Bavarian Environment
Agency

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With a review of ellipsocephalid, solenopleurid and conocoryphid trilobites

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Geologica Bavarica 129

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Hat je ein Petrefact in unsern Zeiten die Aufmerksamkeit der Naturforscher auf sich gezogen, so ist es gewis die concha triloba rugosa, wie man sie gemeiniglich zu nennen pflegt.

J.E.I Walch, Nürnberg 1771

Abstract

Probably lowermost Wuliuan (mid-Cambrian) rocks in the Franconian Forest compose the Wildenstein Member of the Tannenknock Formation. They include a surprisingly diverse fauna with a characteristic West Gondwanan, Atlas-type trilobite assemblage. The assemblage – hitherto having been inadequately characterised and poorly described – includes *Condylopyge* sp. A, *Peronopsis* (*P.*) sp. A, *Dawsonia densiserrata* n. sp., *Tchernyshevioides*? sp. A, *Kingaspis dolosus* n. sp., *Kingaspis* sp. A, *Kingaspis* sp. B, *Kingaspidoides frankenwaldensis*, *Kingaspidoides epimetheus* n. sp., *Kingaspidoides* sp. aff. *destombesi*, *Kingaspidoides wildensteinensis* n. sp., *Kingaspidoides* sp. cf. *brevifrons*, *Kingaspidoides alberti*, *Kingaspidoides* sp. A, *Kingaspidoides*? sp. B, *Kingaspidoides*? sp. C, *Kingaspidoides*? sp. D, *Cambrosaurura* sp. indet., *Latikingaspis* sp. aff. *alatus*, *Latikingaspis tenuis* n. sp., *Ornamentaspis frequens*, *Ornamentaspis*? sp. A, *Ellipsostrenua*? sp. A, *Protolenus* (*Protolenus*) *undulatus* n. sp., *Latoucheia*? (*Latoucheia*?) sp. A, *Enixus* sp. aff. *juvenis*, *Acadoparadoxides* sp. A, "*Paradoxides*" sp. A, *Eccaparadoxides* sp. A, *Eccaparadoxides*? sp. B, *Cambrophatictor meieri* n. sp., *Cambrodaimona parablepta* n. gen., n. sp., *Exapinepiphania wurmi*, *Exapinepiphania*? sp. A, *Exapinepiphania* sp. B, *Exapinepiphania* sp. C, "*Exapinepiphania*" sp. D, undetermined solenopleurid genera and species, *Prioscutarius max* n. gen., n. sp., *Prioscutarius moritz* n. gen., n. sp., *Prioscutarius* sp. A, *Prioscutarius*? sp. B, dorypygid genus and species A, corynexochid genus and species A, and *Acanthomicmacca franconica* Geyer, 2016. The Agnostina are formally separated from the Trilobita, and the class Agnostomorpha n. cl. is suggested for them.

In addition to a precise documentation of the species'/form' morphology and ontogenetic developments, this study exemplifies allometric developments and effects of deformation and distortion caused by diagenesis and tectonics. It further discusses aspects of the trilobites' ecology and taphonomy. Special emphasis is placed on ellipsocephaloid morphology and systematics, and additional chapters are dedicated to the taxonomy of the Solenopleuridae as well as *Bailiella* and related genera. Newly introduced taxa in these chapters include Agnostomorpha n. cl., *Protolenus* (*Hupeolenus*) *deani* n. sp., *Solenopleura westergaardi* n. nom., *Exapinepiphania* n. nom., *Exapinepiphania marionae* n. sp., *Balticomerope* n. gen., *Balticomerope bornholmensis* n. gen., n. sp., *Balticoglaucus* n. gen., *Bailiella marginalis* n. sp., *Bailiella niuxinshanensis* n. sp., *Prioscutarius* n. gen., *Emarginobailiella* n. gen., *Courtessolia* n. gen. and *Courtessolia lemdadensis* n. sp. Conclusive remarks discuss the recognition and significance of trilobite assemblages from the Cambrian Series 2–Miaolingian (Stage 4–Wuliuan) boundary interval in West Gondwana and their coeval/ synchronous conversions and quality in key areas of the palaeocontinent.

Keywords

Cambrian Agnostomorpha Trilobita Biostratigraphy Taxonomy West Gondwana Baltica Avalonia Sibiria Sinokorean Platform Germany Morocco

Kurzfassung

Die Gesteine des ältesten Mittelkambriums/Wuliuums im Frankenwald bilden das Wildenstein-Schichtglied der Tannenknock-Formation. Sie enthalten eine erstaunlich diverse Fauna mit typischen Faunenelementen für West-Gondwana. Die bisher unzureichend charakterisierte und kaum beschriebene Vergesellschaftung besteht vor allem aus seiner Trilobiten-Assoziation vom Typus, der aus den marokkanischen Atlas-Ketten bekannt ist und – angesichts der tektonischen Geschichte – oft erstaunlich gut erhaltene Stücke aufweist. Die Vergesellschaftung enthält folgende Trilobiten und Agnostiden: *Condylopyge* sp. A, *Peronopsis* (*P.*) sp. A, *Dawsonia densiserrata* n. sp., *Tchernyshevioides*? sp. A, *Kingaspis dolosus* n. sp., *Kingaspis* sp. A, *Kingaspis* sp. B, *Kingaspidoides frankenwaldensis*, *Kingaspidoides epimetheus* n. sp., *Kingaspidoides* sp. aff. *destombesi*, *Kingaspidoides wildensteinensis* n. sp., *Kingaspidoides* sp. cf. *brevifrons*, *Kingaspidoides alberti*, *Kingaspidoides* sp. A, *Kingaspidoides*? sp. B, *Kingaspidoides*? sp. C, *Kingaspidoides*? sp. D, *Latikingaspis* sp. aff. *alatus*, *Latikingaspis tenuis* n. sp., *Ornamentaspis frequens*, *Ornamentaspis*? sp., *Ellipsostrenua*? sp. A, *Protolenus* (*Protolenus*) *undulatus* n. sp., *Enixus* sp. aff. *juvenis*, *Acadoparadoxides* sp. A, “*Paradoxides*” sp. A, *Eccaparadoxides* sp. A, *Eccaparadoxides*? sp. B, *Cambrophatictor meieri* n. sp., *Cambrodaimona parablepta* n. gen., n. sp., *Exapinepiphania wurmi*, *Exapinepiphania*? sp. A, *Exapinepiphania* sp. B, *Exapinepiphania* sp. C, “*Exapinepiphania*” sp. D, nicht näher bestimmbare Arten der Solenopleuriden, *Prioscutarius max* n. gen., n. sp., *Prioscutarius moritz* n. gen., n. sp., *Prioscutarius* sp. A, *Prioscutarius*? sp. B, Dorypygidae genus et species A, Corynexochidae genus et species A und *Acanthomicmacca franconica* Geyer, 2016, zudem weitere, taxonomisch nicht näher bestimmbare Sklerite. Die Agnostina werden formell von den Trilobita getrennt, und die Klasse Agnostomorpha n. cl. wird dafür als neues Taxon vorgeschlagen.

Ergänzend zu einer präzisen Dokumentation der Morphologie und ontogenetischen Entwicklung der beteiligten Arten bzw. Formen zeigt diese Studie die allometrischen Veränderungen und die Effekte der Deformation und Verzerrung durch Diagenese und tektonische Beanspruchung. Außerdem werden Aspekte der Ökologie, Erhaltungsbedingungen und Taphonomie der Trilobiten diskutiert. Weitergehende Erläuterungen befassen sich mit der Morphologie und Systematik der Ellipsocephaloidea, und weitere spezielle Abschnitte diskutieren die Taxonomie innerhalb der Solenopleuridae und der Gruppe um *Bailiella*. In diesem Zusammenhang werden folgende neuen Taxa eingeführt: Agnostomorpha n. cl., *Protolenus* (*Hupeolenus*) *deani* n. sp., *Solenopleura westergaardi* n. nom., *Exapinepiphania* n. nom., *Exapinepiphania marionae* n. sp., *Balticomerope* n. gen., *Balticomerope bornholmensis* n. sp., *Balticoglaucus* n. gen., *Bailiella marginalis* n. sp., *Bailiella niuxinshanensis* n. sp., *Prioscutarius* n. gen., *Emarginobailiella* n. gen., *Courtessolia* n. gen. und *Courtessolia lemdadensis* n. sp. Abschließende Betrachtungen diskutieren die Erkennbarkeit und Signifkanz von Trilobiten-Vergesellschaftungen des Grenzbereichs Unter-/Mittelkambrium (Stufe 4/Wuliuum) in West Gondwana und deren synchrone Veränderungen und Qualitäten in den Schlüsselregionen des Paläokontinents.

Schlüsselwörter

Kambrium Agnostomorpha Trilobita Biostratigraphie Taxonomie West-Gondwana Baltica
Avalonia Sibiria Sinokoreanischer Palaeokontinent Deutschland Marokko

1 Introduction

The Cambrian of the Franconian Forest area (Frankenwald) in north-eastern Bavaria is among the most important and stratigraphically most complete occurrences of Cambrian rocks outside Scandinavia and the British Isles in Europe, but had remained largely unstudied since its first discovery during a mapping season for the Bayerisches Oberbergamt in 1923 by Adolf Wurm and his preliminary publications. As summarised in Geyer (2017) and Geyer et al. (2019a), Wurm's initial publications (Wurm 1924a, 1924b, 1925a, 1925b) recognised an early middle Cambrian fauna with trilobites, brachiopods, hyoliths and echinoderm remains, which were subsequently attributed to two different formations. Sdzuy (1964) named these units the Galgenberg and Wildenstein strata ("Galgenberg-Schichten," "Wildenstein-Schichten"), and Geyer & Wiefel (1997) formalised them as the Galgenberg and Wildenstein formations, respectively. The differentiation of both was based on slightly different lithologies, but Sdzuy (1964) also had differences in the biostratigraphic context in mind. In his strictly taxonomic article on his first findings of the strata, Wurm (1925b) recognised only four trilobite species, which he attributed to the classical Bohemian species *Paradoxides spinosus* (Boeck, 1827), *Ptychoparia striata* (Emmrich, 1839) and *Agraulos ceticephalus* (Barrande, 1846), and the only newly introduced species *Agraulos frankenwaldensis* Wurm, 1925. The report of this fauna stimulated considerable interest among scientists concerned with early Palaeozoic trilobites. The results were also pre sented on the International Geological Congress in Madrid 1926 (Wurm 1927a), but all subsequent studies did not deal again with the lower middle Cambrian faunas from north of Wildenstein in a taxonomic approach.

Adolf Wurm later became professor of geology at the Würzburg University and in 1956 sent Klaus Sdzuy to the original localities in the Franconian Forest to study these faunas in a post-doctoral project. Sdzuy collected numerous fossils in this field season, which, however, remained largely unstudied. Nevertheless, Sdzuy subsequently started a series of publications on the Cambrian of the Franconian Forest with a stratigraphic appraisal (Sdzuy 1964), in which he distinguished between the rock units, which include the Galgenberg and Wildenstein faunas in a semi-formal lithostratigraphic way. However, his further publications on the Cambrian of the Franconian Forest dealt with the faunas of the Bergleshof (Sdzuy 1966) and Lippertsgrün formations (Sdzuy 2000) only. A brief note on the Galgenberg trilobites is included in Sdzuy (1957).

The present author revised several aspects of the Cambrian rocks and fossils in the Franconian Forest during the recent years, including aspects of the Galgenberg and Wildenstein strata (e.g., Geyer 2017, 2018; Geyer et al. 2019a, 2019b, 2020, 2023; Streng & Geyer 2019a; Geyer & Malinky 2019). This study presents for the first time a complete record of trilobites from the Wildenstein fauna, based on more than one thousand of specimens investigated by the author.

2 Geological setting and stratigraphy

The Franconian Forest region is situated in north-eastern Bavaria, southern Germany, and lies at the southern margin of the Saxothuringian Zone (Fig. 1). This structural "zone" is a West Gondwana-associated terrane or, better, represents a marginal West Gondwanan succession. Rock successions with ages ranging from Cambrian through Carboniferous of the Saxothuringian Zone have been interpreted as giant olistoliths in the wildflysch of the Variscan orogen (e.g., Linnemann & Schauer 1999). The Cambrian formations (except for the Rauschbach beds; see Geyer et al. 2019a) are distributed in disconnected fault-bounded areas ('slices') such as the Wildenstein and Triebenreuth slices that include the Wildenstein fauna studied herein. Nevertheless, the Cambrian rocks in this part of the Saxothuringian Zone show a geographically coherent facies succession that does not suggest regional allochthony and transport for most of the zone (e.g., Göthel 2001). The small Cambrian blocks in the Franconian Forest are obviously related to the presence of the so-called Münchberg Gneissmass (or Münchberg allochthon), a genetically and chronologically controversially debated block of metamorphic rocks (e.g., Stettner 1972; Behr et al. 1980; Gandl 1998) (Fig. 1).

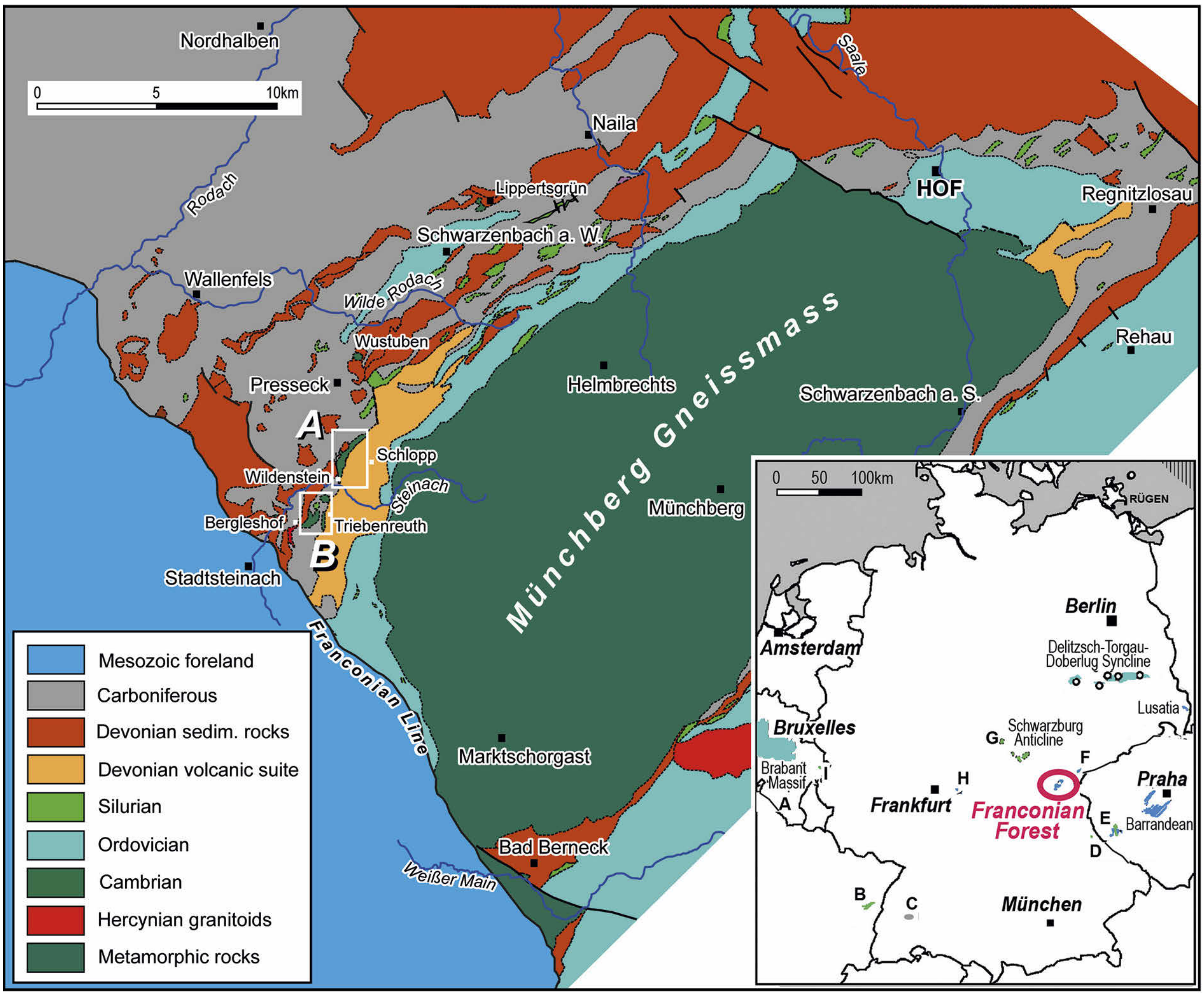

Fig. 1: Generalised geological map of the Saxothuringian Zone in north-eastern Bavaria, southern Germany. Small-scale insert map shows the modern political boundaries of Germany and adjacent regions with outcrop areas of Cambrian rocks (black), outcrop areas of rocks with supposed Cambrian age (grey), and subsurface Cambrian (hatched). Small black rectangles outline the map areas with the Wildenstein slice (A; Fig. 4) and the Triebenreuth slice (B; Fig. 5). Modified from Geyer (2017, fig. 1).

The lower to middle Cambrian succession in the Franconian Forest region are dominated by siliciclastic shallow marine, fossiliferous units of West Gondwanan aspect, similar to those described from the

Moroccan Atlas ranges (Geyer 1990a; Geyer et al. 1995; Geyer and Landing 1995, 2006). This succession primarily bears West Gondwanan trilobites in its lower part (Galgenberg and Wildenstein members of the Tannenknock Formation), a large proportion of exotic trilobites (lower part of the Triebenreuth Formation; unknown from coeval rocks in Central and Southern Europe as well as northwestern Africa), typical “Mediterranean” trilobites in the Lippertsgrün Formation, and with a slight increase in the proportion of Baltic genera in its upper part (Bergleshof Formation) (e.g., Geyer et al. 2008, 2019a; Heuse et al. 2010; Geyer 2010, 2014, 2017). Although the middle Cambrian formations of the Franconian Forest are fault-bounded, biostratigraphically important trilobites and agnostoid arthropods allow for the recognition of a relatively complete middle Cambrian faunal succession (Fig. 2).

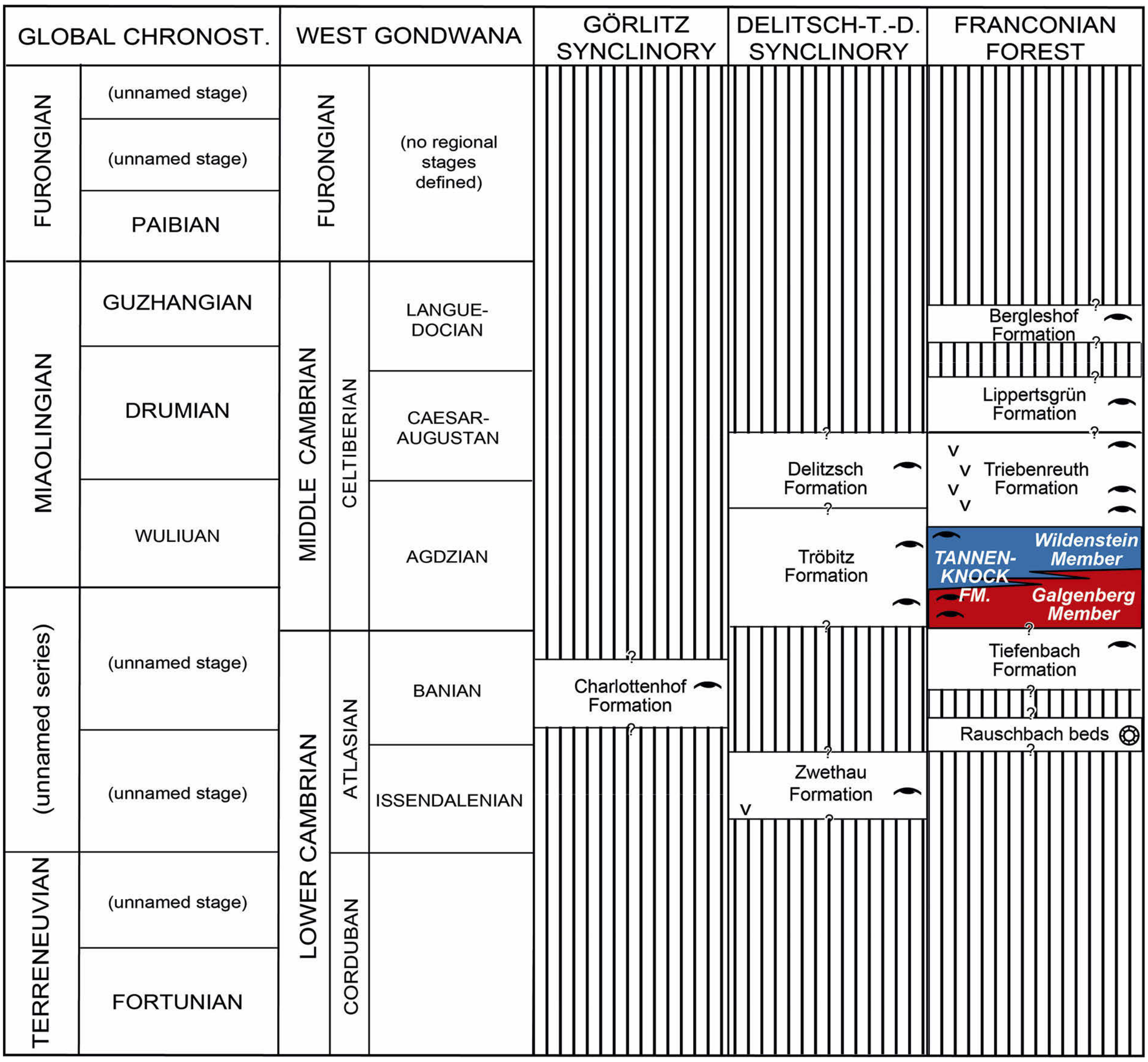

Fig. 2: Lithostratigraphic succession of the lower and middle Cambrian in the Franconian Forest area, Germany, compared with the succession of the Moroccan Atlas ranges. Lithostratigraphy from Geyer & Wiefel (1998) and Geyer et al. (2019a). West Gondwanan standard chronostratigraphy from Geyer & Landing (2004). Modified from Geyer (2017, fig. 2).

As detailed by Geyer (2017), Wurm’s initial publications (Wurm 1924a, 1924b, 1925a, 1925b) on the Cambrian of the Franconian Forest dealt with an early middle Cambrian (in traditional concept) fauna from probably four adjacent localities in the vicinity of the so-called Galgenberg (“Gallow Hill”) near Wildenstein. This fauna included fossils that can be assigned to two stratigraphic horizons or zones. Due to the fact that typical fossils from the two different levels occur in slightly different lithologies, Sdzuy (1964) distinguished two different formations termed the Galgenberg and Wildenstein ‘Schichten’ (‘strata’), or Galgenberg and Wildenstein beds (Erdtmann 1991). These strata were referred to in the sense of formations, and the units were later revised to formal formations by Geyer and Wiefel (1997). Later, Geyer (2017) and Geyer et al. (2019a), based on revised faunal composition, biofacies characteristics and spatial relation of the known occurrences, concluded that the Galgenberg and Wildenstein “strata” are best regarded as members of the same unit, which was formally introduced as the Tannenknock Formation.

Fossils preserved in rocks of the typical Galgenberg facies occur in light coloured sandy, slightly calcareous blue-grey shales, which tend to weather with whitish outer surfaces, whereas the fossils of the Wildenstein facies can be found in fine- to middle-grained, slightly calcareous, commonly feldspathic sandstones or ochre-weathering arenitic calcareous bodies or nodules (Geyer et al. 2008, 2019a; Geyer 2010, 2017). It needs to be emphasised that (1) no sections which characterise the formations were known; (2) no determinable contact between the formations was recognisable in any (even temporal) outcrop; and (3) sandstone units locally appear in the shaly Galgenberg strata as well.

The reinvestigations of the surface areas with the Tannenknock rocks and all available data (Geyer 2017, Geyer et al. 2019b) indicate that the two faunas are more-or-less clearly distinguished and characterise two distinct zones (the *Kingaspidoides frankenwaldensis* and *Ornamentaspis frequens* biozones). However, it became also evident that the Galgenberg fauna occurs, rarely, in rocks of the typical Wildenstein fcies as well and vice versa. Such interbeds of micaceous, stratified sandstone with rich limonitic particles of the Wildenstein facies are concentrated to the upper part of the Galgenberg Member so that they record a slight change in depositional character, particularly a progressive input of coarser siliciclastics. This situation indicates that rocks of Galgenberg facies interfinger with those of the Wildenstein facies within a relatively short interval around the *Kingaspidoides frankenwaldensis*–*Ornamentaspis frequens* zone boundary. The Galgenberg and Wildenstein members are thus primarily lithofacies associations with local microdiachronous contact. For practical purposes, Geyer (2017) suggested that the two units are the Galgenberg and Wildenstein members of a single Tannenknock Formation, and the contact between is distinguished at the base of the *Ornamentaspis frequens* Zone because the minute differences in the onset of the Wildenstein facies cannot be reconstructed in detail. Therefore, the descriptions in the present study distinguish between Wildenstein facies for lithological characters and Wildenstein Member for stratigraphic data.

The spatial arrangement of the fossil localities in the Wildenstein slice and its faunal composition allows for a tentative reconstruction of a lithologic profile (Fig. 3) despite the lack of well recognisable and unequivocally continuous sections. In this context, it becomes evident that localities such as W1, W2, W11, W13d (see Fig. 4) record a slightly mixed fauna with *Kingaspidoides* co-occurring with *Ornamentaspis*. However, the samples indicate to various degrees a transition from the Galgenberg into the Wildenstein facies in different depositional developments. As an example, sample W13a appears to illustrate the known occurrence of rocks in Galgenberg facies in the area, whereas sample horizon W2 appears to record the oldest assemblage with *Ornamentaspis* already having a Wildenstein facies signature.

Rocks of the Galgenberg and Wildenstein members are known from only two isolated blocks, termed the Wildenstein and Triebenreuth slices (Fig. 1, A and B). The geological situation has been studied in detail by Ludwig (1969) and remapped in the course of recent studies. A description of the lithofacies characteristics, and the spatial and temporal distribution was provided by Geyer et al. (2019a). Due to the poor outcrop situation, the varying lithofacies, and structural complications, it is difficult to provide detailed geological maps. However, the situation for the surface distribution of the Galgenberg and Wildenstein members is sketched for the Wildenstein slice in Fig. 4, and for the Triebenreuth slice (including the Teufelsstein localities) in Fig. 5.

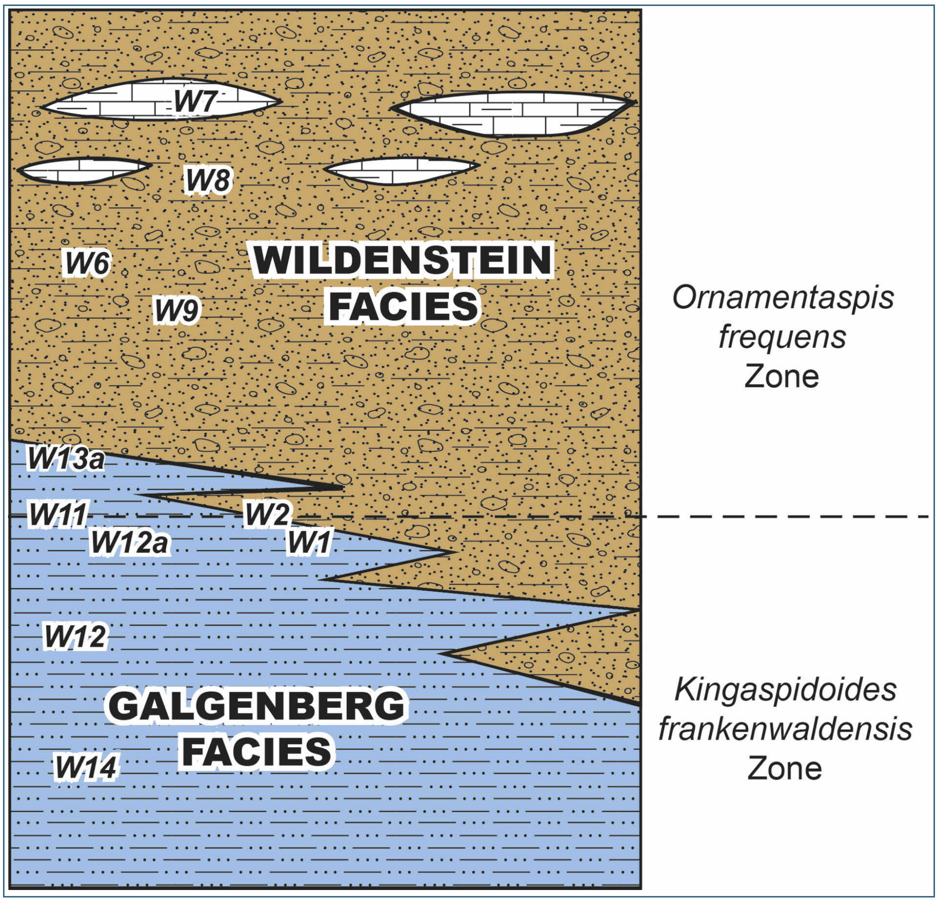

Fig. 3: Tentative reconstructions of the facies relationships in the succession of the Tannenknock Formation, with stratigraphic arrangement of fossil localities in the Wildenstein slice and biostratigraphic zones. For further explanations see text. Based on unpublished field data from K. Sdzuy and data from Geyer et al. (2019a). Modified from Geyer (2017, fig. 3).

The Wildenstein slice records a fairly complicated multiple succession of the Tannenknock Formation, with certain units folded and hashed into small blocks. Strike and dip of the strata are usually difficult to measure, and the map in Fig. 4 does not indicate the probably numerous faults which can be derived from the structural data.

Nevertheless, the outcrops in the Wildenstein segment allow for a relatively precise characterisation of the member's lithology. As detailed in Geyer et al. (2019a), the rocks composing the Wildenstein Member are dominated by light grey to greenish-grey greywacke and fine- to medium-grained sandstones. The carbonate content in these siliciclastics varies considerably and is often visible as limonitic layers or lenses concentrated around fossil shells (Geyer et al. 2019a, fig. 11C), but also forms seams at the change from sandstone to shale intercalations. Calcareous nodules may comprise decimetre-long bodies within the sandstones and contain accumulations of disarticulated trilobite sclerites and mollusc shells. Most of the smaller trilobite specimens were collected from this type of rocks, particularly from sample locality W8, which allowed access to an extended calcareous marlstone–sandstone horizon stretching out under the unpaved vehicle track. The concretions enclose rare quartz-arenitic horizons with mica flakes. More often, the rocks weather to yellowish slabs in which feldspar grains are visible as small white spots. Microscopic investigations indicate that the majority of these feldspars are plagioclase with varying amount of anorthite, but a smaller portion consists of microcline (Emmert et al. 1960).

A second typical rock type for the Wildenstein Member is a dark, fine-grained sandstone to siltstone, occasionally slaty. This rock is more rarely found than others but was long regarded as typical due to the fact that most fossils of the Wildenstein Member were collected from the small abandoned quarry (W9). The fossils from these rocks are dominated by larger trilobites, particularly large specimens of *Kingaspidoides*, *Paradoxides* (s.l.), and *Bailiella*, but also large hyoliths (see Geyer 2018; Geyer et al. 2019b).

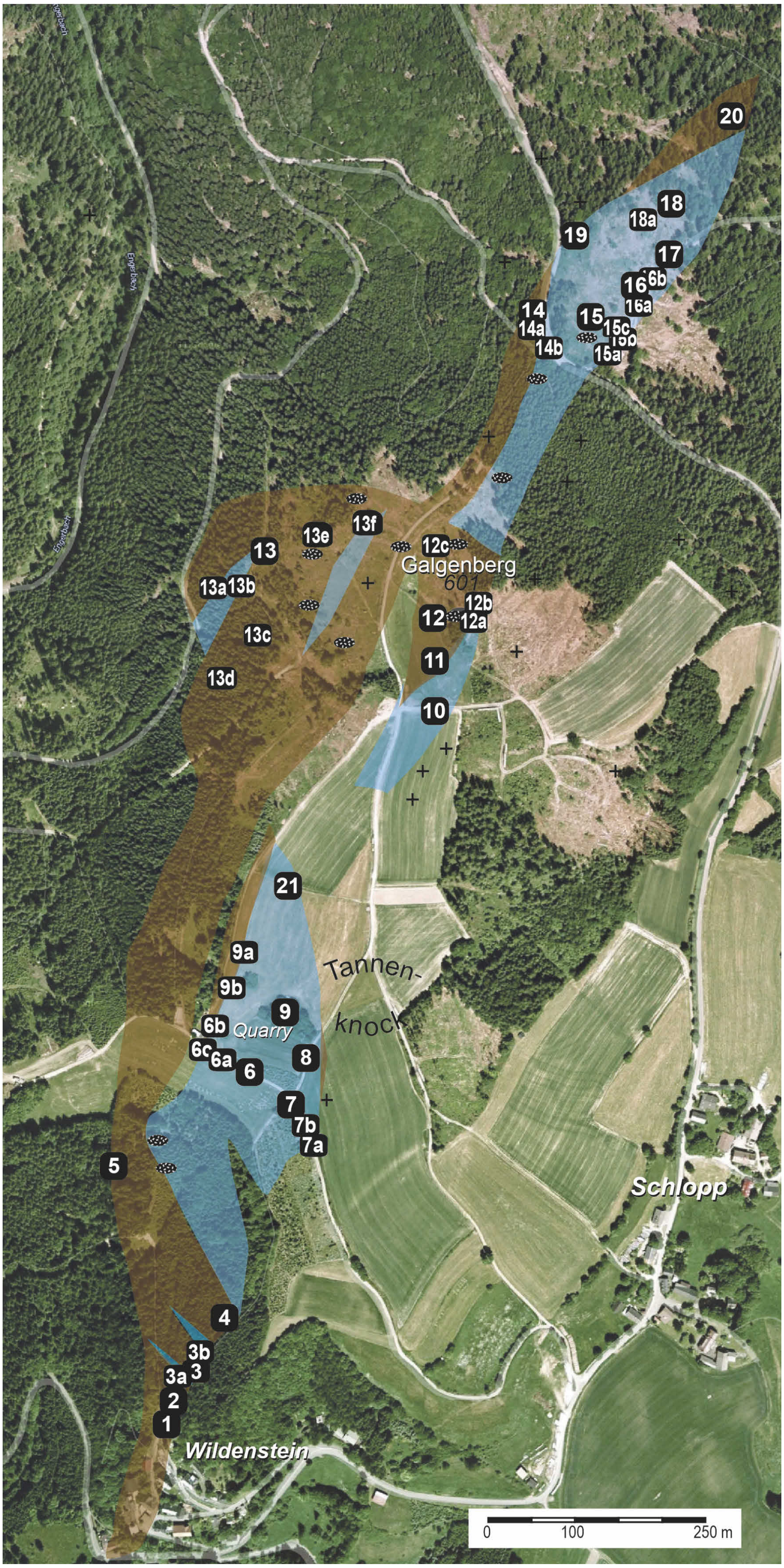

Fig. 4:
Areas with outcrops of Cambrian rocks and fossil localities in the Wildenstein slice (modified from Geyer 2017 and Geyer et al. 2019a). Based on maps of Wurm (1925b), Sdzuy (1964), Ludwig (1969), Horstig & Stettner (1976), unpublished data from field notes of K. Sdzuy, new data from S. Meier and data of field investigations by the author and E. Landing, and new data. Brown colour marks outcrop areas dominated by the Galgenberg Member strata, blue colour marks outcrop areas dominated by the Wildenstein Member strata. Numbers refer to exposures mentioned in the text and appendix. Aerial map from Google Earth.

Fig. 5: Areas with outcrops of Cambrian rocks and fossil localities in the Triebenreuth slice (modified from Geyer 2017 and Geyer et al. 2019a). Based on maps of Emmert et al. (1960), Trapp (1964), Ludwig (1969), and new data of field investigations by the author and E. Landing. Brown colour marks outcrop areas dominated by the Galgenberg Member strata, blue colour marks outcrop areas dominated by the Wildenstein Member strata, dark brown colour marks extended outcrops of the Tiefenbach Formation, bluish purple colour marks the dark mudstone previously assigned to the Tiefenbach Formation. Numbers refer to exposures mentioned in the text and appendix. Aerial map from Google Earth.

The Triebenreuth slice includes a small surface outcrop of Wildenstein Member, which appears to be in fault-bounded contact with highly fossiliferous rocks of the Galgenberg Member in the northern part (T1 in Fig. 5). The rocks are dominated by middle-grained, almost greywacke-type sandstones, but with finer grained sandstone present as well. Due to poor accessibility, only a relatively small assemblage has been collected. The lithofacies–biofacies relations are described in more detail below under “Ecological aspects.”

3 Age and correlation

Acadoparadoxides, which is present throughout the Tannenknock Formation, is following Brøgger's concept (1878) in use as the traditional index fossil for the traditional Middle Cambrian in the "Acado-baltic Realm." The genus *Parasolenopleura* (in the traditional broad concept; see revision below), also already present in the underlying Galgenberg Member of the Tannenknock Formation, is similarly typical for traditional Middle Cambrian strata and one of the most frequent genera throughout the formation. However, *Ornamentaspis frequens* is an ellipsocephalid trilobite species, which can be used as the index fossil of the zone represented by the Wildenstein Member. This trilobite species has originally been described from the High Atlas and Anti-Atlas ranges of the Moroccan Atlas ranges, where it is also used as an index fossil (Geyer 1990b, 1990c; Geyer & Landing 2006). Accordingly, the regions can be perfectly correlated. The *Ornamentaspis frequens* Zone also anchors the Wildenstein Member to the middle part of the Agdzian Stage in the West Gondwanan standard chronostratigraphical scheme (Geyer & Landing 2004) (Fig. 2).

The decision on the GSSP of the lower boundary of the Cambrian Series 3 and Stage 5 led to the introduction of the Miaolingian Series and Wuliuan Stage with the golden spike placed in a relatively high position in the Wuliu-Zengjiayan section in the Guizhou province, South China (Zhao et al. 2019; see discussion in Landing et al. 2023). This decision generated the unfortunate situation that considerable parts of the traditional lowermost to lower Middle Cambrian strata in the palaeocontinents West Gondwana, Avalonia and Sibiria are now in the upper part of the lower Cambrian Stage 4, and also that the Series 2–Miaolingian and Stage 4–Wuliuan boundary are not recognisable with any precision in Cambrian continents such as West Gondwana, Avalonia and Baltica. A best guess for the position of the base of the Miaolingian and Wuliuan in West Gondwana and in the Franconian Forest is at about the base of the *Ornamentaspis frequens* Zone (although with caveat). Therefore, it is suggested here to regard the boundary between the Galgenberg and Wildenstein members as coeval with the base of the Miaolingian and the Wuliuan.

The composition of the Wildenstein fauna in particular and the Tannenknock fauna in general is typical for West Gondwana and enables a precise correlation with other Cambrian areas of West Gondwana. Particularly similar are the trilobite faunas from the Jbel Wawrmast Formation of the Moroccan Atlas ranges. As mentioned above, one of the characteristic trilobites for the Wildenstein Member is *Ornamentaspis frequens* Geyer, 1990, a species that has been found in the eponymous zone of the High Atlas and Anti-Atlas ranges (Geyer 1990b) and is used as an index fossil in the Moroccan standard biostratigraphical scheme (Geyer 1990b, 1990c, 2019a). Other faunal elements of the Wildenstein Member have closely related counterparts in the same zone in the Atlas ranges. Such trilobites include species of the genera *Kingaspis*, *Kingaspidoides*, *Cambrophatictor*, *Prioscutarius* ("*Bailiella*" see below) *Exapinepiphania* ("*Parasolenopleura*" see below), some of which are also found in other regions of the "Mediterranean" Cambrian belt (such as northern and central Spain, the Montagne Noire, and Sardinia). Other trilobite genera, such as the agnostoids *Dawsonia*, *Peronopsis* and *Condylopyge*, as well as *Bailiella*, *Parasolenopleura* and *Acanthomicmacca* are semi-cosmopolitans of the "Acado-baltic Realm", i.e. the plate assemblage around the Rheic Ocean, which includes most part of the British Isles, New Brunswick, Nova Scotia and south-eastern Newfoundland as parts of Avalonia, Bohemia, and southern Scandinavia. Trilobite species which occur also on the Sibiria palaeocontinent include *Dawsonia*, *Peronopsis*, *Condylopyge*, *Acadoparadoxides*, *Eccaparadoxides*, "*Bailiella*", "*Parasolenopleura*", and *Acanthomicmacca*, but particularly *Enixus*, which has long been regarded as a Siberian endemic genus (under the name *Schistocephalus*).

4 Localities

The Tannenknock Formation is almost without any true outcrops. Only thin parts of the rock succession in place can be seen at a few sites along tracks and within forested areas. Due to these extremely small outcrop areas and dense forested vegetation or agricultural use of the studied region, fossil collecting is strenuous or depends on fortunate temporary conditions. As mentioned by Geyer (2017), the fossils used in this series of publications to present the fauna of the Galgenberg and Wildenstein members, are an assemblage of collections started by A. Wurm in the 1920s (now in the Bayerische Staatssammlung für Geologie und Paläontologie, Munich, and the collections of the Bayerisches Landesamt für Umwelt, Hof), unstudied collections of K. Sdzuy (mostly from 1956; now in the repositories of the Mineralogisches Museum, Universität Würzburg), collections of unknown origin left in the former Institut für Paläontologie, University of Würzburg (abandoned 2004/2005; in the repositories of the Mineralogisches Museum, Universität Würzburg), collections of the author (1979–2019; in the repositories of the Mineralogisches Museum, Universität Würzburg), collections of the late Erwin Albert (Burgkunstadt, now in the Naturmuseum Senckenberg, Frankfurt am Main), particularly collections by Stefan Meier (Marktredwitz; homepage www.fichtelgebirgs-mineralien.de/41332.html), occasional collections made during teaching field trips of the University of Frankfurt am Main (now in the Naturmuseum Senckenberg) and the University of Munich (now in the Bayerische Staatssammlung für Geologie und Paläontologie), the Naturkundemuseum Stuttgart, as well as small amounts of samples provided by various amateur collectors (see Acknowledgments).

Unfortunately, most of the early collections were left without an indication of the precise location so that the somewhat uncertain origin partly led to a tentative attribution (based in lithologic characters and details of the preservation) in the specimen lists under the relevant taxa below. The material of K. Sdzuy comes from numerous different locations in the Wildenstein slice, but the recent discovery of his field notes allows to locate the majority of them with fair precision although most of them resulted from better outcrop conditions and small dig-outs that now have completely perished. Fossil localities relevant for this study are shown in Figs. 4 and 5. Additional data in the material lists of the systematic section refer to those localities and indicate further tentatively assigned and unknown sources of material.

For available data on the sampled localities and horizons see Appendix A (pp. 404–409).

5 Ecological aspects

Three different lithologies can be distinguished for the Wildenstein Member: (A) fine- to (less frequently occurring) medium-grained polymictic sandstones with an arkosic aspect and with a relatively high amount of disperse mica and with more or less distinct calcareous matter in the matrix; (B) dark, argillaceous slaty shales (or slates), but with thin quartzitic or greywacke-type sandstones intercalated; and (C) large calcareous nodules or bodies of sandy limestones up to more than 1.5 m in extension with layers of accumulated fossil sclerites with a wackestone-type aspect for some of its layers (Fig. 6).

- Lithofacies (A) appears to be the most widespread habit of Wildenstein lithology, but its spatial extension and microstratigraphic persistence is largely unknown. This lithofacies is typically developed in localities such as W6a, W7, W9b, W10, W10c, W15 and W21.
- Lithofacies (B) is the typical lithology seen in the abandoned small quarry (locality W9), but rare and very limited in its extension elsewhere. It is also seen in apparently thin strata elsewhere (e.g., locality W13b).
- Lithofacies (C) forms the rocks on which the field road at locality W8 is build. It can be seen as loose blocks in the adjacent fields and elsewhere. Due to the weathering of the calcareous matter, such loose blocks on the fields have the appearance of yellowish to ochre-coloured, porous or jagged sandstone rather the dark grey aspects of the fresh carbonatic rock.

Macrofossils of the Wildenstein Member are found in all three lithological types, but the studied samples also record different levels of biodiversity for the three lithofacies types. Macrofossils are typically scattered in rocks of lithofacies (A). Those rocks usually weather to yellowish or multi-coloured chunks, which mostly include medium-sized to large, mostly fragmented sclerites with an imperfect preservation. Fossil sclerites are sometimes accumulated, but distinct shell horizons have not been observed. The aspects of fossil preservation and sedimentological features suggest deposition under moderate to high energy conditions in a shallow marine environment. Lithofacies (A) displays a moderate faunal diversity, with trilobites dominating the assemblages, but other fossil groups such as brachiopods, helcionelloids, and hyoliths being regular faunal elements. Typical trilobites from this lithology include (for example) *Acadoparadoxides* sp. A, *Kingaspidoides frankenwaldensis*, *Latikingaspis* sp. aff. *alatus*, *Ornamentaspis frequens*, *Cambrodaimona parablepta*, *Exapinepiphania wurmi*, and *Prioscutarius max* (Fig. 7, W10/W10c).

Lithofacies (B) reflects quiet water conditions with little recognisable wave action. Distinct arenitic portions are completely lacking, but the rocks are dominantly dark siltstones with large fossil remains. Articulated trilobite exoskeletons are rare, but cephala and associated hyolith conchs (e.g., *Aladraco schloppensis*; Geyer 2018; Geyer et al. 2019b) are partly of considerable size. Lithofacies (B) has a fairly low diversity of the trilobites with only ca. 13 species or forms being recorded, of which only 6–8 are fairly common or frequent. Typical trilobites from this lithology include (for example) *Kingaspis dolosus*, *Kingaspidoides* sp. aff. *destombesi*, *Kingaspidoides* sp. cf. *brevifrons*, *Kingaspidoides frankenwaldensis*, *Acadoparadoxides* sp. A, *Prioscutarius max*, and comparatively regular occurrence of *Exapinepiphania wurmi* and *Cambrophatictor meieri* (Fig. 7, W9). Hyoliths are relatively frequent compared with their occurrence in the other lithofacies types, particularly large ones (length > 2 cm) such as *Aladraco*.

The calcareous rocks of lithofacies (C) are often abundantly fossiliferous, but the sclerites were deposited after some transport and partly winnowed. Remarkably, relatively few of the trilobite sclerites (except for some delicate thoracic segments) are fragmented (Fig. 6A), which is taken as an indication of limited transport and wave energy. However, in addition to the fossil particles, the rocks include small chunks of reworked material giving evidence for a transport from shallow nearshore conditions towards the deeper part of the basin. The rocks are certainly the results of storm-induced sedimentation on a moderately deep shelf. Remarkably, the accumulation of bioclasts into densely packed sclerites layers in lithofacies (C) affected a faunal assemblage that strongly differs from the fossil assemblages in lithofacies (A) and lithofacies (B).

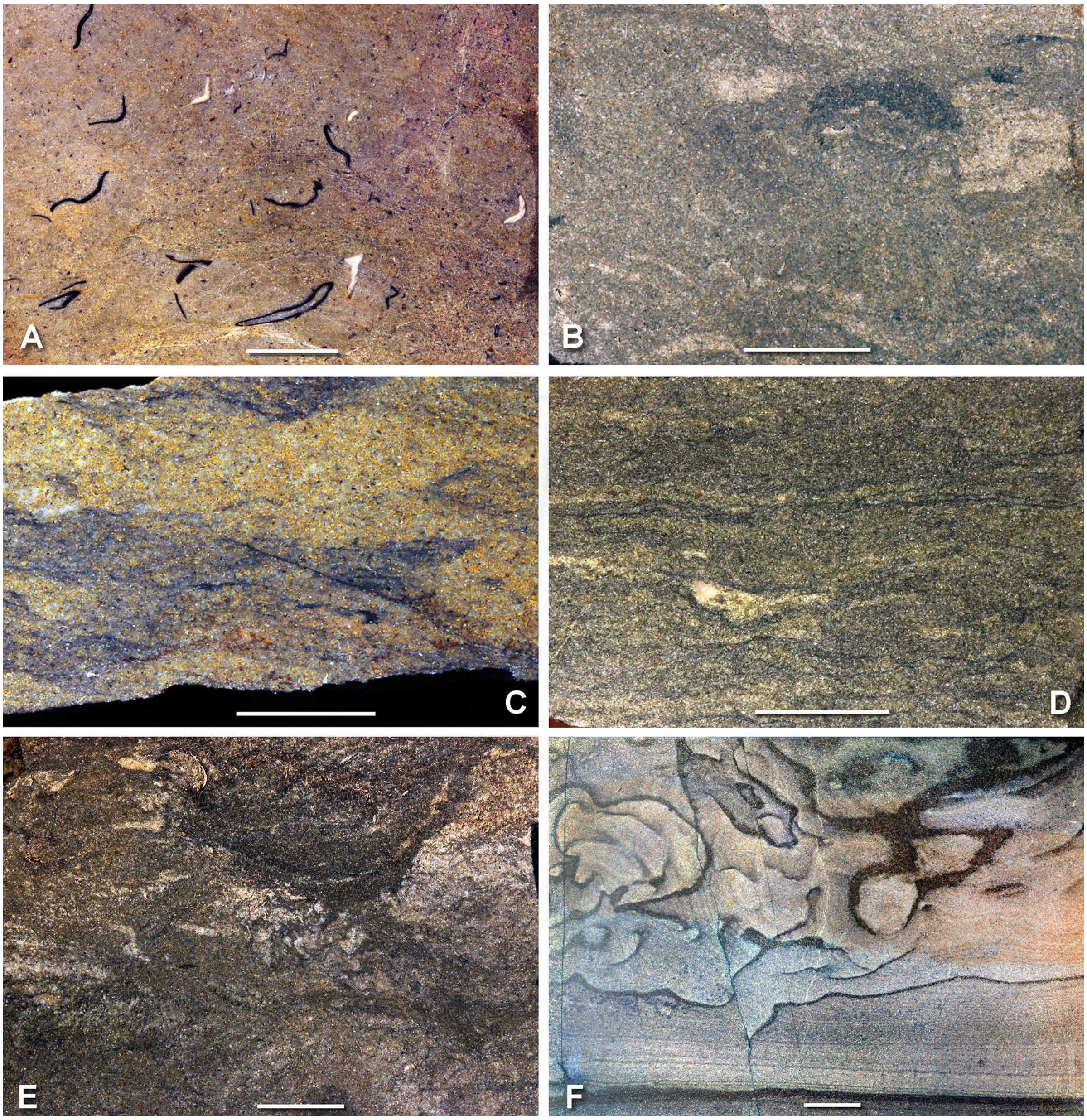

Fig. 6: Examples for lithofacies developed in the Wildenstein Member of the Tannenknock Formation. Polished sections perpendicular to the assumed bedding plane. Scale bars equal 5 mm.

A Sample from locality W8; calcareous sandstone with numerous fragments of trilobite sclerites (slightly phosphatised). MMUW-2022-A-1.

B Sample from locality W8; calcareous sandstone, bioturbated, with high amounts of argillaceous matter and organic substance. MMUW-2022-A-3.

C Sample from locality W19a; shaly sandstone, slightly bioturbated and notably chloritised. MMUW-2022-A-4.

D Sample from locality W9c/II 8; alternation of sandstone and shale, more or less laminated, rich in mica, with local indications of burrowing and occasional small sub-lenticular recrystallizations. MMUW-2022-A-11.

E Sample from locality W6a/I 6; alternation of sandstone and shale with conspicuous bioturbation. MMUW-2022-A-15.

F Sample from locality W13e/GALGENBERG-WEST; sandstone, lowermost part laminated, middle and upper parts affected by soft sediment deformation and secondary mineralisation. From the Collection S. Meier, Marktredwitz.

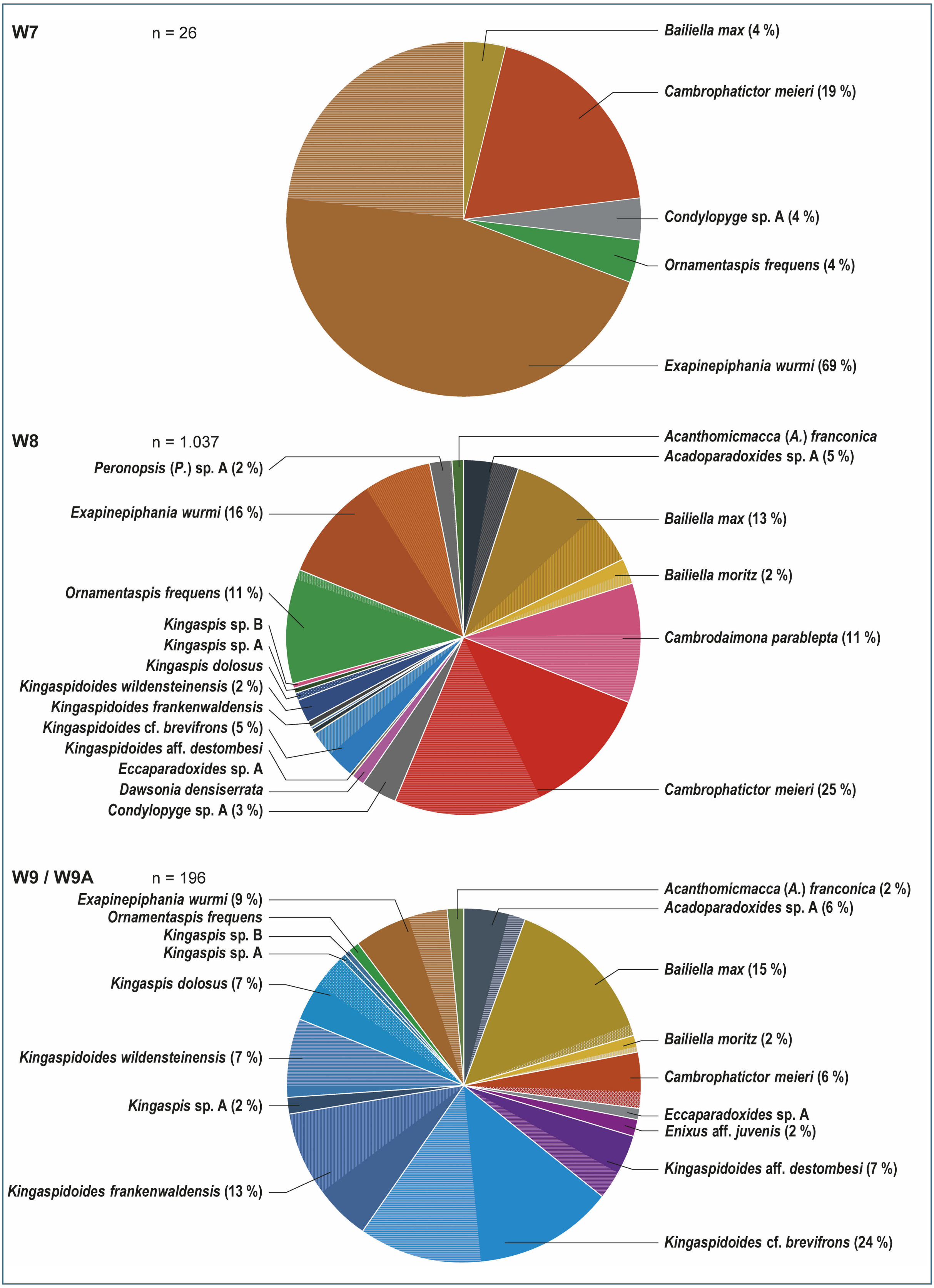

Fig. 7a: Pie charts illustrating the relative frequency of trilobite species exemplified for samples of the Wildenstein-type localities W7, W8 and W9/W9a. Tentatively assigned specimens included in the respective species, but marked by a hatched or cross-hatched signature, with total number of counted specimens (n).

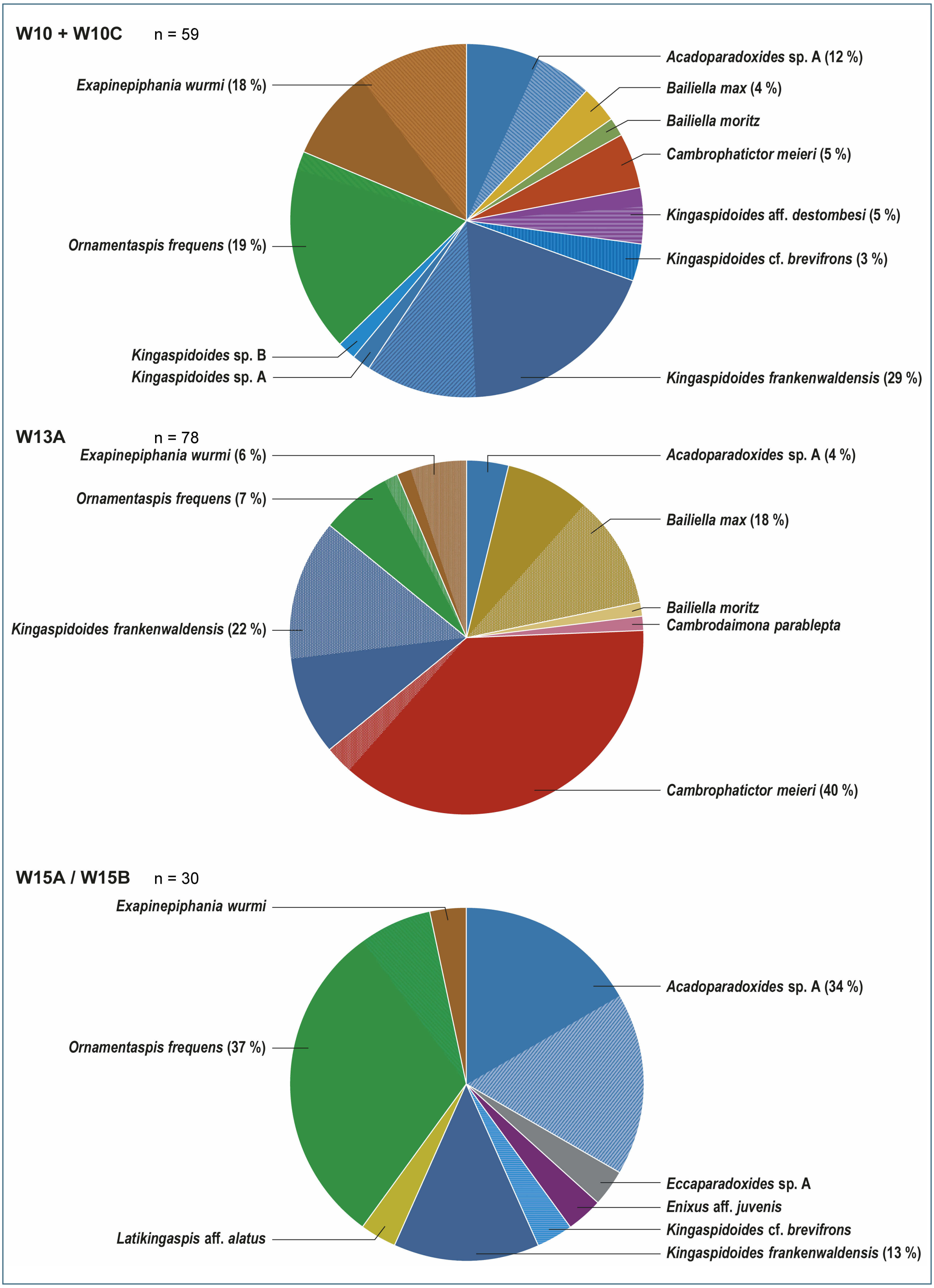

Fig. 7b: Pie charts illustrating the relative frequency of trilobite species exemplified for samples of the Wildenstein-type localities W10/W10c, W13a, and W15a/15b. Tentatively assigned specimens included in the respective species, but marked by a hatched or cross-hatched signature, with total number of counted specimens (n).

Lithofacies (C) has by far the highest diversity, with the assemblages being dominated by trilobites. Twenty-two species or forms being recorded, of which only 10 are common or fairly frequent (Fig. 7a, W8). Particularly frequent are small cranidia of small ptychoparioids such as *Cambrophatictor meieri* n. sp. and *Cambrodaimona parablepta* n. gen., n. sp. Other frequent species include *Kingaspis dolosus*, *Kingaspidoides* cf. *brevifrons*, *Ornamentaspis frequens*, *Prioscutarius max*, and *Exapinepiphania wurmi*. Regular occurrences are noted for *Condylopyge* sp. A, *Peronopsis* (*P.*) sp. A, *Dawsonia densiserrata*, *Kingaspidoides wildensteinensis*, *Kingaspidoides frankenwaldensis*, *Acadoparadoxides* sp. A, and *Eccaparadoxides* sp. A, as well as *Prioscutarius moritz* (Fig. 7a, W8). Other fossil groups such as brachiopods, helcionelloids, and hyoliths are also regular faunal elements.

In total, the assemblages of invertebrates include a fairly large number of species from other animal groups compared with coeval faunal assemblages in West Gondwana, which record a normal diversity for strata of comparable stratigraphic position. They include acrotretoids, rhynchonelliform brachiopods, bradoriids, at least five different echinoderm species, one graptoloid (Geyer et al. 2023), and various ichnofossils identified during the investigations to this study.

It is remarkable that bioturbation is also a regular feature in rocks of the Wildenstein Member, with the three lithofacies being roughly equally affected. However, a particularly heavily burrowed horizons was not seen in any stratum. Fine, intricately branched networks of shallow burrows of the *Planolites beverleyensis* type occur and are usually preserved with iron-mineral infillings and now displaying discrete limonitic threads (ichnofabric index 2 and 3, respectively).

The fossils preserved in the medium-grained polymictic, subarkosic sandstones of lithofacies (A) are generally preserved as isolated sclerites which record a moderate transport with some winnowing and deposition during probably temporal pronounced wave action. Given the connection with lithofacies (C) at locality W8, it is very probable that the majority of the trilobites in lithofacies (A) results from reworked and redeposited fossil remains which were primarily preserved in a lithofacies (C)-type situation.

A few trilobite specimens from lithofacies (A) show damages of the sclerites in the form of broken off marginal portions. These damages are tentatively interpreted as mutilations resulting from predaceous actions, but are more frequently a product of scavenging.

Episodes of rapid deposition are indicated by a considerable amount of articulated remains of trilobites. Such specimens are of different growth stages, and they include strongly or partially enrolled specimens. The articulated or nearly complete exoskeletons are partly to almost completely enrolled (e.g., Fig. 9D, L) or exhibit typical post-mortem deformation (e.g., Fig. 25C, K). Accordingly, they represent individuals embedded in live condition, which suggests rapid burial of the individuals, which caused them to enrol as an ineffective protective reaction. This situation is similar to that recorded from the Galgenberg Member of the Tannenknock Formation (Geyer 2017), but the amount of such specimens is restricted to the coarser siliciclastic rocks and not as frequent as in the Galgenberg Member.

The specimens from the Wildenstein shale facies (lithofacies B) show little winnowing, and no sorting is recognisable. Preserved trilobite sclerites sometimes have large sizes, with paradoxidine librigenae known of up to 7 cm in length. However, the available number of adequately preserved fossil remains is too small to allow a reliable estimation of the ratio of isolated sclerites and exoskeletons found in the strata in order to compare it with the expected ratio of the number of thoracic segments, librigenae and pygidia in respect to the original number, resulting from decay and short-distance transport, modified by the lack of small sclerites, lack of entire large, and an underrepre sentation of thoracic segments, librigenae and pygidia (which would have to be attributed to biased sampling). Nevertheless, some of the larger sclerites as well as a considerable amount of isolated thoracic segments are fragmented, although the amount of breakage is comparatively low. An example for the obvious low energy conditions is indicated when large librigenae are only damaged in a way that the end of the genal spine is broken off.

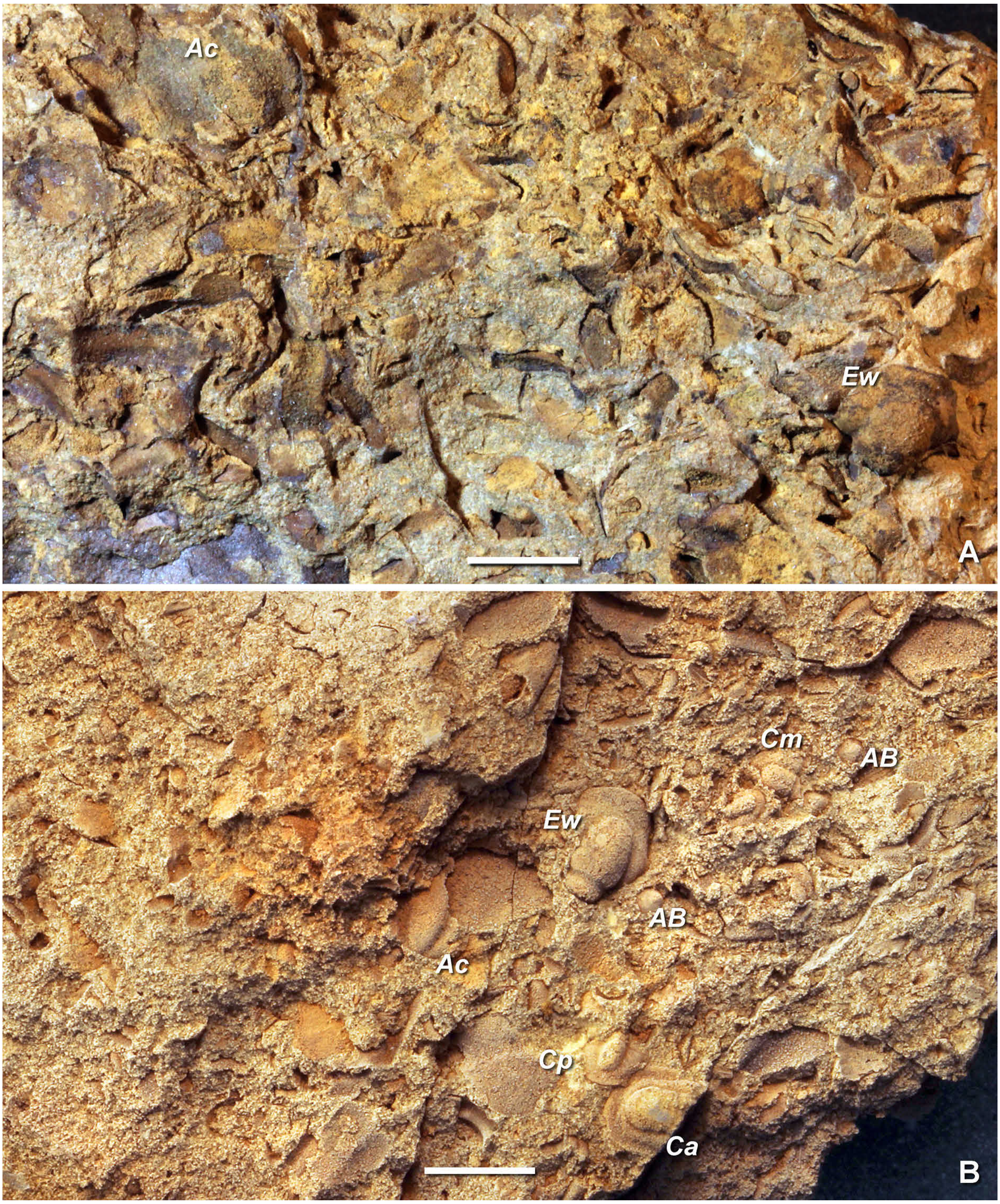

Fig. 8: Preservations of shelly accumulations (predominantly composed of trilobite sclerites) of the Wildenstein Member lithofacies C from locality W8 with different average size of components.
A Sample composed of comparatively large components with a reasonable amount of ferritic minerals. Note high volume of dissolved shells/cuticles.**B** Sample composed of dominantly small components with a fairly high amount of calcareous material. Preservation partly as composite moulds. Note relatively high diversity. Abbreviations: *AB*, articulate brachiopod; *Ac*, *Acadoparadoxides* sp. A; *Co*, *Condylopyge* sp. A; *Cp*, *Cambrodaimona parablepta*; *Cm*, *Cambrophatictor meieri*; *Ew*, *Exapinepiphania wurmi*. Scale bars 5 mm.

As mentioned above, the calcareous rocks of lithofacies (C) probably represent a primary type of Wildenstein sediments, which were often affected by periods during which pronounced energy conditions on the shallow shelf prevailed. Those conditions caused a secondary modification with removal of fine calcareous particles and a transport and winnowing of fossil sclerites. The preserved lithofacies (A) rocks are partly abundantly fossiliferous, with the sclerites partly winnowed and sorted. Accumulated bioclasts are sometimes densely packed although stratification is often poorly developed in parts with a particularly high amount of calcareous matter (Fig. 8).

Nearly quantitative sampling from the Wildenstein localities W8, W9 and W10 by the author, by Klaus Sdzuy, Erwin Albert and Stefan Meier allows a reliable reconstruction of the diversities for the typical associations of the Wildenstein Member. Other localities (W13a, W13b, W15, W15b, W16a) belong to coherent strata with a similar composition of trilobite species. The relative compositions of the trilobite assemblages illustrated in Fig. 7 indicates the dominance of *Kingaspidoides* species, *Prioscutarius max* and *Exapinepiphania wurmi* specimens in the lithofacies that reflect soft substrates and limited wave-action during the lifetimes of the animals, suggesting their ecological fitness for the particular habitat conditions. A different faunal composition is demonstrated by calcareous rocks (such as from localities W7 and W8), where the trilobites are typically dominated by small ptychoparioids such as *Cambrophatictor meieri*, *Exapinepiphania wurmi*, and *Cambrodaimona parablepta* as well as *Ornamentaspis frequens*. Mixed assemblages with supposedly vacillating conditions in respect to wave action and the amount of sand on the seafloor appear to indicate a relatively high proportion of ellipsocephalid species, such as *Kingaspidoides frankenwaldensis, K.* sp. cf. *brevifrons*, and *Ornamentaspis frequens*, with *Exapinepiphania wurmi* also occurring relatively frequently.

6 Arthropod preservation and taphonomy

Trilobites and agnostomorphs of the Wildenstein Member are variably preserved, their particular mode of preservation dependent on the lithofacies (and substrate settings) as well as on early diagenetic and specific taphonomic conditions. It can even be shown that burrowing activities and mottling affected the specific preservation of trilobite sclerites.

Trilobites embedded in finer-grained siliciclastics are typically preserved as quasi-composite moulds. In these cases, the original cuticle has been recrystallised and replaced by carbonate minerals with a varying amount of iron minerals. Phosphatisation of parts of the cuticle, which is regularly seen in the typical rock facies of the Galgenberg Member, is very rare and was only seen in parts of lithofacies C (Fig. 6A). As in the Galgenberg Member, phosphatisation appears to have been connected with a particularly high organic content in the relevant stratum.

Tectonic overprint resulted in consecutive secondary mineralization of the calcareous cuticles and fossil shells with iron minerals or chlorite to various degrees. Sub-recent weathering and leaching associated with iron staining derived from the weathering of (supposedly) pyrite ultimately created limonitic coats or crusts of varying composition, often with a minor amount of (tertiary) calcification. Such ferritic/limonitic replacements of the cuticle co-occur in several variants which are often difficult to distinguish. The typical eye-catching preservation known from fine-grained sandstone of the Galgenberg trilobites occurs in a few localities of Wildenstein rocks as well. These are as orange-yellow (e.g., Figs. 9A, B, 10J, K), reddish brown or maroon (e.g., Figs. 9E, 10F) coats on specimens embedded in yellowish or greenish shaly sandstones. The coats are often decomposed to an orange-brown powdery matter (e.g., Fig. 9E, F) and result from multiple decomposition of the original skeletal material.

This development of the composition predominantly did not produce true external moulds as the preserved surfaces of the mineralised sclerites are usually either corroded to some degree or display an overgrown morphology of the exterior surface of the cuticle. Similarly, the interior surfaces are often not true internal moulds, and early diagenetic deformation had led to conditions, which are here termed as “quasi-composite” moulds (e.g., Fig. 9F). The multiple recrystallisation variably resulted in thin coats replacing the original cuticle as dark brown layers with a high amount of Fe oxides (e.g., Figs. 9C, E, 10E), which sometimes preserve details of the largely removed cuticle (Fig. 10O); in thin yellowish coats (Figs. 9J, 10J); but occasionally in conspicuous thick coats (Fig. 9A). Of particular interest is the formation of replacement cuticles composed of two layers of slightly different mineralogical composition as recognisable by slight differences in the preservation (e.g., Fig. 10B, N).

Near complete weathering and removal of the original cuticular matter led to internal moulds which again may be preserved in several different ways. The calcareous parts of lithofacies C are commonly altered to grumous rock matrix so that the internal moulds are often chimaeras of the original sclerites (e.g., Figs. 9M, 10E). An extreme case with large holes almost concealing the trilobite morphology is illustrated in Fig. 9G. Replacement of original cuticles may have produced thick calcareous layers which are subsequently removed by weathering leaving conspicuous hollows (Fig. 9B). Decomposition of a thin coat in composite mould may lead to an imprint of fine details (e.g. cuticular ornament or prosopon) onto the internal mould.

Trilobite sclerites and carcasses in the Wildenstein Member have been affected by compaction and differential compression in various degrees. Simple and moderate dorsoventral compaction is a general feature that affected almost all specimens and is often only apparent if the sclerites were embedded at various degrees to the bedding plane. However, different aspects of deformation are regular features in the Wildenstein specimens.

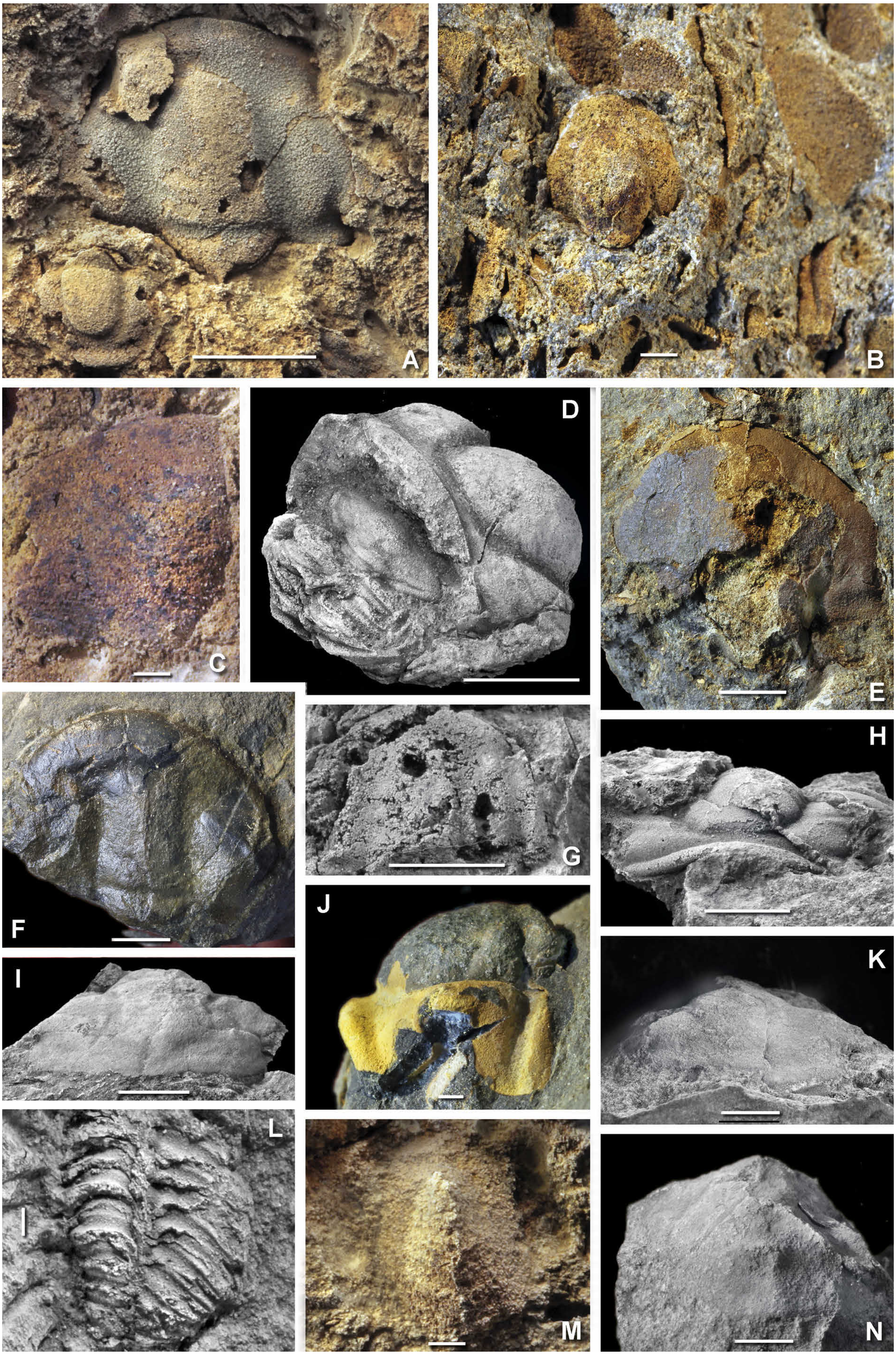
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Fig. 9: Taphonomic aspects illustrated by trilobitic skeletal remains from the Wildenstein facies and Member of the Tannenknock Formation. **A** *Ornamentaspis frequens* Geyer, 1990 and *Cambrophatictor meieri* n. sp., SSMM 11111b and 11111c, cranidia preserved as internal mould with relics of the cuticle developed as a recrystallised, thick secondary coat composed of a large amount of Fe-oxides and other weathering minerals; from locality W8. **B** Weathered bioclastic grainstone with trilobite hash composed of clasts with different sizes; matrix formed by a fine greywacke-type rock from which calcareous particles were removed during subrecent weathering; cranidium in the centre belongs to *Exapinepiphania wurmi* (SSMM 10398a); from locality W8. **C** *Kingaspis dolosus* n. sp., SSMM 11211, fragment of cranidium, internal mould shows remnants of the weathered cuticle; dark brown spots represent strongly ferritic parts of the secondary cover, whereas the yellowish brown areas indicate subrecently weathered parts with high amounts of goethite and limonite; from locality W8. **D** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-380; oblique view of completely enrolled dorsal exoskeleton, largely exfoliated; from locality W8. **E** *Kingaspis dolosus* n. sp., SSMM 10423, incomplete cranidium, partly exfoliated, with remnants of the weathered cuticle preserved as greyish brown coats representing strongly ferritic parts of the secondary cover, whereas the rest of the cuticle is predominantly weathered to orange-brown powder. The space below the shield-like cranidium obviously has been incompletely filled by mud so that this part collapsed during weathering and is also composed of a powdery matter; from locality W8. **F** *Kingaspidoides* sp. aff. *destombesi* (Geyer, 1990), SSMM 10351, composite mould of cranidium with few centripetal cracks and deformations testifying for plastic deformation (primarily on the left side); from locality W9. **G** Incomplete cranidium probably representing *Ornamentaspis frequens* Geyer, 1990, MMUW 2017D-591, strongly weathered sclerite with holes typical for the decomposed rock-type of lithofacies C; from locality W7b. **H** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-391a, anterior view of cranidium affected by oblique fracture and with slight offset of sclerite parts; from locality W8. **I** *Kingaspis* sp. A, MMUW 2017D-014, anterior view of cranidium affected by slightly curved fracture along the axis and with obliquely transverse fracture dissipated into short sections with differing directions; from locality W8. **J** *Exapinepiphania* sp. B, SSMM 19274-II, left lateral view of a cranidium with exfoliated glabella showing filled worm-tubes and with yellowish remnant of the weathered cuticle; from locality T2. **K** *Kingaspis dolosus* n. sp., MMUW 2017D-592, anterior view of cranidium with slightly curved fracture along the axis with slight offset of the sclerite parts; from locality W8. **L** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-239, detail of incomplete dorsal exoskeleton tentatively assigned to the species, shows incompletely enrolled thorax; thoracic segments tilted and slightly telescoped during compaction so that they are now partly detached; from locality W8. **M** Poorly preserved cranidium tentatively identified as *Cambrodaimona parablepta* n. gen., n. sp., SSMM 11111d; internal mould of strongly weathered specimen, divided by fracture along left side of the axis thereby mimicking a tapering, subacute glabella; from locality W6. **N** *Kingaspis dolosus* n. sp., MMUW 2017D-082I, anterior view of cranidium with a fracture along the axis and crushed right flank dissected into small differently tilted platelets; from locality W8.Dorsal views if not otherwise noted.
Scale bars equal 1 mm in B, C, J, L, and M, 5 mm in A, D, E, F, G, H, I, K, and N.

Soft-sediment deformation during compaction has affected all trilobite sclerites, albeit to different degrees. It commonly led to variable appearances of fossils of the same species so that a relatively high percentage of specimens of genera such as *Kingaspidoides* and *Parasolenopleura* are not determinable to the species with confidence. Examples of deformational features include simple flattening of sclerites (particularly cranidia) during dorsoventral compaction, but also plastic deformation of parts of the cranidium or pygidium resulting in wrinkled surfaces (e.g., Fig. 9F, I) or an enhanced relief following lateral compression (Fig. 10A, D) or slight shearing of the sclerites as results of compaction oblique to the axis of the sclerites (e.g., Fig. 10C, I, L). Specimens may also show upwarped lateral parts.

The majority of the trilobites sclerites shows compaction-related fractures although the fractures are often small and inconspicuous. These fractures indicate moderate compaction of the sediments during burial followed by dissolution of the original exoskeleton.

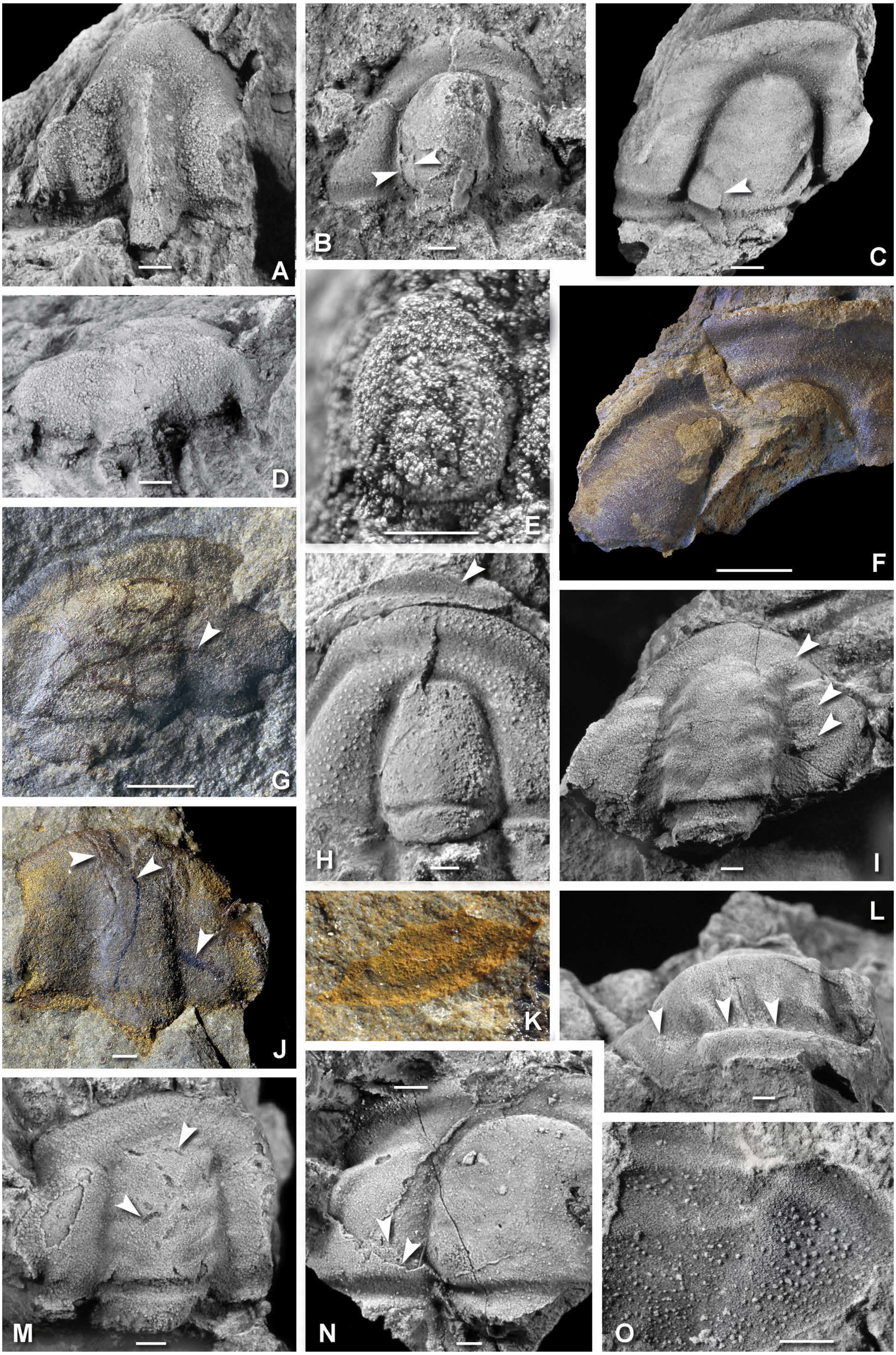
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Fig. 10: Taphonomic aspects illustrated by trilobitic skeletal remains from the Wildenstein facies and Member of the Tannenknock Formation. **A** *Kingaspidoides* sp. A, MMUW 2017D-795, dorsal view of transversely compressed cranidium resulting in exaggerated convexity of glabella, fixigenae and palpebral lobes as well as a longitudinal fracture along the centre of the glabella and a bent crest-line along right-hand eye ridge; from locality W17. **B** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-196, slightly distorted cranidium with curved longitudinal axis and two layers of the replicated cuticle (best visible parts marked by arrows); from locality W8. **C** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-869, cranidium (latex cast of mould) showing slight oblique lateral and oblique dorsoventral distortion resulting in an apparent plectrum-type swelling on the preglabellar field, a slit-like (right) glabellar furrow S1, and the progressive development of a fracture proceeding from the end of the (left) glabellar furrow S1 towards the posterior margin of the occipital ring; from locality W8a. **D** *Kingaspidoides* sp. A, MMUW 2017D-791, longitudinally and slightly obliquely compressed cranidium with anterior part slightly folded ventrally; compare with cranidium of similar size in Fig. 10A; from locality W17. **E** *Peronopsis* (*P.*) sp. A, MMUW 2017D-037a, internal mould of a cephalon formed by coarse granules of the weathered rock; from locality W8. **F** *Prioscutarius max* n. gen., n. sp., SSMM 10457, fragmentary cranidium, internal mould with relics of the ferritised cuticle (dark brown), dismembered by a fracture into two parts with the left parts offset towards the posterior; from locality W8. **G** Incomplete cranidium of *Kingaspidoides wildensteinensis* n.sp,.SSMM 10368, internal mould exposing criss-crossing network of *Planolites*-type burrows; note that the tubes proceed from underneath glabella to genae without change (arrow) so that they must have been aligned to the ventral face of the at that time still existing stiff cuticle; from locality W9. **H** *Prioscutarius max* n. gen., n. sp., MMUW 2017D-079, close-up of a cranidium affected by fracture along the axis in the anterior part and cast of rostral plate disintegrated from cranidium and shifted slightly forward (arrow); from locality W8. **I, L** *Ornamentaspis frequens* Geyer, 1990, MMUW 2017D-074, dorsal and left lateral views of internal mould of slightly distorted cranidium which made muscle attachment sites at lateral glabellar lobes S1, S2 and S3 visible; also visible are three slight uplifts on the genae and the preocular area on the right-hand side (arrows) which most probably represent swellings originating from parasitic infestation; from locality W8. **J** *Kingaspidoides frankenwaldensis* (Wurm, 1925), SSMM 10155, internal mould of slightly distorted cranidium with different types of “worm-tubes” (arrows): thin filled tube on right-hand fixigena, thin filled tube along axis of the glabella, and “hollow” tube to the left of it (probably with dark matter removed during (sub)recent weathering; from locality W14. **K** Librigena tentatively assigned to *Cambrodaimona parablepta* n. gen., n. sp., MMUW 2017D-515, external mould with decomposed cuticle preserved as orange-brown powdery matter largely made up by limonite; from locality W1. **M** *Ornamentaspis frequens* Geyer, 1990, MMUW 2017D-085, incomplete cranidium with secondary cuticular cover penetrated by burrows visibly by short curved sections (arrows); from locality W8. **N** *Exapinepiphania wurmi* (Geyer, 2017), MMUW 2017D-037b, close-up of largely exfoliated cranidium; remaining cuticle composed of two layers (arrows); from locality W8. **O** *Prioscutarius max* n. gen., n. sp., MMUW 2017D-568, fragmentary pygidium tentatively assigned to the species, close-up of external mould with infillings of tubules penetrating the original cuticle; from locality W9b.
Dorsal views if not otherwise noted. Scale bars equal 1 mm in A–E and H–O, 5 mm in F, and G.

Very common are specimens with small fractures that follow the principal directions of mechanical stress, i.e. the longitudinal axis of a convex part (such as the glabella or the pygidial rhachis), the maximum concavity of furrows, or centrifugal directions from the most elevated part of a bulge. Examples for fractures along the axis of the glabella are show in Figs. 9I, K, M, N and 10A, B, D, H, centrifugal fractures in Figs. 9D, F and 10F. Fig. 10C illustrates how a fracture develops from a simple deformation out of a furrow, and similarly growing offsets of fractured sclerite parts are shown in Figs. 9M, 10F and 10H. Complex small-scale fracturing may result in irregularly crushed parts dissected into small and differently tilted platelets (Fig. 9N).

Larger scale fracturing of sclerites, however, mostly took place before embedding as demonstrated by the distinctive predominance of small pieces of thoracic segments and partial cranidia with angular margins (e.g., Fig. 9C). Such damages during transport may lead to prefabricated cracks that led to small-scale lateral shifts caused by low stress during the earliest phase of compaction (Fig. 10F).

The fractures discussed above should not be confused with cracks generated tectonically. These are overwhelmingly common features in the rocks of the Franconian Forest (being part of the Saxo-Thuringian slice of the Hercynian orogenic belt). Such fractures are hardly visible on the sedimentary surfaces of the Cambrian rocks, but they affect most of the specimens although usually remain inconspicuous. They are recognisable in dissecting the trilobite specimens along roughly straight planes without any particular preference to the convexities of the sclerites (e.g., see fracture obliquely cutting the preocular area and glabella in Fig. 10N). Small-scale downthrows of such micro-faults are sometimes seen in fossil specimens, as demonstrated in Fig. 9H).

The observed specimens include exoskeletal elements spanning various degrees of articulation. The vast majority of trilobite sclerites are isolated cranidia and fractured parts of disarticulated thoracic segments, with librigenae and pygidia are regularly occurring. Due to the obvious transport of the specimens, fully articulated dorsal exoskeletons are rare and apparently dominated by enrolled specimens (Fig. 9D), with partially disarticulated exoskeletons or exoskeletal fragments also recognised (Fig. 9L). It is commonly believed that enrolled specimens generally testify rapid burial that subsequently caused the decease of the individual (e.g., Bergström 1973; Esteve & Hughes 2010; Ortega-Hernandez et al. 2013) so that some specimens with slightly disarticulated parts of the (partially) enrolled exoskeleton appear to indicate burrowing activity in the soft sediment after the individuals' decay. The latter case, exemplified by the specimen in Fig. 9L, also demonstrates a common post-mortem modification of the exoskeleton: the thoracic segments are tilted and were slightly telescoped during compaction and after decay of the soft parts that kept adjacent tergites in place so that they are now partly detached.

Most trilobite sclerites of the Wildenstein Member have been distorted during the Variscan tectonic events. An estimate of the distortion (i.e., of the relative amount of shortening or lengthening) can be determined from the specimens by the analysis of the tectonic strain. A semiquantitative approach for a few samples with two or more cranidia on a single slab from the Wildenstein slice localities W8 and W9 as well as W12 (Galgenberg Member) allowed for the reconstruction of the strain ellipses (e.g., Wellman 1962), which show a considerably varying shortening to lengthening ratios from 0.73 to 0.91 (see Geyer 2017).

A common feature in the trilobite sclerites of the Galgenberg Member are small burrows which can be seen on numerous internal moulds of cranidia (Geyer 2017). Such burrows are present in the small quantity of shaly rocks of Galgenberg-type facies interbedded in the Wildenstein rocks at a few localities. These “simple” trace fossils of the *Planolites beverleyensis*- to *Gordia*-type occur in three apparently different types: (a) as moderately broad, dark tubular tracks; (b) as thin, dark tubular tracks; and (c) as furrows of presently “opened” tubes, all immediately below the now removed cuticle (Fig. 10J). All three are gently curved to slightly looping. Sometimes they occur as criss-crossing networks (Fig. 10G), but careful analysis indicates that no connections (and thus no true branching) existed between the loops. Comparison with similar trace fossils from upper Wuliuan and lower Drumian strata of the Bohemian Cambrian (e.g., Mikuláš et al. 2012) suggests that the type (b) and (c) traces are just different preservational variants of the same ichnospecies, and type (a) may indeed also represent the same trace fossil. All of them developed during the period in which the sclerites resting on the seafloor were buried by sediment with the soft parts already decayed so that the animals which created the traces had contract with the still stiff, mineralised cuticle (see Fig. 10G).

A different type of trace fossil is seen in other specimens such as in Fig. 10M. Here, a cranidium shows short, curved sections of burrows, which penetrated a secondary cuticular cover. The fact that the burrows retreat almost immediately into the substrate suggests that the behaviour of the trace-maker was governed by tactile stimulus.

7 Systematic palaeontology

The material used in this study is in the repositories of

- the Mineralogisches Museum, Universität Würzburg (abbreviated MMUW),
- the Bayerische Staatsammlung für Geologie und Paläontologie, Munich (SNSB-BSPG),
- the Bayerisches Landesamt für Umwelt, Hof (BLfU),
- the Naturkunde-Museum Stuttgart, Museum am Löwentor (SMSN),
- the Naturmuseum Senckenberg, Frankfurt (SMF),
- the collections of Sveriges Geologiska Undersökning, Uppsala (SGU),
- the collections of the Lunds Universitet, Lund (LO),
- the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN),
- the collections of the Bundesanstalt für Geowissenschaften und Rohstoffe, Außenstelle Geowissenschaftliche Sammlungen, in Berlin-Spandau (GSB),
- the collection of Matthias Svojtka, Vienna (Sv1),
- the collection of Georges and Joëlle Devoille, Pierrefeu-du-Var, France (DEV),
- the collections of the New Brunswick Museum, St. John (NBMG),
- the collection of Stefan Meier, Marktredwitz (SSMM),
- the collection Frank Rudolph, Steinfeld (FR), and
- the collection of the Naturwissenschaftliches Museum Flensburg (NMF)

under the numbers provided in the material lists and figure captions.

Class Agnostomorpha n. cl.

Etymology. Name derived from that of the Order Agnostida Salter, 1864.

Diagnosis. Class of the Trilobitomorpha with dorsal exoskeleton composed of cephalic and pygidial shield of subequal size; eyes and facial suture absent; thorax composed of two segments; cephalic axis composed of anterior and posterior lobe, with a pair of basal lobes attached; pygidium generally with wide and long axis; ventral cephalic appendages consisting of a single pair of antennules and additional five pairs of appendages.

Discussion. Careful analysis of little- and non-sclerotised parts in *Agnostus pisiformis* led Müller & Walossek (1987) to suggest that the species and probably all agnostoids have character sets of their appendages that do not allow to assign them to the class Trilobita. In addition, Shergold (1991) showed in a prescient paper that agnostoids are distinct from eodiscoids. These conclusions are in line with earlier discussions on agnostoid classification by Öpik (1979) who summarised the basic characters of the *Agnostus* clade in some detail: proportions of tagmata, spines and fulcral structures; homologous structures of the tergite, variations in the appendage morphology and its position (through analysis of muscle scars), notulae and apodemes; positions of nodes; articulation; and suggestions of merocyclism. This results in a concept of functional morphology of the agnostoids as a clade. Öpik's (1979) observations agreed well with the subsequent morphological observations by Müller & Walossek (1987) and the functional morphology and derived from the anatomical details of the immature *orsten* specimens of *Agnostus pisiformis*. Öpik's (1967) general systematic conclusions lead to the assignment of all agnostoids within a single suborder and superfamiy, Agnostacea, principally following Rasetti (1945, 1948,

1952) in recognising the Order Agnostida Salter, 1864, but using it in the same way as the Miomera Jaekel, 1909, which united agnostoids and eodiscoids. However, Shergold et al. (1990) used this order exclusive of the eodiscoids, the latter being considered as a suborder of the Ptychopariida. Unfortunately, Shergold & Laurie (1991) were obviously forced to group the Order Agnostida Salter, 1864 composed of two suborders, Agnostina Salter, 1864 and Eodiscina Kobayashi, 1939, among the Trilobita.

The conclusions about the pronounced differences between agnostoids and trilobites have been often tacitly accepted but neglected in most systematic studies. Meanwhile it is widely accepted that agnostids cannot be furnished under the taxon Trilobita Walch, 1771. Also, an overwhelming majority of trilobitologists share the opinion that eodiscoids are in fact trilobites and not closely related to agnostids. This generates the need for a name of a class composed of the traditional suborder Agnostina and for a revised concept of the order Agnostida that does not include the suborder Eodiscina. The name Agnostomorpha n. cl. is suggested here for this class.

It should be emphasised that the term “polymeroid trilobite” was originally coined to include all trilobites except agnostoids and eodiscoids which then were regarded as representing a clade. Under the present-day concepts, this term denotes a paraphyletic group and is thus nomenclaturally invalid.

The immature specimens from the Orsten limestone nodules (e.g., Müller & Walossek 1987) were interpreted to record a stem-crustacean systematic position. However, exceptionally preserved mature individuals of the agnostinid genera *Peronopsis* and *Ptychagnostus* (Moysiuk & Caron 2019) from the middle Cambrian Burgess Shale of British Columbia, Canada, demonstrates similarities with the Trilobita rather than the Crustacea. However, Moysiuk & Caron (2019) showed that the cephalon carries one pair of elongate spinous antennules, two pairs of appendages with distally setose, oar-like exopods, and three pairs of presumably biramous appendages with endopods sporting club-shaped exites. While the antennules resemble the antennae of trilobites, the presence of six pairs of appendages contrasts the condition in the Trilobita, with four appendiferous segments

Accordingly, the Agnostina must be regarded as a sister group of the Trilobita. In contrast, no convincing data on the ventral appendages of the Eodiscina are known. Their exoskeletons, however, share the general morphology of primordial “polymeroid trilobites.” Briefly summarised, they can be parsimoniously regarded as the result of neotenic developments in trilobite phylogeny.

Order Agnostida Salter, 1864, emended

Discussion. The discussion above under Class Agnostomorpha accentuated that the distinctive morphological differences between the Agnostina and Eodiscina requires to restrict the Order Agnostida to the traditional suborder Agnostina.

Suborder Agnostina Salter, 1864

Superfamily Condylopygoidea Raymond, 1913

Family Condylopygidae Raymond, 1913

Genus *Condylopyge* Hawle & Corda, 1847

Type species. Battus rex Barrande, 1846, from the *Eccaparadoxides pusillus* Zone, middle Miaolingian (Drumian/Caesaraugustan), of Bohemia.

Diagnosis. Condylopygid trilobites with anterior lobe of glabella semicircular to rounded-triangular in outline. Pygidial axis with median ridge and two pairs of lateral furrows.

Condylopyge sp. A

Fig. 11

v 2008 *Condylopyge* – Geyer et al.: p. 168.
v 2010 *Condylopyge* – Geyer: p. 82.
v 2019a *Condylopyge* – Geyer et al.: p. 395.

Studied material. About 18 cephala, 30 pygidia, all disarticulated. In repository: from sample locality and stratum W7 (pygidium under MMUW 2017D-530); locality W8 (12 cephala under MMUW 2017D-006, -245a, -294bII, -737, -785a-I, 785-II, SSMM 10403b, 10494d, 11015b, 11140b, 11190, 11370, 11372; 25 pygidia under MMUW 2017D-007, -008, -010, -068, -233d, -303f, -632c, -652a, -706-I, -706-II, -709, -718, -759, -1011, SSMM 10305a, 11109e, 11116b, 11123b, 11361, 11362, 11363, 11371, 11604, 11615a, 11618, 11629a and 11634); locality W13e (cephalon under MMUW 2017D-480, pygidium under MMUW 2017D-616d); and locality W18a (two cephala under MMUW 2017D-546b, -547a, pygidium tentatively assigned to *Condylopyge* sp. A under MMUW 2017D-544); from locality W19b (cephalon under MMUW 2017D-935d). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Description. Cephalon with a gently curved frontal margin, length about 1.2–1.4 maximum width. Cephalic axis convex, ca. 77–82 % total cephalic length, and ca. 60 % width of cephalon. Anterior lobe subtriangular to subsemicircular in outline with gently curved anterior and posterolateral margins, posterior margin of anterior lobe slightly concave, sagittal length ca. three-quarters width. Posterior lobe subquadrate to slightly longer than wide, 70–75 % width of the anterior lobe, with median tubercle at posterior end, faint crest extends slightly forward from tubercle. Occipital lobe low, short, nearly as wide as anterior glabellar lobe, divided into sagittally narrow median part with median tubercle and pair of swollen basal lobes. Cheeks confluent in front, narrow opposite anterior glabellar lobe, with slightly higher sagittal width. Border furrow a moderately wide groove, relatively well incised. Border narrow, forms a fulcrum with a short spine posterolaterally.

Thoracic segments unknown.

Pygidium subrectangular in outline, length subequal to width. Lateral margins slightly curved, subparallel or slightly converging in the anterior third, gently curved in the posterior half. Posterior margin slightly to gently curved. Axis variably of about 76–83 % length and half width of pygidium, roughly parallel-sided or slightly tapering rearwardly, with slight constriction at about one-third of its length from anterior tip, posterior margin of axis more or less strongly curved to subacute. Anterior and second pair of lateral furrows shallow, not joined across the axis; posterior pair very weak. Median tubercle relatively large, elongated, located slightly anterior to mid-length of axis. Flanks of acrolobe less than or equal to half width of axis anteriorly, slightly narrowing posteriorly, connected posterior to axis.

Border furrow moderately wide, shallow, gutter-like. Border moderately broad (sag., exsag.) at posterior margin, slightly wider at well-rounded posterolateral corners, slightly tapering forward, without marginal spines.

Discussion. The specimens from the Wildenstein Member of the Tannenknock Formation are mostly poorly preserved and occur only in a facies characterised by slightly calcareous arenites.

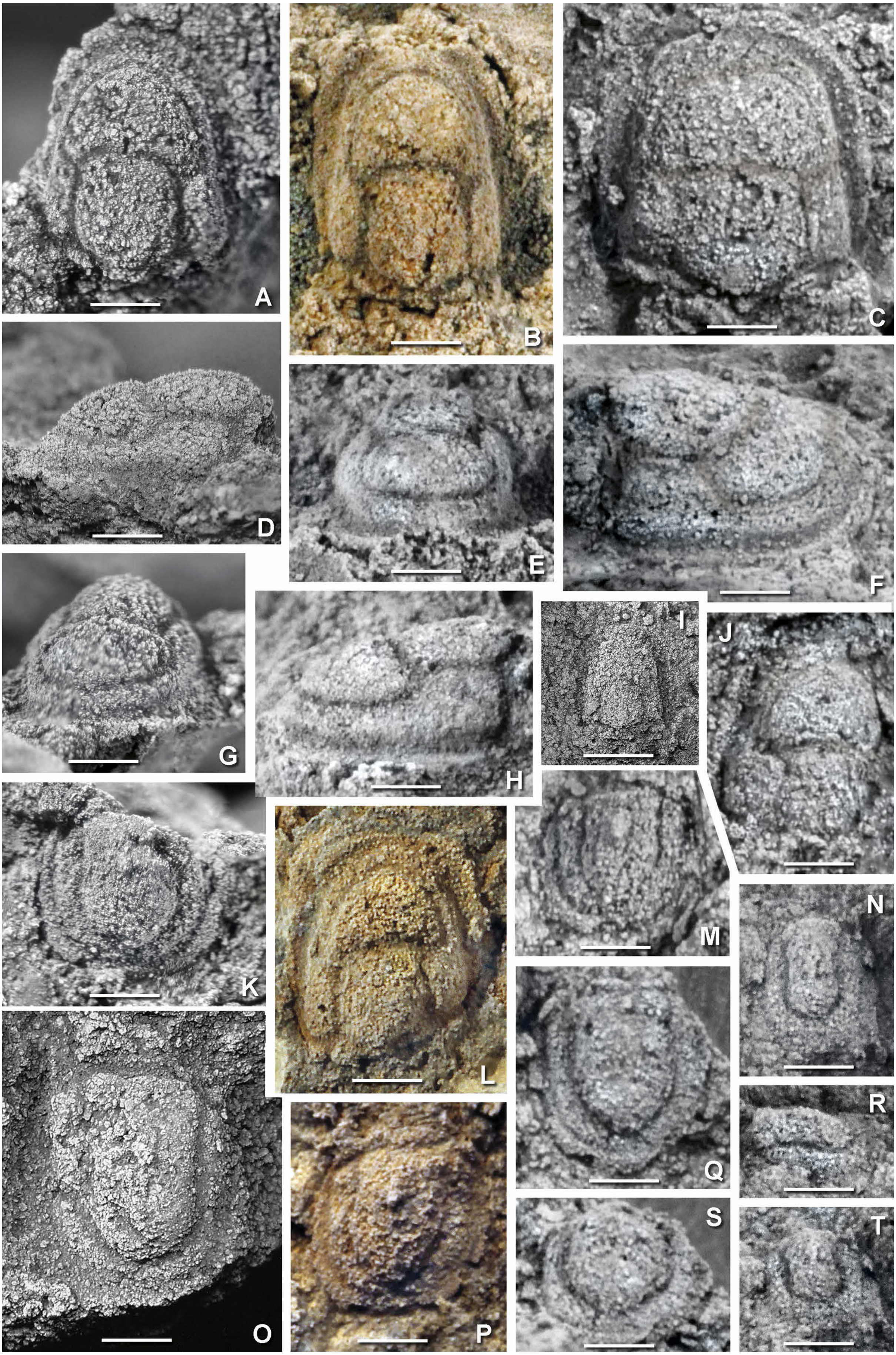
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Fig. 11: *Condylopyge* sp. A, all specimens from the Wildenstein Member, Tannenknock Formation. **A, D, G** MMUW 2017D-006, cephalon, internal mould, dorsal, lateral and anterior views; from locality W8. **B, E, H** MMUW 2017D-1100, cephalon, internal mould, dorsal, anterior and lateral views; locality W8. **C, F** MMUW 2017D-737, cephalon, slightly longitudinally compressed internal mould, anterior and oblique lateral views; locality W8. **I** MMUW 2017D-480, minute cephalon of immature individual; locality W13c. **J** MMUW 2017D-546b, partial cephalon; locality W18a. **K** MMUW 2017D-010, incomplete pygidium; locality W8. **L** MMUW 2017D-547a, cephalon; locality W18a. **M** MMUW 2017D-718, incomplete pygidium; locality W8. **N, R, T** MMUW 2017D-068, pygidium of immature individual, dorsal, oblique lateral and oblique posterior views; locality W8. **O** MMUW 2017D-007, incomplete pygidium; locality W8. **P** SSMM 1116b, incomplete pygidium; locality W8. **Q, S** MMUW 2017D-530, pygidium, dorsal and oblique posterior views; locality W7. Dorsal views if not noted otherwise. All scale bars 1 mm.

Despite of the generally imperfect preservation, the material displays a relatively good picture of the morphology, which does not conform perfectly with any of the 12 formally described and presently recognised species of *Condylopyge*. *Condylopyge* sp. A belongs to the morphogroup of species within the range of *Condylopyge* characterised by the most similar species *Condylopyge carinata* Westergård, 1936, known from the Wuliuan “*Eccaparadoxides*” *pinus*–*Pentagnostus praecurrens* Zone of Sweden and the *Agraulos affinis* Zone of the Chamberlain’s Brook Formation of Avalonian Newfoundland (Fletcher 2006). Rees et al. (2014) suggested that *C. cambrensis* (Hicks, 1871) from the upper Wuliuan Newgale Formation (= Lower Solva beds) of Pembrokeshire, South Wales, is a synonym of *C. carinata*. *Condylopyge carinata* shares a similar morphology of the cephalon, albeit having in most specimens a shorter anterior cephalic lobe with a more equally curved anterior margin and slightly wider flanks. Stronger differences can be seen in the pygidium with distinctly rearward tapering flanks and a relatively blunt posterior margin of the pygidial axis as well as a slightly more posteriorly located median tubercle on the axis in *C. carinata*.

Even more similar is a species originally introduced as *Condylopyge carinata vicina* Egorova, 1972, from the *Oryctocara* and *Kounamkites* zones of the Amgan Stage in the Nekekit River region of the Siberian Platform (see also Egorova et al. 1976). Although this form shows a morphology that resembles that of *C. carinata* from Sweden (= *C. carinata carinata*), *C. carinata* is somewhat transitional to the species of the *C. rex* morphogroup. Accordingly, there is no reason why the two forms with their distinctly dispersed occurrences should be treated as subspecies of the same species and thus different than other closely related species in the genus. Thus, it is suggested here to treat the Siberian form described as *Condylopyge carinata* as a separate species, *C. vicina* (Egorova, 1972). Indeed, *Condylopyge vicina* closely resembles *C.* sp. A from the Wildenstein Member, but is distinguished by its narrower posterior cephalic lobe, a slightly longer pygidial axis and a less pointed posterior tip of this pygidial axis. It needs to be emphasised that the small specimens discovered in the Wildenstein Member (e.g., Fig. 11I, N, R, T) are more slender shaped cephala and pygidia. The same more elongate shape of the cephala and pygidia is also seen in *C. vicina* (e.g., Egorova et al. 1976, pl. 52, figs. 9, 11.

Nevertheless, *Condylopyge* sp. A has some resemblance with the morphogroup exemplified by *Condylopyge rex* (Barrande, 1846) and *C. regia* (Sjögren, 1872). The form differs from the widely distributed *C. rex* (known from the early/lower Drumian *Eccaparadoxides pusillus* Zone of Bohemia; the *aurora*/*gibbus* and *Tomagnostus fissus* zones of England; the *Hypagnostus parvifrons* Zone of Sweden; the *Mawddachites hicksii* and *Paradoxides davidis* zones of Avalonian Newfoundland; the Cantabrian Mountains, Iberian Chains and West Asturian–Leonesian Structural Zone, Spain; the *Solenopleuropsis* Zone of the Franconian Forest, Bavaria, and the *Badulesia tenera* Zone of the boreholes in the Delitzsch–Torgau–Doberlug Syncline, Saxony, Germany) in having slightly larger anterior glabellar lobe and a wider posterior glabellar lobe, as well as particularly a distinctly wider and barely constricted pygidial axis, the axial tubercle in a much more anterior position and narrower flanks (e.g., Fatka et al. 2015, fig. 2). *Condylopyge regia* (Sjögren, 1872), from the *Eccaparadoxides*? *insularis* Zone of Sweden and the *Badulesia tenera* Zone in the Delitzsch–Torgau–Doberlug Syncline, Germany, is distinguished from *C.* sp. A by more-or-less the same characters as *C. rex*, but also by a wider cephalic border.

A superficially more closely similar species appears to be *Condylopyge globosa* (Illing, 1916) from the *Tomagnostus fissus* Zone of the Abbey Shales of Warwickshire, England. This species is particularly similar in the relative widths of the anterior and posterior cephalic lobe and the pygidial axis, the barely constricted pygidial axis, and the more anteriorly located median tubercle. However, *C. globosa* is distinguished by a shorter cephalon and the distinctly curved lateral margins in the cephalon and pygidium as well as a median furrow posterior to the pygidial axis (Rushton 1979, fig. 1B–F).

Superfamily Agnostoidea M'Coy, 1849

Family Peronopsidae Westergård, 1936

Genus *Peronopsis* Hawle & Corda, 1847

Type species. Battus integer Beyrich, 1845; from the *Eccaparadoxides pusillus* Zone, Miaolingian, Jince Formation, Bohemia (by original designation).

Subgenus *Peronopsis* Hawle & Corda, 1847

Type species. Battus integer Beyrich, 1845; from the *Eccaparadoxides pusillus* Zone, Miaolingian, Jince Formation, Bohemia.

Remarks. The comprehensive reappraisal of the *Peronopsis* clade by Naimark (2012) clarified a number of problems within the phylogenetically complex family Peronopsidae and particularly the *Peronopsis–Itagnostus* clade. She was able to demonstrate evolutionary pathways, but also illustrate deficiencies in the knowledge of morphology and the subsequently arising difficulties in a correct weighting of characters for the established taxa.

Peronopsis (*Peronopsis*) sp. A

Fig. 12

Studied material. About 14 cephala, 18 pygidia, all disarticulated. In repository: from sample locality and stratum W8 (8 cephala under MMUW 2017D-036c, -037a, -233c, -291c, -674g, -739, -985, SSMM 11365b, 11365c and 11368; 13 pygidia under MMUW 2017D-036a, -067, -651, -716, -1016b, SSMM 10788c, 11116c, 11364, 11369, 11490a, 11490b, 11614 and 11646b, five pygidia tentatively assigned to *Peronopsis* (*Peronopsis*) sp. A under MMUW 2017D-057, -058, -245b, -503b and -1037). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Description. Cephalon strongly convex, subrectangular in outline, with distinctly and subevenly curved anterior margin and slightly curved lateral margins; length/width ratio ca. 0.80 to 0.85. Glabella bilobate, tapering forward. Posterior lobe with length about three-quarters width, slightly longer than 1.5 times length of anterior lobe, highest elevation about one-third from well-rounded posterior end; with low longitudinal node. Anterior lobe with subevenly rounded frontal margin, slightly constricted towards posterior margin. Transverse furrow straight. Anterior lobe well-defined by moderately deep dorsal furrow. Occipital ring narrow, continuous with the simple, triangular, inequilateral basal lobes, which are somewhat oblique to axis.

Genae convex, preglabellar median furrow absent. Border moderately convex, slightly growing in width from genal angles anteriorly, widest on sagittal line; posterolateral corners not preserved in any of the known specimens. Border furrow narrow, moderately deep.

Thorax unknown.

Pygidium consists of moderately convex flanks and strongly convex axis, subrectangular in outline, with weakly curved lateral and distinctly curved posterior margins, but median part of posterior margin with low curvature; length/width ratio ca. 0.85–0.90. Axis variably of 69–75 percent pygidial length, 40–47 percent pygidial maximum width across anterior segment, which is defined by a distinct lateral furrow, lateral axial furrows obscure; posterior two-thirds or almost three-quarters of axis with subparallel sides and posterior margin with narrow curvature; median tubercle elliptical in outline, ca. 40 percent from anterior end.

Postaxial area wide (sag.), without median furrow. Pleural lobes moderately convex. Border with low convexity, growing in breadth from anterolateral corners to a maximum of ca. twice this breadth on sagittal line; wider than on the cephalon; with somewhat variably developed, small marginal thorns located slightly posterior to a transverse line drawn at tip of axis. Anterior border confluent with lateral border at distinct anterolateral corners. Border furrow shallow, relatively broad, subequal in width throughout.

Lengths of cranidia in the present material 1.2–2.9 mm, lengths of pygidia 1.5–3.3 mm.

Discussion. The poorly preserved specimens from the Wildenstein Member do not allow a precise determination of the species. However, the visible characters indicate a morphology that is distinctly different from all well-known species of the *Peronopsis* clade. Particularly important characters include (1) the relatively slender pygidial axis with subparallel sides and a rounded posterior margin; (2) the absence of a postaxial furrow; (3) the broad (sag.) postaxial area; (4) small to minute posterolateral thorns at the pygidial margin; (5) a moderately large anterior lobe of the glabella; and moderately large basal lobes. These characters suggest that the form belongs to *Peronopsis* (*Peronopsis*), albeit the characters are not entirely distinctive for the species of that subgenus. Among the apparently most similar species is *Peronopsis* (*Svenax*) *inarmata* Hutchinson, 1962, which is known from the (poorly constrained) *Eccaparadoxides bennetti* Zone of Avalonian south-eastern Newfoundland (Hutchinson 1962), but also identified from the *Ptychagnostus gibbus* Zone of the Olenek River region of the Siberian Platform (Naimark 2008, 2012, Naimark & Pegel 2018). If one follows the descriptions in Naimark (2008, 2012), the species has a large morphologic plasticity, but is clearly distinguished from the specimens from the Wildenstein Member by a distinctly wider and posteriorly more acute axis and several other characters. Another similar species was described as *Peronopsis huzhuensis* Chu, 1965, from the late/upper Changhian of North Qilianshan (e.g., Zhou & Dean 1996), but is known from relatively poorly preserved specimens as well. The Chinese species is distinguished by its apparently more strongly developed posterolateral spines and the median node on the pygidial axis in a more anterior position. Other superficially similar species are placed under the genus *Archaeagnostus* Kobayashi, 1939, such as *A. primigeneus* Kobayashi, 1939 from the upper part of the *Bonnia-Olenellus* Zone of the Taconic Allochthon in the New York State and the *Ovatoryctocara* Zone and the *Kounamkites* Zone on the Siberian Platform; *A. evansi* (Rasetti & Theokritoff, 1967) from the upper part of the *Bonnia-Olenellus* Zone of the Taconic Allochthon in the New York State; and *A. majiangensis* (Lu & Chen in Lu et al., 1974) from the *Oryctocephalus orientalis* Zone of south-eastern Guizhou, South China (see additional data in Naimark 2012). However, *Archaeagnostus* is characterised by a rearwardly tapering pygidial axis resulting in a subacute posterior end.

Surprisingly, the specimens from the Franconian Forest are clearly not closely related to the species known from adjacent regions and similar stratigraphic horizons, such as *Peronopsis* (*P.*) *integer* (Beyrich, 1845) (from the Jince Formation of Bohemia) and Scandinavia, although that species has been (erroneously) reported from an extremely extended stratigraphic range and almost subglobally distributed areas (for precise morphology of *P.* (*P.*) *integer* see, e.g., Šnajdr 1958; Pek 1971; Laurie 1990; Robison 1994; Naimark 2012).

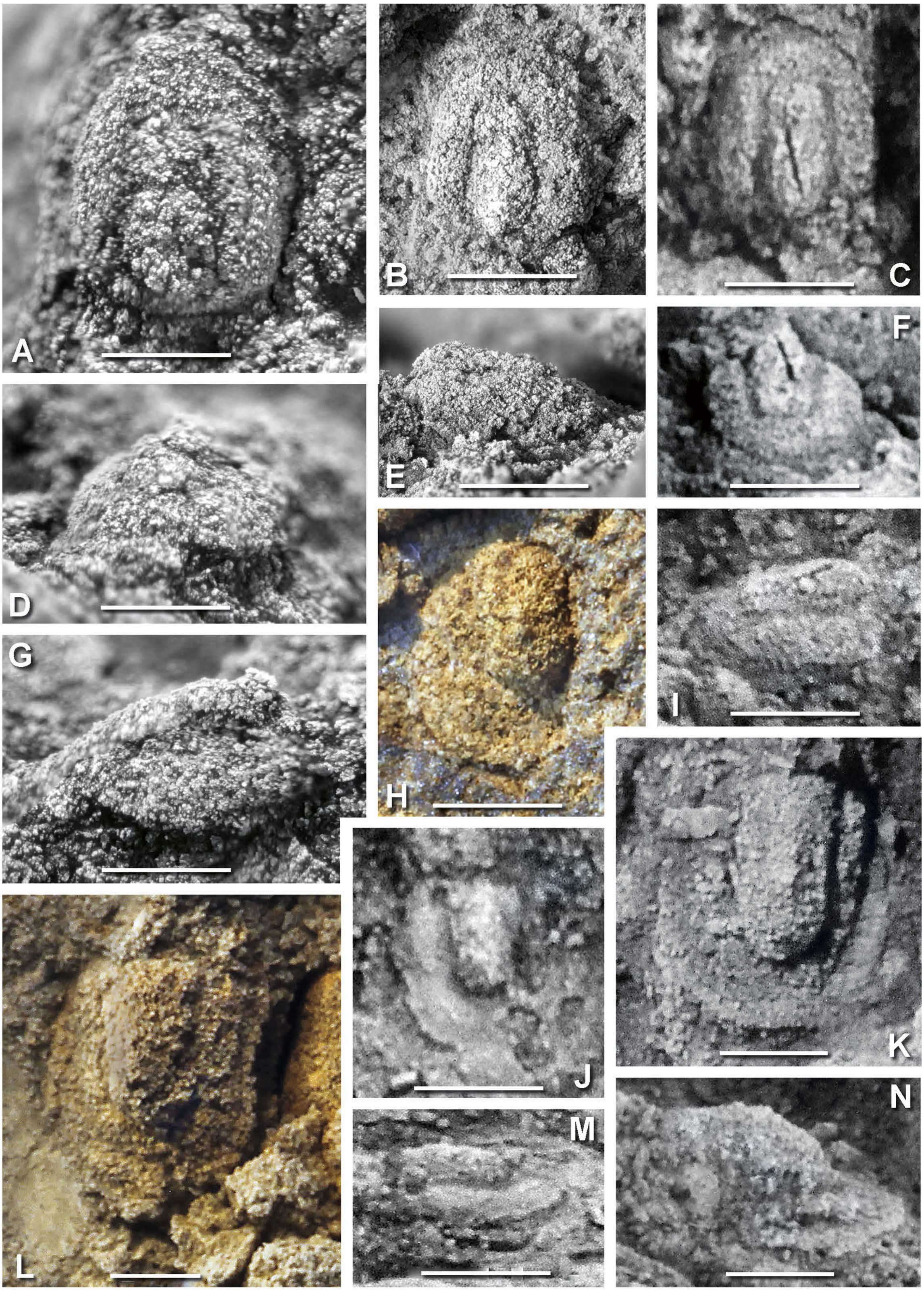

Fig. 12: *Peronopsis* (*Peronopsis*) sp. A, all specimens from the Wildenstein Member, Tannenknock Formation. **A, D, G** MMUW 2017D-037a, cephalon, internal mould, dorsal, anterior and lateral views; from locality W8. **B, E** MMUW 2017D-674g, cephalon of immature individual, internal mould, dorsal and anterior views; locality W13f. **C, F, I** MMUW 2017D-739, cephalon, internal mould, dorsal, oblique anterior and lateral views; locality W8. **H** Partial pygidium; locality W8?; specimen apparently lost. **J, M** MMUW 2017D-716, partial cephalon of juvenile individual, dorsal and lateral views; locality W8. **K, N** MMUW 2017D-067, pygidium, dorsal and lateral views; locality W8. **L** SSMM 11116c, pygidium; locality W8. Dorsal views if not noted otherwise. All scale bars 1 mm.

A somewhat similar form of *Peronopsis* has been recorded from more-or-less coeval strata of the Iberian Chains, which first has been identified as "*Peronopsis* sp." (Liñán et al. 2004), as "*Peronopsis normata* (Whitehouse, 1936)" (e.g., Gozalo et al. 2013) and as "*Peronopsis* aff. *longinqua* Öpik, 1979" (e.g., Liñán et al. 2008, Gozalo et al. 2008), both obviously referring to the same form. The known illustration suggests that the imperfect preservation of those specimens does not allow an even somewhat reliable identification as well as a confident comparison with the specimens from the Wildenstein Member.

Class Trilobita Walch, 1771

Order Eodiscida Kobayashi, 1939, new

[nom. transl. ex Eodiscina Kobayashi, 1939]

Discussion. The separation of agnostoids and eodiscoids requires to raise the former suborder Eodiscina to an order.

Suborder Eodiscina Kobayashi, 1939

Superfamily Eodicoidea Raymond, 1913

Family Eodiscidae Raymond, 1913

Genus *Dawsonia* Hartt *in* Dawson, 1868

Type species. Microdiscus dawsoni Hartt in Dawson, 1868, p. 655, from the Fossil Brook Member of the Chamberlain's Brook Formation, New Brunswick.

Occurrence. The regionally restricted occurrence of *Dawsonia* is quite striking and coincides with that of several other trilobites: It is a genus typical for a sea archipelago realm which existed during the Cambrian Series 2–Miaolingian interval and included Avalonia, the north-western margin of West Gondwana, the Siberian Platform and Baltica (Fig. 13). Species of the genus have been reported from regions such as Massachusetts, USA (Geyer & Landing 2001), New Brunswick, Canada (Rasetti 1952), Wales, UK, Öland and Jämtland, Sweden (Westergård 1936, 1946; Axheimer 2006), Sardinia, Italy, Montagne Noire, France (Howell 1935; Álvaro & Vizcaïno 2000), the Cantabrian Mountains, Spain (Sdzuy 1995), Bohemia (Šnajdr 1958), and the Siberian Platform (Egorova et al. 1982), but also from south-central China (Zhou in Zhou et al. 1977). Specimens from the Franconian Forest have been mentioned by Sdzuy (1960), but this report for the first time characterises the species.

Discussion. The genus *Dawsonia* has been a matter of confusion regarding its authorship as well as that of its species and their precise generic assignment. Discussions in Rasetti (1952), Sinclair (1953) and Geyer and Landing (2001) clarified these questions.

Following Rasetti (1952) and Axheimer (2006), *Dawsonia* is regarded here as a genus with a considerable morphoplasticity so that it includes in this concept species with differences in the pattern of the scrobicules in the anterior border, the shape of the glabella and the occipital spine. Consequently, *Metadiscus* Kobayashi, 1943b (type species *Microdiscus sculptus* Hicks, 1871) is regarded as a junior synonym of *Dawsonia*.

The species of *Dawsonia*, however, are relatively stable in its morphology if they are evaluated by assemblages that appear to represent actual communities. Particularly specific criteria are seen in different shapes and lengths of the glabella, and the dimensions of the anterior border with its differently developed furrows in terms of depth, length and distances between them.

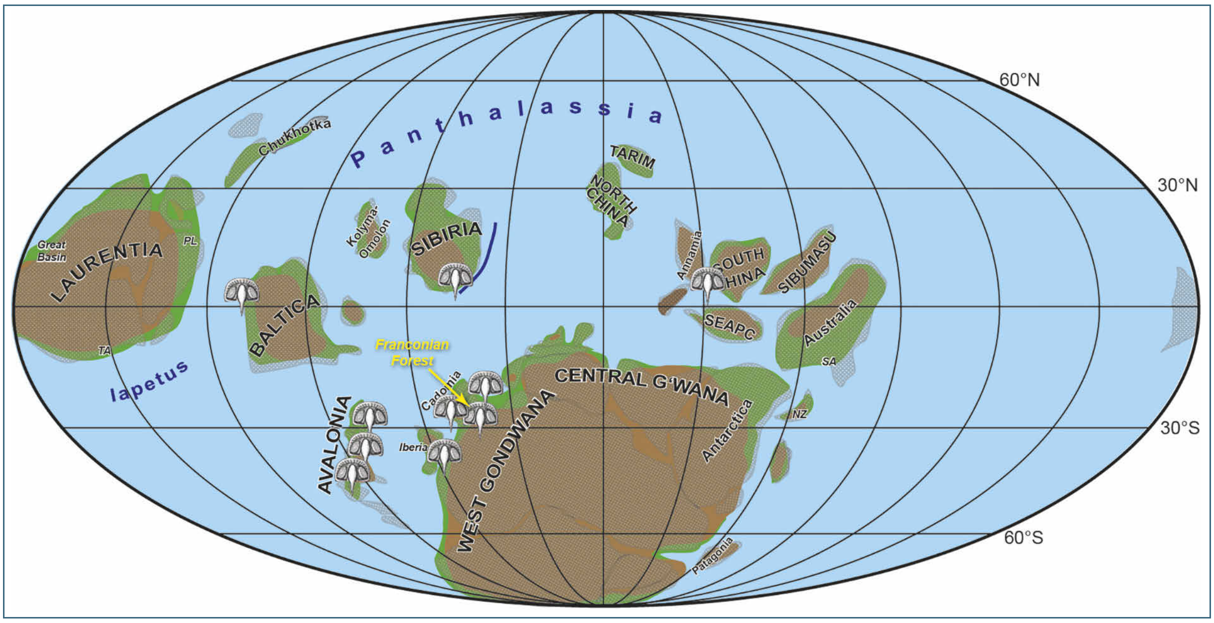

Fig. 13: Palaeogeographic map for the Cambrian (Stage 4–Wuliuan) boundary interval illustrating the occurrence of *Dawsonia*. Map modified from Mghazli et al. (2023, fig. 17).

Dawsonia densiserrata **n. sp.**

Fig. 14

Holotype. Incomplete cephalon, MMUW 2017D-735aI (Fig. 14B, E).

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Type locality and type stratum. Sample locality W8 in the Wildenstein slice near Wildenstein. Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; Agdzian Stage, probably lower Wuliuan.

Etymology. From the Latin *densus*, dense, and *serratus*, jagged; a reference to the densely arranged scrobicules on the anterior cephalic border.

Paratypes. Ten cephala, 9 pygidia, all disarticulated, mostly incomplete or fragmentary. From sample locality and stratum W8 (8 cephala under MMUW 2017D-182b, -219a, -735aII, SSMM 11375, 11378, 11379, 11380, 11469a; 7 pygidia under MMUW 2017D-034, -223, -225b, -746, -752a, -1017 and SSMM 10787a). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Diagnosis. Species of *Dawsonia* without distinct furrows or depressions on the glabella; glabella narrow, tapering forward, with narrow perfectly rounded front; occipital spine probably moderately long; anterior cephalic border with relatively narrowly spaced furrows that reach closed to the anterior cephalic margin and are slightly irregularly arranged; cephalic border furrow moderately wide, tapering posterolaterally. Pygidium with slightly tapering axis composed of up to six rings, terminal axial piece reaching to posterior border furrow; lateral pygidial border narrow, brim-like, grading into border furrow, with smooth abaxial margin.

Description. Cephalon subelliptical in outline, ca. 1.4 times wider than long (excl. glabellar spine). Glabella strongly convex (tr.), evenly tapering forward to ca. 60 percent maximum width across occipital ring, with front evenly curved; maximum glabellar width at occipital ring ca. one-fourth maximum cephalic width, glabellar length ca. two-thirds cephalic length on sagittal axis; glabella without any furrows, but apparently with faint constrictions which are difficult to precisely recognise in the studied poorly preserved specimens. Occipital furrow appears to be obsolescent medially, vaguely developed close to the axial furrow; occipital ring without a conspicuous glabellar spine, but apparently short to median spine present.

Axial furrows and preglabellar furrow deep. Preglabellar field absent, confluent with preglabellar furrow, represented by a distinctly sunken depression which separates the anterior parts of the genae.

Genae subsemicircular in outline, inflated, well-defined by deep axial and border furrows. Faint ridges resembling eye ridges vaguely indicted on two specimens, running obliquely on anterior parts of genae towards anterior part of glabella.

Anterior cephalic border broad (sag., exsag.), tapering posterolaterally and grading into lateral border, distinctly convex (sag., exsag.). Lateral border moderately wide, slightly elevated. Anterior and lateral border serrate, intersected by radially arranged furrows, which end ca. one-fifth of respective border width from anterior, anterolateral, and lateral margins, dividing border into ca. 30 segments of slightly irregular width. Length of grooves decreases posterolaterally, with genal angle apparently smooth.

Thoracic segments unknown.

Posterior border not entirely preserved in any of the present specimens, narrow in the adaxial and middle part, slightly broader (exsag.) abaxially. Posterior border furrow developed as a relatively deep, abaxially continuously broadening groove.

Pygidium subelliptical in outline, strongly convex, about 1.2 times wider than long. Four pleural furrows, curved backwards, reaching border furrow. Pleural furrows deep, dividing the pleural field into five pleural bands.

Pygidial axis tapering rearward, with six axial rings plus a short terminal axial piece, which is separated by a furrow from the terminal axial ring and reaches to posterior border furrow. At least second and third axial ring each probably bear a median node or short spine.

Pleurae with four distinct, but relatively shallow furrows, which are nearly straight and slightly rearward directed from axial furrows. Most posteriorly located, fifth furrow shallow, indistinct.

Lateral and posterior border narrow, uniform in width, brim-like, grading into border furrow, with smooth abaxial margin. Lateral and posterior border furrows moderately deep grooves of up to nearly double width of the adjacent part of the border.

Anterior border relatively narrow to moderately broad (exsag.), prominent, slightly growing in width toward the anterolateral corners, with distinctive curvature in transverse profile. Anterior border furrow quite deeply incised, slightly wider and deeper than pleural furrows, curving slightly backward laterally.

Discussion. The material from the Wildenstein Member is relatively sparse and mostly very poorly preserved. However, the specimens are known from different sample locations and clearly designate a species confined to certain facies preferences of fine-grained calcareous deposits. The recognisable characters identify the specimens unequivocally as a new species of *Dawsonia*.

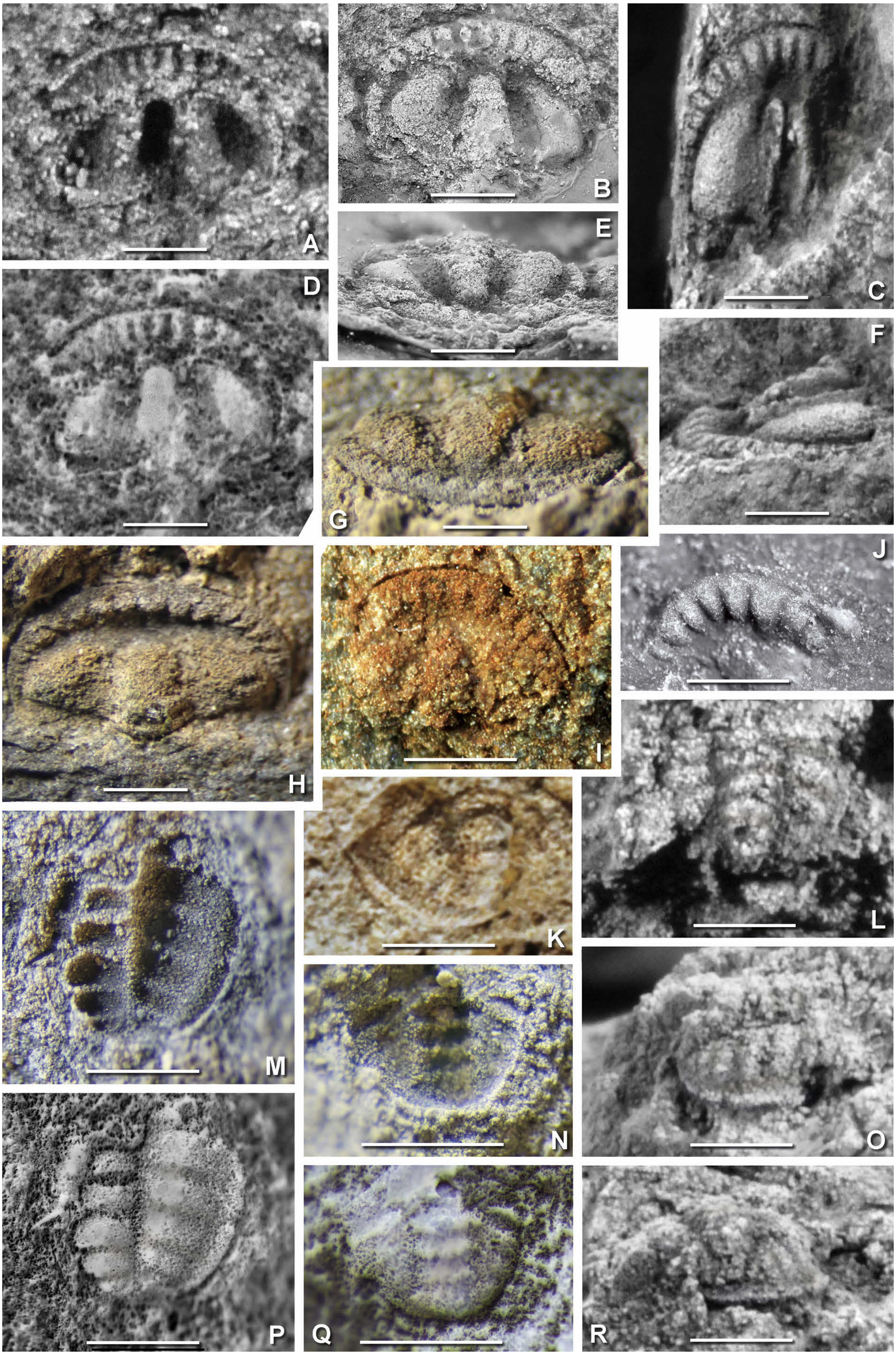
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Fig. 14: *Dawsonia densiserrata* n. sp., all specimens from the Wildenstein Member, Tannenknock Formation. **A, D** MMUW 2017D-735a-II, counterpart of holotype, cephalon, external mould, ventral view and inverted photo; locality W8. **B, E** MMUW 2017D-735a-I, holotype, cephalon, internal mould, dorsal and oblique anterior views; locality W8. **C, F** MMUW 2017D-182b, paratype, partial cephalon, internal mould, dorsal and lateral views; locality W8. **G, H** SSMM 11380, paratype, distorted cephalon, internal mould, oblique anterior and dorsal views; locality W8. **I** SSMM 11378, paratype, partial cephalon, internal mould showing faint submarginal impression at the anterior termination of the scrobicules; locality W8. **J** MMUW 2017D-219a, paratype, partial cephalon, latex cast of external mould showing more-or-less original morphology the anterior border; locality W8. **K** SSMM 10787b, paratype. incomplete pygidium, internal mould; locality W8. **L, O, R** MMUW 2017D-752, paratype, incomplete pygidium, internal mould, dorsal, oblique lateral and posterior views; locality W8. **M, P** MMUW 2017D-034, paratype, partial pygidium, ventral view of external mould and dorsal view of latex cast; locality W8. **N, Q** MMUW 2017D-223, paratype, incomplete pygidium, ventral view of external mould and dorsal view of latex cast; locality W8.
Dorsal views if not noted otherwise. All scale bars 1 mm

The new species closely resembles *Dawsonia bohemica* (Šnajdr, 1950), a well-known species from the *Eccaparadoxides pusillus* Biozone, Jince Formation of the Barrandian region, Czech Republic, introduced as *Aculeodiscus bohemicus* by Šnajdr (1950). That species is distinguished from *D. densiserrata* n. sp. in have less frequent and more irregularly spaced scrobicules on the anterior and lateral border; a broader anterior border; a less strongly tapering glabella with a strongly developed and long genal/ occipital spine; and a lateral border in the pygidium, which is subdivided into segments defined by slight rises.

As noted in Geyer & Landing (2001), the type material for *Dawsonia dawsoni* (Hartt in Dawson, 1868) in Dawson's "Acadian Geology" (1868, pp. 653–655, fig. 228) came from "carbonaceous shales" of the Middle Cambrian at Coldbrook, New Brunswick. Additional material from the same group at Ratcliff's Brook in southern New Brunswick, was described by Walcott (1884a, 1886), but the species is also known from the *Eccaparadoxides eteminicus* Zone of the Chamberlain's Brook Formation of New Brunswick. This purely West Avalonian type species of *Dawsonia* is characterised by relatively irregularly spaced radial grooves, which dissect the wide anterior and lateral cephalic border for approximately three-quarters of its breadth; a glabella with a pair of lateral indentations and therefore not tapering evenly, with the front having a parabolic outline; with a distinct and relatively deep groove in front of the glabella which clearly separates the genae; and with a strongly developed, extended occipital/glabellar spine of clearly less than the length of the rest of the cephalon (see Rasetti 1952, pl. 54, figs. 1–9). A similar form has been described from relatively poorly preserved cephala of the Braintree Member of Massachusetts (Geyer & Landing 2001, fig. 4), but these specimens differ in having a relatively broad (sag.) groove in front of the glabella, with the genae separated medially but with quite closely located anteroproximal ends; and having only an obviously short glabellar spine.

The description of *Dawsonia dawsoni* from south-central China (Zhou in Zhou et al. 1977, p. 116) is based on imperfectly preserved material that probably represents a new species.

Dawsonia canadensis Kobayashi, 1943b, based on a specimen from the *Protolenus* Fauna of Hanford Brook, New Brunswick, is most probably a junior synonym of *Eodiscus scanicus* (Linnarsson, 1883).

Dawsonia spinifera Kobayashi, 1943b has been erected based on specimens collected by G.F. Matthew and regarded as different from *Dawsonia dawsoni* – simply based on wrong assumptions generated by the incorrect illustrations provided in Dawson's monograph. Therefore, the species is a junior synonym of *D. dawsoni* as well (as already considered in Rasetti 1952).

Dawsonia oelandica (Westergård, 1936) had been introduced as *Calodiscus oelandicus* from the *Ptychagnostus praecurrens* Zone (formerly the *Paradoxides pinus* Zone) of Öland, Sweden, and has been described subsequently from coeval strata in Jämtland, but also identified from the Siberian Platform (Savitsky et al. 1972; Egorova et al. 1982). Sdzuy (1960) identified specimens from the

Franconian Forest as *Dawsonia oelandica* but did not provide any photos (Sdzuy 1960, p. 108), and it is almost certain that his record refers to the species described here. In addition, Sdzuy (1968, p. 51) also reported *D. oelandica* without a photo from the Cantabrian Mountains, northern Spain, and this report must be regarded as uncertain. *Dawsonia densiserrata* is clearly distinguished from *D. oelandica* by its more numerous and longer furrows on the anterior and lateral borders, which stretch relatively close to the external margin of the anterior border, whereas the abaxial one-third of the anterior border in *D. oelandica* is unfurrowed (e.g., Axheimer 2006, fig. 2). In addition, the glabella in *D. densiserrata* tapers more strongly and appears to lack a long posterior spine. The pygidial axis in *D. densiserrata* reaches to the posterior border furrow rather than being separated by a narrow band as in *D. oelandica*.

The type material of *Dawsonia sculpta* (Hicks, 1871) comes from the “Harlech Series” of Nun’s Well in Pembrokeshire, Wales (now the Newgale Formation; see Rees et al. 2014). The species was assigned to the type species of *Metadiscus* Kobayashi, 1943a. Rasetti (1952) emphasised that the cephalic and pygidial characters match those seen in *Dawsonia* so that the species should be assigned to this genus. However, Lake (1907) reported that *Microdiscus sculptus* Hicks, 1871 has probably three, possibly even four thoracic segments. This advocates that the species does not belong to *Dawsonia*. One problem is that Kobayashi (1943a) did not consider this character as valuable when introducing *Metadiscus*. In addition, the author of the present study examined material from the *sculpta* beds at Nun’s Well and discovered a few isolated thoraces, mostly with two attached thoracic segments, but also two others that appear to belong to a species with three segments. This seems to indicate that the morphologic plasticity of this species surprisingly allowed individuals to develop a different number of thoracic segments. This, in turn, devalues the number of thoracic segments as a diagnostic character within the clade and suggests assignment of that species to *Dawsonia* as well.

Dawsonia sculpta has been considered a junior synonym of *D. dawsoni* (e.g., Rees et al. 2014). Although the specimens from the type locality are usually considerably distorted and difficult to assess in most details (see lectotype figured by Axheimer 2006, fig. 5), the species is distinguished by its larger and wider ribs between the scrobicules on the anterior border; a more slender glabella; and median tubercles on nearly every axial ring of the pygidium. *Dawsonia densiserrata* differs from *D. sculpta* in the narrower and much more numerous as well as longer scrobicules; a slightly longer and more evenly tapering glabella; less well-developed pleural ribs in the pygidium; and an axis without nodes or spines on the posterior half of the pygidial axis.

Dawsonia weljae Bognibova in Chernysheva, 1971 is a poorly known species described from the Mundybash “horizon” of the Batenev Range of the Altay-Sayan Foldbelt. The species is only known from a single, quite well-preserved cephalon with clear pagetiid characters, which exclude its assignment to *Dawsonia*.

Poorly preserved and incomplete specimens of *Dawsonia densiserrata* may be confused with the well-known species *Kiskinella cristata* Romanenko & Romanenko, 1962, which is known from the Siberian Platform (e.g., Romanenko & Romanenko 1962), the Altay-Sayan Foldbelt (Chernysheva 1971), and Avalonian south-eastern Newfoundland (Fletcher 2003). However, *Kiskinella* and *K. cristata* differs from *Dawsonia* in having small, but distinct, elevated palpebral lobes and eyes, as well as minute librigenae.

It is worth to emphasise that the discussion on the species of *Dawsonia* and their discrimination might raise doubts about the taxonomic significance and validity of most species. This is affected, however, by the mostly imperfect preservation and the difficulties to recognise minor but nevertheless significant characters. The majority of the species of *Dawsonia* are what might be called pseudocryptic species, including the new species *D. densiserrata*. The same phenomenon of largely disesteeming intricate differences that are significant enough to discriminate similar species is a pervasive practice in modern trilobitology, often under the shield of morphometric analysis. Westrop et al. (2018), in contrast, were able to prove that critical morphological characters may be latent features in imperfectly preserved material, but clearly decipherable in well-preserved specimens. Their study on pseudocryptic species of *Eodiscus* encourages critical revision of long known trilobites. One example in this context is the problem of *Eodiscus scanicus* (Linnarsson, 1883) recorded from the Menevia Formation of South Wales. Fig. 15 illustrates specimens of such traditional records. These specimens from the classical Nun's Well locality (e.g., Hicks 1871) differ in several minor characters (e.g., the precise pattern of the scrobicules in the cephalic border and the morphology of the pygidial border) from *E. scanicus* as seen in specimens from Scania, Sweden, and probably represent another but closely related species.

Fig. 15: *Eodiscus* cf. *scanicus* (Linnarsson, 1883). **A** MMUW 2023A-030a, cephalon; **B** MMUW 2023A-031a, cephalon (except occipital spine); **C** MMUW 2023A-032a, incomplete cephalon; **D** MMUW 2023A-033a, articulated thorax composed of three segments; **E** MMUW 2023A-034a, b, isolated pygidium and cephalon with attached thorax composed of three segments; **F** MMUW 2023A-035a, pygidium; **G** MMUW 2023A-036a, pygidium; **H** MMUW 2023A-037a, pygidium; **I** MMUW 2023A-038a, pygidium; **J** MMUW 2023A-039a, detached dorsal exoskeleton consisting of obliquely embedded detached cephalon and pygidium with attached thorax of three segments.
All specimens from the lower part of the Menevia Formation, lower part of *Mawddachites hicksii* Zone, Drumian Stage, Nun's Wells, St. David's Peninsula, south-western Wales. Dorsal views. Scale bars 1 mm.

Stratigraphical range. Dawsonia densiserrata n. sp. comes from strata that can be quite confidently assigned to the lowest part of the Wuliuan Stage. The species is thus older than most of the established species of the genus, but has approximately the same stratigraphic occurrence as *Dawsonia dawsoni* from Avalonian North America.

Family Hebediscidae Kobayashi, 1944a

[nom. transl. Jell in Whittington et al., 1997, ex Hebediscinae Kobayashi, 1944a].

Genus *Tchernyshevioides* Khayrullina *in* Repina et al., 1875

Type species. Tchernyshevioides ninae Khayrullina in Repina et al., 1975, from strata with *Pseudanomocarina* in the Turkestan range, south-western Kyrgyzstan.

Discussion and remarks. See discussion below under *Tchernyshevioides*? sp. A.

Tchernyshevioides? sp. A

Fig. 16A, 16B?

Material. Single incomplete cranidium, MMUW 2017D-374, from locality W8; Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Discussion and description. Tchernyshevioides is an insufficiently known and poorly characterised genus. Nevertheless, the only formally established species is *T. ninae* Khayrullina in Repina et al., 1975 described to date, is based on fairly well-preserved material from the Sulyukty area in the Turkestan range, Kyrgyzstan (Repina et al. 1975, pp. 101–102, pl. VII, figs. 1–8, pl. VIII, figs. 1–6). The hitherto only other report on the genus was based on two well-preserved cranidia from two different localities of the High Atlas in Morocco exposing rocks of the Brèche à *Micmacca* Member of the Jbel Wawrmast Formation (Geyer 1988), both from the *Morocconus notabilis* Zone, which correlates with the *Kingaspidoides frankenwaldensis* Zone of the Franconian Forest. Although the Moroccan specimens clearly share the cranidial characteristics of *Tchernyshevioides* such as the submarginal position of the ocular suture and the well incised furrows that separate the eye ridges from the fixigenae, Geyer (1988) only tentatively assigned the Moroccan specimens to *Tchernyshevioides* because of the unknown morphology of the pygidium, but noted that the specimens differ in lacking a distinctive occipital spine and their narrower glabella.

One incomplete and poorly preserved, minute cranidium was discovered in the Wildenstein Member. Despite its imperfect preservation, it can be recognised that it shares most characters with the specimens from the High Atlas of Morocco, but differs in having an occipital ring which is slightly broader that the posterior part of the faintly club-shaped glabella and in the straight course of the furrows that define the eye ridges posteriorly perpendicular to the longitudinal axis of the cranidium rather than being curved or slightly anteriorly directed from the occipital furrows as in the Moroccan specimens. This suggests that the specimen from the Wildenstein Member represents a third species of *Tchernyshevioides*.

A hebediscid pygidium (Fig. 16B) has been recovered from the same locality and possibly represents the same species. It is preserved with a recrystallised cuticle, but represents the concave ventral side so that the specimen is difficult to portray photographically. It is a roughly semicircular shield with a moderately broad axis that reaches to or at least nearly to the posterior pygidial margin and showing numerous (>7) axial rings, and pleural fields divided by at least six pleurae with shallow pleural and interpleural furrows, but without a lateral and posterior border. Although the pygidium is not typical for the Hebediscidae, it may represent the pygidium of *Tchernyshevioides*? sp. A.

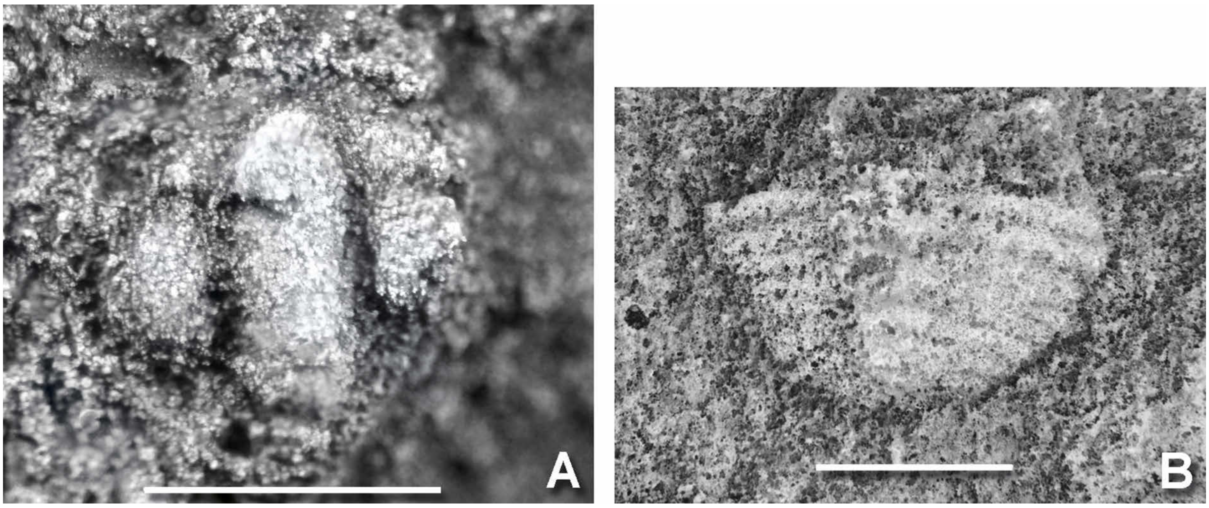

Fig. 16: **A** *Tchernyshevioides*? sp. A, MMUW 2017D-374, incomplete cranidium, internal mould, dorsal view; from locality W8, Wildenstein Member, Tannenknock Formation; scale bar 1 mm.
B Hebediscid genus and species, possibly representing *Tchernyshevioides*? sp. A, MMUW 2017D-1028a, pygidium, ventral view (electronically inverted); from locality W8, Wildenstein Member, Tannenknock Formation; scale bar 500 µm.

Order Redlichiida Richter, 1933

Superfamily Ellipsocephalacea Matthew, 1887b

Discussion. The Ellipsocephalacea have been assigned to the Order Ptychopariida by most authors since Fortey's (1990) emphasis of the cephalic ventral anatomy of the trilobites and particularly the hypostomal and rostral condition. The author of this article variously argued that this systematic placement is premature and does not take into account close morphological similarities between the earliest ellipsocephaloid trilobites and some groups of redlichioids. Meanwhile, Laibl et al. (2015) reviewed the ontogeny of *Ellipsocephalus hoffi* (Schlotheim, 1823) and *E. polytomus* Linnarsson, 1877, and also concluded that the family Ellipsocephalidae is closely related to members of Redlichiida rather than those of the Ptychopariida.

In addition, the Ptychoparioida, regardless whether viewed in the traditional concept of the old Treatise volume (Moore et al. 1959) or in the revised concept of Adrain (2011) must be seen as a polyphyletic grouping. However, the Redlichiida also cannot be identified as a monophyletic group. Systematics and taxonomy of the Redlichiida are not the topic of this study, but it should be emphasised again that the earliest fallotaspidids (such as *Eofallotaspis* Sdzuy, 1978 and *Fallotaspis* Hupé, 1953a) can be identified as non-sutured neoredlichiids (i.e., *Pararedlichia* Hupé, 1953a and *Neoredlichia* Saito, 1934), whereas the co-occurring earliest bigotinid trilobites (e.g., *Bigotina* Cobbold, 1935, *Hupetina* Sdzuy, 1978, *Bigotinops* Hupé, 1953a, or *Bigotinella* Suvorova, 1960) differ morphologically and certainly represent a different phylogenetic line (see Geyer 2019b). Such bigotinid-type trilobites, however, appear to be prime candidates as ancestors of the earliest occurring ellipsocephaloids. In turn, bigotinids may also be suspicious to have given rise to the early ptychoparioid trilobites. However, this would raise another palaeogeographic paradox: bigotinids are distributed mainly in the palaeocontinents West Gondwana and Sibiria, where ptychoparioids are "last arrivals" in the geological record, whereas they are absent in Laurentia, which has the earliest diverse occurrences of ptychoparioids.

At any rate, ellipsocephaloids provide many more characters demonstrating that they are more closely related to redlichioid rather than ptychoparioid trilobites. Among the particularly significant criteria is their ontogenetic development, which was well illustrated by Laibl et al. (2015). Other data were presented in Geyer (1990a, 1998), Elicki & Geyer (2013), Weidner et al. (2015) and Cederström et al. (2022) with discussions on the taxonomy, characters, and systematic affinities of the superfamily.

A phylogenetic development from bigotinid-type trilobites to ellipsocephaloids and a possible further evolution into trilobites that are presently dealt with as members of the order Ptychopariida of course indicates that none of the established suborders and superfamilies involved in these evolutionary developments represent true clades, and they must be eliminated if consequent phylogenetic analysis is applied. However, given the lack of valuable characters and the difficulties to recognise autapomorphies among most trilobites, it is regarded as momentarily appropriate to arrange phylogenetically closely related species and genera into systematic groupings, which are labelled above the genus level as “subfamilies” and “families” although they cannot be regarded as being equivalent to such categories as used for recent organisms in biological classification.

Neontology has developed different concepts of species over the last decades, which lead to perceptions of taxonomical constructs such as species flocks and cryptic or pseudocryptic species. Such concepts are nearly impossible to confidently apply in palaeontology.

Family Ellipsocephalidae Matthew, 1887b

Discussion. As discussed earlier, “clades” within the Ellipsocephalidae or Ellipsocephaloidea have been traditionally grouped according to easily recognisable morphologic features of the cranidia, and these groupings were based on “iconic” genera such as *Ellipsocephalus* Zenker, 1833, *Kingaspis* Kobayashi, 1935, *Protolenus* Matthew, 1892, *Termierella* Hupé, 1953a, *Palaeolenus* Mansuy, 1912, *Antatlasia* Hupé, 1953a and *Strenuella* Matthew, 1887 (see Hupé, 1953a; Henningsmoen in Treatise, 1959). In addition, these “clades” have been variably grouped as subfamilies or families, respectively. However, careful examination of characters and character states demonstrates that the Ellipsocephalidae constitute a heterogenous group with frequently converging morphological features as well as a mosaic pattern which occur in numerous genera and species. Accordingly, the splitting into a considerable number of subfamilies does not feature phylogenetic entities and should not be maintained. Geyer (1990b) showed that not only *Kingaspis*- and *Ellipsocephalus*-type trilobites constitute a systematic group which cannot be divided on a supra-generic level, but even the *Protolenus* group is so closely related to the Ellipsocephalinae that they consequently should be united under a single family. Reduction of convexity and smoothening of the cephalic relief obviously took place independently at least twice among the Ellipsocephalidae (leading to *Kingaspis*- and *Berabichia*-type cephalic morphologies) and created convergent morphologies so that the precise nature of relative cephalic sagittal and transverse profiles is required to allow a confident assessment of the taxon. Cederström et al. (2022) recently demonstrated this for Scandinavian ellipsocephalids.

As emphasised earlier (e.g., Geyer 1990b, 2017; Geyer et al. 2020; Cederström et al. 2022), confident identification of genera within the Ellipsocephalinae requires an understanding of the morphology of the exterior as well as of the interior of the cranidial exoskeleton. However, of particular importance is the morphology of the librigena and the pygidium, which have received very little attention to date because most of the taxa have been solely based on the morphology of the cranidium. Ellipsocephalid pygidia are generally small relative to the cephalon; in assemblages composed of (fractured) sclerites, such minute pygidia are rarely well-preserved and also often overlooked in the bulk material. However, the importance of pygidia for taxonomy is is illustrated by the frequent lumping of species under the genus *Ellipsocephalus* albeit its long known and very distinctive pygidium (see *Ellipsostrenua* in Cederström et al. 2022). Further emphasis must be based on the analysis of the functional morphology recognisable in the thoraces, which may be used to decipher differences in the mode and specific capability of enrolment in the various species.

A tabular overview of the generic concepts among the Ellipsocephalidae is presented in Cederström (2022, fig. 14).

Subfamily Ellipsocephalinae Matthew, 1887b

Discussion. The systematic position and characterisation of the *Ellipsocephalus*-clade has long been controversially discussed and is still circumnavigated in several articles that were published during the last two decades. The genus *Ellipsocephalus* Zenker, 1833 has long served as an icon of the family Ellipsocephalidae. The genus is characterised by a largely effaced morphology of the dorsal exoskeleton in holaspid individuals, particularly in the cephalon. This morphology resembles some of the similarly sagittally and transversely convex cephala seen in adult specimens of *Kingaspis* Kobayashi, 1935 and *Mesetaia* Hupé, 1953a, and also in *Germaropyge* Šnajdr, 1957 and *Comluella* Hupé, 1953a.

Nevertheless, this effacement is an adaptive consequence of the mode of life and cannot be used as a synapomorphic character. *Ellipsocephalus* as well as *Kingaspis* and *Mesetaia* possess devices that helped the individuals to enter a soft substrate, and probable sensory organs aided orientation of their bodies. This indicates that *Ellipsocephalus*, *Kingaspis* and *Mesetaia* obviously preferred a semi-infaunal lifestyle for which the effaced surface and a sort of streamlining of the body and particularly the cephalon was beneficial. Consequently, other characters without a fundamental connection to lifestyle are needed to identify systematic relationships within the Ellipsocephalidae. Such characters include (a) the shape of the glabella and particularly its frontal lobe; (b) the pattern of glabellar furrows; and (c) the morphology of the pygidium. These characters and their problems in specific variation are briefly summarised in the following paragraphs, partly reiterating the characterisation in Cederström et al. (2022).

Shape of the glabella. Ellipsocephaloid trilobites are commonly portrayed with an iconic image of an hour-glass outline of the glabella. However, ellipsocephaloids in fact have quite diverse shapes of the glabella. These include the ordinary condition of subparallel lateral glabellar margins, slightly or distinctly tapering outlines, the conspicuous medially constricted glabellas seen in some species of *Ellipsocephalus* and *Kingaspis* as well as a few exceptional forms. The lateral margins of the glabella are either curved and slightly convex in respect to the axis, more-or-less straight, or faintly to considerably indented.

Specifically, characteristic in respect of systematic relationships is the outline of the frontal lobe and its contact, or connection with the eye ridges. The primordial condition of the frontal lobe's outline is a relatively strong and subeven curvature (Gf2) as seen, e.g., in (the true!) *Strenuella* or in the species of *Ellipsostrenua*. The condition in which the anterior margin of the frontal lobe is gently curved (Gf1) is a derived condition. It is seen in genera such as *Kingaspis* Kobayashi, 1935, *Kingaspidoides* Hupé, 1953, or *Germaropyge* Šnajdr, 1957.

Notwithstanding the specific strength of the curvature, a faint (Ga1) or distinct (Ga2) angulation may occur at the tip of the frontal lobe. In this case, a low triangular outline can be recognised. The presence of such an angulation is accentuated by the mode in which a parafrontal band is developed or recognisable. Such a parafrontal band may be (apparently) absent in which case the margin of the frontal lobe generally lacks a frontal angulation. The parafrontal band may be distinctly developed (as in some species of *Protolenus* Matthew, 1892 and *Latoucheia* Hupé, 1953a) or semifused with the frontal lobe. In the latter case, an incomplete parafrontal band (interrupted across the sagittal line) may cause the notion of a nearly subtruncate anterior margin of the glabella (as in *Kingaspidoides lunatus* Bergström & Ahlberg, 1981; see Cederström et al. 2022, fig. 28K).

A distinct angulation is predominantly absent (Ga0) among the Ellipsocephalidae. However, parafrontal bands may be developed with little curved and almost straight and obliquely directed lateral sections which meet at the anterior tip of the glabella in a distinctively angular contact. This condition creates the impression of an acute tip of the frontal lobe as present in such species as *Kingaspidoides neglectus* Geyer, 1990b, *Ornamentaspis crassilimbata* Geyer, 1990b and *Comluella platycephala* (Cobbold, 1910).

The connection between the lateral glabellar margin and the margin of the frontal lobe is variably developed among the Ellipsocephalidae. The type of contact ranges from a faint change from a weak curvature of the lateral margins to more distinctly curved anterolateral sections of the frontal lobe via a pronounced, stronger curvature at the contact to more-or-less well-developed anterolateral corners. In the latter case, slightly extended acute projections are developed which are connected with the eye ridges. This condition is particularly obvious on internal moulds (e.g., in *Kingaspis* and *Kingaspidoides*).

Glabellar furrows. The pattern of the lateral glabellar furrows provides insights into systematic relationships. However, the evolutionary pathways of the glabellar furrows are not easily decoded. Ellipsocephaloid trilobites present three or four pairs of lateral glabellar furrows, which differ in their spatial arrangement. The fact that the furrows are often weakly developed on the exterior of the cuticle hampers easy distinction of differences in their patterns. The primordial condition is similar to the generally developed pattern in early redlichioid trilobites such as *Wutingaspis* Kobayashi, 1944b and *Kuanyangia* Hupé, 1953a, with three pairs of furrows, all being slightly rearwardly directed and interrupted medially. Among them, S1 is slightly longer than S2 and S3. This pattern is therefore termed here the *redlichioid condition*. This pattern is modified in ellipsocephaloid trilobites into five types, which were recently summarised in Cederström et al. (2022):

- The *strenuellid type* (LGF1) consists of three pairs of glabellar furrows of similar length and impression in a more-or-less equidistant grouping. S1 is slightly longer and more strongly backward directed from the lateral margins of the glabella than S2; S2 displays a faint curvature and is only slightly backward directed; and S3 is more-or-less normal to the length axis or directed slightly forward from its origin at the axial furrows. All furrows are narrow and do not show a broadening towards the adaxial end and the tendency to bifurcate. A fourth pair may be vaguely indicated on well-preserved specimens. The strenuellid type is seen in most trilobites of the *Strenuella* plexus, such as *Strenuella*, but also in genera not closely related to *Strenuella* such as *Kymataspis* Geyer, 1990b, *Planolimbus* Geyer, 1990b, and *Dellingia* Cederström et al., 2022. A similar pattern of lateral glabellar furrows is frequently developed in some solenopleurid and conocoryphid trilobites, but it differs in that S3 commences at short distance from the lateral margins of the glabella.
- The *protolenid type* of the lateral glabellar furrows pattern (LGF2) appears to be derived directly from the strenuellid type. In this pattern, three pairs of furrows are arranged in subequal distance or with a slightly shorter distance between S2 and S3. All furrows are slightly bent and directed slightly backwardly from their origins at the axial furrows. However, the lateral glabellar furrows display a progressive rearward development of such characters, and all tend to be slightly broader than the furrows in LGF1. A fourth pair of furrows (S4) is occasionally developed but only as a short and faint impression. Well-preserved specimens with the protolenid type usually have a weakly to conspicuously developed parafrontal band. This type of arrangement of the lateral glabellar furrows is best seen in genera such as *Protolenus*, *Hamatolenus* Hupé, 1953a and *Cambrunicornia* Geyer, 1990b.
- The *kingaspidoidid type* of the lateral glabellar furrows pattern (LGF3) is composed of four pairs of furrows. As reviewed in Cederström et al. (2022), S1 is longer, better developed, generally more curved and more rearwardly directed from the lateral margins of the glabella than S2; S2 is somewhat curved and faintly to slightly rearward directed from its abaxial origin; S3 is also curved, but directed almost normal to the length axis or even faintly forward. S4 consists of a pair of short furrows or grooves which are directed slightly forward from the lateral margins of the

glabella; they commence at a short distance from the lateral margin of the glabella. S1 is located slightly more distant from S2 than S2, S3 and S4 from each other. A fifth pair of lateral glabellar furrows may be mimicked on internal moulds by a parafrontal band that develops from the eye ridges and runs (incompletely) along the front of the glabella. Typical examples of the LGF3 are seen in *Kingaspidoides*, *Cambrosaurura* Geyer in Cederström et al., 2022, *Latikingaspis* Geyer, 1990b, *Ornamentaspis* Geyer, 1990b and *Ellipsostrenua* Kautsky, 1945. In some cases, S2 and S3 tend to be broadened and may exhibit muscle scars that testify attachment sites of dorsoventral muscles responsible for the movement of ventrally located appendages. An example is shown for *Kingaspidoides lunatus* (Bergström & Ahlberg, 1981) in Cederström et al. (2022, fig. 28Q).

- The *kingaspidid type* of the lateral glabellar furrows pattern (LGF4) is similar to the kingaspidoidid type. It consists of four or five pairs of furrows, of which S1 is slightly longer, better developed and more rearwardly directed from the lateral margins of the glabella than S2. In addition, S1 is located fairly close to the occipital ring. S2 is slightly curved and directed either only faintly or moderately backward from its origin. S3 is also curved, but directed almost normal to the length axis or runs even at bit forward from its origins. S4 consists of a pair of short furrows that are directed slightly forward and start recognisably distant from the lateral margins of the glabella. In contrast to the condition in LGF3, S1 is slightly more distant from S2 than are S2, S3 and S4 from each other. A fifth pair of lateral glabellar furrows may be present and is then developed as a short, oblique incision distant from the lateral margins of the glabella. An additional pair of lateral furrows is occasionally mimicked on internal moulds by a parafrontal band that develops from the eye ridges. As the name suggests, this type is best seen in species of *Kingaspis* (particularly well visible in the specimens of *Kingaspis campbelli* (King, 1923) from the Dead Sea region of Jordan), but also developed in some species of *Ellipsocephalus*.
- *Ellipsocephalus hoffi* (Schlotheim, 1823), the type species of the genus, as well as *E. polytomus* (Linnarsson, 1877) have weakly developed lateral glabellar furrows that are rarely recognisable on the exterior of the cuticle. Developed are four pairs, S1 through S3 are more-or-less transversely directed and slightly bent. The adaxial tips of S1 and S2 are more rearwardly directed than that of S3. S4 is anteriorly directed from its abaxial origin. All commence at an apparently short distance from the lateral margins. However, this is difficult to recognise exactly because these glabellar furrows have the character of muscle attachment sites rather than “ordinary” glabellar furrows. A fifth pair of lateral glabellar furrows is occasionally mimicked on internal moulds by a parafrontal band. This ellipsocephalid type is a modified kingaspidid type and regarded here as a subtype (LGF4a).
- The *strenuaevid type* of lateral glabellar furrows (LGF5) is a modification from the primordial condition which developed early during the phylogeny of the ellipsocephaloids according to the fossil record. This type of lateral glabellar furrow pattern exhibits three principal pairs of furrows which are short and located roughly in subequal distance from each other. Glabellar furrow pair S1 is directed slightly backward, whereas S2 and S3 are directed more-or-less transverse to the axial line. This pattern is typically developed in *Strenuaeva* Richter & Richter, 1940 (see *Strenuaeva primaeva* (Brøgger, 1878) in Cederström et al. 2022, fig. 19), *Issafeniella* Geyer, 1990b, and *Epichalnipsus* Geyer, Popp, Weidner & Förster, 2004 (see *E. bergstroemi* in Cederström et al. 2022, fig. 23).
- The development of the lateral glabellar furrows varies in response to changing conditions on the external face of the cuticle. Frequent factors are differences in the strengths of indentation and also changes in the sculpture on the cuticle or in the external prosopon.
- *Pygidial morphology.* A recently published discussion on the Ellipsocephalidae already emphasised the significance of pygidial morphology in taxonomic and phylogenetic context (Cederström et al. 2022). As discussed in that study, at least five different types of pygidia can be distinguished

among the ellipsocephalid trilobites although unfortunately pygidia are only known from relatively few genera and species with certainty. Cederström et al. (2022) emphasised that a ‘primordial’ condition of pygidial morphology is seen in such genera as *Ellipsostrenua* and *Kingaspidoides*, in which the pygidium consists of a highly convex axis that extends to the posterior margin, and this type of pygidium offers narrow pleural areas defined abaxially by a raised lateral border. It is termed “volucent”.

- A relatively broadly volucent type with well-developed pleural furrows is known from *Germaropyge germari* (Barrande, 1852). This pygidium (Fig. 40) resembles those seen in typical solenopleurid trilobites (e.g., *Erratojincella brachymetopa*, Fig. 57, or *Exapinepiphania marionae*, Fig. 72). This type is not mentioned in Cederström et al. (2022), but should be recognised as a separate, independent type, and I suggest the term “eosolenopleurid” for it.
- A contrasting condition is seen in the pygidium of *Ellipsocephalus*, which is developed as a relatively short, transverse plate with a lenticular or narrow sub-triangular outline. It usually has a low relief and is covered to large extent by terrace ridges. This type of pygidium must be regarded as a terminal condition and is called “ellipsocephaline”.
- Pygidia of kingaspidoid trilobites are poorly known. They are either volucent or derived from the volucent type. Some genera (such as *Cambrosaurura* Geyer in Cederström et al., 2022) possessed a pygidium with a long, subparallel-sided or slightly tapering axis reaching nearly to the posterior border, but a modest convexity, with narrow and usually smooth pleural areas. This type is termed “collispathulate”.
- Another type of pygidium is developed in *Protolenus* and closely related genera such as *Hamatolenus*. However, this type of pygidium is also derived from the volucent type. This pygidium is subrectangular to semicircular in outline with a relatively straight posterior margin. As detailed in Cederström et al. (2022), the axis is well elevated and tapers rearward, often having a sub-triangular outline, with one or two ribs developed, often with a low semilunate crest along the terminal axial piece that rests on a low scale. The pleural field is moderately wide, with a distinct, raised anterolateral border, and the pleural area may be slightly depressed or has a single oblique rib. This pygidial morphology is the “semialate” type.

Stratigraphic position as well as morphological gradients suggest an “evolutionary landscape” for the development of the pygidium, which resembles a phylogenetic tree. Given the still poor fossil record of ellipsocephalacean pygidia, the pathways include certain uncertainties and apparent conundrums. Nevertheless, the small and well-structured volucent pygidium is doubtlessly the primordial condition, which occurs in all early members of the ellipsocephalacean families and subfamilies except for the Protoleninae, for which the semialate type appears to have been developed already in early representatives. The ellipsocephaline and collispathulate pygidia are restricted to genera such as *Ellipsocephalus* and *Cambrosaurura*, respectively, the general morphology and particularly that of their thoraces indicates special adaptation to burrowing activities. Accordingly, the pygidial characters must be regarded as indicating terminal links of evolutionary pathways. The eosolenopleurid pygidium as seen in *Germaropyge* derives from the volucent pygidium by a growth in relative size and appears to attest a beneficial morphology for a life on relatively coarse siliciclastic substrate.

Genus *Kingaspis* Kobayashi, 1935

Type species. Anomocare campbelli King, 1923; from the Burj Formation of Wadi Zerqa Ma’in, Dead Sea region, Jordan; by original designation.

Discussion. The genus *Kingaspis* Kobayashi, 1935 offers only an extremely limited number of readily recognisable morphological characters which can be counted as apomorphic in nature. This entails that since its introduction the taxon has been subject of differing opinions about its definition and systematic relationships. The systematic and taxonomic uncertainties are echoed by strongly opposing assessments of different authors and have their origin and cause partly in the scantly instructive depictions in a number of early publications on species assigned to the genus or to closely related genera. Sdzuy (1961, p. 308) already pointed out that substantial differences exist between the type species of *Kingaspis*, *Anomocare campbelli* King, 1923 from the Dead Sea shore of Jordan (e.g., Elicki & Geyer 2013, fig. 12), and species known at that time from Morocco, which have been described by Hupé (1953a) and assigned to *Kingaspis*. Nevertheless, Sdzuy's (1957, p. 18) concept of the differences had been based on the lengths of the palpebral lobes. This concept has been rejected in Geyer (1990b), who presented a complete revision of the generic concepts within the ellipsocephaloids. The differentiation of the subgenera *Kingaspis* and *Kingaspidoides* Hupé, 1953 was founded by Hupé (1953a) solely on the presence or absence of an occipital spine, and this was shown to be misleading as this feature is of little taxonomic relevance (Geyer 1990b).

Several species from Moroccan sections described by Hupé (1953a) and assigned to the genus *Kingaspis*, however, differ from the genotype by a heterogenous transverse profile as well as by an imperfect connection of their eye ridges with the anterolateral corners of the glabella so that they require an assignment to genera other than *Kingaspis*. Species with a typical kingaspidoid glabella and with palpebral areas that slope ventrally from the axial furrows but show a convexity on the external side of the cuticle in transverse profile which clearly differs from that of the glabella can be assigned to *Kingaspidoides* Hupé, 1953a when raised to generic level as proposed by Geyer (1990b). Species with a transverse profile across the exterior of the cuticle, in which the major regions of the cranidium are separated by relatively well-developed furrows and the palpebral areas raise dorsally from the axial furrows and the anterior area of the cephalon slopes moderately, were united under the genus *Ornamentaspis* Geyer, 1990b. The same morphological features distinguish *Ellipsostrenua* Kautsky, 1945 from *Kingaspis*. The genus *Latikingaspis* differs from the general transverse and sagittal convexities seen in *Ornamentaspis* primarily by a distinct dilatation of the axial furrows. The genus *Mesetaia* Hupé, 1953 (type species: *Hartshillia maroccana* Gigout, 1951) differs from *Kingaspis campbelli* only gradually by its less distinct convexity and can be regarded as a junior synonym of *Kingaspis*.

Kingaspis campbelli (King, 1923) from the Dead Sea area of Jordan has been dealt with in a plethora of articles, but its true identity has been frequently mistaken, probably following Hupé's (1953a) ambiguous reconstruction and the similarly misleading line drawing in the Treatise volume (Henningsmoen 1957, figs. 36B, 148,12). Characteristic photos of specimens have been published in Rushton & Powell (1998) and Elicki & Geyer (2013, fig. 12), and the case has been reviewed in Geyer & Landing (2020), who reported and characterised a single occurrence of the species outside Jordan. This report reconfirmed the earlier notes in Geyer (1990b) on *K. campbelli* from the Tamlelt inlier, eastern High Atlas, in the Moroccan–Algerian border region. The species has also been identified from Iberia, but most of these specimens assigned to the species cannot be unequivocally accepted as representing *K. campbelli*. The only exception are specimens from the Valdoré section in the Cantabrian Mountains, Spain, illustrated by Liñán et al. (2003), which proof an additional occurrence of the species.

Specimens from the Jarque section of the Iberian Chains, Zaragoza province, Spain, identified by Liñán et al. (2003, fig. 4a–i) as *K. campbelli* most probably belong to a species originally described as *Kingaspidoides neglectus* by Geyer (1990b) from the Jbel Wawrmast Formation of the Moroccan Anti-Atlas. The assignment of that species to *Kingaspidoides* has been discussed with caveat in Geyer (1990b), and restudy of material of *Comluella platycephala* (Cobbold, 1910) from the Comley area, Shropshire, U.K., suggests that the Moroccan species belongs to the genus *Comluella* Hupé, 1953a. The characters of *Comluella* and their phylogenetic relations within the Ellipsocephalidae will be discussed elsewhere.

Another species assigned to *Kingaspis*, *K. velatus* Sdzuy, 1961 (pp. 308–310, pl. 15 figs. 1–8 and text-fig. 18), has also been reported from several localities in Spain. The holotype of the species is difficult to assess from Sdzuy's original figures, but has been refigured in Liñán et al. (2003, fig. 3a, e). Liñán et al.'s photos prove that the species is characterised by a relatively short, tapering glabella with nearly straight lateral margins; by an unusually long (sag.) occipital ring with a moderately curved posterior margin which lacks an occipital spine; by a fairly broad (sag.) anterior area; and by short palpebral lobes which are weakly defined by faint furrows, but are slightly upturned in profile. The convexities of the cephalon match the typical morphology of *Kingaspis*, but the mentioned characters not only distinguish *K. velatus* from all other species of the genus, but also suggest that some of the reports of the species from Iberia are incorrect.

Kingaspis glabrata Geyer, 1990b, also from the Jbel Wawrmast Formation of the central Anti-Atlas, is a species with a nearly uniformly convex cranidium in both transverse as well as sagittal profile, with only faint furrows so that the glabella has an only faintly defined front and lacks clearly recognisable lateral glabellar furrows. The occipital ring is relatively long and lacks an occipital spine.

Kingaspis leonica Álvaro, 2007 has been introduced based on material from strata of the Láncara Formation of the Cantabrian Mountains, northern Spain, which underlie the supposed *Acadoparadoxides mureroensis* Zone. The species is characterised by a distinctly tapering glabella with a subacute anterior margin of the frontal lobe; lacks an occipital spine; has a stepwise differentiated sagittal and transverse convexity of the cranidium on both the internal as well as the external surface of the cuticle; a fairly well-recognisable, faintly raised anterior border; and show laterally extended corners of the frontal lobe that progress into the eye ridges (Álvaro 2007, fig. 3). Therefore, this species possesses the characters of *Kingaspidoides* rather than *Kingaspis*. It is morphologically reminiscent of some species of *Ellipsostrenua*, such as *E. simrica* Cederström, Geyer, Ahlberg, Nilsson & Ahlgren, 2022 and *E. sularpensis* Cederström, Geyer, Ahlberg, Nilsson & Ahlgren, 2022. However, all species of *Ellipsostrenua* lack the obvious connection between the frontal lobe of the glabella and the eye ridges, which is developed in *Kingaspidoides*.

Kingaspis? *brdensis* Fatka, Mergl, Šarič & Kordule, 1992 (Fatka et al. 1992, pp. 90–91, pl. III, figs. 1, 2, text-fig. 4) was found in an *Ellipsocephalus vetustus*–*Rejkocephalus*-bearing horizon in the Jince Formation of the Barrandean region[1], Bohemia, and would be the youngest known species of the genus on a global scale. However, the species was chosen as the type species of the genus *Sternbergaspis* Szabad & Valíček in Vaněk & Valíček, 2002. This species has a relatively wide (tr.) glabella; an occipital ring with a distinctly triangular outline but without an occipital spine; a short (sag.) anterior area; and a pronouncedly narrow (sag.) anterior border. The palpebral lobes are somewhat upturned from the abaxial portions of the palpebral areas. The shape of the glabella seen in the figured cranidia does not match the reconstruction shown in Fatka et al.'s text-fig. 4 and shows a slightly tapering glabella without distinct anterolateral corners. Although the overall convexity in transverse and sagittal profile match perfectly that seen in *K. campbelli*, the species from Bohemia differs in the mentioned features to a degree that does not allow a confident assignment to *Kingaspis*, so that the separation as a genus *Sternbergaspis* appears to be justified.

Kingaspis avalonensis Geyer & Landing, 2001 was described from the *Acadoparadoxides harlani* Zone of the Braintree Member of the Chamberlain's Brook Formation in Massachusetts and is the only known species of *Kingaspis* from the palaeocontinent Avalonia. The species distinguished from most of the other species of *Kingaspis* by the presence of a slender and relatively long occipital spine and a

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[1] This region is generally termed "Barrandian". However, the name refers to Joachim Barrande (1799–1883) so that the correct spelling is "Barrandean" as used herein.

strongly ventrally deflected anterior area. Its glabella is moderately wide, faintly tapers forward and possesses moderately long palpebral lobes slightly oblique to the axis. The most similar species is *K. maroccana* (Gigout, 1951) which differs in its broad-based occipital spine, a slightly wider occipital ring, and more anteriorly located palpebral lobes.

Kingaspis (*Kingaspis*) *henningsmoeni* Orłowski, 1964 (Orłowski 1964, pp. 86–88, pl. X, figs. 1–9, text-fig. 18; Orłowski 1971, p. 353, pl. 1, fig. 8) from the Klimontów Anticlinorium of the Holy Cross Mountains, southern Poland, is almost exclusively known from incompletely preserved specimens preserved in relatively coarse sandstones and do not offer the diagnostic characters to a satisfying degree. However, a complete exoskeleton of the species was mentioned to exist in Żylińska & Szczepanik (2009). The species is characterised by a glabella with relatively well developed lateral glabellar furrows; a frontal lobe with distinct median kink, but without distinctly extended anterolateral corners; and it has a short (sag.) preglabellar field. The species has been assigned to *Ornamentaspis* by Żylińska & Szczepanik (2009) and Żylińska (2013). However, the species possesses a few characters that suggest a placement under the genus *Ellipsostrenua* Kautsky, 1945 according to the revised concept by Cederström et al. (2022).

