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EMERALDELLA AND *LEANCHOILIA*, TWO ARTHROPODS FROM THE BURGESS SHALE, MIDDLE CAMBRIAN, BRITISH COLUMBIA

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[Plates 1–18]

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The type species of two much discussed but hitherto poorly known genera of arthropods are described in detail from new preparations. Illustrations are by photographs, explanatory line drawings, and reconstructions including three-dimensional models. The convex body of *Emeraldella brocki* was not trilobed, and was divided into a cephalon with labrum and 13 trunk somites, the first 11 having pleurae which were progressively narrower (transversely (tr.)) and more backwardly curved posteriorly, the last two somites being cylindrical, with a long posterior spine inserted into the 13th. A bilobed, spinose, ventral anal plate was probably attached to the 12th somite; the alimentary canal may have terminated in the 13th somite. The cephalon bore long antennae and five pairs of limbs, the first short, uniramous and jointed, the second to fifth biramous, the outer branch elongate–oval and having marginal filaments, the inner branches jointed and progressively longer. Trunk somites 1–11 each bore a pair of biramous limbs, the outer branch bilobed and with filaments on the distal margins, the jointed inner branches long on the anterior six or seven pairs. The coxae of the entire limb series bore a spinose gnathobase on the mesial edge, and the proximal podomeres of the leg branches were spinose. The outer branches were attached to the coxa and possibly the first podomere of the inner leg branch. The maximum known length of the body (excluding the posterior spine) was 65 mm; the animal lacked eyes, and was a benthonic predator and scavenger, walking on and digging into the muddy bottom, the gnathobases enabling soft food to be squeezed, shredded and passed forward along the midline to the backward-facing mouth. The outer branches were presumably gills, and may have aided in feeble swimming.

Leanchoilia superlata had a smooth, convex, faintly trilobate exoskeleton. The head shield was subtriangular with an upturned snout. The 11 tergites had broad (tr.) pleurae, behind the fifth progressively narrower (tr.) and more backward-curving; the 11th was curved back beside a short, triangular tail spine, which bore lateral spines. Anteriorly the cephalon bore the great appendage, which consisted of a basal section and four additional stout podomeres shaped to curve through 90°. The second and third podomeres were each extended by a tapering shaft continued by a longer, annulated portion. The distal podomere consisted of a tapering shaft terminating in three claws and a long, annulated extension. The remainder of the body had 13 pairs of biramous appendages (two on the cephalon, one on each trunk somite), the outer branch a lobe having overlapping lamellae on the distal and posterior margins, the inner branch tapering, of some eight podomeres and terminal spines. The proximal portions of the appendages are not preserved, but the outer branch was attached so that the inner branch lay below the anterior border of the outer branch; the two branches were of similar length (tr.) and hung down below the body. The alimentary canal is preserved, filled anteriorly with apatite, the filling showing segmentation and annulation. The mouth was apparently downward- and forward-facing, and led into a bulbous foregut situated beneath the cephalon. The anus opened on the 11th trunk somite. The maximum known length of the body was 68 mm. The animal lacked eyes and was probably benthonic in habit, able to rest on the sediment surface on the great appendage and the tips of the inner branches and to swim over it by metachronal movements of the outer branches (which also acted as gills), the great appendage swung back beneath the body to reduce resistance. It was probably a detritus feeder, the food pushed into the midline by the limbs, the mouth presumably suctorial. There is no evidence of a labrum, or of gnathobasic basal podomeres, but the inner margin of the leg branch was setiferous.

The single species of *Emeraldella*, *E. brocki*, is recognized, and the type and only specimen of '*Emeraldoides*' is referred to it. Synonymous with *Leanchoilia superlata* are Walcott's three species *L. major*, *Bidentia difficilis* and *Emeraldella micrura*, and Simonetta's *Leanchoilia amphiction*, *L. persephone* and *L. protogonia*. *Emeraldella brocki* may be allied with *Molaria spinifera*; problematical is any relationship to aglaspidids. *Leanchoilia superlata* may be most closely related to *Actaeus armatus*. *Emeraldella* and *Leanchoilia* are very different from one another, and from either *Sidneyia* or *Naraoia*; these four genera are so heterogeneous that Størmer's grouping of them into the taxon Merostomoidea is rejected as no longer useful.

1. INTRODUCTION

As part of a detailed re-examination of the Burgess Shale arthropods, or supposed arthropods (Briggs, 1976, 1977, 1978, 1979, 1981; Bruton 1977, 1981; Hughes 1975, 1977; Whittington 1971 *a*, *b*, 1974, 1975 *a*, *b*, 1977, 1978, 1980 *a*, 1981), we describe here two relatively large forms, giving much new information derived from our preparations of the appendages. This study was begun by D.L.B. in 1972, while on a visit to the U.S. National Museum, and has been continued in Oslo and during two visits to Cambridge. The work on *Leanchoilia superlata* is by D.L.B.; we have collaborated in the study of *Emeraldella brocki* and in preparation of this account. Each genus is known from a single species, *L. superlata* from over 100 specimens, *E. brocki* from 26, predominantly from collections made by C. D. Walcott from the Burgess Shale in 1910–1917, but, for *L. superlata*, from additional smaller collections made by P. E. Raymond in 1930 and the Geological Survey of Canada's party in 1966–1967. *L. superlata* was one of the species on which Walcott's posthumous paper gave additional information, while Raymond and L. Størmer each commented on other specimens in their possession at Harvard and Oslo Universities respectively. Thus the head of this animal, with its upturned snout and striking frontal pair of appendages, became apparently well known, though how many and what other appendages were borne on the cephalon remained uncertain, and the nature of the trunk limbs debatable. The understanding of *Emeraldella brocki* has been handicapped by Walcott's misidentification of two specimens with appendages as *Sidneyia inexpectans*, and these, the lectotype, and one additional specimen were all that Raymond and Størmer had on which to base their views on its morphology. Additional, better preserved specimens of *Emeraldella* in the Walcott collection were briefly described and figured, and a reconstruction was provided, by A. M. Simonetta in 1964, and of *Leanchoilia* in 1970. Regrettably his photographs were poor and gave little new information, and the restorations show features for which either no, or inadequate, evidence was brought forward. Some confusion also arises from his attribution of an isolated appendage to *Leanchoilia*, which Bruton in 1973 recognized as that of *Emeraldella*. In subsequent papers by Simonetta acceptance of this change is incorporated in the text and in amended restorations. No species other than the type of *Emeraldella*, *E. brocki*, has been described. Simonetta's genus *Emeraldoides* was based on a single specimen; we consider the supposedly distinctive features to be misinterpretations, and regard the specimen as an obliquely compressed example of *E. brocki*. Walcott proposed an additional species of *Leanchoilia*, *L. major*, and Simonetta erected three more, *L. amphiction*, *L. protogonia* and *L. persephone*. None of these appears to be valid, the specimens being either unidentifiable or probably of the type species *L. superlata*.

It is important for our study to elucidate the nature and position of the appendages, so that we have prepared for the first time particular specimens with the micro-drill, taken photographs by various methods, and provided drawings facing them to explain our interpretations. From these the reconstructions (figures 63–65, 111–113) have been made, and models (plates 10, 18) have been constructed as a visual aid and check on the reconstructions. The abstract provides the only summary description of each species, and shows how different they are from one another, as are almost all the arthropod species from the Shale. This diversity, and the isolation in time and space of the fauna, make relationships difficult to discern. Conventional diagnoses, distinguishing each genus from related genera, cannot be given. Until recently the views of palaeontologists on the relationships of these oldest, well preserved arthropods have been dominated by the great contribution made by L. Størmer. Using the name Trilobitoidea, he brought the whole assemblage under the umbrella of being trilobite-like, individual genera being distinguished by the possession of particular non-trilobite characters; this class was subdivided into at least three groups, one being the Merostomoidea which included *Emeraldella* and *Leanchoilia*. The new knowledge that has come from the re-examination now in progress shows that Størmer's views were an oversimplification based on the erroneous information available to him. A new assessment of relationships has to be made; for a beginning see Whittington (1979) and Briggs & Whittington (1981). Here we do not use higher taxonomic groupings but suggest possible relationships of the two genera concerned, pending the wider survey.

2. Locality and stratigraphical horizon

All the specimens of *Emeraldella brocki*, and about half of those of *Leanchoilia superlata*, came from what Walcott (1912, pp. 151–153) called the 'Phyllopod Bed', 2.3 m thick, in which he excavated his quarry. This quarry was in the Burgess Shale member, Stephen Formation, Middle Cambrian, *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field at an elevation of approximately 2286 m, 4.8 km north of Field, southern British Columbia. These specimens are all in the United States National Museum collections and are labelled 35k. This label gives no indication of the level in the Phyllopod Bed from which the specimen came. Walcott (1912, pp. 152–153) remarks that these two species were present only in his layer 10, i.e. 7.6 to 48.3 cm above the base of the bed, and lists the accompanying fauna. We do not know whether these species were discovered at a different level in his subsequent quarrying in the 1912, 1913 and 1917 seasons. Walcott also collected from higher layers some 23 m above the base of the Phyllopod Bed, and in the U.S.N.M. collections such specimens are labelled 35k/1 or 35k/10. The balance of the specimens of *L. superlata* are from this source, or from collections made by Geological Survey of Canada parties from levels 21–22.3 m (69 to 73 ft) above the base of the Phyllopod Bed. A detailed account of the discovery and collection of the fossils has been given by Whittington (1971*a*, pp. 1171–1180), and since then a collection has been made by a party from the Royal Ontario Museum (Collins 1978) from talus.

3. Terminology and methods

The divisions of the dorsal exoskeleton of these arthropods have been referred to as *cephalic shield*, tergites of the *trunk*, and either a *tail spine* or *posterior spine*. Other terms are defined in the list of abbreviations and symbols used on the drawings. To avoid ambiguity when referring to directions, the median longitudinal line in the body is termed *sagittal* (abbreviation sag.), a line parallel to, but outside, the sagittal line as *exsagittal* (abbreviation exs.), and a direction at right angles to these as *transverse* (abbreviation tr.). The dorsal exoskeleton and cuticle of the appendages are preserved as extremely thin layers in the shale, the original relief having been profoundly modified. The bodies were not buried with the horizontal plane parallel to the bedding planes, but all or parts of the body were entombed in a variety of attitudes. These attitudes of the horizontal plane of the body relative to the bedding have been described as *parallel*, *oblique*, *lateral* and *vertical*. These terms are used in the explanations of the plates, qualified as parallel oblique, lateral oblique, etc., to indicate that the specimen is approximately or partly parallel, lateral, etc. When the rock was split to reveal a specimen, portions of the specimen adhered to each side of the split, the *part* and *counterpart*. The former is the side that has the dorsal side of the animal toward the observer. This means that in a lateral, as in a dorsal, compression the part has the exoskeleton nearer to the observer than the underlying appendages. In the explanations of the plates the statement 'part only' or 'counterpart only' means that only one side of the specimen is known; specimens are from the Phyllopod Bed, Walcott's locality 35k, unless otherwise noted. The photographs have been taken on panchromatic film, most in ultraviolet radiation after focusing in ordinary light. The radiation was directed at 30° to the horizontal, and the direction from which it came is given as west, northwest, etc., relative to north at the top of the page. The direction from which such low-angle radiation comes is critical in revealing particular details; these photographs are referred to only by the direction. Photographs referred to as reflected were taken in radiation coming from 65° to the horizontal, and the specimen was tilted about 12° so that the maximum amount of reflected radiation was directed into the camera. As noted in the plate explanations, a few photographs were taken in ordinary light, or in such light after submersion in alcohol. The latter technique proved particularly advantageous in photographing specimens of *L. superlata* that had a pale yellow surface. Camera-lucida drawings face the plates and show how a particular specimen has been interpreted. Minute scarps separate changes in level between one part of the body and another, and reveal their relationship. The scarps are delineated by a line along the upper edge, with hachures running downslope from this line. The scarps were formed either when the rock was split, or by preparation, the changes in level resulting from the mode of preservation. Drawings described as *explanatory* show part or counterpart; *composite* drawings show the part and counterpart superimposed, to explain the relationships of parts of the body. The abbreviations listed include letters denoting the institution in which a particular specimen is housed. These letters are placed before the catalogue number in § 6 and the plate and figure explanations, but omitted in § 5 for brevity, since all the specimens are from U.S.N.M. collections.

4. Preservation

Recent general accounts of the Burgess Shale fauna (Conway Morris & Whittington 1979; Conway Morris 1979; Whittington 1980*b*) have summarized ideas on the environment in which the animals lived and that in which they were buried and preserved. The former environment was at the foot of a submarine cliff, in light, oxygenated waters about 100 m in depth, the animals living above, on and in the fine-grained, muddy sediment. These wet muds were unstable, and periodically a portion of them slumped downslope, as a turbulent cloud of sediment in suspension, which carried with it live or dead animals, empty shells or exoskeletons, that were on or in that particular portion of mud. The suspension slowed down as the slope was reduced, presumably in a small basin. Here the sediment settled out, burying the randomly oriented carcasses in what Conway Morris called the post-slide environment. Such a process explains the varied orientations of the specimens in the rock. All those described here have appendages preserved and not greatly displaced relative to the dorsal exoskeleton. Some trace of the alimentary canal is present in many specimens, as a dark band in low-angle radiation (figure 2, plate 1; figure 12, plate 3), or a strongly reflective band (figure 79, plate 13); these two features may be coincident. In *L. superlata* the anterior portion of the gut in the trunk is filled with apatite (figures 83, 84, plate 14), while in *E. brocki* patches of comminuted fragments of shells are present (figure 24, plate 5). These features are the remains, after diagenesis and compaction, of gut contents. The implication is that the animals were probably alive when trapped in the mud cloud, and killed during transport and burial. A reaction between organic matter and the enclosing sediment is suggested by the halo around the specimen of *L. superlata* (figure 89, plate 15), and the rare dark stain (figures 2, 3, plate 1) may result from organic matter seeping from the carcass. The evidence points to the animals having been benthonic in habit, to allow them to have been caught and buried in this way. That burial was in an oxygen-poor environment is suggested by the pyrite associated with the fossils, as fine-grained patches beside the gut in *L. superlata* (indicated by stipple in figure 100) and minute spheres (figures 17–20, plate 4; figure 81, plate 13).

The bodies of the arthropods with appendages do not lie in one plane in the rock, because of the mode of burial. Appendages are separated by a thin layer of rock from the dorsal exoskeleton, and the two branches of an individual appendage, as well as the members of a series, are imbricated with a thin layer of rock separating them. This mode of preservation enables appendages to be revealed beneath the exoskeleton by preparation (see, for example, figures 12–16, plate 3), including revealing the inner branch. In such specimens it is most valuable to have part and counterpart, so that the mutual relationship of exoskeleton and appendage branches may be seen and summarized in a composite drawing (e.g. figures 21, 22). The split between part and counterpart of a specimen moves from one level to another, so that in some areas it is through portions of the exoskeleton, in others through one branch or another of the appendages, through or around the filling of the alimentary canal (figures 23, 27, plate 5; figure 68, plate 11; figures 93, 95, plate 16).

The mud in which the animal was entombed was compacted, compressing the body in whatever attitude it was buried. The original form and convexity of the exoskeleton, attitude and arrangement of appendages, etc., has to be deduced from these flattened specimens (cf. discussion of form of the cephalic shield of *Naraoia compacta* in Whittington (1977, p. 420, fig. 3)). The samples of the two species considered here reveal a sufficient variety of compressions to enable us to feel reasonably confident of the accuracy of the models (plates 10, 18).

5. *EMERALDELLA BROCKI* WALCOTT, 1912

(Figures 1–65, including plates 1–10.)

1911 Walcott, p. 26, pl. 2, figs 2, 3 (as *Sidneyia inexpectans*).
1912 Walcott, pp. 153, 155, 158, 163, 203–205, 220, pl. 30, fig. 2; text-fig. 8.
1912 Walcott, pp. 205–206, text-fig. 10 (as *Sidneyia inexpectans*).
1918 Walcott, p. 118.
1920 Raymond, pp. 119–120, 149.
1925 Fedotov, pp. 389, 392.
1928 Henriksen, pp. 16–17.
1935 Raymond, pp. 214, 216.
1939 Størmer, pp. 234–235, fig. 29*c*.
1944 Størmer, pp. 84–85, 124, 134, fig. 17 (3).
1949 Størmer *in* Grassé, p. 201, fig. 35, 3.
1953 Dechaseaux *in* Piveteau, pp. 29–30, fig. 1.
1959 Størmer *in* Moore, p. *O*30, fig. 17 (copy Størmer (1944)).
1964 Simonetta, pp. 223–228, figs 4, 5, pls 39–43 (i.e. to include the type of '*Emeraldoides problematicus*').
1970 Simonetta, pl. ii, fig. 1*c*; pl. iii, figs 3*a*, 3*b*.
1975 Simonetta & Delle Cave, pp. 19, 24, 27, 31–32, pl. ii, figs 1*a–i*; pl. xxii, fig. 6; pl. xxiii,

figs 1–4; pl. xxiv, figs 1–4; pl. xxv, figs 1–5; pl. xxvi, figs 1–6; pl. xxvii, figs 1–4, 6 (not fig. 5); pl. xxviii, fig. 1 (copies of Simonetta (1964), with some additions).

1976 Simonetta, p. 116, fig. 3*a–i.*
1979 Bergström, p. 25.
1980 Bergström, p. 34.
1980 Whittington, p. 139, pl. 4, fig. 4.
1980 Simonetta & Delle Cave, pp. 2, 5–6, figs 1, 2; pl. i, fig. 9; pl. iii, fig. 3.
1981 Simonetta & Delle Cave, pp. 428, 431; figs 1, 4, 14, 16, 17.
1981 Whittington, pp. 342, 346.
1981 Conway Morris & Bruton, p. 53; fig. 4.

(*a*) *Material, occurrence, associated fauna*

Lectotype (here selected) U.S.N.M. 57702, original of Walcott's (1912), pl. 30, fig. 2 (figures 2–4, plate 1).

Other material: U.S.N.M. 136439, original of Walcott's (1912) text-fig. 8; U.S.N.M. 57488, 136442, originals of Walcott's (1911) pl. 2, figs 2, 3 and (1912) text-fig. 10, respectively, which he first identified as *Sidneyia inexpectans*, but subsequently (1918) recognized as *E. brocki*; U.S.N.M. 144917–144930, 144932–144934, studied by Simonetta (1964); U.S.N.M. 250227, 250230, two incomplete individuals; U.S.N.M. 155636, 250228, fragments of limbs; and R.O.M. 37850, a poorly preserved individual. These specimens include portions of 26 individuals, 16 of them having part and counterpart, and all showing appendages. Those from the Walcott collection are labelled 35k, and so are from his Phyllopod Bed, possibly from his layer no. 10 (Walcott 1912, p. 153). R.O.M. 37850 was from the talus of Walcott's quarry (Collins 1978). No specimens were obtained by the Geological Survey of Canada parties. Associated with the Walcott specimens is the eodiscid *Pagetia bootes*, agnostids, *Naraoia compacta*, and the other arthropods *Marrella splendens*, *Canadaspis perfecta* and *Waptia fieldensis*.

(*b*) *Description*

The restorations (figures 63–65) on which the model (figures 60–62, plate 10) is based summarize our views on morphology. The length (sag.) of the exoskeleton, excluding the posterior spine, ranges from·11 to 65 mm, overlapping that of *Molaria spinifera* (Whittington 1981, fig. 1) and giving a maximum size more than twice that of *M. spinifera*. The convexity of the exoskeleton is taken from 144930 (figures 7, 8, plate 2) which appears to be an almost exactly lateral compression, and the dorsal outline is based on such specimens as 136440–136442 (plates 3–5). These show the eleven tergites of the thorax which are progressively more strongly curved posteriorly. The lectotype also shows the eleven tergites, the left pleura of the 11th being preserved on the counterpart (figures 2–4, plate 1). Behind the 11th somite of the trunk were two further somites (numbered 12 and 13, figures 11, 21; figure 24, plate 5) and a tapering, posterior spine. Lateral (figures 7, 8, plate 2) and oblique (figures 2, 3, plate 1) specimens do not show the boundary between the last two somites, but suggest that the exoskeleton was cylindrical. The trace of the alimentary canal extends as a darker (figure 2, plate 1; figure 12, plate 3) or reflective (figure 58, plate 9) band through both these somites to the base of the posterior spine. Whether the anal opening was situated in the last somite, or the base of the posterior spine, is uncertain. The spinose lateral margins of a ventral plate are visible beside the 13th somite (figure 24, plate 5) or beside both 12th and 13th somites (figure 17,

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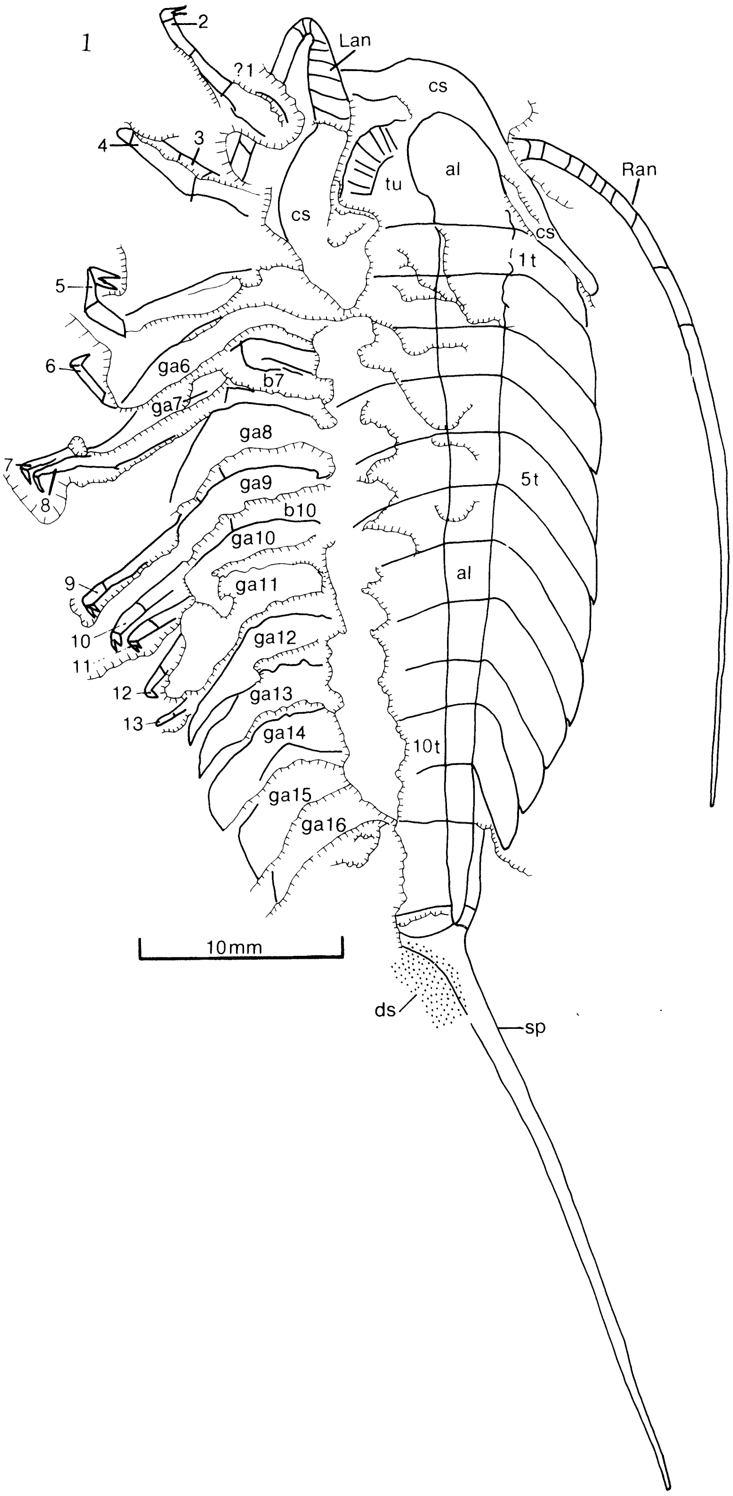
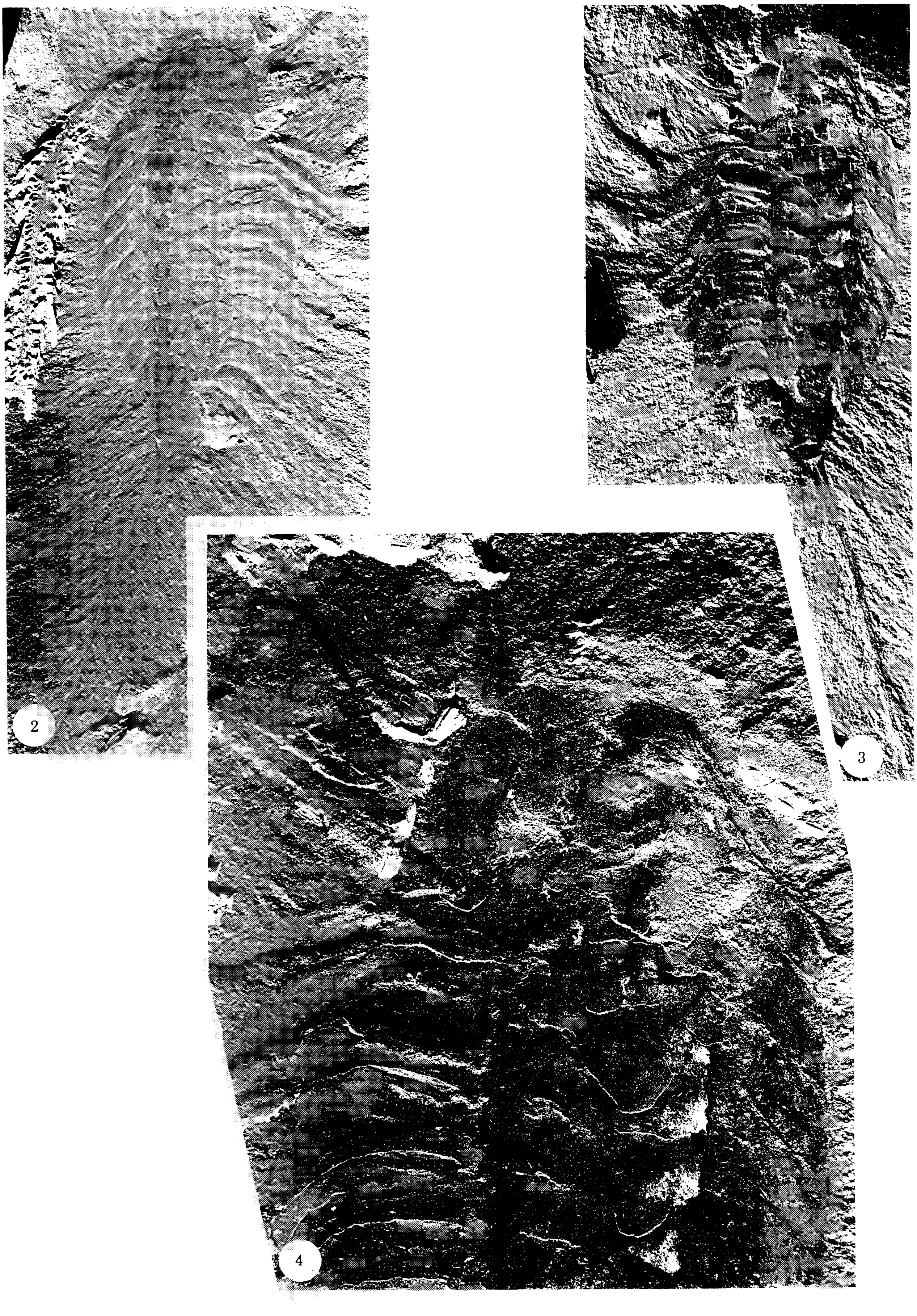


Description of figure 1 and plate 1

Emeraldella brocki Walcott, 1912.

Figure 1. Composite explanatory drawing of U.S.N.M. 57702.

Figures 2–4. U.S.N.M. 57702, lectotype, oblique. Respectively: counterpart, west-northwest (magn. × 1.7); part, east-northeast (magn. × 1.7) and north (magn. × 5).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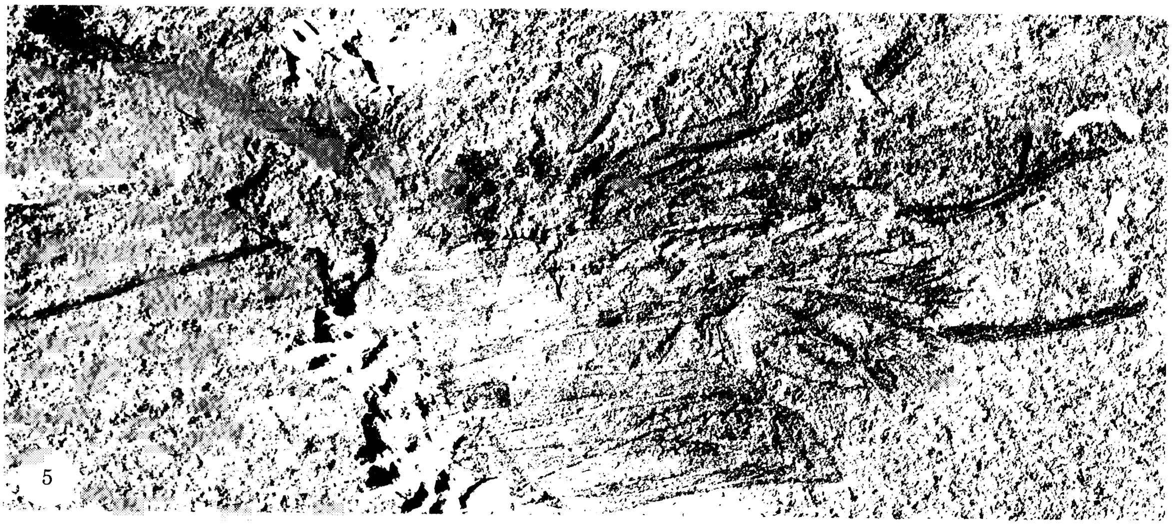
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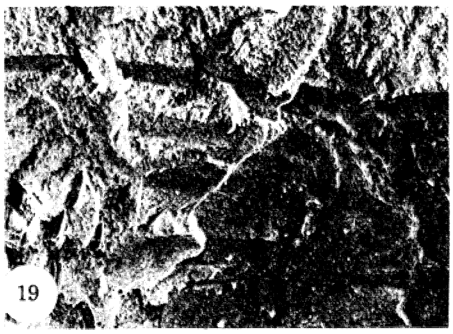

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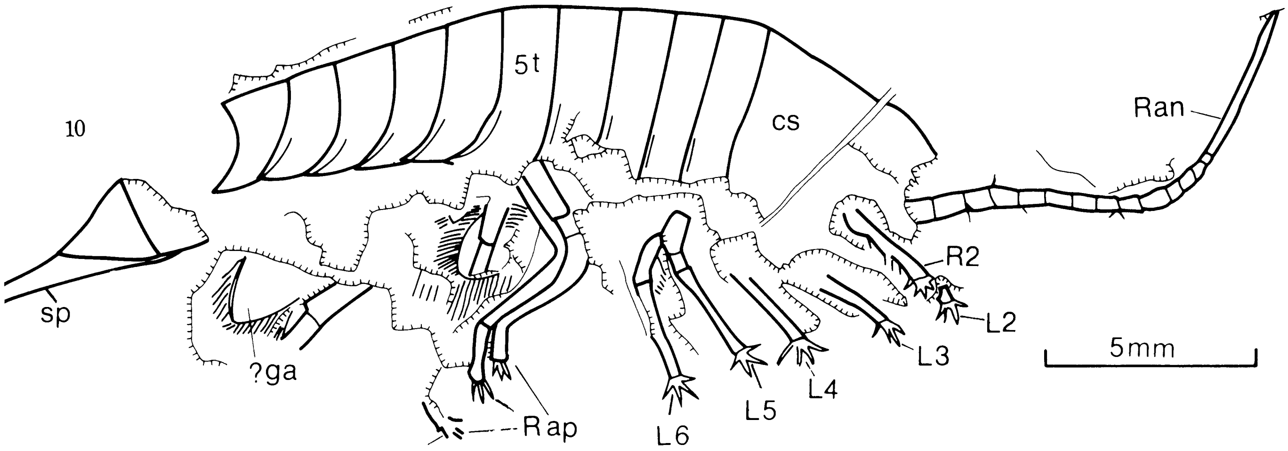

Description of plate 2 and figures 9 and 10

Emeraldella brocki Walcott, 1912.

Figures 5 and 6. U.S.N.M. 144924, parallel, counterpart: (5) west; (6) reflected (magn. × 6.7).

Figures 7 and 8. U.S.N.M. 144930, lateral, part only: (7) northwest (magn. × 3.5); (8) reflected to show appendages (magn. × 7).

Figures 9 and 10. Explanatory drawings of U.S.N.M. 144924 and 144930 respectively.

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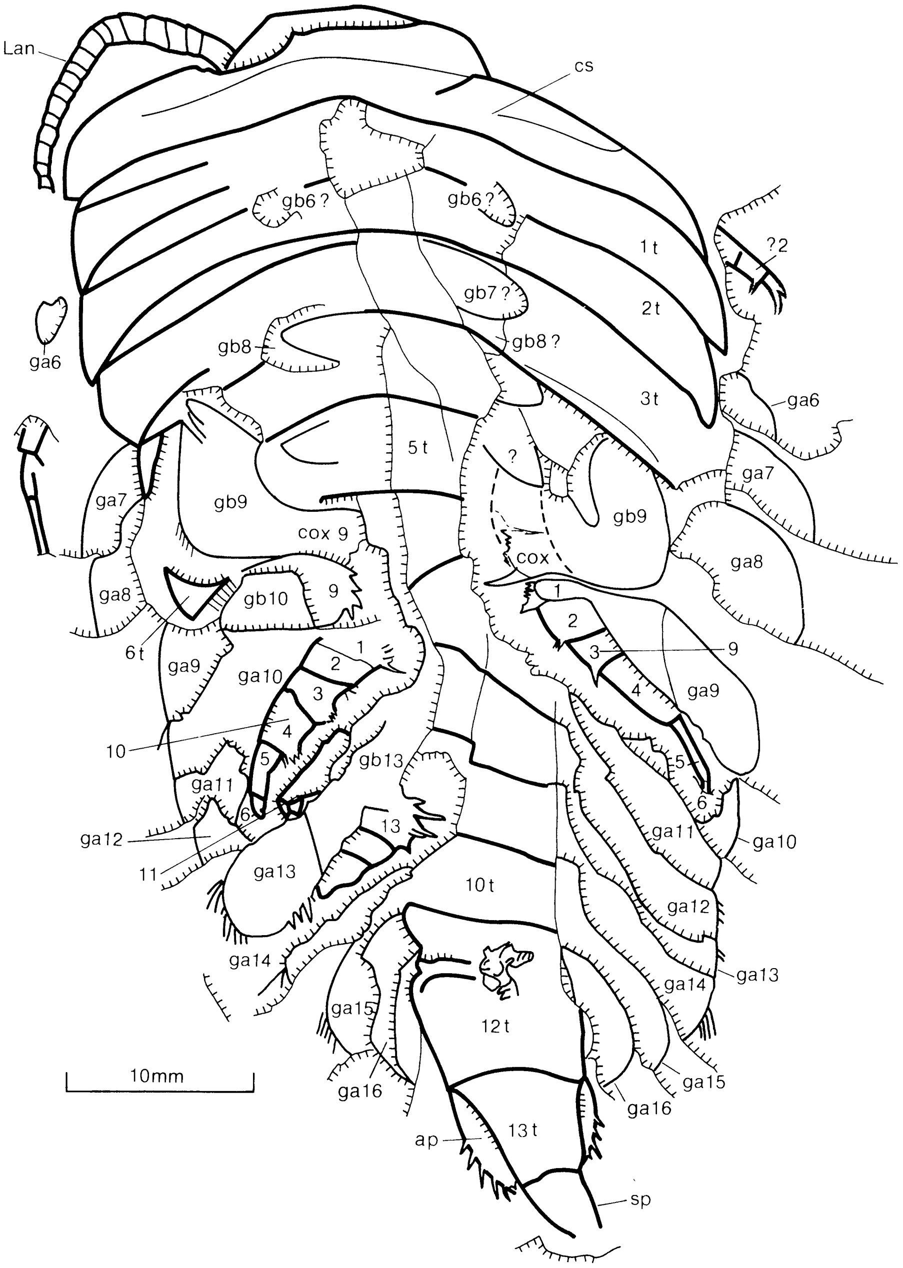
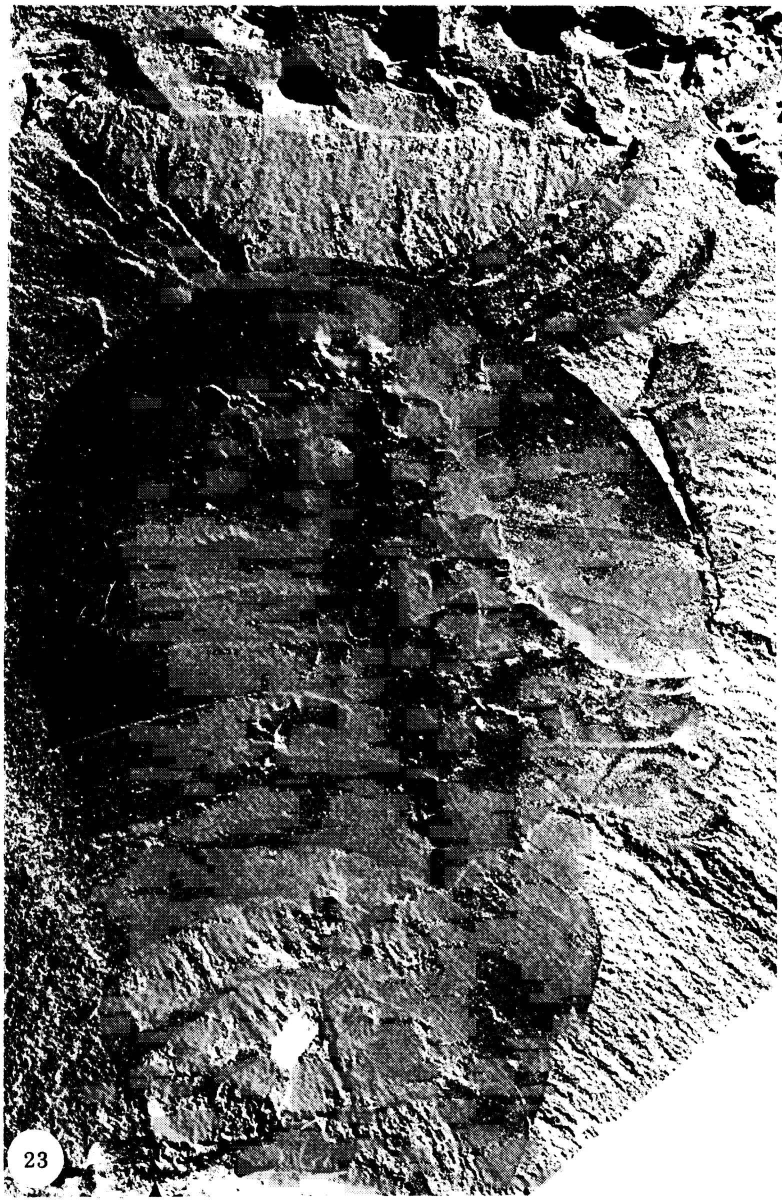


Description of figure 11 and plate 3

Emeraldella brocki Walcott, 1912.

Figure 11. Explanatory drawing after preparation of U.S.N.M. 136440.

