

Early ontogeny of the Furongian (Cambrian) olenid trilobites *Sphaerophthalmus alatus* (Boeck, 1838) and *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922 from Bornholm, Denmark

Kristina Månsson¹ and Euan N. K. Clarkson²

¹ Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden
Email: kristina@forlagshuset.hagern.se

² School of Geosciences, University of Edinburgh, Kings Buildings, West Mains Road, Edinburgh EH9 3JW, Scotland UK
Email: euan.clarkson@ed.ac.uk

ABSTRACT: The early stages in ontogenetic development are described in the co-occurring *Sphaerophthalmus alatus* (Boeck, 1838) and *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922, using fragmentary but otherwise well-preserved material from Bornholm, Denmark. The former species is a senior synonym of *Ctenopyge* (*Eoctenopyge*) *angusta* Westergård, 1922, as has been recently proposed, but the early stages of *S. alatus* from Bornholm are appreciably more spiny than those found of the same species in other places in Scandinavia, and spinosity is retained until later in development. Increasing convexity with development and other morphological changes are noted. Pygidia were previously unknown in *C. (M.) tumida*. Here, they are represented by early pygidia. These are shield-shaped, with a very spiny margin and a strong axial spine. The distinction between *Sphaerophthalmus* and *Ctenopyge* is discussed.



KEY WORDS: Alum Shale, olenids, Leptoplastinae, Scandinavia, Trilobita

Trilobites of the Family Olenidae occur in immense numbers in the Furongian Alum Shales of Scandinavia, and are by far the most dominant fossils. The middle Cambrian through Tremadocian Alum Shales are some 100 metres thick at their maximum, in Skåne, Sweden, the traditional middle Cambrian portion being c.30 m, and the upper Cambrian (Furongian) c.50 m at most. Though the middle Cambrian bears a highly diverse trilobite fauna, that of the upper Cambrian is much more restricted, and most of these are olenids. The environment the olenid inhabited here has been interpreted as being relatively deficient in oxygen (e.g., Anderson *et al.* 1985; Dworatzek 1987; Schovsbo 2000, 2001). However, even though olenids seem to have adapted to a low-oxygen environment, Balseiro *et al.* (2011) showed that some olenids, especially those which lived later in time, are not restricted to dysoxic facies. In the Lower Ordovician of the Argentine Cordillera Oriental, olenids dominated both oxygenated and dysoxic environments. The olenids are usually very well preserved in the Alum Shale; both in three dimensions in carbonate concretions, and flattened in shales. Moreover, juvenile forms commonly occur along with the adults. Many genera and species have been described, and their order of succession is well established; as, in general terms, are their evolutionary relationships. In Norway (Henningsmoen 1957), Sweden (Westergård 1922), and Denmark (Bornholm) (Poulsen 1923), the Cambrian successions in the Alum Shales permit research in many interlinked fields of palaeobiology, sedimentology, evolution and environment; and, arguably, this region of Scandinavia is one of the few places anywhere in the world where such research can be effected. The ultimate objective of this work would be a synthesis of current knowledge of an extinct environment

and the evolution and adaptations of the extinct marine invertebrates that lived within it.

Many studies of the sedimentology, geochemistry and stratigraphical ordering of the Scandinavian Furongian have been undertaken (e.g., Schovsbo 2000, 2001; Terfelt *et al.* 2008, 2010), and tie-points using agnostoids have been established for various levels in the sequence (e.g., Ahlberg & Terfelt 2012). The most recent stratigraphical paper resurrects the concept of superzones for the Scandinavian Furongian (Nielsen *et al.* 2014). In addition, since well-preserved juveniles are often found with the adults, several studies of the ontogeny of Scandinavian olenids have been undertaken in recent years (Clarkson & Taylor, 1995a, b; Clarkson *et al.* 1997, 2003; 2004; Månsson 1998; Clarkson & Ahlberg 2002; Bird & Clarkson 2003; Månsson & Clarkson 2012). Ontogenies of other Cambrian olenids outside Scandinavia have been described from, for example, Argentina (Tortello & Clarkson 2003, 2008), Canada (Lee & Chatterton 2007) and Korea (Lee & Choi 1999). The present paper is a contribution to this databank. Its main purpose is palaeobiological; the study of comparative ontogeny within a close-knit group has a bearing not only on taxonomy but also upon questions of heterochrony and adaptation, as part of the overall interlinked synthesis.

1. Material and stratigraphy

The material upon which this study is based was collected from Bornholm by Dr Arne Torshøj Nielsen some thirty years ago, and was stored in the collections of the Geological Museum, Copenhagen, Denmark. The material was collected at the site

that Poulsen (1923) named Locality 6, located along the Læsaa Rivulet on southern Bornholm. For a detailed map, see Poulsen (1923, fig. 1). Poulsen 1923 (pp 14, 74) described the section as the most accessible one at Læsaa. The section was about 60 metres long (the northern end of the profile is now almost inaccessible) and about 10 m high. The inclination of the section is such that the older zones are found at the northern end of the section. A number of anthraconite concretions of different sizes may be observed. The section contains six zones. These zones are here reinterpreted according to the most recent zonal schemes (Terfelt *et al.* 2008, Nielsen *et al.* 2014). Zone 8 (*Parabolina spinulosa* Zone) is followed by Zone 12 (layers with *Eurycare latum* and *Leptoplastus ovatus*), then Zone 13 (*L. angustatus* and *L. stenotus*), Zone 16 (*Ctenopyge flagellifera*) and Zone 19 (shale with great numbers of *Ctenopyge* (*M.*) *tumida* and *Sphaerophthalmus alatus*). The thickness of Zone 19 is about 2.50 metres. These layers contain four big concretions of aragonite, the greatest of which has axes of about 2.50 m and 0.50 m. The highest zone exposed is that containing *Peltura scarabaeoides* (Zone 22 of *Ctenopyge linnarssoni*). There are undoubtedly hiatuses within the sequence, which require to be investigated further.

The material described here belongs to *Sphaerophthalmus alatus* and *Ctenopyge* (*Mesoctenopyge*) *tumida*, the former being the more abundant. There are rare sclerites, belonging to other species but, despite an extensive search, we found no agnostoids. All the specimens of *S. alatus* and *C. (M.) tumida* are disarticulated, with uncountable numbers of isolated and usually broken sclerites lying on the bedding planes. This is the usual way in which *Sphaerophthalmus* is found, with great numbers of disarticulated exuviae, and complete or nearly complete specimens have been found only rarely. Since there are no complete individuals in the Bornholm material, and most of the larger sclerites are broken so as to be too fragmentary to use for studies of ontogeny, it is usually only the smaller sclerites that are well preserved. Accordingly, we have limited our studies to the early ontogenetic stages. Even here, specimens that can be used for this purpose are not common, and the fragmentary nature of the material necessitated an extended search for intact sclerites. This has imposed two particular limitations on what could be established. The first is that it was not possible to produce any kind of morphometric analysis, such as bivariate plots of length and width; there was simply not enough appropriate material. Secondly, many of the reconstructions are inevitably composite, based upon several specimens; though we trust that this has not diminished their accuracy. The quality of preservation is quite variable, being excellent at some levels, where, for example, long thin spines may be preserved, but less so at others. Eyes are found to be well preserved at some horizons, and lacking in others. It has recently been shown (Schoenemann & Clarkson 2015), on the basis of their optical systems, that although *S. alatus* and *C. (M.) tumida* are found together, the two trilobite species lived at different depths, and it seems appropriate to describe their ontogenies comparatively in the same paper. *S. alatus* is believed to have occupied a vagrant benthic habitat, whereas *C. (M.) tumida* was probably a pelagic swimmer (Schoenemann & Clarkson 2015).

1.2. Is *Sphaerophthalmus* distinct from *Ctenopyge*?

One major problem that has affected the taxonomic ordering of olenid trilobites is that at least some genera were highly labile; subject to morphological and developmental change through even short time periods (Kaufmann 1933, Clarkson *et al.* 1997, Lauridsen & Nielsen 2005, Ahlberg *et al.* 2006). Although some olenids seem to follow a constrained ontogenetic pathway, others do not (Månsson & Clarkson 2012)

and, because of the limitations of the available material, it is not yet known to which category those of the *Sphaerophthalmus*/*Ctenopyge* complex pertain. It is also quite likely that there was a fair degree of regional variation in some geographically widespread olenids. Such issues as these have clouded the production of a sound taxonomy and this has particularly been the case with the leptoplastines of the *Sphaerophthalmus*/*Ctenopyge* complex. Where to draw the boundary between these two genera has taxed generations of olenid specialists, as commented upon by Henningsmoen (1957) and Clarkson *et al.* (2003).

A recent important study by Høyberget & Bruton (2012) addressed the issue of the confused taxonomy of the *Sphaerophthalmus*/*Ctenopyge* complex, based on material from a classic section at Slemmestad, near Oslo, Norway. This work presented a revision of both *Sphaerophthalmus* and *Ctenopyge*, and a new genus *Triangulopyge* was proposed. A detailed stratigraphical log was also given, recording the vertical ranges of all the olenids from the *S. postcurrens* to the *C. linnarssoni* Zones. This new work has gone a long way towards resolving a difficult and complex question. One major issue affecting our present work is the proposal, based on fresh and critical material, that what Clarkson *et al.* (2003) described as *Ctenopyge* (*Eoctenopyge*) *angusta* Westergård 1922 was considered by Høyberget & Bruton (2012) to be *Sphaerophthalmus alatus*. If this is indeed the case, then at first sight this might seem to make our present work redundant, since the ontogeny of *S. alatus* has already been described in full. We agree with Høyberget & Bruton (2012) that *C. (Eoctenopyge)* is a junior synonym of the genus *Sphaerophthalmus*, and that *C. (Eoctenopyge) angusta* described by Clarkson *et al.* (2003) should be regarded as properly belonging to *S. alatus*. However, we recognise *S. alatus* as a highly variable species, and most likely geographically clinal; the Bornholm morphs are not identical to those from Västergötland, south-central Sweden, upon which the study of Clarkson *et al.* (2003) were based. Intermediate morphs of *S. alatus* and *S. angustatus* have been reported from the Oslo area in Norway by Høyberget & Bruton (2012). The Bornholm material described herein differs in several respects from that from Norway and Sweden, and in this paper we present some further observations on various aspects of the early ontogeny of *S. alatus*, based upon specimens from Bornholm.