Kingaspis guerichi (Orłowski, 1959) is another species from the Holy Cross Mountains (e.g., Orłowski 1964, pl. 4, figs. 4, 6, 7, 9; Orłowski 1985, pl. 2, figs. 9–14; Żylińska & Szczepanik 2009, pl. 3, figs. 9, 10). It was originally introduced as *Ellipsocephalus gürichi* by Orłowski (1959, pl. I, figs. 6, 7, 10), but clearly offers morphological features that are typical for *Kingaspis*. Specific characters of this species include a particularly short pre-glabellar region (in dorsal view) with the anterior border relatively well recognizable on internal moulds; a broad glabella; a short occipital ring without an occipital spine; and a quite conspicuous ventral deflection abaxially in front of the palpebral lobes. See Table 1 für further features.

Kingaspis (*Kingaspis*) *borealis* Lendzion, 1972 has been reported from the so-called “*Protolenus* Zone” of the Polish sector of the Peri-Baltic Depression of the East-European Platform and dealt with, or refigured several times (Lendzion 1972, p. 135, text-fig. 6, pl. V, figs. 5, 6; Lendzion 1978, p. 41, pl. III, fig. 14; Lendzion 1979, p. 102, pl. LXXXIII, fig. 12). The species would be the only representative of the genus known from Baltica. It has a relatively strongly tapering glabella with a slightly truncated front, which clearly separates it from the species from the Mediterranean sector of West Gondwana.

Kingaspis? *convexus* Palmer, 1995 is a species from the Shackleton Formation of the Transantarctic Mountains (Palmer & Rowell 1995). This species is characterised by a highly convex (sag., tr.) cephalon with a long, tapering glabella with extended anterolateral corners; a narrow anterior border; and a short to medium-sized, crescentic occipital ring without a spine: The associated librigena without a genal spine dealt with in Palmer & Rowell (1995) as *Kingaspis*? sp. 2 appears to depict the librigenal morphology of the *Kingaspis*? *convexus* librigenae although they might not belong to this species.

As similarly discussed in Palmer & Rowell (1995, p. 12), the progressive effacement of the cephalon as exemplified by *Kingaspis*? *convexus* does not necessarily prove a close relationship to the species which can be confidently assigned to *Kingaspis*, and Palmer’s earlier tentative assignment of the very similar *Glabrella*? *pitans* Palmer & Gatehouse, 1972 from the Argentina Range of Antarctica to *Glabrella* indicates the uncertainties of the systematics and taxonomy. It is concluded herein that the morphology of *Kingaspis*? *convexus* suggests the species probably not being closely related to *Kingaspis* and representing a yet unestablished genus.

The Wildenstein Member of the Tannenknock Formation yields remains of *Kingaspis* which appear to represent three different species. Although a quite large amount of cranidia were collected, the considerable diagenetic deformation and subsequent distortion during tectonic processes as well as the weathering condition of most sclerites make it difficult to precisely reconstruct their original morphology and thus apply a reliable comparison with the numerous published reports from other areas. Thus, the description of the material is restricted to the forms which can be sufficiently characterised while fragments with partly different features are not considered for formal descriptions in this study.

Table 1: Occurrence and characters of species confidently assigned to Kingaspis. Abbreviations: cel cephalic length; crw cranidial width; gll length of glabella (including occipital ring, excl. of occipital spine); glw transverse width of cranidium across centre of palpebral libes; glsh shape of glabella; gsl length of genal spine; mod. moderately/moderately long; orl length of occipital ring (excl. occipital spine); os occipital spine; paw transverse width of palpebral area; pll exsag. length of palpebral lobes; sp subparallel; stap slightly tapering; tap tapering; ? unknown.

Species	Occurrence	gll/cel	glw/crw	glsh	orl	os	paw	pll	gsl
amouslekensis	Anti-Atlas	75–81	35–43	stap	mod.	very long	21–28	25–28	mod.
avalonensis	Massachusetts	75–83	40–45	stap to sp	mod.	mod. long	24–28	23–27	?
campbelli	Jordan, Tamlelt, Cantabrian Mountains	80–84	40–44	sp	short	absent	24–27	22–25	mod.
dolosus	Franconian Forest	82–85	42–46	sp	mod.	mod. long	19–23	23–29	long
glabrata	Anti-Atlas	89–94	43–47	sp	mod	absent	25–30	16–24	long
guerichi	Holy Cross Mountains	ca. 87-89	ca. 44-46	sp	mod	absent	ca. 20-24	ca. 26-32	?
maroccana	Moroccan Meseta	80–84	45–48	tap	mod.	mod. long	24–29	21–24	?
sarhroensis	Anti-Atlas	73–78	36–40	tap	short	absent	24–28	26–29	mod.
velatus	Iberian Chains	ca. 70–75	ca. 40–43	stap	long	absent	ca. 22–25	ca. 25	?

Kingaspis dolosus **n. sp.**

Fig. 17

Holotype. Cranidium, SSMM 10118a (Fig. 17I, L, O).

LSID. urn:lsid:zoobank.org:act:376F0446-89C7-417D-A272-894D2181B7CF

Type locality and type stratum. Sample locality W8 in the Wildenstein slice near Wildenstein. Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Etymology. From the Latin *dolo*, dagger, sword cane, or big spine; a reference to the presence of the slender, foil-shaped occipital spine.

Paratypes. Single cephalon, ca. 30 cranidia. From sample locality and stratum W8 (15 cranidia under MMUW 2017D-052a, -076, -169b, -264, -592, -599, -657, -779a-I, 779a-II, -781, -782, SSMM 10331, 10520, 10538, 11045); from locality W9 (cephalon under MMUW 2017D-760; 12 cranidia under MMUW 2017D-764, -765, SSMM 10382, 10385, 12364a, 12367, 12369, 12390, SMF 88314a, 88314b, 88315, 88322); from locality W9d (“Grauwacke”) (two cranidia under MMUW 2017D-336, -339); from locality “W15” (“forest road north of Galgenberg”) (cranidium under SSMM 10118b in addition to the holotype).

Additional material. Cranidia tentatively assigned to *Kingaspis dolosus* from locality W8 (eight cranidia MMUW-2017D-082, -632d, -633, SSMM 10423, 10517, 10812, 11038c, 11211); from locality W9 (five cranidia under MMUW 2017D-766, SSMM 10383, 10384, SMF 88316, 88319); and from locality W13e (two cranidia under MMUW 2017D-467, SSMM 10215).

Localities and strata. All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Diagnosis. Species of *Kingaspis* with relatively long and wide glabella, occipital ring with slender occipital spine; palpebral lobes relatively well-defined.

Description. Cranidium with relatively uniform transverse convexity, glabella slightly elevated above axial furrows. Sagittal profile with faint to gentle curvature of the glabella, anterior part progressively sloping ventrally; transverse section shows a slightly elevated glabella, which is faintly more convex than the palpebral areas; axial furrows are defined by a low step from glabella, but its magnitude is larger on internal mould and usually enforced by a slight angular deformation during dorsoventral compaction (compare Fig. 17G with Fig. 17L).

Glabella in non-deformed, adult individuals of ca. 82–85 percent (n=6) cephalic length, maximum glabellar width across occipital ring ca. 42–46 percent (n=5) cranidial width across midlength of palpebral lobes; glabella with straight to faintly concave sides, tapering forward, frontal lobe at anterolateral corners ca. 76–83 percent (n=6) width across L1; frontal lobe with a gently curved anterior margin, occasionally with a tendency to develop a faint median angulation that creates a low triangular outline dorsal view; on the exterior surface the glabella slopes continuously into axial furrows, whereas on internal moulds the glabella forms a minor step-like raise above the axial furrows; with three or four pairs of lateral glabellar furrows, S1 to S3 visible as shallow, poorly defined depressions on internal moulds and faint to barely visible on the exterior surface of the cuticle; S1 gently curved backward from about axial furrows, moderately long, disconnected medially; S2 and S3 relatively short. Occipital furrow relatively broad (sag. and exsag.), with slightly narrower lateral sections. Occipital ring moderately broad, ca. 16–19 percent (n=5) cephalic length (sag.), extended into a slender, moderately long subterminal spine, which is obliquely backward directed (Fig. 17E).

Palpebral areas transversely of 19–23 percent (n=6) maximum cranidial width across mid-length of the palpebral lobes, and fixigenae posterior to eye ridges and adjacent to axial furrows exsagittally ca. 42–46 percent (n=6) cephalic length; slightly to distinctly convex in transverse as well as exsagittal section on internal moulds and on the exterior surface; poorly demarcated from axial furrow; most elevated part of the genal sector lies adjacent to the axial furrow, but genal sector in general slopes ventrally abaxially.

Palpebral lobe exsag. of 23–29 percent (n=5) cranidial length and ca. 10 percent maximum cranidial width; distinctly convex in transverse profile, faintly curved, with anterior end at approximately the level of S3, in a slightly more adaxial position than posterior end; posterior tip about at level of anterior part of L1; ocular suture slightly more curved in dorsal view than adaxial margin of the palpebral lobe. Palpebral furrow a shallow, nearly straight longitudinal depression, relatively well impressed, usually slightly enforced because of the slightly upturned palpebral lobes. Eye ridge developed on the exterior of the cuticle as a faint ridge oblique to axis, more-or-less only a slight change in convexity, poorly demarcated from the palpebral area, but defines the increased slope of the preocular area; better marked on internal moulds; extends anteriorly to anterolateral corners of the glabella.

Preglabellar field convex, fused with anterior border, but fairly well-defined from glabellar front; grades laterally into preocular areas without any recognisable distinction. Anterior border not defined on sagittal line, but faintly marked near facial suture. Border furrow obsolescent on sagittal line, faintly marked near facial suture.

Posterior border a moderately broad (exsag.), slightly to moderately convex torus, transverse to the sagittal axis in the proximal part and slightly growing in exsag. width from near axial furrow, slightly reduced in width and slightly curved towards palpebral lobes in the distant section.

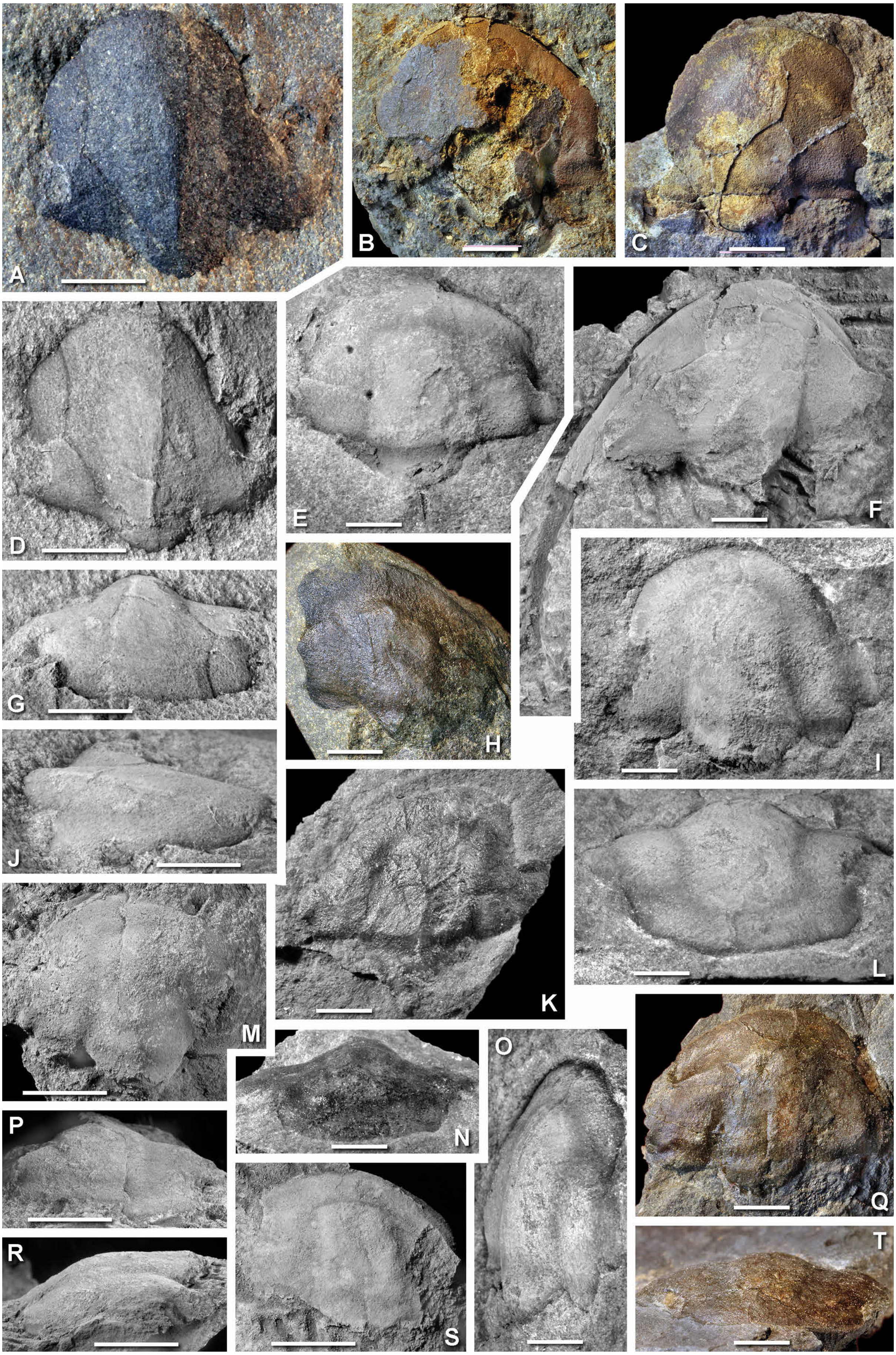
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Fig. 17: *Kingaspis dolosus* n. sp. **A, D, G, J** SSMM 10382, paratype, cranidium, internal mould; from locality W9; A, D, dorsal view, coated in D; G, anterior view; J, oblique lateral view; **B** SSMM 10423, paratype, cranidium, corroded, dorsal view showing remnants of the recrystallised cuticle; from locality W8; **C** SSMM 10538, paratype, cranidium, exfoliated on right side, dorsal view; from locality W8; **E** SSMM 10118b, paratype, internal mould, from locality W14b; **F** MMUW 2017D-760, paratype, cranidium with attached left librigena; from locality W9; **H** SSMM 10520, paratype, cranidium, internal mould, from locality W8; **I, L, O** SSMM 10118, holotype, cranidium, internal mould, dorsal, oblique anterior and oblique lateral views; from locality W14b; **K** SSMM 12367, paratype, cranidium, internal mould, distorted and with centrifugal cracks; from locality W9; **M, P, R** MMUW 2017D-592, paratype, cranidium, internal mould, dorsal (M), anterior (P) and lateral (R) views; most probably from locality W8; **N** SSMM 12369, paratype, cranidium with recrystallised cuticle showing more or less original morphology, anterior view; from locality W9; **Q, T** SSMM 10517, paratype, cranidium, internal mould, dorsal and anterior views; from locality W8; **S** MMUW 2017D-076, paratype, cranidium, composite mould; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation; scale bars 5 mm.

Posterior border furrow a shallow, moderately broad (exsag.) depression, commences adjacent to the occipital ring close to the posterior margin; anterior rim of posterior border furrow with only slight curvature in the abaxial sector so that it is clearly distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture approximately straight and parallel to the sagittal axis from the anterior end of the ocular suture forward, swing adaxially in a gentle curve from about the centre of the anterior border. Posterior branches directed obliquely abaxially from the posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the maximum abaxial level of the palpebral lobes.

Librigena unequivocally assignable to this form only known from a single specimen, where it is distinctly distorted (Fig. 17F). Librigena moderately wide, with a fairly robust and conspicuously long genal spine of nearly the same length as the anterior part. Genal spine with a moderately broad base that defines a gentle curvature from the posterior margin to the adaxial rim of the genal spine, slightly tapering in width. Lateral margin gently and homogeneously curved, without a recognisable change in curvature at the base of the genal spine. Palpebral section of the suture moderately large. Librigenal field slightly convex, fused with lateral border; lateral border furrow absent.

Hypostome, thorax and pygidium unknown.

Surface of cuticle not preserved in a manner that allows precise recognition of fine details. One specimen suggests presence of fine terrace ridges near anterior cephalic margin.

Discussion. Kingaspis dolosus n. sp. is known only from a fairly large number of specimens in different ways of preservation and different size so that its original morphology can be satisfyingly reconstructed. The diagnostic characters of the species include a relatively long and wide, slightly tapering glabella; the presence of a slender, moderately long occipital spine; moderately long, relatively straight and comparatively well-defined palpebral lobes; and the presence of a long genal spine. A comparably slender occipital spine is not known from any other species of *Kingaspis*, and a long genal spine are only known from very few true species of *Kingaspis*, such as *Kingaspis amouslekensis*, *K. sarhroensis*, and *K. avalonensis*, which are distinctly differentiated from *K. dolosus* by a number of other characters. A species with a superficially similar morphology is *Kingaspidoides obliquoculatus* Geyer, 1990b, known from the Moroccan Anti-Atlas, which is placed under *Kingaspidoides* because of its distinctly lowered palpebral areas, but it has similar proportions of the glabella and palpebral lobes and a similar sagittal profile as *K. dolosus*. Nevertheless, *Kingaspidoides obliquoculatus* is distinguished by its characteristically obliquely arranged palpebral lobes and a librigena with a long genal spines having a conspicuously broad base and then progressively reduced in width, with the radius of curvature of the genal angle being large.

Kingaspis sp. A

Fig. 18

Studied material. About 10 cranidia, few fragments of thoracic segments tentatively assigned to *Kingaspis* sp. A. In repository: From sample locality and stratum W8 (three cranidia under MMUW 2017D-014, SSMM 10521, SSMM 11199; cranidium tentatively assigned to *Kingaspis* sp. A under SSMM 10537); from locality W9 (two cranidia under MMUW 2017D-395b and -395c; two cranidia tentatively assigned to *Kingaspis* sp. A under MMUW-2017D-395d and -396a; thoracic segment under MMUW 2017D-395e). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Description. Cranidium with relatively uniform transverse convexity, glabella slightly elevated above axial furrows. Sagittal profile with gentle curvature of the glabella, anterior part only slightly more convex; transverse section shows a glabella, which is slightly more convex than the palpebral areas.

Glabella in nondeformed, adult individuals of ca. 85 percent cephalic length, maximum glabellar width across occipital ring ca. 35–40 percent cranidial width across midlength of palpebral lobes; glabella with slightly concave sides, slightly tapering forward, frontal lobe at anterolateral corners ca. 90 percent (n=6) width across L1; frontal lobe with a gently curved anterior margin, but with a tendency to develop a faint median angulation that creates a low triangular outline dorsal view (although this angulation is commonly enforced by dorsoventral compaction); on the exterior the glabella slopes continuously into axial furrows, whereas on internal moulds the glabella forms a low raise above the axial furrows; three pairs of lateral glabellar furrows recognisable, all marked only as shallow, poorly defined depressions on internal moulds; S1 gently curved backward from about axial furrows, moderately long, disconnected medially; S2 and S3 relatively short. Occipital furrow relatively broad (sag. and exsag.), median section shallower and wider (sag., exsag.) than lateral sections. Occipital ring moderately broad, extended into a probably moderately long an obviously moderately strong subterminal spine, which is not preserved in any of the studied specimens.

Palpebral areas transversely of ca. 25 percent maximum cranidial width across mid-length of the palpebral lobes, and fixigenae posterior to eye ridges and adjacent to axial furrows exsagittally ca. 40–45 percent (n=6) cephalic length; with low convexity in transverse as well as exsagittal section on internal moulds and on the cuticle’s exterior surface; poorly demarcated from axial furrow; most elevated part of the genal sector lies adjacent to the axial furrow.

Palpebral lobe exsag. of ca. 35 percent cranidial length and less than 10 percent maximum cranidial width; slightly convex in transverse profile, relatively curved along the ocular suture, less so at palpebral furrow, with anterior end at approximately the level of S3, in a slightly more adaxial position than posterior end; posterior tip about at level of middle part of L1. Palpebral furrow a shallow, moderately curved longitudinal depression, moderately well recognisable on internal moulds. Eye ridge developed on the exterior of the cuticle as a faint ridge oblique to axis, more-or-less only a slight change in convexity, poorly demarcated from the palpebral area, but defines the increased slope of the preocular area; better marked and slightly raised on internal moulds; extends anteriorly to the apparently extended anterolateral corners of the glabella.

Preglabellar field convex, fused with anterior border, but fairly well-defined from glabellar front; grades laterally into preocular areas without any recognisable distinction. Anterior border not defined on sagittal line, but faintly marked near facial suture, occasionally better recognisable in dorsoventrally compacted specimens and then apparently broader (sag.) than adjacent preglabellar field (Fig. 18A). Border furrow obsolescent on sagittal line, faintly marked near facial suture.

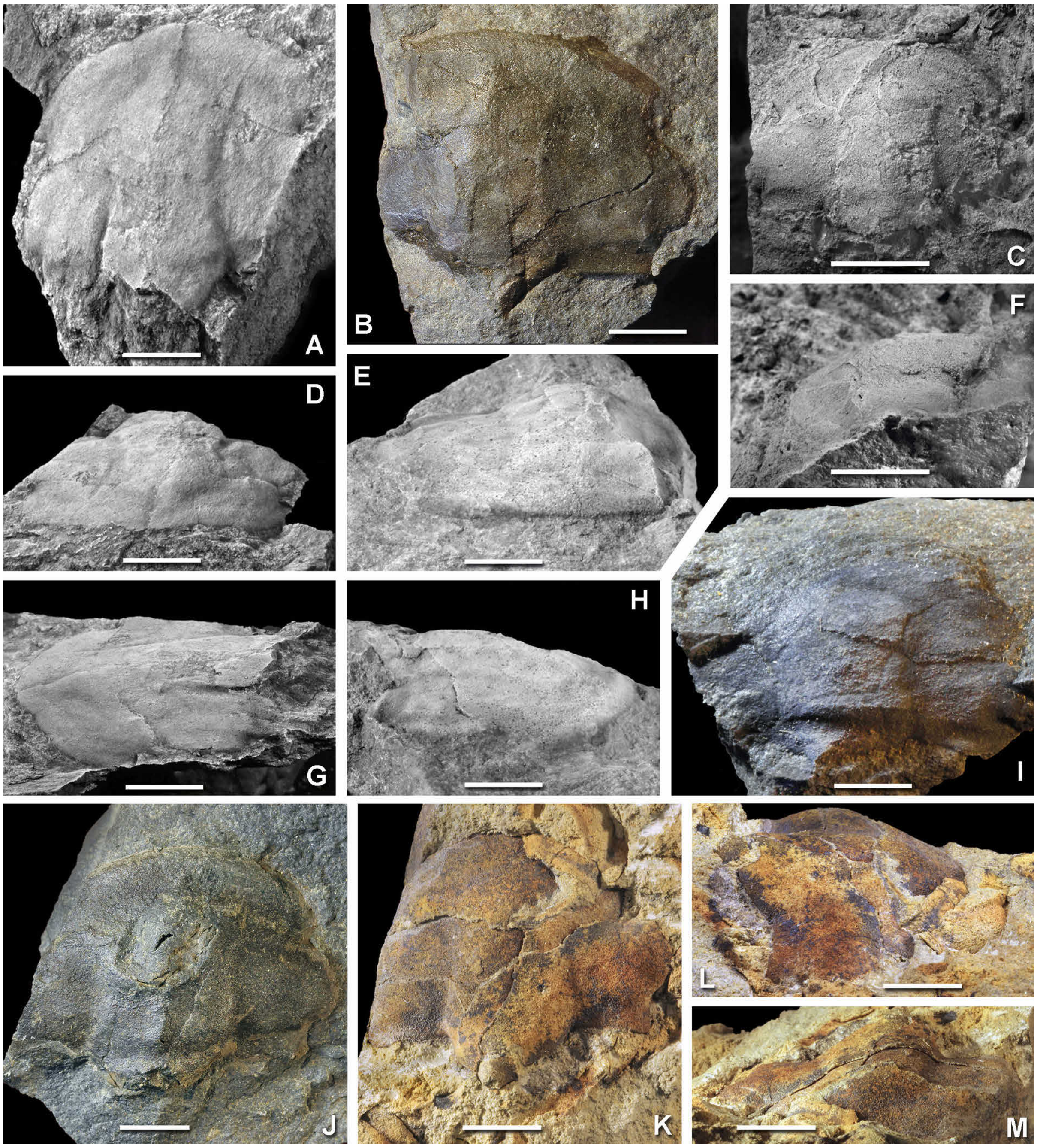

Fig. 18: *Kingaspis* sp. A. **A, D, G** MMUW 2017D-014, incomplete cranidium, largely exfoliated and with notable oblique dorsoventral compression, dorsal, anterior and lateral views; from locality W8; **B, E, H** SSMM 10521, partial cranidium, composite mould, slightly dorsoventrally compressed, dorsal, anterior and lateral views; from locality W8; **C, F** Incomplete cranidium, largely exfoliated; from locality W8 (specimens apparently lost); **I** SSMM 10356, partial cranidium, internal mould with fractures resulting from differential compaction, dorsal view; from locality W9; **J** SSMM10537, cranidium, composite mould, with imprint of slightly detached and rotated hypostome from ventral, dorsal view; from locality W8; **K, L, M** SSMM 11199, incomplete cranidium, with exfoliated left posterior part and massive base of occipital ring, with notable dorsoventral compression; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation; scale bars 5 mm.

Posterior border a moderately broad (exsag.), slightly to moderately convex torus, nearly straight and transverse to the sagittal axis in the proximal part, slightly reduced in width and slightly curved towards palpebral lobes in the distant section. Posterior border furrow a shallow, moderately broad (exsag.) depression, commences adjacent to the occipital ring close to the posterior margin; anterior rim of posterior border furrow with only slight curvature in the abaxial sector, clearly distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture nearly straight and parallel to the sagittal axis from the anterior end of the ocular suture forward, swing adaxially in a gentle curve from the posterior part of the anterior border. Posterior branches directed obliquely abaxially from the posterior ends of the ocular suture, not completely preserved in any of the studied specimens.

Librigena, hypostome, thorax and pygidium unknown.

Surface of cuticle not preserved in a manner that allows precise recognition of fine details.

Discussion. The specimens described here as *Kingaspis* sp. A represent a species distinct from the partly co-occurring *Kingaspis dolosus* n. sp. described above. Significant differences include a longer, less tapering glabella; an obviously more strongly developed occipital spine; slightly shorter and more strongly curved palpebral lobes; and wider (tr.) fixigenae; as well as minor other differences. Most of the specimens of this form are larger than those assigned to *K. dolosus*, but the differences in size cannot be made responsible for the differences in morphology. The very limited number of specimens and the imperfect preservation does not allow a formal taxonomic treatment.

Among the formally introduced species of *Kingaspis*, *K. campbelli* (King, 1923) and *K. sarhroensis* Geyer, 1990b are easily distinguished by the absence of an occipital spine, whereas *K. amouslekensis* Geyer, 1990b has a distinctly narrower and shorter glabella and a triangularly extended occipital ring, and *K. maroccana* (Gigout, 1951) is distinguished by a shorter and more strongly tapering glabella, shorter and more obliquely directed palpebral lobes, and wider palpebral areas.

Kingaspis sp. B

Fig. 19

Studied material. About six cranidia. In repository: From sample locality and stratum W8 (four cranidia under MMUW 2017D-108a, SSMM 10416, 10417, 11626c; cranidium tentatively assigned to *Kingaspis* sp. B under SSMM 11196b); from locality W19b (cranidia under MMUW 2017D-935b, c). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Description. Cranidium with relatively uniform transverse convexity, glabella slightly elevated above axial furrows. Sagittal profile with gentle curvature of the glabella, anterior part only slightly more convex; transverse section shows a glabella, which is slightly more convex than the palpebral areas.

Glabella of ca. 80 percent cephalic length, maximum glabellar width across L1 ca. 40–43 percent cranidial width across mid-length of palpebral lobes; glabella with faintly concave sides, with subparallel lateral margins or slightly tapering forward, frontal lobe at anterolateral corners ca. 90–95 percent width across L1; frontal lobe with a slight median angulation that creates a low triangular outline dorsal view; glabella forms a low raise above the axial furrows; three pairs of lateral glabellar furrows recognisable, all marked only as shallow, poorly defined depressions; S1 gently curving rearward from axial furrows, moderately long; S2 slightly bent, almost normal to axis, moderately long; S3 relatively short, slightly forward directed from lateral origin. Occipital furrow relatively broad (sag. and exsag.), median section shallower and wider (sag., exsag.) than lateral sections. Occipital ring moderately broad, extended into a probably moderately long, delicate subterminal spine.

Palpebral areas transversely of ca. one-quarter maximum cranidial width across mid-length of the palpebral lobes, and fixigenae posterior to eye ridges and adjacent to axial furrows exsagittally ca. half cephalic length; with low convexity in transverse section and moderate convexity in exsagittal section; poorly demarcated from axial furrow; most elevated part of the genal sector lies adjacent to the axial furrow.

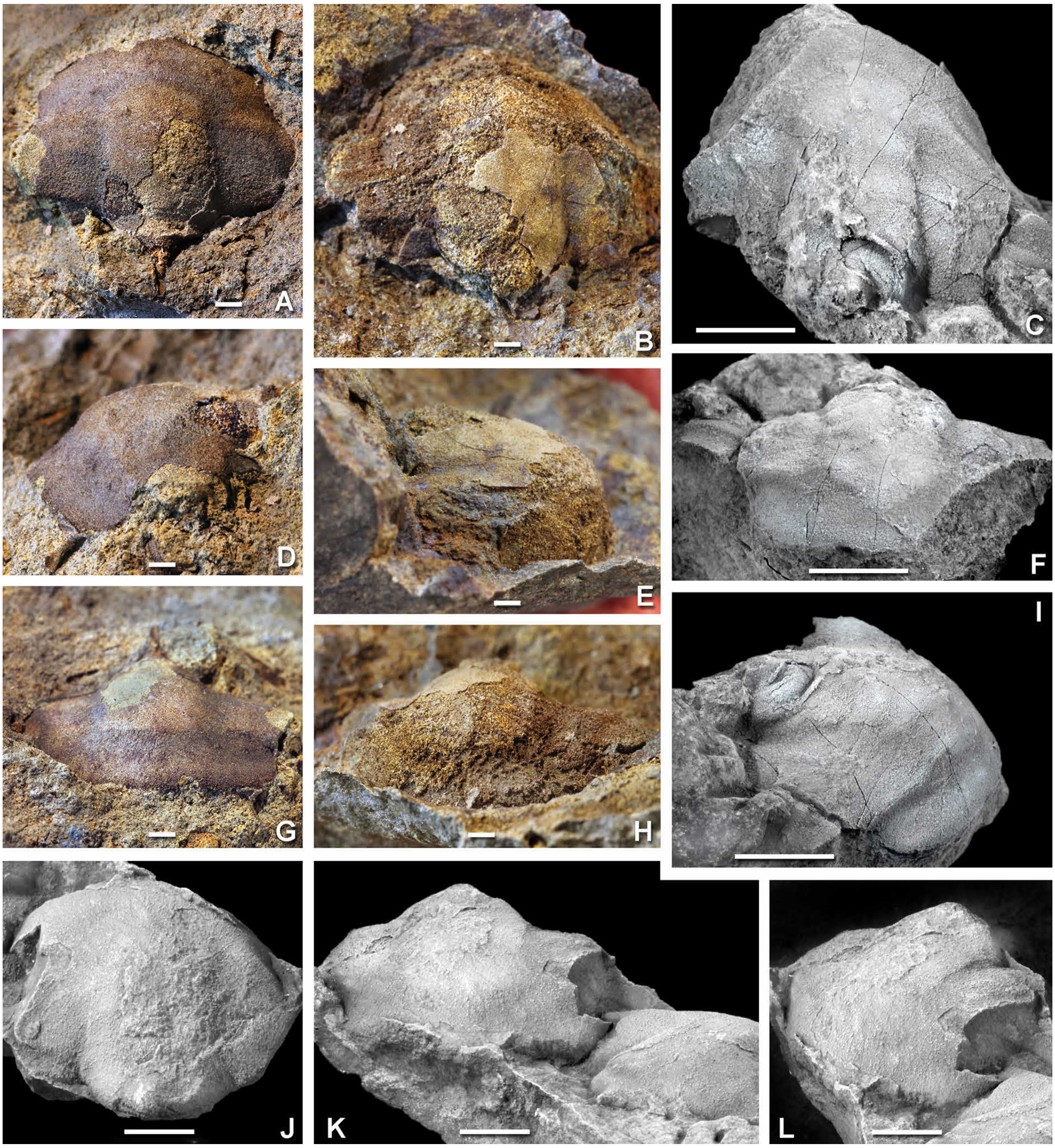

Fig. 19: *Kingaspis* sp. B. **A, D, G** SSMM 10416, cranidium, internal mould, dorsal, lateral and anterior views; from locality W8; **B, E, H** SSMM 10417, cranidium, internal mould with rests of the recrystallised cuticle, dorsal, lateral and anterior views; from locality W8; **C, F, I** MMUW 2017D-108, incomplete cranidium, composite mould, dorsal, anterior and oblique lateral views; note apparently bifid eye ridge in I; from locality W8; **J, K, L** MMUW 2017D-395b, cranidium, composite mould, dorsal, anterior and oblique anterolateral views, K with additional cranidium (MMUW 2017D-395c) in oblique lateral views on right; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 1 mm in A, B, D, E, G and H, 5 mm in C, F, I–L.

Palpebral lobe exsag. of ca. 30 percent cranidial length and ca. 6–8 percent maximum cranidial width; slightly convex in transverse profile, moderately curved along the ocular suture, less so at palpebral furrow, with anterior end at approximately the level of S3, in a slightly more adaxial position than posterior end; posterior tip about at level of anterior part of L1. Palpebral furrow a shallow, moderately curved longitudinal depression. Eye ridge developed on the interior of the cuticle as a low ridge oblique to axis, more or less only a slight change in convexity, usually poorly demarcated from the palpebral area, but defines the increased slope of the preocular area; better marked and slightly raised on one cranidium which is slightly distorted and apparently developed as a bifid ridge (Fig. 19**I**); extends anteriorly to the extended anterolateral corners of the glabella.

Preglabellar field convex, fused with anterior border, but fairly well-defined from glabellar front; grades laterally into preocular areas without any recognisable distinction. Anterior border not well-defined, but marked by a change in convexity. Border furrow obsolescent on sagittal line.

Posterior border a moderately broad (exsag.), a low ridge, nearly straight and transverse to the sagittal axis in the proximal part. Posterior border furrow a shallow, fairly broad (exsag.) depression, commences adjacent to the occipital ring close to the posterior margin; anterior rim of posterior border furrow with only slight curvature in the abaxial sector, distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture are nearly straight and run parallel to the sagittal axis from the anterior end of the ocular suture forward, swing adaxially in a gentle curve from the posterior part of the anterior border.

Librigena, hypostome, thorax and pygidium unknown.

Details of the cuticle surface not preserved in any of the present specimens.

Discussion. The specimens described here as *Kingaspis* sp. B represent a species which is distinguished from the partly co-occurring *Kingaspis dolosus* n. sp. and *Kingaspis* sp. A in its relatively wide and weakly tapering glabella and the cephalic frontal area with a moderately convexity only, as well as some minor differences (including the width of the palpebral areas, the occipital ring and the palpebral lobes). Furthermore, *Kingaspis dolosus* lacks the distinct angulation of the glabellar front, and *Kingaspis* sp. A has an unequivocally longer, more strongly tapering glabella. The limited number of available specimens, however, and the imperfect preservation do not allow a formal taxonomic treatment of this form.

Among the formally introduced species of *Kingaspis*, *K. campbelli* (King, 1923) and *K. sarhroensis* Geyer, 1990b are easily distinguished by the absence of an occipital spine, whereas *K. amouslekensis* Geyer, 1990b has a distinctly narrower and shorter glabella. *Kingaspis maroccana* (Gigout, 1951) is distinguished by a shorter and more strongly tapering glabella, shorter and more obliquely directed palpebral lobes, and wider palpebral areas.

Genus *Kingaspidoides* Hupé, 1953a, emend. Geyer 1990b

Type species. Kingaspis (*Kingaspidoides*) *armatus* Hupé, 1953 [=*Kingaspis* (*Kingaspis*) *brevifrons* Hupé, 1953]; from the *Morocconus notabilis* Biozone, Jbel Wawrmast Formation, of Ourika Wawrmast, central Anti-Atlas, Morocco.

Discussion. The identification and discrimination of genera among the subfamily Ellipsocephalinae has been a matter of debate over many years, which indicates pronounced problems that result from both different opinions of the weighting and significance of characters as week as the foundation of many species on imperfectly preserved material. As emphasised earlier (e.g., Geyer 1990b, 2017; Cederström et al. 2022), a confident identification of clades that can be used as genera requires insights in the morphology of the exterior as well as the interior of the cranidium. Particularly instructive examples for these conditions (or character states) are the species assigned to *Kingaspidoides*. This genus is characterised by a marked reduction of the glabellar and genal convexity toward a *Kingaspis*-like aspect on the dorsal surface of the cephalon, whereas internal moulds of *Kingaspidoides* show distinct axial furrows, well-defined glabellar margins and palpebral areas, which are domed independently from the glabellar convexity.

Two other genera provide analogous cranidial morphology on internal moulds, but differ in the aspects of the exterior of the cuticle: The cranidia of *Ornamentaspis* provide similar internal moulds, but the morphology of the exterior of the cuticle is similar to its internal moulds. The glabella in the species of *Ornamentaspis* is well demarcated and shows a triangular anterior margin. The palpebral areas have a convexity which develops independent from that of the glabella. In addition, the palpebral lobes of *Ornamentaspis* are convex in transverse section and of subequal width throughout. They form an arc subparallel to the slightly curved elongated raise that forms the most elevated part of the fixigena, with the palpebral furrows developed as equally curved grooves of subequal width (e.g., Fig. 35H, K, P). On internal moulds, these palpebral furrows proceed into well-developed depressions that separate the palpebral lobes from the eye ridges. These depressions are much less well developed in the species of *Kingaspidoides*. The palpebral lobe in *Kingaspidoides* is in its average form a torus-shaped bar with an elevation independent from the morphology of the fixigena. Consequently, the palpebral lobe in *Kingaspidoides* may be curved or almost straight. The palpebral furrow in *Kingaspidoides* is thus not evenly curved and frequently shows a nearly straight adaxial margin (e.g., Figs. 21A, 23B, 27A).

Ellipsostrenua Kautsky, 1945 is also closely related to *Kingaspidoides* and until recently was missing a clear-cut diagnosis so that its species have been mistaken as species of *Ornamentaspis*, *Kingaspidoides* or even *Ellipsocephalus*. The genus has its peak distribution on Baltica (Cederström et al. 2022), but species of the genus are also known from the Holy Cross Mountains, Iberia, Morocco and now the Franconian Forest region (see below). Even slightly distorted specimens can be mistaken as species of other ellipsocephalid genera so that the distribution record of *Ellipsostrenua* is expected to grow in future. *Ellipsostrenua* is characterised by a glabella that tapers forward (which unequivocally distinguishes the species with a distinctively tapering glabella from the species of *Kingaspidoides* and *Ornamentaspis*). The fixigenae have a low to moderate convexity, and the genal sector slopes ventrally from axial furrows in transverse section. Accordingly, the palpebral lobes are situated below the level of axial furrows. The palpebral lobes are moderately long, with only a low relief, and they are generally poorly defined from the fixigenae. The eye ridges are similar to those in *Kingaspidoides*: low, poorly defined, and slightly to clearly oblique to the transverse axis, but they are also better separated from the frontal lobe of the glabella. The anterior area of cephalon is slightly convex, ventrally deflected from glabellar front and mostly relatively short by comparison with the remaining part of the cephalon. *Ellipsostrenua* has a typical volucent pygidium.

Kingaspidoides also appears to have a relatively typical volucent pygidium, but its specific morphology appears to vary considerably. A precise characterisation is challenging because despite the frequent occurrence of *Kingaspidoides* species in the Cambrian rocks of the Atlas Ranges, Morocco, pygidia are rare. The standard preservation in shell hash limestones (“Bréche à *Micmacca*”) caused a separation of the small pygidia from the cranidia during transport. Accordingly, pygidia are unknown for the majority of the species, including the type species, *K. brevifrons* (Hupé, 1953a). The knowledge on pygidia is thus based on articulated dorsal exoskeletons from the shaly sandstone facies of the Jbel Wawrmast Formation in the Jbel Ougnate area, eastern Anti-Atlas, where two different types of pygidia can be distinguished: One type consists of a highly convex rhachis the posterior margin of which reaches to the posterior margin of the pygidium. This type of pygidium has narrow pleural areas defined abaxially by a raised lateral border. This type of pygidium, representing the typical volucent pygidium, is also known from *K. frankenwaldensis* (Geyer 2017, fig. 13M, N) and is obviously the normal and primordial condition (see remarks in Cederström et al. 2022). Another type of pygidium with a modest convexity and narrow and usually almost smooth pleural areas without a raised border can be seen in some species which have been previously assigned to *Kingaspidoides* or *Ornamentaspis*. This collispathulate type is usually associated with a laterally reduced posterior part of the thorax. The cephala of the species that possess such a rearwardly reduced thorax and a collispathulate pygidium do not differ significantly from the cephala of true species of *Kingaspidoides* except that their glabellas are slightly narrower and the palpebral areas tend to show a longitudinally extended somewhat torus-like moderately well-developed swelling. The librigenae appear to show typically a relatively short and stout, distinctly curved genal spine. These species have been assigned to the genus *Cambrosaurura* Geyer in Cederström et al., 2022. That genus was previously known only from the Atlas ranges of Morocco but is now apparently also identified in the Franconian Forest region (see below under *Cambrosaurura*? sp. indet.).

Composite moulds of *Kingaspidoides* are often difficult or even impossible to distinguish from those of *Ornamentaspis*, which in fact led to misidentifications of the generic identity of poorly known species. This was also the case for *Kingaspidoides frankenwaldensis* (Wurm, 1925) from the Galgenberg fauna, which had been tentatively assigned to *Ornamentaspis* (Geyer & Wiefel 1997; Elicki & Geyer 2010) based on poorly preserved and often distorted material. In addition, immature specimens of *Kingaspidoides* and *Ornamentaspis* are more-or-less indistinguishable from each other. It is particularly remarkable that the juvenile morphology of *Kingaspidoides* in fact equals the adult morphology of *Ornamentaspis* in respect to the palpebral lobes (e.g., Geyer 2017, fig. 11N, Q, S–U) so that this aspect of *Ornamentaspis* morphology suggests a neotenic development.

An additional misleading aspect arises from the fact that emblematic species of *Ornamentaspis* possess a distinct surface prosopon composed either of a clear bertillon pattern or a similar bertillon pattern of ordered small, elongated granules. This feature was interpreted as a character typical of *Ornamentaspis* by Geyer (1990b) and led to the generic name. However, such surface patters have been identified subsequently in some species of *Kingaspidoides* as well, such as *Kingaspidoides frankenwaldensis* (e.g., Geyer 2017, fig. 10I). A few species that have been tentatively attributed to *Ornamentaspis* because of their bertillon pattern on the cuticle are now recognised as species of *Kingaspidoides* in its emended form. Such species include *Ornamentaspis*? *kissanensis* Geyer, 1990b from the central Anti-Atlas of Morocco as well as *Ornamentaspis destombesi* Geyer, 1990b from the eastern Anti-Atlas of Morocco.

Latikingaspis Geyer, 1990b [type species *Kingaspis* (*Kingaspis) alatus* Hupé, 1953a] is a close relative to both *Kingaspidoides*, *Ornamentaspis*, *Cambrosaurura* and *Ellipsostrenua*. It differs from these other genera mainly in the laterally extended axial furrows, a slender glabella, and in relatively broad librigenae. The palpebral lobes of *Latikingaspis* have the aspects seen in the species of *Kingaspidoides*, but are slightly shorter, and the frontal portion of the cranidium consists of a merged unit of the anterior border and the preglabellar field/preocular areas, but is shorter than in all known species of *Kingaspidoides*.

Other genera of the Ellipsocephalinae are more easily distinguished from *Kingaspidoides*. Such differences are discussed in Cederström et al. (2022).

Kingaspidoides frankenwaldensis (Wurm, 1925b)

Figs. 10J, 20

v * 1925b *Agraulos frankenwaldensis* nov. spec. – Wurm: pp. 85–87, 89, 90, pl. III, figs. 14, 15 (only).
non v 1925b *Agraulos frankenwaldensis* nov. spec. – Wurm: pp. 85–87, 89, 90, pl. III, fig. 13.
1925c *Agraulos frankenwaldensis* Wurm – Wurm: p. 285 (pars).
1927a *Agraulos frankenwaldensis* – Wurm: p. 3 (pars).

non v	1944	*Strenuella frankenwaldensis* – Schmidt: p. 384, pl. 24, figs. 14–20.
	1954	*Strenuella frankenwaldensis* (Wurm) – Horstig: p. 453 (pars).
	1957	*Strenuella frankenwaldensis* (Wurm) – Wurm: p. 21 (pars).
non v	1957	*Kingaspidoides frankenwaldensis* – Sdzuy: pp. 18–19, fig. 7.
	1958b	*Kingaspidoides frankenwaldensis* – Sdzuy: p. 456 (pars).
	1960	*Kingaspidoides frankenwaldensis* (Wurm 1925) – Sdzuy: p. 108 (pars).
	1960	*Kingaspidoides frankenwaldensis* (Wurm) – Emmert et al.: p. 75 (pars).
	1964	*Kingaspidoides frankenwaldensis* – Sdzuy: p. 207.
	1976	*Kingaspidoides frankenwaldensis* (Wurm) – Horstig and Stettner: p. 51 (pars).
	1997	*Ornamentaspis frankenwaldensis* (Wurm) – Geyer & Wiefel: p. 100.
	2005	*Kingaspidoides frankenwaldensis* – Shergold & Brasier: p. 304.
	2009	*Ornamentaspis*? *frankenwaldensis* (Wurm, 1925) – Basse: p. 24.
v	2010	*Ornamentaspis*? *frankenwaldensis* (Wurm 1925) – Elicki & Geyer: p. 109, fig. 4.1.
v	2010	*Kingaspidoides* sp. – Elicki & Geyer: p. 109, fig. 4.2.
	2010	*Ornamentaspis*? *frankenwaldensis* – Geyer: p. 81.
	2014	*Kingaspidoides frankenwaldensis* (Wurm 1925) – Geyer et al.: p. 242.
	2015	*Kingaspidoides frankenwaldensis* (Wurm 1925) – Weidner et al.: p. 68.
v?	2015	*Ornamentaspis* cf. *frankenwaldensis* (Wurm, 1925) – Geyer & Vincent: p. 347, figs. 8, 26b.
v	2017	*Kingaspidoides frankenwaldensis* (Wurm, 1925) – Geyer: p. 5, 6, 7, 11, 13, 15, 16–19, 21, 23, 25–28, 30, 32, 33, 38, 43, 46, 65, 66, 67, figs. 7, 8, 9c, 9e, 9f, 10, 11a–j, 11k?, 11l–t, 11u?, 11v, 12, 13.
v	2019b	*Kingaspidoides frankenwaldensis* (Wurm, 1925) – Geyer et al.: p. 381, 392, 395, 397, 407, 408, 425, fig. 14, fig. 15D.

Lectotype (selected in Geyer 2017). SNSB-BSPG 1924-XII-4 (Geyer 2017, fig. 12D; originally figured by Wurm 1925, pl. III, fig. 15).

Type locality. Locality W1, near the northernmost house in Wildenstein village, Franconian Forest.
Type stratum: Galgenberg Member, Tannenknock Formation.

Studied material. About 10 dorsal exoskeletons, two cranidia with attached thorax, about 130 cranidia, several librigenae, few fragments of thoracic segments tentatively assigned to *Kingaspis frankenwaldensis*. Material from the Galgenberg Member listed in Geyer (2017, pp. 19, 21, 23). Material from the Wildenstein Member and additional material from the Galgenberg Member used for this study: From locality W6 (cranidia under MMUW 2017D-907, -909I/II, -913 and -914); from locality W8 (two cranidia under SSMM 10552a, 11466); from locality W9 (cranidium with detached librigenae under SMF 96553a; cranidium under SMSN 75643-3); from locality W9b (8 cranidia under MMUW 2017D-573, -574, -575, -576, -578a, -584, -586, -587b); from locality W10 (cranidium under SMF 88330); from locality W11 (four dorsal exoskeletons under SSMM 10668, 10680, 10734, 10735, cranidium with disarticulated thorax under SSMM 10671, 43 cranidia under SSMM 10657, 10658, 10659, 10660, 10661, 10662, 10663, 19666, 10667, 10670, 10672, 10673, 10674, 10675a, 10676, 10677, 10678, 10679, 10682, 10683, 10684, 10685, 10688a, 10688b, 10689, 10690, 10691, 10693, 10694, 10703, 10704, 10705, 10706, 10707, 10708, 10709, 10710, 10712, 10713, 10717a, 10717b, 10718, 1070, 10724, 10755, 10756, 10757, 10780, SMF 90018, 90020, 90021a, 90021b); from locality W11 or W12 (cranidia under SNSB-BSPG 1924-XII-2c [on the same slab as SNSB-BSPG 1924-XII-2a, *Exapinepiphania wurmi*, original of Wurm 1925c], SNSB-BSPG-1924-XII-3 [original of Wurm 1925c, pl. III, fig. 13], SNSB-BSPG-1959-IV-62, SNSB-BSPG-1959-IV-63, and SNSB-BSPG--A31a); from locality W12 (dorsal exoskeleton under SSMM 10277); from locality W12a (5 dorsal exoskeletons under SSMM 10572, 10574a and 10574b, 10615, 10616, 10617, cranidium with disarticulated thoracic segments under 10606, cephalon under SSMM 10594, 39 cranidia under SSMM 10573, 10575, 10576, 10577, 10578, 10579, 10580, 10582, 10583, 10584, 10585, 10586, 10587, 10588, 10589, 10590, 10591, 10592, 10593, 10595, 10596, 10597, 10598, 10600, 10602, 10603, 10604, 10605, 10610, 10618b, 10619a, 10635a, 10635b, 10637, 10638, 10639, 10648b, 10649, 10650, thoracic segments under 10607b, 10653); from locality and stratum W13b (6 cranidia under MMUW 2017D-553, -556a, -556b, -556c. -556d, -556e; librigena under MMUW 2019-D-555); from locality W15b (four cranidia under MMUW 2017D-636, -637, -638, -639); from locality W16a (cranidium under MMUW 2017D-823); from locality W17 (12 cranidia under MMUW 2017D-787, -804a, -805, -806, -814, -815, -819, -821, -823, -1032 and -1033); from locality T2 (cranidium under SSMM 10272). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Tentatively assigned to *K. frankenwaldensis*: From locality W8 (three cranidia under SSMM 10813a, 11024, 11028); from locality W9 (5 cranidia under SSMM 10349, SMF 88320, 88329, 96581, 96582); from locality W9b (4 cranidia under MMUW 2017D-566, -567a, -579, -585; librigena under MMUW 2017D-563c; thoracic segment under MMUW 2017D-578b); from locality W10 (cranidium under MMUW 2017D-934, librigena under MMUW 2017D-932); from locality W11 (two dorsal exoskeletons under SSMM 10669 and SSMM 10733; 5 cranidia under MMUW 2017D-894, SSMM 10664, 10686, 10687, 10692, 10729; librigena under MMUW 2017D-899; partial thorax under SSMM 10730); from locality W12a (cephalon with attached thoracic segments under 10633; partial exoskeleton under SSMM 10614; three cranidia under SSMM 10608, 10613, 10630); from locality W16a (cranidium under MMUW 2017D-829); from locality W17 (cranidia under MMUW 2017D-799, -817); from locality W18a (thoracic segment under MMUW 2017D-550); from locality T2 (two cranidia under SSMM 10270, 10274-I).

Diagnosis (emended, Geyer 2017). Species of *Kingaspidoides* having a glabella with subparallel sides or faintly tapering forward, generally with faint to slight constriction across L2 and L3 and extended anterolateral corners; lateral glabellar furrows faint, generally developed as low swales on the exterior of the cuticle; frontal lobe in dorsal view with gently curved anterior margin on the cuticle's exterior surface, but with a faint median indentation on internal moulds; occipital ring with slender, moderately long subterminal spine; preglabellar field and anterior border subequal in sagittal breadth, fused on the exterior of the cuticle.

Description (modified from Geyer, 2017). Cranidium in undeformed condition with relatively uniform transverse convexity, but glabella slightly raised above palpebral areas. Sagittal convexity roughly uniform, but with progressively ventrally sloping anterior part; glabella in transverse section slightly elevated and more convex than palpebral areas so that axial furrows create shallow concave depressions that define the glabella. Glabella in undeformed, adult individuals of ca. 77–85 percent (n=19) cephalic length, maximum cephalic width across L1 ca. 42–48 percent (n=19) cranidial width across mid-length of palpebral lobes; glabella with subparallel lateral margins or faintly tapering forward, generally with a faint constriction across L2 and L3 and thus with slightly extended anterolateral corners at frontal lobe; the glabella slopes continuously into axial furrows on the exterior of the cuticle, whereas on internal moulds the glabella forms a minor step-like raise above the axial furrows; three, rarely four pairs of lateral glabellar furrows recognisable, S1 to S3 developed as well poorly defined depressions on internal moulds and faint to barely visible swales on the exterior of the cuticle; S1 to S3 pairs of lateral glabellar furrows are simple, fairly long and curving gently backward, disconnected medially; S1 slightly more distinct than S2 and S3, commences at or very close to the axial furrow; S4 a short depression, slightly anteriorly directed from axial furrow and barely visible; front of glabella gently and more-or-less evenly curved on the exterior of the cuticle or faintly pointed. Occipital furrow broad (sag. and exsag.), almost straight, with a slightly less broad and shallow middle section. Occipital ring moderately broad (sag.), extended into a slender, moderately long subterminal spine, which is obliquely rearwardly directed; lateral terminations of the occipital ring extend into faint threads that proceed into the postero-proximal extensions of the palpebral areas.

Palpebral areas transversely of 19–24 percent (n=15) maximum cranidial width across mid-length of the palpebral lobes, fixigenae posterior to eye ridges along axial furrows exsagittally of ca. 45–50 percent (n=15) cephalic length; palpebral areas slightly to considerably convex in transverse section on internal moulds, less so on the cuticle's exterior surface; poorly defined from axial furrow; most elevated part of the genal sector lies close to the palpebral furrows, but in general, the genal sector slopes downward abaxially.

Palpebral lobe variable during ontogeny, distinct reduction in length during growth, in adult individuals exsag. of ca. 32–42 percent (n=15) cranidial length and in the order of 5 percent maximum cephalic width; transversely convex, distinctly curved along suture toward visual surface, weakly to slightly curved toward palpebral furrow, with anterior end at approximately the level of S3 or slightly anterior to it, in a slightly more adaxial position than posterior end; posterior end blunt, at level of anterior half of L1 to mid-length of L1; better defined and slightly narrower on internal moulds. Palpebral furrow on the exterior of the cuticle a shallow but distinct depression without clearly defined margins, grades into the palpebral lobes as well as the palpebral areas, better developed toward the anterior and posterior ends, faintly curved; extends anteriorly into a broad, extremely shallow and poorly defined depression that separates palpebral lobe from eye ridge. Eye ridge developed on the exterior of the cuticle as a low, obliquely transverse ridge, which is poorly defined from the palpebral areas, but defines the clearly sloping preocular area; poorly marked on internal moulds; extends into two low and faint threads that traverse the axial furrows and merge with the anterolateral corners of the glabella. Eye ridges and glabellar front tend to form a uniformly curved arch in dorsal view.

Frontal area of the cranidium more-or-less uniformly convex on the exterior of the cuticle, with anterior border generally not defined on the exterior of the cuticle. Preglabellar field on internal moulds of ca. 11–14 percent (n=19) cephalic length, faintly convex, often barely demarcated from anterior border, but relatively well demarcated from the front of the glabella; grades laterally into preocular areas without any recognisable distinction. Anterior border of ca. 10–13 percent (n=19) cephalic length in dorsal view of non-deformed specimens, of nearly equal breadth (sag., exsag.) throughout, subequal in sag. breadth with preglabellar field, forms subequally convex preglabellar convexity. Border furrow shallow to faint, better visible on internal moulds, where it often forms a slight kink in sagittal section when seen in lateral view.

Posterior border a moderately broad (exsag.), slightly to moderately convex lobe, transverse to the length axis in the proximal part, its course swinging anteriorly in the distal part, with slight reduction in exsag. width and with slight curvature of the section posterior to palpebral lobes. Posterior border furrow a shallow, moderately broad (exsag.) groove, commences close to the posterior margin adjacent to the occipital ring; anterior rim of posterior border furrow curved posteriorly in the abaxial sector so that it is clearly distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture more-or-less straight and parallel to the sagittal axis from the anterior end of the ocular suture, swing adaxially with a gentle curvature from about mid-length of the anterior border. Posterior branches of the suture directed obliquely abaxially from posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the distal rim of the palpebral lobes.

Librigena moderately wide (tr.), with a moderately long, relatively plump genal spine of roughly half length of the anterior part. Genal spine with a broad base that defines a gentle curvature from the posterior margin to the adaxial rim of the genal spine, tapers on short distance.

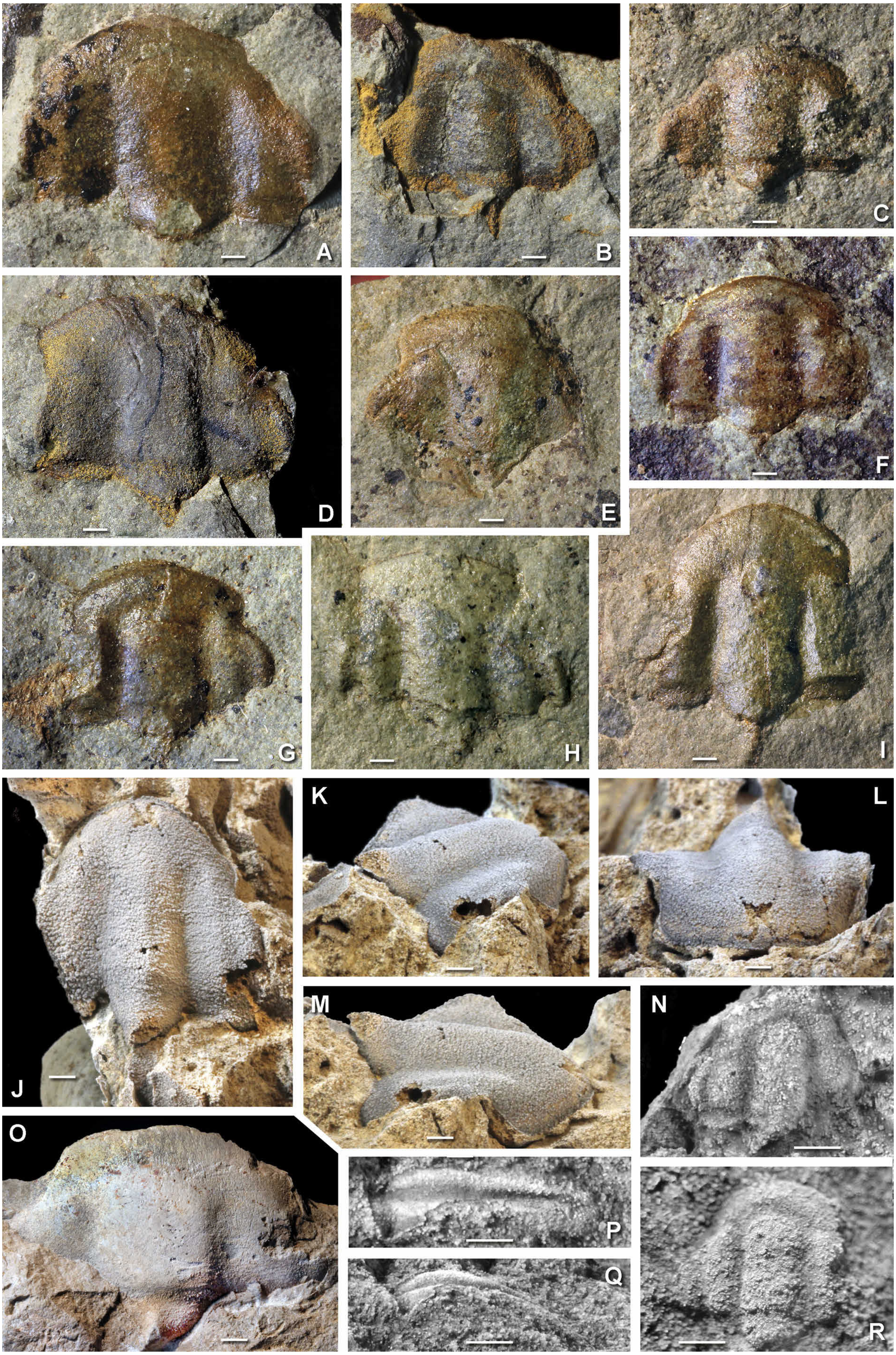
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Fig. 20: *Kingaspidoides frankenwaldensis* (Wurm, 1925). **A** SSMM 10145, cranidium, composite mould; from locality W14; **B** SSMM 10152a, cranidium, internal mould; from locality W14; **C** SSMM 10113, cranidium, internal mould; from locality W14; **D** SSMM 10155, cranidium, internal mould, with *Planolites beverleyensis*-type ichnofossils; from locality W14; **E** SSMM 10135, cranidium, internal mould; from locality W14; **F** SSMM 10178, cranidium, internal mould; from locality W14; **G** SSMM 10179, incomplete cranidium, composite mould; from locality W14; **H** SSMM 10143, incomplete cranidium, internal mould; from locality W14; **I** SSMM 10137, cranidium, internal mould; from locality W14; **J–M** SSMM 11466, cranidium, internal mould, dorsal (J), oblique posterolateral (K), oblique anterior (L) and lateral (M) views; from locality W8; **N** MMUW 2017D-566, incomplete cranidium of immature individual, internal mould; from locality W13b; **O** SSMM 10552a, incomplete cranidium, internal mould; from locality W8; **P, Q** MMUW 2017D-560, pleura of thoracic segment assigned to *K. frankenwaldensis*, internal mould, dorsal (P) and posterior (Q) views; from locality W13b; **R** MMUW 2017D-553, cranidium of immature individual, internal mould; from locality W13b. Dorsal view if not otherwise noted.
All specimens from the Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

Lateral margin gently and evenly curved, at most with a faint flaw at the base of the genal spine. Palpebral section of the suture large. Librigenal field slightly convex, slopes gently ventralward from the palpebral section toward the moderately broad (tr.) border furrow. Lateral border flat, of half to one-third of the librigenal field's transverse width, with a moderately broad doublure. Posterior border narrower (exsag.) than lateral border.

Hypostome unknown.

Thorax composed of 13 to 15 (or possibly 16) segments in adult individuals. Axial rings of segment 3 to 15 of more-or-less uniform shape (sag. and exsag.), length and width reduced progressively posteriorly to less than half maximum width across segment 3, whereas the reduction in sagittal and exsagittal directions are less affected by allometric growth. Transverse width of average axial ring about one-third overall width of the segment, growing slightly in relative width to ca. 45 percent in the posterior segments. Narrow (sag. and exsag.) articulating furrow with distal apodemal pit. Surface of axial ring with a less distinct convexity in exsagittal profile. Each axial ring has a (usually low) axial node and distinct lateral inflations indicating attachment sites for ventral musculature. Axial nodes tend to be better developed and more prominent in the mid-thoracic segments. Greatest overall width (tr.) of thorax across segments 2 to 4, decreasing in width (tr.) rearward, with slightly but progressively backward directed distal parts of pleurae, particularly posterior to segment 10. Pleural furrows moderately broad to broad (exsag.), forming furrows of lenticular outline slightly oblique to transverse axis, which fade short distance from pleural tips. Pleural tips blunt, somewhat obliquely subtruncate, but either with short, acicular and slightly posterolaterally directed spine or with tiny triangular thorn. In anterior view, the pleurae have a distinct geniculation adaxial to the transverse mid-length, which corresponds to the articulation of the adjacent segments by means of a fulcral point. As a result, the anterior flanks of the distant pleural portions have an almost flat, anteriorly tilted articulating facet, whereas the posterior margin of the distal pleura turns slightly forward to allow a limited overlap of adjacent segments during inclination of the segments. The first thoracic segment differs in having an axial ring with an anterior margin that swings clearly backward to allow a distinctive dorsal flexure of the cephalon against the thorax. Its pleurae are straight in the proximal sector, but reveal a well-developed fulcral point to fit into the socket of the cephalon's posterior border; distal part of pleura reduced in size, with a somewhat backward directed anterior margin and an obliquely ventrally deflected articulating facet. This configuration is repeated in a less distinct manner in the second thoracic segment.

Pygidium only known from imperfectly preserved material, of volucent type: generally small, subelliptical to subcordate in outline, with distinctly curved posterior margin, about as wide as long. Axis longitudinally elongate, distinctly elevated and well-defined, with subparallel sides in the anterior two-thirds, evenly curved posteriorly, posterior end at short distance from posterior margin of pygidium, half to two-thirds maximum pygidial width and more than 90 percent pygidial length; with only one or two rings plus articulating half-ring defined; articulating half-ring moderately broad (sag.), gently convex, almost as wide (tr.) as anterior margin of rhachis, with distinctly curved anterior margin. Pleural fields narrow, sublunate, sunken between axis and lateral borders, without recognisable furrows. Anterior and lateral borders form a convex, curved frame, which fades in width and height and grades into the low and poorly defined posterior border.

Exterior of the cuticle seemingly smooth in most specimens, but well-preserved specimens show a delicate bertillon pattern of low ridges on the glabella and, less well recognisable, on the palpebral areas. Fine terrace ridges occur near the anterior border and the lateral border of the librigena.

Discussion. Kingaspidoides frankenwaldensis (Wurm, 1925) has been one of the early reported and frequently quoted ellipsocephalid species of the Central European sector of Gondwana. However, it has never been precisely defined and characterised until the revision of the Galgenberg trilobite fauna (Geyer 2017). As detailed therein, Wurm's original figures and type material include two distinctly different species: one occurring primarily in the Galgenberg Member, and a second species which is found in the Wildenstein Member. The more frequently distributed species comes from the rocks of the Galgenberg facies, and this species has been introduced as *Agraulos frankenwaldensis* and subsequently dealt with as *Kingaspidoides frankenwaldensis* and *Ornamentaspis frankenwaldensis*, respectively. Geyer (2017) accepted this concept and formally restricted the taxon to the specimens from the Galgenberg Member. The material from the Wildenstein Member has been figured by Wurm (1925b) on his plate III, fig. 13 only. It represents a new species which is described in detail below under the name *Kingaspidoides wildensteinensis* n. sp. Wurm's (1925b) "true" specimens of *K. frankenwaldensis* are incomplete cranidia in which several diagnostic characters are lacking. Nevertheless, Geyer (2017, fig. 12D) selected a lectotype from the available specimens of Wurm's type lot (SNSB-BSPG 1924-XII-4; figured by Wurm 1925b, pl. III, fig. 15).

Wurm's concept of the species is far too broad to restrict the assignment of specimens from the Tannenknock Formation to one biological species. Nevertheless, it is clear what type of cranidia he regarded as typical for his *Agraulos frankenwaldensis*, and this restricted concept can be used to define *Kingaspidoides frankenwaldensis* as suggested in Geyer (2017).

Nonetheless, this species, *Kingaspidoides frankenwaldensis* in the revised concept, is not completely restricted to the Galgenberg Member. The youngest specimens of *Kingaspidoides frankenwaldensis* are found in relatively fine-grained sandstones which resemble the Galgenberg facies, but already belong to the (obviously) oldest strata of the Wildenstein Member. They occur rarely with *Ornamentaspis frequens* which indicates an overlap with this index fossil of the eponymous biozone so that specimens of *K. frankenwaldensis* from these strata are portrayed in this study.

A further complication of the situation arises from the fact that five species or forms with fairly similar morphologies occur in the Galgenberg Member and even eight in the Wildenstein Member of the Tannenknock Formation. These species/forms are often difficult to discriminate if the specimens are even slightly distorted. All kingaspidoid trilobites of the Tannenknock Formation have been previously regarded as conspecific, and the often very minor differences resulting from a slight deformation and the preservation as internal, external and composite moulds led to an unsettled amalgamation of different species, which were then placed into *Kingaspidoides* and *Ornamentaspis*. However, the enormous amount of available specimens from the Tannenknock Formation allowed to recognise the presence of both *Kingaspidoides* and *Ornamentaspis* in the Galgenberg facies samples and to specify the identity of *K. frankenwaldensis*.

As already detailed by Geyer (2017), *Kingaspidoides frankenwaldensis* is by far the most frequent kingaspidoid species of the Galgenberg Member in the classical localities, and its morphological plasticity is enhanced if the specimens were affected by distortion due to both tectonic strain and deformation during early diagenesis (see Geyer 2017, figs. 9–11). Nevertheless, the species is characterised by a typical shape of the glabella with slightly indented lateral sides, slightly protruding anterolateral corners with weak connections to the eye ridges, and a frontal lobe that is curved in dorsal view or faintly pointed. Slight compaction often creates a weak, low crest on the sagittal line of the glabella, with the lateral glabellar furrows visible as faint sunken paired swales on both sides. The occipital ring extends into a small to median-sized subterminal spine. The frontal area of the cranidium has a uniform convexity, but a faint anterior border furrow is recognisable on internal moulds, with the anterior border being slightly narrower or subequal in sagittal length with the preglabellar field. If preserved without striking compaction, the frontal area forms a relatively characteristic collar-like platform. The palpebral lobes of *Kingaspidoides frankenwaldensis* are moderately long in adults, but long in juveniles, in which they reach backward to the border furrow. The palpebral lobes form slightly upturned, bulbous lobes on the exterior surface of the cuticle of large specimens, but are well separated by palpebral furrows on internal moulds. This situation is further complicated if the specimens are preserved as composite moulds.

The distinction from the kingaspidoid species *Kingaspidoides alberti* Geyer, 2017, *K. meieri* Geyer, 2017, *K*. sp. aff. *destombesi* and *Ornamentaspis* cf. *crassilimbata* which co-occur with *K. frankenwaldensis* in the Galgenberg Member is difficult if the species are imperfectly preserved. Large, adult specimens of *Kingaspidoides alberti* are distinguished from *Kingaspidoides frankenwaldensis* in having a slightly to distinctly tapering glabella with only minor anterolateral corners; a tendency to develop a faint median angulation of the glabellar front; an anterior border of at least half the sagittal length of the frontal area; and slightly broader palpebral areas.

Kingaspidoides meieri Geyer, 2017 is distinguished by its more conspicuously elevated glabella and sunken posteroproximal portions of the fixigenae as well as a distinctly deflected anterior part of the cephalon so that it has an unusually strong relief for *Kingaspidoides*. This morphology, however, is only clearly recognisable in adult and non-deformed specimens. An additional, conspicuous difference is the extended occipital ring in *K. meieri*, which is also typical for adult specimens only, and the clear ventral deflection of the anterior part of the cephalon in *K. meieri* requires a fair preservation to be reliably identified. For additional discussion on the differences between the two species see Geyer (2017).

The fairly infrequent *Ornamentaspis* sp. cf. *crassilimbata* from the Galgenberg Member is easily distinguished by its more strongly convex glabella with a triangular frontal lobe and better developed lateral glabellar furrows, its longer terminal occipital spine, and longer palpebral lobes the posterior tips of which reach to, or almost to the posterior border furrow even in large specimens.

The differences to other species (and forms described under open nomenclature) of *Kingaspidoides* are explained in the following chapters.

Kingaspidoides epimetheus n. sp.

Fig. 21

Holotype. SMF 79016a, cranidium, internal mould (collected by K. Sdzuy, most probably in 1956).

LSID. urn:lsid:zoobank.org:act:CB9969F0-DE61-4C31-AA02-0674609684DF

Locus typicus and stratum typicum. From locality W8, Wildenstein slice, Franconian Forest; Wildenstein Member, Tannenknock Formation.

Etymology. Named after the Greek mythological character Ἐπιμηθεύς, literally meaning the “after-thinker”; a reference to the general resemblance of the cephalic morphology to that of the older species of *Protolenus*.

Studied material. The holotype is the only specimen of this species known to date, preserved as part (SMF 79016a) and counterpart (SMF 79016b).

Diagnosis. Species of *Kingaspidoides* with glabella (including occipital ring, but without occipital spine) of ca. 80 percent cephalic length, faintly tapering forward; occipital ring extended into moderately long, terminal occipital spine of moderately length, obliquely dorsally directed; maximum width of fixigenae about half maximum glabellar width; palpebral lobes of subequal width throughout, gently curved, of slightly less than 40 percent cephalic length; preglabellar field and anterior border on sagittal line of subequal breadth (sag.), frontal area gently sloping ventrally from anterior tip of glabella.

Description. Cranidium with subtrapezoidal outline in dorsal view, glabella slightly raised above palpebral areas. Sagittal convexity with roughly uniform gently curvature, but frontal area progressively ventrally sloping; glabella in transverse section slightly elevated and more convex than palpebral areas so that the axial furrows create shallow concave depressions that define the glabella. Glabella including occipital ring (but excl. occipital spine) of ca. 80 percent cephalic length, maximum cephalic width across L1 ca. 38 percent cranidial width across mid-length of palpebral lobes; glabella faintly tapering forward, without a readily recognisable constriction across L3; anterolateral corners faintly subacute; glabella with faint crest-line medially which continues into a indistinct plectrum on the preglabellar field on sagittal line; glabellar lateral areas slope distinctly into axial furrows to form a minor step-like raise above the axial furrows; three to four pairs of lateral glabellar furrows recognisable, S1 to S3 developed as poorly defined depressions on the internal mould, forming simple, fairly long and gently backward curving depressions, which are disconnected medially; S1 slightly more distinct than S2 and S3, commences at or very close to the axial furrow; S4 a short depression, slightly anteriorly directed from axial furrow and barely visible; front of glabella gently and more-or-less evenly curved. Occipital furrow broad (sag. and exsag.), almost straight. Occipital ring moderately broad on sagittal line, extended into a slender, moderately long subterminal spine, which is obliquely rearwardly and dorsally directed.

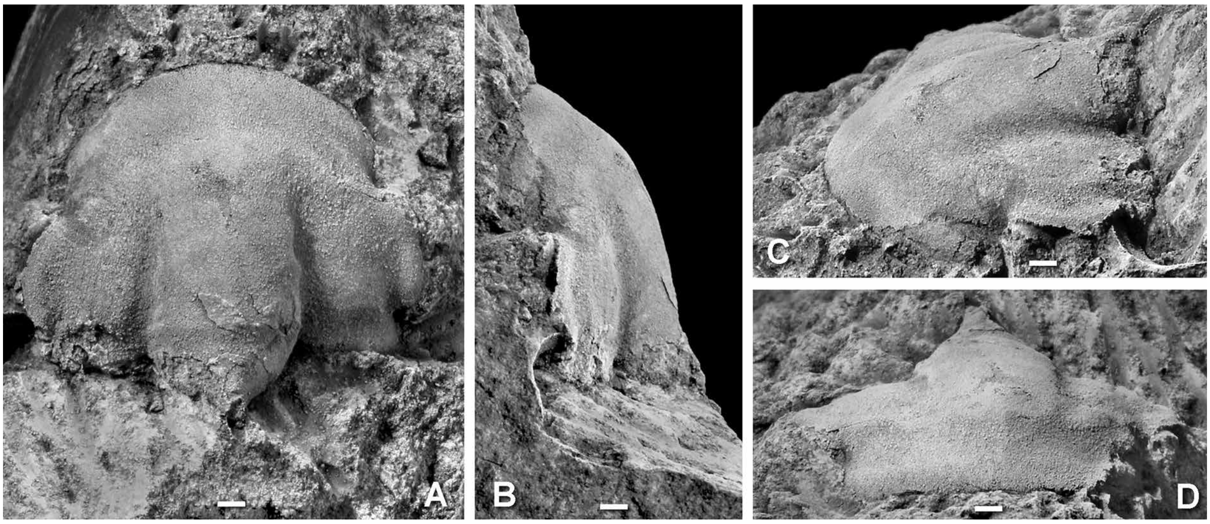

Fig. 21: *Kingaspidoides epimetheus* n. sp. **A–D** SMF 79016a, holotype, cranidium, internal mould; dorsal (A), lateral (B), oblique anterolateral (C) and anterior (D) views. From locality W8; Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

Palpebral areas transversely of 50–55 percent maximum glabellar width and slightly less to 20 percent maximum cranidial width across mid-length of the palpebral lobes, fixigenae posterior to eye ridges exsagittally along axial furrows of slightly less than 40 percent cephalic length; palpebral areas slightly convex in transverse section; relatively well distinguished from axial furrow; most elevated part of the genal sector lies close to the palpebral furrows, but in general, the genal sector slopes downward abaxially.

Palpebral lobe relatively long, exsag. of slightly less than 40 percent cranidial length and in the order of 5 percent maximum cranidial width; transversely convex, of nearly equal width throughout, distinctly curved along suture toward visual surface, with anterior end at approximately the level of S3 or slightly anterior to it, in a slightly more adaxial position than posterior end; posterior end at level of mid-length of L1, reaching nearly to posterior border furrow. Palpebral furrow a shallow but distinct depression without clearly defined margins, gently curved; extends anteriorly into a broad, very shallow and poorly defined depression that separates palpebral lobe from eye ridge. Eye ridge developed as a low, obliquely transverse ridge, which is poorly defined from the palpebral areas, but defines the clearly sloping preocular area; extends into two low and faint threads that traverse the axial furrows and merge with the anterolateral corners of the glabella.

Frontal area of the cranidium roughly uniformly convex on the exterior of the cuticle, with anterior border generally not defined from preglabellar field on the sagittal line. Preglabellar field on sagittal line of subequal breadth to anterior border, of ca. 12 percent cephalic length, faintly convex, barely demarcated from anterior border, but relatively well demarcated from the front of the glabella; grades laterally into preocular areas without any recognisable distinction. Anterior border of ca. 11–12 percent cephalic length in dorsal view, of nearly equal breadth (sag., exsag.) throughout. Border furrow faint to obsolescent on sagittal line, but progressively better developed towards facial suture.

Posterior border a moderately broad (exsag.), slightly to moderately convex lobe, transverse to the length axis in the proximal part, its course swinging slightly anteriorly in the distal part. Posterior border furrow a shallow, moderately broad (exsag.) groove, commences close to the posterior margin adjacent to the occipital ring; anterior rim of posterior border furrow almost straight throughout its course, but with a faint forward curvature in its most distant section so that it reaches almost to the posterior ends of the palpebral lobes.

Anterior branches of the suture more-or-less straight and parallel to the sagittal axis from the anterior end of the ocular suture, swing adaxially in a gentle curve from about mid-length of the anterior border. Posterior branches of the suture directed obliquely abaxially from posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the distal rim of the palpebral lobes.

Librigena, hypostome, thorax and pygidium unknown.

Discussion. Kingaspidoides epimetheus n. sp. is only known from a single cranidium, which is fairly well-preserved and provides the diagnostic characters in a way that allows a confident discrimination from the other ellipsocephalid trilobites – not only of the Franconian Forest strata, but also all other similar species. It is characterised by its faintly tapering glabella, the robust terminal occipital spine, quite long palpebral lobes, relatively broad fixigenae, and a preglabellar field of about the same width as the adjacent anterior border. A faint crest-line is recognisable on the glabella, and the fixigenae are clearly below the lateral margins of the glabella; both characters that resemble the features seen in the species of *Ornamentaspis* so that the species indeed can be seen as indicating a transitional morphology between *Kingaspidoides* and *Ornamentaspis*. However, the gently sloping frontal region is typical for the species of *Kingaspidoides* and differs from that of the *Ornamentaspis* morphology, and the palpebral lobes are obliquely oriented in respected to the horizontal line in the cross-section so that the slope ventrally from the axial furrow in its general orientation.

Kingaspidoides epimetheus is distinguished from the frequent and partly co-occurring species *Kingaspidoides frankenwaldensis* by its noticeably longer palpebral lobes, the shorter glabella and the correspondingly longer frontal region, and by the narrower anterior border.

The species' somewhat unusual cephalic morphology for a species of *Kingaspidoides* easily discriminates *K. epimetheus* from most species of *Kingaspidoides*. There is a close resemblance to species such as *K. brevifrons* (Hupé, 1953) and *K. destombesi* (Geyer, 1990b) in respect to the typical Moroccan specimens of these species. However, the shape of the palpebral lobes and the curved palpebral furrows of subequal breath clearly distinguish *K. epimetheus* from these Moroccan taxa.

***Kingaspidoides* sp. aff. *destombesi* (Geyer, 1990b)**

Fig. 22A–C, D?, E, F?, G, H?, I, J, K?, L?, M, N?, O–R, S?, T

v 2017 *Kingaspidoides* sp. aff. *usitata* (Geyer, 1990) – Geyer: pp. 5, 26, 28, 30, 38, fig. 14a–o.

Studied material. About 20 to possibly 30 cranidia, tentatively assigned librigenae and few fragments of thoracic segments tentatively assigned to *Kingaspis* aff. *destombesi*. From locality W8 (two cranidia under SSMM 10519 and SSMM 10555); from locality W9 (5 cranidia under MMUW 2017D-763, -764, -765, SSMM 10348, 10351 and 10374); from locality W13a (four cranidia under SSMM 10220, 10221, 10223 and 10231; from locality W17 (cranidium under MMUW-2017D-790). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Tentatively assigned to *Kingaspis* sp. aff. *destombesi*: from locality W1a (cranidia under MMUW 2017D-945, -946, -947, -948, 949, -950, -956, -957, -963a, -964b, -967, -968, -970a, -970b, -970c, 970d, -970e, -970f, -970g, -970h, -970i and -971); from locality W8a (cranidium under MMUW 2017D-858); from locality W9 (6 cranidia under SSMM 10336a, 10358, 10367, 10374, 10380b and SMF 96592); from locality W9b (cranidium under MMUW 2017D-576); from locality W13a (8 cranidia under SSMM 10218, 10219, 10226, 10230, 10232, 10233, 10237 and 10256b); from locality W17 (two librigenae under MMUW-2017D-792 and -816); from an unknown locality of the Wildenstein slice (cranidium under MMUW 2017D-702); from locality T2 (cranidium under SMF 88572).

Description (modified from Geyer 2017). Cranidium in original relief with convex and slightly upturned palpebral areas, glabella elevated above palpebral areas. Sagittal convexity in original relief generally uniform, but with progressively ventrally sloping anterior part; axial furrows create quite distinct depressions that define the glabella. Glabella in adult individuals of ca. 70–80 percent (n=5) cephalic length, maximum cephalic width across L1 ca. 36–42 percent (n=5) cranidial width across palpebral lobes; glabella with subparallel sides or faintly tapering forward, generally with slight constriction across L2 and L3 and thus with slightly extended but indistinct anterolateral corners at frontal lobe; glabella slopes continuously into axial furrows on the exterior of the cuticle, whereas on internal moulds the glabella forms a low step-like raise above the axial furrows; three to four pairs of lateral glabellar furrows recognisable, S1 to S3 visible as poorly defined depressions on internal moulds and faint to barely visible swales on the exterior surface; S1 to S3 simple, moderately long, adaxial sections gently backward curved from near axial furrows, disconnected medially; S4 a short, slightly anteriorly directed and poorly visible depression; front of glabella in dorsal view with shallow, more-or-less uniform curvature or with faint angulation on the exterior of the cuticle, on internal moulds composed of paired arcs separated by a faint indentation on sagittal line (Geyer 2017, fig. 14C, F). Occipital furrow moderately broad (sag. and exsag.), almost straight, with a slightly less broad and shallow middle section. Occipital ring moderately broad (sag.), extended into a slender, short to moderately long subterminal spine, which is obliquely backward directed.

Palpebral areas of 16–23 percent (n=5) maximum glabellar width across centre of the palpebral lobes; fixigenae posterior to eye ridges exsagittally ca. 43–53 percent (n=5) cephalic length along axial furrows; slightly to considerably convex in transverse profile on internal moulds, less so on the exterior surface of the cuticle; poorly separated from axial furrow; most elevated part of the genal sector lies closer to the palpebral furrow than to the axial furrow.

Palpebral lobe variably developed, exsag. of ca. 32–38 percent (n=5) cranidial length and in the order of 5 percent (n=5) maximum cephalic width; transversely convex, distinctly curved along suture toward visual surface, weakly to slightly curved adjacent to palpebral furrow, with anterior end slightly anterior to S3, in a faintly more adaxial position than posterior end; posterior tip of palpebral lobe blunt, at level of anterior half of L1 to mid-length of L1. Palpebral furrow relatively broad and shallow, but well recognisable. Palpebral lobe separated from eye ridges by a poorly defined depression. Eye ridge developed as a shallow, obliquely transverse ridge, which is poorly demarcated from the palpebral areas, but defines the clearly sloping preocular area; extends into one or two low, faint threads that traverse the axial furrows and merge with the anterolateral corners of the glabella, the anterior of these threads sometimes developing into a well visible parafrontal band in front of the glabella (Geyer 2017, fig. 14C).

Frontal area of the cranidium uniformly convex on the exterior surface, with anterior border mostly not defined on the exterior of the cuticle. Preglabellar field on internal moulds variably of 12–16 percent (n=9) cephalic length, faintly to gently convex, often barely demarcated from anterior border, but quite well-defined from glabellar front; grades into preocular areas without any recognisable distinction. Anterior border of 10–13 percent (n=9) cephalic length in dorsal view of non-deformed specimens, of nearly equal breadth (sag., exsag.) throughout, on sagittal line slightly to clearly narrower in breadth than preglabellar field. Border furrow shallow to very faint, better visible on internal moulds than on the exterior of the cuticle, often forming a slight kink in sagittal section on internal moulds.

Posterior border a moderately broad (exsag.), slightly to moderately convex lobe, directed transverse to the sag. axis in the proximal part, swinging posteriorly in the distal part, slightly reduced in width posterior to palpebral lobes, with posterior cranidial margin swinging forward in this section. Posterior border furrow a shallow, moderately broad (exsag.) depression, commences adjacent to the occipital ring close to the posterior margin.

Anterior branches of facial suture more-or-less straight and parallel to the sagittal axis from the anterior end of the ocular suture, adaxially swinging forward in a gentle curve from about mid-breadth of the anterior border. Posterior branches of facial suture directed obliquely abaxially from the posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the distal rim of the palpebral lobes.

Librigena, hypostome and pygidium unknown.

Thorax known only from fragments attributed to the species. Its morphology equals that known from the thoracic segments of *Kingaspidoides frankenwaldensis*.

Surface of cuticle probably partly covered with a bertillon pattern of terrace ridges, but internal surface occasionally with moderately large pits (Fig. 22P).

Discussion. Kingaspidoides sp. aff. *destombesi* closely resembles *K. destombesi* (Geyer, 1990b) as well as *K. usitata* (Geyer, 1990b) from the Moroccan Anti-Atlas ranges in most aspects. The form from the Tannenknock Formation has been dealt with as *K.* aff. *usitata* in Geyer (2017). However, restudy of material from Morocco in the course of contributions to the recent monography by Cederström et al. (2022) and for this present study indicated that the comparison with *K. destombesi* is more appropriate.

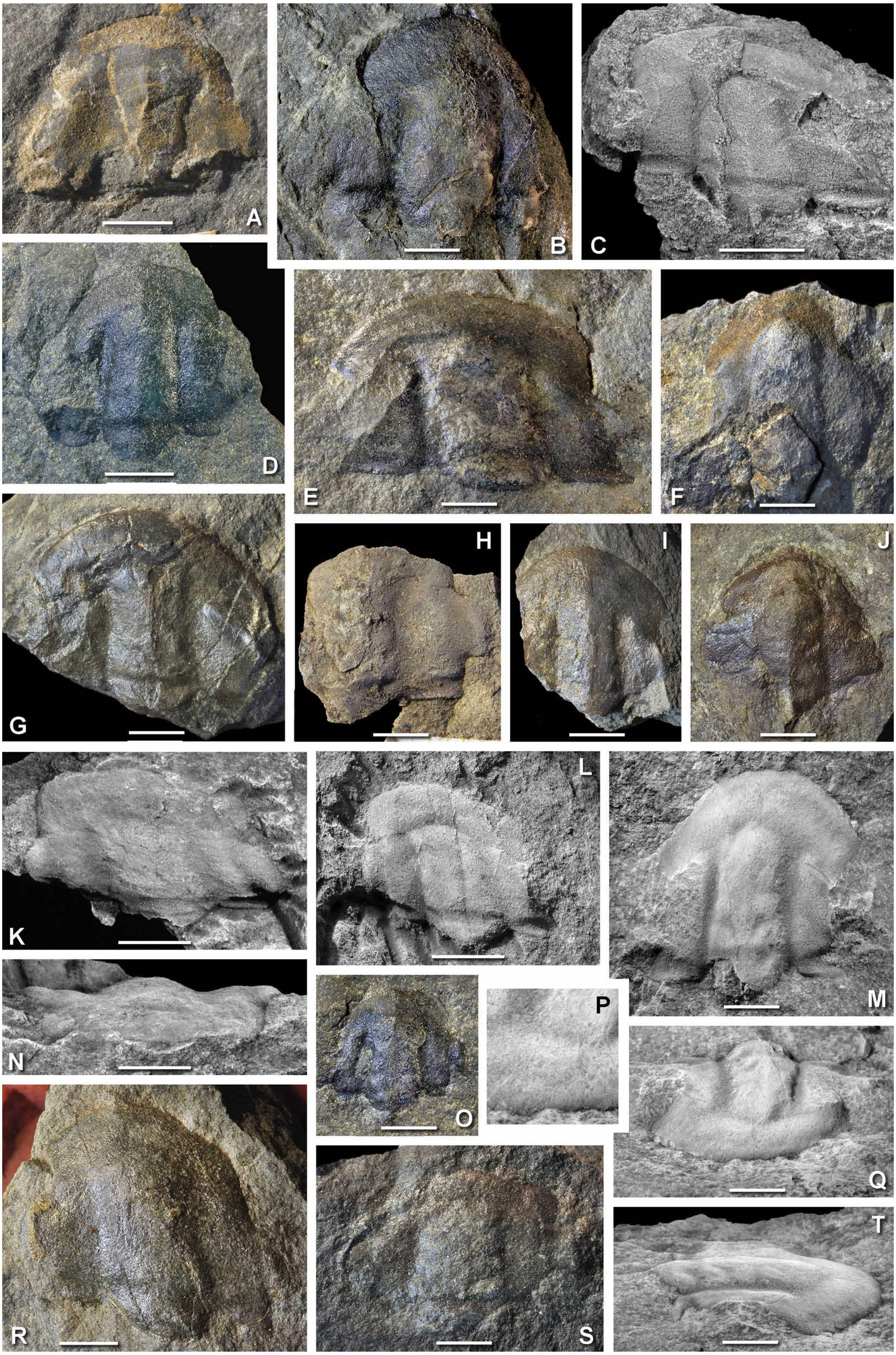
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Fig. 22: A–C, D?, E, F?, G, H?, I, J, K?, L?, M, N?, O–R, T, S? *Kingaspidoides* sp. aff. *destombesi* (Geyer, 1990). **A** SMF 88538, incomplete cranidium, internal mould with remnants of the cuticle, dorsoventrally and obliquely distorted and fractured; from locality W9; **B** SSMM 10555, incomplete cranidium, internal mould with thick secondary coat on left side; from locality W8; **C** MMUW 2017D-763, incomplete cranidium, exfoliated on right half, showing crest-line on glabella; from locality W9; **D** SSMM 10374, incomplete cranidium preserved in silicified quartz arenite, internal mould; from locality W9; **E** SSMM 10231, incomplete cranidium, internal mould; from locality W13a; **F** SSMM 10109, partial cranidium, internal mould, laterally compressed, with *Planolites*-type traces developed underneath the cuticle; from locality T2a; **G** SSMM 10351, incomplete cranidium, internal mould, dorsoventral compression led to wrinkles and various fractures; from locality W9; **H** SSMM 11018, partial cranidium, internal mould; from locality W8; **I** SSMM 10220, incomplete cranidium, internal mould, laterally compressed; from locality W13a; **J** SSMM 10519, incomplete cranidium, mostly composite mould; from locality W8; **K, N** MMUW 2017D-576, incomplete, obliquely sheared cranidium, internal mould, obliquely and dorsoventrally compressed, dorsal and anterior views; from locality W9b; **L** SMF 88572, incomplete cranidium, internal mould, with notable dorsoventral compaction and crack along longitudinal axis; from locality T2; **M, P, Q, T** SSMM 10223, incomplete cranidium, internal mould, obliquely compressed; M dorsal view, P detail of oblique anterior view showing tip of the glabella, preglabellar field and anterior border; Q oblique anterior view; T lateral view; from locality W13; **O** SSMM 10371a, incomplete cranidium of immature individual, internal mould; from locality W9; **R** SSMM 10264, incomplete cranidium, composite mould; from locality T2; **S** SSMM 10358, incomplete cranidium, largely exfoliated; from locality W9.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted.
All scale bars equal 5 mm.

The specimens of *K. destombe*si from the eastern Anti-Atlas are distinguished from the specimens from the Franconian Forest by a generally slightly more tapering glabella; a more frequently developed slight plectrum; and more obliquely directed palpebral lobes which taper anteriorly in large individuals. Major differences between *K.* aff. *destombesi* and *K. usitata* include the slightly longer (sag.) preglabellar areas, the more prominent anterior border, and an apparently more dorsally directed occipital spine. The imperfect preservation of the material from the Franconian Forest limits the identification of robust additional differences, and the specimens from the Wildenstein Member are even less clearly identifiable than the specimens from the Galgenberg Member (see Geyer 2017, fig. 14).

One cranidium (SSMM 10109) with a similar morphology has been collected from sample locality T2a. This cranidium (Fig. 22F) differs from the specimens described above in having a slightly longer and apparently much more pointed glabella; slightly more convex fixigenae in exsagittal direction; and slightly shorter palpebral lobes. This specimen, however, is distorted in a manner that enforces a pointed anterior margin of the glabella and may also influence the apparent length of the palpebral lobes and the convexity of the fixigenae so that it may fall into the morphological range of *K.* sp. aff. *destombesi*.

The specimens of *Kingaspidoides* sp. aff. *destombesi* also resemble those of *K. frankenwaldensis* in most morphological aspects. They are distinguished from most other species of *Kingaspidoides* by the same features, such as the typical shape of the glabella with slightly indented lateral sides, and slightly protruding anterolateral corners with delicate connections to the eye ridges. One of the main differences between *K.* sp. aff. *destombesi* and *K. frankenwaldensis* is the more distinct convexity of the palpebral areas and better impressed axial furrows that are responsible for the differences in the transverse section: *K. frankenwaldensis* has a relatively uniform transverse convexity, in which the slightly convex palpebral areas slope abaxially. By contrast, the palpebral furrows in *K.* sp. aff. *destombesi* are barely lower in transverse section than the axial furrows. In this respect, *K.* sp. aff. *destombesi* resembles the typical species of *Ornamentaspis*. It needs to be emphasised that this species is known from both the Galgenberg and the Wildenstein members, but only from two adjacent localities of the Galgenberg Member combined under W13a. Both localities and sample horizons also yielded a species of *Ornamentaspis* and other faunal elements, which indicate a younger age than almost all of the other localities of Galgenberg facies samples. These samples are thus believed to have delivered the oldest fauna of the *Ornamentaspis frequens* Zone known from the Franconian Forest.

Consequently, *Kingaspidoides* sp. aff. *destombesi* is younger than *K. frankenwaldensis* and may be interpreted as a direct descendent that indicates the morphological transition from *Kingaspidoides* to *Ornamentaspis* (although it cannot be identified as an ancestor of all species of *Ornamentaspis* because of the co-occurring *Ornamentaspis* cf. *crassilimbata*). In addition, the form is more frequent and widespread in the Wildenstein Member.

Particularly similar to *Kingaspidoides* sp. aff. *destombesi* is *Kingaspidoides wildensteinensis* n. sp. (see below). This new species is only known from the Wildenstein Member and often difficult to discriminate from *K.* sp. aff. *destombesi* if the specimens are distorted or generally imperfectly preserved. The most obvious differences between the species/forms are: (1) the relatively subequal breadth of the preglabellar field and anterior border on the sagittal line in *K. wildensteinensis* compared with the different breadth in *K.* sp. aff. *destombesi*; (2) the slightly longer and more strongly tapering glabella in *K. wildensteinensis*; (3) the relatively clearly developed crest-line on the sagittal line of the glabella and its frequent extension onto the preglabellar field in *K. wildensteinensis*; (4) the shorter and more obliquely oriented palpebral lobes in *K. wildensteinensis*; and (5) the slightly more posteriorly directed eye-ridges in *K. wildensteinensis*.

Large, adult specimens of *Kingaspidoides wildensteinensis* n. sp. are distinguished from *Kingaspidoides* sp. aff. *destombesi* by their slightly to distinctly tapering glabella with only weakly developed anterolateral corners; a tendency to develop a faint median angulation of the glabellar front; a broader anterior border of at least half the sagittal length of the frontal area; and slightly broader palpebral areas.

For comparison to other species of *Kingaspidoides* see discussion under *K. frankenwaldensis*.

Kingaspidoides wildensteinensis **n. sp.**

Fig. 23

v	1925c	*Agraulos frankenwaldensis* nov. spec. – Wurm: pl. III, fig. 15.
?	1960	*Kingaspidoides frankenwaldensis* (Wurm 1925) – Sdzuy: p. 108 (pars).

Etymology. Named after the village of Wildenstein, a reference to the occurrence of the species in the Wildenstein Member of the Tannenknock Formation.

Holotype. SNSB-BSPG-1955-VII-8a,b, cranidium, from the original collection of Adolf Wurm (see Wurm 1925b) (Fig. 23B, E, G).

LSID. urn:lsid:zoobank.org:act:6F89DBEC-D733-4CA7-B023-0133F1FD35B2

Type locality. Almost certainly locality W9 in the Wildenstein slice between Wildenstein and Premeusel villages, Franconian Forest.

Type stratum: Wildenstein Member, Tannenknock Formation; *Ornamentaspis frequens* Zone, Agdzian Stage (probably lowermost Wuliuan).

Paratypes. About 10 cranidia (possibly up to 40 cranidia known), one incomplete dorsal exoskeleton, several incomplete thoraxes, few fragments of thoracic segments and several librigenae tentatively assigned to *Kingaspidoides wildensteinensis*. From locality and stratum W1 (cranidium under SNSB-BSPG 1924-XII-4 [originally figured by Wurm 1925, pl. III, fig. 15]; from locality W8 (cranidia under MMUW 2017D-582 and SSMM 10500); from locality W9 (incomplete dorsal exoskeleton under SMF 96569b; five cranidia under SSMM 10353, 10368, SMF 96554, 96602a and 96602b); from locality W11 or W12 (cranidia under SNSB-BSPG 1955-VII-8a and SNSB-BSPG 1955-VII-9a); from locality

W16a (cranidium under MMUW 2017D-853). All specimens from Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Tentatively assigned to *Kingaspidoides wildensteinensis*: from locality W1 (cranidia under MMUW 2017D-517 and -518); from W8 (four librigena under MMUW 2017D-595b, SSMM 10518, 10528, and 11018); from loc. W9 (10 cranidia under SSMM 10347, 10356, 10363, 10369, 10371a, 10375, 10378, 10379a, 10379b and SMF 96573a; partial thorax under SMF 96569a); from loc. W10 (cranidium under SMF 88323); from loc. W11 (cranidium under MMUW 2017D-593); from locality W13a (10 cranidia under SSMM 10194a, 10195, 10196, 10197, 10198b, 10209, 10225, 10228, 10235 and 10236).

Diagnosis: Species of *Kingaspidoides* with a generally tapering glabella of ca. 74–78 percent cephalic length, with faintly extended anterolateral corners; lateral glabellar furrows faint; frontal lobe in dorsal view with faint median angulation; occipital ring extended into a strong, moderately long subterminal spine; palpebral lobes of roughly one-third cephalic length, clearly oblique to axis; preglabellar field and anterior border subequal in sagittal breadth, fused on the exterior of the cuticle, but shallow to faint anterior border furrow progressively well-developed toward cephalic suture; preglabellar field with faint plectrum on internal moulds.

Description. Cranidium with relatively uniform transverse convexity, glabella slightly elevated above axial furrows. Sagittal profile with faint to gentle curvature of the glabella, anterior part progressively sloping ventrally; transverse section shows a slightly elevated glabella with a faint crest-line (Fig. 23D, I), which is more convex than the palpebral areas; axial furrows create shallow depressions that define the glabella. Glabella in nondeformed, adult individuals of ca. 73–80 percent (n=7) cephalic length, maximum glabellar width across occipital ring ca. 37–43 percent (n=7) cranidial width across mid-length of palpebral lobes; glabella with straight to faintly concave sides, tapering forward, frontal lobe at anterolateral corners ca. 77–87 percent (n=7) width across occipital ring; frontal lobe with a gently curved anterior margin, occasionally with a tendency to develop a faint median angulation that creates a low triangular outline dorsal view; internal mould with a complete, relatively broad (sag., exsag.) parafrontal band (Fig. 23B, 23C, J, 23M); on the exterior surface the glabella slopes continuously into axial furrows, whereas on internal moulds the glabella forms a minor step-like raise above the axial furrows; with three or four pairs of lateral glabellar furrows, S1 to S3 visible as shallow, poorly defined depressions on internal moulds and faint to barely visible on the exterior of the cuticle; S1 and S2 simple, gently curved backward from about axial furrows, disconnected medially; S1 slightly more distinct than S2, commences at or very close to the axial furrow; S3 relatively short, broad, transverse to axis, commencing distant from axial furrows; S4 short, narrow to slit-like, slightly anteriorly directed, poorly visible. Occipital furrow relatively broad (sag. and exsag.). Occipital ring moderately broad, ca. 16–19 percent (n=7) cephalic length (sag.), extended into a strong, moderately long subterminal spine, which is obliquely backward directed.

Palpebral areas transversely of 20–23 percent (n=7) maximum cranidial width across mid-length of the palpebral lobes, and fixigenae posterior to eye ridges and adjacent to axial furrows exsagittally ca. 40–45 percent (n=7) cephalic length; slightly convex in transverse section on internal moulds and on the exterior surface; poorly demarcated from axial furrow, with faint branched caeca occasionally recognisable on internal moulds; most elevated part of the genal sector lies closer to the palpebral furrows than to the axial furrow, but genal sector in general slopes ventrally abaxially.

Palpebral lobes exsag. of 27–33 percent (n=7) cranidial length and 8–10 percent (n=7) maximum cranidial width; transversely moderately convex und the exterior of the cuticle, less so on internal moulds, faintly curved, with anterior end at approximately the level of S3, in a slightly more adaxial position than posterior end; posterior tip slightly reduced in width, about at level of mid-length of L1; ocular suture more curved in dorsal view than adaxial margin of the palpebral lobe.

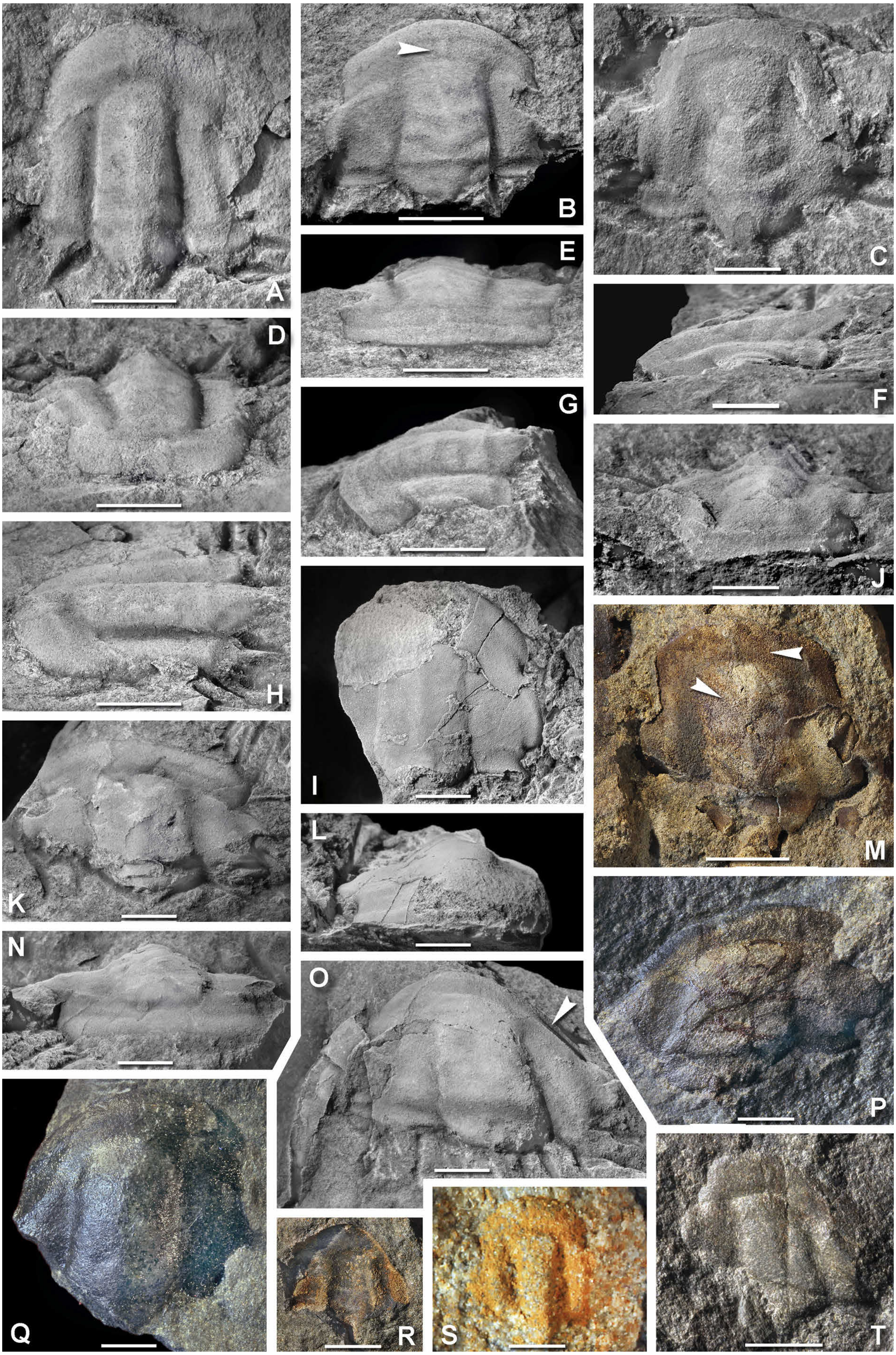
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Fig. 23: A–Q, R–T? *Kingaspidoides wildensteinensis* n. sp. **A, D, H** SMF 96574a, paratype. incomplete cranidium, internal mould, slightly laterally compressed, dorsal (A), oblique anterior (D) and oblique lateral (H) views; from locality W9; **B, E, G** SNSB-BSPG-1955-VII-8a, holotype, incomplete cranidium, internal mould, dorsal (B), anterior (E) and lateral (G) views; from locality W9; **C, F, J** SMF 96602a, paratype, cranidium, internal mould, laterally compressed; from locality W9; **I, L** MMUW 2017D-782, paratype, incomplete cranidium, internal mould with partially preserved cuticle, dorsal (I) and anterior (L) views; from locality W8; **K, N** MMUW 2017D-853, paratype, cranidium, internal mould, slightly longitudinally compressed, dorsal (K) and anterior (N) views; from locality W16a; **M** SSMM 10500, paratype, cranidium, internal mould, showing relics of a granulose sculpture on the glabella developing from a Bertillon pattern (left arrow) and centrifugally arranges caeca on the preglabellar field (right arrow); note the low convexity of the palpebral lobes on the interior of the cuticle and the faint parafrontal band visible at the right anterior margin of the frontal lobe; from locality W8; **O** SMF 96553a, paratype, incomplete cranidium with slightly detached left librigena, internal mould; note distinctive furrow resulting from folding during early diagenesis (arrow); from locality W9; **P** SSMM 10368, paratype, incomplete cranidium, internal mould showing network of numerous *Planolites beverleyensis*-type traces underneath the now removed cuticle; from locality W9; **Q** SSMM 10375, paratype, partial cranidium, internal mould; from locality W9; **R** SMF 88330, cranidium of immature specimen, internal mould; from locality W10; **S** SSMM 10209, incomplete late meraspid cranidium, internal mould; from locality W13a; **T** SMF 88323, incomplete cranidium of immature individual, internal mould with crack subparallel to longitudinal axis; from locality W9.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 5 mm in A–R and T, 1 mm in S.

Palpebral furrow a shallow, nearly straight longitudinal depression, but well recognisable because of the slightly upturned palpebral lobes, slightly better developed in the central and anterior portions, more-or-less straight and slightly oblique to axis; extends anteriorly into a faint to obsolescent depression that separates the palpebral lobe from the eye ridge. Eye ridge developed on the exterior of the cuticle as a low ridge or an extended elongate swelling clearly oblique to axis, which is poorly demarcated from the palpebral area, but defines the clearly sloping preocular area; poorly marked on internal moulds; extends anteriorly into two low, faint threads that traverse the axial furrows and merge with the anterolateral corners of the glabella and posterolaterally into a narrow ridge that connect it with the anterior end of the palpebral lobe (Fig. 23B).

Preglabellar field of ca. 11–13 percent (n=7) cephalic length, faintly convex, mostly barely demarcated from anterior border, but well-defined from glabellar front; with a faint median ridge/plectrum on well preserved internal moulds; grades laterally into preocular areas without any recognisable distinction. Anterior border of ca. 11–14 percent (n=7) cephalic length in dorsal view of undeformed (or nearly undeformed) specimens, slightly reduced in exsag. width towards facial suture, subequal in breadth with preglabellar field, forms subequally convex preglabellar convexity. Border furrow shallow, mostly faint in internal moulds, slightly better developed toward suture; often obsolescent on the exterior of the cuticle.

Posterior border a moderately broad (exsag.), slightly to moderately convex torus, transverse to the sagittal axis in the proximal part, slightly reduced in width and slightly curved posterior to palpebral lobes. Posterior border furrow a moderately shallow, moderately broad (exsag.) depression, commences adjacent to the occipital ring close to the posterior margin; anterior rim of posterior border furrow curved posteriorly in the abaxial sector so that it is clearly distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture nearly straight and parallel to the sagittal axis from the anterior end of the ocular suture forward, swing adaxially in a gentle curve from about mid of the anterior border. Posterior branches directed obliquely abaxially from the posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the maximum abaxial level of the palpebral lobes.

Librigena only known from two specimens, one of them showing slightly detached and distorted librigenae (SMF 96553a; Fig. 23O). Librigena moderately wide, with a moderately long genal spine of roughly half length of the anterior part. Genal spine with a broad base that defines a gentle curvature from the posterior margin to the adaxial rim of the genal spine, slightly tapering in width. Lateral margin gently and homogeneously curved. Palpebral section of the suture large. Librigenal field slightly convex.

Hypostome, thorax and pygidium unknown or not known with any certainty.

Surface of cuticle partly covered with a bertillon pattern of terrace ridges preserved only in some of the specimens, where it is best developed on the glabella (Fig. 23M, arrow). Centrifugally arranged caeca sometimes visible on the preglabellar field and preocular areas (Fig. 23M, right arrow). Terrace ridges partly preserved on the marginal face of the anterior border.

Discussion. Kingaspidoides wildensteinensis n. sp. is known from a number of specimens, which come from lithologically different rocks of the Wildenstein Member of the Tannenknock Formation, such as slaty siltstones and fine-grained sandstones, calcareous shales and ferritic marlstones. The occurrence in such different rocks led to distinct differences in preservation, exemplified by preservation as internal, external and composite moulds affected in different ways and intensities by distortion, by compaction and tectonic deformation. This deformation modifies the cranidia often in a way that they resemble those of other species (or unnamed forms) of *Kingaspidoides* or *Ornamentaspis*. Thoraces are only known from fragments of single isolated sclerites. Pygidia and ventral sclerites are unknown. However, the recognisable characters unmistakeably indicate that the material represents a hitherto unknown species. The most important diagnostic characters include the frontal area with the preglabellar field and the anterior border being subequal in sagittal breadth; a faint plectrum developed on the preglabellar field visible on internal moulds; a relatively short, but moderately broad glabella which is faintly reduced in width towards the frontal lobe; a subequally curved anterior margin of the frontal lobe; and relatively short, slightly crescentic palpebral lobes the posterior end of which is clearly distant from the posterior border furrow.

Several species or forms of *Kingaspidoides* are similar to *K. wildensteinensis*: These include the co-occurring *K.* sp. aff. *destombesi*, which is distinguished by is narrower glabella with a distinct median kink of the anterior margin of the frontal lobe; the preglabellar field being clearly broader (sag.) than the anterior border; the absence of a plectrum on the preglabellar field; and broader, more upturned palpebral lobes.

The most similar formal trilobite species is *Kingaspidoides destombesi* (Geyer, 1990b) from co-eval strata of the eastern Anti-Atlas of Morocco. This species has been first described as *Ornamentaspis destombesi* Geyer, 1990b and was transferred to *Kingaspidoides* by Geyer (2017). The species is distinguished from *K. wildensteinensis* by more-or-less the same characters as *K*. sp. aff. *destombesi*. Typical Moroccan specimens have a slightly broader, shorter and more strongly tapering glabella with a more frequently developed faint boss, slightly more oblique palpebral lobes and a preglabellar field which is clearly broader (sag.) than the anterior border.

The differences between *Kingaspidoides wildensteinensis* and the co-occurring *K. frankenwaldensis* are also minor on the first glance, but very distinct in well-preserved specimens. The glabella of *Kingaspidoides frankenwaldensis* is relatively longer in respect to the length of the cephalon; the frontal lobe in *K. wildensteinensis* extends slightly beyond the arc described by the eye ridges, whereas eye ridges in *K. frankenwaldensis* describe an almost evenly curved arc; *K. frankenwaldensis* lacks the boss on the preglabellar field, and the preglabellar field is broader (sag.) than the anterior border; the palpebral lobes in *K. frankenwaldensis* are broader (tr.) and extend laterally more distinctly than they do in *K. wildensteinensis*.

Kingaspidoides epimetheus n. sp. shares with *K. wildensteinensis* the subequally broad preglabellar field and anterior border as well as a faint crest-line and the tendency to form a plectrum on the preglabellar field. However, *K. epimetheus* differs distinctly from *K. wildensteinensis* by slightly wider (tr.) palpebral areas and markedly longer palpebral lobes of subequal width as well as some minor other characters (see descriptions).

The librigena of *Kingaspidoides wildensteinensis* is only known from one of the studied specimens where the two detached librigenae are clearly distorted. However, it is obvious that the librigena of the species is quite broad and belongs to a type characterised by a long and strong genal spine with a somewhat curved lateral margin. This morphology distinguishes it from that in most other species of the genus. Similar is the librigena of *Kingaspidoides destombesi* from Morocco and also that of *K.* sp. aff. *destombesi* from the same strata as *K. wildensteinensis* in the Franconian Forest region. It is apparently barely distinguishable from that of *Kingaspidoides frankenwaldensis*.

Kingaspidoides sp. cf. *brevifrons* (Hupé, 1953a)

Figs. 24 A–M, N?, O–Q, R–T?, 25 A–D, E?, F–K

? v 1923a Gedornte Rhachis eines Trilobiten – Wurm: pl. III, fig. 18a, b.
v 2020 *Kingaspidoides* sp. D – Geyer et al.: p. 15, fig. 6f.

Studied material. Ca. 40 cranidia (possibly up to 100), about 8 complete or partial exoskeletons or more-or-less complete thoraces with attached or slightly detached cranidia. In repository: from locality W8 (enrolled exoskeleton under 10529, 27 cranidia under MMUW 2017D-088, -143a, -147, -153, -154, -180, -350b, -706c, -710, -758, -773b, -783, SSMM 10402a, 10402c, 10430, 10432a, 10432b, 10450, 10501, 10502, 11001, 11002, 11114, 11331, 11332, 11333 and 12411); from locality W9 (exoskeleton under MMUW 2017D-326; 24 cranidia under MMUW 2017D-077, SSMM 10373, 12364b, 12365, 12366, 12368, 12373, 12374, 12375, 12376, 12384, 12386, 12388, 12389, 12391, 12393, 12395, 12397, 12402b, 12402c, 12403 and SMF 96574); from locality W13e (two cranidia under MMUW 2017D-437 and -477); from locality “W14b” (cranidium under SSMM 10191); from locality W18a (cranidium under MMUW 2017D-546a); from locality T2 (three cranidia under SSMM 10164, 10266 and 10271); from locality T2b (two cranidia under SSMM 10086 and SSMM 10087).

Material tentatively assigned to *Kingaspidoides* sp. cf. *brevifrons*: From locality W6 (cranidia under MMUW 2197-D-911, -912 and -920); from locality W8 (three dorsal exoskeletons under SSMM 10436, 11335 and 10452; 23 cranidia under MMUW 2017D-053c, -303h, -779dI, -1021a, SSMM 10433, 10435, 10440, 10441, 10453, 10455, 10503, 10533, 10552b, 10562, 11016, 11025, 11026, 11027, 11035, 11071, 11082, 11195 and 11337; librigena under MMUW 2017D-244b); from locality W9 (incomplete dorsal exoskeleton under SSMM 12382; partial thorax under BLfU 5735SG015017, = original specimen of Wurm 1923, pl. III, fig. 18a, 18b; 21 cranidia under SSMM 10364, 10376a, 10376b, 10377, 12370, 12371, 12377, 12378, 12379, 12380, 12381, 12383, 12387, 12392, 12394, 12400, 12405, SMF 88318, 88325, 88331 and 96593); from locality W12a (cranidium under MMUW 2017D-906I/-906II); from locality W13e (5 cranidia under MMUW 2017D-454, -460, -471, -474 and -475); from locality “W15”/Waldweg (single cranidium under SSMM 10120); from locality W15a (cranidium under MMUW 2017D-688); from locality W17 (cranidia under MMUW 2017D-813, -1030 and -1031); from locality T2 (four cranidia under SSMM 10163, 10265, 10268 and 10273); from locality T2b (cranidium under SSMM 10110-I).

Description. Cranidium in undeformed condition relatively uniformly convex in sagittal profile, with genae clearly sloping ventrally from axial furrows. Glabella relatively convex (tr., sag.) and moderately elevated above the palpebral areas; anterior part of the cephalon ventrally deflected. Glabella in adult individuals of ca. 80–86 percent (n=6) cephalic length, maximum cephalic width across L1 varies between ca. 37 and 43 percent (n=6) cranidial width across palpebral lobes; glabella typically with almost subparallel lateral margins, but with a slight constriction across L2/L3; with small, mostly indistinct anterolateral corners at frontal lobe, often with faint connection with eye ridges; glabella forms a minor step-like raise above the axial furrows in internal moulds; three, rarely four pairs of lateral glabellar furrows visible, S1 to S3 preserved as poorly defined depressions on internal moulds and faint to barely visible swales on the exterior; S1 to S3 simple and disconnected medially (except for slightly dorsoventrally compressed specimens); S1 slightly more distinct than S2 and S3, commences at or very close to the axial furrow and more distinctly rearward curving from origin near lateral margin; S4 never well visible in the studied specimens; front of glabella in dorsal view apparently with faint angulation medially. Occipital furrow moderately broad (sag. and exsag.), more-or-less straight, with a slightly wider (sag.) middle section. Occipital ring extends into a terminal spine with a moderately broad base running into a slender, obliquely directed middle and terminal part.

Palpebral areas in large individuals transversely of 19–25 percent (n=6) maximum cranidial width across mid-length of the palpebral lobes; fixigenae posterior to eye ridges exsagittally of ca. 45–51 percent (n=6) cephalic length along axial furrows; slightly to considerably convex in transverse section, sloping ventrally along anterior and middle section of palpebral furrows; poorly demarcated from axial furrow; most elevated part of the genal sector lies close to the axial furrow.

Palpebral lobe of variable shape and length, obviously with slight reduction in length during growth, in adult individuals variably of ca. 28–35 percent (n=6) cranidial length (exsag.) and in ca. 5–10 percent maximum cranidial width; transversely convex, moderately curved along suture toward visual surface, less curved toward palpebral furrow, with anterior end at approximately the level of S3 or slightly anterior, in a faintly more adaxial position than posterior end; posterior end at about level of S1. Palpebral furrow shallow, often without clear margins, faintly curved; extends anteriorly into a shallow and poorly defined depression that separates palpebral lobe from eye ridge. Eye ridge a shallow, obliquely transverse ridge, which is poorly demarcated from the palpebral areas. Eye ridges and glabellar front form a somewhat evenly curved arch in dorsal view.

Frontal area of the cranidium convex, distinctly deflected ventrally, with anterior border generally not defined medially, but usually progressively visible towards suture, mainly as a result of compression. Preglabellar field faintly convex, slightly broader (sag.) than anterior border; grades laterally into preocular areas without any recognisable distinction. Anterior border of less than 10 percent cephalic length in dorsal view, of nearly equal breadth throughout. Border furrow faint to obsolescent.

Posterior border relatively narrow to moderately broad (exsag.), slightly convex, transverse to the sagittal axis in the proximal part, swinging slightly to the posterior in the distal part, posterior to palpebral lobes slightly reduced in width and slightly curved. Posterior border furrow a moderately shallow and moderately broad (exsag.) swale, commences adjacent to the occipital ring close to the posterior margin; anterior rim of posterior border furrow curved posteriorly in the abaxial sector so that it is distant from the posterior ends of the palpebral lobes.

Anterior branches of the suture more-or-less straight and parallel to the sagittal axis forwardly from the anterior end of the ocular suture. Posterior branches directed obliquely abaxially from the posterior ends of the ocular suture, describe a gentle curve to meet posterior margin of the cephalon posterior to the distal rim of the palpebral lobes.

A librigena which appears to belong to this species represents the only known record of this sclerite (Fig. 24N). It is moderately wide, with a moderately long genal spine of slightly less length of the anterior part. Genal spine with a broad base that defines a minor curvature from the posterior margin to the adaxial rim of the genal spine so that it tapers slowly backward. Lateral margin gently and almost evenly curved, at most with a faint flaw at the base of the genal spine. Palpebral section of the suture large. Librigenal field convex, slopes gently ventrally from the palpebral section. Lateral border slightly convex, fused with librigenal field. Posterior border narrow.

Hypostome and pygidium unknown.

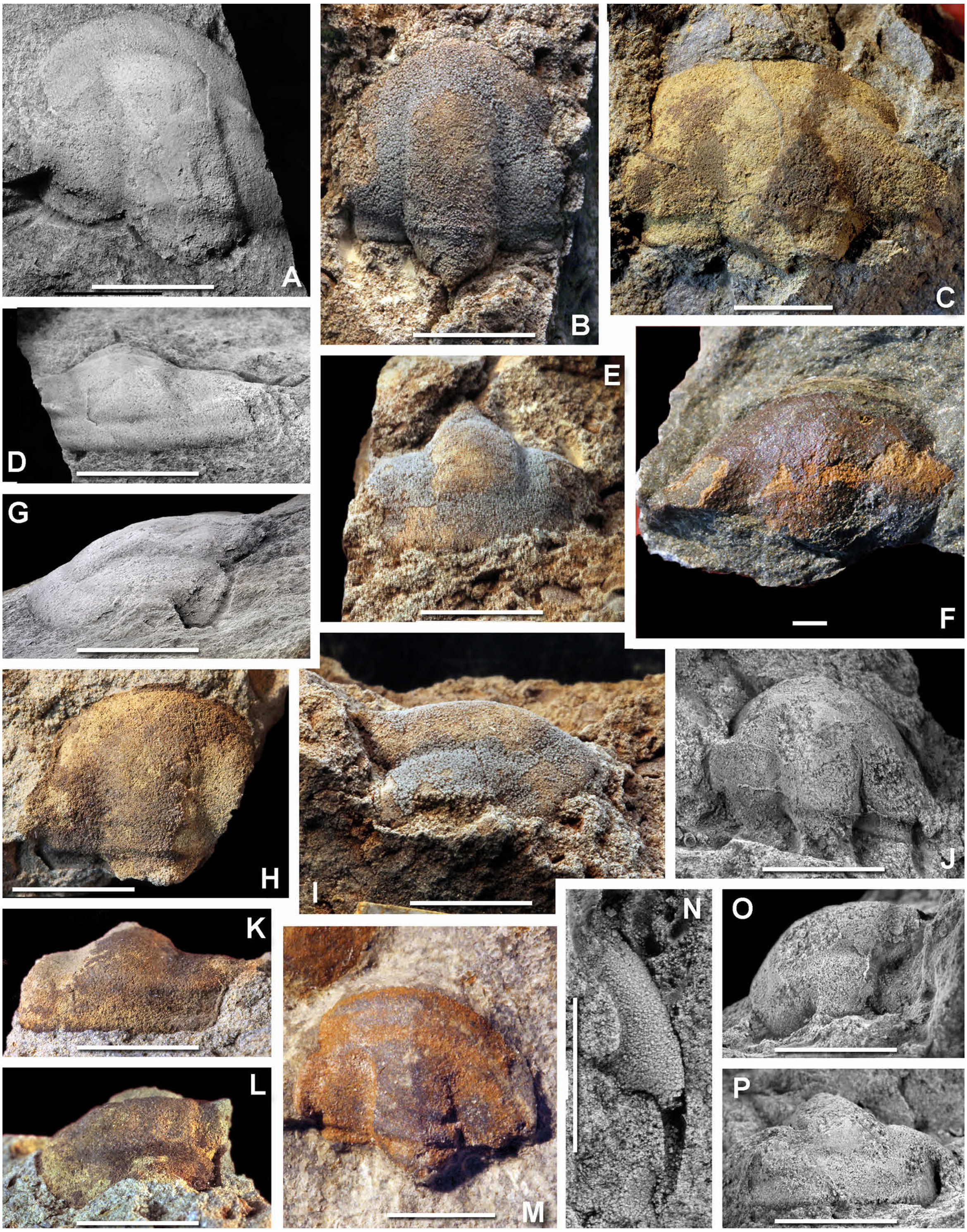

Fig. 24: A–Q, R–T? *Kingaspidoides* sp. cf. *brevifrons* (Hupé, 1953). **A, D, G** SMF 88314a, incomplete cranidium, internal mould, slightly obliquely distorted, dorsal (A), oblique anterior (D) and lateral (G) views; from locality T2; **B, E, I** SSMM 11114, incomplete cranidium, internal mould with replacement coat of remineralised cuticle, dorsal (B), oblique anterior (E) and lateral (I) views; from locality W8; **C** SSMM 10402a, incomplete cranidium, internal mould, longitudinally compressed; from locality W8; **F** SSMM 10276, partial cranidium, composite mould; from locality T2; **H, K, L** SSMM 10501, incomplete cranidium, internal mould, dorsal (H), oblique anterior (K) and oblique lateral (L) views; from locality W8; **J, O, P** MMUW 2017D-783, cranidium, internal mould, dorsal (J), lateral (O) and anterior (P) views; from locality W8; **M** SMF 88550b, cranidium, internal mould with limonitic coat; from locality T2; **N** MMUW 2017D-244b, librigena, internal mould and external cast of genal spine; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars 5 mm in A–E, H–P and T, 1 mm in F.

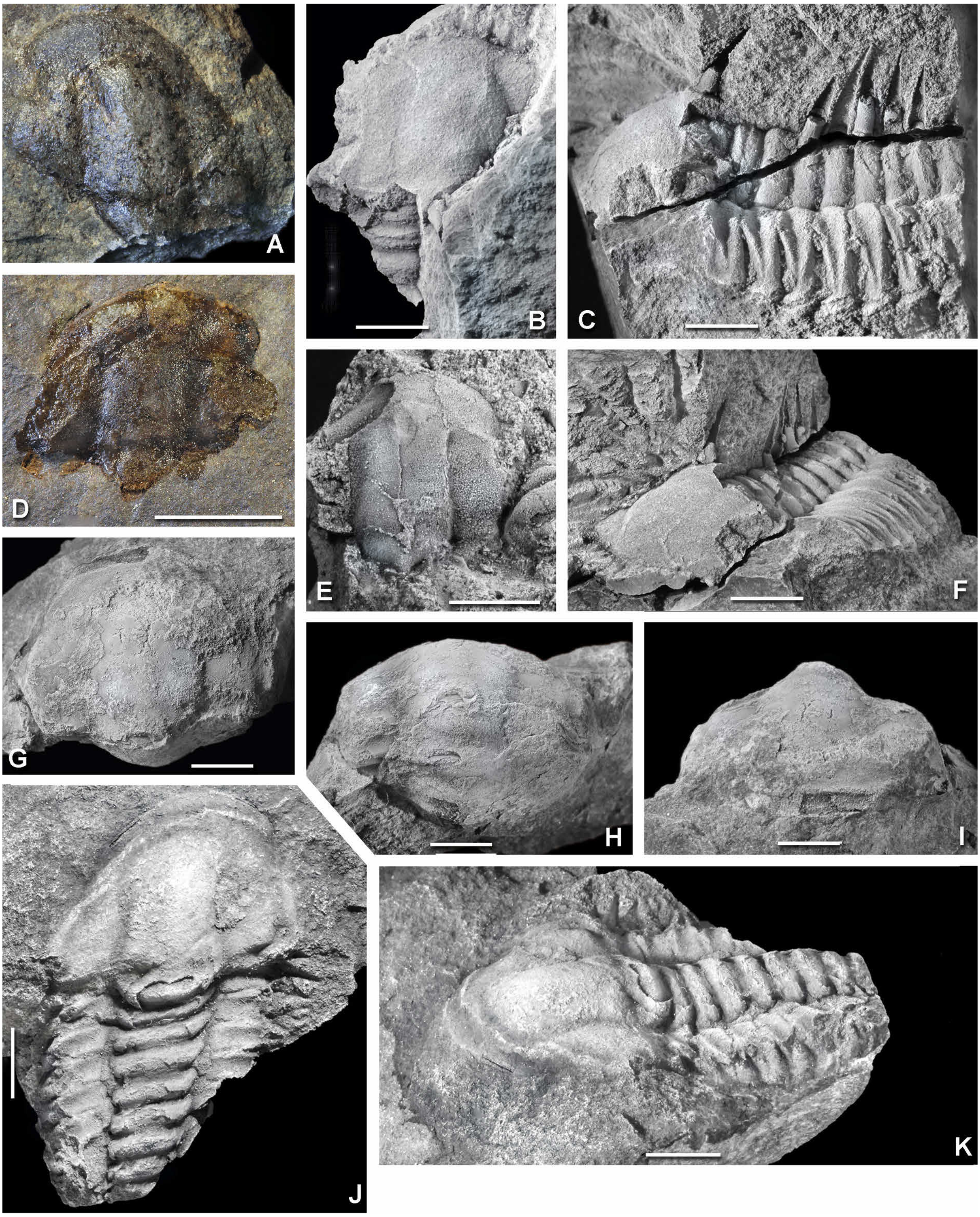

Fig. 25: **A–D, E?, F–K** *Kingaspidoides* sp. cf. *brevifrons* (Hupé, 1953). **A** SSMM 10373, incomplete cranidium, internal mould, obliquely distorted; locality W9; **B, C, F** SMF 96569a, partial dorsal exoskeleton, internal mould, dorsal (B), lateral (C) and oblique anterolateral (F) views; concave flexure of anterior part of the thorax and steeply dorsally directed long axial spines; locality W9; **D** SSMM 10712, small cranidium, composite mould, dorsoventrally compressed; locality W8; **E** MMUW 2017D-053c, partial cranidium tentatively assigned to *Kingaspidoides* sp. cf. *brevifrons*, internal mould; locality W8; **G, H, I** SSMM 10529, cranidium, internal mould, dorsal and oblique anterior views; locality W8; **J, K** MMUW 2017D-326, incomplete dorsal exoskeleton, internal mould, obliquely distorted, dorsal (J) and oblique anterolateral (K) views; locality W9.
Wildenstein Member. Dorsal view if not otherwise noted. Scale bars equal 5 mm.

Thorax only known from three incomplete dorsal exoskeletons. The most informative of these is an incomplete cephalon with a (semi)attached thorax with nine segments partly preserved (Fig. 25B, C, F). Posterior to the inclined cephalon with a conspicuous, dorsally directed occipital spine follow the first post-cephalic segment with slightly reduced pleurae and thoracic segment with pleurae of normal length and morphology, but both without a spine on the axial ring. Axial spines are strongly developed on segments 3–8, similar to the occipital spine, strongly dorsally directed, with growing length from 3 to 5 and slightly decreasing in length in segments 5 through 8. In accordance to the well-developed ability for an advanced inclination is the development of articulation devices such as fulcral sockets and points (Fig. 25C).

Exterior of the cuticle not well preserved in any of the available specimens, appears to have been smooth or covered by minute granules.

Discussion. The specimens from the Wildenstein Member described here closely resemble the specimens of *Kingaspidoides brevifrons* (Hupé, 1953b), the type species of the genus. The latter species is known only from the central Anti-Atlas of Morocco with certainty. The specimens from the Franconian Forest show the same characters, but they are imperfectly preserved, and only a limited number of them is available. In addition, the specimens of *K. brevifrons* from the Anti-Atlas are only known from the *Morocconus notabilis* Biozone, whereas the specimens from the Wildenstein Member come from the *Ornamentaspis frequens* Biozone, which correlates with the slightly younger zone of the Atlas ranges defined by the same trilobite species. Nevertheless, it cannot be ruled out that the specimens from the Wildenstein Member belong to the same species.

The specimens of *Kingaspidoides* cf. *brevifrons* from the Wildenstein Member differ from most of the other species and forms found in the Tannenknock Formation by its glabella having nearly subparallel lateral margins; by its relatively short anterior cephalic area with more or less fused preglabellar field and anterior border; by the fairly uniformly convex sagittal cephalic section except for the occipital spine, which appears to be less strongly developed and more obliquely dorsally directed than in the other species and forms; and by the palpebral areas with are more distinctly ventrally deflected from the axial furrows.

Imperfectly preserved cranidia which appear to represent the same form are shown in Fig. 25A and 25D. They apparently have a longer frontal area and thus a shorter glabella, but this morphology is interpreted as a result of dorsoventral compression which upfolded the anterior part of the cephalon so that the original convexity was lost to some degree.

One specimen is preserved in a somewhat enrolled fashion (Fig. 25H), whereas another partial exoskeleton is preserved in a typical post-mortem configuration. This latter specimen (Fig. 25B, C, F) has a slightly curved, moderately long occipital spine which is fairly distinctly dorsally directed, and similarly strongly developed axial spines on segments 3–8, with growing length from 3 to 5 and slightly decreasing in length in segments 5 through 8. However, spines on thoracic segments 1 and 2 are absent. The sigmoidal curvature of the axis in lateral view with a slightly inflected cephalon is known to be a result of a body movement of entombed individuals as well as a mild post-mortem deformation. The specific development and arrangement of the spines, its length and directions accounts for a protective device against predatorial stress and has been discussed in some detail in Geyer et al. (2020).

Kingaspidoides alberti Geyer, 2017

Fig. 26A, B, C? D–H, I?

v * 2017 *Kingaspidoides alberti* sp. nov. – Geyer: pp. 1, 26, 27, 30–33, 38, 65, 66, 67, figs. 15a–i, j?, i?, l–n, o?, p?, q.

Studied material. See material studied in Geyer (2017). In addition: six cranidia. From locality W8 (cranidium under SSMM 11199); from locality W9 (cranidia under SMF 88207, SMF 88564 and SSMM 12372a); from locality W11/12? (single cranidium under SMF 96557); from locality T2b (cranidium under SSMM 10107).

Material tentatively assigned to Kingaspidoides alberti. From locality W1 (cranidium under MMUW 2017D-509); from locality W19 (two cranidia under MMUW 2017D-923I/II and -924); from locality T2/2a (cranidium under SMF 88560).

Stratigraphy. Galgenberg and Wildenstein members, Tannenknock Formation.

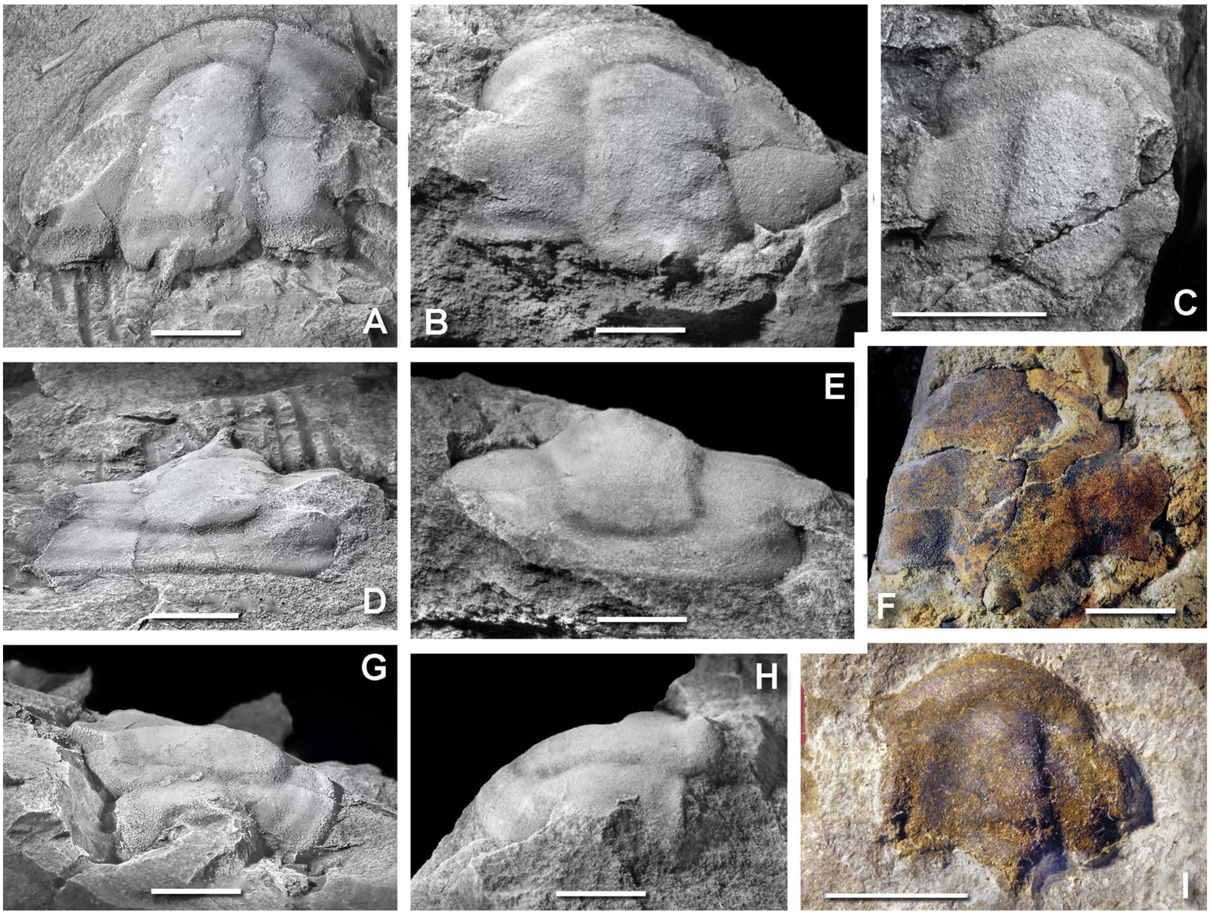

Fig. 26: **A, B, C?, D–H, I?** *Kingaspidoides alberti* Geyer, 2017. **A, D, G** SMF 96557, cranidium, internal mould, dorsal (A), anterior (D) and oblique lateral (G) views; from locality W11/12?; **B, E, H** SSMM 10350, cranidium, internal mould, dorsal (B), anterior (E) and lateral (H) views; from locality W13; **C** MMUW 2017D-509, small incomplete cranidium tentatively assigned to *K. alberti*, internal mould; from locality W1; **F** SSMM 11199, cranidium, internal mould; from locality W8; **I** SMF 88560, small cranidium tentatively assigned to *K. alberti*, internal mould; from locality W9.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 5 mm.

Description and discussion. A further species of *Kingaspidoides* represented in the rocks of the Wildenstein Member is *Kingaspidoides alberti* Geyer, 2017. This species has been described from the Galgenberg Member of the Tannenknock Formation, where it appears to occur more frequently as in the Wildenstein Member. The species is characterised by a slender, tapering glabella of ca. 80–85 percent cephalic length with faintly extended anterolateral corners; faint lateral glabellar furrows which are generally developed as low swales on the exterior surface of the cuticle; a frontal lobe with a slight median angulation; and an occipital ring with strong subterminal spine.

The palpebral lobes are of ca. one-third cephalic length and arranged oblique to axis, with their posterior tips located at about mid-length of L1 to S2 and clearly separated from the posterior border furrow. The frontal area of the cephalon is ventrally deflected in a manner that it continues more-or-less the sagittal convexity of the anterior part of the glabella; the preglabellar field and anterior border are subequal in sagittal breadth, fused on the exterior of the cuticle, but shallow to faint anterior border furrow progressively well-developed toward cephalic suture. Although the specimens assigned to this form are all distinctly dorsoventrally compacted so that the furrows are at least somewhat enhanced, the preglabellar field and anterior border were almost certainly defined by a weakly impressed border furrow in original morphology.

These specimens from the Wildenstein Member differ from all other species/forms of *Kingaspidoides* known from the Franconian Forest by their more strongly tapering glabella and the slender frontal lobe. They resemble some of the specimens of *Kingaspidoides* sp. aff. *destombesi* in most aspects, but still have a longer glabella and, resultantly, a shorter anterior area as well as narrower palpebral areas. This amount of tapering of the glabella with the almost pointed front and the absence of anterolateral corners of the glabella and also the absence of a connection between the glabella and the eye ridges is unique among the hitherto established species of *Kingaspidoides*.

A form with a similarly slender and tapering glabella was discovered in the Galgenberg Member of the Tannenknock Formation and dealt with as *Kingaspidoides*? sp. nov. A (see Geyer 2017). This form is also imperfectly known and is distinctly distinguished by it less developed sagittal and transverse convexity, with the palpebral areas being almost level for most part.

Kingaspidoides alberti appears to represent a species with a relatively short existence. It seems to be distributed only in the upper part of the Galgenberg Member and in the lower part of the Wildenstein Member.

Kingaspidoides sp. A

Fig. 27

Studied material. Ca. 10 cranidia. From locality W8 (cranidium under SSMM 10429); from locality W10? (cranidia under SMF 90020, probably also SMF 90018); from locality W17 (cranidia under MMUW 2017D-791, -795, -804, -807 and -808a). Librigena tentatively assigned to *Kingaspidoides* sp. A from locality W17 under MMUW 2017D-793.

Stratigraphy. Wildenstein Member, Tannenknock Formation.

Description and discussion. A few imperfectly preserved cranidia from sample locality W8, W10(?) and W17 represent a species of *Kingaspidoides* characterised by a cranidium with a relatively slender, slightly forward tapering glabella with a low curvature of the frontal lobe's anterior margin, and with a distinctly convex, slightly inflated frontal area of the cephalon, and with the preglabellar field fused with the anterior border. The palpebral lobes are somewhat upturned and gently curved, with the posterior ends reaching to the mid-level of L1. The occipital ring is extended into a moderately large subterminal spine.

The specimens collected from the Wildenstein Member with this morphology resemble some specimens of *Kingaspidoides frankenwaldensis*, but are distinguished by a longer and slightly narrower glabella (compare with the width of the palpebral areas!), the apparently more elevated frontal area and the slightly longer palpebral lobes. The cranidia also resemble some belonging to *Cambrosaurura usitata* (Geyer, 1990b), but differ in having the front of the glabella less clearly separated from the frontal area of the cephalon and longer palpebral lobes.

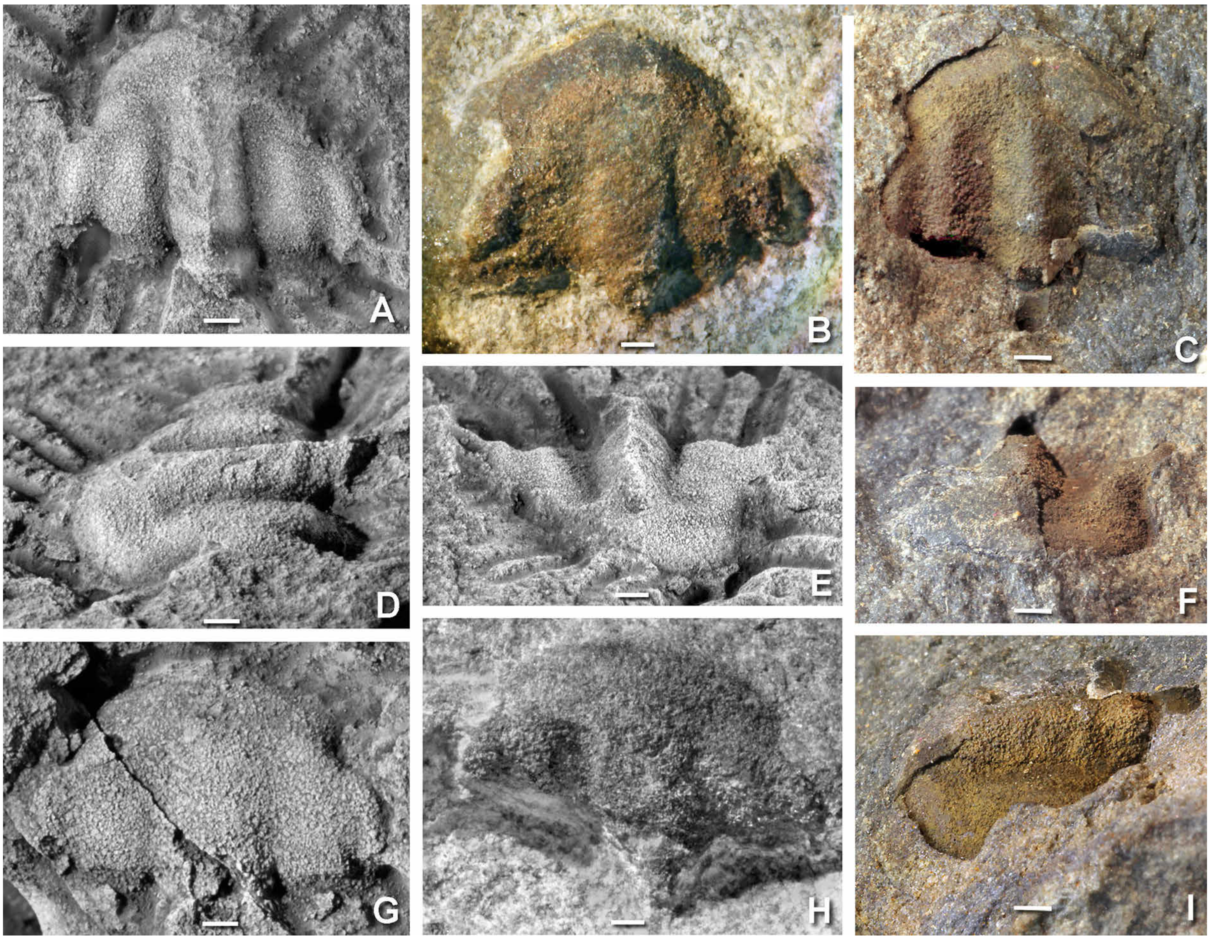

Fig. 27: *Kingaspidoides* sp. A. **A, D, E** MMUW 2017D-807, cranidium, internal mould, laterally compressed, dorsal (A), oblique lateral (D) and oblique anterior (E) views; from locality W17; **B** SMF 88207, cranidium, internal mould; from locality W10?; **C, F, I** SSMM 10429, cranidium, internal mould with remnants of the recrystallised cuticle on right half, dorsal (C), oblique anterior (F) and lateral (I) views; from locality W8; **G** MMUW 2017D-804a, obliquely cracked cranidium, internal mould; from locality W17; **H** SMF 90020, cranidium, internal mould with rests of the cuticle in posterior part; from locality W10?.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 1 mm.

Kingaspidoides? sp. B

Fig. 28

Studied material. Eight (possibly 13) cranidia and a librigena possibly belonging to the same form; from locality W8 (six cranidia under MMUW 2017D-753, -754, SSMM 11321a, SSMM 11328, SSMM 11329 and SSMM 11334); from locality W15d (cranidium under MMMUW 2017D-888a); from locality T2 (single cranidium under SSMM 10276). Tentatively assigned to *Kingaspidoides*? sp. B: three cranidia, one librigena; from locality W8 (MMUW 2017D-674e, SSMM 12420b) and from locality W9 (MMUW-2017D-767-I, -767-II).

Stratigraphy. All specimens from Wildenstein Member, Tannenknock Formation.

Description. The six fairly complete cranidia from locality W8 are preserved as internal moulds, a specimen with a remnant, recrystallised cuticle, an external mould, and a largely exfoliated cranidium with a mineralised cuticle, respectively, showing characters which distinguish them from all other species of *Kingaspidoides* found in the studied strata of the Franconian Forest. The specimens are cranidia with a typical kingaspidoid morphology presenting a relatively low and broad glabella with slightly indented lateral margins and a relatively strongly developed occipital spine, which is obliquely dorsally directed.

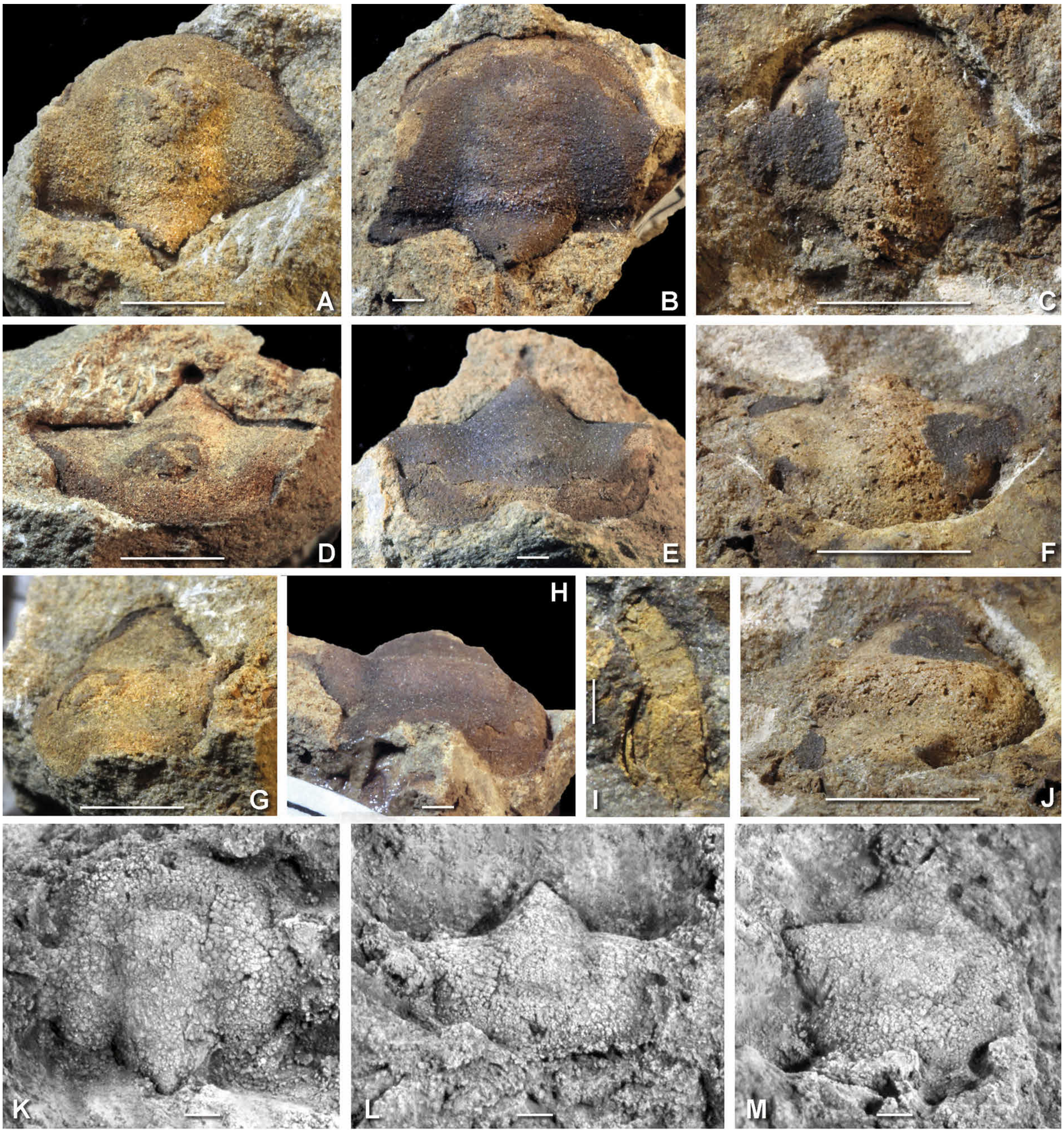

Fig. 28: *Kingaspidoides*? sp. B. **A, D, G** SSMM 11321, cranidium, internal mould, dorsal (A), anterior (D) and oblique lateral (G) views; from locality W8; **B, E, H** SSMM 11328, cranidium, internal mould with mineral coat originating from the degraded cuticle, dorsal (B), anterior (E) and oblique lateral (H) views; from locality W8; **C, F, J** SSMM 11334, cranidium, internal mould with mineral coat on left gena and palpebral lobe, dorsal (C), oblique anterior (F) and oblique anterior (J) views; from locality W8; **I** SSMM 12420b, librigena, internal mould; from locality W8; **K–M** MMUW 2017D-753, cranidium, internal mould, dorsal (K), oblique anterior (L) and oblique lateral (M) views; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 5 mm in A, C, D, F, G and J, 1 mm in B, E, H and I.

The glabella has a relatively low convexity in sagittal profile, but proceeds into a ventrally sloping frontal area. Particularly characteristic is that the palpebral areas are without a pronounced convexity in transverse profile and fairly horizontally arranged, defined by low axial and palpebral furrows so that the palpebral lobes are only faintly below the level of the centre of the palpebral areas (Fig. 28D, E, F);

accordingly, the palpebral areas have a slightly stronger convexity in exsagittal section than in transverse profile. The palpebral lobes are relatively long and distinctly curved in dorsal view. The preglabellar field and anterior border are fused.

Discussion. The sketched morphology is not typical for *Kingaspidoides* and also not for the closely related genera. Two species formally described to date with a similar morphology of glabella, anterior cephalic regions and palpebral area are known. One was introduced under the name *Ornamentaspis*? *personata* Geyer, 1990b. The similarity is best seen in a cranidium shown in Geyer (1990b, pl. 34, fig. 15a–c), which also illustrates differences in the preservation of internal moulds and specimens with the exterior preserved. That species has been tentatively attributed to *Ornamentaspis* based on characters discussed in Geyer (1990b), but the author also emphasised important differences so that the assignment has been claimed as a placeholder for future better generic assignments. Despite the similarities, the specimens from the Franconian Forest certainly do not represent the same species as indicated by the much larger, triangular occipital ring with the strong spine, the broader glabella, the longer palpebral lobes and other characters in the Franconian Forest specimen.

The second species with a somewhat similar morphology is *Kingaspidoides meieri* Geyer, 2017 from the Galgenberg Member of the Tannenknock Formation. That species has a similar transverse profile of the cranidium with pronouncedly elevated palpebral lobes united with the palpebral areas to a near-platform topography and a similar outline of the slightly tapering glabella. Nevertheless, *K. meieri* differs in having more strongly developed palpebral furrows, markedly dropping preocular areas and a broader (sag., exsag.) anterior part of the cephalon, and a distinctly more pronounced, strong occipital spine. However, it appears plausible that *Kingaspidoides*? sp. B may be a direct descendant of *K. meieri*.

More and better preserved material of this form from the Wildenstein Member is needed to allow a confident assessment of the generic identity and to permit a formal taxonomic assignment.

Kingaspidoides? sp. C

Fig. 29

Studied material. Two cranidia, SSMM 10561 and SMSN 73643-1a.

Localities and strata. From W8 (SSMM 10561) and probably from locality W14a (SMSN 75643-1a); Wildenstein Member, Tannenknock Formation.

Description and discussion. A single, fairly complete cranidium most probably from locality W14a presents characters that distinguish it from all typical species of *Kingaspidoides*. The particular characters include a cranidium with relatively low convexity of the glabella in sagittal profile, but a ventrally sloping frontal area; palpebral areas that are convex, but fairly horizontally arranged in transverse section and defined by distinct axial and palpebral furrows so that the palpebral lobes are only faintly below the level of the centre of the palpebral areas (Fig. 29B); a distinctly tapering glabella with a subacute frontal lobe; a triangular occipital ring with only a terminal cusp, but without a distinct thorn or spine; relatively long and prominent palpebral lobes; preglabellar field and anterior border being fused. A second specimen from locality W8 shares the features with the specimen described above, but its palpebral lobes are not entirely visible. Interestingly, it has a striking imprint of another skeletal fossil, which almost certainly was an ossicle of an unknown echinoderm (Fig. 29D).

This morphology is atypical for *Kingaspidoides* so that the questionable assignment of the form just attempts to underline similarities. A somewhat similar form has been described (Geyer 2017) from the Galgenberg Member under the name *Kingaspidoides* sp. nov. A, but the only known specimen of that form has a distinctly shorter glabella, a less ventrally deflected anterior area of the cephalon and a slender terminal occipital spine.

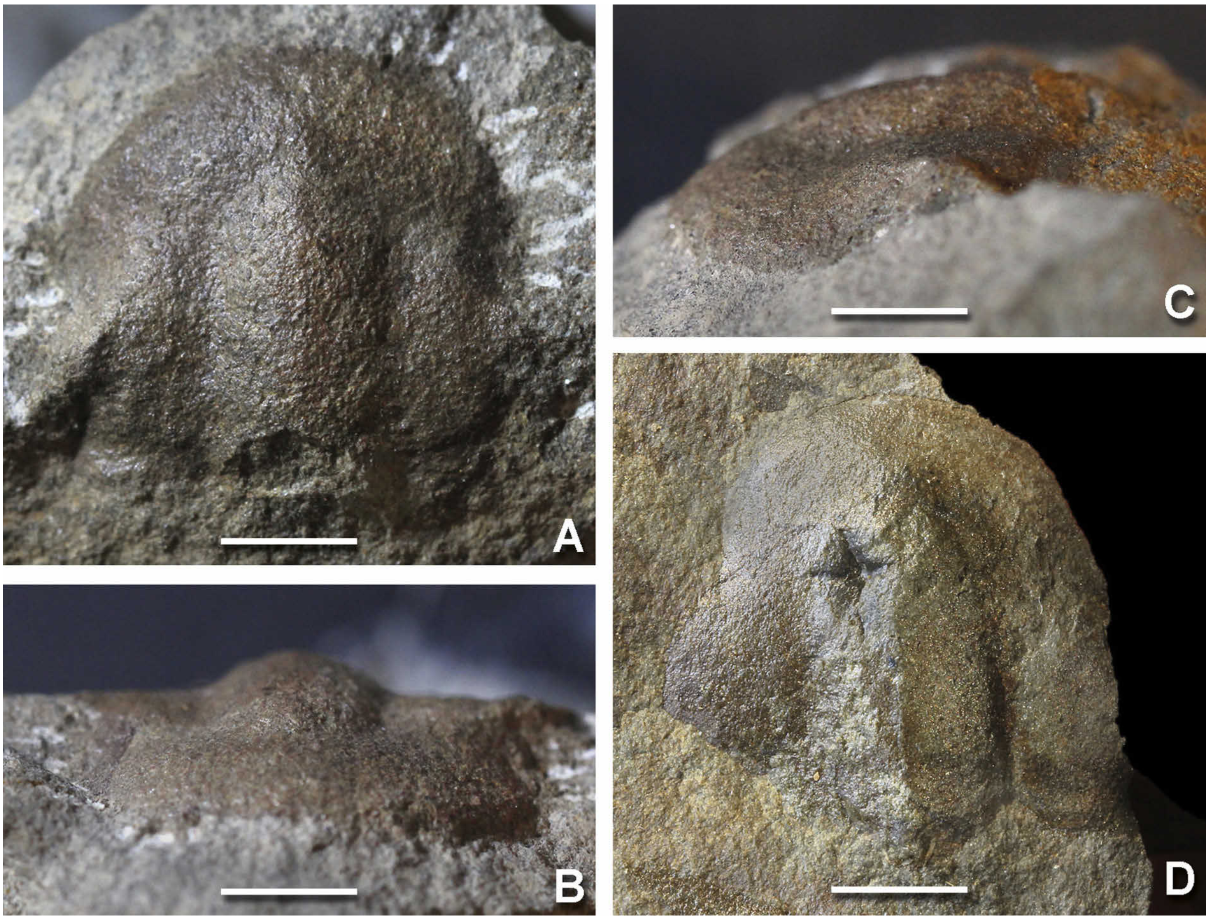

Fig. 29: *Kingaspidoides*? sp. C. **A–C** SMSN 73643-1a, cranidium, internal mould, dorsal (A), anterior (B) and lateral (C) views; most probably from locality W14a; **D** SSMM 10561, cranidium, internal mould, with imprint of echinoderm ossicle on glabella, dorsal view; from locality W8.
Both specimens from Wildenstein Member, Tannenknock Formation. Scale bars equal 5 mm.

More and better preserved material of this form from the Wildenstein Member is needed to allow a confident assessment of the generic identity and also to permit a formal taxonomic assignment.

Kingaspidoides? sp. D

Fig. 30

Studied material, localities and strata. Three cranidia, MMUW 2017D-577, MMUW 2017D-580a and MMUW 2017D-580b. From locality W9b of the Wildenstein slice, Franconian Forest region; Wildenstein Member, Tannenknock Formation. Possibly belonging to the same form: MMUW 2017D-1038I/II, from locality W6b.

Description and discussion. Another not yet established species is represented in the studied samples by at least three cranidia, all from samples collected at locality W9b, which differ slightly in lithology from the typical rocks found at W8 and W9. The best preserved of these cranidia (Fig. 30A–C) shows features which differ from the typical species of *Kingaspidoides*, particularly in the tapering glabella with a relatively prominent convexity and a transverse profile which shows the curvature being only slightly reduced in the peak region. The glabella is defined from the occipital ring by a marked occipital furrow, and the occipital ring extends into a short and broad terminal thorn. The frontal lobe is relatively narrow. The fixigenae are slightly convex, but do not slope markedly towards the palpebral lobes so that the palpebral furrows lie only slightly below the axial furrows. The palpebral lobes are moderately long and located in a relatively posterior position, which the posterior tips at approximately the posterior margin of L1. The anterior border and the preglabellar field are subequal in sag. width and separated by a faint border furrow. However, the anterior border fades in width abaxially from the sagittal line (Fig. 30D), which is also atypical for *Kingaspidoides*.

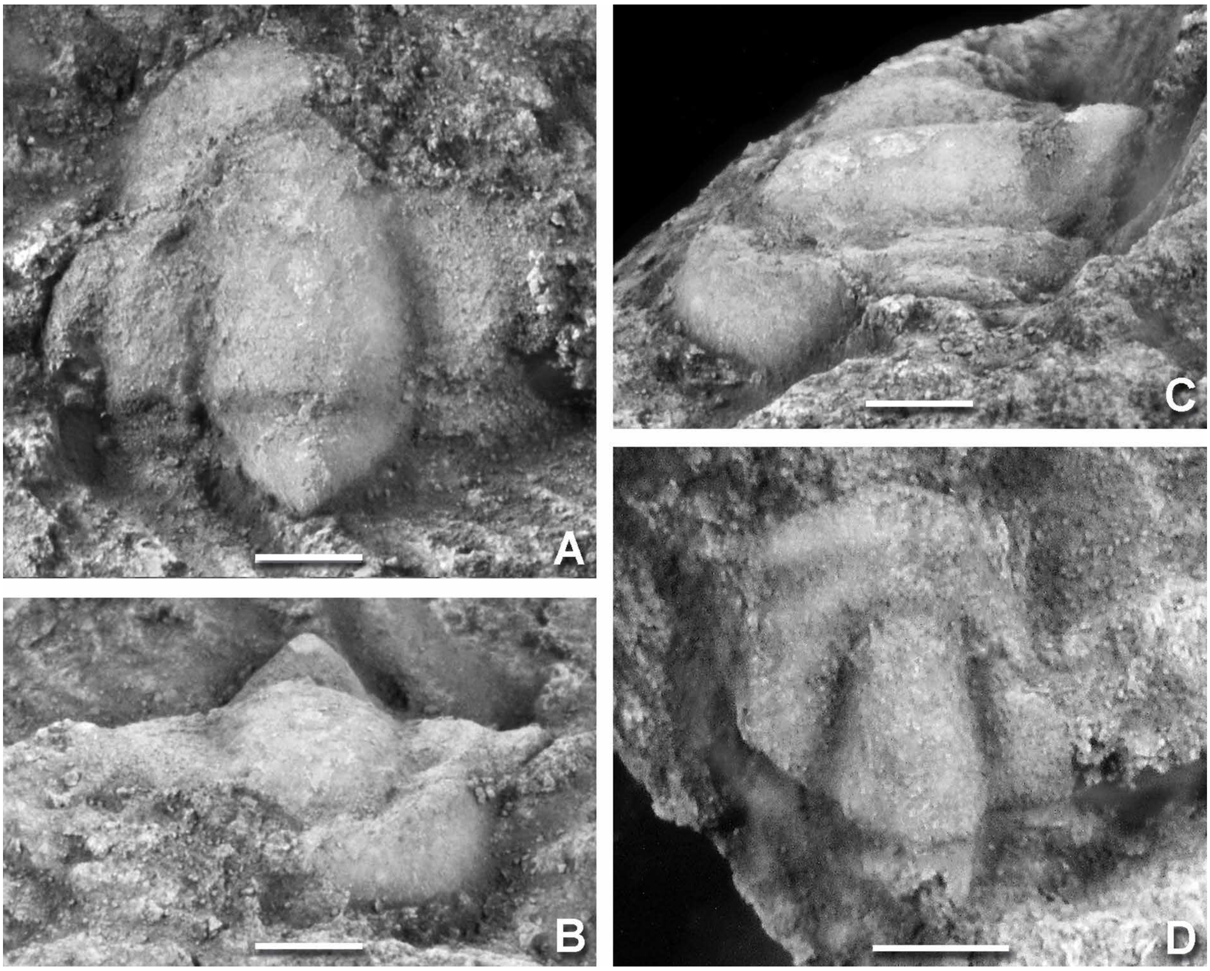

Fig. 30: *Kingaspidoides*? sp. D. **A–C** MMUW 2017D-577, cranidium, dorsal (A), anterior (B) and oblique lateral (C) views; **D** MMUW 2017D-580, small partial cranidium, dorsal view.
Both specimens from locality W9b, Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

Based on the visible characters, the form belongs to the *Kingaspis*–*Kingaspidoides* clade, but according to conventional taxonomic procedures would have to be dealt with as a separate genus. Nevertheless, more and better preserved material appears to be necessary to confidently characterise such a taxon.

Kingaspidoides spp. indeterminate

Fig. 31

Material. Ca. 25 librigenae, ca. five partial thoraces, ca. 40 pleural fragments, ca. four pygidia. In repository: Librigenae from locality W8: MMUW 2017D-257d and MMUW 2017D-676; from locality W8a: MMUW-2017D-863; from locality W13e: MMUW 2017D-487. Partial thorax from locality W8: MMUW 2017D-245c. Thoracic pleural fragments from locality W8: MMUW-2017D-119, MMUW 2017D-184, MMUW 2017D-311c, MMUW 2017D-361a; from locality W9: MMUW 2017D-769; from locality W18a: MMUW 2017D-548. All from Wildenstein-Member, Tannenknock Formation.

Discussion. The fact that even cranidia of *Kingaspidoides* are often difficult to determine confidently to a species with sufficient accuracy already suggests that isolated sclerites of the rest of the exoskeleton are usually impossible to assign to species with sufficient accuracy. Fig. 31 illustrates typical sclerites and fragments of sclerites that belong to species/forms of *Kingaspidoides*, but cannot be determined to species. Nevertheless, most of them offer features that suggests differences in librigenal, thoracic and pygidial morphology so that findings of well-preserved complete exoskeletons would assist in the recognition of specific characters.

Fig. 31: Indeterminate species of *Kingaspidoides* and forms tentatively assigned to *Kingaspidoides*. **A** *Kingaspidoides*? sp. indet., MMUW 2017D-062b, incomplete thoracic segment; from locality W8; **B, E** *Kingaspidoides* sp. indet., MMUW 2017D-538, thoracic pleura, internal mould, dorsal (B) and posterior (E) views; from locality W18e; **C** *Kingaspidoides* sp. indet., MMUW 2017D-184, thoracic pleural tip, internal mould; from locality W8; **D, G** *Kingaspidoides* sp. indet., SSMM 11030, partial thorax, dorsal (D) and oblique lateral (G) views; from locality W8; **F** *Kingaspidoides* sp. indet., MMUW 2017D-058, thoracic pleural tip; from locality W8; **H** *Kingaspidoides* sp. indet., MMUW 2017D-755, thoracic pleural tip; from locality W8; **I** *Kingaspidoides* sp. indet., MMUW 2017D-487, incomplete librigena; from locality W8; **J** *Kingaspidoides* sp. indet., SSMM 11376b, pygidium; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 5 mm in A, 1 mm in B–J.

Plenty of mostly incomplete librigenae are known, mostly separated from locality W8. They differ in several aspects, for example (a) the length and curvature along the ocular suture; (b) the length and curvature of the anterior branch of the facial suture; (c) the width of the ocular platform; (d) the course of the lateral margin; and (e) the length and strength of the genal spine.

A limited transport of trilobite carcasses in the Tannenknock Formation and at least temporary currents that let to different degrees of winnowing are responsible for rare preservation of articulated dorsal exoskeletons of *Kingaspidoides*. However, several incomplete thoraces composed of several articulated segments are known, and they indicate that considerable morphological differences existed between species. Those differences include: (a) the size and convexity of the axial ring, particularly the length of the axial spine or node and the expression of a faint swelling adjacent to the axial furrow which indicates the attachment of ventral muscles (see Fig. 25C, 25J, 31A, 31D); (b) the depth and length of the pleural furrow (see Fig. 25C, 31A–C, F, H); (c) the shape of the pleural spines, i.e. its length, curvature and definition from the rest of the pleura (e.g., Fig. 25C, 31A, C, F); and (d) the presence and development of articulating devices (Fig. 25C, 31A, B, C, F, H). Pleural tips are mostly extended into terminal thorns or short spines in the species of *Kingaspidoides*, which are moderately posterolaterally directed, but moderately long spines with a distinct curvature of its posterior margin are known as well (Fig. 31A). A differential development of distal parts of the pleurae is a functional adaptation to different amounts of inclination of adjacent thoracic segments, resulting in more-or-less distinctly developed pleural facets, which allow overlapping of the pleura (Fig. 31B, C, F, G). Similarly, a short process can be seen at the anterior margins of the pleurae which terminates the abaxial part of the pleural facet and acts as an articulation device (Fig. 31A, C).

Despite of the probably more than one-thousand specimens of *Kingaspidoides* examined from samples of the Moroccan Atlas ranges and the Franconian Forest, only very few pygidia have been identified, which can be primarily ascribed to their small size and a slightly inclined position between somewhat backward directed pleurae of the terminal thoracic segments. A typical morphology has been described in Cederström et al. (2022) and summarised above. A further example of a pygidium attributed to *Kingaspidoides* is shown in Fig. 31J. This pygidium (less than two mm in length) has a slightly subtrapezoidal outline and is mainly made up by a very large gently convex axis composed of a well-defined axial ring and a roughly subrectangular rest of the axis without any recognisable subdivision and a slightly curved posterior margin, with the posterior end being close to the posterior margin of the pygidium. The pleural areas are narrow, without a separation to a lateral border. The posterior border is a low and very thin thread.

Genus *Cambrosaurura* Geyer *in* Cederström, Geyer, Ahlberg, Nilsson & Ahlgren, 2022

Type species. Ornamentaspis usitata Geyer, 1990b; from the lower traditional 'Middle' Cambrian (now probably lowest Wuliuan Stage) Jbel Wawrmast Formation of the Jbel Ougnate region, eastern Anti-Atlas, Morocco; by original designation.

Remarks. The recently erected genus *Cambrosaurura* was known from several sclerites since the 1950s, which had been neglected or assigned to *Ornamentaspis*. Findings of complete or near-complete exoskeletons elucidated the characteristic morphology of the posterior thorax and pygidium, with the mostly conspicuous reduction of the pleurae in the terminal part of the thorax and a collispathulate-type pygidium. See further discussions on the genus above under Ellipsocephalidae and in Cederström et al. (2022).

Cambrosaurura sp. indet.

Fig. 32A?, B?, C

Material. Incomplete articulated thorax with attached pygidium, MMUW 2017D-520b, probably from locality W14c. Two isolated librigenae (MMUW 207D-005) from locality W8 possibly belong to *Cambrosaurura* as well.

Discussion. A single incomplete thorax with attached pygidium from the Wildenstein Member certainly represents a species of *Cambrosaurura* and extends the geographic range of the genus to Central Europe. Most characteristic is the collispathulate pygidium with a blade-shaped outlined with abaxially swinging anterolateral parts. The well-defined axis with one transverse ring differs slightly from the other species/forms of the genus known to date. In addition, the reduction of the pleurae at the very back thoracic segments is less dramatic than in *Cambrosaurura robusta* Geyer in Cederström et al., 2022 or *C. bommeli* Geyer in Cederström et al., 2022, but comparable to that in *C. usitata* (Geyer, 1990b), the type species of the genus. It appears that only the segment articulating to the pygidium has very strongly reduced pleura, and the segment anterior to it has slightly reduced and distinctly rearward directed pleura, whereas the segments anterior to them show small pleurae but with a relatively "ordinary" morphology (Fig. 32C). Accordingly, the posterior part of the thorax and the pygidium will have had a less pronounced ability to incline ventrally and act as a functional unit.

A particular morphologic feature can be seen in at least two librigena, which possibly belong to *Cambrosaurura* as well based on the similarity with specimens known from the Moroccan Anti-Atlas: In those specimens the ocular platform is slightly depressed and generates a shallow concavity adaxially of the lateral border, but a low flange borders the ocular suture (Fig. 32A, B).

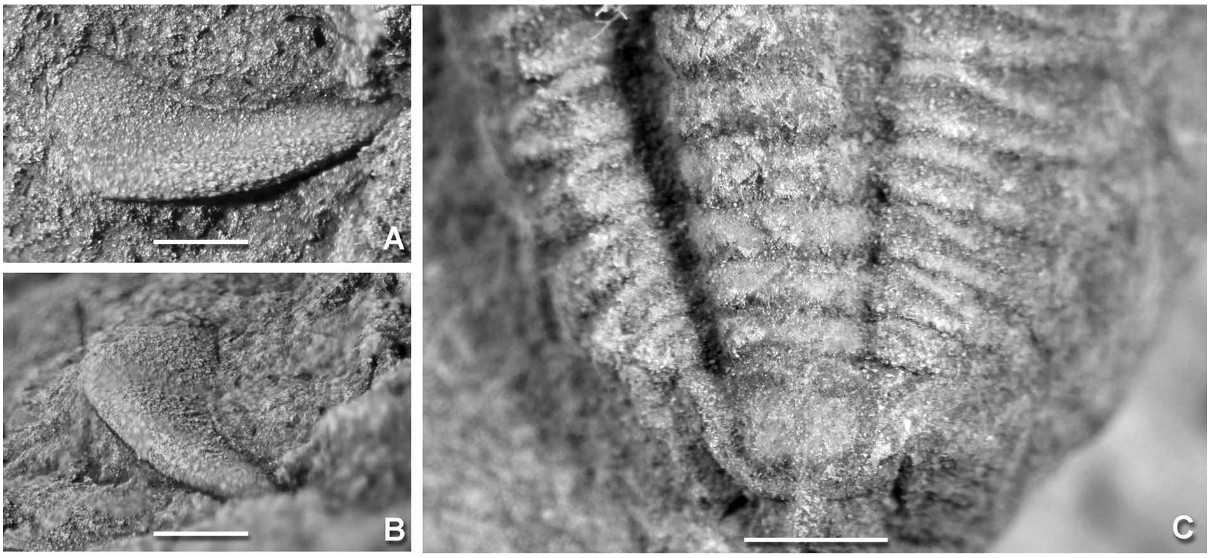

Fig. 32: **A, B** *Cambrosaurura*? sp. indet., MMUW 2017D-005, incomplete librigena, oblique anterolateral (A) and oblique anterior views showing slightly concave, poorly defined ocular platform and very low flange at ocular suture; from locality W8.
C *Cambrosaurura* sp. indet., MMUW 2017D-520b, incomplete thorax with attached pygidium, internal mould, dorsal view; probably from locality W14.
Both specimens from Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

Genus *Latikingaspis* Geyer, 1990b

Type species. Kingaspis (Kingaspis) alatus Hupé, 1953a (termed "*Kingaspis (Kingaspidoides) alatus*" in the figure caption of plate XI of Hupé's initial publication); from the *Morocconus notabilis* Zone of the Moroccan Atlas ranges; by original designation.

Discussion. Latikingaspis Geyer, 1990b is characterised by considerably broadened palpebral areas and axial furrows when compared with other ellipsocephaline genera. The maximum convexity of the palpebral areas lies closer to the palpebral lobes than to the glabella. The eye ridges are therefore separated from the anterolateral corners of the glabella by a fairly broad (although shallow) depression. The glabella of *Latikingaspis* is narrow in respect to the maximum width of the cranidium than in any other ellipsocephaloid genus. It tapers gently forward. The palpebral lobes are elevated and often slightly raised above the level of the palpebral areas and characteristically extended abaxially beyond the level of the palpebral furrow. They are usually located in a relatively posterior position compared with other genera, e.g., *Kingaspidoides*.

These characters unambiguously separate *Latikingaspis* from all other genera of the kingaspidoid genera except for *Kymataspis* Geyer, 1990b, which is differentiated by a narrow (tr.) and sunken preglabellar field.

Latikingaspis **sp. cf.** ***alatus*** **(Hupé, 1953a)**

Fig. 33A, B, C?, D, E, F?, G–I, J?, K?, L, M?

v 2010 *Latikingaspis* cf. *alatus* – Geyer: p. 81.
v 2017 *Latikingaspis* sp. aff. *alatus* (Hupé, 1953) – Geyer: pp. 5, 39–41, 67, fig. 18a, b, d, e?, f.

Studied material. Ca. 6 cranidia. In repository: from locality W11 (three cranidia under SMF 90017, SMF 90019 and SMF 90020); from locality W17 (MMUW 2017D-800 and MMUW 2017D-819).

Material tentatively assigned to *Latikingaspis* sp. aff. *alatus*: from locality W8 (cranidium under SSMM 11047); from locality W7b (cranidium under MMUW 2017D-589); from locality W15b (cranidium under MMUW 2017D-635); from locality T2b (cranidia under SMF 88560 and SMF 88564).

Description. Cranidium subquadratic to transversely subrectangular in outline, with strongly abaxially extended palpebral lobes. Sagittal convexity relatively minor, only anterior part of the cephalon moderately deflected (Fig. 33I). Transverse profile shows platform-like parts, with a low to moderately convex glabella which is only slightly more elevated than the palpebral areas and the palpebral lobes the most elevated point of which lies above the level of the palpebral areas (Fig. 33E, J).

Glabella slender, of ca. 80 percent cephalic length, maximum cephalic width across L1 less than 40 percent cranidial width across centre of palpebral lobes; glabella with straight or slightly indented lateral margins, slightly tapering forward; frontal lobe at anterolateral corners of ca. 80–85 percent tr. width across L1; three or four pairs of lateral glabellar furrows visible, S1 and S2 gently curved backward from near axial furrow, disconnected medially; S3 short, almost normal to axis or directed slightly forward from near axial furrow; S4 usually not recognisable, developed as a short transverse incision fairly close to S3 (Fig. 33C). Occipital furrow relatively broad (sag. and exsag.), almost straight, with distinctly shallower middle section. Occipital ring triangular in dorsal view, with distinctly tapering lateral parts, extended into a robust, long, obliquely upward directed terminal spine (Fig. 33B).

Palpebral areas transversely of almost two-thirds maximum glabellar width across palpebral lobes, fixigenae posterior to eye ridges exsagittally of ca. 45 percent cephalic length adjacent to axial furrows; maximum convexity short distance from palpebral furrows; poorly separated from axial furrow.

Palpebral lobe exsag. of ca. 35 percent cephalic length and transversely up to ca. 40 percent maximum glabellar width; transversely convex, with most elevated part in the distal third, with moderate curvature, anterior end at approximately the level of L4, in a slightly more adaxial position than posterior end; posterior end blunt, at about mid-length of L1, almost reaching to the posterior border furrow. Palpebral furrow a broad, shallow depression, clearly shallower in its anterior third than in the posterior two-thirds; extends anteriorly into a broad, poorly defined depression that separates palpebral lobe from eye ridge. Eye ridge developed on the exterior surface of the cuticle as a low, poorly defined elongate swell oblique to axis.

Preglabellar field moderately broad (sag.), slightly convex, developed as a low elongate pad which is more-or-less fused with the anterior border to form an increasingly ventrally sloping anterior platform;

grades laterally into the preocular areas with an indistinct slope which is usually enhanced in dorso-ventrally compacted specimens. Anterior border relatively narrow to moderately broad (sag.), only close to the suture defined by a shallow and faint border furrow.

