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OLENELLOID TRILOBITES: TYPE SPECIES, FUNCTIONAL MORPHOLOGY AND HIGHER CLASSIFICATION

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Type or topotype specimens of the type species of the genera *Olenellus*, *Nevadia*, *Wanneria* and *Elliptocephala* are redescribed, together with similar specimens of *O. vermontanus* and *O. robsonensis*. Entire, or almost entire, exoskeletons of all these species are known. In the light of this re-investigation, and of recent descriptions of Canadian, Scandinavian and Russian material, the exoskeletal morphology of olenelloids is reviewed. The exoskeleton was convex, sloping gently downwards from the axial furrow, more steeply distally. The perrostral suture and probably a circumocular suture were present, dorsal sutures are unknown. A macropleural third segment, a large axial spine on the fifteenth segment, and a subdivision of the thorax at this segment, appear to characterize species of *Olenellus* and its close relatives. In species of other genera there may be a transition between the subdivisions of the thorax, either the macropleura or the axial spine may be absent, or none of these features may be developed. Articulating flanges in the thoracic exoskeleton of *O. thompsoni* are described, and may occur in other genera; it appears probable that olenelloids could partly enrol. The small pygidium consisted of few segments, the convex axis being ill-defined, the posterior margin of the pleural region entire, bilobed, or spinose; the doublure extended under much of the posterior pleural region. The olenelloid pygidium included the telson and a few segments, and was a terminal tagma of the body, as in all trilobites. On the external dorsal surface of the exoskeleton a reticulate pattern of raised ridges is present in some species, in others the ridges anastomose, or granulation may occur. The doublure bore terrace ridges.

From the earliest olenelloid developmental stages the perrostral suture is present, the dorsal branches of the sutures absent, and the macropleura may disappear, or be retained, during ontogeny. The configurations of holaspid moults suggest that partial enrolment was essential to the process of exuviation. The perrostral and circumocular sutures facilitated such exuviation, this sutural arrangement being different from, but as effective as, the arrangements in contemporaneous and younger trilobites. Exoskeletal characters considered distinctive of olenelloids are all known in other trilobites; none is unique. The developmental stages of olenelloids, redlichioids and paradoxidoids show similarities, and holaspides have many characters in common. The order Redlichiida, embracing these groups and possibly also ellisocephaloids, is advocated, heavy weight being placed on similarities in growth stages as evidence of relationship. There is no basis for K.-E. Lauterbach's concept of the 'telosoma', or for the pygidium being an intercalary, rather than a terminal, tagma of the body in trilobites. Characters of the olenelloid exoskeleton are not like those of any Cambrian or younger chelicerate.

1. INTRODUCTION

Trilobites of *Olenellus* type were first found in New York State and Vermont, about the middle of the 19th century. Discoveries of similar trilobites in western North America, Britain and Scandinavia followed later in the century, and these striking, relatively large trilobites were recognized as characteristic of Lower Cambrian rocks in these areas. Charles D. Walcott amassed a large collection of North American material, including several entire specimens, and he summarized knowledge of olenelloids in his classic work of 1910. Since then many new finds have been described, and the geographical range of the group extended, notably by specimens from Canada, Greenland, Morocco and Siberia. Olenelloids differ from the majority of Cambrian trilobites, which have many thoracic segments and a small pygidium, in that dorsal facial sutures do not cross the gena to the large eye lobe. This lack has been regarded as separating olenelloids from other trilobites so markedly that the taxonomic rank accorded to them has risen from family to as high as order. Another morphological feature of some olenelloids is a prominent median spine arising from the fifteenth thoracic segment. Walcott thought that it was a telson, arising from the terminal segment, but this idea was derived from imperfect specimens, which lacked the posterior thoracic segments and pygidium. Walcott noted the resemblance to the telson of *Limulus*, cautiously going on to remark that 'this resemblance does not necessarily indicate that *Olenellus* was the ancestor of *Limulus*' (Walcott, 1910, p. 246). Nevertheless, the notion that such a trilobite might be ancestral to *Limulus* and its allies arose, and has had its advocates. A recent one is K.-E. Lauterbach, who goes on to argue that any such olenelloid could not be a trilobite, and that trilobites as generally understood (Moore 1959) are not a natural group. Any attempt to assess the validity of these contentions must be based on an appreciation of the morphology of olenelloids, and in particular of specimens of entire exoskeletons of the olenellids to which Lauterbach referred. Such entire specimens are rare, and some of the finest of these, from Walcott's collection, are redescribed herein, together with a much-discussed species from Canada which shows many thoracic segments. A particular attempt is made to describe the olenelloid pygidium, which featured in Lauterbach's discussion, and was said by Harrington (in Moore 1959, p. O73) to be formed of a single tergite and not homologous with that of other trilobites. Throughout this work, the term 'olenelloids' is used to embrace the superfamily that includes all trilobites of *Olenellus* type, whereas 'olenellids' is used to refer to the more restricted family-group centred on *Olenellus*.

In the light of this review, the olenelloid pygidium, though of few segments, is homologous with that of other trilobites. The olenelloids appear to constitute a related group within the trilobites, none being ancestral to limuloids. They may well be classified with other groups of Cambrian trilobites, with which they have many characters in common, in a single order. As usual from such a review, it is evident that more precise information is needed on olenelloid morphology, particularly that to be derived from further study of the Moroccan material. Lauterbach's views are couched in terms of the cladistic method, and a short rejoinder has been made in these terms (Fortey & Whittington 1989) by using some of the information given herein.

2. Systematic palaeontology

(*b*) Superfamily Olenelloidea Walcott, 1890

The family-group name Olenellidae was first proposed by Walcott (1890*b*, p. 635, as Olenellidiae), but he considered it should not be used because of its similarity to the name Olenidae Burmeister, 1843. The name Olenellidae may not be rejected on such grounds, and should therefore date from Walcott, 1890. Walcott (1890*b*, p. 635) proposed the name Mesonacidae (as Mesonacidiae) as a substitute, taking the subgenus *Olenellus* (*Mesonacis*) as the type. A family-group name must be based on a genus contained in the taxon, hence the name Mesonacidae was invalidly proposed, though widely used until Resser (1928, pp. 3–5) showed the difficulties of distinguishing between species referred to *Olenellus* or to *Mesonacis*. Subsequently, the latter name has been accepted as a synonym of the former, and the family-group name Olenellidae used rather than Mesonacidae (Raw 1936, pp. 242–243; 1937, pp. 575–576).

Poulsen (in Moore 1959) divided this group into two families and several subfamilies of olenellids, largely following Hupé (1953*a*). Bergström (1973*b*) increased the number of families to three, using, in addition to characters of the cephalon, some features of the thorax and the supposed capacity to enroll. Repina (1979) took account of the sequence of appearance of cephalic characters during the Lower Cambrian in deriving a phylogeny of olenelloids, dividing them into six families. A modification of this classification has been proposed by Ahlberg *et al.* (1986), changing the rank of previously proposed families and subfamilies. I make no choice between these differing views, my concerns here being whether the superfamily is a natural group, and how it may be related to taxa of similar rank. Classification of olenelloids needs reconsideration, in view of the discussion of early Cambrian morphological plasticity, and the role of heterochrony in evolution of Cambrian trilobites, (McNamara (1986*a*)). It would be desirable, as Repina stressed, to use in classification characters in addition to those of the cephalon in dorsal view. As the present account shows, knowledge of the olenelloid exoskeleton is inadequate to assess the importance of characters such as spines on the border of the hypostome, length (tr.) of pleural furrows, and external sculpture as used by Bergström, and Ahlberg *et al.*

(*b*) *Olenellus* Hall, 1861
(= *Fremontia* Raw, 1936; *Mesonacis* Walcott, 1885; *Paedeumias* Walcott, 1910)
Type species: *Olenus thompsoni* Hall, 1859

Shaw (1955, p. 790) and Poulsen (1958, p. 10; in Moore 1959, p. O192) attributed this genus to Billings rather than to Hall, contrary to previous practice. Hall (1862, p. 114) proposed the name *Olenellus* as a substitute for the name *Barrandia*, which he (Hall 1860, p. 115) had proposed for the species *Olenus thompsoni* Hall, 1859 (p. 59, fig. 1) and *O. vermontanus* Hall, 1859 (p. 60, fig. 2). This substitution was necessary because the name Hall first proposed was preoccupied by *Barrandia* M'Coy, 1849. Billings (dated 21 November 1861, p. 10, footnote) records that he had seen what must have been page 114 of Hall (1862) as a single loose sheet, and hence his use of the name *Olenellus* subsequently (Billings (1865, p. 11), which contains an amended version of the 1861 paper and lacks the footnote) shows that he was aware of Hall's proposal in 1861. I conclude that authorship of *Olenellus* should be attributed to Hall, 1861. The earliest designation of a type species appears to be that of Walcott (1886, p. 163).

(i) *Olenellus thompsoni* (Hall, 1859)

Figures 1–3; figures 4–8, plate 1; figures 9, 10 and 12, plate 2; figures 13 and 15; figures 17 and 19, plate 3; figure 27; figures 29, 31, and 34, plate 5.

Holotype. AMNH 244, reported by Resser & Howell (1938, p. 220) to be missing; confirmed by Dr G. D. Edgecombe, AMNH, as still missing in 1988. Resser & Howell (1938, pl. 3, fig. 19) figured a cast thought to be of this type. The type locality is in the Lower Cambrian Parker Slate, Parker Quarry, Georgia, northwestern Vermont, U.S.A.

Other material. AMNH 226 (515670), Hall Collection; AMNH 223, original of Whitfield (1884, pl. 15, fig. 1; Bell 1931, fig. 4), from the type locality. In his new genus and species *Paedeumias transitans* Walcott (1910, pp. 304–310) included specimens from the Parker Slate and material from the Kinzers Formation found at localities in the York area in southeastern Pennsylvania. It is considered (Fritz 1972, p. 11; Palmer & Halley 1979, p. 66) that *P. transitans* and *O. thompsoni* are conspecific, and the present account is based on some of the specimens used by Walcott (1910).

Description. Glabella narrowest (tr.) at slightly backward-directed S1, width across occipital ring only slightly greater than across frontal lobe; S2 and S3 successively shorter (tr.) and less deep, detached from axial furrow. Occipital ring with small median tubercle at posterior edge, occipital furrow deep distally. The long, curved eye surface is not preserved, but is outlined by a sharply defined edge (figure 13), which suggests the surface has been lost at a circumocular suture. The narrow (tr.), inflated interocular area contrasts with the broad (tr.), outward sloping extraocular genal area. In these features, and in its outline, border and slightly advanced genal spine, the cephalon accords well with Fritz's generic diagnosis (1972, pp. 11–12). The cephalic border is gently convex and of moderate width (sag. and tr.); border furrow shallow. Distally the posterior border bears a short, thorn-like intergenal spine; the border bends forward slightly outside this spine and merges into the base of the genal spine. An intergenal ridge, curving from the posterior end of the eye lobe, along the border and into the base of the intergenal spine, is visible in some specimens (figure 8, plate 1), but it is uncertain whether or not such a structure can be distinguished from the posterior border. On the extraocular gena (figures 4 and 8, plate 1) are the radiating, anastomosing ridges of the genal caecae and the genal ridge directed outwards from the mid-length of the eye lobe to the genal angle. The doublure, convex ventrally, lay beneath the lateral and anterior borders, and formed with them a tubular cephalic border which is crushed in all the specimens. The doublure was traversed by raised, concentric terrace ridges and subdivided by the perrostral suture. The narrow (sag. and tr.), sickle-shaped rostral plate may be displaced slightly (figures 9 and 12, plate 2) or swung back beneath the thorax (figure 8, plate 1). This is presumably because this latter specimen was a moult (cf. Hupé 1953*a*, p. 121, fig. 18, 3). Presumably the originals shown in figures 9 and 12, plate 2, and figures 29 and 34, plate 5, were entire animals when entombed, with the hypostome approximately in place. The outline of the hypostome is visible in both, and in the former specimen there are traces of the short spines on the posterolateral border (cf. Walcott 1910, pl. 34, figs 5–7). The external surface of the middle body bore anastomosing, raised ridges. The hypostome in small cephala of *Olenellus* (Whittington 1988*a*, p. 581) was connected to the rostral plate by a narrow (tr.) median strip (Walcott 1910, pl. 34, figs 5–7; Resser & Howell 1938, pl. 9, figs 6 and 7). The present, larger specimens show that the rostral plate was wider (sag.) medially, the inner edge curving back. The anterior margin of the hypostome lay close to the posterior edge of the rostral plate, and was probably joined to it by a short (tr.) hypostomal suture, rather than a short (sag.) mineralized strip.

Thorax composed of 18 or 19 segments, the axial region narrowing progressively backwards, of moderate convexity. Because of compaction most specimens have a fracture between axial ring and pleura, which follows and obscures the axial furrow. Where this fracture is less marked, as in the left side of segments 1–3 of figure 12, plate 2, or the right side of figures 29 and 34, plate 5, the axial furrow is shallow beside the axial ring, but deepens into a pit between the outer end of the articulating furrow and the inner, inflated end of the anterior pleural band. Presumably this pit is the exterior expression of an articulating process at the anterior margin, that fitted into a socket at the posterior margin of the next anterior ring and the cephalic margin. The first 14 rings bore a median tubercle or short spine at the posterior margin, progressively larger and more backward projecting, forming a series with the occipital tubercle. The 15th ring bore a long, upward-curving median spine, broad at the base (occupying the entire width of the ring), narrowing rapidly proximally. The cross section of this spine is difficult to determine, but it may have been subtriangular, the underside gently convex, the side broad and flat, the upper edge narrow and rounded (figures 17 and 19, plate 3).

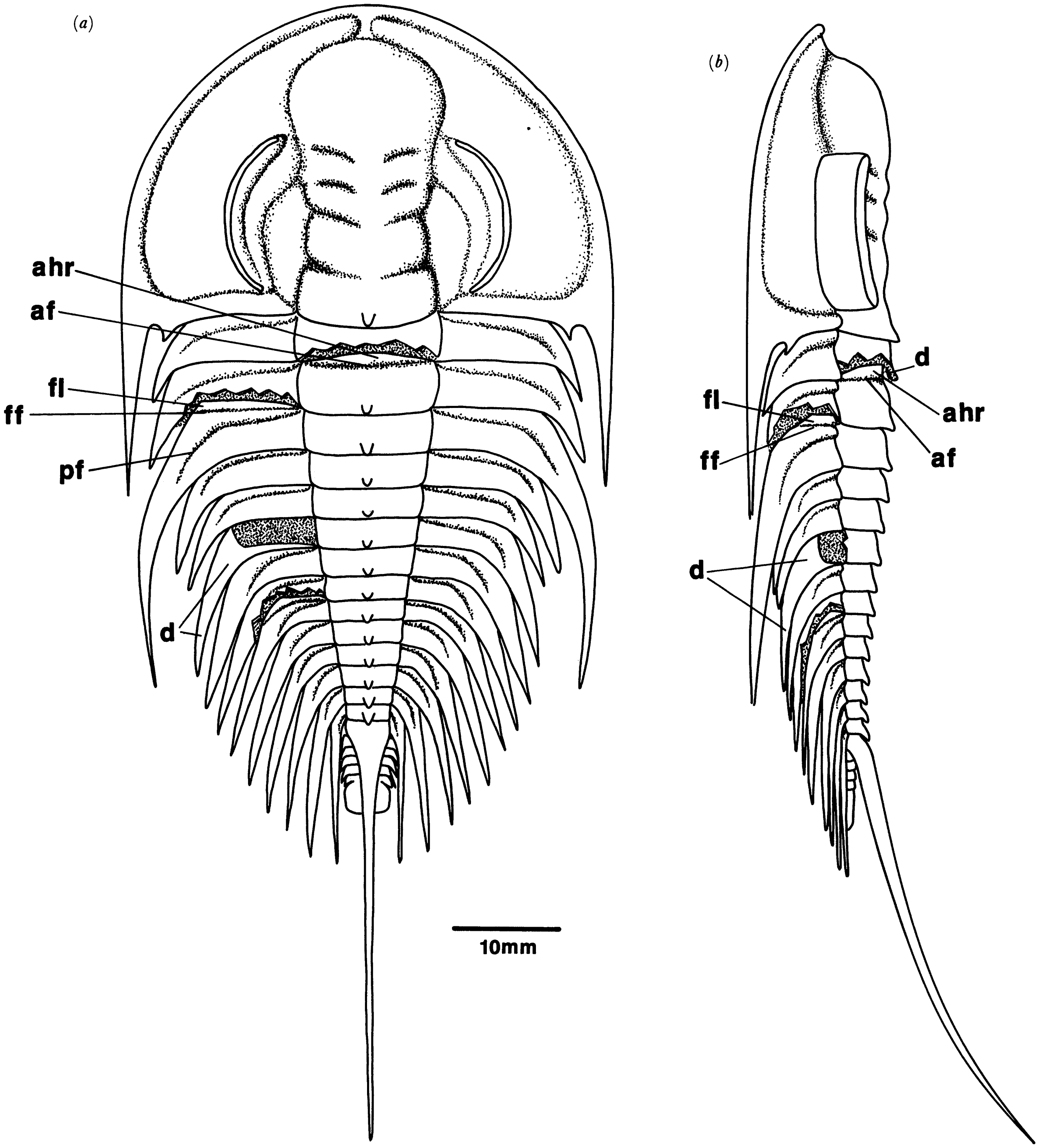


Figure 1. Restoration of exoskeleton of *Olenellus thompsoni*, based on original of figure 8, plate 1, and figures 9 and 12, plate 2. (*a*) Dorsal view with portions of thorax cut away to show concealed features. (*b*) Left lateral view, corresponding portions cut away.

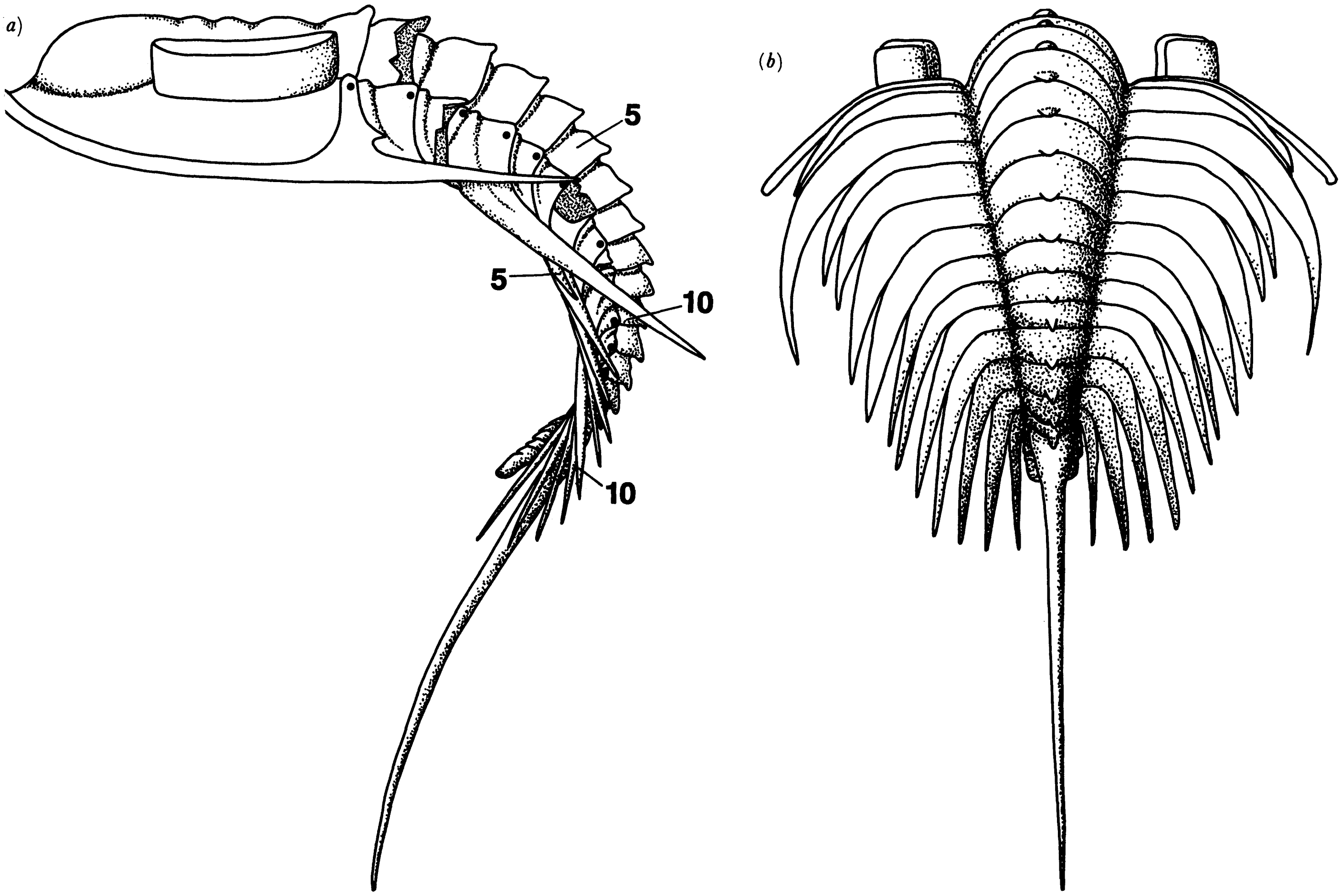
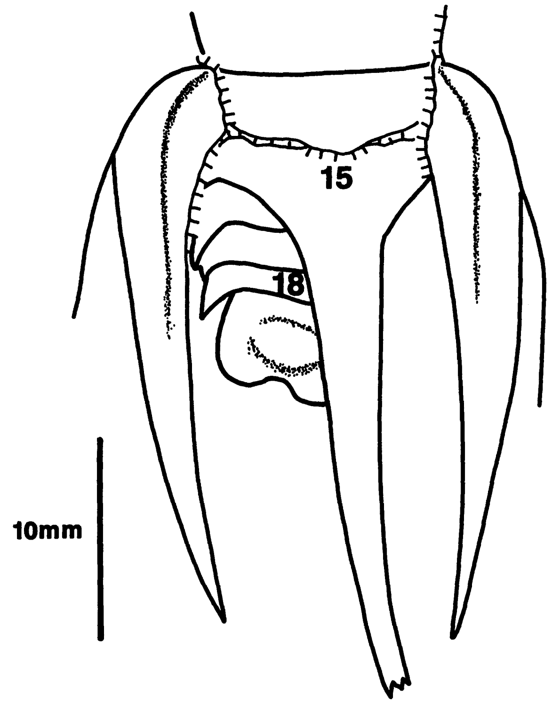


Figure 2. Restoration of exoskeleton of *Olenellus thompsoni* of figure 1, shown partly enrolled in (*a*) left lateral, and (*b*) posterior views. Filled circles in (*a*) show approximate position of axis of rotation between segments.

Proximally the underside may have been concave where it overlay the axial rings of thoracic segments 16–18 or 19. This relation is suggested by the counterpart moulds (figures 9 and 12, plate 2; figures 29 and 34, plate 5); the internal mould has the spine partly broken away and shows the axial rings of segments 14–19, convex, narrowing rapidly backwards. In the cast of the external mould the spine is complete, though crushed proximally, and must have extended close above the axial rings of segments 16–19 (cf. figure 15). Articulating furrow moderately deep, transverse, articulating half-ring longest sagittally, this length slightly less than half of the ring. Pleurae of segments 1–14 formed a series, extending at first transversely outward, then curving backwards into a spine. In the graded series the inner transversely directed portion of the pleura was progressively reduced in width (tr.), and at segment 14 had almost vanished. Pleural spines were directed successively more strongly backwards. Length of the spines differed. Those of segments 1 and 2, that lay inside the genal spine, were short. Pleura 3 was macropleural, the inner portion becoming markedly wider (exs.), the spine long and curved, backwardly directed. Pleural spines 4 and 5 were relatively short, and lay inside the macropleural spine; pleural spines 6–14 were longer and formed a series progressively more strongly backwardly directed. The doublure of the pleura ran exsagittally at the base of the pleural spine, and indicated the boundary between inner and outer portions of the pleura. Near the posterior edge of the pleura the inner margin of the doublure curved inward and ran inside this margin, to the axial furrow, giving a narrow posterior strip of doublure along the inner portion of the pleura. An internal mould (figure 8, plate 1) shows the margin of the doublure as a step in level. Along the anterior edge of the inner portion of the pleura was a flange which widened (exs.) outward; flanges have been revealed by excavation (figure 19, plate 3) or are partly exposed where the posterior edge of a pleura is broken away. The flange projected below the doublure of the next segment in front (compare figures 17 and 19, plate 3), or posterior border of the cephalon, and appears to have been bounded along the posterior side by a furrow or change in slope. On pleurae 1–14 a pleural furrow curved backwards, and outwards, across the inner portion of the pleura and on to the base of the spine; the anterior slope was steep, giving a well-defined anterior pleural band, the posterior slope gentle. Pleural spines 1–14 were hollow structures, but their cross section may well have been ovoid, the spines blade-like distally. Pleurae 15–18 or 19 are partly concealed in specimens crushed dorsoventrally by pleura 14. Pleurae 16–19 were revealed by excavation of pleura 14 (figure 31, plate 5), and by

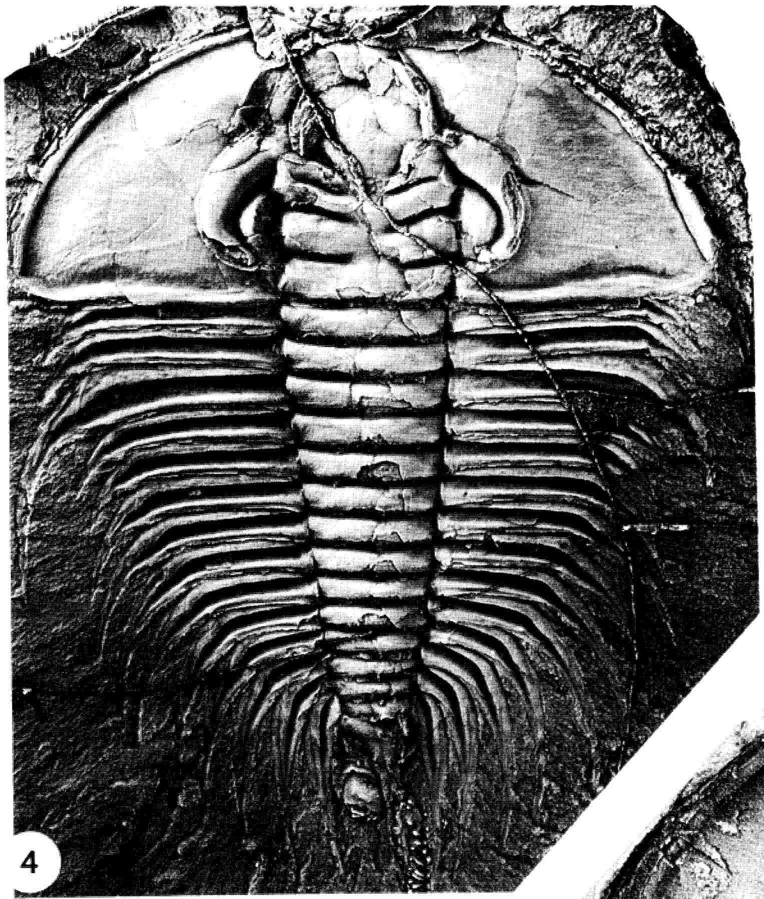


Description of figure 3 and plate 1

Olenellus thompsoni (Hall, 1859)

Figures 3, 4, 5 and 7. USNM 56808, latex cast from external mould of original of Walcott (1910, pl. 33, fig. 1), Parker Slate, Georgia, Vermont, U.S.A. Figures 3 and 5, respectively explanatory drawing, dorsal view (magn. ×3.0) of posterior portion of thorax and pygidium (cf. Walcott 1910, pl. 24, fig. 12). Figures 4 and 7, respectively dorsal view of entire specimen (magn. ×1.0), left posterior portion of cephalon and first two thoracic segments (magn. ×3.0).

Figures 6 and 8. USNM 56810j. Dorsal views of internal mould, respectively posterior portion of thorax and pygidium (magn. ×5.0), entire specimen (magn. ×2.5). Original of Walcott (1910, pl. 32, fig. 10), from Kinzers Formation, near York, Pennsylvania, U.S.A.



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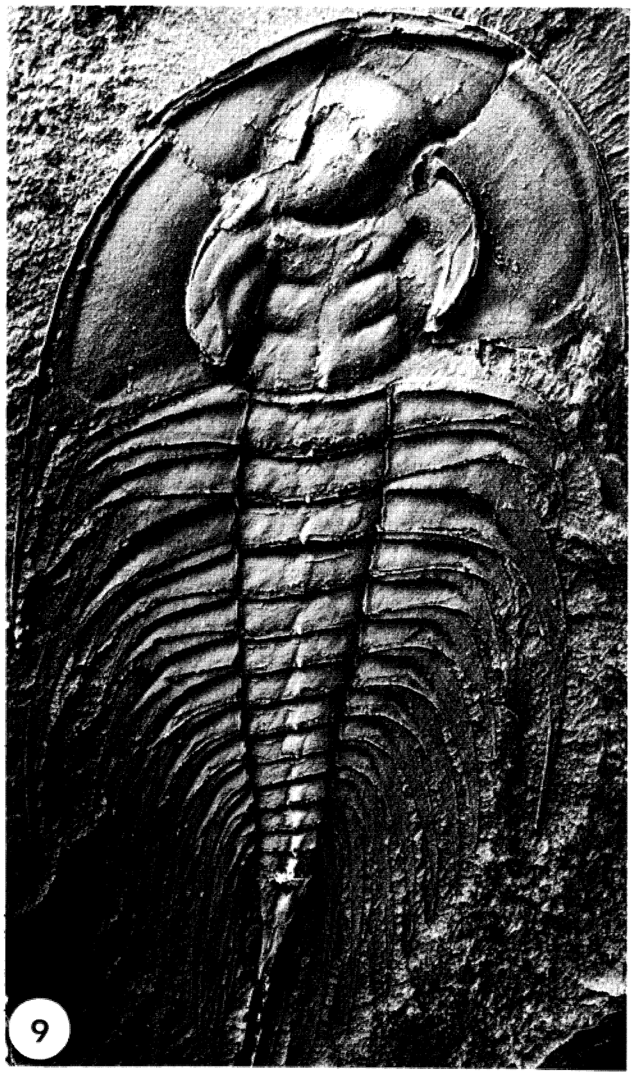
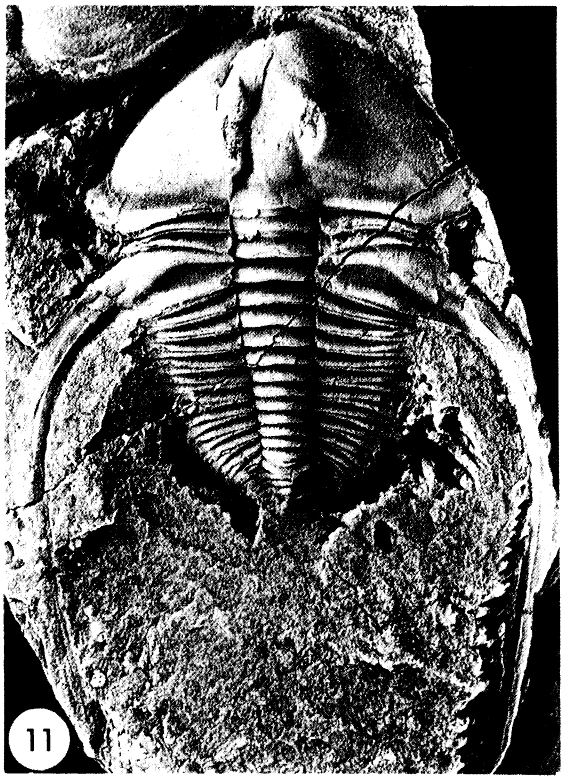
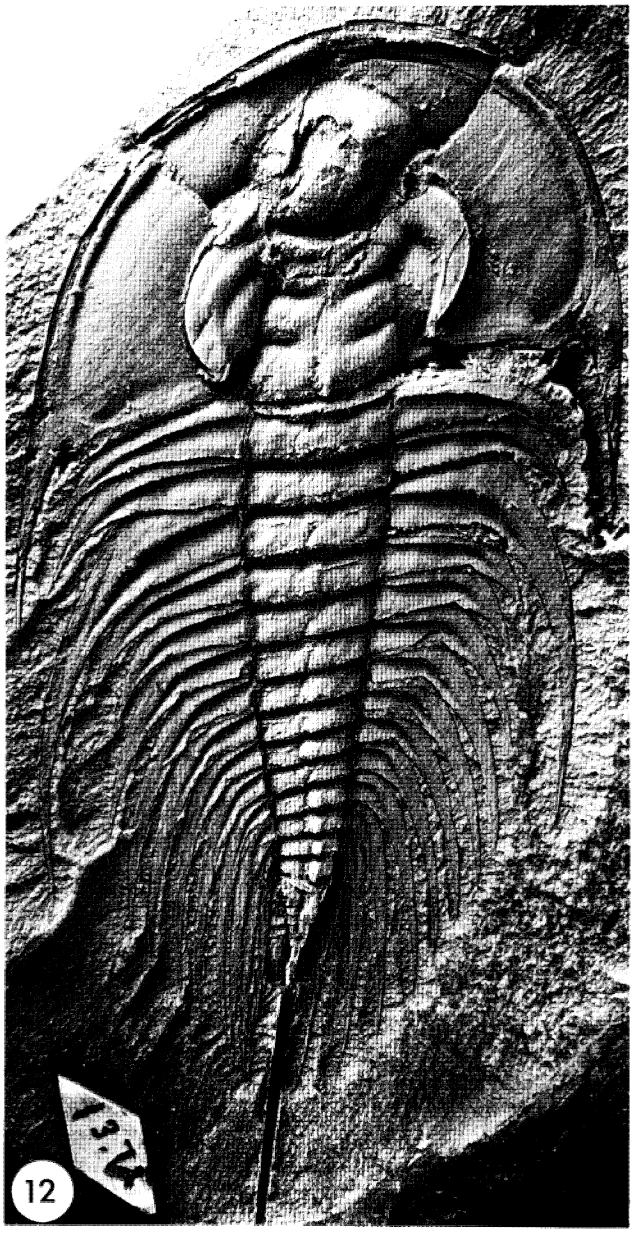
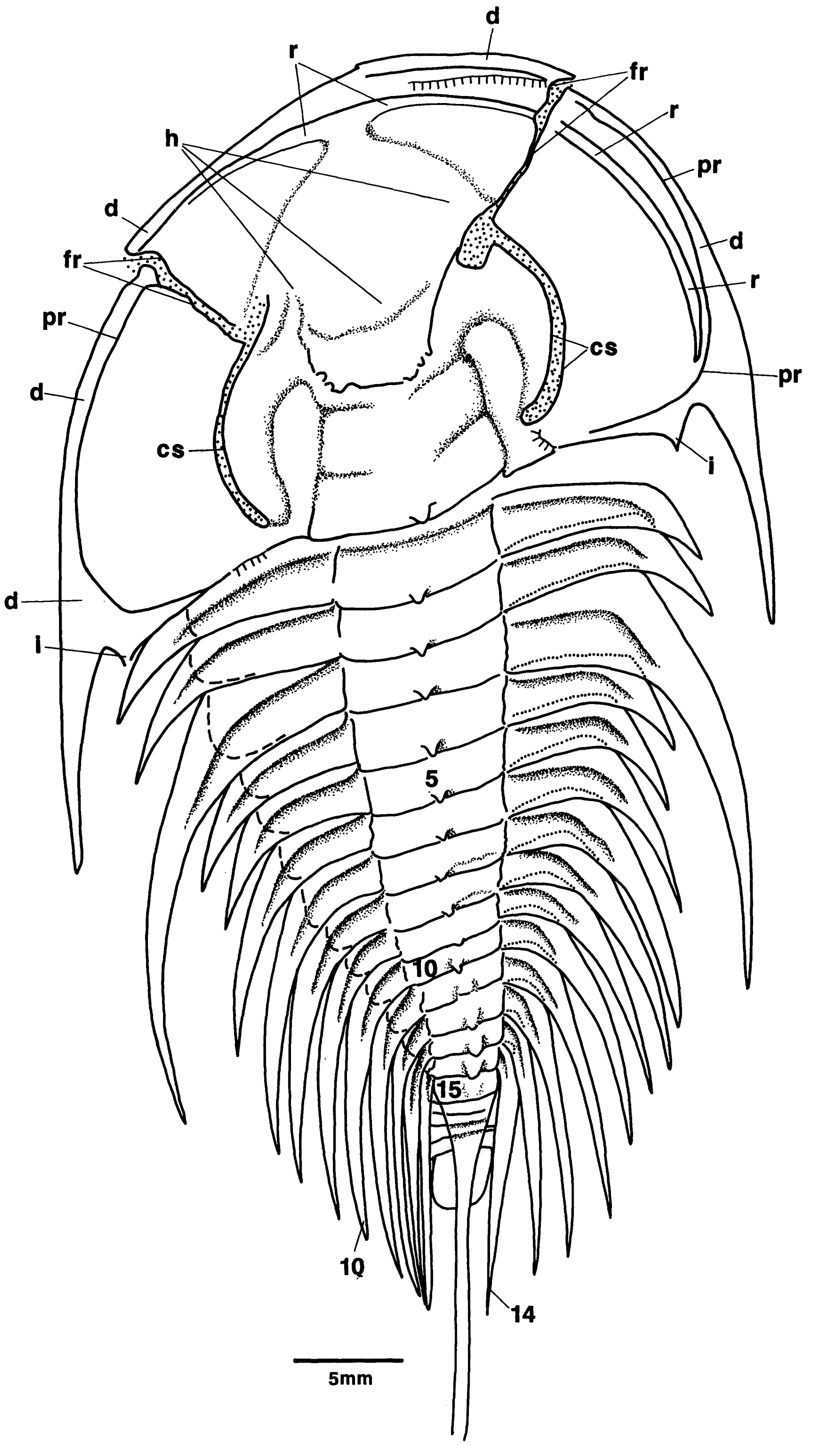
FIGURES 4–8. For description see opposite.







