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Exotic trilobites from the uppermost Cambrian Series 3 and lower Furongian of Sweden

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ABSTRACT:

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Seventeen taxa of exotic trilobites representing eight families are described from the olenid- and agnostoid-dominated strata of the uppermost Cambrian Series 3 and lower Furongian alum shale facies of Sweden and from glacial erratic boulders of Denmark. Only five taxa are assigned to species level, i.e., *Maladioidella abdita* (Salter, 1866), *Olentella rara* (Westergård, 1922), *Pedinocephalus peregrinus* (Henningsmoen, 1957), *Ptychoparia pusilla* (Westergård, 1922), and *Westergaardella olenorum* (Westergård, 1922), whereas the others are left under open nomenclature or remain unrecognized. Most are described for the first time from the Cambrian of Scandinavia. Their affinities point to a strong connection with East Gondwana, Laurentia, Kazakhstania and Siberia. Exotic trilobites appear in the succession directly after periods of very low oxygen concentration in the Alum Shale Sea; their occurrences correspond to the ranges of agnostoid arthropods in the succession and seem to be linked to global transgressive events causing an influx of cool and/or oxygen-depleted waters onto the shelf of the Baltica palaeocontinent.

Key words: Trilobita; Cambrian Series 3; Furongian; Alum Shale; Glacial erratic boulders; Sweden; Denmark; Scandinavia; Exotic trilobites.

INTRODUCTION

The uppermost Cambrian Series 3 and Furongian alum shales of Scandinavia are characterized by olenid trilobites, which may occur in immense numbers (Bergström and Gee 1985). Agnostoid arthropods are common in the uppermost part of Cambrian Series 3 and in the lowermost Furongian, but generally become rare at higher levels (Terfelt *et al.* 2011; Ahlberg and Terfelt 2012). The succession also yields rare representatives of non-olenid trilobites, referred to as 'invaders' (Conway Morris and Rushton 1988), 'exotics' (Żylińska *et al*. 2004; Weidner and Żylińska 2005; Terfelt and Ahlgren 2007; Żylińska and Weidner 2012, 2013) or 'immigrants' (Terfelt 2006; Terfelt and Ahlgren 2009). Specimens collected over the last 25 years from a number of localities in Sweden (by TW and JA) and glacial erratic boulders in Denmark (by TW) allow a detailed taxonomic study for the first time. Their biogeographical significance and appearances in the succession are discussed herein with an attempt to tie the occurrences to global events. The study is based on specimens of non-olenid trilobites from the uppermost Cambrian Series 3 *Agnostus pisiformis* Zone[1] and the lower part of the Furongian (*Glyptagnostus reticulatus* Zone to the lower part of the *Pseudagnostus cyclopyge* Zone in the agnostoid biozonation after Terfelt *et al.* 2008); this interval is equivalent to the *Agnostus pisiformis* Zone and the *Olenus* and *Parabolina* superzones in the revised scheme of Nielsen *et al.* (2014). The original specimens of *Acrocephalites* (?) *rarus* Westergård, 1922 and *Taenicephalus*? *peregrinus* Henningsmoen, 1957 from Västergötland, Sweden, *Liostracus pusillus* Westergård, 1922 and *Conokephalina olenorum* Westergård, 1922 from Scania, Sweden, as well as a number of specimens from glacial erratic boulders collected in Denmark are re-illustrated for the first time since their original descriptions (Westergård 1922; Henningsmoen 1957b; Rudolph 1997; Weidner 2001).

ALUM SHALES AND THEIR FAUNAL COMPOSITION

The alum shales of Scandinavia (Text-fig. 1) developed from Cambrian Epoch 3 through the Furongian to the Early Ordovician (Tremadocian) as kerogen-rich black shales and mudstones with concretions and beds of dark grey, organic-rich limestones ('orsten', stinkstones or anthraconite; e.g., Westergård 1922; Martinsson 1974; Bergström and Gee 1985; Buchardt *et al.* 1997; Nielsen and Schovsbo 2006). Very low rates of deposition (1–10 mm/1000 years), high contents of organic carbon (up to 25% total organic carbon), sulphur and syngenetic trace elements, along with the predominance of parallel lamination and lack of sedimentary structures typical of tidal environments, suggest deposition in an upwelling regime in an epicontinental sea that covered part of the Baltica palaeocontinent, in depths generally below the storm wave base (in the range of 50–150 m), and under low oxygen concentrations (e.g., Andersson *et al.* 1985; Thickpenny 1987; Eklöf *et al.* 1999; Lauridsen and Nielsen 2005). The alum shales, formalized as the Alum Shale Formation by Nielsen and Schovsbo (2006), are present on Bornholm, in the Oslo region, southern and central Sweden, and as a thin stretch along the foot of the Caledonides (Text-figs 1, 2). The thickness of the formation is commonly about 20 m; it thins out to the east and attains thicknesses up to 160 m to the west in off-shore Denmark (Westergård 1922; Buchardt *et al.* 1997; Nielsen and Schovsbo 2006). Thin successions (up to 25 m), a high proportion of limestone (up to 50%) and numerous stratigraphic gaps, as well as evidence of current- and storm-influenced sedimentation characterize the inner shelf deposits, e.g., in Västergötland, whereas relatively continuous sections, low content of limestone (less than 10% of the succession) and greater thicknesses are a feature of the outer shelf sedimentation, e.g., in Scania (Dworatzek 1987; Buchardt *et al.* 1997; Terfelt 2003; Text-fig. 2). The limestone and conglomeratic horizons within the formation are often of regional nature and are important in the sequence stratigraphy context (see Nielsen and Schovsbo 2006 for overview). One such marker bed in the study interval is the Kakeled Limestone Bed.

The fairly diverse agnostoid–paradoxidid–solenopleurid–conocoryphid assemblages that characterize the Scandinavian Middle Cambrian are replaced by an agnostoid-dominated fauna in the *Agnostus pisiformis* Zone. The subsequent major change in the faunal composition (e.g., Lauridsen and Nielsen 2005; Ahlberg *et al.* 2006; Eriksson and Terfelt 2007) is reflected in the predominance of the Olenidae in the Furongian (e.g., Westergård 1922, 1946, 1947b; Henningsmoen 1957a), i.e., a family of highly specialized, generally small trilobites, adapted to dysoxic, or occasionally even anoxic environments (e.g., Clarkson and Taylor 1995; Clarkson *et al.* 1998; Fortey 2000; Schovsbo 2000, 2001; Clarkson 2011). Monospecific assemblages are common, with rarely more than three species at one level (Westergård 1922, 1947b; Clarkson and Taylor 1995). This basal-Furongian faunal turnover coincides with the onset of the SPICE event (Steptoean Positive Carbon Isotope Excursion) as recognized by Saltzman *et al.* (2000) and Ahlberg *et al.* (2009).

Assemblages of endemic olenids form the basis for high-resolution biostratigraphic schemes in the Furongian of Scandinavia (Westergård 1947b; Henningsmoen 1957a; see Nielsen *et al.* 2014 for the most recent scheme), the Holy Cross Mountains in Poland (Żylińska 2001, 2002), England and Wales (Rushton *et al.* 2011), and also eastern Canada (Martin and Dean 1988). In Scandinavia, the scheme based on olenids has been tied to that based on agnostoid arthropods (Terfelt *et al.* 2008). Global correlation of the Furongian in Baltica with other palaeocontinents is possible

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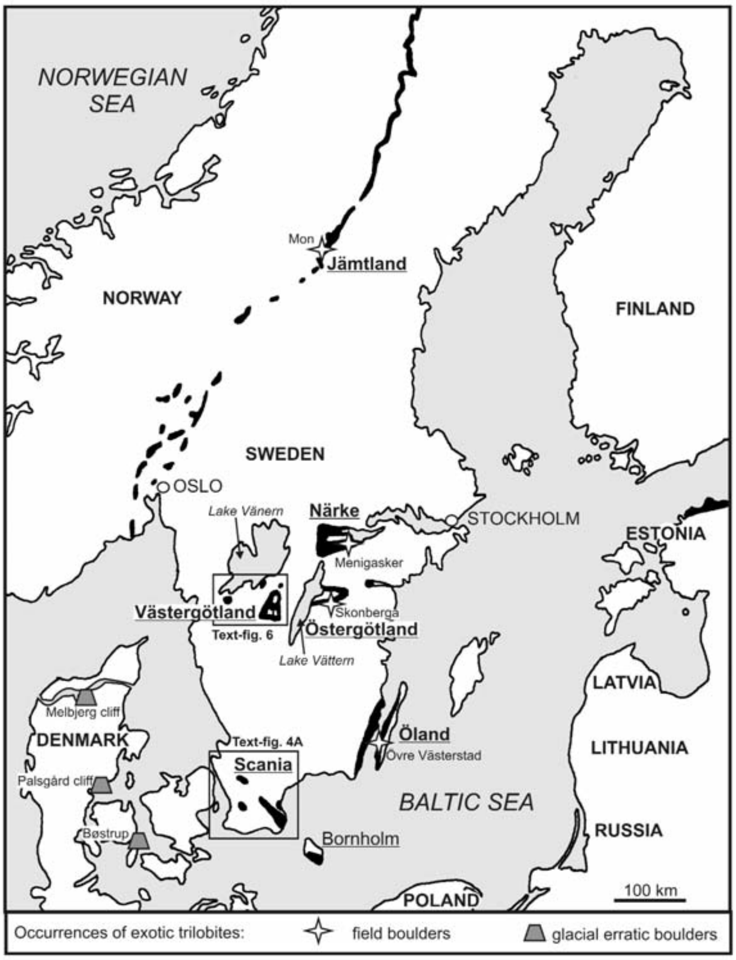
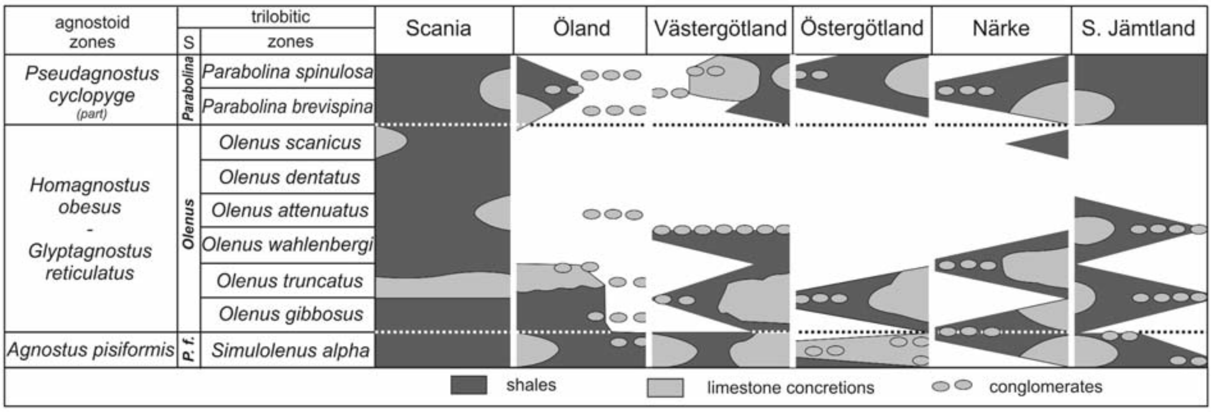
[1] Cambrian stage names are still in the progress of establishment (see Peng and Babcock 2011 for a most recent account). Herein, the term Lower Cambrian is used as the rough equivalent of the Terreneuvian and Cambrian Series 2, and Middle Cambrian as the rough equivalent of Cambrian Series 3. The Furongian Series roughly encompasses the traditional Upper Cambrian; its base is marked by the worldwide appearance of *Glyptagnostus reticulatus* (Angelin, 1851) (Peng *et al.* 2004). Therefore, the *Agnostus pisiformis* Zone, which used to form the base of the traditional Scandinavian Upper Cambrian, is now considered the uppermost zone in the Scandinavian Cambrian Series 3; it represents the uppermost agnostoid zone in the *Paradoxides forchhammeri* Superzone *sensu* Nielsen *et al.* (2014).

through the presence of several intercontinentally distributed agnostoids (Ahlberg and Ahlgren 1996; Ahlberg and Terfelt 2012).

The uppermost Cambrian Series 3 and Furongian faunal assemblages also contain representatives of non-olenid trilobites, termed exotics herein. These



Text-fig. 1. Distribution of Cambrian deposits (black) in the Baltic Sea region (modified from Martinsson 1974) showing localities with the examined exotic trilobites from the uppermost Cambrian Series 3 and lower Furongian

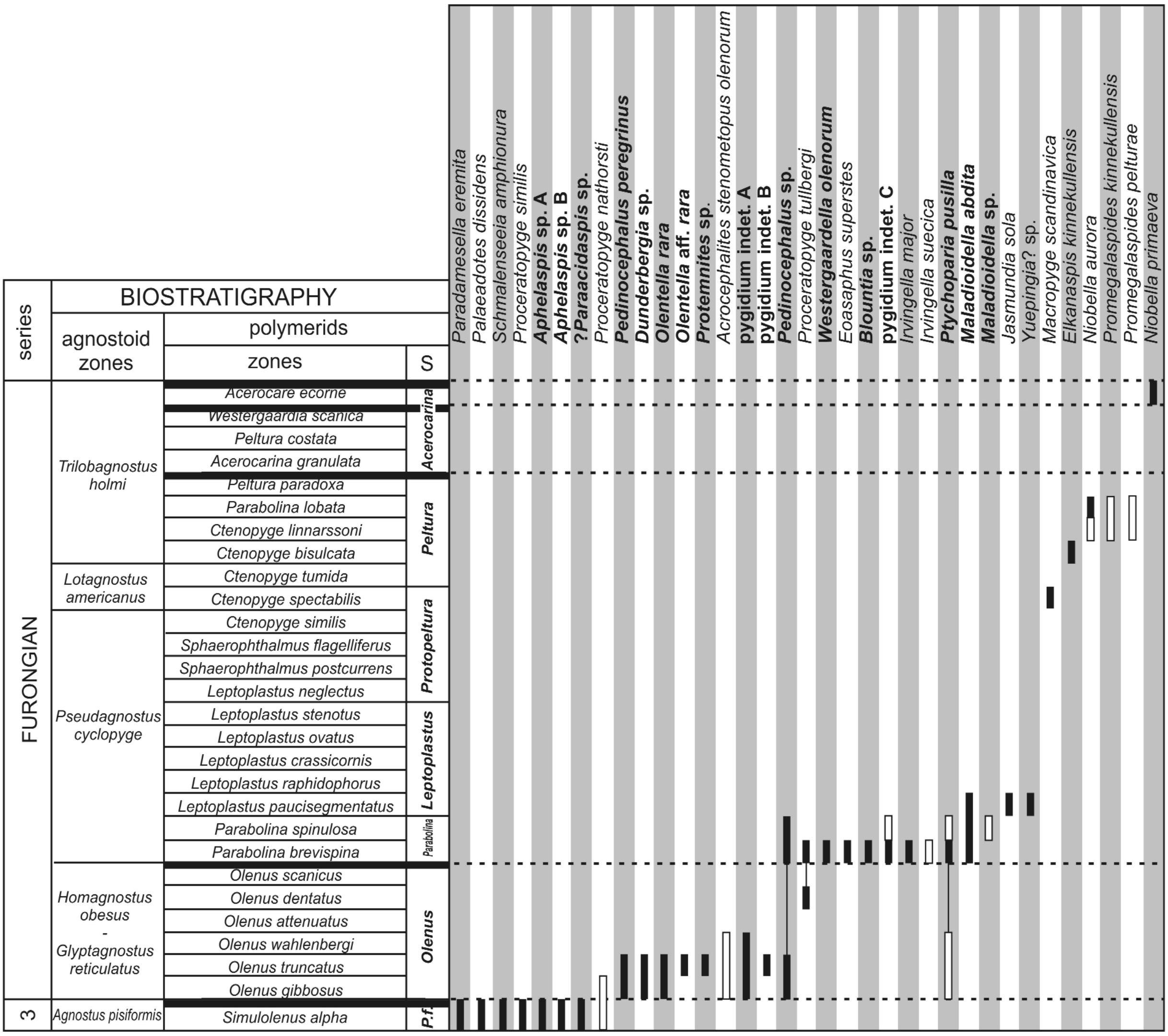


Text-fig. 2. Correlation of the Alum Shale Formation in the uppermost Cambrian Series 3 through lower Furongian successions between various parts of Sweden discussed herein, modified from Martinsson (1974, his fig. 5). Dotted lines mark the base of the *Glyptagnostus reticulatus* and *Pseudagnostus cyclopyge* zones, respectively. Biostratigraphic subdivision after Terfelt *et al*. (2008), with modifications of Nielsen *et al.* (2014). *P.f.* stands for *Paradoxides forchhammeri*. S stands for superzones trilobites occur with variable but generally low abundance throughout the succession (Text-fig. 3), and are known from Swedish sections as well as from glacial erratic boulders in Denmark and northern Germany (Linnarsson 1875; Moberg and Möller 1898; Moberg 1903; Persson 1904; Westergård 1909, 1922, 1939, 1947b, 1949; Henningsmoen 1957b, 1958; Rushton 1983; Buchholz 1991, 1997, 1998b, 2005; Rudolph 1997; Weidner 2001; Żylińska *et al*. 2004; Weidner and Żylińska 2005; Terfelt and Ahlgren 2007, 2009; Mischnik 2008; Rushton and Weidner 2010; Weidner and Nielsen 2010; Żylińska and Weidner 2012, 2013).

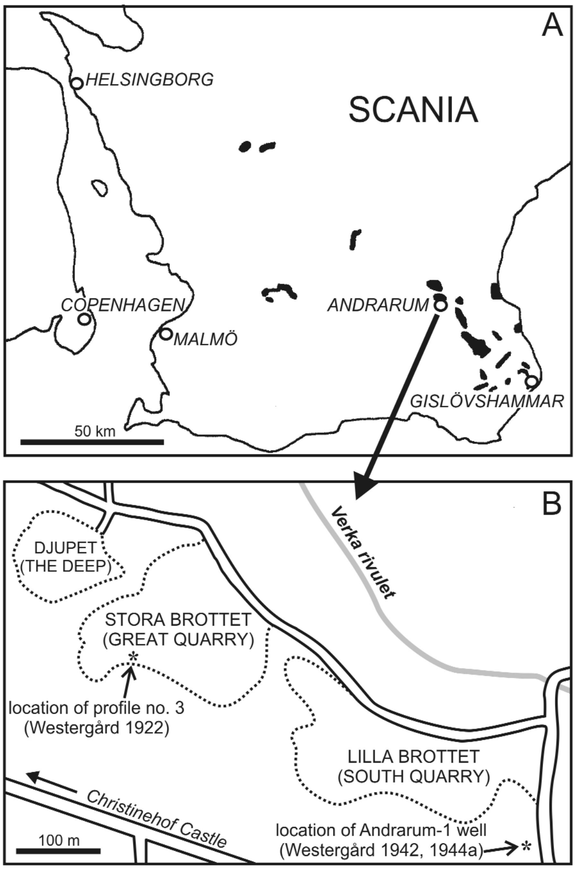
LOCALITIES

Scania

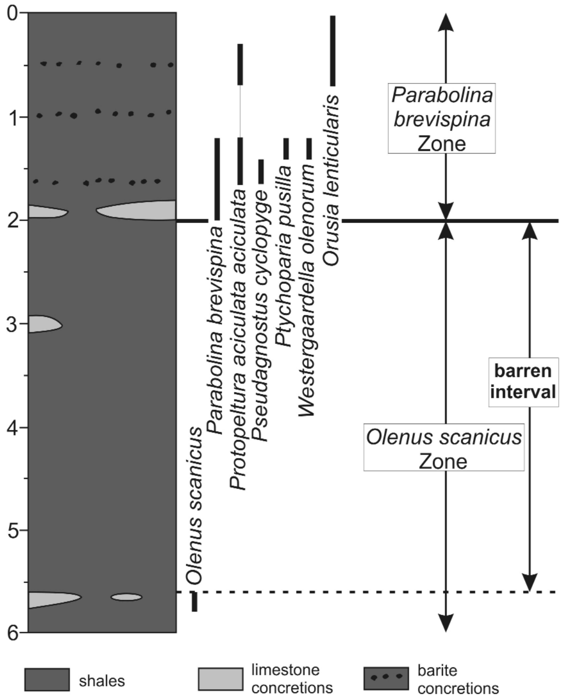
Lower Palaeozoic rocks of the area (Regnéll and Hede 1960; Norling and Skoglund 1977; Text-fig. 1) are exposed within the NW–SE-trending fault-bounded Colonus Shale Trough and have also been encountered below the Mesozoic strata in several boreholes (Terfelt *et al*. 2005; Calner *et al.* 2013). The Colonus Shale Trough is a distinct, elongated trough structure that forms part of the Sorgenfrei–Tornquist tectonic Zone in the Fennoscandian Border Zone (e.g., Erlström *et al*. 1997; Calner *et al*. 2013).



Text-fig. 3. Range chart of non-olenid trilobites in the uppermost Cambrian Series 3 and Furongian of Scandinavia (data from: Westergård 1922, 1947b; Zhang 1996; Buchholz 1998b, 2005; Terfelt and Ahlgren 2007, 2009; Rushton and Weidner 2010; Weidner and Nielsen 2010; Terfelt *et al.* 2011, and this paper). Biostratigraphic subdivision after Terfelt *et al*. (2008), with modifications of Høyberget and Bruton (2012) and Nielsen *et al.* (2014). Vertical thick black lines mark definite occurrences, vertical thick white lines mark estimated occurrences. Taxa discussed in this paper are in bold. Horizontal thick black lines and horizontal dashed lines indicate the position of barren intervals (after Conway Morris and Rushton 1988; Terfelt 2006). 3 stands for Cambrian Series 3, *P.f.* stands for *Paradoxides forchhammeri*, S stands for superzones



Text-fig. 4. **A** – Outcrop areas of the Alum Shale Formation (black) in Scania (southern Sweden) and the location of Andrarum and Gislövshammar. **B** – Sketch-map showing the old quarries at Andrarum and the location of profile no. 3 (compiled from Westergård 1922, 1942, 1944a)



Text-fig. 5. Lithological succession of profile no. 3 at Andrarum in Scania, Sweden, with ranges of trilobites and biostratigraphy. Compiled from Westergård (1922) and Eriksson and Terfelt (2007). Note that by analogy with the Andrarum-3 borehole core, the lower part of the barren interval contains phosphatocopines, i.e., *Cyclotron angelini* (Barrande, 1872). For location see Text-fig. 4B

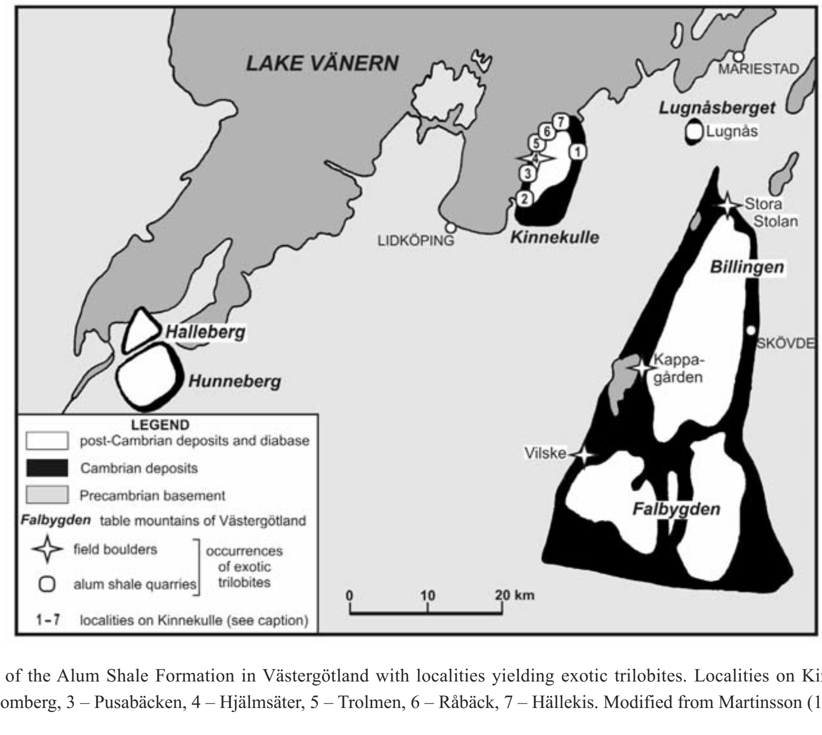
The Alum Shale Formation in Scania is relatively complete (Martinsson 1974; Bergström and Gee 1985; Nielsen and Schovsbo 2006; Text-fig. 2) and rather thick (up to 100 m) compared to other parts of Scandinavia (Westergård 1944a; Martinsson 1974). The Forsemölla–Andrarum district of Scania (Text-fig. 4A) is one of the classic Lower Palaeozoic outcrop areas with the most accessible and complete sections in Scandinavia (see Calner *et al.* 2013 for a most recent account). Strata exposed in the closed-down quarries (Text-fig. 4B) reach up to 80–90 m in thickness and encompass the Cambrian Series 3 to the lower Tremadocian (Westergård 1944a). The section yielding the original specimens of *Ptychoparia pusilla* (Westergård, 1922) and *Westergaardella olenorum* (Westergård, 1922) is Westergård's (1922) profile no. 3 which lies in the southern part of the Great Quarry (Text-fig. 4B). It comprises 6 m of the Alum Shale Formation with calcareous and barite concretions and limestone beds (Text-fig. 5). The associated fauna indicates the *Parabolina brevispina* Zone (Text-fig. 5). *Ptychoparia pusilla* (as *Liostracus pusillus*) was cited by Westergård (1942, 1944a) from the *Parabolina brevispina* Zone in the Gislövshammar and Andrarum 1 borehole cores (Text-fig. 4A, B), but the specimens have not been traced in the SGU collections at Uppsala.

