Phosphatised olenid trilobites and associated fauna from the Upper Cambrian of Vastergotland, Sweden

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Secondarily phosphatised olenid trilobites from organic-rich limestones (*orsten*) in the Furongian (Upper Cambrian) of Västergötland, south-central Sweden, are described and illustrated. All trilobites originate from the *Peltura scarabaeoides* Zone and were collected on the western slope of Kinnekulle. Only the dorsal exoskeletons have become secondarily phosphatised, and the ventral appendages are not preserved. Yet the material is otherwise remarkably well preserved and reveals the morphology of the olenid trilobites in greater detail than hitherto known. Species belonging to the genera *Ctenopyge*, *Sphaerophthalmus*, *Parabolina*, and *Peltura* are identified, and several juvenile specimens are present in the material. The material is disarticulated and fragmentary, and it has only been possible to identify a few specimens to species level. In addition to chaetognaths and conodonts, the trilobites are associated with pelmatozoan columnals, a possible camaroid, and fossils of uncertain affinities. These fossils, along with a probable conulariid fragment from the *Peltura minor* Zone, are also described and discussed. The presence of a benthic fauna of pelmatozoans, and possible conulariids and camaroids, indicates that at least parts of the *Peltura* zones were deposited during dysoxic rather than anoxic periods. Moreover, the sea floor must have been firm enough to allow colonisation by sessile organisms.

Key words: Olenidae, Trilobita, Problematica, phosphatisation, Cambrian, Alum Shales, Västergötland, Sweden.

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Introduction

Intensive research during the past three decades on small and extremely well preserved, secondarily phosphatised arthropods, isolated from limestone nodules and lenses (*orsten*) in the topmost part of the Middle Cambrian and the Furongian (Upper Cambrian) of Sweden, has added a new dimension to the study of the Scandinavian Alum Shales. These tiny, three-dimensionally preserved fossils have been described in numerous publications by Klaus Müller and Dieter Walossek from 1979 and onwards (e.g., Müller and Walossek 1985a, 1985b, 1987, 1988; Walossek 1993). Although the rocks are replete with trilobites, particularly olenids, no phosphatised polymeroid trilobites have hitherto been described from the middle Cambrian–lowermost Ordovician (Tremadocian) Alum Shale Formation of Scandinavia.

Secondarily phosphatised olenid trilobites were discovered by Hubert Szaniawski while he was searching for conodonts in etched residues of organic-rich limestones (*orsten*) from the Furongian of Västergötland, south-central Sweden. The trilobite material is all from the *Peltura scarabaeoides* Zone in the two neighbouring old quarries Trolmen and Råbäck on the western side of Kinnekulle (Fig. 1). Only the dorsal exoskeletons have become phosphatised, and the ventral appendages are not preserved. Yet the material is otherwise remarkably well preserved and reveals the morphology of the olenid trilobites in greater detail than was known hitherto. Species belonging to the genera *Ctenopyge*, *Sphaerophthalmus*, *Parabolina*, and *Peltura* have been identified, and several juvenile specimens are present. This new material of phosphatised trilobites adds significantly to our understanding of the morphology and ontogeny of Furongian olenid trilobites. The material is disarticulated and fragmentary. In addition, the specimens are all small, many are juveniles, and consequently only a few sclerites could be identified to species level.

Geological setting

The Alum Shale Formation (*sensu* Buchardt et al. 1997) of Scandinavia consists of dark, organic-rich, and finely laminated shales with lenses and beds of dark grey limestones (stinkstones or *orsten*). The sediments were formed under

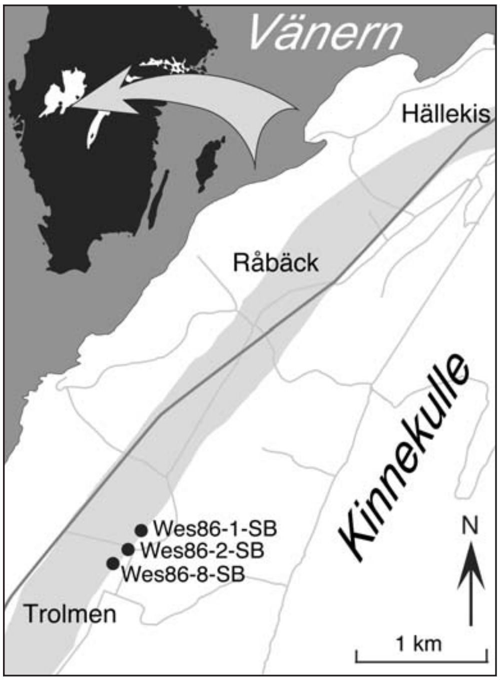

Fig. 1. Sketch-map of northwestern Kinnekulle at Lake Vänern, south-central Sweden, showing the collecting sites in the Råbäck and Trolmen quarries. The broad grey band shows the outcrop area of the Alum Shales in the region. The thin grey lines are roads, and the thicker line shows the railroad. Sample 1 (full designation: Wes86-1-SB) was collected from the Råbäck quarry, and samples 2 (Wes86-2-SB) and 8 (Wes86-8-SB) were collected from the adjacent Trolmen quarry. For stratigraphical position of the samples, see Szaniawski and Bengtson (1998: fig. 2).

poorly oxidised (dysoxic to anoxic) and extremely stable tectonic conditions (e.g., Thickpenny 1984, 1987; Andersson et al. 1985; Bergström and Gee 1985; Buchardt et al. 1997; Schovsbo 2001). The succession is highly condensed, and the net rate of sedimentation was very low.

The faunal succession as a whole is generally dominated by trilobites. Apart from the topmost zone (the *Agnostus pisiformis* Zone), the Middle Cambrian faunas are remarkably diverse, especially in the Exsulans and Andrarum Limestones (Westergård 1946, 1953; Clarkson and Taylor 1995). The Furongian faunas, however, are taxonomically restricted and dominated by trilobites, especially olenids, which, along with agnostoids, generally constitute the bulk of the fauna. Brachiopods, phosphatocopids, conodonts (incl. paraconodonts as well as euconodonts), and chaetognaths (= protoconodonts) may also be common, particularly in certain intervals with stinkstones (e.g., Müller and Hinz 1991; Hinz-Schallreuter 1993; Szaniawski and Bengtson 1993, 1998; Clarkson et al. 1998; Szaniawski 2002; Maas et al. 2003).

The thickest and stratigraphically most complete Furongian successions are in Scania (Skåne), southernmost Sweden, and in the Oslo Region of Norway. In Västergötland, the Furongian is considerably thinner, and there are several gaps in the succession (Westergård 1922; Terfelt 2003). The proportion of limestone relative to shale is considerably greater in Västergötland than in most other areas of Sweden. Numerous old quarries testify to the former importance of lime extraction. These quarries provide many good exposures, and are noted for the abundance of trilobites, which are often well preserved and form the basis for the zonal subdivision (Westergård 1922, 1947; Henningsmoen 1957; Martinsson 1974; Ahlberg 2003).