FIGURES 9–12. For description see opposite.



DESCRIPTION OF PLATE 2 AND FIGURE 13

FIGURES 9, 10, 12 AND 13. *Olenellus thompsoni* (Hall, 1859). USNM 56810n. Original of Walcott (1910, pl. 33, figs 2 and 3), Kinzers Formation, near York, Pennsylvania, U.S.A. Figures 9, 12 and 13 respectively cast from external mould (magn. × 2.5), internal mould (magn. × 2.5), explanatory drawing. In latter broken line shows inner margin of doublure of segment; dotted line the anterior margin of the flange. Figure 10, internal mould, posterior portion of thorax and pygidium (magn. × 5.0).

FIGURE 11. GSM FOR 2604. *Biceratops nevadensis* Pack & Gayle, 1971. Original of Pack & Gayle (1971, pl. 102, fig. 5), Pioche Shale near Las Vegas, Nevada, U.S.A. Internal mould (magn. × 3.0).

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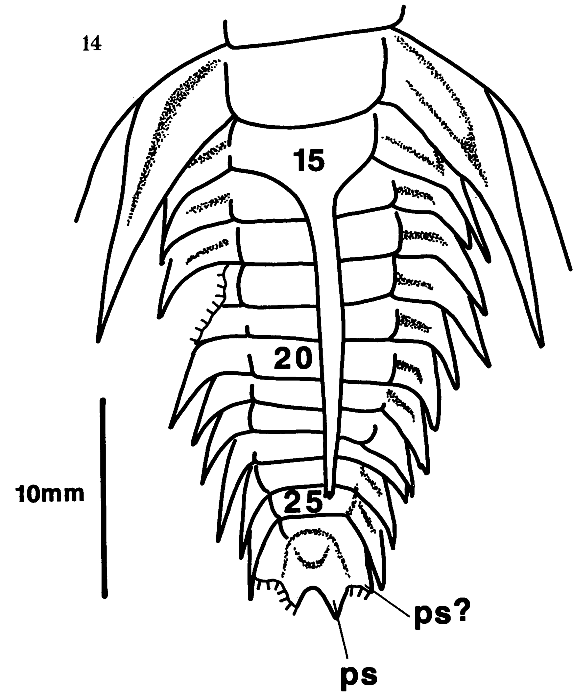

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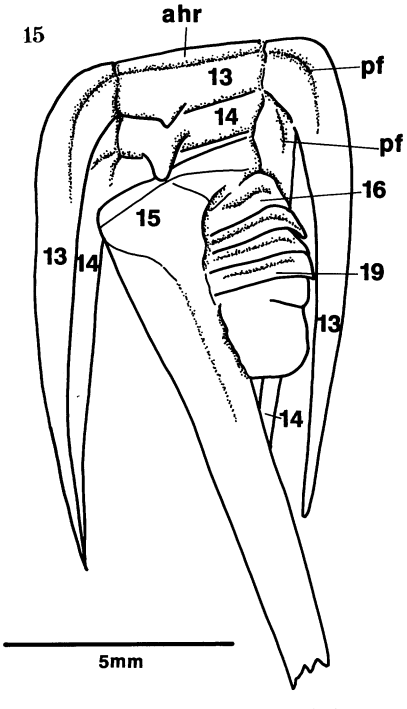
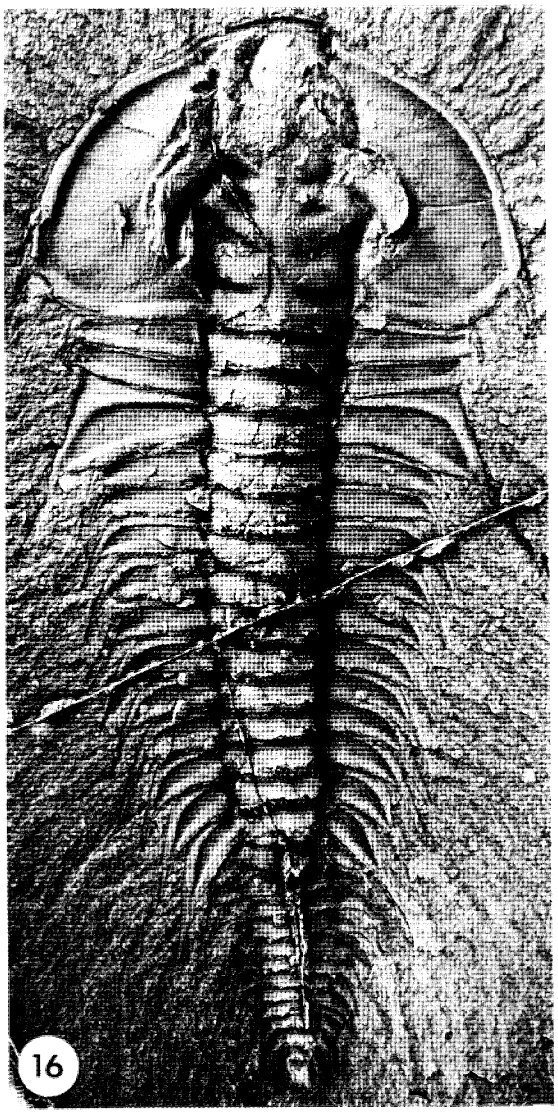


DESCRIPTION OF FIGURES 14, 15 AND PLATE 3

FIGURES 14, 16 AND 18. *Olenellus vermontanus* (Hall, 1859). USNM 15399. Latex cast from external mould of original of Walcott (1910, pl. 26, figs 1 and 2), Parker Slate, Georgia, Vermont, U.S.A. Respectively explanatory drawing of posterior portion of thorax and pygidium, entire specimen (magn. × 1.5), posterior portion (magn. × 3.0).

FIGURES 15, 17 AND 19. *Olenellus thompsoni* (Hall, 1859). USNM 56810i. Original of Walcott (1910, pl. 32, fig. 9), Kinzers Formation, near York, Pennsylvania, U.S.A. Respectively explanatory drawing of posterior portion of thorax and pygidium, latex cast from external mould, internal mould (magn. × 4.0).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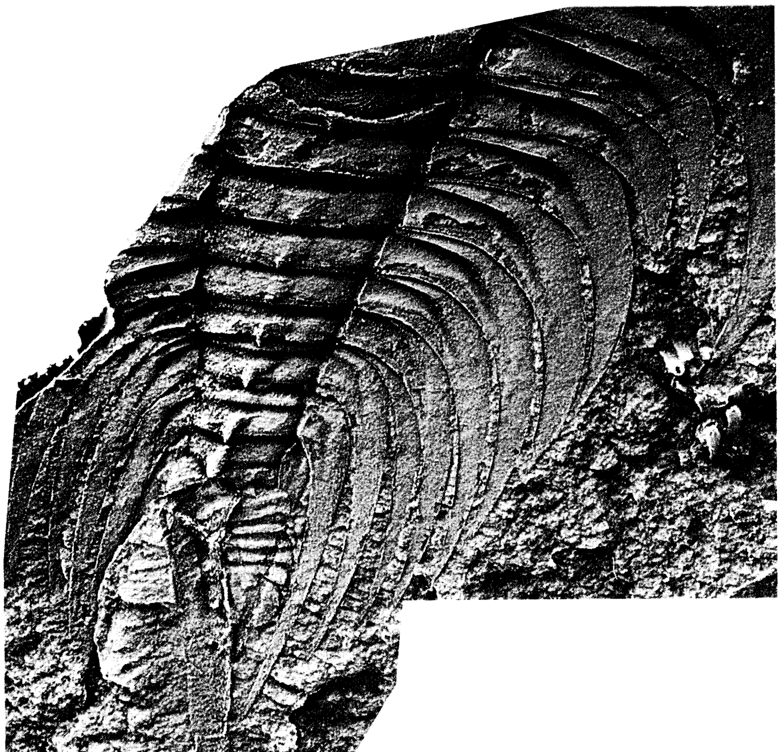
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FIGURES 16–19. For description see opposite.


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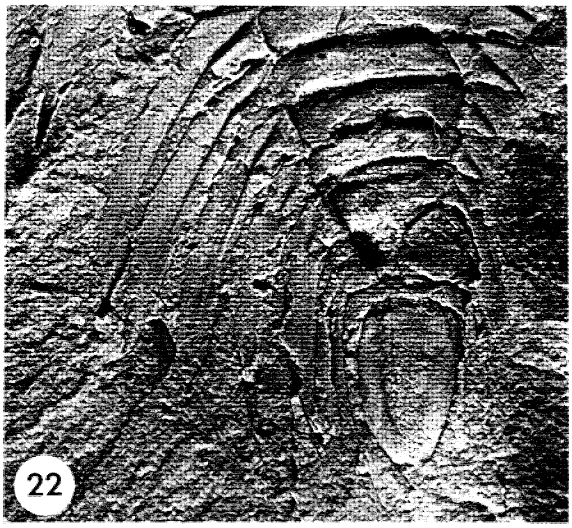
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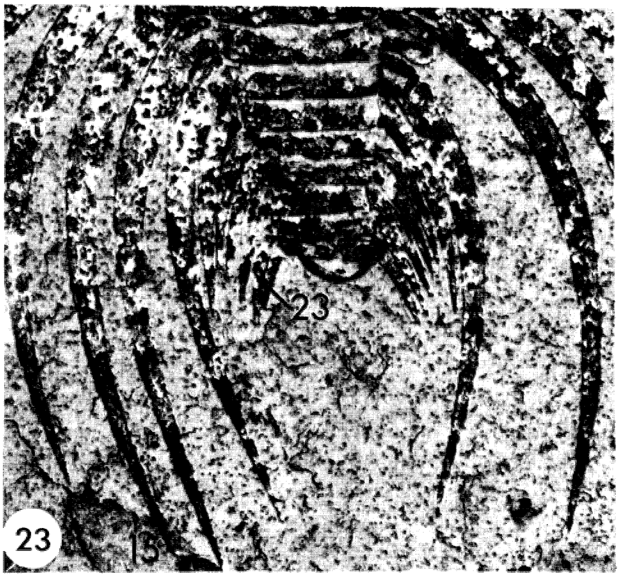

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FIGURES 20–24. For description see opposite.

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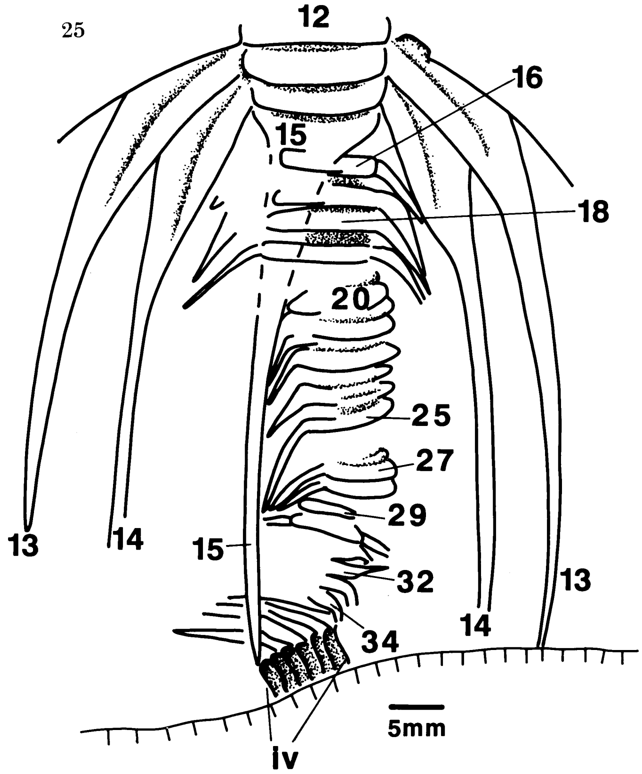

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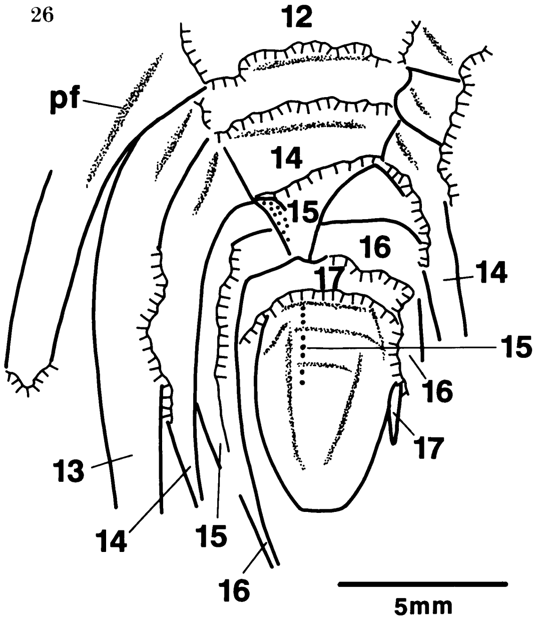

DESCRIPTION OF PLATE 4 AND FIGURES 25 AND 26

FIGURES 20 AND 25. *Olenellus robsonensis* (Burling, 1916), GSC 5272, holotype, probably Mahto Formation, near Mount Robson, British Columbia. Respectively dorsal view (magn. × 1.0), explanatory drawing of posterior portion of specimen. Photograph by GSC, reproduced with permission of the Minister of Supply and Services, Canada.

FIGURES 21, 22 AND 26. Olenelloid gen. et sp. ind., GSC 14332, lower part of *Bonnia–Olenellus* Zone, Rosella Formation, Cassiar Mountains, north–central British Columbia. Respectively dorsal view (magn. × 1.5) of entire specimen, dorsal view (magn. × 3.3) of posterior portion of thorax and pygidium, explanatory drawing of latter (dotted line is impression of edge of axial spine of segment 15). Photographs by GSC, reproduced with permission of the Minister of Supply and Services, Canada.

FIGURE 23. *Nevadia weeksi* Walcott, 1910. USNM 56792a, enlargement of posterior portion of original of figure 44, plate 7, under liquid (magn. × 2.0).

FIGURE 24. *Wanneria walcottanus* (Wanner, 1901). USNM 56807j, Kinzers Formation, York, Pennsylvania. Incomplete internal mould of posterior portion of thorax and pygidium (magn. × 4).

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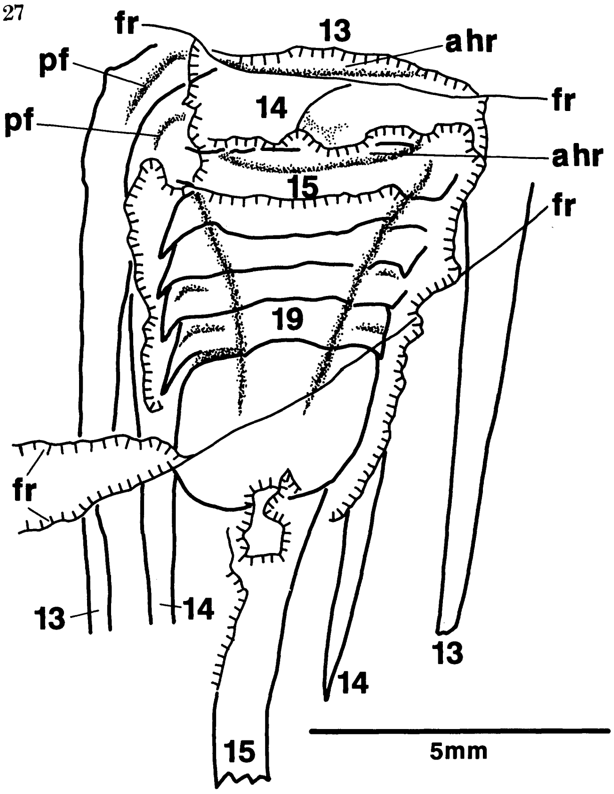

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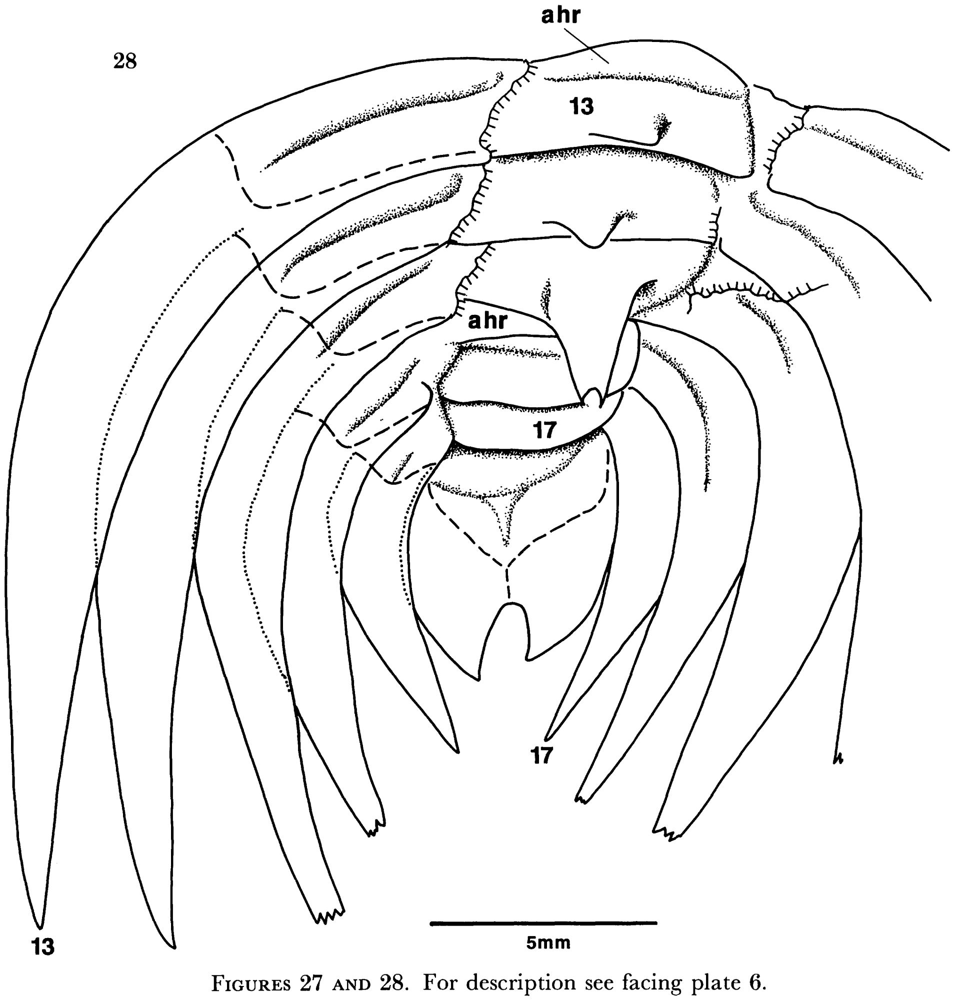
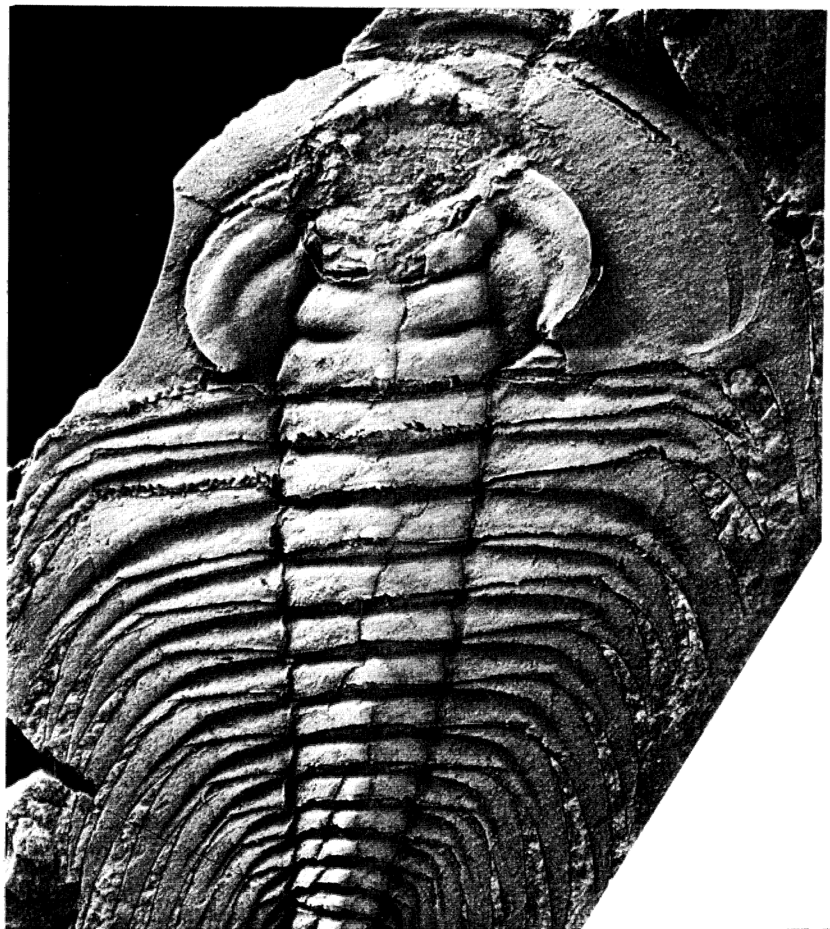


Figures 27 and 28. For description see facing plate 6.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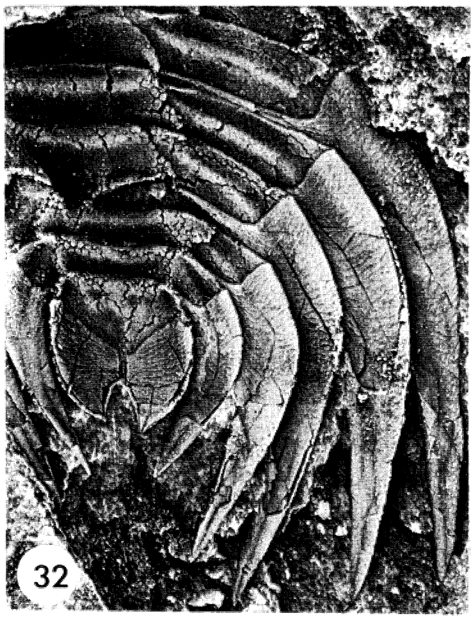
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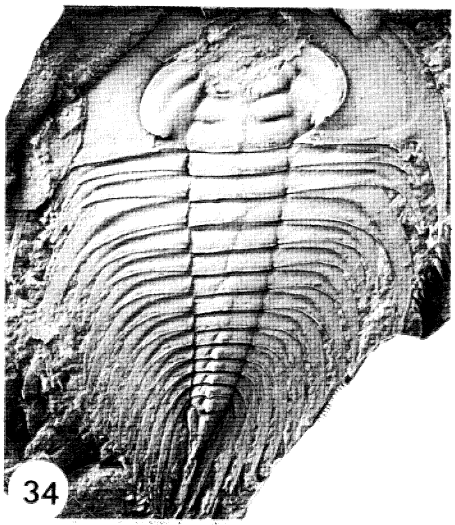
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FIGURES 29–34. For description see facing plate 6.


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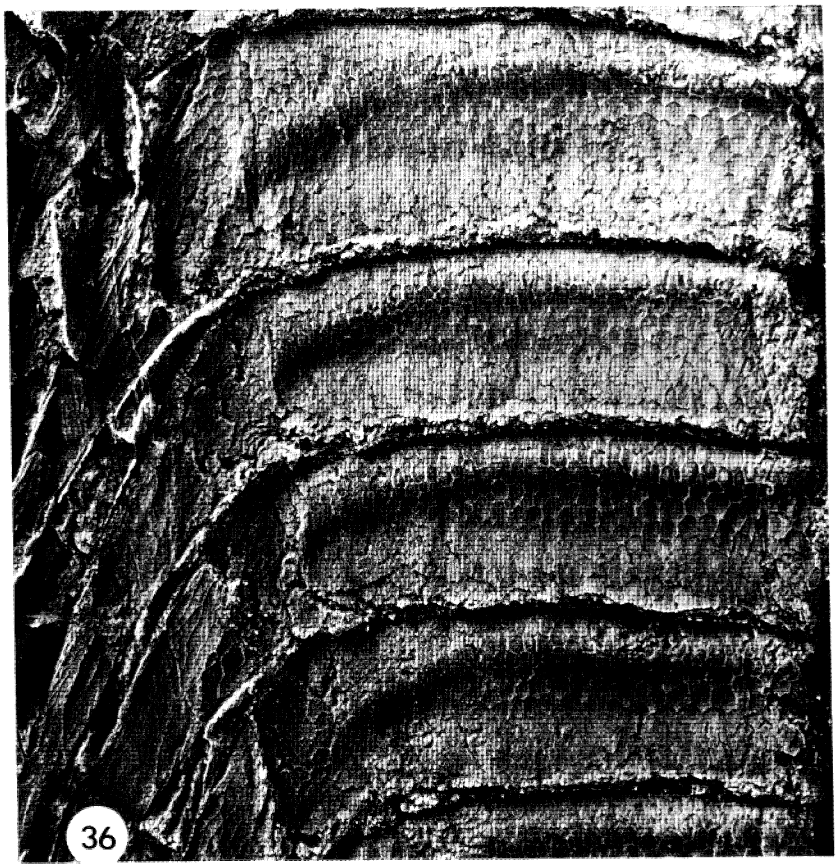
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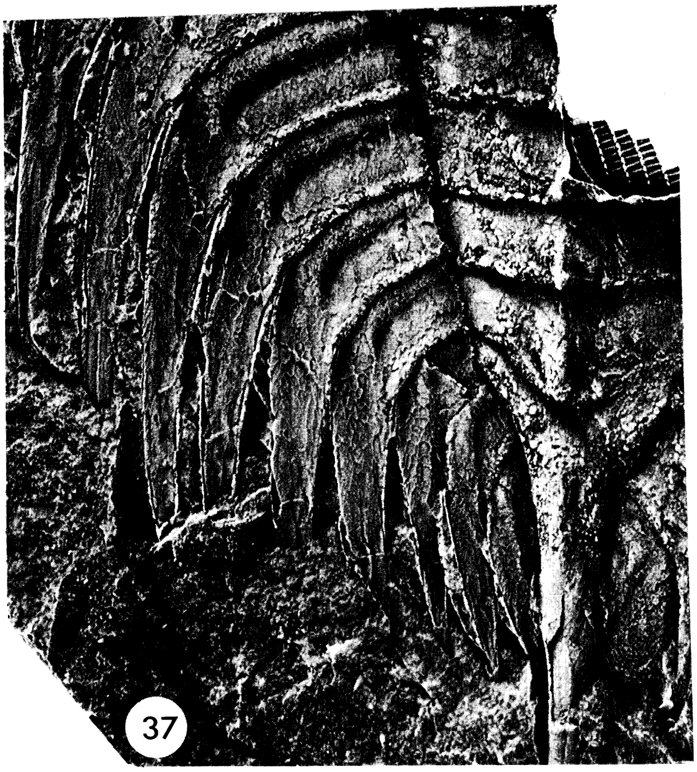
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38

FIGURES 35–38. For description see opposite.

DESCRIPTION OF FIGURES 27, 28 AND PLATE 5

FIGURES 27, 29, 31 AND 34. *Olenellus thompsoni* (Hall, 1859), Kinzers Formation, near York, Pennsylvania, originals of Walcott (1910, pl. 33, figs 4 and 5). Respectively explanatory drawing of posterior portion, entire specimen, internal mould, USNM 56810p (magn. × 3.0), posterior portion of latter (magn. × 5.0), cast from external mould, USNM 56810o (magn. × 1.5).

FIGURES 28, 30 AND 32. *Wanneria walcottanus* (Wanner, 1901). USNM 56807l, original of Walcott (1910, pl. 30, figs 10 and 12), Kinzers Formation, near York, Pennsylvania. Respectively explanatory drawing (broken line, margin of doublure; dotted line, margin of flange), cast from external mould, cast from counterpart internal mould (magn. × 4.0).

FIGURE 33. *Wanneria walcottanus* (Wanner, 1901). USNM 56807o, original of Wanner (1901, pl. 32, fig. 4), Kinzers Formation, near York, Pennsylvania. Internal mould of posterior portion of thorax and pygidium (magn. × 2.0).

DESCRIPTION OF PLATE 6

Wanneria walcottanus (Wanner, 1901), Kinzers Formation, near York, Pennsylvania

FIGURES 35, 36 AND 37. USNM 56807k, original of Walcott (1910, pl. 30, fig. 11). Cast of external mould of incomplete exoskeleton, respectively entire specimen (magn. × 1.0), portion of thoracic segments 2–7 (magn. × 4.0), posterior portion of thorax and pygidium (magn. × 3.0).

FIGURE 38. USNM 56807a, original of Walcott (1910, pl. 30, fig. 1). Internal mould (magn. × 1.5).