Öland

The Alum Shale Formation underlies an Ordovician limestone-dominated succession throughout the island (Westergård 1944b, 1947a; Text-fig. 1). It attains a thickness of up to 24 m in the south of Öland, decreasing to less than 2 m in the northern part of the island. The uppermost Cambrian Series 3 through Furongian succession contains numerous stratigraphic gaps (Martinsson 1974; Text-fig. 2) and comprises black shales with a high frequency of limestone and organic-rich concretions (c. 14 m) followed by lower Tremadocian black shales with subordinate concretions. Non-olenid trilobites represented by *Protemnites* sp., pygidium indet. A and pygidium indet. B have been encountered in field boulders near Övre Västerstad in the south-western part of the island (Text-fig. 1). The associated fauna indicates that the boulders derive from the *Olenus gibbosus* and *Olenus truncatus* zones (Text-fig. 3).

Västergötland

The Lower Palaeozoic deposits of Västergötland occur as erosional outliers on the Precambrian crystalline basement, and form the famous table mountains of the area, grouped in four regions: Billingen–Falbygden to the south-east, Kinnekulle at the shore of Lake Vänern, and Halle- and Hunneberg to the west; a small outlier located to the north of Billingen is the Lugnåsberget (see Calner *et al.* 2013 for a most recent account; Text-fig. 6). The Alum Shale Formation comprises Cambrian Series 3 through Furongian black shales (up to 26 m) with limestone beds or bituminous concretions, and locally conglomerates and calcareous sandstones resting on Lower Cambrian siliciclastics (c. 35 m; Jensen and Ahlberg 1998). The alum shales are covered by Ordovician limestones and Ordovician to Silurian mudstones and shales. The Lower Palaeozoic succession is generally capped by a thick sheet of Carboniferous–Permian diabase; Lugnåsberget is the only outlier without a diabase cap (Text-fig. 6). Several significant limestone units can be recognized over a large area in the Alum Shale Formation in Västergötland (Andersson *et al*. 1985; Nielsen and Schovsbo 2006). They include the 'Hypagnostus limestone bank' of Weidner *et al.* (2004); the Hyolithes Limestone Bed and the coeval conglomerates (Weidner *et al.* 2004); the Andrarum Limestone Bed; and the Kakeled Limestone Bed (see Nielsen and Schovsbo 2006 for an overview). The latter marker bed, earlier referred to as the Great Stinkstone Bank (*stora orstensbanken*), spans the *Olenus gibbosus* through the *Parabolina spinulosa* zones (with a stratigraphic gap from the top of the *Olenus wahlenbergi* Zone to the base of the *Parabolina brevispina* Zone), and may locally reach down to the *Agnostus pisiformis* Zone, as well as upwards to the *Sphaerophthalmus flagelliferus* Zone (Westergård 1922; see Terfelt *et al.* 2011 and Høyberget and Bruton 2012 for zonal nomenclature; Text-fig. 2). The faunal composition within the Kakeled Limestone Bed indicates significant reworking and condensation, hampering in many cases precise age assignment of the exotic trilobites. Locally on Kinnekulle, the topmost part of this bed shows an overlap of ranges of trilobites representing the *Parabolina brevispina* and *Parabolina spinulosa* zones with ranges of trilobites from the underlying *Olenus gibbosus* Zone (see Westergård 1922, his figs 19–21, 23); apart from condensation, a stratigraphic gap is evident. A slightly different case may be observed at Kakeled (also on Kinnekulle), where the *Parabolina spinulosa* Zone lies directly on the *Olenus wahlenbergi* Zone (Terfelt 2003, his fig. 3), recording a clear stratigraphic gap but no mixing of the zone-indicative trilobites. Such variable positions of stratigraphic gaps and their ranges coupled with the presence of strati-



Text-fig. 6. Exposures of the Alum Shale Formation in Västergötland with localities yielding exotic trilobites. Localities on Kinnekulle: 1 – Krokagården, 2 – Blomberg, 3 – Pusabäcken, 4 – Hjälmsäter, 5 – Trolmen, 6 – Råbäck, 7 – Hällekis. Modified from Martinsson (1974, fig. 9) graphically condensed beds and/or conglomerates in neighbouring successions may reflect synsedimentary block tectonic movements leading to the formation of localized high-energy environments or even emersion, variations in sediment supply, current action, or possible sea-level changes (Miall and Miall 2004), as indicated by, for instance, Devonian–Carboniferous (e.g., Szulczewski 1978) or Mesozoic examples (e.g., Bergström *et al.* 1973; Callomon 1995). Resolving this interesting but complex problem for the Västergötland successions requires further studies. Tectonic factors have been suggested as being responsible for relative sea-level changes in Baltoscandia (Artyushkov *et al.* 2000), and the first evidence of subaerial exposure at regressions during the sedimentation of the alum shales has been provided for Kinnekulle by Lehnert *et al.* (2012).

A rich assemblage of non-olenid trilobites comprising *Maladioidella abdita* (Salter, 1866), *Olentella rara* (Westergård, 1922), *Pedinocephalus peregrinus* (Henningsmoen, 1957), *Westergaardella olenorum* (Westergård, 1922), *Aphelaspis* sp. A., *Blountia* sp., *Dunderbergia* sp., *Pedinocephalus* sp., *Protemnites* sp., ?*Paraacidaspis* sp., pygidium indet. A., pygidium indet. B, and pygidium indet. C has been recorded from almost all outliers (Text-figs 3, 6), with the exception of Halle- and Hunneberg, where no collecting was made due to the fact that the Kakeled Limestone Bed is concealed by debris derived from the *Peltura* zones and diabase. The specimens come either directly from the Kakeled Limestone Bed and loose boulders lying in closed-down alum shale quarries (Krokagården, Blomberg, Pusabäcken, Trolmen, Råbäck, and Hällekis), or from field boulders located close to the alum shale outcrops (Hjälmsäter, Stora Stolan, Kappagården, and Vilske) (Text-figs 6 and 7A). The associated fauna indicates the *Agnostus pisiformis*, *Glyptagnostus reticulatus* (*Olenus gibbosus*, *Olenus truncatus*, and *Olenus wahlenbergi* zones of the *Olenus* Superzone *sensu* Nielsen *et al*. 2014) and the lower part of the *Pseudagnostus cyclopyge* Zone (*Parabolina brevispina* Zone of the *Parabolina* Superzone *sensu* Nielsen *et al*. 2014) (Text-fig. 3). In a number of cases the studied specimens adopt a dorsal-up attitude exactly at the boundary between the black, pelitic, *Olenus* spp.-bearing limestone and the light-grey, sparitic limestone with abundant *Orusia lenticularis* (Wahlenberg, 1818), a brachiopod characteristic of the *Parabolina brevispina* Zone. Such an attitude of fossils is considered to indicate surface currents (e.g., Webster *et al.* 2008). Consequently, the exact stratigraphic position of these specimens is not clear, as they could derive either from the older, *Olenus*-spp.-bearing interval or represent a fauna from the *Parabolina brevispina* Zone. In two cases studied, the specimens do not show evident abrasion marks that would point to the erosive action of currents prior to sedimentation at the base of the layer with *Orusia lenticularis* (Text-figs 14H and 23D), and therefore we assume that they could be derived from the *Parabolina brevispina* Zone.

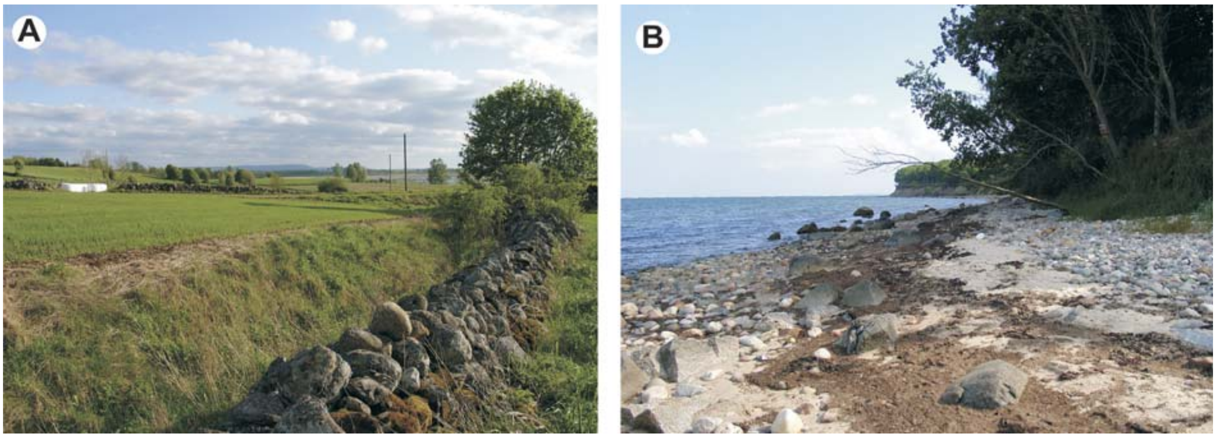
The original specimens of *Taenicephalus*? *peregrinus* come from the Kakeled Limestone Bed in the Trolmen quarry with an associated fauna indicating the *Olenus gibbosus* Zone (Henningsmoen 1957b). The original specimen of *Acrocephalites* (?) *rarus* was collected on Lugnåsberget, Västergötland, but the locality is uncertain as reflected by a question mark on the museum label and in the original publication (Westergård 1922, p. 124); apparently, the specimen was found in a loose block near an abandoned quarry. The associated fauna is suggestive of the *Olenus gibbosus* Zone (Westergård 1922, p. 76).

Östergötland

On the eastern side of Lake Vättern (Text-fig. 1), the Alum Shale Formation occurs in an E–W-trending faulted syncline. It reaches thicknesses from 14 m in the east to over 20 m in the west (Andersson *et al*. 1985). The Kakeled Limestone Bed has a thickness of up to 3 m, comprises the *Olenus gibbosus*, *Olenus truncatus*, *Parabolina brevispina* and *Parabolina spinulosa* zones, and may locally also embrace the *Agnostus pisiformis* Zone (Westergård 1922; Martinsson 1974; Text-fig. 2). Non-olenid trilobites represented by *Aphelaspis* sp. A and *Aphelaspis* sp. B have been found in field boulders on Skonberga hill. The associated fauna indicates the *Agnostus pisiformis* Zone (Text-fig. 3).

Närke

The Lower Palaeozoic succession of the area (Text-fig. 1) comprises Lower Cambrian through Lower Ordovician strata. The Alum Shale Formation reaches 13–19 m in thickness, largely spans the uppermost Cambrian Series 3 through Furongian with many gaps in the succession, and has a relatively low content of stinkstones (Westergård 1922; Martinsson 1974; Text-fig. 2). Non-olenid trilobites represented by *Pedinocephalus peregrinus* have been found in field boulders near Menigasker, where the Furongian is down-faulted and covered by several metres of local moraine (Westergård 1940). The associated fauna indicates the *Olenus gibbosus* and *Olenus truncatus* zones (Text-fig. 3).



Text-fig. 7. **A** – Heap of field boulders at Kappagården in Västergötland, Sweden (for location see Text-fig. 6). **B** – View of Palsgård cliff in central Denmark (for location see Text-fig. 1)

Jämtland

In central Jämtland (Text-fig. 1), Cambrian Series 3 and Furongian strata are dominated by black shales with stinkstone concretions in a narrow strip of autochthonous strata along the Caledonian front and in the Lower Allochton of the Caledonides further to the west (Asklund 1938; Martinsson 1974; Karis and Strömberg 1998; Text-fig. 2). The stinkstones are locally extremely fossiliferous and indicate the presence of almost all Cambrian Series 3 and Furongian zones up to the *Peltura*-bearing interval, albeit with numerous stratigraphic gaps (Martinsson 1974; Karis and Strömberg 1998; Text-fig. 2). One specimen of a non-olenid trilobite representing *Olentella* aff. *rara* (Westergård, 1922) has been collected from a loose boulder in a closed-down quarry at Mon in the Autochthon. The associated fauna indicates the *Olenus truncatus* Zone (Text-fig. 3).

Glacial erratic boulders

Glacial erratic boulders of Cambrian rocks found in moraines deposited during the Pleistocene ice-sheet advances south of the Baltic Sea in Denmark, Germany and Poland have recently been recognized as an important source of data on the succession of rocks in their mother area (Geyer *et al*. 2004; Weidner *et al*. 2004). Uppermost Cambrian Series 3 through Furongian trilobites are quite common in Quaternary deposits of glacial origin (Schrank 1973; Buchholz 1991, 1997, 1998a, 1999, 2000, 2003, 2005; Bilz 1996; Schöning 2002), and have also been noted as far south as in the Czech Republic (Pek and Šnajdr 1981). The boulders also yield non-olenid trilobites (Buchholz 1991, 1998b, 2005; Rudolph 1997; Weidner 2001; Mischnik 2008; Weidner and Nielsen 2010). Seven specimens discussed herein and representing *Maladioidella abdita*, *Ptychoparia pusilla, Pedinocephalus* sp., *Maladioidella* sp. and pygidium indet. C come from two localities: Melbjerg cliff at the Limfjord in northern Denmark and the Palsgård cliff (As Hoved) in central Denmark (Text-figs 1, 7B). Two of the specimens were illustrated and discussed by Weidner (2001). An associated fauna is rare allowing only for a rough estimation of the stratigraphic interval as the *Parabolina* Superzone *sensu* Nielsen *et al.* (2014), i.e., the *Parabolina brevispina* and *Parabolina spinulosa* zones (Text-fig. 3).

DISCUSSION

Affinities of the exotic trilobites

Analysis of the palaeobiogeographical distribution of exotic trilobites at generic level (Text-figs 8–10) clearly indicates that the assemblage shows the strongest affinities with East Gondwana (particularly its Australian – Antarctic – Chinese segment), Laurentia, Kazakhstania, and Siberia, that is palaeogeographic areas located in low-latitude positions (e.g., Cocks and Torsvik 2006; Álvaro *et al.* 2013; Text-figs 8, 9). Interestingly, genera considered to be typical and/or most numerous in specific palaeogeographic areas also have a wide palaeogeographic distribution. *Aphelaspis*, which is most diverse and abundant in Laurentia, has, for example, also been recorded from Kazakhstania, Siberia, Avalonia, East Gondwana and the marginal seas of Baltica (Text-figs 8–10A). This also applies to *Proceratopyge* Wallerius, 1895, which belongs to the most cosmopolitan Cambrian trilobite

Baltica		Laurentia	Kazakhstania	Siberia	Kipchak Arc (Gorny Altai)	Kara terrane (Severnaya Zemlya)	Avalonia	Gondwana												
								Argentina	Antarctica	Australia	South China	North China + Korea	Himalaya	Afghanistan	Iran	Oman	Turkey	France	Spain	Morocco
1	*Palaeadotes*		1	1					1	1	1	1		1	1		1	2		
1	*Paradamesella*		1		1						1	1								
1	*Schmalenseeia*			1			1			1	1		1							
1,2,3	*Proceratopyge*	3	1,2,3	1,2,3			1,2,3	?	2,3	2,3	2	2						2		
1,3*	***Aphelaspis***	1,2	3	2			2		2,3	3	2									
2	***Olentella***	2/3	2	2/3	1				2/3									2		?
2	***Dunderbergia***	2			?							?								
2	***Protemnites***								2	2,3	2									
2,3	***Pedinocephalus***		2						2				2		2					
2,3	***Ptychoparia***											3								
3	***Maladioidella***			3		3	3			3	3	3			3	3	3		3	
3	***Westergaardella***				1							2								
3	***Blountia***	1,2								1			2							
3	*Irvingella*	3	3	3	3		3	3		3	3	3								

Text-fig. 8. Distribution of exotic trilobite genera in various biogeographical areas (for references see text). The examined genera are in bold. 1, 2, 3 represent the *Agnostus pisiformis*, *Glyptagnostus reticulatus* and *Pseudagnostus cyclopyge* zones (or their correlatives), respectively; separation by a comma – occurrences in both zones, separation by a slash – unclear occurrences. 3* marks the occurrence of *Aphelaspis* in the Holy Cross Mountains of Poland

genera, and has been recorded from Laurentia, Kazakhstania, Siberia, Avalonia, various parts of Gondwana (Antarctica, Australia, China, Argentina, Korea, France) and Baltica (Text-fig. 8; see also Shergold *et al.* 2000; Zhang *et al.* 2003), and to *Irvingella* Ulrich et Resser in Walcott, 1924, which occurs in Laurentia, Kazakhstania, Siberia, Gorny Altai Mountains[2] (Kipchak Arc), Avalonia, East Gondwana (Argentina, Australia, China and Korea) and Baltica (Text-fig. 8; see also Hong *et al*. 2003). Taxa with the widest distribution, i.e., *Aphelaspis*, *Maladioidella, Olentella*, *Proceratopyge* and *Irvingella*, have also occurrences beyond low-latitude positions (Text-fig. 10A, D, I; see also Shergold *et al.* 2000; Hong *et al.* 2003; Zhang *et al.* 2003).

A Laurentian influence (*Aphelaspis*, *Dunderbergia*, *Blountia*) can be observed in all of the stratigraphic intervals studied. *Aphelaspis* began its dispersal in Laurentia in the Marjuman *Crepicephalus* Chron and appeared approximately at the same time in the Alum Shale Sea of Baltica during the *Agnostus pisiformis* Chron (see Palaeontological notes for details and references; Text-figs 8, 10A, 11). Later, in the Steptoean *Glyptagnostus reticulatus* Chron and its equivalents, it flourished in Laurentia and dispersed into Siberia, Avalonia, as well as East Gondwana (Antarctica and South China). A slightly later occurrence has been observed in Kazakhstania, East Gondwana (Antarctica), and the marginal seas of Baltica (Holy Cross Mountains). *Dunderbergia* is known from the mid-Steptoean *Dunderbergia* Zone of North America and has also been observed in the Furongian of the Gorny Altai Mountains and North China (Text-figs 8, 10B, 11). *Blountia* is known from Marjuman as well as Steptoean (*Aphelaspis* Zone) strata in Laurentia, and from upper Mindyallan and lower Idamean rocks in East Gondwana (Australia) (Text-figs 8, 10C, 11). Occurrences from the Himalayas are from the lower Upper Cambrian. In the Alum Shale Formation of Baltica, the genus appears stratigraphically slightly higher, and is associated with *Parabolina spinulosa* (Wahlenberg, 1818). Of Laurentian affinity are also some of the exotic trilobites described from younger stratigraphic intervals in Scandinavia, i.e., *Yuepingia*? sp. from the *Leptoplastus paucisegmentatus* Zone and *Elkanaspis kinnekullensis* Terfelt et Ahlgren, 2009 from the *Ctenopyge bisulcata* Zone (Text-fig. 3; Terfelt and Ahlgren 2009; Weidner and Nielsen 2010).