The remarkable variability found amongst the olenids of the *Sphaerophthalmus*/*Ctenopyge* complex, and the problem of intergrading character states and geographical variation, does not make it easy to determine what is rightly a *Sphaerophthalmus* and what is a *Ctenopyge*. The study of comparative ontogenies so far has not really contributed to the resolution of this question. It may well be that any future distinction would be best based on relative spinosity of the thorax, rather than on the more traditional characters.

We also describe the early stages of the ontogeny of *C. (M.) tumida*, including the pygidia, which have not been recorded before. In Clarkson *et al.* (2004), the earlier stages were not described; thus, the present work augments the description of this species.

2. Systematic palaeontology

Illustrated, described and cited specimens are deposited at the Department of Geology, Lund University, Sweden (LO), and at the Geological Museum, University of Oslo, Norway (PMO). Due to the fragmentary nature of the material, the ontogenetic development of the cranidium, librigena, hypostome and pygidium is described separately.

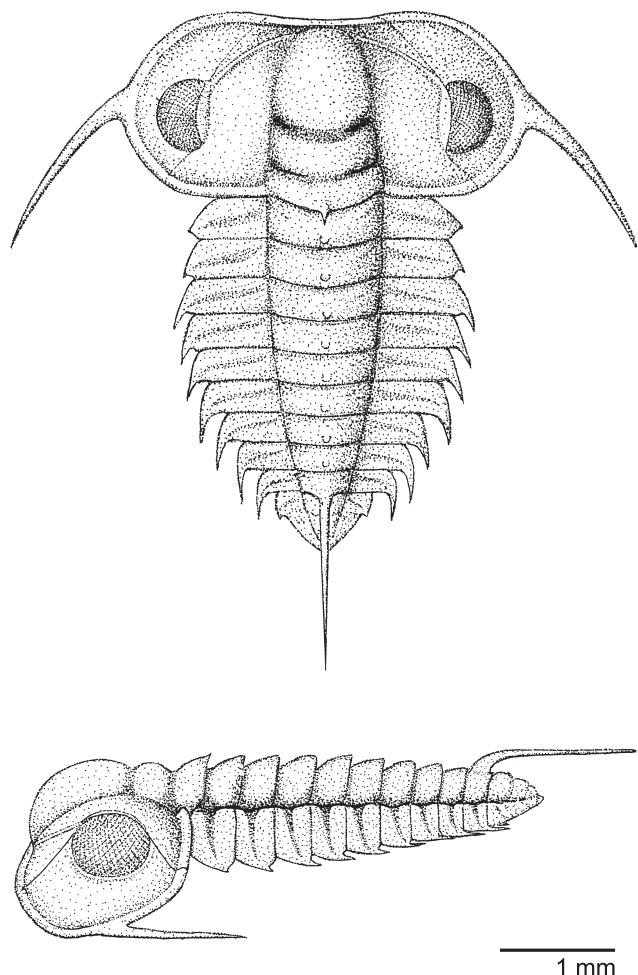


Figure 1 *Sphaerophthalmus alatus* (Boeck, 1838), reconstruction of a late meraspis with nine segments, equivalent to Group 4, in dorsal and lateral views. Based on material from Bornholm.

Subclass Libristomata Fortey, 1990
 Order Olenida Adrain, 2011
 Family Olenidae Burmeister, 1843
 Subfamily Leptoplastinae Angelin, 1854
 Genus *Sphaerophthalmus* Angelin, 1854

Type species. Subsequently designated by Linnarsson (1880) *Trilobites alatus*, Boeck, 1838.

Sphaerophthalmus alatus (Boeck, 1838)
 Figs 1–6

For complete synonymy lists see Henningsmoen (1957), Żylińska (2001) and Høyberget & Bruton (2012).

Type data. Størmer (1940, p. 145) selected a lectotype (PMO 56371) from Gamleby, Oslo, Norway, from Boeck's material. The lectotype has been figured by Henningsmoen (1957, pl. 22, figs 23–24) and by Høyberget & Bruton (2012, fig. 5A, D).

Protaspis stage. (Figs 2a, 3a). The smallest specimens represented in our material are two protaspides, representing an earlier ontogenetic stage than that, for example, figured by Clarkson *et al.* (2003). Each of these is almost circular, being 280 µm long and 280 µm wide, with a well-marked central axis having four axial rings, and a distinct furrow separating the cranidium from the protopygidium. There is a pair of short, sharp intergenal spines. The palpebral lobes are faintly developed.

Development of the meraspis cranidium. (Figs 2b–j, 3b–i). Because the material is fragmentary, we have allocated it into

Groups 1, 2, etc., following Whitworth (1970), Clarkson & Taylor (1995b) and Månsson (1998), rather than attempting to assign detached sclerites to any particular meraspis degree. These groups are mainly based on size and morphological features. These groups do not correspond to moults or instars.

Group 1. (Figs 2b–c, 3b). The two smallest meraspides are 320 µm long (exclusive of spines) and 320 µm wide. The external contour is trapezoidal, with an almost straight anterior border, and the cranidium is widest posteriorly. The axis remains fairly narrow, extending as far as the very narrow anterior border; there are four lobes and the palpebral lobes lie opposite L3. A prominent posterior border has developed, and the occipital ring bears an anterior node with a short, though stout occipital spine. The two intergenal spines are still present. These specimens are likely to represent a degree 1 meraspis.

Group 2. (Figs 2d–e, 3c). The next developmental stage is 350 µm long (excluding spines), and 415 µm wide. It retains the morphology of the preceding stage, though is somewhat narrower posteriorly, so that the paired intergenal spines appear to be a little closer together. This cranidium is slightly more inflated than that of the previous stage.

Group 3. (Figs 2f–i, 3d–g). The smallest cranidium within this group is represented by a single imperfectly preserved specimen 370 µm long and 500 µm wide (excluding the spines), and of similar shape to that of the previous degree. There are only three distinct axial lobes; L4 is now effaced. The occipital and intergenal spines are still very distinct, as is the occipital node. The occipital spine is inclined upwards at about 30 degrees. In profile, the cranidium appears moderately convex. A larger specimen still belonging to Group 3 is 400 µm long (excluding spines) and 610 µm wide. Whereas it is generally similar in form to the preceding stage, the S2 furrow is much fainter, and the intergenal spines have become much shorter, though the occipital spine and node remain prominent. There is a distinct increase in convexity and the anterior slope of the glabella is greater, the highest point being at L2. Figure 2i illustrates an oblique anterior view of the largest cranidium in Group 3, which shows an increasing convexity and an upwards inclined short broken off occipital spine.

Group 4. (Figs 2j, 3h–i). In the latest stage represented in our material, the cranidium is virtually of adult proportions and convexity. The example illustrated is approximately 1.3 mm long and 2.0 mm wide. It probably represents a late meraspis, or an early holaspis. The glabella has broadened so that, as in the adult, it now occupies a third of the total width. There is no trace of the occipital node, and the occipital spine has shrunk to form a small, posteriorly-directed projection. There are no traces of intergenal spines, and the posterior branch of the facial suture now swings slightly outwards as it cuts the posterior border. The palpebral lobes are somewhat longer, lying in front of S1. Of the glabellar furrows, only S0 and S1 remain, and these have become deep and broad, as in the adult. Narrow, curving ocular ridges are now well developed. The convexity of the cranidium is very strong, the anterior part of the glabella sloping almost vertically, and there is hardly any indication of a preglabellar field.

Librigena and eye. (Figs 2k, 4a–i). A small detached librigena, belonging to *S. alatus*, is illustrated in Figure 2k. It is 0.8 mm long, from the anterior point to the base of the genal spine, and 1.5 mm long to the tip of the spine, as preserved. Exclusive of the eye, the maximum width is about 0.3 mm. The spine is narrow and juts out slightly from the margin of the librigena. The eye, set slightly more than half way along the length of the librigena (excluding the spines), is approximately 250 µm long and is nearly circular; it is crushed down, though still in place. Some traces of the lenses can be discerned. The size would fit a relatively late meraspis. Some eyes of this species

