Furongian (upper Cambrian) trilobites and agnostoids from the Alum Shale Formation of Bornholm, Denmark: revised taxonomy and biostratigraphy

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The Furongian (upper Cambrian) trilobite-agnostoid fauna from the Alum Shale Formation of Bornholm, Denmark, is reviewed and revised. The study is based on the museum material stored at the Natural History Museum of Denmark, including the material originally monographed by C. Poulsen (1923) [Bornholms Olenuslag og deres fauna. Danmarks Geologiske Undersøgelse II. Række, Vol. 40, 83 pp]. A total of 8502 specimens, mostly disarticulated sclerites, have been registered. The taxonomy of all species is updated and the best preserved specimens are illustrated. A total of 39 olenid and 5 agnostoid taxa (incl. the Miaolingian *Agnostus pisiformis*) are recorded including one new species, *Ctenopyge magna* n. sp. Two specimens of *Ctenopyge*, treated in open nomenclature as *Ctenopyge* sp. 1 and sp. 2, may also represent new species. 14 taxa have not been previously reported from Bornholm, viz. *Ctenopyge ahlbergi, Ctenopyge tumidoides, Eurycare brevicauda, Leptoplastus abnormis, Leptoplastus crassicornis, Olenus transversus, Parabolina lobata praecurrens, Peltura acutidens, Peltura minor, Peltura westergaardi, Protopeltura planicauda, Protopeltura praecursor, Pseudagnostus leptoplastorum?* and *Sphaerophthalmus drytonensis. Ctenopyge pecten* and *Ctenopyge affinis* are also new to Bornholm as the material formerly described under these names represent *Ctenopyge tenuis* and *C. magna* n. sp., respectively. *Lotagnostus americanus, Ctenopyge fletcheri, Sphaerophthalmus alatus* and *Triangulopyge humilis* were described under different names by C. Poulsen (1923). *Peltura westergaardi* and *Ctenopyge tenuis* are elevated from subspecies to species rank. A redescription of *Leptoplastus bornholmensis* is presented; the species is transferred to *Eurycare*. The identification of isolated skeletal parts of *L. abnormis* and *Leptoplastus ovatus* and *Sphaerophthalmus flagellifer* and *S. drytonensis* are remarked on.

The presence of three agnostoid and 14 trilobite zones is confirmed by fossils and all six Furongian superzones are developed on Bornholm. At least the *Leptoplastus paucisegmentatus* and *Leptoplastus raphidophorus* zones seem to be absent. Other undocumented zones may be unfossiliferous, not exposed or truly absent. Three different trilobite assemblages (potential subzones) are discerned in the *Peltura acutidens–Ctenopyge tumida* Zone; *Ctenopyge tumidoides* and *Sphaerophthalmus angustus* range into the basal part of this zone. All exposures of the Furongian Alum Shale Formation along the Læså and Øleå streams on southern Bornholm are briefly described including GPS coordinates.

Keywords: Furongian, biostratigraphy, taxonomy, trilobites, olenids, Alum Shale, Bornholm, Denmark.

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The Cambro–Ordovician Alum Shale Formation has long been known from discontinuous exposures along the Læså and Øleå streams on southern Bornholm, Denmark (e.g. Grönwall 1902, 1916; C. Poulsen 1922, 1923; Hansen 1945; Berg-Madsen 1985a, b, 1986); for location of outcrops, see Figs 1–2. The shale has also been penetrated by several wells, both cored and uncored, showing that the total thickness of the unit varies between 27 and 39 m on the island (Nielsen *et al.* 2018). The present paper reviews the trilobites found in the Furongian interval, which is 17–23 m thick (Nielsen *et al.* 2018). Regarding stratigraphic terminology, the traditional designations 'Lower', 'Middle' and 'Upper' Cambrian are now discarded (e.g. Babcock *et al.* 2005; Peng *et al.* 2012) and henceforth, the new terms Miaolingian and Furongian replace the former 'Middle' and 'Upper' Cambrian series, respectively. However, the new and old series are not corresponding precisely as the *Agnostus pisiformis* Zone previously was classified as 'Upper' Cambrian in Scandinavia (e.g. Westergård 1922; C. Poulsen 1923), but now is assigned to the Miaolingian (e.g. Terfelt *et al.* 2008; Nielsen & Ahlberg 2019). The revised classification is readily applicable in Scandinavia as a major faunal turnover marks the Miaolinigian–Furongian boundary with the introduction of olenid trilobites coinciding with the near disappearance of agnostoids.

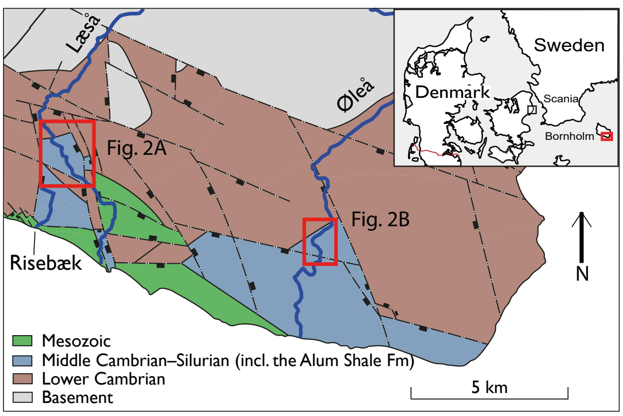


Fig. 1. Simplified geological map of southeastern Bornholm showing location of the Læså, Øleå and Risebæk streams. For locality details, see Fig. 2. Small insert shows location of the island of Bornholm in eastern Denmark.

Parts of the Furongian are highly fossiliferous, and the local trilobite fauna on Bornholm was monographed by C. Poulsen (1923), who described four agnostoid (incl. the Miaolingian *A. pisiformis*) and 24 trilobite taxa. A few additional trilobites have been described subsequently by Kaufmann (1933a), Whittington (1958), V. Poulsen (1963), Rasmussen *et al.* (2015), Schoenemann & Clarkson (2015) and Månsson & Clarkson (2016). C. Poulsen (1923) correlated the succession with the zonation established by Westergård (1922). The chronostratigraphy was later summarized by V. Poulsen (1966) who introduced the revised zonal scheme published by Henningsmoen (1957), but without discussing subzones. This is relevant as the many subzones defined by Henningsmoen (1957) with minor changes were elevated to zonal rank by Terfelt *et al.* (2008). The Furongian zonation for Scandinavia was further revised by Nielsen *et al.* (2014, 2020) and that

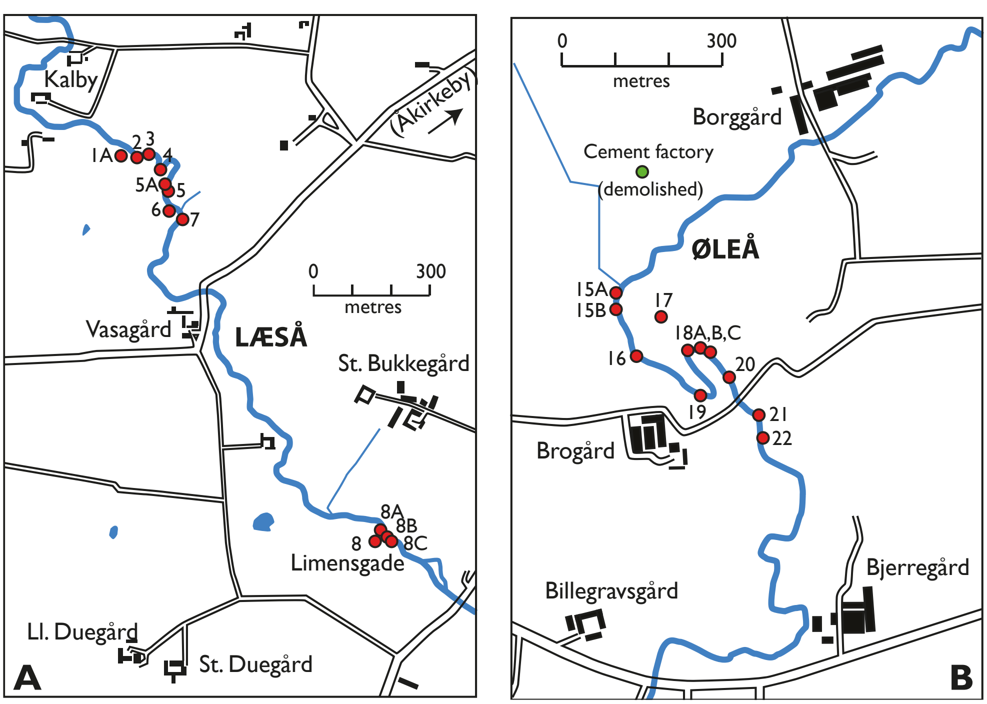


Fig. 2. Maps showing location of the Furongian Alum Shale exposures on Bornholm; see text for details. **A:** Detailed map of the Læså stream between Kalby and Limensgade SW of the town of Åkirkeby, showing location of exposures. **B:** Detailed map of the Øleå stream between Borggård and Sdr. Landevej east of the village of Pedersker, showing location of exposures.

scheme, comprising 23 zones allocated to six superzones, is adopted here (Fig. 3).

The aim of the present study is to document the Furongian trilobites and agnostoids recovered from Bornholm and to present an updated review of the local biostratigraphy. The recorded total of 43 species and subspecies (incl. agnostoids) are characteristic of 14 trilobite zones representing all six Furongian superzones. Overall, the study confirms the biostratigraphy established by C. Poulsen (1923) with only minor corrections.

Material and methods

The study is based on the fossil material from the Alum Shale Formation on Bornholm stored at the Natural History Museum of Denmark (SNM), including the specimens originally described by C. Poulsen (1923), as well as extensive new material collected by ATN in the 1970s. The studied material comprises 8502 counted and identified specimens, mostly disarticulated sclerites of trilobites plus a few agnostoids, but many more uncounted specimens are present in the samples at hand. They have been left out as they require preparation to be safely identified. The majority of the fossils are preserved in so-called anthraconite (early diagenetic bituminous carbonate), and only a few hundreds of specimens have been collected from the shale itself. The older anthraconite samples in the SNM collection are typically penetrated by numerous cracks, due to desiccation of the organic matter and/or pyrite oxidation. The newer material collected by ATN derives from loose limestone nodules found in the Læså stream near Vasagård and Limensgade (Fig. 2A). The nodules were numbered so that the material from each nodule is kept together, which is relevant for its use in biostratigraphic context.

The best preserved specimens of each taxon are illustrated. After preparation, the specimens were coated with ammonium chloride and photographed with a full-frame Canon EOS 5D Mark III camera. A series of 3–30 photos were taken of each specimen and subsequently stacked using the program Helicon Focus. The photographic illustrations were processed using Adope Photoshop software.

Illustrated specimens are numbered individually with the prefix MGUH. Samples in the so-called main collection at the Natural History Museum of Denmark are numbered with the prefix GM; nearly all of this material was collected in the early 1920s or earlier. The samples collected by ATN in the 1970s are numbered using the prefixes ATN and L. Please note that the fossiliferous samples labelled GM, ATN and L typically contain several specimens which therefore are referred to by the same sample number.

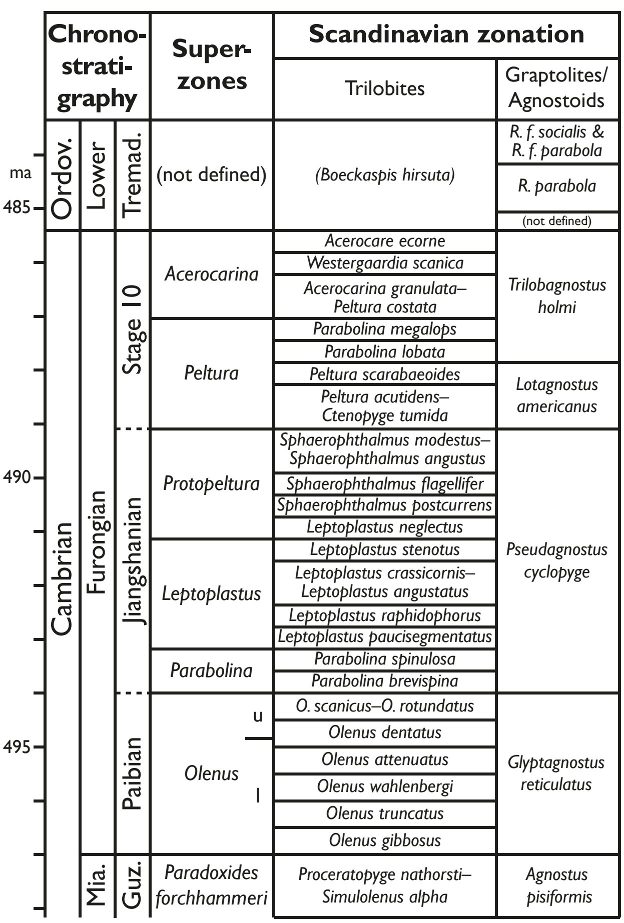
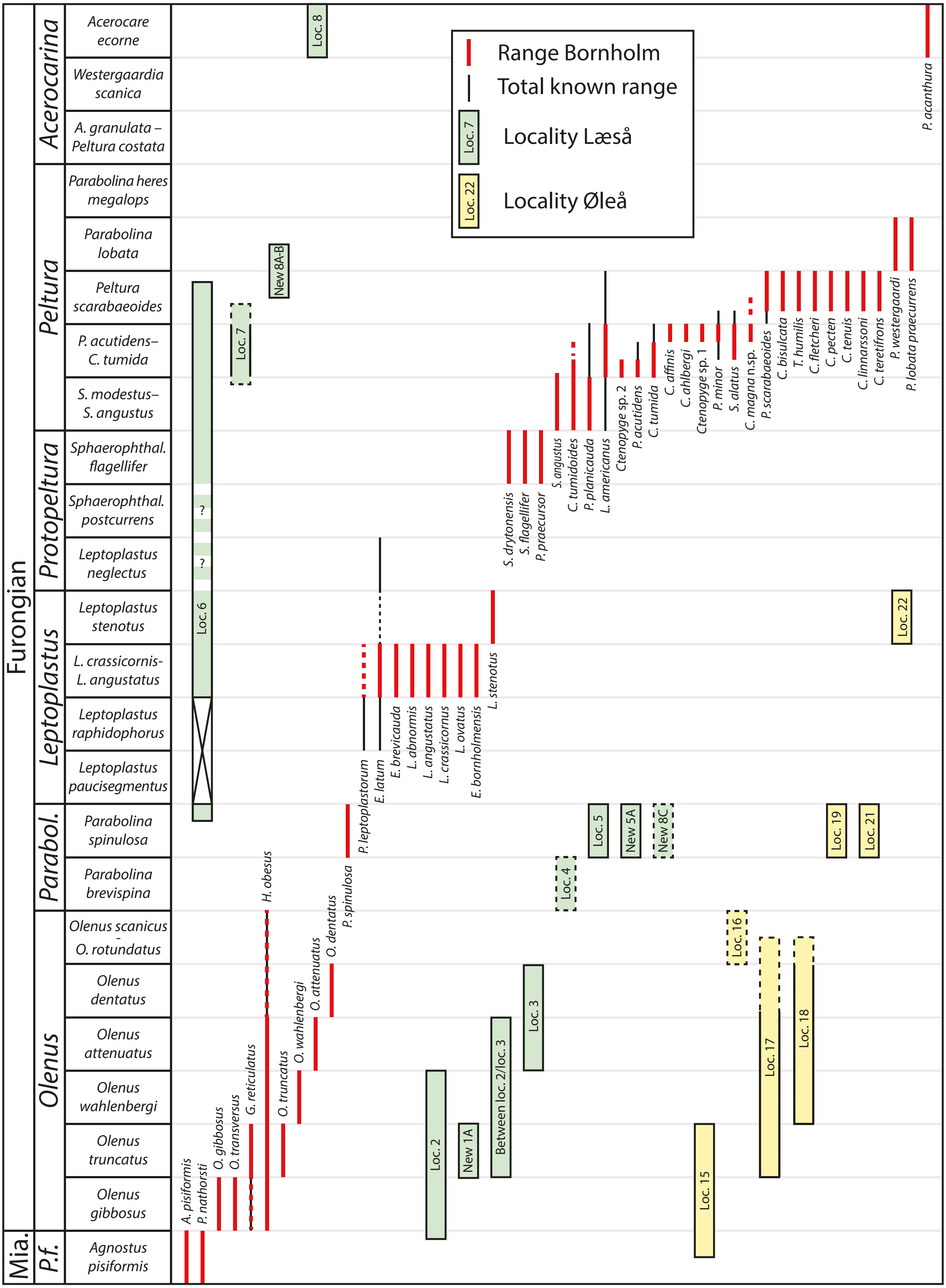


Fig. 3. Current biozonation scheme for the Furongian of Scandinavia (from Nielsen *et al.* 2020; slightly modified with regard to agnostoid zonation, see text). Abbreviations: Mia.: Miaolingian; Guz.: Guzhangian; u: upper; l: lower; Ordov.: Ordovician; Tremad.: Tremadocian; *R.f.*: *Rhabdinopora flabelliformis*.

Localities

All exposures of Furongian Alum Shale along the Læså and Øleå streams, existing at that time, were described by C. Poulsen (1923) and Hansen (1945). We here briefly describe the localities and provide GPS coordinates (using World Geodetic System 1984, WGS84) measured with a handheld Garmin eTrex model 30. The uncertainty in positioning is typically <3 m. The locality number system introduced by C. Poulsen (1923) is maintained and emended to include new exposures (Figs 2A–B). Miaolingian exposures are not discussed and for this reason some of Poulsen's upper Cambrian localities with the *Agnostus pisiformis* Zone are omitted.


Furongian
Mia.
P.f.
Olenus
Parabol.
Leptoplastus
Protopeltura
Peltura
Acerocarina
Agnostus pisiformis
Olenus gibbosus
Olenus truncatus
Olenus wahlenbergi
Olenus attenuatus
Olenus dentatus
Olenus scanicus - O. rotundatus
Parabolina brevispina
Parabolina spinulosa
Leptoplastus paucisegmentus
Leptoplastus raphidophorus
L. crassicornis- L. angustatus
Leptoplastus stenotus
Leptoplastus neglectus
Sphaerophthal. postcurrens
Sphaerophthal. flagellifer
S. modestus– S. angustus
P. acutidens– C. tumida
Peltura scarabaeoides
Parabolina lobata
Parabolina heres megalops
A. granulata – Peltura costata
Westergaardia scanica
Acerocare ecorne
Range Bornholm
Total known range
Loc. 7
Locality Læså
Loc. 22
Locality Øleå
A. pisiformis
P. nathorsti
O. gibbosus
O. transversus
G. reticulatus
H. obesus
O. truncatus
O. wahlenbergi
O. attenuatus
O. dentatus
P. spinulosa
P. leptoplastorum
E. latum
E. brevicauda
L. abnormis
L. angustatus
L. crassicornus
L. ovatus
E. bornholmensis
L. stenotus
S. drytonensis
S. flagellifer
P. praecursor
S. angustus
C. tumidoides
P. planicauda
L. americanus
Ctenopyge sp. 2
P. acutidens
C. tumida
C. affinis
C. ahlbergi
Ctenopyge sp. 1
P. minor
S. alatus
C. magna n.sp.
P. scarabaeoides
C. bisulcata
T. humilis
C. fletcheri
C. pecten
C. tenuis
C. linnarssoni
C. teretifrons
P. westergaardi
P. lobata praecurrens
P. acanthura
Loc. 8
New 8A-B
Loc. 6
?
?
Loc. 2
New 1A
Between loc. 2/loc. 3
Loc. 3
Loc. 4
Loc. 5
New 5A
New 8C
Loc. 15
Loc. 16
Loc. 17
Loc. 18
Loc. 19
Loc. 21

The outcrops in the Læså stream between Kalby and Vasagård (Fig. 2A) intermittently expose the *Olenus*, *Parabolina*, *Leptoplastus*, *Protopeltura* and lower part of the *Peltura* superzones, whereas at Limensgade only the uppermost part of the Furongian is accessible (sporadic exposures of the *Peltura* Superzone plus the very top of the *Acerocarina* Superzone). In the Øleå stream, parts of the *Olenus*, *Parabolina* and *Leptoplastus* superzones are exposed. Figure 4 outlines the zones present (or assumed present) in the different outcrops.

Furongian Alum Shale is also exposed in the Risebæk stream north of Sdr. Landevej (the road from Rønne to Nexø); for location of Risebæk, see Fig. 1. Where the Risebæk stream turns sharply west-northwestwards some 460 m north of the road, the Alum Shale contains *Orusia lenticularis* and represents the *Parabolina* Superzone (ATN, unpublished). The strata tilt *c.* 4–5° southwards and are overlain by Tremadocian Alum Shale and the Dapingian Komstad Limestone Formation immediately north of Sdr. Landevej (Nielsen 1995). Hence, the *Leptoplastus*, *Protopeltura*, *Peltura* and *Acerocarina* superzones are theoretically exposed in the Risebæk stream, at least intermittently, between the sharp turn of the creek and the road, but these exposures have never been investigated.

Læså

For location of exposures, see Fig. 2A.

New locality 1A
55°3′30.25″N, 14°53′6.44″E

A section of highly weathered Alum Shale can be seen along a tractor track in the field some 20 m west of the Læså creek, adjacent to the classical 'Kalby section' through the Miaolingian lower part of the Alum Shale Formation (locality II *sensu* Hansen 1945). The exposed succession, here referred to as new locality 1A, is normally *c.* 0.2 m high and *c.* 3 m long but trenching in 2020 exposed 1.15 m of strongly disturbed shale in a 9 m long section, including one large anthraconite lens in the middle of the exposure. The shale contains common *Olenus truncatus* and some *Homagnostus obesus* [this newly sampled fossil material is not included in the present study] showing that the section represents the basal Furongian. The bedding was measured at $52^0/16^0$ SE (n=3) in the northern part of the section and at $155^0/14^0$ E (n=2) in the southern part of the section. However, the shale is strongly disturbed due to glacio-tectonics.

Locality 2 (Hansen 1945, locality IV)
55°3′29.97″N, 14°53′8.67″E

Ca. 2.5 m long exposure in the southern bank and creek bed, including a limestone bed some 35 cm thick outcropping in the western part. This bed is a proxy for the Miaolingian/Furongian boundary in most wells on Bornholm penetrating this level (Nielsen *et al.* 2018). The dark grey limestone is fine-grained, compact and splintery, and contains sporadic phosphatic shells of bradoriid arthropods but no trilobites. The orientation of the limestone is 10°/5°E. *Olenus* occurs in the upper part of the section (downstream) according to C. Poulsen (1923), whereas Hansen (1945) reported *Olenus* from the entire section.

The studied material from this locality includes *Agnostus pisiformis, Homagnostus obesus, Glyptagnostus reticulatus, Olenus attenuatus, O. gibbosus, O. transversus, O. truncatus* and *O. wahlenbergi.* This assemblage is indicative of the *A. pisiformis* Zone and various zones in the lower part of the *Olenus* Superzone.

Locality 3 (Hansen 1945, locality V)
West end: 55°3′30.07″N, 14°53′9.97″E; east end: 55°3′29.98″N, 14°53′10.55″E

This locality is a *c.* 12 m long outcrop of shale in the northern bank of the creek with a height of up to 0.8 m. Shale is also exposed in the adjacent creek bed but is usually below the water table. The bedding orientation is 20°/10° SE (n = 2). C. Poulsen (1923) found common *H. obesus* at this locality and Kaufmann (1933a) described *O. dentatus* from a 1 cm thick horizon. Hansen (1945) noted that the shale in some places exhibits undulations, suggesting that hidden limestone concretions are present.

The studied material from this locality includes only *H. obesus* and *O. attenuatus*, showing that the exposed strata represent the *Olenus* Superzone. A shale sample 'from the Læså' without proper label contains a fragmentary cranidium that resembles *O. dentatus* (Fig. 7K) and may derive from this locality.

Locality 4 (Hansen 1945, locality VI)
West end: 55°3′28.77″N, 14°53′11.35″E; east end: 55°3′28.84″N, 14°53′12.11″E

A *c.* 14 m long and up to 1.3 m high exposure in the southern bank and adjacent creek bed continuing almost all the way to the opposite bank. 1.55 m of shale are exposed in total, some below the water table most of the year. An anthraconite lens, *c.* 100 × 14 cm in size, is seen in the upper part of the bank. Three smaller

▲ **Fig. 4.** Ranges of trilobites recorded from Bornholm; standard zonation adopted from Nielsen *et al.* (2020). Inferred stratigraphic ranges of exposures are also shown. For location of exposures, see Fig. 2. Dashed locality boxes: Uncertain age of exposed strata.

lenses, *c.* 45 × 15 cm in size, are exposed near the top in the western end of the section, but they are partially hidden by vegetation. Small barite lenses up to *c.* 15 × 10 cm in size, often smaller ('fist size', Hansen 1945), are common in the shale exposed in the creek bed, i.e. in the lower part of the succession. The bedding orientation is 85°/7° S (n=4). C. Poulsen (1923) found a few poorly preserved *Orusia lenticularis* at this locality suggesting a correlation with the *Parabolina* Superzone.

Locality 5 (Hansen 1945, locality VII)
55°3′26.64″N, 14°53′11.82″E

Exposure in the creek bed adjacent to the eastern bank. Only the top of two anthraconite lenses are now exposed, measuring *c.* 1 × 1 m and *c.* 0.5 × 0.5 m, respectively. No shale is exposed, and it is impossible to measure the orientation of strata. C. Poulsen (1923) found *Orusia lenticularis* at this locality together with a few *Parabolina spinulosa*, which is confirmed by the present study. From this site, Hansen (1945) described four anthraconite lenses, up to 1 m in diameter, and a limestone bed, partly coqinoid, with *Orusia*. The exposed strata represent the *Parabolina* Superzone.

New locality 5A
West end: 55°3′27.12″N, 14°53′12.13″E; east end: 55°3′27.17″N, 14°53′12.48″E

Slightly tilting shale beds are exposed in the creek bed along the western bank on the opposite side of locality 5. The exposure is *c.* 12 m long, but only up to 15 cm high; in total *c.* 0.5 m of shale is exposed. Five anthraconite lenses were observed *in situ*; the lenses are up to *c.* 40 × 30 cm in size. The bedding orientation was measured at 19°/9° E and 42°/6° SE; the scatter is likely due to the presence of limestone nodules.

Locality 6 (Hansen 1945, locality VIII)
Northwest end: 55°3′26.22″N, 14°53′12.00″E; southeast end: 55°3′25.20″N, 14°53′13.07″E

This is the best known Alum Shale section in the Læså stream, originally described by Grönwall (1916) and C. Poulsen (1923). It is *c.* 40 m long and *c.* 6 m high and is located in the southern bank of the creek. Grönwall (1916) reported 25 limestone nodules from this exposure; note that not all concretion levels are shown in the synoptic profile published by C. Poulsen (1923, fig. 2). Fifteen anthraconite lenses, up to 63 × 155 cm in size, can still be seen in the section. The bedding orientation was measured at 112°/9° S (n=6) but is a little irregular due to the common presence of limestone nodules. In the western end of the section, the creek bank is overgrown, but anthraconite lenses and a little shale are exposed here and there, notably in the upper part; this rather covered part is not included in the stated total length of the section.

Several trilobite zones are exposed (C. Poulsen 1923, fig. 2); all stated thicknesses are cited from that publication. *Orusia lenticularis* is common at the base of the section and this basal interval represents the upper 2 m of the *Parabolina* Superzone. Then follows a limestone-dominated horizon, *c.* 0.5 m thick, consisting of more or less amalgamated limestone nodules representing the *Leptoplastus* Superzone. This level is overlain by *c.* 1.1 m of shale with several large anthraconite lenses, representing the *Protopeltura* Superzone. Then follows shale with scattered anthraconite lenses representing the *Peltura* Superzone, where the *Peltura acutidens–Ctenopyge tumida* Zone, 2.10 m, and the *Peltura scarabaeoides* Zone (>1.8 m) are confirmed to be present. Nielsen *et al.* (2018) inferred that the former zone is up to 1.7 m thick in the Læså area based on correlation of gamma logs in wells. C. Poulsen (1923, fig. 2) assigned the uppermost part of the section, exposed high in the rather overgrown western end, to the *Parabolina 'longicornis'* Subzone [now *P. lobata* Zone], but this is incorrect. The sparse material labelled as *Parabolina 'longicornis'* in the museum collection (a couple of free cheeks only) represents *Ctenopyge tenuis* and derives from the *Peltura scarabaeoides* Zone and no specimens of *P. lobata* have been found at localities 6 or 7. Loose slabs of limestone sampled from the scree high in the western part of the section (i.e. immediately below the level suggested to represent the *P. lobata* Zone by C. Poulsen 1923) contain only *P. scarabaeoides* and *T. humilis*, suggesting that the *P. scarabaeoides* Zone extends to the very top of the succession. This is also in better accordance with the thickness of this zone indicated by Nielsen *et al.* 2018 (4.5 m in a nearby well).

The studied material from this locality includes *Ctenopyge affinis, C. bisulcata, C. fletcheri, C. linnarssoni, C. magna* n. sp., *C. pecten, C. tenuis, C. teretifrons, C. tumida, C. tumidoides, Eurycare bornholmensis, E. brevicauda, E. latum, Leptoplastus abnormis, L. angustatus, L. crassicornis, L. ovatus, L. stenotus, Lotagnostus americanus, Parabolina spinulosa, Peltura acutidens, P. minor, P. scarabaeoides, Protopeltura planicauda, P. praecursor, Pseudagnostus leptoplastorum*?, *Sphaerophthalmus alatus, S. angustus, S. drytonensis, S. flagellifer* and *Triangulopyge humilis*. This assemblage confirms the biozonation outlined by C. Poulsen (1923) except for the lack of the *P. lobata* Zone.

Locality 7 (Hansen 1945, locality IX)
55°3′24.57″N, 14°53′14.32″E

This outcrop, *c.* 8 m long and up to 1.3 m high, is located in the eastern bank, where the creek bends south-westwards shortly downstream of locality 6. The bedding orientation is 104°/7° S. Please note that this exposure is incorrectly located on the map shown by C. Poulsen (1923, fig. 1); the exposure farther downstream labelled as 7 on his map represents Tremadocian Alum Shale. However, it is obvious from the adjoining description that locality 7 in fact is positioned as indicated on Fig. 2A (see also Hansen 1945, fig. 8). The studied material from this locality includes *Ctenopyge ahlbergi*, *C. affinis*, *C. bisulcata*, *C. fletcheri*, *C. magna* n. sp., *C. tenuis*, *C. tumida*, *C. tumidoides*, *Sphaerophthalmus alatus* and *S. angustus*, showing that the exposed strata represent the lower part of the *Peltura* Superzone and probably also the *S. modestus–S. angustus* Zone. C. Poulsen (1923) reported also *Ctenopyge teretifrons*, *Peltura scarabaeoides* and *Triangulopyge humilis* (under the name *S. alatus*) from locality 7, but no museum material of these taxa is preserved from the locality. The presence of *C. bisulcata* indicates, however, that the top of the section represents the *P. scarabaeoides* Zone.

The tops of several large anthraconite lenses are exposed in the creek bed downstream of locality 7. C. Poulsen (1923) did not find fossils in these nodules but as the stream here is oriented along strike, they most probably represent the lower part of the *Peltura* Superzone.

Locality 8 (Hansen 1945, locality X)
North-western end: 55°2′55.86″N, 14°53′38.96″E; south-eastern end: 55°2′54.92″N, 14°53′39.21″E

This locality is the abandoned limestone-shale quarry at Limensgade. The quarry was thoroughly cleaned in 2017, providing extensive and excellent exposures – probably the best since the quarry was active in the 1840s. The upper 4.5 m of the Alum Shale Formation is exposed on the lower terrace and the lower 2.3 m of the overlying Middle Ordovician Komstad Limestone is exposed on the upper terrace. The shale succession on the lower terrace is *c.* 30 m long and exposes mainly the Tremadocian Alum Shale but with Furongian Alum Shale near the base (lower 0.5 m). No anthraconite lenses were seen in the basal part in 2017–18 despite intensive search and these concretions seem to be rare (lenses were apparently still visible when Hansen 1945 investigated the site). The bedding orientation is 3°/4° W (n=6) but is rather variable due to the small dip.

In anthraconite lenses in the lowermost part of the section, C. Poulsen (1923) found sparse *Parabolina acanthura*, indicative of the *Acerocarina* Superzone. This level is in turn overlain by 0.1 m of unfossiliferous shale, followed by graptolitic Tremadocian Alum Shale, 4.0 m thick (von Jansson 1979). The smaller thickness of the Tremadocian stated by C. Poulsen (1922, 1923) reflects that he failed to find graptolites lower down.

New exposures in the Læså stream near the Limensgade quarry

For location, see Fig. 2A.

New locality 8A
55°2′56.53″N, 14°53′40.04″E

Low outcrop of highly weathered shale in the south-western bank of the creek. The exposure is *c.* 0.35 m high and *c.* 4 m long. The shale contains a few limestone lenses, and several nodules can be seen lying loose in the creek. Loose material of this kind was sampled by ATN in the late 1970s and has been investigated here (including several anthraconite nodules that were collected downstream of this exposure). The material contains *Ctenopyge linnarssoni*, *C. tenuis*, *Parabolina lobata praecurrens*, *Peltura scarabaeoides*, *P. westergaardi* and *Triangulopyge humilis*, indicating the presence of the *Peltura scarabaeoides* and the *Parabolina lobata* zones (*Peltura* Superzone).

New locality 8B
55°2′55.88″N, 14°53′41.18″E

Shale with some limestone lenses is exposed in the south-western bank of the creek just north of the wooden pedestrian bridge. The section is *c.* 10 m long, and the exposed succession is *c.* 0.7 m thick. The bedding orientation is 4°/12° W. Regarding fossil content, see locality 8A. No fossils have been sampled *in situ.*

New locality 8C
55°2′55.28″N, 14°53′42.04″E

A small outcrop of coarse anthraconite (concretion) and a little shale can be seen in the creek bed near the north-eastern bank, about 20 m downstream of the wooden pedestrian bridge. The total exposed thickness is *c.* 0.4 m. The shale bedding is affected by the concretion, but the general bedding orientation is about 1°–10°/up to 28°W. The rather strong dip suggests proximity of a fault. An articulate brachiopod, *Orusia*?, was found in the anthraconite and the exposed strata likely represent the *Parabolina* Superzone.

Øleå

For location of exposures, see Fig. 2B. Several Furongian trilobites in the SNM collection are labelled 'Cementen' or 'Cementfabrikken, Ølenå' [Cement factory, Øleå], which refer to a former cement factory at Borggård east of Pedersker, which was in operation 1846–1915 (for location, see Fig. 2B). The fossils are said to have been collected from the limestone that was intended to be crushed for cement fabrication. These Furongian fossils must derive from local ice-rafted limestone that apparently also was used for manufacturing cement in addition to the quarried Miaolingian limestone.

Locality 15A (Hansen 1945, locality 8, upstream part)
North end: 55°1′34.95″N, 15°0′20.82″E; south end: 55°1′34.68″N, 15°0′20.68″E

C. Poulsen's (1923) locality 15, which is located in the western bank of the creek, is subdivided here into 15A and 15B. Site 15A is 12 m long and exposes 1.5 m of shale, of which 0.4 m is below the water table (even in 2018 when the water level was exceptionally low). The bedding orientation is 86°/4° S (n=3).

The material studied from locality 15 (undivided) contains only *Olenus truncatus.* Investigations of locality 15B in 2020 suggested that the shale at locality 15A probably represents the Miaolingian *Agnostus pisiformis* Zone.

Locality 15B (Hansen 1945, locality 8, downstream part)
North end: 55°1′34.43″N, 15°0′20.53″E; south end: 55°1′33.86″N, 15°0′20.75″E

This exposure starts 10 m downstream of site 15A and is 1.3 m high and 18 m long. The section is shale dominated, but a large limestone lens, 150 × 23 cm in size, is seen in the southern end of the outcrop. It contains bradoriid arthropods and the horizon may correspond to the limestone bed seen at locality 2 in the Læså stream. Investigations in 2020 showed that *Olenus* representatives turn up immediately below this limestone and not 0.5 m above it, as stated by C. Poulsen (1923). A pygidium of *Proceratopyge nathorsti* (indicative of the Miaolingian *Proceratopyge nathorsti–Simulolenus alpha* Zone) was found 10 cm below the first occurrence of *Olenus*. The bedding orientation is 54°/5° S (n=2).

Locality 16 (Hansen 1945, locality 9)
West end: 55°1′31.41″N, 15°0′21.67″E; east end: 55°1′30.40″N, 15°0′24.56″E

This is the most extensive exposure of Alum Shale in the Øleå stream. The section in the southern creek bank is 4 m high and 60 m long, although it is partially overgrown and covered by soil. The bedding orientation is 110°/3° S (n=13).

In the eastern end of the section the shale contains five anthraconite lenses, of which the largest measures 55 × 190 cm. The shale contains also common small limestone concretions (c. 10 cm in diameter); the limestone is greyish, very fine-grained, splintery and unfossiliferous except for bradoriid arthropods. At this locality, C. Poulsen (1923) found poorly preserved *Homagnostus obesus* at about 1.25 m above the creek level, showing that the exposed succession represents the *Olenus* Superzone, presumably its upper part. The studied material from this locality includes only *H. obesus.*

Locality 17 (obliterated)
This small pit, from which shale had been excavated for road material, was located in the field east of the Øleå stream, but is now infilled. C. Poulsen (1923) reported *Glyptagnostus reticulatus*, *Homagnostus obesus* and *Olenus truncatus* from this site; the studied material from the locality includes also *Olenus attenuatus* and *Olenus wahlenbergi.*

Locality 18 (Hansen 1945, locality 10)
Western end: 55°1′31.09″N, 15°0′27.80″E; eastern end: 55°1′31.22″N, 15°0′27.96″E

This shale exposure, 7 m long and up to 0.35 m high, is located in the northern bank of the creek. The bedding orientation is 21°/2° E (n=3). C. Poulsen (1923) found common *Homagnostus obesus* at this site. The studied material from this locality includes also *Glyptagnostus reticulatus, Olenus wahlenbergi* and *O. dentatus*, showing that the shale represents the *Olenus* Superzone.

More Alum Shale has been exposed downstream of this site since C. Poulsen's (1923) investigations. Approximately 10 m downstream of site 18 (GPS coordinates north end: 55°1′31.26″N, 15°0′28.29″E; south end: 55°1′30.97″N, 15°0′28.87″E), a shale exposure, 14 m long and up to 0.5 m high, is present in the north-eastern bank of the creek. The bedding orientation is 20°/5° E (n=3). Slightly farther downstream (GPS coordinates 55°1′30.60″N, 15°0′29.09″E) occurs a small exposure of shale in the north-eastern creek bank, up to 0.35 m high and extending for 3.5 m. The bedding orientation is 39°/3°E (n=3).

The three exposures constitute almost one long outcrop, separated by small areas covered by vegetation, mainly tree roots.

Locality 19 (Hansen 1945, locality 11)
Eastern end: 55°1′28.42″N, 15°0′29.60″E; western end: 55°1′28.66″N, 15°0′28.39″E

This shale exposure, 24 m long and up to 1.4 m high, is located in the southern creek bank. Much vegetation is present with tree roots growing in between the shale. The shale can be seen also in the northern creek bank and in the creek bed itself. The bedding orientation is 106°/4° S (n=6) in the southern end of the exposure. At this locality both C. Poulsen (1923) and Hansen (1945) found common *Orusia lenticularis*, indicative of the *Parabolina* Superzone.

Locality 20 (Hansen 1945, locality 12)
Northern end: 55°1′30.13″N, 15°0′30.88″E; southern end: 55°1′29.85″N, 15°0′31.11″E

Highly weathered unfossiliferous shale is exposed here in the north-eastern creek bank for a stretch of *c.* 14 m; *c.* 0.9 m of shale is exposed (some below the water table under normal circumstances). The bedding orientation is 40°/3° E (n=7).

On the map shown by C. Poulsen (1923, fig. 1) this locality is placed a little too far south.

Locality 21 (Hansen 1945, locality 13)
Northern end: 55°1′27.08″N, 15°0′33.92″E; southern end: 55°1′26.89″N, 15°0′34.09″E

About half of this exposure was below the water table even in August 2018 when the water level in the stream was unusually low. Shale, *c.* 0.65 m thick, is exposed in the north-eastern bank and can be followed for *c.* 7.5 m. A (?loose) lens is exposed in the southern end of the exposure immediately below the Quaternary strata. The exposure yields *Orusia lenticularis* as described also by C. Poulsen (1923), indicative of the *Parabolina* Superzone. The bedding orientation is 143°/11° E (n=5).

Locality 22A (Hansen 1945, locality 14)
55°1′26.16″N, 15°0′34.5″E

C. Poulsen (1923) reported findings of a few anthraconite lenses containing *Leptoplastus stenotus* within the creek bed at this site and his species identification is confirmed by the present study. A shale exposure, *c.* 5 m long, was seen in May 2019 in the creek bed (below the water table).

Locality 22B
55°1′25.8″N, 15°0′34.2″E

An anthraconite lens, *c.* 0.8 m in diameter, is exposed here in the creek bed adjacent to the eastern bank. Since no shale is visible, the bedding orientation could not be measured.

Hansen 1945, locality 16
Hansen (1945, p. 20) reported an anthraconite lens and almost horizontally lying Alum Shale from this site, which was not mentioned by C. Poulsen (1923). Reconnaissance field work in May 2019 failed to locate the exposure and it may have referred to a loose raft of Alum Shale embedded in Quaternary till.

Furongian zones on Bornholm

Olenid trilobites are typically extremely abundant in the Furongian part of the Scandinavian Alum Shale Formation and a detailed biostratigraphy was established by Westergård (1922, 1947) and Henningsmoen (1957), with subsequent revisions introduced by Ahlberg (2003), Terfelt *et al.* (2008), Høyberget & Bruton (2012), Nielsen *et al.* (2014), and Rasmussen *et al.* (2015, 2016). In the present study we use the modified zonation recently introduced by Nielsen *et al.* (2020), and we refer to that paper for further comments on the Scandinavian zonal scheme. The zonation used in the current study is shown in Fig. 3. Agnostoids are generally rare (except for *Homagnostus obesus*) and of very low diversity in the Furongian of Scandinavia. Terfelt et al. (2008) outlined four agnostoid zones (see Fig. 3), which primarily are of relevance for correlation out of Baltica.

The Furongian trilobite zones on Bornholm were remarked on by Johnstrup (1874, 1891) and Grönwall (1916), but C. Poulsen (1923) is the only detailed study published so far. He investigated eight localities along or near the Læså stream, 12 localities along or near the Øleå stream and two localities in the vicinity of Risebæk (for location of these watercourses, see Fig. 1). C. Poulsen (1923) recorded altogether 24 different species and 'variants' of olenids and four agnostoids and he recognized six zones and 11 subzones (including the *A. pisiformis* Zone), following the stratigraphy introduced by Westergård (1922). In the present study, 43 different taxa are reported from the Furongian of Bornholm and they are characteristic of 14 trilobite and three agnostoid zones (Fig. 4).

Some of the material stored at the Natural History Musem of Denmark must have been collected *in situ* (see C. Poulsen 1923, fig. 6) but no records of sampling levels are preserved. Hence, the precise collecting levels of the studied material are essentially unknown. In terms of biostratigraphy, this obviously is not ideal but since most olenid trilobites range through only one or two zones (see summary of ranges in Nielsen *et al.* 2020, fig. 1), it is possible to establish which fossiliferous Furongian zones are exposed on Bornholm with a high degree of confidence.

Agnostoid zonation

The uppermost Miaolingian *Agnostus pisiformis* Zone is characterized by the eponymous index fossil, which is common on Bornholm (recorded at localities 1, 2, 11, 13 and 14 as well as downstream of locality 8C, see taxonomic section). It co-occurs with common phosphatocopines, but no other agnostoids have been collected from the zone. A single pygidium of *Proceratopyge nathorsti* has recently been collected from the very top of the *A. pisiformis* Zone at locality 15B (not illustrated, sample GM 2019-100). The overlying *Glyptagnostus reticulatus* Zone, straddling the entire *Olenus* Superzone (Fig. 3), is defined by the FAD of *G. reticulatus*, which is infrequent on Bornholm, whereas *Homagnostus obesus* is common. Both species have been recorded from the lower part of the *Olenus* Superzone (localities 2–3 and 16–18). Only one agnostoid cephalon, assigned to *Pseudagnostus leptoplastorum*?, have been found at locality 6 in the overlying *Pseudagnostus cyclopyge* Zone, in which agnostoids are exceedingly rare on Bornholm as elsewhere in Scandinavia. The index fossil itself, *P. cyclopyge*, has not been found and identification of the zone remains open to interpretation. The only agnostoid reported from the overlying *Lotagnostus americanus* agnostoid Zone is the eponymous species, of which just one specimen is preserved in the studied collection. According to C. Poulsen (1923) it derives from the *Ctenopyge tumida–Peltura acutidens* olenid Zone at locality 6. This seems to be the level where *L. americanus* turns up in Scandinavia (Westergård 1922, 1947); there are no documented reports from the *Sphaerophthalmus modestus–Sphaerophthalmus angustus* Zone (cf. Ahlberg & Terfelt 2012). No agnostoids from the *T. holmi* Zone have been recorded on Bornholm. In previous literature the zone was inferred starting from about the base of the *P. scarabaeoides* olenid Zone, based on the record of a single pygidium from the conglomerate at the top of the Alum Shale Formation at Uddagården, Falbygden, Sweden (Westergård 1922, p. 69). However, everywhere else in Scandinavia is *T. holmi* known exclusively from the *P. lobata* Zone and we envisage that the conglomerate at Uddagården, which marks an extensive hiatus, in part formed during the *P. lobata* Zone.

Olenid zonation

Olenus Superzone

The *Olenus* Superzone comprises six zones (Fig. 3), and index fossils from five of these are present in the studied material, viz. *O. gibbosus, O. truncatus, O. wahlenbergi, O. attenuatus* and *O. dentatus*. The material derives from localities 2–3, 15, 17 and 18. The base of the superzone is defined by the FAD of *O. gibbosus.* Only a few specimens of that species are at hand, all from locality 2, and apparently *O. gibbosus* is rare or perhaps the eponymous zone is thin and/or not well-exposed. Kaufmann (1933a) did not observe *O. gibbosus* in the Læså sections (localities 2–3) and in a recent unpublished study of the Miaolingian/Furongian boundary beds at locality 15B in the Øleå no specimens were found. Here the base of the Furongian is marked by the FAD of *O. transversus* and maybe this is the general pattern in the Øleå area. The latter species has been found at locality 2, in the creek bed between localities 2 and 3 and at locality 15B. It is conceivable that it characterizes a thin separate interval like in Scania (see Kaufmann 1933b; Westergård 1942, 1944); elsewhere in Scandinavia it co-occurs with *O. gibbosus* (Westergård 1922; Henningsmoen 1957). *Olenus truncatus* and *O. wahlenbergi* are common on Bornholm. The former has been found at locality 2, in the riverbed between localities 2 and 3, and at locality 15. The latter occurs commonly at localities 17 and 18 and one free cheek is from locality 2. Kaufmann (1933a) described *O. dentatus* from a 1 cm thick horizon in the Læså stream (locality 3). None of that material is kept in the SNM collection, but given Kaufmann's extensive knowledge on *Olenus*, his determination is regarded reliable. A fragmentary cranidium in the SNM collection, likely deriving from locality 3, is tentatively assigned to *O. dentatus* (Fig. 7K). Another safely assigned specimen of *O. dentatus* (external mould of complete specimen) derives from locality 18 (Fig. 7J). Hence, all zones of the *Olenus* Superzone except for the *O. scanicus–O. rotundatus* Zone are proven present by fossils. Nielsen *et al.* (2018) concluded, based on correlation of gamma logs in wells, that also the *O. scanicus–O. rotundatus* Zone is developed on Bornholm. The shale at locality 16, where only *H. obesus* has been recorded, is a likely candidate for this horizon. The lower richly fossiliferous part of the *Olenus* Superzone (*O. gibbosus* Zone to the Last Appearance Datum of *O. dentatus*) is 1.8–2.9 m thick in wells in the Læså area according to gamma log stratigraphy (Nielsen *et al.* 2018, table 5). Kaufmann (1933a, text-fig. 1) measured this interval at close to 2 m in the Læså stream (localities 2–3).

Parabolina Superzone

This superzone comprises two zones (Fig. 3), of which the *Parabolina spinulosa* Zone is confirmed present on Bornholm through findings of the eponymous species at localities 5–6. Nielsen *et al.* (2018) inferred, based on correlation of gamma logs in wells, that also the *Parabolina brevispina* Zone is developed, although perhaps only in the Læså area, but the index fossil has not been found so far. The zone may be non-trilobitic or is not exposed. The shale at locality 4 is a potential candidate; here only sparse *Orusia lenticularis* has been found (C. Poulsen 1923). This brachiopod is very common in both zones of the *Parabolina* Superzone (recorded at localities 4–6, 19, 21).

Leptoplastus Superzone

This superzone is characterized by representatives of *Leptoplastus* and *Eurycare* and comprises four zones (Figs 3–4). The superzone is thin, just *c.* 0.5 m at locality 6 (see C. Poulsen 1923, fig. 2), which is the general trend in wells on Bornholm (Nielsen *et al.* 2018). Only the *Leptoplastus crassicornis–Leptoplastus angustatus* and *Leptoplastus stenotus* zones are developed (localities 6 and 22) and the *Leptoplastus paucisegmentatus* and *L. raphidophorus* zones appear to be absent on Bornholm. In the limestone lenses at locality 6, *Eurycare latum* is very common in a *c.* 5 cm thick basal horizon, but rare specimens of *E. brevicauda*, *L. crassicornis* and *L. ovatus* have also been found in this interval. Then follows *c.* 5 cm of coarse-grained unfossiliferous anthraconite, in turn overlain by limestone containing *Eurycare bornholmensis, Leptoplastus abnormis, L. angustatus, L. crassicornis, L. ovatus* and *Pseudagnostus leptoplastorum*?, indicative of the *L. crassicornis*–*L. angustatus* Zone. This zone is presumably about 0.3 m thick (+/- 5 cm). *Leptoplastus angustatus, L. crassicornis* and *L. ovatus* co-occur in the same samples supporting the abandonement of three individual zones (see Rasmussen *et al.* 2015). We note, however, that in 25% of the 85 samples containing *L. angustatus,* the species occurs alone, typically in profusion, showing that at least one horizon (a single bedding plane?) is characterized by this species occurring alone, probably for ecological reasons. The upper part of the superzone contains only *L. stenotus*; it is characteristic of the eponymous zone (?10–20 cm thick). *Leptoplastus stenotus* has been recorded also at locality 22.

Protopeltura Superzone

In the revised zonal scheme for Scandinavia, this superzone is subdivided into four zones (Fig. 3). *Leptoplastus neglectus* has not been found on Bornholm, but correlation of gamma logs in wells suggests that the eponymous zone is developed (Nielsen *et al.* 2018). It is thin, 0.2–0.5 m (maybe even including the overlying *Sphaerophthalmus postcurrens* Zone) and requires detailed sampling to be located. A resampling of the section exposed at locality 6 should be made in order to verify its assumed presence. The absence of samples with *L. neglectus* in the museum collection indicates that the interval contains no limestone. *Sphaerophthalmus postcurrens*, characterizing the overlying zone, likewise has not been encountered on Bornholm, but considering that the zone is very thin in Scania (Westergård 1942, 1944) it may be only a few centimetres thick if developed at all.

Sphaerophthalmus flagellifer, the index species of the overlying zone, is common in the studied museum collection. It co-occurs with common *Sphaerophthalmus drytonensis* and one pygidium of *Protopeltura praecursor* has also been found. This is the first record of the latter two species on Bornholm. *Protopeltura praecursor* is known from the lower three zones of the *Protopeltura* Superzone in Scandinavia (Nielsen *et al.* 2020, fig. 1). *Sphaerophthalmus drytonensis* has been described from the *S. postcurrens* and *S. flagellifer* zones in the Oslo Region and from the latter zone in Sweden (Henningsmoen 1957, Høyberget & Bruton 2012, Rasmussen *et al.* 2016). The *S. flagellifer* Zone is exposed at locality 6 and was stated to be 1.1 m thick by C. Poulsen (1923), but this figure probably includes the *S. modestus–S. angustus* Zone (see below). Nielsen *et al*. (2018, table 5) indicated that the *S. flagellifer* Zone is only *c.* 0.5 m thick in the Læså area. *Sphaerophthalmus flagellifer* or *S. drytonensis* (the material is preserved in shale and cannot be differentiated) have been found also at 106.0 m in the Billegrav-2 core (erroneously recorded as *Leptoplastus* resembling *L. neglectus* by Nielsen *et al.* 2018, p. 250). *Sphaerophthalmus angustus* was reported as *Ctenopyge flagellifera* var. *angusta* by C. Poulsen (1923) from "the upper part of the *S. flagellifer* Zone" at locality 6, indicating the presence of the *Sphaerophthalmus modestus–Sphaerophthalmus angustus* Zone. Nielsen *et al.* (2018) also inferred that this zone is developed on Bornholm, based on correlation of gamma logs in wells. *Sphaerophthalmus angustus* and *Ctenopyge tumidoides*, generally considered indicative of the *S. modestus–S. angustus* Zone (Henningsmoen 1957; Nielsen *et al.* 2020), have been found in many limestone samples; the latter species is new to Bornholm. One specimen of *Protopeltura planicauda* has also been found; this is its first report from Bornholm. Elsewhere in Scandinavia, this species is known also from the overlying *Peltura acutidens*–*Ctenopyge tumida* Zone, but the one specimens at hand co-occurs with *S. angustus* and *C. tumidoides,* showing a probable derivation from the *S. modestus–S. angustus* Zone. However, several cranidia of *Ctenopyge tumida* (e.g. Fig. 29J, K, Q) and a few specimens of *Peltura acutidens* have been found in 25% of the samples containing *C. tumidoides* and *S. angustus,* showing that these species range into the *Peltura* Superzone. This raises the question whether the *S. angustus–C. tumidoides* assemblage without *C. tumida* and/or *P. acutidens* represent the *S. modestus–S. angustus* Zone or whether the two younger species (of which *P. acutidens* is very rare) fortuitously are missing in 75% of the samples. In order to examine this question, we looked into the derivation and frequency of the trilobites in the different limestone nodules sampled *ex situ* by ATN in the 1970s (which was numbered and kept apart during sampling):

- The *S. angustus–C. tumidoides* assemblage is recorded in 12 individual limestone lenses
- The same 12 lenses also yielded assemblages typical of the *P. acutidens–C.tumida* Zone (see below)
- The mixed *S. angustus–C. tumidoides* assemblage including *C. tumida* and/or *P. acutidens* was recorded in only two of these lenses (four out of 27 samples collected by ATN)
- The mixed assemblage including *C. tumida* and/or *P. acutidens* is observed in a total of 11 out of the 41 samples at hand containing *S. angustus* and *C. tumidoides* (including older museum material not deriving from the discussed 12 lenses)
- The faunal mixing is real and not due to occurrence of the discussed species in different parts of the samples

Based on these figures and given that *C. tumida* is fairly common in the mixed assemblage, we conclude that a majority of the samples containing the *S. angustus–C. tumidoides* assemblage without younger faunal elements probably derives from the *Protopeltura* Superzone. The fact that the transitional mixed assemblage is seen in only two lenses indicates that the horizon is thin or discontinuous. For further remarks, se discussion on the *Peltura* Superzone below.

Peltura Superzone

The base of this superzone is defined by the FAD of *Peltura acutidens* (Nielsen *et al.* 2014) and it is subdivided into four zones, see Fig. 3. The *Peltura* Superzone is exposed at localities 6–7 and poorly so at Limensgade (localities 8A–B).

The *Peltura acutidens–Ctenopyge tumida* Zone is represented by three different trilobite assemblages that potentially may serve to recognize local subzones on Bornholm. The oldest assemblage contains very common *S. angustus* co-occurring with fairly common *C. tumidoides* and *C. tumida* as well as very rare *P. acutidens*. This transitional assemblage, discussed above, shows that *S. angustus* and *C. tumidoides* range into the basal part of the *Peltura* Superzone. In fact, very rare specimens of *C. tumidoides* have been found associated with *S. alatus*, demonstrating an even longer upwards range of this species. The two younger assemblages from the *P. acutidens–C. tumida* Zone are both characterized by *S. alatus*, which is overwhelmingly common in nearly all samples. In addition to the omnipresent *S. alatus*, one set of samples is characterized by common *C. tumida* co-occuring with very rare *C. tumidoides* and pelturids which could not be assigned to species. The other set of samples contains *S. alatus*, which is predominant, co-occurring with common *Ctenopyge affinis*, moderately common *C. ahlbergi* and *C. magna* n. sp. and infrequent *Peltura minor*. This latter assemblage seemingly corresponds to the abandoned *C. affinis* (Sub)Zone (see Høyberget & Bruton 2012; Nielsen *et al.* 2020); no *C. tumida* has been found in these samples. The stratigraphically important *P. acutidens* and *P. minor* have not been previously reported from Bornholm and *C. ahlbergi* is also new to the local fauna.

All three assemblages of the *P. acutidens–C. tumida* Zone have been recorded from the same 12 anthraconite nodules that also yielded samples with a *S. angustus–C. tumidoides* assemblage as discussed above. Even the largest nodules in the Alum Shale Fm are ≤1 m thick, implying that the two older assemblages of the *P. acutidens–C. tumida* Zone as well as the *S. angustus–C. tumidoides* assemblage must derive from rather thin intervals each measuring a few decimetres at most. This also entails that the main upper part of the *P. acutidens–C. tumida* Zone, which is 1.5–1.7 m thick in the Læså area (Nielsen *et al.* 2018), likely is characterized by the *C. affinis* assemblage, but no individual nodules containing exclusively this fauna were found by ATN in the 1970s. This suggests that the upper part of the zone is devoid of limestone concretions, or that they are rare. Judging from C. Poulsen (1923, fig. 2), *C. tumida* may have a longer range upwards than indicated by the sampled anthraconite nodules from the *Protopeltura/Peltura* boundary interval.

The overlying horizon is now referred to as the *Peltura scarabaeoides* Zone (Fig. 3). It broadly corresponds to the *Ctenopyge bisulcata* and *Ctenopyge linnarssoni* (sub)zones in the schemes published by Henningsmoen (1957) and Terfelt *et al.* (2008), but *P. scarabaeoides* appears before *C. bisulcata*. Both of these former index species are present in the studied material, but *C. bisulcata* is rare. C. Poulsen (1923) reported the latter species from the upper part of the *P. scarabaeoides* Zone at locality 6, but it should be observed that the exposed section represents only the lower half of that zone (cf. Nielsen *et al.* 2018). We also note that *C. bisulcata* has been found at locality 7, indicating a range from near the base of the *P. scarabaeoides* Zone as that section represents mainly the *P. acutidens–C. tumida* Zone.

Ctenopyge linnarssoni is common at locality 6 according to C. Poulsen (1923); new material collected by ATN demonstrates that it is present also at Limensgade (localities 8A–B), where it co-occurs with common *C. tenuis*, *C. teretifrons*, *P. scarabaeoides* and *T. humilis*. These taxa are all characteristic of the *P. scarabaeoides* Zone (Nielsen *et al.* 2020). *Ctenopyge pecten* also occurs sparsely in the zone and has been found mainly at locality 6; it is new to Bornholm as *C. pecten sensu* C. Poulsen (1923) represents *C. tenuis*. No samples contain *P. scarabaeoides* co-occurring with *S. alatus* as seen in the basal part of the *P. scarabaeoides* Zone in the Oslo Region (Høyberget & Bruton 2012). This level may not be developed on Bornholm or it is devoid of limestone concretions.