Furongian deposits are well exposed in several quarries surrounding the hill Kinnekulle, southeast of Lake Vänern (Westergård 1922: fig.18; Müller and Hinz 1991: fig. 2). Of these the large old, neighbouring quarries of Trolmen and Råbäck (N58°35´41´´, E13°21´18´´) on the western side of Kinnekulle have been described in detail by Westergård (1922), Thorslund and Jaanusson (1960), and Ahlberg (1998). Stratigraphically, the sections exposed range from the *Agnostus pisiformis* Zone to the *Parabolina lobata* Subzone of the *Peltura scarabaeoides* Zone.

Material

Conodonts were described from several limestone horizons in the Trolmen and Råbäck quarries by Szaniawski and Bengtson (1993, 1998). The limestones occur as lenses and beds interlaminated by black alum shales. While searching for conodonts in the etched residues, Szaniawski found numerous disarticulated olenid trilobites. EDAX microprobe analyses show that they consist of calcium phosphate with fluorine, probably fluorapatite, and small irregularly distributed admixtures of silica, aluminium, iron, sulphur, potassium, and sodium. It is evident that the trilobite sclerites are secondarily phosphatised. Biostratigraphic comparisons indicate that the specimens come from the *Parabolina lobata* Subzone (the *P. longicornis* Subzone of Westergård 1947) at the very top of the quarries (samples 1 and 2 of Szaniawski and Bengtson 1998: fig. 2). Only these two samples out of 16 from the quarries yielded well-preserved phosphatised olenids, though a probable conulariid fragment (Fig. 5C) was recovered from the *Peltura minor* Zone (sample 8 of Szaniawski and Bengtson 1998: fig. 2).

It may be significant that the olenid and other fragments, from a taphonomic point of view, are all very small. Many of the olenid sclerites seem to represent juvenile stages. In this respect there are evident similarities with the preservational state of the orsten arthropods described by, e.g., Müller and Walossek (1985a, 1987, 1988) and Walossek (1993); these also are minute, less than 2 mm long (Müller and Walossek 1985b). This may suggest that secondary phosphatisation of external surfaces affected only tiny organisms.

Following the initial discovery of these trilobites they were preliminarily determined and photographed by Szaniawski using the SEM. The photographs were sent to Gunnar Henningsmoen in Oslo, who made some corrections and comments in 1989. After Henningsmoen's death in 1996 the photographs were given to Ahlberg and Clarkson for further study.

Institutional abbreviations.—The illustrated material has been deposited in the Swedish Museum of Natural History, Stockholm (abbreviated SMNH). The numbers within brackets after the individual museum numbers indicate the SEM stub number and specimen number as used by us (e.g., "(3.13)" means specimen no. 13 on stub no. 3).

Other abbreviations.—exsag., exsagittally; sag, sagittally; tr., transversely.

Systematic palaeontology

The trilobite sclerites preserved in our material consist of nearly intact or broken cranidia, librigenae, hypostomes, thoracic tergites, and pygidia. Most of these reveal details of the exoskeletal surface structure and sculpture not previously described in olenid trilobites. Only a few specimens can be assigned to known species, either because they are too fragmentary or because they belong to undescribed species. In addition several juvenile specimens are present, and since the ontogeny is imperfectly known in most cases precise identification is generally not possible.

The morphological terminology used for the description of trilobites follows that of Nikolaisen and Henningsmoen (1985: fig. 2) and Whittington in Kaesler (1997).

Family Olenidae Burmeister, 1843

Genus *Parabolina* Salter, 1849

Parabolina sp.

Fig. 2A.

Material and remarks.—A single juvenile pygidium probably representing a species of *Parabolina*. It is 0.67 mm broad and 0.36 mm long, trapezoidal in shape, with a posteriorly tapering axis almost reaching the posterior border. The axis consists of a prominent articulating half-ring with four axial rings and a terminal piece. Three, possibly four, pairs of pleural furrows are lightly impressed on the pleural fields. The postero-lateral borders are slightly raised with three, possibly four, marginal nodes. The posterior margin is slightly embayed.

Genus *Ctenopyge* Linnarsson, 1880

Ctenopyge sp.

Fig. 2B–H.

Material.—Two left librigenae with intact eyes but broken genal spines, and five pygidia can be assigned to a species of *Ctenopyge*. Two fragmentary cranidia are tentatively referred to the same species.

Description.—The extraocular cheeks are narrow, less than half the width of the eye, and the genal spine is directed outwards at angle of about 90° to the palpebral suture. The genal spine is ovoid in cross-section, probably curving gently backwards, and the base of the spine is slightly narrower than the width of the extraocular cheek. A scale-like ornament is present, particularly distinct on the genal spine. The posterior branch of the facial suture is strongly curved anteriorly behind the eye and then sweeps backwards to make a sharp angle with the lateral margin. The eye is large, reniform, and inflated, occupying at least half the length of the librigena, as inferred. There are at least 100 lenses, regularly arranged in a standard system of hexagonal close-packing in subconcentric rows below the almost straight palpebral suture.

The pygidia are subtriangular with a tapering axis continuing into a prominent, stoutly-based caudal spine. Anteriorly the axis is narrower than the pleural field. The axis consists of a distinct, semicircular half-ring and four or five axial rings. Subdued axial nodes are present on the axial rings, fading posteriorly. The posterior axial ring carries a prominent, broad-based spine, directed backwards and upwards. The spines are broken to reveal a circular cross-section. The pleural fields have shallow pleural furrows, directed outwards and increasingly backwards towards the rear. The postero-lateral margins are almost straight and bear five or six pairs of thorn-like spines. The anterior spines are directed sharply upwards. The angle these marginal spines make with the horizontal plane decreases posteriorly so that the rearmost pair is horizontal. In this respect the pygidia are similar to that of *Ctenopyge ceciliae* Clarkson and Ahlberg, 2002 from the *Peltura scarabaeoides* Zone of Scania, southern Sweden.

A single pygidium (Fig. 2E) represents a juvenile stage in development. It may well belong to the same species. This transitory pygidium is more semicircular in outline and the first segment is defined posteriorly by a transverse furrow and an incipient articulating half-ring, as almost ready for release. It has four axial rings and a terminal piece. The spine on the posterior axial ring is broken off at the base, but the horizontal caudal spine is nearly complete. Six pairs of marginal spines are present, more closely spaced and longer posteriorly than in other pygidia.

The glabella of the fragmentary cranidia (Fig. 2B) tapers forwards, but in both specimens it is broken off anteriorly. The occipital ring (about 0.8 mm wide) has an evenly rounded posterior margin, and a slender, tapering spine extends from its middle part. S0 is transglabellar with two lateral indentations. L1 is about the same length (sag.) as L0 and is bounded anteriorly by S1, which is broad and transglabellar. A granular ornament is present over all parts of the surface, except for the furrows.

Genus *Sphaerophthalmus* Angelin, 1854

Sphaerophthalmus humilis (Phillips, 1848)

Fig. 2I–K.