Olentella and *Pedinocephalus* represent two genera typical of Kazakhstania, where they occur in the Sakian *Aphelaspis*–*Kujandaspis* Zone, and Siberia (including the Gorny Altai Mountains), where they have been noted in coeval strata (see Palaeontological notes for details and references; Text-figs 8, 10D, E,

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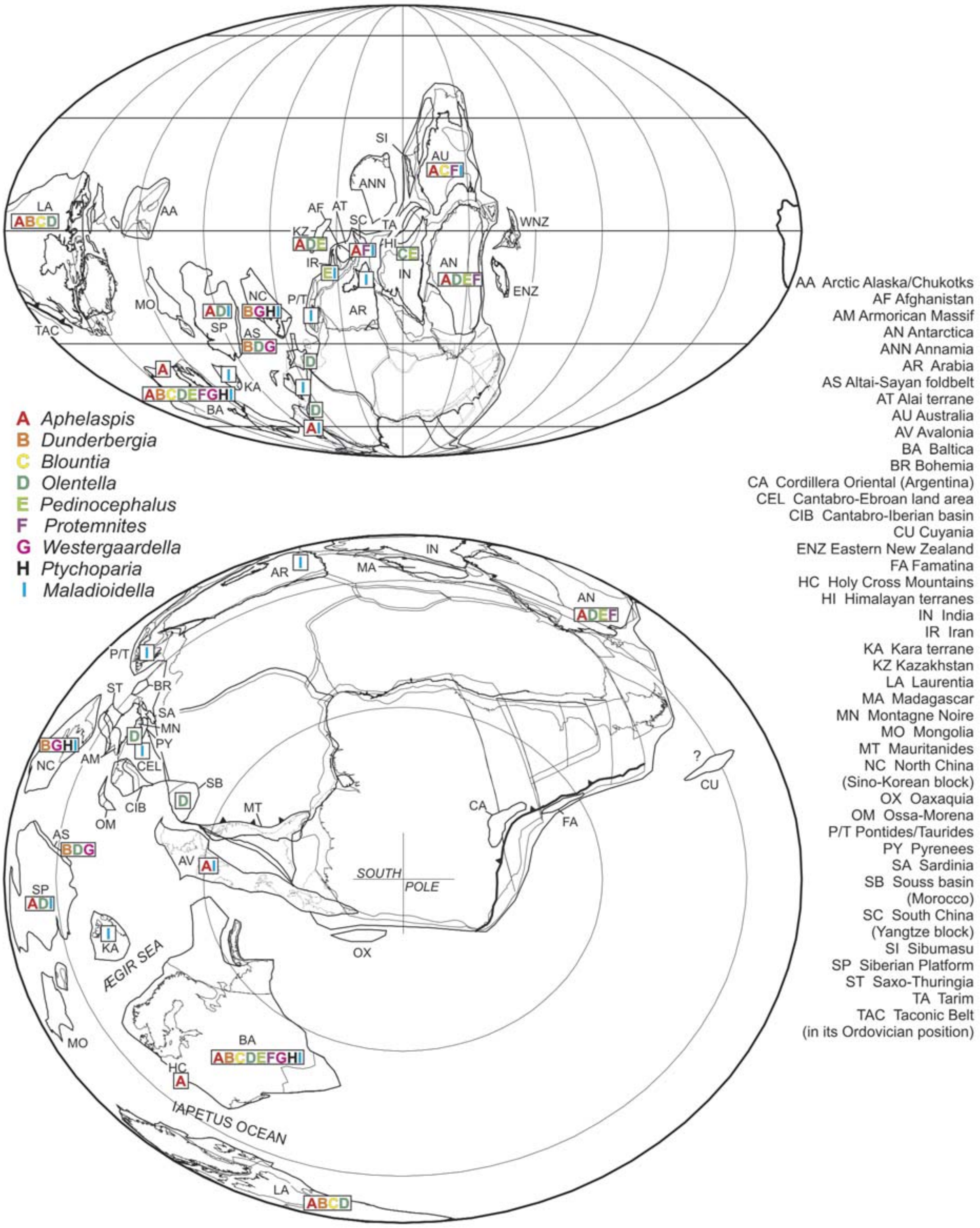
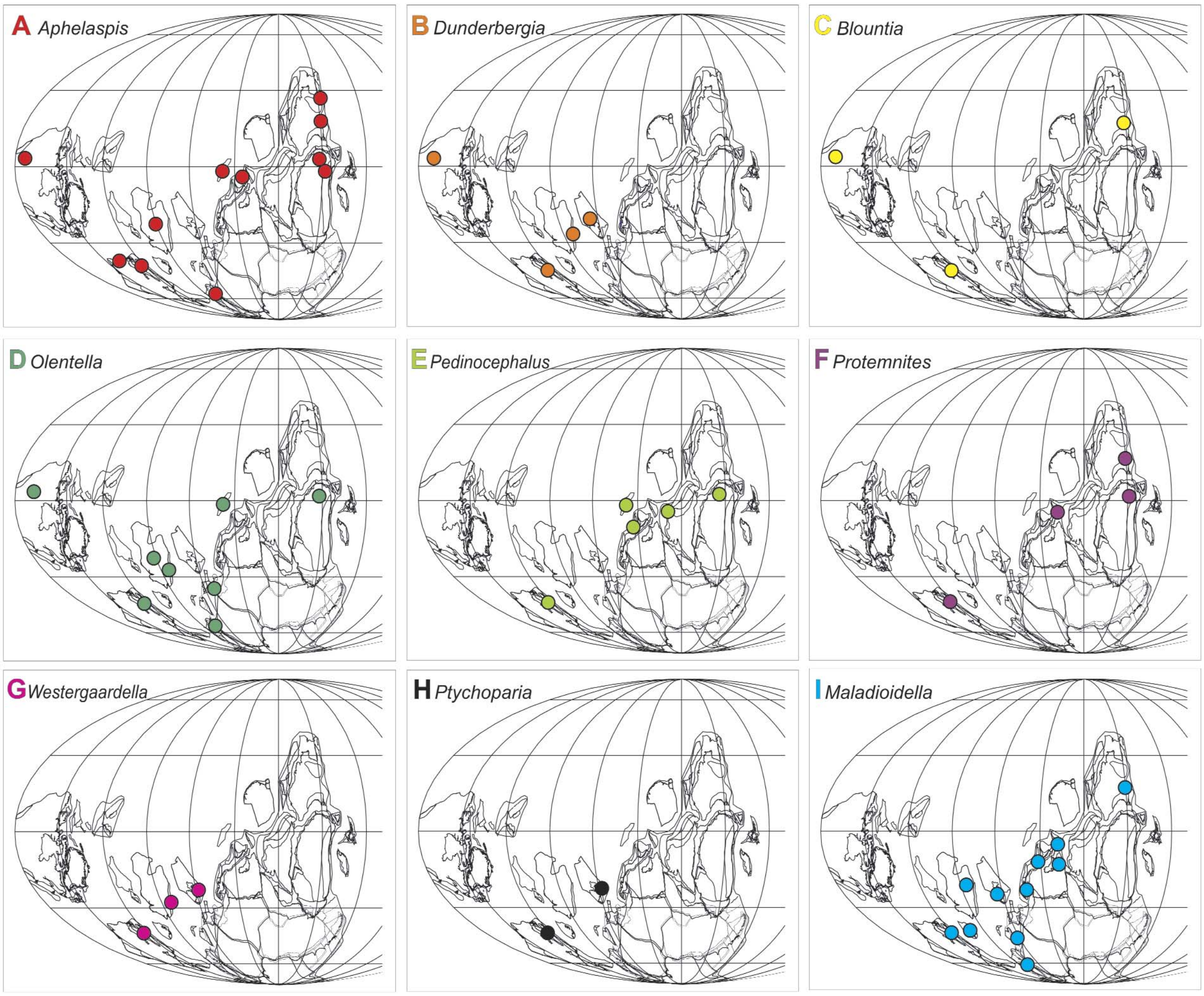
[2] The Gorny Altai Mountains are considered part of the Palaeozoic Kipchak Arc – see e.g., Şengör *et al.* (1993) and Safonova (2014), for details.

11). *Olentella* is quite widespread and has also been noted in the upper Idamean–lower Iverian of Northern Victoria Land, Antarctica (East Gondwana), the upper Steptoean of the Northwest Territories of Canada (Laurentia), the Furongian of Morocco, and the lower Furongian of the Montagne Noire, France (West Gondwana) (Text-fig. 11). Apart from the Sakian of Kazakhstan, *Pedinocephalus* has been recorded from the



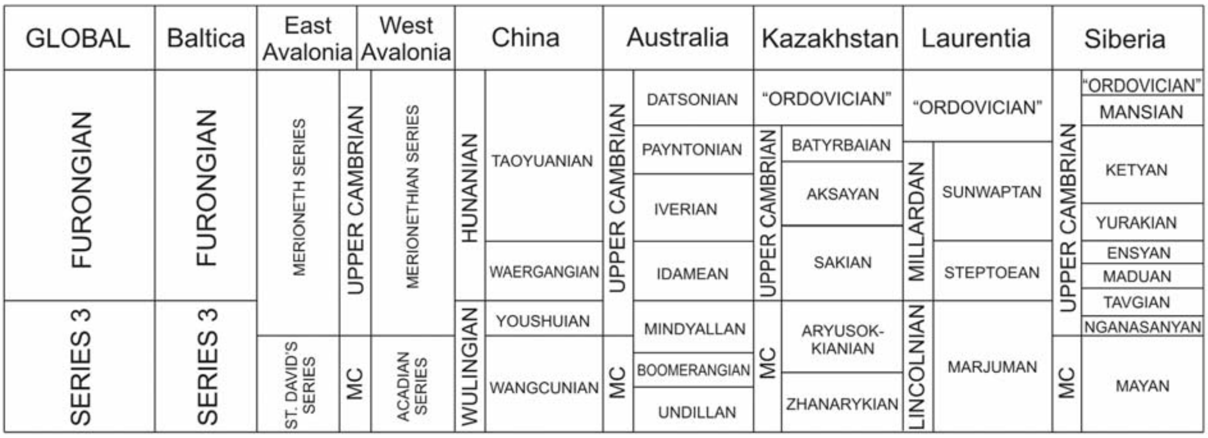
Text-fig. 9. Tentative palaeogeographical reconstruction for the Cambrian, slightly modified from Álvaro *et al.* (2013), with distribution of the examined genera



Text-fig. 10. Individual palaeogeographical distribution of the examined genera. Maps as in Text-fig. 9

upper Idamean–lower Iverian of Northern Victoria Land, Antarctica (East Gondwana), and the lower Furongian of the Himalayas and Iran (Text-fig. 11). A pygidium assigned to ?*Paraacidaspis* sp. may also point to affinities with Kazakhstania and Siberia, as representatives of *Paraacidaspis* Poletaeva, 1960 occur in Kazakhstania, Siberia and China (see Shergold *et al.* 2000).

Most common among the exotic trilobites of Baltica are Gondwanan genera, particularly genera described from East Gondwana (its Australian – Antarctic – Chinese segment). Among the taxa examined, those characteristic of East Gondwana include representatives of *Maladioidella*, *Protemnites*, *Westergaardella* and *Ptychoparia*. Species with such affinities that also occur in Scandinavia in the studied interval include *Palaeadotes dissidens* Öpik, 1967, *Paradamesella eremita* (Westergård, 1947), *Schmalenseeia amphionura* Moberg, 1903*, Proceratopyge similis* Westergård, 1947*, P. nathorsti* Westergård, 1922 and *P. tullbergi* Westergård, 1922 (Westergård 1922, 1947b; Whittington 1994; Zhang 1996; Ebbestad and Budd 2003; Text-fig. 3). *Macropyge* (*Promacropyge*) *scandinavica* Terfelt et Ahlgren, 2007 from the stratigraphically younger *Ctenopyge spectabilis* Zone of Sweden is also of East Gondwanan affinity (Terfelt and Ahlgren 2007). *Maladioidella* is the palaeogeographically most widespread genus in the assemblage discussed herein, being present in very diverse facies of shelf and slope settings (see Palaeontological notes for details and references; Text-figs 8, 10I). Its occurrences beyond the palaeoequatorial area include Avalonia (Wales), West Gondwana (Spain) and the Kara terrane (Severnaya Zemlya). *Protemnites* has been noted in the upper Idamean of Australia, the Idamean of Antarctica, as well as the Iverian of Australia and correlative units in South China (see



Text-fig. 11. Correlation chart of the upper part of Cambrian Series 3 and the Furongian in various biogeographic areas. Modified from Peng *et al.* (2004). MC stands for Middle Cambrian

Palaeontological notes for details and references; Text-figs 8, 10F, 11). Species of *Westergaardella* are rare but have been described from the Furongian of northern China and the Gorny Altai Mountains (Text-figs 8, 10G). *Ptychoparia* is best known from its Middle Cambrian representatives (e.g., Kordule 2006); Furongian species have been described from the Machari Formation of South Korea (Text-figs 8, 10H). Representatives of *Palaeadotes* Öpik, 1967 are known from Kazakhstania, Siberia, the Kipchak Arc, various parts of Gondwana (Antarctica, Australia, China, Afghanistan, Iran, Turkey, France) and Baltica (Text-fig. 8; see also Zhang 1998; Shergold *et al.* 2000). Species of *Paradamesella* Yang in Zhou *et al.*, 1977 have been noted in the Kipchak Arc, Kazakhstania, East Gondwana (China) and Baltica (Text-fig. 8; see also Zhang 1998; Zhang *et al.* 2003). Apart from Baltica, burlingiids of the genus *Schmalenseeia* Moberg, 1903 occur in Siberia, Avalonia, and Gondwana (Australia, China and the Himalayas) (Text-fig. 8; see also Whittington 1994; Ebbestad and Budd 2003).

Appearances of exotic trilobites in the stratigraphic column of Scandinavia

The exotic trilobites from the discussed interval appear in the succession in three phases (Text-fig. 3). Phase 1 is recorded in the uppermost Cambrian Series 3 and coincided with the appearance of the agnostoid-dominated fauna of the *Agnostus pisiformis* Zone, separating the agnostoid–paradoxidid–solenopleurid–conocoryphid assemblages of the Scandinavian Middle Cambrian and the olenid assemblages of the Furongian. The exotic trilobites in this phase include: the damesellids *Paradamesella eremita* (Westergård, 1947) and *Palaeadotes dissidens* Öpik, 1967 (Zhang 1996); the burlingiid *Schmalenseeia amphionura* Moberg, 1903 (Ahlberg 1989; Whittington 1994; Ebbestad and Budd 2003); the ceratopygids *Proceratopyge similis* Westergård, 1947 and *Proceratopyge nathorsti* Westergård, 1922 (Westergård 1922, 1947b); the aphelaspidids *Aphelaspis* sp. A and *Aphelaspis* sp. B; and the lichakephalid ?*Paraacidaspis* sp. (this paper).

Phase 2 recorded the appearance of: the parabolinoidids *Pedinocephalus peregrinus* (Henningsmoen, 1957) and *Pedinocephalus* sp.; the aphelaspidids *Olentella rara* (Westergård, 1922) and *Olentella* aff. *rara* (Westergård, 1922); the acrocephalitid *Acrocephalites stenometopus olenorum* Westergård, 1948; the ceratopygid *Proceratopyge tullbergi* Westergård, 1922; the ptychopariid *Ptychoparia pusilla* (Westergård, 1922); and the elviniids *Dunderbergia* sp. and *Protemnites* sp.; pygidium indet. A and pygidium indet. B also appear in this phase (Text-fig. 3; Westergård 1948; Henningsmoen 1957b; and this paper). Strata representing this phase follow a barren interval in the uppermost *Agnostus pisiformis* Zone (Text-fig. 3).

Phase 3 is, as the preceding one, linked to a barren interval in the uppermost *Olenus scanicus* Zone (Ahlberg *et al.* 2009; Text-figs 3, 5). The assemblage yields: the parabolinoidid *Pedinocephalus* sp.; the ceratopygid *Proceratopyge tullbergi*; and the ptychopariid *Ptychoparia pusilla* from the previous phase; the changshaniid *Westergaardella olenorum* (Westergård, 1922); the asaphid *Eoasaphus superstes* (Linnarsson, 1875); the kingstoniid *Blountia* sp.; the elviniids *Irvingella major* Ulrich et Resser in Walcott, 1924 and *Irvingella suecica* Westergård, 1947; the idahoiids *Mal-*

adioidella abdita (Salter, 1866) and *Maladioidella* sp.; as well as pygidium indet. C from the *Parabolina* Superzone (Westergård 1922, 1947b; Rushton and Weidner 2010; and this paper); the parabolinoidid *Jasmundia sola* Buchholz, 1998 and the ceratopygid *Yuepingia*? sp. are from the *Leptoplastus* Superzone (Buchholz 1998b; Weidner and Nielsen 2010; Text-fig. 3).

Phases 2 and 3 have been recorded directly after barren intervals, i.e., unfossiliferous intervals in the alum shale succession, already recognized by Westergård (1944a). The Cambrian Series 3 to Furongian succession in Scandinavia bears five such unfossiliferous intervals (Text-fig. 3; see also Terfelt 2006, his fig. 9). These unfossiliferous or barren intervals were considered to reflect the primary lack of organisms in the environment, commonly considered to be a result of reduced oxygen conditions (e.g., Berry and Wilde 1978; Conway Morris and Rushton 1988; Clarkson *et al*. 1998). An alternative model was proposed by Schovsbo (2001), who assumed that the barren intervals correspond to parts of the succession that do not preserve a calcareous fauna. Removal of calcareous carapaces from the sediment could be the result of precompaction dissolution by corrosive pore water related to the reoxidation of sulphur compounds in the sediment when the content of oxygen in the environment exceeded that typical of the alum shale facies deposition (Schovsbo 2001). In this interpretation, the barren intervals would correspond to those parts of the succession which are either completely unfossiliferous (‘true’ or primary barren intervals) or contain noncalcareous fossil fauna (secondary barren intervals), represented by phosphatocopines and protoconodonts (see e.g., Eriksson and Terfelt 2007). Detailed studies of the lower two barren intervals in the Andrarum-3 borehole core have shown that in both cases the intervals comprise an unfossiliferous horizon and a horizon with phosphatocopines (Eriksson and Terfelt 2007; Ahlberg *et al.* 2009; see also Text-fig. 5). It was concluded that the phosphatocopines, i.e., nektobenthic arthropods with morphological adaptations for swimming (Vannier and Abe 1992), preferred oxygen-poor, cooler waters (Ahlberg *et al.* 2009); correlating the presence of the phosphatocopine facies in the succession with the appearance of the exotic trilobites shows that the latter was preceded by an influx of cooler sea-water with low oxygen levels into the Alum Shale Sea of Baltica.

Another issue that needs to be discussed with regard to the appearances of the exotic trilobite fauna is the occurrence of agnostoid arthropods in the studied succession. As shown by Ahlberg and Ahlgren (1996) for Västergötland and by Ahlberg and Terfelt (2012) for Scania, several lower Furongian agnostoid species appear at the base of intervals characterizing the onset of new assemblages of the olenid fauna, i.e., *Olenus* spp. at the base of the *Glyptagnostus reticulatus* Zone and *Parabolina* spp. at the base of the *Pseudagnostus cyclopyge* Zone. A few species of *Olenus* spp. have also been recorded in glacial erratic boulders representing the *Agnostus pisiformis* Zone collected in northern Germany, i.e., *O. amplus* Buchholz, 2003, *O. erraticus* Buchholz, 1991 and *O. maturus* Buchholz, 2003 (Buchholz 1991, 2003), although it is not clear if the erratic boulders represent conglomeratic limestones with a stratigraphically mixed fauna. The number of agnostoid species decreases distinctly upwards in each of these intervals, and there are, for example, no agnostoid species in the *Olenus scanicus* Zone in the first case and extremely few agnostoid species in the interval between the base of the *Parabolina spinulosa* Zone to the base of the *Ctenopyge spectabilis* Zone (Buchholz 1999; Ahlberg and Terfelt 2012, their fig. 2). Comparison of the first occurrence (FO) of the exotic trilobites and the FO of the agnostoid arthropods in the Furongian shows an evident correlation between their occurrences: phase 2, beginning at the base of the *Olenus gibbosus* Zone (Text-fig. 3), corresponds to the ranges of *Glyptagnostus reticulatus reticulatus* (Angelin, 1851), *Aspidagnostus lunulosus* (Kryskov in Borovikov and Kryskov, 1963), *Hypagnostus* aff. *parvifrons* (Linnarsson, 1869) and *Agnostus* (*Homagnostus*) *obesus* (Belt, 1867), whereas phase 3, beginning at the base of the *Parabolina brevispina* Zone (Text-fig. 3), corresponds to the re-appearance of *Agnostus* (*Homagnostus*) *obesus*, and the ranges of *Pseudagnostus cyclopyge* (Tullberg, 1880), *Tomagnostella orientalis* (Lazarenko, 1966), and *Agnostus* (*Homagnostus*) *ultraobesus* Lermontova, 1940 (Ahlberg and Ahlgren 1996; Ahlberg and Terfelt 2012).

In the *Agnostus pisiformis* Zone of the Cambrian Series 3 only the eponymous species is common throughout the zone, whereas the remaining agnostoid species, i.e., *Linguagnostus reconditus* Poletaeva et Romanenko, 1970, *Kormagnostus*? sp., *Hypagnostus* sp. and *Peratagnostus obsoletus* (Kobayashi, 1935), appear in its upper part (Ahlberg and Ahlgren 1996; Ahlberg 2003). So far, no barren interval has been observed at the base of this zone. Interestingly, the zone separates the generally fairly diverse agnostoid–paradoxidid–solenopleurid–conocoryphid assemblages of the Scandinavian Middle Cambrian and the olenid assemblages of the Furongian, and contains very few, in some cases questionable, *Olenus* spp. (Henningsmoen 1957a; Nikolaisen and Henningsmoen 1985; Buchholz 1991, 2003) as well as exotic polymerid trilobites.

The mode of life of agnostoid arthropods is a matter of an ongoing debate, with the inferred life strategies ranging from pelagic (Öpik 1961, 1979; Robison 1972), epifaunal (Pek 1977; Havlíček *et al.* 1993), to benthic (Jaekel 1909; Nielsen 1995, 1997) and nektobenthic (Müller and Walossek 1987). Recent studies have brought strong evidence for a benthic life mode of adult agnostoids (Slavíčková and Kraft 2001; Chatterton *et al.* 2003; Fatka *et al.* 2009; Fatka and Szabad 2011; Ahlberg and Terfelt 2012; Esteve and Zamora 2014). Assuming a benthic mode of life of agnostoids, the correspondence of their ranges and the ranges of exotic trilobites suggests that their appearances are linked with a common factor that resulted in widely distributed benthic organisms.

Dispersal mechanism

Among the exotic trilobite taxa, only species of *Irvingella* display morphological features suggestive of a pelagic mode of life, i.e., large eyes, an elongated body with reduced pleurae, a wide thoracic axis serving as an attachment for large muscles, and flattened pleural spines, coupled with a worldwide distribution in a narrow stratigraphic interval (Rushton 1967; Ahlberg 2003; Rushton and Weidner 2010; see also Text-fig. 8). They are morphologically comparable to the most widely distributed trilobite, the Ordovician *Carolinites genacinaca* Ross, 1951, which is considered to have been epipelagic (Fortey 1985; McCormick and Fortey 1999). Of the remaining exotic trilobite species from Scandinavia, none has morphological properties of the exoskeleton suggestive of a pelagic lifestyle, a point that was already brought up in the case of *Maladioidella* (e.g., Rushton and Hughes 1996). Thus, another factor was responsible for the wide geographical distribution of these trilobites. This factor remains to be explored.

Correlation with global events

As noted above, the appearances of the exotic trilobites are associated with barren intervals in the succession (Text-fig. 3). These barren intervals have been shown to correspond broadly with the biomere boundaries in Laurentia (e.g., Conway Morris and Rushton 1988; Terfelt 2006; Ahlberg *et al.* 2009). The biomere concept, first introduced by Palmer (1965b), refers to significantly thick stratigraphic intervals in the Cambrian of Laurentia, bounded by extinction horizons, recording the decimation of diverse shallow marine trilobite faunas and subsequent immigration of genera from deeper outer-shelf or off-shelf environments (see Taylor 2006 for a detailed overview). The biomeres thus defined include (in ascending order): the Marjumiid, Pterocephaliid, Ptychaspid and "Symphysurinid" biomeres.

Four evolutionary phases have been recognized in each biomere (Stitt 1971, 1975; Palmer 1984; Taylor 2006): 1) an initial phase of adaptive radiation at the base of a biomere; the resulting assemblage is of low diversity, with short stratigraphic ranges, high intraspecific variability and a limited range of morphologies; 2) and 3) represent a stable shelf community; the species have longer stratigraphic ranges, reduced intraspecific variability, and a greater range of morphologies. The top of stage 3 is a mass extinction event that erased most of the taxonomic diversity and morphologic variation gained during phases 1–3; and 4) a thin, critical stratigraphic interval dominated by one opportunistic genus or species that survived the extinction. Phase 4 may contain exotic taxa that migrated from deep water environments. The base of each biomere is marked by the appearance of a low-diversity, olenimorph-dominated fauna immediately above the highest occurrence of the dominant families of the underlying biomere (Taylor 1997).

Ludvigsen (1982) and Westrop (1995) have shown that the biomere boundaries cannot be clearly recognized in deep-shelf to upper-slope settings, and are almost unrecognizable in deeper slope to basinal deposits. In the latter case, the pre-extinction assemblages contain numerous olenimorphs and other deep-water forms, such as agnostoids, and few shallow-water taxa (Pratt 1992) and may also yield some of the exotic taxa that appear for the first time as immigrants in the critical interval in more proximal facies (Ludvigsen 1982).