Figures 12–16. U.S.N.M. 136440, oblique, part only: (12) northwest, ordinary light, before preparation (magn. × 1.5); (13) west, after preparation (magn. × 1.7); (14) reflected, left limbs 10–13 (magn. × 4); (15) north-east, left limbs 9–13 (magn. × 5); (16) west-northwest, right limb 9 (magn. × 5). See also figure 24, plate 5.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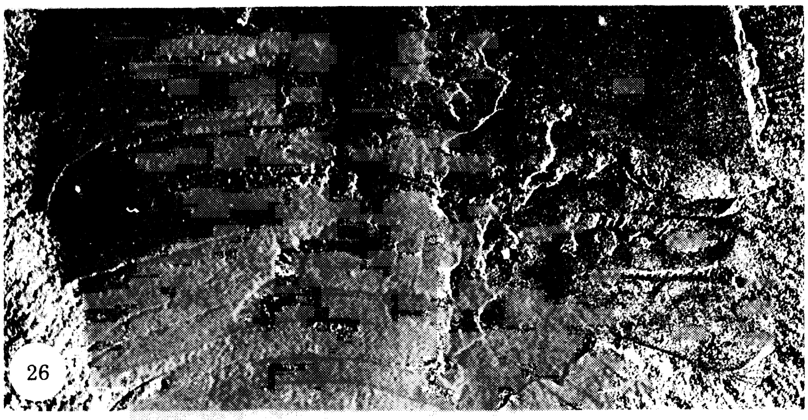
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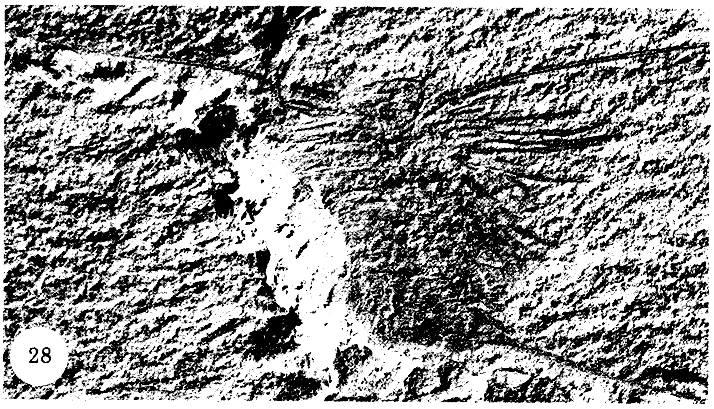
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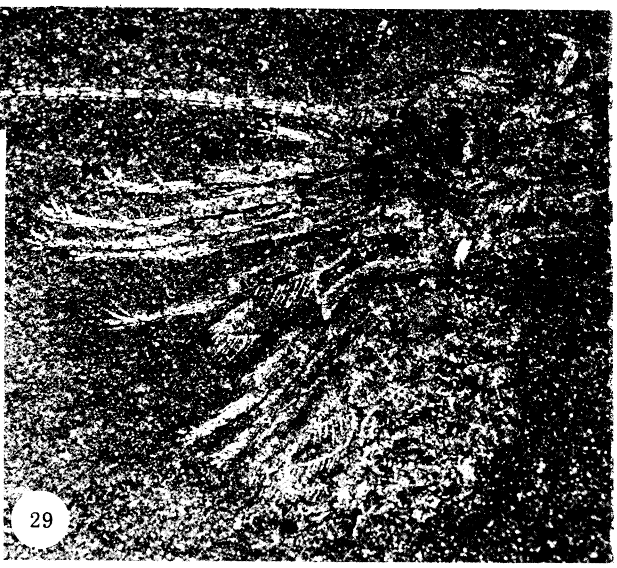
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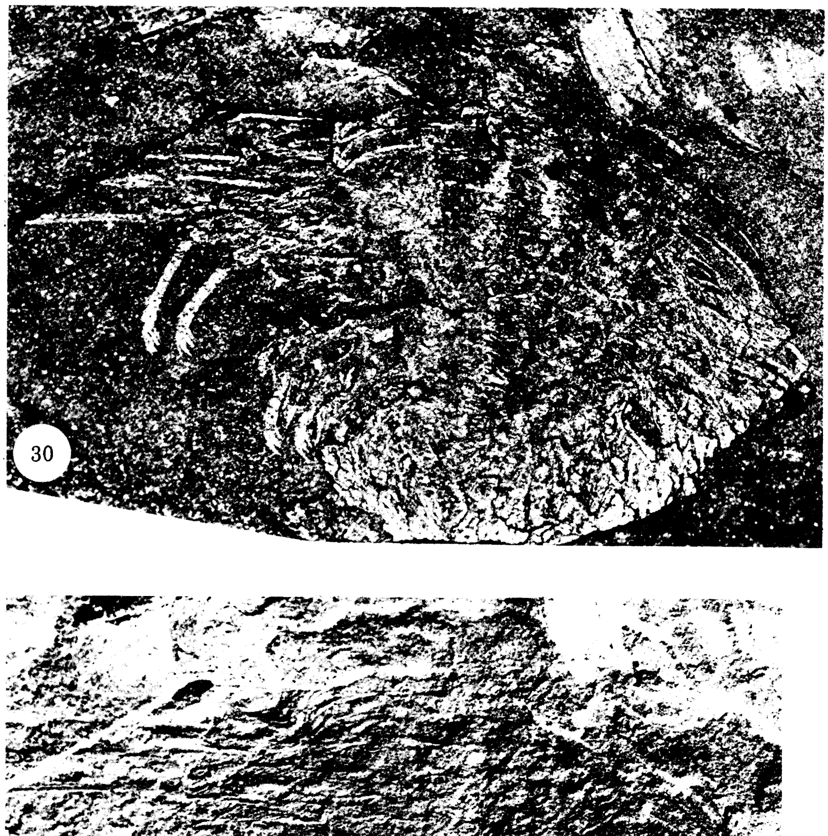
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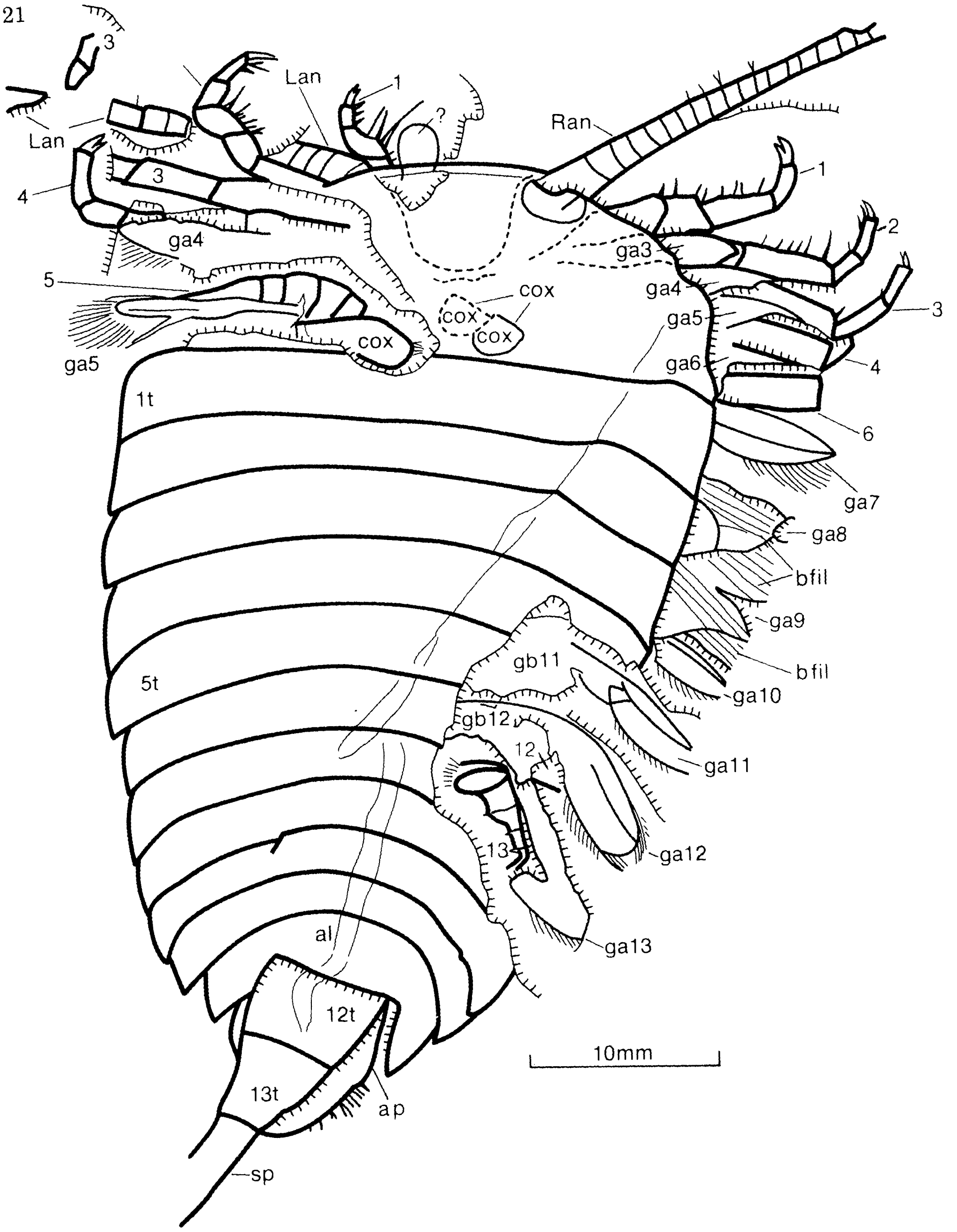

Description of plate 4 and figure 21

Emeraldella brocki Walcott, 1912.

Figures 17–19. U.S.N.M. 136441, parallel, part: (17) east-northeast, ordinary light, after preparation (magn. × 4); (18) west, right half before preparation (magn. × 3); (19) west, left anterior before preparation (magn. × 3).

Figure 20. U.S.N.M. 136441, parallel, counterpart, northwest (magn. × 3.5).

Figure 21. Composite explanatory drawing, after preparation, of U.S.N.M. 136441.

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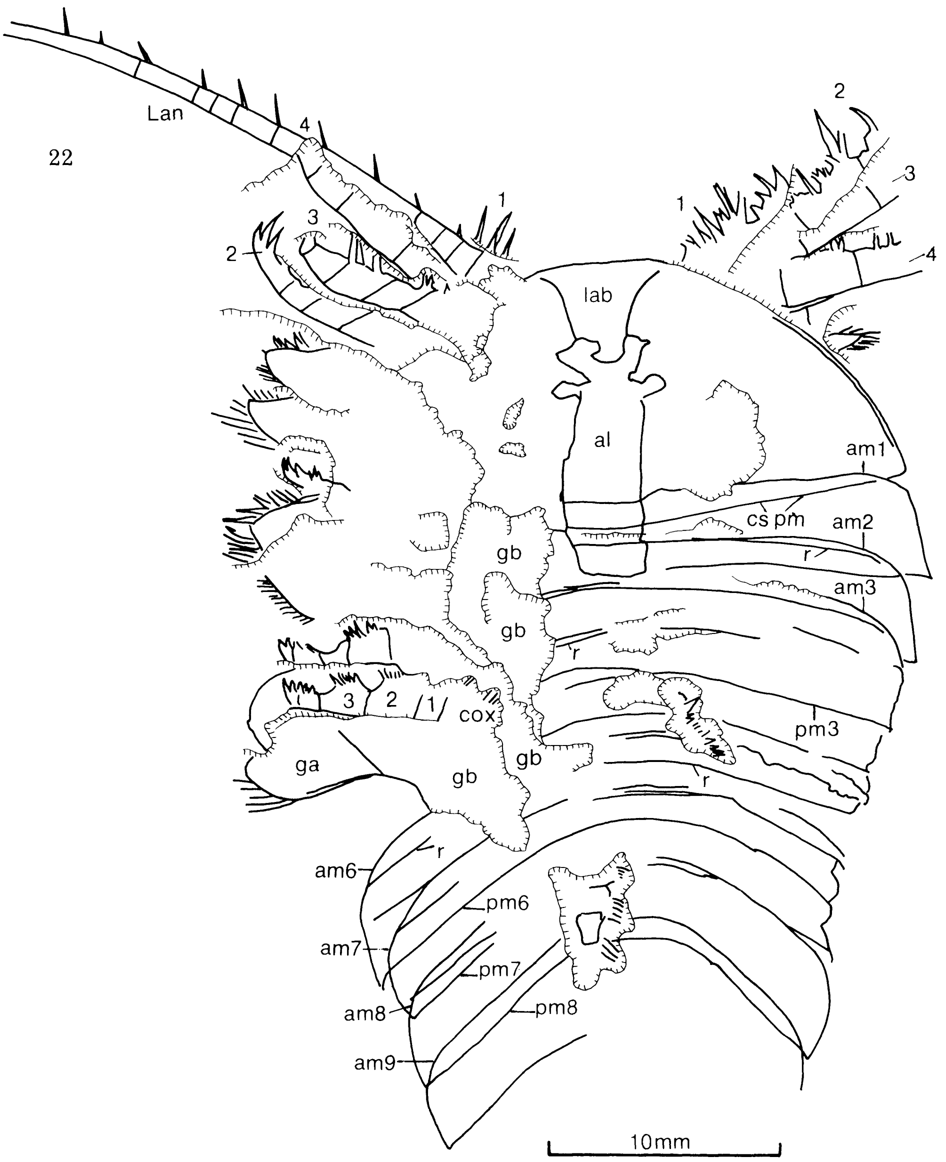

DESCRIPTION OF FIGURE 22 AND PLATE 5

Emeraldella brocki Walcott, 1912.

FIGURE 22. Composite explanatory drawing of U.S.N.M. 136442.

FIGURES 23 AND 26. U.S.N.M. 136442, parallel, counterpart: (23) northeast; (26) west. (Magn. × 3.)

FIGURE 24. U.S.N.M. 136440, part, showing trunk tergites 12 and 13, and margins of anal plate, west. (Magn. × 6.) See also figures 12–16, plate 3.

FIGURES 25 AND 27. U.S.N.M. 136442, parallel, part: (25) midtrunk limbs on left side, reflected (magn. × 4); (27) northeast (magn. × 1.7).


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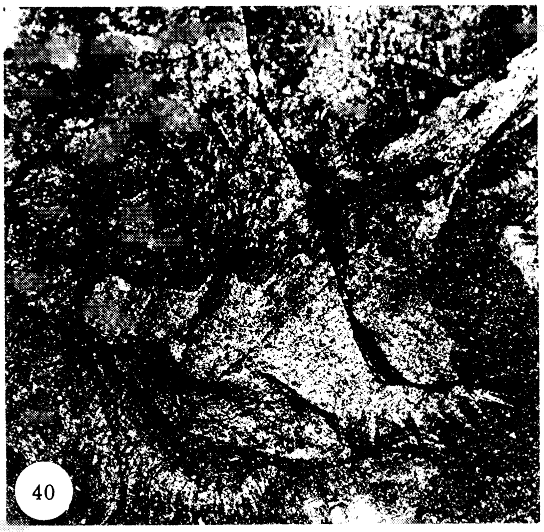
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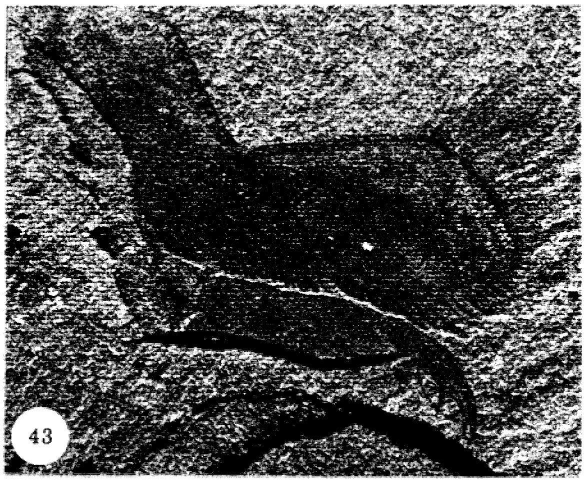
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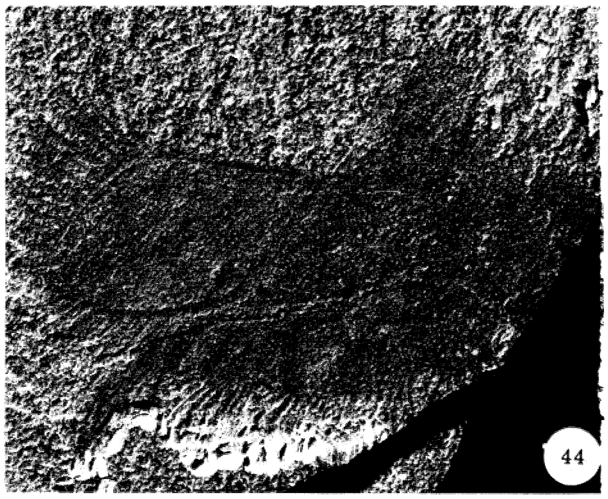
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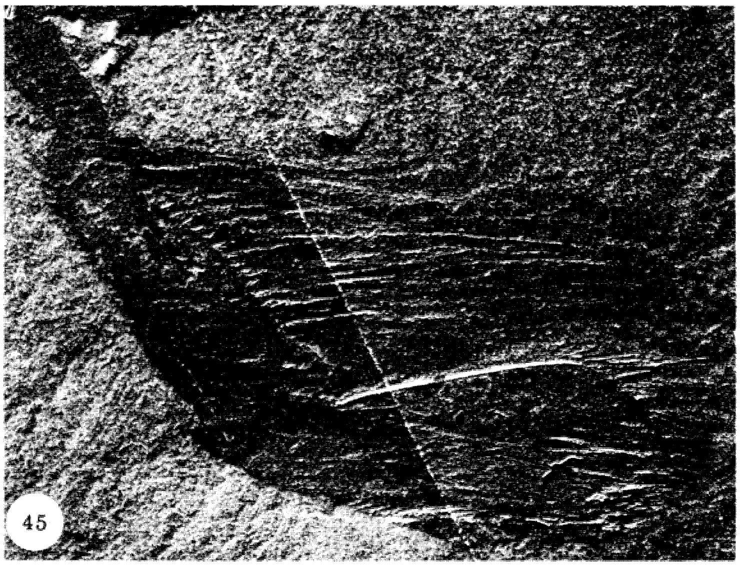
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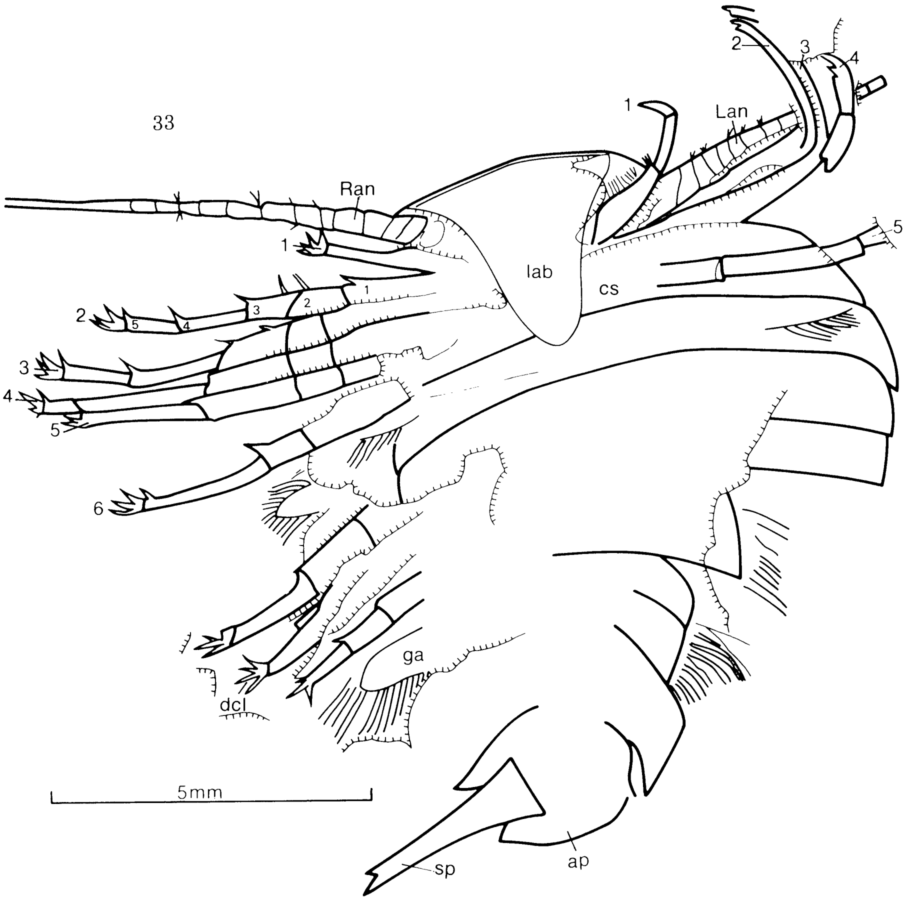

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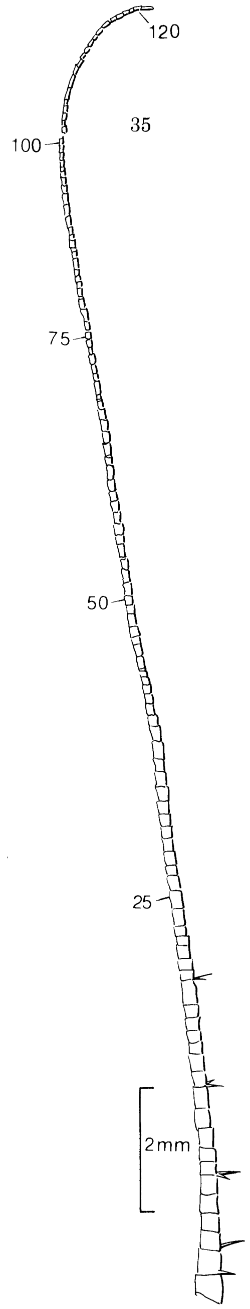

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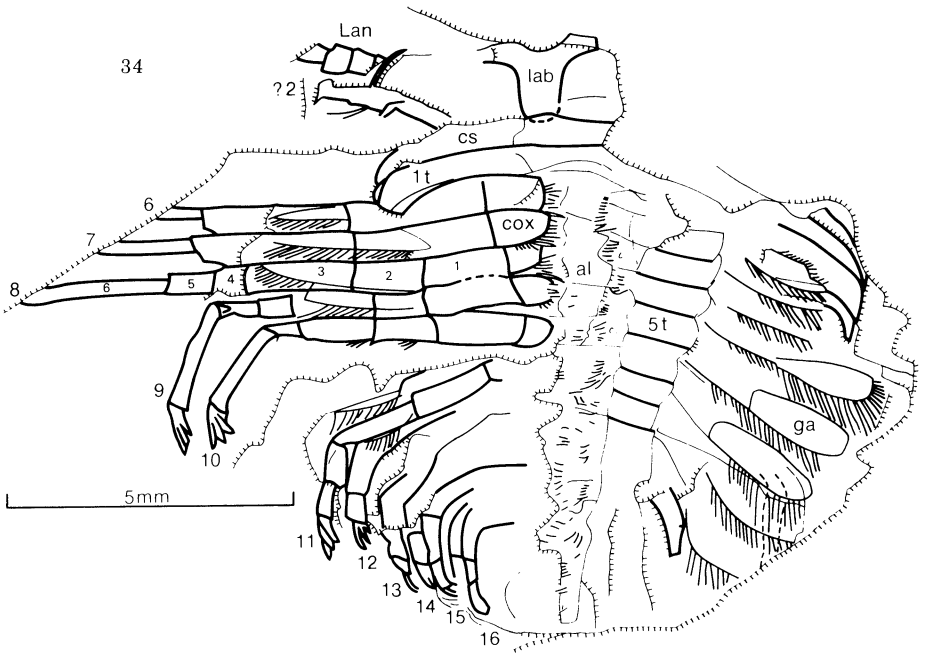

DESCRIPTION OF PLATE 6 AND FIGURES 33–35

Emeraldella brocki Walcott, 1912.

FIGURES 28 AND 29. U.S.N.M. 144923, parallel: (28) part, northwest (magn. ×4); (29) counterpart, reflected (magn. ×7).

FIGURES 30 AND 31. U.S.N.M. 144934, parallel, counterpart only: (30) reflected; (31) northwest. (Magn. ×6.5.)

FIGURE 32. U.S.N.M. 144933, parallel, counterpart only, reflected. (Magn. ×4.) See also figure 48, plate 8.

FIGURES 33 AND 35. U.S.N.M. 144923: (33) composite explanatory drawing of entire specimen from ventral; (35) detail of right antenna, showing number of annulations.

FIGURE 34. Explanatory drawing of U.S.N.M. 144934.

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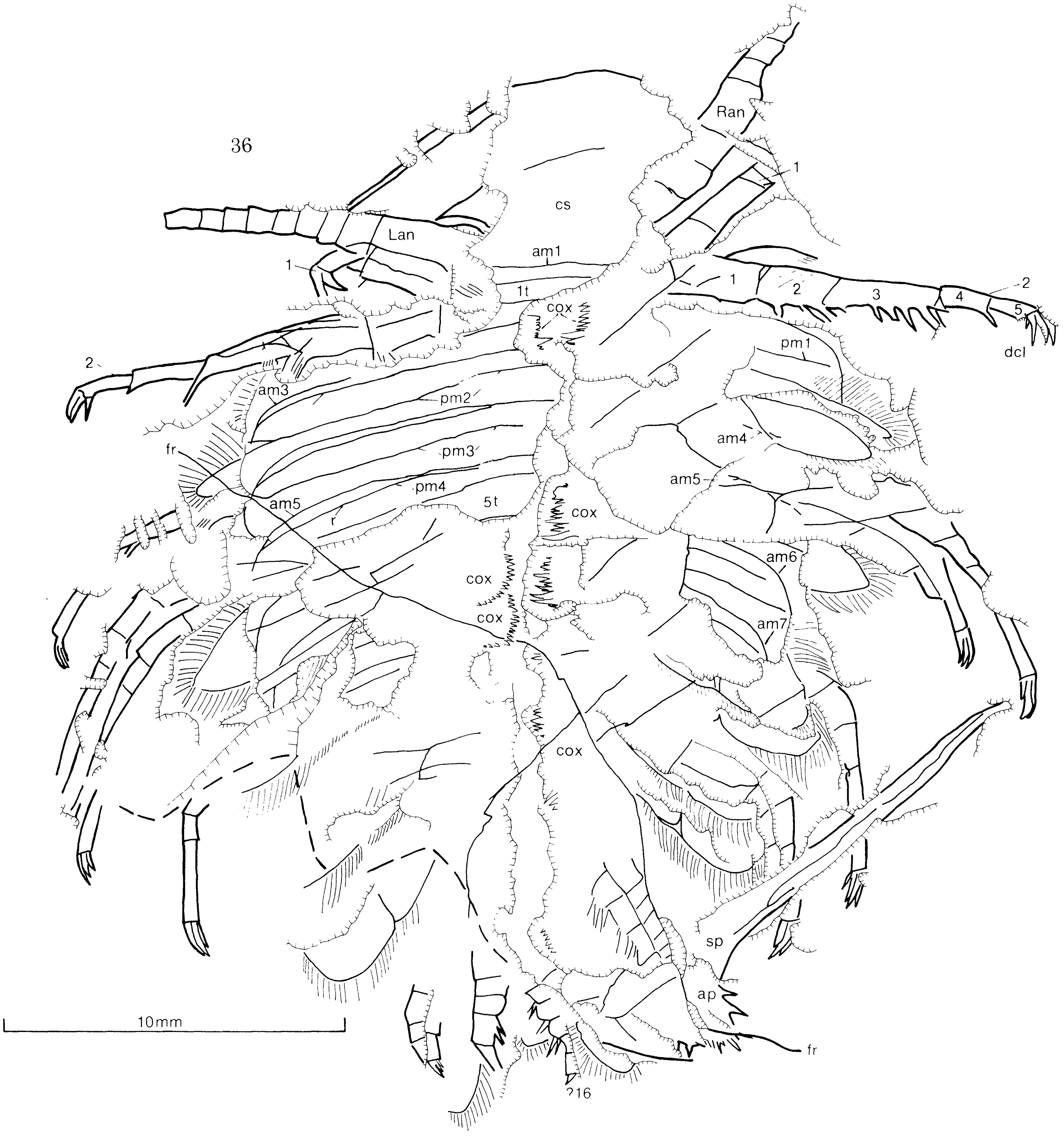


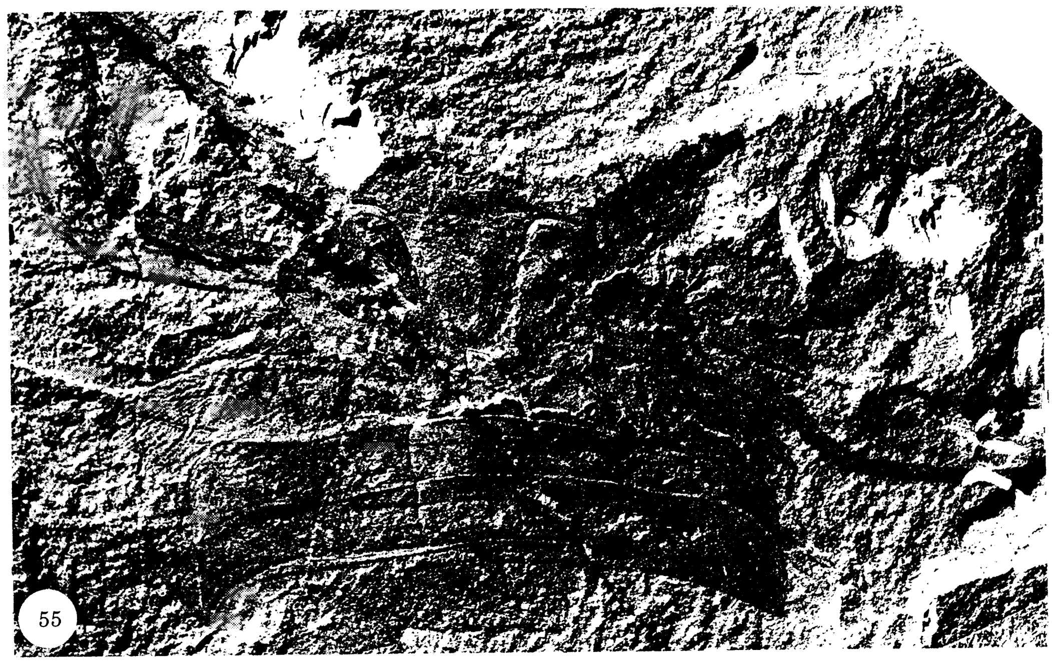
Description of figure 36 and plate 7

Emeraldella brocki Walcott, 1912.

Figure 36. Composite explanatory drawing of U.S.N.M. 144928; portion below dashed line preserved only on counterpart.

Figures 37, 39, 40 and 42. U.S.N.M. 144928, parallel, part: (37) entire, west-northwest (magn. × 3.3); (39) median region showing gnathobases, northwest (magn. × 10); (40) posterior region showing anal plate and base of posterior spine, reflected (magn. × 10); (42) right limb 2 (magn. × 10).

Figures 38 and 41. U.S.N.M. 144928, parallel, counterpart: (38) entire, northwest (magn. × 3.3); (41) median region showing gnathobases, northwest (magn. × 10).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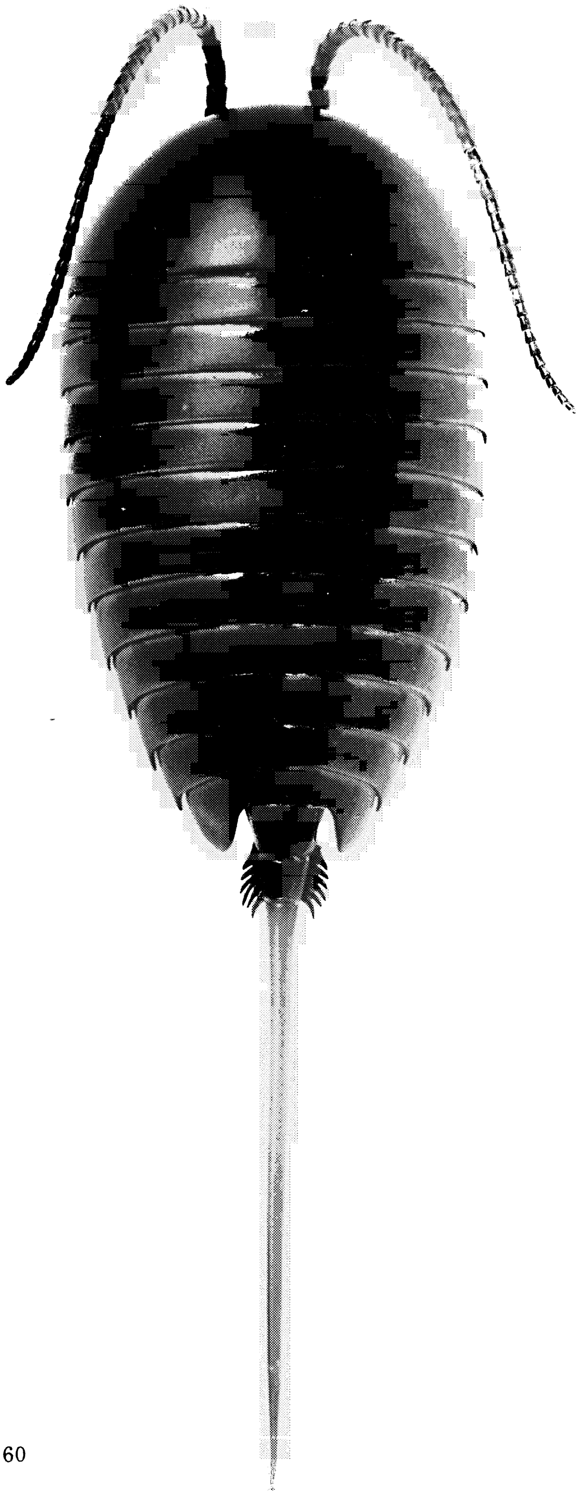

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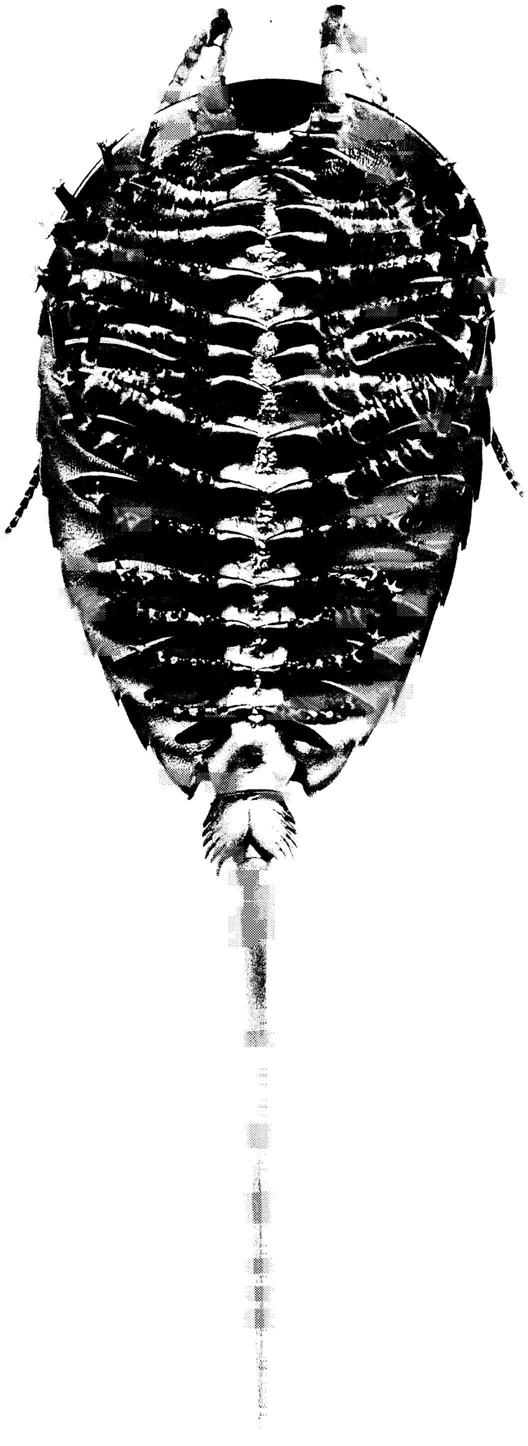

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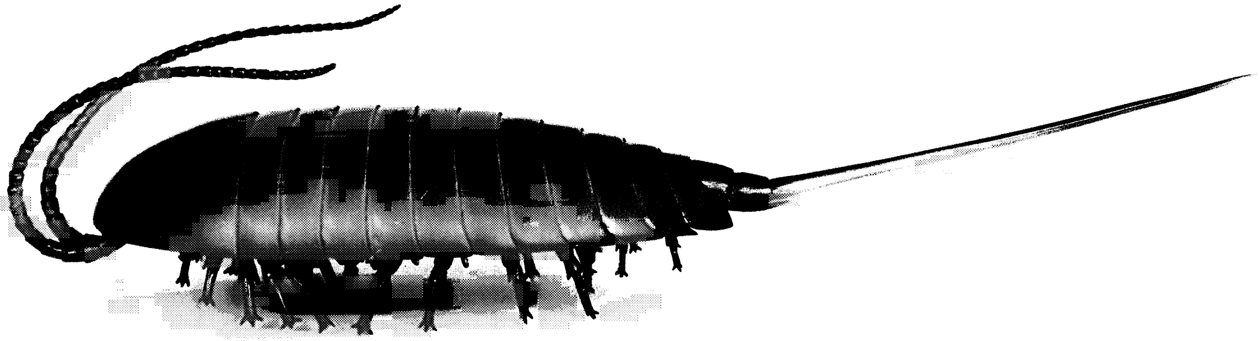

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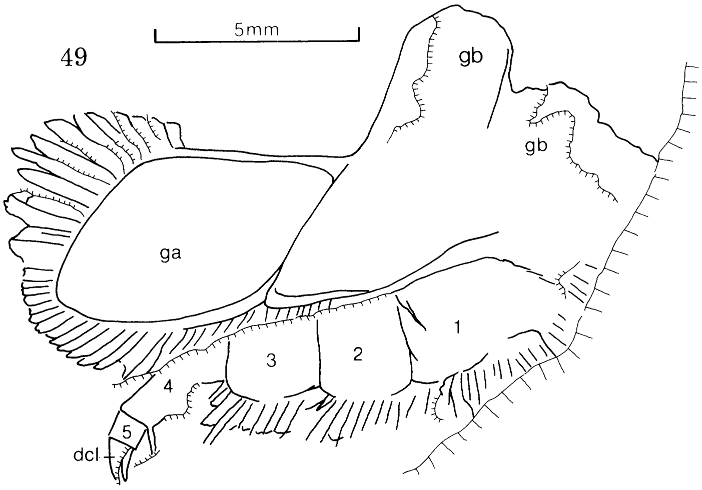

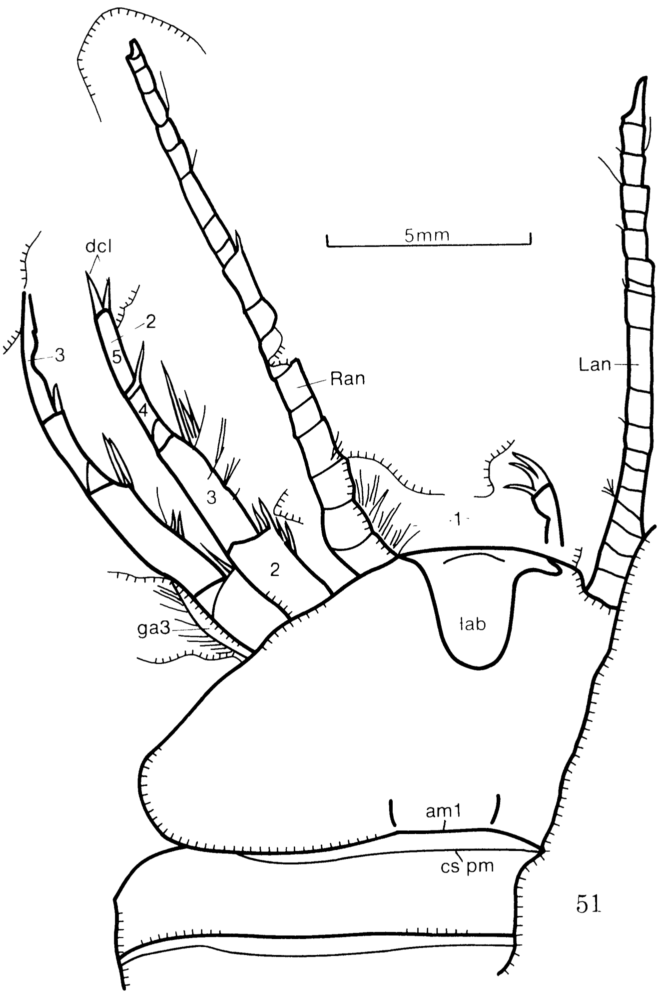

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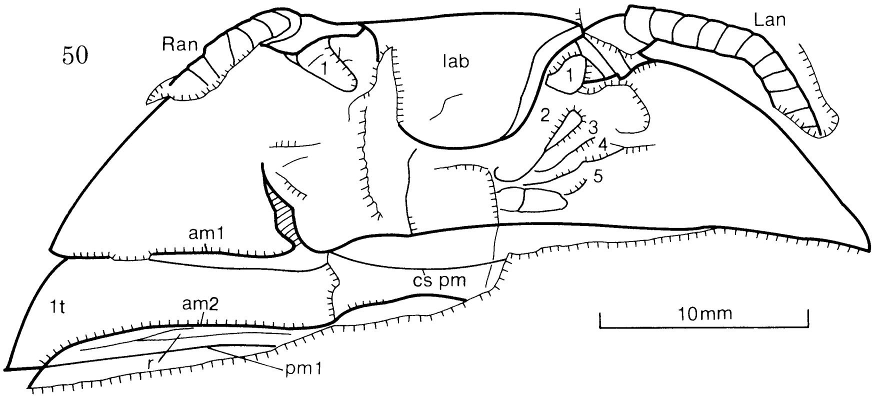

Description of plate 8 and figures 49–51

Emeraldella brocki Walcott, 1912.

Figures 43 and 44. U.S.N.M. 155636, isolated, incomplete trunk limb, counterparts: (43) northeast; (44) north. (Magn. × 5.)

Figures 45 and 47. U.S.N.M. 250228, distal portions of outer lobes ga and gb of trunk limb: (45) south (magn. × 5); (47) reflected (magn. × 10).

Figure 46. U.S.N.M. 144920, parallel, counterpart, northwest. (Magn. × 3.)

Figure 48. U.S.N.M. 144933, parallel, counterpart only, northwest. (Magn. × 3.2.) See also figure 32, plate 6.

Figures 49–51. Explanatory drawings of U.S.N.M. 155636 (composite), 144920 and 144933 respectively.

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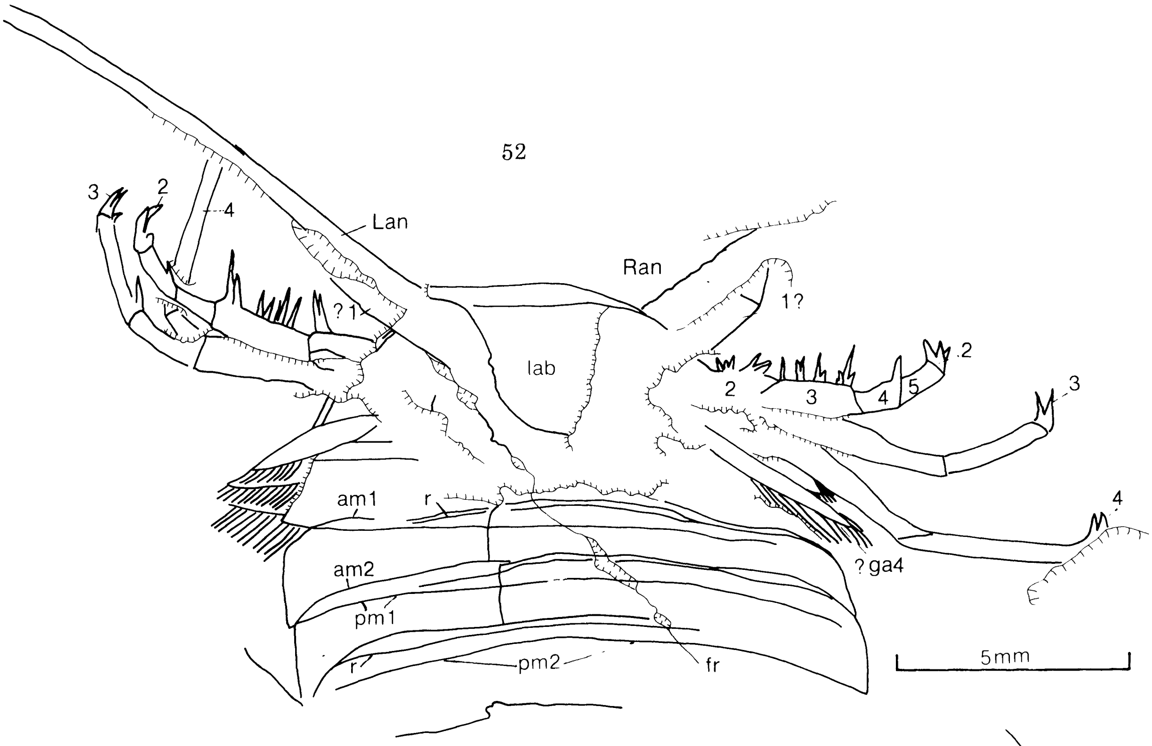

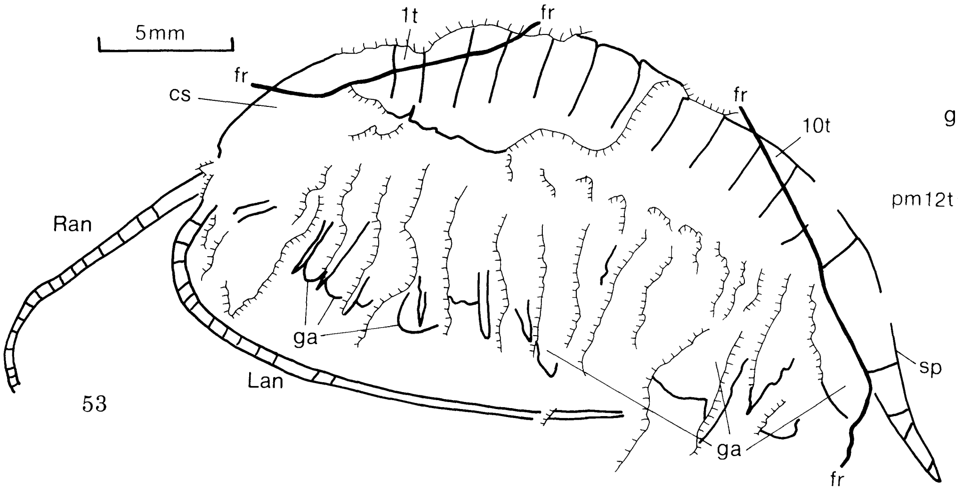

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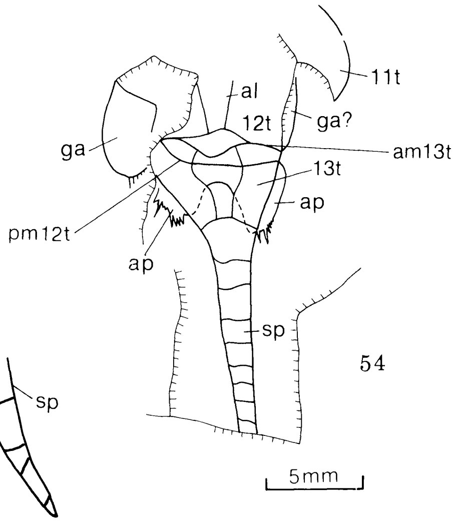

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DESCRIPTION OF FIGURES 52–54 AND PLATE 9

Emeraldella brocki Walcott, 1912.

