Revision of the trilobite genus Sphaerophthalmus and relatives from the Furongian (Cambrian) Alum Shale Formation, Oslo Region, Norway

Article *in* Norsk Geologisk Tidsskrift · January 2012

Revision of the trilobite genus *Sphaerophthalmus* and relatives from the Furongian (Cambrian) Alum Shale Formation, Oslo Region, Norway

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Høyberget, M. & Bruton, D. L.: Revision of the trilobite genus *Sphaerophthalmus* and relatives from the Furongian (Cambrian) Alum Shale Formation, Oslo Region, Norway. *Norwegian Journal of Geology,* Vol 92, pp. 433–450. Trondheim 2012, ISSN 029-196X.

A section through Furongian strata in the classical Slemmestad area of the Oslo Region, Norway, is described together with collected new material of selected zonal trilobites and their stratigraphical ranges within the Alum Shale Formation. This includes hitherto unknown mature and immature pygidia of certain species of *Sphaerophthalmus*, allowing the distinction between this and *Ctenopyge* to be clarified. Seven *Sphaerophthalmus* species are described of which five have previously been assigned to *Ctenopyge (Eoctenopyge)*, a taxon considered redundant. These are *Sphaerophthalmus angustus* (Westergård, 1922), *S. drytonensis* (Cobbold, 1934), *S. flagellifer* Angelin, 1854, *S. modestus* (Henningsmoen, 1957) and *S. postcurrens* (Westergård, 1944). Others are the type species, *S. alatus* (Boeck, 1838) and *S. arcus* n. sp. *Triangulopyge* n. gen. is proposed for a small, but distinct group of olenids earlier assigned to *Sphaerophthalmus*. The new genus includes *T. humilis* (Phillips, 1848), *T. major* (Lake, 1913) and *T. majusculus* (Linnarsson, 1880). It is proposed that the *Ctenopyge affinis* Zone be replaced by a broadened *Ctenopyge* tumida Zone. The round and reduced exoskeletal spines of the *Sphaerophthalmus* species, rather than the very long and flattened exoskeletal spines of *Ctenopyge*, suggest that the former were adapted for a more pelagic life style.

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Introduction

Trilobites of the family Olenidae occur in abundance in the Furongian and Tremadocian Alum Shale Formation of the Oslo Region, Norway, and have attracted the attention of palaeontologists for nearly 180 years, among these being Boeck (1838), Brøgger (1882), Holtedahl (1910), Størmer (1920), Strand (1927, 1929), Henningsmoen (1957, 1958) and Bruton et al. (1982, 1988). The faunas of corresponding strata in Sweden have been described and figured by Angelin (1854), Linnarsson (1880), Moberg & Möller (1898), Westergård (1922, 1940, 1944, 1947) and more recently from here by Clarkson & Taylor (1995), Clarkson et al. (1997, 2003, 2004), Clarkson & Ahlberg (2002), Terfelt (2003) and Ahlberg et al. (2005, 2006). The defined biozones for the Scandinavian Furongian Series proposed by Terfelt et al. (2008) were based on the works of Westergård (1947) and Henningsmoen (1957) and are followed here, save for our reservation of the validity of the *Ctenopyge affinis* Zone. Henningsmoen (1957, p. 211) noted that the distinction between the genera *Ctenopyge* and *Sphaerophthalmus* of the family Olenidae was arbitrary. Linnarsson (1880) erected *Ctenopyge* for a group of species, which had earlier been included in *Sphaerophthalmus*. The characters separating *Ctenopyge* from *Sphaerophthalmus* were mainly based on poorly known pygidia. Unfortunately, Linnarsson's description of *Sphaerophthalmus* was not based on the pygidium of the type species, *S. alatus* (Boeck, 1838), but on another distinct species, *Olenus humilis* (Phillips, 1848; *Triangulopyge humilis* n. gen. herein). Both Westergård (1922) and Henningsmoen (1957) erected a large number of *Ctenopyge* species, for which pygidia were not known and only few diagnostic characters are included for both *Ctenopyge* and *Sphaerophthalmus* in the work of the latter author. Thus, Henningsmoen notes the lack of adult pygidia of *Ctenopyge* s.l. available among collections from Scandinavia, However, we have identified them and propose below the distinction between *Sphaerophthalmus* and *Ctenopyge* together with a refined stratigraphical range of certain species.

Despite the overwhelming abundance, articulated or complete specimens of olenid trilobites are rare in the Oslo Region. We describe the following seven species of *Sphaerophthalmus*: *S. alatus* (Boeck, 1838), *S. arcus* n. sp., *S. angustus* (Westergård, 1922), *S. drytonensis* (Cobbold, 1934), *S. flagellifer* Angelin, 1854, *S. modestus* (Henningsmoen, 1957) and *S. postcurrens* (Westergård, 1944), and two species of *Triangulopyge* n. gen.: *T. humilis* (Phillips, 1848) and *T. majusculus* (Linnarsson, 1880).

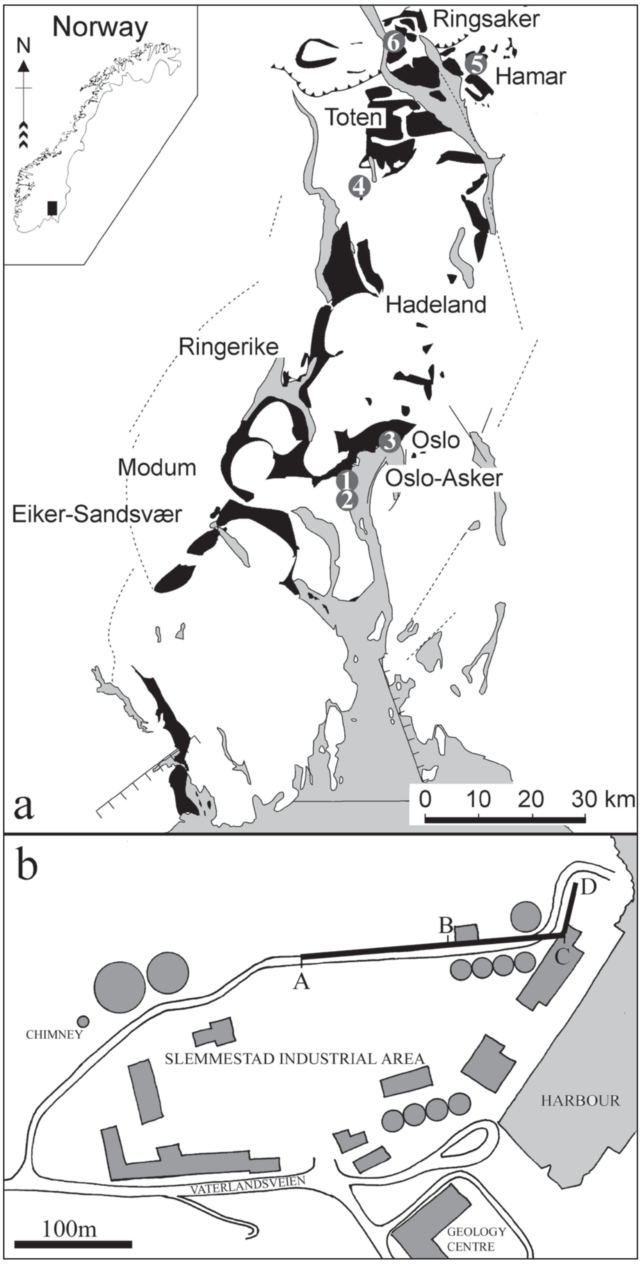

Figure 1. (a) Map of the Oslo Region showing outcrops of Lower Palaeozoic rocks in black, structural elements including thrust faults (single lines), normal faults (hachured lines) and front of Lower Allochthon (hachured triangles). Lakes and fiords shaded. Numbers refer to localities for those specimens figured in the text: 1: Slemmestad; 2: Nærsnes; 3: Oslo; 4: Hennung; 5: Løten; 6: Ringsaker. (b) Map showing the Slemmestad industrial area, buildings shaded, with a large exposed section of the Alum Shale Formation. Section A–B consists of the Tremadocian part of the Alum Shale Fm., with the upper boundary to the Bjørkåsholmen Fm. at A. The Ordovician/ Cambrian boundary is recognised at B, where limestone nodules contain the trilobites Boeckaspis *and* Jujuyaspis *and the graptolite* Rhabdinopora *used in worldwide correlation. Section B–C consists of the upper part of the Furongian Alum Shale Fm. with large limestone lenses more than 2 m in diameter. The stratigraphically lowest part of the section, C–D, is logged and described herein.*

Geological setting

The Alum Shale Formation is present throughout much of Baltoscandia and includes strata from Middle Cambrian (Series 3) to close to the top of the Lower Ordovician Tremadocian Series. At its maximum extent, the 'Alum Shale Sea' covered areas from western Norway to St. Petersburg in the east and from Poland in the south to Finnmark in northern Norway (Buchardt et al., 1997). The term Alum Shale Formation is used for the entire lithostratigraphic unit throughout Scandinavia (Nielsen & Schovsbo, 2007) and the type section is defined in the Gislövshammar-2 core, southern Sweden (Buchardt et al., 1997). The shale consists of sediments deposited under dysoxic to anoxic conditions, with an average sedimentation rate of 1 to 10 mm per one thousand years (Thickpenny, 1984). Bituminous limestone concretions ('Stink Stones') and thin limestone beds occur in many places throughout the unit. The Furongian alum shale of the Oslo Region itself is usually unfossiliferous, strongly folded and cleaved, but the limestone concretions can be extremely rich in fossils of low diversity and strongly dominated by olenid trilobites. The exposed section at Slemmestad (Fig. 1), which forms the basis for this work, is fenced in by the harbour owners and is not easily accessible. This forms the earliest Furongian part of a section which continues westwards and can be studied at the Slemmestad industrial area, where the upper half of the Furongian is present and includes the Cambrian/ Ordovician boundary, followed by a complete section of the Tremadocian.

The succession of the traditional *Ctenopyge* zones is tectonically distorted at the top of the logged section, but is estimated to be 6.5 m thick; 2.5 m above and 4 m below the *Peltura scarabaeoides* marker bed (Fig. 2). The thickness of corresponding zones in Skåne, Sweden is 2.5 to 3 m (Westergård, 1944) and 3.7 m at Kinnekulle, Västergötland, Sweden (Terfelt, 2003).

Discussion on the zonal division

Henningsmoen (1957), in his monumental olenid work, erected several zones and subzones based on material from museum collections, drillcores, in situ limestone concretions and those found loose or in float. Eight of his trilobite subzones were based on ubiquitous species of *Ctenopyge*, all with short vertical ranges. Regrettably, the absolute stratigraphical ranges were not always accurate, especially where material was from float, and some of the subzones were not documented in situ. Thus, the *Ctenopyge similis* Zone (Henningsmoen, 1957, p. 38) was based on morphological characters of the co-occurring *C. modesta*, characterised as being intermediate between the stratigraphically well-known taxa *C. flagellifera* and *C. angustus*. We record herein in situ material of *Sphaerophthalmus modestus* from the new Slemmestad section (Fig. 2) and this supports the validity of the *C.*

similis Subzone, which, like all other subzones, has since been raised to a zonal level (Terfelt et al., 2008).

The *Ctenopyge affinis* Zone was established on the occurrence of its eponymous species. Originally, Westergård (1922) included two different forms under *C. affinis* and Henningsmoen (1957) recognised the co-occurring morphotypes *C. (Ctenopyge) affinis affinis* and *C. (C.) affinis gracilis*. Clarkson et al. (2004) revised the species, elevated *C. gracilis* to species rank and described two additional taxa, *C. ahlbergi* and *C. rushtoni*, all very closely related and co-occurring with *C. tumida*, but *C. affinis s.s.* was not treated. *C. gracilis* is common in Scandinavia, but *C. affinis s.s.* is extremely rare and therefore not suitable for zoning. This was not discussed by Terfelt et al. (2008) when formally defining the *Ctenopyge affinis* Zone on the first appearance (FAD) of the eponymous species. Earlier, Westergård (1922) reported *C. affinis s.l.* as practically coeval with the lowest occurrence of *C. tumida* and later he reported *C. affinis* to occur in the *C. bisulcata* Zone (Westergård, 1947). The *C. affinis* specimens he recorded from the older *C. spectabilis* Zone were later separated into a new taxon, *C. tumidoides*, by Henningsmoen (1957). Terfelt (2003) reported *C.* cf. *affinis* from Västergötland, Sweden, but this is similar to *C. gracilis* or one of the closely related species described by Clarkson et al. (2004). Żylińska (2002, p. 229) reported a randomly distributed trilobite assemblage representing both the *C. tumida* and the *C. affinis* zones limited to a limestone concretion from Poland.