A presence of the *Parabolina lobata* Zone on Bornholm was indicated by C. Poulsen (1923) [in his terminology: Subzone with *Parabolina longicornis* and *Peltura scarabaeoides*], but the free cheeks he assigned to *P. longicornis* are here identified as *C. tenuis* (see taxonomic section). The one sample with these free cheeks also contains various other taxa, erroneously listed from the *P. 'longicornis'* Subzone by C. Poulsen (1923) (see 'Discussion and conclusions' below). Scree samples collected from just below the uppermost anthraconite horizon in the western end of locality 6 (level G in C. Poulsen 1923, fig. 2) yielded a meagre *P. scarabaeoides* Zone assemblage dominated by *T. humilis*. Since no material of *P. lobata* has been found in the numerous limestone samples available from locality 6, we conclude that the *P. lobata* Zone is not developed at this locality, which is in accordance with the thicknesses of the *P. scarabaeoides* Zone in the Læså area indicated by Nielsen *et al.* (2018). However, *Parabolina lobata praecurrens* is actually recorded in several samples collected by ATN in the 1970s at Limensgade (localities 8A–B); this subspecies is characteristic of the *P. lobata* Zone in Scania and the Oslo Region (Henningsmoen 1957; Terfelt *et al.* 2011; Nielsen *et al.* 2020).

Peltura westergaardi also occurs in the *P. lobata* Zone on Bornholm; it is characteristic of the same stratigraphic level in Sweden and Norway (Henningsmoen 1957; Terfelt *et al.* 2011), although it has its FAD in the very top of the underlying *P. scarabaeoides* Zone in the Oslo Region (Nielsen *et al.* 2020). This taxon has not been previously reported from Bornholm and very little of the material labelled as *P. scarabaeoides* in the original museum collection studied by C. Poulsen (1923) represents this species. A few orthid brachiopods have also been found in the *P. lobata* Zone on Bornholm.

Parabolina megalops, characteristic of the uppermost zone in the *Peltura* Superzone (Fig. 3), has not been recorded from Bornholm and Nielsen *et al.* (2018) inferred that this zone is probably absent, based on correlation of gamma logs in wells. However, the *Peltura*/*Acerocarina* superzone boundary interval is not exposed and it is thus inaccessible for sampling.

Acerocarina Superzone

This superzone comprises three zones (Fig. 3), but only the uppermost part is exposed at locality 8 (C. Poulsen 1922, 1923). Findings of rare *Parabolina acanthura* at the base of the section exposed in the Limensgade shale/limestone quarry (C. Poulsen 1923) is taken as indicative of the *Acerocare ecorne* Zone (see e.g. Terfelt 2006), although this species locally ranges into the basal Ordovician in the Oslo area (Bruton *et al.* 1988; see also Nielsen *et al.* 2020).

Nielsen *et al.* (2018) inferred that also the lower parts of the *Acerocarina* Superzone are developed on Bornholm, but the biozones are too thin to be tracked individually on the basis of gamma log correlation. This interval may theoretically be exposed in the Risebæk creek but those outcrops have never been examined.

Discussion and conclusions

The studied museum material of Furongian olenids and agnostoids from Bornholm represents 43 taxa. Fourteen of these have not been reported from the island previously, viz. *Ctenopyge ahlbergi*, *C. tumidoides*, *Eurycare brevicauda*, *Leptoplastus abnormis*, *L. crassicornis*, *Olenus transversus*, *Parabolina lobata praecurrens*, *Peltura acutidens*, *P. minor*, *P. westergaardi*, *Protopeltura planicauda*, *P. praecursor*, *Pseudagnostus leptoplastorum?* and *Sphaerophthalmus drytonensis*. Five species described by C. Poulsen (1923) are here transferred to other taxa that technically speaking also are new to Bornholm, viz. *Lotagnostus americanus* (*'Agnostus trisectus'*), *Ctenopyge magna* n. sp. (*'Ctenopyge affinis'*), *Ctenopyge fletcheri* (*'Ctenopyge directa'*), *Sphaerophthalmus alatus* (*'Sphaerophthalmus major'*) and *Triangulopyge humilis* (*'Sphaerophthalmus alatus'*) (names in brackets are those used by C. Poulsen 1923). The material treated as *Ctenopyge pecten* by C. Poulsen (1923) represents *C. tenuis* (see also V. Poulsen 1963), which is common on Bornholm. However, *C. pecten s.str.* is actually present as well but it is comparatively infrequent. The sparse museum material assigned to *Parabolina longicornis* [now *P. lobata*] by C. Poulsen (1923) is here identified as *C. tenuis*. The cranidia assigned to *C. affinis* by C. Poulsen (1923) are separated as *C. magna* n. sp. and a different group of *Ctenopyge* is identified as *C. affinis*, which is quite common on Bornholm. Strangely, this morph was not dealth with by C. Poulsen (1923).

Eurycare bornholmensis is common in the material at hand. Findings of nearly complete specimens with 16 thoracic segments suggest an affiliation with *Eurycare* rather than *Leptoplastus*, although the interocular cheeks are slightly narrower than typical for representatives of *Eurycare*. The free cheek with a robust long spine is also of *Eurycare* type. *Eurycare bornholmensis* has a well-defined preglabellar area, a trait shared with several species of *Leptoplastus*. *Eurycare bornholmensis* is endemic to Bornholm, but it strongly resembles the Norwegian *E. explanatum* and a separation only at subspecies level may be contemplated.

Leptoplastus abnormis is overall quite similar to *L. ovatus*. The former may possibly have slightly longer genal spines (Westergård 1944; Ahlberg *et al.* 2006) and perhaps a more elongate, usually slightly tapering glabella (this study), but the long pleural spines in the rear part of the thorax are the salient distinguishing feature. However, cranidia and pygidia of the two species - and probably also the free cheeks, as the genal spine often is broken - are very difficult to distinguish, and complete specimens seem to be required for safe differentiation of these taxa. In the material at hand no complete specimens of *L. ovatus* are available and we strongly suspect that the extensive material of disarticulated skeletal parts is mixed with *L. abnormis*. This suspicion also concerns Scandinavian material in general assigned to *L. ovatus* by various authors.

Our study shows that *S. angustus* and *C. tumidoides* range into the basal part of the *Peltura* Superzone, which has not been reported previously from Scandinavia. However, Høyberget & Bruton (2012, p. 440; fig. 5i) mentioned that a morph of *S. angustus* approaching *S. alatus* occurs together with *C. tumida* and *P. acutidens* in the lowermost part of the *C. tumida* Zone, but no further details were provided, and this occurrence was not shown on their range chart (*ibid*. fig. 2). Terfelt & Ahlgren (2009, fig. 3) reported a co-occurrence of *Ctenopyge* (*Eoctenopyge*) *angusta* with *C. tumida* and *P. minor* in a section on eastern Kinnekulle, but no material was illustrated, and the identification remains uncertain. The absence of *S. alatus* in the section is a concern. *Ctenopyge tumidoides,* reported as *C. tumida* by Clarkson *et al.* (2004), seems to range into the *C. tumida* Zone also in Västergötland; for details, see the taxonomic section.

In general, no information on sampling levels is available for the studied museum material and identification of biozones is based on comparison with ranges recorded elsewhere in Scandinavia (see summary in Nielsen *et al.* 2020, fig. 1). This approach is fairly straightforward given that the majority of trilobites known from the Alum Shale have short ranges, typically only through one zone and very rarely through more than two zones. The taxa found on Bornholm indicate that all six Furongian superzones established by Nielsen *et al.* (2014) are developed. Of the 23 trilobite zones, recognized by Nielsen *et al.* (2020) (see Fig. 3), 14 fossiliferous zones are confirmed present on Bornholm (Fig. 4). Correlations based on gamma log stratigraphy in wells suggest that also the *Olenus scanicus–O. rotundatus*, *Parabolina brevispina*, *Leptoplastus neglectus* and at least one and more likely both of the basal zones in the *Acerocarina* Superzone are developed on Bornholm (Nielsen *et al.* 2018). The *S. postcurrens* Zone may be very thin or absent; theoretically it may be accessible for sampling at locality 6. The *Leptoplastus paucisegmentatus* and *L. raphidophorus* zones in the basal *Leptoplastus* Superzone seem to be absent. The *Parabolina megalops* Zone in the upper *Peltura* Superzone was inferred absent (or thin) by Nielsen *et al.* (2018), but the *Peltura*/*Acerocarina* superzone boundary interval is not exposed and, thus, the faunal succession across the boundary cannot be sampled.

Overall, the present revision of Furongian trilobites from Bornholm corroborates the zonation outlined by C. Poulsen (1923) and essentially all additions to the faunal list support his original conclusions.

The present study calls for reinvestigation of the exposure at locality 6 in the Læså stream, which should be sampled in order to ascertain whether or not the *Leptoplastus neglectus* and *Sphaerophthalmus postcurrens* zones are developed.

We note that some details regarding specific occurrences reported by C. Poulsen (1923) are inaccurate, which in ascending order concern:

- *Ctenopyge neglecta* var. *bornholmensis* [here *Eurycare bornholmensis*] was reported to occur in the uppermost part of the horizon with *Eurycare angustatum* [here *L. crassicornis*–*L. angustatus* Zone]. However, *E. bornholmensis* seems to be common throughout the *L. crassicornis*–*L. angustatus* Zone above the basal *E. latum* dominated interval
- *Ctenopyge magna* n. sp. was reported (as *C. affinis*) from the *P. scarabaeoides* Subzone [here Zone] based on alleged co-occurrence with *T. humilis* [reported as *S. alatus*] and *C. pecten* (?). A reinvestigation of the museum samples in question shows that they contain *C. magna* n. sp., *S. alatus* [*s.str.*], *C. ahlbergi* and *C. affinis s.str.* and must derive from the upper part of the *P. acutidens–C. tumida* Zone
- *Ctenopyge fletcheri* – under the name *C. directa* – was reported from the *C. tumida* subzone [here *P. acutidens*–*C. tumida* Zone]. However, no material of *C. fletcheri* associated with trilobites characteristic of that zone is preserved in the museum collection. It remains speculative, but maybe the report was based on misidentification of detached thoracic segments of *C. ahlbergi* that superficially resemble the broad, flat genal spines of *C. fletcheri*
- *Ctenopyge bisulcata* was reported from the upper part of the *P. scarabaeoides* Zone, but it should be observed that the section exposed at locality 6 in fact represents only the lower half of that zone (cf. Nielsen *et al*. 2018). The record of *C. bisulcata* from locality 7 demonstrates that this species occurs from near the base of the *P. scarabaeoides* Zone also on Bornholm
- *Ctenopyge pecten* [here *C. tenuis*], *C. teretifrons*, *C. linnarssoni* and *Sphaerophthalmus alatus* [here *T. humilis*] were all reported to range into the *Parabolina longicornis* Subzone [here: *P. lobata* Zone]; a statement repeated for *C. tenuis* by V. Poulsen (1963). However, the free cheeks identified as *P. longicornis* by C. Poulsen (1923) represent *C. tenuis* and derive from the *P. scarabaeoides* Zone. Hence, the four species listed do not range into the *P. lobata* Zone
- No *P. lobata* Zone is developed at locality 6 as indicated by C. Poulsen (1923, fig. 2)

In general, the thickness of the individual zones cannot be established, partly due to the fact that the fossils are sampled *ex situ* and partly due to discontinuous exposure. The reader is instead referred to the study based on well log correlation published by Nielsen *et al*. (2018). A few details on thicknesses were provided by C. Poulsen (1923; see in particular his description of locality 6), and Kaufmann (1933a, text-fig. 1).

Taxonomy

Most olenid taxa are described in detail by Westergård (1922) and/or Henningsmoen (1957) and the reader is referred to these authoritative monographs for details. The latter author also provided a brief summary of diagnostic characters for each taxon. The descriptive terminology used by Henningsmoen (1957) is adopted here. The studied material is stored at the Natural History Museum of Denmark. Regarding specimen and samples numbers, see section on 'Material and methods'.

Trilobites are exceedingly abundant in many of the limestone samples and the common species (e.g. *L. ovatus*, *S. alatus* and *T. humilis*) are each represented by many more specimens than counted here (>>1000), registering only relatively well preserved and/or easily observable skeletal parts.

Class Trilobita Walch, 1771

Order Agnostida Salter, 1864

FamilyAgnostidae M'Coy, 1849

Genus *Agnostus* Brongniart, 1822
Type species: *Entomostracites pisiformis* Wahlenberg, 1818, designated by Jaekel (1909).

***Agnostus pisiformis* (Wahlenberg, 1818)**
Fig. 5

1922 *Agnostus pisiformis* (L.) – Westergård, pp. 115–116, pl. 1, figs 1–3.
v 1923 *Agnostus pisiformis* Linné – C. Poulsen, pp. 21–22, pl. 1, fig. 1.
1958a *Agnostus (Agnostus) pisiformis* Linnæus 1757 – Henningsmoen, pp. 181–182, pl. 5, figs 1–12.
1996 *Agnostus pisiformis* (Wahlenberg, 1818) – Ahlberg & Ahlgren, pp. 130–131.
2003 *Agnostus pisiformis* (Wahlenberg, 1818) – Terfelt, p. 411; fig. 4A.
2017 *Agnostus pisiformis* (Wahlenberg, 1818) – Rasmussen *et al.*, pp. 8–9.
2017 *Agnostus pisiformis* (Wahlenberg 1818) – Jackson & Budd, pp. 467–484.

See Ahlberg & Ahlgren (1996) and Rasmussen *et al.* (2017) for additional synonymy.

Lectotype. Cephalon Vg. 819 from Hönsäter, Kinnekulle, Sweden. Originally figured by Wahlenberg (1818, pl. 1, fig. 5) and refigured by Reyment (1976, fig. 3a–b). Designated by Shergold *et al.* (1990).

Material. Four complete specimens, 173 cephala (see remarks) and 148 pygidia. The species occurs alone and has been found at localities 1, 2, 11, 13 and 14 as well as downstream of locality 8C in the Læså riverbed (exposure not numbered, GPS coordinates 55°2′54.81″N, 14°53′43.04″E).

Occurrence. Very common in the eponymous upper Miaolingian zone throughout Scandinavia with a lower range from the uppermost part of the *Lejopyge laevigata* Zone (Ahlberg & Ahlgren 1996; Rasmussen *et al.* 2017 and references therein). Within south-central Sweden, it is often reworked into the basal *Olenus* Superzone. *Agnostus pisiformis* is reported also from Poland, Great Britain, Canada (Newfoundland) and Russia (Bennett Island) (Lendzion & Orlowski 1991, Ahlberg 2003, Danukalova *et al.* 2014). On Bornholm, it is common in the eponymous zone which prior to ratification of the Furongian (Peng & Babcock 2003) was classified as 'Upper' Cambrian.

Comparison. *Agnostus pisiformis* is a larger species than *H. obesus* (maximum length of cephala/pygidia *c.* 6 mm vs. *c.* 3.5 mm in *H. obesus*). The cephala of these species are identical (see remarks by Westergård 1947, p. 4) and pygidia are required for safe identification. In *H. obesus,* the pygidial axis is wider, strongly inflated and has a rounded terminal piece. *Agnostus pisiformis* has a more slender axis with a pointed terminal piece.

Remarks. The cephala assigned to *A. pisiformis* are identified by co-occurring with safely identified pygidia. The length of marginal spines in the pygidium varies and cephala may exhibit weak scrobiculation (see Fig. 5). The many species and subspecies recognized by Mischnik (2006a, 2006b) and Buchholz (1991, 1999, 2000, 2016) including *A.? confusus, A. distinctus, A. procerus, A. pisiformis dissimilis,* and *A. pisiformis vastificus*, all based on material from ice-rafted boulders collected in Germany, are here regarded as within the variation range of *A. pisiformis.*

Genus *Homagnostus* Howell, 1935
Type species: *Agnostus pisiformis* var. *obesus* Belt, 1867, by original designation.

***Homagnostus obesus* (Belt, 1867)**
Fig. 6D–E

1922 *Agnostus pisiformis obesus* Belt [*partim*] – Westergård, p. 116, pl. 1, figs 4a–b; non pl. 1, figs 5–6 [= *H. ultraobesus?* Lermontova, 1940].
v 1923 *Agnostus pisiformis* Linné var. *obesus* Belt – C. Poulsen, pp. 22–23, pl. I, fig. 2.
1958a *Agnostus (Homagnostus) obesus* BELT 1867 – Henningsmoen, pp. 182–184, pl. 5, figs 13–16.

1996 *Homagnostus obesus* (Belt, 1867) – Ahlberg & Ahlgren, p. 131, figs 3A–G.

2003 *Homagnostus obesus* (Belt, 1867) – Terfelt, p. 411; fig. 4B.

2016 *Homagnostus obesus* – Ahlberg *et al.*, p. 496, figs 4; 6I, J.

2017 *Homagnostus obesus* (Belt, 1867) – Rasmussen *et al.*, p. 9.

For further synonymy, see Ahlberg & Ahlgren (1996) and Rasmussen *et al.* (2017).

Lectotype. Nearly complete specimen BM I7646, fig-

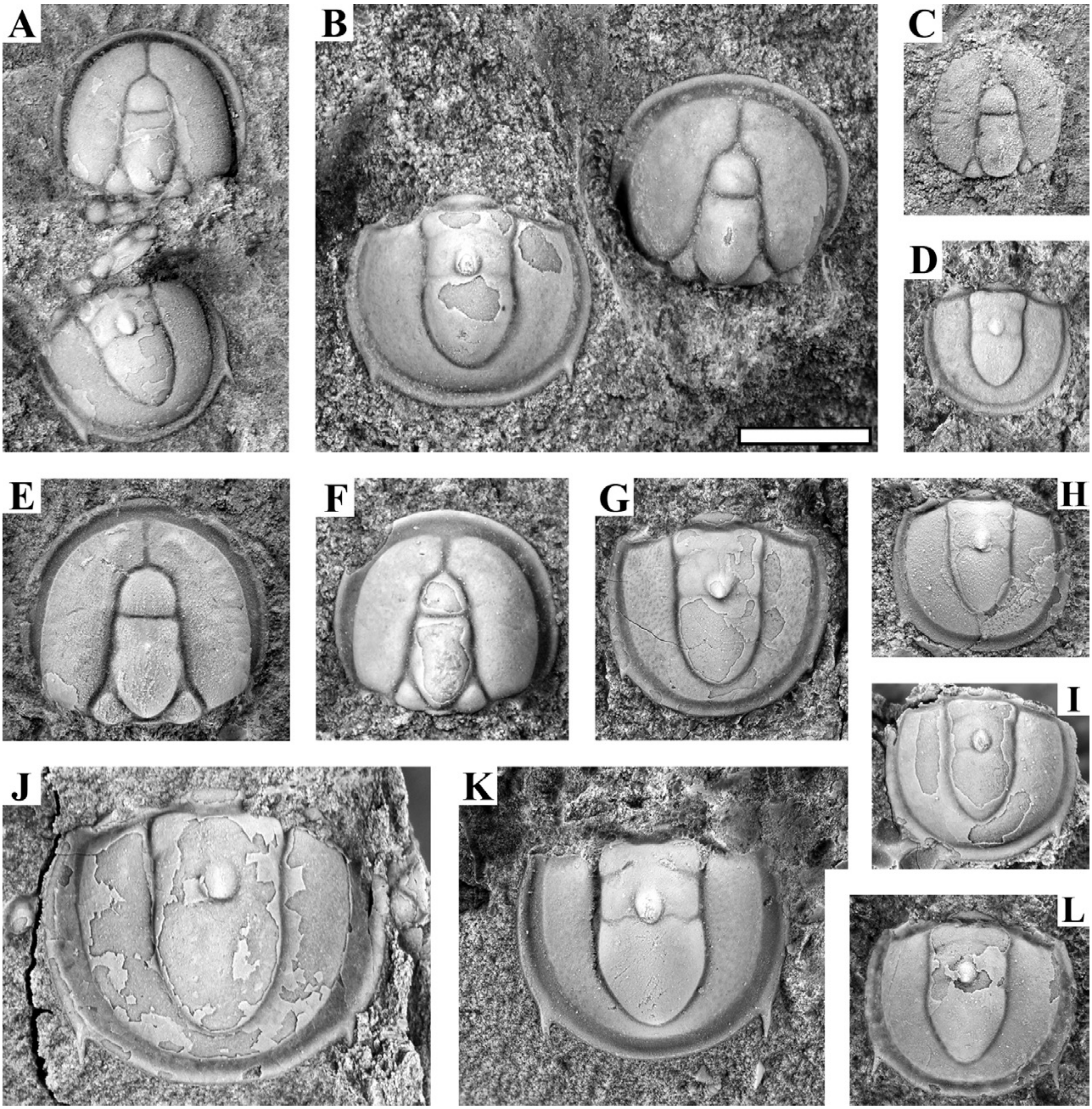


Fig. 5. *Agnostus pisiformis*, all preserved in anthraconite. White scale bar: 2 mm. **A:** Complete specimen, loc. 2, sample L2 (MGUH 33536). **B:** Cephalon and pygidium, loc. 14, sample GM 2019-91 (MGUH 33537). **C:** Slightly scrobiculate cephalon, loc. 2, sample L1 (MGUH 33539). **D:** Pygidium, loc. 1, sample GM 1877-2002 (MGUH 33543). **E:** Cephalon showing very indistinct scrobiculation, loc. 2, sample L1 (MGUH 33540). **F:** Cephalon, loc. 14, sample GM 2019-91 (MGUH 33538). **G:** Pygidium, loc. 1, sample GM 1877-2002 (MGUH 33544). **H:** Pygidium, loc. 2, sample L1 (MGUH 33541). **I:** Pygidium, loc. 1, sample 1877-2002 (MGUH 33545). **J:** Pygidium with relatively long marginal spines, loc. 1, sample GM 1922-132B (MGUH 33547). **K:** Pygidium with relatively long marginal spines, loc. 2, sample L1. (MGUH 33542). **L:** Pygidium with relatively long marginal spines, loc. 1, sample GM 1877-2002 (MGUH 33546).

ured by Belt (1867, pl. 12, fig. 4a) from the Maentwrog Formation of North Wales, *Olenus* Superzone, United Kingdom, designated and refigured by Rushton in Allen *et al.* (1981, pl. 16, fig. 2).

Material. Ten complete specimens and 82 pygidia. 70 associated cephala are tentatively assigned (see comments on *A. pisiformis*). *Homagnostus obesus* co-occurs with *Olenus truncatus* and *O. wahlenbergi* in the material at hand, which derives from localities 2, 3, 16, 17 and 18.

Occurrence. Olenus Superzone (all zones) in all districts of Scandinavia including Bornholm; *H. obesus* is reported also from Great Britain, Newfoundland, Siberia, Kazakhstan, Korea and North America (Ahlberg & Ahlgren 1996; Ahlberg & Terfelt 2012).

Comparison. See *A. pisiformis.*

Genus *Glyptagnostus* Whitehouse, 1936
Type species: *Glyptagnostus toreuma* Whitehouse, 1936 [= *Agnostus reticulatus* Angelin, 1851], by original designation.

***Glyptagnostus reticulatus* (Angelin, 1851)**
Fig. 6A–C

1922 *Agnostus reticulatus* Angelin – Westergård, p. 117, pl. 1, figs 9–10.
v 1923 *Agnostus reticulatus* Angelin – C. Poulsen, p. 23, pl. 1, fig. 3.
1947 *Glyptagnostus reticulatus nodulosus* subsp. n. – Westergård, p. 7, pl. 1, fig. 7–9.
1958a *Glyptagnostus reticulatus reticulatus* Angelin 1851 – Henningsmoen, pp. 184–185, pl. 5, fig. 17.
1996 *Glyptagnostus reticulatus reticulatus* (Angelin, 1851) – Ahlberg & Ahlgren, pp. 135–136, figs 4I–P.
2012 *Glyptagnostus reticulatus* (Angelin, 1851) – Ahlberg & Terfelt, pp. 1004–1006, figs 3a–b.

See Ahlberg & Ahlgren (1996) for additional synonymy.

Lectotype. Cephalon SGU 120, figured by Westergård (1922, pl. 1, fig. 2), one of Angelin's cotypes from Andrarum, southern Sweden, designated by Henningsmoen (1958a).

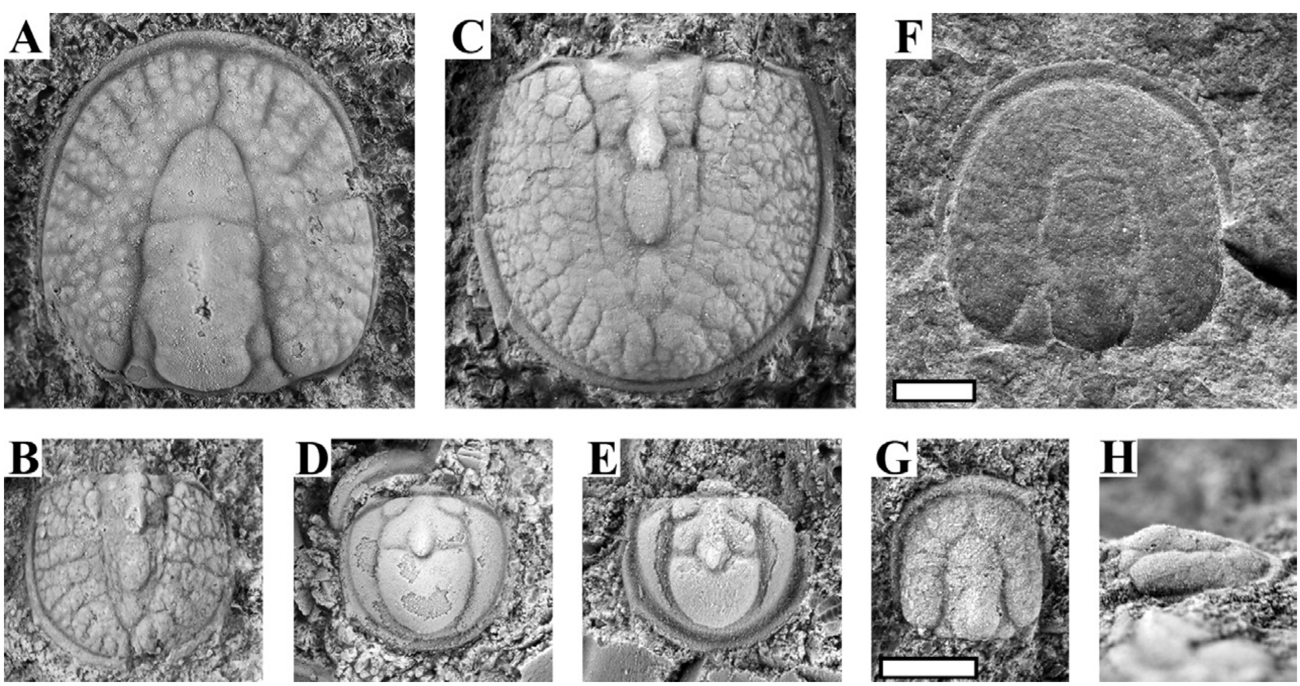


Fig. 6. Various agnostoids, all preserved in anthraconite except F. White scale bars: 1 mm; please note that G–H are shown at larger magnification. **A:** *Glyptagnostus reticulatus*, cephalon, sample GM 1871-602, 'Cement factory', Øleå (MGUH 33548). **B:** *Glyptagnostus reticulatus*, pygidium, loc. 17, sample GM 2019-36 (MGUH 33549). **C:** *Glyptagnostus reticulatus*, pygidium, loc. 17, specimen MGUH 1956 (previously illustrated by C. Poulsen 1923, pl. I, fig. 3). **D:** *Homagnostus obesus*, pygidium, sample GM 2019-51, loc. 17 (MGUH 33550). **E:** *Homagnostus obesus*, pygidium, sample GM 2019-74, loc. 17 (MGUH 33551). **F:** *Lotagnostus americanus*, external mould of cephalon preserved in shale (the corresponding positive is fragmentary), loc. 6, sample GM 1922-141O (MGUH 33552). **G–H:** *Pseudagnostus leptoplastorum*?, dorsal and side view of small cephalon, loc. 6, sample ATN-123 (MGUH 33553).

Material. Four complete specimens, four cephala and six pygidia, occurring alone. The material derives from localities 2, 17 and 18. The complete specimens at hand (all preserved in shale) are poorly preserved and not suitable for illustration.

Occurrence. In Scandinavia, this species occurs sparsely in the *O. gibbosus* and *O. truncatus* trilobite zones (Ahlberg & Terfelt 2012). *Glyptagnostus reticulatus* has a nearly cosmopolitan distribution (Terfelt *et al.* 2008) and is the primary marker for the base of the Furongian (Peng & Babcock 2003).

Comparison. Glyptagnostus reticulatus is readily distinguished from the associated *H. obesus* by its scrobiculate cephalon and pygidium and comparatively narrow glabella and pygidial axis.

Remarks. Glyptagnostus reticulatus nodulosus, characterized by a finer scrobiculation, is here regarded as within the variation range of the main form.

Genus *Lotagnostus* Whitehouse, 1936
Type species: *Agnostus trisectus* Salter, 1864, by original designation.

***Lotagnostus americanus* (Billings, 1860)**
Fig. 6F

1922 *Agnostus trisectus* Salter – Westergård, p. 117, pl. 1, figs 11–12.
v 1923 *Agnostus trisectus* Salter – C. Poulsen, pp. 24–25, textfig. 5.
1996 *Lotagnostus trisectus* (Salter, 1864) – Ahlberg & Ahlgren, pp. 133–135, figs 4A–B.
2005 *Lotagnostus americanus* (Billings, 1860) – Peng & Babcock, pp. 110–113, fig. 2.
2012 *Lotagnostus americanus* (Billings, 1860) – Ahlberg & Terfelt, pp. 1004–1006, figs 4a–f.
2015 *Lotagnostus americanus* (Billings, 1860) – Peng *et al.*, pp. 281–303, figs 1–11.

For further synonymy, see Ahlberg & Ahlgren (1996), Peng & Babcock (2005) and Peng *et al.* (2015).

Holotype. Pygidium GSC 859 from the Lévis Formation, North Ridge, Lévis, Quebec, by monotypy (see Rushton 2009, p. 276). Figured by Westrop *et al.* (2011, fig. 5A–C).

Material. A single cephalon from locality 6, preserved in shale. No associated fauna.

Occurrence. *Lotagnostus americanus* ranges through the eponymous agnostoid zone in Scandinavia, corresponding to the *P. acutidens–C. tumida* and *P. scarabaeoides* olenid zones (cf. Westergård 1922; Ahlberg & Terfelt 2012). There are no confirmed reports of an occurrence in the upper part of the *Protopeltura* Superzone. It has a near global distribution (Peng *et al.* 2015) but is rare in Scandinavia. The specimen at hand derives from the *P. acutidens–C. tumida* Zone according to C. Poulsen (1923).

Remarks. The variability of this species and whether or not it is a senior synonym of various younger names (e.g. *Trilobagnostus trisectus*) is a contentious issue (e.g. Westrop *et al.* 2011; Peng *et al.* 2015). *Lotagnostus americanus* is a potential index species for the as yet unnamed Cambrian Stage 10. We here follow the majority of trilobite specialists, accepting *Lotagnostus americanus* as a rather variable species including forms described under different names; for discussion, see Peng *et al.* (2015). At any rate, the very sparse material from Bornholm does not contribute to this ongoing discussion.

Genus *Pseudagnostus* Jaekel, 1909
Type species: *Agnostus cyclopyge* Tullberg, 1880, by original designation.

***Pseudagnostus leptoplastorum* Westergård, 1944?**
Fig. 6G–H

? 1944 *Pseudagnostus leptoplastorum* sp. n. – Westergård, p. 39, pl. 1, fig. 1.
? 1962 *Pseudagnostus leptoplastorum* Westergard, 1944 – Ivshin, pp. 16–18, textfig. 3; pl. 1, figs 8–18.
? 1971 *Pseudagnostus* cf. *leptoplastorum* Westergaard – Taylor & Rushton, p. 28.

Holotype. By monotypy, flattened pygidium SGU 4214, preserved in shale from the *Leptoplastus raphidophorus* Zone, Andrarum, southern Sweden, illustrated by Westergård (1944, pl. 1, fig. 1).

Material. One cephalon from locality 6. It is associated with *Eurycare bornholmensis*.

Occurrence. Westergård (1944) reported this extremely rare species (based on a single pygidium) from the *L. raphidophorus* Zone at Andrarum, Sweden, while Taylor & Rushton (1971) reported a cephalon referred to as *Pseudagnostus* cf. *leptoplastorum* from the *L. crassicornis* Zone in England. The single specimen from Bornholm derives from the *L. crassicornis–L. angustatus* Zone. No additional material has been described from Scandinavia (cf. Ahlberg & Terfelt 2012) whereas extensive material was described by Ivshin (1962) from the *Irvingella* Zone in central Kazakhstan (see remarks).

Remarks. The specimen presumably represents *P. leptoplastorum* and is the first cephalon of this taxon recorded from Scandinavia. Ivshin (1962) described *P. leptoplastorum* from Kazakhstan, including illustrations and description of cephala. In comparison, the specimen at hand has a parallel-sided non-tapering glabella and there seems to be a minute mesial tubercle in the transglabellar furrow as well as barely perceptible scrobiculation, not seen in the Kazakhstan material (cf. Ivshin 1962, text-fig. 3). Hence identification remains uncertain – but it is obviously also questionable whether the Kazakhstanian material represents *P. leptoplastorum s. str.* considering how poorly known this taxon is. The cephalon referred to by Taylor & Rushton (1971) was neither illustrated nor described. Attempts to obtain photos of that specimen were unsuccessful.

Order Ptychopariida Swinnerton, 1915

Family Olenidae Burmeister, 1843

Genus *Olenus* Dalman, 1827
Type species: *Entomostracites gibbosus* Wahlenberg, 1818, designated by Salter (1864).

***Olenus attenuatus* (Boeck, 1838)**
Fig. 7A–C
1922 *Olenus attenuatus* (Boeck) – Westergård, pp. 128–130, pl. IV, figs 15–19, pl. V, figs 1–9.
v 1923 *Olenus attenuatus* Boeck – C. Poulsen, pp. 27–28, pl. I, fig. 7.
1957 *Olenus attenuatus* (Boeck, 1838) – Henningsmoen, pp. 102–104, textfig. 16; pl. 3.
2017 *Olenus attenuatus* (Boeck, 1838) – Rasmussen *et al.*, pp. 14–15, fig. 8H.
For further synonymy, see Rasmussen *et al.* (2017).

Neotype. Complete specimen Ar 1640 (Naturhistoriska Riksmuseet, Stockholm) from Andrarum, southern Sweden, probably Angelin's original, figured by Westergård (1922, pl. V, fig. 2) and designated by Henningsmoen (1957).

Material. Nine cranidia with up to eight contiguous thoracic segments, two pygidia and one free cheek (tentatively assigned, but associated with thoracic segments showing imprints of axial nodes). The material derives from localities 2, 3 and 17. *Olenus attenuatus* occurs alone in the material at hand.

Occurrence. Index fossil for the eponymous zone in Scandinavia incl. Bornholm (Westergård 1922, 1947; Henningsmoen 1957; Terfelt *et al.* 2008; Nielsen *et al.* 2020).

Comparison. The salient distinguishing feature of this species is the presence of small axial spines on the thoracic segments, but the cranidium is also fairly easily identified due to the relatively wide postocular cheeks, so it is 2.1–2.4 times as wide as long. The pygidium can be confused with *O. gibbosus*, but *O. attenuatus* has only 1 pair of marginal spines, 4–7 axial rings, a pleural field that is narrower than the axis and the overall pygidial outline is subtriangular. The free cheeks of *O. attenuatus, O. dentatus* and *O. truncatus* are essentially identical.

***Olenus dentatus* Westergård, 1922**
Fig. 7J, K?
1922 *Olenus dentatus* n. sp. – Westergård, p. 130, pl. V, figs 10–15.
1933a *Olenus dentatus* (Westergård) – Kaufmann, pp. 58–62.
1957 *Olenus dentatus* Westergård, 1922 – Henningsmoen, pp. 104–105, pl. 3.
2005 *Olenus dentatus* (Westergård, 1922) – Lauridsen & Nielsen, pp. 1043, 1044, 1051, 1053, textfig. 5, pl. 1, figs 2, 13, 14.
For further synonymy, see Henningsmoen (1957).

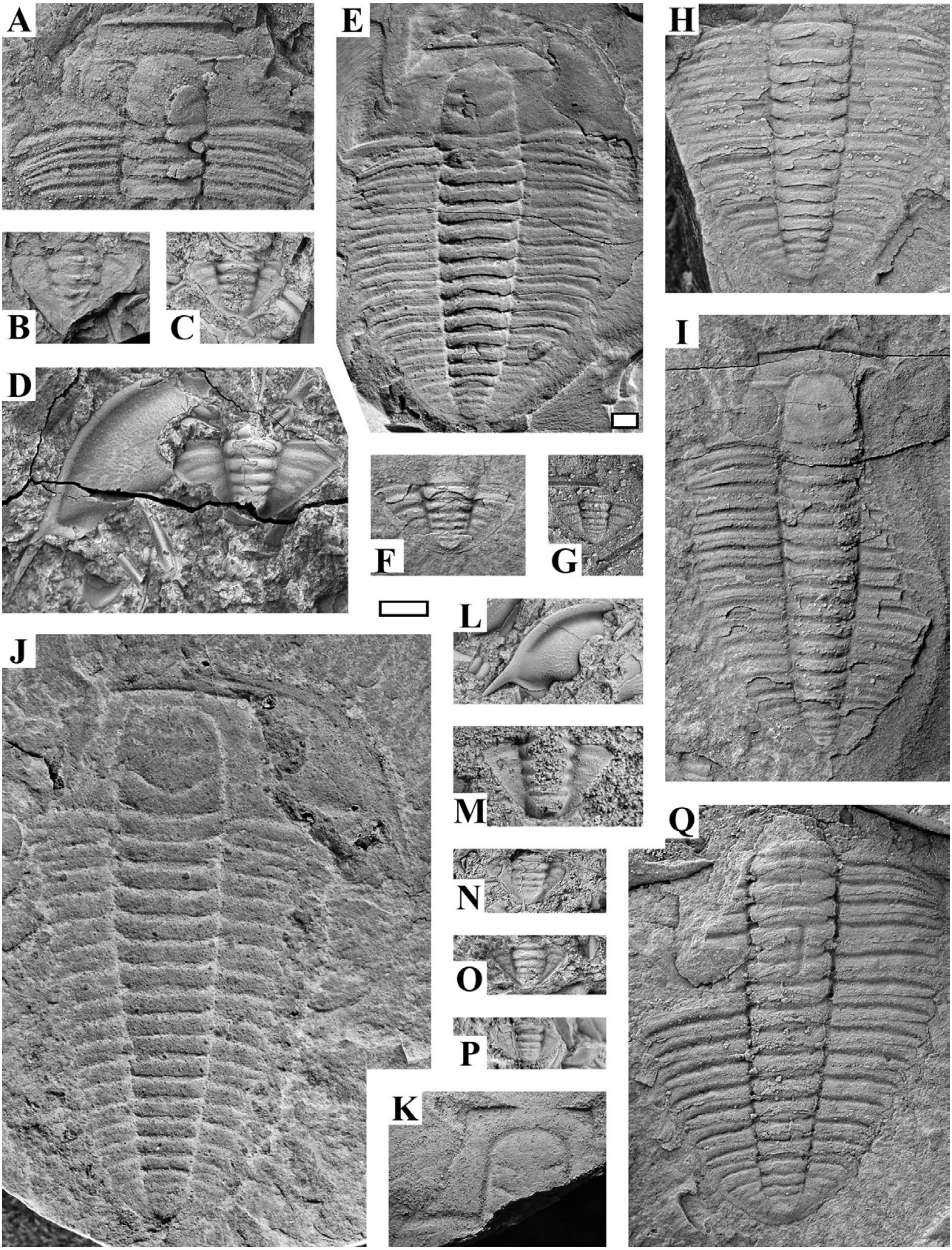
Lectotype. Cranidium SGU 208 from Andrarum, southern Sweden, figured by Westergård (1922, pl. V, fig. 10) and designated by Henningsmoen (1957).

Material. One external mould of a complete specimen from locality 18 and one fragmentary cranidium (tentatively assigned) from the Læså (probably locality 3). Both specimens are preserved in shale and occur alone. The complete specimen is the first articulated specimen recorded of this species (cf. Westergård 1922, Henningsmoen 1957).

Occurrence. Index fossil for the eponymous zone in Scania and Bornholm; the species possibly occurs also in Great Britain (Henningsmoen 1957; Terfelt *et al.* 2008; Nielsen *et al.* 2020). It has previously been reported from Bornholm by Kaufmann (1933a).

Comparison. Olenus dentatus is characterized by having a wide and long glabella, a rather narrow thorax with 15 segments, tapering rearwards, and a comparatively wide axis, and a relatively short pygidium with one pair of marginal spines and a conical axis consisting of only 3–4 axial rings. It is readily separated from the other species of *Olenus*.

Remarks. Kaufmann (1933a) reported 15 cranidia and two pygidia of *O. dentatus* from the Læså stream, probably locality 3, collected from a 1 cm thick horizon at 7 cm above the *O. attenuatus* Zone. No specimens were illustrated, and no material was deposited in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the Geological Museum collection in Copenhagen but given Kaufmann's detailed knowledge on *Olenus* his identification is presumably correct.

***Olenus gibbosus* (Wahlenberg, 1818)**
Fig. 7D

1922 *Olenus gibbosus* (Wahlenberg) – Westergård, pp. 124–125, pl. III, figs 1–10.
v 1923 *Olenus gibbosus* Wahlenberg – C. Poulsen, pp. 26–27, pl. 1, figs 4, 5?
1957 *Olenus gibbosus* (Wahlenberg, 1821) – Henningsmoen, pp. 105–106, pl. 1, fig. 1, pl. 3, pl. 9, fig. 7.
2003 *Olenus gibbosus* (Wahlenberg, 1821) – Terfelt, p. 411, fig. 4E, F.
2016 *Olenus gibbosus* – Ahlberg *et al.*, p. 496, figs 4; 6E–G, M, N.
2017 *Olenus gibbosus* (Wahlenberg, 1818) – Rasmussen *et al.*, p. 15, figs 8A–B.

For further synonymy, see Henningsmoen (1957) and Rasmussen *et al.* (2017).

Type material. Not designated, see Henningsmoen (1957).

Material. One cephalon with three thoracic segments, two free cheeks and four pygidia; all from locality 2.

Occurrence. Index fossil for the eponymous zone in Scandinavia and England (Westergård 1922; Henningsmoen 1957; Terfelt *et al*. 2008).

Comparison. Olenus gibbosus can be distinguished from almost all other *Olenus* species by its free cheek with an obtuse inner spine angle, the only exception being *O. transversus*. However, it is most easily identified by its pygidium having one or two pairs of marginal spines and relatively wide pleural fields. For comparison with *O. attenuatus*, see that species.

Remarks. Olenus gibbosus appears to be rare on Bornholm and/or maybe the zone in question is very thin and perhaps developed only in the Læså area. In a recent study of locality 15B (unpublished), this species was not recorded and the base of the Furongian is here marked by the FAD of *O. transversus*.

***Olenus transversus* Westergård, 1922**
Fig. 7Q

1922 *Olenus transversus* Linnarsson in museo – Westergård, pp. 125–126, pl. III, figs 11–17, pl. 5, figs 16–17?.
1957 *Olenus transversus* Westergård, 1922 – Henningsmoen, p. 108, pl. 3.
2017 *Olenus transversus* Westergård, 1922 – Rasmussen *et al.*, p. 16, fig. 8C–D.

For further synonymy, see these references.

Lectotype. An almost complete specimen (SGU 173) preserved in shale from Andrarum, southern Sweden, figured by Westergård (1922, pl. III, fig. 11) and designated by Henningsmoen (1957).

Material. One almost complete specimen, two free cheeks and four pygidia with up to 13 contiguous thoracic segments attached. Another two pygidia with up to six thoracic segments are tentatively assigned. The almost complete specimen derives from the Læså riverbed between localities 2 and 3, while the other material derives from locality 2. In early March 2020, *O. transversus* was found also at locality 15B (material not included in the present study). This species occurs alone in the samples at hand. Neither C. Poulsen (1923) nor Kaufmann (1933a) recorded this species from Bornholm.

Occurrence. Olenus transversus occurs in the *O. gibbosus* Zone in Scandinavia (Westergård 1922, 1947; Henningsmoen 1957). In SE Scania, the species occurs alone in a thin horizon in between the intervals with

▲ **Fig. 7.** Species of *Olenus*. White scale bars: 2 mm; D is shown at lower magnification. **A–C:** *Olenus attenuatus*. **A:** Cranidium with two thoracic segments, preserved in shale, loc. 2, sample L104 (MGUH 33555). **B:** Pygidium, preserved in shale, loc. 3, sample GM 1897-1300 (MGUH 33556). **C:** Pygidium, preserved in anthraconite, loc. 17, sample GM 2019-63 (MGUH 33557). **D:** Free cheek and pygidium of *Olenus gibbosus*, preserved in anthraconite, loc. 2, MGUH 1957 (previously illustrated by C. Poulsen 1923, pl. I, fig. 4). **E–I:** *Olenus truncatus*, loc. 2, all preserved in shale. **E:** External mould of almost complete specimen, sample GM 1870-876 (MGUH 33558). **F:** Pygidium, sample GM 1922-133B (MGUH 33559). **G:** Pygidium, sample L112 (MGUH 33561). **H:** Pygidium with ten thoracic segments, sample GM 1922-133B (MGUH 33560). **I:** Almost complete specimen, sample GM 1922-133D (MGUH 33562). **J:** *Olenus dentatus,* external mould of almost complete specimen preserved in shale, sample GM 2019-102, loc. 18 (MGUH 33563). **K:** *Olenus dentatus*?, fragmentary cranidium preserved in shale, Læså, probably loc. 3, sample GM 2019-98 (MGUH 33564). **L–P:** *Olenus wahlenbergi,* all preserved in anthraconite, loc. 17. **L:** Free cheek, sample GM 2019-62 (MGUH 33565). **M:** Pygidium, sample GM 2019-59 (MGUH 33566). **N:** Pygidium, sample GM 2019-55 (MGUH 33567). **O:** Pygidium, sample GM 2019-68 (MGUH 33569). **P:** Pygidium, sample GM 2019-55 (MGUH 33568). **Q:** Thorax and pygidium of *Olenus transversus*, preserved in shale, loc. 2, sample L111 (MGUH 33570).

O. gibbosus and *O. truncatus* (Westergård 1922, 1944). Presumably a similar separate *O. transversus* level is developed on Bornholm considering that the species occurs alone in all samples at hand.

Comparison. *Olenus transversus* can be distinguished from the other *Olenus* species, except *O. gibbosus*, by its free cheek with an obtuse inner spine angle. In most other *Olenus* species the inner spine angle is 90º. *Olenus transversus* is, however, most readily identified by its pygidium. It has no marginal spines, and the pleural fields are markedly wider than the axis; the more rounded overall pygidial outline is also characteristic. *Olenus truncatus* has a subtriangular pygidium where each pleural field is as wide as the axis, while in *O. wahlenbergi* the pygidium is triangular in outline and the pleural fields are markedly narrower than the axis.

***Olenus truncatus* (Brünnich, 1781)**

Fig. 7E–I

1922 *Olenus truncatus* (Brünnich) – Westergård, pp. 126–127, pl. III, figs 18–19, pl. IV, figs 1–4.

v 1923 *Olenus truncatus* Brünnich – C. Poulsen, pp. 25–26, textfig. 6; pl. I, fig. 6.

1957 *Olenus truncatus* (Brünnich 1781) – Henningsmoen, pp. 109–110, pl. 3.

2017 *Olenus truncatus* (Brünnich, 1781) – Rasmussen *et al.*, pp. 16–17, fig. 8E–F.

For further synonymy, see Rasmussen *et al.* (2017).

Type material. Not designated, see Henningsmoen (1957).

Material. Six almost complete specimens and 19 pygidia, including one with ten contiguous thoracic segments. Additionally, one cephalon, ten cranidia and eight free cheeks are tentatively assigned, these specimens derive from samples containing safely identified pygidia. The material derives from locality 2 and the riverbed between localities 2 and 3; one sample (GM 1922-147) is from locality 15. C. Poulsen (1923) reported the species also from locality 17 and one shale sample (GM 1922-147B) from this site is in fact labelled *O. truncatus*. However, only cranidia are present and given the high similarity between cranidia of various species of *Olenus* they cannot be identified with certainty. *Olenus truncatus* co-occurs with *H. obesus* and *O. wahlenbergi* in the samples at hand (see remarks).

Occurrence. Index fossil for the eponymous zone in Scandinavia. *Olenus truncatus* has been reported also from Great Britain and Texas (Westergård 1922, 1947; Henningsmoen 1957; Terfelt *et al.* 2008; Rasmussen *et al.* 2017; Nielsen *et al.* 2020).

Comparison. For comparison with *O. transversus* and *O. wahlenbergi*, see *O. transversus*.

Remarks. *Olenus truncatus* and *O. wahlenbergi* are both present in sample L103. However, the two species occur on separate bedding planes, and the sample apparently straddles the boundary between the two zones. According to Kaufmann (1933a p. 59), the *O. truncatus* Zone is only 12 cm thick in the Læså stream.

***Olenus wahlenbergi* Westergård, 1922**

Fig. 7L–P

1922 *Olenus wahlenbergi* n. sp. – Westergård, p. 128, pl. IV, figs 5–14.

v 1923 *Olenus wahlenbergi* Wgd. – C. Poulsen, pp. 29–29, textfig. 7.

1957 *Olenus wahlenbergi* Westergård 1922 – Henningsmoen, pp. 110–111, pl. 3.

1995 *Olenus wahlenbergi* Westergård, 1922 – Clarkson & Taylor, pp. 13–34, figs 1–16.

2003 *Olenus wahlenbergi* Westergård, 1922 – Terfelt, p. 411, fig. 4C, D.

2005 *Olenus wahlenbergi* (Wahlenberg, 1821) [*sic*] – Lauridsen & Nielsen, pp. 1041–1056; pl. 1, figs 8–10.

For further synonymy, see Henningsmoen (1957).

Lectotype. Almost complete specimen (SGU 186) from Andrarum, southern Sweden, figured by Westergård (1922, pl. IV, fig. 5) and designated by Henningsmoen (1957).

Material. 26 free cheeks and 11 pygidia. 176 tentatively assigned cranidia derive from samples containing safely identified pygidia and/or free cheeks. The majority of the material derives from locality 17, with a few samples from locality 18 and one free cheek from locality 2. In the latter sample, *Olenus truncatus* has also been found (see remarks on that species). Kaufmann (1933a) also recorded *O. wahlenbergi* from the Læså stream (probably locality 2) but no material was illustrated. *Olenus wahlenbergi* is often associated with *H. obesus* in the samples at hand.

Occurrence. Index fossil for the eponymous zone in Scandinavia and Great Britain (Henningsmoen 1957; Terfelt *et al.* 2008; Nielsen *et al.* 2020).

Comparison. For comparison with *O. transversus* and *O. truncatus,* see the former. *Olenus wahlenbergi* is characterized by its free cheek having a large eye aperture and the course of the spine deviating slightly outwards from the direction of the lateral margin.

Genus *Parabolina* Salter, 1849
Type species: Entomostracites spinulosus Wahlenberg, 1818 by monotypy.

SubGenus *Parabolina* (*Parabolina*) Salter, 1849
Type species: As for genus.

***Parabolina* (*Parabolina*) *acanthura* (Angelin, 1854)**
Fig. 8A–B
v 1923 *Parabolina acanthura* Angelin – C. Poulsen, pp. 31–32, textfigs 10–11.
1957 *Parabolina acanthura* (Angelin 1854) – Henningsmoen, p. 116, pl. 7, pl. 10, figs 1–6.
2006 *Parabolina (Parabolina) acanthura* (Angelin, 1854) – Terfelt, pp. 1341–1342, pl. 1, figs 1–7.
For further synonymy, see Terfelt (2006).

Lectotype. Cranidium (RM 1655a) selected from Angelin's (1854) syntypes, designated and figured by Terfelt (2006, pl. 1, fig. 4).

Material. One cephalon, three cranidia and two free cheeks. A hypostome and an isolated thoracic pleura from the same horizon are also labelled as *P. acanthura*, but their identification remains tentative. All material is from locality 8. C. Poulsen (1923) described the species as very rare.

Occurrence. Upper part of the *Acerocare ecorne* Zone in Scandinavia and Great Britain (Westergård 1922; Henningsmoen 1957; Terfelt 2006). In Norway, *P. acanthura* ranges into the basal part of the Tremadocian (Henningsmoen 1957; Bruton *et al.* 1988).

Comparison. Parabolina acanthura is distinguished from *Parabolina heres heres* by having a shorter preglabellar field, an acute inner spine angle (right angled in *P. h. heres*), and a pygidium with only 3 pairs of marginal spines (4–5 pairs in *P. h. heres*). The pygidium of *P. heres hexacantha* [= *P. lata sensu* Heningsmoen 1957, see Nielsen *et al.* 2020] has three pairs of marginal spines that are longer than in *P. acanthura.*

***Parabolina* (*Parabolina*) *spinulosa* (Wahlenberg, 1818)**
Fig. 8E–H
1818 *Entomostracites spinulosus* – Wahlenberg, pp. 38–39, pl. I, fig. 3.
1922 *Parabolina spinulosa* (Wahlenberg) – Westergård, pp. 134–135, pl. VI, figs 14–20.
v 1923 *Parabolina spinulosa* Wahlenberg – C. Poulsen, pp. 29–31, textfig. 8.
1957 *Parabolina spinulosa* (Wahlenberg 1821) – Henningsmoen, pp. 126–128, pl. 1, fig. 2, pl. 3, textfig. 12.
1973 *Parabolina spinulosa* (Wahlenberg, 1821) – Schrank, p. 814, pl. I, figs 1–12, pl. II, figs 1–2.
1976 *Parabolina spinulosa* (Wahlenberg) – Reyment, fig. 1a–b.
2003 *Parabolina spinulosa* (Wahlenberg, 1818) – Terfelt, p. 411, fig. 4G, H.
2017 *Parabolina spinulosa* (Wahlenberg, 1818) – Rasmussen *et al.*, pp. 17–18.
For further synonymy, see Rasmussen *et al.* (2017).

Lectotype (designated here). Complete specimen PMU Sk-1 from Andrarum, Scania, originally illustrated by a drawing (Wahlenberg 1818, pl. 1, fig. 3); refigured by Reyment (1976, fig. 1a).

Material. 20 cranidia, seven free cheeks and eight pygidia. Most of the material derives from locality 6, but the species has been found also at locality 5. *Parabolina spinulosa* is associated with extremely common articulate brachiopods (*Orusia lenticularis*) in the samples at hand.

Occurrence. Index fossil for the eponymous zone. *Parabolina spinulosa* occurs widespread in Scandinavia, England and Canada (Westergård 1922; Henningsmoen 1957; Taylor & Rushton 1971; Rasmussen *et al.* 2015; Nielsen *et al.* 2020). It has also been reported from the overlying *Leptoplastus paucisegmentatus* Zone (Westergård 1947), based on co-occurrence with *Leptoplastus minor*, synonymized with *L. paucisegmentatus* by Westergård (1944, 1947). However, this interpretation is questioned by Nielsen *et al*. (2020), inferring reworking.

Comparison. The cranidium of *Parabolina spinulosa* can be distinguished from that of *P. brevispina* e.g. by its wider postocular cheek. Pygidia of *P. spinulosa* have 5–6 axial rings and 3–5 pairs of long marginal spines, while *P. brevispina* pygidia only have three axial rings and 3–4 pairs of short marginal spines.

Subgenus *Parabolina* (*Neoparabolina*) Nikolaisen & Henningsmoen, 1985
Type species: *Parabolina frequens* (Barrande, 1868), by original designation.

***Parabolina* (*Neoparabolina*) *lobata praecurrens* Westergård, 1944**
Fig. 8C–D
1944 *Parabolina longicornis praecurrens* var. n. – Westergård, p. 39, pl. 1, figs 9–11.
1957 *Parabolina lobata praecurrens* Westergård 1944 – Henningsmoen, pp. 123–124.
1973 *Parabolina lobata praecurrens* Westergård, 1944 – Schrank, p. 814–815, pl. II, figs 3–5, ?6.

2004 *Parabolina (Neoparabolina) praecurrens* Westergård 1944 – Buchholz, pp. 17–18, pl. 6, figs 7–10, pl. 7, figs 1–8.

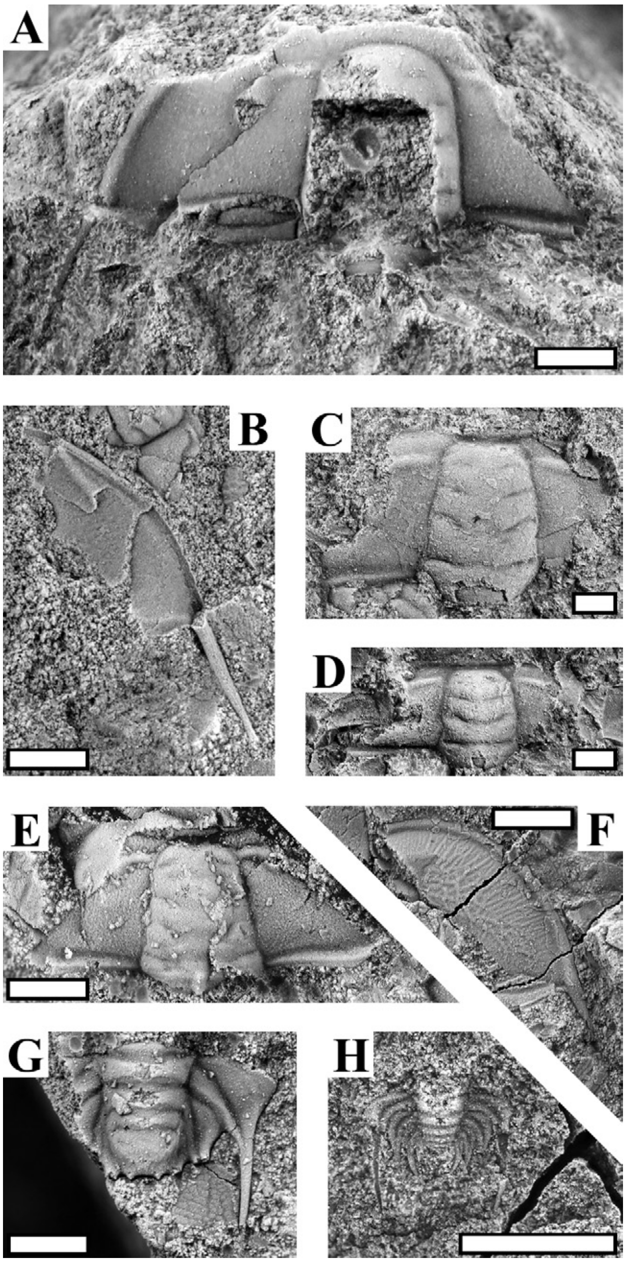


Fig. 8. Various species of *Parabolina*, all preserved in anthraconite. White scale bars: 1 mm. **A–B:** *Parabolina acanthura*, loc. 8. **A:** Fragmentary cephalon, sample GM 1924-1A (MGUH 33571). **B:** Free cheek seen from ventral side (partial external mould), loc. 8, MGUH 1980 (previously illustrated by C. Poulsen 1923, textfig. 11b). **C–D:** *Parabolina lobata praecurrens*, loc. 8B. **C**. Cranidium, sample L16 (MGUH 33572). **D:** Cranidium, sample L12 (MGUH 33574). **E–H:** *Parabolina spinulosa*, loc. 6. **E:** Cranidium, sample GM 1922-137B (MGUH 33575). **F:** Free cheek, sample GM 1922-137B (MGUH 33576). **G:** Pygidium, sample GM 1922-137B (MGUH 33577). **H:** Juvenile pygidium, sample GM 1922-137B (MGUH 33578).