FIGURES 52–54. Explanatory drawings of U.S.N.M. 57488 (composite), 144925 (composite) and 250227 respectively.

FIGURES 55–56. U.S.N.M. 57488, parallel, part: (55) northwest (magn. × 6.7); (56) reflected (magn. × 6).

FIGURES 57 AND 59. U.S.N.M. 144925, holotype of '*Emeraldoides problematicus*', lateral; (57) counterpart reflected; (59) part, west, ordinary light. (Magn. × 3.5.)

FIGURE 58. U.S.N.M. 250227, parallel, part, posterior portion of exoskeleton, under alcohol. (Magn. × 4.)

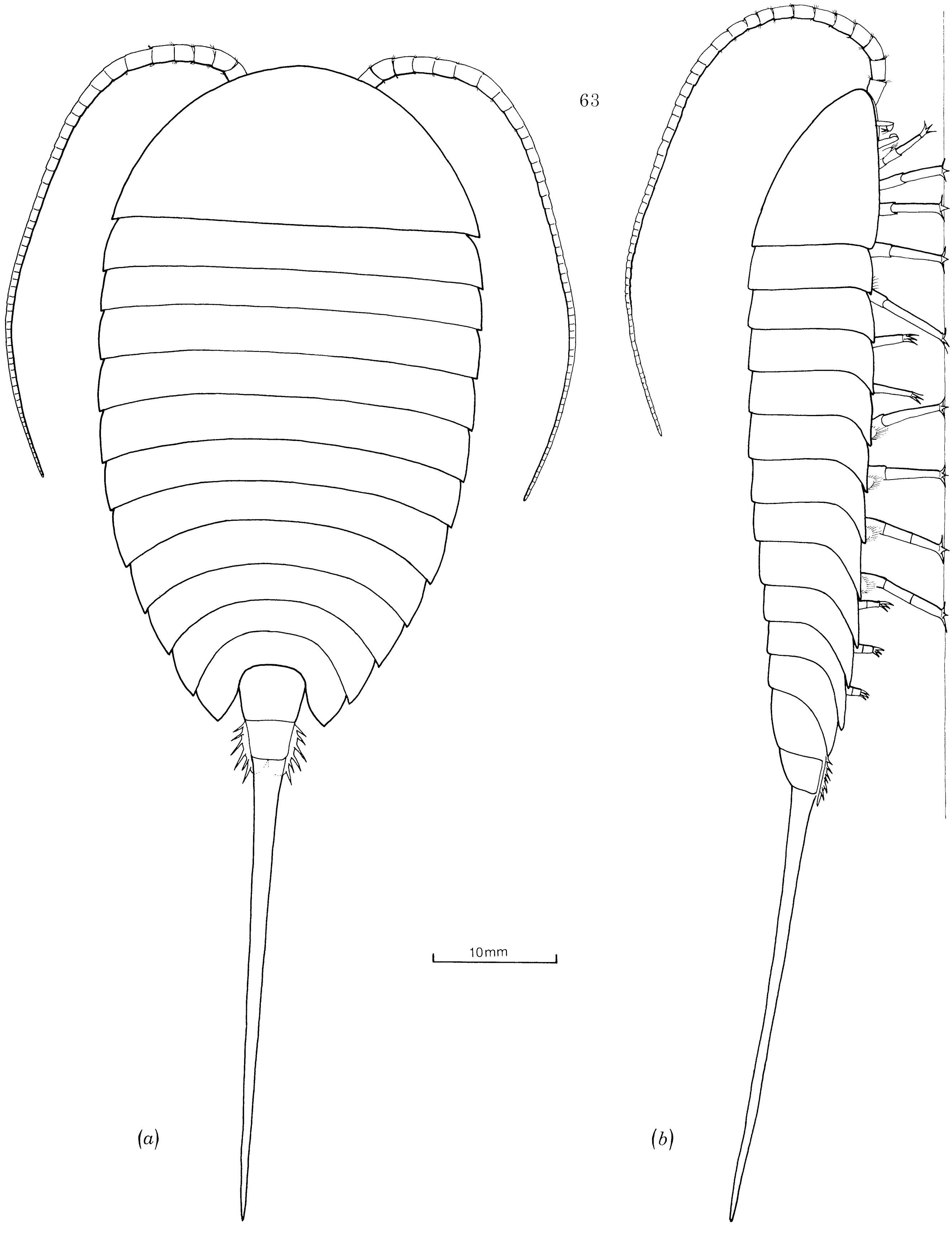

FIGURE 63. Reconstruction of *Emeraldella brocki*; dorsal (*a*), right lateral (*b*) views; limbs in 'still' position of gait discussed in text.

DESCRIPTION OF PLATE 10

FIGURES 60–62. Model of *Emeraldella brocki*; respectively dorsal, ventral, left lateral views; limbs in 'still' position of gait, approximately twice natural size.

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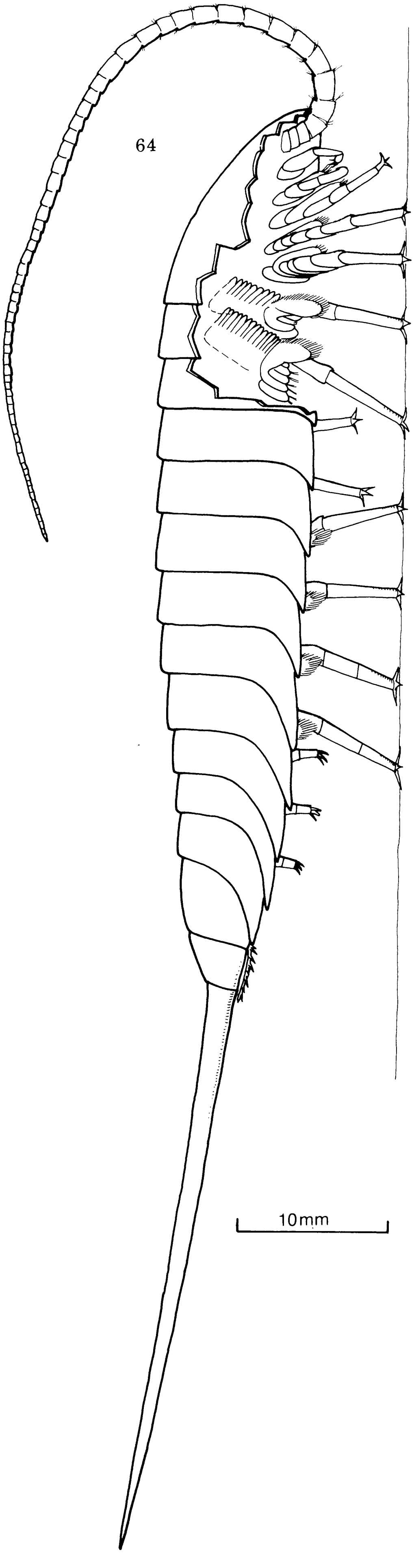

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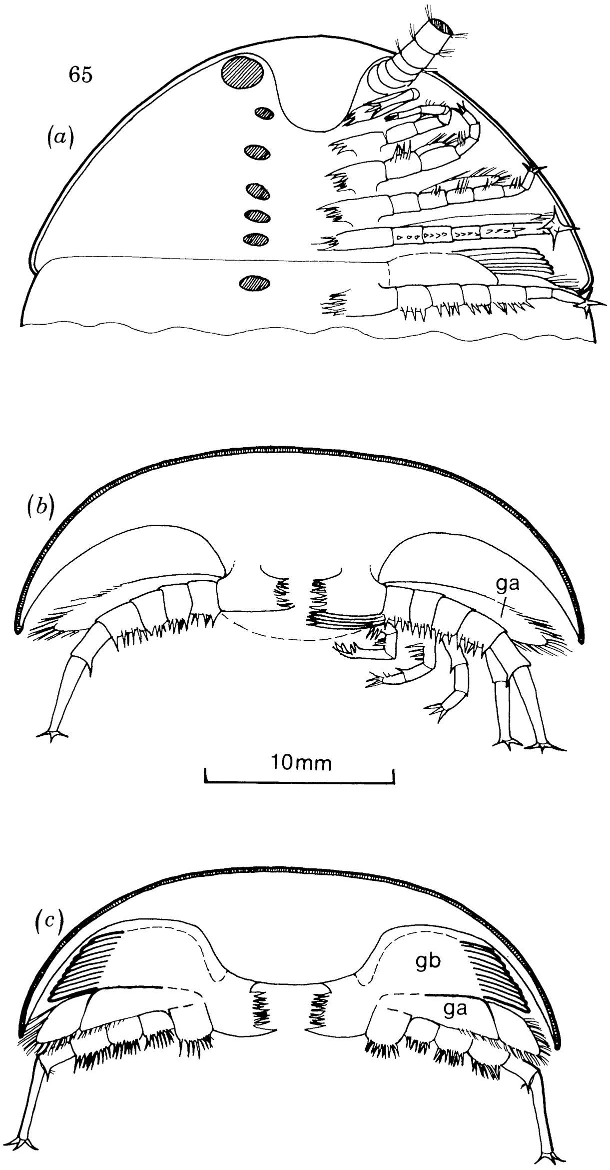


FIGURE 64. Reconstruction of *Emeraldella brocki*; right lateral view of figure 63*b*; portions of cephalic shield and first two trunk tergites cut away to show proximal portions of limbs and possible attitudes of gill lobes.

FIGURE 65. Reconstruction of *Emeraldella brocki*. (*a*) Ventral view of cephalon and first trunk tergite, showing left limbs and (shaded) attachment areas of right limbs. (*b*) Transverse section through posterior edge of cephalon showing fifth pair of biramous limbs (ga is gill branch) in posterior view; on right, coxae and leg branches 1–4 are shown. Dashed line indicates level of labrum. (*c*) Transverse section through posterior edge of sixth trunk tergite, showing limbs in posterior view. Uncertainties in knowledge of the outline of the two lobes (ga and gb) of the outer branch, and of their attachment are indicated by dashed lines (see §5(*c*)).

plate 4). The median posterior notch in the plate may be traced in 250227 (figure 58, plate 9); the margins of the plate are clear in 144928 (figure 40, plate 7), but the apparently triangular outline is a result of fracturing, so that there is a change in level between the two sides. We suggest (figures 60, 61) that this plate was attached on the ventral side of the 12th somite, was bilobed and extended back on either side of the anal opening. The posterior spine was similar in length (sag.) to the thorax (figures 2, 3, plate 1); in 250227 (figure 58, plate 9) the spine appears to be segmented. Such segmentation is visible also in 144917 but not in other specimens (figures 2, 3, plate 1; figure 37, plate 7) in which the spine is straight or only very slightly curved and apparently had limited flexibility. These observations are like those on *Molaria spinifera* (Whittington 1981, p. 338), but the evidence for segmentation and flexure is greater in that species.

The external surface of the exoskeleton was smooth, and there is no evidence of an eye lobe on the cephalic shield (see, for example: figures 17, 20, plate 4; figure 23, plate 5; figure 32, plate 6). There does not appear to have been a raised, longitudinal axial region of the cephalic shield or thorax, the appearance of such a region (figures 2, 3, plate 1; figures 23, 27, plate 5) being caused by infilling of the gut. Overlap between successive thoracic tergites, and between the first tergite and the cephalic shield, was almost half the length (sag.) of the tergite (figure 23, plate 5; figures 55, 56, plate 9), the overlap either being reflective or appearing as a dark band in low angle illumination. The anterior margin of the tergite is curved outward and backward to emerge from beneath the posterior margin of the preceding segment close to the lateral extremity. The anterior portion of each tergite thus forms an articulating flange and shows a narrow ridge, parallel and close to the anterior edge of the flange, which dies out distally. In ventral view (figure 20, plate 4; figure 48, plate 8) the broken edges of successive articulating flanges are visible laterally. The thoracic tergites were thus similar to those of *Molaria spinifera* (Whittington 1981, p. 337), the lateral doublure in *E. brocki* being represented by an extremely narrow, dark, reflective band (figure 32, plate 6). A narrow doublure was also present on the lateral and anterior margins of the cephalic shield, from which the shield-shaped labrum extended back (figures 17, 20, plate 4; figures 46, 48, plate 8; figures 55, 56, plate 9) to about half the length (sag.) of the shield. The labrum also had a narrow border.

Appendages of the cephalon and thorax are preserved in all the specimens, projecting beyond the margins of the exoskeleton, and revealed beneath it either by the level of the split or by preparation. The series consists of one pair of antennae and 16 pairs of limbs, all but the first pair biramous; the five pairs following the antennae were cephalic. If these cephalic limbs are incompletely revealed, but the trunk series are all visible, the limbs have been numbered forward from the hindmost in the explanatory diagrams. This procedure reveals that in an oblique specimen (figures 2–4, plate 1), or one in which the cephalon was flexed down at burial (figures 12, 13, plate 3), there was some backward displacement of the limbs during burial and compaction, but in some dorsoventral compressions (figures 17–20, plate 4; figure 23, plate 5) there appears to have been little such displacement. The entire series of limbs, or all those visible, have either been swung so that the anterior surface faces dorsally, imbricated to slope below the one in front (figures 5, 6, plate 2; figure 23, plate 5; figures 28, 29, plate 6), or the reverse (figures 12–16, plate 3; figures 30, 31, plate 6; figure 37, plate 7); in one specimen (figure 17, plate 4) limbs 1–6 are in the former position, posterior limbs in the latter. The regularity of these arrangements is occasionally interrupted, as in left limbs 1–5 in 136442 (figure 23, plate 5), or in the cephalic limbs of 57488 (figures 55, 56, plate 9). In a lateral (figures 7, 8, plate 2) and an oblique (figures 2, 3, plate 1) specimen, each biramous limb in a left or right series passes below the one in front, suggesting that each pair may have been directed outward and slightly backward. The long antenna, having over 110 annulations in an almost complete example (figure 29, plate 6), was evidently highly flexible. It was inserted into the ventral wall of the cephalon so that it emerged beside the incurved anterolateral margin of the labrum. Broadest proximally, it tapered progressively, the annulations becoming shorter as they narrowed. Groups of bristles (figure 6, plate 2) emerged from the junctions between the annulations on one side, and if the antenna was rotated in conformity with the limbs, the bristles were on the ventral side. Behind the antennae there were five additional pairs of limbs on the cephalon; the distal podomeres of the leg branches are well shown in figures 5 and 6, plate 2, figure 29, plate 6, and figures 55 and 56, plate 9. Only in 144928 (figures 37, 42, plate 7) has the second cephalic limb been exposed more or less complete, although the coxa is not clearly outlined on the right side, and largely hidden on the left. However, the opposed gnathobases are revealed, showing a large spine at the inner, ventral angle. This second leg branch consisted of five podomeres, and a comparable number is present in other specimens. The second and third podomeres are heavily spinose on the ventral side, a distal spine evident on the fourth and fifth podomeres. The first leg branch (figures 5, 6, plate 2) is considerably shorter than the second, having a short distal podomere into which four long claws are inserted, the next two podomeres having many long, close-spaced ventral spines. We infer that this branch consisted of three podomeres. Leg branches 3–5, similar in length, are longer than 2; the distal podomere is elongate. The number of podomeres is not clearly shown, but may have been six in branches 4 and 5, as in the adjacent leg branches of the trunk. Three long, curved spines are inserted into the distal podomere to form a foot. The counterpart of 144920 (figure 46, plate 8) shows the proximal portions of the antennae emerging beside the labrum and impressions of the most proximal portions of the limbs. The arrangement of these limbs appears radial, as it does also in 136441 (figures 17–20, plate 4). No specimen shows an outer branch of the first cephalic limb, but a small such branch is present on the second limb in 144928 (figure 42, plate 7), and is evident lying on the anterior face of limbs 3–5 of 144924, (figures 5, 6, plate 2). This branch appears relatively narrow, it is boat-shaped at the pointed tip, the edges are thickened, and it bears long filaments on the lateral and distal margins. It was attached proximally, but whether to the coxa or to the first podomere is not shown.

The biramous limbs 6–16, on the first 11 somites of the trunk, are all visible on the right side of 144934 (figures 30, 31, plate 6), though in this small specimen details are obscure. The spines of the gnathobases lie along each side of the trace of the alimentary canal, as they do in 144928 (figures 37, 39, 41, plate 7). In neither specimen are the coxae clearly outlined, but they appear to be subrectangular in outline in posterior aspect at the beginning of the series, changing gradually backward to a subsquare outline. The mesial and ventromesial margins bore the overlapping spines that formed the gnathobase, including a large spine at the ventromesial corner; gnathobases were present on the posterior coxae. In the anterior five or six somites of the trunk, i.e. limbs 6–11, the number of podomeres in the leg branch appears to have been six, to judge by 144934 and the leg branches excavated in 136440 (figures 14–16, plate 3). The distal podomere was long, as in the last two or three cephalic limbs. Behind this level the length of the leg branch diminished progressively by shortening of the podomeres, especially of the long sixth podomere of leg branches 6–11. The posterior few leg branches (figures 30, 31, plate 6; figures 37, 38, 40, plate 7) may have consisted of only five podomeres. Inserted into the distal podomere were three relatively long, curved spines and a shorter fourth spine, which formed the foot. To judge by the stepped ventral outline in anterior or posterior view, joints between podomeres 3–6 were hinge joints, with a spine at the distal, ventral margin of each podomere. Possibly the coxa–leg branch joint and the joint between leg branch podomeres 1 and 2 were pivot joints; the joint between podomeres 2 and 3 possibly was a hinge. The profiles of midtrunk leg branches (figures 14–16, plate 3; figures 23, 25, 26, plate 5) shows that podomeres 1–3 were deep, elongate–oval in cross section and armoured on the ventral side by a group of spines; the distal podomeres were narrower and subcircular in cross section. The distal portions of a series of elongate–oval outer branches of the trunk limbs, pointed or rounded, the margins bearing filaments, is evident in most specimens. In 57702 (figures 2–4, plate 1) they lie outside the leg branch, each sloping inward and forward so that the anterior edge lies against the most proximal portion of the leg branch. Filaments are not visible in this specimen. In dorsoventral compressions (figures 15, 16, plate 3; figure 17, plate 4), in which the posterior surface of the leg branch faces dorsally, they lie on the posterior surface of the branch, each sloping downward and backward below the one following (like the leg branch). An opposite orientation is shown by midtrunk limbs of 136442 (figures 23, 26, plate 5), but the outer branch lies partly upon the anterior face of the leg branch. In either orientation the outer and leg branches are most widely separated from one another distally, by a layer of rock which diminishes in thickness proximally, so that the two branches merge and lie at the same level at the base of the limb. The margins of the outer branches are thickened, the lamellae overlapping, blade-shaped, longer laterally than at the tip (figure 47, plate 8). A distinct division runs diagonally upward and inward across the boat-shaped outer branch, commencing at about the midlength (tr.) at a slight emargination of the ventral edge (figures 23, 25, plate 5). The inner portion of the gill lobe of right limb 9, and left limbs 10 and 13 of 136440 (figures 15, 16, plate 3), appears to merge into podomere 1 of the leg branch. In right limb 9 of this specimen, a fold or break separates the coxa from podomere 1, and dorsal of the coxa is a large, smooth area labelled gb 9, separated by the fold or break from the proximal portion of lobe ga. Similar smooth areas, labelled gb 6–8, lie beneath tergites 1–3 of the trunk. On the left side are similar smooth areas, in the same relation to coxae 9, 10 and 13 and also separated by a line or change in level from the proximal portions of lobes ga. A series of similar smooth areas are visible adjacent to the axial region, on the left side of 136442 (figures 23, 25–27, plate 5). No break separates proximally lobes ga and gb in the hindmost of these limbs. In 136441 (figures 17–20, plate 4) corresponding smooth areas are seen on the right side, below trunk tergites 4–6. This same specimen shows an additional feature, imbricated layers of outwardly directed filaments, labelled bfil (figure 21), lying between the exoskeleton and the imbricated tips of the series of lobes labelled ga 7–10. We interpret these filaments as arising from the outer edge of the smooth areas (labelled gb in the drawings). This interpretation is supported by the isolated fragment (figures 45, 47, plate 8), which shows the gill branch with its blade-like marginal lamellae, the dividing line between inner and outer portion, and this dividing line continued dorsally as the outer margin of lobe b, from which flat filaments arise which have a rounded tip and hairs along the margins. A second isolated specimen (figures 43, 44, plate 8) shows part of a leg branch and gill lobe, and dorsal to it a broken portion of lobe gb; there appears to be no clear boundary or change in level between the proximal portions of lobes ga and gb. Since lobe gb extends so far adaxially (figures 12–16, plate 3; figures 23, 26, plate 5) we conclude that it must have been attached to the dorsal side of the coxa, outside the coxa–body junction (figure 65*c*), and these specimens indicate this probability. In 136440 (plate 3) the proximal portions of the lobes ga and gb in limbs L9, L10 and R9 are separated by a fold or slight change in level. In a left trunk limb of 136442 (figures 23, 25, 26, plate 5) and in the isolated fragment 155636 (figures 43, 44, plate 8) no such separation is apparent; the proximal portions merge into one another. The most proximal portion of lobe ga lies adjacent to leg branch podomere 1, and in 136440, 136442 is not separated from it. It may be that lobes ga and gb were parts of a single structure and were attached both to the first podomere of the leg branch and to the coxa or perhaps only to the coxa. It is possible that lobes ga and gb were separate structures, arising from the first podomere and coxa respectively, but the specimens are equivocal on this matter. Accordingly the reconstruction (figure 65*c*) shows only a partial division between lobes ga and gb, and suggests that lobe ga may have arisen from the base of the leg branch and lobe gb from the coxa. In the cephalon (figure 65*a*, *b*), how, and exactly where, lobe ga was attached is not made clear. The exact outline of lobe gb is uncertain, but it was apparently large, and lay beneath the pleural region. It is preserved imbricated with, and facing in the same way as, the gill lobe, leg branch and coxa. The regularity of this imbrication indicates that the entire limb swung as a single unit, about the coxa–body junction, the junction between the two branches being rigid. The outer branch is thus restored (figures 64, 65*c*) as lying in the same plane as the leg branch and coxa, extending dorsad. Thus in the cross section of a trunk somite the pleural region of the body has to be portrayed as thin and the proximal portion of the leg branch as directed downward and outward (i.e. not a hanging stance (Manton 1977, p. 200)) in order to accommodate lobe gb. The alternative would have been to incline or curve the outer branch forward or backward, in which case a more hanging stance of the walking legs may have been possible. Preservation of the few relevant specimens offers little clue to the attitude in life of the outer branch, i.e. whether it was inclined at an angle to the leg branch. The outer portions of lobes ga do show a variation in outline, being rounded in midtrunk limbs (figures 15, 16, plate 3; figures 23, 25, 26, plate 5), whereas they are more pointed and boat-shaped in these limbs and the more anterior limbs in other examples (figures 17, 20, plate 4; figures 37, 38, plate 7; figures 55, 56, plate 9). This boat shape may be the result of compaction of a rounded lobe lying at an oblique angle in the rock. The attitude and position (in front of the cephalic limbs, behind the trunk limbs) of the outer branches shown in figures 64 and 65 is a reflection of our uncertainties. There is no evidence of the presence of lobe gb in the outer branch of the cephalic limbs.

The dark band that runs along the trunk and into the base of the posterior spine in 136440 (figure 12, plate 3) is the trace of the alimentary canal. A similar band in 57702 (figures 2–4, plate 1) is broadest in the cephalon, is slightly raised, is reflective, and has dark patches adhering to it. In 136442 (figures 23, 26, 27, plate 5) the band is gently convex, most so anteriorly, and in the cephalon shows two pairs of irregularly infilled, anterior lobes. Nodular patches of comminuted fragments extended halfway along the tract in a poorly preserved, oblique specimen (144918), and may be present posteriorly (figure 24, plate 5). The most anterior portion of the alimentary canal may have been U-shaped, leading forward and upward from the backward-facing mouth. In the oblique compression 57702, what appears to be the trace of this anterior portion, traversed by darker lines, is barely visible.

(*c*) *Discussion*

Walcott's (1912) original brief description is contradictory, in that he stated that there were ten (p. 203) or eleven (p. 158) thoracic segments and that the eye was unknown though it is mentioned in the legend (p. 220) but not indicated on the figure. Walcott (p. 203, fig. 8) considered that a short antennule was visible in the counterpart of 136439, but the specimen offers no evidence for this claim. His view (p. 203) that the 'abdomen' (the posterior cylindrical segments of the trunk) included three somites appears incorrect. Raymond (1920) saw no eyes, and stated that the cephalon bore the antennae and four additional pairs of limbs. Størmer (1939, 1944, *in* Grassé 1949, *in* Moore 1959) followed this lead, and gave a reconstruction. Both these authors considered the appendages 'trilobitic', presumably because the leg branch, and the tip of what is here called the gill lobe, were visible outside the exoskeleton. Simonetta's (1964) description was based on two (unspecified) of Walcott's originals and U.S.N.M. 136440, 136441, 144917–144934. He makes no mention of either 57488 (which Walcott first attributed to *Sidneyia inexpectans*) or 136442. The description is brief and the photographs are of poor quality and offer vague support to a sketchy reconstruction. In 1975 Simonetta & Delle Cave reproduced the same photographs, and others, so that all Walcott's originals and the additional specimens were illustrated, albeit poorly. In § 5 (*a*) we exclude 144931, as too fragmentary to be identifiable. The number 144925 (that of the type of '*Emeraldoides problematicus*') was also applied by Simonetta & Delle Cave (1975, pl. xxvii, fig. 1) to a different specimen, here numbered U.S.N.M. 250230 and referred to *E. brocki*. In 1975 (pl. xxvii, fig. 5) Simonetta & Delle Cave attributed an additional specimen to *E. brocki*; it belongs to an undescribed taxon, and is now re-numbered U.S.N.M. 274195. Simonetta (*in* Simonetta & Delle Cave 1975, p. 19, pl. 2, fig. 1 *d*) modified a cross section of the thorax of *E. brocki* from that originally given by him (1964, fig. 5, upper left), based on his acceptance of Bruton's recognition (*in* Hessler & Newman 1975, p. 457) that the isolated limb 155636 (figures 43, 44, plate 8) was that of *E. brocki*. This specimen has been prepared to show the leg branch more clearly, which may have included only five podomeres and so have belonged to the posterior portion of the thorax. The dorsomesial edge of lobe gb is ragged and incomplete, and the upwardly directed abaxial edge appears folded over, to give an irregular, slightly darker band. Because this lobe is incomplete we cannot accept Simonetta's restoration of it as an upwardly projecting, subparallel-sided flap, with lamellae on the upper edge. There appears to be no justification for this outline, or for the dorsal lamellae, but the outer margin (figures 45, 47, plate 8), broken in 155636, bore broad lamellae. As described in § 5 (*b*), uncertainties remain regarding the outer branch of the trunk limb, epitomized in the cross section, figure 65*c*. It cannot be stated unequivocally (Hessler & Newman 1975, p. 457) that the trunk limb is 'triramous', because we cannot be sure that lobes ga and gb were separate structures, independently attached to the limb; they may have been portions of a bilobed structure. Exactly where the lobe or lobes were attached is obscure, as is the exact outline of lobe gb. There is no evidence of lobe gb on the cephalic limbs. We conclude that the outer branch of the limb in *Emeraldella* may have been a single structure, bilobed only in trunk limbs, attached to the coxa and perhaps also to the first podomere of the leg branch. The attitude of the large lobe gb in life is also problematical. We portray it as upwardly directed (figures 64, 65*c*), but acknowledge that it may have been curved beneath the pleural region of the trunk.

In his reconstruction Simonetta (1964, fig. 4, and subsequent publications) misrepresented the form of the trunk tergites, did not distinguish the two cylindrical somites 12 and 13, and regarded the posterior spine as the telson. He represented the ventral plate as a pair of plates attached at the base of the posterior spine. This plate may have been a single bilobed structure and was attached farther forward, probably to somite 12. We have obtained much new information on the appendages, particularly on the coxa and gnathobase, so that Simonetta's restorations (1964, fig. 5, and subsequent publications) are emended here. This author did refer to (unspecified) differences in shape of the body, questioning whether these might be of systematic value, an effect of preservation, or evidence of sexual dimorphism. Measurements of dorsoventral compressions suggest a large but continuous range in the ratio of maximum width to length (sag.) of cephalon and thorax, and it is doubtful that 'broad' and 'narrow' forms can be distinguished. The length (sag.) of the body, excluding the posterior spine, ranges from about 12 mm (figures 28, 29, plate 6) to 60 mm (figures 12, 13, plate 3), overlapping that of *Molaria spinifera* (Whittington 1981, fig. 1) and extending to more than twice the maximum known size of that species. The smallest specimen of *E. brocki* exhibits the characteristic appendages, so that this species is quite distinct from any other in the Burgess Shale.

Walcott (1912, p. 205, fig. 9) described a second species, *Emeraldella micrura*, founded on a poorly preserved specimen from the Raymond quarry, some 70 ft above the Phyllopod Bed. This specimen is referred (§6(*f*)) to *Leanchoilia superlata*.

The genus *Emeraldoides*, type species *E. problematicus*, was based by Simonetta (1964, pp. 227–228, fig. 6, pl. xliii, upper two figures; Simonetta & Delle Cave 1975, pp. 21, 27, 32, pl. iii, fig. 4; pl. xxiii, figs 1*a*, 1*b*) on a lateral compression (figures 57, 59, plate 9). The part is bounded dorsoposteriorly by a break, the counterpart is also broken anterodorsally. The dorsal outline of the exoskeleton of figure 53 (in which the breaks are shown by a thick line labelled fr) is thus a composite, the margin of the cephalic shield derived from the part, the posterior tergites and spine from the counterpart. The long, multisegmented antenna is well preserved, but other appendages are represented only by irregularly outlined, darker areas that are reflective. The specimen is like 144930 (figures 7, 8, plate 2) in curvature and dorsal outline of the exoskeleton, and in form and size of the appendages, but in 144930 the curved tips of trunk tergites 6–10 are preserved, as are the characteristic long, distal podomeres of walking legs. Neither of these features is visible in 144925, but the form of the exoskeleton, combined with the long antenna, appears diagnostic for *E. brocki*. Presumably the other appendages in 144925 are of the right side, each imbricated to slope inside the one in front, and while the rounded tips of some of the anterior gill lobes are preserved, the walking legs are not conspicuous, as was the case in 57702 (figures 2–4, plate 1), particularly before preparation. Thus it appears that 144925 is a moderately well preserved, perhaps slightly oblique, lateral compression of *E. brocki*, and not an example of a distinct species. The eye lobe, the trunk tergites, and the distinctive appendages reconstructed by Simonetta (1964, fig. 6), cannot be substantiated, and the supposed 'pygidium' is presumably a misinterpretation of the last appendage preserved beside the fractured edge in the part.

(*d*) *Functional morphology*

The 24 partially or almost complete specimens of *Emeraldella brocki* all have appendages, not greatly displaced, and, based on the arguments deployed for *Molaria spinifera* (Whittington 1981, p. 341), *E. brocki* was probably a benthonic animal. No specimen of *E. brocki* shows the amount of dorsoventral flexure evidenced by those of *M. spinifera* (Whittington 1981, figs 50, 51, pl. 5; fig. 54, pl. 6), nor was the posterior spine strongly curved, but straight. Flexure in the horizontal plane (figures 12, 13, plate 3; figure 17, plate 4; figures 28, 29, plate 6) appears to have been limited, and to have taken place only between posterior trunk tergites. Presumably a flexible membrane extended between successive tergites, from the posterior margin forward towards the anterior margin of the succeeding tergite; perhaps the ridge near this margin served as a line of attachment. The ridge may also, or alternatively, have been a site for attachment of longitudinal and diagonal muscles that effected movements between tergites. In form, and in the position and extent of the articulating ridge, the tergites of *E. brocki* resemble those of *Aglaspis spinifer* (Briggs *et al.* 1979).

The long leg branches of the last two cephalic somites, and the first six or seven of the trunk, in *E. brocki* may have been used mainly in walking (figure 63*b*), the more posterior branches being progressively shorter. The spinose inner podomeres of the leg branches (figure 65) could have been used when the branch was flexed to grasp soft food, the terminal claws to push it into the midline, and the armature of gnathobases to shred the food and push it forward along the midline to the mouth, situated at the hind margin of the labrum. Detailed arguments for the attitude and activities of the limbs were developed for the trilobite *Olenoides* (Whittington 1980*a*), and seem also to be applicable to the present animal as well as to *Molaria spinifera* (Whittington 1981, pp. 341–342). The anterior cephalic limbs in *E. brocki* appear well adapted to assist in conveying food to the mouth. Possibly the animal could tilt the cephalon down and plough in the sediment in search of food, and the posterior portion of the body, and the long posterior spine, could have been flexed upward to maintain balance. The gill branches, including the large lobe gb of the trunk limbs, presumably were primarily for respiration. The division on the boat-shaped lobe ga may imply that the distal section could be flexed at the division, to create water currents when moved in a metachronal rhythm, or even to aid in swimming. It may have been that the animal launched itself off the bottom by swinging a few successive limbs back in a wave, and swam by metachronal movements of the limbs. *E. brocki* was a benthonic predator and scavenger, seeking its food in the muddy bottom, seemingly able to capture and tear up small soft-bodied animals as well as attack carcasses.

(*e*) *Affinities*

Walcott (1912) regarded *Emeraldella* as most closely related to *Molaria* and *Habelia*, and allied these genera with *Sidneyia* and aglaspidids. He considered this group to have been derived from trilobites, and to have given rise to eurypterids. Established by Walcott's authority, these views have persisted, but they were based on two serious errors. First was the attribution to *Sidneyia* of certain isolated appendages (Walcott 1911, pl. 4, figs 1–4), and secondly the identification of appendage-bearing specimens of *Emeraldella brocki* (Walcott 1911, pl. 2, figs 2, 3; Walcott 1912, text-fig. 10) as *Sidneyia inexpectans*. This second error was corrected by Walcott (1918), but the first has only recently been recognized (Bruton 1981; see also Briggs 1979, pp. 653–654) and corrected. Simonetta (*in* Simonetta & Delle Cave 1975, pp. 19–20; 1981, pp. 424–425) has not accepted this correction. So radically has this recent work revised knowledge of morphology of these genera, that earlier views on relationships cannot be examined profitably in any detail. Except for Fedotov (1925), who considered that *Emeraldella* was a malacostracan, authors including Raymond (1920), Henriksen (1928) and Størmer (1944, *in* Moore 1959) have based their assessment of relationships of this genus on the aglaspidid-like form of the exoskeleton and supposed trilobite-like appendages. *Sidneyia* has been associated more or less closely with *Emeraldella* as 'merostomoid', a view that Simonetta (1964) first accepted, but later (*in* Simonetta & Delle Cave 1975, pp. 28, 30–33; 1981, pp. 424–425, 427–429) rejected. The reasons given for this rejection can no longer be considered valid, but we accept the conclusion.

The present work shows that the exoskeleton of *Emeraldella* is broadly like that of *Molaria spinifera* (Whittington 1981, fig. 73), differing in having 11 rather than eight trunk tergites with pleurae, two cylindrical somites following rather than one, a ventral plate rather than a spine, and a sclerotized labrum. The appendages of *M. spinifera* are trilobite-like in a general way, in that the antennae are followed by a series of biramous appendages, alike on cephalon and trunk, the outer branch arising from the base of the limb. The form of the limb differs from those known of trilobites, but in the small individuals of *M. spinifera* details of the limbs are obscure. Specimens of *E. brocki* reach twice the size of those of *M. spinifera*, and in some appendages are well preserved. The antenna is longer and more prominent than in *M. spinifera*; the biramous limbs of cephalon and trunk are differentiated, both for walking and in the size and form of the outer branch; the outer branch is quite distinct in structure and attachment. In *E. brocki* gnathobases are prominent along the length of the body. The differences imply that *Emeraldella* and *Molaria* should be separated at the family if not at a higher level, and neither shows a close resemblance to *Habelia* (Whittington 1981). It remains an open question whether the exoskeletal similarities should be taken to imply a relationship of *Emeraldella* and *Molaria* to aglaspidids, because appendages of the latter group are poorly known (Briggs *et al.* 1979), though it appears that the anterior appendage was not chelate. If such a relationship is assumed, we regard it as doubtful that there is any relationship to merostomes, i.e. to xiphosurids or eurypterids. Recent studies on the functional morphology of eurypterids (Waterston 1979; Selden 1981) do not suggest any relationship to aglaspidids, and on other grounds Selden has questioned the naturalness of the group Merostomata. Thus, while *Emeraldella* and *Molaria* may be related to each other and possibly to *Aglaspis*-like forms, they cannot be grouped with *Sidneyia* and are quite unlike eurypterids.

6. *LEANCHOILIA SUPERLATA* WALCOTT, 1912

(Figures 66–113, including plates 11–18.)

1912 *Leanchoilia superlata* sp.nov. Walcott, p. 170, pl. 31, fig. 6.
1912 *Bidentia difficilis* sp.nov. Walcott, p. 174, pl. 30, fig. 1.
1912 *Emeraldella micrura* sp.nov. Walcott, p. 205, fig. 9.
1928 *Leanchoilia superlata*; Henriksen, p. 7.
1931 *Leanchoilia superlata*; Walcott, p. 8, pl. 12, figs 1–3; pl. 13, fig. 2; *non* fig. 1 = *Olenoides serratus* (see Størmer 1939, p. 199); pl. 14, fig. 5; *non* fig. 4 = *Sidneyia inexpectans*.
1931 *Leanchoilia major* sp.nov. Walcott, p. 9, pl. 13, fig. 3.
1935 *Leanchoilia superlata*; Raymond.
1939 *Leanchoilia superlata*; Størmer, p. 235, pl. 12, fig. 3.
1944 *Leanchoilia superlata*; Størmer, p. 18, figs 16, 17 (1, 2).
1949 *Leanchoilia superlata*; Størmer *in* Grassé, p. 200, fig. 26, p. 208, figs 1, 2.
1953 *Leanchoilia superlata*; Dechaseaux *in* Piveteau, p. 33, figs 7*a*, 8.
1953 *Bidentia* (= *Leanchoilia*?) *difficilis*; Dechaseaux *in* Piveteau, p. 33, fig. 7*b*.s
1959 *Leanchoilia superlata*; Størmer *in* Moore, p. *O*32, fig. 20.
1966 *Leanchoilia superlata*; Sharov, p. 34, fig. 19, D, E.

1970 *Leanchoilia superlata*; Simonetta, p. 36, pl. i, figs 1–8; pl. ii, figs 1*a*, *b*, *non* fig. 1*c* = *Emeraldella brocki*; pl. iii, figs 1–2*c*, *non* figs 3*a*, *b* = *Emeraldella brocki*.

1970 *Leanchoilia protogonia* Simonetta, p. 38, pl. iv, fig. 2.

1970 *Leanchoilia persephone* Simonetta, p. 38, pl. iv, fig. 4, *non* figs 3*a*, *b*.

1970 *Leanchoilia amphiction* Simonetta, p. 39, pl. iii, fig. 4; pl. iv, fig. 1.

1975 *Leanchoilia superlata*; Simonetta & Delle Cave, p. 19, 27, 33, pl. i, figs 1*a*, *b*; pl. xxviii, figs 2*a*–7*b*; pl. xxix, figs 1*a*–6; pl. xxx, figs 2*a*, *b*, 4, *non* figs 1*a*, *b*?

1975 *Leanchoilia amphiction*; Simonetta & Delle Cave, pl. i, fig. 2; pl. xxx, figs 5, 6.

1975 *Leanchoilia persephone*; Simonetta & Delle Cave, pl. xxxi, figs 4, 6; *non* pl. xxx, fig. 3; *non* pl. xxxi, figs 2, 3, 5, 7, 8.

1975 *Leanchoilia protogonia*; Simonetta & Delle Cave, pl. 1, fig. 6; pl. xxxi, fig. 1.

1976 *Leanchoilia superlata*; Simonetta, fig. 6 (23).

1976 *Leanchoilia amphiction*; Simonetta, fig. 6 (24).

1976 *Leanchoilia protogonia*; Simonetta, fig. 6 (26).

1980 *Leanchoilia superlata*; Simonetta & Delle Cave, p. 9, pl. iv, fig. 1.

1980 *Leanchoilia amphiction*; Simonetta & Delle Cave, p. 9, pl. iv, fig. 2.

1980 *Leanchoilia protogonia*; Simonetta & Delle Cave, p. 9, pl. iv, fig. 4.

1980 *Leanchoilia persephone*; Simonetta & Delle Cave, p. 9, pl. iv, fig. 3.

1980 *Leanchoilia superlata*; Whittington, p. 139, pl. 3, fig. 3.

1981 *Leanchoilia superlata*; Simonetta & Delle Cave, pp. 403, 422, 423, figs 5, 14.

1981 *Leanchoilia amphiction*; Simonetta & Delle Cave, p. 423, fig. 14.

1981 *Leanchoilia protogonia*; Simonetta & Delle Cave, p. 423.

1981 *Leanchoilia persephone*; Simonetta & Delle Cave, fig. 14 (modified from 1980, pl. iv, fig. 3).

1981 *Leanchoilia superlata*; Whittington, p. 350.

1981 *Leanchoilia protogonia*; Whittington, pp. 331–332, 334, 351, fig. 116; pl. 13, figs 120–122.

1981 *Leanchoilia amphiction*; Whittington, p. 353.

1981 *Leanchoilia superlata*; Conway Morris & Bruton, p. 53 (cover illustration).