Olenus humilis n. sp.; Phillips 1848: 55, 347, figs. 4–6.

Sphaerophthalmus humilis (Phillips, 1848); Żylińska 2001: 344, pl. 2: 1a, pl. 3: 2–3 [see for complete synonymy].

Material.—Two cranidia and three pygidia.

Description.—The two cranidia are 0.8 and 1.3 mm long, respectively. The smaller one (Fig. 2I) is almost complete except for the occipital ring. The specimens agree in most respects with Henningsmoen´s (1957) description of the spe-

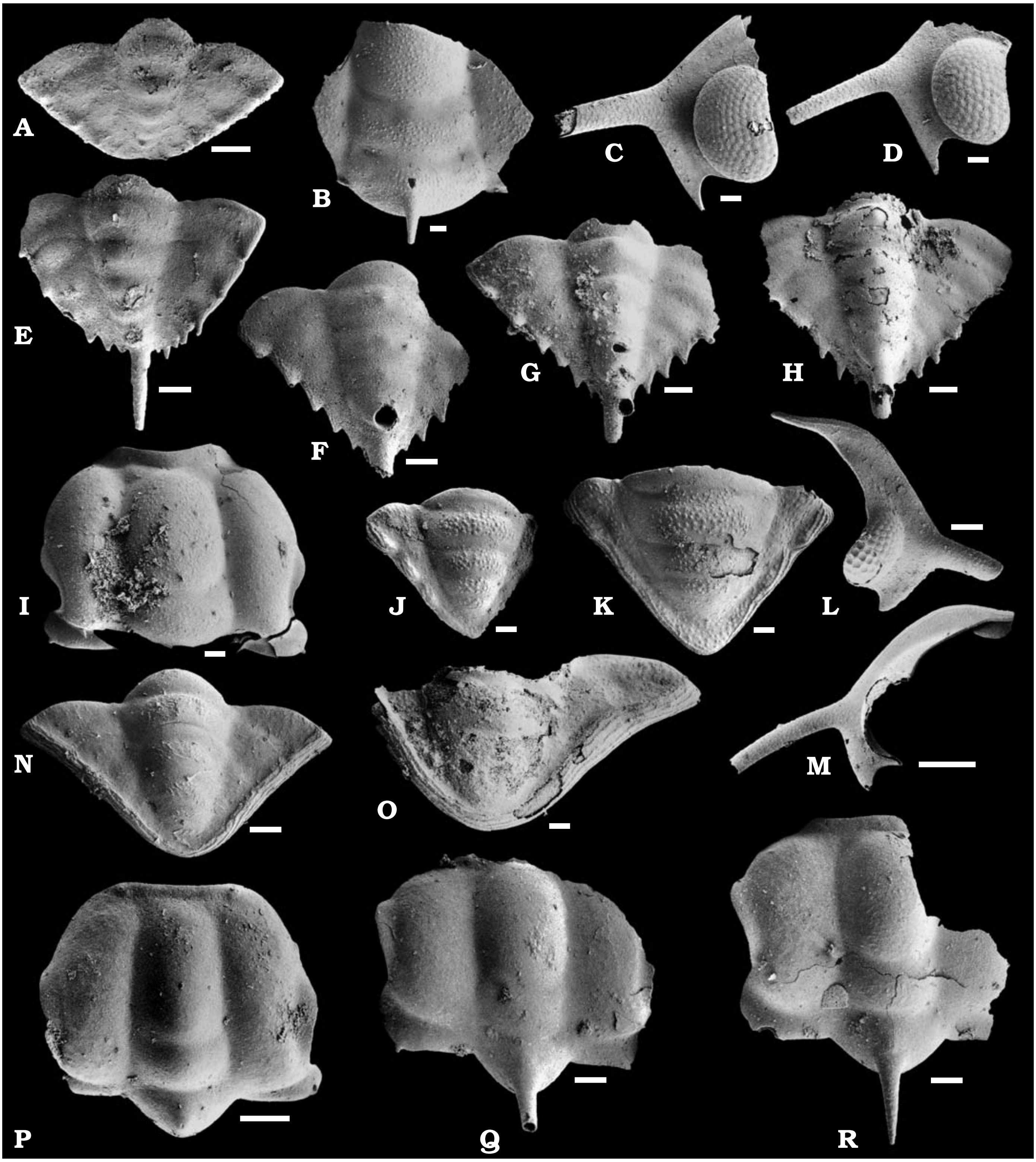

Fig. 2. **A**. *Parabolina* sp., juvenile pygidium, SMNH Ar59711 (3.13), sample 2. **B**–**H**. *Ctenopyge* sp. **B**. Fragmentary cranidium, SMNH Ar59712 (2.8), sample 2. **C**. Left librigena with intact eye, SMNH Ar59713 (1.12), sample 1. **D**. Left librigena with intact eye, SMNH Ar59714 (1.13), sample 1. **E**. Small pygidium, SMNH Ar59715 (1.23), sample 1. **F**. Pygidium, SMNH Ar59716 (2.6), sample 2. **G**. Pygidium, SMNH A59717 (2.2), sample 2. **H**. Pygidium, SMNH Ar59718 (1.4), sample 1. **I**–**K**. *Sphaerophthalmus humilis* (Phillips, 1848). **I**. Cranidium, SMNH Ar59719 (2.20), sample 2. **J**. Pygidium, SMNH 59720 (1.5), sample 1. **K**. Pygidium, SMNH Ar59721(2.5), sample 2. **L**, **M**. *Sphaerophthalmus* cf. *alatus* (Boeck, 1838). **L**. Right librigena with intact eye, SMNH Ar59722 (1.20), sample 1. **M**. Left librigena, SMNH Ar59723 (1.14), sample 1. **N**, **O**. *Sphaerophthalmus* cf. *majusculus* Linnarsson, 1880. **N**. Pygidium, SMNH Ar59724 (1.15), sample 2. **O**. Pygidium, SMNH Ar59725 (2.1), sample 2. **P**. *Sphaerophthalmus* sp. A?, juvenile cranidium, SMNH Ar59726 (2.11), sample 2. **Q**–**R**. *Sphaerophthalmus* sp. A, sample 1. **Q**. Cranidium, SMNH Ar59727 (1.8). **R**. Cranidium, SMNH Ar59728 (1.10). Scale bars 0.1 mm.

cies. The palpebral lobes are very narrow, becoming wider anteriorly, with their centres situated on a transverse line slightly in front of S1. A tiny intergenal spine is present on the rounded postero-lateral margin. The surface is very finely granulated.

The three pygidia (0.7, 0.8, and 0.9 mm long) can confidently be assigned to the species. They are triangular in shape with nearly straight and slightly undulating postero-lateral margins. The axis is very broad, anteriorly occupying six-tenths of the total width, and tapers backwards almost to the tip of the pygidium. It consists of a prominent articulating half-ring, three axial rings, and a terminal piece. The pleural fields are very narrow and there is a distinct, raised postero-lateral border with two, possibly three, elongated lobes opposite the axial rings, arranged parallel to the margin. The surface of the pygidium is covered with granules except on the articulating half-ring. These are most prominent on the central part of the axial rings and behind the axis. On the pleural fields the granules are more elongated, subparallel with the postero-lateral margin. Terrace lines are present on the postero-lateral borders, being especially well developed on the most anterior lobes.

