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THE LARGEST CAMBRIAN ANIMAL, *ANOMALOCARIS*, BURGESS SHALE, BRITISH COLUMBIA

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Isolated specimens of the appendage *Anomalocaris canadensis* have long been known; a single incomplete specimen of an animal having a pair of these appendages attached anteriorly is described. Seven dorsoventrally compressed, partly complete individuals of a similar animal that had a different pair of appendages ('F' of Briggs 1979) attached anteriorly are described, together with two obliquely compressed individuals that are thought to be conspecific. Surrounding the mouth of this latter species is a circlet of plates identical with the supposed medusoid coelenterate *Peytoia nathorsti*; this species is referred to *Anomalocaris*; *Laggania* is a junior synonym. As now understood, *Anomalocaris* was an animal that reached a length of 0.5 m, the elongate body having a head region bearing one pair of large, lateral eye lobes, each borne on a short stalk, the single pair of appendages attached at the ventral, anterior margin. The 13 segments of the appendage in *A. canadensis* bore paired spines on the inner side, short spines on the outer side, and there was a terminal, spinose 14th segment. The appendage in *A. nathorsti* consisted of 11 segments, the 2nd to 10th bearing on the inner side a graduated series of spinose blades, and spines on the lateral and outer sides, the terminal 11th segment ending in a group of spines. The circlet of plates surrounding the mouth was situated ventrally on the head region immediately behind the appendages; the plates bore teeth and the circlet constituted a jaw mechanism; additional groups of spines were present in the buccal cavity. Beneath the head region, behind the mouth, were three pairs of semicircular flaps, strongly overlapping: on the tapering trunk were 11 pairs of triangular lateral lobes, widest at the mid-length of the trunk, reduced progressively in size backward. These lobes were strongly overlapping in the same sense as the flaps on the head, and attached low on the sides. The trunk termination was short and blunt, without any projecting spine or lobe. Attached to the side of the body, above each flap and lateral lobe, was a multi-lamellar structure, apparently a gill. A thin cuticle covered the head region dorsally, and ventrally around the appendages and jaw circlet, behind this becoming a lateral strip that narrowed backward. It is suggested that a thin cuticle covered the trunk region dorsally and hung down beside the gills; this covering may have been continuous, but possibly was divided into tergites. Irregular patches of apatite, and some matrix, occur in the trace of the alimentary canal, which extended to the tip of the trunk. Mineralized patches occur in association with the gills, and as transverse strips, presumed traces of some internal organ or structure. The cuticle of the appendages and jaw circlet was presumably stout, hence these parts of the body were more resistant to decay and so were preserved in isolation. The thin cuticle of the lateral lobes shows rays which were presumably thicker and strengthening in function.

We suggest that this animal, the largest known from Cambrian rocks, swam by using the series of closely spaced lateral lobes essentially as a lateral fin along which waves of motion were propagated. If the waves were moved in either the same, or opposite, sense on each side, considerable manoeuvrability would have resulted. The anterior pair of appendages, and jaw mechanism, would have made *Anomalocaris* a formidable predator, particularly on soft-bodied benthos including the abundant arthropods without a mineralized exoskeleton. No fragments of hard parts have been observed in the gut, but there is evidence that it may have inflicted wounds on trilobites.

Anomalocaris was a metameric animal, and had one pair of jointed appendages and a unique circlet of jaw plates. We do not consider it an arthropod, but the representative of a hitherto unknown phylum. It is best known from *A. nathorsti*, the single specimen of *A. canadensis* having a different appendage but the rest of the body similar, probably including the jaw circlet. The evidence is insufficient to reach any conclusion on whether or not these two 'species' may be sexual dimorphs of a single species.

The single specimen of *Amiella ornata* is redescribed. It shows what may be lateral lobes like those of *Anomalocaris*, but other features unlike it. We conclude that this specimen is not an example of *Sidneyia inexpectans*, and is too incomplete for its relationship to be determined.

1. INTRODUCTION

Strange soft-bodied animals are known at intervals throughout the Palaeozoic, creatures that do not fit into any phylum of living animals. They are usually known from one or few localities and so have a limited range in time and space. Examples are the Burgess Shale, Middle Cambrian, *Opabinia* (Whittington 1975) and *Hallucigenia* (Conway Morris 1977), the late Silurian *Ainiktozoon* (Scourfield 1937), and the Upper Carboniferous *Tullimonstrum* (Johnson & Richardson 1969), which Foster (1979) interprets as a prosobranch gastropod. Such animals have frequently been regarded as interesting curiosities, and have not been given serious consideration in evolutionary studies. The present account deals with an additional example, of which entire specimens have now been found in the Burgess Shale section. Isolated specimens of the more heavily sclerotized parts of these animals have long been known, and are widespread in North America in both Lower and Middle Cambrian rocks. Thus these animals are more widely distributed in time and space than most 'curiosities', and in addition were far and away the largest known animals of their time. It is hoped that these descriptions will help to emphasize the importance of soft-bodied fossils preserved in unusual conditions, for they are not insignificant but constitute all we know about what may have been the majority of invertebrates living in the ancient past.

Briggs (1979), as part of a comprehensive revision of Burgess Shale arthropods, re-investigated large isolated, jointed limbs, and concluded that one, *Anomalocaris canadensis*, was probably ambulatory, the other, informally designated as 'appendage F', was used in feeding. Bruton (1981) has shown conclusively that 'appendage F' does not belong to *Sidneyia inexpectans*, as Walcott (1911 *a*) and Simonetta (1963) have claimed. Thus one could only speculate as to what kind of animal these limbs belonged, until the preparation of the specimen illustrated in figure 3; figures 4–6, plate 1; figures 8 and 10, plate 2; and figure 12. This revealed quite unexpectedly a pair of the appendages known as *A. canadensis*, attached at the anterior end of an otherwise superficially *Opabinia*-like animal. Investigation of the very few similar specimens in the Walcott collection provided additional surprises. A pair of jointed appendages was found attached anteriorly (figures 25, 26, 29, plate 6; figure 30), but these proved to be 'appendage F' of Briggs 1979. In addition, another specimen (figure 17, plate 4; figures 20, 21; figures 22, 23, plate 5) showed that, situated anteriorly between the appendages on the ventral side, was a circlet of toothed plates. In isolation, the identical circlet has been regarded as the supposed medusoid *Peytoia nathorsti*. There thus seem to be two kinds of animals, and the size of isolated specimens of the appendages, and of the supposed medusoid, indicates that they attained a length of up to 0.5 m. Isolated examples of *A. canadensis* are known from Lower and Middle Cambrian rocks of varied facies in North America, and isolated *Peytoia* has been found at Middle Cambrian localities other than that of the Burgess Shale section. 'Appendage F' is known only from the Burgess Shale section and nearby localities in the Stephen Formation. Here we describe these two animals in detail, and discuss problems of morphology, nomenclature and affinities. The better known one is reconstructed, and was probably a bethonic predator, swimming near the bottom and capturing prey. These animals are by far the largest known Cambrian predators.

We (Whittington & Briggs 1982) gave a preliminary account of three of the specimens. In the same year Simonetta & Delle Cave (1982) illustrated others that we re-figure here in detail, after preparation. They did not recognize the nature of the anterior appendage, nor the 'Peytoia' circlet, and interpreted the mineralized patches as the axial portion of appendages. The conspicuous mineralized bands across the axial region in 274142 and its counterpart (figure 31; figures 32–34, plate 7), were regarded as representing a sclerotized axis connecting the pair of appendages. The reflective dorsal cuticle at the anterior margin of the head in 274148 (figures 44, 45, 47 and 48, plate 10; figure 50) was interpreted as an 'epistomium'. They suggested comparisons of the animal with certain Precambrian genera (which we do not think can be sustained) but their belief that it cannot be classed in any recognized phylum is upheld here in the light of the much more detailed knowledge now available. The abstract provides a summary description of *Anomalocaris* as we reconstruct it (figures 101, 102).

2. STRATIGRAPHICAL AND GEOGRAPHICAL OCCURRENCE

All the specimens illustrated herein are from the Burgess Shale section in the Stephen Formation, Middle Cambrian, *Pagetia bootes* faunule of the *Ptychagnostus praecurrens* Biozone (Robison 1976, p. 104) 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. The great majority are from what Walcott (1912, pp. 151–153) called the 'Phyllopod bed', 2.3 m thick, in which he excavated his quarry; these specimens are all in the U.S. National Museum collections and are labelled 35k with no indication of the level in the bed from which a specimen came. 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. These higher layers are referred to as the Raymond quarry, and Geological Survey of Canada parties collected from them, and the Phyllopod bed, at measured intervals. A detailed account of the discovery and collection of the fossils has been given by Whittington (1971, pp. 1171–1180), and since then a collection has been made by a party from the Royal Ontario Museum (Collins 1978) from talus. Figure 1 summarizes the occurrence of isolated appendages and mouth parts in the Burgess Shale section. The complete specimen of *Anomalocaris canadensis* is from the Raymond quarry, and complete specimens of *A. nathorsti* from the Phyllopod bed and 65 m higher in the section; only one other incomplete body is known from the lower Marjum Formation of west central Utah (Briggs & Robison 1984).

The work of Briggs (1979), Briggs & Mount (1982) and Collins *et al.* (1983) has shown that isolated appendages of *canadensis* type are far more widespread, not only in the Stephen Formation south of Mount Field, but from Lower and Middle Cambrian rocks of Pennsylvania, California and British Columbia. 'Appendage F' is known only from the Stephen Formation in British Columbia (Collins *et al.* 1983, table 1), the incomplete specimens from the Lower

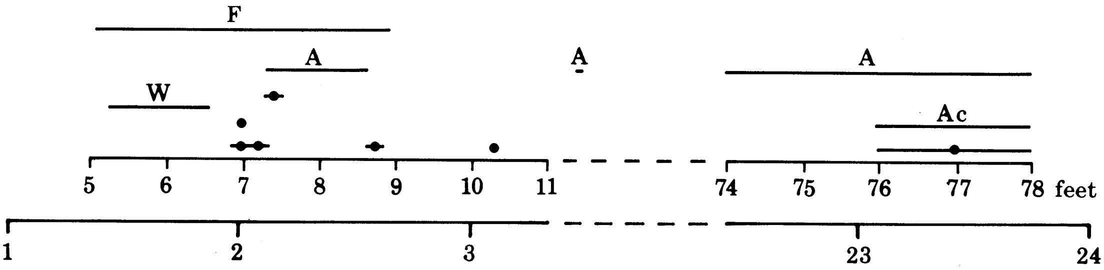


FIGURE 1. Stratigraphical levels in feet (with equivalent metric scale) from which portions of, and one entire, specimen have been collected in the Burgess Shale section. Solid circles indicate levels in the Walcott and Raymond quarries (Whittington 1971) from which seven specimens of 'Peytoia' were collected by the G.S.C. parties of 1966 and 1967. Where these levels were recorded as a range it is shown by a bar. Other ranges of level are shown as follows: W, occurrence of 'Peytoia' recorded by Walcott (1912, pp. 152–153); A, isolated appendage of *A. canadensis* and F, 'appendage F', collected by G.S.C. parties, from Briggs 1979, figure 2; Ac, entire specimen of *A. canadensis* described herein.

Cambrian of Pennsylvania (Briggs 1979, pp. 659–670, plate 81, figures 9–11; text-figures 33, 34) being only superficially similar to 'appendage F'. 'Peytoia' has been found in the Middle Cambrian of west central Utah (Conway Morris & Robison 1982).

3. TERMINOLOGY AND METHODS

The nomenclatural complexities associated with *Anomalocaris* are dealt with in § 5. For brevity, the circlet of mouth plates is referred to as 'Peytoia'. The designation 'appendage F' of Briggs (1979, text-figure 20) is used, but the broad, flat projections from each segment are called blades rather than spines, and the auxiliary spines of Briggs called spines. 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 *exsaggital* (abbreviation, exs.), and a direction at right angles to these as *transverse* (abbreviation, tr.). The exoskeleton is 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, as revealed, for example, by the lack of symmetry between left and right lobes. These attitudes of the horizontal plane of the body relative to the bedding have been described as *parallel* or *oblique*, the amount of obliquity varying between specimens or along the length of an individual. These terms are used in the explanations of the plates, together with *parallel oblique* to indicate that the specimen is approximately parallel. When the rock was split to reveal a specimen, the split followed particular layers of exoskeleton, other layers may be buried on either side of the split. A *part* and *counterpart* are produced by the split, the former has what is considered to be the dorsal side of the animal toward the observer, that is, in a complete specimen, the eye lobe is nearer to the observer, the 'Peytoia' and appendages farthest away. The part of an isolated appendage, or a 'Peytoia' is the side that presents the external surface to the observer. In the explanations of the plates the statement 'part only' or 'counterpart only' denotes 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, the majority 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. Similarly directed radiation, the specimen not tilted but submersed under alcohol, gives a different effect of reflection. 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 down-slope 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; dashed lines show margins derived from the opposite side. The specimens described herein do not show an obvious tectonic lineation (that crosses some Burgess Shale specimens) but a less conspicuous lineation is indicated in figure 94 by dashed lines. Veins that cut the rock, and fractures, are indicated in the drawings as a guide to relating the drawing to photographs. The abbreviations listed include letters denoting the institution in which a particular specimen is housed. These letters are placed before the catalogue numbers in lists of specimens and in plate and figure explanations, but omitted in the descriptions for brevity.

4. Preservation and interpretation

Recent general accounts of the Burgess Shale fauna (Conway Morris & Whittington 1979; Conway Morris 1979; Whittington 1980) have summarized ideas on the environment in which the animals lived, and in which they were buried and preserved. The former environment was at the foot of a submarine cliff, in light, oxygenated waters of 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 down-slope, 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 (1979) called the post-slide environment. Such a process explains the varied orientations of the specimens in the rock, and in the post-slide environment decay was inhibited.

That only seven parallel or parallel oblique, fairly complete and well preserved specimens of *Anomalocaris* were found by Walcott, and one by the Canadian Geological Survey party, places such specimens among the greater rarities of the Shale. Isolated examples of the more sclerotized portions of *Anomalocaris*, that is of the appendage or the 'Peytoia', are much more common and of larger size than those known from complete specimens. Such isolated portions show that some individuals must have grown to a maximum size twice or three times the size of the largest known complete specimen. Some fine-grained pyrite is present on the surface of the specimens (figure 30) and small spheres are visible on right lateral lobes 3 to 5 in 274146 (figure 56, plate 12). These features are consistent with the animals having been benthonic in habit and hence caught in the mud slides as live animals or as carcasses that had suffered little decay and no dismemberment. The presence of pyrite supports the view that the burial environment was anaerobic, and inhibited further decay.

When the rock was split originally to reveal the parallel or parallel oblique specimens, the parting followed the large and flat surfaces of the lateral lobes, parts of the well-sclerotized appendage, the eye lobe and margins of the anterior region, stepping in level from one to another. As the photographs show, mechanical excavation was successful in revealing the 'Peytoia', portions of appendages, lateral lobes and flaps, and dorsal or ventral cuticle of the anterior region, because the rock will part along such areas. The parting did not follow the dorsal or ventral cuticle in the median region of the body, but an irregular surface through the body. Attempts to reveal dorsal or ventral cuticle in this region have failed because the rock did not part along any such layer, neither when lateral lobes were followed inward or at the broken posterior edge of 274147 (figure 16, plate 3). Possibly compaction of the median region of the trunk produced so irregular a surface in the (presumably) thin dorsal or ventral cuticle, that insufficient flat areas remain to be followed at any one place by mechanical excavation. Characteristic of the median region of the body of *A. nathorsti* are the nodular mineralized areas (stippled in figures 20, 30, 31, 50, 51 and 59). Some are paired and laterally situated, and may be connected across the mid-portion of the trunk, others are antero-medially situated. The black mineral is apatite or a calcite–apatite mixture; the median apatite-filled areas seem to be associated with the alimentary canal, but the lateral areas and transverse strips may be fillings of some other organ. Strong reflectivity is not characteristic of the alimentary canal in *Anomalocaris*, in contrast to the situation in many Burgess Shale animals.

Lamellar areas are well preserved only in 274143, where on the left anterior side the split has stepped down below the dorsal cuticle and downwards and outwards across successively more ventral lamellae (figures 18, 20). On the right anterior side (figures 23, 24) the split goes inward from the lateral margin across the dorsal cuticle, then steps successively downward and inward across the distal edges of more ventral lamellae, and on to the underlying flap. Figure 2*a* shows the stepwise course of the split through the lamellae, and figure 2*c* the edges of the lamellae as seen in the part (figures 20, 21), figure 2*b* the edges as seen in the counterpart (figure 13).

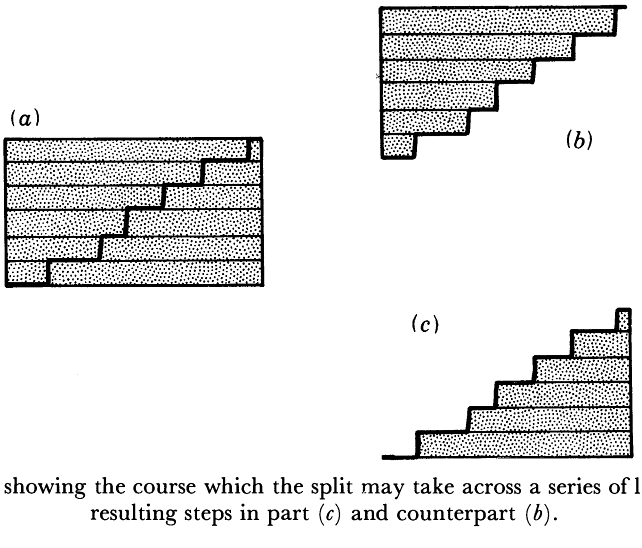


FIGURE 2. Diagram showing the course which the split may take across a series of lamellae (*a*), and the resulting steps in part (*c*) and counterpart (*b*).

The lack of a lateral compression of *A. nathorsti* makes reconstruction hazardous because the convexity of the body remains unknown. Most difficult was the interpretation of the specimens described in §7*c* and §9, in ascending order of difficulty, because of their obliquity and incompleteness; they also lack a median region showing nodular mineralized patches. The first-mentioned (figures 72–74, plate 16; figure 99) shows a fragmentary 'appendage F' and the only known lateral-oblique compression of 'Peytoia', hence despite the lack of clearly preserved lateral lobes, this specimen seems to be of *A. nathorsti*. On the other hand, the original of figure 100 shows lateral lobes with rays, lamellar areas and a doubtful scrap of 'Peytoia'. It probably belongs within *A. nathorsti*, but if so is the only specimen showing plates that may be trunk tergites. The holotype and only known example of *Amiella ornata* (figures 90–92, plate 20; figure 94) has presented the greatest difficulties, only the left anterior areas labelled 2 and 3 suggest affinity with *A. nathorsti*.

5. GENUS *ANOMALOCARIS* WHITEAVES, 1892

Type species: *Anomalocaris canadensis* Whiteaves, 1892

Synonyms: *Laggania* Walcott, 1911, type species *L. cambria* Walcott (1911*b*); *Peytoia* Walcott, 1911, type species *P. nathorsti* Walcott (1911*b*).