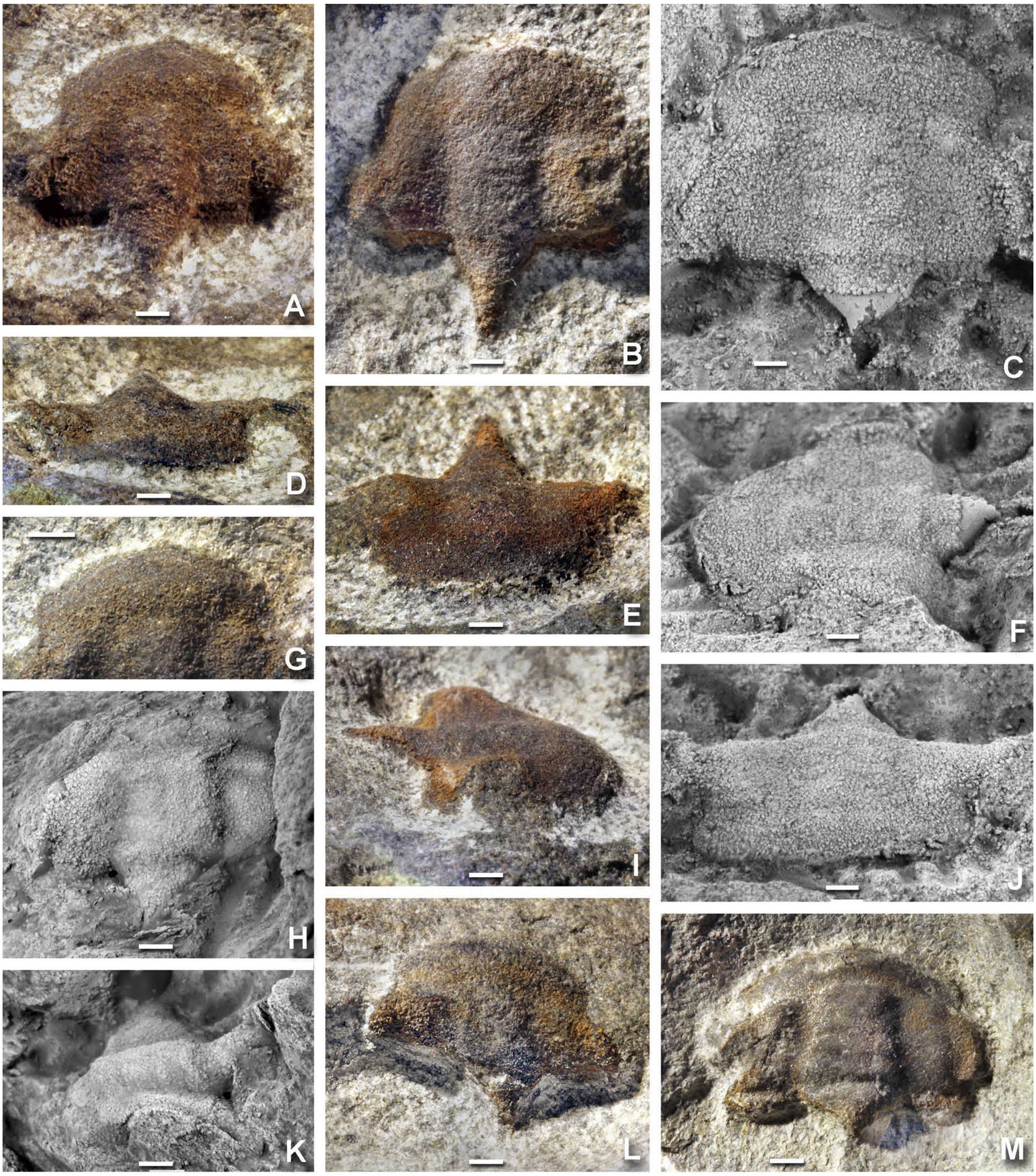

Fig. 33: **A, B, C?, D, E, F?, G–I, J?, K?, L, M?** *Latikingaspis* sp. aff. *alatus* (Hupé, 1953). **A, D, G** SMF 90017, cranidium, composite mould, dorsal view (A), anterior view (D) and magnified view of anterior part of cranidium; most probably from locality W11; **B, E, I** SMF 90019, cranidium, internal mould with limonitised remnants of the cuticle, dorsal (B), anterior (E) and lateral (I) views; from locality W11; **C, F, J** MMUW 2017D-819, cranidium, internal mould, dorsal (C), oblique lateral (F) and oblique anterior (J) views; from locality W17; **H, K** MMUW 2017D-800, cranidium, internal mould, dorsal (H) and oblique lateral (K) views; from locality W17; **L** SMF 90020, cranidium, internal mould; from locality W11; **M** SMF 88564, longitudinally compressed cranidium, internal mould; from locality T2b.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 1 mm.

Posterior border close to the axial furrow a low, poorly defined and narrow (exsag.) lobe, growing in exsag. width abaxially. Posterior border furrow a shallow, moderately broad (exsag.) depression, marked by a conspicuous posterior escarpment formed by the drop of the posterior margin of the fixigena.

Anterior branches of the suture more-or-less straight and parallel to the sagittal axis. Posterior branches directed obliquely abaxially from the posterior ends of the ocular suture.

Librigena not known with certainty. Hypostome, thorax and pygidium unknown.

Discussion. This form is known from both the Galgenberg and Wildenstein members of the Tannenknock Formation and has already been characterised in Geyer (2017). The available material is limited, and all known specimens are incomplete cranidia with often poor preservation of details. Five specimens from the (supposedly) upper part of the Galgenberg Member have been studied and described in Geyer (2017), and the additional material from the Wildenstein Member does not differ significantly and is therefore covered herein under the same informal assignment.

Characteristic for the genus *Latikingaspis* is the relief of the cranidium with sagittal and transverse profiles that distinctly differ from other similar and coeval ellipsocephaloid genera such as *Kingaspidoides*, *Ornamentaspis*, *Cambrunicornia* or *Ellipsostrenua*: The convexity on the sagittal line is relatively minor in *Latikingaspis*, with the anterior area only moderately deflected as perfectly indicated in the cranidium in Fig. 33I. More important, the cranidium shows a transverse profile in which the glabella has a low to moderately convexity and is barely or only slightly more elevated than the palpebral areas so that the cephalon is almost a platform-like plate. The palpebral lobes are distinctly convex and slightly upturned from the palpebral furrow so that the most elevated part lies above the level of the palpebral areas (Fig. 33E, J).

As for the Galgenberg specimens, all characters visible are similar to or almost identical with those seen in the specimens of *Latikingaspis alatus* (Hupé, 1953a), the type species of the genus, inclusive of the conspicuously long, occipital spine (Fig. 33B, I). This species is hitherto known only from the Anti-Atlas and High Atlas regions of southern Morocco, where it appears to occur exclusively in the *Morocconus notabilis* Zone. Therefore, the occurrence in the *Ornamentaspis frequens* Zone of the Wildenstein Member extends the range slightly upward. As far as the characters can be estimated with some precision, the specimens from the Franconian Forest differ only in slightly narrower palpebral areas.

Nomenclatural remark. The gender of *Latikingaspis* has been chosen by Hupé (1953a) as male, without an obvious and objective mistake. Therefore, the suggestion to change the name of *Latikingaspis alatus* to *Latikingaspis alata* has no legal base.

Latikingaspis tenuis n. sp.

Fig. 34

Holotype (and only present specimen). SSMM 12401, cranidium.

LSID. urn:lsid:zoobank.org:act:4FF045A8-0F97-4363-9897-3B26AEB75F4E

Type locality and type stratum. Sample locality W9 in the Wildenstein slice near Wildenstein. Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Etymology. From the Latin *tenuis*, thin, slender; a reference to the shape of the glabella and the general width of the cranidium.

Diagnosis. Species of *Latikingaspis* with a cranidial length of ca. 90 percent cranidial width; glabella with a slight broadened L1; fixigenae of moderate width (tr.); preglabellar field fused with anterior border, considerably convex in sagittal profile; surface finely granulose.

Description. Cranidium with glabella moderately elevated, well separated from palpebral areas by distinct but poorly defined, broad axial furrows; most elevated parts of the palpebral areas close to the shallow palpebral furrows (Fig. 34B). Sagittal profile shows a poorly convex glabella and step-like lowered anterior area, which is distinctly convex (Fig. 34C).

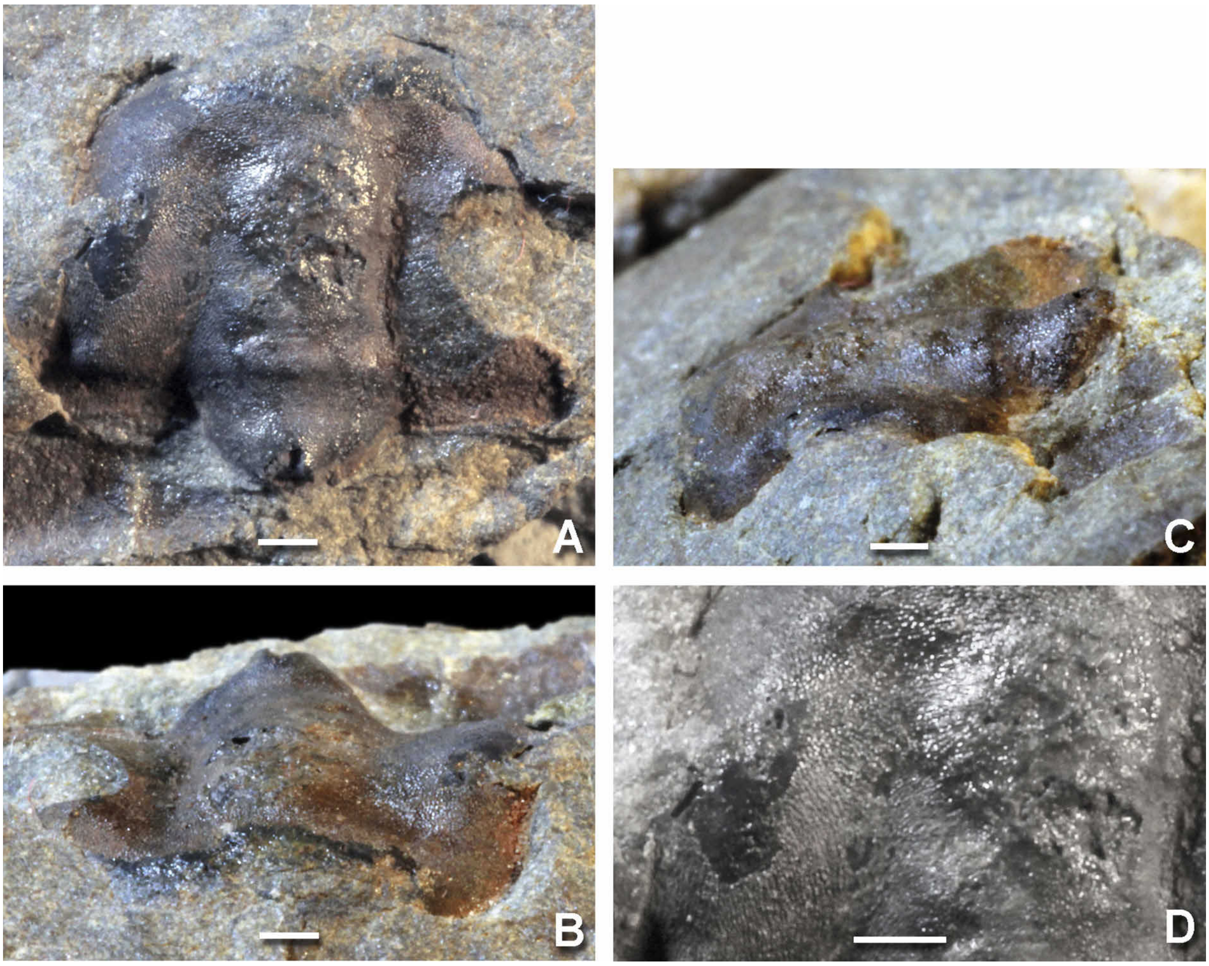

Fig. 34: *Latikingaspis tenuis* n. sp. SSMM 12401, holotype, cranidium, composite mould, dorsal view (A), slightly oblique anterior view (B), oblique lateral view (C) and magnified view of anterior part of cranidium and left anterior part of the cranidium showing Bertillon-type patterns on the palpebral area (D); from sampling locality W9.
Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

Glabella of slightly less than 80 percent cephalic length, maximum width of axis across L1 ca. 40 percent cranidial width across palpebral lobes; glabella with subparallel to faintly convergent lateral margins anterior to S1, L1 slightly extended when compared with L2 and L3, frontal lobe at anterolateral corners of ca. two-thirds transverse width across L1; glabella is well elevated above axial furrows and above the preglabellar field, slopes down to axial furrows without a distinct drop. Anterior margin of frontal lobe with low curvature or possibly a faint kink medially; three pairs of shallow lateral glabellar furrows recognisable; S1 commences near axial furrows (in dorsal view), rearward directed from its origin, faintly bifurcated adaxially, but broadly disconnected medially; S2 slightly shorter than S1, rearward directed from its origin near the axial furrow and slightly curved; S3 not precisely preserved in the specimen, apparently transversely or even slightly forward directed, short. Occipital furrow distinct, broad, almost straight throughout. Occipital ring subtriangular in outline in dorsal view, almost completely fading laterally, but well extended on sagittal line, of ca. 20 percent cephalic length (sag.), extended into a fairly strong, moderately long subterminal spine, which is distinctly dorsally directed in lateral profile.

Palpebral areas transversely of slightly less than 20 percent maximum glabellar width across midlength of the palpebral lobes, fixigenae posterior to eye ridges exsagittally of ca. 40–45 percent cephalic length along axial furrows; slightly convex in transverse profile, ascending from axial furrows to its most prominent point close to the axial furrow; poorly defined from axial furrow on the exterior of the cuticle.

Palpebral lobe exsag. of ca. 30 percent cephalic length and tr. ca. 6 percent maximum cranidial width; transversely convex, subequal in transverse width, slightly curved, anterior end approximately at the level of S3, in a faintly more adaxial position than posterior end; posterior end at mid-level of L1, some distance from posterior border furrows. Palpebral furrow a very shallow depression on the exterior of the cuticle.

Eye ridge on the exterior of the cuticle a low, poorly defined ridge slightly oblique to axis, poorly demarcated from the palpebral area, but defined by a narrow furrow from preocular area; appears to extend anteriorly into a low ridge that traverse the axial furrow.

Preglabellar field fused with anterior border to form a distinctly convex (sag.) area of slightly less than 20 percent cephalic length in dorsal view; grades laterally into preocular areas without any recognisable distinction. Anterior border obsolescent on the sagittal line, but recognisable laterally in front of the preocular areas when defined by a poorly developed border furrow.

Posterior border a moderately broad (exsag.), moderately convex, transverse to sagittal axis in the proximal part, slightly posteriorly reclined towards facial suture. Posterior border furrow a moderately deep, moderately broad (exsag.) groove.

Anterior branches of the suture more-or-less straight, slightly diverging forward from the anterior end of the ocular suture, swing adaxially in a gentle curve slightly anterior to the border furrow. Posterior branches strongly diverging from the posterior ends of the ocular suture.

Other parts of the dorsal exoskeleton unknown.

Exterior of the cuticle covered with fine granules, which turn into delicate wavy ridges that approach Bertillon pattern on the preglabellar field and on the palpebral areas (Fig. 35D) as well as near-terrace ridges on the occipital ring.

Discussion. The single cranidium from locality W9 represents a hitherto unknown species, which offers the characteristics of *Latikingaspis*: It has fairly broad palpebral areas, which ascend from the poorly defined but well developed and broad axial furrows abaxially to its highest elevation close to the palpebral furrows; the glabella is slender, but distinctly convex; the occipital ring is subtriangular in outline and terminates into an obliquely dorsally directed spine; and the anterior part of the cephalon is formed by a fused to semifused unit composed of preglabellar field and anterior border, both being distinctly convex in sagittal direction. Given the broad spectrum of ellipsocephalid trilobites from the *Kingaspidoides* clade, one might assume that the differences between *Kingaspidoides* and *Latikingaspis* could be considered as “fluent”. However, the quite characteristic morphology of the occipital ring in *Latikingaspis tenuis* n. sp. reconfirms the separation of the two genera: As in *L. alatus*, it has the unique morphology of a sub-bulbous element crowned by an obviously long and distinctly dorsally directed spine; a configuration which is unknown from any of the species of *Kingaspidoides*.

The species differs from *Latikingaspis alatus* Hupé, 1953, the type species of the genus, is clearly narrower palpebral areas and less wing-like extended palpebral lobes, as well as the broadened L1 and a most probably shorter occipital spine.

The prosopon on the cranidium and the shape of the glabella offer some similarities with *Ornamentaspis* so that the species may be interpreted on a first glance as an unusually preserved, slightly deformed specimen of *Ornamentaspis frequens*. However, the occipital ring as well as the palpebral areas and the preglabellar region clearly distinguish *Latikingaspis tenuis* n. sp. from that species and falsify this possible assumption.

Genus *Ornamentaspis* Geyer, 1990b

Type species. Ornamentaspis frequens Geyer, 1990b; from Agdzian *Ornmentaspis frequens* Zone of the Moroccan High Atlas ranges; by original designation.

Ornamentaspis frequens Geyer, 1990b

Figs. 35, 36

Studied material. Ca. 170 confidently identifiable cranidia and ca. 30 cranidia tentatively assigned to the same form, ca. 8 (15) librigenae, numerous fragments of thoracic segments. In repository: From sample locality W1 (two cranidia under MMUW 2017D-510, -512); from locality W6 (cranidia under MMUW 2017D-908a and -910); from locality W7 (cranidium under MMUW 2017D-536); from locality W8 (ca. 100 cranidia under MMUW 2017D-019, -074, -085, -099b, -129, -130, -132b, -137, -138, -141c, -146aI, -149, -152, -165, -166, -172, -177c, -181a, -181b, -183e, -228b, -237a, -247b, -248, -249a, -255, -274a, -279a, -279b, -284a, -301, -302d, -303c, -304a, -305e, -311d, -352, -354, -357, -364, -376, -496, -603b, -646, -646-I, -646-II, -649a, -649b, -650, -654, 655, 656, -674a, -707b, -714, -719a, -723, -725a, -738, -740, -857, -1005, -1016a, -1020, -1021b, SSMM 10401a, 10409a, 10410, 10411, 10412a, 10413, 10414, 10415, 10434, 10438, 10451b, 10459, 10476c, 11006, 11030b, 11021, 11074, 11075, 11077, 11086, 11087, 11111b, 11115, 11116a, 11120b, 11122a, 11139, 11180, 11191, 11203, 11205, 11206a, 11321b, 11502d, 11626d, 11628d, 11642b, 11642c, 11643, 11644a; five librigenae under MMUW 2017D-131, -181b, -361b, -649c, -751; incomplete thoracic segments under MMUW 2017D-724a, -724b, -725b, and SSMM 11644c); from locality W9 (two cranidia under MMUW 2017D-653, SSMM 10372b); from W11 or W12: MMUW 2015A-454 (single cranidium); most probably from locality W11 (three cranidia under MMUW 2015A-560, -561-I and -561-II, -563); from locality W12 (cranidium under MMUW 2015A-584); from locality W13a (8 cranidia under MMUW 2015A-401, -402, -403, -404, -406, SSMM 10222, 10229 and 10245); from W13b (two cranidia under MMUW 2017D-421I/II and -554); from locality W13e (7 cranidia under MMUW 2017D-440a, -442b, -446, -453, -458, -463 and -468; thoracic pleura under MMUW 2017D-490); from locality W14 (cranidium under MMUW 2017D-520); from locality W14b (cranidium under SSMM 10192); from locality W15 (two cranidia under SSMM 10119 and 10120); from locality W15a (9 cranidia under MMUW 2017D-682b, -684, -685, -686, -687, -690, 692, -694 and -695); from locality W16a (8 cranidia under MMUW 2017D-822, -824, -826, -829, -849-I/-II, -850-I/-II, 851 and -852); from locality W17 (five cranidia under MMUW 2017D-788, -796, -798, -810 and -1029); from locality W19b (cranidium under MMUW 2017D-935e); and from locality T2/T2a (single cranidium under SMF 90101). Specimens of samples W1 (in part), W7, W8, W13b, W13e and W14 from Wildenstein Member, specimens from sample localities W1 (in part), W11, W12, W13a, W14a and T2/2a from Galgenberg Member, Tannenknock Formation.

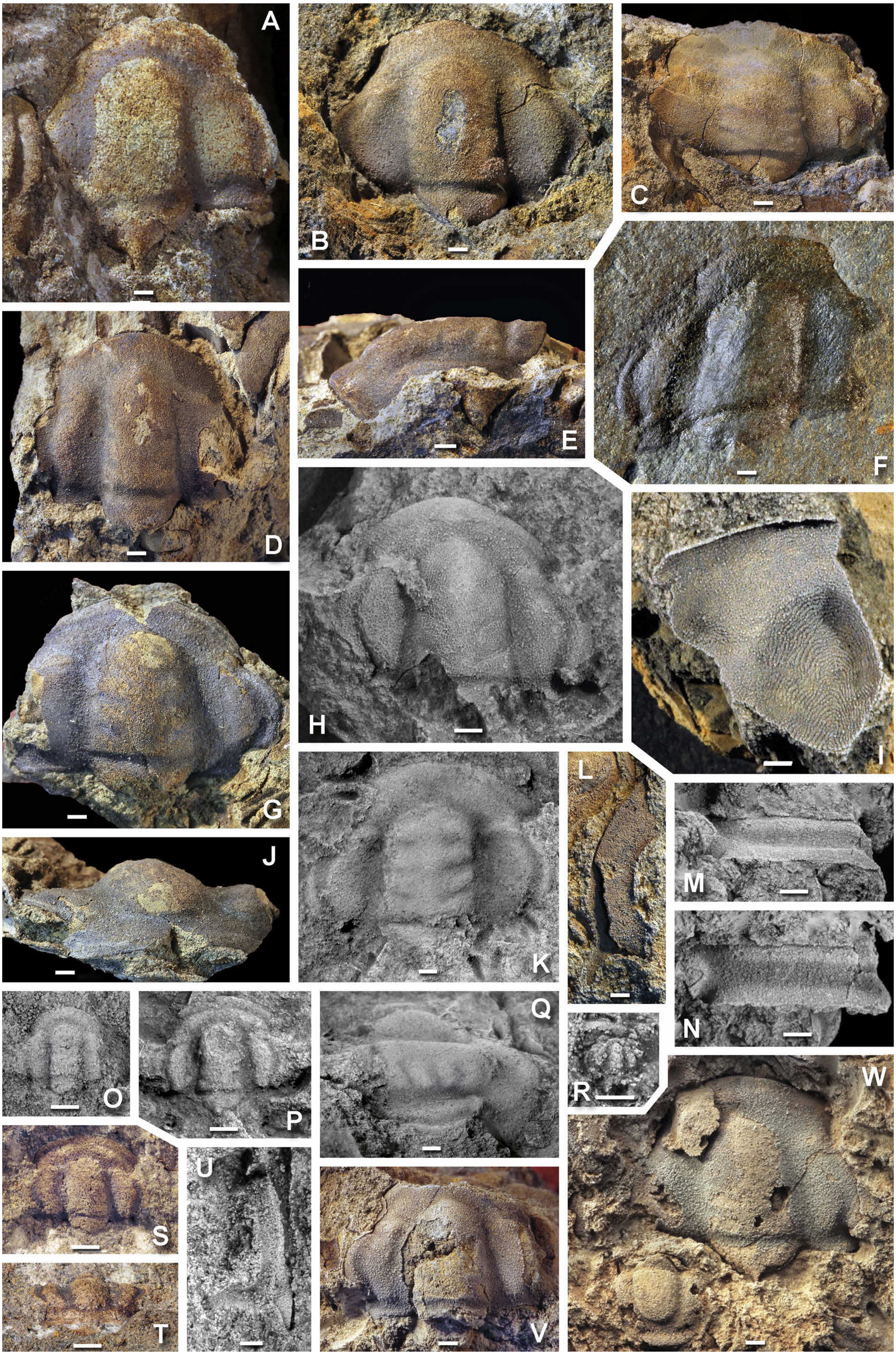
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Fig. 35: *Ornamentaspis frequens* Geyer, 1990. **A** SSMM 11205, cranidium, internal mould; from locality W8; **B** SSMM 10401, cranidium, internal mould; from locality W8; **C** SSMM 10476c, cranidium, internal mould; from locality W8; **D, E** SSMM 10409a, cranidium, internal mould, dorsal (D) and lateral (E) views; from locality W8; **F** SSMM 10222, cranidium, internal mould; from locality W13a; **G, J** SSMM 10459, cranidium, internal mould, dorsal (G) and anterior (J) views; from locality W8; **H** MMUW 2017D-019-I, cranidium, exterior; from locality W8; **I** MMUW 2017D-723, fragment of cranidium, external mould, ventral view showing Bertillon pattern; from locality W8; **K, Q** MMUW 2017D-849, cranidium, internal mould, dorsal (K) and oblique lateral (Q) views; from locality W16a; **L** SSMM 11129b, librigena, internal mould with slight indentation of lateral margin near the base of the genal spine; from locality W8; **M, N** MMUW 2017D-490, partial pleura from most probably middle part of thorax, internal mould, oblique posterior (M) and dorsal (N) views; from locality W13e; **O** MMUW 2017D-553, cranidium of immature individual, internal mould; from locality W13b; **P** MMUW 2017D-137, cranidium of immature individual, internal mould; from locality W8; **R** MMUW 2017D-423, meraspid cranidium, internal mould; from locality W13; **S, T** SSMM 11206a, small cranidium, internal mould, dorsal and oblique anterior views; from locality W8; **U** MMUW 2017D-131, small librigena, internal mould; from locality W8; **V** SSMM 11006, incomplete cranidium, middle part with glabella exfoliated; from locality W8; **W** SSMM 11111b, cranidium (in central part) together with small cranidium of *Cambrophatictor meieri* n. sp. (in lower left part; SSMM 11111c), internal mould; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 1 mm.

Material tentatively assigned to *Ornamentaspis frequens*: from locality W1 (immature cranidium under MMUW 2015A-531); from locality W1a (cranidium under MMUW 2017D-973); from locality W7b (four cranidia under MMUW 2017D-591, 704, 705 and 706); from locality W8 (four cranidia under SSMM 10449, 10494c, 10515 and MMUW 2017D-026b; librigena under MMUW 2017D-255d and -302a; fragments of thoracic segments under MMUW 2017D-020b, -146bI, -268, -275a, -302c and -756); from sample locality W11 (two cranidia under MMUW 2017D-893 and -896); from locality W12 (librigena under SMF 88697); from locality near W13a (cranidium under MMUW 2017D-904); from locality W13b (juvenile cranidia under MMUW 2017D-416f and MMUW 2017D-423, librigena under MMUW 2017D-416d); from locality W13e (cranidium under MMUW 2017D-457); from locality W14a (6 cranidia under MMUW 2015A-238a, -362, -363, -364, -366 and -367); from locality W15a (cranidia under MMUW 2017D-697 and -699); from locality W16a/b (two cranidia under MMUW 2017D-925 and -926); from locality W18 (librigena under MMUW 2017D-541a; fragments of thoracic segments under MMUW 2017D-547c); from locality T2/T2a (3 cranidia under SMF 90043, SMF 90053 and SMF 90060).

Description. Cranidium with glabella moderately elevated, well separated from palpebral areas by distinct axial furrows. Sagittal profile shows moderately convex glabella and step-like lowered anterior area (Fig. 35E).

Glabella in adult individuals of 80–85 percent (n=9) cephalic length, maximum width of axis at occipital ring 40–45 percent (n=9) cranidial width across palpebral lobes; glabella with subparallel, faintly concave lateral margins, frontal lobe at anterolateral corners of 90–95 percent (n=9) transverse width across occipital ring; the glabella is fairly well elevated above the axial furrows and above the preglabellar field on the exterior of the cuticle and slopes down to axial furrows without a distinct drop, whereas on internal moulds the glabella forms a minor step-like raise above the axial furrows and the preglabellar field.

Anterior margin of frontal lobe with a distinct kink that creates a triangular shape in dorsal view; with three pairs of well-developed lateral glabellar furrows, S1 to S3 shallow depressions on the cuticle's exterior, but well visible although progressively faint toward the anterior on internal moulds; S1 commences at axial furrows, distinctly curves rearward from its origin adjacent to the axial furrow, moderately long and broadly disconnected medially; S2 slightly shorter than S1, slightly curved and weakly rearward directed from near axial furrow; S3 commences close to the axial furrow, short, slightly curved and slightly backward directed from near axial furrows, distinctly less impressed than S1 and S2; S4 occasionally indicated as a narrow, slit-like indentation marked solely by the absence of the prosopon on the exterior of the cuticle close to the frontal margin, obliquely forward directed. Occipital furrow distinct, with almost straight median section and faintly obliquely directed lateral sections. Occipital ring moderately broad, variably of 14–18 percent (n=9) cephalic length (sag.), extended into a moderately strong, moderately long subterminal spine, which is obliquely backwardly directed in lateral profile.

Palpebral areas transversely of slightly less than 20 percent (n=9) maximum glabellar width across mid-length of the palpebral lobes, fixigenae posterior to eye ridges exsagittally of ca. 45 percent (n=8) cephalic length along axial furrows; slightly convex in transverse profile on internal moulds and on the exterior surface of the cuticle, but occasionally with the tendency to show a diagonal depression when affected by a mild dorsoventral compaction (Fig. 35B); poorly defined from axial furrow on the exterior of the cuticle, but fairly well demarcated on internal moulds; most elevated part of the genal sector lies closer to the palpebral furrows than to the axial furrow.

Palpebral lobe in adult individuals exsag. of 39–47 percent (n=9) cephalic length and tr. ca. 6–8 percent maximum cranidial width; transversely convex and subequal in transverse width, distinctly curved, with anterior end at the level of S3 or slightly anterior to it, in a faintly more adaxial position than posterior end; posterior end curved, at level of posterior part of L1, closely adjacent to or at posterior border furrows. Palpebral furrow a shallow depression on the exterior surface, but moderately indented and a well recognisable groove on internal moulds; extends anteriorly into a shallow, poorly defined depression that separates palpebral lobe from eye ridge. Eye ridge developed on the exterior of the cuticle as a low ridge or an extended elongate uplift, transverse or faintly oblique to axis, poorly demarcated from the palpebral area on the exterior of the cuticle, but defined by a narrow furrow on internal moulds; occasionally developed as an indistinctly bifid ridge on internal moulds (Fig. 35D, G); extends anteriorly into one or two low, delicate threads that traverse the axial furrows and merge with the anterolateral corners of the glabella; occasionally grading into a parafrontal band which is nearly fused with the frontal lobe of the glabella (Fig. 35K).

Preglabellar field of ca. 10 percent cephalic length, slightly convex (sag. and exsag.); occasionally flat or slightly sunken medially (Fig. 35G, H), rarely with a faint plectrum on the sagittal line in internal moulds which grades into a swelling at the posterior margin of the anterior border (Fig. 35H, K); it grades laterally into preocular areas without any recognisable distinction. Anterior border on sag. line of ca. 10 percent cephalic length in dorsal view of undeformed specimens, of subequal sag. and exsag. breadth throughout. Border furrow shallow and frequently faint but always recognisable, slightly better developed toward suture; better visible on internal moulds.

Posterior border a moderately broad (exsag.), slightly to moderately convex, transverse to sagittal axis in the proximal part, slightly reduced in width and slightly curved posterior to palpebral lobes. Posterior border furrow a moderately deep, moderately broad (exsag.) groove.

Anterior branches of the suture more-or-less straight, often slightly diverging forward from the anterior end of the ocular suture, swing adaxially in a gentle curve slightly anterior to the border furrow. Posterior branches strongly diverging from posterior ends of the ocular suture, describe a distinct curve to meet posterior margin of cephalon posterior to the maximum abaxial level of the palpebral lobes.

Librigena incompletely known, relatively narrow (tr.), with a relatively short to moderately long, slender genal spine of clearly less than half length of anterior part. Genal spine with a narrow base and directly obliquely abaxially so that it defines a gentle curve from the posterior margin to the adaxial rim of the genal spine. Lateral margin gently and evenly curved, with a distinctly concave curvature at the base of the genal spine. Palpebral section of the suture large. Librigenal field very narrow, merely formed by a minute strip along the vertical face at the suture. Lateral border furrow obsolescent. Lateral border weakly convex in tr. profile, with a moderately broad doublure.

Hypostome unknown.

Thorax only known from fragments of thoracic segments. Axial rings distinctly convex in tr. and sag. profile, with a narrow, relatively shallow axial furrow close to the anterior margin. Pleurae moderately long (tr.), nearly straight for most part in dorsal view and transverse profile, with moderately broad to broad, well developed pleural furrow, which is straight and in an almost constant position relative to the pleura, slightly anterior to the midline; distal part of the pleura steeply ventrally deflected with a notable kink into the pleural spine section, with articulating devices developed at the bend.

Pygidium unknown. However, an isolated pygidium which may belong to *Ornamentaspis frequens* is known from locality W8 (Fig. 35B). This pygidium (an internal mould) is characterised by a broad axis consisting of one clearly defined ring and a subquadrate, relatively highly elevated main part with slightly rounded posterolateral corners. Its posterior end lies only short distance from the posterior pygidial margin. The pleural areas are narrow, with a moderately defined lateral border recognisable for approximately two-third exsagittal length.

Exterior of the cuticle covered generally with small granules except for furrows, but glabella and palpebral areas develop a conspicuous prosopon of bertillon pattern (Fig. 35I, 36A, M, N) the preservation of which various considerably depending on the lithofacies of the embedding rock. The palpebral areas are rarely covered with honeycomb-type polygons (Fig. 36L).

Ontogeny. A number of immature cranidia assigned to *Ornamentaspis frequens* have been found. They feature considerable morphological changes during ontogeny. Although not all of these specimens can be unequivocally identified as individuals of *Ornamentaspis frequens*, selected specimens record a reliable history of the modifications with allometric growths in the usual range that is known from ellipsocephaloid trilobite species. Particularly informative examples are included in the study of Scandinavian species of *Ellipsostrenua* (see Cederström et al. 2022).

The smallest specimen from the Wildenstein Member which almost certainly belongs to *Ornamentaspis frequens* has a length of 1.2 mm (Fig. 35R) and is characterised by well incised axial and palpebral furrows, a tapering, subacute glabella and a conspicuously short anterior area. Indeed, the glabella progressively shortens in respect to the total cephalic length during ontogeny, whereas the palpebral areas become increasingly wider. Synchronously, the palpebral lobes are slightly shorter in larger specimens, but also of a more slender shape and have a stronger curvature compared with the smaller specimens. In addition, a relatively well-incised anterior border furrow is developed in small cranidia, but this seems to be visible only on internal mould whereas the anterior border furrow is faint to obsolescent on the exterior of the cuticle (compare Fig. 35P, S with Fig. 35O).

Discussion. The specimens from the Franconian Forest described here fall into the variability of *Ornamentaspis frequens* Geyer, 1990b from the High Atlas Mountains of Morocco. Despite of minor differences (such as a slightly larger size of the fully grown specimens and a more strongly developed kink at the anterior margin of the frontal lobe), the Moroccan material cannot be distinguished by any significant character from the species of the Wildenstein Member, and even the presence of a faint plectrum, the slightly variable breadth of the preglabellar field or the differential development of a para-frontal band is visible in the specimens of the Anti-Atlas and the Franconian Forest region. It is noteworthy that the Moroccan specimens of *O. frequens* are known almost exclusively in a different rock facies (with a considerable amount of tuffitic/volcanoclastic particles in a sort of marlstone that makes it look like a sandstone) which may contribute to some slight differences of the trilobite's preservation. It should be emphasised that this is the first confident record of the species outside the Atlas region, which is particularly noteworthy because *O. frequens* has been used as an index fossil for the eponymous biozone for the middle Agdzian, which appears to correspond with the base of the Wuliuan Stage and Miaolingian Series and thus would be an important level for international/intercontinental/ global correlation.

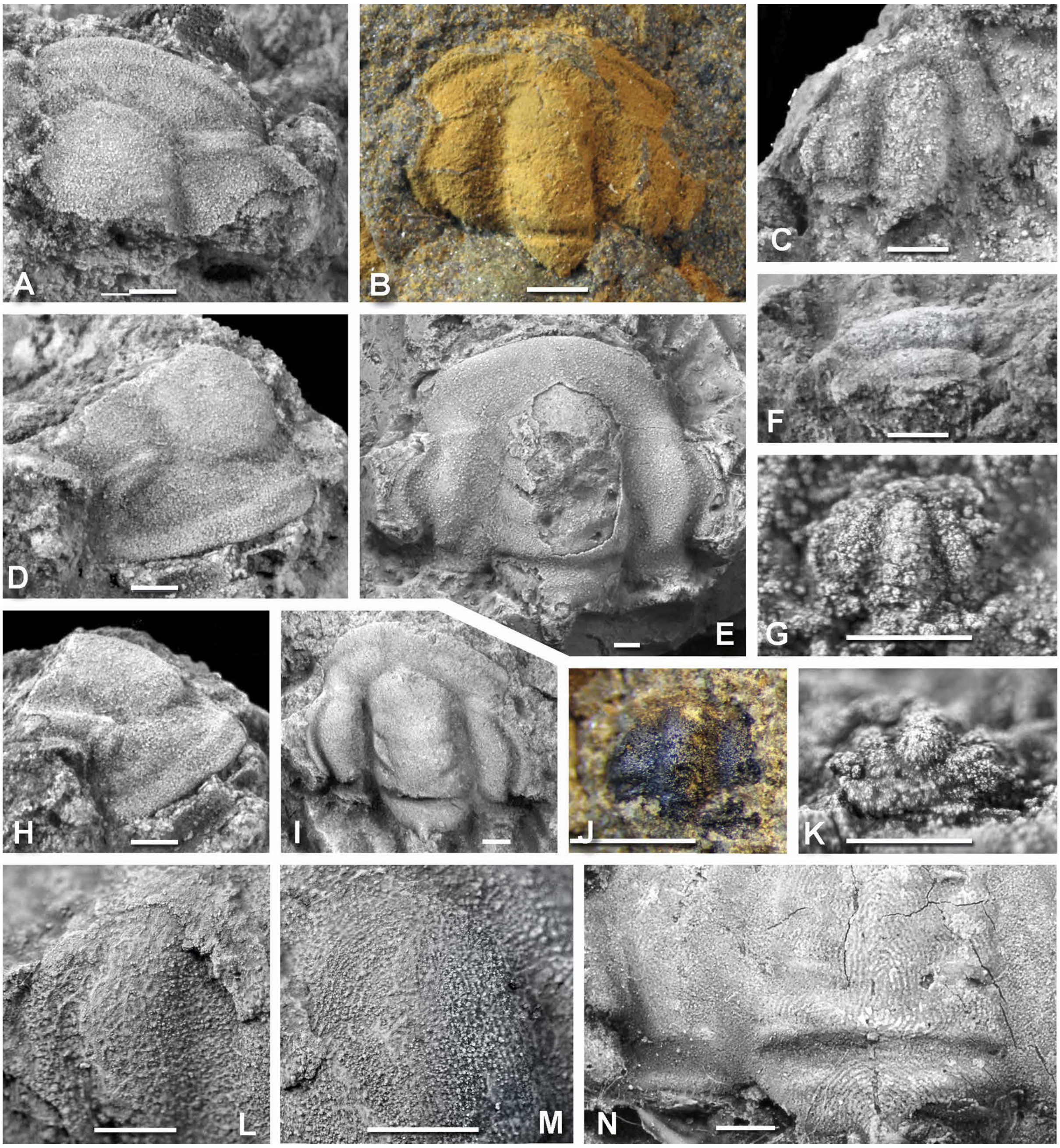

Fig. 36: *Ornamentaspis frequens* Geyer, 1990. **A, D, H** MMUW 2017D-364, partial cranidium, internal mould, dorsal (A), oblique anterolateral (D) and lateral (H) views; from locality W8; **B** SSMM 10434, small cranidium; from locality W8; **C, F** MMUW 2017D-566, cranidium of immature individual, dorsal (C) and lateral (F) views; from locality W9b; **E** MMUW 2017D-129, cranidium, exterior of cuticle with eroded glabella; from locality W8; **G, K** MMUW 2017D-423, cranidium, internal mould, dorsal (G) and anterior (K) views; from locality W8; **I** MMUW 2017D-402I, cranidium, internal mould, slightly distorted; from locality W13b; **J** SSMM 10815, cranidium of immature individual; from locality W8; **L, M** MMUW 2017D-301, cranidium, exterior, details showing polyfavolate pattern on palpebral areas (L) and Bertillon pattern on glabella (M); from locality W8; **N** MMUW 2017D-181aL, cranidium, latex cast of external mould; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars equal 1 mm.

Nevertheless, it needs to be emphasised that a form identified as *Ornamentaspis* cf. *crassilimbata* has been collected from strata assigned to the Galgenberg Member of the Tannenknock Formation. As discussed in Geyer (2017), this occurrence appears to challenge the simple biostratigraphic scheme, in which the development of the Tannenknock Formation in Galgenberg shale facies took place only during an interval that represents the *Kingaspidoides frankenwaldensis* Biozone, whereas the typical

Wildenstein facies trilobites belong only to the *Ornamentaspis frequens* Biozone. As detailed in earlier studies (e.g., Geyer 1990b, 1990c, 1998; Geyer et al. 1995; Geyer & Landing 2006), *Ornamentaspis crassilimbata* Geyer, 1990b occurs in it type region in the Moroccan High Atlas in the *O. frequens* Zone only so that the occurrence of specimens that possibly belong to the same plexus should represent the same zone in the Franconian Forest. Indeed, *O.* cf. *crassilimbata* is found almost exclusively in localities W13a and W14 (Sdzuy's samples "i" and "K2"), which both include "mixed" faunas and partly fossils preserved in Wildenstein facies characteristic for both zones. Consequently, those faunas are assumed to indicate a late development of the Galgenberg shale assigned to the Galgenberg Member at the basal part of the *O. frequens* Zone.

The specimens of the Franconian Forest identified as *Ornamentaspis* cf. *crassilimbata* match the type material of *O. crassilimbata* Geyer, 1990b from the High Atlas Mountains of Morocco in nearly all of the recognisable character, but have a slightly less convex anterior border (sag.), slightly narrower palpebral areas, and a slightly broader (sag.) preglabellar field. As discussed in Geyer (2017), these differences may be interpreted as to fall within intraspecific plasticity and are partly assignable to a minor distortion of the specimens from the Franconian Forest. In addition, differences of diagenetic history resulting from the differing host sediments (calcareous mud in the High Atlas, muddy sands in the Franconian Forest) may also be made responsible for the differences. It could be regarded as puzzling, why *O.* cf. *crassilimbata* and *O. frequens* are restricted to the Galgenberg and Wildenstein members, respectively. This, in fact, conforms with the occurrences in the High Atlas Mountains of Morocco, where both species indeed occur in coeval strata of neighbouring localities, but have never been found to co-occur in the same localities: It seems as if both species have an unusually high requirement to specific environmental conditions, which is reflected by the different types of host rocks in the High Atlas as well as in the Franconian Forest regions.

The pygidium that possibly belongs to *Ornamentaspis frequens* (Fig. 35B) differs considerably from the pygidia known from other genera of the kingaspidoid clade (such as *Kingaspidoides*, *Kingaspis*, *Cambrosaurura*, *Ellipsostrenua* or *Kymataspis*). It is slightly reminiscent of the pygidia known from *Protolenus* with the relatively large and well-elevated axis and fairly small pleural fields defined by strongly posteriorly directed lateral borders [compare *Hamatolenus* (*H.*) *draensis* (Hupé, 1953a) in Geyer 1990b, pl. 42, fig. 6].

Ornamentaspis? sp. A

Fig. 37

Studied material. Two incomplete cranidia: From sample locality W8 (SSMM 11336) and sample locality W13b (MMUW 2017D-420), respectively.

Locality and stratum. Wildenstein Member, Tannenknock Formation.

Description and discussion. One of the cranidia from locality W8 is an incomplete internal mould, which shows the characters of *Ornamentaspis*, and specifically of *O. frequens* (see above) and *O. crassilimbata* Geyer, 1990b. Differences can be seen in the slightly broader glabella, but particularly in the shorter frontal regions, which is further characterised by a slightly raised, moderately broad (sag., exsag.) anterior border and correspondingly a slightly sunken preglabellar field and preocular areas (Fig. 37D). The specimen was preserved in a marly limestone layer of the Wildenstein Member and is affected by subrecent weathering. Despite the resulting poor preservation, the preglabellar field and the preocular areas still preserve relics of radial caeca.

A second cranidium from locality W13b shares the morphology of the frontal lobe with slightly sunken preglabellar field and preocular areas as well as the relatively posterior position of the palpebral lobes but differs in having a more slender and tapering glabella and a narrower occipital furrow as well as an apparently broader (sag.) preglabellar field (Fig. 37A–C). These differences are seemingly significant, but more material would be needed to rule out that both specimens are opponent peaks of a broad morphological range.

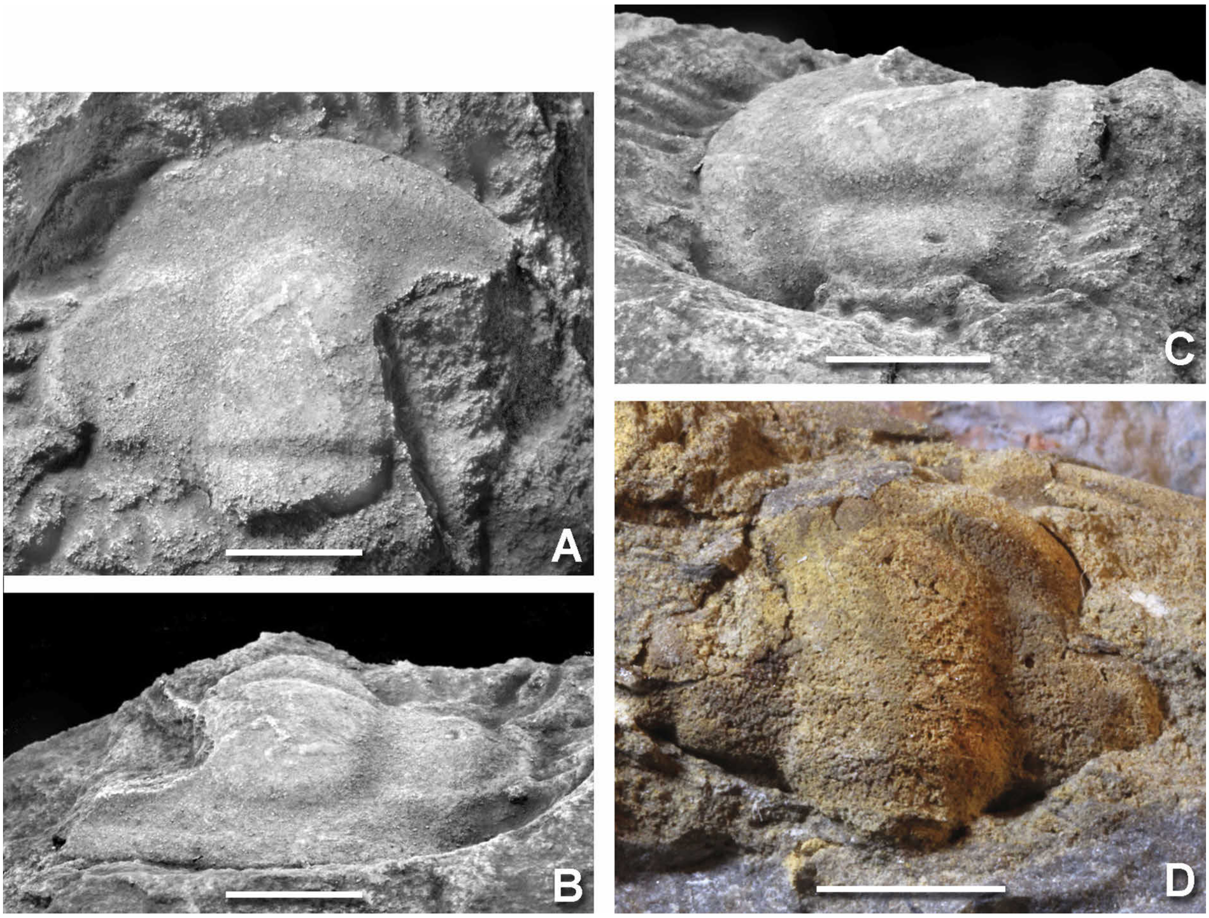

Fig. 37: *Ornamentaspis* sp. A. **A–C** MMUW 2017D-420, cranidium, internal mould, dorsal view (A), oblique anterior view (B) and oblique lateral view showing slightly concave preglabellar field (C); from locality W13b; **D** SSMM 11336, cranidium, dorsal view; from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars equal 5 mm.

The morphology of the frontal region is unlike that known from the species of *Ornamentaspis*, although a specimens of *O. frequens* from the High Atlas of Morocco were found with a similar, albeit not as strongly sunken preglabellar field and preocular areas (see Geyer 1990b, pl. 24, fig. 1a, b). Thus, it should be ruled out that the specimen from locality W8 (Fig. 37D) is an unusually preserved specimen of *O. frequens* although this interpretation is regarded as highly improbable herein. However, the specimen from locality W13b certainly cannot be identified as *O. frequens*. It should be noted that the morphological plasticity within the closely related genus *Ellipsostrenua* (see below) includes a fairly broad variation in the morphology of the frontal regions in the different species (Cederström et al. 2022) with slightly raised anterior borders and faint depression posterior to it.

Genus *Ellipsostrenua* Kautsky, 1945

Type species. *Strenuella* (*Ellipsostrenua*) *gripi* Kautsky, 1945; from the upper traditional Lower Cambrian Grammajukku Formation at Mount Assjatj in the Laisvall area, central Swedish Lapland; by monotypy.

Discussion. *Ellipsostrenua* has been a long-time neglected or misinterpreted genus of ellipsocephalid/kingaspidoid trilobites, but has been scrutinised recently by Cederström et al. (2022). The genus has been erected originally as a subgenus of *Strenuella* by Kautsky (1945), based on a single new species, *Strenuella* (*Ellipsostrenua*) *gripi* Kautsky, 1945, although Kautsky (1945, p. 161) mentioned that he regarded "forms of *Strenuella*, which mutate in direction to *Ellipsocephalus* as belonging to *Ellipsostrenua*" (translated from the German text). As suggested by Cederström et al. (2022), Kautsky (1945) obviously regarded *linnarssoni*, which was discussed in another part of his article, as a species of *Strenuella (Ellipsostrenua)*. However, that species was only dealt with as *Strenuella linnarssoni* in Kautsky's publication.

Ellipsostrenua was raised to generic rank by Henningsmoen (1959), a classification which was maintained by Sdzuy (1961), Rushton (1966), Poulsen (1969), Lendzion (1972), Bergström (1973) and Geyer (1990b). However, Ahlberg & Bergström (1978) suggested that the taxon is better regarded as a junior synonym of *Ellipsocephalus*, which was generally followed in subsequent publications of Scandinavian authors. Høyberget *et al.* (2015) retained the species under *Ellipsocephalus* but clearly indicated that this placement is regarded as provisional.

Cederström et al. (2022) included nine species under *Ellipsostrenua*, which had been previously allocated to several different genera, such as *Ellipsocephalus*, *Proampyx*, *Strenuella*, *Strenuaeva*, and tentatively also to *Ornamentaspis*. The authors also presented an emended diagnosis for the genus. Although the confusion in generic placement of the species is mainly a result of similarities in the cephalic morphology, some important differences can be recognised, which are summarised in the following paragraphs following the discussions in Cederström et al. (2022):

(1) Adult individuals of *Ellipsostrenua* have a glabella that generally tapers considerably forward, whereas *Ornamentaspis* and *Kingaspidoides* are characterised by species with a subparallel glabella or a glabella which tapers only faintly from the occipital ring forward to the anterolateral corners of the frontal lobe.

(2) The genal sector of *Ellipsostrenua* is characterised by almost flat to slightly convex fixigenae in transverse section and a general ventral deflection of the genae from the axial furrows toward the ocular suture so that the palpebral lobes are situated below the level of the axial furrows.

(3) The cephalic anterior area is somewhat variably developed in species of *Ellipsostrenua*, but in general forms a faintly to moderately convex, ventrally deflected platform. In most species of *Ellipsostrenua*, the medial portion of the preglabellar field is slightly more convex than the abaxial parts of the preocular fields so that a slight differential development can be recognised.

(4) The anterior cephalic margin has a relatively strong curvature in dorsal view compared with other genera of the Ellipsocephalinae.

Ellipsostrenua? sp. A

Fig. 38

Material. Single incomplete cranidium, MMUW 2017D-460; from locality W13e.

Stratigraphy. Wildenstein Member, Tannenknock Formation.

Description and discussion. The single cranidium described here is mainly characterised by a relatively effaced kingaspidoid morphology with a subrectangular glabella elevated above the genae and having a gently curved anterior margin, with the anterolateral corners extending into shallow, indistinct eye ridges. Particularly important for the generic and specific characteristic is the conspicuous sagittal convexity (Fig. 38C) as well as the transverse profile with the glabella well-elevated above the genae, but without distinct axial furrows, and the palpebral areas/fixigenae gently deflected from the axial furrows toward the palpebral lobes. The frontal area consists of a gently convex, ventrally sloping unit of the preglabellar field and anterior border with an obsolescent anterior border furrow. The palpebral lobes are not preserved, but were almost certainly of moderate length, with the posterior ends distant from the posterior border furrow.

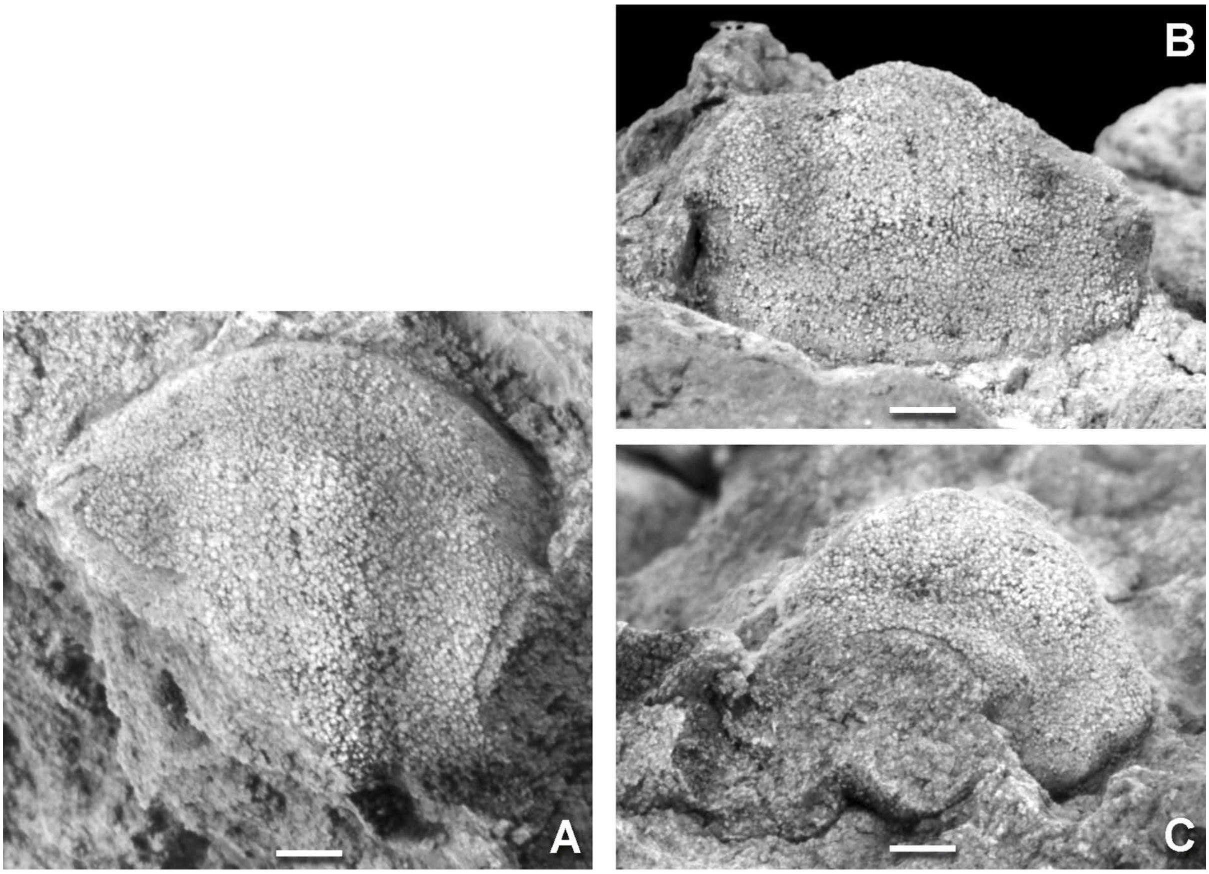

Fig. 38: *Ellipsostrenua*? sp. A. MMUW 2017D-460, cranidium, internal mould, dorsal view (A), oblique anterior view (B) and oblique lateral view illustrating considerable convex curvature of glabella in sagittal profile (C); from locality W13e. Wildenstein Member, Tannenknock Formation. Scale bars equal 1 mm.

This cranidium has the general morphology seen in typical species of *Ellipsostrenua*, but differs in the subparallel glabella with the slightly indented lateral margins and a relatively low curvature of the frontal margin of the glabella. This shape of the glabella is typical for *Kingaspidoides*. However, the conspicuous sagittal and transverse convexity is unknown from species of *Kingaspidoides*. It should be emphasised that this convexity cannot be ascribed as being a product of post-mortem deformation.

Genus *Germaropyge* Šnajdr, 1957

Type species. Ellipsocephalus germari Barrande, 1852; from the *Eccaparadoxides pusillus* Zone of the Skryje Shale Member, Barrandean region, Czech Republic.

Discussion. Germaropyge Šnajdr, 1957 is a genus that suffered from its restricted occurrence and the unsettled concept of *Ellipsocephalus*, as well and uncertainties about diagnostic characters among ellipsocephaline trilobites. Until today the genus is mostly considered a synonym of *Ellipsocephalus* although differences were discussed in several publications.

Briefly summarised, the type species of *Germaropyge*, *G. germari* (Barrande, 1852), has indeed a glabella which superficially resembles that of *Ellipsocephalus hoffi* in its outlines. Despite the reconstruction in Šnajdr (1958, text-fig. 16) the lateral margins of the glabella are never constricted, and the frontal lobe has a somewhat variable shape, but usually lacks distinct anterolateral corners as seen in *E. hoffi* and the other unequical species of *Ellipsocephalus*. In transverse section, the glabella shows a gentle convexity without a central crestline (Fig. 39D), and the glabella slopes gently towards the axial furrows as well as to the preglabellar field without a stepwise drop (Fig. 39B, D). The anterior part of the cephalon lies clearly below the front of the glabella (Fig. 39B, E) and does not show the stepwise deflection seen in typical species of *Ellipsocephalus*. The palpebral lobes are moderately upturned so that they project above the palpebral areas (Fig. 39D), unlike the palpebral lobes in *Ellipsocephalus*.

The thoracic segments in *Germaropyge germari* are of similar shape, but are reduced in size from the largest one (segment 3) towards the end of the thorax. The pleural tips have relatively large articulating facets that differ from those seen in species of *Ellipsocephalus*. In addition, moderately well-developed lateral swellings are developed at the axial rings which mark the attachment sites of strong muscles on the ventral side (Fig. 38C, I).

The pygidium of *Germaropyge germari* unmistakably distinguishes the species from those of *Ellipsocephalus*. This pygidium has a broadly sublenticular outline with a gently convex axis composed of three axial rings and a terminal axial piece. The posterior end of the axis reaches to almost the posterior margin of the pygidium. The pleural areas have moderately well-defined pleural and interpleural furrows, but the anterior two ribs are better developed and appear to incompletely fused although the ventral doublure that is visibly in Fig. 38F suggests a uniform sclerite. Some specimens known from *G. germari* seem to indicate that a low crest subparallel to the lateral and posterior margin of the terminal axial piece was developed in the living individuals – similar to the structure seen in species of *Hamatolenus*. This pygidium is a modified volucent-type pygidium that resembles the pygidium known from typical solenopleurids and is termed *eosolenopleurid* herein.

A further species assigned to *Germaropyge* was first published as "*Ellipsocephalus S-ta Cruzensis*" by Czarnocki (1927), which in fact is a *nomen nudum*. Samsonowicz (1959) formally introduced the species as "*Germaropyge sancta-crucensis* (Czarnocki)" (Samsonowicz 1959, 527, 529, pl. II, figs. 4–12). The species was then dealt with in Orłowski (1973) as "*Ellipsocephalus* cf. *sanctacrucensis* Samsonowicz" while "*Germaropyge* cf. *sancta-crucensis*" in Lendzion (1972) represents a different genus and species. Orłowski (1975) eventually described the species in a monographic article under the name *Ellipsocephalus sanctacrucensis*.

The species from the Ociesęki Formation of the Holy Cross Mountains is characterised by a ellipsocephaline morphology of the cephalon with a relatively voluminous glabella with slightly constricted lateral margins and a subtriangular front similar to some species of *Kingaspidoides*. The species certainly does not belong to *Ellipsocephalus* as mostly done following Orłowski's suggestion, but it also does not represent a species of *Germaropyge*.

The pygidium of "*Ellipsocephalus*" *sanctacrucensis* (Samsonowicz, 1959) is small and subtriangular in outline so that it resembles the pygidia in true species of *Ellipsocephalus* in that respect. However, the pygidium is of a volucent type, with the axis being well defined and gently convex, subdivided into axial rings, relatively short, with its posterior end being distant from the posterior margin of the pygidium. The pleural areas are low and show only poorly developed furrows (Orłowski 1975, pl. 1, fig. 1b). Żylińska & Masiak (2007) and Nawrocki et al. (2007) transferred the species to *Kingaspidoides*, and this assignment was maintained in Żylińska (2013) and Nowicki & Żylińska (2018). It can be considered as a reasonable placement although several aspects of the species are not typical for that genus.

Germaropyge? *mendosa* Chernysheva in Korkutis, 1971 was described from the Gargzdai-6 drill-core in western Lithuania. As discussed in Cederström et al. (2022), the species shows characters resembling *Strenuaeva* and *Epichalnipsus* rather than *Germaropyge*, and it needs careful reconsideration.

Germaropyge germari (Barrande, 1852)

Fig. 39

Studied material. Incomplete dorsal exoskeleton, Sv1-331; cephalon with articulated anterior thorax, Sv1-330; thorax with attached pygidium, Sv1-332. All specimens collected from Skryje Shale Member, Tyřovice (Pod trnim), Skryje-Týřovice Basin, Barrandean region, Czech Republic.

Discussion. The significant characters of *Germaropyge germari* are described above under the genus. Nevertheless, other interesting features include the fact that the facial suture in *G. germari* appears to be weakly developed so that in several specimens the suture is barely recognisable. The two cranidia illustrated in Fig. 39E and 39G show a crack close to the true position of the suture, but in both cases caused by dorsoventral compaction.

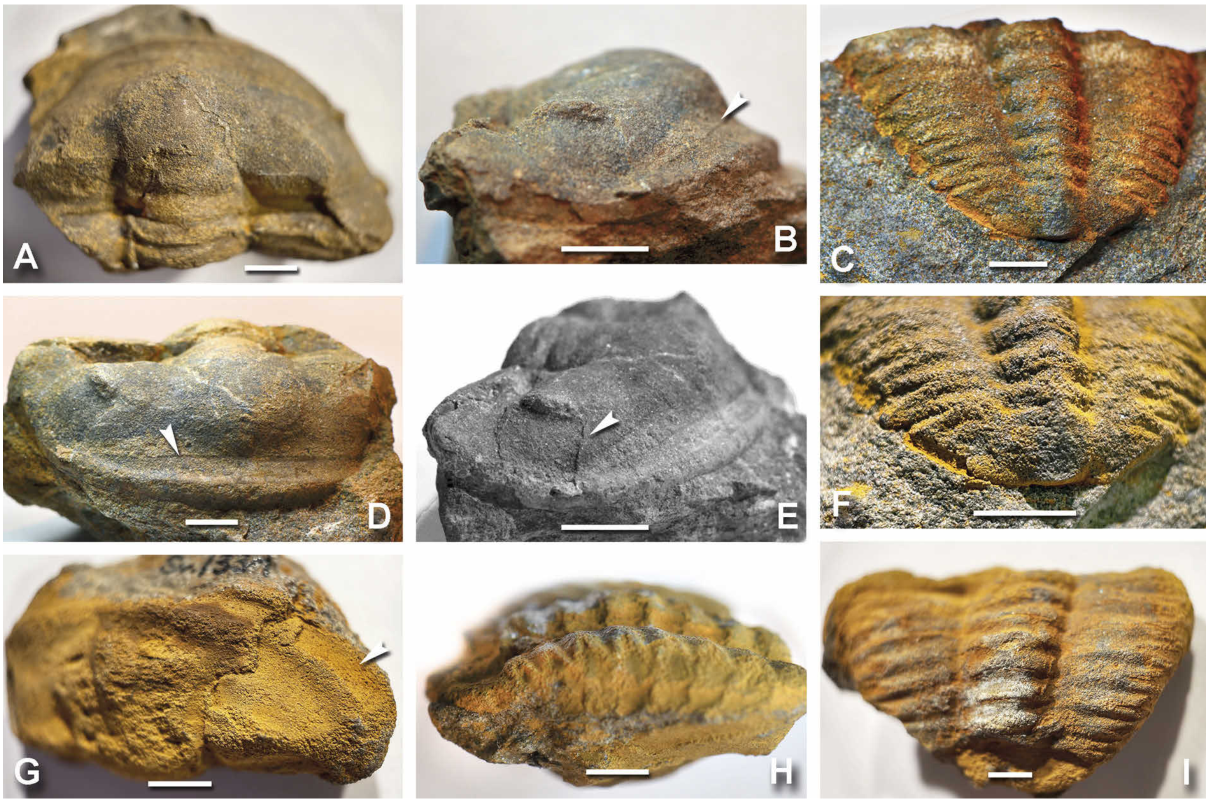

Fig. 39: *Germaropyge germari* (Barrande, 1852). **A, B, D, E** Sv1–330, cephalon with articulated anterior thorax, partially enrolled, internal mould; A dorsal view of cephalon; B lateral view of cephalon illustration relief of the cephalon, upturned palpebral lobes and imprint of rostral plate (arrow); D anterior view showing gently convex glabella and relatively low relief of palpebral areas as well as imprint of rostral plate (arrow); E oblique anterolateral view showing weakly developed facial suture and crack slightly posterior to actual anterior branch of facial suture, resulting from compression. **C, F** Sv1–332, incomplete, slightly enrolled exoskeleton, internal mould; C posterior part of thorax consisting of seven segments visible in the photo and attached pygidium; F magnified view of pygidium with axis of three axial rings and terminal axial piece reaching to almost the posterior margin of the pygidium and well defined pleural ribs. **G–I** Sv1–331, incomplete, enrolled dorsal exoskeleton; G distorted cephalon showing ventral doublure of lateral border with several terrace ridges; H lateral view of thorax illustrating pleurae of similar morphology and articulating facets; I thorax in dorsal view, with moderately well-developed lateral swellings of the axial rings which mark the attachment sites of strong muscles on the ventral side.
All specimens collected from Skryje Shale Member, Tyřovice (Pod trnim), Skryje-Týřovice Basin, Barrandean region, Czech Republic. Scale bars 5 mm.

Fig. 39G also illustrates an exposed surface of the ventral doublure with several quite distinctly developed terrace ridges. These appear to be better developed than in most ellipsocephaline trilobites from which terrace ridges on the doublure are known.

Specimen Sv1-330 shows the imprint of a surprisingly large rostral plate (Fig. 39B, D).

Trivial remark. These trilobites are perhaps more popular in the Czech Republic than elsewhere. One contribution to this popularity is a phone card with an instructive photo of and information on *Germaropyge germari* issued by Česky Telecom in September 2000.

Stratigraphic occurrence. The precise stratigraphic range of *Germaropyge germari* is somewhat unresolved. The confidently assigned specimens are from the lower and middle part of the *Eccaparadoxides pusillus* Zone of the Skryje Shale Member in the Skryje-Týřovice Basin, particularly from the *Ptychoparia dubinka* and the *Mikaparia mutica* assemblage zones (Kordule 2006), but records range from the *Ornamentaspis*–*Conocoryphe* Horizon to the lower part of the *Acadolenus snajdri*–*Litavkaspis rejkovicensis* Subzone and the *Doryagnostus* Subzone in the Přibram-Jince Basin (see Fatka et al. 2014).

Subfamily Protoleninae Richter & Richter, 1948

Remarks. For the modern concept of the subfamily Protoleninae see discussions in Geyer (1990b) and Cederström et al. (2022).

Genus *Protolenus* Matthew, 1892

Type species. Protolenus elegans Matthew, 1892; from the Cambrian Series 4, Hanford Brook Formation of Hanford Brook, New Brunswick, Canada.

Remarks. For the modern concept of *Protolenus* see discussions in Geyer (1990b).

Subgenus *Protolenus* (*Protolenus*) Matthew, 1892

Type species. As for genus.

Protolenus (*Protolenus*) *undulatus* n. sp.

Fig. 40

Holotype (and only available specimen). SMF 79015, cranidium.

LSID. urn:lsid:zoobank.org:act:B0139BB0-6203-4F2E-847C-24B049E45BE9

Type locality and type stratum. Sample locality W8 in the Wildenstein slice near Wildenstein. Tannenknock Formation, Wildenstein Member, *Ornamentaspis frequens* Zone; probably lower Wuliuan.

Etymology. From the Latin *undulatus*, undulated, as with waves; a reference to the relief of the cranidium.

Diagnosis. Species of *Protolenus* (*Protolenus*) with a cranidial length of ca. 85 percent cranidial width; glabella with a moderately long (sag) occipital ring, terminating into in a moderately large occipital spine; fixigenae with only a very shallow median depression, most elevated relatively close to palpebral furrows; preglabellar field slightly sunken, defined from the anterior border only by a change in convexity; anterior border moderately broad (sag., exsag.), low, slightly convex.

Description. Cranidium with glabella moderately elevated, separated from palpebral areas by poorly defined axial furrows and a considerable slope at lateral margins; most elevated parts of the palpebral areas relatively close to the palpebral furrows (Fig. 40B). Sagittal profile shows a poorly convexity of the glabellar axis, a nearly step-like lowered anterior area with a low convexity and a ventral deflection (Fig. 40C).

Glabella of ca. 85 percent cephalic length, maximum width of axis across L1 ca. 35 percent cranidial width across palpebral lobes; glabella with subparallel to faintly convergent lateral margins anterior to occipital furrow, frontal lobe at anterolateral corners of ca. 90 percent transverse width across L1; glabella moderately well elevated above axial furrows and above the preglabellar field, slopes down to axial furrows with a moderate drop. Anterior margin of frontal lobe subtriangular, with a somewhat curved kink medially; three pairs of shallow lateral glabellar furrows recognisable; S1 commences near axial furrows (in dorsal view), rearward directed from its origin, broadened or faintly bifurcated near the sagittal axis, but disconnected medially; S2 similar to S1, but more transversely directed; S3 not precisely preserved in the specimen, apparently transversely or even slightly forward directed, short. Occipital furrow distinct, broad, almost straight throughout. Occipital ring with rearward swinging posterior margin, narrow laterally, on sagittal line of ca. 15 percent cephalic length (sag., excl. occipital spine), extended into a moderately strong, moderately long subterminal spine, which is distinctly dorsally directed in lateral profile.

Palpebral areas transversely of ca. 23 percent maximum glabellar width across mid-length of the palpebral lobes, fixigenae posterior to eye ridges exsagittally of ca. 45 percent cephalic length along axial furrows; slightly convex in transverse profile, ascending from axial furrows to its most prominent point short distance from the palpebral furrow; poorly defined from axial furrow on the exterior of the cuticle, with only a very shallow, slightly obliquely directed central depression.

Typical *Protolenus*-type palpebral lobe of exsag. ca. 40 percent cephalic length and tr. ca. 6–7 percent maximum cranidial width; transversely distinctly convex, subequal in transverse width, with considerable curvature in dorsal view, anterior end approximately short distances anterior to the level of S3, in a faintly more adaxial position than posterior end; posterior end short distances anterior to the level of the occipital furrow, reaching to posterior border furrows. Palpebral furrow a moderately well-developed depression on the exterior of the cuticle.

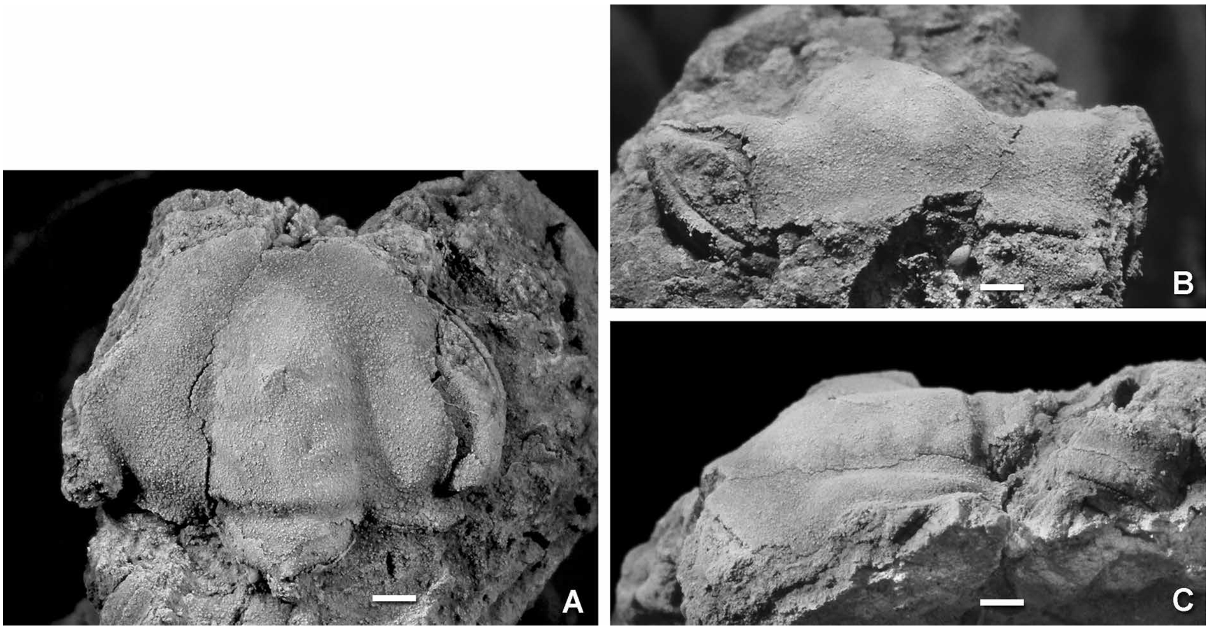

Fig. 40: *Protolenus* (*Protolenus*) *undulatus* n. sp. SMF 79015, holotype, cranidium, dorsal (A), anterior (B) and lateral (C) views; from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Eye ridge on the exterior of the cuticle a low, poorly defined ridge faintly oblique to axis, poorly demarcated from the palpebral area, but defined by its slope from preocular area; appears to extend anteriorly into a low ridge that traverse the axial furrow and appears also to extend into a faint parafrontal band around the frontal lobe of the glabella.

Preglabellar field slightly sunken, forming a shallow, moderately broad groove, of ca. 8 percent cephalic length (sag.); defined from anterior border only by a change in surface ornamentation and a faint anterior border furrow. Anterior border with only low curvature, of 8 percent cephalic length on the sagittal line and of subequal breadth as preglabellar field. Preglabellar field and anterior border form a somewhat ventrally deflected platform.

Posterior border a moderately broad (exsag.), moderately convex, transverse to sagittal axis in the proximal part, slightly posteriorly reclined towards facial suture; with a small knob-like swelling posterior to the abaxial part of the palpebral areas, which acted as a connective device to the first thoracic segment. Posterior border furrow a moderately deep, moderately broad (exsag.) groove.

Anterior branches of the suture straight for most part, more-or-less parallel to axis, swing adaxially in a small when reaching the anterior border. Posterior branches strongly diverging from the posterior ends of the ocular suture.

Other parts of the exoskeleton unknown.

Exterior of the cuticle apparently covered with fine granules; palpebral areas, particularly in their posterior half, probably with delicate caeca, which run oblique to the axis.

Discussion. The single cranidium from locality W8 is an unexpected occurrence of a species of *Protolenus*. Unfortunately, only one specimen is present among the rich material, which suggests that the species was quite rare even during it lifetime. Nevertheless, the preservation is sufficiently good enough to unequivocally characterise the species.

The subgenus *Protolenus* was often used as a basket for protolenoid or ellipsocephaloid genera, obviously because the type species and associated other species from New Brunswick have not been adequately illustrated in the early publications. The revision of the genus and subgenus by Geyer (1990b) emphasised that the species are characterised by a glabella with subparallel margins or slightly tapering forward; palpebral areas which are convex, but show a shallow diagonal depression; eye ridges that include an angle to the palpebral lobes and are further separated by a distinct groove; a preglabellar field without lateral grooves; and a convex anterior border of a maximum width of that of the preglabellar field. In addition, the species of *Protolenus* are now known to have a pygidium with a fused axis and pleural areas with crest-like ridges similar to those known from the closely related genus *Hamatolenus* Hupé, 1953.

Protolenus (*Protolenus*) *undulatus* n. sp. differs from the typical species of *Protolenus* such as *P.* (*P.*) *elegans* Matthew, 1892 and *P.* (*P.*) *paradoxoides* Matthew, 1892 from Avalonian New Brunswick (see also Matthew 1895) as well as *P.* (*P.*) *interscriptus* Geyer, 1990b and *P.* (*P.*) *densigranulatus* Geyer, 1990b from the Moroccan Atlas ranges in the somewhat ventrally sloping frontal area of the cephalon with a fairly low anterior border and also in a less well developed diagonal depression on the palpebral areas. However, the new species from the Franconian Forest shares all other characteristic features with those typical species, particularly the shape of the glabella with the subacute frontal lobe and the (apparent) parafrontal band; the arcuation between the eye ridges and the palpebral lobes; and the shape and size of the palpebral lobes. Unfortunately, no pygidium was found that could be assigned with some confidence to the species. The morphology of the frontal area of the cephalon resembles the morphology seen in a number of species assigned to *Kingaspidoides* or *Ornamentaspis*, but the anterior border remains relatively short for the species of those genera, and the other listed characters exclude a placement under *Kingaspidoides* or *Ornamentaspis*.

Typical species of *Protolenus* occur in a relatively short interval assigned to the uppermost Stage 4 of the Cambrian. Hence, *Protolenus* (*Protolenus*) *undulatus* appears to be among the youngest species or the youngest species of the genus.

Genus *Latoucheia* Hupé, 1953a

Type species. Protolenus latouchei Cobbold, 1910; from the Comley Limestone Formation, "Protolenus limestone" (Ac5), Cambrian Series 4 of the Comley area, Shropshire, UK.

Discussion. Latoucheia has been introduced as a subgenus of *Protolenus* by Hupé (1953a), but tacitly raised to genus level by Repina (1966, p. 122). Its type species, *Protolenus latouchei* Cobbold, 1910, is poorly known, but superbly preserved similar species from the Moroccan Atlas ranges assist to allow a clear-cut concept of the genus. *Latoucheia* is characterised by a shallow transverse furrow that traverses the fixigenae in diagonal direction, a well-recognisable parafrontal band (as in *Protolenus*) and eye ridges that are oriented almost perpendicular to the longitudinal axis of the cephalon and are well separated from the palpebral lobes (also as in *Protolenus*). In addition, the species of *Latoucheia* have a less sunken preglabellar field and show a delicate transverse groove on the occipital ring.

Two subgenera have been placed under *Latoucheia* by Geyer (1990b): *Latoucheia* (*Latoucheia*) is characterised by a relatively slender glabella with nearly straight lateral margins and a reduced frontal lobe. Species and not formally defined forms of *Latoucheia* (*Latoucheia*) are known primarily from West Gondwanan Morocco and Avalonian England as well as from an uncertain occurrence in Spain and a species tentatively assignable to *Latoucheia* [described as *Latoucheia* (*L.*) *longa* in Żylińska & Szczepanik 2009] from the Holy Cross Mountains of Poland, all in stratigraphical levels that correlate with most probably the uppermost part of Cambrian Stage 4. *Latoucheia* (*Pseudolenus*) has a clearly wider glabella with a somewhat different shape of the frontal lobe. It is only known from the Moroccan Anti-Atlas, also from strata which seem to represent the uppermost Stage 4.

Latoucheia? (*Latoucheia*?) sp. A

Fig. 41

Material. Single cranidium, MMUW 2017D-075I.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest area. Wildenstein Member, Tannenknock Formation.

Description and discussion. This form is represented in the studied material by only one cranidium, which superficially resembles the species of *Latoucheia* (*Latoucheia*) in having a relatively slender glabella without well-incised glabellar furrows and with nearly straight lateral margins; a quite broad (sag.) occipital ring; eye ridges arranged almost transverse to the cephalic axis; and a quite long (sag.) preglabellar field. The cranidium, however, lack the diagonal groove that runs across the fixigenae in typical species of *Latoucheia*, and the palpebral lobes are much thicker and somewhat shorter.

The specimen differs from all other ellipsocephaloid trilobites found in the Cambrian of the Franconian Forest, but its identity can only be dealt with strong proviso. It is somewhat laterally compressed so that the palpebral areas are certainly more strongly convex than they were during lifetime of the animal, and the same accounts for the palpebral lobes. However, the differences are so striking that the form cannot be assigned to *Latoucheia* according to the present state of knowledge about the genus' species. More and better preserved specimens are necessary to reconstruct the precise morphology, which also bears some resemblance to the species of the *Kingaspidoides* clade, which is represented by so many different forms in the same strata.

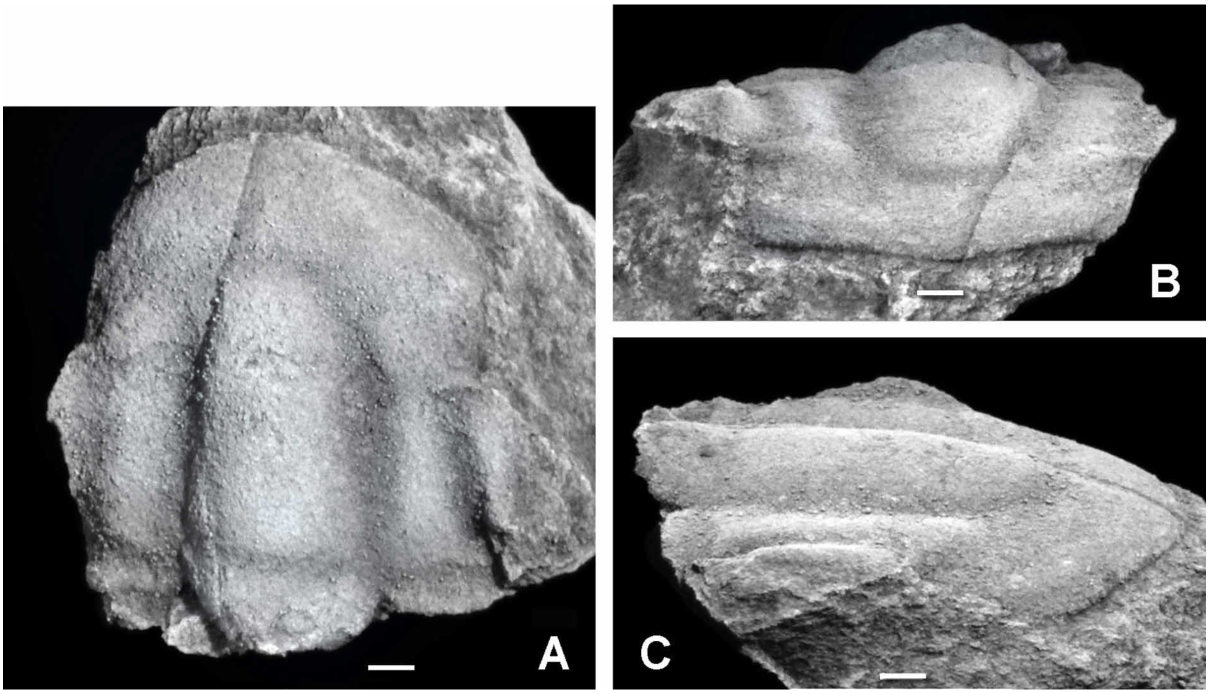

Fig. 41: *Latoucheia*? (*Latoucheia*?) sp. A. MMUW 2017D-075, cranidium, dorsal (A), anterior (B) and lateral (C) views; from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Family Palaeolenidae Hupé, 1953a

Genus *Enixus* Özdikmen, 2009

[pro *Schistocephalus* Chernysheva, 1956]

Discussion. Specimens of *Enixus* Özdikmen, 2009 were described from the Galgenberg assemblage (Geyer 2017), and additional material from the Wildenstein Member complements the record. These specimens further extend the known occurrences of the genus *Enixus*, which has been introduced under the name *Schistocephalus* Chernysheva, 1956 and has long been regarded as a typical Siberian taxon which was almost exclusively restricted to the Siberian Platform and the adjacent Altay-Sayan Foldbelt. Long known only from the Siberian Platform and adjacent regions, the genus has subsequently identified from the Moroccan Atlas region (Geyer 1998), the Dead Sea area of Jordan (Rushton & Powell 1998; Elicki & Geyer 2013), and the Cantabrian Mountains of Spain, from where Gozalo et al. (2007, fig. 4F–4H) figured two incomplete cranidia assigned to *Palaeolenus*, which in fact represent another species of *Enixus*.

As emphasised by Geyer (2017), the occurrence in the Tannenknock Formation is the first of the genus from predominantly siliciclastic rocks. For further remarks on the species' morphological groupings see discussion in Elicki & Geyer (2013).

Enixus sp. aff. *juvenis* (Chernysheva, 1956)

Fig. 42

v	1960	*Wurmaspis rarus* Sdzuy 1960 – Sdzuy: p. 108. [nom. nud.].
v	1976	*Wurmaspis rarus* Sdzuy – Horstig & Stettner: p. 51 (pars). [nom. nud.].

	1997	*Wurmaspis rarus* Sdzuy – Geyer & Wiefel: p. 100. [nom. nud.].
	2009	*Wurmaspis rarus* Sdzuy, 1960 – Basse: pp. 26, 42. [nom. nud.].
	2010	*Wurmaspis rarus* Sdzuy 1962 – Geyer: p. 81. [nom. nud.].
v	2017	*Enixus* sp. aff. *juvenis* (Chernysheva, 1956) – Geyer: pp. 43–46, 66, fig. 20.
v	2019a	*Enixus* sp. aff. *juvenis* (Chernysheva, 1956) – Geyer et al.: fig. 15I.

Studied material. Eight cranidia or cranidial fragments. In repository: From sample locality W8 (single cranidium; appears to be lost); from locality W9 (three cranidia under SMF 79020, MMUW 2017D-314 and MMUW 2017D-317); from locality W11 (cranidium under SSMM 10760); from locality W11/12 (cranidium under SMF 11790a and SMF 11790b, part and counterpart); from W15a (cranidium under MMUW 2017D-330).

Specimens from locality W9 and W15a from Wildenstein Member of the Tannenknock Formation; specimens from W11 and W11/12 from Galgenberg Member of the Tannenknock Formation.

Description (modified from Geyer 2017). Cranidium slightly wider than long. Axial furrows shallow on the exterior of the cuticle, weakly defined from palpebral areas.

Glabella faintly clavate, maximum width 1.10–1.15 times occipital width; length ca. 85 percent of cephalic length, width across occipital ring ca. 45 percent cranidial width across centre of palpebral lobes. Glabella moderately convex, frontal lobe with relatively strongly curved anterior margin, but with a low curvature in the median part; four pairs of lateral glabellar furrows visible: S1 and S2 well impressed, S3 and S4 shallower; S1 relatively broad and deep, with clear onset at axial furrows, with slightly rearward bend to a weakly bifurcated, shallower median section; S2 narrower and slightly less incised than S1, faintly curved to a double sigmoidal course, in total view normal to axis, deepest slightly distant from axial furrows; S3 shallow, commences slightly distant from axial furrow, slightly anteriorly directed from origin, then with a rearward curvature that suggests a shallow, chevron-shaped median sector; S4 short, directed slightly anterior from near axial furrows, short distance from and with only a small angle to S3. Frontal lobe with a faint parafrontal band, which is generally difficult to recognise. Occipital furrow more-or-less straight, with quite distinctly incised lateral sections. Occipital ring moderately long (sagittal length about 15 percent cephalic length), without medial node or with only faint tubercle.

Palpebral areas posterior to eye ridges subelliptical to subsemicircular in outline; maximum width (tr.) about 40 percent width of occipital ring, maximum length (exsag.) adjacent to axial furrows about 40 percent of sag. cephalic length. Palpebral lobes relatively narrow, moderately convex in transverse profile, a moderately curved arc of about equal width throughout. Palpebral furrow a moderately wide groove, which extends transversely to about double palpebral lobe width in the centre (opposite S1); advances anteriorly with a faint kink into a shallow and weakly demarcated furrow that delimits the palpebral lobe from the fixigena. Eye ridge exsagittally about as wide as transverse width of palpebral lobe, weakly angulate relative to palpebral lobe; clearly oblique to axis and faintly curved; distinguished from preocular field by greater relief and a marked slope.

Anterior branches of facial suture diverge considerably forward from ocular suture, ventrally inclined, slightly curved toward sagittal line from half-distance to border furrow and with a distinct curvature toward sagittal line halfway through anterior border. Anterior wings extend slightly more distally than palpebral lobes. Posterior branches of facial suture diverge strongly, moderately curved, clearly ventrally deflected, extend distinctly beyond abaxial level of palpebral lobes.

Preglabellar field in front of glabella slightly narrower (sag.) than anterior border. Preocular fields more than twice width of anterior border, with distinct ventral deflection from eye ridges, and with low convexity.

Anterior border arched against the convexity of the anterior part of the cephalon; surrounds preglabellar field and preocular fields as a moderately raised ribbon with weakly convex dorsal surface. Anterior border furrow moderately sharp. Posterior margin of cranidium with minor sigmoidal curvature; posterior border slightly broader distally. Posterior border furrow deep near axial furrow, widens distally, directed slightly oblique to axis.

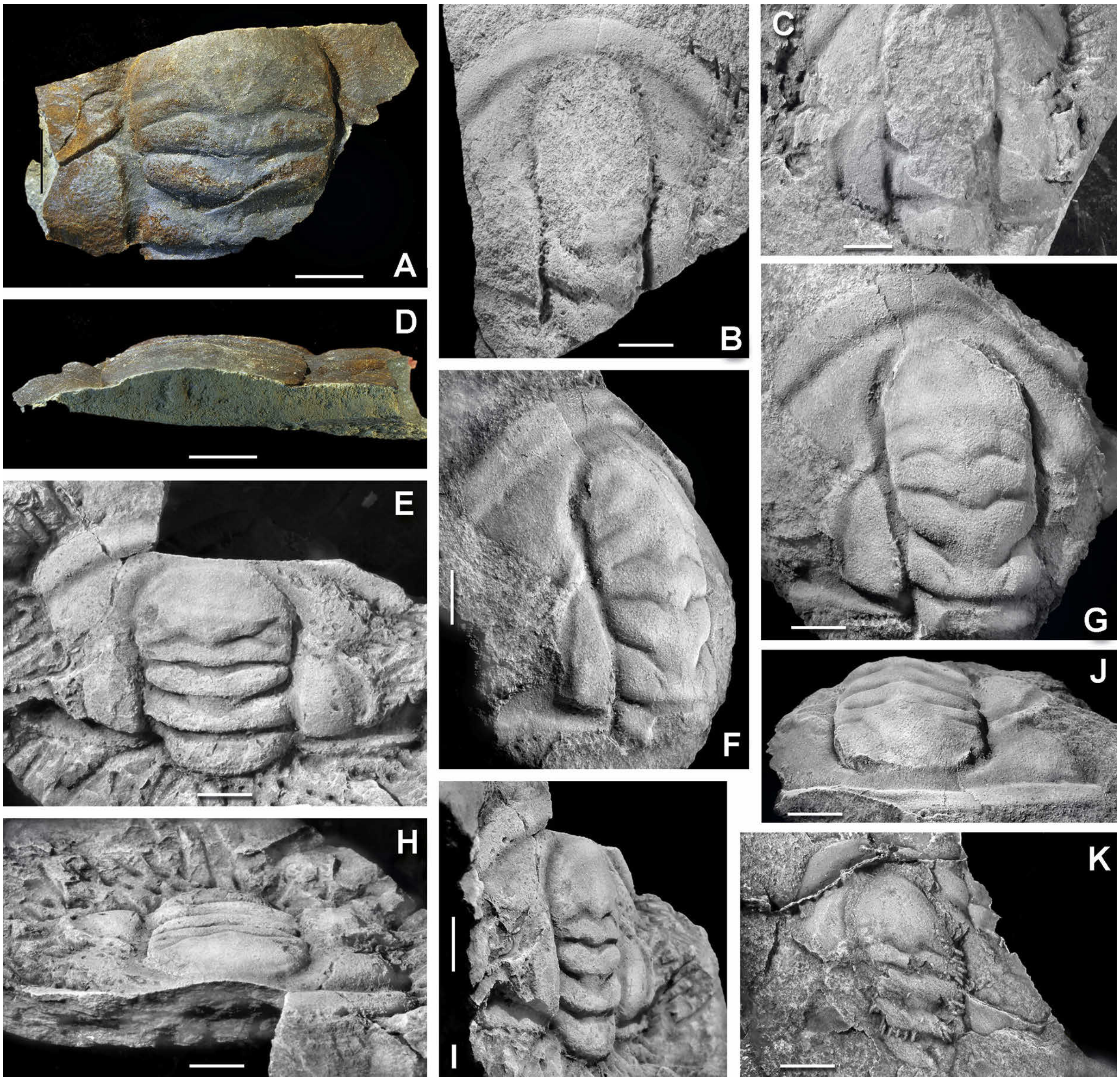

Fig. 42: *Enixus* sp. aff. *juvenis* (Chernysheva, 1956). **A, D** SSMM 10760, fragment of cranidium, internal mould, dorsal (A) and posterior (D) views; from Galgenberg Member, locality W11; **B** MMUW 2017D-314, incomplete cranidium, dorsal view; from Wildenstein Member, locality W9; **C** MMUW 2017D-317, incomplete cranidium, internal mould, transversely compressed; from Wildenstein Member, locality W9?; **E, H, I** SMF 11790a; incomplete cranidium, internal mould, dorsal (E), oblique anterior (H) and oblique lateral (I) views; from Wildenstein Member, locality W11?; **F, G, J** SMF 79020, partial cranidium, internal mould, oblique lateral (F), dorsal (G) and anterior (J) views; Wildenstein Member, from locality W9; **K** MMUW 2017D-127, distorted cranidium, latex cast of external mould; Wildenstein Member, from locality W9. All specimens from Tannenknock Formation. Dorsal view if not otherwise noted. Scale bars 5 mm.

Exterior of cuticle finely granulose (except for furrows), internal moulds covered by moderately large grooves.

Hypostome, rostral plate, thorax, and pygidium unknown.

Discussion. As discussed in Geyer (2017), the material from the Franconian Forest is the only known representative of *Enixus* found in West Gondwana, which belongs to the *enigmaticus* clade of the genus, whereas the species from the Moroccan Atlas region (Geyer 1998), the form described from the Cantabrian Mountains of Spain (Gozalo et al. 2007), and the species from the Dead Sea area of Jordan (Rushton & Powell 1998; Elicki & Geyer 2013) are close relatives of *Enixus antiquus* (Chernysheva, 1956), the index fossil of the lower Amgan *Enixus antiquus* Zone, which defines the basal middle Cambrian in the Siberian Anabar–Sinsk facies region.

The form that occurs in the Tannenknock Formation is characterised by a slightly clavate glabella with a relatively stout anterior part, a more-or-less transglabellar S3, but shorter S4, and anterior wings of the cranidium that extend beyond the distal margin of the palpebral lobes (Geyer 2017). Therefore, the specimens are most similar to *Enixus juvenis* (Chernysheva, 1956) from the Amgan *Pseudanomocarina* (=*Kounamkites*) Zone of the Siberian Platform, which is comparable in most characters. As noted by Geyer (2017), the Siberian species differs, however, in having a slightly longer glabella (relative to the length of the cephalon) with a more expanded and slightly longer anterior part, and less extending anterior wings (see Chernysheva 1961, pl. IV, figs. 1–8). In addition, the palpebral lobes in the specimens from the Tannenknock Formation appear to be slightly shorter than those of *E. juvenis*.

Another similar species from Siberia has been described as “*Schistocephalus* ex gr. *juvenis*” from the Amgan *Kounamkites* Zone by Egorova et al. (1976). The species represented by those specimens has a clearly longer, more strongly clavate glabella with S3 and S4 in a distinctly more anterior position on the glabella, and with a nearly evenly curved anterior margin of the frontal lobe, with narrower palpebral areas and a narrower (sag.) preglabellar field.

Enixus amzassiensis (Fedyanina, 1971) (in Chernysheva 1971) from the Altay-Sayan Foldbelt is distinguished as well by a longer and more slender glabella with a nearly evenly curved frontal lobe of the glabella. Other species described from the Altay-Sayan Foldbelt are similar to *E. amzassiensis* so that all of them are distinguished more-or-less easily by their relatively longer glabella. *Enixus tchernyshevae* (Bognibova, 1971) (in Chernysheva 1971) is superficially the most similar species, distinguished by a weakly clavate glabella and a very convex axis as well as a subterminal occipital node. Also similar is *Enixus ishinicus* (Romanenko, 1971) (in Chernysheva 1971), which has a more strongly expanding glabella, a nearly evenly curved anterior margin of the frontal lobe, and narrow palpebral areas. *Enixus anormalis* (Bognibova, 1971) (in Chernysheva 1971) is only known from a single figured cranidium and a pygidium. The glabella in this species has a similar shape and pattern of the lateral glabellar furrows as in *Enixus* sp. aff. *juvenis* from the Franconian Forest area, but reaches almost to the relatively thin (sag. and exsag.) anterior border. *Enixus elandicus* (Romanenko, 1971) (in Chernysheva 1971) is known from evidently distorted specimens only, which exhibit palpebral areas that are distinctly wider (tr.) than those in the specimens from the Franconian Forest and appear to belong to the *antiquus* clade rather than the *enigmaticus* clade. *Enixus planus* (Fedyanina, 1971) (in Chernysheva 1971) also belongs to the *Enixus antiquus* plexus and is thus distinguished by lacking a transcurrent S3. *Enixus impressus* (Fedyanina, 1971) (in Chernysheva 1971), by contrast, is very closely related to the type species of *Enixus*, *E. enigmaticus* (Chernysheva, 1956), and shares an almost subparallel glabella. It has long and relatively prominent palpebral lobes. *Enixus enigmaticus* (Chernysheva, 1956) from the Siberian Platform, finally, is clearly distinguished from the species represented by the material from the Franconian Forest in having a slender glabella with subparallel sides, a terminal occipital thorn, a gently rearward curvature of the median sector of S3, and a granulose ornament of the cuticle.

Stratigraphy. *Enixus* sp. aff. *juvenis* occurs in both the Galgenberg and Wildenstein members of the Tannenknock Formation. However, only one specimen (SSMM 10760) has been discovered to date in rocks of Galgenberg shale facies at locality W11. The other specimens come from rocks of the Wildenstein facies, from rocks assigned to the younger *Ornamentaspis frequens* Biozone. The rare occurrence of *Enixus* sp. aff. *juvenis* does not permit to indicate a precise stratigraphic range. However, the species ranges at least from the upper part of the *Kingaspidoides frankenwaldensis* Zone in Gal-genberg shale facies into the *Ornamentaspis frequens* Zone in Wildenstein facies in accordance with what is expected from the range of the similar species from the Siberian Platform.

Superfamily Paradoxidacea Emmrich, 1839

Family Paradoxididae Emmrich, 1839

Subfamily Paradoxidinae Emmrich, 1839

Genus *Acadoparadoxides* Šnajdr, 1957

Type species. Paradoxides sacheri Barrande, 1852, from the *Eccaparadoxides pusillus* Biozone, Jince Formation of the Barrandean region, Czech Republic; by original designation.

Discussion. For taxonomic concept of the *Paradoxides* group and the early phylogeny of *Acadoparadoxides* see extended discussion in Geyer & Vincent (2015) and Nowicki & Żylińska (2018).

Acadoparadoxides sp. A

Figs. 43, 44A?, 45

v 1923 *Paradoxides spinosus* Boeck – Wurm, pl. III, figs. 8, 9.
? 1960 *Paradoxides* aff. *pinus* – Sdzuy: p. 108.
1997 *Acadoparadoxides* aff. *pinus* – Geyer & Wiefel: p. 100.
v 2017 *Acadoparadoxides* sp. A – Geyer: p. 46, 48–49, fig. 21a–l.

Studied material. Ca. 55 confidently identified and ca. 30 tentatively assigned cranidia or cranidial fragments, several partial dorsal exoskeletons, ca. 6 (6) librigenae, ca. 12 (11) hypostomata, ca. 5 (1) incomplete pygidia, numerous fragments of thoracic pleurae. In repository: From locality W6 (cranidium under MMUW 2917-D-916); from locality W8 (ca. 20 cranidia and cranidial fragments under MMUW 2017D-078, -213a, -234b, -236, -249b, -251a, 258a, -267, -303e, -309a, -502, -775a, -777, -1012, SSMM 10514, 10571, 11103b, 11104a and 11111a; 6 hypostomata under MMUW 2017D-048, -250a, -265, -780, SSMM 10512 and 10513; librigena under MMUW 2017D-051a; partial thorax under MMUW 2017D-259); from locality W9 (10 cranidia under SNSB-BSPG 1924-XII-1 [original specimen of Wurm 1923, pl. III, fig. 8], BLfU 5735SG015018, presently under SMF 79018; original specimens of Wurm 1923, pl. III, fig. 9, MMUW 2017D-127, -701, SSMM 10333, 10335, 10336a, 10337, 10338 and 10381; pygidium under MMUW 2017D-198a); from locality W12 (three cranidia under MMUW 2015A-580a and -558; cranidium with detached fixigena under MMUW 2015A-580); from locality W12a (four partial cranidia under SSMM 10631, 10632, 10640 and 10642; cranidium with loosely attached librigena and slightly disarticulated first thoracic segment under SSMM 10628; three incomplete hypostomata under SSMM 10641, 10644a and 10645; incomplete thoracic segment under SSMM 10654; two partial pygidia under SSMM 10634 and SSMM 10643); from locality W13a (four cranidia under MMUW 2015A-482, -483, -484-I and -484-II, -487); from locality W14a (cranidial fragment under MMUW 2015A-435; incomplete thoracic segment under MMUW 2015A-434); from locality W14b (incomplete cranidium under SSMM 10189, thoracic segment under SSMM 10190); probably from locality W14b (two incomplete cranidia under SMSN 75643-1b and SMSN 75643-3); from locality W15 (three cranidia under SSMM 10340, 10342 and 10344; hypostome under SSMM 10343); from locality W15a (five incomplete cranidia under MMUW 2017D-679, -680, -681, -682a and -683).

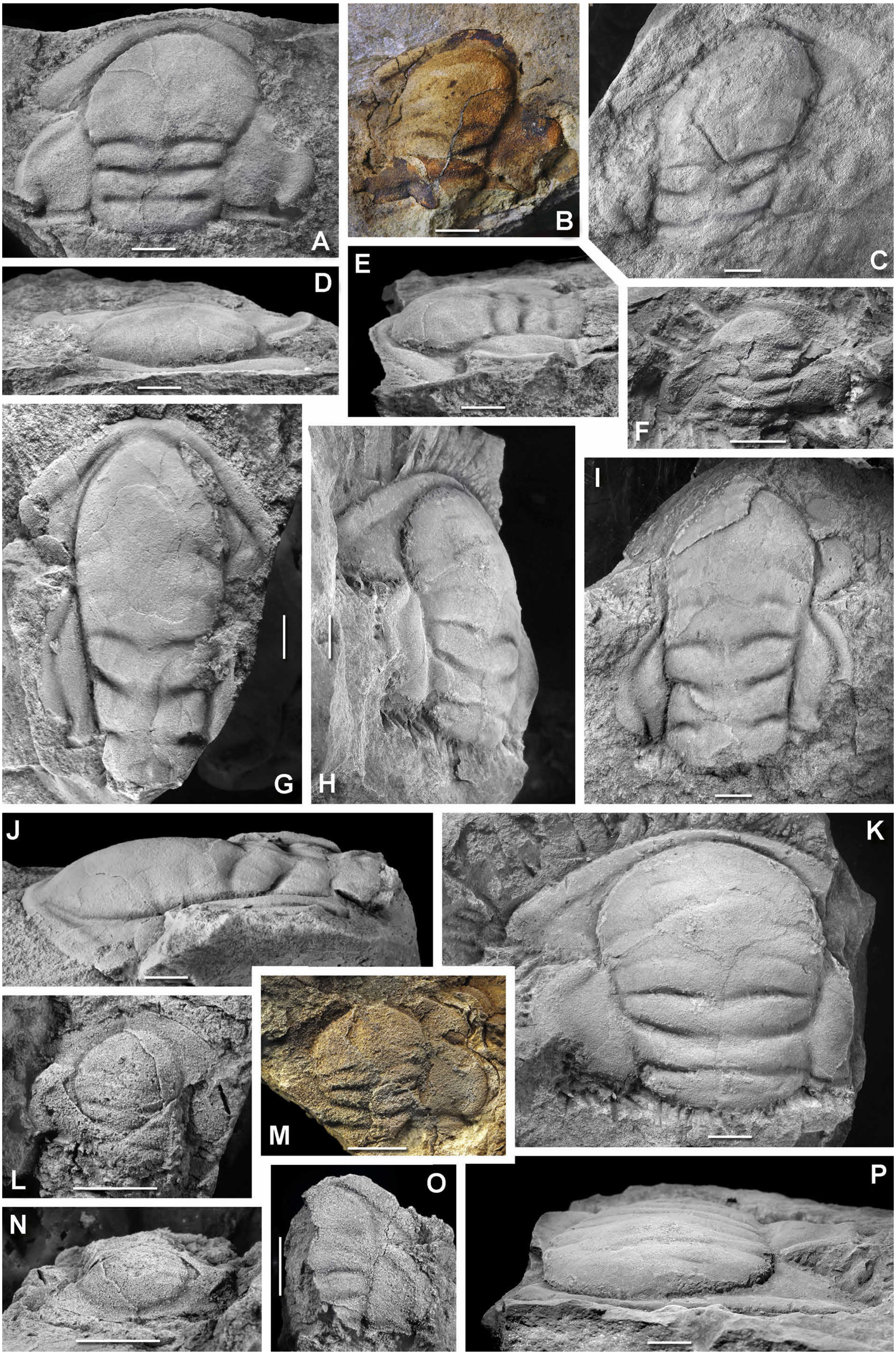
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Fig. 43: *Acadoparadoxides* sp. A. **A, D, E** SNSB-BSPG 1924-XII-1, original specimen of Wurm 1923, pl. III, fig. 8, cranidium, internal mould, dorsal (A), anterior (D) and lateral (E) views; from locality W9; **B** SSMM 10514, cranidium, internal mould; from locality W8; **C** SSMM 10337, cranidium, internal mould; from locality W9; **F** SSMM 11103b, incomplete cranidium, internal mould; from locality W8; **G, J** SSMM 10333, incomplete cranidium, internal mould, dorsal (G) and lateral (J) views with well recognisable ocular lines; from locality W9; **H, K, P** SMF 79018 (= BLfU 5735SG015018), partial cranidium, internal mould, oblique lateral (H), dorsal view with well recognisable ocular lines (K) and oblique anterior (P) views; from locality W9; **I** MMUW 2017D-327, partial cranidium, internal mould; from locality W9; **L, N** MMUW 2017D-249b, incomplete cranidium, internal mould, dorsal (L) and anterior (N) views; from locality W8; **M** SSMM 11111a, partial cranidium, internal mould; from locality W8; **O** MMUW 2017D-303e, fragment of small cranidium, internal mould; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Material tentatively attributed to Acadoparadoxides *sp. A:* From locality W8 (13 cranidia and cranidial fragments under MMUW 2017D-017, -212a, -261, -775cI, -1009a, SSMM 10569, 10570, 11053b, 11071b, 11131b, 11135a, 11135b and 11135c; 9 hypostomata under MMUW 2017D-066, -295, -356, -497, -499, -722, -754b, -1021c and SSMM 11022; three (partial) librigenae under MMUW 2017D-049b, -652b and SSMM 11118c; thoracic pleurae under MMUW 2017D-083, -260c and -266b); from locality W9 (two cranidial fragments under SSMM 10345 and 10380a; hypostome under SSMM 10339; pygidium under MMUW 2017D-198a; thoracic pleurae under MMUW 2017D-397b and -397c); from locality W11 (cranidial fragment under SSMM 10753; partial hypostome, SSMM 10774b; incomplete thoracic segment, SSMM 10774a; genal spine, SSMM 10775); from locality W12 (cranidium under SMF 90982; librigena under SMF 90981); from locality W12a (cranidial fragment, SSMM 10622; fragment of cranidial ventral doublure, SSMM 10648a); from locality W13a (four cranidial fragments under SSMM 10249, 10255, 10256a-I and 10256a-II; hypostome under SSMM 10234); from locality W13e (thoracic pleurae under MMUW 2017D-449 and -464); from locality W15 (cranidial fragment under SSMM 10341); from locality W15a (four cranidia under MMUW 2017D-689, -693, -696 and -698; librigena under MMUW 2017D-691); from locality W17 (two cranidia under MMUW 2017D-802 and -803; librigena under MMUW 2017D-794); from locality T2/T2a (incomplete thoracic segments under SMF 88938 and 88987); from locality T2a (cranidial fragment under SSMM 10055).

Localities and strata. Sample localities W11, W12, W12a, W13a, W14a, T2/T2a, and T2a from Galgenberg Member of the Tannenknock Formation; *Kingaspidoides frankenwaldensis* Zone, probably topmost Cambrian Stage 4. Sample localities W8, W9 and W13e from Wildenstein Member of the Tannenknock Formation; *Ornamentaspis frequens* Zone, probably lowest Wuliuan.

Description. Cephalon subsemicircular, anterior border more-or-less evenly curved in non-deformed, original condition. Lateral border moderately curved, extends into moderately long genal spines. Posterior border almost straight abaxial of cephalic suture, normal to axis.

Glabella pyriform, expands forward to a maximum width of about 1.40 to 1.55 times width across occipital ring in non-deformed, original condition. Posterior section with slightly diverging sides. Frontal lobe convex in transverse profile, glabellar front evenly curved. S1 and S2 well impressed, connected medially by a shallower section; S1 quite strongly indented, connected with axial furrows, clearly posteriorly directed and faintly curved, lateral sections connected by slightly backward curved, broader (sag.) but shallow median section; S2 slightly backward directed from axial furrows, gently curved, connected medially by a short shallow section; S3 and S4 developed as pairs of shallow furrows; S3 slightly forward directed from axial furrow, moderately long; S4 poorly marked to barely visible, anteriorly directed. Occipital furrow well impressed, consisting of moderately broad and moderately deep, nearly straight lateral sections and relatively long (tr.), shallower median section of about the same breadth (sag.) as the lateral sections and with a gentle forward curvature. Occipital ring moderately convex in transverse section, with well-marked median tubercle located slightly posterior to centre. Posterior margin of occipital ring with moderate overall curvature in dorsal view, projects well beyond posterior border.

Axial furrows shallow for most of its extension, narrow, best developed adjacent to posterior part of palpebral areas. Palpebral areas relatively narrow, tr. around one-fifth width of cranidium across mid-length of palpebral lobes, continue into narrow to moderately broad (exsag.) posterolateral projection of fixigenae; small bacculae-type swelling present in posteroproximal corner adjacent to L1 (Fig. 43A, K). Palpebral lobe relatively long, exsagittally of 38–47 percent cephalic length in the studied specimens, posterior end at level of centre of L1; moderately wide (ca. one-fifth transverse width of occipital ring), gently convex and well raised, generally slightly narrower in the frontal one-third. Palpebral furrow relatively shallow, shallowest around mid-length. Palpebral lobe proceeds into short eye ridge that tapers slightly toward glabella and swings forward with an almost rectangular curvature to run along glabella.

Anterior border well developed, bar-like elevated in sagittal and exsagittal section, with almost flat median surface; relatively narrow on sagittal line in front of the glabella, 5–8 percent cephalic length in the large specimens, expands to about double of this exsag. breadth close to the facial suture. Preocular field trapezoidal.

Posterior border moderately broad (exsag.), strongly convex in section, barely tapering toward axial furrow, with a slight node-like swelling posterior to the end of the palpebral lobe where it curves ventrally. Posterior border furrow well incised, nearly straight and subequal in exsag. breadth throughout.

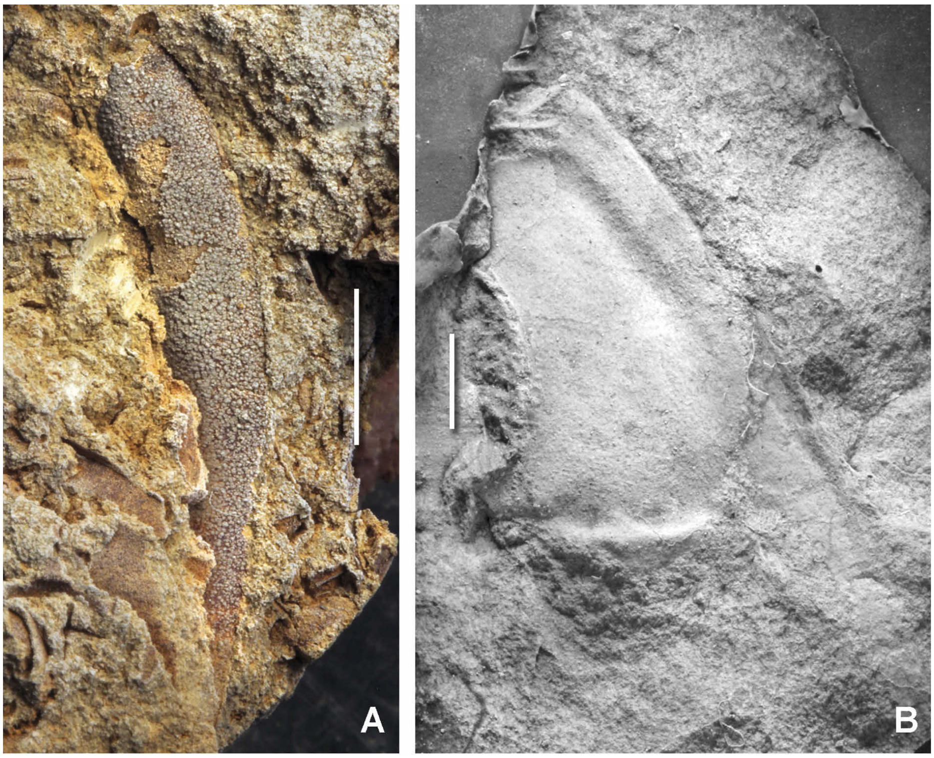

Fig. 44:
A *Acadoparadoxides* sp. A?, SSMM 11118c, librigena, internal mould, ventral view of doublure; from locality W8.
B "*Paradoxides*" sp. A, MMUW 2017D-318L, librigena, latex cast of external mould, dorsal view; from locality W9?.
Both specimens from Wildenstein Member, Tannenknock Formation. Scale bars 5 mm.

Facial suture with moderately diverging anterior branches, sharply curved adaxially when reaching anterior border to meet anterior cephalic margin at an acute angle. Anterolateral corner of cranidium projects slightly beyond the distal margin of palpebral lobe.

Librigena only known from specimens of the Galgenberg Member, with moderately curved lateral border. Genal spine gently curved, appears to have been slightly longer than anterior part of librigena or of approximately the same length. Base of genal spine moderately broad, abaxially developed with curved subrectangular corner from posterior border. Border furrow well-defined. Librigenal field ("ocular platform") moderately broad (tr.).

Rostral plate unknown.

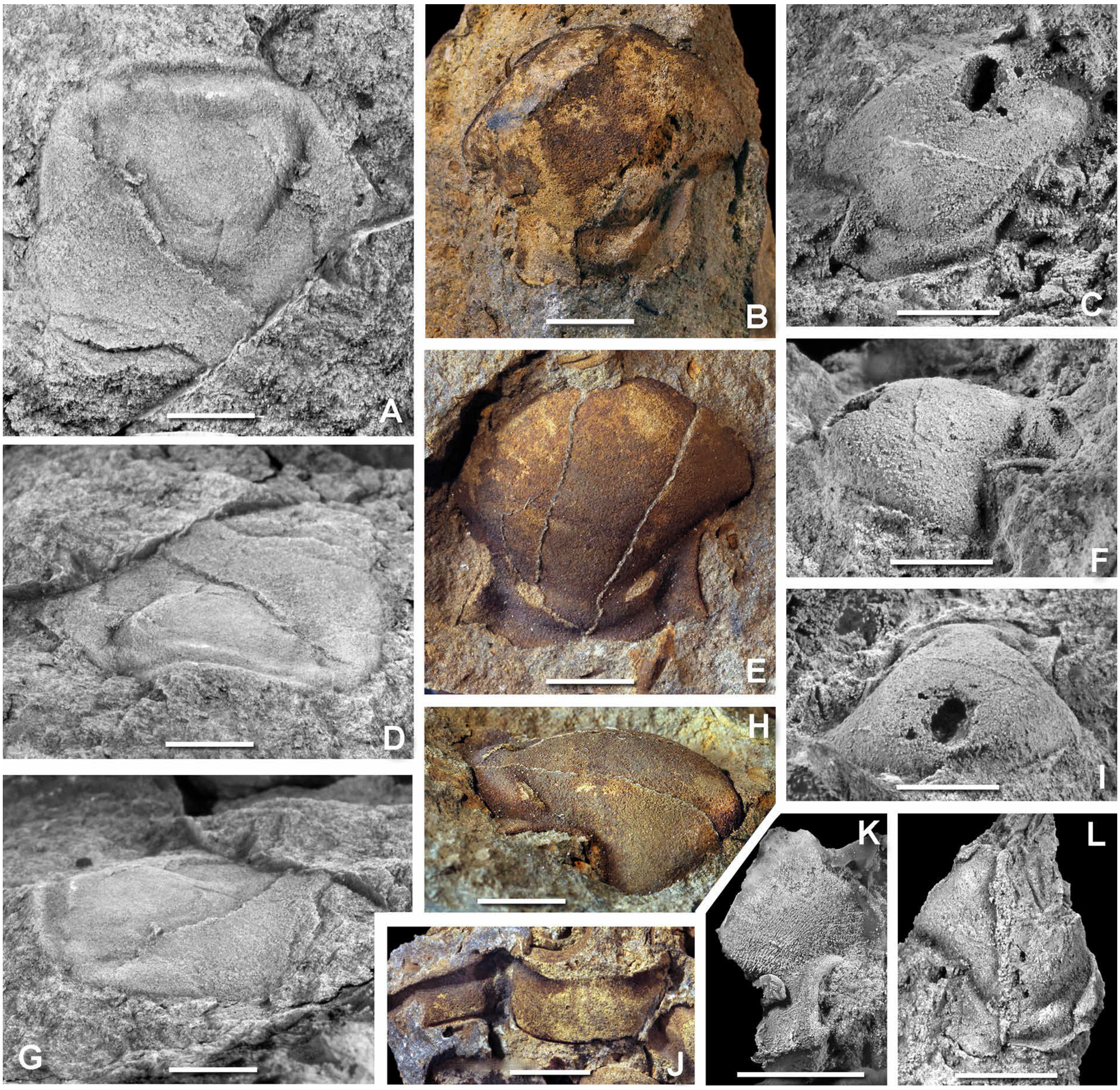

Fig. 45: *Acadoparadoxides* sp. A. **A, D, G** MMUW 2017D-916, partial pygidium, partly exfoliated, dorsal (A), oblique anterior (D) and oblique lateral (G) views; from locality W6; **B** SSMM 10513, hypostome, internal mould; from locality W8; **C, F, I** MMUW 2017D-048, hypostome, internal mould, dorsal, lateral and oblique anterior views; from locality W8; **E, H** SSMM 10512, hypostome, internal mould, dorsal and oblique lateral; from locality W8; **J** SSMM 11071a, fragment of thoracic segment with incomplete axial ring and fragment of left pleura, internal mould; from locality W8; **K** MMUW 2017D-250a, fragment of small hypostome, latex cast of external mould showing terrace ridges on main body and Bertillon pattern on posterior part; from locality W8; **L** MMUW 2017D-265, fragment of small hypostome, internal mould; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Hypostome with anterior lobe of middle body more than 1.5 times wider (tr.) than posterior lobe. Middle furrow transverse, with moderate rearward curvature, shallow and broad (sag.) medially, laterally extending into a pair of maculae. Lateral borders of hypostome subparallel in anterior section, but with distinct posterolateral curvature toward the slightly expanded spines. Posterior border with gentle indentation on median section and with distinct embayment towards bases of posterolateral spines.

Thorax only known from few fragments of disarticulated thoracic segments. Pleurae slightly curved, pleural furrow moderately deep to well indented, with sharply demarcated anterior margin and less distinct posterior margin, crosses pleuron obliquely and fades close to posterior margin.

Pygidium subquadrate to spathulate in outline, slightly longer than wide, lateral margins weakly to gently curved, proceeding with gentle curvature into the slightly curved posterior margin. Pygidial flanks slope ventrally around rhachis and platform to form a more-or-less flat or slightly convex base.

Axis on a prominent but weakly defined platform, broad anteriorly (about half maximum pygidial width), subtriangular, tapers toward the posterior tip with its narrowly curved margin; sag. about 0.5 to 0.6 total pygidial length; axis with only one distinctly marked ring, defined by moderately broad (sag.) transverse furrow that has a broader median section indicating weak scrobiculae seen in other species of *Acadoparadoxides* (e.g., Geyer & Vincent 2015, figs. 26N, 29A); relatively large subterminal depression well-defined in one of the specimens collected from the Galgenberg Member (see Geyer 2017, fig. 21f). Articulating half-ring moderately broad (sag.), about as broad (sag.) as the transverse furrow, which separates it from the first axial ring; laterally obliquely truncated.

Pleural field smooth, fused with almost flat posterolateral and posterior border. Anterolateral border low to moderately convex. Ventral doublure wide (sag. and tr.) in the posterior half (see Geyer 2017, fig. 21f).

Dorsal surface of cranidium with terrace ridges on anterior border. Middle body of hypostome covered by a bertillon pattern. Thoracic pleurae smooth, occasionally with terrace ridges. Dorsal surface of pygidium smooth except for a few lines on the flanks. Ventral doublure of pygidium with coarse terrace ridges subparallel to the posterior margin.

Dimensions. The best preserved cranidia are relatively small and point to a total width of the cranidium of ca. 2 to 5 cm only. However, this is certainly a sampling artefact. Large specimens are only preserved as comparatively small fragments and thus rarely recognised or collected. A very large fragment of a cranidium attributed to *Acadoparadoxides* sp. A (SSM 10648) is part of the ventral doublure of an anterior wing that points to a total width of the cranidium of more than 15 cm. Best preserved pygidium is ca. 17 mm wide (Fig. 45A, D, G).

Discussion. Specimens of the form described herein have also been collected from the Galgenberg Member of the Tannenknock Formation and characterised and illustrated in Geyer (2017) under the same name. The material of *Acadoparadoxides* sp. A represents a hitherto unknown species. However, the sclerites are too incomplete to allow a precise discrimination in respect to further findings elsewhere. The issue of the intricate pattern of phylogenetic development and the problems that may arise with species based on insufficiently known material have been discussed by Geyer & Vincent (2015).

The specimens from the Wildenstein Member described here are generally in accordance with that of the Galgenberg Member. However, the Wildenstein specimens supplement the morphological characteristics provided in Geyer (2017) in a few aspects. The pygidia from the Wildenstein Formation indicate that the lateral margin of the pygidium may develop a gentle curvature rather than being almost straight.

The hypostomata have lateral borders which are subparallel or slightly diverging in the anterior section, but show a distinctive posterolateral curvature toward the curved spines, which extend well beyond the level of the posterior margin – characters that were not well developed in the hypostomata known from the Galgenberg Member, but are typical for species of *Acadoparadoxides*.

The few known pygidia that can be assigned to *Acadoparadoxides* sp. A have a spathulate outline of (roughly) subequal length and width, which is unique among *Acadoparadoxides*. A single pygidium with a similar outline has been reported from the well-studied Tarhoucht section in the eastern Anti-Atlas, Morocco (*Acadoparadoxides* sp. A in Geyer & Vincent 2015, fig. 29A, 29B) and originated from coeval strata. The Moroccan form differs obviously in having a slightly more elongate pygidial rhachis and lacks a subterminal depression on the rhachis which is seen in the specimen(s) from the Franconian Forest. A few other characters also differ in minor aspects, but it cannot be excluded that the pygidium from the Anti-Atlas represents the same species.

A complete dorsal exoskeleton with a similar morphology of its pygidium and probably recovered at Tarhoucht is known from the fossil market (erroneously assigned to *A. briareus* under https://sgfossil-hoarder.wordpress.com/2012/02/10/largest-trilobites-acadoparadoxides-briareus/). However, this specimen is largely restored by artificial materials and was not available for this study.

“*Paradoxides*” sp. A

Figs. 44B, 46, 47?

Material and localities. Ca. 15 incomplete cranidia or cranidial fragments, four incomplete librigenae. From locality W9 (11 cranidia under MMUW 2017D-312, -313, -315, -316, -320, -323, -327, -331, -332, -341 and -347; four librigenae under MMUW 2017D-318, -319, -321 and -322); from locality W15a (cranidium under MMUW 2017D-348).

Specimens tentatively assigned to “*Paradoxides*” sp. A: From locality W9 (three cranidia under MMUW 2017D-329, -334, -340 and SMNS 75643-4); from locality W14b (SMNS 75643-1a).

Description. Cephalon subsemicircular, anterior border more-or-less evenly curved in non-deformed, original condition. Glabella pyriform, expands forward to a maximum width of about 1.40 to 1.45 times width across occipital ring. Posterior section with slightly diverging sides. Frontal lobe convex in transverse profile, glabellar front nearly evenly curved. S1 and S2 well impressed, connected medially by a shallower section. S1 quite strongly indented, connected with axial furrows, posteriorly directed from its origin and faintly curved, lateral sections connected by slightly backward curved, broader (sag.) but shallow median section; S2 only slightly backward directed from axial furrows, gently curved, connected medially by a short shallow section. S3 and S4 developed as pairs of shallow furrows; S3 slightly foward directed from axial furrow, moderately long; S4 shallow and but always well recognisable, anteriorly directed. Occipital furrow well impressed, consisting of moderately broad and moderately deep, nearly straight lateral sections and a relatively long (tr.), shallower median section of about the same breadth (sag.) as the lateral sections and with a gentle forward curvature. Occipital ring moderately convex in transverse section, with median tubercle located slightly posterior to centre. Posterior margin of occipital ring with moderate overall curvature in dorsal view.

Axial furrows shallow for most of its extension, narrow, best developed adjacent to posterior part of palpebral areas. Palpebral areas narrow, transversely ca. 10–15 percent width of cranidium across mid-length of palpebral lobes, continue into narrow to moderately broad (exsag.) posterolateral projection of fixigenae; small bacculae-type swelling present in is posterior part. Palpebral lobe relatively long, exsagittally of 37–43 percent cephalic length among the studied specimens, posterior end at level of posterior part of L1 or almost at level of occipital furrow; moderately wide (ca. one-fifth transverse width of occipital ring, but variable in its width, with a tendency to be broader in large/gerontic specimens), gently convex and well raised, slightly to notably narrowing towards anterior end. Palpebral furrow relatively shallow, shallowest around mid-length. Palpebral lobe proceeds into short, ante-riorly directed eye ridge that tapers slightly toward glabella and swings forward to run along glabella.

Anterior border well developed, bar-like elevated in sagittal and exsagittal section, with almost flat median surface; relatively narrow on sagittal line in front of the glabella, 5–9 percent cephalic length in the large specimens, expands to about 1.5 to 1.8 times exsag. breadth close to the facial suture. Preocular field subtriangular.

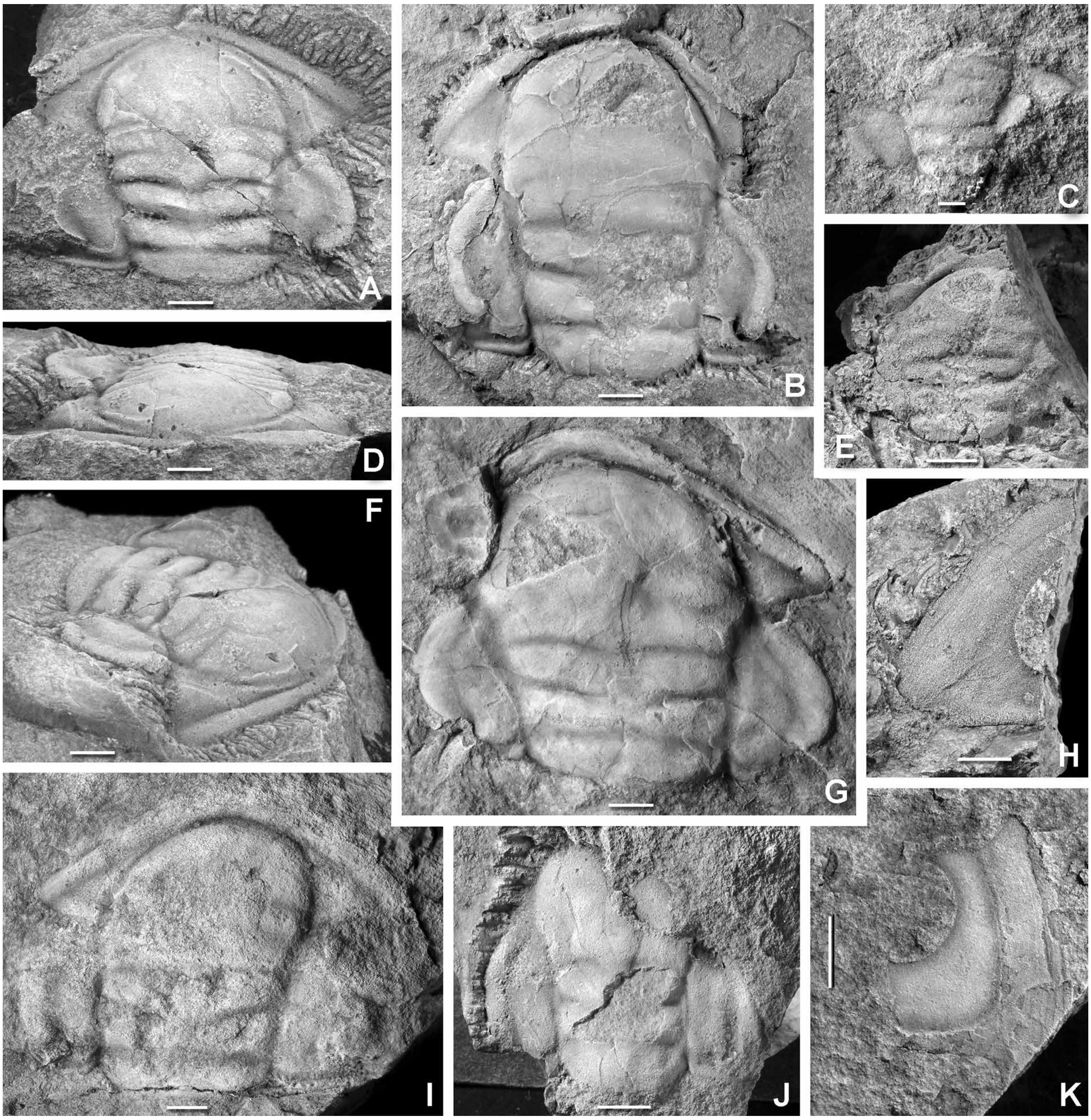

Fig. 46: "*Paradoxides*" sp. A. **A, D, F** MMUW 2017D-701, cranidium, internal mould, dorsal (A), anterior (D) and oblique anterolateral (F) views; from locality W9; **B** MMUW 2017D-328, cranidium, internal mould; from locality W15a; **C** MMUW 2017D-332, fragment of small cranidium, internal mould; from locality W15a; **E** Incomplete small cranidium tentatively assigned to "*Paradoxides*" sp. A, internal mould; from locality W8 (specimen appears to be lost); **G** SSMM 10336, large, gerontic cranidium, internal mould; from locality W9; **H** MMUW 2017D-051, partial librigena, internal mould; from locality W8; **I** SSMM 10335, cranidium, internal mould; from locality W9; **J** MMUW 2017D-313, partial cranidium, internal mould; from locality W9; **K** MMUW 2017D-703, partial librigena, internal mould; possibly from locality W9.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm except for C (1 mm).

Posterior border moderately broad (exsag.), strongly convex in section, barely tapering toward axial furrow, with a slight node-like swelling posterior to the end of the palpebral lobe where it curves ventrally. Posterior border furrow well incised, nearly straight and subequal in exsag. breadth throughout.

Facial suture with moderately diverging anterior branches, sharply curved adaxially when reaching anterior border to meet anterior cephalic margin at an acute angle. Anterolateral corner of cranidium projects slightly to distinctly beyond the distal margin of palpebral lobe.

Librigena only known from incomplete sclerites, with relatively weakly curved lateral border. Genal spine not preserved completely in any of the studied specimens, gently curved, appears to have been somewhat longer than anterior part of librigena. Base of genal spine broad, abaxially developed with curved subrectangular corner from posterior border. Lateral border broad, with low transverse convexity and broad ventral doublure (Fig. 46K). Border furrow well-defined. Librigenal field ("ocular platform") relatively narrow (tr.) (Fig. 46H).

Rostral plate, hypostome, thorax and pygidium are unknown.

Dorsal surface of cephalon with terrace ridges on anterior border, lateral border and ventral doublure of the librigena.

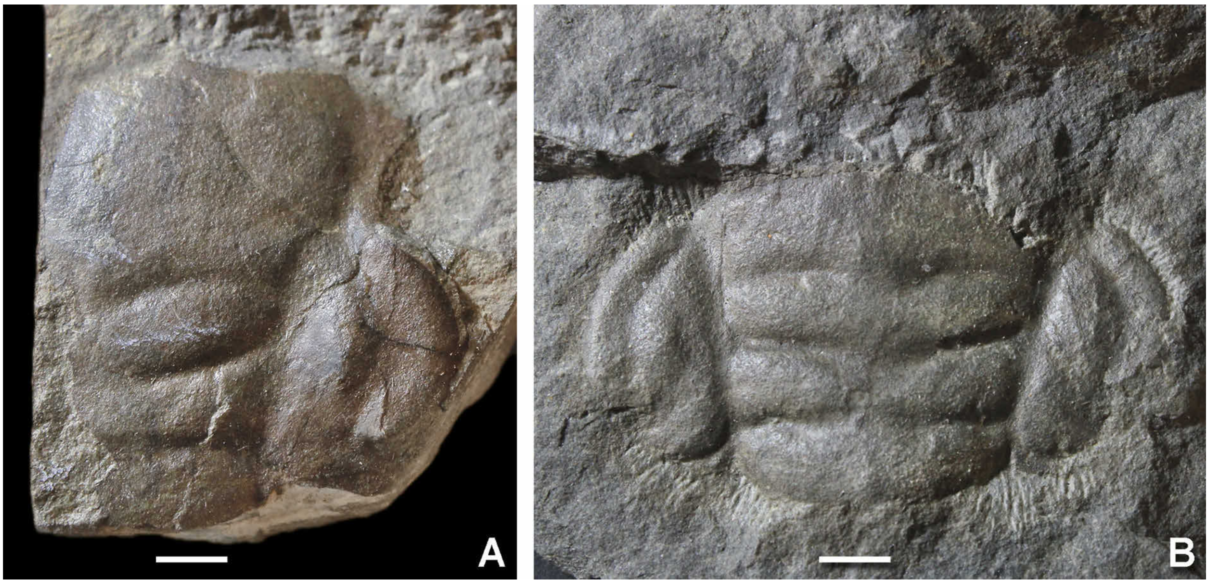

Fig. 47: "*Paradoxides*" sp. A? **A** SMNS 75643-1b, partial cranidium, internal mould; from locality W14b; **B** SMNS 75643-4, partial cranidium, internal mould; from locality W9. Wildenstein Member, Tannenknock Formation. Dorsal views. Scale bars 5 mm.

Discussion. The specimens that represent this form cannot be assigned to an existing species and even a paradoxidine genus because of the lacking knowledge on the pygidial morphology. The cranidia resemble those of *Acadoparadoxides* Šnajdr, 1957 "*en grande tenue*" in the shape of the glabella, the pattern of glabellar furrows, the length and shape of the palpebral lobes and the morphology of the librigenae as far as known, but differ in the large glabella which dominates the cranidium, and in the narrow palpebral areas. The few small cranidia which almost certainly belong to the same form (e.g., Fig. 46C, E) possess a more strongly pyriform glabella with a relatively slender posterior portion and much wider palpebral areas, resembling semi-adult, early holaspid cranidia seen in the *pusillus* clade of *Eccaparadoxides* (see discussion in Geyer et al. 2021/2023). Although this change in shape is immense, it still falls within the range of allometric growth changes.

A number of relatively large sclerites are known, which appear to represent the same species but cannot be assigned to it confidently due to their incomplete preservation. Examples of such specimens are illustrated in Fig. 47.

Other genera within the Paradoxidinae do not readily stand by to furnish this form so that it is kept in open nomenclature even on the generic level. Discussions about the morphological range of the species of *Hydrocephalus* Barrande, 1846 are not included here, but it needs to be emphasised that given the morphological characteristics of its type species, *Hydrocephalus carens* Barrande, 1846, a number of species assigned to the genus during the last two decades are certainly ill-placed and need careful reassessment.

Genus *Eccaparadoxides* Šnajdr, 1957

Type species. Paradoxides pusillus Barrande, 1846, from the Jince Formation, lower Drumian/Caesaraugustan, of the Barrandean region, Czech Republic (by original designation).

Eccaparadoxides sp. A

Fig. 48A–F, H, J, K, G?, I?

Material and occurrence. Six confidently and three tentatively assigned incomplete cranidia and one librigena from most probably the same species. From locality W8 (cranidia and cranidial fragments under MMUW 2017D-234b, 236, -251a, -295 and -309a); from locality W10 (cranidia under SSMM 10361 and SSMM 10362).

Tentatively assigned to *Eccaparadoxides* sp. A: from locality W8 (partial cranidia under SSMM 11010 and SSMM 11136, librigena under MMUW 2017D-234c); from locality W15a (incomplete cranidium under MMUW 2017D-703); from unknown locality of the Wildenstein slice: fragmentary librigena under MMUW 2017D-703.

Description. Cephalon subsemicircular, anterior border more-or-less evenly curved. Glabella pyriform, expands subevenly forward to a maximum width of about 1.40 to 1.50 times width across occipital ring. Frontal lobe convex in transverse profile, glabellar front nearly evenly curved. S1 through S4 all well impressed; S1 and S2 connected medially by a shallower section. S1 quite strongly indented, connected with axial furrows, slightly posteriorly directed from its origin and faintly curved, lateral sections connected by slightly backward curved, broader (sag.) but shallow median section; S2 slightly backward directed from axial furrows or subtransversely directed, gently curved, connected medially by a short shallow section. S3 moderately long, connected across glabella by a broader depression which appears to result from weakly delimited, branching, centrally located furrows, lateral parts slightly forward directed from axial furrows; S4 a pair of moderately well impressed, obliquely anteriorly directed, gently curved furrows. Occipital furrow well impressed, consisting of moderately broad and moderately deep, nearly straight lateral sections and relatively long (tr.), shallower median section of about the same breadth (sag.) as the lateral sections and with a gentle forward curvature. Occipital ring moderately convex in transverse section, with small median tubercle located approximately at centre. Posterior margin of occipital ring with moderate overall curvature in dorsal view.

Axial furrows shallow for most of its extension, narrow, best developed adjacent to posterior part of palpebral areas. Palpebral areas moderately wide, tr. ca. 19–23 percent width of cranidium across mid-length of palpebral lobes; small to moderately large bacculae present adaxially in is posterior part. Palpebral lobe relatively long, exsagittally of ca. 35 percent cephalic length in the studied specimens, posterior end at level of occipital furrow or anterior part of occipital ring; moderately wide, gently convex and well raised, with blunt posterior termination, of more-or-less equal width throughout except for notably tapering anterior end. Palpebral furrow moderately well impressed, shallowest around mid-length. Palpebral lobe proceeds into moderately long, obliquely directed eye ridge that tapers slightly toward glabella and swings forward to run along glabella.

Anterior border well developed, elevated and with gentle convexity in sagittal and exsagittal section, but changing to almost flat median surface near facial suture; relatively narrow on sagittal line in front of the glabella, expands to about 1.5 times exsag. breadth close to the facial suture. Preocular area subtrapezoidal. Posterior border moderately broad (exsag.), strongly convex in exsag. section, of more-or-less subequal breadth throughout, with a slight node-like swelling posterior to the end of the palpebral lobe where it curves ventrally. Posterior border furrow well developed, nearly straight and subequal in exsagittal breadth throughout.

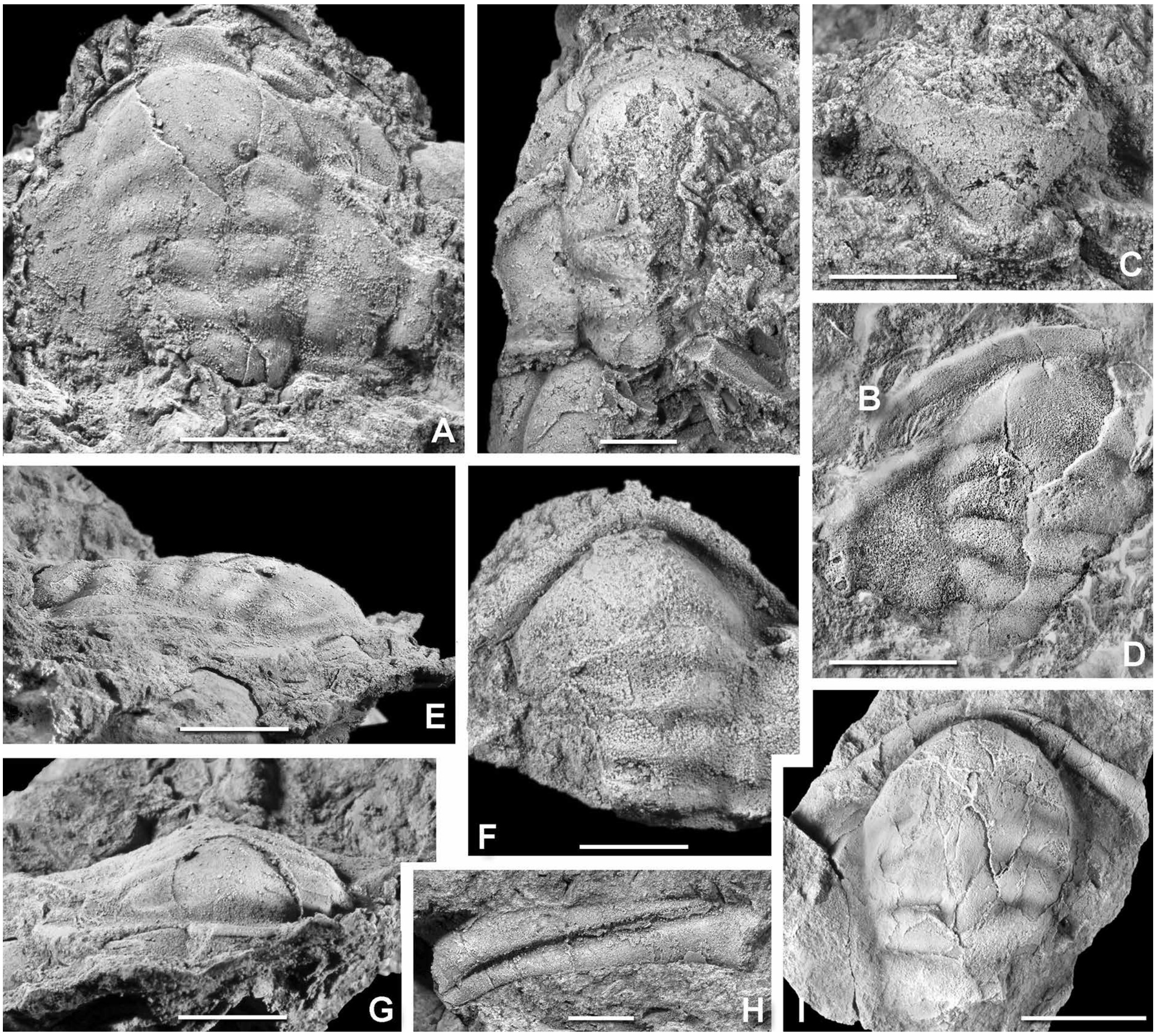

Fig. 48: A–F, I? *Eccaparadoxides* sp. A **A, E, G** MMUW 2017D-251a, cranidium, partially exfoliated, dorsal (A), lateral (E) and anterior (H) views; from locality W8; **B** 2017D-309a, partial cranidium, internal mould; from locality W8; **C** MMUW 2017D-295, incomplete small hypostome, internal mould; from locality W8; **D** MMUW 2017D-234b, partial small cranidium, cast of internal mould, photographically reversed; from locality W8; **F** MMUW 2017D-236, partial cranidium, internal mould; from locality W8; **I** SSMM 10361, incomplete cranidium, internal mould; from locality "Rand Kartoffelacker" (uncertain location).
H "*Paradoxides*" sp. incert., MMUW 2017D-259, partial pleura of anterior thoracic segment, internal mould; from locality W8.
Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Facial suture with moderately diverging anterior branches, sharply curved adaxially at about one-third width of anterior border to meet anterior cephalic margin at an acute angle. Anterolateral corner of cranidium projects to level of central part of palpebral furrow or to adaxial part of centre of palpebral lobe.

A fragmentary librigena from an unknown locality in the Wildenstein slice is tentatively assigned to this form. It has almost now specific characters but shows the typical features known from typical species of *Eccaparadoxides*, i.e., an apparently moderately long genal spine and a relatively distinctly extending librigenal platform portion adjacent to the anterior branch of the facial suture.

Hypostome assigned to this form (Fig. 48C) with anterior lobe of middle body ca. 1.5 times wider (tr.) than posterior lobe. Middle furrow transverse, with moderate rearward curvature, shallow and broad (sag.) medially, laterally extending into a pair of maculae. Lateral borders of hypostome subparallel in anterior section, with slight posterolateral curvature toward the probably slightly extended spines. Posterior border with gentle indentation on median section and with distinct embayment towards bases of posterolateral spines.

Thorax not known with any certainty. However, a few fragments of pleura are known which possibly represent this form. One of them is shown in Fig. 48H, which originates from an obviously robust segment the pleura of which has a relatively sharp and deeply incised, gently curved pleural furrow, anterior and posterior faces of pleurae convex in exsag. profile, with indistinct kink representing an articulating process at anterior margin and indistinct fulcral groove at posterior margin.

Rostral plate and pygidium unknown.

Discussion. The shape of the glabella and the presence of four pairs of distinctly developed glabellar furrows suggest that this form represents a species of *Eccaparadoxides* although the relatively uniform expansion is not typical for the *pusillus* plexus with their curved lateral glabellar margins which has to be regarded as characteristic feature for the genus. The species of *Hydrocephalus* have a superficially similar cranidium in holaspid stages, but their S4 is short and located distant from the axial furrows, and they have distinctly shorter palpebral lobes and a different type of hypostomata.

It needs to be emphasised that the stratigraphic position is surprisingly low for this kind of paradoxidine morphology and makes this form the oldest known *Eccaparadoxides*, regardless of the uncertainty of its precise taxonomy.

Eccaparadoxides? sp. B

Fig. 49

Material and occurrence. Six confidently and three tentatively assigned incomplete cranidia and one librigena from most probably the same species. From locality W8 (cranidia and cranidial fragments under MMUW 2017D-234b, 236, -251, -295 and -309a); from locality W10 (cranidia under SSMM 10361 and SSMM 10362).

Material and occurrence. Single, incomplete pygidium, from locality W8, under SSMM 11141. Wildenstein Member, Tannenknock Formation.

Description. Pygidium longitudinally suboval, maximum transverse width near mid-length, in the order of 70 percent sagittal pygidial length; lateral margin nearly uniformly curved in anterior two-thirds as far as recognisable in the incomplete specimen. Posterior margin unknown. Axis subtriangular in outline, posterior margin with narrow curvature, rests on indistinctly defined socle, axis of ca. two-thirds pygidial length; only one axial ring distinctly defined by a faintly posteriorly curving furrow; remaining part of axis possibly with a pair of shallow, indistinct impressions at about mid-length; with well-defined, moderately broad (sag.) articulating half-ring. Pleural fields apparently smooth, with low longitudinally directed ridge near axis in anterior sector. No pygidial border and border furrow developed for most part, but border developed as a low, poorly defined lobe anterolaterally. Doublure wide/broad as visible on the exfoliated dextral posterolateral part.

Discussion. The single pygidium of this form collected from the Wildenstein Member has a quite typical morphology as seen in the species of the *pusillus* and *lamellatus* clades of *Eccaparadoxides* so that there is little doubt that the species represented by the specimen would need to be placed under this genus if sufficiently known. The genus *Eccaparadoxides* has recently reviewed in detail (Geyer et al. 2021/2023) and has shown to be best characterised by the species of these two clades. It differs, however, from the species of the *pusillus* clade (*E. pusillus* (Barrande, 1846), *E. rohanovicus* Šnajdr, 1986, possibly also *E. kozaki* Kordule, 1999 and *E. oppanol* Šnajdr, 1978, all from Bohemia, *E. epimetheus* Geyer et al., 2021 from the Moroccan Anti-Atlas and *E. zelus* Geyer et al., 2021 from Saxony, Germany) in having an apparently slenderer outline and a longer pygidial axis. The species from the *lamellatus* clade all come from Avalonia and partly have a similar outline (*E. lamellatus* (Matthew, 1883) and *E. acadicus* (Hartt *in* Dawson, 1868), both from south-eastern Newfoundland), but also have a shorter pygidial axis. A similar morphology can be seen in the pygidium of *Acadoparadoxides*? *pinus* (Holm in Westergård, 1936) from Sweden, which is distinguished by a longer pygidial axis and the presence of a pair of faint and strongly rearwardly directed pleural ribs.

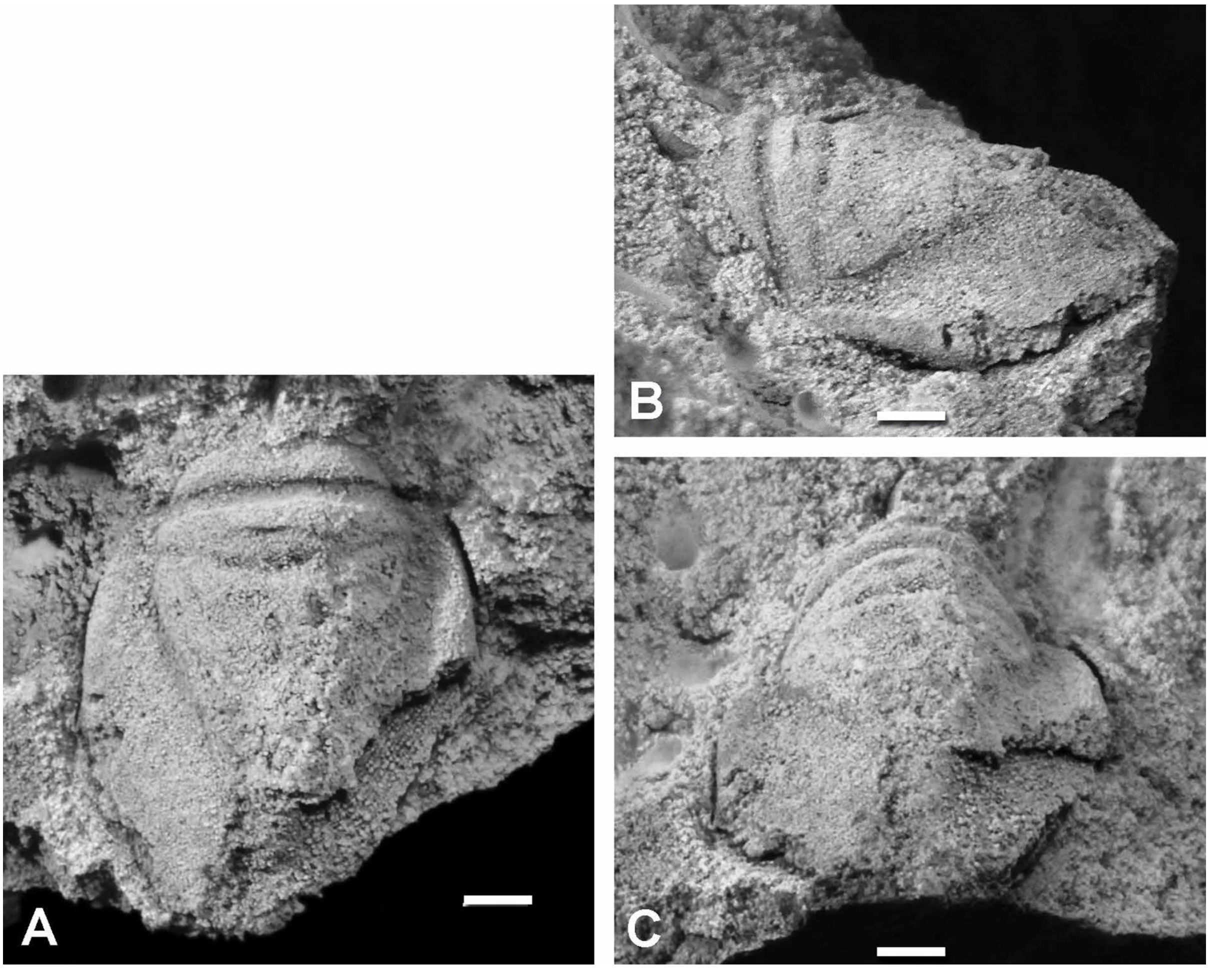

Fig. 49: *Eccaparadoxides*? sp. B. SSMM 11141, incomplete pygidium, internal mould with exposed ventral doublure (with terrace ridges) on right posterior side, dorsal (A), lateral (B) and ob-lique posterior (C) views. From locality W8. Wildenstein Member, Tannenknock Formation. Dorsal views, Scale bars 1 mm.

The pygidium has not been collected from the same localities and comes most probably not from the precise stratigraphic horizon as the cranidia described above under *Eccaparadoxides* sp. A. It is therefore kept separately in open nomenclature.

As discussed above for the cranidia assigned to *Eccaparadoxides*, the stratigraphic position of this pygidium is also surprisingly low and makes it the oldest known *Eccaparadoxides* pygidium, regardless of the uncertainty of its precise taxonomy.

“Order Ptychopariida Swinnerton, 1915”

“Suborder Ptychopariina Richter, 1933”

Discussion. The order Ptychopariida Swinnerton, 1915 as well as the suborder Ptychopariina Richter, 1933 have long been recognised to be paraphyletic taxa. A series of re-groupings of certain clades which have been previously assigned to the Ptychopariida (e.g., the taxa of the newly erected orders Aulacopleurida Adrain, 2011 and Olenida Adrain, 2011) led to a certain clearing, but has not provided an even vaguely satisfying concept for the remaining taxa, with a plethora of families left unassigned to any of the existing orders (e.g., Adrain 2011).

A taxonomy of the former core-group Ptychopariacea has to some degree focused on the nature of the hypostome, which is known to have a natant condition in small to middle-sized ptychoparioids (e.g., Fortey 1990, 1997; Adrain et al. 2004). However, more important for a concise classification is the morphology of the pygidium, in addition to the precise characters of the glabella and the palpebral lobes. These “traditional” taxa of obviously erroneously understood relationships include the superfamilies Ptychopariacea with the families Ptychopariidae Matthew, 1887, Antagmidae Hupé, 1953a, Solenopleuridae Angelin, 1854 and Conocoryphidae Angelin, 1854, which are of critical interest in this study. These families in traditional sense include (according to my count in April 2023) at least 280 genera with more than 1200 formally described species.

This study does not attempt to solve any of the taxonomic issues of these four existing families. However, several remarks need to be made to shed some light on some basic dilemmas. The name Ptychopariidae refers to its type genus *Ptychoparia* Hawle & Corda, 1847 from the Miaolingian of Bohemia; see e.g., Šnajdr (1958) for it morphology and intraspecific variation of its type species, *P. striata* (Emmrich, 1838). This genus and species is typical for “Acadobaltic” Miaolingian ptychoparioids, but differs considerably from the typical ptychopariid(!) trilobites from the Wuliuan and Drumian of Laurentian North America so that an “ordinary” North America ptychopariid is certainly not very closely related to *Ptychoparia*. They are mostly more closely related to what had been assigned to the obsolete family Antagmidae (see below under *Cambrophatictor*). Accordingly, the family Ptychopariidae needs to be strongly restricted.

The core groups of both the Solenopleuridae and Conocoryphidae share the same bauplan types of their glabellas and pygidia. The main difference between the families is the presence/absence of eye and the morphologic structures related to the visual organs. As it can be recognised in several taxa, the loss of visual organs is not a character of high taxonomic significance so that the two families cannot be separated based on this criterion. A few genera, however, which are traditionally assigned to the Conocoryphidae are most probably not closely related to *Conocoryphe* and should be placed outside the family. Solenopleuridae and Conocoryphidae are regarded as subjective synonyms, and Solenopleuridae is given priority.

The family Solenopleuridae in the hitherto used concept includes more than 80 genera with more than 330 species. Debates in the literature pay tribute to widely diverging opinions on the classification.

Particularly the *Solenopleura* plexus of genera with their occurrence centred in the palaeocontinents of Baltica, West Gondwana and Sibiria indicates a mosaic pattern of characters, which according to the general taxonomic procedures forces recognition of numerous different genera with changing character sets.

Superfamily Ptychopariacea Matthew, 1887

Family unassigned

Genus *Cambrophatictor* Geyer, 1998

Type species. Cambrophatictor cataractis Geyer, 1998; from the Jbel Wawrmast Formation of the High Atlas, Morocco, *Ornamentaspis frequens* Zone, Agdzian Stage (by original designation).

Discussion. Cambrophatictor belongs to the group of genera with a "primitive" ptychoparioid morphology, which unfortunately does not allow a precise systematic placement, both due to an overwhelming amount of ptychoparioids with similar morphologies and a regrettably high amount of genera introduced based on material with incompletely known morphological features. With its median occipital node and highly convex glabella, *Cambrophatictor* resembles some of the trilobite genera assigned to the Antagmidae (or "Antagminae") – a grouping that has been shown to be illegitimate since it is based on a *nomen dubium* because of the inappropriate holotype of *Antagmus* (Sundberg 2007). In any case, the shape of the glabella with its subevenly curved front, a weak swelling of the anterior border, and a narrow but convex preglabellar field (not a depression or a clear plectrum) distinguish *Cambrophatictor* from most other genera of Antagmidae-type trilobites. In addition, similar genera are assigned to the Namanoiidae, which differ by a narrow preglabellar field. As discussed in Geyer (1998), more similar are species of the genus *Onchocephalina* Repina, 1960 which typically occur in the upper traditional Lower Cambrian of the Altay-Sayan Foldbelt. Like the glabella of *Cambrophatictor*, the glabella of *Onchocephalina* has a bifurcate S1 with a strongly backward curving posterior branch, a glabella with gentle curvature of the frontal margin, and a similar morphology of the occipital ring. However, *Onchocephalina* has an anterior border which is swollen medially, a preglabellar field developed as a depression, and more prominent palpebral lobes.

A superficially similar species has been described under the name *Chondagraulos fraudulentus* Semashko in Chernysheva, 1971. This species from the Wuliuan Mundybash "horizon" of the Batenev Ridge in the Altay-Sayan Foldbelt differs in major aspects from the typical species of the utiid genus *Chondagraulos* Lermontova, 1940 (Chernysheva 1971, pl. 14, figs. 8, 9) that suggest a placement distant from that genus. The species appears to be closely related to the two species of *Cambrophatictor*. However, that species differs from *Ca. cataractis* and the new species *Ca. meieri* in such features as a subrectangular glabella and shorter palpebral lobes as well as a notably shorter preglabellar part of the cephalon with a relatively short anterior border.

Generally similar in its overall morphology and quite related phylogenetically is *Spencella*? *buttsi* (Resser, 1938) from the *Ehmaniella* Zone of Laurentia (see Sundberg 1994, fig. 7l). The species, introduced as *Solenopleurella buttsi* Resser, 1938, probably represents a new, unnamed genus. *Spencella*? *buttsi* differs from *Cambrophatictor* in having a more transverse cranidium, a clearly truncate front of the glabella, deeper lateral glabellar furrows, and more upwardly directed palpebral lobes.

Another similar genus is *Altikolia* Khayrullina in Khayrullina & Yaskovich, 1961. The type species of that genus, *A. posochovae* Khayrullina in Khayrullina & Yaskovich, 1961, is known from the Cambrian Stage 4 of the Alty-Kol River area in Uzbekistan, where it defines the eponymous biozone in the Stage 4 – Wuliuan boundary interval of the Turkestan Range in Uzbekistan (Khayrullina & Yaskovich, 1961; Khayrullina 1970). A second species, *A. kurshabica* Ghobadi Pour & Popov, 2009, was reported from the Wuliuan Stage of the Alai Range, Kyrgyzstan, but is known only from olistolith boulders in the Silurian Pulgon Formation (Ghobadi Pour & Popov 2009). These species (partly in need of more and better preserved material for a precise portrayal) are characterised by a more regularly tapering and narrower as well as less convex glabella, a broader (sag.) preglabellar field, and medially expanding anterior border. At least the type species bears a faint plectrum. The pygidium of *A. kurshabica* has a morphology quite similar to that of *C. meieri* (see below), unlike that of Laurentian so-called ptychopariine trilobites and clearly different from the Bohemian *Ptychoparia*.

An additional possible species of this genus has been identified as a juvenile form of the agraulid *Skreiaspis affinis* (Billings, 1874) in an unpublished thesis by Fletcher (1972, pl. LXVI, fig. 5a–c), occurring in the *Skreiaspis affinis* Biozone of Avalonian Newfoundland. The single figured specimen of this form is distinguished from *Skreiaspis affinis* by its much more strongly convex glabella defined from the adjacent parts of the cranidium by sharply incised furrows and a subterminal rather than terminal occipital spine. In addition, it has an anterior border, which is quite well demarcated from the preglabellar field.

Cambrophatictor meieri n. sp.

Figs. 50, 51A–I, J?, K–R, 52A–E, F–H?

Holotype. Cranidium, MMUW 2017D-570 (Fig. 50J, M, Q).

LSID. urn:lsid:zoobank.org:act:E074A02E-0E45-4523-A6A5-41FCEF2A536E

Type locality and type stratum. Locality W9b, Wildenstein slice. Wildenstein Member, Tannenknock Formation. Most probably earliest Wuliuan.

Etymology. Named in honour of Stefan Meier (Marktredwitz), who collected a great number of the specimens and provided additional material for this study.

Paratypes. Six incomplete dorsal exoskeletons, ca. 340 cranidia. From locality W1 (two cranidia under MMUW 2017D-511 and -519); from locality W7 (five cranidia under MMUW 2917D—534a, -534b, -534c, -534d and -539); from locality W8 (ca. 255 cranidia under MMUW 2017D-018a, -020a, -026a, -027, -031, -049c, -051c, -061, -069b, -092, -094, -099a, -103c, -116a, -116b, -120, -133, -134, -140b, -167, -170, -171, -173, 175a, -175b, -176, -181d, -182c, -182d, -186, -194a, -194b, -194c, -194d, -197a, -197b, -197c, -201, -202, -206, -207, -208a, -210, -211b, -217, -218, -219b, -220a, -220b, -221, -222a, -222b, -222c, -225a, -226a, -227, -228a, -229a, -229b, -232a, -232b, -232c, -237b, -241, -242a, -242b, -243, -251b, -253b, -256, -257a, -257b, -258b, -272a-h, -274b, -276a, -277a, -278a, -280b, -282a, -287, -288a, -288b, -288c, -289a, -289b, -289c, -290a, -290b, -291a, -299a, -300a, -305c, -205d, -306, -307, -351a, -361c, -367, -369, -388, -389a, -404a, -405, -416a, -417, -601, -602a, -603c, -630a, -645, -707a, -719b, -720, -721, -728, -729, -732a, -732b, -733, -734a, -734b, -741, -744a, -744b, -748, -752b, -772, -785bl, -976b, -977a, -978, -980, -983a, -984b, -989, -1000, -1004, -1007a, -1007b, -1008c, -1015, -1018b, -1018c, -1023, -1024, -1025, SSMM 10392, 10393, 10394a, 10395, 10396, 10397, 10398a, 10399, 10400, 10412b, 10478, 10479, 10480, 10481, 10482, 10484, 10485, 10787e. 10814, 10815, 10819, 11000b, 11000c, 11043a, 11048a, 11048b, 11048c, 11057a, 11104c, 11104e, 11105, 11107, 11108a, 11109b, 11109c, 11109f, 11111c, 11120a, 11120c, 11120e, 11122b, 11187, 11197, 11198a, 11338, 11342a, 11345b, 11348a, 11348b, 11367a, 11443d, 11444, 11445, 11446, 11448, 11450, 11451, 11455b, 11456, 11462, 11463, 11464a, 11464b, 11465, 11468, 11472a, 11472b, 11480, 11481a, 11482, 11483, 11484b, 11485, 11486, 11487, 11488, 11489, 11493, 11497b, 11501a, 11502a, 11502b, 11600b, 11601a, 11607a, 11607b, 11609, 11610, 11611a, 11611b, 11612, 11616, 11620, 11622, 11627c, 11627d, 11627e, 11627f, 11628b, 11628c, 11628g, 11631a, 11632, 11633a, 11635, 11636b, 11637, 11639, 11640, 11641, 11644b, 11645a, 11645b, 11646c, 11647a, 11647b and 12318); from locality W9 (two cranidia under MMUW 2017D-768 and -770); from locality W9b (five cranidia under MMUW 2017D-565, -571, -572 and -581); from locality W13a (6 dorsal exoskeletons under 10243a, 10243b, 10244a, 10244b, 10244c and 10244d; 6 cranidia under SSMM 10217, 10241, 10242, 10244e, 10246 and 10248); from locality W13b (17 cranidia under MMUW 2017D-398a, -399a, -401a, -401b, 402, -403, -425, -427, -428, -429, -430 and -431a–f); from locality W13e (25 cranidia under MMUW 2017D-438, -488, -489a, -491a, -491b, -491c, -491d, -604, -605, -606, -607, -608, -611, -614a, -614b, -614c, -615a, -615b, -615c, -616a, -616b, -619a, -619b, -622 and -624); from locality W13f (two cranidia under MMUW 2017D-1035 and -1036); from locality W16a (cranidium under MMUW 2017D-825); from locality W17 (two cranidia under MMUW 2017D-804b and -811); from locality W18a (three cranidia under MMUW 2017D-540a, -540c and -547d); from locality W19b (cranidia under MMUW 2017D-935b, -935c, and -937b); from locality T2b (cranidium under SSMM 10106).

Tentatively assigned to Cambrophatictor meieri*.* From horizon W8 (enrolled exoskeleton under SSMM 10468; 22 juvenile cranidia under MMUW 2017D-114, -155, SSMM 10419a, 10444, 10445, 10446, 10447, 10448, 10474, 11008, 11083a, 11083b, 11123c, 11123e, 11124a, 11128b, 11479a, 11500b, 11502c, 11627a, 11628h and 11644d; 9 pygidia under 11116d, 11481b, 11623a, 11624, 11625, 11626a, 11627a, 11628e and 11628f); from locality W9b (three juvenile cranidia under MMUW 2017D-567c, -569 and -583); from locality W12a (cranidium under SSMM 10647); from locality W13a (28 cranidia under SSMM 10239a-k [15 cranidia], 10240a-i [13 cranidia]); from locality W13e (four cranidia under MMUW 2017D-483, -617a, -671a and -672); from locality W13f (cranidium under MMUW 2017D-1034b); from locality W19a (cranidium under MMUW 2017D-830).

Diagnosis. Species of *Cambrophatictor* with glabella of ca. 50 percent cranidial width across its widest part at L1; ey-e ridges nearly straight in its adaxial part and with faint continuation to frontal lobe across axial furrow, only slightly oblique to axis; preglabellar field narrow on sagittal line, of less than half sagittal breadth of anterior border.

Description of adult morphology. Cranidium subtrapezoidal in outline, with curved anterior margin and extending posterolateral portions. Ratio length on sagittal line (excl. occipital spine) to transverse width across palpebral lobes ca. 0.90–0.95 (0.87–0.96; n=12).

Glabella transversely moderately to strongly convex, lateral profile gently convex in the posterior half, progressively sloping towards anterior; of subovoid outline when occipital ring included, widest across anterior part of L1, width across L2 barely smaller, pronouncedly tapering forward from L3; frontal lobe with rounded anterolateral corners and a gently curved anterior margin, occasionally with feeble straight portion across sagittal line; length ca. 69 to 78 percent cephalic length (n=12), transverse width across widest portion at L1 ca. 50 percent (47–56 percent) transverse cranidial width across centre of palpebral lobes (n=12). Generally with three pairs of glabellar furrows, all shallow and barely recognisable on the exterior of the cuticle, better developed on internal moulds, with better impressed parts near axial furrows, and fading towards midline; S1 bifurcate, anterior branch roughly normal to axis, posterior branch directed backward and gently curved, very shallow for most distance; S2 slightly curved, backward directed, shallow; S3 faint, slightly forward directed or more or less normal to axis. Occipital furrow well-defined throughout, with slightly backward directed narrow and deep lateral sections and a slightly wider and somewhat shallower median section. Occipital ring of narrow subtriangular outline in dorsal view, with narrow lateral portions developing into a subacute tip with a prominent subterminal thorn or short spine; sagittal length ca. 10 percent cephalic length.

Axial furrows well-defined, moderately deep, slightly shallower in front of the glabella. Palpebral lobe short to moderately long, in adult individuals exsag. of ca. 26–29 percent cephalic length (longer in juveniles), slightly oblique to axis, anterior end in transverse line with posterior part of L4 or S3, posterior end about in transverse line with S1; palpebral lobe prominent, rises steeply from cheek, defined by shallow and narrow palpebral furrow, which is slightly curved adaxially near anterior end.

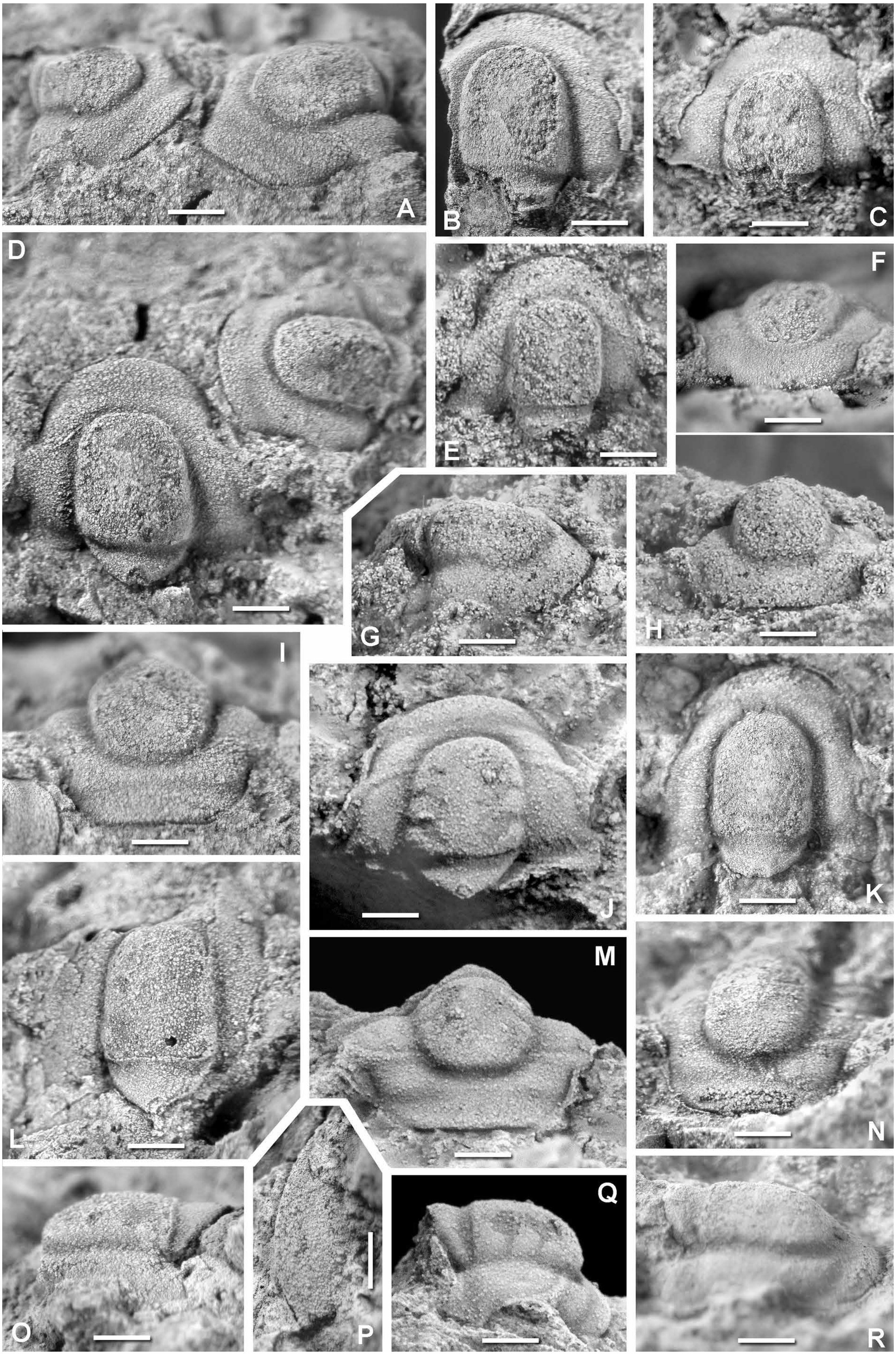
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Fig. 50: *Cambrophatictor meieri* n. sp. **A, D, I** MMUW 2017D-232a, b, paratypes, two cranidia, internal moulds, oblique anterolateral (A), (oblique) dorsal (D) and anterior (I) views; from locality W8; **B** MMUW 2017D-220a, paratype, incomplete cranidium, internal mould with relics of the cuticle at right palpebral lobe; from locality W8; **C, F** MMUW 2017D-218, paratype, incomplete cranidium, internal mould, dorsal and anterior views; from locality W8; **E, G, H** MMUW 2017D-222a, paratype, incomplete cranidium, internal mould, dorsal (E), oblique lateral (G) and anterior (H) views; from locality W8; **J, M, Q** MMUW 2017D-570, holotype, incomplete cranidium, internal mould, dorsal (J), anterior (M) and lateral (Q) views; note fine granules; from locality W9b; **K, N, R** MMUW 2017D-242a, paratype, incomplete cranidium, internal mould, dorsal (K), oblique anterior (N) and lateral (R) views; from locality W8; **L, O** MMUW 2017D-221, paratype, incomplete cranidium, internal mould, dorsal (L) an lateral (O) views; from locality W8; **P** MMUW 2017D-231a, paratype, librigena, internal mould; from locality W8. From locality W8. Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 1 mm.

Eye ridge forms shallow elevated lobe directed inward and forward to axial furrow anterior to S3, with nearly straight adaxial part and faint continuation to frontal lobe across axial furrow. Palpebral area gently convex, moderately wide (tr.), transverse width between posterior ends of palpebral lobe and axial furrow ca. 45 percent maximum glabellar width. Posterior area of fixigena extends into an exsagittally relatively narrow posterolateral projection.

Anterior border convex, moderately broad, growing in width from the suture to the sagittal line to more than double breadth, on the sagittal line variably of ca. 12–16 percent cephalic length; anterior margin with considerable curvature in dorsal view, with faint dorsal bulge in anterior view. Anterior border furrow a moderately wide (sag. and exsag.) depression, distinctly shallower in its median sector.

Preglabellar field present, but narrow on sagittal line, of less than half width of anterior border, slightly sunken in front of the glabella; developing into convex, moderately broad (exsag.) genal fields, which slope distinctly towards anterior border furrow and abaxially towards facial suture. Anterior branch of suture parallel from anterior ends of eyes, then curving inward in a gentle arc and with a clear adaxial curvature after meeting the anterior border, cutting it very obliquely. Posterior border fairly narrow (exsag.) next to axial furrow, growing in width abaxially, directed slightly posterolaterally with a gentle curvature and growing in breadth up to a fulcral point about one-third distance from posterolateral tips; distinctly convex. Posterior border furrow moderately wide (exsag.) and relatively deep, slightly shallower adaxially.

External surface of cranidial cuticle appears to have been smooth or densely covered with minute granules (except for smooth lateral glabellar, axial, and border furrows).

Thorax only known from incomplete dorsal exoskeletons, composed of up to at least 15 segments in the present material (Fig. 52A–C). Axial rings of segments 4 to 15 of more-or-less uniform shape (sag. and exsag.), the length and width reduced progressively posteriorly. Transverse width of axial ring ca. 30 percent overall width of the segment. Each ring has a relatively narrow articulating half-ring, a narrow articulating furrow, and a slight lateral inflation indicating the attachment site of ventral muscle.

Pleurae widest (tr.) at about segments 3 and 4, decreasing progressively in width (tr.), becoming slightly more strongly rearwardly directed in the posterior fifth of the thorax. Pleural furrows relatively narrow and moderately well impressed, more-or-less straight or faintly s-shaped, fading short distance from pleural tips. Pleural ends probably developed as bluntly rounded tips. In anterior view, the pleurae show a distinct geniculation at ca. two-thirds of its transverse length from axial furrow, which corresponds with the articulating of adjacent segments.

First thoracic segment not well enough preserved in any of the available specimens to recognise morphological details. Segments 2 and 3 differ from posterior ones in having axial rings the anterior margin of which swings slightly backward to allow a dorsal flexure against the anteriorly adjacent segment. Its pleurae seem to have a slightly rearwardly directed abaxial part.


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Fig. 51: **A–I, J?. K–R** *Cambrophatictor meieri* n. sp. **A, D** MMUW 2017D-280b, paratype, cranidium, internal mould, dorsal (A) and anterior (D) views; from locality W8; **B** MMUW 2017D-217, paratype, incomplete cranidium, internal mould; from locality W8; **C, F** MMUW 2017D-210a, paratype, incomplete cranidium, internal mould, dorsal and lateral views; from locality W8; **E** MMUW 2017D-935b, paratype, incomplete cranidium, internal mould; from locality W19b; **G** SSMM 11104e, paratype, cranidium of immature individual, internal mould; from locality W8; **H** SSMM 10787c, paratype, cranidium of immature individual, internal mould; from locality W8; **I** SSMM 11105, paratype, incomplete cranidium of immature individual, internal mould; from locality W8; **J** MMUW 2017D-935f, meraspid cranidium, internal mould; from locality W19b; **K** SSMM 10479, paratype, incomplete cranidium, internal mould; from locality W8; **L** SSMM 10488, paratype, cranidium of immature individual, internal mould; from locality W8; **M** SSMM 11057b, paratype, meraspid cranidium, internal mould; from locality W8; **N, Q, S** MMUW 2017D-222b, paratype, incomplete cranidium, internal mould, dorsal (N), lateral (Q) and anterior (S) views; from locality W8; **O** incomplete cranidium, internal mould showing typical occipital thorn; from locality W8 (specimen apparently lost); **P, R** incomplete cranidium with preserved finely granulose cuticle, dorsal and lateral views; from locality W8 (specimen apparently lost). Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 1 mm except for J (=500 µm).

Rostral plate and hypostome are unknown.

Pygidium (Fig. 52F, G) subsemielliptical in outline, length (sag.) ca. 60–65 percent maximum width (tr.). Axis reaches almost to the posterior pygidial margin, slightly tapering backward, width (tr.) at anterior ring ca. 55 percent maximum pygidial width; composed of 2 or 3 axial rings and a terminal axial piece; axial rings separated by shallow, broad depressions; posterior rim of axial piece with low curvature in dorsal view. Pleural fields without well-developed pleural furrows. Anterior pygidial border well recognisable, defined by moderately well indented furrow, with considerable angulation in posterior view that defines a well-developed articulation process at ca. one-fourth to one-third transverse width from axial furrow; lateral and posterior pygidial borders obsolescent. Surface covered with small granules except for well-developed furrows.

Ontogenetic and preservational differences. *Cambrophatictor meieri* n. sp. shows a considerable morphologic variation, which is a result of changes in growth rate during ontogeny as well as preservational modifications.

The relatively large number of immature cranidia available for this study suggests obvious ontogenetic trends which affect the following characters:

(1) The palpebral lobes decrease in length with increasing overall size from more than one-third cephalic length to less than 30 percent. During the same interval they turn from a slight to a more oblique position.

(2) Juvenile cranidia have a narrower (sag., exsag.) anterior border which is approximately as wide as the preglabellar field, being better defined medially by a distinct anterior border furrow.

(3) Cranidia of immature specimens have a less ovoid glabella, often with nearly parallel lateral margins or tapering forward with straight lateral margins. Consequently, the anterior margin of the glabella has a more pronounced curvature than in large cranidia, sometimes with better developed anterolateral corners.

Among the preservational variation, the following differences between external and internal moulds should be emphasised:

(1) Internal moulds of cranidia show much better impressed lateral glabellar furrows than recognisable on the exterior.

(2) The axial furrows as well as the anterior and posterior border furrows are more markedly developed in internal moulds as well as the visibility of the eye ridges.

(3) The occipital spine is developed on internal moulds only as a narrow prominent node.

(4) Some internal moulds show a faint median crest-line on the glabella which cannot be seen on the exterior.