(*a*) *Material, occurrence, associated fauna*

Holotype U.S.N.M. 57709, an incomplete part, consisting of cephalic shield and four trunk tergites (Walcott 1912, pl. 31, fig. 6) (figure 82, plate 13). The estimated number of *L. superlata* individuals available for this study, excluding counterparts, is 109. Of these 51 have been studied in detail, including seven figured by Walcott (1912, 1931), U.S.N.M. 57709 (holotype), 83943a–e, 83944 (holotype of *L. major*), and eight topotype specimens figured by Simonetta (1970) and Simonetta & Delle Cave (1975), U.S.N.M. 155637, 155638, 155642–155645, 155655, 155656. New topotypes identified are U.S.N.M. 250217, 250219, 250220–25, 250229. This material is variously labelled 35k, 35k/1, and 35k/10. Among additional material in the United States Museum of Natural History are 32 specimens labelled under the first category and 26 specimens under the second category.

In the Geological Survey of Canada party's measured section (Whittington 1971*a*, fig. 3) 17 specimens were collected from levels 21–22.6 m (69–74 ft) above the base of the Phyllopod Bed. These are numbered G.S.C. 49747–49753, and 49755–49764. Material from similar levels was collected by Raymond (1935) from what has since become known as the Raymond Quarry (Whittington 1971*a*). This material is deposited in the Museum of Comparative Zoology, Harvard University, U.S.A., under catalogue numbers M.C.Z. 1841, 1843–1846, 5962, 5965.

Additional material includes the specimen P.M.O. A5116 figured by Størmer (1939, 1944), P.M.O. A5142 and part and counterpart specimens (R.O.M. 35351) collected on the spoil tips at the Burgess Quarry by members of the Royal Ontario Museum (Collins 1978).

Specimens labelled 35k/1 and 35k/10, which almost certainly correspond to the higher horizons of the Raymond Quarry, and those collected from the same locality in 1967, are found in association with the brachiopod *Dictyonina* sp., the sponge *Vauxia* sp., the non-trilobite arthropod *Sidneyia inexpectans* (Bruton 1981) and scales of the worm *Pollingeria*. The holotype, from 35k, is associated with the crustacean *Canadaspis perfecta*, and two additional specimens from this horizon occur together with fragments of this crustacean and with the trilobite *Olenoides serratus*. Walcott (1912, p. 153) lists *Leanchoilia superlata* from layer 10 of the Phyllopod Bed but new collections have not produced further material of this species from equivalent layers.

(*b*) *Description*

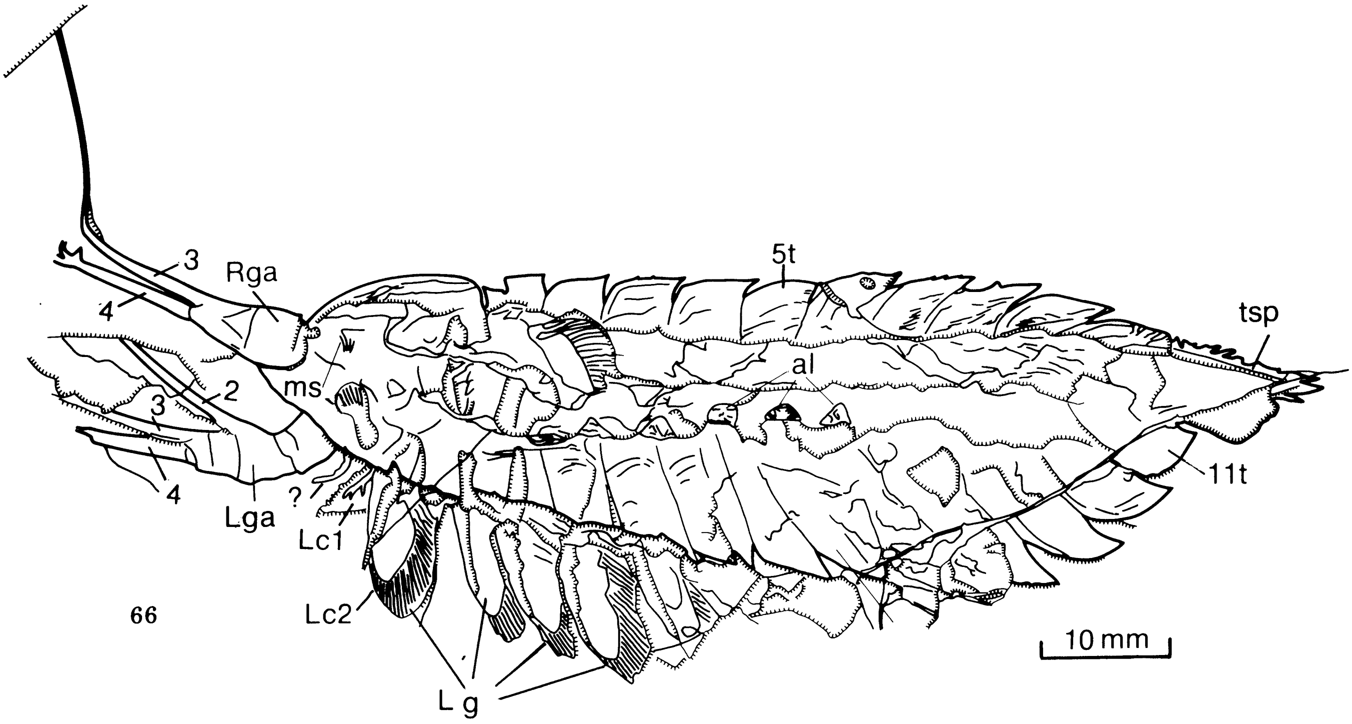
The convexity of the exoskeleton (plate 18; figures 111–113) is taken from U.S.N.M. 250217 (figure 104, plate 17) and U.S.N.M. 250222 (figure 91, plate 16), which are lateral compressions, and the dorsal outline is based on U.S.N.M. 250221 (figure 93, plate 16), G.S.C. 49748 (figure 79, plate 13) and G.S.C. 49750 (figure 81, plate 13). These and others clearly show that the body was composed of a cephalic shield, a trunk of 11 tergites and a tapered tail spine. The largest specimen (figure 104, plate 17) has a sagittal length, excluding the tail spine, of 6.8 cm; the average length of eight other specimens is 5.0 cm. The trunk widens backwards to the maximum width (tr.) at the fifth tergite and curves progressively inwards to the 11th tergite, which is directed alongside the tail spine. The external surface of the skeleton was smooth, although suitably preserved specimens, such as G.S.C. 49748 (figure 79, plate 13) and U.S.N.M. 250221 (figure 93, plate 16), show short spines along the lateral margin of the cephalic shield and tergites. Eyes were lacking on the cephalic shield, and the oval areas on U.S.N.M. 83943b (figure 67, plate 11) and U.S.N.M. 57709 (figure 82, plate 13) are interpreted as being compressions around the base of the foremost cephalic appendages. Shallow dorsal furrows outline the rachis which extends from the posterior one-third of the cephalic shield down the length of the trunk. In dorsal view (figures 79, 81, plate 13) this area is often accentuated owing to compression around the infilled alimentary canal, while in oblique lateral compressions (figure 83, plate 14) the crest of the rachis is displaced laterally and overlaps adjacent tergites. In true lateral compression (figures 88, 89, plate 15; figure 104, plate 17) the crest of the rachis is smooth, but a lateral oblique compression results in a spine-like shape of the posterior edge of each tergite (figure 70, plate 12; figure 84, plate 14). In specimens such as G.S.C. 49751 (figure 83, plate 14), in which the posterior part of the trunk is seen in oblique lateral aspect, such spiny processes are the distal margins, on the side away from the observer, of tergites. Specimens in dorsal and lateral view show the successive overlap of tergites from front to back, and anterior and posterior margins are clearly visible. The amount of overlap increases from the fifth tergite as these become fanned and directed backwards. When tergites are displaced, a raised articulating ridge, labelled r on figure 98, occurs on the upper surface some distance behind the anterior margin. This ridge might have been connected with articulation between tergites, but its exact function is not clear. Movement between the tail spine and the trunk would have been possible in a dorsoventral plane, but not laterally because of the surrounding 11th trunk tergite (figure 79, plate 13) and the lateral fringing spines of the tail. These spines, 11 in number (figure 80, plate 13), were splayed downwards and backwards from the lower margin and were inserted in sockets, as shown by reflective pyrite surrounding the base of each spine (figure 92, plate 16). This dorsal oblique specimen, U.S.N.M. 155655, shows that on the left the fringing spines lie below the lateral margin, while on the right side they have been pushed through the exoskeleton and lie dorsally. Also visible on this specimen are the tail spine doublures, which, as other specimens (figure 72, plate 12; figure 79, plate 13) show, are extensions of the dorsal exoskeleton onto the ventral side. The doublures are fused, forming a solid tip to the spine, but are separated elsewhere along the length of the spine, leaving an open central portion. In life, this area was presumably bridged by a thinner integument.

In lateral view, the front of the cephalic shield is prolonged into a dorsally curved snout, the shape of which varies depending on the angle of compression. In parallel specimens (figures 79, 81, plate 13), the snout may be flattened in the plane of compression or folded over (figure 93, plate 16). The tip of the snout appears to have been a solid spine, while the base was hollow, to judge from U.S.N.M. 250229 (figure 89, plate 15), in which right and left margins of the cephalic shield are visible anteriorly.

Numerous specimens show the broad alimentary canal containing masses of black apatite infilling. This is restricted in most examples to the anterior trunk region (plate 14; figures 88, 89, plate 15; figures 93, 95, plate 16), but on U.S.N.M. 155644 (figure 80, plate 13) it is present where the alimentary canal opens on the 11th trunk somite, in front of where the tail spine is attached. Three specimens show what is interpreted as being the foregut, an area infilled with fine-grained material beneath the cephalic shield. This area extends far forward on U.S.N.M. 250217 and U.S.N.M. 250223 (figures 104, 107, plate 17), while on U.S.N.M. 250229 (figures 88, 89, plate 15) it appears to be a curved sac-like area extending from the mouth region. The mouth is directed forwards and downwards and opens ventrally along the midline behind the base of the foremost cephalic appendages. On U.S.N.M. 250223 (figure 107, plate 17), two highly reflective areas on each side of the foregut (labelled ?fgd on figure 103) may be gut diverticulae, that on the right side showing a spiral structure interpreted as part of the folded gut wall.

Appendages on the cephalon and trunk are preserved on the majority of specimens and are best seen in lateral compressions, where they extend ventrally below the margin of the dorsal exoskeleton. Only the foremost cephalic appendages, the great appendages, are seen in parallel specimens (figure 79, plate 13), while these and the distal portions of the succeeding cephalic appendages are seen in lateral compressions. An oblique specimen such as U.S.N.M. 250221 (figure 93, plate 16) shows trunk appendages on one side and both great appendages have been folded so that lateral faces are uppermost. On U.S.N.M. 83943a (figures 70, 73, plate 12), the ventral surface of the appendage faces dorsally, without seemingly having been twisted at the basal joint, and two other specimens, U.S.N.M. 250223 (figure 107, plate 17) and G.S.C. 49751 (figure 83, plate 14), show the great appendages to be swung backwards to lie beneath the body between the trunk appendages. Whether this is a natural position in U.S.N.M. 250223 is not certain but it is interpreted as such on G.S.C. 49751 and is shown to be a possible swimming position in the reconstruction (figure 112*b*). Otherwise, in the majority of specimens, the great appendages are directed forwards and are, excluding the annulated portion, of length (exs.) two-thirds that of the trunk.

The great appendage consists of four parts, numbered in succession on the explanatory drawings from the broad first podomere. The first podomere seems to have been attached by a basal section to the underside of the cephalon, and the raised oval area on the counterpart of U.S.N.M. 83943b (figure 68, plate 11) is this point of attachment. Podomere 1 is long, with a curved posterior surface; podomeres 2 and 3 are shorter, approximately equal in size, and the dorsal surface of each is extended in a straight, tapering shaft, which is continued by a much longer annulated, flexible distal portion. Podomere 4 consists of a long tapering shaft terminating distally in three claws and an annulated, flexible ramus which fits into a socket below the claws. In lateral view (figure 89, plate 15; figure 104, plate 17) the great appendage hangs beneath the cephalic shield and could presumably be held at varying angles. In those specimens where the appendage has been swung backwards, the basal area of attachment seems to have been very flexible and may well have consisted of arthrodial membrane. Traces of the distal and proximal margins of the podomeres in U.S.N.M. 83943a (figure 73, plate 12), U.S.N.M. 250221 (figure 93, plate 16) and U.S.N.M. 250223 (figure 107, plate 17), indicate that articulation was pivotal, that between 2 and 3, and 3 and 4, being greater to allow separation of the shafts. Greater movement of these distally was afforded by the annulated portion or flagellum, best displayed on U.S.N.M. 83943b (figure 73, plate 12). The distal claws on podomere 4 do not appear to have been movable and consist of a dorsally directed claw flanked by a pair of smaller claws. On the third podomere of well preserved specimens occurs a circular area filled with dark phosphatic material, similar in appearance to the apatite infilling of the alimentary canal, for



66

Description of figure 66 and plate 11

Leanchoilia superlata Walcott, 1912.

Figure 66. Explanatory drawing of U.S.N.M. 83943b.

Figures 67–69. U.S.N.M. 83943b, parallel–oblique. Respectively: part, reflected (magn. × 1.75); counterpart, west, ordinary light (magn. × 3.5); counterpart, reflected (magn. × 3.5). Original of Walcott's (1931) pl. 12, figs 2, 3.

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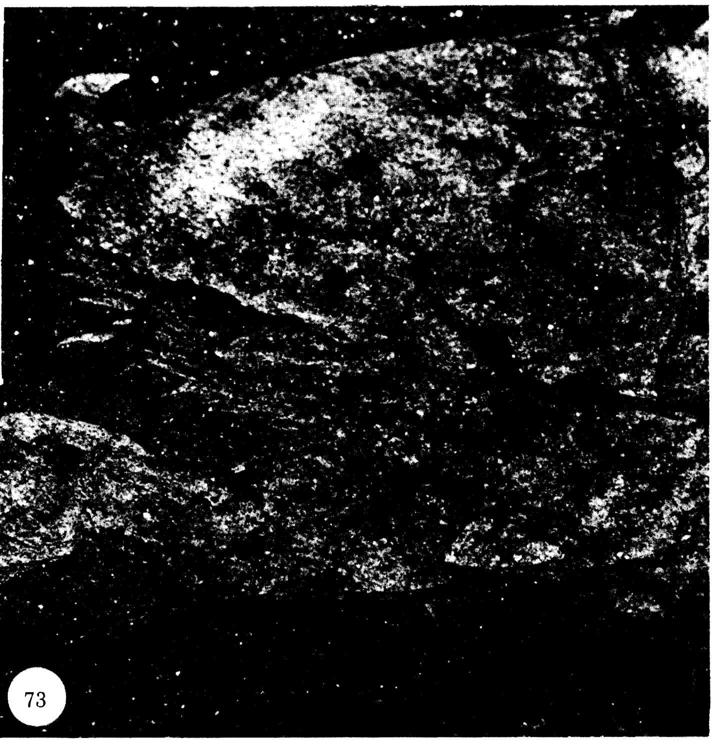
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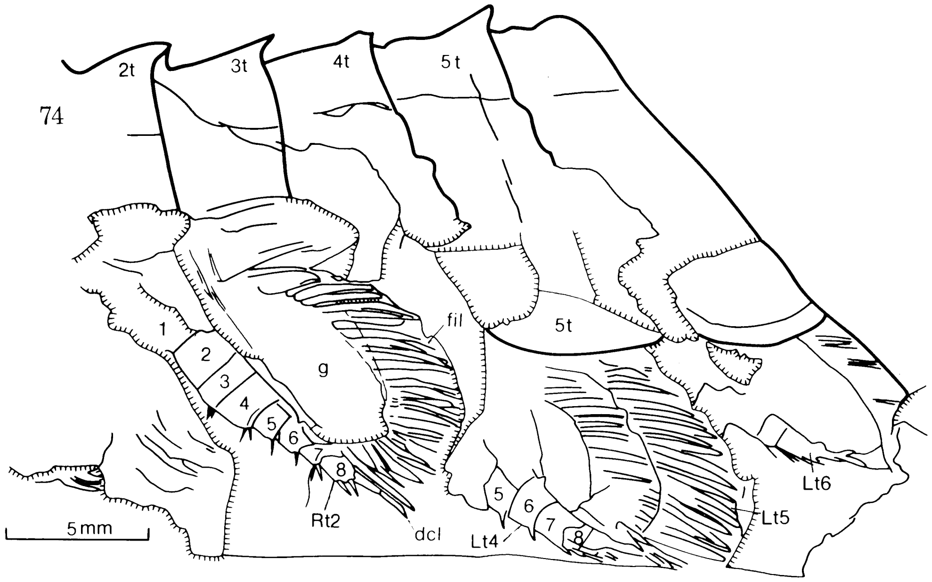

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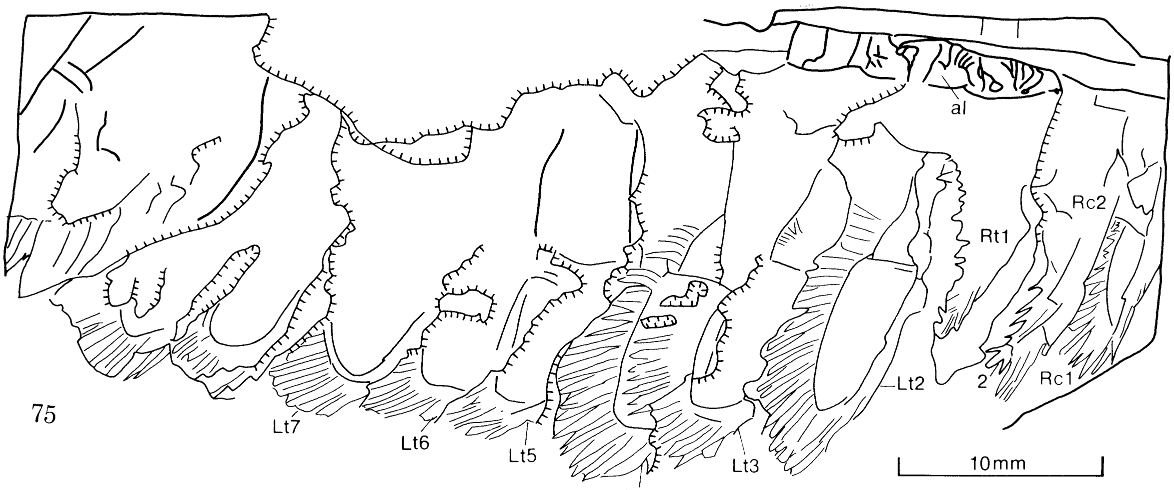

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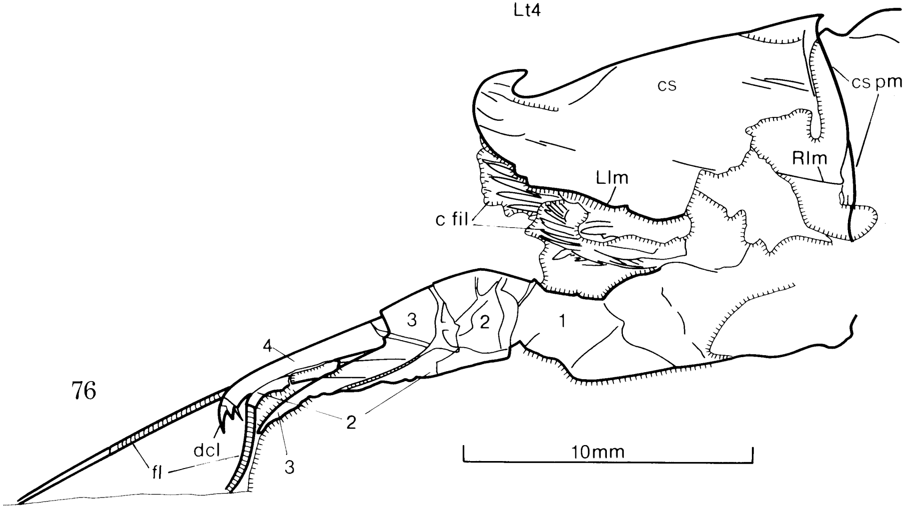

DESCRIPTION OF PLATE 12 AND FIGURES 74–76

Leanchoilia superlata Walcott, 1912.

FIGURES 70 AND 73. U.S.N.M. 83943a. (70) Lateral, part, reflected (magn. × 4). (73) Detail of cephalic shield and great appendage rotated about basal joint, reflected. Note annulated flagellum. (Magn. × 7.) Original of Walcott's (1931) pl. 12, fig. 1.

FIGURE 71. G.S.C. 49749, oblique, part, under alcohol. (Magn. × 3.5.) Raymond Quarry 21–21.6 m (69–71 ft).

FIGURE 72. G.S.C. 49753, oblique, part, under alcohol, showing doublure of tail spine. (Magn. × 3.5.) Raymond Quarry 21–21.6 m (69–71 ft).

FIGURES 74 and 76. Explanatory drawings of U.S.N.M. 83943a: (74) right and (76) left halves of specimen, latter showing both lateral margins of cephalic shield.

FIGURE 75. Explanatory drawing of G.S.C. 49749.

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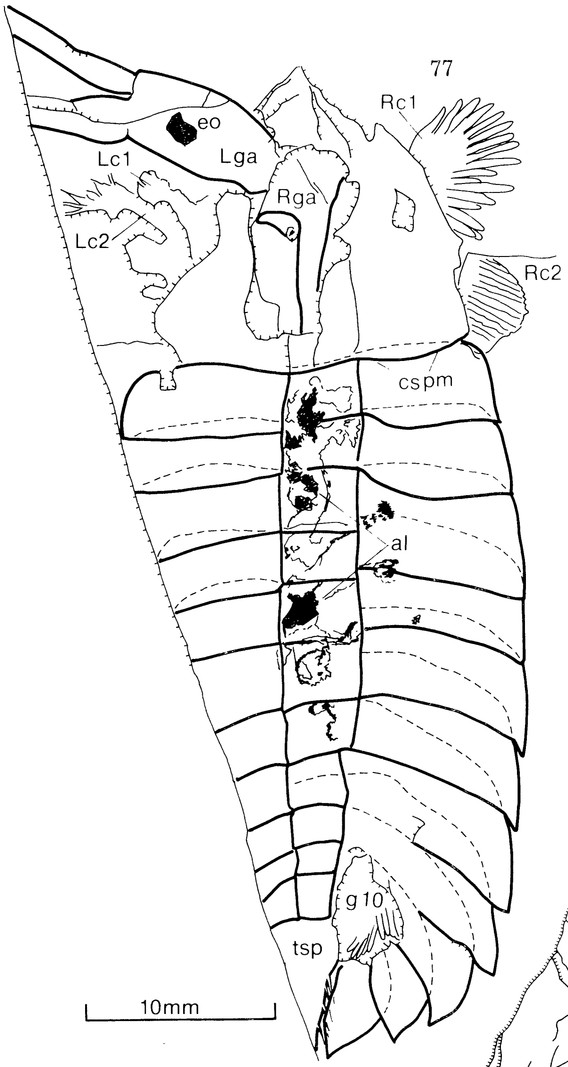

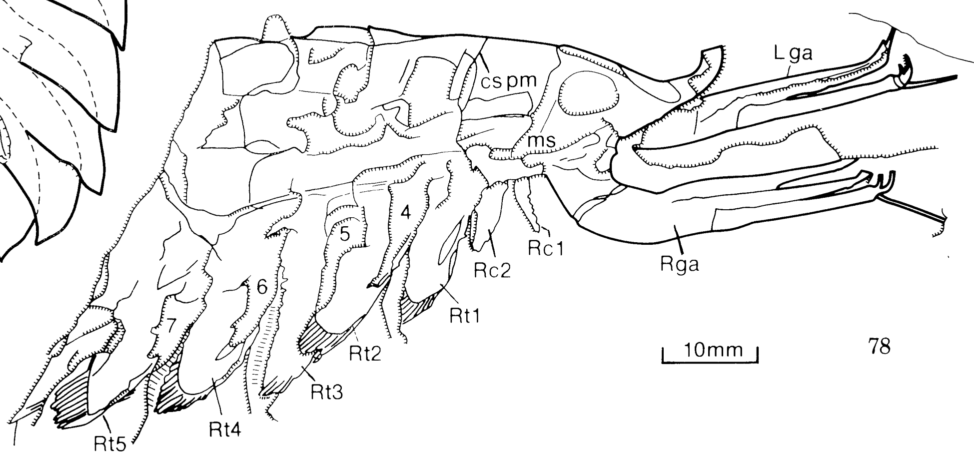

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Description of figures 77 and 78 and plate 13

Leanchoilia superlata Walcott, 1912.

Figure 77. Explanatory drawing of G.S.C. 49750.

Figure 78. Explanatory drawing of U.S.N.M. 57709.

Figure 79. G.S.C. 49748, parallel, part only, under alcohol. (Magn. × 4.) Raymond Quarry, 21.9 m (72 ft).

Figure 80. U.S.N.M. 155644, parallel, counterpart, showing junction of tail spine and 11th trunk tergite. Note alimentary canal opening in front of tail spine, reflected. (Magn. × 8.)

Figure 81. G.S.C. 49750, parallel, part, under alcohol. (Magn. × 6.) Raymond Quarry, 21.9–21.6 m (72–71 ft).

Figure 82. U.S.N.M. 57709, holotype, part only, west. (Magn. × 1.5.) Original of Walcott's (1912), pl. 31, fig. 6.


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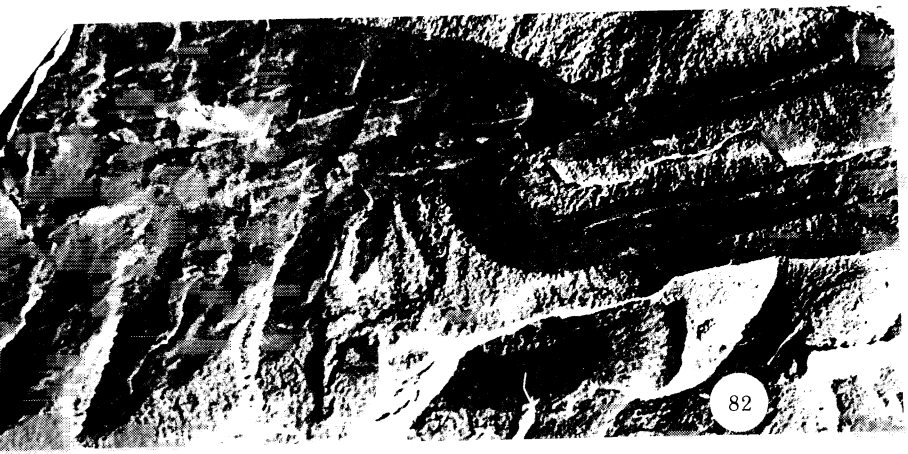
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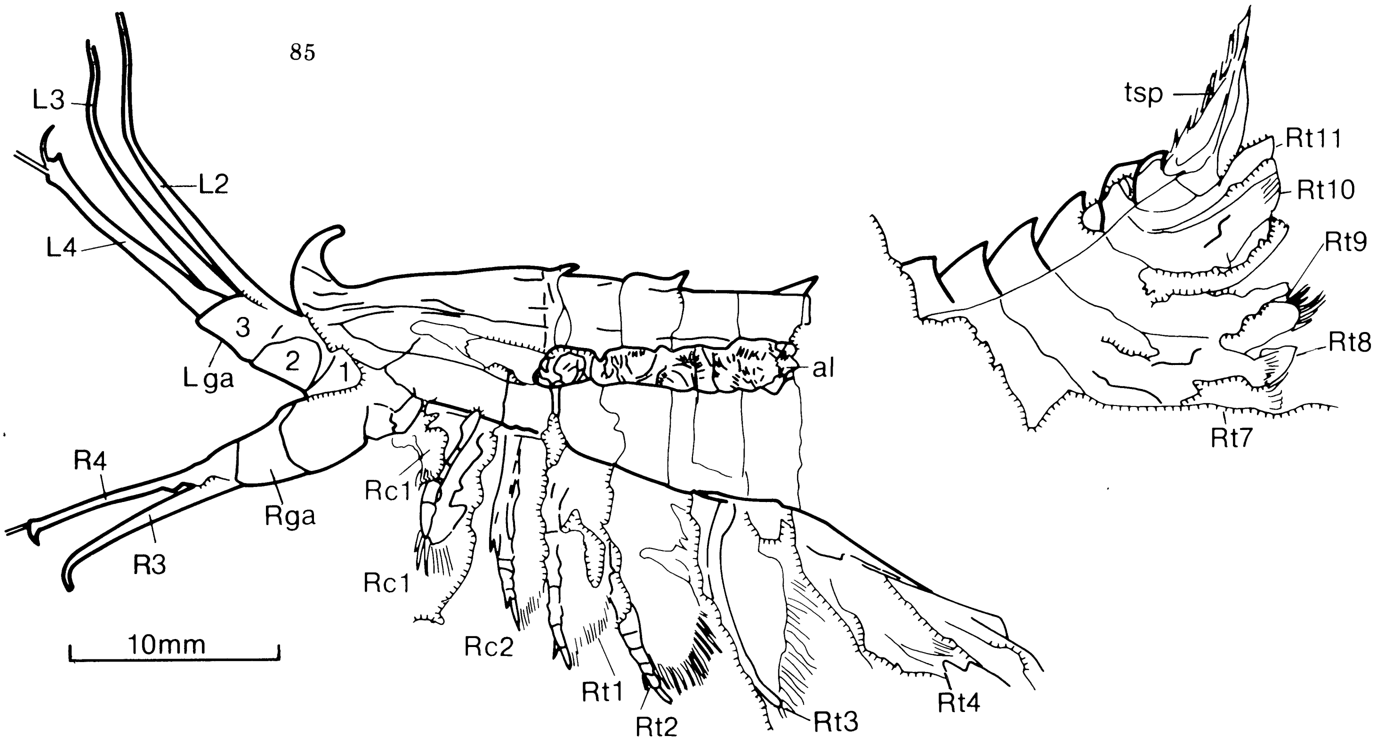

Description of plate 14 and figure 85

Leanchoilia superlata Walcott, 1912.

Figure 83. G.S.C. 49751, lateral oblique, part only, showing great appendages swung backwards beneath trunk, under alcohol. (Magn. × 3.5.) Raymond Quarry, 21.6–22.2 m (71–73 ft).

Figure 84. P.M.O. A5116, lateral, counterpart only, anterior portion of specimen under alcohol. (Magn. × 3.5.) 35k/1. Original of Størmer (1939, 1944).

Figure 85. Explanatory drawing of P.M.O. A5116.

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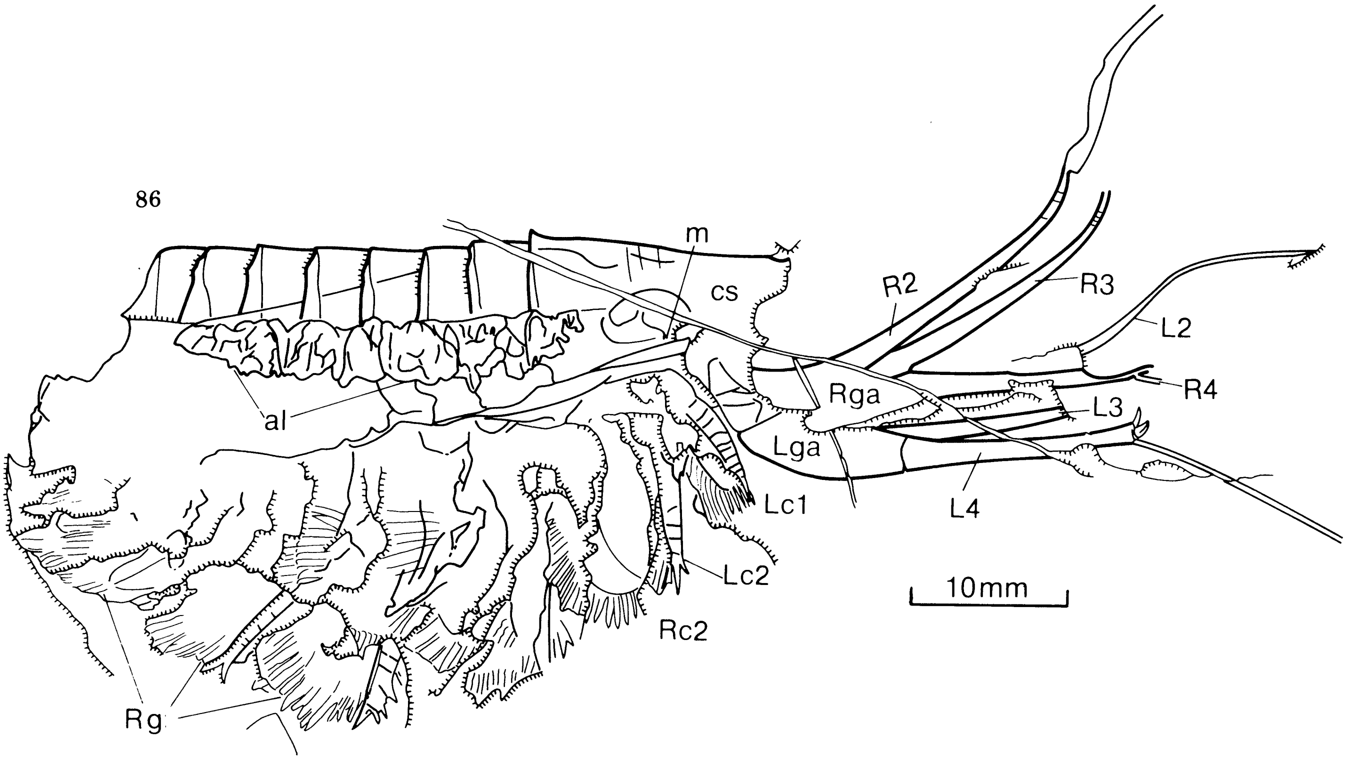

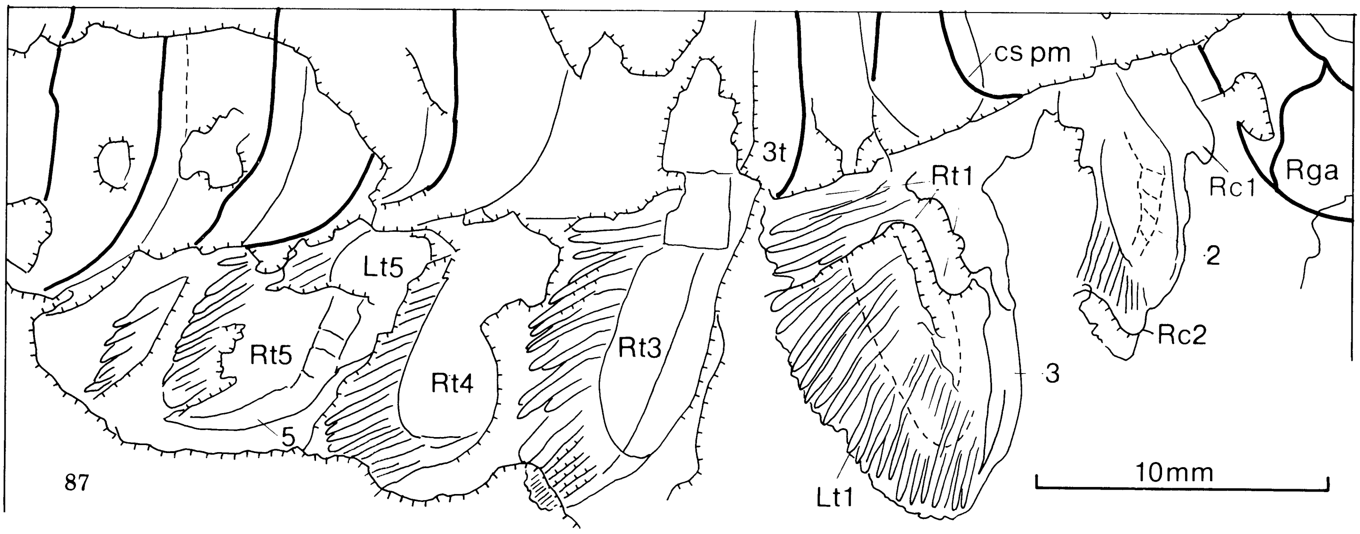

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Description of figures 86 and 87 and plate 15

Leanchoilia superlata Walcott, 1912.

Figure 86. Explanatory drawing of U.S.N.M. 250229.

Figure 87. Explanatory drawing of U.S.N.M. 250219, showing compression of L1 and R1 trunk appendages on each other.

Figures 88 and 89. U.S.N.M. 250229, lateral, portions of specimen, part: (88) ordinary light, east (magn. × 3.5); (89) under alcohol. (Magn. × 3.5.) Most probably from Raymond Quarry.

Figure 90. U.S.N.M. 250219, lateral, oblique, part only, under alcohol. (Magn. × 3.5.) See also figure 94, plate 16.

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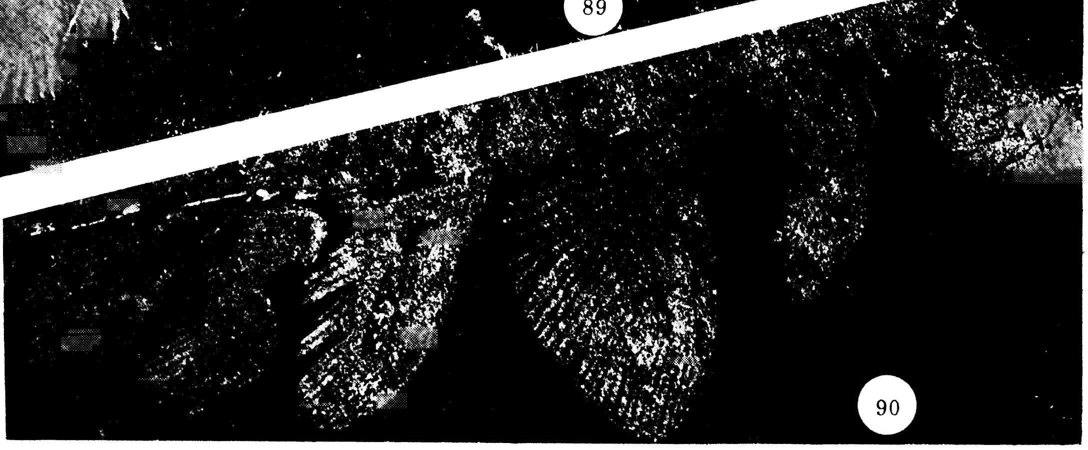

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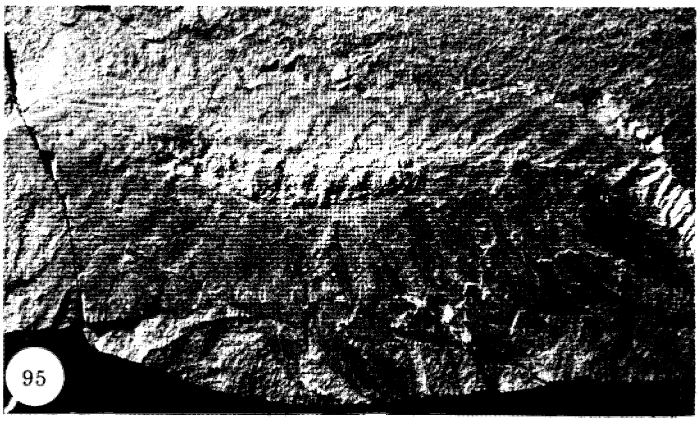

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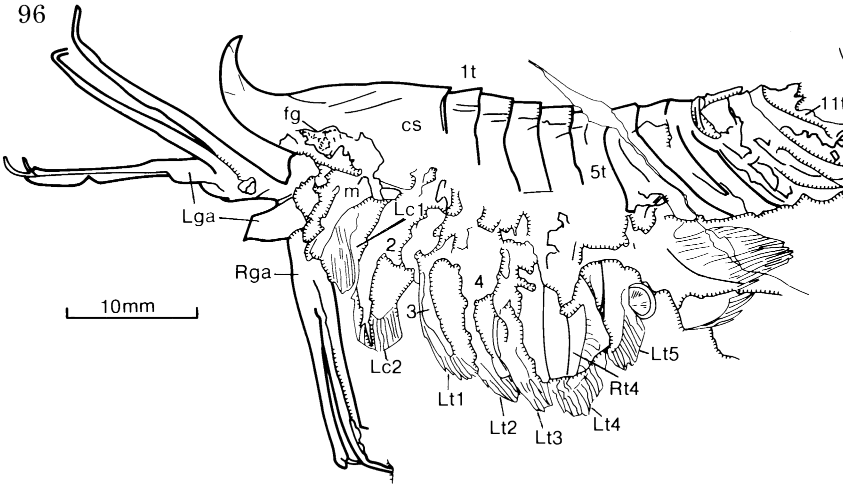

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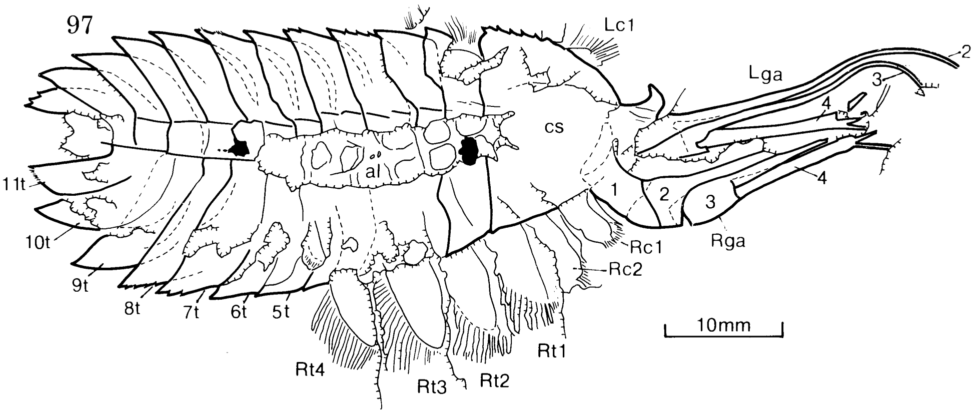

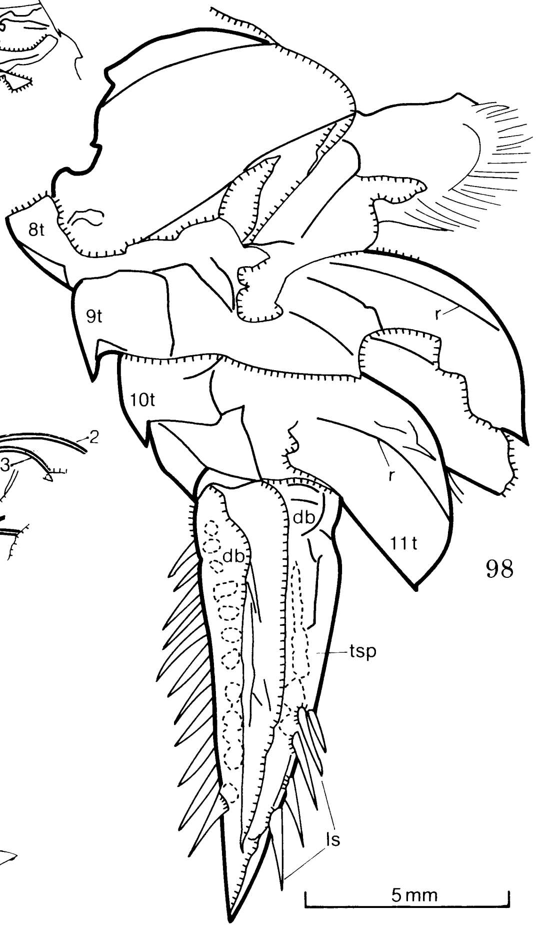

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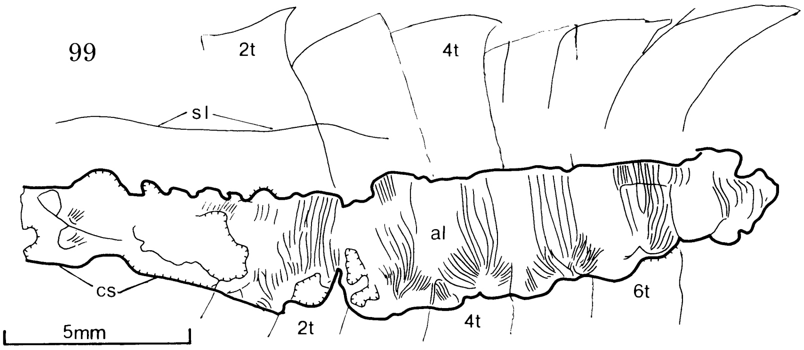


Description of plate 16 and figures 96–99

Leanchoilia superlata Walcott, 1912.