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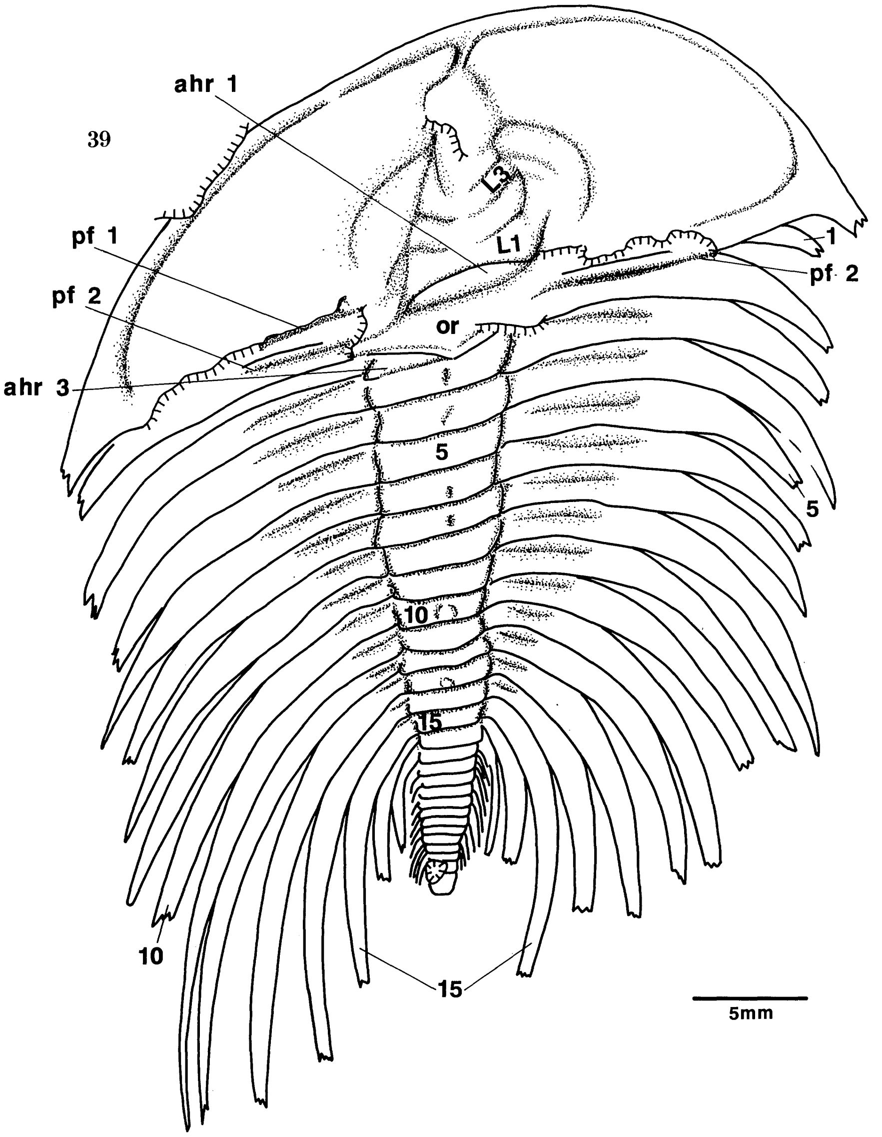

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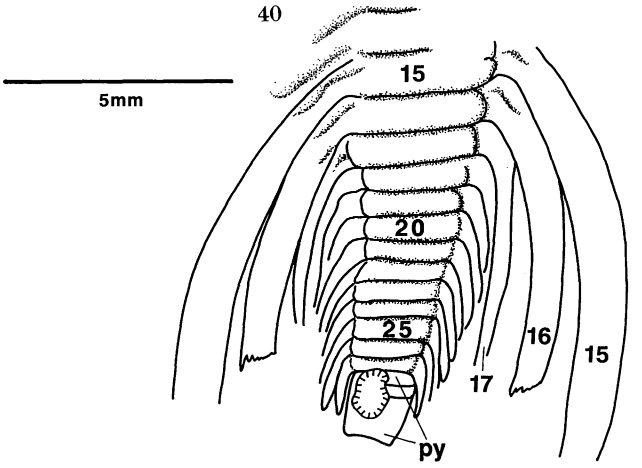


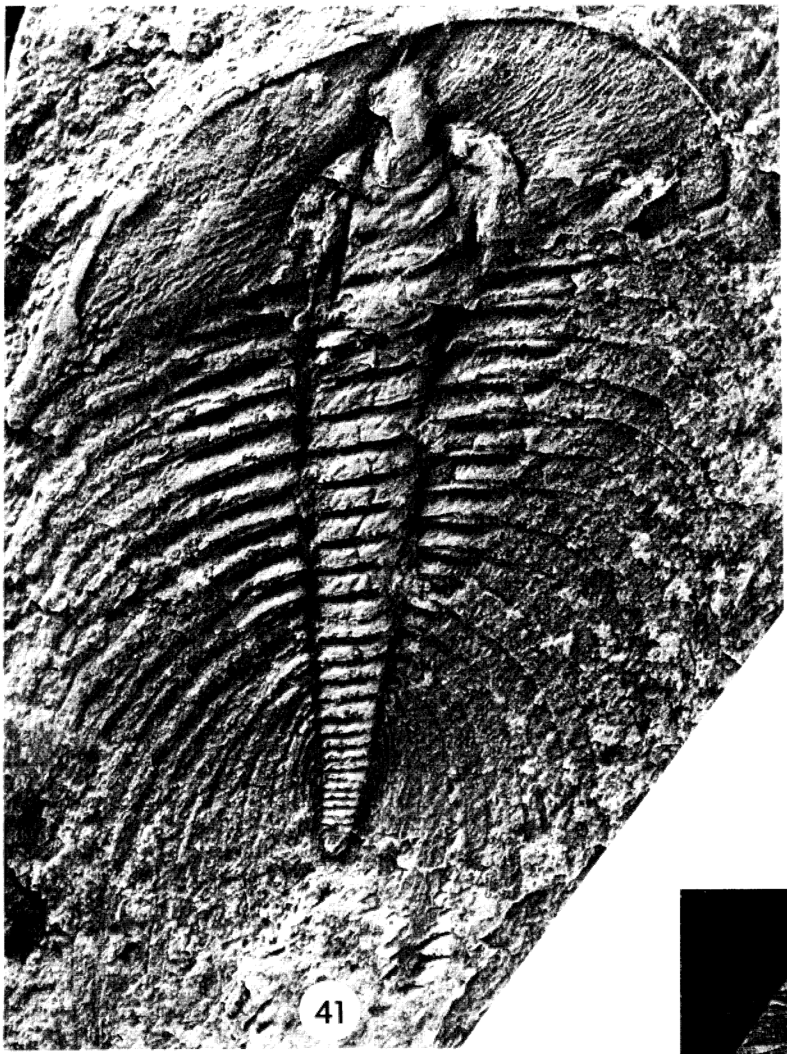
Description of figures 39, 40 and plate 7

Nevadia weeksi Walcott, 1910, south of Silver Peak, Esmerelda County, Nevada

Figures 39, 41 and 42. USNM 56792b, lectotype, original of Walcott (1910, pl. 23, fig. 2). Respectively explanatory drawing, entire exoskeleton (magn. × 3.0), entire exoskeleton under liquid (magn. × 2.0).

Figures 40 and 43. USNM 56792b, posterior of thorax and pygidium, respectively explanatory drawing, photographed under liquid (magn. × 6.0).

Figure 44. USNM 56792a, original of Walcott (1910, pl. 23, fig. 1), photographed under liquid (magn. × 1.0).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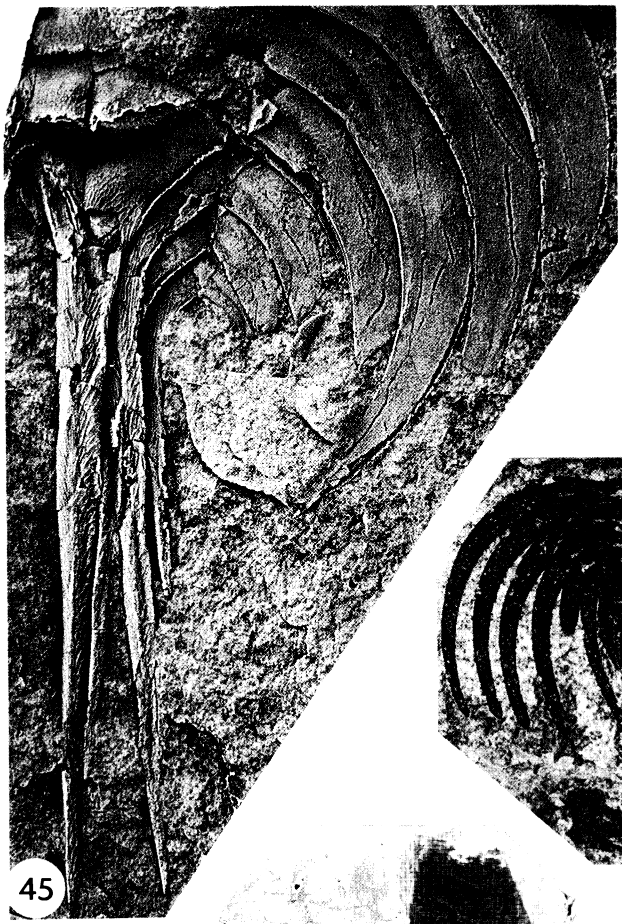
FIGURES 41–44. For description see opposite.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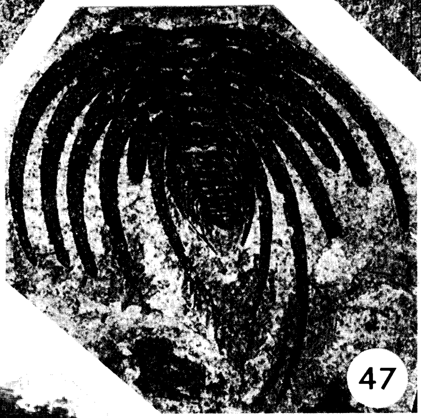
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FIGURES 45–49. For description see opposite.

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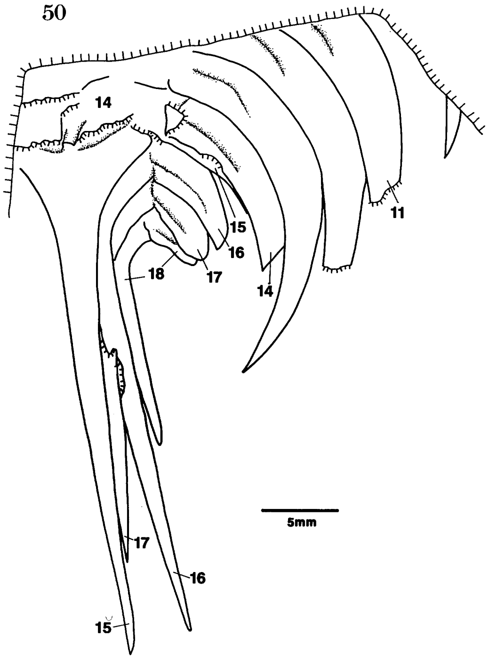

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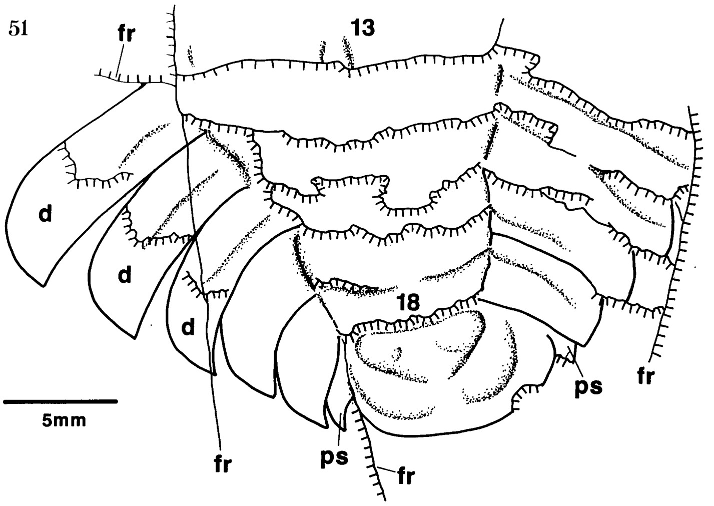

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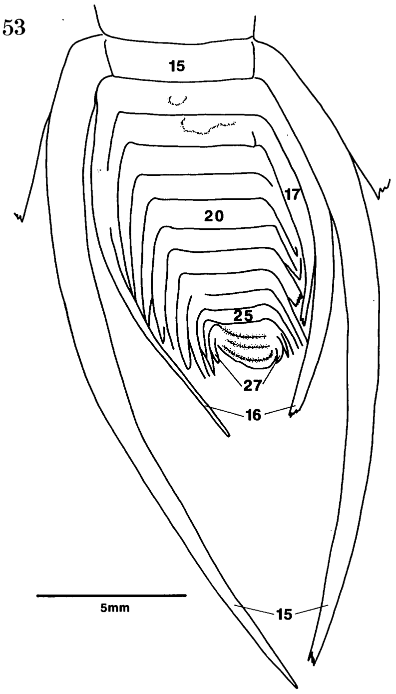

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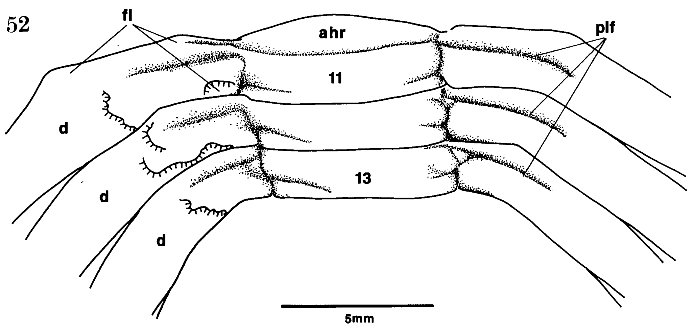

Description of plate 8 and figures 50–53

Elliptocephala asaphoides Emmons, 1844, near North Greenwich, Washington County, New York State

Figures 45 and 50. USNM 18350b, original of Walcott (1890*b*, pl. 90, fig. 1a; 1910, pl. 24, fig. 9). Respectively cast from external mould of posterior portion of thorax (magn. × 3.0), explanatory drawing.

Figures 46, 48 and 51. USNM 18350a, original of Walcott (1890*b*, pl. 89, figs 1 and 1a; 1910, pl. 24, figs 1 and 2). Respectively posterior portion of thorax and pygidium (magn. × 3.0), entire specimen (magn. × 1.0), explanatory drawing of thoracic segments 13–18 and pygidium.

Nevadia weeksi Walcott, 1910, south of Silver Peak, Esmerelda County, Nevada

Figures 47, 49, 52 and 53. USNM 56792d, original of Walcott (1910, pl. 23, fig. 4). Posterior portion of thorax and pygidium, respectively entire specimen (magn. × 1.5), posterior portion of specimen (magn. × 5.0), explanatory drawings of thoracic segments 11–13, of thoracic segments 15–27 and portion of pygidium. Photographs under liquid.

the rotation that took place (figures 17 and 19, plate 3) to bring them above pleura 14. Pleura 15 was hidden in all the specimens and was probably narrow (tr.). The inner portion of pleurae 16–19 appears to have been horizontal, narrow (tr.), the outer portion likewise narrow, steeply bent down and drawn into a short, backwardly directed spine.

Pygidium in the Vermont specimen (figure 5, plate 1; cf. Walcott (1910, pl. 24, fig. 12)) of similar maximum width and length (exs.), shallow first inter-ring furrow, axis poorly defined except posteriorly where it slopes steeply, not separated laterally from pleural region. Posterior margin having broad, shallow notch and pleural region posterolaterally a lobate outline; no border. In the Pennsylvania specimens (figure 10, plate 2; figure 31, plate 5) the axis may appear well defined laterally because the median spine of the 15th segment was crushed down upon it. The same crushing obscures the median posterior outline of the pygidium, which may have been notched. The first inter-ring furrow is preserved, and in figure 17, plate 3, a first interpleural furrow and the free margin of the pleura. Resser & Howell (1938, pl. 5, fig. 5) figured a specimen from Pennsylvania (as *O. getzi*) showing thoracic segments 14–18 and the pygidium with a median posterior notch and a pointed tip to the posterolateral pleural lobe.

The sculpture of the external surface is well preserved in the Vermont specimen (figures 4, 5 and 7, plate 1). On the axial region a scale-like pattern is formed by terrace ridges, anastomosing in curves convex forward, which swing more strongly back close to the axial furrow. Axial rings of the thorax have a posterolateral smooth area. On the cephalon a pattern of anastomosing ridges is impressed transversely on the palpebral lobe, on the extraocular gena the ridges run parallel to the margin, curving back as they approach a furrow, and swinging forward and back across the border. Stronger ridges, not anastomosing but parallel to the margin, traverse the cephalic doublure. On the thoracic pleurae the scale-like anastomosing pattern of ridges is present on the convex anterior and posterior bands, but fades out in the deepest part of the pleural furrow. On the outer portion of the pleura the ridges become stronger, closer together, and run out to meet the margin at an acute angle. The scale-like pattern of anastomosing ridges runs across the pleural regions and axis of the pygidium, swinging back as it approaches the lateral margin. In these terrace ridges the steeper, scarp slope faced backward or inward in the convex–forward curves; on the cephalic doublure it faces inward. On the Pennsylvania specimens the sculpture is poorly preserved, except for the strong terrace ridges on the cephalic doublure (figure 12, plate 2), and granulation on the median 15th thoracic spine, which becomes elongated and sharply pointed distally (figures 17 and 19, plate 3).

Discussion. The specimens from Vermont and Pennsylvania are all flattened in shale, so that the original convexity is not revealed. The convexity of the restoration is therefore based on illustrations by Fritz (1972, pl. 11, figs 13–18; pl. 15, figs 17 and 18) of cephala of other species. Convexity of thorax and pygidium is derived from that given to the cephalon, but the exact form of the pleural region remains problematical. Bergström (1973*a*, p. 17, pl. 2, figs 3 and 4) studied olenellids from Greenland in which the pleural region curved downwards and outwards from the axial furrow, and concluded that little movement between successive segments was possible. However, Fritz's illustrations suggest that the inner portion of the pleural region was almost horizontal or only very slightly downwardly inclined, the outer portion sloping more steeply downwards and outwards. In the present specimens the inner portion of the pleura appears parallel-sided, the margin directed transversely to the axial furrow (with the exception of the posterior margin of the macropleura). This portion has the doublure only along the posterior edge, narrows (tr.) and disappears posteriorly, and merges distally into the outer portion, the pleural spine. A boundary between the two portions is apparently not signalled by a flexure, the fulcrum, nor a fulcral process and socket, but the flange attains its maximum width (exs.) about here, and the margin of the doublure swings to run exsagitally. In the restoration (figures 1 and 2) it is suggested that the inner portion of the pleura was gently curved, not horizontal, that the transverse axis of swing between successive segments passed through the axial process, and that the articulating halfring and flanges acted (in opposite directions) as guides in flexure of the thorax. At least the amount of enrolment shown in figure 2 appears to have been possible, and some flexure in the opposite sense, restricted by contact between successive axial rings. The devices associated with articulation between segments in *Olenellus* are like those described in the corynexochoid *Olenoides* (Whittington 1980, pp. 173–179). In redlichids (Öpik 1970, pp. 3–5) the flange has not been described, but Öpik referred to the pleural guide, a short process at the anterolateral corner of the pleura; this guide corresponds in position with the anterolateral angle of the flange. Öpik drew attention to the possible use in classification of the presence of a clearly defined fulcrum and horizontal hinge line along the edge of the inner portion of the pleura, in contrast to the apparent absence of these features in olenellids and redlichids.

The restoration (figures 1 and 2) is based on specimens from Pennsylvania. The complete specimen from the type locality in Vermont (figure 4, plate 1) is about twice as large as these specimens, and differs from them in being relatively broader (tr.), in the deep, channel-like pleural furrow and in having only 18 thoracic segments. Tectonic distortion may have made this specimen broader, and a smaller specimen from Vermont (Resser & Howell 1938, pl. 3, fig. 17) is relatively narrower and much more like those from Pennsylvania. Reference has been made above to the specimen from Pennsylvania, attributed to *O. getzi*, which has 18 thoracic segments, and a median posterior notch in the pygidium. It is one of eight of the species of *Olenellus* from the York area of Pennsylvania described by Resser & Howell (1938), which are considered by Fritz (1972, p. 11) to be synonyms of *O. thompsoni*. Acceptance of Fritz's views thus implies the variation within this species illustrated herein.

Meraspid stages in the ontogeny of this species (Whittington 1957, p. 431, fig. 2) are known from Pennsylvania. They show up to 12 thoracic segments, including the third macropleural segment but nothing of the transitory pygidium. Shaw (1955, pp. 790–794, pl. 75, figs 1–3 and 10) recognized two additional species, *O. brachycephalus* and *O. vermontanus*, as coming from the slate of the Parker Quarry. Shaw's figures of the former species, the type of which he reports as missing, suggest that it may be difficult to maintain it as distinct from *O. thompsoni*.

(ii) *Olenellus vermontanus* (Hall, 1859)

Figure 14; figures 16 and 18, plate 3.

Holotype. AMNH 230, original of Hall (1859, p. 60, fig. 2) from Lower Cambrian Parker Slate, Parker Quarry, Georgia, northwestern Vermont, U.S.A. Missing from AMNH collections (Dr G. D. Edgecombe, personal communication, January 1988).

Discussion. The counterparts of the complete specimen described by Walcott (1886, pp. 158–162, 1890*b*, p. 637, 1910, pp. 264–266) came from the same type locality as *Olenellus thompsoni*. The entire exoskeleton is narrower (tr.) than any of *O. thompsoni*, and the eye lobe is shorter (exs.) reaching back only to the midlength of L1, not to the occipital furrow. There appear to be 25 thoracic segments (Walcott showed 26 in his 1886 work, only 25 in 1910), and a small pygidium. The axial region of the thorax shows a gradual taper and reduction in size of the axial rings, from first to last, and there is a further reduction in the pygidial ring. Axial ring of thorax moderately convex, shallow articulating furrow. Axial furrow shallow beside mid-portion of ring, deepening, anteriorly and posteriorly, the marked anterior deepening descending to the axial articulating process. Pleurae are directed transversely in the first eight segments, with a macropleural third pleura. Because of the rapid expansion abaxially in length (exs.) of the macropleura, the margins are diagonally directed rather than transverse, and the shape of pleurae 1, 2 and 4 are modified to accommodate this expansion. From pleura 9 backwards the pleurae are directed outwards and progressively more strongly backwards, pleura 14 directed at some 50° to the sagittal line. Behind the macropleural spine the slim pleural spines become progressively longer to pleura 14. The 15th segment bears a slim axial spine that appears to reach back almost to the pygidium, the pleura is reduced to about half the size of that of the 14th segment, and bears a thin pleural spine. This 15th segment may be considered as the first of the opisthothorax. In the next four segments (16–19) the pleurae are directed transversely, narrow (tr.) the inner portion impressed by a shallow furrow, the pleural spine slim. In segments 20–26 the pleurae are directed successively more strongly backwards, and reduced progressively in size. The transition from prothorax to opisthothorax takes place between segments 14 and 15, and in segment 16 the pleura is directed transversely, as it is in the anterior portion of the prothorax. The anterior edge of the inner portion of each pleura in the entire thorax passes below the posterior edge of the pleura in front, and there was evidently a narrow flange along this edge. The pygidium has the posterolateral margins incomplete, but it appears to have the axis divided into an anterior ring and small terminal portion. Laterally the axis slopes into the pleural regions without any axial furrow. Walcott portrayed a pair of spines flanking a median spine on the posterior border of the pygidium, but there appears to be a median notch flanked by a larger inner pair of spines, and there probably was a smaller, outer spine. The pygidium may have included, therefore, two fused segments and a small terminal axial portion.

(iii) *Olenellus robsonensis* (Burling, 1916)

Figure 20, plate 4; figure 25.

Holotype. GSC 5272, Lower Cambrian, probably Mahto Formation, drift block on the slope of the Mural glacier below Mumm Peak, near Mount Robson, British Columbia.

Discussion. This single specimen on which Burling founded his species is of interest because of the healed injury on the right anterior side of the thorax (Rudkin 1979) and the many segments that follow the 15th thoracic segment. Figure 25 is an interpretation of what can be seen of these segments, 16–34 being partly disarticulated, an additional six segments inverted behind them. The convex axial region tapers gradually posteriorly, the rings and deep, straight articulating furrows like those of the more anterior segments, portions of the articulating halfrings being revealed by the disarticulation. Pleurae are partly hidden by matrix or broken, that of segment 15 concealed beneath the posterior pleural band of 14. The visible portions of more posterior pleurae show them to be straight, tapering, and directed outwards and backwards, more strongly so posteriorly, where they are also diminished in length (tr.). Pleura 14, like those in front of it, bears a deep, channel-like pleural furrow, but there is no such furrow in pleurae labelled 16–19. These and more posterior pleurae may be pleural spines, equivalent only to the outer portions of pleurae 1–14; the inverted segments at the rear of the specimen appear to show the doublure of the pleurae extending in to the axial furrow. The long median axial spine of segment 15 is partly preserved and appears to have curved upward above the axis posteriorly. The pleural spine of the segment labelled 16 passes distally under pleura 14, and this segment appears to be disarticulated. When in place behind segment 15 it must have extended below pleura 14 almost entirely, as must pleurae 17 and 18 in part. This implies that either pleura 14 was somewhat upwardly directed, or perhaps more probably pleura 14 and those behind it were downwardly directed. The restoration of *O. robsonensis* by Hupé (1953*b*, fig. 76) likewise implies this, though the pleurae from 16 onwards are shown as shorter and less spine-like than appears to be the case, and there is no clear evidence of the short pleural furrows Hupé showed. The probable existence of a pleural flange is shown particularly by posterior segments of the prothorax, by the way each passes below the next anterior. A similar relation is shown by pleurae 16–19 of the opisthothorax. Segments along the entire length of the thorax appear to have been articulated with one another.

This single specimen shows more segments in the opisthothorax than any other olenellid known; the pygidium is missing. It was regarded as perhaps aberrant by Raw (1936, p. 239, footnote), and it may be that this exceptional number resulted from injury. As a guide to the maximum number of segments in the olenellid thorax it should be treated with caution. Judging by the present material, segments 1–14 of the thorax of *O. robsonensis* are characterized by a deeper, more channel-like pleural furrow than those of *O. thompsoni*, the posterior slope of the furrow being steeper so that a posterior pleural band is defined. The pleural spines in *O. robsonensis* are relatively slimmer and slightly differently disposed to those of *O. thompsoni*. The cephala of the two species appear generally similar. Fritz (1972, p. 15) refers to the similarities between *O. robsonensis* and *O. puertoblancoensis* (Lochman in Cooper *et al.* 1952), and of the latter to *O. thompsoni*.

(*c*) *Nevadia* Walcott, 1910

Type species: *Nevadia weeksi* Walcott, 1910

(i) *Nevadia weeksi* Walcott, 1910

Figure 23, plate 4; figures 39 and 40; figures 41–44, plate 7; figures 47 and 49, plate 8; figures 52 and 53.

Lectotype (*here selected*). USNM 56792b, original of Walcott (1910, pl. 23, fig. 2), unit no. 12 in Barrel Spring Section of Walcott (1908, p. 189), 3 miles† northeast of Barrel Spring, which is 16 miles south of Silver Peak, Esmerelda County, Nevada.

Other material. USNM 56792 a, c–j, originals of Walcott (1910, pl. 23, figs 1, 3–7 and 8; figs 14 and 15, p. 257), all from the same horizon and locality.

Description. The lectotype (figures 41–43, plate 7) is an almost complete dorsal exoskeleton, an internal mould, flattened in siliceous, micaceous shale. Walcott (1910, pl. 23, fig. 2) did not show the pleural spine of the first thoracic segment (figure 39), which appears below the cephalic border on the right side. This segment lies almost entirely below the posterior cephalic borders, which are broken away adaxially, and the axial ring of the second thoracic segment is hidden below the occipital ring. Thus what may be thought to be the posterior border furrow extending straight outwards to the left of the occipital furrow, is the impression of the underlying pleural furrow of the first segment. A similar impression is less clearly visible on the

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† 1 mile ≈ 1.61 km.

right side. This telescoping of thorax below the cephalon appears to have brought the articulating furrow of the first thoracic segment to a position below the occipital furrow so that the articulating halfring of the first segment has been impressed upon the basal glabellar lobes. The larger specimen of the thorax and a portion of the cephalon (figure 44, plate 7) is an external mould. The outlines of all three specimens studied are best revealed when submersed in alcohol.

The cephalon (see also Walcott 1910, pl. 23, figs 3 and 6) is sub-semicircular in outline, about $2\frac{1}{2}$ times as wide (tr.) across the genal angles as long (sag.). The glabella tapers forward from the occipital ring, S1–3 straight, slightly backwardly directed, S1 extending inward about one-third the width (tr.) at that point, S2 and S3 successively slightly longer; frontal lobe crushed, and probably slightly forward tapering and moderately inflated. Occipital furrow appears deep in the lectotype, but this appearance may be the impression of the articulating furrow of the first segment; the portion of this furrow preserved in 56792a shows it as deep abaxially, shallowing inwards. The long, curved eye lobe is close to the glabella, and extends back from opposite the posterior portion of the frontal lobe almost to the level of the occipital furrow. Genal field includes the broad (tr.) extraocular area and a short (sag.) preglabellar field, anterolateral border narrow, broadening as it approaches the genal angle and less markedly so in front of the glabella; a low, narrow median preglabellar ridge may extend between border and frontal glabellar lobe. Posterior border transverse, narrow (exs.) and faintly defined adaxially, broader and better defined in the outer portion that was directed slightly forwards to the genal angle; only broad basal portion of genal spine preserved. The radiating, anastomosing genal caecae are well preserved on the extraocular area of the genal field.

The thorax appears to consist of 27 segments (figures 39 and 40) the axial region tapering uniformly, the axial rings successively shorter (sag. and exs.). The external surface is not visible, the external mould (figure 44, plate 7) having a thin layer (light in the photograph) clinging to it. This layer is presumably the exoskeleton, and retains traces of reticulate sculpture outlined by shallow grooves on the inner surface. Because the external surface is not seen, one cannot be certain whether or not there were median nodes on the axial rings, but structures on the internal mould (figure 39), particularly on the 10th and 13th rings, suggest that there may have been such nodes. No evidence of a median axial spine is preserved on any segment. The articulating halfring of the 1st axial ring is preserved in the lectotype and of the 11th in the original of figure 52. The axial furrow is well defined, the posterior pleural band rising steeply from it on segments 1–17. The inner portions of the pleurae in these segments appear gently convex (tr.), the posterior band broad (exs.) and prominent, the anterior a narrow (exs.) ridge that descends very steeply to the pleural furrow. This furrow dies out beyond the inner portion of the pleura, and this portion is widest (tr.) in segments 1–3, then diminishes rapidly in width so that it cannot be distinguished beyond segment 15. The outer portion of the pleura is preserved as a flat, curved blade. The step in level between inner and outer portions shown by internal moulds (figure 41, plate 7), and the curved, well-defined inner edge of the exoskeletal layer shown by anterior segments in the original of figure 44, plate 7, suggest that the doublure underlies these outer portions, and that they were hollow, blade-like pleural spines. The length and backward curvature of these spines increases progressively in segments 1–15, the 15th curving directly backwards and slightly inwards (figures 40 and 53). The pleural spines of 16–18 show a rapid reduction in length, and at their bases pass into an extremely short inner portion in which a pleural furrow may be discerned. Pleural spines 19–27 are directed backwards and slightly outwards, one inside the other, successively reduced in length at a much lower rate than between pleurae 15–18. In the largest individual (figure 23, plate 4; figure 44, plate 7) pleural spines 16 and 17 are only slightly shorter than 15, whereas 18 is half the length of 17. Further, only additional axial rings and pleural spines 19–23 are preserved, the axis ending in a narrow (tr.) sub-semicircular section bounded posteriorly by a groove. It appears that the axis was curved up towards the observer beyond segment 23, and the semicircular section is all that is preserved of segment 24, seen in cross section in this external mould, the remainder of the exoskeleton being in the missing counterpart. A similar downward flexure of the pygidium, so that it is partly concealed in the matrix, would explain the small, semicircular plate, that has a single transverse division, behind the axial ring of segment 27 in the original of figure 53. Thus the pygidium, longer (sag.) than wide, is preserved more completely only in the lectotype (figure 40). It forms a slightly tapered termination to the axial region and appears to have a raised axis (damaged) and a flatter pleural region; two axial rings are visible anteriorly. The pygidium is so small, however, that details are difficult to observe.

The presence of the articulating halfring, and the interpretation of the appearance of the termination of the axial region given above, imply that flexure was possible between segments 1–27, and between them and cephalon and pygidium. The lectotype shows no gaps between the edges of the inner portions of pleurae 1–16, rather that the anterior edge of one passed below the posterior edge of the one in front (figure 41, plate 7). The broken posterior edge of the left interior portion of segment 3, for example, suggests the presence of a flange, as does a break in segment 11 of 56762d (figure 52). A gap, widening abaxially, separates the pleural spines. Assuming an original convexity of the exoskeleton similar to that in *Olenellus*, then enrolment was possible, the pleural spines fitting one behind and below the other along the length of the thorax.

Discussion. In his description Walcott (1910, p. 258) refers to the 'body portion' of the pleura, referred to here as the inner portion. The mineralized doublure did not extend beneath this portion (except perhaps for a narrow (exs.) posterior band as in *Olenellus*). The abaxial margins of these portions lie in a line (exs.) that extends from the slight angulation in the posterior cephalic border, to the axial furrow opposite the 18th segment. Morphologically this line corresponds to the fulcrum, the angulation in pleurae of trilobites that have the inner portion horizontal. In *Nevadia* and other olenellids it may be that this inner portion was not horizontal, but gently curved or sloping outwards and downwards; uncompressed specimens are needed for investigation of this question.