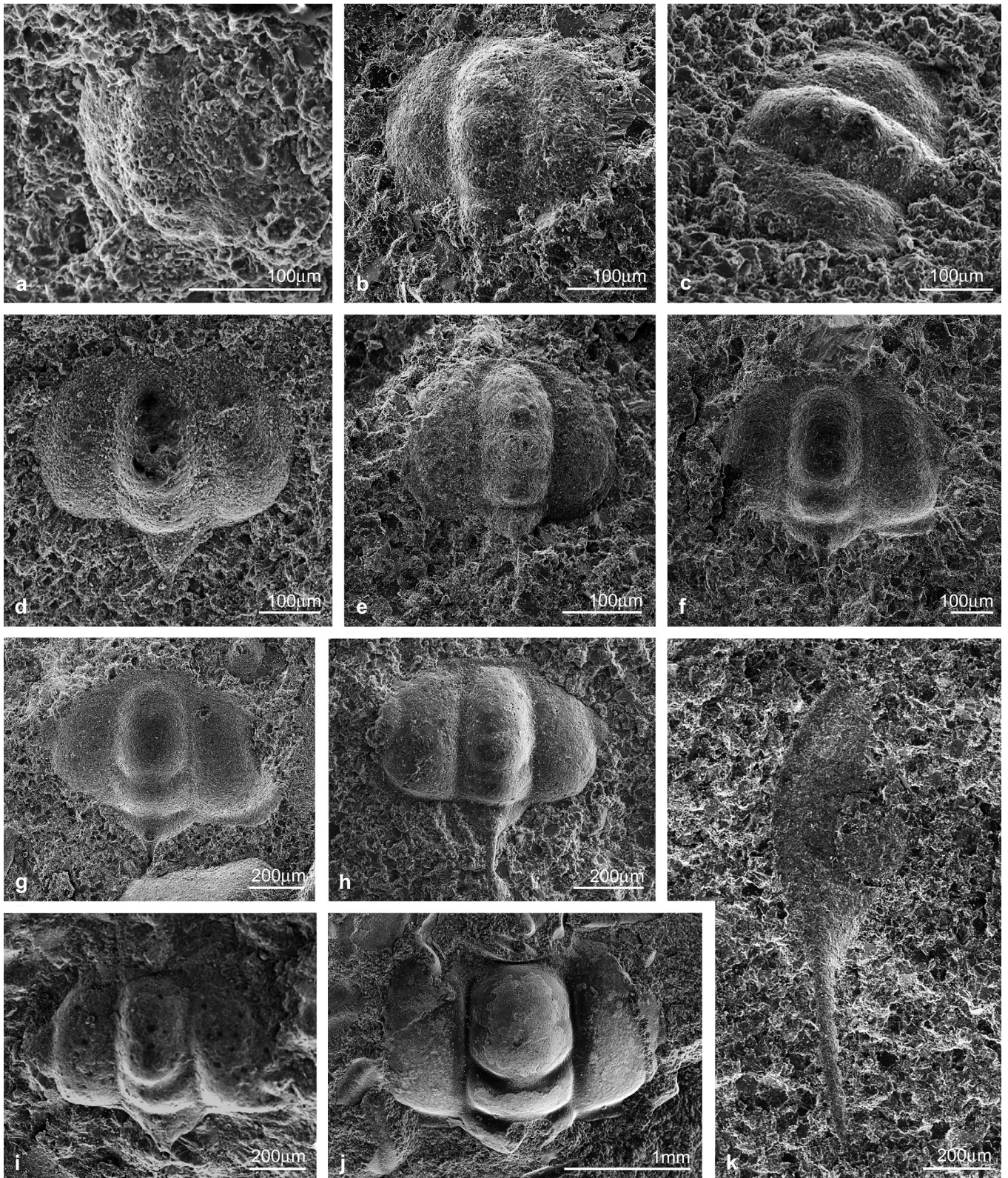


Figure 2 *Sphaerophthalmus alatus* (Boeck, 1838). (a) Protaspis, LO 12297t. (b–c) Group 1 meraspid cranidia: (b) LO 12298t; (c) LO 12299t. (d–e) Group 2 meraspid cranidia: (d) LO 12300t; (e) LO 12301t. (f–i) Group 3 meraspid cranidia: (f) LO 12302t; (g) LO 12303t; (h) LO 12304t; (i) LO 12305t. (j) Group 4 cranidium of adult proportions, LO 12306t. (k) Librigena, likely belonging to a relatively late meraspid, LO 12307t.

were described and figured by Clarkson (1973, p. 754, pl. 95, figs 1–2, text-fig. 7a–d). His description was based on material from Andrarum, Skåne and Gamlebyen, Oslo. At some horizons, very well preserved compound eyes of *S. alatus* are to be found in some abundance. Whereas in some cases the external surfaces are preserved (Fig. 4i), it is more commonly the inter-

nal moulds that are seen (Fig. 4a–e, g–h), the lenses having been retained by the external matrix and, thus, wholly or partially stripped off during preparation (Fig. 4f). These illustrations show clearly (Fig. 4a–e, g–i) the original curvature of the visual surfaces, the shapes of the lenses and variation of lens size across the eye. Figure 4b–d shows the same eye in

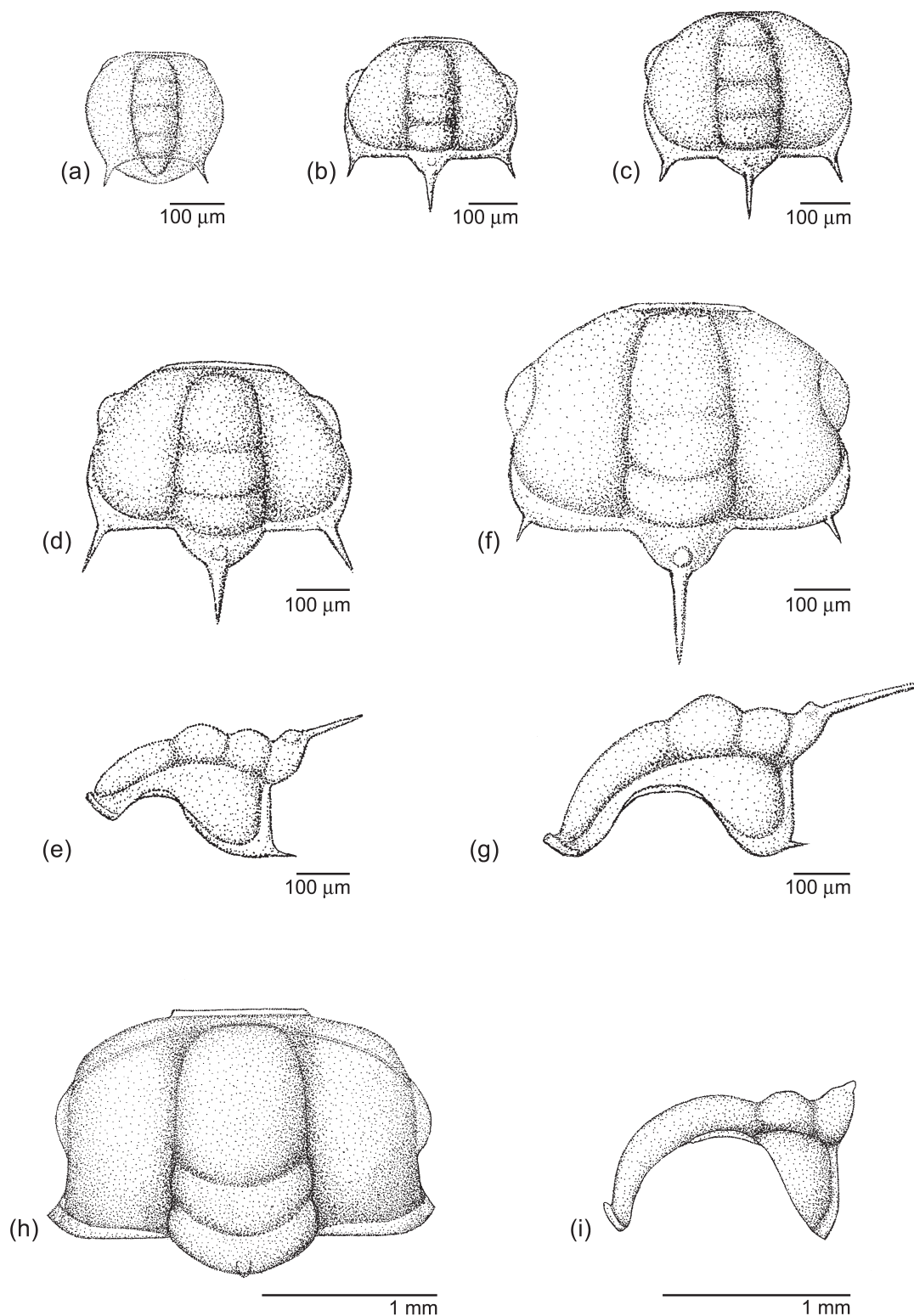


Figure 3 Reconstructions of protaspis and cranidia of *Sphaerophthalmus alatus* (Boeck, 1838): (a) protaspis, dorsal view; (b) Group 1 meraspis cranium; (c) Group 2 meraspis cranium; (d–e) Group 3 meraspis, in dorsal and lateral views; (f–g) Group 3 meraspis, in dorsal and lateral views; (h–i) Group 4 cranium, late meraspis/early holaspis in dorsal and lateral views.

lateral, dorsal and posterior views; this eye is c 400 µm long and 300 µm in height. The lenses average 20 µm in diameter, though there is some variation in lens size; the somewhat larger lenses being in the upper part of the eye in the specimen illustrated in Figure 4e, though this is by no means a constant feature. The contours of the upper and lower surfaces of the thin lenses are visible in the broken surfaces in Figure 4g–i. They are very similar to those illustrated by Lindström (1901) and

Clarkson (1979). A discussion of the optics and the eyes of *S. alatus* is given by Schoenemann & Clarkson (2015).

Development of the hypostome. (Figs 5h–i, 6e–f). A juvenile hypostome (Figs 5h, 6e) is 400 µm long and 300 µm wide. It has a relatively broad brim, lacking the U-shaped platform of the adult, and is widest at about three-quarters of the total length from front to rear. The adult hypostome greatly resembles the material found in Västergötland, figured by Clarkson *et al.*