2005 *Parabolina (Neoparabolina) lobata praecurrens* Westergård, 1944 – Terfelt *et al.*, pp. 197–200, fig. 4G–H.

For complete synonymy, see Henningsmoen (1957) and Terfelt *et al*. (2005).

Holotype. Cranidium SGU 4222 from the Gislövhammar-1 drill core, Sweden, figured by Westergård (1944, pl. 1, fig. 9).

Material. 21 cranidia, all rather poorly preserved and more or less fragmentary. The material derives from loose limestone boulders in the Læså creek bed at Limensgade (localities 8A–B). *Parabolina lobata praecurrens* co-occurs with *Peltura westergaardi* and rare articulate brachiopods.

Occurrence. Parabolina lobata Zone in Scania and the Oslo Region (Westergård 1944, 1947; Henningsmoen 1957). According to Westergård (1944) and Terfelt *et al.* (2005), *P. lobata praecurrens* is characteristic for the lower part of this zone.

Comparison. In comparison with *P. lobata lobata, P. lobata praecurrens* lacks a preglabellar field and also tends to have narrower fixed cheeks (see remarks). For description of pygidia, see Buchholz (1999, 2004).

Remarks. This is the first report of this subspecies from Bornholm. The free cheeks that C. Poulsen (1923) assigned to *Parabolina longicornis* [= *P. lobata*] are here allocated to *Ctenopyge tenuis* (*q.v.*) and thus no original museum material represents *P. lobata*. Henningsmoen (1957) and Terfelt *et al.* (2005) mentioned that *P. lobata praecurrens* has narrower fixed cheeks than *P. lobata lobata*, but Terfelt *et al.* (2005) remarked on the presence of intermediate forms with narrower fixed cheeks and a shorter preglabellar field than typical for *P. lobata lobata*. Terfelt *et al.* (2005) assigned cranidia with a pronounced preglabellar field to *P. lobata lobata* and cranidia lacking or having a very short preglabellar field to *P. lobata praecurrens*. The cranidia from Bornholm have a very short or no preglabellar field.

Genus *Leptoplastus* Angelin, 1854

Type species: Leptoplastus stenotus Angelin, 1854, designated by Vogdes (1890).

***Leptoplastus abnormis* Westergård, 1944**

Figs 9–10.

v 1923 *Leptoplastus ovatus* Angelin [*partim*] – C. Poulsen, pp. 35–36.

v 1923 *Leptoplastus stenotus* Angelin [*partim*]– C. Poulsen, pp. 36–37.

1944 *Leptoplastus abnormis* sp. n. – Westergård, p. 41, pl. 1 fig. 23; pl. 2, fig. 1.
1973 *Leptoplastus ovatus* Angelin, 1854 [*partim*] – Schrank, p. 817, pl. III, fig. 13.
2006 *Leptoplastus abnormis* Westergård, 1944 – Ahlberg *et al.*, pp. 105–106, figs 6G, 7B.
2015 *Leptoplastus ovatus* (Angelin, 1854) [*partim*] – Rasmussen *et al.*, pp. 14–15, fig. 6C–D.
2017 *Leptoplastus abnormis* Westergård, 1944 – Rasmussen *et al.*, p. 13, fig. 5A.
For further synonymy, see Rasmussen *et al.* (2017).

Holotype. Almost complete specimen SGU 4235 from Andrarum, southern Sweden, figured by Westergård (1944, pl. 1, fig. 23).

Material. The highly characteristic thorax of *L. abnormis* with long spines in the rear part has been found in ten samples including a nearly complete specimen and external moulds of three nearly complete specimens, all without free cheeks (e.g. Figs 9A–D). The remaining skeletal parts are exceedingly alike *L. ovatus* but one cephalon, 352 cranidia and nine free cheeks, all from locality 6, are tentatively assigned to *L. abnormis* (see remarks). Please note that the extensive material listed as *L. ovatus* in Appendix 1 rather likely still contains some *L. abnormis* and no differentiation of pygidia has been attempted. *Leptoplastus abnormis,* as interpreted here, co-occurs with *Eurycare bornholmensis, Leptoplastus angustatus, L. crassicornis* and *L. ovatus*.

Occurrence. Leptoplastus crassicornis–L. angustatus Zone in Scania and Öland, Sweden, perhaps Slemmestad in the Oslo Region, Norway (see remarks), and Bornholm (Westergård 1944, 1947; Ahlberg *et al.* 2006; Rasmussen *et al.* 2017; this study).

Comparison. In comparison with *L. angustatus* and *L. crassicornis*, the cranidium of *L. abnormis* has a more bulbous and short glabella, the interocular area is significantly narrower (tr.) and the postocular cheeks are shorter (exsag.); the free cheek has a much shorter spine and shorter posterior margin. For comparison with *L. ovatus*, see remarks.

Remarks. Nearly all identifiable thoraxes of *Leptoplastus* in the material at hand represent *L. abnormis* whereas no contiguous thoracic segments assignable to *L. ovatus* have been recorded. Initially all detached skeletal parts of *ovatus*-type (i.e. cranidia with relatively short, wide glabella, narrow interocular cheeks and short (exsag.) postocular cheeks; free cheeks with short almost straight spine) were identified as *L. ovatus* and none as *L. abnormis,* making it obvious that the disarticulated slerites of these species were mixed up.

According to Henningsmoen (1957), *L. abnormis* has an elongate glabella, interocular cheeks that are ½ as wide as glabella at eye-line and postocular cheeks that are ¾ as wide (tr.) as the occipital ring, whereas *L. ovatus* was diagnosed as having a glabella that is approximately as wide as long, interocular cheeks that are ¼ as wide as the adjacent glabella and postocular cheeks that are somewhat narrower (tr.) than the occipital ring. Ahlberg *et al.* (2006, fig. 7B) indicated that *L. abnormis* has its palpebral lobes situated relatively far forwards opposite L2, while the lobes are located opposite L1–S1 in *L. ovatus.* The free cheek of *L. abnormis* may have a slightly longer genal spine than *L. ovatus* (Westergård 1944; Ahlberg *et al.* 2006). No separating characters for pygidia have been published.

All material studied here is preserved in limestone, whereas the few semi-complete specimens of *L. abnormis* from Scania described by Westergård (1944) and Ahlberg *et al.* (2006) are preserved in shale. This is relevant as compaction may have distorted the outline of the material hitherto described, and also influenced the drawn reconstruction published by Ahlberg *et al.* (2006, fig. 7B).

A closer examination of the *ovatus*-type cranidia was based on photos of 101 fairly preserved specimens of different sizes. The pilot study revealed that three morphs can be distinguished based on visual appearance: i) one with a short glabella+occipital ring that essentially does not taper (Fig. 14), ii) one with a slightly to clearly elongate glabella+occipital ring that essentially does not taper (Figs 9J, 10E–L) and iii) one where the elongate glabella+occipital ring tapers (Figs 9E–I, 10C–D, M). In order to characterize these morphs further, several cranidial features were measured; the results are summarized in Table 1 and illustrated in Fig. 11. In the non-tapering morph with short glabella, tentatively treated as *L. ovatus,* the width of the occipital ring corresponds on average to 0.83 of the combined length of glabella+occipital ring, whereas this ratio averages 0.86 in the two other morphs that both are assumed to represent *L. abnormis* (Table 1 and Fig. 11, ratio A).

The key difference between the two taxa, based on visual examination, is the relative length of the glabella. Most unexpectedly, the measured length/width ratio of the glabella itself (i.e. without the occipital ring) is identical in the two groupings (Table 1 and Fig. 11, ratio D). Hence, one of the few measurable differences is the laterally expanded occipital ring seen in most (but not all) medium-sized and larger cranidia of *L. abnormis* (Table 1 and Fig. 11, ratio A). Increased tapering of the glabella+occipital ring during growth is a phenomenon seen also in other olenids, e.g. *C. affinis* (Fig. 20) and *S. alatus* (Fig. 32) and which justifies the assignment of small cranidia with non-tapering,

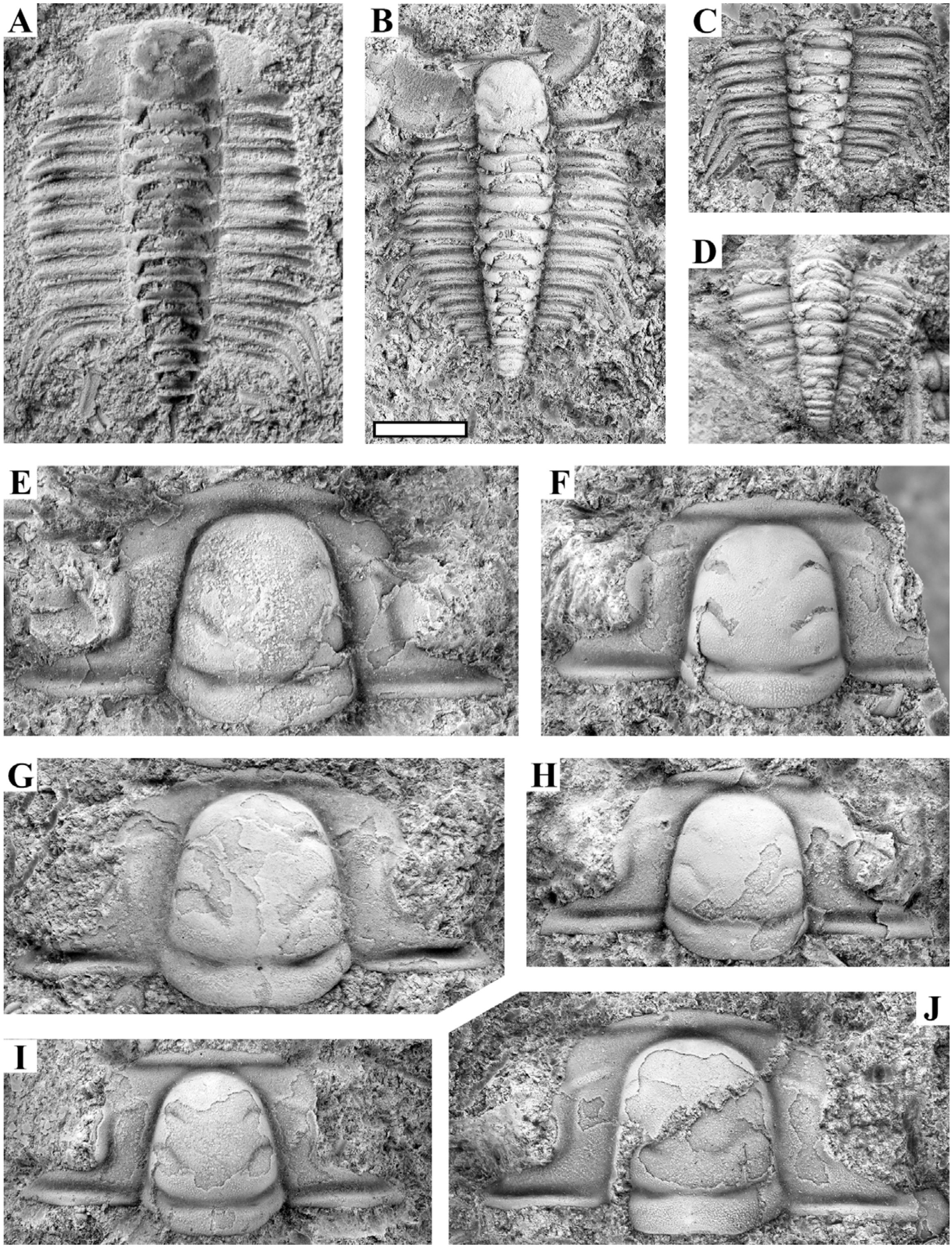


Fig. 9. *Leptoplastus abnormis*, all preserved in anthraconite from locality 6; regarding assignment of cranidia, see text. White scale bar: 2 mm. **A:** External mould of almost complete specimen, sample ATN-304 (MGUH 33579). **B:** Small, almost complete specimen (somewhat damaged), sample ATN-260 (MGUH 33582). **C:** Part of thorax, sample ATN-301 (MGUH 33583). **D:** Small thorax with attached pygidium; the pleural spines are broken and the specimen is tentatively assigned, sample ATN-265 (MGUH 33585). **E:** Cranidium, sample ATN-261 (MGUH 33588). **F:** Cranidium, sample ATN-331 (MGUH 33589). **G:** Cranidium, sample ATN-288 (MGUH 33592). **H:** Cranidium, sample ATN-262 (MGUH 33597). **I:** Cranidium, sample ATN-276 (MGUH 33599). **J:** Cranidium with non-tapering glabella, tentatively assigned, sample ATN-288 (MGUH 33593) (see also Fig. 10I–L).

barely elongate glabella to *L. abnormis* (Fig. 10E–G). Otherwise, the cranidial ratios of *L. ovatus* and *L. abnormis* are quite similar (Table 1, Fig. 11) except that the postocular cheek in large cranidia is relatively wider in *L. ovatus* than in *L. abnormis*, and which is also reflected in the cranidial W/L ratio in adults (ratio B2). The relative width of the occipital ring (ratio C, Table 1 and Fig. 11) increases hardly at all during growth and

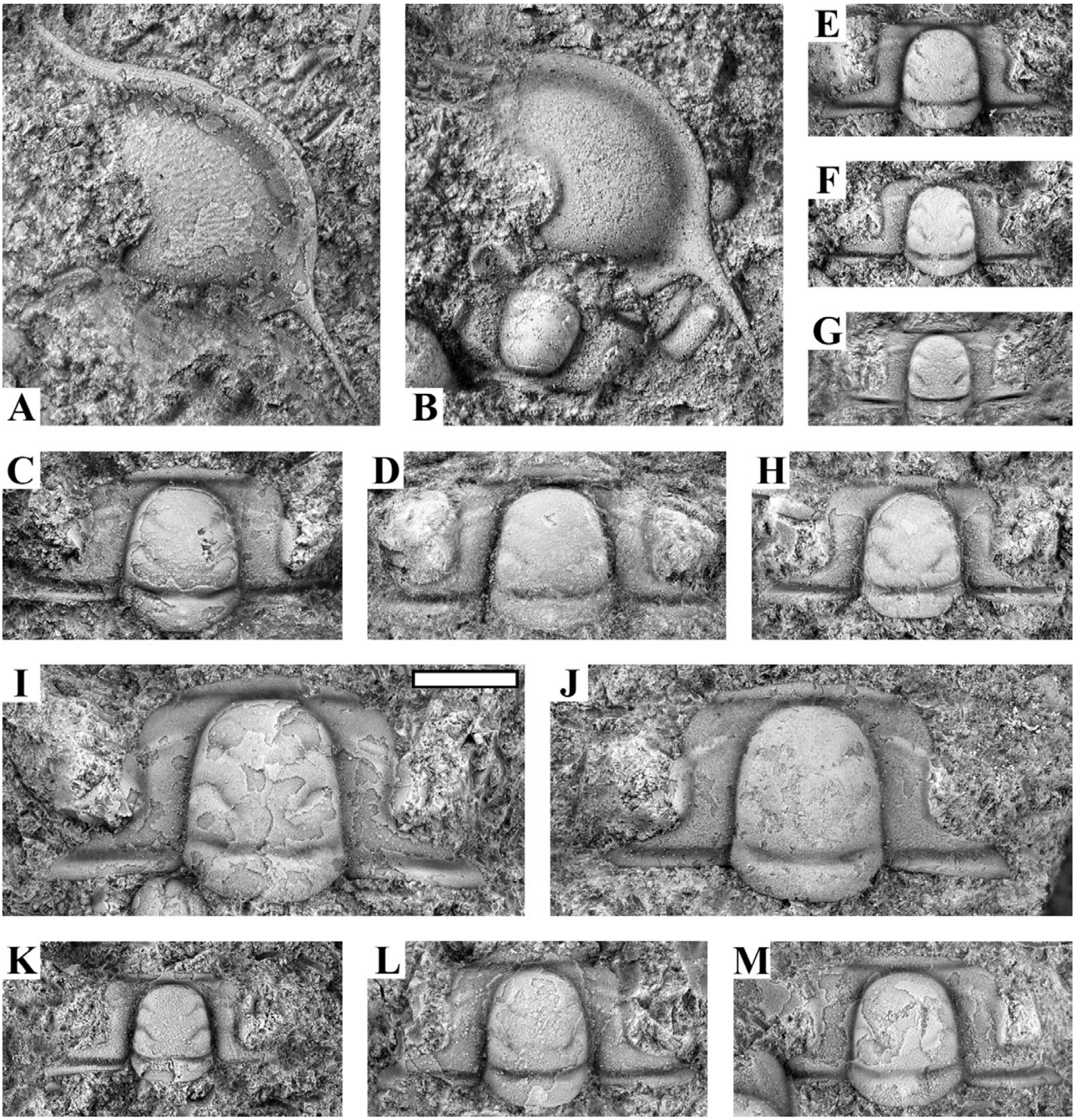


Fig. 10. *Leptoplastus abnormis* (*s.l.*), all preserved in anthraconite from locality 6; regarding assignment of cranidia and free cheeks, see text. White scale bar: 2 mm. **A–B:** Free cheeks, tentatively assigned to *Leptoplastus abnormis*, samples ATN-119 and ATN-288 (MGUH 33601, 33594). **C–H:** Medium sized cranidia. **C:** Sample L126 (MGUH 33603). **D:** Sample ATN-332 (MGUH 33607). **E:** Sample ATN-301 (MGUH 33584). **F:** Sample ATN-265 (MGUH 33586). **G:** Sample ATN-335 (MGUH 33609). **H:** Sample ATN-265 (MGUH 33587). **I–L**. Cranidia with essentially non-tapering, slightly elongate glabella, identified as *Leptoplastus* cf. *abnormis*. **I:** Sample ATN-347 (MGUH 33611). **J:** Sample ATN-331 (MGUH 33590). **K:** Cranidium, sample ATN-241 (MGUH 33612). **L:** Sample ATN-293 (MGUH 33613). **M:** Cranidium, sample ATN-346 (MGUH 33614).

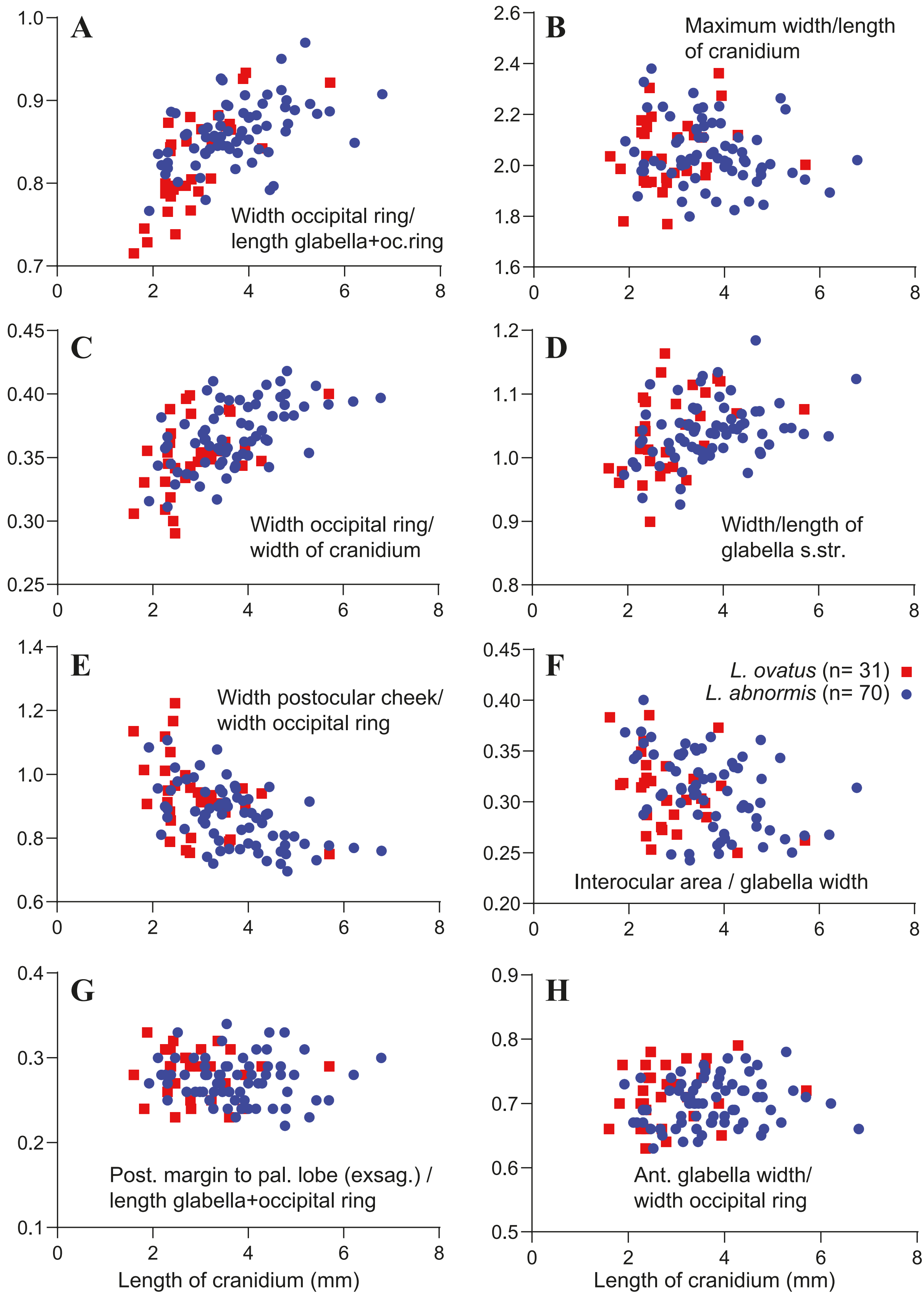


Fig. 11. Scatter plots of various cranidial features of *Leptoplastus abnormis* and *Leptoplastus ovatus*. See text for discussion; average values and variation ranges are listed in Table 1. All x-axes are length of cranidium (mm). Legend in F.

is surprisingly similar in the two taxa. The distance (exsag.) between the posterior cranidial margin and posterior corner of the palpebral lobe is also identical in both taxa (ratio G, Table 1). The eyes are thus not located more forwards in the specimens assigned to *L. abnormis* (cf. Ahlberg *et al*. 2006), and midpoint of the palpebral lobes is located opposite S1 to L1 (Figs 9–10). Also, the width of the interocular cheek at eye-line (tr.) is identical in the two taxa (ratio F, Table 1).

As it appears, the only measurable differences between the discussed species are the slightly wider postocular cheeks in adult *L. ovatus* cranidia and the wider occipital ring of the medium-sized and larger cranidia assigned to *L. abnormis,* which engenders a tapering appearance of the glabella+occipital ring. In this connection, please note that the complete specimen of *L. abnormis* illustrated in Fig. 9B has a cranidium only 2.4 mm long. The two specimens of *L. abnormis* originally illustrated by Westergård (1944) both have cranidia *c.* 3.5 mm long. One of them shows a tapering glabella (*ibid*. pl. 2, fig. 1) whereas the other (the holotype) does not (*ibid*. pl. 1, fig. 23).

A biometric study, including complete specimens of *L. ovatus* as well as disarticulated *ovatus*-type material from across Scandinavia, should be undertaken. For instance, the cranidium and free cheek from Slemmestad assigned to *L. ovatus* by Rasmussen *et al.* (2015) in our opinion resemble the morph identified here as *L. abnormis* as the glabella is tapering and the genal spine is comparatively sturdy.

Table 1. Cranidial ratios of *Leptoplastus ovatus* (morph with short, essentially non-tapering glabella) and *Leptoplastus abnormis* (morphs with relatively longer glabella, tapering or non-tapering) based on measurements of 101 well-preserved cranidia

	L. ovatus (n=31)	*L. abnormis* (n=70)
A. Width occipital ring (tr.) / length of glabella+occipital ring	avg. 0.83 (0.72–0.93)	avg. 0.86 (0.77–0.97)
A1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.79 (0.72–0.88)	avg. 0.83 (0.78–0.89)
A2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.88 (0.81–0.93)	avg. 0.87 (0.78–0.99)
B. Cranidial maximum width/maximum length	avg, 2.05 (1.77–2.36)	avg. 2.05 (1.80–2.38)
B1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 2.01 (1.77–2.30)	avg. 2.09 (1.88–2.38)
B2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 2.11 (1.96–2.36)	avg. 2.03 (1.80–2.28)
C. Width occipital ring (tr.) / width of cranidium	avg. 0.35 (0.29–0.40)	avg. 0.37 (0.31–0.42)
Ca. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.35 (0.29–0.40)	avg. 0.35 (0.31–0.38)
Cb. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.36 (0.34–0.40)	avg. 0.37 (0.32–0.42)
D. Max. width/length ratio of glabella s.str.	avg. 1.04 (0.90–1.16)	avg, 1.04 (0.93–1.18)
Da. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 1.02 (0.90–1.16)	avg. 1.02 (0.94–1.12)
Db. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 1.07 (0.96–1.12)	avg. 1.05 (0.93–1.18)
E. Width (tr.) of postocular cheek / width occipital ring	avg. 0.93 (0.75–1.22)	avg. 0.87 (0.70–1.11)
E1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.96 (0.75–1.22)	avg. 0.95 (0.81–1.11)
E2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.88 (0.75–0.96)	avg. 0.84 (0.70–1.08)
F. Width (tr.) of interocular cheek /width of adjacent glabella at eye-line (n= 30 and 67, respectively)	avg. 0.31 (0.25–0.39)	avg. 0.31 (0.24–0.40)
F1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.32 (0.25–0.39)	avg. 0.33 (0.25–0.40)
F2. Cranidia ≥3 mm long (n=10 and 52, respectively)	avg. 0.30 (0.25–0.37)	avg. 0.30 (0.24–0.37)
G. Distance (exsag.) post. cranidial margin to post. corner of palpebral lobe / length of glabella+occipital ring	avg. 0.28 (0.23–0.33)	avg. 0.27 (0.22–0.34)
G1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.28 (0.23–0.33)	avg. 0.28 (0.25–0.33)
G2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.28 (0.23–0.32)	avg. 0.27 (0.22–0.34)
H. Width of glabella (tr.) at eye ridge/width of occipital ring	avg. 0.71 (0.63–0.79)	avg. 0.70 (0.63–0.78)
H1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.71 (0.63–0.78)	avg. 0.69 (0.63–0.74)
H2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.73 (0.65–0.79)	avg. 0.70 (0.64–0.78)
I. Width of glabella (tr.) at eye ridges/max. width of glabella immediately in front of occipital ring	avg. 0.74 (0.64–0.81)	avg. 0.75 (0.66–0.84)
I1. Cranidia < 3 mm long (n=20 and 15, respectively)	avg. 0.73 (0.64–0.79)	avg. 0.73 (0.66–0.81)
I2. Cranidia ≥3 mm long (n=11 and 55, respectively)	avg. 0.77 (0.69–0.81)	avg. 0.76 (0.71–0.84)

See also Fig. 11, where the ratios are plotted vs. cranidial length.
Much of the dataset is obtained from an unpublished student project (Holm 2020).
For remarks on identification of *L. ovatus* and *L. abnormis*, see text.

Findings of the characteristic thorax shows that *L. abnormis* unquestionably occurs in the *Leptoplastus* Superzone on Bornholm. A few *ovatus*-type free cheeks with comparatively long spines have also been tentatively assigned (Fig. 10A–B), following Westergård (1944). We presume, but cannot prove beyond doubt, that also *L. ovatus* is present and it is stressed that the indicated identification of disarticulated sclerites remains preliminary.

***Leptoplastus angustatus* (Angelin, 1854)**
Fig. 12.

1904 *Eurycare angustatum* Ang. [*partim*] – Persson, pp. 517–520, pl. 9, figs 11–13; non pl. 9, figs 9–10 [= *Eurycare*? sp.].
1922 *Eurycare angustatum* Angelin – Westergård, p. 150, pl. X, figs 4–9.
v 1923 *Eurycare angustatum* Angelin [*partim*] – C. Poulsen, pp. 34–35, pl. 1, fig. 10; non pl. 1, fig. 9 [= *L. crassicornis*, see Fig. 13D]. [The museum material labelled as *Eurycare angustatum* includes *L. crassicornis* and *L. ovatus*].
v 1923 *Leptoplastus stenotus* Angelin [*partim*] – C. Poulsen, pp. 36–37.
1957 *Leptoplastus angustatus* (Angelin 1854) – Henningsmoen, pp. 164–165, pl. 4; pl. 16, figs 10–13.
1973 *Leptoplastus angustatus* (Angelin, 1854) – Schrank, pp. 818–819, pl. IV, fig. 13–22; pl. V, fig. 1–4.
2004 *Leptoplastus angustatus* (Angelin 1854) – Mischnik, pp. 109–110, pl. 3, fig. 2.
2006 *Leptoplastus angustatus* (Angelin, 1854) [*partim*] – Ahlberg *et al.*, pp. 102, 105, figs 4B–C, 6B–C, 7D; non fig. 6A [= *L. crassicornis*].
2016 *Leptoplastus angustatus* (Angelin, 1854) – Rasmussen *et al.*, p. 13.

For further synonymy, see Rasmussen *et al.* (2016).

Type material. Not designated, see Henningsmoen (1957).

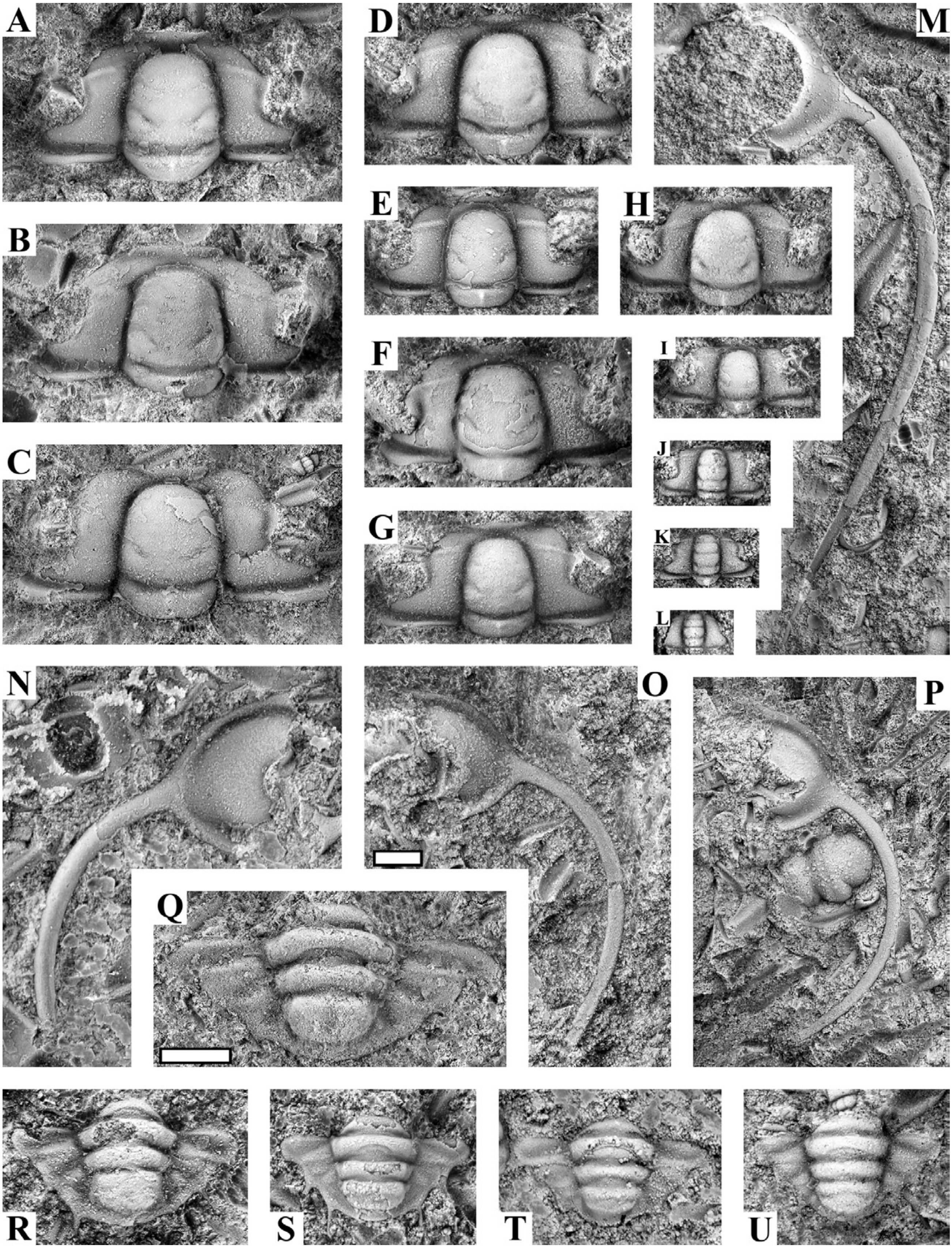
Material. 457 cranidia, 203 free cheeks and 28 pygidia; all from locality 6 (a few older museum specimens just labelled 'Læså' must also derive from this locality). Four additional pygidia may belong to the species but are too poorly preserved to be safely assigned. *Leptoplastus angustatus* co-occurs with *E. bornholmensis*, *L. abnormis*, *L. crassicornis* and *L. ovatus* in the samples at hand.

Occurrence. Characteristic for the *L. crassicornis–L. angustatus* Zone in Scandinavia (Rasmussen *et al.* 2015; Nielsen *et al.* 2020 and references therein).

Comparison. Leptoplastus crassicornis is distinguished from *L. angustatus* by having a more elongate glabella. These species have rather similar looking free cheeks with a very long curved spine, but in *L. crassicornis*, the spine is wider, somewhat flattened and provided with a central keel (Fig. 13H–J), whereas in *L. angustatus* the spine is more slender and rounded in cross-section (Fig. 12M–P). For comparison with free cheeks of *E. bornholmensis*, see that species. In comparison with *L. angustatus,* the crania of *L. ovatus* and *L. abnormis* have a less elongate, more bulbous glabella, the interocular cheeks are narrower and the postocular cheeks are shorter (exsag.). Due to the longer (exsag.) postocular cheeks of *L. angustatus*, the eyes are positioned more anteriorly than in *L. ovatus* and *L. abnormis*.

Remarks. The fact that *L. angustatus* co-occurs with *L. ovatus* and *L. crassicornis* on Bornholm corroborates the zonal revision proposed by Rasmussen *et al.* (2015), abandoning separate *L. crassicornis, L. ovatus* and *L. angustatus* zones. The latter taxon seems, though, to predominantly occur towards the top of the zone at several Scandinavian localities (e.g. Westergård 1944, 1947; Henningsmoen 1957; Rasmussen *et al.* 2015). Its distribution within the zone on Bornholm cannot be unravelled based on the material at hand, but it co-occurs with all the other nominate zonal index species (see above). However, in 25% of the samples containing *L. angustatus,* the species occurs alone, usually in profusion and with many juveniles. Hence, at least

▼ **Fig. 12.** *Leptoplastus angustatus*, all preserved in anthraconite from locality 6. White scale bars: 1 mm; please note that juvenile cranidia J–L and pygidia R–U are shown at a greater magnification (scale bar in Q). **A:** Cranidium, sample ATN-110 (MGUH 33615). **B:** Cranidium, sample ATN-223 (MGUH 33622). **C:** Cranidium, sample ATN-252 (MGUH 33624). **D:** Cranidium, sample ATN-153 (MGUH 33626). **E:** Cranidium, sample ATN-110 (MGUH 33616). **F:** Cranidium, sample ATN-288 (MGUH 33595). **G:** Cranidium, sample ATN-153 (MGUH 33627). **H:** Cranidium, sample ATN-335 (MGUH 33610). **I:** Small cranidium, sample ATN-304 (MGUH 33580). **J:** Juvenile cranidium, sample GM 1888-289A (MGUH 33628). **K:** Juvenile cranidium, sample ATN-334 (MGUH 33630) **L:** Juvenile cranidium, sample GM 1888-289A (MGUH 33629). **M:** Free cheek, sample ATN-110 (MGUH 33617). **N:** Free cheek, sample ATN-224 (MGUH 33631). **O:** Free cheek, sample ATN-223 (MGUH 33623). **P:** Free cheek, sample ATN-278 (MGUH 33633). **Q:** Pygidium, sample ATN-332 (MGUH 33608). **R:** Pygidium, tentatively assigned, sample ATN-224 (MGUH 33632). **S:** Pygidium, sample L32 (MGUH 33636). **T:** Pygidium, sample GM 1888-289C (MGUH 33637) (same sample as MGUH 1962). **U:** Pygidium, sample ATN-110 (MGUH 33618).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one level within the *L. crassicornis–L. angustatus* Zone on Bornholm is characterized by sole occurrence of *L. angustatus*, but it may just be a single bedding plane.

Leptoplastus crassicornis (Westergård, 1944)

Fig. 13.

v 1923 *Eurycare angustatum* Angelin [*partim*] – C. Poulsen, pp. 34–35, pl. I, fig. 9. [The specimen is here re-illustrated in Fig. 13D].
v 1923 *Leptoplastus stenotus* Angelin [*partim*] – C. Poulsen, pp. 36–37.
1944 *Eurycare angustatum crassicorne* var. n. – Westergård, pp. 41–42, pl. 2, figs 2–4.
1957 *Leptoplastus crassicorne* (Westergård 1944) – Henningsmoen, p. 167, pl. 4; pl. 14, figs 1–13.
1958a *Leptoplastus crassicornis* – Henningsmoen, p. 187.
1973 *Leptoplastus crassicorne* (Westergård, 1944) – Schrank, pp. 816–817, pl. III, figs 5?, 6, 7?, 8–11.
2004 *Leptoplastus crassicornis* (Westergård 1944) – Mischnik, p. 108, pl. 2, fig. 7.
2006 *Leptoplastus crassicornis* (Westergård, 1944) – Ahlberg *et al.*, p. 102, figs 5H–I, 7E.
2006 *Leptoplastus angustatus* (Angelin, 1854) [*partim*] – Ahlberg *et al.*, fig. 6A.
2017 *Leptoplastus crassicornis* (Westergård, 1944) – Rasmussen *et al.*, pp. 13–14.

For further synonymy, see Rasmussen *et al.* (2017).

Holotype. Complete specimen SGU 4237 from Andrarum, southern Sweden, figured by Westergård (1944, pl. 2, fig. 2).

Material. 37 cranidia, 12 free cheeks and six pygidia; all from locality 6. *Leptoplastus crassicornis* co-occurs with *Eurycare bornholmensis*, *E. latum*, *Leptoplastus angustatus*, *L. abnormis* and *L. ovatus* in the material at hand.

Occurrence. Index fossil for the *L. crassicornis–L. angustatus* Zone in Scandinavia (Rasmussen *et al.* 2015; Nielsen *et al.* 2020). *Leptoplastus crassicornis* has been reported also from England (Taylor & Rushton 1971).

Comparison. The free cheek of *L. crassicornis* with a long, robust, somewhat flattened genal spine is distinctive and safely confirms the presence of this species on Bornholm. The cranidium reminds of *L. angustatus*, for comparison, see that species. The free cheek somewhat resembles that of *E. latum*, but the spine curves stronger and the genal field of *E. latum* is more vaulted.

Remarks. This species was mentioned from Bornholm by Henningsmoen (1957, p. 167) but its presence has never been documented. Only sparse material has been found and *L. crassicornis* appears to be comparatively infrequent. This should be evaluated in light of the fact that a very extensive sample material from the *Leptoplastus* Superzone is at hand.

Leptoplastus ovatus Angelin, 1854

Fig. 14

1904 *Leptoplastus ovatus* Ang. – Persson, pp. 520–522, pl. 9, figs 17–23.
1922 *Leptoplastus ovatus* Angelin – Westergård, pp. 145–146, pl. VIII, figs 18–21.
v 1923 *Leptoplastus ovatus* Angelin [*partim*] – C. Poulsen, pp. 35–36, textfig. 12. [The material includes *L. abnormis*].
v 1923 *Leptoplastus stenotus* Angelin [*partim*] – C. Poulsen, pp. 36–37.
v 1923 *Eurycare angustatum* Angelin [*partim*] – C. Poulsen, pp. 34–35.
1957 *Leptoplastus ovatus* Angelin 1854 – Henningsmoen, pp. 173–174, pl. 4; pl. 13, figs 8–10.
1973 *Leptoplastus ovatus* Angelin, 1854 [*partim*] – Schrank, p. 817, pl. III, fig. 12, 14–16; non pl. III, fig. 13 [= *L. abnormis*].
2004 *Leptoplastus ovatus* Angelin 1854 – Mischnik, p. 108, pl. 2, fig. 6.
2015 *Leptoplastus ovatus* (Angelin, 1854) [*partim*] – Rasmussen *et al.*, pp. 14–15, non fig. 6C–D [= *L. abnormis*].
2017 *Leptoplastus ovatus* (Angelin, 1854) – Rasmussen *et al.*, p. 14, fig. 7C, E, F.

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Complete specimen Ar 1721 (Naturhistoriska Riksmuseet, Stockholm) from Andrarum, southern Sweden, figured by Westergård (1922, pl. VIII, fig. 18), and supposed to be Angelin's type specimen. Designated by Henningsmoen (1957).

Material. 401 cranidia, 429 free cheeks, one hypostome? and 35 pygidia (free cheeks, hypostome and pygidia are tentatively assigned and probably include specimens of *L. abnormis*); all from locality 6. *Leptoplastus ovatus* co-occurs with *Eurycare bornholmensis, E. latum, L. abnormis, L. angustatus* and *L. crassicornis.*

Occurrence. Leptoplastus crassicornis–L. angustatus Zone in Scandinavia (Westergård 1944; Ahlberg *et al.* 2006; Rasmussen *et al.* 2015; Nielsen *et al.* 2020). *Leptoplastus ovatus* is reported also from England (Taylor & Rushton 1971) and possibly maritime Canada (Henningsmoen 1957).

Comparison. For comparison with *L. angustatus* and *L. abnormis*, see those taxa. Disarticulated skeletal parts of *L. ovatus* and *L. abnormis* are almost indistinguishable and despite detailed study the may still be mixed to some extent.

Remarks. Measurements of cranidia of the morph we here identify as *L. ovatus* (see remarks on *L. abnormis*) show that width of the interocular cheeks at eye-line (tr.) corresponds to 0.25–0.4 of the adjacent glabella width (Table 1), a range slightly wider than indicated for this species by Henningsmoen (1957).

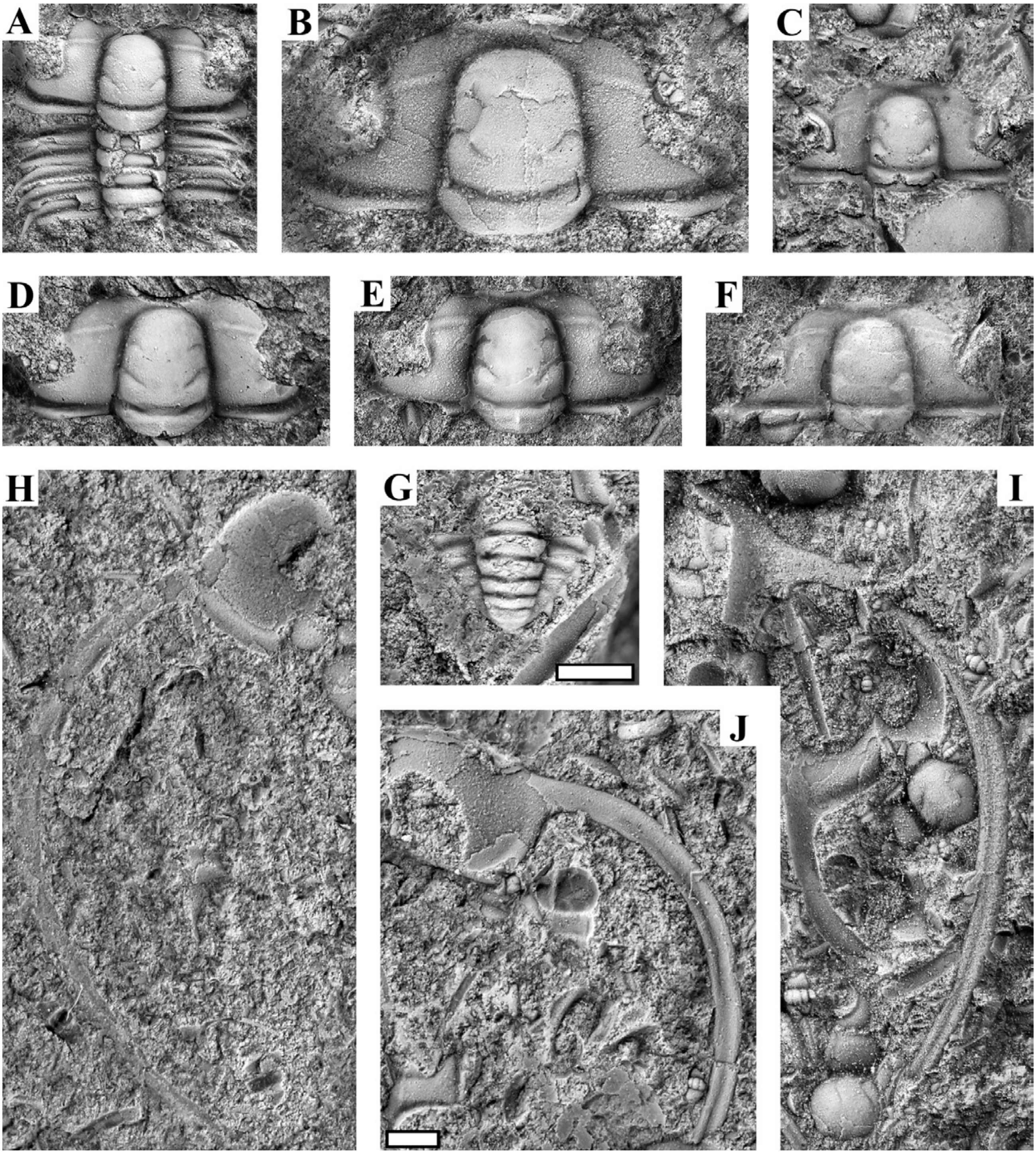


Fig. 13. *Leptoplastus crassicornis*, all preserved in anthraconite from locality 6. White scale bars: 1 mm; pygidium (G) is shown at greater magnification. **A:** Cranidium with four thoracic segments, sample ATN-110 (MGUH 33619). **B:** Large cranidium, sample ATN-216 (MGUH 33638). **C:** Small cranidium, sample GM 1888-289D (MGUH 33639). **D:** Cranidium illustrated as *Eurycare angustatum* by C. Poulsen (1923, pl. I, fig. 9) (MGUH 1962). **E:** Cranidium, sample ATN-278 (MGUH 33634). **F:** Cranidium, sample ATN-110 (MGUH 33620). **G:** Pygidium, sample ATN-278 (MGUH 33635). **H:** External mould of free cheek, sample ATN-220 (MGUH 33640). **I:** Free cheek, sample ATN-178 (MGUH 33641). **J:** Free cheek, sample ATN-252 (MGUH 33625).

***Leptoplastus stenotus* Angelin, 1854**

Fig. 15

1904 *Leptoplastus stenotus* Ang. – Persson, pp. 522–523, pl. 9, figs 14–16.

1922 *Leptoplastus stenotus* Angelin – Westergård, pp. 146–147, pl. IX, figs 1–6.

v 1923 *Leptoplastus stenotus* Angelin [*partim*] – C. Poulsen, pp. 36–37, textfigs 13–14, 21. [The material also contains *L. abnormis*, *L. angustatus*, *L. crassicornis* and *L. ovatus*, see remarks].

1957 *Leptoplastus stenotus* Angelin 1854 – Henningsmoen, pp. 177–178, pl. 2, fig. 16; pl. 4.

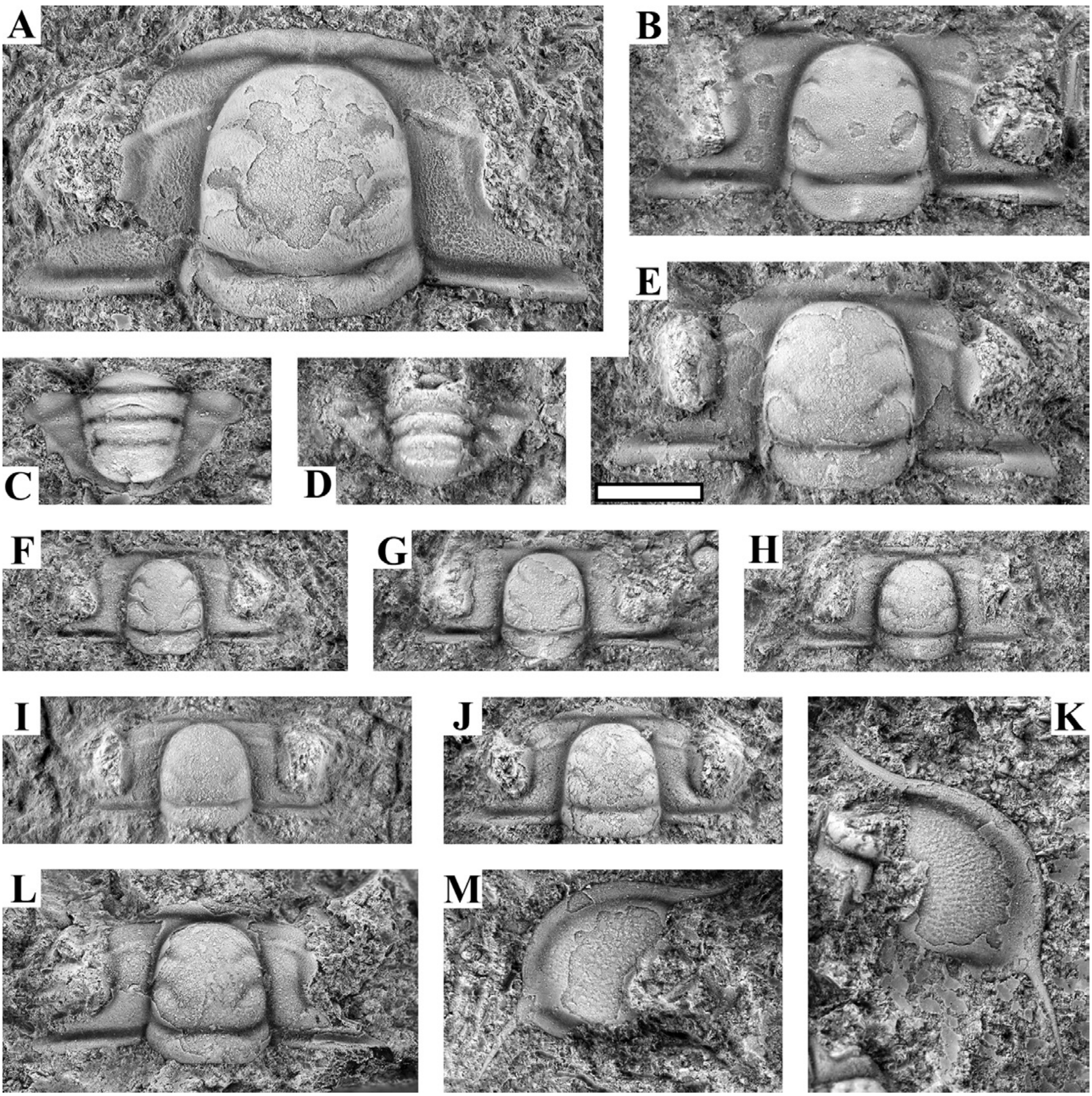


Fig. 14. *Leptoplastus ovatus*, all preserved in anthraconite from locality 6. Regarding assignment of disarticulated sclerites, see text. Free cheecks and pygidia (O–S) may alternatively belong to *L. abnormis*. White scale bar: 2 mm. **A:** Large cranidium, sample ATN-270 (MGUH 33642). **B:** Cranidium, sample ATN-276 (MGUH 33600). **C:** Pygidium, sample ATN-110 (MGUH 33621). **D:** Pygidium, sample ATN-119 (MGUH 33602). **E:** Cranidium, sample ATN-263 (MGUH 33643). **F:** Cranidium, sample ATN-306 (MGUH 33645). **G:** Cranidium, sample L126 (MGUH 33604). **H:** Cranidium, sample ATN-108 (MGUH 33649). **I:** Cranidium, sample ATN-288 (MGUH 33596). **J:** Cranidium, sample ATN-331 (MGUH 33591). **K:** Free cheek, sample ATN-263 (MGUH 33644). **L:** Cranidium, sample ATN-251 (MGUH 33650). **M:** Free cheek, sample ATN-156 (MGUH 33652).

1973 *Leptoplastus stenotus* Angelin, 1854 – Schrank, pp. 819, pl. V, fig. 5–11.
2015 *Leptoplastus stenotus* (Angelin, 1854) – Rasmussen *et al.*, p. 16, fig. 12.
For further synonymy, see Rasmussen *et al.* (2015).

Neotype. Designated here, complete specimen LO 3073, from Andrarum, southern Sweden, illustrated by Westergård (1922, pl. IX, fig. 4).

Material. 142 cranidia, 12 free cheeks and 5 pygidia. Six specimens are from locality 22 and the remaining material is from locality 6. *Leptoplastus stenotus* occurs alone.

Occurrence. Index fossil for the eponymous zone in Scandinavia (Henningsmoen 1957; Terfelt *et al.* 2008; Rasmussen *et al.* 2015; Nielsen *et al.* 2020).

Comparison. The cranidium of *L. stenotus* is distinguished from the cranidia of *L. angustatus* and *L. crassicornis* by its preglabellar field. The free cheek differs from that of *L. ovatus* by having a longer genal spine, which, however, often is broken.

Remarks. Two museum samples, both numbered GM 1922-139E, are labelled as *L. stenotus* but contain several cranidia, free cheeks, and two pygidia here identified as *L. abnormis*, *L. ovatus*, *L. crassicornis* and *L. angustatus.* The samples also contain an *E. bornholmensis* cranidium and some *L. abnormis* thoracic segments, but no *L. stenotus*.

Genus *Eurycare* Angelin, 1854
Type species: *Eurycare brevicauda* Angelin, 1854, designated by Vogdes (1925).

***Eurycare bornholmensis* (Poulsen, 1923)**
Figs 16–18
v 1923 *Ctenopyge neglecta*, Westergård var. *bornholmensis* n. var. – C. Poulsen, pp. 37–38, pl. I, fig. 11.
1957 *Leptoplastus bornholmensis* (Poulsen, 1923) – Henningsmoen, p. 165.
1973 *Leptoplastus bornholmensis* (Poulsen, 1923) – Schrank, pp. 817–818, pl. IV, figs 10–12.

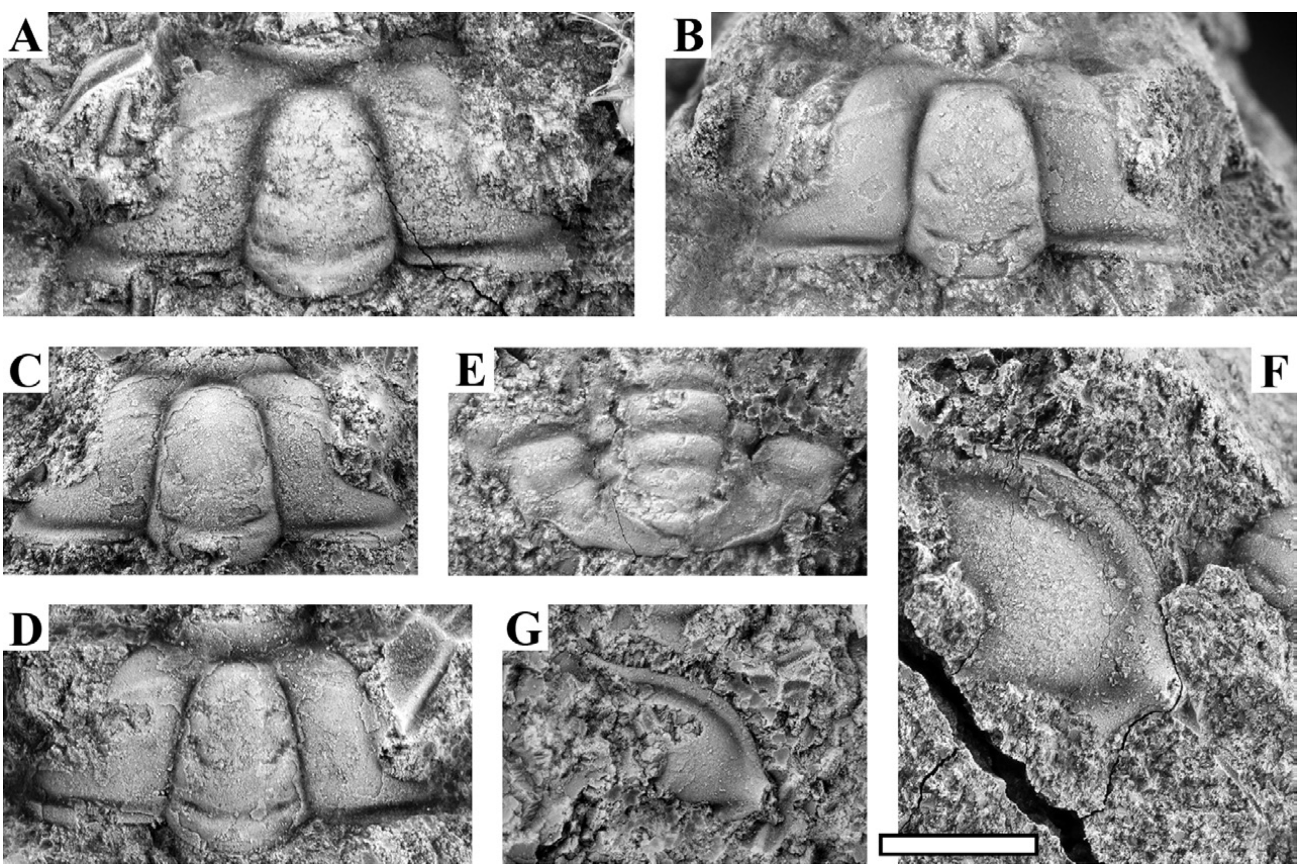


Fig. 15. *Leptoplastus stenotus*, all preserved in anthraconite. White scale bar: 2 mm. **A:** Cranidium, sample L125, loc. 6 (MGUH 33655). **B:** Cranidium, sample ATN-266, loc. 6 (MGUH 33657). **C:** Cranidium, sample ATN-266, loc. 6 (MGUH 33658). **D:** Cranidium, sample L125, loc. 6 (MGUH 33656). **E:** Pygidium, sample GM 1922-152, loc. 22 (MGUH 33659). **F:** Free cheek, sample GM 1922-152, loc. 22 (MGUH 33660). **G:** Free cheek, sample GM 1922-152, loc. 22 (MGUH 33661).

v 2015 *Leptoplastus bornholmensis* (Poulsen, 1923) – Rasmussen *et al.*, pp. 11–12, fig. 8.