Discussion: the lectotype of *A. canadensis* is an isolated appendage (Briggs 1979, p. 633, plate 77, figure 1; text-figure 3), and here we describe the complete animal to which this appendage is attached. A similar complete animal is here described as a second species of *Anomalocaris*, *A. nathorsti*. Specimens of this latter have a circlet of mouth plates identical with that described by Walcott as *Peytoia nathorsti*; thus the holotype of *A. nathorsti* is an isolated circlet of mouth plates, and *Peytoia* a synonym of *Anomalocaris*. Conway Morris (1978) showed that *Laggania* Walcott was a synonym of *Peytoia*, and chose the latter name as the senior synonym; both names are now synonyms of *Anomalocaris*. Whittington & Briggs (1982, p. 573) were in error in overlooking Conway Morris' choice (1978, p. 130) and in using the name *Laggania*. The only known specimen of *Amiella ornata* Walcott (1911*a*) is re-described in detail (§9), because it shows two areas of cuticle that resemble lateral lobes of *Anomalocaris nathorsti*. Other characters of the specimen cannot be matched with those shown by any specimen of *A. nathorsti*, nor with those of other species from the Burgess Shale. This unique combination of characters means that the name *Amiella ornata* can be applied only to the holotype; it was published by Walcott on 8 April 1911, before the name *nathorsti* on 13 June 1911. These two specific names cannot be shown to be subjective synonyms, so that *Amiella* is not a subjective synonym of *Anomalocaris*.

We thus conclude that two species of a whole animal should now be regarded as belonging within one genus (*Anomalocaris*) but the type of each species is a specimen of only a portion of the animal. The type of *A. canadensis* is an appendage unique to the species, so recognition of that species may be based on the appendage alone. The type of *A. nathorsti* is the isolated circlet of mouth plates referred to herein as 'Peytoia'. The only known whole specimen of *A. canadensis* shows a fragment of a similar circlet. We do not know if the circlets of mouth plates in the species *canadensis* and *nathorsti* were identical or not; the species are distinguished by the appendages. An isolated circlet of mouth plates (figures 61, 62, plate 13) could have belonged to either species; we have not been able to discern two kinds of such circlets. Arbitrarily we assign all isolated circlets of mouth plates to *Anomalocaris nathorsti*.

6. *ANOMALOCARIS CANADENSIS* WHITEAVES, 1892

(Figures 3–12, including plates 1 and 2.)

1979 Briggs, pp. 633–641: synonomy and description of numerous specimens, including lectotype, of the isolated appendage.

1982 Briggs & Mount: new occurrence of isolated appendage and distribution of genus.

1982 Whittington & Briggs: plate 1, figure 3, brief description of entire animal.

1983 Collins *et al.*: distribution in Stephen Formation.

(*a*) *Material*

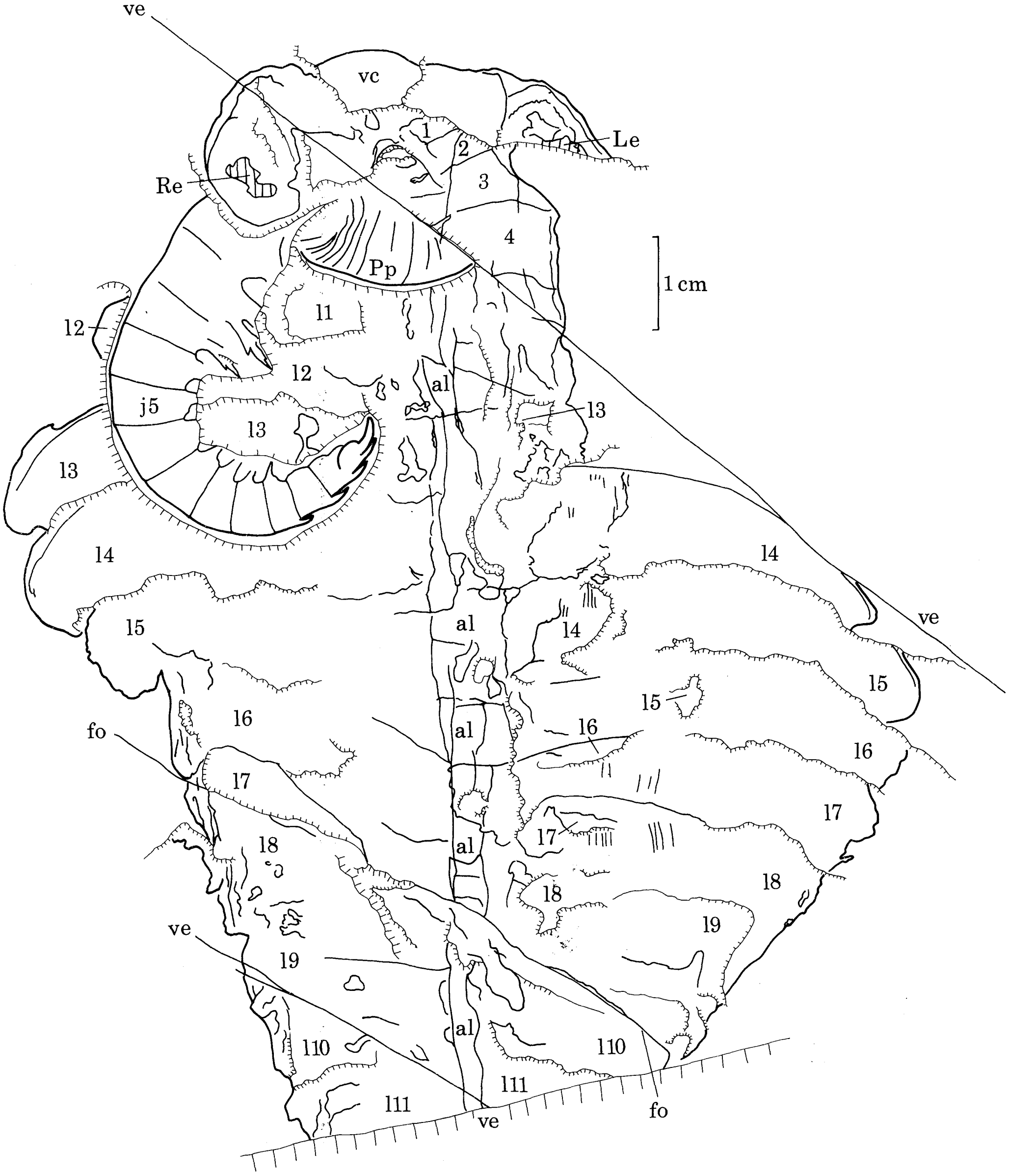
Lectotype: GSC 3418, an isolated appendage from the *Ogygopsis* Shale, Mt Stephen; see Briggs (1979), plate 77, figure 1, text-figure 3.

Material: the isolated appendages listed by Briggs (1979); Briggs & Mount (1982); Collins *et al.* (1983). GSC 75535, a single incomplete specimen of the entire animal, the counterpart more complete than the part, from 76–78 feet (23.2–23.8 m, figure 1), in the Raymond quarry, Burgess Shale section.

(*b*) *Description*

The specimen is incomplete posteriorly, and lacks the anterolateral portion of the part (figure 6) because of a break along a vein. The anterior end of the body appears to narrow forward and be bluntly rounded. A trapezoidal fragment of the ventral surface is preserved medially in the counterpart (figure 5, vc in figure 3). On either side of this fragment (appearing from underneath it in the counterpart, that is, dorsal to it) is a strip which ends in a rounded area. That on the left (right in the counterpart) is incomplete, that on the right has been revealed by preparation (figure 5); both rounded areas have a central patch of a yellowish mineral which is moderately reflective. This rounded area is tentatively interpreted as an eye, borne on a stalk and directed upward and outward. This conjecture is based on the unusual mineral in the outer rounded area, and analogy with *Anomalocaris nathorsti* which also appears to have a stalked eye.

Behind this most anterior portion the body widens to a maximum across lateral lobes 3–5, the changes in level between successive lobes clearly shown on the right side (left side of counterpart, figures 5 and 3). This distal portion of the first right lobe is concealed beneath the base of the appendage in the counterpart, the rounded outer margins of succeeding right lobes 2–4 preserved, that of right lobe 5 incomplete. Each lobe slopes below that following, and this overlap, combined with the position of the split, conceals the anterolateral and posterolateral margins of the lobes. Because this specimen is unique, no attempt has been made to reveal either of these margins of a lobe in part or counterpart. On the left side of the body (right in the counterpart, figures 3–5), opposite to right lobes 1–3, the margin runs almost straight and exsagittally. This is because the split has passed dorsal to the lobes and intersected the margin of the body above them; the level of the split changes abruptly behind here and passes through left lobe 4. In the left anterior portion of the body, beside and behind the supposed left eye lobe, are lines along which mineral matter is concentrated; these lines (figures 4, 5) suggest segmentation, tentatively numbered 1–4 in figure 3. In the part (figures 6, 8, 10) almost the entire right appendage has been revealed by preparation, and is in all respects typical of *A. canadensis* (cf. Briggs 1979). Only a portion of the left appendage has been so revealed (the proximal portion was in the missing upper left side of the part), but it shows the symmetrical arrangement of the pair and removes all doubt that they were part of the animal and not an accidental association. Adjacent to the base of the right appendage, lying just dorsal to it, a fragment is preserved (figure 10) that has a curved posterior margin and faint, radially arranged divisions; the median of these is wider than the others and oriented subparallel to the sagittal line (p in figure 12). This fragment may be a portion of 'Peytoia'.



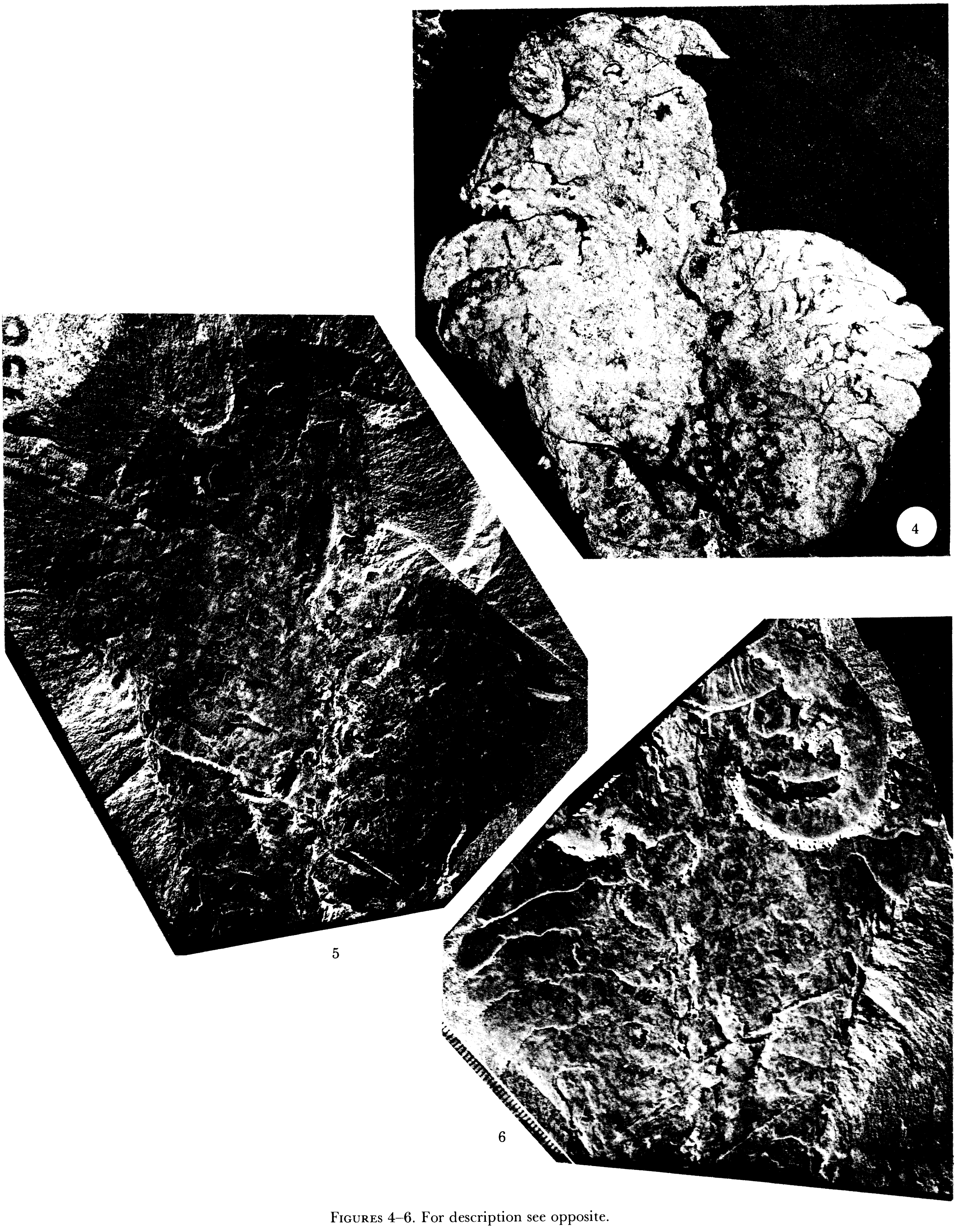
DESCRIPTION OF FIGURE 3 AND PLATE 1

Anomalocaris canadensis Whiteaves, 1892

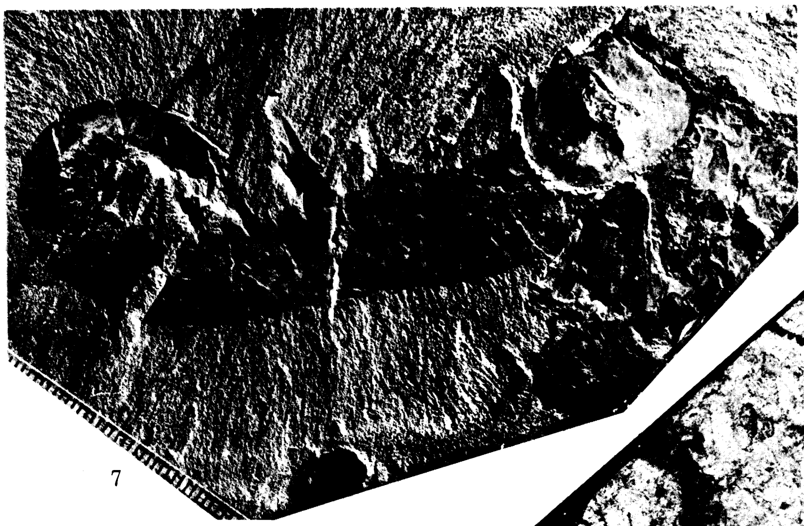
G.S.C. 75535, parallel oblique.

FIGURE 3. Composite explanatory drawing from ventral.

FIGURES 4–6. Respectively: counterpart, under alcohol, northwest, and part, northeast (magn. ×1). Raymond quarry, 76–78 feet.



FIGURES 4–6. For description see opposite.



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Figures 7–10. For description see opposite.

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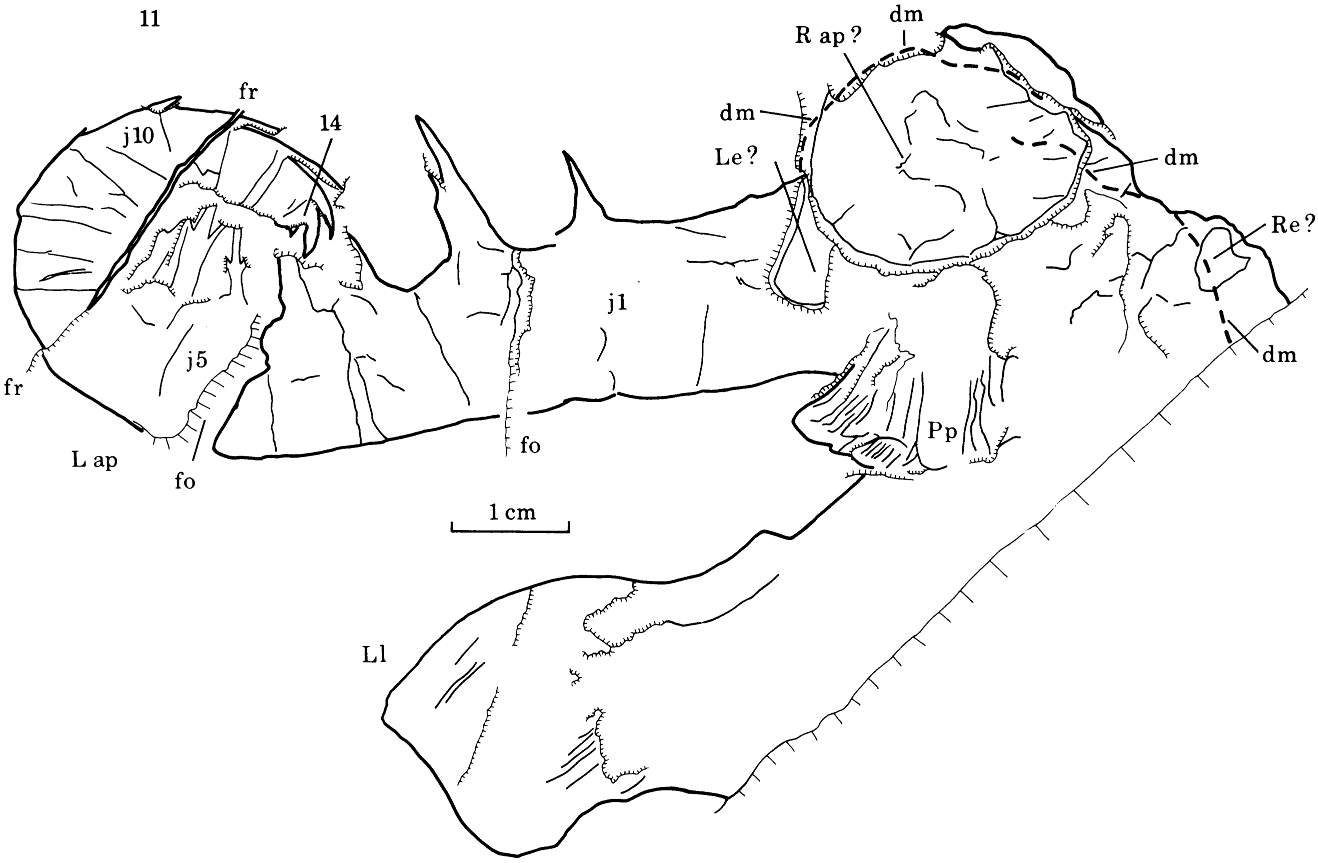