C. tumida is very characteristic, easily identified and occurs frequently throughout the *Ctenopyge* tumida and *Ctenopyge affinis* zones in the Oslo Region, and is common in Sweden, Denmark, Britain and Poland. We therefore propose to replace the *Ctenopyge affinis* Zone by a broadened *Ctenopyge tumida* Zone (Fig. 2).

Material

We have collected well-preserved material from bituminous limestone lenses and beds, exhibiting detailed structures of specimens less than 10 mm in length. None is complete, but moulted exuviae of detached cranidia or cranidia with thorax attached are known for most of the described species. Detached sclerites occur in great abundance on certain surfaces, commonly representing two or three taxa. The minute, adult pygidia associated with detached *Sphaerophthalmus* cranidia, certainly belong to the same species. Mostly, the co-occurring species belong to another genus or subfamily (*Protopeltura, Peltura, Parabolina* and *Ctenopyge*), which leaves no doubt to which species the pygidia belong. All the *Sphaerophthalmus* and *Triangulopyge* species treated herein occur commonly in the Oslo Region.

Material figured below was collected by MH except when stated and deposited in the type collection of

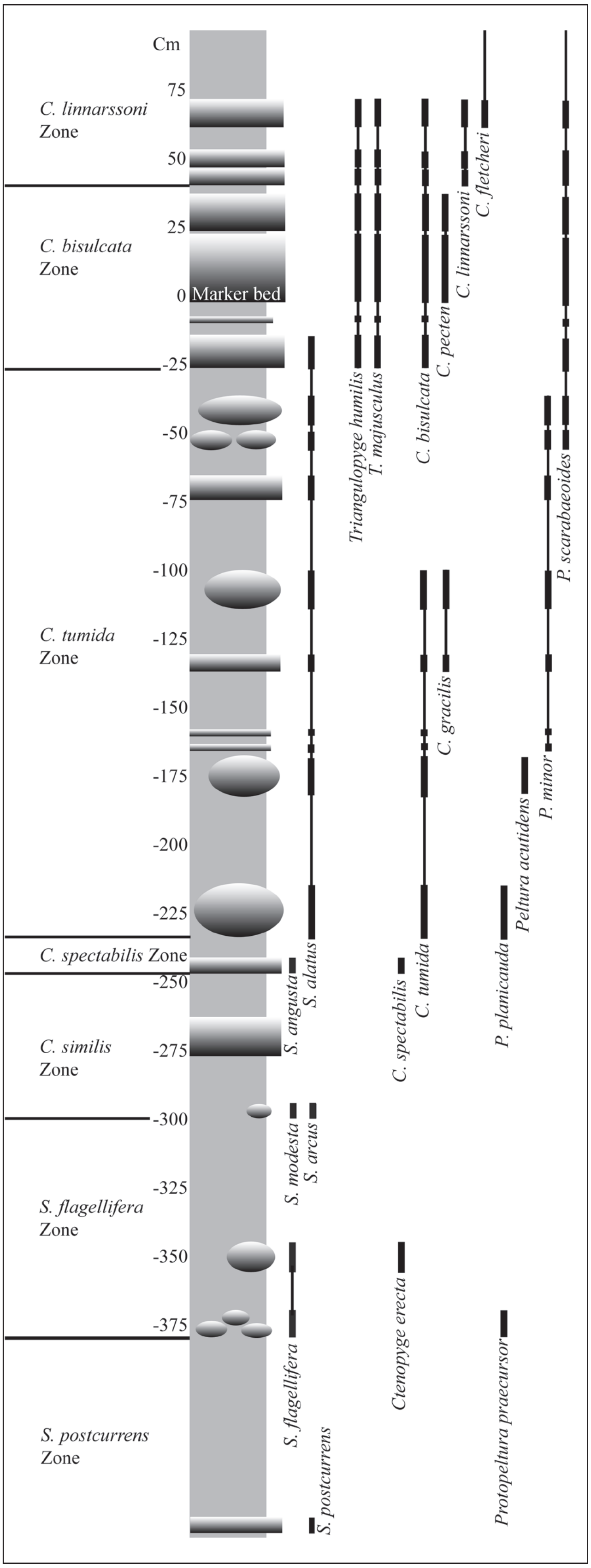

Figure 2. *Log of the investigated section in the Slemmestad industrial area showing trilobite zonation, limestone horizons of nodules and beds with gradient shade and species range chart. The 35 cm-thick limestone bed yielding abundant* Peltura scarabaeoides *occurs at several localities in the Slemmestad area. Here the base of this bed corresponds to 0 cm.*

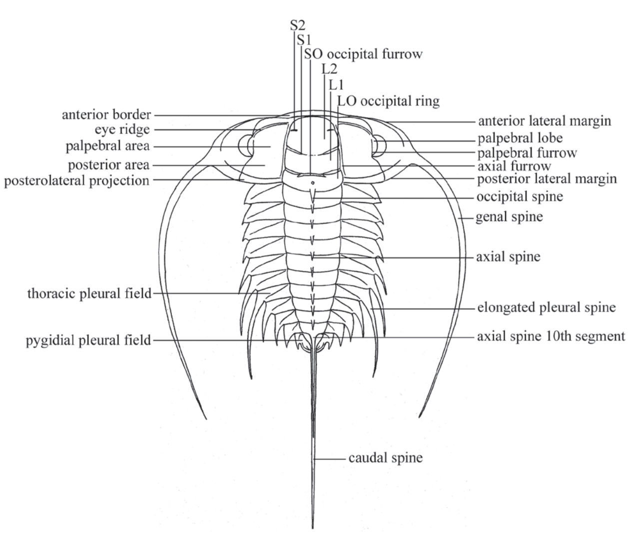

Figure 3. Morphological terms used in the text (after Whittington & Kelly, 1997).

the Geological Museum, University of Oslo (hereafter abbreviated PMO). Other material mentioned is in collections of the Swedish Geological Survey, Uppsala (SGU) and the Oxford University Museum (Ox). Morphological terms applied to the figured olenids are shown in Fig. 3.

Systematic palaeontology

Family Olenidae Burmeister, 1843.

Subfamily Leptoplastinae Angelin, 1854.

Genus *Sphaerophthalmus* Angelin, 1854.

Type species: Trilobites alatus Boeck, 1838, designated by Linnarsson (1880). A lectotype (PMO 56371) was selected by Størmer (1940, p. 145) from Boeck's material, originating from an old alum shale quarry in Gamlebyen, Oslo, Norway. The lectotype is refigured herein (Fig. 5A, D).

Diagnosis: (Emended from Henningsmoen 1957). Glabella convex, slightly tapering, longer than wide. Distinct occipital furrow, S1 pronounced abaxially. S2 and S3 short, shallow to obsolete. Anterior border upturned, moderately to strongly convex in frontal view. Centres of palpebral lobes opposite S1 to L2. Eye ridges oblique. Palpebral area markedly narrower than glabella at eye line. Posterior area as wide as to slightly wider than occipital ring (tr.). Posterolateral projection ventrally downflexed. Librigena with long and curved spine rounded in cross-section. Thorax consists of ten segments, pleural fields about as wide (tr.) as axis. Tenth segment with long axial spine. Pleural spines short, seventh pair elongated. Pygidium minute and triangular, one to two axial rings. Very long, backwardly curved caudal spine. One pair of short marginal spines. Pleural field less than half the width of axis.

Discussion: In the light of a new diagnosis of the genus, three previously assigned species are here excluded and others are now included. Together, these are: *S. alatus* (Boeck, 1838), *S. angustus* (Westergård, 1922), *S. drytonensis* (Cobbold, 1934), *S. flagellifer* Angelin 1854, *S. modestus* (Henningsmoen, 1957), *S. postcurrens* (Westergård, 1944) and *S. arcus* n. sp.

Linnarsson (1880) erected the genus *Ctenopyge* to separate a group of species which had earlier been included in *Sphaerophthalmus*. These species, since Henningsmoen (1957) assigned to *Ctenopyge* (*Ctenopyge*), have a more flattened cranidium, palpebral areas as wide as or wider than the glabella at eye line, anteriorly situated palpebral lobes, almost transverse eye ridges and a parallel–sided glabella. The thorax has very long and curved pleural spines on each segment.

The separation was mainly based on characteristic features of the insufficiently known pygidia (Linnarsson, 1880, pp. 16, 17). The pygidia of the *Ctenopyge* species are proportionally larger and have more axial rings and marginal spines than those belonging to *Sphaerophthalmus*. Unfortunately, Linnarsson mixed *Sphaerophthalmus humilis* (Phillips, 1848) from the *Ctenopyge bisulcata* Zone with the type species *Sphaerophthalmus alatus* (Boeck, 1838) from the older *Ctenopyge tumida* Zone. This has caused some confusion by later authors (Brøgger, 1882; Lake, 1913; Westergård, 1922; Poulsen, 1923; Strand, 1929).

There are few differential characters in Henningsmoen's (1957, p. 211) diagnoses of *Ctenopyge* and *Sphaerophthalmus*, which include the comparatively narrower (tr.) posterior area and the relatively short pleural spines in *Sphaerophthalmus*. In Moore (1959, p. O264), a few additional diagnostic features are provided, but the described pygidium is based on *Sphaerophthalmus majusculus* Linnarsson, 1880 and *Olenus humilis* Phillips, 1848, whose pygidia are so different from those of *Sphaerophthalmus* that they are now assigned to *Triangulopyge* n. gen. (see below).

In our view, the species assigned by Henningsmoen (1957) to *Ctenopyge (Eoctenopyge)* share features of cephalon, thorax and pygidium with those of *Sphaerophthalmus*, indicating that they are best assigned to that genus, making *C. (Eoctenopyge)* redundant.

Henningsmoen (1957, p. 185) points out the lack of adult pygidia, but we now have these for species of both *Sphaerophthalmus* and *Triangulopyge* n. gen. During moulting the long, curved, caudal spine in *Sphaerophthalmus* appears to have caused the pygidium to become buried on its side. When collecting, the rock splits and the spine with part of the pleura is detached, leaving behind the minute pygidium still embedded in matrix. The extremely long caudal spine (probably among the proportionally longest known in trilobites) is more than ten times the length of the pygidium, longer than the rachial spines and with a curve similar to the genal spine. We have abundant immature pygidia in our collections. These lack the large caudal spine, but in the largest immature examples a tiny spine occurs on the last axial ring. Immature transitory pygidia show up to six axial rings, each with spines on transitory pleurae. The posterior area of transitory pygidia is curled down, as seen in other immature leptoplastines (Whitworth, 1970; Clarkson & Ahlberg, 2002; Clarkson et al., 2004; Ahlberg et al., 2005). Meraspid pygidia of *Sphaerophthalmus* have recently been figured and described by Clarkson et al. (2003).

Adult pygidia of *Ctenopyge* are only known for *C. similis*, *C. erecta*, *C. pecten* and the miniaturised *C. ceciliae*. The pygidium of *C. similis* has not previously been described, but new material (Høyberget collection) shows that it is proportionally large with 3–4 pairs of marginal spines and 4–5 axial rings lacking a caudal spine. The pleural fields are wider (tr.) than the axis. So far, no pygidia have been identified for *C. oelandica, C. affinis, C. bisulcata* and *C. fletcheri*, all of which have cranidia resembling that of *Sphaerophthalmus* in the following way: (1) the centres of the palpebral lobe are situated opposite S1 to L2 and the eye ridges run obliquely backward; (2) The palpebral area is narrower than the glabella at eye line. However, the posterolateral projection is more flattened and is not curved downwards ventrally as in *Sphaerophthalmus*. In *C. (Ctenopyge) gracilis*, *C. (Ctenopyge) rushtoni* and *C. (Ctenopyge) ahlbergi* the pygidium seems to be small and triangular, but is poorly known (Clarkson et al., 2004) and the thorax is typical for *Ctenopyge* with wide (tr.) pleural fields and paired, very long, pleural spines on each thoracic segment (see Westergård, 1922; Henningsmoen, 1957; Clarkson et al., 2004).

Clarkson (1973) discussed the long, curved, librigenal spines of both *Sphaerophthalmus* and *Ctenopyge* species. The length and flattening of librigenal and pleural spines in *Ctenopyge* suggest that they functioned as a large snowshoe giving support to the body when resting on a muddy sea floor (Clarkson, 1973, p. 752; Clarkson et al., 2004). Our figured material of *Sphaerophthalmus* (Fig. 4) shows a reduced spinosity and may be an adaptation to a more pelagic mode of life (see Fortey, 1974; Bruton & Høyberget, 2006).