Lectotype. External mould of cranidium MGUH 1964, originally illustrated by C. Poulsen (1923, pl. 1 fig. 11) and designated by Henningsmoen (1957). The lectotype was re-illustrated by Rasmussen *et al.* (2015, fig. 8).

Diagnosis (emended Henningsmoen 1957): Glabella elongate, parallel-sided and moderately vaulted. Well-developed preglabellar field. Very slightly oblique eye ridges, almost transverse. Midpoint of palpebral lobes opposite L2. Interocular cheeks from ¾ to as wide as glabella at eye-line and postocular cheeks from 1.6 to 1.8 times as wide as the occipital ring. Thorax with 16 thoracic segments having short pleural spines. Pygidium triangular, with four axial rings and at least three pairs of marginal spines.

Material. Two semi-complete specimens, 123 cranidia (including one with 13 and one with 14 contiguous thoracic segments), eight free cheeks, one hypostome (tentatively assigned) and seven pygidia. All material derives from locality 6. *Eurycare bornholmensis* co-occurs with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus* and *P. leptoplastorum?*.

Occurrence. Known only from the *L. crassicornis–L. angustatus* Zone on Bornholm (C. Poulsen 1923; this study), but see comparison with *E. explanatum* below.

Description: Cranidium 2 ½ times as wide as long, trapezoidal in overall outline. Glabella about 1.2 times as long as wide, parallel-sided, moderately vaulted, with up to three pairs of lateral glabellar furrows directed obliquely backwards-inwards (Figs 17D, G, I), but usually only two pairs are visible. Well-developed preglabellar field; anterior border form a swollen ridge along the anterior margin, being widest mesially. Mesial arc visible in frontal view. Eye ridges very slightly oblique, almost transverse. Midpoint of palpebral lobes situated opposite L2. Palpebral lobes slightly less than 1/3 as long (exsag.) as glabella (incl. occipital ring). Interocular cheeks from ¾ to as wide as glabella at eye-line (tr.). Postocular facial suture divergent sinuous. Postocular cheeks 1.6 to 1.8 times as wide as occipital ring; gently curving border furrow present, most deeply impressed centrally. Distinct occipital furrow. Elongate mesial tubercle on occipital ring seen in well preserved specimens (Fig. 17B). Fragmentary hypostome (tentatively assigned) oval in outline with entire posterior margin and strongly swollen median body overhanging posterior margin (median body lost during preparation; specimen not suited for illustration). Free cheek with rounded lateral margin showing flattened, moderately narrow border; posterior margin short. Stout genal spine situated far back, curving gently backwards and inwards (Fig. 16). The genal spine reminds of the one in *L. angustatus* but it is more sturdy, oval in cross-section and the spine base is broader and raised a little (Figs 16, 17E–F). Thorax with 16 segments, each provided with short pleural spines. The anterior 5 segments increase gently in width, the following segments taper rearwards. Pleural regions twice as wide as axis where the thorax is widest (excluding the short pleural spines). Pygidium triangular in outline and almost twice as wide as long. Axis consists of four rings in addition to anterior half ring and terminal piece; it occupies 0.3 or a little more of the total pygidial width at the anterior margin. At least three pairs of marginal spines (broken in all specimens).

Comparison. The cranidium of *E. bornholmensis* somewhat resembles the cranidium of *E. brevicauda* but has a more distinct preglabellar field and significantly wider (tr.) postocular cheeks. The pygidium of *E. bornholmensis* is more distinctly triangular in shape compared to the sub-semicircular and relatively broader pygidium in *E. brevicauda*. *Eurycare bornholmensis* differs from *L. neglectus* and *L. norvegicus* by having wider interocular and postocular cheeks and 16 thoracic segments. The long, curved genal spine of *E. bornholmensis* reminds of that in *L. angustatus*, but the free cheek of the latter has a much longer posterior margin and the spine and spine base are less sturdy.

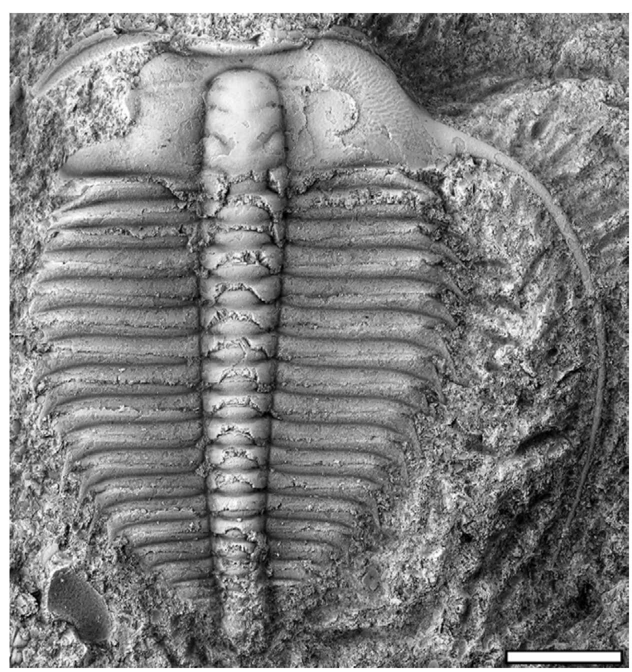


Fig. 16. *Eurycare bornholmensis*, almost complete specimen preserved in anthraconite from locality 6, sample ATN-329 (MGUH 33662). White scale bar: 3 mm. See also Fig. 17F.

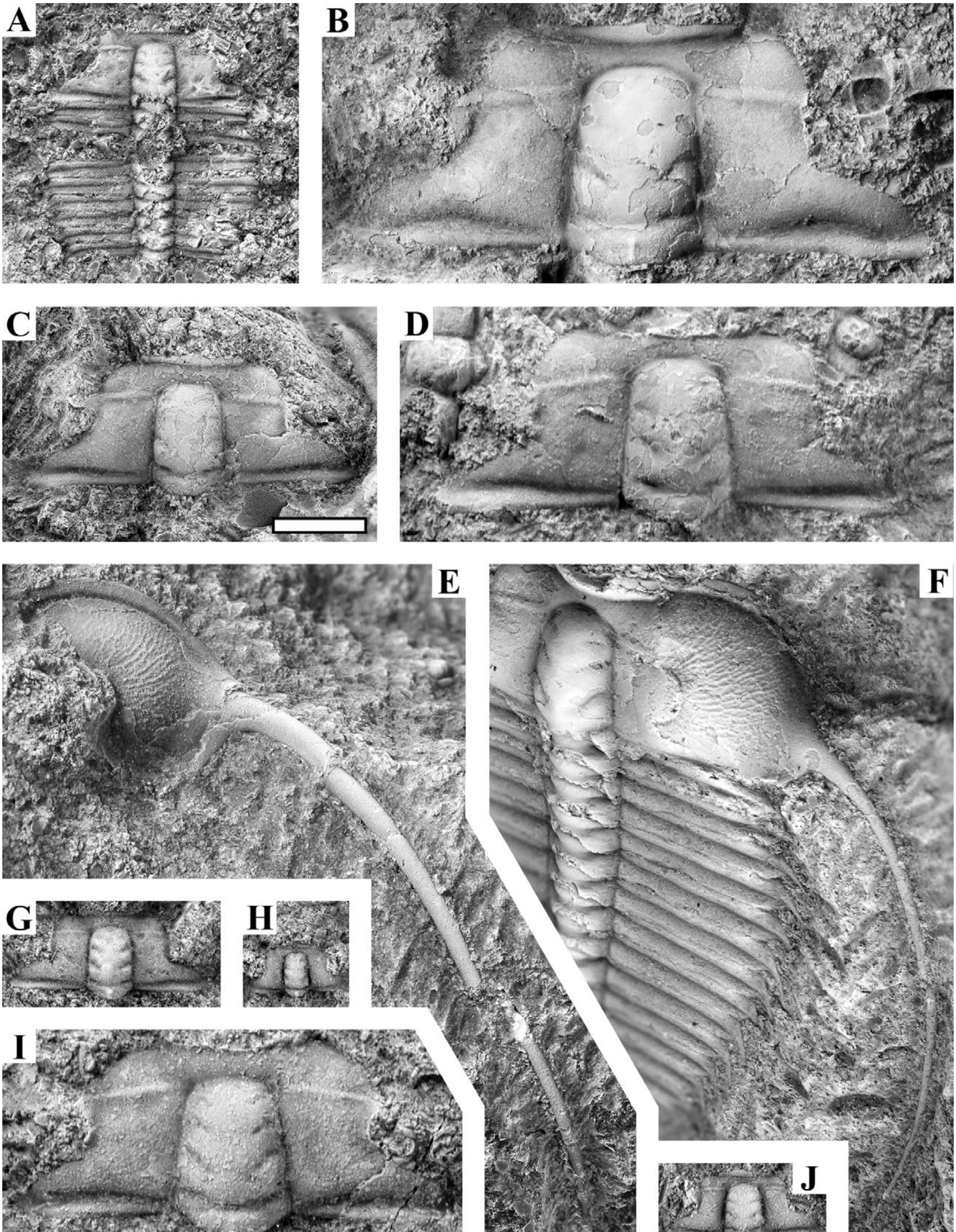


Fig. 17. *Eurycare bornholmensis*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A:** Cranidium with eight thoracic segments, sample ATN-136 (MGUH 33663). **B:** Cranidium, sample L126 (MGUH 33605). **C:** Cranidium, sample L126 (MGUH 33606). **D:** Cranidium, sample ATN-157 (MGUH 33665). **E:** Free cheek, sample ATN-251 (MGUH 33651). **F:** Free cheek, sideview, sample ATN-329 (MGUH 33662), the complete specimen is shown in Fig. 16. **G:** Small cranidium, sample ATN-154 (MGUH 33666). **H:** Juvenile cranidium, sample ATN-156 (MGUH 33653). **I:** Cranidium, sample ATN-156 (MGUH 33654). **J:** Small cranidium, sample ATN-306 (MGUH 33646).

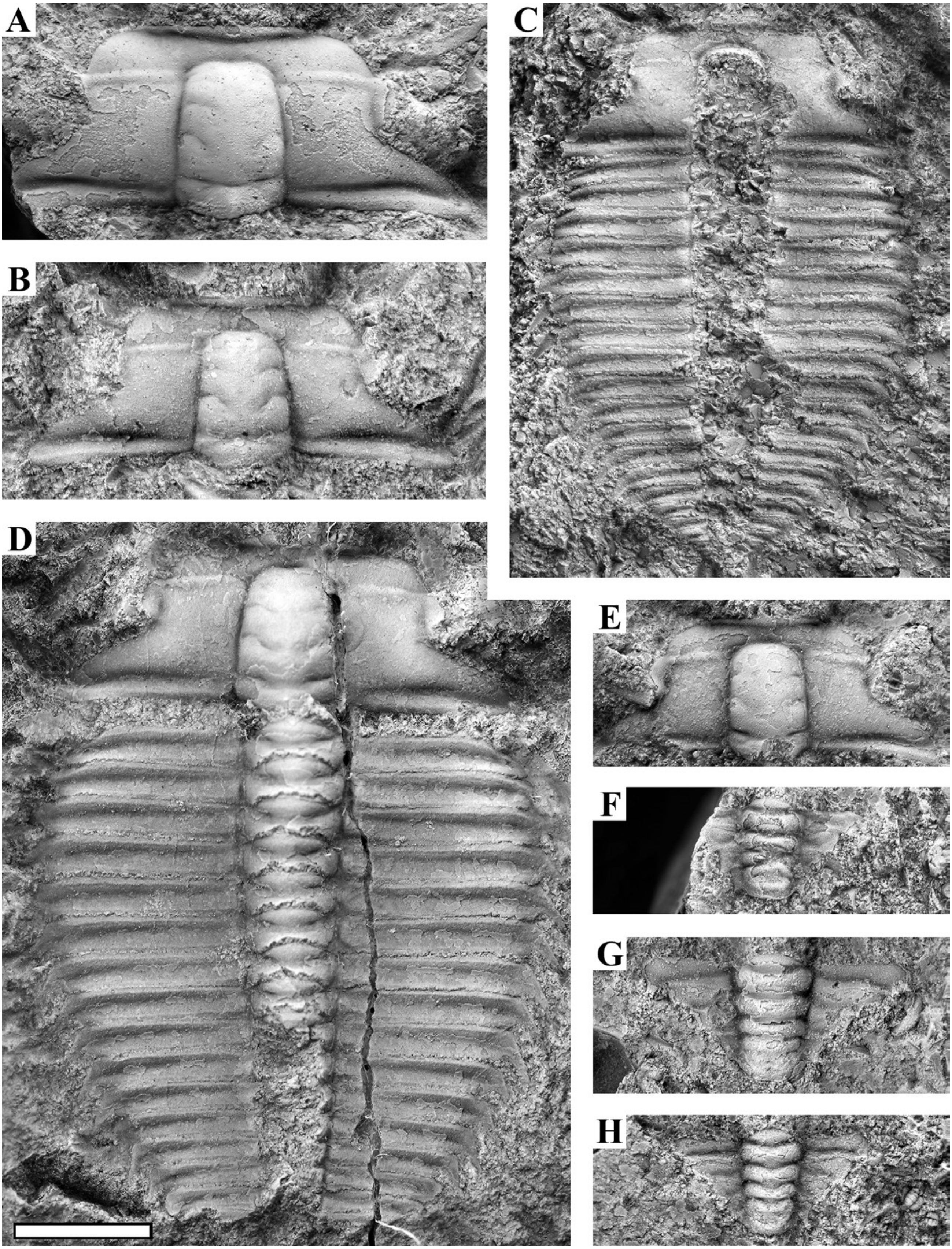


Fig. 18. *Eurycare bornholmensis*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A:** Cranidium, sample ATN-306 (MGUH 33647). **B:** Cranidium, sample ATN-248 (MGUH 33667). **C:** Almost complete specimen, sample ATN-136 (MGUH 33664). **D:** Almost complete specimen, sample ATN-120 (MGUH 33668). **E:** Cranidium, sample ATN-262 (MGUH 33598). **F:** Pygidium, sample ATN-306 (MGUH 33648). **G:** Pygidium, sample ATN-123 (MGUH 33554). **H:** Pygidium, sample ATN-304 (MGUH 33581).

The cranidium of *Eurycare intermedium* (regarding generic assignment, see Ahlberg *et al.* 2006) is quite similar to that of *E. bornholmensis*, but the glabella appears slightly wider and the postocular cheeks are narrower (tr.). In *E. intermedium,* the postocular cheek is thus *c.* 1.4 times as wide as the occipital ring (see Westergård 1944 and Ahlberg *et al.* 2006, fig. 6D) vs. 1.6 – 1.8 times as wide as the occipital ring in *E. bornholmensis*. The outline of the genal spine base also differs, being much broader in *E. bornholmensis,* and *E. intermedium* has >9, probably 12, thoracic segments (Westergård 1944), whereas *E. bornholmensis* has 16 thoracic segments.

The cranidium of *E. explanatum* is almost indistinguishable from that of *E. bornholmensis* but again appears to have slightly narrower (tr.) postocular cheeks (however, up to 1.63 times as wide as the occipital ring, see Henningsmoen 1957, pl. 16, fig. 5); they also seem to be marginally longer (exsag.), reflecting that the eyes are located slightly more forwards in the Norwegian form (centre of palpebral lobes opposite S2 vs. L2 in *E. bornholmensis*). Nonetheless, the differences are subtle and maybe these taxa should be separated only as subspecies. The number of thoracic segments in *E. explanatum* is unknown. The pygidium of a suspected *E. explanatum* illustrated by Henningsmoen (1957, pl. 16, fig. 4) has wider pleural fields than the pygidia of *E. bornholmensis* (Fig. 18F–H).

Remarks. C. Poulsen (1923) erected this species as a variant of 'C.' *neglecta* and described it as fairly common in the upper part of the '*Eurycare angustatum* Subzone'. It was transferred to *Leptoplastus* by Henningsmoen (1957). A large material is at hand, including a few almost complete specimens with 16 thoracic segments, suggesting a closer affinity with *Eurycare* as representatives of *Leptoplastus* have only up to 12 thoracic segments (Henningsmoen 1957). The many new cranidia also demonstrate that *E. bornholmensis* has wider postocular cheeks than most representatives of *Leptoplastus*, whereas the width of the interocular cheeks is intermediate between the two genera. The genal spine is stout like in other species of *Eurycare.* The presence of a well-developed preglabellar field is a trait shared with some species of *Leptoplastus.*

Eurycare brevicauda **Angelin, 1854**
Fig. 19A

1922 *Eurycare brevicauda* Angelin – Westergård, pp. 148–149, pl. IX, figs 11–12.
1957 *Eurycare brevicauda* Angelin 1854 – Henningsmoen, p. 179, pl. 2, fig. 19; pl. 4.
2006 *Eurycare brevicauda* Angelin – Ahlberg *et al*., fig. 5.
2015 *Eurycare brevicauda* Angelin 1854 – Rasmussen *et al*., p. 9, fig. 6G.
2017 *Eurycare brevicauda* Angelin 1854 – Rasmussen *et al*., p. 12, fig. 7A.

Lectotype. Not designated, but see remarks by Westergård (1922, p. 149) and Henningsmoen (1957).

Material. One small cranidium from locality 6. It is associated with common *E. latum*.

Occurrence. Known only from the *L. crassicornis–L. angustatus* Zone in Scandinavia (Henningsmoen 1957; Rasmussen *et al.* 2015). This is the first report from Bornholm.

Comparison. For comparison with *E. latum*, see that species. *Eurycare brevicauda* and *E. spinigerum* have identical cranidia and almost identical pygidia and are separated primarily by having different numbers of thoracic segments (14 in *E. brevicauda* vs. 12–13 segments in *E. spinigerum*). For this reason, the assignment of the single detached cranidium from Bornholm may be taken as tentative.

Eurycare latum **(Boeck, 1838)**
Fig. 19B–J

1904 *Eurycare latum* Boeck – Persson, pp. 513–517, pl. 8, figs 1–7.
1922 *Eurycare latum* (Boeck) – Westergård, p. 148, pl. IX, figs 7–10.
v 1923 *Eurycare latum* Boeck – C. Poulsen, pp. 32–33, pl. I, fig. 8.
1957 *Eurycare latum* (Boeck 1838) – Henningsmoen, pp. 181–182, pl. 4; pl. 16, figs 6–9.
1973 *Eurycare latum* (Boeck, 1838) – Schrank, pp. 819–820, pl. IV, figs 1–5.
2004 *Eurycare latum* (Boeck 1838) – Mischnik, pp. 110–111, pl. 2, fig. 8.
2017 *Eurycare latum* (Boeck, 1838) – Rasmussen *et al.*, p. 12, fig. 7B.

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Small cranidium PMO 56383a from Gamlebyen, Oslo, Norway; designated and illustrated by Henningsmoen (1957, pl. 16, fig. 9).

Material. 156 cranidia including one with six contiguous thoracic segments, 23 free cheeks and 18 pygidia; all from locality 6. The species mostly occurs alone (in profusion), but in a few samples it is associated with rare specimens of *E. brevicauda*, *L. crassicornis* and *L. ovatus*.

Occurrence. Common in the *L. crassicornis–L. angustatus* Zone in Norway and Sweden (Westergård 1947; Ahlberg *et al.* 2006; Rasmussen *et al.* 2015, 2016, 2017),

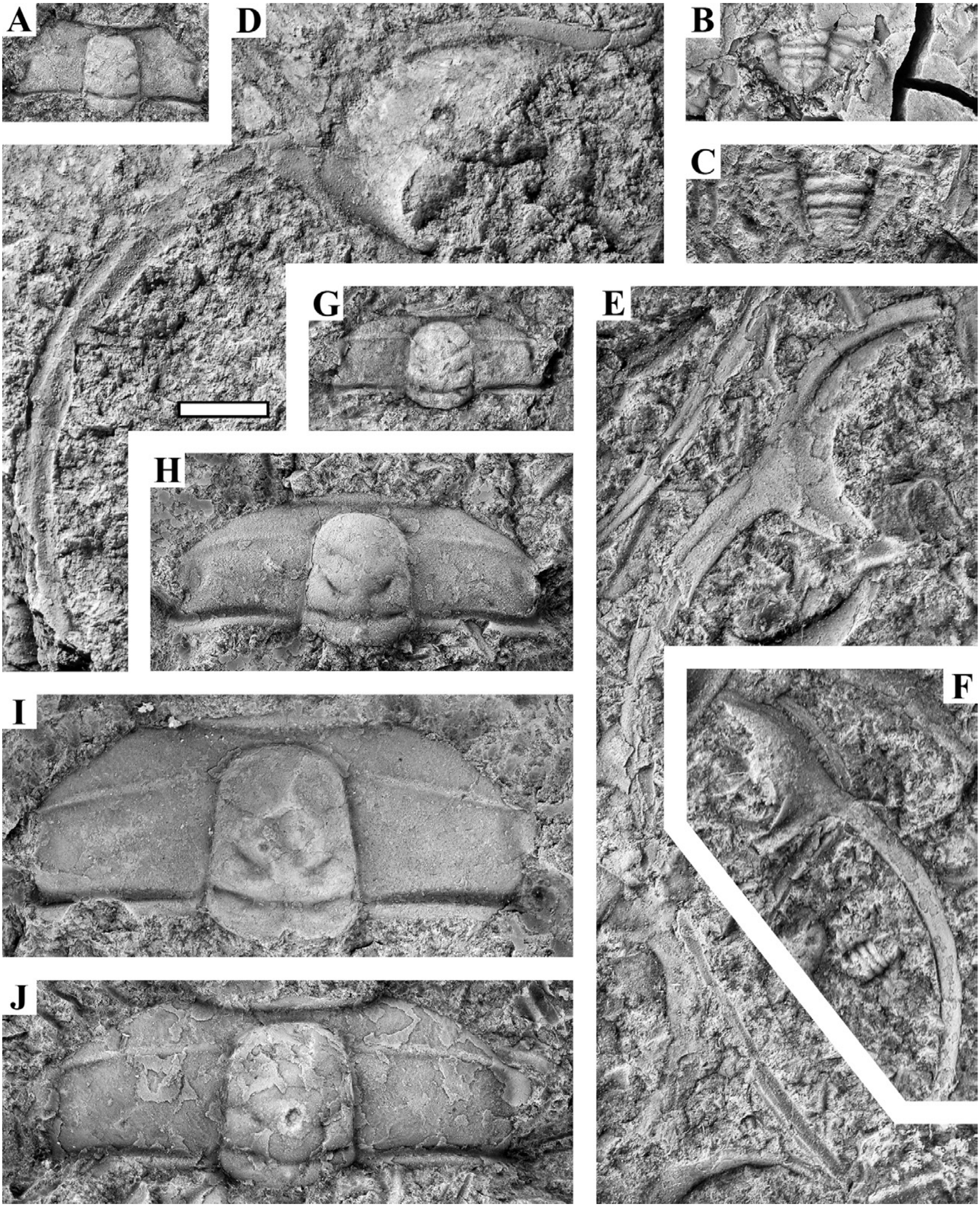


Fig. 19. *Eurycare brevicauda* (**A**) and *Eurycare latum* (**B–I**), all preserved in anthraconite from locality 6. White scale bar: 3 mm; please note that these specimens are shown at a lower magnification than used for most of the illustrations. **A:** Small cranidium, sample ATN-282 (MGUH 33669). **B:** Pygidium, sample GM 1922-138B (MGUH 33670). **C:** Pygidium, sample ATN-114 (MGUH 33671). **D:** Free cheek, sample ATN-272 (MGUH 33373). **E:** Free cheek, sample ATN-114 (MGUH 33672). **F:** Free cheek, sample ATN-159 (MGUH 33675). **G:** Cranidium, sample ATN-280 (MGUH 33677). **H:** Cranidium, sample ATN-272 (MGUH 33674). **I:** Cranidium, sample ATN-279 (MGUH 33678). **J:** Cranidium, sample ATN-159 (MGUH 33676).

and also mentioned from England (Taylor & Rushton 1971). Rasmussen *et al.* (2015) recorded it also from the *L. raphidophorus* and *L. neglectus* zones at Slemmestad, Norway. On Bornholm, *E. latum* occurs only in the basal part of the *Leptoplastus* Superzone, distinguished as the *E. latum* Subzone by C. Poulsen (1923). The co-occurrence with rare *L. crassicornis* and *L. ovatus* is suggestive of the *L. crassicornis–L. angustatus* Zone. At locality 6, *E. latum* is very common in a lower horizon, *c.* 5 cm thick, separated by coarse-grained unfossiliferous anthraconite, also *c.* 5 cm thick, from an overlying fine-grained limestone containing a more diverse *L. crassicornis–L. angustatus* Zone fauna without *E. latum*.

Comparison. Eurycare latum is readily distinguished by its unusually wide fixed cheeks. However, the cranidium can resemble that of *E. brevicauda* and *E. spinigerum*, but the interocular cheeks of those species are only as wide as glabella at eye-line, while *E. latum* has interocular cheeks that are 1 ⅕ to 1 ⅖ times as wide as the adjacent glabella. The free cheek of *E. latum* resembles that of *L. crassicornis;* for comparison, see the latter species.

Genus *Ctenopyge* Linnarsson, 1880
Type species: *Olenus (Sphaerophthalmus) pecten* Salter, 1864, designated by Vogdes (1890).

Subgenus *Ctenopyge* (*Ctenopyge*) Linnarsson, 1880
Type species: As for genus.

***Ctenopyge (Ctenopyge) affinis* Westergård, 1922**
Fig. 20

1922 *Ctenopyge affinis* n. sp. [*partim*] – Westergård, pp. 157–158, pl. XII, figs 1–6, 14; non pl. XII, figs 7–13 [= *Ctenopyge gracilis*]; non pl. XII, fig. 15 [= *C. pecten*?].

v non 1923 *Ctenopyge affinis* Westergård – C. Poulsen, pp. 41–42, pl. 2, fig. 5 [= *C. magna* n. sp.].

1957 *Ctenopyge affinis affinis* Westergård 1922 – Henningsmoen, pp. 200–201, pl. 5; pl. 19, fig. 22.

Lectotype. Cranidium SGU 327 from Andrarum, southern Sweden, figured by Westergård (1922, pl. XII, fig. 1) and designated by C. Poulsen (1923).

Material. 222 cranidia and 15 free cheeks. The far majority of the material is from locality 6, but a few specimens derive from locality 7. *Ctenopyge affinis* co-occurs with *C. magna* n. sp., *C. ahlbergi, Ctenopyge* sp. 1, *P. minor* and *S. alatus*.

Occurrence. Upper part of the *Peltura acutidens–Ctenopyge tumida* Zone, Scandinavia (Henningsmoen 1957; Høyberget & Bruton 2012). The report from the lower part of the *Peltura scarabaeoides* Zone (Westergård 1947) probably refers to *C. gracilis*. On Bornholm, the species has been found only in the upper part of the *P. acutidens–C. tumida* Zone.

The *C. affinis* Zone *sensu* Terfelt *et al.* (2008) was amalgamated with the *C. tumida* Zone by Høyberget & Bruton (2012) since *C. affinis* is rare in most regions of Scandinavia and, hence, not suitable as an index fossil. This approach is followed here, but on Bornholm a subzone characterized by *C. affinis, C. ahlbergi* and *C. magna* n. sp. actually seems to be developed in the upper part of the *P. acutidens*–*C. tumida* Zone (see section on 'Olenid zonation').

Comparison. Ctenopyge affinis is separated from *C. gracilis* by having a broader, tapering glabella, most distinctly so in larger specimens, with a less inflated anteroglabella. *Ctenopyge affinis* also reaches larger maximum sizes. The free cheek of *C. affinis* has a less curving spine that follows the general course of the cheek margin and the posterior cheek margin is very short in comparison with the free cheeks of *C. gracilis*.

For comparison with *C. magna* n. sp., see that species. The cranidium of the co-occurring *C. ahlbergi* has a much more inflated anteroglabella, the front of the cranidium is therefore significantly higher and the rear part of glabella also shows a characteristic distinct constriction in front of the occipital furrow and deep lateral pits accentuate the occipital furrow, so well-preserved specimens are readily separated from *C. affinis*.

Ctenopyge oelandica is based on a single juvenile cranidium from the *P. acutidens–C. tumida* Zone at Degerhamn, Öland (Westergård 1922). The tiny cranidium is characterized by a parallel-sided glabella and unusually strongly curving eye ridges, reflecting that the eyes are situated far back. Buchholz (2000) illustrated a larger cranidium from erratics in Germany, also assigned to *C. oelandica*. The latter cranidium overall looks like the holotype, but it is relatively slightly less wide (ontogenetic change?), and therefore the eye ridges are shorter. The German cranidium resembles several of the smaller to medium-sized cranidia here assigned to *C. affinis* (e.g. Fig. 20Ø), but in all specimens from Bornholm the eyes are situated more anteriorly and thus the eye ridges curve less strongly rearwards. However, this feature exhibits some variation (e.g. Fig. 20Q vs. Y). Additional material of *C. oelandica* is needed to constrain its variation range.

Without complete specimens at hand it is impossible to discuss *C. rushtoni*, described by Clarkson *et al.* (2004).

Remarks. Henningsmoen (1957) recognized two subspecies of *C. affinis*, viz. *C. a. affinis* (larger and with a distinctly tapering glabella) and *C. a. gracilis* (smaller and with an almost parallel-sided glabella). *Ctenopyge gracilis* was treated at species level by Clarkson *et al.* (2004) and we also prefer to rank *C. gracilis* and *C. affinis* as separate species.

The sparse material identified as *C. affinis* by C. Poulsen (1923) is here assigned to *C. magna* n. sp. and a smaller form, which is much more common on Bornholm, is identified as *C. affinis*. Strangely, this common species was not treated by C. Poulsen (1923) (15 cranidia of *affinis s.str.* are registered in the 1902-samples containing "*C. affinis*" discussed by C. Poulsen, see Appendix 1). *Ctenopyge affinis* shows ontogenetic changes and juvenile cranidia are rather *C. gracilis*-like having a parallel-sided, slender glabella. However, the anteroglabella is less inflated than in equal-sized *C. gracilis* cranidia, although we note that the anteroglabella exhibits considerable variation in shape and degree of inflation in *C. affinis* (e.g. Fig. 20A, F, I; juvenile condition illustrated in Fig. 20L–O, Ø). Larger cranidia have a clearly tapering glabella, which is the salient distinguishing character of *C. affinis* in comparison with *C. gracilis.* It appears also to be a consistent character of *C. affinis* cranidia to have a weakly impressed pair of S3 indentations situated close to the axial furrows, visible in dorsal view; this feature is not so distinctive in *C. gracilis*, maybe due to the stronger inflation of the anteroglabella, concealing the S3 in dorsal view.

The Scanian holotype of *C. affinis* has a comparatively little inflated antero-glabella (Westergård 1922, pl. XII, fig. 1), whereas the second Scanian specimen illustrated by Westergård (ibid. pl. XII, fig. 2) is very similar to most of the similar-sized cranidia from Bornholm. The free cheeks in the material at hand also comply with the description of *affinis* cheeks provided by Westergård (1922).

***Ctenopyge (Ctenopyge) ahlbergi* Clarkson, Ahlgren & Taylor, 2004**

Fig. 21

? 2003 *Ctenopyge* cf. *affinis* – Terfelt, fig. 4L–N.

2004 *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp. – Clarkson *et al.*, pp. 125–127, textfigs 11; 12A, B, E, F; 13–14.

Holotype. Complete juvenile specimen LO 8976T from Blomberg, Kinnekulle, Västergötland, illustrated by Clarkson *et al.* (2004, textfig. 11A).

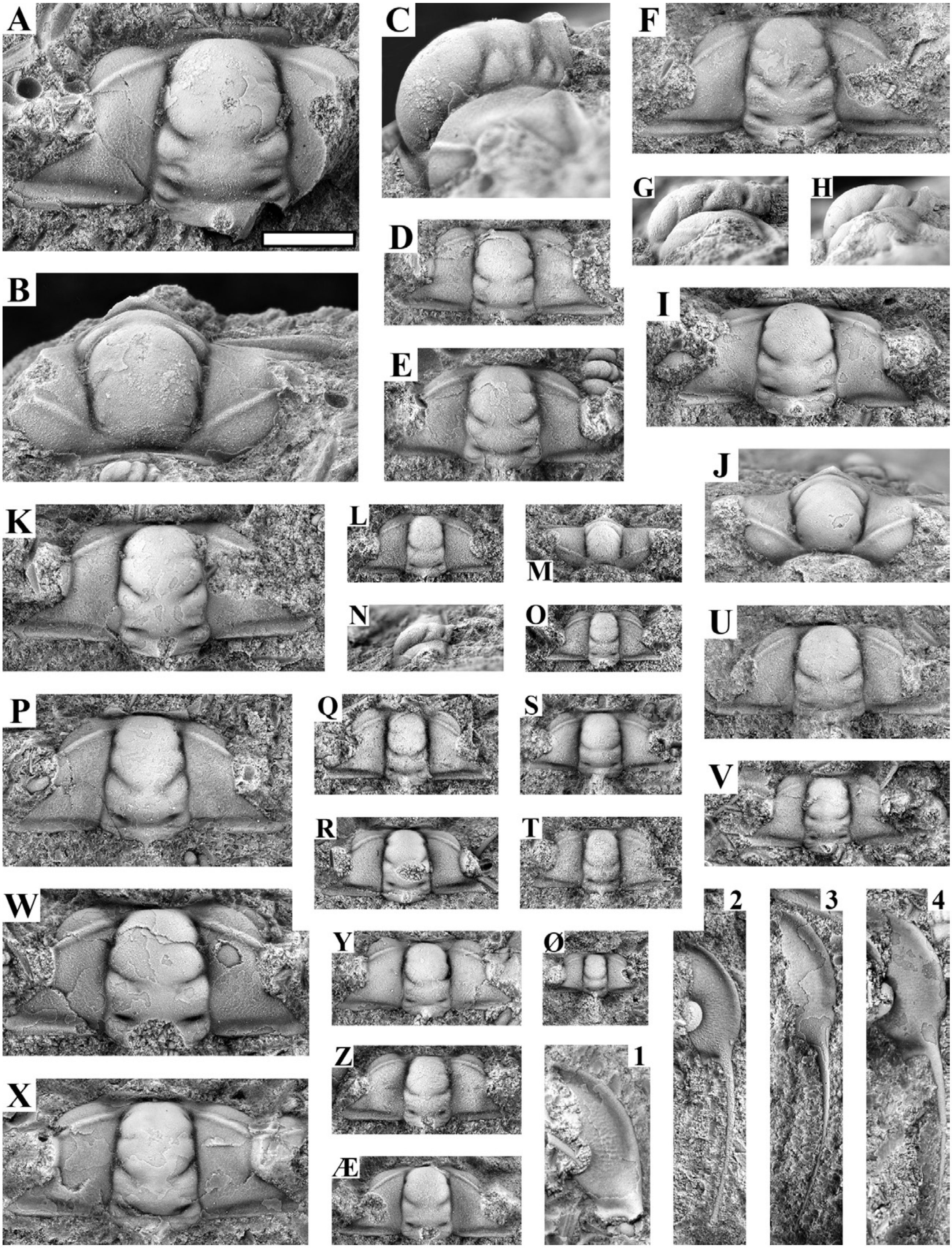
Material. 38 cranidia incl. two external moulds, and seven free cheeks. Most of the specimens are from locality 6, but a few derive from locality 7. Several disarticulated thoracic segments probably also belong to this species. *Ctenopyge ahlbergi* co-occurs with *C. affinis, C. magna* n. sp., *Ctenopyge* sp. 1, *S. alatus* and *P. minor.*

Occurrence. Known only from the *P. acutidens*–*C. tumida* Zone in Västergötland and on Bornholm (Clarkson *et al*., 2004, this study). The cranidia from Västergötland identified as *C.* cf. *affinis* by Terfelt (2003) resemble *C. ahlbergi* but may alternatively represent *C. gracilis.*

Comparison. The cranidium is very distinctive and cannot be confused with any of the associated species. The deep lateral impressions in the occipital furrow, the outline of the deep S1 and the distinctly inflated anteroglabella creating a high front of the cranidium are distinctive traits. The closest relative may be *C. gracilis* that also has a rather inflated anteroglabella, but this species has only a shallow or no indentation of the rear part of glabella. The pleural spines on the thoracic segments also have a different outline in these species, being flattened in *C. ahlbergi* (for details, see Clarkson *et al.* 2004).

Remarks. This is the first report of this species outside Västergötland; regarding identification, see especially

▼ **Fig. 20.** *Ctenopyge affinis*, all preserved in anthraconite from locality 6; the free cheeks may alternatively belong to *C. magna* n. sp. In order to save space the cheeks are rotated clockwise relative to life position. Note the non-tapering glabella in juveniles and smaller cranidia. White scale bar: 2 mm. **A–C:** Large cranidium, dorsal, frontal and side views, sample ATN-117 (MGUH 33679). **D:** Cranidium, sample ATN-117 (MGUH 33680). **E:** Cranidium, sample ATN-130 (MGUH 33688). **F–G:** Large cranidium, dorsal and side view, sample ATN-134 (MGUH 33690). **H–J:** Cranidium with unusually inflated anteroglabella, dorsal, frontal and side views, sample ATN-130 (MGUH 33689). **K:** Large cranidium, sample ATN-222 (MGUH 33703). **L–N:** Small cranidium, dorsal, frontal and side views, sample ATN-116 (MGUH 33706). **O:** Small cranidium, sample ATN-117 (MGUH 33681). **P:** Large cranidium, sample ATN-113 (MGUH 33711). **Q:** Cranidium, sample ATN-103 (MGUH 33719). **R:** Cranidium, sample ATN-134 (MGUH 33691). **S:** Cranidium, sample ATN-147 (MGUH 33723). **T:** Cranidium, sample ATN-146 (MGUH 33725). **U:** Large cranidium, sample ATN-222 (MGUH 33704). **V:** Cranidium, sample ATN-113 (MGUH 33712). **W:** Large cranidium, sample ATN-113 (MGUH 33713). **X:** Large cranidium, ATN-146 (MGUH 33726). **Y:** Cranidium, sample ATN-117 (MGUH 33682). **Z:** Cranidium, sample ATN-113 (MGUH 33714). **Æ:** Cranidium, sample ATN-134 (MGUH 33692). **Ø:** Juvenile cranidium, note the occipital spine, sample ATN-134 (MGUH 33693). **1:** Free cheek, sample ATN-146 (MGUH 33727). **2:** Free cheek, sample ATN-103 (MGUH 33720). **3:** Free cheek, sample ATN-116 (MGUH 33707). **4:** Free cheek, sample ATN-132 (MGUH 33730).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the largest Swedish specimen illustrated by Clarkson *et al.* (2004, fig. 11C–D), clearly showing the characteristic cranidium albeit in a slightly oblique view. The cranidia at hand are significantly larger than the material originally described from Västergötland.

***Ctenopyge (Ctenopyge) bisulcata* (Phillips, 1848)**
Fig. 22A–B

1922 *Ctenopyge bisulcata* (Phillips) [*partim*] – Westergård, pp. 159–160, pl. XII, figs 19–20, 22–25, non fig. 21 [= *C. tumida*].
v 1923 *Ctenopyge bisulcata* Phillips – C. Poulsen, pp. 46–47, pl. 2, fig. 4.
1957 *Ctenopyge (Ctenopyge) bisulcata* (Phillips 1848) – Henningsmoen, pp. 203–204, pl. 5.
1973 *Ctenopyge (Ctenopyge) bisulcata* (Phillips, 1848) – Schrank, pp. 827–828, pl. VIII, fig. 9–16, 17?, 18; pl. IX, figs 1–2.
2016 *Ctenopyge (Ctenopyge) bisulcata* (Phillips 1848) – Rasmussen *et al*. pp. 10–11, fig. 5.

For a more comprehensive list of synonymy, see Rasmussen *et al*. (2016).

Lectotype. Original of Phillips (1848, fig. 1 on p. 55) from the White-Leaved Oak Shales (Merioneth Series) of the Malvern Hills, United Kingdom, was selected as 'holotype' by Stubblefield (1938). The whereabouts of the type specimen is currently unknown (Morris 1988).

Material. Six cranidia preserved in shale from locality 6 (no associated fauna) and locality 7 (co-occurring with common *C. fletcheri*).

Occurrence. Ctenopyge bisulcata was coined as index fossil for a lower subzone of the *P. scarabaeoides* Zone by Henningsmoen (1957), later elevated to zonal rank by Terfelt *et al.* (2008). This interval is assigned here to the *P. scarabaeoides* Zone following Nielsen *et al.* (2020). The sparse material of *C. bisulcata* from Bornholm derives from the "upper part of the *P. scarabaeoides* (Sub)Zone" according to C. Poulsen (1923). However, the species occurs near the base of the zone at locality 7 and the section exposed at locality 6 only represents the lower half of the *P. scarabaeoides* Zone (cf. Nielsen *et al.* 2018). Hence, *C. bisulcata* is characteristic of the lower part of the *P. scarabaeoides* Zone on Bornholm as elsewhere in Scandinavia. The species is known also from Great Britain and Canada (Nova Scotia) (Henningsmoen 1957).

Comparison. The cranidium resembles that of *C. fletcheri* but is wider. In *C. bisulcata,* the postocular cheeks are thus about 1.5 times as wide as the occipital ring vs. about as wide as the occipital ring in *C. fletcheri*. The cranidium of *C. linnarssoni* is also rather wide, but in *C. bisulcata* the eye ridges are oblique and not transverse as in *C. linnarssoni*. Furthermore, in *C. bisulcata,* the postocular cheeks are divergent sinuous while they are divergent convex in *C. linnarssoni* (terminology according to Henningsmoen 1957, fig. 2).

Remarks. Peltura scarabaeoides appears earlier than *C. bisulcata* and correlation of the lower boundary of the now abandoned *C. bisulcata* Subzone with the base of the *P. scarabaeoides* Zone (Henningsmoen 1957) was an inaccurate approximation (for details, see Nielsen *et al*. 2020).

***Ctenopyge (Ctenopyge) fletcheri* (Matthew, 1901)**
Fig. 22C–G

1922 *Ctenopyge directa* Lake [*partim*] – Westergård, pp. 158–159, pl. 12, fig. 17.
v 1923 *Ctenopyge directa* Lake – C. Poulsen, pp. 45–46, pl. III.
1957 *Ctenopyge (Ctenopyge) fletcheri* (Matthew 1901) – Henningsmoen, pp. 205–207, pl. 5; pl. 22, figs 1–6.
1973 *Ctenopyge (Ctenopyge) fletcheri* (Matthew, 1901) – Schrank, p. 833, pl. X, figs 16–20.
2017 *Ctenopyge (Ctenopyge) fletcheri* (Matthew, 1901) – Rasmussen *et al*., pp. 10–11, figs 6A–B.

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Free cheek figured by Matthew (1901, pl. IV, fig. 7d and 1903, pl. XVII, fig. 7d) from Band C3b, Escasonie Shore, East Bay, Nova Scotia, designated by Henningsmoen (1957).

Material. 41 cranidia and 15 free cheeks from localities 6 and 7. The species is associated with cranidia of *Peltura* sp. (probably *P. scarabaeoides*), *C. bisulcata* and *T. humilis.*

Occurrence. Peltura scarabaeoides Zone in Scandinavia, Great Britain, Poland and Canada (Henningsmoen 1957; Żylińska 2001, 2002). *Ctenopyge fletcheri* – under the name *C. directa* – was recorded from the *C. tumida* and *P. scarabaeoides* subzones at localities 6 and 7 by C. Poulsen (1923). However, the report from the *P. acutidens*–*C. tumida* Zone seems to be an error; no museum material derives from that level.

Comparison. See *C. linnarssoni* and *C. bisulcata*.

Remarks. The discussed material was assigned to *C. directa* by C. Poulsen (1923). However, that species has interocular cheeks that are as wide as or just slightly wider than the glabella at eye-line (Henningsmoen 1957; see also Westergård 1922, pl. XII, fig. 16). The material at hand has interocular cheeks that are about ¾ as wide (tr.) as the glabella at eye-line and which fits with the description of *C. fletcheri* (see Henningsmoen

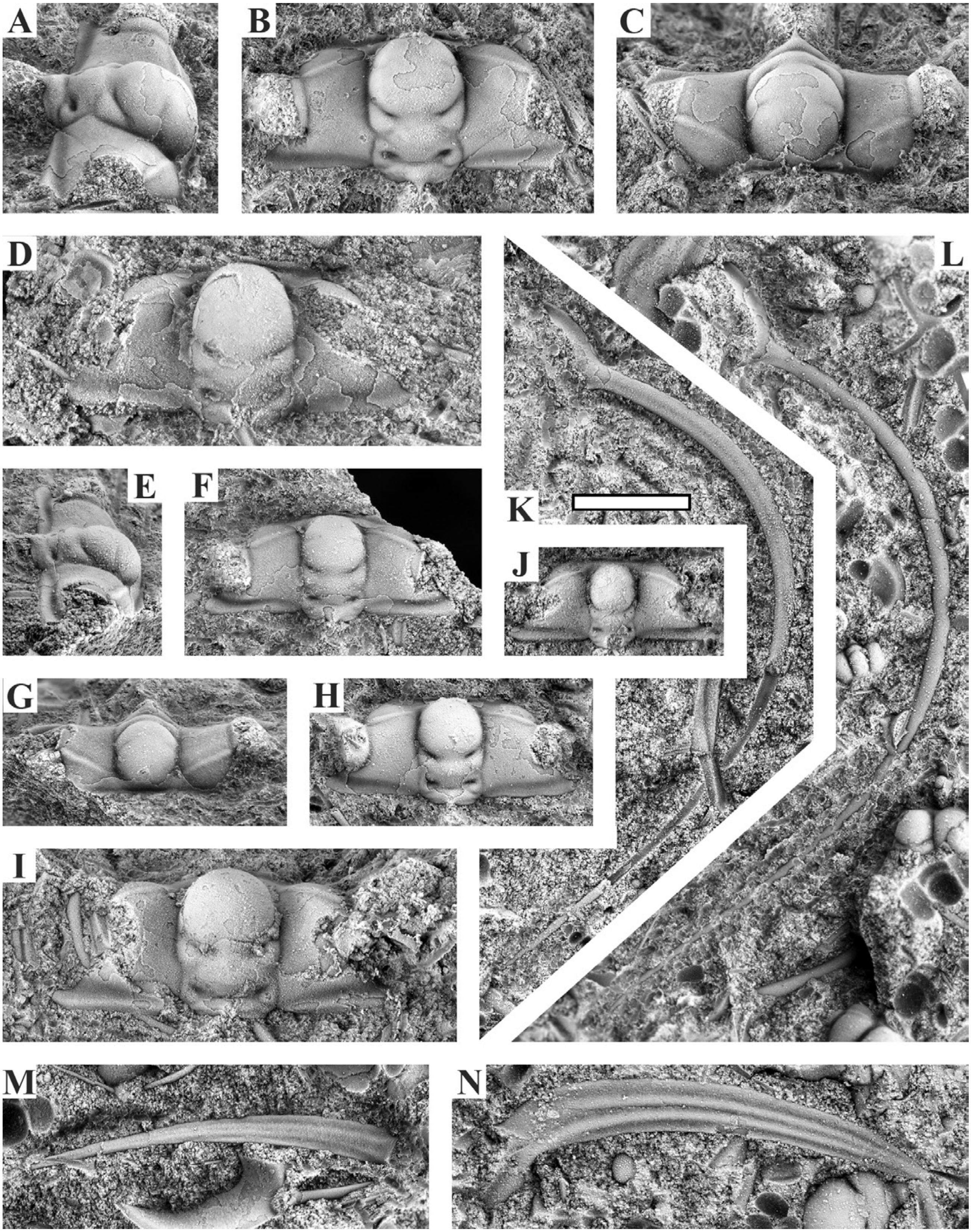


Fig. 21. *Ctenopyge ahlbergi*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A–C:** Cranidium, different views, sample ATN-117. (MGUH 33683). **D:** Largest cranidium found, sample ATN-205. (MGUH 33733). **E–G:** Cranidium, different views, sample ATN-117. (MGUH 33684). **H:** Cranidium, sample ATN-134. (MGUH 33694). **I:** Cranidium, sample ATN-132. (MGUH 33731). **J:** Cranidium, sample ATN-134. (MGUH ¤33695). **K:** Free cheek, sample ATN-117. (MGUH 33685). **L:** Free cheek, sample ATN-134. (MGUH 33696). **M:** Pleural spine of thoracic segment, sample ATN-134. (MGUH 33697). **N.** Pleural spine of thoracic segment, sample ATN-113. (MGUH 33715).

1957). The characteristic free cheeks with long, flattened spines also match *C. fletcheri* as described and illustrated by Henningsmoen (1957).

Ctenopyge (Ctenopyge) linnarssoni Westergård, 1922

Fig. 23

1922 *Ctenopyge Linnarssoni* n. sp. – Westergård, pp. 162–163, pl. XIII, figs 2–5.

v 1923 *Ctenopyge Linnarssoni* Westergård – C. Poulsen, p. 45, pl. 1, fig. 17.

1957 *Ctenopyge (Ctenopyge) linnarssoni* Westergård 1922 – Henningsmoen, p. 207, pl. 5; pl. 22, fig. 8.

1973 *Ctenopyge (Ctenopyge) linnarssoni* Westergård, 1922 – Schrank, pp. 830–831, pl. IX, figs 13–17.

?2003 *Ctenopyge (Ctenopyge) linnarssoni* Westergård, 1922 – Terfelt, p. 413, fig. 4O.

2016 *Ctenopyge linnarssoni* – Ahlberg *et al.*, p. 498, figs 4, 6C.

2017 *Ctenopyge (Ctenopyge) linnarssoni* Westergård, 1922 – Rasmussen *et al.*, p. 11, fig. 6C.

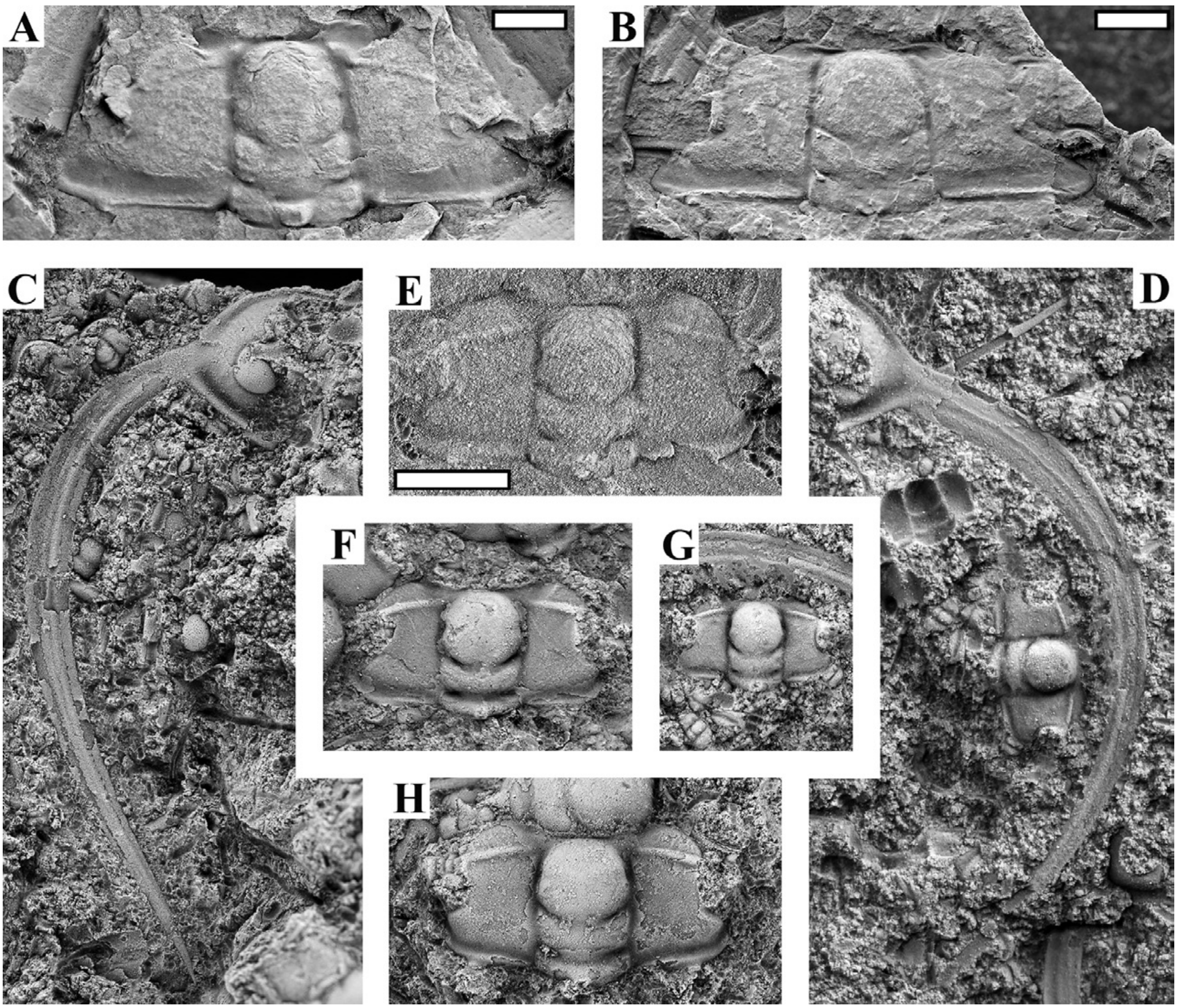


Fig. 22. *Ctenopyge bisulcata* (**A–B**) and *Ctenopyge fletcheri* (**C–H**). White scale bars: 2 mm; please note that the cranidia of *C. bisulcata* are shown at a smaller magnification. **A:** Cranidium preserved in shale from loc. 6, sample GM 1922-142R (MGUH 33735). **B:** Cranidium preserved in shale from loc. 6, specimen MGUH 1974 (previously illustrated by C. Poulsen 1923, pl. II, fig. 4). **C:** Free cheek preserved in anthraconite, loc. 6, sample GM 1881-337A (MGUH 33736). **D:** Free cheek preserved in anthraconite, loc. 6, specimen MGUH 1978a. The specimen is located on a bedding surface in sample GM 1881-337B illustrated by C. Poulsen (1923, pl. III). This surface also includes the specimens illustrated here as F and G. **E:** Cranidium preserved in shale, loc. 7, sample GM 1922-143 (MGUH 33738). **F–G:** Two cranidia preserved in anthraconite, loc. 6, specimens MGUH 1978b–c. **H:** Cranidium preserved in anthraconite, loc. 6, sample GM 1881-337A (MGUH 33737).

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Cranidium SGU 356 from Andrarum, southern Sweden, figured by Westergård (1922, pl. XIII, fig. 2) and designated by Henningsmoen (1957).

Material. 38 cranidia and two free cheeks. Twelve of these cranidia derive from sample L17, found in the Læså stream at Limensgade (localities 8A–8B). Two cranidia and one free cheek are labelled "between Hjulmagergård and Vasagård" and another two cranidia are labelled "from the Læså area" (unspecified). These specimens are probably from locality 6 like most of the remaining material. *Ctenopyge linnarssoni* co-occurs with *C. pecten*, *C. tenuis*, *C. teretifrons*, *P. scarabaeoides* and *T. humilis* in the studied samples.

Occurrence. Ctenopyge linnarssoni is characteristic for the upper part of the *P. scarabaeoides* Zone and has been reported from Scandinavia, Poland, Great Britain and Canada (Westergård 1922; Henningsmoen 1957; Żylińska 2001; Terfelt *et al.* 2008; Rasmussen *et al.* 2017). The report from the *P. lobata* ['*longicornis*'] Zone on Bornholm (C. Poulsen 1923) is an error, see 'Discussion and conclusions'.

Comparison. The cranidium of *C. linnarssoni* reminds of that of *C. fletcheri,* but the latter has oblique eye ridges, whereas they are transverse or only slightly oblique in *C. linnarssoni. Ctenopyge fletcheri* also has narrower fixed cheeks, the interocular cheek is only ¾ as wide as the glabella at eye-line, while the postocular cheeks are about as wide as the occipital ring. *Ctenopyge linnarssoni* has interocular cheeks as wide as the glabella at eye-line, and the postocular cheeks are almost 1½ times as wide as the occipital ring. For comparison with *C. bisulcata*, see that species.

Ctenopyge (Ctenopyge) magna **n. sp.**

Fig. 24

v 1923 *Ctenopyge affinis* Westergård – C. Poulsen, pp. 41–42, pl. 2, fig. 5.

Derivation of name: Latin *magna*, meaning great or large, alluding to the extraordinary size of this *Ctenopyge* species.

Holotype. Cranidium MGUH 1975 from locality 6, Læså, Bornholm, originally illustrated as *C. affinis* by C. Poulsen (1923, pl. 2, fig. 5); here re-illustrated in Fig. 24A–C.

Diagnosis: Large *Ctenopyge* species. Glabella unusually broad, tapering, most pronouncedly so in the largest specimens; occipital furrow deeply impressed laterally with low swellings on the occipital ring behind the impressions; S1 deeply impressed laterally, oblique, not transglabellar; glabellar front truncate; eye ridges oblique; midline of eye situated opposite S1; moderately long spine on occipital ring; interocular cheek *c.* half as wide as the adjacent glabella at eye line (slightly narrower in large specimens, slightly wider in small specimens); postocular cheek triangular and ¾ as wide (tr.) as the occipital ring in large specimens; free cheek assumed belonging to this species of *affinis*-type with long, only gently curving spine almost forming a contuinuation of the course of the lateral margin; posterior margin short, straight.

Material. 41 cranidia, two free cheeks (tentatively assigned) and one hypostome. Most of the material is from locality 6, but a few specimens derive from locality 7. *Ctenopyge magna* n. sp. co-occurs with *C. affinis*, *C. ahlbergi*, and *S. alatus*. A single sample contains a cranidium of *C. magna* n. sp. in association with *T. humilis, C. tenuis* and *P. scarabaeoides*.

Occurrence. The material at hand derives almost exclusively from the upper part of the *P. acutidens*–*C. tumida* Zone; one specimen (Fig. 24I) is from the *P. scarabaeoides* Zone. The new species is currently known only from Bornholm.