Fritz (1973, p. 15, pl. 4, figs 16–18) figures three small cephala that he refers to *Nevadia*? sp. The forwardly tapering glabella and long eye lobe make this reference plausible, an intergenal ridge and spine are prominent, and the extraocular area of the genal field is relatively narrower (tr.) than in the larger cephala. Fritz mentions that these small cephala might belong to *Nevadella* Raw, 1936. The diagnosis of this latter genus given by Fritz (1972, p. 22) embraces characters seen in *Nevadia weeksi*, except that the posterior border of the cephalon does not curve back so that distally it lies behind the occipital ring, as it does in the type species *Nevadella eucharis* (Walcott 1913, pl. 53, fig. 1). This character is probably not significant at the generic level, and is a difficult one to use because the form of the posterior border may be different in compressed and uncompressed specimens. Thus it is questionable whether the name *Nevadella* should continue to be used to separate species from those placed in the older genus *Nevadia*.

Raw's (1936, pp. 249–250) original characterization of species to be referred to *Nevadella* is far from convincing. The new genus *Buenellus* proposed by Blaker (1988), was based on a new species from Greenland considered to differ from any referred to *Nevadia* or *Nevadella*. The diagnosis of the new taxon includes characters seen in species of *Nevadia*, and the significance of supposedly distinctive characters is uncertain. The taxonomic problems posed by olenelloids at the generic level are well illustrated by these species.

(*d*) *Wanneria* Walcott, 1910

Type species: *Olenellus* (*Holmia*) *walcottanus* Wanner, 1901

(i) *Wanneria walcottanus* (Wanner, 1901)

Figure 24, plate 4; figure 28: figures 30, 32 and 33, plate 5; figures 35–38, plate 6.

Lectotype. USNM 56807e, original of Wanner (1901, pl. 31. fig. 1), and Resser & Howell (1938, pl. 10, fig. 9), entire exoskeleton exposed from the dorsal side, from Kinzers Formation, about 3 miles north and northwest of York, Pennsylvania. As Resser & Howell show, on the same slab as the lectotype is a portion of cephalic doublure and an attached hypostome, originally figured by Wanner (1901, pl. 32, fig. 2) and subsequently by Walcott (1910, pl. 30, fig. 5).

Other material. USNM 56807a, j, k, l, originals respectively of Walcott's (1910, plate 30, figures 1, 10–12), and USNM 56807o, original of Wanner (1901, plate 32, figure 4), all from same horizon and locality as the lectotype.

Description. The glabella narrows forward from the occipital ring to 2L, in front of here widening (tr.) to a maximum width across the frontal lobe; latter appears to reach the border furrow. Occipital furrow a deep slot inside axial furrow, shallow medially; occipital ring with strong, rounded median node. 1L and 2L defined by inward and backward directed 1S and 2S, having low independent convexity, 3L lower and 3S fainter, 3S commencing opposite anterior end of eye lobe. What appears to be a faint 4S curves forwards and inwards, indenting the frontal lobe immediately in front of the eye lobe. Eye lobe of length (exs.) about one third length (sag.) of cephalon, having a narrow, convex palpebral rim set off by a moderately deep furrow from the gently inflated palpebral lobe; latter extends inward from eye lobe and merges with L3 and frontal glabellar lobe. Extraocular genal area broad (tr.), anterior and lateral borders gently convex, shallow border furrow, posterior border apparently narrow (exs.), distally joining lateral border to form a blunt short genal spine; no evidence of an intergenal spine. This description of the cephalon is based on the original of figure 38, plate 6; the lectotype and the original of Walcott (1910, plate 30, figure 2), appear to show the same features. In 56807a, around the lateral borders, are exposed portions of the doublure showing terrace ridges parallel to the margin. Anteriorly and on the right side inside this doublure, are broken and probably displaced portions of the gently convex rostral plate, also bearing ridges. The course of the perrostral suture is not shown. Wanner (1901, pl. 32, figs 1–3; cf. Walcott 1910, pl. 30, figs 5 and 7) figured portions of the cephalic doublure and the hypostome, the former showing a row of ventrally facing pits along the inner margin. Traces of such pits (as spines) are not visible along the inner margin of doublure or rostral plate in 56807a. *Olenellus thompsoni* and possibly other species of *Olenellus* are also present at this locality (see list in Resser and Howell (1938, p. 205), and compare Fritz (1972, p. 11)), so that the detached fragments of the doublure and hypostome may not be attributable to *W. walcottanus* as Wanner and Walcott assumed.

Thorax of 17 segments. Axial region tapers backward evenly so that 17th axial ring is approximately one third the width (tr.) of the 1st. Shallow articulating furrow curves slightly backwards so that ring is shortest sagittally; articulating halfring of length (sag.) almost equal to that of ring. Axial rings 1–15 each bear a median node, these nodes posteriorly becoming pointed and backward projecting; that of the 15th segment large and elongated into an upward, and backward directed spine that extended well beyond the pleural spines. No median node on axial rings 16 and 17 (figure 28). Axial furrow shallow beside mid-portion of axial ring, descending steeply forward in a manner strongly suggesting the presence of an axial process at the anterior margin; a corresponding socket would have been present on the posterior margin. Pleural region divided into inner and outer portions, the inner impressed by the pleural furrow, the outer a curved pleural spine. In the anterior 10 or 11 segments the inner portion of the pleura was directed transversely proximally, successive segments curved back more strongly distally; behind this the inner portions were directed more strongly backward. The inner portion diminishes progressively in width (tr.) posteriorly, on segment 17 being much shorter than the pleural spine. Pleural spines curved back and tapered, a series that increases in length and backward direction from segments 1–13, the spines of 13–15 similar in length, 14 and 15 slightly incurved, those of 16 and 17 successively shorter and more inwardly curved. The doublure extends (figure 32, plate 5) beneath the spine to the boundary between the two portions at the extremity of the pleural furrow, and a narrow (exs.) strip of doublure continues along the posterior edge of the inner portion, diminishing in width as it approaches the axial furrow. Pleural furrow broad (exs.) and shallow, bounded by an anterior ridge that slopes more steeply down to the furrow than does the posterior ridge. The anterior ridge bounding the pleural furrow also slopes steeply down on its anterior, outer side, and passes into narrow (exs.) flange along the inner portion of the pleurae that projected beneath the doublure of the segment (or posterior cephalic border) in front. This flange extended part-way along the outer, anterior margin of the curved pleural spine, where it fitted below and inside the spine (or posterior cephalic border) in front of it. Latex casts from counter-part moulds (figures 30 and 32, plate 5) show how the segments fitted one beneath the other. Internal moulds (figure 24, plate 4; figure 33, plate 5) show a sharp break (Wanner's (1901, p. 268), 'prominent line of demarcation') between the mould of the exoskeleton of the inner portion of the pleura and the mould of the outer surface of the doublure of the pleural spine.

Pygidium (figures 30 and 32, plate 5) of length (exs.) similar to maximum width (tr.), lying between curved pleurae of 17th segment and not reaching as far posteriorly as these pleurae. A low axial ring, articulating furrow and halfring, forms the anterior margin, the lateral margins curving backward and slightly outward from the edge of this ring, and inward posteriorly. A faint inter-ring furrow (deep distally in internal moulds, figure 33, plate 5) separates the axial ring from a low median region, so that no more of the axial region is clearly defined. The lateral and posterior portions of the pygidium form the pleural regions, a deep, V-shaped median notch separating the incurved, pointed posterior tips. The doublure extends inwards beneath the pleural region to a line that continues the direction of the transverse margin of the doublure of the 17th segment; these margins meet well in front of the inner end of the median posterior notch.

The network of raised ridges that covers the external surface of the axial region, genal field and inner portion of the pleurae, is well shown by the external mould of Resser & Howell (1938, pl. 11). Over the anterior glabellar lobe the network changes to a Bertillon pattern of ridges, and to such ridges subparallel to the margin on the anterolateral cephalic borders and genal spine. At the transition from inner to outer portion of the thoracic pleurae (figures 36 and 37, plate 6), the network of ridges expands and passes into anastomosing ridges that run out to meet the anterior edge of the pleural spine at an acute angle. In portions of the exoskeleton subjected to stress on compaction, such as the transition between inner and outer portions of the pleurae, or adjacent to the axial furrow, the exoskeleton has fractured along the margins of the polygons of raised ridges. This suggests that these margins were lines of weakness in the exoskeleton. On the doublure of the pleural spines (figures 32 and 33, plate 5) the anastomosing ridges are directed at approximately a right angle to the anterior edge, but as they approach the posterior edge curve inwards and run towards the posterior edge at an acute angle. This change of direction causes the ridges on the posterior edge of the doublure, that lies above the flange of the succeeding segment, to run transversely. On the pygidial doublure the ridges are in a direction like that over the anterior part of the pleural spine.

Discussion. Cephala of species attributed to *Wanneria* were described by Fritz (1972, pp. 29–31). The lateral views of his plate 13, figure 2, plate 14, figures 9 and 10, and plate 16, figure 7, show the moderate convexity, the glabella and eye lobe standing well above the genal region, the latter horizontal or gently outward-sloping adaxially, the extraocular portion curving downward more steeply. The fracturing evident in the cephalon and along the axial furrows in the flattened specimens of *W. walcottanus* suggests a similar original convexity. If so, then the axial region of the thorax stood well above the inner pleural region, which may have been gently curved in cross section, the outer pleural region down-sloping. Thus a reconstruction similar in form to that of *Olenellus thompsoni* would be reasonable, and the articulating halfring, axial articulating process and flange made enrolment possible. The pleural spines would have fitted successively inside one another, the short first two spines inside the genal spine, the pygidium between the 17th spines.

None of the cephala described by Fritz, nor those of *Wanneria anneria* cf. *W. walcottanus* described by Palmer (1964, p. F4), exceeds about 10 mm in length (sag.), about one third the size of the lectotype of *W. walcottanus*. The reticulate pattern of raised ridges is preserved in the small cephala, and pits in the lateral border furrow, features not evident in the large specimen; the smallest cephala show radiating genal caecae rather than reticulate ridges. Hypostomes described by Fritz and Palmer are like that attributed to the type species by Wanner. In describing *W.* cf. *W. walcottanus*, Palmer (1964, p. F4, pl. 1, fig. 11) noted that perforations on the inner surface of the exoskeleton outlined the polygons, and that the exoskeleton broke along the margins of these polygons. Palmer suggested that this was because the perforations continued part way (but not to the external surface) through the exoskeleton as canals. Preservation of the present specimens supports the view that the polygons were outlined through the exoskeleton in a manner than made them lines of weakness. Fritz (1972, p. 29) regarded the reticulate network of ridges on the external surface of the exoskeleton of *Wanneria* as characteristic, and described in his species *W. parvifrons* (1972, p. 30) a granule in the centre of each polygon. This latter sculpture has been assumed to be diagnostic of *Wanneria* by Theokritoff (1985, pp. 283–284, fig. 1). A granule is not present in the centre of each polygon in the best-preserved specimens examined here (figures 30 and 32, plate 5; figures 36 and 37, plate 6) nor in *W. logani* (Fritz 1972, p. 29). Theokritoff referred fragments of exoskeletons showing the network and a central granule (Walcott 1910, pl. 24, fig. 10; Lochman 1956, pl. 6, figs. 11, 19 and 21) to *Wanneria* rather than to *Elliptocephala asaphoides*, but such an assignment of fragments may be open to question.

(*e*) *Elliptocephala* Emmons, 1844

Type species: *Elliptocephala asaphoides* Emmons, 1844

(i) *Elliptocephala asaphoides* Emmons, 1844

Figures 45, 46 and 48, plate 8; figures 50 and 51.

Material. Where Emmons's original specimens may be is not known; they are not in the collections of the New York State Museum (Dr E. Landing, personal communication). The two specimens described here were obtained by Walcott (1890*a*, p. 41) from the type locality, and described by him (Walcott, 1890*b*, p. 637, pls 89 and 90), together with a third specimen which has the most posterior portion of the thorax and the pygidium missing. Earlier, Ford (1877, 1881) and Walcott (1910) described small growth stages; these have been restudied (Whittington 1957, pp. 935–937; see comments by McNamara 1978, fig. 2, p. 646). Lochman (1956, pp. 1376–1377, pl. 6, figs 2–21) described cephala from various localities in New York State; the fauna associated with *E. asaphoides* (Lochman 1956; Bird & Rasetti 1968; Theokritoff 1985) is correlated with approximately the middle portion of the *Bonnia–Olenellus* zone. Although there is a considerable difference in size between the largest cephala described by Walcott (1910, pl. 25, fig. 14) and Lochman (1956, p. 1376, pl. 6, figs 2 and 9), which are about 25 mm in length (sag.), and the original of figure 48, plate 8, it appears reasonable to conclude that only one species is represented. The only other olenelloid recorded from this fauna are the fragments attributed to *Wanneria* by Theokritoff (1985, pp. 283–284, fig. 1), an attribution I regard as doubtful (§2*d*(i)).

Description. As noted above, the dorsal side of the cephalon and its development are reasonably well known and illustrated, and McNamara (1978, pp. 641–642) summarizes some of the morphological changes that took place during development. In larger cephala the deep, outer portion of S2 and S3, and probably also S1, were connected across the median portion of the glabella by a shallow depression; the glabella appears to have been widest (tr.) across the frontal lobe, immediately in front of the anterior extremity of the eye lobe. As McNamara (1978, p. 644) noted, the preglabellar field appears to have increased in length (sag.) during the meraspid and early holaspid developmental stages, but subsequently become relatively shorter. The intergenal spine, prominent in the meraspis, is lost early in the holaspid period, but a relatively short (exs.), broad-based genal spine is present in large holaspides (Walcott 1890*b*, pl. 90). Small hypostomes were illustrated by Walcott (1890*b*, pl. 88, fig. 1g; 1910, pl. 24, fig. 8) and Lochman (1956 , pl. 6, fig. 14), and the external mould of the posterior portion is visible where L3 and the frontal lobe are broken away in 18350a (figure 48, plate 8).

Thorax of 18 segments, axial region tapering back evenly to a width (tr.) slightly more than one third that of the first ring. Axial ring slightly narrower (sag.) medially than distally (exs.), shallow articulating furrow curves slightly backward. Articulating halfring present but none is exposed. A median node close to the posterior margin is evident on the 7th axial ring, and increases in prominence backward to the 14th ring. The fragment of the posterior portion of the thorax (figure 45, plate 8), known only from an external mould, shown the long median spines on the 15–18th rings, which decrease in length posteriorly. These spines may have been triangular in cross section, the sharp crest on the dorsal side. These spines are not shown by the internal mould (18350a), and it is uncertain whether or not the median node of ring 14 was extended as a spine, as Walcott (1890*b*, p. 638) apparently thought. Inner portions of pleurae of first six or seven segments directed transversely, behind here directed successively more strongly backwards. Outer portions in the form of a curved spine, shortest (tr.) on the 1st pleura, increasing gradually in length and backward curvature to the 13th pleura, diminishing in length and becoming lobe-shaped in pleurae 17 and 18. Inner portion traversed by a shallow, slightly diagonally directed pleural furrow. Near the outer end of this furrow internal moulds show a step in level (figure 46, plate 8) that indicates approximately the position of the inner edge of the doublure of the pleural spine. In the cast from the external mould (figure 45, plate 8) no such step is visible, the cast showing the dorsal surface of the pleura. Each pleura passes below the next pleura in front, strongly suggesting that an articulating flange was present along the anterior edge of the inner portion of the pleura. This flange may have extended outwards a short distance along the anterior edge of the pleural spine, for these edges appear to pass below the spine in front.

Pygidium wider than longer, anterior axial ring outlined by a shallow inter-ring furrow, lateral portion of ring slightly inflated. Behind the inter-ring furrow the triangular tip of the axis is outlined by shallow furrows. Pleural region flattened distally, pleura of first segment having a free tip, outlined by the marginal notch.

External surface of axial region, and inner portion of pleural region of thorax (Lochman 1956, pl. 6, fig. 21) bearing a network of raised ridges (figure 46, plate 8), and genal caecae are present on the extraocular genal field and preglabellar field (Lochman 1956, pl. 6, fig. 6; Whittington 1957, pl. 115, fig. 6). At the base of the median axial spines of the last four thoracic segments (figure 45, plate 8) the reticulate pattern of raised ridges changes into a pattern of branching sub-parallel ridges that curve upwards and backwards on the sides of the spine and join along the dorsal ridge.

Discussion. In outline of the glabella and form of the lobation, *E. asaphoides* resembles *W. walcottanus*, the frontal glabellar lobe being wider (tr.) in the latter; in both species the palpebral rim is narrow and prominent. The resemblance between these species was commented on by Bergström (1973*b*, pp. 307–308), and neither shows a subdivision of the thorax or a macropleural third thoracic segment; a prominent median spine was developed on the 15th segment in each, and on more posterior segments in *E. asaphoides*. In the characters mentioned these two species are like *Holmia kjerulfi* (Kiaer 1917, figs 8 and 9), and Bergström (1973*b*, p. 285) placed these three genera in the same family.

3. Morphology of holaspid olenelloids

This account is based upon the important North American material re-examined here, supplemented by reference to more recent descriptions of Scandinavian, Moroccan and Russian material.

(*a*) *Cephalon*

Sub-semicircular in outline, moderately convex. Moore (1959, p. O191) thought that the olenelloid exoskeleton was nearly flat or of low convexity, but this is a misapprehension derived from flattened specimens. Bergström (1973*a*, p. 17, pl. 2, figs 3 and 4) drew attention to the arched cross section, and how the gena sloped outwards and downwards from the axial furrow. This convexity is amply confirmed by material preserved in relief, such as that described by Poulsen (1958,) Fritz (1972) and Egorova & Savitskii (1969, pls 9–11). The glabella stood above the gena, divided by an occipital furrow and up to four pairs of glabellar furrows. The latter deepest abaxially, S1, 2 or 3 may be connected across the median region by a faint depression or a more definite furrow. The frontal glabellar lobe may be narrower (tr.) than the remainder of the glabella and low in convexity, or wider than the portion behind it, subcircular in outline and moderately or quite strongly inflated. The outline of the glabella may hence taper forward, approach parallel-sided, or be hour-glass in shape if the glabella narrowed forwards to L2 and L3 and expanded in front of these lobes. The glabella may, or may not, extend forward close to, or in contact with, the anterior border. The eye lobe was prominent, curved, standing well above the gena, the palpebral lobe continued by the eye ridge (the palpebro-ocular ridge, see Bergström (1973*b*, fig. 1) for terminology) to the glabella opposite L4. The axial furrow was shallow or barely discernible beside L4. Some olenelloids have a prominent palpebral rim, the furrow on the inner side of this rim continued by the ocular striga, a furrow that divides the palpebro-ocular ridge. The anterior palpebro-ocular ridge may be continued forwards around a portion of the margin of the frontal glabellar lobe, or to the median line, where it may join a median preglabellar ridge (Fritz 1972, pl. 1, fig. 1). These ridges were observed by Hupé (1953*a*, text-fig. 16) in the Moroccan olenelloids. The partial flattening of the Moroccan material may have accentuated these features in some specimens, but the material preserved in relief illustrated by Fritz (1972) and Bergström (1973*b*, fig. 17) shows their nature less equivocally. In many olenelloids a ridge runs from the posterior end of the eye lobe (or of the interocular area) outwards and backwards to the base of the intergenal spine. This ridge is here called the intergenal ridge, and although it was a feature of meraspid and early holaspid stages (Whittington 1957, pl. 115, figs 1–5; Palmer 1957) of development, it is less conspicuous (Bergström 1973*b*, fig. 2) or may be absent (Fritz 1972) in larger holaspides.

The inner portion of the posterior border of the cephalon is narrow (exs.), the border widening as the posterior margin curves back at the base of the intergenal spine. Outside this spine the border is wider (exs.) and it is only this outer portion of the border that is directed outward and forward in such genera as *Bristolia* (Palmer & Halley 1979, pl. 1). The position where the posterior border widens is recognizable in olenelloids generally, by the widening itself, or by the position of the intergenal spine or of the outer end of the intergenal ridge, or some combination of these characters. Its position corresponds to that of the boundary between inner and outer portions of the pleurae. The form of the posterior cephalic border is revealed in the illustrations of material preserved in relief by Poulsen (1958), Fritz (1972), Bergström (1973*b*) and Palmer & Halley (1979), for example. These figures also show that the inner portion of the border curved downwards and outwards from the axial furrow, and was not horizontal.

In the smallest meraspides of the silicified specimens described by Palmer (1957) the eye lobe appears smooth, the exact limits of any visual surface cannot be seen, nor any lenses within it. In larger specimens (Palmer 1957, pl. 19, figs 16, 17, 19 and 20) the eye surface is outlined and may be missing, partly missing or preserved. Specimens of the former type led Öpik (1967, pp. 54–55) to claim that a circumocular suture was present in olenellids. As Öpik pointed out, the clear-cut edge of the visual surface argues that it was a sutural boundary. The evidence for such an edge in the specimens figured by Fritz (1972) and Palmer & Halley (1979) is not convincing, but suggestive in that the outline of the visual surface is, in portions on particular specimens, clean-cut, not ragged, as in the originals of figures 4 and 8, plate 1, for example. The evidence for or against such a suture should be sought, and the nature of the eye surface itself needs investigation. Clarkson (1973, text-fig. 1a) figured the impressions of lenses in a meraspid of *Olenellus*, Kiaer (1917, p. 65, pl. 7, figs 1–3) described the facets and clearly bounded eye surface in holaspid *Holmia*, and Palmer & Halley (1979, pl. 1, fig. 12) illustrate a small holaspid of *Bristolia* in which the eye surface is outlined and preserved, but the surface smooth. If there was a circumocular suture in olenellids, moults should have the eye surface missing, but specimens derived from dead animals at an inter-moult stage may show the line of the suture around the edge of the preserved eye surface.

Radiating, anastomosing ridges on the genal field, the genal caecae, are present in many species of olenelloids, more evident in the younger stages of development, but retained in some large specimens. Not part of this pattern is the intergenal ridge and the genal ridge (Fritz 1972, pl. 11, figs 17 and 21) that runs out from the outer margin of the eye lobe to the genal angle. A ridge commencing at the outer, anterior edge of the eye lobe, and curving around to the genal angle, in one species continuing across the posterior border inside the base of the genal spine, was described as the anterior ocular line by Hupé (1953*a*, pp. 116–117, text-fig. 16). Størmer (1942, pl. 2, figs 1 and 3) showed a similar faint line in *Kjerulfia* and *Holmia*.

The form of the hypostome, rostral plate, and course of the suture in olenelloids has recently been reviewed, and a reconstruction of the cephalon of *Holmia* given (Whittington 1988*a*, pp. 579–581). More information is needed, but although in early meraspides of *Olenellus* the hypostome was apparently detached (Whittington 1988*a*, fig. 4), in holaspides of this and other genera it was attached by a narrow (tr.) hypostomal suture to the rostral plate, the suture possibly having been functional only at exuviation. The hypostome was braced against the rest of the cephalic exoskeleton at the tip of the anterior wing, where it lay close beneath the axial furrow immediately in front of the palpebro-ocular ridge. During life the hypostome was held firmly in this position, a position seen, for example, in the large specimen of *Elliptocephala* (figure 48, plate 8).

(*b*) *Thorax*

Thorax of 9 segments in *Olenellus* (*Olenelloides*) (McNamara 1978), of 13 or more segments in other olenelloid species. The inner portion of the pleura is reduced in width (tr.) backwards, the outer portion a spine that is curved backwards progressively more strongly. In *O. thompsoni* (figures 4 and 5, plate 1) the pleura of the 14th segment is long and directed almost straight backwards, and in the restricted space between these pleurae, those of succeeding segments 14–19 must necessarily have been narrow (tr.), the spines short and directed backwards and downwards. This abrupt change in the pleural region suggested to Hupé (1953*a*, pp. 117–118, 122–123) a division of the thorax into a prothorax and post thorax, the latter having the pleurae 'reduced or absent'. This subdivision was accepted by Harrington *et al.* (*in* Moore 1959, p. O123, 125) the term 'opisthothorax' being substituted for post thorax, and the division described as having 'reduced pleurae'. In *O. vermontanus* (figures 16 and 18, plate 3) and *O. robsonensis* (figure 20, plate 4) a division in the thorax may be recognized, though the space between the 14th pleurae is less restricted; in *O. vermontanus* the relatively narrow (tr.) body makes the change less obvious. In the opisthothorax of *O. vermontanus* pleurae 15–25 show an inner portion and pleural furrow, and appear to have the articulating flange. In *O. robsonensis* the inner portion is more reduced, but in both species the gradation in size from segment 16 onward is gradual compared with the abrupt change between 14 and 15. In such other olenelloids as *O. multinodus* Palmer & Halley (1979, pl. 4, fig. 7), *Bristolia insolens* (Riccio 1952, pl. 6, figs 1–3), *Biceratops nevadensis* (figure 11, plate 2) (Pack & Gale 1971, pl. 102, fig. 4), and *Peachella brevispina* (Stitt & Clark 1984, figs 2 and 3) the 14th pleura is directed moderately outwards and backwards, and impressed by the pleural furrow. The 15th pleura is apparently narrower (tr.) and shorter (exs.) than the 14th, and only faintly, if at all, impressed by a pleural furrow. Succeeding pleurae show a gradual reduction posteriorly, lack the pleural furrow, and adaxially are separated from the axial ring by a change in slope rather than an axial furrow. The specimens referred to do not show the two or three pleurae following the 14th clearly, except the right side of *O. multinodus*. It is uncertain in this specimen which is the 14th segment, and Palmer & Halley (1979, p. 73) describe the passage from prothorax to opisthothorax as transitional. Nevertheless, a prothorax that is broad anteriorly and rapidly tapered in outline behind the macropleural segment (except in *O. vermontanus*), and a narrow opisthothorax that tapers gradually, may be seen in all the specimens, the transition between them taking place between the 14–17th segments; the 15th segment bears a prominent median axial spine (except possibly in *O. multinodus*). In *Nevadia* (figures 39 and 40) the transition takes place in a rapid reduction in size in the pleurae of segments 15–17, and an opisthothorax of segments 18–27 may be recognized, graded posteriorly more slowly in size. On such criteria a subdivision of the thorax cannot be recognized in *Wanneria* (figure 38, plate 6), *Elliptocephala* (figures 46 and 48, plate 8), *Callavia* (Walcott 1890*b*, pl. 91), *Holmia* or *Kjerulfia* (Kiaer 1917, figs 9 and 12), or *Judomia* (Savitskii *et al.* 1972, pl. 8, fig. 2). Hupé did not consider that the sub-division was recognizable in *Bondonella* or *Daguinaspsis* (1953*a*, figs, 27 and 28), although his claim that it was present in *Fallotaspis* and *Neltneria* (Hupé 1953*a*, figs 19 and 25) appears doubtful. The last few segments in the thorax of these last two examples differ slightly from those in front, but not as pronouncedly as in the instances given above. A pronounced division of the thorax appears to be characteristic only of certain North American species.

In the undivided thorax, or the prothorax, axial rings are convex, and are separated by a shallow articulating furrow from the articulating halfring. Kiaer (1917, p. 79) first described the articulating process at the anterior margin of the axial furrow and the corresponding socket on the posterior margin. A median node may be present adjacent to the posterior margin of the axial ring, and such nodes may increase in strength posteriorly and form one or more backwardly directed spines. A pleural furrow crosses the inner portion of the pleura, ending at the base of the pleural spine. It is shown here (figure 32, plate 5) that the doublure extended inwards to the base of the hollow pleural spine, and may have extended as a thin strip along the posterior margin of the inner portion of the pleura. Photographs of the thorax preserved as an internal mould (e.g. *Holmia* in Størmer (1942, pl. 2, fig. 4); *Fallotaspsis* and *Neltneria* in Hupé (1953*a*, pl. 1, fig. 1; pl. 3, figs 2 and 6) show the marked step in level separating the mould of the dorsal and ventral (doublure) surfaces at the boundary between the two portions of the pleurae. These latter photographs also show that the pleural furrow terminates adaxial to the base of the pleural spine, this base defined by the inner edge of the doublure. In *Olenellus* (figures 4 and 8, plate 1) the furrow extends on to the spine. Bergström (1973*b*, pp. 285, 309) introduced this difference in the extent of the pleural furrow as a character of familial rank. An exception to the pleurae being impressed by a pleural furrow is provided by one specimen of *Judomia tera* (Demokidov & Lazarenko 1964, pl. 7, fig. 8; pl. 8, fig. 8), whereas another specimen referred to the same species (Savitskii *et al.* 1972, pl. 8, fig. 2) has a narrow, diagonal pleural furrow on the inner portion of the pleura. The flange along the anterior edge of the pleura (figure 1) was an important articulatory device. In *Olenellus* (figures 4 and 8, plate 1), *Biceratops* (figure 11, plate 2), *Bristolia* (Riccio 1952, pl. 6) and *Peachella* (Stitt & Clark, 1984) a macropleura was developed on the third thoracic segment. The axial ring of this segment is not exceptionally long (sag. or exs.), but fits in size with the series of the thorax. The inner portion of the pleura, however, expanded rapidly in length (exs.) distally, moderately so in *Olenellus*, but in other genera to three or four times its length adjacent to the axial furrow. In these other genera, the form of the second, and fourth to sixth inner portions of adjacent pleurae was modified to accommodate the expansion. The outer portion of the macropleura formed a long, stout pleural spine that extended well beyond the rest of the exoskeleton. The thorax of these four genera also had a long, backward- and upward-directed median axial spine on the 15th segment, the first of the opisthothorax. This latter consisted of between 4 and 25 segments in species of *Olenellus*, and respectively a minimum of 10, 17 and 8 or 9 in *Biceratops*, *Bristolia* and *Peachella*. The axial rings of these segments conformed in width (tr.) to the even taper of the rings of the prothorax, and showed a progressive reduction in width and length (sag. and exs.) posteriorly. As noted above, the axial furrow is not impressed in the opisthothorax, being rather a change in slope. The disarticulation in *O. robsonensis* (figure 25) reveals fragments of articulating halfrings and deep articulating furrows, showing that the opisthothoracic segments freely articulated with one another. The combination of a subdivided thorax, the prothorax with the third segment macropleural, and the first opisthothoracic segment with a long axial spine, is known only in species of *Olenellus* (the axial spine may not be present in *O. multinodus*), *Bristolia*, *Biceratops* and *Peachella*. In other genera only one of these thoracic characters may be present, for example, only the subdivided thorax in *Nevadia* (figure 39), or only the axial spine on the 15th segment in *Wanneria* (figure 35, plate 6). In species in which the thorax is not subdivided, a macropleura is developed in *Fallotaspsis* (Hupé 1953*a*, p. 127) and *Andalusiana* (Sdzuy 1961, p. 247). The macropleura may be lost during development, for it is present in the early holaspid of *Elliptocephala* (Whittington 1957, p. 936) but not in larger individuals. Median axial spines are developed on segments 15–18 of *Elliptocephala* (figure 50), on segments 10–14 of *Holmia* (Kiaer 1917, p. 63, fig. 8) and on posterior segments, especially 16 and 17, of *Kjerulfia* (Kiaer 1917, p. 78, fig. 12). The number of thoracic segments in forms that lack a division of the thorax varies from 16 in *Holmia* (Kiaer 1917) to 18 in *Elliptocephala* and *Callavia* (Walcott 1890*b*, pl. 91).

As mentioned in §3*a*, in a wide variety of olenelloid cephala the inner portion of the posterior border slopes downwards and outwards from the axial furrow. The inner portion of the thoracic pleura must have conformed to this convexity, as shown here in the reconstruction of *Olenellus* (figures 1 and 2), and by an almost entire specimen of *Judomia tera* (Demokidov & Lazarenko 1964, pl. 7, fig. 8). Thus, so far as appears to be known in olenelloids, there was no straight, horizontal hinge between the inner portion of the posterior border of the cephalon, the inner portions of the pleurae of successive segments, and the pygidium. Enrolment (to an unknown maximum extent) was evidently possible, in a manner much as shown here in *Olenellus*.

(*c*) *Pygidium*

As the entire specimens show, the olenelloid pygidium was narrow (tr.) in relation to the cephalon. The maximum width of the pygidium was related to how strongly backward-directed were the pleurae of the last thoracic segment (compare figures 1*a* and 51). In specimens of *Olenellus* (figures 3, 14, 15 and 27) the pygidium may be partly concealed by the axial spine, but appears to have had a convex axis, the pleural region of a width (tr.) similar to that of the axis, extending behind it, the outline of the margin convex backward, bilobed, or extended by one or two pairs of posteriorly directed spines. The pygidium of *Nevadia* (figure 40) also appears to have consisted of more than two segments and like *Olenellus* to have had a short (sag. and exs.) portion of the pleural region posteriorly. Best preserved is that of *Wanneria* (figure 28), which shows the anterior axial ring, the pleural region composed of the fused pleurae, and an obscure tip of the axis. In *Elliptocephala* (figure 51) the pleura of the first segment ends in a short pleural spine, the posterolateral margin of the pleural region apparently entire. The pygidium of *Schmidtiellus* (Bergström 1973*b*, fig. 14*d*) has a convex axis divided into two rings and a terminal portion, and a narrow (tr.) pleural region that may be notched or spinose on the posterior margin. In *Holmiella* (Fritz 1972, p. 25, pl. 4, figs 4–6; pl. 7, figs 14–17; Ahlberg *et al.* 1986, fig. 13) the axis is also divided into two rings and a terminal portion, and the pleural region divided by backward curving interpleural furrows into two pairs of pleurae with spinose tips, a third pair of tiny spines posteromedially. The relatively great width of this pygidium, commented on by Fritz, is clearly related to the gently backward direction that the inner portion of the last thoracic segment must have had to have fitted the pleural region. Two examples of the pygidium of the Siberian *Judomia tera* have been illustrated. The first (figure 54*a*) has two axial rings, separated by straight inter-ring furrows, the anterior showing a short (sag.) articulating halfring. The axial rings slope down distally and merge into the curved, blade-like pleurae, the anterior pair directed slightly outwards, the second directly backwards. These pleurae are almost entirely separated from one another, and from the remaining posterior portion of the pygidium. One incomplete specimen shows that the doublure extended inwards to more than half the length of the pleura, there was no pleural furrow. In the remaining portion of the pygidium a gently convex anterior region merged posteriorly into a pair of pleurae that reached back to a lesser distance than the first two pairs and were similarly pointed. The second example (figure 54*b*) is attached to 12 thoracic segments, the last four of which are shown here. The axis of the pygidium was divided into two rings, and the long (sag. and exs.) pleural region divided posteriorly into a pair of flattened spines. The posterior portion of the pleural region is exfoliated, and shows that the doublure, concave ventrally, extended inwards to the ill-defined tip of the gently convex axis. The pygidium attributed to *Callavia* by Raw (1936, pl. 21, figs 3*a–c*) is composed largely of one pair of spines similar in form to those of *J. tera.* Photographs of an undescribed olenelloid (figures 21 and 22, plate 4) from western Canada were sent to me by Dr W. H. Fritz. These show a species having an advanced genal spine, and apparently no macropleura in the undivided thorax. There was a prominent axial spine on the 15th segment, largely broken away, an impression of one edge remaining on the axis of the pygidium (figure 26). Part of the left pleural spine of segment 15 is preserved, and the succeeding segments 16 and 17 show progressive reduction in size of the pleurae. The pygidium, elongate–oval in outline, is divided by a faint change in slope into an axial region and slightly narrower (tr.) pleural region; the pleural region extends behind the rounded tip of the axis, length (sag.) of this posterior portion about equal to width (tr.) of the region laterally. The axial region appears slightly abraded, but anteriorly shows two distinct rings and faint inter-ring furrows; behind these are faint suggestions of further divisions.