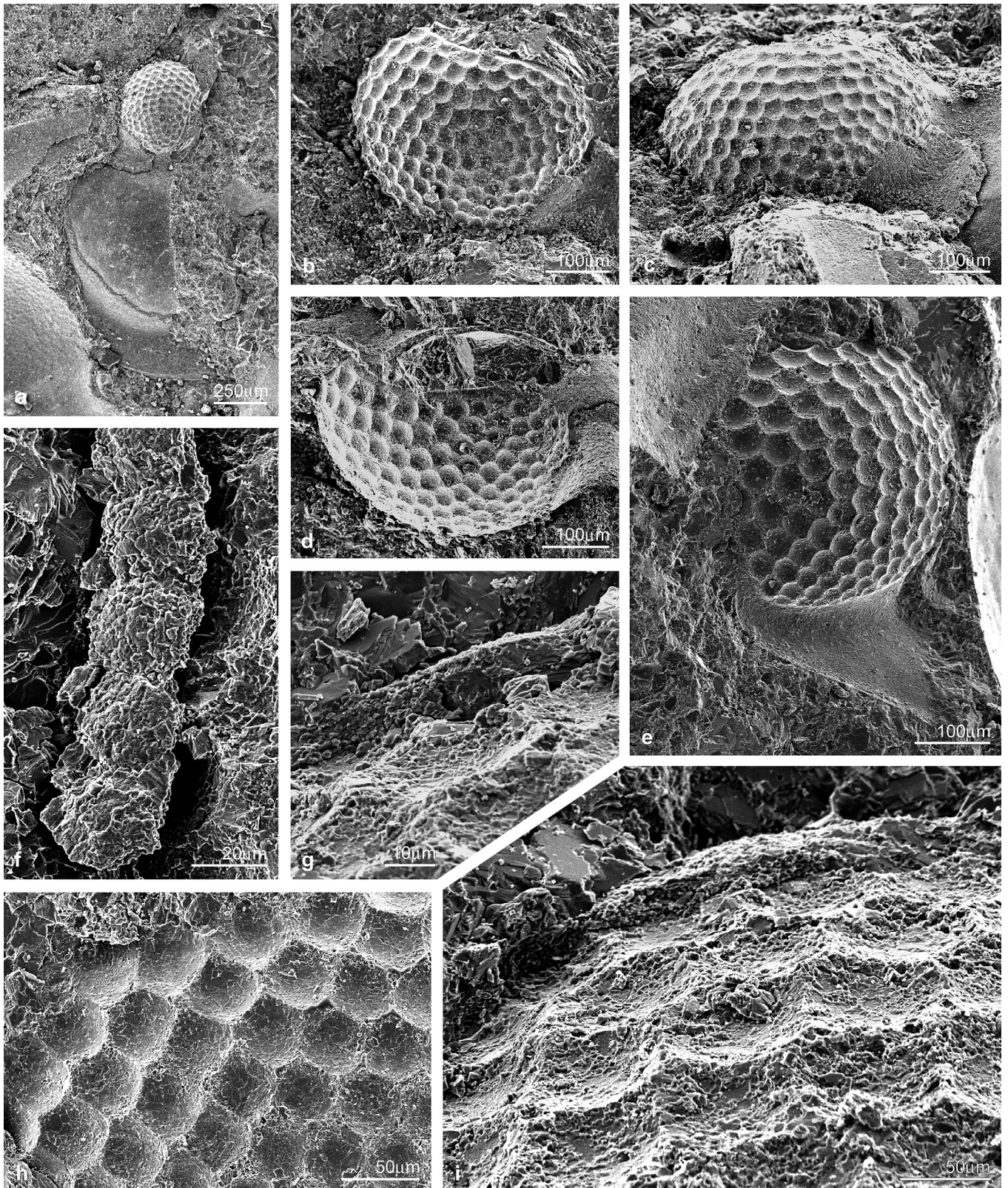


Figure 4 *Sphaerophthalmus alatus* (Boeck, 1838): (a) internal mould of eye attached to librigena, anterior view, LO 12308t; (b–d) internal mould of eye in lateral, posterior and dorsal views, LO 12309t; (e) well-preserved eye attached to librigena, LO 12310t; (f) string of lenses, partially detached, LO 12311t; (g) vertical broken section through lenses, showing bioconvex form, LO 12312t; (h) internal mould, showing proximal surface of lenses, LO 12313t; (i) internal mould, oblique view showing vertical section of lenses (top) and proximal surfaces of lenses, LO 12314t.

(2003, pl. 6, figs 1–5, 8) in having a very similar external contour, pointed anterior wings and a raised middle body tapering posteriorly. The middle body is situated on a U-shaped raised platform, more distinct than that found in the material from Västergötland, outside which lies the brim proper, curled pos-

teriorly, and with a few subdued terrace lines concentric with the margin. The brim is widest at about two-thirds of the distance from front to rear of the hypostome. That figured here (Figs 5i, 6f) belongs to a small holaspis; it is 750 µm long, with a maximum width of 530 µm.

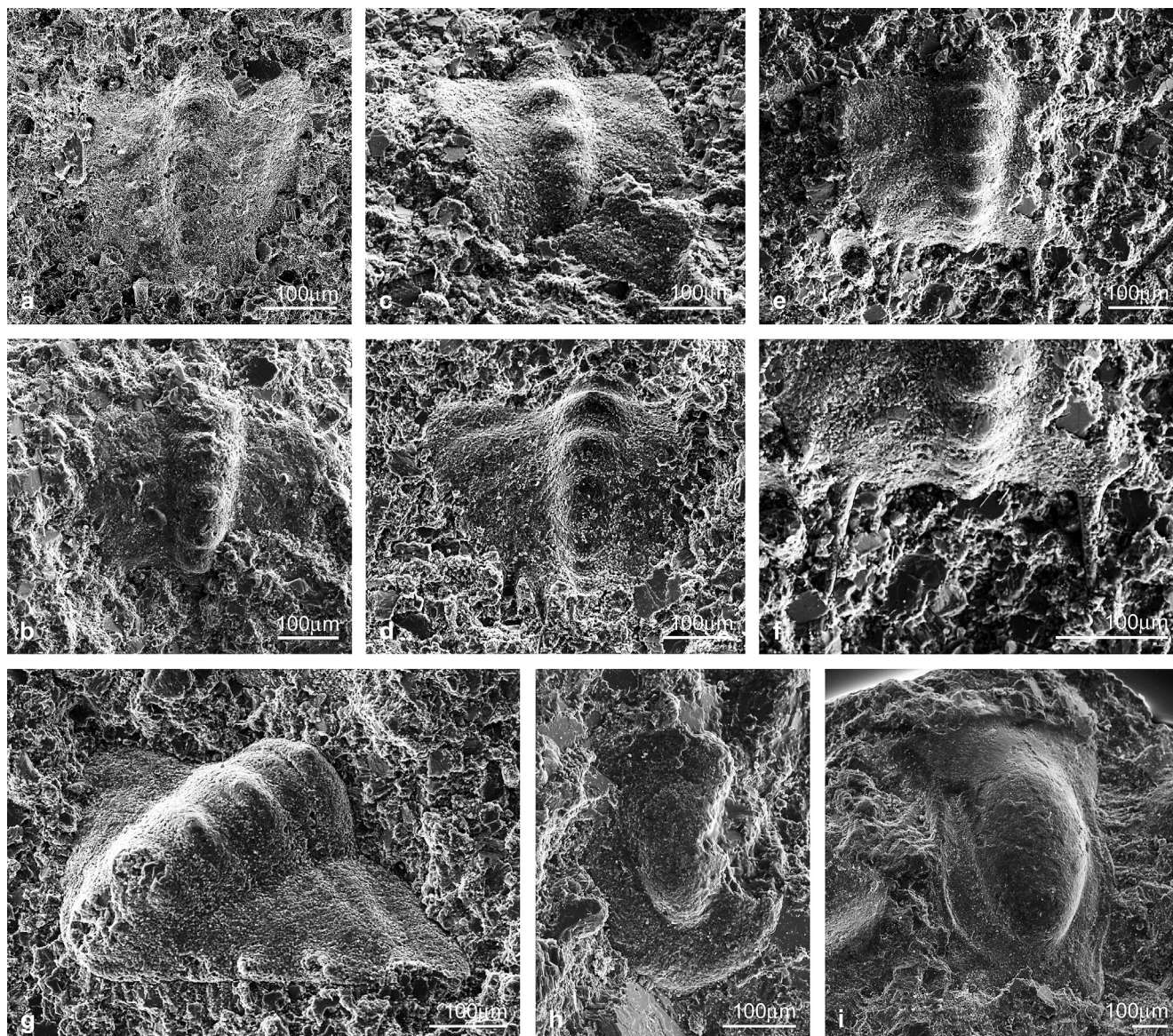


Figure 5 *Sphaerophthalmus alatus* (Boeck, 1838). (a) Group 1 meraspid pygidium, LO 12315t. (b–d) Group 2 meraspid pygidia: (b) LO 12316t; (c) slightly broken and obscured posteriorly, though the posterior downward curling is clear, LO 12317t; (d) LO 12318t. (e–f) pygidium, Group 3: (e) LO 12319t; (f) enlargement of posterior spines of (e). (g) Group 4 meraspid pygidium, showing triangular form, short, upturned marginal spines, and broken spine bases on axial rings, LO 12320t. (h) Meraspid hypostome, LO 12321t. (i) Young holaspid hypostome, LO 12322t.

Development of the meraspid pygidium. (Figs 5a–g, 6a–d). We have assigned the pygidia to four groups, as used above in the development of the cranidium, and though some assumptions have been made, we believe that the numbered groups of cranidia and pygidia correspond.

Group 1. (Fig. 5a). Pygidia, being very delicate, are rare in the Bornholm material, and there are no perfect specimens representing the early developmental stages. The smallest, slightly distorted pygidium is 300 μm wide, which would put it in the range of meraspid degree 0–1, by comparison with the specimens figured by Clarkson *et al.* (2003). It is similar in form and dimensions to these, being slightly longer than wide, and apparently flattened by compaction.

Group 2. (Figs 5b–d, 6a). Pygidia in this size range are 320 μm long and 350 μm wide; they are shield-shaped, with a narrow tapering axis, having 5–6 axial rings and faint impressions of the pleural furrows anteriorly. The posterior part remains somewhat downwardly coiled. There are five pairs of short marginal spines.

Group 3. (Figs 5e–f, 6b–c). The pygidium remains shield-shaped; it is 425 μm long and 400 μm wide (excluding spines). There are six axial rings and six pairs of marginal spines. The anterior axial rings are more differentiated and strap-shaped, with a small axial node, and the marginal spines are appreciably longer. Whether or not there is a posterior spine at this stage remains unknown; the reconstruction is made without one.

Group 4. (Figs 5g, 6d). The largest of the pygidia is small and triangular, being 450 μm long and 600 μm in width, and with a faint posterior downward coiling. Although the external contour is like that of the adult, the axis conserves the juvenile state, with six rings, the first being raised and strap-like, the rest decreasing in elevation posteriorly. A pronounced cicatrice on the terminal piece may well indicate the base of a broken pygidial spine (cf. Clarkson *et al.* 2004, pl. 8, fig. 5, text-fig. 2). Four pairs of short, stubby marginal spines are present, lining the pleural fields and inclined slightly upwards, and the lateral furrows are faintly impressed.