Description: Large olenid, the holotype cranidium is 20 mm wide across the postocular cheeks and the largest cranidium found must originally have been ≈25 mm wide, judging from the with of the occipital ring (Fig. 24E). The cranidium is subtrapezoidal in overall outline. Glabella occupies a large proportion of the cranidium; it tapers fairly strongly, most pronouncedly so in the largest specimens. Glabellar front truncate; anteroglabella not as strongly inflated as in *C. ahlbergi* and *C. gracilis* and in sagittal profile descends evenly to the preglabellar furrow (Fig. 24C, O); glabella also moderately convex transversely; highest point behind S1. Three pairs of lateral glabellar furrows of which S1 is developed as elongate deep lateral impressions, directed obliquely inwards-backwards, reaching the axial furrows abaxially, but not united across the glabella. S2 and S3 are much shallower, but always visible; they are both directed inwards at an almost right angle to the axial furrows. Occipital ring wider than the rear part of glabella; it carries a fairly long spine (preserved in only two specimens, Fig. 24F) and a small mesial node is located immediately in front of the raised spine base (Figs 24E–F). The occipital furrow is laterally strongly accentuated by a pair of oblong deep pits; the furrow is shallow mesially, so the occipital ring appears as an integrated continuation of the glabella. A pair of elongate low swellings are seen on the occipital ring

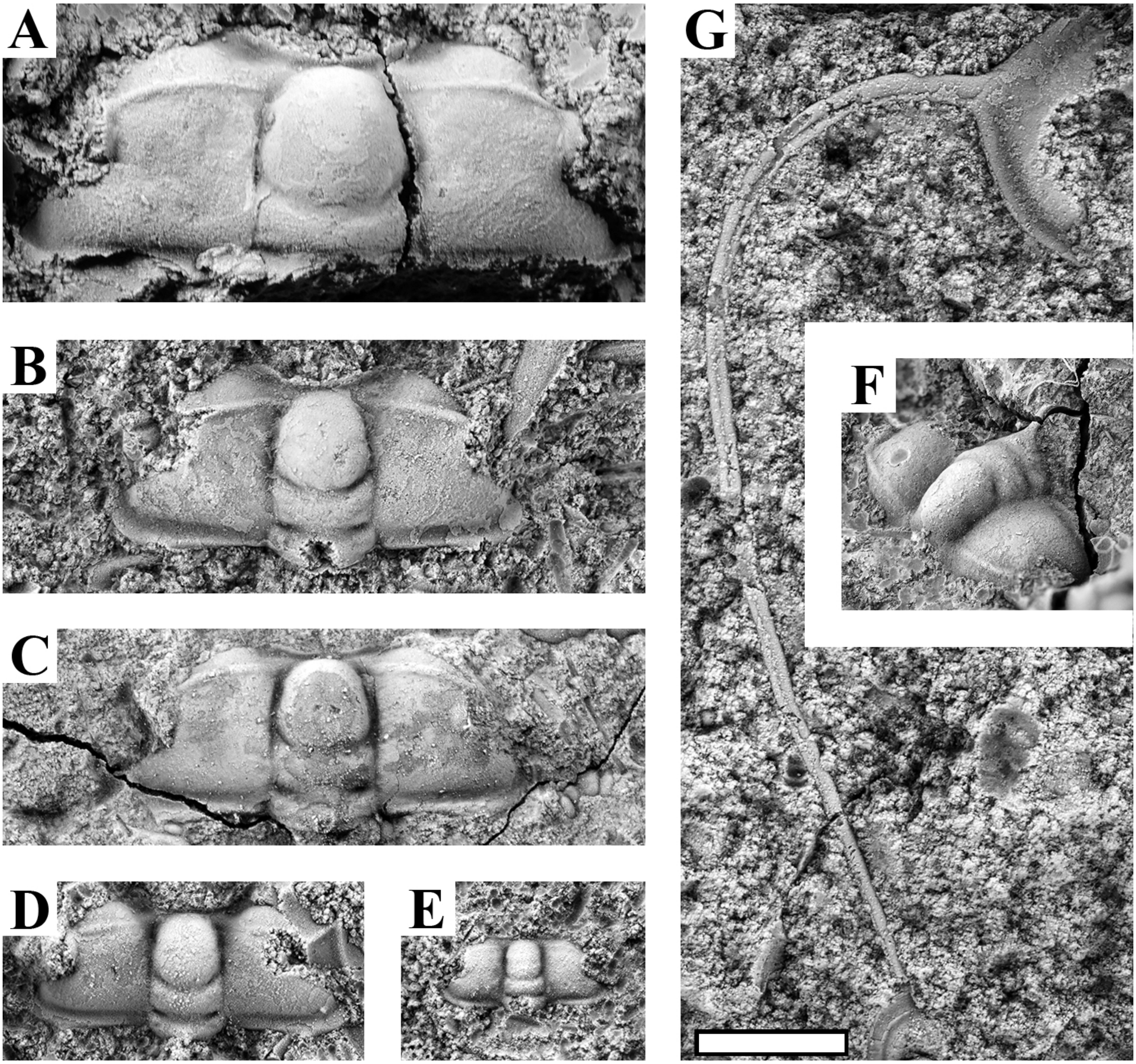
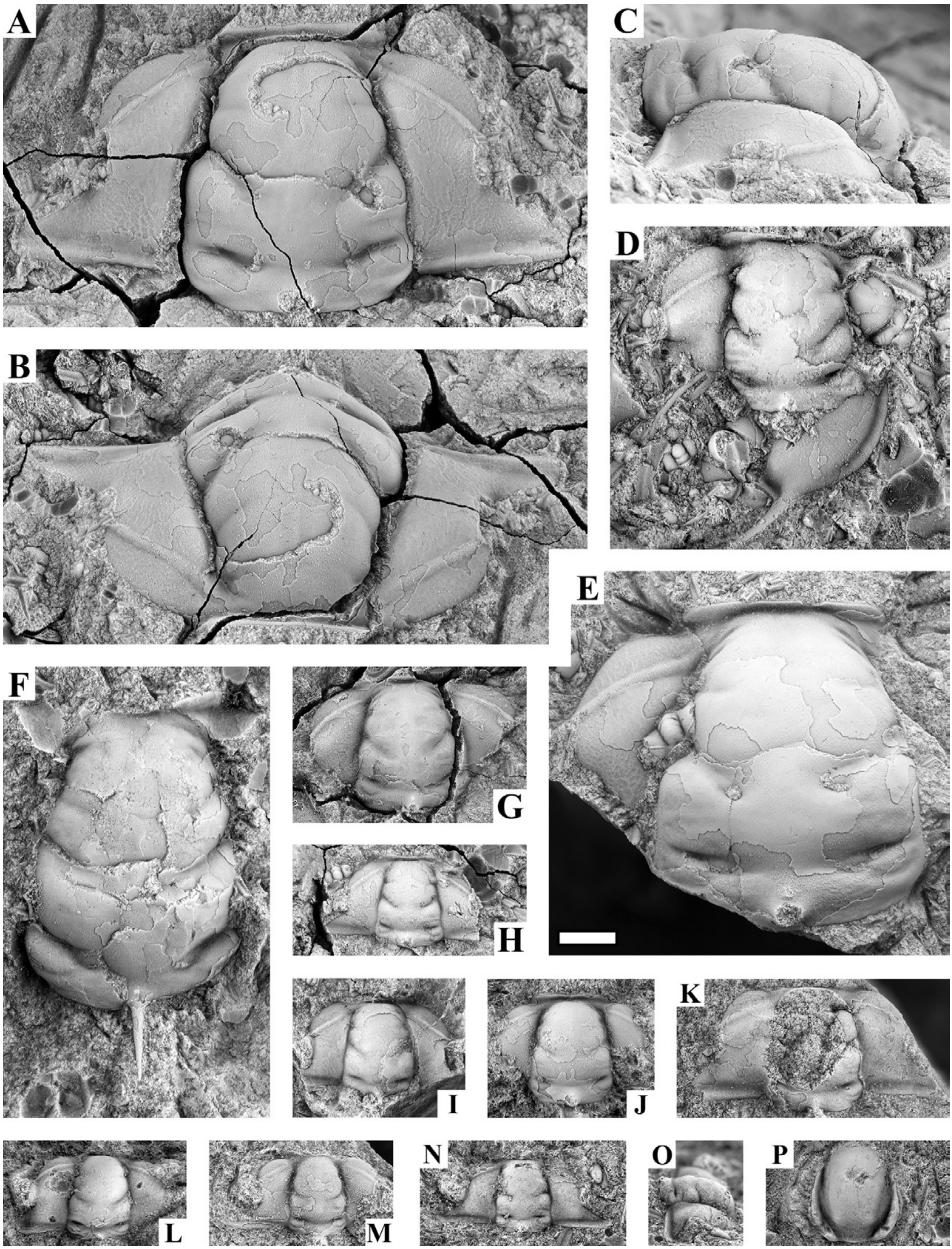


Fig. 23. *Ctenopyge linnarssoni*, all preserved in anthraconite. White scale bar: 2 mm. **A:** Cranidium, locs 8A–B, sample L17 (MGUH 33739). **B:** Cranidium, loc. 8A–B, sample L17 (MGUH 33740). **C:** Cranidium MGUH 1970, loc. 6; previously illustrated by C. Poulsen (1923 pl. 1, fig. 17). **D:** Cranidium, locs 8A–B, sample L17 (MGUH 33741). **E:** Juvenile cranidium, Læså area unspecified [probably loc. 6], sample GM 1877-2000 (MGUH 33745). **F:** Cranidium with occipital spine partially preserved, loc. 6, sample GM 1922-142I (MGUH 33746). **G:** Free cheek, Læså area between Hjulmagergård and Vasagård [probably loc. 6], sample GM 1871-666 (MGUH 33758).

▼ **Fig. 24.** *Ctenopyge magna* n. sp., all preserved in anthraconite from locality 6. Note the less pronounced tapering of the glabella in the smaller cranidia. White scale bar: 2 mm; please observe that the specimens are shown at a lower magnification than used for most of the illustrations in this paper. **A–C:** Different views of large cranidium, MGUH 1975, previously illustrated by C. Poulsen (1923, pl. II, fig. 5). **D:** Dislocated free cheek, assumed belonging to this species, and cranidium, sample ATN-116 (MGUH 33709). **E:** Fragmentary cranidium, sample ATN-147, the largest specimen at hand. A small cranidium of *C. affinis* in the axial furrow is kept as curiosum (MGUH 33724). **F:** Fragmentary cranidium with intact occipital spine. Note the small occipital node in front of the spine. Sample ATN-137 (MGUH 33759). **G:** Medium sized cranidium, sample GM 1902-1212 (MGUH 33760). **H:** Small cranidium, sample GM 1902-1209 (MGUH 33761). **I:** Small cranidium, the only one found in the *P. scarabaeoides* Zone, sample GM 1922-142S (MGUH 33764). **J:** Small cranidium, sample GM 1902-1209 (MGUH 33762). **K:** Medium sized cranidium, sample ATN-113 (MGUH 33716). **L.** Small cranidium, sample ATN-103 (MGUH 33721). **M:** Small cranidium, tentatively assigned, sample ATN-117 (MGUH 33686). **N–O:** Different views of small cranidium, tentatively assigned, sample ATN-116 (MGUH 33709). **P:** Hypostome, sample ATN-134 (MGUH 33698).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posterolaterally of the oblong deep pits in the occipital furrow; these swellings are separated by shallow furrows from the remainder of the occipital ring. Similar very shallow furrows with the same orientation are sometimes visible also on the rear part of glabella in front of the deep occipital pits, i.e. between the occipital furrow and S1 (see e.g. Fig. 24A, C). Axial furrows deep, gently undulating with indentations at the occipital furrow and each of the lateral glabellar furrows. Glabella is delimited anteriorly by a deep preglabellar furrow coincident with the anterior border furrow; no preglabellar area. Frontal area extremely narrow, consisting only of the narrow, upturned anterior border. Anterior margin of cranidium is gently concave in anterior view, truncate in dorsal view. Midline of palpebral lobes situated opposite S1; interocular cheek only *c.* half as wide as glabella at eye line (slightly narrower in large specimens and a little wider in small specimens); it is very slightly convex, sloping gently towards the palpebral lobes. The palpebral lobes are broken in most specimens, but apper to be rather narrow (tr.); they are delimited by wide and shallow but clearly defined palpebral furrows. Eye ridges distinct, directed obliquely backwards-outwards from the axial furrows and usually appear slightly curved in dorsal view. Postocular cheeks triangular in overall outline, comparatively long (exsag,) and short (tr.), gently down-sloping outwards. Posterior border furrow wide, rather shallow, running parallel with the posterior cranidial margin, but terminating adaxially a little short of the axial furrows. Posterior border moderately convex (exsag.), almost straight (tr.), widening slightly and getting less convex abaxially. Anterior sections of the facial suture are directed outwards-forwards for a short stretch in front of the eyes, then turn inwards, curving gently forwards-inwards and intersect the anterior cranidial margin level with maximum glabellar width (excl. of the occipital ring); the posterior sections of the facial suture are straight, diverging backward at an angle of *c.* 60° to the sagittal line. In some cranidia the surface of the cheeks exhibits a reticulate pattern (e.g. 24A, E). Nearly all cranidia are more or less fragmentary and compacted, suggesting that the test is thin and fragile.

Free cheek associated with cranidium (Fig. 24D) is assumed belonging to this species. It appears very similar to the free cheeks attributed to *C. affinis* (Fig. 20:1–4) having a presumably rather straight spine almost continuing the course of the lateral margin, a narrow border petering out close to the spine base and a short, straight posterior margin.

An unusually large hypostome (Fig. 24P) likely belongs to the new species.

Pygidium unknown.

Comparison. The cranidium of *C. magna* n. sp. somewhat resembles that of the co-occurring *C. affinis* but the glabella is significantly more 'bulbous' and tapers more in similar-sized specimens. *Ctenopyge magna* n. sp. also attains considerably larger maximum size. It is, however, difficult to separate small cranidia of *C. magna* n. sp. with a less tapering and narrower glabella (Fig. 24L–O) from those of *C. affinis* and identification remains tentative, based on the degree of glabella inflation.

Remarks. Several free cheeks (e.g. Fig. 20:1–4) have been assigned to *C. affinis* but may alternatively represent small *C. magna* n. sp.; compare with Fig. 24B.

C. Poulsen (1923) described ten large cranidia identified as *C. affinis* from five museum samples collected in 1902, which according to him also contain *S. alatus* [in C. Poulsen's terminology a mislabel for *T. humilis*] and fragments of *C. pecten* (?). The samples, numbered GM 1902-1208 to GM 1902-1212, are now intensively cracked, but a total of six cranidia and five external moulds of cranidia of *C. magna* n. sp. were recorded. Sample GM 1902-1208 has been impregnated with epoxy and the fossil content can no longer be observed. The samples also contain *S. alatus* [*s.str.*], *C. ahlbergi* and *C. affinis* [*s.str.*] and it is probably the latter that was misidentified as *C. pecten* (?) by C. Poulsen. In any case, these samples are not from the *P. scarabaeoides* Zone.

***Ctenopyge (Ctenopyge) pecten* (Salter, 1864)**
Fig. 25A–F

1922 *Ctenopyge pecten* (Salter) [*partim*] – Westergård, pp. 160–161, pl. XII, figs 26?, 27–28, 30–33; pl. XIII, fig. 1; non pl. XII, fig. 29 [= *C. tenuis*].
? 1922 *Ctenopyge affinis* n. sp. [*partim*] – Westergård, pp. 157–158, pl. XII, fig. 15.
Non 1923 *Ctenopyge pecten* Salter – C. Poulsen, pp. 42–44, pl. II, figs 1–3 [= *C. tenuis*].
1947 *Ctenopyge pecten* (Salter) – Westergård, pl. 3, fig. 12.
1957 *Ctenopyge (Ctenopyge) pecten* (Salter 1864) – Henningsmoen, pp. 208–209; pl. 2, fig. 18?; pl. 5; pl. 22, figs 9–10.
1959 *Ctenopyge (Ctenopyge) pecten* (Salter, 1864) – C. Poulsen, p. O264, fig. 195:7.
1973 *Ctenopyge (Ctenopyge) pecten pecten* (Salter, 1864) – Schrank, pp. 828–829, pl. IX, figs 3–6.
2004 *Ctenopyge (Ctenopyge) pecten pecten* (Salter 1864) – Mischnik, p. 116, pl. 4, figs 6, ?7–8.
For further synonymy, see Henningsmoen (1957).

Type material. Not designated. Syntypes BGS GSM 8960, 8981, ?8914-19 are from the White-Leaved Oak Shales, Malvern, United Kingdom (Morris 1988).

Material. 21 cranidia. Three cranidia are labelled 'between Hjulmagergård and Vasagård' (locality 6?), one is from 'the Læså area' (also most likely locality 6), two are from 'Cementen' (i.e. ice-rafted material, Øleå), while the remaining cranidia are from locality 6. *Ctenopyge pecten* co-occurs with *C. linnarssoni*, *C. tenuis*, *C. teretifrons*, *P. scarabaeoides* and *T. humilis* in the studied samples.

Occurrence. *Ctenopyge pecten* occurs comparatively infrequently in the *P. scarabaeoides* Zone and has been reported from Scandinavia, Great Britain and Canada (Westergård 1922; Henningsmoen 1957; Terfelt *et al.* 2008; Høyberget & Bruton 2012). It occurs at the same stratigraphic level on Bornholm.

Comparison. The cranidium of *C. pecten* reminds of that of *C. tenuis*, but the eyes are situated further back so the postocular cheeks are shorter (exsag.) and typically also longer (tr.). The free cheeks has a more strongly curving and presumably longer genal spine than *C. tenuis* and the location of the eye incision should also differ, but so far this inference has not been verified. See also 'comparison' with *C. tenuis* below.

Remarks. The material assigned to *C. pecten* by C. Poulsen (1923) represents *C. tenuis* (see V. Poulsen 1963) which is common in the *P. scarabaeoides* Zone on Bornholm. However, *C. pecten s.str.* is also present although much more sparsely. Not all cranidia of *C. pecten* have as wide (tr.) and gracile postocular cheeks as those illustrated by Westergård (1922 pl. XII, figs 30–31) and some approaches the additional specimens he illustrated (*ibid*., pl. XII, figs 26–27) with shorter (tr.) and slightly longer (exsag.) postocular cheeks. The latter two cranidia illustrated by Westergård were synonymized with *C. tenuis* by V. Poulsen (1963), but we consider them as within the range of variation of *C. pecten*, whereas another cranidium illustrated by Westergård (1922, pl. XII, fig, 29) clearly belongs to *C. tenuis*.

***Ctenopyge (Ctenopyge) tenuis* Poulsen, 1963**
Figs 26–27

1922 *Ctenopyge pecten* (Salter) [*partim*] – Westergård, pl. XII, fig. 29.
v 1923 *Parabolina longicornis* Westergård [*partim*] – C. Poulsen, p. 31; non textfig. 9 [= *P. lobata lobata*].
v 1923 *Ctenopyge pecten* Salter – C. Poulsen, pp. 42–44, pl. II, figs 1–3.
v 1963 *Ctenopyge (Ctenopyge) pecten tenuis* n. subsp. – V. Poulsen, pp. 1–9, figs 1a–c.
1973 *Ctenopyge (Ctenopyge) pecten tenuis* V. Poulsen, 1963. – Schrank, pp. 829–830, pl. IX, figs 7–12; pl. X, figs 12, 13?.

Holotype. Incomplete thorax with pygidium (MGUH 1973) and external mould of the same specimen (MGUH 1972), figured by C. Poulsen (1923, pl. 2, figs 2–3) and V. Poulsen (1963, figs 1a–b). The holotype and matching external mould are refigured here in Figs 26N and 27D.

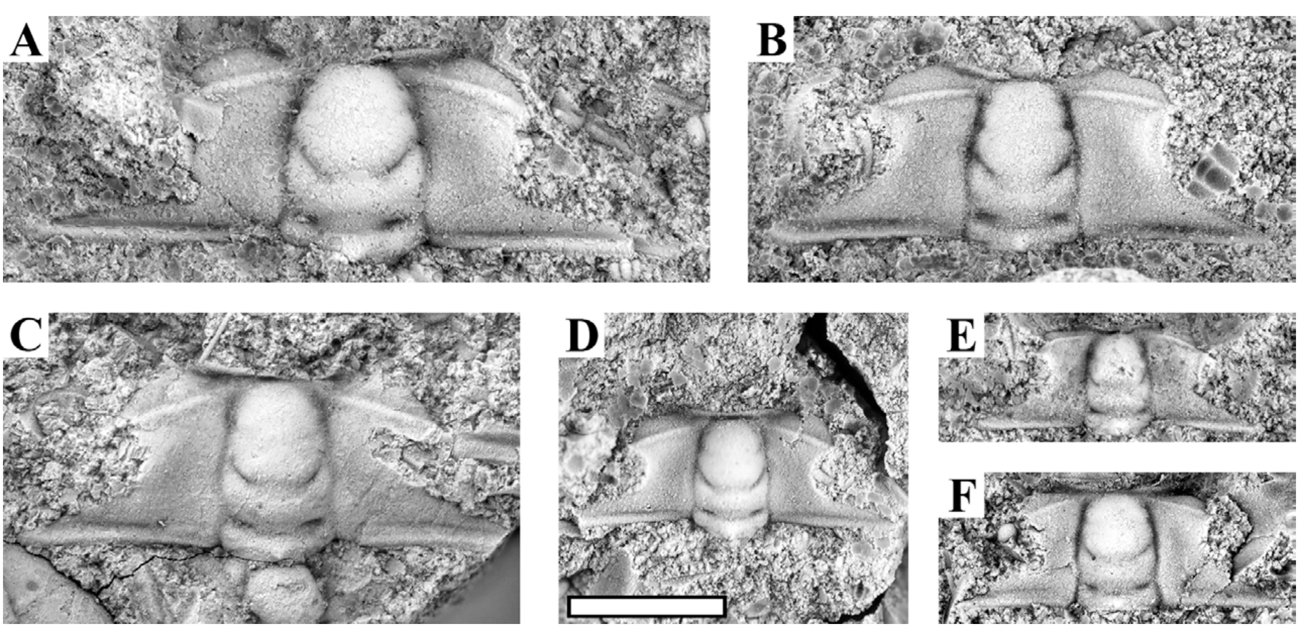


Fig. 25. Cranidia of *Ctenopyge pecten*, all preserved in anthraconite. B and C are labelled 'Cementen, Øleå', the remaining specimens are from locality 6. White scale bar: 2 mm. **A:** Sample L43 (MGUH 33767). **B:** Sample GM 1874-28 (MGUH 33771). **C:** Sample GM 1871-655 (MGUH 33772). **D:** Sample GM 1922-142I (MGUH 33749). **E:** Sample L52 (MGUH 33773). **F:** Sample GM 1874-27 (MGUH 33774).

Material. 327 cranidia, seven free cheeks, one thorax with 4–5 contiguous segments and 24 pygidia with up to nine attached thoracic segments. One cranidium was found in sample L17 at Limensgade (localities 8A–8B), 20 cranidia and one free cheek are labelled 'Cementen' (i.e. ice-rafted material, Øleå), while all other material derives from locality 6. C. Poulsen (1923) listed *C. tenuis* [as *C. pecten*] also from locality 7, but no museum material of the species is at hand from that locality. *Ctenopyge tenuis* co-occurs with *C. linnarssoni*, *C. pecten*, *C. teretifrons*, *P. scarabaeoides* and *T. humilis* in the studied samples.

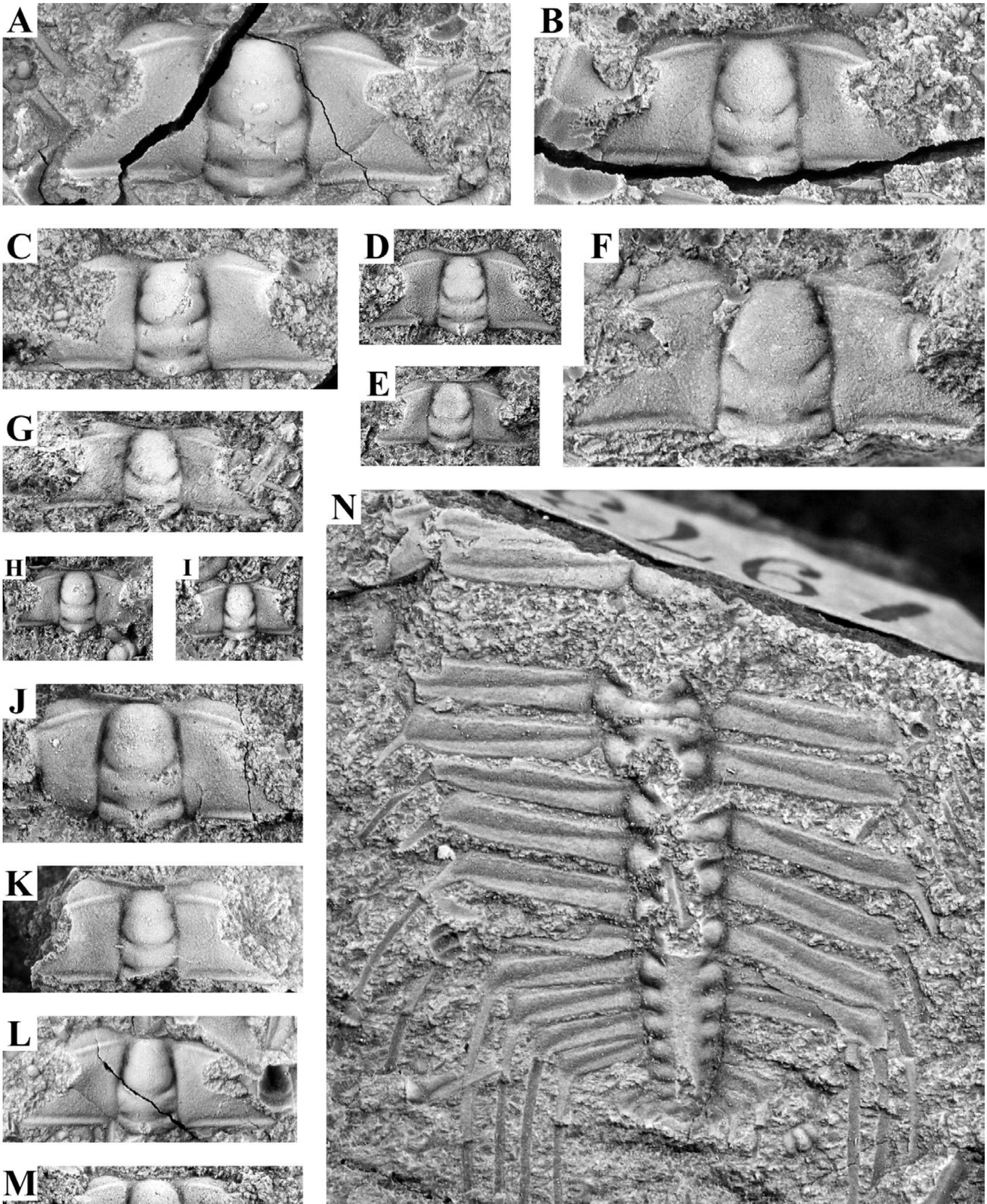
Occurrence. Peltura scarabaeoides Zone on Bornholm and in Sweden (V. Poulsen 1963; present study). *Ctenopyge tenuis* does not range into the *P. lobata* [*'longicornis'*] Zone as reported by C. Poulsen (1923) (see 'Discussion and conclusions').

Diagnosis (new): A *Ctenopyge pecten*-like species with almost parallel-sided glabella; S1 oblique, distinctly impressed abaxially, shallow mesially; S2 and S3 short, indistinct; eye ridges slightly oblique; centres of palpebral lobes opposite L2; interocular cheeks about three-fourths as wide as glabella at eye line in adult specimens; postocular cheeks on average *c.* 1.4 times as wide as occipital ring; postocular facial suture diverges rearwards-outwards at an angle of 50–60º from sagittal line; free cheeks with long rounded spine, curving gently, short straight posterior lateral margin, and markedly longer, gently convex anterior lateral margin; thorax with long flattened pleural spines; pleural region of thorax (excluding spine) up to two times as wide as the axis; pygidium with 7-8 axial rings in addition to the articulating half ring and terminal piece; long axial spine; pleurae (not united with each other?) with long flattened pleural spines.

Supplementary description: For a general description, see V. Poulsen (1963). Glabella almost parallel-sided with three pairs of lateral glabellar furrows, of which S1 is well-impressed laterally and shallow mesially whereas S2 and S3 are indistinct, short and not transglabellar. The shape of the anteroglabella varies from being slightly trapezoidal, tapering forwards with truncate front in some specimens (e.g. Fig. 26F), to more parallel-sided with rounded front in other specimens (e.g. Fig. 26J). Slightly oblique eye ridges; rear edge of palpebral lobe roughly level with S1, so midline of palpebral lobes level with L2. Interocular cheeks are *c.* ¾ as wide as the glabella at eye-line in adult specimens; the ratio varies between 0.73–0.84, averaging 0.76 (n = 7). The interocular cheeks are relatively narrower in small cranidia less than 1.5 mm long; here the corresponding width varies between 0.55–0.73 and averages 0.65 (n=4). Postocular cheeks rather variable in width (tr.) irrespective of cranidial size; in measured specimens the width varies from 1.24 to 1.66 times the width of the occipital ring, averaging 1.39 (n= 13). Postocular facial suture sinuous, diverging backwards at an angle of 50–60º from sagittal line, which is an important distinguishing feature. Free cheek has a long, moderately curving and slender spine. Thorax consists of >9 segments, widest across the middle segments, tapering backwards in the posterior part, all with long, flattened pleural spines. The axis constitutes about ⅕ of the total width of the thorax (excluding spines) where the thorax is widest. The pygidium is rounded to semi-triangular in outline. At least the anterior six pygidial segments are provided with long marginal spines. The axis is slightly tapering and consists of 7–8 segments in addition to the articulating half ring and terminal piece. Axial rings nos 5–7 provide a base for a long axial spine. For further details, see V. Poulsen (1963).

Comparison. Ctenopyge tenuis is distinguished from *C. pecten* by the angle of the postocular facial suture relative to the sagittal axis. In *C. tenuis,* this angle is between 50–60º vs. 70º–80º in *C. pecten* (with a few specimens showing 65º), so overall the cranidium of *C. pecten* is wider. The genal spine seems to be only gently curving in *C. tenuis* versus strongly curving in *C. pecten*. Besides, in *C. tenuis* the thoracic axis constitutes slightly more than 1/5 of the total thoracic width (where the thorax is widest, excluding spines), while

▼ **Fig. 26.** *Ctenopyge tenuis*, all preserved in anthraconite and from locality 6 unless otherwise stated. White scale bar: 3 mm. **A:** Cranidium MGUH 1971, previously illustrated by C. Poulsen (1923, pl. II, fig.1). **B:** Cranidium, sample GM 1922-142I (MGUH 33747). **C:** Cranidium, sample GM 1922-142I (MGUH 33754). **D:** Small cranidium, sample GM 1922-142A (MGUH 33777). **E:** Small cranidium, sample GM 1881-1804; no information on locality (MGUH 33780). **F:** Cranidium, sample L43 (MGUH 33768). **G:** Cranidium, sample L48 (MGUH 33781). **H:** Small cranidium, sample GM 1922-142B; locality 6 (MGUH 33783). **I:** Small cranidium, sample GM 1874-27, 'Cementen', Øleå (MGUH 33775). **J:** Cranidium, sample GM 1881-1797 (MGUH 33784). **K:** Cranidium, sample GM 1922-142I (MGUH 33755). **L.** Cranidium, sample GM 1922-142I (MGUH 33750). **M:** Cranidium, sample L41 (MGUH 33785). **N:** Holotype, incomplete thorax with pygidium, MGUH 1973 (previously illustrated by C. Poulsen 1923, pl. II, fig. 3 and V. Poulsen 1963, fig. 1a; see also Fig. 27D).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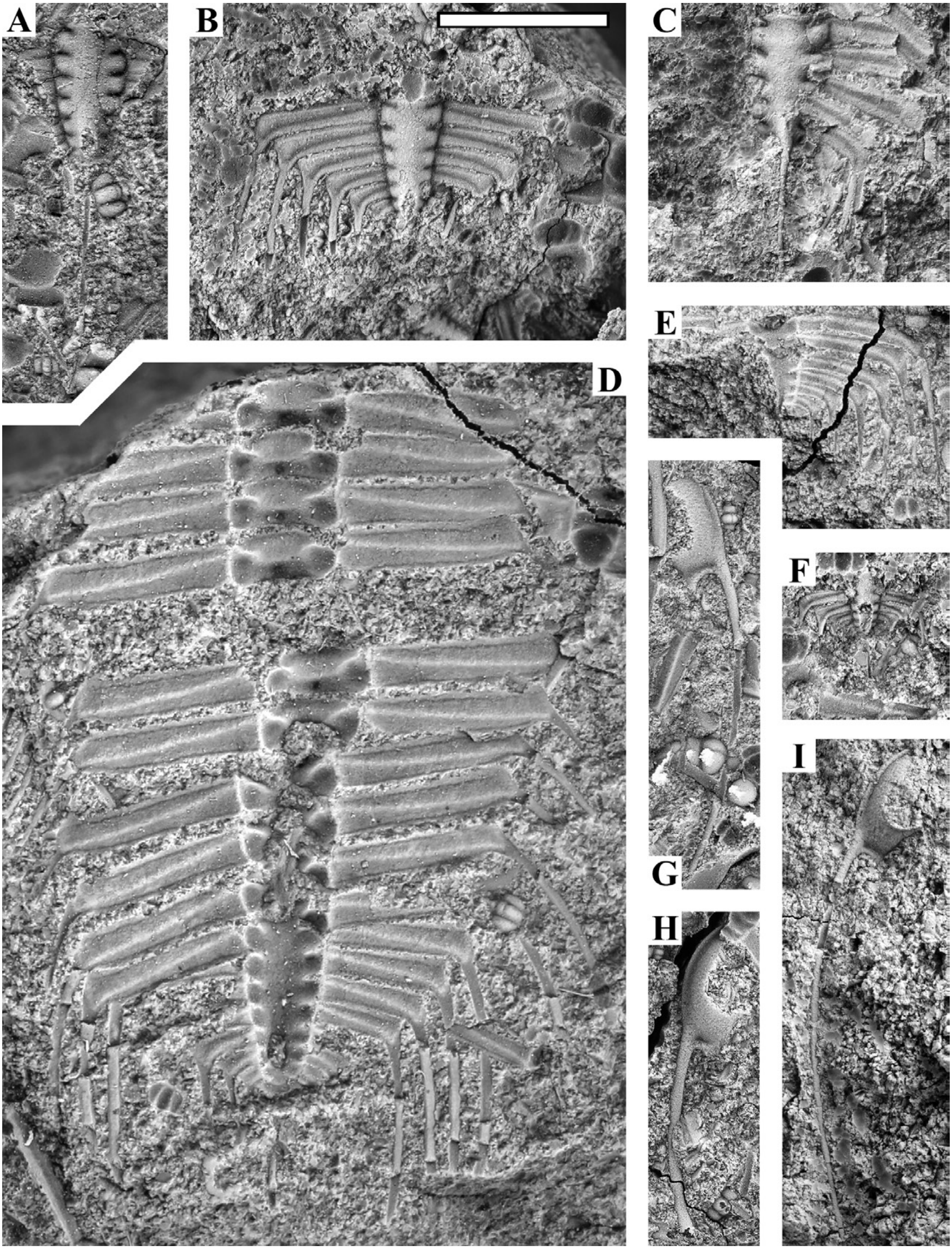
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in *C. pecten* the axis occupies only slightly more than 1/10 of the thoracic width. *Ctenopyge pecten* also has a more rapidly tapering posterior part of the thorax. The pygidia of the two species are apparently essentially identical.

Remarks. Westergård (1922) and Henningsmoen (1957) included two different forms under the name *C. pecten.* Westergård (1922) illustrated both, whereas Henningsmoen (1957) only showed the wider form assigned here to *C. pecten.* V. Poulsen (1963) separated *tenuis* as a subspecies of *C. pecten*; we prefer a separation at species level as these taxa co-occur on Bornholm. A diagnosis in the style of Henningsmoen (1957) is provided for *C. tenuis* as no summery of characteristics was given by V. Poulsen (1963).

V. Poulsen (1963) described the thoracic axis of *C. tenuis* as being ⅔ as wide as the pleural regions (excluding spines). However, in the holotype specimen, the axis is less than 0.6 times as wide as the adjacent pleural region (measured where the thorax is widest) and about ⅕ of the total width of the thorax.

Two free cheeks assigned to *P. 'longicornis'* by C. Poulsen (1923) are identified here with *C. tenuis* together with additional free cheeks. The specimens are not well-preserved, but it is obvious that the genal spine is long and slender. The genal field is elongate and the outer lateral margin is convex and much longer than the posterior lateral margin. Although the spine is less curved, these free cheeks (Figs 27G–I) overall resemble those of *C. pecten* figured by Westergård (1947, pl. 3, fig. 12) and Schrank (1973, pl. IX figs 7, 10), and given the otherwise strong resemblance between *C. tenuis* and *C. pecten* we conclude that they belong to *C. tenuis*. Besides, the specimens do not look like any other species of *Ctenopyge* occurring at that level.

***Ctenopyge (Ctenopyge) teretifrons* (Angelin, 1854)**
Fig. 28

1922 *Ctenopyge teretifrons* (Angelin) [*partim*] – Westergård, p. 162, pl. XIII, fig. 6; non pl. XIII, figs 7–8 [= *C. fletcheri*].

v 1923 *Ctenopyge teretifrons* Angelin – C. Poulsen, pp. 44–45, pl. 1, fig. 16.

1957 *Ctenopyge (Ctenopyge) teretifrons* (Angelin 1854) – Henningsmoen, pp. 209–210, pl. 5.

1973 *Ctenopyge (Ctenopyge) teretifrons* (Angelin 1854) – Schrank, pp. 831–832, pl. X, fig. 1–2, ?3.

For further synonymy, see Henningsmoen (1957).

Type material. Not designated (see Henningsmoen 1957).

Material. 71 cranidia, mostly from locality 6. A single specimen is labelled 'Cementen' (i.e. ice-rafted material, Øleå) and there is no locality information on four specimens. C. Poulsen (1923) reported this species also from locality 7, but no museum material is available from that locality. *Ctenopyge teretifrons* co-occurs with *C. linnarssoni, C. pecten, C. tenuis, P. scarabaeoides* and *T. humilis* in the studied samples.

Occurrence. Peltura scarabaeoides Zone, Sweden, England and Wales (Henningsmoen 1957). *Ctenopyge teretifrons* occurs at the same level on Bornholm and the report from the *P. lobata* ['*longicornis*'] Zone (C. Poulsen 1923) is an error, see 'Discussion and conclusions'.

Comparison. In comparison with *C. linnarssoni,* the cranidium of *C. teretifrons* is wider, with interocular cheeks that are almost 1 ½ times as wide as the glabella at eye-line and postocular cheeks that are about twice as wide as the occipital ring (see remarks), while *C. linnarssoni* has interocular cheeks as wide as the glabella at eye-line and the postocular cheeks are only *c.* 1 ½ times as wide as the occipital ring. *Ctenopyge teretifrons* has also a distinctive, rather inflated 'globular' anteroglabella.

Remarks. In a few measured cranidia, the width of the interocular area at eye line is 1.1–1.7 times the width of the adjacent glabella, averaging 1.4 (n=8). The postocular cheeks are 1.6–2.1 times as wide as the occipital ring, averaging 1.9 (n=8). The narrowest interocular area and postocular cheeks are seen in the smaller cranidia (<1.5 mm long).

Subgenus *Ctenopyge (Mesoctenopyge)* Henningsmoen, 1957
Type species: *Ctenopyge spectabilis* Brøgger, 1882 by original designation.

▲ **Fig. 27.** *Ctenopyge tenuis*, all preserved in anthraconite and from locality 6, unless otherwise stated. White scale bar: 3 mm. **A:** Fragmentary pygidium, sample GM 1922-142M (MGUH 33788). **B:** Pygidium, sample GM 1922-142M (MGUH 33789). **C:** Fragmentary pygidium, sample L38 (MGUH 33790). **D:** Incomplete thorax with pygidium (external mould of holotype MGUH 1973 illustrated in Fig. 26N), specimen MGUH 1972. **E:** External mould of pygidium, sample GM 1871-636, Læså area from between Hjulmagergård and Vasagård [loc. 6 or 7] (MGUH 33793). **F:** Fragmentary small pygidium, sample GM 1874-27, collected at 'Cementen', Øleå (MGUH 33776). **G:** One of two free cheeks, sample GM 1922-142J, labelled as *Parabolina longicornis* by C. Poulsen, see text (MGUH 33794). **H:** Free cheek, sample GM 1922-142I (MGUH 33748). **I:** Free cheek, sample GM 1922-142S (MGUH 33765).

***Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922**

Fig. 29

1922 *Ctenopyge tumida* n. sp. [*partim*] – Westergård, pp. 155–156, pl. XI, figs 15–18; non pl. XI, figs 19–20 [= *Ctenopyge tumidoides*].

1922 *Ctenopyge bisulcata* (Phillips) [*partim*] – Westergård, pl. XII, fig. 21.

v 1923 *Ctenopyge tumida* Westergård [*partim*] – C. Poulsen, pp. 39–41, pl. 1, fig. 14; non textfig. 16 [= *Ctenopyge tumidoides*].

1957 *Ctenopyge (Mesoctenopyge) tumida* Westergård 1922 – Henningsmoen, pp. 198–199, pl. 5, pl. 20, fig. 16.

1973 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922 – Schrank, pp. 825–826, pl. VII, figs 13–20, 22–23.

non 2004 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922 – Clarkson *et al.*, pp. 129–130, 134, 137, figs 17, 18A–D, 19, 20A–D. [= *C. tumidoides*].

2015 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922 – Schoenemann & Clarkson, pp. 133–139, figs 1F–H, 3.

2016 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922 – Månsson & Clarkson, pp. 178–182, figs 7–11.

2016 *Ctenopyge tumida* – Ahlberg *et al.*, p. 498, figs 4, 6O.

2017 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922 – Rasmussen *et al.*, pp. 11–12, fig. 6E.

For further synonymy, see Månsson & Clarkson (2016) and Rasmussen *et al.* (2017).

Lectotype. Cranidium SGU 315 figured by Westergård (1922, pl. XI, fig. 16) from Andrarum, southern Sweden, designated by Henningsmoen (1957).

Material. 141 cranidia and nine free cheeks. Nearly all of the material is from locality 6; one cranidium and a free cheek were found at locality 7. *Ctenopyge tumida* co-occurs with *C. tumidoides*, *Ctenopyge* sp. 2, *P. acutidens, S. alatus* and *S. angustus* in the studied samples.

Occurrence. Ctenopyge tumida is characteristic of the *P. acutidens*–*C. tumida* Zone (Terfelt *et al.* 2008; Nielsen *et al.* 2020). It has been recorded from Scandinavia (incl. Bornholm), Great Britain and Poland (Henningsmoen 1957; Żylińska 2001, 2002; Terfelt *et al.* 2008).

Comparison. Ctenopyge tumida is quite similar to *C. tumidoides* but has a transverse postocular facial suture whereas it runs obliquely backwards in *C. tumidoides.*

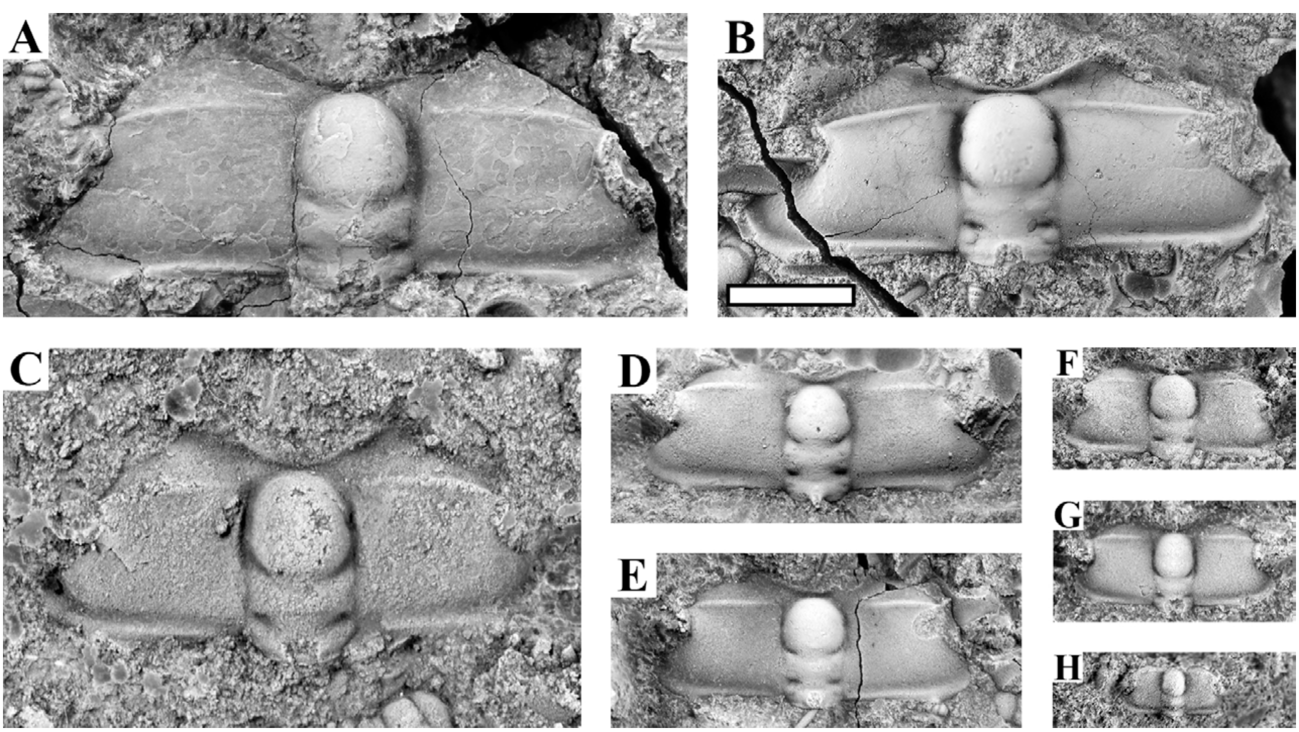


Fig. 28. Cranidia of *Ctenopyge teretifrons,* all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A:** Sample GM 1922-142T (MGUH 33796). **B:** MGUH 1969, previously illustrated by C. Poulsen (1923, pl. 1, fig. 16). **C:** Sample L41 (MGUH 33786). **D:** Sample GM 1922-142D (MGUH 33797). **E:** Sample GM 1922-142I (MGUH 33751). **F:** Sample GM 1922-142S (MGUH 33766). **G:** Sample GM 1922-142B (MGUH 33798). **H:** Sample GM 1881-1796 (MGUH 33800).

Hence, the adaxial parts of the postocular cheeks are shorter (exsag.) in *C. tumida* compared with *C. tumidoides*. *Ctenopyge tumida* also has slightly wider (tr.) postocular cheeks being almost 1 ½ times as wide as the occipital ring, while they are only slightly wider than the occipital ring in *C. tumidoides*. The strong resemblance between *C. tumida* and *C. tumidoides* makes identification difficult if the postocular cheeks are broken or not fully visible.

Remarks. 23 cranidia of *C. tumida* (examples shown in Fig. 29J–K, Q) have been found associated with *C. tumidoides* and *S. angustus*. The latter two species are usually regarded as indicative of the *S. modestus–S. angustus* Zone, but apparently they range into the basal *Peltura* Superzone (see section on 'Olenid zonation').

One of the cranidia illustrated as *C. bisulcata* by Westergård (1922, pl. XII, fig. 21) has a course of the posterior branches of the facial suture entirely similar to that of *C. tumida.*

The cranidia described as *C. tumida* by Clarkson *et al.* (2004) have oblique postocular facial sutures and are here identified as *C. tumidoides*.

***Ctenopyge (Mesoctenopyge) tumidoides* Henningsmoen, 1957**

Fig. 30

1922 *Ctenopyge tumida* n. sp. [*partim*] – Westergård, pp. 155–156, pl. XI, figs 19–20.

1923 *Ctenopyge tumida* Westergård [*partim*] – C. Poulsen, pp. 39–41, textfig. 16.

1957 *Ctenopyge (Mesoctenopyge) tumidoides* n. sp. – Henningsmoen, pp. 199–200, pl. 5; pl. 20, fig. 15.

2004 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922 – Clarkson *et al.*, pp. 129–130, 134, 137, figs 17, 18A–D, 19, 20A–D.

Holotype. Cranidium with five attached thoracic segments (SGU 318) figured by Westergard (1922, pl. XI, fig. 19) from Andrarum, southern Sweden.

Material. 141 cranidia (including 21 external moulds) and 11 free cheeks, co-occurring with common *S. angustus*, very rare *P. planicauda*, *P. acutidens* and *Ctenopyge* sp. 2, and occasional *C. tumida*, see remarks on the latter species. Most specimens are from locality 6, but a few were found at locality 7.

Occurrence. Sphaerophthalmus modestus–S. angustus Zone in the Oslo Region and Scania (see Henningsmoen 1957). *Ctenopyge tumidoides* has not been reported from Bornholm previously due to mixing with *C. tumida*; it is, in fact, quite common. The majority of the specimens derive from samples with common *S. angustus*, but a few samples also contain *C. tumida* and/or *P. acutidens*. One sample (ATN-197) even contains several cranidia of *C. tumidoides* associated with *S. alatus* and *C. tumida*. *Ctenopyge tumidoides* thus seems to range into the lowermost part of the *Peltura* Superzone, which apparently also is the case in Västergötland (see remarks).

Comparison. For comparison with *C. tumida*, see that species.

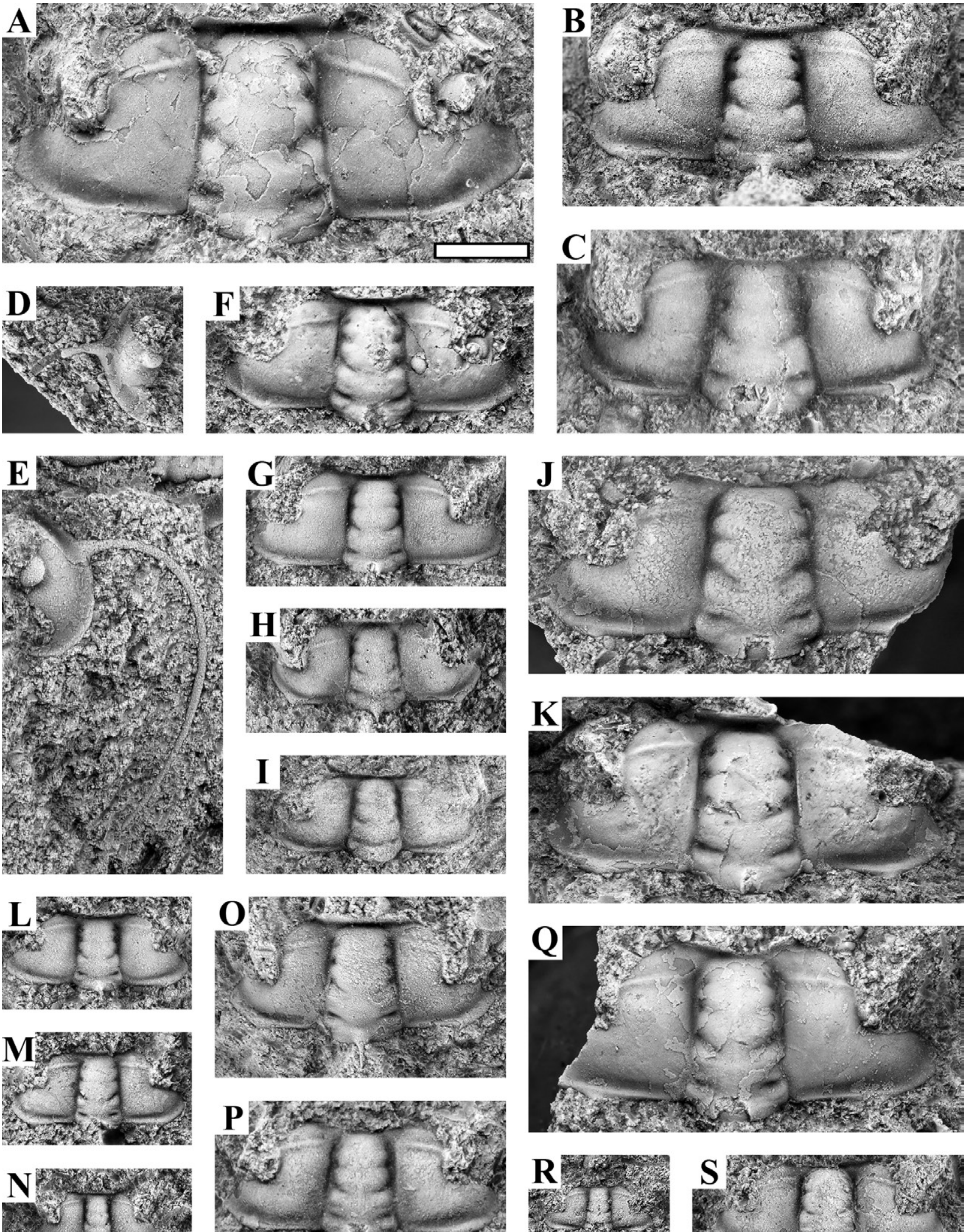
Remarks. The small cranidia allocated to *C. tumida* by Clarkson *et al.* (2004) have oblique postocular facial sutures and short (tr.) postocular cheeks and are here assigned to *C. tumidoides*; compare with the smallest cranidia of *C. tumida* (Fig. 29N, R) and *C. tumidoides* (Fig. 30L) illustrated from Bornholm vs. Clarkson *et al.* (2004 fig. 17B). The material from Västergötland described by Clarkson *et al*. (2004) co-occurs with *C. ahlbergi* and apparently derives from the *P. acutidens–C. tumida* Zone. On Bornholm, *C. tumidoides* co-occurs with *C. tumida* and *P. acutidens* in the lower part of the *P. acutidens–C. tumida* Zone but not with *C. ahlbergi* (see section on 'Olenid zonation').

***Ctenopyge* sp. 1**

Fig. 31A

Material. One cranidium from sample L77 found at locality 7. It co-occurs with *C. affinis*, *C. ahlbergi* and *S. alatus* and this assemblage is indicative of the upper part of the *P. acutidens–C. tumida* Zone.

Remarks. The cranidium, which is 3.35 mm wide and *c.* 1.95 mm long (the anterior margin is damaged) has unusually narrow cheeks. The glabella morphology suggests that it is a representative of *Ctenopyge* but it cannot be assigned to any known species. The little-known *C. oelandica* (see Westergård 1922, Buchholz 2000) has strongly curving eye ridges, which clearly sets it apart from *Ctenopyge* sp. 1. *Ctenopyge rushtoni* – of which only juveniles are described (Clarkson *et al.* 2004) – has a cranidium that is quite *C. gracilis*-like with much wider cheeks than *Ctenopyge* sp. 1 and the glabella of *C. rushtoni* and notably the anteroglabella is also significantly more inflated. *Ctenopyge affinis* has posterior indentations in the glabella immediately in front of the occipital furrow and the postocular cheeks are clearly wider than the occipital ring (*c.* 1.2 times as wide in adult specimens). In *Ctenopyge* sp. 1, the glabella has no lateral indentations in the rear part and it tapers evenly and gently forwards; the postocular cheeks are also markedly narrower (tr.) than the occipital ring (*c.* ¾ as wide). Unless it is a pathological specimen, it likely represents a new species.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***Ctenopyge* sp. 2**
Fig. 31B

Material. One free cheek from sample GM 1922-141P that also contains *S. angustus*, *C. tumidoides* and *C. tumida*. This assemblage is indicative of the lowermost part of the *P. acutidens*–*C.tumida* Zone. The sample is from locality 6.

Remarks. The free cheek is 3 mm long excl. spine and *c.* 5.5 mm incl. spine, but which is broken. The spine is rather straight for a *Ctenopyge* and overall, the specimen resembles the free cheeks assigned to *C. affinis* and *C. magna* n. sp. The co-occurring *C. tumida* and *C. tumidoides* have free cheeks with a much different morphology and no other cranidia of *Ctenopyge* have been found at this level. In comparison with the free cheeks assigned to *C. affinis* and *C. magna* n. sp., *Ctenopyge* sp. 2 is relatively wider, and it also has a broader lateral border and a posterior margin that appears to be approximately twice as long. Hence, the discussed free cheek is not likely to be an early representative of *C. affinis* or *C. magna* n. sp., and it may represent a new species.

Genus *Sphaerophthalmus* Angelin, 1854
Type species: *Trilobites alatus* Boeck, 1838, designated by Linnarsson (1880).

***Sphaerophthalmus alatus* (Boeck, 1838)**
Fig. 32

1922 *Sphærophthalmus major* Lake – Westergård, pp. 163–165, pl. XIII, figs 9–19.
Non 1922 *Sphærophthalmus alatus* (Boeck) – Westergård, pp. 165–166, pl. XIII, figs 20–29 [= *Triangulopyge humilis*].
v 1923 *Sphaerophthalmus major* Lake [*partim*] – C. Poulsen, pp. 47–48, pl. 1, fig. 15; non textfig. 17a–b [= *S. angustus*].
v Non 1923 *Sphaerophthalmus alatus* Boeck – C. Poulsen, pp. 49–50 [= *Triangulopyge humilis*].
1957 *Sphaerophthalmus alatus* (Boeck 1838) – Henningsmoen, pp. 212–215, pl. 2, fig. 15; pl. 5; pl. 22, figs 18–26.
1973 *Sphaerophthalmus alatus* (Boeck, 1838) – Schrank, pp. 834–835, pl. X, figs 21–23; pl. XI, figs 1–15.
2012 *Sphaerophthalmus alatus* (Boeck, 1838) [*partim*] – Høyberget & Bruton, pp. 438–439, figs 4A, H, 5A–H, J–K, non fig. 5i [= *S. angustus*].
2015 *Sphaerophthalmus alatus* (Boeck, 1838) – Schoenemann & Clarkson, pp. 133–139, figs 1A–E, 2.
2016 *Sphaerophthalmus alatus* (Boeck, 1838) – Månsson & Clarkson, pp. 173–178, figs 1–6.
2016 *Sphaerophthalmus alatus* – Ahlberg *et al.*, p. 498, figs 4, 6A–B.
2017 *Sphaerophthalmus alatus* (Boeck, 1838) – Rasmussen *et al.*, pp. 21–22, fig. 6F.

For further synonymy, see Høyberget & Bruton (2012) and Rasmussen *et al.* (2017).

Lectotype. Cranidium PMO 56371 from Gamlebyen, Oslo, Norway. Designated by Størmer (1940) and figured by Henningsmoen (1957, pl. 22, figs 23, 24) and Høyberget & Bruton (2012, figs 5A, D).

Material. Extremely abundant cranidia of which *c.* 1011 are registered, whereas only 23 free cheeks and 2 pygidia have been identified. Most of the material derives from locality 6 (a few older museum samples labelled 'Læså between Hjulmagergård and Vasagård' or just 'Læså' probably also originate from this locality), but a few specimens derive from locality 7. In the studied samples, *S. alatus* co-occurs with *C. affinis*, *C. ahlbergi*, *C. magna* n. sp., *C. tumida*, *C. tumidoides*, *Ctenopyge* sp. 1 and *P. minor.*

Occurrence. Very common in the *P. acutidens*–*C. tumida* Zone in Scandinavia and Poland; *S. alatus* has been recorded also from the lowermost part of the *P. scarabaeoides* Zone (Henningsmoen 1957; Żylińska 2001, 2002; Høyberget & Bruton 2012). From Bornholm, C. Poulsen (1923) reported it (under the name *S. major*) from the *C. tumida* Subzone [= *P. acutidens*–*C. tumida* Zone], which is confirmed by the present study. No co-occurrence with *P. scarabaeoides* has been observed in the samples at hand.

