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Ontogeny, structure and functional morphology of some spiny *Ctenopyge* species (Trilobita) from the upper Cambrian of Västergötland, Sweden

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ABSTRACT: This paper completes the description of intact and three-dimensional *Ctenopyge* species from the upper Cambrian *Peltura minor* Zone in Västergötland, central Sweden. All these species are present together, on the same bedding planes. The most abundant species, *Ctenopyge* (*Eoctenopyge*) *angusta* Westergård, 1922 has previously been described, and an almost complete ontogeny worked out. *C.* (*Ctenopyge*) *gracilis* Henningsmoen, 1957 is a small trilobite with nine thoracic segments and very long, thin curving and subparallel thoracic spines; the genal spines partially encircle the body. Two axial spines at the rear are of considerable length. When reconstructed in side view, the posterior thoracic spines rise upwards as an inclined fan, but when relaxed the tips of all the thoracic and axial spines come to lie in the same plane as the horizontal genal spines. An almost complete ontogeny is described for this species, and individuals show an evident spinosity from an early stage, but the body size at which thoracic segments are liberated is highly variable. *C.* (*Ctenopyge*) *ahlbergi* n. sp. is a larger, robust and broad species distinguished by long, stout genal spines, ten thoracic segments, and a very spiny body with the first three to four spines expanded into lateral flanges. A degree 6 meraspis shows these flanges already developing. *C.* (*Ctenopyge*) *rushtoni* n. sp has likewise ten thoracic segments, and has stout, broad-based and tapering spines. Incomplete meraspides 6 and 7 are known for this species. In both *C.* (*Ctenopyge*) *ahlbergi* and *C.* (*Ctenopyge*) *rushtoni* there are also two axial spines at the rear, and the extended body would have had a similar rising tail fan to that of *C.* (*Ctenopyge*) *gracilis*. *C.* (*Mesoctenopyge*) *tumida* is also present as a single large adult and several smaller holaspides. In this species the first thoracic segment is confirmed as bearing a pair of long curving spines, somewhat smaller than the encircling genal spines. The remaining thoracic spines are straight and sharp, and evidently longer in young holaspides. There is a single long axial spine on the last segment. No adult pygidium has been found.

Some comments on the diversity of the fauna as a whole and the range of functional types are appended.

KEY WORDS: Olenidae, spinosity, trilobite.

Ctenopyge is a genus of the trilobite Family Olenidae, distinguished by a remarkable spinosity of the body, and it is the most highly modified of all the olenid genera. This genus occurs in the upper Cambrian *Peltura* Zones in Scandinavia and elsewhere, and though widely distributed and stratigraphically useful, few specimens of any of its species have been preserved intact and in three dimensions. In recent years, however, a remarkable fauna has been collected in Västergötland by John Ahlgren, which contains five species of *Ctenopyge*, in addition to the subzonal index fossil *Peltura minor*, These are exceptionally well preserved, and in this material some or all of the juvenile stages are present. For the most abundant of these, *C.* (*Eoctenopyge*) *angusta* Westergård, 1922, a complete post-protaspid ontogeny has recently been described (Clarkson *et al*. 2003), and morphological details of the adult form have been illustrated in dorsal and lateral views.

In the present paper the remaining four species are described. One of these, the least abundant species in our material, is readily identified as *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922. We have, however, encountered a problem with the identification and interpretation of the other three species. They are evidently closely related, in a group centring round *Ctenopyge* (*Ctenopyge*) *affinis gracilis* Henningsmoen, 1957, as we noted in our previous work. This subspecies and related forms have been known hitherto only from detached cranidia and librigenae, all of which are remarkably similar. It is evident from our material, however, that it is the structure of the thorax which most clearly distinguishes them, and this has not been described before. There are various ways of interpreting this plexus of related, though different morphologies. One would be to regard all three morphs as belonging to a single, highly variable species, but this approach is not taken here since the morphs do not intergrade, and ontogenetic stages (in various degrees of completeness) can be established for each. Instead we regard them as three separate species, *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957, *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp. and *Ctenopyge* (*Ctenopyge*) *rushtoni* n. sp.

1. Material

The described material comes from two localities only, on the lower slopes of Mount Kinnekulle. Most originates from a series of small quarries near Blomberg, where the fossils show up as white against the pale pinkish-brown limestone, and occur on the same bedding planes. The rest comes from a black

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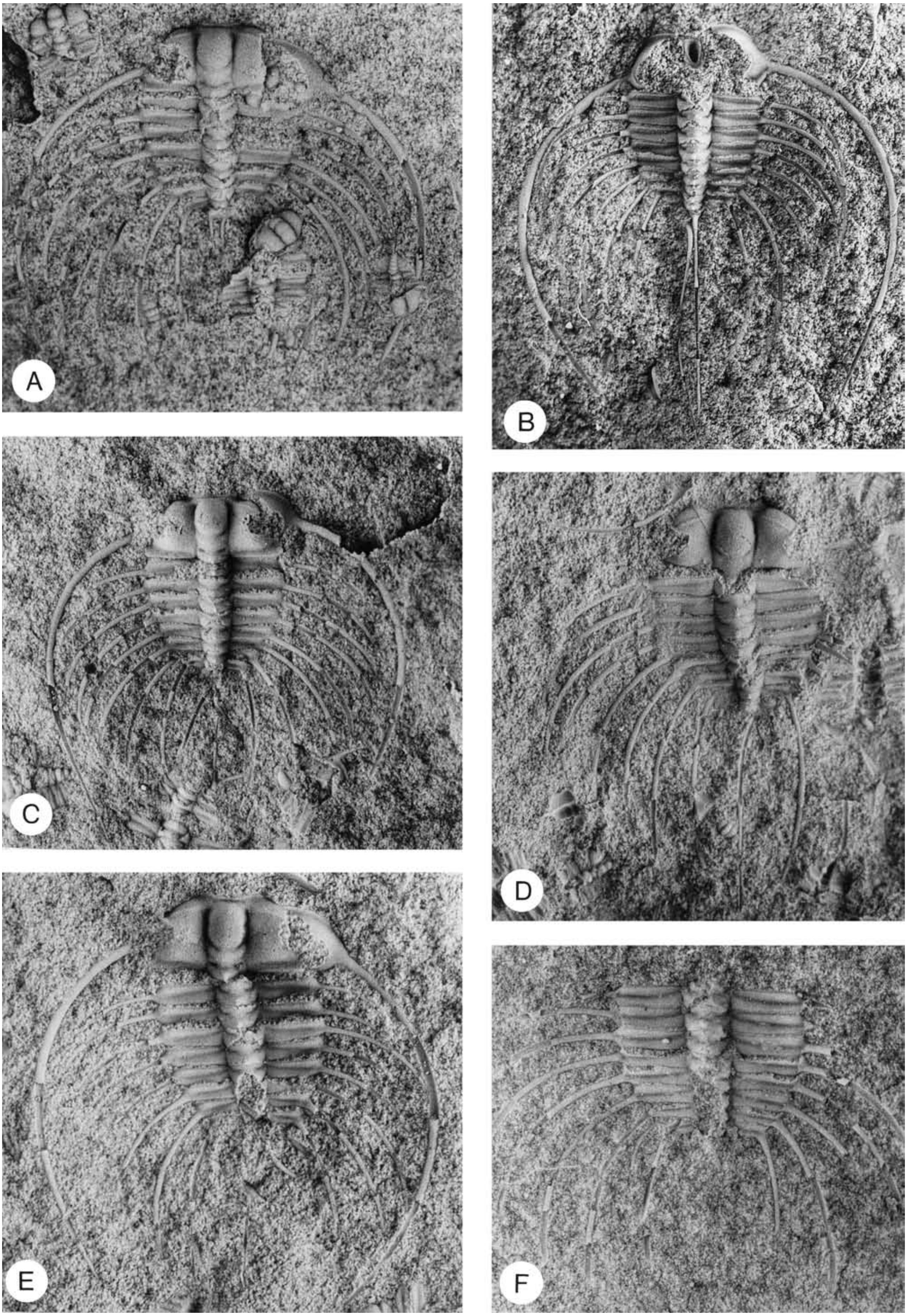
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limestone at Toreborg, which was found only as loose boulders in a ploughed field (for map and description of lithologies see Clarkson *et al*. 2003). While the exact stratigraphical relationship of these two localities remains to be determined, all five *Ctenopyge* species are present in each, and are found on the same bedding planes. The co-occurrence of these various *Ctenopyge* species in Västergötland contrasts dramatically with that in Norway and in Skåne. Henningsmoen (1957) included four subzones within the zone of *Peltura minor*; in ascending order these are the subzones of *C. similis*, *C. spectabilis*, *C. tumida* and *C. affinis*. He noted Westergård's (1944) comment that in Skåne *C. affinis* occurs above *C. tumida*. The order of succession amongst *Ctenopyge* species in continuous sequences elsewhere is not sustained in the condensed successions in Västergötland. Ahlgren & Ahlberg (1996) indicate that subzones of the *Olenus* Zone recognisable in Skåne have their typical species co-mingled in Västergötland. The same is evidently true of the *Peltura minor* Zone, where species hitherto thought to be indicative of three separate subzones co-occur. At Blomberg the most abundant fossil is *C.* (*Eoctenopyge*) *angusta* (ca. 40 intact adults or degree 9 meraspides), *C.* (*Ctenopyge*) *gracilis* is less so (ca. 15 of same), *C.* (*Ctenopyge*) *ahlbergi* and *C.* (*Ctenopyge*) *rushtoni* are comparatively uncommon (ca. five intact adults or degree 9 meraspides), and *C.* (*Mesoctenopyge*) *tumida* is represented only by three specimens altogether. We have less material from Toreborg, and although all five species are present, it is from here that our largest and best preserved specimens of *C.* (*Ctenopyge*) *ahlbergi*, *C.* (*Ctenopyge*) *rushtoni* and *C.* (*Mesoctenopyge*) *tumida* have been collected.

2. Descriptive section

Ctenopyge (*Ctenopyge*) *gracilis* Henningsmoen, 1957
Figs 1–10; 12C, D; ?18J–L

1922 *Ctenopyge affinis* n. sp [partim]: Westergård, p. 157, pl XII, figs 7–13
1929 *Ctenopyge affinis* Westergård: Strand p. 359 (Recorded)
1957 *Ctenopyge* (*Ctenopyge*) *affinis gracilis* n. sp: Henningsmoen, p. 201, Pl. 5: Pl. 19, figs 17, 19–21
1973 *Ctenopyge* (*Ctenopyge*) *affinis gracilis* Henningsmoen: Schrank, p. 826 Taf. VIII, figs 3–5, 6?, 7, 8.

Material. Five near-intact fully adult holaspides ranging in overall length from 6·5 mm to 7·75 mm (spines included), and many other nearly complete or partial individuals representing various degrees of ontogenetic development. Here we treat *C.* (*Ctenopyge*) *gracilis* as a full species rather than a subspecies of *C.* (*Ctenopyge*) *affinis*. Henningsmoen's (1957, p. 201) description was based upon disarticulated material, but the new information, especially on the construction of the thorax and the hypostome, emphasises the distinctiveness of this form, and it seemed appropriate to raise it to species level. The holotype cranidium in the Oslo Museum (PMO 19993b (wrongly indicated in the text as PMO 19993a)) is 3·3 mm long, contrasting with a length of only 1·2 mm in our largest holaspis. We must assume therefore that none of our specimens were fully grown, but still adolescent and yet to develop fully adult morphology. The appreciably larger eyes in our material may likewise be an immature feature.

2.1. Description of the adult

Cephalon. Cranidium convex, somewhat broader than long, glabella occupying the central third interocularly, and the central quarter postocularly, as measured across the posterior border. External contour trapezoidal, anterior border transverse, forming a turned-up flange when seen in plain view; anterior arch pronounced. Anterior branch of facial suture forming an ogival curve running out at about 65° to the sagittal plane, palpebral suture about half the length (sag.) of the cranidium; its posterior edge is set opposite S1. Posterior branch of facial suture curving out very sharply behind the eye, making an angle of some 75° to the sagittal plane, curving slightly and extending to cut the posterior border distal to the outermost curve of the visual surface. Ocular ridges narrow and pronounced, almost parallel with the posterior branch of the facial suture, palpebral lobe relatively broad.

Glabella quadrate, nearly twice as long as it is broad, extending to anterior margin, almost parallel-sided except where S1 furrow form a minor constriction or 'waist'. Occipital furrow narrow, curving posteriorly medially, continuous throughout but much more deeply incised laterally. L1 narrow (hardly more than one-eighth of the total length of the cranidium), S1 is of similar form to S0, though less indented posteriorly. S2 represented only by faint lateral impressions, glabella anterior to S2 about a third of the total glabella length (including L0), curving down anteriorly to meet the flanged anterior border. Occipital ring, slightly shorter (sag.) and wider than L1 projects backwards from the cranidium and bears a short central spine. Eye large, subspherical, about half the length (sag.) of the cranidium, otherwise resembling that of *C.* (*Eoctenopyge*) *angusta*. Librigena broad, with curving anterior and posterior margins; in plan view the eye is set slightly more than halfway between the axial furrow and the rest of the genal spine. Genal spine relatively thin and ovoid in cross-section, springing out at an angle of some 60° to the transverse plane, each spine describing a near semicircle outside the thoracic spines and terminating at a distance of the total length of the body (caudal spine omitted) beyond the pygidium.

Hypostome. Several specimens were found with the hypostome still in place, and these were used as the basis for description and illustration. Many detached hypostomes are found scattered on the bedding planes, but since this sclerite is similar in all species of *Ctenopyge*, there can be no certainty as to which species these isolated hypostomes belong. As we suggested previously (Clarkson *et al*. 2003) the hypostome was probably conterminant. The two holaspid hypostomes illustrated here (Fig. 12C, D) are respectively 0·65 mm long (sag.) and 0·4 mm wide, and 0·75 mm long (sag.) and 0·48 mm wide centrally; 0·65 mm across the lateral wings. In the larger and better preserved of the two (Fig. 12D) the anterior margin curves forwards and is broadest at the outwardly projecting wings, each of which terminates at an acute angle. Hypostome narrowest at approximately a quarter of the distance from front to rear, shoulders laterally expanded and set almost exactly half way along the total length. Middle body prominent, tapering posteriorly with a rounded margin, and highest towards the rear. Anteriorly it virtually merges with the frontal margin. A thin external rim is present on each side at the 'waist', but this fades out posteriorly and is in any case more clearly defined in the smaller specimen illustrated in

Figure 1 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland: (A) Almost-complete small holaspis. LO 8945t, × 10·5; (B) Almost-complete larger holaspis, lacking cranidium but showing the hypostome in place, and with two posterior spines. LO 8946t, × 8; (C) Almost-complete degree 8 meraspis, right librigena hardly displaced. LO 8947t, × 12; (D) Degree 8 meraspis, lacking librigenae. LO 8948t, × 12·5; (E) Almost-complete holaspis, right librigena hardly displaced, though lacking posterior region. LO 8949t, × 9; (F) Well-preserved holaspid thoracopygon. LO 8950t, × 9. All these specimens are latex replicas of external moulds, except for (F). See also Figure 3.

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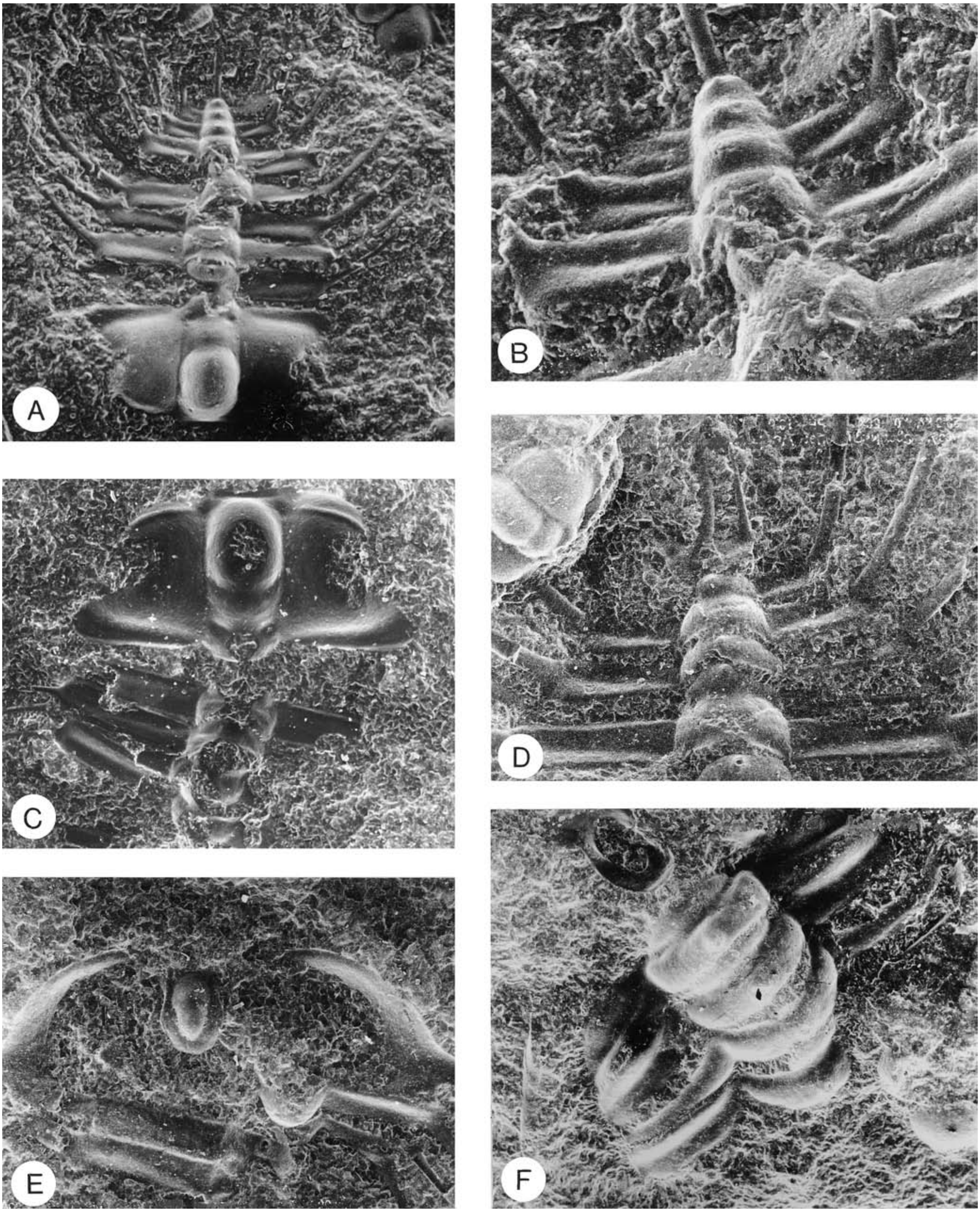

Figure 2 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland. Holaspid individuals selected to show details of construction: (A, B) Specimen in antero–dorsal view showing posterior thoracic spines inclined and rising above the horizontal plane. LO 8951t: (A) × 28; (B) Details of posterior region. × 100; (C) A well-preserved cranidium with three detached thoracic segments. LO 8952t, × 28; (D) Posterior region of an individual showing inclined thoracic spines and displaced caudal and axial spines. LO 8953t, × 92; (E) Hypostome in place, with detached librigenae. LO 8954t, × 36; (F) Anterior part of thorax of a partially-enrolled specimen, showing articulating half rings, and a central node on the axial rings. A hypostome lies to the NW. LO 8955t, × 28. All SEM photographs of latex replicas.