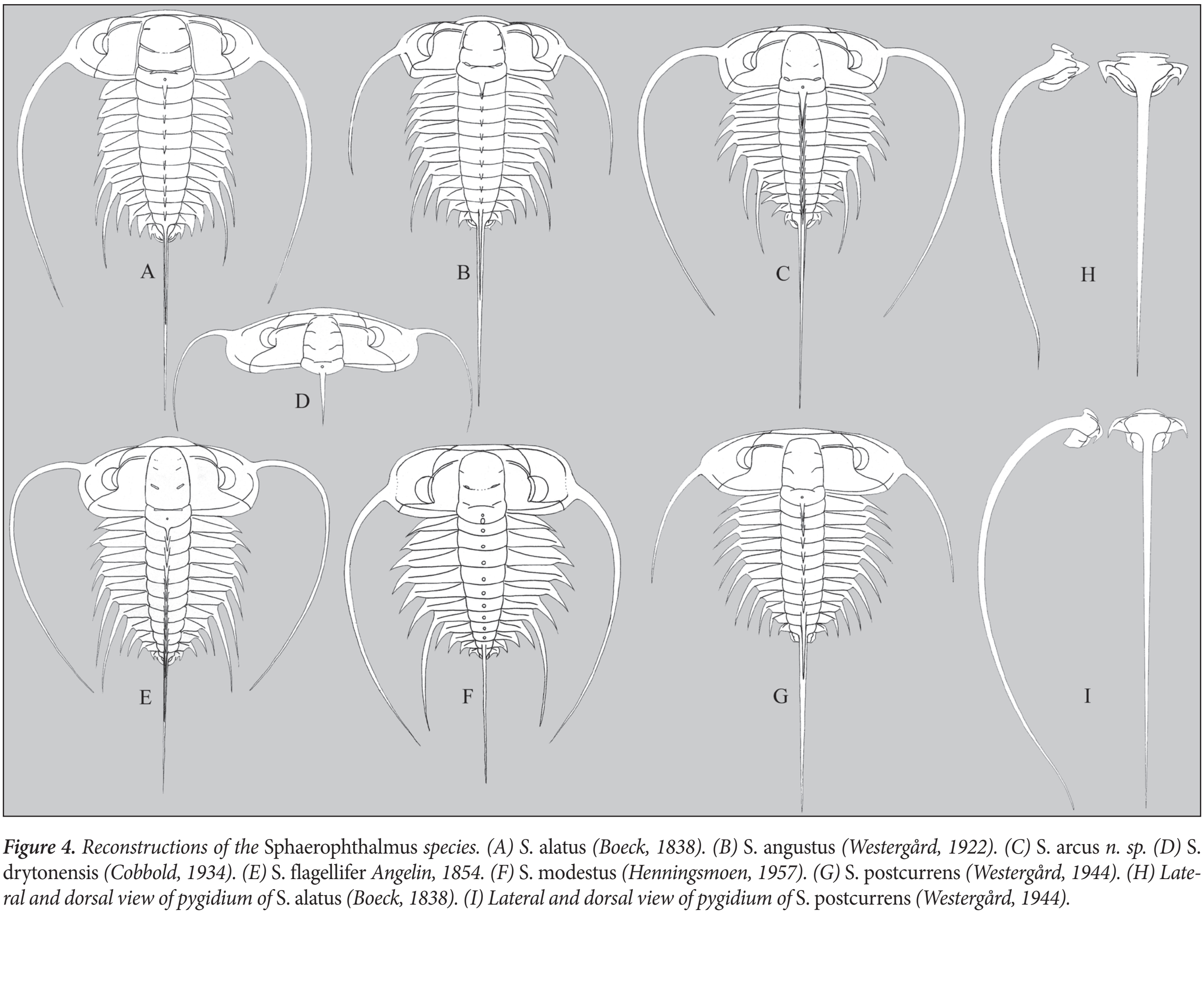

Figure 4. *Reconstructions of the* Sphaerophthalmus *species. (A) S.* alatus *(Boeck, 1838). (B)* S. angustus *(Westergård, 1922). (C)* S. arcus *n. sp. (D)* S. drytonensis *(Cobbold, 1934). (E)* S. flagellifer *Angelin, 1854. (F)* S. modestus *(Henningsmoen, 1957). (G)* S. postcurrens *(Westergård, 1944). (H) Lateral and dorsal view of pygidium of* S. alatus *(Boeck, 1838). (I) Lateral and dorsal view of pygidium of* S. postcurrens *(Westergård, 1944).*

Characters used in distinguishing species of *Sphaerophthalmus* are mainly the shape and position of the glabellar furrows, the convexity of the anterior border, the position of the palpebral lobes, the shape of the lateral margins on the librigena and the morphology of the thoracic spines.

Sphaerophthalmus alatus **(Boeck, 1838).**
Figs. 4A, H and 5A–K

1838 *Trilobites alatus* Boeck, p. 143.
1957 *Sphaerophthalmus alatus* (Boeck) – Henningsmoen, pp. 212–215, pl. 2, fig. 15, pl. 5, pl. 22, figs. 18–26.
1958 *Sphaerophthalmus alatus* (Boeck) – Henningsmoen, pp. 190, 192, pl. 3.
1968 *Sphaerophthalmus alatus* (Boeck) – Rushton, p. 415, pl. 78, figs. 9–10, text fig. 3d.
1973 *Sphaerophthalmus alatus* (Boeck) – Clarkson, p. 754, pl. 95, figs. 1, 2, text fig. 7 a–d.
1992 *Sphaerophthalmus alatus* (Boeck) – Cope and Rushton, pl. 5, figs. e–h.
2002 *Sphaerophthalmus majusculus* Linnarsson – Schöning, fig. 50 (fig. 51 = *T. humilis*).
2003 *Ctenopyge (Eoctenopyge) angusta* Westergård – Clarkson, Ahlgren and Taylor, pp. 1–27, pls. 1–8.

For further synonymy, see Henningsmoen (1957).

Lectotype: PMO 56371 selected by Størmer (1940, p. 145) from Boeck's material, collected at an old alum shale quarry in Gamlebyen, Oslo, Norway. Henningsmoen (1957, pl. 22, figs. 23, 24) figured the lectotype, which is refigured herein (Fig. 5A, D).

Diagnosis: A *Sphaerophthalmus* species with the cranidium both sagittally and transversally very convex. Centres of palpebral lobes opposite S1. S1 transglabellar, deep abaxially and connected with axial furrows. Palpebral area strongly convex, elevated above palpebral lobes. Librigenal posterior lateral margin convex, shorter than convex anterior lateral margin. Thoracic pleural regions narrower than axial rings in holaspid specimens.

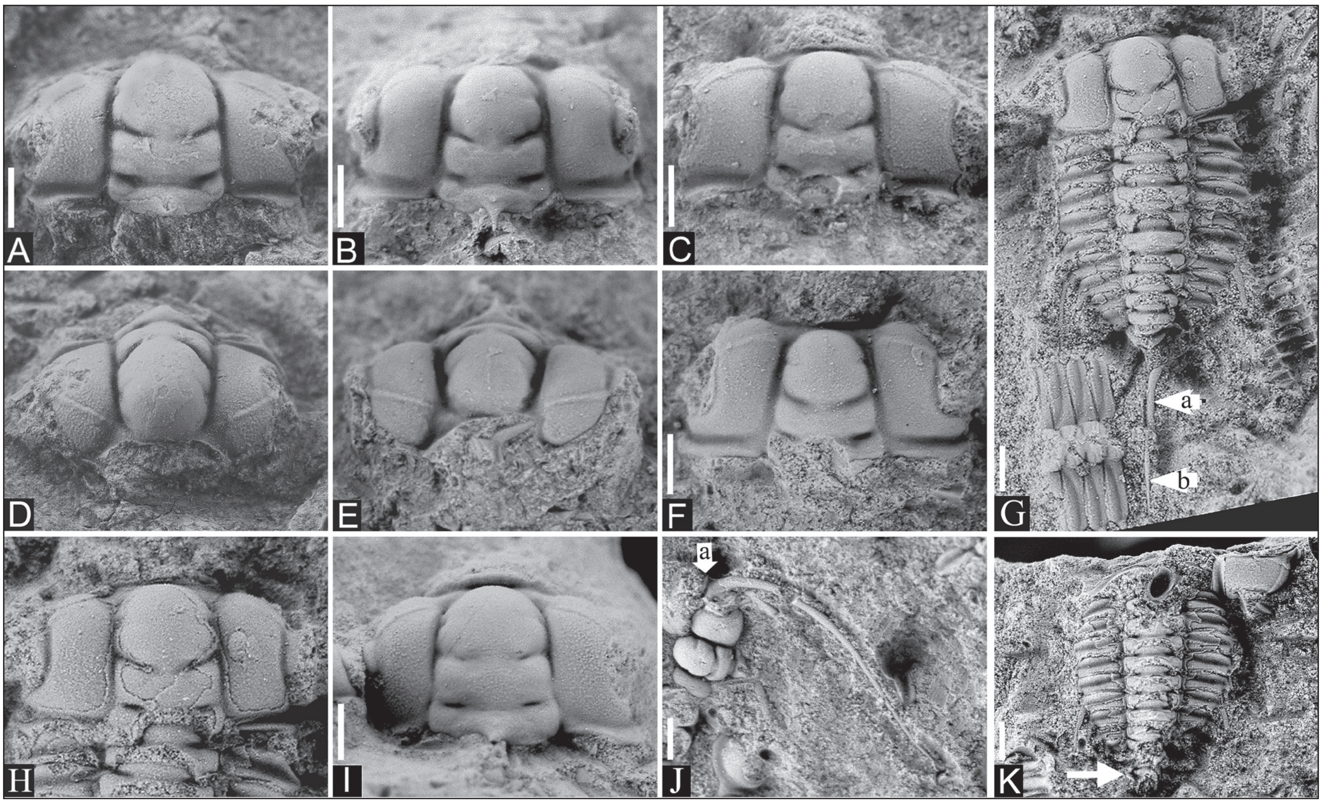

Figure 5. Sphaerophthalmus alatus *(Boeck, 1838). All scale bars: 1mm. (A) and (D) Dorsal and frontal view of lectotype cranidium* (PMO 56371). *Old Alum Shale Quarry, Gamlebyen, Oslo,* Ctenopyge tumida *Zone (Coll.: Boeck, 1830's). (B) and (E) Dorsal and frontal view of cranidium* (PMO 223.407/1), *length 2.9 mm. Yongstorget, Oslo,* C. tumida *Zone, upper part (former* C. affinis *Zone). (C) Cranidium* (PMO 223.407/2), *length 2.6 mm, faintly granulated. On the same slab as (B). (F) Cranidium* (PMO 223.408), *length 2.8 mm. Note the tapering glabella. Slemmestad,* C. bisulcata *Zone. (G) Exoskeleton* (PMO 223.409/1), *length 6.7 mm. Arrow a marks the caudal spine, arrow b the axial spine on the tenth segment. Four thoracic segments of* C. gracilis *are seen on lower left. Backeborg, Kinnekulle, Sweden,* C. tumida *Zone, uppermost part. (H) Close-up of (G), cranidium 2.5 mm long. (I) Cranidium* (PMO 223.410), *length 3.4 mm, with proportionally large glabella and shallow S1 medially. Ringsaker,* C. tumida *Zone, lower part. (J) Oblique lateral view of pygidium* (PMO 223.411), *length 0.6 mm excl. the caudal spine, with marginal spine broken off. Arrow a marks the connecting half ring. Backeborg, Kinnekulle, Sweden,* C. tumida *Zone. (K) Thoracopygon* (PMO 223.409/2), *length 4.5 mm long. Arrow points the left border of damaged pygidium. External mould of hypostoma in situ, right fixigena turned 90° clockwise. On the same slab as (G).*

Remarks: Clarkson et al. (2003, pp. 5, 6) gave a thorough description of *Ctenopyge (Eoctenopyge) angusta*, considered a subjective synonym of *Sphaerophthalmus alatus* (Boeck), see discussion below. Little is added to the description, except that the sixth to eighth segments have elongated pleural spines. In large specimens the axial rings become wider than the pleural region. The pygidium is small, triangular in outline and with only one axial ring, possessing an extremely long caudal spine more than ten times the length of the pygidium. The pleural field has one pair of very short pleural furrows and is less than half the width of the axis. One pair of short marginal spines is present. An upturned border occurs posteriorly, extending from the base of each pleural spine to the posterior.

Discussion: Clarkson et al. (2003) thoroughly described and figured specimens from Västergötland, Sweden, as *Ctenopyge (E.) angusta* Westergård, 1922. The specimens are here assigned to *S. alatus* because of the distinctly transglabellar S1, absent or very shallow in *S. angustus*. Moreover, the posterior area is narrower and more strongly flexed ventrally. The glabellar furrows in *S. alatus* are laterally deeper and more distinctly connected with the axial furrows than in all other species of *Sphaerophthalmus*. The material figured by Clarkson et al. (2003, p. 4) occurs together with *C. tumida* and *C. gracilis*, which are known to appear above the *Ctenopyge spectabilis* Zone to which *S. angustus* (Westergård, 1922) is confined.