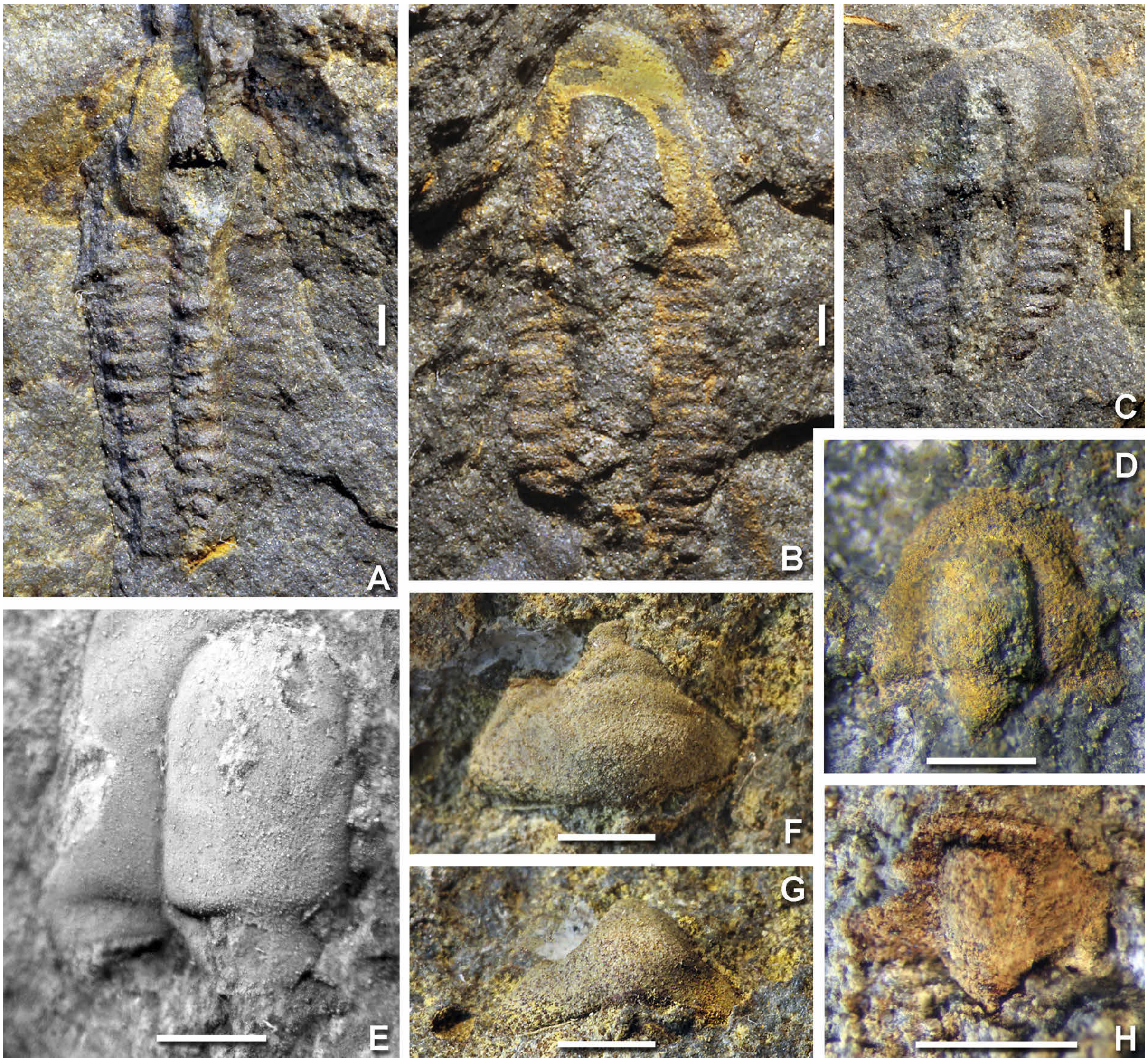

Fig. 52: A–E, F–H? *Cambrophatictor meieri* n. sp. **A** SSMM 10243a, paratype, incomplete dorsal exoskeleton, internal mould; from locality W13a; **B** SSMM 10248, paratype, incomplete dorsal exoskeleton, internal mould; from locality W13a; **C** SSMM 10243c, paratype, incomplete dorsal exoskeleton, internal mould; from locality W13a; **D** MMUW 2017D-581, paratype, partial cranidium with preserved cuticle; from locality W9a; **E** MMUW 2017D-369, paratype, partial cranidium with preserved punctate cuticle; from locality W8; **F, G** SSMM 11019a, pygidium, internal mould, dorsal (F) and posterior (G) views; from locality W8; **H** SSMM 11611a, cranidium of immature individual, internal mould; from locality W8. Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 1 mm.

Discussion. Cambrophatictor meieri n. sp. is the second species of this unusual ptychoparioid genus, which shows an exotic morphology compared with the other trilobites from this stratigraphic level in West Gondwana. The type species, *C. cataractis* Geyer, 1998, in known only from a single locality in the High Atlas of Morocco, from the *Ornamentaspis frequens* Zone and thus with a synchronous occurrence. The Moroccan species has a very similar morphology to *C. meieri* but differs in having a slightly broader (sag.) preglabellar field; a glabella with the broadest part across at the middle part of L1 or immediately in front of the occipital furrow; and the eye ridges are more strongly obliquely directed and having a less curved abaxial portion.

Genus *Cambrodaimona* n. gen.

Type species. Cambrodaimona parablepta n. gen., n. sp.

LSID. urn:lsid:zoobank.org:act:7624833D-EC78-482B-B71A-903AEC131CED

Etymology. Name composed of *Cambrium*, Cambrian, and δαίμωνα (*Daimona*), a Greek mythological figure as a personification of obliviousness; a reference to obscure presence of the type species in the Wildenstein Member.

Diagnosis. Ptychoparioid genus with a moderately to strongly convex glabella in transverse profile, lateral profile gently convex in the posterior half, progressively sloping towards anterior; glabella tapering forward, with subtrapezoidal outline (occipital ring excluded); palpebral lobe short to moderately long, slightly oblique to axis, prominent, rises conspicuously from cheek; eye ridge slightly elevated, direc-ted inward and forward to axial furrow, with nearly straight adaxial part; anterior part of cephalon step-like downthrown, preglabellar field sunken in respect to the frontal lobe forming an inclined ramp in combination with the anterior border furrow; anterior border slightly raised to form a snout-like continuation of this ramp.

Discussion. Cambrodaimona n. gen. is one of the genera of ptychoparioid trilobites with “primordial” characters and represented only by a single species. Accordingly, this raises the question whether the introduction of this additional genus is necessary and indispensable. However, *Cambrodaimona* is unique in respect to the morphology of its anterior part of the cephalon. This is step-like downthrown with respect to the glabella and the fixigenae. Hence, the preglabellar field lies clearly below the level of the frontal lobe and is generally developed as an inclined ramp together with the anterior border furrow, and the anterior border with its morphology of a slight raise forms a snout-like continuation of this ramp. Such a morphology is unknown from any of the genera with a similar morphology and from this stratigraphic interval. The even more platform-like development of the anterior part of the cephalon in the agraulids can be interpreted as a further development of this trend. Insofar, *Cambrodaimona* might represent an ancestor of the Agraulidae.

Cambrodaimona shares most characters with other “primordial” ptychoparioids, such as the co-occurring *Cambrophatictor* (see above), *Litavkaspis* Fatka, Kordule & Šnajdr, 1987 from the upper Wuliuan to lower Drumian *Eccaparadoxides pusillus* Zone of Bohemia, or an unnamed new genus and species from the *Ovatoryctocara granulata* assemblage of the Henson Gletscher Formation of Peary Land, North Greenland (lumped with other taxa under the name *Ptychoparella* sp. A in Blaker & Peel 1988). *Cambrodaimona* differs in at least two characters which reflect important constructional principles and are thus believed to indicate systematically distinctive differences: the shape of the glabella; and the morphology of the anterior part of the cephalon. The glabella of *Cambrodaimona* has a subtrapezoidal outline in dorsal view (occipital ring excluded) and is transversely moderately to strongly convex. Its lateral margins are gently curved and the frontal lobe shows rounded anterolateral corners and a weakly to gently bowed anterior margin. This subtrapezoidal outline with the relatively low curvature of the anterior margin of the frontal lobe distinguishes the genus from most of the classical “ptychopariid” genera and again suggests a similarity with agraulid taxa (such as *Skreiaspis* and *Litavkaspis*). However, the convexity of the glabella is clearly more prominent in *Cambrodaimona* than in the true agraulids, and agraulids have smaller palpebral lobes which raise from the palpebral areas and show only obsolescent palpebral furrows on the exterior of the cuticle (e.g., Fatka et al. 1987, pl. I, figs. 2, 3).

Cambrodaimona parablepta n. gen., n. sp.

Figs. 53, 54A?, B, C, D?, E, F, G? H–N, O?

Holotype. Cranidium, MMUW 2017D-674c (Fig. 53H).

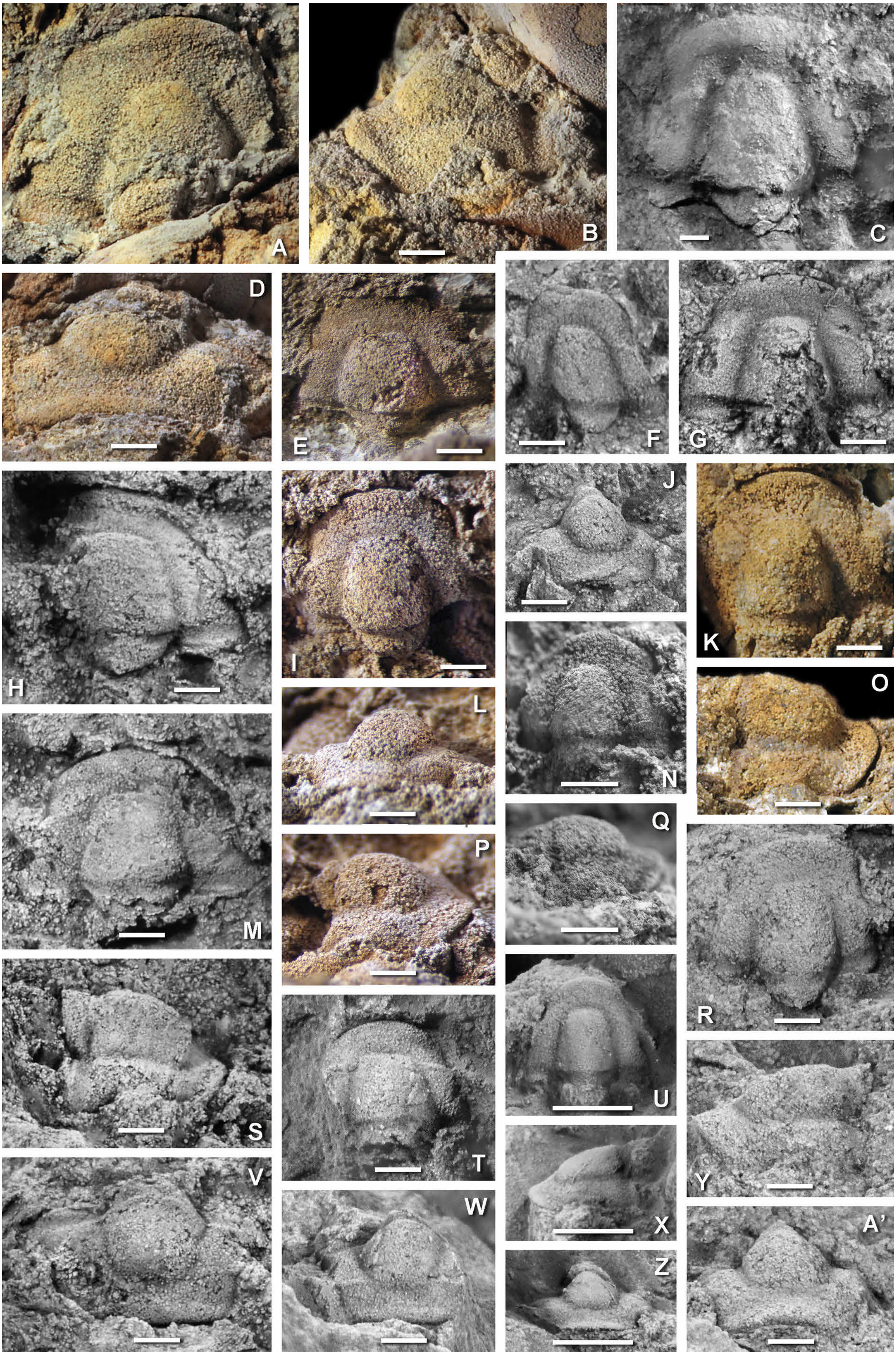
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Fig. 53: *Cambrodaimona parablepta* n. gen., n. sp. **A, B, D** SSMM 11020a, paratype, partial cranidium, internal mould, anterior (A), lateral (B) and anterior (D) views; from locality W8; **C** MMUW 2017D-507a, paratype, cranidium, internal mould; from locality W1; **E** SSMM 11117, paratype, cranidium, internal mould; from locality W8; **F, J** cranidium, internal mould, dorsal and anterior views; from locality W8 (specimen apparently lost); **G** MMUW 2017D-368, paratype, incomplete cranidium, internal mould; from locality W8; **H** MMUW 2017D-674c, holotype, cranidium, internal mould; from locality W8; **I, L, P** SSMM 11106, paratype, cranidium, internal mould, dorsal (I), anterior (L) and oblique lateral (P) views; from locality W8; **K, O** SSMM 11076a, paratype, cranidium, internal mould, dorsal and oblique lateral views; from locality W8; **M, S, V** MMUW 2017D-547b, paratype, cranidium, internal mould, dorsal (M), lateral (S) and oblique anterior (V) views; from locality W18a; **N, Q** SSMM 11104d, paratype, cranidium of immature individual, internal mould, dorsal (N) and oblique lateral (Q) views; from locality W8; **R, Y, A'** MMUW 2017D-096, paratype, cranidium, internal mould, dorsal (R), lateral (Y) and anterior (A') views; from locality W8; **T, W** MMUW 2017D-1034a, paratype, incomplete cranidium, internal mould with deformed frontal lobe of the glabella, dorsal (T) and oblique anterior (W) views; from locality W13f; **U, X, Z** MMUW 2017D-308, paratype, late meraspid cranidium with mineralised cuticle, dorsal (U), lateral (X) and anterior (Z) views; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 1 mm.

LSID. urn:lsid:zoobank.org:act:F570D164-799A-40F4-BCFB-986BFC0FAAE4

Type locality and type stratum. Locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation. Most probably earliest Wuliuan.

Etymology. From the Greek παραβλέπω, ignored, overlooked; a reference to the relatively frequent occurrence of the species in the Wildenstein Member, but having been completely disregarded to date by every record.

Paratypes. Ca. 121 cranidia, single librigena. From locality W1 (cranidium under MMUW 2017D-507a); from locality W8 (105 cranidia under MMUW 2017D-032a, -032b, -033, -051b, -060, -071, -091a, -093, -096, -098, -199, -214, -215, -230, -235a, -260a, -262, -275b, -283b, -283c, -291b, -303g, -308, -368, -379a, -390, -626, -627, -628, -632b, -634, -674c, -708a, -712, -722, -730, -745, -984a, -1006c, -1019, SSMM 10403a, 10421b, 10427, 10443, 10477a, 10788a, 10788b, 10817a, 10818a, 11014a, 11020a, 11057b, 11058, 11076a, 11104d, 11106, 11108b, 11109a, 11123d, 11192a, 11212, 111339b, 11340, 111341a, 11341b, 11342c, 11343, 11344, 11345b, 11346a, 11346b, 11347, 11349a, 11349b, 11350a, 11350c, 11350d, 11443a, 11447, 11449, 11452, 11453a, 11453d, 11454, 11455a, 11459, 11460a, 11460b, 11467, 11469b, 11470a, 11473, 11474, 11475, 11476, 11477a, 11484a, 11494, 11496a, 11496d, 11496e, 11503b, 11608, 11628a and 11638a; librigena under SSMM 11350b); from locality W13b (cranidium under MMUW 2017D-409a); from locality W13e (three cranidia under MMUW 2017D-439b, -443 and -481); from locality W13f (cranidium under MMUW 2017D-1034a).

Tentatively assigned to Cambrodaimona parablepta*:* In repository: Single enrolled exoskeleton, 9 cranidia, single librigena, several incomplete/fragmented thoracic segments: From locality W1 (librigena under MMUW 2017D-515); from sample W8 (enrolled exoskeleton under 10469, cranidia under MMUW 2017D-990, 11059a, 11063, 11065, 11111d, 11117, 11458, 11492, 11500a and 11500c; thoracic segments under 11350e, 11350f).

Diagnosis. Diagnosis of the genus (because of monotypy).

Description of adult morphology. Cranidium subtrapezoidal in outline, with gently curved anterior margin and extending posterolateral portions. Ratio length on sagittal line (excl. occipital spine) to transverse width across centres of palpebral lobes ca. 0.92–1.00 (0.87–1.06; n=11).

Glabella transversely moderately to strongly convex, lateral profile gently convex in the posterior half, progressively sloping towards anterior; of subtrapezoidal outline when occipital ring excluded, widest across central part of L1, lateral margins gently curved; frontal lobe with rounded anterolateral corners and a weakly to gently curved anterior margin; length (including occipital ring) ca. 73–78 percent cephalic length (n=10), transverse width across widest portion at L1 ca. 55 percent (51–60 percent) transverse cranidial width across centre of palpebral lobes (n=10). With three pairs of glabellar furrows, all shallow and barely recognisable on the exterior of the cuticle, slightly better developed on internal moulds, fading towards midline, all directed more-or-less normal to axis. Occipital furrow well-defined laterally, with slightly backward directed narrow and deep lateral sections and a slightly wider and shallower median section. Occipital ring of subtriangular outline in dorsal view, with narrow lateral portions developing into a subacute tip with a prominent subterminal thorn or short spine; its sagittal length ca. 20 percent cephalic length.

Axial furrows shallow, poorly defined from fixigenae. Palpebral lobe short to moderately long, in adult individuals exsag. of 21–28 percent cephalic length (slightly longer in juvenile individuals), slightly oblique to axis, with distinctly curved abaxial margin, anterior end in transverse line with posterior part of L4 or S3, posterior end about in transverse line with S1; palpebral lobe prominent, rises conspicuously from cheek, defined by a moderately well developed, narrow palpebral furrow, which is slightly curved adaxially near anterior end. Eye ridge forms slightly elevated lobe directed inward and forward to meet axial furrow distinctly anterior to S3, with nearly straight adaxial part and faint continuation to frontal lobe across axial furrow. Palpebral area gently convex, moderately wide (tr.), transverse width between posterior ends of palpebral lobe and axial furrow ca. half (varies between 42 and 55 percent in the studied specimens) maximum glabellar width. Posterior area of fixigena extends into an exsagittally relatively narrow posterolateral projection.

Anterior border gently convex but varying between individuals and between internal moulds and the exterior of the test; moderately broad (sag., exsag.), growing in width from the suture to the sagittal line to more than double breadth, on the sagittal line variably of ca. 13–16 percent cephalic length; anterior margin with considerable curvature in dorsal view, with faint dorsal bulge in anterior view. Anterior border furrow a moderately wide (sag. and exsag.) depression with more-or-less equal depth throughout, poorly defined from and progressing into the preglabellar field. Preglabellar field present, moderately broad on sagittal line, slightly varying in breadth, wider in larger specimens and then of up to two-thirds width of anterior border on sagittal line; variably developed in respect to its relief, from slightly sunken in front of the glabella to faintly convex, with the tendency of developing a joint depression with the anterior border furrow in large specimens; developing into slightly convex, moderately broad (exsag.) genal fields, which slope distinctly towards anterior border furrow and abaxially towards facial suture.

Anterior branch of suture parallel from anterior ends of eyes, then curving inward in a gentle arc and with a clear adaxial curvature after meeting the anterior border. Posterior border narrow (exsag.) next to axial furrow, growing slightly in width abaxially, directed posterolaterally in a gentle curvature and growing in breadth up to a fulcral point about one-third distance from posterolateral tips; distinctly convex. Posterior border furrow moderately wide (exsag.) and moderately deep, slightly shallower adaxially.

Thorax only known from isolated segments tentatively assigned to the species. Transverse width of axial ring ca. 30 percent overall width of the segment, with a relatively narrow articulating half-ring and a narrow articulating furrow. Pleural furrows relatively narrow and moderately well impressed, more-or-less straight or faintly s-shaped, fading short distance from pleural tips. Pleural ends probably developed as bluntly rounded tips.

Librigena not known with any certainty. Rostral plate and hypostome unknown.

Pygidium only known small fragmentary specimens tentatively assigned to the species; outline elliptical in dorsal view; axis reaching close to the posterior margin of the pygidium, probably with two or three poorly defined axial rings and a terminal axial piece, which has a curved posterior rim; pleural regions apparently without well recognisable furrows; lateral and posterior borders obsolescent.

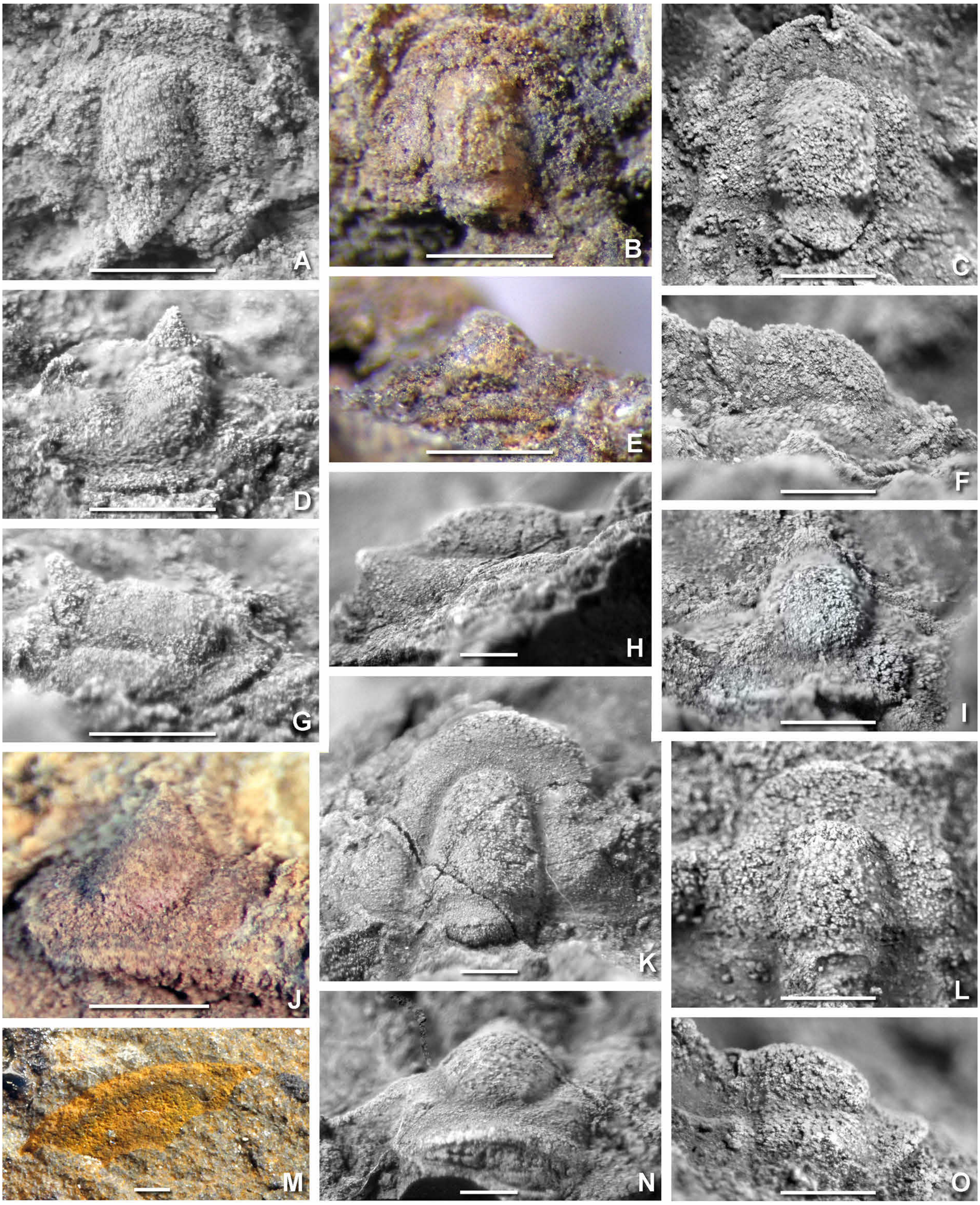

Fig. 54: **A?, B, C, D?, E, F, G? H–N, O?** *Cambrodaimona parablepta* n. gen., n. sp. **A, D, G** SSMM 11476, cranidium of immature individual with extended occipital ring tentatively assigned to *Cambrodaimona parablepta*, internal mould, dorsal (A), oblique anterior (D) and oblique lateral views; from locality W8; **B, E** MMUW 2017D-235a, paratype, cranidium of immature individual, internal mould, dorsal (B) and anterior (E) views; from locality W8; **C, F, I** MMUW 2017D-060, paratype, cranidium of immature individual, internal mould, dorsal (C), lateral (F) and anterior (I) views; from locality W8; **H, K, N** MMUW 2017D-481, paratype, cranidium, internal mould, lateral (H), dorsal (K) and anterior (N) views; from locality W13e; **J** SSMM 11602, paratype, cranidium, internal mould, oblique anterior view; from locality W8; **L, O** MMUW 2017D-379a, paratype, cranidium of immature individual, internal mould, dorsal (L) and lateral (O) views; from locality W8; **M** MMUW 2017D-515, librigena assigned to *Cambrodaimona parablepta*, external mould with relictic weathered limonitised cuticle, dorsal view; from locality W1. All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Discussion. Important relationships and similarities of *Cambrodaimona parablepta* n. gen., n. sp. with other taxa are discussed above under the genus. Particularly significant characters include the subtrapezoidal shape of the glabella with the sometimes almost subtruncate front; the nearly spathulate preglabellar region; and the length and topography of the palpebral lobes and their connection with the eye ridges.

It should be mentioned that *Cambrodaimona parablepta* has some similarity with *Asturiaspis* Sdzuy, 1968, particularly with the flattened specimens from the Iberian Chains northern Spain that are determined as *A. inopinatus* Sdzuy, 1968, which also have a tapering glabella with a mostly narrow, subtruncate front. However, *Asturiaspis* is clearly distinguished by the different type of convexity of the frontal area with a broader (sag., exsag.) and more regularly convex anterior border, the tendency to develop a faint swelling at the anterior preglabellar field on the sagittal line, and longer and more obliquely rising palpebral lobes. The two genera are not closely related, and *Asturiaspis* appears to an early representative of the *Braintreella*–*Badulesia* clade.

Superfamily Solenopleuracea Angelin, 1854

Family Solenopleuridae Angelin, 1854

Discussion. The taxonomic situation within the family Solenopleuridae has been discussed in various articles over the last decades (e.g., Poulsen 1954; Ahlberg & Bergström 1978; Rudolph 1994; Geyer 1998; Rushton & Berg-Madsen 2002; Álvaro et al. 2004; Esteve 2015). However, correctly deciphered morphological criteria and the phylogenetic pathways are still far from being appropriately understood. This state of affairs arises partly from the fact that the genus *Solenopleura* Angelin, 1854 and closely related taxa were described in an early phase of trilobite taxonomy from Scandinavia and neither well characterised nor appropriately illustrated. Subsequent works by Westergård (e.g., 1953) contributed to a beneficial and valuable documentation of the Scandinavian genera and species, but the author largely ignored closely related species from elsewhere, particularly Avalonian North America and North China. Meanwhile more than 320 species assigned to at least 120 named genera were accommodated (at least temporarily) under the family Solenopleuridae and presented in at least 190 different publications (according to my count in March 2023). These genera were recorded from nearly all Cambrian palaeocontinents and include a stratigraphic range from the upper part of Cambrian Stage 3 through the Miaolingian up to the Jiangshanian. However, the distribution shows tremendous differences in both generic and species diversity as well as stratigraphic occurrence, and these differences provide some clues for systematic relations and affinities in this plethora of similar morphologic features in varying combinations.

Several subfamilies have been introduced for the Solenopleuridae, nearly all of them without a formal diagnosis and without any diagnostic criteria being generally accepted. The main source of a hypertrophied classification with little support by morphological criteria is Hupé's (1953b) chapter on the solenopleurids, which he dealt with as a Superfamily Solenopleuroidæ Hupé, 1953b, which (among several other families) included the families Solenopleuridæ Angelin, 1854 and Solenopariidæ Hupé, 1953b (with 13 genera). Hupé (1953b) erected three subfamilies under the Solenopleuridæ: the Solenopleurinæ (with the 6 genera *Solenopleura* Angelin, 1954; *Asthenopsis* Whitehouse, 1939; *Solenopleuropsis* Thoral, 1948; *Deckera* Frederickson, 1949; *Aposolenopleura* Raymond, 1937; and *Onchopeltis* Rasetti, 1944), the Menocephalinæ Hupé, 1953b (with *Menocephalites* Kobayashi, 1937; *Liaotungia* Resser & Endo, 1937; and *Menocephalus* Owen, 1852); and the Heterocaryoninæ Hupé, 1953b (with *Heterocaryon* Raymond, 1937; *Pseudopetigurus* Prantl & Příbyl, 1949; and tentatively *Welleraspis* Kobayashi, 1935). From the present viewpoint, this systematic approach is so far from true evolutionary pathways that it does not merit a serious discussion. A vast majority of the listed genera that are now not regarded as being closely related to *Solenopleura* are thus not considered as members of the Family Solenopleuridae. On the other hand, Hupé (1953b) introduced a family Saoidæ under the Superfamily "Ptychoparioidæ" (with *Sao* Barrande, 1852; *Pardailhania* Thoral, 1947; and *Rimouskia* Resser, 1938), which was placed as an additional subfamily under the Solenopleuridae by some subsequent authors.

Ahlberg & Bergström (1978, fig. 1) attempted a reconstruction of phylogenic pathways among what they interpreted as solenopleuracean trilobites. They considered a subdivision of the Solenopleuridae into 9 subfamilies: Ellipsocephalinae Matthew, 1887 (including Antagminae and Strenuellinae); Conocoryphinae Angelin, 1854; Agraulinae Raymond, 1913; Solenopleurinae Angelin, 1854 (including Ptychopariinae Matthew, 1887); Saoinae Hupé, 1953b; Plethopeltinae Raymond, 1924; Eulomatinae Kobayashi, 1955; Dimeropyginae Hupé, 1953b; and Hystricurinae Hupé, 1953b. Of these, only the Solenopleurinae are presently unequivocally accepted as representing solenopleurid trilobites. Given the close relationship of *Sao* and *Solenopleuropsis*, the Saoidae/Saoinae are actually a junior synonym of the family Solenopleuropsidae Thoral, 1947, which was transferred to the solenopleurid subfamily Solenopleuropsinae by Dean & Krummenacher (1961).

It is evident that subfamilies of the Solenopleuridae as well as the family itself are based on traditional concepts of similar character set rather than the recognition of apomorphies, and that these entities are therefore paraphyletic (as in the case of the Solenopleuropsinae) or even polyphyletic. The flaws in solenopleurid evolution and taxonomy start from the fact that the shape of the glabella is seen as a distinctive character although in most genera the tapering glabella with three pairs of faint subparallel, slightly backward directed lateral glabellar furrows is simply a plesiomorphy that belongs to the groundplan of ptychopariine trilobites and can be seen in other, related families as well. However, deviations from this blueprint are important references to derived and therefore relevant primary characters. This study attempts provide at least criteria for a robust concept of the Solenopleurinae (see below).

Jell (2021, p. 4) diagnosed the Solenopleuridae as "Ptychoparioidea with a rather gibbous, tapering forward, rounded anterior glabella with relatively faint, short, lateral glabellar furrows; occipital ring with median node or spine; a convex preglabellar field, upstanding anterior border; anterior facial sutures inclined inward; small- to medium-size eyes [palpebral lobes] slightly forward of cephalic midpoint; eye ridges faint or absent." This diagnosis denotes important characters, but delimits a broad concept, which brought Jell (2021) to include traditional ptychopariid genera such as *Modocia* Walcott, 1924. This family concept is the result of a strict application of the nominal system which defines the Solenopleuridae as the clade specified by the relationship to *Solenopleura holometopa* (Angelin, 1851) and the Ptychopariidae as the clade typified by the relationship to *Ptychoparia striata* (Emmrich, 1839) which is best characterised by a less convex glabella tapering to a subtruncate anterior margin of the glabella.

To present complete and reliable discussions on even the well-known and clearly definable species of Solenopleuridae is beyond the scope of this study. However, the following pages attempt to clarify characters and differences of the most important and representative genera and species from Scandinavian Baltica, West Gondwana and Western Avalonia. This approach attempts to apply consequent taxonomic principles which allow discrete groupings rather than using broad generic concepts which avoid tentative placement but also fail to characterise phylogenetic pathways.

Subfamily Solenopleurinae Angelin, 1854

[nom. transl. ex Solenopleuridae Angelin, 1854]

Critical characters. Taxonomic subdivision should be a factual and objective approach and generate an identical result regardless of its starting point. Unfortunately, this is often not the case, and the results depend on the historical development of research. Certainly, this indicates deficiencies of the *modus operandi*, which could be avoided. However, the fact that a type species strongly rules the tenor and concept of a genus and the type genus dictates the concept of a subfamily or family contributes to fallacies in taxonomic entities.

In the case of the Solenopleuridae/Solenopleurinae, the basic genera were all Scandinavian and Avalonian in origin, and the Scandinavian and Avalonian genera have not been accurately portrayed and assessed in the early literature of the 19th and early 20th century. A plethora of taxa subsequently described from the Sibiria palaeocontinent were largely lumped into the existing Scandinavian genera, whereas taxa from North and South China were dealt with in a quasi-separate systematic universe. While the Scandinavian taxa are lumped into poorly defined "primordial" genera, the East Asian ones are split into a plethora of genera. Nevertheless, a correct treatment of the Scandinavian taxa is a prerequisite for a practicable taxonomy under the subfamily.

The Scandinavian solenopleurid species are frequently preserved in such an excellent condition that they allow the recognition of fine details. The ca. 20 different species recognised from that region can be precisely differentiated and nicely indicate almost a dozen different morphological characters recognisable at the dorsal exoskeleton that clearly suggest a separation of ca. 8 different genera when the customary practices of generic differentiation of Cambrian trilobites is applied to them. Such characters include:

(1) Shape of the glabella;

(2) size and convexity of the preglabellar field;

(3) size and shape of the anterior border;

(4) size, shape and position of the palpebral lobes;

(5) outline and convexity of the palpebral areas;

(6) outline of the librigena;

(7) outline of the pygidium;

(8) shape and length of the pygidial axis;

(9) relief of the pygidial pleural areas;

(10) development of the lateral and posterior pygidial border; and

(11) ornamentation of the different parts of the dorsal exoskeleton.

Particularly the morphological features of the pygidium, the overall convexity of the cephalon and the course of the anterior border in the Scandinavian solenopleurid trilobites have not been seriously taken into account as taxonomic criteria for solenopleurid genera to date. The results of the examination in this respect and the resulting taxonomy are presented on the following pages. It is regarded as forming a modern approach to a sound generic subdivision among the true solenopleurids. Summarised, a subdivision of the family based on robust criteria leads to a consequent recognition of numerous distinguishable genera in the way that was started by Rudolph (1994).

Previous approaches to a robust taxonomy. Rudolph (1994) introduced additional members of the *Solenopleura* clade and restricted *Solenopleura* to species with a glabella characterised by well-defined lateral glabellar furrows on both exterior and on internal moulds, quite well-developed eye ridges, and a sunken and concave (actually barely visible) preglabellar field, so that the preocular fields are not connected in front of the glabella. This concept, however, excludes all of the non-Scandinavian species previously assigned to this genus. In fact, Rudolph's concept is largely followed in this study. The genus *Solenopleura* in the revised concept proposed here is characterised by a quite strongly convex (tr.), distinctively tapering glabella of parabolic outline with a narrow curvature of its front; by strongly deflected anterior part of the cephalon; a narrow (sag.) and low preglabellar field that is sunken between the preocular area; by a moderately broad (sag.) and moderately convex anterior border that lies clearly below the front of the glabella and describes a conspicuous curvature in frontal view; by short to moderately long palpebral lobes with a distinctive curvature, which are obliquely upturned in axial view and located in a relatively anterior position; by relatively narrow palpebral areas with a distinctive convexity in exsag. direction and with a strong ventral deflection of the posterolateral wings; by a pygidium consisting of an axis of ca. four rings plus a terminal axial piece the tip of which is fused with the posterior border, well divided pleural areas, and a relatively broad, undivided border; and by a prosopon composed of granules of very different sizes, the largest of them with a central canal.

Of principal importance for the systematics of the solenopleurids is the genus *Parasolenopleura*. It was proposed by Westergård (1953) for a group of trilobites with similar aspects and a typical solenopleurid morphology. This morphology varies among the genera in a number of apparently minor characters, primarily in respect to the convexity of the cephalon, the convexity and shape of the palpebral areas, and the size and convexity of the preglabellar field. Westergård (1953) was aware that the characters proposed by him were not critical when isolated from other morphological features, but emphasised their combination to be a reliable criterion for distinguishing *Solenopleura* Angelin, 1854 from *Parasolenopleura*. This, however, is not the case for all of the species included in the two genera. Both genera developed subsequently into taxonomic wastebaskets, and the situation became even more complicated when *Jincella* Šnajdr, 1957 was introduced, because that genus was originally poorly characterised. Taking into account the genera *Brunswickia* Howell, 1937 (in its revised concept suggested by Fletcher 2006) and *Solenopleurina* Růžička, 1938 further complicates the situation. Nevertheless, the simplistic morphology of many solenopleurid trilobites with a paraboloid outline of the glabella, well incised axial furrows, moderately convex palpebral areas, short palpebral lobes, a short to absent preglabellar field and a moderately broad, distinctly convex anterior border made *Parasolenopleura* a convenient collective taxon.

Restudy of the type species of *Parasolenopleura*, *P. aculeata* (Angelin, 1851), based on well-preserved specimens from the original collections indicates that the glabella bears valuable differences compared to all of the other species assigned to *Parasolenopleura* (Fig. 55). The glabella of this species tapers forward to almost subacute anterolateral corners so that the front appears subtruncate, and the lateral margins of the glabella are almost straight. These features result from a pair of anterolaterally developed incomplete parafrontal bands which are recognisable in juvenile individuals and are fused with the glabella in adults. They contribute to a marked incision that defines the glabellar front anteriorly. The preglabellar field is moderately broad (sag.) and slightly convex on the sagittal axis, but sunken between the preocular areas, and it proceeds with a feeble swelling anterior into the anterior border furrow. The quite different front of the glabella is also proven by an unpaired muscle attachment site located on the sagittal axis and reaching almost to the front of the glabella. In addition, a pygidium of *P. aculeata* nicely illustrates that the anterior axial ring and pleural band were incompletely fused to the remaining part of the pygidium, as well as some other characters which are unknown from the other species assigned to *Parasolenopleura*.

Accordingly, it is suggested herein to restrict the genus to its type species, *P. aculeata*. All other species which were previously regarded as typical for *Parasolenopleura* need to be transferred to a separate genus. As discussed below, the genus *Herse* Hawle & Corda, 1847 would have been a suitable replacement. Its type species, *Herse neubergii* Hawle & Corda, 1847, is a senior subjective synonym of *Solenopleurina tyrovicensis* Růzička, 1938. However, the name *Herse* is preoccupied and requires a replacement name. *Exapinepiphania* is suggested for it (see below).

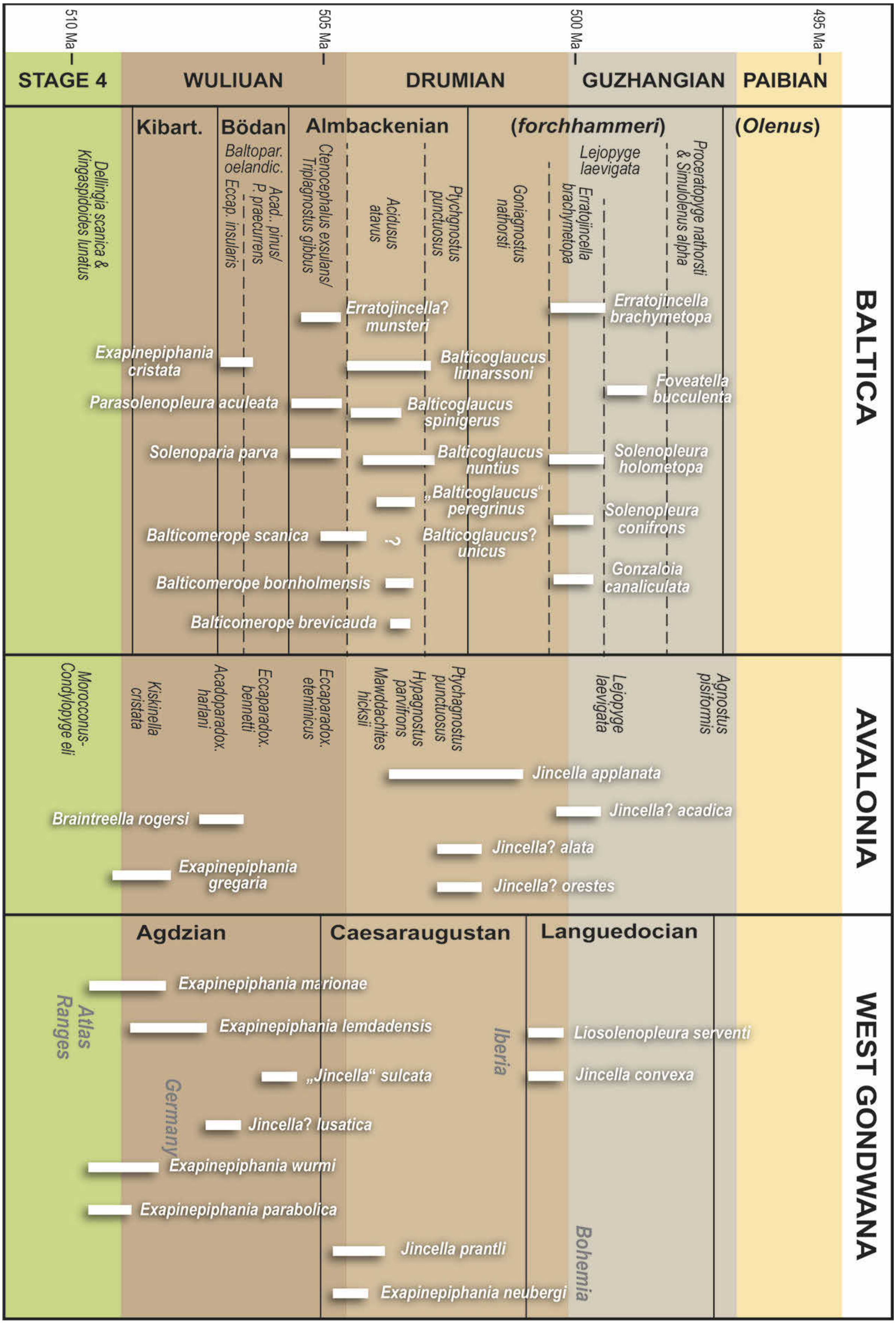

Fig. 55: Stratigraphic occurrence of solenopleurine key species in the palaeocontinents Baltica, Avalonia and West Gondwana. For explanations see discussion in the text.

Additional members of the *Solenopleura* clade were introduced by Rudolph (1994), who restricted *Solenopleura* to species with a glabella characterised by well-defined lateral glabellar furrows on both exterior and internal moulds, fairly well-developed eye ridges, and a sunken and concave (actually barely visible) preglabellar field, so that the preocular fields are not connected in front of the glabella. This concept, however, excludes all of the non-Scandinavian species previously assigned to this genus. A further problem arises by Rudolph's (1994) erroneous restriction of *Solenopleura* to *S. canaliculata* Westergård (1953). *Calymene holometopa*, assigned to *Solenopleura* by Westergård (1953) and subsequently placed under *Jincella* Šnajdr, 1957, clearly differs from typical species of *Jincella* so that no difficulty exists for the distinction between *Solenopleura* and *Jincella*. The features that separate *Solenopleura* from *Jincella* include (i) highly raised palpebral areas; (ii) a sagittally narrow preglabellar field; (iii) strongly upturned palpebral lobes in a strikingly anterior position; (iv) inward-curving anterior branches of the facial suture; (v) a strongly curved lateral cephalic margin (that provides a shape similar to an arc of a circle to the librigenae); (vi) an anterior cephalic margin with a distinct curvature in anterior view; (vii) a prosopon composed of coarse spiniform tubercles; and (viii) a pygidium with a subelliptical rather than transverse outline and few but fairly strongly developed furrows. These characters require a separation of *Calymene holometopa* from the genera discussed above under this section, so that the genus *Solenopleura* needs to be restricted (a priori) to *S. holometopa*. This problem will be discussed by the author in detail in a separate study.

SP- and PL-type morphologies. All genera discussed above are characterised by a cephalon, in which the axial furrows are well incised and relatively broad so that the genae are considerably convex in transverse section and well separated from the glabella. The cephalic profile of these species shows three "hills" separated by relatively deep "valleys". This kind or morphology is termed the "SP-type" (derived from *Solenopleura* and *Parasolenopleura* as characteristic examples) in the following paragraphs. Nevertheless, superficially similar species exist, in which the genae are separated from the axis by relatively sharp, narrow axial furrows, which do not attain the ventral depth as in the true *Solenopleura*-type morphology. Such cephala are characterised by an overall dome-shape in transverse profile, in which the adaxial margins of the palpebral areas are clearly more elevated than the abaxial parts and in which the margin to the axial furrow is marked by a relatively steep drop. This kind or morphology is termed the "PL-type" in the following paragraphs. Both morphological types occur in the Miaolingian of Scandinavia (with a strong prevalence of SP-type genera) as well as in North China (where the PL-type is much more common) and partly elsewhere with species that are superficially very similar. This similarity, however, is mimicked by the prevalence of "primordial" characters and proportions.

It is a truism that the dorsal topography of the trilobite cephalon reflects the internal anatomy. Consequently, apparently small differences of the dorsal morphology of the head shield do often have a v aluable meaning for the organisation and systematic relationship of a trilobite. Zhang & Jell (1987, p. 88) briefly discussed minor differences in the shapes of the glabellar front, the preglabellar field and the anterior border in respect to assumed evolutionary changes in the alimentary canal and feeding habits. Although these assumptions must be regarded as largely hypothetical, the differences do have anatomical reasons and clearly reflect evolutionary trajectories. Such changes in life habits are easily derived from ontogenetic changes, which are quite impressive in some solenopleurid species recorded from North China (e.g., *Trachoparia* spp., *Kaipingella* spp.). Zhang & Jell (1987) considered the expansion of the glabella to be a result of the morphology of the part of alimentary canal that lies beneath it, certain developments in vessels of the circulatory or nervous system that ran beneath them. Insofar, the and the changing expression of structures such as the parafrontal band and the eye ridges to reflect convexity of certain parts of the cephalon plays a role for systematics and taxonomy as well as the expression of a parafrontal band, eye ridges, the width and relative position of the preglabellar field and anterior border. Extremely prominent positions of the palpebral lobes appear to reflect the need for the visual organ to be in a prominent position, perhaps because the animal lived partly infaunally. In addition, a curved course of the anterior border of the cranidium in frontal view suggests an intake of seawater, which may point to a filter-feeding mode of nutrient retrieval. This is of course also an important feature, which sometimes allows a confident differentiation of roughly similar taxa (e.g., *Solenopleura* vs. *Erratojincella*, see below) and under normal circumstances escapes standard morphometric analysis (which has received a lot of applauding recognition during the last two decades).

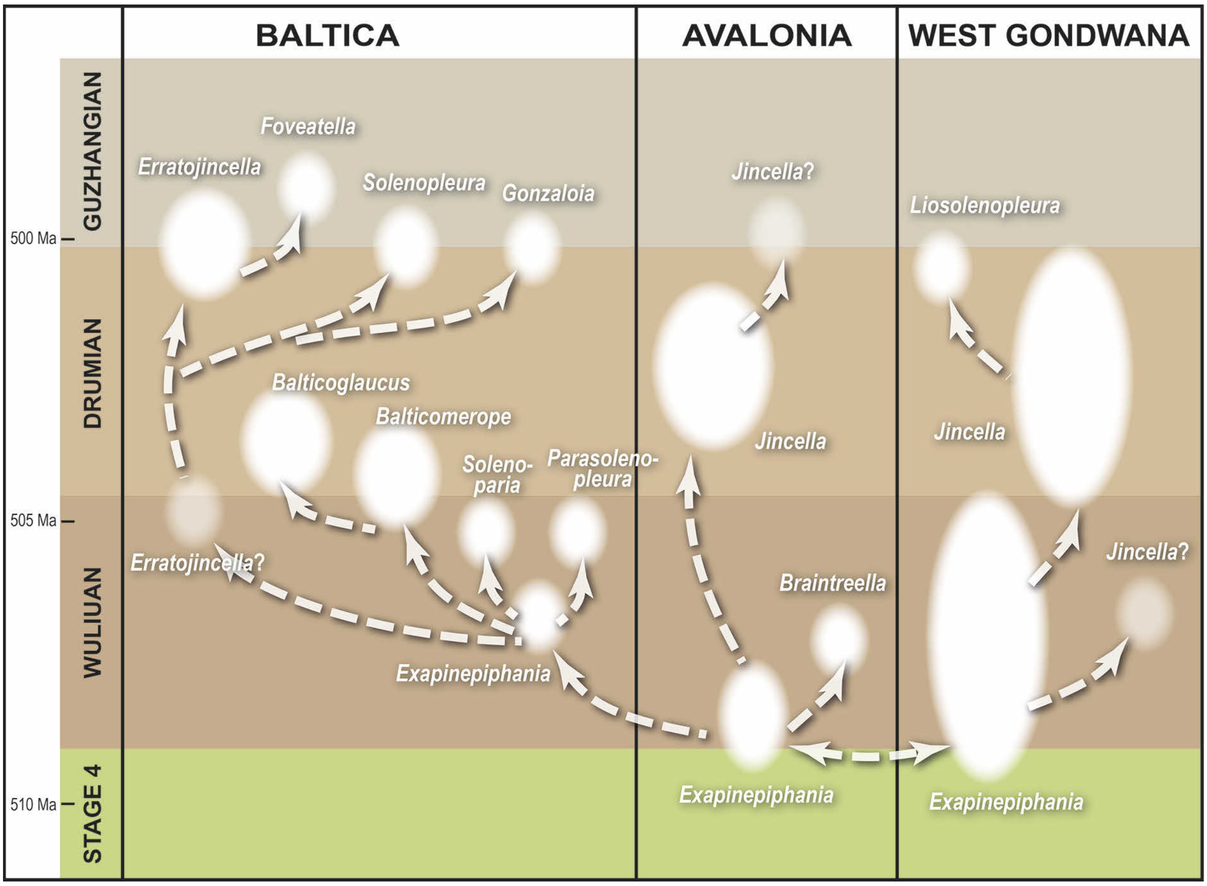

Fig. 56: Stratigraphic occurrence, systematic relationships and probable phylogenetic pathways of key genera among the Solenopleurinae in Baltica, Avalonia and West Gondwana. For explanations see discussion in the text.

Typical examples for the SP-type are the species of *Solenopleura*, *Erratojincella*, *Gonzaloia*, *Foveatella* and the typical species of what was hitherto termed *Parasolenopleura*. *Jincella*, *Liosolenopleura* and *Exapinepiphania* (previously *Solenopleurina*) also belong to the SP-type. The PL-type is represented by species such as *Parasolenopleura parva*, *P. linnarssoni* and *P. spinigera*. It is also known by plenty of taxa described from the Miaolingian of the North China/Sinokorean palaeocontinent, including species assigned to such genera as *Solenoparia* Kobayashi, 1935, *Solenoparops* Chang, 1963, or *Austrosinia* Zhang & Jell, 1987.

Unfortunately, to nearly all of the East Asian genera with typical PL-type species such with a SP-type morphology are also assigned. Important cases are discussed below. In addition, the PL-type shows transitions to species with less convex genae and less domed cranidia as seen in *Parasolenopleura scanica*. When taking into account the stratigraphic occurrence of the relevant species, there is little doubt that the development from forms with rather independently vaulted regions of the cephalon of the SP-type to PL-type occurred several times independently and also the reversed development took place. Nevertheless, lumping species just on the basis of similar proportions obscures true relationships and will lead to paraphyletic genera.

Discussion on selected genera. A comprehensive revision of the nearly 100 genera assigned to the Solenopleurinae is a Herculean task and is probably even beyond the scope of a monograph. Nonetheless, it is regarded as a helpful step stone to clarify a few of the problems in the light of the cephalic morphology, and these are addressed below for some of the genera.

In addition to the Scandinavian genera and species (the majority of which is dealt with in some detail below), a plethora of relatively similar solenopleurine trilobites with a comparatively uniform morphology is distributed in the upper Wuliuan to Drumian of the North China/Sinokorean palaeocontinent, with a number of them also known from South China. They appear to constitute a monophyletic clade, but the generic assignments are far from being satisfactorily resolved. One of the major genera is *Solenoparia* Kobayashi, 1935, to which almost a dozen species were (partly temporarily) assigned. Aspects of this genus are discussed below.

Austrosinia Zhang & Jell, 1987 (type species: *Solenopleura chalcon* Walcott, 1911) is a genus, which according to the concept of Zhang & Jell (1987) includes at least 7 species from the North China Platform and Australia, with a stratigraphic range in the *Crepicephalina* Zone of the Changhian Stage (mid Drumian in the global chronostratigraphic scale). Unfortunately, the genus as presented by Zhang & Jell (1987) includes species with distinctly different morphologies. Its type species, *A. chalcon* (Walcott, 1911) from the Shandong Province, North China, has a subtransverse cranidium with comparatively wide palpebral areas of moderate convexity and little abaxial deflection so that the axial furrows clearly dissect the cephalon in an SP-type manner (e.g., Zhang & Jell 1987, pl. 40, fig. 10–15). The same accounts for *A. puteata* (Resser & Endo, 1937) from the Liaoning Prince, North China (e.g., Zhang & Jell 1987, pl. 34, figs. 9–12).

Austrosinia intermedia (Walcott, 1906b) is a perfect example for the PL-type cephalon with a considerable overall convexity and the most elevated parts of the fixigenae adjacent to the axial furrows as illustrated by the lectotype (e.g., Walcott 1913, pl. XVII, fig. 16, refigured in Zhang & Jell 1987, pl. 39, fig. 8). *A. intermedia* resembles *Solenopleura parva* in most aspects. Both species should be assigned to the same genus despite of the unknown pygidium of *A. intermedia*.

Austrosinia beroe (Walcott, 1906a) represents another different type of morphology. This species has a parabolic outline of the glabella and well indented axial furrows, with the genae showing a moderate convexity in transverse profile with the most elevated part slightly adaxial to the centre. The preglabellar field is narrow and sunken between the preocular areas. The anterior border is relatively prominent and moderately broad (e.g., Zhang & Jell 1987, pl. 40, figs. 4–7). This species actually shows the characters typical for *Exapinepiphania* n. gen. However, differences in the species of that genus can be seen in the surface ornamentation of the cuticle which is composed of granules of very different sizes including large ones, and longer, medium-sized palpebral lobes. Unfortunately, pygidia of *Austrosinia beroe* appear to be unknown.

Austrosinia inaii (Resser & Endo, 1937) has the same critical characters as *A. beroe*, but differs in less important features such as a shorter occipital ring and a narrower preglabellar field. It is somewhat imperfectly known, but certainly represents the same genus as *A. beroe*.

Solenoparops Chang, 1963 was introduced based on *Solenoparia luna* Endo, 1944, from the upper part of the Changhia Formation of the Liaoning Province, North China. That species is in fact a junior synonym of *Solenoparia taitzuensis* Resser & Endo, 1937. *Solenoparops taitzuensis* has a PL-type cephalon with a very thick (sag.) anterior border defined by a narrow anterior border furrow. The most striking diagnostic character is that the preglabellar field is laterally defined by two shallow depressions and tends to proceed faintly forward forming an indistinct boss. A similar species is *Solenoparops salebrosa* (Resser & Endo, 1937) in which the preglabellar field is almost entirely reduced.

The species of *Menocephalites* Kobayashi, 1935 from the upper Changhian of northern and north-eastern China can be generally regarded as a progression of the *Austrosinia* morphology. Its type species, *Menocephalus acanthus* Walcott, 1913, has a typical SP-type morphology. The holotype of *Menocephalites acanthus* (Walcott, 1913) from the *Taitzuia-Paoshania* Zone of the Changhia Formation in the Shandong Province is characterised by a conical glabella with a subevenly curved frontal that reaches to the anterior border furrow and even sticks slightly more forward by comparison to the anterior margins of the preocular areas (Zhang & Jell 1987, pl. 44, figs. 4, 5). The anterior border is very prominent and quite thick (sag.), its anterior being gently curved in dorsal view, whereas the anterior border furrow is only faintly curved. The eye ridges are located in a strikingly anterior position so that the preocular areas are narrow (exsag.) in dorsal view. The cuticle is covered by loose distributed very coarse granules.

Several other species assigned to *Menocephalites* differ strongly from this morphology and cannot be assigned to the genus. These include *Menocephalites pauperata* (Walcott, 1906b) from the *Dorypyge richthofeni* faunal assemblages of the Changhia Formation of the Liaoning Province; *M. acidalia* (Walcott, 1906a) from the *Taitzuia-Poshania* Zone of the Changhia Formation of the Shandong Province; and *M. agave* (Walcott, 1906a), also from the *Taitzuia-Poshania* Zone of the Changhia Formation of the Shandong Province. Particularly *Menocephalites pauperata* shows has a morphology that closely resembles that seen in *Herse neubergii/ Solenopleurina tyrovicensis* and other species of the new genus *Exapinepiphania* and is transferred to that genus as discussed in some detail below. The other mentioned species can be seen as indicating a transition to the morphology of the glabella and anterior cephalic region in *M. acanthus*.

Trachoparia Chang, 1963 has almost a morphology which is commonly regarded as typical for ptychoparioids. Its type species, *Solenoparia bigranosa* Endo, 1937 occurs in the Changhia Formation of the Liaoning Province; it lacks a distinct preglabellar field and has a broad anterior border furrow and a relatively narrow anterior border on the sagittal line. The best known species of the genus is *Trachoparia acis* (Walcott, 1906a) from probably the *Amphoton* Zone of the Changhia Formation of the Shandong Province. The SP-type cranidium is characterised by long, slightly tapering glabella that reaches forward to nearly the narrow, brim-like anterior border.

Pompeckj (1896) introduced a solenopleurid species from the Barrandean region (now Czech Republic), which he called “*Solenopleura (?) conifrons*”. The type material originated from the Buchava Formation at the classical Kamenná hůrka locality near Týřovice (Pompeckj 1896, pl. XVI, figs. 11a, b, 12a, b). This species also suffered a nomenclatural imbroglio: Růžička (1940) introduced the species *Perneria lata* with two subspecies, *P. lata lata* and *P. lata quadrata*. He also assigned *S.*? *conifrons* to *Perneria*. Both represent the same species and are therefore synonyms. In addition, the subspecies of *P. lata* cannot be distinguished and maintained as separate taxa. However, *Perneria* Růžička, 1940 could not be used as a genus name for the species because it was a junior homonym of the arachnid genus *Perneria* Fritsch, 1904. This was early recognised, and Prantl (1947) suggested *Perneraspis* as a replacement name. However, he regarded *P. lata* and *P. conifrons* as different species so that *P. lata* was regarded as the type species of *Perneraspis*. Recognising the synonymy of *S.*? *conifrons* and *P. lata* (first suggested by Šnajdr 1958) made *Perneraspis conifrons* (Pompeckj, 1896) the type species of the genus.

Perneraspis conifrons differs considerably from typical solenopleurids. The genus and species is characterised by a strongly tapering glabella with curved lateral margins on L1, whereas the lateral margins in front of S1 are nearly straight. The occipital ring has a broadly (sag.) lenticular outline and carries a subterminal node. The preglabellar field is lacking or consists of a depression which slightly enlarges the anterior border furrow. The fixigenae are narrow, the palpebral lobes moderately long and slightly curved, but not clearly dorsally upturned. Thus, *Perneraspis conifrons* obviously cannot be assigned to the family Solenopleuridae.

A further complication arose from the fact that Westergård (1953) introduced a new species from Sweden under the name *Solenopleura conifrons*. Although the Bohemian species was formally belonging to a different genus at that time, the name *Solenopleura conifrons* was not available, and the species requires a replacement name, which has not been formally proposed to date. It is therefore proposed here to name the species from Sweden as *Solenopleura westergaardi* n. nom.

Genus *Solenopleura* Angelin, 1854

Type species. Calymene holometopa Angelin, 1851 (by subsequent designation; Walcott 1884a).

Diagnosis (emended). Genus of the Solenopleuridae with strongly convex (tr.) and distinctively tapering glabella of parabolic outline, with narrow curvature of its front, decreasing transverse convexity towards the glabellar front; occipital ring without a spine or a conspicuous median node, subequal in breadth (sag., exsag.) for most of its transverse extension; anterior part of the cephalon strongly ventrally deflected; preglabellar field narrow (sag.), sunken between the preocular area; anterior border comparatively narrow (sag.) and short (tr.) in ventral view, with conspicuous curvature in frontal view; border furrow nearly straight in dorsal view; palpebral lobes short to moderately long, with distinctive curvature; palpebral areas with a strong convexity in exsag. direction, and with a severe ventral deflection of posterolateral wings; eye ridges with well-marked anterior margin, nearly horizontal in frontal view; facial sutures strongly ventrally directed from the anterior and posterior ends of the ocular suture; pygidium with axis consisting of ca. three rings plus a terminal axial piece, pleural areas well divided by sharp pleural and less sharp interpleural furrows; pygidial lateral border relatively broad, undivided; prosopon composed of granules of different sizes.

Discussion. The genus *Solenopleura* was erected by Angelin (1954) in the dawn of phylogenetic considerations for trilobites and consequently became an iconic type of Cambrian ptychoparioid trilobites in what has once been called the Acadobaltic realm. Walcott (1884) coined what became a sketchy concept of the Solenopleuridae, and Westergård (1936, 1953) recognised the necessity to split the taxon.

Once assigned to *Solenopleura* were at least 126 valid species, most of which are now assigned to other genera, some of them now regarded as not even closely related to *Solenopleura* (such as *Menocephalites* Kobayashi, 1935; *Poulsenia* Resser, 1936; *Yorkella* Kobayashi, 1942; *Erbia* Lermontova, 1940; *Loganellus* Devine, 1863; *Fordaspis* Lochman, 1956; *Oligometopus* Resser, 1936; *Glyptometopus* Rasetti, 1944; *Wuhuia* Kobayashi, 1933; *Welleraspis* Kobayashi, 1935; *Pseudatops* Lake, 1940; or *Sudanomocarina* Jell, 1978). Numerous species from the palaeocontinent Sibiria are in need of careful revision, but for most of them this task will remain futile without more complete and better preserved material.

The key to the genus is of course the morphology of its type species. Fig. 57 illustrates the precise morphology of *Solenopleura holometopa* in well-preserved specimens of different size, which makes some of the subsequent, partly tentative assignments doubtful and illustrates differences to other species which are now regarded as representing different genera such as *Erratojincella* Rudolph, 1994, *Foveatella* Rudolph, 1994, and *Gonzaloia* Geyer, 1998. In fact, this morphology of *S. holometopa* designates several characters that place the genus in a strongly decentral position in the morphological range of solenopleurids. Consequent application of morphological range clusters strongly limits the number of species that are closely related to *S. holometopa*.

Geyer (1998, 2017) suggested a revised concept of *Solenopleura* which is illustrated and more comprehensively explained here. According to this concept, the genus is characterised by:

(1) a strongly convex (tr.) and distinctively tapering glabella of parabolic outline with a narrow curvature of its front, but a decreasing transverse convexity (Fig. 57A, B, K);

(2) an occipital ring without a spine or a conspicuous median node, without clearly tapering laterally;

(3) a strongly ventrally deflected anterior part of the cephalon (Fig. 57G, J);

(4) a narrow (sag.) and low preglabellar field which is sunken between the preocular area (Fig. 57A, B, D, E);

(5) a comparatively narrow (sag.) and short (tr.), moderately convex anterior border that lies clearly below the front of the glabella and describes a conspicuous curvature in frontal view (Fig. 57B, E, H, L), defined by a border furrow that is nearly straight in dorsal view;

(6) short to moderately long palpebral lobes with a distinctive curvature, which are obliquely upturned in axial view and are located in a relatively anterior position (Fig. 57A, H, L);

(7) relatively narrow palpebral areas with a distinctive convexity in exsagittal direction, and with a strong ventral deflection of the posterolateral wings (Fig. 57H, K, O);

(8) eye ridges that are relatively weakly defined at its posterior margins, but have a well-marked anterior margin and have a nearly horizontal course in frontal view (Fig. 57D, E);

(9) facial sutures, which are quite strongly ventrally directed from the anterior and posterior ends of the ocular suture (Fig. 57G, O);

(10) a pygidium consisting of an axis of ca. three rings plus a terminal axial piece, the tip of which is fused with the posterior border, well divided pleural areas, and a relatively broad, undivided border (Fig. 57M, P, O); and

(11) a prosopon composed of granules of very different sizes, the largest of them with a central canal (Fig. 57C, N, R).

The characters that are particularly diagnostic for *Solenopleura* and distinguish it from closely related genera are the low, comparatively narrow anterior border defined by a nearly straight border furrow; the elongated palpebral lobes with their crescentic outline; the relatively constant width of the occipital ring without a spine of distinct node; and the outline of the pygidium, the subdivision of its pleural fields and distinctness of the lateral border.

The species which is most closely related to *S. holometopa* is *Solenopleura conifrons* Westergård, 1953. Its morphology and nomenclature are discussed below.

Despite of the non-consideration or their uncertain treatment, the closely related genera *Erratojincella*, *Foveatella*, and *Gonzaloia* can be distinguished fairly easily from *Solenopleura* based on this morphological concept.

Erratojincella has a similar parabolic outline of the glabella and a similar vertical drop of the area in front of the glabella and the eye ridges. However, the front of the glabella in *Erratojincella* tends to show a slight subtruncate median part. The preglabellar field lies below the level of the preocular areas, but is not sunken but always convex in sagittal profile. The anterior border is moderately broad and always crescentic in dorsal view, defined posteriorly by a curved anterior border. The eye ridges are directed obliquely backward from their origins near the axial furrows, and in frontal view they ascend slightly along their course towards the palpebral lobes. The pygidium of *Erratojincella* is somewhat similar to that of *Solenopleura*, but it has a narrower and less well-developed lateral border. Internal moulds of *E. brachymetopa* show a dense pattern of minute punctae, which is not known with certainty in *Solenopleura*.

Gonzaloia differs from *Solenopleura* in having a broader, clearly more prominent anterior border, which is distinctly swollen across the sagittal line due to the posteriorly curving (rather than nearly straight) anterior border furrow. The palpebral lobes in *Gonzaloia* are short and knob-like, and located very prominent due to the fact that the palpebral areas reach their highest elevation close to the palpebral lobes. The occipital ring in *Gonzaloia* tapers markedly from the sagittal axis abaxially to relatively narrow lateral margins. The pygidium of *Gonzaloia* is more broadly elliptical than that of *Solenopleura*, has a higher number of axial rings and shows larger pleural areas subdivided by more pleural furrows.

Foveatella has a very different overall convexity of the cephalon, with a much less ventrally sloping anterior pre-glabellar area and a quite prominent, crescentic-shaped anterior border. The occipital ring is prominent, tapers laterally and has a conspicuous median tubercle. The axial furrows are sharply incised and cause a distinct subvertical drop at the adaxial margins of the fixigenae. The palpebral lobes in *Foveatella* are short and knob-shaped rather than crescentic and of moderate length.

Solenopleura holometopa (Angelin, 1851)

Fig. 57

v *	1851	Calymene holometopa n. sp.– Angelin: p. 23, pl. XVIII, fig. 8a.
v	1854	Solenopleura holometopa – Angelin; p. 26, pl. 18, fig. 8, 8a.
	1876	*Solenopleura holometopa* Ang. 1851 – Linnarsson: p. 30 (table).
?	1878	*Solenopleura holometopa*, (Angelin) – Brøgger; p. 53 [37], pl. 3, fig. 9.
	1884a	*Solenopleura holematopa* – Walcott: p. 346, pl. VI, fig. 3.
?	1902	*Solenopleura holometopa* Ang. – Grönwall: pp. 153, 155–156, 157, 158, table on p. 169, pl. 4, figs 20, 21, 23.
	1913	*Solenopleura holometopa* (Angelin) – Walcott: p. 167, pl. 17, fig. 12, 12a–c.
	1930	*Solenopleura holometopa* Ang. – Wallerius: p. 54.
	1936	*Solenopleura holometopa* (Ang.) – Westergård: p. 60.
	1946	*Solenopleura holometopa* (Angelin) – Thoral: p. 14.
v	1953	*Solenopleura holometopa* (Angelin) – Westergård: pp. 7, 8, 14–16, pl. 4, figs. 1–8.
v	1953	*Solenopleura holometopa humilis* (Westergård, 1952) – Westergård: pp. 9, 16, pl. 4, fig. 9a–c.
	1953b	*Solenopleura holometopa* Angelin – Hupé in Piveteau: fig. 122.1.
	1957	*Jincella holometopa* (Angelin) – Šnajdr: p. 241.
	1958	*Jincella holometopa* (Angelin) – Šnajdr: pp. 197, 198.
?	1984	*Solenopleura holometopa* – Berg-Madsen: fig. 8.
?	1985	*Solenopleura holometopa* subsp. indet. – Berg-Madsen: p. 136, table 1.
?	1985	*Solenopleura holometopa humilis* – Berg-Madsen: p. 136, table 1.
	1994	*Jincella holometopa holometopa* (Angelin 1851) – Rudolph: pp. 73, 137, 188, 202, pl. 25, figs. 8, 9.
	1994	*Jincella holometopa humilis* (Westergård 1953) – Rudolph: pp. 73, 203, pl. 25, figs. 10, 11.
	1998	*Solenopleura holometopa* (Angelin, 1851) – Geyer: pp. 390, 391.
	2000	*Solenopleura holometopa* (Angelin, 1851) – Bruton & Harper: p. 35.
v	2004	*Solenopleura holometopa* (Angelin, 1851) – Álvaro et al.: fig. 3.1.
	2007	*Solenopleura holometopa* (Angelin, 1851) – Fletcher: p. 48.
pars v	2016	*Solenopleura holometopa* (Angelin, 1851) – Esteve: pp. 185, 186, 187–189, figs. 3A–3, 4A–4H.
	2023	*Solenopleura holometopa* (Angelin, 1851) – Weidner et al.: p. 204.

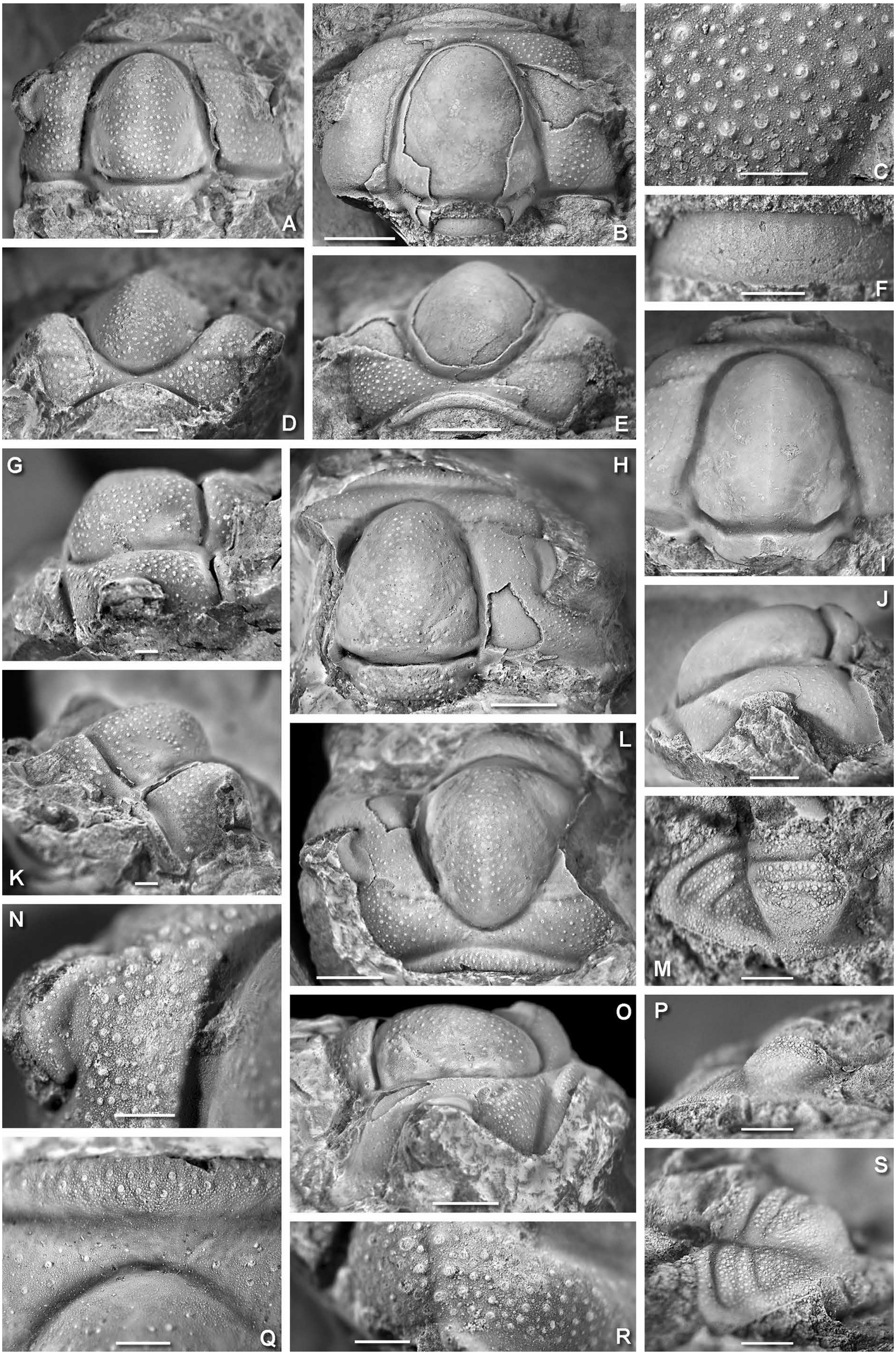
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Fig. 57: *Solenopleura holometopa* (Angelin, 1851**). A, D, G, K, N, R** SGU 6267, incomplete cranidium with largely preserved cuticle; from Andrarum, Scania (collected by G. von Schmalensee), original of Westergård (1953, pl. 4, fig. 2); A dorsal view; D, anterior view illustrating dorsally swinging anterior cephalic margin; G lateral view; K oblique posterolateral view showing profound convexity of distal palpebral areas and prominent palpebral lobes; N detail of abaxial part of palpebral areas, well impressed palpebral furrows with a central incision, and curved palpebral lobes; R oblique lateral view of anterior palpebral areas, eye ridge and preocular areas covered by a cuticle with distinctly different sizes of granules, the largest of them with distinct central tubes. **B, C, E, F** SGU 9753, incomplete cranidium, partially exfoliated; from Andrarum, Scania (collected by G. von Schmalensee, 1877); B dorsal view showing conical glabella and rise along anterior border furrow; C detail of palpebral area and palpebral lobe showing cuticular ornamentation consisting of large wart-like swellings with central canals, smaller uplifts and numerous minute granules; E anterior view illustrating profound ventral deflection of preocular areas and distinct dorsally swinging anterior cephalic margin; F detail of occipital ring showing ventral doublure with edge as stopping device in dorsal view. **H, L, O, Q** SGU 6268, incomplete cranidium, partly exfoliated; H dorsal view; L oblique anterior view; from Andrarum, Scania (collected by G. von Schmalensee), original of Westergård (1953, pl. 4, fig. 4); O oblique lateral view; Q detail of cranidium with anterior border with granules of different sizes, anterior border furrow with indistinct, obliquely running folds, and tip of glabella with nearly fused parafrontal band. **I, J** SGU 9754, incomplete cranidium, internal mould; from Andrarum, Scania (collected by G. von Schmalensee 1877); I, dorsal view showing conical glabella with smooth internal side and sagittal crest-line; J lateral view. **M, P, S** SGU 9744, incomplete pygidium with preserved cuticle, dorsal (M), posterior (P) and lateral (S) views; from Andrarum, Scania. All specimens from Andrarum Limestone Bed, Alum Shale Formation, *Erratojincella brachymetopa* Biozone, Andrarum, Scania. Scale bars 5 mm in B, E, H, I, J, L, O, 1 mm in A, C, D, F, G, K, M, N, P–S.

Discussion. Solenopleura holometopa is characterised by its distinctly conical glabella with slightly curved lateral margins; by quite long lateral furrows S1 which are steeply backward directed from their origins near the axial furrows and weakly curved; by its very short or sometimes nearly absent preglabellar field; by an anterior border furrow relatively with a weak curvature in dorsal view; distinctly upturned, moderately long palpebral lobes; by a pygidium with an axis consisting of three axial rings, two interpleural and two weaker pleural furrows; and by a prosopon with granules of very different sizes.

Solenopleura westergaardi n. nom.

LSID. urn:lsid:zoobank.org:act:2D42FB86-B87D-44AA-956A-7AF59C681E65

Discussion. A species that shares its morphology with *Solenopleura holometopa* (Angelin, 1851) and is closely related to that species is *Solenopleura conifrons* Westergård, 1953. This species is only known from few cranidia and requires restudy. Westergård's holotype (1953, pl. 4, fig. 10a–d) from the Andrarum Limestone Bed of Andrarum, Scania, is associated with *S. holometopa* and shows a more regularly conical and slenderer glabella, slightly wider (tr.) palpebral areas and a transversely more extended anterior border as well as a broader preglabellar field. Westergård (1953, p. 17) also stated that the cranidium from the Andrarum Limestone Bed of Bornholm described and illustrated by Grönwall (1902) as "*Solenopleura acadica* Whiteaves var. *elongata* Matthew" in fact also represents *S. conifrons*.

A specimen described under the name "*Solenopleura acadica elongata* Matthew" from the Salop area, Shropshire in Cobbold & Pocock (1934, pl. 42, fig. 17) was tentatively assigned to *S. conifrons* as well by Westergård (1953), but despite of a superficial similarity this specimen is imperfectly preserved (lacking most part of its anterior border and shows a number of characters that suggest it does not represent *S. conifrons* nor a species assignable to *Solenopleura* in its revised concept.

A further complication arose from the fact that Westergård (1953) introduced this additional species of *Solenopleura* from Sweden under the name *Solenopleura conifrons*. Although the Bohemian species *conifrons* was formally belonging to a different genus at that time, the name *Solenopleura conifrons* was not available, and the species requires a replacement name, which has not been formally proposed to date. It is therefore proposed here to name the species from Sweden *Solenopleura westergaardi*.

Genus *Erratojincella* Rudolph, 1994

Type species. Calymene brachymetopa Angelin, 1851; from the Alum Shale Formation, *Erratojincella brachymetopa* Zone/*Lejopyge laevigata* Zone, lower Guzhangian; Scandinavia (by original designation).

Diagnosis (emended). Genus of the Solenopleuridae with strongly convex (tr.) and distinctively tapering glabella of parabolic outline, with narrow curvature of its front; occipital ring subequal in breadth (sag., exsag.) for most of its transverse extension; anterior part of the cephalon strongly ventrally deflected; preglabellar field convex in sagittal profile; anterior border moderately broad (sag.), crescentic in dorsal view, barely curved in frontal view; border furrow moderately in dorsal view; palpebral lobes short to moderately long, gently curvature; palpebral areas with strong convexity in transverse and exsag. direction, posterolateral wings strongly deflected; eye ridges ascending from their origin at the axial furrows; facial sutures strongly ventrally directed from the anterior and posterior ends of the ocular suture; pygidium with axis consisting of ca. three rings plus a terminal axial piece, pleural areas divided by pleural furrows, which decrease rearward in depth; pygidial lateral border relatively narrow, undivided, poorly defined; prosopon composed of granules of different sizes, internal mould with densely-spaced minute punctae.

Discussion. The genus *Erratojincella* was erected by Rudolph (1994) based on profound differences between its type species, *E. brachymetopa*, and the type species of *Solenopleura*, *S. holometopa*. Apart from the jumble about the type species which was illegally selected as *Calymene canaliculata* by Miller (1889) and erroneously identified as such by Westergård (1953), it appears as if Rudolph's unfortunate choice of the generic name prevented many authors to accept and apply the name.

The taxon was erected with the morphological concept based on just *Solenopleura brachymetopa*. However, Rudolph (1994) introduced a second species, *Erratojincella nigra*, based on a single cranidium recorded from an erratic boulder found at the coast of Holstein, Germany, that originally originated from the Andrarum Limestone of the Alum Shale Formation (Rudolph 1994, pl. 25, fig. 3). Rudolph (1994) suggested that the species is distinguished from *E. brachymetopa* by its wider and more elevated preglabellar field, a shallower border furrow across the sagittal line, longer posterolateral wings of the palpebral areas, and a less convex glabella without a tubercle. In fact, the differences offered by this specimens are more intricate and are discussed below.

Quite surprisingly, *Erratojincella lata* Yuan & Zhang in Yuan et al., 2016, *Erratojincella convexa* Yuan & Zhang in Yuan et al., 2016, and *Erratojincella*? *truncata* Yuan & Zhang in Yuan et al., 2016 were introduced as additional species, all three from the Wuliuan of the Ordos Platform, China. Despite of superficial similarity in the morphology of the cranidium, particularly of *E. lata* (see Yuan et al., 2016, pl. 80, fig. 1), the three species are ill-placed under *Erratojincella*.

Erratojincella brachymetopa (Angelin, 1851)

Fig. 58

*1851 *Calymene brachymetopa.* n. sp. – Angelin: p. 23, pl. XIX, fig. 1, 1a.
1854 *Solenopleura brachymetopa.* n. sp. – Angelin: p. 27, pl. XIX, fig. 1, 1a.
1873 *Conocoryphe* (*Selenopleura) brachymetopa* Ang. – Linnarsson: p. 246.
1876 Selenopleura brachymetopa Ang. – Brøgger: p. 196.
1876 Selenopleura brachymetopa Ang. 1851 – Linnarsson: p. 30 (table).
1878 Selenopleura brachymetopa Ang. var. – Brøgger: pp. 35 [table], 51, pl. III, fig. 8.
1883 *Selenopleura brachymetopa* – Linnarsson: p. 48.
1902 *Solenopleura brachymetopa* Ang. – Grönwall: pp. 4, 15, 16, 27, 153–155, 156, 169 (table), pl. 4, figs. 15, 22.
1902 *Solenopleura brachymetopa* var. *alutacea* Br. – Grönwall: pp. 27, 153–154.

1929 *Solenopleura brachymetopa* Ang. – Strand: pp. 322, 352, 353.
1930 *Solenopleura brachymetopa* Ang. – Wallerius: p. 54.
1935 *Solenopleura brachymetopa* – Asklund & Thorslund: pp. 9, 92, 94.
1940 *Solenopleura brachymetopa* (Ang.) – Westergård; pp. 48, 63.
1944 *Solenopleura brachymetopa* (Ang.) – Westergård; pp. 29 (table), 34 (table), pl. 5.
1946 *Solenopleura brachymetopa* – Westergård; pp. 8, 75.
1947 *Solenopleura brachymetopa* – Thoral: p. 14.
v 1953 *Solenopleura brachymetopa* (Angelin) – Westergård: pp. 7, 11, 16, 18–19, 20, 40 (table), pl. 3, figs. 4–10.
v 1953 *Solenopleura brachymetopa alutacea* – Westergård: p. 10.
1957 *Jincella brachymetopa* (Angelin) – Šnajdr: p. 241.
1958 *Jincella brachymetopa* (Angelin) – Šnajdr: p. 197.
1966 *Jincella brachymetopa* (Angelin) – Poulsen: pp. 121, 122.
non 1966 *Jincella* cf. *brachymetopa* (Angelin) – Sdzuy: p. 71, pl. 8, figs. 24–27.
1974 *Jincella brachymetopa* – Martinsson: p. 205.
1979 *Solenopleura brachymetopa* (Angelin) – Neben & Krueger: p. 16, pl. 117, figs. 20–22.
1981 *Solenopleura brachymetopa* – Anderberg & Johansson: p. 77.
1985 *Solenopleura brachymetopa* –Berg-Madsen: pp. 360, 366, 368, text-fig. 8.
pars 1994 *Erratojincella brachymetopa* (Angelin 1851) – Rudolph: pp. 21, 22, 26, 27, 37, 38, 73, 94, 119, 136, 188, 205, 220, 243, 261.
non 1994 *Erratojincella brachymetopa* (Angelin 1851) – Rudolph: 206–206, 208, 209, tab. 12, text-fig.91, pl. 25, fig. 1, pl. 33, fig. 5. [=*Erratojincella* sp. cf. *brachymetopa*]
non 1994 *Erratojincella brachymetopa* (Angelin 1851) – Rudolph: pl. 25, fig. 2. [uncertain affinity]
2002 *Solenopleura brachymetopa* (Angelin) – Rushton & Berg-Madsen: p. 339, tab. 2.
2003 *Erratojincella brachymetopa* – Jell & Adrain: p. 374.
2003 *Erratojincella brachymetopa* – Álvaro et al.: p. 139.
2003 *Solenopleura brachymetopa* – Axheimer & Ahlberg: pp. 141, 143.
2004 *Solenopleura? brachymetopa* (Angelin, 1851) – Weidner et al.: pp. 42, 44.
2006 *Solenopleura*? *brachymetopa* – Axheimer et al.: p. 448.
non 2010 *Erratojincella* cf. *brachymetopa* – Elicki & Geyer: p. 110.
non 2010 *Erratojincella* cf. *brachymetopa* – Geyer: p. 84.
2014 *Solenopleura*? *brachymetopa* (Angelin, 1851) – Weidner & Nielsen: pp. 37, 61.
2014 *Erratojincella brachymetopa* – Yuan & Li: p. 507.
2016 *Erratojincella brachymetopa* (Angelin, 1851) – Yuan et al.: pp. 215, 216.
2017 *Erratojincella brachymetopa* – Geyer: p. 49.
2023 *Solenopleura*? *brachymetopa* (Angelin, 1851) – Weidner et al.: pp. 11, 16, 104–106, 120 (table), tab. 2, fig. 54A–F.
2023 *Solenopleura*? *nigra* (Rudolph, 1994) – Weidner et al.: p. 104.
2023 *Solenopleura brachymetopa* – Weidner et al.: fig. 2.

Diagnosis (emended herein). Species of *Erratojincella* with glabella moderately parabolic in outline; frontal lobe with faint para-frontal band; eye ridges originating slightly anterior to S3; anterior border furrow with median swelling; anterior border distinctly growing in breadth; anterior branches of facial suture subparallel from anterior tips of ocular suture; pygidium with relatively strong transverse convexity; surface of cuticle covered with granules of different diameters up to relatively coarse ones.

Discussion. See under genus.

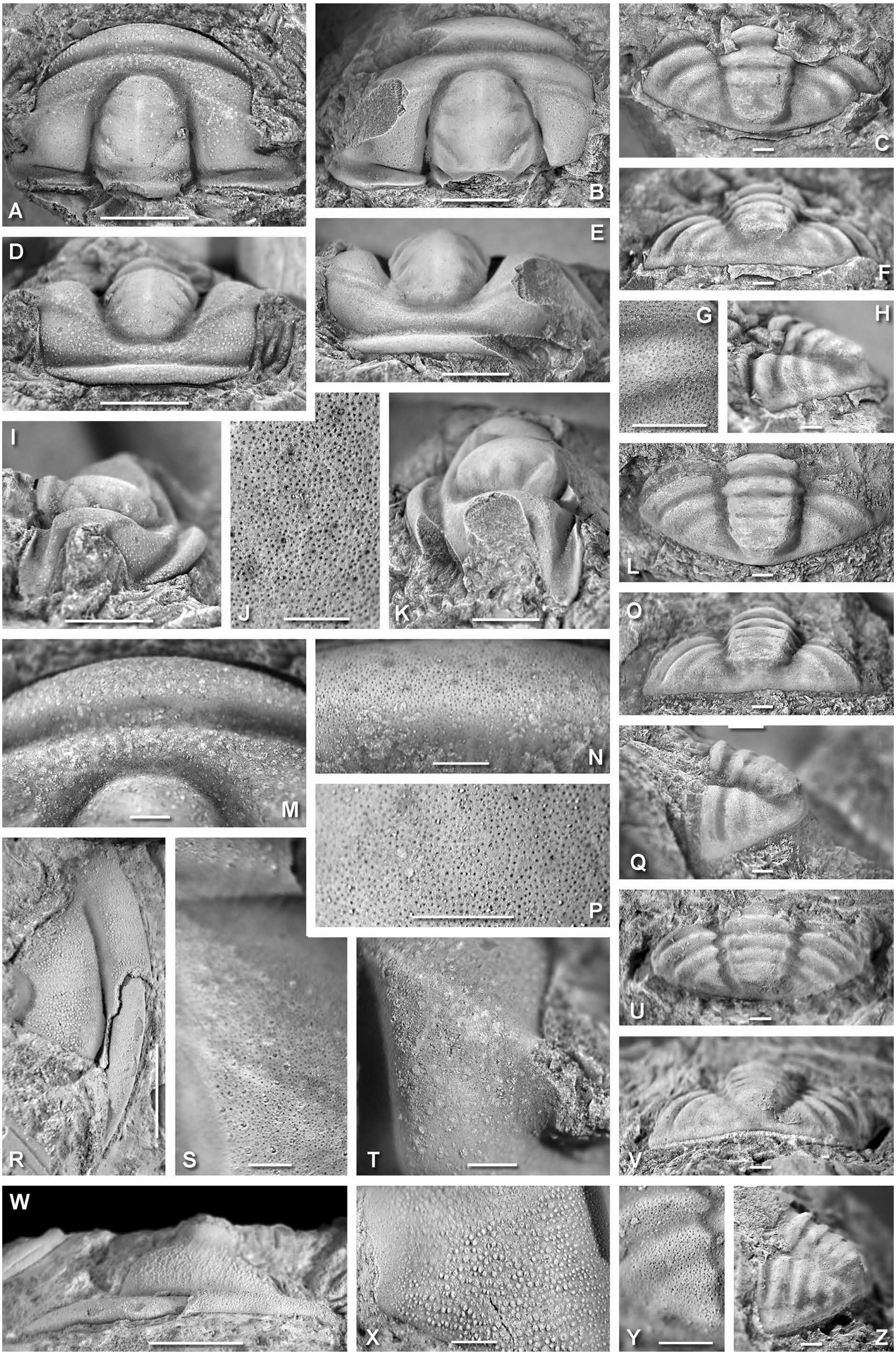
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Fig. 58: *Erratojincella brachymetopa* (Angelin, 1851). **A, D, I, T** SGU 6264, cranidium, internal mould, dorsal (A), anterior (D) and oblique lateral (I) views; magnified view of anterior part of fixigena, eye ridge and palpebral lobe (T) illustrates fine punctae as well as elevated granules with a central tube; original of Wester-gård 1953, pl. 3, fig. 5a, b. **B, E, J, K, M, P** SGU 9745, incomplete cranidium, internal mould, dorsal (B), anterior (E) and oblique lateral (K) views, detail of fixigena in J shows internal surface with minute punctae and more extended depressions with a tube exhibiting a central filling; preglabellar field and front of glabella in M; similar fine punctae (partly with central filled tube) and larger depressions on the glabella shown in P; previously unfigured specimen collected by G. von Schmalensee 1878. **C, F, G, H** SGU 9747, pygidium, internal mould, dorsal (C), posterior (F) and lateral (H) views, G shows detail of left pleural field with fine punctate surface; from Andrarum, Scania, previously unfigured specimen collected by G. von Schmalensee 1878. **L, O, Q** SGU 9746, pygidium, internal mould, dorsal (L), posterior (O) and lateral (Q) views; previously unfigured specimen collected by G. von Schmalensee 1878. **R, W, X** SGU 6265a, librigena, genal spine exfoliated, dorsal (R and lateral (W) views, magnified dorsal view in X shows arrangement of moderately coarse granules in slightly curving rows; original of Westergård 1953, pl. 3, fig. 6 (upside down), collected by G. Holm in 1891. **S** SGU 6265b, partial cranidium, internal mould, magnified view of anterior part of fixigena, eye ridge and preocular area showing fine punctae as well as elevated granules with a central tube; on the same piece of rock as SGU 6265a; **U, V, Z** SGU 6266, pygidium, internal mould, dorsal (U), oblique posterior (V) and lateral (Z) views; original of Westergård 1953, pl. 3, fig. 7. All specimens from Andrarum Limestone, Andrarum, Scania. Scale bars 5 mm in A, B, D, E, I, K, R, W, 1 mm in C, F, G, H, J, L–Q, S–V, X–Z.

Occurrence. Erratojincella brachymetopa is restricted to Scandinavia although the terms "*Solenopleura brachymetopa* Zone" or "*Erratojincella brachymetopa* Zone" are also in use in Western and Eastern Avalonia. The species is common and widely distributed in Scandinavia, from where it was recorded from the Andrarum Limestone Bed and the coeval Exporrecta Conglomerate Bed of the lower part of the *Lejopyge laevigata* Zone in Scania, on Öland, in Västergötland (Westergård 1953) and the Swedish Caledonides (Weidner & Nielsen 2023). It was also reported from Norway (Brøgger 1878), Bornholm (Grönwall 1902; Weidner & Nielsen 2023) and ice-rafted boulders in Germany (Rudolph 1994) and at As Hoved, Denmark (Weidner & Nielsen 2023).

Erratojincella sp. cf. *brachymetopa* (Angelin, 1851)

Fig. 59A, D, G, H

v 1994 *Erratojincella brachymetopa* (Angelin 1851) – Rudolph: pp. 21, 22, 26, 27, 37, 38, 73, 94, 119, 136, 188, 205, 206–207, 208, 209, 220, 243, 261, text-fig. 91, tab. 12, pl. 25, fig. 1, pl. 33, fig. 5. [only].

non 1994 *Erratojincella brachymetopa* (Angelin 1851) – Rudolph: pl. 25, fig. 2.

Studied material and stratigraphy. Cranidium, FR 7122, from erratic boulder collected a Mucheln, Plön County, Holstein, Germany; and partial cranidium, external mould, FR 7745, collected near Jagel, Rendsburg-Eckernförde County, Schleswig, Germany; Both originating from Andrarum Limestone Bed, Alum Shale Formation, Drumian.

Description and discussion. The two cranidia collected from Pleistocene erratic boulders in northern Germany and illustrated by Rudolph (1994, text-fig. 91, pl. 25, fig. 1, pl. 33, fig. 5) and identified as *Erratojincella brachymetopa* resemble that species in most aspects. However, a few minor features distinguish them from the typical specimens known from the Scandinavian source rocks of the Alum Shale Formation.

The glabella in the specimens from the erratic boulders has a glabella with a relatively slender posterior part tapering quite moderately towards an almost subtruncate front (Fig. 59A) and thus lacks the distinctly parabolic outline seen in the typical specimens of *Erratojincella brachymetopa* (Fig. 58A, C). A sagittal crestline is developed, but remains inconspicuous. The lateral glabellar furrows are illustrated in Rudolph (1994, pl. 33, fig. 5) and perfectly equal those seen in the Swedish specimens of *E. brachymetopa* except for an apparently slightly longer S2. The occipital ring is, accordingly, narrower than those in *E. brachymetopa* and has a low node of moderate size in central position. The sagittal and exsagittal profiles of the occipital ring exhibit the subrectagular shape typical for *Erratojincella* in general and also a faint obliquely running furrow that separates the central and lateral portions of the occipital ring.

The genal areas in the cranidium from Holstein are well raised, but show a less steeply sloping adaxial margin than developed in *E. brachymetopa* and a slightly less pronounced convexity (compare Fig. 59D with Fig. 58D, E). The eye ridges are quite prominent and gently curved. They extend into the distinctly curved palpebral lobes, which are narrow (tr.) in the internal mould and adaxially defined by a broad palpebral furrow as seen in *E. brachymetopa*. A remarkable feature is that the eye ridges are anteriorly defined by a quite well developed, distinctly incised furrow (Fig. 59D, G, arrows).

Fig. 59: **A, D, G, H** *Erratojincella* sp. cf. *brachymetopa* (Angelin, 1851), FR 7122, incomplete cranidium, internal mould with relics of the recrystallised cuticle, dorsal (A), anterior (D), oblique lateral (G) and oblique anterolateral views; note abruptly ending low swelling in the anterior order furrow (arrow in A) and distinctly incised furrow delimiting the eye ridge from the proucular areas (arrows in D and G) as well as the poorly branched caeca on th preocular areas (arrow in H); from Andrarum Limestone, erratic boulder from near Muchel, Plön County, Germany; original of Rudolph 1994, pl. 25, fig. 1.
B, C, E, F, I *Erratojincella nigra* Rudolph, 1994, holotype, AfG G134/8, partial cranidium, internal mould, dorsal (B), oblique posterolateral (C), anterior (E) and lateral (I) views as well as an enlarged oblique anterior view in (F); note subangular exsagittal profile of lateral parts of the occipital ring and shallow indentation of short furrow (arrowed in C); arrows in (F) point to moderate-sized granules showing a central canal; from Andrarum Limestone, erratic boulder from near Kasseedorf, Ostholstein County, Holstein, Germany; original of Rudolph 1994, pl. 25, fig. 3.
Scale bars 5 mm in A, B, D, E, G–I, 1 mm in C and F.

The preglabellar field in *Erratojincella* sp. cf. *brachymetopa* is in dorsal view slightly broader (sag.) than the anterior border furrow, which is clearly different to the situation seen in the Scandinavian specimens of *E. brachymetopa*, in which the preglabellar field is narrower (compare Fig. 59A with Fig.

58A, B). The anterior border furrow shows a relatively well recognisable transverse swelling which is quite abruptly delimited laterally (Fig. 59A, arrow).

Differences between the specimens from the erratic boulders of northern Germany and the specimens of *Erratojincella brachymetopa* from Sweden can be seen in the surface ornament of the cuticle. As illustrated in Fig. 58, the exterior of the cuticle in *E. brachymetopa* is beset with numerous, moderate to densely spaced granules of slightly varying diameter, whereas well-preserved internal moulds show a characteristic pattern of dense minute punctae and occasional larger tubes (Fig. 58J). Caeca are nowhere developed in a well-developed pattern. The internal mould FR 7122 from Holstein, however, has widely spaced small to moderately large low granules only. In addition, caeca are well-developed on the preocular areas (Fig. 59D, G, H), partly axtending onto the anterior border and onto the areas of the genae in vicinity to the eye ridges. The vessel patterns are poorly branched and originate into comparatively straight centrifugal directions from the eye ridges (Fig. 59H, arrow). Both cranidia from the erratic boulders of Germany are smaller than those of the typical specimens of *Erratojincella brachymetopa* from Sweden and may therefore be seen as offering juvenile features. However, Scandinavian specimens with the same morphology as the cranidium illustrated herein are unknown so that the erratic boulder specimens may represent a species different from *Erratojincella brachymetopa*.

A pygidium assigned to *Erratojincella brachymetopa* as well in Rudolph's monograph (1994, pl. 25, fig. 2) exhibits a broad lateral border poory defined from the pleural areas and certainly cannot be assigned to *E. brachymetopa* as well as *E.* sp. cf. *brachymetopa* and the Solenopleuridae in general. It is more plausible that it represents a species of the Anomocarioidea.

Erratojincella nigra Rudolph, 1994

Fig. 59B, C, E, F, I

v * 1994 *Erratojincella nigra* n. sp. – Rudolph: pp. 73, 137, 206, 207–209, text-fig. 92, tab. 12, pl. 25, fig. 3.

Studied material and stratigraphy. Partial cranidium, holotype, NMF AfG G134/8, from erratic boulder collected near Kasseedorf, Ostholstein County, Holstein, Germany; originating from Andrarum Limestone Bed, Alum Shale Formation, Drumian.

Diagnosis (emended herein). Species of *Erratojincella* with glabella moderately parabolic in outline (maximum width across L1 ca. 45 percent width across palpebral lobes); frontal lobe with faint parafrontal band; eye ridges clearly oblique to axis, commence opposite origins of S3; swelling in the anterior border furrow insignificant an nearly fused with anterior margin of ptreglabellar field; anterior border distinctly growing in breadth towards sagittal line; facial suture directed inward to intersect border in at a relatively adaxial position.

Description. Cephalon trapezoidal in outline, with quite strong curvature in sagittal profile (Fig. 59I). Axial furrows moderately wide, deeply incised. Glabella parabolic in outline, lateral margins curved; maximum glabellar width across L1 of ca. 45 percent cranidial width across centre of palpebral lobes; frontal lobe across anterolateral corners of approximately 45 percent width across L1; anterior margin of frontal lobe with low curvature in dorsal view, with vaguely indicated anterolateral corners; three pairs of lateral glabellar furrows; S1 moderately long, indistinctly bifurcated, in dorsal view strongly rearwardy directed from its origin; S2 moderately long, slightly rearwardly directed; S3 short, almost normal to axis. Low, indistinct crestline developed on the sagittal axis.

Occipital furrow quite broad and more-or-less normal to axis in its central sector, with narrower, well-incised lateral parts directed obliquely backward from axial furrow. Occipital ring sagittally of about 12 percent cephalic length, extreme lateral parts narrow, middle part subequal in sag. and exsag. breath, sag. and exsag. Profile subrectangular, defined from lateral parts by a low, oblique and quite broad furrow (Fig. 59C); moderately large occipital node in central position.

Fixigena in the area posterior to the eye ridge of nearly 45 percent sagittal cephalic length near axial furrow, width of palpebral area across palpebral lobes variably of ca. 45 percent maximum glabellar width (across L1), extends into a narrow (exsag.) posterior limb of the fixigena; gently to moderately convex, most elevated point roughly in central position, but with a fairly steep slope to drop towards axial furrow.

Eye ridge developed as a moderately raised “rib”, gently curved aligned with an angle of ca. 20° to the transverse axis, well visible on the studied internal mould, meet axial furrows opposite S3. Palpebral lobe not preserved in the holotype, relatively small, aacording to the preserved socle exsagittally of ca. 21–22 percent sag. cephalic length, anterior end opposite posterior part of L3, posterior end opposite anterior part of L1.

Preglabellar field comparatively short, of less than 10 percent cephalic length in dorsal view, forms a gently convex, anteriorly sloping swelling in front of the glabella, generally less well demarcated from the anterior border than from the glabella. An indistinct, poorly defined parafrontal band appears to be developed (Fig. 59F). Preocular areas gently to distinctly convex, developed as steeply sloping trapezoidal fields, separated from eye ridges by a considerable drop (Fig. 59F).

Anterior border moderately to distinctly convex, fairly broad (sag., exsag.), faintly swollen and of ca. 15 3percent cephalic length on sagittal line, clearly tapering to less than half-width next to suture. Anterior margin gently curved in its central sector in dorsal view, faintly arched upward in frontal view. Lateral sections of the anterior border quite distinctly narrowimg due to its dissection by the inward curvature of the facial suture. Anterior border furrow moderately deep in front of preocular fields, slighty wider in front of the glabella. An indistinct and poorly demarcated low swelling is developed in the central sector, where it is more-or-less attached to the preglabellar field.

Posterior border with straight, fairly narrow adaxial part, slightly broadening abaxially, but almost straight and prominent for most of its course. Posterior border furrow narrow adjacent to axial furrows, broadening conspicuously abaxially to an exsagittally wide, moderately deep groove toward the posterior branches of the suture.

Anterior branches of facial suture obviously straight short distance on its course from the anterior tips of the eyes, the with strong inward curvature anteriorly leading to a strong oblique intersecting of the border. Posterior branches probably diverging markedly from posterior ends of ocular suture.

Surface of the internal mould covered with up to moderately largegranules with moderate distances between them, except for the major furrows (axial furrows, lateral glabellar furrows, anterior and posterior border furrows) and the occipital ring, which are smooth. Some eroded granules offer the aspect of a central lacune indicating the presence of a tube during lifetime (Fig. 59F, arrows). Surface between these granules smooth. Parts of the preocular areas, the anterior border furrow and parts of the anterior border show relictic caeca (Fig. 59B).

Discussion. Erratojincella nigra Rudolph, 1994 was introduced based on a single partial cranidium collected from an erratic boulder found in Holstein, northern Germany. According to the lithology of the rock, it undoubtedly originated from the Andrarum Limestone of the Alum Shale Formation (Rudolph 1994, pl. 25, fig. 3).

Rudolph (1994) suggested that his newly introduced species is distinguished from *Erratojincella brachymetopa* by its wider and more elevated preglabellar field; a shallower border furrow across the sagittal line; longer posterolateral wings of the palpebral areas; and a less convex glabella without a tubercle. However, these criteria either fall into the morphologic plasticity known from the Swedish material of *E. brachymetopa*, or they may be interpreted as hypertrophied and therefore inappropriate to differentiate *E. nigra* from *E. brachymetopa*. Nonetheless, the Rudolph's holotype indeed differs from the specimens of *E. brachymetopa* in some characters that must be regarded as of taxonomic significance.

The most signifant of these characters are: (1) the weakly developed swelling in the anterior border furrow that is nearly fused with the preglabellar field rather than being well-defined and in a central position of the anterior boder furrow as in E. brachymetopa; (2) the eye ridges commencing at the axial furrow opposite the origin of S3; (3) strongly adaxially curving anterior branches of the facial suture that intersect the anterior border considerably and thus traverse the anterior border furrow at a distinctly more adaxial position that those in *E. brachymetopa* (compare Fig. 59E with Fig. 58D); (4) different surface ornament seen in internal moulds, consisting of widely spaced moderate-sized granules and occasional facial lines, but the absence of fine punctae in *E. nigra*. Several other differences between *E. nigra* and *E. brachymetopa* are difficult to estimate and cannot be regarded as being taxonomically meaningful.

Although it is evident that more and more completely preserved material is needed to provide an accurate picture of the *Erratojincella nigra*, the species must be regarded as actual and identifiable taxon.

***Erratojincella*? *munsteri* (Strand, 1929)**

Fig. 60

non	1879	Selenopleura parva n. sp. – Linnarsson: p. 15, pl. 1, fig. 20.
*	1929	*Solenopleura munsteri* n. sp.– Strand: pp. 320, 352–353, pl. II, figs. 12a, b, 13, 14?, 15, 18?.
	1940	*Solenopleura munsteri* Strand – Westergård: p. 12.
v	1953	*Solenopleura munsteri* (Strand, 1929 – Westergård: pp. 8, 9, 11–12, 13, 40 (table), pl. 2, figs. 6a–d, 7–10.
	1958	*Jincella munsteri* (Strand) – Šnajdr: p. 197.
non	1964	*Jincella munsteri* (Strand) – Orłowski: pp. 550, 552, 558, 560.
	1974	*Jincella* (?) *munsteri* – Martinsson: p. 204.
non	1985	*Solenopleura munsteri* (STRAND) – Orłowski: p. 252, text-fig. 1.
	1994	*Jincella munsteri* (Strand 1929) – Rudolph: pp. 27, 55, 202, 203–204, 205, tab. 12, pl. 24, fig. 12.
	1998	“*Solenopleura munsteri*” – Geyer: p. 398.
non	2003	*Solenopleura* cf. *munsteri* (Strand, 1929) – Axheimer & Ahlberg: pp. 143, 152–153, 156, fig. 8F. [new, yet unnamed species]
	2007	*Solenopleura munsteri* – Nielsen & Schovsbo: p. 84.
non	2007	*Solenopleura munsteri* (Strand) – Nawrocki et al.: p. 414.
	2014	*Solenopleura munsteri* – Weidner & Nielsen: pp. 6, 61.
	2015	*Jincella munsteri* – Weidner et al.: p. 63.
	2016	*Solenoparia munsteri* (Strand, 1929) – Yuan et al.: p. 224.
	2017	“*Solenopleura munsteri*” – Geyer: p. 50.
	2023	*Solenopleura*? *munsteri* Strand, 1929 – Weidner et al.: pp. 104, 121 (table).

Diagnosis (emended). Species tentatively assigned to *Erratojincella* with glabella broadly parabolic in outline (maximum width across L1 ca. 45 percent width across palpebral lobes); frontal lobe with faint parafrontal band; eye ridges moderately rearward directed from axial furrows; anterior border furrow with medial swelling; anterior border growing moderately in breadth towards sagittal line; pygidium with relatively strong transverse convexity; anterior branches of facial suture with long, straight section subparallel to axis from ocular suture; surface of cuticle covered with fine granules only.

Discussion. Strand (1929) introduced a species based on material from the *Ctenocephalus exsulans* Zone of southern Norway under the name *Solenopleura munsteri*. Westergård (1953) restudied the type material and assigned specimens from Scania, Västergötland and Östergötland, Sweden to the species. Nevertheless, the known material is limited and except for pygidia fragmentary.

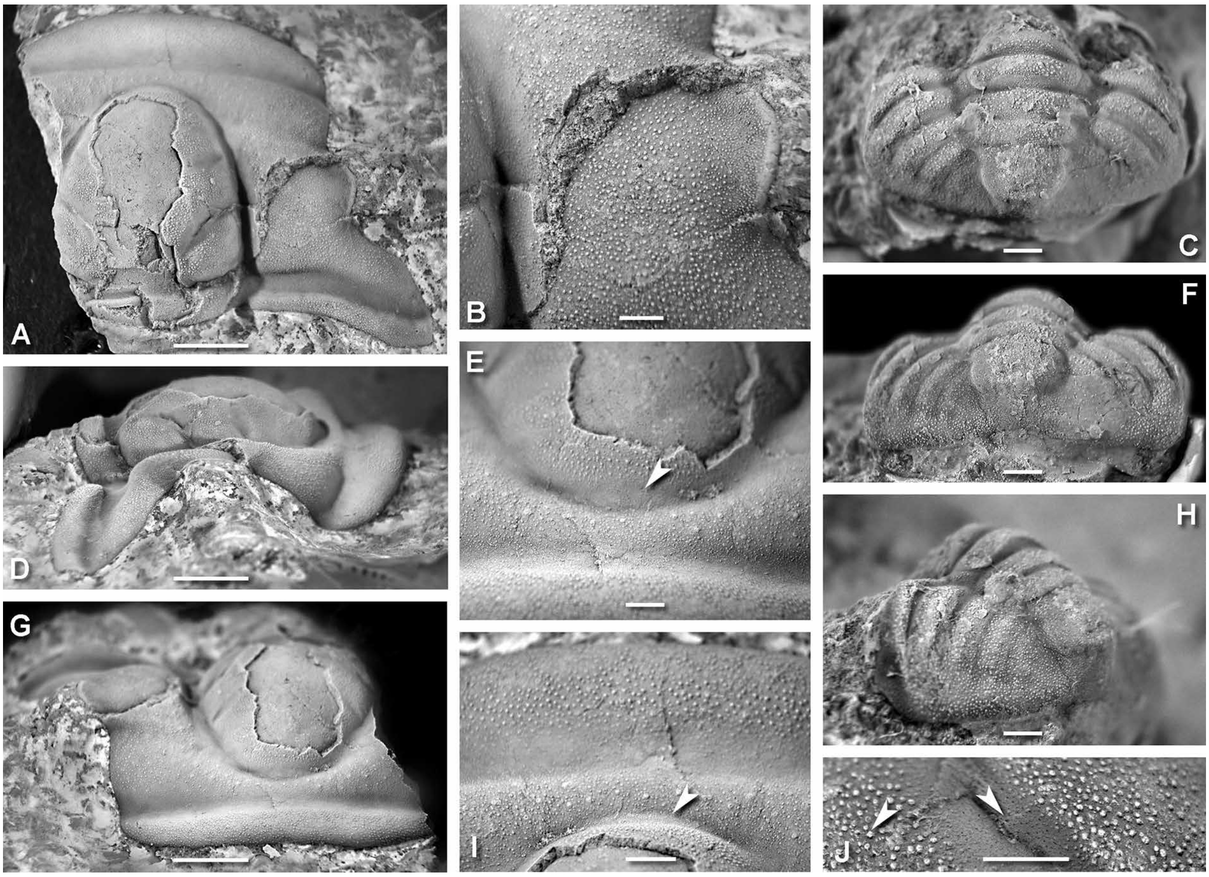

Fig. 60: *Erratojincella*? *munsteri* (Strand, 1929). **A, B, D, E, G, I, J** SGU 6258, partial cranidium with preserved cuticle, dorsal (A), lateral (D) and oblique anterior (G) views; magnified view of fixigena, eye ridge and palpebral lobe (in B) illustrates dense granulation grading into finer granules in the wide palpebral furrow as well as narrow, curved palpebral lobe; oblique anterior (E) and dorsal (I) views of frontal portion shows larger granules with filled central tubes and delicate low, crescentic parafrontal band (arrows); magnified oblique lateral view of glabella shows S1 with minute punctae (central arrow) and elevated granules on L1 and L2, partly with central canal (left arrow); original of Westergård 1953, pl. 2, fig. 9. **L, O, Q** SGU 6259, pygidium with largely preserved cuticle, dorsal (C), posterior (F) and posterolateral (H) views; original of Westergård 1953, pl. 2, fig. 10a, b. Both specimens from Exsulans Limestone, Brantevik, Scania, collected by K.A. Grönwall in 1915.
Scale bars 5 mm in A, D, G, 1 mm in B, C, E, F, H–J.

The species characterised by a quite highly convex glabella of parabolic outline, which extrudes from between a domed platform formed by highly convex (particularly in exsagittal direction) palpebral areas with strongly ventrally deflected posterolateral wings. The lateral glabellar furrows are quite shallow as usually for the *Solenopleura* clade, but L1 is better developed, considerably indented and curves strongly backward from its origin near the axial furrows (Fig. 60A). The front of the glabella shows a small, incomplete parafrontal band in well preserved specimens, which is almost fused with the frontal lobe (Fig. 60E, I). The preglabellar field is relatively narrow on the sagittal line and much narrower than the anterior border furrow, convex, but with a steeper drop anterior towards the anterior border furrow. The anterior border is fairly broad, moderately convex and moderately crescentic in dorsal view.

Particularly diagnostic is the configuration of the eye ridges and the palpebral lobes: The eye ridges are distinctly obliquely backward directed from the axial furrows and relatively broad. The palpebral lobes, in contrast, are relatively narrow and almost thread-like in some specimens (Fig. 60A, B), show a moderate curvature in dorsal aspect and are defined by a shallow, but relatively broad (tr.) palpebral furrow. The surface of the cuticle is densely beset with moderately large granules on the glabella, the palpebral area, preglabellar field and anterior border, which grade into much smaller granules in some furrows (e.g., palpebral furrow, Fig. 60B), but the palpebral lobes, lateral glabellar furrows, occipital furrow, axial furrow and border furrows are smooth. Preocular areas and preglabellar furrows as well as some of the glabellar lobes have a few widely spaced larger granules, which show the infilling of a central tube (Fig. 60E).

The known pygidia have subelliptical outline in dorsal view but are quite convex in sagittal section and show pronouncedly dropping lateral flanks (Fig. 60C). The axis tapers more-or-less continuously rearward, with the tip reaching almost to the posterior margin in dorsal view, but being distant in posterior view, connected with the posterior margin by a low boss (Fig. 60F). The axis is composed of three well defined axial rings and a fourth axial ring barely defined from the terminal axial piece, as well as a relatively broad (sag.) articulating half-ring (Fig. 60C). The pleural fields are subdivided by four deep pleural furrows, whereas the interpleural furrows are shallow and demarcate very thin anterior pleural parts only. The lateral border is only weakly convex, subdivided by very shallow prolongations of the pleural furrows which create a weakly wavy surface, and they are directed almost vertically in posterior aspect. The posterior border shows a slight embayment of the posterior margin visible in posterior view (Fig. 60F) which suggests its function as an articulating device during enrolment. The surface of the pygidial cuticle is almost entirely densely covered with small, but relatively prominent granules (Fig. 60F, H).

Axheimer & Ahlberg (2003, fig. 8F) illustrated an incomplete, but nicely preserved cranidium which they identified as *Solenopleura* cf. *munsteri*. Indeed, this cranidium is closely related to *E. munsteri*, but differs in a number of important features, such as the width (sag.) of the preglabellar field, the precise position and length of the palpebral lobes, and the surface ornamentation. It is considered here that it certainly represents a new species tentatively referable to *Erratojincella*.

Occurrence. Erratojincella? *munsteri* appears to be restricted to the *Ptychagnostus gibbus* Zone (lower *P. paradoxissimus* Superzone, lower Drumian).

Genus *Foveatella* Rudolph, 1994

Type species. Solenopleura bucculenta Grönwall, 1902; from the *Erratojincella brachymetopa* Zone of the Alum Shale Formation, Sweden (by original designation).

Diagnosis (emended). Genus of the Solenopleuridae with a glabella of ca. 70 to 75 percent cephalic length; palpebral areas with highest elevation adjacent to palpebral lobes; axial furrows deep; palpebral lobes short, knob-like, raised above the palpebral areas, at a relatively anterior position; facial sutures strongly ventrally directed from anterior and posterior ends of ocular suture; preglabellar field narrow to moderately broad (sag.), convex; anterior border relatively broad, prominent, crescentic in dorsal view, anterior margin moderately curved in frontal view; cuticle (except for furrows) covered with granules of different size, with a considerable among of large ones.

Discussion. Foveatella was erected by Rudolph (1994) as a monotypic genus based on *Solenopleura bucculenta* Grönwall, 1902 from the Guzhangian Stage of Bornholm, Denmark. Rudolph's (1994) concept was mainly based on a depression in the preglabellar field, which (according to Rudolph) was unique among the Solenopleurinae. In addition, Rudolph (1994, p. 209) emphasised the shallow dorsal and border furrows as being unusual for the subfamily as well. Also, the protruding palpebral lobes

– according to Rudolph – are reminiscent of *Solenopleurina* (see discussion below under *Exapinepiphania*), which is distinguished by deeper glabellar furrows and longer palpebral lobes. The species assigned by Rudolph to *Jincella* are believed to have a less prominent anterior border and (relatively) longer glabella, as well as their occipital rings are shorter and carry a less prominent occipital tubercle.

Rudolph (1994) accentuated that these differences are not gradual in nature, but clearly distinguish the species from other clades. I concur with this opinion, but regard *Foveatella* as being characterised by other features than those highlighted by Rudolph. A complication arises from the fact that discrepancies seem to exist in the concept of the typical morphology of the species. Grönwall's type specimen from Hoved, Bornholm, is figured as a sclerite with a relatively large, prominent glabella and a convex preglabellar field of moderated width (sag.) (Grönwall 1902, pl. 4, fig. 18).

This appears to contradict Grönwall's description and also the morphology seen in quite characteristic cranidia figured by Westergård (1953, pl. 3, figs. 1a–c, 2, 3a–c). Westergård (1953, p. 14) based his description on 18 cranidia from Andrarum and Gislöv in Scania, Sweden. However, he mentioned that he had examined specimens from Bornholm as well. Accordingly, we have to assume that Westergård's identification and characterisation of "*Solenopleura bucculenta*" is correct. Hence, two of Westergård's (1953) specimens are refigured and used herein for an enhanced characterisation the taxon.

Important characters shown by these cranidia include:

(1) A quite strong differentiation of the convexity of different parts of the cranidium. The glabella is relatively strongly convex in transverse profile but not raised significantly above the palpebral areas, which are also quite strongly convex in transverse profile. The same accounts for the sagittal and exsagittal convexity of the anterior and posterior borders.

(2) The palpebral lobes and preglabellar field are arranged like a frame for the glabella due to the deep axial and preglabellar furrows. In fact, the "fovea" suggested as a main character of the genus is only a result of the slightly obliquely running parts of the preglabellar furrows as processing from the axial furrows. Their meeting point just in front of the glabellar tip is slightly arcuate, and thus causes a minor extension of the furrow which mimics a pit (or fovea).

(3) The occipital ring has a quite strongly curved posterior margin so that the lateral parts of the occipital ring are narrow (exsag.). A large and very prominent node (or tubercle) which is developed at a subcentral position enforces the impression of a very prominent occipital ring, and indeed this tubercle marks the most prominent part of the cranidium (Fig. 60C, E).

(4) Other very prominent parts of the palpebral areas are located adjacent to the palpebral lobes, which causes the anterior and posterior branches of the facial suture to be strongly ventrally directed (Fig. 60C, E).

(5) The palpebral lobes are short (exsag.), but thick (tr.) and located at a relatively anterior position short distance posterior to the anterolateral corners of the glabella.

(6) The anterior border is relatively broad (sag.) and crescentic in dorsal view of the cranidium, but its abaxial narrowing is partly an effect of the strongly adaxially directed course of the facial suture.

(7) The cuticle carries numerous relatively coarse granules of very different size. The largest of them are easily recognised to possess a central tube.

(8) In particular, the knob-like palpebral lobes in a pronouncedly prominent and anterior position; the relatively short glabella; the highly elevated occipital ring; and the broad anterior border, all covered with coarse granules, distinguish the genus and species from all other taxa of the family.

Although *Foveatella bucculenta* is relatively easily distinguished from other genera, a number of features in the cranidium of this species are analogous to those seen in *Solenopleura holometopa* and suggest a fairly close relationship. Among them is the shape of the glabella, the inclination of the palpebral lobes, the course of the suture, and the surface sculpture of the cuticle.

Foveatella bucculenta (Grönwall, 1902)

Fig. 61

*	1902	*Solenopleura bucculenta* n. sp.– Grönwall: pp. 152–153, pl. 4, figs 18.
?	1927	*Solenopleura bucculenta* Grönwall– Czarnocki: p. 196.
non	1934	*Solenopleura* cf. *bucculenta,* Grönwall – Cobbold & Pocock: p. 366.
non	1934	*Solenopleura bucculenta,* Grönwall – Cobbold & Pocock: pl. 42, fig. 18a, b.
v	1953	*Solenopleura bucculenta* Grönwall, 1902 – Westergård: pp. 7, 13–14, 16, 40 (table), pl. 3, figs. 1a–c, 2, 3a–c.
	1958	*Jincella bucculenta* (Grönwall) – Šnajdr: p. 197.
	1974	*Jincella bucculenta* – Martinsson: p. 205.
	1974	*Solenopleura bucculenta* (Grönwall) – Neben & Krueger: pl. 115, fig. 113.
	1984	*Solenopleura bucculenta* – Berg-Madsen: fig. 8.
non	1988	*Solenopleura* cf. *bucculenta* – Morris: pp. 212–213.
non	1989	*Solenopleura* sp. – Bruton et al.: fig. 3.13.
	1991	*Solenopleura bucculenta* Grunw. – Astashkin: p. 61.
	1994	*Solenopleura bucculenta* – Wolfart: p. 83.
	1994	*Foveatella bucculenta* (Grönwall 1902) – Rudolph: pp. 209, 210, 261.
?	1994	*Foveatella bucculenta* (Grönwall 1902) – Rudolph: pp. 73, 137, 210 [pars], tab. 12, pl. 24, fig. 13.
	1994	*Solenopleura bucculenta* – Babcock: pp. 107–108, tab. 1, fig. 4, fig. 22.1–22.8, 22.9?.
	1998	*Foveatella bucculenta* (Grönwall, 1902) – Geyer: p. 391.
non	2000	*Solenopleura bucculenta* Grönwall, 1902 – Bruton & Harper: pp. 30, 35, fig. 4A–G.
non	2002	*Solenopleura* sp. – Rushton & Berg-Madsen: pp. 339, 341, tab. 2, fig. 5g, h. [Revision of Cobbold & Pocock's reported specimens]
non	2002	*Solenopleura* cf. *bucculenta* – Rushton & Berg-Madsen: p. 341.
	2002	*Solenopleura bucculenta* – Rushton & Berg-Madsen: p. 341.
	2016	*Foveatella bucculenta* (Grönwall, 1902) – Yuan et al.: pp. 244, 644.
	2023	*Solenopleura*? *bucculenta* Grönwall, 1903 – Weidner et al.: pp. 104, 121 (table).

Diagnosis. Diagnosis of genus (because of monotypy).

Discussion. See under genus.

Occurrence. Foveatella bucculenta is a quite rare species which was originally described from specimens from the so-called Hyolithes limestone and Andrarum limestone bed, both from the *Erratojincella brachymetopa* Zone. The localities include Scania (Andrarum and Gislöv) and Bornholm (*Paradoxides davidis* and *P. forchhammeri* zones). A reliable further identification is a single specimen from the Kap Stanton Formation, *Ptychagnostus punctuosus* Subzone of the *Lejopyge laevigata* Zone, of Peary Land, North Greenland (Babcock 1994).

Czarnocki (1927, p. 9) recorded the species from the Holy Cross Mountains of southern Poland, but the precise identification must be challenged. The species has also been reported from the Ogon'or Formation (*Corynexochus perforatus*/*Anopolenus henrici* Zone. upper Maya Stage) in the vicinity of the Bulkur Anticline in the Lena River region on the Siberian Platform, which bears a faunal assemblage with some resemblance to the Scandinavian fauna (e.g. Astashkin 1991).

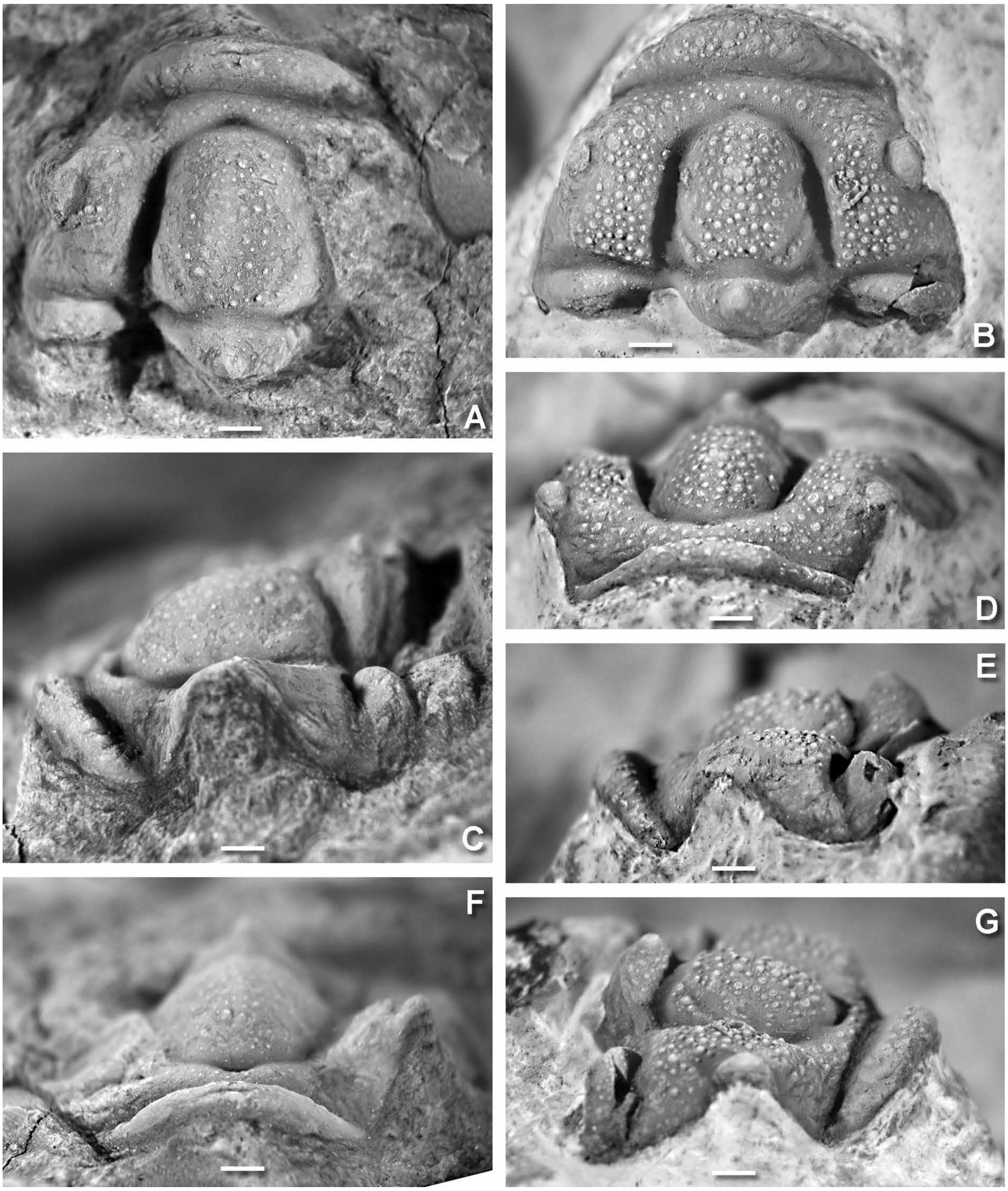

Fig. 61: *Foveatella bucculenta* (Grönwall, 1902). **A, C, F** SGU 6262, incomplete cranidium with preserved cuticle, dorsal (A), oblique lateral (C) and frontal (G) views; from the so-called Hyolithes Limestone Bed, Andrarum, Scania; original of Westergård, 1953, pl. 3, fig. 1a, b. **B, D, E, G** SGU 6263, cranidium with preserved cuticle, dorsal (B), frontal (D), lateral (E and oblique lateral views; from the Andrarum Limestone Bed, Andrarum, Scania; original of Westergård, 1953, pl. 3, fig. 2a–c. All scale bars 1 mm.

Genus *Gonzaloia* Geyer, 1998

Type species. Calymene canaliculata Angelin, 1851, from the *Erratojincella brachymetopa* Zone of the Alum Shale Formation, Andrarum, Scania, Sweden.

Diagnosis (emended). Cephalon subrectangular in outline; glabella distinctly convex, front bluntly rounded to subtruncate; occipital ring with median node; palpebral lobes convex in transverse profile, separated by a moderately deep and broad (sag., tr.) depression in front of the glabella; eye ridge relatively well developed, transverse to sagittal axis for most of its course, ascending in frontal view from its origin near the axial furrow; palpebral lobe short (exsagittally), conspicuously upturned; anterior branches of facial suture steeply ventrally deflected; preglabellar field a short, sunken strip with a low sagittal convexity; anterior border moderately to strongly convex, with median swelling that forces anterior border furrow to a conspicuous rearward curvature across the sagittal line. Pygidium subelliptical in outline, pygidial axis with four to six axial rings plus terminal axial piece and at least five well developed pleural ribs on a relatively broad pleural field.

Discussion. Although *Gonzaloia* is one of the best characterised and easiest recognisable solenopleurid genera, its separation as a distinct genus different from *Solenopleura* by Geyer (1998) has been astoundingly ignored, misunderstood or simply not accepted by most authors. This can be partly ascribed to the fact that many authors obviously believed in the erroneous assumption that Miller (1889) correctly selected *Solenopleura canaliculata* Angelin, 1851 as the type species of *Solenopleura* (e.g., Bruton & Harper 2000, Pegel et al. 2016) although Walcott (1884) had already selected the genotype in the figure captions to his plate VI assuming that this was already done by Angelin (1951) and despite of misspelling the species "*holematopa*". Regarding *Gonzaloia* as a synonym of *Solenopleura* is an extreme case of pre-modern generic concept (Esteve 2015). However, assigning the species tentatively to *Solenopleura* based on reasons other than the morphological criteria appears to indicate deficiencies of taxonomic expertise.

The genus has several characters which distinguish it more-or-less readily from other genera of the Solenopleuridae. They include the distinctly transverse outline of the cephalon; the rearward curved anterior border furrow which causes a distinctly swollen anterior border (in dorsal and frontal views) although the anterior cephalic margin is only weakly curved; the narrow, low preglabellar field which is covered by coarse granules; the relatively well-developed eye ridges with their transverse direction for most of their course their ascending orientation from the axial furrows when seen from anteriorly.

A second, very similar species has been introduced as *Solenopleura patula* Egorova in Egorova et al., 1976. That species easily is distinguished from *G. canaliculata* by a broader (sag.) and less clearly rearward curving anterior border furrow and more posteriorly located palpebral lobes (Egorova et al. 1976, pl. 35, fig. 14, pl. 58, fig. 13, pl. 50, figs. 24, 25). The original material was collected from strata in the Lena and Amga River areas of the Siberian Platform, which represent the *Tomagnostus fissus* Zone of the at that time upper part of the Amgan Stage. A second occurrence was record from the Nizhniy Imbak 219 borehole at the north-western margin of the Siberian Platform (Pegel' et al. 2017). This species was used to characterise the *Solenopleura patula* Zone of the Suorbalakh "Horizon" (lowest part of the Mayan Stage/equivalent to the lower Drumian) in the outer shelf Anabar-Sinsk facies region of the Siberian Platform.

A third species of *Gonzaloia* is probably recorded from the Holy Cross Mountains of southern Poland, where it occurs in Alum Shale equivalents. The species that represent the species are imperfectly preserved in sandstone and were identified as *Solenopleura* cf. *canaliculata* by Orłowski (1985, pl. 7, fig. 13). However, differences are seen in the broader glabellar front, a less posteriorly extended anterior border, and palpebral lobes in a slightly more anterior position than in *G. canaliculata*. However, more and better preserved material is required to formally define this species.

Whitehouse (1939) assigned *Solenopleura canaliculata* to his newly erected genus *Asthenopsis*, which was based on *Asthenopsis levior* Whitehouse, 1939, from the "*Papyriaspis* Stage" (now the Boomerangian; = lower Guzhangian) of north-western Australia. However, the similarity of *A. levior* with *G. canaliculata* is very superficial, and both species are not closely related.

Gonzaloia canaliculata (Angelin, 1851)

Fig. 62

*1851 *Calymene canaliculata*. n. sp. – Angelin: p. 23, pl. 18, fig. 9, 9a.
1854 *Selenopleura canaliculata*. n. sp. – Angelin: p. 27, pl. 18, fig. 9, 9a.
? 1869 *Selenopleura canaliculata* – Linnarsson: p. 72.
? 1876 *Selenopleura canaliculata* Ang. 1851 – Linnarsson: p. 30 (table).
1878 *Selenopleura canaliculata*. n. sp. – Angelin: p. 27, pl. 18, fig. 9, 9a.
1889 *Solenopleura canaliculata* Angelin 1852 – Miller: p. 567.
1902 *Solenopleura canaliculata* Ang. – Grönwall: p. 151, pl. 4, figs. 16, 17.
1937 *Solenopleura canaliculata* – Howell: p. 1176.
1939 *Asthenopsis canaliculata* Angelin sp. – Whitehouse: pp. 213, 214.
v 1953 *Solenopleura canaliculata* (Angelin 1851) – Westergård: pp. 7, 8, 9, 19–21, 40 (table), pl. 5, figs. 1a–c, 2a–c, 3a, b, 4, 5a, b.
1954 *Solenopleura canaliculata* (Angelin, 1851) – Poulsen: p. 444.
1957 *Solenopleura canaliculata* (Angelin) – Rasetti: p. 965.
1959 *Solenopleura canaliculata* (Angelin, 1851) – Poulsen in Harrington et al.: p. *O*275, text-fig. 203.
1967 *Solenopleura canaliculata* (Angelin) – Öpik: pp. 184, 188.
1972 *Solenopleura canaliculata* (Angelin, 1851) – Palmer & Gatehouse: pp. D25, D26.
1973 *Solenopleura canaliculata* – Bergström: p. 27.
1974 *Solenopleura canaliculata* – Martinsson: p. 205.
non 1985 *Solenopleura* cf. *canaliculata* (Angelin 1851) – Orłowski: pp. 252, 260, 263, text-fig. 1, pl. 7, fig. 13.
1994 *Solenopleura canaliculata* (Angelin 1851) – Wolfart: pp. 79, 83, 84, 105, 121, text-fig. M42.
1994 *Solenopleura canaliculata* (Angelin 1851) – Rudolph: pp. 73, 137, 201, 208, pl. 25, figs. 4, 5.
1998 *Gonzaloia canaliculata* (Angelin 1851) – Geyer: p. 392.
2000 *Solenopleura canaliculata* (Angelin 1851) – Bruton & Harper: p. 35.
2002 *Solenopleura canaliculata* (Angelin 1851) – Rushton & Berg-Madsen: p. 341.
2003 *Gonzaloia canaliculata* (ANGELIN, 1851) – Jell & Adrain: p. 380.
2004 *Gonzaloia canaliculata* (Angelin 1851) – Álvaro et al.: pp. 136, 139.
non 2007 *Solenopleura* cf. *canaliculata* (Angelin) – Nawrocki et al: p. 414.
2015 *Solenopleura*? *canaliculata* (Angelin, 1851) – Esteve: pp. 1, 2, 3, 6, 7, fig. 4I–Q.
2016 *Gonzaloia canaliculata* (Angelin, 1851) – Yuan et al.: pp. 222, 247, 645.
2017 *Gonzaloia canaliculata* (Angelin, 1851) – Geyer: p. 49.
2017 *Solenopleura canaliculata* (Angelin, 1851) – Pegel et al.: p. 1283.
2023 *Solenopleura*? *canaliculata* (Angelin, 1851) – Weidner et al.: pp. 104, 120 (table).

Diagnosis. Species of *Gonzaloia* with anterior cephalic border moderately wide (exsag.), distinctly broadened on the sagittal line; anterior border furrow with a rearward swing across the sagittal line; palpebral lobes located in a moderate to slightly anterior position relative to the longitudinal axis.

Occurrence. Erratojincella brachymetopa Zone, particularly Andrarum limestone bed of the Alum Shale Formation. Known from Scania, Västergötland and Jämtland in Sweden; Bornholm, Denmark; southern Norway; and from erratic boulders in northern Germany.

Fig. 62: *Gonzaloia canaliculata* (Angelin, 1851), SGU 6269, incomplete cranidium with preserved cuticle, dorsal (A), frontal (C) and oblique lateral (D) views; magnified view of frontal area (in B) with medially swollen anterior border, subtruncate front of the glabella and low, sunken preglabellar field; E shows anterior part of left fixigena and preocular area separated by transverse, well-developed, slightly raised eye ridge; note coarse granules with a central tube and interspersed low, delicate granules; from Andrarum Limestone Bed, Alum Shale Formation, Andrarum, Scania; original of Westergård, 1953, pl. 5, fig. 3a, b. Scale bars 5 mm in A, C, D, 1 mm in B, E.

Genus *Parasolenopleura* Westergård, 1953

Type species. Calymene aculeata Angelin, 1851 (by original designation); from the *Acrothele granulata* Conglomerate of Borgholm on the island of Öland, Sweden (by original diagnosis).

Diagnosis (emended). Genus of the Solenopleuridae with moderately convex (tr.) and distinctively tapering glabella with almost straight lateral margins and a low curvature of its front; occipital ring with a (sub)terminal spine, strongly tapering towards the abaxial tips; preglabellar field short to moderately broad (sag.), slightly sunken between the preocular areas, defined from glabella by a sharp furrow; anterior border moderately broad (sag.), with low convexity (sag., exsag.), slightly and subevenly curved in frontal view; border furrow with slight to moderate curvature, relatively shallow, with even shallower section in the sagittal sector; palpebral lobes moderately long, crescentic in outline, moderately curved, with oblique inclination; palpebral areas moderately convex in transverse and distinctly convex in exsag. direction; pygidium short, sublenticular in outline, with axis consisting of three rings plus a terminal axial piece, pleural areas divided by shallow pleural furrows; pygidial lateral border poorly defined; prosopon composed of fine to moderately large granules.

Discussion. The genus *Parasolenopleura* is a key genus for the understanding of solenopleurid morphology. Nevertheless, the precise morphological plasticity of the genus has not received much attention over several decades after its introduction and has been regarded as of typical Baltica aspect. In fact, *Parasolenopleura* is a genus typical for the lower half of the middle Cambrian in the so-called Acadobaltic faunal realm. In addition to Scandinavian species *Parasolenopleura cristata* (Linnarsson, 1877), *P. aculeata* (Angelin, 1851), *P. linnarssoni* (Brøgger, 1878), and *P. spinigera* Westergård, 1953, other species have been described from the West Gondwanan areas of the Delitzsch–Torgau–Doberlug Syncline of Germany (*P. lusatica* Sdzuy, 1970), the Franconian Forest region (*P. horstigi* Sdzuy, 1966), northern Spain (*P. demanda* Sdzuy, 1958a), and the Atlas ranges of Morocco (*P. lemdadensis* Geyer, 1998), from where a number of other species await formal description. *Parasolenopleura gregaria* (Billings, 1865) and *P. ouangondiana* (Hartt in Dawson, 1868) are species known from Avalonian Newfoundland. The genus will be discussed in more detail elsewhere.

A number of other species have been assigned or tentatively assigned to *Parasolenopleura*, including species from the Siberian Platform and the Sayan-Altay Foldbelt (*Parasolenopleura composita* Rozova in Egorova et al., 1960; *P. bella* Rozova in Egorova et al., 1960; *P. priva* Khayrullina in Repina, Petrunina & Khayrullina, 1975; *P. schoriensis* Poletaeva, 1955; and *P. subconsocialis* Poletaeva, 1955) as well as Antarctica (*Parasolenopleura amundseni* Wolfart, 1994 and *P.*? *cooperi* Wolfart, 1994), all of them with morphological features which clearly separate them from the typical *Parasolenopleura* species, particularly *P. aculeata*.

Parasolenopleura schoriensis Poletaeva, 1955 and *P. subconsocialis* Poletaeva, 1955, both from the Gornaya Shoriya range of western Sibiria, has been erected as species of a newly introduced genus *Parasolenopleura* Poletaeva, 1955, with *P. subconsocialis* as the type species. Obviously, Poletaeva was not aware during the preparation of the manuscript that a genus with the name *Parasolenopleura* had been recently erected by Westergård (1953). Both poorly known species from the Sanashtykgol “horizon” are known only from considerably distorted specimens and need careful reconsideration of its systematic position.

Other species that were at least temporarily assigned to *Parasolenopleura* and also differ considerably include four species from the British Midlands of eastern Avalonia, such as *Parasolenopleura bruno* (Cobbold & Pocock, 1934), *P. comleyensis* (Richter 1919), *P. dubia* (Cobbold, 1911), *P. elegans* (Illing, 1916), and *P. rushtonensis* (Cobbold & Pocock, 1934).

Parasolenopleura was restricted by Rudolph (1994) to solenopleurid species with a cranidium with a relatively moderate relief, moderately convex palpebral areas (other than *Erratojincella* Rudolph, 1994 with its pronouncedly vaulted cheeks), fairly shallow axial and border furrows, and a weakly to moderately convex anterior border. In addition to the type species of *Parasolenopleura*, *Calymene aculeata* Angelin, 1851, Rudolph (1994) assigned *Solenopleura cristata* Linnarsson, 1877; *Parasolenopleura scanica* Westergård, 1953; *Liostracus linnarssoni* Brøgger, 1878; and *Parasolenopleura vestgothica* Westergård, 1953 to *Parasolenopleura*. This concept portrays more-or-less the generic model which was used for *Parasolenopleura* since its introduction by Westergård (1953), including the publications of the present author (e.g., Geyer 1998, 2017). Indeed, *C. aculeata* and *S. cristata* have palpebral areas which are relatively convex in well-preserved specimens, and the general convexity does not differ from that of species assigned to *Jincella*. As noted earlier, *Calymene aculeata* and *S. cristata* are characterised by a very narrow to nearly entirely reduced preglabellar field and a tendency to exhibit a subtruncate glabellar front (despite of rare specimens of both species with a narrow glabellar front). Another species with an extremely narrow to absent preglabellar field and a usually narrow glabellar front is *P. lemdadensis* Geyer, 1998, from the High Atlas of Morocco.

A contrasting morphology can be seen in *Parasolenopleura scanica*, *L. linnarssoni*, and *P. vestgotica*, which possess a well-developed, convex preglabellar field and other characters described for *Jincella*. The three species *C. aculeata*, *S. cristata*, and *P. lemdadensis* have librigenae with broadly curved genal angles and lack genal spines, whereas all Scandinavian species with a morphology regarded as typical for *Jincella* and from which librigenae are known, possess a small to moderately long genal spine. These species include *S. munsteri*, *S. parva*, *P. scanica*, *L. linnarssoni*, and *Lonchocephalus* *peregrinus* Wallerius, 1930. Geyer (1998, 2017) suggested that the morphology of the genal spines has not been discussed earlier, but appears to be more distinctive than the set of characters, which has been suggested previously to define the genus. The librigenae of *P. vestgothica* are unknown, but there is little doubt that this species also agrees with the characters seen in *Jincella*.

Nonetheless, the averaged cephalic morphology of these species deviates from the morphology of *Calymene aculeata* so that a re-examination of the typical material is required to characterise the genus and to re-evaluate its morphological range. A fundamental character of *Parasolenopleura aculeata* is the shape of its glabella, which has not been played a central role in the characterisation of the genus *Parasolenopleura* and the discussion of relationships between its (suggested) species. The glabella of *P. aculeata* tapers forward to a seemingly subtruncate front (Fig. 63). As it is shown by well-preserved immature specimens, this nearly straight anterior border of the frontal lobe develops from a pair of lobes that are fused with the frontal lobe in adult individuals (Fig. 63F, J, L). The lobes are divided medially, which is indicated by a discrete muscle attachment site on the sagittal line at the tip of the glabella (Fig. 63J). The preglabellar field is relatively narrow, but slightly convex in sagittal profile. However, it is slightly sunken between the preocular areas and proceeds anteriorly into a slight raise in the anterior border furrow. The best preserved of the known pygidia of *P. aculeata* has two normal axial rings plus a terminal axial piece and pleural areas that border to a smooth posterolateral margin, but it also shows a semifused anterior axial ring and a not entirely fused anterior pleura causing a notch at the lateral margin.

Almost all of the other species assigned to *Parasolenopleura* differ slightly or significantly from the morphologies of the glabella, frontal area and pygidium so that *Parasolenopleura* falls out of the average morphology. When compared to other solenopleurids and the existing genera, these features suggest to limit the genus to its type species if principles of consequent morphological analysis are applied.

Parasolenopleura aculeata **(Angelin, 1851)**

Figs. 63, 88S, X

*	1851	Calymene aculeata n. sp. – Angelin: pp. 23–24, pl. XIX, fig. 2.
	1854	Liostracus aculeatus (ANGELIN) – Angelin: p. 27, pl. XIX, fig. 2.
non	1869	*Liostracus aculeatus* Ang. – Linnarsson: pp. 39, 41, 55, 71, 87 (table). [= *P. linnarssoni*].
non	1873	*Liostracus aculeatus* Ang. – Linnarsson: p. 245. [= *P. linnarssoni*].
non	1873	*Liostracus aculeatus* Ang. – Kjerulf: p. 84, text-fig. 14. [= *P. linnarssoni*].
	1878	Calymene aculeata n. sp. – Angelin: pp. 23–24, pl. XIX, fig. 2.
non	1878	Liostracus aculeatus (Angelin?) – Brøgger: p. 46 (30), pl. 3, fig. 3. [= *Parasolenopleura spinigera*]
v	1879	*Liostracus aculeatus* Ang. – Linnarsson: pp. 5, 11–13, pl. I, figs. 12–15.
pars	1883	*Liostracus aculeatus* Ang. – Linnarsson: pp. 7, 22–23, 24, 37 (table), 40, 41.
	1884a	*Solenopleura holematopa* – Walcott: p. 346, pl. VI, fig. 3.
	1884a	*Liostracus aculeatus* – Walcott: p. 346, pl. VI, fig. 6.
	1889	*Liostracus aculeatus* – Lesley: p. 351, unnumbered figure.
	1906	*Liostracus aculeatus* – Wiman: p. 19.
	1913	*Liostracus aculeatus* (Angelin) – Walcott: pp. 137, pl. 13, fig, 6, 6a, 6b.
pars	1929	*Liostracus aculeatus* (Angelin) – Strand: pp. 313, 314, 315, 320, 321, 322, 331, 339, 351, 352, pl. 2, fig. 5a, b.
	1936	*»Liostracus« aculeatus* (Ang.) – Westergård: pp. 19, 21, 52.
	1940	*»Liostracus« aculeatus* (Angelin) – Westergård: pp. 40, 48, 62–63.
	1944	*»Liostracus« aculeatus* (Ang.) – Westergård: p. 35.
	1948	*Liostracus« aculeatus* – Westergård: p. 13.

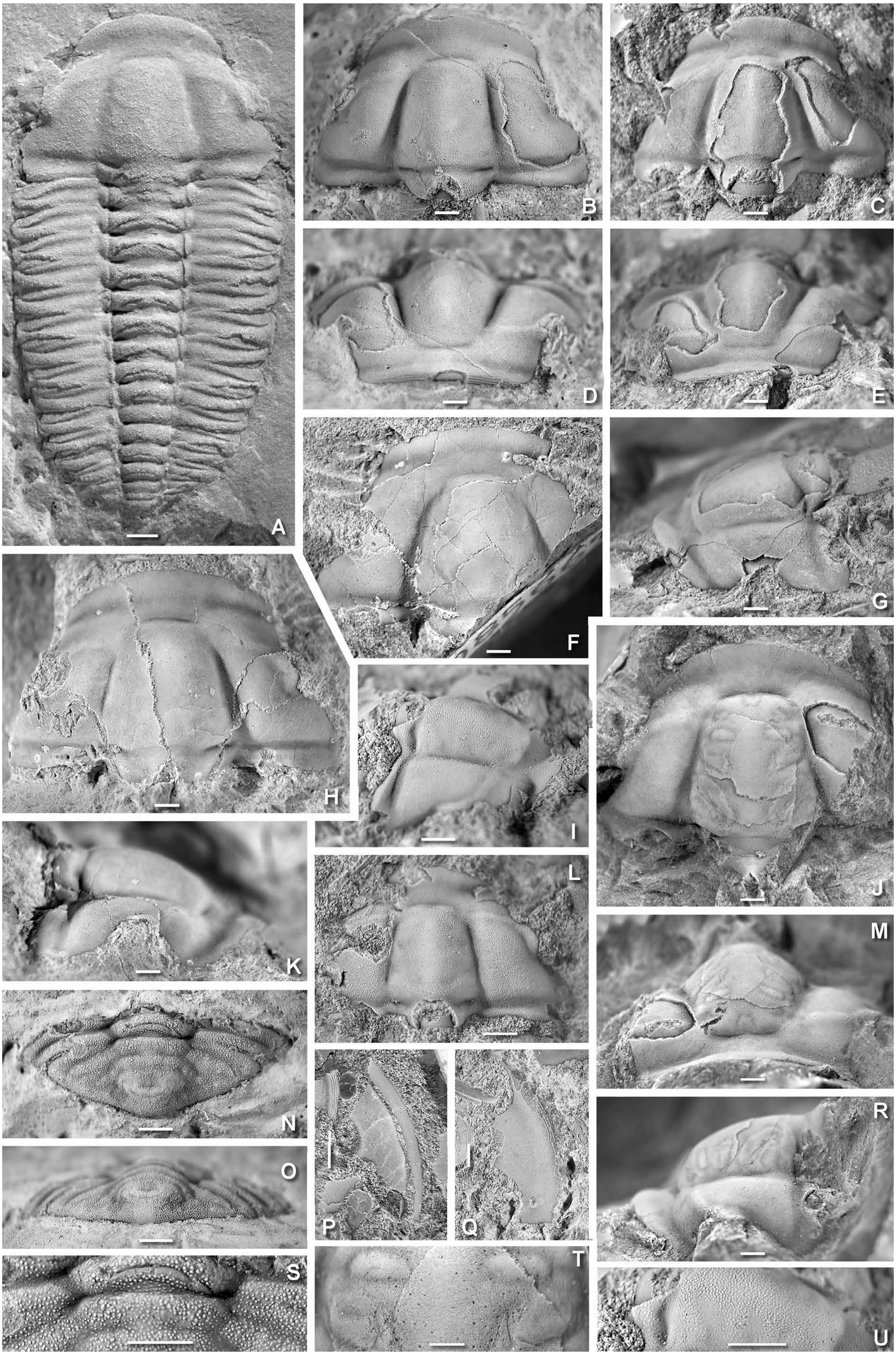
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Fig. 63: *Parasolenopleura aculeata* (Angelin, 1851). **A** SGU 6270a, dorsal exoskeleton without librigenae, internal mould, dorsal view; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 6, fig. 3a, b, c). **B, D** SGU 6272, cranidium, partly exfoliated, dorsal (B) and anterior (D) views; note faint crestline on glabella; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 5, fig. 6a, b). **C, E, G** SGU 4518, cranidium, largely exfoliated, dorsal (C), anterior (E) and lateral (G) views; note incised furrow defining the glabellar front; from Kiviks Esperöd; original of *Liostracus aculeatus* in Linnarsson (1879, pl. I, fig. 12) (collected by G. von Schmalensee 1877). **F** SGU 6273a, small incomplete cranidium, dorsal view; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 5, fig. 9). **H, K** SGU 6272, cranidium, partly exfoliated, dorsal and anterior views, with well visible incision immediately in front of the glabella; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 5, fig. 8). **I, L, U** SGU 6276b, incomplete immature cranidium, internal mould, oblique anterolateral (I) and dorsal (L) views illustrating bilobate frontal lobe of the glabella; U magnified oblique lateral view showing projection of occipital spine and dense granulation of the cuticle's surface; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 6, fig. 4). **J, M, R, T** SGU 4520, cranidium, internal mould with distinct muscle scars; dorsal, anterior and lateral views; T magnified view of glabella showing areas of lateral furrows S2 and S3 illustrating distinct muscle attachment sites and relatively coarse punctae; from Kiviks Esperöd (collected by G. von Schmalensee 1877). **N, O, S** SGU 6276a, pygidium with preserved cuticle; N dorsal view; O anterior view; S magnified dorsal view showing well-preserved surface ornamentation of granules and incompletely fused first axial ring; from Öv. Åkerby, Bh. Nivå; original of Westergård (1953, pl. 6, fig. 4). **P** SGU 6273b, librigena, dorsal view; from Berg, Östergötland, boulder 4 of Westergård (1953). **Q** SGU 6276c, librigena of immature individual, dorsal view; from Berg, Östergötland, boulder 4 of Westergård (1953); original of Westergård (1953, pl. 5, fig. 9).
All scale bars 1 mm.

v 1953 *Parasolenopleura aculeata* (Angelin, 1851) – Westergård: pp. 8, 9, 10, 21, 22, 23–25, 26, 29, 30, 31, 38, pl. 5, figs. 6–10, pl. 6, figs, 1-4.
1958 *Liostracus aculeatus* – Krasnopeeva: p. 109.
1958 *Solenopleurina aculeata* (Angelin) – Šnajdr: p. 200.
1958a *Parasolenopleura aculeata* (Angelin) – Sdzuy: p. 72.
1959 *Parasolenopleura aculeata* (Angelin) – Poulsen in Harrington et al.: p. *O*275, fig. 204,*12*.
non 1966 *Parasolenopleura* cf. *aculeata* (Angelin) – Rushton: p. 47, pl. 6, fig. 14a, b.
non 1973 *Parasolenopleurina? cf. aculeata* – Courtessole: p. 178, pl. 17, fig. 9.
1974 *Parasolenopleura aculeata* – Martinsson: pp. 202, 231.
1979 *Parasolenopleura aculeata* (Angelin) – Neben & Krüger: pl. 115, fig. 5.
1981 Parasolenopleura aculeata – Anderberg & Johansson: pp. 77, 103 (figure).
non 1988 *Parasolenopleura* cf. *aculeata* (Angelin, 1851) – Morris: p. 168.
1994 *Parasolenopleura aculeata* (Angelin, 1851) – Babcock: p. 106, tab. 1, fig. 2, fig. 21.
1994 *Parasolenopleura aculeata* (Angelin 1851) – Rudolph: pp. 27, 48, 49, 50, 51, 52, 54, 57, 72, 99, 100, 211–212, 213, 215, 261, 262, tabs. 12, 15, pl. 26, figs. 10–13 [non pl. 26, fig. 14].
1998 *Parasolenopleura aculeata* (Angelin, 1851) – Geyer: pp. 391, 392.
2000 *Parasolenopleura aculeata* (Angelin, 1851) – Bruton & Harper: pp. 35, 37.
non 2003 *Parasolenopleura* cf. *aculeata* (Angelin, 1851) – Axheimer & Ahlberg: pp. 143, 150, 156, tab. 1.
non 2003 *Parasolenopleura* cf. *aculeata* (Westergård, 1953) – Axheimer & Ahlberg: fig. 7l.
non 2006 *Parasolenopleura aculeata* (Angelin, 1851) – Fletcher: pp. 1077, 1078, 1084, 1086, text-fig. 2.
non 2006 *Parasolenopleura aculeata* (Angelin 1851) – Fletcher: text-fig. 3.
non 2006 *Parasolenopleura aculeata* (Angelin, 1841) – Fletcher: text-fig. 5J.
? 2009 *Parasolenopleura aculeata* (Angelin, 1851) – Weidner & Nielsen: pp. 254, 255, 258, 266–267, text-fig. 17F, 17G.
2022 *Parasolenopleura aculeata* (Angelin, 1851) – Unger et al.: p. 1056.
2023 *Parasolenopleura aculeata* (Angelin, 1851) – Weidner et al.: pp. 12, 106, 121.

Diagnosis (emended). Diagnosis of the genus (because of monotypy).

Discussion. See under genus.

Occurrence. The specimens examined by Angelin (1851) were collected from the *Acrothele granulata* Conglomerate of the Alum Shale Formation at Borgholm on the island of Öland, Sweden. Those specimens and the ones reported by Westergård (1953) from Sweden and Norway are from the *Ptychagnostus gibbus* Interval-zone. Additional specimens were recorded from the *Ptychagnostus atavus* Zone of the upper part of the Henson Gletscher Formation in Nyeboe Land, North Greenland (Babcock 1994), which extends the geographic distribution of the species to Laurentia.

“*Parasolenopleura*” sp. A

Fig. 64

Studied material. Two cranidia, LO 12512t and LO 12513t.

Locality and stratum. Specimens labelled as Cambrian “Div. 1.^{C}, St. John, N. B.”, probably referring to the Fossil Brook Member of the Chamberlain’s Brook Formation at St. John, New Brunswick.

Description and discussion. G.F. Matthew presented two cranidia from St. John, N.B., determined as “*Liostracus ouangondianus* var. *aurora*”, to K.A. Grönwall. These cranidia do not match the descriptions and figures given in Dawson (1868), Walcott (1884b, pl. v, fig. 5) and Matthew (1888, pl. II, fig. 7). They are characterised by a relatively broad glabella with a subtruncate front. The occipital ring is relatively broad o the sagittal line and extends into an apparently moderately long terminal spine, whereas the breadth (exsag.) of the occipital ring decreases considerably towards the fairly broad and poorly defined axial furrows. The palpebral areas are moderately convex, with the most elevated parts located one-third breadth from the axial furrows. The palpebral lobes are moderately long, slightly oblique to axis, with a considerably curved margin at the ocular suture and a weakly curved palpebral furrow. The preglabellar field is moderately long, but only weakly convex in sagittal profile and poorly defined from a shallow anterior border furrow. The anterior border is relatively broad, with a low convexity, weakly ascending in its anterior part.

The specimens are clearly distinguished from *Parasolenopleura aculeata* by a less well-defined anterior margin of the cranidium, a broader preglabellar field and a lower anterior border with a different character as in *P. aculeata*. More and better preserved material is needed to accurately characterise the species represented by the two cranidia. Accordingly, it remains uncertain whether they can be confidently assigned to *Parasolenopleura*.

The specimens are much larger than the other material published as *Conocephalites aurora* Hartt in Dawson, 1868 and subsequent names. The furthermore differ from these specimens in having a relatively low and broad rather than narrow and considerably upturned anterior border; a broader glabella; a short terminal occipital spine; shallow axial furrows; a broad anterior border furrow; and longer, obliquely directed palpebral lobes.

Genus *Exapinepiphania* n. nom.

Type species. Herse neubergi Hawle & Corda, 1847 (junior objective synonym: *Solenopleurina tyrovicensis* Růzička, 1938), name replaced herein by *Exapinepiphania neubergi*; from the Wuliuan of the Barrandean region, Czech Republic.

LSID. urn:lsid:zoobank.org:act:1DFD9A1F-FCB4-429B-9963-5D0915E88C03

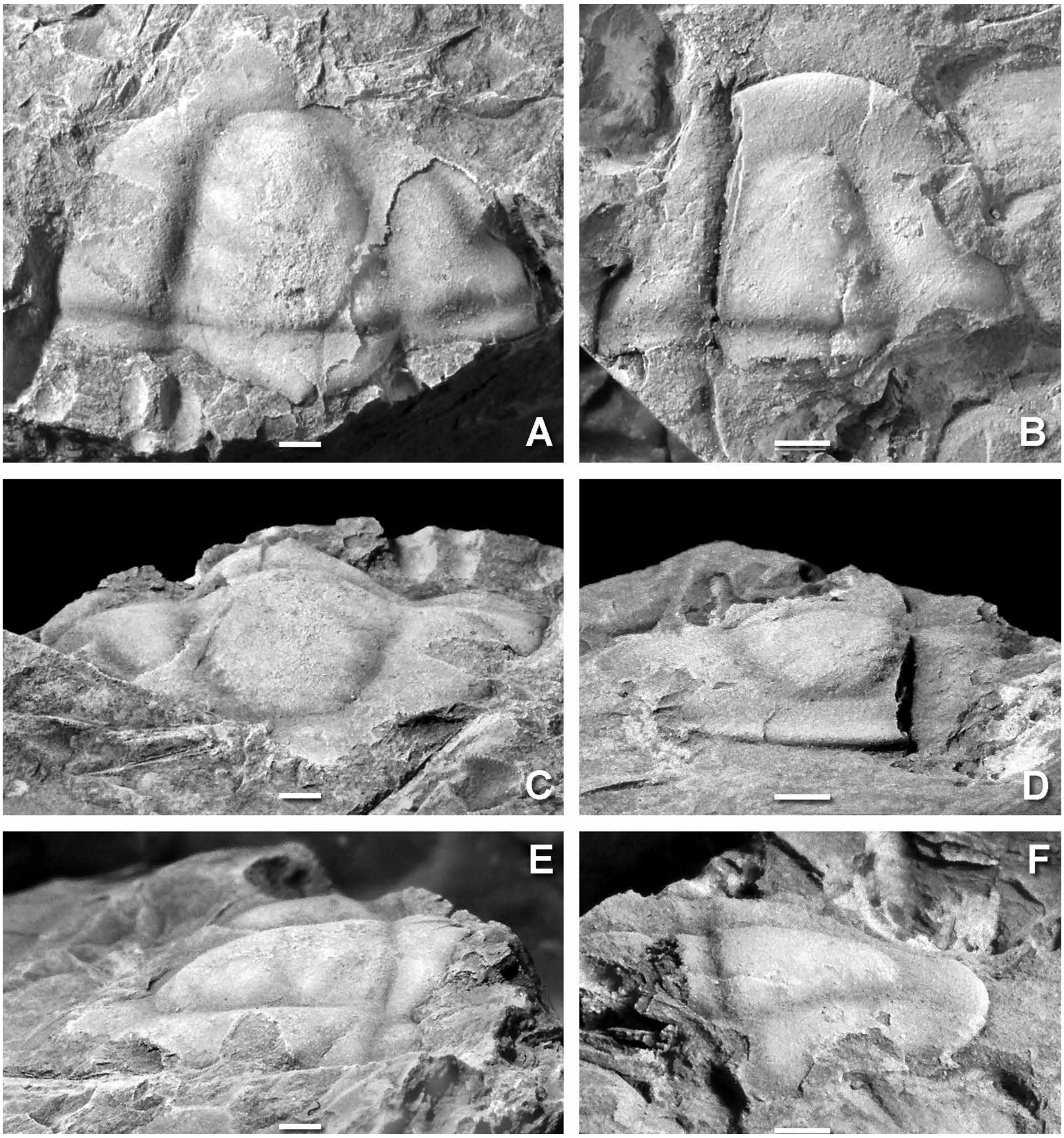

Fig. 64: “*Parasolenopleura*” sp. A. **A, C, E** LO 12512t, incomplete cranidium, partly exfoliated, considerably flattened during compaction, dorsal (A), anterior (C) and oblique lateral (E) views. **B, D, F** LO 12513t, incomplete cranidium, considerably flattened during compaction, partly exfoliated, dorsal (B), anterior (D) and oblique lateral (F) views.
Specimens collected by G. F. Matthew from probably the Fossil Brook Member of the Chamberlain’s Brook Formation at St. John, New Brunswick. All scale bars 1 mm.

Diagnosis. Genus of the Solenopleuridae with a moderately convex (tr.) and tapering glabella with parabolic outline; occipital ring with a (sub)terminal node, thorn or short spine, tapering towards the abaxial tips; preglabellar field short (sag.), slightly sunken between the preocular area, flat to moderately convex in sagittal profile; anterior border moderately broad (sag.), moderately convex (sag., exsag.), slightly and subevenly curved in dorsal view; border furrow with slight to moderate curvature, relatively shallow; palpebral lobes short, distinctly curved at facial suture, but with low curvature at palpebral furrow, obliquely inclined; palpebral areas moderately convex in transverse and exsagittal direction; eye ridges horizontal under frontal view; pygidium with subelliptical outline, axis consists of three rings plus a terminal axial piece, pleural areas divided by distinct pleural furrows; pygidial lateral border poorly defined; prosopon composed of fine to moderately large granules.

Discussion. The problems of the genus *Parasolenopleura* have been shortly discussed above. *Herse* Hawle & Corda, 1847 is a hitherto inadequately characterised and monotypic genus with a confusing nomenclatural history, but its type species, *H. neubergii* Hawle & Corda, 1847, agrees with most species previously assigned to *Parasolenopleura*. *Herse* would have been suitable to accommodate the species that do not fit into the revised concept of *Parasolenopleura*, being distinguished mainly by the precise morphology of the glabella, the palpebral lobes, and the pygidium. Accordingly, *Parasolenopleura* is restricted to its type species, *P. aculeata*.

As for the synonymy of *Herse*, Šnajdr (1958) selected a lectotype for *Herse neubergi* Hawle & Corda, 1847, the type species of the monotypic genus *Herse* Hawle & Corda, 1847. This specimen (Šnajdr 1958, pl. IX, fig. 20) clearly includes the characters of *S. tyrovicensis* and was assigned to this species by Šnajdr (1958). This procedure, however, made *S. tyrovicensis* an objective synonym of *H. neubergi* and the genus *Solenopleurina* consequently an objective junior synonym of *Herse*, as already noted by Sdzuy (1967, p. 108). The name *Herse* had been almost ignored since Hawle & Corda's publication in 1847 – a situation that led to the introduction of the homonymous replacement name *Herse* Gistel, 1848 (for the extant cavolinoid pteropod genus *Cuvieria* Rang, 1827; now *Cuvierina* Boas, 1886).

Unfortunately, the name *Herse* was itself preoccupied by the generic names of the sphingid butterflies *Herse* Oken, 1815 and *Herse* Agassiz, 1846 (which ironically are now both regarded as synonyms as well). *Herse* Hawle & Corda, 1847 is therefore not available, but has never been formally replaced. *Exapinepiphania* is therefore suggested herein as a replacement name. It should also be emphasised that Pompeckj (1896) regarded *Herse* as a synonym of *Agraulos* Hawle & Corda, 1847, but spelled it "*Herze*" and assumed that only the Botanist August Carl Joseph Corda (initials "A. J. C." on the title page of the *Prodrom*) is the author.

A clear-cut concept of *Exapinepiphania* n. nom. compels a precise selection of diagnostic features. These, in turn, put a number of existing species with incomplete record or deficient preservation into only tentative generic assignment.

Jincella Šnajdr, 1957 is a genus with a very close resemblance to *Exapinepiphania*, and species of *Parasolenopleura* were variously re-assigned to *Jincella* and vice versa. The important characters of *Jincella prantli* (the type species of *Jincella*) include the distinctly tapering glabella with a relatively narrow front and almost straight lateral margins; a short, but clearly convex (sag.) preglabellar field, which is only slightly sunken between the preocular areas; and a moderately broad (sag.), convex anterior border defined by a normal, well indented anterior border furrow of equal width throughout of its course. The axial furrows in *J. prantli* are relatively broad and gully-shaped in transverse section rather than relatively deep and more-or-less incised as in the species of *Exapinepiphania*. In addition, the surface of the cuticle in *J. prantli* is covered with fine to moderate granules, whereas the species of *Exapinepiphania* typically show a smooth or nearly surface of the cuticle.

It needs to be emphasised that *Parasolenopleura* had been regarded as a junior synonym of *Solenopleurina* Růžička, 1938 (type species *Solenopleurina tyrovicensis* Růžička, 1938) by Šnajdr (1958), and this proposed synonymy would now apply to *Exapinepiphania*. Earlier studies suggested that *Solenopleurina* differs from *Parasolenopleura* (in the traditional concept) in having relatively deep lateral glabellar furrows and longer palpebral lobes (Sdzuy 1961; Rudolph 1994; Geyer 2017). In fact, this applies to a certain degree for *H. neubergi*, but the figured specimens from the Barrandean region are almost all internal moulds or composite moulds which show much deeper glabellar furrows than they were on the exterior of the cuticle, and the longer palpebral lobes are regarded as specific characters. All other morphologic features seen in *H. neubergii* agree well with those seen in the other species now assigned to the genus.

As discussed earlier, *Parasolenopleura lusatica* Sdzuy, 1970 has been described from material found in boreholes of Agdzian (lower Wuliuan) rocks in the Delitzsch–Torgau–Doberlug Syncline (not of the Lusatia region as the name would suggest). The holotype is shown in Sdzuy (1970, pl. II, fig. 8) in a composite picture and comprises a partial exterior and a cast of the internal mould. It shows a relatively small cranidium with five attached partial thoracic segments and a relatively slender glabella with a narrow curvature of the frontal lobes anterior margin and a narrow occipital ring with only a small median node, narrow palpebral areas, small palpebral lobes, and a narrow (sag.) preglabellar field of about half the breadth of the anterior border. Other cranidia provide little insight into the species' ontogeny and morphological plasticity. Sdzuy (1970, pl. II, fig. 13) assigned a librigena to the species, which, however, was discovered in a horizon well below the horizons in which the cranidia were found. This librigena appears to indicate the presence of a short genal spine, which would suggest *P. lusatica* to be placed under *Jincella*. A pygidium tentatively attributed to *P. lusatica* also comes from a level below the occurrence of cranidia and has a number of characters that would not be typical for *Parasolenopleura*. Accordingly, the species must be regarded as a solenopleurid from the *Exapinepiphania–Jincella* plexus of uncertain generic assignment.

Solenopleura picardi Schmidt, 1942, described from the Doberlug IV drill-core of the Delitzsch–Torgau–Doberlug Syncline, is an imperfectly known species that according to the figures in Schmidt (1944) shows similarities with the species of *Jincella*. However, restudy of the original material suggests that the specimens in fact represent two different species. The holotype belongs to a species which is difficult to assign to an existing genus, but has strong affinities to *Oreisator* Geyer & Malinky, 1997 and is described and discussed below under "*Oreisator*" *picardi*.

Parasolenopleura horstigi Sdzuy, 1966 from the Guzhangian Bergleshof Formation of the Franconian Forest is the youngest species previously assigned to the genus. The species is unusual for the genus in several aspects, particularly the small size and a relatively broad (sag. and exsag.), collar-like anterior border, but – despite the imperfect preservation of the known specimens – has morphological features previously assumed to be characteristic of *Parasolenopleura*. This includes librigenae without a genal spine and with a gently curved genal angle and a relatively well-defined lateral and posterior border (Sdzuy 1966, pl. 9, figs. 7, 8). Nevertheless, no pygidia have been attributed to the species with confidence. Sdzuy (1966, p. 73) stated that the species is very frequent in the type stratum and it would thus be surprising if no pygidia were found, but assumed that these were more or less identical in morphology with those attributed to *Proampyx anceps medianus* Sdzuy, 1966. This of course appears to exclude the species from *Exapinepiphania*.

Species included.

- *Herse neubergi* Hawle & Corda, 1847; from the Skryje Formation, *Eccaparadoxides pusillus* Biozone, Wuliuan, Barrandian region, Czech Republic
- *Parasolenopleura wurmi* Geyer, 2017; from the Galgenberg and Wildenstein members of the Tannenknock Formation, *Kingaspidoides frankenwaldensis* and *Ornamentaspis frequens* biozones, uppermost Cambrian Stage 4 and lowest Wuliuan, Franconian Forest region, Germany
- *Parasolenopleura parabolica* Geyer, 2017; from the Galgenberg Member of the Tannenknock Formation, *Kingaspidoides frankenwaldensis* Zone, uppermost Cambrian Stage 4, Franconian Forest region, Germany

- *Parasolenopleura lemdadensis* Geyer, 1998; from the Bréche à *Micmacca* Member, Jbel Wawrmast Formation, *Ornamentaspis frequens* and *Kymataspis arenosa* biozones, lower Wuliuan, High Atlas, Morocco
- *Solenopleura cristata* Linnarsson, 1877; from the Alum Shale Formation, *Eccaparadoxides*? *insularis* and "*Eccaparadoxides*" *pinus* zones, Wuliuan, Öland, Östergötland, Närke, and southern Jämtland(?), Sweden
- *Bathyurus gregarius* Billings, 1865; from the "Big Gully Member" (=upper Braintree Member), Chamberlain's Brook Formation, *Agraulos affinis* Zone, middle Wuliuan, Avalonian south-eastern Newfoundland
- *Solenopleura pauperata* Walcott, 1906b; from the *Amphoton* Zone, Changhia Formation, Shanxi and Liaoning provinces, northern China
- *Exapinepiphania marionae* n. sp.; from the *Morocconus notabilis* and *Ornamentaspis frequens* zones of the Jbel Wawrmast Formation in the eastern Anti-Atlas, Morocco.

Exapinepiphania wurmi (Geyer, 2017)

Figs. 65–67, 68(pars), 69 (pars), 71N, O

v	1925b	*Ptychoparia striata* Emmr. sp. – Wurm: pp. 83–85, 89, 90, pl. III, figs. 10–12.
v	1925b	*Agraulos ceticephalus* Barr. sp. – Wurm: pp. 87–88, 89, 90, pl. III, fig. 16 (only).
non	1925b	*Agraulos ceticephalus* Barr. sp. – Wurm: pl. III, fig. 17.
v	1925c	*Ptychoparia striata* Emmr. sp. – Wurm: p. 285 (pars).
v	1925c	*Agraulos ceticephalus* Barr. sp. – Wurm: p. 285 (pars).
v	1927a	Ptychoparia striata – Wurm: p. 3 (pars).
v	1927a	Agraulos ceticephalus – Wurm: p. 3 (pars).
v	1927b	*Ptychoparia striata* Emmr. – Wurm: p. 13.
?	1957	*Parasolenopleura* sp. – Wurm: p. 21.
?	1957	*Agraulos ceticephalus* (Barrande) – Wurm: p. 21 (pars).
v	1960	*Solenopleura* aff. *munsteri* Strand 1929 – Sdzuy: p. 108.
	1960	*Solenopleura* aff. *munsteri* Strand – Emmert et al.: p. 75.
	1976	*Solenopleura* aff. *münsteri* Strand – Horstig & Stettner: p. 51 (pars).
v	1997	„*Jincella*“ aff. *munsteri* (Strand) – Geyer & Wiefel: p. 100.
v	2010	*Parasolenopleura* sp. A – Elicki & Geyer: p. 109, fig. 4.3.
v	2010	*Parasolenopleura* sp. B – Elicki & Geyer: p. 109, fig. 4.5.
v	2010	*Parasolenopleura* sp. A – Geyer: p. 81, unnumbered figure on p. 82.
v	2010	*Parasolenopleura* sp. B – Geyer: p. 81.
v	* 2017	*Parasolenopleura wurmi* sp. nov. – Geyer: pp. 5, 13, 16, 19, 51–60, 62, 63, 65, 66, 67, figs. 7, 9d, 9g, 9m, 9n, 22, 23, 24, 25a–d, 25e?, 25f?, 25g, 25h?, 25i?, 25j–x, 25y?, 25z?.
v	2019a	*Parasolenopleura wurmi* – Geyer et al.: pp. 247, 248, 249.
v	2019a	*Parasolenopleura wurmi* Geyer, 2017 – Geyer et al.: p. 397, fig. 15C.

Type locality. Most probably from locality W12 on Fig. 4, a classical Galgenberg locality where Adolf Wurm collected the first specimens of the species.

Type stratum. Galgenberg Member, Tannenknock Formation.

Studied material. More than 210 cranidia, two dorsal exoskeletons, cephalon with attached partial thorax, 13 librigenae, 9 partial thoraces, several thoracic fragments and thoracic segments, two pygidia, single pygidium with attached partial thoraces. In repository: From locality W1 (five unregistered cranidia); from locality W1a (cranidia under MMUW 2017D-944, -951, -952, -953, -955, -958, -959,

-961, -962, -964a, -966, -969a, -969b, -969c, -969d, -969e, -969 and -969g); from locality W6 (cranidia under MMUW 2017D-908b and -918); from locality W7 (10 cranidia under MMUW 2017D-524a, -524b, -524c, -524d, -524e, -524f, -524g, -525, -526 and -537; two librigenae under MMUW 2017D-527a, -527b); from locality W7b (single cranidium under MMUW 2017D-588); from locality W8 (dorsal exoskeleton under MMUW 2017D-380; ca. 125 cranidia under MMUW 2017D-015, -016a, -016b, -021, -022, -023, -035, -037b, -039, -040, -049a, -053a, -053b, -080b, -080c, -084, -089, -090, -112, -115, -118a, -118b, -126, -141a, -141b, -143b, -150a, -150b, -151, -156, -157, -158, -159, -160, -161, -162a, -163, -168, -183a, -183b, -185, -187, -191, -195, -196, -211b, -212b, -213b, -216, -224, -237d, -237e, -240a, -247a, -249c, -253a, -273a-g, -293, -294, -303a, b, -304b, -305a, -310a, -310d, -349, -355a, -372, -375, -391, -392, -597a, -600, -629b, -659, -674b, -674d, -677c, -678, -708b, -713, -726, -731, -735b, -743, -775b, -778, -784a, -975, -979, -981, -983a, -983b, -986a, -987, -988, -991, -992, -993, -994, -995, -996, -997. -999, -1001, -1003, -1006a, -1008a, -1008b, -1010, -1013, -1014, -1018a, SSMM 10402b, 10421c, 10472, 10483, 10488, 10491, 10811a, 10811b, 10816, 10818b, 11023, 11038b, 11038d, 11057c, 11062c, 11067, 11073, 11113, 11208, 11441, 11642a and 11848a; 10 librigenae under MMUW 2017D-189, -231, -237c, -238a, -238b, -675, -677a, -677b, -727 and -773a); from locality W8a (five cranidia under MMUW 2017D-861, -866b, -869, -880a and -880b); from locality W9 (two cranidia under SSMM 11503a and 12402a); from locality W9a (6 cranidia under SSMM 10287, 10289, 10290a, 10290b, 10293 and 10294); from locality W9b (two cranidia under MMUW 2017D-562 and -587a); very probably from locality W10 (three cranidia under SMF 88213a, 88213c and MMUW 2017D-933); from locality W11 (31 cranidia under SSMM 10656a, 10656b, 10675c, 10681, 10695, 10696, 10697, 10698, 10699, 10700, 10701, 10702a, 10702b, 10714, 10715, 10716b, 10721, 10722, 10723, 10725, 10726, 10727, 10728, 10731, 10732, 10736a, 10758, 10759, 10761, SMF 90022a and SMF 90022b); from locality W11 (cranidium under MMUW 2017D-895); from locality W11 or W12 (five cranidia under SNSB-BSPG 1924-XII-2a [original specimen of Wurm 1925c, pl. III, fig. 11]; SNSB-BSPG 1924-XII-2b [original specimen of Wurm 1925c, unfigured], SNSB-BSPG 1955-VII-13, SNSB-BSPG 1955-VII-18b and SNSB-BSPG 1959-IV-64; pygidium under SNSB-BSPG 1924-XII-2d [on the same slab as the specimen of Wurm 1925c, SNSB-BSPG 1924-XII-2b]); from locality W12a (10 cranidia under SSMM 10618a, 10619b, 10620, 10621, 10623, 10624, 10625, 10626a, 10651 and 10652); from locality W13b (cranidia under MMUW 2017D-559, -927i/II, -928I/II and -930I/II); from locality W13e (seven cranidia under MMUW 2017D-451, -462, -465, -623, -625a, -625b and -625c); from locality W14 (incomplete dorsal exoskeleton under SSMM 10144; 11 cranidia under SSMM 10122, 10123, 10129, 10130a, 10131a, 10131b, 10132, 10133, 10134, 10181 and 10182); from locality W15b-15c (single cranidium under MMUW 2017D-643); from locality W16a (single cranidium under MMUW 2017D-828); from locality W17 (librigena under MMUW 2017D-818); from locality W19b (cranidia under MMUW 2017D-936a, -936b, -937a, -938a and -938b); from locality T2a (two dorsal exoskeletons under SSMM 10011 and SSMM 10012; cephalon with articulated partial thorax under SSMM 10010a; 14 cranidia under SSMM 10006, 10009, 10010b, 10010c, 10018, 10052, 10056, 10069, 10070, 10082, 10089a, 10089b, 10102a and 10102b.

Material tentatively assigned to Exapinepiphania wurmi*:* In repository: ca. 170 cranidia, ca. 25 librigenae, ca. 25 thoracic fragments and thoracic segments, 17 pygidia. From locality W1 (four cranidia under MMUW 2017D-507b, -508, -516 and -921a; thoracic segments and pleurae under MMUW 2017D-513, -514 and -757); from locality W1a (cranidia under MMUW 2017D-972a, -972b and -972c; librigena under MMUW 2017D-974; pygidium under MMUW 2017D-963b); from locality W6 (cephalon under MMUW 2017D-915, cranidia under MMUW 2017D-917 and -919a, librigena under MMUW 2017D-919b); from locality W7 (6 cranidia under MMUW 2017D-529, -533a, -533b, -533c, -533d and -537; librigena under MMUW 2017D-528; pygidium under MMUW 2017D-531); from locality W8 (58 cranidia under MMUW 2017D-041a, -055, -056, -069a, -097a, -103a, -104, -115, -123a, -128b, -150c, -178a, -181c, -183c, -183d, -200, -250b, -252, -284b, -296b, -297, -298, -302e, -304c, -305b, -309b, -309d, -311b, -371a, -371c, -381a, -389b, -616c, -621a, -644, -779b-I, 779b-II, -1007c, -1009b, -1028, SSMM 10428, 10465, 10466a, 10466b, 10467, 10476b, 10486, 10489, 10495b, 10522, 10525, 10534, 11000a, 11004, 11005, 11079 and 11121; 19 librigenae under MMUW 2017D-009, -072, -106, -121, -122, -124, -164, -254a, -263, -363a, -370, -381b, -381c, -385, -595a, -621b, -717, -982a, -986b and -1006b; 8 pygidia under MMUW 2017D-110, -233b, -296a, -311a, -353a, -360, -378b, 383, and -976a; thoraces, thoracic segments and pleurae under MMUW 2017D-028, -042, -162b, -237f, -353b, -355b, -363b, -381d, -784b, -977b and 1026); from locality W8a (partial cephalon with partial thorax under MMUW 2017D-864, 10 cranidia under MMUW 2017D-865, -870, -871a, -874, -875, -877, -878, -879, -885 and -886, librigena under MMUW 2017D-868, articulated thorax under MMUW 2017D-860 and -882, pygidia with articulated posterior thorax under MMUW 2017D-871b and -883, 6 pygidia under MMUW 2017D-859, -866a, -867, -872, -873 and -876); from locality W9 (five cranidia under MMUW 2017D-771, SSMM 12396, SSMM 12398, SSMM 12399 and SMF 96580); from locality W9b (two cranidia under MMUW 2017D-567b and -582; librigena under MMUW 2017D-801); from locality W16b (librigena under MMUW 2017D-827); very probably from locality W10 (two cranidia under SMF 88203 and SMF 88210); from locality W11 (six cranidia under MMUW 2017D-898, SSMM 10655, 10675b, 10711, 10719 and 10736b; librigena under MMUW 2017D-897); from locality W12 (two cranidia under SSMM 10178 and SSMM 10279); from locality W12a (three cranidia under SSMM 10601, 10636 and 10654); from locality W12d (cranidium under MMUW 2017D-905); from locality W13a (cranidia under MMUW 2017D-609, -610, -612, -613 and SSMM 10208); from locality W13b (three librigenae under MMUW 2017D-422, -557 and -929; thoracic pleura under MMUW 2017D-931b; pygidia under MMUW 2017D-405 and 931a); from locality W13e (12 cranidia under MMUW 2017D-436, -440b, -456, -459, -470, -472, -476a, -476b, -476c, -482, -485 and -489c; two librigenae under MMUW 2017D-455 and -488c; pygidium under MMUW 2017D-466; dorsal exoskeleton under MMUW 2017D-447); from locality W14 (6 cranidia under MMUW 2017D-521, -522, -523, SSMM10124, 10125, 10128a and 10142); from locality W15a (almost complete exoskeleton under MMUW 2017D-333); from locality W15b (cranidium under MMUW 2017D-891); from locality W15d (cranidial fragments under MMUW 2017D-889a and -889b); from locality W17 (two cranidia under MMUW 2017D-786 and -797); from locality W18a (six cranidia under MMUW 2017D-540d, -542, -545, -546c, -552a and -552b; thoracic segments and pleurae under MMUW 2017D-551); from locality W19 (cranidia under MMUW 2017D-922a, -922b, -922c and -922d); from locality W19a (three cranidia under MMUW 2017D-833, -834-I and 834-II; two librigenae under MMUW 2017D-831 and -832); from locality W19b (thoracic pleura under MMUW 2017D-935g); from locality T2a (12 cranidia under SSMM 10035, 10068, 10073, 10075, 10076, 10078, 10080, 10083, 10084, 10085, 10089c and 10275); from locality T2b (four cranidia under SSMM 10105, 10108, 10110-II and 10111).