Sphaerophthalmus cf. *alatus* (Boeck, 1838)

Fig. 2L, M.

Material.—Two librigenae, one left and one right.

Description.—Nearly intact left and right librigena (1.2 and 0.7 mm long respectively), the latter with an intact eye, probably belong to this species. They are very narrow, curving and tapering anteriorly, and with the eyes set in the posterior third, where the librigena is widest. Long genal spines (broken) emerge from a level opposite the eye at an angle of 70–80° to the sagittal line. The postero-lateral margin between the spine and the facial suture is almost straight and very short, less than the length of the eye. The antero-lateral margin in front of the spine is three to four times as long as the postero-lateral margin. It is almost straight laterally and then curves forwards and inwards to terminate very sharply against the facial suture. The anterior branch of the facial suture is almost straight anteriorly, and then slightly curved to meet the eye, where it curves sharply inwards and outwards again, encompassing the rear part of the eye. The posterior branch is short and curves slightly inwards to meet the posterior margin.

The eye is ovoid, slightly expanded posteriorly, and provided with about 50 thin lenses, which are slightly larger towards the rear. The librigenae are very small and clearly belong to juvenile specimens, and the eyes have fewer lenses and are more elongated than in adult specimens from Andrarum, Scania, southern Sweden (see Clarkson 1973: 756).

Sphaerophthalmus cf. *majusculus* Linnarsson, 1880

Fig. 2N, O.

Material.—Two pygidia, 0.6 and 0.8 mm long.

Description.—The pygidia are subtriangular, wider than long, and with the postero-lateral margins slightly concave and a somewhat rounded posterior end. The axis occupies slightly more than the central third of the total width anteriorly, tapers regularly backwards and almost reaches the posterior border. It consists of an articulating half-ring, three axial rings, and a terminal piece. The pleural fields become distinctly narrower backwards and have two or three shallow pleural furrows. The pygidial border is raised and continuous, lacking undulations, and provided with several distinct, subparallel terrace lines. The pygidial surface lacks distinct ornamentation other than the terrace lines and some faint granulation on the central part of the axial rings, and, on the larger specimen (Fig. 2O), on the anterior part of the pleural field.

Sphaerophthalmus sp. A

Figs. 2P?, 2Q–R, 3A.

Material.—Six cranidia, ranging in length (excluding the occipital spine) from 0.5 to 0.8 mm.

Description.—The larger cranidia (Figs. 2Q, R, 3A) are subquadrate in outline and slightly wider than long. The anterior and posterior margins are almost straight and transverse. The anterior branch of the facial suture is curved backwards at approximately 45° from the anterior margin. The palpebral lobe is narrow, curved, and long, approximately half the total length of the glabella (L0 excluded), and narrows posteriorly. The centre of the palpebral lobe is situated opposite the posterior third of the glabella excluding L0 to S1. The posterior branch of the facial suture extends from opposite S1 to the posterior margin, and curves backwards and slightly outwards from the palpebral lobe, then runs backwards and inwards. A pair of tiny intergenal spines is present where the facial suture terminates against the posterior margin. The glabella is parallel-sided, broadly rounded in front, extends to the anterior border, and occupies about a third of the total width of the cranidium. S1 is prominent, transglabellar, and curved backwards medially. There is no indication of S2 or S3. L0 is subtriangular and is provided with a long and stoutly-based occipital spine, circular in cross-section, and arising backwards and upwards from the posterior half of L0. The spine is about three-quarters the length of the glabella (L0 excluded), and is sharply pointed at its tip. Some specimens show a subdued, somewhat reticulate surface ornament.

Remarks.—The smallest cranidium (Fig. 2P) is provisionally referred to the same species, though it differs in being slightly longer relative to its width, having a slightly tapering glabella, and in having an occipital node rather than a spine. Two small nodes are present on the anterior border on either side of the glabella. The palpebral lobe is less sharply marked off, and is set further backwards. Moreover, the anterior branch of the facial suture curves backwards more sharply from the anterior margin. This small cranidium probably represents a juvenile form.

Sphaerophthalmus sp. B

Fig. 3B.

Material.—A damaged right librigena (width excluding spine about 0.5 mm) lacking the anterior part.

Remarks.—This specimen is in many ways comparable to the librigenae of *Sphaerophthalmus* cf. *alatus* (Fig. 2L, M) in terms of the genal spine set opposite the eye and in the course of the posterior branch of the facial suture. The eye, however, is relatively larger, not so elongated, and has about 80 lenses. The librigena may represent a more adult individual than the librigenae described above as *S*. cf. *alatus*.

Sphaerophthalmus sp. C

Fig. 3C.

Material.—An incomplete thoracic tergite (estimated width 2.9 mm).

Remarks.—The axial ring is convex (tr.) and very wide, about twice as wide as the pleura, and has a narrow crescentic articulating half-ring separated by a deep continuous furrow, and a slight swelling medially in front of a short, sharp axial spine. The pleura is horizontal proximally, but distally sharply bent down at approximately two-thirds of the distance to the outer edge. The lateral margin is straight, exsagittally orientated, and forms a fine ridge. The pleural furrow is distinctly incised and nearly reaches the lateral margin. The integument is very thin, as indicated by the intact anterior margin seen from the anterior edge. The external surface is almost smooth. The closest resemblance may lie with *S. humilis* in terms of the proportion of the axial ring to the pleura.

Genus *Peltura* Milne Edwards, 1840

Peltura cf. *transiens* (Brögger, 1882)

Fig. 3D–F.

Material.—Three pygidia, 0.4, 0.6, and 0.8 mm long (the latter estimated).

Description.—The pygidia are subsemicircular in outline and more than twice as wide as they are long. The axis is wider than the pleural fields, slightly tapering backwards, and broadly rounded posteriorly, not reaching the posterior margin. It consists of an articulating half-ring, two axial rings, and a terminal piece. The pleural field narrows backwards and has two shallow furrows extending almost to the postero-lateral margins. A very narrow, curving articulating facet is present on the antero-lateral margin. Three pairs of marginal spines, directed backwards and inwards, are present lateral to the posterior margin behind the axis.

Remarks.—In the smallest pygidium (Fig. 3F) the marginal spines are relatively longer than in the larger pygidia. The development of the surface sculpture can be traced from the smallest to the largest specimen. In the smallest specimen the ornament consists of granules, slightly elongated and, on the pleural fields, subparallel with the postero-lateral margin. On the axial rings these granules have coalesced into incipient transverse terrace lines. Less developed terrace lines are present at the posterior margin. In the next larger specimen (Fig. 3D) the terrace lines are much more distinctly developed on the pleural fields and behind the axis. In the largest specimen (Fig. 3E) the terrace lines are very well developed as raised ridges forming short, linked sections, but continuous behind the axis. On the terminal piece of the axis they are again continuous and subconcentric with the axial furrow surrounding the posterior end of the axis.