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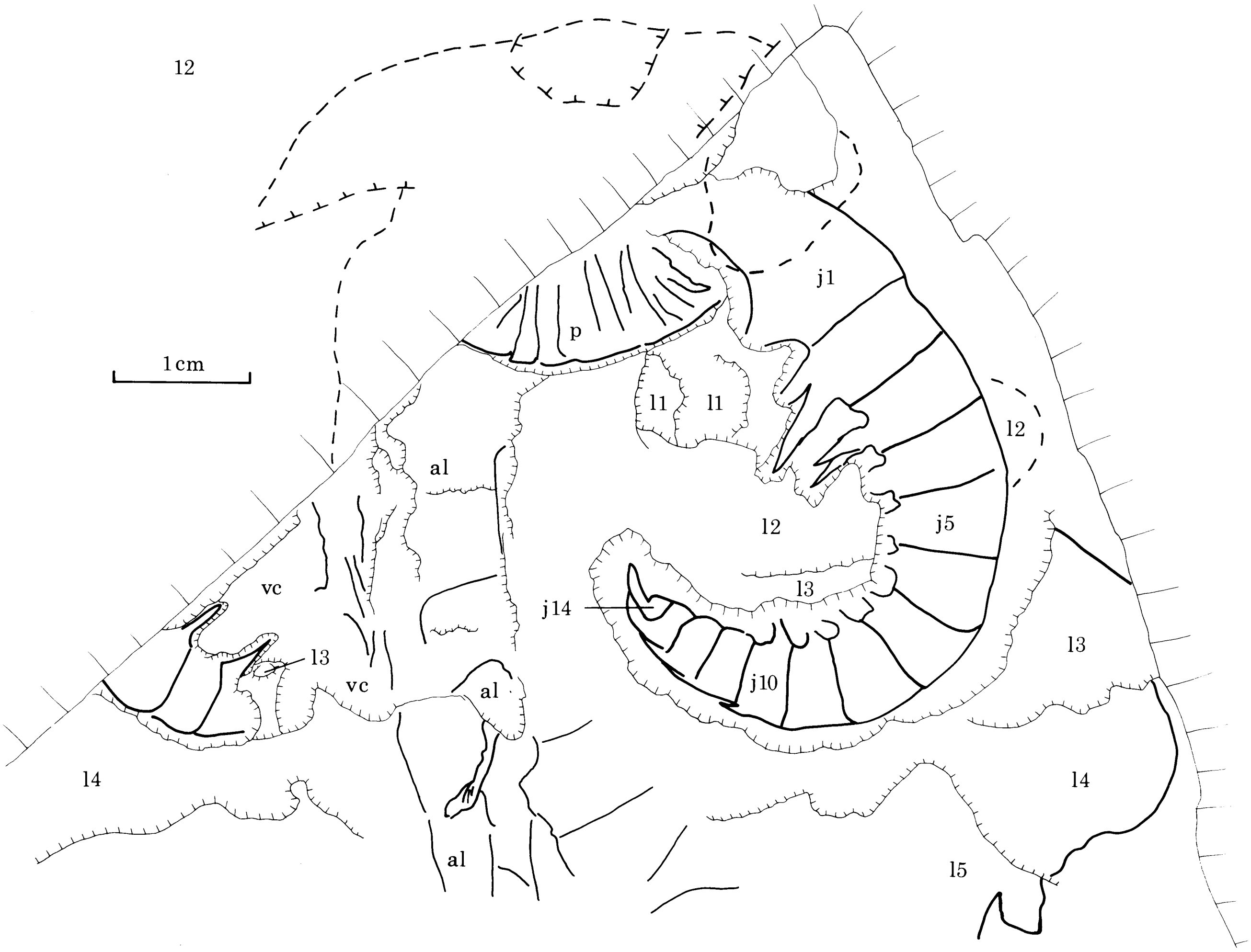


Description of plate 2 and figures 11, 12

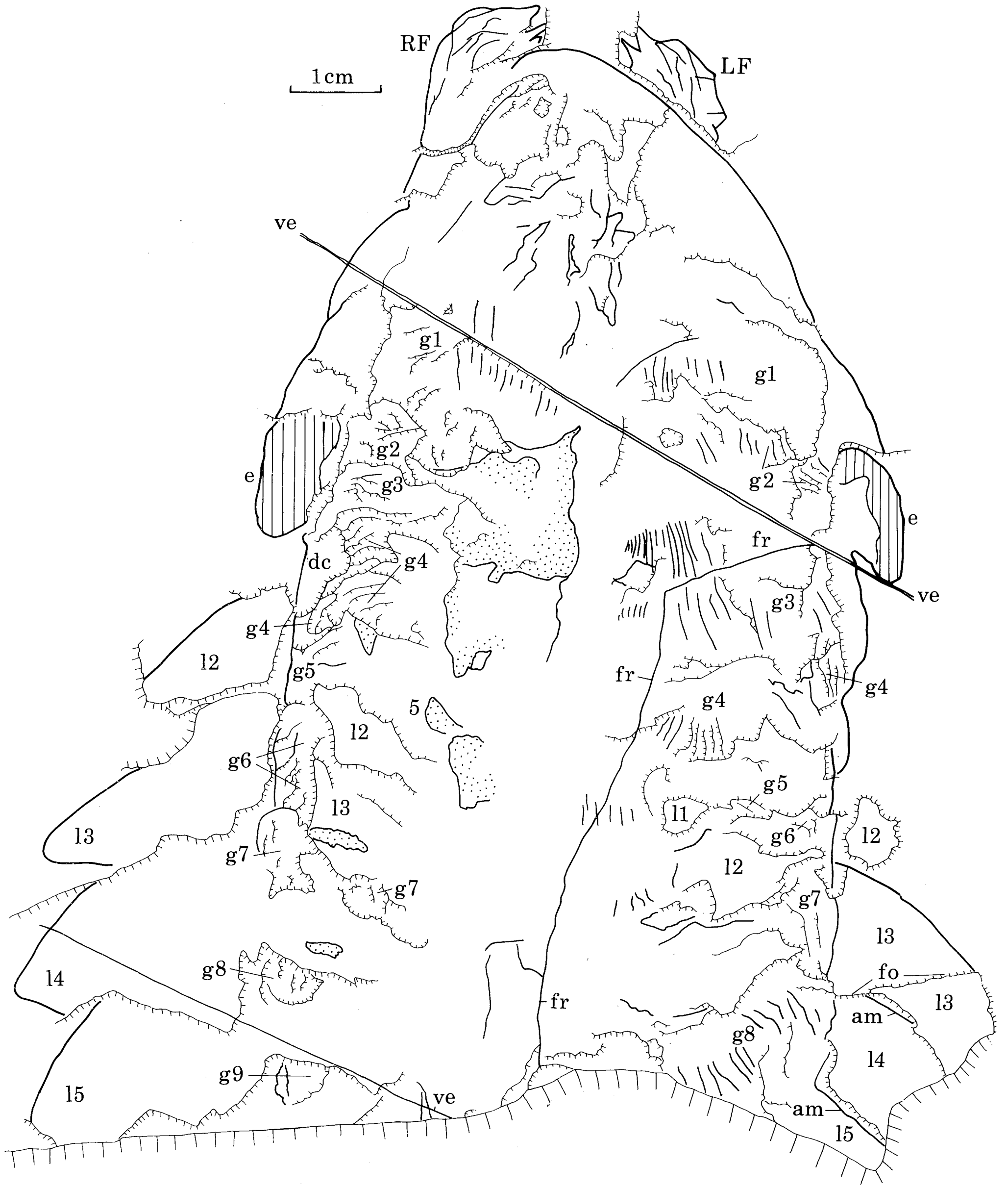
Anomalocaris canadensis Whiteaves, 1892

Figures 7, 9. U.S.N.M. 189024, left appendage and fragment of body, respectively part, northeast, counterpart, northwest (magn. × 1). Raymond quarry, locality 35k/1.

Figures 8, 10. G.S.C. 75535, part, respectively under alcohol, west (magn. × 1.7).

Figure 11. Composite explanatory drawing of U.S.N.M. 189024.

Figure 12. Explanatory drawing of part, dashed lines from outline of counterpart, G.S.C. 75535.



Description of figure 13 and plate 3

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274147 (counterpart of 274143), parallel.

Figure 13. Explanatory drawing.

Figures 14–16. Respectively, left gills 2–9, prepared to show margins, north (magn. × 1.7), right gills 2–8, similarly prepared, northeast (magn. × 1.7), entire, north–northwest (magn. × 0.9), before preparation.

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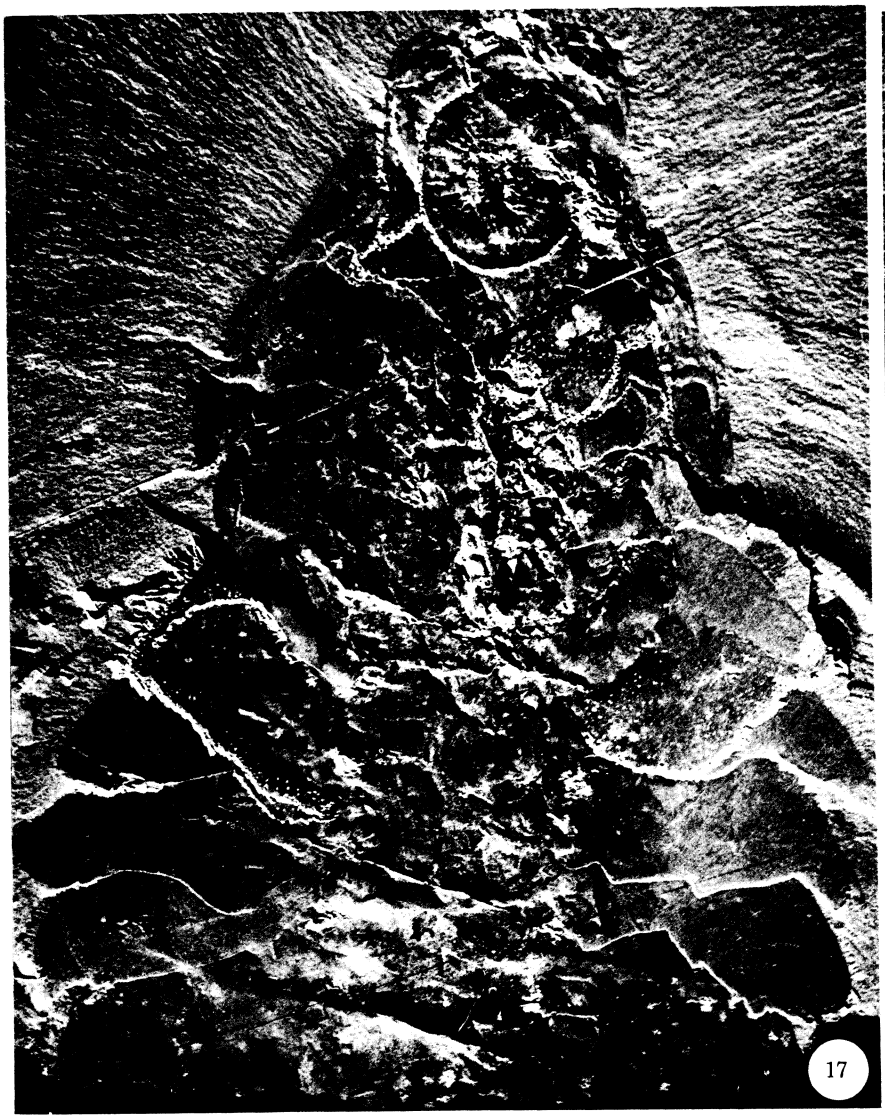
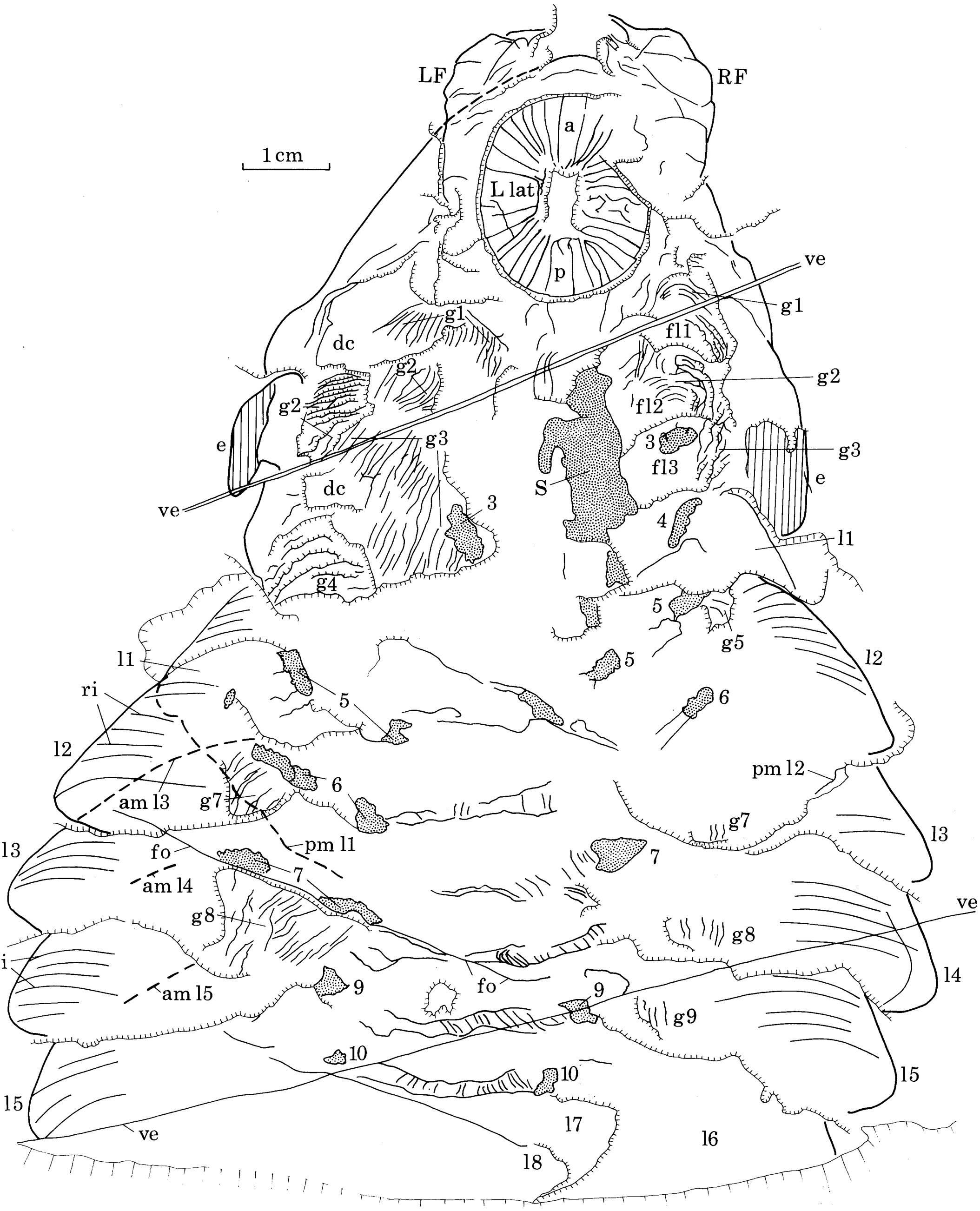
FIGURES 14–16. For description see opposite.



FIGURES 17–19. For description see opposite.



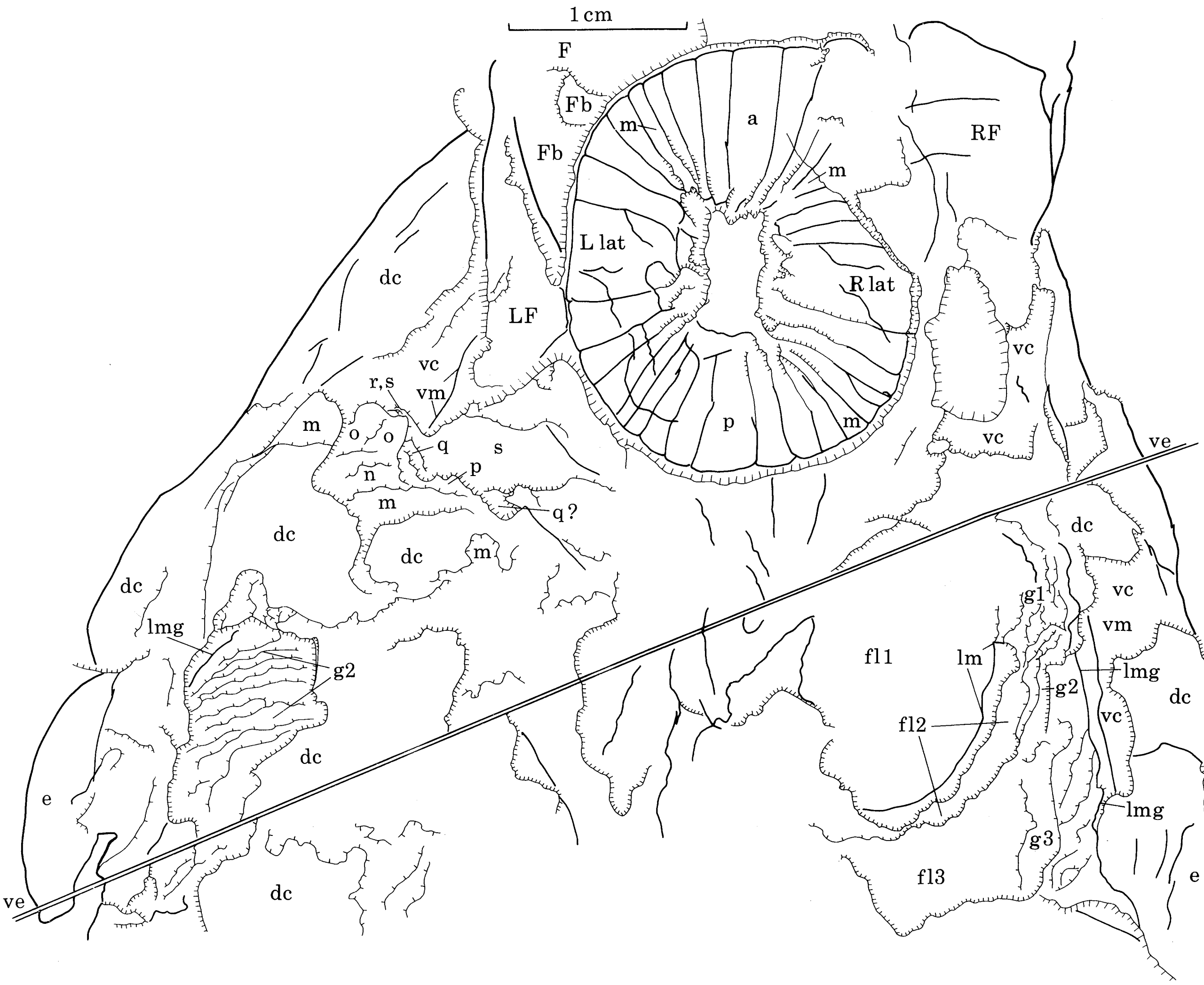
Description of plate 4 and figure 20

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274143, parallel, part (counterpart is 274147).

Figures 17–19. Respectively entire northeast, after all preparation (magn. × 1.0), left gills 1–4, north–northwest (magn. × 2.5), right posterior portion, west (magn. × 2.5).

Figure 20. Explanatory drawing.