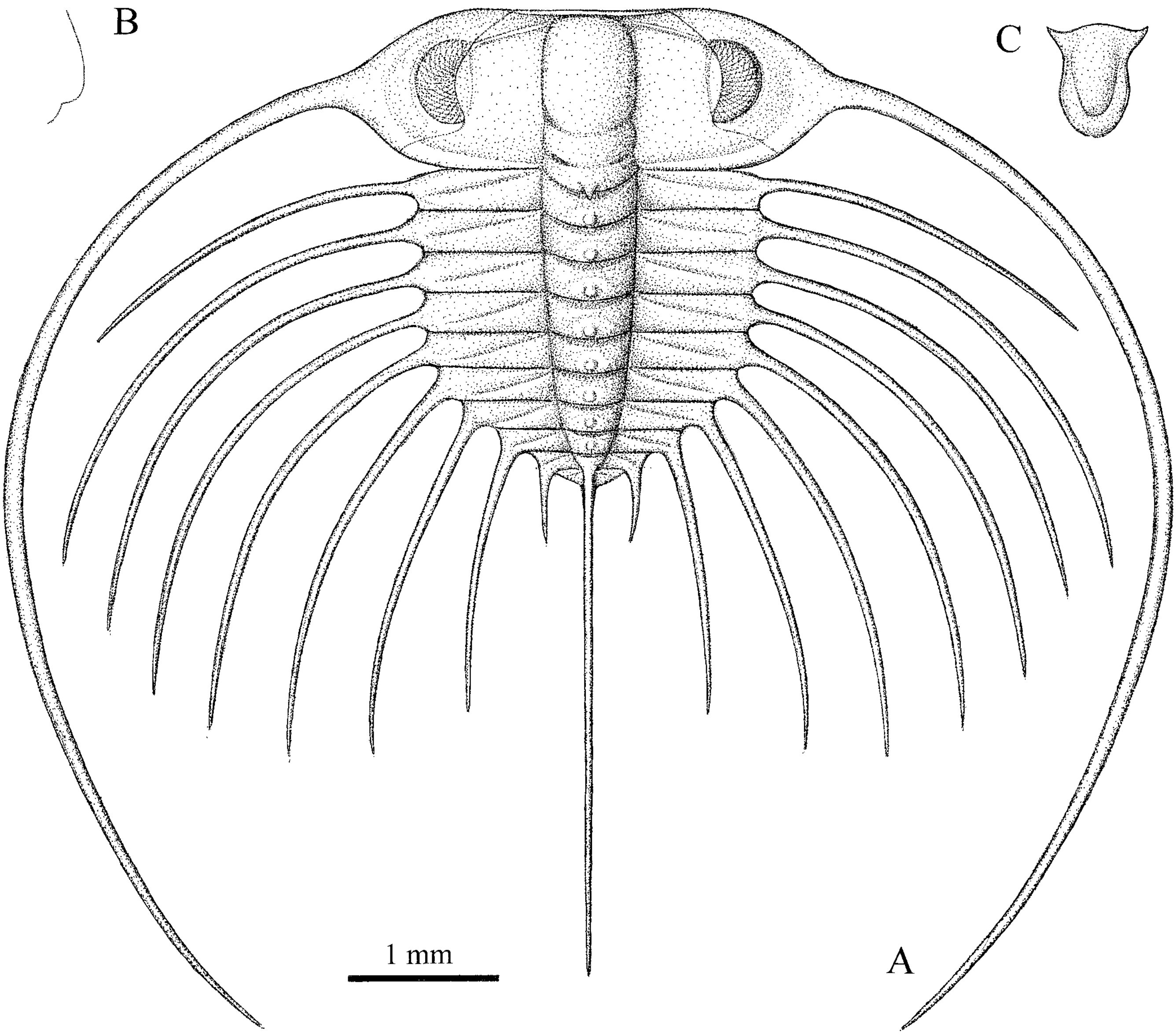

Figure 3 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957: (A) Reconstruction of adult in dorsal view; (B) Hypostomal profile; (C) Hypostome.

Figure 12C. Posterior border (brim of Henningsmoen 1957, Fig. 1) in the full-grown specimen is long (sag.), being over a quarter of the total hypostomal length. In the smaller specimen, however, it is less than a fifth of the total length, and an evident feature of late ontogeny is the extension of the brim. In most respects the hypostome of *C.* (*Ctenopyge*) *gracilis* is similar to that of *C.* (*Eoctenopyge*) *angusta*, *C.* (*Ctenopyge*) *ahlbergi* and *C.* (*Ctenopyge*) *rushtoni*, except that the posterior border is longer.

Thorax. Thorax consisting of nine segments and (spines excluded) slightly broader than long, almost parallel-sided until about the level of the fifth segment, tapering sharply thereafter. Axis occupying about the central fifth of the total width, excluding spines, and tapering sharply towards the rear. Each axial ring projects slightly backwards, is raised centrally, and each of the first eight segments has a distinct node. The ninth axial ring, however, has a very long thin spine, raked upwards at an angle of some 45° from the horizontal, and slightly curving. Anteriorly the pleurae are about two and a half times as wide as they are long (sag.); they become much shorter (sag.) and narrower posteriorly. Each pleura bears a long, thin, curving spine, much narrower than the pleura which gives rise to it, so that the margins of the thorax appear scalloped between spine bases. The outer terminations of these spines all lie within the semicircle formed by the long genal spine. Of this spine array the second pair are the longest, and the first few pairs are subconcentric, in plan view, while the most posterior spines become shorter and increasingly inclined to the sagittal plane. The much shorter ninth pair is parallel with the axis. Whereas in the outstretched animal the first two pairs of thoracic spines are almost straight and nearly horizontal, they become progressively more angled upwards and increasingly curved towards the rear. They thus form an en echelon pattern with the most posterior pair rising at an angle of some 45° to the horizontal.

Pygidium. Adult pygidium tiny and triangular, bearing a very long thin caudal spine, subparallel with the axial spine of the ninth thoracic segment, rising upwards at some 40° to the horizontal plane.

Surface sculpture appears to the almost entirely absent.

Lateral view. The body of *C.* (*Ctenopyge*) *gracilis* may be reconstructed in two alternative positions (Fig. 4). If we assume that the body is outstretched horizontally, then the thorax is carried at a high level, though parallel with the

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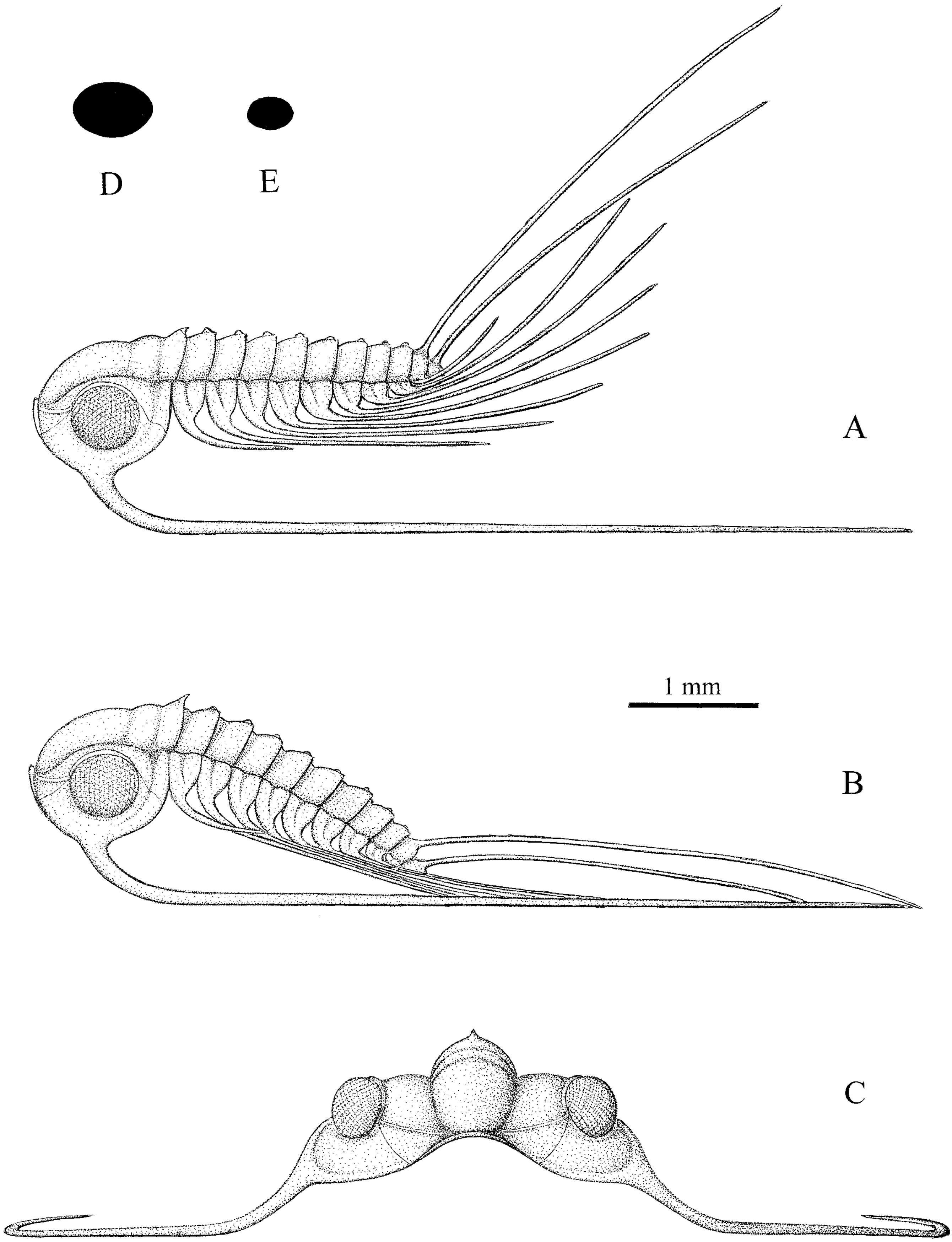

Figure 4 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957: Reconstruction in lateral view in (A) outstretched and (B) relaxed posture; (C) Frontal view; (D) Cross-section through genal spines, enlarged; (E) Cross-section through thoracic spines, enlarged.

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horizontal genal spines, as is typical of *Ctenopyge* generally. In this attitude the more posterior thoracic spines rise upwards as an inclined, slightly curving fan, flanking the highly raked axial and caudal spines. The body may be reconstructed in an alternative posture, into which it would naturally fall if the muscles were relaxed. In this half-curled attitude, the tips of the axial and caudal spines would come to lie in the same horizontal plane as the thoracic spines, which is the same as that in which the long genal spines lie; evidently this was a resting attitude. These two alternative postures are more fully discussed under 'Functional Morphology'.

Remarks. Of the known spinose *Ctenopyge* species *C.* (*Ctenopyge*) *gracilis* most closely resembles *C.* (*Ctenopyge*) *ahlbergi* n. sp., and *C.* (*Ctenopyge*) *rushtoni* n. sp. It differs from these mainly in the slender, rounded genal and thoracic spines. *C.* (*Ctenopyge*) *pectin* has a much broader body, a longer pygidium, and the genal spines lie below and within the outer tips of the thoracic spine array.

2.2. Description of ontogeny

Individuals of *C.* (*Ctenopyge*) *gracilis* are not as abundant as those of *C.* (*Eoctenopyge*) *angusta*, and fewer specimens representing early growth stages are present. It is relatively easy to distinguish these from those of *C.* (*Eoctenopyge*) *angusta*, since the earliest meraspides are appreciably broader, and the thoracic spines develop very early. It is easier, however, to confuse the early developmental stages of *C.* (*Ctenopyge*) *gracilis* with those of *C.* (*Ctenopyge*) *ahlbergi* and *C.* (*Ctenopyge*) *rushtoni* since these were probably very similar when young. *C.* (*Ctenopyge*) *gracilis* is the commonest species after *C.* (*Eoctenopyge*) *angusta*, and the growth series described here remain coherent. The few protaspides present cannot confidently be assigned to any one of the five *Ctenopyge* species present in our material, and are described later as 'unassigned protaspides'.

2.2.1. Degree 0 meraspis (M0). **Material**. We have only one well-preserved specimen (Fig. 5A), which forms the basis for the reconstruction given in Figure 9.

Description. The specimen is about 0·38 mm long, lacking librigenae. Cranidium forming a laterally stretched hexagon, 0·35 mm wide and 0·22 mm long (sag.), glabella occupying less than the central third, parallel-sided, reaching the anterior margin, and rounded anteriorly. S0 (occipital) furrow distinct, and S1, S2 and S3 are clearly visible, approximately equally spaced and quite well impressed. Incipient palpebral lobes present, set at the anterior corners of the cranidium; no clear indication of ocular ridges. Posterior border well-marked but there is no evidence of intergenal spines at this or later stages. In this specimen the occipital ring is broken off.

Transitory pygidium semicircular, of width 0·25 mm and length (sag.) 0·18 mm, rachis occupying about the central third and extending to the rear margin, tapering posteriorly. Articulating half-ring distinct, as are four to five axial rings on the rachis. Whereas the margin of the transitory pygidium is frayed, possible spine bases are visible. The transitory pygidium, like that of leptoplastines generally, curves down posteriorly.

2.2.2. Degree 1 meraspis (M1). **Material**. Only one specimen is available to us (Fig. 5B), but it is largely intact, with the librigenae detached and lying below the transitory pygidium.