Peltura cf. *paradoxa* (Moberg and Möller, 1898)

Fig. 3G.

Material.—An incomplete pygidium, about 0.7 mm long and 1.8 mm wide (estimated).

Remarks.—The specimen agrees fairly well with Henningsmoen's (1957) diagnosis and description of *Peltura paradoxa*, but the pleural field is slightly wider, and medially the posterior margin is slightly curved anteriorly. In the latter respect the pygidium resembles one from the Oslo Region, Norway, figured by Henningsmoen (1957: pl. 26: 5). The granulose ornament present on the pleural fields is also evident on the axis though here the granules are linked into transverse terrace lines. Several subparallel terrace lines are extended along the posterior margin, most distinct medially.

Peltura sp. A

Fig. 3H, I.

Material.—One almost complete pygidium, 0.8 mm long (excluding spines) and 1.5 mm wide, and one transitory pygidium, 0.4 mm long (estimated) and 0.9 mm wide.

Remarks.—The larger pygidium (Fig. 3H) resembles that of typical *Peltura* species, but the three pairs of marginal spines are relatively long and directed inwards. The posterior pair of spines is situated quite close to the midline, as in *P. acutidens* Brögger, 1882 and *P. scarabaeoides westergaardi* Henningsmoen, 1957. An ornament of granules is present on the axial rings and on the pleural fields, especially along the anterior edge. Terrace lines are visible on the marginal spines, orientated roughly along the axis of the spines. The transitory pygidium (Fig. 3I) has four pairs of marginal spines directed inwards. In this respect it differs from *P. scarabaeoides westergaardi*, which has three pairs of spines in a transitory pygidium of similar size (see Bird and Clarkson 2003).

Peltura sp. B

Fig. 3J.

Material.—One transitory pygidium with a length of about 0.5 mm and an estimated width of 1.0 mm.

Remarks.—The pygidium is subtriangular in outline with three axial rings and a terminal piece. There are four pairs of stout marginal spines, the outermost directed backwards and the innermost directed backwards and slightly inwards. While this pygidium is noted here as a separate species, it may merely represent a different growth stage of *Peltura* sp. A.

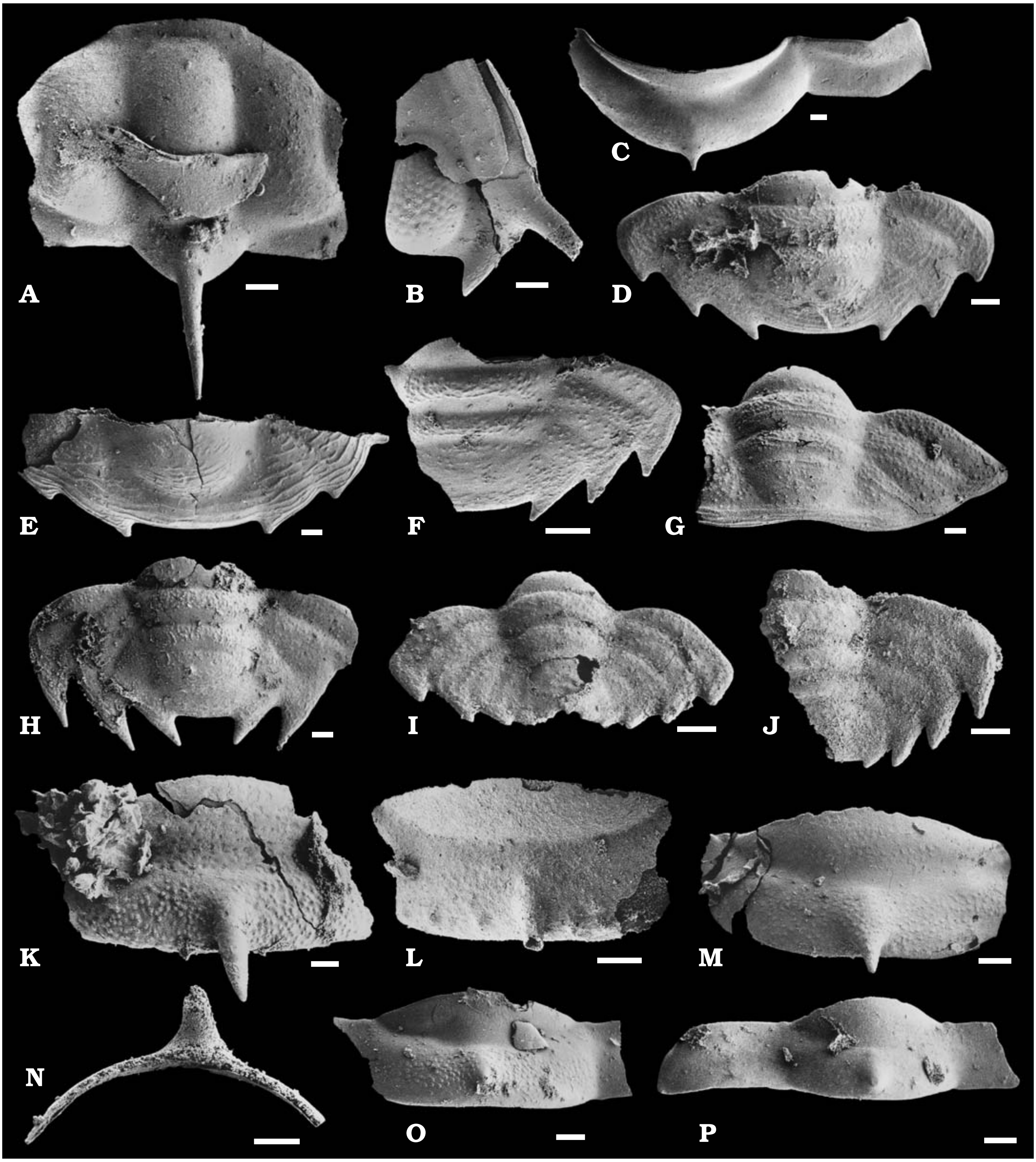

Fig. 3. **A**. *Sphaerophthalmus* sp. A, cranidium, SMNH Ar59729 (2.21), sample 2. **B**. *Sphaerophthalmus* sp. B, right librigena with intact eye, SMNH Ar59730 (3.11), sample 2. **C**. *Sphaerophthalmus* sp. C, incomplete thoracic tergite, SMNH Ar59731 (2.19), sample 2. **D**–**F**. *Peltura* cf. *transiens* (Brögger, 1882). **D**. Pygidium, SMNH Ar59732 (1.3), sample 1. **E**. Pygidium, SMNH Ar59733 (2.7), sample 2. **F**. Small pygidium, SMNH Ar59734 (3.12), sample 2. **G**. *Peltura* cf. *paradoxa* (Moberg and Möller, 1898), pygidium, SMNH Ar59735 (1.7), sample 1. **H**, **I**. *Peltura* sp. A. **H**. Pygidium, SMNH Ar59736 (1.2), sample 1. **I**. Transitory pygidium, SMNH Ar59737 (1.21), sample 1. **J**. *Peltura* sp. B, transitory pygidium, SMNH Ar59738 (1.6), sample 1. **K**–**P**. Indeterminate olenid fragments. **K**–**M**. Occipital rings. **K**. SMNH Ar59739 (1.19), sample 1. **L**. SMNH Ar59740 (1.15), sample 1. **M**. SMNH Ar59741 (2.14), sample 2. **N**. Axial ring seen edge on, SMNH Ar59742 (1.18), sample 1. **O**. Axial ring, SMNH Ar59743 (2.22), sample 2. **P**. Incomplete thoracic tergite, SMNH Ar59744 (1.24), sample 1. Scale bars 0.1 mm.