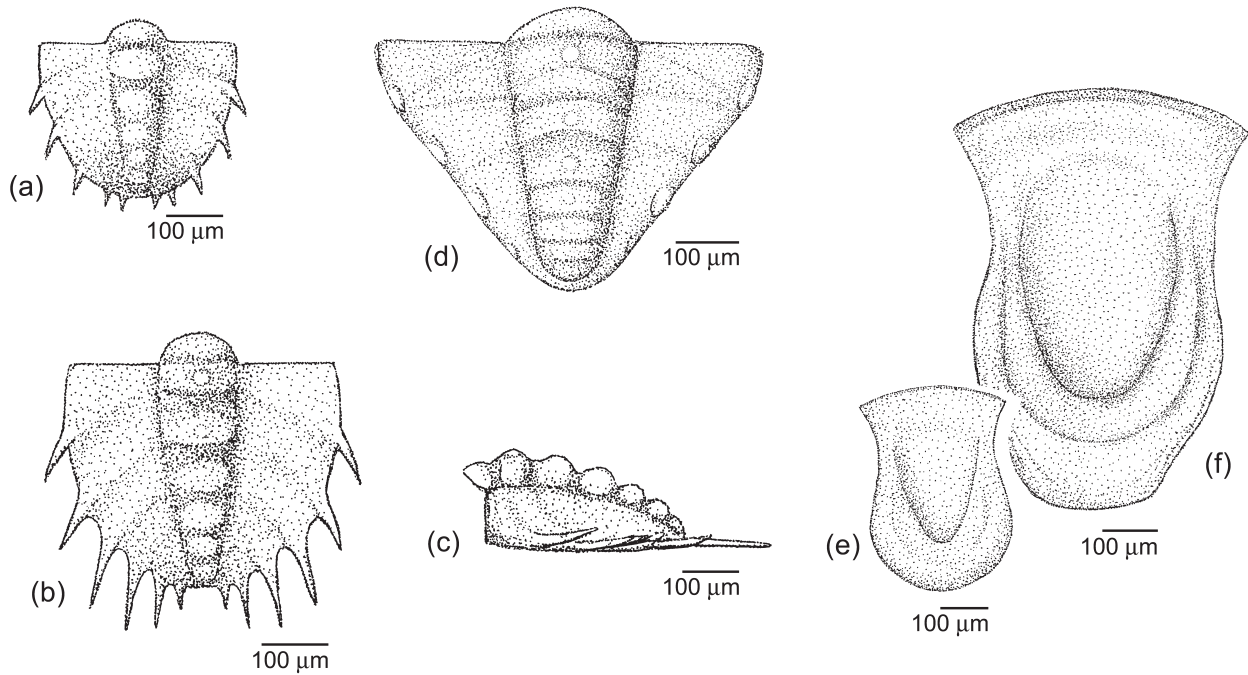


Figure 6 Reconstructions of pygidia and hypostomes of *Sphaerophthalmus alatus* (Boeck, 1838): (a) Group 2 meraspid pygidium; (b–c) Group 3 meraspid pygidium, dorsal and lateral views; (d) Group 4 meraspid pygidium; (e) meraspid hypostome; (f) young holaspid hypostome.

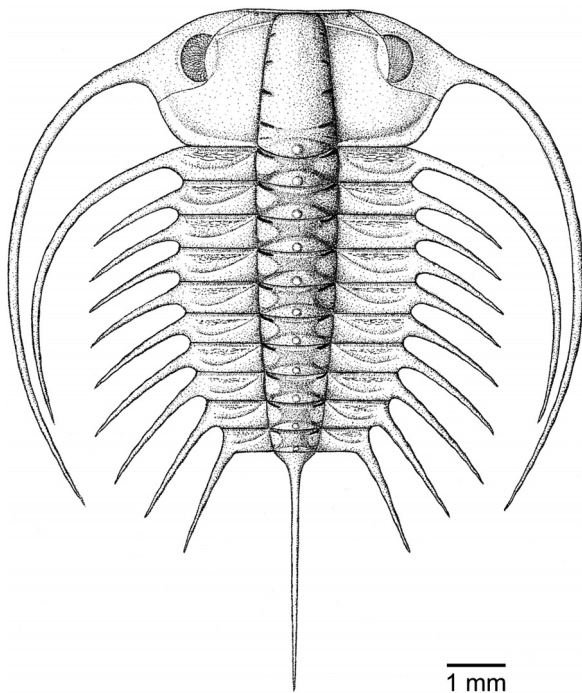


Figure 7 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922. Reconstruction in dorsal view (from Clarkson *et al.* 2004).

Remarks. The morphology of the cephalon in *S. alatus* from Västergötland is virtually identical with that of the reconstruction of *S. alatus* given by Høyberget & Bruton (2012), based on the Oslo Fjord specimens; it differs from that of Clarkson *et al.* (2003) only in minor details: a better developed S2 glabellar furrow, a wider axis, genal spines which extend further from the body, and a very long caudal spine. The main difference between the two morphs is in the length of the genal spines. The genal spines of *S. alatus* found in Västergötland extend horizontally, far under the body, whereas those of *S.*

alatus, as illustrated by Westergård (1922) and Henningsmoen (1957), and as found in all the Bornholm material, are relatively short. A holaspid librigena referred to *S. alatus* from Västergötland, however, with an unusually short spine, was figured by Clarkson *et al.* (2003, pl. 8, fig. 8). Although there are evident similarities between the stages of development of *S. alatus* from Bornholm and Västergötland, there are some differences; and in particular that the former retains intergenal and occipital spines until relatively late in meraspid ontogeny, while in the latter, such spines are absent from the beginning. Likewise, the marginal spines on the pygidium are appreciably longer in *S. alatus* from Bornholm during development than they are in the material from Västergötland, and the small triangular pygidium does not closely resemble that of the latter species at any stage of development.

Moreover, throughout ontogeny, each of the occipital rings of the Bornholm *S. alatus* material invariably bears an occipital spine, whereas only a node is present in the specimens from Västergötland. A reconstruction of *S. alatus*, based on the Bornholm material, is given in Figure 1.

Lee & Chatterton (2007) stated that olenid protaspides show morphological differences depending on oxygenation conditions. The protaspides of *S. alatus* are small and round, with spindle shaped axis and a smaller protopygidium, and are lacking anterior and mid fixigenal spine pairs. It fits very well into a description of an olenid protaspid found in a low oxygen environment.

Genus *Ctenopyge* Linnarsson, 1880

Type species. *Olenus (Sphaerophthalmus) pecten* Salter, 1864, from the Merioneth Series of Herefordshire and Worcestershire, England, UK, designated by Vogdes (1890).

Subgenus *Ctenopyge (Mesoctenopyge)* Henningsmoen, 1957

Type species. *Ctenopyge spectabilis* Brøgger, 1882, from the Furongian of Norway.

Ctenopyge (Mesoctenopyge) tumida Westergård, 1922
Figs 7–11

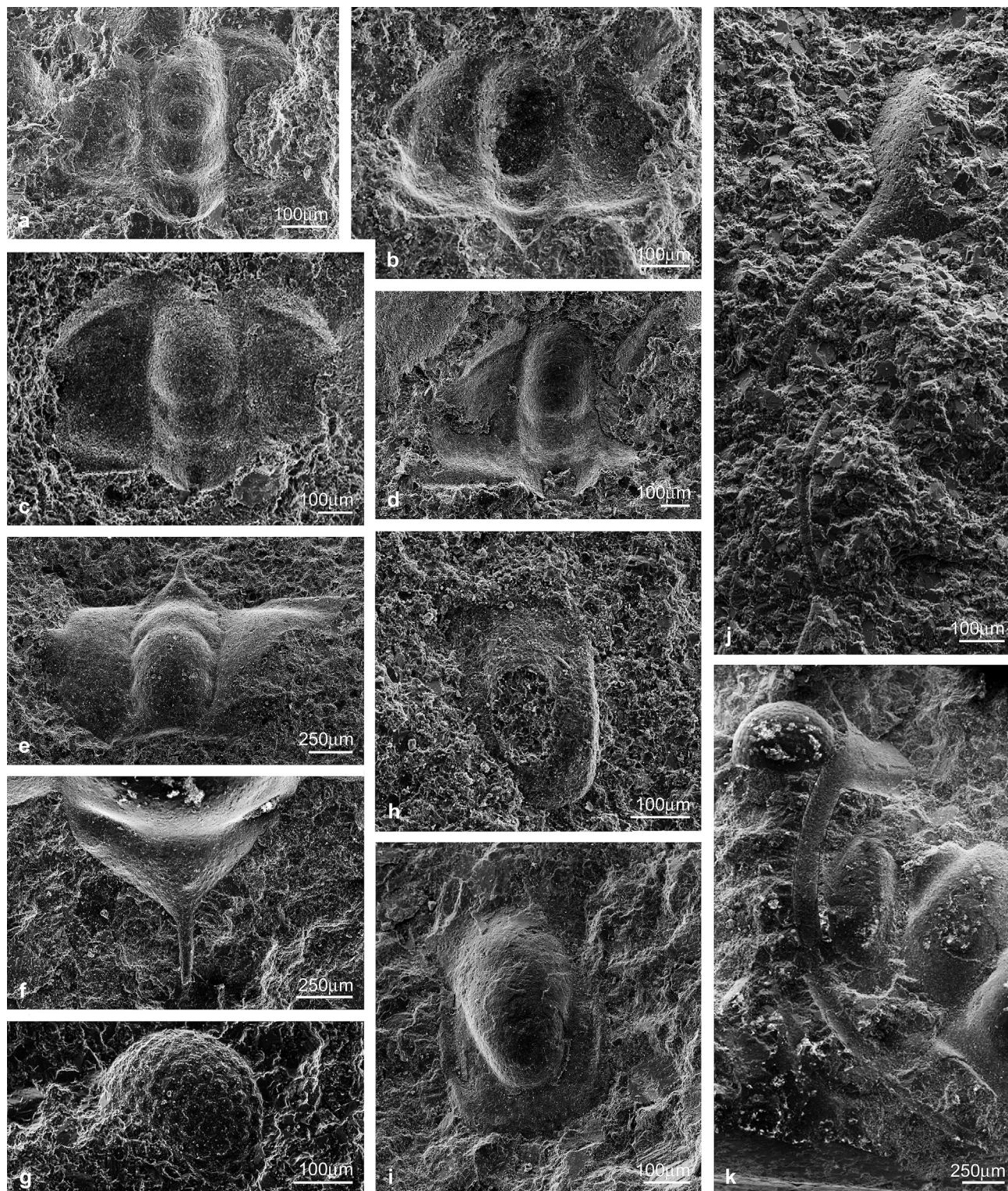


Figure 8 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922: (a) cranium degree 3–4, LO 12323t; (b) cranium degree 3–4, LO 12324t; (c) late meraspid, cranium LO 12325t; (d) partial cranium of a late meraspid, LO 12326t; (e) cranium of late meraspid or early holaspid, oblique anterior view, LO 12327t; (f) occipital ring and spine of an early holaspid showing tiny tubercles, LO 12328t; (g) juvenile eye, LO 12329t; (h) meraspid hypostome, LO 12330t; (i) young holaspid hypostome, LO 12331t; (j) two librigena, showing distinct curving spines, eyes broken off, LO 12332t; (k) curving genal spine of a late meraspid/early holaspid, LO 12333t.