The olenelloid pygidium thus appears to have been formed of at least two, and perhaps as many as five or six, fused segments. The axis was convex, and where the inner portions of the anterior one or two pleurae were outwardly and backwardly directed, as in *Elliptocephala* or *Holmiella*, the pleural region was relatively wide, in contrast to the condition in *Olenellus.* In some species the pleural region was extended posteriorly, the margin of this portion bilobed or

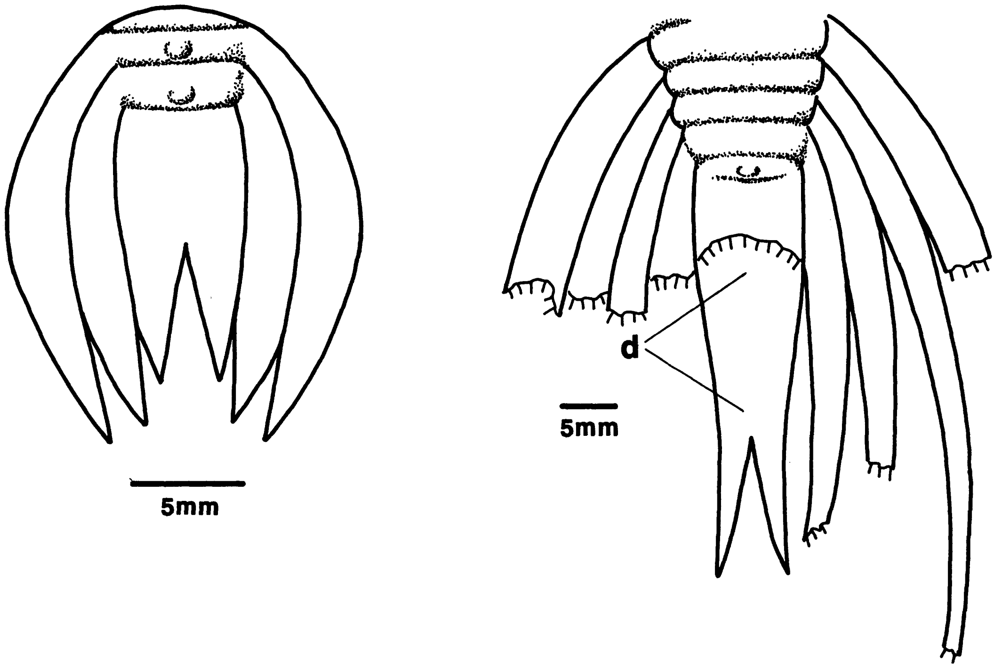

Figure 54. *Judomia tera* Lazarenko, 1960. (*a*) Pygidium after Demokidov & Lazarenko (1964, pl. 8, figs 2, 6 and 8). (*b*) Posterior four thoracic segments and pygidium, after Savitskii *et al.* (1972, pl. 8, fig. 2). Hachures indicate edge of exoskeleton.

showing one or more pairs of pleural spines. It is probable that the doublure extended beneath these fused pleural spines towards the tip of the axis, as it did in *Wanneria*.

(*d*) *Sculpture of external surface*

A reticulate pattern of raised ridges, on the external surface of the axial region (except the anterior glabellar lobe), genal field and inner part of the pleural region is well known in *Wanneria* (figure 36, plate 6) (Resser & Howell 1938, pl. 11), and a similar sculpture is present in *Elliptocephala* (figure 46, plate 8), *Nevadia*, *Holmia* and *Kjerulfia* (Kiaer 1917, pl. 14), *Callavia* (Raw 1936, pl. 18, figs 1, 3 and 21) and in some specimens of *Olenellus* (Fritz 1972, pl. 11, fig. 20; pl. 12, figs 20, 24 and 25). In the large specimen of *O. thompsoni* (figure 7, plate 1), however, the pattern formed by the raised ridges is anastomosing rather than reticulate. The reticulate sculpture appears to be confined in the dorsal exoskeleton to portions not underlain by the doublure or hypostome. In these anterior and distal portions of the exoskeleton the network changes into anastomosing terrace ridges, and on the cephalic doublure similar ridges run subparallel to the outer margin; on the doublure of the pleural region the pattern is more complex (e.g. in *Wanneria*, figure 32, plate 5). In describing *Wanneria* cf. *W. walcottana*, Palmer (1964, p. F4, pl. 1, fig. 11) noted that perforations on the inner surface of the exoskeleton outlined the polygons, and that the exoskeleton broke along the margins of these polygons, showing that the perforations extended part-way through the exoskeleton, but not to the dorsal surface. The polygons in *Wanneria* (figure 36, plate 6) and *Elliptocephala* (figure 46, plate 8) are outlined in a manner that suggests they extended through the exoskeleton, as are those of *Schmidtiellus* of Bergström (1973*b*, fig. 13*a*). This structure may be peculiar to olenelloids, and deserves further investigation. Granulation on the external surface occurs in *Andalusiana* (Sdzuy

1961, p. 249, pl. 3, fig. 5*b*, *c*), *Bradyfallotaspis* and *Parafallotaspis* (Fritz 1972, pl. 1, fig. 5; pl. 6, figs 6 and 8), and a Bertillon pattern of anastomosing ridges in *Holmiella* (Fritz 1972, pl. 4, figs 5 and 12) and *Bristolia* (Palmer & Halley 1979, pl. 1, fig. 10). Bergström (1973*b*, p. 286) referred to a reticulate sculpture of raised ridges in *Elliptocephala*, in which there is a node in each polygon, as a character of taxonomic significance. Presumably Bergström had in mind illustrations by Walcott (1910, pl. 24, fig. 10) and Lochman (1956, pl. 6, figs 11 and 19). Fritz (1972, p. 30) described this sculpture in *Wanneria parvifrons*, but it has not been observed in the type and other species of *Wanneria* (§2*d*) nor in *Elliptocephala* (§2*e*). To regard this sculpture as diagnostic of *Wanneria* (Theokritoff 1985) is questionable. Its significance needs further study, and how it may be preserved in internal and external moulds.

4. Discussion

(*a*) *Development of exoskeleton*

McNamara (1978, pp. 641–643, text-fig. 2; 1986*a*, fig. 4*a–f*) has summarized the changes that took place in development of the dorsal exoskeleton. One of these in *Elliptocephala* is the increase in width of the inner portion of the thoracic pleurae, which took place more rapidly than the width of the axial region increased. This increase in width of the thorax parallels the outward migration of the intergenal spine. The exsagittal line joining the bases of the intergenal and thoracic pleural spines is an important line in the exoskeleton, outside which it is underlain by the doublure and slopes more steeply outwards and downwards. This line is the morphological equivalent of the fulcrum in trilobites in which the inner pleural region is horizontal. The ontogeny of *Elliptocephala* (Whittington 1957, pl. 115, figs 4 and 5) also shows that the macropleural segment, the third of the thorax, loses its enlargement and becomes a normal segment in the series early in the holaspid stages. Perhaps most significant is that the best-preserved developmental series of *Olenellus* known (Palmer 1957, p. 126) show no trace of anterior or posterior branches of a dorsal facial suture. Hence it may be agreed that there is no evidence of such sutures in olenelloids, and Palmer's observations also showed that the perrostral suture was present in the earliest developmental stages, and maintained a constant position on the cephalic doublure throughout development. The development of the procranidial, genal and intergenal spines (Palmer 1957; McNamara 1978, text-fig. 2) shows that no credence can be given to the idea of the metaparial head plan, and the rotation of these spines so ingeniously developed by Raw (1925, p. 312; 1927). The material studied by Palmer (1957) shows no sign of the supposed circumocular suture in his stages I–IV. However, in some of the small holaspides (Palmer 1957, pl. 19, figs 16, 17 and 20) the presumed visual surface is sharply outlined, wholly or in part, suggesting the development of such a suture at this stage.

(*b*) *Functional morphology*

The enrolment of olenelloids was investigated by Bergström (1973*a*, pp. 16–17), and some of the rare, partly enrolled specimens commented on. Newly described here is the pleural flange (figure 1), curved down distally. It appears probable that *Olenellus* lacked a horizontal hinge, as Bergström thought, but I do not agree with him that successive segments 'were almost immovably connected with one another' (1973*a*, p. 17). I suggest that the flexible ventral cuticle extended outwards as far as the longitudinal edge of the doublure of the thorax, and that a flexible membrane connected the anterior edge of the flange to the edge of the narrow strip of doublure along the posterior edge of the segment in front. A similar flexible membrane would have connected articulating halfring and doublure of the ring in front. Figure 2 suggests rotation about the axial process and socket, and portrays perhaps a minimum possible enrolment. The maximum possible may have brought the pygidium closer towards the cephalon, in what Bergström called partial or incomplete enrolment, presumably a protective posture with the genal, macropleural and median axial spines differently directed. When the body was outstretched on the substrate these and other spines were presumably also protective, the genal and macropleural spines providing stability and preventing excessive lateral roll, when appendages were used in digging (cf. Ingham (1968) on the role of similar spines in *Cybeloides*) in search of food or for partial concealment. When the animal was drifting or swimming (feebly?) the median axial spine would have aided in balance. In the case of an olenid with a prominent axial thoracic spine, Fortey (1974, fig. 4, pp. 27–28) suggested that this spine may have aided in righting the animal if it were overturned. Such an activity would also have required concave–dorsal arching of the body, which may have been possible for *Olenellus* (§2*b*(i)). The function of the macropleural spine is thus considered to have been largely to assist in propping the animal in position on the substrate, including cases in which it was very long and stout, as in *Biceratops* (figure 11, plate 2) and *Peachella* (Stitt & Clark 1984). Both of these genera had either extremely short pleural spines on other segments, or rounded tips. *Biceratops* also lacked the genal spine, but the macropleural spine extended far back, well behind where the pygidium presumably was situated. *Peachella* had a short, lobe-shaped genal spine and a long macropleural spine. These large macropleural spines, with the median axial spine, may also have played a role in buoyancy and balance. In these two genera the inner portion of the macropleura expands in width (exs.) abaxially to three times the proximal width, and pleurae ahead and behind are shaped to accommodate this expansion. Probably these inner portions of the pleurae were not horizontal, but curved gently downward abaxially. It appears, however, that the shape of the macropleura, and of adjacent pleurae, was such that partial enrolment of the body was possible.

Exuviation in olenelloids was discussed by Hupé (1953*a*, pp. 120–122, fig. 18), with reference to the cranidium and inverted rostral plate and hypostome of *O. thompsoni* (Resser & Howell 1938, pl. 9, fig. 6), and an entire dorsal exoskeleton of *W. walcottanus* with an inverted rostral plate and hypostome beside it (Resser & Howell 1938, pl. 10, fig. 9). A complete dorsal exoskeleton (figure 8, plate 1) of *O. thompsoni* has the inverted rostral plate situated below it, the tips of the rostral plate situated beneath the genal angle almost exactly below where they would have been in life. Resser & Howell's specimen shows the same relation, and similar ones have been observed in other trilobites (see McNamara & Rudkin 1984, pp. 164–171, figs 9, 12 and 13). Such configurations of preserved exoskeletal parts are explained (McNamara & Rudkin 1984, fig. 11) as resulting from an initial arching of the body until the cephalon was vertical, separation of the old exoskeleton along the perrostral suture, and inversion of the rostral plate as the animal moved forward over it in resuming a horizontal position. These authors suggest that the purpose of arching the body was to initiate a split of the old exoskeleton between cephalon and thorax. Such a split would explain the Resser & Howell specimen of *O. thompsoni* as resulting from subsequent separation of the cast thoracic and pygidial exoskeleton from that of the cephalon. The failure of such a split to develop in the original of figure 8, plate 1, presumably left the animal to free itself by crawling forward out of the entire exoskeleton. The sharply defined edges of the visual area suggest that freeing the eye surfaces at the circumocular suture may have helped this process. The hypostome may not be in place against the inverted rostral plate in this specimen. Possibly it was carried away on the post-ecdysial animal and shed elsewhere, as McNamara & Rudkin (1984) suggest. If exuviation in olenelloids took place in the manner outlined, the macropleural or median axial spines may have assisted in propping up the arched body. The ability to partly enrol the body (figure 2) was essential to this process, as McNamara (1986*b*, p. 412) remarks as a result of considering exuviation in *Redlichia*.

5. CHARACTERS DISTINCTIVE OF OLENELLOIDS

The olenelloid exoskeleton (§3) exhibits many structures that are typical of all trilobites. Yet such authors as Rasetti (1972, p. 44) regarded olenelloids as 'susceptible of a perfectly sharp definition', and Bergström (1973*b*, p. 285) considered that 'Olenellaceans constitute one of those trilobite groups which is most easily distinguished and morphologically most isolated'. Characters that have been considered (Hupé 1953*a*, pp. 116–118; Bergström 1973*b*, pp. 284–285; Repina 1979, p. 11) to be distinctive of olenelloids are as follows.

1. Lack of anterior and posterior branches of the dorsal facial suture. No evidence of such sutures is present in ontogeny, and it is doubted that particular ridges on the gena of holaspides are fused remnants of such sutures. Other trilobites, such as agnostids, trinucleids and harpetids, lack dorsal facial sutures at any stage in development. Peculiar to olenelloids is the presence of a large eye lobe, despite the lack of dorsal sutures; this eye lobe may have been that of a holochroal eye, and there was probably a circumocular suture.

2. The crescentic rostral plate, extending between the genal angles, and perrostral suture separating it from the cephalic doublure. The rostral plate in *Xystridura* (Öpik 1975*a*, pp. 26, 84) extends between the genal angles, as it does in the Carboniferous proetid *Brachymetopus* (Whittington 1988*b*, p. 328) in which it occurs in combination with the lack of dorsal facial sutures and presence of a compound eye.

3. The thorax was of many segments, in some species the third was macropleural, a median axial spine present on the 15th segment and on adjacent segments, and in species of *Olenellus* and related genera there was a subdivision of the thorax. Bergström (1973*b*, p. 284) pointed out that the pleural region was not divided by a fulcrum into an inner, horizontal portion and outer, flexed-down portion. None of these characters is unique to olenelloids.

There are as few as 9 thoracic segments in the tiny *Olenelloides* (McNamara 1978), and although 40 segments are known in *O. robsonensis*, a maximum of 32 are known in *Alokistocare* (Robison 1971) and 61 in emuellids (Pocock 1970). A macropleural segment is not present in all olenelloid species, but when it is developed it is on the third thoracic segment. A macropleura is present, for example, in the raphiophorid *Cnemidopyge* (Hughes 1969, p. 62) and the encrinurid *Cybeloides* (Ingham 1968). A median spine on the axial ring of thoracic segment 15, the first of the opisthothorax, characterizes *Olenellus* and related genera, but in other olenelloids such spines are absent, in others (e.g. *Elliptocephala*) developed on several segments. A long axial spine on the thorax is present, for example, in the olenid *Balnibarbi* (Fortey 1974, fig. 4), in *Encrinurus* (Ramsköld 1986, pl. 39, fig. 1) and the aulacopleurids *Cyphaspis* and *Harpidella* (Thomas 1978, pl. 7, figs 9, 11, 17 and 18). It has been explained (§3*b*) that a subdivision of the thorax into prothorax and opisthothorax appears limited to *Olenellus* and related genera. This subdivision resulted from the sharp change in size between the pleurae of the 14th and the immediately succeeding segments. A similar change occurs behind the 6th, macropleural segment (which is fused to the 5th segment) of the thorax in emuellids (Pocock 1970). This change was related (Pocock 1970, pp. 551–552) to the restriction in width imposed by the backward- and outward-directed posterior edge of the macropleura, and Pocock referred to the necessity of maintaining ability to articulate between segments. In such olenelloids as *Bristolia insolens* (Riccio 1952, pl. 6, figs 2 and 3) and *Biceratops nevadensis* (figure 11, plate 2) the macropleura, despite its great width (exs.) distally, does not produce this effect. The inner portions of succeeding pleurae accommodated to the change in direction, and became transverse again, the transition to the opisthothorax taking place at a later stage. A change in the thorax akin to the subdivision in some olenelloids is seen in *Hapalopleura clavata* (Harrington & Leanza 1957, p. 205, figs 109 and 110), if these many posterior segments are not fused into a pygidium, as these authors thought. There was a gradual transition from a wider, rapidly narrowing anterior portion to a posterior portion that tapered more gradually. Though the evidence is limited, it appears probable that in olenelloids the inner portion of the pleura was not horizontal, but curved and downwardly inclined, and that there was no fulcrum. Articulation appears to have been facilitated by the flange. In *Paradoxides* (Bergström & Levi-Setti 1978), *Redlichia* (Öpik 1970, p. 4), and the corynexochoid *Olenoides* (Whittington 1980, pp. 173–178) there was no horizonal inner portion of the pleura and fulcrum, and in the latter genus a flange similar to that in *Olenellus* aided articulation.

4. The small pygidium, formed by the telson and a few segments (Bergström 1973*b*, p. 284). Accepting the definition of Manton (1977, p. 150) that the telson is not a segment, there are no grounds for maintaining the interpretation (Harrington in Moore 1959, p. O73) that the olenelloid pygidium was a 'telson', a single segment, and not homologous with the pygidia of other trilobites. The specimens described herein show that the olenelloid pygidium, which must have included the telson, the unsegmented posterior portion of the body bearing the anus, consisted of few segments, the doublure being best known in *Wanneria*. Many other trilobites had a pygidium that was much smaller than the cephalon, and included few segments.

Thus none of the characters that have been used to define olenelloids is unique to the group, but is shared with other trilobites. The olenelloids may hardly be described as morphologically isolated, but as differing from other, generally similar Cambrian trilobites in having a large eye lobe but lacking dorsal facial sutures.

6. Classification of olenelloids

Harrington (in Moore 1959, pp. O153–O154) assumed that functional dorsal, rostral, connective and hypostomal sutures were primary in trilobites. In his classification he followed the lead of Richter (1932) in placing olenelloids, redlichioids and paradoxidoids in the order Redlichiida, associating with them ellipsocephaloids and Bathynotidae. Pocock (1970) added the Emuellidae to the suborder that included redlichioids and their allies. Judging by the diagnoses (Moore 1959, pp. O191, O198), what was considered to be the suborder Olenellina was separated from the suborder Redlichiina because the facial sutures were 'ankylosed', in contrast to the other groups that had opisthoparian facial sutures. Since then Bergström (1973*b*; cf. Ahlberg *et al.* 1986) has argued that olenelloids may be contained within a single superfamily of such distinctive character as to deserve ordinal status, whereas Repina (1979) deferred the question of this status. Öpik (1970, pp. 4–5) took the view that the order

Redlichiida should include only redlichioids and olenelloids, excluding from it paradoxidoids and ellipsocephaloids; subsequently Öpik (1975*b*, pp. 10–13) placed these last two groups in the order Corynexochida. A different approach by Lauterbach (1980) claimed that some olenelloids are to be classified as Chelicerata, and that a sister group includes the emuellids and the 'Eutrilobita', a group that embraces all other trilobites (as generally recognized). Two questions that arise from this welter of conflicting opinions are addressed here, as a result of the present examination of some olenelloids.

(*a*) *Do olenelloids merit ordinal status?*

There are many general resemblances between olenelloids, redlichioids, paradoxidoids and emuellids. In the meraspid growth stages the subparallel-sided glabella was divided into occipital ring, L1–3, and an anterior lobe; the long, curved eye lobe was joined to the anterior lobe by a prominent palpebro-ocular ridge. Procranidial spines were unique to olenelloids, but genal and intergenal spines are known in olenelloids, redlichioids and paradoxidoids (including xystridurids); macropleural spines are developed in olenelloids, paradoxidoids and emuellids. Sources for illustrations of these growth stages include McNamara (1978, 1986*a*), Öpik (1975*a*), Palmer (1957), Pocock (1970) and Whittington (1957); Zhang *et al.* (1980) refigure growth stages of *Redlichia*. Changes that take place in the glabella during further development have been discussed by McNamara (1986*a*, pp. 132–133, fig. 5), and include retraction from the anterior border, the reverse process of protraction, and anterior expansion. The hypostomes of *Holmia*, *Redlichia*, *Paradoxides* and *Xystridura* (Whittington 1988*a*) are similar in the way the convex anterior lobe of the middle body is extended into a large anterior wing that lacks a wing process, the posterior portion narrow (tr.) and having a spinose border. In the holaspid the hypostome is attached, in *Paradoxides* fused with the rostral plate; this rostral plate is of very different width in these four genera. The distinctive features of the olenelloid cephalon are the lack of anterior and posterior branches of the suture, and the presence of a perrostral suture confined to the margin and ventral side, not extending on to the dorsal side of the border as in *Xystridura*. Many of the trilobites under discussion, apart from xystridurids, had a pygidium that was considerably narrower (tr.) than the cephalon and of few segments. With the exception of the peculiar *Olenelloides* (McNamara 1978), all had a dozen or more thoracic segments. A subdivision of the thorax has been recognized in some olenelloids and in emuellids. Long axial spines characterize species of olenelloids and redlichioids, and long, backwardly curved pleural spines are a widely distributed feature. A furrow in the inner portion of the pleura, and the doublure extending in beneath the pleural spine to the abaxial edge of the inner portion, are widely recognized. In olenelloids the pleura lacks the fulcrum, the inner portion curved rather than horizontal, the outer not flexed abruptly down at the fulcrum and without the facet. A flange along the anterior edge of the pleura acted as a guide in articulation. Thoracic structures in *Redlichia* (Öpik 1970, p. 3) were similar, there being a projection at the anterolateral angle of the pleura rather than a flange. It was this similarity in structure and manner of articulation in the thorax that led Öpik (1970, pp. 3–5) to consider the order Redlichiida as comprising only redlichioids and olenelloids, which he regarded as the early 'non-fulcrates', i.e. lacking the inner, horizontal portion of the pleura and the flexure downward at the fulcrum. However, in one species of *Paradoxides* (Bergström & Levi-Setti 1978, p. 9) the inner portion of the pleura was not horizontal, whereas in other species (Bergström 1973*a*, p. 18) it apparently was; among xystridurids only in *Galahetes* (Öpik 1975*a*, p. 23, pl. 18) is the fulcrum developed along the entire thorax, and facets on the outer portions of the pleurae. Supposed differences in thoracic structures need further study, but I do not consider they outweigh other characters sufficiently to exclude paradoxidoids from Redlichiida.

The similarities between olenelloids and *Redlichia* have been stressed by Henningsmoen (1951, p. 185), Öpik (1970, p. 4), Rasetti (1972, p. 45) and Zhang *et al.* (1980; cf. Zhang 1987), and if paradoxidoids are included in Redlichiida, the group would embrace the Centropleuridae (Öpik 1961, pp. 96–133). Distinctive of *Centropleura* are the inward and backwardly directed S4, the retrodivergent anterior branch of the facial suture, the flat, narrow (tr.), first thirteen thoracic pleurae, which widen posteriorly, the much wider last three pleurae that bear large pleural spines, and the relatively large pygidium. Öpik discussed the primitive and specialized characters of *Centropleura*, reaching only a vague conclusion about its ancestry, but a firm conclusion that it was highly specialized compared with other Cambrian trilobites. Ellipsocephaloids, including protolenids, have not been considered here, but the argument for including them in an order Redlichiida must rest on the form of the glabella and the nature of its furrows, combined with the long (exs.) eye lobe and prominent palpebro-ocular ridge. Inclusion of them adds a group in which the inner portion of the pleura hinges along the straight, horizontal edge, the outer portion bent down at the fulcrum and facetted. This manner of articulation between thoracic segments, known in the early Cambrian *Crassifimbria* (Palmer 1958), is otherwise rare in Redlichiida. Lochman-Balk (in Moore 1959, p. O216) placed *Bathynotus*, type genus of the Bathynotidae, in Redlichiida, but the unique cephalic structure (Whittington 1988*a*, pp. 581–584) makes any such classification highly questionable.

In classification the result arrived at depends on the weight given to a particular character, or whether it is called a primitive or a derived condition (cf. Fortey & Chatterton 1988, pp. 165–177). The presence of a submarginal, perrostral suture in olenelloids, was considered primitive by Bergström (1973*b*, p. 285) because it was a character shared with groups of arthropods other than trilobites. The heavy weight given to this character (expressed as the lack of dorsal sutures) by Bergström (1973*a*, p. 39) led to his considering them a separate order. Fortey & Whittington (1989) also regard the lack of dorsal facial sutures in olenelloids as primitive, for essentially the same reasons as did Bergström. Relative stratigraphical occurrence cannot be used in the Lower Cambrian as a guide to whether this condition is 'primitive', i.e. occurs in trilobites in substantially older rocks than those yielding trilobites having dorsal sutures. Olenelloids occur in early Lower Cambrian rocks in North America, northwestern Europe, Morocco and Siberia (Fritz 1972), whereas in China (Zhang 1985, 1987) redlichioids with dorsal facial sutures characterize these rocks. It has been argued in §4*b* that in exuviation olenelloids were as well served by the perrostral and presumed circumocular sutures as other groups were by the dorsal, rostral and connective sutures (cf. Öpik 1975*a*, p. 26). I assume that this character difference had little functional significance, being an expression of the morphological plasticity of early Cambrian trilobites (cf. McNamara 1986*a*, pp. 128–131). I therefore give it little weight, and hence consider that the case falls for separating olenelloids from other trilobites by a gap of ordinal or subordinal rank, merely because they lack dorsal facial sutures. There is no evidence from ontogeny that this lack is secondary, that the dorsal sutures were ankylosed. The similarity between olenelloid, redlichioid, paradoxidoid and emuellid early growth stages, and between holaspides, of glabellar form and furrows, and of the long eye lobe and prominent palpebro-ocular ridge, are characters here thought to be indicative of relationship. They are therefore given heavy weight in advocating an order

Redlichiida, the similarities in development being of special significance as probably expressive of common ancestry.

(*b*) *Are some olenelloids not trilobites?*

In the light of §3, this appears an unlikely question to raise. Raw (1925, p. 312; 1957) and Størmer (1944, pp. 76–79) advocated the idea that an *Olenellus*-like form was ancestral to chelicerates; the case against this suggestion was made by Öpik (1958, pp. 22–23). Nevertheless, it has been revived by Lauterbach (1980, 1983), with the added view that *Olenellus*-like trilobites must therefore be chelicerates, not trilobites. Lauterbach also goes on to argue that Trilobita includes two major groups of equal rank, the emuellids and the 'Eutrilobita' (i.e. all trilobites other than emuellids and olenelloids). A cardinal assumption in such a view appears to be that the dorsal facial suture is the most important character that unites trilobites, any loss of such sutures being secondary. Olenelloids, on the other hand, are characterized by Lauterbach as lacking such sutures, but having a marginal suture. Certain olenelloids referred to by Lauterbach (1980, p. 175, figs 4 and 5) as 'olenellines' (that is, species of genera included in this subfamily by Poulsen (in Moore 1959, p. O192), and in Olenellidae by Bergström (1973*b*, p. 312)), are characterized as having a prothorax of 15 segments, the third macropleural, the 15th having borne a long axial spine. He considered that the opisthothorax was terminated by a telson, and constituted a unit termed the 'telosoma', asserting that a pygidium was not developed. Behind these views lies the image of the superficial similarity between *Olenellus*, with its wide cephalon, tapering thorax and long median spine on the 15th segment, and the Recent *Limulus*, an image portrayed by Størmer (1944, fig. 15) in a diagram conveying overtones of recapitulation. Attractive as this may seem, any similarities are exceedingly superficial and do not withstand examination, as the following points emphasize.

1. It is argued in §6*a* that the lack of dorsal sutures in olenelloids may not have been an all-important character that excluded them from Trilobita; rather that the many similarities between olenelloids and other trilobites outweigh this difference. The perrostral suture and the presumed circumocular suture may have been part of an effective means of exuviation. Neither of these kinds of suture is unique to olenelloids.

2. The post-cephalic exoskeleton of few olenelloids is known, but it appears (§3*c*) that the thorax terminated in a pygidium that consisted of a few fused segments and the telson.

3. The subdivision of the thorax (§3*b*) in olenelloids is a transition that took place in the pleurae of a few segments, followed by a more gradual diminution in size of the opisthothoracic pleurae; the axial region of the thorax showed a gradual reduction in size of the rings posteriorly along its entire length, a reduction not affected by changes in the pleurae. This subdivision, in *Nevadia* for example, is not invariably associated with a macropleura or an axial spine on a particular segment. Subdivision of the thorax (rarely), and development of a macropleura or of an axial spine, are morphological characters that appear singly or in combination in many other groups of trilobites.

4. Lauterbach (1980, figs 6 and 7) regarded both the opisthothorax of emuellids, and the 'post-pygidial abdomen' of *Triarthrus* (Cisne 1975) as examples of his telosoma. These were used in his argument that the pygidium in trilobites was an intercalary, not a terminal, tagma, of the body, developed after reduction and loss of the 'telosoma'. The evidence of the fossils does not support these arguments. The transition between prothorax and opisthothorax in

emuellids takes place between three or four pleurae, and the axial region is unaffected. The small pygidium was inadequately figured by Pocock (1970), and described as minute, segmented, and without border spines. This description, and the description of the transitory pygidium in the development of one species, implies that the pygidium of emuellids was of a few, fused segments, as in olenelloids. Whittington & Almond (1987) consider that there was no 'post-pygidial abdomen' in *Triarthrus*. The evidence from the appendages of *Triarthrus*, and from those of the Middle Cambrian *Olenoides* (Whittington 1975), is that the trilobite pygidium included the telson and several segments, and was a terminal structure of the body. Although knowledge of the small pygidium of olenelloids and emuellids is inadequate, there seems no reason to consider that it was different. On the contrary, what is known argues that this pygidium included the telson and a few additional segments. Harrington's view that the olenellid pygidium was 'a true telson or caudal piece, the pygidia of other trilobites being the equivalent of the ensemble of opisthothorax plus "pygidium" of the Olenellidae' (in Moore 1959, p. O73), is regarded as having been unfounded.

5. A Cambrian chelicerate with appendages has recently been described (Briggs & Collins 1988), and its relationships with other early Palaeozoic chelicerates discussed. Only the antennae (Dunbar 1925) are known in *Olenellus*, so that discussion of any similarities between olenelloids and chelicerates has to be confined to exoskeletal characters. It appears obvious that the exoskeleton of *Olenellus* is more like that of other trilobites than that of any Lower Palaeozoic fossil considered to be a chelicerate. Ahlberg *et al.* (1986, p. 40) make cryptic mention of some ten characteristics of trilobites in this connection. Here it is sufficient to mention that in the mineralized exoskeleton, including the hypostome braced against the rest of the cephalon, the pleural furrows of the thorax, and the terminal tagma of the pygidium, *Olenellus* is allied with other olenelloids and other trilobites, and was not a chelicerate.

The evidence from the present review and other recent studies of relevant fossils argues against acceptance of the classification of Lauterbach (1980, figs 1, 23 and 24). It is concluded here that *Olenellus* and its allies were related most closely to other olenelloids, which were part of a larger group of Lower and Middle Cambrian trilobites, the Redlichiida.