The factor(s) causing the extinctions remain(s) unknown. Various mechanisms have been suggested. Palmer (1965b, 1984) and Stitt (1971, 1975, 1977) strongly advocated for a rise of the oceanic thermocline that allowed cooler waters from the ocean to invade the shelf and thus exterminate the thermophilic platform taxa. These ideas were strongly opposed by Westrop and Ludvigsen (1987), who excluded the incursion of cool and/or poorly oxygenated waters from the ocean because there was no physical evidence of environmental changes at biomere boundaries. Evidently, the scenario involving cooler and/or anoxic water was most commonly considered to trigger the extinctions and explains the migration of olenimorphs into shallow marine settings (Fortey 1989; Loch *et al.* 1993). This mechanism has gained independent evidence from isotope studies; at biomere boundaries lower $^{87}Sr/^{86}Sr$ ratios pointed to a progressive sea-level rise, whereas more positive $\delta^{13}C$ values upward indicated reduced oxygen concentrations (Saltzman *et al.* 1995; Perfetta *et al.* 1999; Saltzman 1999). Eventually, these studies have resulted in the recognition of a large positive, globally recorded, carbon isotope excursion, known as the Steptoean Positive Carbon Isotope Excursion (SPICE) (Saltzman *et al.* 2000), recognized also in Sweden (Ahlberg *et al.* 2009).

The SPICE, beginning at the first appearance of *Glyptagnostus reticulatus*, and the DICE (a negative Drumian Carbon Isotope Excursion), recorded from the Cambrian Series 3 *Ptychagnostus atavus* Zone and its correlatives (Ahlberg *et al.* 2009), are considered to be associated with rapid eustatic deepening events and with the appearances of agnostoids immediately following the flooding of the shelves (Babcock *et al.* 2006). Global migration of cosmopolitan agnostoids must have been a rapid and synchronous event (Ahlberg *et al.* 2009). The onset of SPICE correlates with biomere extinctions in Laurentia, as well as extinctions recognized in correlatable beds in Australia and South China (Saltzman *et al.* 2000; Peng *et al.* 2004). Thus, as shown by Ahlberg *et al.* (2009), the barren and phosphatocopine intervals recognized by Eriksson and Terfelt (2007) coincide with the extinction event at the end of the Marjumiid Biomere and the same driving mechanism is postulated. If so, then the appearances of the exotic trilobites, following the pattern of agnostoid arthropods in the succession, could also be a result of the same scenario.

A very strong influence of East Gondwanan taxa, similar to that in the studied assemblage (Text-figs 8–10), has been observed in the Furongian of West Gondwana (Shergold and Sdzuy 1984, 1991; Shergold *et al.* 2000; Álvaro *et al.* 2003). The recognized trilobite biofacies include: 1) an Idamean/Steptoean biofacies with aphelaspidoid elements; 2) an Iverian/Sunwaptan biofacies with *Maladioidella*; and 3) a terminal Cambrian assemblage with *Cordylodus proavus* Müller, 1959 (Álvaro *et al.* 2003). The two lower biofacies seem to correspond to phase 1/phase2 and phase 3 assemblages as recognized in Sweden (Text-fig. 3). The occurrence of trilobite assemblages with similar characteristic morphologies suggests that a common factor was responsible for their wide distribution.

In conclusion, the appearances of exotic trilobites in the Furongian succession of Sweden appear to be an effect of an influx of cooler sea water with low oxygen levels into the Alum Shale Sea (a eustatic sea-level rise) that resulted in the colonization of the shelf areas by benthic organisms: agnostoid arthropods, exotic trilobites and new assemblages of olenids (*Olenus* spp. at the base of the *Olenus* Superzone and *Parabolina* spp. in the *Parabolina* Superzone). With their morphologies and life habits highly adapted to an oxygen-depleted environment (e.g., Clarkson and Taylor 1995; Clarkson *et al.* 1998; Fortey 2000; Schovsbo 2000, 2001; Balseiro *et al.* 2011; Clarkson 2011), the olenid trilobites successfully evolved during these events in the Alum Shale Sea of Baltica.

CONCLUSIONS

The uppermost Cambrian Series 3 and lower Furongian Alum Shale facies of Sweden have yielded seventeen taxa of exotic trilobites representing eight families. Most taxa are described for the first time from the Cambrian of Scandinavia and supplement the data on exotic trilobites from the area. The exotic fauna shows strong affinities with East Gondwana, Laurentia, Kazakhstania, and Siberia. Exotic trilobites appear in the succession directly after periods of very low oxygen concentrations in the Alum Shale Sea and their occurrences correspond to the appearances of agnostoid arthropods in the succession. Global transgressive events causing the influx of cool and/or oxygen-depleted waters onto the shelf of the Baltica palaeocontinent, coinciding with the biomere boundaries in Laurentia, seem to be the driving factors for the appearances of these trilobites in the Alum Shale Sea.

PALAEONTOLOGICAL NOTES

Material and methods

The material includes 48 specimens collected by TW and JA in Sweden as well as seven specimens from glacial erratic boulders collected by TW in Denmark. Additionally, the original specimens of *Acrocephalites* (?) *rarus* Westergård, 1922, *Taenicephalus*? *peregrinus* Henningsmoen, 1957, *Conokephalina olenorum* Westergård, 1922, and *Liostracus pusillus* Westergård, 1922, from Västergötland and Scania were also studied. All newly collected specimens are housed at the Department of Geology, Lund University; figured specimens are numbered with the prefix Lund Original (LO). The type specimens of *Acrocephalites* (?) *rarus* and *Taenicephalus*? *peregrinus* are housed in the Museum of Evolution of Uppsala University (PMU) and those of *Conokephalina olenorum* and *Liostracus pusillus* are in the Main Collection of Sveriges Geologiska Undersökning (Geological Survey of Sweden) in Uppsala (SGU). Accompanying specimens of olenid trilobites and/or agnostoid arthropods were studied to determine the stratigraphic position of the samples. The specimens are represented by variably preserved detached parts of the exoskeleton, with cranidia prevailing over pygidia and librigenae. In many cases the test is also partly preserved, but the specimens are usually damaged and corroded. Large-sized cranidia often occur. The specimens were measured with callipers with an accuracy of 0.1 mm. Various parameters were calculated and the values are presented as percentages; a range of values is given for 2 to 4 specimens, over 5 specimens measured give a mean value with standard deviation; in the latter case the number of specimens measured is given in parentheses. The specimens were photographed with a digital camera after coating with ammonium chloride. Abbreviations used for the localities: DK – Denmark; J – Jämtland; N – Närke; Ög – Östergötland; Ö – Öland; S – Scania; Vg – Västergötland.

Systematic descriptions

Class Trilobita Walch, 1771
Order Olenida Adrain, 2011[3]
Family Aphelaspididae Palmer, 1960
Subfamily Aphelaspidinae Palmer, 1960

Genus *Aphelaspis* Resser, 1935

TYPE SPECIES: *Aphelaspis walcotti* Resser, 1938, from the Furongian (Steptoean) Nolichucky Formation, Virginia, USA, subsequently designated by Palmer (1953). The type species of the genus stated by Jell and Adrain (2003), *Conocephalites depressus* Shumard, 1861, is not valid as explained earlier by Palmer (1953).

REMARKS: Palmer (1953, 1954, 1960, 1962, 1965a) discussed the concept of the genus, provided emended diagnoses, and described the Laurentian species. Shergold and Cooper (1985), Shergold and Webers (1992) and Cooper *et al.* (1996) described species from the Furongian of Antarctica. Representatives of the genus have also been recorded from the lower Furongian of Wales (Allen *et al*. 1981; Rushton 1983; Allen and Jackson 1985), the Holy Cross Mountains in Poland (Żylińska 2001, 2002; Żylińska *et al.* 2006), north-central Kazakhstan (Ivshin 1956), Australia (Henderson 1976; Powell *et al*. 1981; Shergold 1982), South China (Peng 1992) and Siberia (Zhuravleva and Rozova 1977). The North American, Antarctic (Heritage Range), Chinese and Siberian occurrences are generally from beds with *Glyptagnostus reticulatus sensu lato*, whereas the genus appears in slightly younger strata in Australia and Antarctica (Northern Victoria Land), and probably also in Kazakhstan (Ivshin 1961; Shergold and Webers 1992). The occurrence of *Aphelaspis* spp. in the *Agnostus pisiformis* Zone of Sweden (see below), i.e., in beds below the first appearance of *Glyptagnostus reticulatus*, is interesting because it may be the earliest record of the genus on a global scale. However, *Glyptagnostus reticulatus sensu lato* is a species composed of at least two morphotypes, the weakly reticulated *G. reticulatus angelini* (Resser, 1938) and the strongly reticulated *G. reticulatus reticulatus* (Angelin, 1851). The two taxa are regarded either as valid (Palmer 1962) or invalid subspecies, with the two morphotypes intergrading into one another (Pratt 1992). On a global scale, the weakly reticulated morphotype always precedes the strongly reticulated one (Peng *et al.* 2004). In Scandinavia, *G. reticulatus* is represented by the strongly reticulated morphotype, i.e., *G. reticulatus reticulatus*, which occurs in the *Olenus gibbosus* through the *Olenus truncatus* zones (Ahlberg and Ahlgren 1996). In Laurentian sections, the FAD of *Aphelaspis* generally falls within beds with the strongly reticulated morphotype of *G. reticulatus s.l.*, and the base of the *Olenus* Superzone *sensu* Nielsen *et al.* (2014) can be correlated with the base of the *Aphelaspis* Zone. However, Palmer (1962) has also shown that *Aphelaspis* spp. may co-occur with *G. reticulatus angelini*. The Swedish occurrences of *Aphelaspis* (see below) in the *Agnostus pisiformis* Zone may correspond to the Laurentian occurrences of *Aphelaspis* in the Marjuman *Crepicephalus* Zone (see Palmer 1962, his table 1), rather than representing an early appearance of *Aphelaspis* in Baltica.

Aphelaspis sp. A
(Text-fig. 12A–C)

MATERIAL: Three incomplete cranidia: LO12047t and LO12048t from Hjälmsäter (Vg); LO12049t from Skonberga (Ög).

DESCRIPTION: Cranidium with low relief, trapezoidal, width at level of palpebral lobes almost equal to total cranidial length; posterior width about 1.5 of total cranidial length. Glabella 68–73% of total cranidial length, forwardly tapering, bluntly terminated anteriorly. Faint traces of three backwardly oblique, wide, shallow, almost effaced lateral glabellar furrows becoming gradually shorter towards the anterior. Distance between S1 and S2 larger than between S2 and S3. Distinct, low-relief eye-ridges, only slightly back-

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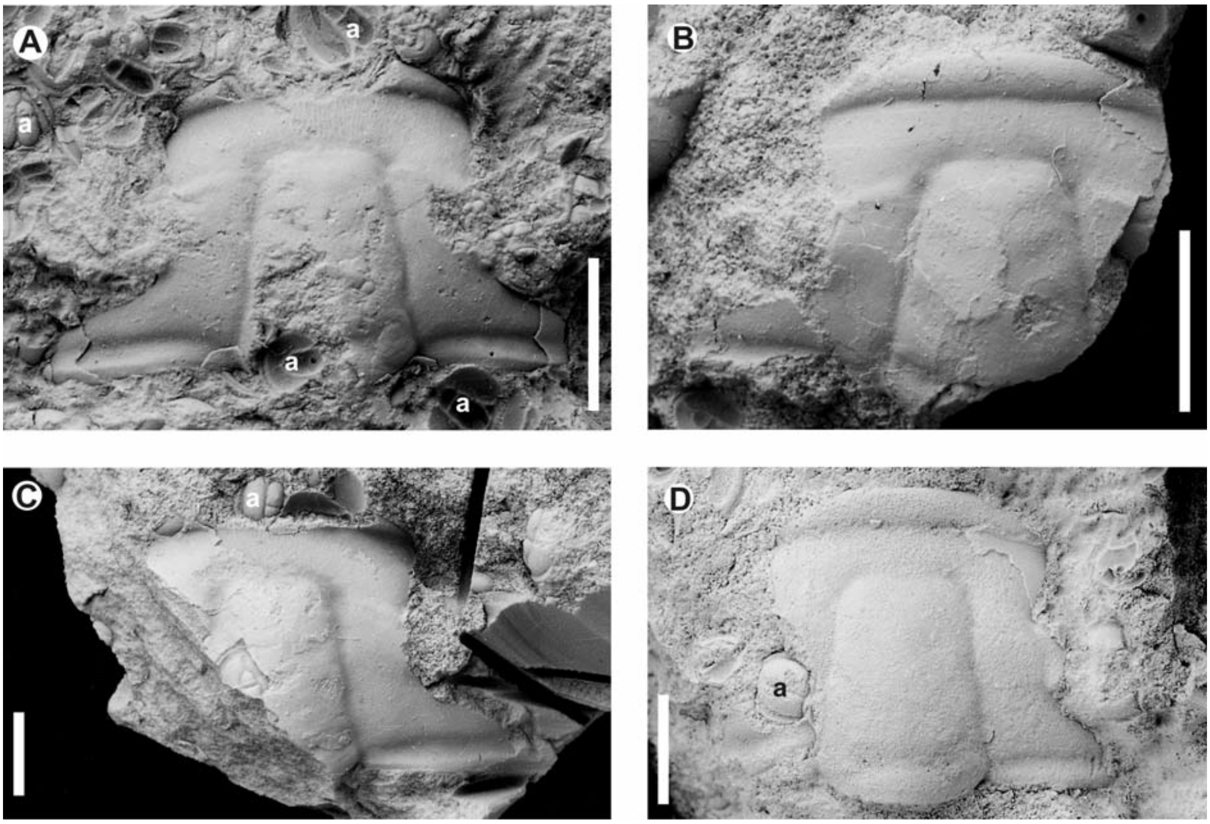
[3] According to Adrain (2011, p. 107), this new ordinal concept includes all trilobites with a highly specialized cephalic border structure, often reflected by the presence of pits in the anterior border furrow.



Text-fig. 12. A-C – *Aphelaspis* sp. A from the Cambrian Series 3, *A. pisiformis* Zone of Sweden. A – almost complete cranidium, LO12049t, Skonberga (Ög); B – incomplete cranidium, LO12047t, Hjälmsäter (Vg); C – incomplete cranidium, LO12048t, Hjälmsäter (Vg). D – *Aphelaspis* sp. B, incomplete cranidium, LO12050t, Cambrian Series 3, *A. pisiformis* Zone at Skonberga (Ög). Accompanying fauna: a – *Agnostus pisiformis* (Wahlenberg, 1818). Scale bars represent 0.5 cm

wardly oblique. Anterolateral corners of glabella with distinct pits. Frontal area well-developed, with convex, slightly upturned anterior border separated from preglabellar field by distinct, almost straight anterior border furrow. Preglabellar field 57–63% of frontal area, with a distinct longitudinal caecal pattern. Preocular areas almost flat, only slightly sloping forwards anterolaterally. Palpebral lobes not preserved, but slight swellings on the fixigenae indicate that they had attained about 20% of total cranidial length; the lobes are barely defined by a palpebral furrow and are located from the glabella at a distance of less than half of the glabellar width at mid-palpebral level. Occipital ring only partly preserved on the counterpart of one specimen (LO12047t), probably undifferentiated. Anterior facial sutures diverging slightly, then turning strongly inwards across border to meet anterior margin lateral to the side of the glabella. Posterior facial suture sigmoidal, enclosing transversely triangular, long posterolateral limbs bearing relatively deep and wide posterior border furrows. Posterior margin with faintly marked fulcrum.

MEASUREMENTS: Cranidial length 10.3–15 mm, cranidial width at palpebral mid-length 9–14 mm, posterior cranidial width 18–24 mm.

REMARKS: Assignment of the specimens to *Aphelaspis* is justified by a forward-tapering glabella with a bluntly rounded or truncated anterior lobe, faint lateral glabellar furrows, and a well-defined, slightly upturned anterior border. The species is morphologically most similar to the type species, *A. walcotti* (see Rasetti 1965), but differs in having a flatter preglabellar field and glabella, and slightly wider interocular cheeks. *Aphelaspis* cf. *walcotti* from the lower Furongian of the Heritage Range, West Antarctica (Shergold and Webers 1992) has a more convex glabella and anterior border, which is slightly wider sagittally, and narrower interocular cheeks. *Aphelaspis* sp. A differs from *Aphelaspis* sp. B from contemporary strata (see description below) in having a more tapering glabella, a cranidium slightly wider posteriorly, a slightly shorter glabella, eye ridges and pits in the anterolateral corners of the glabella, probably a slightly shorter palpebral lobe that is poorly distinguished from the fixigena by an indistinct palpebral furrow, an undifferentiated occipital ring, and lacking an indentation in the anterior margin of the glabella.

Another trilobite from the *Agnostus pisiformis* Zone, *Olenus alpha* Henningsmoen, 1957 of Norway was considered a representative of *Simulolenus* Palmer, 1965[4] (Henningsmoen 1957a; Nikolaisen and Henningsmoen 1985), a genus characteristic of the Steptoean *Dunderbergia* Zone of the Great Basin, USA (Palmer 1965a). The specimens at hand differ from *Simulolenus alpha* (Henningsmoen, 1957) in having much larger dimensions, eye-ridges that are more backwardly oblique, and a sagittally much wider anterior border.

OCCURRENCE: Cambrian Series 3, *Agnostus pisiformis* Zone in Sweden.

Aphelaspis sp. B
(Text-fig. 12D)

MATERIAL: One incomplete cranidium: LO12050t from Skonberga (Ög).

DESCRIPTION: Cranidium with low relief, trapezoidal, width at mid-palpebral level equal to total cranidial length; posterior width about 1.3 of total cranidial length. Glabella 73% of total cranidial length, forwardly tapering, bluntly terminated anteriorly; anterior margin of glabella with small indentation. Faint traces of three backwardly oblique, almost effaced lateral glabellar furrows. Eye-ridges not visible. Anterolateral corners of glabella poorly marked. Frontal area well-developed, with convex, slightly upturned anterior border separated from preglabellar field by distinct, almost straight anterior border furrow. Preglabellar field 58% of anterior border. Preocular areas relatively flat, slightly sloping forwards anterolaterally. Palpebral lobe gently arcuate, 24% of total cranidial length, defined by narrow palpebral furrow, located from glabella at a distance of less than half of glabellar width at mid-palpebral level. Occipital ring composite, with faint trace of median knob located slightly posteriorly, separated from glabella by wide and shallow occipital furrow. Anterior facial sutures diverging from glabella, then turning strongly inwards across border to meet anterior margin lateral to the side of the glabella. Posterior facial suture almost straight, enclosing transversely triangular posterolateral limbs bearing moderately wide posterior border furrows. Posterior margin with very faintly marked fulcrum.

MEASUREMENTS: Cranidial length 14.8 mm, cranidial width at palpebral mid-length 15.5 mm, posterior cranidial width 20 mm.

REMARKS: Assignment to *Aphelaspis* is justified by the following features: a tapering forward glabella with a truncated anterior lobe, faint lateral glabellar furrows, and a well-defined, slightly upturned anterior border. The specimen is closest to *A. subdita* Palmer, 1962 from the Steptoean *Aphelaspis* Zone in Nevada, USA (Palmer 1962, 1965a) but differs in having more distinct lateral glabellar furrows, a narrower glabella and a sagittally shorter preglabellar field. *Aphelaspis* cf. *subdita* from the lower Furongian of the Heritage Range, West Antarctica (Shergold and Webers 1992) has a distinctly longer preglabellar field and a flatter glabella. For differences between *Aphelaspis* sp. B and *Aphelaspis* sp. A, see above.

OCCURRENCE: Cambrian Series 3, *Agnostus pisiformis* Zone in Sweden.

Genus *Olentella* Ivshin, 1955[5]

TYPE SPECIES: *Olentella olentensis* Ivshin, 1955, *Aphelaspis*–*Kujandaspis* Zone, Sakian, Furongian, central Kazakhstan, OD.

REMARKS: The genus was erected for specimens from the Furongian *Aphelaspis*–*Kujandaspis* Zone in Kazakhstan (Ivshin 1955, 1956). Species assigned to *Olentella* are listed in Shergold *et al.* (1976, 2000) and Romanenko (1988). Its representatives have been found in Kazakhstan, Siberia, the Gorny Altai Mountains, Antarctica, Morocco, southern France and northwest Canada (Romanenko 1988; Shergold *et al.* 2000; Text-fig. 8).

Olentella rara (Westergård, 1922)
(Text-fig. 13A–F)

1922. *Acrocephalites* (?) *rarus* n. sp.; Westergård, pp. 123, 124, fig. 39.

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[4] Pratt (1992) and Jell and Adrain (2003) consider *Simulolenus* Palmer, 1965 as a junior subjective synonym of *Olenus* Dalman, 1827.

[5] According to Shergold and Cooper (1985) and Shergold *et al.* (2000), the year of establishing the genus is 1955 and not 1956 as commonly accepted (e.g., Rozova 1968; Shergold *et al*. 1976; Destombes and Feist 1987; Romanenko 1988).

non 1981. *Olentella rara* Orłowski [sic]; Allen, Jackson and Rushton, p. 308 [= *Aphelaspis rara* (Orłowski, 1968)].
non 1983. *Olentella rara* (Orłowski); Rushton, p. 112 [= *Aphelaspis rara* (Orłowski, 1968)].
non 1985. *Olentella rara* (Orłowski); Rushton in Allen and Jackson, pl. 4, fig. 2 [= *Aphelaspis rara* (Orłowski, 1968)].
1997. *Boestrupia rara* (Westergård, 1922); Rudolph, pp. 40, 41, text-figs 1, 2; pl. 5, figs 1, 2.
2013. *Olentella rara* (Westergård, 1922); Żylińska and Weidner, p. 71, fig. 2A.