Intermediate morphs of *S. angustus* and *S. alatus* seem to occur in the lowermost part of the *Ctenopyge tumida* Zone at Slemmestad and in Ringsaker. The morph (Fig. 5I) from the latter area is similar to *S. alatus*, but S1 and SO are slightly shallower and the glabella is wider. A cranidium figured by Henningsmoen (1957, pl. 22, fig. 25) from approximately the same stratigraphic level also shows similar features, but the specimens are best assigned to *S. alatus* because of their strong, transverse convexity and the fact that S1 reaches the axial furrow.

The distinguishing characters between figured material of *S. angustus* provided by Westergård (1922, pl. 11, figs. 2–5, 8) and Henningsmoen (1957, pl. 19, figs. 11–16, 18) and the well- preserved specimens by Clarkson et al. (2003) were regarded to fall within the range of local variants by the latter authors. It could be argued as unnecessary to recognise *S. alatus* and *S. angustus* as separate species, but we believe that the morphological differences between the two are consistent in Norway, Sweden and Wales (cf., Cope and Rushton, 1992, pl. 5, figs. e–h, for the latter). The separation of the two species is therefore maintained, though we do not follow Henningsmoen (1957, p. 211) who considered the difference to be of generic rank separating *Ctenopyge* and *Sphaerophthalmus*.

A few cranidia found in the lowermost part of the *Ctenopyge bisulcata* Zone with a more tapering glabella are tentatively also assigned to *S. alatus* (Fig. 5F).

Distribution: The species is widespread and very common. It is abundant in the *Ctenopyge tumida* Zone in association with *C. (Mesoctenopyge) tumida*, *C. (Ctenopyge) gracilis*, *Peltura minor*, *P. acutidens* and *Protopeltura planicauda*. A few cranidia were also found in the lowermost part of the *Ctenopyge bisulcata* Zone, associated with *Triangulopyge humilis, C. (Ctenopyge) bisulcata* and *Peltura scarabaeoides*.

***Sphaerophthalmus angustus* (Westergård, 1922).**
Figs. 4B and 6A–F

1922 *Ctenopyge flagellifera angusta* n.var. [partim] Westergård, p. 153, pl. 11, figs. 2–5, 8.
1957 *Ctenopyge (Eoctenopyge) angusta* Westergård – Henningsmoen, p. 187, pl. 5, pl. 19, figs. 11–16, 18.
1958 *Ctenopyge (Eoct.) angusta* Westergård – Henningsmoen, pp. 190, 192, pl. 3.
2003 non *Ctenopyge (Eoctenopyge) angusta* Westergård – Clarkson, Ahlgren & Taylor, pp. 1–27, pls. 1–8 (= *Sphaerophthalmus alatus*).

For further synonymy, see Henningsmoen (1957).

Lectotype: Selected by Henningsmoen (1957), a cranidium (SGU305) figured by Westergård (1922, pl. 11, fig. 3) from the *C. spectabilis* Zone, Andrarum, Scania, Sweden.

Diagnosis: A *Sphaerophthalmus* species with centres of palpebral lobes opposite S1. Glabellar furrows shallow. Palpebral area convex, elevated above palpebral lobes. Librigenal posterior lateral margin nearly straight and shorter than convex anterior lateral margin.

Description: Glabella tapering. S1 shallow and not joined across glabella. S2 short and weakly defined abaxially. Occipital furrow distinctly pronounced as pits abaxially and shallower medially. Centres of palpebral lobes located opposite S1. Eye ridges and the furrow on the palpebral lobes distinct. Anterior border as wide as (tr.), or slightly wider than occipital ring and moderately to strongly convex in frontal view. Preglabellar field lacking. Occipital ring bearing a short spine. Palpebral area, between half to three-fourths as wide as glabella at eye line and convex in frontal view. Posterior area as wide as (tr.) or slightly narrower than the occipital ring.

Librigena with round and slender spine, posterior lateral margin nearly straight and shorter than the convex, anterior margin.

Thorax of ten segments. Pleura, excluding spine, slightly narrower to about as wide as the axial ring in the anterior six segments. The five anteriormost pleural spines short, sixth to the eighth are elongated and directed backward. All pleural spines are round in cross section. A long spine

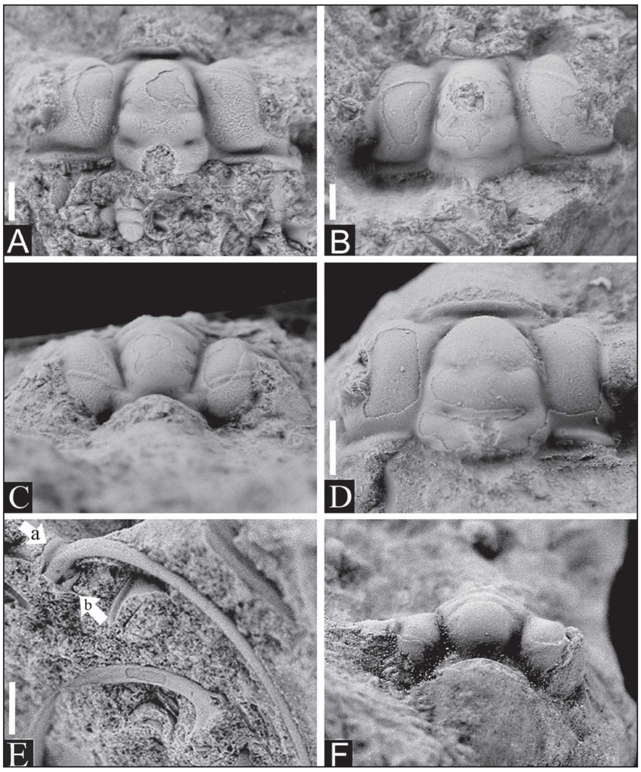

Figure 6. Sphaerophthalmus angustus *(Westergård, 1922). All scale bars: 1mm. (A) and (C) Dorsal and frontal view of granulated cranidium* (PMO223.412/1)*, length 3.5 mm. Slemmestad,* Ctenopyge spectabilis *Zone, -240 cm level. (B) Cranidium* (PMO223.412/2)*, length 3.7 mm. On the same slab as (A). (D) and (F) Dorsal and frontal view of cranidium* (PMO 223.413)*, length 3.3 mm. Note unusually wide glabella, tentatively assigned to the species. Professor Aschehougs Plass, Oslo,* C. tumida *Zone, lower part. (E) Oblique postero-lateral view of pygidium* (PMO 223.414)*, length 0.8 mm excl. spine, from the same limestone nodule as (D). Arrow a marks the connecting half ring, b the minute spine on posterior border.*

is presumably positioned on the tenth axial ring and the other rings seem to have nodes or short spines at least in the anterior part of the thorax.

Pygidium with very long spine on the single axial ring. One pygidium (Fig. 6E), thought to belong here, has a second pair of minute marginal spines.

Remarks: S. angustus is very similar to *S. alatus* and Clarkson et al. (2003) thoroughly described and figured specimens from Västergötland, Sweden as *Ctenopyge (E.) angusta* (=*S. alatus*, see above). Henningsmoen (1957, p. 187) recorded *S. angustus* from the *Ctenopyge spectabilis* Zone in Norway and Sweden, but erroneously stated that the lectotype figured by Westergård (1922, pl. 11, fig. 3) occurs together with *C. (Mesoctenopyge) tumida*. According to Westergård (1922, p. 21) the lectotype occurs together with *C. spectabilis*, but in a later range chart (Westergård, 1947, pp. 24–25), *S. angustus* is shown with *C. tumida* and species from older zones. Clarkson (1973, p. 752) reports *C. angusta* and *C.* cf. *tumida* to be associated. These specimens have a narrower posterior area, approaching *S. alatus* as an intermediate morph. A similar intermediate morph has been collected from the lower part of the *Ctenopyge tumida* Zone at Professor Aschehougs Plass in Oslo (Fig. 6D, F). These specimens show a strongly tapering glabella with shallow glabellar furrows and are here tentatively assigned to *S. angustus*.

Distribution: Slemmestad and Oslo (Tøyen and Professor Aschehougs Plass). *S. angustus* is common in the *Ctenopyge spectabilis* Zone where it is associated with the eponymous species. A morph approaching *S. alatus* is found in the lowermost part of the *Ctenopyge tumida* Zone together with *C. tumida* and *Peltura acutidens*.

***Sphaerophthalmus* arcus n. sp.**
Figs. 4C and 7A–H

Holotype: A nearly complete specimen (PMO 223.444) lacking librigenae, 5.2 mm long excluding spines, from a loose limestone concretion from the *Ctenopyge similis* Zone at the beach section, Nærsnes, Oslo Region.

Other material: One nearly complete specimen, which is an external mould, one librigena, immature pygidia and several thoracic segments on the same slab as the holotype (PMO 223.444), ten cranidia, one librigena and several sclerites of immature specimens (PMO 223.447).

Derivation of name: Arcus alludes to the highly convex anterior border when the specimen is seen in frontal view.

Diagnosis: A *Sphaerophthalmus* species with centres of palpebral lobes opposite S1. Glabellar furrows very shallow. Palpebral area weakly convex. Anterior margin strongly convex in frontal view. Librigenal posterior lateral margin weakly convex, slightly shorter than anterior convex margin. Thorax rapidly tapering backward from third segment. Pleural spines on eighth segment short, directed outwards in a crossing direction under the spines on seventh segment.

Description: Glabella tapering, S1 weak, S2 absent or very faint. Occipital furrow pit-like abaxially and shallow medially, composite and not connected with the axial furrows. Stout occipital spine present. Centres of palpebral lobes opposite S1. Palpebral furrows distinct in their full length. Posterior area as wide as to slightly wider (tr.) than occipital ring. Palpebral area about three-fourths as wide as glabella at eye-line. Raised anterior border as wide (tr.) or slightly wider than the occipital ring. Preglabellar field absent. Anterior border strongly convex in frontal view and palpebral area not highly inflated (Fig. 7E). Largest cranidium is approximately 3 mm long.

Librigena with long spine, round in cross- section. Posterior lateral margin weakly convex and only slightly shorter than lateral anterior convex margin. Subspherical

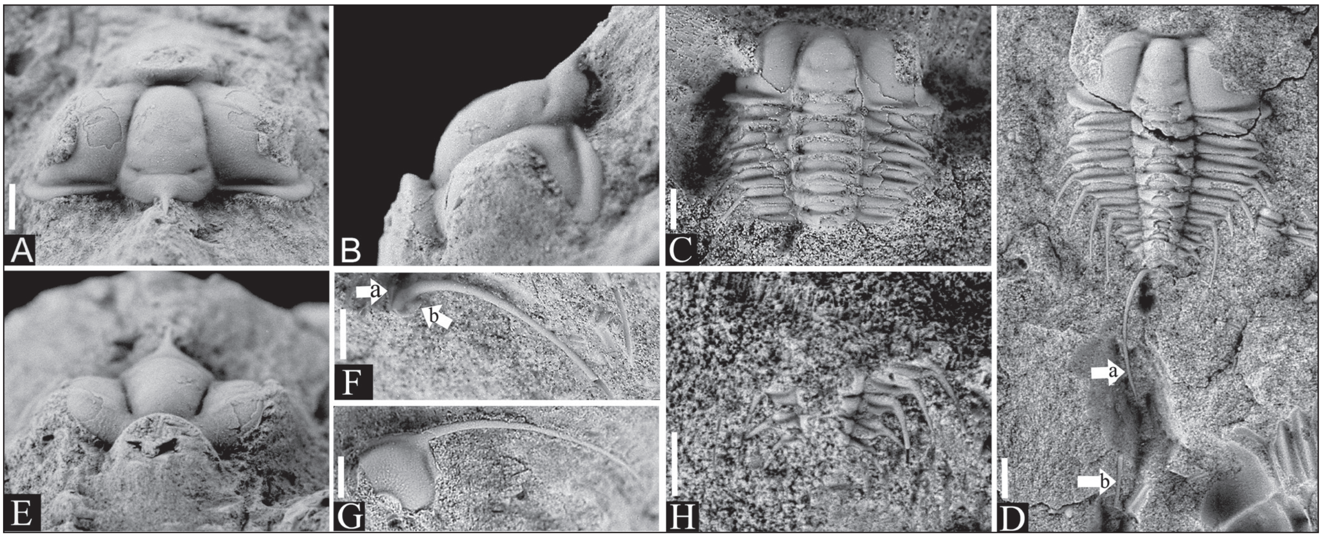

Figure 7. Sphaerophthalmus arcus *n. sp. All scale bars: 1mm. (A), (B) and (E) Dorsal, lateral and frontal view of cranidium* (PMO 223.445)*, length 3.4 mm excl. occipital spine. Note the strongly convex anterior margin in (E). (C) Cranidium with six attached thoracic segments* (PMO 223.446/1)*, length 5.2 mm. A shadow on anterior part of glabella makes the frontal lobe appear shorter. (D) Holotype* (PMO 223.444)*. Nearly complete specimen lacking free cheeks, 5.2 mm long excl. spines. Arrow a marks the caudal spine, b the posterior portion of the axial spine on the tenth segment, which was broken off during preparation. An external mould of a second nearly complete specimen is to be found on the same slab. (F) Pygidium* (PMO 223.446/2)*, length 0.8 mm excl. caudal spine. Pleural spine broken off. Arrow a marks the connecting half ring, b the posterior margin. On the same slab as (C). (G) Librigena* (PMO 223.447)*, length 2.5 mm excl. spine. (H) Fifth to ninth thoracic segments* (PMO 223.448)*. Note the crossing of the elongated seventh and the short eighth pleural spines. All specimens from the* Ctenopyge simils *Zone at Nærsnes.*

eye positioned at midlength or just posterior of midlength adjacent to the base of the genal spine. Very shallow caeca visible near the eye socle.