1880 *Ctenopyge?* sp. Indet. [partim] Linnarsson, p. 156, pl. 6, fig. 15.

1922 *Ctenopyge tumida* n. sp. [partim] Westergård, p. 155, pl. 11, figs 15–18.

1923 *Ctenopyge tumida* Westergård [partim] Westergård; Poulsen, p. 39, pl. 1, fig. 14.

1947 *Ctenopyge tumida* Westergård; Westergård, p. 24.

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

1971 *Ctenopyge (Mesoctenopyge) tumida* Westergård; Rushton, in Taylor & Rushton, p. 32–33, fig. 8a.

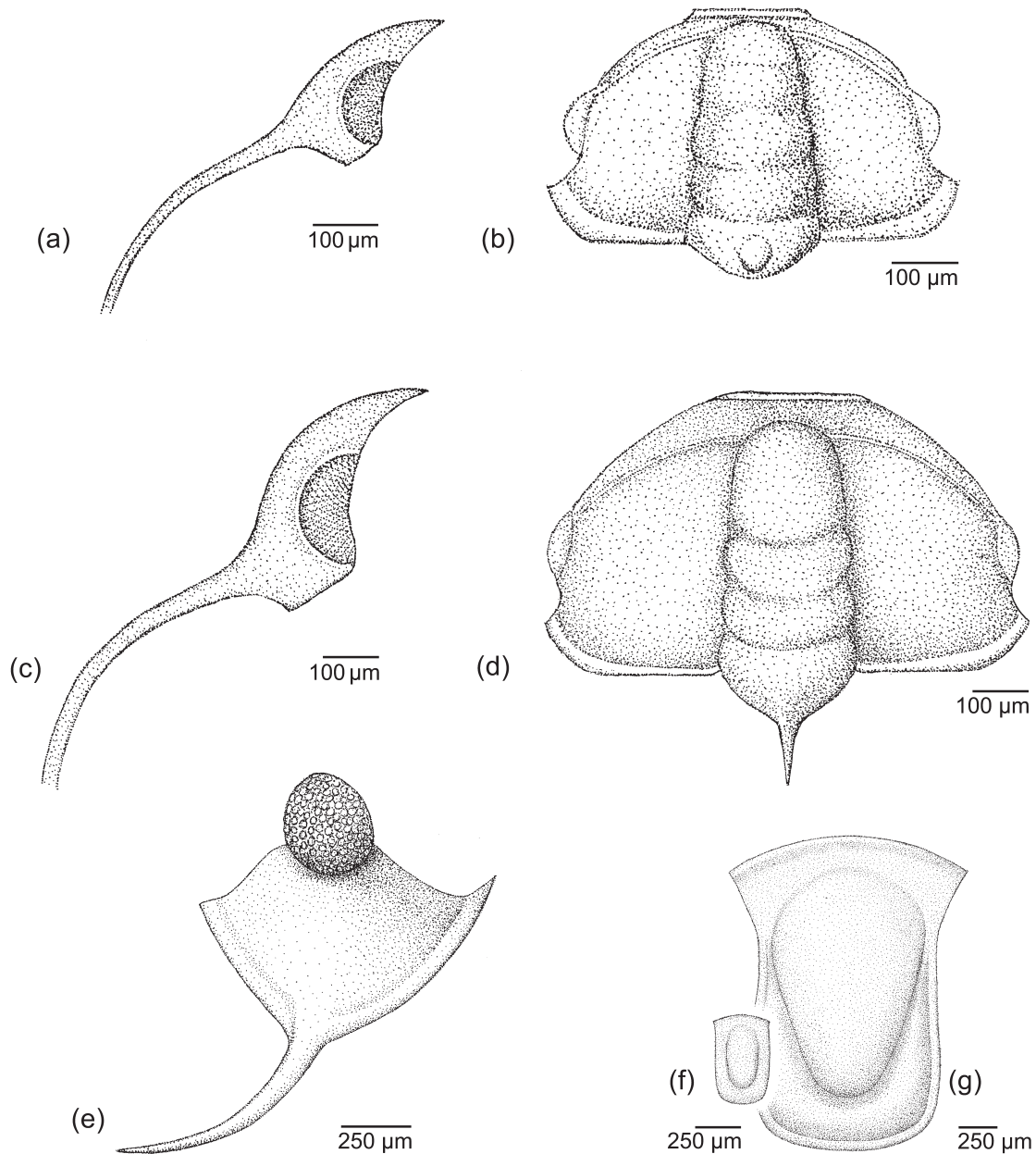


Figure 9 Reconstructions of librigenae, cranidia and hypostomes of *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922: (a, c) librigenae, probably representing similar developmental stages to the cranidia figured here; dimensions of eyes uncertain; (b) meraspid cranidium degree 3 or 4; (d) later meraspid cranidium; (e) librigena in lateral view; (f) juvenile hypostome; (g) adult hypostome.

1973 *Ctenopyge (Mesoctenopyge) tumida* Westergård; Schrank, p. 825, pl. 7, figs 13–20, 22, 23.

1992 *Ctenopyge (Mesoctenopyge) tumida* Westergård; Cope & Rushton, p. 547, fig. 5 m–o.

2001 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922; Żylińska, pp 341–342, pl. 1, figs 11–12.

2004 *Ctenopyge (Mesoctenopyge) tumida* Westergård; Clarkson *et al.*, pp 129ff, figs 17, 18A–D, 19, 20A–D

Type data. As the lectotype, Henningsmoen (1957) selected a cranidium figured by Westergård (1922, pl. 11, fig. 16) from Andrarum, Skåne, Sweden.

Description. This species was fully described by Westergård (1922) and Henningsmoen (1957). A further description was given by Clarkson *et al.* (2004), based upon excellent material from Västergötland. In all the specimens described so far, however, the pygidium is lacking, and those described below are the only ones so far known.

Development of the cranidium. (Figs 8a–f, 9b, d). A few meraspid stages from Västergötland were figured by Clarkson *et al.* (2004). The smallest is a hexagonally shaped cranidium with a single attached thoracic segment, of length 0.43 mm and width 0.5 mm. A larger specimen with five thoracic segments (interpreted as a degree 5 meraspis) has a cranidium of length 0.6 mm and width 0.8 mm. A further individual is a young holaspis with a cranial length of 0.8 mm and a width of 1.25 mm. The cranidia figured here can be compared with those described from Västergötland. Figures 8a–b and 9b illustrate a cranidium of length 400 µm and width 700 µm. They may belong to a degree 3, or possibly a degree 4 meraspis, compared to that described by Clarkson *et al.* (2004). A larger sized cranidium (Figs 8c, d, 9d), interpreted as a late meraspid stage, appears to be of length 600 µm and width 800 µm, but since both are frayed at the lateral edges, the width is somewhat uncertain. These two specimens resemble those previously figured by Clarkson *et al.* (2004), but the distinctive, very short,