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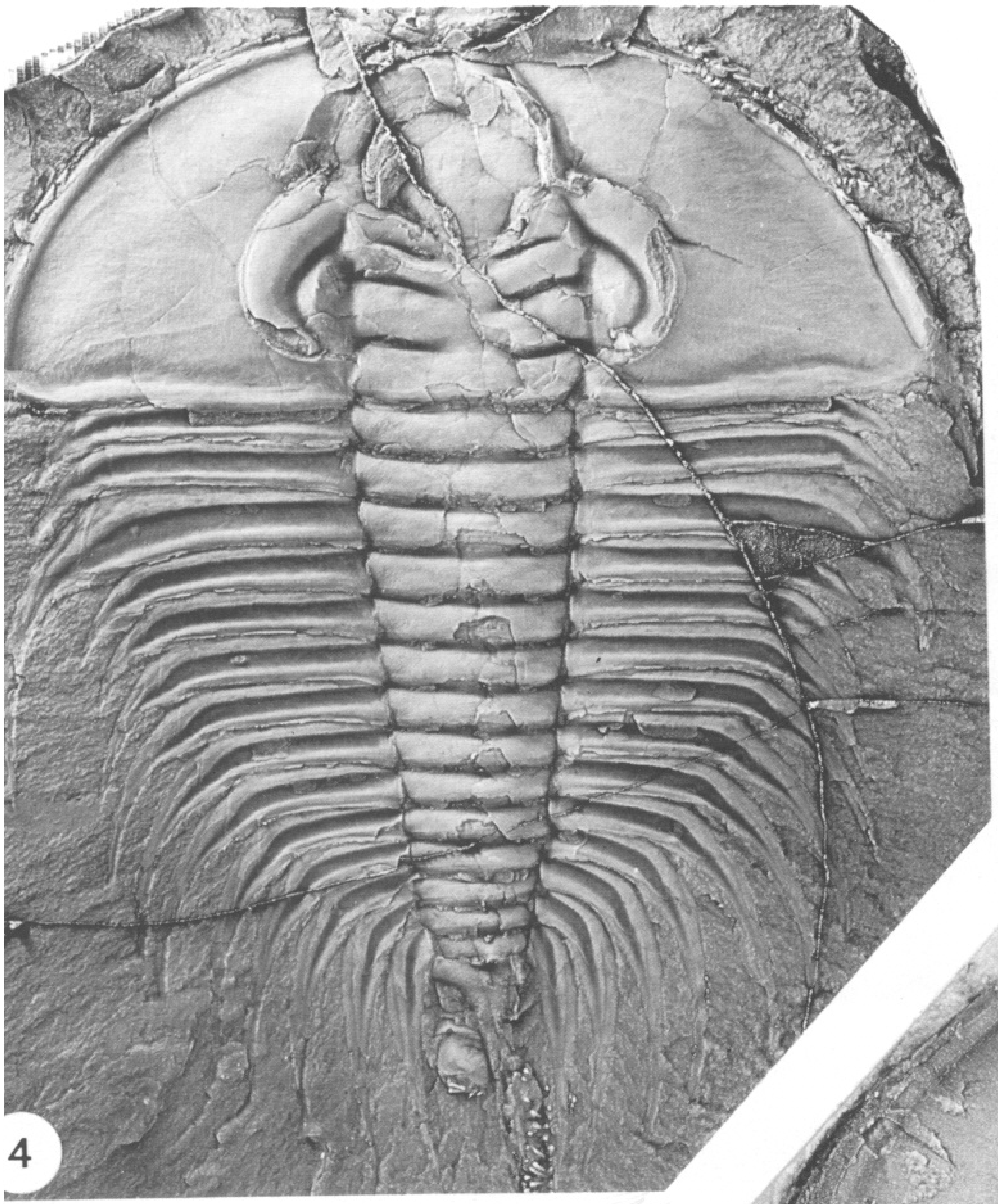
LIST OF ABBREVIATIONS

af	articulating furrow
ahr	articulating halfring
AMNH	American Museum of Natural History
cs	circumocular suture
d	doublure
exs.	exsagittal line, a line parallel to, but outside the sagittal line
ff	flange furrow
fl	flange
fr	fracture
GSC	Geological Survey of Canada
GSM	Geological Survey and Museum (now British Geological Survey)
h	hypostome
i	intergenal spine
iv	inverted segments
L	glabellar lobe
or	occipital ring
pf	pleural furrow
pr	perrostral suture
ps	pleural spine of pygidium
py	pygidium
r	rostral plate
S	glabellar furrow
sag.	sagittal, a median longitudinal line in the body
tr.	transverse, a direction at right angles to the sagittal line
USNM	United States National Museum of Natural History
I–*n*	serial numbering of glabellar lobes and furrows, axial rings, thoracic segments and pleural spines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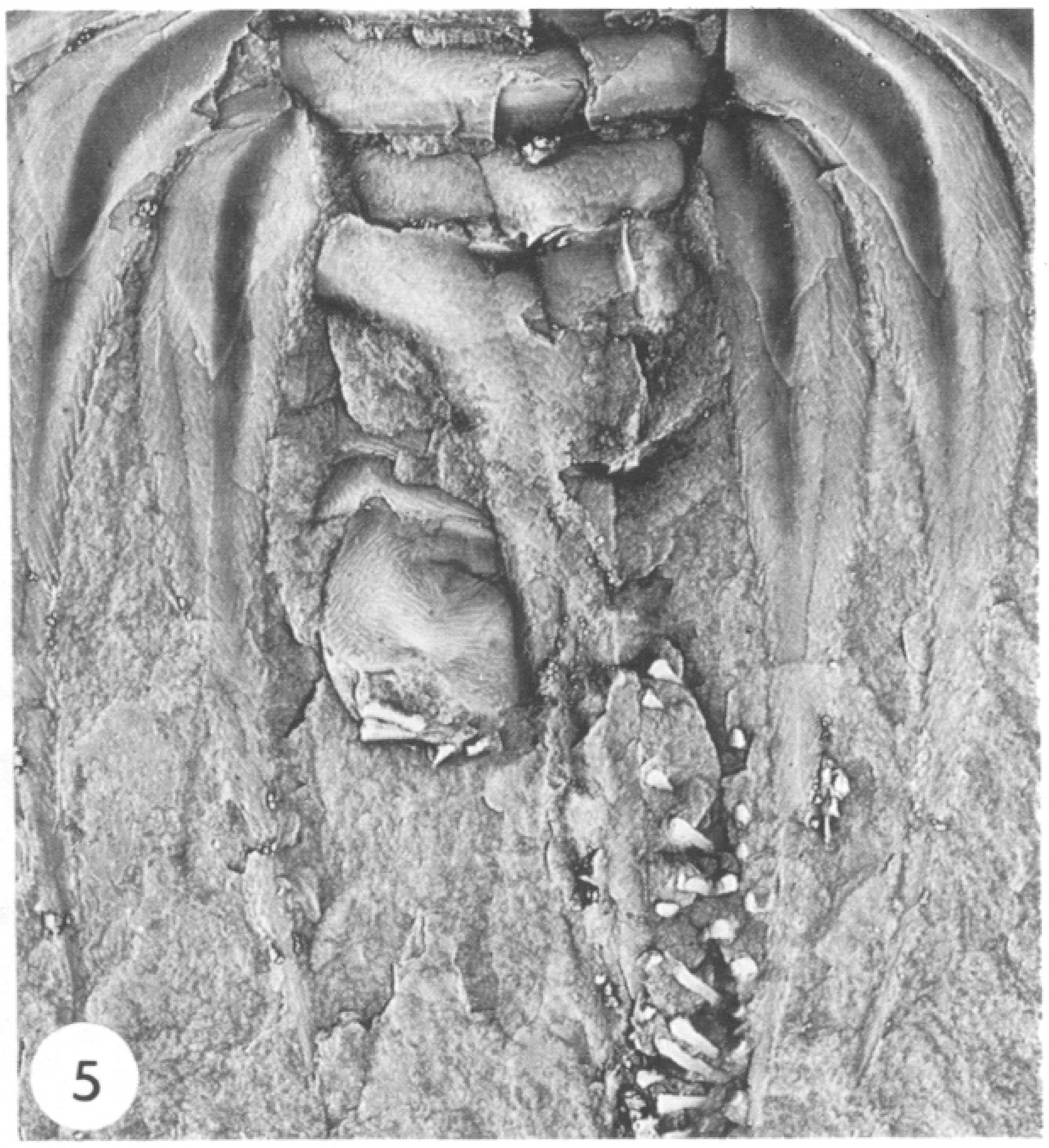
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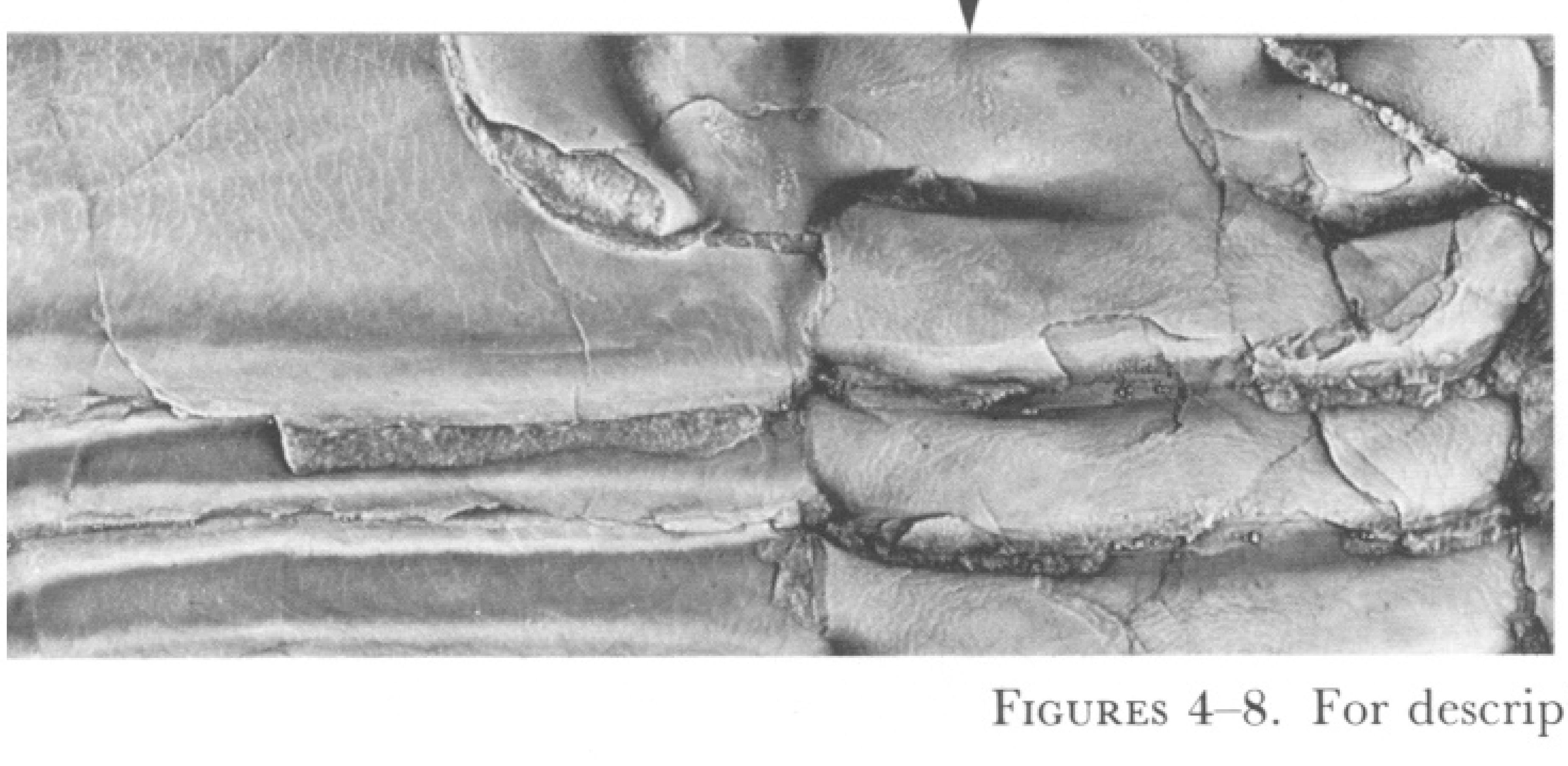
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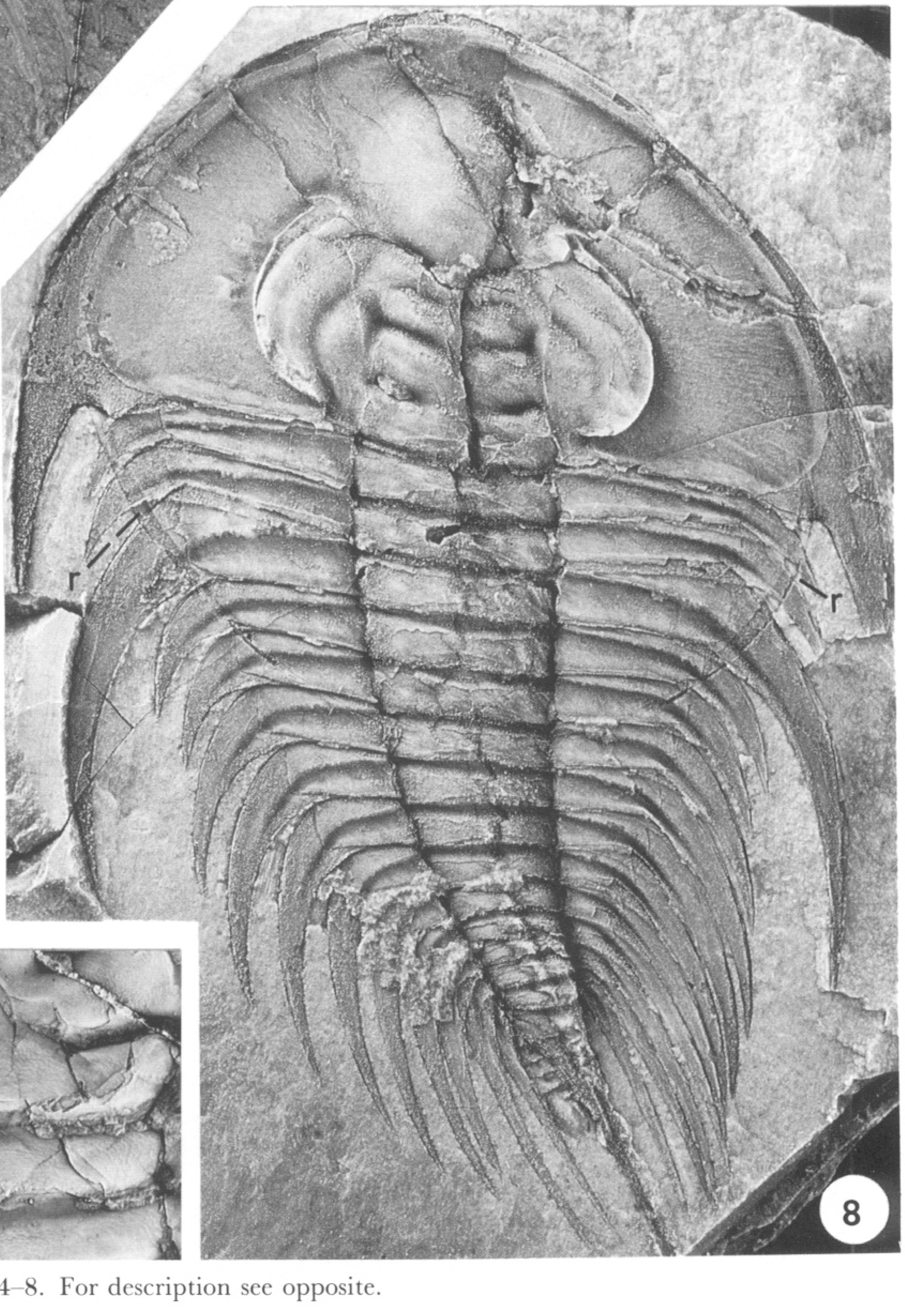

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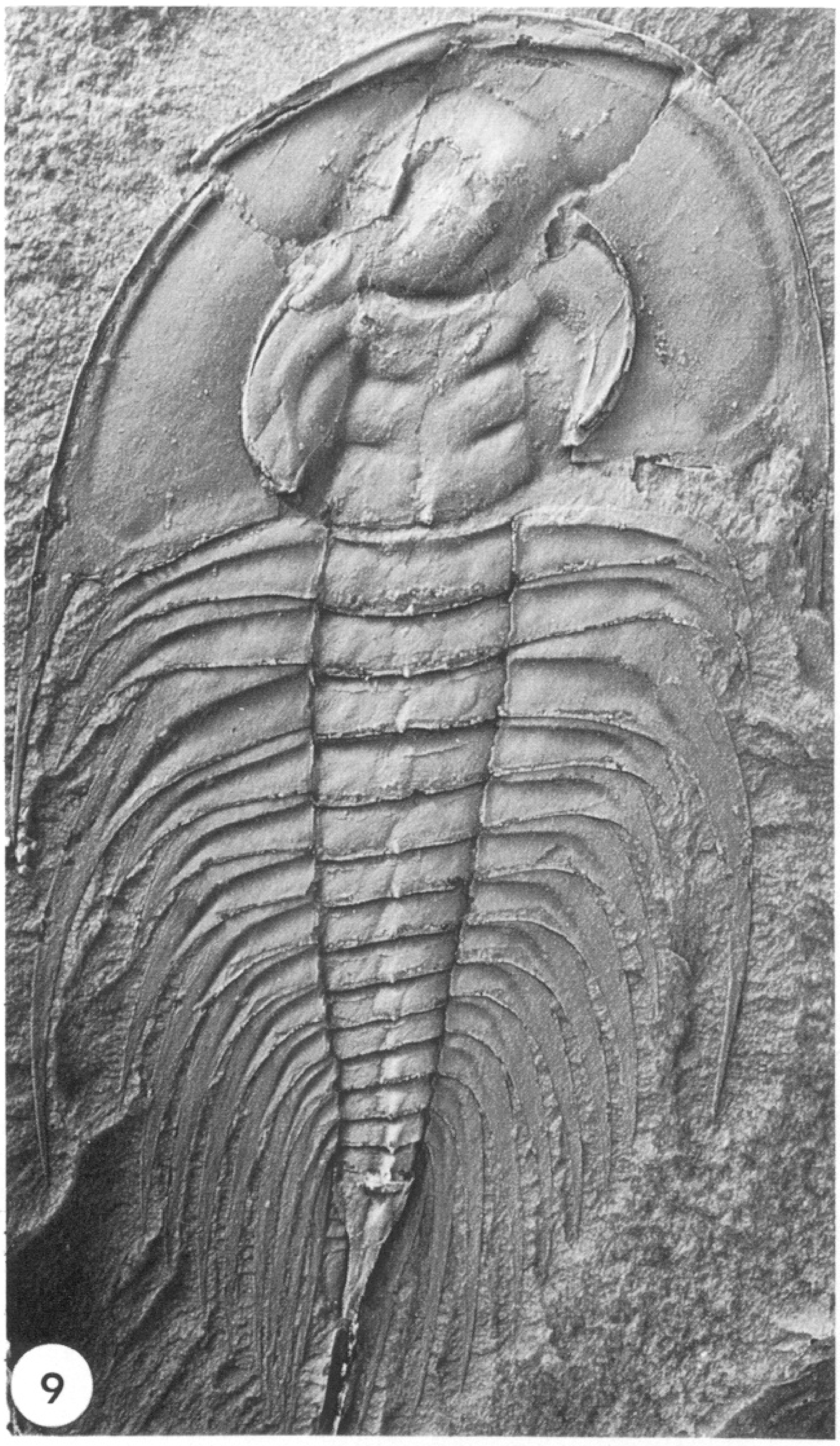
FIGURES 4–8. For description see opposite.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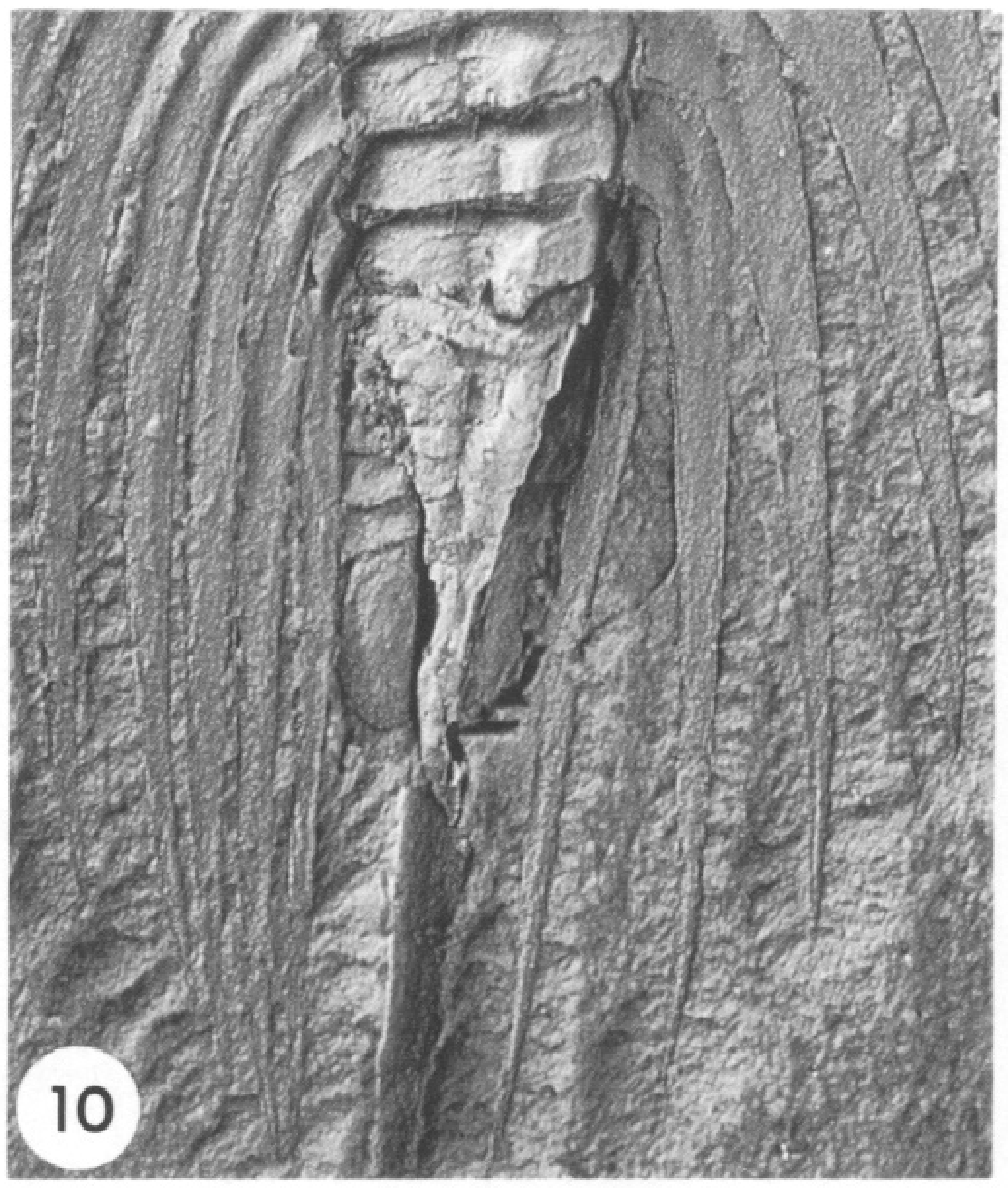
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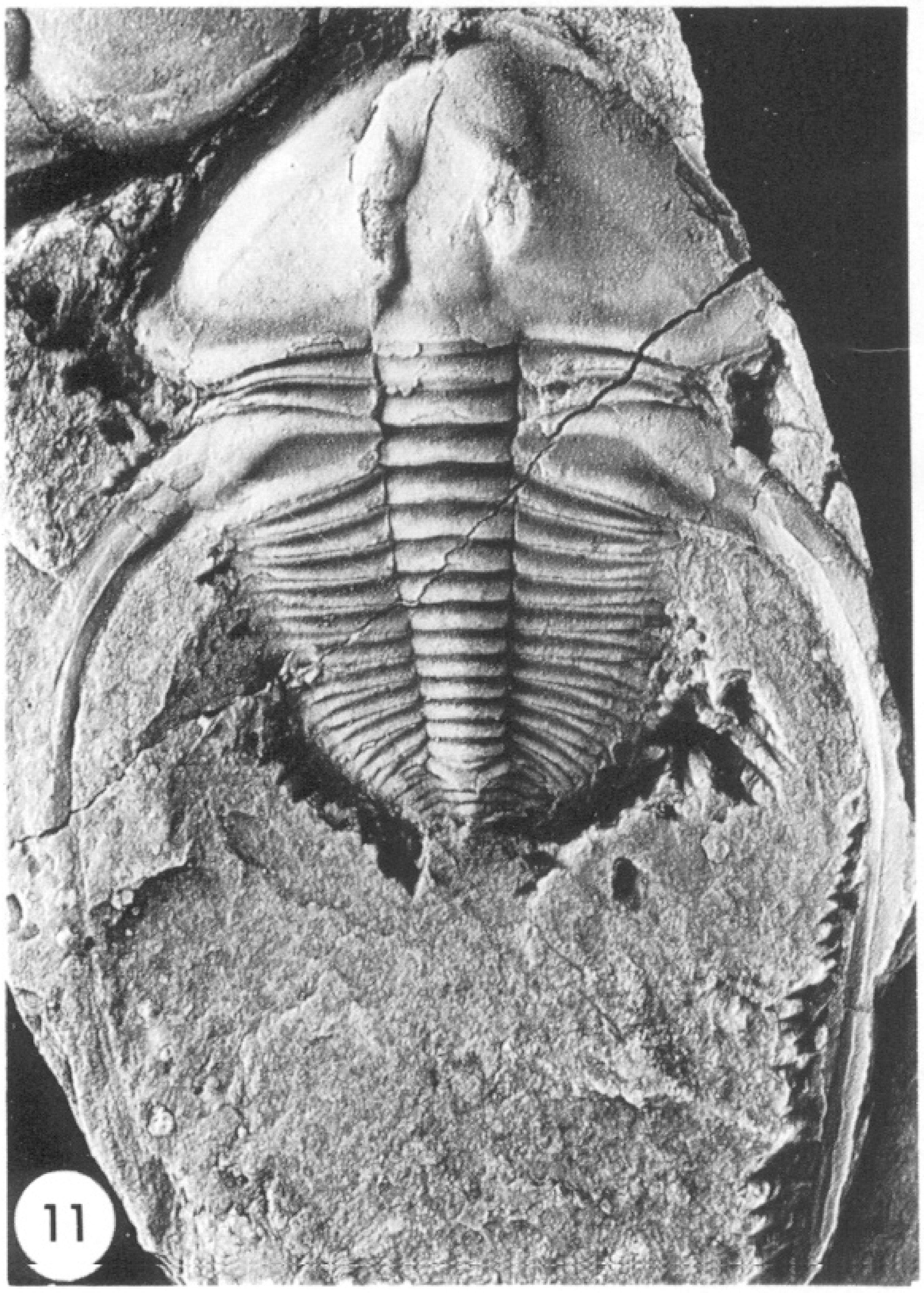
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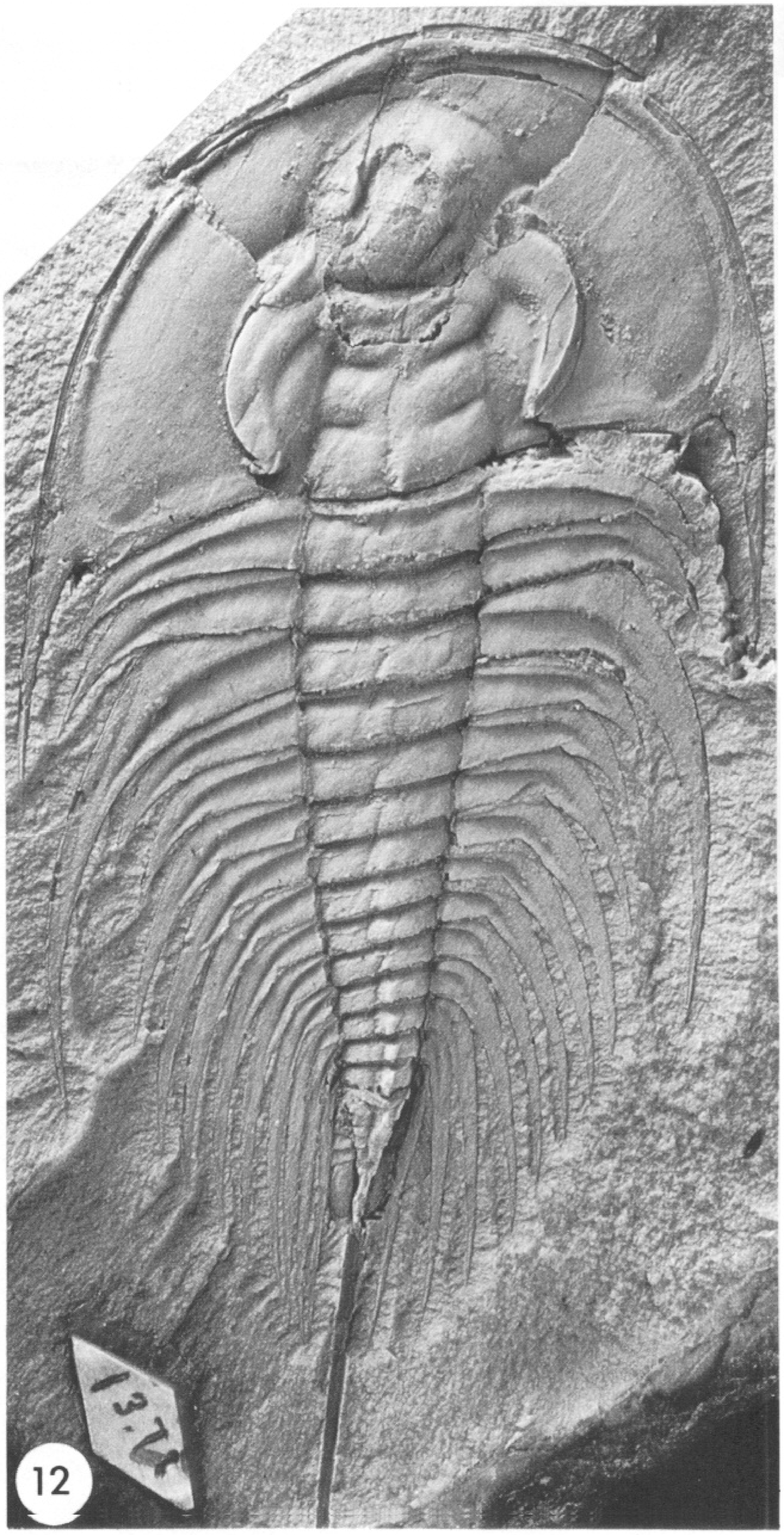

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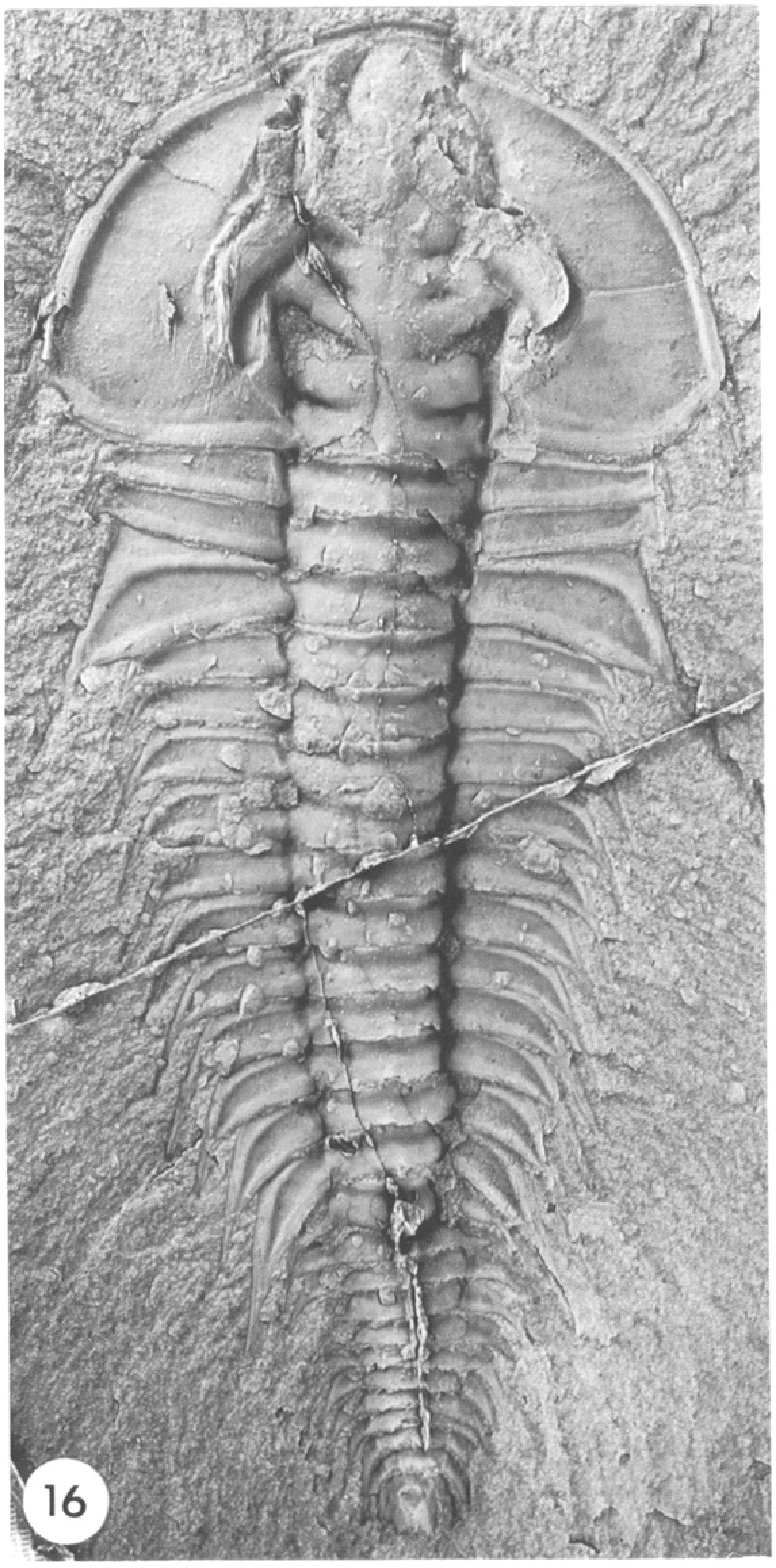
Figures 9–12. For description see opposite.