Thorax of 10 segments, tapering backwards from the third segment, axis tapers gradually backwards from the third ring. Pleural regions, excluding spines, about as wide as axial ring in the anterior five segments. Anterior three segments with short spines. The fourth to seventh pleural spines are longer, the seventh being very long and directed backwards. The eighth to tenth segments have short spines directed outward. As viewed, the eighth pleural segment with spine is directed laterally and crossed by the elongated spine of the seventh segment (Fig. 7D, H). A long and slender spine as long as the thorax or longer occurs on the tenth axial ring, the other rings have short spines.

Adult pygidia triangular in outline with only one axial ring with a long, backward curved spine and an end lobe. This spine is more robust than the thoracic axial spines with a base occupying the whole length (sag.) of the ring. Pleurae very narrow (tr.) with one pair of marginal spines. An upturned border present posteriorly.

Remarks: S. arcus n. sp. is closely related to *S. flagellifer*, but is distinguished by the more posteriorly positioned palpebral lobes and a shorter and straighter posterior lateral margin on the librigena. The species occurs with *S. modestus*, from which it is easily distinguished by the shape of the spines and the position of the ocular lobes. *S. arcus* n. sp. differs from all other species in the highly convex anterior border and in the way the pleural spines on the seventh and eighth segments cross.

Distribution: Nærsnes, Slemmestad, Oslo (Tøyen and Professor Aschehougs Plass) and Sønstebygda, Modum. *S. arcus* is common in the *Ctenopyge similis* Zone and occurs together with *S. modestus, Ctenopyge (Mesoctenopyge) similis, C. (M.) erecta, Parabolina mobergi, Protopeltura bidentata* and *P. planicauda*.

***Sphaerophthalmus drytonensis* (Cobbold, 1934).**
Figs. 4D and 8A–D

1934 *Ctenopyge drytonensis* n. sp. Cobbold, p. 352, pl. 45, figs. 9, 15a, 19.
1957 *Ctenopyge (Eoctenopyge)* n. subgen. *drytonensis* Cobbold [partim] – Henningsmoen, p. 188, pl. 5, pl. 18, figs. 5–9 and 11–14 [fig. 10 = *S. flagellifer*].
1958 *Ctenopyge (Eoct.) drytonensis* Cobbold – Henningsmoen, pp. 191, 192, pl. 3.
2002 *Ctenopyge (Eoctenopyge) drytonensis* Cobbold 1934 – Schöning, p. 83, figs. 38–40.
2004 *Ctenopyge (Eoctenopyge) drytonensis* Cobbold 1933 – Mischnik, p. 112, pl. 3, fig. 5.

For further synonymy, see Henningsmoen (1957).

Holotype: A cranidium figured by Cobbold (1934, pl. 45, fig. 9) from a loose block in Dryton Brook, Rushton area, Shropshire, England. The holotype was refigured by Henningsmoen (1957, pl. 18, fig. 8).

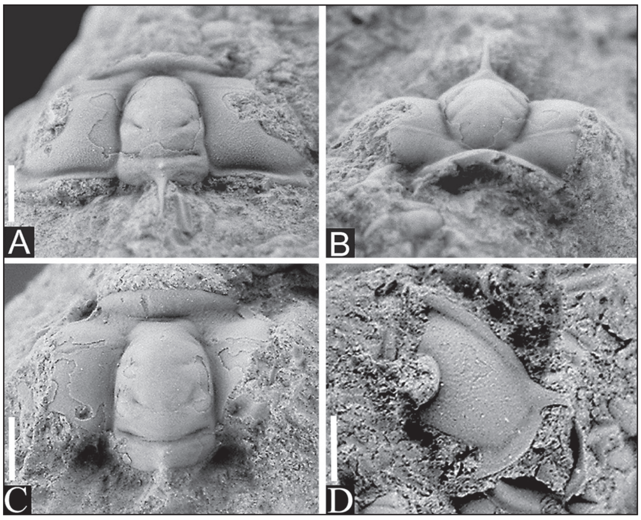

Figure 8. Sphaerophthalmus drytonensis *(Cobbold, 1934). All scale bars: 1mm.* ***(A)*** *and* ***(B)*** *Dorsal and frontal view of cranidium* (PMO 224.150)*, length 3 mm excl. spine. Note moderately convex frontal margin in (B).* ***(C)*** *Fragmentary cranidium* (PMO 223.449)*, length 3.3 mm.* ***(D)*** *Librigena* (PMO 223.415)*, length 2.9 mm. All specimens from the* Sphaerophthalmus postcurrens *Zone at Hennung, Gran.*

Diagnosis: A *Sphaerophthalmus* species with centres of palpebral lobes opposite L2. Glabella with three pairs of furrows, S1 and S2 geniculate. Palpebral area gently convex. Anterior border distinctly wider (tr.) than occipital ring, moderately convex in frontal view. Librigena with moderately long spine. Inner spine angle more lateral than outer spine angle.

Description: Glabella tapering, with three pairs of furrows not expressed medially. S1 and S2 geniculate, the former bigeniculate in larger specimens. S3 rather distinct in larger specimens, located at adaxial end of eye ridge. Occipital furrow transglabellar. A small node is present in front of a long and straight occipital spine. Centres of palpebral lobes opposite L2. Anterior border sagittally long, distinctly wider (tr.) than occipital ring and moderately convex in frontal view (Fig. 8B). Preglabellar field absent, but in some specimens the anterior border furrow is wide (sag.). Posterior area as wide as, or slightly wider than occipital ring. Palpebral area weakly convex in frontal view. The largest cranidium is about 4 mm in length.

Librigena with round and very slender spine, proportionally shorter than in other species. Posterior lateral margin strongly convex, anterior border longer and less convex with shallow border furrow adjacent to spine. Inner spine angle more laterally placed than outer spine angle, asymmetric to the base of the spine.

Hypostome, thorax and pygidium not known.

Remarks: Cobbold (1934) described the species from Shropshire, England, along with *Sphaerophthalmus*? *parabola, Ctenopyge flagellifera, Ctenopyge flagellifera angusta* and *Eurycare angustatum*. Henningsmoen (1957, p. 189) considered all specimens to represent *C. drytonensis* and refigured these in addition to the holotype. Regrettably, the photographs are small, poorly focused and several of the diagnostic features are not visible. Some of the specimens from Shropshire may actually belong to *S. postcurrens*, which is associated with *S. drytonensis* in the Oslo Region. The specimen figured by Henningsmoen (1957, pl. 18, fig. 7) shows a long (sag.) anterior border, which corresponds well with the material of *S. drytonensis* we have available. The anterior border of the holotype (Henningsmoen, 1957, pl. 18, fig. 8) is missing, but the lateral areas present indicate that the border was long (sag.). *S. drytonensis* is easily separated from *S. postcurrens* in the narrower and more tapering glabella and the anterior border is longer (sag.) and more convex in frontal view. Further, S1 and S2 are more distinctly geniculate and the preglabellar field is absent. The librigena of the two are very different.

Distribution: Nærsnes, Gran (Hennung) and Hamar area (Løten and Stange). The species occurs in the *Sphaerophthalmus postcurrens* Zone together with the zonal fossil and *Protopeltura praecursor*.

Sphaerophthalmus flagellifer **Angelin, 1854.**
Figs. 4E and 9A–H

1854 *Sphaerophthalmus flagellifer* n. sp. Angelin, p. 49, pl. 26, fig. 7.
1957 *Ctenopyge (Eoctenopyge)* n. subgen. *flagellifera* (Angelin) – Henningsmoen, p. 189, pl. 2, fig. 17, pl. 5, pl. 18, figs. 1–4.
1958 *Ctenopyge (Eoct.) flagellifera* (Angelin) – Henningsmoen, pp. 191, 192, pl. 3.
2002 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) – Schöning, figs. 33, 35, 36.
2004 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) – Mischnik, pp. 112–113, pl. 3, fig. 6.
2005 *Ctenopyge (Eoctenopyge) flagellifera* (Angelin 1854) – Buchholz, pl. 3, fig. 10.

For further synonymy, see Henningsmoen (1957).

Neotype: In the absence of Angelin's type specimen, considered lost, Henningsmoen (1957) selected a neotype (SGU5510) from the type material of Linnarsson (1880, pl. 1, fig. 14) from the same locality at Andrarum, Scania, Sweden. This librigena was also figured by Westergård (1922, pl.10, fig. 20).

Diagnosis: A *Sphaerophthalmus* species with centres of palpebral lobes opposite L2. S1 pit-like, S2 shallow to absent. Palpebral area horizontal to gently downward sloping. Librigena with convex posterior lateral border longer than anterior lateral border in large specimens.

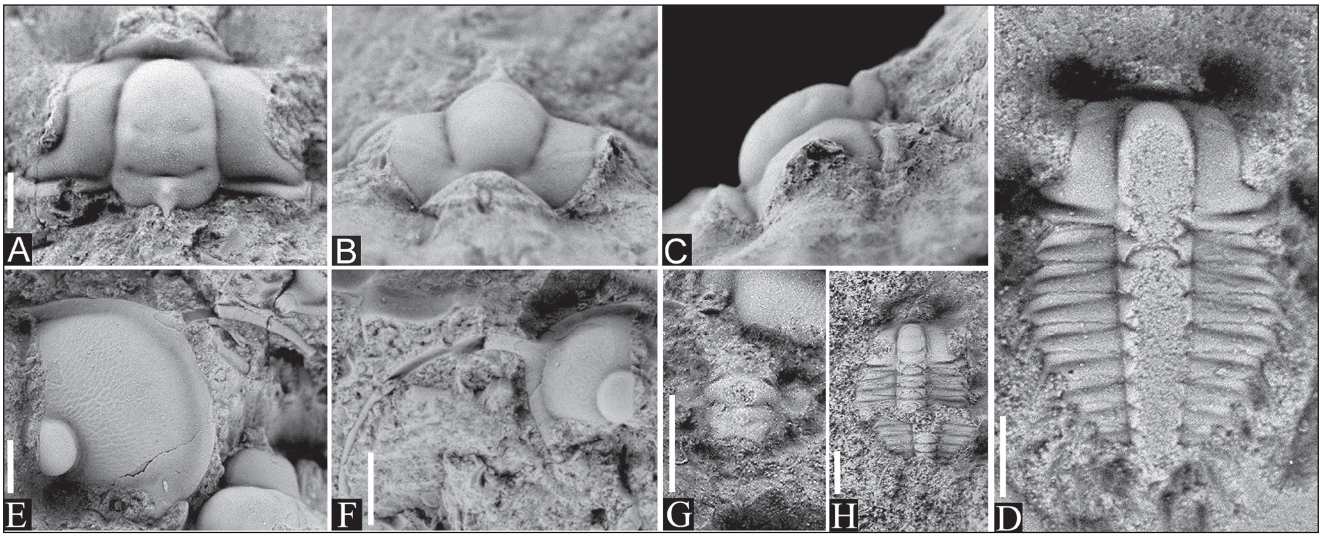

Figure 9. Sphaerophthalmus flagellifer *Angelin, 1854. All scale bars: 1mm.* ***(A), (B)*** *and* ***(C)*** *Dorsal, frontal and lateral views of cranidium* (PMO 223.416), *length 3.1 mm. Note laterally downsloping interocular cheeks in (B).* ***(D)*** *Small cranidium with eight attached segments* (PMO 223.417), *length 4.3 mm.* ***(E)*** *Large librigena (PMO 223.418), length 5.5 mm, showing distinct caeca.* ***(F)*** *Small librigena* (PMO 223.419/1), *length 2.9 mm with the posterior margin slightly shorter than anterior margin.* ***(G)*** *Dorsal view of pygidium* (PMO 223.419/2), *length 0.8 mm, possessing two axial rings with a base of a broken spine on anterior ring and a node on the posterior. On the same slab as (F).* ***(H)*** *Small cranidium with seven attached thoracic segments (PMO 223.420), length 2.5 mm. All specimens from the* Sphaerophthalmus flagellifer *Zone at Nærsnes, Røyken.*

Description: Glabella of large cranidia, weakly tapered, parallel sided in juveniles (Fig. 9D, H). S1 expressed as abaxial pits detached from axial furrow, S2 faint to absent. Occipital furrow transglabellar. Centres of palpebral lobes situated opposite L2. In large specimens, the anterior border is wider (tr.) than occipital ring, long medially (sag.) and strongly convex in frontal view. Palpebral area horizontal or sloping downwards from axial furrows (Fig. 9B). Preglabellar area absent. A small node is present in front of a short, straight occipital spine.