A total of 539 cranidia, 9 cranidia with attached partial thoraces, 79 librigenae, 19 thoraces, thoracic fragments and thoracic segments, 62 pygidia, 4 pygidia with attached partial thoraces, and 35 exoskeletons were listed in Geyer (2017) as paratypes from the studied localities of the Galgenberg Member (localities W1; W1 or W2; W8; W9a; probably from W10; W11; W11 or W12; W12; W12a; W13c; W14; W14a; W14b; T2/T2a; T2a; and T3/T4). Material tentatively assigned to *P. wurmi* in Geyer (2017) included 95 cranidia, 96 librigenae, 24 thoraces, thoracic fragments and thoracic segments, 28 pygidia, two pygidia with attached partial thoraces, 14 exoskeletons.

Diagnosis (emended herein). Species of *Exapinepiphania* with the following characters (in adult individuals): glabella strongly convex, having a nearly evenly curved to faintly subacute anterior margin of the frontal lobe; maximum width across S1 ca. 50 percent width across mid-length of palpebral lobes, glabella slightly tapering forward, with distinctly curved lateral margins; occipital ring with postero-median or sub-terminal node or thorn; anterior branches of facial suture subparallel between anterior ends of palpebral lobes and anterior border furrow; palpebral areas moderately convex; eye ridges moderately elevated, generally well visible, distinctly oblique to axis, meet axial furrows opposite S3; preglabellar field sagittally narrow, forming a low swelling in front of the glabella; anterior border a moderately broad (tr.) torus of ca. 12–15 percent cephalic length, considerably tapering from its sagittal maximum breath toward the facial suture, moderately raised in lateral view; anterior margin gently curved in front of the glabella, less so close to the facial suture.

Description. Cephalon trapezoidal in outline, with broadly curved anterolateral and posterolateral corners. Axial furrows moderately wide, relatively deeply incised. Glabella tapers forward, paraboloid in outline; maximum glabellar width across L1 of 46–53 percent (n=17) cranidial width across centre of palpebral lobes; frontal lobe across anterolateral corners of ca. half width across L1; anterior margin of frontal lobe variably developed, generally gently curved in dorsal view, with vaguely indicated anterolateral corners and occasionally faintly subacute on the sagittal line so that in such cases the front appears obliquely subtruncate (Fig. 65P), rarely slightly truncate, often with reduced curvature to subtruncate in distorted specimens; three pairs of lateral glabellar furrows; S1 moderately long, bifurcated, with strongly backward curved posterior branch and slightly shorter and less well impressed (Fig. 65O), roughly transverse anterior branch, moderately deep on internal moulds near axial furrows, shallow adaxially and on exterior surface; S2 and S3 comparatively short, S2 slightly directed backward from near axial furrows, S3 almost normal to axis. Internal moulds occasionally allow recognition of muscle scars, which appear to consist of a composite pair (e.g., Fig. 67G, left pair of arrows; Fig. 66Y). Occipital furrow with narrow, well-incised lateral parts directed obliquely backward from axial furrow, and quite broad (sag.) and moderately shallow, transverse middle part. Occipital ring sagittally of about 14–18 percent (n=17) cephalic length, extreme lateral parts narrow, its low abaxial extensions traverse axial furrows; moderately large occipital node in posteromedian to slightly subterminal position.

Fixigena posterior to eye ridge of about 40 percent sagittal cephalic length near axial furrow, width of palpebral area across palpebral lobes variably of 35–42 percent (n=17) maximum glabellar width (across L1), extends into broad (tr.) posterior limb of the fixigena; gently to moderately convex, most elevated point roughly in central position. Eye ridge developed as a low ridge, weakly demarcated on the exterior of the cuticle and aligned with an angle of ca. 25° to the transverse axis, well visible on internal moulds, meet axial furrows opposite S3. Palpebral lobe relatively small to moderately long, depending on the size of the individual, exsagittally 22–27 percent (n=14) sag. cephalic length in adult specimens, anterior end opposite posterior part of L3, posterior end opposite S1 or anterior part of L1, moderately upturned at an angle of roughly 30° to the slope of the abaxial part of the gena. Palpebral furrow a relatively broad, shallow, almost straight depression slightly oblique to sagittal axis. Palpebral lobes and eye ridges separated by a constriction, which is distinct and well preserved on internal moulds (e.g., Fig. 67G, arrow).

Preglabellar field short, forms a poorly convex, anteriorly sloping swelling in front of the glabella, generally less well demarcated from the anterior border than from the glabella (e.g., Figs. 65K, 67C). Preocular area gently convex, developed as steeply sloping trapezoidal fields.

Anterior border moderately to clearly convex, but relatively low in lateral view, moderately broad (sag., exsag.), faintly swollen and of ca. 12–15 percent (n=17) cephalic length on sagittal line, clearly tapering to about half-width next to suture. Anterior margin gently curved in dorsal view, faintly arched upward in frontal view; in anterior view, the anterior border forms a moderately curved arch in its middle section, but has a faint sigmoidal curvature with less curved lateral sections (Fig. 65L, Q).

Anterior border furrow moderately deep in front of preocular fields, shallower and developed merely as a change in convexity in front of the glabella. Posterior border with straight adaxial part, weakly sigmoidally curved distally, moderately narrow, relatively prominent. Posterior border furrow narrow adjacent to axial furrows, broadening abaxially to an exsagittally wide, moderately deep groove toward the posterior branches of the suture, with straight adaxial part and slight sigmoidal curvature distally.


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Fig. 65: *Exapinepiphania wurmi* (Geyer, 2017). **A, D, G** SNSB-BSPG-1924-XII-2a, cranidium, internal mould, dorsal (A), anterior (D) and lateral (G) views; original of Wurm 1925a, pl. III, fig. 11; from locality W11 or W12; **B, E** MMUW 2017D-151, incomplete cranidium, internal mould, dorsal (B) and anterior (E) views; from locality W8; **C, F, J** MMUW 2017D-157, cranidium, internal mould, dorsal (C), lateral (F) and anterior (J) views; from locality W8; **H, K** MMUW 2017D-163, cranidium, internal mould, lateral (H) and dorsal (K) views; from locality W8; **I** MMUW 2017D-216, cranidium, internal mould, slightly distorted; from locality W8; **N, Q** MMUW 2017D-158, cranidium, internal mould, dorsal (N) and anterior (Q) views; from locality W8; **L, M, O, R** MMUW 2017D-159, cranidium, internal mould, anterior view (L), magnified view of dextral side showing caeca arising from eye ridge into palpebral areas and preocular areas (M), lateral view with muscle attachment scars (O) and dorsal view with indistinct radial caeca extending across preglabellar field and anterior border furrow (R); from locality W8; **P, S** MMUW 2017D-156, cranidium, internal mould, dorsal and lateral views; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Anterior branches of facial suture straight and almost parallel from anterior ends of the palpebral lobes to border furrow, with strong inward curvature anteriorly. Posterior branches diverge markedly from posterior ends of ocular suture, with moderate general curvature, curve markedly backward and inward from centre of border furrow at posterolateral angles.

Librigena moderately large, with broadly curved genal angle (Fig. 68P, S). Genal field fairly wide (tr.), gently convex, adjacent to ocular suture with narrow plane band and flange (Fig. 618C, G). Lateral border moderately wide. Border furrow shallow, but relatively well demarcated.

Thorax composed of 13 (rarely 14 or even 15) segments. Thoracic axis narrows slightly and progressively backward from third axial ring. Axial rings moderately convex, separated from articulating half-ring by a very distinct, fairly deep articulating furrow with slightly broader medial part; with lateral, swollen bacculae that indicate attachment sites for a well-developed musculature for the ventral appendages. Middle section commonly narrower (sagittally), reflects an ability to perform a ventrally concave curvature during enrolment in segments 3 to 9. Axial rings of segments 4 to 8 with small to moderately large median axial spines.

Pleurae of tergites 3 to 11 with more-or-less straight adaxial section, distal parts conspicuously deflected ventrally and slightly backward directed (Geyer 2017, fig. 23A). Anterior margins of these pleurae nearly straight, posterior margin of distal part slightly curved and convex toward posterior. Distal section of pleura with conspicuous, large anterior facet that permitted considerable overlap of adjacent pleurae. First tergite with especially large facets and slightly truncated distal portion of pleurae; second tergite with similar morphological modifications, but less strikingly developed. Pleural tips generally broadly curved in dorsal view, posterior half obliquely subtruncate. Pleural furrow well-defined, relatively deep, commences close to axial ring and swings faintly back to stay roughly in centreline of pleura, but with a slight swing toward the anterior in the distal portion of the pleura; fade relatively close to pleural tips. Pleurae of tergites 10 to 13 with site of ventral deflection close to axis and slightly curved backward; facets large, allow distinct ventral deflection of pygidium and posterior tergites.

Pygidium relatively small, subpentagonal in outline, or with gently arched posterior margin, length/width ratio roughly 0.4 to 0,5. Axis moderately convex, with two relatively well-defined axial rings, one additional faintly marked ring and a terminal axial piece; articulating half-ring a moderately prominent, narrow ring, separated by a broad (sag.) and moderately deep articulating furrow; first axial ring well marked by a moderately deep transverse ring furrow, transversely of ca. 40 percent maximum pygidial width; second axial ring defined by a shallow to barely visible furrow; terminal axial piece of ca. 70 percent width across anterior axial ring, with evenly curved posterior tip, which is separated from the posterior margin by more than 5 percent of the pygidial length; no plectrum developed, but often with low, posteriorly downward sloping median swelling adjacent to posterior tip of the rhachis (Fig. 69E, H).


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Fig. 66: *Exapinepiphania wurmi* (Geyer, 2017). **A, D, G** MMUW 2017D-196, distorted cranidium with partially preserved cuticle, dorsal (A), anterior (D) and lateral (G) views; from locality W8; **B** MMUW 2017D-158, partial cranidium, internal mould, lateral view; from locality W8; **C, F, I** MMUW 2017D-160, incomplete cranidium, internal mould, anterior (C), lateral (F) and anterior (I) views; from locality W8; **E** MMUW 2017D-216, cranidium, internal mould, oblique anterolateral view; from locality W8; **H, K** MMUW 2017D-371a, partial cranidium, internal mould, dorsal (H) and anterior (K) views; from locality W8; **J, L** MMUW 2017D-161, cranidium of immature individual, internal mould, dorsal (J) and anterior (L) views; from locality W8; **M, R, S** MMUW 2017D-861, cranidium of immature individual, external mould, dorsal (M), oblique lateral (R) and anterior (S) views; from locality W8a; **N, P** MMUW 2017D-303b, cranidium of immature individual, internal mould, anterior (N) and dorsal (P) views; from locality W8a; **O** SSMM 11108b, cranidium of immature individual, internal mould; from locality W8; **Q** MMUW 2017D-159, cranidium, internal mould, partial lateral view illustrating the connection between palpebral lobe and eye ridge as well as a low ridge on the preocular area (see also Fig. 65); from locality W8; **T** MMUW 2017D-211b, cranidium of immature individual, internal mould; from locality W8; **U, Y** MMUW 2017D-224, partial cranidium, internal mould, dorsal (U) and lateral (Y) views; note loop-shaped muscle scars on glabella (arrows); from locality W8; **V–X** MMUW 2017D-215, cranidium of immature individual, internal mould, dorsal (V), lateral (W) and anterior (X) views; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated.
Scale bars 5 mm in B, C, E, F, H–L, P, Q, 1 mm in A, D, G, M–P, R–T, U–Y.

Pleural fields with two or three pleural furrows, which are progressively ill-defined backward (Fig. 69M); anterior, faint interpleural furrows sometimes visible (Fig. 69C, J). Posterior and lateral borders not defined, lateral and posterior rims consist of convex, rapidly sloping deflected marginal portions.

External surface smooth except for weakly developed terrace ridges alone anterior and lateral margins of the cephalon. Indistinct caeca visible on internal moulds on the preocular areas, sometimes extended onto the anterior border (Fig. 67G, arrow).

Discussion. Exapinepiphania wurmi (Geyer, 2017) is alongside with *Kingaspidoides frankenwaldensis* (Wurm, 1923) the most frequent trilobite in the Galgenberg Member of the Tannenknock Formation. The species also occurs in the Wildenstein Member of this formation, but clearly less frequently. The species is stratigraphically the oldest species of *Exapinepiphania* known thus far, but its morphological characters do not indicate any “primordial” status.

The species was among the first trilobites described from the Tannenknock Formation by Wurm (1924b). However, Wurm misidentified the specimens discovered by him from both rocks of the Galgenberg and Wildenstein members (not distinguished in Wurm 1924b and subsequent publications of that author) as the well-known trilobite species *Ptychoparia striata* Emmrich, 1839 and also as *Agraulos ceticephalus* Barrande, 1852. Sdzuy (1960) recognised the species as a new solenopleurid, but identified it provisionally as *Solenopleura* aff. *munsteri* Strand, 1929.

The difficulties of identifying a species within this notoriously difficult genus and family from imperfectly preserved material have been discussed in Geyer (2017). *Exapinepiphania wurmi* is characterised by a combination of features.

The species has: (1) a comparatively large glabella in both longitudinal as well as transverse directions; (2) a sagittally narrow preglabellar field, which has a low convexity (best seen in lateral view); (3) a fairly prominent anterior border, which is not conspicuously raised in lateral view because of the distinctive deflection of the anterior part of the cephalon; (4) relatively moderately convex (tr. and exsag.) palpebral areas; (5) palpebral lobes with a relatively strong oblique direction in dorsal view; (6) a moderately large occipital node in a median to slightly subterminal position; and (7) pygidial pleural fields with only weak pleural furrows.

The species is accompanied in the Galgenberg Member by a second species of *Exapinepiphania*, *E. parabolica* (Geyer, 2017), which is easily distinguished by its more slender shaped glabella with the eponymous outline (see Geyer 2017 for additional discussion).

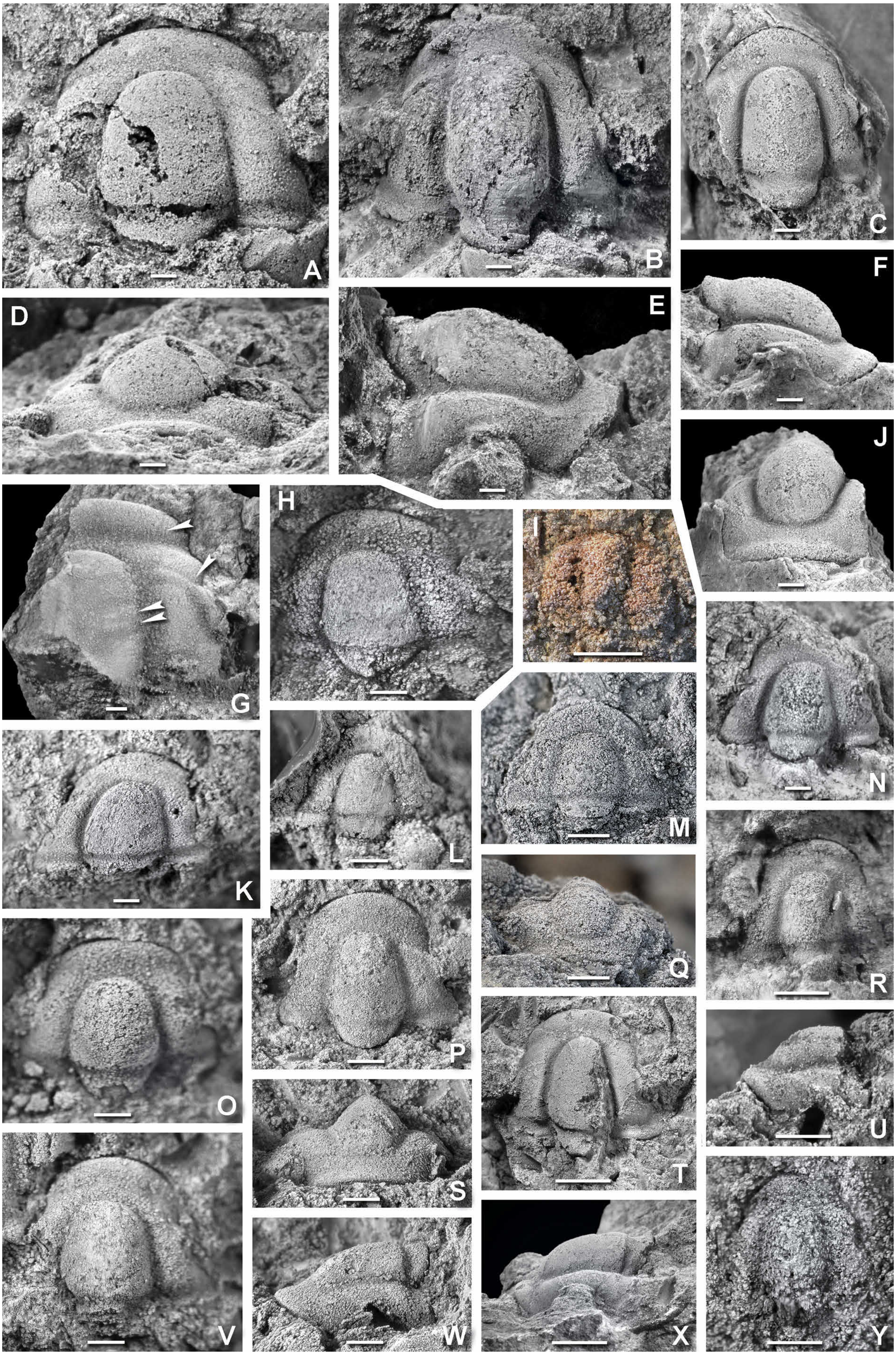
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Fig. 67: **A–H, I?, J–S, T?, U–W, X?, Y** *Exapin-epiphania wurmi* (Geyer, 2017). **A, D** MMUW 2017D-183a, cranidium, internal mould, dorsal (A) and anterior (D) views; from locality W8; **B, E** MMUW 2017D-084, cranidium, internal mould, dorsal (B) and lateral (E) views, slightly compressed cranidium reminds to the morphology of *Parasolenopleura*? sp. A; from locality W8; **C, F, J** MMUW 2017D-185, partial cranidium, internal mould, dorsal (C), lateral (F) and anterior (J) views; from locality W8; **G** MMUW 2017D-866b, partial cranidium, internal mould; arrows point to radial caeca extending onto anterior border, to notable constriction between palpebral lobe and eye ridge, and to paired muscle scar below L2; from locality W8a; **H** MMUW 2017D-303i, cranidium of immature individual tentatively assigned to *E. wurmi*, internal mould; from locality W8; **I** MMUW 2017D-935h, meraspid cranidium, internal mould; from locality W19b; **K** MMUW 2017D-253a, cranidium of immature individual, internal mould; from locality W8; **L** MMUW 2017D-115L, cranidium of immature individual, latex cast of external mould; from locality W8; **M, Q** MMUW 2017D-035, cranidium of immature individual, internal mould, dorsal (M) and anterior (Q) views; from locality W8; **N** MMUW 2017D-489c, cranidium of immature individual, internal mould; from locality W13e; **O** MMUW 2017D-303a, cranidium of immature individual, internal mould; from locality W8; **P, S, W** MMUW 2017D-674b, cranidium of immature individual, internal mould, dorsal (P), anterior (S) and oblique lateral (W) views; from locality W8; **R, U** MMUW 2017D-743, cranidium of immature individual, internal mould, dorsal and lateral views; from locality W8; **T, X** MMUW 2017D-266l, cranidium of immature individual, internal mould, dorsal (T) and lateral (X) views; from locality W8; **V** MMUW 2017D-310a, cranidium of immature individual, internal mould; from locality W8; **Y** cranidium of immature individual, internal mould; from locality W8? (specimen apparently lost). All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated.
Scale bars 1 mm except for I (= 500 µm).

However, *E. wurmi* is accompanied in the Wildenstein Member by two more species and two additional informally described forms of *Exapin-epiphania* or closely related taxa. These forms are characterised and compared with *E. wurmi* below. They are often difficult to confidently identify if affected by tectonic distortion. The principal distinguishing characters are the width and relative of the preglabellar field and the transition to the neighbouring preocular areas; the height, convexity and breadth (sag., exsag.) of the anterior border; and the size and prominence of the palpebral lobes. Although these characters may seem to range (at least partly) under the specific variability, this is clearly not the case if specimens of the same size are compared. As in the case of the *Kingaspidoides*, the taxonomic proliferation of the genera is unexpected and challenging to explain, but it should be taken into account that the different species, or forms partly come from different localities with different lithological signatures and may also represent strata of somewhat different ages.

It is demanding or impossible to precisely determine isolated non-cranidial sclerites of *Exapinepiphania wurmi* and the other species/forms. For this reason, the librigenae and pygidia of the Wildenstein Member from the *wurmi* clade are collectively dealt with herein and illustrated in Figs. 68 and 69.

Another very similar species is *Exapinepiphania cristata* (Linnarsson, 1877) from the slightly younger *Eccaparadoxides oelandicus* Superzone of Sweden. The Swedish species has a slightly smaller and more strongly tapering glabella, more distinctly convex palpebral areas, a broader (sag. and exsag.) anterior border, and a relatively small occipital node in a perfectly median position (Figs. 73, 74).

As discussed in Geyer (2017), *E. cristata* has been regarded as a junior synonym of *E. gregaria* (Billings, 1865) from Avalonian Newfoundland (dealt with as species of *Parasolenopleura* in Fletcher 2005). However, *E. gregaria* is distinguished from *E. cristata* (and *E. wurmi*) by a distinctly broader (sag.) and more prominent anterior border. This broad border is also developed on the librigenae of *P. gregaria*, where it causes a reduction in width of the librigenal field width (see Fletcher 2005, pl. 2, figs. 8–11). *Exapinepiphania gregaria* has an occipital node in a perfectly median position, whereas the occipital node in *E. wurmi* is located at a slightly subterminal position, and *E. wurmi* and *E. cristata* have their occipital nodes as well mostly slightly posterior to the centre of the occipital ring. The exoskeleton of *E. gregaria* includes 14 thoracic segments, whereas specimens with 14 and 15 segments are known of *E. cristata*. The number of thoracic segments in *E. wurmi* is usually 13, but varies to reach up to 15 in number.

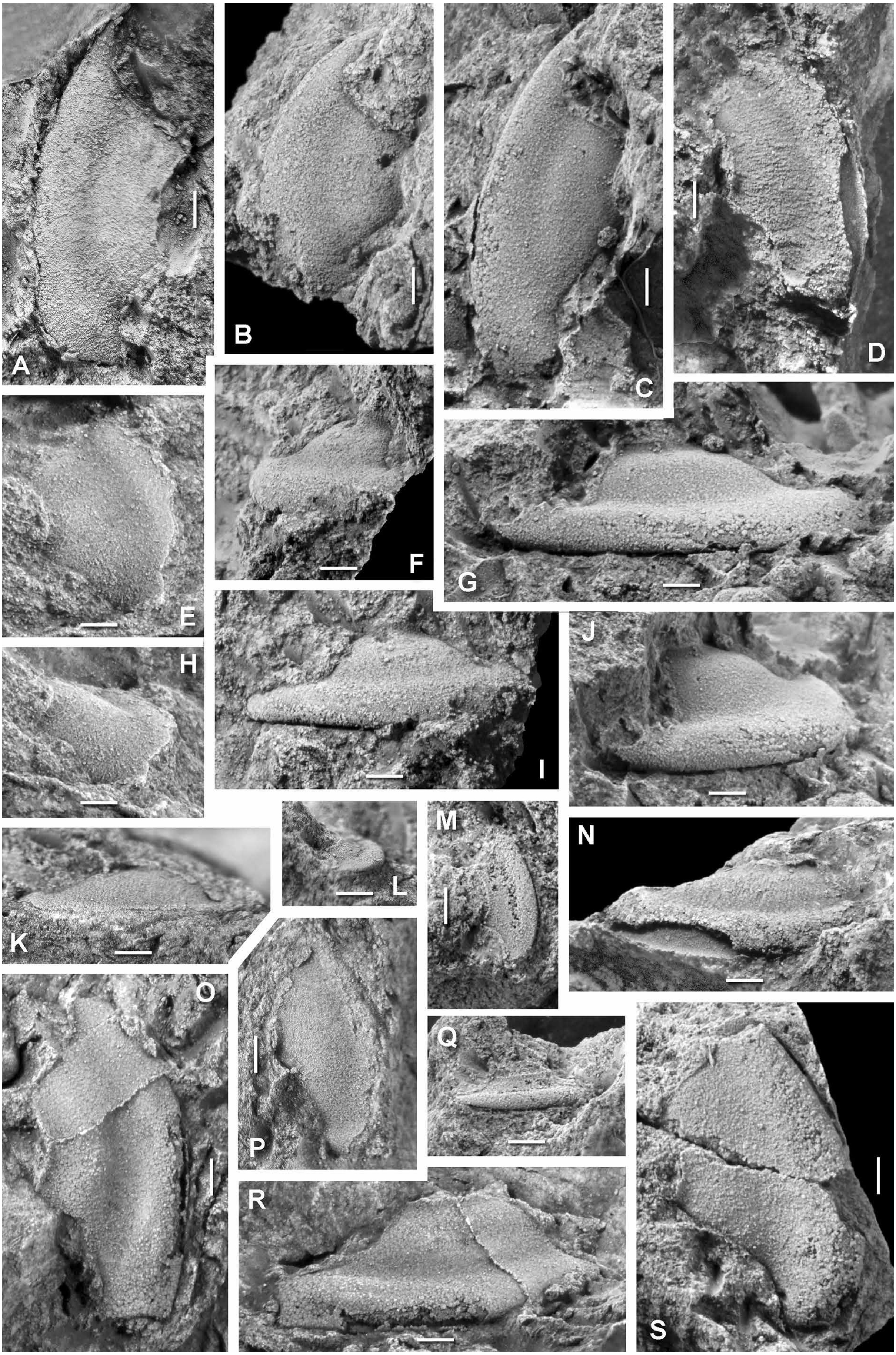
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Fig. 68: Librigenae of *Exapinepiphania* spp. **A** MMUW 2017D-238aL, left librigena, latex cast of internal mould; from locality W8; **B, F, I** MMUW 2017D-263, left librigena, internal mould, dorsal (B), oblique posterior (F) and lateral (I) views; from locality W8; **C, G, J** MMUW 2017D-164, left librigena, internal mould, dorsal (C), lateral (G) and oblique anterior (J) views; from locality W8; **D, N** MMUW 2017D-122, incomplete right librigena, internal mould with broken right margin exposing part of the ventral doublure, dorsal (D) and anterolateral (N) views; from locality W8; **E, H** MMUW 2017D-106, partial right librigena, internal mould, dorsal (E) and oblique posterior (H) views; from locality W8; **K, L, P** MMUW 2017D-121, right librigena, internal mould, lateral (K), posterior (L) and dorsal (P) views; from locality W8; **M, Q** MMUW 2017D-148, right librigena of immature individual, internal mould, dorsal (M) and lateral (Q) views; from locality W8; **O, R** MMUW 2017D-124, right librigena, internal mould, dorsal (O) and oblique lateral (R) views; from locality W8; **S** MMUW 2017D-189, right librigena, internal mould, dorsal view; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

The pygidia of *E. gregaria* figured by Fletcher (2005, pl. 3) apparently differ considerably In their morphology. However, the specimens all share at least three conspicuous characters that discriminate them from *E. wurmi* and *E. cristata*:

(1) The first/anterior axial ring shows vestiges of an overlapping of the anterior segment over the articulating half-ring of the second axial ring (now fused) as if the dorsal cover of the first ring was too small for an entire coverage.

(2) The posterior end of the pygidial axis sits close to the posterior rim of the pygidium and carries a pair of small bulbs, similar to the features in the pygidium from Krekling, Norway, figured by Westergård (1953, pl. 7, fig. 3) and assigned to '*P. linnarssoni*' or *P. spinigera*, and as seen in the type material of *Elrathina cordillerae* (see Geyer & Peel 2017). A shallow sagittal groove commences close to this pair of bulbs and is visible at least on internal moulds (Fletcher 2005, pl. 3, figs. 4, 9, 10).

(3) In well preserved specimens, the pleural fields in the pygidium have distinct pleural and interpleural furrows, of which the interpleural furrow between segment 1 and the pleural furrow of segment 2 converge to form a narrow lobe at about the axial furrow (Fletcher 2005, pl. 3, figs. 3, 7, 9, 10).

The ontogeny of *Exapinepiphania wurmi* can be illustrated very well (Figs. 66, 69). It indicates that the morphologies of this species and of *E. gregaria* were quite different during ontogeny. This is best seen in the broadly rectangular outline of the glabella in immature cranidia (see specimens in Fletcher 2005, plate 1).

Exapinepiphania parabolica (Geyer, 2017) occurs together with *E. wurmi* in the Galgenberg Member of the Tannenknock Formation. Although it was expected that its range also extends into the Wildenstein Member, surprisingly no specimen has been observed with a clear *E. parabolica* morphology. The species closely resembles *E. wurmi* and is difficult to distinguish from that species. As noted by Geyer (2017), the most striking difference between the two species is that *P. parabolica* is characterised by a glabella that tapers more distinctly forward because of its less curved lateral margins. The glabella is less blunt and generally slightly narrower.

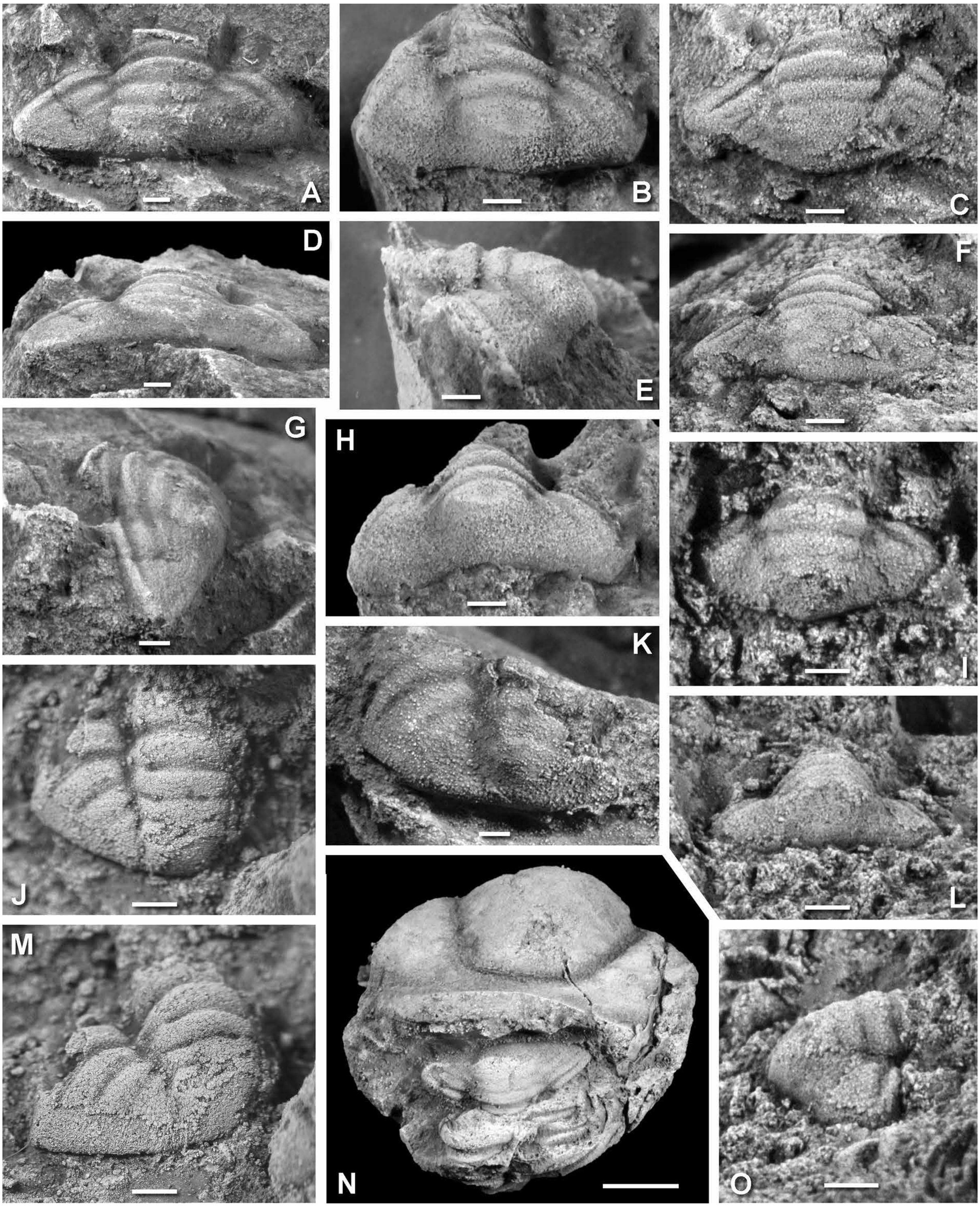

Fig. 69: Pygidia of *Exapinepiphania* spp. **A, D, G** MMUW 2017D-466, pygidium, internal mould, dorsal (A), posterior (D) and lateral (G) views; from locality W8; **B, E, H** MMUW 2017D-873, pygidium, internal mould, dorsal (B), lateral (E) and posterior (H) views; from locality W8a; **C, F** MMUW 2017D-107, pygidium, internal mould, dorsal (C) and oblique posterior (F) views; from locality W8; **I, L, O** MMUW 2017D-531, pygidium, internal mould, dorsal (I), posterior (L) and lateral (O) views; from locality W7; **J, M** MMUW 2017D-296a, partial pygidium, internal mould, dorsal (J) and oblique posterolateral (M) views; from locality W8; **K** MMUW 2017D-383, partial pygidium, internal mould, dorsal view; from locality W8; **N** MMUW 2017D-380, *Exapinepiphania wurmi* (Geyer, 2017), enrolled exoskeleton with slightly detached pygidium, internal mould; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 1 mm except in N (5 mm).

The eye ridges in *E. parabolica* are more obliquely rearward directed so that they meet the axial furrows at a more anterior position than those in *E. wurmi*. Accordingly, the palpebral areas are slightly longer close to the glabella than those of *E. wurmi* and are more subtrapezoidal in outline. In addition, the occipital ring in *E. parabolica* has a subterminally located node, whereas that in the cephala of *E. wurmi* is slightly more anteriorly located on the occipital ring.

Exapinepiphania lemdadensis (Geyer, 1998) is easily distinguished from *E. wurmi* by its extremely narrow or mostly absent preglabellar field and a narrow, blade-like and upturned anterior border.

Exapinepiphania? *lusatica* (Sdzuy, 1970) (see discussion above) is only known from material which is distinctly smaller than the normal adult specimens of *E. wurmi* except for one specimen with a similar aspect (Sdzuy 1970, pl. III, fig. 9). That species from the Delitzsch–Torgau–Doberlug Syncline is distinguished by a narrower (sag. and tr.) occipital ring and smaller palpebral lobes; immature cranidia have a broader subrectangular to slightly tapering glabella with a subtruncate front, and the librigena (provided its correct assignment) indicates the presence of a small genal spine rather than having a distinctly curved genal angle as in *E. wurmi*.

***Exapinepiphania*? sp. A**

Fig. 70

Studied material: 15 cranidia. From locality W8 (13 cranidia under MMUW 2017D-1101, -1102, -1103, SSMM 11033a, 11037a, 11037b, 11038a, 11040, 11041, 11042, 11044, 11046, 11103a and 11196a); from locality W18 (single cranidium under MMUW 2017D-547b).

Material tentatively assigned to Exapinepiphania*? sp. A:* Single cranidium from locality W8 under SSMM 11131a.

Discussion. A number of cranidia from the Wildenstein Member represent specimens, which superficially resemble *Exapinepiphania wurmi* and equal that species in most aspects. However, distinct and undebatable differences can be seen in the morphology of the anterior part of the cranidium.

These species all share an anterior border which is more obliquely upturned and broader (sag. and exsag.) with respect to the cephalic length. This border is always broader than the preglabellar field on the sagittal line, mostly even more than double that sagittal width (typically developed in Fig. 70D, H). The sagittal and exsagittal profile also shows a distinctly less pronounced convexity of the anterior border when compared with specimens of similar size of *Exapinepiphania wurmi*. In addition, the anterior border furrow has the tendency to be less curved (except in laterally compressed specimens). Also, the lateral margins of the cranidium are in general less bowed.

Specimens with a more-or-less well preserved exterior of the cuticle show that the cuticle was covered with fine, moderately spaced granules (Fig. 70C, P). Relatively large caeca originating from the eye ridges are seen in some specimens (Fig. 70D).

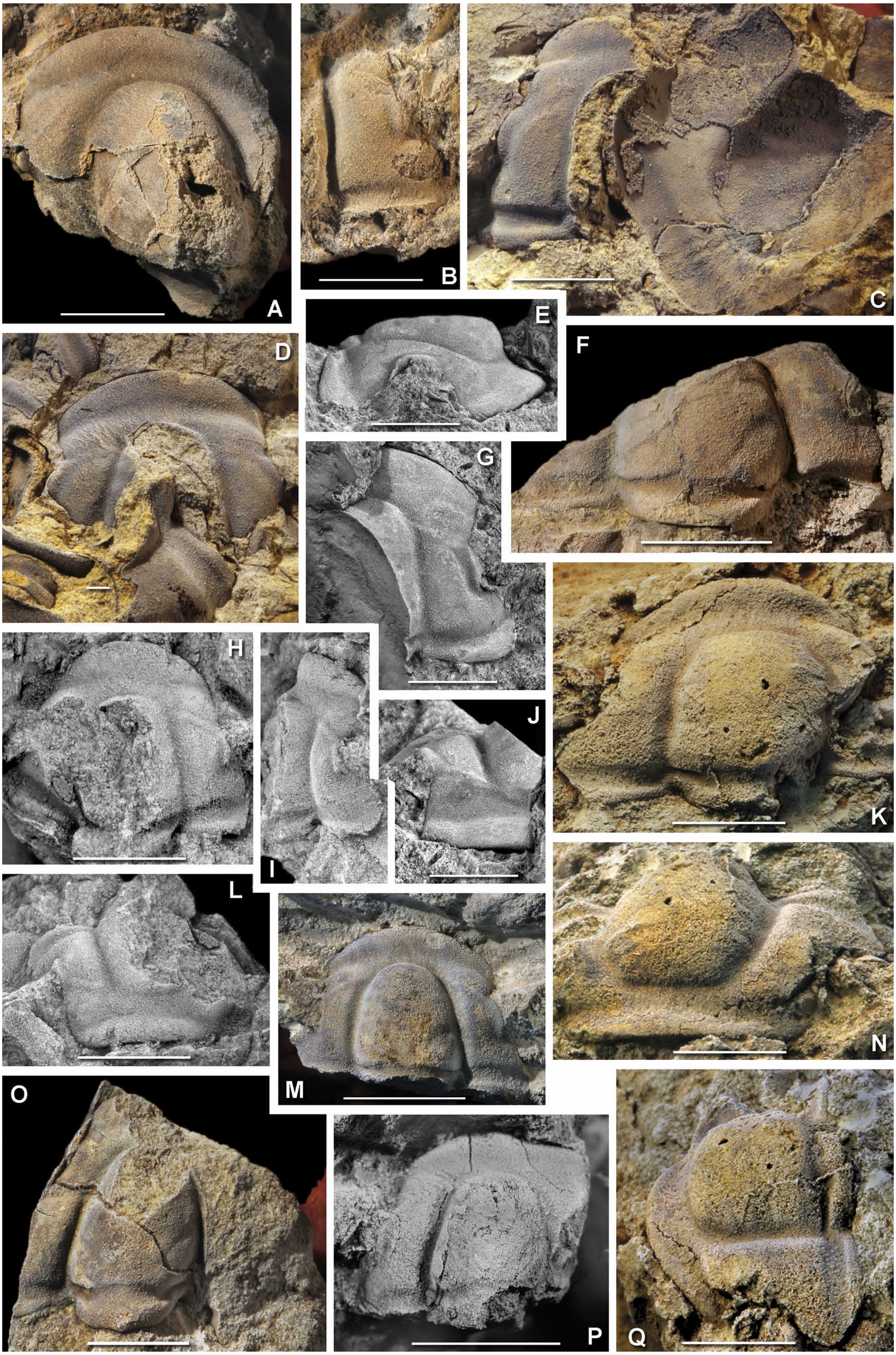
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Fig. 70: *Exapinepiphania*? sp. A. **A** SSMM 11041, partial cranidium, internal mould; from locality W8; **B** SSMM 11040, partial cranidium, internal mould; from locality W8; **C** SSMM 11037a, b, two partial cranidia, internal mould and cast of exterior; from locality W8; **D** SSMM 11038a, b, partial cranidium and cranidia fragment, internal moulds; from locality W8; **E, G, J** MMUW 2017D-1103, partial cranidium, internal mould, lateral (E), dorsal (G) and anterior (J) views; from locality W8; **F** SSMM 11046, partial cranidium, internal mould; from locality W8; **H, I, L** MMUW 2017D-1101, partial cranidium, internal mould, dorsal (H), lateral (I) and oblique anterior (L) views; from locality W8; **K, N, Q** SSMM 11103a, incomplete cranidium, internal mould, dorsal (K), oblique anterior (N) and oblique lateral (Q) views; from locality W8; **M** SSMM 11044, incomplete cranidium, internal mould; from locality W8; **O** SSMM 11042, partial cranidium, internal mould; from locality W8; **P** MMUW 2017D-1102, incomplete cranidium, internal mould; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm except in D (1 mm).

Exapinepiphania sp. B

Fig. 71A–L, M?

Studied material: 10 cranidia. From locality W8 (9 cranidia under SSMM 10463, 10473, 10488, 11130, 11036a, 11078, 11194, 11204 and 11204); from locality T2 (cranidium under SSMM 10274-II).

Material tentatively assigned to Exapinepiphania *sp. B:* From locality W8 (six cranidia under MMUW 2017D-1022, SSMM 10475, 10486, 10492, 10494a and SSMM 10494b); from locality W10? (cranidium under SMF 88201); from locality W13e (cranidium under MMUW 2017D-618).

Discussion. Several cranidia from the Wildenstein Member differ from *Exapinepiphania wurmi* in having a slightly narrower and more strongly upturned anterior border and a more sunken preglabellar field of approximately equal breadth as the anterior border on the sagittal line. These features are combined in all typical cranidia with a narrower front of the glabella devoid of the faint anterolateral "corners" that are seen in well-preserved specimens of *Exapinepiphania wurmi*.

The anterior border in *Exapinepiphania* sp. B merits a close investigation to highlight the differences to *E. wurmi*: In contrast to the latter species, the anterior border fades only moderately towards the facial suture so that is has anterior to the mid-level of the palpebral areas clearly more than half of its breath on the sagittal line. In transverse section, the posterior and anterior slope are steeper than in the anterior border of *E. wurmi* so that the dorsal face is relatively gently convex only. Well-preserved specimens indicate that the preglabellar field is depressed in front of the glabella in a way that its raises faintly towards the preocular areas, which is much less so in *E. wurmi*.

This specific morphology of the anterior border and the preglabellar appears to arise in relatively late stages of the ontogeny which makes precise identification of small and moderately sized specimens impossible. Fig. 71M illustrates a relatively small specimen with a clearly sunken preglabellar field which appears to indicate a moderate growth stage. However, this specimen shows a much wider (sag., exsag.) anterior border as seen in *E. wurmi*.

Fig. 71N, O shows a specimen that illustrates the observed maximum morphological plasticity of *Exapinepiphania wurmi* in direction to the *E.* sp. B morphology. This partial cranidium demonstrates the delicate anterolateral corners typical for the cranidium of *E. wurmi*, which lacks in *E.* sp. B, and it shows a less well defined posterior definition of the anterior border.

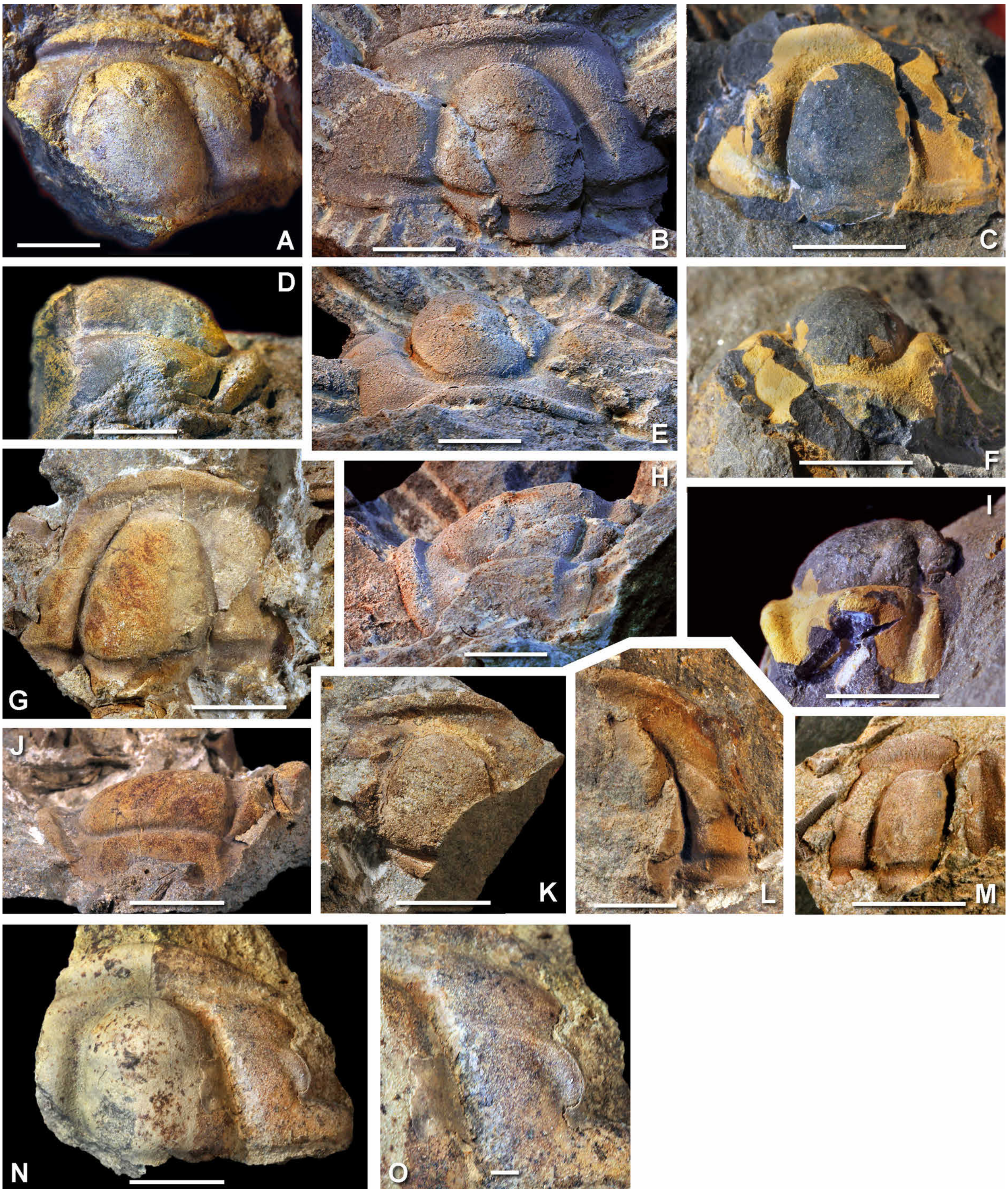

Fig. 71: **A–L, M?** *Exapinepiphania* sp. B. **A, D** SSMM 10463, cranidium, internal mould, dorsal (A) and lateral (D) views; from locality W8; **B, E, H** SSMM 11130, incomplete cranidium, internal mould, slightly fractured, dorsal (B), anterior (E) and lateral (H) views; from locality W8; **C, F, I** SSMM 10274-II, cranidium, internal mould with limonitised remains of the cuticle (yellow), dorsal (C), anterior (F) and lateral (I) views; from locality T2; **G, J** SSMM 11204, cranidium, internal mould, slightly fractured, dorsal (G) and lateral (J) views; from locality W8; **K** SSMM 11078, partial cranidium, internal mould; from locality W8; **L** SSMM 11194, partial cranidium, internal mould; from locality W8; **M** MMUW 2017D-1022, small cranidium, internal mould; from locality W8.**N, O** *Exapinepiphania wurmi* (Geyer, 2017), SSMM 10491, partial cranidium, internal mould, dorsal view of entire specimen (N) and magnification of right fixigena and palpebral lobes illustrating a delicate external flange along the ocular suture and a bifid eye ridges with a very thin posterior thread; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm except in O (1 mm).

Exapinepiphania sp. C

Fig. 72A?, B?, C, D?, E?, F, G?, H, I?, J–Q

Fig. 72: **A?, B?, C, D?, E?, F, G?, H, I?, J–Q** *Exapinepiphania* sp. C. **A** SSMM 10464, cranidium, internal mould; from locality W8; **B** SSMM 10536a, cranidium with mineralised, weathered and partly removed cuticle; from locality W8. **C, F, H** SSMM 11051, small cranidium, internal mould, dorsal (C), lateral (F) and anterior (H) views; from locality W8; **D, I** SSMM 10355, cranidium, composite mould, dorsal (D) and oblique anterior (I) views; from locality W9; **E, G, L** MMUW 2017D-395a, cranidium, internal mould, dorsal (L), oblique anterior (E) and oblique lateral (G) views; from locality W9; **J, M** SNSB-BSPG-1955-VII-13, cranidium, internal mould, dorsal (J) and oblique lateral views; probably from locality W12; **K, N, Q** MMUW 2017D-365, cranidium with largely preserved cuticle, dorsal (K) and anterior (N) views; from locality W8. All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 5 mm.

Studied material: Eight cranidia. From locality W8 (three cranidia under SSMM 11051, SSMM11464 and MMUW 2017D-365); from locality W9 (cranidium under MMUW 2017D-395a); from locality W10? (three cranidia under SMF 88204, 88205 and 88212); from locality W11 or W12 (single cranidium under SNSB-BSPG-1955-VII-13).

Material tentatively assigned to Exapinepiphania *sp. C:* From locality W8 (four cranidia under MMUW 2017D-660a, MMUW 2017D-660b, SSMM 10335 and SSMM 10464).

Description and discussion. The cranidia illustrated in Fig. 72 portray a species of *Exapinepiphania* n. nom., which also closely resembles *E. wurmi*. Nonetheless, these cranidia and several others collected from the Wildenstein Member show a few characters that are developed differently in *E. wurmi*.

Among the most conspicuous differences is the shape of the glabella: Typically preserved specimens of *Exapinepiphania* sp. C have a glabella which tapers less distinctly forward than the glabella in *E. wurmi*, and thus has a broader and less narrowly curved front that is never subacute (e.g., Fig. 72J, K, L). The occipital ring appears to be slightly narrower (sag.) than that in *E. wurmi*. Differences are also recognisable in the morphology of the anterior part of the cephalon of *Exapinepiphania* sp. C: The preglabellar field is narrow in dorsal view, but it has always a slightly convex profile in specimens which did not suffer oblique deformation (Fig. 72F, P, Q), whereas compaction from oblique anterior angles tilts the cranidium in a way that alters the dorsal aspect considerably so that a confident identification is impossible. Not only will the anterior border and the preglabellar field be flattened so that the anterior border as well as the preglabellar field are slightly turned dorsally, resulting in their breadth appearing greater than during lifetime. In addition, the dorsoventral compaction which accompanies this type of deformation widens the posterior part of the glabella in respect to the anterior part. Two examples of specimens which show this type of deformation and thus resemble much more *Exapinepiphania wurmi* or even *Exapinepiphania*? sp. A are illustrated in Fig. 72A, D, I.

Exapinepiphania marionae **n. sp.**

Figs. 73, 74A–E, F?, G?, H–J, K?, L

v	1995	*Parasolenopleura* sp. A – Geyer et al.: p. 110.
v ?	1995	*Parasolenopleura?* sp. – Geyer et al.: p. 111.
v	1995	“*Parasolenopleura*” sp. – Geyer et al.: p. 116.

Holotype. Dorsal exoskeleton, MMUW 2023A-001a (Fig. 73A).

LSID. urn:lsid:zoobank.org:act:95D1A147-1784-4BCD-B1E2-71CCCC9BEAE8

Type locality. Bou Tiouit section, Jbel Ougnate, eastern Anti-Atlas, Morocco.

Type stratum. Sample horizon TAR-75, upper briareus bed, *Morocconus notabilis* Zone, Jbel Wawrmast Formation. Most probably uppermost Cambrian Stage 4.

Etymology. Named in honour of Marion Kraßnitzer-Geyer (Würzburg), in appreciation of her help for the preparation of this study.

Paratypes. Cranidium under MMUW 2023A-018, from sample horizon TAR-75, Bou Tiouit section near Tarhoucht; dorsal exoskeletons (partly incomplete) under MMUW 2023A-001c, -001e, -001f, -001g, -001h, -001i, -001j, -001k, -001l, -001m, -001n, -002 and -019, three cranidia under MMUW 2023A-001o, -001p and -010, three librigenae under MMUW 2023A-001b, -001d and -001q, all from sample horizon TAR-75, Bou Tiouit section near Tarhoucht; two dorsal exoskeletons (MMUW 2023A-003a, -003b), cranidium with attached thoracic segments (MMUW 2023A-005), partial thorax with attached pygidium (MMUW 2023A-004) and librigena (MMUW 2023A-011) from TAR-77.8–78.2 of Bou Tiouit section; incomplete dorsal exoskeleton (MMUW 2023A-017) from sample horizon TAR-82.9 of Bou Tiouit section; eight incomplete or partial dorsal exoskeletons (nos. 1–8) and two librigenae (nos. 9–10) under DEV 24-02a through DEV 24-02j, incomplete dorsal exoskeleton under DEV 24-02b, all from temporal outcrop northwest of Tarhia (geographic coordinates N 31° 24’ 15”, W 5° 1’); dorsal exoskeleton under DEV 24-01b from Jbel Touist in the Jbel Ougnate region; cranidium (MMUW 2023A-009) from sample horizon TNI-01, Tizi n’Izem section (see Geyer 1990b for exact location). All specimens from Jbel Ougnate region, eastern Anti-Atlas, Morocco.

Specimens tentatively assigned to E. marionae: Cranidium under MMUW 2023A-006 from TAR-71; cranidium (MMUW 2023A-020) from TAR-77.8–78.2; cranidium (MMUW 2023A-016) from sample horizon TAR-109.7 of Bou Tiouit section; cranidium (MMUW 2023A-007a) and pygidium (MMUW 2023A-008) from TAR-141.0; Bou Tiouit section near Tarhoucht. For detailed data on stratigraphy and location of the samples see Geyer (1990a), Geyer et al. (1995) and Geyer & Vincent (2015).

Diagnosis. Species of *Exapinepiphania* characterised by a glabella with a relatively high length:width ratio; frontal lobe with considerable curvature of anterior margin, anterolateral corners barely developed; preglabellar field moderately long, clearly convex in sagittal section; anterior border with moderate convexity, not ascending towards anterior margin, moderately expanded in the central sector in comparison to the exsag. breadth at facial sutures; librigenae with short to moderately long genal spine.

Description. Cephalon trapezoidal in outline, with broadly curved anterolateral corners. Glabella tapers forward, with almost straight, slightly or slightly concave lateral margins, length ca. 75–82 percent (n=8) cephalic length on sagittal line; maximum glabellar width across L1 in adult specimens of 47–52 percent (n=6) cranidial width across centre of palpebral lobes; frontal lobe across anterolateral corners of 75–81 percent width across L1; anterior margin of frontal lobe generally with gentle to considerably curvature in dorsal view, anterolateral corners vaguely indicated by a pronounced arc; three pairs of lateral glabellar furrows; S1 moderately long, bifurcated, with strongly backward curved posterior branch and slightly shorter and less well impressed, roughly transverse anterior branch, moderately deep on internal moulds near axial furrows; S2 and S3 comparatively short to moderately long, S2 slightly directed backward from their origin near axial furrows, S3 almost normal to axis or slightly anteriorly directed from near axial furrow. Occipital furrow with quite narrow, well-incised lateral parts and slightly broader (sag.) and moderately shallow transverse middle part. Occipital ring sagittally of about 13–17 percent (n=6) cephalic length, extreme lateral parts narrow, its low abaxial extensions traverse axial furrows; moderately large occipital node in posteromedian position.

Fixigena posterior to eye ridge of about half sagittal cephalic length near axial furrow, width of palpebral area across palpebral lobes variably of 38–42 percent (n=4) maximum glabellar width (across L1), extends into broad (tr.) posterior limb of the fixigena; gently to moderately convex, most elevated point in subcentral position. Eye ridge developed as a low ridge, weakly demarcated on the exterior of the cuticle and aligned with an angle of ca. 25° to the transverse axis, well visible on internal moulds, meet axial furrows slightly anterior to position of S3. Palpebral lobe moderately long, but slightly variable depending on the size of the individual, exsagittally 24–28 percent (n=4) sag. cephalic length in adult specimens, anterior end opposite anterior part of L3, posterior end opposite S1, moderately upturned in respects to abaxial part of gena. Palpebral furrow a relatively broad, almost straight depression oblique to sagittal axis.

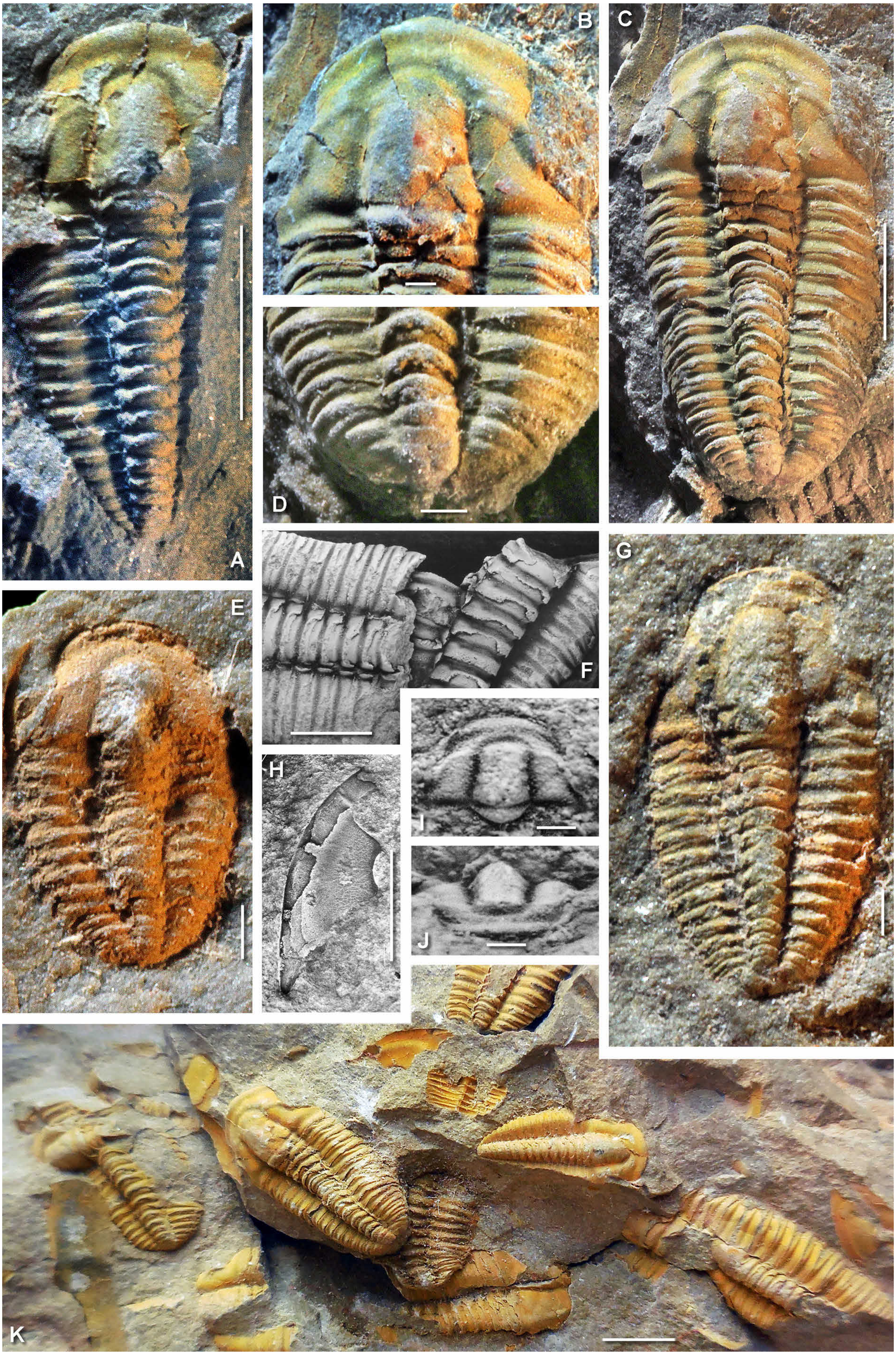
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Fig. 73: *Exapinepiphania marionae* n. sp. **A** DEV C5.4a-1, paratype, incomplete exoskeleton; from temporal outcrop due to road works north of Tarhia. **B–D** DEV C5.4a-2, paratype, dorsal exoskeleton, with magnified view of cranidium and attached anterior part of thorax (B), entire specimen (C), and posterior part of thorax and articulated pygidium (D); from temporal outcrop north of Tarhia. **E** DEV C14.1a, paratype, dorsal exoskeleton of immature individual; from unspecified locality in the norther Jbel Ougnate region. **F** MMUW 2023A-001c, f, paratypes, incomplete exoskeleton and partial thorax illustrating articulation of thoracic segments and extension of doublure. **G** DEV 24-01b, paratype, incomplete dorsal exoskeleton; from temporal outcrop north of Tarhia. **H** MMUW 2023A-011, paratype, librigena, from TAR-77.8–78.2, Bou Tiouit section near Tarhoucht. **I, J** MMUW 2023A-010, paratype, meraspid cranidium, from TAR-75, Bou Tiouit section near Tarhoucht. **K** DEV 24-02, slab with 8 incomplete or partial dorsal exoskeletons and librigena, all paratypes; from temporal outcrop north of Tarhia. All specimens from Jbel Wawrmast Formation, upper part of *Morocconus notabilis* Zone; Jbel Ougnate region, eastern Anti-Atlas, Morocco. Dorsal views. Scale bars 10 mm in K, 5 mm in A, C, F, H, 1 mm in B, D, E, G, I, J.

Preglabellar field moderately long, of ca. 10 percent cephalic length in dorsal view, forms a gently convex swelling in front of the glabella, which is well demarcated from the anterior border and from the glabella; slightly oblique to horizontal line in sagittal profile. Preocular area gently convex, developed as moderately steeply sloping trapezoidal fields.

Anterior border moderately convex, relatively low in lateral view, moderately broad (sag., exsag.) and of ca. 8–10 percent cephalic length on sagittal line; slightly broadened on sagittal line, clearly tapering to about two-thirds width next to suture. Anterior margin gently curved in dorsal view; in anterior view, the anterior border forms a moderately curved arch in its middle section. Anterior border furrow shallow to moderately deep, of subequal breadth throughout of its course. Posterior border with straight adaxial part, weakly sigmoidally curved distally, moderately narrow, relatively prominent. Posterior border furrow narrow adjacent to axial furrows, slightly broadens abaxially.

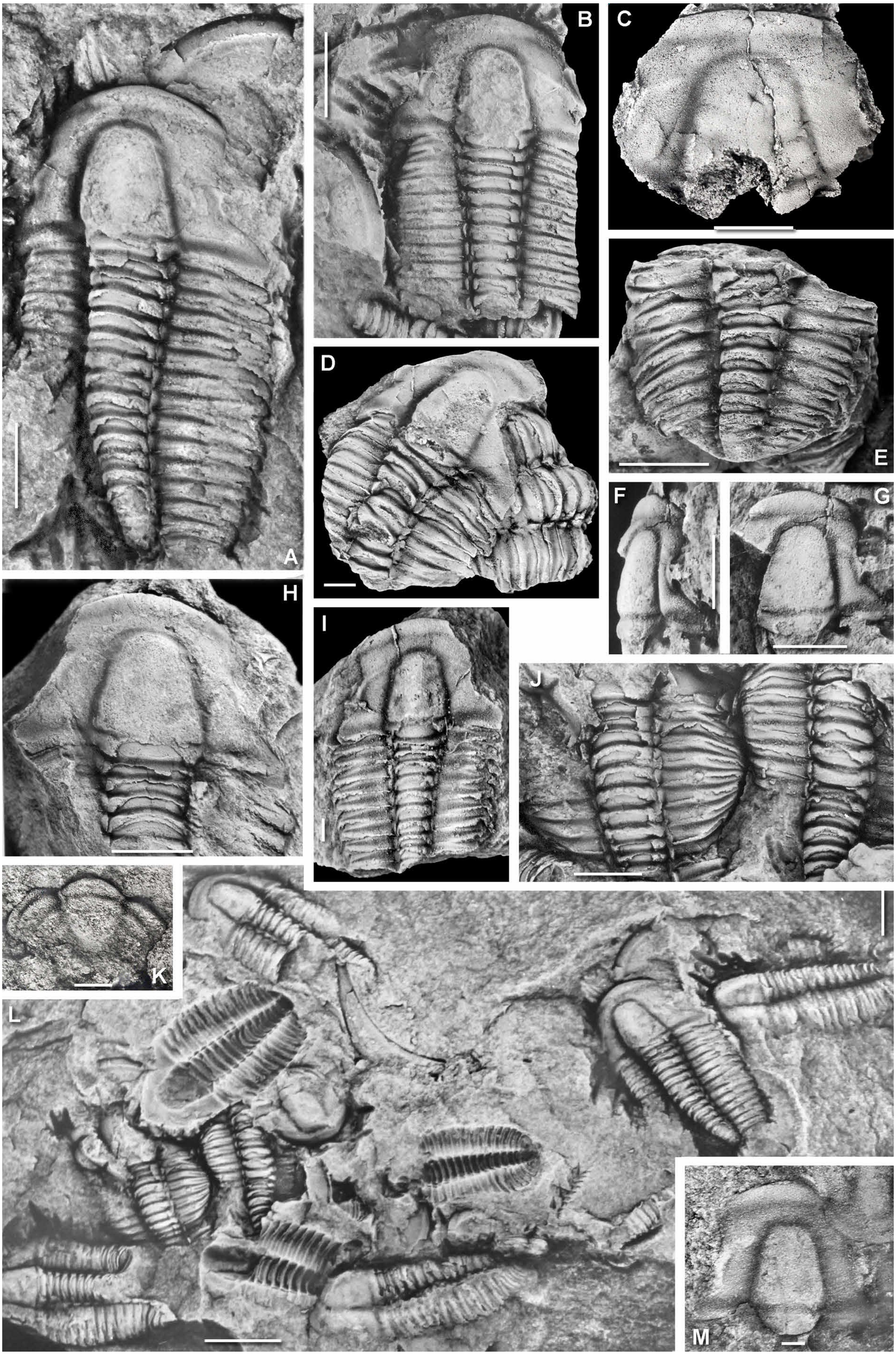
Anterior branches of facial suture straight and almost parallel from anterior ends of the palpebral lobes to mid-sector of the preocular fields, with inward curvature anteriorly. Posterior branches diverge markedly from posterior ends of ocular suture, straight for short distance from ocular suture, with moderate general curvature posteriorly, curve markedly backward and inward from centre of border furrow at posterolateral angles.

Librigena moderately large, with gently curved lateral margin and short to moderately large genal spine (Fig. 73H). Genal field fairly wide (tr.), gently convex, adjacent to ocular suture with narrow plane band. Lateral border moderately wide. Border furrow shallow.

The thorax consists of 14 or 15 segments in adult individuals. Thoracic axis narrows slightly and progressively backward starting from second or third axial ring. Axial rings moderately convex, separated from articulating half-ring by a distinct, fairly deep articulating furrow; with lateral, swollen bacculae that indicate attachment sites for a well-developed musculature for the ventral appendages. Middle section commonly narrower (sagittally), reflects an ability to perform a ventrally concave curvature during enrolment in segments 2 to 7 or 8. Axial rings of segments 4 to 9 with small to moderately large median axial node (or short spine?).

Pleurae of tergites 13 and 14 (and 15, if present) with more-or-less straight adaxial section, distal parts conspicuously deflected ventrally and slightly backward directed. Anterior margins of these pleurae straight, posterior margin of distal part slightly curved; facets large to allow ventral deflection of pygidium and posterior tergites.

First tergite with slightly larger facets. Pleural tips generally broadly curved in dorsal view, posterior half obliquely subtruncate. Pleural furrow well-defined, relatively deep, commences close to axial ring and swings faintly back to stay roughly in centreline of pleura, but with a slight swing toward the anterior in the distal portion of the pleura; fade relatively close to pleural tips.


A
B
C
D
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M

Fig. 74: **A–E, H–J, L** *Exapinepiphania marionae* n. sp. **A** MMUW 2023A-001a, holotype, dorsal exoskeleton, and -001b, paratype, librigena (b). **B** MMUW 2023A-001c, paratype, incomplete dorsal exoskeleton, and -001d, paratype, librigena. **C** MMUW 2023A-009, paratype, partial cranidium, flattened and cracked. **D** MMUW 2023A-003a, -003b, paratypes, two enrolled dorsal exoskeletons, oblique views. **E** MMUW 2023A-004, paratype, partial thorax with attached inclined pygidium. **H** MMUW 2023A-005, paratype, cranidium with articulated thoracic segments. **I** MMUW 2023A-002, paratype, cranidium with attached partial thorax. **J** MMUW 2023A-001e, f, paratypes, partial dorsal exoskeletons, enrolled (left) and in post-mortem deformation (right). **L** MMUW 2023A-001, slab with 12 dorsal exoskeletons, two cranidia and three librigenae (specimens paratypes and the holotype). **F, G, K, M** Specimens tentatively assigned to *Exapinepiphania marionae* n. sp. **F, G** MMUW 2023A-008, partial cranidium, oblique lateral (F) and dorsal views. **K** MMUW 2023A-006, pygidium, internal mould. **M** MMUW 2023A-007a, cranidium with a subtruncate frontal lobe, internal mould. Specimens in A, B, I, J, L from TAR-75, specimens in D, E, H from TAR-77.8–78.2, specimen in F, G from TAR-71, specimens in K, M from TAR-141.0, all from Bou Tiouit section, near Tarhoucht; specimen in C from TNI-01, Tizi n'Izem; all specimens from Jbel Ougnate region, Anti-Atlas. Dorsal views if not noted otherwise.
Scale bars 10 mm in L; 5 mm in A–H, J; 1 mm in I, K, M.

Pygidium of moderate size; with gently arched lateral and posterior margins, length/width ratio roughly 0.4. Axis moderately to distinctly convex, with two relatively well-defined axial rings, one additional less clearly marked ring and a terminal axial piece; articulating half-ring a moderately prominent, narrow ring, separated by a broad (sag.) and moderately deep articulating furrow; first axial ring well marked by a moderately deep transverse ring furrow, transversely of ca. 30 percent maximum pygidial width; second axial ring defined by a shallow furrow; terminal axial piece of ca. three-quarters width across anterior axial ring, with evenly curved posterior margin, which is separated from the posterior margin by one very short distance. Pleural fields with two or three pleural furrows, which are progressively less well-defined backwards; anterior interpleural furrows visible in well-preserved specimens. Posterior and lateral borders not defined, lateral and posterior rims consist of convex, rapidly sloping deflected marginal portions.

Discussion. Exapinepiphania marionae n. sp. is characterised by its relatively long and slender glabella with a distinctly curved anterior margin of the frontal lobe devoid of distinct anterolateral corners; by the moderately broad, convex preglabellar field of almost the same sagittal breadth as the anterior border; and by an anterior border with is only moderately convex in sagittal profile and neither distinctly swollen nor upturned. The librigenae has a genal spine developed. These features permit an easy distinction of the species from most other species assigned to the genus.

Exapinepiphania wurmi has a similar general morphology, but is easily distinguished by its lower, less convex and slightly narrower (sag.) preglabellar field and a broader, slightly bulging anterior border, as well as a wider and more strongly tapering glabella. The same differences can be seen in *E. gregaria* and *E. parabolica*. *Exapinepiphania lemdadensis* differs by its narrow (sag.) and sunken preglabellar field and the often collar-like and prominent anterior border. *Exapinepiphania cristata* differs in having a narrower (sag.) and weakly convex preglabellar field, a broader anterior border, and a narrow frontal lobe of the glabella.

Taphonomy. The specimens of *Exapinepiphania marionae* nicely illustrate how taphonomic effects may affect the apparent morphological variability of trilobites. Although the specimens from the quarried mass occurrences of *Acadoparadoxides briareus* (the so-called Briareus beds; Geyer 1993) show distinct plastic deformation resulting from early diagenetic effects, the morphology of the glabella and the frontal parts of the cranidia remained fairly close to its original relief. Isolated sclerites from other beds in approximately the same stratigraphic position, however, often show a much stronger deformation that leads to a less convex and apparently short preglabellar field (e.g., Fig. 74I), a more strongly tapering glabella (e.g., Fig. 74H), and other features. Dorsoventral compaction may also exaggerate the tapering of the glabella and often created fractures that follow more-or-less the maximum convexity directions (Fig. 74A).

It is noteworthy that the nearly complete dorsal exoskeletons are frequently enrolled. Stretched out specimens often show a certain degree of post-mortem deformation (e.g., Figs. 73C, E, 74A). Sometimes, enrolled specimens and specimens with a double s-shaped thorax are found next to each other (Fig. 74J).

Ecological data, stratigraphic and geographic range. Exapinepiphania marionae n. sp. is a common species in the upper part of the *Morocconus notabilis* Biozone of the Jbel Ougnate region in the eastern Anti-Atlas of Morocco. It is unknown outside that region. Interestingly, the species is not found in the lower and the middle part of the *Morocconus notabilis* Zone in the Tarhoucht area, where the sections where intricately studied (see Geyer & Vincent 2015). However, the species ranges up into the *Ornamentaspis frequens* Zone. It is remarkable that the species appears to have almost the same stratigraphic range as *Exapinepiphania wurmi* has in the Franconian Forest.

Mass occurrences of *Exapinepiphania marionae* are recorded in the strata with complete dorsal exoskeletons of *Acadoparadoxides briareus*, which are commercially quarried at Bou Tiouit (Geyer 1993; Geyer et al. 1995). These prolific occurrences of *E. marionae* consist of nearly complete dorsal exoskeletons that lack the librigenae which occur as isolated sclerites between the carcasses. The specimens generally show mild post-mortem deformational features and are not spread on a single sedimentary surface but with a certain angle to the bedding plane (Figs. 73K, 74L). Accordingly, the specimens appear to indicate preferred locations of synchronised ecdysis.

Exapinepiphania cristata **(Linnarsson, 1877)**

Figs. 75, 76

*	1877	*Selenopleura cristata* n. – Linnarsson: p. 370, pl. 15, figs. 5, 6.
v	1879	*Solenopleura cristata* Lnrs. – Linnarsson: p. 14, pl. I, figs. 12–15.
	1884a	*Ptychoparia cristata* – Walcott: p. 12.
	1884a	*Ptychoparia* (= *Solenopleura*) *cristata* Linnarsson – Walcott: p. 37.
	1884a	*Ptychoparia* (*Solenopleura*) *cristata*, Linnarsson – Walcott: p. 38.
non	1929	*Solenopleura cristata* Lnrs. – Strand: p. 353, pl. II, fig. 19.
non	1929	*Solenopleura* aff. *cristata* – Strand: pp. 320, 354, pl. 2, fig. 20.
v	1936	*Solenopleura cristata* Linnarsson, 1877 – Westergård: pp. 14, 18, 57, 59–60, 63 (table), pl. XII, figs. 1–7.
	1940	*Solenopleura cristata* Linrs. – Westergård: pp. 24, 61.
	1944	*Solenopleura cristata* Linrs. – Westergård: p. 21.
?	1952	Solenopleura cristata Linnarsson – Henningsmoen: p. 26.
v	1953	*Parasolenopleura cristata* (Linnarsson, 1877) – Westergård: pp. 22–23, 24, 38 (table), pl. 2, figs. 5, 6.
	1958	*Pseudosolenopleura cristata* (Linnarson) – Šnajdr: p. 199 [probably a type mistake].
	1974	*Parasolenopleura cristata* – Martinsson: p. 202.
?	1983	*Parasolenopleura cristata* (Linnarsson) – Lendzion: p. 679.
?	1983	*Parasolenopleura cristata* (Linnarsson) – Lendzion: text-fig. 5.
	1994	*Parasolenopleura cristata* (Linnarsson 1877) – Rudolph: pp. 24, 46, 212–213, tabs. 12, 15, pl. 26, fig. 8.
?	1994	*Parasolenopleura cristata* (Linnarsson 1877) – Rudolph: pl. 26, fig. 9 [only].
	1994	*Parasolenopleura cristata* (Linnarsson 1877) – Wolfart: p. 84.
non	1996	*Parasolenopleura cristata* (Linnarsson, 1877) n. ssp. – Sdzuy: p. 116.
	1998	*Parasolenopleura cristata* (Linnarsson, 1877) – Geyer: pp. 377, 391, 393.
pars	2005	*Parasolenopleura cristata* (Linnarsson, 1877) – Fletcher: pp. 1075, 1077, 1079, 1084.
non	2006	*Parasolenopleura cristata* – Fletcher: p. 74 [used as a synonym of *H. gregaria*].
	2017	*Parasolenopleura cristata* (Linnarsson, 1877) – Geyer: pp. 49, 50, 59, 60.

non 2017 *Parasolenopleura cristata* (Linnarsson, 1877) – Fletcher: p. 197 [used as a synonym of *H. gregaria*].

2023 *Parasolenopleura cristata* (Linnarsson, 1877) – Weidner et al.: pp. 106, 121 (table).

Diagnosis (emended). Species of *Exapinepiphania* characterised by a glabella with a relatively low length:width ratio; frontal lobe with low curvature of anterior margin, anterolateral corners form narrow arc; preglabellar field short, low; anterior border with low convexity, ascending towards anterior margin; librigenae with strongly curved genal corner.

Description and discussion. Although devoid of conspicuous autapomorphic characters, *Exapinepiphania cristata* is well recognisable and clearly distinguishable from other species of the genus by its stout glabella, a low preglabellar field which is defined posteriorly by the furrow that separates it from the front of the glabella and which is more indented that the quite shallow anterior border furrow in front of the preglabellar field (Fig. 75A, B), and by a slightly anteriorly ascending anterior border with only a fairly moderate convexity (Fig. 75F).

A particularly instructive specimen illustrates several features that merit attention (Fig. 75A): The glabella preserves the low and poorly impressed lateral glabellar furrow by the absence of the otherwise well-developed granulation. The anterior margin of the glabella appears to have a faint rise along the frontal lobe, which would point to the presence of a nearly completely fused parafrontal band. The moderately large median occipital node shows at least two perforations which suggests relics of a cephalic median organ (Fig. 76D).

The palpebral lobes are fairly simple and slightly obliquely upturned. Their anterior ends are in a position slightly anterior to the connection with the faintly bilobate eye ridges. The preocular areas are covered by granules but allow recognition of weakly developed centrifugal caeca.

The librigena of *Exapinepiphania cristata* lacks a genal spine, but has a narrow curvature of its genal corner (Fig. 75N–P).

The thorax consists of 13 segments in adult individuals of *Exapinepiphania cristata*. Thoracic segment 1 is modified in a way that the axial ring is shifted into a posterior position and the pleurae are shorter than those in the segments following posterior to it, and the external parts of the pleurae are ventrally deflected and somewhat obliquely twisted, thus allowing an inclination of segment 1 in respect to the cranidium. The axial rings of segments 3 through 13 have an axial spine which is dorsally directed from its base, but rapidly deflected towards the posterior. These axial spines are small in segment 3 and rapidly increase to a moderately large size, but are again reduced from segment 11 to the pygidium. Articulating devices are developed in all segments, such as fulcral joints and distinct pleural facets (Fig. 76C, I).

The pygidium is moderately large. The axis consists of three moderately distinct rings plus a low terminal axial piece, which carries a low crest subparallel to its margin. The anterior axial ring shows an incomplete state of fusion, with the former articulating half-ring of the adjacent second ring not entirely covered (Fig. 76B). Only two interpleural furrows are visible on the pleural fields. The lateral and posterior borders are fused and not defined. In addition, the cuticle of *E. cristata* is covered by dense, small granules except for the furrows and sometimes also adjacent areas (Fig. 75I, J). The particularly illustrative specimen in Fig. 76 (collected from Strandtorp on the island of Öland) shows gradients in the density of the granules on various parts of the dorsal exoskeleton, such as on the lateral parts of the glabella including the occipital ring, the axial rings, the thoracic pleural regions and the posterior parts of the pygidium (Fig. 76A, B, D, H, I). Terrace ridges are developed on the anterior border (Fig. 76G).

Fletcher (2005) regarded this Scandinavian species as a junior synonym of *Parasolenopleura gregaria* (Billings, 1865) from western Avalonia, as well as the Moroccan species *P. lemdadensis* Geyer, 1998.

Despite of a quite large morphological plasticity, *Exapinepiphania gregaria* is characterised in fully adult individuals by a relatively broad (sag.) and moderately upturned anterior border, by a sunken preglabellar field, which is developed as a narrow, band-shaped platform, and an anterior border furrow with a normal arcuation and without being shallower on the sagittal line. The palpebral lobes are obliquely upward directed and relatively thick (tr.). *Exapinepiphania lemdadensis* completely lacks a preglabellar field and has a conspicuously upturned, collar-like upturned anterior border distinctly different from *E. cristata* and *E. gregaria*.

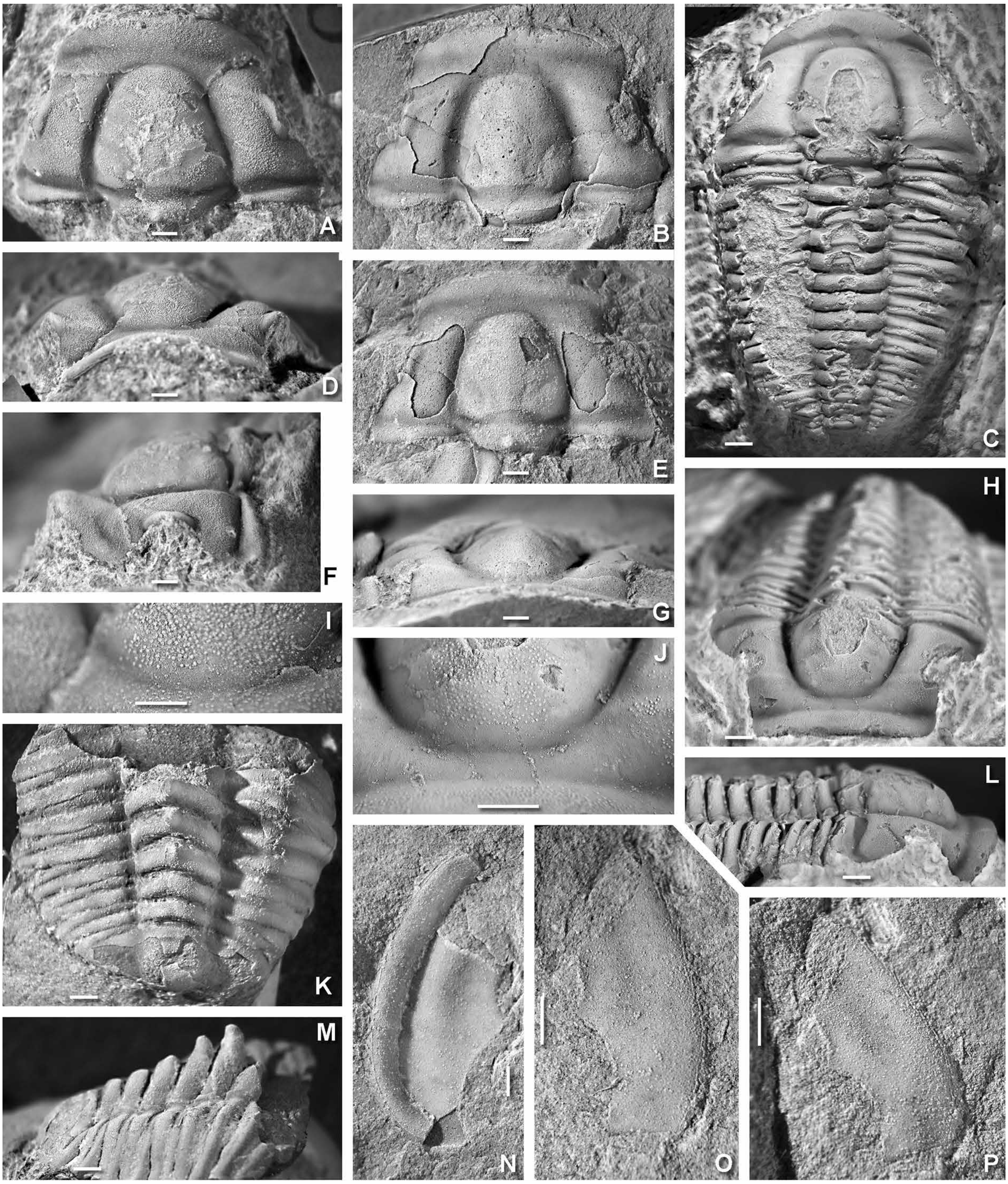

Fig. 75: *Exapinepiphania cristata* (Linnarsson, 1877). **A, D, F, I** SGU 6239, cranidium with preserved cuticle, dorsal (A), anterior (D) and lateral (F) views, magnified view of glabellar front and preglabellar field in (I) showing variation in fine granulation of the cuticular surface; from Oelandicus beds, Alum Shale Formation, Alböke, Öland; original of Westergård (1936, pl. XII, fig. 2). **B** SGU 6242a, cranidium, partly exfoliated, dorsal view; from Oelandicus beds, Alum Shale Formation, Mossberga drillcore, Öland; original of Westergård (1936, pl. XII, fig. 5a). **C, H, J, L** SGU 6240, exoskeleton without librigenae, dorsal (C), oblique anterior (H) and lateral (L) views, magnified view of glabellar front, preglabellar field and anterior border in (J); from Oelandicus beds, Alum Shale Formation, Borgholm, Öland; original of Westergård (1936, pl. XII, fig. 3), collected by G. von Schmalensee. **E, G** SGU 6242b, cranidium, largely exfoliated, dorsal and anterior views; from Oelandicus beds, Alum Shale Formation, Mossberga drillcore, Öland; original of Westergård (1936, pl. XII, fig. 5a, b). **K, M** SGU 6241, posterior part of thorax with articulated pygidium, dorsal (K) and lateral views showing decreasing size of axial spines on thoracic segments; from Oelandicus beds, Alum Shale Formation, Borgholm, Öland; original of Westergård (1936, pl. XII, fig. 4a, b), collected by G. von Schmalensee. **N** SGU 6241, librigena, ventral view indicating curved genal "corner"; from Oelandicus beds, Alum Shale Formation, Mossberga drillcore, Öland; original of Westergård (1936, pl. XII, fig. 7). **O, P** SGU 6243, librigena, internal mould, dorsal view; from Oelandicus beds, Alum Shale Formation, Mossberga drillcore, Öland; original of Westergård (1936, pl. XII, fig. 6). All scale bars 1 mm.

It remains doubtful whether the specimens collected in the Mjøsa area of southern Norway indeed belong to *E. cristata*. Strand (1929) described two forms determined as *Solenopleura cristata* and *S.* aff. *cristata*, respectively, which both differ in having a slender glabella, a granulose surface of the cuticle and a clearly raised preglabellar field. They resemble much more the cranidia of *Balticoglaucus linnarssoni* (Brøgger, 1878).

Exapinepiphania **sp. aff.** ***cristata*** **(Linnarsson, 1877)**

Fig. 77

Material. Four specimens, two in repository (MMUW 2023A-038a, b); both from Jbel Taouist, northern part of the Jbel Ougnate region, eastern Anti-Atlas, Morocco (donated by Georges Devoille). From Jbel Wawrmast Formation, upper part of the *Morocconus notabilis* Zone or from the *Ornamentaspis frequens* Zone, Stage 4–Wuliuan boundary beds.

Description and discussion. The typical beds of the Brèche à *Micmacca* Member of the Jbel Wawrmast Formation are quarried at a few localities in the Jbel Ougnate region of the Anti-Atlas between Alnif and Tinejdad for large trilobites, particularly species of *Acadoparadoxides* and *Cambropallas*, but also specimens of *Kingaspis*, *Cambrosaurura*, *Protolenus* and *Hamatolenus*. Commercial collecting of trilobites from this amply fossiliferous interval is conducted as well at other localities for some time, and such localities often remain unregistered, but the specimens occasionally turn up on the fossil market. A new, yet undescribed species of *Exapinepiphania* with a morphology similar to *E. cristata* (Linnarsson, 1877) is known from such collections, and its stratigraphic occurrence is proven by co-occurring trilobites. The apparently best specimen of the known remains is illustrated in Fig. 77, but introduction of a formal taxon needs to await material from a well recorded section.

The informally characterised species has a relatively short glabella which is fairly broad across L1 and tapers distinctly towards the narrowly curved anterolateral corners; the lateral margins are more-or-less straight, and the frontal lobe has a relatively weakly curved anterior margin. The preglabellar field is moderately long, but on the sagittal line slightly narrower than the anterior border; it has a gentle convexity towards the preocular areas, but is almost flat on the sagittal line (Fig. 77B). The anterior border is moderately broad and moderately convex and not markedly reduced in breadth and convexity towards the facial suture. The palpebral lobes are quite simple in their morphology and of more-or-less constant width, and they are obliquely upturned. The eye ridges run forward from the anterior ends of the palpebral lobes to meet the axial furrow just posterior to the anterolateral corners of the glabella.

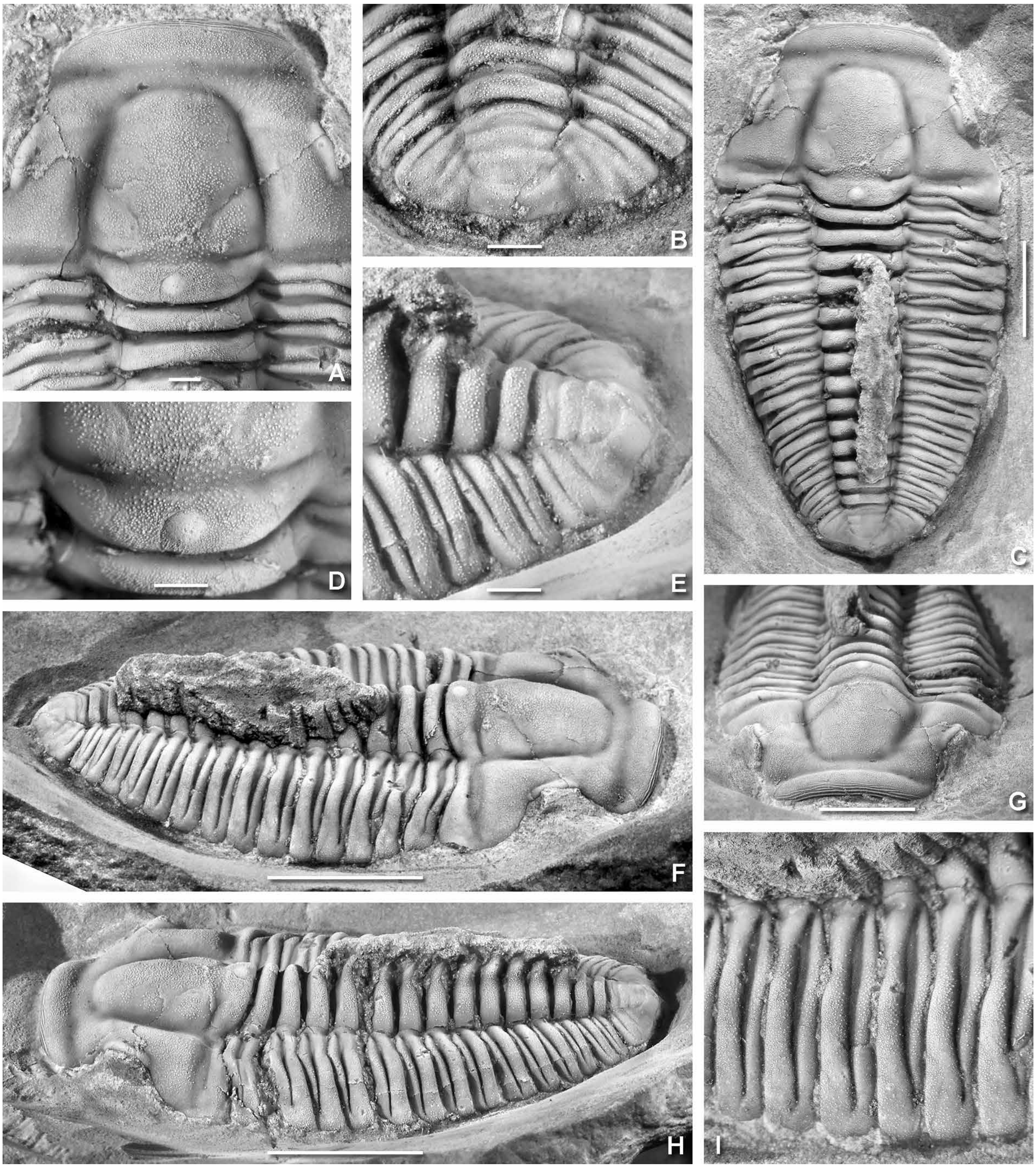

Fig. 76: *Exapinepiphania cristata* (Linnarsson, 1877). MMUW 2023A-021, dorsal exoskeleton without librigenae; A, magnified view of cranidium with anterior part of thorax; B, posterior part of thorax with attached pygidium in dorsal view; C, entire specimen in dorsal view; D, magnified view of posterior glabella and occipital ring illustrating the cephalic median organ on the occipital node; E, oblique lateral view of posterior thorax and slightly inclined pygidium; F, oblique right lateral view of entire exoskeleton; G, oblique anterior view of cranidium showing pattern of terrace ridges on anterior border; H, oblique left lateral view of entire exoskeleton illustration dorsal spines on axial rings; I, detail of thorax in oblique lateral view shows articulating devices and slight lateral swellings on axial rings that indicate muscle attachment sites on the ventral side. Specimen from Oelandicus beds, Alum Shale Formation, Strandtorp, south of Borgholm, Öland. Scale bars 1 mm in A, B, D, E, G, I, 5 mm in C, F, H.

The thorax consists of 14 segments. The pygidium is relatively small, with gently arched lateral and posterior margins. Its axis has two relatively well-defined axial rings, one additional poorly marked ring which tends to be fused with the short terminal axial piece. The pleural fields have two or three well-defined pleural furrows. The posterior and lateral borders are not defined.

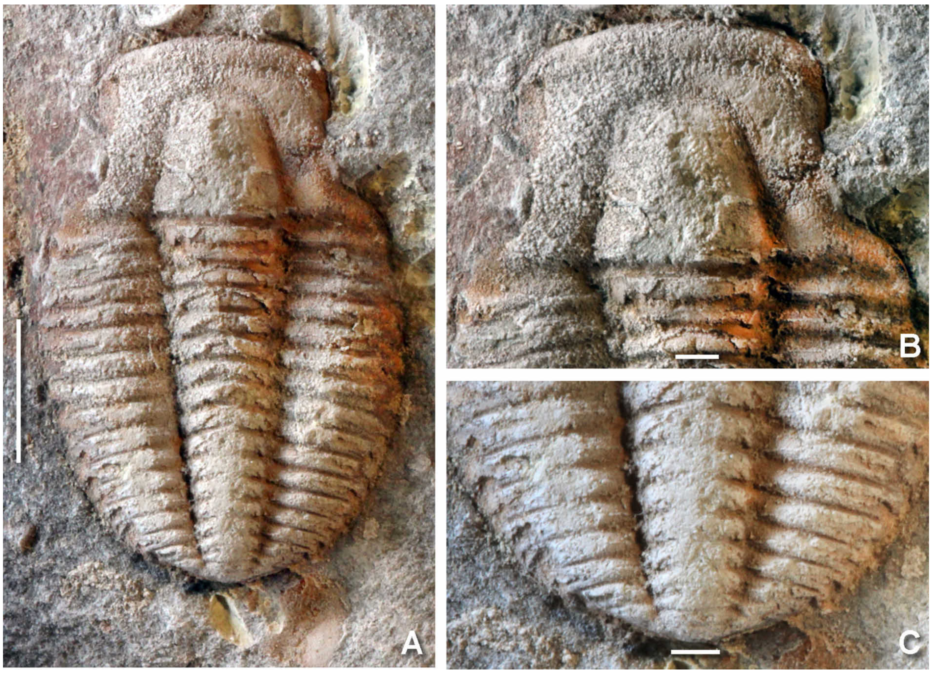

Fig. 77: *Exapinepiphania* sp. aff. *cristata* (Linnarsson, 1877). MMUW 2023A-038a, incomplete dorsal exoskeleton, specimen with weathered mineralised cuticle; **A** view of entire specimen; **B** magnified view of cranidium with attached anterior part of thorax; **C** magnified view of posterior thorax and attached pygidium. Jbel Wawrmast Formation, most probably from upper part of *Morocconus notabilis* Zone. From unspecified locality of the Jbel Ougnate region, eastern Anti-Atlas, Morocco.

This form resembles *Exapinepiphania cristata* in several aspects, particularly the shape and size of the glabella, and the preglabellar field. However, it is clearly distinguished by a slightly broader preglabellar field and anterior border on the sagittal line; a lower curvature of the frontal lobe; palpebral lobes in a more posterior position; and a generally longer and slightly larger pygidium.

Exapinepiphania pauperata (Walcott, 1906a)

* 1906b *Solenopleura pauperata*, new species – Walcott: pp. 565, 593–594.

1913 *Solenopleura pauperata* Walcott – Walcott: p. 291.

1913 *Solenopleura pauperata* – Walcott: pp. V, 169, 210, pl. 17, fig. 18.

1916 *Menocephalus pauperata* (Walcott, 1905) – Walcott: pp. 30, 65.

1937 *Solenoparia triangularis* new species – Resser & Endo: p. 289, pl. 47, figs. 18–22 [only].

non 1937 *Solenoparia triangularis* new species – Resser & Endo: pl. 34, figs. 1, 2 [only].

1942 *Solenopleura pauperata* Walcott – Resser: p. 52.

1943 *Solenopleura pauperata* Walcott – Howell: p. 243.

1953 *Solenopleura pauperata* Walc. – Ivshin: p. 98.

1965 *Trachoparia pauperata* (Walcott) – Chang in Lu et al.: pp. 210–211, pl. IV, figs. 1, 2.

1977 *Eilura*? cf. *triangularis* (Resser & Endo, 1937) – Schrank: pp. 148–149, pl. 4, figs. 1, 2.

1987 *Menocephalites pauperata* (Walcott, 1906) – Zhang & Jell: p. 105, pl. 43, figs. 1, 7–11.

2012 *Trachoparia pauperata* (Walcott, 1906) – Yuan et al.: pp. 224, 235, 238–239, 247, 256, 548, 637, 645, 652, pl. 236, figs. 3–6.

Discussion. Exapinepiphania pauperata was introduced by Walcott (1906b) as *Solenopleura pauperata*, transferred by Chang (in Lu et al. 1965) to *Trachoparia* and by Zhang & Jell (1987) to *Menocephalites*. Walcott's (1906b) type material was collected from the *Amphoton* Zone of the Changhia Formation in the Shanxi Province, northern China. Resser & Endo (1937) described material from the Changhia Formation of the Liaoning Province under the name *Solenoparia triangularis*, but part of their specimens collected from the Changhia Formation of the Liaoning Province most probably represent *Exapinepiphania pauperata* as well.

The cranidia of *Exapinepiphania pauperata* resemble those of typical species of the genus, such as *E. neubergii* (Hawle & Corda, 1847) and *E. wurmi* (Geyer, 2017). They have a distinctly convex (tr.) and forward tapering glabella with barely curved lateral margins anterior to L1 and a frontal margin with a relatively gentle curvature and S1 being better developed and recognisable on the exterior of the cuticle. The occipital ring is moderately long (sag.), but tapers abaxially to thin (exsag.) lateral threads and has a quite massive node in a subterminal position. The axial furrows are deeply indented. The palpebral areas are also distinctly convex in transverse profile, with the most elevated part slightly adaxial to the centre. The eye ridges are moderately well developed and form well-recognisable, relatively thick lobes directed slightly backward from their origins near the axial furrows. They are well separated by a depression from the palpebral lobes, which a moderately long (exsag.) and defined by a weakly curved palpebral furrow, but show a moderate curvature at the suture (e.g., Zhang & Jell 1987, pl. 43, fig. 9).

The anterior border and preglabellar field allow to distinguish *Exapinepiphania pauperata* from the other species of the genus: The preglabellar field is extremely thin (sag.) or missing so that the furrow which curves around the front of the glabella would coalesce with the anterior border furrow. However, the “pre-frontal furrow” is deeper and separates the anterior border furrow into two lateral sections, which are nearly interrupted by thin, slightly forward directed threads originating from the adaxial tips of the preocular areas (e.g., Zhang & Jell 1987, pl. 43, fig. 8). The anterior border is moderately thick (sag., exsag.) moderately prominent. A further character that distinguishes *E. pauperata* from the Baltican, West Gondwanan and Avalonian species of the genus is the distinct granulation on the cuticle with some quite coarse granules on the glabella and the genae.

The pygidium of *Exapinepiphania pauperata* is probably only known from a single, well-preserved specimen figured in Zhang & Jell (1987, pl. 43, fig. 11). It has a morphology which closely resembles that known from other species of the genus, but is relatively short and thus sublenticular in outline with sharp anterolateral corners. The axis consists of three decreasingly well-defined rings; a moderately broad articulating half-ring; a terminal axial piece with a nearly even curvature of its posterior margin, but a faint median indentation, and it has a well-recognisable posterior boss. The pleural fields a defined by three broad pleural furrows which are generally shallow and even decrease in their depth rearwards. The lateral margin is relatively narrow, low and poorly defined from the pleural fields.

Exapinepiphania? *acidalia* (Walcott, 1906a)

*	1906a	*Solenopleura acidalia*, new species – Walcott: pp. 6, 89.
	1913	*Menocephalus acidalia* (Walcott, 1905) – Walcott: pp. V, 10, 19, 174–175, pl.16, fig. 8, 8a.
	1914	*Menocephalus acidalia* (Walcott, 1905) – Walcott: p. 72.
	1916	*Menocephalus acidalia* (Walcott, 1905) – Walcott: pp. 16, 24.
	1935	*Menocephalites acidalia* (Walcott) – Kobayashi: p. 268.
	1942	*Taitzuia acidalia* (Walcott) – Resser: p. 53.
	1965	*Taitzuia acidalia* (Walcott) – Chang in Lu et al.: p. 221, pl. 38, figs. 11, 12, 13?.
	1987	*Menocephalites acidalia* (Walcott, 1905) – Zhang & Jell: p. 104, pl. 42. figs. 6, 7, pl. 43, fig. 12.
	2012	*Menocephalites acidalia* (Walcott, 1905) – Yuan et al.: pp. 194, 196, 235, 236, 247, 614, 637, 645.

Discussion. A species similar to *Exapinepiphania pauperata* (Walcott, 1906) was described as *Solenopleura acidalia* Walcott, 1906a. That species was collected from the *Taitzuia-Poshania* Zone of the Changhia Formation in the Shandong Province, northern China. The species was transferred to *Menocephalus* by Walcott (1913), to *Menocephalites* by Kobayashi (1935) and to *Taitzuia* by Resser (1942). Zhang & Jell (1987) reassigned it to *Menocephalites*, which documents the uncertainty in the assessment of its character.

In fact, that imperfectly known species shares all significant characters with *Exapinepiphania pauperata*. The only significant difference is the morphology of the anterior border, which is less broad and has a nearly straight to faintly concave course of the anterior margin in dorsal view (see refigured holotype in Zhang & Jell 1987, pl. 43, fig. 12), resulting from a considerable curvature of the anterior border in frontal view.

A disarticulated pygidium assigned to the species, however, seems to differ from the typical pygidial morphology known from the species of *Exapinepiphania* n. nom. It has a subelliptical outline and an axis consisting of ca. 6 axial rings (see Zhang & Jell 1987, pl. 42, fig. 7). It remains somewhat uncertain whether the pygidium indeed belongs to the species. Accordingly, the species should be tentatively assigned to *Exapinepiphania*.

Yuan et al. (2012) considered the librigena assigned to *Exapinepiphania*? *acidalia* as belonging to a species originally introduced as *Menocephalus agave* Walcott, 1906, which also was subsequently as signed to *Menocephalites* and *Taitzuia*. Yuan et al. (2012) placed that species under the genus *Trachoparia*, but kept *E.*? *acidalia* tentatively as a species of *Menocephalites*.

“*Exapinepiphania*“ sp. D

Fig. 78

Studied material. Single cranidium, MMUW 2017D-747a; with possibly two additional cranidia, MMUW 2017D-747b and -747c; from locality W8.

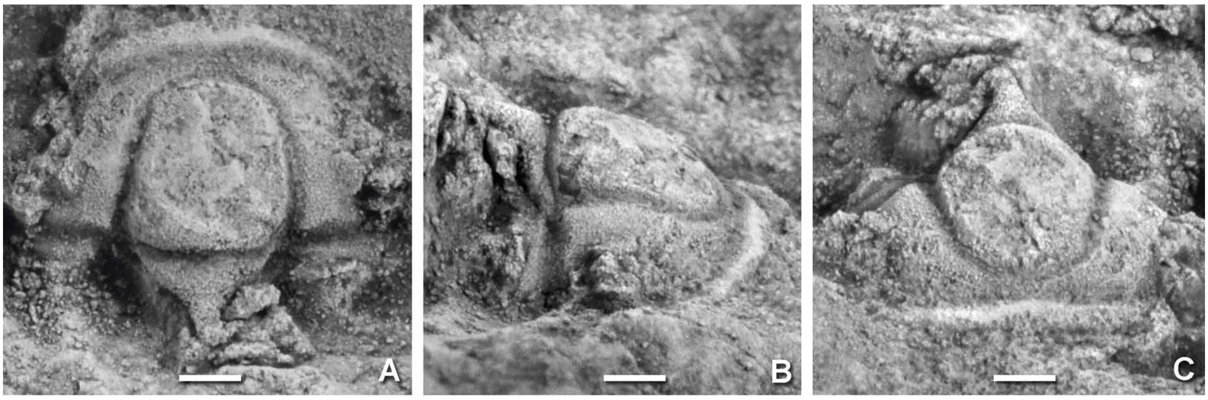

Fig. 78: “*Exapinepiphania*” sp. D. MMUW 2017D-747a, cranidium, internal mould, dorsal (A), oblique lateral (B) and oblique anterior (C) views; from locality W8; Wildenstein Member, Tannenknock Formation. Scale bars 5 mm.

Description and discussion. The cranidium shown in Fig. 78 exhibits a morphology that resembles that of typical species of *Exapinepiphania* n. nom., such as *E. wurmi* (Geyer, 2017) and *Exapinepiphania* sp. C which co-occur in the locality W8 of the Tannenknock hill. However, this cranidium differs considerably in having a long and relatively strong occipital spine, which is unquestionably not developed in any of the other species/forms of the Wildenstein Member and Tannenknock Formation in general and is also rarely found in other species assigned to the genus *Parasolenopleura* in the revised concept suggested by Geyer (1998) and applied herein. In addition, other, more minor differences seen in this cranidium when compared with *E. wurmi* are the slightly narrower anterior border with a less clear growth in width towards the sagittal line; the more strongly sloping palpebral areas; and the slightly less obliquely positioned palpebral lobes.

The imperfect preservation of the anterior portion of the glabella makes it difficult to recognise the exact morphology of the glabella. However, it appears as if the glabella in MMUW 2017D-747a has slight angulations at the anterolateral corners. This can be seen in a much more distinct preservation in two other cranidia which are preserved on the same slab as MMUW 2017D-747a. These two cranidia possibly represent the same form as they appear to have possessed a similar long occipital spine. However, both are preserved as external moulds with the exact length of the occipital spine being difficult to assess.

"*Exapinepiphania*" sp. E

Fig. 79

v 1944 *Solenopleura* cf. *vermontensis* Howell. – Schmidt: pp. 374–376, pl. 23, fig. 16a, b.

Studied material. Two cranidia, GSB X 4733c and GSB X 4754.

Locality and stratum. Both specimens from the Doberlug IV/1929 drill site, northwest of Kirchhain, Delitzsch–Torgau–Doberlug Syncline, Northern Saxony, Germany. Delitzsch Formation, *Badulesia tenera* Zone, Wuliuan–Drumian boundary interval, Miaolingian Series. From 187 m depth in the core (see Geyer & Malinky 2019: fig. 2).

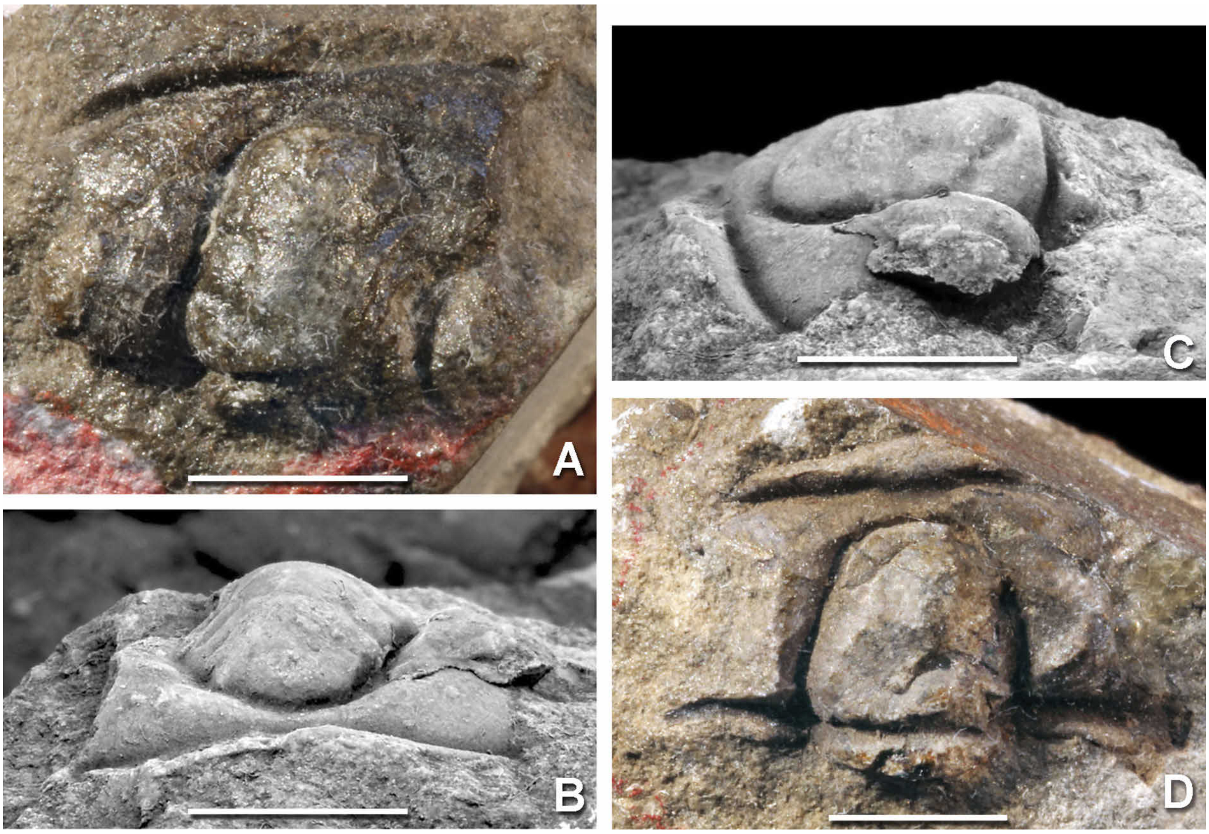

Fig. 79: "*Exapinepiphania*" sp. E. **A–C** GSB X 4754, partial cranidium, dorsal (A), anterior (B) and lateral (C) views. Doberlug IV/1929 drill core, depth 187 m; original specimen of Schmidt (1944, pl. 23, fig. 16a, b). **D** GSB X 4733c, cranidium, dorsal view. Doberlug IV/1929 drill core, depth 187 m. Scale bars 5 mm.

Description and discussion. Two cranidia from the core of the Doberlug IV/1929 drilling were identified by Schmidt (1944) as *Solenopleura* cf. *vermontensis*. These specimens are characterised by strongly convex, relatively broad, clearly tapering glabella with a low curvature of its anterior margin. Remarkably, the partial cranidium (Fig. 79A) exhibits an occipital ring that appears to have been distinctly narrower (tr.) than the maximum width of the glabella across the centre of L1. The palpebral areas are relatively narrow (tr.), approximately less than 40 percent of the transverse maximum width of the glabella across L1. The palpebral lobes are imperfectly preserved in one of the specimens, but their relics suggest a moderate length and a slight oblique direction in respect to the axis. They are at a relatively posterior position when compared with those of other solenopleurine trilobites, its anterior tips approximately at the level of S2 or slightly anterior to it. The eye ridges are poorly marked and have an oblique course towards the axial furrow.

The preglabellar field is moderately broad in dorsal view, moderately convex in sagittal profile and drops ventrally from the anterior tip of the glabella. Its breadth on the sagittal line is (in dorsal view) equals approximately the breadth of the anterior border. The anterior border furrow is well incised and has a gently curvature. The anterior border is quite narrow laterally and certainly broader in the sagittal sector, but the preservation in the specimen in Fig. 79D exaggerates its breadth due to a dorsoventral compression. The anterior border is distinctly elevated and decreases in breadth from the sagittal line towards the facial suture, which has a relatively long anterior branch with a straight course for most of its stretch anterior to the ocular suture.

The cranidia appear to represent another, yet undefined species of the *Exapinepiphania* clade. The shape of the glabella agrees well with most of the species of *Exapinepiphania*, as well as the convexity of the palpebral areas, the laterally extended anterior border and most other recognisable features. Differences with regard to these species can be seen in the longer palpebral lobes and the slightly narrower occipital ring. The anterior border appears to have a prominence that exceeds those seen in most species of *Exapinepiphania*, and the deceasing breadth (exsag.) towards the facial suture is also larger than known from true species of *Exapinepiphania*.

Genus *Jincella* Šnajdr, 1957

Type species. Solenopleura prantli Růžička, 1944a; from the Jince Formation, *Eccaparadoxides pusillus* to *Onymagnostus hybridus* biozones; Příbram-Jince Basin, Barrandean region, Czech Republic.

Diagnosis (emended). Genus of the Solenopleuridae with moderately convex (tr.) glabella which tapers forward to a relatively narrow, subevenly curved front, with nearly straight lateral margins; occipital ring with a (sub)median node, slightly tapering towards the abaxial tips; preglabellar field short (sag.), slightly sunken between the preocular areas, with low convexity in sagittal profile; anterior border moderately broad (sag.), moderately convex (sag., exsag.), gently and subevenly curved in dorsal view; border furrow with low curvature; palpebral lobes short, distinctly curved at facial suture, but with low curvature at palpebral furrow, obliquely inclined; palpebral areas moderately convex in transverse and exsagittal directions; eye ridges horizontal in frontal view; pygidium with subelliptical outline, axis consists of three rings plus a terminal axial piece, pleural areas divided by fairly distinct pleural furrows; pygidial lateral border poorly defined; prosopon composed of moderately large or large granules.

Discussion. Jincella Šnajdr, 1957 is a genus based on *Solenopleura prantli* Růžička, 1946a from the present-day Jince Formation in Bohemia. The genus and species have relatively “residual” features without apparent apomorphic characters. The genus closely resembles *Exapinepiphania* n. nom., and species of *Parasolenopleura* were variously re-assigned to *Jincella* and vice versa. Šnajdr (1957, 1958) chose *Solenopleura prantli* as the type species of the genus, but assigned *S.*? *conifrons* Pompeckj, 1896 from Bohemia, the Scandinavian species *Solenopleura holometopa* (Angelin, 1851), *S. bucculenta* Grönwall, 1902, *S. brachymetopa* (Angelin, 1851), *S. munsteri* (Strand, 1929), *S. parva* (Linnarsson, 1879) and tentatively also *S. ferganensis* Lermontova, 1951 from the Shody-Mir/Turkestan Range to the genus (generic assignments at that time), an opinion shared for *S. holometopa*, *S. munsteri* and *S. parva* by Rudolph (1994).

Jincella prantli has a tapering glabella with a relatively narrow front and almost straight lateral margins. Its preglabellar field is quite short (sag.), but well vaulted and only slightly sunken. The anterior border is convex, moderately broad (sag.) and defined by a normal, well incised anterior border furrow of equal width throughout of its course. Remarkably, the curvature of the border furrow is low in dorsal view and thus similar to that seen in *Solenopleura* and unlike in *Exapinepiphania*. Palpebral lobes and palpebral furrows are similar in convexity and dimensions to those seen in the species now assigned to *Exapinepiphania*. However, the axial furrows are relatively broad and gully-shaped in transverse section rather than relatively sharply incised as in the species of *Exapinepiphania*. In addition, *Jincella prantli* shows a prosopon of fine to moderately large granules, whereas the species of *Exapinepiphania* typically show a smooth external surface of the cuticle. These criteria allow to confidently distinguish *Jincella* from *Exapinepiphania*.

The genus suffered a complicated history in respect to which characters were regarded as significant and to which species should be assigned to *Jincella*. Various authors placed earlier introduced species to the genus and frequently challenged the differences between *Parasolenopleura* and *Jincella*. A comprehensive study was published by Álvaro et al. (2004), and the concept and composition of *Jincella* suggested therein is largely followed herein, except for different criteria considered to be diagnostic.

A species closely related to *Jincella prantli* is *Jincella convexa* Álvaro, Vizcaïno, Kordula, Fatka & Pillola, 2004 from the middle Languedocian of the Montagne Noire, France, and probably Sardinia, Italy. That species has a relatively broad, prominent, crescentic anterior border, a preglabellar field carrying two or three rows of tubercles, and fairly well impressed lateral glabellar furrows.

Jincella cannati had been first mentioned as *Solenopleura cannati* by Grönwall & Miquel in Miquel (1910), but firmly established by Thoral (1948). The species was transferred to *Jincella* by Courtessole (1973). The species (tentatively assigned to *Jincella* in the figure captions in Courtessole 1973 and in Courtessole et al. 1988) is only known from specimens that are so poorly preserved (best specimens illustrated by Pillet in Courtessole et al. 1988, pl. VIII, figs. 3–6) that diagnostic characters are impossible to recognise. A further uncertainty results from different stratigraphic positions of the material assigned to *J. cannati*, and the species needs to be regarded as doubtful. Álvaro et al. (2004) considered the species as a junior synonym of *J. prantli*, but their assignment is also uncertain.

Jincella? *brianensis* Courtessole, 1973 is another species recorded from the Montagne Noire, southern France. Again, the species is based only on strongly distorted incomplete cranidia, which are characterised by relatively coarse granules on the exterior and an apparently faintly subtruncate glabellar front. It seems as if the palpebral lobes are in a relatively posterior position and of larger size than known from true species of *Jincella*. The species has been transferred to *Derikaspis* by Dean (1982), but it remains doubtful whether the visible characters qualify this action.

The species of *Jincella* with probably the broadest regional occurrence of all species comes from the Avalonian palaeocontinent: *Conocoryphe applanata* Salter, 1865 (see also Salter & Hicks 1869) was first reported from Menevian Lingula Flags Formation (*P. aurora* Biozone) at Porth-y-rhaw near St. Davids, South Wales (Hicks in Salter & Hicks 1969), and also identified from the Maentwrog valley and at Tafarn Hellig, Nant-pig Mudstones and doubtfully in the Upper Caered Mudstones, Abersoch, Wales. Specimens from the Abbey Shales, *Paradoxides hicksi* Biozone, at Hartshill, England, were also assigned to the species (Rushton 1979). The species has also been identified from the Manuels River Formation of Avalonian Newfoundland, from where it was claimed to have an extended range from the *Tomagnostus fissus*, *Ptychagnostus atavus*, and *Mawddachites hicksii* into the *Paradoxides davidis* Zone (Martin & Dean 1988; Fletcher 2006, 2007; Unger et al. 2022). Its occurrence in Wales (Salter & Hicks 1869; Nicholas 1915; Young et al. 1994) and England was claimed to be restricted to the *Tomagnostus fissus* to *Solenopleura brachymetopa* zones and *Ptychagnostus atavus* Zone (Illing 1916; Rushton & Berg-Madsen 2002). Subsequently described material from Bornholm (Weidner & Nielsen 2013) extends the species' range confidently to the *Ptychagnostus atavus* Zone of Baltica.

Jincella applanata suffered an extended nomenclatural odyssey. It has been re-assigned to *Solenopleura* by Reed (1900), Illing (1916), Nicholas (1916) and Lake (1936). It was tentatively assigned to *Parasolenopleura* by Martin & Dean (1988) and then firmly to *Parasolenopleura* (Young et al. 1994), but transferred to *Jincella* by Álvaro et al. (2004) and Fletcher (2006). Fletcher (2007) lastly suggested to name it *Brunswickia* (*Jincella*) *applanata*, and Unger et al. (2022) assigned the species tentatively to *Jincella*.

Jincella applanata is fairly easily recognised by the course of its anterior border furrow, which is quite weakly curved in dorsal view, but usually has a slight extension or rearward swing on the sagittal line thereby forming a small indentation that reduced the width of the preglabellar field. The palpebral areas are somewhat domed, unlike the situation in *J. prantli*, but the fixigenae are defined by a relatively steep adaxial face at the axial furrows. Unger et al. (2022, fig. 6) illustrate specimens from the Manuels River Formation of south-eastern Newfoundland which properly show these morphological features. However, two of these cranidia (Unger et al. 2022, fig. 6D, E) have a less tapering glabella with a broader frontal lobe and an anterior border furrow without a median expansion and a broader preglabellar field and certainly belong to a different, but not yet established species.

Álvaro et al. (2004) also assigned *Parasolenopleura linnarssoni brevicauda* Westergård, 1953 from Sweden to *Jincella*; interestingly obviously as a subspecies although *Parasolenopleura linnarssoni* was not discussed. However, the taxon is discussed below and regarded as a species of the newly introduced genus *Balticomerope*.

Solenopleura picardi Schmidt, 1944 from Saxony, Germany, was also considered as a species of *Jincella* by Álvaro et al. (2004). However, that species differs considerably in several principal characters and is tentatively assigned to *Oreisator* (see below).

Jincella? *sulcata* Sdzuy, 1968 is a species originally described from the Cantabrian Mountains, and subsequently recorded from the Iberian Chains and the Ossa-Morena Zone, Spain. It is also known from the Triebenreuth Formation of the Franconian Forest, which overlies the Wildenstein Member of the Tannenknock Formation (Geyer & Elicki 2024). It was assigned to *Jincella* by Álvaro et al. (2004). The species has a number of characters that differ significantly from those known from *Jincella*, particularly the quite unique shape, morphology and position of the palpebral lobes and the anterior part of the cranidium, that it must be regarded as representing a yet undescribed genus. This will be dealt with in detail in a subsequent study on the fauna of the Triebenreuth Formation.

Solenopleura zverewi Lermontova, 1940 was originally described from the Mayan of the Maya River area of the Aldan region. It was also spelled "*S. zverevi*" in Lermontova (1940) and is subsequently mostly mentioned as "*S. zwerewi*" or "*S. zwerevi*". The species is probably known as well from the Mayan *Anomocarioides limbataeformis* Zone of the Yunkyulyabi-Yuryakh Formation in Khorbusuonka River region of the Olenek Uplift. It was also identified from the same zone in the overlying Tyussala (Tyuss-Sala) Formation in that region. In addition, the species was reported from the *Anomocarioides limbataeformis* Zone in the Dzhakhtar Formation of the Arga-Sala River area in the south-eastern Prianabar region and Olenek River region. Unfortunately, cranidia determined as *S. zverewi* (or any of the other spellings) differ in some characters and proportions so that a precise analysis is needed to define the morphological plasticity. Nevertheless, in respect to its characters, the species can be tentatively assigned to *Jincella*.

Fletcher (2007) grouped *Jincella* as a subgenus of the genus *Brunswickia* Howell, 1937. This is regarded as of little justification here as discussed below under that genus.

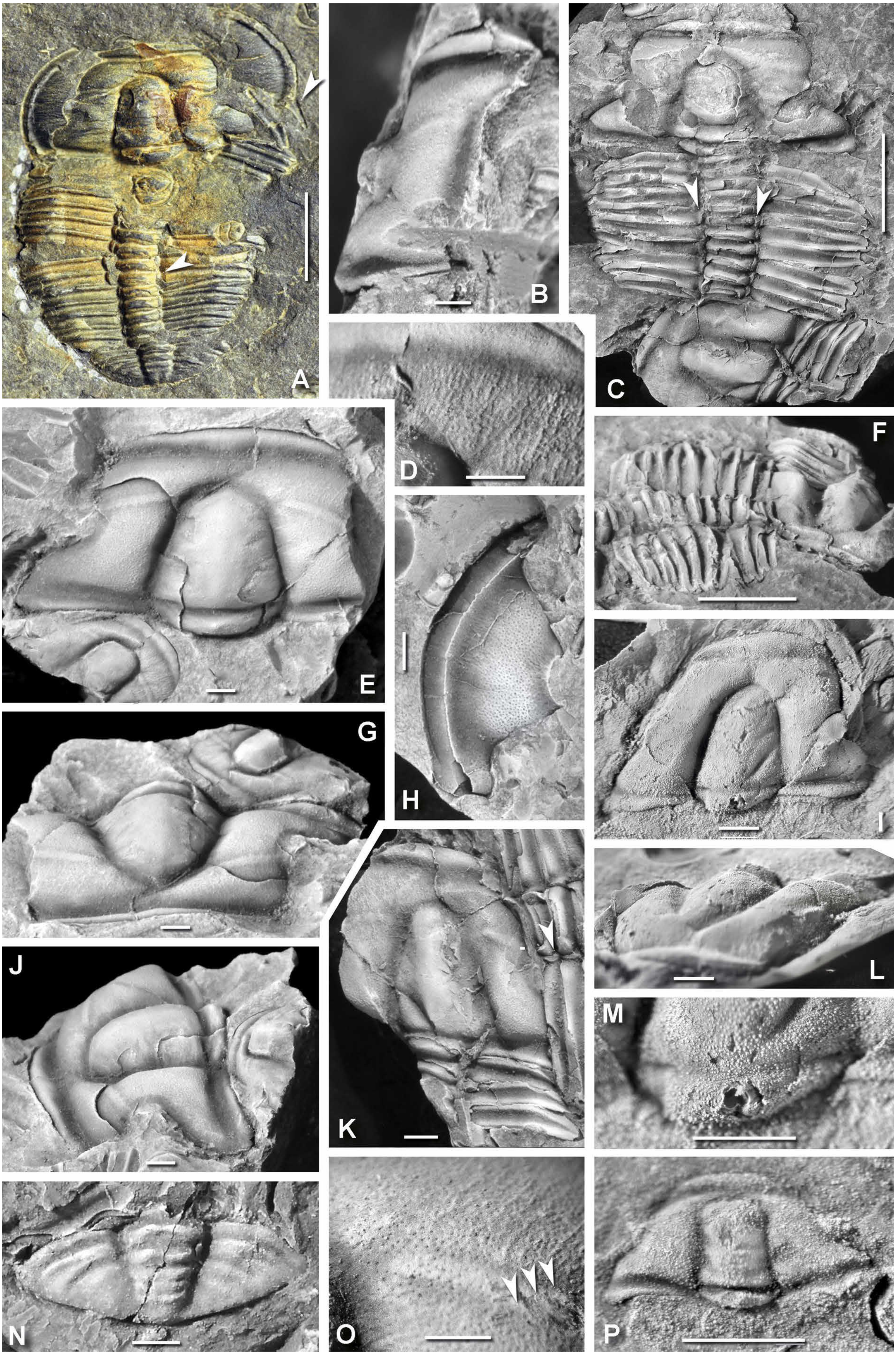
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Fig. 80: **A–O, P?** *Jincella*? *acadica* (Whiteaves in Matthew, 1885). **A** NBMG 6041, incomplete dorsal exoskeleton with dislocated thorax and librigenae; photo from New Brunswick Museum (reproduced with permission). **B** LO 12514t, fragment of cranidium with original relief, internal mould showing characteristic preservation of palpebral lobe. **C, F, K** LO 12515ta, b, partial dorsal exoskeletons, internal moulds with parts of the cuticle, dorsal and oblique lateral/anterior views; arrows indicate bulbous lateral parts of the axial rings indicating attachment sites of strong muscles (arrows). **D, E, G, J, O** LO 12516ta, b, large and moderate-sized cranidia, with largely preserved cuticle, dorsal (E), anterior/oblique anterolateral (G) and lateral/ oblique posterolateral (J) views, detail of smaller specimen in D shows multiple branching of caeca on anterior cephalic area vaguely proceeding onto the anterior border, magnified view of large specimen in O illustrates the punctate surface of the cuticle, the branching of the distal part of the eye ridge (arrows) and low caeca on the preocular area. **H** LO 12516t, librigena, internal mould with broken genal spine; note punctate surface on librigenal field. **I, L, M** LO 12518t, cranidium of moderate size, obliquely distorted, with largely replaced cuticle, dorsal (I) and oblique anterolateral (L) views, magnified view of posterior glabella and occipital ring in M shows eroded median occipital node and granulose surface ornament. **N** LO 12519t, pygidium, internal mould. **P** LO 12520t, meraspid cranidium with subparallel glabella having a vaguely bilobate frontal lobe, narrow preglabellar field, and granulose surface ornament.
Specimens collected by G.F. Matthew from Manuels River Formation at Porter's Brook, St. Martins, New Brunswick. Dorsal views if not noted otherwise. Scale bars 5 mm in A, C, F, 1 mm in B, D, E, G–P.

Jincella? *acadica* (Whiteaves *in* Matthew, 1885)

Fig. 80A–O, P?

*1885 *Selenopleura acadica* Whiteaves, ms. – Matthew: pp. 76–77, pl. VII, fig. 15.
1887a *Selenopleura Acadica,* Whiteaves – Matthew: p. 155.
1888 *Solenopleura Acadica,* Whiteaves – Matthew: pp. 157–158, pl. II, fig. 5a.
non 1888 *Solenopleura Acadica,* Whiteaves, Narrow Form – Matthew: pp. 158–159, pl. II, fig. 5b.
1891 *Solenopleura acadica* of Whiteaves – Walcott: pp. 83, 86.
1894 *Solenopleura Acadica*, Whiteav. – Matthew: p. 118.
1910 *Solenopleura acadica* Whiteaves – Grabau & Shimer: p. 277, fig. 1577.
1937 *Solenopleura acadica* Whiteaves – Howell: pp. 1179, 1180.
1953 *Solenopleura acadica* Whiteaves (M. S.) – Ivshin: p. 95, 100.
1972 *Jincella acadica* (Whiteaves in Matthew, 1885) – Fletcher: p. 264, pl. LXIII, fig. 3.
1998 *"Jincella" acadica* – Landing & Westrop: pp. 18, 66.
non 2007 *Brunswickia*? cf. *acadica* (Whiteaves in Matthew 1886) – Rushton et al.: pp. 132, 139, fig. 7h.
2007 *Brunswickia*? *acadica* – Rushton et al.: p. 141.
2007b *Brunswickia*. (*Jincella*) *acadica* (Whiteaves in Matthew, 1885) – Fletcher: pp. 157–159, fig. 7U.
2018 *Solenopleura acadica* – Bicknell & Paterson: p. 764, tab. 1.

Material. Two partial dorsal exoskeletons, LO 12515ta, LO 12515tb; four cranidia of holaspid individuals, LO 12514t, LO 12516ta, LO 12516tb, LO 12518t, meraspid cranidium under LO 12520t; librigena, LO 12516t; pygidium, LO 12518t.

Locality and stratum. Specimens from Manuels River Formation at Porter's Brook, St. Martins, New Brunswick.

Discussion. Jincella? *acadica* is only known from limited material with different quality of preservation, and it is demanding to determine the characters that distinguish the species from other similar ones, particularly *Jincella applanata*. Fletcher (1972, 2007) illustrated a topotypic specimen from Porter's Brook, New Brunswick, and emphasised its broad librigena and the less granulose surface ornament (when compared with *J. applanata*). These differences are also suggested by the specimens figured herein (Fig. 80).

In addition, the eye ridges and palpebral lobes in *Jincella*? *acadica* are located more posteriorly than those of *Jincella applanata*, which results in broader (exsag.) preocular furrows. Further characteristics include:

(1) the tendency to develop a subacute front of the glabella in large adult specimens (Fig. 80A, E);

(2) relatively narrow palpebral lobes which are moderately curved along the ocular suture and slightly upturned, separated by a distinct angle and a broad furrow from the eye ridges (Fig. 80B);

(3) the presence of faint caeca on the preocular areas (Fig. 80D, O);

(4) a moderately broad (sag.) anterior border, which is well convex, but slightly narrower than the preglabellar field (Fig. 80I, J);

(5) a librigena with a broad and distinctly elevated lateral border and a moderately long and strongly abaxially curving genal spine (Fig. 80A, H);

(6) thoracic segments with axial rings having clearly recognisable, bulbous lateral swellings that mark the attachments sites of the muscles that enable the movement of the ventral appendages (Fig. 80A, C, K);

(7) a clearly tapering pygidial axis composed of five rings plus an articulating half-ring and a terminal axial piece which reaches to the posterior margin of the pygidium (Fig. 80N); and

(8) pleural fields of the pygidium with at least three pleural ribs separated by pleural and quite weakly developed interpleural furrows and clearly decreasing in elevation rearward (Fig. 80N).

These characters are illustrated in Fig. 80 for specimens collected by G.F. Matthew and donated to K.A. Grönwall (now housed in the collections of Lund University, Sweden). They include the probably best preserved cranidium, a well-preserved librigena as well as a meraspid cranidium which almost certainly belong to the species. The well-preserved large cranidium of an adult individual exhibits an overall shape that reminds specimens of *Ptychoparia striata* and differs considerably from that of *Jincella prantli* so that the species is only tentatively assigned to *Jincella*. It also exhibits fine perforations on the internal mould, but also shows a double bifurcation at the abaxial part of the eye ridge (Fig. 80). An associated incomplete cranidium shows the pattern of multiply and irregularly branched caeca on the frontal area (Fig. 80D). The meraspid cranidium (Fig. 80P) has a nearly parallel-sided glabella with a faintly bilobate frontal lobe and fine, widely spaced granules on its surface.

Occurrence. The material of Matthew (1885, 1888) was collected by R.W. Ells from the "*Paradoxides*" *abenacus* Zone of the Manuels River Formation (previously termed "Porter Road Formation" for the locality by Hayes & Howell 1937; Div. 1d of Matthew) at "Porter's Stream" (now Porter's Brook), St. Martins, St. John Co., and is known only from this area in New Brunswick.

Jincella? *alata* (Matthew, 1888)

Fig. 81

* 1888 *Ptychoparia linnarssoni* Narrow Form (var. *alata*) – Matthew: pp. 147–149, pl. II, fig. 2a–f.

Material. Four cranidia of holaspid individuals, LO 12521t, LO 12522t, LO 12523t, LO 12524t, meraspid cranidia under LO 12525t, LO 12526t; protaspid under LO 12527t; two librigenae under LO 12528t and LO 12529t; two pygidia und LO 12530t and LO 12531t.

Locality and stratum. Specimens from Manuels River Formation at Porter's Brook, St. Martins, New Brunswick.

Discussion. Matthew (1888) briefly introduced this taxon as a "variety" of the Swedish species '*Ptychoparia linnarssoni*.' His figures do not provide a reliable picture of the morphology, and hitherto the taxon appears to have been completely ignored. The Royal Ontario Museum houses almost 50 specimens collected by Matthew and assigned to his "form". Matthew donated few more specimens to K.A. Grönwall, which are now in the Lund University collection and were examined during the course of this study.

The normal-sized of these specimens are cranidia of a simple ptychoparioid morphology without any readily recognisable peculiar characters. They may even be misidentified on the first glance as small specimens of *Jincella*? *acadica* (see above), which was collected from the same locality, and one of the original labels suggests that it has been identified by Matthew as "Solenopleura Acadica narrow form". Indeed, undistorted cranidia have a higher length:width ratio and a narrower glabella with almost straight lateral margins which terminates in a frontal defined by a subevenly curved anterior margin. However, at least some of the specimens identified as "Solenopleura Acadica narrow form" are most probably somewhat laterally compressed specimens of *Jincella*? *acadica* (such as the cranidium LO 12518t in Fig. 80I, L, M).

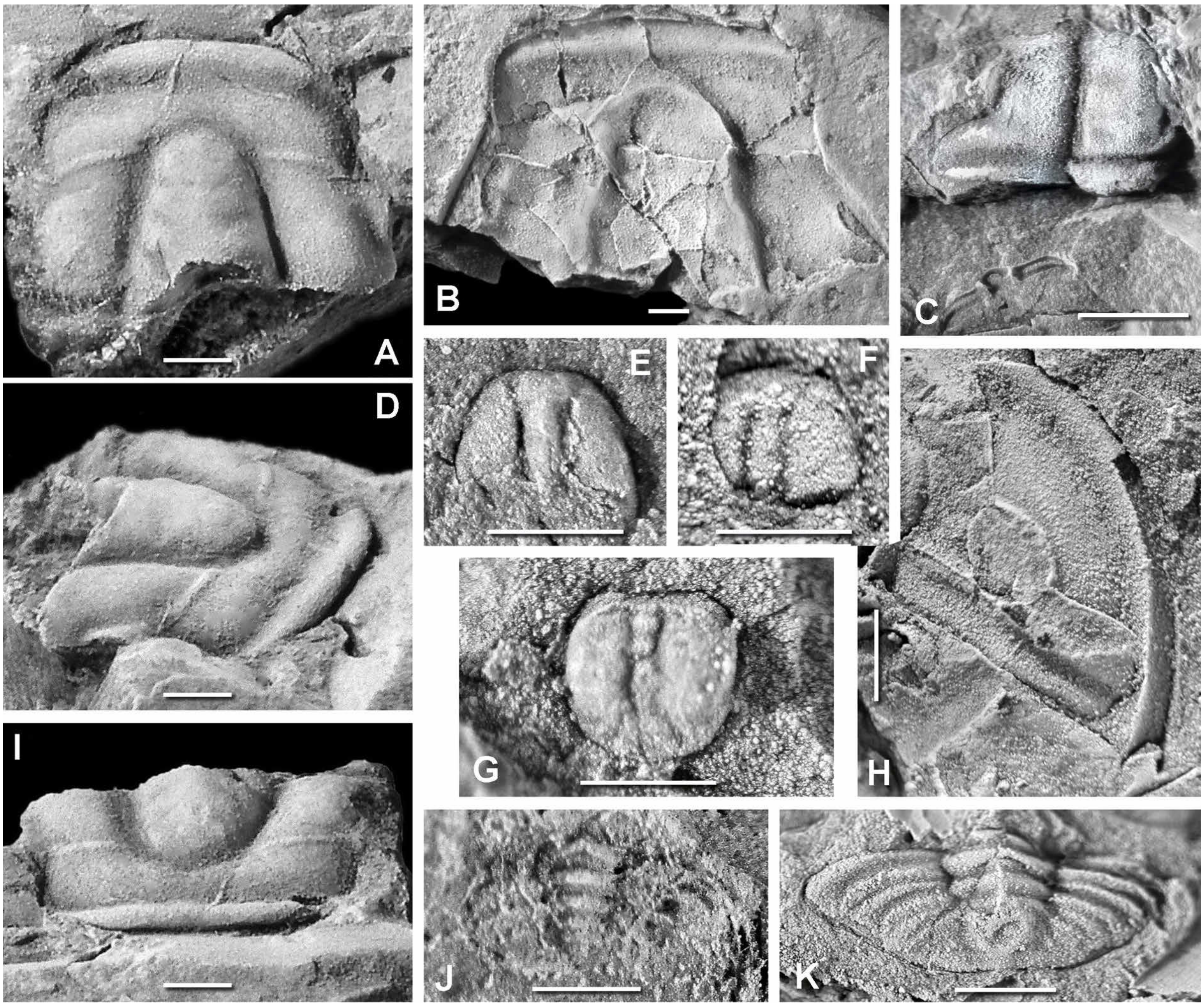

Fig. 81: *Jincella*? *alata* (Matthew, 1888). **A, D, I** LO 12521t, incomplete cranidium with original relief, composite mould, dorsal (A), oblique lateral (D) and oblique anterior (I) views. **B** LO 12522t, fractured partial cranidium, external moulds, ventral view. **C** LO 12524t, partial cranidium, composite mould, and thoracic segments of immature specimen, external mould, ventral view. **E** LO 12525t, meraspid cranidium, internal mould with relics of the cuticle. **F** LO 12526t, meraspid cranidium, internal mould. **G** LO 12527t, protaspid, internal mould. **H** LO 12528t, LO 12529t, librigena, internal mould with broken genal spine; note relics of caeca on librigenal field; associated incomplete thoracic pleura. **J** LO 12530t, incomplete pygidium of immature individual, internal mould. **K** LO 12531t, pygidium, partly exfoliated; note incomplete fusion of anterior axial ring and pleura. Dorsal views if not noted otherwise.
Specimens collected by G.F. Matthew from Manuels River Formation at Porter's Brook, St. Martins, New Brunswick. Scale bars 1 mm in A–D, H, I, K, 0.5 mm in E–G, J.

The presently available material is rendered as insufficient to estimate the morphological plasticity of the species. Fig. 81 illustrates an assemblage of specimens collected by G.F. Matthew from his “type locality” near St. Martins and identified as *Ptychoparia linnarssoni* var. *alata*. The specimens include a cranidium which certainly does not belong to *Jincella*? *acadica* (which occurs in the same strata at St. Martins), and the other specimens are dispersed on the same slab leaving little doubt that they belong to the same taxon. The SP-type cranidium (Fig. 81A, D, I) has a slender and strongly tapering glabella with almost straight lateral margins and an evenly curved frontal margin. The eye ridges are relatively prominent and only slightly rearward directed, with a stronger curvature near its abaxial end. The palpebral lobes appear to be longer than in *Jincella applanata*, *J.*? *acadica* and the other species assigned to *Jincella*, and they are strongly upturned. The preglabellar field is relatively broad (sag.), about as broad as the anterior border, and moderately convex. The anterior border is also moderately broad and moderately convex and has a straight anterior margin in anterior view (Fig. 81I). It is more-or-less of subequal breath in the sagittal and adaxial sector and decreases in exsag. width towards the facial suture starting at about mid-width of the fixigenae. However, a delicate swelling appears to exist on the sagittal axis which causes a slightly shallower central sector of the anterior border furrow. The cuticle surface is smooth. A second, larger partial cranidium is preserved as a fractured external mould, but exhibits the same characters except for a slightly narrower (sag., exsag.) anterior border and preglabellar field. A cranidial fragment exhibits the occipital ring which does not strongly taper towards the axial furrows, and the extended posterolateral extensions of the palpebral areas (Fig. 81C).

An associated librigena that fits to the cranidium has a strongly curved lateral margin as seen in *Jincella*? *acadica*, but the section of the ocular suture is larger, the lateral border slightly narrower and proceeds into an apparently short spine without a notably lateral curvature. The genal field appears to show relics of radial caeca (Fig. 81H).

Two pygidia are associated with the cranidia and librigena, the larger one of which has a generally similar morphology as *Jincella*? *acadica*. However, this pygidium differs unequivocally in its axis composed of four axial rings (plus a transversely narrow articulating half-ring and a terminal axial piece with a low curvature of its posterior margin), which does not reach to the posterior margin of the pygidium (Fig. 81K). The pleural fields are subdivided by distinctly developed pleural and (less deep) interpleural furrows slightly decreasing in depth rearward. The anterior axial ring and pleural unit appears to be incompletely fused with the remaining part of the pygidium.

At least four larval specimens are associated with the described sclerites, which probably represent specimens of *Jincella*? *alata* as well. Three are early meraspid cranidia with a slender cephalic axis and a clearly broadened anterior section that reaches to the anterior margin of the cephalon. The small one is ca. 0.5 mm wide and long, whereas the larger one is approximately 0.7 mm wide (Fig. 81E, F). The latter shows an anterior axial sector with a pair of indistinctly defined bulbous swellings, relatively long, anterolaterally located palpebral lobes, and appears to have short posterolateral genal spines. A protaspid (Fig. 81G) has a narrow axis proceeding into a considerably broadened posterior sector, with at least seven rings being recognisable, the anterior of which is connected with transversely directed, thin and relatively prominent eye ridges.

Occurrence. The material of Matthew (1888) was collected from the “*Paradoxides*” *abenacus* Zone of the Manuels River Formation (previously termed “Porter Road Formation” for the locality by Hayes & Howell 1937; Div. 1d of Matthew) at Porter’s Brook, St. Martins, St. John Co., and is known only from this area in New Brunswick.

Jincella? *orestes* (Matthew, 1888)

Fig. 82

1868 *Conocephalites Orestes*, Hartt, MS – Hartt in Dawson: pp. 649–650, fig. 225.
1868 *Conocephalites Halli*, Hartt, MS – Hartt in Dawson: pp. 650, 654, fig. 227.
1878 *Conocephalites Orestes*, Hartt, MS – Hartt in Dawson: pp. 649–650, fig. 225.
1878 *Conocephalites Halli*, Hartt, MS – Hartt in Dawson: pp. 650, 654, fig. 227.
1884 *Ptychoparia orestes* – Walcott: pp. 39–40, 41, pl. II, fig. 3, 3a.
1887 Conocephalites (Ptychoparia) orestes, *Hartt* – Whiteaves in Matthew: p. 149
* 1888 *Solenopleura Robbii* var. *Orestes* – Matthew: pp. 154–155, pl. II, fig. 4a–e.
1889 *Ptychoparia orestes* – Lesley: pp. 140, 141.
1889 *Solenopleura orestes* – Matthew in Lesley: p. xvi.
1891b *Ptychoparia orestes* – Walcott: pp. 80, 81.
1894 *Solenopleura Robbii* v. *Orestes*, Hartt, sp. – Matthew. p. 118.

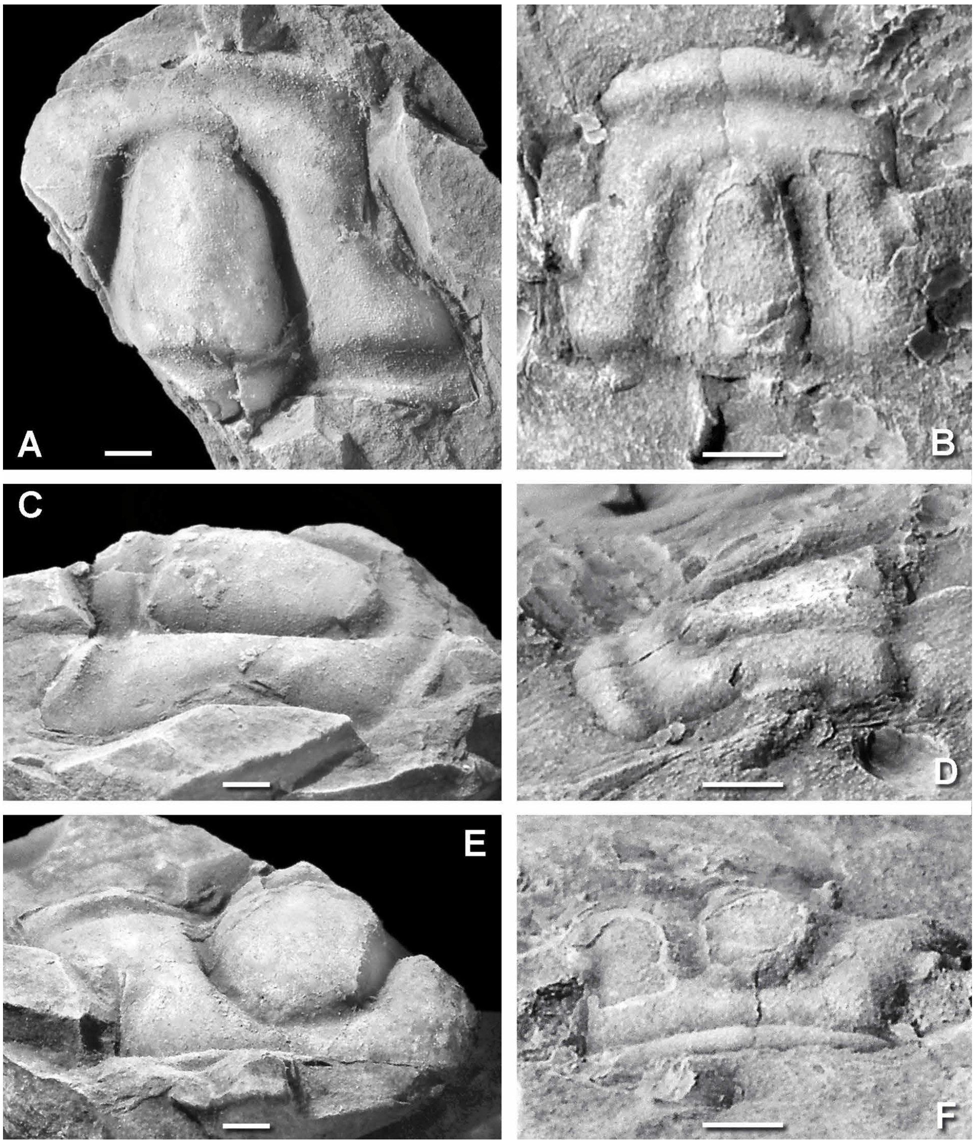

Fig. 82: *Jincella*? *orestes* (Matthew, 1888). **A, C, E** LO 12532t, partial cranidium, composite mould, dorsal (A), oblique lateral (C) and anterior (E) views. **B, D, F** LO 12533t, incomplete cranidium, composite mould, dorsal (B), oblique lateral (D) and anterior (F) views. Specimens collected from the Fossil Brook Member of the Chamberlain's Brook Formation by G. F. Matthew at Ratcliffe Brook/Ratcliff's Millstream, New Brunswick. Scale bars 1 mm.

Studied material. Two incomplete cranidia, LO 12532t and LO 12533t.

Locality and stratum. Specimens from the Fossil Brook Member of the Chamberlain's Brook Formation at Ratcliffe Brook/Ratcliff's Millstream, New Brunswick.

Discussion. Another fairly obscure *Jincella*-type trilobite from New Brunswick has been introduced as *Conocephalites Orestes* by Hartt (in Dawson, 1868). The little-known species exhibits a quite simple morphology very similar to that of *J.*? *acadica*. Fig. 82 illustrates two cranidia collected by Matthew and identified as *Solenopleura robbii* var. *orestes*. These cranidia show a tapering glabella with a relatively narrow frontal lobe having a subevenly curved anterior margin. The palpebral areas appear to be slightly narrower than those in *J.*? *acadica*. The preglabellar field is well developed and appears to be (on the sagittal line) at least as broad as the moderately broad, well elevated anterior border.

Walcott studied the type material of Hartt and claimed to have been unable to find any characters that distinguish *Conocephalites Orestes* from *C. Halli*, and although the illustrations in Dawson (1868) differ profoundly, both must be regarded as synonymous.

Occurrence. Fossil Brook Member of the Chamberlain's Brook Formation at Ratcliffe Brook/Ratcliff's Millstream (type locality) and Seely St., St. John, New Brunswick.

Genus *Braintreella* Wheeler, 1942

Type species. Ptychoparia rogersi Walcott, 1884; from the *Acadoparadoxides harlani* Assemblage Zone of the Braintree Formation at Quincy, Massachusetts, U.S.A.

Discussion. The type species of *Braintreella*, *Ptychoparia rogersi* Walcott, 1884a, is poorly preserved in its type locality. This fact led to the suggestion that the species should be restricted to the material from Massachusetts, USA (e.g., Geyer & Landing 2001; Fletcher et al. 2005). Nevertheless, the case of *B. rogersi* is challenging as outlined by Geyer & Landing (2001): Wheeler (1942) had collected material in 1940 and recognised that (among other minor inaccuracies) the eye ridges in Walcott's (1884a, p. VII, fig. 2) original figure of *Ptychoparia rogersi* are exaggerated which brought Howell & Mason (1938) to propose affinities with *Ehmania*. Wheeler (1942) introduced for the Braintree material the new genus *Braintreella*, which he placed into the subfamily Nassovinae (original spelling in Wheeler 1938). He also proposed similarities with *Vermontella* Howell, 1937 and *Champlainia* Howell, 1937 from the traditional Middle Cambrian of Vermont. However, neither of these genera appears to have a close phylogenetic relationship to *Braintreella*, and the subfamily Nassoviinae as introduced by Howell (1937) is not a natural group.

Wheeler (1942) indeed introduced another species assigned to his genus *Braintreella*, *B. currieri* Wheeler, 1942, which is regarded as a junior synonym of *B. rogersi*. Accordingly, *Braintreella* was restricted to the genotype species, *Ptychoparia rogersi* Walcott, 1884, by Geyer & Landing (2001).

Howell (1959) referred *Braintreella* to the subfamily Ptychopariinae, but this systematic position is incorrect as the taxon does not share any recognisable apomorphic-type characters with *Ptychoparia*. Instead, *Braintreella rogersi* provides characters that suggest a close affinity with morphologically simple Solenopleuridae. The following relevant characters can be recognised:

(1) The glabella tapers forward and is defined by almost straight lateral margins anterior to L1; with the frontal lobe showing a tendency to develop a low curvature of the frontal margin;

(2) the preglabellar field is narrow and slightly sunken in adult specimens in respect to the pre-ocular areas, with the anterior border of at least double breadth of the preglabellar field in the sagittal line;

(3) the palpebral lobes are short and located at a relatively anterior position;

(4) the palpebral areas are relatively narrow, but gently convex (tr., sag.) and defined adaxially by well incised, sharp axial furrows so that the transverse profile is of SP-type topography.

All of these characters are subtle and apparently insufficient to allow a confident definition of a genus. Confusion with other solenopleurid genera is possible, particularly if specimens are unfavourably preserved. As noted by Geyer & Landing (2001), distorted specimens of *Braintreella rogersi* may be difficult to distinguish from species which have been previously assigned to *Parasolenopleura* or *Jincella*, which were also characterised by narrow to obsolescent preglabellar fields, a glabella with a low curvature of the frontal lobe and transversely convex palpebral areas defined by well incised axial furrows.

Characters that distinguish *Braintreella rogersi* from such similar genera may be considered as subtle and inadequate in respect to consequent phylogenetic analysis (e.g., Hennig 1950). However, the present generic concepts among the solenopleurids mostly fail to fulfil the requirements of consequent genus-level taxa. Accordingly, an existing genus *Braintreella* is useful if it appropriately reflects systematic relationships and phylogenetic developments. *Braintreella* can be defined as being distinguished from similar genera by its distinctly tapering glabella with its nearly straight margins in the anterior two-thirds, a narrow, sunken preglabellar field, narrow palpebral areas which contribute to the PL-type transverse morphology of the cephalon, as well as a strongly curved lateral cephalic margin, which gives the librigenae a shape similar to an arc of a circle, devoid of a genal spine.

The superficially most similar genus is *Jincella*, which has broader axial furrows, broader fixigenae, strongly upturned palpebral lobes, an anterior margin with a distinct curvature in anterior view, and a prosopon of coarse granules.

Genus *Balticomerope* n. gen.

Type species. Parasolenopleura scanica Westergård, 1953; type material from the Exsulans Limestone, Alum Shale Formation, Andrarum, Scania, Sweden.

LSID. urn:lsid:zoobank.org:act:DBDA4211-AC58-4EFE-A346-FF6E8F47D625

Etymology. Name composed of *Baltica* as a reference to the occurrence of the type species on that lower Palaeozoic continent; and *Merope* (Μερόπη in Ancient Greek), daughter of Atlas in Greek mythology, one of the Pleiades, also known as the “lost star” which is understood in this context as a reference to the nescience about the taxonomic significance of the type species.

Diagnosis. Genus of the Solenopleurinae with cephalon of PL-type architecture; glabella moderately tapering forward, with almost straight lateral margins; frontal lobe with a feeble parafrontal band; occipital ring with tubercle or node in a median position; axial furrows narrow, sharp; eye ridges faintly marked, in relatively anterior position; palpebral lobes short, in a relatively anterior position; palpebral areas of ca. two-thirds width of the glabellar frontal lobe across the level of the palpebral lobes. with modest transverse and exsag. convexity; preglabellar field moderately broad (sag.), convex; anterior border moderately broad, with low arcuation of its margin in anterior view; anterior border furrow moderately deep, with a slightly flattened central sector; pygidium of lenticular outline, with a relatively broad, weakly tapering axis of ca. 80 percent pygidial length, consisting of three fairly well-defined axial rings, posteriorly continuing into a short and relatively low boss; pygidial pleural fields with fairly well-developed pleural furrows; pygidial lateral and posterior border poorly defined.

Discussion. Some of the well preserved solenopleurine trilobites grouped under *Parasolenopleura* by Westergård (1953) seem to represent a closely related group with fairly “primordial” morphologic features and without obvious apomorphic characters. They all have a distinctly tapering glabella with a subevenly rounded front; a short to moderately broad (sag.), convex preglabellar field; a rather simple, short to moderately broad and convex anterior border; quite narrow, well incised axial furrows of moderate depth; transversely and sagittally moderately convex palpebral areas; and short, moderately prominent palpebral lobes at a “normal” intermediate position. The pygidia of these species are relatively short and typically sublenticular in outline, with an axis of 3 or 4 more-or-less well-marked axial rings (plus an articulating half-ring and a terminal axial piece). The pleural areas are subdivided by pleural furrows; the lateral and posterior borders are relatively narrow, poorly defined from the pleural areas and without any recognisable subdivision, forming smooth margins.

As for the Scandinavian taxa, the species introduced as *Parasolenopleura scanica* Westergård, 1953 closely resembles *P. linnarssoni*, *P. spinigera* and *P. brevicauda*, but more than those species it unites characters of solenopleurid and ptychopariid trilobites, with mainly the morphology of the palpebral lobes and the specific character of the anterior border distinguishing them from the latter group and from other Scandinavian species assigned to the subfamily Solenopleurinae. The placement under *Parasolenopleura* by Westergård (1953) reflects the state of taxonomic approach at that time, and the uncertainty of subdivision of solenopleurid trilobites has been commented upon above. Close examination of the available material of the species listed here reveals important differences between it and superficially similar species assigned to *Parasolenopleura*, *Jincella* and *Liosolenopleura* as described herein.

Both *Parasolenopleura* and *Jincella* are characterised by species with a relatively stout glabella (with a width:length ratio larger than 0.80 in adult individuals); with a sunken or almost absent preglabellar field; broad and distinctly developed axial furrows; relatively prominent, upturned palpebral lobes; and a pygidium with a subelliptical outline, a broad axis and a poorly defined, but broad lateral and posterior border. *Parasolenopleura scanica* has a relatively slender glabella (with a width:length ratio of less than 0.73 in adult individuals); a short to moderately broad, clearly convex preglabellar field; well incised axial furrows, which are sharp rather than broad and do not extend distinctly into ventral direction; small, indistinct palpebral lobes, which are nearly flap-like; and a pygidium with a sublenticular outline, a moderately wide axis and a poorly defined, relatively narrow lateral and posterior border. Similar characters and dimensions can be seen in *Parasolenopleura linnarssoni* Westergård, 1953, *P. spinigera* Westergård, 1953 and *P. vestgothica* Westergård, 1953, and it has been variously suggested that these constitute a closely related group (e.g., Weidner & Nielsen 2013). These three species differ from the species described as *P. scanica* primarily in the overall convexity of the cephalon, the exact way in which the axial furrow is developed and the resulting convexity of the fixigenae as well as some slightly different aspects in the pygidial morphology.

Summarised, the basic architecture of the cephalon of *Parasolenopleura scanica* Westergård, 1953 differs quite fundamentally from that of the *linnarssoni* clade (which is formally distinguished as the newly introduced genus *Balticoglaucus*). The cephalon of *P. scanica* is composed of a clearly elevated glabella that projects well above the genae with their comparatively modest convexity in both transverse and exsagittal directions. Insofar, the species is a paradigmatic example for an SP-type morphology. The anterior part of the cephalon dips considerably, but the anterior border is constructed like a framing brim, although its anterior margin forms a low arc in anterior view. The axial furrows are quite sharply incised.

Although this design and also the pygidium are fairly similar to those of *Jincella* or *Exapinepiphania* n. nom., the precise shape of the glabella, the different character of the axial furrows and the width and convexity of the palpebral area suggest principal differences so that the species cannot be assigned to those genera and is considered to present a separate new genus for which the name *Balticomerope* n. gen. is proposed. A second species, previously also identified as *Parasolenopleura scanica* in Weidner & Nielsen (2013) and introduced here as *B. bornholmensis* n. gen., n. sp., has the same characters. A third species, previously dealt with as *Parasolenopleura brevicauda* (Westergård, 1953), is assigned to the genus as well.

In addition, at least two species from the Siberian Platform can be assigned to Balticomerope; these are *Solenopleura flerovae* Lermontova in Chernysheva, 1953 and *S. djainensis* Lermontova in Chernysheva, 1953. Both are discussed below under *Balticomerope flerovae*.

The principal diagnostic characters include a moderately tapering glabella with almost straight lateral margins and a subevenly curved anterior margin of the frontal lobe with a feeble parafrontal band which is fused with the glabellar front except for its continuation into the axial furrow; a moderately broad (sag.) occipital ring which tapers considerably towards the axial furrows and bears a low, but relatively large median tubercle; an occipital furrow with narrow, sharp but relatively shallow central sector; narrow axial furrows; faintly marked eye ridges at an anterior position and with only a slightly oblique direction; short, obliquely directed and moderately upturned palpebral lobes in a relatively anterior position at the level between S2 and S3; comparatively wide palpebral areas with ca. two-thirds width of the glabellar frontal lobe across the level of the palpebral lobes and a fairly modest transverse convexity; a moderately broad (sag.), convex preglabellar field; a moderately broad anterior border of more-or-less equal breadth of the preglabellar field on the sagittal line, continuously decreasing in exsag. width towards the facial sutures and with a moderate curvature of the anterior margin in dorsal view, moderately convex in sag. profile but slightly elbowing in respect to the general drop of the anterior cephalic region, with a low arcuation of its margin in anterior view; a moderately deep, subevenly curved anterior border furrow with a slightly flattened central sector; a pygidium of lenticular outline in dorsal view, with a relatively broad, weakly tapering axis of ca. 80 percent pygidial length, consisting of three fairly well-defined axial rings, a visibly projecting articulating half-ring and a short terminal axial piece, posteriorly continuing into a short and relatively low boss; pygidial pleural fields with three segments indicated by fairly well-developed and broad pleural and faint interpleural furrows; pygidial border poorly defined; cuticle on the cranidium covered with densely arranged fine granules of varying sizes.

The genus, as defined herein, is formally based on *Parasolenopleura scanica*. However, Weidner & Nielsen (2013) reported specimens from the *Ptychagnostus atavus* Zone of Bornholm which they assigned to *Parasolenopleura scanica*. These two cranidia are closely reminiscent of the morphology seen in the (slightly older, *Ptychagnostus gibbus* Zone) type material of Westergård (1953). However, they show a slightly narrower (sag., exsag.) anterior border defined by a more sharply incised and less curved anterior border furrow. In addition, the eye ridges initiated slightly posterior to the location in which they start in *B. scanica*, are slightly more rearward directed, and the palpebral lobes are thus at a slightly more posterior position at the level of S2. The pygidium illustrated in Weidner & Nielsen (2013, fig. 52C, D) resembles very much the pygidium of *B. scanica* (Fig. 83F, J), differing only in minor aspects. Nevertheless, the cranidial morphology does not match that seen in the cranidia of the type lot of *Parasolenopleura scanica*. It must be regarded as a second species of *Balticomerope* which is formally introduced herein as *B. bornholmensis* n. gen., n. sp.

The species of the *linnarssoni* clade are generally similar in dorsal view, with similar shapes of the glabella, preglabellar field and anterior border as well and the small palpebral lobes and also in the principal morphology of the pygidium. However, all these features are plesiomorphic characters. As discussed above, a fundamental difference exists in the cephalon which has a morphology derived from a domal vault that is intersected by axial furrows rather than being an arcuated upfold composed of more-or-less independently convex glabella and genae. There is little doubt that this construction is a functional morphology caused by an enlarged digestive tract on the ventral side of the dorsal exoskeleton. Such an organisation of the ventral organs must be valued as reflecting an evolutionary progress which testifies a quality that claims taxonomic significance. In addition, the species of *Balticomerope* possess a median tubercle on the occipital ring, whereas the species *Balticoglaucus* have a terminal occipital node, thorn or spine. Close examination of well-preserved specimens of these species reveals that a segmental boundary exists on the occipital ring (see Fig. 83A), which indicates that the tubercle in *Balticomerope* and the terminal occipital node/spine in *Balticoglaucus* arise from different segments and are thus not homologous.

Species with a roughly similar morphology of the cephalon are also known from North China, for example *Austrosinia chalcon* (Walcott, 1911), but they have utterly different pygidia. This, in turn, suggests that the PL-type morphology composed of these plesiomorphic characters is insufficient to merge relevant species with similar morphologies under a few traditional genera with a hypertrophied morphological range.

Balticomerope scanica (Westergård, 1953)

Fig. 83

v *	1953	*Parasolenopleura scanica* sp. n. – Westergård: pp. 25–26, 38 (table), pl. 6, figs. 5a–c, 6–8.
	1974	*Parasolenopleura scanica* – Martinsson: p. 204.
	1994	*Parasolenopleura scanica* (Westergård 1953) – Rudolph: pp. 27, 48, 54, 213, 227–228, 238, 264, tab. 12, pl. 26, figs. 1–6.
	1998	*Parasolenopleura scanica* – Geyer: p. 391.
non	2003	*Parasolenopleura* cf. *scanica* Westergård – Axheimer & Ahlberg: pp. 143, 151, 156, tab. I.
	2007	*Parasolanopleura scanica* – Rushton et al.: p. 139.
?	2009	*Parasolenopleura scanica* Westergård, 1953 – Weidner & Nielsen: pp. 258, 267.
?	2014	*Parasolenopleura scanica* Westergård, 1953 – Weidner & Nielsen: pp. 63, 65, fig. 52A–D.
	2017	*Parasolenopleura scanica* Westergård, 1953 – Geyer: pp. 49, 50.
	2023	*Parasolenopleura scanica* Westergård, 1953 – Weidner et al.: pp. 107, 121 (table).

Diagnosis. Species of *Balticomerope* with eye ridges initiating near anterolateral corners and relatively poorly rearward directed; palpebral lobes located at the level of L3; anterior border (in dorsal view) of subequal width to preglabellar field; anterior border furrow moderately well developed, with minor curvature in dorsal view; pygidium with indistinct, very short plectrum posterior to axis.

Description and discussion. The general morphology and its diagnostic characters of *Balticomerope scanica* are discussed above under the genus. Nevertheless, a few details merit some additional remarks. Particularly interesting is the frontal lobe with its parafrontal band, which is usually difficult to recognise. It is fused for most of its extension, but appears to be better recognisable in smaller specimens. Fig. 83B shows a parafrontal band fused with the frontal lobe. They form a roof-shaped chevron with anterolateral corners formed by two knob-like extensions into the axial furrow, which create delicate grooves posterior to it (Fig. 83E). The lateral extensions of the parafrontal band may develop into delicate threads traversing the axial furrows and continuing into the eye ridges as in Fig. 83M or better visible in internal moulds (e.g., Fig. 83C).

The palpebral lobes are short and located in relatively anterior position at the level between S2 and S3. They are directed oblique to the axis and moderately are slightly upturned, but often more lid-like than in related species of the Solenopleurinae (Fig. 83E, I). On internal moulds, they are subdivided into a trapezoidal, slightly curved, low area and a slightly more elevated, narrow ridge (Fig. 83H).

The occipital ring bears a median tubercle of considerable size, but generally poorly defined. Anterior to it, the surface sculpture of small to minute granules is modified to show transversely lengthened granules with a vaguely subelliptical arrangement around the tubercle (Fig. 83O). These scale-like granules proceed into a relatively sharp occipital ring further reducing its width.

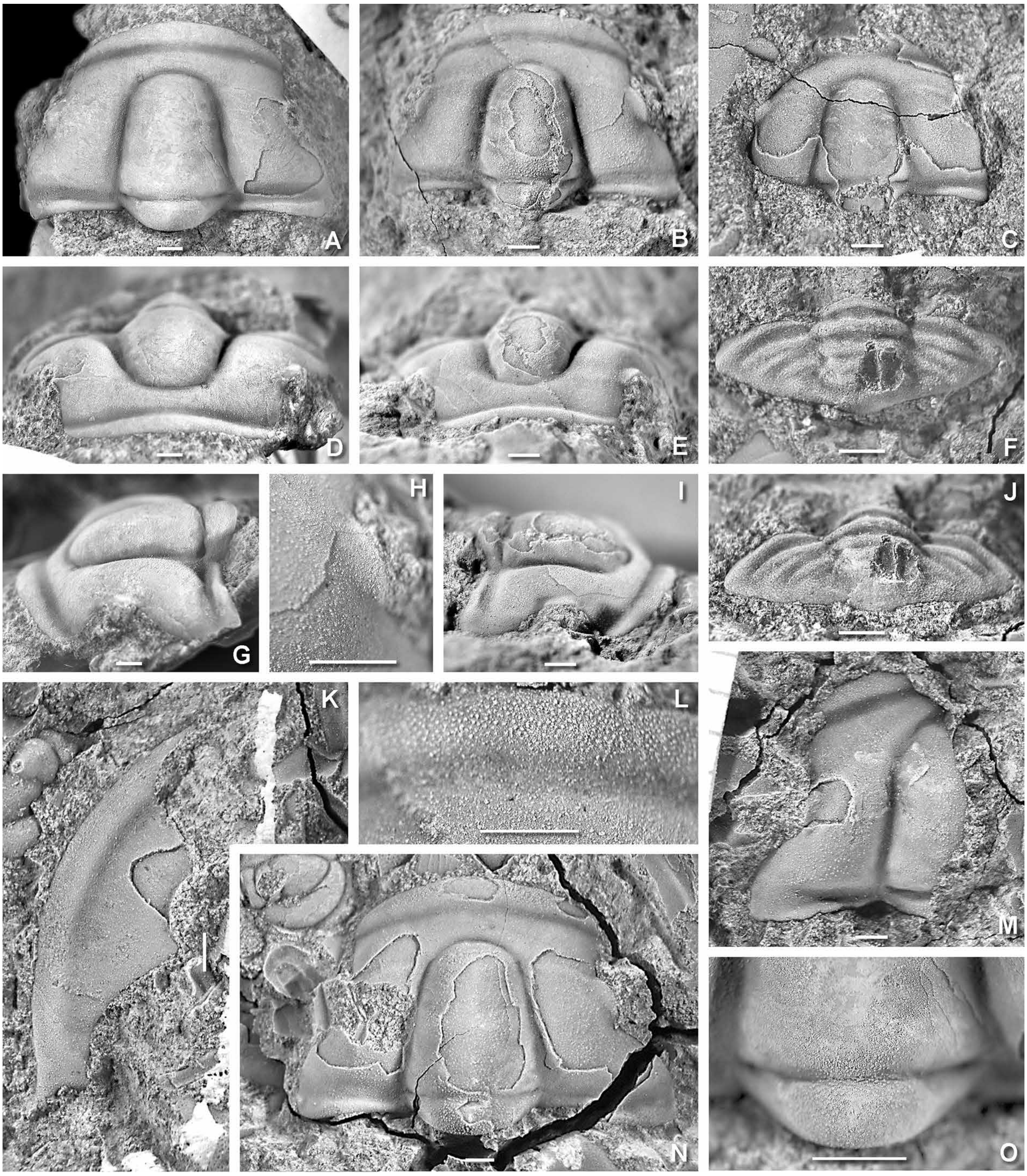

Fig. 83: *Balticomerope scanica* (Westergård, 1953). **A, D, G, O** SGU 6277, holotype, cranidium with preserved cuticle; dorsal (A), anterior (D) and lateral (G) views; O shows magnified view of occipital ring illustrating prosopon of small granules and faint occipital node; original of Westergård (1953, pl. 6, fig. 5a–c). **B, E, H, I, L** SGU 6278, paratype, cranidium, partly exfoliated; dorsal (B), anterior (E) and lateral (I) views; H magnified view of palpebral lobe and palpebral furrow documenting the flap-like upturn of a poorly convex (tr.) palpebral lobe; L detail of anterior border, border furrow and preglabellar field with faint, low swelling in the anterior border furrow; original of Westergård (1953, pl. 6, fig. 6). **C** SGU 6279Bc, cranidium of immature individual, largely exfoliated, dorsal view; original of Westergård (1953, unfigured). **F, J** SGU 6280, pygidium, dorsal (F) and oblique posterior views; original of Westergård (1953, pl. 6, fig. 8). **K** SGU 6279b, librigena, dorsal view; original of Westergård (1953, pl. 6, fig. 7). **M** SGU 6279Bb, partial cranidium, partly exfoliated, dorsal view; original of Westergård (1953, pl. 6, unfigured). **K** SGU 6279Ba, cranidium, partly exfoliated, dorsal view; original of Westergård (1953, pl. 6, unfigured). All specimens from Exsulans Limestone, Alum Shale Formation, Andrarum, Scania. Scale bar 1 mm.

A faint swelling is developed in the central sector of the anterior border furrow (Fig. 83L). Its definition from the anterior border is enhanced by granules of different diameters.

A librigena that almost certainly belongs to *Balticomerope scanica* (Fig. 83K) has a short genal spine with a moderate arcuation in respect to the evenly curved lateral margin and continuous into a very short posterior border section. The genal field fairly wide (tr.), gently convex, and has a low fringe along the ocular suture. It shows very delicate radial caeca. The lateral border moderately wide and flattened in transverse profile.

The pygidium of *Balticomeropa scanica* is only known from a single isolated specimen. This pygidium, however, agrees well with the size and expected morphology of the species and co-occurs with cranidia of the species (Fig. 83F, J). It has a lenticular outline in dorsal view, with the axis elevated distinctly above the pleural regions which slope moderately towards the lateral and posterior margins. The axis has a maximum width (across the anterior axial ring) of slightly less than one-third maximum width of the pygidium and a length of ca. 80 percent pygidial length. It is subdivided into three rings which are quite distinctly defined by well-developed axial furrows, plus an anteriorly projecting articulating half-ring and a short ring-like terminal axial piece, which continues posteriorly into a short and relatively low, poorly defined plectrum or swelling, which terminates into an indistinct blunt corner at the margin on the sagittal line. The pleural fields are subdivided by fairly well-developed and broad pleural and faint interpleural furrows, the ribs slightly extended onto a poorly defined pygidial border.

Occurrence. Balticomerope scanica was originally only known from the upper part of the *Ptychagnostus gibbus* Zone Exsulans Limestone Bed of the Alum Shale Formation of Scania and erratic ice-rafted boulders from northern Germany (Rudolph 1994). The species was recorded by Axheimer & Ahlberg (2003) from the lower part of the *Ptychagnostus atavus* Zone of Scania. Additional specimens reported from the *Ptychagnostus atavus* Zone of Bornholm are distinguished here as *Balticomerope bornholmensis* n. gen., n. sp.

***Balticomerope bornholmensis* n. gen., n. sp.**

2013 *Parasolenopleura scanica* Westergård, 1953 – Weidner & Nielsen, pp. 6, 63, 65, fig. 52A–52D.

Holotype. MGUH 30208, cranidium, partly exfoliated (Weidner & Nielsen 2013, fig. 52A).

LSID. urn:lsid:zoobank.org:act:B62A6339-7168-4FE5-A0F2-0190C9CC8FAC

Type locality and stratum. Lower part of *Ptychagnostus atavus* Zone of the Alum Shale Formation; Øleå creek near Borggård, Bornholm, Denmark.

Etymology. Named after the occurrence of the species on the island of Bornholm.

Paratypes. One cranidium, MGUH 30209; one pygidium, MGU 30310; all from the upper part of the of *Ptychagnostus atavus* Zone of the Alum Shale Formation; Øleå creek, Bornholm, Denmark.

Diagnosis. Species of *Balticomerope* with eye ridges initiating slightly posterior to the anterolateral corners, moderately rearward curving; palpebral lobes located at the level of S2; anterior border (in dorsal view) slightly narrower than preglabellar field; anterior border furrow quite well developed, with minor curvature in dorsal view; pygidium with indistinct, relatively short, but moderately well-defined plectrum posterior to axis.

Description and discussion. The species is based on material from Bornholm, which was figured and shortly discussed in Weidner & Nielsen (2013), and assigned by them to *Parasolenopleura scanica*. As noted above, the two cranidia are closely reminiscent of the morphology seen in the type material of *Parasolenopleura scanica*, but differs in a slightly narrower (sag., exsag.) anterior border defined by a more sharply incised and less curved anterior border furrow. This furrow, however, shows a shallower median section as similarly developed in *Balticomerope scanica*. The glabella in *B. bornholmensis* n. gen., n. sp. is very similar to that in *B. scanica*, but seems to be slightly shorter. Similar to the situation in *B. scanica*, the frontal lobe has a nearly completely fused parafrontal band with laterally extending faint threads that proceed into the eye ridges. However, the frontal margin in *B. bornholmensis* appears to have a lower curvature. The eye ridges start slightly posterior to the antero-lateral corners of the glabella and have a more pronounced curvature as in *B. scanica*. As a consequence, the palpebral lobes are located at a slightly more posterior position, at the level of S2.

The pygidium of *Balticomerope bornholmensis* (Weidner & Nielsen 2013, fig. 52C, D) has a similarly broad axis with three well marked axial rings. The axis appears to taper a bit more strongly than that seen in the pygidium of *B. scanica*, and the posterior margin of the terminal axial piece is bilobate and shows a well visible indentation on the sagittal line. It is noteworthy that the anterior axial ring appears to have been incompletely fused. A low, but much better laterally defined and longer plectrum can be seen. The posterior pygidial margin lacks the blunt tip on the sagittal line that can be seen in *B. scanica*. In addition, the poorly defined lateral border is slightly thicker than in the pygidium of *B. scanica*. Nevertheless, all these differences in the pygidium may be ascribed to intraspecific variation so that more material is needed to evaluate the morphologic ranges.

The differences to similar species are as discussed for *Balticomerope scanica* (above).

***Balticomerope brevicauda* (Westergard, 1953)**

Fig. 84

pars	1883	*Liostracus Linnarssoni* Brögger – Linnarsson: p. 24.
v *	1953	*Parasolenopleura linnarssoni brevicauda* subsp. n. – Westergård: pp. 28–29, 38 (table), pl. 6, figs. 13, 14.
	1974	*Parasolenopleura linnarssoni brevicauda* – Martinsson: p. 204.
	2004	*Parasolenopleura linnarssoni brevicauda* – Álvaro et al.: p. 139.
	2013	*Parasolenopleura brevicauda* Westergård, 1953 – Weidner & Nielsen: pp. 63, 65, fig. 52Q.

Discussion. Westergård (1953) introduced this taxon as a subspecies of *Parasolenopleura linnarssoni*. He referred only two specimens to the species of which he only regarded the holotype (Westergård 1953, pl. 6, fig. 13) as confidently representing the subspecies. That specimen is an incomplete dorsal exoskeleton, which from a collection by Schmalensee and was already referred to in Linnarsson (1883), who regarded it as representing his *Liostracus linnarssoni*. Westergård (1953) considered the pygidium as characteristic. It is short (almost three times as broad as long), and its axis consists of only two recognizable rings plus a barely recognizable terminal axial piece. The pleural regions accordingly are subdivided by only two interpleural furrows.

Given the imperfect preservation of the pygidium in the holotype, this reference appears to be insufficient to confidently distinguish the taxon. However, as already mentioned by Westergård (1953), the cuticle of the holotype is beset with granules. This granulation is relatively coarse and differs indisputably from the surface ornamentation seen in *Balticoglaucus linnarssoni*. A second specimen figured by Westergård (1953, pl. 6, fig. 14) is an isolated, quite well preserved cranidium, which was only tentatively assigned to *Parasolenopleura linnarssoni brevicauda*, probably because it is smaller than the holotype and lacks an associated pygidium. Nevertheless, this specimen shows the same type of surface ornament of moderate-sized granule in a fairly loose arrangement on the cuticle (Fig. 84A–C), and there can be little doubt that it represents the same taxon. In addition, this specimen has a median tubercle on the occipital ring rather than a terminal spine. Most of all, it does not show the domed transverse profile as *Balticoglaucus linnarssoni*, but genae with a lower convexity surmounted by a distinctly more elevated glabella.