Figure 91. U.S.N.M. 250222 lateral, part, under alcohol. (Magn. ×2.75.) 35k/1.

Figure 92. U.S.N.M. 155655, oblique, counterpart, tail spine showing sockets of lateral spines, under alcohol. (Magn. ×4.)

Figure 93. U.S.N.M. 250221, oblique, anterior portion of part, ordinary light, east. (Magn. ×2.) 35k/10.

Figure 94. U.S.N.M. 250219, lateral oblique, anterior portion of part, under alcohol. (Magn. ×2.) See also figure 90, plate 15.

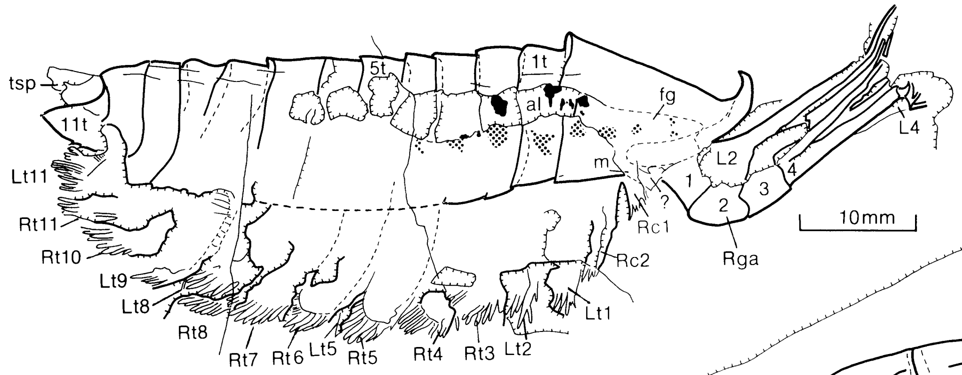
Figure 95. U.S.N.M. 155638A, oblique, part, northwest, showing gut infilling and gut wall striations. (Magn. ×1.5.)

Figure 96. Explanatory drawing of U.S.N.M. 250222.

Figure 97. Explanatory drawing of U.S.N.M. 250221. Snout of cephalic shield has been folded over on left side; left great appendage turned to lie under that of right side.

Figure 98. Explanatory drawing of U.S.N.M. 155655.

Figure 99. Explanatory drawing of portion of U.S.N.M. 155638.



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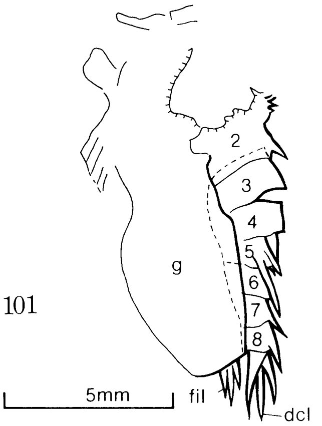

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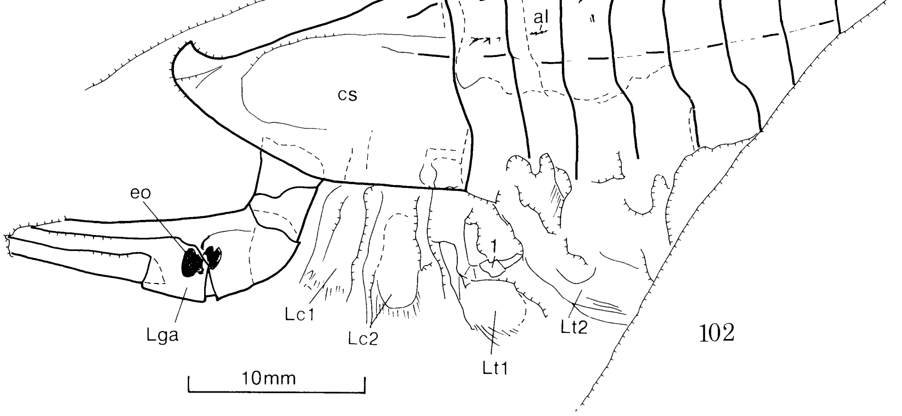

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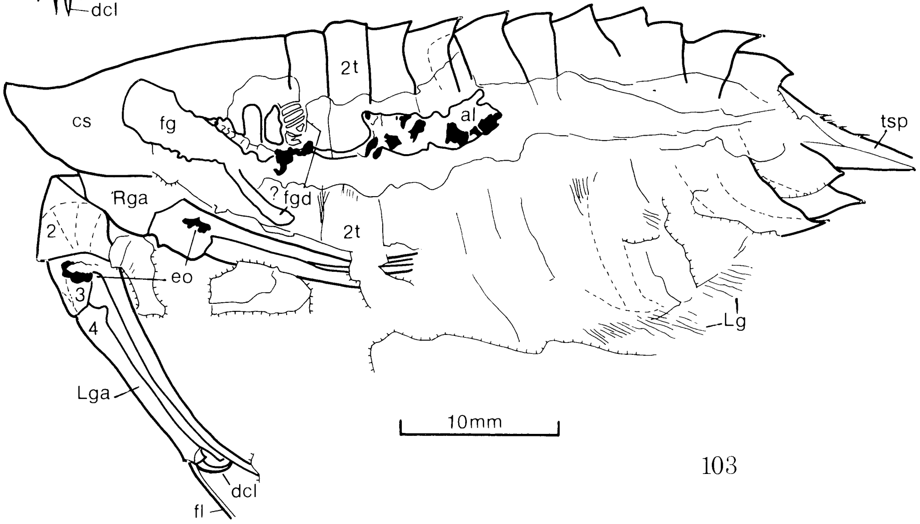

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Description of figures 100–103 and plate 17

Leanchoilia superlata Walcott, 1912.

Figures 100 and 101. U.S.N.M. 250217, explanatory drawings of (100) entire specimen and (101) detached limb.

Figure 102. Explanatory drawing of U.S.N.M. 155645.

Figure 103. Explanatory drawing of U.S.N.M. 250223.

Figures 104 and 105. U.S.N.M. 250217, lateral, part only: (104) entire, under alcohol (magn. × 2.5); (105) detached appendage lying below entire specimen, under alcohol (magn. × 4). 35k/1.

Figure 106. U.S.N.M. 155645, lateral, part only, under alcohol. (Magn. × 3.5.) 35k/1.

Figure 107. U.S.N.M. 250223, lateral oblique, counterpart, under alcohol. (Magn. × 3.) The sponge *Vauxia* sp. lies beneath the specimen. 35k/1.

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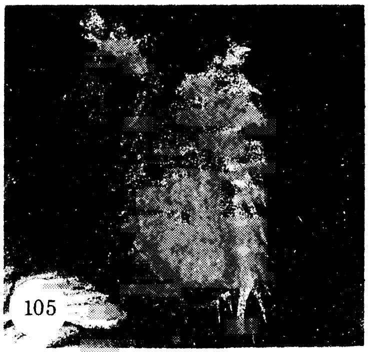

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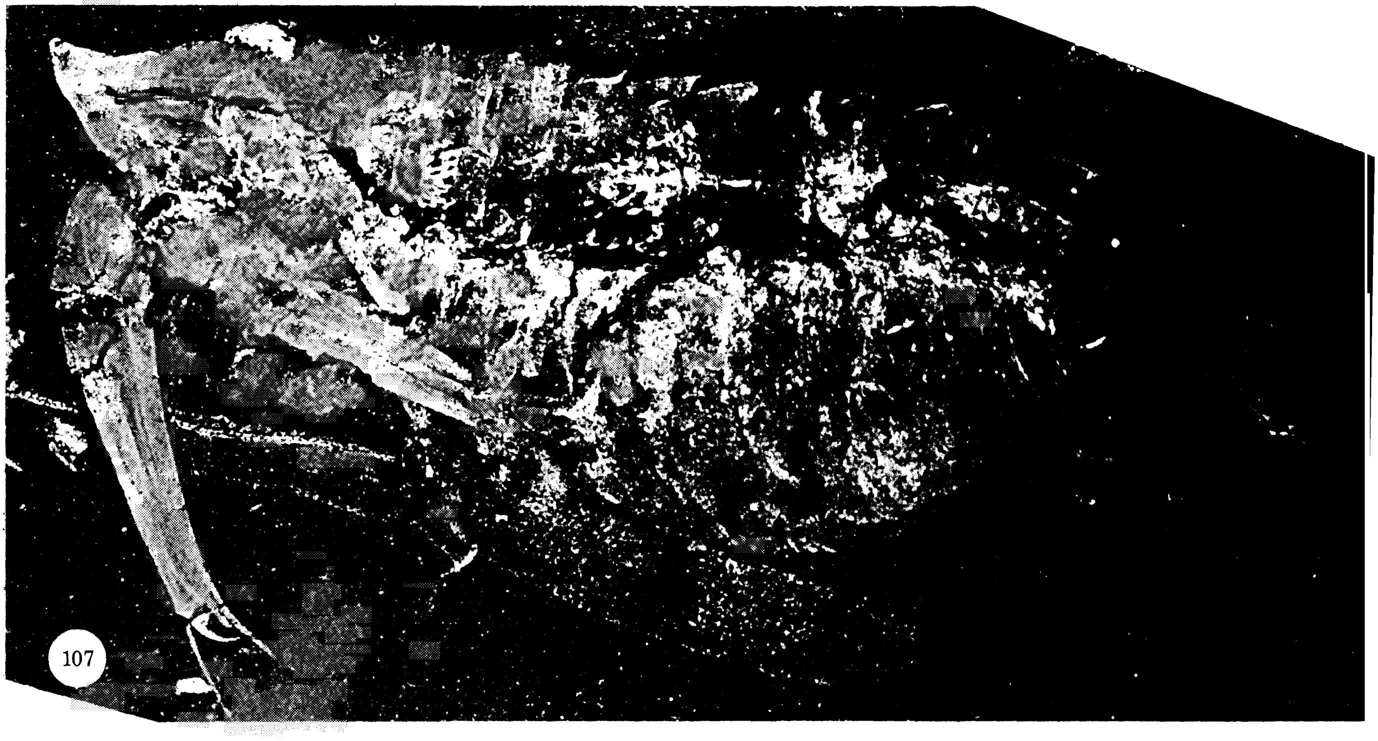

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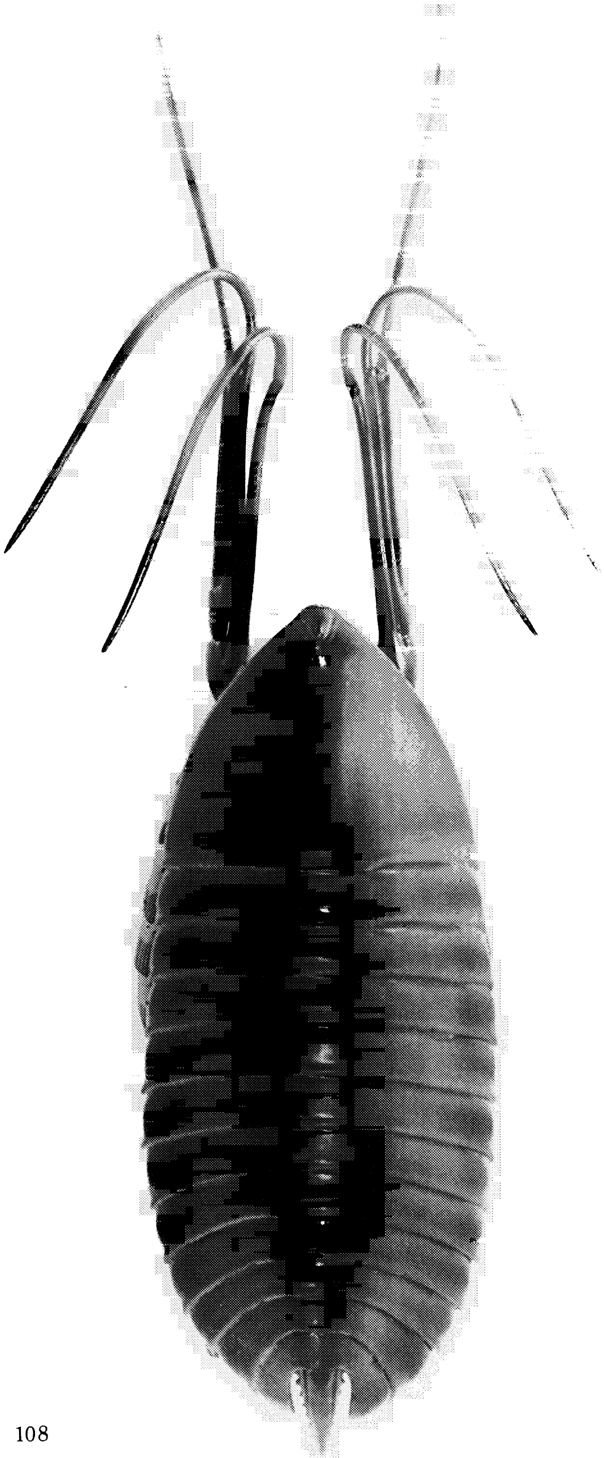

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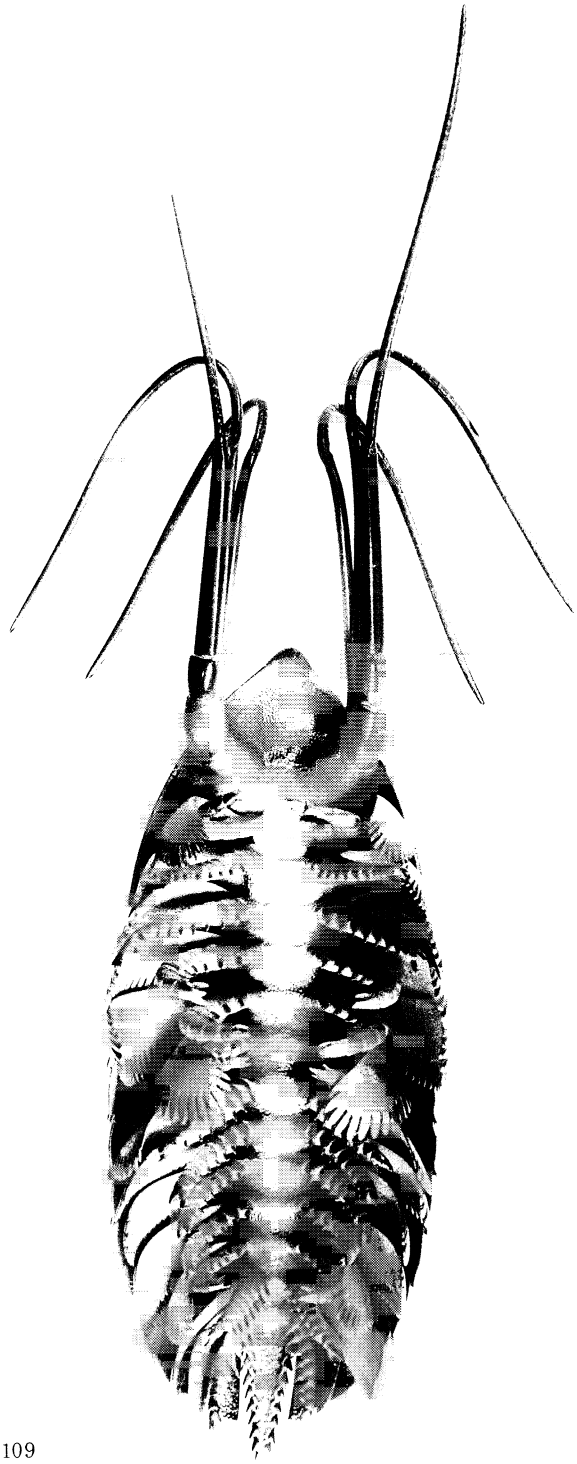

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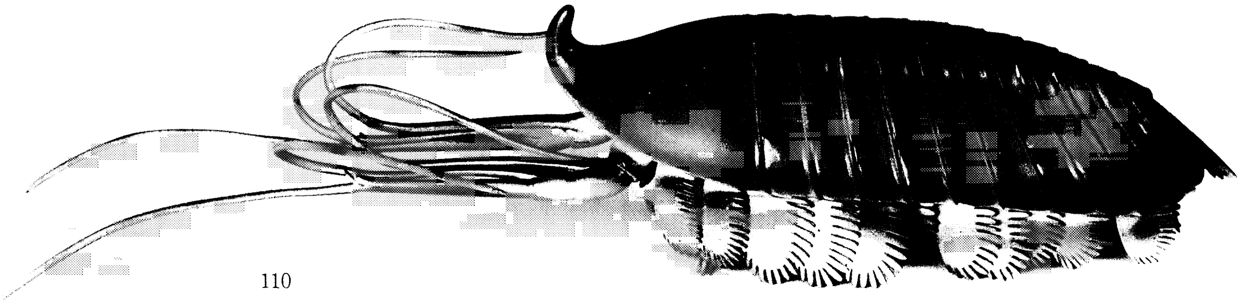

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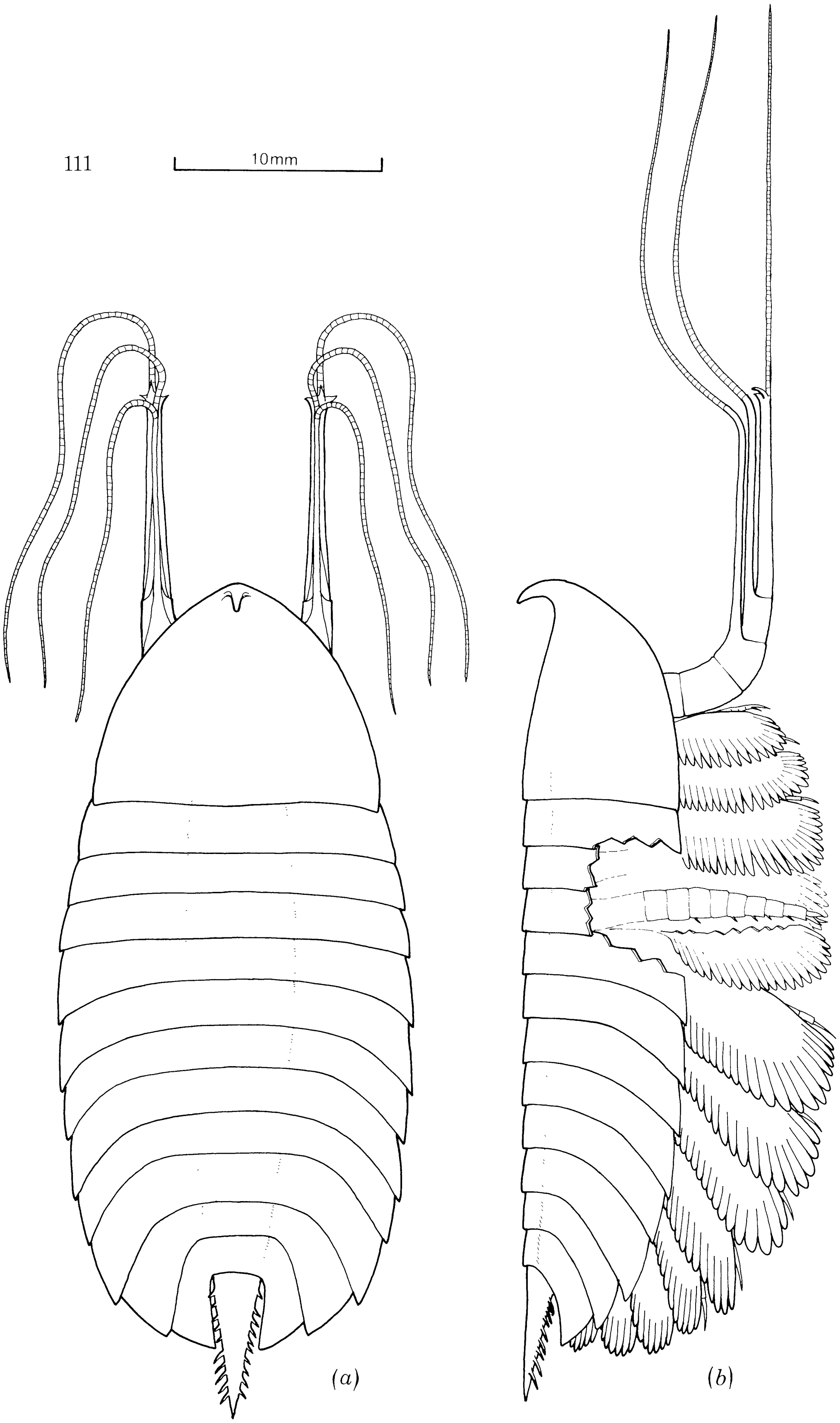

Figure 111. Reconstruction of *Leanchoilia superlata* Walcott, 1912; (*a*) dorsal view; (*b*) right lateral view with parts of trunk tergites and gills cut away to reveal leg branch of third trunk appendage.

Description of plate 18

Figures 108–110. Model of *Leanchoilia superlata* Walcott, 1912, approximately $1\frac{1}{2}$ times maximum known size. (108) Dorsal, (109) ventral and (110) left lateral views. Appendages in 'still' position of rhythm discussed in §6(*d*).

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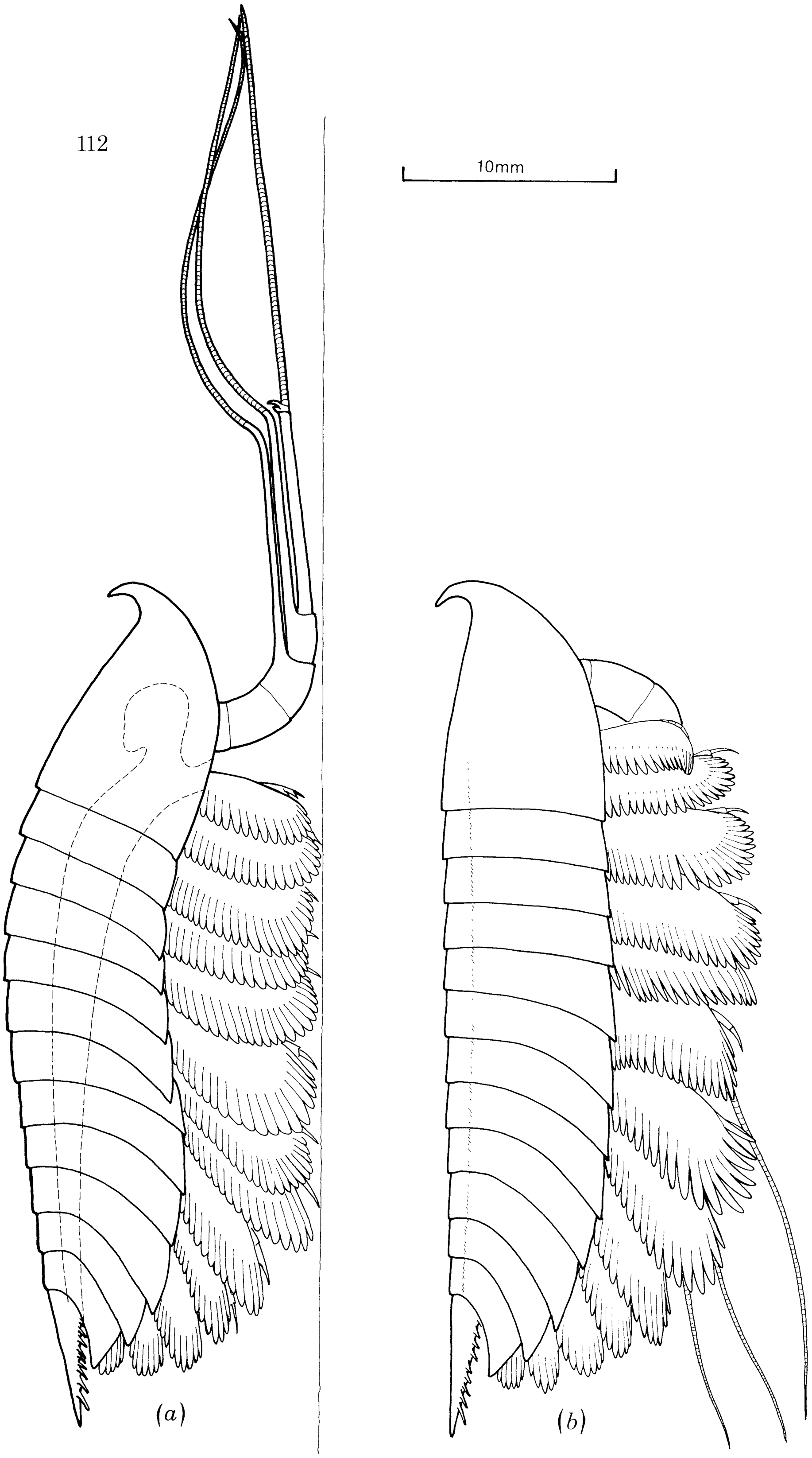

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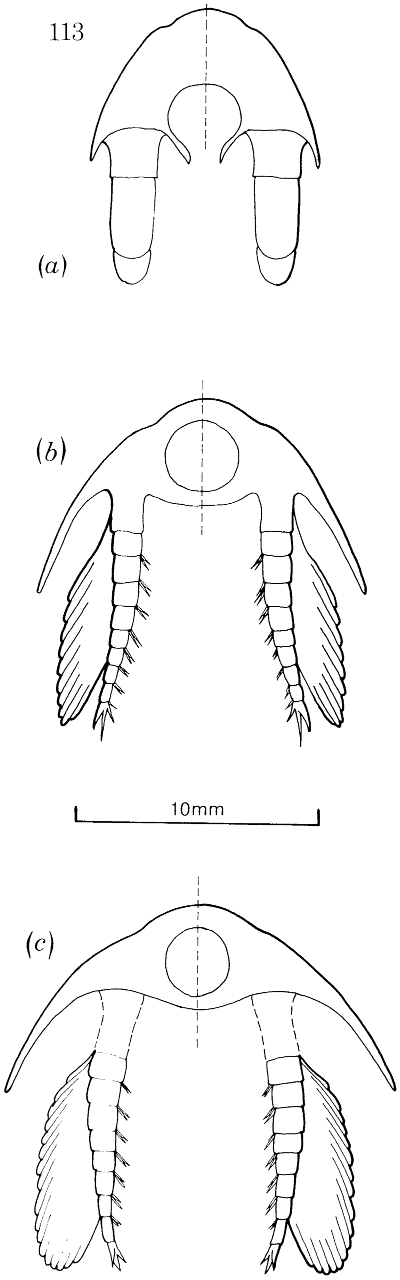

FIGURE 112. Reconstruction of *Leanchoilia superlata* Walcott, 1912. (*a*) Assumed feeding position with animal resting on the bases of the great appendages and tips of the anterior leg branches; outline of alimentary canal shown by dashed lines. A greater arching of the trunk than shown would bring the cephalon and mouth nearer the sediment surface. (*b*) A possible swimming position with great appendages feathered backwards beneath the trunk; other appendages in 'still' position of metachronal rhythm discussed in §6(*d*).

FIGURE 113. Cross sections of cephalon and trunk of *Leanchoilia superlata*, showing appendage immediately in front of section in posterior view: (*a*) behind great appendage through mouth opening; (*b*) at posterior margin of cephalic shield, limb beginning inward swimming stroke; (*c*) at posterior margin of third trunk tergite, limb moving out in swimming stroke.

example in G.S.C. 49748 (figure 79, plate 13) and U.S.N.M. 155645 (figure 106, plate 17). It is interpreted as a posssible excretory organ, and labelled as such. To judge from U.S.N.M. 250229 (figures 88, 89, plate 15) and U.S.N.M. 250217 (figure 104, plate 17), the great appendages were attached just forward of the mouth. On U.S.N.M. 83943b (plate 11) a smooth sickle-shaped structure (?in figure 66) seems to be attached near the base of podomere 1, and on U.S.N.M. 250217 (?in figure 100) a similar structure projects backwards towards the opening of the mouth. Whether this is a structure associated with feeding or a form of endite is not certain, and these are the only two specimens showing this feature.

In lateral compressions (figure 82, plate 13; figure 104, plate 17), the two cephalic appendages behind the great appendage, and the succeeding 11 trunk appendages, hang vertically below the animal; those of one side, observed from the outer surface, being flap-like structures which overlap each other from front to back and bear filaments from posterior and distal margins. When observed from the inner surface in similar specimens (figure 68, plate 11; figure 70, plate 12), however, these appendages are seen to be biramous and consist of a jointed, inner leg branch, attached at its base to the outer, filamentous branch, or gill. Details of the attachment are not clear but it does appear to have been such that during burial the leg was always compressed onto the gill approximately parallel to the anterior margin. Such is the regularity of this feature that Størmer (1944) considered the jointed structures shown on P.M.O. A5116 (figure 84, plate 14) to be the thickened anterior margins of the gill branches. These are clearly gills from the right side of the animal viewed from the inside, and show the leg branch compressed upon the inner surface of the gill. Preparation from the right side of better preserved lateral specimens has revealed left side appendages with leg branches, such as those of U.S.N.M. 250217 (figure 104, plate 17) and G.S.C. 49749 (figure 71, plate 12). Furthermore, a convincing overlapping relationship is seen on the isolated appendage (figure 105, plate 17) and on U.S.N.M. 155645 (figure 106, plate 17), where the distal part of the leg branch is curved backwards on the first trunk appendage, while the proximal part is straight and clearly lies beneath the gill. From these specimens and U.S.N.M. 83943a (figure 70, plate 12), the leg branch was armed with a double row of spines along the inner surface, and tapered distally from a broad base. Eight cylindrical podomeres appear to have articulated and had simple overlapping margins, the eighth podomere articulated with a stout distal claw flanked by two slimmer spines.

In lateral (figure 71, plate 12) and oblique specimens (figure 93, plate 16), the regularity of overlap of the gills along the length of the body is remarkable, as is the way that the outer face of the gill in lateral view is always at a slightly oblique angle to the plane of compression. That this was a primary feature can be seen from the holotype (figure 82, plate 13), in which the wedge of sediment separating one gill from another is thickest below the filaments. Many previously illustrated specimens give the impression that the posterior gill margins were fringed with thick setal spines, but recently collected material, including G.S.C. 49750 (figure 81, plate 13) and G.S.C. 49749 (figure 71, plate 12), shows them to be broad, flattened in the plane of the gill body, and with rounded ends.

(*c*) *Discussion*

The reconstructions (figures 111–113), and the model based on them (plate 18), summarize the evidence presented above, and show how the animal may have looked when swimming and/or feeding. All complete specimens clearly have 11 trunk tergites, and reports of specimens with nine (Walcott 1912, p. 170; 1931, p. 8), ten (Raymond 1935, p. 206; Størmer 1944, p. 82) and occasionally 12 or 13 tergites (Simonetta 1970, p. 37) are incorrect. The recognition of oblique compressions explains much of the variation in shape of the dorsally curved snout of the cephalic shield (Simonetta 1970, p. 37), and confirms the observations of Raymond (1935), that the apparent dorsal angular peaks along the midline are a result of compression of the rachial region. Likewise, the oblique carinae alongside the rachis (figure 70, plate 12; figure 107, plate 17) are the result of compression along gut infilling. The latter is similar in appearance to that described for *Sidneyia inexpectans* (Bruton 1981), and an X-ray analysis shows it likewise to be composed of the mineral apatite. Study of U.S.N.M. 155638 (figure 95, plate 16) confirms the segmented arrangement of the alimentary canal and the annulated striations of the wall of the gut as observed by Raymond (1935, pp. 211–212). It was this same specimen on which Simonetta (1970, p. 38) interpreted the gut infilling as being a polychaete worm, but this is clearly not correct.

Walcott (1912, p. 171; 1931, p. 9) believed there to be a large opening for an eye on the side of the cephalic shield, and, although such an opening was shown not to exist by Raymond (1935, p. 213), he interpreted reniform depressions as representing sessile eyes. Størmer (1944, p. 82) and Simonetta (1970, p. 37) cast doubt on this interpretation, and study of the holotype (figure 82, plate 13), on which Walcott based his observations, shows the area (labelled ms in figure 78) to be no more than a compression around the area of attachment of the cephalic great appendage. No structures resembling eyes are present on any of the material studied and we conclude that *Leanchoilia superlata* was a blind form.

Details of structures around the mouth are lacking and beyond the margin of the cephalic shield there is no evidence for structures in front of the great appendage, only evidence for two appendages behind it. This is contrary to Raymond (1935, pp. 208–209, figure 3) and Størmer (1944, fig. 17, 1, 2), who inserted paired 'antennules' in front of the great appendages and two pairs of appendages behind, making a total of four such pairs on the cephalon. Simonetta (1970, p. 37, pl. ii, figs 1*a*, *b*; cf. Simonetta & Delle Cave 1975, pl. i, figs 1*a*, *b*) gave no evidence in support of his view that the cephalon bore the great appendages followed by three pairs of limbs like those of the trunk. Raymond's material at Harvard University is not well preserved and, while it supports some of his observations, does not support all his conclusions (Raymond 1935, pp. 213–214). Our interpretation of the first or great appendage differs from that of Raymond (1935, pp. 207–208, fig. 1), in that we regard the shafts of podomeres 2 and 3 as separate structures and not inner branches of podomere 2 only, as did Simonetta (1970, pl. ii, fig. 1*a*; cf. Simonetta & Delle Cave 1975, pl. i, fig. 1*a*). Clearly, different angles of compression produced varying relationships between the distal portions of the shafts, but the articulation between podomeres 2 and 3 in U.S.N.M. 83943b (figure 68, plate 11), U.S.N.M. 250217 (figure 104, plate 17) and U.S.N.M. 250223 (figure 107, plate 17) favours our interpretation, especially since one is viewing the outer faces of the appendage. There is no reason to believe that the great appendage was post-oral in position as suggested by Størmer (1944, fig. 17, 1) and whether or not it was equivalent to the antenna (Raymond 1935, p. 213) of other arthropods is debatable. As discussed in § 6 (*d*) it could have had both a swimming and a sensory function, and so have functioned in part like an antenna.

The remaining biramous cephalic and trunk appendages are interpreted in a way similar to that of Raymond (1935, p. 211), though he had no specimens showing details of the inner branch as clearly as U.S.N.M. 250222 (figure 91, plate 16) and U.S.N.M. 250217 (figures 104, 105, plate 17). These show that the appendage is unlike that illustrated for *Leanchoilia* by Simonetta (1970, pl. ii, fig. 1*c*; pl. iii, fig. 3*a*, *b*), which was later referred to *Emeraldella* (see Simonetta & Delle Cave 1975, p. 19; also §5(*b*)). Simonetta & Delle Cave (1975, p. 19, pl. i, fig. 1*a*) rightly consider the *Leanchoilia* limb to be biramous, but wrongly attribute to Bruton a personal communication in which he was said to interpret the limb as being uniramous, consisting of a filamentous gill body strengthened by an annulated process along the anterior edge. This interpretation is that of Størmer (1939, p. 235; 1944, pp. 82–83), based on P.M.O. A5116 (figure 84, plate 14). Had it not been for U.S.N.M. 155645 (figure 106, plate 17) and several new specimens, among them U.S.N.M. 250217 (figures 104, 105, plate 17), we would have considered many specimens to have favoured Størmer's interpretation, or that the biramous nature of the appendages was equivocal. The new material is still not sufficiently well preserved to show details of the proximal portions of the biramous appendages but there is no evidence of there having been gnathobasic lobes, as suggested by Raymond (1935, p. 211, 214). In the cross sections (figure 113) the filamentous gill is shown as having been attached to the proximal portion of the limb. Evidence for this basal portion, and the leg branch, is present on G.S.C. 49749 (figure 71, plate 12), while details of the leg branch may be seen in U.S.N.M. 83943a (figure 70, plate 12). While the latter clearly shows an overlapping relationship between leg branch and gill, there is, without exception, never any layer of sediment separating the two. We take this, and their mutual flattening, to indicate that the leg branch was composed of thin integument similar to the gill branch and was not strongly sclerotized; nor did it possess knee or hinge joints or the type of articulation between podomeres associated with a walking function.

Recognition of left and right side gill branches in lateral specimens such as U.S.N.M. 250222 (figure 91, plate 16) and U.S.N.M. 250217 (figure 104, plate 17) explains how an apparent double row of filaments can arise fortuitously from the superposition of one gill branch on another. This has happened between Rt1 and Lt1 on U.S.N.M. 250219 (figure 90, plate 15; figure 94, plate 16), and is clearly the same as observed by Raymond (1935), who thought that the filaments might have formed a double row.

(*d*) *Mode of life*

All the specimens of *L. superlata* considered here are complete, with the appendages in place and traces of gut contents preserved in many; detached fragments are exceedingly rare. It is therefore probable that the animal was benthonic, and so could have been trapped alive when the muddy sediment slumped and formed a suspension in which carcasses were transported and buried. *L. superlata* lacked eyes but had long, annulated, presumably sensory appendages anteriorly; *E. brocki* and some, but by no means all, Burgess Shale arthropods are similar in these respects. Strikingly unusual in *L. superlata* are the great appendages, which bore not only the three annulated flagellae but also a shaft terminating in fixed claws, and the curtain along the sides of the body formed by the overlapping lamellate lobes, below which the inner, jointed branches do not project. This latter is in sharp contrast to *E. brocki*, in which the inner branches are conspicuous and adapted for walking. A peculiarity of *L. superlata* is that the two branches of the appendage are not separated by a thin layer of rock (implying that they were held close together in life), and the inner branch was not constructed with the hinge joints characteristic of walking legs. The proximal portions of the biramous limb series are poorly preserved, but if the coxae had been gnathobasic, and therefore well sclerotized, one would have expected them to be preserved, as they are in *E. brocki*. It has not been possible to identify gut contents as in

Sidneyia inexpectans (Bruton 1981, p. 648), although the phosphatic debris is similar but fine-grained. As shown in §6(*c*), the assumption by Simonetta (1970, p. 38) that *L. superlata* swallowed worms whole is without foundation, the supposed worm being a phosphatic infilling of the gut. Examination of the hindgut shows the presence of coarse particles suggesting that *L. superlata* was a detritus feeder, yet there is no trace of gnathobases or of a labrum covering the mouth, which was apparently ventrally directed. We suggest (figure 112*b*) that the animal moved about close to the bottom by swimming, with the great appendages swung back to lie under the body in the midline, a 'feathered' position preserved in some specimens (figure 83, plate 14). The gill branches are depicted in various positions of a metachronal rhythm that involved a cycle of six branches. The appendage may have flexed about the most proximal portion, the surface of the gill branch not lying in an exsaggital direction but at an angle to the body, as suggested by the overlap between successive branches. Thus the branch would have been swung outward and forward, and backward and inward, the leg branch moving and flexing with it (figure 113*b*, *c*). In figure 112*b* the first cephalic gill branch is almost at the maximum outward position, the second cephalic branch has started the inward movement (cf. figure 113*b*), and the first trunk branch is at the maximum inward position. The second and third (figure 113*c*) trunk branches are at successive stages of the outward swing, the fourth at almost the maximum outward position, repeating the position of the first cephalic branch. Thus water is being either sucked in (between branches 1c and 2c, 2c and 1t) or forced out (between branches 1t–4t) in waves along the body, so that the gill branch surfaces could have been oxygenated and the animal pushed forward through the water. The filaments of the gill branches may have aided in oxygen absorption, but would also have aided in directing water currents. While moving in this way the flagellae of the great appendages would have been used to explore the environment, and figure 112*a* suggests a possible resting and feeding position, achieved by flexure of the body. By greater flexure and some digging in the bottom, the mouth could have been brought closer to the sediment surface. In this position the mud could have been stirred up and pushed toward the midline, by the distal claws and fringing setae of the leg branches, and the mouth may have been suctorial.

(*e*) *Affinities*

The class or subclass Merostomoidea (Størmer 1944, p. 134; *in* Moore 1959, p. *O*29) was proposed to include genera from the Burgess Shale, all of which have now been re-examined: *Sidneyia* in Bruton (1981), *Naraoia* in Whittington (1977), *Molaria* and *Habelia* in Whittington (1981), and *Emeraldella* and *Leanchoilia* herein. Discussion of affinities has made clear that these genera are so disparate that this taxon loses any usefulness, is impossible to define, and does not imply any but the most generalized relationship. Thus the cephalon of *Sidneyia* had only one appendage, an uniramous antenna which was pre-oral. *Emeraldella* had two uniramous appendages of which the first was pre-oral and antenniform, and four biramous post-oral appendages. *Leanchoilia* had three appendages, a multiramous pre-oral great appendage which had three long, annulated extensions, and two biramous post-oral appendages. Whether this total number of head appendages, *Sidneyia* (one), *Emeraldella* (six) and *Leanchoilia* (three), reflects original segmentation is not known, and from the fossils it is not possible to say how many primary segments may have been lost during tagmatization of the head. Nor is it possible to say whether the apparent pre-oral position is primary or secondary. Thus discussion on fossil arthropod relationships based on head segmentation (Stürmer & Bergström 1978; Bergström 1971;

Simonetta & Delle Cave 1981) appears to be largely irrelevant and, at best, speculative. In trying to classify *Leanchoilia*, Walcott (1912, 1931), Fedotov (1925) and Simonetta & Delle Cave (1980, 1981) pointed to its crustacean features, while Henriksen (1928), Hutchinson (1930) and Størmer (1944) argued more strongly for supposed merostome characters. Raymond (1935, p. 216) considered the Crustacea to have been derived from forms with a 'trilobite limb' and features like those found in *Leanchoilia*, and on balance referred it to that group. In terms of the assumed feeding method (§6(*d*)), the prehensile limb of *Leanchoilia*, hanging below the body and attached to some form of flattened coxa, does resemble that of the crustacean *Hutchinsoniella* (Hessler 1969, fig. 41D), though it differs from this and the contemporaneous Burgess Shale crustacean *Canadaspis* (Briggs 1978) in lacking setae along the midline and modified oral appendages. Simonetta & Delle Cave (1981, p. 423) included *Leanchoilia* in the Leanchoiliidae Raymond, 1935, and argued (1980, p. 9) for a relationship between members of this family and crustaceans. However, restudy (Whittington 1981) of the genera on which their arguments depended removes the bases for their view.