Librigena in large specimens with a round spine positioned far forward (Fig. 9E). Posterior lateral margin very long and convex, anterior margin shorter and convex. Younger individuals with proportionally longer and coarser spines situated more posteriorly (Fig. 9F). Well-preserved specimens show distinct caeca, strongest near the eye.

Thorax of 10 segments, widest (tr.) at third segment, tapering rapidly backwards. The pleural region, excluding spine, as wide as or wider than axial ring. The fifth to eighth segments with elongated, slender spines, the seventh pair being the longest. An axial spine is present on all thoracic segments, the posterior-most long and slender.

Adult pygidia with one to two axial rings with a long and curved spine on anterior ring. Spine more than six times as long as the pygidium. An upturned border is present posteriorly. Pleura half as wide (tr.) as axis with one pair of marginal spines.

Remarks: Henningsmoen (1957, p. 190) emphasised the long and convex posterior lateral margin of the librigena as the most characteristic feature of the species. The posterior margin is longer than the anterior margin, which causes the cheek spine to be based far forwards. Small specimens have a shorter posterior lateral margin (Fig. 9F). The posterior lateral margin becomes longer only in large specimens with cranidia exceeding 4 mm in length, indicating a change of form in the late holaspid stage. The reconstruction (Fig. 4E) was drawn from small individuals with cranidia shorter than 3 mm. Henningsmoen's figures of the Norwegian material are restricted to only one cranidium with 8 attached thoracic segments and a librigena (Henningsmoen, 1957, pl. 18, figs. 1, 3). It is difficult to detect diagnostic features in the figured cranidium, but the centres of the palpebral lobes are situated opposite L2 and not S2 as stated in his diagnosis (Henningsmoen, 1957, p.190). This is confirmed by the material figured by Westergård (1922 pl.10, figs. 19, 21a, pl. 11, fig. 1) and Poulsen (1923, pl. 1, figs. 12, 13).

S. flagellifer is easily distinguished from the associated *S. modestus* by the presence of an occipital spine and by the more slender pleural spines that are round in cross section, but flattened in *S. modestus*. The librigenae of the two species are distinctly different. *S. flagellifer* is readily distinguished from both *S. modestus* and *S. arcus* n. sp. by the more anteriorly situated centres of the palpebral lobes and from *S. drytonensis* by the sagittally shorter anterior border. S1 in *S. drytonensis* is distinctly geniculate.

Distribution: S. flagellifer is very common in the *Sphaerophthalmus flagellifer* Zone and the lowermost part of the overlying *Ctenopyge similis* Zone at Nærsnes, Slemmestad, Eiker–Sandsvær and Oslo (Gamlebyen) and occurs together with *S. modestus, C. (Mesoctenopyge) erecta* and *Protopeltura praecursor*.

***Sphaerophthalmus modestus* (Henningsmoen, 1957).**
Figs. 4F and 10A–H

1957 *Ctenopyge (Eoctenopyge)* n. subgen. *modesta* n. sp. Henningsmoen, p. 191, pl. 5, pl. 19, figs. 1–10.
1958 *Ctenopyge (Eoct.) modesta* Henningsmoen – Henningsmoen, pp. 190, 192, pl. 3.
1973 *Ctenopyge (Eoctenopyge) modesta* Henningsmoen – Clarkson, p. 751, text fig. 5. a–d, pl. 94, fig. 5.

For further synonymy, see Henningsmoen (1957).

Holotype: PMO 29497a, free cheek figured by Henningsmoen (1957, pl. 19, fig. 2) from the *Ctenopyge similis* Zone at Slemmestad in Røyken.

Diagnosis: A *Sphaerophthalmus* species with long (sag.) and narrow (tr.) palpebral lobes, centre opposite S1. Glabella parallel-sided, S1 shallow, S2 very shallow or absent. Palpebral area gently raised towards palpebral lobes. Librigena with long and strongly convex anterior lateral border, posterior lateral border short and straight. Thorax with short and flattened pleural spines, macropleural spines on seventh segment.

Description: Glabella parallel-sided and well raised above the level of the cheeks. S1 deepest abaxially, usually not extended to axial furrows and not transglabellar, but shallow medially. S2 weak or absent. Occipital furrow transglabellar, but not connected with axial furrows. Occipital ring lacking spine, but two nodes closely spaced medially can form a keel-like node. In rare, large specimens the posterior node becomes a very short spine. In frontal view (Fig. 10B) the palpebral area is elevated towards the palpebral lobes. Posterior area commonly wider than the occipital ring. Preglabellar field absent. Centres of palpebral lobe placed opposite S1. Palpebral lobes long and transversally narrow with palpebral furrow distinct in full length (Fig. 10A). Raised anterior border wider (tr.) than the occipital ring. The anterior margin is strongly convex in frontal view. Largest cranidia are approximately 3 mm long.

Librigena with long, slightly flattened spine. Posterior lateral margin short and straight, anterior lateral margin is characteristically long and strongly convex (Fig. 10C). Eyes are large and spherical.

Thorax of 10 segments, the third being the widest (tr.). Pleural spines flattened, broad and short, except the long and slender spines on the seventh segment. The tenth segment has a long, almost straight axial spine; other segments have only a small node.

Adult pygidia are triangular in outline with one axial ring and an end lobe. The long caudal spine is placed on the single axial ring. Base of caudal spine occupies the whole sagittal length of the ring. An upturned border is present posterior to paired marginal spines. The pleural region is half as wide as the axis.

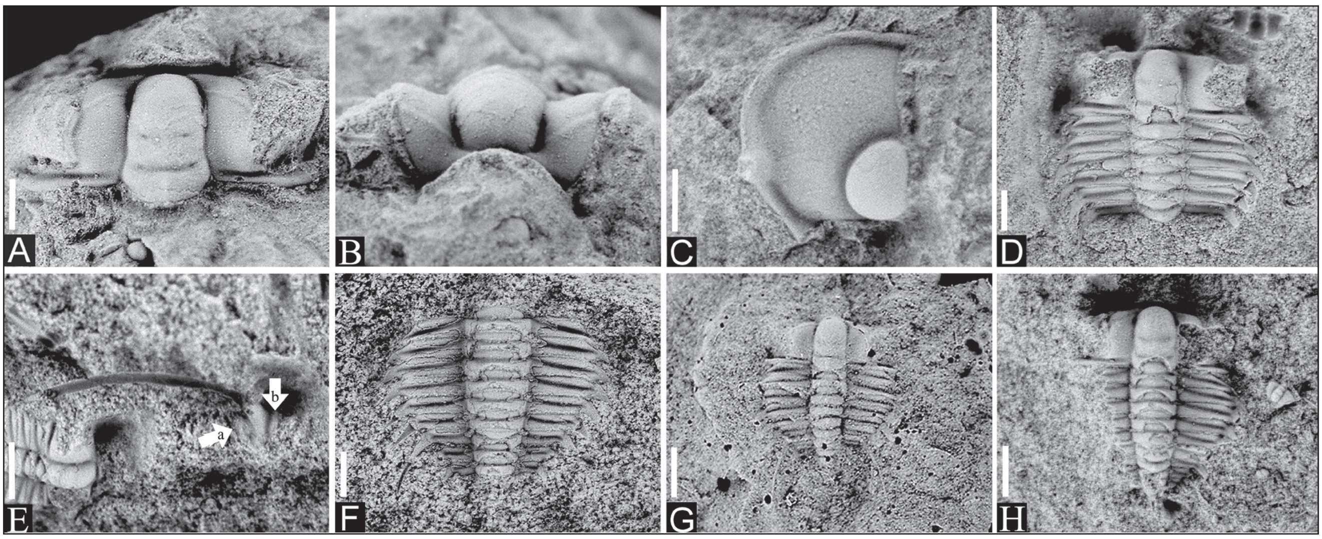

Figure 10. Sphaerophthalmus modestus *(Henningsmoen, 1957). All scale bars: 1mm. (A) and (B) Dorsal and frontal view of cranidium* (PMO 223.421), *length 2.8 mm. Professor Aschehougs Plass, Oslo. (C) Librigena* (PMO 223.422) *with spine broken off. Length 3.2 mm. Nærsnes. (D) Cranidium with six attached segments* (PMO 223.423), *length 3.6 mm. Note wide and flattened pleural spines. Nærsnes. (E) Lateral view of pygidium* (PMO 223.424), *length 0.7 mm excl. spine. Arrow a marks the posterior margin, b the connecting half ring. Nærsnes. (F) Thorax* (PMO 223.425) *lacking the tenth segment, length 3.8 mm. Note elongated spine on the seventh segment. Nærsnes. (G) Latex cast of cranidium with 9 attached thoracic segments* (PMO 223.426), *length 3.2 mm. Nærsnes. (H) Fragmentary cranidium with ten attached thoracic segments* (PMO 223.427), *length 3.7 mm. Nærsnes. All specimens from the* Ctenopyge similis *Zone.*

Remarks: Henningsmoen (1957, p. 191) based this species on a large number of isolated parts but no pygidia. The present new material includes several cranidia with up to 10 attached thoracic segments and detached parts of the thorax with pygidium. The new material agrees well with specimens figured by Henningsmoen (1957, pl. 19, figs. 1–10). In his description, Henningsmoen (1957, p. 192) emphasised the very distinct occipital furrow, but this is no more distinct than in any other *Sphaerophthalmus* species and is not a diagnostic feature. He also mentioned that the anterior border of the cranidium is concave in dorsal view, but when the shield is oriented in assumed life position, it appears transversally straight (Fig. 10A). This is in contrast to the cranidia figured by Henningsmoen (1957, pl. 19, figs. 1, 6) which are tilted to a very oblique frontal view and the anterior furrow thus appears convex. The cranidium figured by Westergård (1922, pl.11, fig. 6) as *S. angustus* and transferred to *S. modestus* by Henningsmoen (1957), has a short preglabellar field and the centres of the palpebral lobes are situated more anteriorly, which are not features of *S. modestus*. This specimen may therefore belong to another species, probably a small *S. postcurrens*.

S. modestus differs from all other species of the genus by the lack of axial spines on all segments with the exception of the tenth and the pygidium. Centres of the long palpebral lobes are situated more posteriorly than in most other species of the genus, making the posterolateral projection sagittally very short. The anterior lateral margin of the librigena of *S. modestus* is strongly convex and the posterior lateral margin is shorter and straighter than in any other species of the genus.

Distribution: The species is common in the *Ctenopyge similis* Zone at Nærsnes, Slemmestad, Sønstebygda in Modum and Oslo (Tøyen, Nedre Slottsgate, Professor Aschehougs plass) and is associated with *S. arcus* n. sp., *C. (M.) similis, C. (M.) erecta, Parabolina mobergi, Protopeltura bidentata* and *P. planicauda*.

***Sphaerophthalmus postcurrens* (Westergård, 1944).**
Figs. 4G, I and 11A–G

1944 *Ctenopyge neglecta postcurrens* n. var. Westergård, p. 42, pl. 2, figs. 15–17.

1957 *Ctenopyge (Eoctenopyge)* n. subgen. *postcurrens* Westergård – Henningsmoen, p. 193, pl. 5, pl. 17, figs. 8–10.

1958 *Ctenopyge (Eoct.) postcurrens* Westergård – Henningsmoen, pp. 191, 192, pl. 3.

2004 *Ctenopyge (Eoctenopyge) postcurrens* Westergård 1944 – Mischnik, pp. 111, 112, pl. 3, fig. 4.

For further synonymy, see Henningsmoen (1957).

Holotype: A cranidium, SGU4250, figured by Westergård (1944, pl. 2, fig. 15) from a drillcore at Andrarum, Scania, Sweden.