Indeterminate olenid fragments

Figs. 3K–P, 4A–H.

Material.—Three broken occipital rings, two thoracic "axial rings", one broken thoracic tergite, four thoracic pleurae, one hypostome, one partial librigena with the eye, and two detached visual surfaces.

Remarks.—None of these fragments can be referred with certainty to any genus. The occipital rings (Fig. 3K–M), of width 0.6, 0.9, and 1.0 mm respectively, all of which have an occipital spine, appear to belong to three different species. They differ in their surface sculpture. The occipital ring shown in Fig. 3L has broadly spaced nodules along the posterior margin, the one shown in Fig. 3M is granulose, whereas the occipital ring shown in Fig. 3K has dense, closely packed and prominent granules.

The axial rings (Fig. 3N, O) again appear to belong to two different species. The axial ring shown in Fig. 3O has a smooth, lensoidal articulating half-ring (0.7 mm wide), approximately the same length (sag.) as the main part of the axial ring, which has a straight posterior margin, a distinct medial node, and a granular sculpture. The axial ring in Fig. 3N is seen edge on and is strongly arched with a broad-based and stout axial spine.

The incomplete thoracic tergite (Fig. 3P; estimated width 1.3 mm) has a smooth external surface. The axial ring proper is slightly wider than the pleura and about the same length (sag.) as the articulating half-ring. It has a conspicuous medial node. The pleurae lack a distinct pleural furrow and the lateral margins are somewhat rounded anteriorly, posteriorly making an angle of about 80° with the posterior margin.

Three pleurae (1.2, 1.3, and 1.6 mm wide; Fig. 4A–C) are all broken off at the axial furrow, but can be referred to the same species. They are 0.4 times as long (exsag.) as they are wide with nearly straight and transversely parallel margins. The curving antero-lateral margin terminates in a broad-based spine, directed posteriorly and slightly laterally. Articulating facets are absent. An oblique pleural furrow traverses the pleura almost as far as the base of the spine. The external surface is granulose, except antero-laterally. Three to five larger nodes, irregularly spaced, are present along a transverse line in front of the posterior margin. A thin ridge, subparallel with the pleural furrow, extends from the anterior margin about a third of the way from the axial furrow to the middle part of the antero-lateral margin. Terrace lines run along the outer edge of the pleura, particularly on the spine.

The fourth pleura (Fig. 4D; 0.6 mm long exsag.) consists of the lateral part only and is seen in ventral view. It appears to have been very long (exsag.) and extends laterally into a sharp, postero-laterally directed spine. The doublure is clearly visible as a subtriangular area joining with the spine. It has an almost straight inner edge in the exsagittal plane, sharply curved posteriorly into a narrow shelf along the posterior margin of the pleura. Anteriorly the inner edge of the doublure curves slightly inwards to meet the anterior margin of the pleura. Seven terrace lines are arranged subparallel with the inner edge of the doublure. The inner surface of the

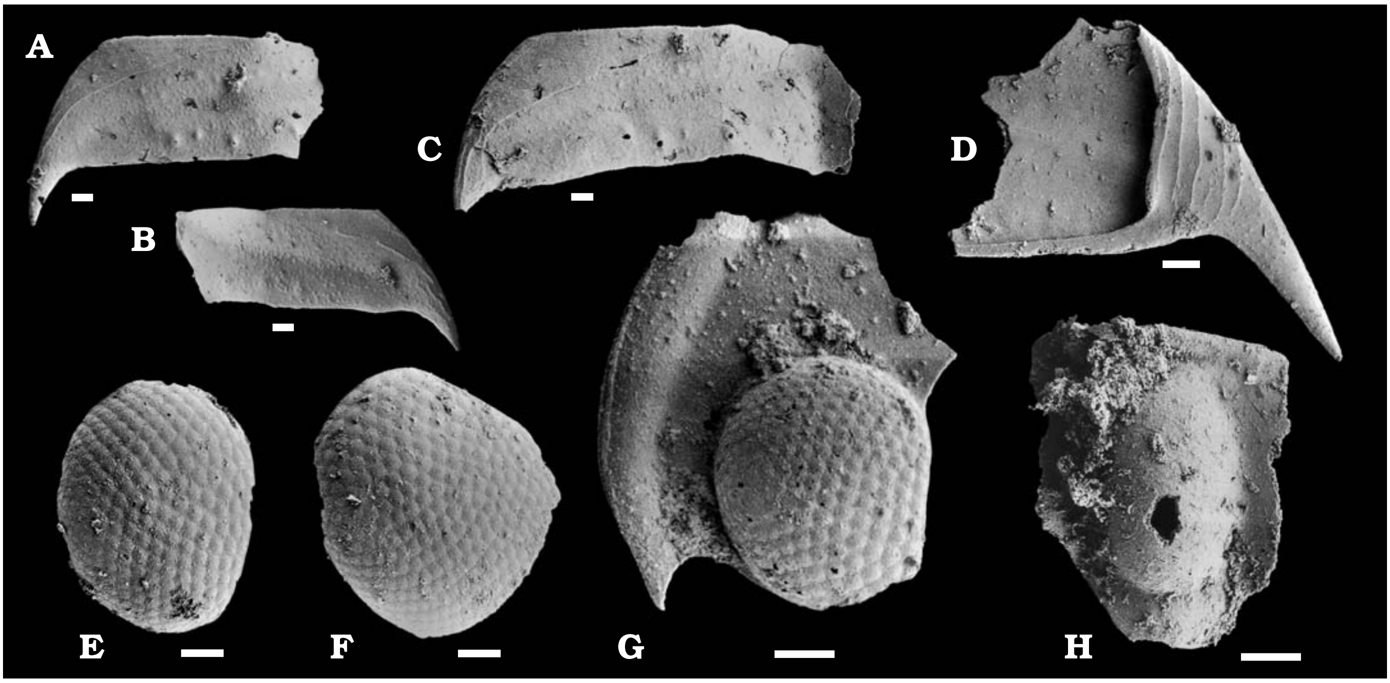

Fig. 4. Indeterminate olenid fragments. **A**. Left pleura, SMNH Ar59745 (2.13), sample 2. **B**. Right pleura, SMNH Ar59746 (1.17), sample 1. **C**. Left pleura, SMNH Ar59747 (1.16), sample 1. **D**. Pleura in ventral view, SMNH Ar59748 (2.16), sample 2. **E**. Detached eye, SMNH Ar59749 (2.17), sample 2. **F**. Detached eye, SMNH Ar59750 (2.18), sample 2. **G**. Librigena with intact eye, SMNH Ar597451 (2.15), sample 2. **H**. Poorly preserved hypostome, SMNH Ar59752 (1.22), sample 1. Scale bars 0.1 mm.

pleura is smooth. There seems to be a hollow space between the doublure and the dorsal exoskeleton.