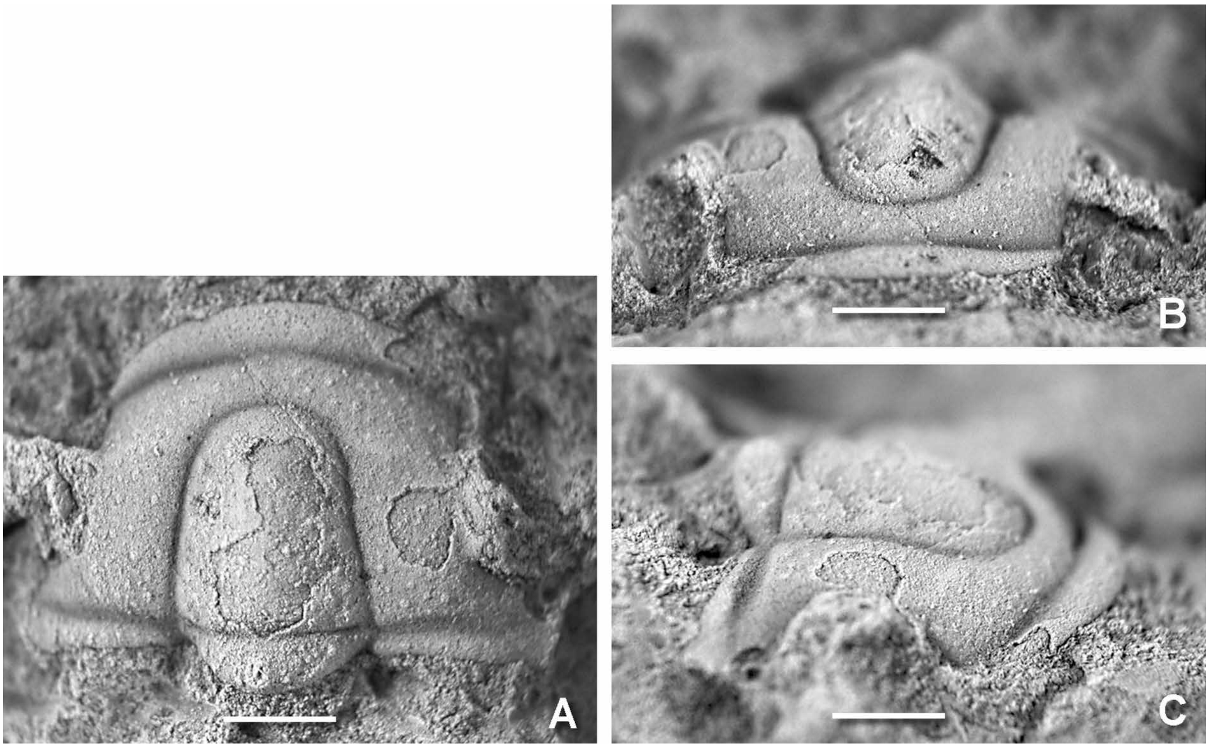

Fig. 84: *Balticomerope brevicauda* (Westergård, 1953). **A–C** SGU 6283a, cranidium, partly exfoliated; dorsal (A), anterior (B) and oblique lateral (C) views with prosopon of loosely spaced moderately large granules; original of Westergård (1953, pl. 6, fig. 14). From Aborfallet at Sjougdälven River, Angermanland, Sweden. Scale bars 1 mm.

Despite of the imperfect knowledge on the taxon based on the two specimens, it is certain that it is valid and cannot be regarded as a synonym of *Balticoglaucus linnarssoni*. Apart from the surface ornamentation and the shape of the pygidium, the specimens also suggest differences to *L. linnarssoni* in the less clearly developed raise in the anterior border furrow, a slightly broader (sag.) preglabellar field (by comparison with the anterior border) and a slightly more convex (sag.) anterior border. Accordingly, it is proposed here to raise the taxon to the species level as tacitly suggested by Weidner & Nielsen (2013). All characters discussed above fit those of *Balticomerope* n. gen. rather than *Balticoglaucus*.

Weidner & Nielsen (2013) discussed the species and its relationship to the coeval species *Parasolenopleura linnarssoni*, *P. spinigera* and *P. vestgothica*, all known from the *Ptychagnostus atavus* Zone of Sweden. They figured a fairly large cranidium as *Parasolenopleura brevicauda* which was collected from an ice-rafted erratic boulder found at As-Hoved, Denmark. That specimen, however, differs from Westergård's original specimen in showing a narrower anterior border with a faint kink of the anterior cephalic margin on the sagittal line and having slightly wider palpebral areas.

Stratigraphic occurrence. Hypagnostus parvifrons Zone, i.e. upper *Ptychagnostus atavus* Zone, Alum Shale Formation, Scania, Sweden.

Balticomerope flerovae (Lermontova in Chernysheva, 1953)

Figs. 85, 86

v * 1953 *Solenopleura flerovae* Lerm. – Chernysheva, pp. 36, 41, 42–45, 52, pl. V, figs. 1–4.
1960 *Solenopleura flerovae* Lermontova – Chernysheva, p. 466, pl. III, fig. 5.

1964 *Solenopleura flerovae* Lerm. – Rozova, p. 466, table on p. 14.
1978 *Solenopleura flerovae* Lerm. – Gogin et al., pp. 83, 84.
1978 *Solenopleura flerovae* Lerm. – Dymovich et al., p. 61.

Lectotype (chosen herewith). Incomplete dorsal exoskeleton, figured in Chernysheva (1953, pl. V, fig.1) and Chernsheva (1960, pl. III, fig. 5); refigured by its latex cast on Fig. 85).

Diagnosis. Species of *Balticomerope* with relatively narrow frontal lobe, eye ridges initiating near anterolateral corners; palpebral lobes located at the level of S2 to L3; anterior border (in dorsal view) narrower than preglabellar field; anterior border furrow moderately well developed, shallower medially with moderate curvature in dorsal view; pygidium with indistinct, very short plectrum posterior to axis, lateral border obsolescent; posterolateral pygidial margins poorly curved.

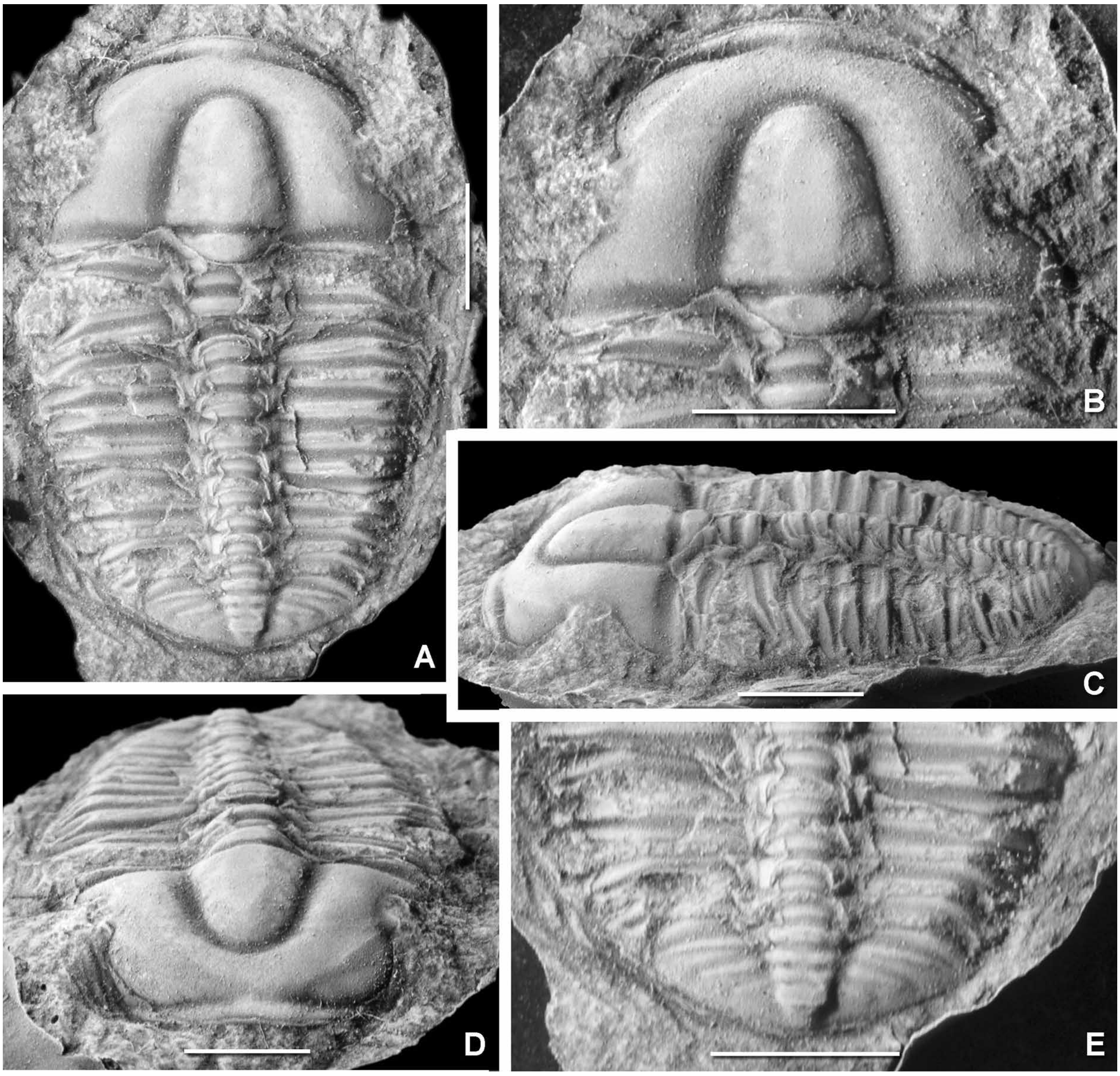

Fig. 85: *Balticomerope flerovae* (Lermontova in Chernysheva, 1953), latex cast of the lectotype (Chernysheva 1953, pl. V, fig. 1), incomplete, slightly decomposed dorsal exoskeleton, oblique anterior view (A), magnified view of cranidium (B), oblique lateral view (C), dorsal view of entire specimen with detached librigena (D) and magnified view of pygidium with slightly detached posterior thoracic segments (E). From the Tuaeva collection so-called *Paradoxides davidis* Zone (= *fissus-perforatus* Zone, lower Maya Stage/Olenek Horizon). Scale bars 5 mm in A–D, 1 mm in E.

Description. The general morphology of *Balticomerope flerovae* (Lermontova in Chernysheva, 1953) resembles that of *B. scanica*. Typical characters of Balticomerope include the shape and convexity of the glabella, the position and course of the eye ridges and the palpebral lobes, and the morphology of the anterior part of the cephalon with the particular expression of the anterior border and the anterior border furrow. Particularly noteworthy in the shape and size of the pygidium.

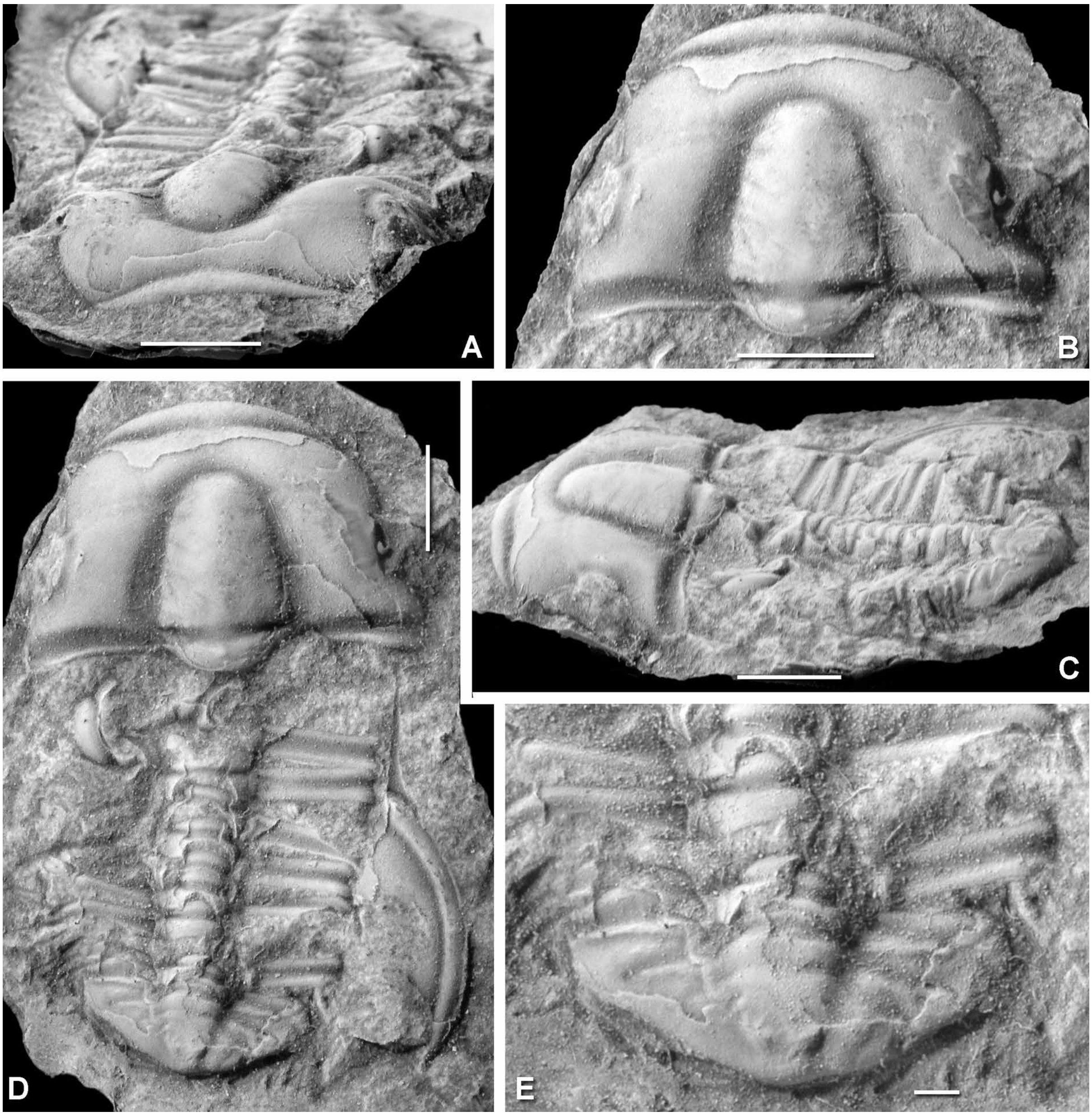

Fig. 86: *Balticomerope flerovae* (Lermontova in Chernysheva, 1953), latex cast of the lectotype (chosen herein; figured in Chernysheva1953, pl. 5, fig. 5, and in Chernysheva 1060, pl. II, fig. 5 [with incorrect magnification]), incomplete, slightly decomposed dorsal exoskeleton, oblique anterior view (A), magnified view of cranidium (B), oblique lateral view (C), dorsal view of entire specimen with detached librigena (D) and magnified view of pygidium with slightly detached posterior thoracic segments (E). From the Tuaeva collection, from the so-called *Paradoxides davidis* Zone (= *fissus-perforatus* Zone, lower Maya Stage/ Olenek Horizon). All scale bars 5 mm.

The glabella of *Baltimerope flerovae* has fairly narrow parabolic shape with an evenly curved frontal margin. Three weakly impressed lateral furrows can be recognised, S1 being quite strongly rearward curved from its origin at the lateral margins. The occipital ring is narrow near the axial furrows, with a distinct growth in length to the midline so that it extends clearly backward on the axial line. A weakly developed median node seems to have been present.

The eye ridges initiate near the (evenly curved) anterolateral corners of the glabella and are slightly backward directed and moderately thick near the axial furrow, but more strongly curved and slightly thinner in the abaxial section. The palpebral lobes are moderately curved, somewhat crescent-shaped and oriented slightly oblique to the axis.

A weakly developed parafrontal band appears to have been present, but both specimens are not well enough preserved to exhibit this delicate line with any certainty. The preglabellar field is convex in sagittal profile, but clearly ventrally deflected. Nevertheless, in dorsal view it has about double breadth of the anterior border on the sagittal line. The anterior border is a crescent-shaped, relatively narrow lobe, which subevenly narrows towards the facial suture. However, it is faintly raised on the sagittal line. The anterior border furrow shows the shallower median section across the sagittal line that is typical for *Balticomerope*.

A librigena is preserved as a detached sclerite in one of the specimens (Fig. 86D). It is moderately large and has a broadly curved genal angle. The genal field is fairly wide (tr.), gently convex, and shows moderately wide and clearly raised lateral border. The border furrow is well demarcated and moderately deep. A short, but well visibly acute genal spine extends rearwards.

The thorax consists of 10 segments in the lectotype (Fig. 85A, C) and apparently also 10 segments in the other figured specimens (Fig. 86). All segments are characterised by extended and straight adaxial pleurae, a distinct kink at the articulation lines at each pleura, quite highly convex axial rings with fairly large bulbous lateral swellings, and subrounded pleural tips without well-developed pleural spines. Segments 1 and 2 show a progressive rearward direction of the distal pleural parts.

The pygidium is relatively large and has a transversely subtriangular outline, which is primarily a result of the poorly curved posterolateral margins. The axis tapers evenly and is composed of ca. four moderately well-defined rings plus a terminal axial piece with a subtruncate posterior margin. A low ridge continues from it towards the posterior margin, but appears to end shortly before the margin.

The pygidial pleurae are defined by low, but moderately well visible pleural and interpleural furrows which decrease in visibility rearwards. A lateral or posterolateral margin is not developed by the termination of the pleural ribs well before the lateral margins.

Although the name “*Solenopleura flerovae*” turns up in a number of subsequent publications on Middle Cambrian strata of the Siberian Platform (e.g., Rozova 1964; Gogin et al. 1978; Dynovich et al. 2012), it appears to have been figured only once except for Chernysheva’s original monograph, i.e. in the trilobite part of the Osnovy Paleontologii (Chernysheva 1960), where one of the specimens of the type lot is refigured (Chernysheva 1960, pl. II, fig. 6; with erroneous magnification).

The species’ generic affinity to *Balticomerope* is demonstrated by a number of characters, such as the shape and course of the preglabellar field, anterior border furrow and border in the cephalon, and the shape and morphology of the pygidium. The species appears to have the longest (tr.) preglabellar field known from any of the species of *Balticomerope*.

Another species of *Balticomerope* from the Siberian Platform was described as *Solenopleura djainensis* Lermontova in Chernysheva, 1953. It originates from strata of similar age or even coeval strata and is also among the poorly known species. *Balticomerope djainensis* differs from *B. flerovae* in having a distinctly more strongly tapering glabella due to a broader occipital ring, more adaxially located and strongly upturned palpebral lobes, and a narrower pygidium. The complete dorsal exoskeleton figured in Chernysheva (1953, pl. V, fig. 6) has 12 thoracic segments. As for *B. flerovae*, the species has never been reported subsequently with any certainty.

Stratigraphy. The precise stratigraphic range is not indicated in the original publication by Chernysheva (1953), Subsequent references of "*Solenopleura flerovae*" suggest that the species occurs in the Chaya Formation and/or coeval strata of the Uchur-Maya region of the Siberian Platform, in a stratigraphic interval of the lower Mayan defined by the *Tomagnostus fissus* and *Corynexochus perforatus* zones.

Genus *Balticoglaucus* n. gen.

Type species. Liostracus linnarssoni Brøgger, 1878; from the *Ptychagnostus atavus* Zone, Alum Shale Formation, Scania, Sweden.

LSID. urn:lsid:zoobank.org:act:F4EFA95D-67EF-4583-AB00-5551AC677848

Etymology. Name composed of *Baltica* as a reference to the occurrence of the type species on that lower Palaeozoic continent; and *Glaukos* (Γλαῦκος in Ancient Greek), son of Merope in Greek mythology, a reference to the direct ancestry of the genus' species from *Balticomerope*.

Diagnosis. Genus of the Solenopleurinae with cephalon of PL-type architecture; glabella tapering forward, with almost straight lateral margins; frontal lobe with a feeble parafrontal band; occipital ring with a terminal node or spine; eye ridges faintly marked, commencing short distance posterior to frontal lobe; palpebral lobes moderately long, in moderate position; palpebral areas of clearly less than half width of occipital ring, sloping ventrally from most elevated point near axial furrow; preglabellar field moderately broad (sag.), convex; anterior border moderately broad, with a very minor arcuation of its margin in anterior view; anterior border furrow moderately deep, with flattened central sector; pygidium lenticular in outline, pygidial axis moderately broad, weakly tapering, of almost 90 percent pygidial length, consisting of four axial rings, posteriorly continuing into a short and relatively low boss; pygidial pleural fields with relatively well-developed pleural furrows; pygidial border poorly defined.

Discussion. The species of *Balticoglaucus* n. gen. have been assigned to *Parasolenopleura* in earlier publications. They are closely related to *Balticomerope* n. gen. and appear to be direct descendants. The differences have been shortly discussed above: *Balticoglaucus* differs primarily in the domed cephalon with abaxially sloping genae. The glabella surmounts the palpebral areas, but has the aspect as resting on a socle. The palpebral lobes in *Balticoglaucus* are moderately long rather than short as in *Balticomerope* and are in a central rather than anterior position in respect to the length axis. The pygidial axis *Balticoglaucus* appears to be longer and slightly narrower than in *Balticomerope*. In addition, several minor features distinguish *Balticoglaucus* from *Balticomerope*, but these are delicate and only well recognisable in well-preserved specimens:

(1) The anterior border furrow in *Balticoglaucus* has a shallower central section as in *Balticomerope*, which is obviously a result of more anteriorly positioned organs on the ventral side. This location of ventral organs appears to be indicated by surface ornament on a lunate area on the posterior part of the anterior border in this central sector, which differs from the ordinary prosopon in the anterior part and elsewhere on the cephalon (Fig. 87M). It shows the presence of obscurely developed caeca.

(2) The occipital ring in *Balticoglaucus* carries a terminal or subterminal node (as in *B. linnarssoni*) or spine (as in *B. spinigerus* and *B. vestgothicus*). Well-preserved specimens show a delicate transverse furrow (Fig. 87A), which is the relic of a segment boundary as also suggested by the position of the doublure (Fig. 87B). The median nodes in the species of *Balticomerope*, by contrast, belong to an anteriorly located segment.

The frontal lobe in both *Balticomerope* and *Balticoglaucus* is merged with a parafrontal band, which is thus only recognizable in most well-preserved specimens as delicate threads extending anterolaterally from the front of the glabella. The cranidium of *Balticoglaucus linnarssoni* illustrated in Fig. 87A features vaguely visible extended anterolateral bulges representing the parafrontal band, separated in the sagittal line by a low pit at the tip of the glabella.

The difference between *Balticoglaucus* and other morphologically similar genera are mostly the same as for *Balticomerope*. In respect to the cephalic architecture, the species of *Balticoglaucus* show an intermediate morphology between *Balticomerope* and the more homogeneously vaulted cupola seen in typical species of *Solenoparia* Kobayashi, 1935 (see below).

Differences between the species of *Balticoglaucus* are discussed below. *Balticoglaucus spinigerus* and *B. vestgothicus* show a moderately long, subterminal occipital spine. Westergård (1953) suggested that this spine is more prominent in *B. vestgothicus* than in *B. spinigerus*. However, Weidner & Nielsen (2023) regarded both species as being synonymous. They also noted that investigations on extensive material from Sweden, Norway and Bornholm (Weidner & Nielsen, in prep.) appear to indicate for all three species a considerable variation of certain characters during ontogeny, often also among specimens of similar size. These are similar to observations on *Exapinepiphania gregaria* from Newfoundland (Fletcher 2005).

Also assigned to *Balticoglaucus* is a species described originally as *Solenopleura brachymetopa* var. *nuntia* by Grönwall (1902). The taxon from the *Ptychagnostus atavus* and *P. punctuosus* biozones of Bornholm was raised to species level as *Solenopleura nuntia* by Rushton & Berg-Madsen (2002). It is also known from the *Ptychagnostus punctuosus* Zone of England. Weidner & Nielsen (2014, fig. 51B) refigured the lectotype, a cranidium, which is characterised by a relatively narrow preglabellar field, a short occipital ring and short, subelliptical palpebral lobes. The palpebral areas are arranged in a way that causes a slight doming of the cephalon in transverse section, unlike the situation in *Balticomerope scanica*, but similar to the situation in *Balticoglaucus linnarssoni* and *B. spinigerus*. The pygidium (Weidner & Nielsen 2014, fig. 51E) shows at least three rings and is similar in other aspects to that known from *Balticomerope scanica*, but has a more subelliptical outline.

Agraulos robustus Cobbold in Cobbold & Pocock, 1934 clearly does not represent an agraulid species, but agrees in most characters with *Balticoglaucus linnarssoni* and *B. spinigerus* (see Cobbold & Pocock 1934, p. 376, pl. XLIII, figs. 6–9 and Rushton & Berg-Madsen 2002, fig. 3a–d). This species has an even more pronounced SP-type cephalic morphology. The preglabellar field is elevated and drops less that in the Scandinavian species of *Balticoglaucus*, and the anterior border furrow is a broader groove. The occipital furrow in *Agraulos robustus* is deeply incised, and the occipital ring extends into a long and strong, posteriorly directed spine. These characters do not match impeccably with the morphology seen in *Balticoglaucus linnarssoni* and *B. spinigerus*, but under a broad concept, the species can be regarded as a species of that genus. It is thus suggested to deal with the species as *Balticoglaucus*? *robustus* (Cobbold in Cobbold & Pocock, 1934).

Rushton & Berg-Madsen (2002) considered *Agraulos robustus* as a junior synonym of *Lonchocephalus peregrinus*. Despite a general similarity, that species differs in several aspects which are regarded herein as of taxonomic significance, such as a less pronounced SP-type topography of the cephalon, a less subacute front of the glabella, a distinctly longer (sag.) preglabellar field, a less well developed occipital furrow, and a longer occipital spine. The species introduced by Wallerius (1930) as *Lonchocephalus peregrinus* was tentatively assigned to *Parasolenopleura* by Westergård (1953). This species superficially resembles *Balticoglaucus linnarssoni* and *B. spinigerus* and could be considered as a progression of the growing size of the occipital spine in those species. However, other characters clearly distinguish that species from the typical species of *Balticoglaucus.* Nevertheless, no genus exists to which *Lonchocephalus peregrinus* can be confidently assigned. It is provisionally dealt with herein as "*Balticoglaucus*" *peregrinus*.

A further species of *Balticoglaucus* was recorded and illustrated by Bruton & Harper (2000, fig. 5A–D) as *Parasolenopleura* cf. *peregrina* (Wallerius, 1930) (and "*Parasolenopleura* cf. *perigrina*", respectively). The specimens from Ritland, western Norway, show a cranidial morphology similar to that of *B. spinigerus*, but with more strongly curved lateral margins of the glabella and a narrower, strongly curved front of the glabella as well as a mostly stronger and longer occipital spine. The specimens resemble "*Balticoglaucus*" *peregrinus* in dorsal view, but the cranidium of "*B.*" *peregrinus* has a less strongly developed PL-type topography, the glabella is narrower with almost straight lateral margins and an almost subtruncate front, and the preglabellar field is much broader (sag.). The Norwegian specimens certainly represent a yet undefined species, but additional material (including pygidia) is needed for a precise morphological assessment.

The species has been considered as similar to *Conocoryphe applanata* Salter, 1865 in several publications. However, that species from Eastern and Western Avalonia is regarded as a distinct species of *Jincella* (see also Álvaro et al. 2004; Fletcher 2006) or is tentatively assigned to *Jincella* (Unger et al. 2022).

A generally similar species was described from the Lena River region, Siberian Platform, under the name *Solenopleura lenaica* Lermontova, 1940. The precise locality was not noted in Lermontova (1940), but the first record probably came from the Botoma River area. It was later reported from the Amgan "*Tomagnostus fissus/Paradoxides sacheri*" Zone to the Mayan *Anopolenus henrici* Zone of the Chaya Formation in the Yudoma River area in the Yudoma-Maya rivers region of the Siberian Platform. Unfortunately, the figured specimens display some morphological disparity and are difficult to precisely assess. The original material came from the lower Mayan Stage of the Siberian Platform (Lermontova 1940; Chernysheva 1953) and features a cranidium with a relatively slender glabella tapering to a narrow, evenly curved anterior margin; a moderately broad (sag.) occipital ring; a relatively short preglabellar field; a moderately broad anterior border which slightly thickens at some distance on the sagittal line and next to it; and moderately long, well-defined palpebral lobes. Subsequently reported are occurrences of *Solenopleura lenaica* from the Eldakh "horizon", upper Amgan Stage, of the Batenev Range in the Altay-Sayan Foldbelt (Chernysheva 1971) as well as from the upper Amgan Maydan "Horizon" of central Kazakhstan (Ivshin 1978), but these specimens are less well-preserved, and its precise identification is difficult. Egorova et al. (1976, 1982) illustrated numerous specimens from various stratigraphic levels, including strata corresponding to the *Ptychagnostus atavus* Zone. The best preserved and most characteristic cranidia (e.g. Egorova et al. 1976, pl. 32, fig. 10; Egorova et al. 1982, pl. 4, figs. 3, 9, 10, 11) portray a morphology which resembles that seen in *Balticoglaucus*, but is estimated here as a result of convergent evolution. However, most of these specimens do not agree precisely with the type specimen figured by Lermontova (1940). These specimens exhibit a glabella which tapers forward to a front which tends to exhibit slight oblique truncations resulting in a short, nearly straight median part of the front. The preglabellar field is convex, but drops ventrally in a much stronger manner as in the typical species of *Balticoglaucus*. The anterior cephalic border in these specimens is convex, relatively short and quite prominent. More important, however, are the fixigenae and palpebral lobes: The palpebral areas are quite convex, including a considerable vaulting in exsag. direction, which is stronger than that seen in the species of *Balticoglaucus*. The palpebral lobes are relatively prominent, defined by a relatively sharp palpebral furrow and located slightly more posteriorly than those in the species of *Balticoglaucus*. Several specimens assigned to *Solenopleura lenaica* in various publications obviously do not represent that species nor the one illustrated by Lermontova (1940).

Fletcher (2007) refigured a cranidium of "*Solenopleura lenaica*" previously illustrated in Egorova (1982, pl. 4, fig. 9) and regarded its morphology as an argument for taxonomic rearrangements on the genus and subgenus level. He dealt with the species as *Brunswickia* (*Jincella*) *lenaica*, thereby changing the concept of *Jincella* and considering it a subgenus of *Brunswickia*.

Weidner & Nielsen (2014, fig. 51A) discussed and refigured a cranidium from an erratic boulder of the *Ptychagnostus atavus* Zone collected in north-western Poland, which was previously used by Buchholz (2004, pl. 4, fig. 5) to introduce a new solenopleurid species under the name *Jincella unica*. This specimen indeed resembles “*Solenopleura lenaica*”, but it differs in several important aspects and therefore must be regarded as a valid, independent species. It has a quite strongly tapering glabella with a nearly subacute front, a much shorter preglabellar field, and shorter, almost-knob-like palpebral lobes in a clearly more anterior position. The more strongly tapering glabella with the almost subacute front, the short occipital ring, the relatively strong exsagittal convexity of the palpebral areas, and the narrow anterior border distinguish the species from the species confidently assigned to *Balticoglaucus*, but the similarity with those suggest a tentative assignment to that genus.

A genus with superficially similar morphology and proportions to *Balticoglaucus* is known as *Aiaiaspis* Nazarov, 1973, occurring in the *Lejopyge laevigata*–*Aldanaspis truncata* zones of the Mayan Stage in parts of the Siberian Platform. The similarities, however, must be regarded as due to convergent evolution. Among other differences, the genal areas have a different transverse convexity as they grow up from the axial furrows. The anterior border is brim-like and arranged like a secondary addition to the cephalon. The anterior border furrow lacks a shallow median section. *Aiaiaspis* can be confidently assigned to the family Lonchocephalidae.

Balticoglaucus linnarssoni **(Brøgger, 1878)**

Fig. 87

	1869	*Liostracus aculeatus* – Linnarsson: p. 71.
	1873	*Liostracus aculeatus* – Kjerulf: p. 84, fig. 14.
?	1878	*Liostracus aculeatus* – Brøgger: pl. 3, fig. 3.
	*1878	*Liostracus Linnarssoni* n. sp. – Brøgger: pp. 47 [31], 50 [34], pl. 3, fig. 4, 4a–c.
	1879	*Liostracus Linnarssoni* – Linnarsson: p. 13.
v	1883	*Liostracus Linnarssoni* Brögger – Linnarsson: pp. 7, 8, 23–25, 37 (table), 40, 42, pl. IV, figs. 6?, 7–11.
cf.	1883	*Liostracus Linnarssoni* Brögger – Linnarsson: pl. IV, fig. 5.
pars	1888	*Liostracus Linnarssoni* Brögger – Matthew: pp. 143–147, pl. 2, fig. 1a–m.
	1902	*Liostracus Linnarssoni* Br. – Grönwall: pp. 11, 23, 24, 144–145, 169 (table), 188.
	1925	*Liostracus linnarssoni* Brögger – Warburg: p. 25.
non	1927	*Liostracus Linnarssoni* Ang. – Czarnocki: p. 196.
non	1927	*Liostracus Linnarssoni* Brögg. – Czarnocki: p. 196.
?	1929	*Liostracus linnarssoni* Br. – Strand: pp. 314, 315, 321, 322, 324, 326, 328, 329, 330, 339, 348, 351–352, pl. I, fig. 19, pl. II, fig. 6.
	1930	*Liostracus Linnarssoni* Brögger – Wallerius: p. 48.
	1931	*Liostracus linnarssoni* – Lake: pp. 144, 147.
	1935	*Liostracus linnarssoni* – Asklund & Thorslund: pp. 93, 94.
	1936	*Liostracus linnarssoni* Brögger – Westergård: p. 55.
	1940	*Liostracus linnarssoni* Brögg. – Westergård: p. 62.
	1944	*»Liostracus« linnarssoni* Brögg. – Westergård: p. 35 (table).
	1946	*Liostracus linnarssoni* – Westergård: pp. 7, 12–13 (table), pl. 6, figs. 5a–c, 6–8.
v	1953	*Parasolenopleura linnarssoni* (Brögger, 1878) – Westergård: pp. 26–28, 30, 38 (table), pl. 6, figs. 9–12.
	1953	*Parasolenopleura* cf. *linnarssoni* (Brögger, 1878) – Westergård: pp. 29, 38 (table), pl. 7, figs. 6–8.

non 1964 *Solenopleurina linnarssoni* (Brögger) – Orłowski: p. 551.
1974 *Parasolenopleura linnarssoni* – Martinsson: p. 204.
non 1985 *Solenopleurina linnarssoni* (BRÖGGER, 1879) – Orłowski: pp. 252, 261, text-fig. 1.
1998 *Parasolenopleura linnarssoni* – Geyer: p. 391.
? 2003 *Parasolenopleura* cf. *linnarssoni* (Brögger, 1878)? – Axheimer & Ahlberg: pp. 143, 150, 156, tab. I, fig. 8B.
? 2009 *Parasolenopleura linnarssoni* (Brøgger, 1878) – Weidner & Nielsen: pp. 258, 267.
2014 *Parasolenopleura linnarssoni* (Brøgger, 1878) – Weidner & Nielsen: pp. 63, 65, fig. 52E–J.
2017 *Parasolenopleura linnarssoni* (Brøgger, 1878) – Geyer: pp. 49, 50, 60.
2023 *Parasolenopleura linnarssoni* (Brøgger, 1878) – Weidner et al.: pp. 8, 13, 107–108, tab. 2, fig. 55A–D.

Diagnosis (emended). Species of *Balticoglaucus* with subterminal to terminal node or thorn on the occipital ring.

Description and discussion. Balticoglaucus linnarssoni (Brøgger, 1878) is a species which is relatively frequently reported from various regions in Scandinavia. One might be suspicious that this frequency is partly a result of the fact that the cranidium of the species shows a fairly simple, average condition for ptychoparioid trilobites with a tapering glabella with slightly curved lateral margins; an occipital ring with a median node; a short, convex preglabellar field; an anterior border of moderate breadth (sag., exsag.); moderately broad (tr.) palpebral areas; and short palpebral lobes in a “normal” position. This morphology devoid of any apomorphic characters makes it even difficult to confidently assign the species to a genus.

A further complication is seen in a quite large morphological plasticity of the species, if the concept as developed since Brøgger’s (1978) introduction of the species is accepted. The variation in cephalic dimensions can be partly ascribed to differential preservational conditions as documented in Fig. 87: Specimens preserved in limestones generally have a broader glabella, a slightly shorter (sag.) preglabellar field, and less clearly marked eye ridges, among other differences than those preserved in shaly rock types (Fig. 87A–H, P vs. 87O, Q–U). This appears to be a consequence of dorsoventral compaction. However, differences are also recognisable between specimens from different localities and source strata, which appears to indicate a morphological shift with geographic and stratigraphic divergence.

The morphological variability also hampers the identification of imperfectly preserved specimens. Closely related are *Balticoglaucus linnarssoni*, *B. spinigerus* (Westergård, 1953) and *B. vestgothicus* (Westergård, 1953). *Balticoglaucus linnarssoni* is distinguished by several minor features from the others, but easiest recognition is based on the presence of a subterminal node on the occipital ring rather than a spine as in *B. spinigerus* and *B. vestgothicus*. Differences to the species of *Balticomerope* are discussed above. In particular, the pygidium attributed to *Balticomerope scanica* differs from that of *Balticoglaucus linnarssoni* in its more lenticular rather than subtriangular outline, the broader axis with three rather than four axial rings and the better developed lateral and posterior border.

The figures of cranidia in Linnarsson (1884) suggest that the occipital rings normally lack a node and a spine as suggested by Westergård (1953), who therefore excluded them from the species. Weidner & Nielsen (2023) thus concluded that these may constitute a different (third) species within in this *linnarssoni* clade. However, Linnarsson’s (1883) original specimens in the SGU collection show that this is mainly a preservational artefact: The specimens from shales are preserved as more-or-less compressed internal moulds, which only show relics of the occipital node (Fig. 87R, T). Nonetheless, one specimen (Linnarsson 1884, pl. IV, fig. 5; Fig. 87Q, U) shows a relatively short (sub)terminal occipital spine and can be differentiated from typical specimens of *B. linnarssoni*.

Weidner & Nielsen (2023) also emphasised that their extensive material from Sweden, Norway and Bornholm (Weidner & Nielsen, in prep.) indicates a considerable variation of some of the cranidial features during ontogeny and often also among specimens of similar size (similar to what has been recorded for *Exapinepiphania gregaria*; Fletcher 2005).

Balticoglaucus spinigerus (Westergård, 1953)

Fig. 88

? 1878 *Liostracus aculeatus* – Brøgger: pl. 3, fig. 3.
v * 1953 *Parasolenopleura spinigera* sp. n. – Westergård: pp. 23, 26, 28, 29, 30, 40 (table), pl. 6, figs. 15a–c.
v 1953 *Parasolenopleura vestgothica* sp. n. – Westergård: pp. 28, 29, 40 (table), pl. 6, figs. 16a–c.
v 1953 *Parasolenopleura linnarssoni* (Brögger) or *P. spinigera* sp. n. – Westergård: pl. 7, fig. 5 [only].
1974 *Parasolenopleura spinigera* – Martinsson: pp. 204, 205.
1974 *Parasolenopleura vestgothica* – Martinsson: p. 204.
1991 *Parasolenopleura vestgothica* (Westergård) – Buchholz: p. 220, pl. 2, fig. 5.
1994 *Parasolenopleura spinigera* – Rudolph: p. 211, 216.
1994 *Parasolenopleura vestgothica* Westergård 1953 – Rudolph: pp. 61, 69, 212, 215, tab. 4, pl. 26, fig. 7.
1998 *Parasolenopleura vestgothica* Westergård, 1953 – Geyer: p. 391.
2014 *Parasolenopleura spinigera* Westergård, 1953 – Weidner & Nielsen: pp. 6, 63, 65, fig. 52K–P.
2014 *Parasolenopleura vestgothica* Westergård, 1953 – Weidner & Nielsen: pp. 63, 65.
2017 *Parasolenopleura linnarssoni* Westergård, 1953 – Geyer: pp. 50, 60.
2017 *Parasolenopleura vestgothica* Westergård, 1953 – Geyer: pp. 49, 50.
2019 *Parasolenopleura spinigera* Westergård, 1953 – Høyberget et al.: p. 6, fig. 7C–F.
2023 *Parasolenopleura spinigera* Westergård, 1953 – Weidner et al.: pp. 106, 107, tab. 2, fig. 55A–D.
2023 *Parasolenopleura vestgothica* Westergård, 1953 – Weidner et al.: pp. 106, 107, tab. 2.

Diagnosis (emended). Species of *Balticoglaucus* with terminal spine on the occipital ring.

Discussion. Balticoglaucus spinigerus (Westergård, 1953) was introduced as *Parasolenopleura spinigera*, based only on a single cranidium (Fig. 88A, C, F) from the *Ptychagnostus atavus* Biozone of Oltorp, Västergötland. As it turned out, a second, partial cranidium is on the same piece of rock as the holotype, and this cranidium has a slightly thicker glabella, a faintly more robust occipital spine and a slight forward bent of the preglabellar field on the sagittal line (Fig. 88B). The morphology of this cranidium increases the differenced to *B. linnarssoni* (see above), but still suggests a close relationship to that species.

Parasolenopleura vestgothica Westergård, 1953 closely resembles *Balticoglaucus spinigerus.* It has variously been suggested that both species are synonyms and that the larger occipital spine claimed by Westergård (1953) as a distinguishing character is less clearly developed and thus the differences less evident (e.g., Weidner & Nielsen 2013). In fact, the second cranidium figured herein with its slightly larger spine bridges the morphological gap between the holotypes of *Parasolenopleura spinigera* and *P. vestgothica*, which are even loco- and stratotypic. Hence, there is little doubt that Westergård's type material indeed represents the same species. Moreover, Weidner & Nielsen (2013) referred to specimens from glacial erratic boulders identified as *P. vestgothica* (e.g., Buchholz 1991) which have the characters of *Balticoglaucus spinigerus*.

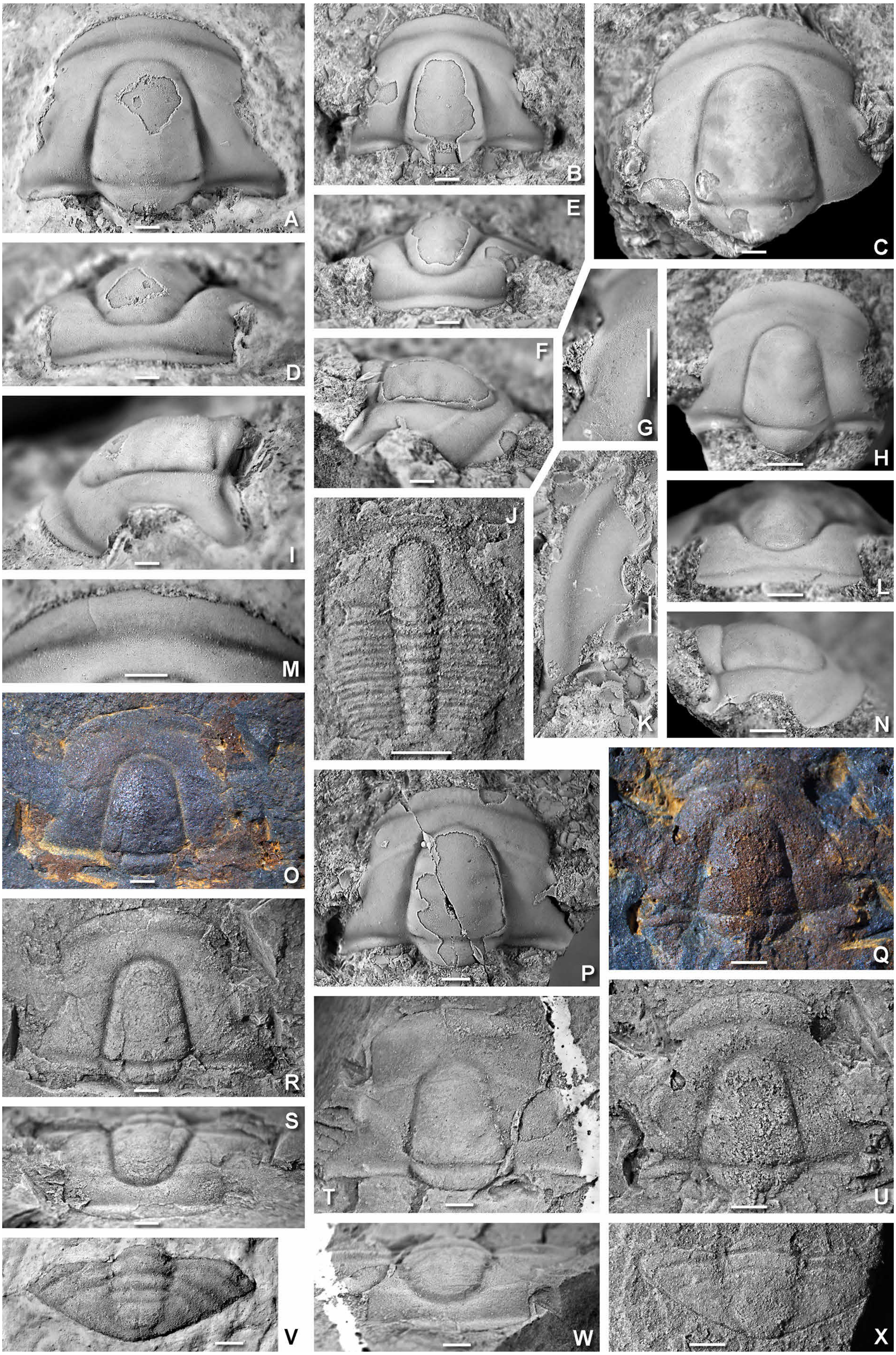
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Fig. 87: **A–T, V, W** *Balticoglaucus linnarssoni* (Brøgger, 1878). **A, D, I, M** SGU 6282a, cranidium with largely preserved cuticle; dorsal (A), anterior (A) and lateral (I) views; M shows magnified view of anterior border, anterior border furrow and preglabellar field showing faint swelling with an lenticular outline proceeding onto the anterior border; Alum Shale Formation, *Ptychagnostus atavus* Zone, Oltorp, Västergötland; original of Westergård (1953, pl. 6, fig. 10a, b), collected by G. von Schmalensee 1878. **B, E, F** SGU 6286c, cranidium partly exfoliated, dorsal (A), anterior (E) and oblique anterolateral (F) views; Alum Shale Formation, *Ptychagnostus atavus* Zone, Oltorp, Västergötland; collected by G. von Schmalensee 1878. **C** SGU 6286a, cranidium with preserved cuticle, dorsal view; Alum Shale Formation, *Ptychagnostus atavus* Zone, Oltorp, Västergötland; original of Westergård (1953, pl. 6, fig. 9). **G, H, L, N** SGU 6281b, cranidium with preserved cuticle; dorsal (H), anterior (L) and oblique lateral (L) views; G shows magnified view of palpebral lobe, palpebral furrow and adjacent areas, note delicate lobe projecting anteriorly from anterior tip of palpebral lobe; Alum Shale Formation, Andrarum, Scania. **J** SGU 5594, incomplete dorsal exoskeleton, internal mould, dorsal view; Alum Shale Formation, Andrarum, Scania; original of Linnarsson (1883, pl. IV, fig. 9), collected by G. von Schmalensee 1877. **K** SGU 6286b, librigena with preserved cuticle, dorsal view; Alum Shale Formation, *Ptychagnostus atavus* Zone, Oltorp, Västergötland; collected by G. von Schmalensee 1878. **O, R, S** SGU 5590a, cranidium, internal mould, dorsal (O, R) and oblique anterior (S) views; Alum Shale Formation, Andrarum, Scania; collected by G. von Schmalensee 1877. **P** SGU 6282b, cranidium, largely exfoliated, dorsal view; Alum Shale Formation, *Ptychagnostus atavus* Zone, Oltorp, Västergötland; collected by G. von Schmalensee 1878. **T, W** SGU 5592, cranidium, internal mould, dorsal (T) and oblique anterior (W) views; Alum Shale Formation, Andrarum, Scania; original of Linnarsson (1883, pl. IV, fig. 7), collected by G. von Schmalensee 1877. **V** SGU 5596, pygidium, dorsal view; Alum Shale Formation, Andrarum, Scania; original of Linnarsson (1883, pl. IV, fig. 11) and Westergård (1953, pl. 6, fig. 12), collected by G. von Schmalensee 1877. **X** SGU 5594, pygidium, dorsal view; Alum Shale Formation, Andrarum, Scania; original of Linnarsson (1883, pl. IV, fig. 10), collected by G. von Schmalensee 1877. **Q, U** *Balticoglaucus* cf. *linnarssoni* (Brøgger, 1878), SGU 5590b, cranidium, internal mould, dorsal views of specimen in natural condition (Q) and coated with ammonium chloride; occipital ring with short terminal spine; Alum Shale Formation, Andrarum, Scania; original of Linnarsson (1883, pl. IV, fig. 5), collected by G. von Schmalensee 1877.
All scale bars 1 mm.

Westergård (1953) did not present a pygidium which he confidently assigned to *Parasolenopleura spnigera*. However, two pygidia are known from the Oltorp samples, both determined as belonging to "*Parasolenopleura linnarssoni* (Brögger) or *P. spinigera* sp. n." One of them (Westergård 1953, pl. 7, fig. 5; Fig. 88D, E, G, H) differs from those known to belong to *Balticoglaucus linnarssoni* and almost certainly represents a pygidium of *B. spinigerus*. It is characterised by a relatively broad and low axis with only two well-marked axial rings (plus an articulating half-ring and a subdivided terminal axial piece) and pleural areas with pleural and interpleural furrows grading into a relatively narrow, undivided lateral and posterior border with an evenly curved outer margin. It should be noted that the first axial ring shows relics of an incomplete fusion, and the cuticle is beset with densely arranged granules of varying sizes. Weidner & Nielsen (2013, fig. 52O, P) figured a pygidium from Bornholm which very much resembles that from Oltorp.

Occurrence. The species was originally recorded from the lower part of the *Ptychagnostus atavus* Zone in the Alum Shale Formation of Västergötland, Sweden. Unverified records suggest that the species ranges from the *Tomagnostus fissus*/*Goniagnostus nathorsti* into the *Hypagnostus parvifrons* and up into the *Ptychagnostus punctuosus* Biozone. In addition to the report by Weidner & Nielsen (2013) from the *Atavus* Zone of Bornholm, Denmark, another report suggests the presence of the species in the basal conglomerate of the Alum Shale Formation at Flagstadelva in Mjøsa area of southern Norway (Høyberget et al. 2019).

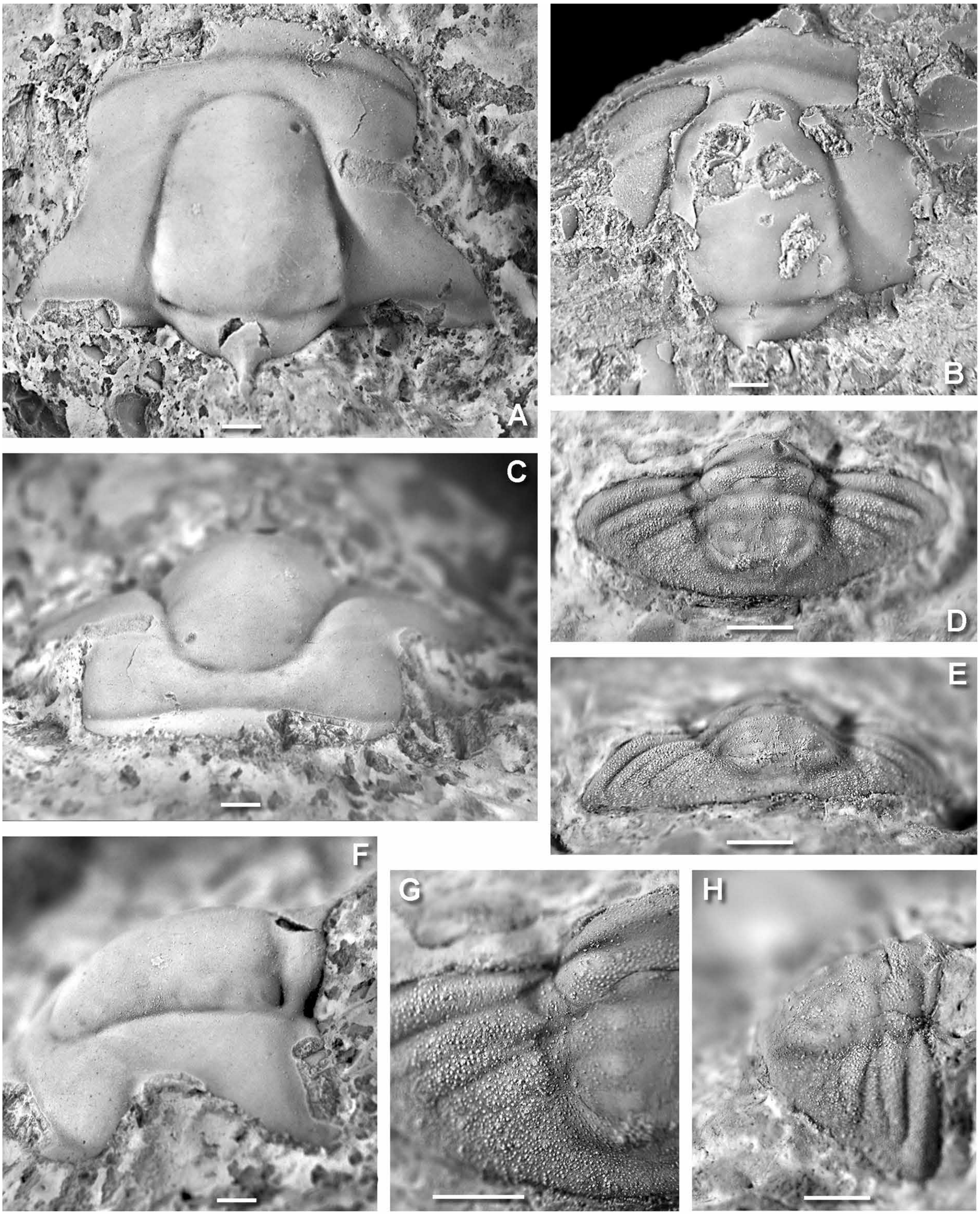

Fig. 88: *Balticoglaucus spinigerus* (Westergård, 1953). **A–C** SGU 6284a, holotype, cranidium with cuticle retained; dorsal (A), anterior (C) and oblique lateral (F) views; original of Westergård (1953, pl. 6, fig. 15a–c). **B** SGU 6284b, previously unfigured partial cranidium, dorsal view; on the same rock fragment as the holotype. **D, E, G, H** SGU 6287, pygidium with preserved cuticle, dorsal (D), oblique posterior, and lateral (H) views; magnified view in G illustrates surface ornamentation consisting of densely spaced granules of varying size; original of Westergård (1953, pl. 7, fig. 5) previously identified as pygidium of *Parasolenopleura linnarssoni* or *P. spinigera*. All specimens from Oltorp East of near Falköping, Västergötland, Sweden, collected by G. von Schmalensee 1878. All scale bars 1 mm.

“*Balticoglaucus*” *peregrinus* (Wallerius, 1930)

Fig. 89

*	1930	*Lonchocephalus peregrinus* n. sp. – Wallerius: pp. 51–52, text-fig. 2.
non	1934	*Agraulos robustus*, sp. nov. – Cobbold in Cobbold & Pocock: pp. 376–377, 378, 390, pl. 43, figs. 6, 7, 8?, 9.
v	1953	*Parasolenopleura*? *peregrina* (Wallerius, 1930) – Westergård: pp. 30–31, 40 (table), pl. 7, fig. 9–12.
	1974	*Parasolenopleura spinigera* – Martinsson: p. 205 [only].
	1998	*Parasolenopleura*? *peregrina* – Geyer: p. 391.
pars	2002	*Parasolenopleura*? *peregrina* (Wallerius) – Rushton & Berg-Madsen: pp. 338, 341.
non	2002	*Parasolenopleura*? *peregrina* (Wallerius) – Rushton & Berg-Madsen: tab. 2, fig. 3a–d. [= *Balticoglaucus*? *robustus*]
	2023	*Parasolenopleura*? *peregrina* – Weidner et al.: p. 121 (table).

Discussion. Balticoglaucus? *peregrinus* is a little known species. The original specimens of Wallerius (1930) appear to be lost so that the revising descriptions by Westergård (1953) and herein are based on the few specimens recollected by A.H. Westergård from the type locality. Representative are two imperfectly preserved cranidia, which are characterised by a tapering glabella with faintly curved lateral margins and a low curvature of its frontal margin causing blunt anterolateral corners and obviously also faint depressions immediately posterior to them; an occipital ring with a very long, posteriorly directed occipital spine; narrow palpebral areas of moderate convexity surmounted distinctly by the raised glabella; moderately long palpebral lobes in a subcentral position in respect to the length axis of the cephalon; eye ridges that are obliquely rearward directed, but commence at an anterior position near the anterolateral corners of the glabella; a broad, convex preglabellar field; a broad, convex anterior border; and moderately well impressed anterior border furrow with a medially located shallower segment.

A librigena which was collected from the same locality and stratum as the cranidia fits well to the suture of the cranidium (Fig. 89C). It is characterised by a wide genal field with a long anterior branch of the suture and a relatively broad (tr.) lateral margin. The genal corner extends into a moderately long, obliquely abaxially directed genal spine.

A pygidium collected together with the other specimens may represent the pygidium of the species (Fig. 89E, H, I). It has a subtrapezoidal outline with a low curvature of its posterior margin. The axis is quite short, broader than long, with only one clearly defined axial ring plus an articulating half-ring and a broad, faintly bilobate terminal axial piece. Posterior to the axis is a low, apparently subtriangular torus that covers more than two-thirds the distance to the posterior margin of the pygidium.

The poor preservation of the pygidium does not allow the recognition of details on the pleural areas, which seem to be almost smooth. Recognisable is a moderately prominent rib along the anterior border. No lateral and posterior borders are identifiable, but appear to have not been developed or defined in any way.

The proportions and also the topography of the cranidium agree fairly well with *B. linnarssoni* and *B. spiniferus* as the quintessential species of *Balticoglaucus* n. gen. However, the eye ridges commence more anteriorly this in those species, the palpebral areas are less dipping laterally, and the anterior part of the cranidium is distinctly extended. The pygidium differs considerably from those of *B. linnarssoni* and *B. spinigerus*. Nevertheless, they can be derived from a common basic concept seen in the *Balticomerope*–*Balticoglaucus* clade.

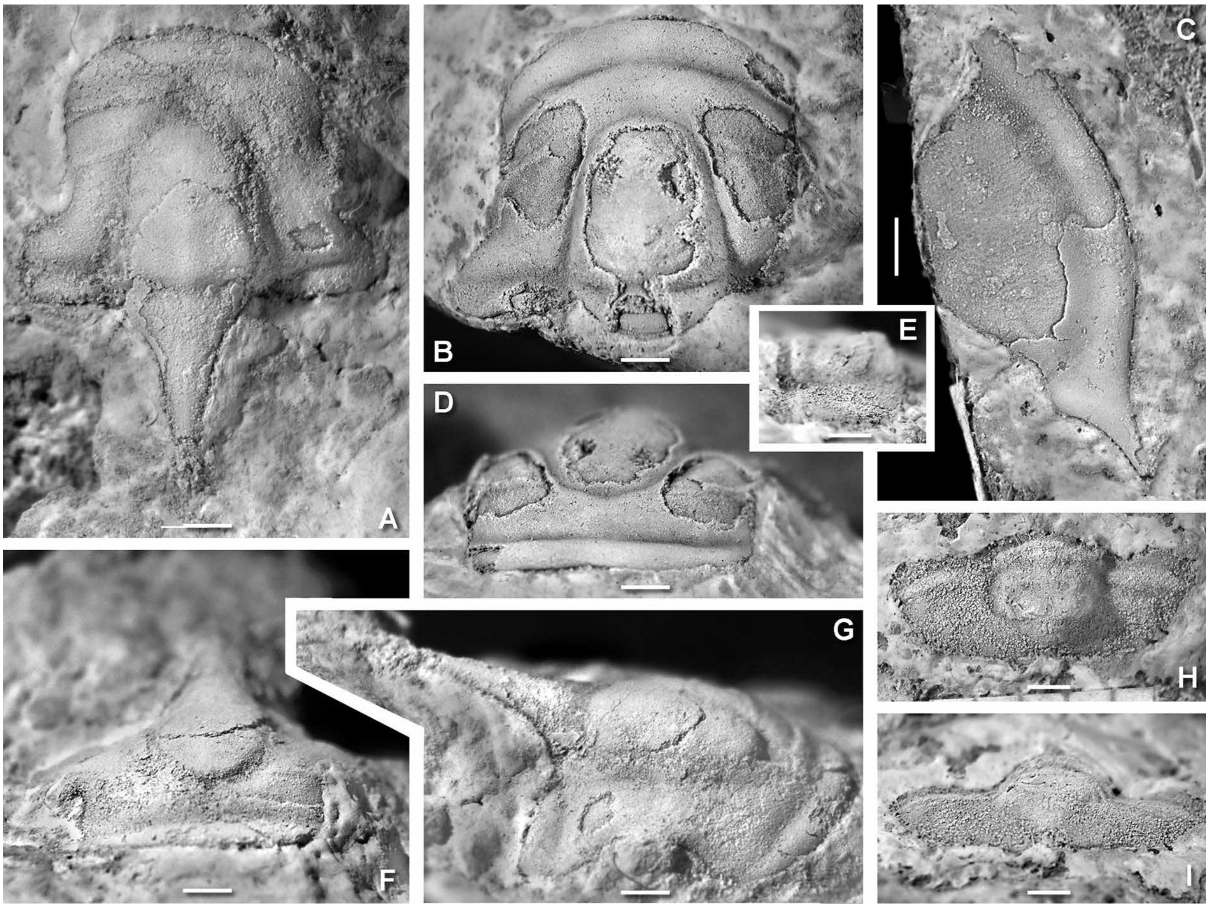

Fig. 89: "*Balticoglaucus*" *peregrinus* (Wallerius, 1930). **A, F, G** SGU 6290, cranidium, largely exfoliated; dorsal (A), anterior (F) and oblique lateral (G) views; original of Westergård (1953, pl. 7, fig. 9). **B, D** SGU 6291, incomplete cranidium, partly exfoliated; dorsal (B) and anterior (D) views; original of Westergård (1953, pl. 7, fig. 10a. b). **E** SGU 6292a, librigena, partly exfoliated; oblique dorsal view; original of Westergård (1953, pl. 7, fig. 11). **E, H, I** SGU 6293, incomplete cranidium, partly exfoliated; lateral (E), dorsal (H) and posterior (I) views; original of Westergård (1953, pl. 7, fig. 12).
All specimens from the *Ptychagnostus punctuosus* Zone at Byklev, Hunneberg, Västergötland, Sweden, collected by A. H. Westergård 1930. All scale bars 1 mm.

Occurrence. The type material of this species was collected from the *Ptychagnostus punctuosus* Zone of the Alum Shale Formation, from the uppermost *orsten* layer at Byklev, Hunneberg, Västergötland.

Genus *Solenoparia* Kobayashi, 1935

Type species. Ptychoparia (*Liostracus*) *toxeus* Walcott, 1906a; from the *Inouyops* Zone of the Hsuchuang Formation, Shandong Province, northern China.

Discussion. Solenoparia Kobayashi, 1935 was founded on *Ptychoparia* (*Liostracus*) *toxeus* Walcott, 1906a from the *Inouyops* Zone of the Hsuchuang Formation of Shandong, North China. Other species assigned to the genus occur in the upper part of the Hsuchuangian and the lower and middle part of the Changhian Stage of the North China Platform, corresponding to the upper/late Wuliuan to lower/early Drumian (Geyer 2018). The type species is consistently dealt with in the previous literature as *Solenoparia toxeus* although the species name needs to be declined to a female ending. Accordingly, the correct species name is *Solenoparia toxea* (Walcott, 1906).

Solenoparia toxea possesses a fairly typical PL-type cephalon with a considerable overall convexity as illustrated by the holotype (e.g., Walcott 1913, pl. XIX, fig. 10, refigured in Zhang & Jell 1987, pl. 39, fig. 1). The species also shows a parafrontal band, which causes a slight broadening of the frontal lobe so that the outline of the glabella is not perfectly parabolic. In addition, the species has a slightly shallower median sector of the anterior border furrow. This morphology and also that of very similar species assigned to *Solenoparia* elucidate evolutionary pathways among the Solenopleurinae, with a transition from SP- to PL-type morphology and the doming of the cephala. *Solenoparia* can be seen as an end-link of a series leading from *Balticomerope* n. gen. via *Balticoglaucus* n. gen. to *Solenoparia*. The supposed reason for this transition of the dorsal morphology has been discussed above as the enlargement of the anterior part of the alimentary canal below the dorsal exoskeleton.

Solenoparia lilia (Walcott, 1906b) from the *Metagraulos* Zone of the Hsuchuangian is a species based on only poorly preserved cranidia, which seems to have a similar morphology as *S. toxea*.

Solenoparia talingensis (Dames, 1883) (synonym: *Ptychoparia* (*Liostracus*) *subrugosa* Walcott, 1906a) has a quite strongly convex glabella with parabolic outline, broad and deep axial furrows, and palpebral areas with a moderate convexity in transverse profile with the most elevated part slightly adaxial to the centre so that it provides a typical PL-type morphology. The preglabellar field is moderately broad and moderately convex, the anterior border moderately prominent and lies below the preglabellar field (e.g., Zhang & Jell 1987, pl. 39, figs. 9, 10, pl. 40, figs. 1, 2). This species is clearly of the SP-type and shows characters that are fairly typical for *Exapinepiphania* n. nom.

Solenoparia agno (Walcott, 1906a) from the *Taitzuia-Poshania* Zone of the Changhia Formation has similar characters as *S. talingensis* and also represents a typical SP-type morphology.

Solenoparia trogus (Walcott, 1906a) from the *Amphoton* Zone of the Changhia Formation is an insufficiently known species, which certainly cannot be assigned correctly to *Solenoparia*.

Solenoparia parva (Linnarsson, 1879)

Fig. 90A–R, T–W

v *1879 *Selenopleura parva* n. sp. – Linnarsson: pp. 5, 14–15, pl. I, fig. 16–20.
v 1883 *Selenopleura parva* Linrs. – Linnarsson: pp. 7, 25.
1896 *Solenopleura parva Linnarsson* – Pompeckj: p. 546.
1902 *Solenopleura parva* Lnrs. – Grönwall: pp. 21, 23, 151–152, 169 (table).
1929 *Solenopleura parva* Linnarsson – Strand: pp. 320, 321, 328, 353, pl. II, fig. 21.
1931 *Solenopleura parva*, Linnarsson – Lake: p. 139.
1936 *Solenopleura parva* Linnarsson – Westergård: p. 60.
1942 *Solenopleura parva* Linnarsson – Poulsen: pp. 214, 226.
1944 *Solenopleura parva* (Linnarsson) – Westergård: p. 35.
1946 *Solenopleura parva* – Westergård: p. 12.
v 1953 *Solenopleura parva* Linnarsson, 1929 – Westergård: pp. 11, 12–13, 26, 40 (table), pl. 2, figs. 11a–c, 12, 13.
1957 *Solenopleura parva* Linnarsson – Rasetti: p. 965.
1957 *Jincella parva* (Linnarsson) – Šnajdr: p. 241.
1958 *Jincella parva* (Linnarsson) – Šnajdr: p. 197.
1963 *Jincella parva* – Poulsen: p. 9.
1965 *Solenopleura parva* – Chernysheva: p. 169.
1966 *Jincella parva* (Linnarsson) – Poulsen: p. 119.
1994 *Jincella parva* (Linnarsson 1879) – Rudolph: pp. 25, 27, 33, 55, 78, 79, 203, 204–205, 227, 264, text-fig. 97, tab. 12, tab. 15, pl. 25, figs. 6, 7.
1998 “*Solenopleura parva*” – Geyer: p. 391.
2002 *Jincella parva* (Linnarsson, 1879) – Schöning: pp. 75, 76, figs. 2, 3.
? 2003 *Solenopleura parva* Linnarsson, 1879 – Axheimer & Ahlberg: pp. 143, 152, 153, 156, fig. 8D, 8E.

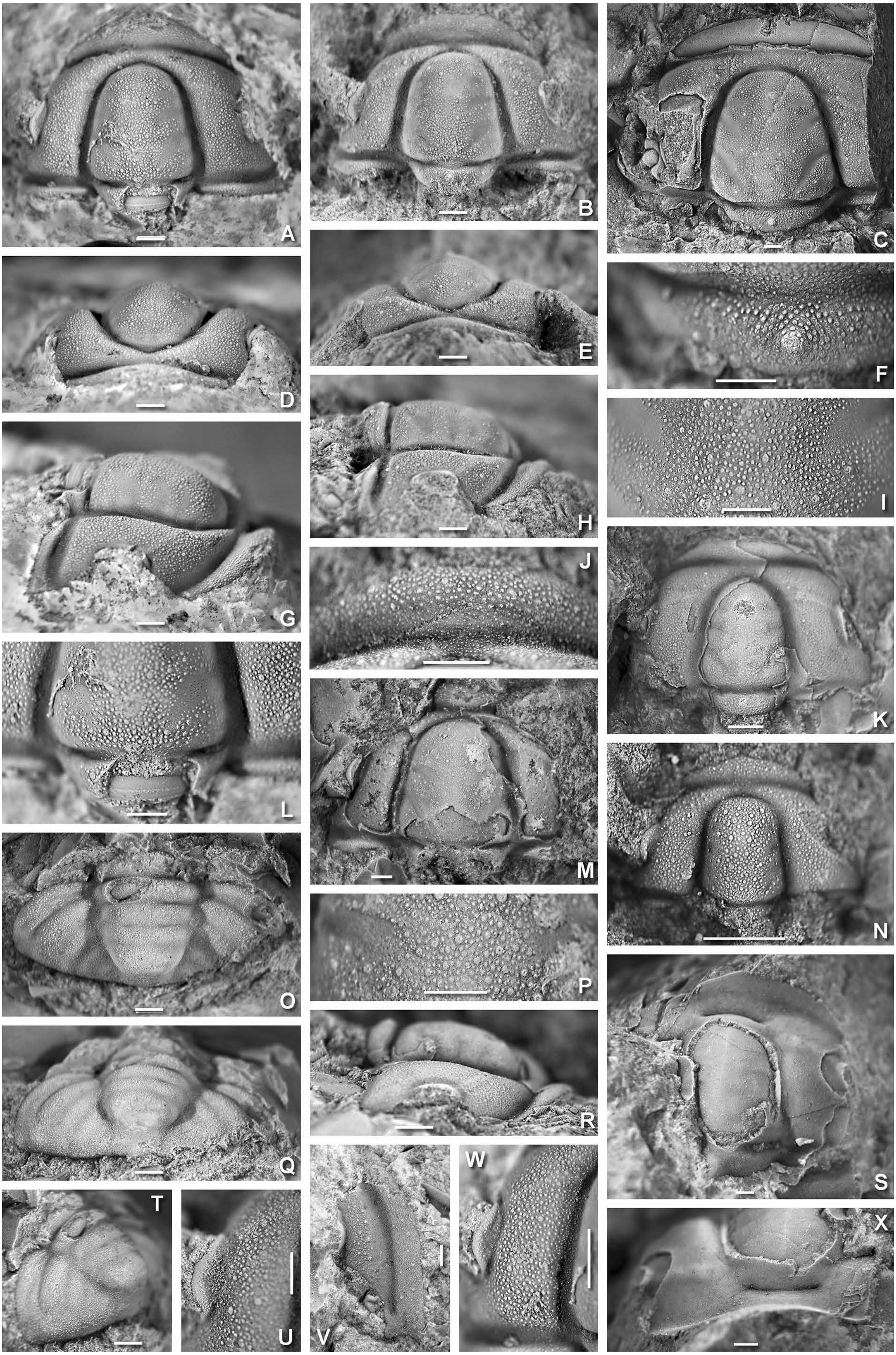
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Fig. 90: **A – R , T – W** *Solenoparia parva* (Linnarsson, 1879). **A, D, F, L, W** SGU 4521, lectotype (termed "holotype" in Westergård 1953), middle-sized cranidium with preserved cuticle, dorsal (A), anterior (D) and oblique lateral (G) views; magnified view (in L) of the posterior part of glabella an occipital ring shows granulation with different sizes of granules and smooth lateral glabellar furrows as well as exposed ventral doublure of occipital ring with low ridge that served as a stopping device for the articulating half-ring of the first thoracic segment; magnified view of left palpebral area and palpebral lobe in W illustrates narrow palpebral lobes with less curved anterior part of palpebral lobe, spindle-shaped palpebral furrow and surface ornamentation; from Gislöv near Brantevik, Scania, original of Linnarsson 1879, pl. I, fig. 17? and Westergård 1953, pl. 2, fig. 11a, b. **B, E, H, J, U** SGU 6260a, middle-sized cranidium with preserved cuticle, dorsal (B), anterior (E) and lateral (H) views; magnified view of anterior part of the cranidium (in J) illustrates slightly sunken, narrow preglabellar field, different sizes of granules on the slightly ascending anterior border and a growth stop on the posterior part of the border probably resulting from a healed injury; magnified view of left palpebral area and palpebral lobe in U illustrates narrow palpebral lobes with less curved anterior part of palpebral lobe and surface ornamentation; from Andrarum, Scania; original of Westergård 1953, pl. 2, fig. 12, collected by G. von Schmalensee 1877. **C, F, I** SGU 9755a, incomplete large cranidium with preserved cuticle and very small cranidium of immature individual on the left (SGU 9755d, see N), dorsal view (B), magnified view of occipital ring in F showing prominent occipital node with subcircularly arranged, lengthened granules, and magnified view of mid-glabella (I) showing small and slightly larger simple granules as well as interspersed larger granules with a central tube; from Andrarum, Scania, collected by G. von Schmalensee 1877. **K, R** SGU 9757, cranidium of moderate size, glabella and right part exfoliated, dorsal (K) and lateral (R) views; from Andrarum, Scania, collected by G. von Schmalensee 1877. **M, P** SGU 6260b, incomplete large cranidium, partly exfoliated, dorsal view in M, detail of glabella in P illustrating surface ornamentation; from Andrarum, Scania, collected by G. von Schmalensee 1877. **N** SGU 9755d, small cranidium with preserved cuticle, dorsal view from Andrarum, Scania, collected by G. von Schmalensee 1877. **O, Q, T** SGU 4522, pygidium with largely preserved cuticle, dorsal (O), oblique posterior (Q) and oblique posterolateral (T) views; from Kiviks-Esperöd, Scania, original of Linnarsson 1879, pl. I, fig. 20. **V** SGU 6261b, librigena, dorsal view; from Andrarum, Scania, from Kiviks-Esperöd, Scania, original of Westergård 1953, pl. 2, fig. 13. **S, X** *Parasolenopleura aculeata* (Angelin, 1851), SGU 6261a, partial cranidium, partly exfoliated, dorsal (S) and oblique anterior (X) view; note sharp furrow that defined anterior margin of glabella and faint swellings at anterolateral corners of glabella; from Kiviks-Esperöd, Scania. All specimens from Exsulans Limestone Bed, Alum Shale Formation, upper *Ptychagnostus gibbus* Zone. All scale bars 1 mm.

2007	*Solenopleura parva* – Nielsen & Schovsbo: p. 84.
2009	*Solenopleura parva* – Weidner & Nielsen: pp. 253, 254.
2014	*Solenopleura parva* – Weidner & Nielsen: pp. 6, 61.
2016	*Solenoparia parva* (Linnarsson, 1879) – Yuan et al.: p. 224.
2017	"*Solenopleura parva*" – Geyer: p. 50.
2023	*Solenopleura*? *parva* Linnarsson, 1879 – Weidner et al.: pp. 12, 104, 121 (table).

Diagnosis (emended). Species of *Solenoparia* with transverse glabellar width across L1 in adult individuals of ca. 46–50 percent width across centre of palpebral lobes; glabella slightly tapering forward, with nearly straight margins anterior to L1; frontal lobe with apparent faint acute tip due to coalescent parafrontal band sections; palpebral lobes moderately long, gently curved in the posterior two-thirds of their length, but almost straight in the anterior third; anterior border distinctly convex; anterior border furrow with short (tr.) shallow section in the centre; exterior of the cuticle covered by quite numerous granules of different diameters.

Discussion. The species first described as *Selenopleura parva* by Linnarsson (1879) is a key for understanding part of the morphological evolution in the Solenopleurinae. The species has a PL-type cranidium that shows a considerably general doming in transverse profile, with the adaxial margins of the palpebral areas being clearly more elevated than the abaxial parts. The margins of the fixigenae to the axial furrow are marked by a relatively steep drop (Fig. 90D, E). It should be noted that this morphology is perfectly seen in specimens of adult individuals, whereas cranidia of immature individuals have more deeply incised axial furrows and palpebral areas with a more strongly developed transverse convexity. A gradient from this almost SP-type to the PL-type topography can be recorded (Fig. 90K, N).

Solenoparia parva has a glabella with a subparabolic outline, in which the lateral margins anterior to L1 are nearly straight. The frontal margin of the glabella is quite well-rounded on the first glance, but close examination shows feeble variations with apparent oblique parts resulting in a faintly acute tip (Fig. 90A, M) or even a nearly subtruncate central section (Fig. 890C, N). This variation is partly caused by changes during ontogeny, but also by a variably developed parafrontal band. The parafrontal band is sometimes composed of two anterolateral threads, which coalesce to a slightly broader (sag.), subtriangular low knot directly in front of the tip of the glabella and forces the anterior processes of the axial furrows to proceed and meet at a minute angle (Fig. 90A, B). The parafrontal band is sometimes developed as an isolated low lobe, which appears as a swelling in the preglabellar furrow (Fig. 90C). The anterior border furrow has a gentle subeven curvature in dorsal view, but houses a faint swelling for almost one-third of its sagittal stretch on the cranidium. This raise obviously corresponds to anatomical structures beneath the dorsal skeleton, and some specimens appear to indicate that this structure (which is supposedly related to a forward expansion of the digestive tract) proceeds as far as to almost the centre of the anterior border (Fig. 90J). This anterior border is slightly crescentic, with a considerably decrease in exsagittal width towards the facial suture. In frontal view, the anterior margin of the border shows a slight curvature which is almost subangular in some specimens (Fig. 90E).

The breadth of the preglabellar field varies considerably among the individuals. It is usually of about half the sagittal breadth of the anterior border on the sagittal line. Sometimes it is relatively broad and gains almost the sagittal width of the anterior border in front of it (Fig. 90C), but occasionally it is reduced to a thin, sunken thread (Fig. 90B).

Remarkable is the morphology of the palpebral lobes. These are of more-or-less moderate length and gently curved in the posterior two-thirds of their extension, but almost straight in the anterior third and tend to show a delicate abaxial swing at the anterior tips. The palpebral furrow has a straight adaxial margin for its posterior two-thirds turning into an abaxial bent anteriorly, whereas the abaxial part is more curved which causes a slightly inflected sigmoidal area (Fig. 90U, W).

The exterior of the cuticle is covered by numerous granules of different diameters, the largest of which show a central tube (Fig. 90I, L, P). As the granules do not grow markedly in relative size during ontogeny, the smallest specimens appear to have a coarser surface ornamentation than the largest ones (Fig. 90N vs. 90C). The occipital ring has a moderately large tubercle around which the granules are slightly laterally extended and elliptical or almost scale-like in shape (Fig. 90F).

Linnarsson (1879) assigned a pygidium (figured on his pl. I, fig. 20) tentatively to the species, and this caveat was repeated by subsequent authors or the pygidium assigned tentatively to *Erratojincella munsteri*. This pygidium has been located and re-examined in the course of this study (Fig. 90O, Q, T). It differs clearly from that assigned to *Erratojincella munsteri* and therefore is considered to represent the only known pygidium of *S. parva*.

Occurrence. Strand (1929) introduced a species based on material from the Exsulans Limestone Bed. The species has meanwhile been recorded from the Exsulans Limestone, *Ptychagnostus gibbus* Zone, of Scania, Öland and Jämtland in Sweden, the Oslo and Mjøsa areas in Norway, and from the island of Bornholm, Denmark. Rudolph (1994) reported it also from erratic boulders of the *Tomagnostus fissus* Conglomerate in Holstein, and Schöning (2002) from the Osnabrück area, Niedersachsen, Germany.

Subfamily Solenopleuropsinae Angelin, 1854

Genus *Badulesia* Sdzuy, 1968

Type species. Liostracus granieri Thoral, 1935; from the Coulouma Formation of the Montagne Noire, southern France (by original designation).

Discussion. Badulesia was introduced as a genus by Sdzuy (1968), who selected *Liostracus granieri* Thoral, 1947 as the type species. The genus depicts a progressive development of ostentatious ridges on the palpebral area and, in later species, also on the glabella which start to transmute into series of pustules. This arrangement of papillate pustules characterises the species of *Pardailhania*. Degradation of the serial arrangement of the pustules into more randomly arranged elevated granules is recognised in the genera *Solenopleuropsis* and *Manublesia* (see Álvaro & Vizcaïno 2001). However, taxa without the spectacular ridges and papillae on the genae and glabella are also known suggesting that *Velieuxia* Courtessole, 1973 and *Liosolenopleura* Thoral, 1948 as well as the proto-*tenera* forms of *Badulesia* are also members of the Solenopleuropsinae.

The demarcation of the genus *Badulesia* is difficult and a matter of approaches to traditional, or non-objective and non-phylogenetic generic concepts. The most striking feature seen in “typical” species of *Badulesia* are the conspicuous ridges on the genae, but these cannot be accepted as apomorphic characters as they vary tremendously even among individuals of obviously the same species. *Badulesia ouangondiana* (Hartt in Dawson, 1868) is certainly a direct ancestor of *B. tenera* (Hartt in Dawson, 1868), or at least the *tenera* plexus, and could be regarded as separable on generic level. However, early specimens of *B. tenera* from the Iberian Chains in Spain and also from subsurface strata in Saxony, Germany, occasionally exhibit partially developed fixigenal ridges. Sometimes, these ridges are totally absent on one of the palpebral areas. In strata below the initial *B. tenera* onset in Spain, a species identified as *Badulesia* sp. A has been recognised, which lacks any fixigenal ridges. K. Sdzuy (unpubl. data) reconstructed the phylogenetic development of the early *Badulesia* species in a section near the eponymous Badules village in the Iberian Chains, northern Spain. He noted that even rare specimens without any ridges occur in the lowest horizons with *B. tenera*. Sdzuy also reconstructed a complicated pathway to *B. granieri* and *B. paschi* with some regressive development and obvious dead-end branches (clearly less simple than depicted in Sdzuy 1968 and Álvaro & Vizcaïno 2001, fig. 1). Accordingly, the different types of ridges and the changes of their orientation must have formed rapidly. Thus, the presence/absence of such ridges cannot be valued as diagnostic for separation on generic level. Therefore, *B. ouangondiana* must be regarded as a species of *Badulesia*.

The same situation is found in strata of the Delitzsch–Torgau–Doberlug Syncline in Saxony, Germany (e.g., Schmidt 1944, Geyer et al. 2008, Geyer & Elicki 2024). Cores from the Doberlug D IV/1929 borehole include specimens of an apparently proto-*tenera* species or morphotype which was predominantly identified as “*Andrarina quadrata*” by Schmidt (1944). Examples for this “species” are illustrated in Fig. 91. That “species” certainly does not represent an Avalonian species introduced as *Conocephalites quadrata* Hartt in Dawson, 1868 (see below), but also cannot be identified as *Badulesia ouangondiana*. They may be regarded as a new species, but its differentiation from early representatives of *Badulesia tenera* is puzzling and requires a careful statistical analysis. Typical specimens of *Badulesia tenera* from the Doberlug D IV/1929 core are illustrated in Fig. 91. Large cranidia of adult individuals of that species are differentiated by having a narrower anterior border, better developed crests on the genae and a notable arcuation of the anterior cephalic margin on the sagittal line. However, cranidia of juvenile individuals generally lack distinct ridges on the palpebral lobes and the genae.

Specimens identified as *Badulesia* sp. A from various Spanish sections (e.g., Álvaro & Vizcaïno 2001, pl. 1, fig. 1) were regarded as in fact representing *B. ouangondiana*. However, they clearly differ in having a narrower (sag., exsag.) anterior border that is almost blade-like in internal moulds, and clearly broader fixigenae, and certainly represent a different species. Subsequently, Chirivella Martorell et al. (2020) synonymised all of the relevant species, or varieties described from New Brunswick (*Conocephalites orestes* Hartt in Dawson 1868; *Conocephalites ouangondianus* Hartt in Dawson, 1868; *Conocephalites aurora* Hartt in Dawson, 1868; *Conocephalites quadratus* Hartt in Dawson, 1868) with *Calymene aculeata* Angelin, 1851 so that this species – as *Parasolenopleura aculeata* – was claimed to occur in the *Eccaparadoxides asturianus* Zone and in the basal parts of the *Badulesia tenera* Zone of the Spanish Mansilla Formation. However, *Parasolenopleura aculeata* (redescribed in detail above) differs in several characters from *B. ouangondiana* and most of the other species and is considered as a species which cannot be assigned to even the same subfamily.

Badulesia tenera **(Hartt *in* Dawson, 1868)**

Fig. 91

Material used in this present study. 17 dorsal exoskeletons under GSB X4735 (illustrated in Schmidt 1944, pl. 22, fig. 18a, b; from unknown depth); GSB X4736 (illustrated in Schmidt 1944, pl. 22, fig. 19; from unknown depth); GSB X4737 (illustrated in Schmidt 1944, pl. 22, fig. 20; from unknown depth); GSB X4738 (illustrated in Schmidt 1944, pl. 23, fig. 1a, b; from unknown depth); GSB X4739/1 and X4739/2 (illustrated in Schmidt 1944, pl. 23, fig. 2a, b; from unknown depth); GSB X13391 (from depth 194 m); GSB X13397/1, X13397/2 and X13397/3 (from unknown depth); GSB X13409 (from unknown depth); GSB X13411 (from unknown depth); GSB X13412/1 (from depth 189 m); GSB X13417/1 (from depth 189 m), GSB X13429/2, X13429/3 and X13429/4 (from unknown depth); four cephala under GSB X4733/4 (from depth 187 m), GSB X12946/1 (from depth 187 m), GSB X13426 (from depth 179 m) and GSB X13428 (from depth 179 m); 55 cranidia under GSB X4743 (illustrated in Schmidt 1944, pl. 23, fig. 6; from depth 198 m); GSB X4744 (illustrated in Schmidt 1944, pl. 23, fig. 7; from depth 190 m); GSB X4747 (illustrated in Schmidt 1944, pl. 23, fig. 9a–c; from depth 189 m); GSB X12998/1 (from depth 195 m); GSB X12999/5 (from unknown depth); GSB X13382/1, GSB X13382/2 and GSB X13382/3 (from depth 190 m); GSB X13383 (from depth 186 m); GSB X13384 (from unknown depth); GSB X13385/1 and X13385/4 (from depth 189 m); GSB X13393 (from depth 195 m); GSB X13395/1 and X13395/2 (from depth 189 m); GSB X13396 (from unknown depth); GSB X13400 (from unknown depth); GSB X13403/1 and X13403/3 (from depth 190 m); GSB X13423/1 and X13423/2 (both from depth 190 m); GSB X13406 (from depth 189 m); GSB X13407 (from unknown depth); GSB X13408/1 and X13408/2 (from depth 191 m); GSB X13410 (from depth 193 m); GSB X13415 (from depth 195 m); GSB X13416 (from unknown depth); GSB X13418/1, X13418/2, X13418/3 and X13418/6 (from depth 188 m); GSB X13420/1, X13420/2 and X13420/3 (from depth 186 m); GSB X13421 (from unknown depth), GSB X13422/1, X13422/2, X13422/3 and X13422/4 (from depth 184 m); GSB X12423/1 and X13423/2 (from depth 190 m); GSB X13424/3 (from unknown depth); GSB X13427 (from depth 179 m); GSB X13432/1, X13432/2, X13432/3, X13432/4 and X13432/7 (all from unknown depth); GSB X13439 (from depth 184 m); GSB X13441/1 and X13441/2 (from depth 190 m); nine librigenae under GSB X13385/2 (from depth 189 m); GSB 13386 (from unknown depth); GSB 13388 (from depth 198 m); GSB 13389 (from unknown depth); GSB X13399/1 and X13399/2 (from depth 190 m); GSB X13420/4 (from depth 186 m); GSB X13424/1 (from unknown depth); GSB X13432/5 (from unknown depth); two thoraces under GSB X13385/3 (from depth 189 m), thorax under GSB X13402 (from depth 198 m); thoracic segments under GSB X13403/2 (from depth 190 m); thorax with attached pygidium under GSB X4740 (illustrated in Schmidt 1944, pl. 23, fig. 43a, b; from depth 186 m) and GSB X13429/1 (from unknown depth); articulated thorax with attached pygidium under GSB X13432/6 (from unknown depth) and GSB X13431 (from unknown depth); five pygidia under GSB X06239/9 (from depth 186 m), GSB X13390/1 (from depth 190 m), GSB X13418/4 and X13418/5 (from depth 188 m), GSB X13430 (from depth 189 m).

Material tentatively assigned to Badulesia tenera: Thoracic segments under GSB X13412/2 (from depth 189 m), GSB X13420/5 (from depth 186 m) and GSB X13425/1, X13425/2 and X13425/3 (from unknown depth).

Locality and strata. All specimens from core of D IV/1929 drillhole near Kirchhain in the Delitzsch–Torgau–Doberlug Syncline, northern Saxony. *Badulesia tenera* Zone, Delitzsch Formation, Caesaraugustan Stage of West Gondwana, Drumian Stage.

Discussion. A plethora of specimens with a rather typical *Badulesia tenera* morphology occurs in strata of the core of the D IV/1929 drillhole near Kirchhain. A number of them have been illustrated in Schmidt (1944) under the name *Andrarina tenera*. Selected specimens with particular characters are shown in Fig. 91. These specimens of the quite well-known species merit supplementary remarks on various aspects.

Typical cranidia of adult individuals show a distinctly forward tapering glabella with a relatively narrow front with a low arcuation of the anterior margin (Fig. 91A–E). The front of the glabella appears to be formed by a weakly curved lobe which creates delicate lateral extensions (e.g., Fig. 91A, B). The subtruncate front of the glabella is also seen in cranidia of immature individuals (Fig. 91J–L, N–P, S, T, V, W). Some of the small cranidia exhibit even a pair of anterolateral low bulbs (Fig. 91L, O, P, T).

The preglabellar field is usually low, almost flat, but well-preserved specimens indicate that a slight swelling was originally developed, which is formed like a low plectrum in juveniles (Fig. 91O), but like a hump in large cephala (Fig. 91A). A slight longitudinal extension of the preglabellar field during growth is responsible for a forward shift of the swelling in large specimens and leads to a slight arcuation of the anterior border on the sagittal line (Fig. 91A, B, G) and a low curvature of the anterior cephalic margin in anterior view (Fig. 91R).

Dorsoventral compaction frequently led to deformation or fractures with a faint offset of the different sections along the fracture lines (Fig. 91B, F, V). Their location appears to correspond with the position of the rostral plate on the ventral side. The hypostome is occasionally portrayed by impressions printed on the glabella (Fig. 91J).

The typical set of ridges on adult cranidia of *Badulesia tenera* in the D IV/1929 drill-core consists of (a) a prominent gently curved crest along the eye ridge and palpebral lobe; (b) a prominent crest on the proximal part of the palpebral area parallel to the lateral margin of the glabella; and (c) a ridge nearly normal to the length axis that commences approximately at the posterior end of (b) and curving forward from posterior to the posterior tips of the palpebral lobes, terminating almost abaxially of the posterior tips of the eyes (Fig. 91F, I). A very short branch extends adaxially from the fusion point of (b) and (c), and this node marks the initial growth point of the ridges as indicated in juveniles with ridges *in statu nascendi* (Fig. 91K, N, O).

A non-elevated crest is formed in large cephala in form of a sharp blade that marks the margin of the glabella to the occipital furrow, with a slightly overhanging blade (Fig. 91C, M, R).

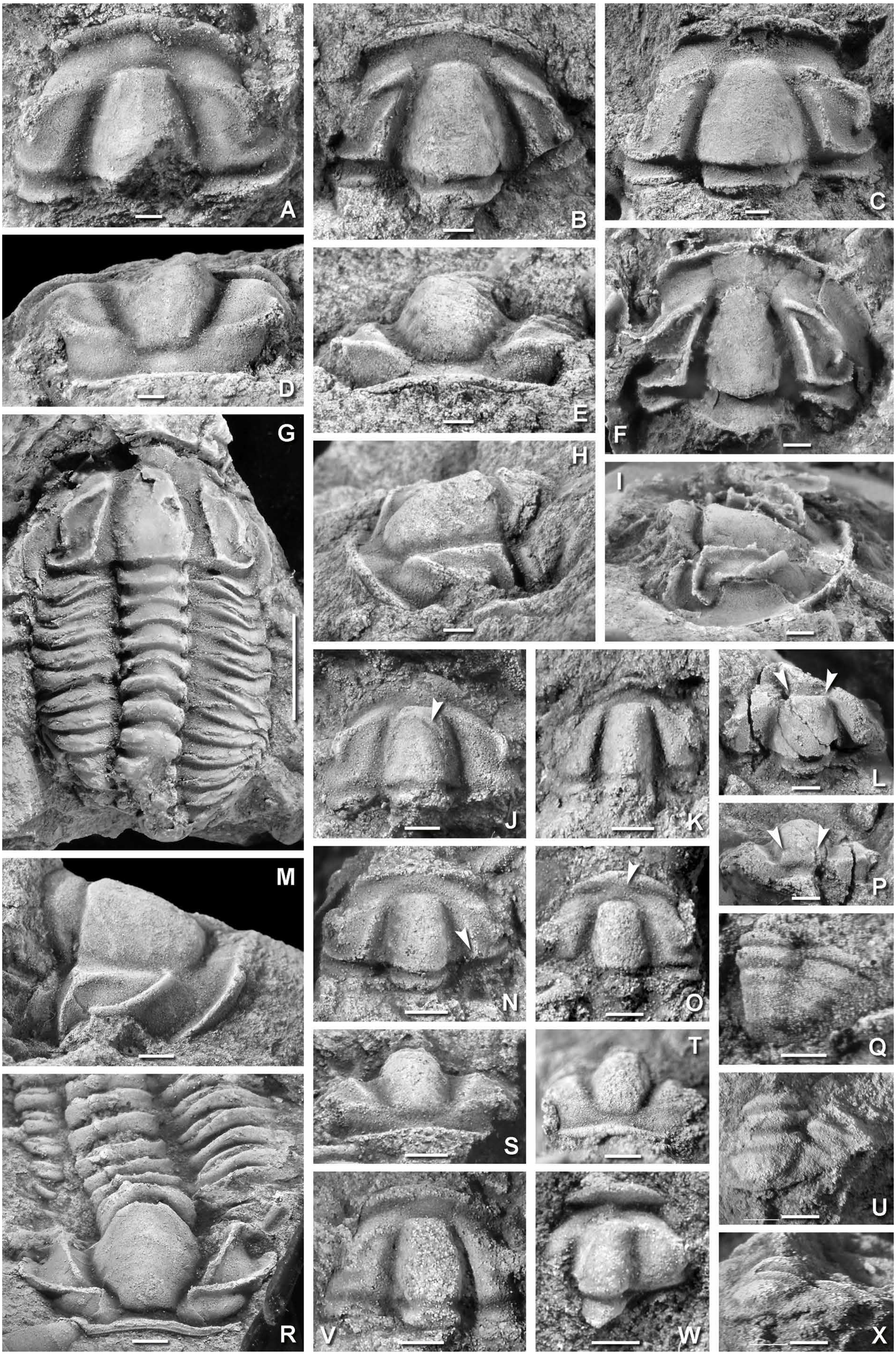
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Fig. 91: *Badulesia tenera* (Hartt in Dawson, 1868). **A, D** GSB X13432/1, incomplete cranidium, internal mould, dorsal (A) and oblique anterior (D) views. Doberlug IV/1929 drill core, from unknown depth. **B, E, H** GSB X13408/1, incomplete cranidium, internal mould, dorsal (B), anterior (E) and oblique anterolateral (H) views. Doberlug IV/1929 drill core, depth 191 m; original of Schmidt 1944, pl. 23, fig. 8. **C** GSB X4747, incomplete cranidium, internal mould, dorsal view. Doberlug IV/1929 drill core, depth 189 m; original of *Andrarina tenera* in Schmidt 1944, pl. 23, fig. 9a–c. **F, I** GSB X4742, cranidium, latex cast of external mould, dorsal (F) and oblique lateral (I) views. Doberlug IV/1929 drill core, depth 198 m; original of *Andrarina tenera* in Schmidt 1944, pl. 23, fig. 5a, b. **G** GSB X4738, dorsal exoskeleton, internal mould, dorsal view. Doberlug IV/1929 drill core, from unknown depth; original of *Andrarina tenera* in Schmidt 1944, pl. 23, fig. 1a, b. **J** GSB X13432/7, incomplete cranidium, internal mould, dorsal view, with impression of hypostome from ventral side (arrow). Doberlug IV/1929 drill core, from unknown depth. **K** GSB X13406, incomplete cranidium, internal mould, dorsal view. Doberlug IV/1929 drill core, depth 189 m. **L, P** GSB X13398, incomplete fractured cranidium, internal mould, dorsal (L) and anterior (P) views; arrows point to low knobs developed at the anterolateral corners of the frontal lobe. Doberlug IV/1929 drill core, from unknown depth. **M** GSB X12998/1, incomplete cranidium, internal mould, oblique lateral view. Doberlug IV/1929 drill core, depth 195 m; original of Schmidt 1944, pl. 23, fig. 9b. **N, S** GSB X13383, incomplete cranidium, internal mould, dorsal (N) and anterior (S) views; arrow points to oblique adaxially directed short crest. Doberlug IV/1929 drill core, depth 186 m. **O, T** GSB X13432/3, incomplete cranidium of immature individual, internal mould, dorsal (O) and anterior (T) views. Doberlug IV/1929 drill core, from unknown depth. **Q** GSB X13390/1, partial pygidium, latex cast of internal mould, dorsal view. Doberlug IV/1929 drill core, depth 190 m. **R** GSB X13397/1, incomplete dorsal exoskeleton, latex cast of external mould, oblique anterior view. Doberlug IV/1929 drill core, from unknown depth. **U, X** GSB X13430, partial pygidium, internal mould, dorsal (U) and posterior (X) views. Doberlug IV/1929 drill core, depth 189 m. **V** GSB X13392, incomplete cranidium of immature individual, internal mould, dorsal view. Doberlug IV/1929 drill core, from unknown depth. **W** GSB X13407, incomplete cranidium of immature individual, latex cast of external mould, dorsal view. Doberlug IV/1929 drill core, from unknown depth. All scale bars 1 mm.

Badulesia barthouxi (Mansuy, 1922)

Fig. 92A–H

Material. Ca. 5 specimens on a single slab; from the sample locality of Jean Barthoux in the Oued Djemat section, southern Moroccan Méséta. Unnamed formation, probably late Wuliuan to early Drumian in age.

Discussion. The first trilobites in the Jbilet region in the southern part of the Moroccan Méséta were discovered by Jean Barthoux. He collected trilobites from slaty argillaceous shales, which he correctly identified as Middle Cambrian in age (Barthoux 1924). Before his paper, Mansuy (1922) published a short note on these trilobites in which he determined the well-known Bohemian “*Paradoxides rugulosus* Corda”, “*Paradoxides* (?)”, “*Conocephalites* sp. ? aff. *C. Sulzeri* Schlotheim”, “*Conocephalites* sp. (?)”. The only new species of this fauna was “*Ptychoparia Barthouxi* n. sp.”. Mansuy was obviously influenced by the (at that time) low number of Middle Cambrian trilobites, which were dominated by Bohemian species. However, he recognised a new species which he named “*Ptychoparia Barthouxi* n. sp.”, which he compared with “*Ptychoparia striata* Emmr.” from Bohemia. The species is fairly common in the Oued Djemat section, and original material from the collections by Barthoux in 1923 is shown in Fig. 92.

In fact, Mansuy introduced “*Ptychoparia Barthouxi*“ without considering “*Conocephalites tener*” of Hartt (in Dawson, 1868). *Badulesia barthouxi* is most similar to *Badulesia tenera*. The only differences between them are the probably slightly broader (sag.) occipital ring in *B. barthouxi* with an apparently better developed terminal occipital spine (Fig. 92B, C, F) and a minimally shorter glabella in that species. In addition, all specimens known from *B. barthouxi* appear to have slightly better developed crests on the genae, particularly with an angulate posteroproximal part. However, a few specimens from the D IV/1929 drill core of the Doberlug area are almost identical except for the differences in the occipital ring (e.g. Fig. 92F). Consequently, it might be considered whether *B. barthouxi* represent a morphological expression typical for late individuals of *B. tenera*.

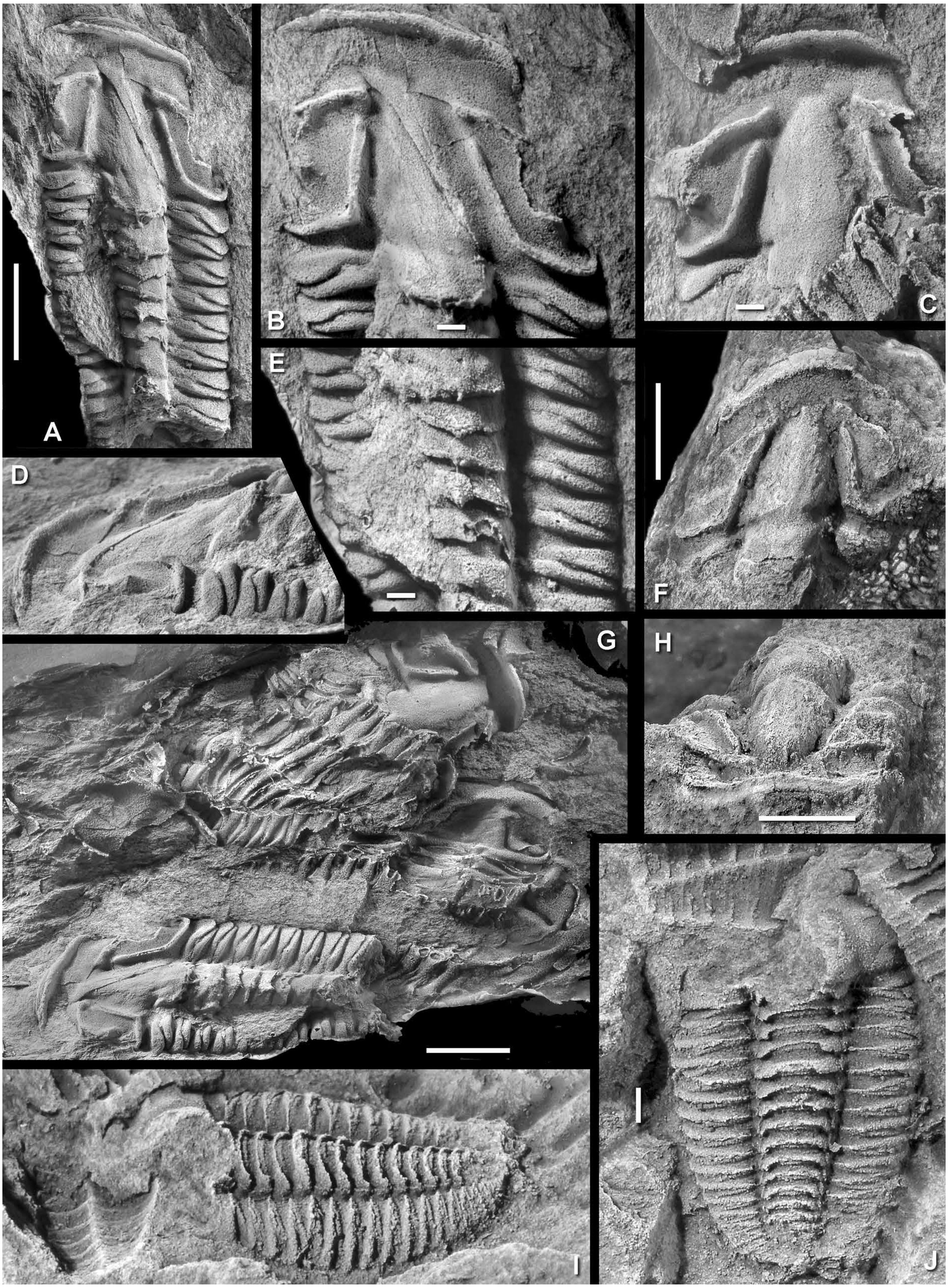

Fig. 92: **A–H** *Badulesia barthouxi* (Mansuy, 1922). **A, B, D, E** IGR 23004a, partial dorsal exoskeleton, latex casts of external mould, dorsal view of entire specimen (A), magnified view of cranidium (B), oblique lateral view of cranidium (D) and magnified view of anterior thorax in dorsal aspect. C IGR 23004c, incomplete cranidium, latex cast, dorsal view. **F, H** IGR 23004b, incomplete cranidium, exterior of cuticle. **G** IGR 23004, view of nearly entire slab, latex cast. **I, J** *Exapinepiphania*? sp., IGR 23005, incomplete dorsal exoskeleton internal mould. All specimens from Barthoux' sample locality, Oued Djemat section, southern Méséta, Morocco; collected by Jean Barthoux in 1923. Scale bars 5 mm in A, F–H, 1 mm in B–E, I, J.

Given the morphologic proximity and the other species in the *B. barthouxi* assemblage, they seem to have a comparable stratigraphic range so that these occurrences are of high significance for biostratigraphy and intercontinental correlation.

Badulesia sp. aff. *tenera* (Hartt *in* Dawson, 1868)

Fig. 93

v 1944 *Andrarina quadrata* (Hartt) – Schmidt: pp. 373–374, pl. 23, figs. 4, 10, 15.
v 1957 *Pardailhania* sp. – Sdzuy: p. 26, text-fig. 14.

Material. Dorsal exoskeleton under X4741/1 (original of Schmidt 1944, pl. 23, fig. 4; from unknown depth); cephalon under GSB X4748/1 (illustrated in Schmidt 1944, pl. 23, fig. 10; from unknown depth); cranidium with detached librigena under GSB X4753/1 (illustrated in Schmidt 1944, pl. 23, fig. 15; from unknown depth); 13 cranidia under GSB X13387 (from depth 187 m); GSB X13392 (from unknown depth), GSB X13394/1 (from unknown depth), GSB X13398 (from unknown depth), GSB X13401 (from depth 188 m), GSB X13404/1 and X13404/2 (both from unknown depth), GSC X13414/1, GSB X13414/2, GSB X13414/3 and X13414/4 (all from unknown depth), GSB X13429/1 and GSB X13419/2 (both from unknown depth); three librigenae under GSB X13394/2 and X13394/3 (both from unknown depth), GSB X13405 (from depth 191 m); enrolled thorax with attached pygidium under GSB X4753/2 (from unknown depth).

Material tentatively assigned to Badulesia sp. *aff.* tenera*:* librigena under GSB X13405 (from depth 191 m).

Locality and strata. All specimens from core of D IV/1929 drillhole near Kirchhain in the Delitzsch–Torgau–Doberlug Syncline, northern Saxony. *Badulesia tenera* Zone, Delitzsch Formation, Caesaraugustan Stage of West Gondwana, Drumian Stage.

Discussion. Specimens of a trilobite species or morphotype that very much resemble *Badulesia tenera*, but are devoid of clearly developed ridges on the genae, occur in about the same strata of the Delitzsch Formation in the D IV/1929 drill-core. These specimens have been identified (for its greatest amount) as *Andrarina quadrata* or *Andrarina* cf. *quadrata* by Schmidt (1944). Except for the absence of crests, slight differences can be seen in an apparently slightly narrower glabella, a slightly stronger curvature of the anterior margin of the frontal lobe, and possibly the lack of a slight kink of the anterior border on the sagittal line. Accordingly, the specimens could be interpreted as a morphotype of *Badulesia tenera* although such differences would require acceptance of a very broad species concept.

A parsimonious assumption of evolutionary pathways would expect the specimens of *Badulesia* sp. aff. *tenera* as pre-dating those of *B. tenera*. However, this is not the case. Unfortunately, numerous specimens of *Badulesia* sp. aff. *tenera* and *B. tenera* have been collected from cores without a documentation of the precise depth, but the known cases indicate an overlap of the specimens of both forms, with *Badulesia* sp. aff. *tenera* seemingly slightly post-dating the specimens of *B. tenera*. Accordingly, the exact stratigraphic range of both forms cannot be indicated, and additional data are needed to clarify the taxonomy.

Badulesia ouangondiana (Hartt in Dawson, 1868)

* 1868 *Conocephalites Ouangondianus*, Hartt, MS. – Hartt in Dawson: pp. 648, 651–652, fig. 226.
? * 1868 *Conocephalites Aurora*, Hartt, MS. – Hartt in Dawson: p. 653.
? * 1868 *Conocephalites quadratus*, Hartt, MS. – Hartt in Dawson: p. 654.
1878 *Conocephalites Ouangondianus*, Hartt, MS. – Dawson: pp. 651–652, fig. 226.
? 1878 *Conocephalites aurora*, Hartt, MS. – Dawson: p. 653.

? 1878 *Conocephalites Thersites*, Hartt, MS. – Dawson: p. 653.

1884a *Ptychoparia Ouangondiana*, Hartt, 1868 – Walcott: pp. 11 [291], 37 [317]–38 [318], 40 [320], pl. V, fig. 4, 4a–f.

? 1884a *Ptychoparia Ouangondiana*, var. *Aurora*, Hartt – Walcott: pp. 11 [291], 38 [318]–39 [319], pl. V, fig. 5.

? 1884a *Ptychoparia quadrata*, Hartt – Walcott: pp. 11 [291], 39 [319], pl. V, fig. 1.

1888 *Liostracus Ouangondianus* – Matthew: pp. 138–139, pl. I, fig. 4a–q, pl. II, fig. 7a–f.

? 1888 *Liostracus Ouangondianus*. Var. *Aurora* – Matthew: pp. 139–140, pl. II, fig. 7a–f.

1889 *Liostracus ouangondianus*, Hartt, 1868 – Miller: pp. 539, 555.

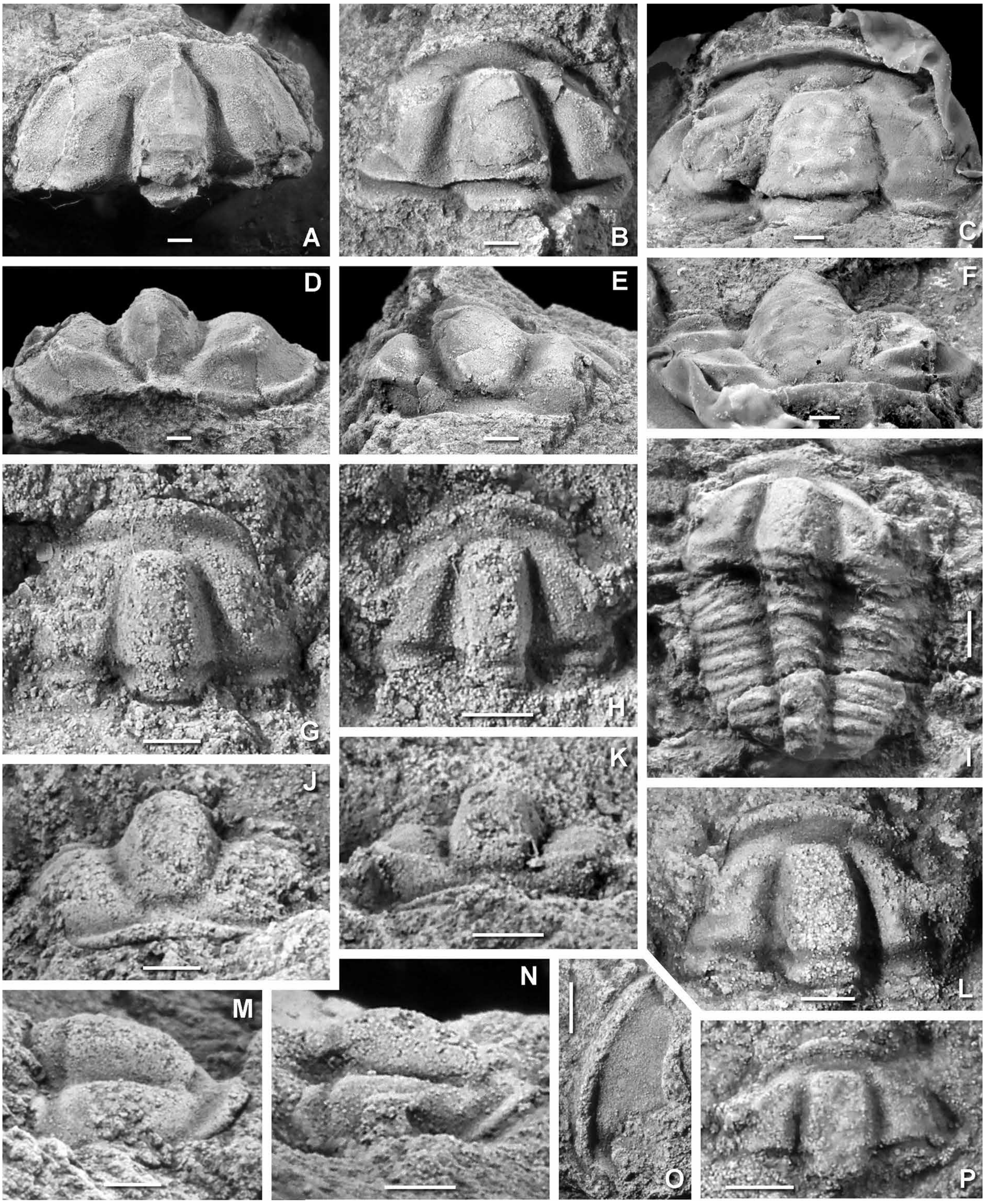

Fig. 93: *Badulesia* sp. aff. *tenera* (Hartt in Dawson, 1868). **A, D** GSB 4748/1, cephalon, laterally compressed internal mould, dorsal (A) and oblique anterior (D) views. Doberlug IV/1929 drill core, from unknown depth; original of *Andrarina quadrata* in Schmidt (1944, pl. 23, fig. 10), and *Pardailhania* sp. in (Sdzuy 1957, fig. 14). **B, E** GSB X13414/1, cranidium, internal mould, dorsal (B) and oblique anterior (E) views. Doberlug IV/1929 drill core, from unknown depth. **C, F** GSB X 4753/1, cranidium, latex cast of slightly distorted internal mould, dorsal (C) and anterior (F) views. Doberlug IV/1929 drill core, from unknown depth; original of *Andrarina quadrata* in Schmidt (1944, pl. 23, fig. 15). **G, J, M** GSB X13404/1, cranidium of immature individual, dorsal (G), anterior (J) and lateral (M) views. Doberlug IV/1929 drill core, from unknown depth. **H, K, N** GSB X13401, incomplete cranidium of immature individual, internal mould, dorsal (H), anterior (K) and lateral (N) views. Doberlug IV/1929 drill core, depth 188 m. **I** GSB X4741/2, dorsal exoskeleton, internal mould, dorsal view showing post-mortem deformation resulting in a sigmoidal inclination of the thorax. Doberlug IV/1929 drill core, from unknown depth; original of *Andrarina quadrata* in Schmidt (1944, pl. 23, fig. 4). **L** GSB X13392, cranidium of immature individual, internal mould, dorsal view. Doberlug IV/1929 drill core, from unknown depth. **O** GSB X13394/2, librigena, internal mould, oblique lateral view. Doberlug IV/1929 drill core, from unknown depth. **P** GSB X13387, cranidium of immature individual, internal mould, dorsal view. Doberlug IV/1929 drill core, depth 187 m. Scale bars 1 mm except in I (= 5 mm).

? 1889 *Liostracus aurora*, Hartt, 1868 – Miller: pp. 539, 555.
? 1889 *Liostracus quadratus*, Hartt, 1868 – Miller: pp. 539, 555.
1889 *Ptychoparia ouanagondiana,* var. *aurora*. – Lesley: p. 140.
1889 *Liostracus ouanagondianus* – Lesley: p. 351.
1889 *Liostracus ouangondianus* var. *aurora* – Matthew in Lesley: p. XV.
1891b *Ptychoparia ouangondiana* – Walcott: pp. 80, 81, 85.
? 1891b *Ptychoparia ouangondiana* var. *aurora* – Walcott: pp. 80, 81, 85.
? 1891b *Ptychoparia quadrata* – Walcott: pp. 80, 81, 226.
1894 *Liostracus Ouangondianus*, Hartt, sp. – Matthew: p. 118.
1894 *Liostracus Ouangondianus* var. *aurora*, Hartt, sp. – Matthew: p. 118.
1897 *Liostracus Ouangondianus* – Matthew: p. 179.
1910 *Ptychoparia ouangondiana* Hartt – Grabau & Shimer: p. 277, fig. 1576d, e.
1925 Liostracus ouangondianus (Hartt) – Howell: pp. 51, 52, 53.
? 1925 Liostracus ouangondianus (Hartt) – Howell: pp. 53, 54.
1927 *Liostracus ouangondianus* (Hartt) – Dale: p. 179.
non 1929 *Liostracus aculeatus* Ang. – Strand: pp. 313, 339, 351, pl. II, fig. 5a, b.
1944 *Andrarina ouangondiana* (Hartt) – Shimer & Shrock: pp. 605, 617 fig. 276-26.
non 1944 Andrarina quadrata (Hartt) – Schmidt: pp. 373–374, pl. 23, fig. 4.
1961 *Andrarina ouangondiana* – Dean & Krummenacher: p. 79.
1962 *Liostracus ouangondianus* (Hartt) – Hutchinson: p. 32.
1972 *Braintreella ouangondiana* (Hartt *in* Dawson, 1868) – Fletcher: pp. 180, 181, 200, pl. LVIII, figs. 10, 11.
? 1972 *Braintreella ouangondiana* (Hartt *in* Dawson, 1868) – Fletcher: pl. LIX, fig. 1a–c.
? 2005 *Parasolenopleura aculeata* (Angelin, 1841) – Fletcher, text-fig. 5J.
2005 *Parasolenopleura ouangondiana* (Hartt, *in* Dawson, 1868) – Fletcher: p. 1086, text-fig. 5K, 5L, 5N, 5O.
2006 *Parasolenopleura ouangondiana* (Hartt *in* Dawson, 1868) – Fletcher: p. 79.
non 2008 *Parasolenopleura ouangondiana* (Hartt *in* Dawson, 1868) – Gozalo et al.: p. 143.
non 2008 *Parasolenopleura ouangondiana* (Hartt *in* Dawson, 1868) – Liñán et al.: p. 17.
2011a *Parasolenopleura ouangondiana* (Hartt *in* Dawson, 1868) – Gozalo et al.: p. 77.
2011b *Parasolenopleura ouangondiana* (Hartt in Dawson, 1868) – Gozalo et al.: p. 143.
pars 2020 *Parasolenopleura aculeata* (Angelin, 1851) – Chirivella Martorell et al.: pp. 6, 8, 9.

Description. Glabella highly convex, tapering forward to narrow front, with distinctly curved lateral margins, frontal lobe with low curvature of its anterior margin or subtruncate, with slight to notable anterolateral corners. Occipital ring moderately broad (sag.), clearly tapering towards the axial furrows; with short to moderately long, obliquely posterodorsally directed terminal spine. Axial furrows moderately deep, relatively broad. Palpebral areas narrow, about equal width as palpebral lobes plus palpebral furrows, distinctly convex in transverse section, with most elevated part slightly adaxially to midline; posterolateral wings distinctly abaxially/ventrally extended.

Eye ridges short, obliquely rearward curving from its origins at the axial furrows, relatively low, moderately narrow, proceeding into the palpebral lobes and not separated from them by a recognizable depression. Palpebral lobes thick and prominent on the exterior of the cuticle, clearly narrower and less upturned on internal mould; moderately to strongly curved on both the abaxial and adaxial margins, with widest (tr.) parts in the central and posterior parts. Palpebral furrow moderately wide and moderately well impressed. Preglabellar field short, in dorsal view shorter than anterior border, clearly sunken between preocular areas, faintly convex in sagittal profile. Anterior border moderately broad (sag., exsag.), prominent, bulging on specimens with preserved cuticle, but more blade-like and slightly obliquely upturned at internal moulds; moderately tapering towards the facial suture. Anterior border furrow a shallow, moderately wide (sag., exsag.) depression, which appears to have a shallower central sector in slightly distorted specimens. Surface of cuticle smooth.

Discussion. Badulesia ouangondiana (Hartt *in* Dawson, 1868) is a species which caused various confusions in respect to its precise identity and the amount of intraspecific variation. This trouble was certainly caused by the misleading figures in the first publications, but also by the fact that the species is indeed quite variable and almost devoid of characters that permit a simple identification. Already Matthew (1888, p. 138) claimed that this “species is one of the most difficult to deal with among those of the fauna described by Hart.” Indeed, the specimens figured by Matthew (1888) probably represent not only this species, and on the other hand some of the specimens assigned to different species or forms possibly belong to *B. ouangondiana*. The uncertainty about the estimation of its characters led to the changeful generic assignment of the species, from the early collective bins such as *Conocephalites*, *Ptychoparia* and *Liostracus* to a position within undoubtable solenopleurids.

Tectonic distortion and the lack of obvious (not apomorphic!) characters even led to such errant assumption as the synonymy of *Badulesia ouangondiana* and *Parasolenopleura aculeata* and *Badulesia quadrata* (together with *Jincella*? *orestes* and others) (Chirivella Martorell et al. 2020).

Fletcher (1972) assigned *Badulesia ouangondiana* to *Braintreella* because of its apparent affinity to *Braintreella rogersi*. Subsequently (Fletcher 2005) regarded the species as closely related to both *Parasolenopleura aculeata* and *Badulesia tenera*. He considered the species as representing de facto a *Badulesia tenera* without the spectacular fixigenal ridges, and assigned both species to *Parasolenopeura*. Indeed, *B. ouangondiana* occurs in strata of the Fossil Brook Member of the Chamberlain’s Brook Formation at Porter Road, southern New Brunswick, associated with *Badulesia tenera*. *Badulesia tenera* was considered by Fletcher (1972) as a species of *Braintreella* as well. However, *Badulesia tenera* as well as true specimens of *B. ouangondiana* have a tapering glabella with a relatively wide occipital ring, but a nearly subtruncate front, narrow and more strongly elevated fixigenae and broader palpebral lobes than *Braintreella rogersi*, and can be relatively easily distinguished so that they should be separated on generic level.

Conocephalites aurora Hartt in Dawson, 1868 has not been figured in the original publication. The first illustration is found in Walcott (1884, pl. V, fig. 5), who regarded the taxon as a “variety” of *Ptychoparia ouangondiana*. Walcott’s description and figure do not provide a precise image of the taxon, but given the characters shown in Walcott’s figure and the co-occurrence with *B. ouangondiana*, it is highly probable that *Conocephalites aurora* was based on specimens of *B. ouangondiana* with somewhat unusual features.

G.F. Matthew presented two cranidia from St. John, N.B., determined as “*Liostracus ouangondianus* var. *aurora*” to K.A. Grönwall. These two cranidia differ clearly from *B. ouangondiana* despite of superficial similarity in some of the aspects such as the larger size, the relatively flat anterior border, and a terminal occipital spine. They also do not match the descriptions given in Dawson (1868), Walcott (1884a, pl. v, fig. 5) and Matthew (1888, pl. II, fig. 7), particularly because of an obviously much narrower and considerably upturned anterior border and a broader glabella. They are described above under “*Parasolenopleura*” sp. A.

Although having a proto-*tenera* morphology like *Badulesia* aff. *tenera* (discussed above), *Badulesia ouangondiana* differs significantly from that form in at least two features of considerable importance: *B. ouangondiana* has a bulging anterior border rather than a relatively narrow, elevated border, and relatively wide (tr.) palpebral lobes. According to present knowledge, *B. ouangondiana* predates the occurrences of *B. tenera*, except for a claimed common occurrence recorded by Fletcher (2005, 2006) the latter of which could be based on small cranidia with incipient ridge forming from immature specimens.

Occurrence. The original material of Hartt (in Dawson 1868) has been collected at Ratcliff's Millstream with additional material collected by Walcott (1884) at the adjacent Ratcliff’s Millstream, New Brunswick, whereas Matthew’s specimens originate from Porters Brook, all from the *Eccaparadoxides eteminicus* Zone of the Fossil Brook Member of the Chamberlain’s Brook Formation, New Brunswick (see Hayes and Howell 1937, p. 88, fig. 3). Additional records from the *Badulesia tenera*, *Hartella bucculenta* and *Agraulos longicephalus* zones of the uppermost Chamberlain’s Brook and lower Manuels River formations, Branch Cove, St. Mary’s Bay, Newfoundland.

Genus *Liosolenopleura* Thoral, 1948

Type species. Liosolenopleura serventi Thoral, 1948; from the Coulouma Formation, *Solenopleuropsis* (*Solenopleuropsis*) Biozone, Montagne Noire, France.

Discussion. Thoral (1947, 1948) introduced a new genus and species under the name *Liosolenopleura serventi*. The first publication in 1947 only raised a numen nudum, but Thoral formally erected the taxon in 1948. Unfortunately, it is based on relatively rare material from the Montagne Noire in southern France, which mostly consists of strongly distorted specimens so that the genus and species from the upper Drumian *Solenopleuropsis* (*Solenopleuropsis*) Biozone received little attention. Its precise morphology is mostly difficult to assess, but the best preserved of the published illustrations (Courtessole 1973, pl. XVI, fig. 16; Álvaro et al. 2004, fig. 4.14, 4.15) depict a cranidium with generally the same morphological features as the Scandinavian grouping described above.

Its specific characters include relatively weakly curved lateral margins of the glabella; a preglabellar field of subequal breadth (sag.) as the relatively thin (sag.) anterior border which tapers notably towards the facial suture; and a relatively short (sag.) occipital ring with a quite thick median node. Unfortunately, no pygidium is known that can be confidently assigned to *Liosolenopleura serventi*. The genus and species suggests – by the combination of its morphology and stratigraphic position – that it probably belongs to the *Badulesia*–*Solenopleuropsis* clade and thus the Solenopleuropsinae. It may be seen as an exceptional genus of the group devoid of ridges and papillae the exterior of the cuticle.

Whether other species can be assigned confidently to the genus remains unsettled until better preserved cranidia and pygidia of *Liosolenopleura serventi* are known. For the moment, it should be considered whether *Conocephalites robbii* Hartt in Dawson, 1868 may represent a species of *Liosolenopleura*.

“*Liosolenopleura*” *robbii* (Hartt in Dawson, 1868)

Fig. 94

Studied material. Two cranidia, LO 12534t and LO 12535t; librigena, LO 12536t.

Locality and stratum. Specimens from the Fossil Brook Member of the Chamberlain’s Brook Formation at St. John, New Brunswick.

Description and discussion. The species was based on material collected from the Fossil Brook Member of New Brunswick, which appear to be difficult to characterise. Matthew (1888) presented study on apparently abundant material, but merged Hartt’s (in Dawson, 1868) species *Conocephalites Robbii*, *Conocephalites formosus*, *Conocephalites Orestes*, *Conocephalites Thyrsites* and *Conocephalites hallii* under *Solenopleura Robbii*. However, he acknowledged morphological differences among the specimens so that he discussed a “narrow form” under which he united *Conocephalites Orestes* and *C. hallii* without providing a suggestion for a formal taxon name.

It would require a thorough study on all available material from New Brunswick and probably additional specimens to achieve a robust concept for the species. Fig. 94 illustrates two specimens from G.F. Matthew’s collections at St. Martins, New Brunswick, which exemplifies the morphologic plasticity of the *robbii* plexus and also illustrates that the size of the specimens appears to vary considerably so that the specimens figured in previous publications probably represent medium-sized individuals.

Additional specimens of *“Brunswickia” robbii* are illustrated in Fletcher (2007a, fig. 7A, B) with some correction of tectonic distortion. They have a distinctly tapering glabella with almost straight lateral margins anterior to L1 and a gently curved anterior margin without a recognisable tendency towards a low curvature or subtruncate front (e.g., Fletcher 2007a, text-fig. 5R, 2007b, fig. 7A, B). The occipital ring is moderately broad (sag., exsag.) almost to the abaxial margins and carries a tubercle in a median position. The preglabellar field is present and of more-or-less equal breadth to the anterior border, being moderately convex, but slightly sunken in respect to the preocular areas. The anterior border is moderately broad and distinctly convex, moderately tapering towards the facial suture. The palpebral lobes are almost moderately long, with a conspicuous curvature at the circumocular suture, distinctly upturned and located at a medial position in respect to the cephalic length axis. Eye ridges are moderately elevated, slightly to gently curved and somewhat posteriorly directed from their origins at the axial furrows. The palpebral areas are moderately wide (tr.), considerately convex in transverse and exsag. profiles, with a distinct slope towards the well incised axial furrows, and the most elevated parts are located close to the palpebral lobes. Their posterior wings extend considerably beyond the palpebral lobes and are quite strongly ventrally deflected.

This morphology indicates that the species does not exhibit any readily recognisable derived characters so that a conclusive generic assignment is presently not possible. Given the morphology of Howell’s (1937) type species of *Brunswickia*, an assignment to that genus is obviously incorrect, which also invalidates Fletcher’s (2007a) concept of *Brunswickia* with two subgenera, *Brunswickia* and *Jincella*.

Despite of the obvious “primordial” morphology, the species cannot be regarded as a representative of an early solenopleurine lineage. Instead, its morphology agrees largely with that of *Liosolenopleura serventi* Thoral, 1947. Whether these similarities are simply superficial is difficult to decide. Nevertheless, the recognizable characters as well as the stratigraphic positions suggest that *Liosolenopleura serventi* as well as *“L.” robbii* may have been related to the lineage that developed into typical solenopleurine species. Accordingly, the species is provisionally termed *“Liosolenopleura” robbii* herein, pending further studies on the plexus based on more material with careful stratigraphic collecting.

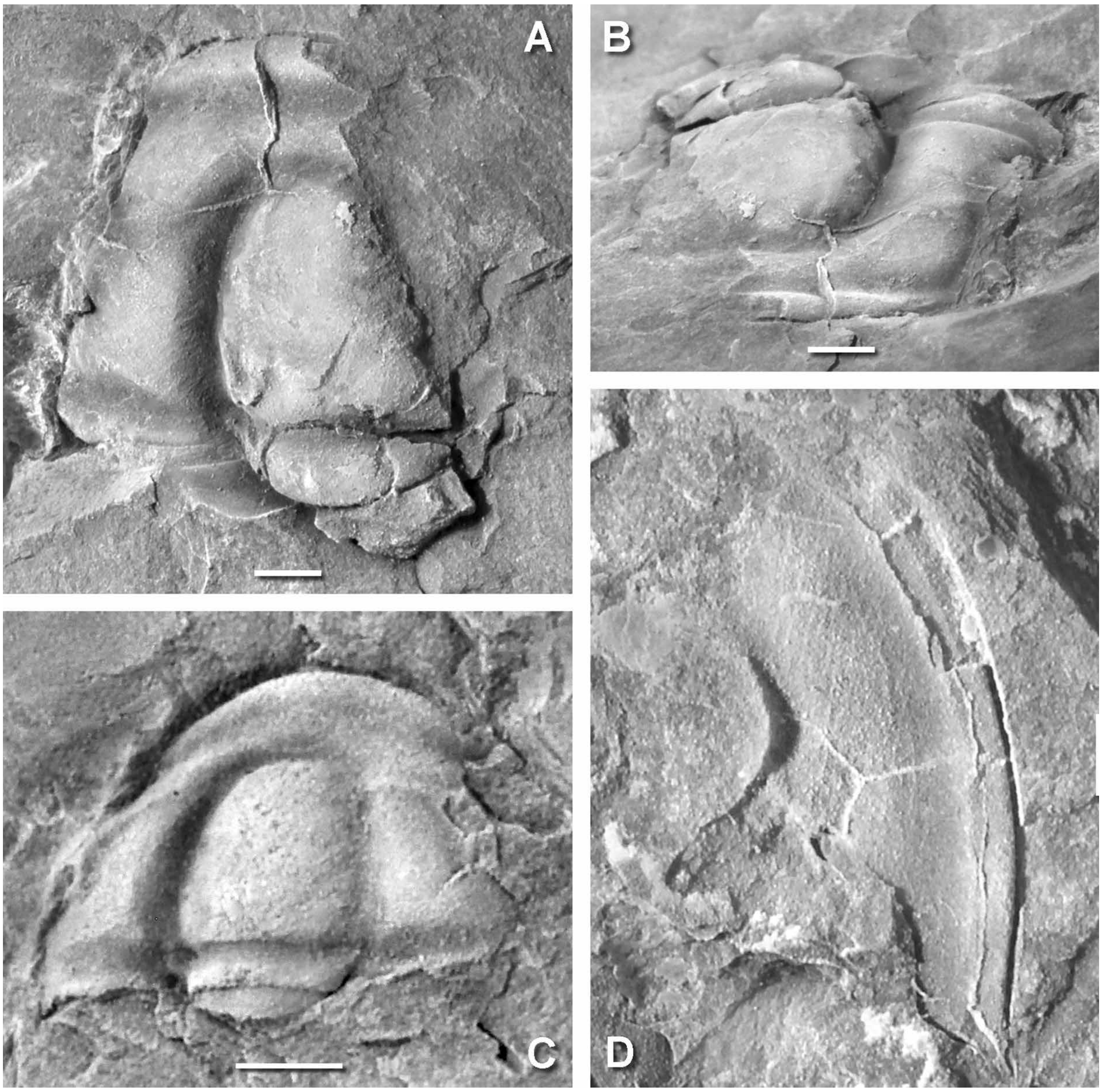

Fig. 94: *"Liosolenopleura" robbii* (Hartt *in* Dawson, 1868). **A, B** LO 12534t, partial cranidium, composite mould, dorsal (A) and oblique anterior (B) views. **C** LO 12535t, cranidium, composite mould, dorsal view. **D** LO 12536t, librigena, composite mould, partly exfoliated, broken lateral border in the anterior part exposes ventral doublure. Specimens collected from the Fossil Brook Member of the Chamberlain's Brook Formation by G.F. Matthew at St. John, New Brunswick (LO 12535t in C determined as *Liostracus Ouangondianus*). Scale bars 1 mm).

Occurrence. The type material of Hartt (in Dawson 1868) was collected from the *Eccaparadoxides eteminicus* Zone of the Fossil Brook Member of the Chamberlain's Brook Formation at Ratcliffe's Millstream, New Brunswick. Additional material was presented by Matthew from Hanford Brook near St. Martins, New Brunswick (Matthew 1888, pl. II, figs. 4g–4l). Fletcher (2005) recorded the species from the *Hartella bucculenta* Zone of the Cape Shore Member, Chamberlain's Brook Formation, of south-eastern Newfoundland.

Solenopleurid genera and species indeterminate

Fig. 95

Discussion. Several isolated sclerites found in the Wildenstein Member of the Tannenknock Formation cannot be matched to a determinable cranidium. Their morphology, however, suggests that they are sclerites of solenopleurid genera and species. Examples for these sclerites are assigned to indeterminate genera and species and are illustrated in Fig. 95: Numerous fragments of isolated thoracic segments are known from the Wildenstein samples. The specimens in Fig. 95A–D originate from anterior thoracic segments recognizable from a relatively short pleural part, with the pleural furrow obliquely rearward directed and tapering from their subcentral position in the proximal part of the pleura.

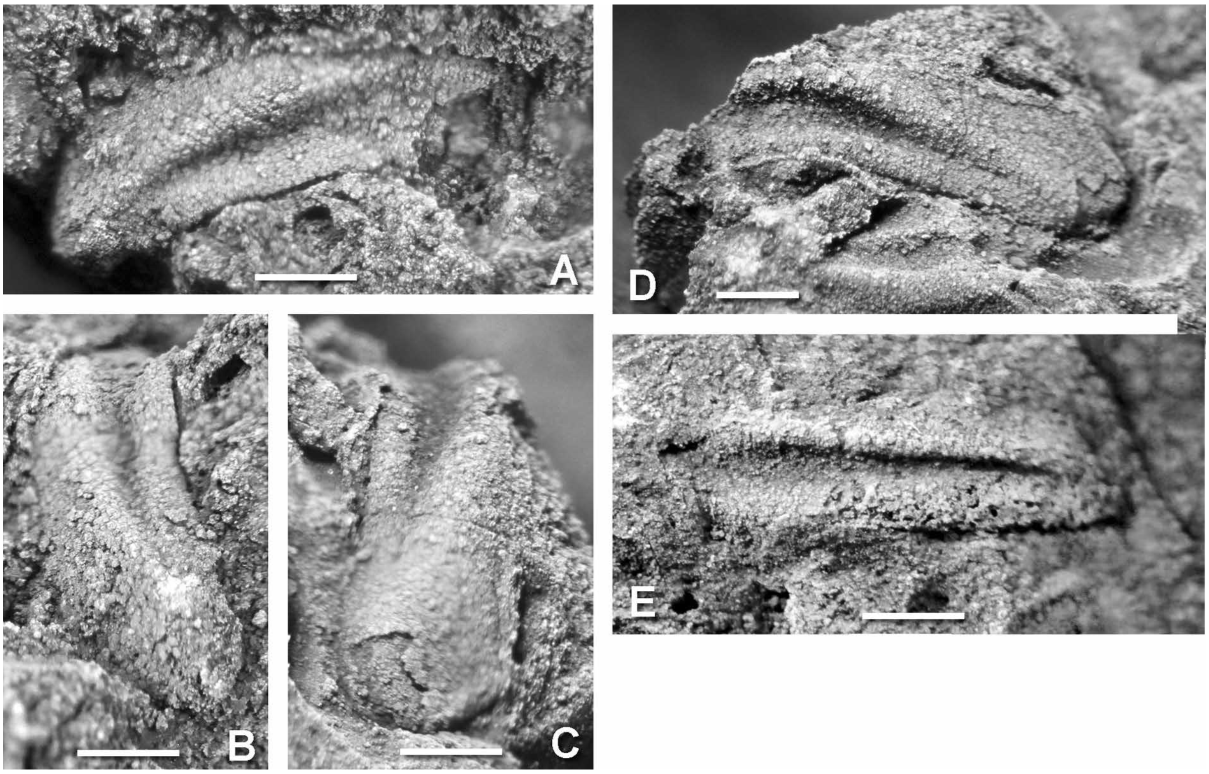

Fig. 95: Solenopleurid genus and species indeterminate. **A, B** MMUW 2017D-064, fragment of thoracic pleura, dorsal (A) and oblique lateral (B) views; **C, D** MMUW 2017D-065, fragment of thoracic pleura, lateral (C) and dorsal (D) views; **E** MMUW 2017D-101, fragment of thoracic pleura, dorsal view. All specimens from locality W8; Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

A relatively broadly triangular articulating facet is developed in the anterodistal part of the pleura. The posterior margin shows a relatively distinct kink towards dorsal which corresponded to a small socle on the posteriorly adjacent segment. The pleural tip lacks a pleural spine and instead has a pointed termination with a subtriangular cross-section.

An example for a segment from the middle and posterior parts of a solenopleurid thorax is shown in Fig. 95E. It has a nearly straight, slightly abaxially tapering pleural furrow the posterior margin of which runs parallel to the posterior margin of the pleural, whereas an anteriorly dipping facet that slightly increases in exsag. breadth is developed in front of the pleural furrow.

All known pleurae have a more-or-less pronounced kink or bend at approximately mid-length (tr.) of the pleura corresponding to the external points of articulation, which attests a pronounced ability to enrol the dorsal exoskeleton.

Family uncertain

Genus *Oreisator* Geyer & Malinky, 1997

Type species. Oreisator tichkaensis Geyer & Malinky, 1997, from the Bréche à *Micmacca* Member, Jbel Wawrmast Formation, at Tizi n’Tichka, central High Atlas, Morocco (by original designation).

Discussion. Oreisator is characterised by a highly convex glabella with subparallel lateral margins and a frontal lobe having a strongly and subevenly curved anterior margin; a sagittally narrow, but convex preglabellar field; a relatively narrow (sag. and exsag.), simple anterior border. The pygidium is broadly subtriangular in outline, its axis convex, with two well-delineated and two poorly defined axial rings plus terminal section; weakly convex pleural regions, which are connected behind the rhachis. The lateral and posterior pygidial border furrow is indistinct to obsolete. The cuticle is covered with granules of different sizes.

The systematic position of *Oreisator* poses problems because the genus unites characters that have been regarded variously as of ptychoparioid, solenopleurid and even chengkouiid signature. These have been discussed in some detail Geyer (2016, p. 772–773). Given the additional aspect discussed above, the genus is best regarded as of uncertain position.

"*Oreisator*" *picardi* (Schmidt, 1944)

Figs. 96 A–H, J–L, 97A, D, I, J?, K?, N–P

v * 1944 *Solenopleura picardi* n. sp. – Schmidt: pp. 376–377, pl. 23, figs. 14, 17, 18.
v 1944 *Dorypyge cf. lakei* Cobb. – Schmidt: pl. 22, fig. 12 [only].
v 1959 *Solenopleura picardi* W. E. Schmidt 1942 – Sdzuy: p. 25.

Material. 10 cranidia under GSB X4755 (holotype, Schmidt 1944, pl. 23, fig. 17a, 17b; from depth 195 m); GSB X4756 (paratype, Schmidt 1944, pl. 23, fig. 18a, 18b; from depth 184 m), GSB X4757/1, X4757/3, X4757/4, X4757a (all from unknown depth), X06239/8 (from depth 186 m), GSB X13434 (from depth 188 m), GSB X13435/1 (from unknown depth), and GSB At364 (from depth 395 m; determined and figures as *Dorypyge* cf. *lakei* in Schmidt 1944, pl. 22, fig. 12); two librigenae under GSB X4752 (Schmidt 1944, pl. 23, fig. 14; from unknown depth) and GSB X13433 (from depth 195 m); single pygidium under GSB x4757/4.

Locality and strata. Doberlug IV/1929 drill site, northwest of Kirchhain, Delitzsch–Torgau–Doberlug Syncline, Northern Saxony, Germany. Various horizons in the Delitzsch Formation, *Badulesia tenera* Zone, Wuliuan–Drumian boundary interval, Miaolingian Series.

Description. Cranidium subtrapezoidal in outline, with distinctly curved anterior margin and extending occipital ring. Glabella strongly convex in transverse section, lateral profile gently convex in the posterior half, steeply sloping towards anterior margin; lateral margins slightly converging forward in dorsal view from L1 to faint anterolateral corners anterior to S2; frontal lobe with anterolateral parts evenly curved curvature, but frontal median section of the anterior margin flattened front; length about 80 % cephalic length (inclusive occipital ring). Three pairs of glabellar furrows recognisable, all shallow and poorly impressed, broadly separated over midline; S1 directed strongly backward from axial furrows and gently curved; S2 short, vaguely bifurcated; S3 short, indistinct. Occipital furrow with faintly backward directed narrow and deep lateral sections and a slightly shallower, nearly straight median section. Occipital ring with back ward swinging posterolateral and posterior margins; with median node. Axial furrows deeply incised.

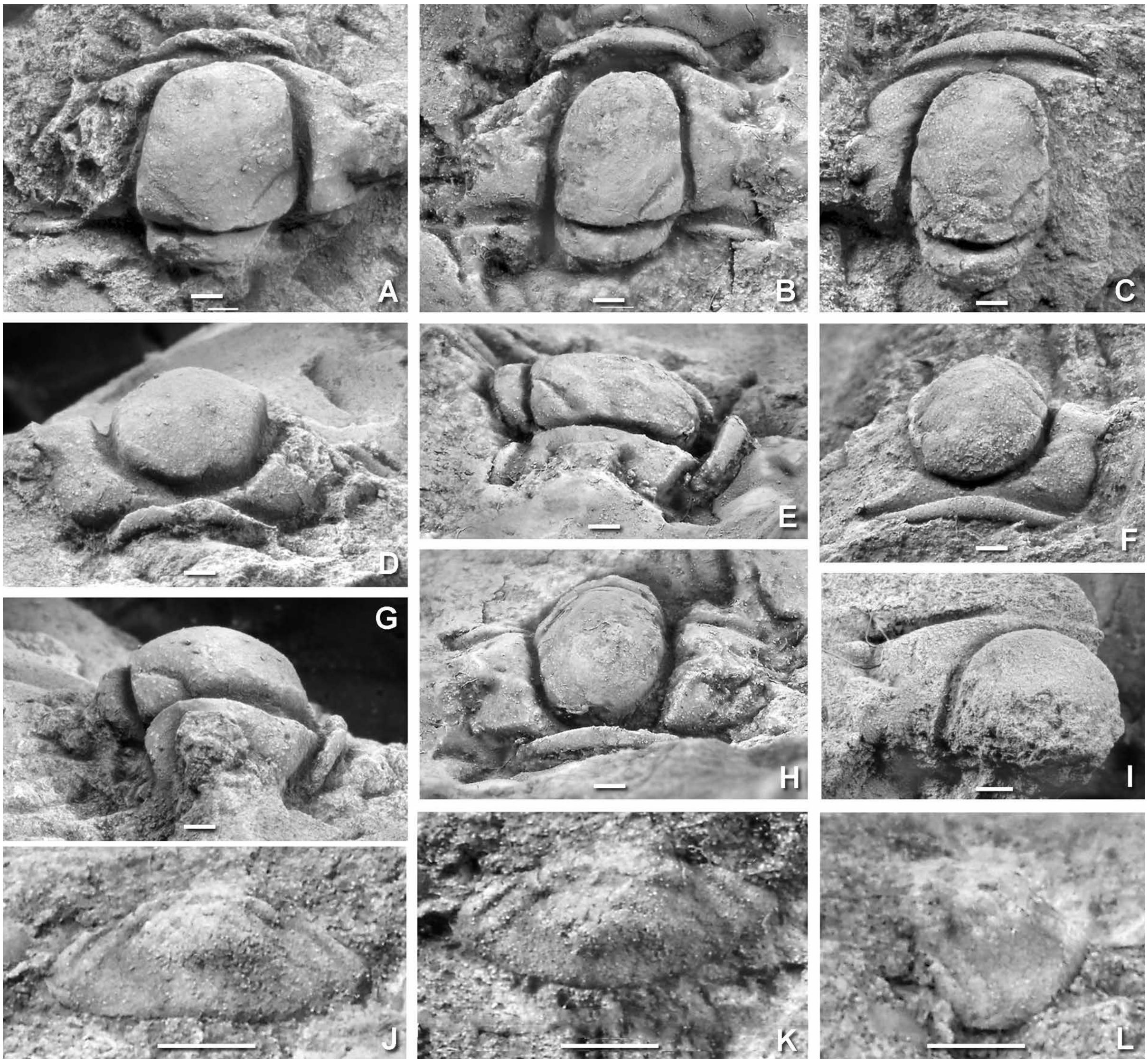

Fig. 96: **A–H, J–M** "*Oreisator*" *picardi* (Schmidt, 1944). **A, D, G** GSB X 4755, holotype, incomplete cranidium, composite mould with relics of the granulose surface, dorsal (A), anterior (D) and lateral (G) views, Doberlug IV/1929 drill core, depth 195 m; original specimen of Schmidt (1944, pl. 23, fig. 17a, b). **B, E, H** GSB X 4756, paratype, cranidium, internal mould, dorsal (B), oblique lateral (E), and oblique anterior views, Doberlug IV/1929 drill core, depth 179 m; original specimen of Schmidt (1944, pl. 23, fig. 18a, b). **C, F** GSB X 4757a, partial cranidium, composite mould with granulose surface, dorsal (C) and anterior (F) views, Doberlug IV/1929, depth 190 m; original specimen of Schmidt (1944, pl. 23, fig. 19). **J, K, L** GSB X 4757/4, pygidium, internal mould, posterior (J), dorsal (K) and lateral (L) views, Doberlug IV/1929 drill core, depth 190 m.
I Genus and species indeterminate aff. "*Oreisator*" *picardi* (Schmitt, 1944), GSB X 4746/1, paratype, cranidial fragment with granulose surface, Doberlug IV/1929 drill core, from unknown depth; original specimen of Schmidt (1944, pl. 23, fig. 8), identified as "*Andrarina tenera* (Hartt, 1868)".
Dorsal views if not indicated otherwise. All scale bars 1 mm.

Palpebral lobe moderately long, exsag. of ca. one-fourth cephalic length, almost normal to or slightly oblique to axis, anterior end in transverse line with S2, posterior end about in transverse line with S1 or anterior part of L1; slightly raised above fixigenae; defined by a shallow, moderately broad, slightly curved palpebral furrow. Eye ridge forms shallow lobe directed strongly obliquely inward and forward to meet axial furrow opposite to S3, with obsolescent continuation to frontal lobe across axial furrow. Palpebral area gently convex, moderately wide (tr.), transverse width between posterior ends of eye lobe and axial furrow ca. 40 percent maximum glabellar width across L1. Posterior area of palpebral area extends into moderately broad (tr.) posterolateral projection.

Anterior border distinctly convex and clearly elevated to a conspicuous anterior bulge, moderately broad on sagittal line, reduced in exsag. width towards the facial suture; anterior margin with more-or-less equal curvature in dorsal view and slight curvature in anterior view (Fig. 96F). Anterior border furrow relatively narrow (sag. and exsag.), forms a conspicuous groove with a slightly shallower median section on sagittal line.

Preglabellar field typically of ca. half breadth of the anterior border on the sagittal line, gently convex in front of the glabella, but slightly sunken between preocular fields, particularly in dorsoventrally or laterally compressed specimens. Preocular areas gently convex, exsag. moderately broad, sloping towards anterior border furrow.

Anterior branch of suture subparallel from anterior ends of eyes, distinctly curving inward at ca. one-third distance posterior to anterior border.

Posterior border relatively narrow (exsag.) near axial furrow, directed in slightly posterolateral direction with a gentle curvature and growing in breadth abaxially. Posterior border furrow moderately wide (exsag.) and moderately deep near axial furrow, broader (exsag.) and shallower near posterior branches of suture.

Librigena known from a single specimen; considerably elevated from the lateral margin to the ocular suture, characterised by wide (tr.), gently convex genal field and relatively long anterior and posterior branches of facial suture. With notable, moderately high flange along ocular suture. Lateral border moderately broad (tr.), broken for most of its extension in the studied specimen. Lateral border furrow relatively narrow, moderately deep. Visible parts of the librigena suggest that the suture ran almost into the genal angle and that the genal angle was narrowly curved, lacking a genal spine.

A single specimen is believed to represent a pygidium of the species. This pygidium (Fig. 96J–L) is sublenticular in outline, width/length ratio ca. 0.8, anterolateral margins slightly posterolaterally directed from axial furrow; lateral and posterior margin entire, evenly curved throughout. Axis fairly of ca. two-thirds total pygidial length inclusive of articulating half-ring, fairly wide anteriorly, tapering to ca. two-thirds width across terminal axial piece; consists of ca. two axial rings and a terminal axial piece. Terminal axial piece appears to be bilobate. Low plectrum extends from the terminal axial piece to the posterior pygidial margin (Fig. 96K). Pleural field divided into two or three low, pleural ribs separated by shallow interpleural furrows. Lateral border poorly defined.

Surface of cuticle covered by relatively small granules of subequal diameter except for the smooth furrows.

A meraspid cranidium associated with adult cranidia probably represents an ontogenetic stage of "*Oreisator*" *picardi* (Fig. 97J, K). This cranidium shows a relatively broad glabella with a subrectangular outline and a nearly straight anterior glabellar margin. The anterior border is moderately elevated and relatively broader (sag., exsag.) than in adult individuals. The axial furrows are much wider than in adults, and the palpebral lobes short, slightly broader and more upturned. The morphology of the specimen resembles immature specimens of *Badulesia* spp.

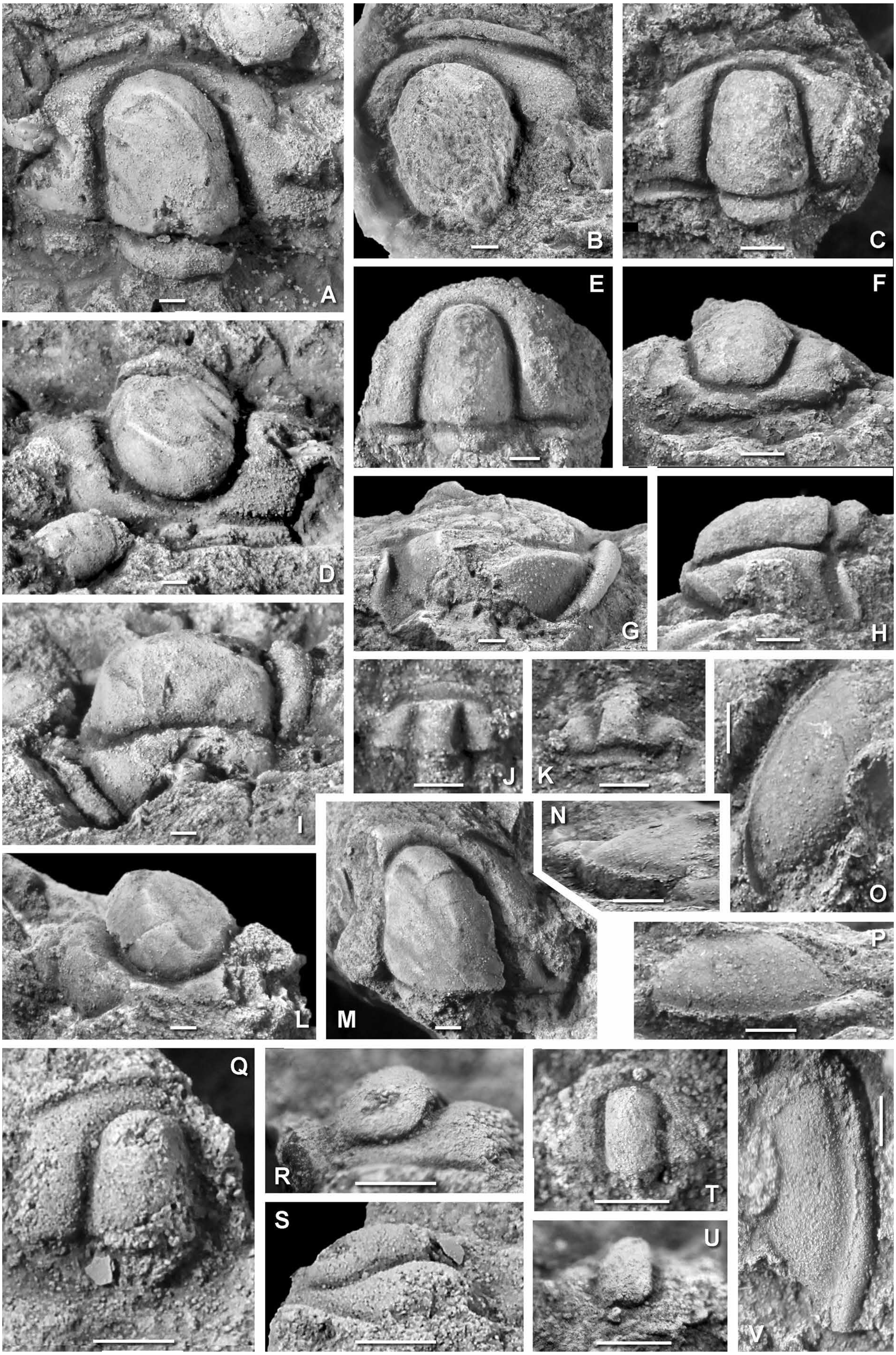
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Fig. 97: **A, D, I, J?, K?, N–P** “*Oreisator*” *picardi* (Schmidt, 1944). **A, D, I** GSB X06239/8, cranidium, composite mould with relics of the granulose surface, dorsal (A), oblique anterior (D) and lateral (I) views, Doberlug IV/1929 drill core, depth 186 m. **J, K** GSB X13436/1, meraspid cranidium, dorsal and oblique anterior views, Doberlug IV/1929 drill core. **N–P** GSB X 4752, paratype, librigena, composite mould, anterior (N), dorsal (O) and lateral (P) views, Doberlug IV/1929 drill core, from unknown depth; original specimen of Schmidt (1944, pl. 23, fig. 14). **B, C, E, F, G, H. L, M, Q–V** Genus and species indeterminate aff. “*Oreisator*” *picardi* (Schmidt, 1944). **B** GSB X13436/1, partial cranidium, latex cast of external mould, Doberlug IV/1929 drill core, depth 179 m. **C, F, H** GSB X06238/2, incomplete cranidium, internal mould, dorsal (C), anterior (F) and lateral (H) views, Doberlug IV/1929 drill core, from unknown depth. **E** GSB X13438, incomplete cranidium, internal mould, Doberlug IV/1929 drill core, depth 191 m. **G** GSB X13437, partial cranidium, lateral view, cuticle with granules, Doberlug IV/1929 drill core, from unknown depth. **L, M** GSB X14440, partial cranidium, anterior (L) and dorsal (M) views, Doberlug IV/1929, depth 189 m. **Q, R, S** GSB X06277/3, partial small cranidium, dorsal (Q), anterior (R) and oblique anterolateral (S) views, Doberlug IV/1929 drill core, depth 199.5 m. **T, U** GSB X06277/4, cranidium of juvenile individual, dorsal (T) and oblique anterior (U) views, Doberlug IV/1929 drill core, from unknown depth. **V** GSB X06277/5, librigena, composite mould, Doberlug IV/1929 drill core, from unknown depth.
Dorsal views if not indicated otherwise. All scale bars 1 mm.

Discussion. “*Oreisator*” *picardi* was introduced by Schmidt (1944) as *Solenopleurina picardi*. The species is based on distorted cranidia from the Doberlug D IV/1929 borehole from Saxony, Germany, which fundamentally differ from *Solenopleurina sensu* Růžička (1938).

The morphology of the species resembles that seen in *Oreisator tichkaensis* Geyer & Malinky, 1995, from the High Atlas of Morocco. However, the specimens from Saxony differ in a broader glabella, longer palpebral lobes with a slightly different character, a librigena without a distinct genal spine and a quite different morphology of the pygidium tentatively assigned to the species. In addition, “*Oreisator*” *picardi* occurs in strata of the Wuliuan–Drumian boundary interval and is thus clearly younger than the *O. tichkaensis* from Morocco. These differences suggest that the species should most probably be assigned to a closely related, different genus. Such a suitable genus, however, does not exist yet. Accordingly, the species is here provisionally dealt with as “*Oreisator*” *picardi*.

Specimens of a similar trilobite species co-occur with “*Oreisator*” *picardi* in the strata of the Doberlug D IV/1929 borehole and appear to have been included into the species by Schmidt (1944). These are discussed below under Genus and species indeterminate aff. “*Oreisator*” *picardi*.

Genus and species indeterminate aff. “*Oreisator*” *picardi* (Schmidt, 1944)

Figs. 96I, 97B, C, E, F, G, H. L, M, Q–V

Material. Eight cranidia under GSB X06238/2 (from unknown depth); GSB X13436/1, GSB X13436/2 (from depth 179 m); GSB X06277/3 (from depth 199,5 m); GSB X06277/4 (from unknown depth); GSB X13437 (from unknown depth); GSB X13438 (from depth 191 m); and GSB X13440 (from depth 189 m); librigena under GSB X06277/5 (from unknown depth).

Locality and strata. Doberlug IV/1929 drill site, northwest of Kirchhain, Delitzsch–Torgau–Doberlug Syncline, Northern Saxony, Germany. Various horizons in the Delitzsch Formation, *Badulesia tenera* Zone, Wuliuan–Drumian boundary interval, Miaolingian Series.

Discussion. Eight cranidia and cranidial fragments from the Doberlug D IV/1929 borehole provide a morphology which superficially resembles that of “*Oreisator*” *picardi* (Schmidt, 1944), with which they are partly associated. They differ, however, in having a glabella that tapers forward to a subevenly curved anterior margin of the frontal lobe. The occipital ring is slightly narrower (sag.) than that of “*O.*” *picardi*. The palpebral areas are more strongly dipping into abaxial direction. The preglabellar field is always completely developed and not notably depressed in front of the glabella, and its sagittal width is usually at least as great as that of the anterior border, partly up to 1.5 times that breadth. The anterior border has a relatively constant breadth for most of its stretch, but is reduced in breadth close to the facial suture.

The imperfect preservation of these cranidia and the lacking information on the morphology of the librigena and pygidium does not allow a precise reconstruction and systematic assignment. The species, however, suggests a stronger affinity to the Solenopleuridae than *Oreisator*, but shares most characters with that genus.

Family Conocoryphidae Angelin, 1854

Discussion. Modern approach of phylogenetic principles has made clear that the traditional concept of the family Conocoryphidae (e.g., Poulsen 1959) maintains an artificial grouping of taxa based on the lack of eyes and marginal or submarginal sutures, which cannot be interpreted as autapomorphic characters that define a monophyletic group (e.g., Fortey, 1990; Geyer, 1998). Cotton (2001, 2002) presented a phylogenetic analysis which demonstrated that the family is polyphyletic and comprises four distantly related clades. A monophyletic family Conocoryphidae must be restricted, according to Cotton (2001, 2002), to the genera *Conocoryphe* Hawle & Corda, 1847, *Parabailiella* Thoral, 1946, *Ctenocephalus* Hawle & Corda, 1847, *Hartella* Matthew, 1885, *Elyx* Angelin, 1854, *Holocephalina* Salter, 1864, *Bailiella* Matthew, 1885, *Bailiaspis* Resser, 1936, *Cainatops* Matthew, 1890, and *Tchaiaspis* Korobov, 1966.

Nevertheless, Kim et al. (2002) emphasised that in-group relationships of the conocoryphid genera were partly imperfectly resolved in Cotton's analysis (2002) so that a number of species require a better understanding of the sister groups of the Conocoryphidae among the "ptychoparioids" to define the morphologic ranges of the genera. In addition, comprehensive analyses of the conocoryphid species are needed rather than a subset of representative species.

Genus *Bailiella* Matthew, 1885

Type species. Conocephalites baileyi C.F. Hartt in Dawson, 1868; from the Chamberlain's Brook Formation of New Brunswick, Canada; subsequent designation by Miller (1889).

Discussion of the generic concept. The *Bailiella* plexus is another insufficiently clarified clade of solenopleuroid trilobites. As already discussed by Kim et al. (2002), the introduction of genera to subdivide the earlier "collective genus" *Bailiella* created taxa which were based on diagnostic characters of different weight, or phylogenetic significance. The genus *Bailiaspis* Resser, 1936, was erected for species which differ from *Bailiella baileyi* Hartt in Dawson, 1868 by possessing a slight to marked rearward extension of the anterior border (or "plectrum") in front of the glabella and, thus, an anterior border furrow which curves backward on the sagittal line (e.g., Walcott 1884a, pl. 4, fig. 2, 2b; Westergård 1950, pl. 6, figs. 4, 5; Egorova et al. 1982, pl. 1, fig. 8, pl. 11, fig. 11; Kim et al. 2002, fig. 4.1–4.4). Species with a considerably thickened anterior border on its median part but a more-or-less straight anterior border furrow were placed among *Bailiella* by Resser (1936), e.g. *B. emarginata* (Linnarsson, 1877). The absence of this extension of the anterior border leads to a border which is virtually identical in *Bailiella*, *Conocoryphe* (e.g., Šnajdr 1958, pl. 31, figs. 8–13; Hutchinson 1962, pl. 13, fig. 8a) and other genera of the family, thus illustrating a plesiomorphic state. Species of *Bailiella* have moderately inflated fixigenae (e.g., Westergård 1950, pl. 5, figs. 5b, 6b, 6c, 10c) very similar to those seen in the species of *Conocoryphe* (e.g., Hutchinson 1962, pl. 13, fig. 7b) and *Elyx* (e.g., Hutchinson 1962, pl. 12, fig. 5b; Westergård 1950, pl. 7, fig. 3c). This character state also represents a plesiomorphic condition. It should be emphasised, however, that considerable differences exist in the way in and degree to which the preglabellar area is depressed around the sagittal line. Typical species of *Bailiaspis*, such as *B. glabrata* (Angelin, 1854) and *B. dalmani* (Angelin, 1864), show a markedly sunken preglabellar area and adjacent part of the anterior border furrow so that the genae/"preocular areas" are distinctly separated.

A number of conocoryphid genera have a cephalic suture in a marginal to submarginal position. In this case, the librigenae consist of only part of the lateral cephalic border or the lateral cephalic border and (part of) the adjacent border furrow. Accordingly, at least part of the border and border furrow can be traced along the lateral margin to the level of the occipital furrow (e.g., Westergård 1950, pl. 6, fig. 9a, pl. 7, figs. 1–4; Hutchinson 1962, pl. 10, fig. 18a; Dean 1982, fig. 11). In contrast, the sutures in the species of *Bailiella* swing adaxially at, or in front of, the glabella's mid-length thereby dissecting the lateral border and border furrow and the most distant parts of the fixigenae (e.g., Westergård 1950, pl. 5, figs. 1–3, 6–8, 10–12, pl. 6, figs. 1–3; Šnajdr 1958, pl. 35, fig. 1; Geyer 1998, pl. 4, fig. 4; Kim et al. 2002, fig. 3.1). The same condition is also present in *Bailiaspis* (e.g., Westergård 1950, pl. 6, figs. 4, 5) and in some species of *Conocoryphe* (e.g., Sdzuy 1968, pl. 10, figs. 7–15, 18–21, 23). Therefore, this feature does not provide an unequivocal criterion for a monophyletic status of *Bailiella*. Moreover, some species which are currently assigned to *Bailiella* (e.g., Zhang & Jell 1987, pl. 35, figs. 1–7) have lateral borders that extend backward and are connected with the abaxial parts of the posterior border.

Unfortunately, more-or-less complete dorsal exoskeletons are only known from a limited number of species assigned to *Bailiella*, such as *B. baileyi* (see Matthew 1891), *B. levyi* Munier-Chalmas & Bergeron in Bergeron, 1889 (see Thoral 1946), *B. lyelli* (Hicks, 1871 (see Lake 1940), *B. lantenoisi* (Mansuy, 1916), and *B. emarginata* (Linnarsson, 1877) (see Westergård 1936). Accordingly, possible differences in the characters of the post-cephalic exoskeleton are largely unknown.

Sdzuy (1961, pp. 671–672) discussed the problems of *Bailiella*, but concentrated on the species united under *Bailiella* by Resser (1936) and subsequent authors. He suggested that two groups may be recognisable: one group, represented by *B. lyelli* and *B. emarginata*, is characterised by a cephalic border which does not taper distinctly from the anterior towards the lateral parts; with the suture running distinctly into the area of the fixigenae; and with 15 thoracic segments. A second group, with *B. levyi* and *B. lantenoisi*, is characterised by a cephalic border that tapers distinctly along the lateral margin, almost fading posteriorly; by a cephalic suture that runs in the lateral border furrow or at a very abaxial position on the genae adjacent to the border furrow; and by a thorax composed of 14 segments. *Bailiella baileyi* is only known from slightly distorted specimens, and no well-preserved, complete, unequivocally determinable exoskeleton seems to be known from the species. Matthew (1891, pl. XI, fig. 10) presented a reconstruction of *B. baileyi*, which shows 16 thoracic segments on the left and 17 segments on the right side, but in the text noted that the species has 14 segments. Nevertheless, the cephalic suture in *B. baileyi* is in a decidedly marginal position as in *B. levyi* and *B. lantenoisi* and also shows a clearly tapering lateral border (see Kim et al. 2002, fig. 4.7, 4.8; also contra Matthew's reconstruction of 1891, pl. XI, fig. 10).

Another difference between the two morphogroups identified by Sdzuy (1961) is the subtle difference in the shape of the glabella. This difference is regarded herein as of even higher taxonomic significance: According to Sdzuy (1961), the "*levyi-lantenoisi* group" has glabellas with a relatively acute frontal lobe, tapering more-or-less uniformly and with almost straight lateral margins in the middle part. The species of the "*lyelli-emarginata* group" have glabellas with a broader frontal lobe and curved middle portions of the lateral glabellar margins. In conclusion, it is suggested that the two groups identified by Sdzuy (1961) require taxonomical distinction and should be separated on the genus level. According to the morphological characters known from *B. baileyi*, this species belongs to the "*levyi–lantenoisi* group" so that this group represents the true genus *Bailiella*.

This indicates that the "*lyelli-emarginata* group" of Sdzuy appears to represent a genus different from *Bailiella*, which requires a new name. Sdzuy (1961) suggested that this genus may be termed *Tangshiella* Hupé, 1953b. However, the case of appropriate nomenclature is more complicated: Hupé (1953b) intended to introduce a new genus based on *Bailiella ulrichi* Resser & Endo, 1937, which could have been available as a name for the new genus. Hupé (1953b) used the name "*Tangshiella*" in his fig.

121.8, but "*Tangshihella* n. g." on p. 194. In addition to the name, no diagnosis or data of its discrimination are provided. Also, *B. ulrichi* is a doubtful taxon: Resser & Endo's (1937, pl. 41, figs. 5, 6, 8) description does not fit with the figured specimens so that it appears to be confused with another species. Furthermore, the figured specimens of *B. ulrichi* match the characters seen in *B. lantenoisi* so that *B. ulrichi* appears to be a junior synonym of *B. lantenoisi*. In any case, Hupé's (1953b) introduction of new genus must be regarded as an illegitimate act. Instead, the *Emarginobailiella* n. gen. is suggested as a genus name for the group in the strongly revised concept presented here (see below).

A few early species hitherto assigned to *Bailiella* have a glabella which tapers moderately and has a gently rounded and relatively broad anterior margin of its front. In addition, these species have a shield-like outline of the cephalon with a high length:width ratio. Also, the anterior border in these species is typically of low convexity in profile, and it is defined by a broad anterior border with a tendency to include a low swelling in the sagittal sector. A typical species for this group was introduced as *Bailiella dilatata* Geyer, 1998 from the (probably earliest Wuliuan) *Ornamentaspis frequens* Zone of the High Atlas. Two new species introduced herein from the same stratigraphic level of the Tannenknock Formation of the Franconian Forest show the same combination of such features, and *Bailiella inconspicua* Geyer, 1998 can be assigned to the same clade. This group is separated here as the new genus *Prioscutarius* (see below).

Furthermore, the *levyi-lantenoisi* group is only uniform in terms of the shape of the glabella and the position of the cephalic suture, but its species require a careful analysis in respect to other features. *Bailiella levyi* and *B. lantenoisi* differ considerably in the areal extensions of the glabella and the preglabellar areas. The glabella in *B. levyi* is relatively short, but with a higher width:length ratio, and the preglabellar field and the anterior border are much broader. The same configuration is seen in other species from the Languedocian of West Gondwana, such as *Bailiella barriensis* Sdzuy, 1958a, *B. griffei* Courtessole, 1967, *B. souchoni* Courtessole, 1967, *B. seguieri* Courtessole, 1967 and *B. sepulcra* Álvaro & Vizcaïno 2018. This group certainly represents a clade derived from the *Bailiella* stock and should be separated taxonomically. It is suggested to separate the group formally as the new genus *Courtessolia* (see below).

Summarised, unambiguous apomorphies are unknown to date from *Bailiella* so that the genus in its traditional concept is paraphyletic. Although there seems to be no practical procedure to solve this problem in all aspects to date, it is suggested to split the genus into an emended genus *Bailiella*, the new genus *Emarginobailiella* for the Baltic, West Gondwanan, Avalonian and Sibirian species of the *emarginata* group, and the new genus *Courtessolia* for the relevant species of the *levyi* clade of West Gondwana.

Discussion on species assigned to Bailiella. More than 50 named species are or have been assigned to *Bailiella*. A short assessment of the most important of these species follows (in alphabetical order):

Bailiella aequalis (Linnarsson, 1883) is an insufficiently known species based on a few poorly preserved, distorted cranidia from the *Ptychagnostus punctuosus* Biozone in the Alum Shale Formation of Scania. Additional reports claim the species to occur in Bornholm (Grönwall 1902) and in the *Ptychagnostus gibbus–Mawddachites hicksii* Zone of Avalonian south-eastern Newfoundland (Howell 1925; Fletcher 2006). The species has a more-or-less equally tapering glabella with a narrow (tr.) front; an anterior border of subequal breadth throughout its extension, a more-or-less equally curved anterior border furrow continuing into the lateral sector without a notable bow, and a moderately broad preglabellar field (Fig. 98). These characters remind to species of *Conocoryphe*. Unfortunately, the precise position of the facial suture is unknown, and the specimens refigured in Westergård (1950, pl. 5, fig. 12, pl. 6, figs. 1–3) are slightly ambiguous in this aspect.

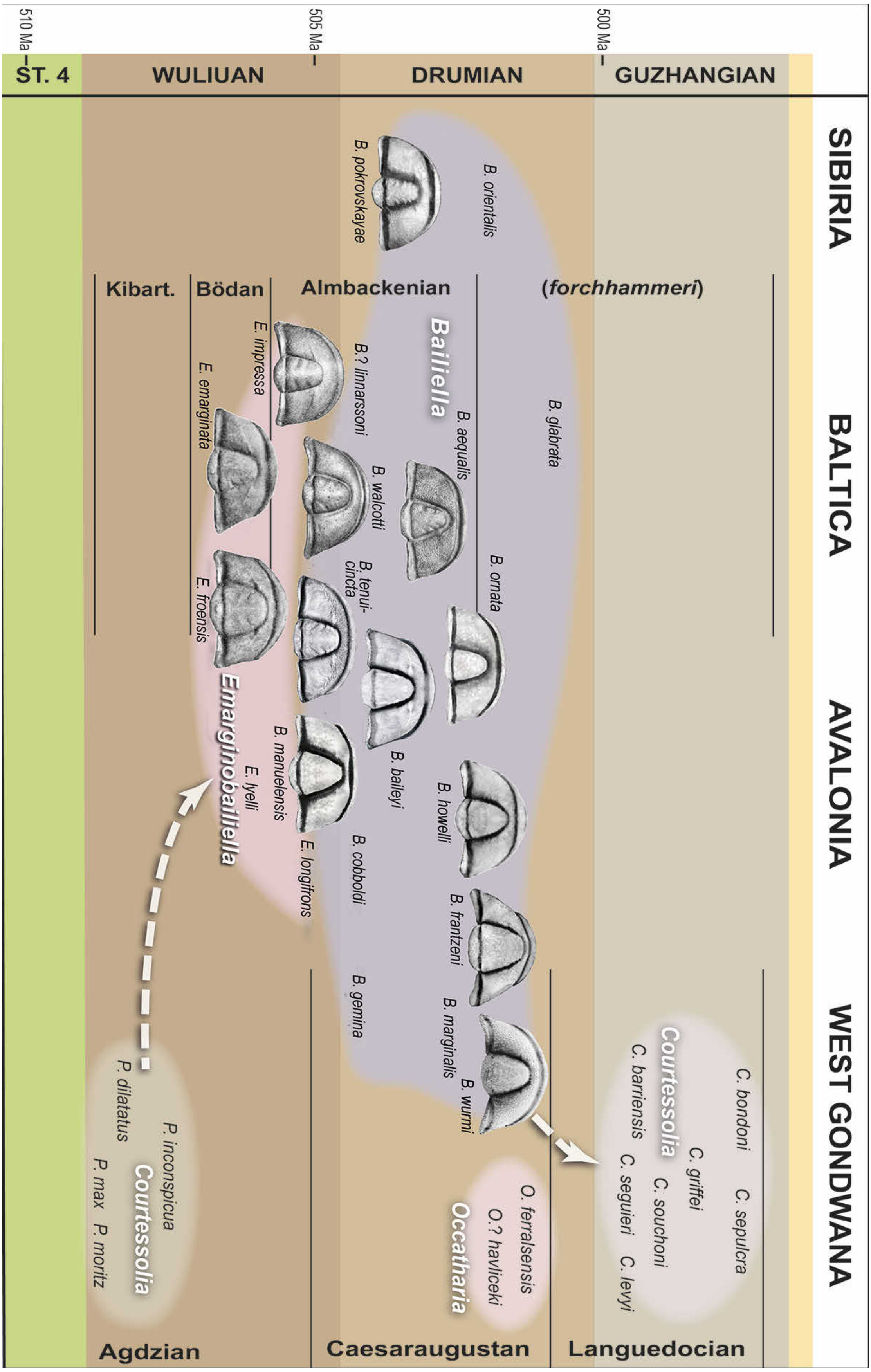

Fig. 98: Cranidia of key species of the *Bailiella* clade with suggested generic affinities. The reconstruction are graphic reconstructions from primarily the type material of the species.

Sdzuy (2000) assigned specimens of *Bailiella* from the Lippertsgrün Formation of the Franconian Forest area, Germany, from the *Solenopleuropsis* Zone, to the same species. The specimens from the Franconian Forest (Sdzuy 2000, pl. 3, figs. 11–14, pl. 7, figs. 4*–6*) are all relatively strongly distorted. From what can be seen, they are somewhat similar to *B. aequalis*. However, the preglabellar field in the specimens from the Lippertsgrün Formation is distinctly broader (sag.) that that in *B. aequalis*, and the precise position of the facial suture almost certainly is in an even more lateral position so that the lateral border in the cranidium is still present at the level of L2. Despite the imperfect preservation of the specimens, it is obvious that the specimens represent a new species which is introduced below under the name *Bailiella marginalis* n. sp.

A further specimen of *Bailiella* from the Lippertsgrün Formation was assigned tentatively to *B. aequalis* by Sdzuy (2000, pl. 3, fig. 15). This specimen is an incompletely preserved cranidium with similar the characters discussed above for *B. marginalis* n. sp. However, the single cranidium is clearly distinguished in having a narrow occipital ring with a subtriangular outline in dorsal view due to a pronounced terminal thorn. In addition, the cranidium appears to have a denser granulation of the exterior of the cuticle.

Bailiella angusta Kobayashi, 1960 is a species from the Taiki Formation of South Korea, “Bailiella Zone”, based on a single cranidium which is slightly distorted and lacks most of the surface structures (Kobayashi 1960, p. 373–373, pl. XIX, fig. 18). Kobayashi’s short description and discussion indicates that the precise relationship to other species of the genus was poorly investigated. The specimen has a relatively slender glabella with apparently almost straight lateral margins and a narrow frontal lobe. The anterior border appears to be of moderate width with a conspicuous growth in width towards the axial line. The anterior border furrow is shallow, but probably in part due to the deformation. The preglabellar field is apparently relatively wide, at least slightly broader than the anterior border, but this is also a result of compression. Other characters are hardly recognisable. Summarised, the species must be regarded as either doubtful and not well recognisable, and it should be restricted to the holotype.

Bailiella arcuata (Matthew, 1885) was described as “*Conocoryphe* (*Bailiella*) *baileyi* var. *α. arcuata*”. According to Matthew (1895), the material was collected from his “horizon c^2”, thus from the same strata as *B. baileyi* and *B. elegans* (Hartt in Dawson, 1868), of the *Paradoxides davidis* Zone (Matthew 1885, pl. I, fig. 23, 23b). However, the way in which Matthew (1885) described and characterised it sheds doubt whether he intended to introduce a new taxon (in modern sense). He emphasised that it “is quite possible that it may be only a sexual variation of form” (Matthew 1885, p. 113). None of the differences described by Matthew are of particularly taxonomic significance. Resser (1936, p. 16) raised Matthew’s form to species level with one of his two-line remarks, albeit wrongly citing Matthew’s remark.

Bailiella artagena (Howell, 1937) was described as *Conocoryphe*? *artagena* from the St. Albans Formation of Vermont, based on a single cranidial fragment which consists of the right gena and part of the glabella (Howell 1937, pl. 3, fig. 7). Resser (1938) transferred the species to *Bailiella*, but Shaw (1962) showed that the species is a junior synonym of *Meneviella venulosa* (Salter, 1865).

Bailiella baileyi (Hartt in Dawson, 1868) was first described from the Fossil Brook Member of the Chamberlain’s Brook Formation, New Brunswick, and later reported from the distinctly younger *Hartella bucculenta* Zone of Avalonian Newfoundland (Fletcher 2006). The species has a distinctly tapering glabella with barely curved lateral margins and a narrow frontal lobe with a more-or-less evenly curved anterior margin. The occipital ring is moderately wide adjacent to the axial furrow and grows in sag. width, with a subevenly curved posterior margin and an inconspicuous subterminal node. The anterior border grows in breadth towards the sagittal line, but is only moderately wide (sag.), slightly broader than the anterior border furrow and half to two-thirds the sag. breadth of the preglabellar field. The anterior border furrow is curved throughout its course, with distinctly more pronounced curvature in the anterolateral sector, but without a narrow bow or kink. The facial suture lies at a pronouncedly marginal position so that it intersects the lateral border furrow at the level of S1 or slightly anterior to it, and the genal corner is completely preserved on the cranidium, indicating that no genal spine was developed at this species. Bulbous swellings are developed on the genae close to the axial furrow (Fig. 98). These structures proceed into relatively well visible relics of the eye ridges and are larger than those in other species of the *Bailiella* group.

Pygidia assigned to the species (e.g., Kim et al. 2002, fig. 4.5, 4.6) have a slightly tapering axis composed of 3 axial rings which are progressively less well marked towards the posterior, and a relatively large terminal axial piece. The pleural areas show relatively shallow furrows, which also fade towards the posterior and with indistinct interpleural furrows only. The lateral and posterior borders are very narrow and poorly defined, and a faint plectrum is visible posterior to the rear end of the axis.