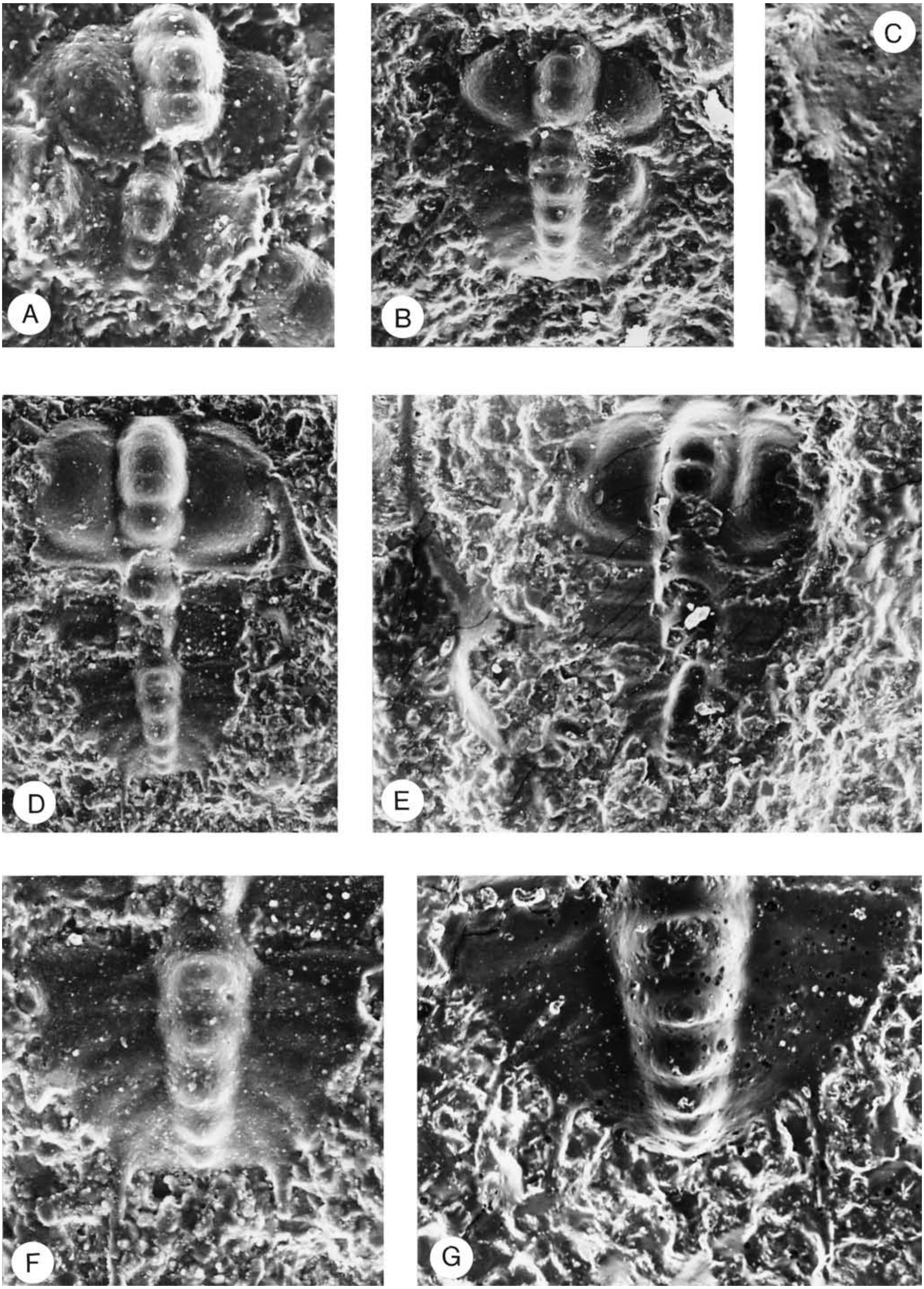
Description. As reconstructed (Fig. 9), the complete animal is 0·60 mm long and 0·50 mm broad across the widest part of the cranidium. The cranidium is 0·33 mm long (sag.), including occipital ring. Of this, the glabella occupies the central third, and bears distinct S0, S1, and S2 furrows; the most anterior part, however, is broken off so that the presence of S3 remains uncertain. The occipital ring is also broken off. Posterior border furrow very distinct. Both librigenae are present in this individual though displaced. Each bears a large eye, though no lenses can be discerned. Genal spines arise at about half-way down the cephalon, slightly curved, taping, and in life would have projected outwards, inclined at some 40° posteriorly, to terminate at about the level of the posterior cranidial border. The total width of the reconstructed cephalon, with spines is 0·95 mm.

The single thoracic segment is (like the occipital ring) partially broken off. Transitory pygidium semicircular and somewhat curled down posteriorly; rachis distinct with five axial rings, each with incipient central node; border with short slender spines, most distinct posteriorly. At this stage there is no indication of a caudal spine.

2.2.3. Degree 2 meraspis (M2). **Material**. (i) An almost complete individual with slightly frayed margins (Fig. 5D, F), and with the right librigena broken and reversed; (ii) An individual of similar size, with a displaced transitory pygidium (Fig. 5E). A nearby left librigena, likewise reversed, probably belongs to this specimen. When reconstructed, individuals representing this degree are 0·90 mm long (caudal spines excluded); (iii) A well-preserved transitory pygidium with intact margins and spines (Fig. 5G); (iv) A partial transitory pygidium with long marginal spines (Fig. 5C); (v) An individual with a damaged thorax and rotated pygidium, margin frayed (Fig. 6A, C); (vi) A transitory pygidium with marginal spines and a caudal spine, all of remarkable length (Fig. 6B).

Description. As reconstructed (Fig. 9), M2 is 1·1 mm long and 1·8 mm wide, spines included. The cranidium 0·42 mm long (occipital ring included) and 0·75 mm broad, glabella occupying 35% of the total width. Palpebral lobes still set relatively far forwards, opposite S2; both they and the ocular ridges are by now well defined. Other features of the cephalon remain much as before, but a pair of small nodes has appeared just behind the anterior margin, on either side of the glabella. There is some variation in the structure of the glabella between the two figured specimens. Figure 5D shows an individual in which S1 is deeply incised, and the glabella is constricted at this level. L1 is ovoid and isolated. S2 and S3, however, are poorly defined. In the specimen illustrated in Figure 5E, on the other hand, S2 is as deeply incised as is S1, and S3 is also evident though less deep. In both these specimens the occipital ring is broken, and the hypostome remains unknown.

The associated librigena (Fig. 5E) has a long, thin, tapering, and curving spine which in life would terminate at about the level of the thorax, and would extend the body to an overall width of 1·7 mm. The two thoracic segments are of similar length (sag.), each with a central axial node. Whereas traces of thoracic spines are present, their length can only be estimated with reference to those of the transitory pygidium. Transitory pygidium, rounded to triangular in form, is 0·30 mm long and 0·575 mm broad, excluding spines. Rachis occupying the central 35% of the total width, anteriorly extending to a large articulating half-ring, and tapering posteriorly to reach the rear edge. Five axial rings and an incipient sixth are present, with subdued nodes anteriorly. Pleural field traversed by shallow pleural furrows, becoming more inclined posteriorly. Round the margin are four pairs of radially arranged spines, the more posterior being parallel with the axis; these are long, slender, and curving. A possible trace of a caudal spine is visible (Fig. 5G), but since the transitory pygidium in larval leptoplastines curls down posteriorly, this remains unclear. The caudal spine, however, is clearly visible in Figure 6B, where it is arched and curved downwards posteriorly; this and the marginal spines are much longer than in other specimens, testifying to a high degree of intraspecific variation.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2.2.4. Degree 3 meraspis (M3). **Material**. (i) An individual with somewhat separated thoracic segments and a frayed pygidial margin, but with a long, curving genal spine still in place (Fig. 6D); (ii) An individual with the lateral parts of the cranidium damaged, and the thorax and transitory pygidium slightly detached (Fig. 6E).

Description. As reconstructed (Fig. 9), M3 (spines included) is of maximum length 1·5 mm, and width c. 2 mm. Cranidium is 0·45 mm long (including the occipital ring) and 0·75 mm broad, closely similar in form to that of degree 2. The main changes in cranidial structure are a slightly overall broadening, and the virtual disappearance of the two small anterior nodes. As regards the librigena, the eyes are appreciably larger than before, and have migrated somewhat posteriorly, and the genal spine now reaches beyond the posterior end of the body. The thorax, of three segments, is 0·325 mm long (sag.), and 0·65 mm wide (excluding spines) and the transitory pygidium, 0·3 mm long, and 0·53 mm wide, is nearly semicircular in form with four pairs of lateral spines and a caudal spine. Overall, the main differences between M3 and M2 are in the longer spines, and possession of three thoracic segments.

2.2.5. Degree 4 meraspis (M4). **Material**. (i) An almost-complete individual with excellent details of thoracic spines on the right hand side and a well-preserved transitory pygidium (Fig. 7C, D); (ii) An individual with fine derails of the cranidium, but frayed edges to the thorax and pygidium (Fig. 7E).

Description. As reconstructed (Fig. 9), individuals are 2·1 mm long, and 2·3 mm wide (spines included). Cranidium, including occipital ring, is now 0·5 mm long and 0·95 mm wide, broadly similar in form to that of the preceding degree, and the proportions are much the same, though the posterior branch of the facial suture is more curved and swings posteriorly. S2 is more faintly impressed than before. Thorax, spines excluded, 0·5 mm long and 1 mm wide. Thoracic spines, and those of the transitory pygidium, are already very long (Figs 7C, D; 9). With the release of the fourth thoracic segment the transitory pygidium now appears relatively broader and shorter, being 0·3 mm long, and 0·85 mm broad. An increase in spine length is again evident, though we have no specimens with intact genal spines, hence the incomplete reconstruction in Figure 9.

2.2.6. Degree 5 meraspis (M5). **Material**. (i) A slightly disarticulated but otherwise intact individual within the size range of M5, in which the damaged transitory pygidium exhibits the sixth thoracic segment ready for release (Fig. 7A); (ii) A disarticulated specimen, with the thoracic segments rotated, but the genal spines preserved to their full length (Fig. 7B); (iii) A slightly flattened individual, with a displaced left librigena and broken thoracic spines but with an intact caudal spine (Fig. 7F); (iv) A somewhat smaller individual with well-preserved thoracic spines and transitory pygidium (Fig. 8E, F).

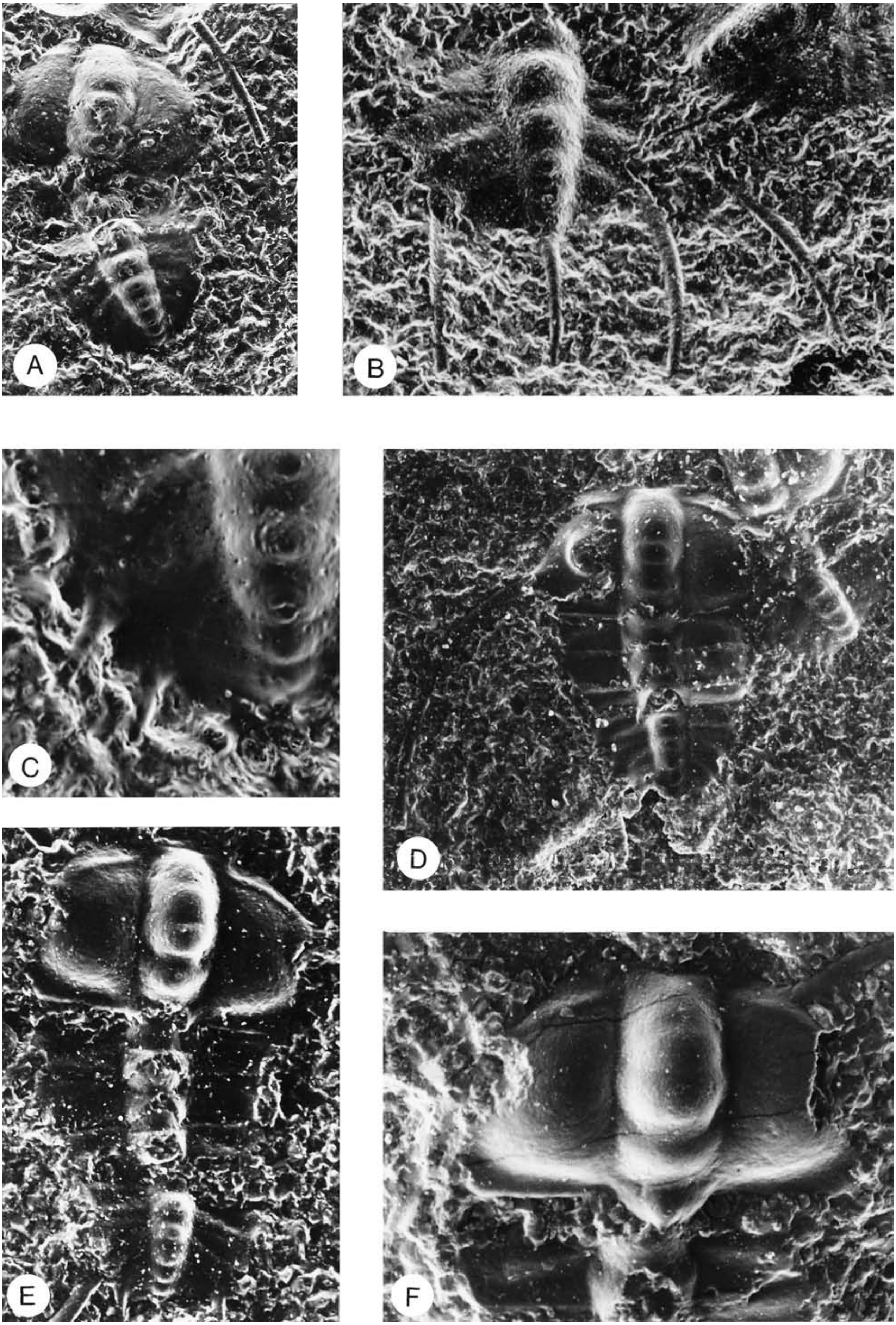
Description. Of the various individuals representing this stage of development, two kinds of variations are apparent (a) in overall size, which is relatively minor and (b) in angle of thoracic spines. These specimens, however, are all incomplete or crushed to some degree, so we have not attempted a reconstruction. In the best-preserved, though slightly crushed individual figured in Figure 8E and F the cranidial width is 1·3 mm and length (sag.) 0·7 mm. An estimate of the original length of the body (spines included) would be 1·8 mm, i.e. well within the expected size range following the growth trajectory from M0 onwards. In this specimen, however, the thoracic spines, while all long and subparallel, are set at some 60° to the transverse plane, rather than the 40° or so encountered in other specimens. The transitory pygidium now has a length (sag.) of 0·42 mm and a width of 0·85 mm. Otherwise the only real changes from M4 are the release of a further segment and larger size. S2 if faint and pit-like, though still evident in some individuals (e.g. Fig. 1E).

2.2.7. Degree 6 meraspis (M6). **Material and description**. The individual described and figured here (Figs 8A, C; 10) is 2·8 mm long and 3·5 mm wide including spines). The cranidium, including the occipital ring, is now 0·65 mm and 1·6 mm. The main differences between degree 6 and previous degrees lie in the broadening of the cranidium, and the larger eyes, which are set further back. With the release of the sixth thoracic segment the pygidium has shortened sagitally, being no more than 0·3 mm long (sag.) and 1·0 mm wide (excluding spines).

2.2.8 Degree 7 meraspis (M7). **Material and description**. Of the specimens we have of this degree, most are damaged, but fall within the expected size range, estimated as c. 3·6 mm long and c. 4·5 mm broad. The best-preserved individual, however, is appreciably smaller than would be expected. That illustrated in Figure 8B would only be 3 mm long, which is actually about the same size as some of the individuals belonging to degree 6. Even more extreme is a poorly preserved (unfigured) individual, which though lacking a pygidium exhibits seven distinct thoracic segments. Yet its length, as estimated, would hardly be more than 2·5 mm – virtually the same as our reconstructed degree 5 meraspis. These two specimens suggest that the relationship between overall size and number of liberated thoracic segments is not exact. Whereas most individuals will lie within a 'normal' size range for the species, having followed a standard growth trajectory, others may achieve a more mature form when still very small. Since the only really well-preserved specimen of degree 7 of this kind, we have included a photograph thereof (Fig. 8B) but not a reconstruction.

2.2.9. Degree 8 meraspis (M8). **Material**. The dimensions of seven individuals ranging in length (as estimated) from 4·8 mm to 5·5 mm plot out as a cluster lying between plots of degree 7 meraspides and undoubted large holaspides (Fig. 21). Some of these retain displaced axial spines, but the fragile pygidium and eighth thoracic segment are damaged or missing. The position of the size cluster on the graph, however, and the morphological similarity between these and the holaspides strongly indicates that these are indeed degree 8 meraspides. Of those figured here (i) is an almost complete individual with the left librigena half buried, and the right one only slightly displaced (Fig. 1C); (ii) lacks the librigenae but along axial spine is present and the specimen exhibits very extended thoracic spines (Fig. 1D).

Figure 5 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland. (A) Degree 0 meraspis, lacking librigenae and with the occipital ring damaged and the transitory pygidium slightly displaced. Librigenae absent. (See Figure 9.) LO 8956t, × 172; (B) Degree 1 meraspis with librigenae detached and lying slightly under the damaged transitory pygidium; an eye is shown clearly on the right hand side. (See Figure 9.) LO 8957t, × 86; (C) Degree 2 meraspis, spines on left side of transitory pygidium. LO 8958t, × 250; (D, F) Degree 2 meraspis, almost complete specimen, right librigena reversed and with most of the spine broken. LO 8959t: (D) × 70, (F) Transitory pygidium of same, × 165; (E) Degree 2 meraspis, almost-complete specimen, pygidium displaced; right librigena, probably of the same individual reversed and lying to left. LO 8960t, × 70; (G) Degree 2 meraspis, transitory pygidium with marginal and a possible caudal spine. LO 8961t, × 185. All SEM photographs of latex replicas.


A
B
C
D
E
F

Comments. While the specimens are smaller than the holaspides, and (presumably) have one less thoracic segment, they do not perceptively differ otherwise from holaspides.

Ctenopyge (*Ctenopyge*) *ahlbergi* n. sp.
Figs 11; 12A, B, E, F; 13; 14

Derivation of name. In honour of our research colleague, Professor Per Ahlberg.

Material. Several nearly complete and partial specimens from both Blomberg and Toreborg, Västergötland, in the collections of Lund University (LO).

Holotype. A largely complete small holaspis, part only, LO 8976T (Fig. 11A), Blomberg.

Paratypes. LO 8978t (Fig. 11B), LO 8980t (Fig. 11F), LO 8981t (Fig. 11G), LO 8982t (Fig. 11H), LO 8983t (Fig. 12A), LO 8984t (Fig. 12B), all from Blomberg; LO 8979t (Fig. 11C–E), LO 8986t (Fig. 12E), LO 8987 (Fig. 12F), all from Toreborg.

Type locality and horizon. Small quarry at Blomberg, western slope of Mount Kinnekulle, Västergötland, Sweden.

Diagnosis. A broad species of *Ctenopyge* with long curving genal spines, lacking flanges, curving round the outside of the thorax. Thorax of ten segments, with the first three segments bearing very long curving spines with flanges. Only the proximal part of the fourth pair is flanged, that of the fifth hardly at all, the remaining spines tapering and slender, and angled upwards posteriorly. The tenth segment bears a long axial spine, and the tiny triangular pygidium has a long caudal spine.