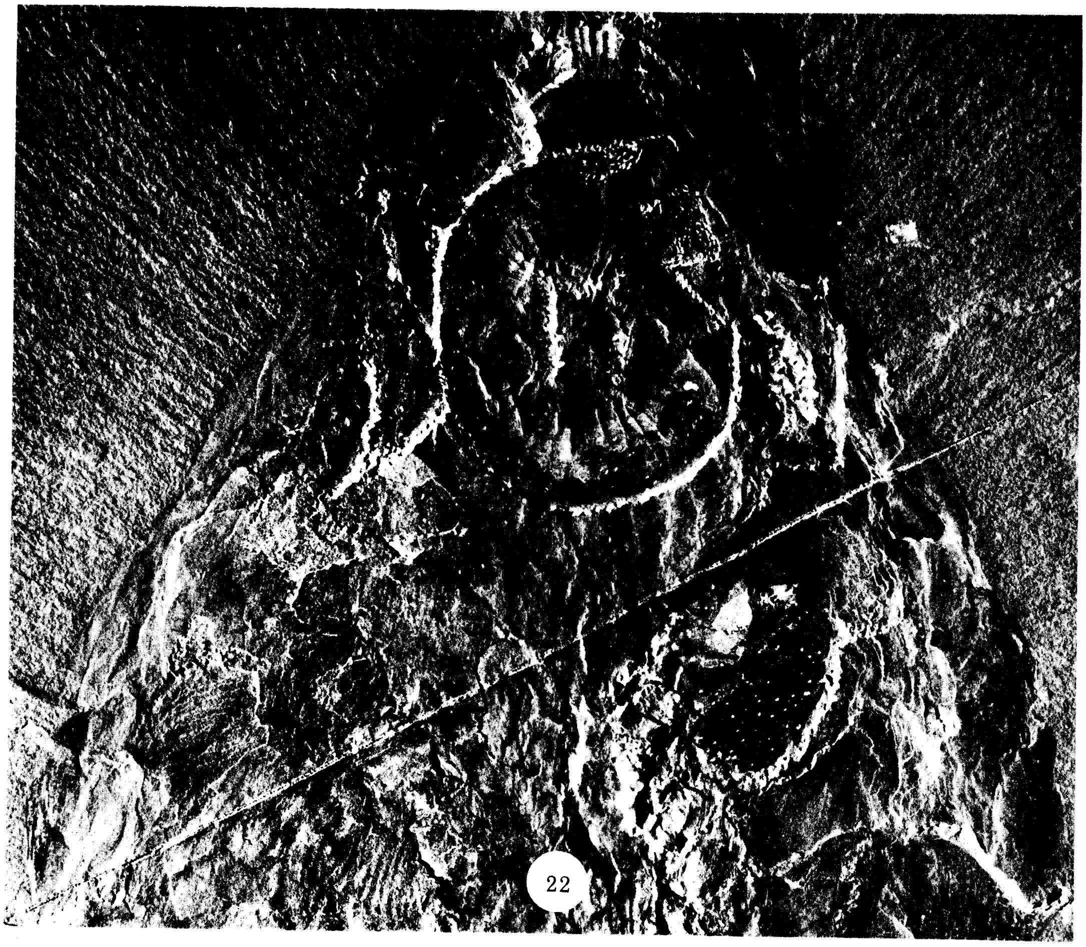
Description of figure 21 and plate 5

Anomalocaris nathorsti (Walcott, 1911)

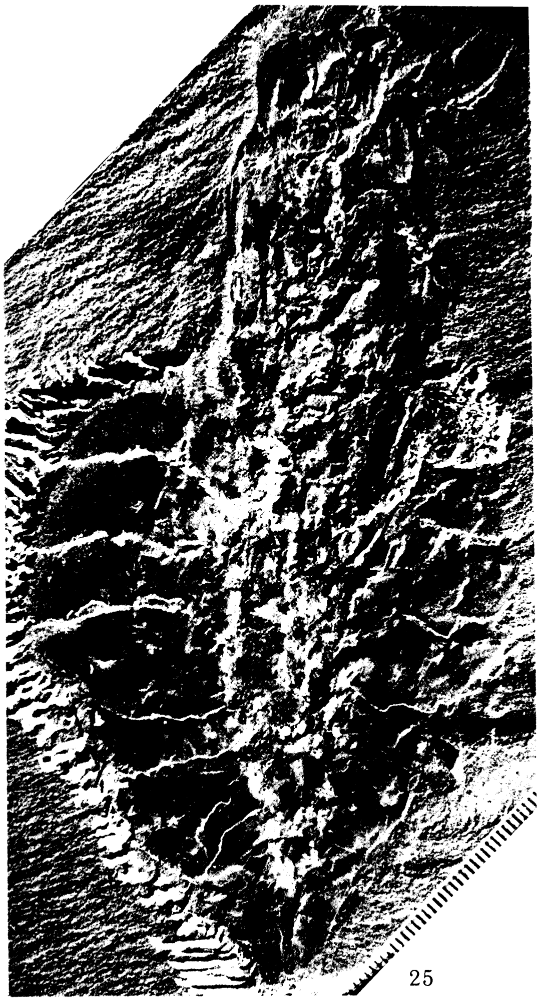
U.S.N.M. 274143 part, anterior portion (counterpart is 274147).

Figure 21. Explanatory drawing.

Figures 22–24. Respectively anterior portion, west, after all preparation (magn. × 1.7), right anterior portion, west, before preparation of flap 1 (magn. × 1.7) and detail of right anterior, north, to show flap 1 (magn. × 2.5).



FIGURES 22–24. For description see opposite.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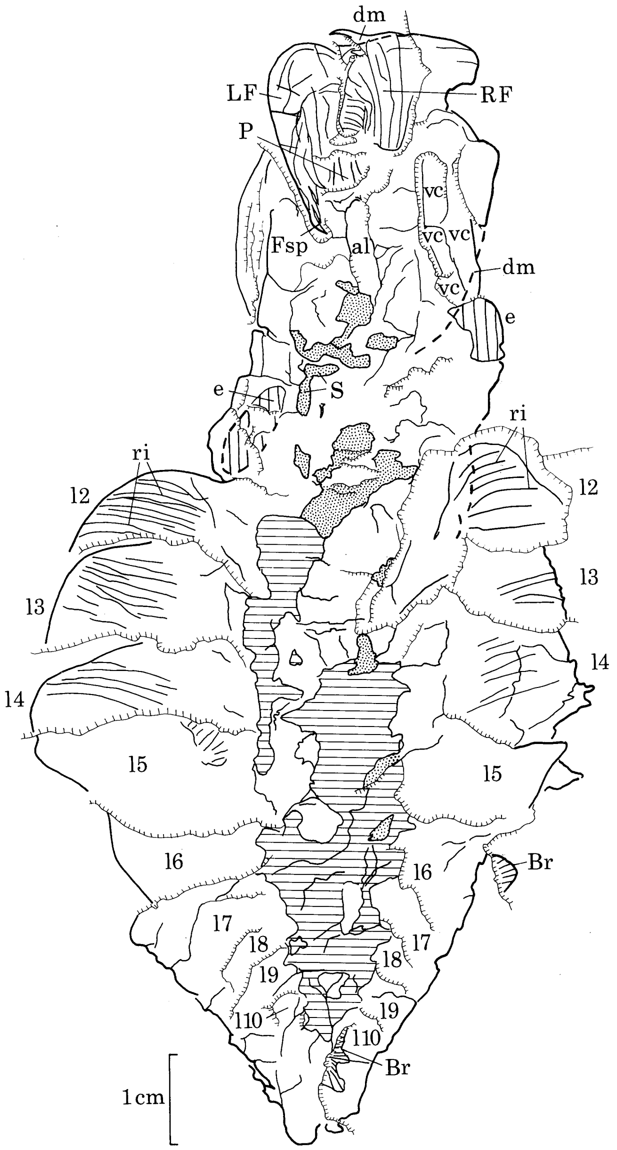
FIGURES 25–29. For description see opposite.



Description of plate 6 and figure 30

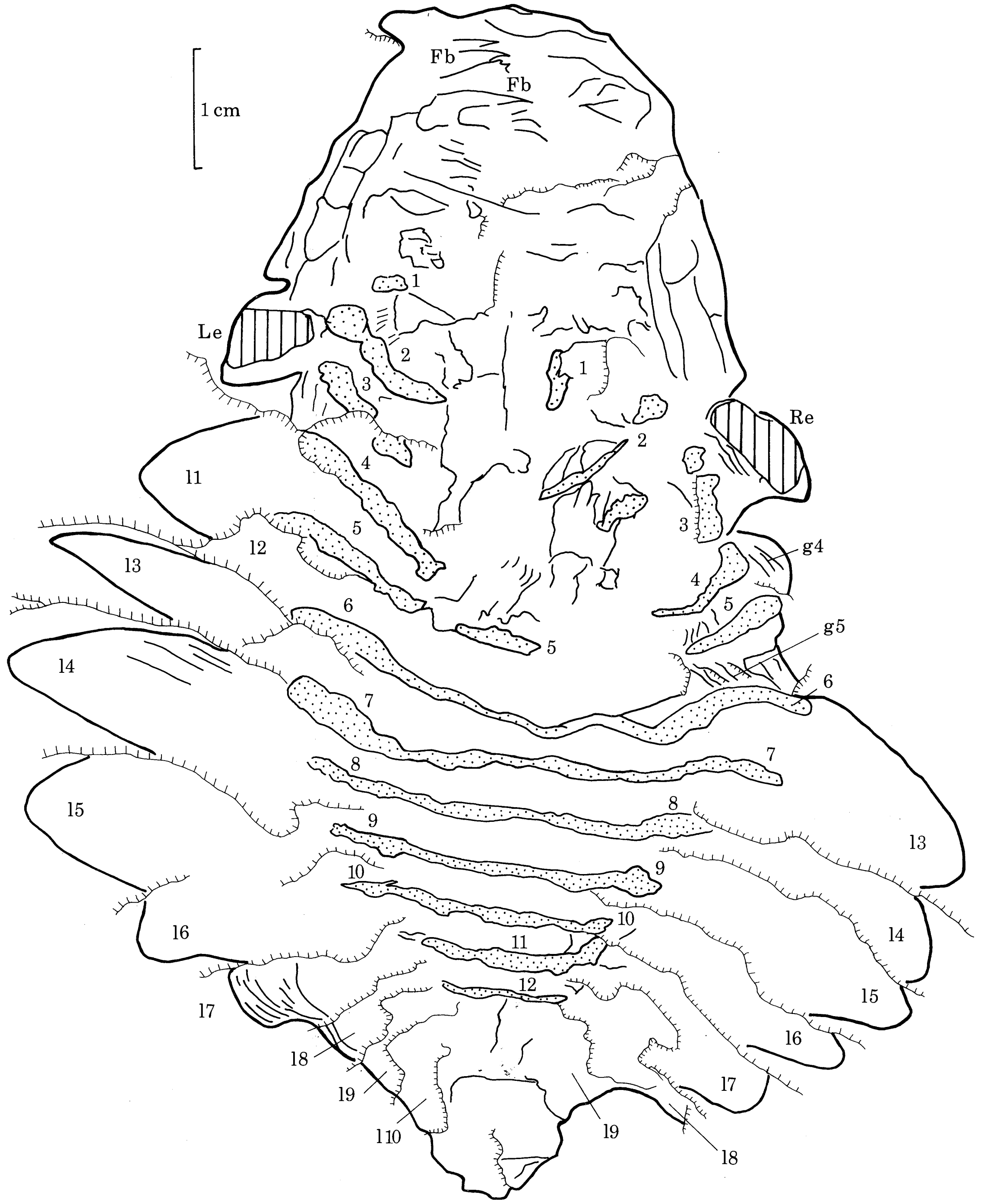
Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274164, parallel.

Figures 25, 26, 28, 29. Part, respectively entire, northwest (magn. × 1.0) anterior portion, northwest (magn. × 2.5), entire, under alcohol (magn. × 1.0), anterior portion, reflected (magn. × 2.5).

Figure 27. Counterpart, entire, north (magn. × 1.0).

Figure 30. Explanatory drawing of part.



DESCRIPTION OF FIGURE 31 AND PLATE 7

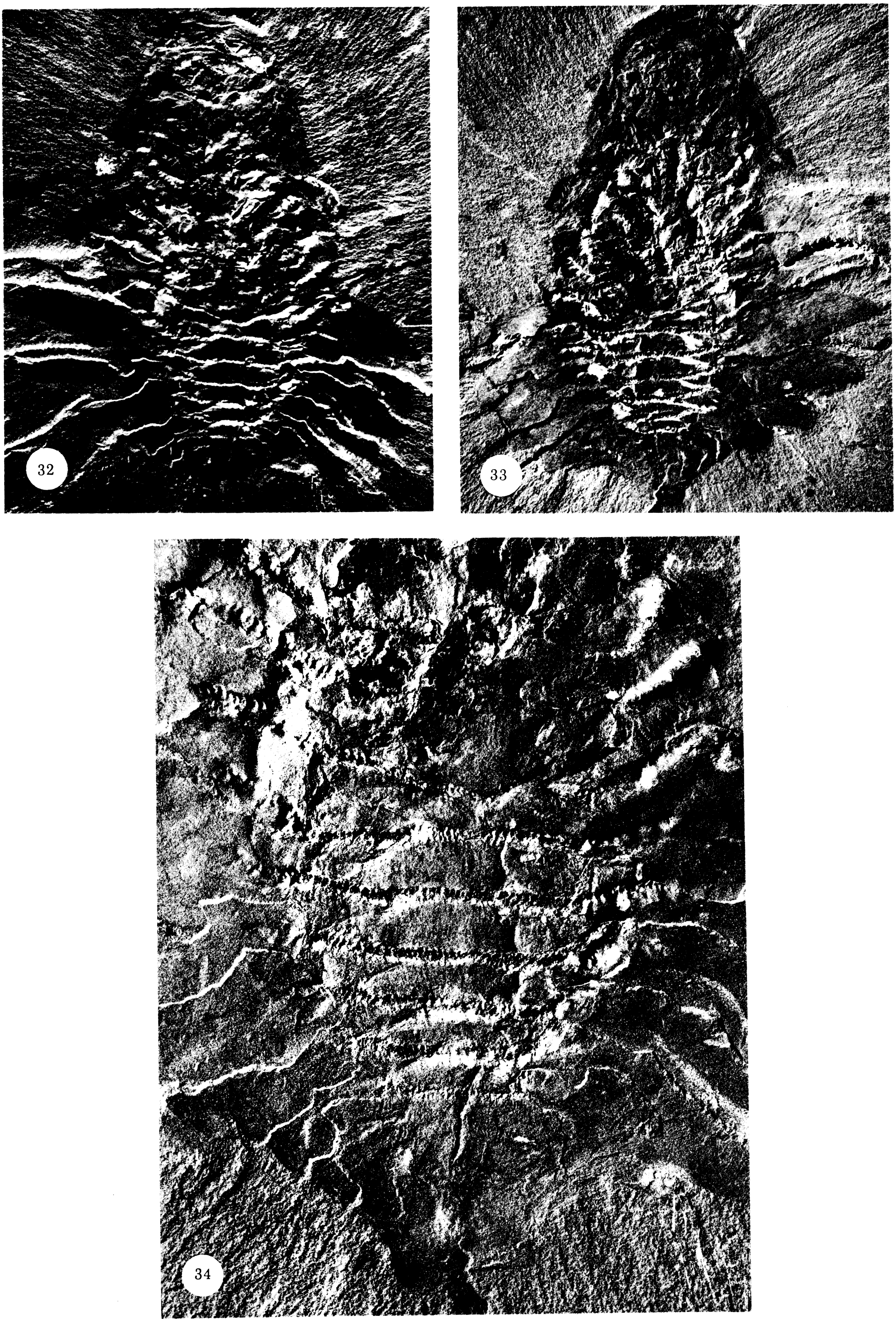
Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274141, counterpart of U.S.N.M. 274142, the part, parallel oblique.

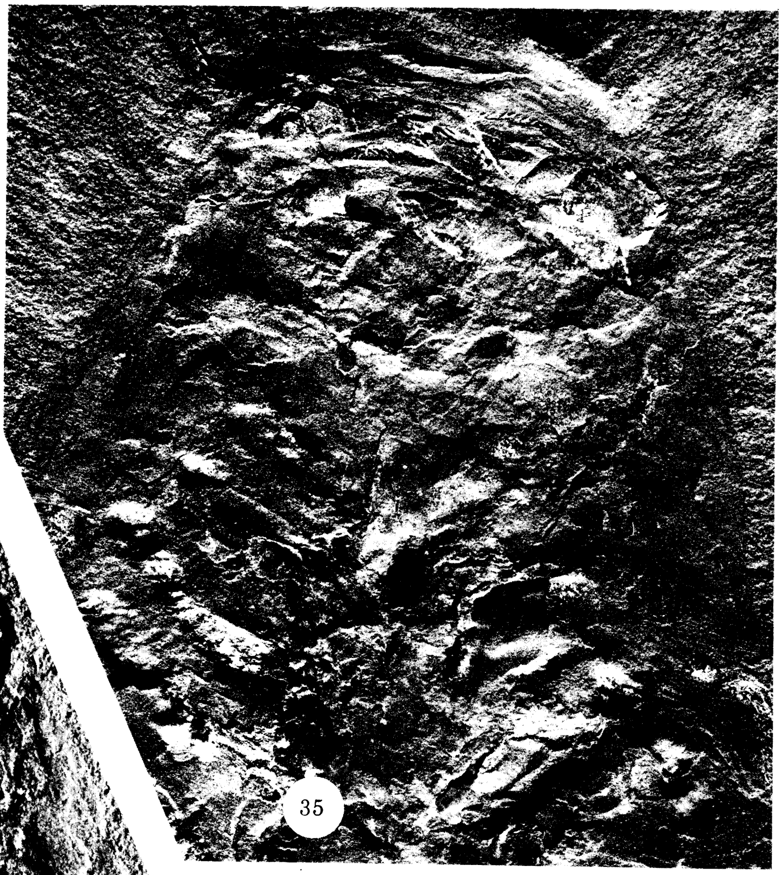
FIGURE 31. Explanatory drawing of part, before preparation.

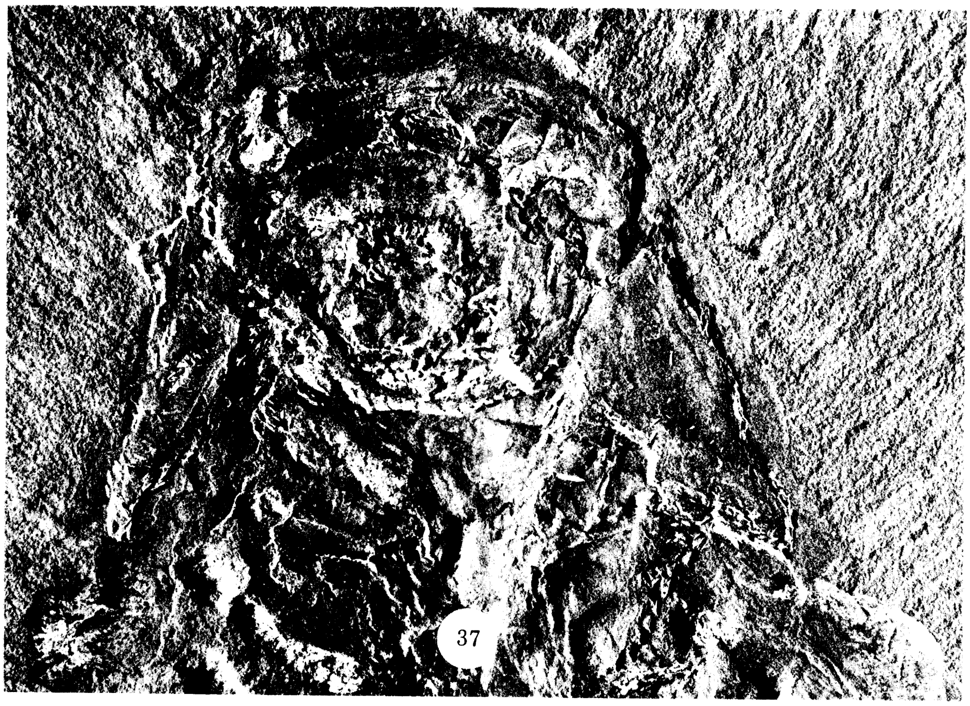
FIGURES 32, 34. Part, respectively entire, before preparation, northwest (magn. × 1.0), median–posterior region, northwest (magn. × 2.5).