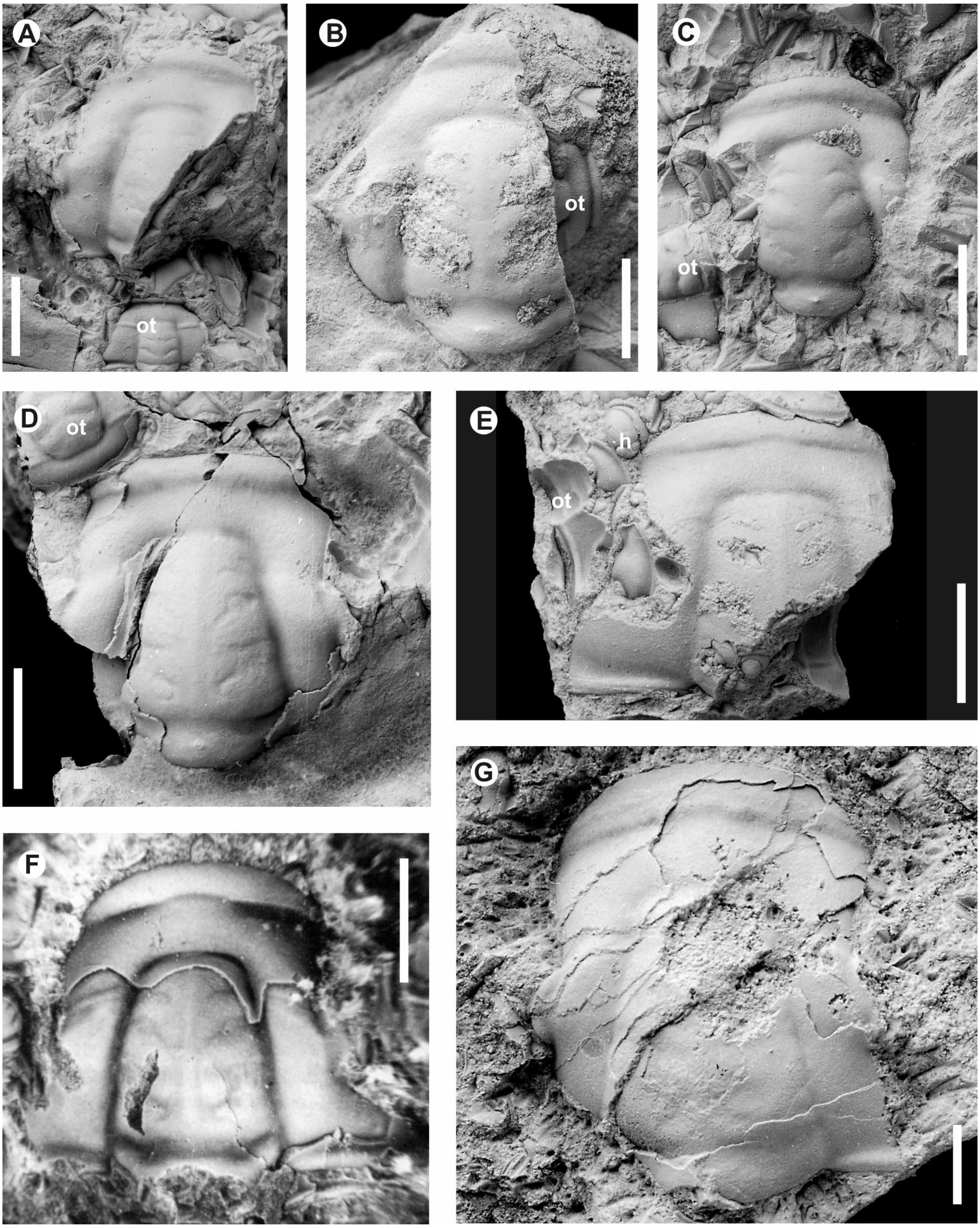
TYPES: According to Rudolph (1997), the holotype is specimen PMU Vg. 11 (Text-fig. 13A), illustrated also by Westergård (1922, fig. 39) and Rudolph (1997, Textabbildung 1), from the *Olenus gibbosus* Zone of Lugnåsberget, Västergötland. However, Westergård (1922, pp. 123, 124) never selected the holotype, therefore the specimen illustrated in Westergård (1922, fig. 39) should be treated as a lectotype.

MATERIAL: Five incomplete cranidia: PMU Vg. 11 from Lugnåsberget (Vg); LO12051t from Kappagården (Vg); LO12052t and LO12053t from Vilske (Vg); LO12054t from Pusabäcken (Vg).

DESCRIPTION: Cranidium fairly convex, trapezoidal, width at level of palpebral lobes equal to total cranidial length; posterior width not measurable but probably about 1.5 of total cranidial length. Glabella 71–76% of total cranidial length, forwardly tapering, anterior lobe bluntly terminated to vaguely triangular anteriorly. Anterolateral corners of glabella relatively well marked. Glabella with faint median keel. Four distinct lateral glabellar furrows, directed obliquely backwards; S1 short, rather straight, directed backwards, covering inner half of glabella; S2 long, rather straight, directed only slightly backwards, reaching axial furrow; S3 longest, arched, directed backwards and reaching axial furrow. Faint trace of fourth lateral glabellar furrow visible in specimens without the test (Text-fig. 13C, D, F); it is shortest, slightly arched, transverse or slightly directed forwards and reaches the axial furrow. Ocular ridges barely visible, strongly oblique, extending from axial furrows outwards and backwards at level slightly anterior to S3. Frontal area well developed, 24–29% of total cranidial length, with faintly visible caecal pattern. Preglabellar field 67–71% of frontal area, anterior border convex, separated from almost flat preglabellar field by shallow anterior border furrow, which becomes shallower to slightly anteriorly curved medially. Preocular areas slightly convex, sloping forwards anterolaterally. Palpebral lobe gently arcuate, 17–22% of total cranidial length, defined by faint palpebral furrow which is deeper at anterior and posterior terminations of the palpebral lobe, located from glabella at a distance of less than half of glabellar width at mid-palpebral level. Occipital ring longest sagittally, with small median knob, separated from glabella by wide and deep sigmoidal occipital furrow. Anterior facial sutures diverging slightly from glabella, then turning strongly inwards across border to meet anterior margin lateral to the side of the glabella. Posterior facial suture not preserved in the studied specimens; its course on a specimen from a glacial erratic boulder in Denmark (Rudolph 1997, his pl. 5 and Text-fig. 13F herein) suggests that it is almost straight and encloses transversely triangular posterolateral limbs that bear wide and deep posterior border furrows.

MEASUREMENTS: Cranidial length 11.6–14.7 mm, cranidial width at mid-palpebral level 11.5–14.5 mm (cranidial posterior width not measurable).

REMARKS: Assignment of the studied specimens to *Olentella* is justified by a forward-tapering, truncated glabella with a slight median keel, a sagittally wide preglabellar field, an anterior border furrow which is shallower and slightly anteriorly curved medially, a convex anterior border, a relatively deep occipital furrow and the presence of a median knob on the occipital ring. From *O. olentensis*, the type species, they differ in having a less tapering glabella which is more truncated and a sagittally slightly shorter preglabellar field and anterior border (Ivshin 1956). In comparison to the specimens at hand, *Olentella* cf. *olentensis* from the lower Furongian of the Northern Victoria Land, Antarctica, has a sagittally shorter preglabellar field (Shergold *et al.* 1976). *Olentella shidertensis* Ivshin, 1956 from the same strata as the type species has the preglabellar field and anterior border of approximately the same sagittal length (Ivshin 1956; Shergold and Cooper 1985). *Olentella ivshini* Romanenko, 1988 from the Furongian of the Gorny Altai Mountains has a slightly wider glabella with relatively deeper axial and anterior furrows, exsagittally longer palpebral lobes, and the anterior border and the preglabellar field are subequal in length (Romanenko 1988). The specimens at hand are quite similar to *Olentella africana* Feist, 1987 from the Moroccan Anti-Atlas (Destombes and Feist 1987) and *Olentella* sp. cf. *africana* from the Montagne Noire, France (Shergold *et al.* 2000), but differ in having the preglabellar field sagittally longer than the anterior border.



Text-fig. 13. A-E – Cranidia of *Olentella rara* (Westergård, 1922) from the Furongian of Sweden. A – lectotype, PMU Vg. 11, exact horizon unclear, probably from Lugnåsberget (Vg); original of Westergård (1922, text-fig. 39); B – LO12052t, *O. truncatus* Zone at Vilske (Vg); C – LO12051t, *O. gibbosus* Zone at Kappagården (Vg); D – LO12053t, *O. truncatus* Zone at Vilske (Vg); E – LO12054t; *O. gibbosus* Zone at Pusabäcken (Vg). F – *Boestrupia rara* (Westergård, 1922) from the *O. gibbosus* Zone in a glacial erratic boulder collected at Bøstrup (DK); original of Rudolph (1997, pl. 5). G – Cranidium of *Olentella* aff. *rara* (Westergård, 1922), LO12055t, *O. truncatus* Zone at Mon (J). Accompanying fauna: ot – *Olenus truncatus* (Brünnich, 1781), h – *Homagnostus obesus* (Belt, 1867). Scale bars represent 0.5 cm

The genus *Boestrupia* Rudolph, 1997 was based on *Acrocephalites*(?) *rarus* Westergård, 1922. Following assignment of *A*.(?) *rarus* to *Olentella*, *Boestrupia* becomes a junior subjective synonym of the latter.

The binomen *Olentella rara* has also been used by Allen *et al.* (1981), Rushton (1983) and Allen and Jackson (1985) to describe specimens from the Furongian of Wales and the Holy Cross Mountains, Poland, that have previously been assigned to *Olenus rarus* Orłowski, 1968. This affiliation was later questioned e.g., by Shergold *et al.* (2000); as shown by Żylińska (2001), the specimens are best assigned to *Aphelaspis rara* (Orłowski, 1968) and clearly represent a different taxon than *Olentella rara* (Westergård, 1922). According to ICZN Code (Ride *et al.* 1999), Article 59.2, the specific name *Olentella rara* (Orłowski, 1968) does not have to be replaced on account of the homonymy with *Olentella rara* (Westergård, 1922), because the two taxa are now not considered congeneric.

OCCURRENCE: Furongian, *Olenus gibbosus* and *Olenus truncatus* zones in Sweden (this paper) and in glacial erratic boulders in Denmark (Rudolph 1997).

Olentella aff. *rara* (Westergård, 1922)
(Text-fig. 13G)

MATERIAL: One incomplete cranidium: LO12055t from Mon (J).

DESCRIPTION: Cranidium sagittally convex and transversely flat, narrowly trapezoidal, width at level of palpebral lobes is 0.8 of cranidial length, posterior width not measurable. Glabella 70% of total cranidial length, strongly forwardly tapering. Anterior lobe bluntly terminated. Axial furrows narrow and shallow. Faint traces of two of the probably four lateral glabellar furrows are visible in the posterior half of the glabella. Ocular ridge narrow, strongly oblique, extending from the axial furrow outwards and backwards. Frontal area well-developed, 30% of total cranidial length. Preglabellar field 64% of frontal area, anterior border convex, separated from preglabellar field by shallow and wide anterior border furrow. Preglabellar field with faint median knob, so that the anterior border furrow is medially slightly curved towards the anterior. Preocular areas slightly curved downwards anterolaterally. Palpebral lobe gently arcuate, 17% of total cranidial length, defined by a narrow and shallow palpebral furrow, located from glabella at a distance of less than half of glabellar width at mid-palpebral level. Occipital ring longest sagittally, with small median knob, separated from glabella by a shallow and sigmoidal occipital furrow. Anterior facial sutures diverging slightly from glabella, then turning strongly inwards across border to meet anterior margin lateral to the side of the glabella. Posterior facial suture not preserved.

MEASUREMENTS: Cranidial length 28.6 mm, cranidial width at mid-palpebral level 25.4 mm (cranidial posterior width not measurable).

REMARKS: Although bearing a number of features typical of *Olentella rara* (Westergård, 1922), the studied specimen differs in having a relatively longer frontal area and anterior border. Because it is represented only by one large cranidium (approximately twice as large as the specimens of *O. rara* described above), it is not clear whether this difference results from maturity/gerontism or the specimen represents a separate taxon; hence it is left under open nomenclature. Most illustrated specimens of *Olentella* are medium-sized trilobites, with cranidia less than 20 mm in length (see above for references); larger cranidia have been noted only in material from Kazakhstan (Ivshin 1956, pp. 67, 69).

OCCURRENCE: Furongian, *Olenus truncatus* Zone in Sweden.

Family Idahoiidae Lochman, 1956

Genus *Maladioidella* Endo in Endo and Resser, 1937

TYPE SPECIES: *Maladioidella splendens* Endo in Endo and Resser, 1937, from the Furongian Taishan Formation, Liaoning Province, China, OD.

REMARKS: Species assigned to this genus were listed and discussed by Shergold (1975, 1993), Shergold *et al.* (1983), Shergold and Sdzuy (1984), Fortey (1994), Rushton and Hughes (1996) and Rushton *et al.* (2002). *Aphelaspis* sp. from Tasmania (Jell *et al.* 1991, their fig. 13A–E) may also represent a species of *Maladioidella*. Due to high variation of pygidial morphologies coupled with considerable conservatism in cranidial morphology, the genus has been considered polyphyletic (Rushton and Hughes 1996). Based on the shape of the glabella, degree of effacement, structure of the preglabellar area, relationship of the preglabellar field to the glabella and the morphology of the librigena it has been assigned to the Idahoiidae (e.g., Shergold and Sdzuy 1984; Rushton and Hughes 1996;

Jell and Adrain 2003), and this view is followed here. Species of the genus show an unusually wide palaeogeographic and facies-independent distribution, having been reported from shelf and slope settings along the northern margin of Gondwana and Siberia, occurring equatorially and at higher latitudes on both sides of the palaeoequator (Rushton and Hughes 1996; Rushton *et al.* 2002; Text-fig. 10I). The genus is characteristic of a narrow stratigraphic interval and co-occurs with e.g., *Parabolina spinulosa* and/or *Pseudagnostus cyclopyge*, suggesting a correlation with the Iverian Stage of Australia (Shergold and Sdzuy 1984; Rushton and Hughes 1996).

Maladioidella abdita (Salter, 1866)
(Text-fig. 14A–J)

1866. *Conocoryphe abdita*, n. sp.; Salter, p. 306, pl. 5, fig. 13.
1996. *Maladioidella abdita* (Salter); Rushton and Hughes, pp. 249–252, figs 2–4 [with full synonymy].
2000. *Maladioidella abdita* (Salter); Pegel, fig. 14.7.
part 2001. *Pedinocephalus peregrinus* Henningsmoen, 1957; Weidner, pp. 65, 66, figs 5 (left cranidium only), 7.
2005. *Anomocare*? *jarmenensis* n. sp.; Buchholz, pp. 17, 18, pl. 1, fig. 7.
part 2008. *Maladioidella abdita* (Salter); Lazarenko *et al.* in Rozanov and Varlamov, pl. 18, figs 1, 4, non fig. 2 = probably a species of *Olentella*.
2013. *Maladioidella abdita* (Salter, 1866); Żylińska and Weidner, p. 71, fig. 2C.

TYPES: The lectotype is cranidium GSM 19826 (British Geological Survey), figured by Lake (1931, pl. 16, fig. 12), from the Furongian *Parabolina spinulosa* Zone in the Ogof Ddû section, east of Criccieth, Gwynedd, North Wales, UK, selected and re-illustrated by Rushton and Hughes (1996, p. 249, fig. 3a1).

MATERIAL: Five incomplete cranidia, five librigenae, one pygidium and three doublure fragments: LO12056t, LO12057t, LO12058t, LO12059t, LO12060t and an unnumbered specimen from Hällekis (Vg); an unnumbered specimen from Trolmen (Vg); an unnumbered specimen from Hjälmsäter (Vg); LO12061t, LO12062t and LO12063t from Råbäck (Vg); LO12064t from Vilske (Vg); an unnumbered specimen from a glacial erratic boulder at Palsgård cliff (DK); LO12065t from a glacial erratic boulder at Melbjerg cliff (DK).

DESCRIPTION: Cephalon broadly semi-circular. Cranidium trapezoidal, with low relief, posterior width about 1.7 of total cranidial length. Glabella long, 70–74% of total cranidial length, convex sagittally (especially in juveniles), slightly forwardly tapering and truncated anteriorly. Anterolateral corners of glabella well marked. Glabella with faint median keel. Faint traces of three lateral glabellar furrows that are backwardly oblique. Ocular ridges narrow, distinct, extending from the axial furrows at a level that is slightly posterior to the glabellar anterolateral corner, and directed slightly backwards. Frontal area well developed, 26–30% of total cranidial length. Preglabellar field about 40% of frontal area, with strongly convex anterior border, separated from preglabellar field by a narrow and distinct anterior border furrow. Palpebral lobe not preserved in the available specimens. Occipital ring with small median knob, separated from glabella by narrow and deep, slightly sigmoidal occipital furrow which becomes shallower laterally. Anterior facial suture diverging strongly from glabella, then turning strongly inwards across border to meet anterior margin slightly lateral to the side of the glabella. Posterior facial suture diverging strongly from glabella, straight, then curving backwards to enclose narrow, triangular posterolateral limbs with wide and relatively deep posterior border furrows. Anterior border and doublure with densely spaced terrace lines (Text-fig. 14J).

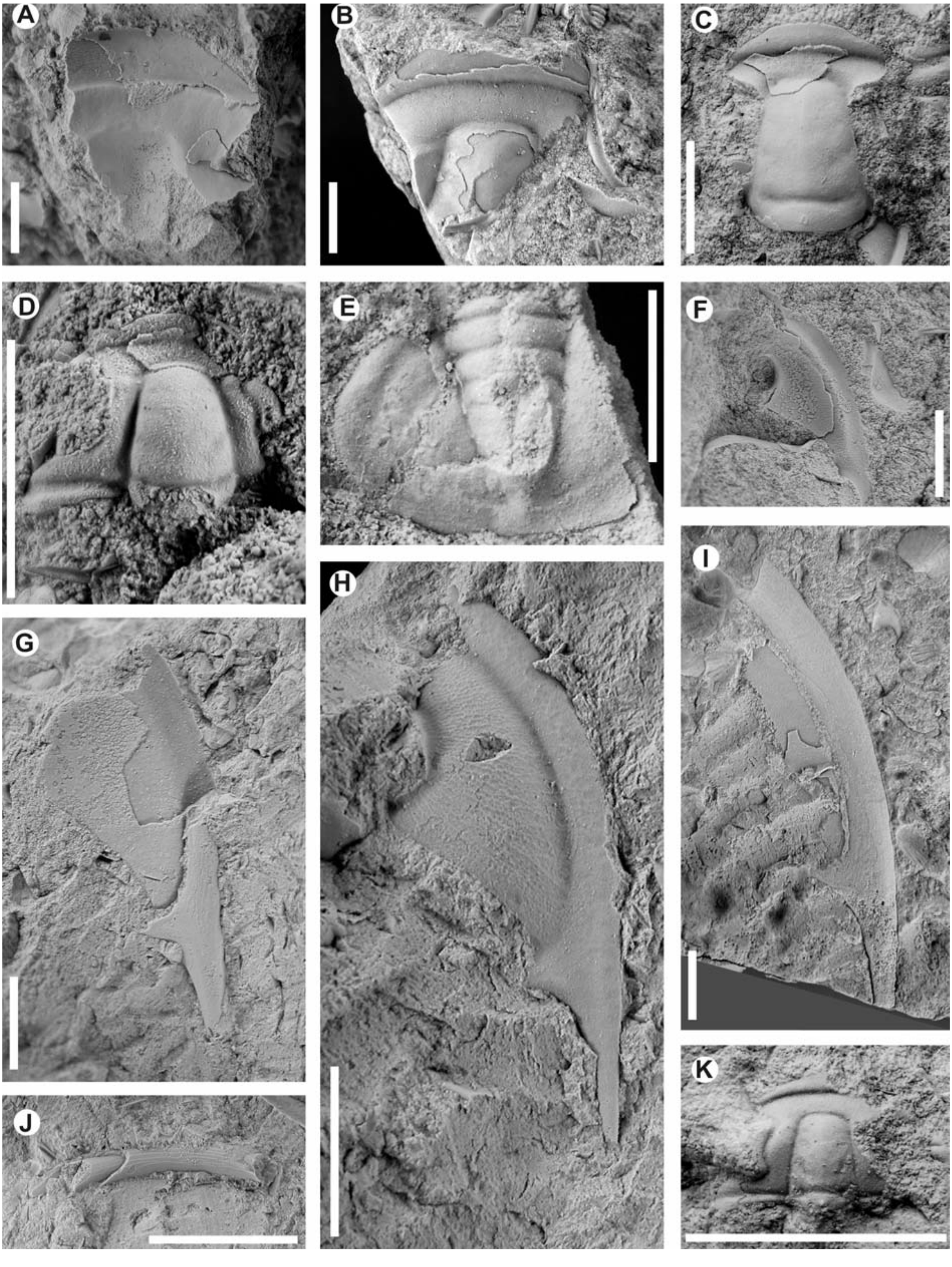
Librigena with short, stout-based spine, in line with course of lateral margin. Border wide, lateral border furrow well defined and wide. Posterior border furrow very short and shallower. Inner spine angle slightly obtuse. Palpebral socle distinctly elevated. Surface of librigena covered by caecae, doublure of the librigenae covered by dense terrace lines.

Pygidium oval-shaped, slightly wider than long. Axis tapering strongly backwards, sub-divided into three segments and a fairly long, fused terminal piece. Pleural fields with shallow and wide pleural furrows. Border flat, not delineated from pleural fields.

Text-fig. 14. A-J – *Maladioidella abdita* (Salter, 1866) from the Furongian of Sweden and glacial erratic boulders in Denmark. A – incomplete cranidium, LO12063t, *P. brevispina* or *P. spinulosa* Zone at Råbäck (Vg); B – incomplete cranidium, LO12056t, probably *P. brevispina* Zone at Hällekis (Vg); C – incomplete cranidium, LO12065t, probably *P. spinulosa* Zone in a glacial erratic boulder collected at Palsgård cliff (DK); original of Weidner (2001, text-fig. 5, left cranidium); D – incomplete juvenile cranidium, LO12062t, probably *P. brevispina* Zone at Råbäck (Vg); E – incomplete pygidium, LO12064t, *P. brevispina* Zone at Vilske (Vg); F – negative of librigena, LO12061t, probably *P. brevispina* Zone at Råbäck (Vg); G – incomplete librigena, LO12059t, *P. brevispina* or *P. spinulosa* Zone at Hällekis (Vg); H – librigena, LO12058t, *P. brevispina* Zone at Hällekis (Vg); I – incomplete librigena, LO12060t, *P. brevispina* or *P. spinulosa* Zone at Hällekis (Vg); J – doublure fragment, LO12057t, *P. brevispina* or *P. spinulosa* Zone at Hällekis (Vg). K – *Maladioidella* sp., incomplete cranidium, LO12066t, probably *P. spinulosa* Zone in a glacial erratic boulder collected at Melbjerg cliff (DK). Scale bars represent 0.5 cm

MEASUREMENTS: Cranidial length 4.0–8.4 mm, fragmentary specimens indicate individuals possessing cranidia that were at least 23 mm long.

REMARKS: The specimens at hand, although incomplete, have all the features of *Maladioidella abdita* as described by Rushton and Hughes (1996). The only illus-



trated cranidium of *Anomocare? jarmensis* Buchholz, 2005 from the *Leptoplastus paucisegmentatus* Zone in a glacial erratic boulder collected in Germany (Buchholz 2005, pl. 1, fig. 7) is characterized by a well developed frontal area, sub-divided into a sagittally long preglabellar field and a strongly convex anterior border; a glabella that tapers slightly forwards and is truncated anteriorly; three backwardly oblique lateral glabellar furrows, a faint median keel and an occipital ring with a small median knob, separated from the glabella by a narrow and deep, slightly sigmoidal occipital furrow. The proportions of the illustrated cranidium are also comparable to the studied specimens. Thus, *Anomocare*? *jarmensis* should be regarded as a junior subjective synonym of *M. abdita*.

OCCURRENCE: Furongian; *Parabolina brevispina* and *Parabolina spinulosa* zones in Sweden (this paper) and North Wales (Rushton and Hughes 1996); probably *Parabolina spinulosa* Zone in glacial erratic boulders in Denmark (this paper); *Leptoplastus paucisegmentatus* Zone in a glacial erratic boulder in Germany (Buchholz 2005); *Maladioidella abdita* Zone in exposures along the Khos-Nelege River, Siberia (Lazarenko *et al.* in Rozanov and Varlamov 2008). *Maladioidella* aff. *abdita* has been noted in the Furongian of Severnaya Zemlya, Russia (Rushton *et al.* 2002), in beds coeval with the lower part of the *Protopeltura* Superzone of Nielsen *et al*. (2014).

Maladioidella sp.
(Text-fig. 14K)

MATERIAL: One incomplete cranidium: LO12066t from a glacial erratic boulder at Melbjerg cliff (DK).