2.3 Description of the adult

Cranidium. The largest cranidium is 1·3 mm long (sag.), including the short occipital spine, and 3 mm broad, trapezoidal in outline, anterior margin is almost straight, slightly indented, and broadest posteriorly where the posterior branch of the facial suture cuts the pronounced posterior border. Anterior branch of the facial suture making an angle of some 40° to the exsagittal plane, cutting the distal edge of the raised anterior border. Posterior branch making an angle of 70° to the exsagittal plane, subparallel with the slightly curving ocular ridges. About a third of the total width is taken up by the convex glabella, as measured interocularly, and a quarter across the posterior border. Glabella parallel-sided, rounded anteriorly, and reaching to the anterior margin. S0 (occipital furrow) continuous but deeply indented laterally, defining a short (sag.) occipital ring only one eighth the overall length of the cranidium. A short, sharp, posteriorly projecting occipital spine is present. L0 is a third of the length of the cranidium, defined anteriorly by S1, continuous and slightly broadened medially, and like the occipital furrow sharply indented laterally. It is set slightly behind the centre of the eye. Glabella anterior to S1 occupies about half the total length of the cranidium, forming the anteriorly rounded frontal region.

Librigena. This tapers laterally to a very long, stout and highly curved genal spine, rounded in cross-section and lacking flanges. The librigena curls round the outer tips of the thoracic spines, tapering slightly, to terminate well behind the body (apart from the axial and caudal spines). Eye holochroal, semicircular, and very large, with many lenses. Below it the sloping surface of the librigena has a faint sculpture of fine veins.

Hypostome. The hypostome (Figs 11F; 12E, F) illustrated from intact specimens, is very similar to that described for *C.* (*Ctenopyge*) *gracilis* and other species of the subgenus though there is an evident intraspecific variation in the dimensions of the posterior border. Illustrated specimens are 0·5 mm long (sag.) and 0·7 mm wide across the anterior wings.

Thorax. Thorax of ten segments. Anteriorly, excluding spines, it is as broad as the cranidium, and the axis is about a quarter of the total width. It is parallel-sided up to about the fifth thoracic segment, quite sharply tapering thereafter, and the same is true of the external contour (without the spines). Each axial ring is strongly arched, about a third as long (sag.) as it is broad, and equipped with a short, stout medial spine. At the outer anterior edge of each axial ring there is a pair of short, deep indentations, like those of S0 and S1. Thoracic segments each with an oblique pleural furrow, and distally bearing long spines. Of these, the first three thoracic segments have spines of similar form, being slightly constricted at the base, then curving posteriorly to terminate at a distance of about three times the width of the proximal part of the thoracic segment. These spines are borne horizontally; they are flattened and extend into broad flanges proximally while being pointed at the tips. The proximal part of each of these is oblate in section, but with sharp edges (Fig. 13G); distally they become trapezoidal (Fig. 13E, F) with a narrow central ridge on the upper surface and a corresponding groove below. The spines of the fourth segment are flanged proximally, distally becoming narrower, while the spines of the fifth thoracic segment are swollen at the base. The remaining posterior spines, forming a radial fan, are of ‘normal’ appearance, rounded in cross-section (Fig. 13H) and becoming straighter and shorter posteriorly. The final spine pair, of the tenth thoracic segment, is very short, almost subparallel, like that of the occipital ring, that of the tenth segment is remarkably long as is the caudal spine of the tiny triangular pygidium; both of these extend well posteriorly, beyond the tips of the genal spines.

Whereas the flanged spines extend horizontally from the body, the thinner spines towards the rear appear to be directed upwards at an increasing angle posteriorly, but how steeply they rose, and what the original angle of the axial and caudal spines actually was remains unknown.

Remarks. As for *C.* (*Ctenopyge*) *gracilis*. The flanged thoracic spines resemble those of *C.* (*Ctenopyge*) *falcifera*, though the latter is known only from distorted specimens. There is a superficial similarity to the flanged genal spines of *C.* (*Ctenopyge*) *fletcheri*, for which the thoracic segments have not been described. In *C.* (*Ctenopyge*) *fletcheri*, however, the lateral flanges of the genal spines are broad and flat, and the central plateau has a groove rather than a ridge.

2.4. Observations on earlier developmental stages

It is possible that the earliest developmental stages of *C.* (*Ctenopyge*) *ahlbergi* are similar to those of the other *C.* (*Ctenopyge*) species described here. Yet in the well-preserved degree 6 meraspis illustrated here, 3·5 mm long and 3·8 mm

Figure 6 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland. (A, C) Degree 2 meraspis, thorax damaged, transitory pygidium rotated. LO 8962t: (A) × 65, (C) Enlargement of pygidium showing marginal spines, × 260; (B) Degree 2 meraspis showing marginal and caudal spines of remarkable length. LO 8963t, × 85 (D) Degree 3 meraspis with long, intact, left genal spine, margins of transitory pygidium damaged; degree 2 meraspis overlying on right side. LO 8964t, × 55; (E) Degree 3 meraspis with detached thorax and pygidium, librigenae missing. LO 8965t, × 75; (F) Degree 4 meraspis cranidium showing occipital node. LO 8966t, × 80. All SEM photographs of latex replicas.

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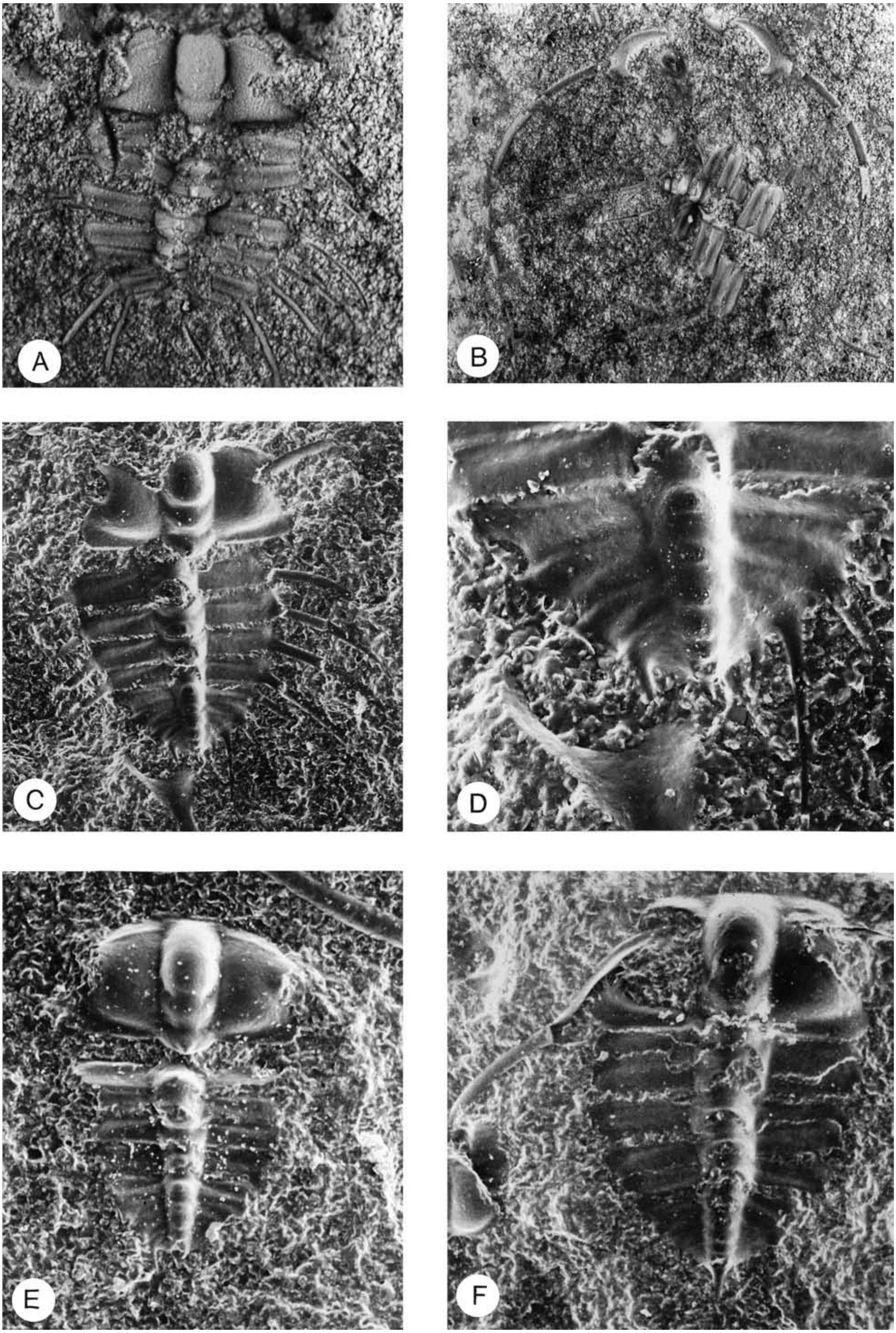

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wide (Figs 11B; 12A; 14), the distinguishing features of the adult are already present though less well developed. Thus there is an evident broadening of the body, with the genal spines becoming strongly curved round the outside of the spinose thorax, and the first three or four thoracic spines flatter and broader than those posteriorly. We interpret these as incipient flanges.

A single degree 8 meraspis (Fig. 12B) is virtually of adult form.

Ctenopyge (*Ctenopyge*) *rushtoni* n. sp.
Figs 12G–H; 15; 16A–H

Derivation of name. In honour of Dr Adrian Rushton, in recognition of his class work on British Cambrian faunas.

Material. Several nearly complete and partial specimens from Blomberg and Toreborg, deposited in the collections of Lund University (LO).

Holotype. An almost complete specimen with a slightly rotated cranidium. LO 8989T (Fig. 15A).

Paratypes. LO 8991t (Figs 12G; 15C), LO 8992t (Fig. 15D), LO 8993t (Fig. 15E), LO 8994t (Fig. 15F), LO 8984t (Fig. 12B all from Blomberg; LO 8988t (Fig. 12H)) from Toreborg.

Type locality and horizon. Small quarry at Blomberg, western slope of Mount Kinnekulle, Västergötland, Sweden.

Diagnosis. A medium-sized species of *Ctenopyge* with long curving genal spines, and a thorax of ten segments, each bearing a pair of spines, nearly straight, broad at the base and tapering to a point. These spines are arranged radially, increasing in length posteriorly, but those of the tenth segment being short. The tenth segment bears a long axial spine, and the pygidium is small, forming a broad triangle, and has a long caudal spine.

2.5. Description of the adult

As reconstructed, and including spines, the body is 5 mm long and 5·5 mm broad.

Cranidium. In the holotype the cranidium is 1·3 mm long and 2·6 mm broad, including the occipital ring, trapezoidal, with a straight anterior margin and broadest posteriorly. Anterior branch of the facial suture makes an angle of some 40° to the exsagittal plane, while the posterior branch is set at some 60° thereto, subparallel with the slightly curving ocular ridges. Glabella about a third of the interocular width, and about a quarter of the total width as measured across the posterior border. Glabella parallel-sided, rounded anteriorly and reaching the raised anterior margin. S0 (occipital furrow) almost transverse and continuous, broadest medially and somewhat indented laterally. Occipital ring about a fifth of the total length of the cranidium. The posterior margin of the occipital ring is gently rounded. A prominent occipital node is present. L1 is slightly longer (sag.) than the overall length of the occipital ring, and S1 is almost identical in form to the occipital furrow. S2 presents as a pair of faint lateral pits. Glabella anterior to L2 slightly less than half the total length of the cranidium. Palpebral lobes narrow, 0·4 times the overall cranidial length, and are set slightly forward of centre.

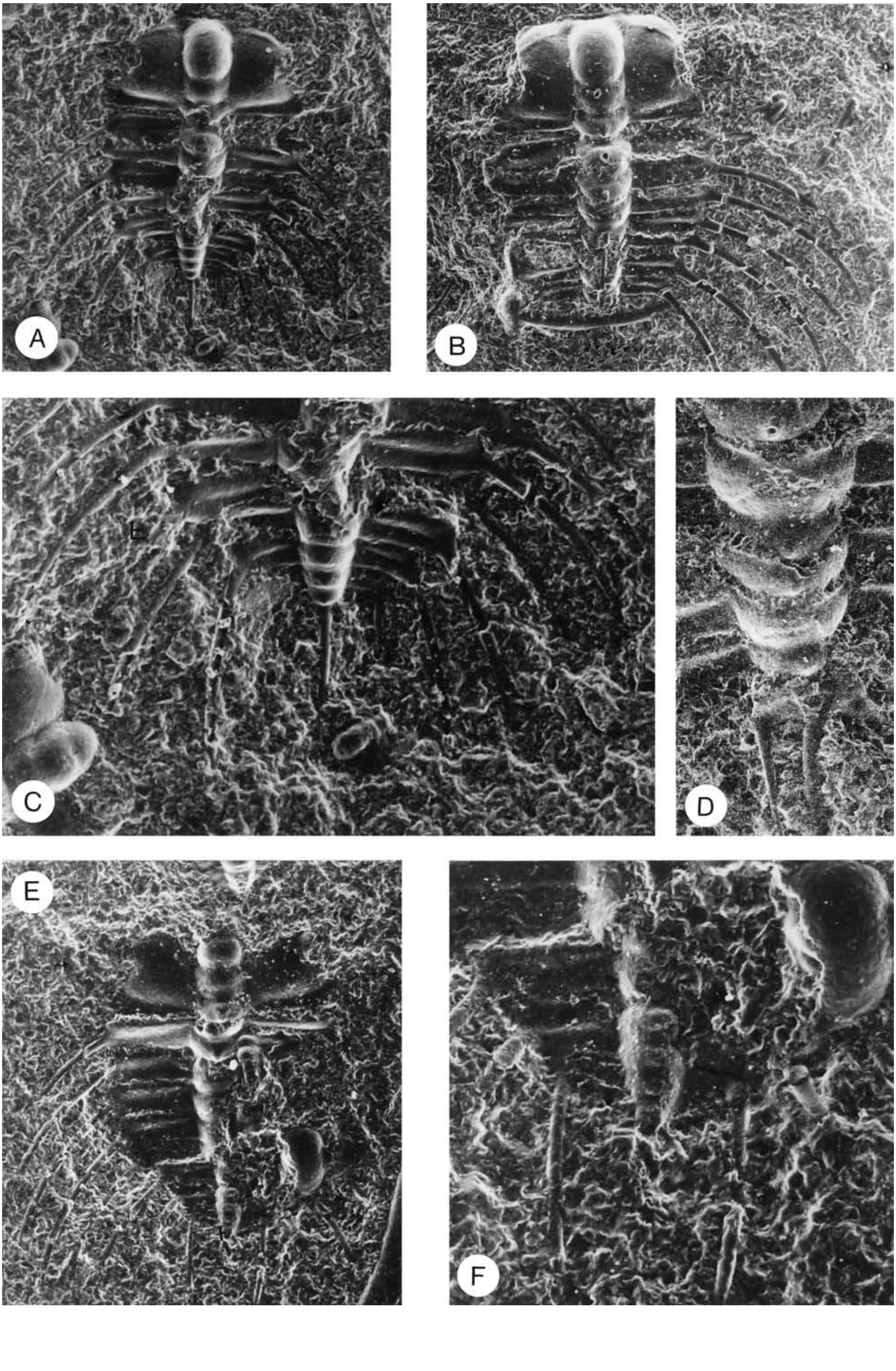
Librigena. Librigena tapers proximally quite sharply to the genal spine, anterior part of the eye is quite close to the curving anterior edge of the cephalon. Genal spine projecting outwards at an angle of some 45°, and curving posteriorly round the outside of the spinose thorax, the curvature decreasing so that the rear part is almost straight, tapering posteriorly, terminating at a sharp point, and is rounded in cross-section for its whole length. The distance between the genal spine, the short anterior thoracic spines and the longer posterior spines decreases rearwards. Eye holochroal, large, and with many small lenses. There is no discernible surface sculpture on the librigena or any part of the cephalon.

Hypostome. The hypostome (Figs 12G, H; 13B, C) illustrated from intact specimens, is very similar to that described for *C.* (*Ctenopyge*) *gracilis* and other species of the subgenus. Illustrated specimens are 0·75 mm long (sag.) and 0·65 mm wide across the anterior wings.

Thorax. The thorax consists of ten segments; slightly longer than broad, excluding spines, and is widest at the level of the fourth thoracic segment. Axis is about a quarter of the total width; it is parallel sided anteriorly, but posteriorly from about the fourth segment taping towards the rear. Axial rings, of very similar form to the occipital ring, strongly arched, half as long as broad, and each has a central node. Pleurae about three times wider than they are long (sag.), each traversed by an oblique pleural furrow. Each segment bears a pair of very strong tapering spines, broad-based and with pointed tips, and all these spines originate slightly below the level of the pleura from which it arises. They are arranged radially so that the spines of the first segment arise at about 60° to the exsagittal plane, whereas those of the tenth segment are nearly parallel with the axis. The spines of the first thoracic segment are triangulate in form, curving slightly backwards, and about half the length of the adjacent pleura. In section these spines are ridges, the anterior surface being the steeper, and the lower surface is slightly concave. While a triangulate, broad-based form is evident in the succeeding segments, they become increasingly elongated towards the rear so that those of the ninth segment are two and a half times as long as the pleurae from which they originate; this pair may be slightly sinuous in form and in the holotype are inclined at some 25° to the exsagittal plane. The relative length and inclination of these spines, however, is a very variable feature, but they always seem to have near-equal spaces between them. Final pairs of spines much shorter, parallel with the axis, and this tenth thoracic segment bears a long, narrow axial spine, similar to that of the caudal spine of the small, broad-based triangular pygidium; this spine lies directly below the axial spine. The more posterior spines, like those of the other species of *Ctenopyge* described here, are raked upwards, their inclination increasing posteriorly, at an angle which is as yet indeterminate.