FIGURE 33. Counterpart, entire, northwest (magn. × 1.0).



Figures 32–34. For description see opposite.





FIGURES 35–37. For description see opposite.

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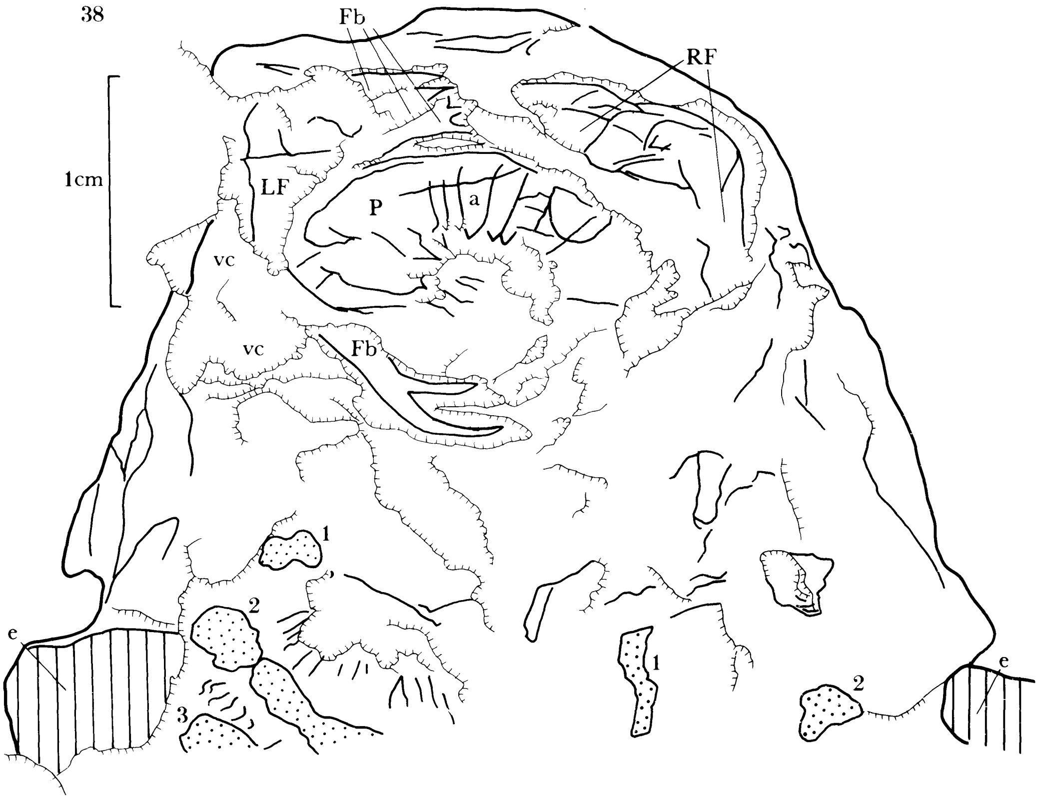

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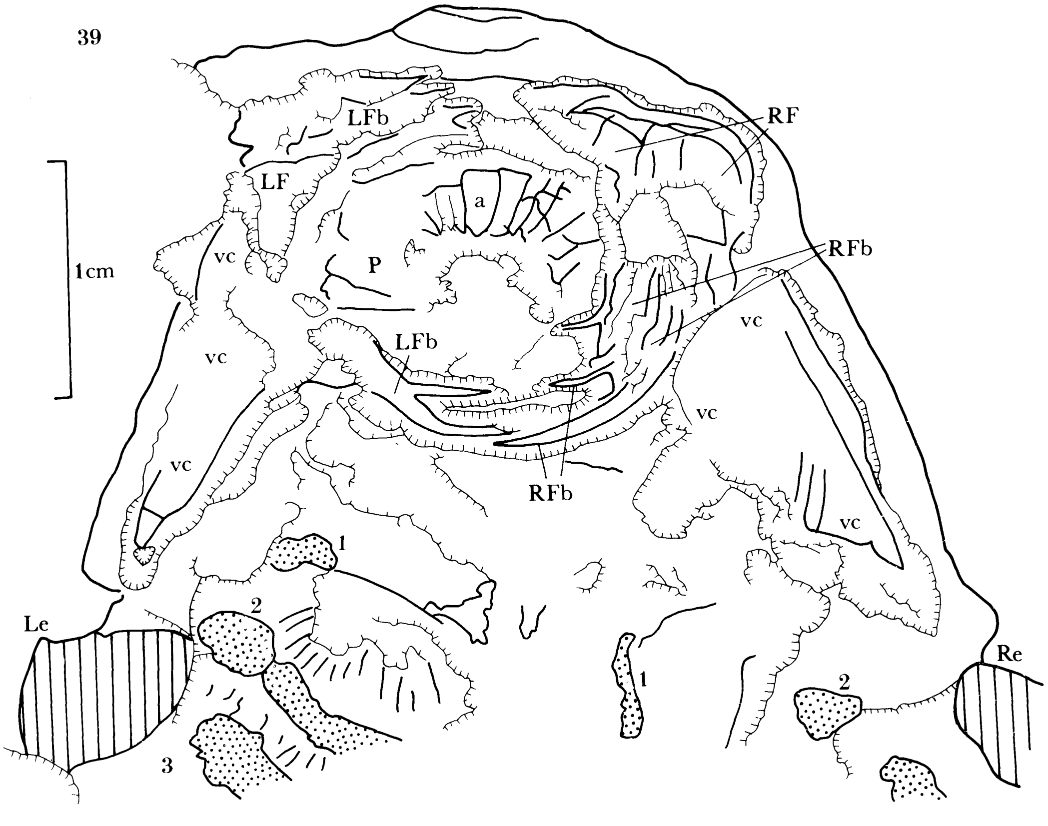


DESCRIPTION OF PLATE 8 AND FIGURES 38, 39

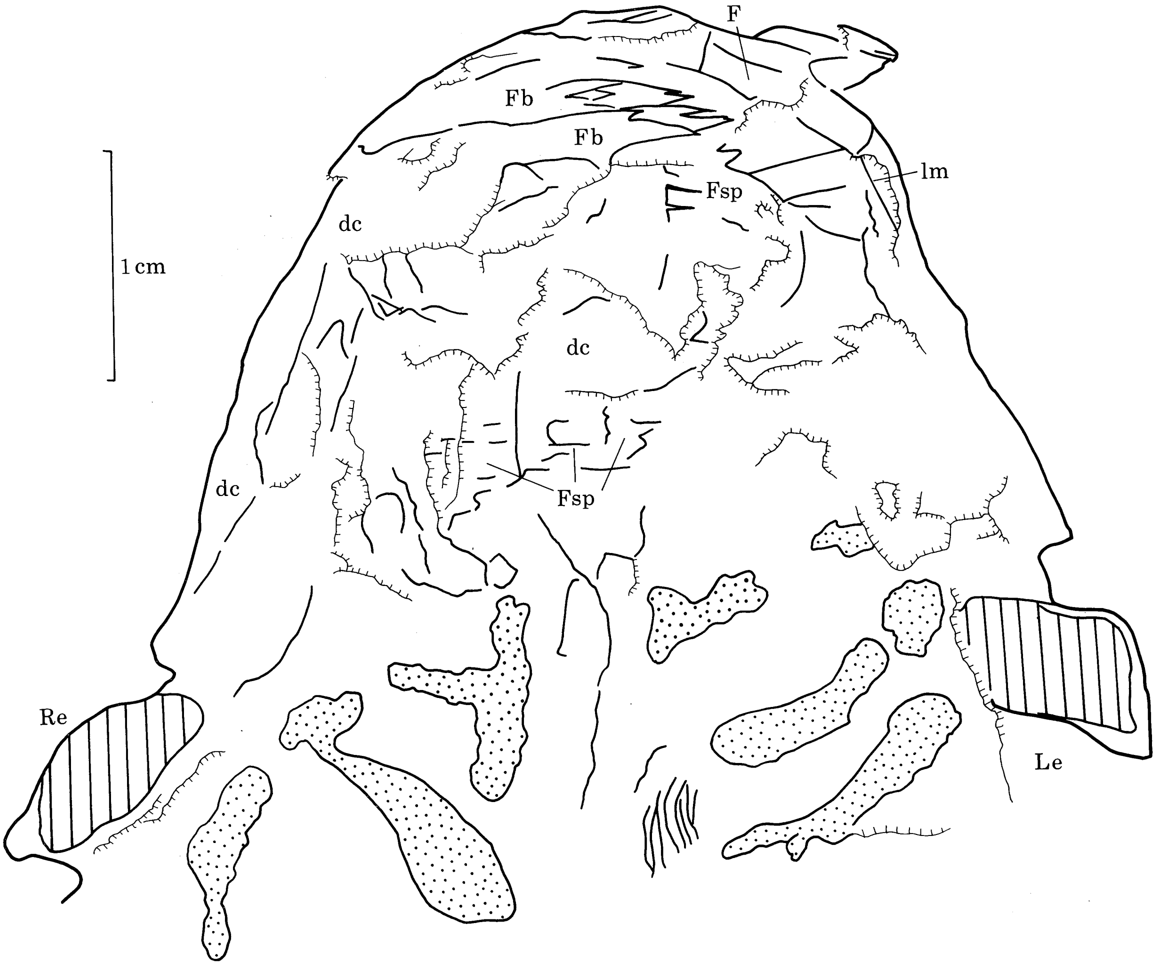
Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274142, anterior portion of part (magn. × 2.5).

FIGURES 35–37. Respectively before preparation, north (compare figure 32, plate 7), at first stage of preparation, east, at second stage, east.

FIGURE 38. Explanatory drawing, first stage of preparation.

FIGURE 39. Explanatory drawing, second stage of preparation.



Description of figure 40 and plate 9

Anomalocaris nathorsti (Walcott, 1911)

Figure 40. U.S.N.M. 274141, explanatory drawing of anterior portion after preparation.

Figure 41. U.S.N.M. 274141, anterior portion, counterpart, after preparation (compare figure 33, plate 7) (magn. × 2.5).

Figures 42, 43. U.S.N.M. 274145, part (compare figure 51), left hand portion showing lateral lobes 3–10 and rays, respectively northwest, reflected (magn. × 2.5).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FIGURES 41–43. For description see opposite.


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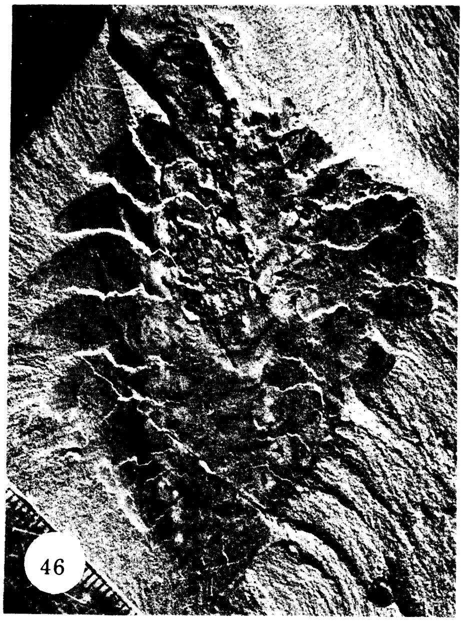
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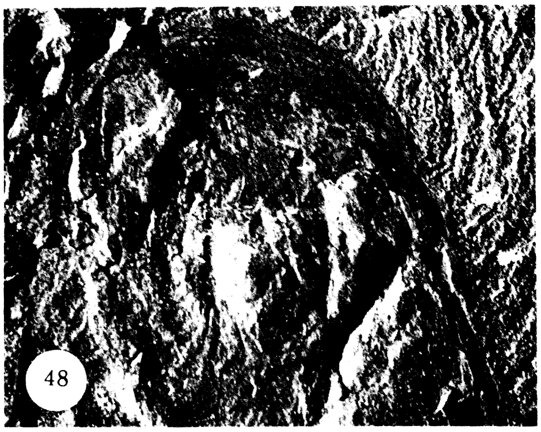
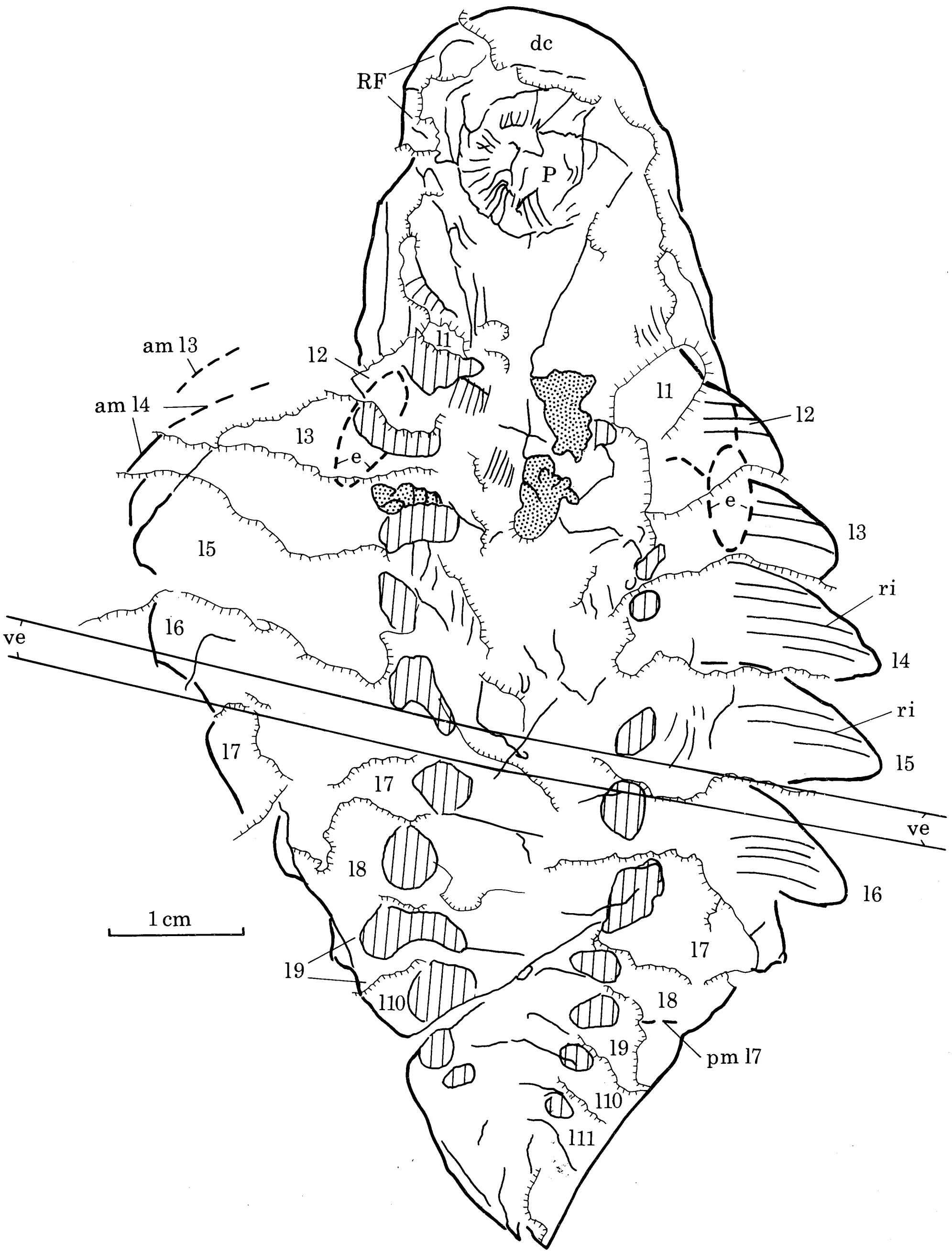

48

FIGURES 44–49. For description see opposite.



Description of plate 10 and figure 50

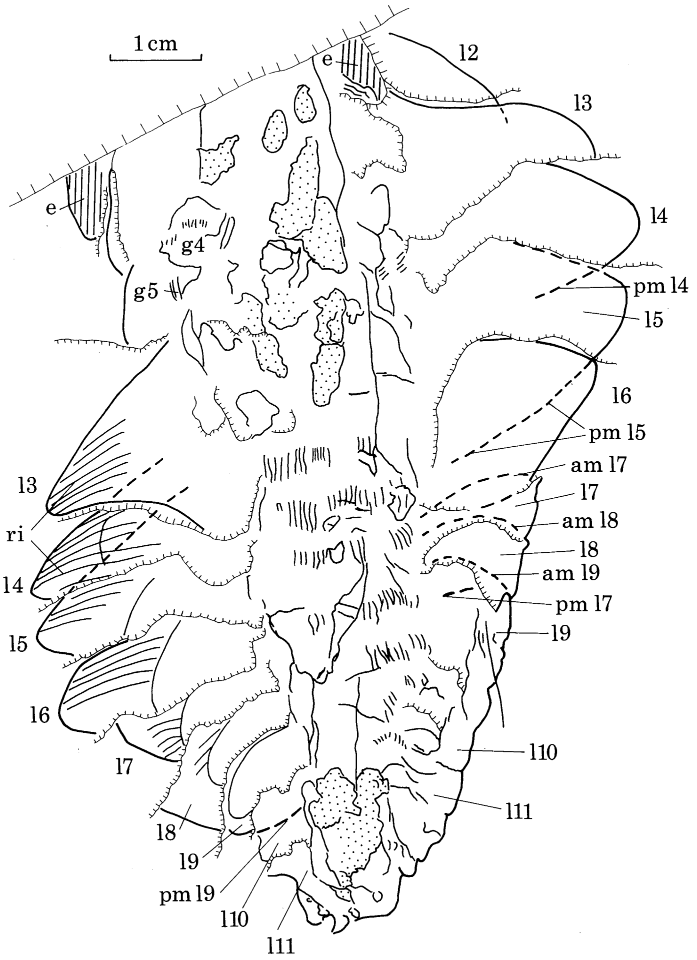
Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274144, part, and U.S.N.M. 274148, counterpart, parallel oblique.

Figures 44, 45, 47–49. Counterpart, respectively before and after preparation to expose eye lobes, northwest (magn. × 1.0), under alcohol (magn. × 1.0), anterior portion, west (magn. × 2.5), postero-median portion, north (magn × 5.0).