▲ **Fig. 29.** *Ctenopyge tumida*, all preserved in anthraconite from locality 6. J–K and Q are from samples dominated by *Ctenopyge tumidoides* and *Sphaerophthalmus angustus*, see text. White scale bar: 2 mm. **A:** Large cranidium, sample L61 (MGUH 33801). **B:** Cranidium, sample ATN-197 (MGUH 33802). **C:** Cranidium, sample ATN-238 (MGUH 33809). **D:** Free cheek, sample ATN-175 (MGUH 33811). **E:** Free cheek, sample ATN-197 (MGUH 33803). **F:** Cranidium, specimen MGUH 1967, originally illustrated by C. Poulsen (1923, pl. 1, fig. 14). **G:** Cranidium, sample ATN-171 (MGUH 33813). **H:** Cranidium, sample GM 2019-17 (MGUH 33816). **I:** Cranidium, sample ATN-197 (MGUH 33804). **J:** Cranidium, sample GM 1922-141J (MGUH 33818). **K:** Cranidium, sample GM 1922-141P (MGUH 33819). **L.** Cranidium, sample ATN-197 (MGUH 33805). **M:** Cranidium, sample ATN-197 (MGUH 33806). **N:** Juvenile cranidium, sample ATN-171 (MGUH 33814). **O:** Cranidium, sample GM 2019-17 (MGUH 33817). **P:** Cranidium, sample L53 (MGUH 33828). **Q:** Cranidium, sample GM 1922-141P (MGUH 33824). **R:** Cranidium, sample ATN-197 (MGUH 33807). **S:** Cranidium, sample ATN-175 (MGUH 33812).

Comparison. For comparison with *S. angustus*, *C. affinis* and *T. humilis*, see these species and remarks below.

Remarks. In general, *S. alatus* and *S. angustus* were not separated by C. Poulsen (1923) and except for GM 1922-141P, all the museum samples with *S. alatus* and *S. angustus* listed in Appendix 1 were labelled as *S. major*.

Large cranidia of *S. alatus* have a tapering glabella (Fig. 32A–D) whereas the glabella is parallel-sided in smaller specimens (Fig. 32E–O). The distinct S1, which

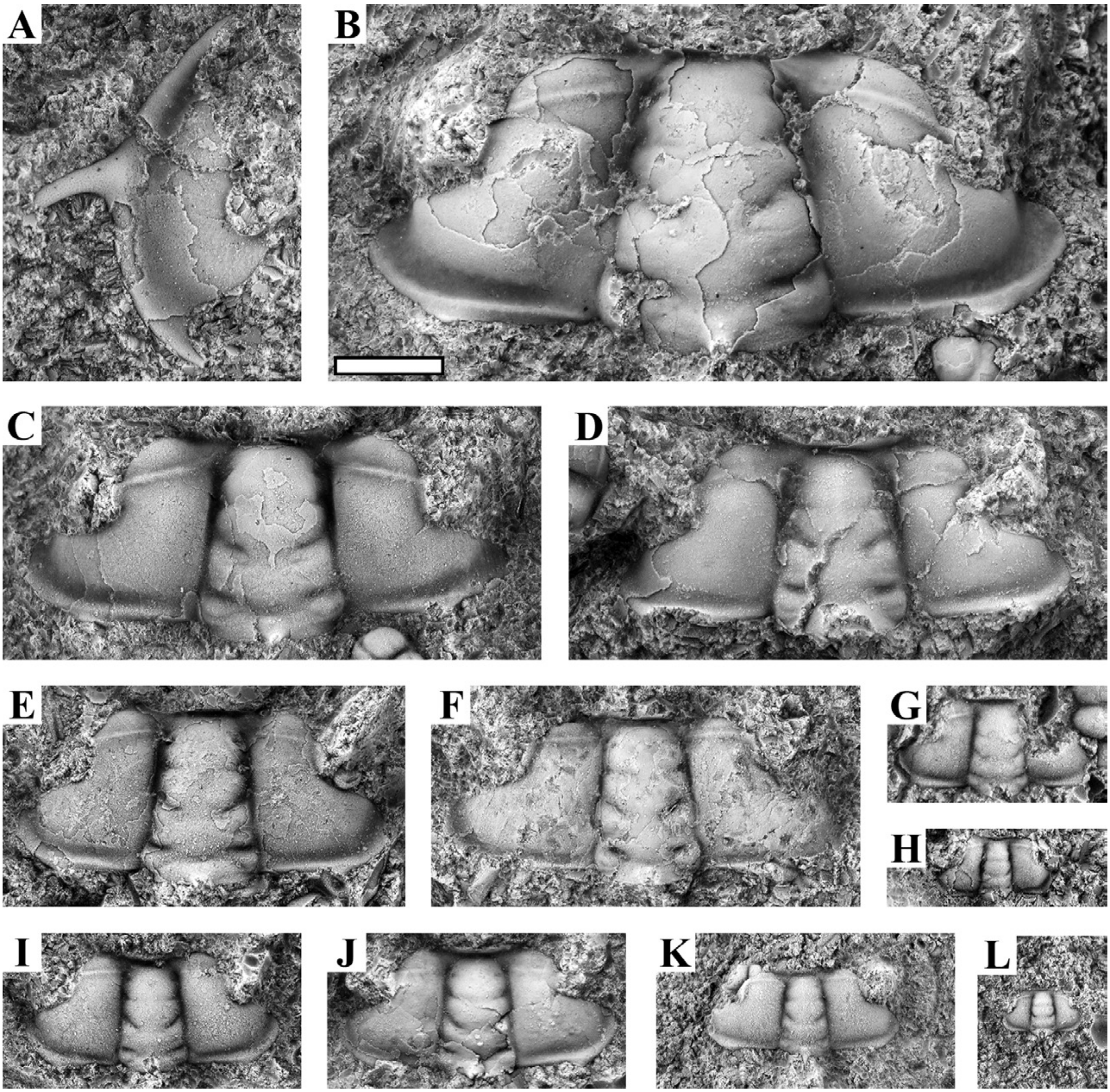


Fig. 30. A–L. *Ctenopyge tumidoides*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. The specimens shown in B and C are from the *P. acutidens–C. tumida* Zone; the remaining material is assumed to be from the *S. modesta–S. angustus* Zone. **A:** Free cheek, sample L87 (MGUH 22829). **B:** Very large cranidium, sample L57 (MGUH 33832). **C:** Large cranidium, Sample L87 (MGUH 33830). **D:** Large cranidium, Sample L87 (MGUH 33831). **E:** Cranidium, sample L71 (MGUH 33834). **F:** Cranidium, sample L80 (MGUH 33835). **G:** Cranidium from sample ATN-190, which contains many cranidia of *Ctenopyge tumida* and *Sphaerophthalmus alatus* as well as several cranidia of *C. tumidoides* (MGUH 33838). **H:** Juvenile cranidium, sample ATN-145 (MGUH 33839). **I:** Cranidium from sample ATN-197, which contains many cranidia of *Ctenopyge tumida* and *Sphaerophthalmus alautus* as well as *C. tumidoides* (MGUH 33808). **J:** Cranidium from sample GM 1922-141P, which is dominated by *Ctenopyge tumida* and *Sphaerophthalmus alatus* (MGUH 33820). **K:** small cranidium GM 1922-141N (MGUH 33842). **L**. Juvenile cranidium GM 1922-141G (MGUH 33843).

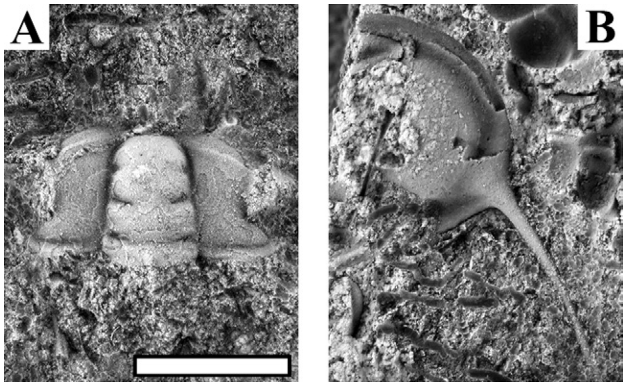


Fig. 31. A: *Ctenopyge* sp. 1, cranidium, sample L77, anthraconite, loc. 7 (MGUH 33844). **B:** *Ctenopyge* sp. 2, free cheek, sample GM 1922-141P, anthraconite, loc. 6 (MGUH 33821). The white scale bar: 2 mm.

is important for identification, is shallower in larger cranidia, especially mesially. Due to these changes, cranidia become increasingly *S. angustus*-like with size and very large cranidia are exceedingly similar (Fig. 32A–B). Still, S1 is marginally more distinct and the postocular cheeks bend down just slightly stronger, but small and medium-sized cranidia are much easier to distinguish. It is emphasized that the illustrated '*angustus*-like' very large *S. alatus* cranidia derive from samples containing numerous, readily identified smaller cranidia of *S. alatus* co-occurring with *C. tumida*.

Pygidia are mostly overlooked, as they are lying sideways in the sediment due to the long caudal spine (cf. Høyberget & Bruton 2012); no attempt has been made to identify isolated spines from free cheeks and pygidia.

***Sphaerophthalmus angustus* (Westergård, 1922)**
Fig. 33

1922 *Ctenopyge flagellifera angusta* n.var. [*partim*] – Westergård, p. 153, pl. 11, figs 2–5, 8.
v 1923 *Ctenopyge flagellifera* Angelin var. *angusta* Westergård [*partim*] – C. Poulsen, p. 39.
v 1923 *Sphaerophthalmus major* Lake [*partim*] – C. Poulsen, pp. 47–48, textfig. 17a–b.
1957 *Ctenopyge (Eoctenopyge) angusta* Westergård – Henningsmoen, p. 187, pl. 5, pl. 19, figs 11–16, 18.
2012 *Sphaerophthalmus angustus* (Westergård, 1922) – Høyberget & Bruton, pp. 439–440, Figs 4B and A–F.
2012 *Sphaerophthalmus alatus* (Boeck, 1838) [*partim*] – Høyberget & Bruton, pp. 438–439, fig. 5i.
2016 *Sphaerophthalmus angustus* (Westergård, 1922) – Rasmussen *et al*., pp. 19–20, fig. 9A.

For further synonyms, see Henningsmoen (1957) and Høyberget & Bruton 2012.

Lectotype. Cranidium SGU305, figured by Westergard (1922, pl. 11, fig. 3) from Andrarum, southern Sweden, designated by Henningsmoen (1957).

Material. >911 cranidia and at least 23 free cheeks. The far majority of the material is from locality 6, but a few specimens derive from locality 7. On Bornholm, the species co-occurs with *C. tumidoides*, *Ctenopyge* sp. 2, *P. planicauda*, *P. acutidens* and *C. tumida*.

Occurrence. This species has hitherto been considered characteristic of the *S. modestus*–*S. angustus* Zone in Scandinavia (Henningsmoen 1957; Høyberget & Bruton 2012; Nielsen *et al.* 2020). From Bornholm, C. Poulsen (1923) reported "var. *angusta*" as common in the upper part of what he called the *C. flagellifer* Subzone (see remarks). However, the material at hand suggests that *S. angustus* on Bornholm ranges from the *S. modestus*–*S. angustus* Zone, where it is associated with *C. tumidoides*, into the basal part of the *P. acutidens*–*C. tumida* Zone, where it is associated with *C. tumidoides*, *C. tumida* and *P. acutidens* (for details, see section on 'Olenid zonation').

Comparison. This species resembles *S. alatus*, but in the latter the glabellar furrows are deeper and more distinct and confluent with the axial furrows. S1 is particularly distinct in *S. alatus* and there is no shallowing towards the axial furrow. In *S. angustus,* the occipital furrow and S1 are less distinctly impressed and with some shallowing towards the axial furrow. The postocular cheeks of *S. alatus* are more strongly bent downwards than in *S. angustus*, hence the cranidial width across the postocular cheeks (tr.) is larger in the latter. In the free cheeks, the posterior border is straight in *S. angustus* and typically a little curved in *S. alatus*, but atypical specimens with a straight posterior margin occurs also (Fig. 32R).

Remarks. The taxon was described as occurring commonly in the section at locality 6 (C. Poulsen 1923, p. 39), but the few samples labelled as '*Ctenopyge flagellifera* var. *angusta*' (GM 1922-140B) contain only *S. flagellifer* and *S. drytonensis* (examples are shown in Figs 34M, 35E–F, H, J). Sample GM 1922-141P (originally labelled as *S. major* [i.e. *S. alatus*]) was exhibited in the Geological Museum in 1960 as *Ctenopyge angusta*, showing that C. Poulsen realized the misidentification of the cranidia at that stage. Several additional museum samples contain *S. angustus* (listed in Appendix 1), but all were labelled as *S. major*.

***Sphaerophthalmus drytonensis* (Cobbold, 1934)**
Fig. 34, Fig. 35P–T.

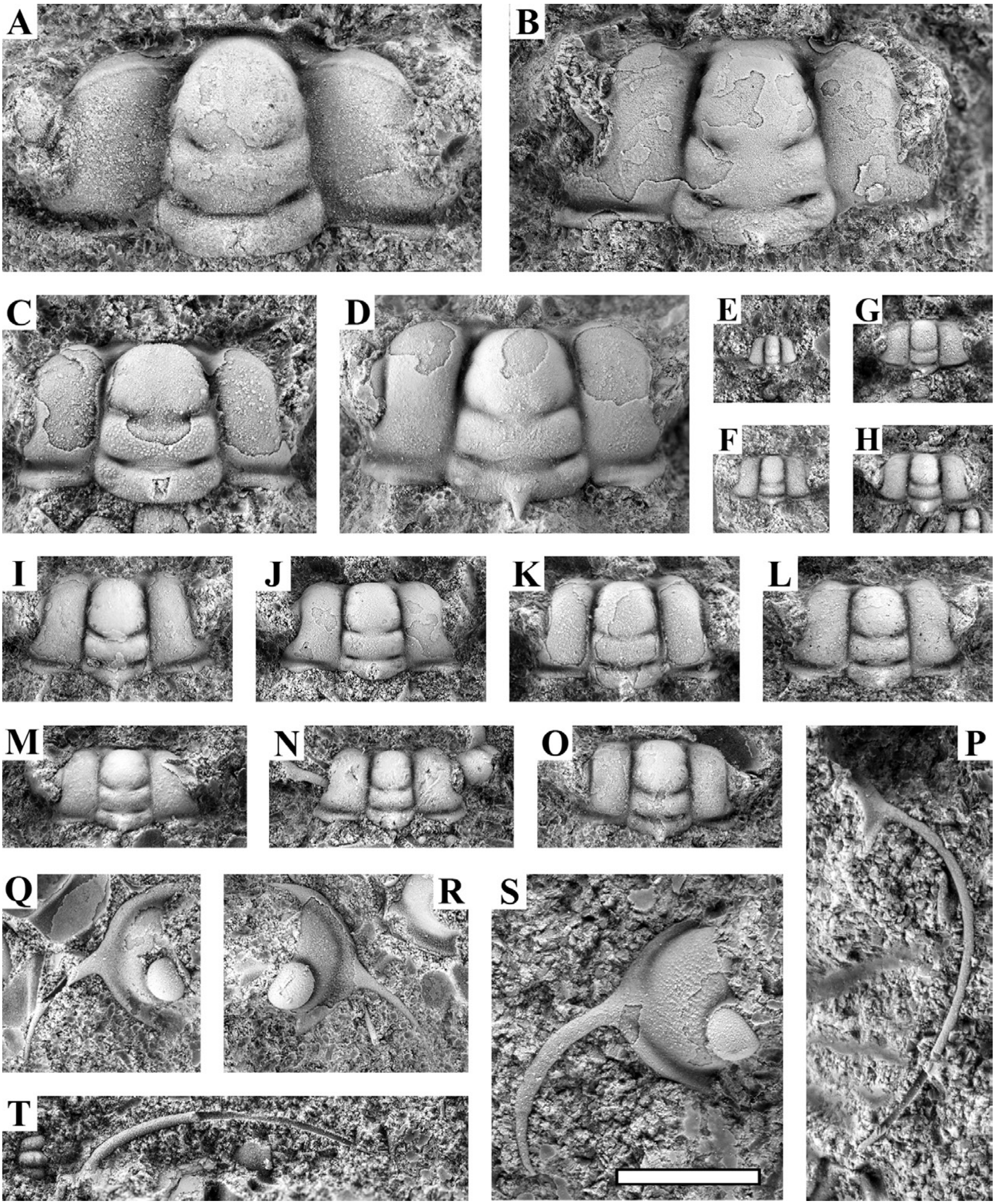
? 1894 *Ctenopyge Acadica*, n. sp. – Matthew, pp. 109–110, pl. XVII, fig. 13a–e.

1922 *Ctenopyge flagellifera* (Angelin) [*partim*] – Westergård, pp. 152–152, pl. X, figs 19, 21a; pl. XI, fig. 1 [see remarks].

v 1923 *Ctenopyge flagellifera* Angelin [*partim*] – C. Poulsen, pp. 38–39, textfig. 15; pl. 1, figs 12?–13.

v 1923 *Ctenopyge flagellifera* Angelin var. *angusta* Westergård [*partim*] – C. Poulsen, p. 39.

1957 *Ctenopyge (Eoctenopyge) drytonensis* Cobbold



1934 [*partim*] – Henningsmoen, pp. 188–189, pl. 5, pl. 18, figs 5–9 and 11–14; non fig. 10 [= *S. flagellifer*].

1957 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) [*partim*] – Henningsmoen, pp. 189–191, pl. 18, fig. 1.

2012 *Sphaerophthalmus drytonensis* (Cobbold, 1934) – Høyberget & Bruton, pp. 441–442, fig. 8.

2016 *Sphaerophthalmus drytonensis* Cobbold, 1934 – Rasmussen *et al*., p. 20, fig. 9D,

For further synonymy, see these publications.

Holotype. Cranidium GSM 51776 from Dryton Brook, Rushton area, Shropshire, England. Figured by Cobbold (1934, pl. 45, fig. 9) and Henningsmoen (1957, pl. 18, fig. 8).

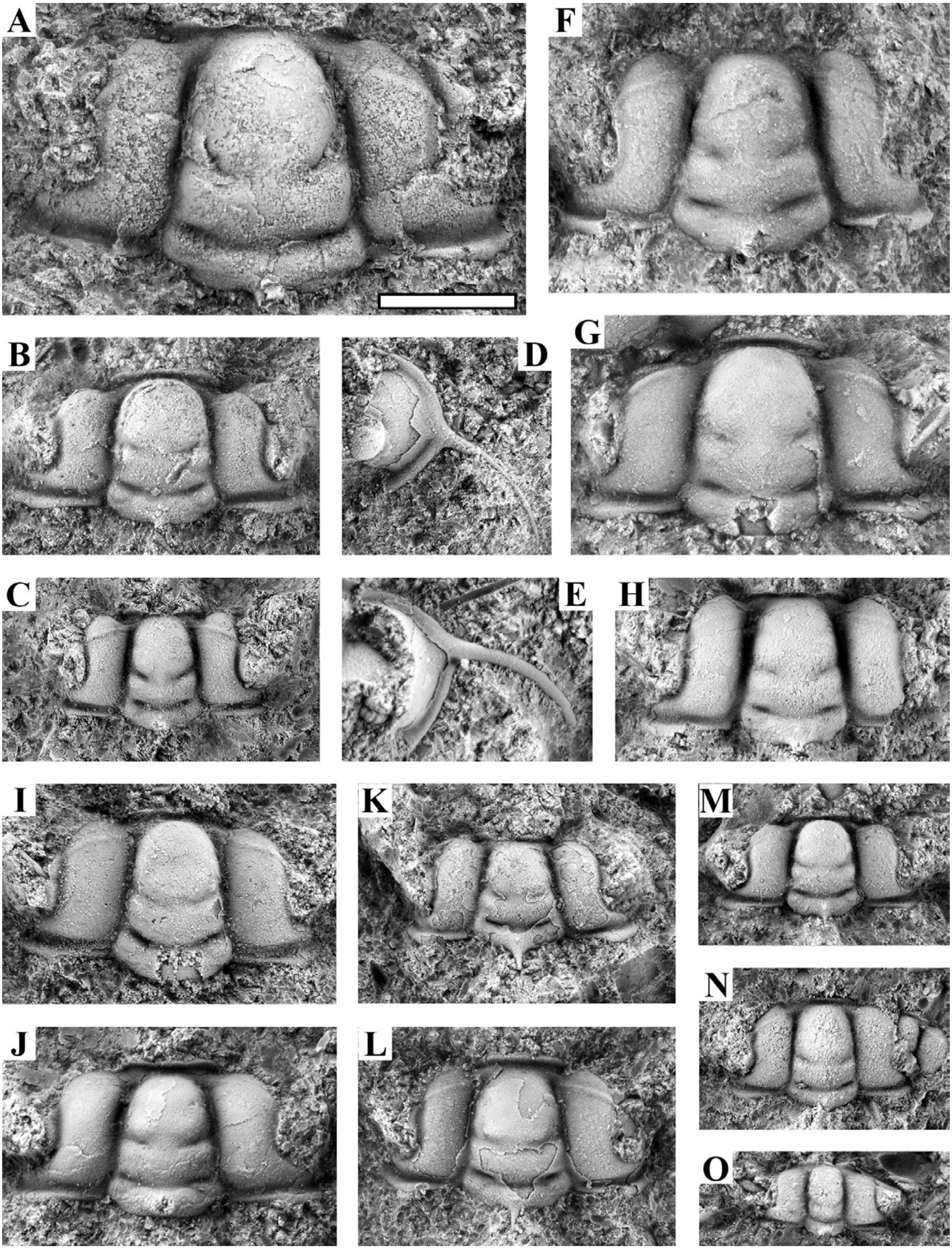
Material. External mould of one complete specimen, 486 cranidia and 114 free cheeks from the *C. flagellifer* Zone at locality 6. The species is associated wth common *C. flagellifer;* a single pygidium of *Protopeltura praecursor* has been found in one sample.

Occurrence. In the Oslo Region, the species ranges from the *S. postcurrens* Zone into the *S. flagellifer* Zone (Henningsmoen 1957, Høyberget & Bruton 2012). From Sweden, *S. drytonensis* has been reported only from the *S. flagellifer* Zone at Hunneberg (Rasmussen *et al.* 2016), but it has most likely been mixed with *S. flagellifer* in previous studies. In our interpretation, much of the material described as *S. flagellifer* by Westergård (1922) from Andrarum, Scania, represents *S. drytonensis* (see remarks). This is the first report of *S. drytonensis* from Bornholm, where it occurs commonly in the *S. flagellifer* Zone.

Comparison. The free cheek is distinguished from those of the co-occurring *S. flagellifer* by having a slightly more sturdy, less curving and shorter spine; the posterior lateral margin is rather strongly convex (dorsal view) and shorter than the less convex anterior lateral margin; the posterior border is comparatively wide and clearly wider than the anterior lateral border; the border furrow is indistinct inside the spine base. The most characteristic separating feature is, however, the asymmetry of the lateral margin behind and in front of the spine base: The obtuse inner spine angle is placed more laterally relative to the base of the spine than the outer spine angle. In comparison, the free cheek of *S. flagellifer* has a moderately narrow lateral border of nearly equal width throughout (minor widening posteriorly); the spine is a more gracile, longer and curves more strongly; the border furrow continues without shallowing inside the spine base; there is no asymmetry in the position of the lateral margin behind and in front of the spine base; the posterior margin is longer than the anterior margin so the spine is situated relatively anteriorly and overall, the lateral margin of the free cheek curves evenly throughout. The cranidia of the two species are very alike. The key separating feature is a fairly impressed, elongate, often but not always geniculate S1 in *S. drytonensis* that extends to the axial furrows, as opposed to the pit-like, rather shallow S1 in *S. flagellifer* that does not reach the axial furrows. Other differences like a longer frontal area (sag.) in *S. drytonensis,* a more strongly tapering glabella, a shallowing of the axial furrow at the anterior corners of the glabella, presence of shallow S2 and S3 and convex versus flat gently sloping interocular area (Henningsmoen 1957, Høyberget & Bruton 2012) have proven impossible to apply as consistent separating characters in the material from Bornholm; for further comments, see remarks.

Remarks. Sphaerophthalmus drytonensis is very common on Bornholm and actually more common than the associated *S. flagellifer.* The cranidium illustrated as *C. flagellifera* by C. Poulsen (1923 pl. I, fig. 13) is here assigned to *S. drytonensis* whereas the illustrated second cranidium with attached thoracic segments (*ibid*., pl. I, fig. 12) has a slightly dissolved test and cannot be identified with certainty, but it may also represent *S. drytonensis*.

▲ **Fig. 32.** *Sphaerophthalmus alatus*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. Note the tapering glabella in large cranidia vs. the parallel-sided glabella in small cranidia; see text for further remarks. **A:** Very large cranidium, sample ATN-112 (MGUH 33845). **B:** Very large cranidium with comparatively narrow occipital ring (sag.), sample L81 (MGUH 33846). **C:** Large cranidium, sample ATN-133 (MGUH 33848). **D:** Large cranidium, sample ATN-205 (MGUH 33734). **E:** Juvenile cranidium, sample ATN-134 (MGUH 33699). **F:** Juvenile cranidium, sample GM 1902-1209 (MGUH 33763). **G:** Juvenile cranidium, sample ATN-134 (MGUH 33700). **H:** Juvenile cranidium, sample ATN-134 (MGUH 33701). **I:** Cranidium, sample ATN-116 (MGUH 33710). **J:** Cranidium, sample ATN-139 (MGUH 33849). **K:** Cranidium, sample ATN-222 (MGUH 33705). **L:** Cranidium, sample ATN-103 (MGUH 33722). **M:** Cranidium, sample ATN-146 (MGUH 33728). **N:** Cranidium, sample ATN-117 (MGUH 33687). **O:** Cranidium, sample ATN-113 (MGUH 33717). **P:** Free cheek, sample ATN-238 (MGUH 33810). **Q:** Free cheek, sample ATN-146 (MGUH 33729). **R:** Free cheek with atypical straight posterior margin (i.e. *S. angustus*-like), sample ATN-134 (MGUH 33702). The associated fauna shows that this free cheek is from the upper part of the *P. acutidens–C. tumida* Zone well above the range of *S. angustus.* **S:** Free cheek, sample L81 (MGUH 33847). **T:** Pygidium with large spine (side view), sample ATN-171 (MGUH 33815).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The cranidia of *S. flagellifer* and *S. drytonensis* are exceedingly alike and identification has been based exclusively on the morphology of S1 as stated above. A slight dissolution of the test surface is a problem in several samples (see e.g. Figs 34I, 35L–M) and this obviously does not make it easier to differentiate the cranidia. Flattened cranidia preserved in shale cannot be assigned. In addition to the morphology of S1, there seems to be a trend that S2 and S3 often are visible in *S. drytonensis*, but this is not always the case. S1–S3 seem to be more distinctly impressed in juvenile cranidia, probably including juveniles of *S. flagellifer*, and small specimens appear impossible to assign safely.

The free cheeks are very characteristic and readily separated. We note that the ratio in this study between identified cranidia of *S. flagellifer*/*S.drytonensis* is 0.43 (207 counted specimens vs. 486 specimens) which compares reasonably well with the ratio between the more readily identified free cheeks (0.36), indicating that the chosen approach to identification of cranidia is plausible although some mixing may persist, in part due to the intermittent dissolution of the test surface.

According to the criterion used herein for separation of *S. flagellifer* and *S. drytonensis,* the cranidia of *S. flagellifer* illustrated by Westergård (1922) all represent *S. drytonensis* and the only safely assigned skeletal part of *S. flagellifer* illustrated is the free cheek (*ibid*. pl. X, fig. 20 [neotype]). This indicates that *S. drytonensis* is more widespread in Sweden than currently reported. It is, however, difficult to ascertain whether or not S1 reaches the axial furrows based on illustrations in dorsal view, so the reassignment of Westergårds illustrated material may be taken as tentative.

The semi-complete specimen illustrated by Henningsmoen (1957, pl. 18, fig. 1) as *C. flagellifera* has distinct, elongate S1 and is here allocated to *S. drytonensis*.

Ctenopyge acadica Matthew, 1894 was synonymized with *S. flagellifer* by Henningsmoen (1957). However, the drawn illustration of the *C. acadica* cranidium (Matthew 1894, pl. 17, fig. 13a) shows a transglabellar S1 as well as short S2 and S3 furrows and this pattern was described also in the accompanying text. Hence, it is unlikely that *C. acadica* is a synonym of *S. flagellifer*. The genal spine is also drawn rather short, *drytonensis*-like, but there is not indicated an asymmetry of the inner and outer genal angle and the posterior border is not widening. For the time being we prefer an assignment of the Bornholm material to *S. drytonensis*, which in Scandinavia is a well-defined taxon. A restudy of the type material of *C. acadica* and notably its free cheek is needed to unravel whether or not it is a senior synonym of *S. drytonensis*; for the time being we regard *C. acadica* as a *nomen dubium*.

***Sphaerophthalmus flagellifer* Angelin, 1854**

Fig. 35A–O.

1922 *Ctenopyge flagellifera* (Angelin) [*partim*] – Westergård, pp. 152–152, pl. X, fig. 20; non figs 19, 21a; pl. XI, fig. 1 [= *S. drytonensis*; see remarks on this species above].

v 1923 *Ctenopyge flagellifera* Angelin [*partim*] – C. Poulsen, pp. 38–39, non textfig. 15; pl. 1, figs 12–13 [= *S. drytonensis*].

v 1923 *Ctenopyge flagellifera* Angelin var. *angusta* Westergård [*partim*] – C. Poulsen, p. 39.

Non 1952 *Ctenopyge flagellifera* (Angelin) – Hutchinson, pp. 87–88, pl. IV, fig. 11.

1957 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) [*partim*] – Henningsmoen, pp. 189–191, pl. 2, fig. 17; pl. 5; pl. 18, figs 2–4, non fig. 1 [= *S. drytonensis*].

1973 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) – Schrank, p. 822, pl. VI, figs 13, ?14, ?15.

2012 *Sphaerophthalmus flagellifer* Angelin, 1854 – Høyberget & Bruton, pp. 442–444, figs 4E, 9A–H.

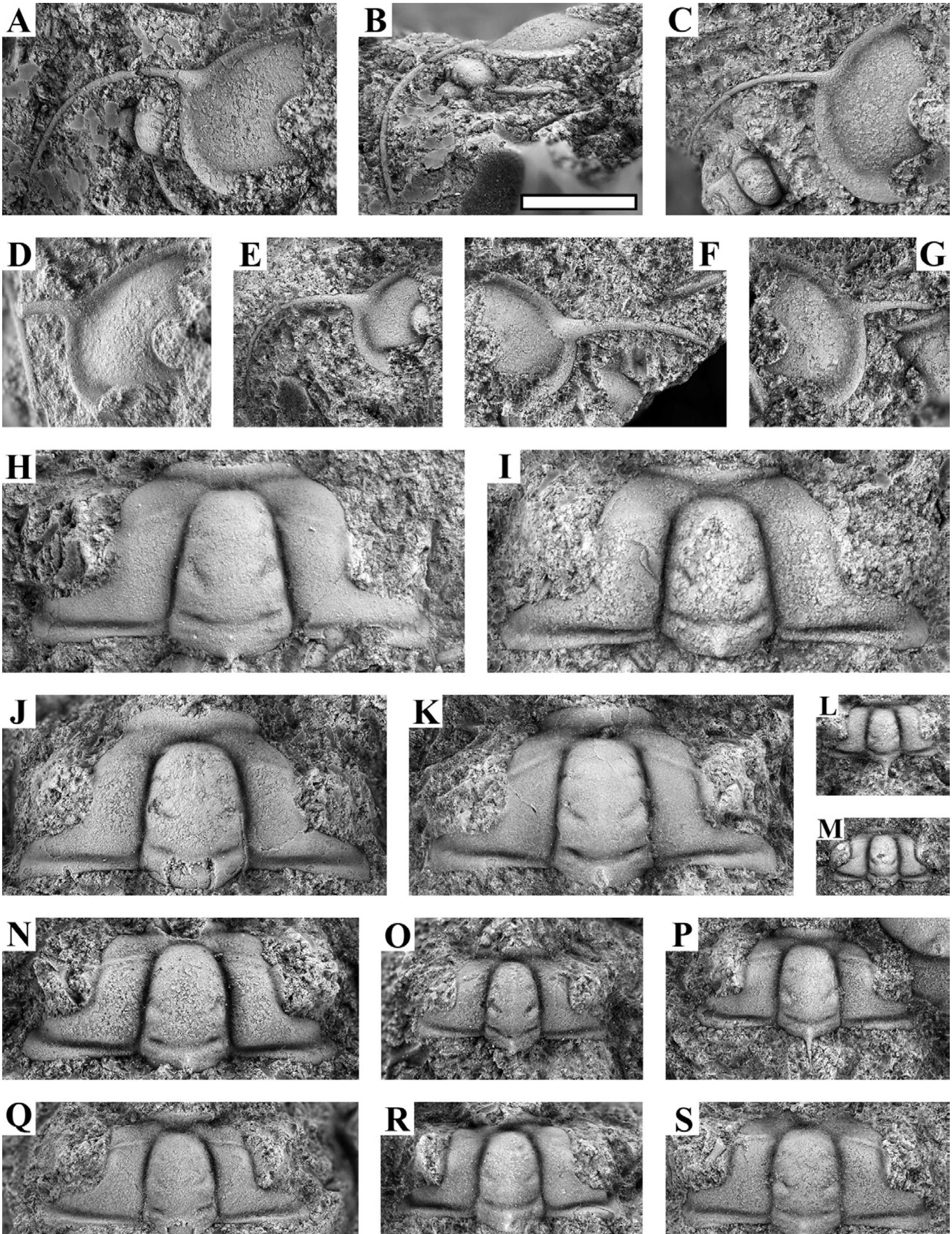
2017 *Sphaerophthalmus flagellifer* Angelin, 1854 – Rasmussen *et al.*, p. 22.

For further synonymy, see Høyberget & Bruton (2012) and Rasmussen *et al.* (2017).

Neotype. Free cheek SGU 5510 from Andrarum, southern Sweden, the same locality as Angelin's lost type specimen derived from, designated by Henningsmoen (1957). Illustrated by Linnarsson (1880, pl. 1, fig. 14) and Westergård (1922, pl. X, fig. 20).

Material. 207 cranidia and 41 free cheeks, all from locality 6. The species is associated with common

▲ **Fig. 33.** *Sphaerophthalmus angustus*, all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A:** Large cranidium, sample L60 (MGUH 33851). **B:** Cranidium, sample GM 1922-141P (MGUH 33825). **C:** Cranidium, sample L92 (MGUH 33852). **D:** Free cheek, note the straight posterior margin, sample L80 (MGUH 33836). **E:** Free cheek, note the straight posterior margin, sample ATN-145 (MGUH 33840). **F:** Large cranidium, sample L78 (MGUH 33853). **G:** Large cranidium, sample GM 1922-141P (MGUH 33826). **H:** Cranidium, sample L124 (MGUH 33854). **I:** Cranidium, sample GM 1922-141P (MGUH 33822). **J:** Cranidium, sample L124 (MGUH 33855). **K:** Cranidium with preserved occipital spine and unusually short glabella, sample L80 (MGUH 33837). **L:** Cranidium with preserved occipital spine, sample L57 (MGUH 33833). **M:** Cranidium with preserved occipital spine, sample GM 1922-141P (MGUH 33827). **N.** Cranidium, sample ATN-151 (MGUH 33856). **O:** Juvenile cranidium, sample GM 1922-141P (MGUH 33823).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Sphaerophthalmus drytonensis whereas *Protopeltura praecursor* has been found in only one sample.

Occurrence. Common in the eponymous zone in Scandinavia, Great Britain and Canada (Westergård 1922; Henningsmoen 1957; Høyberget & Bruton 2012). In the Oslo Region, the species ranges into the lowermost *S. modestus–S. angustus* Zone (Høyberget & Bruton 2012). C. Poulsen (1923) reported '*Ctenopyge*' *flagellifera* only from the eponymous (sub)zone on Bornholm but the majority of the specimens in the museum collection represents *S. drytonensis*.

Comparison. *Sphaerophthalmus flagellifer* can be differentiated from *S. modestus* by the presence of an occipital spine, and by having more slender (exsag.) and longer (tr.) postocular cheeks. The genal spine is also located much further forwards in the free cheeks of *S. flagellifer*. *Sphaerophthalmus flagellifer* has wider (tr.) and longer (exsag.) postocular cheeks than *S. angustus* and midline of the eyes is situated opposite S2 compared to S1 in *S. angustus*. For comparison with *S. drytonensis,* see that species.

Remarks. Høyberget & Bruton (2012) gave a thorough description of *S. flagellifer* including a drawn reconstruction of a complete specimen (*ibid*. fig. 4E). This was, however, based on small specimens, and they stated that the posterior lateral margin of the free cheek becomes longer in larger specimens (and thus displaces the genal spine forwards). For comments on assignment of the cranidia illustrated by Westergård (1922) and C. Poulsen (1923), see remarks on *S. drytonensis*. The thoraxes and pygidia illustrated by Westergård (1922) cannot be assigned to species for the time being, as these skeletal parts of *S. drytonensis* are unknown.

The poorly illustrated *C. flagellifera* from Cape Breton Island, Canada, reported by Hutchinson (1952), has a distinct S1 and is not likely to represent *S. flagellifer*. The illustration does not permit a reassignment.

Westergård (1922) and Henningsmoen (1957) discussed *Ctenopyge falcifera* Lake, 1923 as a possible synonym of *S. flagellifer*. The specimen is preserved in shale and the free cheek is unknown. Lake (1913) described S1 as 'decidedly oblique' which is not bringing the rounded outlined typical for *S. flagellifer* to mind, but further considerations are pointless until better preserved material (including free cheeks) becomes available.

Genus *Triangulopyge* Høyberget & Bruton, 2012

Type species: *Olenus humilis* Phillips, 1848, by original designation.

***Triangulopyge humilis* (Phillips, 1848)**

Fig. 36.

1922 *Sphærophthalmus alatus* (Boeck) – Westergård, pp. 165–166, pl. XIII, figs 20–29.

v 1923 *Sphaerophthalmus alatus* Boeck – C. Poulsen, pp. 49–50.

1957 *Sphaerophthalmus humilis* (Phillips 1848) – Henningsmoen, pp. 215–217, pl. 5; pl. 22, figs 7, 11–15.

1973 *Sphaerophthalmus humilis* (Phillips, 1848) – Schrank, pp. 837–838, pl. XII, figs 14–30.

2012 *Triangulopyge humilis* (Phillips, 1848) – Høyberget & Bruton, p. 447, figs 12A, 13A–J.

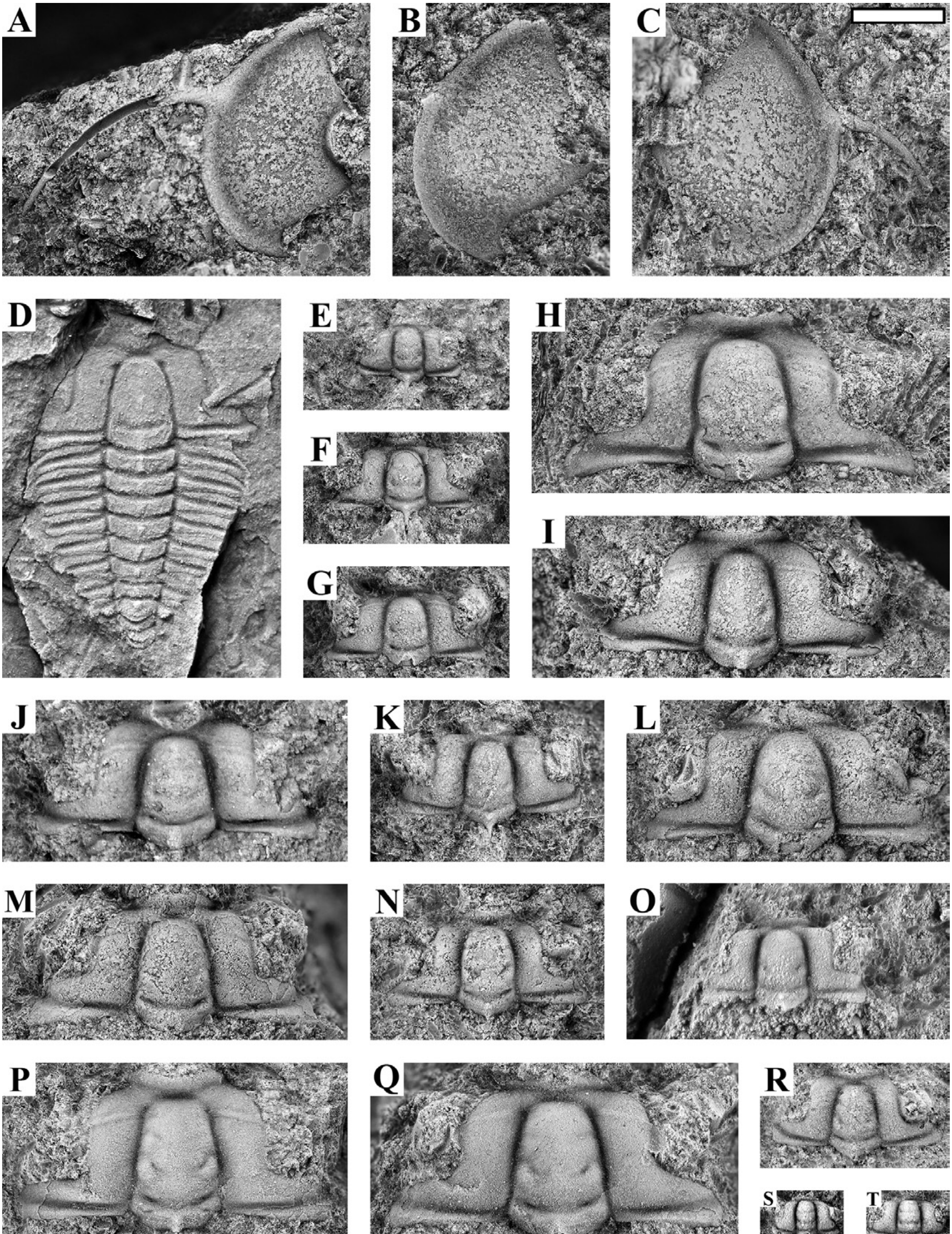
2017 *Triangulopyge humilis* (Phillips, 1848) – Rasmussen *et al.*, pp. 22–23, fig. 10B.

For further synonymy, see Høyberget & Bruton (2012) and Rasmussen *et al.* (2017).

Lectotype. Cranidium Ox A287a from the Phillips collection, collected from the White Leaved Oak Shale, Malvern, United Kingdom. Figured by Rushton (1968, pl. 78, fig. 13) and designated by Høyberget & Bruton (2012).

Material. 610 cranidia, five free cheeks and eight pygidia, but the far majority of specimens have not been registered as preparation is needed for safe assignment. The material predominantly derives from locality 6, but a few specimens were collected at Limensgade (localities 8A–B), three samples are from 'Cementen' (i.e. ice-rafted material, Øleå) and one is not labelled. C. Poulsen (1923) reported the species (as *S. alatus*) also from locality 7 but no material from that site is

▲ **Fig. 34.** *Sphaerophthalmus drytonensis,* all preserved in anthraconite from locality 6. White scale bar: 2 mm. **A–B:** Free cheek, dorsal and posterior view, sample L23 (MGUH 33857). **C:** Free cheek, sample ATN-105 (MGUH 33858). **D:** Free cheek, sample ATN-256 (MGUH 33869). **E:** Free cheek, small specimen, sample ATN-105 (MGUH 33859). **F:** Free cheek, sample GM 1922-140C (MGUH 33870). **G:** Free cheek, sample L24 (MGUH 33871). **H:** Large cranidium, sample ATN-105 (MGUH 33860). **I:** Large cranidium, previously illustrated by C. Poulsen (1923 pl. I, fig. 13) as *C. flagellifera* (MGUH 1966). **J:** Cranidium, sample ATN-131 (MGUH 33872). **K:** Cranidium, sample ATN-105 (MGUH 33861). **L:** Small cranidium with intact occipital spine, sample L19 (MGUH 33873). **M:** Cranidium, sample GM 1922-140B (MGUH 33875). **N:** Cranidium, sample L29 (MGUH 33880). **O:** Cranidium, sample L29 (MGUH 33881). **P:** Cranidium with intact occipital spine, sample ATN-105 (MGUH 33862). **Q:** Cranidium, sample ATN-181 (MGUH 33883). **R:** Cranidium, sample ATN-105 (MGUH 33863). **S:** Cranidium, sample L27 (MGUH 33884).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kept in the museum collection. *Triangulopyge humilis* co-occurs with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons* and *P. scarabaeoides* in the studied samples. The report of this species (under the name *S. alatus*) from the *P. lobata* [*'longicornis'*] Zone (C. Poulsen 1923) is an error, see 'Discussion and conclusions'.

Occurrence. Extremely common in the *P. scarabaeoides* Zone in Scandinavia (Høyberget & Bruton 2012) including Bornholm (this study). *Triangulopyge humilis* was listed also from the *P. lobata* Zone by Terfelt *et al.* (2008), based on Ahlberg *et al.* (1995) who reported phosphatized juvenile specimens from Västergötland. However, that material is considered reworked herein. Outside Scandinavia, *T. humilis* is known from Poland, England, Wales and Canada (Westergård 1922, 1947; Henningsmoen 1957; Żylińska 2001, 2002).

Comparison. In comparison with *T. majusculus*, the cranidium of *T. humilis* is narrower with interocular cheeks that are less than half as wide as glabella at eye-line and postocular cheeks that are about ⅔ as wide (tr.) as the occipital ring, while *T. majusculus* has interocular cheeks that are just slightly narrower than glabella at eye-line and the postocular cheeks are about as wide as the occipital ring. *Triangulopyge humilis* also has an occipital spine, a feature not seen in *T. majusculus* (however, often the spine is not preserved). *Triangulopyge majusculus* has a more rounded and wider pygidium compared to *T. humilis* which has pleural fields markedly narrower than the axis and a more equilateral triangular pygidial outline.

The small cranidia of *T. humilis* and *S. alatus* are superficially somewhat alike, but the palpebral lobes are situated opposite L1 in *T. humilis* and opposite S1 in *S. alatus* and the fixed cheeks are widening (tr.) in front of the palpebral lobes in *T. humilis*, which is very characteristic. Comparing larger cranidia, *S. alatus* has a more distinctly tapering glabella with a rounded front; in *T. humilis* the glabella is less pronouncedly tapering and the antero-glabella is parallel-sided with a more truncate front; S1 is also shallow mesially in *S. alatus*, unlike in *T. humilis*. The two species are readily separated by their pygidia, as *S. alatus* has a long caudal spine, unlike *T. humilis*, but the tiny pygidia are easily overlooked, and registered specimens are rare in the material at hand.

Remarks. We have observed that the occipital spine is longer in small specimens than in large cranidia (Fig. 36).

Genus *Protopeltura* Brøgger, 1882

Type species: *Peltura praecursor* Westergård, 1909, designated by Henningsmoen (1958b).

***Protopeltura planicauda* (Brøgger, 1882)**

Fig. 37E

1922 *Peltura planicauda* Brögger – Westergård, p. 173, pl. XV, fig. 2.

1957 *Protopeltura planicauda* (Brögger 1882) – Henningsmoen, pp. 228–229, pl. 6; pl. 24, figs 11–13.

2017 *Protopeltura planicauda* (Brøgger, 1882) – Rasmussen *et al.*, p. 20, figs 9A–B.

For further synonymy, see these references.

Lectotype. Pygidium PMO H2715a from Slemmestad, Norway, originally figured by Brøgger (1882, pl. II, fig. 8). Designated and refigured by Henningsmoen (1957, pl. 24, fig. 13).

Material. One pygidium from locality 6. This is the first record of this species from Bornholm.

Occurrence. Sphaerophthalmus modestus–S. angustus and *P. acutidens–C. tumida* zones in Scandinavia (Westergård 1947; Henningsmoen 1957; Rasmussen *et al.* 2016, 2017). The single specimen at hand co-occurs with *C. tumidoides* and *S. angustus*, suggestive of the *S. modestus–S. angustus* Zone (but see section on 'Olenid zonation').

▲ **Fig. 35.** *Sphaerophthalmus flagellifer* (A–O) and *Sphaerophthalmus drytonensis* (P–T), preserved in anthraconite except D (flattened, preserved in shale). All specimens are from locality 6. White scale bar: 2 mm. *Sphaerophthalmus flagellifer*: **A:** Free cheek, sample L26 (MGUH 33885). **B:** Free cheek, spine is not preserved, sample L26 (MGUH 33886). **C:** Free cheek, sample L28 (MGUH 33889). **D:** Cranidium with thorax, tentatively assigned; this specimen may alternatvely represent *S. drytonensis*, sample GM 1872-1070 (MGUH 33891). **E–F:** Small cranidia with comparaticely distinct S1, sample GM 1922-140B (MGUH 33876 & 33877). **G:** Small cranidium, sample ATN-215 (MGUH 33892). **H:** Large cranidium, sample GM 1922-140B (MGUH 33879). **I:** Cranidium, sample L26 (MGUH 33887). **J:** Cranidium, sample GM 1922-140B (MGUH 33878). **K:** Cranidium, sample L26 (MGUH 33888). **L:** Cranidium with slightly elongate S1, but which do not reach the axial furrows, sample L19 (MGUH 33874). **M:** Cranidium, with slightly elongate but very shallow S1 that do not reach the axial furrows, sample GM 1897 (MGUH 33893). **N:** Cranidium, sample L28 (MGUH 33890). **O:** Cranidium, sample ATN-125 (MGUH 33894). **P:** Large cranidium with comparatively distinct S2 and S3 furrows, sample ATN-105 (MGUH 33864). **Q:** Large cranidium, sample ATN-105 (MGUH 33865). **R:** Cranidium, sample L29 (MGUH 33882). **S:** Juvenile cranidium, tentatively assigned, sample ATN-105 (MGUH 33866). **T:** Juvenile cranidium, tentatively assigned, sample ATN-105 (MGUH 33867).

Comparison. In comparison with *P. bidentata*, the pygidium of *P. planicauda* is wider with a rounded outline, while the former has a slightly more triangular overall shape.

Protopeltura praecursor **Westergård, 1909**
Fig. 37D

1922 *Protopeltura præcursor* (Westergård) – Westergård, p. 171, pl. XIV, figs 23–29, 31; pl. XV, fig. 1.
1957 *Protopeltura praecursor* (Westergård 1909) – Henningsmoen, pp. 229–230, Pl. 2, fig. 2; pl. 6; pl. 24, figs 1-5.
2017 *Protopeltura praecursor* (Westergård, 1909) – Rasmussen *et al*., p. 21.

For a complete list of synonymy, see Henningsmoen (1957) and Rasmussen *et al.* (2017).

Lectotype. Pygidium PM0 H 2716b [not 2715a as stated by Henningsmoen 1957, p. 229] from Nærsnæs, Norway, originally figured by Brøgger (1882, pl. I, fig. 14c). Designated and refigured by Henningsmoen (1957, pl. 24, fig. 5).

Material. One pygidium, collected at locality 6. It co-occurs with common *S. drytonensis* and *S. flagellifer.*

Occurrence. Comparatively long-ranging species recorded from the *L. neglectus*, *L. postcurrens* and *S. flagellifer* zones in Scandinavia (Nielsen *et al*. 2020). This is the first record of *P. praecursor* from Bornholm.

Comparison. *Protopeltura praecursor* cannot be confused with any other species occurring in the *S. flagellifer* Zone.

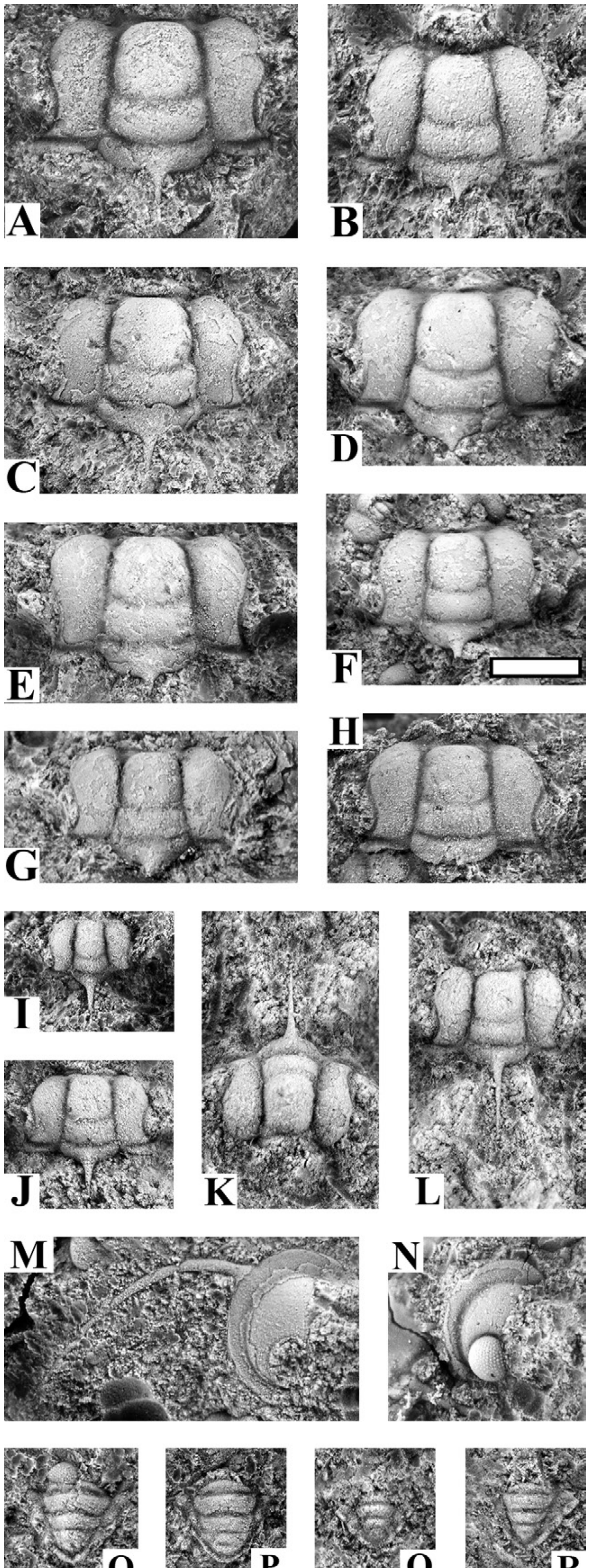

Fig. 36. *Triangulopyge humilis*, all preserved in anthraconite from locality 6. White scale bar is 1 mm. **A**. Large cranidium, sample L41 (MGUH 33787). **B**. Cranidium, sample L45 (MGUH 33895). **C**. Cranidium, sample L39 (MGUH 33896). **D.** Cranidium, sample L38 (MGUH 33791). **E.** Cranidium, sample L39 (MGUH 33897). **F.** Cranidium, sample L43 (MGUH 33769). **G.** Cranidium, sample L42 (MGUH 33898). **H**. Small cranidium with occipital spine, sample GM 1871-671 (MGUH 33899). **I.** Small cranidium with occipital spine, sample GM 1922-142A (MGUH 33779). **J.** Small cranidium with occipital spine, sample GM 1871-671 (MGUH 33900). **K-L.** Small cranidium with occipital spine, frontal and dorsal view, sample GM 1871-675A (MGUH 33901). **M**. Free cheek, sample GM 1922-142I (MGUH 33752). **N**. Free cheek, sample GM 1922-142I (MGUH 33753). **O.** Pygidium, sample L48 (MGUH 33782). **P.** Pygidium, sample L38 (MGUH 33792). **Q.** Pygidium, sample GM 1922-142A (MGUH 33778). **R**. Pygidium, sample GM 1922-142J (MGUH 33795).

Genus *Peltura* Milne Edwards, 1840
Type species: *Entomostracites scarabæoides* Wahlenberg, 1818, designated by Hawle & Corda (1847).

***Peltura acutidens* Brøgger, 1882**
Fig. 37A–C

1922 *Peltura scarabæoides acutidens* Brögger – Westergård, p. 175, pl. XV, figs 14–17.
1957 *Peltura acutidens* Brögger 1882 – Henningsmoen, pp. 233–234, pl. 6; pl. 25, figs 1, 3, 4, 7, 9, 11.
1973 *Peltura acutidens* Brögger, 1882 – Schrank, pp. 940–841, pl. XIV, figs 2–7.

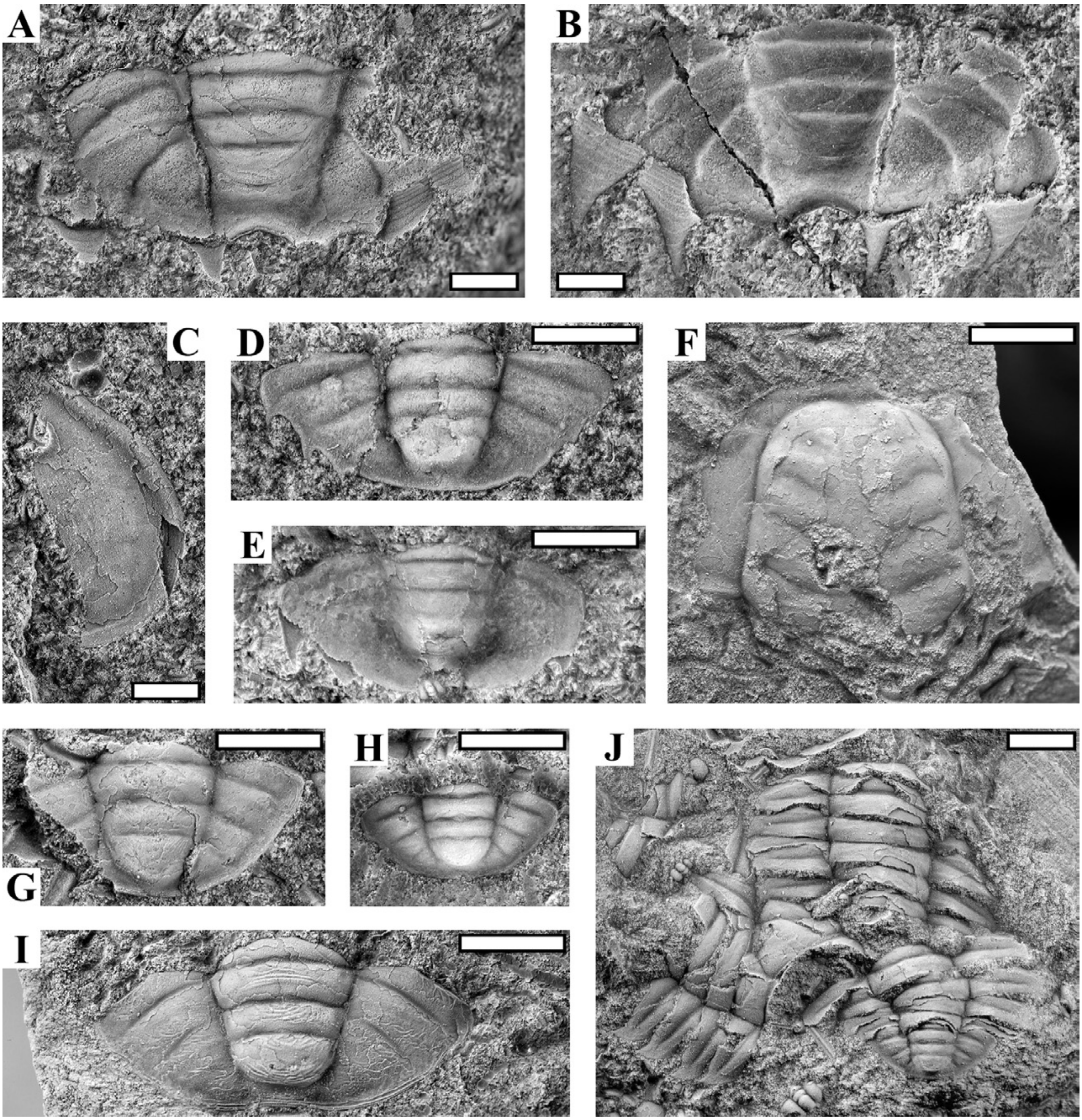

Fig. 37. Pelturids, all preserved in anthraconite from locality 6. White scale bars: 2 mm. **A–C:** *Peltura acutidens.* **A:** Pygidium, sample ATN-327 (MGUH 33902a). **B:** External mould of the specimen illustrated in A showing marginal spines, sample ATN-111 (MGUH 33902b). **C:** Free cheek, sample L82 (MGUH 33903). **D:** *Protopeltura praecursor,* sample ATN-105 (MGUH 33868). **E:** *Protopeltura planicauda,* sample ATN-145 (MGUH 33841). **F–J:** *Peltura minor.* **F:** Cranidium which may belong to one of the thoraxes illustrated in J: Sample ATN-127 (MGUH 33904). **G:** Pygidium, sample ATN-132 (MGUH 33732). **H:** Pygidium, sample ATN-139 (MGUH 33850). **I:** Pygidium, sample ATN-113 (MGUH 33718). **J:** Incomplete thoraxes (two specimens) with pygidium, sample ATN-127 (MGUH 33905).