Remarks. This species closely resembles *C.* (*Ctenopyge*) *gracilis* and *C.* (*Ctenopyge*) *ahlbergi*. The stout-based thoracic spines, however, bear some comparison with those of *C.* (*Eoctenopyge*) *flagellifera*, and the anterior spines of *C.* (*Ctenopyge*) *pecten*. *C.* (*Ctenopyge*) *falcifera*, known only from

Figure 7 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland. (A) Degree 5 meraspis, largely intact apart from librigenae, but with some thoracic and pygidial spines visible, and a caudal spine. LO 8967t, × 19·5; (B) Degree 5 meraspis lacking cranidium, with rotated librigenae; possible moulting configuration. LO 8968t, × 25; (C, D) Degree 4 meraspis, largely intact with well developed thoracic spines, librigenae scattered (under right side of cranidium and south of pygidium). LO 8969t: (C) × 40; (D) Transitory pygidium, showing well-developed marginal spines and scar of broken caudal spine. × 120; (E) Degree 4 meraspis, with well-preserved cranidium, thoracic and pygidial spines broken. LO 8970t, × 43; (F) Degree 5 meraspis, slightly flattened with librigenae somewhat displaced, thoracic and pygidial spines broken off, caudal spine present. LO 8971t, × 38. All SEM photographs of latex replicas.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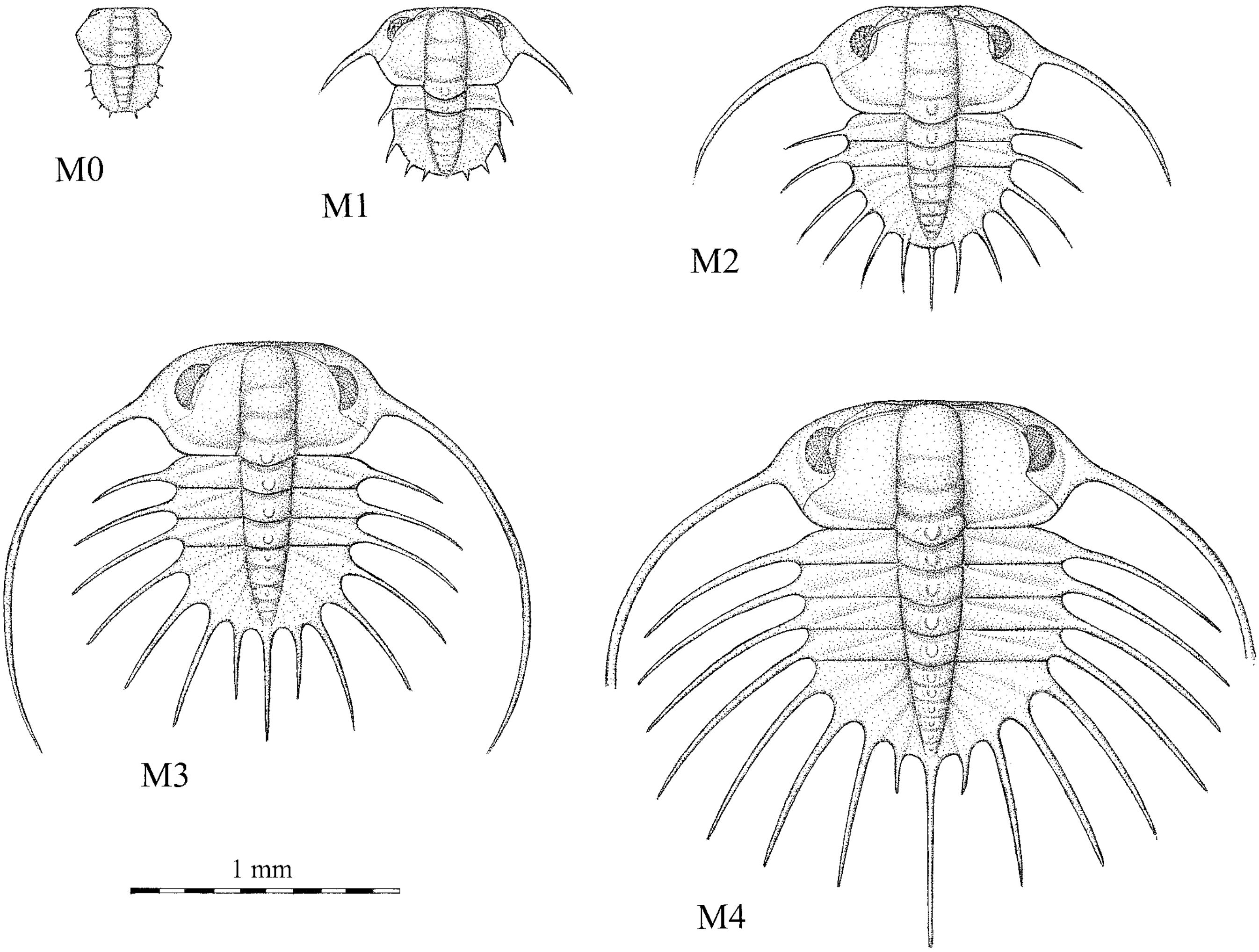

Figure 9 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. Reconstruction of meraspid degrees 0–4.

distorted British specimens, appears to have a longer curved margin to the librigena behind the spines.

2.6. Observations on earlier developmental stages

The incomplete meraspides illustrated here (Fig. 16A, B), tentatively assigned to degrees 6 and 7, are of remarkably similar form to the adult (Fig. 16C). As preserved, lacking the pygidium, they are of length 1·2 mm and 1·9 mm respectively. The distinctive thoracic spines are already present in M6, and in M7 the librigenal spines are of virtually adult form. The only real difference is that the posterior thoracic spines are shorter and less fully developed than in the adult. Even at these meraspid stages *C.* (*Ctenopyge*) *rushtoni* cannot be confused with any other species.

Ctenopyge (*Mesoctenopyge*) *tumida* Westergård, 1922
Figs 17; 18A–D; 19; 20A–D

1880 *Ctenopyge*? sp. indet. Linnarsson, p. 26 (156) pl II (156) fig 15
1922 *Ctenopyge tumida* n. sp. [partim]. Westergård, p. 155, pl XI, figs 15–18
1923 *Ctenopyge tumida* Westergård [partim]. Poulsen p. 39, pl. 1, fig 14
1947 *Ctenopyge tumida* Westergård [partim]. Westergård p. 24
1957 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård. Henningsmoen p. 198, pl 5, pl 20, fig 16
1971 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård. Rushton, in Taylor & Rushton, p 32–33, fig. 8a
1973 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård. Schrank, p. 825, Taf. VII, figs 13–20, 22, 23
1992 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård. Cope & Rushton, p. 547, fig 5 m–o

Material. (i) A very large specimen from Toreborg (Fig. 17A); (ii) Several smaller specimens from Toreborg and Blomberg, representing a partial ontogeny.

2.7. Description of the adult

Cranidium. Cranidium forming a laterally stretched hexagon, slightly more than twice as broad as it is long, including the occipital ring. Anterior margin transverse, with a very thin anterior border separated from the front of the glabella by a narrow furrow. A pair of nodes is set on the

Figure 8 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland. (A, C) Degree 6 meraspis, lacking librigenae; caudal and axial spines present. LO 8972t: (A) × 28, (C) Details of posterior region. A protaspid with frayed edges lies S of the axial spines. × 55; (B) Degree 7 meraspis, lacking librigenae and transitory pygidium, of somewhat smaller dimensions than would be expected (see text). LO 8973t, × 55; (D) Posterior axial region of an adult specimen. The axial and caudal spines are broken off and lie side by side. LO 8974t, × 40; (E, F) Degree 5 meraspis, lacking librigenae, with subconcentric thoracic spines, inclined more posteriorly than is usual. LO 8975t: (E) × 70, (F) Detail of transitory pygidium. × 190. All SEM photographs of latex replicas.

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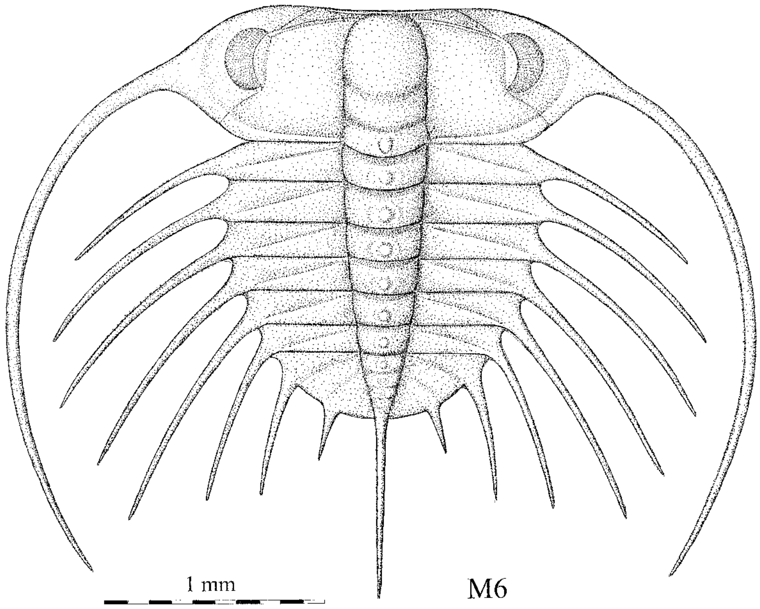


Figure 10 *Ctenopyge* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. Reconstruction of meraspid degree 6.

anterior margin, at the points where the straight anterior border curves slightly backwards to join the palpebral lobes, which are connected to the anterior part of the glabella by slightly oblique ocular ridges. Centres of palpebral lobes set opposite S3 (S4 in the Norwegian material described by Henningsmoen), their rear edges being at about the midpoint of the total length of the cranidium. Anterior branch of facial suture forming an angle of some 70° to the transverse plane. Posterior branch set at cranidial mid-length; usually transverse or directed slightly backwards in smaller individuals. Inter-ocular part of the librigena about the same width as the glabella, while the postocular area is at least 1·5 times the glabellar width. Behind the posterior branch of the facial suture the posterior border is rounded, becoming transverse posteriorly, the posterior furrow is shallow but broad. Occipital furrow, just behind S1, constricted medially, broadening laterally, thereby isolating a raised, oblate, central dome, twice as broad as it is long, with a pronounced occipital node.

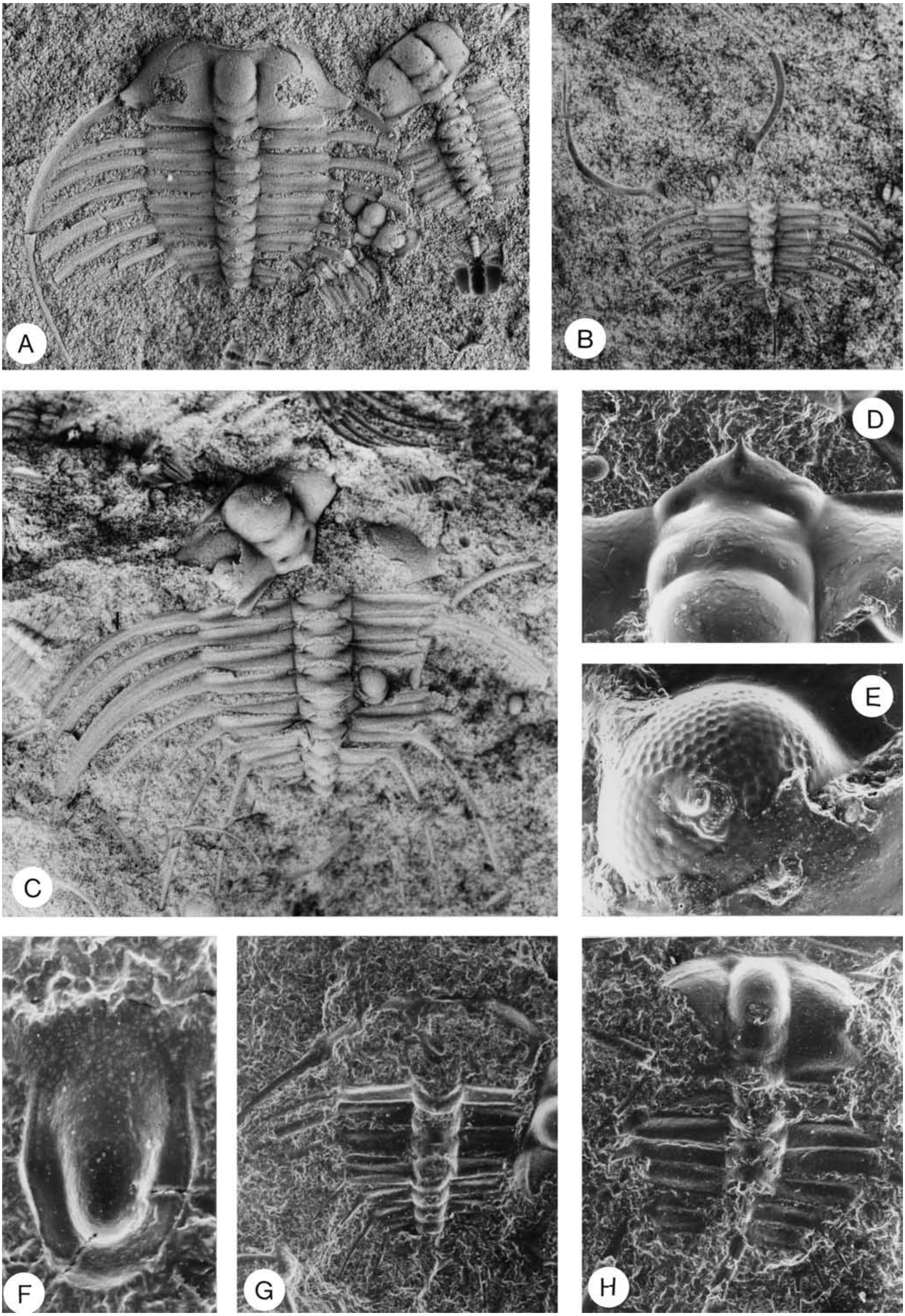
Glabella, as its base, occupying a quarter to a third of the total cranidial width; it tapers forwards and virtually reaches the anterior border, with a transverse or slightly indented anterior margin. Axial furrows straight, each at an angle of some 10° to the sagittal plane. There are four almost equally spaced glabellar furrows, and an intercalary furrow set just anterior to the occipital furrow (S0) and somewhat indented laterally against the axial furrows, but with the transverse central part hardly inscribed. S1 is somewhat deeper centrally, but laterally deeply indented, forming a pair of short, profound impressions, directed posteriorly at some 20° to the transverse plane. In the otherwise similar S2 furrow the lateral parts are very deep, short, and transverse, S3 is represented only by a pair of very small, deep, lateral pockets. The depth of impression of the glabellar furrows seems to be a relatively variable feature.

Librigena. The specimens in our material lack librigenae, apart from the largest individual in which part of the long curving genal spine is present. What can be seen of its morphology agrees with that described by Westergård (1922, p. 201, pl XI, fig. 17) in which he describes the librigena as "small, sloping greatly from the eye to the margin, angulate in outline, spine broad and long, placed backwards". No librigenae were figured by Henningsmoen (1957), but Schrank (1973, Taf VII, figs 18, 19, 21) illustrated three.

Hypostome. A single partial hypostome is associated with the cranidium of a small holaspis (Figs 18A; 20D). It has a slightly curved anterior margin with a very thin, sharp border, and a narrow elongated, strongly upraised middle body with a rounded posterior margin. At the widest point visible the middle body is about a third the overall width. Unfortunately the posterior brim is hidden under the adjacent cranidium; in previously described species of *C.* (*Mesoctenopyge*) this is broad and distinct. An adult hypostome was figured by Schrank (1973, Taf. VII, fig. 7), with a broad and flanged brim.