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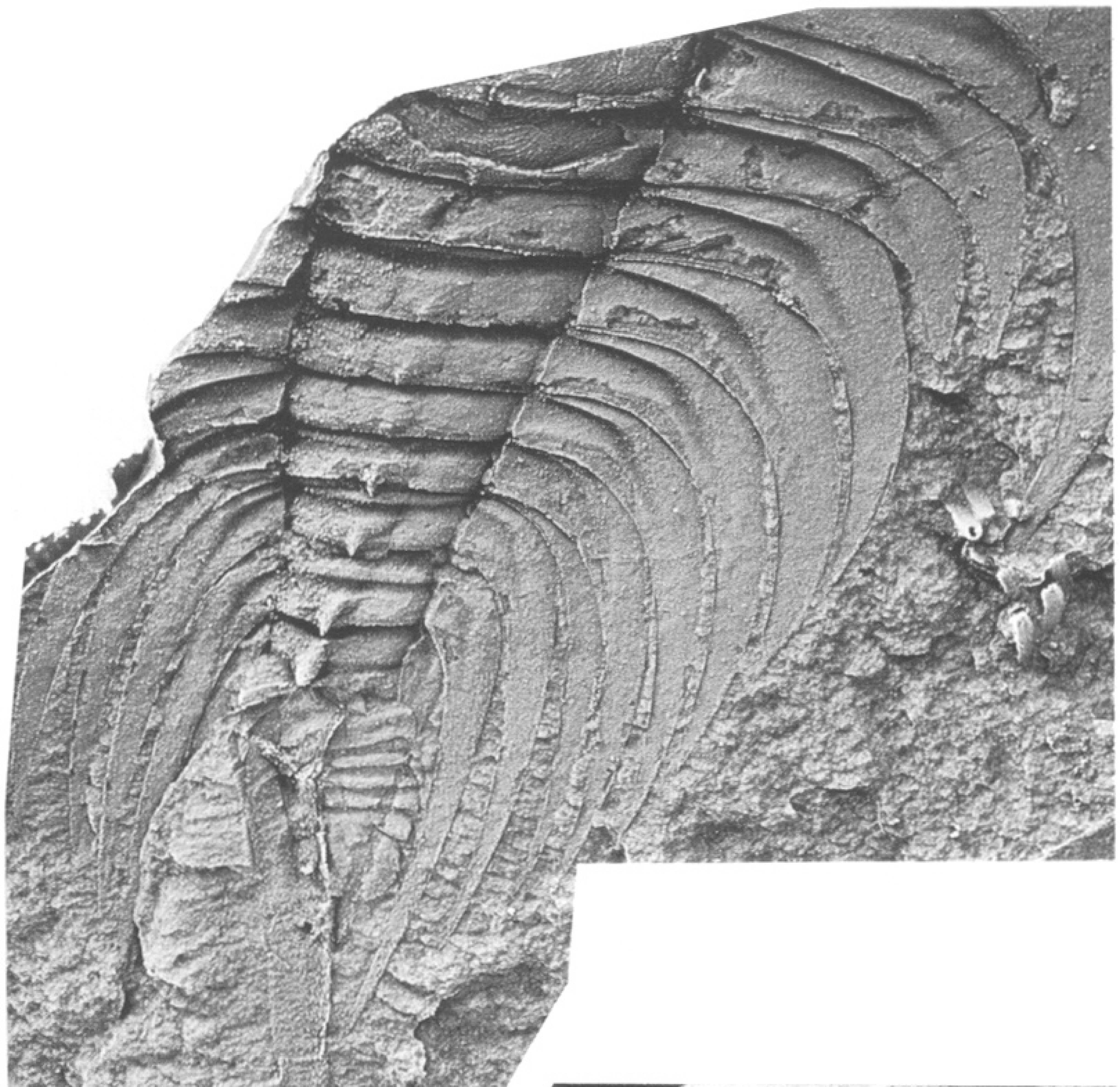

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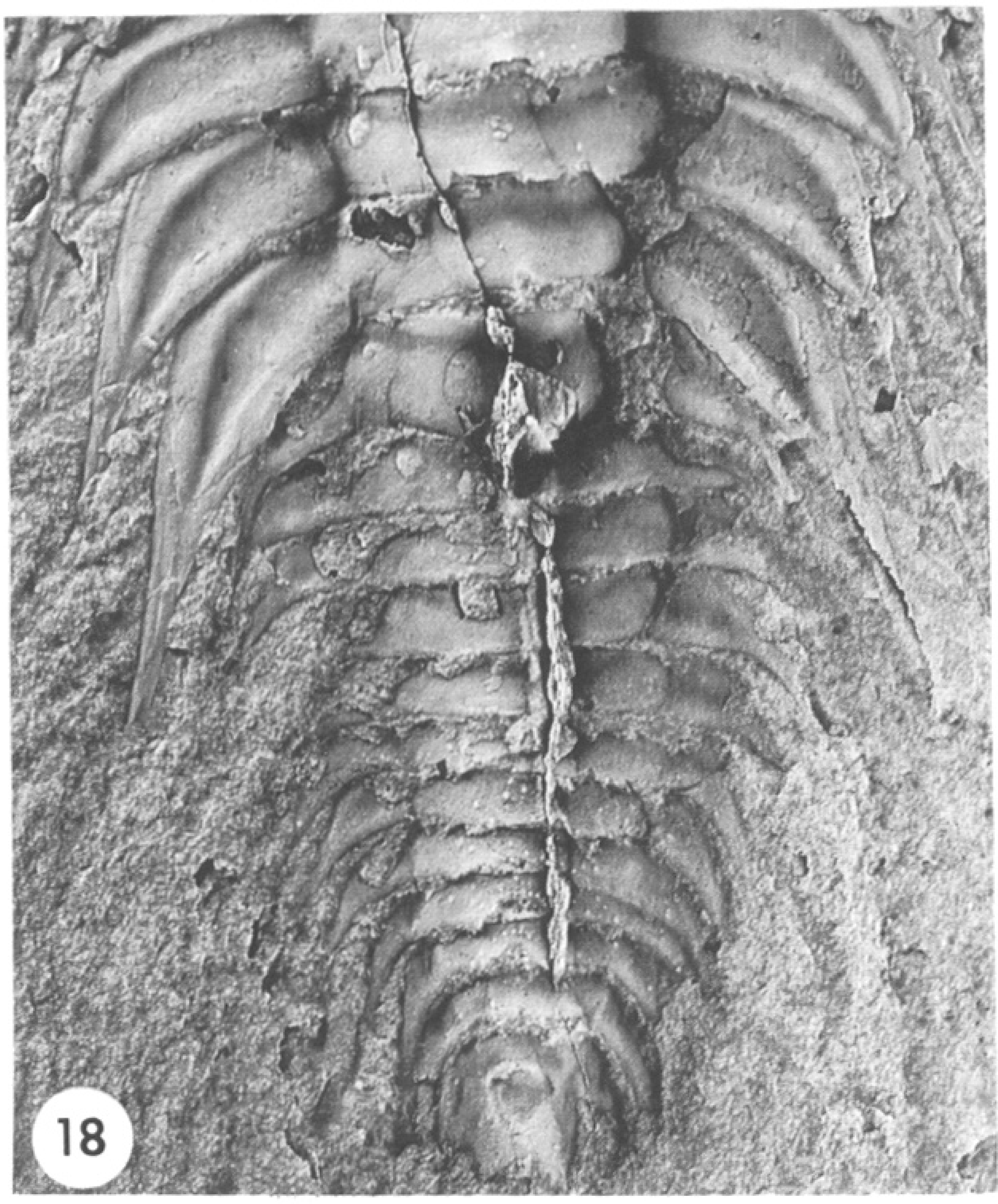

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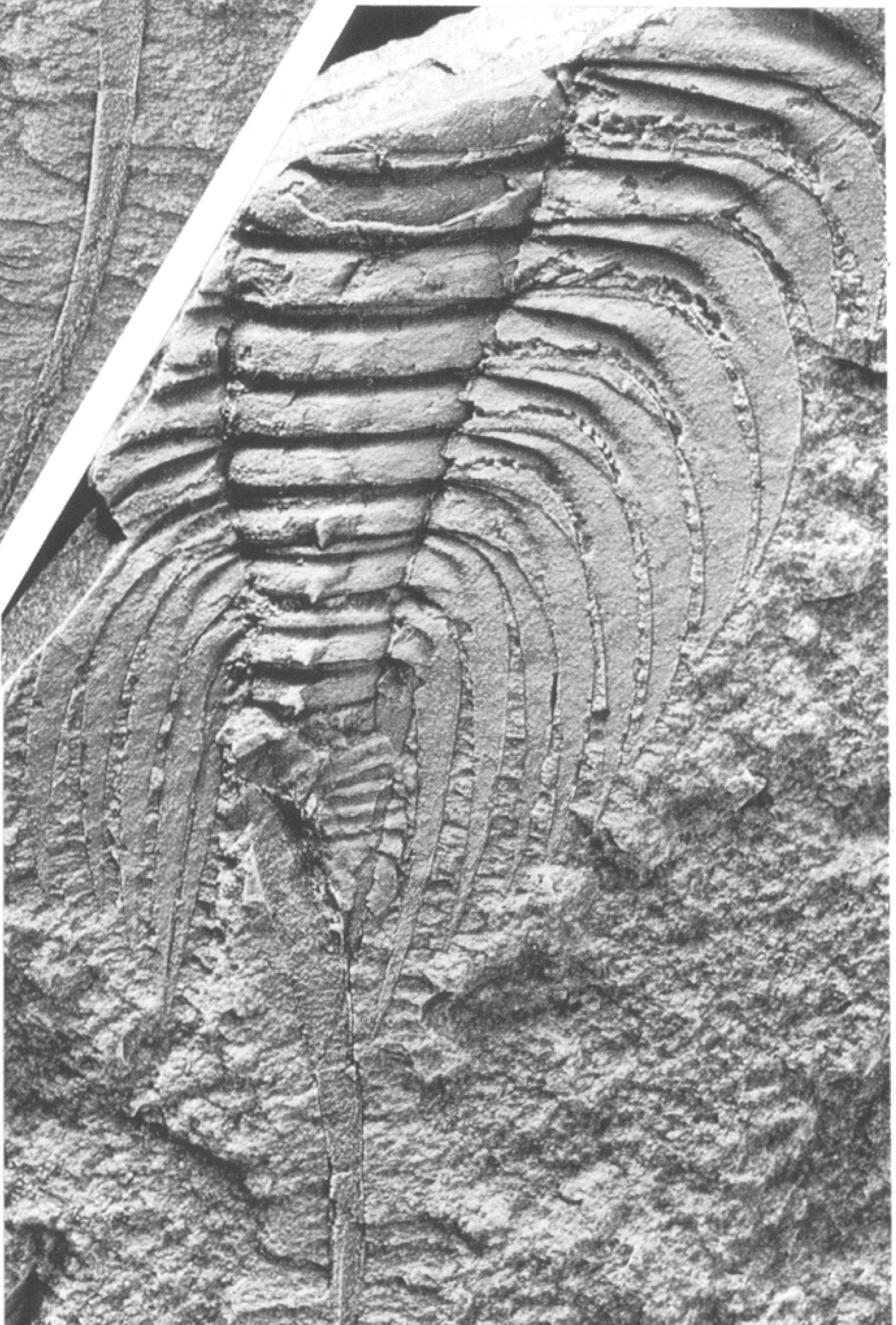

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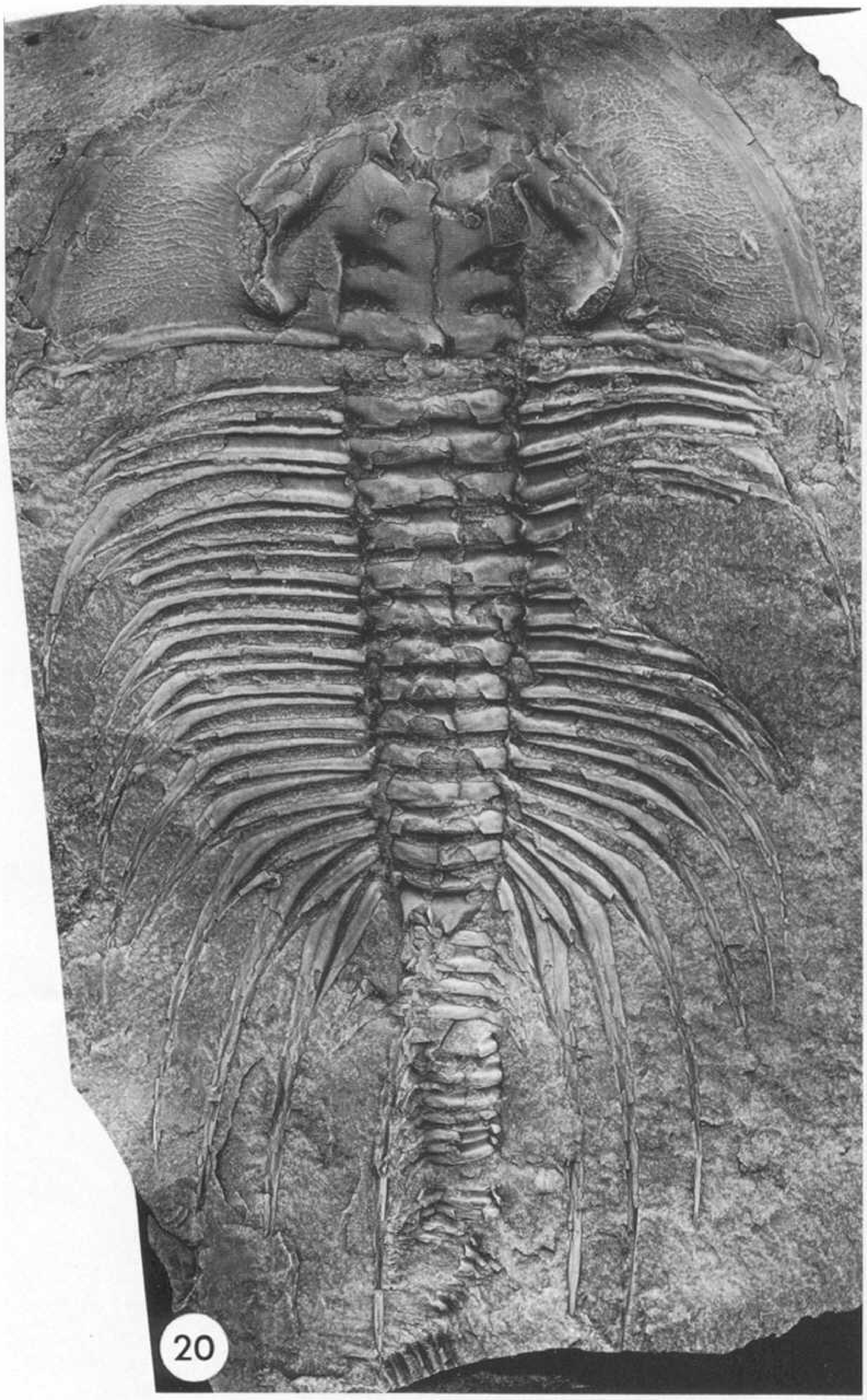
FIGURES 16–19. For description see opposite.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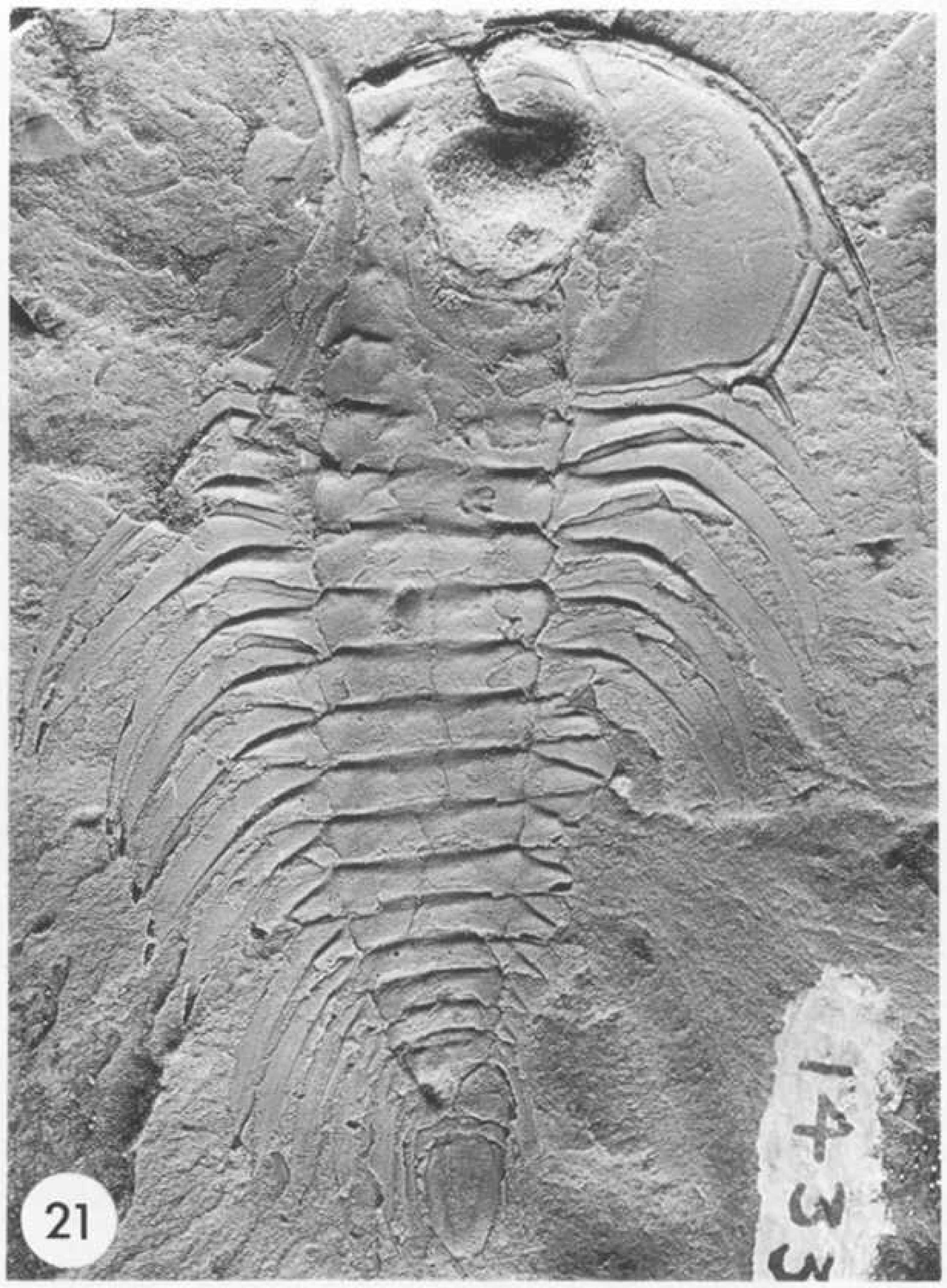
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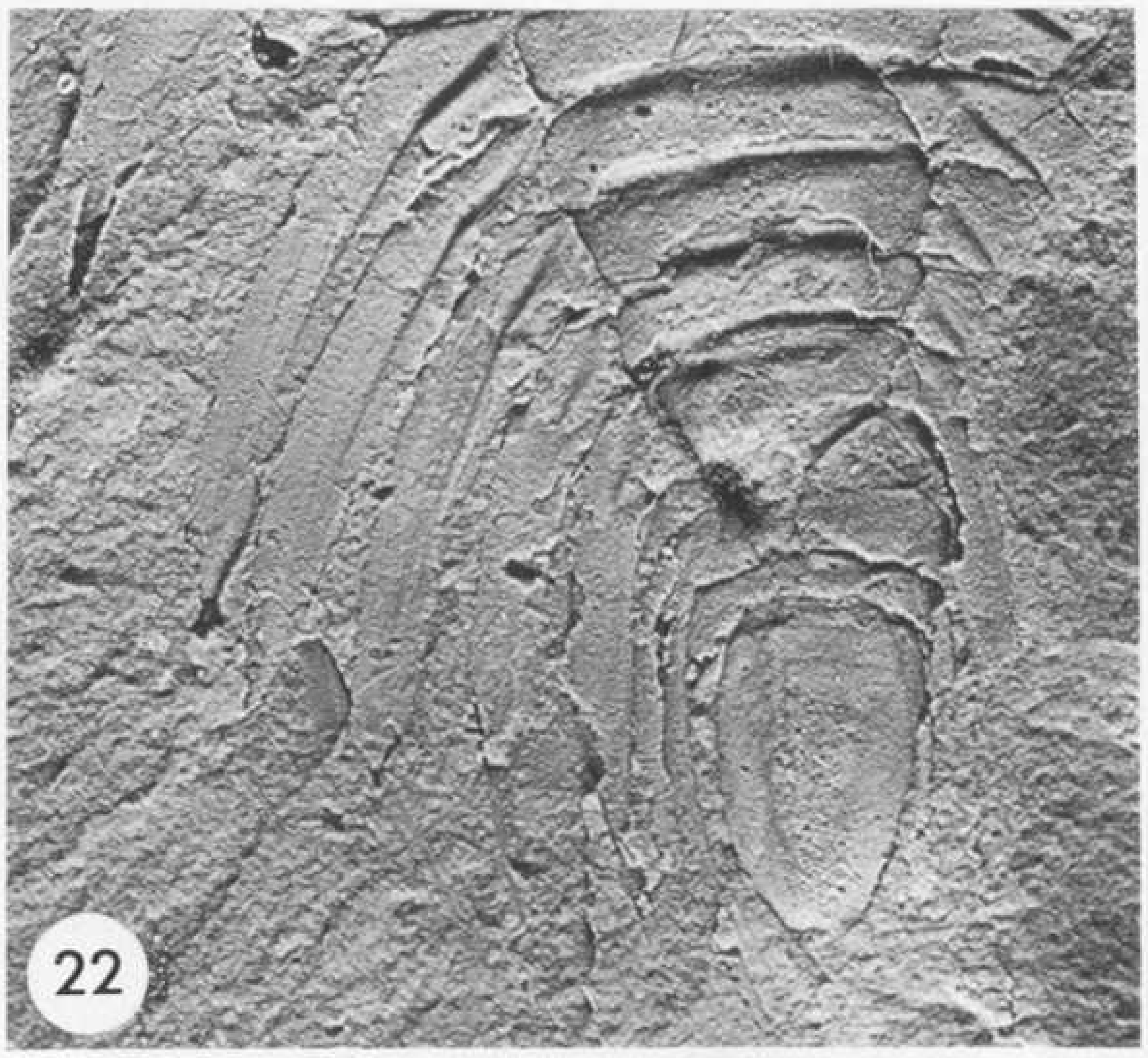
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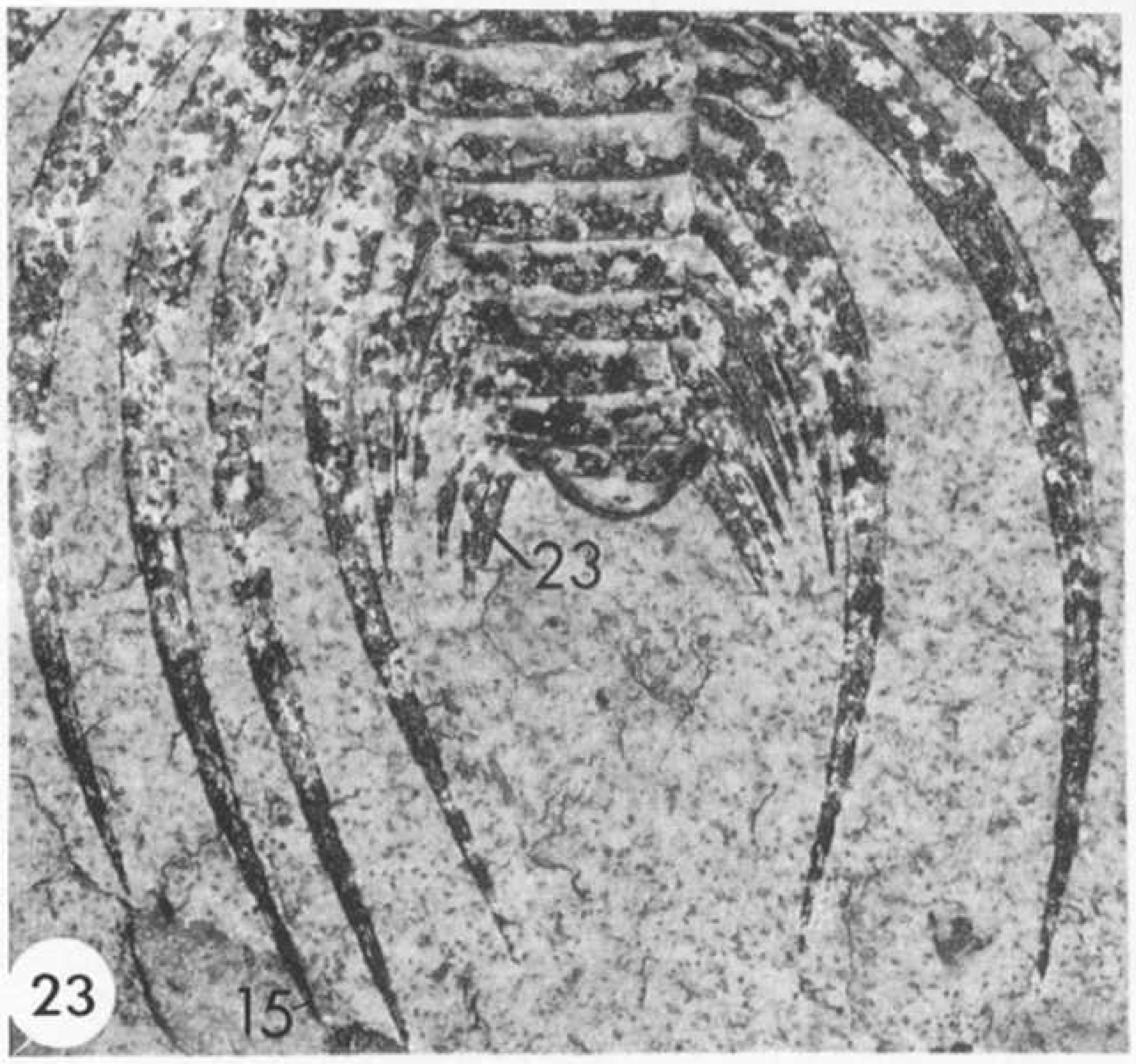
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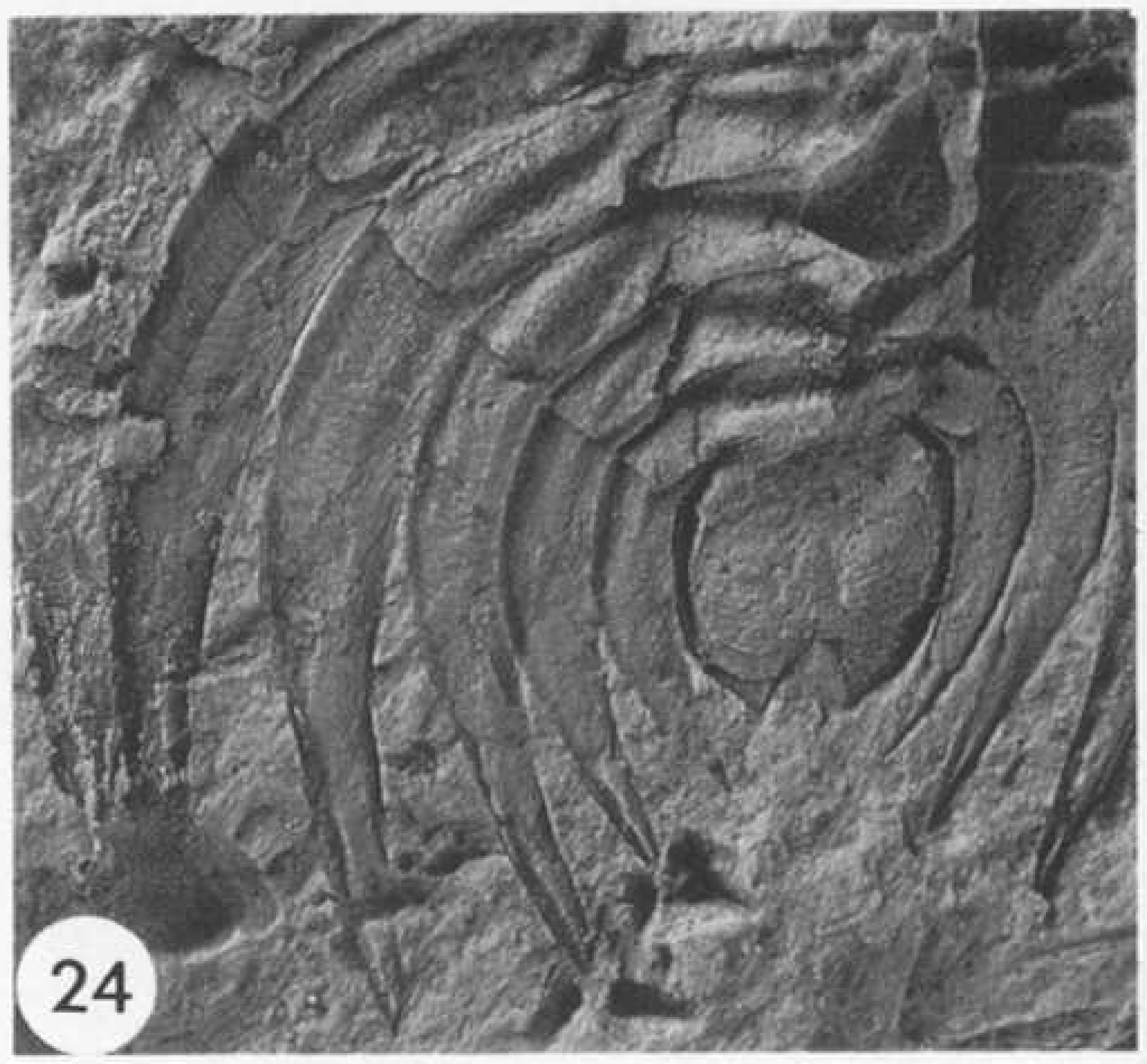
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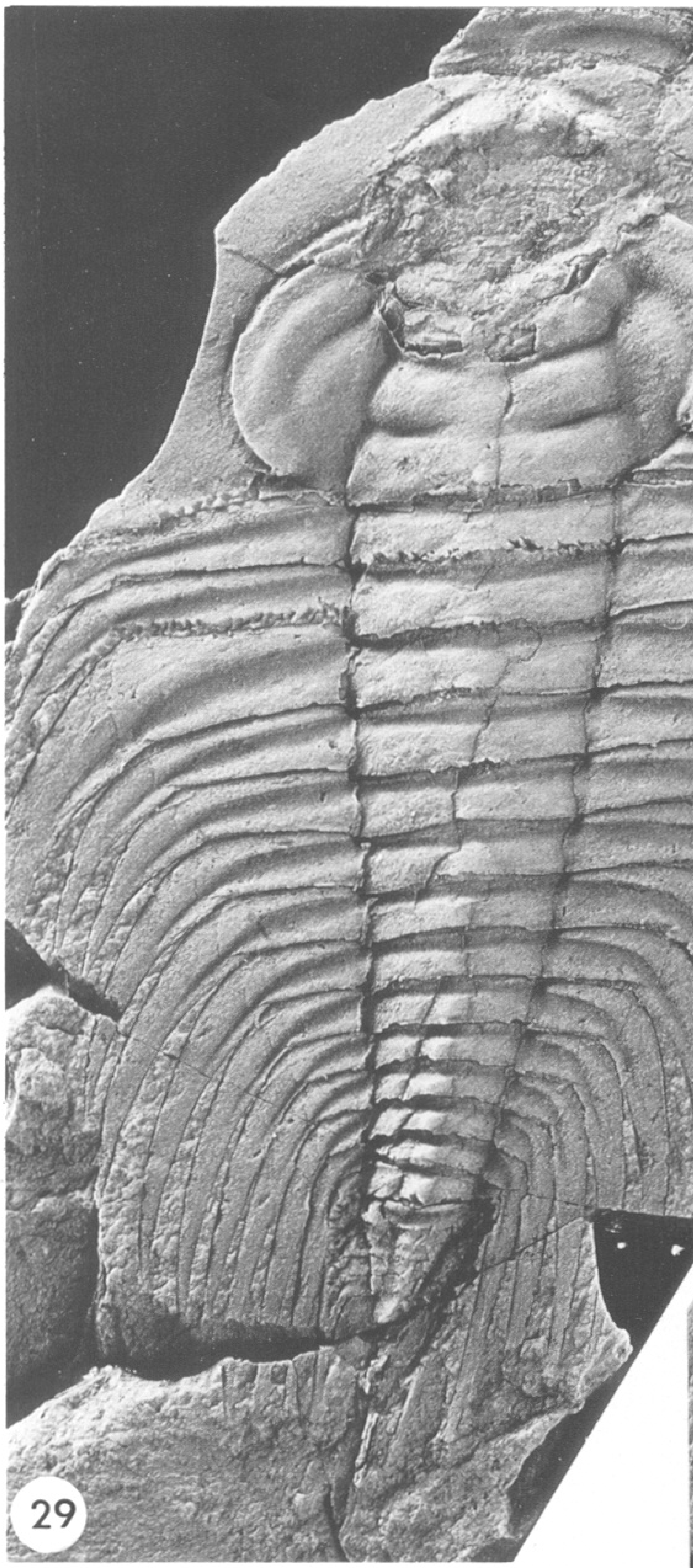
FIGURES 20–24. For description see opposite.