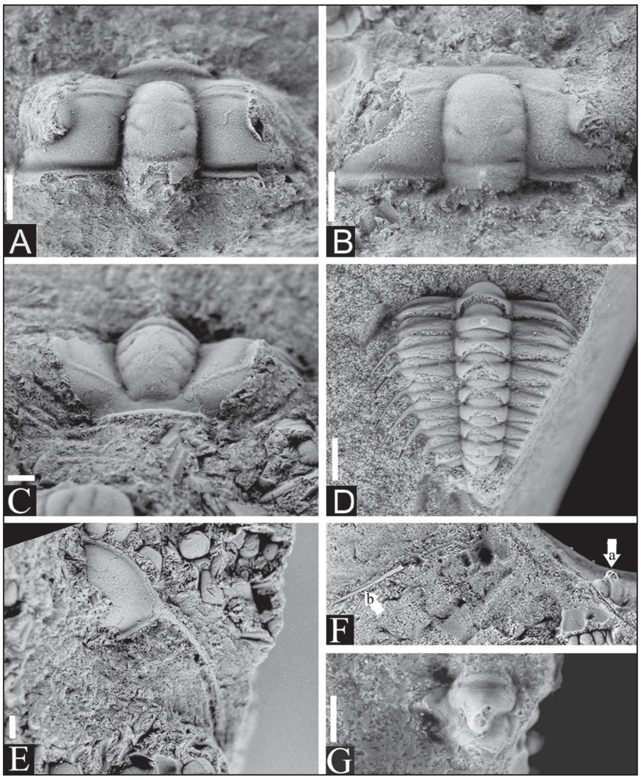

Figure 11. Sphaerophthalmus postcurrens *(Westergård, 1944). All scale bars: 1mm. (A) Cranidium* (PMO 223.428)*, length 3.5 mm. Note nearly horizontal eye ridges. Løten. (B) Cranidium* (PMO 223.429)*, length 2.9 mm. Note oblique eye ridges. Nærsnes. (C) Frontal view of fragmentary cranidium* (PMO 223.430)*, length 5.3 mm. Note moderately convex frontal margin. Nærsnes. (D) Thorax* (PMO 223.431)*, length 5.4 mm with fragmentary tenth segment slightly disarticulated. Løten. (E) Librigena* (PMO 223.432)*, length 4.2 mm excl. spine. Hennung, Gran. (F) and (G) Lateral and dorsal view of pygidium* (PMO 223.433)*, length 1.6 mm excl. spine. Arrow a marks the pygidium with the base of the broken caudal spine, b marks the posterior end of a long caudal spine broken off during preparation. Løten. All specimens from the* Sphaerophthalmus postcurrens *Zone.*

Diagnosis: A *Sphaerophthalmus* species with centres of palpebral lobes opposite L2. Three pairs of glabellar furrows, S3 shallow and S1 geniculate. Short preglabellar field usually developed. Posterior area wider than occipital ring. Anterior border weakly convex in frontal view. Librigena with straight posterior lateral margin, markedly shorter than convex anterior lateral margin. Thorax tapering, lacking elongated pleural spines.

Description: The following is the first description to be given. Largest cranidia approximately 5 mm long (sag.). Glabella slightly tapering, S1 and S2 distinct and in larger specimens S3 occurs at adaxial end of the eye ridge. S1 is not transglabellar, distinctly geniculate and connected to the axial furrow. Eye ridges slightly oblique and centres of the palpebral lobes are opposite L2. Occipital furrow distinct and transglabellar. A small node occurs in front of a short occipital spine. Anterior border slightly wider (tr.) than occipital ring and characteristically weakly convex in frontal view (Fig. 11C). A short preglabellar field is usually present, but may be absent in rare specimens. In frontal view the palpebral area raises from the axial furrow in a sinuous line to the palpebral furrow. The posterior area is wider than the occipital ring.

Librigena with moderately long spine, rounded in cross section. Posterior lateral margin straight, anterior lateral margin markedly longer and convex.

Thorax of at least ten thoracic segments, but exact number not known. The ninth segment with a long axial spine, probably also the tenth. Pleura, excluding spine, about as wide (tr.) as axial ring. The two anterior pleural spines are slightly shorter than spines on the third to the ninth segments, which are approximately equal in length. No elongated pleural spines are present. All spines are round in cross section.

Pygidium triangular in outline with two rachial rings and an end lobe, the latter fused to posterior ring. Anterior ring with very long and curved spine, more than ten times the length of the pygidium. One pair of marginal spines and pleural furrows present. Pleura, excluding marginal spines, is one-fourth the width of the axis. The largest pygidium is 1.4 mm long including the connecting half ring.

Remarks: Westergård (1944, pl. 2, figs. 15–17) described this taxon as a subspecies of *Ctenopyge neglecta* whilst Henningsmoen (1957, p.193) assigned *neglecta* to *Leptoplastus* and *postcurrens* to *Ctenopyge (Eoctenopyge)*. The pygidium of *L. neglectus* figured by Henningsmoen (1957, p. 170, pl. 17 fig. 1) clearly belongs there by the relative size, lack of long caudal spine, the wide (tr.) pleural fields with three pleural furrows and marginal spines. We believe *postcurrens* is best assigned to *Sphaerophthalmus*. Westergård's material lacks a preglabellar field, according to Henningsmoen to be within intraspecific variation. The specimen figured by Westergård (1922, pl. 10, fig. 18) agrees well with our material of *S. postcurrens*, which seems to be quite variable even among specimens on the same slab. Henningsmoen (1957, p. 193) wrongly stated that the palpebral area is as wide as or even wider than the glabella, but his only figured cranidium (1957, pl. 17, fig. 9) has a palpebral area narrower than the glabella, a feature confirmed by material figured by Westergård (1944, pl. 2) and that described herein (Fig. 11A, B).

S. postcurrens differs from other species of the genus in the less convex anterior margin and by the presence of a preglabellar field. The pleural spines are approximately of even length and the thorax is proportionally larger. These features may indicate that *S. postcurrens* is an ancestor of the *Ctenopyge* lineage, but we assign it here to *Sphaerophthalmus*. *S. postcurrens* is readily distinguished from *Leptoplastus neglectus* by having the palpebral lobe more posterior and by the pleura with slender spines as wide as the axial ring. In *L. neglectus* the pleura has short spines and is wider than the axial ring. The pygidia are widely different.

Distribution: The *Sphaerophthalmus postcurrens* Zone is tectonically distorted with poorly preserved trilobites in the new Slemmestad section, but *S. postcurrens* is abundant at Nærsnes, Slemmestad, Gran (Hennung) and Hamar area (Løten and Stange) and occurs with *S. drytonensis* and *Protopeltura praecursor*.

Genus **Triangulopyge** *n. gen.*

Type species: Olenus humilis Phillips, 1848, from the White Leaved Oak Shales at White Leaved Oak, Malvern, Great Britain.

Derivation of name: Referring to the triangular shape of the pygidium.

Diagnosis: Exoskeleton transversally strongly convex. Glabella slightly tapering, distinct occipital furrow and transglabellar S1. S2 very short, shallow to obsolete. Anterior border flattened, distinctly narrower (tr.) than occipital ring. Centres of very narrow palpebral lobes opposite L1 to S1. Palpebral area very convex, elevated above palpebral lobes. Preocular area long (sag.) and projecting anterior tip of glabella at a transverse line. Posterolateral projection strongly flexed ventrally. Librigena with short to moderately long, curved spine, rounded in cross section. Eye socket close to the posterior border. Thoracic pleura almost as wide as axis, rounded distally. Pygidium triangular, with narrow border lacking spines, axis with two to three rings and an end lobe, pleura with two to three pleural furrows.

Remarks: This new genus is established for three species: *T. humilis* (Phillips, 1848), *T. major* (Lake, 1913) and *T. majusculus* (Linnarsson, 1880). These form a small group distinct from *Sphaerophthalmus* to which they were earlier assigned, based on a misidentification of the type species (see discussion under *Sphaerophthalmus*). All above-mentioned species have an extremely convex (tr.) dorsal shield, the eyes are far back and the distal ends of the thoracic pleurae are rounded. The pygidium lacks spines, the pleural field is broader (tr.) and the axis has a larger number of rings than in *Sphaerophthalmus*. In pygidia of *Triangulopyge* n. gen., the number of axial rings increases during ontogeny (Fig. 13H, I), the opposite being the case in *Sphaerophthalmus* (see Westergård, 1922, pl.13, figs. 26–29 and 33–35; Clarkson et al., 2003; Ahlberg et al., 2005, fig. 2).

In *Triangulopyge*, the cranidium is widest (tr.) in front of the narrow palpebral lobes, resulting in a constriction at the eye line in dorsal view. In *Sphaerophthalmus* the palpebral lobes are relatively wider. The anterior cephalic border in *Triangulopyge* is narrow (tr.), flattened and sloping downward whilst it is upturned in

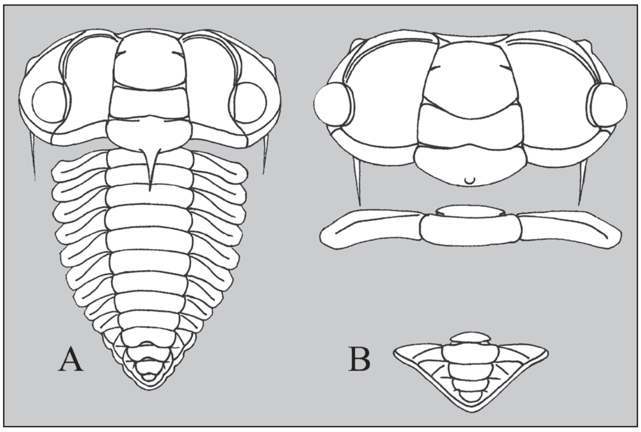

***Figure 12.** Reconstructions of* Triangulopyge *species. (A)* T. humilis *(Phillips, 1848). (B)* T. majusculus *(Linnarsson, 1880).*

Sphaerophthalmus. Both Rushton (1968, text fig. 2) and Clarkson (1973, text figs. 8a–d) provided reconstructions of *T. humilis* showing the high convexity of the cephalon and the ventrally directed genal spines, a situation we interpret from the study of new material of *T. majusculus* (Figs. 12B, 14O, P) as well.

The overall shape of the body seems well adapted to a pelagic mode of life (see Fortey, 1974; Bruton & Høyberget, 2006).

***Triangulopyge humilis* (Phillips, 1848).**
Figs. 12A and 13A–J

1848 *Olenus humilis* Phillips, p. 55, figs. 4–6, p. 347.
1957 *Sphaerophthalmus humilis* (Phillips) – Henningsmoen, pp. 215–217, pl.5 and pl. 22, figs. 7, 11–15.
1958 *Sphaerophthalmus humilis* (Phillips) – Henningsmoen, pp. 190, 192, pl. 3.
1968 *Sphaerophthalmus humilis* (Phillips) – Rushton, p. 415, text figs. 2 and 3a, pl. 78, figs. 11–15.
1973 *Sphaerophthalmus humilis* (Phillips) – Clarkson, pp. 754–756, text fig. 8a–d, pl. 94, fig. 6.
2002 *Sphaerophthalmus majusculus* Linnarsson 1880 – Schöning, fig. 51 (fig. 50 = *S. alatus*).
2005 *Sphaerophthalmus humilis* (Phillips, 1848) – Ahlberg et al., pp. 431, 433, fig. 2I–K.
2005 *Sphaerophthalmus* sp. C, – Ahlberg et al., p. 434, fig. 3C.

For a more complete synonymy list on early works, see Henningsmoen (1957).

Lectotype: Here selected, a cranidium, Ox A287a, from the Phillips collection, figured by Rushton (1968, pl. 78, fig. 13) from the White Leaved Oak Shale at White Leaved Oak, Malvern, England.

Diagnosis: Triangulopyge species with centres of the palpebral lobes opposite L1. S2 very short, shallow to obsolete. Palpebral area less than half the width of glabella at eye line. Posterior area half as wide (tr.) as occipital ring. Librigena with posterior lateral margin long and convex, anterior lateral margin shorter and convex. Thoracic pleurae without spines. Pygidium with up to three axial rings and an end lobe, pleura markedly narrower than axis.

Description: Little can be added to the detailed description of Lake (1913, p. 74) who considered the species a junior synonym of *Sphaerophthalmus alatus*. We note that well-preserved cranidia possess a very fine granulation and an occipital spine of variable length. Pygidia vary in width (tr.) with pleura proportionately narrow (tr.) during growth (Fig. 13H, I). Two shallow pleural furrows are present. The axial rings of the pygidium show a longitudinal constriction at the sagittal line. In the new material studied herein, largest cranidium is 3.5 mm long (Fig. 13C, G), largest pygidium is 2.3 mm long (Fig. 13I).

Remarks: Until Henningsmoen (1957, pp. 215–217) revived the species, all previous authors considered it a junior synonym of *Sphaerophthalmus alatus*. The type material of *Triangulopyge major* from Lake's collection is rather poorly preserved and flattened in tectonically distorted shale (Rushton, 1968). As pointed out by Rushton (1968, p. 416), the general features of the cranidium in *T. major* are very similar to *T. humilis*; the main differences being an occipital spine present in *T. major*, which also has a more rounded and wider pygidium. The width of the pygidium in *T. humilis* is a variable feature, so that it cannot be ruled out that *T. major* and *T. humilis* are conspecific. Other distinguishing features are the more anterior position of the eye lobes and the slightly wider palpebral area in *T. major*, characters that may be developed during growth since *T. major* attains a larger size. The diagnosis of *T. major* given by Rushton (1968, p. 416) includes mention of thoracic pleural spines, though none of the figures show these and the author says that they are generally not preserved.