Figure 46. Part, northeast, after preparation of left lateral lobes 1–3 (magn. × 1.0).

Figure 50. Composite explanatory drawing of U.S.N.M. 274144 and 274148, from ventral.



DESCRIPTION OF FIGURE 51 AND PLATE 11

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274145, part, and U.S.N.M. 274162, counterpart, oblique (magn. × 1.0).

FIGURE 51. Composite explanatory drawing.

FIGURES 52, 53. Part, before and after preparation of posterior margins of lateral lobes, north.

FIGURES 54, 55. Counterpart, before and after preparation of anterior margins of right lateral lobes, north.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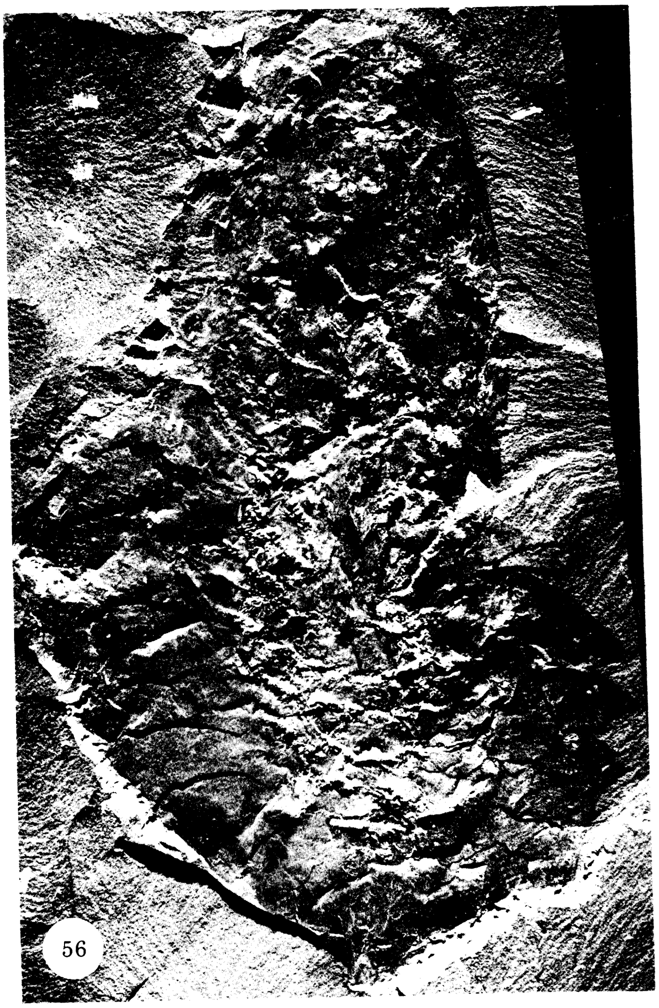
FIGURES 52–55. For description see opposite.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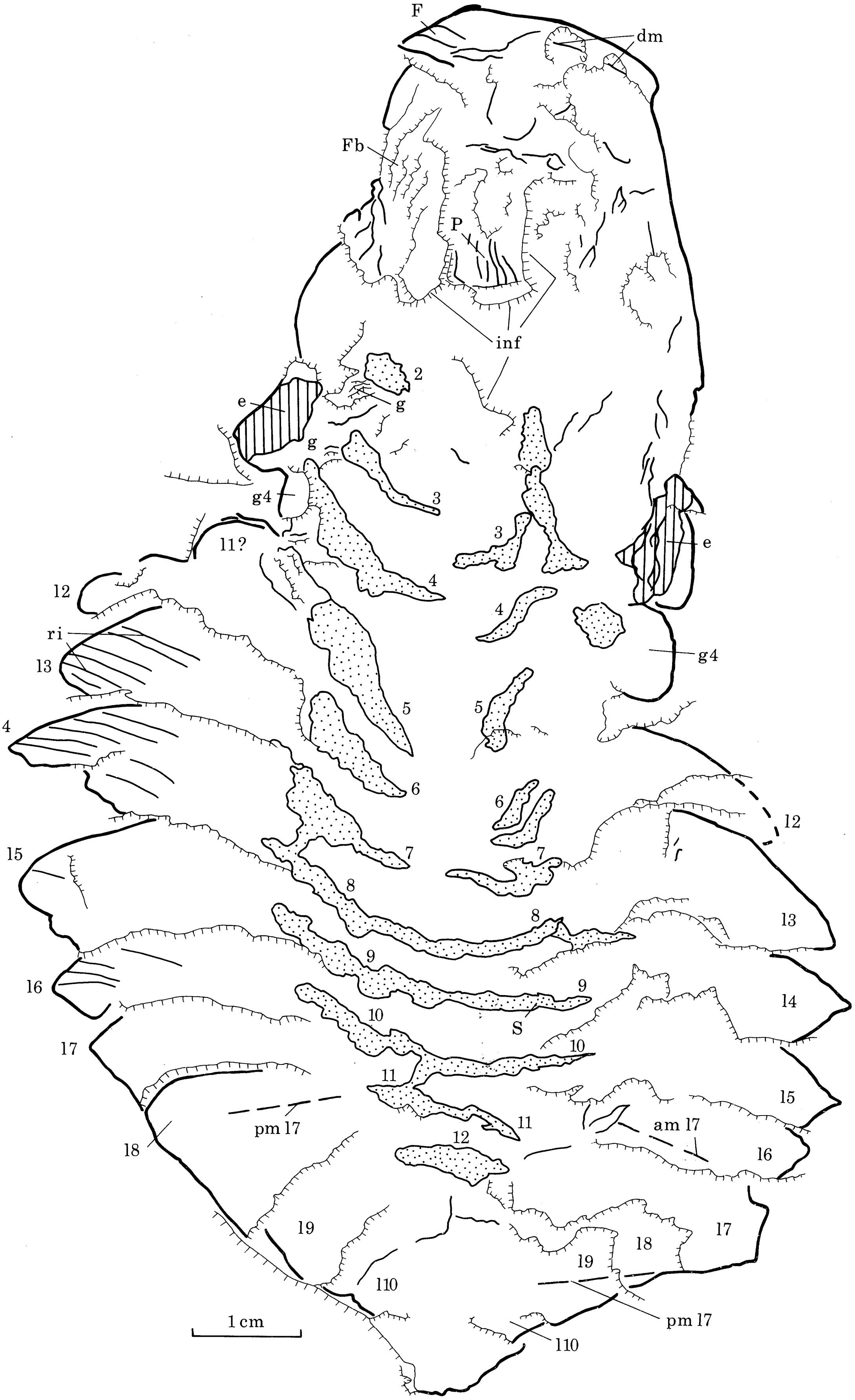
FIGURES 56–58. For description see opposite.



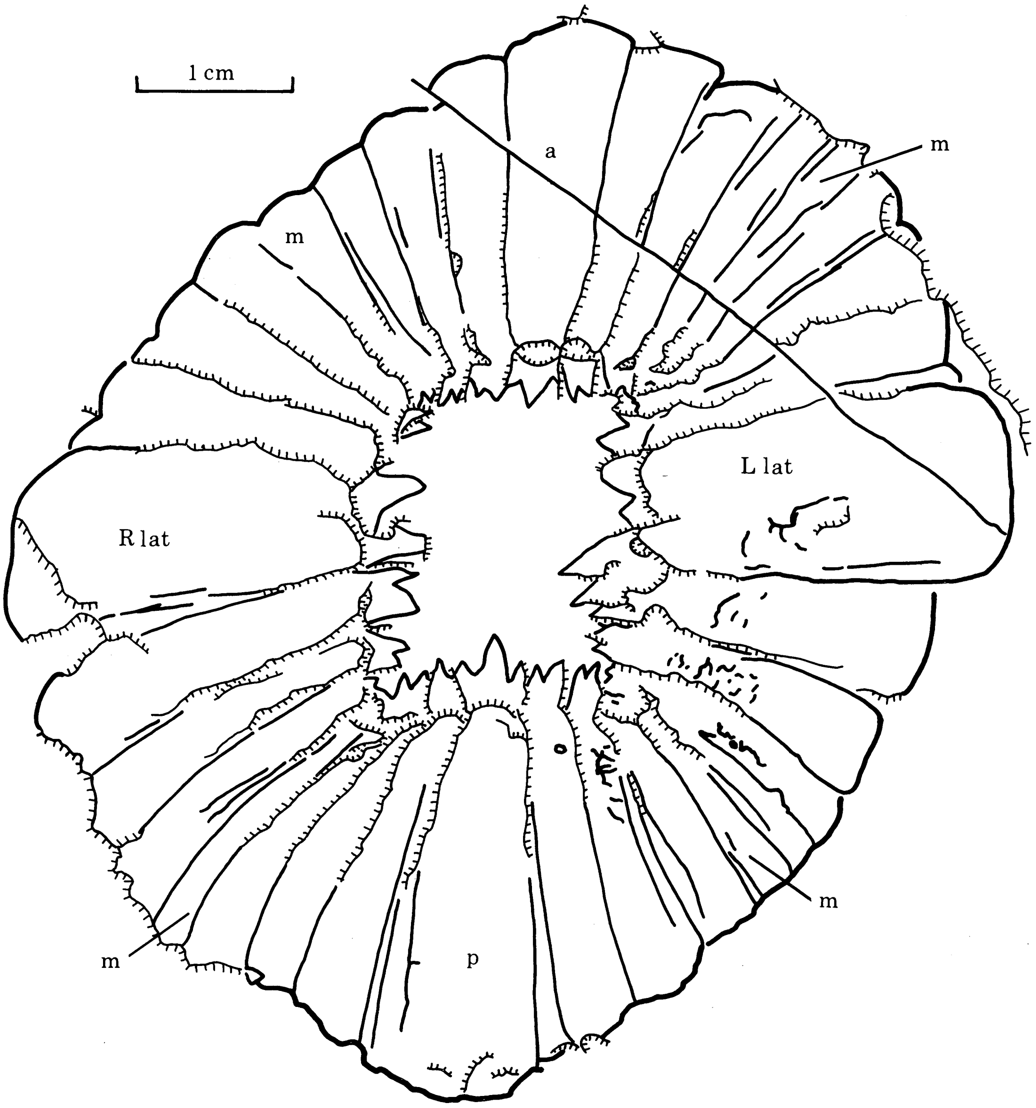
Description of plate 12 and figure 59

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274146, counterpart, parallel oblique.

Figures 56–58. Respectively entire, north, reflected (magn. × 1.0), anterior portion after removal of portion of infilling, northeast (magn. × 2.5).

Figure 59. Explanatory drawing. See text for discussion of numbering of right lateral lobes.



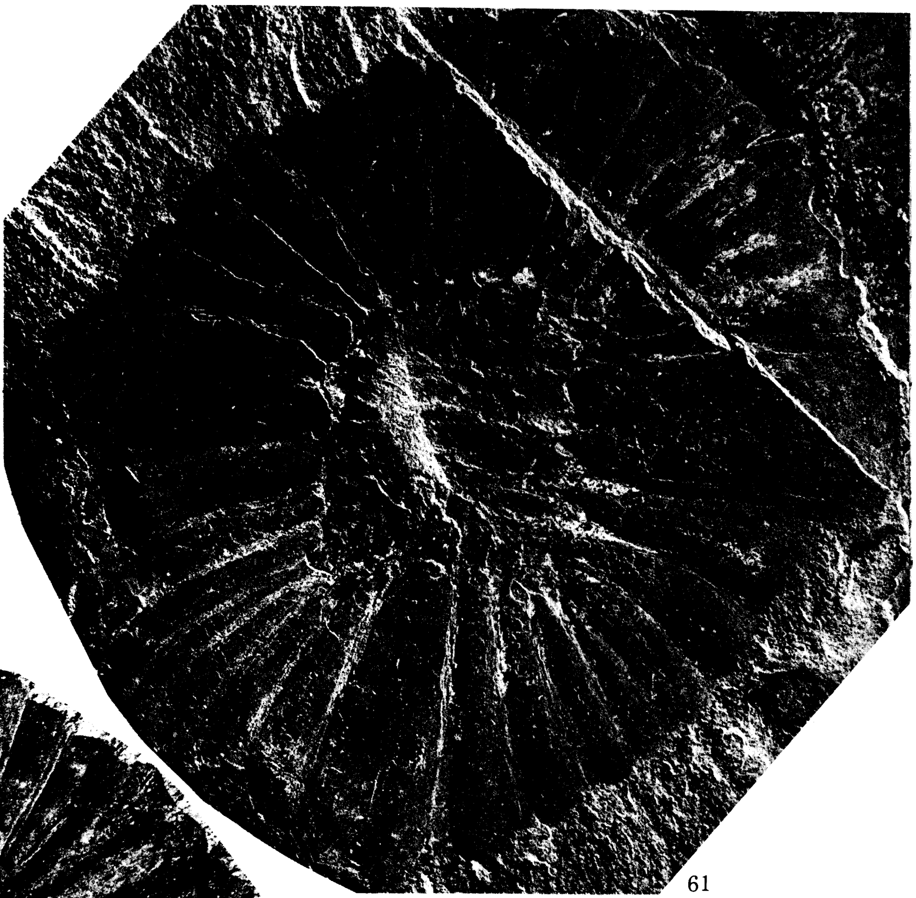
Description of figure 60 and plate 13

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 57538, holotype.

Figure 60. Composite explanatory drawing.

Figures 61–63. Respectively part, northeast, counterpart, northwest (magn. × 1.7), aperture of counterpart, west (magn. × 3.3).



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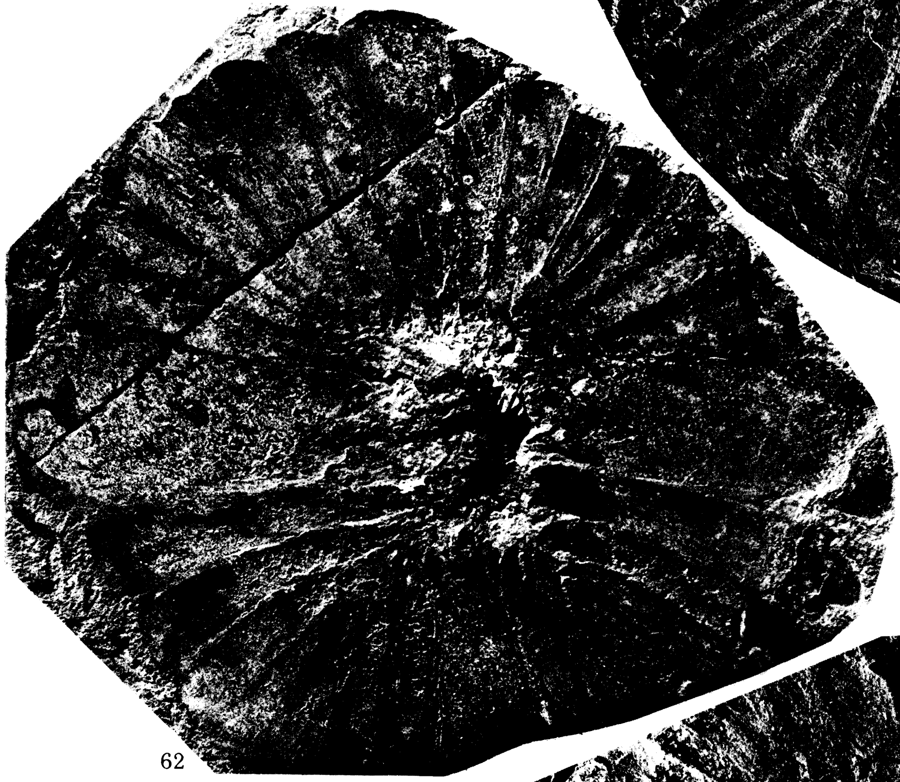

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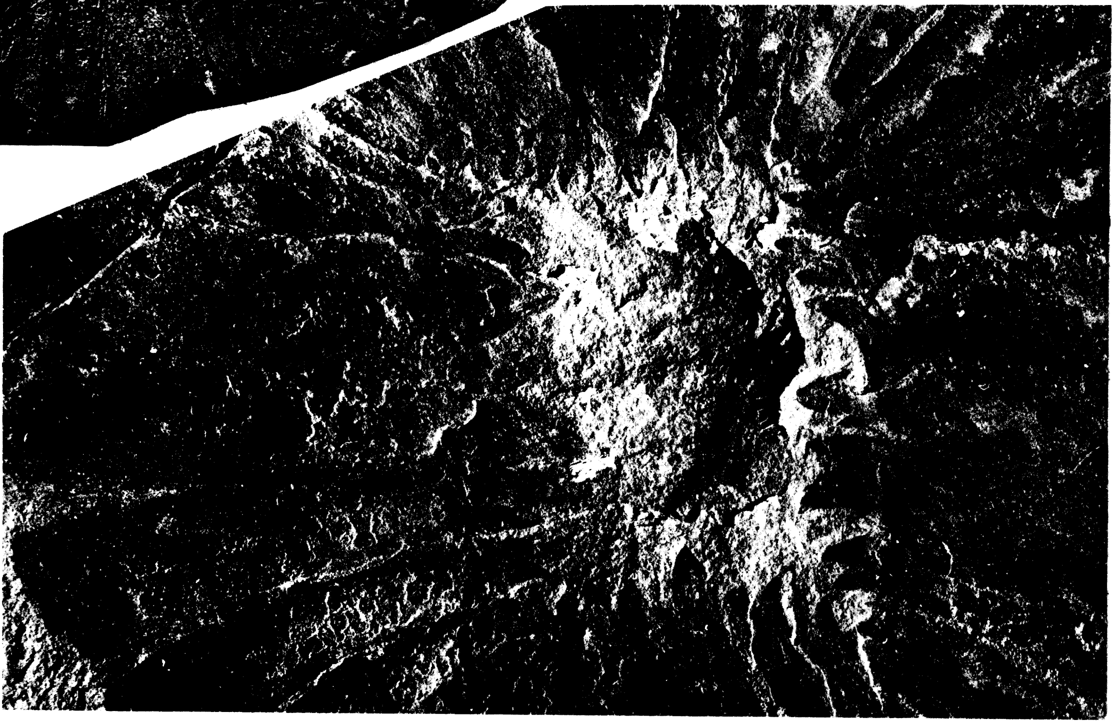
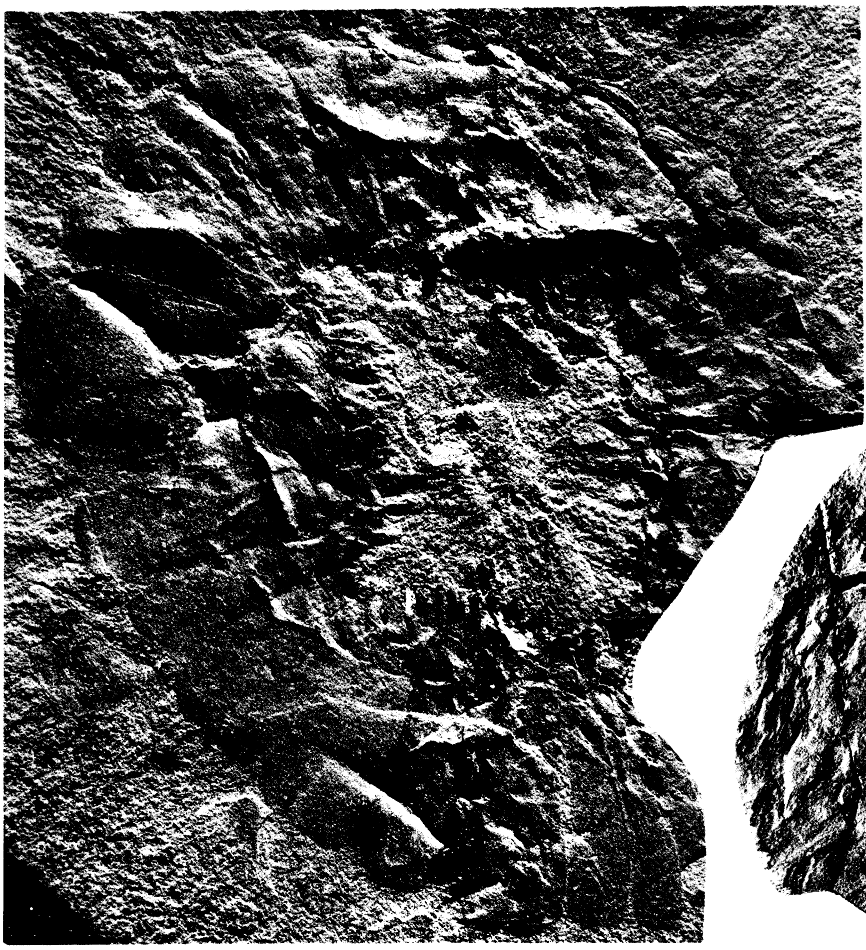


63

FIGURES 61–63. For description see opposite.