Thus *Leanchoilia* cannot be grouped with *Sidneyia* or *Emeraldella*, nor is it a crustacean. It may be most closely related to *Actaeus*, and less closely to *Alalcomenaeus* (Whittington 1981; also Bergström 1980, p. 35), which had a pair of great appendages on the head followed by a number of undifferentiated biramous appendages of which the outer branch had broad, flattened marginal filaments (inner branches differ and reflect different food-gathering methods). Using principal-component analysis, Briggs & Whittington (1981) show how these three genera form a closely knit group, and their study also serves to illustrate the limited number of ways in which the Burgess Shale arthropods were equipped to solve the problems of feeding, locomotion and sensing. This makes recognition of distinct taxonomic groups difficult, since it was only later that certain of these solutions were fixed in combinations that allow the present arthropod groups to be recognized.

(*f*) *Synonymous and unrecognizable species*

The following six species are all considered to be subjective synonyms of *L. superlata*.

Emeraldella micrura

The holotype, U.S.N.M. 139213, figured by Walcott (1912, p. 205, fig. 9), is a poorly preserved, incomplete, dorsal compression from the Raymond Quarry, about 22.6 m (75 ft) above the Phyllopod Bed. The shape of the trunk tergites and tail spine is like those of *L. superlata*, a conclusion that Walcott apparently reached later, according to a label in his handwriting that accompanies the type specimen (see also: Henriksen 1928, p. 9; Størmer 1944, p. 84).

Bidentia difficilis

The holotype, U.S.N.M. 57701, figured by Walcott (1912, p. 173, pl. 30, fig. 1), is listed in the text (Walcott 1912, p. 175) as also coming from beds equivalent to the Raymond Quarry (35k/10), though on the plate explanation the locality is given as the Phyllopod Bed (35k). The specimen is an oblique dorso-ventral compression showing details of left and right great appendages, the latter of which in Walcott's illustrations (later reproduced by Dechaseaux *in* Piveteau 1953, p. 33, fig. 7*b*) was grossly retouched and the 'segmentation' is nothing more than crinkle marks accentuated by weathering. Parts of the three shafts of both great appendages are recognizable, not two as stated by Walcott, but the trunk appendages are too poorly preserved to show any detail. Nevertheless, details of the trunk tergites and tail spine leave little doubt that this species is probably the same as *L. superlata,* and Walcott's remark that the tail consists of paired rami is not correct. This observation was probably based on a second specimen to which Walcott refers, which was originally labelled incorrectly as being the counterpart but has since been renumbered U.S.N.M. 189262 and figured as *Waptia fieldensis* by Simonetta & Delle Cave (1975, pl. xli, fig. 4).

Leanchoilia major

The holotype, U.S.N.M. 83944 (Walcott 1931, p. 9, pl. 13, fig. 3), is an incomplete parallel compression, having both part and counterpart, and showing the left side of a cephalic shield, nine trunk tergites (the ninth poorly preserved but visible on the part, which was not illustrated by Walcott), and a tail spine of *Leanchoilia* type. Several specimens were apparently available to Walcott but now only the holotype is labelled *Leanchoilia major.* It is unique in having two fewer trunk tergites than specimens of *Leanchoilia superlata.* However, no appendages are present and it is difficult to maintain the species based on a single, incomplete specimen.

Leanchoilia amphiction

This species, established by Simonetta (1970, p. 39, pl. iii, fig. 4; pl. iv, fig. 1; see also Simonetta & Delle Cave 1975, pl. xxx, figs 5, 6), is based on two specimens, each with counterparts, the holotype, U.S.N.M. 155660 (see also Whittington 1981, p. 353), and U.S.N.M. 155639. The counterpart of the latter has been prepared to show cephalic and trunk appendages behind the left great appendage. This appendage, both here and on the holotype, is not segmented as shown in the reconstruction (Simonetta & Delle Cave 1975, pl. 1, fig. 2) and is no different from that of *L. superlata. L. amphiction* was mainly distinguished on details of the tail spine, said by Simonetta (1970) to be composed of two rectangular lamellae lacking lateral spines. Faint traces of lateral spines are visible when the tail of the holotype is examined in reflected light, and the 'two rectangular lamellae' are no more than the doublures of a laterally compressed tail spine of *L. superlata* type. *L. amphiction* is here considered a junior subjective synonym of *L. superlata* and the holotype is probably a small individual of the latter.

Leanchoilia persephone

Of the six specimens identified by Simonetta (1970, p. 38), four, U.S.N.M. 155635 (Simonetta 1970, pl. iv, fig. 3; Simonetta & Delle Cave 1975, pl. xxx, fig. 3), 155646, 155652, 155653 (Simonetta & Delle Cave 1975, pl. xxxi, figs 3, 5, 7), are unrecognizable, leaving the holotype, 155651 (Simonetta 1970, pl. iv, fig. 4; Simonetta & Delle Cave 1975, pl. xxxi, fig. 6, *non* fig. 2), and 155649 (Simonetta & Delle Cave 1975, pl. xxxi, fig. 4). These two remaining specimens have a tail spine of *L. superlata* type, and 155649, preserved from the ventral side, also has a poorly preserved left great appendage. They should probably be referred to *L. superlata* and show no characters upon which a separate taxon can be based.

Leanchoilia protogonia

The holotype, U.S.N.M. 155648 (Simonetta 1970, p. 38, pl. iv, fig. 2; Simonetta & Delle Cave 1975, pl. i, fig. 6; pl. xxxi, fig. 1), is interpreted as being a composite fossil consisting of a specimen of *L. superlata* lying on top of an unidentified organism (Whittington 1981, p. 351).

In 1966 and 1967 a re-investigation of the Burgess Shale (Whittington 1971*a*; Fritz 1971) was undertaken by the Geological Survey of Canada, with the cooperation of authorities of the Yoho National Park and Parks Canada, Department of Indian and Northern Affairs, Ottawa. The Geological Survey of Canada invited H.B.W. to be Chairman of the palaeobiological work, and he is indebted to the Natural Environment Research Council (grant GR3/285) for support of field and laboratory work by him and by D.L.B. Every facility for study of the Walcott collection in the National Museum of Natural History (formerly U.S. National Museum), Washington, D.C., was afforded us by Dr Porter M. Kier and Dr Richard E. Grant. D.L.B. acknowledges financial assistance from Norges Almenvitenskapelige Forskningråd (N.A.V.F.) and the University of Oslo, which enabled visits to Cambridge, U.K., and Washington, D.C., U.S.A. In Oslo Mr R. Jacquet redrew many of the illustrations from original pencil drawings and Mr P. Sundhell redrew the reconstructions. We are deeply grateful to Mr Aa. Jensen for his skill in making the plastic models, and to Mr P. Aas for the photographs of them. In Cambridge enlargements from negatives were prepared by Mr D. Bursill, and Miss Adele Prouse converted pencil drawings into the figures.

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LIST OF ABBREVIATIONS AND SYMBOLS USED IN FIGURES AND TEXT

al	alimentary canal
am	anterior margin
ap	anal plate
bfil	filaments of gill lobe b of *Emeraldella brocki*
c	cephalic limb
cox	coxa
cs	cephalic shield
cfil	cephalic filaments
db	doublure
dcl	distal claw
ds	dark stain
eo	excretory organ
exs.	exsagittal
fg	foregut
fgd	foregut diverticulum
fil	filaments
fl	flagellum
fr	fracture
g	gill branch; in *Emeraldella brocki* may consist of two lobes, labelled ga and gb
ga	great appendage; and as subdivision of gill branch
gb	subdivision of gill branch in *Emeraldella brocki*
G.S.C.	Geological Survey of Canada
L	left side of animal, as prefix
lab	labrum
lm	lateral margin
ls	lateral spine
m	mouth
M.C.Z.	Museum of Comparative Zoology, Harvard University
ms	muscle scar
pm	posterior margin
P.M.O.	Palaeontological Museum, University of Oslo
R	right side of animal, as prefix
R.O.M.	Royal Ontario Museum, Montreal
r	articulating ridge
sag.	sagittal
sl	sagittal line
sp	posterior spine
t	trunk tergite or limb of trunk
tr.	transverse, transversely
tu	anterior portion of alimentary canal
tsp	tail spine

Numbers are used serially to denote tergites of trunk (1t, 2t, etc.), annulations of antenna, biramous appendages of cephalon (c1, c2) and trunk (t1, t2, etc.), leg branches in *Emeraldella brocki* (without prefix), and gill branches. They are also used to identify podomeres of a leg branch numbered outwards, and for divisions of the great appendage.


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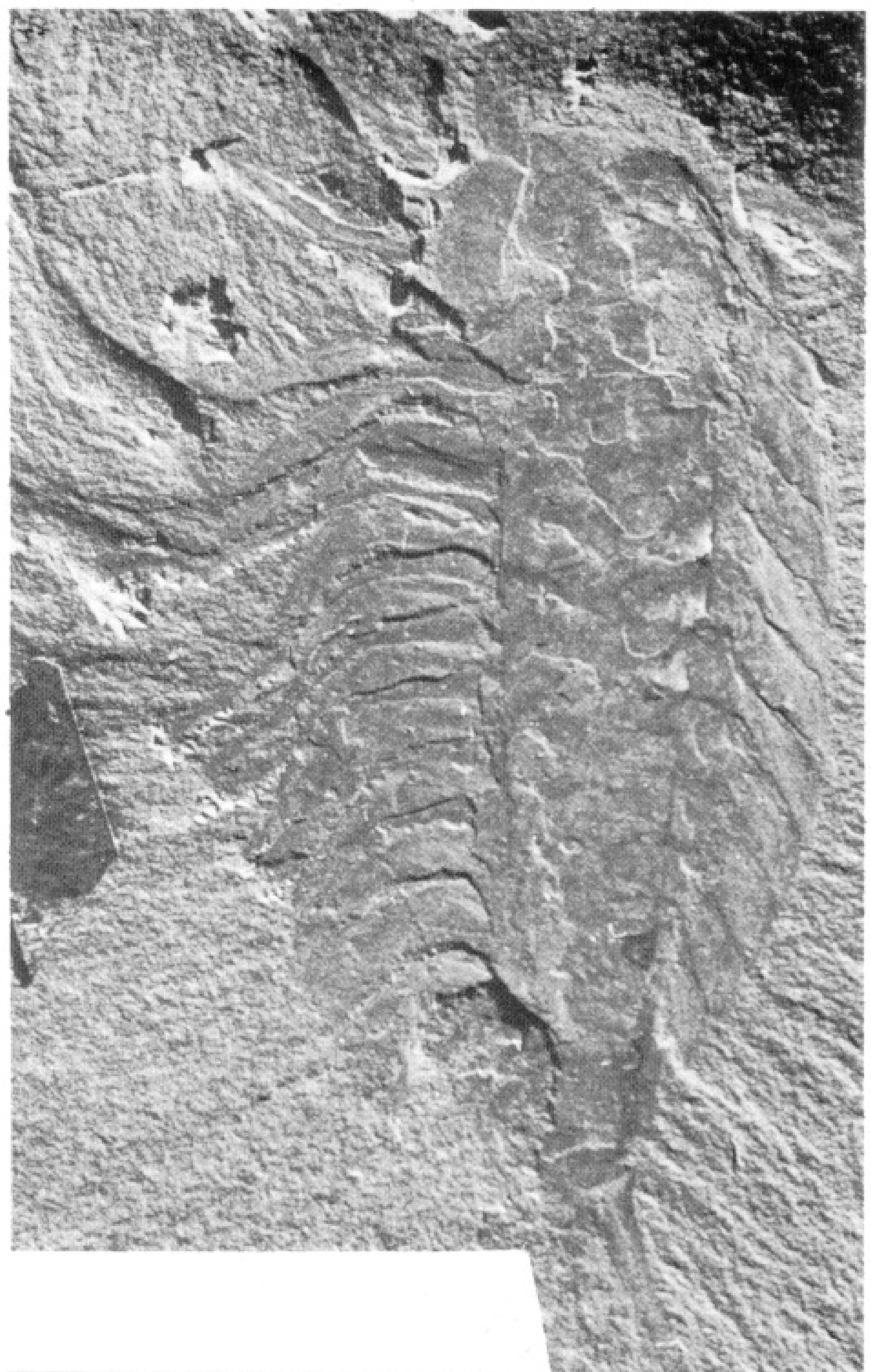
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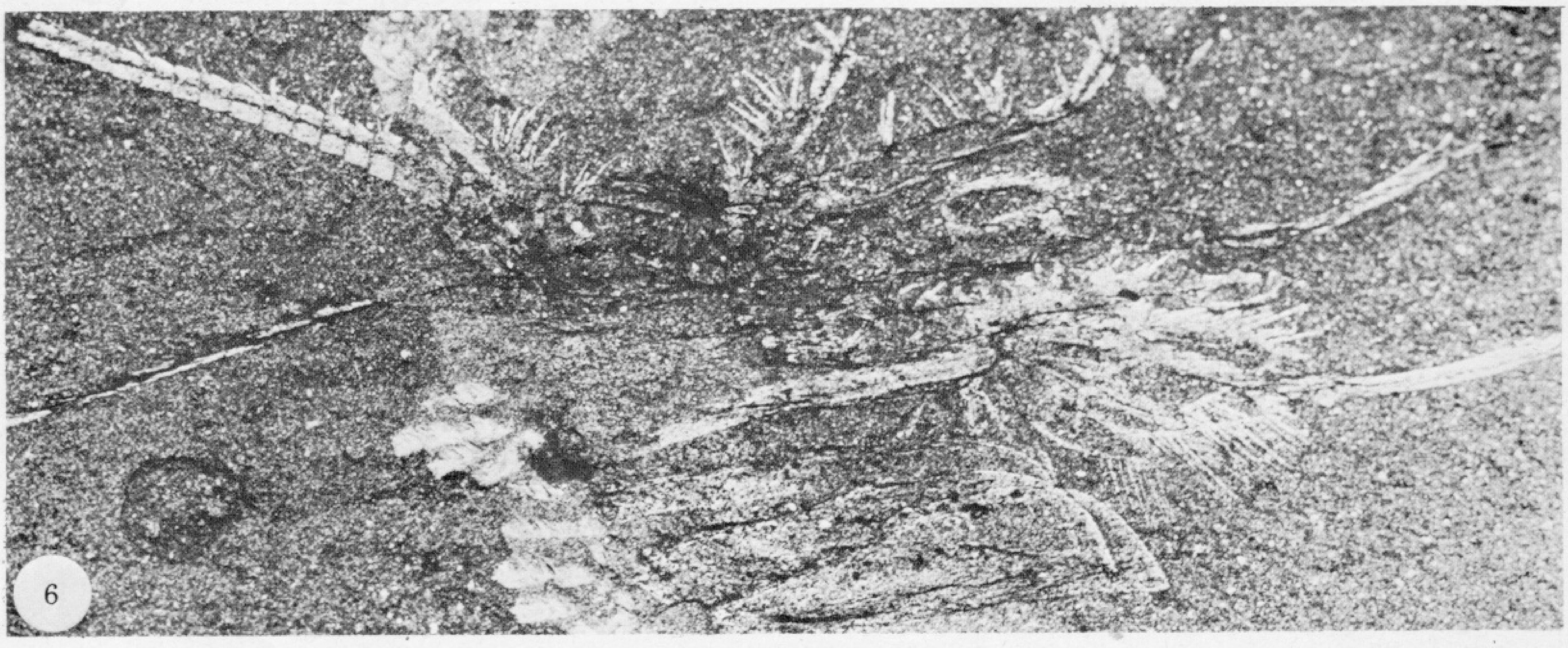
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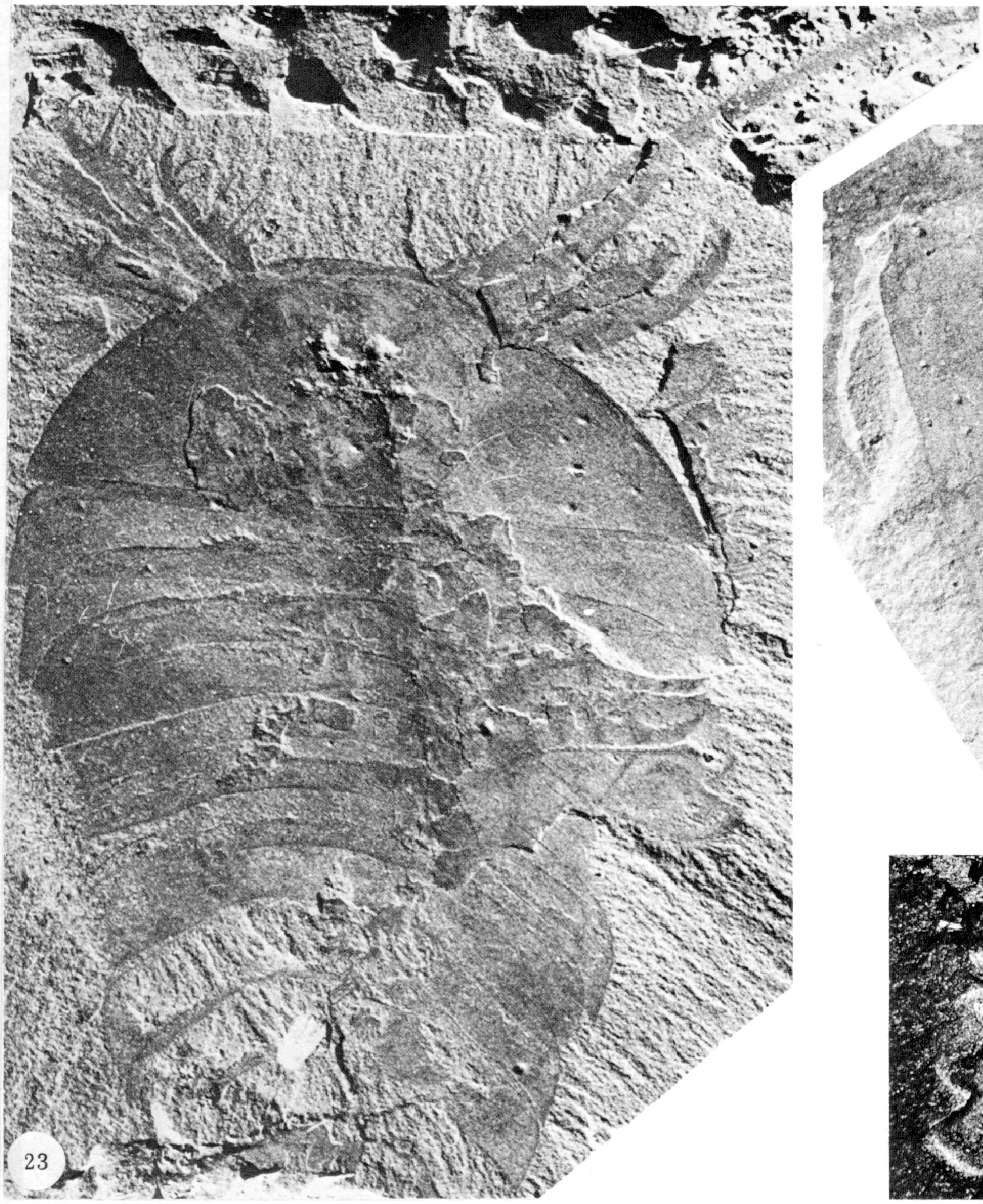
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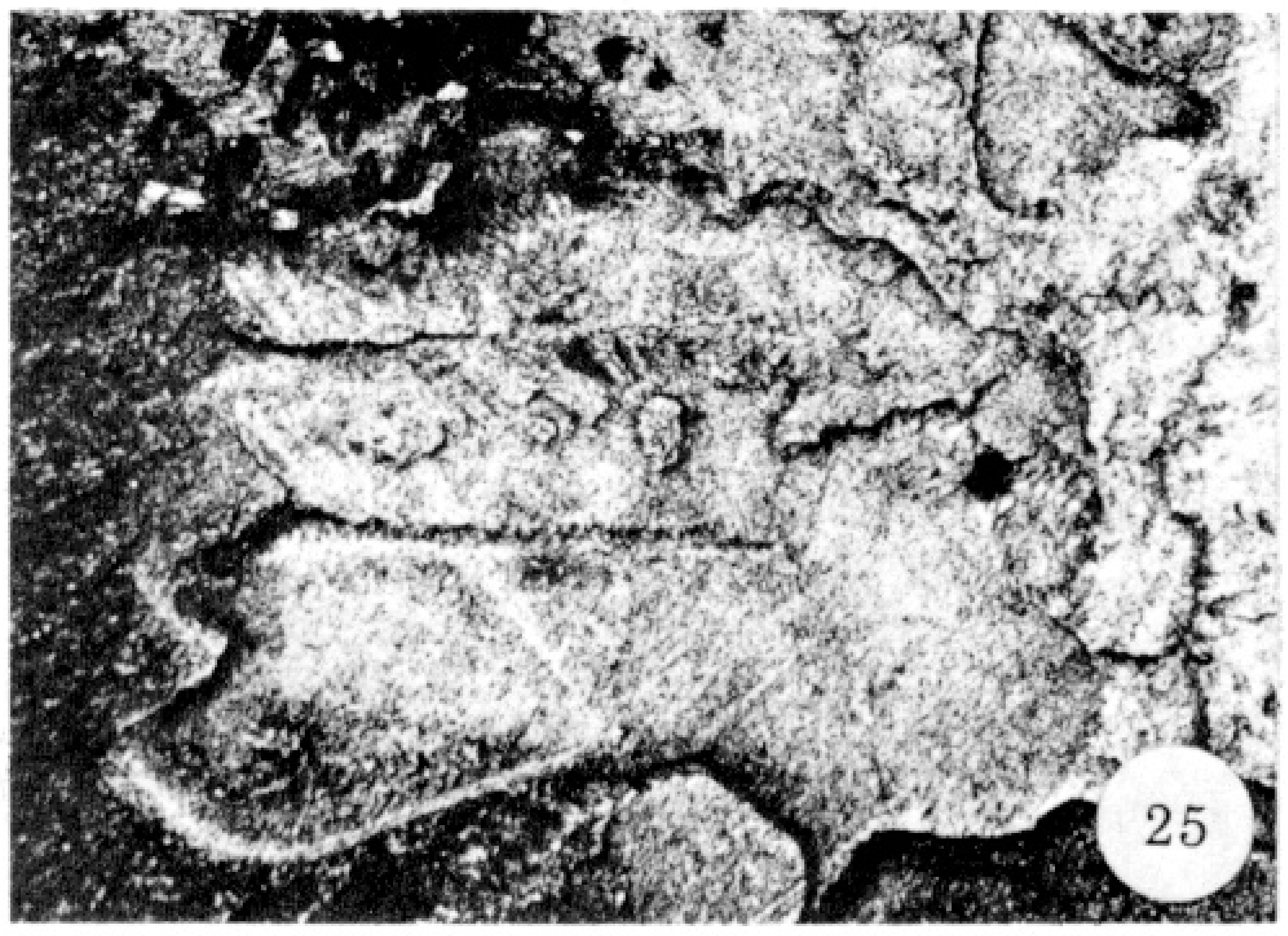
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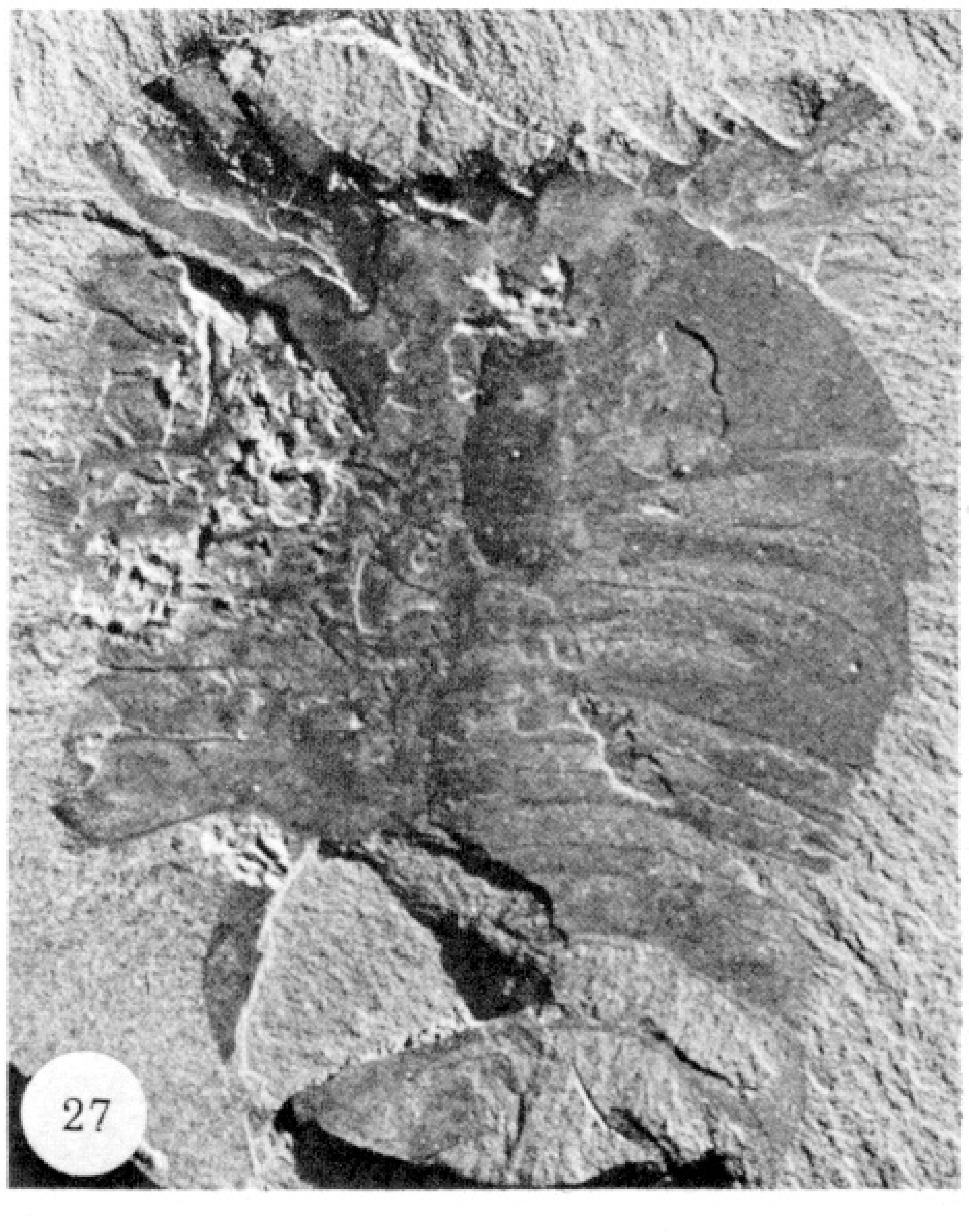
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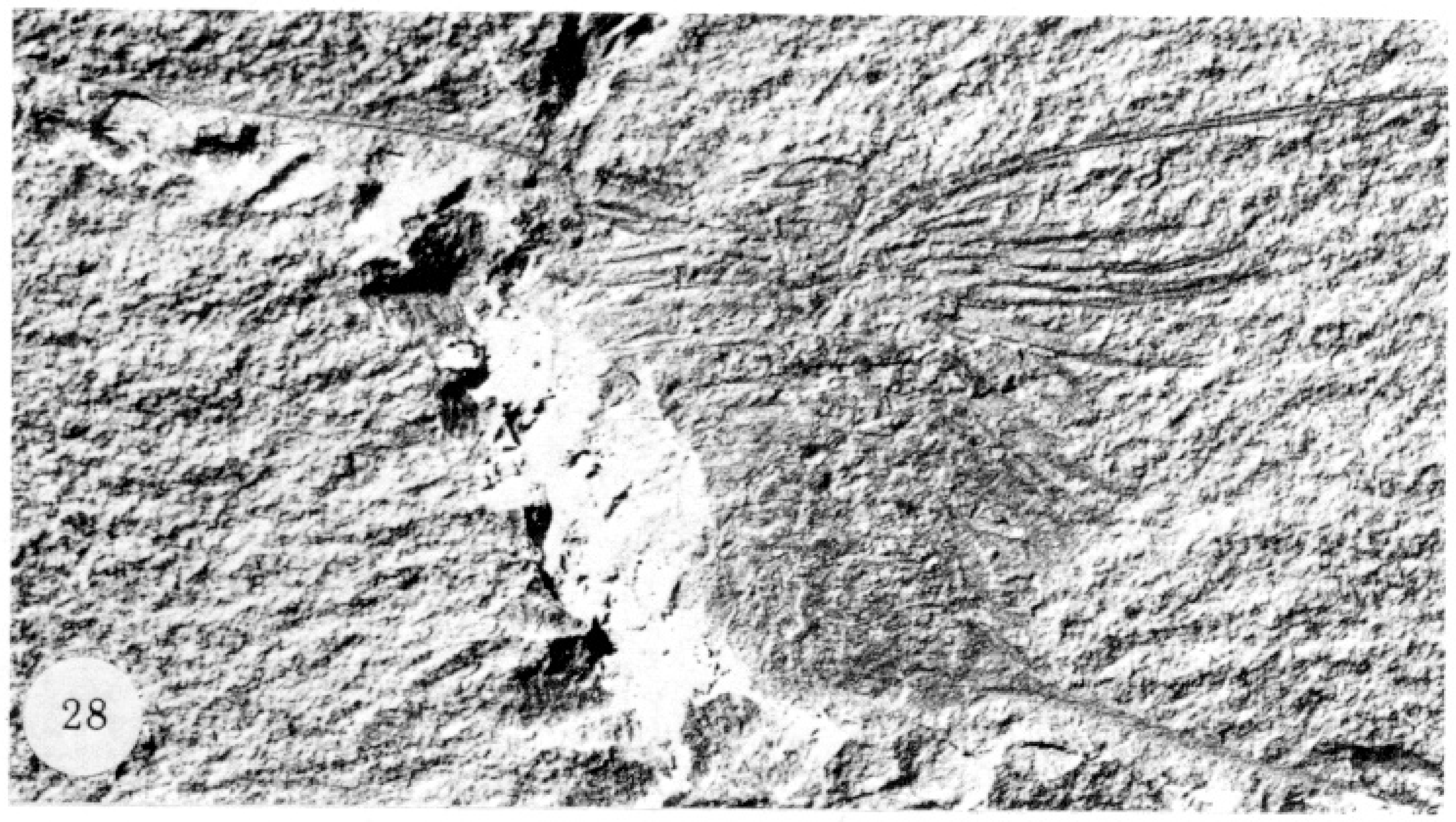
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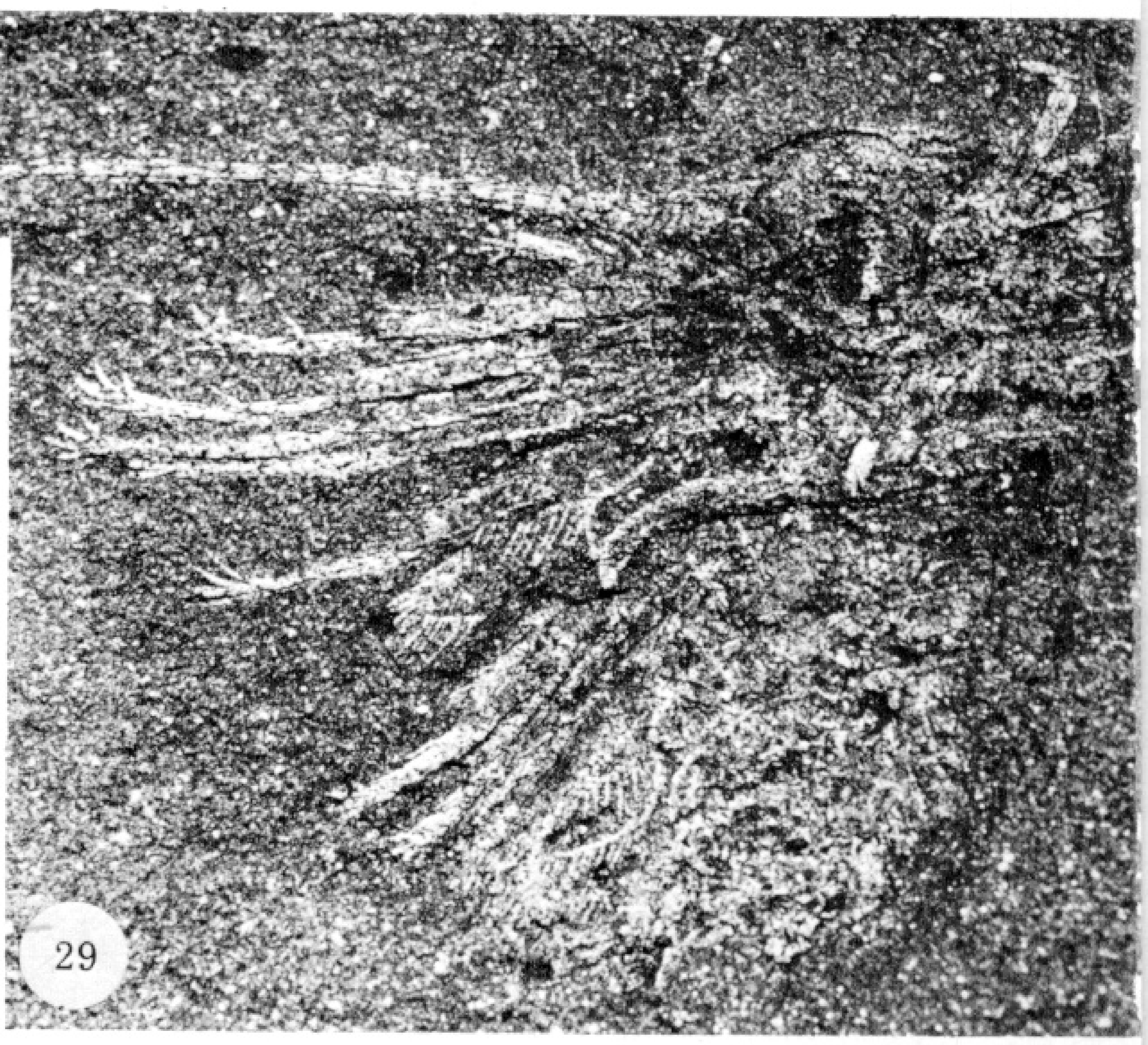
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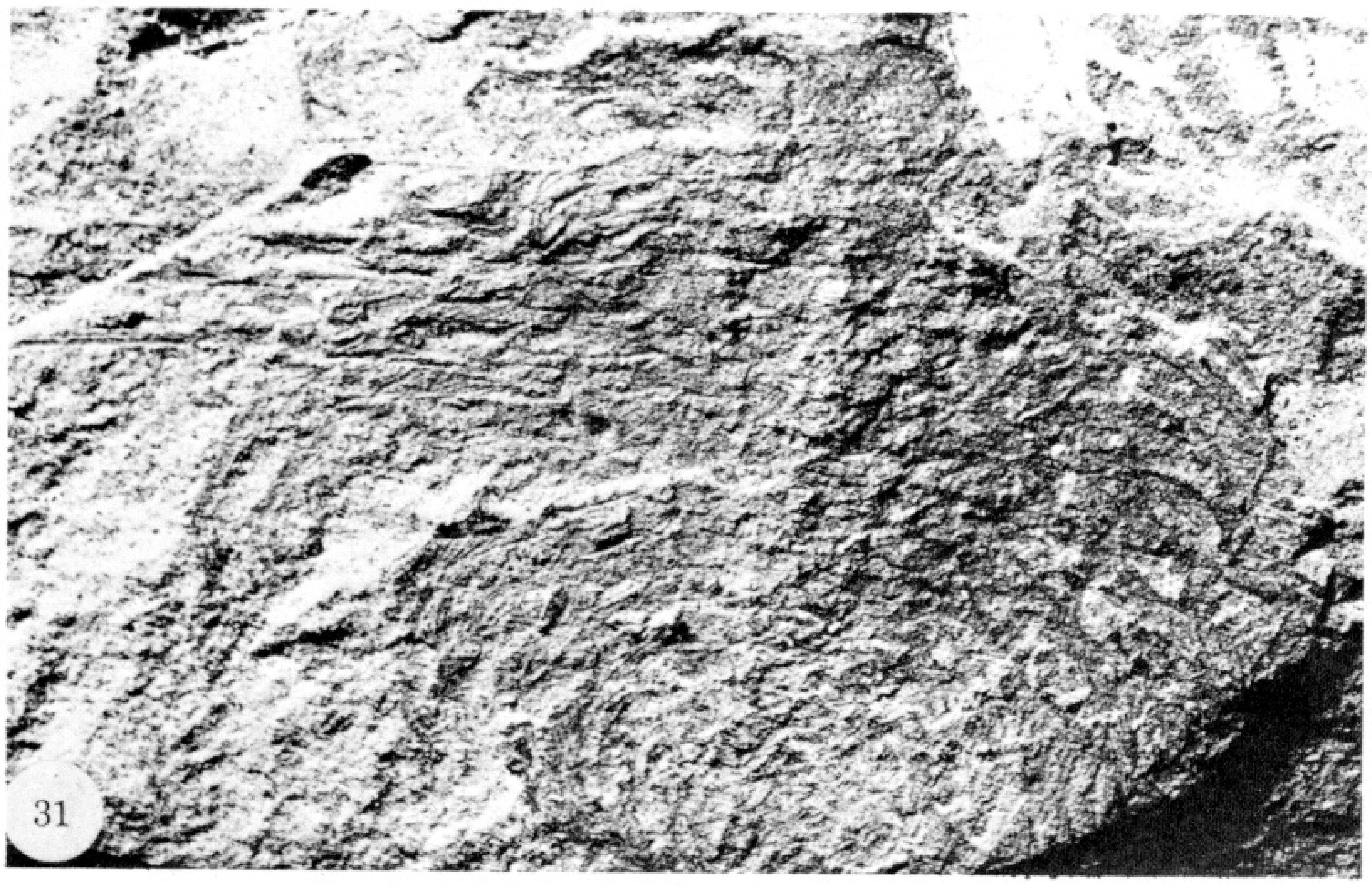
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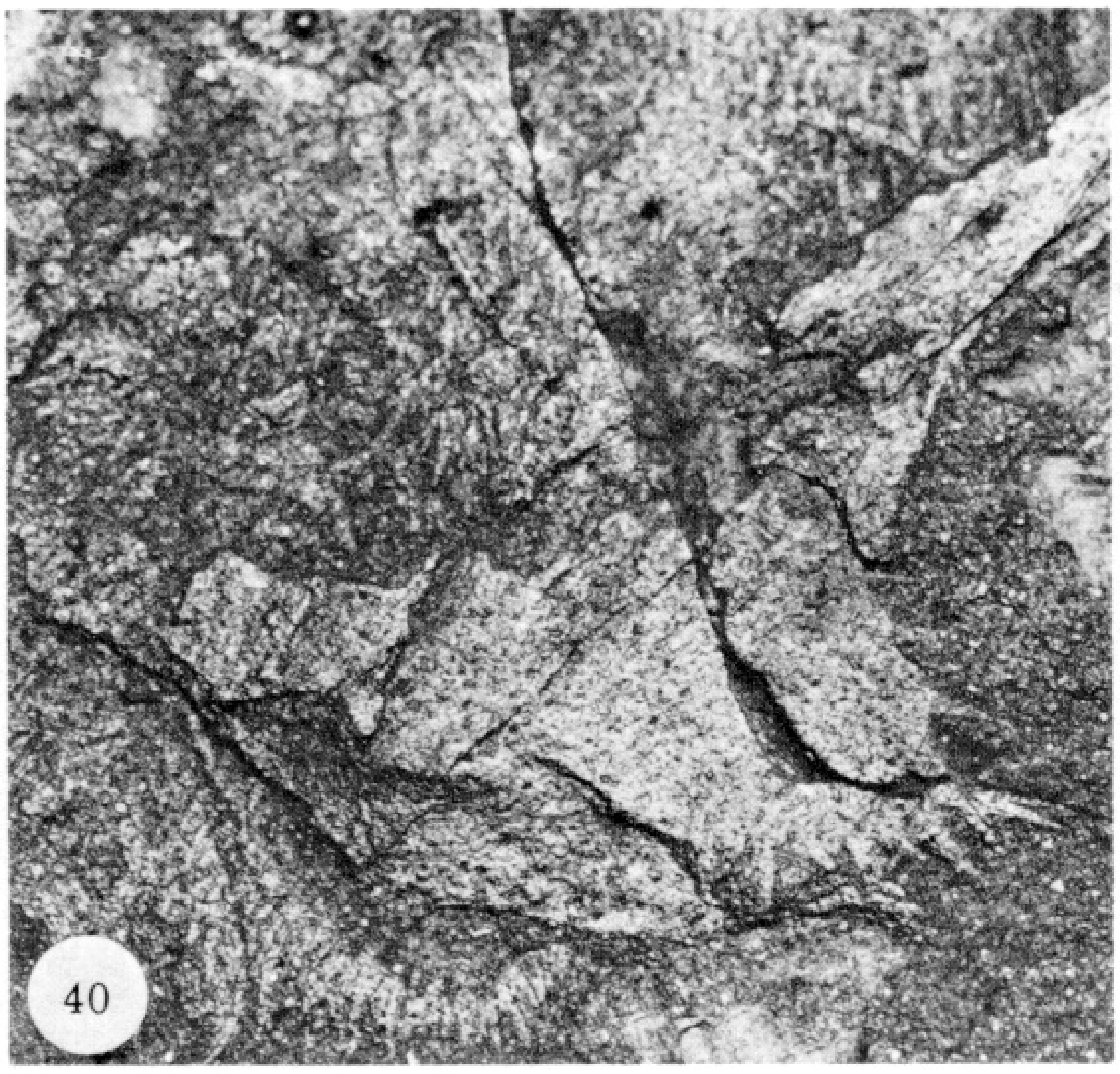
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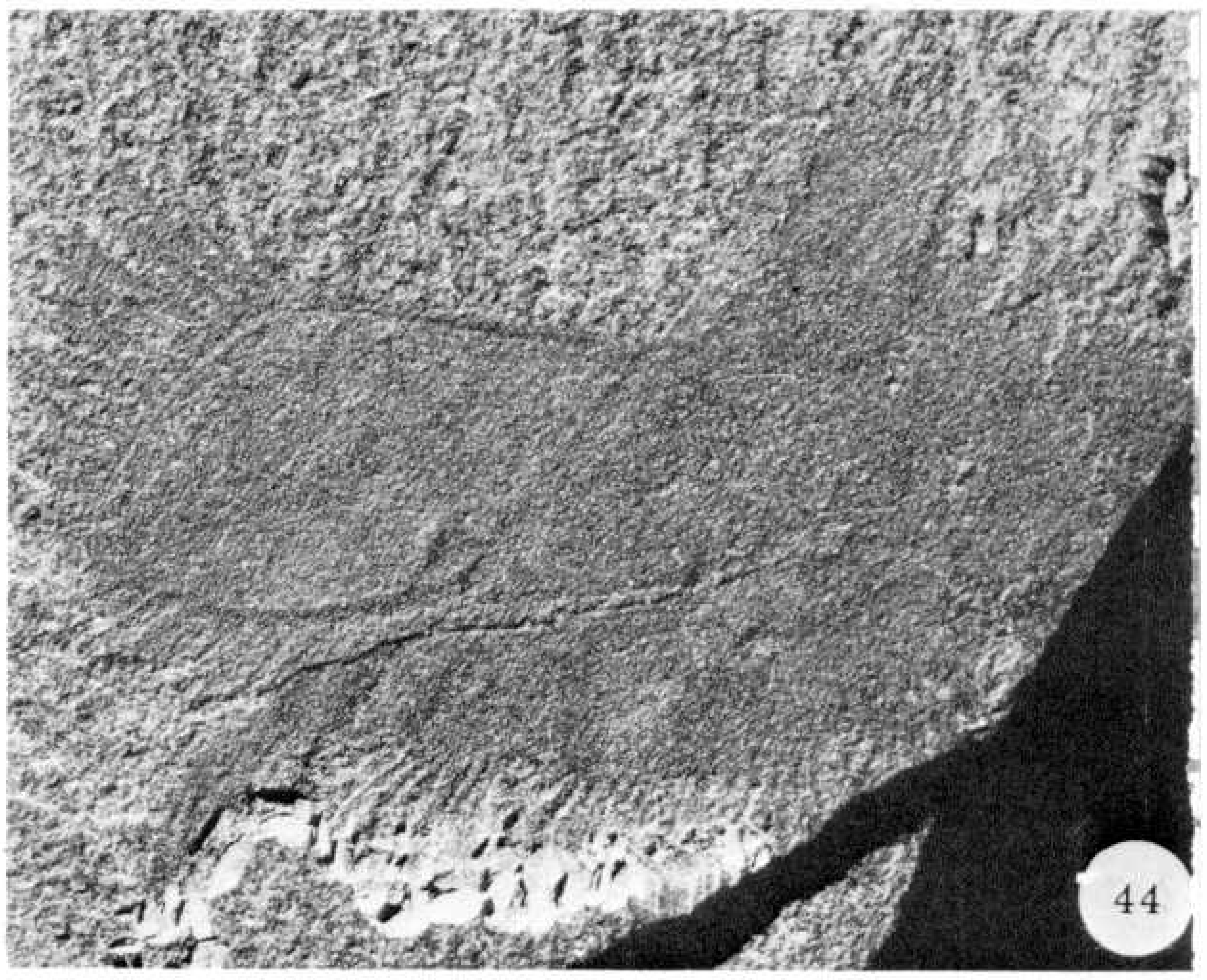
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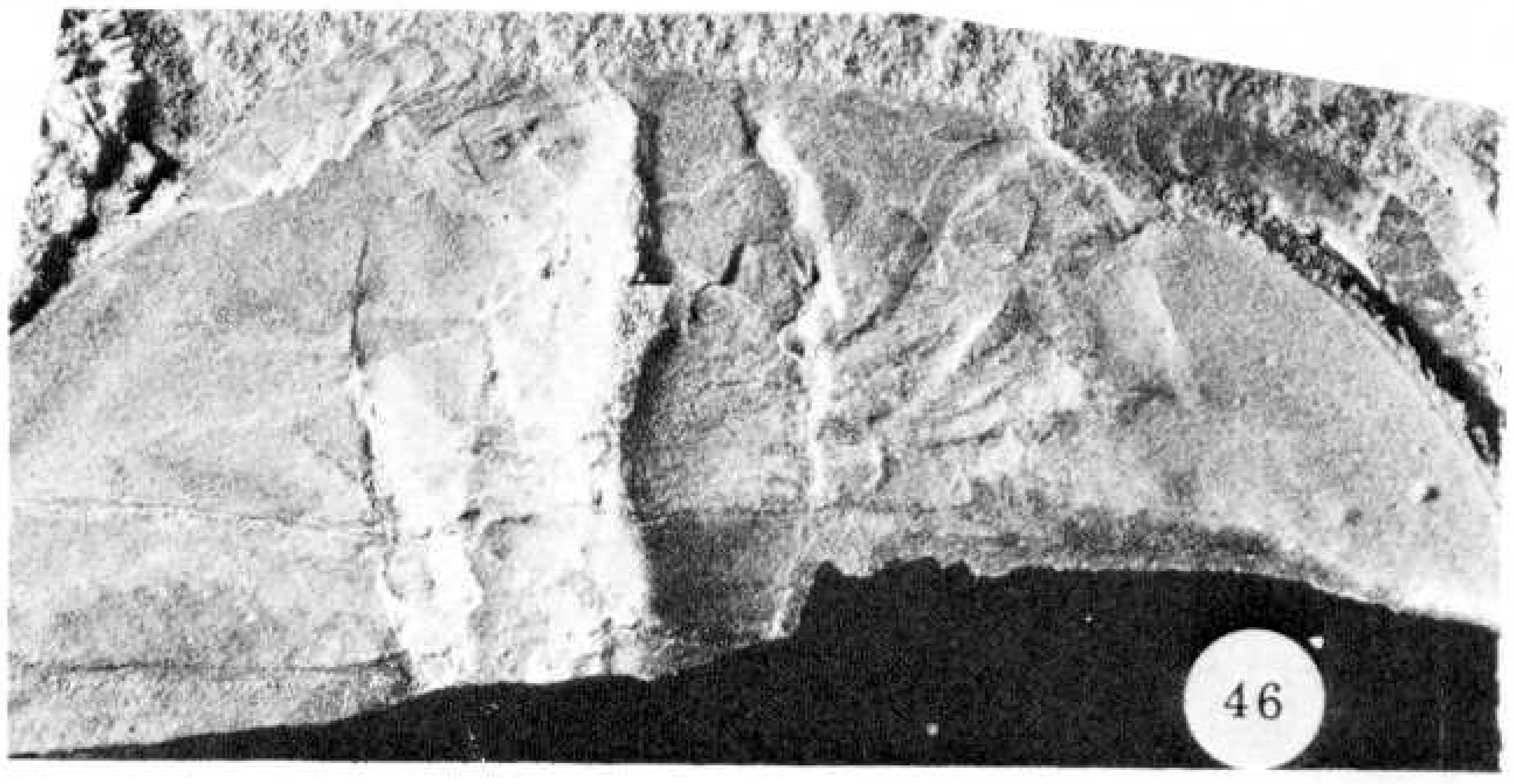
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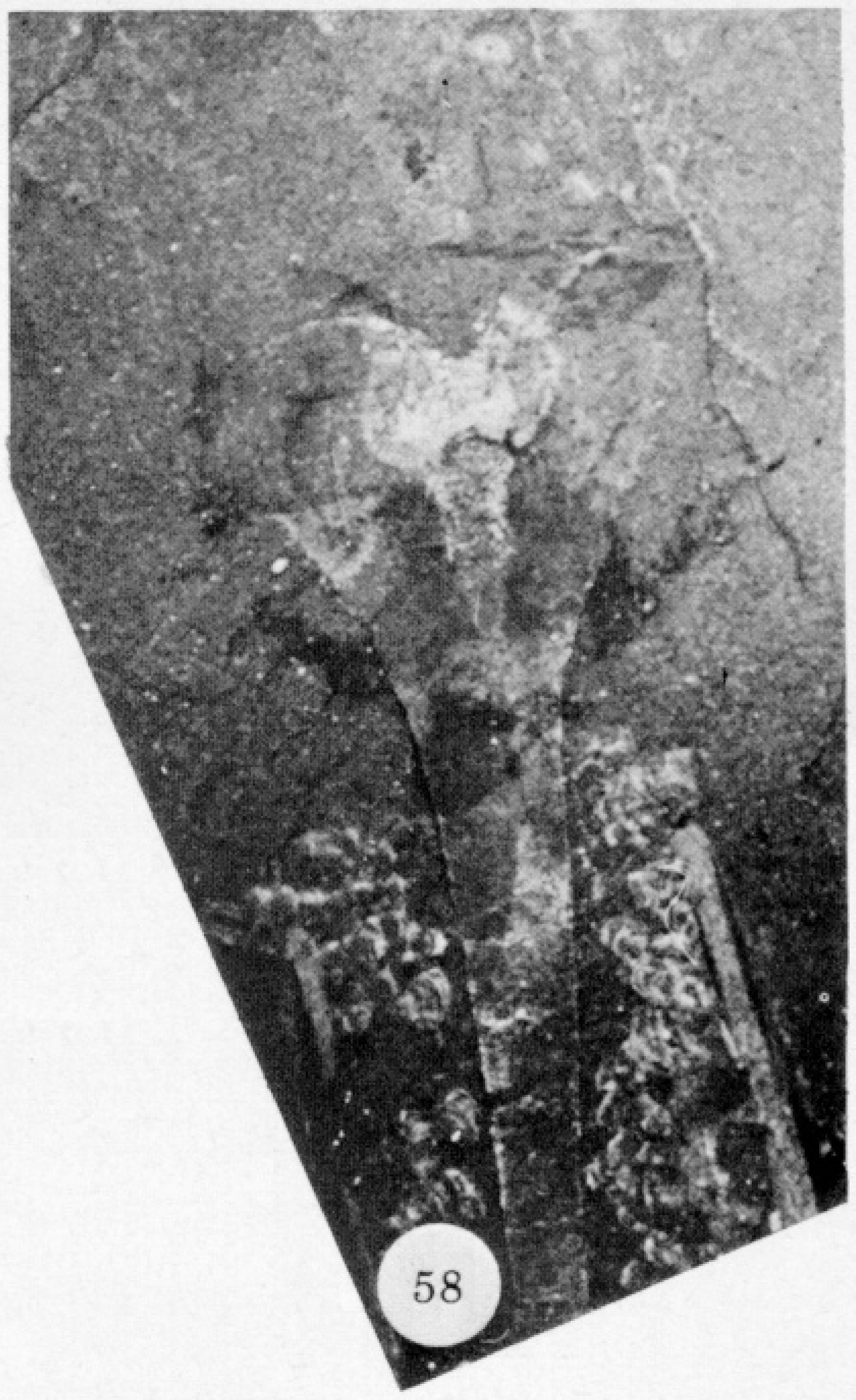
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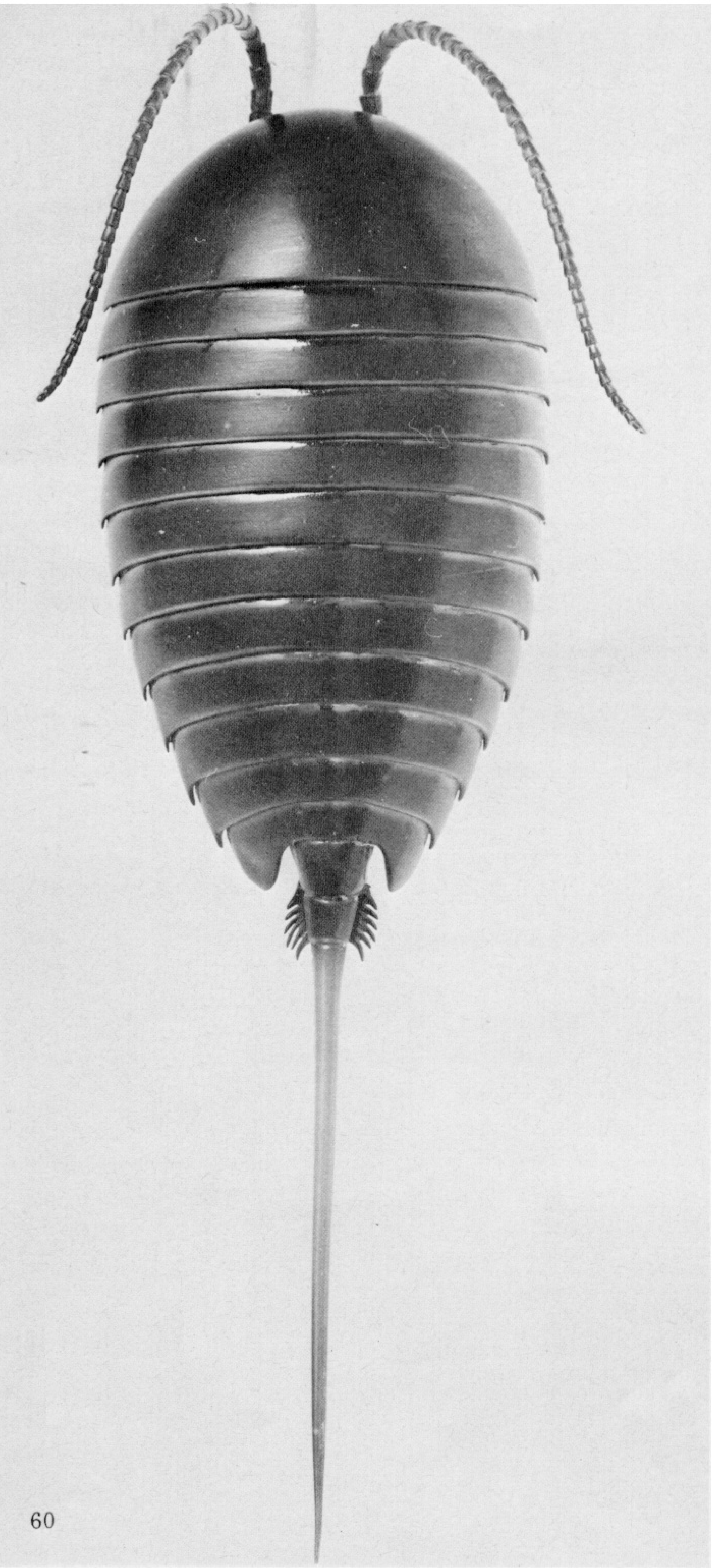