2017 *Peltura acutidens* Brøgger, 1882 – Rasmussen *et al.*, p. 18.

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Pygidium PMO H 2720, collected at Slemmestad, Norway, and originally figured by Brøgger (1882, pl. II, fig. 9). Designated and refigured by Henningsmoen (1957, pl. 25, fig. 11).

Material. One pygidium and one free cheek (?) found at locality 6. *Ctenopyge tumidoides* and *S. angustus* occur in the same samples.

Occurrence. Characteristic for the *P. acutidens*–*C. tumida* Zone and known from Scandinavia and Poland (Westergård 1922, 1947; Henningsmoen 1957; Rasmussen *et al.* 2016, 2017; Żylińska 2001, 2002). This is the first report of *P. acutidens* from Bornholm, where it seems to be exceedingly rare as many limestone samples are at hand from the *P. acutidens*–*C. tumida* Zone.

Comparison. Cranidia and free cheeks of *P. acutidens, P. minor, P. scarabaeoides* and *P. westergaardi* are essentially similar and no effort has been made to assign these skeletal parts; pygidia are needed in order to safely identify these species. *Peltura minor* pygidia are readily identified by their lack of marginal spines. In *P. scarabaeoides,* the distance between the inner pair of marginal spines is slightly wider than the anterior half ring; in *P. westergaardi* the distance is equal to or slightly narrower than the anterior half ring and in *P. acutidens* the distance is marginally narrower than the terminal piece. The axis is relatively wide in pygidia of *P. scarabaeoides*, anteriorly occupying >0.4 of the pygidial width, vs. less than 0.4 in the other species discussed. External terrace lines are more extensive on pygidia of *P. scarabaeoides* than seen on *P. westergaardi* pygidia. The border in *P. acutidens* is also more distinct than in *P. scarabaeoides*. *Peltura scarabaeoides* has moderately short marginal spines that typically are bent downwards, while *P. acutidens* and *P. westergaardi* have significantly longer spines and they are typically horizontal. The pygidium of *P. acutidens* is relatively wide with markedly wider pleural fields than in the pygidia of *P. scarabaeoides* and *P. westergaardi*.

Peltura minor **(Brøgger, 1882)**

Fig. 37F–J

1922 *Peltura minor* (Brögger) – Westergård, p. 175, pl. XV, figs 3–11.

1947 *Peltura minor* (Brögger) – Westergård, pl. 2, fig. 12.

1957 *Peltura minor* (Brögger 1882) – Henningsmoen, pp. 235–236, pl. 6; pl. 25, figs 2, 5.

1973 *Peltura minor* (Brögger, 1882) – Schrank p. 841, pl. XIV, figs 8–9.

2003 *Peltura minor* (Brøgger, 1882) – Terfelt, p. 412, fig. 4K.

2017 *Peltura minor* (Brøgger, 1882) – Rasmussen *et al.*, pp. 18–19.

For further synonymy, see Rasmussen *et al.* (2017).

Lectotype. Pygidium PMO no H 2713a from Slemmestad, Norway, originally figured by Brøgger (1882, pl. II, fig. 10). Designated and refigured by Henningsmoen (1957, pl. 25, fig. 5).

Material. Six pygidia incl. one with nine contiguous thoracic segments, all from locality 6. *Peltura minor* co-occurs with *C. affinis, C. ahlbergi, C. magna* n. sp. and *S. alatus* in the samples at hand.

Occurrence. Characteristic for the *P. acutidens*–*C. tumida* Zone in Scandinavia (Westergård 1922, 1947; Henningsmoen 1957; Rasmussen *et al.* 2016, 2017), but with an upper range into the very base of the *P. scarabaeoides* Zone (e.g. Westergård 1922, figs 11, 26; Høyberget & Bruton 2012, fig. 2). On Bornholm, it appears to be typical of the upper part of the *P. acutidens–C. tumida* Zone. It is a general trait that *P. minor* appears slightly above the base of the *P. acutidens*–*C. tumida* Zone in Scandinavia (cf. Westergård 1922).

Comparison. For comparison with *P. acutidens* and *P. scarabaeoides,* see the former.

Remarks. This species has not been reported from Bornholm previously and it seems to be infrequent, as many samples are at hand from the *P. acutidens*–*C. tumida* Zone. Henningsmoen (1957) defined a *P. minor* Zone, subdivided into four subzones. However, *P. minor* has its FAD in the *P. acutidens*–*C. tumida* Zone and does not occur in the lower two subzones defined for the zone by Henningsmoen. The reported presence in older strata appears to be a *lapsus calami* (Nielsen *et al.* 2020).

Peltura scarabaeoides **(Wahlenberg, 1818)**

Fig. 38

1922 *Peltura scarabæoides* (Wahlenberg) [*partim*] – Westergård, pp. 173–174, pl. XV, fig. 18; non pl. XV, figs 12–13 [= *Peltura westergaardi*, see remarks].

v 1923 *Peltura scarabaeoides* Wahlenberg [*partim*] – C. Poulsen, pp. 50–52, textfig. 18; pl. II, figs 6–7; non pp. 58–59, textfig. 22 [= *P. westergaardi*].

1957 *Peltura scarabaeoides scarabaeoides* (Wahlenberg 1821) – Henningsmoen, pp. 237–239, pl. 2, fig. 1; pl. 6; pl. 25, figs 6, 13–14; pl. 26, figs 1–2.

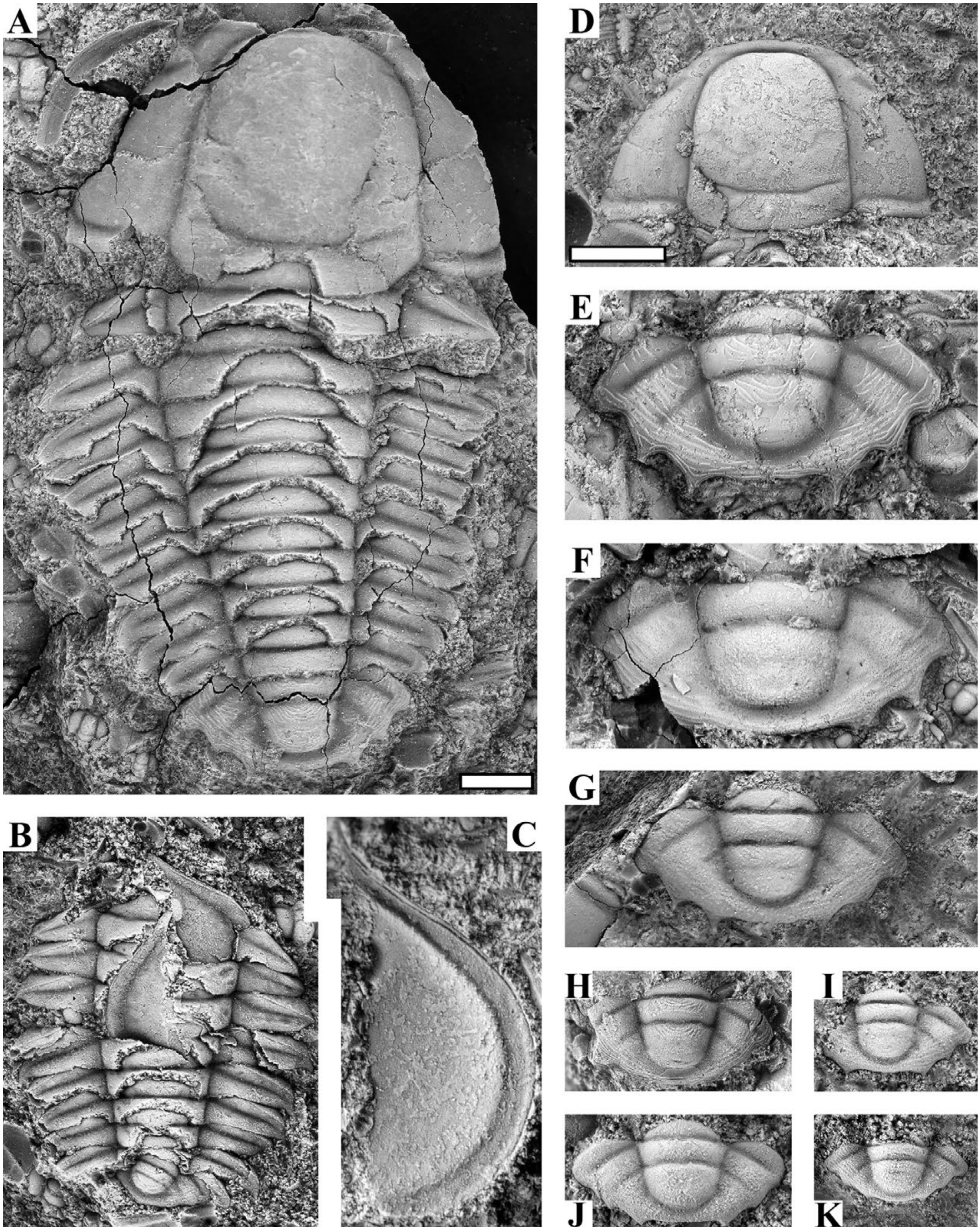

Fig. 38. *Peltura scarabaeoides*, all preserved in anthraconite. White scale bars: 2 mm; note that A is shown at smaller magnification. **A:** Almost complete specimen, found in the Læså stream near Vasagård [probably loc. 6], sample GM 1881-1805 (MGUH 33906). **B:** Pygidium with seven thoracic segments and two partly visible free cheeks, probably exuvium, 'Cementen', Øleå, sample GM 1874-30 (MGUH 33907). **C:** External mould of free cheek, loc. 6, sample L43 (MGUH 33770). **D:** Cranidium possibly belonging to this species, loc. 6, sample GM 1922-142B (MGUH 33799). **E:** Pygidium, found in the Læså area between Hjulmagergård and Vasagård [probably loc. 6], sample GM 1871-626 (MGUH 33908). **F:** Pygidium, loc. 6, sample GM 1922-142C (MGUH 33909). **G:** Pygidium, loc. 6, sample GM 1922-142I (MGUH 33756). **H:** Pygidium, loc. 6, sample GM 1922-142I (MGUH 33757). The broad-based marginal spines point downwards in this small specimen and are difficult to see in dorsal view. **I–K:** Three pygidia, locs 8A–B, sample L17 (MGUH 33742, 33743, 33744).

Non 1958 *Peltura scarabaeoides* (Wahlenberg 1821) – Whittington, pp. 200–206, pl. 38. [= *P. westergaardi*].
1973 *Peltura scarabaeoides scarabaeoides* (Wahlenberg, 1821) [*partim*] – Schrank, pp. 841–842; pl. XIV, fig. 10–15,17–23; non pl. XIV, fig. 16 [= *P. westergaardi*].
2003 *Peltura scarabaeoides* (Wahlenberg 1821) – Terfelt, p. 412, fig. 4I.
2016 *Peltura scarabaeoides scarabaeoides* – Ahlberg *et al.*, p. 498, figs 4, 6H.
2017 *Peltura scarabaeoides scarabaeoides* (Wahlenberg, 1818) – Rasmussen *et al.*, pp. 19–20.
For further synonymy, see Rasmussen *et al.* (2017).

Type material. Not designated, see Henningsmoen (1957).

Material. One almost complete specimen (Fig. 38A) and 84 pygidia, incl. one with eight contiguous thoracic segments. The majority of the material derives from locality 6, with additional material collected at 'Cementen' (Øleå) and Limensgade (localities 8A–B). C. Poulsen (1923) reported the species also from locality 7 but no material from that site is kept in the museum collection. 160 cranidia, including one with ten attached thoracic segments, and 112 free cheeks from samples with safely assigned pygidia are tentatively assigned. *Peltura scarabaeoides* co-occurs with *C. linnarssoni*, *C. pecten*, *C. tenuis*, *C. teretifrons*, and *T. humilis* in the samples at hand.

Occurrence. Characteristic for the eponymous zone in Scandinavia, Poland, Great Britain and Canada (Westergård 1922, 1947; Henningsmoen 1957; Żylińska 2001, 2002). *Peltura scarabaeoides* occurs at the same stratigraphic level on Bornholm.

Comparison. See *P. acutidens*.

Remarks. Three samples from a well south of Lille Duegård (GM 2019-93, GM 2019-94, GM 2019-95), collected by Grönwall, and labelled as *P. scarabaeoides*, contain numerous *P. westergaardi* occurring alone

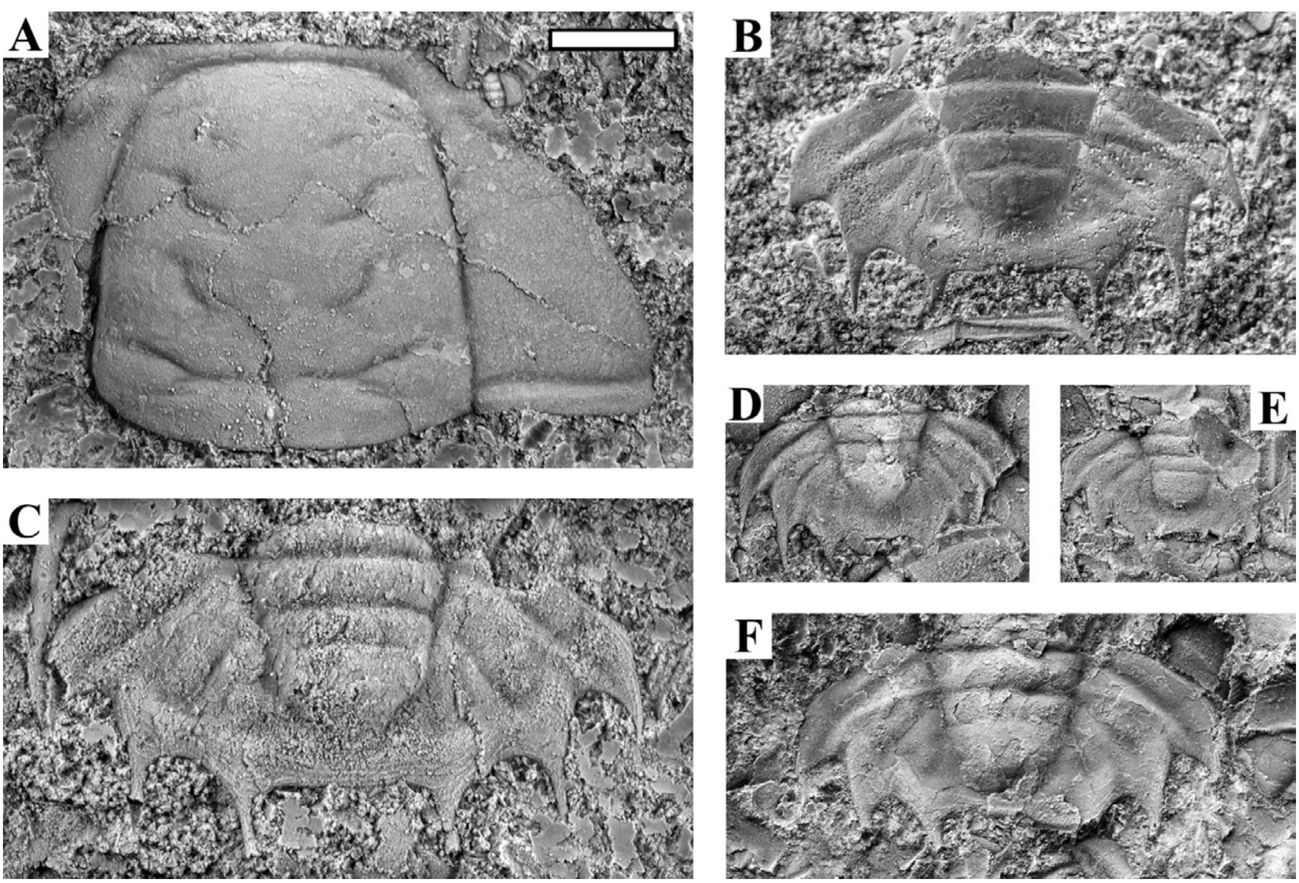

Fig. 39. *Peltura westergaardi*, all preserved in anthraconite from localities 8A–B: White scale bar: 2 mm. **A:** Cranidium presumably belonging to this species, sample L16 (MGUH 33573). **B:** External mould of pygidium, sample L10 (MGUH 33910). **C:** Pygidium, sample L11 (MGUH 33911). **D:** Pygidium, sample L13 (MGUH 33912). **E:** Pygidium, sample L14 (MGUH 33913). **F:** Pygidium, sample L15 (MGUH 33914).

including many juveniles treated by C. Poulsen (1923) and Whittington (1958).

Two complete specimens figured by Westergård (1922, pl. XV, figs 12–13) have pygidia with rather long horizontal marginal spines, relatively narrow axis and the distance between the inner spine pair is smaller than the anterior axial width. Westergård (*ibid*. p. 174) considered these as transitional to *acutidens*, and described that such forms with marginal spines co-occur with *scarabaeoides* in Närke and on Kinnekulle. Unpublished material from the latter locality shows extensive stratigraphical overlap between *P. scarabaeoides* (partly reworked?) and *P. westergaardi*. We identify the discussed specimens illustrated by Westergård as *P. westergaardi*.

Peltura westergaardi **Henningsmoen, 1957**

Fig. 39

1922 *Peltura scarabæoides* (Wahlenberg) [*partim*] – Westergård, pp. 173–174, pl. XV, figs 12–13. [See remarks on *P. scarabaeoides* above].

v 1923 *Peltura scarabaeoides* Wahlenberg [*partim*] – C. Poulsen, pp. 58–59, textfigs 18, 22.

1957 *Peltura scarabaeoides westergaardi* n. subsp. – Henningsmoen, pp. 239–240, pl. 7; pl. 25, figs 8, 10, 12, 15–17.

v 1958 *Peltura scarabaeoides* (Wahlenberg 1821) – Whittington, pp. 200–206, pl. 38.

1973 *Peltura scarabaeoides scarabaeoides* (Wahlenberg, 1821) [*partim*] – Schrank, pl. XIV, fig. 16.

1973 *Peltura scarabaeoides westergaardi* Henningsmoen, 1957 – Schrank, p. 843; pl. XV, figs 1–6.

2017 *Peltura scarabaeoides westergaardi* (Henningsmoen, 1957) – Rasmussen *et al.*, p. 20, fig. 9D.

For further synonymy, see Rasmussen *et al.* (2017).

Holotype. Cranidium SGU 4255 from Åkarpsmölle, Sweden, figured by Westergård (1944, pl. 3, fig. 3).

Material. 25 pygidia. In addition, one cephalon, 116 cranidia, 2 hypostomes and 12 free cheeks from samples with safely identified pygidia are tentatively assigned. The majority of the material derives from Limensgade (localities 8A–B), where *P. westergaardi* co-occurs with *P. (N.) lobata praecurrens* and rare orthid brachiopods. A few samples are from a well south of Ll. Duegård, see remarks.

Occurrence. Parabolina lobata Zone in Scandinavia and possibly Poland (Westergård 1947; Henningsmoen 1957; Żylińska 2001, 2002; Rasmussen *et al*. 2017). This is the first record from Bornholm where *P. westergaardi* occurs at the same stratigraphic level. In the Oslo Region, *P. westergaardi* has its FAD in the uppermost part of the *P. scarabaeoides* Zone (Nielsen *et al*. 2020) and this also seems to be the case on Kinnekulle, Västergötland (unpublished).

Comparison. See *Peltura acutidens.*

Remarks. We prefer to treat this taxon at species rather than subspecies level. Samples GM 2019-93 to -95 collected from a well south of Ll. Duegård (for location, se Fig. 2A) contains many juveniles as well as several adult *P. westergaardi*, occurring alone. The well-preserved juveniles were treated by C. Poulsen (1923) and Whittington (1958) (as *P. scarabaeoides*) (their illustrated specimens are numbered MGUH 1987, 1988, 1989).

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Appendix 1. List of registered material; the samples also contain many non-prepared specimens that have not been counted. The fossils are preserved in anthraconite (bituminous limestone) unless otherwise stated.

Appendix 1: List of material

The fossils are preserved in anthraconite (bituminous limestone) unless otherwise stated.

Agnostus pisiformis **(Wahlenberg, 1818).** *4 complete specimens, 173 cephala and 148 pygidia*. Samples L1 (5 cephala, 6 pygidia), L2 (13 cephala, 10 pygidia, 1 complete specimens), GM 864 (11 cephala, 6 pygidia), GM 1870-538 (8 cephala, 10 pygidia), GM 1870-832 (2 cephala, 1 pygidium), GM 1870-834 (3 cephala, 3 pygidia), GM 1870-835 (14 cephala, 8 pygidia), GM 1870-836 (11 cephala, 9 pygidia), GM 1870-837 (9 cephala, 5 pygidia), GM 1877-2002 (25 cephala, 26 pygidia), GM 1883-340 (12 cephala, 11 pygidia), GM 1922-132A (16 cephala, 11 pygidia), GM 1922-132C (19 cephala, 17 pygidia), GM 1922-132B (4 cephala, 3 pygidia), GM 1922-144 (complete specimen), GM 1922-145 (pygidium), GM 1922-146A (5 cephala, 12 pygidia), GM 1922-146B (cephalon, 2 pygidia, 1 complete specimen), GM 2019-29 (2 cephala), GM 2019-30 (cephalon), GM 2019-31 (4 cephala, 3 pygidia), GM 2019-32 (cephalon), GM 2019-33 (2 cephala, 3 pygidia), GM 2019-91 (2 cephala, 1 pygidium), unnumbered sample incl. MGUH 1954 (3 cephala, 1 complete specimen).

Homagnostus obesus **(Belt, 1867)**. *10 complete specimens, 70 cephala and 82 pygidia.* Samples (all shale): ATN-323 (4 pygidia) (with *O. truncatus*), ATN-325 (3 cephala, 1 pygidium) (with *O. truncatus*), ATN-326 (3 cephala, 5 pygidia), GM 1871-692 (cephalon, 2 pygidia), GM 1871-811 (pygidium), GM 1892-1300 (cephalon, 2 pygidia) (with *O. wahlenbergi*), GM 1922-134 (cephalon, 3 pygidia), GM 1922-148 (cephalon, 5 pygidia), GM 1922-149A (3 cephala, 4 pygidia), GM 1922-150B (11 cephala, 7 pygidia, 7 complete specimens), GM 1922-150C (7 cephala, 6 pygidia, 1 complete specimen), GM 1935-54 (9 cephala, 15 pygidia, 1 complete specimen), GM 2019-37 (pygidium), GM 2019-38 (complete specimen), GM 2019-39 (2 cephala), GM 2019-40 (2 cephala, 2 pygidia) (with *O. wahlenbergi*), GM 2019-45 (cephalon, 1 pygidium) (with *O. wahlenbergi*), GM 2019-51 (2 cephala, 4 pygidia) (with *O. wahlenbergi*), GM 2019-55 (8 cephala, 4 pygidia) (with *O. wahlenbergi*), GM 2019-58 (2 cephala), GM 2019-59 (2 cephala, 1 pygidium) (with *O. wahlenbergi*), GM 2019-61 (cephalon), GM 2019-62 (2 cephala, pygidium) (with *O. wahlenbergi*), GM 2019-64 (3 pygidia) (with *O. wahlenbergi*), GM 2019-67 (3 cephala) (with *O. wahlenbergi*), GM 2019-69 (pygidium) (with *O. wahlenbergi*), GM 2019-70 (cephalon, 3 pygidia) (with *O. wahlenbergi*), GM 2019-74 (pygidium) (with *O. wahlenbergi*), GM 2019-80 (cephalon) (with *O. wahlenbergi*), GM 2019-81 (cephalon) (with *O. wahlenbergi*), GM 2019-83 (pygidium) (with *O. wahlenbergi*), GM 2019-85 (2 cephala) (with *O. wahlenbergi*), GM 2019-86 (cephalon) (with *O. wahlenbergi*), GM 2019-87 (3 pygidia) (with *O. wahlenbergi*), MGUH 1955 (pygidium).

Glyptagnostus reticulatus **(Angelin, 1851)**. *Four complete specimens, 4 cephala and 6 pygidia.* Samples GM 1871-602 (cephalon, 1 pygidium), GM 1902-1196 (pygidium), GM 1922-133 (pygidium) (shale), GM 1922-150A (cephalon), GM 1938-43 (cephalon, 2 complete specimens), GM 1939-22 (cephalon, 2 complete specimens), GM 2019-34 (pygidium), GM 2019-35 (external mould of pygidium) (counter piece to GM 2019-36), GM 2019-36 (pygidium) (positive counter piece to GM 2019-35), MGUH 1956 (pygidium).

Lotagnostus americanus **(Billings, 1860)**. *One cephalon*, sample GM 1922-141O.

Pseudagnostus leptoplastorum **Westergård, 1944?** *One cephalon*, sample ATN-123 (with *E. bornholmensis*).

Olenus attenuatus **(Boeck, 1838)**. *9 cranidia with up to 8 contiguous thoracic segments, 1 free cheek(?) and 2 pygidia.* Samples L104 (cranidium with two thoracic segments), L105 (cranidium), L115 (cranidium), L118 (possible free cheek), GM 1897-1300 (5 cranidia incl. 2 with up to 8 thoracic segments, 1 pygidium), GM 2019-63 (3 cranidia?, pygidium), MGUH 1960 (cranidium with 4 thoracic segments).

Olenus dentatus **Westergård, 1922**. *External mould of one almost complete specimen and 1 tentatively assigned cranidium.* Samples GM 2019-98, GM 2019-102.

Olenus gibbosus **(Wahlenberg, 1818)**. *One cephalon with three thoracic segments attached, 2 free cheeks and 4 pygidia*. Samples MGUH 1958 (cephalon with 3 thoracic segments), GM 2019-41 (pygidium), GM 2019-42 (free cheek), GM 2019-43 (2 pygidia), unnumbered sample (incl. MGUH 1957) (free cheek, pygidium).

Olenus transversus **Westergård, 1922**. *One almost complete specimen, 2 free cheeks and 4 pygidia with up to 13 thoracic segments attached. Additionally, 2 pygidia with up to 6 thoracic segments have been tentatively assigned*. Samples ATN-320 (almost complete specimen), ATN-322 (pygidium), L99? (pygidium), L100 (pygidium), L101? (pygidium with 6 thoracic segments), L108 (pygidium), L111 (pygidium with 13 thoracic segments), L119 (2 free cheeks).

***Olenus truncatus* (Brünnich, 1781)**. *11 almost complete specimens and 21 pygidia, including one with 10 contiguous thoracic segments. Additionally, 1 cephalon, 7 cranidia and 9 free cheeks have been tentatively assigned*. Samples ATN-323 (pygidium) (with *H. obesus*), ATN-324 (cephalon, 3 pygidia), ATN-325 (3 pygidia) (with *H. obesus*), L95 (free cheek, pygidium), L98 (pygidium), L103 (3 pygidia) (with *O. wahlenbergi*), L112 (2 pygidia), GM 1870-876 (3 external moulds of complete specimens, cranidium?, 2 pygidia), GM 1914 (1 almost complete specimen, 3 pygidia), GM 1922-133B (cranidium with 10 thoracic segments, 2 free cheeks, 2 pygidia incl. one with 10 thoracic segments), GM 1922-133C (2 almost complete specimens, 5 free cheeks), GM 1922-133D (complete specimen), GM 1922-136 (almost complete specimen), GM 1922-138 (almost complete specimen), GM 1922-147 (5 cranidia, 1 free cheek), GM 2019-46 (almost complete specimen), MGUH 1959 (almost complete specimen).

***Olenus wahlenbergi* Westergård, 1922**. *26 free cheeks and 11 pygidia. 176 cranidia have been tentatively assigned.* Sample L103 (free cheek) (with *O. truncatus*), GM 1892-1300 (pygidium) (with *H. obesus*), GM 1938-42 (pygidium), GM 2019-40 (2 free cheeks, 3 cranidia) (with *H. obesus*), GM 2019-44 (5 cranidia, 2 free cheeks), GM 2019-45 (14 cranidia, 3 free cheeks) (with *H. obesus*), GM 2019-47 (cranidium), GM 2019-48 (cranidium?, free cheek?), GM 2019-49 (5 cranidia, 1 free cheek), GM 2019-50 (15 cranidia, 1 free cheek), GM 2019-51 (5 cranidia) (with *H. obesus*), GM 2019-52 (cranidium, 2 free cheeks), GM 2019-53 (3 cranidia, 1 free cheek), GM 2019-54 (free cheek), GM 2019-55 (10 cranidia, 1 free cheek, 2 pygidia) (with *H. obesus*), GM 2019-56 (6 cranidia), GM 2019-57 (cranidium), GM 2019-59 (4 cranidia, 1 free cheek, 1 pygidium) (with *H. obesus*), GM 2019-60 (4 cranidia), GM 2019-62 (2 cranidia, 2 free cheeks) (with *H. obesus*), GM 2019-64 (5 cranidia) (with *H. obesus*), GM 2019-65 (3 cranidia, 2 pygidia), GM 2019-66 (2 cranidia), GM 2019-67 (3 cranidia) (with *H. obesus*), GM 2019-68 (6 cranidia, 1 pygidium), GM 2019-69 (5 cranidia, 1 free cheek, 1 pygidium) (with *H. obesus*), GM 2019-70 (10 cranidia, 1 free cheek) (with *H. obesus*), GM 2019-71 (3 cranidia), GM 2019-72 (3 cranidia, 3 free cheeks), GM 2019-73 (3 cranidia, 2 free cheeks), GM 2019-74 (4 cranidia) (with *H. obesus*), GM 2019-75 (2 cranidia), GM 2019-76 (cranidium), GM 2019-77 (10 cranidia), GM 2019-78 (3 cranidia), GM 2019-79 (2 cranidia), GM 2019-80 (3 cranidia) (with *H. obesus*), GM 2019-81 (cranidium) (with *H. obesus*), GM 2019-82 (4 cranidia), GM 2019-83 (4 cranidia, 1 pygidium) (with *H. obesus*), GM 2019-84 (3 cranidia), GM 2019-85 (3 cranidia), GM 2019-86 (5 cranidia), GM 2019-87 (8 cranidia, 1 pygidium).

***Parabolina acanthura* (Angelin, 1854)**. *One cephalon, 3 cranidia and 2 free cheeks. One hypostome and isolated pleura are tentatively assigned.* Samples GM 1924-1A (cephalon), GM 1924-1B (cranidium), GM 1924-1C (cranidium), GM 1924-1D (cranidium, 3 free cheeks – all specimens fragmentary), MGUH 1979 (hypostome), GM 1924.1E incl. MGUH 1980 (cranidium, free cheek), MGUH 1981 (pleura).

***Parabolina spinulosa* (Wahlenberg, 1818)**. *20 cranidia, 7 free cheeks and 8 pygidia*. Samples GM 1870-861 (cranidium) (with *Orusia lenticularis*), GM 1879-861 (cranidium) (with *Orusia lenticularis*), GM 1887-399 (3 cranidia) (with *Orusia lenticularis*), GM 1897-399 (cranidium) (with *Orusia lenticularis*), GM 1922-137A (2 cranidia, 2 free cheeks) (with Orusia lenticularis), GM 1922-137B (6 cranidia, 2 free cheeks, 5 pygidia), GM 1922-137C (2 pygidia), GM 1922-137D (cranidium), GM 1922.137E (cranidium, 1 juvenile cranidium, 1 free cheek, 1 pygidium incl. MGUH 1985), GM 1946-4 (2 free cheeks), GM 2019-92 (3 fragmentary cranidia) (with *O. lenticularis*).

***Parabolina lobata praecurrens* Westergård, 1944**. *21 cranidia*. Samples L3 (cranidium), L10 (cranidium) (with *P. westergaardi*), L11 (9 cranidia) (with *P. westergaardi*), L12 (5 cranidia) (with *P. westergaardi, Peltura* sp.), L14 (cranidium) (with *P. westergaardi, Peltura* sp.), L16 (2 cranidia) (with *P. westergaardi, Peltura* sp., orthid brachiopod), L18 (2 cranidia) (with orthid brachiopod).

***Leptoplastus abnormis* Westergård, 1944**. *4 almost complete specimens, 1 cephalon, 352 cranidia, external mould of one cranidium with ~10 thoracic segments, 3 specimens with continuous thoracic segments and 9 free cheeks.* Samples ATN-108 (2 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-119 (2 possible free cheeks) (with *E. bornholmensis, L. ovatus*), ATN-122 (11 cranidia) (with *E. bornholmensis, L. ovatus*), ATN-124 (15 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-129 (cranidium) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-149 (external mould of complete specimen) (with *L. angustatus*), ATN-154 (3 cranidia) (with *E. bornholmensis*, *L. ovatus*), ATN-155 (cranidium) (with *L. angustatus*), ATN-156 (15 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-157 (6 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-170 (cranidium, 1 thoracic segment) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-176 (3 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-217 (12 cranidia) (with *E. bornholmensis, L. ovatus*), ATN-219 (4 external moulds of cranidia), ATN-228 (cranidium) (with *L. angustatus*), ATN-232 (3 cranidia) (with *L. ovatus*), ATN-241 (4 cranidia) (with *L. ovatus*), ATN-243 (8 cranidia) (with *L. ovatus*), ATN-251 (cranidium) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-252 (cranidium) (with *L. angustatus*, *L. crassicornis*, *L. ovatus*), ATN-254 (cranidium) (with *L. angustatus?, L. ovatus*), ATN-260 (complete specimen) (with *L. angustatus, L.ovatus, E. bornholmensis*), ATN-261 (4 cranidia, 2 free cheeks) (with *L. angustatus*, *L. ovatus*), ATN-262 (2 cranidia) (with *E. bornholmensis*, *L. ovatus*), ATN-263 (5 cranidia, 1 thoracic segment) (with *L. angustatus*, *L. crassicornis*, *L. ovatus*), ATN-264 (cranidium), ATN-265 (4 cranidia, 1 thorax with pygidium) (with *E. bornholmensis, L. angustatus, L. crassicornis, L. ovatus*), ATN-270 (7 cranidia) (with *L. ovatus*), ATN-271 (cranidium, 1 free cheek) (with *E. bornholmensis*, *L. ovatus*), ATN-275 (cranidium) (with *E. bornholmensis*, *L. angustatus*), ATN-276 (14 cranidia) (with *E. bornholmensis*, *L. angustatus, L. crassicornis, L. ovatus*), ATN-277 (external mould of cranidium) (with *E. bornholmensis*, *L. angustatus, L.*

ovatus), ATN-278 (2 cranidia) (with *E. bornholmensis*, *L. angustatus*, *L. crassicornis, L. ovatus*), ATN-283 (cranidium) (with *L. ovatus*), ATN-288 (11 cranidia, 1 free cheek) (with *L. angustatus*, *L. ovatus*), ATN-293 (2 cranidia, thorax) (with *L. angustatus, L. crassicornis?, L. ovatus*), ATN-301 (2 cranidia, 6 contiguous thoracic segments) (with *L. angustatus*, *L. ovatus*), ATN-302 (cranidium) (with *L. ovatus*), ATN-304 (8 cranidia, 2 external moulds of complete specimens, contiguous thoracic segment, 1 free cheek) (with *E. bornholmensis, L. angustatus*, *L. crassicornis*, *L. ovatus*), ATN-306 (3 cranidia) (with *E. bornholmensis, L. ovatus*), ATN-307 (5 cranidia) (with *E. bornholmensis*, *L. ovatus*), ATN-328 (8 cranidia) (with *E. bornholmensis, L. angustatus, L. crassicornis, L. ovatus*), ATN-331 (6 cranidia) (with *L. angustatus, L. ovatus*), ATN-332 (3 cranidia) (with *L. angustatus, L. ovatus*), ATN-335 (2 cranidia) (with *L. angustatus, L. ovatus*), ATN-336 (cranidium) (with *E. bornholmensis*, *L. angustatus, L. ovatus*), ATN-337 (3 cranidia), ATN-338 (cephalon, 1 cranidium with 4 thoracic segments attached) (with *L. ovatus*), ATN-339 (7 cranidia) (with *E. bornholmensis, L. ovatus*), ATN-340 (cranidium) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-341 (5 cranidia) (with *L. angustatus, L. ovatus*), ATN-342 (11 cranidia) (with *E. bornholmensis*, *L. ovatus*), ATN-343 (2 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-346 (15 cranidia) (with *E. bornholmensis, L. angustatus, L. ovatus*), ATN-347 (3 cranidia) (with *L. angustatus, L. ovatus*), ATN-348 (11 cranidia) (with *L. crassicornis, L. ovatus*), L126 (4 cranidia) (with *E. bornholmensis, L. ovatus*), GM 1902-1201 (external mould of cranidium) (with *L. ovatus*), GM 1922-138D (2 cranidia) (with *L. crassicornis, L. ovatus, E. bornholmensis*), GM 1922-139E (2 cranidia, 2 thoracic segments) (with *E. bornholmensis, L. angustatus, L. crassicornis, L. ovatus*), GM 2019-88 (2 cranidia) (with *L. ovatus*), GM 2019-89 (4 cranidia) (with *L. ovatus*), GM 2019-90 (18 cranidia, 2 thoracic segments, 2 possible free cheeks) (with *E. bornholmensis*, *L. angustatus, L. ovatus*).

***Leptoplastus angustatus* (Angelin, 1854)**. *457 cranidia incl. two with up to 9 thoracic segments, 203 free cheeks and 28 pygidia*. Samples ATN-108 (cranidium) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-109 (free cheek) (with *L. ovatus*), ATN-110 (19 cranidia, 2 free cheeks, 2 pygidia) (with *E. bornholmensis*, *L. crassicornis*), ATN-118 (2 free cheeks) (with *E. bornholmensis*, *L. ovatus*), ATN-124 (2 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus, L. ovatus*), ATN-129 (free cheek) (with *E. bornholmensis*, *L. abnormis, L. ovatus*), ATN-136 (free cheek) (with *E. bornholmensis*), ATN-142 (>20 cranidia, >3 free cheeks, 1 pygidium), ATN-149 (cranidium with 9 thoracic segments, 1 free cheek) (with *L. abnormis*), ATN-152 (cranidium, free cheek) (with *L. ovatus*), ATN-153 (11 cranidia, 14 free cheeks, 3 pygidia) (with *L. crassicornis*), ATN-155 (10 cranidia, >10 free cheeks) (with *L. abnormis*), ATN-156 (3 cranidia, 1 free cheek) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-157 (cranidium) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-158 (19 cranidia, >2 free cheeks) (with *L. crassicornis*, *L. ovatus*), ATN-162 (pygidium) (with *L. ovatus*), ATN-163 (cranidium), ATN-170 (cranidium) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-176 (5 cranidia, 1 free cheek) (with *E. bornholmensis*, *L. abnormis*, *L. ovatus*), ATN-177 (2 free cheeks) (with *L. ovatus*), ATN-216 (>25 cranidia, 7 free cheeks) (with *E. bornholmensis*, *L. crassicornis*), ATN-223 (>39 cranidia, >10 free cheeks, 2 pygidia), ATN-224 (3 free cheeks, 1 pygidium?) (with *E. bornholmensis*), ATN-228 (3 cranidia, 1 free cheek) (with *L. abnormis*), ATN-233 (3 cranidia, 3 free cheeks) (with *L. ovatus*), ATN-234 (cranidium), ATN-247 (5 cranidia, 2 free cheeks, 1 pygidium), ATN-251 (free cheek) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-252 (10 cranidia, 1 free cheek, >3 pygidia) (with *L. abnormis*, *L. crassicornis*, *L. ovatus*), ATN-253 (6 cranidia, 2 free cheeks) (with *L. ovatus*), ATN-254 (free cheek?) (with *L. abnormis, L. ovatus*), ATN-259 (cranidium) (with *L. crassicornis*), ATN-260 (pygidium) (with *L. ovatus, L. abnormis, E. bornholmensis*), ATN-261 (cranidium) (with *L. abnormis*, *L. ovatus*), ATN-263 (pygidium) (with *L. abnormis, L. crassicornis*, *L. ovatus*), ATN-265 (3 cranidia, 1 free cheek) (with *E. bornholmensis, L. abnormis, L. crassicornis, L. ovatus*), ATN-269 (free cheek) (with *L. ovatus*), ATN-274 (16 cranidia, 6 free cheeks), ATN-275 (cranidium, 1 free cheek) (with *E. bornholmensis*, *L. abnormis*), ATN-276 (free cheek) (with *E. bornholmensis*, *L. abnormis, L. crassicornis, L. ovatus*), ATN-277 (2 cranidia, 1 free cheek) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-278 (7 cranidia, 4 free cheeks, 1 pygidium) (with *E. bornholmensis*, *L. abnormis, L. crassicornis, L. ovatus*), ATN-281 (6 cranidia, 1 free cheek) (with *L. crassicornis*), ATN-285 (7 cranidia, >4 free cheeks), ATN-288 (cranidium) (with *L. abnormis*, *L. ovatus*), ATN-289 (14 cranidia, 1 pygidium), ATN-292 (14 cranidia, 4 free cheeks) (with *E. bornholmensis, L. ovatus*), ATN-293 (cranidium) (with *L. abnormis, L. crassicornis?, L. ovatus*), ATN-295 (cranidium), ATN-297 (>16 cranidia, 2 free cheeks), ATN-298 (>7 cranidia, 2 free cheeks), ATN-299 (free cheek, 2 pygidia) (with *E. bornholmensis*, *L. ovatus*), ATN-301 (free cheek) (with *L. abnormis, L. ovatus*), ATN-303 (12 cranidia, 4 free cheeks, 1 pygidium), ATN-304 (7 cranidia, >18 free cheek) (with *E. bornholmensis, L. abnormis*, *L. crassicornis*, *L. ovatus*), ATN-305 (25 cranidia, 9 free cheeks, 1 pygidium) (with *L. crassicornis*), ATN-328 (cranidium, 1 free cheek) (with *E. bornholmensis, L. abnormis, L. crassicornis, L. ovatus*), ATN-331 (free cheek) (with *L. abnormis*, *L. ovatus*), ATN-332 (free cheek) (with *L. abnormis, L. ovatus*), ATN-334 (3 cranidia, 16 very small juvenile cranidia, 5 free cheeks), ATN-335 (5 free cheeks) (with *L. abnormis, L. ovatus*), ATN-336 (cranidium) (with *E. bornholmensis*, *L. abnormis, L. ovatus*), ATN-340 (4 free cheeks) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-341 (cranidium, 1 free cheek) (with *L. abnormis, L. ovatus*), ATN-343 (cranidium) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-344 (4 cranidia, 1 free cheek), ATN-346 (2 cranidia, 2 free cheeks) (with *E. bornholmensis, L. abnormis, L. ovatus*), ATN-347 (free cheek) (with *L. abnormis, L. ovatus*), L31 (3 cranidia, 1 free cheek), L32 (2 free cheeks, pygidium), L33 (3 cranidia, 3 free cheeks, 1 pygidium), L54 (>12 cranidia, >4 free cheeks, 1 pygidium), GM 1870-847 (cranidium) (with *L. ovatus*), GM 1870-848 (cranidium) (with *L. crassicornis, L. ovatus*), GM 1871-607 (3 cranidia) (with *E. bornholmensis*, *L. ovatus*), GM 1888-289A (8 cranidia, 7 free cheeks) (with *L. crassicornis, L. ovatus*), GM 1888-289B (cranidium, 4 free cheeks), GM 1888-289C (13 cranidia, 5 free cheeks, 1 pygidium) (with *L. crassicornis*), GM 1888-289D (4 cranidia), (with *L. crassicornis*, *L. ovatus*), GM 1922-139A (2 cranidia, 2 free cheeks) (with *E. bornholmensis*), GM 1922-139B (4 cranidia, 8 free cheeks) (with *L. crassicornis, L. ovatus*), GM 1922-139C (3 cranidia, 2 free cheeks), GM 1922-139D (pygidium), GM 1922-139E (cranidium) (with *E. bornholmensis, L. abnormis, L. crassicornis, L. ovatus*), GM 1922-139G (2 cranidia) (with *E. bornholmensis, L. ovatus*), GM 1930-99/100 (2 cranidia, 2 free cheeks) (with *E. bornholmensis, L. ovatus*), GM 2019-28 (2 cranidia), GM 2019-90 (6 cranidia) (with *E. bornholmensis*, *L. abnormis, L. ovatus*), MGUH 1963 (free cheek).

***Leptoplastus crassicornis* (Westergård, 1944*)*. *37 cranidia, 12 free cheeks and 6 pygidia*. Samples ATN-110 (2 cranidia incl. one with 4 thoracic segments) (with *E. bornholmensis*, *L. angustatus*), ATN-153 (cranidium) (with *L. angustatus*), ATN-158 (2 cranidia) (with *L. angustatus, L. ovatus*), ATN-178 (free cheek) (with juvenile *Eurycare* sp.), ATN-216 (cranidium, 2 free cheeks, 2 pygidia) (with *E. bornholmensis*, *L. angustatus*), ATN-220 (external mould of free cheek), ATN-252 (4 cranidia, 1 free cheek) (with *L. abnormis*, *L. angustatus, L. ovatus*), ATN-259 (cranidium) (with *L. angustatus*), ATN-263 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-265 (pygidium with attached thoracic segments) (with *E. bornholmensis, L. abnormis, L. angustatus, L. ovatus*), ATN-273 (2 cranidia) (with *E. latum*), ATN-276 (2 cranidia incl. one with a few thoracic segments attached) (with *E. bornholmensis*, *L. abnormis*, *L. angustatus, L. ovatus*), ATN-278 (cranidium, 1 pygidium) (with *E. bornholmensis, L. abnormis, L. angustatus, L. ovatus*), ATN-281 (cranidium) (with *L. angustatus*), ATN-284 (cranidium) (with *E. latum*), ATN-293 (cranidium?) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-304 (cranidium) (with *E. bornholmensis*, *L. abnormis, L. angustatus*, *L. ovatus*), ATN-305 (cranidium with contiguous thoracic segments) (with *L. angustatus*), ATN-328 (cranidium) (with *E. bornholmensis, L. abnormis, L. angustatus, L. ovatus*), ATN-348 (free cheek) (with *L. abnormis, L. ovatus*), GM 1870-848 (2 cranidia) (with *L. angustatus, L. ovatus*), GM 1888-289A (cranidium, 1 free cheek) (with *L. angustatus, L. ovatus*), GM 1888-289C (cranidium, 3 free cheeks, 2 pygidia) (with *L. angustatus, L. ovatus*), GM 1888-289D (4 cranidia) (with *L. angustatus*, *L. ovatus*), GM 1922-138D (2 cranidia) (with *L. abnormis, L. ovatus, E. bornholmensis*), GM 1922-139B (cranidium, 2 free cheeks) (with *L. angustatus, L. ovatus*), GM 1922-139E (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), GM 1922-850 (cranidium) (with *L. ovatus*), MGUH 1962 (cranidium).

***Leptoplastus ovatus* Angelin, 1854**. *OBS: Some of the listed cranidia and in particular free cheeks and pygidia probably represent* L. abnormis. *401 cranidia, 429 free cheeks, 1 hypostome? and 35 pygidia*. Samples ATN-106 (2 cranidia) (with *E. bornholmensis*), ATN-108 (2 cranidia, 12 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-109 (cranidium) (with *L. angustatus*), ATN-118 (2 cranidia) (with *E. bornholmensis, L. angustatus*), ATN-119 (10 cranidia, 5 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis*), ATN-120 (3 cranidia, 1 free cheek) (with *E. bornholmensis*), ATN-122 (10 cranidia, >15 free cheeks) (with *E. bornholmensis, L. abnormis*), ATN-124 (21 cranidia, >20 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-129 (6 cranidia, 5 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-152 (4 cranidia, 5 free cheeks) (with *L. angustatus*), ATN-154 (11 cranidia, 24 free cheeks, 1 pygidium) (with *E. bornholmensis*, *L. abnormis*), ATN-156 (6 cranidia, 20 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-157 (8 cranidia, 4 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-158 (2 cranidia) (with *L. angustatus, L. crassicornis*), ATN-160 (cranidium), ATN-162 (2 cranidia, 1 free cheek) (with *L. angustatus*), ATN-167 (2 free cheeks), ATN-170 (5 cranidia. 3 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-172 (4 cranidia, 1 free cheek), ATN-174 (cranidium), ATN-176 (18 cranidia, >28 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis*, *L. angustatus*), ATN-177 (cranidium) (with *L. angustatus*), ATN-217 (7 cranidia, >8 free cheeks) (with *E. bornholmensis, L. abnormis*), ATN-227 (10 cranidia, 1 free cheek), ATN-232 (3 cranidia, 5 free cheeks, 3 pygidia) (with *L. abnormis*), ATN-233 (1 free cheek) (with *L. angustatus*), ATN-237 (free cheek), ATN-241 (cranidium, 1 free cheek, 1 hypostome?) (with *L. abnormis*), ATN-242 (cranidium), ATN-243 (cranidium, 12 free cheeks, 2 pygidia) (with *L. abnormis*), ATN-244 (4 cranidia, 3 free cheeks), ATN-249 (cranidium), ATN-251 (3 cranidia, 7 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-252 (cranidium) (with *L. abnormis*, *L. angustatus, L. crassicornis*), ATN-253 (cranidium) (with *L. angustatus*), ATN-254 (3 cranidia) (with *L. angustatus?, L. abnormis*), ATN-260 (3 cranidia, 1 free cheek) (with *L. abnormis*, *L. angustatus*, *E. bornholmensis*), ATN-261 (2 cranidia, >13 free cheeks, 1 pygidium) (with *L. abnormis, L. angustatus*), ATN-262 (3 cranidia, 4 free cheeks) (with *E. bornholmensis, L. abnormis*), ATN-263 (6 cranidia, >7 free cheeks, 3 pygidia) (with *L. abnormis, L. angustatus, L. crassicornis*), ATN-265 (3 cranidia, 2 free cheeks, 2 pygidia?) (with *E. bornholmensis, L. abnormis, L. angustatus, L. crassicornis*), ATN-269 (free cheek) (with *L. angustatus*), ATN-270 (3 cranidia, 4 free cheeks, 1 pygidium) (with *L. abnormis*), ATN-271 (2 cranidia, 2 free cheeks) (with *E. bornholmensis*, *L. abnormis*), ATN-276 (11 cranidia, >14 free cheeks, 3 pygidia) (with E. bornholmensis, *L. abnormis*, *L. crassicornis*, *L. angustatus*), ATN-277 (2 cranidia, 7 free cheeks) (with *E. bornholmensis*, *L. abnormis*, *L. angustatus*), ATN-278 (free cheek) (with *E. bornholmensis, L. abnormis, L. angustatus, L. crassicornis*), ATN-283 (cranidium) (with *L. abnormis*), ATN-288 (3 cranidia, 6 free cheeks) (with *L. abnormis, L. angustatus*), ATN-290 (4 cranidia), ATN-291 (2 cranidia, 1 free cheek), ATN-292 (free cheek) (with *E. bornholmensis, L. angustatus*), ATN-293 (cranidium, 5 free cheeks) (with *L. abnormis*, *L. angustatus*, *L. crassicornis?*), ATN-296 (cranidium) (with *E. latum*), ATN-299 (free cheek) (with *E. bornholmensis, L. angustatus*), ATN-301 (2 free cheeks) (with *L. abnormis, L. angustatus*), ATN-302 (1 free cheek, 2 pygidia) (with *L. abnormis*), ATN-304 (2 cranidia, >10 free cheeks, 3 pygidia) (with *E. bornholmensis, L. abnormis, L. angustatus, L. crassicornis*), ATN-306 (2 cranidia, >8 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis*), ATN-307 (3 cranidia, 9 free cheeks) (with *E. bornholmensis, L. abnormis*), ATN-328 (8 cranidia, 11 free cheeks, 2 pygidia) (with *E. bornholmensis, L. abnormis, L. angustatus, L. crassicornis*), ATN-329 (20 cranidia, 9 free cheeks) (with *E. bornholmensis*), ATN-331 (3 cranidia, 3 free cheeks) (with *L. abnormis*, *L. angustatus*), ATN-332 (5 cranidia, 1 pygidium) (with *L. abnormis, L. angustatus*), ATN-333 (5 free cheeks) (with *E. bornholmensis*), ATN-335 (cranidium, 1 free cheek) (with *L. abnormis, L. angustatus*), ATN-336 (2 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-338 (2 cranidia, 2 free cheeks) (with *L. abnormis*), ATN-339 (7 cranidia) (with *E. bornholmensis, L. abnormis*), ATN-340 (cranidium, >2 free cheeks) (with *E. bornholmensis, L. angustatus, L. abnormis*), ATN-341 (6 cranidia, >2 free cheeks) (with *L. abnormis, L. angustatus*), ATN-342 (9 cranidia, 3 free cheeks) (with *E. bornholmensis, L. abnormis*), ATN-343 (cranidium) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-345 (3 cranidia), ATN-346 (9 cranidia, >14 free cheeks) (with *E. bornholmensis, L. abnormis, L. angustatus*), ATN-347 (5 cranidia, 8 free cheeks) (with *L. abnormis, L. angustatus*), ATN-348 (7 cranidia, 7 free cheeks) (with *L. abnormis, L. crassicornis*), L126 (5 cranidia, >10 free cheeks) (with *E. bornholmensis, L. abnormis*), GM 1870-847 (6 cranidia) (with *L. angustatus*), GM 1870-848 (cranidium, 2 free cheeks) (with *L. angustatus, L. crassicornis*), GM 1870-850 (3 cranidia, 2 free cheeks) (with *L. crassicornis*), GM 1871-607 (cranidium) (with *E. bornholmensis, L. angustatus*), GM 1888-289A (cranidium) (with *L. angustatus, L. crassicornis*), GM 1888-289D (cranidium), (with *L. angustatus, L. crassicornis*), GM 1902-1199 (cranidium), GM 1902-1200 (2 cranidia, 1 free cheek), GM 1902-1201 (cranidium) (with *L. abnormis*), GM 1902-1202 (cranidium, 2 free cheeks), GM 1902-1204 (2 free cheeks), GM 1902-1207 (cranidium, 3 free cheeks), GM 1922-138D (22 cranidia, 27 free cheeks, 1 pygidium) (*E. bornholmensis, L. abnormis, L. crassicornis*), GM 1922-138F (6 cranidia, 2 free cheeks), GM 1922-139B (4 cranidia, 2 free cheeks, 1 pygidium) (with *L. angustatus, L. crassicornis*), GM 1922-139E (4 cranidia, 5 free cheeks, 1 pygidium) (with *E. bornholmensis, L. abnormis, L. angustatus, L. crassicornis*), GM 1922-139G (cranidium, free cheek) (with *E. bornholmensis, L. angustatus*), GM 1930-99/100 (21 cranidia, 6 free cheeks) (with *E. bornholmensis, L. angustatus*), GM 2019-88 (3 cranidia, 2 free cheeks) (with *L. abnormis*), GM 2019-89 (7 cranidia, 4 free cheeks, 1 pygidium) (with *L. abnormis*), GM 2019-90 (9 cranidia, 8 free cheeks, 2 pygidia) (with *E. bornholmensis, L. abnormis, L. angustatus*).

***Leptoplastus stenotus* Angelin, 1854**. *142 cranidia, 12 free cheeks and 5 pygidia*. Samples ATN-168 (21 cranidia), ATN-182 (3 cranidia), ATN-199 (6 cranidia, 2 free cheeks, 1 pygidium), ATN-255 (11 cranidia), ATN-257 (60 cranidia), ATN-266 (9 cranidia), L125 (20 cranidia), GM 1902-1205 (cranidium, external mould of free cheek), GM 1922-139F (4 cranidia, 1 juvenile cranidium, free cheek, pygidium) (incl. MGUH 1986), GM 1922-152 (6 cranidia, 8 free cheeks, 3 pygidia).