Thorax. Thorax spinose, two and a half times as long as the cranidium (sag.) and consisting of ten segments, somewhat less broad than the postocular cranidium at its widest point (excluding spines), and almost parallel-sided, tapering only slightly towards the rear. The segments are longer (sag.) anteriorly and decrease in this dimension towards the rear. The rachis occupies the central third of the body and likewise tapers only slightly posteriorly. Each of the thorax axial rings bears a pair of short, curving, deeply incised lateral furrows, isolating them from the articulating half-rings. Behind these there is a pair of slightly swollen triangular nodes. Posterior to

Figure 11 *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp. *Peltura minor* subzone, Västergötland: (A) Small holaspis (left), holotype, with flanges and only slightly displaced librigenae, LO 8976T, lying alongside an adult *C.* (*Eoctenopyge*) *angusta*. LO 8977t, both × 10, Blomberg; (B) Degree 6 meraspis, slightly abraded, with librigenae and hypostome rotated; thickening spines are visible. LO 8978t, × 11·25, Blomberg; (C–E). The largest known specimen, cranidium rotated, right librigenae present though genal spine broken off — the curving spine on the right probably belongs here, left librigena partially buried. LO 8979t: (C) × 12, (D) Detail of occipital region, × 26, (E) Detail of eye, × 100, Toreborg (see also Figure 13); (F) Detached hypostome. LO 8980t, × 60, Blomberg; (G) Degree 8 meraspis, lacking cranidium, but with genal spines. Hypostome rotated, axial spine present. LO 8981t, × 42, Blomberg; (H) Degree 6 meraspis, lacking librigenae. LO 8982t, × 70, Blomberg. (A) and (C) are light micrographs of latex replicas of external moulds; (B) of an original specimen; (D–H) are SEM photographs of latex replicas of external moulds.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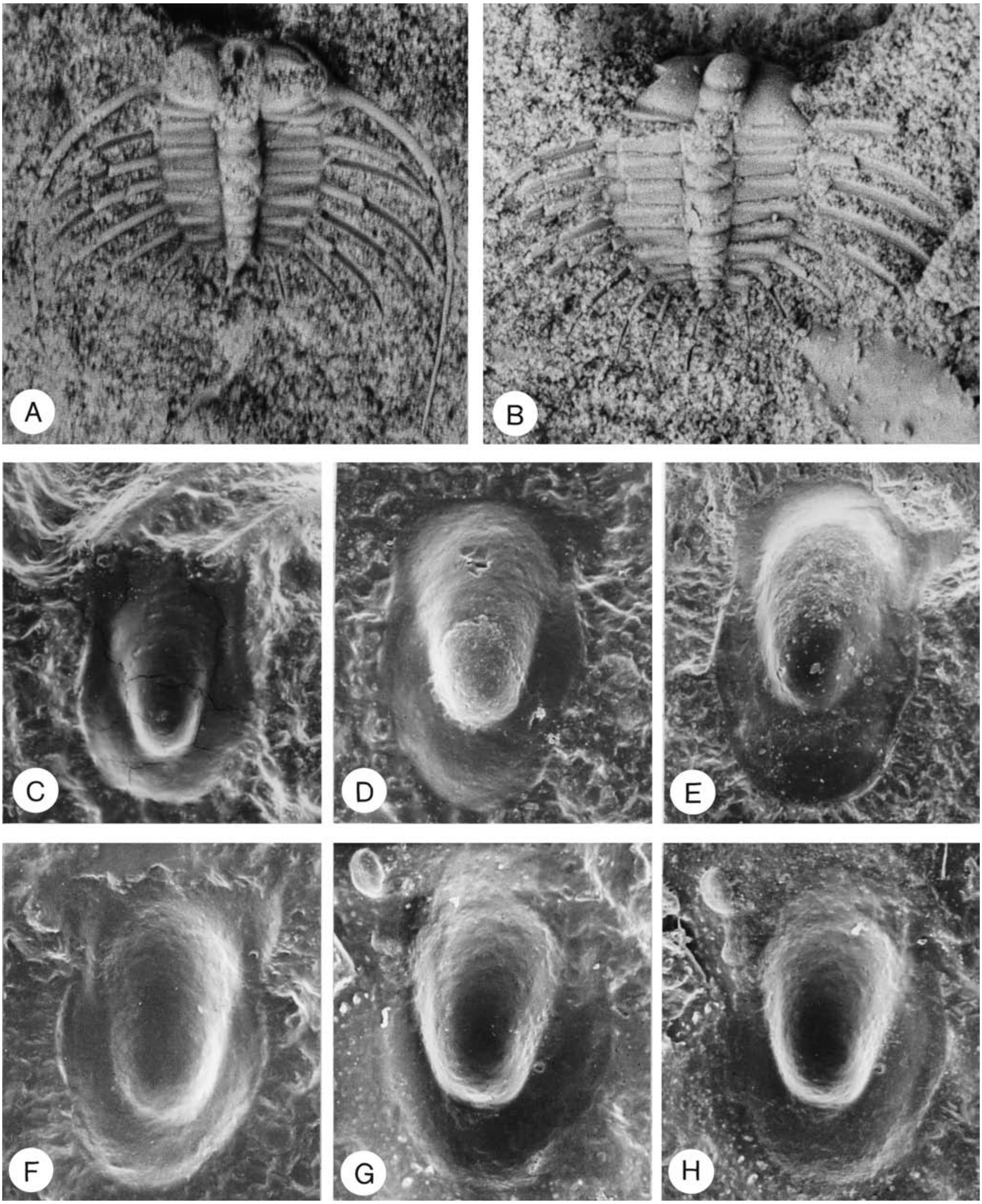

Figure 12 (A, B, E. F) *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp. *Peltura minor* subzone, Västergötland: (A) Degree 6 meraspis, abraded individual lacking cranidium but with the hypostome in place. LO 8983t, × 20, Original specimen, Blomberg; (B) Degree 8 meraspis, lacking librigenae, cranidium tilted forwards and rotated. LO 8984t, × 15, Original specimen, Blomberg; (C, D, G. H) Hypostomes of the three *Ctenopyge* (*Ctenopyge*) species shown for comparison: (C, D) *C.* (*Ctenopyge*) *gracilis* Henningsmoen, 1957. *Peltura minor* subzone, Blomberg, Västergötland: (C) Small adult hypostome. LO 8985t, × 75, (D) Larger adult hypostome. LO 8946t (see also Figure 1B), × 75, Blomberg; (E, F) *C.* (*Ctenopyge*) *ahlbergi* n. sp.: (E) Adult hypostome. LO 8986t, × 60, Toreborg; (F) Adult hypostome. LO 8987t, × 62, Toreborg; (G, H) *C.* (*Ctenopyge*) *rushtoni* n. sp.: (G) Adult hypostome. LO 8991t (see also Figure 15C), × 85, Blomberg; (H) Adult hypostome. LO 8988t, × 85, Toreborg. (A) and (B) are light micrographs of original specimens, (C–H) are SEM photographs of latex replicas of external moulds.

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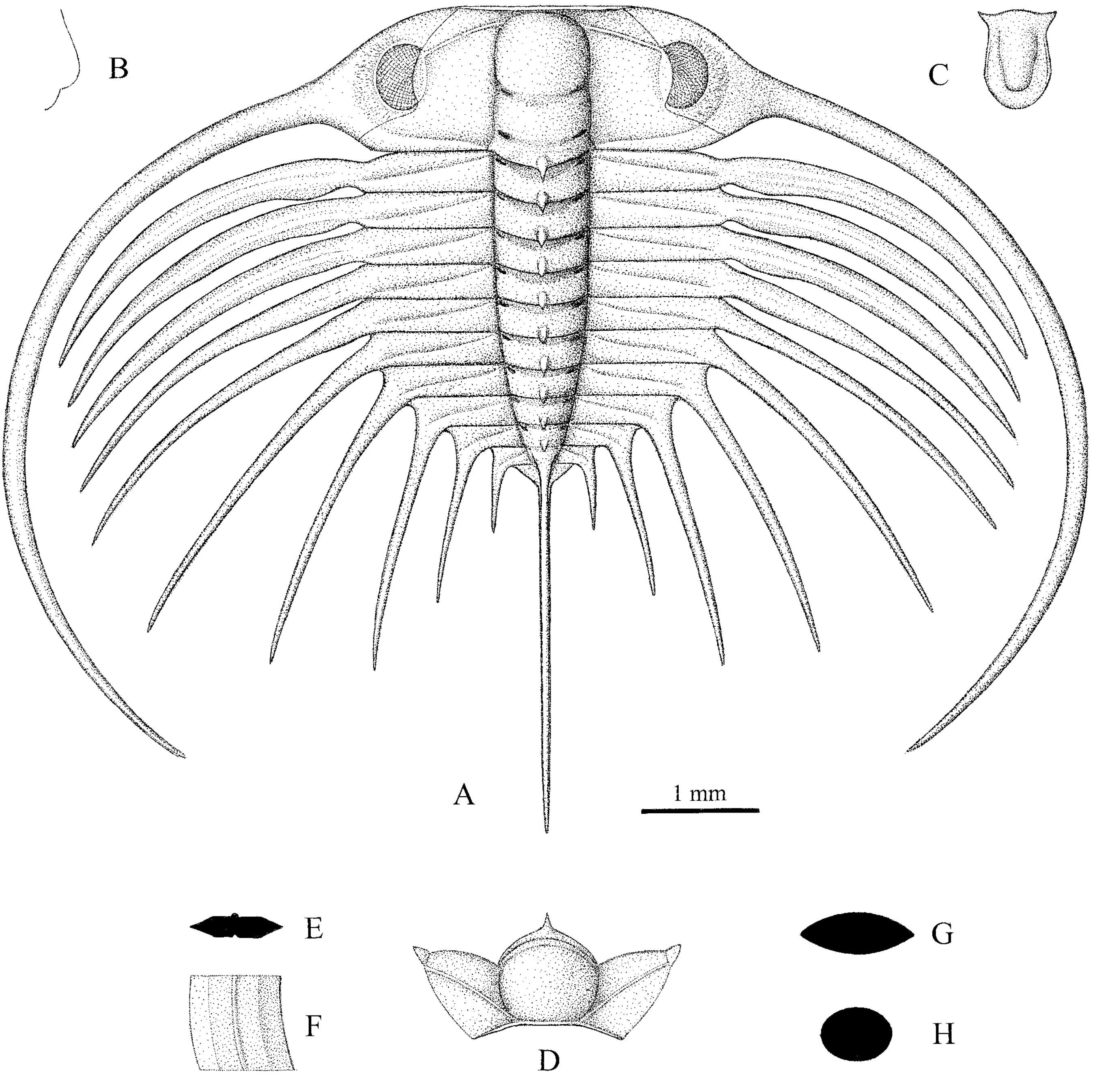

Figure 13 *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp.: (A) Reconstruction of adult in dorsal view; (B) Hypostomal profile; (C) Hypostome; (D) Anterior view of cranidium. A–D all to same scale. (E) Third thoracic spine in section, midway along its length; (F) Surface view of same; (G) Section through proximal part of same spine; (H) Seventh thoracic spine in section. E–H enlarged to the same scale.

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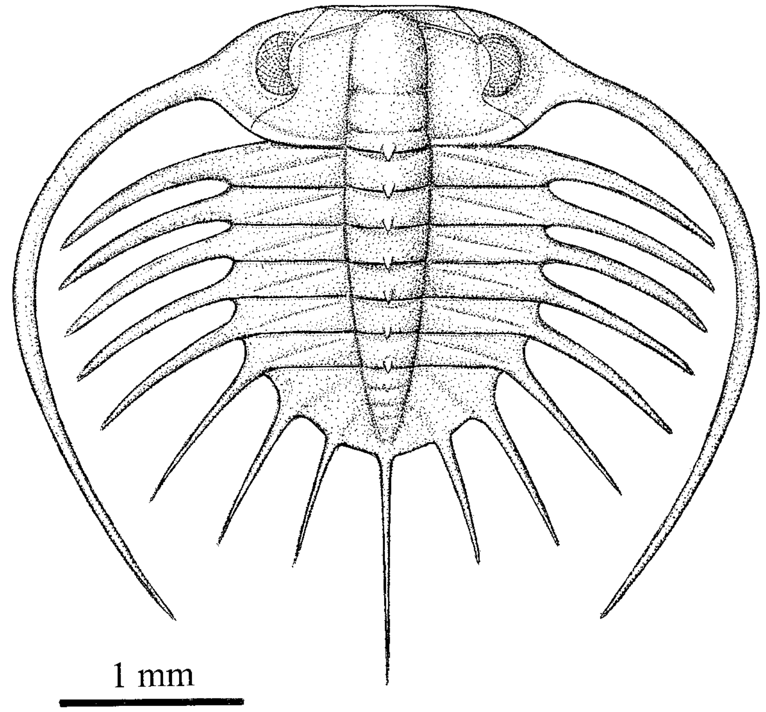


Figure 14 *Ctenopyge* (*Ctenopyge*) *ahlbergi* n. sp.: Reconstruction of meraspid degree 6.

these again is a large, oblate swollen dome, isolated from other parts of the axial ring and bearing a strong central node; this structure is like that of the occipital ring. A very strong dorsal spine, curving at its base but otherwise straight, is present on the tenth segment instead of the usual node. In life it probably rose at an angle of some 30° from the horizontal.

Pleurae of the first thoracic segment indented by a transverse shallow furrow, not reaching the outer margin. From the antero–lateral margin of this segment springs a very long curving spine, extending far posteriorly, and apparently subparallel with the genal spine. Second and subsequent pleurae with an oblique pleural furrow, proximally traversing each pleura, but distally turning forwards slightly, isolating an inflated region on either side. Each pleura bears a broad-based, but otherwise narrow spine, about twice the pleural width, and emerging from the posterior part of the pleura. These spines are almost straight, directed postero-laterally, and subparallel to each other. The spines of the second and third segments make an angle of about 40° to the transverse plane, this angle increasing posteriorly, so that the rearmost of the radial fan of posterior spines form an angle of about 70° to the transverse plane.

Pygidium. No pygidia have been found in any of our specimens; that figured by Schrank (1973, Taf. VII, fig 23) is triangular in form.

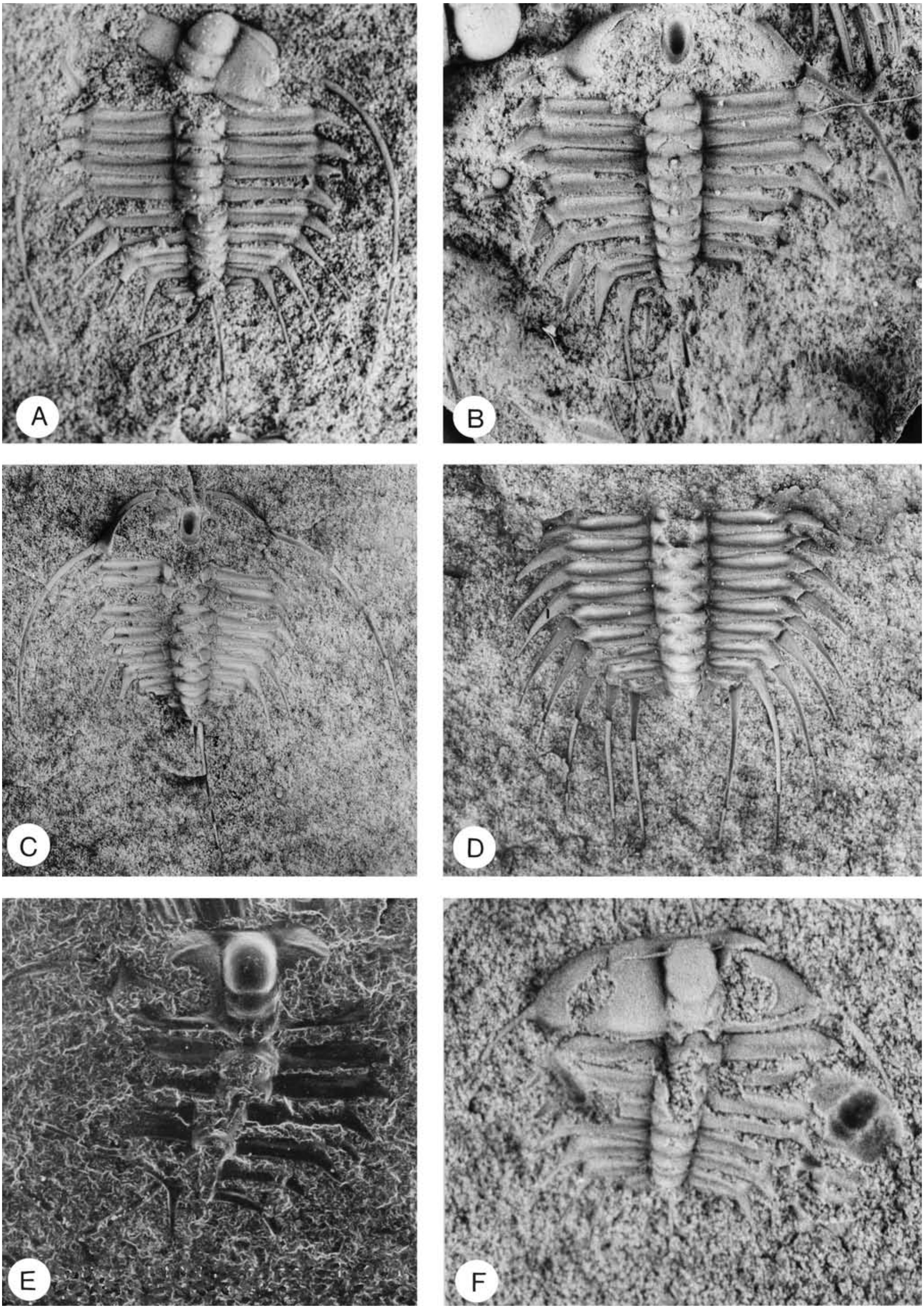
Remarks. While we describe our material as *C.* (*Mesoctenopyge*) *tumida*, even our largest specimen is only half the size of the individuals figured by Westergård (1922, pl 9, figs 15–18), Henningsmoen (1957, Pl. 20, fig. 16), Schrank (1973, Taf. VII, figs 13–20, 22, 23) and Cope & Rushton (1992, fig. 5, m–o). Moreover, in all previously published descriptions, the postocular sutures are perpendicular to the sagittal plane, whilst in our material they are more oblique, as in *C.* (*Mesoctenopyge*) *tumidoides* Henningsmoen (1957, Pl. 20, fig. 15). It is quite possible that our large specimen is still adolescent and that the oblique sutures are a juvenile feature retained from earlier growth stages, and such immaturity may account for the more forward position of the palpebral lobes than in specimens described by previous authors.

2.8. Observations on earlier developmental stages

All figured specimens, except for those shown in Figure 17E and F, are holaspides, though some are appreciably smaller than is the full-grown adult.

Figure 17E illustrates a solitary small specimen, here referred to this species, which is a small cranidium with a single attached thoracic segment. The cranidium is almost perfectly hexagonal to slightly trapezoidal, of length 0·43 mm and width 0·5 mm. The antero-lateral areas are frayed, but a partial librigena, with the proximal part of a stout genal spine, lies adjacent to the left cranidial margin and at right angles to it. This is of equivalent scale to the cranidium and is reconstructed here as belonging to it (Fig. 20A). The glabella occupies the central third of the cranidium and tapers slightly forward. Furrows S1, S2, and S3 are distinct, delimiting four glabellar lobes. The occipital ring is distinct, though damaged. The postero-lateral borders have a pronounced border furrow and the genal angle is about 115° fixigenae slightly inflated. A single thoracic segment with short, stubby pleurae is attached to the cranidium. This specimen is probably a degree 1 meraspis, but could represent a later stage.