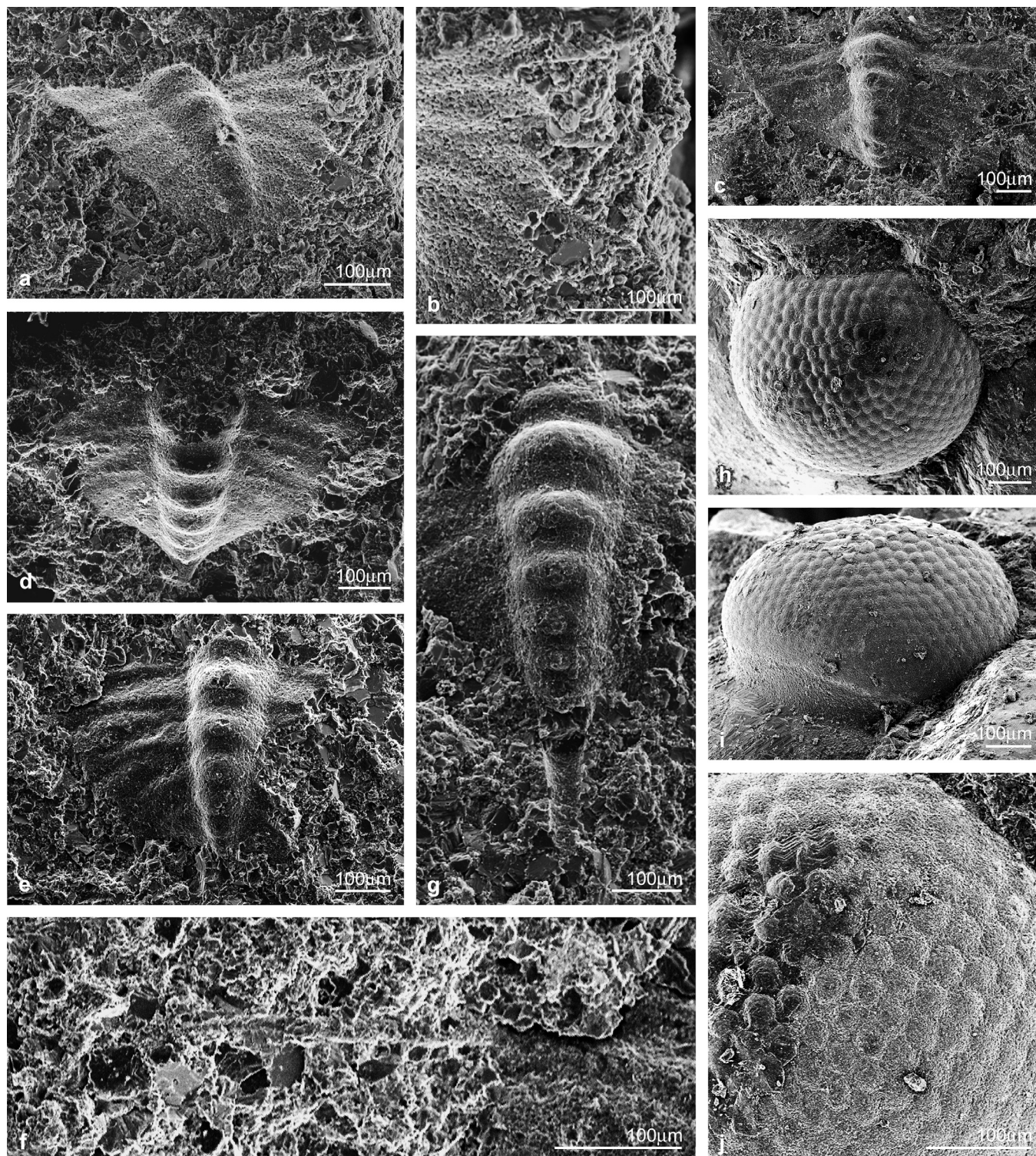


Figure 10 *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922: (a–b) pygidium, early meraspid stage, oblique posterior view, LO12334t; (b) enlargement of part of (a) showing marginal spines on left hand side; (c) pygidium of middle meraspid stage, LO 12335t; (d) oblique anterior view of a pygidium of a middle meraspid stage showing posterior spine, LO 12336t; (e–f) pygidium of an early meraspid stage, LO 12337t: (f) enlargement of the upper left side of (e), showing a single marginal spine; (g) axis and posterior spine of a well-preserved pygidium, middle meraspid stage, a breakage scar is evident where the spine has been crushed down, LO 12338t. (h–j) eye of a small adult, LO11944t; (i) showing the socle at the base; (j) enlargement of the visual surface and lenses.

deeply sunk glabellar furrows of the typical *C. (M.) tumida* are much less developed. In the smaller specimen, furrows S1, S2 and S3 are continuous over the glabella, though slightly effaced centrally. In the larger specimen, there is a short occipital spine, a short preglabellar field, S0 is continuous, S1 more deeply depressed laterally, and S2 continuous but faint. A late meraspid/early holaspid is shown in antero-lateral view in

Figure 8e, showing a short, thin, upturned occipital spine, and tiny tubercles have developed on the occipital ring. Holaspid specimens (Fig. 8f) from Bornholm usually retain the distinct occipital spine, but this seems to be a variable feature. The material from Västergötland, upon which the reconstruction of Clarkson *et al.* (2004, fig. 19; Fig. 7), was based, lacks an occipital spine, though it does have a node.

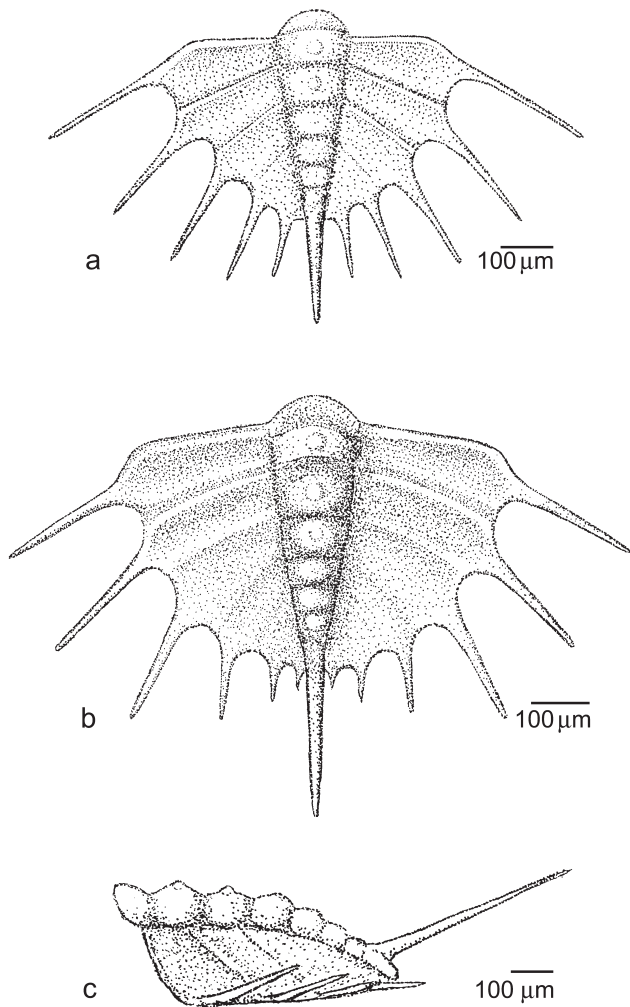


Figure 11 Reconstructions of pygidia of *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922, pygidia: (a) pygidium of early meraspid stage; (b–c) pygidium of middle meraspid stage, showing the upward inclination of the spines, dorsal and lateral views.

Librigena and eye. (Figs 8g, j, k, 9a, c, e, 10h–j). Two small librigenae (Figs 8j, 9a, c) show long curving spines which, clearly, were already well developed during the meraspid stage. The eyes are broken off, and the reconstruction presented is tentative. These obviously belong to meraspid stages, but which stage remains uncertain. Figure 9e shows a librigena in lateral view. Here, the lenses, though imperfectly preserved, are large and separate (Fig. 8g), as is common in juvenile holochroal eyes (e.g., in *Olenus*; Clarkson & Taylor 1995b). In the adults, the eyes, as figured previously (Clarkson *et al.* 2004) and also in the present paper, show many lenses of approximately equal dimensions, set on a panoramic visual surface. A feature not previously recorded is a wide, though featureless socle, upon which the visual surface is set (Fig. 10i). Enlarged lenses are shown in Figure 10j. Schoenemann & Clarkson (2015) described the structure and optics of the visual system of *C. (M.) tumida*.

Development of the hypostome. (Figs 8h–i, 9f–g). A juvenile hypostome (Figs 8h, 9f), 0.55 mm long and 0.32 mm wide, has a slightly curved anterior margin, small anterior wings, and is virtually parallel-sided laterally. The middle body is also almost parallel-sided. A small holaspid hypostome (Figs 8g, 9i) is 2.0 mm long and 1.2 mm wide. The anterior margin is curved and short anterior wings are developed. The middle body is large, inflated and tapering posteriorly to a blunt termination. There is no U-shaped band surrounding the middle body, as in *S. alatus*. Posteriorly from the anterior

wings, the hypostome narrows to a point opposite the widest part of the middle body, thereafter becoming subparallel-sided, expanding slightly rearwards so that it is widest close to the almost transverse posterior margin.

Development of the meraspid pygidium. (Figs 10a–g, 11a–c). The pygidia are assigned to two stages.

Early meraspid stage. A few incomplete pygidia, frayed at the edges, but otherwise retaining much structural detail, provide the only available information on the tails of *C. (M.) tumida*. Some other fragments provide additional information. As previous authors have noted, several *Ctenopyge* species are never found with associated pygidia. Figures 10(a–b, e) and 11 show pygidia retaining long, thin, marginal spines, of which the full length of one of the anterior spines is preserved (Fig. 11g) and others are present, with broken tips. As reconstructed (Fig. 11a), these small pygidia are 320 µm long and 600 µm wide exclusive of spines, and 500 µm long and 1.0 mm wide with spines included. The outline, without the spines, is almost semi-circular, slightly pointed posteriorly. The axis, about 100 µm wide anteriorly and with 5–6 rings, tapers posteriorly, terminating in a strong axial spine. The anterior segments bear an axial node. The anterior pleural field has distinct, rather flattened pleurae, becoming less marked posteriorly and separated by ridges, each with a broad furrow behind, which fade out towards the rear. Each of the pleurae terminates in a long, thin, straight spine, projecting upwards and rearwards at about 20 degrees; each is about as long as the pleura from which it originates. There are five of these marginal spines, decreasing in size posteriorly. Pygidia of this size probably belong to a degree 3 meraspis.

Middle meraspid stage. A few slightly larger pygidia (Figs 10c–d, g, 11b–c) are 400 µm long and 700 µm wide without spines, and 750 µm long and 1.1 mm wide including spines. A transitory pygidium of this size is of similar form to the smaller pygidium and, likewise, has six axial rings, although the marginal spines diminish in size posteriorly. The stout axial spine is seen lying horizontally in Figure 10g, but it has a distinct fracture at the base. It is likely that this spine was originally inclined rearwards and upwards, at about 25 degrees.

3. Concluding remarks

This study has been based on abundant, though generally rather damaged and disarticulated, material from Bornholm, Denmark. It is complementary to previous works on ontogeny of olenid trilobites, and it reveals that the early stages in ontogeny of the Bornholm *Sphaerophthalmus alatus* are much more spinose than those of *S. alatus* found in Västergötland, of which the adult forms are very similar. Whether this is taxonomically significant, or is a consequence of local variation, remains an open question; here, we regard the two morphs as variants of the same species. Early ontogeny of *C. (M.) tumida*, already known in part, is further illuminated by the discovery of very spiny transitory pygidia, the only ones known for this species.

4. Acknowledgements

ENKC would like to thank the SYNTHESYS Foundation for funding a visit to Copenhagen in 2006, and Arne Nielsen for the supply of material, and inviting him to prepare and study it. Assistance with the SEM was given in Copenhagen by Maria Liljeroth, in Lund by Rita Wallén and in Edinburgh by Nicola Cayzer. Brigitte Schoenemann (Cologne) is thanked for helpful discussion; as is Anna Żylińska (Warsaw) for very helpful comments on an earlier draft of this paper. We thank the

reviewers Per Ahlberg (Lund) and Alan Owen (Glasgow) for their valuable suggestions.