***Eurycare bornholmensis* (Poulsen, 1923)**. *2 more or less complete specimens, 123 cranidia (incl. one with 13 and one with 14 contiguous thoracic segments), 8 free cheeks, one hypostome (tentatively assigned) and 7 pygidia*. Samples ATN-106 (cranidium) (with *L. ovatus*), ATN-108 (4 cranidia) (with *L. ovatus*), ATN-110 (cranidium) (with *L. angustatus, L. crassicornis*), ATN-118 (cranidium with 13 thoracic segments) (with *L. angustatus, L. ovatus*), ATN-119 (2 cranidia) (with *L. abnormis, L. ovatus*), ATN-120 (complete specimen, 1 cranidium) (with *L. ovatus*), ATN-122 (5 cranidia, 1 external mould of cranidium) (with *L. abnormis, L. ovatus*), ATN-123 (2 cranidia, 1 pygidium) (with *P. leptoplastorum*?), ATN-124 (5 cranidia, 1 free cheek) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-129 (2 external moulds of cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-136 (3 cranidia incl. one with 14 thoracic segments, the other with 8 thoracic segments; counter piece of ATN-333) (with *L. angustatus*), ATN-154 (2 cranidia) (with *L. abnormis, L. ovatus*), ATN-156 (5 cranidia) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-157 (2 cranidia, 1 external mould cranidium, 2 free cheeks, external mould of pygidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-170 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-176 (2 cranidia, 2 free cheeks) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-216 (cranidium) (with *L. angustatus, L. crassicornis*), ATN-217 (3 cranidia) (with *L. abnormis, L. ovatus*), ATN-224 (2 cranidia) (with *L. angustatus*), ATN-248 (2 cranidia), ATN-251 (free cheek) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-260 (cranidium) (with *L. angustatus, L. ovatus, L. abnormis*), ATN-262 (cranidium) (with *L. abnormis, L. ovatus*), ATN-265 (external mould of cranidium) (with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus*), ATN-271 (external mould of cranidium) (with *L. abnormis, L. ovatus*), ATN-275 (2 cranidia) (with *L. abnormis, L. angustatus*), ATN-276 (cranidium) (with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus*), ATN-277 (external moulds of 3 cranidia, 1 cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-278 (cranidium) (with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus*), ATN-292 (cranidium) (with *L. angustatus, L. ovatus*), ATN-299 (cranidium) (with *L. angustatus, L. ovatus*), ATN-304 (4 cranidia, 4 external moulds of cranidia, 1 pygidium) (with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus*), ATN-306 (4 cranidia, 1 external mould of cranidium, 1 pygidium) (with *L. ovatus*), ATN-307 (1 external mould of cranidium, 1 free cheek) (with *L. abnormis, L. ovatus*), ATN-328 (3 cranidia) (with *L. abnormis, L. angustatus, L. crassicornis, L. ovatus*), ATN-329 (almost complete specimen, 3 cranidia) (with *L. angustatus, L. crassicornis, L. ovatus*), ATN-333 (counter piece to ATN-136) (with *L. ovatus*), ATN-336 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-339 (4 cranidia, 3 external moulds of cranidia, 2 pygidia) (with *L. abnormis, L. ovatus*), ATN-340 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-342 (2 cranidia) (with *L. abnormis, L. ovatus*), ATN-343 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), ATN-346 (pygidium) (with *L. abnormis, L. angustatus, L. ovatus*), L126 (2 cranidia, 1 possible hypostome) (with *L. abnormis, L. ovatus*), GM 1871-607 (cranidium) (with *L. angustatus, L. ovatus*), GM 1881-1784 (2 cranidia), GM 1922-138D (small cranidium) (with *L. abnormis, L. crassicornis, L. ovatus*), GM 1922-139A (5 cranidia) (with *L. angustatus*), GM 1922-139E (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*), GM 1930-99/100 (4 cranidia, 1 free cheek?) (with *L. angustatus, L. ovatus*), GM 1922-139G incl. MGUH 1964 (external mould of cranidium) (with *L. angustatus, L. ovatus*), GM 2019-90 (cranidium) (with *L. abnormis, L. angustatus, L. ovatus*).

.

***Eurycare brevicauda* Angelin, 1854.** *1 cranidium*, sample ATN-280 (with *E. latum*).

Eurycare latum **(Boeck, 1838).** *156 cranidia including one with 6 continuous thoracic segments, 23 free cheeks and 18 pygidia.* Samples ATN-114 (13 cranidia, 1 free cheek, 3 pygidia, 2 external moulds of pygidia), ATN-150 (15 cranidia incl. one with 11 contiguous thoracic segments, 2 free cheeks, 3 pygidia), ATN-159 (21 cranidia, 3 free cheeks), ATN-231 (3 cranidia, 2 free cheeks), ATN-250 (7 cranidia, 3 free cheeks, 1 pygidium), ATN-268 (7 cranidia), ATN-272 (5 cranidia, 1 free cheek), ATN-273 (cranidium, 1 pygidium) (with *L. crassicornis*), ATN-279 (2 cranidia, 1 pygidium), ATN-280 (3 cranidia, 1 free cheek) (with *E. brevicauda*), ATN-282 (10 cranidia, 1 pygidium), ATN-284 (4 cranidia, 1 pygidium) (with *L. crassicornis*), ATN-286 (2 cranidia, 1 pygidium), ATN-287 (7 cranidia, 1 pygidium), ATN-294 (6 cranidia, >10 external moulds of cranidia, 3 free cheeks, 1 pygidium), ATN-296 (9 cranidia) (with *L. ovatus*), ATN-300 (8 cranidia, >2 external moulds of cranidia, 2 free cheeks, 1 pygidium), GM 1922-138A (3 cranidia), GM 1922-138B (5 cranidia, 1 free cheek, 1 pygidium), GM 1922-138C (4 cranidia, 1 free cheek), GM 1922-138E (4 cranidia, 3 free cheeks) (including MGUH 1961), GM 1922-138G (4 cranidia).

Ctenopyge (Ctenopyge) affinis **Westergård, 1922**. *222 cranidia incl. 13 external moulds, and 15 free cheeks (tentatively assigned).* Samples ATN-103 (12 cranidia, 3 free cheeks) (with *Peltura cf. minor*, *S. alatus*), ATN-113 (51 cranidia, 3 external moulds of cranidia, 3 free cheeks) (with *C. magna n.sp.*, *C. ahlbergi*, *P. minor, S. alatus*), ATN-116 (5 cranidia, 1 free cheek?) (with *C. magna n.sp., C. ahlbergi, Peltura cf. minor*, *S. alatus*), ATN-117 (17 cranidia) (with *C. ahlbergi*, *S. magna n.sp.*, *S. alatus*), ATN-127 (2 cranidia, 2 external moulds of cranidia) (with *C. ahlbergi*, *P. minor, S. alatus*), ATN-130 (4 cranidia) (with *C. magna n.sp.*, *S. alatus*), ATN-132 (12 cranidia, free cheek?) (with *P. minor, C. ahlbergi*, *S. alatus*), ATN-133 (6 cranidia) (with *C. magna n.sp.*, *C. ahlbergi*, *P. minor, S. alatus*), ATN-134 (12 cranidia, 1 external mould of cranidum, 1 free cheek?) (with *C. magna n.sp., C. ahlbergi*, *Peltura* sp., *S. alatus*), ATN-137 (cranidium) (with *C. magna n.sp.*, *S. alatus*), ATN-139 (7 cranidia) (with *S. alatus*, *P. minor*), ATN-146 (9 cranidia, 2 free cheeks?) (with *C. magna n.sp.*, *C. ahlbergi*, *S. alatus*), ATN-147 (5 cranidia, 1 free cheek?) (with *C. magna n.sp.*, *S. alatus*), ATN-169 (3 cranidia, 1 external mould of cranidium, 2 external moulds of free cheeks) (with *C. magna* n.sp, *S. alatus*), ATN-173 (cranidium, 1 external mould of cranidium) (with *C. ahlbergi, C. magna* n.sp..*S. alatus*), ATN-191 (cranidium) (with *S. alatus*), ATN-192 (cranidium, 2 external moulds of cranidia) (with *S. alatus*), ATN-205 (external mould of cranidium) (with *C. ahlbergi*, *S. alatus*), ATN-222 (17 cranidia, 1 free cheek) (with *C. ahlbergi, S. alatus*), ATN-246 (11 cranidia, 2 external moulds of cranidia) (with *C. magna* n.sp., *S. alatus*). ATN-330 (5 cranidia including a juvenile) (with *C. magna n.sp., C. ahlbergi, S. alatus*), L76 (2 cranidia, 3 external moulds) (with *S. magna* n.sp., *S. ahlbergi*, *S. alatus*), L77 (cranidium, 1 external mould of cranidium) (with *C. ahlbergi*, *S. alatus* and unknown species?), L84 (6 cranidia) (with *C. magna* n.sp., *S. alatus*), L93 (2 cranidia) (with *C. magna* n.sp., *S. alatus*), GM 1902-1208 (2 cranidia) (with *S. alatus*), GM 1902-1209 (3 cranidia) (with *C. magna n.sp., C. ahlbergi, C. affinis, S. alatus*), GM 1902-1210 (7 cranidia) (with *C. magna n.sp., C. ahlbergi, S. alatus*), GM 1902-1212 (3 cranidia, 1 free cheek?, external mould of 1 free cheek?) (with *C. magna n.sp., C. ahlbergi*, *S. alatus*),

Ctenopyge (Ctenopyge) ahlbergi **Clarkson, Ahlgren & Taylor, 2004.** *38 cranidia incl. 2 external moulds of cranidia and 7 free cheeks.* Samples ATN-113 (3 cranidia, 3 free cheeks) (with *C. magna n.sp.*, *C. affinis*, *P. minor, S. alatus*), ATN-116 (disarticulated thoracic segment) (with *C. magna n.sp., C. affinis, Peltura cf. minor*, *S. alatus*), ATN-117 (2 cranidia, 1 free cheek, disarticulated thoracic segment?) (with *C. affinis, S. magna n.sp., S. alatus*), ATN-127 (cranidium) (with *C. affinis*, *P. minor, S. alatus*), ATN-132 (2 cranidia, 1 external mould of cranidium, disarticulated thoracic segment?) (with *C. affinis*, *P. minor, S. alatus*), ATN-133 (cranidium, disarticulated thoracic segment?) (with *C. magna n.sp., C. affinis*, *P. minor, S. alatus*), ATN-134 (6 cranidia, 1 free cheek, disarticulated thoracic segments?) (with *C. magna n.sp., C. affinis, Peltura* sp., *S. alatus*), ATN-146 (cranidium, 1 free cheek) (with C. *magna n.sp., C. affinis, S. alatus*), ATN-148 (cranidium) (with *S. alatus*, *Peltura cf. minor*), ATN-173 (cranidium, 1 fragmentary free cheek, 1 thoracic segment) (with *C. affinis, C. magna* n.sp., *S. alatus*), ATN-205 (cranidium) (with *C. affinis*, *S. alatus*), ATN-222 (poor cranidium) (with *C. affinis, S. alatus*), ATN-330 (3 cranidia) (with *C. magna n.sp., C. affinis, S. alatus*), L76 (cranidium, external mould of cranidium, disarticulated thoracic segments) (with *C. magna n.sp., C. affinis, S. alatus*), L77 (cranidium) (with *C. affinis*, *S. alatus*, unknown species?) GM 1902-1209 (9 cranidia, disarticulated thoracic segments?) (with *C. magna n.sp., C. affinis, S. alatus*), GM 1902-1210 (cranidium, disarticulated thoracic segment) (with *C. magna n.sp., C. affinis, S. alatus*), GM 1902-1212 (cranidium, fragmentary) (with *C. magna n.sp., C. affinis, S. alatus*).

Ctenopyge (Ctenopyge) bisulcata **(Phillips, 1848).** *6 cranidia*. Samples (in shale): GM 1922-142R (2 cranidia), GM 1922-143 (3 cranidia) (with *Ctenopyge fletcheri*), MGUH 1974 (cranidium).

Ctenopyge (Ctenopyge) fletcheri **(Matthew 1901)**. *41 cranidia and 15 free cheeks*. Samples GM 1881-337A (5 cranidia, 2 free cheeks) (with *T. humilis*), GM 1922-143 (31 cranidia, 5 free cheeks) (with *Peltura* sp., *Ctenopyge bisulcata*), GM 1881-337B (5 cranidia, 8 free cheeks incl. MGUH 1978).

Ctenopyge (Ctenopyge) linnarssoni **Westergård, 1922**. *38 cranidia and 2 free cheeks.* Samples L17 (12 cranidia) (with *C. tenuis, P. scarabaeoides, T. humilis*), L38 (2 cranidia) (with *C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *T. humilis*), L50 (2 cranidia) (with *Peltura* sp., *T. humilis*), L52 (1 small cranidium) (with *C. pecten*, *C. tenuis*), GM 1871-647 (cranidium) (with *Peltura* sp., *P. scarabaeoides, T.*

humilis), GM 1871-657 (free cheek?) (with *C. tenuis, T. humilis*), GM 1871-666 (free cheek), GM 1871-675A (cranidium) (with *T. humilis*), GM 1877-2000 (2 cranidia) (with *Peltura* sp., *T. humilis*), GM 1881-1805 (cranidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142B (cranidium) (with *C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142C (cranidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142E (cranidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142H (cranidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *T. humilis*), GM 1922-142I (cranidium) (with *C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142K (cranidium) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142L (cranidium), GM 1922-142M (cranidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142N (4 cranidia) (with *C. tenuis*, C. t*eretifrons*, *P. scarabaeoides*, *T. humilis*), GM 1922-142U (3 cranidia) (with *C. tenuis*, *Peltura scarabaeoides*, *Peltura* sp., *T. humilis*), MGUH 1970 (cranidium).

***Ctenopyge (Ctenopyge) magna* n.sp.**. *41 cranidia incl. 10 external moulds, 2 free cheeks? and 1 hypostome*. Samples ATN-113 (5 cranidia) (with *C. ahlbergi*, *C. affinis*, *S. alatus, P. minor*), ATN-116 (3 cranidia, 1 free cheek?) (with *C. ahlbergi*, *C. affinis, Peltura cf. minor, S. alatus*), ATN-117 (cranidium) (with *C. affinis, C. ahlbergi, S. alatus*), ATN-130 (cranidium) (with *C. affinis, S. alatus*), ATN-133 (cranidium) (with *C. ahlbergi*, *C. affinis*, *P. minor, S. alatus*), ATN-134 (2 cranidia, external mould of cranidium) (with *C. ahlbergi*, *C. affinis, Peltura* sp., *S. alatus*), ATN-137 (cranidium) (with *C. affinis, S. alatus*), ATN-146 (2 cranidia) (with *C. ahlbergi*, *C. affinis, S. alatus*), ATN-147 (cranidium) (with *C. affinis, S. alatus*), ATN-169 (fragmentary cranidium) (with *C. affinis*, *S. alatus*), ATN-173 (2 cranidia, 2 external moulds of cranidia, 1 fragmentary free cheek?) (with *C. affinis, C. ahlbergi, S. alatus*), ATN-246 (external mould of cranidium) (with *C. affinis*, *S. alatus*), ATN-330 (cranidium) (with *C. ahlbergi*, *C. affinis, S. alatus*), L76 (external mould of cranidium) (with *S. ahlbergi*, *S. affinis*, *S. alatus*), L84 (2 cranidia) (with *C. affinis, S. alatus*), L93 (fragment of cranidium) (with *C. affinis, S, alatus*), GM 1922-142S (cranidium) (with *T. humilis, C. tenuis, C. teretifrons, P. scarabaeoides*), GM 1902-1209 (4 cranidia incl. MGUH 1975) (with *C. ahlbergi, C. affinis, S. alatus*), GM 1902-1210 (1 cranidium, 4 external moulds of cranidia) (with *C. ahlbergi*, *C. affinis, S. alatus*), GM 1902-1212 (cranidium, 1 external mould of cranidium) (with *C. ahlbergi*, *C. affinis, S. alatus*).

Ctenopyge (Ctenopyge) pecten* (Salter, 1864).** *21 cranidia.** Samples L38 (1 external mould of cranidium) (with *C. linnarssoni*, *C. tenuis, C. teretifrons, Peltura* sp., *T. humilis*), L43 (cranidium) (with *C. tenuis, C. teretifrons, P. scarabaeoides, T. humilis*, L52 (1 small cranidium) (with *C. linnarssoni*, *C. tenuis*), GM 1871-651B (cranidium) (with *T. humilis*), GM 1871-655 (2 cranidia) (with *C. tenuis, Peltura* sp, *T. humilis*), GM 1871-674 (cranidium) (with *T. humilis*, *P. scarabaeoides*), GM 1874-27 (2 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1874-28 (cranidium) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 1881-1802 (2 cranidia?) (with *C. teretifrons*, *P. scarabaeoides*, *T. humilis*), GM 1922-142A (cranidium?) (with *C. tenuis*, *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142B (3 cranidia) (with *C. tenuis*, *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142D (cranidium) (with *C. tenuis*, *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142I (cranidium) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*). GM 1922-142T (2 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp., *T. humilis*), GM 2019-99 (cranidium) (with *C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*).

***Ctenopyge (Ctenopyge) tenuis* Poulsen, 1963**. *327 cranidia, 7 free cheeks, thorax with 4-5 contiguous segments and 24 pygidia with up to 9 attached thoracic segments attached*. Samples L17 (cranidium) (with *C. linnarssoni, Peltura* sp., *P. scarabaeoides, T. humilis*), L38 (2 cranidia, 2 external moulds of cranidia, 2 pygidia) (with *C. linnarssoni, C. pecten, C. teretifrons, Peltura* sp., *T. humilis*), L41 (3 cranidia) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), L43 (11 cranidia, 1 poor pygidium) (with *C. pecten*, *C. teretifrons, P. scarabaeoides, T. humilis*), L44 (cranidium) (with *Peltura* sp., *P. scarabaeoides, T. humilis*), L45 (2 cranidia) (with *P. scarabaeoides, T. humilis*), L46 (9 cranidia) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), L47 (cranidium) (with *P. scarabaeoides*), L48 (7 cranidia, 2 external moulds of cranidia, free cheek) (with *T. humilis*), L52 (5 cranidia, 2 external moulds of cranidia) (with *C. linnarssoni*, *C. pecten*), GM 1871-611 (cranidium) (with *Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1871-612 (14 cranidia, 2 external moulds of cranidia, pygidium) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 1871-617 (cranidium) (with *Peltura* sp.), GM 1871-636 (5 continuous thoracic segments, 1 pygidium) (with *Peltura* sp.), GM 1871-655 (2 cranidia?) (with *C. pecten*, *Peltura* sp, *T. humilis*), GM 1871-657 (cranidium, 2 free cheeks) (with *C. linnarssoni*?, *T. humilis*), GM 1871-661 (5 cranidia) (with *Peltura* sp., *T. humilis*), GM 1871-672 (5 cranidia) (with *Peltura* sp., *T. humilis*), GM 1871-673 (cranidium) (with *Peltura scarabaeoides*, *Peltura* sp.), GM 1874-27 (13 cranidia, 2 external moulds of cranidia) (with *C. pecten, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1874-28 (3 cranidia, free cheek, 2 pygidia) (with *C. pecten*, *Peltura* sp., *T. humilis*), GM 1874-30 (4 cranidia) (with *Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1874-661 (2 cranidia) (with *Peltura* sp., *T. humilis*), GM 1881-1796 (including MGUH 1973) (2 cranidia, 1 pygidium with 5 continuous thoracic segments) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 1881-1797 (cranidium, 1 pygidium with 9 continuous thoracic segments) (including MGUH 1972) (with *T. humilis*), GM 1881-1804 (2 cranidia) (with *Peltura* sp., *T. humilis*), GM 1881-1805 (3 cranidia) (with *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1883-341A (2 cranidia) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 1883-341B (4 cranidia) (with *Peltura* sp., *T. humilis*), GM 1886-199 (3 cranidia, 1 pygidium) (with *Peltura* sp.), GM 1922-142A (42 cranidia, 1 pygidium, 2 external moulds of pygidia) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142B (17 cranidia, 1 pygidium) (with *C. pecten*, *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142C (11 cranidia) (with *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142D (6 cranidia, 1 pygidium) (with *C. pecten*, *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142E (7 cranidia) (with *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142F (2 cranidia) (with *Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142H (13 cranidia, 1 pygidium, 1 external mould of pygidium) (with with *C. linnarssoni, C. teretifrons, Peltura* sp., *T. humilis*), GM 1922-142I (45 cranidia, 2 pygidia of which one has 3 thoracic segments attached) (with *C. linnarssoni, C. pecten, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142J (11 cranidia, 2 free cheeks) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142M (3 cranidia, 2 pygidia) (with *C. linnarssoni, C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142N (7 cranidia, 1 pygidium) (with *C. linnarssoni*, *C. teretifrons*, *P. scarabaeoides*, *T. humilis*), GM 1922-142O (4 cranidia) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142P (4 cranidia) (including MGUH 1971) (with *Peltura* sp., *T. humilis*), GM 1922-142Q (including MGUH 1976) (cranidium) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 1922-142S (3 cranidia, 1 free cheek) (with *T. humilis, C. magna n.sp., C. teretifrons, P. scarabaeoides*), GM 1922-142T (5 cranidia) (with *C. pecten*, *C. teretifrons, Peltura* sp., *T. humilis*), GM 2019-7 (cranidium) (with *Peltura* sp., *T. humilis*), GM 2019-8 (2 cranidia, 2 pygidia) (with *Peltura* sp., *P. scarabaeoides*), GM 2019-9 (2 cranidia) (with *Peltura* sp.), GM 2019-10 (3 cranidia of which one is juvenile) (with *Peltura* sp.), GM 2019-11 (3 cranidia) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 2019-12 (2 cranidia) (with *Peltura* sp., *T. humilis*), GM 2019-13 (3 cranidia), GM 2019-14 (cranidium) (with *Peltura* sp., *T. humilis*), GM 2019-15 (11 cranidia) (with *C. teretifrons, Peltura* sp., *T. humilis*), GM 2019-16 (cranidium) (with *Peltura* sp., *T. humilis*), GM 2019-99 (5 cranidia, 2 external moulds of cranidia) (with *C. pecten, Peltura* sp., *P. scarabaeoides, T. humilis*).

***Ctenopyge (Ctenopyge) teretifrons* (Angelin, 1854)**. *71 cranidia*. Samples L38 (4 cranidia) (with *C. pecten, C. tenuis, C. linnarssoni, Peltura* sp., *T. humilis*), L39 (2 cranidia) (with *Peltura* sp., *T. humilis*), L41 (cranidium) (with *C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), L42 (cranidium) (with *Peltura* sp., *T. humilis*), L43 (cranidium, 1 external mould of cranidium) (with *C. pecten*, *C. tenuis, P. scarabaeoides, T. humilis*), L46 (2 cranidia) (with *C. tenuis, P. scarabaeoides, T. humilis*), L49 (cranidium) (with *Peltura* sp., *T. humilis*), GM 1874-27 (cranidium) (with *C. pecten, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1871-612 (2 cranidia) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 1871-648 (cranidium) (with *Peltura* sp., *T. humilis*), GM 1871-658 (cranidium), GM 1871-662 (cranidium), GM 1871-664 (cranidium) (with *T. humilis*), GM 1871-665 (2 cranidia) (with *T. humilis*), GM 1871-667 (cranidium) (with *P. scarabaeoides, T. humilis*), GM 1871-675B (cranidium) (with *T. humilis*), GM 1877-1999 (cranidium) (with with *Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1881-1796 (2 cranidia) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 1881-1802 (2 cranidia) (with *C. pecten, P. scarabaeoides, T. humilis*), GM 1881-1805 (cranidium) (with *C. linnarssoni, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1883-341A (cranidium) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 1922-142A (3 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142B (cranidium) (with *C. linnarssoni, C. pecten, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142C (6 cranidia) (with *C. linnarssoni, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142D (4 cranidia) (with *C. pecten, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142E (cranidium) (with *C. linnarssoni, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142H (3 cranidia) (with *C. linnarssoni, C. tenuis, Peltura* sp., *T. humilis*), GM 1922-142I (3 cranidia) (with *C. linnarssoni, C. pecten, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142J (cranidium) (with *C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142K (2 cranidia) (with *C. linnarssoni, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142M (cranidium) (with *C. linnarssoni, C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142N (2 cranidia) (with *C. linnarssoni*, *C. tenuis*, *P. scarabaeoides*, *T. humilis*), GM 1922-142O (3 cranidia) (including MGUH 1969) (with *C. tenuis, Peltura* sp., *P. scarabaeoides, T. humilis*), GM 1922-142Q (2 cranidia) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 1922-142S (cranidium) with *T. humilis, C. magna n.sp., C. tenuis, P. scarabaeoides*), GM 1922-142T (2 cranidia) (with *C. pecten*, *C. tenuis, Peltura* sp., *T. humilis*), GM 2019-11 (cranidium) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 2019-15 (3 cranidia) (with *C. tenuis, Peltura* sp., *T. humilis*), GM 2019-97 (cranidium) (with *Peltura* sp., *T. humilis*).

***Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922**. *141 cranidia and 9 free cheeks*. Samples ATN-112 (6 cranidia) (with *S. alatus*), ATN-121 (2 cranidia) (with *S. angustus*), ATN-126 (8 cranidia, 2 external moulds) (with *S. alatus*), ATN-138 (5 cranidia, 2 free cheeks) (with *S. alatus*), ATN-151 (7 cranidia) (with *S. angustus*), ATN-171 (5 cranidia, 1 external mould of cranidium) (with *S. alatus*), ATN-175 (2 cranidia) (with *S. alatus*), ATN-188 (2 cranidia, 1 external mould of cranidium) (with *S. alatus*), ATN-193 (6 cranidia, 1 free cheek) (with *S. alatus*), ATN-197 (13 cranidia, 2 external moulds of cranidia, 1 free cheek) (with *S. alatus, C. tumidoides*), ATN-208 (2 cranidia, free cheek?) (with *S. alatus*), ATN-238 (3 cranidia, 1 external mould of cranidium, 1 free cheek) (with *S. alatus*), ATN-239 (4 cranidia) (with *S. alatus*), L53 (cranidium) (with *S. alatus*), L59 (2 cranidia) (with *S. alatus*), L61 (6 cranidia, 4 external moulds of cranidia) (with *S. alatus*), L64 (cranidium) (with *S. alatus*), L65 (cranidium) (with *C. tumidoides, S. angustus*), L67 (cranidium) (with *S. angustus*), L78 (cranidium, one external mould of cranidium, 1 free cheek) (with *S. alatus*), L81 (2 cranidia) (with *S. alatus*), L88 (external mould of cranidium) (with *S. angustatus*), L89 (cranidium) (with *S. alatus*), GM 1922-141A (cranidium) (with *C. tumidoides, S. angustus*), GM 1922-141C (cranidium,) (with *C. tumidoides*, *S. angustus*), GM 1922-141G (2 cranidia?) (with *C. tumidoides*, *S. angustus*), GM 1922-141H (2 cranidia) (with *S. alatus*), GM 1922-141J (2 cranidia) (with *C. tumidoides, S. angustus*), GM 1922-141K (3 cranidia including MGUH 1967) (with *C. tumidoides*, *S. angustus*), GM 1922-141N (2 cranidia) (with C. *tumidoides*, *S. angustus*), GM 1922-141P (2 cranidia) (with *C. tumidoides*, *S. angustus*), GM 1930-101/102 (10 cranidia) (with *C. tumidoides*, *S. angustus*), GM 2019-17 (11 cranidia, 3 external moulds of cranidia, 1 thoracic segment) (with *S. angustus*), GM 2019-18 (6 cranidia) (with *S. alatus*), GM 2019-21 (free cheek) (with *S. alatus*), GM 2019-25 (cranidium) (with *S. alatus*).

***Ctenopyge (Mesoctenopyge) tumidoides* Henningsmoen, 1957.** *141 cranidia, 11 free cheeks.* Samples ATN-111 (cranidium, 3 external moulds of cranidia) (with *P. acutidens, S. angustatus*), ATN-115 (cranidium) (with *S. angustus*), ATN-135 (3 cranidia) (with *S. angustus*), ATN-145 (2 cranidia) (with *P. planicauda, S. angustus*), ATN-190 (4 cranidia) (with *S. angustus*), ATN-197 (5 cranidia, 2 external moulds of cranidia) (with *S. alatus, C. tumida*), ATN-211 (4 cranidia, 1 free cheek) (with *S. angustus*), ATN-218 (2 external moulds of cranidia) (with *S. angustus*), ATN-225 (cranidium) (with *S. angustus*), ATN-226 (6 cranidia, 2 external moulds of cranidia, 1 free cheek) (with *S. angustus*), ATN-258 (cranidium) (with *S. angustus*), ATN-327 (cranidium, 1 external mould of cranidium) (with *P. acutidens, S. angustus*), L55 (3 cranidia) (with *S. angustus*), L56 (6 cranidia) (with *S. angustus*), L57 (3 cranidia) (with *S. angustus*), L58 (cranidium) (with *S. angustus*), L60 (2 poor cranidia) (with *S. angustus*), L62 (cranidium, 2 external moulds of cranidia) (with *S. angustus*), L63 (3 cranidia) (with *S. angustus*), L65 (external mould of cranidium) (with *C. tumida, S. angustus*), L71 (cranidium) (with *S. angustus*), L73 (cranidium) (with *S. angustus*), L75 (cranidium) (with *S. angustus*), L80 (2 cranidia) (with *S. angustus*), L87 (11 cranidia, 2 external moulds of cranidia, 2 free cheeks, 1 external mould of free cheek, 1 thoracic segment) (with *S. angustus*), L92 (2 cranidia) (with *S. angustus*), L124 (1 cranidium) (with *S. angustus*), GM 1922-141A (6 cranidia) (with *C. tumida*, *S. angustus*), GM 1922-141C (4 cranidia, external mould of free cheek?) (with *C. tumida*, *S. angustus*), GM 1922-141D (cranidium, 3 external moulds of cranidia) (with *S. angustus*), GM 1922-141G (8 cranidia and 2 external moulds of cranidia) (with *C. tumida?*, *S. angustus*), GM 1922-141J (cranidium) (with *C. tumida, S. angustus*), GM 1922-141K (cranidium) (with *C. tumida*, *S. angustus*), GM 1922-141N (5 cranidia, 1 external mould of cranidium) (with C. *tumida*, *S. angustus*), GM 1922-141P (6 cranidia and 1 external mould of a cranidium) (with *C. tumida*, *S. angustus*), GM 1930-101/102 (16 cranidia, 2 external moulds of cranidia, 5 free cheeks) (with *C. tumida*, *S. angustus*), GM 2019-19 (cranidium, 1 external mould of cranidium) (with *S. angustus*), GM 2019-20 (cranidium) (with *S. angustus*), GM 2019-22 (external mould of cranidium) (with *S. angustus*), GM 2019-23 (external mould of cranidium) (with *S. angustus*), GM 2019-26 (cranidium).

***Sphaerophthalmus alatus* (Boeck, 1838)**. *Cranidia are extremely abundant of which most are not registered (>> 1000 specimens); ~1011 cranidia, 23 free cheeks, 1 hypostome? and 2 pygidia.* Samples ATN-103 (>20 cranidia) (with *C. affinis, Peltura cf. minor*), ATN-112 (>40 cranidia) (with *C. tumida*), ATN-113 (>30 cranidia, 1 pygidium) (with *C. magna n.sp., C. ahlbergi, C. affinis, P. minor*), ATN-116 (>20 cranidia) (with *C. magna n.sp., C. ahlbergi*?, *C. affinis, Peltura cf. minor*), ATN-117 (>40 cranidia) (with *C. ahlbergi*, *C. affinis, S. magna n.sp.*), ATN-126 (c. 15 cranidia) (with *C. tumida*), ATN-127 (10 cranidia) (with *C. ahlbergi*, *C. affinis, P. minor*), ATN-130 (10 cranidia) (with *C. magna n.sp.*, *C. affinis*), ATN-132 (>20 cranidia) (with *C. ahlbergi*, *C. affinis, P. minor*), ATN-133 (>20 cranidia) (with *C. magna n.sp., C ahlbergi*, *C. affinis, P. minor*), ATN-134 (>30 cranidia, 3 free cheeks) (with *C. magna n.sp.*, *C. ahlbergi*, *C. affinis, Peltura* sp.), ATN-137 (6 cranidia) (with *C. magna n.sp., C. affinis*), ATN-138 (>20 cranidia) (with *C. tumida*), ATN-139 (>30 cranidia) (with *C. affinis*, *P. minor*), ATN-146 (> 20 cranidia, 1 free cheek) (with *C. magna n.sp., C. ahlbergi, C. affinis*), ATN-147 (> 10 cranidia) (with *C. magna n.sp., C. affinis*), ATN-148 (>20 cranidia) (with *C. ahlbergi*, *Peltura cf. minor*), ATN-164 (>20 cranidia), ATN-169 (>30 cranidia) (with *C. affinis*, *C. magna* n.sp.), ATN-171 (>20 cranidia, 1 pygidium) (with *C. tumida*), ATN-173 (>20 cranidia) (with *C. affinis, C. ahlbergi, C. magna* n.sp.), ATN-175 (>20 cranidia, 1 free cheek) (with *C. tumida*), ATN-180 (2 cranidia), ATN-188 (10 cranidia, 1 free cheek) (with *C. tumida*), ATN-191 (>10 cranidia) (with *C. affinis*), ATN-192 (>20 cranidia) (with *C. affinis*), ATN-193 (>30 cranidia) (with *C. tumida*), ATN-197 (>20 cranidia, 2 free cheeks) (with *C. tumida, C. tumidoides*), ATN-205 (>30 cranidia) (with *C. ahlbergi*, *C. affinis*), ATN-208 (>20 cranidia, 2 free cheeks) (with *C. tumida*), ATN-209 (>20 cranidia), ATN-222 (>30 cranidia) (with *C. affinis, C. ahlbergi*), ATN-236 (>10 cranidia), ATN-238 (>20 cranidia, 3 free cheeks) (with *C. tumida*), ATN-239 (>10 cranidia) (with *C. tumida*), ATN-246 (>20 cranidia) (with *C. affinis, C. magna* n.sp.), ATN-330 (>10 cranidia) (with *C. magna n.sp., C. ahlbergi, C. affinis*), L53 (>20 cranidia) (with *C. tumida*), L59 (5 cranidia) (with *C. tumida*), L61 (>15 cranidia, 1 free cheek) (with *C. tumida*), L64 (5 cranidia) (with *C. tumida*), L76 (>20 cranidia) (with *C. magna n.sp., C. ahlbergi, C. affinis*), L77 (6 cranidia) (with *C. affinis*, *C. ahlbergi*, unknown species?), L78 (cranidium, 1 free cheek) (with *C. tumida*), L81 (9 cranidia, 4 free cheeks) (with *C. tumida*), L84 (>20 cranidia) (with *C. affinis, C. magna* n.sp.), L86 (10 cranidia), L89 (8 cranidia, 2 free cheeks) (with *C. tumida*), L93 (8 cranidia) (with *C. affinis, C. magna* n.sp.), L94 (10 cranidia), GM 1870-944 (4 cranidia) (shale), GM 1870-945 (6 cranidia) (shale), GM 1870-947 (>8 cranidia) (shale), GM 1902-1208 (>5 cranidia) (with *C. affinis*), GM 1902-1209 (>20 cranidia) (with *C. magna n.sp.*, *C. ahlbergi, C. affinis, S. alatus*), GM 1902-1210 (> 20 cranidia) (with *C. magna n.sp., C. ahlbergi, C. affinis*), GM 1902-1211 (4 cranidia), GM 1902-1212 (> 20 cranidia) (with *C. magna n.sp., C. ahlbergi, C. affinis*), GM 1922-141B (>15 cranidia), GM 1922-141E (10 cranidia, 1 free cheek), GM 1922-141F (10 cranidia, hypostome), GM 1922-141H (~20 cranidia) (with *C. tumida*), GM 1922-141L (4 cranidia) (including MGUH 1968), GM 2019-18 (>10 cranidia) (with *C. tumida*), GM 2019-21 (5 cranidia) (with *C. tumida*), GM 2019-24 (2 cranidia, 1 free cheek), GM 2019-25 (cranidium) (with *C. tumida*), GM 2019-27 (cranidium).

***Sphaerophthalmus angustus* (Westergård, 1922)**. *>911 cranidia and >23 free cheeks.* Samples ATN-111 (>50 cranidia, >5 free cheeks) (with *C. tumidoides, P. acutidens*), ATN-115 (2 cranidia) (with *C. tumidoides*), ATN-121 (c. 10 cranidia) (with *C. tumida*), ATN-135 (>30 cranidia) (with *C. tumidoides*), ATN-145 (>12 cranidia, 2 free cheeks) (with *C. tumidoides, P. planicauda*), ATN-151 (>50 cranidia) (with *C. tumida*), ATN-183B (23 cranidia, 1 free cheek), ATN-190 (> 20 cranidia) (with *C. tumidoides*), ATN-211 (> 20 cranidia) (with *C. tumidoides*), ATN-218 (> 30 cranidia) (with *C. tumidoides*), ATN-225 (>15 cranidia) (with *C. tumidoides*), ATN-226 (>30 cranidia) (with *C. tumidoides*), ATN-240 (>20 cranidia), ATN-258 (3 cranidia) (with *C. tumidoides*), ATN-327 (>10 cranidia) (with *C. tumidoides*, *P. acutidens*), L55 (>25 cranidia) (with *C. tumidoides*), L56 (>10 cranidia) (with *C. tumidoides*), L57 (>10 cranidia) (with *C. tumidoides*), L58 (>10 cranidia) (with *C. tumidoides*), L60 (6 cranidia, 1 free cheek) (with *C. tumidoides?*), L62 (>5 cranidia) (with *C. tumidoides*), L63 (>20 cranidia) (with *C. tumidoides*), L65 (>10 cranidia, 1 free cheek) (with *C. tumida, C. tumidoides*), L67 (7 cranidia) (with *C. tumida*), L70 (6 cranidia), L71 (3 cranidia) (with *C. tumidoides*), L73 (>20 cranidia) (with *C. tumidoides*), L75 (5 cranidia) (with *C. tumidoides*), L79 (7 cranidia), L80 (3 cranidia, 1 free cheek) (with *C. tumidoides*), L82 (8 cranidia, 1 free cheek) (with *Peltura cf. acutidens*), L83 (>20 cranidia), L85 (>20 cranidia), L87 (>20 cranidia) (with *C. tumidoides*), L88 (7 cranidia) (with *C. tumida*), L90 (>15 cranidia), L91 (10 cranidia, 2 free cheeks), L92 (11 cranidia, 2 free cheeks) (with *C. tumidoides*), L124 (> 10 cranidia) (with *C. tumidoides*), GM 1888-290 (>20 cranidia), GM 1922-141A (>40 cranidia) (with *C. tumida, C. tumidoides*), GM 1922-141C (>30 cranidia) (with *C. tumida, C. tumidoides*), GM 1922-141D (>50 cranidia) (with *C. tumidoides*), GM 1922-141G (>30 cranidia) (with *C. tumida?, C. tumidoides*), GM 1922-141I (c. 25 cranidia), GM 1922-141J (>20 cranidia) (with *C. tumida C. tumidoides*), GM 1922-141K (>10 cranidia) (with *C. tumida, C. tumidoides*), GM 1922-141M (7 cranidia, 1 free cheek, 1 hypostome) (including MGUH 1982), GM 1922-141N (7 cranidia, 3 free cheek (MGUH 1983)) (with *C. tumida, C. tumidoides*), GM 1922-141P (>100 cranidia, 4 free cheeks) (with *C. tumida, C. tumidoides*), GM 1930-101/102 (>40 cranidia) (with *C. tumida, C. tumidoides*), GM 2019-17 (>20 cranidia) (with *C. tumida*), GM 2019-19 (3 cranidia) (with *C. tumidoides*), GM 2019-20 (cranidium) (with *C. tumidoides*), GM 2019-22 (2 cranidia) (with *C. tumidoides*), GM 2019-23 (2 cranidia) (with *C. tumidoides*), GM 2019-96 (cranidium).

***Sphaerophthalmus drytonensis* (Cobbold, 1934).** *One external mould of semi-complete specimen, 486 cranidia including 1 specimen with 7–8 contiguous thoracic segments and 114 free cheeks.* Samples ATN-105 (29 cranidia, 6 free cheeks) (with *P. praecursor, S. flagellifer*), ATN-107 (cranidium) (with *S. flagellifer*), ATN-125 (4 cranidia, 3 free cheeks) (with *S. flagellifer*), ATN-128 (5 cranidia, 3 free cheeks) (with *S. flagellifer*),
ATN-131 (14 cranidia, 3 free cheek) (with *S. flagellifer*), ATN-144 (7 cranidia) (with *S. flagellifer*, problematicum), ATN-166 (4 cranidia, 2 free cheeks) (with *S. flagellifer*), ATN-181 (9 cranidia, 5 free cheeks) (with *S. flagellifer*), ATN-215 (c. 30 cranidia, 10 free cheeks) (with *S. flagellifer*), ATN-256 (25 cranidia, 5 free cheeks) (with *S. flagellifer*), L19 (25 cranidia, 2 free cheeks) (with *S. flagellifer*), L20 (8 cranidia, 2 free cheeks) (with *S. flagellifer*), L21 (14 cranidia, 4 free cheeks) (with *S. flagellifer*), L22 (14 cranidia, 1 free cheek) (with *S. flagellifer*), L23 (22 cranidia, 4 free cheek) (with *S. flagellifer*), L24 (18 cranidia, 4 free cheeks) (with *S. flagellifer*), L25 (24 cranidia, 7 free cheeks) (with *S. flagellifer*), L26 (11 cranidia, 4 free cheeks) (with *S. flagellifer*), L27 (external mould of nearly complete specimen, 20 cranidia, 7 free cheeks) (with *S. flagellifer*), L28 (27 cranidia, 4 free cheeks), L29 (28 cranidia, 6 free cheeks) (with *S. flagellifer*), L30 (6 cranidia, 4 free cheeks) (with *S. flagellifer*), L66 (2 cranidia, 1 free cheek), L72 (16 cranidia, 2 free cheeks) (with *S. flagellifer?*), L74 (free cheek) (with *S. flagellifer*), GM 1897 (7 cranidia, 2 free cheeks), GM 1922-140B (54 cranidia, 13 free cheeks) (with *S. flagellifer*), GM 1922-140C (12 cranidia, 7 free cheeks) (with *S. flagellifer*), GM 1922-140D (9 cranidia, including one (?) with 7 thoracic segments [MGUH 1965], 2 free cheeks) (with *S. flagellifer*), GM 1922-140E (24 cranidia including MGUH 1966) (with *S. flagellifer*), GM 1922-140F (17 cranidia) (with *S. flagellifer*).

Undetermined ***Sphaerophthalmus drytonensis* (Cobbold, 1934) OR *Sphaerophthalmus flagellifer* Angelin, 1854,** most of them preserved in shale.
49 cranidia including 2 with 7-8 contiguous thoracic segments, 3 hypostomes, 1 free cheek and 1 contiguous thorax. Samples ATN-125 (hypostome) (with problematicum), ATN-128 (hypostome, 1 contiguous thorax), GM 1871-882 (2 cranidia), GM 1871-883 (cranidium, 1 free cheek), GM 1871-884 (2 cranidia), GM 1871-885 (cranidium), GM 1871-886 (cranidium), GM 1871-888 (6 cranidia), GM 1871-890 (cranidium), GM 1871-891 (cranidium), GM 1871-898 (cranidium), GM 1871-893 (2 cranidia), GM 1871-895 (5 cranidia), GM 1871-896 (3 cranidia), GM 1871-897 (cranidium), GM 1872-1070 (2 cranidia, incl. one with 8 contiguous thoracic segments), GM 1874-26 (8 cranidia, incl. one with 7 contiguous thoracic segments), GM 1922-140A (12 cranidia), GM 1922-140C (hypostome)

***Sphaerophthalmus flagellifer* Angelin, 1854**. *207 cranidia and 41 free cheeks*. Samples ATN-105 (11 cranidia, 2 free cheeks) (with *P. praecursor, S. drytonensis*), ATN-107 (6 cranidia, 4 free cheeks) (with *S. drytonensis*), ATN-125 (3 cranidia) (with *S. drytonensis*), ATN-128 (4 cranidia, 1 free cheek) (with *S. drytonensis*), ATN-131 (11 cranidia) (with *S. drytonensis*), ATN-144 (6 cranidia, 1 free cheek) (with *S. drytonensis*), ATN-166 (cranidium) (with *S. drytonensis*), ATN-181 (cranidium, 1 free cheek) (with *S. drytonensis*), ATN-215 (c. 30 cranidia, 6 free cheeks), ATN-256 (7 cranidia, 1 free cheek) (with *S. drytonensis*), L19 (12 cranidia) (with *S. drytonensis*), L20 (4 cranidia) (with *S. drytonensis*), L21 (5 cranidia) (with *S. drytonensis*), L22 (5 cranidia, 2 free cheeks) (with *S. drytonensis*), L23 (15 cranidia, 2 free cheeks) (with *S. drytonensis*), L24 (19 cranidia) (with *S. drytonensis*), L25 (7 cranidia, 1 free cheek) (with *S. drytonensis*), L26 (2 cranidia, 3 free cheeks) (with *S. drytonensis*), L27 (7 cranidia, 2 free cheeks) (with *S. drytonensis*), L28 (4 cranidia, 3 free cheeks) (with *S. drytonensis*), L29 (3 cranidia, 1 free cheek) (with *S. drytonensis*), L30 (3 cranidia) (with *S. drytonensis*), L72 (1 free cheek?) (with *S. drytonensis*), L74 (cranidium) (with *S. drytonensis*), GM 1897 (4 cranidia, 2 free cheeks) (with *S. drytonensis*), GM 1922-140B (17 cranidia, 6 free cheeks) (with *S. drytonensis*), GM 1922-140C (5 cranidia, 1 free cheek) (with *S. drytonensis*), GM 1922-140D (2 cranidia) (with *S. drytonensis*), GM 1922-140E (7 cranidia, 1 free cheek) (with *S. drytonensis*), GM 1922-140F (5 cranidia) (with *S. drytonensis*).

***Triangulopyge humilis* (Phillips, 1848)**. *Cranidia are extremely abundant of which most are not registered (>> 1000 specimens). 610 cranidia, 5 free cheek and 8 pygidia*. Samples L17 (2 cranidia, 1 free cheek) (with *C. linnarssoni*, *Peltura* sp., *P. scarabaeoides*), L38 (8 cranidia, 1 pygidium) (with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons, Peltura* sp.), L39 (7 cranidia) (with *C. teretifrons, Peltura* sp.), L40 (5 cranidia) (with *Peltura* sp., *P. scarabaeoides*), L41 (3 cranidia, 1 pygidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides),* L42 (cranidium) (with *C. teretifrons, Peltura* sp.), L43 (cranidium) (with *C. pecten*, *C. tenuis, C. teretifrons, P. scarabaeoides*), L44 (10 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides*), L45 (6 cranidia) (with *C. tenuis, P. scarabaeoides*), L46 (20 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), L48 (pygidium) (with *C. tenuis*), L49 (cranidium) (with *C. teretifrons, Peltura* sp.), L50 (2 cranidia) (with *C. linnarssoni*, *Peltura* sp.), GM 1871-611 (9 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides*), GM 1871-612 (6 cranidia) (with *C. tenuis, Peltura* sp.), GM 1871-619 (5 cranidia) (with *Peltura* sp., *P. scarabaeoides*), GM 1871-625 (7 cranidia) (with *Peltura* sp., *P. scarabaeoides*), GM 1871-626 (6 cranidia) (with *Peltura* sp., *P. scarabaeoides*), GM 1871-647 (8 cranidia) (with *C. linnarssoni, Peltura* sp., *P. scarabaeoides*), GM 1871-648 (7 cranidia) (with *C. teretifrons, Peltura* sp.), GM 1871-649 (3 cranidia) (with *Peltura* sp.), GM 1871-651A (4 cranidia) (with *Peltura* sp.), GM 1871-651B (cranidium) (with *C. pecten*), GM 1871-652 (3 cranidia) (with *P. scarabaeoides*), GM 1871-653 (cranidum) (with *Peltura* sp.), GM 1871-655 (5 cranidia) (with *C. pecten*, *C. tenuis, Peltura* sp.), GM 1871-661 (2 cranidia) (with *C. tenuis, Peltura* sp.), GM 1871-657 (2 cranidia) (with *C. linnarssoni?, C. tenuis*), GM 1871-663 (cranidium), GM 1871-664 (cranidium) (with *C. teretifrons*), GM 1871-665 (10 cranidia) (with *C. teretifrons, P. scarabaeoides*), GM 1871-667 (20 cranidia) (with *C. teretifrons, P. scarabaeoides*), GM 1871-671 (4 cranidia) (with *Peltura* sp.), GM 1871-672 (5 cranidia) (with *C. tenuis, Peltura* sp.), GM 1871-673 (2 cranidia) (with *Peltura* sp.), GM 1871-674 (5 cranidia, 1 pygidium) (with *C. pecten*, *P. scarabaeoides*), GM 1871-675A (2 cranidia) (with *C. linnarssoni*), GM 1871-675B (2 cranidia) (with *C. teretifrons*), GM 1871-868 (2 cranidia) (shale), GM 1871-871 (2 cranidia) (shale), GM 1871-872 (6 cranidia) (shale), GM 1871-874 (cranidium) (shale), GM 1871-876 (cranidium) (shale), GM 1874-27 (14 cranidia) (with *C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1874-28 (2 cranidia) (with *C. pecten, C. tenuis, Peltura* sp.), GM 1874-30 (2 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides*), GM 1874-661 (2 cranidia) (with *C. tenuis*, *Peltura* sp.), GM 1877-1999 (3 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides*), GM 1877-2000 (4 cranidia) (with *C. linnarssoni, Peltura* sp.), GM 1881-337A (11 cranidia) (with *C. fletcheri*), GM 1881-1802 (>30 cranidia, 1 pygidium) (with *C. pecten, C. teretifrons, P. scarabaeoides*), GM 1881-1804 (3 cranidia) (with *C. tenuis, Peltura* sp.), GM 1881-1805 (21 cranidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1881-1796 (3 cranidia) (with *C. tenuis*), GM 1881-1797 (3 cranidia) (with *C. tenuis*), GM 1881-1802 (11 cranidia) (with *C. pecten, Peltura* sp.), GM 1883-341A (4 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp.), GM 1883-341B (2 cranidia) (with *C. tenuis, Peltura* sp.), GM 1884-1828 (5 cranidia) (with *Peltura* sp.), GM 1884-1830 (2 cranidia), GM 1922-142A (30 cranidia, 2 free cheeks, 1 pygidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142B (35 cranidia) (with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142C (32 cranidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142D (9 cranidia) (with *C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142E (8 cranidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142F (4 cranidia) (with *C. tenuis, Peltura* sp., *P. scarabaeoides*), GM 1922-142G (2 cranidia) (with *Peltura* sp.), GM 1922-142H (2 cranidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp.), GM 1922-142I (14 cranidia, 2 free cheeks) (with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142J (17 cranidia, 1 pygidium) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142K (3 cranidia) (with *C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142M (4 cranidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142N (10 cranidia, 1 pygidium) (with *C. linnarssoni*, *C. tenuis*, *C. teretifrons, P. scarabaeoides*), GM 1922-142O (4 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp., *P. scarabaeoides*), GM 1922-142P (5 cranidia) (with *C. tenuis, Peltura* sp.), GM 1922-142Q (3 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp.), GM 1922-142S (25 cranidia) (with *P. scarabaeoides*, *C. magna n.sp., C. tenuis, C. teretifrons*), GM 1922-142T (19 cranidia) (with *C. pecten*, *C. teretifrons, C. tenuis, Peltura* sp.), GM 1922-142U (16 cranidia) (with *C. linnarssoni*, *C. tenuis*, *P. scarabaeoides, Peltura* sp.), GM 2019-7 (5 cranidia) (with *Peltura* sp.), GM 2019-11 (5 cranidia) (with *C. teretifrons, C. tenuis, Peltura* sp.), GM 2019-12 (3 cranidia) (with *C. tenuis, Peltura* sp.), GM 2019-14 (3 cranidia) (with *C. tenuis, Peltura* sp.), GM 2019-15 (7 cranidia) (with *C. tenuis, C. teretifrons, Peltura* sp.), GM 2019-16 (2 cranidia) (with *C. tenuis, Peltura* sp.), GM 2019-97 (cranidium) (with *C. teretifrons, Peltura* sp.), GM 2019-99 (21 cranidia) (with *C. pecten, C. tenuis, Peltura* sp., *P. scarabaeoides*).

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***Protopeltura planicauda* (Brøgger, 1882)**. *One pygidium*, sample ATN-145 (with *C. tumidoides, S. angustus*).

***Protopeltura praecursor* (Westergård, 1909)**. *One pygidium*, sample ATN-105 (with *S. drytonensis*, *S. flagellifer*).

***Peltura acutidens* Brøgger, 1882**. *One pygidium and 1 free cheek (?)*. Samples ATN-111 (external mould of pygidium, counter piece of ATN-327) (with *C. tumidoides, S. angustus*), ATN-327 (pygidium, counter piece of ATN-111) (with *S. angustus, C. tumidoides*), L82 (with *S. angustus*)

***Peltura minor* (Brøgger, 1882)**. *4 cranidia (tentatively assigned), 1 free cheek (tentatively assigned), 1 external mould of free cheek (tentatively assigned)* and 6 pygidia incl. one with 9 thoracic segments attached. Samples ATN-103 (cranidium) with *C. affinis, S. alatus*), ATN-113 (pygidium) (with *C. affinis, C. ahlbergi, C. magna n.sp., S. alatus*), ATN-116 (cranidium, 1 free cheek) (with *C. ahlbergi, C.*

affinis, C. magna n.sp., *S. alatus*), ATN-127 (cranidium, 2 pygidia) (with *C. ahlbergi, C. affinis, S. alatus*), ATN-132 (pygidium) (with *C. ahlbergi, C. affinis, S. alatus*), ATN-133 (pygidium) (with *C. magna n.sp., C. ahlbergi, C. affinis, S. alatus*), ATN-139 (pygidium with 9 thoracic segments) (with *C. affinis, S. alatus*), ATN-148 (cranidium, 1 external mould of free cheek) (with *C. ahlbergi, S. alatus*).

***Peltura scarabaeoides* (Wahlenberg, 1818)**. *One almost complete specimen, 84 pygidia, incl. one with 8 contiguous thoracic segments, 3 hypostomes, 112 free cheeks, and 160 cranidia, including one with 10 contiguous thoracic segments (cranidia and free cheeks are registered as* Peltura *sp.).* Samples L17 (3 cranidia, 7 pygidia) (with *C. linnarssoni, T. humilis*), L39 (cranidium?) (with *C. teretifrons, T. humilis*), L40 (2 cranidia, 3 pygidia) (with *T. humilis*), L41 (3 cranidia, 1 pygidium) (with *C. tenuis, C. teretifrons, T. humilis*), L43 (external mould of free cheek) (with *C. pecten, C. tenuis, C. teretifrons, T. humilis*), L44 (4 cranidia, 1 pygidium) (with *C. tenuis, T. humilis),* L45 (free cheek) (with *C. tenuis, T. humilis*), L46 (4 cranidia, 1 pygidium) (with *C. tenuis, C. teretifrons, T. humilis*), L47 (free cheek) (with *C. tenuis*), L51 (free cheek) (with *T. humilis*), GM 1871-611 (cranidium, 2 free cheeks, 3 pygidia) (with *C. tenuis, T. humilis*), GM 1871-619 (1 free cheek, 1 pygidium) (with *T. humilis*), GM 1871-621 (pygidium), GM 1871-625 (cranidium, 4 free cheeks, 2 pygidia) (with *T. humilis*), GM 1871-626 (cranidium, 1 free cheek, 2 pygidia) (with *T. humilis*), GM 1871-647 (free cheek, 3 pygidia) (with *C. linnarssoni, T. humilis*), GM 1871-652 (pygidium) (with *T. humilis*), GM 1871-665 (pygidium) (with *C. teretifrons, T. humilis*), GM 1871-667 (3 pygidia) (*C. teretifrons, T. humilis*), GM 1871-671 (hypostome?) (with *T. humilis*), GM 1871-673 (3 cranidia, 1 hypostome) (with *C. tenuis*), GM 1871-674 (hypostome) (with *C. pecten, T. humilis*), GM 1874-27 (cranidium, 2 free cheeks, 1 pygidium) (with *C. pecten, C. tenuis, C. teretifrons, T. humilis*), GM 1874-30 (cranidium, 1 free cheek, 1 pygidium with 8 thoracic segments) (with *C. tenuis, T. humilis*), GM 1877-1999 (cranidium, 3 free cheeks, 1 pygidium) (with *C. tenuis, T. humilis*), GM 1881-1802 (6 cranidia, 10 free cheeks, 3 pygidia, incl. MGUH 1977) (with *C. pecten, C. teretifrons, T. humilis*), GM 1881-1805 (1 complete specimen, 9 cranidia, 3 free cheeks, 1 pygidium) (with *C. linnarssoni, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142A (9 cranidia incl. one with 10 thoracic segments, 2 free cheeks, 2 pygidia) (with *C. tenuis, C. teretifrons, T. humilis*), GM 1922-142B (4 cranidia, 9 free cheeks, 2 pygidia) (with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142C (6 cranidia, 8 free cheeks, 6 pygidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142D (5 cranidia, 2 free cheeks, 2 pygidia) (with *C. pecten, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142E (19 cranidia, 8 free cheeks, 4 pygidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142F (8 cranidia, 3 free cheeks, 1 pygidium) (with *C. tenuis, T. humilis*), GM 1922-142I (10 cranidia, 11 free cheeks, 6 pygidia) (with *C. linnarssoni, C. pecten, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142J (10 cranidia, 11 free cheeks, 4 pygidia) (with *C. tenuis, C. teretifrons, T. humilis*), GM 1922-142K (3 cranidia, 1 pygidium) (with *C. linnarssoni C. teretifrons, T. humilis*), GM 1922-142M (6 cranidia, 2 free cheeks, 3 pygidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142N (5 cranidia, 4 free cheeks, 2 pygidia) (with *C. linnarssoni, C. tenuis, C. teretifrons, T. humilis*), GM 1922-142O (4 cranidia, 1 pygidium) (with with *C. tenuis, C. teretifrons, T. humilis*), GM 1922-142S (10 cranidia, 13 free cheeks, 6 pygidia) (with *T. humilis, C. magna n.sp., C. tenuis, C. teretifrons*), GM 1922-142U (2 cranidia, 1 pygidium) (with *C. linnarssoni, C. tenuis, T. humilis*), GM 2019-8 (11 cranidia, 1 free cheek, 5 pygidia) (with *C. tenuis*), GM 2019-99 (7 cranidia, 6 free cheeks, 1 pygidium) (with *C. pecten, C. tenuis, T. humilis*).

***Peltura westergaardi* Henningsmoen, 1957**. *25 pygidia, 1 cephalon, 12 free cheeks, 2 hypostomes and 116 tentatively assigned cranidia (registered as* Peltura *sp.).* Samples L4 (pygidium), L9 (3 cranidia, 1 pygidium), L10 (external mould of pygidium) (with *P. lobata praecurrens*), L11 (2 pygidia) (with *P. lobata praecurrens*), L12 (cranidium, 1 pygidium) (with *P. lobata praecurrens*), L13 (pygidium), L14 (4 cranidia, 3 pygidia) (with *P. lobata praecurrens*), L15 (2 cranidia, 1 free cheek, 1 pygidium), L16 (3 cranidia, 1 pygidium) (with *P. lobata praecurrens*, orthid brachiopod), GM 2019-93 (1 cephalothorax, 18 cranidia (several juvenile), 3 free cheeks, 3 pygidia), GM 2019-94 (32 cranidia (most of them juvenile), 1 hypostome, 4 free cheeks, 6 pygidia), GM 2019-95 (38 cranidia (most of them juvenile), 1 hypostome, 1 free cheek, 4 pygidia), sample 2019-101 (incl. MGUH 1987) (4 juvenile cranidia), sample 2019-104 (incl. MGUH 1988) (8 cranidia of which 5 are juvenile), 2019-105 (incl. MGUH 1989) (3 juvenile cranidia, 3 free cheeks).

***Orusia lenticularis* (Wahlenberg, 1821) (brachiopod).** Specimens not counted; the species is extremely common. Samples ATN-104, ATN-140, ATN-141, ATN-143, ATN-165, ATN-179, ATN-183A, ATN-184, ATN-185, ATN-186, ATN-187, ATN-189, ATN-194, ATN-195, ATN-198, ATN-200, ATN-201, ATN-202, ATN-203, ATN-204, ATN-206, ATN-207, ATN-210, ATN-212, ATN-213, ATN-214, ATN-221, ATN-235, ATN-245

Other samples (Miaolingian samples, lithology samples, samples without determinable fossils). ATN-161, ATN-196, ATN-229, ATN-230, ATN-267, ATN-308, ATN-309, ATN-310, ATN-311, ATN-312, ATN-313, ATN-314, ATN-315, ATN-316, ATN-317, ATN-318, ATN-319, ATN-321, L5, L6, L7, L8, L34, L35, L36, L37, L68, L69, L96, L97, L102, L06, L107, L109, L110, L113, L114, L116, L117, L120, L121, L122, L123.