DESCRIPTION: Cranidium trapezoidal, with low relief, posterior width about 1.6 of total cranidial length. Glabella long, 72% of total cranidial length, forwardly tapering and truncated anteriorly. Three lateral glabellar furrows are present, S1 sigmoidal and long, S2 backwardly oblique and shorter, S3 very short and shallow. Ocular ridges indistinct. Frontal area well developed, 28% of total cranidial length. Preglabellar field flat, 56% of frontal area, anterior border strongly convex, separated from preglabellar field by narrow and deep anterior border furrow. Palpebral lobe arcuate, 41% of total cranidial length, defined by a slightly arcuate, narrow and deep palpebral furrow. Occipital ring with small median knob, separated from glabella by narrow and deep, sigmoidal occipital furrow which becomes shallower laterally. Anterior facial suture diverging strongly from glabella, then turning strongly inwards across border to meet anterior margin slightly lateral to the side of the glabella. Posterior facial suture diverging strongly from glabella, straight, then curving backwards to enclose narrow, triangular posterolateral limbs with a wide and relatively deep posterior border furrow.

MEASUREMENTS: Cranidial length 3.2 mm, cranidial width at mid-palpebral level 3.25 mm, posterior cranidial width 5.5 mm.

REMARKS: The only known specimen is a juvenile; even so, comparison with juvenile specimens assigned to *M. abdita* (see above; Text-fig. 14D) shows that the specimen at hand has three lateral glabellar furrows, almost indistinct ocular ridges, and a relatively longer preglabellar field (56% instead of 40% of the length of the frontal area). So far, such a ratio of the length of the preglabellar field relative to the length of the frontal area is unknown in the illustrated specimens of all known species of *Maladioidella* (see above for references) and therefore the specimen might represent a so far unknown juvenile of a known species or even a new species. Solving this problem would require a larger collection of specimens, and the specimen is left under open nomenclature.

OCCURRENCE: Furongian, probably *Parabolina spinulosa* Zone in a glacial erratic boulder in Denmark.

Family Parabolinoididae Lochman, 1956[6]

Genus *Pedinocephalus* Ivshin, 1956

TYPE SPECIES: *Pedinocephalus bublichenkoi* Ivshin, 1956, Kuyandinian Stage, Sakian, Furongian, central Kazakhstan, OD.

REMARKS: Ivshin (1956) gave a diagnosis of the genus and described three species. Further taxa have been described from Kazakhstan (Ivshin 1962), Antarctica (Shergold *et al.* 1976), Iran (Wittke 1984) and the Himalayas (Shah *et al.* 1991).

Pedinocephalus peregrinus (Henningsmoen, 1957)
(Text-fig. 15A–E)

part 1957b. *Taenicephalus*? *peregrinus* n.sp.; Henningsmoen, pp. 167–170, pl. 1, figs 1–4, non figs 5, 6 = *Pedinocephalus* sp.

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[6] Following Jell and Adrain (2003), *Pedinocephalus* is assigned to the Family Parabolinoididae.

1958. *Taenicephalus*? *peregrinus* […] belongs to the genus *Pedinocephalus* Ivshin 1956; Henningsmoen, p. 180.
1983. *Pedinocephalus peregrinus* (Henningsmoen, 1957b); Rushton, p. 112.
non 2001. *Pedinocephalus peregrinus* Henningsmoen 1957; Weidner, pp. 65–67, figs 5–7 (= left cranidium in fig. 5 and fig. 7 is *Maladioidella abdita*; pygidium in fig. 5 is pygidium indet. C; middle cranidium in fig. 5 and fig. 6 are gen. et sp. indet.).
2008. *Pedinocephalus peregrinus* (Henningsmoen, 1957); Mischnik, p. 9, pl. 2, fig. 2.
2011. *Pedinocephalus peregrinus* Henningsmoen, 1957 [sic]; Terfelt *et al*., table 1, fig. 1.

HOLOTYPE: Cranidium PMU Vg. 705, probably from the *Olenus gibbosus* Zone at Trolmen in Västergötland, Sweden, illustrated in Henningsmoen (1957b, pl. 1, text-figs 1–4) and Text-fig. 15A herein.

MATERIAL: 5 incomplete cranidia: PMU Vg. 705 from Trolmen (Vg); LO12067t from Stora Stolan (Vg); LO12068t from Kappagården (Vg); LO12069t from Menigasker (N); LO12070t from Vilske (Vg).

DESCRIPTION: Cranidium almost flat, trapezoidal, width at level of palpebral lobes almost equal to total cranidial length; posterior width probably slightly exceeding 1.5 of total cranidial length. Glabella 68–71% of total cranidial length, forwardly tapering; glabellar sides slightly concave at level of palpebral lobes; anterior lobe bluntly terminated. Anterolateral corners of glabella fairly indistinct. Three pairs of faintly impressed lateral glabellar furrows, S1 and S2 short and backwardly oblique, S3 slightly shorter and less oblique. Frontal area well developed, 29–32% of total cranidial length. Preglabellar field 49–57% of frontal area, with traces of longitudinal caecal pattern, anterior border slightly convex, separated from almost flat preglabellar field by almost straight, shallow anterior border furrow. Palpebral lobe poorly preserved, 18% of total cranidial length. Occipital ring longest sagittally, with small median knob, separated from glabella by distinct but narrow sigmoidal occipital furrow. Anterior facial sutures diverging slightly from glabella, then turning strongly inwards across border to meet anterior margin lateral to the side of the glabella. Posterior facial suture slightly sigmoidal, enclosing triangular posterolateral limbs that bear wide and shallow posterior border furrows.

MEASUREMENTS: Cranidial length 13.5–24 mm, cranidial width at palpebral mid-length about 10–20 mm (posterior cranidial width not measurable).

REMARKS: Following Henningsmoen (1958) and Shergold *et al*. (1976), *Taenicephalus*? *peregrinus* is considered a species of *Pedinocephalus* Ivshin, 1956. We restrict *P. peregrinus* to the holotype and assign three other specimens from the collection to this species; the second specimen originally assigned to *P. peregrinus* represents a different species of the same genus (for differences, see under *Pedinocephalus* sp.). From the type species, *P. bublichenkoi*, three other species from Kazakhstan (*P. kazachstanensis* Ivshin, 1956; *P. bykovae* Ivshin, 1956; *P. simplex* Ivshin, 1962), and *P. divergens* Wittke, 1984 from Iran, the specimens at hand differ in having a sagittally shorter frontal area. Moreover, *P. bublichenkoi* has more pronounced anterolateral corners of the glabella and a glabella more tapering forwards; *P. kazachstanensis* has a glabella more tapering forwards, a slightly rounded anterior glabellar lobe and more pronounced eye-ridges; *P. bykovae* has a sagittally longer frontal area and stronger eye-ridges; *P. simplex* is characterized by the lack of lateral glabellar furrows; whereas *P. divergens* has a transversely wider glabella and a strongly arched anterior border furrow (Ivshin 1956, 1962; Wittke 1984).

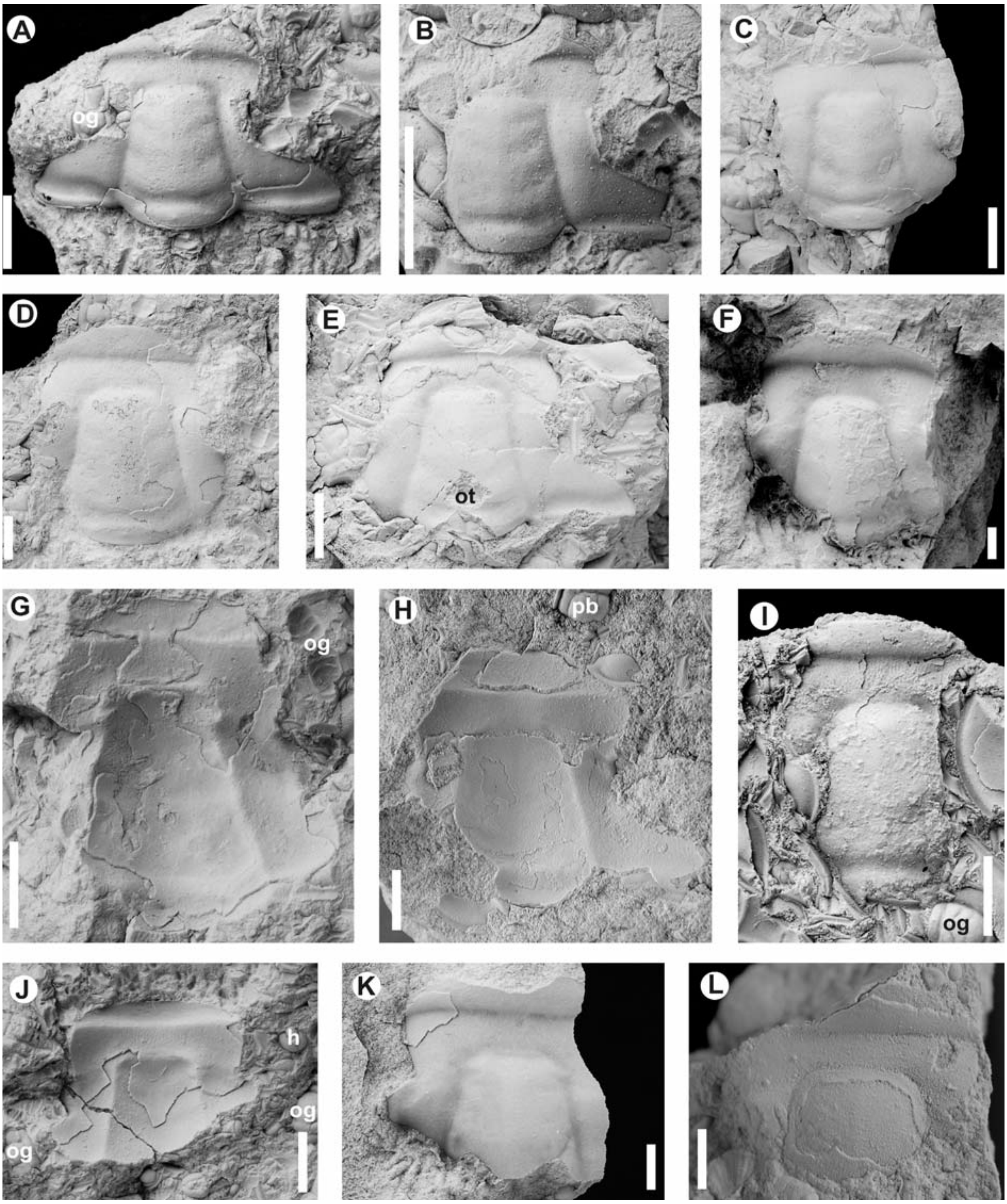
OCCURRENCE: Furongian, *Olenus gibbosus* and *Olenus truncatus* zones in Sweden (Henningsmoen 1957b and this paper) and in glacial erratic boulders in Germany (Mischnik 2008).

Pedinocephalus sp.
(Text-fig. 15F–L)

part 1957b. *Taenicephalus*? *peregrinus* n.sp.; Henningsmoen, pp. 167–170, pl. 1, figs 5, 6, non figs 1–4.

MATERIAL: Seven incomplete cranidia: PMU Vg. 706 from Trolmen (Vg); LO12071t from Krokagården (Vg); LO12072t from Hällekis (Vg); LO12073t from Råbäck (Vg); LO12074t, LO12075t, and LO12076t from glacial erratic boulders at Palsgård cliff (DK).

DESCRIPTION: Cranidium almost flat, trapezoidal, width at level of palpebral lobes slightly smaller than total cranidial length; posterior width probably exceeding 1.5 of total cranidial length. Glabella 69–73% of total cranidial length, tapering strongly forwards; glabellar sides rather straight; anterior lobe bluntly terminated or slightly concave anteriorly (see Text-fig. 15K). Anterolateral corners of glabella almost indistinct. Faint traces of three short and oblique lateral glabellar furrows; S3 is probably the shortest and less oblique than S1 and S2. Frontal area well developed,



Text-fig. 15. A-E – Cranidia of *Pedinocephalus peregrinus* (Henningsmoen, 1957) from the Furongian of Sweden. A – holotype, PMU Vg. 705, *O. gibbosus* Zone at Trolmen (Vg); original of Henningsmoen (1957b, pl. 1, figs 1–4); B – LO12067t, *O. gibbosus* Zone at Stora Stolan (Vg); C – LO12068t, *O. gibbosus* Zone at Kappagården (Vg); D – LO12070t, *O. truncatus* Zone at Vilske (Vg); E – LO12069t, *O. truncatus* Zone at Menigasker (N). F-L – Cranidia of *Pedinocephalus* sp. from the Furongian of Sweden, and glacial erratic boulders in Denmark (DK). F – LO12075t, *P. brevispina* or *P. spinulosa* Zone in a glacial erratic boulder collected at Palsgård cliff (DK); original of Weidner (2001, text-fig. 1); G – PMU Vg. 706, *O. gibbosus* Zone at Trolmen (Vg); original of Henningsmoen (1957b, pl. 1, figs 5–6 as *Taenicephalus*? *peregrinus*); H – LO12073t, *P. brevispina* or *P. spinulosa* Zone at Råbäck (Vg); I – LO12074t, *O. gibbosus* Zone at Menigasker (N); J – LO12071t, *O. gibbosus* Zone at Krokagården (Vg); K – LO12076t, *P. brevispina* or *P. spinulosa* Zone in a glacial erratic boulder collected at Palsgård cliff (DK); original of Weidner (2001, text-fig. 2, left cranidium); L – LO12072t, *P. brevispina* or *P. spinulosa* Zone at Hällekis (Vg). Accompanying fauna: ot – *Olenus truncatus* (Brünnich, 1781), og – *Olenus gibbosus* (Wahlenberg, 1818), pb – *Parabolina brevispina* Westergård, 1922, h – *Homagnostus obesus* (Belt, 1867). Scale bars represent 0.5 cm

27–31% of total cranidial length. Preglabellar field 56±8% of frontal area (n=6), with distinct longitudinal caecal pattern; anterior border distinctly convex, separated from flat preglabellar field by straight and narrow anterior border furrow. Palpebral lobe 17–22% of total cranidial length, almost confluent with level of intraocular cheek. Occipital ring longest sagittally, with small median knob, separated from glabella by shallow and wide, slightly sigmoidal occipital furrow. Anterior facial sutures diverging slightly from glabella, then turning strongly inwards across border to meet anterior margin at level of the anterolateral corners. Posterior facial suture slightly sigmoidal, enclosing triangular posterolateral limbs with wide and shallow posterior border furrows.

MEASUREMENTS: Cranidial length 16.5–22.3 mm, cranidial width at mid-palpebral level about 16–27 mm (posterior cranidial width not measurable).

REMARKS: The specimens at hand differ from *P. peregrinus* in having a slightly smaller cranidial width to length ratio at level of palpebral lobes; a glabella that tapers more strongly forwards; rather straight glabellar sides; an anterior lobe of the glabella that can be slightly concave anteriorly; a distinctly convex anterior border; and eye ridges that are strongly backwardly oblique. The specimens resemble *P. bublichenkoi*, the type species, in having a strongly tapering glabella, but differ in having a shorter frontal area.

OCCURRENCE: Furongian, *Olenus gibbosus* and *Olenus truncatus* zones in Sweden (Henningsmoen 1957b and this paper); *Parabolina brevispina* and *Parabolina spinulosa* zones in Sweden and in glacial erratic boulders in Denmark (Weidner 2001 and this paper).

Order Uncertain[7]
Family Changshaniidae Kobayashi, 1935

Genus *Westergaardella* Kobayashi, 1962

TYPE SPECIES: *Conokephalina olenorum* Westergård, 1922, from the *Parabolina brevispina* Zone at Andrarum, Scania, Sweden, OD.

REMARKS: The genus has been considered to belong to the family Conokephalinidae Hupé, 1953 (Kobayashi 1962; Jell and Adrain 2003); however, we consider Shergold and Sdzuy's (1991) suprageneric assignment more appropriate.

Westergaardella olenorum (Westergård, 1922)
(Text-fig. 16A–L)

part 1922. *Conokephalina olenorum* n. sp.; Westergård, p. 122, pl. 1, figs 22–26, 28, non fig. 27 [= hypostome of *Ptychoparia pusilla*].
1997. *Conokephalina olenorum* Westergård 1922; Buchholz, p. 29, pl. 4, fig. 15.
2000. *Conokephalina* cf. *olenorum* Westergård, 1922; Buchholz, pp. 763, 764, pl. 11, fig. 5.
2013. *Westergaardella olenorum* (Westergård, 1922); Żylińska and Weidner, p. 71, fig. 2D.

TYPES: The lectotype is cranidium SGU 137 (Text-fig. 16A), illustrated in Westergård (1922, pl. 1, fig. 22), selected herein.

MATERIAL: Twenty cranidia, twelve librigenae, numerous pleurae, one pygidium: SGU 137, 138a, 138b, 139, 140a, 141, 9596, 9597 from Andrarum (S); LO12077t from Hällekis (Vg); LO12078t from Trolmen (Vg); LO12079t from Råbäck (Vg); LO12080t, LO12081t and LO12082t from Blomberg (Vg).

DESCRIPTION: Cephalon broadly semicircular, with long librigenal spines. Cranidium subquadrangular, with low relief, total cranidial length slightly smaller than width at mid-palpebral level. Glabella relatively long, 77±1% of total cranidial length (n=8), slightly truncated anteriorly, anterior lobe slightly rounded anteriorly, axial furrows shallow and narrow. Two strongly oblique, faintly impressed lateral glabellar furrows, of equal length and very shallow. Frontal area well-developed, 23±1% of total cranidial length (n=8), with slightly convex anterior border distinctly elevated above flat preglabellar field; exsagittal width of anterior border almost even, only slightly narrowing abaxially; anterior margin curved gently backwards. Course of anterior border furrow gently arcuate, furrow with distinct pits (Text-fig. 16E, L). Preglabellar field slightly more than 2/3 of length of the frontal area. Preocular areas sloping only slightly forwards anterolaterally. Palpebral lobes large, exsagittal length 47±2% of total cranidial length (n=7), flat, separated from fixigenae by narrow palpebral furrow; located from glabella at a distance of more than half of glabellar width at mid-palpebral level, close to axial furrows but not reaching them anteriorly or posteriorly. Palpebral lobes strongly arcuate, slightly narrower anteriorly, almost reaching axial furrows; arching of palpebral lobes asymmetrical, with anterior part slightly longer than the posterior. Occipital ring undifferentiated, 16±2% of total cranidial length (n=8), sep-

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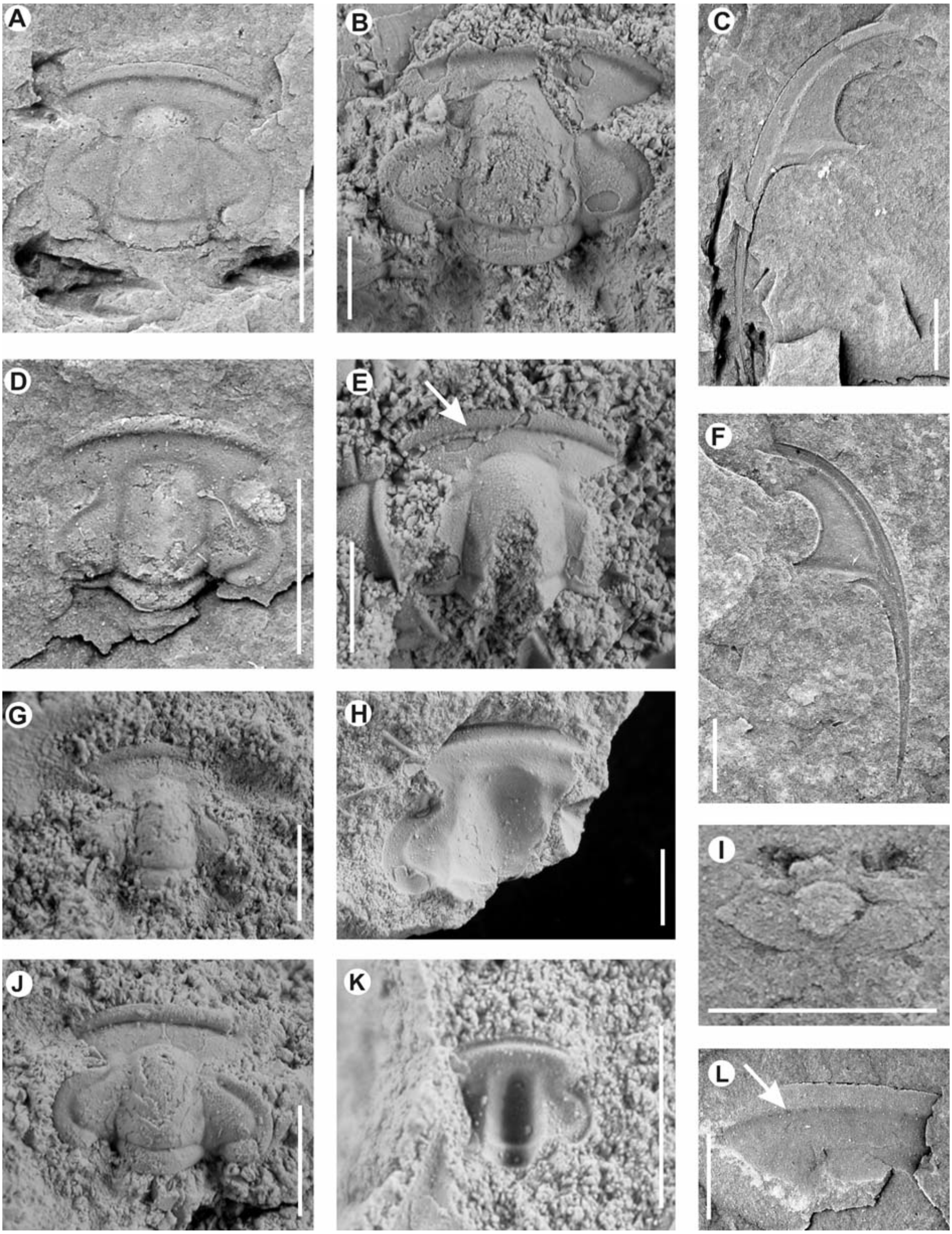
[7] The Order Ptychopariida Swinnerton, 1915, to which all the families mentioned below have once been assigned, is now abandoned (Adrain 2011).

arated from glabella by deep occipital furrow that is medially gently arcuate backwards, without knob or spine. Anterior facial sutures long, slightly sigmoidal, diverging strongly forwards, at about 60° from the axis, then turning strongly inwards to meet anterior margin lateral to the side of the glabella. Posterior facial suture very short, straight, enclosing very small triangular posterolateral limbs.



Librigena with long, slender spine confluent with course of lateral margin; spine almost twice as long as the librigena without spine. Border wide, flat, lateral border furrow well defined, wide, continuing onto spine. Posterior border furrow slightly oblique posterolaterally, wide and shallow. Inner spine angle slightly larger than 90°, inner posterior margin arcuate. Palpebral socle slightly elevated.

Pygidium widely semi-circular, rounded posteriorly. Axis tapering backwards, composed of at least 2 segments and a terminal piece that is rounded posteriorly and does not reach posterior margin; pleurae strongly effaced. Margin entire.

MEASUREMENTS: The lectotype cranidium (SGU 137) is 3.6 mm long and 4.3 mm wide at palpebral mid-length; cranidial length 1.8–7.3 mm, cranidial width at palpebral mid-length 2.1–8.3 mm.

REMARKS: *Conokephalina olenorum* was selected as the type species of *Westergaardella* Kobayashi, 1962, a genus that has been assigned to the family Conokephalinidae Walcott, 1913 (Kobayashi 1962; Jell and Adrain 2003). Öpik (1967) assigned the genus to the family Auritamidae Öpik, 1967, which was erected to encompass anomocaraceans with a parallel-sided glabella and a relatively small pygidium. Following Shergold and Sdzuy (1991), it is herein referred to the family Changshaniidae.