5. References

- Adrain, J. 2011. Class Trilobita Walch 1771. In Zhang, Z. G. (ed.) *Animal biodiversity, an outline of higher-level classification and taxonomic richness*. *Zootaxa* **3148**, 104–09.
- Ahlberg, P., Månsson, K., Clarkson, E. N. K. & Taylor, C. M. 2006. Faunal turnovers and trilobite morphologies in the Upper Cambrian *Leptoplastus* Zone at Andrarum, southern Sweden. *Lethaia* **39**, 97–110.
- Ahlberg, P. & Terfelt, F. 2012. Furongian (Cambrian) agnostoids of Scandinavia and their implications for intercontinental correlation. *Geological Magazine* **149**, 1001–12.
- Anderson, A., Dahlman, B., Gee, D. G. & Snäll, S. 1985. The Scandinavian Alum Shales. *Sveriges Geologiska Undersökning Ca* **56**, 1–50.
- Angelin, N. P. 1854. *Palaeontologica Scandinavica. I: Crustacea formationis transitionis*. Fasc. 2, 21–92. Leipzig, Lund: T. O. Weigel. 93 pp.
- Balserio, D., Waisfeld, B. G. & Buatois, L. A. 2011. Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeontology. *Lethaia*, **44**, 58–75.
- Bird, C. & Clarkson, E. N. K. 2003. Observations on the ontogeny of the upper Cambrian trilobite *Peltura scarabaeoides westergaardi* Henningsmoen 1957. *GFF* **125**, 177–80.
- Boeck, C. P. B. 1838. Uebersicht der bisher in Norwegen gefundenen Formen der Trilobiten-Familie. In Keihau, B. M. (ed.) *Gaea Norvegica* **1**, 138–45. Oslo: Johan Dahl, Christiania.
- Brøgger, W. C. 1882. *Die silurischen Etagen 2 und 3 im Kristianiagebiet und auf Eker*. Universitätsprogramm für 2. Semester 1882. Oslo: Kristiania. 376 pp.
- Burmeister, H. 1843. *Die Organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeiter beschriebenen Arten*. Berlin: Georg Reimer. 148 pp.
- Clarkson, E. N. K. 1973. Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita) *Palaeontology* **16**, 735–65.
- Clarkson, E. N. K. 1979. The visual system of trilobites. *Palaeontology* **22**, 1–22.
- Clarkson, E. N. K., Taylor, C. M. & Ahlberg, P. 1997. Ontogeny of the trilobite *Parabolina spinulosa* (Wahlenberg, 1818) from the upper Cambrian Alum Shales of Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 69–89.
- Clarkson, E. N. K., Ahlgren, J. & Taylor, C. M. 2003. Structure, ontogeny, and moulting of the olenid trilobite *Ctenopyge (Eoctenopyge) angusta* Westergård 1922 from the upper Cambrian of Västergötland, Sweden. *Palaeontology* **47**, 1–27.
- Clarkson, E. N. K., Ahlgren, J. & Taylor, C. M. 2004. Structure, ontogeny, and functional morphology of some spiny *Ctenopyge* species from Västergötland, Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94**(for 2003), 115–43.
- Clarkson, E. N. K. & Ahlberg, P. 2002. Ontogeny and morphology of a new, miniaturised and spiny olenid trilobite from southern Sweden. *Palaeontology* **45**, 1–22.
- Clarkson, E. N. K. & Taylor, C. M. 1995a. The lost world of the olenid trilobites. *Geology Today* **11**, 147–54.
- Clarkson, E. N. K. & Taylor, C. M. 1995b. Ontogeny of the trilobite *Olenus wahlenbergi* Westergård, 1922 from the upper Cambrian Alum Shales of Andrarum, Skåne, Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **86**, 13–34.
- Cope, J. C. W. & Rushton, A. W. A. 1992. Cambrian and early Tremadoc rocks of the Llangynog Inlier, Dyfed, South Wales. *Geological Magazine* **129**, 543–52.
- Dworatzek, M. 1987. Sedimentology and petrology of carbonate intercalations in the Upper Cambrian Olenid Shale facies of southern Sweden. *Sveriges Geologiska Undersökning C* **819**, 1–73.
- Fortey, R. A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* **33**, 529–76.
- Henningsmoen, G. 1957. The trilobite family Olenidae with description of Norwegian material and remarks on the Olenid and Tremadocian Series. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I Matematisk-Naturvidenskapelig Klasse* **1957**, 1–303.
- Høyberget, M. & Bruton, D. L. 2012. Revision of the trilobite genus *Sphaerophthalmus* and relatives from the Furongian (Cambrian) Alum Shale Formation, Oslo Region, Norway. *Norwegian Journal of Geology* **92**, 433–50.
- Kaufmann, R. 1933. Variationsstatistisches Untersuchungen über die “Artabwandlung” und “Artumbildung” and der Oberkambrische Gattung *Olenus* Dalm. *Abhandlungen des Geologischen – Paläontologisches Institut der Universität Greifswald* **10**, 1–54.
- Lauridsen, B. W. & Nielsen, A. T. 2005. The upper Cambrian trilobite *Olenus* at Andrarum, Sweden; a case study of iterative evolution? *Palaeontology* **48**, 1041–56.
- Lee, D.-C. & Chatterton, B. D. E. 2007. Ontogeny of *Parabolina panosa* (Olenidae, Trilobita) from the uppermost Furongian (Upper Cambrian) of northwestern Canada, with discussion of olenid protaspides. *Canadian Journal of Earth Sciences* **44**, 1695–711.
- Lee, G. L. and Choi, D. K. 1999. Ontogeny of the Late Cambrian trilobite *Olenus asiaticus* Kobayashi, 1944 from the Machari Formation of Korea. *Geosciences Journal* **3**, 225–31.
- Lindström, G. 1901. Researches on the visual organs of the trilobites. *Kungliga Svenska Vetenskapsakademiens Handlingar* **34**, 1–86.
- Linnarsson, G. 1880. Om försteningarne i de svenska lagren med *Peltura* och *Sphaerophthalmus*. *Geologiska Föreningens i Stockholm Förhandlingar* **5**, 132–61.
- Månsson, K. 1998. Middle Ordovician olenid trilobites (*Triarthrus Green* and *Porterfieldia Cooper*) from Jämtland, central Sweden. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **89**, 47–62.
- Månsson, K. & Clarkson, E. N. K. 2012. Ontogeny of the upper Cambrian (Furongian) olenid trilobite *Protopeltura aciculata* (Angelin, 1854) from Skåne and Västergötland, Sweden. *Palaeontology* **55**, 887–901.
- Nielsen, A. T., Weidner, T., Terfelt, F. & Høyberget, M. 2014. Upper Cambrian (Furongian) biostratigraphy in Scandinavia revisited: definition of superzones. *GFF* **136**, 193–97.
- Poulsen, C. 1923. Bornholms Olenuslag og deres fauna. *Danmarks Geologiske Undersøgelse* **40**, 1–85.
- Salter, J. W. 1864–1884. A monograph of the British trilobites. *Palaeontographical Society (London) Monographs*. 244 pp.
- Schoenemann, B. & Clarkson, E. N. K. 2015. Eyes and vision in the coeval Furongian trilobites *Sphaerophthalmus alatus* (Boeck, 1938) and *Ctenopyge (Mesoctenopyge) tumida* Westergård, 1922, from Bornholm, Denmark. *Palaeontology* **58**, 133–40.
- Schovsbo, N. H. 2000. Environmental fluctuations in the *Olenus* Zone (Upper Cambrian), southern Scandinavia: a geochemical approach. *Bulletin of the Geological Society of Denmark* **47**, 53–61.
- Schovsbo, N. H. 2001. Why barren intervals? A taphonomic study of the Scandinavian Alum Shale and its faunas. *Lethaia* **34**, 271–85.
- Schrank, E. 1973. Trilobiten aus Geschieben der oberkambrischen Stufen 3–5. *Paläontologische Abhandlungen (A)* **4**, 805–91.
- Størmer, L. 1940. Early descriptions of Norwegian trilobites. *Norsk Geologisk Tidsskrift* **20**, 113–51.
- Taylor, K. & Rushton, A. W. A. 1971. The pre-Westphalian geology of the Warwickshire Coalfield. *Bulletin of the Geological Survey of Great Britain* **35**, 1–152.
- Terfelt, F., Eriksson, M. E., Ahlberg, P. & Babcock, L. E. 2008. Furongian series (Cambrian) biostratigraphy of Scandinavia – a revision. *Norwegian Journal of Geology* **88**, 73–87.
- Terfelt, F., Ahlberg, P. & Eriksson, M. E. 2010. Complete record of Furongian polymerid trilobites and agnostoids of Scandinavia – a biostratigraphical scheme. *Lethaia* **44**, 8–14.
- Tortello, M. F. & Clarkson, E. N. K. 2003. Ontogeny of the Early Ordovician olenid trilobite *Jujuyaspis keideli* Kobayashi from northwestern Argentina. *Ameghiniana* **40**, 257–75.
- Tortello, M. F. & Clarkson, E. N. K. 2008. Ontogeny, structure and moulting of *Parabolina frequens argentina* (Kayser) (Trilobita, Olenidae) from the Furongian of northwestern Argentina. *Ameghiniana* **45**, 13–31.
- Vogdes, A. W. 1890. A Bibliography of Paleozoic Crustacea from 1698 to 1889 including a list of North American species and a systematic arrangement of genera. *US Geological Survey Bulletin* **63**. Washington, DC: United States Geological Survey. 177 pp.
- Westergård, A. H. 1922. Sveriges Olenidskiffer. *Sveriges Geologiska Undersökning. Ca* **18**, 1–205.
- Westergård, A. H. 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. *Sveriges Geologiska Undersökning C* **489**, 1–34.
- Whitworth, P. H. 1970. Ontogeny of the upper Cambrian trilobite *Leptoplastus crassicornis* (Westergård) from Sweden. *Palaeontology* **13**, 100–11.
- Żylińska, A. 2001. Late Cambrian trilobites from the Holy Cross Mountains, central Poland. *Acta Geologica Polonica* **51**, 333–83.