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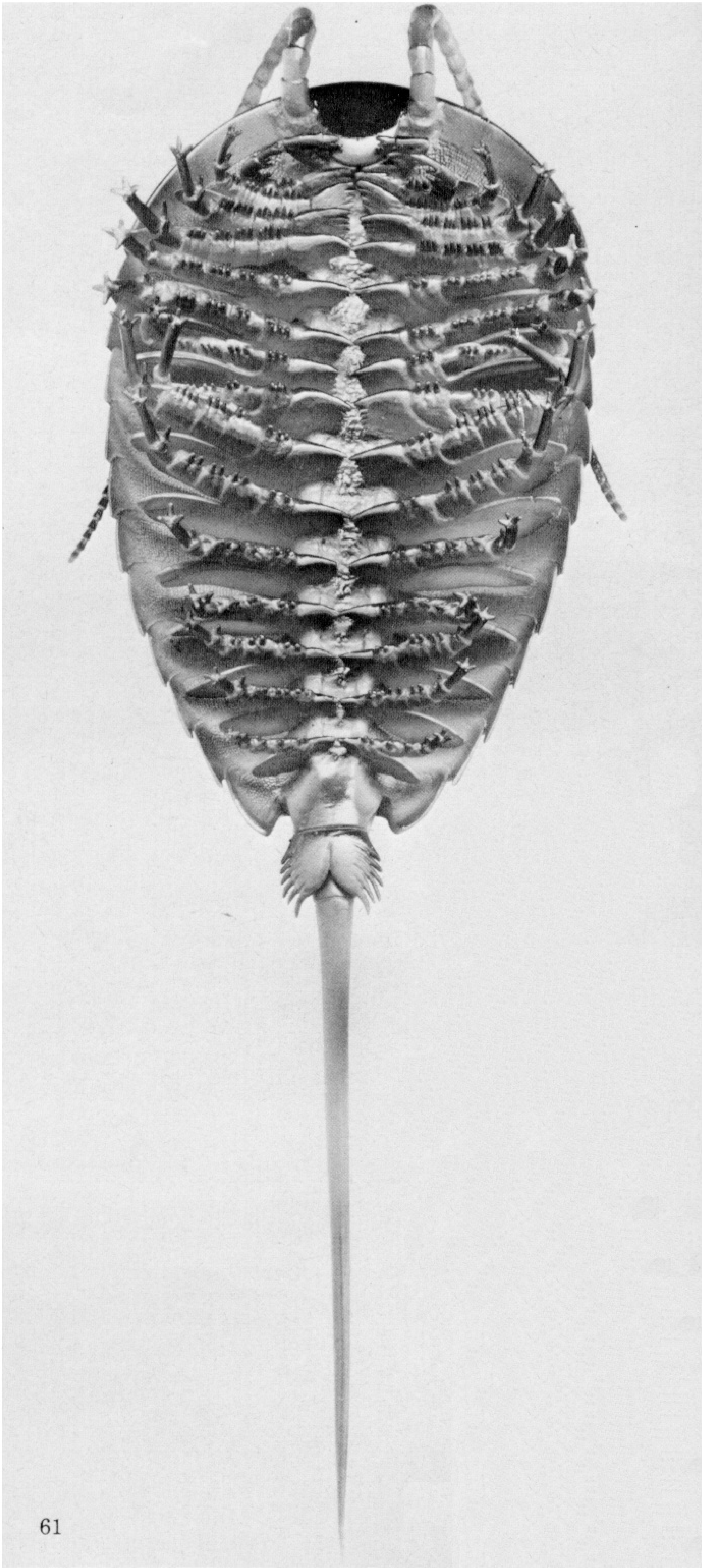

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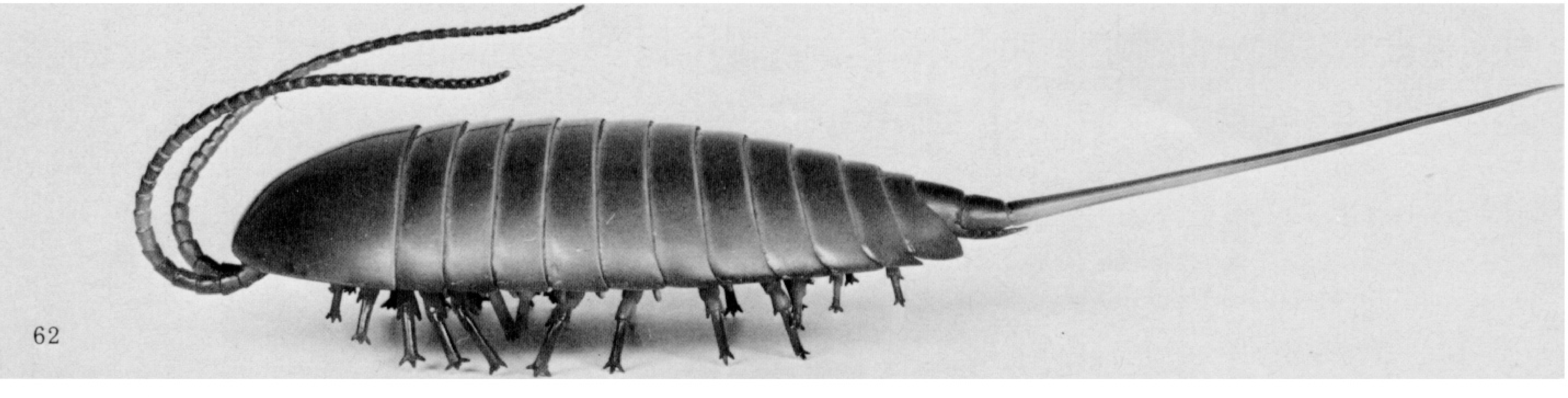

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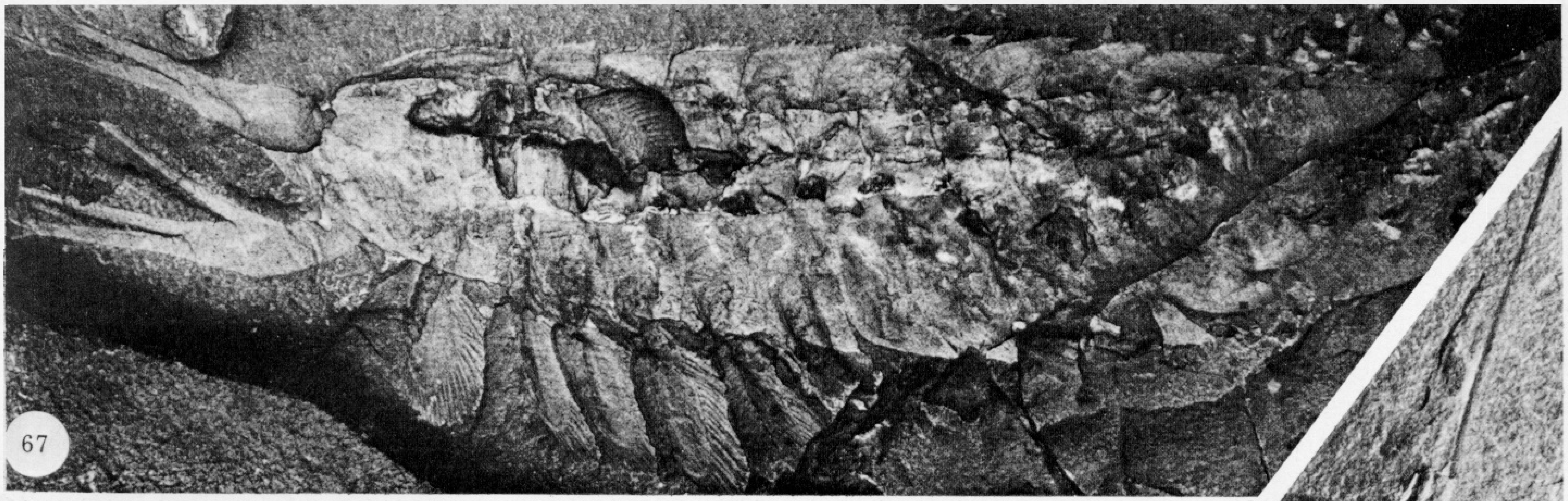
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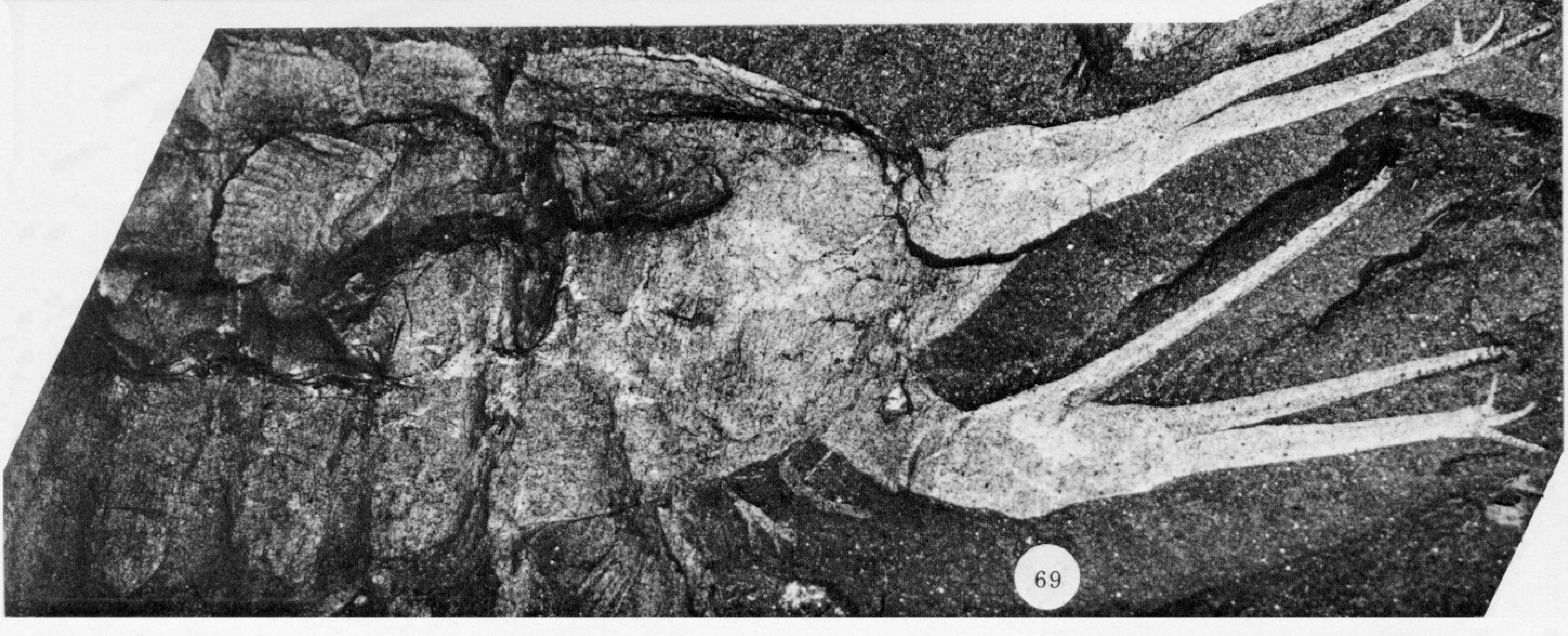
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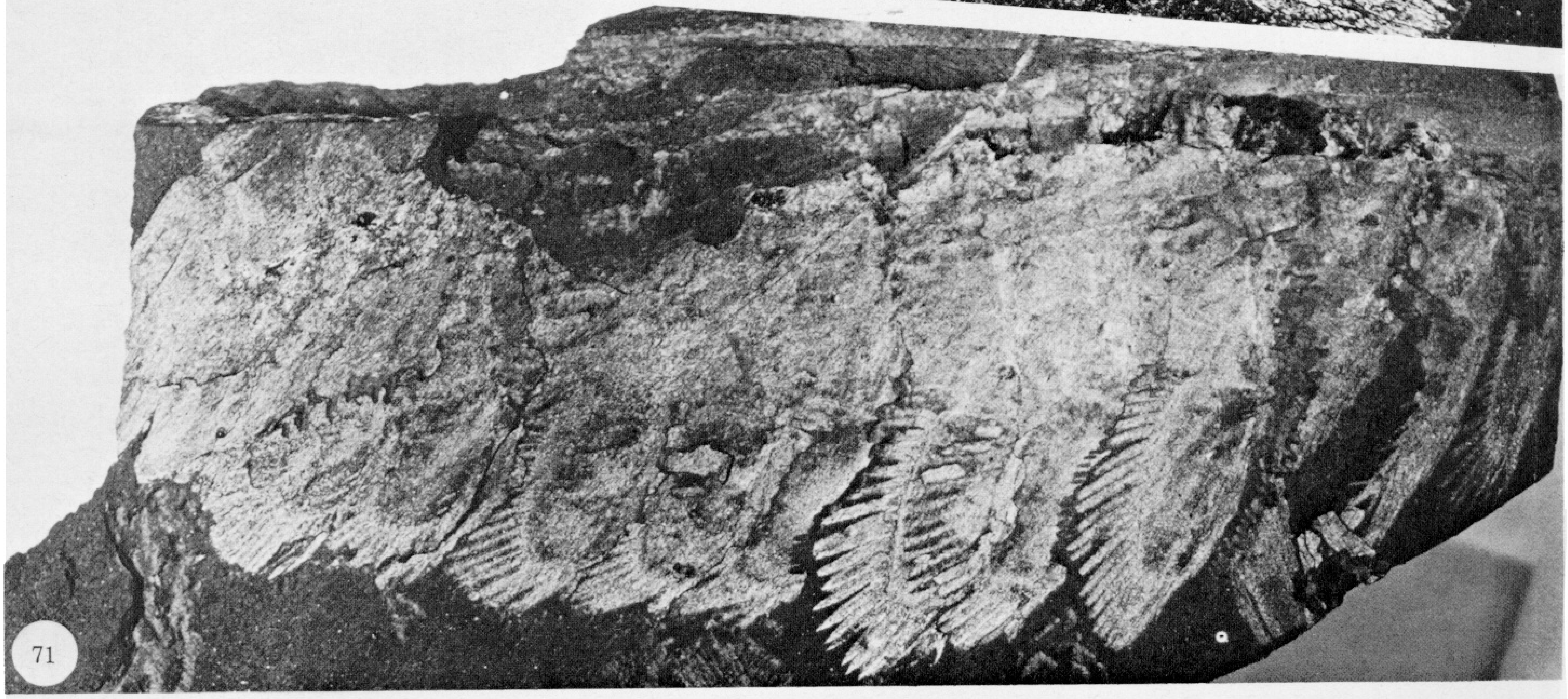

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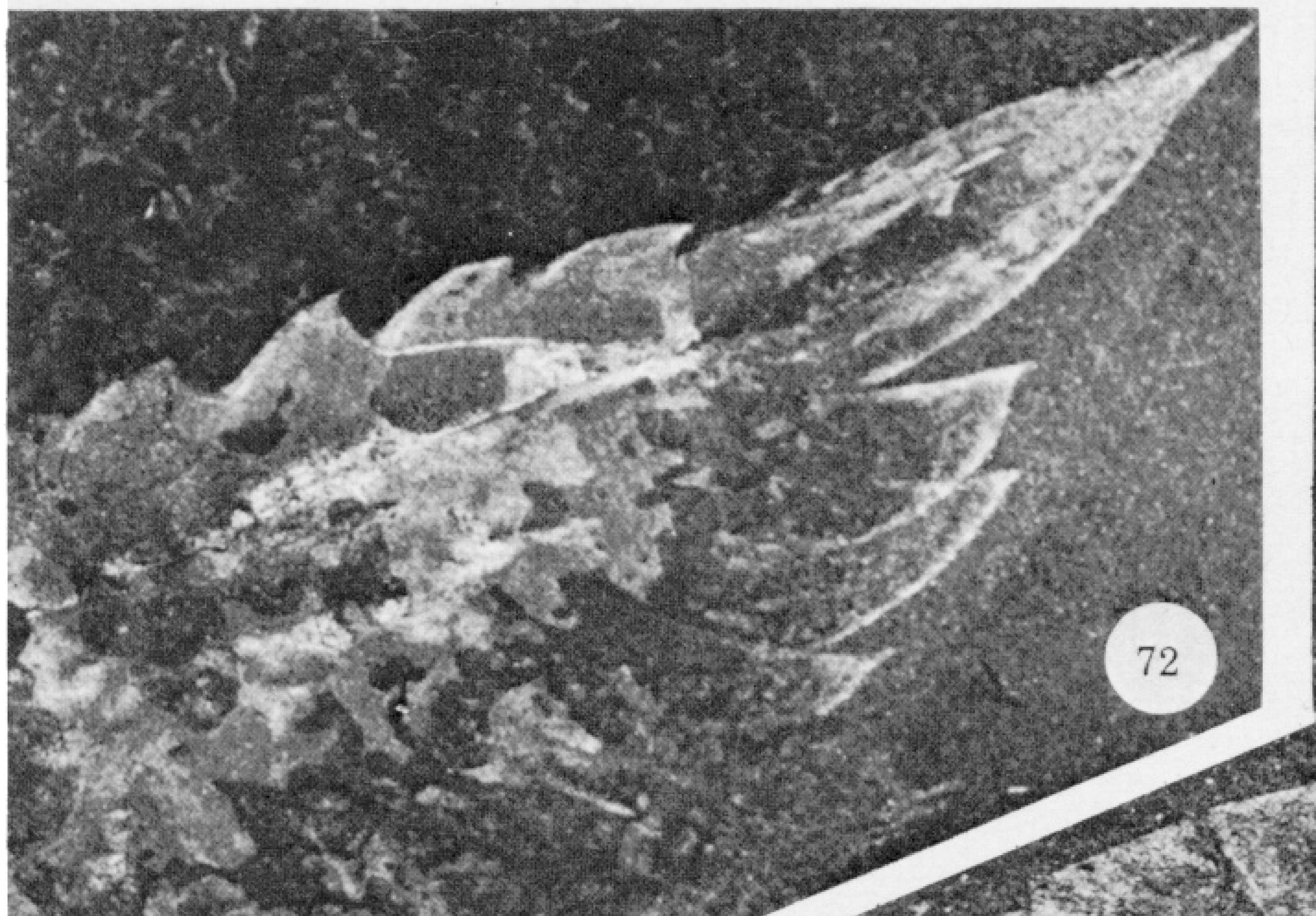

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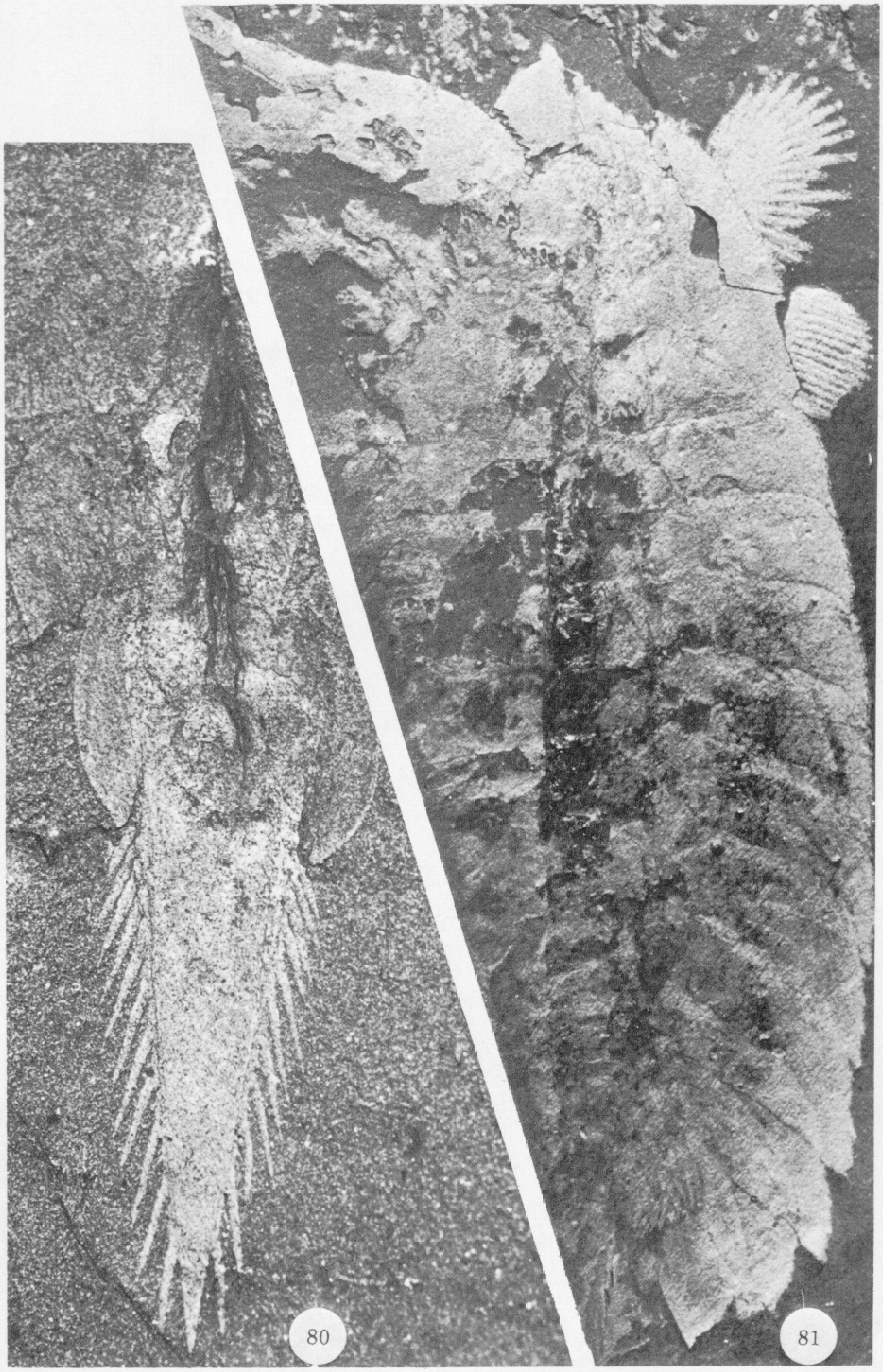

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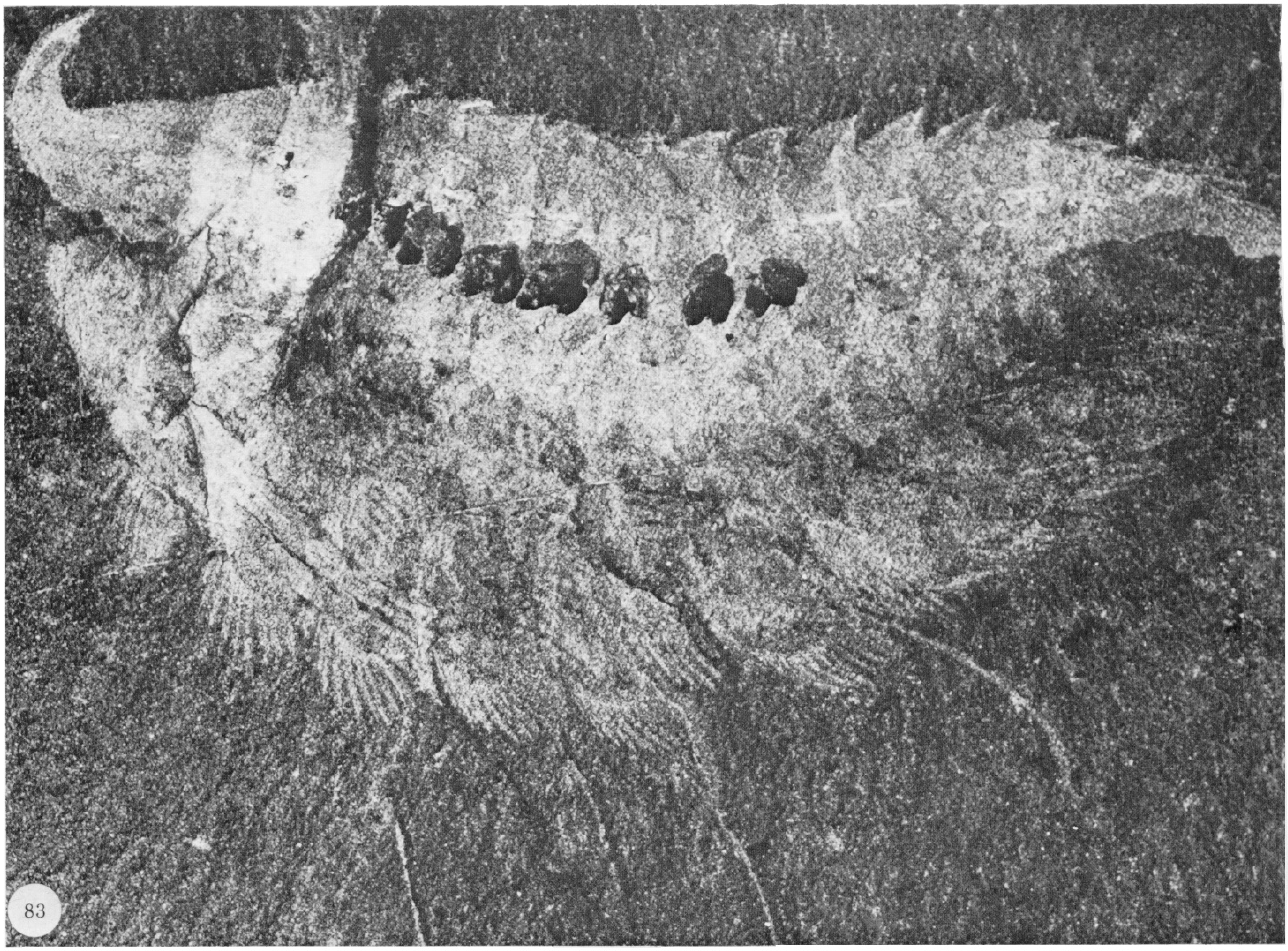

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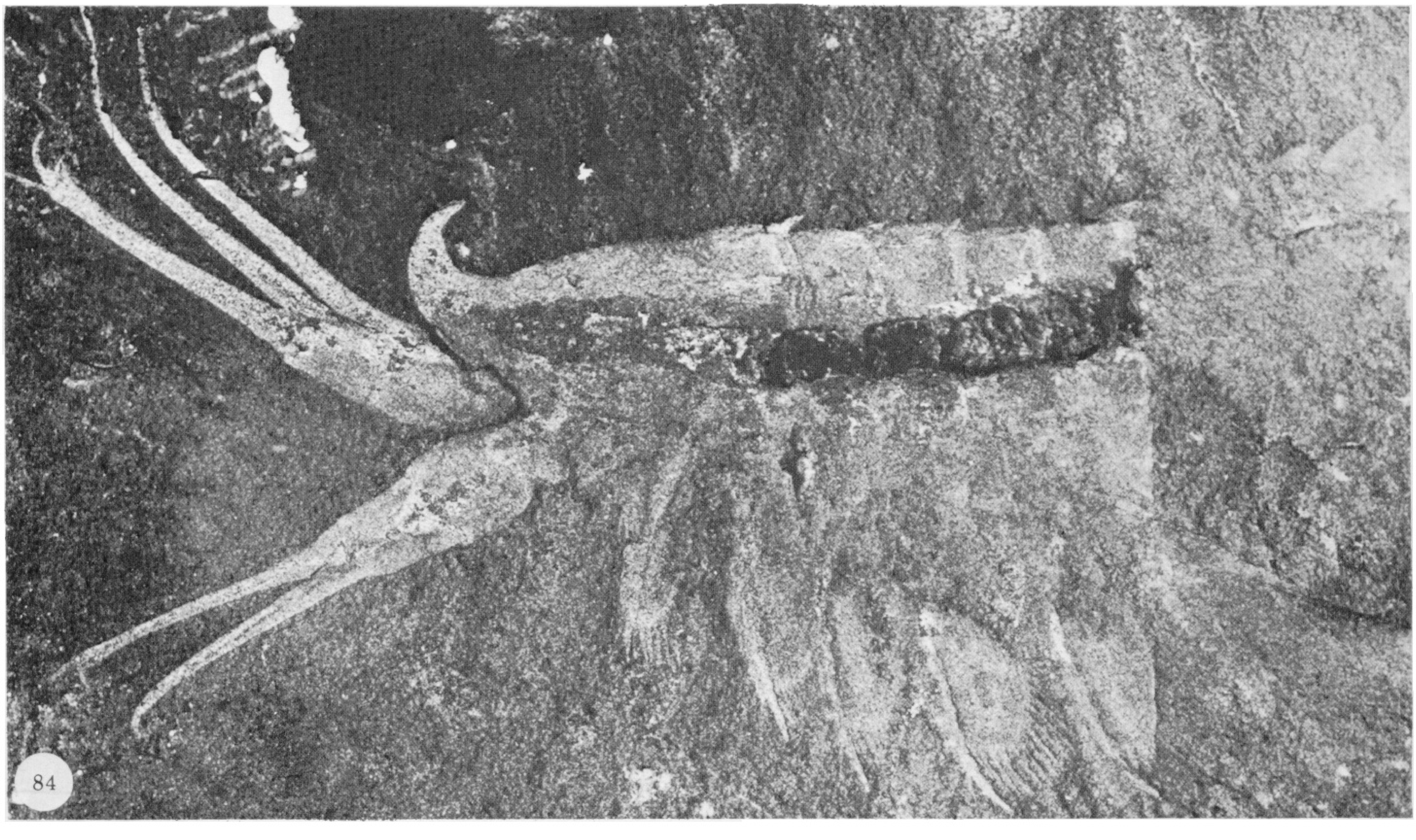