Bailiella barriensis Sdzuy, 1958a is a little-known species based primarily on material from the Los Barrios de Luna section of the Cantabrian Mountains. However, Sdzuy (1961) identified the species from the Valdemiedes sections in the Iberian Chains, Aragón, as well. The species (see Sdzuy 1961, pl. 33, figs.1–4, 5?, text-fig. 52) is similar to *B. levyi* in nearly all aspects. The most conspicuous difference (and usually the only distinct difference in distorted specimens) is the more prominent anterior border, which attains a slightly swollen aspect in large individuals. The Spanish specimens of *B. barriensis* also show a slightly broader frontal lobe of the more suboval glabella with a more rounded rather than subacute glabellar front. *Bailiella barriensis* occurs in the same strata as *B. levyi* so that one could suspicious that both are just morphotypes of the same species or their different morphologies caused by different amounts of deformation, which was ruled out by Sdzuy (1961, p. 673). Indeed, the anterior border of *B. barriensis* seems to have a pronounced dorsal elevation on the sagittal line as visible in anterior views (e.g., Sdzuy 1961, pl. 33, fig. 2), which is much less developed in *B. levyi* and reminds to the morphology seen in *Bailiaspis glabrata* from Sweden.

Bailiella binodosa Bi in Qiu et al., 1983 is usually held for a junior synonym of *B. lantenoisi*. It is only known from a single, incomplete cranidium. The cranidium differs from typical specimens of *B. lantenoisi* in having a more regularly tapering glabella and a broader (sag.) preglabellar field. The anterior border only slightly widens towards the sagittal line, and the anterior border furrow is only moderately broad and thus narrower than in typical specimens of *B. lantenoisi*. In addition, the specimen figured in Qiu et al. (1983, pl. 28, fig. 6) shows the slight lenticular rise in the anterior border furrow located in the central sector. The single specimen is difficult to precisely assess, but it shows enough differences to *B. lantenoisi* that it cannot be definitively synonymised with that species. Accordingly, it should be maintained as a separate species unless more material from the type locality will indicate that the species is just based on an abnormally developed individual.

The mention of a “*Bailiella brevis* (Matthew, 1890)” (e.g., Yuan et al. 2012, p. 122) is obviously a mistake: Matthew (1891) figured a sketch of the dorsal exoskeleton of “*Conocephalites Baileyi* Hartt” on his pl. XI, fig. 10. The relevant lettering on the plate is unfavourable arranged so that the figure number seems to have been mistaken as “13” instead of “10”. This figure (Matthew 1891, pl. XI, fig. 13), however, shows the trace fossil “*Arenocilites brevis* n. sp.” as correctly listed in the figure captions. “*Bailiella brevis* (Matthew, 1890)” is thus a *nomen nullum*.

Bailiella bullata (Howell, 1925) is a species introduced as *Conocoryphe bullata* from the *Paradoxides bennetti* Zone of the Manuels River Formation at Manuels, south-eastern Newfoundland. In fact, this probably indicates that the specimens originated from the upper part of the Chamberlain’s Brook Formation rather than the Manuels River Formation. Howell’s original material consisted of two figured partial cranidia (Howell 1925, pl. 3, figs. 10, 11) which do not provide a precise picture of its morphology. The glabella tapers distinctly and has barely curved lateral margins and a narrow frontal lobe. The anterior border grows in breadth towards the sagittal line. It is slightly more than moderately wide (sag.), slightly broader than the sag. preglabellar field. The anterior border furrow is curved throughout its course, with distinctly more pronounced curvature in the anterolateral sector, but without a narrow bow or kink. The facial suture lies at a pronouncedly marginal position. One of Howell's specimens is a partial cranidium in which the suture appears to run within the lateral border, and the genal angle preserved on the cranidium has a transverse furrow crossing the lateral border. Howell's description does not contribute to a clarification of the characteristics, and the species was not claimed to have been collected in any of the subsequent studies of the Manuels River area.

Bailiella cobboldi Resser, 1936 has been introduced based on specimens published by Cobbold (1913, pl. III, fig. 16a–c) under the name *Conocoryphe* (*Liocephalus*) *impressa* and in Cobbold (1931, pl. CCXXIII, fig. 22) as *Conocoryphe emarginata longifrons*, respectively. from the *Mawddachites hicksii*/*P. aurora* Biozone of the Comley and Rushton area, Shropshire, U.K. Lake (1940, pl. XL, figs. 12–14) redescribed the species, which has an *emarginata*-type glabella with gently curved lateral margins and a moderately broad front; a relatively broad (sag. and exsag.) anterior border of approximately equal width (sag.) as the preglabellar field; facial sutures in a relatively adaxial position so that they intersect the lateral border furrows at a level short distance posterior to the glabellar front, but traverse the posterior border close to the genal angle; and an occipital ring which is fairly narrow laterally, but grows to considerable sagittal length and carries a well-developed occipital node in a central position.

Chernysheva (1953, pl. 1, fig. 6) identified a specimen from the (at that time) "*Paradoxides hicksi* Zone" (now *Corynexochus perforatus*–*Anopolenus henrici* Zone) on the eastern part of the Siberian Platform as *B. cobboldi*. The specimen was refigured by Korobov (1973, pl. XI, fig. 5) and is certainly an immature cranidium with a short, moderately tapering glabella with nearly straight lateral margins and a broadly rounded frontal lobe. The anterior cephalic margin is comparatively strongly arched, resulting in the cranidium having an almost semicircular outline. The lateral and anterior border as preserved on the cranidium have a narrow crescent-shaped outline. The anterior border furrow shows an almost even curvature, but the median section around the sagittal line is shallower and slightly broader, almost a shallow swell as seen in *B. dilatata*. The facial suture lies in a relatively marginal position, intersecting the lateral border furrow at about the level of S2, and the genal corners are partly preserved, suggesting that a distinct genal spine was not developed in this species. The specimen almost certainly represents a new species, but more specimens of adult growth stages will be needed to characterise it.

Bailiella comleyensis Resser, 1936 is another species which Resser erected based on material described and figured by Cobbold (1913, pl. III, fig. 18) as *Conocoryphe aequalis*. The single specimen on which the species was based originated from the *Mawddachites hicksii*/*P. aurora* Biozone of the Comley area, Shropshire. This specimen is preserved as part and counterpart and was redescribed in Lake (1940, pl. XL, figs. 7, 8). The species resembles *B. cobboldensis*, having an *emarginata*-type glabella with gently curved lateral margins and a moderately broad front; a moderately broad (sag. and exsag.) anterior border, which is thinner than the preglabellar field; facial sutures in a relatively adaxial position so that they intersect the lateral border furrows at the level of the frontal lobe or short distance posterior to the glabellar front, but traverse the posterior border close to the genal angle; and an occipital ring which is fairly narrow laterally, but grows in length towards the sagittal line and has an occipital node located slightly anterior to the centre of the occipital ring. The glabella of the holotype is certainly shorter than in the specimens that characterise *B. cobboldi*, but the single fragmentary cranidium is somewhat insufficient to fully characterise *B. comleyensis*.

"*Conocoryphe dalmanni* Angelin?" is just a name applied by Sjögren (1872) to unfigured specimens from the *Oelandicus* beds of Stora Frö on the island of Öland, Sweden. Almost certainly, the brief characterisation applies for *Bailiella emarginata*.

Bailiella dilatata Geyer, 1998 is a very distinct species from the Bréche à *Micmacca* Member of the Jbel Wawrmast Formation, *Ornamentaspis frequens* Biozone, Agdzian Stage (probably lowest/earliest Wuliuan), from the Lemdad Syncline of the High Atlas, Morocco. The species has an anterior border, which grows gently in sag. and exsag. width towards the sagittal line, with faint and inconspicuous anterolateral kinks. The border furrow is strikingly broad, somewhat indistinctly defined from the anterior border, the preglabellar field and the preocular areas, and it has a shallow median rise for most of its course. In large specimens the anterior border furrow is broader than the moderately wide preglabellar field in the sagittal line. The glabellar is quite stout, with a broadly curved anterior margin of the frontal lobe and gently curved lateral margins. The occipital ring is narrow close to the axial furrows but reaches distinctly posteriorly on the sagittal line due to its strongly curved posterior margin. The facial suture lies at a relatively lateral position and dissects the lateral border furrow approximately at the level of L3.

This species is typical for a group of species which differ in these characters from the typical species of *Bailiella* and are also distinguished by their very early occurrence. They are separated under the new genus *Prioscutarius*, and *Bailiella dilatata* is selected as its type species.

A species similar to *Bailiella niuxinshanensis* n. sp. was described under the name *Occatharia dongshankouensis* Yuan & Zhang in Yuan et al., 2016 is a species of the *Bailiella* group that was never formally assigned to that genus. The species co-occurs with specimens identified as *B. lantenoisi* in the Hulusitai Formation of the Ordos Plateau in Inner Mongolia and exemplifies a morphological gradient: It shares most of the characters with these specimens of “*B. lantenoisi*”, but differs primarily in having a sunken preglabellar field, almost straight lateral margins of the glabella and a low curvature of the anterior margin of the frontal lobe. It thus closely resembles this species, which is introduced below as *Bailiella niuxinshanensis* n. sp. *Occatharia dongshankouensis* is also reassigned to *Bailiella* and discussed below.

Bailiella elegans Lee in Zhou et al., 1982, described from the Xuzhuang Formation of Inner Mongolia, is usually held for a junior synonym of *B. lantenoisi*. The type material consists of two figured specimens (Lee in Zhou et al. 1982, pl. 60, fig. 16, p. 61, fig. 1), one very well-preserved cranidium and a well-preserved pygidium from the same stratum. Indeed, the cranidium equals the cranidium of *B. lantenoisi* in most aspects, including the shape and size of the glabella, the shape and topography of the anterior border, and the presence of a minute longitudinal (tr.) elevation developed in the central sector of the anterior border furrow. However, differences can be seen in the distinctly broader occipital ring with broadly elliptical outline and a subcentral tubercle; more anteriorly located adaxial parts of the eye ridges; a slight, but well recognisable depression of the preglabellar field, which causes a minor backward swing of the posterior margin of the anterior border furrow; and a slightly more adaxially located suture, which causes the lateral border furrow to be traversed in a more posterior position, approximately at the level of S2. The pygidium has a moderately broad to broad rhachis with two well developed and one faint ring, the terminal axial piece being relatively broad and having a nearly evenly curved posterior margin. The pleurae show two well-defined rings with well-developed pleural furrows and faint interpleural furrow continuously less well developed towards the posterior. The lateral and posterior border as obsolescent, the marginal parts showing occasional faint swellings. Remarkable is a distinctive angulation of the anterior border, which results in a strong backward deflection of the abaxial parts. Such a striking rearward direction of the anterior border is not known from the pygidium of *B. lantenoisi*.

Summarised, the type material of *B. elegans* differs distinctly from typical specimens of *B. lantenoisi*/ *ulrichi* and cannot be readily synonymised with the latter species. *Bailiella elegans* appears to represent a different species unless additional collection may prove that its type material represents unusual specimens of otherwise typical specimens of *B. lantenoisi* from the Xuzhuang Formation of Inner Mongolia.

Bailiella emarginata (Linnarsson, 1877) is among the best-known species of the genus *Bailiella* in its traditional concept, although it is known only from a few localities on the island of Öland, Sweden, all representing the Wuliuan *Eccaparadoxides*? *insularis* Biozone. Westergård (1936, 1950, pl. 5, figs. 1–4) has nicely characterised the species, which shows a considerably thickened and slightly curved anterior border so that the anterior border furrow is distinctly less curved in its central part across the sagittal line and show a faint kink anterolaterally towards the more anterolaterally located section of the border furrow. The cephalic suture dissects the border furrow clearly posterior to the glabellar front, approximately on the level of the clearly recognisable bulbous swellings close to the axial furrow, which represent the relics of the eye ridges. The glabella has a relatively low front, the margin of which appears to be almost truncated in a shallow, oblique manner on both sides of the sagittal line. Together with the slightly curved lateral margins of the glabella with its faintly bulbous L1, the glabella has an almost parabolic outline. The preglabellar field is relatively short (sag.) and faintly lower than the cheeks in the “preocular areas” (Fig. 98). The librigena includes a well recognisable lateral part of the cheek, and it has a moderately long genal spine. The nearly complete exoskeleton figured in Westergård (1950, pl. 5, fig. 2) has 15 segments, and shows relics of the pygidium with anteriorly well-developed furrows. It needs to be emphasised that these characters are only significant for adult specimens. Two immature cranidia illustrated by Westergård (1950, pl. 5, figs. 1, 2) show specimens with a similarly thickened anterior border and a relatively adaxial position of the suture, but the glabellas in these specimens taper more-or-less equally and thus show nearly straight lateral margins, a narrow glabellar front, and a broader (sag.) preglabellar field.

Bailiella frangtengensis (Reed, 1934), introduced as *Conocoryphe frangtengensis* by Reed (1934, pl. II, figs. 9–12), was assigned to *Bailiella* by Shah (1973), who described a number of *Bailiella* specimens from the Nutunus Formation of the Baramula District, Kashmir, India, which he identified as different species of *Bailiella*, *Holocephalina* and *Bailiaspis*. The relevant specimens studied by Shah (1973) were suggested by Jell & Hughes (1997) to differ in characters because of considerable deformation and to represent just a single species. This species was synonymised with *Bailiella lantenoisi*, well known from Vietnam, Korea and the Liaoning province of Northeast China. Although it is conclusive that all of Shah’s specimens actually represent a single species, the imperfect preservation and lack of precisely recognisable characters prevents the Kashmiri material to be confidently identified as *B. lantenoisi* (see discussion below).

Although Shah (1973, figs. 1e, 1f, 2b) identified some of his specimens from the Baramula District firmly as *Bailiella frangtengensis*, his discussion takes the determination with reservation and mentions differences to Reed’s (1934) specimens, particularly in the glabella. These differences are regarded here (in accordance with Jell & Hughes 1997) as a product of distortion and thus without taxonomic relevance.

Bailiella frantzeni Sdzuy, 2000 was described from the Lippertsgrün Formation, *Solenopleuropsis* Biozone, Drumian, of the Franconian Forest area, Germany. The material consists only of two specimens (Sdzuy 2000, pl. 3, figs. 7, 8, pl. 7, fig. 7*) which Sdzuy confidently assigned to the species. Both are very imperfectly preserved, and it is difficult to assess the critical characters, and the original diagnosis and comparison is of little help when trying to highlight the species’ peculiarities *sensu* Sdzuy (2000). The paratype is a small fragment that does not show any characters of the anterior half and the lateral margins of the cranidium. Thus, only the holotype provides clues for the species’ characteristics. What can be recognised is that the anterior border is of nearly the same width (sag.) as the preglabellar field, with only a minor growth in width towards the sagittal line. The glabella has a moderately wide frontal lobe and slightly curved lateral margins, with an apparently relatively narrow occipital ring. The facial suture appears to intersect the lateral border furrow approximately at the level of S2 (Fig. 98).

Bailiella froeensis Westergård, 1950 is a little known species from the Alum Shale Formation, *Eccaparadoxides*? *insularis* Biozone, of Stora Frö, Öland. Westergård (1950, pl. 5, fig. 5a–c) listed only one specimen of his new species recovered from a limestone, and no further, unequivocally determinable material has been published to date. Nevertheless, the species appears to be distinct, characterised by a relatively curved facial suture and a fairly narrow cephalon relative to its length as well as a proportionally large glabella. The species resembles the co-occurring *Bailiella emarginata*, but differs in the proportions of the cephalon as well as the surface ornamentation and a considerable forward curvature of the occipital furrow (emphasised by Westergård 1950). The course of the cephalic suture is certainly less unique and may be accentuated by the preservational conditions of the holotype, but it runs in a distinctly adaxial position to dissect a lateral part of the genae and traverses the border furrow slightly anterior to the level of the bulbous swellings created by the eye ridges adjacent to the axial furrows. The anterior margin of the frontal lobe of the glabella shows a slight, oblique double truncation with a faint tip on the sagittal line (Fig. 98). Westergård (1950) spelled the species name “fröensis”, which violates the ICZN rules, and it is suggested to be corrected here.

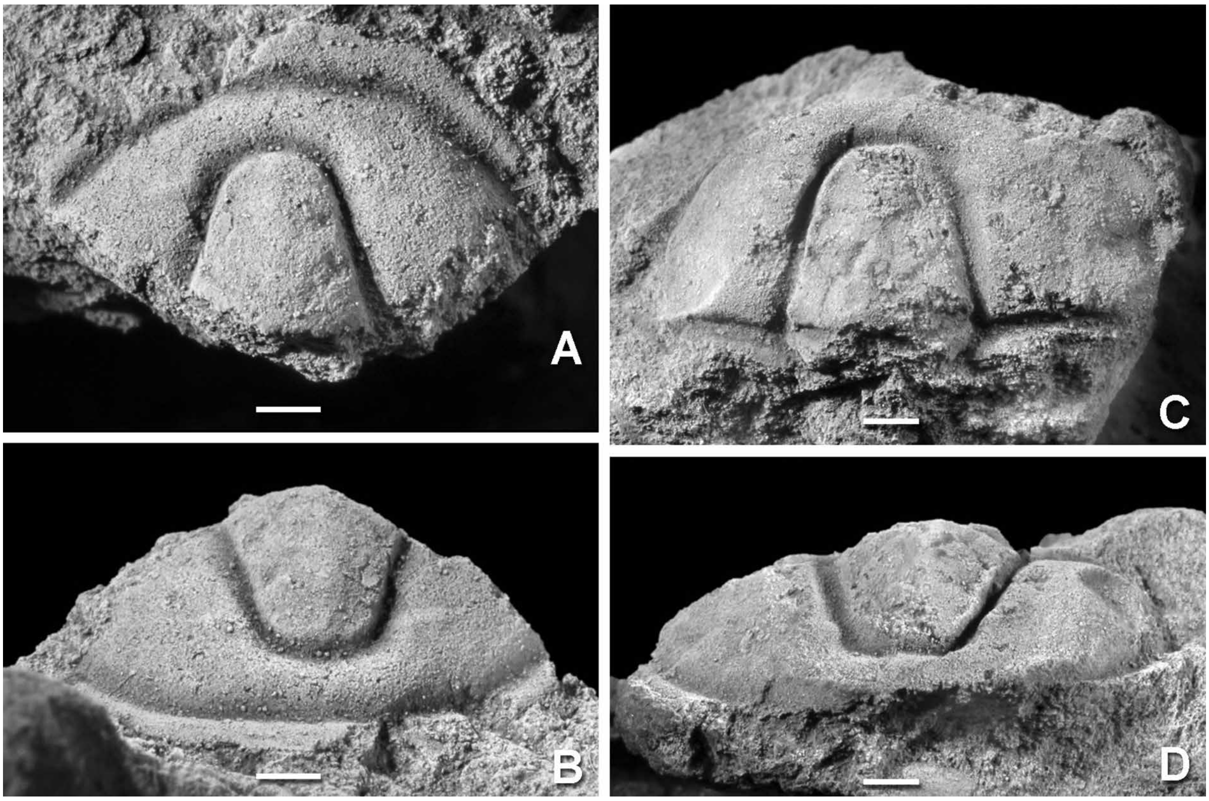

Fig. 99: *Bailiella gemina* (Schmidt, 1944). **A, B** GSB X06277/5, incomplete cranidium, internal mould with relics of the granulose surface, dorsal (A) and anterior (B) views, Doberlug IV/1929 drill core, depth 189 m. **C, D** GSB X06277/6, incomplete cranidium, internal mould with relics of the granulose surface, dorsal (C) and anterior (D) views, Doberlug IV/1929 drill core, from unknown depth. Scale bars 1 mm.

Bailiella gemina (Schmidt, 1944) has been introduced based on specimens from a drill core in the Delitzsch–Torgau–Doberlug Syncline of Saxony, Germany. Unfortunately, the original figures (Schmidt 1944, pl. 24, figs. 11–13) do not provide a satisfying image of the morphology, and it is not clear when-judging from these figures whether the specimens belong to the same species. However, re-examination of the type material indicates that the three figured specimens indeed represent the same species, and that this species is easily distinguished from all other species assigned to *Bailiella*: The facial suture lies in a sub-marginal position so that is only cuts through no more than half of the lateral border, having little change in direction throughout its course. The lateral and anterior borders are relatively thick, with little change in dimensions from the anterior to the lateral border. The glabella is conical, with almost straight lateral margins, but a relatively broad frontal lobe and an almost subtruncate frontal margin. Bulbous swellings are present on the genae, and these are located somewhat distant to the axial furrow. Accordingly, this species appears to differ significantly from almost all typical species of *Bailiella*. Nevertheless, the unpublished material from the D IV/1929 drill-core near Kirchhain includes specimens with a more typical *Bailiella* morphology (Fig. 99) so that it seems as if Schmidt (1944) selected specimens with a particular morphology from an amount of relatively broad variability.

Bailiella glabrata (Angelin, 1854) was first described from the *Ptychagnostus punctuosus* Biozone (now the lower part of the *Lejopyge laevigata* Zone) of the Alum Shale Formation of Andrarum, Scania (Angelin 1854, pl. 37, fig. 8, 8a), particularly from the Andrarum Limestone. It is generally regarded as a characteristic species of the genus *Bailiaspis*. The species belongs to a group of species which is characterised by an anterior border that is considerably broadened on the sagittal line, but defined posteriorly by a straight or almost straight anterior border furrow, This configuration differs distinctly from the group of species with a broadened anterior border, in which the anterior border furrow curved posteriorly in the sagittal sector so that the posterior margin of the anterior border produces a rearward protrusion, but its anterior margin has a relatively even and moderate curvature (as in *Bailiaspis dalmani* (Angelin, 1854), known from the Exsulans Limestone of the Alum Shale Formation in the same area. This is certainly a strong argument with the result that the cladistic analysis by Cotton (2000) suggested *B. glabrata* to be grouped in *Bailiella*. However, gerontic specimens of *Bailiaspis glabrata* show a slight rearward curvature of the anterior border furrow as well.

Bailiella glabrata has also been reported from the Guzhangian (and thus distinctly younger) strata of the Bergleshof Formation in the Franconian Forest, Germany. However, the specimens from the Bergleshof Formation determined in Sdzuy (1966) as *Bailiella glabrata* appear to represent a different, not yet established species.

Bailiella griffei Courtessole, 1967 from the Montagne Noire, southern France, occurs in the *Eccaparadoxides macrocercus* Biozone and thus in the lower Guzhangian. The species indicates a progression of the thickened anterior border and the transverse to even slightly posteriorly swinging anterior border furrow from *B. seguieri* and *B. levyi* – species, which are separated from *Bailiella* in the new genus *Courtessolia* (see below). In *B. griffei*, the anterior border furrow has a gentle rearward curvature that affects a large portion of the furrow. This also causes a slight depression of the preglabellar field relative to the preocular areas. The glabella is similar to that in *B. levyi*, with a fairly narrow frontal lobe and a seemingly small subtruncate tip which, however, is a result of dorsoventral compaction. *Bailiella griffei* thus apparently links *B. l*evyi and *Bailiaspis glabrata*, with *B. glabrata* having an even more similar morphology of the anterior part of the cephalon on the first glance. However, the Scandinavian species has the tendency to show a narrower curvature of the anterior cephalic margin and the distinct uplift on the sagittal ling when viewed from the anterior, which are both absent or developed in a different way in *B. griffei*. In addition, the glabella in the phylogenetic line *B. seguieri* – *B. levyi* – *B. souchoni* – *B. griffei* is smaller in respect to the genae, and the posterior border distinctly narrower so that the species from the Montagne Noire appear to record a parallel, convergent evolution.

Bailiella havličeki [sic] (Šnajdr, 1958) is a recombination by Korobov (1973) of *Couloumania havlíčeki* [sic] Šnajdr, 1957, a relatively rare species from the *Eccaparadoxides pusillus* Biozone of the Jince Formation of the Barrandian region in Bohemia, Czech Republic. The species is characterised by a cranidium with a subtrapezoidal outline; relatively small glabella with faintly curved lateral margins; small palpebral lobes located anterior to the centre of the genae and with probable relictic eyes distant from the facial suture; and a prosopon composed of large granules [similar to *Conocoryphe cirina* (Barrande, 1846)]. The anterior part of the cephalon and the glabella are more ptychoparioid-like than typical for the *Conocoryphe*-*Bailiella* clade (see Šnajdr 1958, pl. XXXVI, figs. 13, 14).

The uncertainty of the generic assignment is reflected by an odyssey of the species through various genera since its first description by Šnajdr (1957). Synonymisation of *Couloumania* Thoral, 1946 led to the identification as *Conocoryphe* (*Conocoryphe*) *havliceki* (Šnajdr, 1957) by Dean (1982). Álvaro & Vizcaïno (2003) introduced the genus *Catharia* based on *Conocoryphe ferralsensis* Courtessole, 1967, a typical conocoryphid species with relictic palpebral lobes, but certainly without functional eyes. Nevertheless, Šnajdr's *Couloumania havlíčeki* was assigned to *Catharia* by Vaněk & Valíček (2001). *Cataria havliceki* (Šnajdr, 1957) is just a subsequent illegitimate writing. However, *Catharia* Álvaro & Vizcaïno, 2003 was recognised to be junior homonym of *Catharia* Lederer, 1863, a genus of extant Crambidae (Insecta, Lepidoptera). Álvaro (2007) suggested the replacement name *Occatharia* for the conocoryphid genus. Obviously, Özdikmen (2009) recognised the homonymy of *Catharia*, but missed Álvaro's suggestion so that he proposed the replacement name *Novocatharia* for it, which is a junior synonym of *Occatharia*.

The Bohemian species is now usually assigned to *Occatharia*. However, the drastic differences in the shape of the glabella and the anterior part of the cephalon clearly indicates that the presence of small palpebral lobes and relictic eyes is a result of convergent evolution rather than proving a close relative. *Couloumania havliceki* Šnajdr, 1957 must be regarded as representing a different, not yet established genus.

Bailiella hebeiensis Zhang & Wang, 1985 is species from North China, which was based on a single registered specimen (Zhang & Wang 1985, pl. 110, fig. 12). This specimen is a cranidium preserved as an internal mould. It is characterised by a tapering glabella with gently curved lateral margin and a narrow, strongly curved front. The occipital ring is narrow laterally and moderately broad on the sagittal line. The anterior border is quite narrow and strongly elevated, slightly thickening from the anterolateral sectors towards the sagittal line. The anterior border furrow is deep and broadens distinctly towards the central sector where it is broader than the adjacent anterior border and approximately as broad (sag.) than the relatively short (sag.) preglabellar field. The swellings on the genae near the frontal lobe are quite conspicuously developed are slightly curved, obliquely transverse rises proceeding into thin, nearly obsolescent eye ridges. The facial suture is in a decidedly abaxial position running within the lateral border for most of its course.

Bailiella hebeiensis is usually considered as junior synonym of *B. lantenoisi*. The characters which were believed to discriminate it from *B. lantenoisi* focus on the broad anterior border furrow and the conspicuous swellings on the genae. However, they can be interpreted as somewhat anomalously developed in the specimen so that the specimen falls into the morphologic variability of *B. lantenoisi*.

Bailiella heberti (Munier-Chalmas & Bergeron, 1889) (in Bergeron 1889) is an apparently widespread species with the facial suture in a marginal position, known from the Montagne Noire, the Cantabrian Mountains, and the Iberian Chains. It is clearly a species of *Conocoryphe* in its traditional sense, but was assigned to *Couloumania* Thoral, 1946. In any case, it cannot be assigned to the *Bailiella* clade discussed here.

Bailiella howelli (Hutchinson, 1962) has been introduced as *Bailiaspis howelli* by Hutchinson (1962, pl. XIV, figs. 1–6) and transferred to *Bailiella* by Kim et al. (2002). It occurs in strata originally identified as belonging to the so-called "*P. forchhammeri* Zone" in the upper part of the Manuels River Formation. The species shows a distinct growth in breadth of the anterior border towards the sagittal line where it is broader than the preglabellar field. It also has a transverse, straight to nearly straight course of the anterior border furrow. However, a number of cranidia are known in which the anterior border is slightly curved so that the species does not perfectly fit into *Bailiaspis* and should be placed under *Bailiella*. Its glabella tapers forward to a narrow frontal lobe and has gently curved lateral margins. The occipital ring is very narrow laterally, but grows distinctly towards the centre so that it sometimes has a markedly triangular outline often with a sharp terminal thorn (which is otherwise unknown from species of *Bailiella*).

The axial furrows are comparatively sharp. The facial suture runs in a moderately marginal position, dissecting the lateral border furrow approximately between the level of S2 and S3 (Fig. 98).

Bailiella huoshanensis Zhang & Wang, 1985 is a second species from the North China Platform which was based on two cranidia and one pygidium (Zhang & Wang 1985, pl. 110, figs. 2–4). The cranidia are preserved as internal moulds. Both are characterised by a tapering glabella with gently curved lateral margins, but the width of the glabella differs considerably: The cranidium on their pl. 110, fig. 2 has a relatively large glabella with a fairly broadly rounded front and a fairly narrow occipital ring, whereas the glabella of the specimen on pl. 110, fig. 3 is distinctly more slender shaped, with a narrower frontal lobe and a slightly broader (sag.) occipital ring. The anterior border in both specimens is similarly developed as a moderately broad (sag.), elevated brim-like structure with only a faint growth in sag. and exsag. breadth towards the sagittal line. The anterior border furrow is well-marked and grows slightly in breadth towards the sagittal line, being distinctly broader in the central sector than in the anterolateral sectors. One of the specimens (pl. 110, fig. 2) shows a relatively conspicuous lenticular swelling in the posterior half of the anterior border furrow stretching across the entire central sector of the furrow. Such a swelling is also visible in the second cranidium (pl. 110, fig. 3), but it is less clearly expanded from the central towards the anterolateral parts. On the sagittal line, this swelling appears to extend from the preglabellar field. The preglabellar field is moderately broad, clearly broader than the anterior border on the sagittal line, but it is broader in the specimen on pl. 110, fig. 3 than in the specimen on pl. 110, fig. 2. The caecal swellings on the genae near the frontal lobe are relatively low and inconspicuously developed in both cranidia. The facial suture is in an abaxial position, but appears to run along the adaxial part of the lateral border for some distance.

The pygidium of *Bailiella huoshanensis* figured in Zhang & Wang (1985, pl. 110, fig. 4) has a comparatively wide axis with 3 to 4 distinctly defined axial rings plus a terminal axial piece, which is only slightly narrower than the anterior axial ring. The pleural fields are subdivided by three well-developed pleural furrows and faint interpleural furrows, and the lateral (and probably also the not preserved posterior border) is well-defined and moderately broad.

Bailiella huoshanensis is treated as a junior synonym of *B. lantenoisi*. The cranidium shown in Zhang & Wang (1985, pl. 110, fig. 3) certainly falls within the morphological range of typical specimens of *B. lantenoisi*. However, this is not the case for the cranidium on pl. 110, fig. 2 (the holotype), which has a larger glabella and accordingly narrower genae, a better developed swelling in the anterior border furrow, a narrower occipital ring and probably less well developed swellings. In addition, the pygidium assigned to *B. huoshanensis* also differs quite distinctly from the typical pygidia of *B. lantenoisi*. It is thus suggested here that the species should be restricted momentarily to the holotype and the pygidium figured in Zhang & Wang (1985), and that it should be regarded as an independent species pending more material to assess the intraspecific variation.

Bailiella impressa (Linnarsson, 1879) occurs in the upper Wuliuan Exsulans Limestone, upper *Ptychagnostus gibbus* Biozone, of the Alum Shale Formation. It was based on material from Kiviks-Esperöd, Scania, but is fairly common in the Exsulans Limestone and also known from other localities in Scania (including allochthonous specimens from the coast near Brantevik) and from Bornholm, Denmark. The species is quite distinct in having a subsemicircular outline of the cephalon; a relatively short glabella with weakly curved lateral margins and a moderately broad frontal lobe; a long (sag.) preglabellar field, which is not defined from the "preocular areas" in any notable way; and a relatively thin anterior border, which grows slightly in breaths towards the sagittal line (Fig. 98).

Despite of the differences, this species is certainly related to *B. emarginata* and thus belongs to the *lyelli-emarginata* group in broad sense. The conspicuous broad preglabellar field suggests a close relationship to similar species from West Gondwana, such as an undescribed species from the

Moroccan High Atlas region. The Swedish specimens are relatively small so that differences between them and the West Gondwana species can be explained by different morphologies due to growth conditions and functional requirements. In his subdivision of the traditional genus *Conocoryphe*, Grönwall (1902) used the species as the type species of his new genus *Liocephalus*. As noted by Westergård (1950, p. 27), Grönwall's concept of *Liocephalus* included a fairly heterogenous assembly of species. However, the name is available for a genus based on *Bailiella impressa*.

Bailiella inconspicua Geyer, 1998 is another distinct species from the Bréche à *Micmacca* Member of the Jbel Wawrmast Formation, *Ornamentaspis frequens* Biozone, Agdzian Stage (probably lowest Wuliuan), from the Lemdad Syncline of the High Atlas, Morocco. The species has an anterior border, which grows in sag. and exsag. width towards the sagittal line, being at least as broad or even distinctly broader than the relatively narrow (sag.) preglabellar field. The anterior border furrow is relatively broad, particularly in large specimens, and then not distinctly defined from the anterior border, but shows a tendency to develop into that. The border furrow is more-or-less evenly curved and intersected by the facial suture at a particularly posterior position at about the level of L2. The glabella is relatively wide, with a broadly rounded front and gently curved lateral margins. The occipital ring is narrow adjacent to the axial furrows and has a distinctly curved posterior margin and a conspicuous node close to the posterior margin. The broad, moderately tapering glabella with its gently curved frontal margin as well as the broad anterior border suggests a close relationship to *Bailiella dilatata*, and the species is also assigned to *Prioscutarius* n. gen.

Bailiella lantenoisi (Mansuy, 1916) from strata characterised by this species at Tiên-fong, northern Vietnam, is the best described and most frequently figured species of *Bailiella*. It is described and discussed in some detail below.

Bailiella lantenoisi has also been reported from the Hulusitai Formation, Hsuchuangian Stage, of the western Shaanxi Province and of the Ordos Plateau in the Inner Mongolia region, China, from the eponymous biozone (Yuan et al. 2016, pl. 16, figs. 1–5, 7–10, non 6!). These specimens are nicely preserved and particularly instructive. However, they do not belong to *B. lantenoisi*, but represent a new, fairly easily recognisable species, which is introduced below as *Bailiella niuxinshanensis*.

Bailiella lata Wu & Lin in Zhang et al., 1980 from the upper Wuliuan Xuzhuang Formation of the Zhongtiao Mountains in the Shanxi province, North China, is usually also considered to be a junior synonym of *B. lantenoisi*. This species, however, differs clearly from *B. lantenoisi* and several characters and cannot be synonymised with it. It is discussed in some detail below under *Bailiella lata*.

Bailiella levyi (Munier-Chalmas & Bergeron in Bergeron, 1889 is a common species known from numerous localities in the Montagne Noire, southern France, from the *Manublesia thorali* to the *Jincella convexa* biozones, lower to middle Languedocian (uppermost Drumian to lower Guzhangian) (see Thoral 1946, pl. I, figs. 1–3, pl. II, figs. 1–7, pl. III, figs. 1, 2; Courtessole 1973, pl. XXI, figs. 9, 10, pl. XXII, figs. 1–9, pl. XXIII, figs. 1–6). The species is characterised by an anterior border growing in breath towards the sagittal line and of subequal breadth with the preglabellar field in this sagittal axis. The anterior border furrow has a nearly straight course in its median part, with distinct rearward curvatures at the anterolateral corners. The facial suture lies at a relatively marginal position dissecting the lateral border furrow approximately at the level of L3. The glabella is quite small, with a narrow to almost subacute front and distinctly curved lateral margins. The occipital ring grows slightly in breath towards the sagittal line, but is relatively broad even at its lateral margins. The genae are of conspicuous width, and this is optically enforced by the absence of a distinct surface ornament of the cuticle. It is worth noting that *B. levyi* has a relatively large pygidium with 4–5 axial rings and a terminal axial piece, and its pleural regions with at least 4 pleural and interpleural furrows and a narrow, poorly defined lateral and posterior border. The pair of nodes in the last well-defined axial ring and the plectrum posterior to the axis seen in other species are not developed. The surface of the cuticle is smooth.

Specimens with a very similar morphology as *B. levyi* are known from Spain, particularly from the Oville Formation of the Cantabrian Mountains, but also from the Acón Group (particularly the Borrobia and Valdeorea formations; Languedocian) of the Iberian Chains, Aragón. They have been dealt with as *Bailiella* cf. *levyi* by Sdzuy (1961, pl. 32, figs. 8, 9). As detailed by Sdzuy (1961), differences between the specimens from the Montagne Noire and the Cantabrian Mountains focus on a more strongly curved anterior margin of the Spanish specimens and the, accordingly, less strongly trapezoidal outline of the cranidium; better developed bulbous swellings as the relics of the eye ridges; and an apparently slightly more sunken preglabellar field in respect to the neighbouring preocular areas. Sdzuy (1961) emphasised that the Spanish specimens might fall into the morphological variation of the species; an opinion which was later followed by most authors (e.g., Liñán et al. 1993, 2004; Álvaro 1996; Gozalo et al. 2008) although no further, detailed examination of Spanish specimens was performed.

Bailiella levyi bondoni Termier & Termier, 1950 from the Moroccan Atlas ranges is an independent species from the *levyi* clade and is described below under *Courtessolia bondoni*.

Bailiella linnarssoni (Grönwall, 1902), introduced as *Conocoryphe* (*Liocephalus*) *linnarssoni*, is a species from the Exsulans Limestone of the Alum Shale Formation, upper part of the *Ptychagnostus gibbus* Biozone, from Hoved/near Borregård on the island of Bornholm. Grönwall's (1902, pl. 2, fig. 1) specimen is a small cranidium, possibly from an immature individual, with an almost semicircular outline, a relatively small glabella which tapers only slightly forward and has a broadly rounded front. The facial suture lies in a very marginal position so that the border is visible all around the cranidium, the lateral and anterior borders of moderate width and growing slightly in breadth towards the sagittal line. The preglabellar field is broad, of at least double sagittal width than the anterior border on the sagittal line. This species cannot be assigned to *Conocoryphe* or *Bailiella*. It somewhat resembles *Bailiella gemina* from the Delitzsch–Torgau–Doberlug Syncline (see above), but clearly differs in the less tapering glabella and a much broader (sag,) preglabellar field.

Bailiella longifrons (Cobbold, 1911) is a species that was introduced as *Conocoryphe emarginata* var. *longifrons* by Cobbold (1911) based on specimens from the Wuliuan "*Paradoxides groomi* fauna" of Comley, Shropshire, England. Although Cobbold (1911, pl. XXIV, figs. 8–14) regarded it as a variety of *B. emarginata*, the differences between them are considerable, and the species appears to be more closely related to *B. froeensis* and *B. impressa*, as already noted by Lake (1940) and Westergård (1950). Lake (1940, pl. XL, figs. 9–11) chose a lectotype which shows the apparently conspicuously extended preglabellar field that is clearly broader (sag.) than the moderately broad anterior border on the sagittal line. The glabella tapers moderately forward towards a modestly broad (tr.) frontal lobe with a fairly low curvature of its anterior margin, and has slightly curved lateral margins. The occipital ring is moderately broad adjacent to the axial furrow. The course of the facial suture is not well preserved, but appears to lie at a relatively adaxial position similar to the situation in *B. cobboldi* and *B. comleyensis*. The lectotype appears to show a relatively distinct eye ridge on the right gena, which curved considerably rearward from near the frontal lobe in a gently arc towards the genal angle. Nevertheless, this little known species must be regarded as a member of the *emarginata* group although better preserved and more complete material is needed for a sufficiently precise concept of the species.

Bailiella lyelli (Hicks, 1871) from the Solva beds (= Solva Group, lower to middle part of the Wuliuan) of the St. David's area, Wales, is based on distorted material which makes the characterisation of its significant features difficult. The species (see Lake 1940, pl. XL, figs. 1–6) has a relatively broad preglabellar field and, accordingly, a relatively short glabella with faintly curved lateral margins and a moderately broad front with a low anterior curvature, as well as a moderately broad anterior border. In this respect, it closely resembles *B. longifrons* from strata of similar age in Shropshire. *Bailiella lyelli* is known to have a small genal spine. It is among the species from which complete dorsal exoskeletons are known. The thorax seems to encompass consistently of 15 segments in adult specimens. The pygidium has an axis consisting of three defined rings plus a terminal axial piece with a posterior margin located very close to the posterior border. The pleural areas of the pygidium have three relatively distinct pleural furrows. The lateral margin appears to be moderately broad (tr.).

Bailiella lyelli was suggested to be closely related to *B. emarginata* (Westergård 1950; Sdzuy 1961). Nevertheless, as noted by Westergård (1950), its cephalic border is proportionally thinner, and the pygidium of. *B. lyelli* has one additional ring in the axis and a faint narrow border. Although it appears to close the morphological gap between *B. emarginata* and *B. levyi* in this respect, the shape of the glabella and the posteriorly tapering cephalic border as well as the number of thoracic segments place it into the new genus *Emarginobailiella*.

Bailiella manuelensis Hutchinson, 1962 is a species similar to *B. baileyi*, known as well from the Fossil Brook Member of the Chamberlain's Brook Formation, *Paradoxides bennetti* Biozone, but from Avalonian south-eastern Newfoundland rather than New Brunswick. It is characterised by a distinctly tapering glabella with barely curved lateral margins and a fairly narrow frontal lobe. The occipital ring is moderately wide adjacent to the axial furrow and grows in sag. width, with a subevenly curved posterior margin and an inconspicuous occipital node in a slightly more anterior position than in *B. baileyi*. The anterior border grows in breadth towards the sagittal line, but is only moderately wide (sag.), distinctly broader than the anterior border furrow and about two-thirds the sag. breadth of the preglabellar field or of equal width. The anterior border furrow is curved throughout its course, with a distinctly more pronounced curvature in the anterolateral sector, but without a narrow bow or kink (Fig. 98). The facial suture lies at a marginal position. It intersects the lateral border furrow probably around the level of S2, and the genal corner is preserved in a way that has the forward curvature of the genal angle lying more-or-less on the cranidium, indicating that most probably no genal spine was developed at this species. Bulbous swellings are developed on the genae close to the axial furrow, but they are distinctly less well developed than in *B. baileyi*. Kim et al. (2002, fig. 3.1) illustrated a dorsal exoskeleton with an attached pygidium, which shows a progressively tapering axis composed of 3 to 4 axial rings that are less well marked towards the posterior, and a terminal axial piece. The pleural areas have relatively shallow furrows, which also fade towards the posterior direction and have indistinct interpleural furrows only.

Bailiaspis meridiana Sdzuy, 1958a is a species only known from very few specimens of the Villafeliche section in the Iberian Chains, Aragón, Spain. The holotype (Sdzuy 1958a, pl. 1, fig. 9; 1961, pl. 34, fig. 5) is a quite well-preserved cranidium, which shows a close resemblance to the species of *Bailiella levyi* clade. It is distinguished by a longer glabella, an almost strictly transverse course of the anterior border furrow bound laterally by narrow rearward bows, and a short (sag.) preglabellar field. The anterior margin of the cephalon shows a relatively even curvature so that the anterior border as a spindle shape in dorsal view. Sdzuy (1958a, 1961) placed the species into *Bailiaspis*, which agrees with the traditional concept, but the species clearly belongs to the *levyi* clade and appears to represent one of the terminal morphologies in evolution within the group.

Bailiella orientalis (Lermontova, 1951) features a generic assignment first suggested by Korobov (1973) for *Conocoryphe aequalis* var. *orientalis* Lermontova, 1951, a taxon described from the *Corynexochus perforatus-Anopolenus henrici* Zone of Shody-Mir (southern periphery of the Fergana Basin, Altay-Sayan Foldbelt). The identity of this taxon is somewhat challenging because Lermontova (1951, pl. I, figs. 15–17) figured three cranidia, which almost certainly belong to two different species. Two of them (Lermontova 1951, pl. I, figs. 15, 17) are characterised by a slender, but distinctly tapering glabella, a short to moderately broad preglabellar field and a relatively narrow and elevated anterior border that tapers laterally and extends far rearward due to a suture in a very marginal position. The genae show only weak indications or remnant eye ridges Its cuticle appears to have been smooth. The third cranidium (Lermontova 1951, pl. I, fig. 16) is distinctly larger, has a broader and even more tapering glabella with curved lateral margins, but a suture in a similarly marginal position. However, the genae are more gently rounder anterolaterally, and the genae appear to be characterised by much better developed bulbous swellings of the eye ridges.

No type was selected in Lermontova (1951), but the description (Lermontova 1951, p. 21–22) appears to be mainly inspired by the specimen on pl. I, fig. 15 so that I select this specimen (termed specimen no. 30 in Lermontova 1951) as the lectotype.

Bailiella ornata Resser, 1937 is a species based on imperfectly preserved material from the *Mawddachites hicksii* and *P. davidis* zones of the Manuels River Formation of south-eastern Newfoundland (Resser 1937, pl. 7, figs. 18–21). The species was redescribed by Hutchinson (1962, pl. 15, figs. 1, 2) and also mentioned to occur the younger *Hartella bucculenta* Zone of Avalonian Cape St. Mary's Peninsula of Newfoundland (Fletcher 2006). It resembles *Bailiella manuelensis* Hutchinson, 1962 in most aspects and is characterised by a glabella with gently curved lateral margins and a narrow frontal lobe; an anterior border which grows faintly towards the sagittal line; a fairly narrow anterior and gently curved border furrow grading anterolaterally into more strongly curved parts of the lateral border furrow; and a relatively thin (sag.) preglabellar field of approximately the sagittal breadth of the anterior border.

Resser's specimens (Resser 1937, pl. 7, figs. 18–21) seem to show cranidia which are dorsoventrally compressed so that the preglabellar field is probably broader than during life of the individual. No distinct swellings appear to be present on the genae. The facial suture lies in a comparatively moderate position, intersecting the lateral border furrow approximately at the level of S2 to L3. The species has a relatively characteristic ornament on the cuticle consisting of closely spaced small granules overlain by a second set of coarser granules (Fig. 98).

Bailiella pingshanensis Zhang & Wang, 1985 is another species from the North China palaeocontinent, which was also based on a single registered specimen (Zhang & Wang 1985, pl. 110, fig. 7). This specimen is a partly exfoliated cranidium characterised by a tapering glabella with gently curved lateral margins and a moderately wide (tr.) frontal lobe. The occipital ring is narrow laterally and moderately broad on the sagittal line. The anterior border is moderately broad (sag., exsag.; although not completely preserved) and distinctly elevated, slightly thickening from the anterolateral sectors towards the sagittal line. The anterior border furrow is well-marked and slightly broadens towards the sagittal line. It is slightly shallower on the sagittal line. The preglabellar field is moderately broad, apparently slightly broader than the anterior border on the sagittal line. The swellings on the genae near the frontal lobe are relatively low and inconspicuously developed, of elongate outline. The facial suture is in a decidedly abaxial position running within the lateral border on its entire course.

Bailiella pingshanensis was treated as junior synonym of *B. lantenoisi* wherever it was mentioned after its introduction by Zhang & Wang (1985). However, the reasons for this synonymy are not strictly conclusive. The glabella of the holotype cranidium is larger (areally and in length) than in typical cranidia of *B. lantenoisi*, and its anterior border is thicker, particularly when compared with the anterior border furrow. The caecal swellings are low. Most importantly, however, the facial suture lies at a more ab-axial position. These features are clear enough to distinguish the holotype from typical specimens of *B. lantenoisi*. Almost certainly it represents a different species. However, more material is needed to allow an assessment of the intraspecific variation until the distinction can be more significantly demonstrated.

Bailiella pokrovskayae Korobov, 1973 is a species based on well preserved material from the Yuryut-Kochega river area on the eastern part of the Siberian Platform. It comes from strata of the Olenek "horizon" of the Chaya Stage, from what is now termed the *Tomagnostus fissus* or "*Solenopleura patula*"

Biozone. Korobov (1973, pl. XI, fig. 7, 7a, 7b) figured only a single cranidium, which is characterised by having a small glabella with nearly straight lateral margins and a moderately narrow frontal lobe which is almost subtruncate. The anterior border grows in breadth towards the sagittal line, being slightly narrower/shorter (sag.) than the preglabellar field; its anterior margin has a low, but subeven curvature in the median sector, but curves more distinctly posteriorly near the anterolateral points. The anterior border furrow is nearly straight and moderately wide on its course, with a pronounced rearward curvature anterolaterally. The facial suture lies in a moderate position when compared with the other species assigned to *Bailiella*, and it intersects the lateral border furrow at about the level of L3. In anterior view, the anterior border shows a slight raise on the sagittal line, which is poorly developed for the lower margin of the border, but much more pronounced for its upper margin due to the growth in width towards the sagittal line (Fig. 98). The holotype is largely an internal mould so that the lateral glabellar furrows are well visible, and in this case four pairs of furrows are clearly visible, which is not known from almost all of the other species assigned to *Bailiella*. The species is of the “eastern type” and similar to *B. orientalis*.

Another cranidium was figured even before Korobov’s book by Savitskiy et al. (1972, pl. 20, fig. 9) under the name “*Bailiella pokrovskayae* Korobov (MS)”, collected from the Amgan *Kounamkites* Zone of the Nekekit river section. This specimen resembles Korobov’s *B. pokrovskayae* from the younger strata, but it differs in having an almost semicircular outline of the cephalon, a slightly larger glabella, and a narrower anterior border without a clear growth in thickness towards the sagittal line. Although the morphological plasticity of *B. pokrovskayae* cannot be assessed, it is very probable that the specimen from the Nekekit river represents a different species.

Liaotungia puteata Resser & Endo, 1937 is a species described from the Taitzu Formation near Liaoyang in the Liaoning province. It was based on a single fragment of a cranidium which lacks most of the anterior part. This species is generally synonymised with *Bailiella lantenoisi* since this was suggested by Zhang & Jell (1987). However, the glabella of the holotype shows a slightly different shape and a distinctly recurved S1, and the course of the facial suture is largely unknown. Accordingly, the species cannot be assessed with sufficient certainty to discriminate it. A slightly reconstructed figure of the holotype pre-published in Kobayashi (1935, pl. XXIV, fig. 25) does not precisely portray its morphology and may have contributed to the synonymisation of *Liaotungia puteata* with *B. lantenoisi*. In addition, the specimen identified by Zhang (in Lu et al. 1965, pl. 37, fig. 23) as *Liaotungia puteata* clearly does not belong to *Bailiella lantenoisi* and the *Bailiella* plexus.

Bailiella seguieri Courtessole, 1973 is a fairly frequent species known from a number of localities in the Montagne Noire, southern France, from the *Solenopleuropsis rouayrouxi* Biozone, Languedocian Stage (see Courtessole 1973, pl. XXIII, figs. 7–14, pl. XXIV, figs. 1–3). The species is similar to *B. levyi* and has a similar stratigraphic range according to Courtessole (1973). It also shares most characters with *B. levyi*, particularly the configuration of the anterior border, the course of the anterior border furrow, the dimensions of the preglabellar field, the shape of the glabella and the course of the facial suture. The differences between the species are more slender and straight genal spines in *B. seguieri*, a better developed occipital node, a more strongly conical glabella, as well as a more conical pygidial axis and better developed pleural furrows in the pygidium.

Courtessole (1973) underlined that adult specimens of *B. seguieri* are difficult to distinguish from not fully grown specimens of *B. levyi* and that the also detailed that the stratigraphic range of *B. seguieri* concentrates on the lower part of the *Solenopleuropsis rouayrouxi* Biozone (his level D) in the Montagne Noire, whereas *B. levyi* is much more frequent above. However, it appears that the species are difficult or impossible to distinguish if strongly affected by tectonic distortion and that *B. seguieri* is simply based on immature specimens of *B. levyi*, but also that the stratigraphically lowest specimens represent populations primarily comprising smaller individuals.

Bailiella sejuncta (Reed, 1934), introduced as *Conocoryphe sejuncta* by Reed (1934, pl. II, figs. 9, 11, 12), was assigned to *Bailiella* by Shah (1973), when describing a number of *Bailiella* specimens from the Nutunus Formation of the Baramula District, Kashmir, which he identified as different species of *Bailiella*, *Holocephalina* and *Bailiaspis*. As mentioned above under *B. frangtengensis*, all relevant specimens studied by Shah (1973) were suggested by Jell & Hughes (1997) to represent just a single species, this species being synonymised with *Bailiella lantenoisi*. Although it is conclusive that all of Shah's specimens represent a single species, the confidently identification as *B. lantenoisi* is hampered by the imperfect preservation (see discussion below).

As for *Bailiella frangtengensis*, Shah (1973, figs. 1a–d, 2a, b) identified some of his specimens from the Baramula District firmly as *B. sejuncta* although his discussion takes the determination with reservation and mentions differences to Reed's (1934) specimens. Shah particularly discusses "characteristic furrows across the preglabellar area" (although not indicated in Shah's fig. 2c) which Jell & Hughes (1997) showed to be a result of deformation.

Bailiella sepulcra Álvaro & Vizcaïno, 2018 is a species from the *Bailiella* Formation of the Anti-Atlas, Morocco, occurring in strata of middle/late Languedocian (=Guzhangian) age. The species is characterised by a distinctly tapering glabella with a narrow, typically subtruncate front and gently curved lateral margins (Álvaro & Vizcaïno 2018, fig. 3A–J, M–O). Its occipital ring is narrow close to the axial furrow and grows conspicuously in length on the sagittal line, terminating in a terminal or subterminal thorn so that it has a subtriangular outline in dorsal view. Lateral glabellar furrows are barely recognisable. The anterior border grows moderately towards the sagittal line. The anterior cranidial margin describes a nearly uniform curvature, but occasionally shows a weak angulation on the sagittal line in large individuals. The anterior border furrow is moderately broad (sag., exsag.) throughout, shallowing a bit towards the lateral border furrow. The preglabellar field is moderately broad (sag.) and moderately convex. It is slightly broader in cephala of small to moderate size than the anterior border on the sagittal line, but slightly thinner (sag.) in large specimens. The genae carry a small node or swelling of subcircular to transversely elliptical shape close to the frontal lobe. Weak lines originate from these swellings and can be recognised in well preserved specimens to extend in a gentle arch in the direction of the genal corners. The facial sutures are located in a pronouncedly abaxial position and intersect the lateral border in a way that they reach the lateral border furrows approximately at the level of S2. The exterior of the cuticle is smooth.

Pygidia of *Bailiella sepulcra* (Álvaro & Vizcaïno 2018, fig. 3K, L) have a wide axis with only one or two recognisable axial rings, defined by progressively shallower furrows towards the posterior, with a broadly rounded posterior end reaching approximately to the posterior border. The pleural fields show two or three pleural furrows, which are also shallower towards the posterior area, and one weak interpleural furrow. The lateral and posterior borders are barely defined by an obsolescent border furrow, shallow, but relatively narrow.

Bailiella sepulcra belongs to the *B. levyi* group, but is distinctly differentiated from the other species of this group by its triangular shape of the occipital ring (see discussion below).

Bailiella souchoni Courtessole, 1967 is a fourth, rare species known from the middle Languedocian (=Guzhangian) of the Montagne Noire, southern France. It occurs fairly late, in strata with *Trochocinctus pardailhanicus*, in strata identified as a *Bailiella souchoni* Biozone (Courtessole's level G). The species is similar to *B. levyi* and differs from that species by a more strongly tapering and slightly shorter glabella and the presence of an occipital node. However, the specimens figured by Courtessole (1967, pl. 3, fig. 10, pl. 4, figs. 1–3, 1973, pl. XXIV, figs. 11–14) clearly indicate the progressive broadening of the anterior border in the middle part, creating a slight backward curvature of the anterior border furrow and a reduction in sag. breadth and convexity of the preglabellar field. In this respect, *B. souchoni* perfectly fits into the morphological gradient illustrated by the progressive evolution of *B. seguieri*/*B. levyi* – *B. souchoni* – *B. griffei* in the Drumian strata of the Montagne Noire. This development, however, challenges a simplistic definition and demarcation of the genus *Bailiaspis* (see below).

Bailiella taurinus (Harrington, 1937) is an erroneous assignment of *Basilicoides taurinus* Harrington, 1937 from the Ordovician of Argentina (now *Thysanopyge taurinus*).

Bailiella tenuicincta (Linnarsson, 1879) is known from the Exsulans Limestone of the Alum Shale Formation, which represent the upper part of the *Ptychagnostus gibbus* Biozone, of Scania and the island of Öland, Sweden, and the island of Bornholm, Denmark, where it occurs quite commonly. The species has an only gently broadened anterior border towards the sagittal axis and a faintly shallower curvature of the anterior border furrow on the median section. In anterior view, the cephalic border shows a very gentle elevation. The preglabellar field is moderately broad (sag.), in the order of twice the width (sag.) of the anterior border (Fig. 98). The glabella has distinctly curved lateral margins and a narrow frontal lobe, very similar to that of *B. emarginata*, and the species clearly belongs to the *lyelli-emarginata* group.

Westergård (1950, pl. 5, fig. 9) figured a partial pygidium, which almost certainly belongs to this species. It shows an axis with ca. four rings and a terminal axial piece and a pair of low swellings on the last axial ring, with a short but well recognisable plectrum, a narrow posterior and lateral border, as well as three well-defined pleurae with pleural and interpleural furrows on the pleural fields.

Bailiella teres (Grönwall, 1902) is a rare species introduced as *Conocoryphe* (*Liocephalus*) *teres* from the Exsulans Limestone of the Alum Shale Formation at Borregård, Bornholm (Grönwall 190, pl. II, fig. 2) and also reported from Scania. It is a relatively typical species of *Conocoryphe*.

Bailiella transversa Zhang & Wang, 1985 is another species from the North China palaeocontinent, which was based on a single registered specimen (Zhang & Wang 1985, pl. 110, fig. 15). This specimen is a cranidium preserved as an internal mould. It is characterised by a tapering glabella with gently curved lateral margins and a narrow frontal lobe. The occipital ring is narrow laterally but moderately broad on the sagittal line. The anterior border is moderately broad (sag., exsag.) and moderately elevated, faintly growing in width from the anterolateral sectors towards the sagittal line. The anterior border furrow is well-marked and of more-or-less constant width throughout its course in the central sector. It has seemingly a slight kink on the sagittal line (see below). It is shallower on the sagittal line due to a quite distinct swell extending from the preglabellar field. The preglabellar field is moderately broad, about as broad as the anterior border on the sagittal line. The caecal swellings on the genae near the frontal lobe are relatively low and inconspicuously developed, of elliptical outline. The facial suture is in a very abaxial position running within the lateral border for most of its course.

Bailiella transversa is generally treated as junior synonym of *B. lantenoisi*. The characters which were believed to discriminate it from *B. lantenoisi* focus on the swelling in the anterior border furrow and a slightly more distinct curvature of the anterior cephalic margin on the sagittal line. However, these features are most probably a result of differential compression/distortion. Accordingly, the specimen falls into the morphologic variability of *B. lantenoisi*.

Bailiella ulrichi Resser & Endo, 1937 was based on rich material from several localities in the Tangshih Formation of the Liaoning province, Manchuria, Northeast China, which includes cranidia and cephala of different sizes and nearly complete exoskeletons (Resser & Endo in Endo & Resser 1937, pl. 41, figs. 5–8, pl. 42, pl. 59, fig. 21). *Bailiella ulrichi* is generally regarded as a junior synonym of *B. lantenoisi*. However, this material from Manchuria is more instructive than the type material of *B. lantenoisi* so that actually the morphology of *B. ulrichi sensu* Resser & Endo (1937) has given the distinction for the general view of *B. lantenoisi*'s morphology and variability.

Particularly instructive is a slab with nearly 30 specimens illustrated in Resser & Endo (1937, pl. 41), which features both the ontogenetic and general morphologic variability of *B. ulrichi sensu* Resser & Endo. Although the slab was collected from sandy shale and thus has suffered some dorsoventral compaction, the cranidia nicely document a fairly uniform morphology for specimens of similar size and a slight to moderate change in allometric growth for some parts of the cephalon. The typical cranidia from this sample have a tapering glabella with gently curved lateral margins and a relatively narrow frontal lobe with a somewhat obliquely truncated front or with a relatively low curvature of the anterior margin. The glabellar furrows S1 and S2 are both bifurcate. The occipital ring is narrow near the axial furrows and grows to moderate size on the sagittal line. It carries a small to moderately large node slightly anterior to the centre. The anterior border grows quite distinctly in width towards the sagittal line and is usually slightly narrower (sag.) than the preglabellar field, but rarely attains approximately the same width. It is moderately elevated and has a moderate convexity in transverse section. The specimens from the Liaoning region appear to differ from the others in having the tendency to develop anteriorly ascending anterior borders on internal moulds so that the border has a faint brim-like aspect with the highest elevation close to the anterior cephalic margin. The border is slightly more elevated and has a more uniformly convex sag. profile on the exterior of the cuticle so that its posterior slope is steeper than on internal moulds. The anterior border furrow is moderately broad, but typically narrows towards the anterolateral portions and is narrower laterally. Well preserved internal moulds show in the broadened median section of the anterior border furrow a faint transverse rise of extended spindle-shape in dorsal view. On the exterior of the cuticle, the anterior border furrow is deeper, narrower and better defined both anteriorly and posteriorly than on internal moulds. The genae carry transversely elongate, slightly curved swellings close to the axial furrow as remnants of the eye ridges, which are much more conspicuously developed on internal moulds. A weak eye ridge trace continuing from the swellings in the genae run in a gentle curve precisely towards the genal angle.

The facial sutures are in a very marginal position and run along the lateral border furrow for most of their course or even within the lateral border, but intersect the posterior border just adaxially of the genal angle: a mode of suturing which appears to differ from that seen in the non-East Asian species assigned to *Bailiella*. Accordingly, the librigena is extremely narrow, but includes a relatively strongly developed and moderately long genal spine which has a length of approximately two-thirds the length of the librigena anterior to it.

The pygidia shown in Resser & Endo (1937, pl. 41, fig. 7, pl. 42) have a relatively wide (tr.) rhachis, which consists of 4 recognisable axial rings plus a terminal axial piece reaching close to the posterior border. The axial rings are decreasingly well-defined towards the posterior end. The pleural fields show three pleural and interpleural furrows, the interpleural furrows being faint and even less clearly visible towards the posterior. The pygidium has a moderately well-defined, low lateral and posterior border, which is moderately broad and relatively well recognisable – unlike that seen in the Scandinavian, West Gondwanan and Avalonian species.

Bailiella walcotti (Matthew, 1885) is a third species from the Fossil Brook Member of the Chamberlain's Brook Formation, also established on material from New Brunswick. It is similar to *B. baileyi* in most aspects (e.g., Kim et al. 2002, fig. 3.3–3.8), having a distinctly tapering glabella with barely curved lateral margins and a fairly narrow frontal lobe with a more or less evenly curved anterior margin. The occipital ring is moderately wide adjacent to the axial furrow and grows in sag. width towards the sagittal line, with a subevenly curved posterior margin. On occipital node is present, but not very prominent and lies at a subcentral position. The anterior border grows only slightly in breadth towards the sagittal line, being fairly narrow (sag., exsag.), slightly broader than the anterior border furrow and slightly shorter (sag.) than the preglabellar field. The anterior border furrow is curved throughout its course, with an only slightly more pronounced curvature in the anterolateral sector without any narrow bow or kink. The facial suture lies at a pronouncedly marginal position, so that it intersects the lateral border furrow as far back as at approximately the level of S1, and the genal corner is completely preserved on the cranidium, indicating that no genal spine was developed at this species (Fig. 98). Large bulbous swellings are developed on the genae close to the axial furrow. These structures proceed into relatively well visible relics of the eye ridges and are almost as large as in *B. baileyi*, which has the most pronouncedly developed swellings known from the species of the *Bailiella* group.

Pygidia assigned to the species (e.g., Kim et al. 2002, fig. 3.5, 3.6) have a slightly tapering axis composed of 3 to 4 axial rings which are progressively less well marked towards the posterior, and a relatively large terminal axial piece. The pleural areas show moderately well-developed furrows, which also fade in expression towards the posterior and with faint interpleural furrows only. The lateral and posterior borders are narrow and poorly defined, and a plectrum is visible posterior to the rear end of the axis.

Bailiella wuanensis Zhang & Wang, 1985 from the North China palaeocontinent was based on a single registered specimen (Zhang & Wang 1985, pl. 110, fig. 11). This specimen is a cranidium preserved as an internal mould. It is characterised by a tapering glabella with gently curved lateral margins and a moderately wide frontal lobe. The occipital ring is narrow laterally but moderately broad on the sagittal line. The anterior border is moderately broad (sag., exsag.) and well elevated, slightly growing in width from the anterolateral sectors towards the sagittal line. The anterior border furrow is well-marked, slightly growing in width towards the sagittal line. It shows a slight swelling in the central sector, developed as a narrow lenticular rise close to the posterior margin of the furrow and apparently proceeding from the preglabellar field. The preglabellar field is moderately broad, broader than the anterior border on the sagittal line. The caecal swellings on the genae near the frontal lobe are relatively low, elongated and directed slightly oblique to the axis, proceeding into faint ridges. The facial suture is in a very abaxial position running within the lateral border on its course.

Bailiella wuanensis is generally considered as junior synonym of *B. lantenoisi*. However, the larger glabella and the very abaxial position of the facial suture as well as the broader (sag.) preglabellar field appear to discriminate it from *B. lantenoisi*. It is difficult to assess the characteristic morphology of a species from a single cranidium, but it is suggested that the holotypes of *Bailiella wuanensis* and *B. pingshanensis*, and possibly also the material of *B. wutaishanensis* represent the same species.

Bailiella wurmi Sdzuy, 2000 is only known from the Lippertsgrün Formation, *Solenopleuropsis* Biozone, lower Languedocian (upper Drumian), of the Franconian Forest area, Germany. All known specimens (Sdzuy 2000, pl. 4, figs. 1–6, 7?, 8?, pl. 7, figs. 1*–3*) are fairly distorted and do not provide unequivocal characteristics of the species, when all of them are examined. The holotype is a cranidium with a relatively thin anterior border growing more-or-less evenly towards the sagittal line, having about half width (sag.) than the preglabellar field on the sagittal line. The anterior border furrow is subequally curved on its entire stretch. The facial suture also lies in a very marginal position, running almost at the adaxial margin of the lateral border furrow, and it intersects the lateral border furrow approximately at the level of S2. The glabella has a relatively narrow frontal lobe and moderately curved lateral margins (Fig. 98). Sdzuy's specimens on pl. 4, figs. 1, 2, and 5, possibly also fig. 6, agree with these characters. However, the specimens illustrated on pl. 4, figs. 6 and 7 probably or certainly belong to different species as indicated by distinctly broadened anterior borders and the course of the border furrow.

Bailiella wutaishanensis Zhang & Wang, 1985 is also species from the Wutai Mountains, Shanxi Province, North China. It is known from two cranidia and one pygidium figured in Zhang & Wang (1985, pl. 110, figs. 8–10), with one of the cranidia and the pygidium refigured in Wang & Zhang (1994, pl. 4, figs. 11, 12). This cranidium have a tapering glabella with gently curved lateral margins and a moderately wide frontal lobe. The occipital ring is narrow laterally but seems to be considerably broader on the sagittal line (not entirely preserved in the illustrated specimens). The anterior border is moderately broad (sag., exsag.) and well elevated, slightly growing in width from the anterolateral sectors towards the sagittal line. The anterior border furrow is well-marked, growing in width towards the sagittal line and broader in the central portion than anterolaterally. It shows a swelling in the central sector, developed as a rise close to and developing from the preglabellar field. The preglabellar field is moderately broad, and thus broader than the anterior border on the sagittal line. The caecal swellings on the genae near the frontal lobe are moderately well developed as elongated and slightly curved rises slightly oblique to the axis, proceeding into faint ridges. The facial suture is in a very abaxial position and seems to run within the lateral border on its course as visible from the cranidium on pl. 110, fig. 8 in Zhang & Wang (1985).

The pygidium assigned to *Bailiella wutaishanensis* (Zhang & Wang 1985, pl. 110, fig. 10) is not very well preserved. It has a wide axis composed of probably three rings plus a terminal axial piece, which is quite well rounded posteriorly, but seems to show a pair of subterminal swellings and reaches almost to the posterior border. The pleural areas are divided by three pleura furrows and also possess faint to obsolescent interpleural furrows. The lateral border (and probably also the partly broken posterior border) are narrow to moderately broad and low, defined from the pleural areas only by the absence of furrows.

Bailiella wutaishanensis is generally considered as a junior synonym of *B. lantenoisi*, which appears to be realistic on a quick glance. However, it has a slightly larger glabella and a very abaxial position of the facial suture which discriminates it from the typical cranidia of *B. lantenoisi*. As mentioned above, it is reasonable to assume that it represents the same species as the holotypes of *Bailiella wutaishanensis* and *B. pingshanensis*.

Despite the step towards a better phylogenetically-based taxon, the emended genus *Bailiella* is used here still with the reservation that it must be regarded as a polyphyletic taxon. It must be assumed that it will not be possible to break down the relationships between the species because of the imperfect preservation of most species.

Table 2: Species previously assigned to *Bailiella* and their taxonomic position as revised herein.

Species	Author, year of introduction	Suggested generic affinity	Regional occurrence
aequalis	Linnarsson, 1883	*Bailiella*	Sweden, Bornholm, Newfoundland
angusta	Kobayashi, 1960	*Bailiella*	South Korea
arcuata	Matthew, 1885	*Bailiella*	New Brunswick
artagena	Howell, 1937	*Meneviella*	Vermont
baileyi	Hartt in Dawson, 1868	*Bailiella*	New Brunswick, Newfoundland
barriensis	Sdzuy, 1958a	*Courtessolia*	Cantabrian Mountains, Iberian Chains
binodosa	Bi in Qiu et al., 1983	*Bailiella*	North China
bondoni	Termier & Termier, 1950	*Courtessolia*	Anti-Atlas
brevis	Matthew, 1890	nomen nullum	
bullata	Howell, 1925	*Bailiella*?	Newfoundland
cobboldi	Resser, 1936	*Emarginobailiella*	British Midlands
comleyensis	Resser, 1936	*Emarginobailiella*	British Midlands
dalmanni	Sjögren, 1872	nomen nudum	
dalmani	Angelin, 1854	*Bailiaspis*	Sweden
dilatata	Geyer, 1998	*Prioscutarius*	High Atlas
dongshankouensis	Yuan & Zhang in Yuan et al., 2016	*Bailiella*	Ordos Plateau
elegans	Lee in Zhou et al., 1982	*Bailiella*	Ordos Plateau
emarginata	Linnarsson, 1877	*Emarginobailiella*	Sweden

Species	**Author, year of introduction**	**Suggested generic affinity**	**Regional occurrence**
ferralsensis	Courtessole, 1967	*Occatharia*	Montagne Noire
frangtengensis	Reed, 1934	*Bailiella*	Kashmir
frantzeni	Sdzuy, 2000	*Bailiella*	Franconian Forest
froeensis	Westergård, 1950	*Emarginobailiella*	Sweden
gemina	Schmidt, 1944	*Bailiella*	Saxony
glabrata	Angelin, 1854	*Bailiaspis*	Sweden
griffei	Courtessole, 1967	*Courtessolia*	Montagne Noire
havlíceki	Šnajdr, 1957	*Occatharia*?	Bohemia
hebeiensis	Zhang & Wang, 1985	*Bailiella*	North China
heberti	Munier-Chalmas & Bergeron, 1889	*Conocoryphe*	Montagne Noire, Cantabrian Mountains, Iberian Chains
howelli	Hutchinson, 1962	*Bailiella*	Newfoundland
niuxinshanensis	this study	*Bailiella*	North China, Ordos Plateau
huoshanensis	Zhang & Wang, 1985	*Bailiella*	North China
impressa	Linnarsson, 1879	*Emarginobailiella*	Sweden
inconspicua	Geyer, 1998	*Prioscutarius*	High Atlas
lantenoisi	Mansuy, 1916	*Bailiella*	Vietnam, North China
lata	Wu & Lin in Zhang et al., 1980	*Bailiella*	North China
levyi	Munier-Chalmas & Bergeron, 1889	*Courtessolia*	Montagne Noire
linnarssoni	Grönwall, 1902	uncertain	Bornholm
longifrons	Cobbold, 1911	*Emarginobailiella*	British Midlands
lyelli	Hicks, 1871	*Emarginobailiella*	South Wales
manuelensis	Hutchinson, 1962	*Bailiella*	Newfoundland
max	this study	*Prioscutarius*	Franconian Forest
marginalis	this study	*Bailiella*	Franconian Forest
meridiana	Sdzuy, 1958a	*Courtessolia*	Iberian Chains
moritz	this study	*Prioscutarius*	Franconian Forest
orientalis	Lermontova, 1951	*Bailiella*	Siberian Platform
ornata	Resser, 1937	*Bailiella*	Newfoundland
pingshanensis	Zhang & Wang, 1985	*Bailiella*	North China
pokrovskayae	Korobov, 1973	*Bailiella*	eastern Siberian Platform
puteata	Resser & Endo, 1937	*Liaotungia*	North China
seguieri	Courtessole, 1973	*Courtessolia*	Montagne Noire
sejuncta	Reed, 1934	*Bailiella*	Kashmir
sepulcra	Álvaro & Vizcaïno, 2018	*Courtessolia*	Anti-Atlas
souchoni	Courtessole, 1967	*Courtessolia*	Montagne Noire
taurinus	Harrington, 1937	*Thysanopyge*	Argentina
tenuicincta	Linnarsson, 1879	*Emarginobailiella*	Sweden, Bornholm
teres	Grönwall, 1902	*Conocoryphe*	Bornholm
transversa	Zhang & Wang, 1985	*Bailiella*	North China
ulrichi	Resser & Endo, 1937	*Bailiella*	North China
walcotti	Matthew, 1885	*Bailiella*	New Brunswick
wuanensis	Zhang & Wang, 1985	*Bailiella*	North China
wurmi	Sdzuy, 2000	*Bailiella*	Franconian Forest
wutaishanensis	Zhang & Wang, 1985	*Bailiella*	North China

Bailiella lantenoisi **(Mansuy, 1916)**

Discussion. The species of *Bailiella* from Asia and particularly the North China/Sinokorean platform differ in some characters from those described from Avalonia, Baltica and West Gondwana. *Bailiella lantenoisi* (as the quintessential species of the group) has a moderately large glabella which tapers forward to a relatively narrow frontal lobe with a more-or-less evenly curved anterior margin on the cuticle, but occasionally a subtruncate front in internal moulds (as seen in the specimens figured in studies such as Wang et al. 1956, Lu 1957, Hsiang 1963, Lu et al. 1963, An 1966, Luo 1974, Schrank 1976, Wu & Lin in Zhang et al. 1980b, Kim 1987, Liu et al. 1987, 1991, Zhang et al. 1995, Luo et al. 2009 and Yuan et al. 2012). The lateral margins of the glabella are faintly curved to almost straight. They include three pairs of which S1 and S2 are distinctly bifurcated. The genae are moderately convex, with the most elevated point close to the axial furrow. Transversely elongate swellings are present near the axial furrows at about the level of the frontal lobe, and they continue into faint to obsolescent ridges that curve in a gentle arc towards the genal angle. The axial furrows are relatively sharply incised so that the glabella appears almost as being squeezed out between the genae. The anterior border is relatively narrow to moderately broad (sag.), never exceeding the breadth of the preglabellar field. It has more or less the same width in the median sector of the anterior border, but is clearly reduced in width anterolaterally. The anterior border furrow is moderately broad and well incised on the exterior of the cuticle. It is gently curved and proceeds into the lateral border furrow without any recognisable arcuation. The posterior border furrow is as well incised and quite narrow. The facial sutures are in a very marginal position and run along the adaxial margin of the lateral border furrow for most part of their course, but intersect the posterior border just adaxially of the genal angle. Furthermore, the pygidia of *B. lantenoisi* have a relatively broad rhachis and moderately broad lateral and posterior borders.

These characters differ in several aspects from those seen in the Avalonian, West Gondwanan and Baltican species assigned to *Bailiella*, including its type species, *B. baileyi*. The species of the *baileyi–aequalis* group have a glabella with a similar shape of the forward tapering glabella, but generally with a broader and less evenly curved front. This glabella has a vaguely bifurcate S1, but such a bifurcation is apparently never developed clearly in S2. The glabella is well separated from the genae by relatively wide axial furrows, which are deeper and developed as moderately broad gullies throughout so that the glabella does not appear as squeezed out from a cephalic platform. The genae are moderately convex, with their highest elevation in a more central position. The swellings as the relics of the eye ridges are subcircular to slightly elongate, and the faint ridges extend from them into obliquely lateral directions, but never into the genal angle. The anterior border is variably developed among the species, and sometimes it clearly exceeds the breadth of the preglabellar field. The anterior border furrow is generally a well-developed transverse groove with changing sag. and exsag. breadth, and it generally shows a slight kink or narrower curvature in anterolateral position. The posterior border furrow is usually moderately broad and never developed as a sharply incised furrow in those species. The facial suture lies usually in a relatively marginal position, but always intersects at least a narrow strip of the abaxial genal part. The known pygidia of the *baileyi–aequalis* group possess a slender to moderate axis and very narrow lateral and posterior borders.

Nevertheless, species with a transitional morphology are known. A particular illustrative species is *Bailiella manuelensis* from the Manuels Formation of Avalonian Newfoundland (see above; Fig. 98), which bridges the discussed morphological disparities.

Bailiella lantenoisi (Mansuy, 1916) was first described as *Conocoryphe lantenoisi* from northern Vietnam (Mansuy 1916, pl. IV, figs. 6, 7?, pl. V, fig. 3) and recognised as an index fossil for the strata in which it occurs. Additional, more instructive material was presented by Endo & Resser (1937, pl. 41, gigs. 5–8, pl. 42, pl. 59, fig. 21) from the Gangshikh Formation of Manchuria and by Kobayashi (1935, pl. 23, figs. 13, 14) from Manchuria as well.

The first mention of the species is under the name *Conocephalites typus* by Dames (1883). However, only the pygidium (pl. II, fig. 12), which was tentatively assigned to C. typus by Dames (1983) is believed to belong to the species. Lorenz (1906) and Walcott (1916) dealt with the cranidium and transferred the species to *Ptychoparia*. The species was later assigned to *Inouyella* Resser & Endo in Kobayashi, 1935 by Kobayashi (1937), but the scarce and incomplete specimens do not belong to *Bailiella lantenoisi* as suggested by its record in the synonymy lists presented by Yuan et al. (2012) and Yuan et al. (2016). Ferdinand von Richthofen had collected the material studied and presented by Dames (1883) in the Liaotung province, Manchuria, with the species coming from loose blocks in a wall. Walcott (1916) reported the same species based on material collected by Joseph Iddings from the "Fouchou series" in the Liaotung province, and this material clearly belongs to a ptychopariod trilobite.

The typical material of *Bailiella lantenoisi* from the Liaoning region of Manchuria (e.g., Yuan et al. 2012, pl. 35, figs. 1–7) and from the Shandong province (e.g., Yuan et al. 2012, pl. 41, figs. 5–8) exhibit cranidia with a moderately transverse shape, with slightly less curved anterior margin. The anterior border grows quite distinctly in width towards the sagittal line and is usually slightly narrower (sag.) than the preglabellar field, but rarely attains approximately the same width. It is moderately elevated and has a moderate convexity in transverse section. Specimens from the Liaoning region appear to differ from the others in having the tendency to develop anteriorly ascending anterior borders so that the border has a faint brim-like aspect with the highest elevation close to the anterior cephalic margin. The anterior border furrow is moderately broad, but typically narrows towards the anterolateral portions and is somewhat narrower laterally. Well preserved specimens exhibit in the broadened median section of the anterior border furrow a faint transverse rise of extended spindle-shape in dorsal view. The glabella is moderately large and tapers forward towards a fairly narrow frontal lobe, which is normally well rounded on the exterior of the cuticle. The lateral margins of the glabella are gently curved. The glabellar furrows S1 and S2 are both clearly bifurcate. The occipital ring is narrow near the axial furrows and grows to moderate size on the sagittal line. It carries a small to moderately large node slightly anterior to the centre. The genae carry transversely elongate, slightly curved swellings close to the axial furrow as remnants of the eye ridges.

The facial sutures are in a very marginal position and run along the adaxial margin of the lateral border furrow for most part of their course or even within the lateral border, but intersect the posterior border just adaxially of the genal angle: a mode of suturing which appears to differ from that seen in the non-East Asian species assigned to *Bailiella*. In addition, the weak eye ridge trace extends from the swellings in the genae run in a gentle curve precisely towards the genal angle.

The pygidium of *Bailiella lantenoisi* has a relatively wide (tr.) rhachis, which consists of 3 to 4 recognisable axial rings plus a terminal axial piece reaching almost to the posterior border. The axial rings are less well-defined towards the posterior end. The pleural fields show three pleural and interpleural furrows, the interpleural furrows being faint and even less clearly visible towards the posterior. The pygidium has a weakly defined, low lateral and posterior border, which is moderately broad and fairly well recognisable – unlike that seen in the Scandinavian, West Gondwanan and Avalonian species.

Since Zhang & Jell's (1987) monograph, *Liaotungia puteata* Resser & Endo, 1937 is generally synonymised with *Bailiella lantenoisi*. However, the specimen identified by Zhang (in Lu et al. 1965, pl. 37, fig. 23) clearly does not belong to *Bailiella lantenoisi* and the *Bailiella* plexus. Kobayashi's (1960, text-fig. 7m) illustration clearly shows that the specimen (and species) has a different shape of the glabella and possessed palpebral lobes and eyes.

Bailiella lantenoisi has also been reported from the Kashmir region of the Himalaya ranges. The first reports of *Bailiella*-type specimens by Reed (1934) led to the introduction of two new species, *Conocoryphe frangtengensis* and *C. sejuncta*. Shah (1973) transferred these species to *Bailiella* and introduced three additional species (*Holocephalina wadiai*, *H. wakhalooi* and *Conocoryphe reedi*) and a form assigned to *Bailiaspis* (as *Bailiaspis* sp.), which subsequently were all interpreted to represent the common *Bailiella lantenoisi* known from the South China and North China continents (Jell & Hughes 1997). As detailed in Jell & Hughes (1997), who studied Reed's (1934) and Shah's (1973) original specimens, Reed's distinction between *Conocoryphe frangtengensis* and *C. sejuncta* based on the absence and presence of genal spines was erroneous, and both represent the same species without a genal spine assigned to *B. lantenoisi* by Jell & Hughes (1997). Shah's purported species from the Nutunus Formation of the Baramula District were all interpreted to be differentially distorted leading to artificial peculiarities mistaken for taxonomically relevant characters. They were all assigned to *B. lantenoisi* although the imperfect preservation of course rules out a confident determination.

The Kashmiri specimens suffer from their imperfect preservation resulting in partly distinct tectonic distortion and compression as well as a deficient preservation of the surface. The circumstances make a confident identification to the species problematic. Nevertheless, the argumentation that all the previously described specimens and additional material studied by Jell & Hughes (1997) most probably belong to a single species is conclusive. In addition, the recognisable characters match those seen in *Bailiella lantenoisi*, and differences with regard to the typical specimens from North China can be interpreted to fall within the morphologic plasticity or are caused by differential deformation. Nevertheless, an authoritative taxonomic determination should name the Himalayan specimens *Bailiella* cf. *lantenoisi*.

A cranidium of *Bailiella lantenoisi* from the Yunnan Province, South China, is presented in Luo (1974, pl. 11, fig. 9). It shows a glabella with a moderately large glabella with progressive tapering towards an almost subacute front and with distinctly curved lateral margins; with a moderately broad (sag.) preglabellar field; a relatively sharp anterior border furrow and an anterior border that grows only slightly in breadth towards the sagittal line. Remarkable is the relatively short occipital ring. The preservation along the anterior border furrow is imperfect, but this specimen appears to lack the slight rise in the median sector seen in most of the specimens from North China. Additional figures of specimens from Yunnan are shown in Luo et al. (2009, pl. 14, figs. 4, 5). One of these specimens is the same as in Luo (1974), but the other is a considerably flattened cranidium, which certainly represents a different species. Characterisation of this species will need additional and better preserved material.

Material assigned to *Bailiella lantenoisi* from the Shandong Province is described and figured in Qiu et al. (1983, pl. 28, figs. 4, 5). One of the specimens is a dorsal exoskeleton that lacks the posterior part of the thorax and the pygidium. However, it displays a complete cephalon with relatively narrow anterior and lateral borders of nearly the same width throughout, defined by a relatively narrow border furrow, and with a glabella with is relatively slender and tapers only moderately forward. Judging from these characters, the specimen cannot be assigned to *B. lantenoisi*. The pygidium from the same strata, also assigned to *B. lantenoisi* in Qiu et al (1983), has relatively distinct pleural furrows and a slender pygidial axis, but is imperfectly preserved in other aspects. The same two specimens are refigured in Lu & Zhu (2001, pl. I, figs. 1 and 4, respectively), whereas most other specimens illustrated in Lu & Zhu (2001) agree well with typical specimens of *B. lantenoisi*/*ulrichi*. Similar specimens assigned to *B. lantenoisi* are figured in Nan (1980, pl. 201, fig. 15–17).

A small and obviously not fully grown cranidium assigned to *Bailiella lantenoisi* from the Hsuchuang Formation of the Shandong Province is figured in Lu & Zhu (2001, pl. II, fig. 13). It has a small, almost evenly tapering glabella with a subacute front and a relatively broad anterior border that grows slightly in width towards the sagittal line. Although the preservation of the specimen is imperfect, it exhibits that a narrow raise is developed in the anterior border furrow. The specimen probably is the only illustrated immature specimen of *Bailiella lantenoisi* and thus merits particular attention.

Zan (1992, pl. 1, fig. 1) illustrated a complete dorsal exoskeleton assigned to *Bailiella lantenoisi*, collected from the Hsuchuang Formation of eastern Liaoning. The cranidium is dorsoventrally compressed so that the shape of the glabella does not feature the original shape, but it agrees with other specimens from the Liaoning Province identified as *B. lantenoisi* and *B. ulrichi*, respectively. Remarkable is the distinctly broadening of the anterior border in its central sector, the relatively short (sag.) occipital ring and the fairly broad (sag.) preglabellar field. The thorax of this relatively large specimen is probably the best preserved of the species portrayed in any of the publications. It consists of 14 segments, all with slender pleurae and an almost centrally running pleural furrow. The attached pygidium has a relatively wide rhachis with two distinct rings and a subevenly curved posterior end. The pleurae are subdivided by two distinct pleural and two faint interpleural furrows.

Similarly, instructive dorsal exoskeletons are illustrated in Guo et al. (1996, pl. 22, figs. 8–13) together with two cranidia and a pygidium, all from the Liaoning Province. The exoskeletons show a thorax with 14 segments in both specimens and similar features as in the specimen shown in Zan (1992). The cranidia of all specimens are somewhat dorsoventrally compressed, showing an almost regularly tapering glabella with a narrow (tr.) frontal lobe. The anterior border grows moderately in width towards the sagittal axis, and the central sector of the anterior border furrow exhibits a relatively well recognisable sickle-shaped raise. The pygidium has a distinctly tapering axis with two distinct rings and a narrow posterior end, but it is affected by post-mortem deformation. The pleurae are subdivided by two distinct pleural and two less distinctly developed interpleural furrows.

Stratigraphical occurrence. Bailiella lantenoisi is generally regarded as an excellent index fossil permitting a correlation throughout most of the East Asian regions. It occurs at the top of the Hsuchuangian regional stage of the North China continent, in both fine siliciclastic and carbonate rocks. It characterises the *Bailiella-Lioparia* Zone in the Hsuchuang Formation, with most characteristic/traditional collections from the Liaoning province. This zone is assumed to correlate with the lowest part of the *Ptychagnostus gibbus* Zone in South China, Australia, Kazakhstania, Baltica and elsewhere.

Bailiella niuxinshanensis n. sp.

2016 *Bailiella lantenoisi* (Mansuy, 1916) – Yuan et al.: pp. 75–76, pl. 16, figs. 1–5, 7–10, non 6.

Holotype. NIGP 62270, incomplete cranidium, external mould (cast figured in Yuan et al. 2016, pl. 16, fig. 1).

LSID. urn:lsid:zoobank.org:act:847698EE-3B37-4B7B-8E94-3E6F3986E7E4

Type locality. Niuxinshan section, western Longxian County, western Shaanxi Province, North China.

Type stratum. Horizon L25, *Bailiella lantenoisi* Biozone, Changia Formation, Hsuchuangian Stage.

Etymology. Named after the type locality of the species at Niuxinshan.

Diagnosis. Species of *Bailiella* with cephalon of transversely elongate outline, anterior and lateral borders describing a more-or-less even curvature; glabella tapering forward towards a narrow frontal lobe, which tends to be subtruncate on internal moulds; S1 and S2 both clearly bifurcate; genae with transversely elongate swellings close to the axial furrow; anterior border slightly narrower (sag.) than the preglabellar field, prominent; anterior border furrow narrows towards the anterolateral portions; facial sutures in a very marginal position, intersect posterior border just adaxially of the genal angle; pygidium with a relatively wide (tr.) rhachis, which consists of 3 to 4 recognisable axial rings plus a terminal axial piece; proceeds into a low and poorly defined plectrum; pleural fields show three pleural and interpleural furrows: pygidial border poorly defined, low, but broad and well recognisable.

Discussion. Bailiella lantenoisi has also been reported from the Changhia Formation of the western Shaanxi Province and from the Hulusitai Formation, Hsuchuangian Stage, of the Ordos Plateau in the Inner Mongolia region, China, from the eponymous biozone (Yuan et al. 2016, pl. 16, figs. 1–5, 7–10, non 6!). These specimens are nicely preserved and particularly instructive. However, they clearly differ from *B. lantenoisi*, but represent a new, fairly easily recognisable species.

Typical cranidia of this new species, *Bailiella niuxinshanensis* n. sp., have a transversely elongated shape, with the anterior and lateral borders describing a more-or less even curvature. The anterior border grows slightly in width towards the sagittal line and is usually slightly narrower (sag.) than the preglabellar field, but can attain approximately the same width. It is quite prominent so that the anterior border furrow is quite deep. This anterior border furrow is moderately broad, but typically narrows towards the anterolateral portions and is somewhat narrower laterally. The glabella tapers forward towards a narrow frontal lobe, which is normally well rounded on the exterior of the cuticle, but tends to be somewhat subtruncate on internal moulds. The occipital ring is quite narrow near the axial furrows and grows to moderate size on the sagittal line. It carries a small to moderately large node slightly anterior to the centre. The genae carry transversely elongate swellings close to the axial furrow as remnants of the eye ridges. The facial sutures are in a very marginal position and run along the adaxial margin of the lateral border furrow for most part of their course or even within the lateral border, but intersect the posterior border just adaxially of the genal angle: a mode of suturing which appears to differ from that seen in the non-East Asian species assigned to *Bailiella*. In addition, the weak eye ridge trace continuing from the swellings in the genae run in a gentle curve precisely towards the genal angle. Another peculiarity is that the glabellar furrows S1 and S2 are both clearly bifurcate.

The pygidium of *Bailiella niuxinshanensis* also differs distinctly from those seen in the Scandinavian and Avalonian species assigned to *Bailiella*, but they resemble very much the pygidia known from *B. lantenoisi*. They have a relatively wide (tr.) rhachis, which consists of 3 to 4 recognisable axial rings plus a terminal axial piece which are les well-defined towards the posterior end. It proceeds into a low and poorly defined plectrum. The pleural fields show three pleural and interpleural furrows, the interpleural furrows being faint and even less clearly visible towards the posterior. The pygidium has a weakly defined, low lateral and posterior border, which is moderately broad and fairly well recognisable – unlike that seen in the Scandinavian, West Gondwanan and Avalonian species.

Bailiella dongshankouensis (Yuan & Zhang in Yuan et al., 2016)

*2016	*Occatharia dongshankouensis* Yuan et Zhang, sp. nov. –Yuan et al.: pp. 77, 345–346, pl. 16, figs. 11–14.

Holotype. NIGP 62538, incomplete cranidium (figured in Yuan et al. 2016, pl. 16, fig. 13).

Type locality. Dongshankou section, Gandeershan, Wuhai City, on Ordos Plateau in the Inner Mongolia region, China.

Type stratum. *Bailiella lantenoisi* Biozone, Hulusitai Formation, Hsuchuangian Stage, Ordos Plateau in the Inner Mongolia region, China.

Diagnosis (emended). Species of *Bailiella* with cephalon of transversely elongate outline, anterior and lateral borders describing a more-or-less even curvature; glabella with nearly straight lateral margins, tapering forward towards a narrow frontal lobe, which is nearly subtruncate and has distinct anterolateral corners; preglabellar field sunken; anterior border quite narrow, elevated; anterior border furrow deep, with little expansion on sagittal line; pygidial axis consisting of five rings with the posterior furrows not continuing across the sagittal line; lateral and posterior borders not developed.

Discussion. A species similar to *Bailiella niuxinshanensis* n. sp. was described under the name *Occatharia dongshankouensis* Yuan & Zhang in Yuan et al., 2016. This species co-occurs with *B. lantenoisi* in the Hulusitai Formation of the Ordos Plateau in Inner Mongolia and exemplifies a morphological gradient: It shares most of the characters with *B. lantenoisi*, but differs primarily in having a sunken preglabellar field, almost straight lateral margins of the glabella and a low curvature of the anterior margin of the frontal lobe. In addition, its pygidium (if correctly identified; see Yuan et al. 2016, pl. 16, fig.12) has five rings with the posterior furrows not continuing across the sagittal line and lacks lateral and posterior borders.

Unfortunately, *Occatharia dongshankouensis* cannot be maintained to be a species of the genus *Occatharia* Álvaro, 2007. This genus has been based on *Conocoryphe ferralsensis* Courtessole, 2007 from the Coulouma Formation in the Montagne Noire region, southern France. Álvaro & Vizcaïno (2003) founded a new genus *Catharia* on the species, but this was a homonym of the genus *Catharia* Lederer, 1863. The homonym was replaced by *Occatharia* Álvaro, 2007. *Occatharia ferralsensis* is primarily characterised by its relics of the eyes and palpebral lobes expressed as strongly curved ridges in a relatively central position on the genae. The preglabellar field is fairly low, but still well convex and of completely different character as that in *Occatharia dongshankouensis*. The latter species thus cannot be accommodated under *Occatharia* and is regarded as a somewhat atypical species of *Bailiella*.

Bailiella lata Wu & Lin in Zhang et al., 1980

Discussion. Bailiella lata Wu & Lin in Zhang et al., 1980 from the upper Wuliuan Xuzhuang Formation of Shuiyu, Ruicheng, in the Zhongtiao Mountains of the Shanxi province, North China, is usually held for a junior synonym of *B. lantenoisi*. This species, however, differs clearly from *B. lantenoisi* in several characters and cannot be synonymised with it although the type material raises questions. Wu & Lin (in Zhang et al., pl. II, figs. 9–11) figured two cranidia and a pygidium, and Zhang & Wang (1985, pl. 110, figs. 13, 14) refigured one of the cranidia and the pygidium.

The holotype (pl. II, fig. 9) is a relatively small cranidium with a tapering glabella having gently curved lateral margins and a moderately wide (tr.) frontal lobe the anterior margin of which is more-or-less evenly curved. Visible are S1 and S2 being distinctly bifurcate. The occipital ring is narrow laterally and carries a low node in a subcentral position. The axial furrows are relatively sharply developed and incised. The anterior margin of the cranidium is considerably curved and describes a more-or-less uniform arc proceeding into lateral parts with only a faint change in curvature anterolaterally. The anterior border is fairly low and relatively narrow and tapers continuously from the sagittal line so that the border is relatively narrow where the facial suture starts to intersect the border in a very anterior position at about the level of the posterior margin of the anterior border furrow. The anterior border is weakly defined against the anterior border furrow in the central sector, where it slopes from the most elevated parts. The anterior border furrow is vaguely crescent shaped, with a moderately curved anterior margin and an almost straight posterior margin, relatively shallow, but includes a low, transversely elongate raise its central part, which is approximately as wide (tr.) as the frontal lobe of the glabella. A similar, but less clearly developed and smaller rise can be seen in some specimens of *B. lantenoisi*, which also have a different outline of the anterior border furrow. The preglabellar field is relatively narrow, of approximately the sag. breadth of the anterior border furrow on the sagittal axis. The facial suture in this species clearly runs entirely within the lateral border, only perhaps touching the abaxial margin of the lateral border furrow at about the level of S1.

A second cranidium of nearly the same dimensions (but figured in a smaller size; Wu & Lin in Zhang et al. 1980, pl. II, fig. 10) differs in several characters and almost certainly represents a different species of *Bailiella*. This specimen has a relatively slender and longer glabella with nearly straight lateral margins and a narrow frontal lobe which is obliquely truncated on both sides of the sagittal line, creating a somewhat pointed tip. The anterior border is of moderate breadth (sag.) and tapers gently from the sagittal line abaxially. The anterior border furrow is of normal width, but seems to show a faint rise medially. The preglabellar field is about as wide (sag.) as the anterior border plus border furrow on the sagittal line. More material is needed to sort out this discrepancy.

The pygidium assigned to *Bailiella lata* (Wu & Lin in Zhang et al. 1980, pl. II, fig. 11) differs considerably from all pygidia known from the *lantenoisi* group as well as the Baltican, West Gondwanan and Avalonian species assigned to *Bailiella*. It has a sublenticular outline and a relatively broad axis with stretches to the posterior border. The pleural field have weakly developed pleural furrows, but are defined anteriorly by a well elevated bulge curving rearwardly at the anterolateral corners. Lateral and posterior borders are obsolescent. This pygidium almost certainly does not belong to the same species as the holotype cranidium. Accordingly, the species is regarded as valid and distinct, but should be restricted to the holotype until more well-preserved specimens are known.

Bailiella marginalis n. sp.

v 2000 *Bailiella aequalis* (Linnarsson 1883) – Sdzuy: pp. 302, 305, 308, pl. 3, figs. 11–14, pl. 7, figs. 4*–6*.
non v 2000 *Bailiella aequalis* (Linnarsson 1883) – Sdzuy: pl. 3, fig. 15 [only].

Holotype. SMF 57646, partial dorsal exoskeleton, cast of external mould (figured in Sdzuy 2000, pl. 3, fig. 13a, b and pl. 7, fig. 5*).

LSID. urn:lsid:zoobank.org:act:D6CDD32C-3656-44CD-9A1E-B1A49FA03D0C

Type locality. Sdzuy's (2000) locality 1 near the Weidstaudenmühle, southwest of Lippertsgrün, Franconian Forest region, north-eastern Bavaria, Germany.

Type stratum. *Solenopleuropsis* Biozone, Lippertsgrün Formation, Languedocian Stage (upper Drumian).

Paratypes. Three cranidia under SMF 57644, SMF 57645 and SMF 57647. All topo- and stratotypic with holotype.

Diagnosis (emended). Species of *Bailiella* with cephalon of transversely elongate outline, anterior border describing a more-or less even curvature; glabella with faintly to slightly curved lateral margins, tapering forward towards a narrow frontal lobe with a low curvature of its anterior margin; preglabellar field moderately broad, distinctly convex; anterior border narrow, elevated, with little expansion towards the sagittal line; anterior border furrow narrow, of subequal breadth throughout it course, with a faint swelling across the sagittal line; facial suture at a pronouncedly abaxial position, dissects the lateral border furrow fairly posterior position posterior to the level of L2.

Discussion. Sdzuy (2000) described several trilobite sclerites from the notoriously poorly preserved fauna of the Lippertsgrün Formation of the Franconian Forest area, which he assigned to *Bailiella*. Some of them were identified as *Bailiella aequalis* (Linnarsson, 1883) (Sdzuy 2000, pl. 3, figs. 11–15, pl. 7, figs. 4*–6*). All of them are quite strongly distorted, and from the description by Sdzuy it becomes clear that he was not completely convinced that they indeed represent *B. aequalis*. Sdzuy's figures suggest that the specimens are similar to the species from Scandinavia. They share with it the narrow anterior border; a slight anterolateral kink in the anterior border furrow; the relatively posterior position at which the facial suture dissects the lateral border furrow; and the shape of the glabella with a narrow frontal lobe and nearly straight lateral margins of the glabella. However, the preglabellar field in the specimens from the Lippertsgrün Formation is distinctly broader (sag.) than that in *B. aequalis*, having at least 1.5 times the width of the anterior border on the sagittal line, and the precise position of the facial suture almost certainly is in an even more lateral position so that the lateral border in the cranidium is still present at the level of L2, which is probably the most marginal position in any species assigned to *Bailiella*.

Despite the imperfect preservation of the specimens, all taxonomically relevant characters are visible, including the occipital ring with a gentle curvature of its posterior margin. The specimens represent a new species introduced here under the name *Bailiella marginalis* n. sp.

The stratigraphic occurrence of *Bailiella marginalis* clearly postdates that of *B. aequalis*. Because of the difficult outcrop situation of the Lippertsgrün Formation, there is unfortunately little hope to collect more and better-preserved specimens.

Genus *Prioscutarius* n. gen.

Type species. Bailiella dilatata Geyer, 1998; from the Jbel Wawrmast Formation, *Ornamentaspis frequens* Zone, Lemdad Syncline, the High Atlas, Morocco.

LSID. urn:lsid:zoobank.org:act:BAACCB0C-B308-4D0B-A463-BF0231C3CE82

Etymology. From the Latin *prius*, early; and *scutarius*, carrier of a shield; a reference to the shape of the cephalon that resembles a shield, and its early stratigraphic occurrence.

Diagnosis. Cephalon subsemicircular in outline; glabella weakly to moderately tapering forward, lateral margins curved, frontal lobe moderately broad; preglabellar field relatively broad (sag.), convex, shorter (sag.) than anterior border; anterior border distinctly growing in width towards the sagittal line, up to moderate convexity in sag. and exsag. profile; anterior border furrow broad (sag.), shallow; facial suture in a relatively adaxial position, with a noticeable part of the distal genal areas located on the librigena.

Discussion. This new genus is characterised by a glabella which tapers moderately forwards and possesses a gently rounded and relatively broad anterior margin of its frontal lobe. The cephalon is shield-like in outline and thus has a relatively high length:width ratio, thus considerably differing from that seen in typical species of *Bailiella*. A prime characteristic feature, however, is the morphology of the anterior part of the cephalon: The anterior border in the species of *Prioscutarius* is typically of low convexity in sagittal and exsagittal profile. It accompanied by a broad anterior border furrow with a tendency to include a low median rise in the sagittal sector. The preglabellar field is well developed and clearly convex on the sagittal line, but narrower (sag.) than the anterior border.

This configuration is typically developed in *Bailiella dilatata* Geyer, 1998 from the (probably lowermost Wuliuan) *Ornamentaspis frequens* Zone of the High Atlas, which is chosen as the type species. Two additional species are introduced below, *P. max* n. gen., n. sp. and *P. moritz* n. gen., n. sp.: They are from the same stratigraphic level as *P. dilatata*, both occurring in the Wildenstein Member of the Tannenknock Formation of the Franconian Forest, and they exhibit the same combination of features. *Bailiella inconspicua* Geyer, 1998 differs in having a shorter cephalon and a more ascending anterior border, but belongs to the same clade and is thus also assigned to *Prioscutarius*.

Prioscutarius max n. gen., n. sp.

Figs. 100–103, 104A, B–K?, 105?

Holotype. MMUW 2017D-410, incomplete cranidium (Fig. 101B, E, H).

LSID. urn:lsid:zoobank.org:act:C89455B7-AC2A-483B-A12E-2ECAE23B23E7

Type locality. Locality W8 on Fig. 4, Galgenberg north of Wildenstein, Franconian Forest.

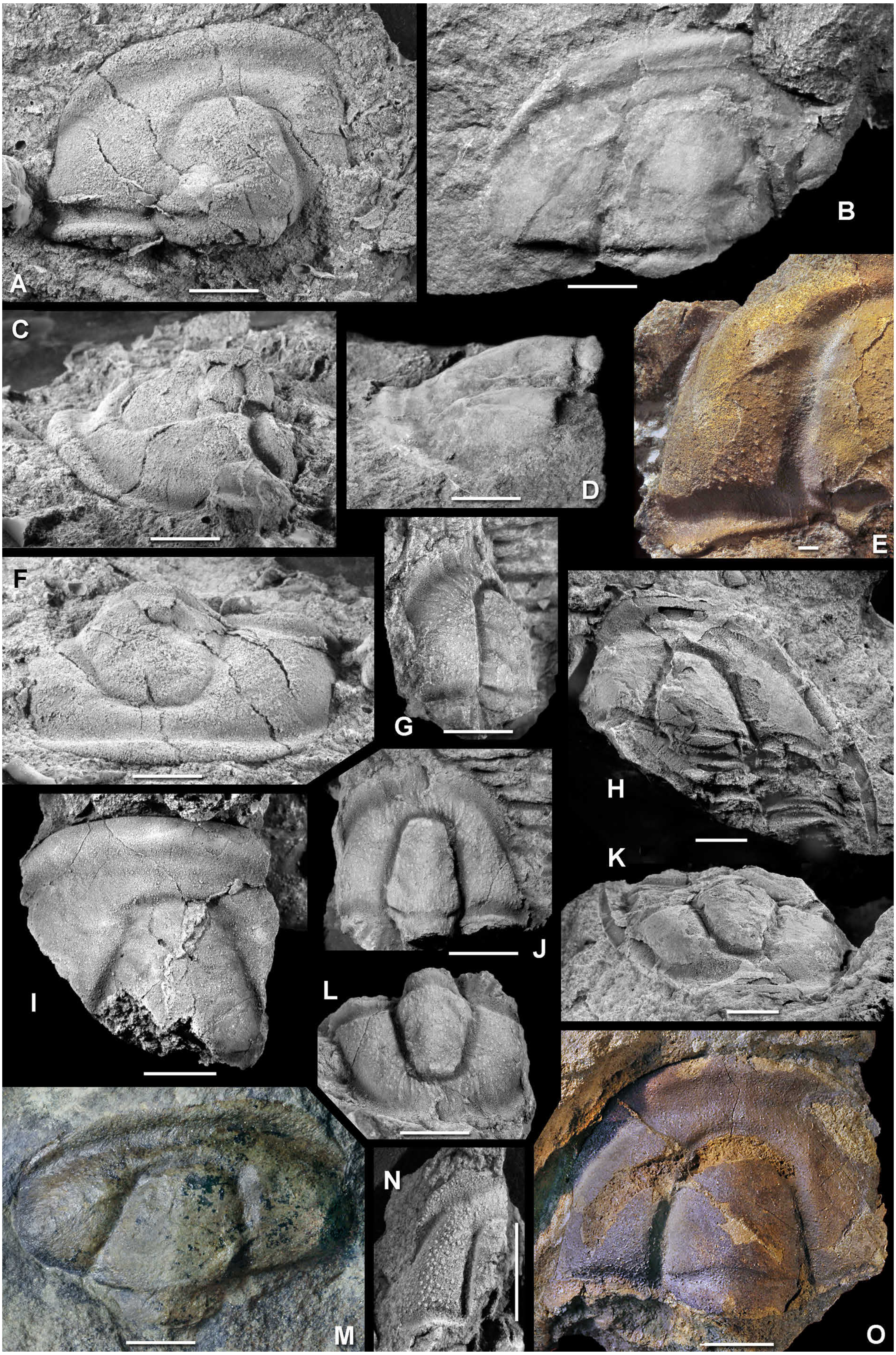
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Fig. 100: *Prioscutarius max* n. gen., n. sp. **A, C, F** SSMM 10426, paratype, incomplete cranidium with centrifugal fractures, dorsal (A), oblique lateral (C) and oblique anterior (F) views; from locality W8; **B, D** SSMM 10508, paratype, incomplete cranidium, internal mould with relics of the cuticle, dorsal (B) and lateral (D) views; from locality W8; **E** SSMM 11069, incomplete cranidium, internal mould, detail of left half; from locality W8; **G, J, L** MMUW 2017D-012, paratype, cranidium, internal mould, oblique lateral (G), dorsal (J) and oblique anterior (L) views; from locality W8; **H, K** MMUW 2017D-054, paratype, incomplete cephalon with attached partial thorax, internal mould with relics of the cuticle, dorsal (H) and oblique anterior (K) views; from locality W8; **I** MMUW 2017D-439, fragment of cranidium; from locality W13f; **M** SSMM 10559, paratype, incomplete cranidium, slightly distorted composite mould; from locality W8; **N** MMUW 2017D-044, paratype, fragment of cranidium, internal mould showing relative coarse granules on the fixigenae; from locality W8; **O** SSMM 10497, paratype, small incomplete cranidium, internal mould; from locality W8.
Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Type stratum. Wildenstein Member, Tannenknock Formation.

Etymology. Named after Max, a literary figure created by the German artist Wilhelm Busch (1832–1908) as one main figure of the coarse boyish protagonists in *Max und Moritz*; a reference to the joint occurrence of the species with *Prioscutarius moritz* n. gen., n. sp. (see below).

Paratypes. Single dorsal exoskeleton, single cephalon, cephalon with attached thoracic segments, 114 cranidia, three rostral plates, one articulated thorax, single pygidium. From locality W1a (cranidia under MMUW 2017D-942 and -965); from locality W8 (cephalon under MMUW 2017D-054; cephalon with attached thoracic segments under MMMUW 2017D-080a, 77 cranidia under MMUW 2017D-004, -011, -012, -013, -043, -044, -045, -050a, -050b, -070, -073, -079, -139, -142, -144, -145, -178, -182a, -188, -203a, -203b, -203c, -203d, -203e, -204, -208b, -233a, -234a, -270, -280, -292, -303d, -371b, -377, -394, -632a, -658, -711, -736, -742, -998, -1002, SSMM 10334, 10425, 10426, 10456, 10457, 10460, 10462, 10471, 10490, 10493, 10495a, 10497, 10498, 10499, 10508, 11003, 11015a, 11050a, 11069, 11125, 11183, 11322, 11442a, 11442b, 11496f, 11600a, 12317, 12412, 12413, 12414, 12415, 12416, 12417, 12418 and 12419; two rostral plates under MMUW 2017D-003, -715; pygidium under MMUW 2017D-596); from locality W9 (dorsal exoskeleton under MMUW 2107-D-345; 18 cranidia under MMUW 2017D-335, -631a, -631b, -648, -661, -662. -663, -664, -665, -666, -667, -668, -669a, -669b, -670, -673, SSMM 12404 and SMSN 75643); from locality W9b (cranidium under MMUW 2107-D-561); probably from locality W11 or W12 (partial cranidium under SNSB-BSPG 1955-VII-14); from locality caW12a (two cranidia under SSMM 10626a and 10627); from locality W12c (cranidia under MMUW 2017D-939I/II, -940I/II and -941); from locality W13b (four cranidia under MMUW 2107-D-400, -410, -418 and -426; rostral plate under MMUW 2107-D-408; articulated thorax under MMUW 2107-D-411); from locality W13e (11 cranidia under MMUW 2107-D-432, -433, -434, -435, -439a, -441, -442a, -444, -450, -478 and -620); from locality W16a (two cranidia under MMUW 2017D-854-I/-II and -855).

Specimens tentatively assigned to Prioscutarius max*:* In repository; single dorsal exoskeleton, 53 cranidia, two librigenae, 8 pygidia, ca. 30 fragments of thoracic segments. From locality W1a (single cranidium under MMUW 2017D-943a); from locality W7 (cranidium under MMUW 2107-D-532); from locality W8 (dorsal exoskeleton under SSMM 10496; 38 cranidia under MMUW 2017D-026c, -037c, -062a, -069c, -081, -140a, -269, -285, -309c, -359, -366, -1027, SSMM 10398b, 10409b, 10242, 10431, 10451a, 10458, 10461, 10493, 10524, 10530, 10536b, 10549, 10551, 10554, 10556, 10558, 10560, 10813b, 11007, 11039a, 11052, 11053a, 11134, 11140a, 11193 and 11443b; two librigenae under MMUW 2017D-102 and -128a; four pygidia under MMUW 2017D-182e, -378a and -393a; thoracic segments/ pleurae under MMUW 2017D-038, -046, -047, -097b, -103b, -179, -229c, -234d, -382, -387, -597b, -629 and -774); from locality W8a (incomplete thorax with attached pygidium under MMUW 2017D-881/L); from locality W9 (two cranidia under MMUW 2017D-343 and -346; single pygidium under MMUW 2017D-324; thoracic segments/pleura under MMUW 2017D-344); from locality W9b (two pygidia

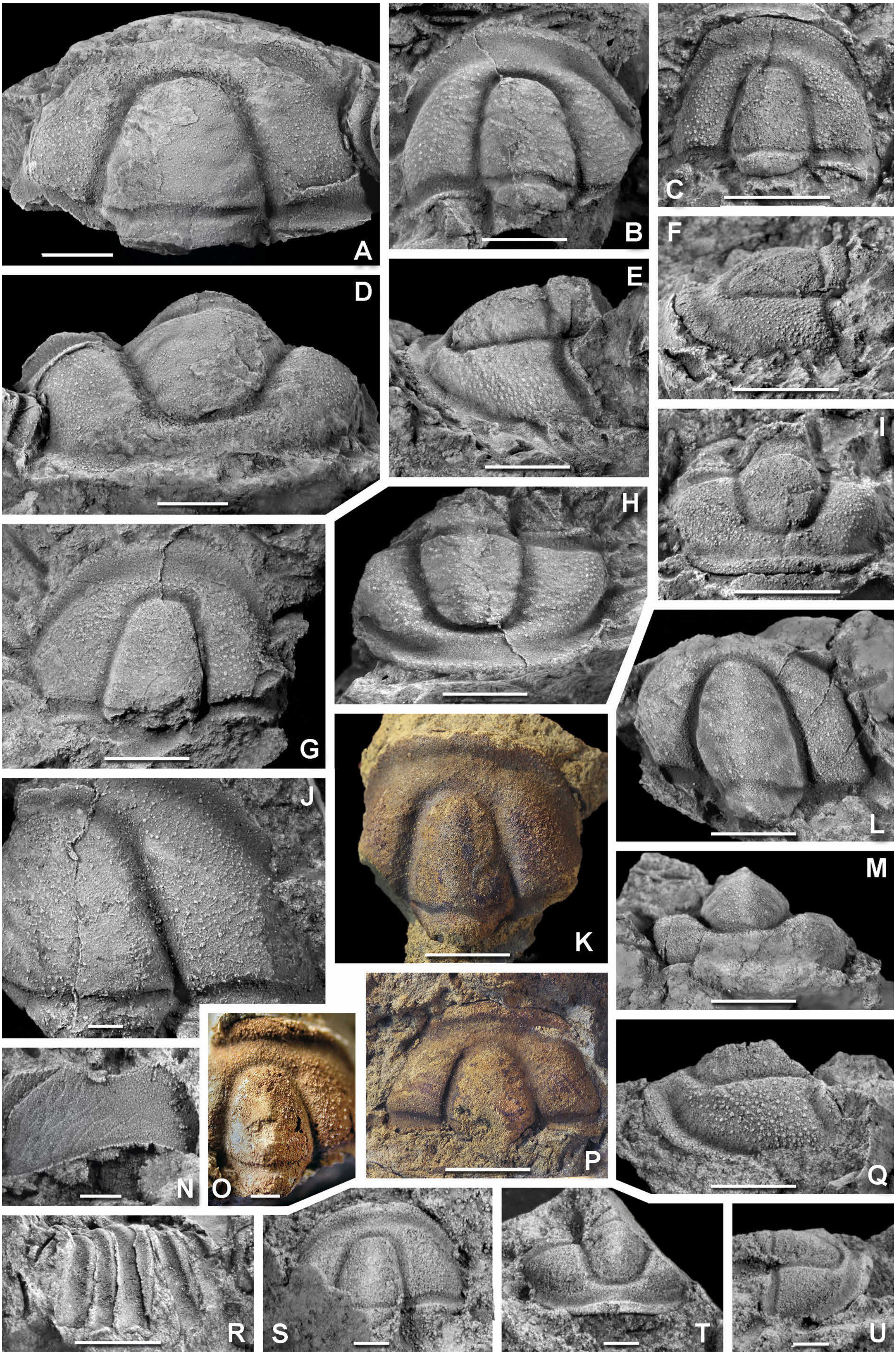
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Fig. 101: *Prioscutarius max* n. gen., n. sp. **A, D** MMUW 2017D-939I, paratype, incomplete cranidium, internal mould with relics of the cuticle, dorsal (A), oblique anterior (D) views; from locality W12c; **B, E, H** MMUW 2017D-410, holotype, incomplete cranidium, internal mould, dorsal (B), lateral (E) and oblique anterior (H) views; from locality W8; **C, F, I** MMUW 2017D-079, paratype, cranidium, internal mould, dorsal (C), oblique lateral (F) and oblique anterior (I) views; from locality W8; **G, J** MMUW 2017D-043, paratype, incomplete cranidium, internal mould, dorsal views of entire specimen (C) and magnification illustrating eye ridges and differences in the density of the granulation and the size of the granules; from locality W8; **K** SSMM 10462, paratype, incomplete cranidium, internal mould; from locality W8; **L, M, Q** MMUW 2017D-561, paratype, incomplete cranidium, internal mould, dorsal (L), anterior (M) and lateral (Q) moulds; from locality W9b; **N** incomplete thoracic segments, view of ventral doublure of the pleural tip covered with terrace ridges, dorsal view; from locality W8 (specimen apparently lost); **O** SSMM 10490, paratype, incomplete cranidium, internal mould; from locality W8; **P** SSMM10498, paratype, incomplete small cranidium, internal mould; from locality W8; **R** MMUW 2017D-411, paratype, partial thorax, internal mould, lateral view, exemplifies articulation of segments under weak concave enrolment; probably from locality W13b; **S–U** MMUW 2017D-004, paratype, incomplete small cranidium, internal mould, dorsal (S), oblique anterior (T) and oblique lateral (U) views; from locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm except for J, N–Q, R–U (1 mm).

under MMUW 2107-D-564 and -568); from locality W11a (two cranidia under MMUW 2017D-892 and -901); from locality W13b (five cranidia under MMUW 2107-D-407, -558, -598a, -598b and -598c; three pygidia under MMUW 2017D-406, -412 and -413); from locality W13e (five cranidia under MMUW 2107-D-448, -455a, -461, -479 and -486; five thoracic segments/pleura under MMUW 2017D-445, -484, -489b, -617b and -671b); from locality W15d (partial cranidium under MMUW 2017D-888b); from locality W17 (cranidium under MMUW 2017D-789; two pygidia under MMUW 2107-D-809 and -812); from locality W18a (single cranidium under MMUW 2107-D-540b); from locality W19a (two cranidia under MMUW 2107-D-835-I and -835-II); from locality T2a (cranidium under SSMM 10088).

Diagnosis. Species of *Prioscutarius* with the following characters in adult individuals: glabella moderately wide (tr.), with gently curved lateral margins and a moderately broad frontal lobe, anterior glabellar margin broadly curved; occipital ring moderately broad (sag.), with subterminal node; anterior border relatively thick (exsag., sag.) moderately prominent, about as wide as the preglabellar field; anterior border furrow moderately broad (exsag., sag.), without precise definition from border and preglabellar field, with low, transverse swelling of approximately the tr. width of the glabella in its posterior two-thirds; facial suture intersecting lateral border to enter lateral border furrow at about the level of S2, with maximal adaxial position in the most abaxial part of the genae at the level of L1; genae with longitudinally elliptical swellings arranged oblique to axis, its proximal ends proceeding into a faint thread that traverses the axial furrows and merges with the front of the glabella; prosopon of loosely spaced granules.

Description. Cephalon subsemicircular to subtrapezoidal in outline. Axial furrows moderately well developed in depth and width, deeper on internal moulds than on the exterior of the cuticle. Glabella tapers forward, lateral margins gently curved from L1 to the frontal lobe, frontal lobe with gentle curvature at anterior margin, but mostly with somewhat lower curvature across sagittal line; length of the glabella 68 to 74 percent (n=8) cephalic length on the sagittal line; maximum glabellar width across L1 of ca. 35 percent (n=6) cranidial width across level of the posterior border; frontal lobe width about 52 to 57 percent (n=5) width across L1; three pairs of lateral glabellar furrows; S1 moderately long, bifurcated, with strongly backward curved posterior branch and shorter and mostly faint, transversely directed anterior branch; S2 moderately long, backward directed from axial furrow, less well developed than S1; S3 comparatively short, slightly posteriorly directed to almost normal to axis, usually barely recognisable. Occipital furrow with narrow, well-incised lateral parts directed obliquely backward from axial furrow, and broader (sag.) and shallower transverse middle part. Occipital ring sagittally of about 12–15 percent (n=6) cephalic length, extreme lateral parts narrow; moderately large occipital node in a position relatively close to the posterior margin of the occipital ring.

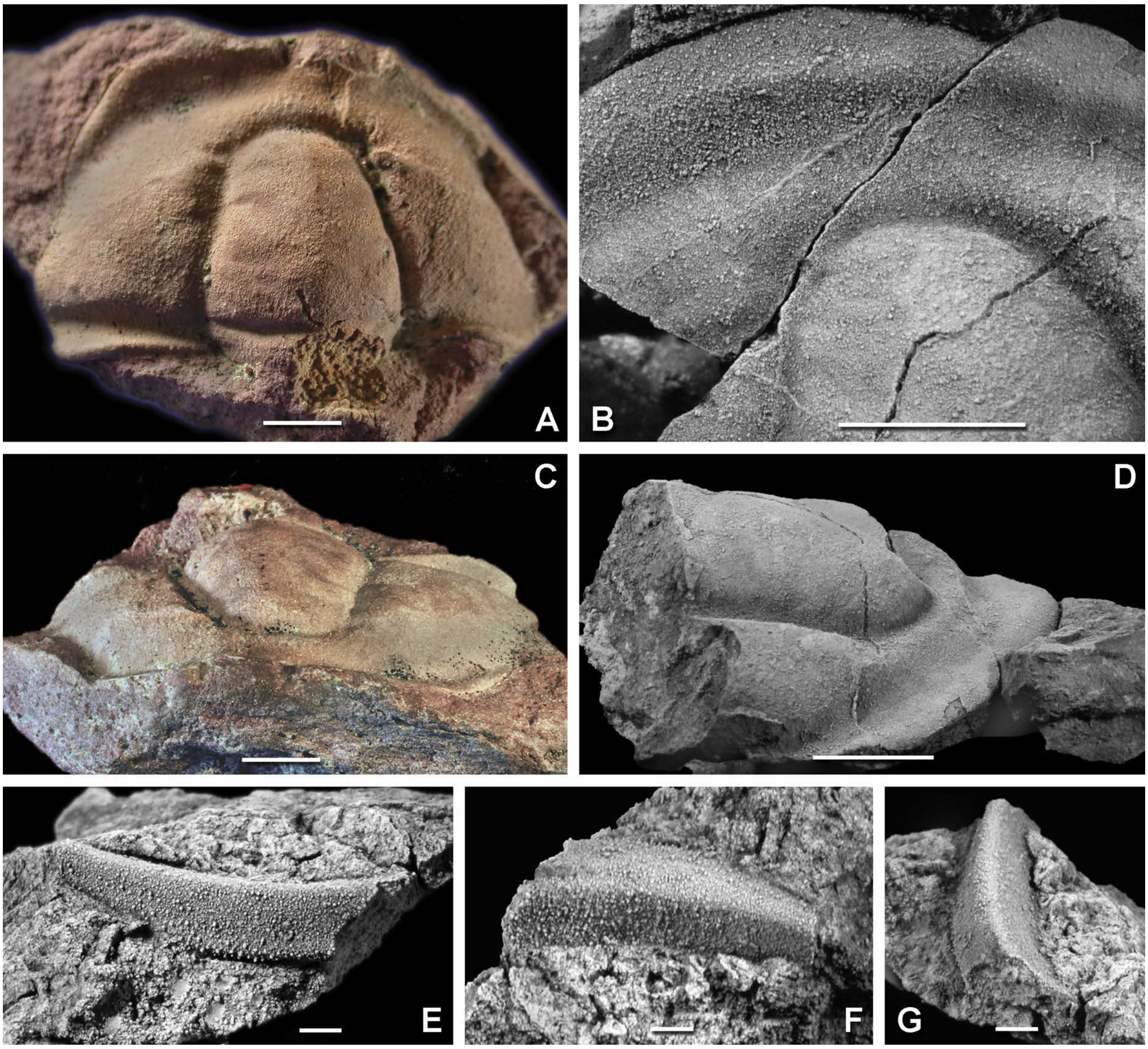

Fig. 102: *Prioscutarius max* n. gen., n. sp. **A, C** SSMM 11183, paratype, incomplete cranidium, internal mould, dorsal (A) and oblique anterior (C) views; from locality W8; **B, D** MMUW 2017D-013, paratype, partial cranidium, internal mould, detail of dorsal view (A) and oblique lateral view (D); from locality W8; **E–G** MMUW 2017D-003, paratype, partial rostral plate, oblique anterior (E), ventral (F) and oblique lateral (G) views; from locality W8.
Specimens from Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm in A–D and 1 mm in E–G).

Gena distinctly convex in transverse and exsagittal profile, with most elevated part relatively close to the axial furrow in the posteroadaxial sector; swelling developed as longitudinally extended elliptical rise oriented slightly to distinctly oblique to axis; abaxial end of swelling proceeds into a low and mostly faint, moderately thick thread that curves posterolaterally in a gentle arc, but is not recognisable in the abaxial half of the gena; adaxial end of swelling extends into a thin thread that traverses the axial furrow and merges with the anterolateral corners of the frontal lobe.

Preglabellar field moderately broad (sag.), 12 to14 percent (n=6) cephalic length, moderately convex (sag.), proceeding into and faintly lower than the preocular areas.

Anterior border moderately convex, moderately broad (sag.), 12 to14 percent (n=6) cephalic length, slightly decreasing in exsag. breadth abaxially to the anterolateral corners, with a more conspicuous decrease in width and elevation from there to the lateral border. Anterior margin gently curved in dorsal aspect, faintly arched upward in frontal view, with a more pronounced curvature at anterolateral corners.

Anterior border furrow quite shallow to moderately deep, poorly defined from anterior border and preglabellar field, fairly broad in its central portion; with a low, transverse rise that occupies the posterior two-thirds of the anterior border furrow stretching for a distance of approximately the maximum width of the glabella. Posterior border with straight adaxial part, weakly sigmoidally curved distally, moderately narrow, but slightly broadening abaxially, relatively prominent. Posterior border furrow well developed, moderately broad, faintly broadening abaxially, with straight adaxial part and slight sigmoidal curvature distally.

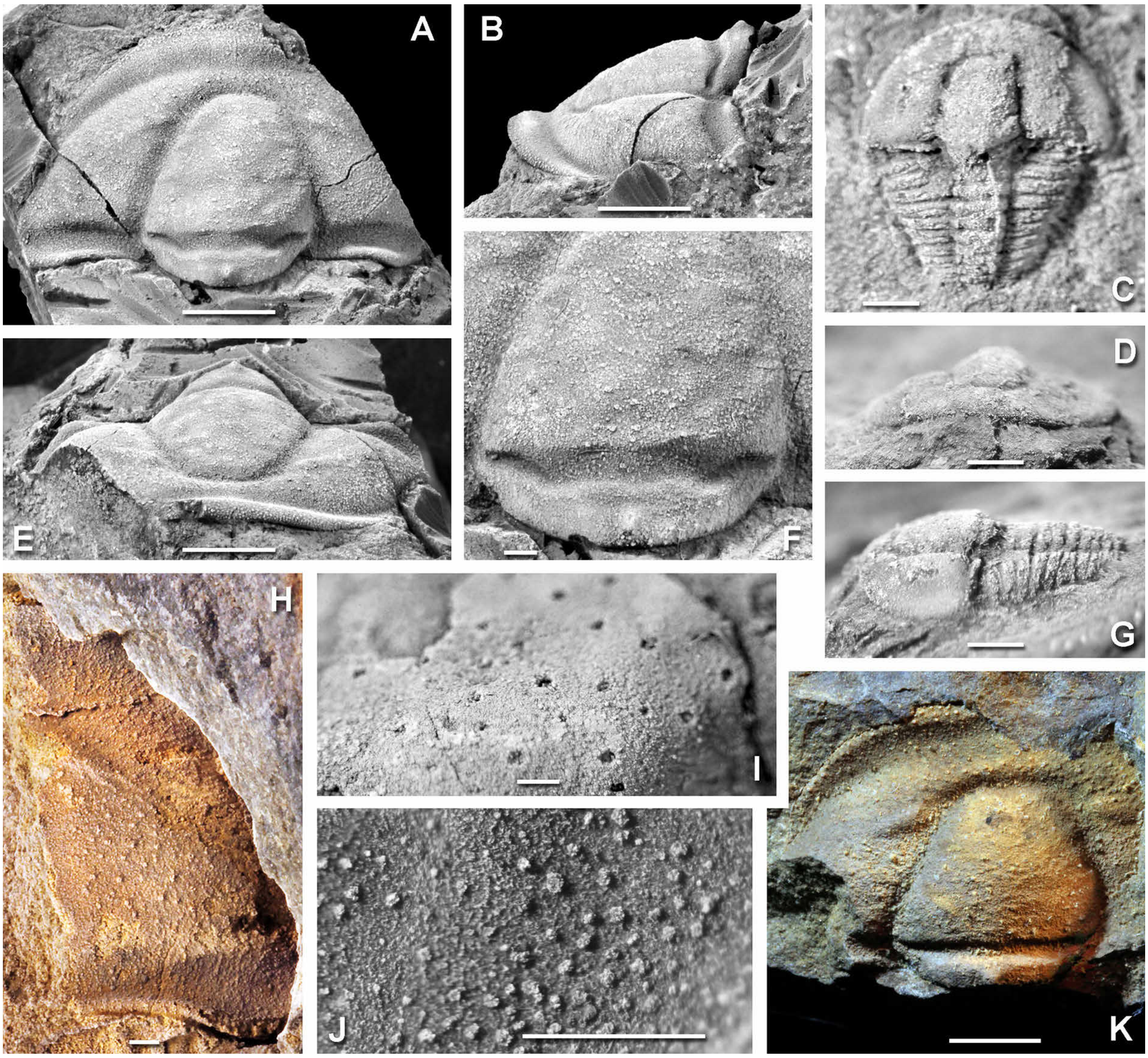

Fig. 103: *Prioscutarius max* n. gen., n. sp. **A, B, E, F** MMUW 2017D-135a, paratype, incomplete cranidium, internal mould, dorsal (A), lateral (B) and anterior (E) views as well as magnified view of glabella illustrating ornamentation by coarser and fine granules (F); from locality W8; **C, D, G** MMUW-2017D-345L, paratype, incomplete dorsal exoskeleton of immature individual, latex cast of internal mould, dorsal (C), anterior (D) and lateral (G) views; probably from locality W9; **H** SSMM 11110, paratype, fragment of cranidium showing eye ridge developing distal bifurcation as well as radial caeca on preocular areas and different granulation on the fixigenae; from locality W8; **I** MMUW-2017D-366, paratype, incomplete cranidium with recrystallised cuticle, oblique anterior view of fixigenae showing tubular openings corresponding to large granules on the internal mould and delicate scrobicules; from locality W8; **J** MMUW 2017D-568, paratype, incomplete pygidium, external mould, magnified ventral view of the pleural field illustrating the infilling of tubular openings on the (now decayed) cuticle; from locality W9b; **K** SSMM 10626a, paratype, partial cranidium, internal mould, dorsal view illustrates short eye ridges and prominent granules on anterior border; locality W8.
All specimens from Wildenstein Member, Tannenknock Formation. Scale bars 5 mm in A, B, E and K, 1 mm in C, D, F–J).

Facial suture in a relatively marginal position, starting at a level slightly posterior to the glabellar front, intersecting the lateral border to arrive at the border furrow approximately at the level of S2, intersecting the most abaxial parts of the genae on a short stretch starting approximately at the level of S1. Posterior branch intersects lateral border anterior to the posterior margin of the genae so that the posterior end of the lateral border furrow lies on the cranidium.

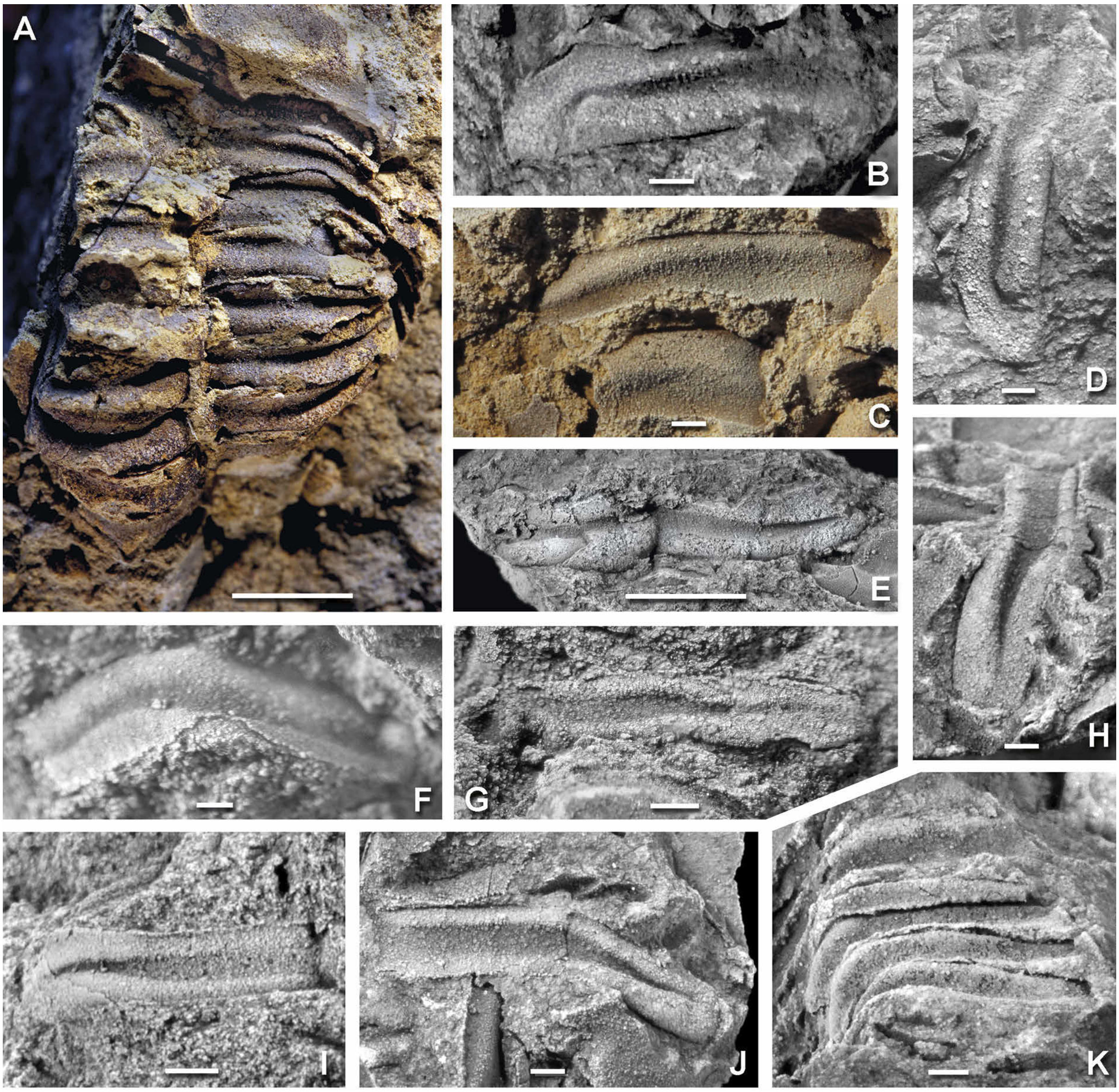

Fig. 104: **A, B–K?** *Prioscutarius max* n. gen., n. sp. **A** SSMM 10496, paratype, partial dorsal exoskeleton, incompletely enrolled, internal mould, dorsal view of anterior thorax illustrating articulation; from locality W8; **B, D** MMUW 2017D-047, fragment of thoracic pleura, internal mould, oblique dorsal (B) and lateral views; from locality W8; **C** SSMM 11012a, partial thoracic segment, dorsal view; from locality W8; **E** MMUW 2017D-136, fragment of thoracic pleura, internal mould; from locality W8; **F** MMUW 2017D-547c, fragment of thoracic pleura, internal mould, oblique view illustrating pronounced kink of the pleura with articulating devices on both sides; from locality W8; **G** MMUW 2017D-046, fragment of thoracic pleura, internal mould; from locality W8; **H, J** MMUW 2017D-102, fragment of thoracic pleura, internal mould, oblique lateral (H) and oblique posterodorsal (J) views; from locality W8; **I** MMUW 2017D-179, fragment of thoracic pleura, internal mould; from locality W8; **K** MMUW 2017D-411, partial thorax, internal mould, oblique posterior view; probably from locality W13b.
Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm in A and E and 1 mm in B–D and F–K.

Librigena only known from a single specimen, where it is attached to the cranidium (Fig. 101H); consists of a relatively prominent lateral border and a very thin (tr.) platform represented almost entirely of the lateral border furrow area; posteriorly extended into a moderately long, gently curved genal spine of ca. half librigenal length that appears to extend posteriorly to about the level of segment 8.

Hypostome not known with certainty. Rostral plate preserved by a quite characteristic fragment, being part of a narrowly crescentic sclerites with a subtriangular transverse section (Fig. 102E–G) and with remarkably steep, poorly curved anterior and posterior faces.

Thorax known from partial dorsal exoskeletons (e.g., Figs. 103C, G, 104A, K) and from isolated, fragmented thoracic segments (Fig. 104). Thoracic segments generally without unusual characters. Axial rings relatively prominent, with well incised furrows defining the articulating half-ring. Pleurae with very distinct pleural furrows directed slightly oblique to the axis of the pleurae, extending into moderately long pleural spines. A fairly well-preserved fragment of a pleura shows that the pleural furrow performs a distinct rearward curvature at the base of the pleural spine and also indicates the development of a distinct fulcral process at the anterior margin and of smooth facets slightly abaxially of this process (Fig. 104B, I).

Pygidium not known with certainty, but pygidia which probably belong to *Prioscutarius max* n. gen., n. sp. are shown in Fig. 105. They are characterised by a lenticular to subpentagonal outline, with gently and relatively evenly curved posterior margin, length/width ratio roughly 2/3.

Axis moderately convex, with two, rarely three axial rings plus articulating half-ring and terminal axial piece; articulating half-ring a prominent, narrowly lenticular ring, separated by a broad (sag.) and deep articulating furrow; first axial ring well marked by a moderately deep transverse ring furrow, transversely of ca. 40 percent maximum pygidial width, occasionally with a faint intra-axial furrow; second axial ring defined by a shallow furrow; terminal axial piece of ca. 80 percent width across anterior axial ring, with a pair of low, poorly marked swellings, posterior end with low curvature, separated by a short distance only from the posterior margin; no plectrum developed. Pleural fields with two or three pleural furrows, which are progressively ill-defined backwards; anterior, faint interpleural furrows sometimes visible.

Posterior and lateral borders not defined, lateral and posterior rims consist of slightly convex, rapidly sloping deflected marginal portions.

Surface of the cuticle beset with granules, which are rarely preserved in the available specimens, but recognisable on fragments of external moulds. Internal moulds show them as small nipples with tiny tubules in the centres (Fig. 103J). These granules are best developed and largest on the central parts of the genae from where they fade in size towards the anterior and abaxial parts. The furrows are smooth. The thoracic segments show a serial arrangement of single nipples on the anterior and posterior parts of the pleurae (Fig. 104B).

Relics of a caecal network develop from the faint genal ridges, particularly in direction to the anterior border furrow (e.g., Figs. 100E, 102B, 103H). However, the present material is not preserved in a quality that allowed a precise reconstruction of details. A ventral doublure of a relatively large pleura reveals a pseudodichotomic branching of vessels on the ventral side (Fig. 101N).

Ontogenetic differences. As usual in ptychoparioid trilobites, moderately pronounced differences in the ratios of different part of the cephalon can be recognised due to allometric growth. Such differences result in a relatively larger/wider glabella in large individuals; a slight relative growth in the length (sag.) of the preglabellar field; a stronger curvature of the frontal margin of the glabella; a broader (sag., exsag.) anterior border; and less densely spaced granules on the cuticle.

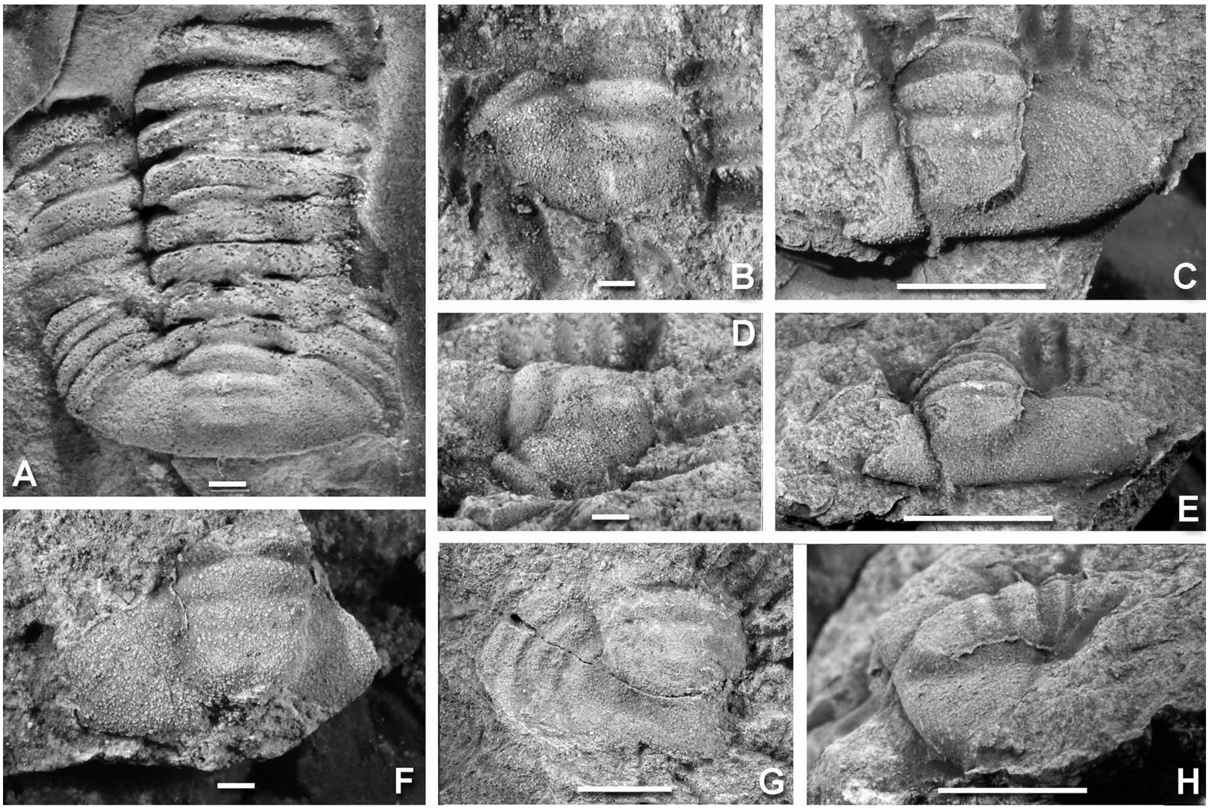

Fig. 105: Pygidia assigned to *Prioscutarius max* n. gen., n. sp. **A** MMUW 2017D-881L, incomplete thorax with attached pygidium, latex cast of internal mould, dorsal view; from locality W8a; **B, D** MMUW 2017D-564, fragment of pygidium, internal mould, dorsal (B) and lateral (D) views; from locality W9b; **C, E, H** MMUW 2017D-596, fragmented pygidium, internal mould, dorsal (C), posterior (E) and oblique lateral (H) views; from locality W8; **F** incomplete pygidium, dorsal view; from locality W8 (specimen apparently lost; **G** MMUW 2017D-324, incomplete pygidium, dorsal view; from uncertain locality in the Wildenstein slice. Wildenstein Member, Tannenknock Formation. Scale bars 5 mm in C, E, G and H, 1 mm in A, B, D, and F.

Discussion. Prioscutarius max n. gen., n. sp. is characterised by the shape of its glabella, the transverse profile of the cephalon and the broad and comparatively low anterior border in combination with the broad and shallow anterior border furrow with its faint swelling as a close relative of *Prioscutarius dimarginatus* (Geyer, 1998) from the Moroccan High Atlas and the co-occurring *P. moritz* n. gen., n. sp. *Prioscutarius dimarginatus* is distinguished from *P. max* by its broader anterior border and the more distinctly developed swelling in the border furrow as well as a higher ratio between cephalic length and cephalic width. *Prioscutarius moritz* n. gen., n. sp. is also very similar but shows a particularly conspicuous allometric growth of the anterior border which is distinctly broader (sag.) than the preglabellar field. This eye-catching anterior border is already seen in specimens of moderate size so that these can be easily distinguished from specimens of *P. max* of the same size. In addition, the facial suture has a slightly more marginal position in *P. moritz*, and the occipital node lies at the centre of the occipital ring.

Prioscutarius moritz n. gen., n. sp.

Figs. 106, 107?

Holotype. SSMM 10546, incomplete cranidium (Fig. 106A, D, F).

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Type locality. Locality W8, Tannenknock north of Wildenstein, Franconian Forest.

Type stratum. Wildenstein Member, Tannenknock Formation.

Etymology. Named after Moritz, a literary figure created by the German artist Wilhelm Busch (1832–1908) as one main figure of the coarse boyish protagonists in *Max und Moritz*; a reference to the joint occurrence of the species with *Prioscutarius max* n. gen., n. sp. (see above).

Paratypes. 16 cranidia, two pygidia. From locality W8 (14 cranidia under SSMM 10509, 10510, 10526, 10532, 10540a, 10541a, 10542, 10548, 10550, 10553a, 10553b, 10559 and 10563; two pygidia under SSMM 10418 and 10420); from locality W9 (two cranidia under MMUW 2017D-325 and SSMM 12363); from locality W11 (cranidium under SSMM 10778).

Specimens tentatively assigned to Prioscutarius moritz*:* Single partial dorsal exoskeleton, ca. 15 cranidia, four pygidia, ca. 10 fragments of thoracic segments. In repository: From locality W8 (10 cranidia under SSMM 10332a, 10332b, 10523. 10527, 10531, 10547, 10557, 10564, 10565 and 11049a; four pygidia under MMUW 2017D-086, -125, -193 and -386); from locality W9 (cranidium under MMUW 2017-D-337); from locality W13b (partial dorsal exoskeleton under MMUW 2017-D-424); from locality W13e (thoracic pleura under MMUW 2017D-440c); from locality W17 (pygidium under MMUW 2017D-820).

Diagnosis. Species of *Prioscutarius* with the following characters in adult individuals: glabella moderately wide (tr.), with gently curved lateral margins and a moderately broad frontal lobe, anterior glabellar margin broadly curved; occipital ring moderately broad (sag.), with subcentral node; anterior border thick (exsag., sag.), moderately prominent, distinctly broader (sag.) than the preglabellar field; anterior border furrow moderately broad (exsag., sag.), without precise definition from border and preglabellar field, with low, transverse swelling in its posterior two-thirds of approximately the tr. width of the glabella; facial suture intersecting lateral border to enter lateral border furrow at about the level of L2, with maximal adaxial position in the most abaxial part of the genae at the level of L1; genae with elliptical swellings arranged oblique to axis; prosopon of loosely spaced granules.

Description. Cephalon subsemicircular in outline. Axial furrows moderately well developed in depth and width, deeper on internal moulds than on the exterior of the cuticle. Glabella tapers forward, lateral margins gently curved from L1 to the frontal lobe, frontal lobe with gentle curvature at anterior margin, but mostly with somewhat lower curvature across sagittal line; length of the glabella 66 to 70 percent (n=5) cephalic length on the sagittal line; maximum glabellar width across L1 of ca. 31 to 36 percent (n=5) cranidial width across level of the posterior border; frontal lobe width about half width across L1; three pairs of lateral glabellar furrows; S1 moderately long, bifurcated, with strongly backward curved posterior branch and faint, transversely directed anterior branch; S2 moderately long, less well developed than S1; S3 short, usually barely recognisable. Occipital furrow with narrow, well-incised lateral parts directed obliquely backward from axial furrow, and broader (sag.) and shallower transverse or slightly anteriorly curving middle part. Occipital ring sagittally of about 12–14 percent cephalic length, extreme lateral parts fairly narrow; occipital node in a subcentral position (e.g., Fig. 106J).

Gena distinctly convex, with most elevated part relatively close to the axial furrow in the posteroadaxial sector; swelling developed as an elliptical rise oriented slightly to distinctly oblique to axis; abaxial end of swelling proceeds into a low and faint thread that curves posterolaterally in a gentle arc.

Preglabellar field relatively narrow (sag.), 7 to 9 percent (n=5) cephalic length, moderately convex (sag.), proceeding into and faintly lower than the preocular areas.

Anterior border moderately convex, fairly broad (sag.), 13 to 17 percent (n=6) cephalic length, distinctly decreasing in exsag. breadth abaxially to the anterolateral corners, having a conspicuous decrease in width and elevation from there to the lateral border. Anterior margin gently curved in dorsal view, faintly arched upward in frontal view, with a more pronounced curvature at anterolateral corners.

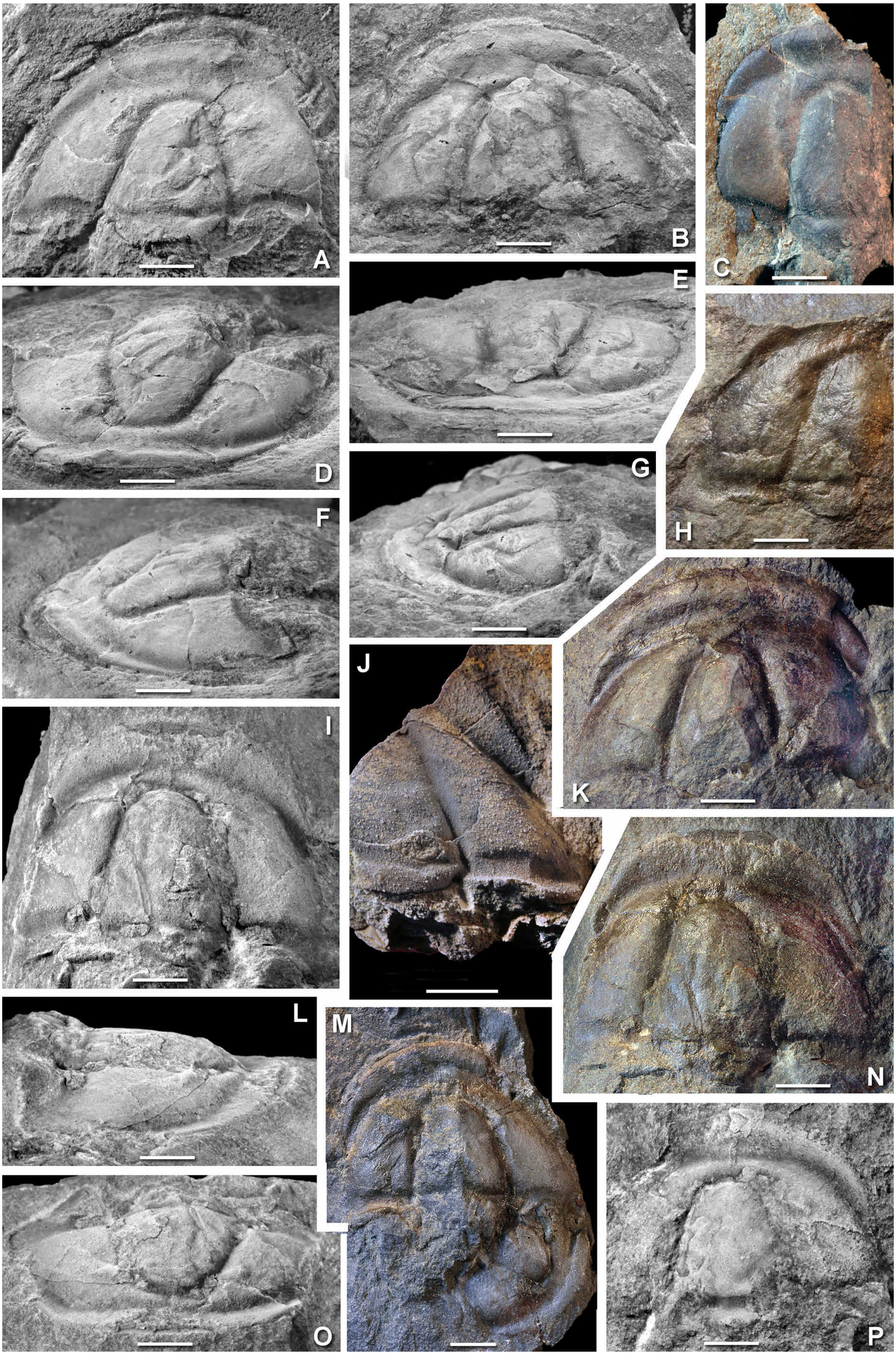
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Fig. 106: *Prioscutarius moritz* n. gen., n. sp. **A, D, F** SSMM 10546, holotype, cranidium, composite mould, dorsal (A), oblique anterior (D) and oblique anterolateral (F) views; from locality W8; **B, E, G** SSMM 10509, paratype, cranidium, composite mould, dorsal (A), oblique anterior (E) and lateral (G) views; from locality W8; **C** SSMM 12404, paratype, partial cranidium, internal mould; from locality W8; **H** SSMM 12412, paratype, incomplete cranidium, internal mould, partial view; from locality W8; **I, L, O** SSMM 10540a, paratype, cranidium, composite mould, dorsal (I), lateral (L) and oblique anterior (O) views; from locality W8; **J** SSMM 11003, paratype, partial cranidium, internal mould; from locality W8; **K** SSMM 10542, paratype, incomplete cranidium, internal mould; from locality W8; **M** SSMM 10553a, b, paratypes, incomplete and partial cranidium, internal moulds; from locality W8; **N** SSMM 10540a, paratype, incomplete cranidium, internal mould; from locality W8; **P** SSMM 10532, paratype, incomplete cranidium, internal mould; from locality W8. Wildenstein Member, Tannenknock Formation. Dorsal views if not otherwise stated. Scale bars 5 mm.

Anterior border furrow shallow to moderately deep, poorly defined from anterior border and preglabellar field, relatively broad in its central portion; with a low, transverse rise that occupies the posterior two-thirds of the anterior border furrow and stretches on a distance of approximately the maximum width of the glabella. Posterior border with straight adaxial part, weakly sigmoidally curved distally, moderately narrow, but slightly broadening abaxially, relatively prominent. Posterior border furrow well developed, moderately broad, faintly broadening abaxially, with straight adaxial part and slight sigmoidal curvature distally.

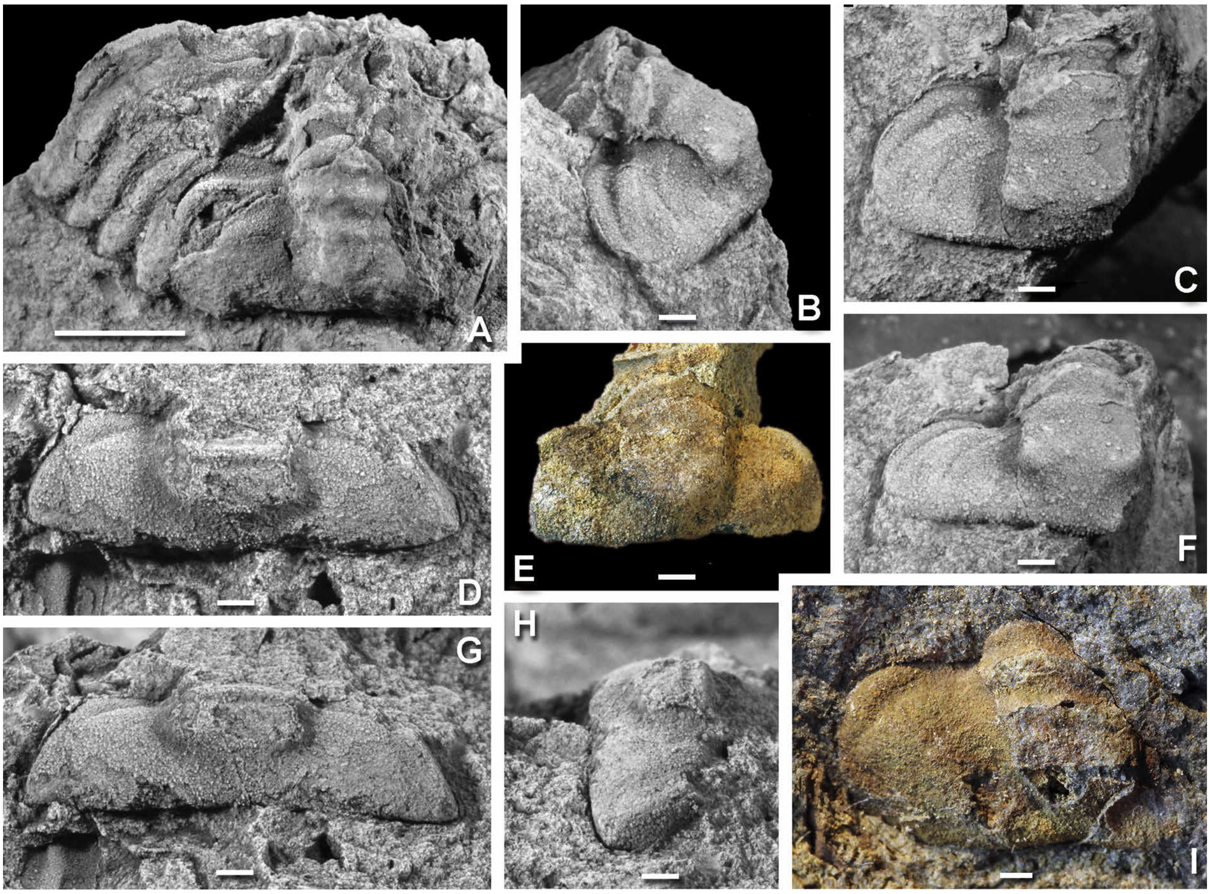

Fig. 107: Pygidia assigned to *Prioscutarius moritz* n. gen., n. sp. **A** MMUW 2017D-424, paratype, pygidium, internal mould, posterior thorax and attached pygidium, oblique posterior view; from locality W13b; **B, C, F** MMUW 2017D-125, paratype, partial pygidium, internal mould, lateral (B), dorsal (C) and posterior (F) views; from locality W8; **D, G, H** MMUW 2017D-086, paratype, partial pygidium, internal mould, dorsal (D), oblique posterior (G) and lateral (H) views; from locality W8; **E** SSMM 10420, incomplete pygidium, internal mould, dorsal view; from locality W8; **I** SSMM 10418, paratype, partial pygidium, internal mould, dorsal view; from locality W8.
Wildenstein Member, Tannenknock Formation. Scale bars 5 mm in A, 1 mm in B–I.

Facial suture in a marginal position, starting at a level anterior to the glabellar front, intersecting the lateral border to arrive at the border furrow approximately at the level of L2, intersecting the most abaxial parts of the genae on a short stretch. Posterior branch intersects lateral border just anterior to the posterior margin of the genae or at this margin so that the posterior end of the lateral border furrow lies on the cranidium.

Librigena, hypostome and rostral plate unknown.

Thorax known from partial dorsal exoskeletons (e.g., Fig. 107A) and from isolated, fragmented thoracic segments tentatively assigned to the species. Thoracic segments generally without unusual characters. Axial rings prominent, with well incised furrows defining the articulating half-ring. Pleurae with distinct pleural furrows directed slightly oblique to the axis of the pleurae, extending into moderately long pleural spines. Abaxial parts of the pleura strongly ventrally deflected in the posterior segments (Fig. 107A).

Pygidium not known with certainty, but pygidia which probably belong to *Prioscutarius moritz* n. gen., n. sp. are shown in Fig. 107. They are characterised by a variable, subpentagonal outline, with posterior margin with a low curvature.

Axis moderately to distinctly convex, with two axial rings plus articulating half-ring and a terminal axial piece; articulating half-ring a prominent, narrowly lenticular ring, separated by a broad (sag.) and deep articulating furrow; first axial ring well marked by a moderately deep transverse ring furrow, transversely of ca. 40 percent maximum pygidial width; second axial ring defined posteriorly by a shallow furrow; terminal axial piece of ca. 80 to 90 percent width across anterior axial ring, with a pair of low, poorly marked swellings, which tend to extend posterolaterally (Fig. 107B, F), posterior end with low curvature or subtruncate, separated by a short distance only from the posterior margin; no plectrum developed, but a faint rise proceeds from the terminal axial piece posteriorly. Pleural fields with two or three pleural furrows, which are progressively ill-defined backward; anterior, faint interpleural furrows sometimes visible. Posterior and lateral borders not defined, lateral and posterior rims consist of slightly convex, rapidly sloping deflected marginal portions.

Surface of the cuticle beset with granules of different sizes (rarely preserved in the available specimens). One partial cranidium nicely illustrates the presence of larger, widely spaced granules between smaller ones with a moderate density (Fig. 106J). The granulation is best developed and largest on the central parts of the genae from where they fade in size towards the anterior and abaxial parts. The furrows are smooth.

Discussion. Prioscutarius moritz n. gen., n. sp. belongs, together with *P. max* n. gen., n. sp., to a group of relatively large *Bailiella*-type species, which have a very low/early stratigraphic occurrence and are characterised by a fairly average shape of its glabella, the transverse profile of the cephalon and the broad and comparatively low anterior border in combination with the broad and shallow anterior border furrow with its faint swelling. *P. moritz* is a close relative of *Prioscutarius dimarginatus* (Geyer, 1998) from the Moroccan High Atlas, which is distinguished from *P. moritz* by its broader anterior border and the more distinctly developed swelling in the border furrow as well as a higher ratio between cephalic length and cephalic width.

The differences to *Prioscutarius max* n. gen., n. sp. are discussed above under that species.

***Prioscutarius* sp. A**

Fig. 108

Material. Single cranidium, SSMM 10778.

Locality and stratum. From locality W11, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. An incomplete cranidium of moderate size (length ca. 2.2 cm) resembles *Prioscutarius max* n. gen., n. sp., which co-occurs with this form. However, the cranidium differs in two features: It has a glabella, which tapers only to a much lesser degree than the glabella seen in the specimens of *P. max*, thus having a much more broadly curved front. The glabella is indeed slightly crushed, but his compaction-related damage did not produce the shape. In addition, the initial part of the facial suture is located more abaxially so that it commences to intersect the (anterior/lateral) border at a more posterior point than it is the case in specimens of *P. max* of comparable size.

The single specimen is insufficient to prove that the cranidium represents a different distinct species of *Prioscutarius*. However, the differences sketched above are in the order that is used to clearly discriminate it from the species of *Bailiella*.

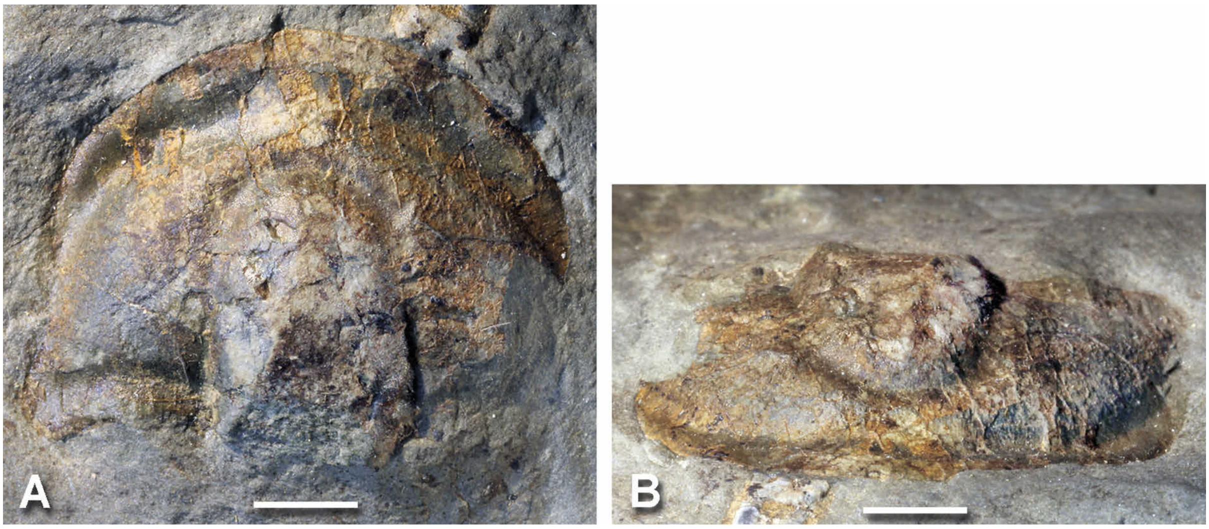

Fig. 108: *Prioscutarius* sp. A. **A, B** SSMM 10778, incomplete cranidium, internal mould with relics of the cuticle, dorsal (A) and anterior (B) views. From locality W11.
Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Prioscutarius? sp. B

Fig. 109

Material. Single cranidium, MMUW 2017D-135.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A partial cranidium with small to moderate size clearly differs from *Prioscutarius max* n. gen., n. sp. and *P. moritz* n. gen., n. sp. although both co-occur in the same strata. This cranidium is differentiated by its relatively strongly tapering glabella with a narrow, but almost subtruncate front.

The visible nearly straight frontal section of the glabella may have been intensified by a minor distortion, which nonetheless is not readily visible. If it indeed took place, the effect can only be minimal so that the front will have been subtruncate in the living animal. In addition, the anterior border in the specimen is strikingly broadened in the middle part along and adjacent to the sagittal axis and thus broader than in any of the morphologically related specimens of *Prioscutarius max*. The convexity of the anterior border is low. If this would be a result of dorsoventral compaction, it would have affected the shape of the glabella as well. Accordingly, this morphology suggests that the species cannot be assigned to *P. max* or *P. moritz*.

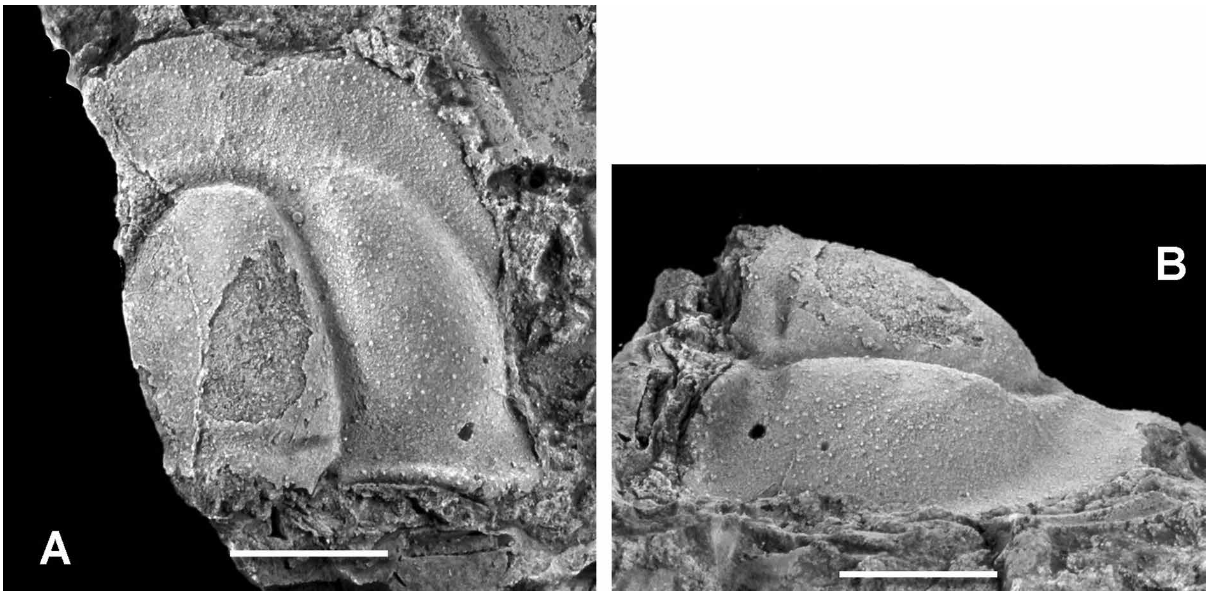

Fig. 109: *Prioscutarius*? sp. B. **A, B** MMUW 2017D-135b, partial cranidium, internal mould, dorsal (A) and lateral (B) views. From locality W8.
Wildenstein Member, Tannenknock Formation. Scale bars 5 mm.

Genus *Emarginobailiella* n. gen.

Type species. Conocoryphe emarginata Linnarsson, 1877; from the *Eccaparadoxides*? *insularis* Biozone of the Alum Shale Formation, Öland, Sweden.

LSID. urn:lsid:zoobank.org:act:66ED20D9-C5D3-4A6D-9FD8-B0283C1EFE7C

Etymology. Name composed of *emarginatus* (Latin for “deprived of its edge”) and the genus name *Bailiella*.

Diagnosis. Cephalon subsemicircular in outline; glabella weakly to moderately tapering forward, lateral margins curved, frontal lobe moderately broad; preglabellar field relatively broad (sag.), convex, at least as long as anterior border; anterior border without distinct growth in width towards the sagittal line; facial suture in a relatively adaxial position, with a considerable part of the distal genal areas located on the librigena.

Discussion. The characters of the new genus are summarised in the diagnosis and discussed above under *Bailiella*. The species of *Prioscutarius* n. gen. have a glabella with a similar shape as the species of *Emarginobailiella* n. gen., but differ in the longer outline of the cephalon and the broader anterior border and anterior border furrow. These features suggest considerable differences in the internal morphology of the cephalon and the anterior part of the digestive tract.

Species included. Conocoryphe emarginata Linnarsson, 1877; *Bailiella cobboldi* Resser, 1936; *Bailiella comleyensis* Resser, 1936; *Bailiella froeensis* Westergård, 1950; *Conocoryphe impressa* Linnarsson, 1879; *Conocoryphe emarginata var. longifrons* Cobbold, 1911: *Conocoryphe lyelli* Hicks, 1871; *Conocoryphe tenuicincta* Linnarsson, 1879 (see Table 2).

Genus *Courtessolia* n. gen.

Fig. 110

Type species. Conocoryphe levyi Munier-Chalmas & Bergeron in Bergeron, 1889; from the *Bailiella levyi* Biozone, Coulouma Formation, Montagne Noire, France.

LSID. urn:lsid:zoobank.org:act:9846AD0D-9FA4-4A82-A0D6-A53E307585E7

Etymology. Named after Abbé Robert Courtessole (1904–1990), in appreciation of his efforts on the Cambrian palaeontology of the Montagne Noire region, southern France.

Diagnosis. Cephalon subtrapezoidal in outline with curved anterolateral corners; glabella distinctly tapering forward, lateral margins curved, frontal lobe narrow, with paraboloid outline; preglabellar field relatively broad (sag.), slightly convex, comparable in sag. width with anterior border; anterior border broad on the sagittal line, moderately convex, distinctly tapering abaxially; anterior border furrow a broad groove, with straight or almost straight median section; facial suture in a pronouncedly abaxial position, with only short distance located in the lateral border furrow.

Discussion. The characters of the new genus are summarised in the diagnosis and discussed above under *Bailiella*. *Courtessolia* n. gen. is best recognizable by (i) its relatively short and distinctly forwardly tapering glabella with a subacute front; (ii) a relatively thick (sag., exsag.) anterior border; (iii) a broad, groove-like anterior border furrow with the straight or nearly straight part across the sagittal line; (iv) a comparatively broad (sag.) preglabellar field; and (v) a smooth surface of the dorsal exoskeleton. The cephalic suture is in a quite marginal position: it runs within the lateral border for most of its extension, but its course lies within the lateral border furrow for a short distance.

Courtessolia levyi (Munier-Chalmas & Bergeron in Bergeron, 1889) (Fig. 110A–F) is a well-known and widely distributed species known from the *Solenopleuropsis* (*Manublesia*) *thorali* Zone (lower Languedocian) to the *Jincella convexa* Zone (middle Languedocian) of the Iberian Peninsula and the Mon-tagne Noire (Álvaro & Vizcaïno 1998). It is characterised by a broad (tr.) anterior border and a relatively long glabella with gently curved lateral margins. The anterior border furrow is more-or-less straight in the central sector, but curves abruptly rearward already on a level equal to the abaxial part of the genae.

Courtessolia seguieri (Courtessole, 1973) from the Montagne Noire (Fig. 110I, K, M) was considered as being simply a name for immature individuals of *Bailiella levyi*, which illustrates difficulties to confidently identify specimens of that species. Indeed, all specimens which were determined as *Bailiella seguieri* are small individuals. However, despite of the fact that they partly co-occur with *C. levyi* the well-preserved specimens of *C. seguieri* all show a well recognisable growth in breadth of the anterior border on the sagittal line, and the pygidia in the specimens of *C. seguieri* appear to have a lower length:width ratio.

Courtessolia souchoni (Courtessole, 1967) is only known from large specimens, which generally resemble very large specimens of *C. levyi* (Fig. 110G, J, L). Differences can be seen in a slightly shorter glabella and a longer (sag.) preglabellar field as well as a more distal position in which the anterior border furrow swings rearward from a relatively straight course across the central sector of the cranidium.

Courtessolia griffei (Courtessole, 1967) is typified by a relatively short glabella with gently curved lateral margins and a quite short (sag.) occipital ring, a moderately broad (sag., exsag.) anterior border, and by an anterior border furrow which curves rearwards at a quite adaxial position (Fig. 110H, N).

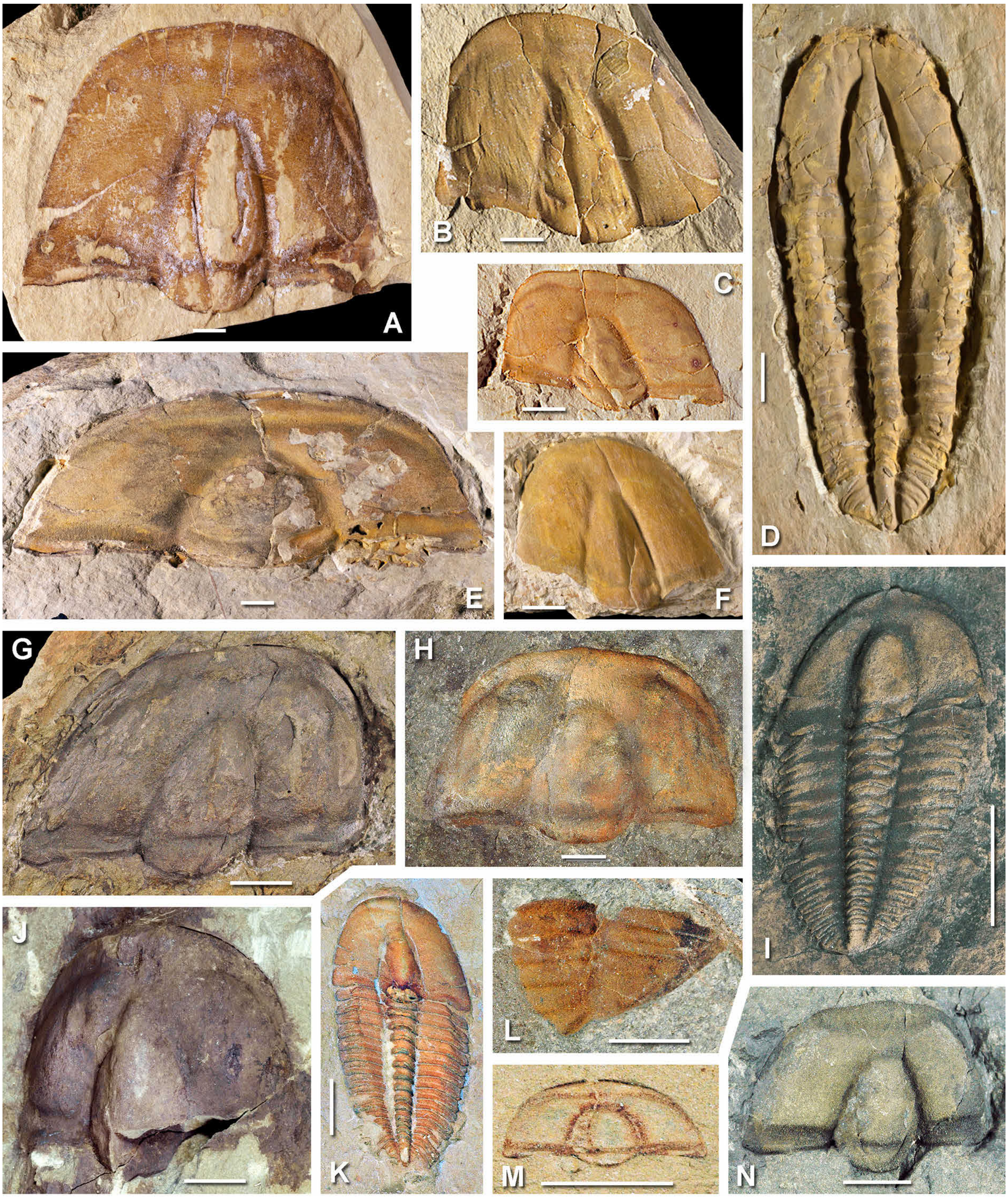

Fig. 110: Species of *Courtessolia* n. gen. from the Montagne Noire, southern France.
A–F *Courtessolia levyi* (Munier-Chalmas & Bergeron, 1889). **A** MNHN F.09892, dorsal exoskeleton, Faveyrolles; **B** MNHN F.R.09887, cranidium, Faveyrolles; **C** MNHN F.R.09888, cranidium, Faveyrolles; **D** MNHN F.09881, dorsal exoskeleton, Ferrals-des-Montagnes; **E** MNHN F.09889, dorsal exoskeleton, Faveyrolles; **F** MNHN F.R.09886, cranidium, Faveyrolles.**G, J, L** *Courtessolia souchoni* (Courtessole, 1967). **G** MNHN F.R09907, holotype, cranidium, Ferrals-les-Montagnes; **J** MNHN F.A33790, paratype, cranidium, Ferrals-le-Montagnes; **L** MNHN F.R09908a, paratype, incomplete pygidium, Faveyrolles. **H, N** *Courtessolia griffei* (Courtessole, 1967). **H** MNHN F.R09905, paratype, cranidium, Le Bois de Vidal; **N** MNHN F.R09906, holotype, cranidium, Le Bois de Vidal. **I, K, M** *Courtessolia seguieri* (Courtessole, 1973). **I** MNHN F.R09895, holotype, dorsal exoskeleton, Cousses. **K** MNHN F.R09896a, paratype, dorsal exoskeleton, Faveyrolles; **M** MNHN F.R09899, paratype, cranidium, Cousses.
All specimens in dorsal views. All specimens collected by Robert Courtessole from Departement Hérault, Montagne Noire, southern France. Scale bars 5 mm except in J (= 10 mm).

Courtessolia griffei is a quite common species from the Montagne Noire. It occurs quite late, in strata with *Eccaparadoxides macrocercus* and *Conocoryphe ferralsensis*, in the *Eccaparadoxides macrocercus* Biozone (Courtessole's level H). The species (see Courtessole 1967, pl. 3, figs. 1–9, 1973, pl. XXIV, figs. 4–10) indicates a progression of the thickened anterior border and the transverse to even slightly posteriorly swinging anterior border furrow from *C. seguieri* and *C. levyi*. In *C. griffei*, the gentle rearward curvature affects a large portion of the furrow, and this also causes a slight depression of the preglabellar field relative to the preocular areas.

Species included. Conocoryphe levyi Munier-Chalmas & Bergeron, 1889; *Bailiella levyi bondoni* Termier & Termier, 1950; *Bailiella griffei* Courtessole, 1967; *Courtessolia lemdadensis* n. gen., n. sp., *Bailiella meridiana* Sdzuy, 1958a; *Bailiella seguieri* Courtessole, 1973; *Bailiella sepulcra* Álvaro & Vizcaïno, 2018; *Bailiella souchoni* Courtessole, 1967 (see Table 2).

***Courtessolia lemdadensis* n. gen., n. sp.**

Fig. 111

v	1995	*Bailiella* cf. *B. levyi* (Munier-Chalmas & Bergeron 1889) – Geyer et al.: p. 96.
v	2006	*Bailiella* cf. *B. levyi* – Geyer & Landing: p. 93.

Holotype. MMUW 2019D-042a, cranidium (Fig. 111B, E).

LSID. urn:lsid:zoobank.org:act:856F8314-8BDE-488C-8E1F-ED40C3420D85

Type locality. Locality X68 near section Le XI, eastern limb of Lemdad Syncline, High Atlas, Morocco (see map in Geyer & Landing 2006, figs. 14, 29.

Type stratum. Equivalent of the Bailiella Formation, Languedocian.

Etymology. Named after its occurrence in the Lemdad Syncline, Massif Ancien, High Atlas.

Paratypes. 16 cranidia, two dorsal exoskeletons, several partial thoraces, single isolated pygidium. From sample horizon X67: two cranidia under MMUW 2019D-043a and -043b; from sample horizon X68: dorsal exoskeleton under MMUW 2019D-035a, isolated cranidia under 2019D-035b, -036a, -036b, -036c, -036d, -036g, -037, -038, -039a, -039b, -039c, -041a, -042b; cranidium with partial thorax under MMUW 2019D-040, partial thoraces under MMUW 2019D-036e and -041b; from sample horizon X70: two dorsal exoskeletons under MMUW 2019D-044a and -044b.

Diagnosis. Species of *Courtessolia* with cephalon having a length:width ratio of ca. 0.65–0.70; glabella of ca. 65–70 percent cephalic length and ca. 40 percent cephalic width across occipital ring, lateral margins distinctly curved; anterior border moderately broad (ca. 15–20 percent cephalic length on sagittal line), with nearly straight posterior margin in its median sector; anterior border furrow nearly straight in the central sector, and with slight kink at mid-level of genae; facial suture intersects lateral border furrow at anterior part of L2.

Description. Cephalon subsemicircular to subtrapezoidal in outline, quite strongly convex in transverse and sagittal profile. Axial furrows moderately well developed in depth and width, deeper on internal moulds than on the exterior of the cuticle.