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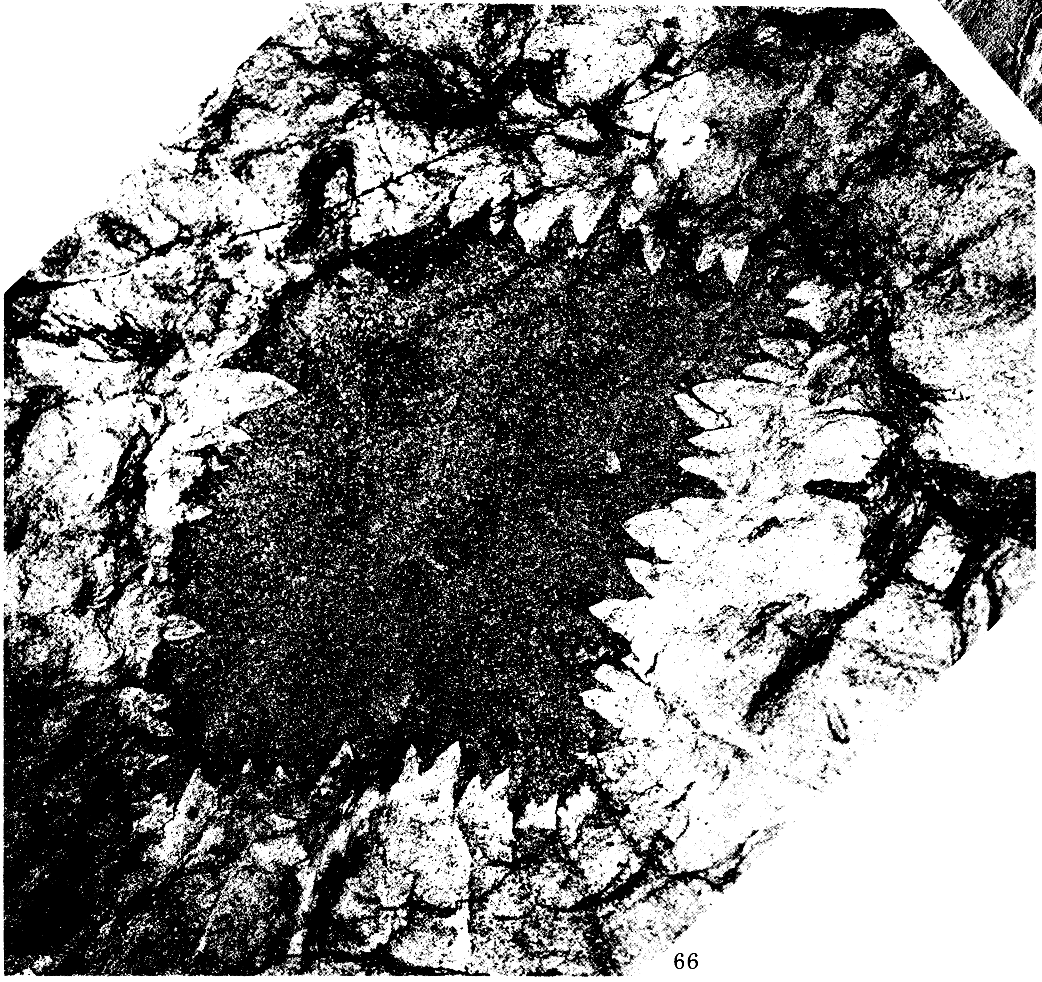
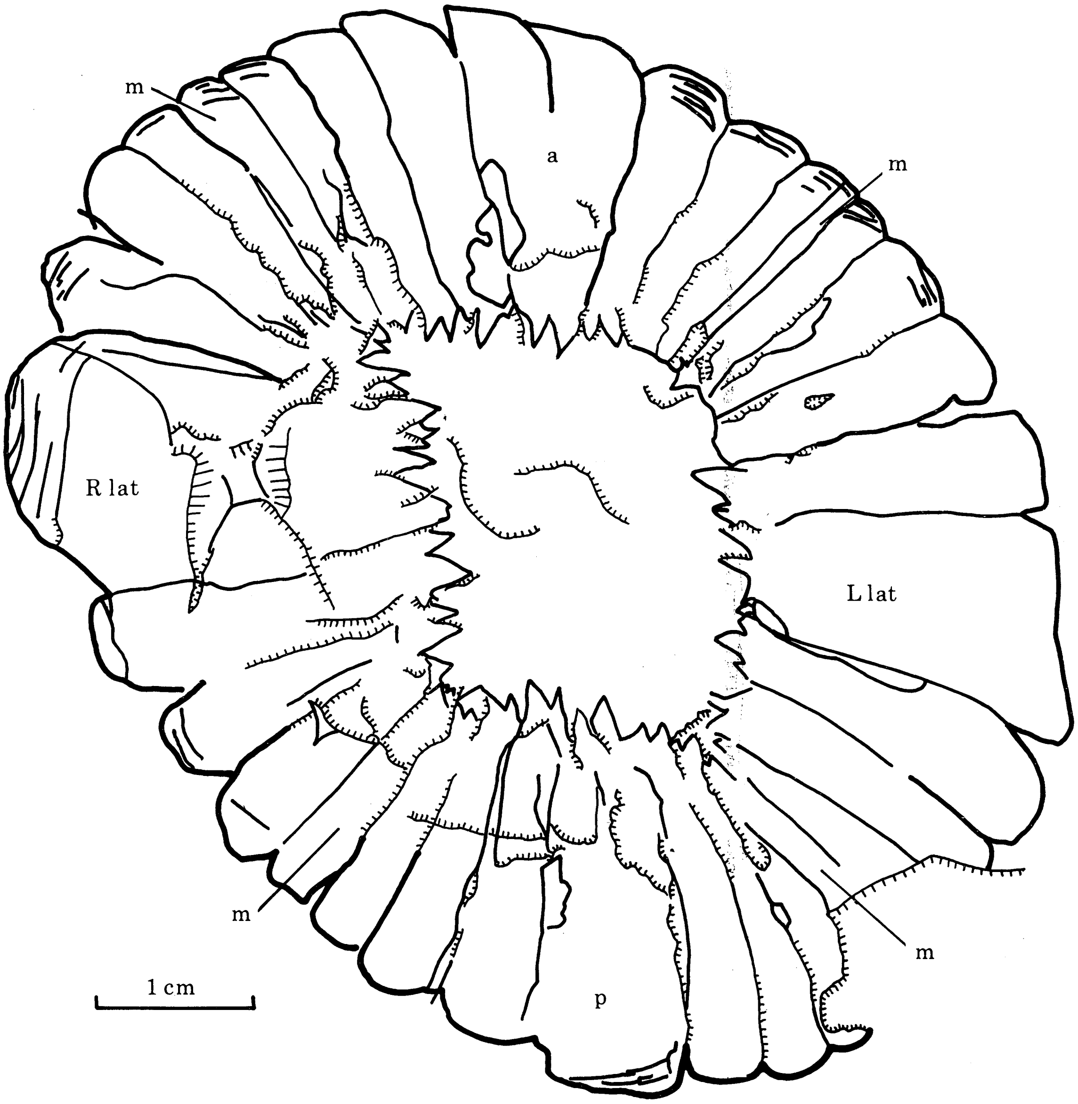


66

FIGURES 64–66. For description see opposite.



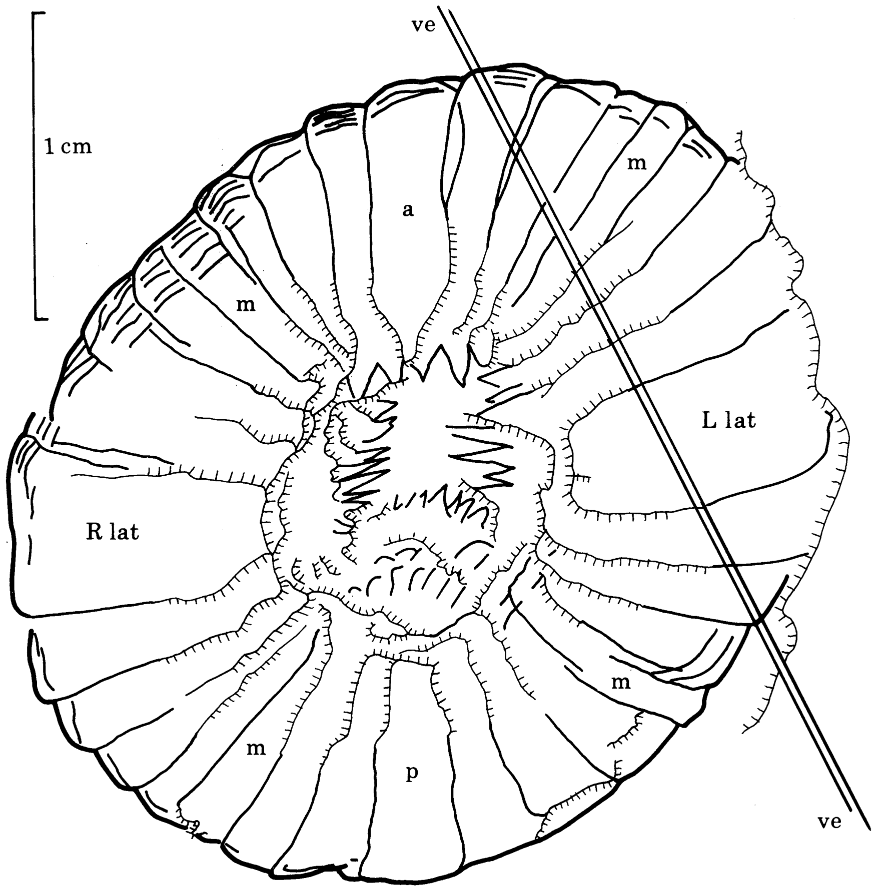
Description of plate 14 and figure 67

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 253216, a 'Peytoia' showing teeth around the aperture.

Figures 64–66. Respectively part, north–northeast, counterpart, west (magn. × 1.7), and aperture of counterpart, reflected (magn. × 3.3).

Figure 67. Composite explanatory drawing.



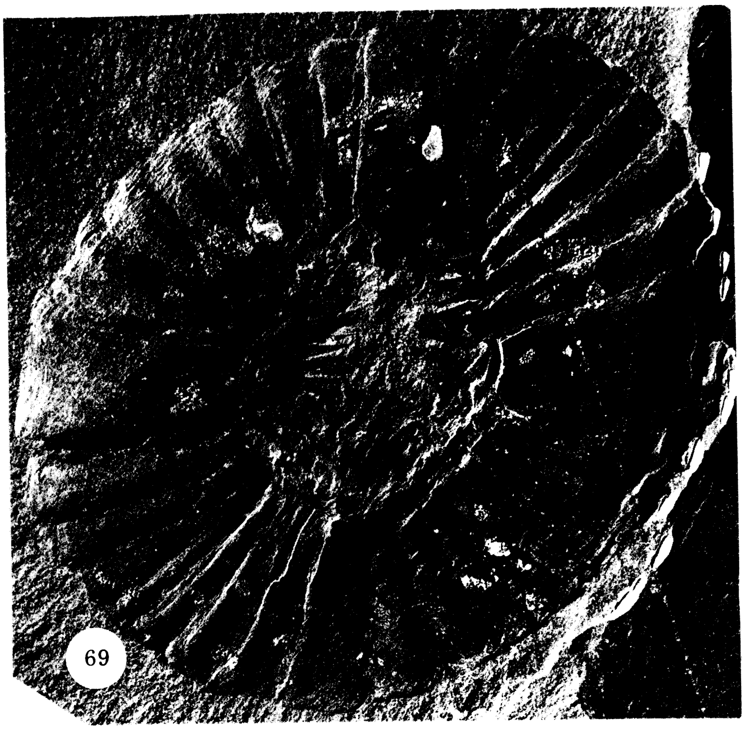
Description of figure 68 and plate 15

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 368583, a 'Peytoia' showing additional groups of spines within the aperture.

Figure 68. Explanatory drawing of part.

Figures 69–71. Respectively part, counterpart, northwest (magn. × 3.3), and part, reflected (magn. × 5.0).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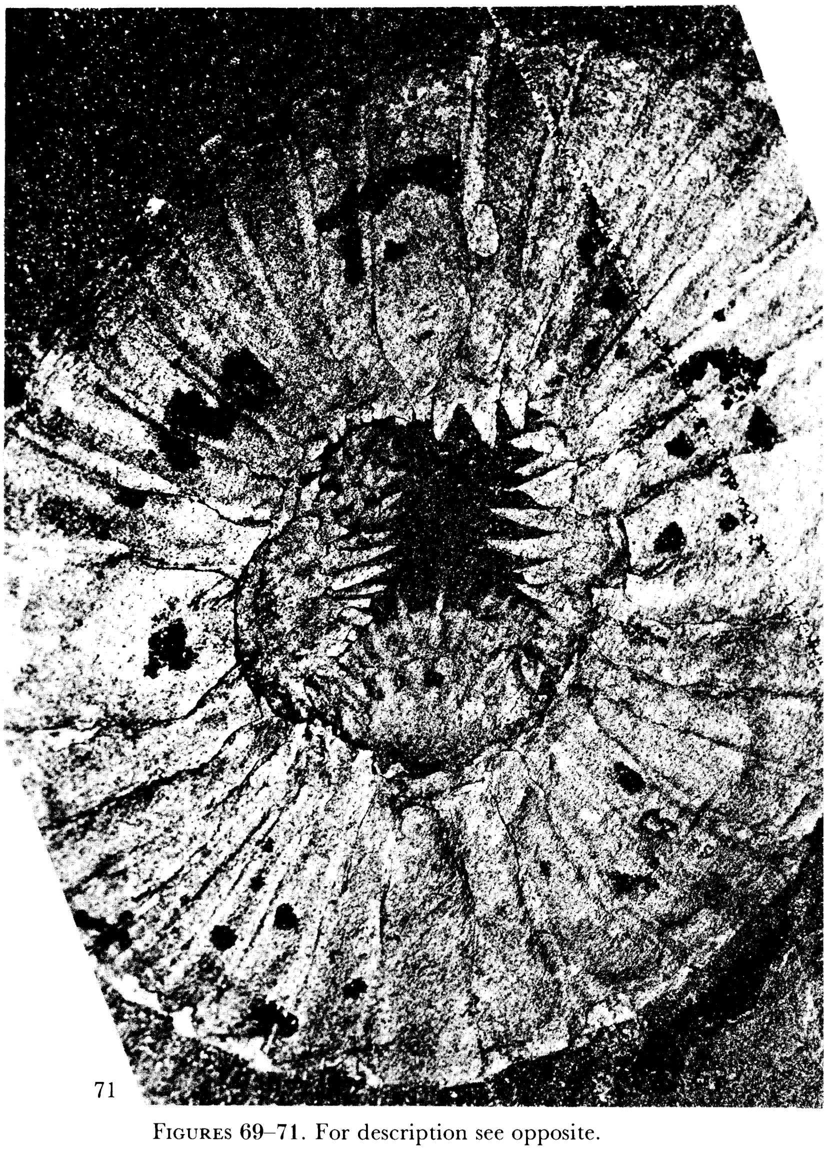
71

FIGURES 69–71. For description see opposite.