The Changshaniidae are typical of East Gondwana and Siberia (see Shergold and Sdzuy 1991 for references). Apart from *W. olenorum* discussed herein, the only changshaniid found outside these areas is *Parachangshania*? species undetermined from the Iberian Mountains of Spain (Shergold and Sdzuy 1991).

OCCURRENCE: Furongian; *Parabolina brevispina* Zone in Sweden (this paper) and in glacial erratic boulders in Germany and Denmark (Buchholz 1997, 2000 and this paper).

Family Elviniidae Kobayashi, 1935

Dunderbergia Walcott, 1924

TYPE SPECIES: *Crepicephalus* (*Loganellus*) *nitidus* Hall et Whitfield, 1877, from the Dunderberg Formation in Nevada, USA, OD.

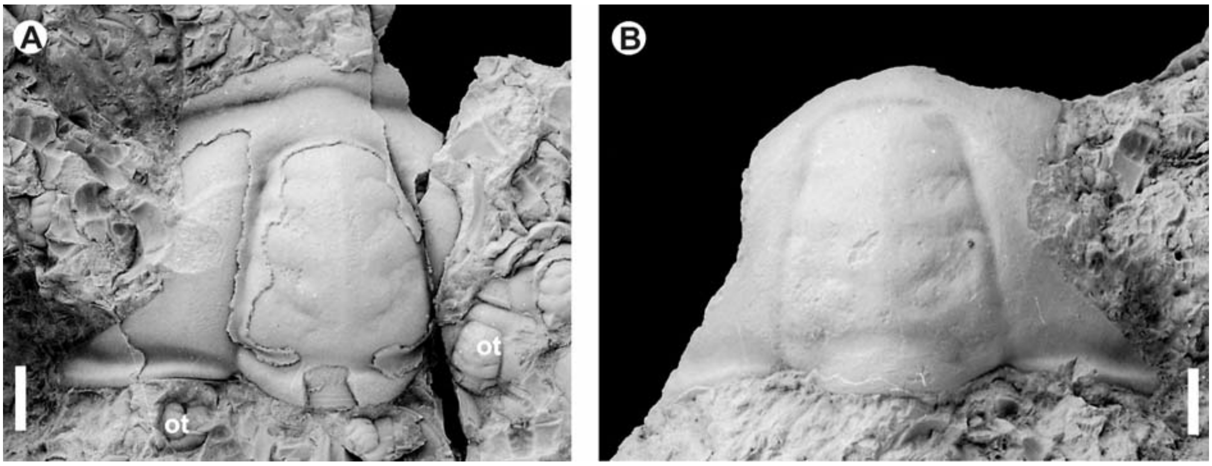
REMARKS: The genus was described in detail by Palmer (1954, 1960, 1965a). It has mainly been recorded from North America (Walcott 1924; Kobayashi 1938; Palmer 1954, 1960, 1965a); other occurrences include the Gorny Altai Mountains (Romanenko and Romanenko 1967) and northern China (Zhu *et al.* 1979).

Dunderbergia sp.
(Text-fig. 17A, B)

MATERIAL: Two incomplete cranidia: LO12083t and LO12084t from Vilske (Vg).

DESCRIPTION: Cranidium strongly convex, trapezoidal, width at level of palpebral lobes slightly larger than total cranidial length; posterior width about 1.7 of total cranidial length. Glabella 74% of total cranidial length, forwardly tapering, frontal lobe slightly triangular in outline. Anterolateral corners of glabella well marked. Glabella with faint median keel, distinctly more convex than fixigenae in lateral view. Four shallow lateral glabellar furrows, directed obliquely backwards, S1 bifurcating, sigmoidal and longest, S2 sigmoidal and slightly shorter, S3 slightly shorter than S2, S4 shortest, slightly curved. Ocular ridges narrow but distinct, running strongly obliquely backwards from a level opposite S4. Anterior fixigenae laterally strongly convex but not elevated above the glabella. Frontal area well developed, 26% of total cranidial length, with a finely granulose surface. Length of preglabellar field about 2/3 of length of frontal area, anterior border strongly convex, separated from almost flat (at sagittal line) preglabellar field by deep anterior border furrow, which becomes slightly shallower and anteriorly curved medially, so that the anterior border and anterior border furrow seem to form a blunt point medially instead of forming an even curve. Palpebral lobe not preserved. Occipital ring longest sagittally, separated from glabella by wide and laterally relatively deep sigmoidal occipital furrow. Anterior facial sutures diverging slightly from glabella, and then turning strongly inwards across border. Contact of anterior facial suture with anterior border not preserved. Posterior facial suture almost straight, running obliquely to enclose transversely triangular posterolateral limbs with deep and wide posterior border furrows that become deeper laterally.

Text-fig. 16. *Westergaardella olenorum* (Westergård, 1922) from the Furongian, *P. brevispina* Zone at Andrarum, Scania (S) and in Västergötland (Vg). A – lectotype cranidium, SGU 137 (S); original of Westergård (1922, pl. 1, fig. 22); B – cranidium, LO12082t, Blomberg (Vg); C – librigena, SGU 9597 (S); D – cranidium; SGU 138a (S); original of Westergård (1922, pl. 1, fig. 23); E – cranidium, LO12079t, Råbäck (Vg); note pits in anterior border furrow (arrowed); F – librigena, SGU 139 (S); original of Westergård (1922, pl. 1, fig. 24); G – cranidium, LO12080t, Blomberg (Vg); H – negative of cranidium, LO12077t, Hällekis (Vg); I – pygidium, SGU 143 (S); original of Westergård (1922, pl. 1, fig. 28); J – cranidium, LO12081t, Blomberg (Vg); K – negative of cranidium, LO12078t, Trolmen (Vg); L – anterior part of cranidium; SGU 9596 (S); note pits in anterior border furrow (arrowed). Scale bars represent 0.25 cm



Text-fig. 17. *Dunderbergia* sp. from the Furongian of Vilske (Vg), Sweden. A – incomplete, partly testaceous cranidium, LO12083t, *O. truncatus* Zone; B – incomplete cranidium, LO12084t, *O. gibbosus* or *O. truncatus* Zone. Accompanying fauna: ot – *Olenus truncatus* (Brünnich, 1781). Scale bars represent 0.5 cm

MEASUREMENTS: Cranidial length 22.9 mm, cranidial width at palpebral mid-length 23.8 mm; the less complete cranidium is even larger (estimated length over 27 mm, estimated width at palpebral mid-length over 25 mm).

REMARKS: The cranidia at hand fit all the features of *Dunderbergia* Walcott, 1924, particularly in having a subquadrate glabella; the anterior border and anterior border furrow meeting medially at a blunt point instead of forming an even curve; long and oblique eye ridges; and a laterally relatively deep occipital furrow. The hardly visible lateral glabellar furrows expressed in the original diagnosis are most probably a result of variable preservation; for example, *D. variagranula* Palmer, 1960 from the Steptoean *Dunderbergia* Zone of Nevada, *D. brevispina* Palmer, 1965 from the Steptoean *Dicanthopyge* Zone of Nevada, and *D. seducta* Palmer, 1968 from the Steptoean of Alaska (Dresbachian-2 fauna) are characterized by quite distinct lateral glabellar furrows (Palmer 1960, 1965a, 1968). The specimens at hand are closest to *Dunderbergia bigranulosa* Palmer, 1960 from the Steptoean *Dunderbergia* Zone of Nevada, but have a slightly longer and narrower glabella in relation to the total cranidial length and width at level of palpebral lobes, a slightly shorter (sag.) preglabellar field and more distinct lateral glabellar furrows (Palmer 1960, 1965a).

OCCURRENCE: Furongian; *Olenus gibbosus* and *Olenus truncatus* zones in Sweden.

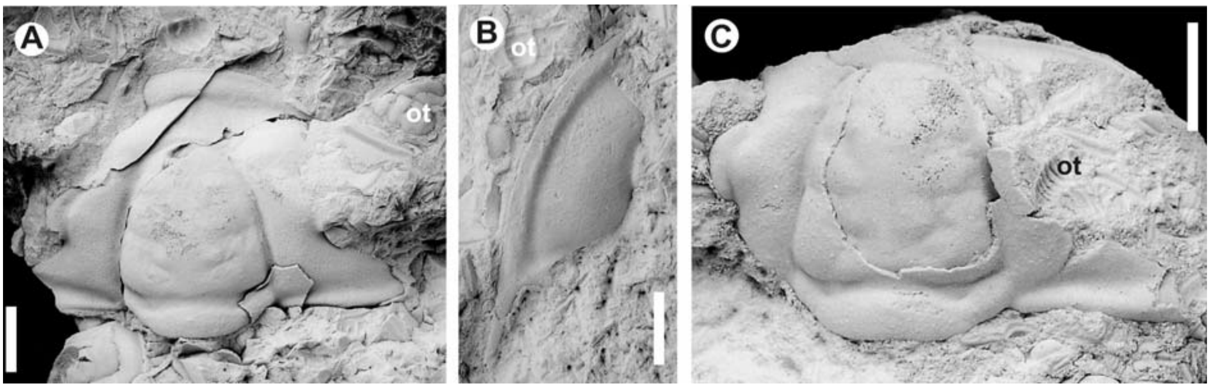
Genus *Protemnites* Whitehouse, 1939 emended Shergold, 1982

TYPE SPECIES: *Protemnites elegans* Whitehouse, 1939, exact stratigraphic horizon and locality unknown, from the Furongian (Idamean) of the Georgina Limestone, Glenormiston area, western Queensland, Australia (see Shergold 1982 for discussion and refigured holotype cranidium), OD.

Protemnites sp.
(Text-fig. 18A–C)

MATERIAL: Two incomplete cranidia, one librigena: LO12085t and LO12086t from Kappagården (Vg); LO12087t from Övre Västerstad (Ö).

DESCRIPTION: Cephalon sub-semicircular, convex sagittally and transversely. Cranidium trapezoidal, moderately convex sagittally, somewhat convex transversely, slightly longer than wide at cranidial mid-length. Glabella long, 71% of total cranidial length, moderately convex sagittally, forwardly tapering and strongly rounded anteriorly. Preglabellar furrow moderately deep. Four pairs of faint lateral glabellar furrows; S1 to S3 directed backwards, S1 slightly sigmoidal, not reaching axial furrows, S2 longer, slightly curved, S3 of similar length as S2, sigmoidal; S4 almost horizontal, barely curved. Occipital ring longest sagittally, with faint median node located slightly anteriorly, separated from glabella by deeply incised, sigmoidal occipital furrow of variable width, slightly narrower medially, then widening slightly and narrowing again at contact with axial furrows. In lateral profile occipital ring located at lower level than preoccipital glabellar lobes. Palpebral lobes relatively flat, transversely narrow, gently arcuate, de-



Text-fig. 18. *Protemnites* sp. from the Furongian *O. truncatus* Zone of Sweden. A – incomplete, partly testaceous cranidium, LO12085t, Kappagården (Vg); B – librigena, LO12086t, same zone and locality as for Text-fig. 18A; C – incomplete, partly testaceous cranidium, LO12087t, Övre Västerstad (Ö). Accompanying fauna: ot – *Olenus truncatus* (Brünnich, 1781). Scale bars represent 0.5 cm

fined by relatively shallow palpebral furrows that are slightly shallower at mid-point of palpebral lobe, 19% of total cranidial length, extending from opposite S3 to front of S2. Fixigenae at level of palpebral lobes slightly elevated. Ocular ridges relatively wide and flat, extending from axial furrows outwards and backwards at level of S3, less distinct at contact with anterior part of palpebral lobes. Palpebral areas convex. Frontal area 29% of total cranidial length, anterior border gently convex, preglabellar field 57% of frontal area length, flat sagittally; preocular areas relatively convex, then sloping strongly forward. Anterior furrow slightly arcuate, deeper and narrower medially. Fixigenae convex, gently inclined to axial furrows, slightly less than half glabellar width at glabellar mid-length. Anterior facial sutures diverging slightly, then turning gradually inwards across anterior border to meet anterior margin lateral to the side of the glabella. Posterior facial suture nearly straight, enclosing transversely triangular, exsagittally relatively narrow posterolateral limbs bearing shallow, distally expanding posterior border furrows. External surface of test with fine, densely spaced granules, of which some are perforated.

Librigena with short, slender spine, diverging only slightly from course of lateral margin. Border relatively wide, lateral border furrow well defined and wide. Posterior border furrow very short and shallow. Inner spine angle close to a right angle. Palpebral socle slightly elevated. Surface covered with faint caecal pattern.

MEASUREMENTS: The best preserved cranidium is 20.7 mm long, 20 mm wide at palpebral mid-length, and 30 mm wide posteriorly.

DISCUSSION: Despite their incompleteness, the cranidia at hand bear all the characteristics of *Protemnites*. Particularly significant is the cranidial convexity, combined with a tapering glabella, a flat preglabellar field, strongly sloping preocular areas and broadly based posterolateral limbs of the fixigenae. The cranidia differ from *P. elegans*, the type species, in the slightly shorter palpebral lobes and in having four pairs of lateral glabellar furrows. The original diagnosis indicates that representatives of *Protemnites* have two pairs of lateral glabellar furrows, and this is apparent from the illustrations of the holotype of the type species in Whitehouse (1939, pl. 22, fig. 12a–b). However, the re-illustrated holotype specimen (Shergold 1982, pl. 9, fig. 1) shows three pairs of lateral glabellar furrows, similarly as *P. brownensis* (Henderson, 1976) from the late Idamean *Stigmatoa diloma* Assemblage Zone, Glenormiston area, western Queensland, Australia, *P. burkensis* Shergold, 1982 from the Iverian *Irvingella tropica* Zone, Burke River Structural Belt, western Queensland, Australia, and *P.*? *magnificans* Shergold and Webers, 1992 from the Idamean of the Heritage Range, west Antarctica (Henderson 1976; Shergold 1982; Shergold and Webers 1992). Three to four lateral glabellar furrows have been noted in *P. waergangensis* Peng, 1992 from the Bitiao Formation, *Agnostotes* (*Pseudoglyptagnostus*) *clavatus – Irvingella angustilimbata* Zone in the Cili–Taoyuan area, north-west Hunan, China (Peng 1992), suggesting that the number of lateral glabellar furrows is not only an inter- but also intra-specific character. In comparison to the discussed specimens, *P. brownensis* has a straight anterior border furrow and less sloping preocular areas (Henderson 1976). Cranidia of *Protemnites* sp. are similar to those of *P.* sp. aff. *P. elegans* from the Idamean of west Antarctica (Shergold and Webers 1992), differing in having more oblique palpebral lobes located at a slightly larger distance from the glabella. The palpebral lobes in *P. waergangensis* are located even further away from the glabella than in the discussed specimens. *Protemnites*? *magnificans* has less oblique palpebral lobes and the frontal area is relatively longer sagittally in comparison to the studied specimens. The proportions of the librigena fit those of the associated cranidium and allow its assignment to the same taxon.

OCCURRENCE: Furongian, *Olenus truncatus* Zone in Sweden.

Family Kingstoniidae Kobayashi, 1933

Subfamily Blountiinae Lochman in Lochman and Duncan, 1944

Genus *Blountia* Walcott, 1916 emended Öpik, 1967

TYPE SPECIES: *Blountia* (*Blountia*) *mimula* Walcott, 1916, from the Middle Cambrian of Tennessee, USA, OD (see Öpik 1967 for discussion on the genus and the subgeneric assignment).

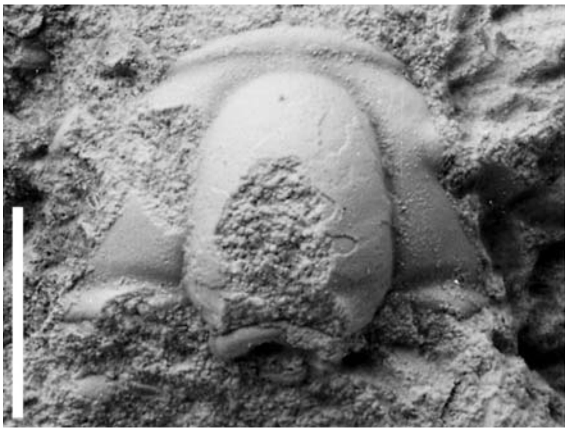
REMARKS: Assignment of *Blountia* to the Family Kingstoniidae follows Westrop (1992) and Jell and Adrain (2003); a different view that the Blountiinae should be retained in the Family Asaphiscidae Raymond, 1924 was expressed e.g., by Pratt (1992) and Stitt and Perfetta (2000).

Blountia sp.

(Text-fig. 19)

MATERIAL: One incomplete cranidium: LO12088t from Vilske (Vg).

DESCRIPTION: Cranidium subtrapezoidal, small, with posterolateral lobes directed backwards, width at level of palpebral lobes almost equal to total cranidial length. Glabella long, 80% of total cranidial length, only slightly forwardly tapering, evenly rounded anteriorly, highly convex sagittally and transversely, rising distinctly above the level of the rest of the cranidium. Preglabellar furrow and axial furrows shallow and narrow but distinct. Lateral glabellar furrows almost effaced, S1 backwardly oblique, preserved only as a short and shallow depression, not connected with axial furrows. Occipital ring not preserved entirely, but seems to be longest sagittally, separated from glabella by shallow and wide occipital furrow, barely connected with axial furrows. Palpebral lobes small, 16% of total cranidial length, situated anterior to glabellar centre, slightly arcuate. Palpebral areas preserved as small swellings, barely differentiated from rest of fixigenae. Ocular ridges not present. Frontal area 20% of total cranidial length, anterior border relatively strongly convex, preglabellar field almost flat, 43% of frontal area, distinguished from anterior border by shallow and narrow anterior border furrow that is slightly less deep at cranidial sagittal mid-length; anterior border furrow curved slightly backwards abaxially. Fixigenae relatively flat, very narrow, only about 1/4 of glabellar width at level of palpebral lobes. Preocular areas downsloping slightly forwards. Anterior facial sutures converging and rounded, then turning inwards across anterior border to meet anterior margin lateral to the side of the glabella. Posterior facial suture diverging, slightly convex, enclosing narrow, flat, triangular posterolateral limbs directed backwards. Posterior border furrow wide and shallow, posterior margin with distinct fulcrum located closer to posterolateral point of fixigenae.



Text-fig. 19. *Blountia* sp., LO12088t, Furongian, *P. brevispina* Zone at Vilske, Västergötland, Sweden. Scale bar represents 0.5 cm

MEASUREMENTS: Cranidial length 7.5 mm, cranidial width at palpebral mid-length 7.4 mm, posterior cranidial width 10 mm.

REMARKS: Despite a poor state of preservation, the cranidium displays features characteristic of *Blountia*, i.e., a strongly convex, forwardly tapering glabella with a rounded front, narrow fixigenae whose posterolateral limbs are distinctly directed backwards, small palpebral lobes anterior to the glabellar centre, and a distinct anterior border furrow. Additionally, its short preglabellar field and anterior border, as well as relatively narrow fixigenae show resemblance to *B. montanensis* Duncan in Lochman and Duncan, 1944 from the Marjuman *Crepicephalus* Zone, Montana, USA and the Marjuman *Cedaria brevifrons* Zone, Canada (Lochman and Duncan 1944; Pratt 1992), but the specimen differs in having slightly larger preocular fixigenae and a less arcuate anterior border furrow.

Laurentian occurrences of the genus are typically from upper Marjuman strata (Lochman and Duncan 1944; Rasetti 1965; Palmer and Peel 1981; Pratt 1992; Stitt and Perfetta 2000). Representatives of the genus were noted also in Australia in correlatable strata (Öpik 1967). Rasetti (1965, p. 59) also recorded some specimens from the Steptoean *Aphelaspis* Zone; likewise, the occurrences from the Himalayas (Shah *et al.* 1991) are from the lower Upper Cambrian. The cranidium under discussion is from slightly younger strata.

OCCURRENCE: Furongian, *Parabolina brevispina* Zone in Sweden.

Family Ptychopariidae Matthew, 1887[8]
Subfamily Ptychopariinae Matthew, 1887

Genus *Ptychoparia* Hawle and Corda, 1847
emended Kordule, 2006

TYPE SPECIES: *Conocephalus striatus* Emmrich, 1839 from the Middle Cambrian of Bohemia, Czech Republic, OD.

REMARKS: The genus was thoroughly revised by Kordule (2006). Following the assignment of *Liostracus pusillus* Westergård, 1922 to *Ptychoparia*, the genus *Mukrania* Buchholz, 1997, based on *L. pusillus* as the type species, is considered a junior subjective synonym of *Ptychoparia*.

Ptychoparia pusilla (Westergård, 1922)
(Text-figs 20A–R and 21A–F)

1922. *Liostracus pusillus* n. sp.; Westergård, p. 121, pl. 2, figs 8–19.
part 1922. *Conokephalina olenorum* n. sp.; Westergård, p. 122, pl. 1, fig. 27 (hypostome only).
? 1984. cf. ‘*Liostracus*’ *pusillus* Westergård; Thomas *et al.*, p. 13.
? 1988. ‘*Liostracus*’ *pusillus* Westergård, 1922; Morris, p. 130.
1997. *Mukrania pusilla* (Westergård, 1922); Buchholz, p. 29, pl. 4, figs 16, 17, ?18.
2001. *Andrarina*? *pusilla* (Westergård); Żylińska, p. 378.
2008. *Mukrania pusilla* (Westergård, 1922); Mischnik, p. 13, pl. 1, fig. 6.

TYPES: The lectotype is cranidium SGU 149 (Text-fig. 20G), illustrated in Westergård (1922, pl. 2, fig. 11); selected by Buchholz (1997, p. 29).

MATERIAL: Over 65 cranidia, 10 pygidia, 7 librigenae, a fragmentary thorax, numerous pleurae and one hypostome: SGU 142, 146–154, 155a, 155b, 156a, 156b, 157, 9601–9607 from Andrarum (S); LO12089t from a glacial erratic boulder at Melbjerg cliff (DK).

EMENDED DIAGNOSIS: Species of *Ptychoparia* with S1 conspicuous, S2 and S3 distinct, S4 poorly marked; anterior border prominent; length of cranidium to length of anterior border (a1/f1 index) averagely 6 (5 to 8 based on diagenetic compaction); pygidial axis with 5 axial rings and terminal piece; pygidial pleural fields with four distinct ribs, fifth rib poorly developed as weak elevation near terminal axial piece.