Rushton (1968, p. 419) comments on the two cranidia of *T. major* figured by Henningsmoen (1957, pl. 22, figs. 7, 15) from Norway and says that the posterior area is too wide and the occipital spines are longer than those found in *T. humilis*. We regard these differences to be within the range of intraspecific variation of *T. humilis*, though we have not studied the British material to confirm this.

Henningsmoen (1957, p. 217) reported that no hypostoma have been found in situ, but there should be no doubt in assigning the commonly occurring very small and narrow hypostoma to *T. humilis* (Henningsmoen, 1957, pl. 22, fig. 11).

Distribution: T. humilis is widespread and very common in the *Ctenopyge bisulcata* and *Ctenopyge linnarssoni* zones, associated with *T. majusculus*, *S. alatus*, *C. bisulcata, C. linnarssoni, C. fletcheri, C. pecten* and *P. scarabaeoides.*

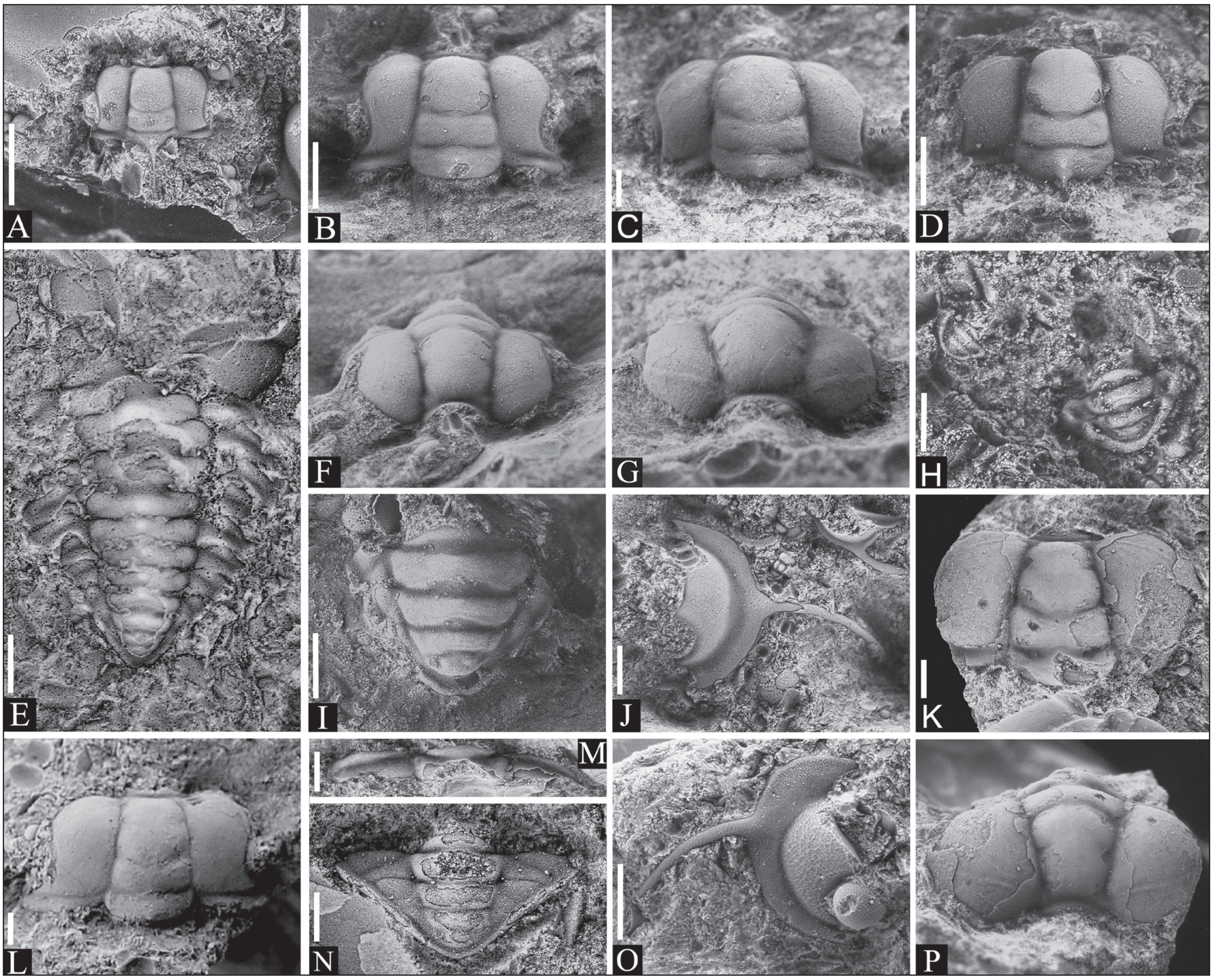

Figure 13. *(A–J)* Triangulopyge humilis *(Phillips, 1848), (K–P)* Triangulopyge majusculus *(Linnarsson, 1880). All scale bars: 1mm. (A) Small cranidium* (PMO 223.434)*, length 1 mm excl. long occipital spine. Akersgata, Oslo,* Ctenopyge bisulcata *or* C. linnarssoni *Zone. (B) and (F) Dorsal and frontal view of cranidium* (PMO 223.435)*, length 2 mm. Slemmestad,* C. bisulcata *Zone. (C) and (G) Dorsal and frontal view of large cranidium* (PMO 223.436)*, length 3.1 mm excl. occipital spine. Slemmestad,* C. bisulcata *Zone, -25 cm level. (D) Dorsal view of cranidium* (PMO 223.437*), length 2 mm with short occipital spine. Akersgata, Oslo,* C. bisulcata *or* C. linnarssoni *Zone. (E) Latex cast of thoracopygon, length 5.9 mm with eight articulated thoracic segments and broken librigenae in front. Sandtorp, Kinnekulle, Västergötland, Sweden,* C. bisulcata *or* C. linnarssoni *Zone. (Coll.: J. Ahlgren). (H) Two pygidia* (PMO 223.438)*, the largest 1.4 mm long. Nærsnes,* C. bisulcata *Zone. (I) Dorsal view of unusually large pygidium* (PMO 223.439)*, length 2.2 mm, with three axial rings and an end lobe. Slemmestad,* C. linnarssoni *Zone, 60 cm level. (J) Librigena (*PMO 223.440*), length 3.1 mm showing distinct border furrow. Slemmestad,* C. bisulcata *Zone, -25 cm level. (K) and (P) Dorsal and frontal view of large cranidium (PMO 223.441), length 4 mm. Slemmestad,* C. bisulcata *Zone, -5 cm level. (L) Dorsal view of cranidium* (PMO 223.442)*, length 3.9 mm. Slemmestad,* C. bisulcata *Zone, -25 cm level. (M) Thoracic segment* (PMO 224.165/1) *with truncate pleural tip 6.4 mm wide (tr.). Råbäck, Kinnekulle, Västergötland, Sweden,* C. bisulcata *Zone. (N) Pygidium* (PMO 224.165/2)*, length 2.2 mm with three axial rings and an end lobe. On the same slab as (M). (O) Librigena (PMO 223.443), length 2.8 mm showing eye, caeca and wide flat border. Slemmestad,* C. linnarssoni *Zone, 60 cm level.*

***Triangulopyge majusculus* (Linnarsson, 1880).**
Figs. 12B and 13K–P

1880 S*phærophthalmus majusculus* Linnarsson, p. 11, pl.1, figs. 11–12.

1957 *Sphaerophthalmus majusculus* Linnarsson - Henningsmoen pp. 218–219, pl. 5, pl. 22, figs. 16–17.

1958 *Sphaerophthalmus majusculus* Linnarsson - Henningsmoen pp. 190, 192, pl. 3.

1968 *Sphaerophthalmus majusculus* Linnarsson - Rushton, text fig. 3c.

2002 non *Sphaerophthalmus majusculus* Linnarsson 1880 - Schöning, figs. 50–51 (fig. 50 = *S. alatus*, fig. 51 = *T. humilis*).

2005 *Sphaerophthalmus* cf. *majusculus* Linnarsson, 1880 - Ahlberg et al. p. 433, fig. 2N, O.

For further synonymy, see Henningsmoen (1957).

Lectotype: Designated by Henningsmoen (1957), the pygidium figured by Linnarsson (1880, pl.1, fig. 12) and refigured by Westergård (1922, pl. 13, fig. 33) from the *Peltura scarabaeoides* Zone, Andrarum, Scania, Sweden.

Diagnosis: Triangulopyge species with centres of palpebral lobes opposite anterior part of L1 to S1. S1 shallow medially. Occipital node faint. Librigena with posterior lateral margin long and convex, anterior lateral margin shorter and convex, border widest anteriorly and flattened. Thoracic pleura narrower than axial ring. Pygidium with two to three axial rings and an end lobe, pleura three-fourths the width of axis.

Description: An emended description is given here after Linnarsson (1880) and Westergård (1922). The former had only access to flattened specimens preserved in shale, whereas librigena and thoracic segments were lacking in Westergård's material. Glabella tapered, S1 transglabellar, S2 short, placed abaxially. Occipital furrow distinct, ring with faint node. Centres of the palpebral lobes opposite anterior part of L1 to S1. Palpebral area slightly narrower than or as wide as glabella at eye line. Preocular area very wide. Anterior border flattened, considerably narrower (tr.) than occipital ring. Glabella in frontal view (Fig. 13P) low, moderately raised from strongly convex cheeks. The largest cranidium studied is 4 mm long.

Librigena with moderately long and slender spine placed far forwards. Border flat, widening anteriorly with the posterior lateral margin curved and longer than the curved anterior lateral margin (Fig. 13O). Caeca distinct, closely spaced at base of spherical eye, situated close to the posterior border.

Number of thoracic segments unknown, pleura almost as wide as axial ring and lacking spines.

Pygidium with two to three axial rings and an end lobe, lacking nodes and spines. Pleural field nearly as wide as axis, with two to three pleural furrows reaching margin. Lateral margin thread-like, weakly concave, lacking spines.

Remarks: Very few cranidia have been figured of this species where only two are well-preserved in limestone (Westergård, 1922, pl.13, fig. 30a–b; Henningsmoen, 1957, pl. 22, fig. 16). The distinction between *T. majusculus* and *T. humilis* was thoroughly covered by Henningsmoen (1957, p. 219), who emphasised the generally wider anterior and posterior areas in *T. majusculus*. Attention was drawn to the fact that the thorax was unknown and associated pygidia and cranidia may be uncertain (Westergård, 1922, p. 166; Henningsmoen, 1957, p. 219). A portion of stinkstone (PMO 224.165) measuring 4 x 6 cm, collected by MH from the *Ctenopyge bisulcata* Zone at Råbäck, Kinnekulle, Sweden, contains approximately fifty cranidia of *T. majusculus* associated with some fragments of *Peltura scarabaeoides* and *Ctenopyge bisulcata*. Additionally, there are four pygidia (Fig. 13N), which strongly tie this pygidium to *T. majusculus*. Thoracic segments (Fig. 13M) on the same block show these to be convex with pleura curved downwards distally and lacking a spine. New specimens of librigena (Fig. 13O) are very like the one figured by Henningsmoen (1957, pl. 22, fig. 17). Fig 12B shows how, in an assumed life position, the genal spine would have been curved ventrally under the thorax in a similar manner to that shown in reconstructions of *T. humilis* given by Rushton (1968, text fig. 2) and Clarkson (1973, text figs. 8a–d). The anterior area of the fixigena becomes inflated during growth and is dominant when the cranidium of a large specimen is viewed from the front (Fig. 13P).

Distribution: T. majusculus rarely occurs in large numbers, but is present in the *Ctenopyge bisulcata* and *Ctenopyge linnarssoni* zones in Nærsnes, Slemmestad, Oslo, Modum, Ringerike and the Mjøsa area, where it occurs with *T. humilis*, *C. bisulcata*, *C. linnarssoni*, *C. fletcheri*, *C. pecten* and *P. scarabaeoides*.

Acknowledgments. - Arne Torshøj Nielsen is thanked for discussions and valuable comments on the manuscript at an early stage, Bjørn Funke is thanked for his companionship on numerous field trips and John Jompa Ahlgren generously provided latex casts of material from his collections. Magnus Høyberget is thanked for his encouragement and for guiding field trips in the Mjøsa area. We are grateful to the two referees, Anna Żylińska and Per Ahlberg for their comments, which have improved the quality of this work.

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