Figure 15 *Ctenopyge* (*Ctenopyge*) *rushtoni* n. sp. *Peltura minor* subzone, Blomberg, Västergötland: (A) Holotype. Nearly intact adult, cranidium rotated. LO 8989T, × 14·5 (see also Figure 16), latex replica of external mould; (B) Nearly intact adult, lacking cranidium but with the hypostome in place. LO 8990t, × 12·5, latex replica of external mould; (C) Small holaspis, lacking cranidium, but with hypostome in place, axial and caudal spines visible. LO 8991t, × 12, latex replica of external mould; (D) Thorax of large adult, with thoracic spines of considerable length. Original specimen. LO 8992t, × 6·5; (E) Degree 6 meraspis with displaced librigenae and separated thoracic segments; caudal spine of transitory pygidium visible. LO 8993t, × 48, latex replica of external mould; (F) Degree 7 meraspis, librigenae almost in place, pygidium missing. LO 8994t, × 22. All light micrographs except for (E) (SEM).



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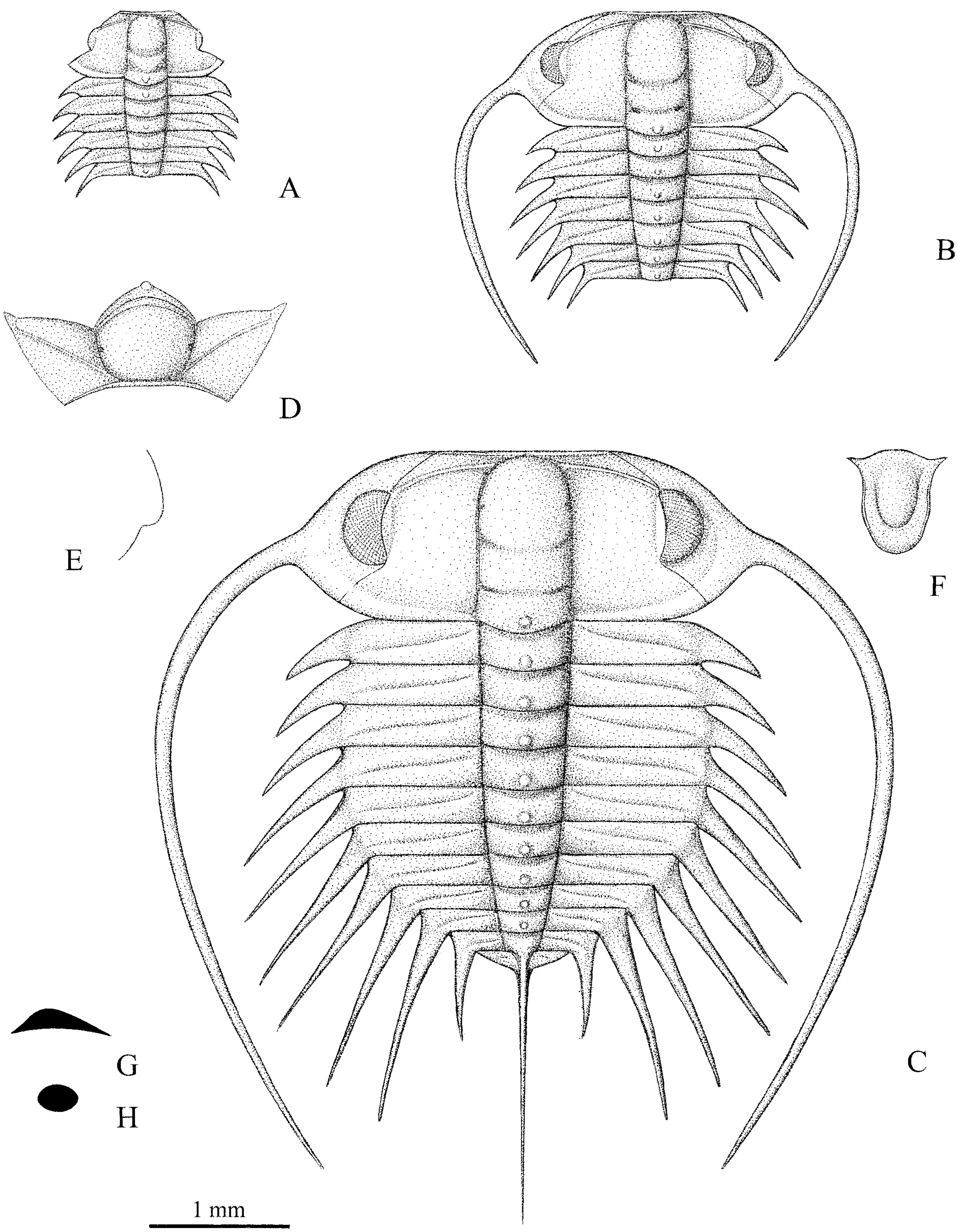

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A partial degree 5(?) meraspis, of preserved length 1·5 mm, is of distinctly adult-like form, though with a less broad cranidium (Figs 17F; 20B). Slender thoracic spines are present on the last three segments. The remaining figured specimens all probably represent young holaspides. They differ from the adult in being smaller, and that figured in Figures 17G; 18A, B and D has long posterior thoracic spines. There is no evidence of whether the long spines of the first thoracic segment are developed in the early holaspides; the reconstruction (Fig. 20C) shows them as of normal length.

3. Unassigned protaspides

Four protaspides (Figs 18E–H), not especially well-preserved, almost certainly pertain to *Ctenopyge*, though to which subgenus or species is uncertain. They are broadly similar to protaspides of other olenids (Strand 1927; Størmer 1942; Clarkson & Taylor 1995; Clarkson *et al*. 1997). The individual shown in Figure 18E, almost circular and 0·26 mm long and wide, may be an anaprotaspis. The protoglabella is about a third of the width of the whole, and has five distinct axial rings. The other three specimens (Figs 18F–H) are larger and are probably metaprotaspides. They are of broadly trapezoidal form, 0·325 mm long and 0·5 mm broad. They differ from the presumed anaprotaspid in having a pronounced postero-lateral border, and a glabella slightly less than a third of the total width. The five axial rings remain distinct. Figure 18F illustrates the best-preserved specimen in which there is a suggestion not only of intergenal spines but also of lateral spines. The protaspis may indeed have had six marginal spines in all, like that of *Jujuyaspis* (Tortello & Clarkson 2003), and *Leptoplastides*, which also has an occipital spine (Raw 1925). This indication, however, remains to be sustained by further discoveries of *Ctenopyge* protaspides. Whereas the protaspides of leptoplastines generally tend to be more highly cambered and coiled down posteriorly than those of other olenids, those figured here are of relatively low convexity.

4. Functional morphology of the five *Ctenopyge* species

Within the Västergötland assemblages, all the trilobites belong to the genus *Ctenopyge*, save for the zonal index fossil *Peltura minor*. All five *Ctenopyge* species are very spiny and show, as has long been understood, a degree of evolutionary convergence with the odontopleuroids. The thoracic spines of *C.* (*Mesoctenopyge*) *tumida*, for instance, are very like those of *Selenopeltis*. What is most remarkable is the great diversity of size and form of contemporaneous species within the one genus *Ctenopyge*. In particular, the spines have become modified in different ways, and presumably for various functions. The extremely spinose aspect of the fauna as a whole contrasts dramatically, for example, with the short-spined *Olenus* species of Zone II. So why should this be so?

Of the five species of *Ctenopyge* present, the easiest to interpret functionally is the previously-described *C.* (*Eoctenopyge*) *angusta*. In this species (Clarkson *et al*. 2003) the genal spines are very long and in lateral view are seen to extend horizontally, parallel with the extended thorax. This is the least spinose of the five species under review, and only the macropleural spines of the seventh, and to a lesser extent the eighth and ninth, thoracic segments are particularly developed. It is significant that these thoracic spines are all parallel with the genal spine. The axial spines on the last segment are likewise horizontal, and the pygidial axial spine rises at an angle of 10°–15° above it. These small trilobites, with their large eyes subtending a wide field of view, appear well adapted both for swimming and for resting on the sea floor. When swimming, the parallel, horizontal spines would act as stabilisers. These trilobites may have swum by darting around in short bursts.

As noted elsewhere, the genal spines, like those of *Leptoplastus crassicornis*, are so constructed as to spread the weight of the body when resting on the sea floor, but with the high carriage of the body ensuring that the gills were clear of the bottom. The early growth stages may have been planktonic as in many other trilobites (Chatterton & Speyer 1997), but the genal spines were well developed enough to allow residence on the sea floor, in the adult manner, from about meraspid degree 4 onwards.

There is a striking contrast here with *C.* (*Ctenopyge*) *gracilis*. Here again the genal spines are long and slender. They curve posteriorly so as to run a little way outside the tips of the thoracic spines, and since they also extend horizontally they are likewise adapted for sea-floor resting. The body is held high above the sea floor, ensuring that the gills would be well clear of any muddy or anoxic sediment on the bottom. But if the body is outstretched horizontally, the more posterior spines rise up as an inclined, slightly curving fan. Elegant and graceful though this may seem, there seems to be no immediately apparent functional reason for it, and the inclined spines must have produced at least some drag effects if the trilobite were swimming forward. It is unlikely that these trilobites were rapid swimmers, unlike *C.* (*Eoctenopyge*) *angusta*. One possibility is that the spine array of the outstretched trilobite was a defensive or threatening armament, a deterrent against conodonts or other predators that lived in the same environment.

Relaxation of the extensor muscles would allow the body to fall into an alternative posture, the 'sad frog' attitude. Here the tips of the axial, caudal, and thoracic spines would come to lie in the same plane as the horizontal genal spines, and the maintenance of such a resting posture for an extended period of time would require little energy. There is a distant parallel here with the two alternative life attitudes (active and resting) described (Clarkson 1969) for the odontopleuroid *Leonaspis deflexa*, but they cannot be matched in detail.

C. (*Ctenopyge*) *ahlbergi* is appreciably larger and has up to ten thoracic segments. The genal spines are stout, though not preserved in the large holotype, and known only from smaller specimens. They curve round the outer edge of the thoracic spines, and presumably functioned like the genal spines of other species of *C.* (*Ctenopyge*) as supports for the body when resting on the sea floor. Where this species differs most dramatically from *C.* (*Ctenopyge*) *gracilis* is in the form of the anterior thoracic spines. The lateral spines of the first three thoracic segments, though shorter than those of *C.* (*Ctenopyge*) *gracilis*, are long and curving, and each is equipped with a pair of lateral flanges on either side of the central rib. These flanges are slightly expanded near the base. The fourth spine pair of likewise swollen at the base but otherwise remain slender and pointed. All these spines lie in the same horizontal plane. The posterior spines are remarkably

Figure 16 *Ctenopyge* (*Ctenopyge*) *rushtoni* n. sp.: (A) Partial reconstruction of meraspid degree 6; (B) Partial reconstruction of meraspid degree 7; (C) Adult in dorsal view; (D) Adult cranidium in anterior view; (E) Hypostomal profile; (F) Hypostome. A–F all to same scale. (G) Third thoracic segment in section; (H) Seventh thoracic segment in section. (G), (H) enlarged to same scale.

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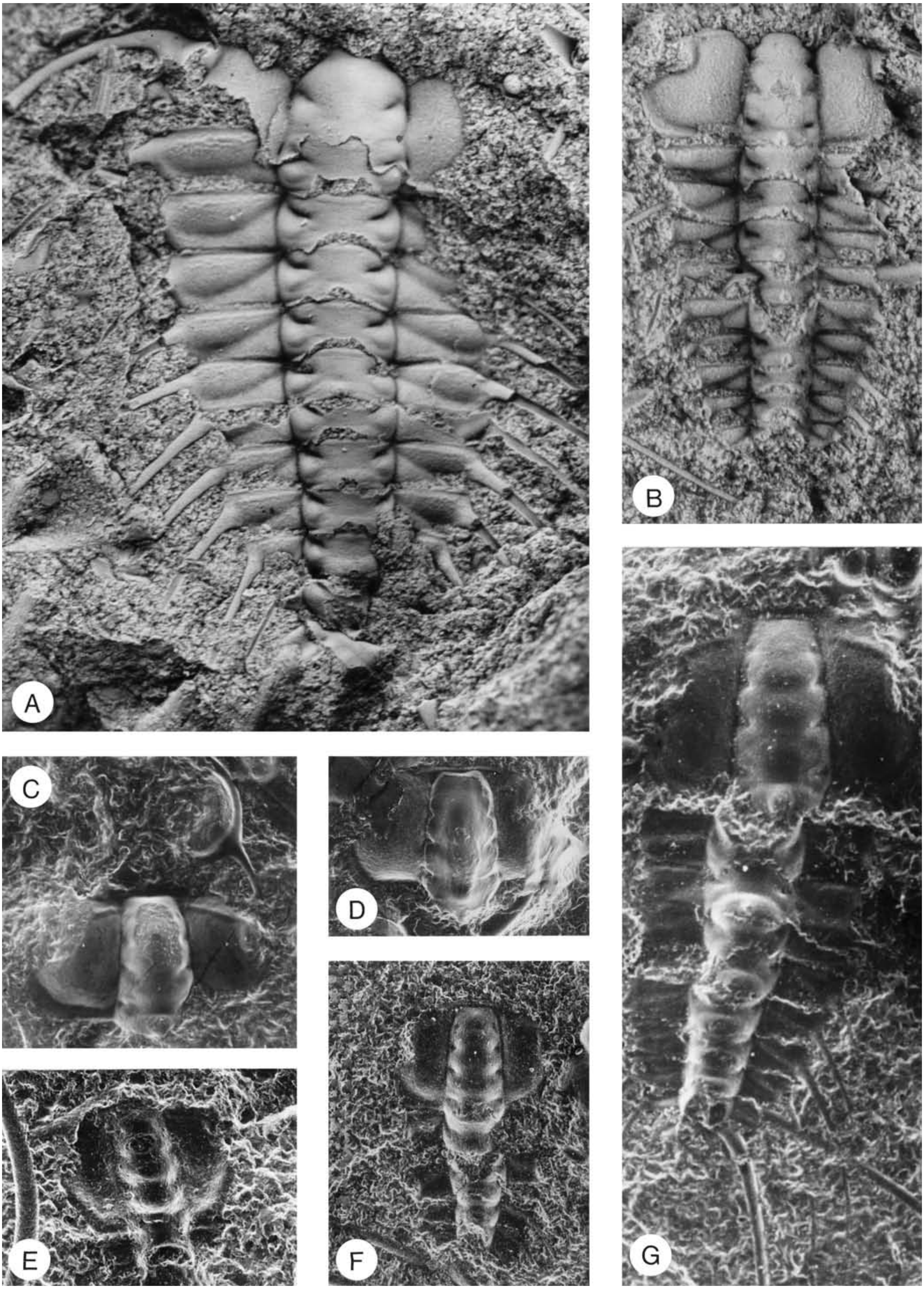
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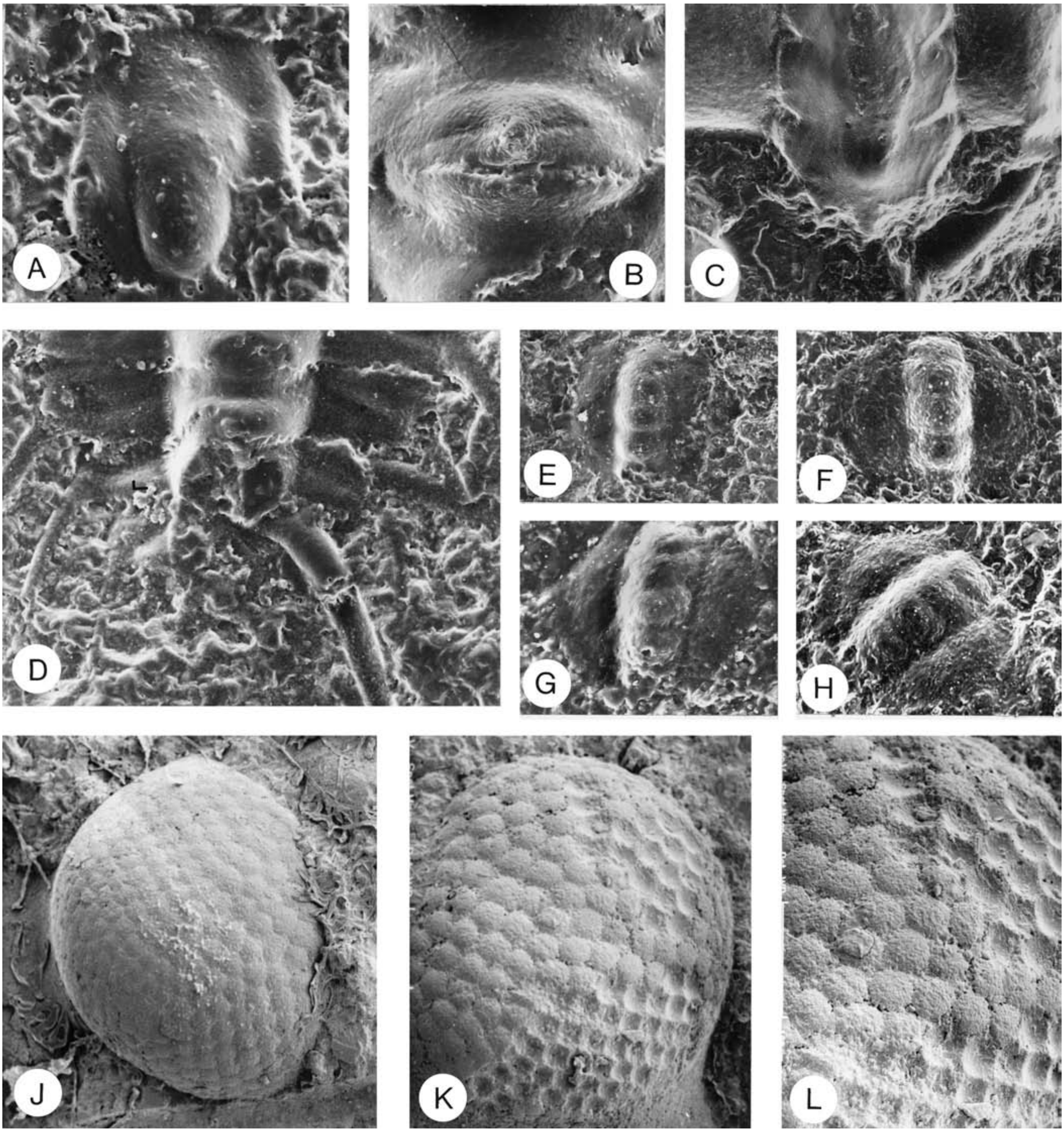

Figure 18 (A–D) *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922. *Peltura minor* subzone, Västergötland: (A) Hypostome of specimen illustrated in Figure 17(G). LO 9152t, − 280, Toreborg; (B) Axial structure of same specimen (Figure 17(G)). × 300, Toreborg; (C) Occipital ring of specimen illustrated in Figure 17(D). LO 9149t, × 40, Blomberg; (D) Posterior region of specimen illustrated in Figure 17(G) showing displaced axial and (?) caudal spines. LO 9152t, × 200, Toreborg. (E–H) Unassigned protaspides, all × 100: (E) LO 9153t; (F) LO 9154t; (G) LO 9155t; (H) LO 9156t, all from Blomberg. (J–L) Eyes, probably belong to *C.* (*Ctenopyge*) *gracilis*, though possibly to another *C.* (*Ctenopyge*) species: (J) LO 9157t, × 110; (K) LO 9158t, × 140; (L) enlargement of same. × 200, Blomberg.