DESCRIPTION: Exoskeleton heteropygous, ovally elongated, small. Cephalon broadly semicircular. Cranidium trapezoidal, relatively flat, slightly shorter than wide at cranidial mid-length, with narrow posterolateral limbs. Glabella trapezoidal, long, tapering forward, truncated to weakly rounded anteriorly, defined by deep and wide axial and preglabellar furrows, with rounded anterior corners and posteriormost lateral lobes. Length of glabella 76±3% of total cranidial length (n=19). Four pairs of lateral glabellar furrows, generally weakly impressed. S1 longest, oblique, curved posteriorly, S2 and S3 shorter and shallower, S2 oblique, S3 almost normal to sagittal line; S4 shortest, transverse or directed slightly anteriorly. Occipital ring 18±2% of total cranidial length (n=18), longest sagittally, with poorly visible median knob, separated from glabella by deep and wide, sigmoidal occipital furrow; axial portion of furrow arched forward; furrow widest medially, narrowing slightly abaxially and confluent with posterior parts of axial furrows. Palpebral lobes transversely narrow, gently arcuate, located at level of S2, only faintly convex, 26±3% of total cranidial length (n=17). Palpebral furrow shallow but distinct. Ocular ridges wide and flat, almost transverse, connecting palpebral lobe with axial furrow at level of S4. Frontal area 25±3% of total cranidial length (n=19), anterior border relatively strongly convex, separated from only slightly vaulted preglabellar field by deep, almost transverse furrow; a1/f1 index averagely 6 (5 to 8 based on diagenetic compaction). Fixigenae transversely slightly narrower than glabella posteriorly. Anterior facial sutures almost parallel to axis or slightly divergent, then curved sharply adaxially to meet at

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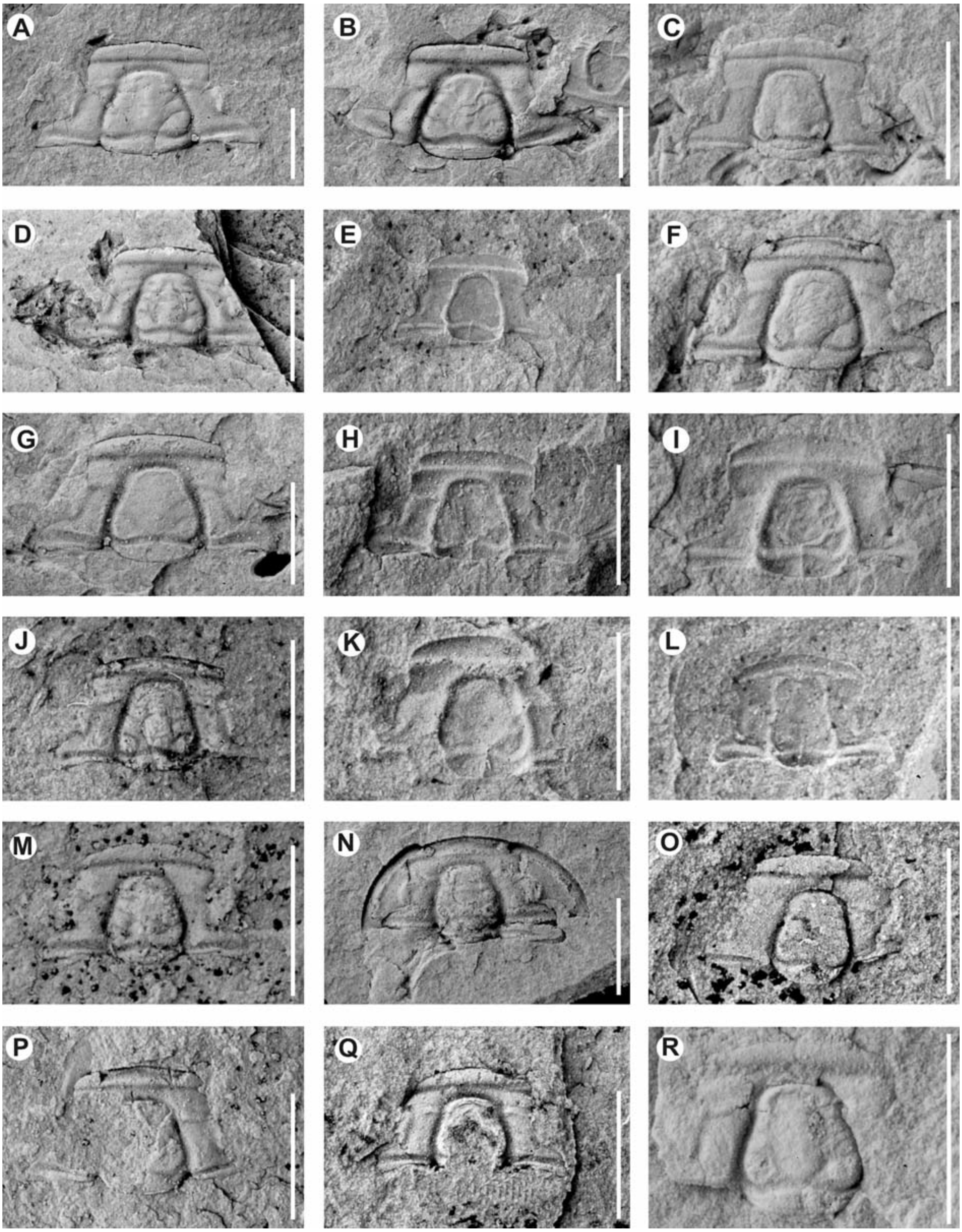
[8] The Family Ptychopariidae is probably polyphyletic but treated as a taxon for convenience (Adrain 2011, p. 108).



Text-fig. 20. Cranidia of *Ptychoparia pusilla* (Westergård, 1922) from the *P. brevispina* Zone at Andrarum, Scania, Sweden. A – SGU 146; original of Westergård (1922, pl. 2, fig. 8); B – SGU 147; original of Westergård (1922, pl. 2, fig. 9); C – SGU 157; original of Westergård (1922, pl. 2, fig. 19); D – SGU 148; original of Westergård (1922, pl. 2, fig. 10); E – SGU 9598; F – SGU 9607; G – lectotype, SGU 149; original of Westergård (1922, pl. 2, fig. 11); H – SGU 9599; I – SGU 9606; J – SGU 150; original of Westergård (1922, pl. 2, fig. 12); K – SGU 9600; L – SGU 9603; M – SGU 151; original of Westergård (1922, pl. 2, fig. 13); N – with librigenae, SGU 152; original of Westergård (1922, pl. 2, fig. 14); O – SGU 155b; P – SGU 9601; Q – SGU 9602; R – SGU 9605. Scale bars represent 0.25 cm midline. Posterior facial sutures slightly sinuous, enclosing transversely triangular posterolateral limbs with deep and wide, distally expanding posterior border furrows.

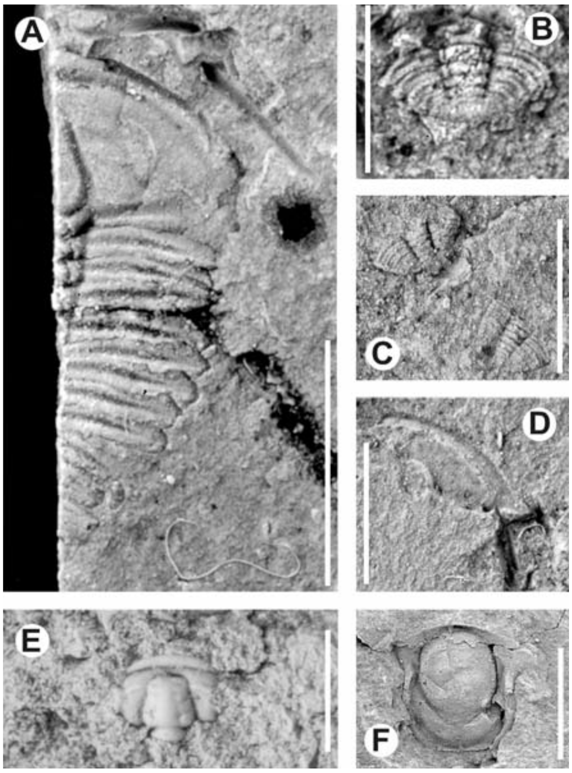
Librigenae subtriangular, narrow, with short, slender spine not deflected from lateral margin. Border relatively wide, of even width, with narrow and shallow border furrow. Inner spine angle close to a right angle. Ocular area of librigena slightly elevated.

Hypostome with prominent anterior lobe, distinct and much shorter posterior lobe separated by narrow but distinct middle furrow. Borders distinctly raised laterally and posteriorly, curved upwards. Anterior margin only slightly differentiated from anterior lobe, passing into pointed anterior wings.

Thorax of at least twelve segments, tapering gently backwards from about thoracic mid-length. Axis relatively strongly convex transversely, separated from pleurae by distinct axial furrows. Pleurae fulcrate, pleural extremities pointed.

Pygidium semicircular. Pygidial axis long, convex, with 5 rings and poorly differentiated terminal piece, separated from lateral lobes by narrow but distinct axial furrows disappearing posteriorly. Lateral lobes with four ribs on each pleural field, separated by distinct pleural furrows. Interpleural furrows shallower, well defined, distinct all the way to border.

MEASUREMENTS: The only preserved incomplete exoskeleton is less than 5 mm long. The lectotype cranidium is 3.1 mm long and 5.8 mm wide posteriorly. The largest cranidium (SGU 147; Text-fig. 20B) is 4 mm long and 8 mm wide posteriorly.



Text-fig. 21. *Ptychoparia pusilla* (Westergård, 1922) from the *P. brevispina* Zone at Andrarum, Scania (S), Sweden and probably *P. spinulosa* Zone in a glacial erratic boulder collected at Melbjerg cliff (DK). A – incomplete exoskeleton, SGU 155a (S); original of Westergård (1922, pl. 2, fig. 17); B – pygidium, SGU 156b (S); C – two pygidia, SGU 9604 (S); original of Westergård (1922, pl. 2, fig. 18); D – librigena, SGU 153 (S); original of Westergård (1922, pl. 2, fig. 15); E – incomplete cranidium, LO12089t (DK); F – hypostome, SGU 142 (S); original of Westergård (1922, pl. 1, fig. 27, as *Conokephalina olenorum*). Scale bars represent 0.25 cm.

REMARKS: Assignment to *Ptychoparia* is justified by the following features: the shape of the glabella; four pairs of lateral glabellar furrows, with S4 transverse or slightly directed anteriorly; a prominent cephalic border; the a1/f1 index averagely 6; a short slender librigenal spine; and a pygidium with 5 rings and terminal piece, without a distinct border. The described species differs from *P. striata*, the type species from the Cambrian Series 3 of Bohemia, in having a mean a1/f1 index of 6 (five in *P. striata*), a less convex anterior border, a straight anterior border furrow, fixigenae narrower than glabella at level of palpebral lobes, lack of ornamentation, and a small size (Šnajdr 1958; Kordule 2006). From *P. dubinka* Kordule, 2006, another species common in the Cambrian Series 3 of Bohemia, it differs in having fixigenae narrower than glabella at level of palpebral lobes, less prominent lateral glabellar furrows, a more prominent hypostomal anterior lobe, and a narrower librigenal lateral border. The a1/f1 index and number of axial rings in the pygidium are as in *P. dubinka* (Kordule 2006). Specimens from the Furongian of Andrarum are preserved in shale and hence strongly compacted, and many diagnostic features have become obscured. For example, the course of the anterior border furrow is almost transverse and not curved backwards as in *P. striata* or *P. dubinka* (see Šnajdr 1958, his pl. 29, figs 2, 3, 5; Kordule 2006, his figs 1B, C, I, K, 2A). The only unflattened specimen studied is a juvenile (Text-fig. 21E); here the anterior border furrow is more distinctly although still very slightly curved backwards abaxially. The generally transverse anterior border furrow is visible in internal moulds of *P. striata* and *P. dubinka* (Kordule 2006, his figs 1J and 2L, respectively). The paradoublural furrow is not visible in specimens of *P. pusilla*, a feature common in well preserved adult individuals from Bohemia representing the genus (Kordule 2006, his figs 2A, 3B, C, E, F); this might be the result of poor preservation of the studied specimens.

Preservation as internal moulds results in lack of distinct ornamentation visible in the specimens illustrated by Šnajdr (1958) or Kordule (2006). *Ptychoparia pusilla* is represented only by small specimens (the only known dorsal exoskeleton is less than 5 mm long); the largest cranidium is 4 mm long, suggesting that the complete exoskeleton could have been about 12 mm, whereas representatives of *Ptychoparia* from Bohemia commonly are 50 to 70 mm and can reach a length of up to 100 mm (Šnajdr 1958; Kordule 2006). Perhaps the assemblage from Andrarum represents an association of juveniles or the Alum Sea environment may have prevented the growth of larger individuals of this taxon. Furongian representatives of *Ptychoparia* could also have attained much smaller dimensions. For example, in the Machari Formation of South Korea an almost complete dorsal exoskeleton of *P. orientalis* Resser and Endo, 1937 is 2.5 mm long and cranidia of *P. kochibei* Walcott, 1911 are 2 to 2.5 mm wide posteriorly (Kobayashi 1962, pl. 11, fig. 13 and pl. 10, figs 1–3, respectively).

In his original description, Westergård (1922, p. 121) noted that the taxon seems to be related to *Liostracus costatus* Angelin, 1854, a species that was later assigned to *Andrarina* Raymond, 1937 (Westergård 1948), although close resemblance to *Ptychoparia* or *Solenopleura* Angelin, 1854, based on the relatively deep furrows around the glabella, was also suggested. Based on this feature, Robison and Pantoja-Alor (1968) considered *P. pusilla* as a member of the ancestral calymenid stock. These authors excluded the species from *Andrarina* and noted its resemblance to *Pharostomina* Sdzuy, 1955 except for slightly larger eyes and a narrower exsagittal width of the posterior limbs. The superficial similarity of *P. pusilla* to trilobites belonging to the calymenid stock is evident particularly in the arrangement of the lateral glabellar furrows and relatively deep axial furrows; however, cranidia of the Calymenina Swinnerton, 1915 are strongly convex, especially at the level of glabellar mid-length. This feature does not occur in the cranidia of *P. pusilla*; there are no indications of crushing in spite of compaction, although their exoskeleton could have been thinner and thus more vulnerable to compaction if the assemblage represents juveniles.

OCCURRENCE: Furongian, associated with *Homagnostus obesus* (Belt, 1867) in glacial erratic boulders in northern Germany (Mischnik 2008); *Parabolina brevispina* Zone in Sweden (this paper) and glacial erratic boulders in Germany (Buchholz 1997); probably *Parabolina spinulosa* Zone in glacial erratic boulders in Denmark (this paper).

Order Lichida Moore, 1959
Family Lichakephalidae Tripp, 1957
Paraacidaspis Poletaeva, 1960

TYPE SPECIES: *Paraacidaspis sibirica* Poletaeva, 1960, from the Gorny Altai Mountains, Siberia, OD (see Shergold *et al.* 2000 and Jell and Adrain 2003 for a detailed discussion of the type species and the availability of the genus name).

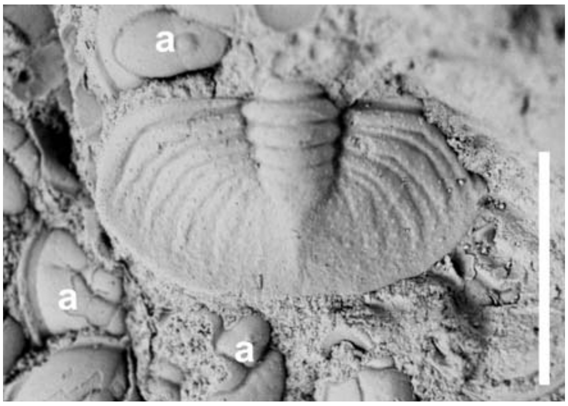
?*Paraacidaspis* sp.
(Text-fig. 22)

2013. Dikelocephalidae indet.; Żylińska and Weidner, p. 71, fig. 2B.

MATERIAL: Two pygidia: LO12090t and an unnumbered specimen from Hjälmsäter (Vg).

DESCRIPTION: Pygidium entire, wider than long, subrectangular. Maximum length about 0.6 of maximum width. Pygidial axis (excluding postaxial ridge) about 0.6 of maximal pygidial length, elevated above surface of pygidium, tapering backwards, terminal axial piece extending rearwards into a postaxial ridge that ends slightly anterior to the posterior margin. Pygidial axis with 4 inter-ring furrows, of which the posteriormost is slightly shallower. Anterior half-ring slightly narrower transversely than axis, separated from it by straight articulating furrow. Pleural fields with at least seven distinct, narrow, strongly sigmoidal pleural furrows. Border flat, of varying width, no border furrow present. Pygidium with slight indentation at posterior midpoint. Surface of entire pygidium covered by small granules.

MEASUREMENTS: Pygidial length 5–6.5 mm, anterior pygidial width 9.4–10 mm.



Text-fig. 22. ?*Paraacidaspis* sp., LO12090t, Cambrian Series 3, *A. pisiformis* Zone at Hjälmsäter (Vg), Sweden. Scale bar represents 0.5 cm

REMARKS: The pygidia have provisionally been assigned to Dikelocephalidae indet. in a conference abstract (Żylińska and Weidner 2013), but close examination of the ranges of the dikelocephalids suggests that an occurrence of trilobites of this family in strata correlatable with the Marjuman Stage seems unlikely (e.g., Palmer 1968; Westrop 1986). It is more probable that the pygidia represent a species of *Paraacidaspis* Poletaeva, 1960, a genus largely restricted to mid-Furongian strata in Siberia, South China and Kazakhstan (see overview in Shergold *et al.* 2000). These occurrences also seem quite young stratigraphically; however, Shergold *et al.* (2000) described an assemblage with *Palaeadotes* and *Paraacidaspis* from Ferrals in the Montagne Noire, France. The Ferrals assemblage was likely recovered from deposits equivalent to the *Glyptagnostus reticulatus*-bearing strata (Shergold *et al.* 2000). Representatives of both *Palaeadotes* and *Paraacidaspis* are known from the *A. pisiformis* Zone of Sweden (Westergård 1922, 1947b; Zhang 1996; Text-fig. 3), suggesting that the pygidia at hand can (with reservation) be attributed to *Paraacidaspis*. There is also an apparent resemblance of the examined pygidia to representatives of the Iwayaspidinae Kobayashi, 1962, such as e.g., *Cermatops* Shergold, 1980 (see Shergold 1980 and Hughes and Rushton 1990), but in the examined pygidia the pleural furrows are sigmoidal and bent strongly backwardly, whereas in *C. vieta* Shergold, 1980 and *C. discoidalis* (Salter, 1866) they are curved only slightly obliquely backwards; moreover, pygidia of iwayaspidines are usually suboval, rarely subtrapezoidal, whereas the pygidia at hand are subrectangular in outline.

OCCURRENCE: Cambrian Series 3; *Agnostus pisiformis* Zone in Sweden.

Pygidium indet. A
(Text-fig. 23A)

MATERIAL: Two pygidia: LO12091t from Övre Västerstad (Ö); an unnumbered specimen from Hällekis (Vg).

DESCRIPTION: Pygidium entire, wider than long. Maximum length about 0.4 of maximum width. Pygidial axis about 75% of maximal pygidial length, distinctly elevated above surface of pleural fields, tapering strongly backwards, with posteriorly rounded terminal axial piece. Pygidial axis with two inter-ring furrows which are wide and shallow. Anterior half-ring slightly narrower than axis, separated from it by straight, wide and shallow articulating furrow. Pleural fields with three relatively wide and shallow pleural furrows, of which the posteriormost is the shallowest. Border narrow, slightly elevated, outlined by narrow border furrow. Pygidium with slight indentation at posterior midpoint.

MEASUREMENTS: Pygidial length 4.5–8.6 mm, anterior pygidial width 10.6–18 mm.

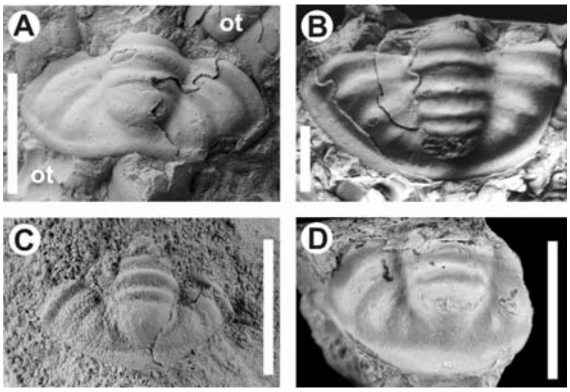
REMARKS: The specimens show characters that can be attributable to pygidia representing different genera and families, e.g., the elviniid *Dunderbergia* (Palmer 1960, pl. 5, figs 20–23; 1965a, pl. 4, figs 4, 10, 11), the aphelaspidid *Olentella* (Ivshin 1956, pl. 7, figs 9–12; Shergold and Cooper 1985, fig. 6L) or the eurekiid *Bandalaspis* Ivshin, 1962 (Ivshin 1962, text-fig. 80, pl. 19, figs 7, 9, 13).

OCCURRENCE: Furongian; *Olenus gibbosus* through *Olenus wahlenbergi* zones in Sweden.

Pygidium indet. B
(Text-fig. 23B)

MATERIAL: 1 pygidium: LO12092t from Övre Västerstad (Ö).

DESCRIPTION: Pygidium entire, wider than long. Maximum length about 0.4 of maximum width. Pygidial axis about 85% of maximal pygidial length, distinctly elevated above surface of pleural fields, tapered slightly backwards, with terminal axial piece



Text-fig. 23. Undetermined pygidia of exotic trilobites from the Furongian of Sweden. A – Pygidium indet. A, LO12091t, *O. gibbosus* or *O. truncatus* Zone at Övre Västerstad (Ö); B – Pygidium indet. B, LO12092t, *O. gibbosus* Zone at Övre Västerstad (Ö); C-D – Pygidium indet. C from the *P. brevispina* Zone at Hällekis (Vg). C – LO12093t; D – LO12094t. Accompanying fauna: ot – *Olenus truncatus* (Brünnich, 1781). Scale bars represent 0.5 cm rounded posteriorly. Pygidial axis with four inter-ring furrows which are wide and shallow. Anterior half-ring slightly narrower that axis, separated from it by straight articulating furrow. Pleural fields with four wide and shallow pleural furrows, of which the posteriormost is the shallowest. Border relatively wide and flat. Pygidium with slight indentation at posterior midpoint, pronounced by slightly narrower border at mid-point.

MEASUREMENTS: Pygidial axial length 13 mm, anterior pygidial width 25.4 mm.

REMARKS: With its proportion of width to length, numerous inter-ring furrows on the axis and inter-pleural furrows on the pleural fields, the specimen probably represents an aphelaspidinae, and appears to be closest to *Aphelaspis* and comparable to the illustrated specimens of *A. brachyphasis* Palmer, 1962 from Nevada (Palmer 1962, pl. 4, figs 6, 10; 1965, pl. 8, figs 19, 20) and *A. australis* Henderson, 1976 from Australia (Henderson 1976, pl. 49, fig. 7).

OCCURRENCE: Furongian; *Olenus truncatus* Zone in Sweden.

Pygidium indet. C
(Text-fig. 23C, D)

part 2001. *Pedinocephalus peregrinus* Henningsmoen 1957 [sic]; Weidner, pp. 65, 66, fig. 5 (pygidium only).

MATERIAL: Three pygidia: LO12093t and LO12094t from Hällekis (Vg); an unnumbered specimen from a glacial erratic boulder at Palsgård cliff (DK).

DESCRIPTION: Pygidium entire, wider than long. Maximum length about 0.45 of maximum width. Pygidial axis about 70% of maximal pygidial length, distinctly elevated above surface of pleural fields, tapered slightly backwards, with terminal axial piece rounded posteriorly. Pygidial axis with two inter-ring furrows. Anterior half-ring slightly narrower that axis, separated from it by straight articulating furrow. Pleural fields with three wide and very shallow pleural furrows, of which the posteriormost is the shallowest. Border relatively wide and flat; border expanding posteriorly to become twice as wide at axial mid-point.

MEASUREMENTS: Pygidial axial length 3.6–10.8 mm, anterior pygidial width 7.5–23 mm.

REMARKS: The pygidia are distinctive in having the border significantly expanded in the postaxial part. So far, it is not possible to assign these specimens with confidence to any known family or genus, although the long and wide pygidial axis (but not reaching the posterior border furrow), suggests affinities with the catillicephalid genus *Buttsia* Wilson, 1951 (Wilson 1951, pl. 89, figs 22, 23).

OCCURRENCE: Furongian; *Parabolina brevispina* Zone in Sweden; probably *Parabolina spinulosa* Zone in glacial erratic boulders in Denmark (Weidner 2001 and this paper).

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