The two detached visual surfaces (Fig. 4E, F) and the librigena with an intact eye (Fig. 4G) probably belong to the same species, maybe a species of *Ctenopyge*. These detached eyes (0.55 and 0.60 mm long) are nearly spherical with between a hundred and two hundred lenses. In one specimen there is clear lens packing discontinuity (running from northeast to southwest in Fig. 4E). The librigena has a regularly curved outer margin with a raised lateral border, about the same width as the narrowest distance from the border furrow to the base of the eye. The posterior branch of the facial suture is short, strongly convex forwards, and cuts the lateral border at a sharp angle. That part of the anterior branch of the facial suture still preserved curves slightly forwards from the top of the eye. The palpebral suture is straight adaxially. The external surface is smooth.

A poorly preserved hypostome (Fig. 4H), 0.5 mm long, is frayed laterally and its original external contour cannot be distinguished. The anterior margin is slightly convex forwards. Only part of the posterior border is preserved, but it is evidently longer (sag.) than the anterior border. The ovoid and convex middle body is distinct.

Remarks on the associated fauna

Numerous fragments of organisms other than chaetognaths and para- and euconodonts are present in the etched residues. Few of these, however, can be referred to any known genera or even to particular phyla. They are briefly described below, but require further study.

Two pelmatozoan echinoderm columnals are figured here. The larger one (Fig. 5A; 1.6 mm in diameter) is rounded pentagonal in axial view, and apparently with a pentagonal lumen occupying the central third of the diameter. Opposite the corners are broad, shallow, and nearly oval depressions convergent on the central lumen. These depressions are separated by a pair of narrow and straight ridges at right angles to the centre of each face. The smaller columnal (Fig. 5B) is an elongated, pentagonal cylinder (0.6 mm long and 0.4 mm in diameter). The facets are weakly crenulated. The stereom structure (Fig. $5B_2$) is well preserved in both specimens and shows them to be holomeric (consisting of a single skeletal piece). The two columnals may represent the proximal and distal portions, respectively, of the stem. Furongian echinoderm faunas are generally of low diversity (Guensburg and Sprinkle 2001); the present columnals may belong to an eocrinoid.

One fossil (Fig. 5C) from the *Peltura minor* Zone (sample 8 of Szaniawski and Bengtson 1998) has the outline of a parallelogram with the length of one face being 1.3 mm. The acute angle is about 50°. The specimen is built up of seven partially connected bars, parallel to the short side of the parallelogram. The external surface of these is sculptured with narrow, subparallel, oblique ridges; in one place these are intersected by another set of less prominent ridges (Fig. $5C_2$). The surface further carries a finely nodular pattern (Fig. $5C_3$, C_4). The frequent alignment of the nodules indicates that this is an original histological structure rather than diagenetic spherules. This specimen bears a certain resemblance to the five times larger scales of the Upper Devonian actinopterygian fish *Krasnoyarichthys* (see Prokofiev 2002: fig. 2d). Most likely, however, it is a fragment of a conulariid test. Conulariids were recently reported from the Furongian (Hughes et al. 2000), and their strongly ribbed phosphatic exoskeletons encompass both the parallelogram geometry and fine wrinkle-like structures oblique to the main ridges (e.g., Babcock and Feldman 1986).

The funnel-like specimen figured in Fig. 5D is shaped like a circular disc (0.5 mm in diameter) with a strongly depressed surface on one side and a cambered face on the other side. The cambered side bears a central, slightly oblique spine of nearly the same length as the diameter of the disc. The specimen bears some resemblance, both in size and shape, to certain cambroclaves, in particular *Cambroclavus absonus* Conway Morris, 1990 (Bengtson et al. 1990: fig. 69K), but the deeply concave side also suggests comparisons with *Archaeopetasus excavatus* Conway Morris and Bengtson, 1990 (Bengtson et al. 1990: figs. 196, 107). Its affinity is unknown.

Fig. 5E illustrates a fragment of a slightly convex sclerite, 1.7 mm long. On the surface there are numerous irregularly spaced subcircular to elongated rings with raised edges, each having a central depression with a small peg-like spine. Most of these spines are broken off to reveal a hollow interior, except for six intact spines along one margin. Most probably, the rings represent larger spines that have been broken off, leaving an internal pulp to form the peg-like spines (cf. Fig. $5E_2$). The surface of the sclerite is otherwise smooth. The surficial pattern resembles that of the vertebrate *Anatolepis*, known from the Furongian to Lower Ordovician. The tubercles of the latter have an internal pulp cavity and are surrounded by laminar material, creating concentric structures where the tubercles are broken; from the pulp cavity there are radiating, branching dentin-like tubules (Smith et al. 1996). We have not observed any tubule-like structures in the illustrated specimen, though this may be an effect of diagenetic infilling.

Fig. 5F illustrates a semicircular sclerite, 0.5 mm in diameter. It may be a fragment of an originally discoidal fossil with a somewhat polygonal margin. It has an incomplete raised margin that splits into two thinner ridges, the inner one more pronounced bearing faint subparallel lines and crossing the face of the sclerite. These ridges are broken on the left hand side. Inside the border are 13 ovoidal raised swellings, separated by furrows and arranged radially. A second and central ring composed of five ovoid swellings lies within this chain. Three of these swellings are of about the same size, the two others are smaller, at least as preserved.