Figure 17 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922. *Peltura minor* subzone, Västergötland: (A) Largest known specimen. LO 9146t, × 18, light micrograph (see also Figure 19); (B) Young holaspis or (possibly) degree 9 meraspis, lacking librigenae, latex replica of external mould. LO 9147t, × 25 (see also Figure 20(C)); (C) Cranidium of small holaspis and associated librigenae (above). LO 9148t, × 24; (D) Cranidium of small holaspis. LO 9149t, × 20 (see also Figure 18(C)); (E) Early meraspid cranidium with one attached thoracic segment. LO 9150t, × 60 (see also Figure 20(A)); (F) Partial degree 5(?) meraspis. LO 9151t, × 32 (see also Figure 20(B)); (G) Young holaspis or degree 9 meraspis, lacking librigenae but with thoracic spines and one (or two) axial spines. A rotated hypostome lies W of the cranidium (partly shown). LO 9152t, × 43 (see also Figure 20(D)). All are latex replicas of external moulds; (A) and (B) are light micrographs, (C–G) SEM photographs. (A–C, E–G) are from Toreborg, (D) from Blomberg.

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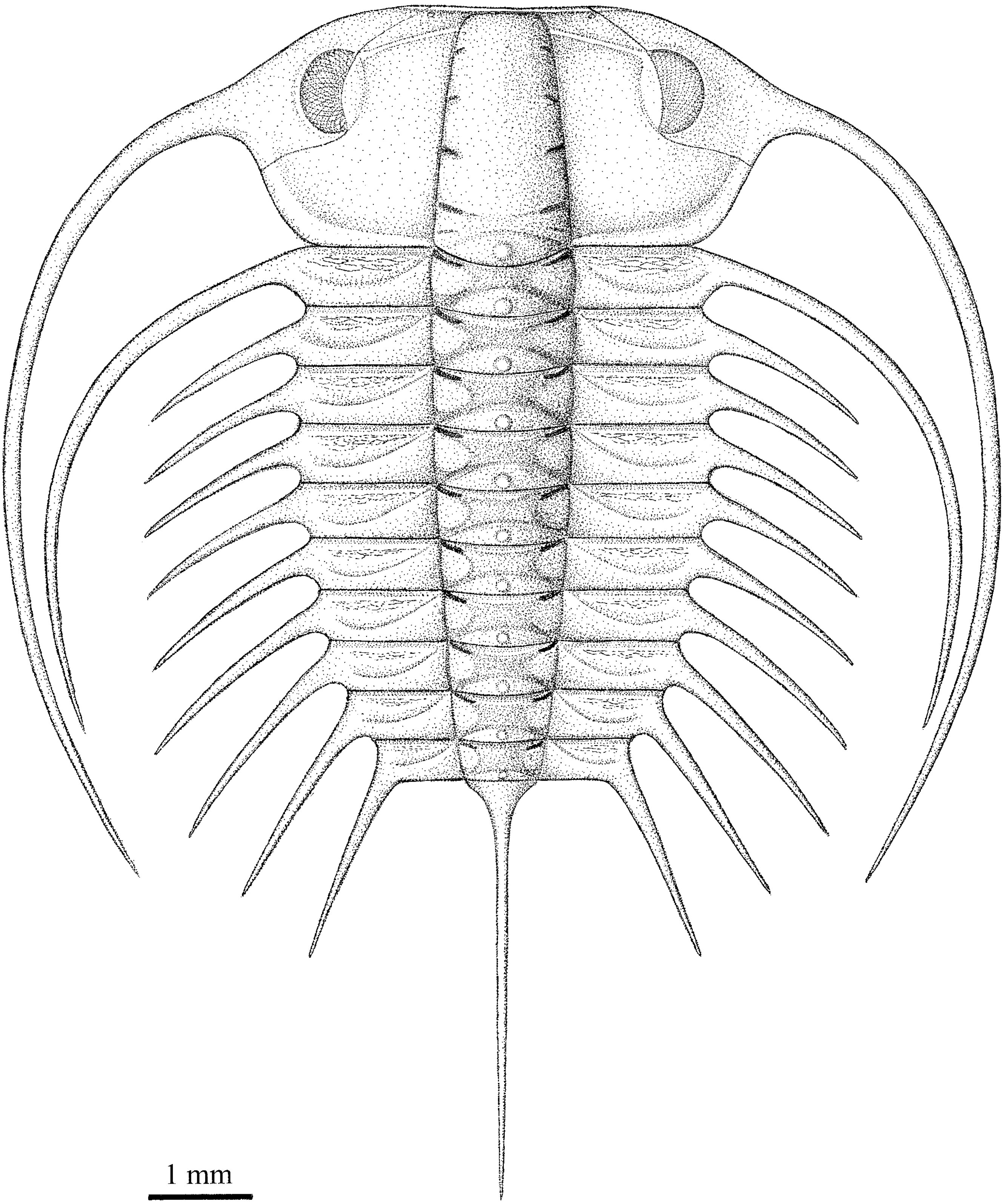

Figure 19 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922. Reconstruction of a large individual in dorsal view.

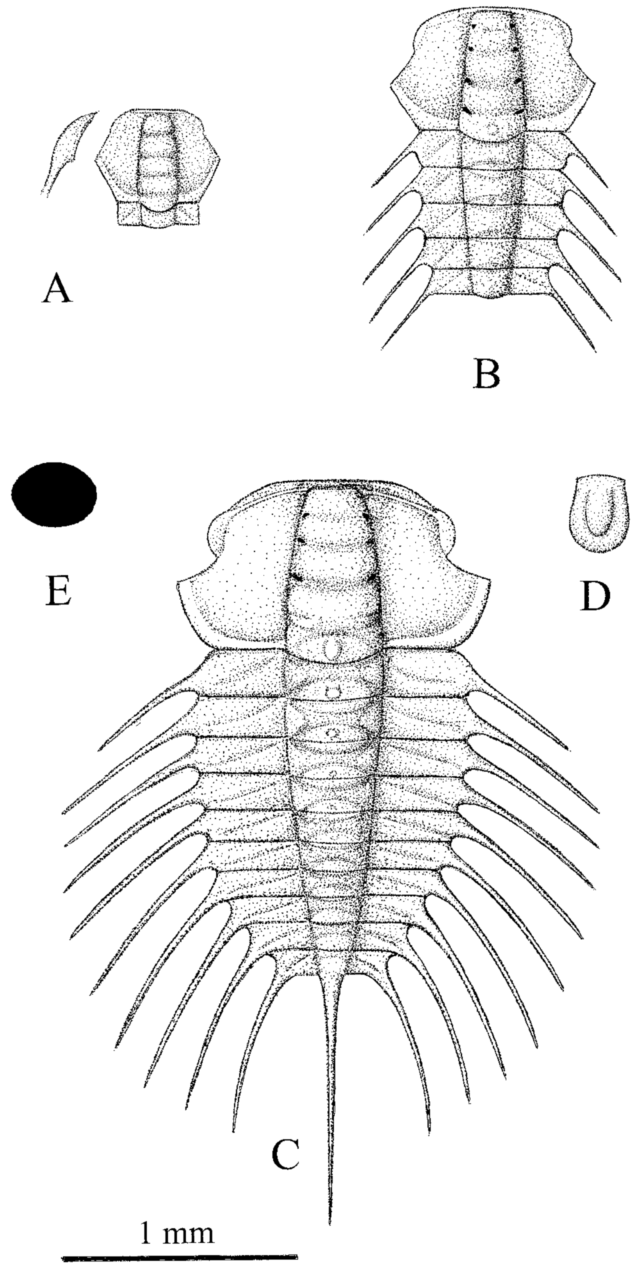

Figure 20 *Ctenopyge* (*Mesoctenopyge*) *tumida* Westergård, 1922: (A–D) Reconstruction of early growth stages; (A) ?Degree 1 meraspis; (B) ?Degree 5 meraspis; (C) Young holaspis; (D) Hypostome thereof. (A)–(D) all to same scale. (E) Section through thoracic spine of adult, enlarged.

like those of *C.* (*Ctenopyge*) *gracilis*, and likewise would form a raised fan if the trilobite were extended horizontally. The flanged spines may have acted as stabilisers in a swimming trilobite, or as protectors for the gills. But Fortey's (1999, 2000) case for olenid trilobites as chemoautotrophic symbionts may suggest an alternative function. Fortey notes that many modern metazoans, tolerant of hypoxic conditions, make use of colourless sulphide bacteria both as a food source and for detoxification, in counteracting the effects of high sulphide concentration. He comments that in symbiotic metazoans, bacteria are cultivated on special regions of the body, or are incorporated in tissues such as the gills. In *C.* (*Ctenopyge*) *ahlbergi* might the flanges have acted as bacterial 'nurseries'? Whilst this cannot be proved, the fact that only the three anterior spine pairs and the proximal parts of the fourth pair have flanges, i.e. in regions which would be accessible for feeding using scraping gills or legs, seems consistent with this suggestion.

C. (*Ctenopyge*) *rushtoni* is more stoutly built than *C.* (*Ctenopyge*) *gracilis*, with stronger thoracic spines. Again, when the body is outstretched, the posterior spines form a rising tail fan and the two axial spines are raked upwards. Whilst a not dissimilar mode of life may be proposed for this species to that of *C.* (*Ctenopyge*) *gracilis*, some kind of niche partitioning must be construed.

The few, and incomplete, specimens we have of *C.* (*Mesoctenopyge*) *tumida* do not permit a functional interpretation. It is worth mentioning, however, that this species does not have the rising tail fan of the *C.* (*Ctenopyge*) species. The peculiar conformation of the axial rings is hard to interpret functionally. We might also point out that in none of the specimens of this species we have, nor in those we have seen in other collections, is the pygidium present. According to Henningsmoen (1957, p. 184), the rarity of pygidia in adult *Ctenopyge* may be a function of the small size thereof, but also of the caudal spine becoming embedded in the mud on death or ecdysis, and the pygidium thereby breaking off more easily.

Comparison of flanged spines in different species reveals minor, but probably significant details in their construction. Whether the presence of flanges can be used to infer relationships remains unclear, and will continue to do so until further morphological information for other species is forthcoming.

5. Growth and variability

In our previous work (Clarkson *et al.* 2003, fig. 6) we presented a graphical plot of growth and development in *C.* (*Eoctenopyge*) *angusta* based upon many specimens of this common species. Here we were able to show distinct instar groupings, as did Clarkson & Ahlberg (2002) for the miniaturised *C. ceciliae*. The other four *Ctenopyge* species are much less common in this fauna, but we present a graph (Fig. 21) which illustrates both isometric growth and some tendency to clustering in *C.* (*Ctenopyge*) *gracilis*. This species is the most variable in the fauna, both in terms of overall morphology and size of meraspid degrees, for, as previously noted, some individuals of degree 7 (M7(s) on Fig. 21) for instance are appreciably smaller than others representing the same degree. A few points are plotted for the rarer *C.* (*Ctenopyge*) *rushtoni* and *C.* (*Ctenopyge*) *ahlbergi*; those for the former species giving a somewhat different growth trajectory, and thereby emphasising that these are indeed separate species. In view of the small sample no further interpretation is possible at this stage.

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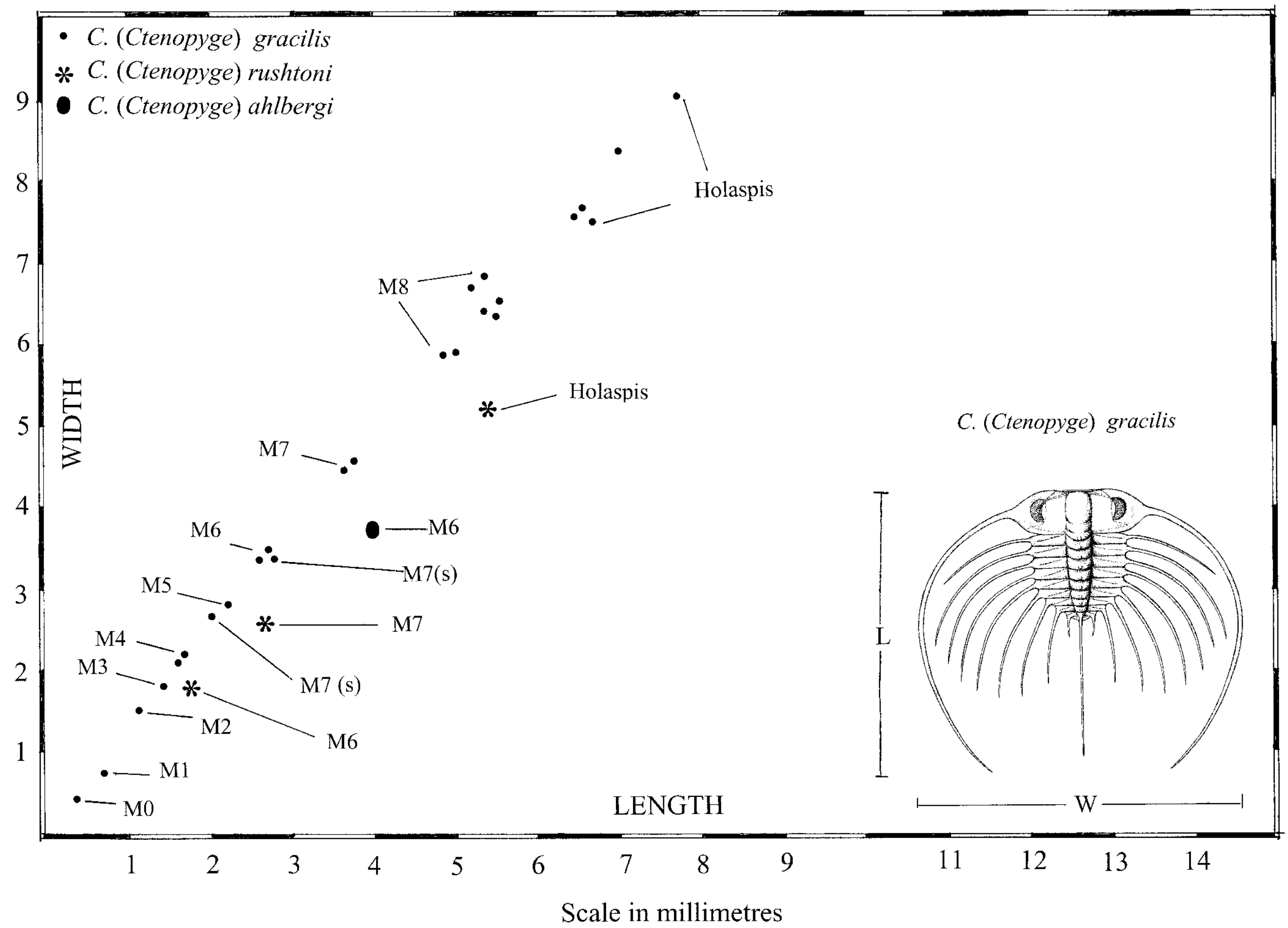

Figure 21 Graphical plot showing length and width, as indicated, for three species of *C.* (*Ctenopyge*); some tendency to clustering is evident for *Ctenopyge* (*Ctenopyge*) *gracilis*, even with the small sample.

and assistance in this respect was given by Professor Kent Larsson.

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