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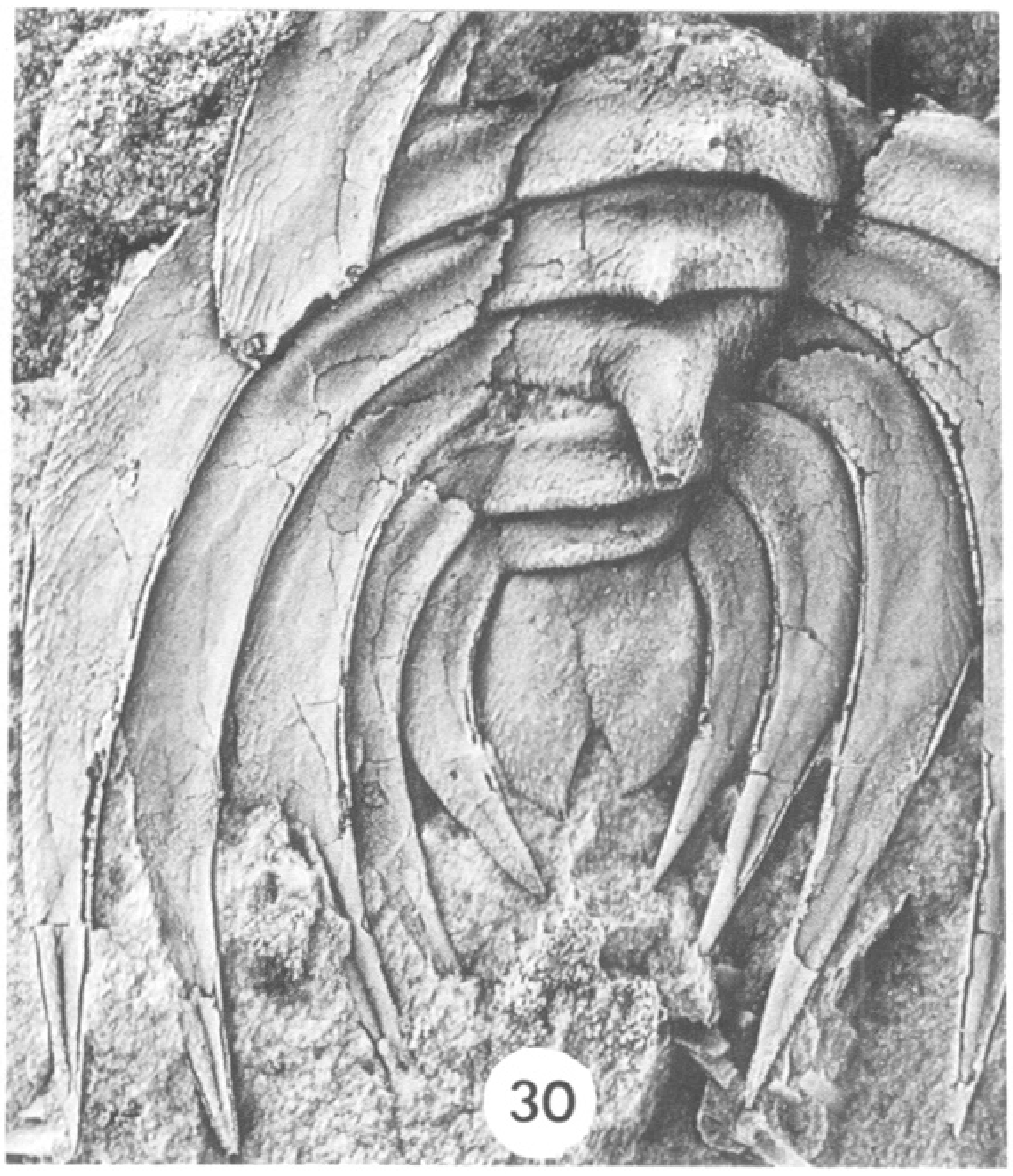

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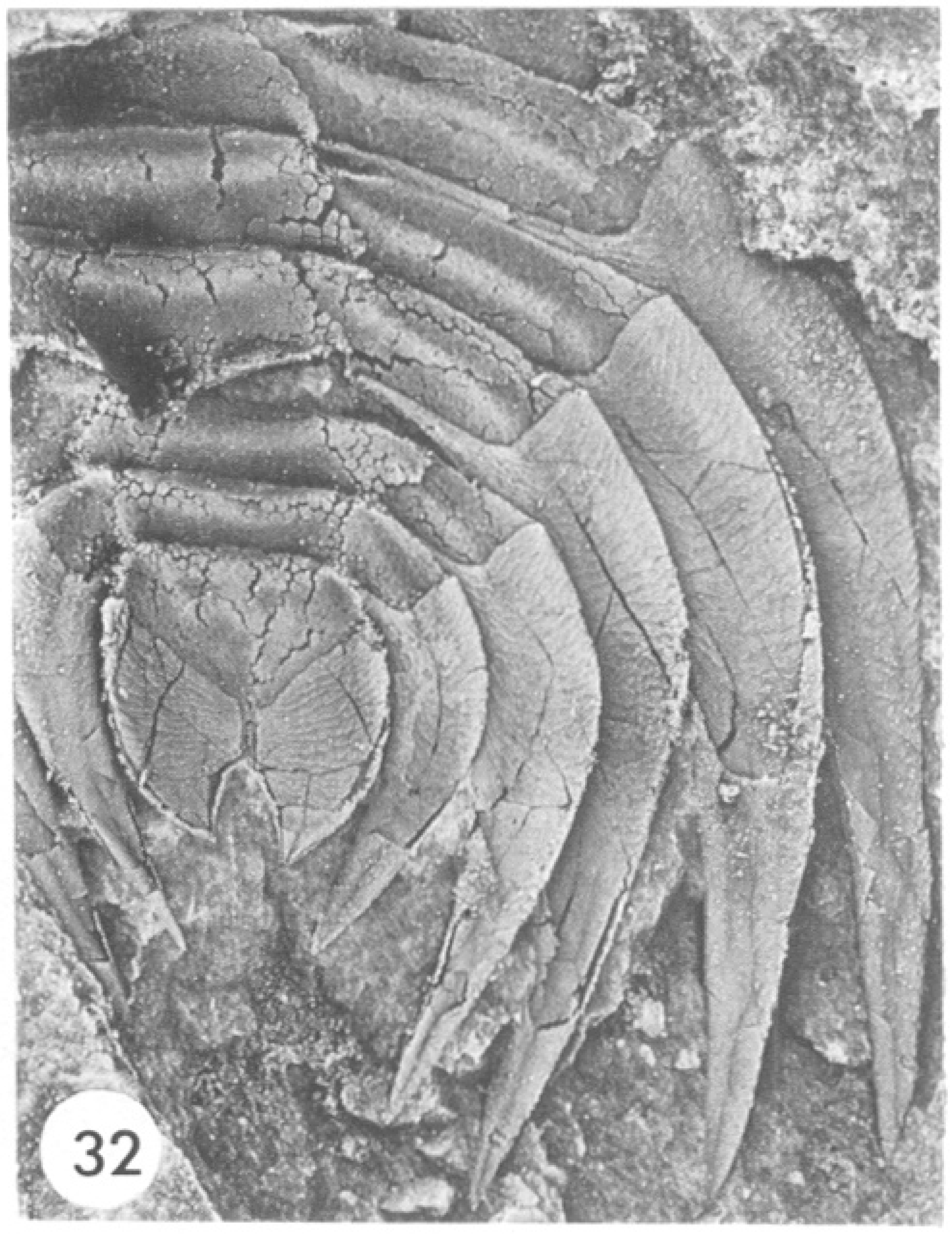

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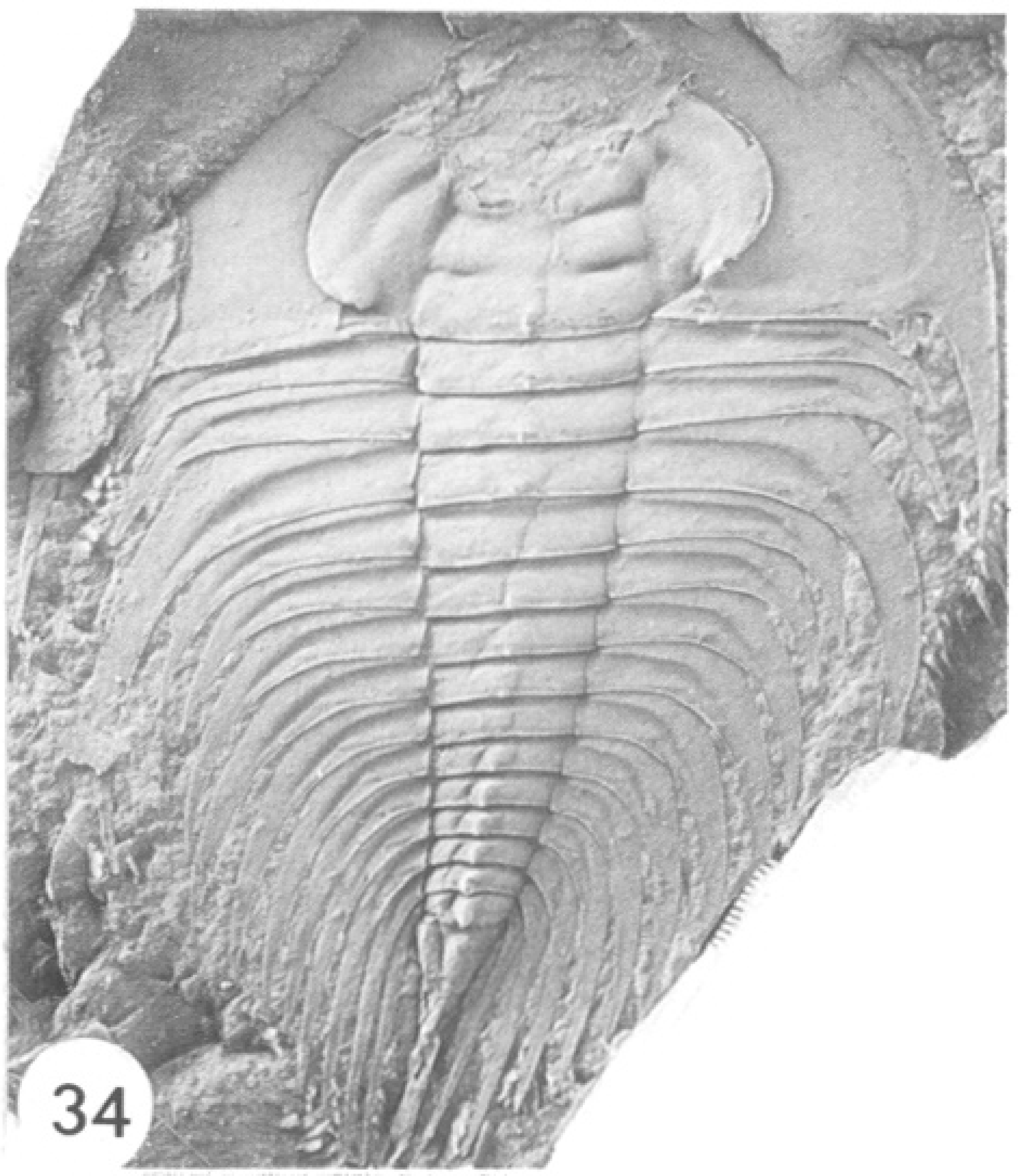

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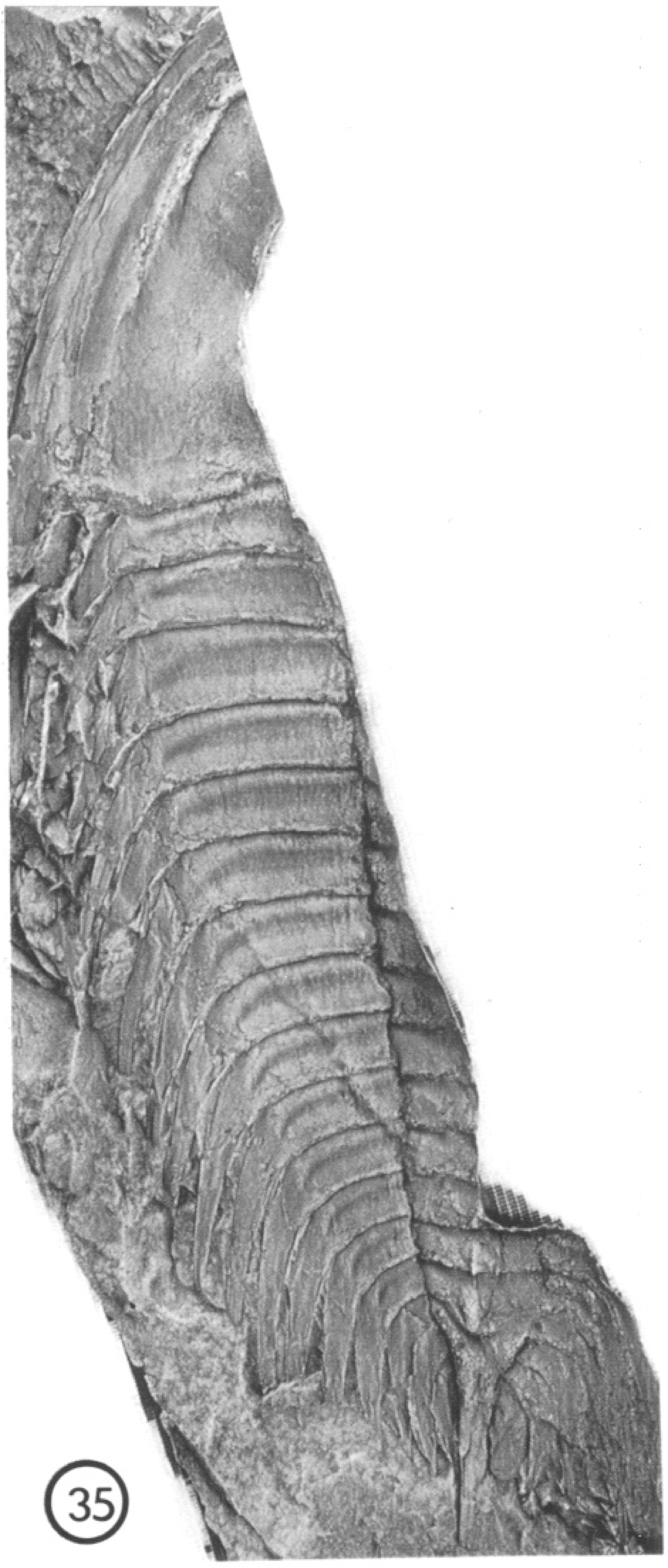
FIGURES 29–34. For description see facing plate 6.



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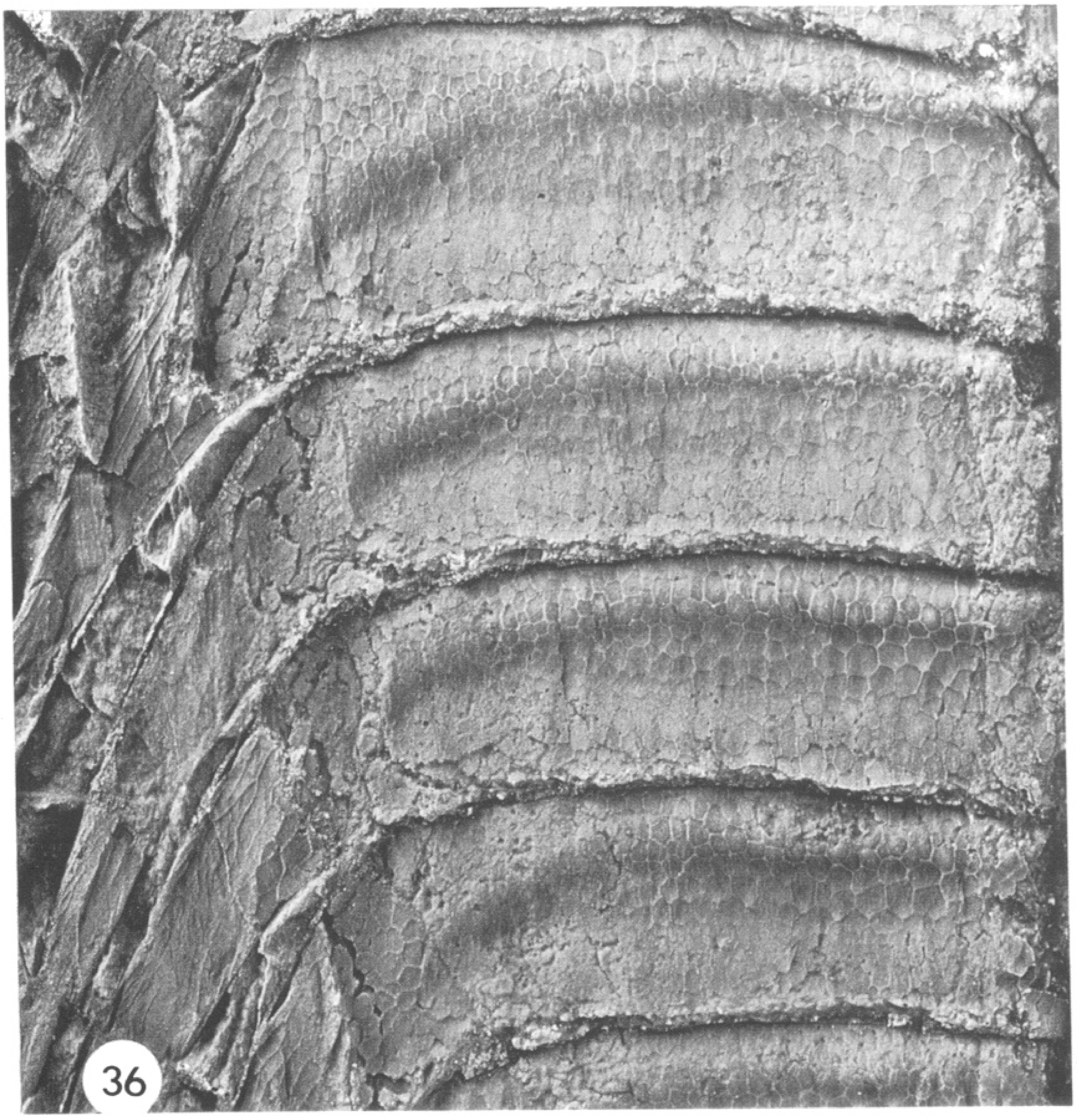

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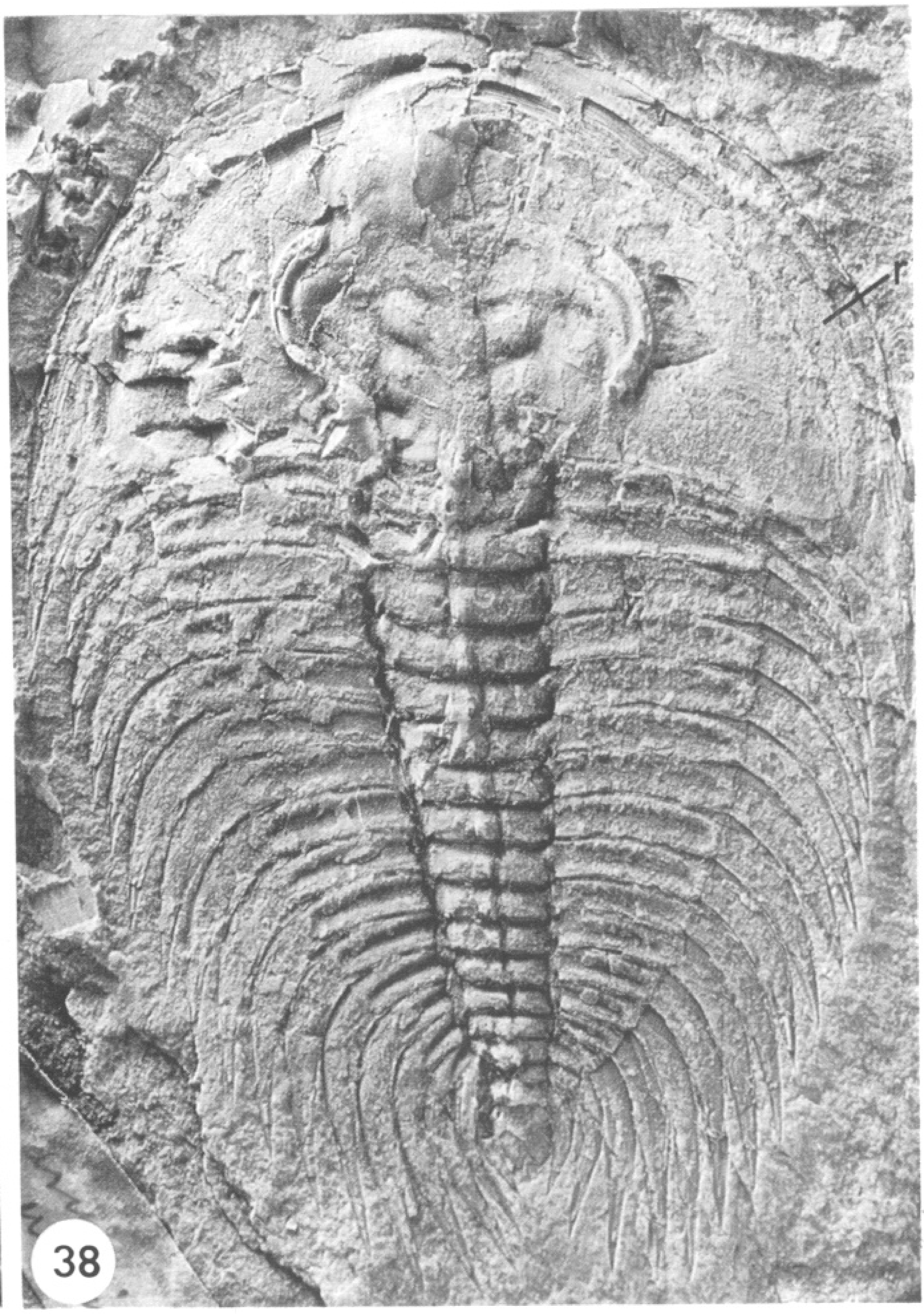

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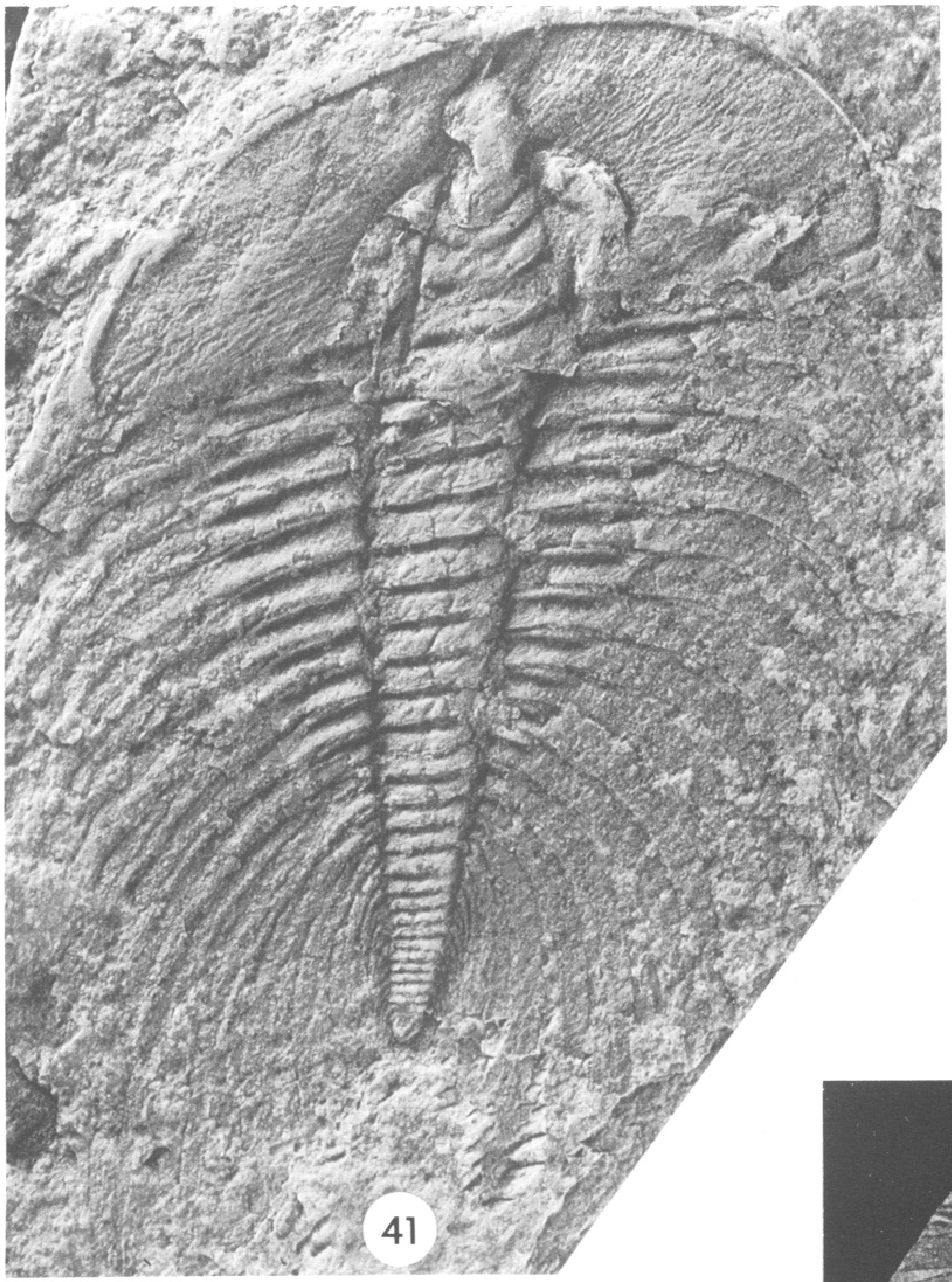
FIGURES 35–38. For description see opposite.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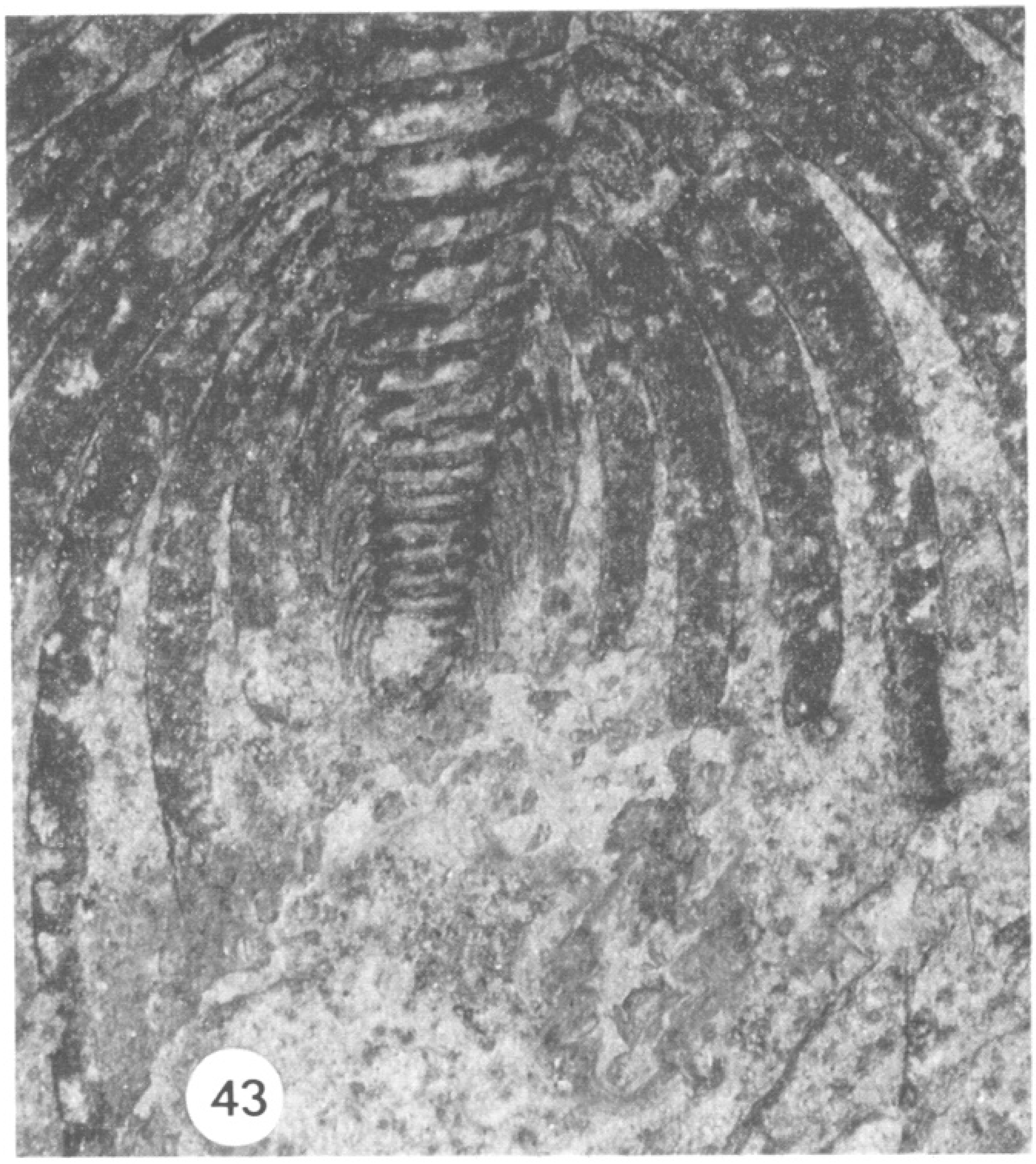
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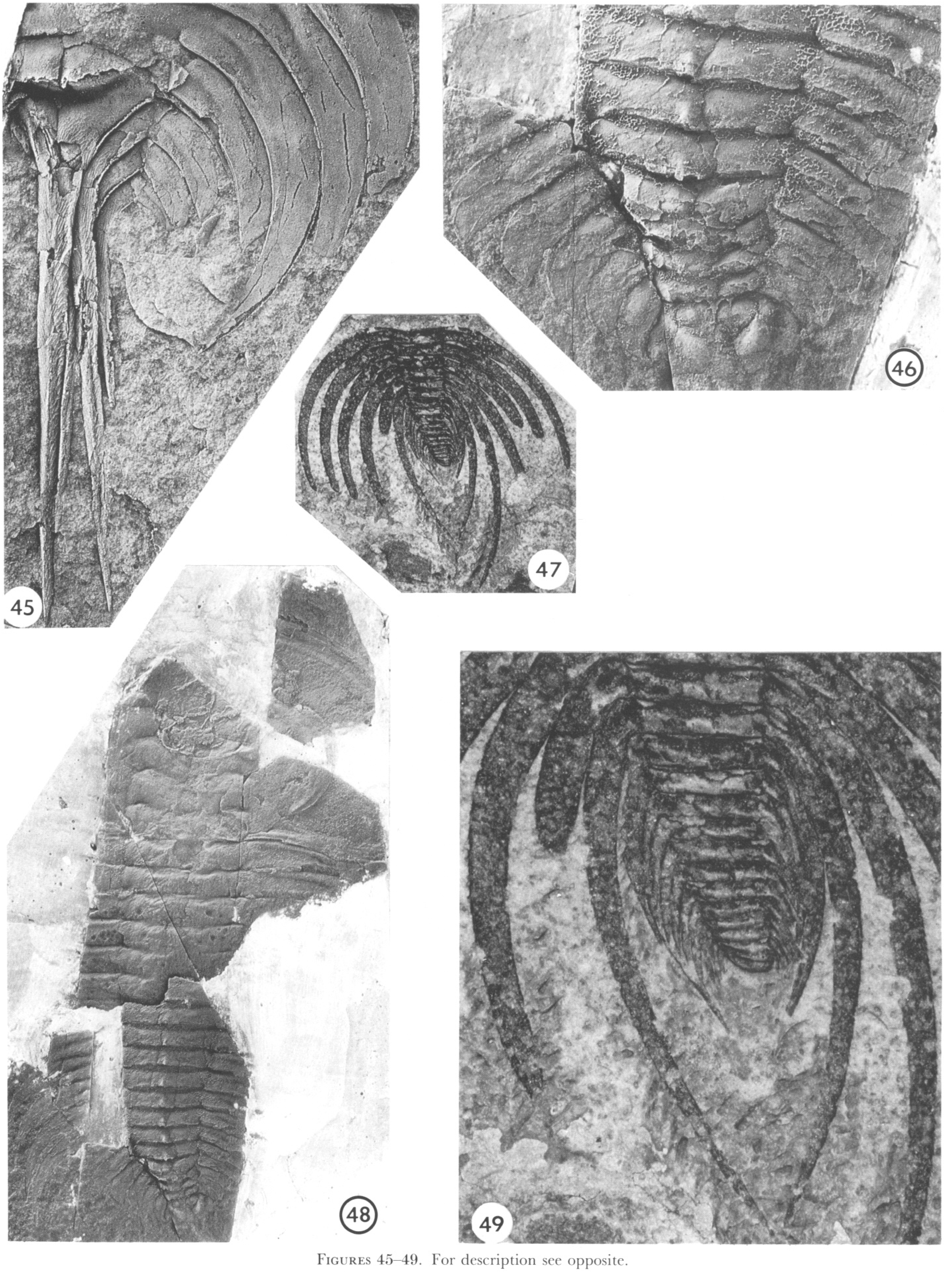
FIGURES 41–44. For description see opposite.



FIGURES 45–49. For description see opposite.