The specimen shown in Fig. 5G is anvil-shaped, 0.4 mm long and 0.2 mm thick. It broadly resembles some fish scales. Both the upper and lower surfaces are nearly flat and wedge-shaped in outline. The upper surface is proportionately much

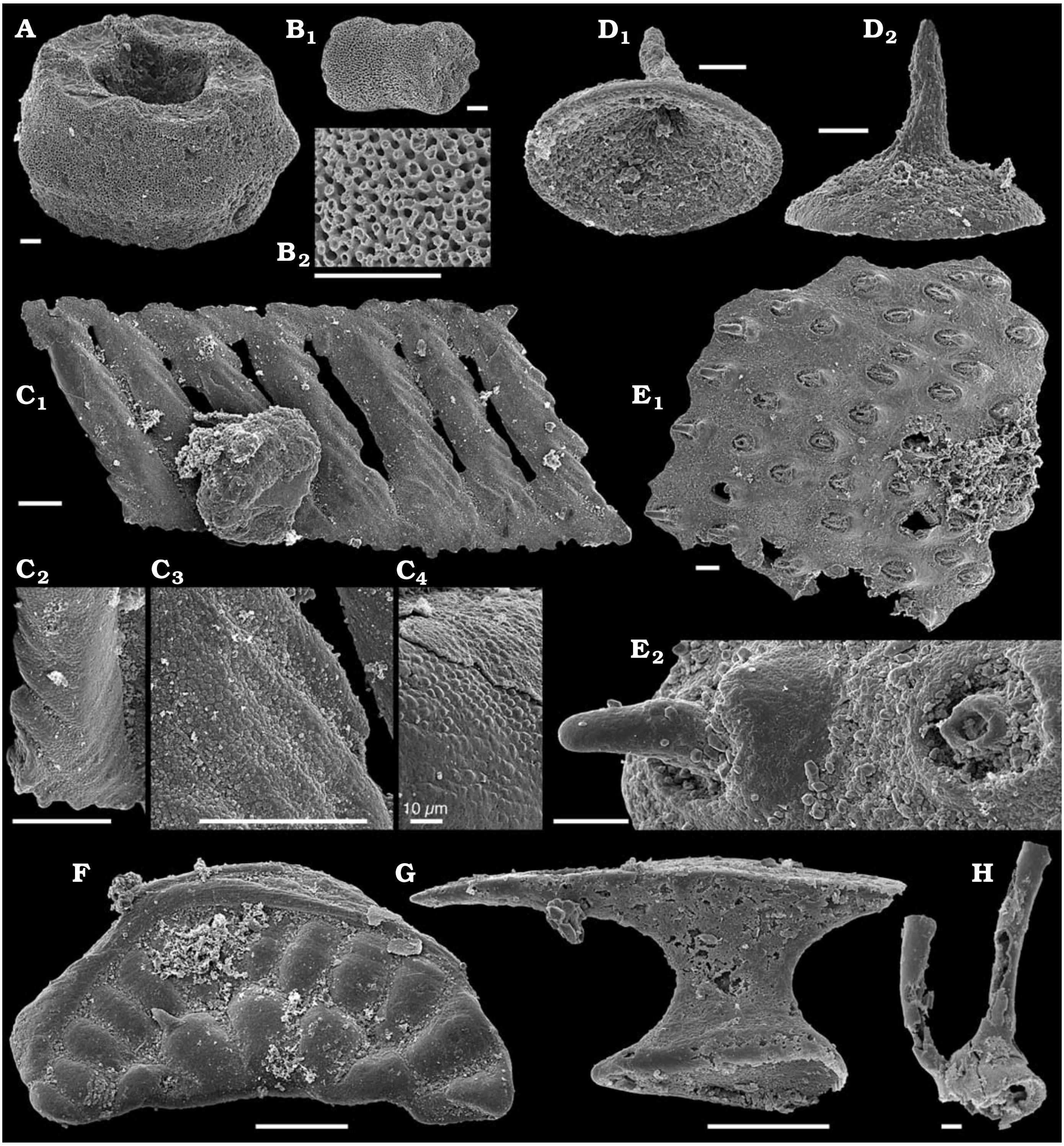

Fig. 5. Non-trilobite fossils from the *orsten* samples. **A**. Echinoderm columnal, SMNH X3566 (3.5), sample 2. **B**. Echinoderm columnal, SMNH X3567 (3.6), sample 2. Stereom structure shown in B_2. **C**. Conulariid(?) fragment, SMNH X3568 (3.16), sample 8 (*Peltura minor* Zone). **D**. Funnel-like fossil, SMNH X3569 (3.16), sample 2. **E**. *Anatolepis*-like fragment, SMNH X3570 (4.1), sample 2. Spines preserved in different degrees of abrasion (E_2). **F**. Semicircular fossil, SMNH X3571 (3.1), sample 2. **G**. Dermal scale(?), SMNH X3572, (3.15), sample 2. **H**. Camaroid graptolite(?), SMNH X3573 (3.9), sample 1. All scale bars, except C_4, are 0.1 mm.

narrower and nearly twice as long as the lower surface. In terms of functional morphology, this may well have been a dermal sclerite having the lower surface anchored in soft tissue and the upper forming part of cover of interlocking or imbricating scales. Without histological information it is not possible to determine its affinity.

The branched specimen in Fig. 5H is 1.6 mm long. It consists of a stout basal part, with two hollows, and two subparallel branches, tube-like, which curve slightly and expand a little distally. Similar fossils of organic composition were described by Kozłowski (1948) from the Tremadocian of Poland as graptolites of the Order Camaroidea; *Bithecocamara gladiator* Kozłowski, 1948 and "Échantillon" No 209 and 210. Later, the same author (Kozłowski 1967) assigned fossils similar to the "Échantillons" to the new genus *Ascosyrinx* Kozłowski, 1967 of unknown systematic position. Both species of *Ascosyrinx* known so far, however, have only one branch (tube), while our specimen (Fig. 5H) has two.

Concluding remarks

This work reports the occurrence of the only known phosphatised fauna from the Alum Shale Formation other than those described by Klaus Müller, Dieter Walossek, and others in numerous publications from 1979 and onwards. The bulk of the material reported on by these authors came from the *Agnostus pisiformis* and *Olenus/Agnostus* (*Homagnostus*) *obesus* zones, whereas the specimens herein described are from the upper part of the *Peltura* zones (the *Peltura scarabaeoides* Zone). The conulariid? fragment (Fig. 5C) is from the *Peltura minor* Zone. Most of our material consists of fragmentary olenid trilobites, which have never been found phosphatised before. Only the dorsal exoskeletons have become secondarily phosphatised, and the ventral appendages are not preserved. Even so, the material is superbly preserved and reveals the morphology and the cuticular sculpture of the olenid trilobites in greater detail than hitherto known. In particular, details of the terrace lines and granulation of the pygidium of *Sphaerophthalmus* and *Peltura* can be distinguished, and new information is presented on their development during successive ontogenetic stages. Indeterminate fragments have also yielded new information on the microstructure of the occipital ring and the thoracic tergites, including the doublure, in olenid trilobites. The presence of other faunal elements, in addition to chaetognaths and para- and euconodonts, but hitherto unrecorded in the Alum Shales, testifies to an originally rather diverse accompanying biota.

The Alum Shales of Scandinavia are known to have been deposited in anoxic to dysoxic environments (e.g., Buchardt et al. 1997; Schovsbo 2001), at least during most of the Furongian (Late Cambrian). The presence of a benthic fauna of pelmatozoans, and possible conulariids and camaroids, indicates that at least parts of the *Peltura* zones were deposited during dysoxic rather than anoxic periods. Moreover, the sea floor must have been firm enough to allow colonisation by sessile organisms. It is possible that this fauna represents a taphonomic window, which gives a more complete picture of the total original fauna.

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