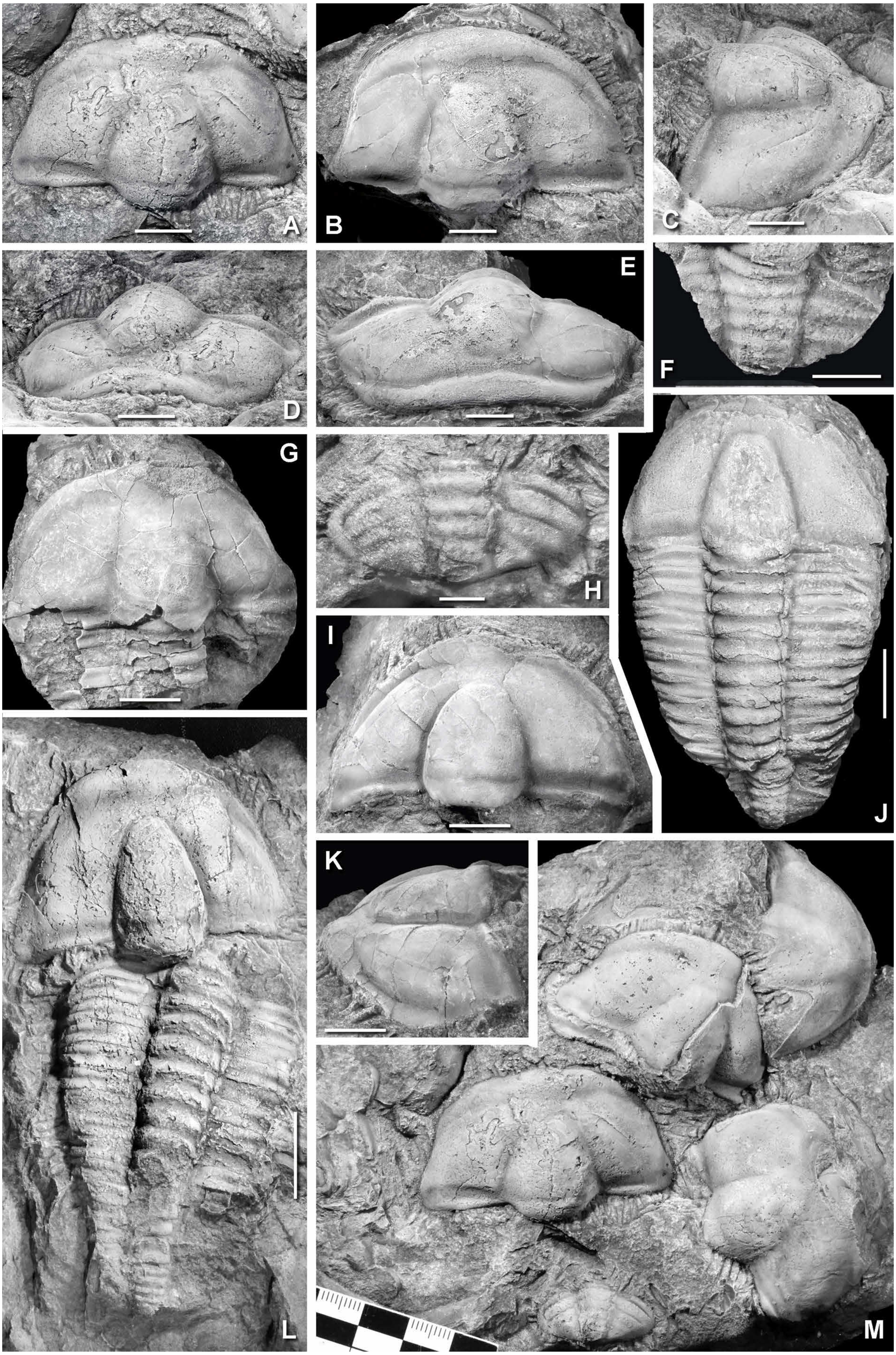
A
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Fig. 111: *Courtessolia lemdadensis* n. sp. **A, C, D** MMUW 2019D-036a, paratype, cranidium, dorsal (A), oblique lateral (C) and anterior views; sample locality X68; **B, E** MMUW 2019D-042a, holotype, cranidium, dorsal (B) and anterior (E) views; sample locality X68; **F, J** MMUW 2019D-044a, paratype, dorsal exoskeleton, dorsal view of slightly enrolled specimen (J) and magnified view of posterior thorax with attached incomplete pygidium (F); sample locality X70; **G** MMUW 2019D-043a, paratype, cranidium with attached partial thorax, dorsal view; sample locality X68; **H** MMUW 2019D-036f, paratype, isolated pygidium, dorsal view; sample locality X68; **I, K** MMUW 2019D-037, cranidium, dorsal (I) and oblique lateral (K) views; sample locality X68; **L** MMUW 2019D-035a, paratype, incomplete dorsal exoskeleton, dorsal view; sample locality X68;. **M** MMUW 2019D-036, slab with several cranidia, fragments of isolated thoracic segments and pygidium; sample locality X68.
All specimens from the eastern limb of the Lemdad Syncline, from an unnamed equivalent of the Bailiella Formation, Languedocian, High Atlas, Morocco. Scale bars 10 mm except in H (= 5 mm).

Glabella tapers forward, lateral margins distinctly curved from L1 to the frontal lobe, frontal lobe with gentle curvature at anterior margin; length of the glabella 69 to 76 percent (n=6) cephalic length on the sagittal line; maximum glabellar width across L1 of ca. 35–40 percent (n=5) cranidial width across level of the posterior border; frontal lobe width about half (n=5) width across L1; three pairs of lateral glabellar furrows, all shallow and poorly marked on the exterior of the cuticle; S1 moderately long, indistinctly bifurcated, with strongly backward curved posterior branch; S2 moderately long, backward directed from axial furrow; S3 short, usually barely recognisable. Occipital furrow with narrow, moderately well-incised lateral parts directed slightly obliquely backward from axial furrow, and shallow to moderately indented transverse middle part. Occipital ring sagittally of about 12–15 percent (n=5) cephalic length, extreme lateral parts narrow; apparently with low occipital node in a median position on the occipital ring.

Genae distinctly convex in transverse and exsagittal profile, with most elevated part relatively close to the axial furrow in the posteroadaxial sector.

Preglabellar field relatively narrow (sag.), 9 to12 percent (n=6) cephalic length, decreasing in relative length during ontogeny, faintly convex (sag.), and lower than the preocular areas.

Anterior border moderately convex, relatively broad (sag.), 13 to18 percent (n=6) cephalic length, growing in size with age, decreasing in exsag. breadth abaxially to the anterolateral corners, with a more conspicuous decrease in width and elevation from there to the lateral border. Anterior margin gently curved in dorsal aspect, faintly to gently arched upward in frontal view, with a more pronounced curvature at anterolateral corners. Anterior border furrow shallow to moderately deep, poorly defined from anterior border and preglabellar field, fairly broad in its central portion and only poorly curved in this section; with a recognisable kink towards the gently and subevenly curved anterolateral sections. Posterior border with straight adaxial part, moderately narrow, slightly broadening abaxially, relatively prominent. Posterior border furrow well developed, moderately broad, broadening abaxially, with adaxial part slightly forward directed from axial furrow, with slight sigmoidal curvature distally.

Facial suture in a relatively marginal position, starting approximately at level of S3, intersecting the lateral border to arrive at the border furrow approximately at the level of the anterior part of L2 (but apparently variable), intersecting the most abaxial parts of the genae on a short stretch starting approximately at the level of S1. Posterior branch intersects lateral border anterior to the posterior margin of the genae so that the posterior end of the lateral border furrow lies on the cranidium.

Librigena, hypostome and rostral plate unknown.

Thorax known from two exoskeletons and partial dorsal exoskeletons (e.g., Figs. 111J, L) and from partial thoracic fragments, consisting of 14 segments. Thoracic segments generally without unusual characters. Axial rings relatively prominent, with well incised furrows defining the articulating half-ring, with moderately well developed lateral swellings. Pleurae with moderate exsagittal convexity, almost straight in its adaxial part, with distinct pleural furrows directed weakly oblique to the axis of the pleurae, extending into moderately long pleural spines.

Pygidium known only from slightly imperfect specimens. These are characterised by a lenticular to elliptical outline, with gently and relatively evenly curved posterior margin, length/width ratio roughly 0.5. Axis moderately convex, with four axial rings plus articulating half-ring and terminal axial piece; articulating half-ring a prominent, narrowly lenticular ring, separated by a deep articulating furrow; first axial ring well marked by a moderately deep transverse ring furrow, transversely of almost half maximum pygidial width; second and third axial ring defined by a moderately well impressed furrow; terminal axial piece of ca. two-thirds width across anterior axial ring, separated by a short distance only from the posterior margin. Pleural fields with three pleural furrows; anterior, faint interpleural furrows developed. Posterior and lateral borders weakly defined, lateral and posterior rims consist of slightly convex, rapidly sloping deflected marginal portions.

Surface of the cuticle smooth.

Dimensions. Some of the studied specimens are extraordinarily large. The nearly complete dorsal exoskeleton MMUW 2019D-035a (illustrated in Fig. 111L) has a length of 113 mm, with its cranidium being 39 mm long. Other cranidia are in the same range, an unfigured partial cranidium suggested a length of 42 mm during life time of the individual.

Discussion. Courtessolia lemdadensis n. gen., n. sp. is characterised by a relatively large and broad glabella with distinctly curved lateral borders so that it is quite similar to the species of the *Courtessolia levyi* group, particularly *C. levyi* (Munier-Chalmas & Bergeron in Bergeron, 1889), *C. seguieri* (Courtessole, 1973) and *C. griffei* (Courtessole, 1973). *Courtessolia seguieri* and *C. griffei* are both distinguished from *C. lemdadensis* by a preglabellar field that is nearly as broad as the anterior on the sagittal line whereas the anterior border is broad and relatively convex in *C. lemdadensis*, while the preglabellar field is much narrower and only poorly convex.

More similar to *C. lemdadensis* is *C. levyi*, but is also distinguished by a slightly narrower (sag.) preglabellar field and a narrower anterior border relative to the cephalic length. The genae in *C. levyi* are areally larger than those in *C. lemdadensis*, and the facial sutures dissect the lateral border furrow at a slightly more anterior position.

Courtessolia sepulcra (Álvaro & Vizcaïno, 2018) and *C. bondoni* (Termier & Termier, 1950) differ in having a narrower and sub-pointed glabella as well as a clearly broader (sag.) preglabellar field in respect to the anterior border as well as in additional, less obvious characters.

Courtessolia sepulcra (Álvaro & Vizcaïno, 2018)

Fig. 112

* 1879 *Bailiella sepulcra* n. sp. – Álvaro & Vizcaïno: pp. 572–573, 584, fig. 3a–o.

Studied material, localities and strata. Ca. one dozen cranidia, two pygidia and a few fragmentary thoracic segments, preserved as internal and external moulds in variably calcareous, fine-grained sandstone. In repository: 18 cranidia under MMUW 2019E-001a, -005d, -008, -009a, -012a, -012d, -015a, -016a, -017a, -018b, -020, 023a, -023b, -023c, -024a, -025a, -025b and -026; pygidia under MMUW 2019E-003c and -027; specimens from horizon D2172, ca. 7 m above the base of the Bailiella Formation, upper/late Languedocian (= early Guzhangian); from section at Jbel Hessikou northeast of Mlal, map sheet Tazzarine, central Anti-Atlas, Morocco (Lambert coordinates 475.9/434.5). Single cranidium under MMUW 2019E-028; from near the base of the Bailiella Formation, upper/late Languedocian (= early Guzhangian); from Aït Mersid section, southern flank of Jbel Sarhro, map sheet

Tazzarine, central Anti-Atlas, Morocco (Lambert coordinates ca. 460/ca. 435). Four cranidia under MMUW 2019E-029, -030. -031 and -032; two pygidia under MMUW 2019E-033 and -034; from near the base of the Bailiella Formation, upper/late Languedocian (= early Guzhangian); from Jbel Bou Ifersikt section/Zaouia Aïnass (“Zawat Aynas”), WSW of Agdz, map sheet Ouarzazate, central Anti-Atlas, Morocco (Lambert coordinates 386.4/404.3).

Diagnosis (emended). Species of *Courtessolia* with cephalon having a length:width ratio of ca. 0.60–0.65; glabella of ca. 65 percent cephalic length and ca. 30 percent cephalic width across occipital ring, lateral margins gently curved; anterior border moderately broad (ca. 15–17 percent cephalic length on sagittal line), distinctly decreasing in breadth from sagittal line; anterior border furrow gently curved in the central sector, with faint swelling across sagittal line and with slight kink at mid-level of genae; facial suture intersects lateral border furrow at anterior part of L2.

Discussion. *Bailiella sepulcra* has been introduced by Álvaro & Vizcaïno (2018) and described as characterised by a smooth test, by cephala being hemispherical in outline and having a convex pre-glabellar field and anterior border and a stout spine on the occipital ring. The pygidium is described as having a long axis of about 85–90% pygidial length and with “one/two axial rings and two pleural furrows” as well as lacking a border (Álvaro & Vizcaïno (2018, p. 573).

Discussion. *Bailiella sepulcra* has been introduced by Álvaro & Vizcaïno (2018) and described as characterised by a smooth test, by cephala being hemispherical in outline and having a convex pre-glabellar field and anterior border and a stout spine on the occipital ring. The pygidium is described as having a long axis of about 85–90% pygidial length and with “one/two axial rings and two pleural furrows” as well as lacking a border (Álvaro & Vizcaïno (2018, p. 573).

Bailiella sepulcra is long known from strata of the central Anti-Atlas and was eponymous for the Bailiella Formation. It has been dealt with informally or identified as *Bailiella levyi* and *Bailiella* cf. *levyi* (Geyer & Landing 1995, 2006; Geyer et al. 1995), respectively, owing to the apparent morphological plasticity of the specimens of *B. levyi* described from Spain and southern France.

In fact, allometric changes during ontogeny must be emphasised, leading to a more acute and shorter glabella in large and nearly gerontic cephala, with a glabella of almost exactly 60% cephalic length (rather that 65–70% as described by Álvaro & Vizcaïno 2018) and with a distinctly subacute front and only slightly curved lateral margins (rather than being “bluntly rounded” as noted in Álvaro & Vizcaïno 2018). The glabellar furrows are weak, but not “obsolete”, and the occipital ring has a median node (Fig. 112A, G) rather than a “stout rearward-directed spine” as claimed in Álvaro & Vizcaïno (2018). These features are of little difference compared with *Bailiella levyi*. However, differential characters between the species can be seen in the (i) the slightly posteriorly extended occipital ring in *B. sepulcra*, and (ii) the pygidium, which is characterised in *B. sepulcra* by a sublenticular outline and a pygidial axis with a subrectangular posterior section. Álvaro & Vizcaïno (2018) described the axis as “comprising one (rarely two) axial ring and rounded terminal piece”, but this is in strong contrast to the material studied herein (Fig. 112F, H, I, R), with the best-preserved pygidia (internal moulds) having three well recognizable axial rings and an additional very weak furrow.

Bailiella levyi, by contrast, is characterised by a slightly less curved anterior margin of the cephalon and a shorter occipital ring with a moderately curved posterior margin (e.g., Esteve 2009, fig. 4b). A particularly informative pygidium was figured by Esteve (2009, fig. 6), showing the longer axis with a tapering posterior portion. *Bailiella souchoni* from the *Bailiella souchoni* Zone (middle Languedocian) of the Montagne Noire is distinguished by more strongly inflated fixigenae, but is too poorly known yet to allow a precise comparison of all characters.

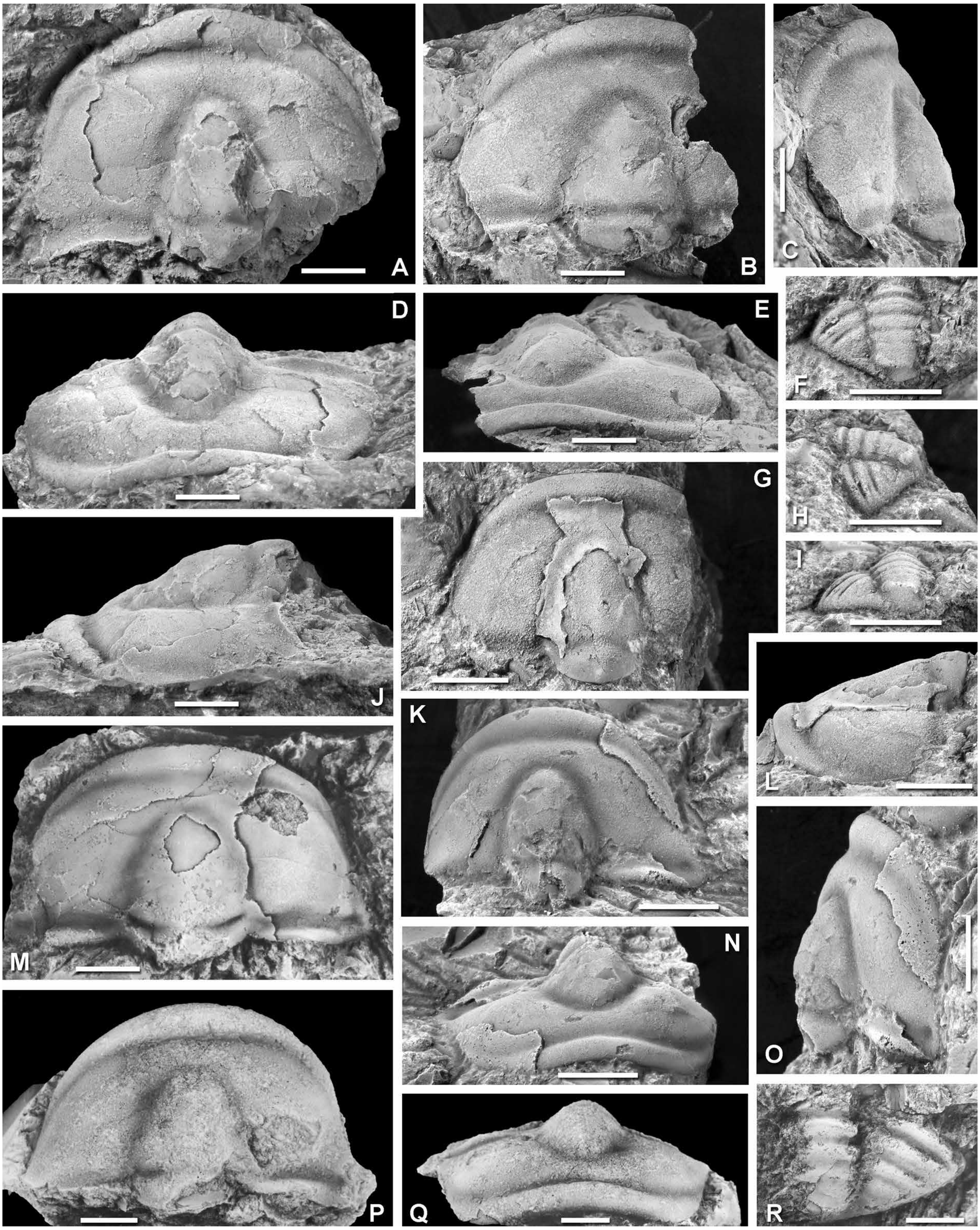


Fig. 112: *Courtessolia sepulcra* (Álvaro & Vizcaïno, 2018). **A, D, J** MMUW 2019E-008, incomplete cranidium, partly exfoliated, dorsal (A), anterior (D) and lateral (J) views; **B, C, E** MMUW 2019E-015a, partial cranidium, dorsal (B), oblique lateral (C) and anterior (E) views; **F, H, I** MMUW 2019E-003c, incomplete pygidium, dorsal (F), lateral (H) and posterior (I) views; **G, L** MMUW 2019E-016a, partial cranidium, dorsal (G) and lateral (L) views; **K, N, O** MMUW 2019E-012a, incomplete cranidium, largely exfoliated,dorsal (K), anterior (N) and lateral (O) views; **M** MMUW 2019E-029, cranidium, partly exfoliated, dorsal view; from Jbel Bou Ifersikt/Zaouia Aïnass section, sample horizon D2095; **P, Q** MMUW 2019E-028, cranidium, dorsal (P) and anterior (Q) views, from Aït Mersid section, sample horizon D2078; **R** MMUW 2019E-033, partial pygidium, dorsal view, from Jbel Bou Ifersikt/Zaouia Aïnass section, sample horizon D2095. Specimens in A–L, N, O from horizon D2172, Jbel Hessikou section; all from Bailiella Formation, *Courtessolia* Zone, central Anti-Atlas, Morocco. Scale bars 5 mm).

Courtessolia bondoni (Termier & Termier, 1950), described below, is a second, similar species of *Courtessolia* that occurs in the Atlas ranges of Morocco. It differs in having a somewhat broader cephalon with a slightly longer glabella, an anterior border that is reasonably constant in breadth in the central sector, and an anterior border furrow without a swelling and being almost straight across the central sector.

Stratigraphic occurrence. Bailiella Formation, *Courtessolia* Biozone, upper/late Languedocian (=early Guzhangian); central Anti-Atlas, Morocco.

***Courtessolia bondoni* (Termier & Termier, 1950)**

Fig. 113

v * 1950 *Bailiella Levyi* Munier-Chalmas et Bergeron var. *Bondoni* var. nov. – Termier & Termier: pp. 28, 50, pl. CLXXXXI, fig. 4.
v 1984 *Bailiella levyi bondoni* Termier & Termier, 1950 – Carriol: p. 18.
v 2018 *Bailiella levyi bondoni* Termier & Termier, 1950 – Lebrun: text-fig. E

Lectotype (chosen herewith). MNHN F.R50872a, cranidium (figured in Termier & Termier 1950, pl. CLXXXXI, fig. 4).

Type locality. Unidentified locality in the Oued Tamsift syncline, High Atlas, Morocco.

Type stratum. Bailiella Formation, *Courtessolia* Biozone, upper/late Languedocian (=early Guzhangian).

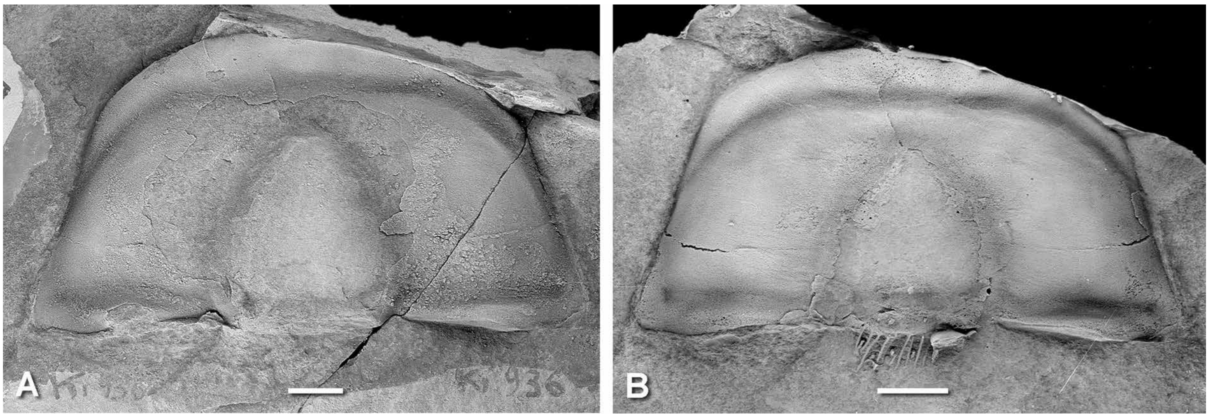


Fig. 113: *Courtessolia bondoni* (Termier & Termier, 1950). **A** MNHN F.R50872A, lectotype (chosen herein), cranidium, largely exfoliated, dorsal view; **B** MNHN F.R50872, paratype, cranidium, latex cast of external mould, dorsal view. Both specimens from the Bailiella Formation, *Courtessolia* Zone, Oued Tamsift syncline, High Atlas, Morocco. Scale bars 5 mm.

Paratypes. MNHN F.R50872b, incomplete cranidium with partial first thoracic segment attached to it (on the same slab as the lectotype); MNHN F.R50872ba-II, cranidium, external mould (counterpart of MNHN F.R50872a).

Diagnosis (emended). Species of *Courtessolia* with cephalon having a length:width ratio of ca. 0.52–0.56; glabella of ca. 70 percent cephalic length and ca. 30 percent cephalic width across occipital ring, lateral margins gently curved; anterior border moderately broad (ca. 15 percent cephalic length on sagittal line), with inconspicuous decrease in breadth along central sector; anterior border furrow weakly curved in the central sector, with slight kink at mid-level of genae; facial suture intersects the lateral border furrow at anterior part of L2.

Discussion. Termier & Termier (1950) figured and shortly described a trilobite that they regarded as a "new variety" of *Bailiella levyi*. Thus trilobite, termed "*Bailiella Levyi* Munier-Chalmas et Bergeron var. *Bondoni*", was shortly characterised as follows: "Nous pensons qu'il est nécessaire de distinguer une variété nouvelle de *Baillella Levyi* pour un échantillon répresente par un céphalon fuse dont la glabelle est subsphérique et dont l'éspace du limbe qui est compris entre la partie anterieure de la glabelle et le bourrelet frontal est égal a la largeur de ce dernier, donc moins grand que chez l'espèce typique." (Termier & Termier 1950, p. 28). Despite of the quite rudimentary information (which is not entirely unusual for the time of publication), the introduction must be regarded as valid. The type material of the Termiers is housed in the Muséum Nationale d'Histoire Naturelle in Paris and consists of two slabs that represent part and counterpart and contain two fairly well preserved cranidia. The Termiers indicated the "Synclinal de Tamsift" as the origin of the sample with Jacques Bondon as the collector of the specimens. The lithology and preservation of the samples (studied by GG in 1996) leaves little doubts that the specimens originate from the *Bailiella* Formation.

The specimens differ from *Courtessolia levyi* as well as *C. sepulcra* in having a glabella which is relatively broad across the occipital ring and with distinctly curved lateral glabellar margins. In addition, the preglabellar field is narrower on the sagittal line than the anterior border, and the cephalic suture is located in a relatively adaxial position so that it cuts off part of the genae and meets the anterior border furrow at or even slightly anterior to the level of S3.

Conocoryphid genus and species A

Fig. 114

Material. Four hypostomata; in repository: MMUW 2017D-750a, SSMM 11055 and SSMM 11374.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Description. Hypostome tongue-shaped in ventral view, with anterior lobe of middle body ca. 2.5 times longer (sag.) than posterior lobe and subequal wide. Middle furrow transverse, with gentle rearward curvature, shallow and broad (sag.) medially. Posterior lobe of middle body crescent-shaped, with nearly evenly curved posterior margin. Lateral borders of hypostome slightly diverging in anterior section and curved in lateral profile, slightly broadening anteriorly, well elevated, defined from middle body by well impressed border furrow; separated from posterior section by a more-or-less distinctive shallower portion; posterior part of the lateral border extending into the posterior border without any recognisable change, both of subequal width and elevation, relatively narrow, with distinct subequal curvature throughout. Border furrow moderately wide, relatively shallow, but well recognisable.

Discussion. The hypostome has a morphology typical for conocoryphid trilobites. Its specific morphological features include the relatively broad (sag.) posterior lobe of the middle body and a fairly narrow border furrow, which distinguishes it from the otherwise similar hypostomata known from species of *Conocoryphe*, such as *C. sulzeri* (Schlotheim, 1823) or *C. granulata* Hawle & Corda, 1847 from Bohemia. According to their relative frequency, their size and the co-occurrence with *Prioscutarius max* n. gen., n. sp. and *P. moritz* n. gen., n. sp., it seems very probable that the hypostoma belong to one of these species, probably the former.

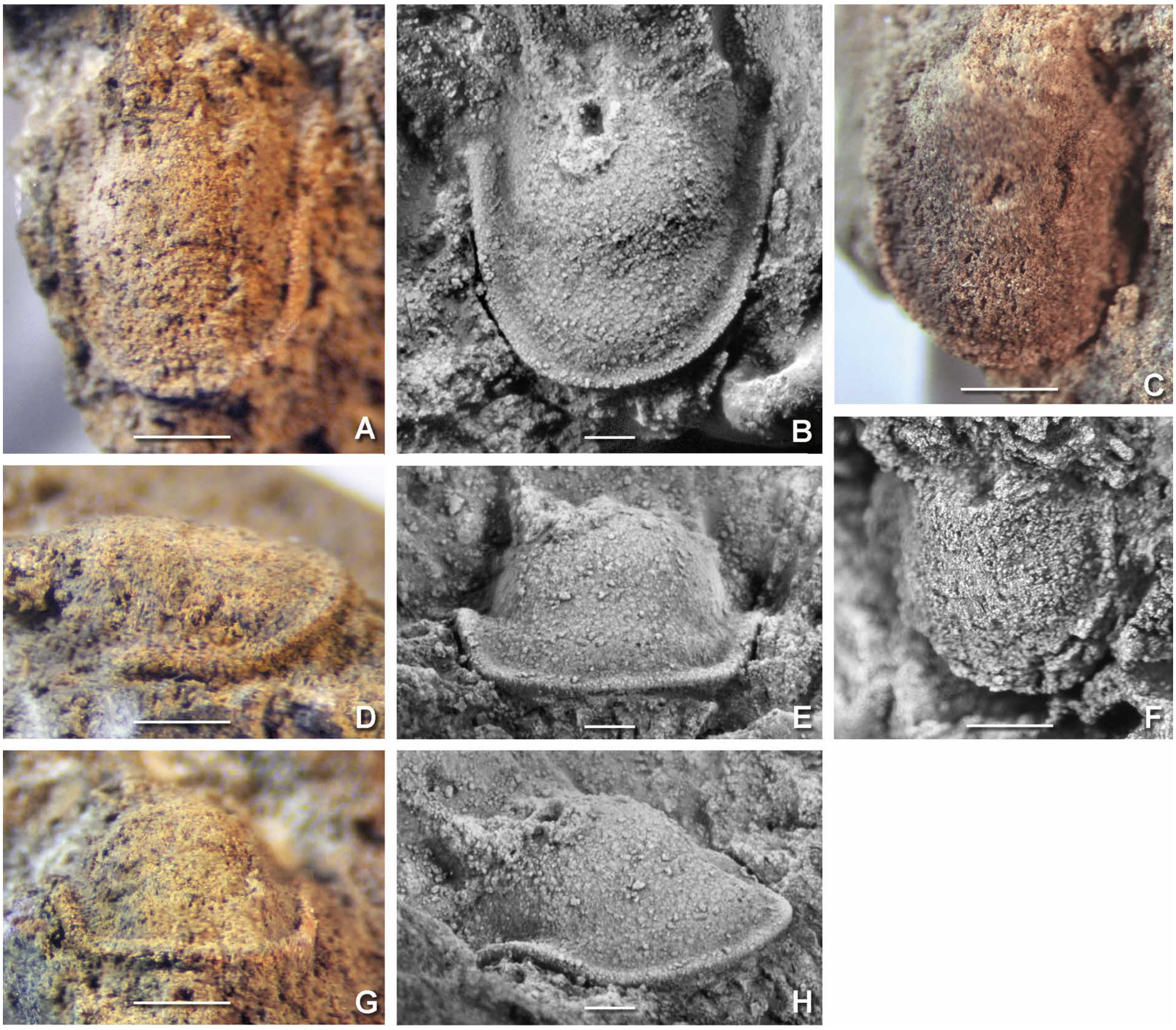


Fig. 114: Conocoryphid genus and species A. **A, D, G** SSMM 11055, incomplete hypostome, internal mould, dorsal (A), oblique lateral (D) and posterior (G) views; **B, E, H** MMUW 2017D-750a, incomplete hypostome, internal mould, dorsal (B), posterior (E) and lateral (H) views; **C** SSMM 11374, hypostome, internal mould, dorsal view; **F** incomplete hypostome, internal mould, dorsal view; specimen apparently lost. All specimens from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Conocoryphid genus and species B

Fig. 115

Material. Partial pygidium, MMUW 2017D-338.

Locality and stratum. Collecting site uncertain, Wildenstein slice, Franconian Forest.

Discussion. The pygidium is slightly distorted, and only the left half and most of the axis preserved. This axis stretched over ca. 80 percent of the pygidial length, with two well-defined axial rings and furrows and a third weakly developed furrow. It tapers slightly towards the bluntly curved and fairly broad terminal axial piece. The pleural areas are well divided by at least three deep pleural and at least three less well developed interpleural furrows. The anterior border is relatively slender and clearly defined by a deep border furrow. The lateral border is comparatively broad and almost flat. A border furrow is not developed, but the lateral border and pleural areas are distinctly separated by a distinct change in convexity.

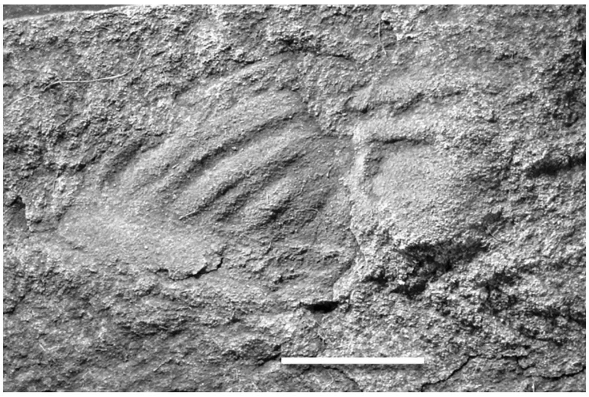


Fig. 115:
Conocoryphid genus and species B. MMUW 2017D-338, partial pygidium, dorsal view; from uncertain locality in the Wildenstein slice. Wildenstein Member, Tannenknock Formation. Scale bar 5 mm.

No cranidium is known from the Wildenstein Member which readily fits to this pygidium. Its morphology resembles pygidia of conocoryphid genera including *Bailiella*. However, roughly similar pygidia of *Bailiella* and *Conocoryphe* occur in species with a much younger stratigraphical occurrence, whereas the two coeval species of *Bailiella* from the Wildenstein Member have morphologically quite different pygidia (see above). A particularly distinguishing character is the broad and almost flat lateral border.

Family uncertain

Genus *Brunswickia* Howell, 1937

Fig. 116

Type species. Brunswickia quadrata Howell, 1937; from the St. Albans Formation at St. Albans, Vermont, U.S.A.

Discussion. The genus *Brunswickia* Howell, 1937 was introduced as a monotypic genus based on *Brunswickia quadrata* Howell, 1937, which was known from only two unfavourably preserved cranidia from the *Bolaspidella* Zone of the St. Albans Formation (Shaw 1958; Mehrtens & Dorsey 1987) of Vermont. The original material and subsequently collected specimens are even less informative than the material of *Braintreella rogersi* (Walcott, 1884) from Massachusetts (see above). Its recognisable characters include a slightly tapering glabella with a considerable transverse convexity and a low curvature of its anterior margin; a moderately broad (sag., exsag.) occipital ring extending into a long terminal occipital spine; a convex (sag.) preglabellar field of nearly the breath (sag.) of the anterior border; an anterior border which appears to taper only slightly towards the facial sutures; moderately wide fixigenae; and palpebral lobes in a central position in respect to the cephalon's length axis. Howell's (1937, pl. 5, figs. 13, 32) figures of the type material may even lump two different species. A specimen interpreted to represent *Brunswickia quadrata* is illustrated in Fig. 116.

Nevertheless, *Brunswickia* has been suggested to be a genus suitable to include further solenopleurid species with a "primordial" morphology, such as "*Conocoryphe applanata* Salter, 1869", "*Jincella prantli* Růžička, 1944", and "*Conocephalites robbii* Hartt in Dawson, 1868." Fletcher (2007, 2017) suggested a broad concept of the genus, but distinguished two subgenera, *Brunswickia* (*Brunswickia*) and *Brunswickia* (*Jincella*) and assigned *Conocephalites robbii* to *B.* (*Brunswickia*). He considered *Brunswickia* and *Jincella* as distinct, but closely related to that he regarded *Jincella* as a subgenus of *Brunswickia*.

These affinities are invalidated by the type species of *Brunswickia*, which must be regarded as of uncertain systematic position. Regardless of the deficiencies in morphological characteristics, distinction as subgenera suggests a degree of relationship, which appears to be based on hypothetic phylogenetic pathways and does not take into account that any other distinction on a subgenus level is considered within the subfamily. Fletcher (2007) assigned not only *Conocoryphe applanata* and *Jincella* *prantli* to the genus, but also the Siberian species *Brunswickia* (*Jincella*) *lenaica* (Lermontova, 1940) from the *Tomagnostus fissus-Eccaparadoxides hicksii* Zone of the Yudoma River area (e.g., Egorova et al. 1982, pl. 4, fig. 9) and *Brunswickia* (*Jincella*) *recta* (Chernysheva, 1953) from the *Ptychagnostus gibbus* Zone of the Khorbusuonka River area (e.g., Savitsky et al. 1972, pl. 21, fig. 3).

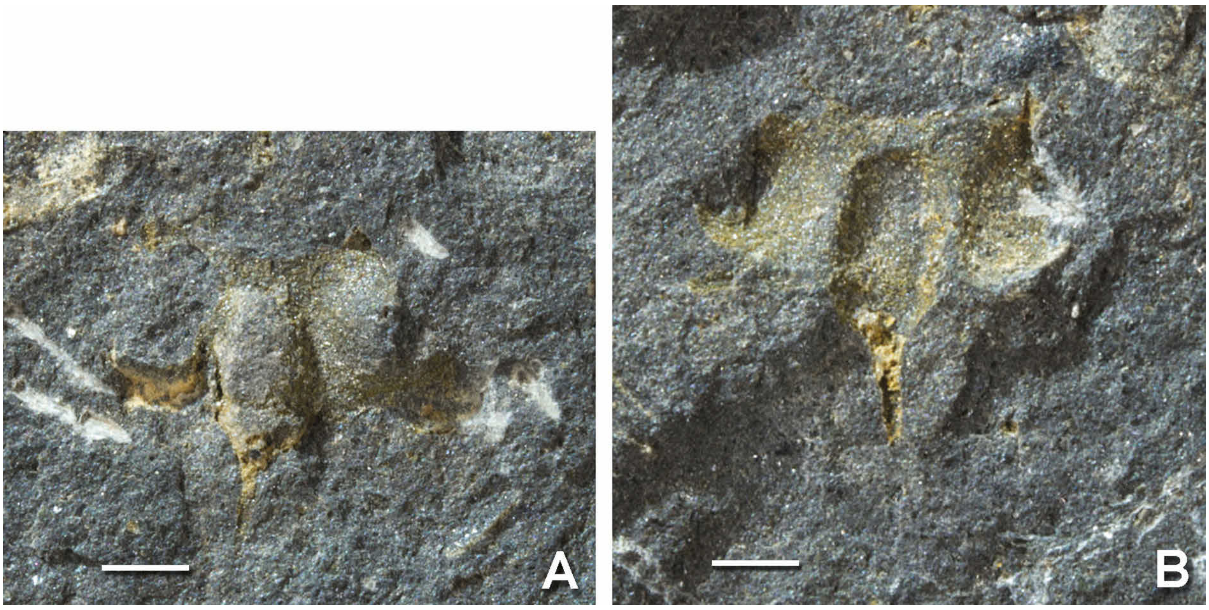


Fig. 116: *Brunswickia quadrata* Howell, 1937. **A** USNM PAL 532304, holotype, partial cranidium, internal mould; original of Howell 1937, pl. 5, fig. 13 (previously Princeton University collection, no. 40092a, now more strongly damaged); **B** USNM PAL 532304, cranidium, external mould; *Centropleura vermontensis* faunal assemblage, St. Albans Formation, near St. Albans, Franklin County, north-western Vermont; National Museum of Natural History, Smithsonian Institution. (2016, February 20). Smithsonian Learning Lab Resource: *Brunswickia quadrata* Howell, 1937. Retrieved October 15, 2023.

Indeterminate ptychopariine trilobites

Remarks. The Wildenstein Member yields a considerable number of isolated trilobite sclerites, which cannot be assigned with any certainty to a genus and species or even a family due to either an imperfect preservation in terms of completeness or the lack of unequivocal characters. The majority of such indeterminate sclerites belongs to the suborder Ptychopariina (in a traditional concept), which is clearly a polyphyletic taxon. Sclerites with more-or-less significant characters are shortly characterised and discussed below in order to portray the faunal spectrum. None of them is presently believed to assist critically in delineating a formal taxon.

Ptychopariine genus and species 1

Fig. 117

Material. Small cranidium, MMUW 2017D-1104, and incomplete cranidium, SSMM 12420a.

Locality and stratum. Both specimens from locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. An imperfectly preserved, small specimen (width ca. 1.2 mm) from locality W8 (Fig. 117A–C) is characterised by a cranidium with a roughly semicircular outline; a relatively wide and faintly tapering, quite long glabella; moderately long palpebral lobes in a fairly posterior position; a narrow preglabellar field, which is convex in sagittal profile, but distinctly lower than the preocular areas; and a relatively narrow, moderately prominent anterior border of nearly equal breadth (sag., exsag.) throughout its course.

A larger, but still relatively small incomplete specimen (Fig. 117D) appears to represent the same species. It has a well demarcated, relatively short (sag.) occipital ring which terminates with a small node, and the eye ridges are clearly recognisable and form a gently backward curved arc.

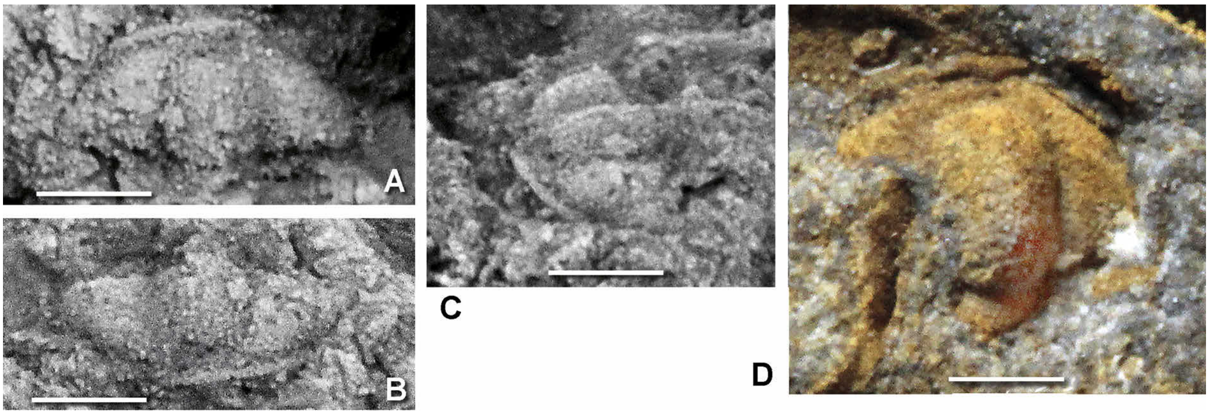


Fig. 117: Ptychopariine genus and species 1. **A–C** MMUW 2017D-1103, cranidium of immature individual, dorsal (A), oblique lateral (B) and oblique anterior views; **D** SSMM 12420a, small partial cranidium, dorsal view. Both specimens from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

This very small specimen represents an immature individual of a ptychopariine trilobite from either the ptychoparioid or solenopleurid clade, whereas the slightly larger cranidium appears to present features that suggest primarily solenopleurid signatures. Although both groups are represented by several species or informally recognised forms in the Wildenstein Member and locality W8, particularly *Exapinepiphania* n. nom., the form epitomised by the two specimens almost certainly does not belong to any of the taxa described herein from sclerites of adult individuals.

Ptychopariine genus and species 2

Fig. 118

Material. Partial cranidium, SSMM 10535.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Fig. 118:
Ptychopariine genus and species 2.
SSMM 10535, partial cranidium, dorsal view. From locality W8.
Wildenstein Member, Tannenknock Formation. Scale bar 5 mm.

Discussion. The larger cranidial fragment shows characters typical for solenopleurine trilobites. It resembles very much species and forms assigned to *Exapinepiphania* n. nom. present in the

Wildenstein Member. However, the specimen is distinguished from them in having a glabella with a front defined by a low curvature and relatively distinctive anterolateral corners of the glabella; a preglabellar field that appears to slope ventrally from the front of the glabella; and an anterior border with a relatively minor convexity in sag. and exsag. profile so that it appears somewhat blade-like and ascending from the anterior border furrow. The palpebral lobes as well as the entire posterior part of the cranidium are unknown so that a reliable determination to a family or even a genus is not possible.

Ptychopariine genus and species 3

Fig. 119A, B, C?, D?

Material. Pygidial fragment, MMUW 2017D-543a, and pygidium tentatively assigned to the same form under MMUW 2017D-469.

Locality and stratum. From localities W18a and W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. The single fragment of a pygidium is characterised by pygidial axis with a relatively high convexity that almost certainly tapers slightly and appears to have been well divided into at least four axial rings, with the posterior tip reaching almost to the posterior margin of the pygidium. An anterior border is well-defined. The pleural field show at least three well-defined pleural ribs, whereas the lateral border is weakly defined and almost flat in transverse profile. Pleural fields and lateral border slope considerably towards ventral from near the well-incised axial furrow.

A somewhat laterally compressed complete pygidium (Fig. 119C, D) probably represents the same form. Due to its poor preservation, it does not show the delicate furrows on the pleural areas. It shows a pygidial axis which tapers rearward, having a least two well recognisable axial rings and a fairly broad (sag.) articulating half-ring. The posterior end of the axis reaches to, or nearly to the posterior margin of the pygidium. A longitudinal furrow is visible on its (undivided) posterior part, but the depth of this furrow was certainly enhanced by the lateral compaction.

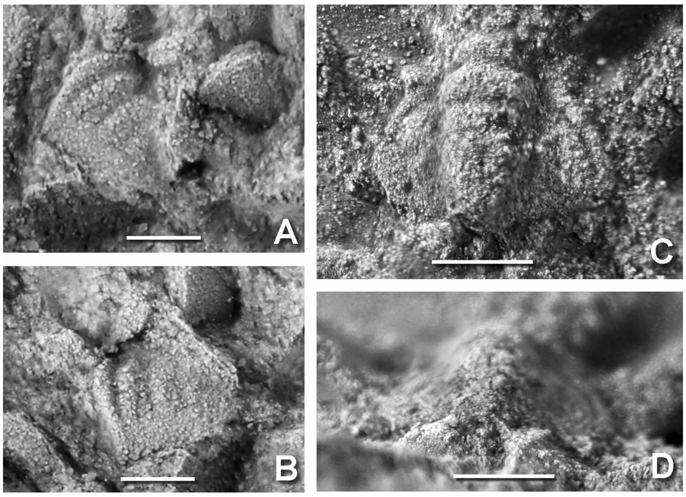


Fig. 119:
A, B Ptychopariine genus and species 3, MMUW 2017D-543a, fragment of pygidium, internal mould, dorsal (A) and lateral views (B); from locality W18a.
C, D Ptychopariine genus and species 3?, MMUW 2017D-469, pygidium, internal mould, dorsal (C) and posterior (D) views; from locality W8. Wildenstein Member, Tannenknock Formation. All scale bars equal to 1 mm.

This pygidium differs noticeably from all other pygidia known from the Tannenknock Formation. It resembles pygidia known from several ptychopariine taxa, but a somewhat reliable identification is not possible. Similarities to corynexochoid taxa can also be seen, but the gently curved lateral margin does not favour such a relationship.

Ptychopariine genus and species 4

Fig. 120

Material. Single small pygidium with loosely attached partial thoracic segments, SSMM 11617.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

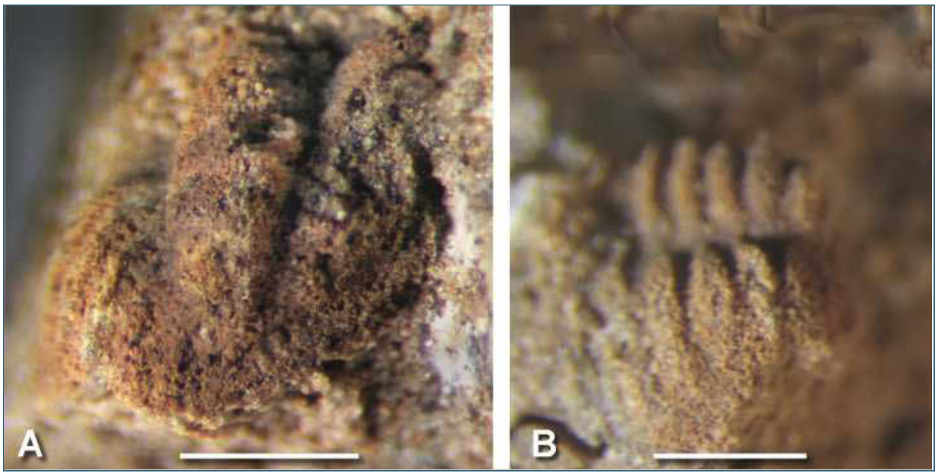


Fig. 120: Ptychopariine genus and species 4. **A, B** SSMM 11617, small pygidium with two more or less attached fragmental thoracic pleurae, internal mould, dorsal (A) and lateral views (B). From locality W8. Wildenstein Member, Tannenknock Formation. Scale bar 1 mm.

Discussion. The slightly laterally compressed cranidium is only ca. 0.85 mm long and has a tapering axis with at least four well-defined rings and a relatively narrow (tr.) terminal axial piece. A well-defined, narrow anterior border is developed. The pleural areas are subdivided by ca. four well incised pleural and an equal number of much shallower interpleural furrows and are gently convex (now slightly exaggerated by the lateral compression) so that they show a steep ventral slope towards the lateral margins. The field posterior to the axis is also intersected by fairly well developed furrows.

Two partial segments of the posterior thorax and more-or-less attached to the pygidium, but do not offer any details of their morphology.

Although on the first glance this single pygidium seems to resemble pygidia known from early ptychopariaceans, it is clearly distinguished from them in the persistence of well-developed pleural furrows throughout the pleural areas and posterior to the axis. In addition, the absence of a lateral border and the considerable ventral slope of the abaxial parts of the pleura also characterise the pygidium.

Ptychopariine genus and species 5

Fig. 121

Material. Several pygidia and pygidial fragments. In repository: five pygidia, MMUW 2017D-190, MMUW 2017D-244a, MMUW 2017D-279b, SSMM 11116d and SSMM 11481b.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. Several small and mostly poorly preserved cranidia of lenticular outline (in dorsal view) and a relatively high convexity were found in the calcareous bodies of the Wildenstein Member. They are characterised by an axis which gently tapers rearward and has a poorly defined posterior margin, with only one well-defined axial ring and a second poorly demarcated ring posterior to it; by a well-defined anterior border, but lateral and posterior border fused with the pleural fields; pleural field almost without a recognisable subdivision; lateral and posterior areas relatively steeply ventrally deflected (Fig. 121B).

These pygidia resemble those of *Exapinepiphania* n. nom., but differ in having steeply inclined lateral and posterior areas, which suggest a functional morphology as an adaptation to a position below the anterior part of the cephalon during enrolment. However, the particular convexity does not fit perfectly to any of the solenopleurid cranidia found in the Wildenstein Member to date and described above so that the precise identity of these pygidia remains unknown.

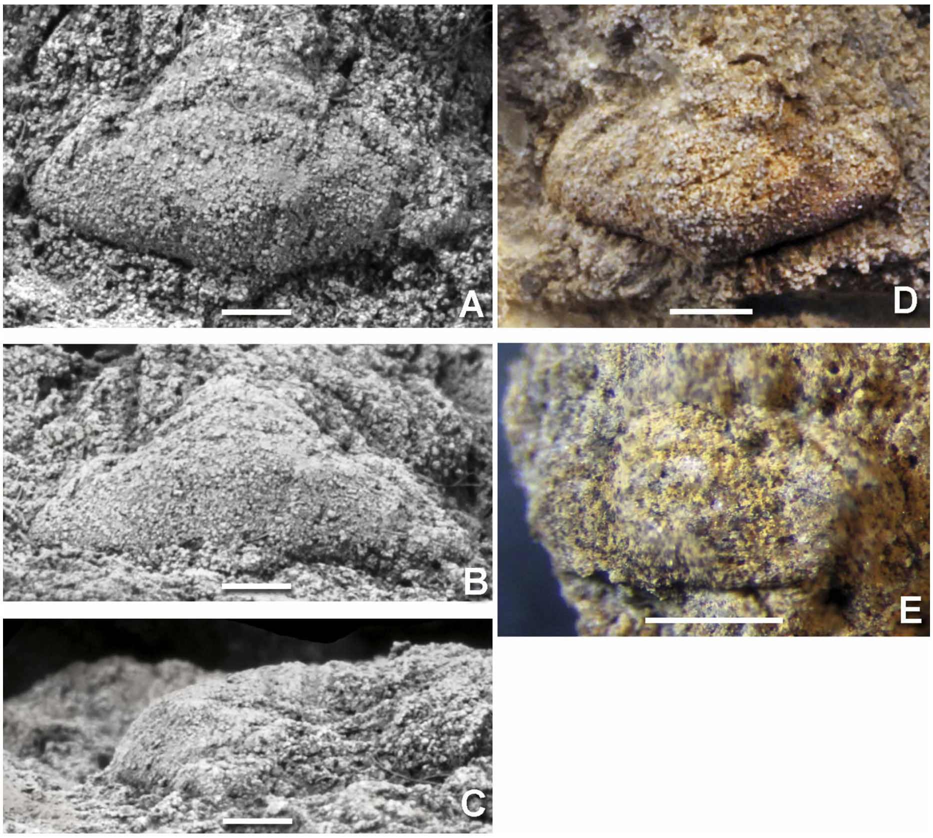


Fig. 121: Ptychopariine genus and species 5. **A–C** MMUW 2017D-190, pygidium, internal mould, dorsal (A), posterior (B) and lateral (C) views; **D** SSMM 11116d, pygidium, internal mould, dorsal view; **E** SSMM 11481b, pygidium, internal mould, dorsal view. All from locality W8. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Ptychopariine genus and species 6

Fig. 122

Material. Several pygidia. In repository: two pygidia, MMUW 2017D-192 and SSMM 11062b.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. Several small and predominantly poorly preserved cranidia of lenticular outline (in dorsal view) and a relatively high convexity, similar to those described above under ptychopariine genus and species 5 were discovered in the calcareous bodies of the Wildenstein Member. Similar to those of ptychopariine genus and species 5 they are characterised by an axis which slightly tapers and has a weakly defined posterior and posterolateral margin, but two to four axial rings are defined by furrows which appear to fade in depths rearward. The anterior border is well-defined, but the lateral and posterior borders are fused with the pleural fields. The pleural field shows several pleural and interpleural furrows which are decreasingly well-developed towards the posterior. The flanks are ventrally deflected, but (in contrast to that seen in ptychopariine genus and species 5) they are gently convex and do not show a recognisable arcuation in transverse profile (Fig. 122C, D).

These pygidia resemble those of *Exapinepiphania* n. nom., but differ by the inclination and slope of the lateral and posterior areas as well as the relatively narrowly spaced pleural furrows.

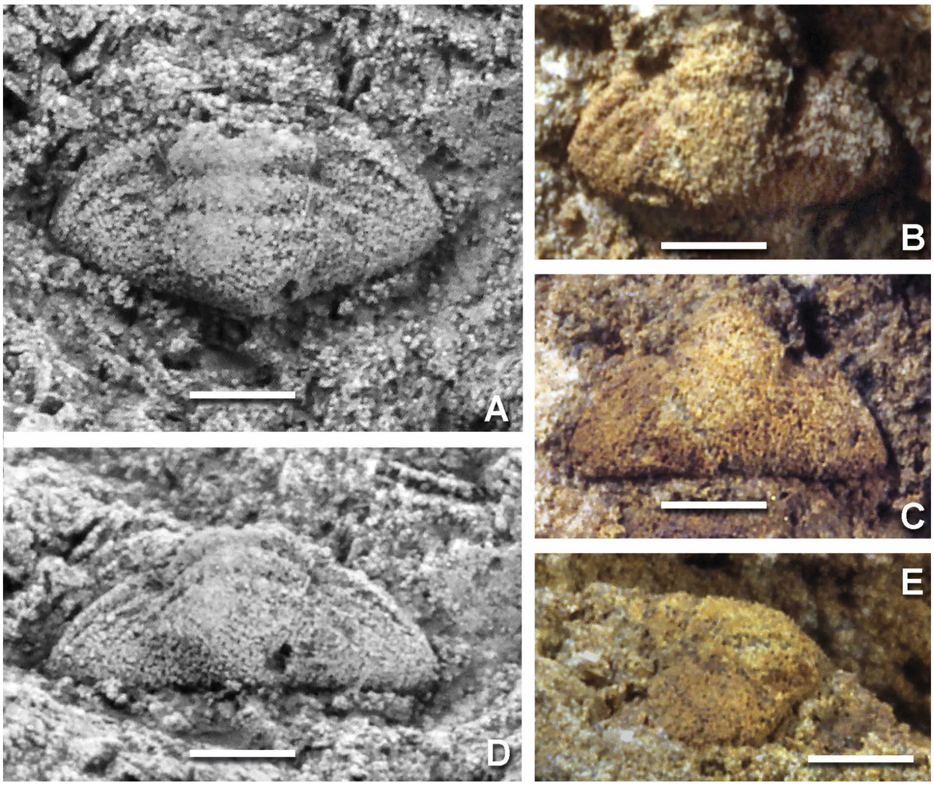


Fig. 122: Ptychopariine genus and species 6.
A, D MMUW 2017D-192, pygidium, internal mould, dorsal (A) and oblique posterior (D) views; from locality W8;
B, C, E SSMM 11062b, cranidium, internal mould, dorsal (B), oblique posterior (C) and lateral (E) views; from locality W8.
Wildenstein Member, Tannenknock Formation.
Scale bars 1 mm.

Ptychopariine genus and species 7

Fig. 123

Material. Ca. 10 pygidia and pygidial fragments. In repository: more or less complete pygidia under SSMM 11623a, SSMM 11624, SSMM 11625, SSMM 11627a and SSMM 11628e; single incomplete pygidium with two articulated thoracic segments under MMUW 2017D-862.

Locality and stratum. All specimens from locality W8 except MMUW 2017D-862 (from W8a), Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A number of pygidia and pygidial fragments from the Wildenstein Member share a general morphology of a broadly lenticular outline and a moderately broad pygidial axis with one to two well recognisable and one or two faint axial rings and a terminal axial piece with a uniformly curved posterior margin. The axis tapers slightly to moderately, and its posterior tip does not reach to the posterior border from which it is separated by a narrow (sag.) transverse band (e.g., Fig. 123H), which is slightly raised from the posterior pleural areas lateral to it as visible om posterior view (e.g., Fig, 123E, F). The pleural areas are relatively broad (tr.; ca. 1.5 times the width of the pygidial axis) and almost devoid any recognisable furrows except for one pleural furrow in the anterior part short distance posterior to the well-developed border furrow which defined a moderately broad (exsag.) anterior border. No lateral border is recognisable, and the marginal lateral parts of the pygidium show a significant ventral deflection.

The specific characters of the pygidia vary to a certain degree, and the photos shown in Fig. 123 are selected for illustration of these variations. Differences can be recognised in the precise relative width (tr.) of the axis, the degree of tapering and the convexity of the axis, the overall convexity as well as the curvature of the posterior margin. These are certainly affected by different amounts of compression and distortion, other preservational conditions, but also by intraspecific variability. Nevertheless, it is perhaps probably that these pygidia represent more than a single species.

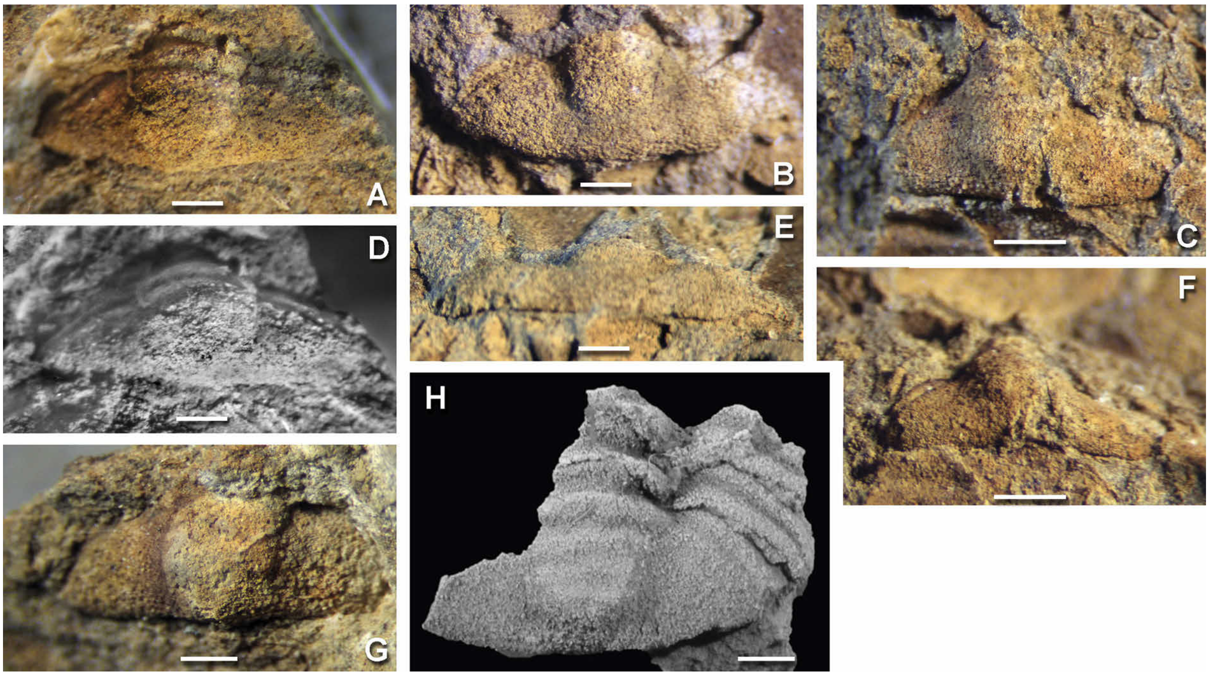


Fig. 123: Ptychopariine genus and species 7. **A, D** SSMM 11623a, pygidium, internal mould, dorsal (A) and oblique posterior (D) views; from locality W8; **B, E** SSMM 11627a, pygidium, internal mould, dorsal (B) and posterior (E) views; from locality W8; **C, F** SSMM 11628e, pygidium, internal mould, dorsal (C) and posterior (F views; from locality W8; **G** SSMM 11625, quite strongly distorted pygidium, internal mould, dorsal view; from locality W8; **H** MMUW 2017D-862, incomplete pygidium with two incomplete thoracic segments attached to it, internal mould, dorsal view; from locality W8a.
Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

“Order Corynexochida Kobayashi, 1935”

Discussion. Sundberg (2008) presented a study of trilobite hypostomata and rostral plates, in which he suggested that the genera of the Corynexochida represent a polyphyletic group. He specifically pointed out the genera *Albertella* Walcott, 1908, *Wenkchemia* Rasetti, 1951, *Parkaspis* Rasetti, 1951, and *Fieldaspis* Rasetti, 1951 (which are grouped among the families Dolichometopidae Walcott, 1916 and Zacanthoididae Swinnerton, 1915) might represent a clade separate from the remaining Corynexochida. Yuan et al. (2001) stated that the members of the corynexochoid family Oryctocaridae have a narrow rostral plate which is not fused with the hypostome. Subsequently, the species *Zacanthopsis palmeri* Hopkins & Webster, 2009 and *Zacanthoides marshalli* Robison & Babcock, 2011 have been shown to possess a functional hypostomal suture in adults so that the earlier suggested diagnostic character of the Corynexochida of having a fused rostrohypostomal plate is not a robust feature. In addition, *Hunanocephalus* Lee in Egorova et al., 1963 and *Taijiangocephalus* Yuan and Zhao in Yuan et al., 2002 (both belonging to the family Cheiruroideidae) have natant hypostomata similar to ptychoparioids (see Yuan et al. 2001, pl. 1, figs. 7, 8; Yuan et al. 2002, pl. 37, figs. 1, 4; Sundberg 2008). As further discussed in Sundberg’s (2014) additional analysis, these examples and other facts indicate that regarding the Corynexochida cannot be regarded as a monophyletic group but are polyphyletic as suggested by Robison & Babcock (2011). Its members are repeatedly derived from ptychoparioid stocks.

Family Chengkouiidae Zhu, 1980

[Chengkouidae Zhu in Zhang et al., 1980, p. 250]

Genus *Acanthomicmacca* Hupé, 1953a

Type species. Micmacca walcotti Matthew, 1899; from the upper lower Cambrian basal Brigus Formation, southeast Newfoundland; original designation by Hupé (1953a, p. 248).

Discussion. See Geyer (2016) for a comprehensive discussion and revision of the *Acanthomicmacca* clade.

Subgenus *Acanthomicmacca* (*Acanthomicmacca*) Hupé, 1953a

Type species. Micmacca walcotti Matthew, 1899, from the upper lower Cambrian basal Brigus Formation, southeast Newfoundland; original designation by Hupé (1953a, p. 248).

Acanthomicmacca (*Acanthomicmacca*) *franconica* Geyer, 2016

Fig. 124

v 1960 *Micmacca* sp. – Sdzuy: p. 108.
v 1960 *Micmacca sera* Sdzuy 1960 – Sdzuy: p. 108. [nom. nud.]
v 1960 *Micmacca* sp. – Emmert et al.: p. 75.
v 1976 *Micmacca* sp. – Horstig & Stettner: p. 51.
v 2009 *Micmacca sera* Sdzuy, 1960 – Basse: p. 23, 42. [nom. nud.]
v 2010 *Acanthomicmacca* sp. – Elicki & Geyer: p. 109.
v 2010 *Acanthomicmacca* sp. – Geyer: p. 81.
v * 2016 *Acanthomicmacca (Acanthomicmacca) franconica* n. sp. – Geyer: pp. 329, 361, 362–364, 384, fig. 13A–F, G–I?
v 2017 *Acanthomicmacca (Acanthomicmacca) franconica* – Geyer: pp. 6, 63, 64–65, fig. 27.

Studied material. Holotype, cranidium, SMF 79017, from locality W9; paratype, MMUW 2015B-120, from W14a; as well as four additional cranidia (SSMM 11498a, SSMM 11498b, SSMM 11504 and SSMM 11505, from locality W8). All from original material of Geyer (2017). Additional specimens: From locality W8 (cranidia under MMUW 2017D-132a, -169a, -205, -603a, -776-I and -776-II). Material from W8 and W9 from Wildenstein Member of the Tannenknock Formation; specimens from W14 from Galgenberg Member of the Tannenknock Formation.

Description and discussion. Acanthomicmacca (Acanthomicmacca) franconica has been introduced and described in a monographic study of the Chengkouiidae and the *Micmacca* group (Geyer 2016) and shortly discussed in the study on the trilobites of the Galgenberg Member. Therefore, it is only briefly described here for the completeness of the Wildenstein fauna and summarises the characterisation in Geyer (2017).

Acanthomicmacca (*A.*) *franconica* is characterised by a stout subrectangular glabella with a width/length ratio of ca. 0.65; a frontal lobe with gently curved anterior margin, but with an almost straight median section; by a short and slender terminal occipital spine; by eye ridges that are more than twice longer than broad; by long palpebral lobes directed slightly oblique to the axis and with gentle arcuation against the eye ridges; by a relatively low anterior border, which is gently convex in sagittal and exsagittal profile, but appear slightly upturned toward the anterior; and by a prosopon of the cuticle consisting of a dense meshwork of delicate crests.

Acanthomicmacca (*A.*) *franconica* is the only species of the genus known so far with a prosopon consisting of a meshwork of delicate crests similar to a longitudinally elongate honeycomb pattern (Fig. 124H). The glabella is characterised by a frontal lobe with a faintly curved median section of the anterior margin and by the presence of a short occipital spine in a terminal position. The slight longitudinal compression probably increases the median constriction visible in the holotype, but the anterior glabellar lobes and L1 were certainly distinctly broader than L2 during lifetime. The palpebral lobes are fairly long and directed slightly oblique to the axis, separated from the eye ridges by a slight arcuation. The anterior border is relatively low, but convex in transverse section.

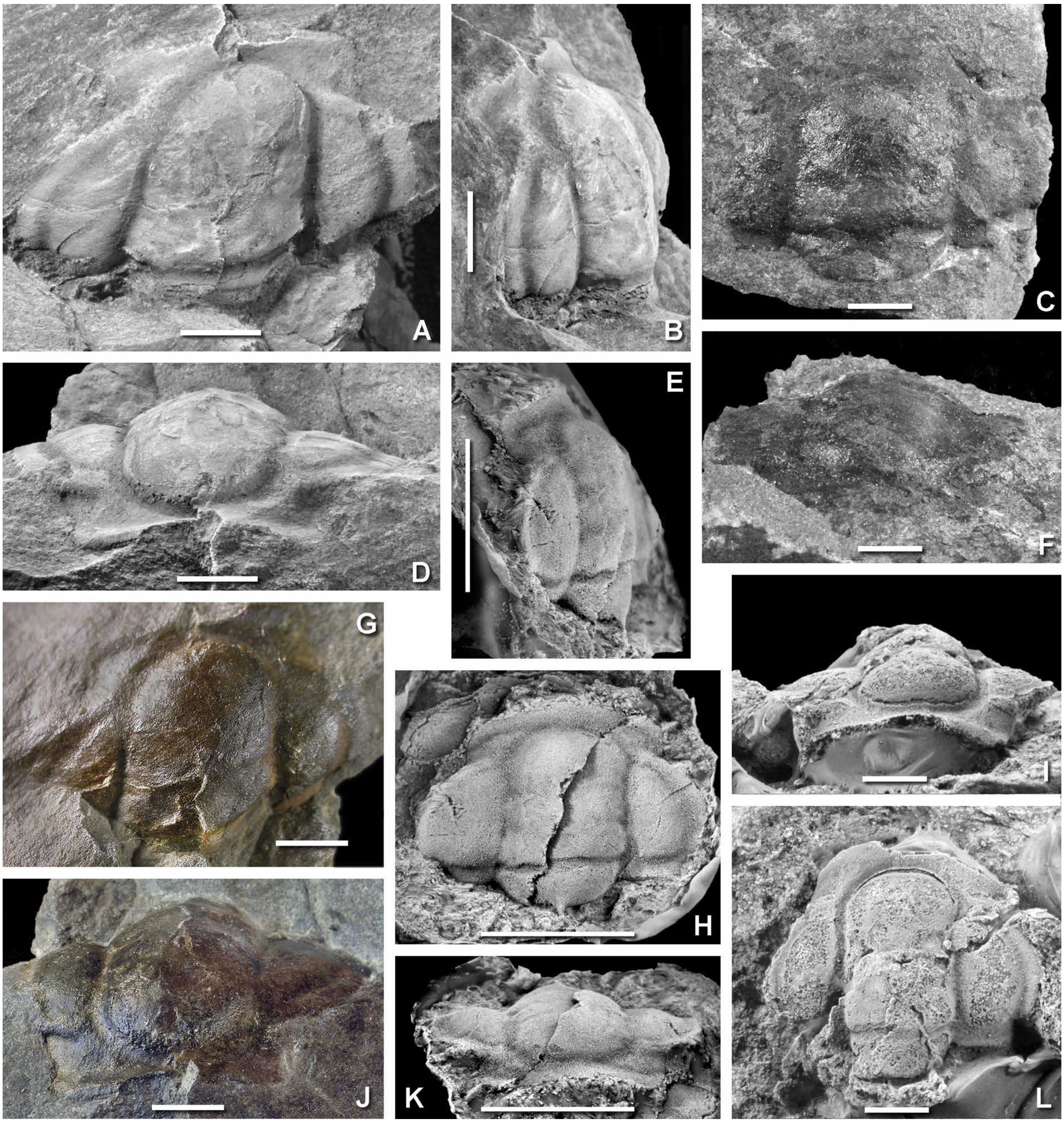


Fig. 124: *Acanthomicmacca* (*Acanthomicmacca*) *franconica* Geyer, 2016. **A, B, D** SSMM 10505-II, cranidium, latex cast of composite mould, dorsal (A), oblique lateral (B) and anterior (D) views; from locality W9; **C, F** SSMM 12405, incomplete cranidium, composite mould, dorsal (C) and anterior (F) views; from locality W9; **E, H, K** SMF 79017, holotype, cranidium, latex cast of external mould, oblique lateral (E), dorsal (H) and anterior (K) views; from locality W9; **G, J** SSMM 10505-I, incomplete cranidium, composite mould, dorsal (G) and anterior (J) views; from locality W9; **I, L** MMUW 2017D-132, small cranidium, internal mould, anterior (I) and dorsal (L) views; from locality W8.
Wildenstein Member, Tannenknock Formation. Scale bars 5 mm except in C, F, I and L (= 1 mm).

As discussed in Geyer (2017), species similar to *Acanthomicmacca* (*A.*) *franconica* are *A.* (*A.*) *neltneri* Hupé, 1953a and *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016, both from more or less coeval strata of the Jbel Wawrmast Formation in the Moroccan Atlas ranges. Both Moroccan species are distinguished from *A.* (*A.*) *franconica* by the granulation of their cuticle, narrower palpebral areas, and shorter palpebral lobes and eye ridges. The only other species of the genus known from Germany, *Acanthomicmacca* (*A.*) *anomocaroides* (Schmidt, 1944) from the middle Cambrian of the Delitzsch–Torgau–Doberlug Syncline, northern Saxony, clearly differs by its glabella with an almost evenly curved front, narrower palpebral areas and moderately long eye ridges.

Remarks on the stratigraphical range, facies and earlier reports. The holotype comes from the small quarry (locality W9) that exposes siltstone-dominated, slate-like rocks of the Wildenstein Member. This occurrence can be regarded as the type locality of the Wildenstein 'strata' or 'beds' of Wurm and Sdzuy and was thus believed to be characteristic for the Wildenstein facies of the Wildenstein Member of the Tannenknock Formation. The specimen was probably discovered around 1957, possibly by H. Klan, and loaned to K. Sdzuy who intended to use it for a description of the fauna. Obviously, Sdzuy prepared a manuscript and placed the specimen in repository of the Naturmuseum Senckenberg, Frankfurt am Main, under the name '*Micmacca sera* Sdzuy, 1960', but the article was never published, and the manuscript appears to be lost. However, the name was used in Sdzuy (1960).

A second relatively well preserved cranidium comes from the slightly older Galgenberg facies of the Galgenberg Member from locality W14 (Sdzuy's collective sample K) and was discovered in 1956, but remained in a collection box until it was unwrapped in 2014. It is thus puzzling why the identification of *Micmacca* sp. in the fossil lists for the Galgenberg 'strata' occurs in several publications (Sdzuy, 1960; Emmert et al. 1960; Horstig & Stettner 1976).

Dimensions. The holotype cranidium is 9 mm long (without occipital spine) and 13 mm wide, paratype cranidium MMUW 2015B-120 is 22 mm long and 30 mm wide. Specimen SSMM 10504 is 19 mm long and specimen SSMM 10505 21 mm long.

Superfamily Dorypygidacea Kobayashi, 1935

[nom. transl. herein ex Dorypygidae Kobayashi, 1935]

Family Dorypygidae Kobayashi, 1935

Dorypygid genus indeterminate

Dorypygid genus and species A

Fig. 125

Material. Cranidial fragments under SSMM 11036b, SSMM 11037f and SSMM 11189a; a pygidium tentatively assigned to this form under MMUW 2017D-100.

Localities and strata. All specimens from locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation.

Description. Both the cranidia and the pygidium of this form are fragmentary, and the lack of information on some of the characters does not allow confident assignments to a genus or species.

The cranidia show a glabella with subparallel lateral margins and a gently curved anterior margin of the frontal lobe, with faintly marked anterolateral corners and a slight constriction across S1. Its transverse convexity is moderate. Lateral glabellar lobes consist of shallow, faintly marked S1 and S2, both broad, and an indistinctly marked S3. The occipital furrow consists of relatively narrow, sharply incised lateral sections and a moderately well impressed median section, which curves anteriorly across the sagittal axis.

The palpebral areas are moderately convex, sloping ventrally towards the palpebral furrows, with a gently exsagittal convexity throughout. The palpebral lobes appear to have been short and upturned from the palpebral furrows. Visible is a low, obliquely directed and nearly straight eye ridge extending from near the origin of S3.

The axial furrows are narrow and sharp, but poorly indented. A moderately elevated, anterior border is located close to the anterior margin of the glabella so that a preglabellar field is lacking. The posterior border curves obliquely rearward from the axial furrow. The posterior border furrow is relatively broad and deep, growing in exsag. width abaxially.

The pygidium is only known from a fragment that allows little clues on the axial morphology. It shows part of the pleural areas which suggest the presence of three pleural ribs defined by well-developed interpleural furrows and shallow pleural furrows as visibly at the anterior pleural rib. The anterior border is well-defined, moderately broad (exsag.) and elevated, defined by a well-developed border furrow. The lateral border is low, barely defined from the shallow border furrow. Both are generally zigzagging, with the lateral border extended into short protrusions with curved tips.

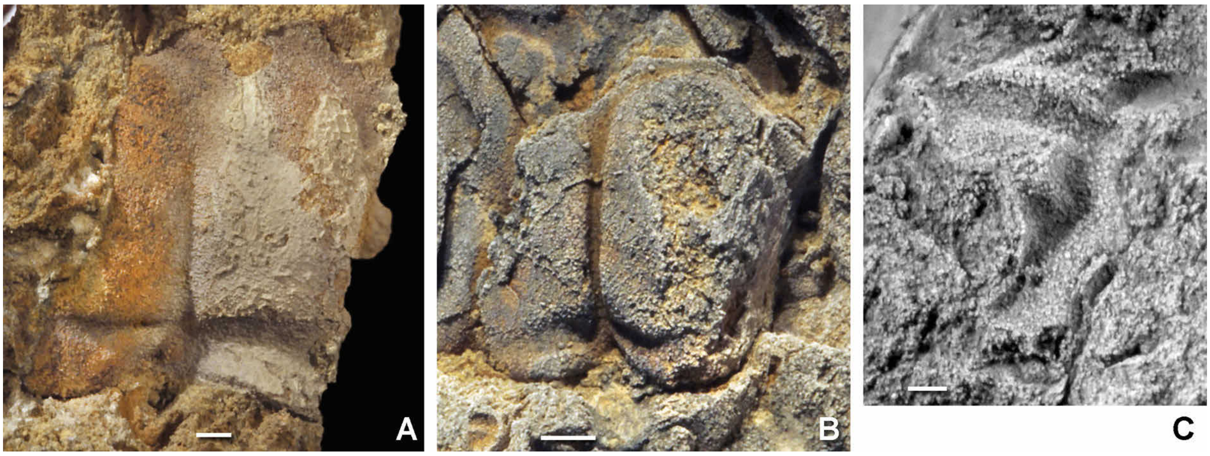


Fig. 125: Dorypygid genus and species indeterminate A. **A** SSMM 11189a, partial cranidium, internal mould; **B** SSMM 11036b, partial cranidium, internal mould; **C** MMUW 2017D-100, partial pygidium, internal mould. All specimens from locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation. All photos show dorsal views. Scale bars 1 mm.

Discussion. The convexity of the glabella and the configuration of the palpebral area with the short upturned palpebral lobe as well as the narrow anterior border and the absence of a preglabellar field and the pygidial pleurae and lateral border are typical for corynexochid genera, particularly those of the family Dorypygidae. However, the subparallel margins and the relatively moderate convexity distinguish the form from nearly all of the well-established dorypygid genera such as *Bonnia*, *Dorypyge*, *Kootenia*, or *Ogygopis*. Cranidia with well-preserved glabella and palpebral lobes are needed to identify the generic affinity.

Suborder Corynexochina Kobayashi, 1935

Discussion. Whittington (2009) discussed a few of the many problems related to the suborder Corynexochina. It is suggested here to restrict the suborder to the family Dolichometopidae Walcott, 1916, Corynexochidae Angelin, 1854, Zacanthoididae Swinnerton 1915, and Dinesidae Lermontova, 1940. Paedomorphic developments in this group obscures the recognition of true apomorphic characters

(McNamara 1986; Whittington 2007, 2009), and particularly the Corynexochidae apparently were rising by means of neoteny. However, stratigraphic occurrences of the various genera indicate that the evolutionary development in the suborder are not easily re-entangled. Further consideration to these problems lie outside the scope of this study and will be expressed elsewhere.

Family Corynexochidae Angelin, 1854

Discussion. The family Corynexochidae is an apparently easily recognisable grouping of trilobites, of which a number of genera are recognised. Its centre of distribution and diversity appears to be the palaeocontinent Sibiria, from which *Abakania* Poletaeva, 1973, *Corynexochina* Lermontova, 1940, *Corynexochella* Suvorova, 1964, *Eocorynexochus* Korobeynikova, 1965, *Milaspis* Sivov, 1960, *Miranella* Pokrovskaya, 1960, *Olinaspis* Suvorova, 1964, *Shivelicus* Pokrovskaya, 1959, *Sanaschtykgolia* Poletaeva, 1960 and *Trinia* Poletaeva, 1956 have been described. *Corynexochus* Angelin, 1854 and *Acontheus* Angelin, 1851 have first been described from Baltica. *Clavigellus* Geyer, 1994 is a genus from West Gondwanan Morocco, subsequently recorded from West Gondwanan Turkey (Dean 2005). *Bonnaspis* Resser, 1936 is a Laurentian genus. *Chatiania* Yang in Zhou et al., 1977 and *Eochatiania* Yuan & Yin, 1998 were first described from the South China/Yangtze continent, but *Chatiania* has been subsequently reported from the Lesser Himalaya (Peng et al. 2004). *Corynexochus* has developed into one of the most widespread genera of Cambrian trilobites with record from West Gondwanan southern France and Sardinia, Laurentian eastern Canada, the Canadian Cordillera, Alaska and North Greenland, South China and south-eastern Australia in addition to its first record from southern Sweden (Baltica). The Corynexochina have also been reported from South China.

The family has been split by authors from the Soviet Union and subsequently Russia in several subfamilies (e.g., Triniinae, Corynexochellinae Suvorova, 1964, Acontheinae, Milaspinae Suvorova, 1964, Abakaniinae Romanenko in Repina et al., 1999) based on strict character sets, e.g., according to the presence/absence of a facial suture and eyes, and the size and position of the palpebral lobes. Geyer (1994) in suggesting a phylogenetically-based taxonomy regarded the Triniinae and Corynexochellinae as synonyms of the Acontheinae. However, Repina et al. (1999) even united corynexochids with a proparian suture, palpebral lobes in an anterior position and small pygidia into a new family Milaspidae (with three subfamilies, Milaspinae, Triniinae and Abakaniinae). Such a separation of proparian and opisthoparian corynexochoids may be an appropriate differentiation, but it needs to consider the trend to a reduction of eyes and a marginalisation of the suture, and should avoid oversplitting which does not portray the phylogenetic developments within the group.

Corynexochid genus indeterminate

Corynexochid genus and species A

Fig. 126

Material. Two incomplete cranidia. In repository: SSMM 11181 and MMUW 2017D-538, both from locality W8. One partial cranidium, MMUW 2017D-642, from locality W6d tentatively assigned to this form.

Localities and strata. From locality W8, possibly locality W6d, Wildenstein slice. Wildenstein Member, Tannenknock Formation.

Description. Cranidium small, opisthoparian. Glabella considerably convex, clavate, extends to anterior border; lateral furrows effaced; front of glabella with a very low curvature to nearly straight, with a faint median indentation in the larger of the specimens which creates the impression of a pair of weakly indicated bulbs in dorsal view (Fig. 126A); occipital ring small, narrower (tr.) than or at best as wide as the posterior margin of L1, short (sag.). Fixigenae subtriangular in outline, moderately wide, with considerable convexity in exsagittal direction. Palpebral lobes very small, with length:width ratio of ca. 2 in the larger of the figured specimens (Fig. 126A), directed slightly oblique to longitudinal axis, placed at approximately one-third of the length of the glabella from front. Anterior border narrow, convex in sag. and exsag. profile, at a "basal" position in the topography of the cranidium.

Discussion. The very small cranidia found in the Wildenstein Member are best characterised by the more-or-less evenly expanding glabella with the almost straight anterior margin; the narrow (tr., sag.) occipital ring; the short palpebral lobes in some distance from the glabella; and the presence of a narrow anterior border anterior to the glabellar front. These characters distinguish this form from the Wildenstein Member from all established genera of the Corynexochidae and also from the otherwise similar genus *Corynexochus* Angelin, 1854, which, however, requires a reconsideration of some of the species assigned to it. The shape of the glabella and the size of the occipital ring also distinguishes the form from the Franconian Forest from *C. delagei* Miquel, 1905, which is one of the few palaeogeographically related corynexochids, known from the Montagne Noire region in southern France (Miquel 1905; Courtessole 1973; Álvaro & Vizcaïno 2000) and Iberia (Álvaro et al. 1999). The same differences are seen in a species described as *Corynexochus* sp. from the Çal Tepe Formation of the central Taurides in southern Turkey (Dean 2005).

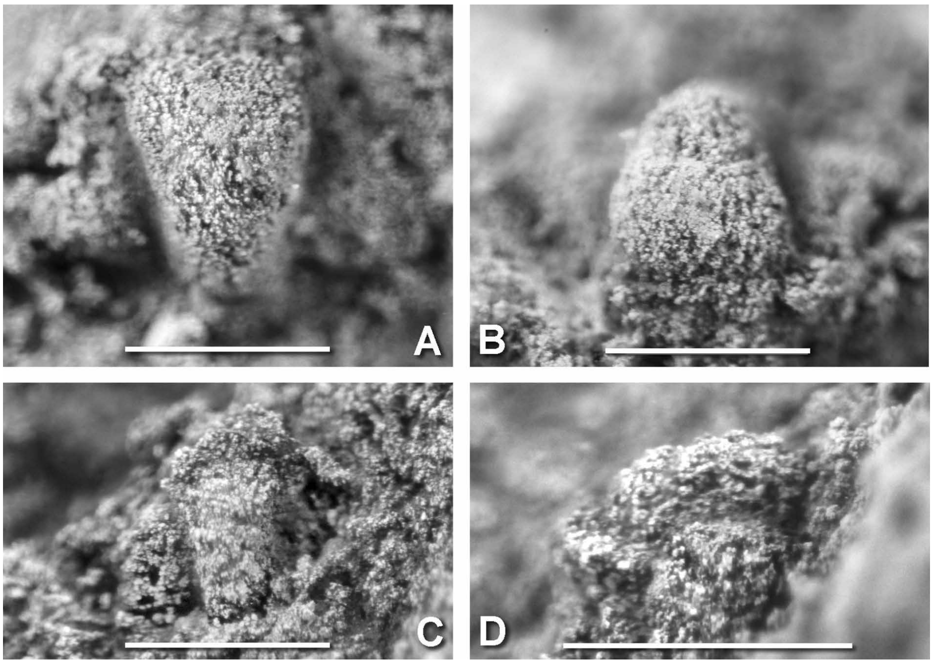


Fig. 126: Corynexochid genus and species indeterminate A. **A, B** SSMM 11181, incomplete cranidium, internal mould, dorsal (A) and anterior (B) views; from locality W8; **C, D** MMUW 2017D-538, partial cranidium, internal mould, dorsal (C) and lateral (D) views; from locality W7. From Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Indeterminate genus and species 1

Fig. 127

Material. Fragment of pygidium, MMUW 2017D-749.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A fragment of a pygidium with unusual morphological features is distinguished from all other pygidia of the Wildenstein trilobites. Preserved is the right side of the pygidium with pleural areas and lateral border and the marginal strip of the pygidial axis. The outline of the pygidium in dorsal view was probably slightly subtrapezoidal, with the posterolateral corners being in a slightly more abaxial position than the anterolateral corners, which have a more curved course of the margin. The anterior border is well-defined, moderately broad (exsag.) and directed almost perpendicular to the longitudinal axis, and it swings into an equally well-defined lateral margin at a faintly indicated arcuation. However, the lateral margin is continuously reduced in width towards posterior, and parallel to it the anteriorly well incised border furrow becomes shallower and fades completely at about two-thirds the pygidial length. The pleural area is only subdivided by one shallow pleural furrow and one very shallow interpleural furrow, which both curved distinctly rearward and fade short distance posterior and anterior (respectively) to the pygidial mid-length. Accordingly, pleural areas, lateral border and posterior border are completely fused in the posterior third of the pygidium.

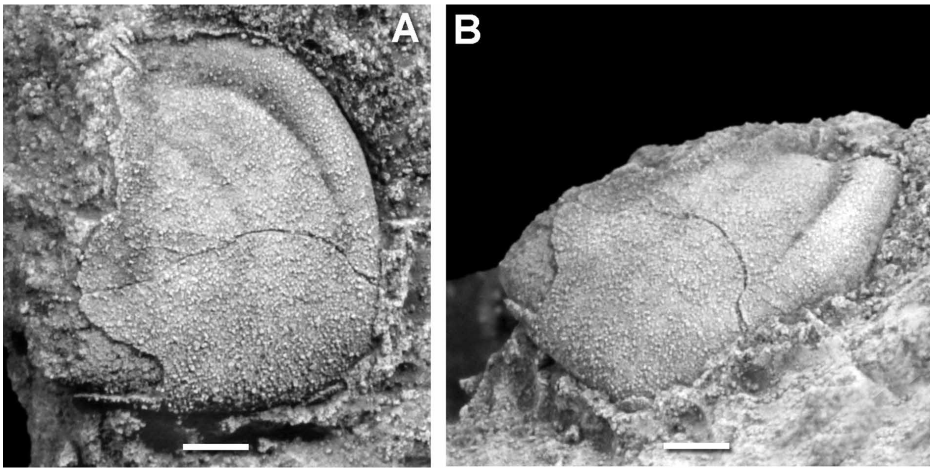


Fig. 127: Indeterminate genus and species 1. MMUW 2017D-749, fragment of pygidium, internal mould, dorsal (A) and lateral (B) views. From locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation. Scale bars 1 mm.

Although the shape of the axis is only vaguely indicated, it appears to have been moderately convex (with the convexity possibly growing rearward), moderately broad, faintly tapering and its posterior tip reaching (at least in dorsal view) to the posterior margin.

This systematic affinity of the pygidium is uncertain. Its length of ca. 6.5 mm and the even greater width in combination with the smoothened morphology of the pleural parts suggest that it very probably does not represent a ptychopariine trilobite. Some resemblance may be seen with paradoxidines, but an axis that reaches to the posterior margin of the pygidium is unknown from any of the described paradoxidines. Better preserved specimens will be needed for a confident taxonomic assignment.

Indeterminate genus and species 2

Fig. 128

Material. Fragment of pygidium, MMUW 2017D-109.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A fragment of a pygidium with unusual morphological features is clearly differentiated from all other pygidia of the Tannenknock Member. It has a subtrapezoidal outline with a curved posterior margin and an almost straight lateral margin, whereas the anterolateral corners tend to form small wing-shaped projections. The axis is very prominent, broad, and it tapers rearward. No subdivision of the axis is recognisable except for the broad (sag.) articulating half-ring defined by a broad transverse furrow. This half-ring has the appearance of an anterior axial ring. The pleural areas and the area posterior to the axis are shallow, slightly convex and devoid of any furrow or subdivision. No lateral or posterior border is indicated.

This pygidium is very unusual and at first glance may be mistaken even as a cranidium. However, the posterior view in Fig. 128C illustrates that it suffered a considerable deformation so that the axis is obliquely folded, with a resulting incision visible to affect the right side of the axis. Accordingly, the existing morphology should be taken with proviso, which is also indicated by the apparent character of the articulating half-ring. Insofar, the lateral margin of the pygidium may mimic an outline that differs to some degree from the original shape, and the convexity of the pleural areas may have undergone a considerable change as well. Nonetheless, there is no pygidium known to me that shows a high degree of conformity with the specimen from the Wildenstein Member.

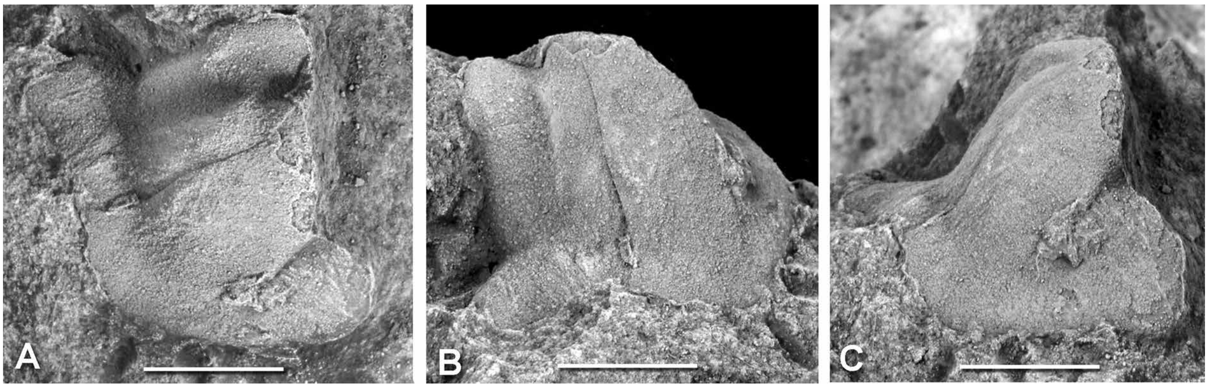


Fig. 128: Indeterminate genus and species 2. MMUW 2017D-109, fragment of pygidium, internal mould, dorsal (A), lateral (B) and posterior (C) views.
From locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation. Scale bars 5 mm.

Indeterminate genus and species 3

Fig. 129

Material. Incomplete librigenae, SSMM 11491.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A relatively large incomplete librigenae from the Wildenstein Member differs from all other known librigenae of the strata in being defined by quite long posterior and anterior sections of the facial suture. The posterior branch, which is complete preserved, is gently curved and passes posteriorly into the base of an apparently moderately long and robust genal spine. The anterior branch is preserved only at its basal part, which allows an estimation of the length. The lateral margin of the librigena is gently curved as well. A moderately broad lateral border with a low convexity is defined only by a poorly demarcated depression that represents the lateral border furrow. It borders a fairly broad (tr.) ocular platform. The visual surface was situated above a relatively well-developed flange, which turns up with a sharp turn from the ocular platform.

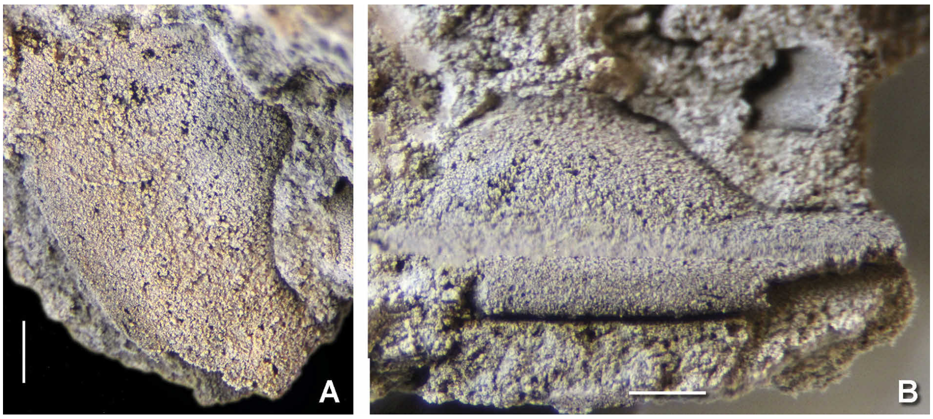


Fig. 129:
Indeterminate genus and species 3.
SSMM 11461a, partial librigena, internal mould, dorsal (A) and lateral (B) views. From locality W8, Wildenstein slice. Wildenstein Member, Tannenknock Formation. Scale bars equal to 1 mm.

The general shape and the relatively small size of the eye suggest that this librigena belongs to a ptychopariine trilobite of which other sclerites are unknown. However, the systematic position remains uncertain.

Indeterminate genus and species 4

Fig. 130

Material. Incomplete rostral plate, SSMM 11118b.

Locality and stratum. From locality W8, Wildenstein slice, Franconian Forest. Wildenstein Member, Tannenknock Formation.

Discussion. A minute sclerite from the Wildenstein Member is a slender, bent mould of a strap-shaped symmetrical plate, which grows slightly in width from its thin centre towards both ends. It shown a relatively well recognisable subcentral longitudinal rib as well as a rib that coincides with the frontal margin and a thinner rib close to the posterior margin so that these ribs were furrows on the surface. Both ends are slightly deflected and intact. Their nature indicates that this sclerite cannot be interpreted as the ventral doublure of the anterior border of a trilobite. It is highly probably that it represents a rare finding of a rostral plate.

Rostral plates are very seldom reported from most of the trilobites from the Cambrian Series 2 and the Miaolingian except for a few taxonomic groups with relatively large individuals. Thus, it remains uncertain from which group of trilobites this rostral plate may originate.

Fig. 130:
Indeterminate genus and species 4.
SSMM 11118b, rostral plate, external mould, dorsal view.
From locality W8, Wildenstein slice.
Wildenstein Member, Tannenknock Formation. Scale bar 1 mm.

8 Stratigraphic conclusions

8.1 Stratigraphic range of the Wildenstein Member

The trilobites recovered from the Wildenstein Member suggest that the entire member as known to date belongs to a single zone, the *Ornamentaspis frequens* Zone. It should be emphasised, however, that the lithofacies, the faunal composition and the frequency of fossils of the different localities vacillates considerably. This can be ascribed *pro parte* to sampling biases, but lithofacies mostly equals biofacies differences, as best seen in localities W8 and W9.

Although in most cases the localities appear to represent tectonically isolated microslices so that their present-day relative position does not indicate a stratigraphic relation, the two localities W8 and W9 (and the closely adjacent ones) most probably belong to a single tilted block so that the faunas may record a stratigraphical succession. Indeed, W8 unites faunas of the (probably uppermost) *Kingaspidoides frankenwaldensis* Zone (dealt with in Geyer 2017) and the *Ornamentaspis frequens* Zone. The faunas are intermingled as they were collected from loose material which turns up after plugging of the fields that form the eastern part of the locality, whereas a pure, astoundingly diverse *Ornamentaspis frequens* fauna is found in the typical Wildenstein rocks in calcareous nodules that underlie the unpaved road of the western margin of W8. At a short distance to the west lies the abandoned small quarry (locality W9), characterised by a slightly different faunal composition and siliciclastic rocks. Particularly noteworthy is that the fossils from W9 are often much larger and typically include a considerably higher amount of specimens of paradoxidids and *Kingaspis*. The larger size of the sclerites may be attributed to differences in the depositional environment and the sampling, but this cannot explain the change entirely. Accordingly, the rocks from W9 probably are the uppermost part of the Wildenstein Member and belong to the upper part of the *Ornamentaspis frequens* Zone. More complete successions may even be able to show that another, younger zone could be seen to start within these higher strata.

The boundary between the Galgenberg and the Wildenstein members is indicated by changes in lithology. However, this does not coincide precisely with the boundary between the *Kingaspidoides frankenwaldensis* and the *Ornamentaspis frequens* zones. Accordingly, this boundary appears to be diachronous, albeit to a small amount. It may be surprising to recognise the differences within such a small area, but it should be kept in mind that the present-day distribution of the Cambrian rocks in the Wildenstein and Triebenreuth slices does not correlate with the original extension of the area in which the strata were deposited. Both occurrences are wildflysch blocks in which the microslices have been accumulated, and the few reliable measurements of bed dip vary between 30 and 70º. Hence, the area of deposition represented in the small slices of roughly 1 x 2 km and 2 x 2 km would have been much larger thus allowing small-scale differences in depositional environments to be concentrated further.

8.2 Fine-scale stratigraphy and faunal associations in West Gondwana

The highest Lower to lower Middle Cambrian in traditional sense has been examined in numerous studies with a plethora of methods (e.g., Khalfin et al. 1960; Rasetti 1967; Chernysheva 1971; Sdzuy 1971, 1972, 1995; Fletcher 1972, 2003, 2006; Egorova et al. 1976; Robison et al. 1977; Palmer & Halley 1979; Palmer & James 1980; Bergström & Ahlberg 1981; Geyer 1983, 1990a, 1990b, 1990c, 1990d, 1998, 1999, 2005, 2015, 2017; Rozanov & Sokolov 1984; Palacios & Moczydłowska 1988; Liñán et al. 1992, 1993; Geyer & Landing 1995, 2000, 2004, 2006; Heldmaier 1997; Yuan et al. 1997, 2003; Landing & Westrop 1998b; Moczydłowska 1998a, 1998b; Orłowski et al. 1998; Brasier &

Sukhov 1998; Yuan & Li 1999; Geyer & Shergold 2000; Sundberg & McCollum 2000, 2003; Peng et al. 2000; Montañez et al. 2000, 2002; Korovnikov 2001, 2004; Sundberg et al. 2016, 2020, 2023; Yang & Yin 2001; Zhao et al. 2001, 2008, 2013, 2015, 2017, 2019; McCollum & Sundberg 2002; Landing et al. 2006, 2023; Clausen & Álvaro 2006; Gozalo et al. 2007; Rozanov et al. 2008; Yuan et al. 2009, 2016; Yin et al. 2009, 2016; Korovnikov et al. 2009; Żylińska & Szczepanik 2009; Webster 2011; Geyer & Peel 2011; Wotte et al. 2012; Geyer & Elicki 2012; Fatka & Szabad 2014; Pratt & Bordonaro 2014; Nielsen & Schovsbo 2015; Høyberget et al. 2015; Weidner et al. 2015; Korovnikov & Shabanov 2016; Singh et al. 2016; Palacios et al. 2017; Zhu et al. 2018; Chang et al. 2019; Lin et al. 2019; Karlstrom et al. 2020; Noriega-Ruiz et al. 2020; Cederström et al. 2022; Handkamer et al. 2022). However, these studies frequently contrast in their results. Traditionally, the occurrence of *Paradoxides* (s. l.) has been regarded as indicating a Middle Cambrian age, following the suggestion of Brøgger (1878). A complication arises from the fact that the first (=lowest) occurrence of *Paradoxides* (s. l.) is diachronous and takes place at considerably different stratigraphic levels even in neighbouring areas. This has been discussed in length in Geyer (2005). Accordingly, the FAD of *Paradoxides* s. l. (represented by *Acado-paradoxides* as the earliest genus of the group in West Gondwana and the majority of other *Paradoxides*-bearing regions) differs considerably even in neighbouring areas of West Gondwana, such as the Moroccan Atlas ranges of Morocco, the Iberian Chains in northern Spain, the Montagne Noire in southern France, south-western Sardinia in Italy, the Delitzsch–Torgau–Doberlug Syncline of Germany, the Taurides in southern Turkey, the Holy Cross Mountains in Poland, but also south-eastern Newfoundland (Western Avalonia) and southern Sweden (Baltica).

Fine-scale stratigraphic subdivisions of the faunal assemblages from these regions are of different resolution, depending on the diversity, richness and preservation of the faunas as well as the presence/ absence of hiatuses in the lithologic successions. An ongoing debate on the correlation and the resolution of such faunal assemblage between the Moroccan Atlas ranges and the Iberian Chains mainly results from the different quality of faunal preservation, but obviously also on different conceptions which themselves are influenced by the quality of the faunal elements (see Geyer 1998, Geyer & Vincent 2015, Geyer et al. 2019 vs. Gozalo et al. 2007, 2013 and Álvaro et al. 2017).

The search for a practical global boundary between the “Lower” and the “Middle Cambrian” has finally ignored all traditional (sub)global concepts. Eventually, a GSSP for the revised Middle Cambrian (=Series 3, now formally termed the Miaolingian) has been established at the FAD of *Oryctocephalus indicus* as seen in the sections of the Guizhou Province in South China, which more or less agrees with the traditional Lower–Middle Cambrian boundary in China, but postdates more-or-less all traditional boundary levels elsewhere. At least two trilobite zones in which *Acadoparadoxides* occurs are found below this level in the Anti-Atlas of Morocco, and at least one zone with *Acadoparadoxides* in other regions of West Gondwana (including the Holy Cross Mountains in Poland) and West Avalonia. Moreover, the exact level of the FAD of *Oryctocephalus indicus* is unknown from all of West Gondwana, Avalonia and Baltica so that the Cambrian Series 2–Miaolingian boundary in not known with certainty in these palaeocontinents.

As discussed elsewhere (e.g., Geyer 2017, Geyer et al. 2019), the Moroccan *Morocconus notabilis* Biozone correlates at least partly with the *Ovatoryctocara granulata* Biozone, which immediately underlies the *Oryctocephalus indicus* Zone in South China. Accordingly, the *Ornamentaspis frequens* Biozone in the Moroccan Atlas ranges probably correlates with the *Oryctocephalus indicus* Zone and thus represents the basal Miaolingian Cambrian Stage 5 (formally termed the Wuliuan). This, in turn, means that the *Kingaspidoides frankenwaldensis* Zone of the Franconian Forest correlates approximately with the *Ovatoryctocara granulata* Biozone and the uppermost Stage 4 whereas the *Ornamentaspis frequens* Biozone of the Franconian Forest correlates approximately with the *Oryctocephalus indicus* Zone and represents the lowermost Wuliuan.

Despite of cumulative faunal lists from the key regions of West Gondwana, no fine-scale correlations were attempted to date. These may help to elucidate regional variations in faunal turnover and significance of certain trilobite occurrences. Four key regions exist in West Gondwana for this stratigraphic interval: the Moroccan Atlas ranges (with particularly informative section in the Lemdad Syncline of the western High Atlas and the central and eastern Anti-Atlas); the Iberian Chains in northern Spain; the Taurid range in Turkey; and the Franconian Forest in Germany. They all record similar faunas, but with differences that can be ascribed to different causes.

8.2.1 Franconian Forest

The only relevant strata for the critical stratigraphic interval is the Tannenknock Formation. The trilobite fauna of the lower Galgenberg Member has been examined in Geyer (2017) with further comments in Geyer et al. (2019). The Wildenstein trilobites are described in this present study. Based on the assumptions discussed above, two slightly different assemblages are distinguished and listed in Fig. 131. Assemblage W2a is characterised by the occurrence of ellipsocephaline trilobites that are otherwise represented in the *Kingaspidoides frankenwaldensis* Zone and biofacies; assemblage W2b primarily by the absence of these faunal elements.

8.2.2 Iberian Chains

The Iberian Chains received the greatest attention among the regions with Cambrian rocks on the Iberian Peninsula. Comprehensive studies started with a monograph on the Cambrian trilobites of Spain by Sdzuy (1961), and the knowledge on the trilobite faunas increased since almost permanently. The lithostratigraphic units for the interval discussed here include a calcareous Ribota Formation, a shaly Huérmeda Formation, a coarsely siliciclastic Daroca Formation, and a Valdemiedes Formation (e.g., Gozalo et al. 2003). The latter is an example for the monotonous siltstone and fine-grained sandstone unit typical for the lower Middle Cambrian formations in the Mediterranean sector of West Gondwana, as elsewhere seen in other parts of the Iberian Peninsula, southern France, Sardinia, and Morocco.

The Cambrian Stage 4–Wuliuan interval in the Iberian Chains has moderately diverse faunal assemblages without considerable breaks. However, the duration of gaps and the morphological plasticity of trilobites has been controversially interpreted. This affects interregional and intercontinental correlation as well as the interpretation of the position of the Stage 4–Wuliuan boundary. Also, a regional stage scheme is used in Spain (Liñán et al. 1993) that partly obscures diachronism. In the following discussion, the taxonomy is updated to the presently best estimation.

Faunal assemblages relevant for this discussion start with a *Serrodiscus* assemblage which defines the base of the upper Marianian regional stage. This assemblage is not well represented in the Iberian Chains.

The base of the traditional Bilbilian regional stage is defined by the FAD of the trilobite genus *Realaspis*. This biozone is in fact a low diversity zone from which only *Realaspis strenoides* has been determined with certainty until a few years ago.

The next younger assemblage recognised in the Iberian Chains – still in the lower part of the Bilbilian Stage – is a *Protolenus dimarginatus* assemblage characterised by *Protolenus* (*Hupeolenus*) *dimarginatus* (Assemblage IC-2 in Fig. 132). This species was originally described from Morocco, where the earliest species of the subgenus *Hupeolenus*, *P.* (*H.*) *hupei* defines the base of the *Hupeolenus* Zone. *Protolenus* (*H.*) *dimarginatus* has a later onset, in the *Morocconus notabilis* Zone.

WULIUAN STAGE	AGDZIAN STAGE	*Ornamentaspis frequens* Zone	**Assemblage W2b**	*Kingaspis dolosus* n. sp. *Kingaspis* sp. A *Kingaspis* sp. B *Kingaspidoides* sp. aff. *destombesi* Geyer, 1990 *Kingaspidoides* sp. cf. *brevifrons* (Hupé, 1953) *Kingaspidoides frankenwaldensis* (Wurm, 1925) *Kingaspidoides wildensteinensis* n. sp. *Ornamentaspis frequens* Geyer, 1990 *Enixus* sp. aff. *juvenis* (Chernysheva, 1956) *Acadoparadoxides* sp. A *Eccaparadoxides* sp. A *Cambrophatictor meieri* n. sp. *Exapinepiphania wurmi* (Geyer, 2017) *Exapinepiphania* sp. A *Prioscutarius max* n. gen., n. sp. *Prioscutarius moritz* n. gen., n. sp. *Acanthomicmacca franconica* Geyer, 2016
			Assemblage W2a	*Condylopyge* sp. A *Peronopsis* (*P.*) sp. A *Dawsonia densiserrata* n. sp. *Tchernyshevioides*? sp. *Kingaspis dolosus* n. sp. *Kingaspis* sp. A *Kingaspidoides elegans* n. sp. *Kingaspidoides* sp. aff. *destombesi* Geyer, 1990 *Kingaspidoides* sp. cf. *brevifrons* (Hupé, 1953) *Kingaspidoides frankenwaldensis* (Wurm, 1925) *Kingaspidoides wildensteinensis* n. sp. *Ellipsostrenua*? sp. *Ornamentaspis frequens* Geyer, 1990 *Latikingaspis* sp. aff. *alatus* (Hupé, 1953) *Latikingaspis tenuis* n. sp. *Protolenus* (*P.*) *undulatus* n. sp. *Enixus* sp. aff. *juvenis* (Chernysheva, 1956) *Acadoparadoxides* sp. A *Eccaparadoxides* sp. A *Cambrophatictor meieri* n. sp. *Cambrodaimona parablepta* n. gen., n. sp. *Exapinepiphania wurmi* (Geyer, 2017) *Exapinepiphania* sp. A *Prioscutarius max* n. gen., n. sp. *Prioscutarius moritz* n. gen., n. sp. *Acanthomicmacca* (*A.*) *franconica* Geyer, 2016 Dorypygid gen. and sp. *Corynexochus*? sp.
STAGE 4		*Kingaspidoides frankenwaldensis* Zone	**Assemblage G1**	*Kingaspidoides frankenwaldensis* (Wurm, 1925) *Kingaspidoides alberti* Geyer, 2017 *Kingaspidoides meieri* Geyer, 2017 *Cambrosaurura*? sp. cf. *usitata* (Geyer, 1990) *Ornamentaspis* sp. cf. *crassilimbata* Geyer, 1990 *Latikingaspis* sp. aff. *alatus* (Hupé, 1953) *Enixus* sp. aff. *juvenis* (Chernysheva, 1956) *Acadoparadoxides* sp. A *Exapinepiphania wurmi* (Geyer, 2017) *Exapinepiphania parabolica* (Geyer, 2017) *Acanthomicmacca* (*A.*) *franconica* Geyer, 2016

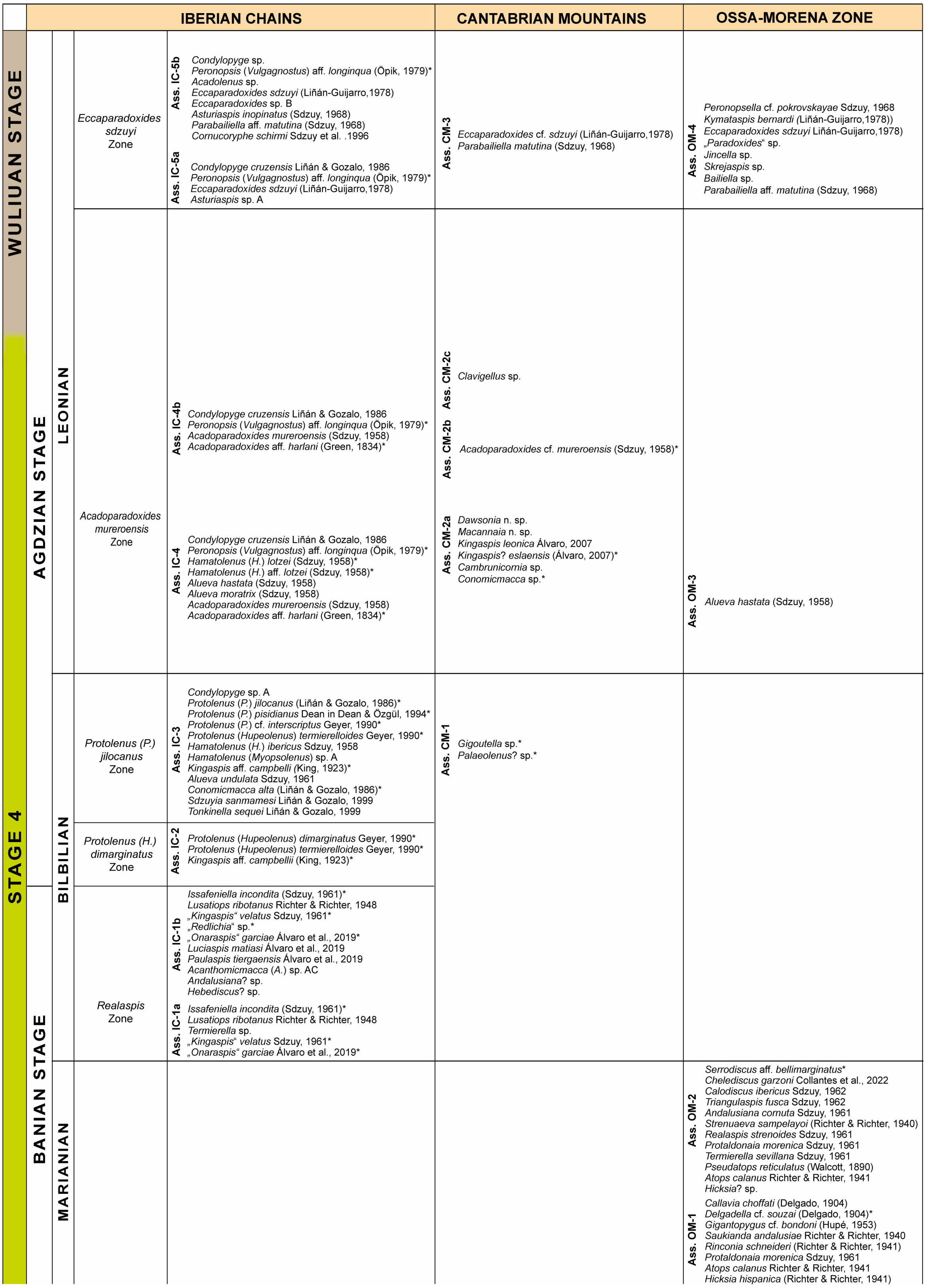
Fig. 131: Biostratigraphic levels for the Lower–Middle Cambrian boundary interval as seen in the trilobite assemblages of the Tannenknock Formation of the Franconian Forest and their bio- and lithostratigraphic position (with global and continental stages).

The biostratigraphy and trilobite ranges in that interval have been intricately studied so that there is little doubt that *P.* (*H.*) *dimarginatus* postdates *P.* (*H.*) *hupei* and partly also *P.* (*H.*) *termierelloides*, which in the Iberian Chains is believed to have the same onset as *P.* (*H.*) *dimarginatus*. Accordingly, the FAD of *P.* (*H.*) *dimarginatus* cannot be correctly correlated with the base of the *Hupeolenus* Zone in Morocco. Instead, the *P.* (*H.*) *dimarginatus* assemblage correlates with the assemblages of the lower to middle *M. notabilis* Zone, in which several species of *Acadoparadoxides* are found in the High Atlas and Anti-Atlas ranges. The only other trilobite species recognised in this zone was determined as *Kingaspis campbelli*, a species known from the Dead Sea region of Jordan. As discussed in Geyer & Landing (2020), the specimens identified from Spain as *K. campbelli* by Dies et al. (1999) and Liñán et al. (2003) and later reconfirmed in Dies et al. (2004), Gozalo et al. (2007, 2008), Liñán et al. (2004, 2008) and García-Bellido et al. (2011) are all distorted and cannot be identified with any certainty, but undoubtedly do not represent *K. campbelli*. Nevertheless, an authentic record of *K. campbelli* from Iberia appears to be that from the Valdoré section in the Cantabrian Mountains (Liñán et al. 2003).

A long neglected fauna in the Tierga region composed of similar trilobites has long been insufficiently described. Remarkably, this fauna from the middle and upper Ribota Formation and from the base of the Huérmeda Formation appears to bracket an interval from the middle Marianian up to the lower Bilbilian (Álvaro et al. 2019, Sepúlveda et al. 2022). It consists of *Issafeniella incondita*, *Lusatiops ribotanus*, "*Kingaspis*" *velatus* and "*Onaraspis*" *garciae* in the Ribota Formation (Assemblage IC-1a in Fig. 132) and a somewhat more diverse assemblage with *Hebediscus*? sp., *Andalusiana*? sp., *Issafeniella incondita*, *Lusatiops ribotanus*, *Pauliaspis tiergaensis*, *Luciaspis matiasi*, and *Acanthomicmacca* sp. in the lowermost Huérmeda Formation (Assemblage IC-1b in Fig. 132) and thus the lower Bilbilian. Interestingly, *Realaspis strenoides* has not been detected in those faunal assemblages. However, Sepúlveda et al. (2022) considered that *Realaspis strenoides* could in fact be poorly preserved specimens of "*Onaraspis*" *garciae*.

The upper Bilbilian regional stage was initially believed to match a *Hamatolenus ibericus* Zone when it was subsequently replaced by the *Protolenus jilocanus* Zone. However, its uppermost part is considered to be represented by an extended regional gap termed the "Valdemiedes event" (Liñán et al. 1992). The plausibility of this hiatus has been discussed in some detail in Landing et al. (2006). The trilobite assemblage of the *Protolenus jilocanus* Zone (Assemblage IC-3 in Fig. 132) includes, in addition to the nominal species, the *Kingaspis* species erroneously identified as *K. campbelli*, *Alueva undulata*, *Protolenus* (*P.*) cf. *interscriptus* (*P. interscriptus* known from the *M. notabilis* Zone of Morocco), *P.* (*P.*) *pisidianus*, *P.* (*H.*) *termierelloides*, *Hamatolenus* (*Myopsolenus*) sp., *Conomicmacca altus*, *Sdzuyia sanmamesi*, *Tonkinella sequei*, and an indeterminate oryctocephalid as well as the agnostine *Condylopyge* sp. This assemblage clearly correlates with the lower to middle part of the *M. notabilis* Zone in southern Morocco.

The traditional Middle Cambrian starts in the Iberian Chains above the Valdemiedes barren interval with the onset of *Acadoparadoxides mureroensis*, which also defines the base of the Leonian regional stage. The morphological plasticity and the problems in the identification of this species were subject to several publications (e.g. Geyer & Vincent 2015, Geyer et al. 2019c). The species defines the base of the eponymous zone, which comprises a considerable amount of strata in the Valdemiedes Formation. Other trilobites in the zone include *Alueva hastata*, *Alueva moratrix*, *Hamatolenus* (*Lotzeia*) *lotzei*, *Acadoparadoxides* cf. *harlani*, as well as the agnostines *Condylopyge cruzensis* and *Peronopsis* cf. *normata* [=*Peronopsis* (*Vulgagnostus*) aff. *longinqua*]. This fauna (Assemblage IC-4 in Fig. 132) appears to correlate with the upper part of the *M. notabilis* Zone in Morocco.



				IBERIAN CHAINS		CANTABRIAN MOUNTAINS		OSSA-MORENA ZONE	
WULIUAN STAGE	AGDZIAN STAGE	LEONIAN	*Eccaparadoxides sdzuyi* Zone	Ass. IC-5b	*Condylopyge* sp. *Peronopsis* (*Vulgagnostus*) aff. *longinqua* (Öpik, 1979)* *Acadolenus* sp. *Eccaparadoxides sdzuyi* (Liñán-Guijarro,1978) *Eccaparadoxides* sp. B *Asturiaspis inopinatus* (Sdzuy, 1968) *Parabailiella* aff. *matutina* (Sdzuy, 1968) *Cornucoryphe schirmi* Sdzuy et al. .1996	Ass. CM-3	*Eccaparadoxides* cf. *sdzuyi* (Liñán-Guijarro,1978) *Parabailiella matutina* (Sdzuy, 1968)	Ass. OM-4	*Peronopsella* cf. *pokrovskayae* Sdzuy, 1968 *Kymataspis bernardi* (Liñán-Guijarro,1978)) *Eccaparadoxides sdzuyi* Liñán-Guijarro,1978) „*Paradoxides*“ sp. *Jincella* sp. *Skrejaspis* sp. *Bailiella* sp. *Parabailiella* aff. *matutina* (Sdzuy, 1968)
				Ass. IC-5a	*Condylopyge cruzensis* Liñán & Gozalo, 1986 *Peronopsis* (*Vulgagnostus*) aff. *longinqua* (Öpik, 1979)* *Eccaparadoxides sdzuyi* (Liñán-Guijarro,1978) *Asturiaspis* sp. A				
STAGE 4			*Acadoparadoxides mureroensis* Zone	Ass. IC-4b	*Condylopyge cruzensis* Liñán & Gozalo, 1986 *Peronopsis* (*Vulgagnostus*) aff. *longinqua* (Öpik, 1979)* *Acadoparadoxides mureroensis* (Sdzuy, 1958) *Acadoparadoxides* aff. *harlani* (Green, 1834)*	Ass. CM-2c	*Clavigellus* sp.		
						Ass. CM-2b	*Acadoparadoxides* cf. *mureroensis* (Sdzuy, 1958)*		
				Ass. IC-4	*Condylopyge cruzensis* Liñán & Gozalo, 1986 *Peronopsis* (*Vulgagnostus*) aff. *longinqua* (Öpik, 1979)* *Hamatolenus* (*H.*) *lotzei* (Sdzuy, 1958)* *Hamatolenus* (*H.*) aff. *lotzei* (Sdzuy, 1958)* *Alueva hastata* (Sdzuy, 1958) *Alueva moratrix* (Sdzuy, 1958) *Acadoparadoxides mureroensis* (Sdzuy, 1958) *Acadoparadoxides* aff. *harlani* (Green, 1834)*	Ass. CM-2a	*Dawsonia* n. sp. *Macannaia* n. sp. *Kingaspis leonica* Álvaro, 2007 *Kingaspis*? *eslaensis* (Álvaro, 2007)* *Cambrunicornia* sp. *Conomicmacca* sp.*	Ass. OM-3	*Alueva hastata* (Sdzuy, 1958)
		BILBILIAN	*Protolenus (P.) jilocanus* Zone	Ass. IC-3	*Condylopyge* sp. A *Protolenus* (*P.*) *jilocanus* (Liñán & Gozalo, 1986)* *Protolenus* (*P.*) *pisidianus* Dean in Dean & Özgül, 1994* *Protolenus* (*P.*) cf. *interscriptus* Geyer, 1990* *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990* *Hamatolenus* (*H.*) *ibericus* Sdzuy, 1958 *Hamatolenus* (*Myopsolenus*) sp. A *Kingaspis* aff. *campbelli* (King, 1923)* *Alueva undulata* Sdzuy, 1961 *Conomicmacca alta* (Liñán & Gozalo, 1986)* *Sdzuyia sanmamesi* Liñán & Gozalo, 1999 *Tonkinella sequei* Liñán & Gozalo, 1999	Ass. CM-1	*Gigoutella* sp.* *Palaeolenus*? sp.*		
			Protolenus (H.) dimarginatus Zone	Ass. IC-2	*Protolenus* (*Hupeolenus*) *dimarginatus* Geyer, 1990* *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990* *Kingaspis* aff. *campbellii* (King, 1923)*				
	BANIAN STAGE		*Realaspis* Zone	Ass. IC-1b	*Issafeniella incondita* (Sdzuy, 1961)* *Lusatiops ribotanus* Richter & Richter, 1948 „*Kingaspis*“ *velatus* Sdzuy, 1961* „*Redlichia*“ sp.* „*Onaraspis*“ *garciae* Álvaro et al., 2019* *Luciaspis matiasi* Álvaro et al., 2019 *Paulaspis tiergaensis* Álvaro et al., 2019 *Acanthomicmacca* (*A.*) sp. AC *Andalusiana*? sp. *Hebediscus*? sp.				
				Ass. IC-1a	*Issafeniella incondita* (Sdzuy, 1961)* *Lusatiops ribotanus* Richter & Richter, 1948 *Termierella* sp. „*Kingaspis*“ *velatus* Sdzuy, 1961* „*Onaraspis*“ *garciae* Álvaro et al., 2019*				
		MARIANIAN						Ass. OM-2	*Serrodiscus* aff. *bellimarginatus** *Chelediscus garzoni* Collantes et al., 2022 *Calodiscus ibericus* Sdzuy, 1962 *Triangulaspis fusca* Sdzuy, 1962 *Andalusiana cornuta* Sdzuy, 1961 *Strenuaeva sampelayoi* (Richter & Richter, 1940) *Realaspis strenoides* Sdzuy, 1961 *Protaldonaia morenica* Sdzuy, 1961 *Termierella sevillana* Sdzuy, 1961 *Pseudatops reticulatus* (Walcott, 1890) *Atops calanus* Richter & Richter, 1941 *Hicksia*? sp.
								Ass. OM-1	*Callavia choffati* (Delgado, 1904) *Delgadella* cf. *souzai* (Delgado, 1904)* *Gigantopygus* cf. *bondoni* (Hupé, 1953) *Saukianda andalusiae* Richter & Richter, 1940 *Rinconia schneideri* (Richter & Richter, 1941) *Protaldonaia morenica* Sdzuy, 1961 *Atops calanus* Richter & Richter, 1941 *Hicksia hispanica* (Richter & Richter, 1941)

Fig. 132: Biostratigraphic levels and trilobite assemblages of the Lower–Middle Cambrian boundary interval (upper part of the Cambrian Stage 4 and Wuliuan) in the Iberian Chains, the Cantabrian Mountains and the Ossa-Morena Zone of Spain, with their bio- and lithostratigraphic position (with global and continental stages). Data from Liñán & Gozalo (1986), Gozalo et al. (1993, 2008, 2013), Sdzuy et al. (1999), Liñán et al. (2003, 2004, 2008), Gozalo (2017), Sepúlveda et al. (2022). The taxonomy of a number of reported species/forms is revised here against the latest taxonomy used in the listed publication. Such revised names are marked by an asterisk.

Only a small number of trilobites and agnostines are known from the overlying *Eccaparadoxides sdzuyi* Zone (=middle Leonian) in the Iberian Chains. In addition to the nominal species, these are *A. mureroensis*, *Acadolenus* sp. (in the upper part only), *Asturiaspis inopinatus* (in the upper part only), *Parabailiella* aff. *matutina* (in the upper part only), *Cornucoryphe schirmi* (in the upper part only), *Condylopyge cruzensis* and *Peronopsis* (*Vulgagnostus*) aff. *longinqua* (Assemblages IC-5a and IC-5b in Fig. 132).

Surprisingly, there is little resemblance of this fauna with that above the *M. notabilis* Zone in Morocco, i.e. that of the *Ornamentaspis frequens* Zone. Rather, the trilobites from the uppermost part of the *E sdzuyi* Zone show some degree of similarity with those of the *Kymataspis* Zone of the Moroccan Atlas ranges, which overlies the *O. frequens* Zone. In accordance, the fauna from the Wildenstein Member described herein also shows little similarity with the assemblages of the *E. sdzuyi* Zone.

8.2.3 Cantabrian Mountains

The Lower–Middle Cambrian succession in the Cantabrian Mountains of northern Spain is represented in the calcareous Láncara Formation. The faunal succession is known from various sections, but the assemblages have the characters of spotty collections to date. The biostratigraphically most useful assemblages have been recorded from the Valdoré section as preliminary notes (e.g., Gozalo et al. 2007, Sdzuy, unpublished data). An assemblage (assemblage CM-1 in Fig. 132) is portrayed by poorly known specimens which appear to represent *Palaeolenus*? and *Gigoutella* (known from Morocco). An assemblage with *Kingaspis leonica*, *Kingaspis*? *eslaensis*, *Cambrunicornia* sp. and *Myopsolenites* sp. (Álvaro, 2007 and unpublished data by K. Sdzuy) appears to be slightly younger and correlates with the *Morocconus notabilis* Zone faunas of the Moroccan Anti-Atlas (assemblage CM-2 in Fig. 132). *Acadoparadoxides mureroensis* has been identified as well, but its precise identity remains problematic. The genus *Clavigellus* occurs as well (as in the *M. notabilis* Zone in the High Atlas of Morocco and in the Taurus ranges of Turkey).

8.2.4 Ossa-Morena “Zone”

The Lower–Middle Cambrian succession in the Ossa-Morena “Zone” of southern Spain is represented in several spatially separated sections and has a character considerably different from that of the Iberian Chains. The lithostratigraphic succession of the relevant interval includes the shaly Santo Domingo Formation, the coarsely siliciclastic Castellar Formation and the Los Villares Formation, the latter representing the quite monotonous siltstone to fine-grained sandstone facies which is typical for the “lower Middle Cambrian” formations in the Mediterranean sector of West Gondwana.

Relatively rich trilobite assemblages are known from the shale unit that can be termed the Santo Domingo Formation and the more calcareous Alconera Formation, but has been subdivided into more-or-less coeval local members termed the Cumbres, Herrerías, La Hoya, Alanís and Benalija beds (e.g., Richter & Richter 1940, 1941; Gozalo et al. 2003; Liñán et al. 2004; Collantes et al. 2022a, b). This unit yields an assemblage with *Callavia choffati*, *Delgadella* cf. *souzai*, *Gigantopygus* cf. *bondoni*, *Saukianda andalusiae*, *Rinconia schneideri*, *Protaldonaia morenica*, *Atops calanus* and *Hicksia hispanica* (Assemblage OM-1 in Fig. 132), which is assigned to the middle Marianian Stage, and an upper assemblage with *Serrodiscus* aff. *bellimarginatus*, *Chelediscus garzoni*, *Calodiscus ibericus*, *Triangulaspis fusca*, *Andalusiana cornuta*, *Strenuaeva sampelayoi*, *Realaspis strenoides*, *Protaldonaia morenica*, *Termierella sevillana*, *Pseudatops reticulatus*, *Atops calanus* and *Hicksia*? sp. (Richter & Richter 1940, 1941; Sdzuy, 1961, 1962; Collantes et al. 2021a, 2021b, 2022; taxonomy updated herein), which represents the upper Marianian biota (Assemblage OM-2 in Fig. 132). These assemblages show moderate congruence with such from the upper Issafen Formation of the Banian Stage in the Anti-Atlas of Morocco and appear to indicate that the Ossa-Morena block rested in a significant distance from that of the Iberian Chains during the times of deposition.

The lower Bilbilian is probably still represented by the uppermost part of the Santo Domingo Formation in the Córdoba region, which is developed as supralittoral to restricted infralittoral environments (Liñán et al. 1993a). The Castellar Formation is a siliciclastic unit that features littoral to shallow sublittoral depositional conditions. Both are devoid of biostratigraphically useful fossils.

The Leonian (~ Agdzian) of the Ossa-Morena Zone (southern Spain) is represented by a 450+ m sequence of shales and sandstones with intercalated coarse siliciclastics of ca. 100 m thickness, represented by the Los Villares Formation (Liñán Guijarro 1978; Liñán et al. 1995; Perejón et al. 1996; Sdzuy et al. 1999). The formation yields *Alueva hastata* at its base (Assemblage OM-3 in Fig. 132), which suggests a correlation with the *Acadoparadoxides mureroensis* Zone of the Iberian Chains so that it represents the lower/early part of the Leonian stage. Additional trilobite assemblages throughout the formation indicate that the Los Villares Formation ranges up into the Caesaraugustan *Badulesia granieri* Zone (Liñán Guijarro 1978; Liñán et al. 1995, 2002, 2004a). Trilobites from the *Acadoparadoxides mureroensis* Zone of the formation in the Córdoba region are extremely sparse and poorly preserved so that they do not provide any useful biostratigraphic data.

The *Eccaparadoxides sdzuyi* Zone has a moderately diverse faunal assemblage at its base, which includes *Peronopsella* cf. *pokrovskayae*, *Kymataspis bernardi*, *Eccaparadoxides sdzuyi*, “*Paradoxides*” sp., *Jincella* sp., *Skrejaspis* sp., *Bailiella* sp. and *Parabailiella* aff. *matutina* (Liñán Guijarro 1978, taxonomy updated). This assemblage (Assemblage OM-4 in Fig. 132) clearly correlates with the *Kymataspis* Zone of the Agdzian Stage in Morocco and is thus younger than the Wildenstein fauna described herein.

8.2.5 The Moroccan High Atlas and Anti-Atlas ranges

The depositional history of the Stage 4–Wuliuan interval in the Moroccan High Atlas and Anti-Atlas ranges has been reconstructed in detail (Landing et al. 2006). It records a two-phased regressive–transgressive development with short episodes of non-deposition and considerable local to regional erosion as well as the formation of mildly condensed horizons. Nonetheless, the trilobite stratigraphy indicates that no gaps in gross stratigraphy took place. All relevant biozones (the *Sectigena*, *Hupeolenus*, *Morocconus notabilis*, *Ornamentaspis frequens* and *Kymataspis* zones) are interval zones so that the index fossils range into the overlying zone, which proves that no substantial gaps exist between them. The overlaps of index taxa are of different extent, being very thin for the *Sectigena* and *Hupeolenus* zones, but considerable between the *Hupeolenus* and the *M. notabilis*, and the *M. notabilis* and the *O. frequens* zones, respectively. Also, the thickness of rocks representing this zone differs enormously between the zones, but also shows regional differences. These differences are results of the sediment accumulation rate as well as the duration of the zones, which appears to have been quite short for the *Hupeolenus* Zone, but quite extended for the *M. notabilis* and moderately long for the *O. frequens* Zone. The *M. notabilis* Zone has been extensively investigated in a case study which indicates that it can be regionally subdivided into at least five subzones based on the occurrence of short-lived species of *Acadoparadoxides* (Geyer & Vincent 2015).

In summary, approximately seven assemblages can be recognised in the High Atlas and six assemblages in the central and eastern Anti-Atlas for the three zones that were originally connected to define the Agdzian Regional Stage (Geyer & Landing 2004). These are shown in Fig. 133 separately for the High Atlas, Central and Eastern Anti-Atlas and Western Anti-Atlas facies regions.

	HIGH ATLAS				CENTRAL & EASTERN ANTI-ATLAS		WESTERN ANTI-ATLAS
WULIUAN STAGE	**AGDZIAN STAGE**	*Ornamentaspis frequens* Zone	**Ass. HA-4b**	*Ornamentaspis frequens* Geyer, 1990 *Ornamentaspis crassilimbatus* Geyer, 1990 *Ornamentaspis* aff. *angustigena* Geyer, 1990 *Kingaspidoides* aff. *laetus* Geyer, 1990 *Condylopyge eli* Geyer, 1998 *Acadoparadoxides* sp. B *Kootenia beethoveni* Geyer, 1994 *Cambroproteus lemdadensis* Geyer, 2015 *Atopiaspis tikasraynensis* Geyer, 1998 *Prioscutarius? inconspicuus* (Geyer, 1998) *Prioscutarius dilatatus* (Geyer, 1998) *Cambrophatictor cataractis* Geyer, 1998 *Exapinepiphania lemdadensis* (Geyer, 1998) *Exapinepiphania* sp. A *Parabailiella* sp.	**Ass. AA-4c**	*Ornamentaspis destombesi* Geyer, 1990 *Kingaspidoides sarhroensis* Geyer, 1990 *Acadoparadoxides* sp. *Eccaparadoxides* sp. *Exapinepiphania* sp. B	
					Ass. AA-4b	*Ornamentaspis crassilimbata* Geyer, 1990 *Ornamentaspis destombesi* Geyer, 1990 *Ornamentaspis? kissanensis* Geyer, 1990 *Cambrosaurura? todraensis* Geyer, 1990 *Cambrosaurura usitata* (Geyer, 1990) *Kingaspidoides* aff. *laetus* Geyer, 1990 *Kingaspidoides spinirecurvatus* Geyer, Pais & Wotte, 2020 *Acadoparadoxides* sp. *Eccaparadoxides* sp. *Exapinepiphania* sp. B *Exapinepiphania* sp. C	*Acadoparadoxides* sp. D *Acadoparadoxides* sp. E *Parasolenopleura*? sp.
			Ass. HA-4a	*Latoucheia* (*L.*) *pusilla* Geyer, 1990 *Ornamentaspis frequens* Geyer, 1990 *Kingaspidoides* aff. *laetus* Geyer, 1990 *Latikingaspis sulcatus* Geyer, 1990 *Morocconus notabilis* (Geyer, 1988) *Condylopyge eli* Geyer, 1998 *Acadoparadoxides* sp. B *Exapinepiphania* sp. A	**Ass. AA-4a**	*Ornamentaspis destombesi* Geyer, 1990 *Cambrosaurura usitata* (Geyer, 1990) *Ornamentaspis? personata* Geyer, 1990 *Kingaspidoides* aff. *laetus* Geyer, 1990 *Condylopyge eli* Geyer, 1998 *Acadoparadoxides* sp. *Eccaparadoxides* sp. *Exapiepiphania* sp. B *Exapinepiphania* sp. C	*Kingaspis amouslekensis* Geyer, 1990 *Acadoparadoxides* sp. D *Acadoparadoxides* sp. E *Acanthomicmacca* (*A.*) sp. C
STAGE 4		*Morocconus notabilis* Zone	**Ass. HA-3c**	*Latoucheia* (*L.*) *pusilla* Geyer, 1990 *Latoucheia* (*L.*) *longicervix* Geyer, 1990 *Latoucheia* (*Pseudolenus*) *ourikaensis* (Hupé, 1953) *Protolenus* (*P.*) *densigranulatus* Geyer, 1990 *Protolenus* (*P.*) *interscriptus* Geyer, 1990 *Hamatolenus* (*H.*) *marocanus* (Neltner, 1938) *Latikingaspis alatus* (Hupé, 1953) *Latikingaspis sulcatus* Geyer, 1990 *Kingaspis* cf. *maroccana* (Gigout, 1951) *Morocconus notabilis* (Geyer, 1988) *Cobboldites tichkaensis* Geyer, 1988 *Pseudocobboldia pulchra* (Hupé, 1953) *Gigoutella atlasensis* Hupé, 1953 *Enixus? ornatus* (Geyer, 1998) *Acadoparadoxides nobilis* (Geyer, 1998) *Exapinepiphania* sp. A *Acanthomicmacca* (*A.*) *neltneri* (Hupé, 1953) *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016 *Acanthomicmacca* (*A.*) *rana* Geyer, 2016 *Acanthomicmacca* (*A.*) *mirandoides* Geyer, 2016 *Acanthomicmacca* (*A.*) *morrisoni* Geyer, 2016 *Oreisator tichkaensis* Geyer & Malinky, 2015 *Clavigellus annulus* Geyer, 1994	**Ass. AA-3c**	*Peronopsis* (*P.*) sp. *Morocconus notabilis* (Geyer, 1988) *Condylopyge eli* Geyer, 1998 *Kingaspidoides laetus* Geyer, 1990 *Kingaspidoides* aff. *laetus* Geyer, 1990 *„Kingaspidoides“ neglectus* Geyer, 1990 *Kingaspidoides larvalis* Geyer, 1990 *Ornamentaspis* cf. *destombesi* Geyer, 1990 *Kingaspidoides* cf. *angustigena* Geyer, 1990 *Cambrosaurura usitata* (Geyer, 1990) *Cambrosaurura bommeli* Geyer in Cederström et al., 2022 *Kingaspidoides* cf. *frankenwaldensis* (Wurm, 1925) *Kingaspis glabrata* Geyer, 1990 *Cambrosaurura robusta* Geyer in Cederström et al., 2022 *Latoucheia* (*L.*) *epichara* Geyer, 1990 *Latoucheia* (*Pseudolenus*) *ourikaensis* Geyer, 1990 *Hamatolenus* (*H.*) *marocanus* (Neltner, 1938) *Hamatolenus* (*H.*) *meridionalis* Geyer, 1990 *Hamatolenus* (*H.*) *vincenti* Geyer & Landing, 2006 *Protolenus* (*P.*) *densigranulatus* Geyer, 1990 *Cambrunicornia agdziensis* Geyer, 1990 *Cambrunicornia vanlooyi* Geyer, 1990 *Acadoparadoxides* cf. *mureroensis* Sdzuy, 1958 *Acadoparadoxides ovatopyge* Geyer & Vincent, 2015 *Acadoparadoxides briareus* Geyer, 1993 *Acadoparadoxides nobilis* (Geyer, 1998) *Eoptychoparia tafilaltensis* Geyer 2015 *Acanthomicmacca* (*A.*) *neltneri* (Hupé, 1953) *Shergoldiella vincenti* Geyer & Landing, 2004	*Morocconus notabilis* Geyer, 1988 *Hamatolenus* (*Myopsolenus*) *magnus* (Hupé, 1953) *Hamatolenus* (*Myopsolenus*) *staminops* (Hupé, 1953) *Kingaspis amouslekensis* Geyer, 1990 *Acadoparadoxides* sp. C *Bailiaspis*? sp.
			Ass. HA-3b	*Latoucheia* (*L.*) *pusilla* Geyer, 1990 *Protolenus* (*Protolenus*) *densigranulatus* Geyer, 1990 *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990 *Kingaspidoides obliquoculatus* Geyer, 1990 *Kingaspidoides* sp. C *Gigoutella atlasensis* Hupé, 1953 *Morocconus notabilis* (Geyer, 1988) *Cobboldites tichkaensis* Geyer, 1988 *Acadoparadoxides* cf. *nobilis* (Geyer, 1998) *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016 *Acanthomicmacca* (*A.*) *neltneri* (Hupé, 1953) *Amslamia rudkini* Geyer, 2016 *Iguidiella schaeri* Geyer, 2016	**Ass. AA-3b**	*Morocconus notabilis* (Geyer, 1988) *Peronopsis* (*P.*) sp. *Cobboldites* cf. *tichkaensis* Geyer, 1988 *Cambropallas telesto* Geyer, 1993 *Kingaspidoides brevifrons* (Hupé, 1953) *Kingaspidoides laetus* Geyer, 1990 *Kingaspidoides* aff. *laetus* Geyer, 1990 *Kingaspidoides borjensis* Geyer, 1990 *„Kingaspidoides“ neglectus* Geyer, 1990 *Latikingaspis alatus* (Hupé, 1953) *Kingaspidoides angustigena* Geyer, 1990 *Ourikaia calva* Geyer, 1990 *Latoucheia* (*L.*) *epichara* Geyer, 1990 *Latoucheia* (*Pseudolenus*) *ourikaensis* Geyer, 1990 *Hamatolenus* (*H.*) *marocanus* (Neltner, 1938) *Hamatolenus* (*H.*) *meridionalis* Geyer, 1990 *Hamatolenus* (*H.*) *vincenti* Geyer & Landing, 2006 *Hamatolenus* (*H.*) *draensis* (Hupé, 1953) *Protolenus* (*P.*) *densigranulatus* Geyer, 1990 *Acadoparadoxides pampalius* Geyer & Vincent, 2015 *Acadoparadoxides levisettii* Geyer & Vincent, 2015 *Granularaspis bommeli* Geyer, 2014 *Conomicmacca alta* (Liñán & Gozalo, 1986) *Onchocephalites permingeati* (Termier & Termier, 1950) *Acanthomicmacca* (*A.*) *neltneri* (Hupé, 1953) *Shergoldiella vincenti* Geyer & Landing, 2004	*Morocconus notabilis* Geyer, 1988 *Protolenus* (*Protolenus*?) sp. *Hamatolenus* (*Myopsolenus*) *magnus* (Hupé, 1953) *Hamatolenus* (*Myopsolenus*) *staminops* (Hupé, 1953) *Hamatolenus* (*H.*) *meridionalis* Geyer, 1990 *Acadoparadoxides* sp. C
			Ass. HA-3a	*Latoucheia* (*L.*) *pusilla* Geyer, 1990 *Protolenus* (*Protolenus*) *densigranulatus* Geyer, 1990 *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990 *Kingaspidoides obliquoculatus* Geyer, 1990 *Tchernyshevioides*? sp. *Calodiscus* sp. A *Acadoparadoxides* sp. *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016 *Strettonia* sp.	**Ass. AA-3a**	*Morocconus notabilis* (Geyer, 1988) *Tschernyshevioides* sp. *Protolenus* (*Hupeolenus*) *dimarginatus* Geyer, 1990 *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990 *Protolenus* (*Hupeolenus*) *hupei* Geyer, 1990 *„Kingaspidoides“ neglectus* Geyer, 1990 *Ourikaia calva* Geyer, 1990 *Latoucheia* (*Latoucheia*) *epichara* Geyer, 1990 *Latoucheia* (*Pseudolenus*) *ourikaensis* (Hupé, 1953) *Acanthomicmacca* (*A.*) sp. A *Acanthomicmacca* (*A.*) sp. B	*Issafeniella turgida* Geyer, 1990 *Strenuaeva nefanda* Geyer, 1990 *Protolenus* (*Protolenus*?) sp. *Hamatolenus* (*H.*) *meridionalis* Geyer, 1990 *Acanthomicmacca* (*A.*) aff. *coloi* (Hupé, 1953)
		Hupeolenus Zone	**Ass. HA-2b**	*Protolenus* (*Hupeolenus*) *hupei* Geyer, 1990 *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990 *Protolenus* (*Protolenus*) *densigranulatus* Geyer, 1990 *Acadoparadoxides* sp. *Kingaspidoides obliquoculatus* Geyer, 1990 *Kingaspis*? sp. *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016			*Geyerorodes schmitti* (Geyer, 1990) *Hamatolenus* (*H.*) *meridionalis* Geyer, 1990 *Protolenus* (*Hupeolenus*?) sp. *Acanthomicmacca* (*A.*) aff. *coloi* (Hupé, 1953)
			Ass. HA-2a	*Protolenus* (*Hupeolenus*) *hupei* Geyer, 1990 *Protolenus* (*Hupeolenus*) *termierelloides* Geyer, 1990 *Protolenus* (*Hupeolenus*) sp. A *Acadoparadoxides* sp. *Acanthomicmacca* (*A.*) *hupei* Geyer, 2016			
	BANIAN	*Sectigena* Zone	**Ass. HA-1d**	*Sectigena sdzuyi* Geyer, 1990 *Sectigena crassa* Geyer, 1990 *Berabichia* sp.			

Fig. 133: Biostratigraphic levels and trilobite assemblages of the Lower–Middle Cambrian boundary interval (upper part of the Cambrian Stage 4 and Wuliuan) in the High Atlas and Anti-Atlas ranges, Morocco and adjacent Algeria. Data from Hupé (1953a), Geyer (1988, 1990b, 1994, 1998, 2015, 2016), Geyer & Landing (2004), Geyer & Malinky (2017), Geyer & Vincent (2016), Geyer et al. (2020, 2021) and additional unpublished data from the author.

8.2.6 Taurides

Several occurrences of Cambrian trilobites have been reported from different areas in Turkey, but most of them achieved relatively little attention. Most of the occurrences come from the Taurides, where trilobites were described from at least eight different areas. The most instructive succession for this study comes from the Çal Tepe Formation of the central Taurides near Seydişehir in southern Turkey (Dean 2005).

The lowest assemblage from the black limestone member of the Çal Tepe Formation includes a fauna with (according to the determinations in Dean 2005) *Condylopyge matutina*, *Alueva venulosa*, *Antatlasia scabra*, *Pamphyliaspis nigra*, and (at the top) *Kingaspis* cf. *velata*, *Lusatiops*? sp., and *Strenuella*? sp.

Alueva venulosa is the most common species and can be regarded as the index fossil of the assemblage. It clearly is a species of *Hupeolenus* and thus treated here as *Protolenus* (*Hupeolenus*) *venulosus* (Dean, 2005). *Antatlasia scabra* in fact appears to be a kingaspidoid species, which is tentatively assigned to *Kingaspidoides* here. Interestingly, none of the species and forms persists into the overlying light-grey limestone member.

Two assemblages can be distinguished in the light-grey limestone member of the Çal Tepe Formation. The lower one includes (according to Dean 2005) *Hamatolenus* (*H.*) *altifrons*, *Alueva* cf. *hastata*, *Acadoparadoxides* (*A.*) *mureroensis* and *Clavigellus venustus*. This assemblage is recognised by Dean (2005) as the *Acadoparadoxides mureroensis* Zone. As for Assemblage 1, none of the species or forms persists upwards into the next assemblage.

Assemblage ÇT-3 from the upper part of the light-grey limestone member includes *Acadolenus*? sp., *Granularia* sp. (=*Granularaspis* sp.), *Acadoparadoxides* (*A.*) sp., *Dorypyge fimbriata*, *Sdzuyella* cf. *stremina* (=*Sdzuyella* aff. *stremina*), *Corynexochus* sp. and *Agraulos* sp. (=*Agraulos*? sp.). Only two horizons with more than a single species were known so that no zone is recognised for this stratigraphic interval above the *Acadoparadoxides mureroensis* Zone.

The overlying red nodular limestone member of the Çal Tepe Formation includes at least three discriminable assemblages. The lowest of these (Assemblage ÇT-4a) includes *Eccaparadoxides marginatus*, *Asturiaspis oezgueli*, *Dorypyge*? sp. and *Corynexochus* spp.; all species which range into a more diverse faunal assemblage (Assemblage ÇT-4b) with *Conocoryphe* (*C.*) *heberti*, *Pardailhania hispida*, *Parasolenopleura*? sp. and *Proampyx* sp. The diversity grows a bit further up, when *Acadolenus*? sp., *Olenoides*? sp., *Ellipsocephalus* sp., *Hartella antiqua* and a second species of *Pardailhania* sp. turn up.

The taxonomy of the trilobites suggested by Dean (2005) requires careful reconsiderations. *Alueva venulosa* Dean, 2005 is in fact clearly recognisable as a species of *Protolenus* (*Hupeolenus*) and is very closely related to *P.* (*H.*) *termierelloides* Geyer, 1990b from the *Hupeolenus* Zone of Morocco. The only striking difference recognisable from the specimens presented by Dean (2005) is a furrow on most of the anterior cranidial border stretching parallel to the anterior cephalic margin. The species from Assemblage ÇT-1 of the Çal Tepe Formation should therefore dealt with as *Protolenus* (*Hupeolenus*) *venulosus* (Dean, 2005). However, this only is valid for some of the holotype of the species (Dean 2005, pl. 1a, d) and a few other specimens illustrated by Dean (2005, pl. Ib, c, e, f, m?) and the specimen figured as *Lusatiops*? sp. (Dean 2005, pl. 1l).

Other specimens determined as *Alueva venulosa* are clearly distinguished by a strikingly upturned anterior part of the anterior border defined by a distinct furrow equivalent to that developed in *P.* (*H.*) *venulosa*, whereas the posterior part of the anterior border is low and often barely distinguishable from the preglabellar field (Dean 2005, pl. 1g, h, j, n?, o–q). Also, the glabella in those specimens is distinctly narrower. Accordingly, the morphology of these specimens resembles more closely that of *P.* (*H.*) *hupei* Geyer, 1990b, also from the *Hupeolenus* Zone of the Moroccan High Atlas. Nonetheless, the specimens from the Çal Tepe Formation are distinguished by the distinct (albeit low) posterior band of the anterior border, which is not developed in *P.* (*H.*) *hupei* and represent a different, new species. It is suggested to separate this species as *Protolenus* (*Hupeolenus*) *deani* n. sp. An appropriate diagnosis of *P.* (*H.*) *deani* is as follows:

> *Diagnosis.* Species of *Hupeolenus* glabella slender, maximum transverse width 30 percent of the maximum cranidial width across centre of palpebral lobes; anterior border consists in sag. and exsag. profile of a narrow, well elevated to prominent anterior lobe of subequal width along its course, defined posteriorly by a moderately broad (sag., exsag.) moderately indented groove and a low posterior band, which is slightly convex in sag. and exsag. profile and weakly defined by a shallow border furrow developed more-or-less inly as a change in convexity.
>
> *Holotype.* Cranidium NMW.95.34G.366, from Bed VII, Locality C.526.
>
> *LSID.* urn:lsid:zoobank.org:act:69AB705C-A193-4A37-A8AD-6D1E4A4E846A

The stratigraphic ranges of both species overlap, similar to the species of *Hupeolenus* in the sections of the High Atlas.

A partial cranidium from the assemblage was tentatively determined as belonging to *Kingaspidoides*, but this generic assignment cannot be maintained based on the observed character. The specimen appears to be a protolenine, but cannot be assigned to a genus with any certainty.

Antatlasia scabra Dean, 2005 from Assemblage ÇT-1 differs considerably from all (true) species of that genus. Its glabella has a clear kingaspidoid morphology as well as the configuration of eye ridges and palpebral lobes, similar to the arrangement in *Kingaspidoides*. The palpebral areas, however, resemble those typical for *Ornamentaspis*. The frontal area with fused preglabellar field, preocular areas and anterior border does neither match the configuration typical for *Kingaspidoides* nor *Ornamentaspis*. Utterly unique is the sculpture on the exterior of the cuticle consisting of imbricate ridges or small scales, partly following a larger pattern resembling short terrace ridges. The species may be regarded as representing a new genus as a morphological intermediate between *Kingaspidoides* and *Ornamentaspis*, but for this moment it is suggested to deal with it as *Kingaspidoides*? *scabra* (Dean, 2005).

Ornamentaspis? sp. from Assemblage ÇT-1 (Dean 2005, pl. 3a–d, f) is not an ellipsocephalid, but most probably a ptychopariine trilobite for which no genus has been erected yet.

Kingaspis cf. *velata* Sdzuy, 1961 is known from relatively poorly preserved cranidia, which almost certainly represent two different species. Dean's specimens figured on pl. 3i, l, m resemble *Kingaspis velata*, although no characters can be recognised which require the suggested identification. The specimen in Dean (2005, pl. 3e, g, h, j) have a slightly tapering glabella with a subacute front and should be kept separate from the other specimens.

The last trilobite from Assemblage ÇT-1 is a specimen identified by Dean (2005, pl. 3k) as *Strenuella*? sp., a strongly deformed trilobite, which in fact possibly represents *Protolenus* (*H.*) *deani* and certainly is not related to *Strenuella*.

Assemblage ÇT-2 has two quite typical endemic species of *Hamatolenus* and *Clavigellus*, introduced as *Hamatolenus* (*H.*) *altifrons* Dean, 2005 and *Clavigellus venustus* Dean, 2005. Both genera are typical and more-or-less restricted to the *M. notabilis* Zone in of Morocco. *Alueva*? cf. *hastata* (Sdzuy, 1958a) is based on poorly preserved specimens (Dean 2005, pl. 4s).

The identification of *Acadoparadoxides* (*A.*) *mureroensis* (Sdzuy, 1958a) is based on numerous partial sclerites (cranidia, hypostomata, librigenae and pygidia; Dean 2005, pl. 5a–p). All of them are comparatively small, and none of the cranidia and pygidia is complete enough to portray confidently the morphology. However, one partial cranidium (Dean 2005, pl. 5n) shows a palpebral lobe, which is wider (tr.) and shorter than that known from the type material of Spain, and the only known pygidium that suggests the outline (Dean 2005, pl. 5p) indicates similarities with the typical specimens of *A. mureroensis* but has a more slender shape with less rearwardly extending lateral margins than the typical pygidium of *A. mureroensis* from Spain. Summarised, the specimens from Assemblage ÇT-2 of the Çal Tepe Formation represent a species of *Acadoparadoxides* from the *A. mureroensis* clade, but should not be confused with that species. The evolutionary lineage seen in the *Morocconus notabilis* Zone of the eastern Anti-Atlas records the rapid change and the re-combination of features so that the presence of additional species elsewhere is not surprising.

Another species of *Acadoparadoxides* can be seen in Assemblage ÇT-3, which is known from better preserved and more complete cranidia (Dean 2005, pl. 6i, j, m, p). However, no pygidium has been found from the level in which the cranidium was collected so that Dean (2005) kept the form in open nomenclature. Nevertheless, this cranidium differs from the (erroneously identified) *A.* (*A.*) *mureroensis* specimens by a glabella with subparallel lateral margins in the posterior part and longer, drop-shaped palpebral lobes, which are not typical for the *mureroensis* clade. A single pygidium of probably *Acadoparadoxides* with a subelliptical outline was found in a somewhat lower level. Whether it belong to the species documented by the cranidia or not cannot be answered, but appears to be improbable when the size relationships are compared.

Acadolenus? sp. is only known from a single partial cranidium, which shows the characters known from *Protolenus* (*Protolenus*). Unfortunately, neither the anterior border nor the occipital ring are known so that the specimen should be identified as *Protolenus*? (*Protolenus*?) sp.

The incomplete cranidia determined as *Granularia* sp. (Dean 2005, pl. 4f, l) are characterised by a slender glabella and thus belong to the *Granularaspis dentata* plexus [see *G. dentata* (Romanenko in Repina & Romanenko, 1978)]. A somewhat similar species is *Granularaspis limbata* (Khayrullina in Repina et al. 1975), a species from the Tyan-Shan Range in Kyrgyzstan, which merits notion because of the joint occurrence of a species of *Sdzuyella* in both regions (see below).

Dorypyge fimbriata Dean, 2005 is an endemic species with a fairly early occurrence for species of this genus.

The specimen identified and illustrated as *Sdzuyella* cf. *stremina* indeed show a large extent of similarity with *Sdzuyella stremina* Khayrullina in Repina et al. 1975, an endemic species of the Tyan-Shan Range in Kyrgyzstan. The Turkish specimen has a larger (sag.) frontal area of the cranidium and narrower (tr.) palpebral areas, but certainly should be assigned to the same genus.

The specimens of *Corynexochus* sp. from Assemblage ÇT-3 indeed represent a species of this genus, apparently even closely related to *C. delagei* Miquel, 1905, known from southern France and Spain.

Cranidia identified by Dean (2005) as *Agraulos* sp. represent an agraulid species, which may be assigned to *Agraulos*, but differs from the type species and other typical species of the genus by the shape of the glabella with a gently curved front and a relatively broad anterior border. Unfortunately, the imperfect preservation does not permit recognition of the pattern of glabellar furrows, which are crucial for a confident determination.

Assemblages ÇT-4a and ÇT-4b obviously represent faunas of a somewhat younger age, probably middle to late Wuliuan. Thus, they are not discussed in detail herein. It is thus probable that a considerable hiatus or a gap in fossil record exists between the Assemblages ÇT-3 and ÇT-4a.

Summarised, three trilobite levels are exemplified by the Assemblages ÇT-1–ÇT-3 in the Çal Tepe Formation for the Lower–Middle Cambrian boundary interval.

8.3 Stratigraphical conclusion

The key trilobite assemblages identified from West Gondwana in this chapter provide a sound scenario and can be correlated quite confidently with assemblages from Baltica (see revised biostratigraphic schemes in Cederström et al. 2022) and western Avalonia (see Landing et al. 2023). They demonstrate transgressive–regressive sea-level changes during this period that were much more complicated than originally presumed in traditional Hawke Bay event models (Fig. 134). The Galgenberg and Wildenstein faunas from the Franconian Forest are important for the fine tuning of faunal turnovers during this interval.

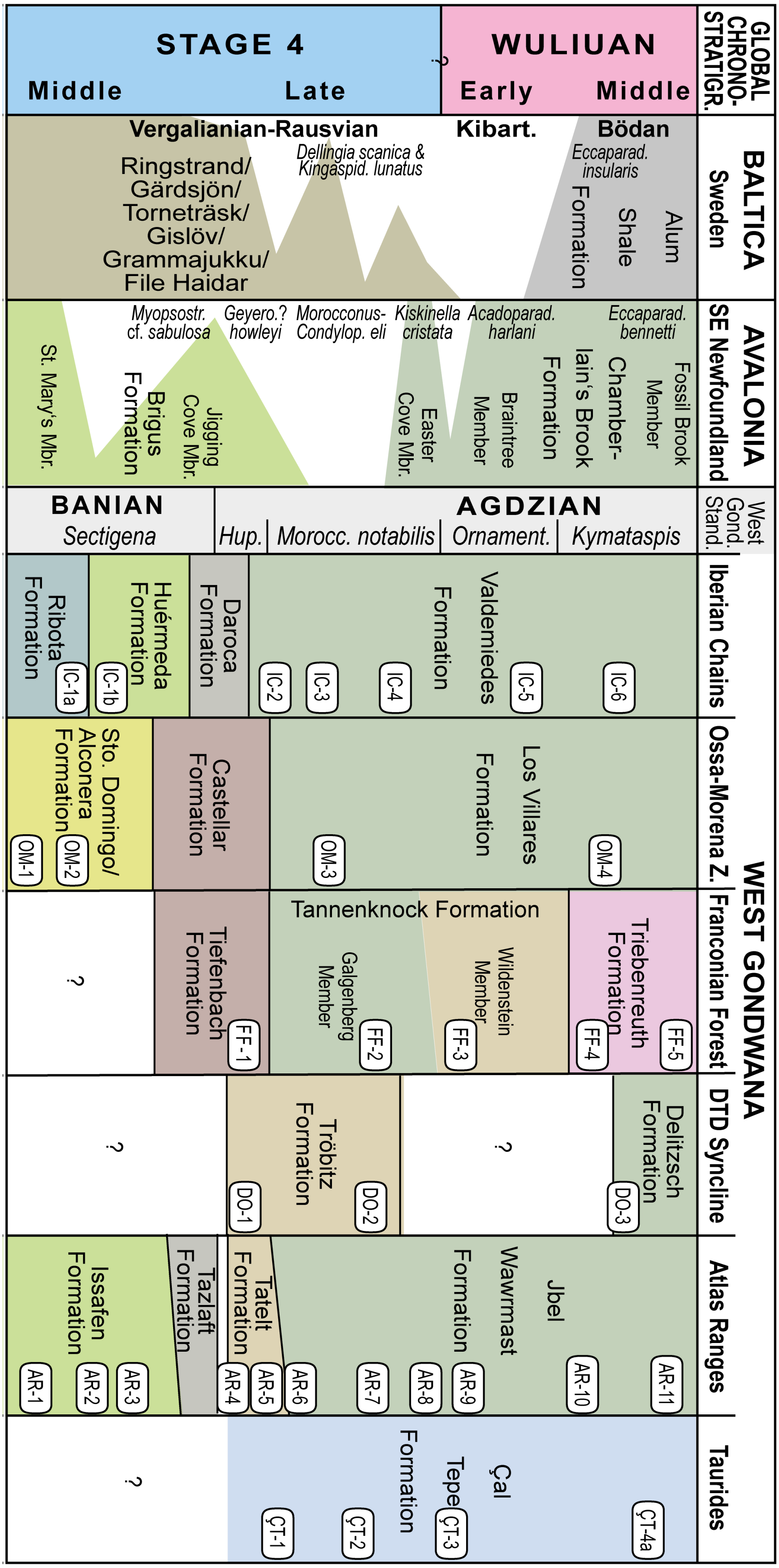


Fig. 134:
Correlation table of the Lower–Middle Cambrian boundary interval in Baltica, Western Avalonia and West Gondwana with position of key trilobite assemblages discussed in this study.

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Appendix A

Samples of Wildenstein facies relevant for the present study

Locality IDs starting with “W” or “T” and with Arabic numbers refer to the Wildenstein and Triebenreuth slices, respectively. Location indicated on the maps in Figs. 4 and 5.

Collectors are (in alphabetic order): Erwin Albert, Burgkunstadt (†); Josef Gandl, Würzburg; Gerd Geyer (author); Wolfgang Hammann, Würzburg (†); Peter Hickethier, Zedtwitz; Jörg Hiltl, Erlangen; Reverent S. G. Kohlmann, Stadtsteinach (†); Hermann Klan, Hof (†); Ed Landing, Albany, NY; Volkmar Ludwig, Würzburg (†); Stefan Meier, Marktredwitz; Bruno Paulus, Munich (†); Rudolf Richter, Frankfurt a. M. (†); Armin Rückert, Würzburg/Neuried; Klaus Sdzuy, Würzburg (†); Harald Tragelehn, Köln/Wallenfels (†); Wolfgang Trapp, Würzburg; Max Urlichs, Stuttgart; and Adolf Wurm, Munich/Würzburg (†). Some specimens in the SMF repository were collected by unidentified members of the University of Frankfurt a. M:

Sample ID*	Alternative sample ID(s)	Trilobites encountered	Remarks	Collector(s)
W1		*Kingaspidoides frankenwaldensis* *Kingaspidoides wildensteinensis* *Kingaspidoides alberti* *Ornamentaspis frequens* *Cambrophatictor meieri* *Cambrodaimona parablepta* *Exapinepiphania wurmi*	with subordinate amounts of Wildenstein facies	Geyer, Sdzuy
W1a	G	*Kingaspidoides* aff. *destombesi*? *Ornamentaspis frequens*? *Exapinepiphania wurmi* *Prioscutarius max*	relatively thick-bedded calcareous sandstone, resistant	Sdzuy
W3a		undetermined sclerites only		Geyer
W3b		undetermined sclerites only		Geyer
W6	D	*Kingaspidoides frankenwaldensis* *Kingaspidoides* cf. *brevifrons*? *Ornamentaspis frequens* *Acadoparadoxides* sp. A *Exapinepiphania wurmi*		Geyer, Sdzuy
W6a	E1, I 6	undetermined sclerites only		Geyer, Sdzuy
W6b	E2	*Kingaspidoides* cf. *frankenwaldensis* *Kingaspidoides*? sp. D? *Exapinepiphania*? sp. D?	partly in Galgenberg facies	Sdzuy
W6c		undetermined ellipsocephalid sclerites Corynexochid genus and species A		Sdzuy
W7		*Condylopyge* sp. A *Ornamentaspis frequens* *Cambrophatictor meieri* *Exapinepiphania wurmi* *Prioscutarius max*?		Sdzuy
W7a		undetermined sclerites only		Sdzuy
W7b	B	*Latikingaspis* aff. *alatus*? *Ornamentaspis frequens*? *Exapinepiphania wurmi*		Sdzuy

Sample ID*	Alternative sample ID(s)	Trilobites encountered	Remarks	Collector(s)
W8	Str	*Condylopyge* sp. A *Peronopsis* (*P.*) sp. A *Dawsonia densiserrata* *Tchernyshevioides*? sp. A *Kingaspis dolosus* *Kingaspis* sp. A *Kingaspidoides frankenwaldensis* *Kingaspidoides epimetheus* *Kingaspidoides* aff. *destombesi* *Kingaspidoides wildensteinensis* *Kingaspidoides* cf. *brevifrons* *Kingaspidoides* sp. A *Kingaspidoides*? sp. B *Kingaspidoides*? sp. C *Cambrosaurura* sp. indet.? *Latikingaspis* aff. *alatus*? *Ornamentaspis frequens* *Ornamentaspis*? sp. A *Protolenus* (*P.*) *undulatus* *Latoucheia*? (*L.*?) sp. A *Enixus* aff. *juvenis* *Acadoparadoxides* sp. A *Eccaparadoxides* sp. A *Eccaparadoxides* sp. B *Cambrophatictor meieri* *Cambrodaimona parablepta* *Exapinepiphania wurmi* *Exapinepiphania*? sp. A *Exapinepiphania* sp. B *Exapinepiphania* sp. C "*Exapinepiphania*" sp. D *Prioscutarius max* *Prioscutarius moritz* *Prioscutarius* sp. A *Prioscutarius*? sp. B Conocoryphid genus and species A Ptychopariine genus and species 1 Ptychopariine genus and species 2 Ptychopariine genus and species 3 Ptychopariine genus and species 4 Ptychopariine genus and species 5 Ptychopariine genus and species 6 Ptychopariine genus and species 7 *Acanthomicmacca* (*A.*) *franconica* Dorypygid genus and species A Corynexochid genus and species A	predominantly in Wildenstein facies	Geyer, Meier, Sdzuy
W8a	Weg II	*Condylopyge* sp. A *Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi*? *Ornamentaspis frequens* *Exapinepiphania wurmi* *Prioscutarius max* Ptychopariine genus and species 7		

Sample ID*	Alternative sample ID(s)	Trilobites encountered	Remarks	Collector(s)
W9	Stbr., Kleiner Steinbruch	*Kingaspis dolosus* *Kingaspis* sp. A *Kingaspis* sp. B *Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi* *Kingaspidoides wildensteinensis* *Kingaspidoides* cf. *brevifrons* *Kingaspidoides alberti* *Kingaspidoides*? sp. B *Latikingaspis tenuis* *Ornamentaspis frequens* *Enixus* aff. *juvenis* *Acadoparadoxides* sp. A "*Paradoxides*" sp. A *Eccaparadoxides* sp. A *Eccaparadoxides* sp. B *Cambrophatictor meieri* *Exapinepiphania wurmi* *Exapinepiphania* sp. C *Prioscutarius max* *Prioscutarius moritz* *Acanthomicmacca* (*A.*) *franconica*		Albert, Geyer, Klan, Kohlmann, Meier, Richter, Sdzuy, Urlichs, Wurm, unknown collector
W9a		*Kingaspidoides frankenwaldensis* *Exapinepiphania wurmi* *Exapinepiphania parabolica* ?		Klan?, Sdzuy
W9b	F	*Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi*? *Kingaspidoides*? sp. D *Cambrophatictor meieri* *Exapinepiphania wurmi* *Prioscutarius max*	mostly in Wildenstein facies	Sdzuy
W9c	II 8	Indeterminate sclerites only		Sdzuy
W9d	Grauwacke	*Kingaspis dolosus* *Enixus* aff. *juvenis* *Paradoxides* sp. A *Prioscutarius max* *Prioscutarius moritz* Ptychoparioid pygidium #4		
W10	WI	*Kingaspidoides frankenwaldensis* *Kingaspidoides wildensteinensis*? *Kingaspidoides* sp. A? *Eccaparadoxides* sp. A *Exapinepiphania wurmi* *Exapinepiphania* sp. B? *Exapinepiphania* sp. C		Geyer, Meier, Sdzuy
W11	Galgen II	*Kingaspidoides frankenwaldensis* *Kingaspidoides wildensteinensis* *Kingaspidoides alberti* *Latikingaspis* aff. *alatus* *Ornamentaspis frequens* *Enixus* aff. *juvenis* *Acadoparadoxides* sp. A? *Exapinepiphania wurmi* *Exapinepiphania* sp. C *Prioscutarius max*		Sdzuy

Sample ID*	**Alternative sample ID(s)**	**Trilobites encountered**	**Remarks**	**Collector(s)**
W11a	Galgen I	*Kingaspidoides* sp. indet. *Acadoparadoxides* sp. A? *Exapinepiphania wurmi* *Prioscutarius max*?		Sdzuy
W12		*Kingaspidoides frankenwaldensis* *Kingaspidoides* cf. *brevifrons* *Ornamentaspis frequens* *Acadoparadoxides* sp. A *Exapinepiphania wurmi*		Sdzuy
W12a		*Kingaspidoides frankenwaldensis* *Kingaspidoides* cf. *brevifrons* *Acadoparadoxides* sp. A *Cambrophatictor meieri*? *Exapinepiphania wurmi* *Prioscutarius max*		Sdzuy
W12c	Lichtung Iu	*Prioscutarius max*		Sdzuy
W12d		*Exapinepiphania wurmi*?		Sdzuy
W13a	i, iu	*Condylopyge* sp. A *Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi* *Kingaspidoides wildensteinensis* *Exapinepiphania wurmi* *Ornamentaspis frequens* *Acadoparadoxides* sp. A *Cambrophatictor meieri* *Parasolenopleura wurmi*?	partly in Galgenberg facies	Geyer, Sdzuy
W13b	j_1, j_2	*Kingaspidoides frankenwaldensis* *Ornamentaspis frequens* *Ornamentaspis*? sp. A *Acadoparadoxides* sp. A? *Cambrophatictor meieri* *Cambrodaimona parablepta* *Exapinepiphania wurmi* *Prioscutarius max* *Prioscutarius moritz*?	Wildenstein facies	Geyer, Sdzuy
W13e		*Condylopyge* sp. A *Kingaspis dolosus*? *Kingaspidoides* cf. *brevifrons*? *Ornamentaspis frequens* *Ellipsostrenua*? sp. A *Acadoparadoxides* sp. A? *Cambrophatictor meieri* *Cambrodaimona parablepta* *Exapinepiphania wurmi* *Exapinepiphania* sp. B? *Prioscutarius max*	predominantly in Wildenstein facies	Meier
W13f	H, H_2	*Peronopsis* (*Peronopsis*) sp. A *Kingaspidoides* sp. *Cambrophatictor meieri* *Cambrodaimona parablepta*	predominantly in Wildenstein facies	Geyer, Sdzuy
W14		*Ornamentaspis frequens* *Exapinepiphania wurmi*		Geyer

Sample ID*	**Alternative sample ID(s)**	**Trilobites encountered**	**Remarks**	**Collector(s)**
W14a		*Kingaspidoides*? sp. C? *Ornamentaspis frequens*? *Acadoparadoxides* sp. A *Exapinepiphania wurmi*? *Acanthomicmacca* (*A.*) *franconica*	partly in Galgenberg facies	Geyer
W14b		*Kingaspidoides* cf. *brevifrons* *Ornamentaspis frequens* *Acadoparadoxides* sp. A “*Paradoxides*” sp. A? *Exapinepiphania wurmi*		Geyer, Klan
W14c	K	*Cambrosaurura* sp. indet.		Sdzuy
W15		*Kingaspis dolosus* *Kingaspidoides* cf. *brevifrons*? *Ornamentaspis frequens* *Acadoparadoxides* sp. A		Geyer, Klan
W15a	N, N1	*Kingaspidoides* sp. cf. *brevifrons* *Ornamentaspis frequens* *Enixus* aff. *juvenis* *Acadoparadoxides* sp. A “*Paradoxides*” sp. A *Eccaparadoxides* sp. A? *Exapinepiphania wurmi*?		Geyer, Sdzuy, Klan
W15b	N2	*Kingaspidoides frankenwaldensis* *Latikingaspis* aff. *alatus*? *Exapinepiphania wurmi*		Geyer, Sdzuy
W15c		*Exapinepiphania wurmi*		Geyer
W15d	North of N2	*Kingaspidoides*? sp. B *Kingaspidoides* sp. C *Exapinepiphania wurmi*? *Prioscutarius max*?		Sdzuy
W16a	O 1	*Kingaspidoides frankenwaldensis* *Kingaspidoides wildensteinensis* *Ornamentaspis frequens* *Cambrophatictor meieri* *Exapinepiphania wurmi* *Prioscutarius max*		Geyer, Sdzuy
W16b	O II	*Kingaspidoides* sp. indet. *Exapinepiphania wurmi*?		Geyer, Sdzuy
W17	O III	*Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi* *Kingaspidoides* cf. *brevifrons* *Kingaspidoides* sp. A *Latikingaspis* aff. *alatus* *Ornamentaspis frequens* *Acadoparadoxides* sp. A *Cambrophatictor meieri* *Exapinepiphania wurmi* *Prioscutarius max*		Geyer, Sdzuy
W18		*Ornamentaspis frequens*? *Exapinepiphania*? sp. A		Geyer, Sdzuy

Sample ID*	**Alternative sample ID(s)**	**Trilobites encountered**	**Remarks**	**Collector(s)**
W18a	Q	*Condylopyge* sp. A *Kingaspidoides frankenwaldensis*? *Kingaspidoides* cf. *brevifrons* *Ornamentaspis frequens*? *Cambrophatictor meieri* *Exapinepiphania wurmi*? *Prioscutarius max*? Ptychopariine genus and species 3		Geyer
W19	P	*Kingaspidoides alberti*? *Ornamentaspis frequens*? *Exapinepiphania wurmi*		Sdzuy
W19a	P1	*Cambrophatictor meieri*? *Exapinepiphania wurmi* *Prioscutarius max*?		Sdzuy
W19b	Q	*Condylopyge* sp. A *Kingaspis* sp. B *Ornamentaspis frequens* *Cambrophatictor meieri* *Exapinepiphania wurmi*		Sdzuy
W21		Indeterminate sclerites only		Sdzuy
W22a	L1	Paradoxidid sclerites *Exapinepiphania wurmi*	partly in Wildenstein facies	Sdzuy
W22b	L2	*Exapinepiphania wurmi* Indeterminate sclerites	partly in Wildenstein facies	Sdzuy
W23	M	*Kingaspidoides* cf. *brevifrons* *Ornamentaspis frequens*? *Cambrophatictor meieri* *Exapinepiphania wurmi*	Galgenberg facies	Sdzuy
T1		*Kingaspidoides* aff. *destombesi*? *Kingaspidoides* cf. *brevifrons* *Kingaspidoides* sp. indet. *Acadoparadoxides* sp. A?	mostly in Wildenstein facies	Geyer, Meier, Sdzuy
T2		*Kingaspidoides frankenwaldensis* *Kingaspidoides* aff. *destombesi*? *Kingaspidoides* cf. *brevifrons* *Kingaspidoides*? sp. B *Acadoparadoxides* sp. A? *Exapinepiphania* sp. B *Exapinepiphania* sp. C	partly in Wildenstein facies	Geyer, Sdzuy
T2a		*Kingaspidoides alberti* *Ornamentaspis frequens* *Acadoparadoxides* sp. A? *Exapinepiphania wurmi* *Prioscutarius max*?	partly in Wildenstein facies	Geyer, Sdzuy
T2b		*Kingaspidoides* cf. *brevifrons*? *Kingaspidoides alberti* *Latikingaspis* aff. *alatus*? *Cambrophatictor meieri* *Exapinepiphania wurmi*?		Geyer, Sdzuy

Tabular systematic palaeontology index (for Chapter 7)

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		Suborder Agnostina Salter, 1864							30
			Superfamily Condylopygoidea Raymond, 1913						30
				Family Condylopygidae Raymond, 1913					30
						Genus *Condylopyge* Hawle & Corda, 1847			30
								Condylopyge sp. A	31
			Superfamily Agnostoidea M'Coy, 1849						34
				Family Peronopsidae Westergård, 1936					34
						Genus *Peronopsis* Hawle & Corda, 1847			34
							Subgenus *Peronopsis* Hawle & Corda, 1847		34
								Peronopsis (*Peronopsis*) sp. A	34
Class Trilobita Walch, 1771									37
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		Suborder Eodiscina Kobayashi, 1939							37
			Superfamily Eodicoidea Raymond, 1913						37
				Family Eodiscidae Raymond, 1913					37
						Genus *Dawsonia* Hartt in Dawson, 1868			37
								Dawsonia densiserrata n. sp.	38
				Family Hebediscidae Kobayashi, 1944a					44

Class	**Order**	**Suborder**	**Superfamily**	**Family**	**Subfamily**	**Genus**	**Subgenus**	**Species**	**Page**
						Genus *Tchernyshevioides* Khayrullina in Repina et al., 1875			44
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			Superfamily Ellipsocephalacea Matthew, 1887b						45
				Family Ellipsocephalidae Matthew, 1887b					46
					Subfamily Ellipsocephalinae Matthew, 1887b				47
						Genus *Kingaspis* Kobayashi, 1935			50
								Kingaspis dolosus n. sp.	54
								Kingaspis sp. A	58
								Kingaspis sp. B	60
						Genus *Kingaspidoides* Hupé, 1953a, emend. Geyer 1990b			62
								Kingaspidoides frankenwaldensis (Wurm, 1925b)	64
								Kingaspidoides epimetheus n. sp.	71
								Kingaspidoides sp. aff. *destombesi* (Geyer, 1990b)	74
								Kingaspidoides wildensteinensis n. sp.	78
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Class	Order	Suborder	Superfamily	Family	Subfamily	Genus	Subgenus	Species	Page
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								Cambrosaurura sp. indet.	96
						Genus *Latikingaspis* Geyer, 1990b			97
								Latikingaspis sp. cf. *alatus* (Hupé, 1953a)	98
								Latikingaspis tenuis n. sp.	100
						Genus *Ornamentaspis* Geyer, 1990b			103
								Ornamentaspis frequens Geyer, 1990b	103
								Ornamentaspis? sp. A	109
						Genus *Ellipsostrenua* Kautsky, 1945			110
								Ellipsostrenua? sp. A	111
						Genus *Germaropyge* Šnajdr, 1957			112
								Germaropyge germari (Barrande, 1852)	114
					Subfamily Protoleninae Richter & Richter, 1948				115
						Genus *Protolenus* Matthew, 1892			115
							Subgenus *Protolenus* (*Protolenus*) Matthew, 1892		115
								Protolenus (*Protolenus*) undulatus n. sp.	115
						Genus *Latoucheia* Hupé, 1953a			118
								Latoucheia? (*Latoucheia*?) sp. A	118
				Family Palaeolenidae Hupé, 1953a					119
						Genus *Enixus* Özdikmen, 2009			119
								Enixus sp. aff. *juvenis* (Chernysheva, 1956)	119
			Superfamily Paradoxidacea Emmrich, 1839						123

Class	**Order**	**Suborder**	**Superfamily**	**Family**	**Subfamily**	**Genus**	**Subgenus**	**Species**	**Page**
				Family Paradoxididae Emmrich, 1839					123
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						Genus *Acadoparadoxides* Šnajdr, 1957			123
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						Genus *Cambrophatictor* Geyer, 1998			137
								Cambrophatictor meieri n. sp.	138
						Genus *Cambrodaimona* n. gen.			145
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			Superfamily Solenopleuracea Angelin, 1854						150
				Family Solenopleuridae Angelin, 1854					150
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						Genus *Solenopleura* Angelin, 1854			159
								Solenopleura holometopa (Angelin, 1851)	161
								Solenopleura westergaardi n. nom.	163

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						Genus *Erratojincella* Rudolph, 1994			164
								Erratojincella brachymetopa (Angelin, 1851)	164
								Erratojincella sp. cf. *brachymetopa* (Angelin, 1851)	167
								Erratojincella nigra Rudolph, 1994	169
								Erratojincella? *munsteri* (Strand, 1929)	171
						Genus *Foveatella* Rudolph, 1994			173
								Foveatella bucculenta (Grönwall, 1902)	175
						Genus *Gonzaloia* Geyer, 1998			176
								Gonzaloia canaliculata (Angelin, 1851)	178
						Genus *Parasolenopleura* Westergård, 1953			179
								Parasolenopleura aculeata (Angelin, 1851)	181
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						Genus *Exapinepiphania* n. nom.			184
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								Exapinepiphania sp. B	203
								Exapinepiphania sp. C	205
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								Exapinepiphania cristata (Linnarsson, 1877)	212
								Exapinepiphania sp. aff. *cristata* (Linnarsson, 1877)	215
								Exapinepiphania pauperata (Walcott, 1906a)	217
								Exapinepiphania? *acidalia* (Walcott, 1906a)	218

Class	Order	Suborder	Superfamily	Family	Subfamily	Genus	Subgenus	Species	Page
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								Jincella? *acadica* (Whiteaves in Matthew, 1885)	225
								Jincella? *alata* (Matthew, 1888)	226
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