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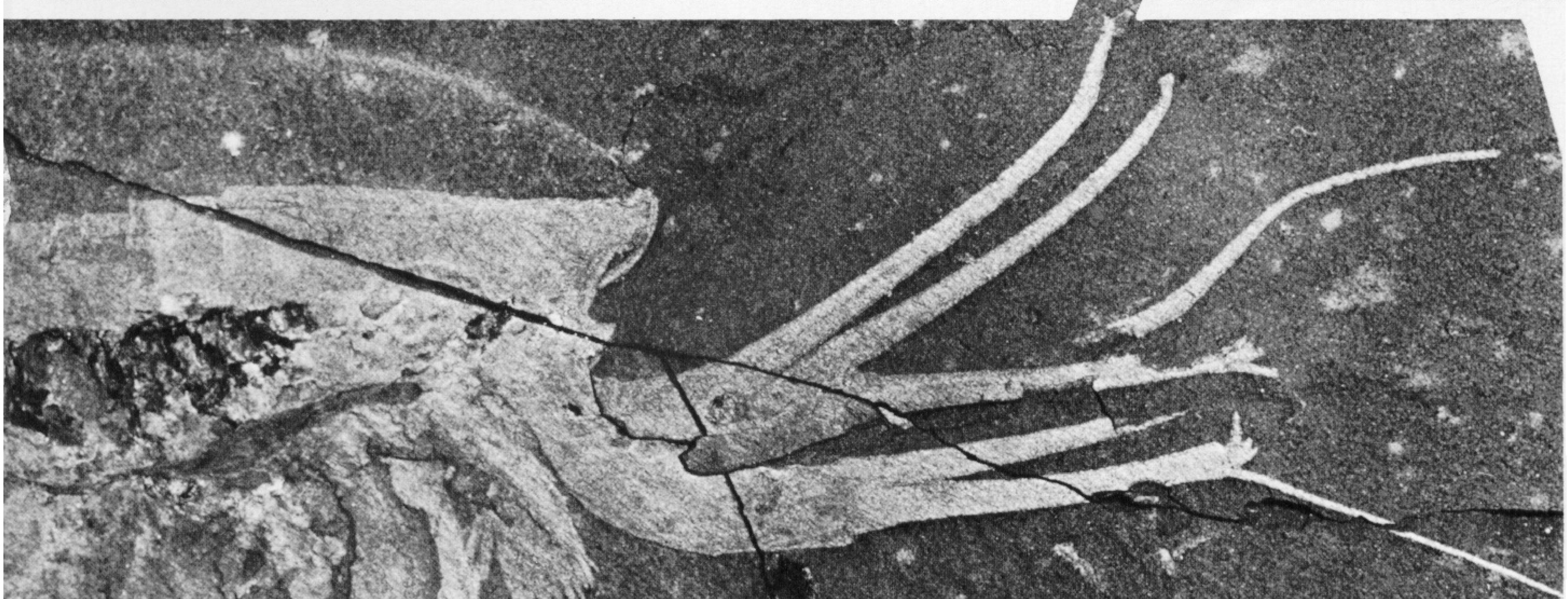

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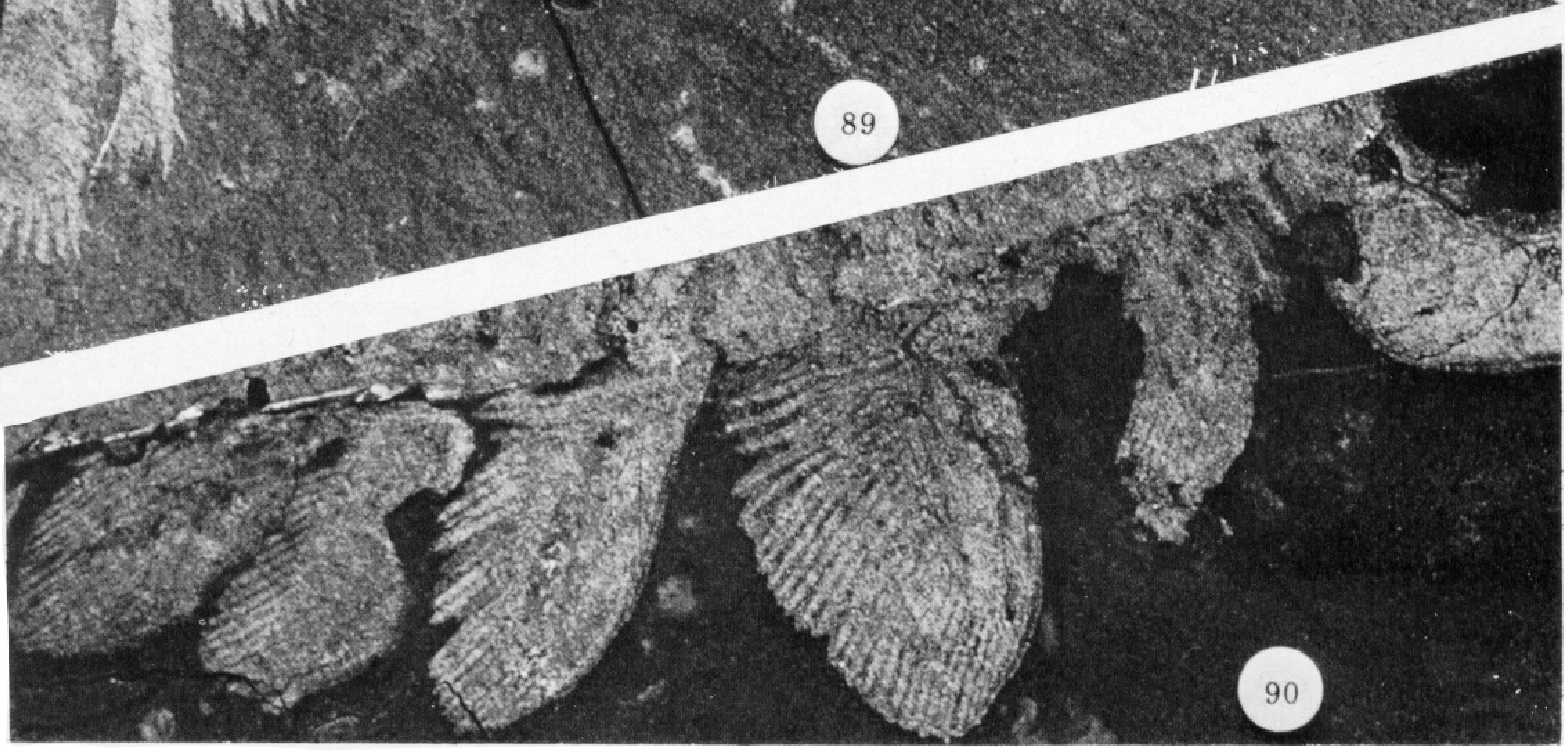

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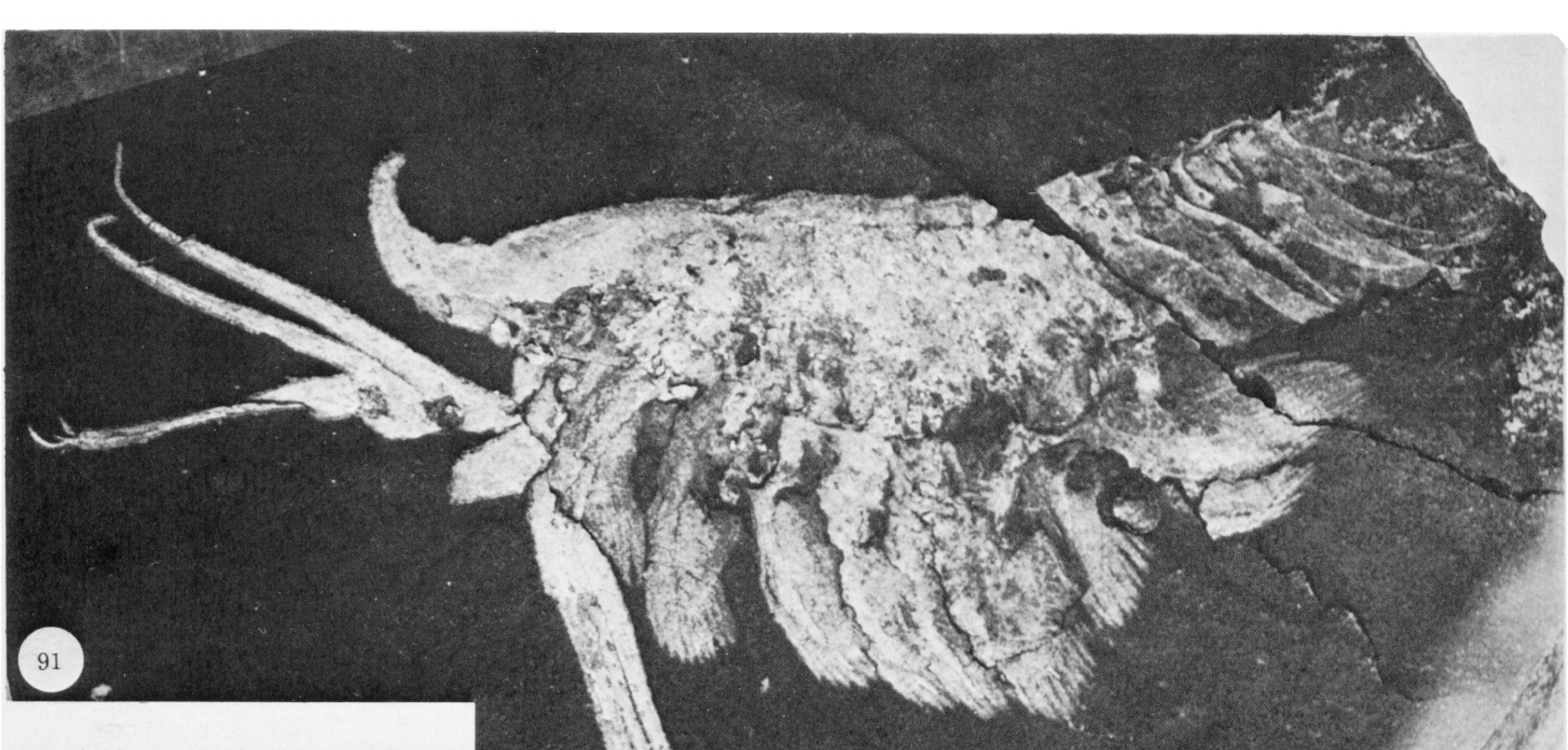

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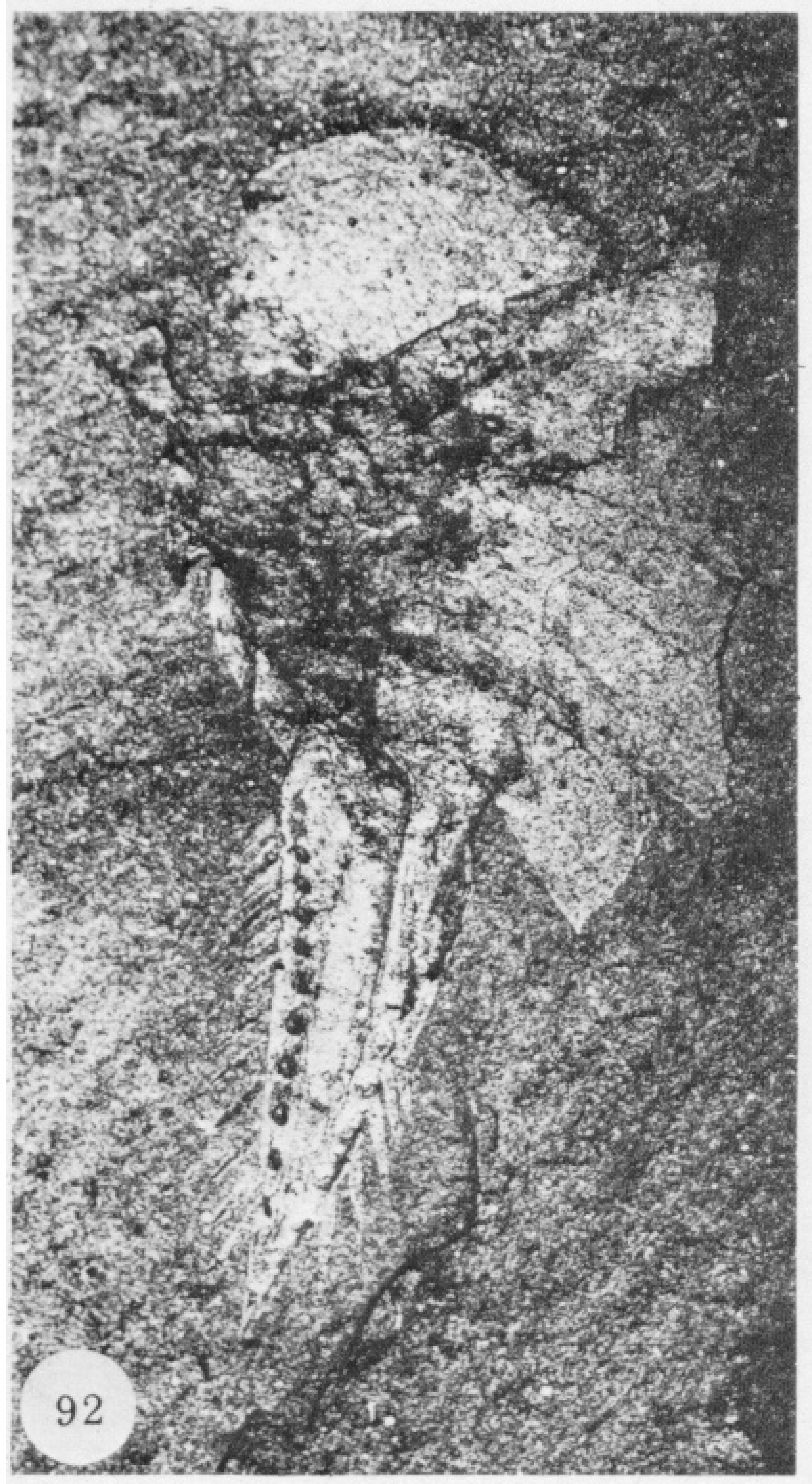

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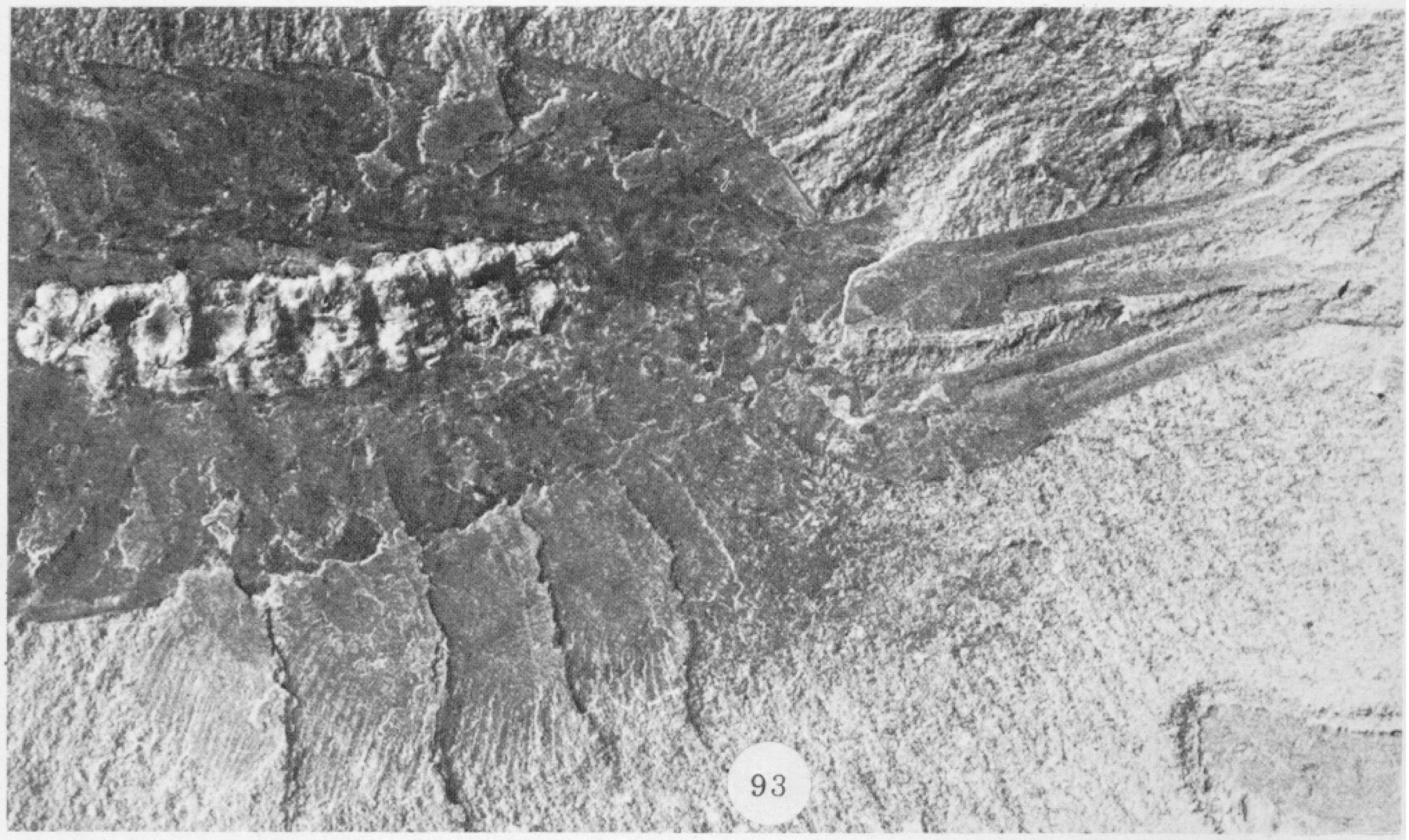

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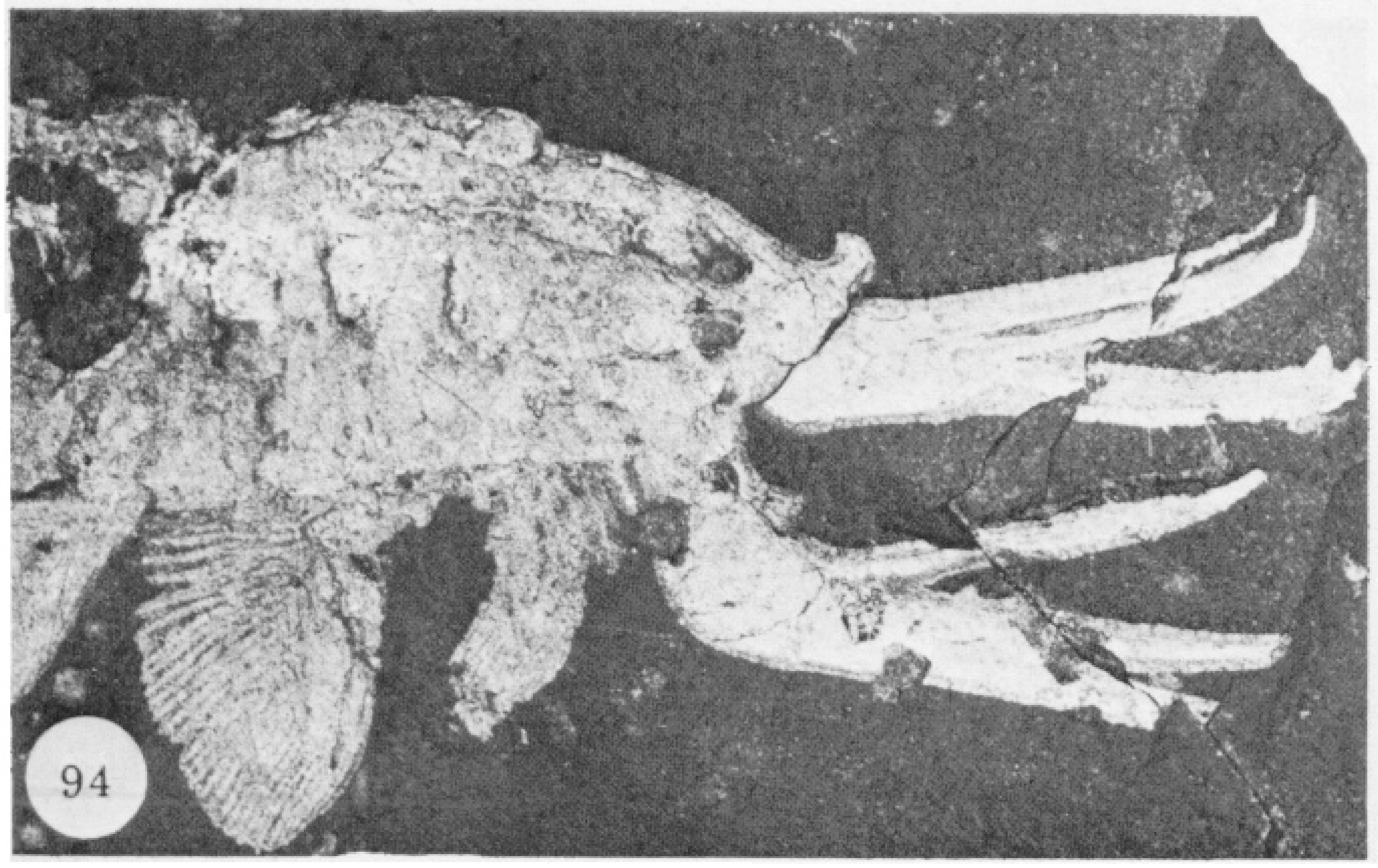

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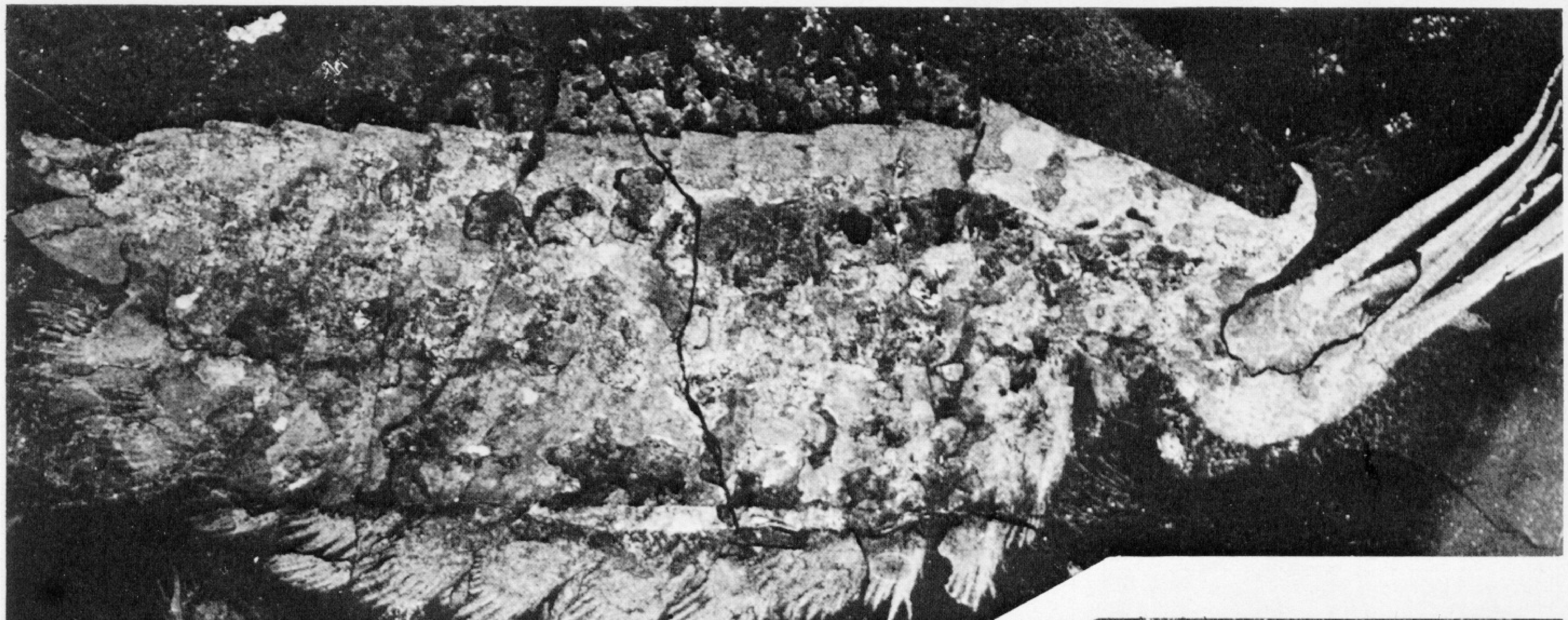

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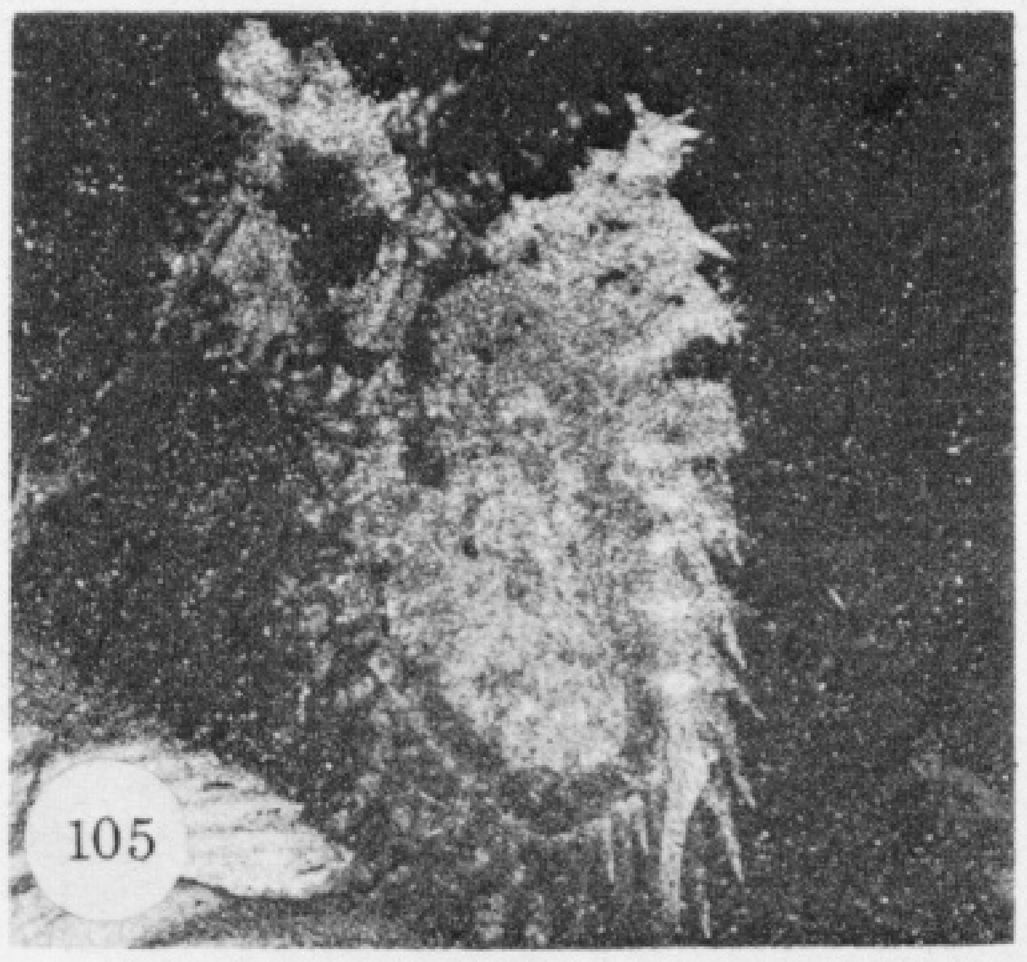

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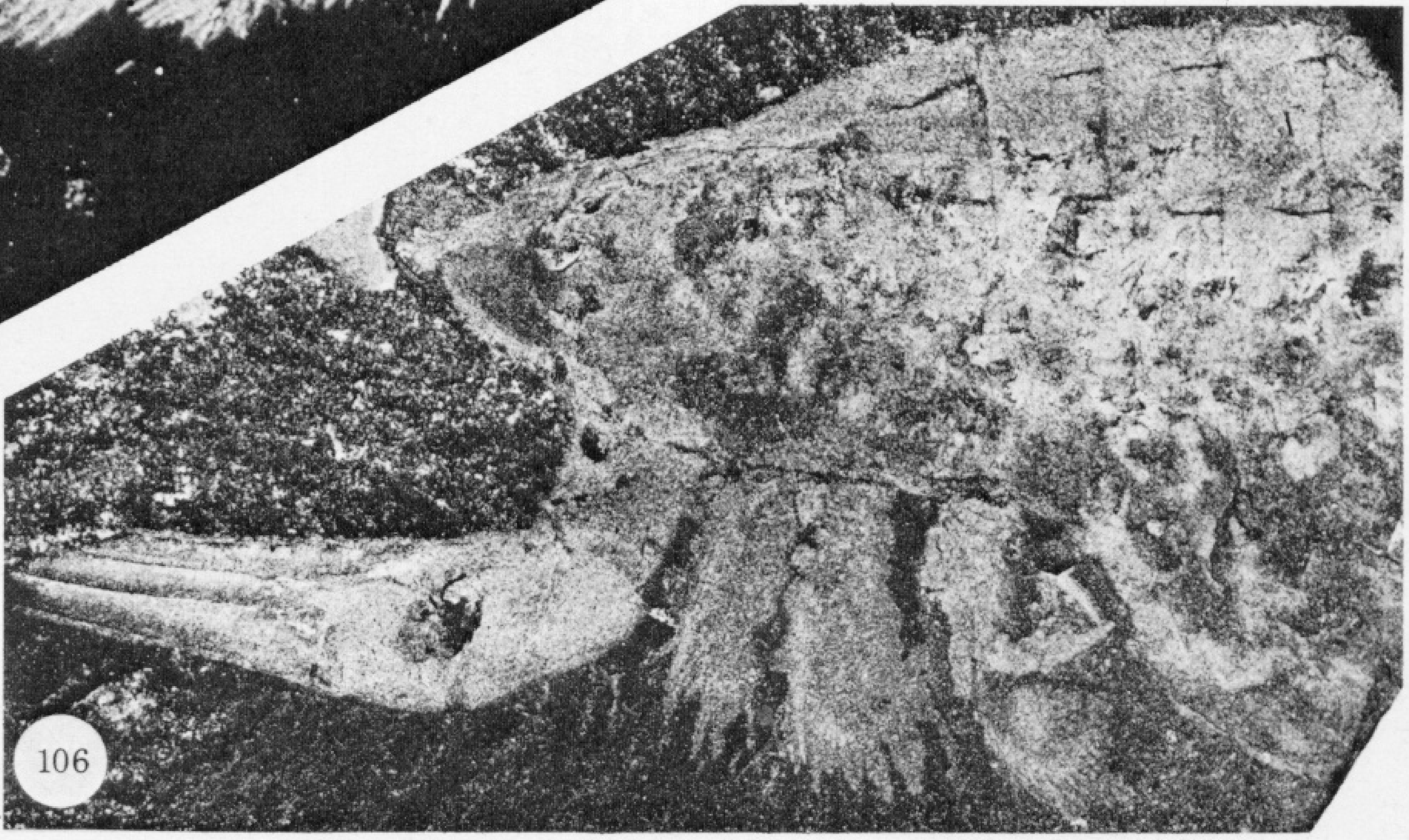

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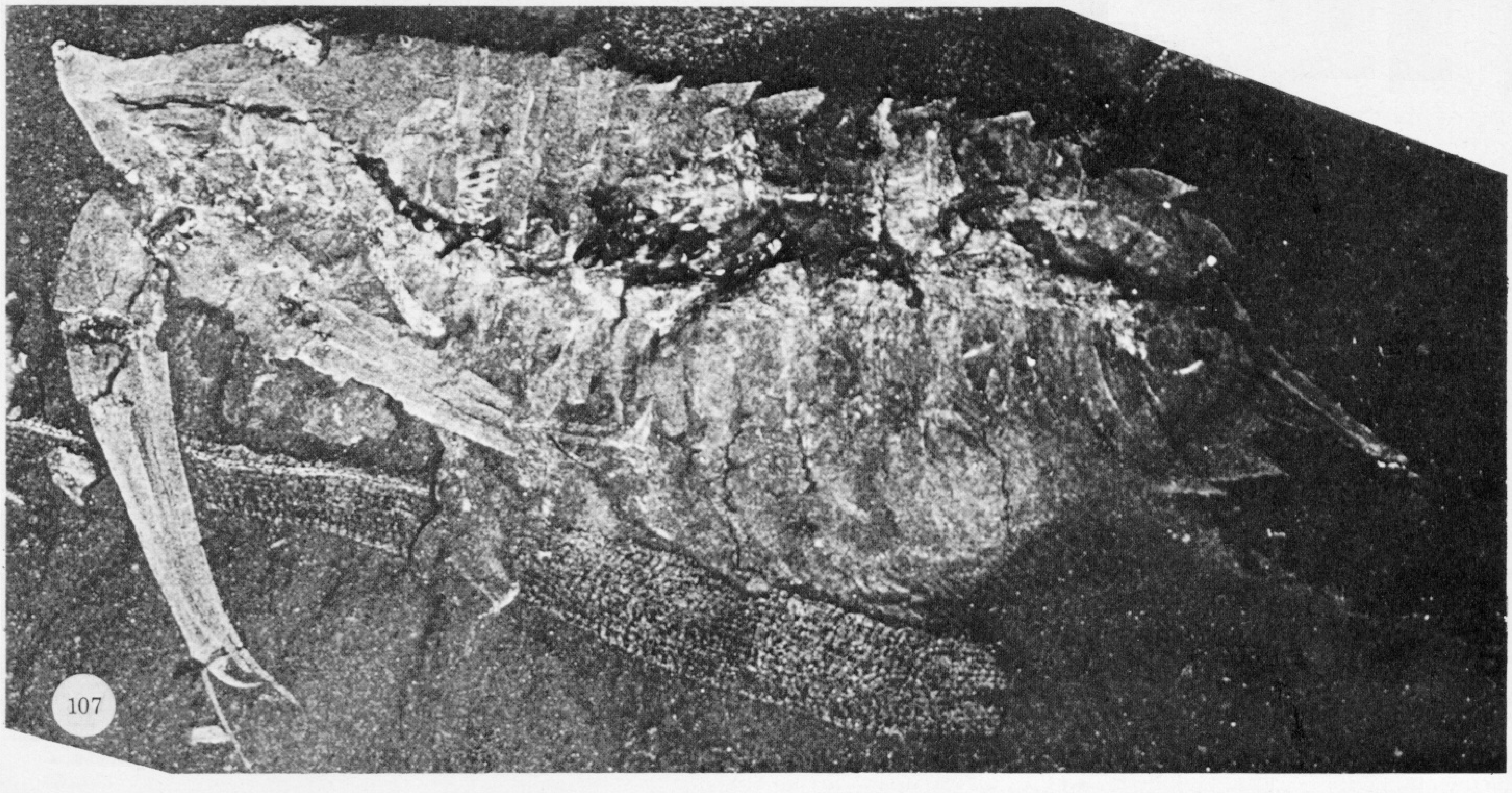

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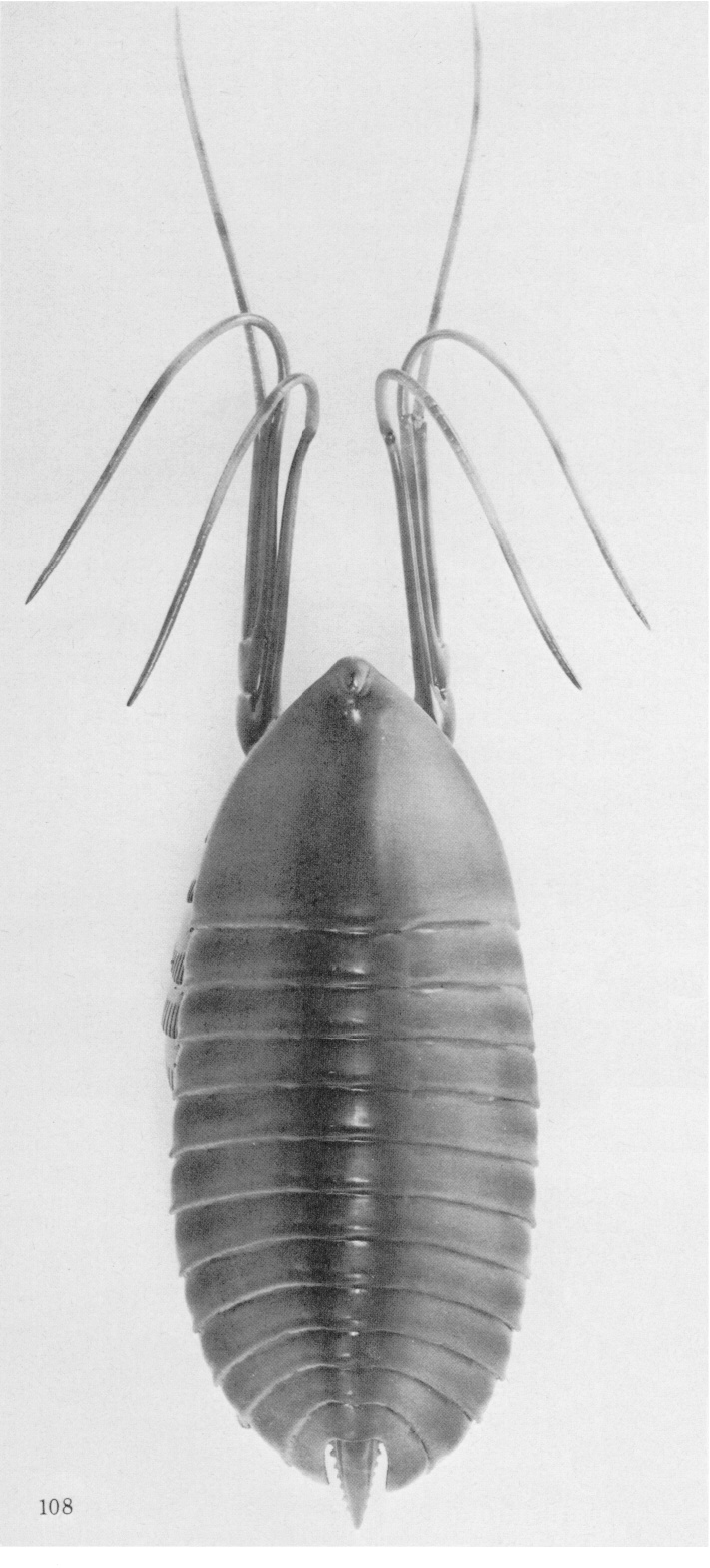

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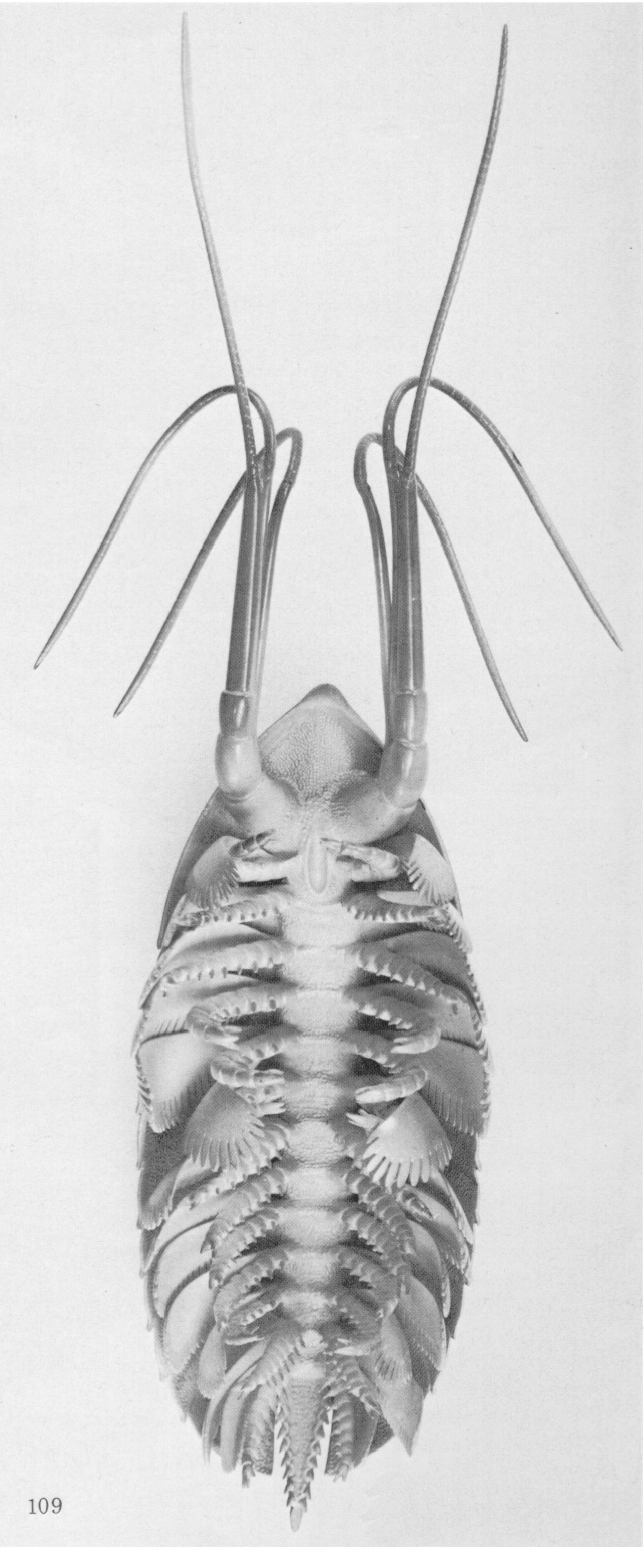

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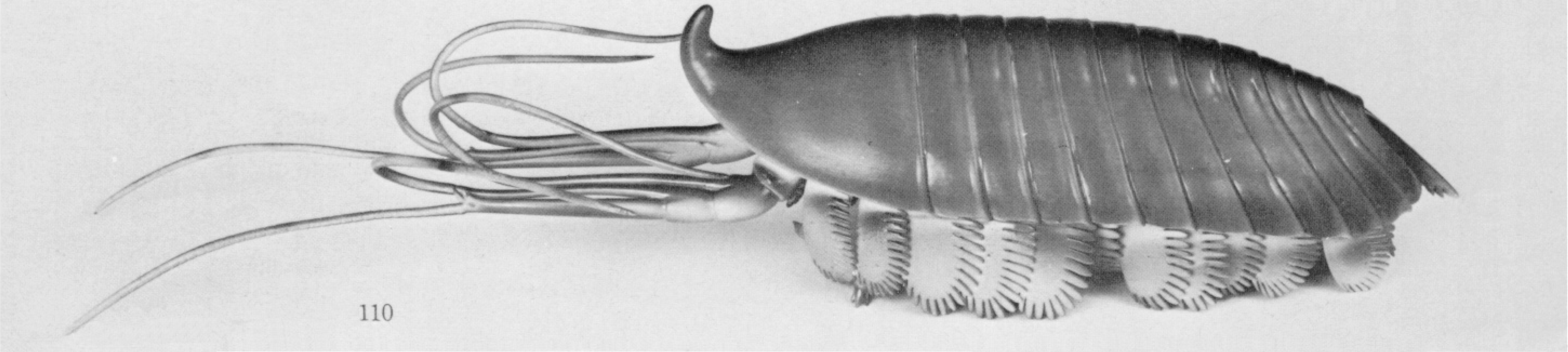

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