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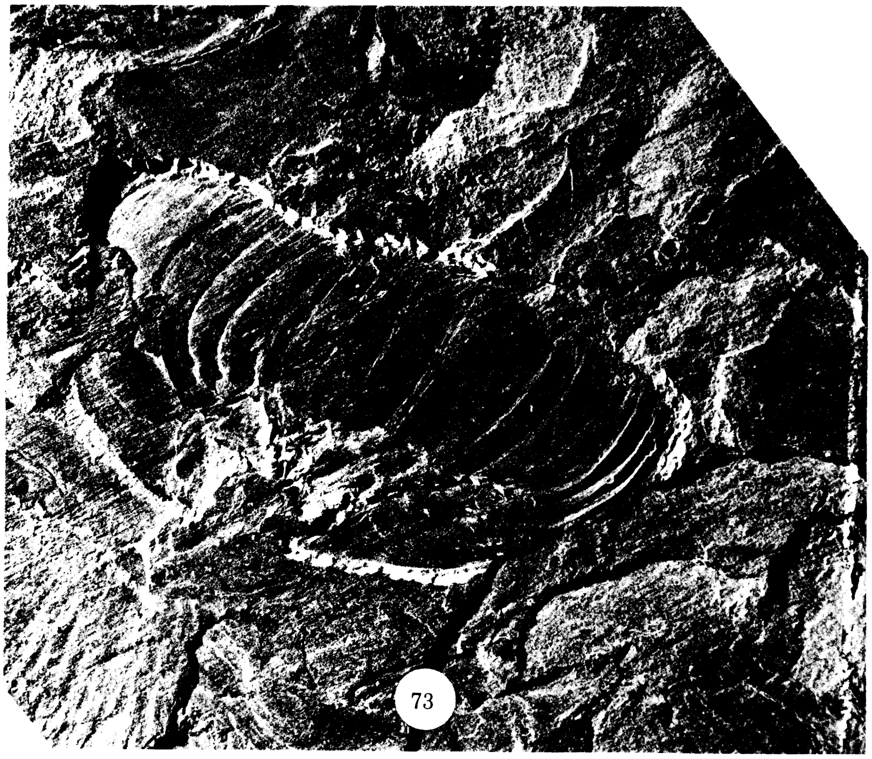
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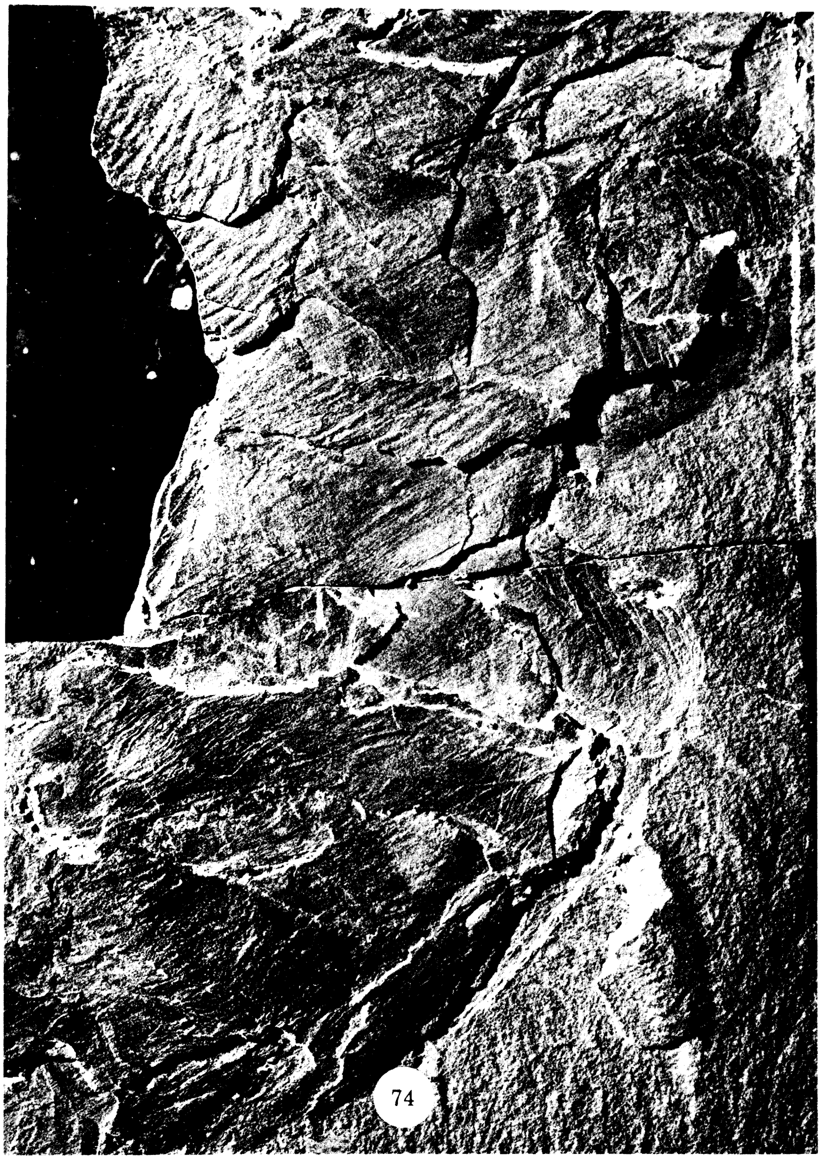

74

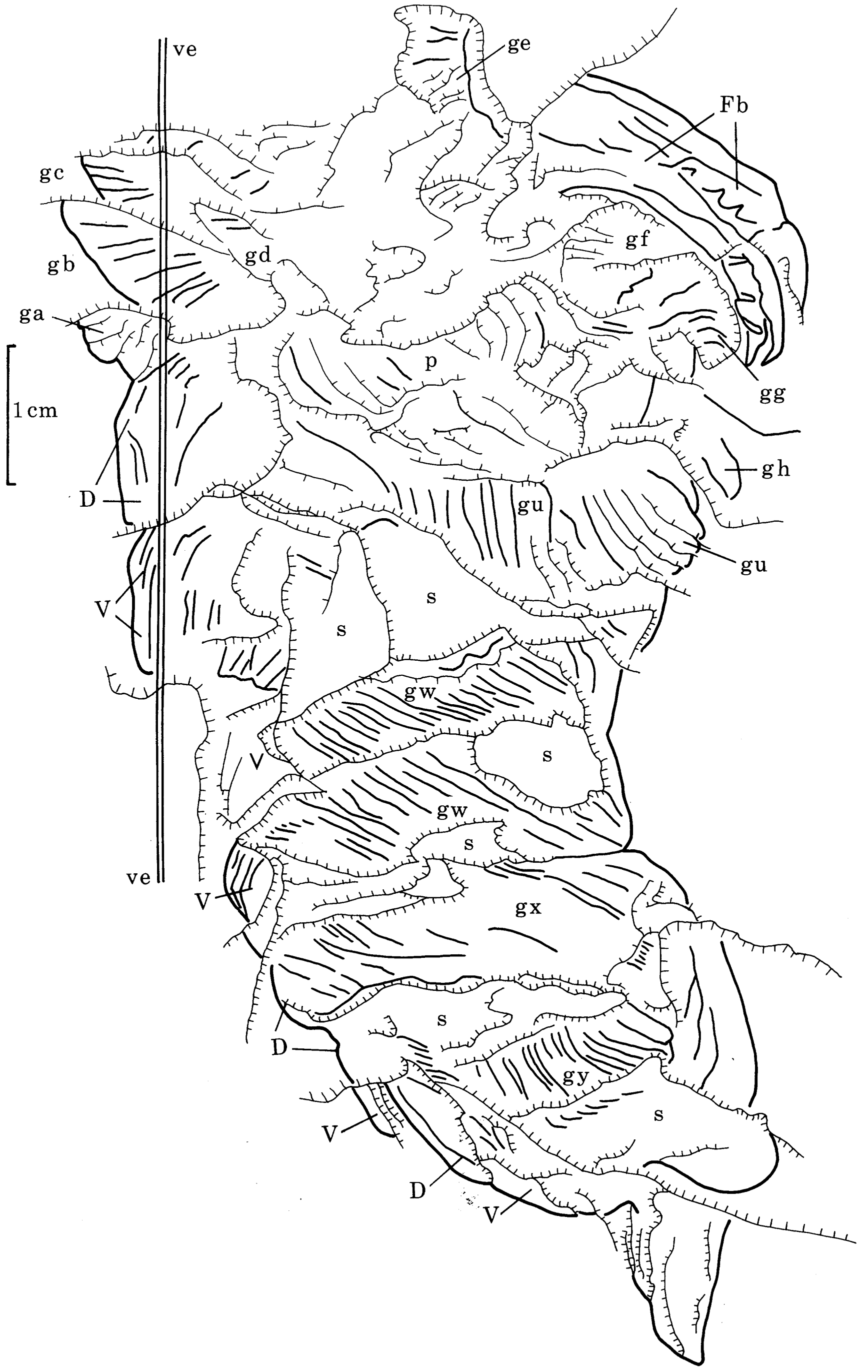
FIGURES 72–74. For description see opposite.

Description of plate 16 and figure 75

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274155, 274158, joined together and forming the part of an oblique specimen (counterpart U.S.N.M. 274159, see figures 76–78).

Figures 72–74. Respectively entire, west (magn. × 1.0), anterior area with 'Peytoia', northwest (magn. × 3.3), and mid-region, west (magn. × 2.5).



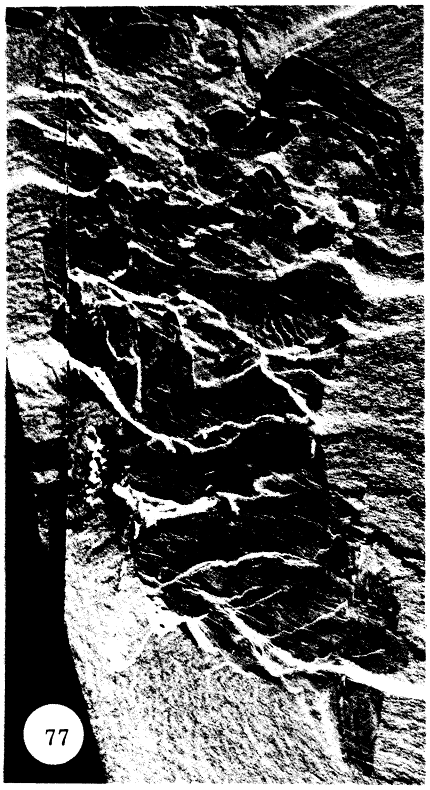
Description of figure 76 and plate 17

Anomalocaris nathorsti (Walcott, 1911)

Figure 76. Explanatory drawing of U.S.N.M. 274159 (counterpart of U.S.N.M. 274155, 274158, see figure 75).

Figures 77, 78. U.S.N.M. 274159 (counterpart of U.S.N.M. 274155, 274158, see figures 72–74, plate 16), respectively entire, northeast (magn. × 1.0), median region, west (magn. × 2.5).

Figures 79, 80. U.S.N.M. 368584, a 'Peytoia' showing darker bands at margins of plates, respectively counterpart, west, part, west (magn. × 3.3).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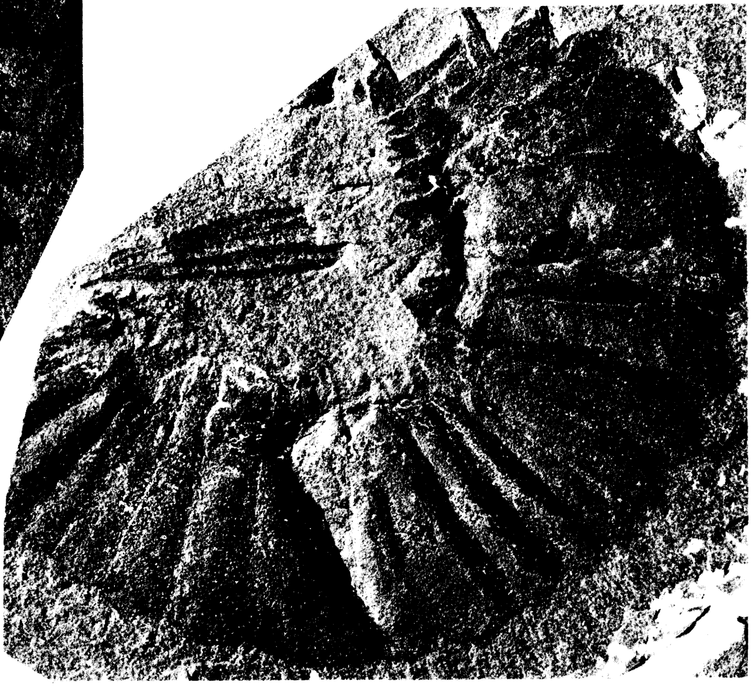
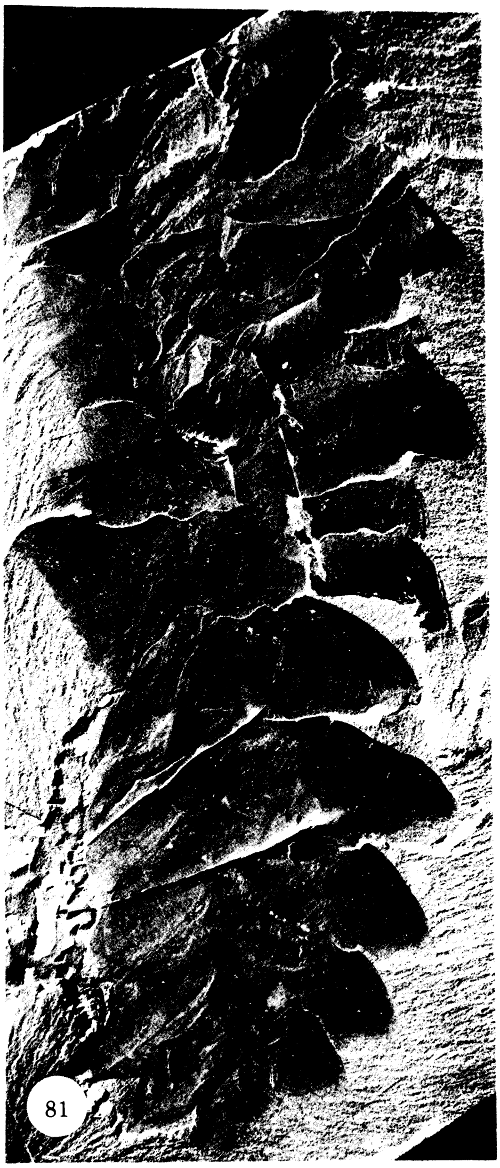

80

FIGURES 77–80. For description see opposite.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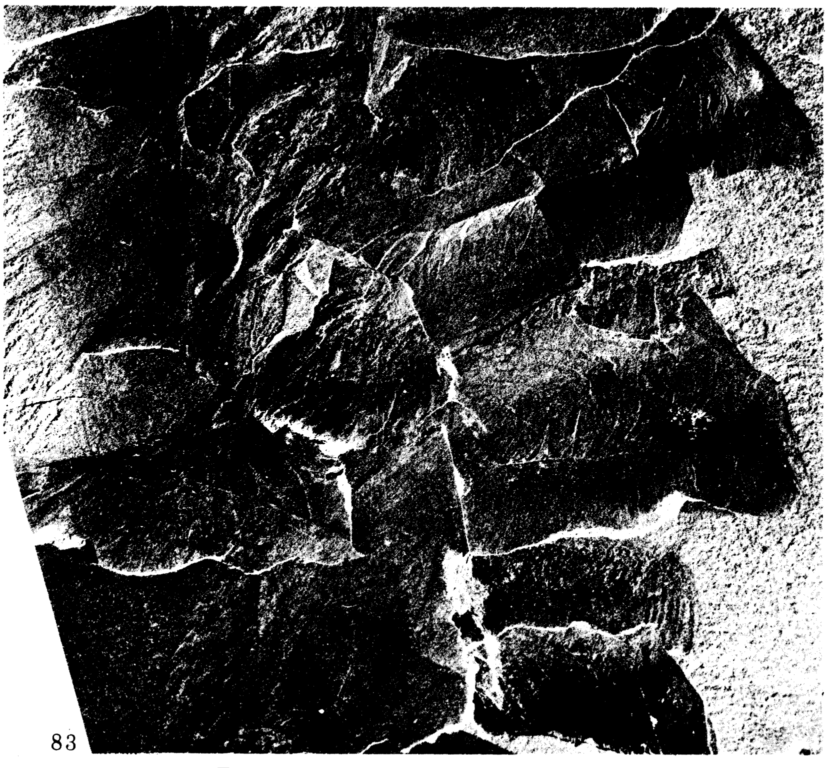
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FIGURES 81–83. For description see opposite.

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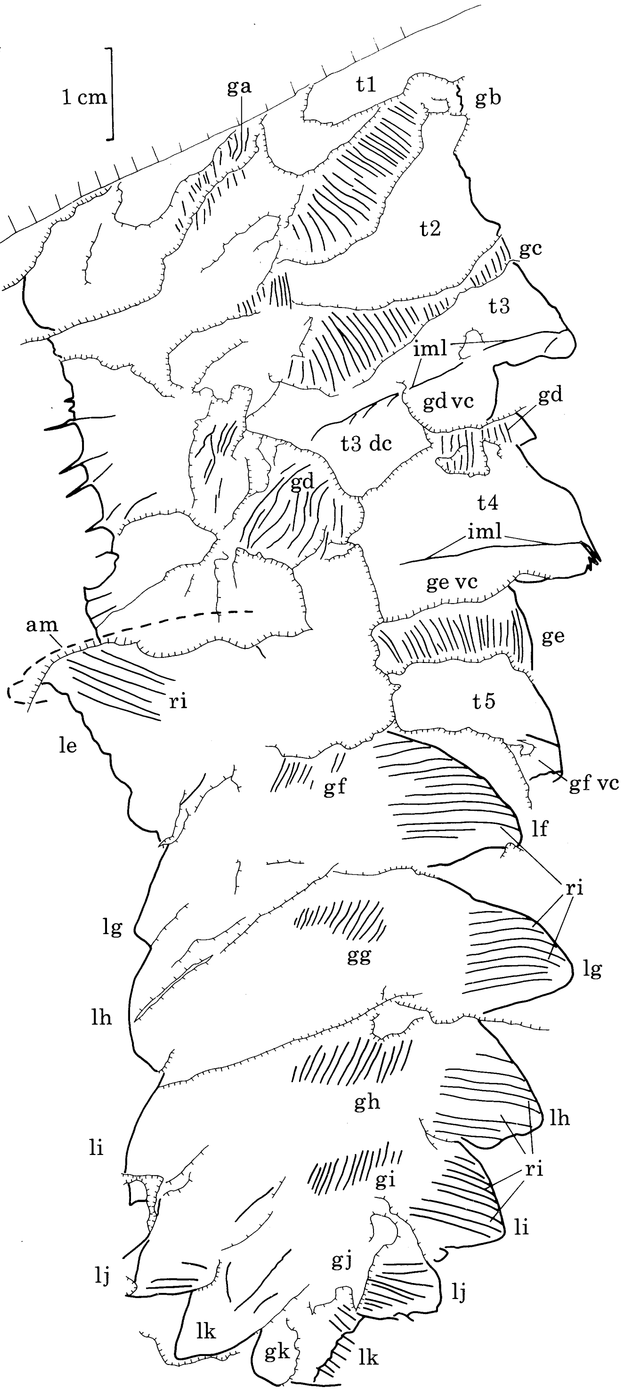
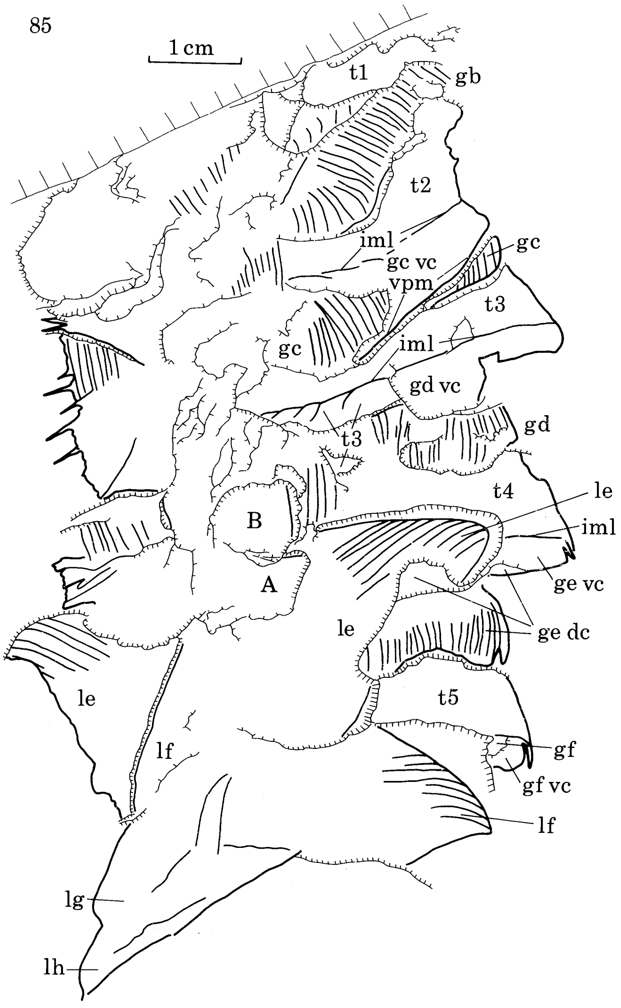


85



DESCRIPTION OF PLATE 18 AND FIGURES 84, 85

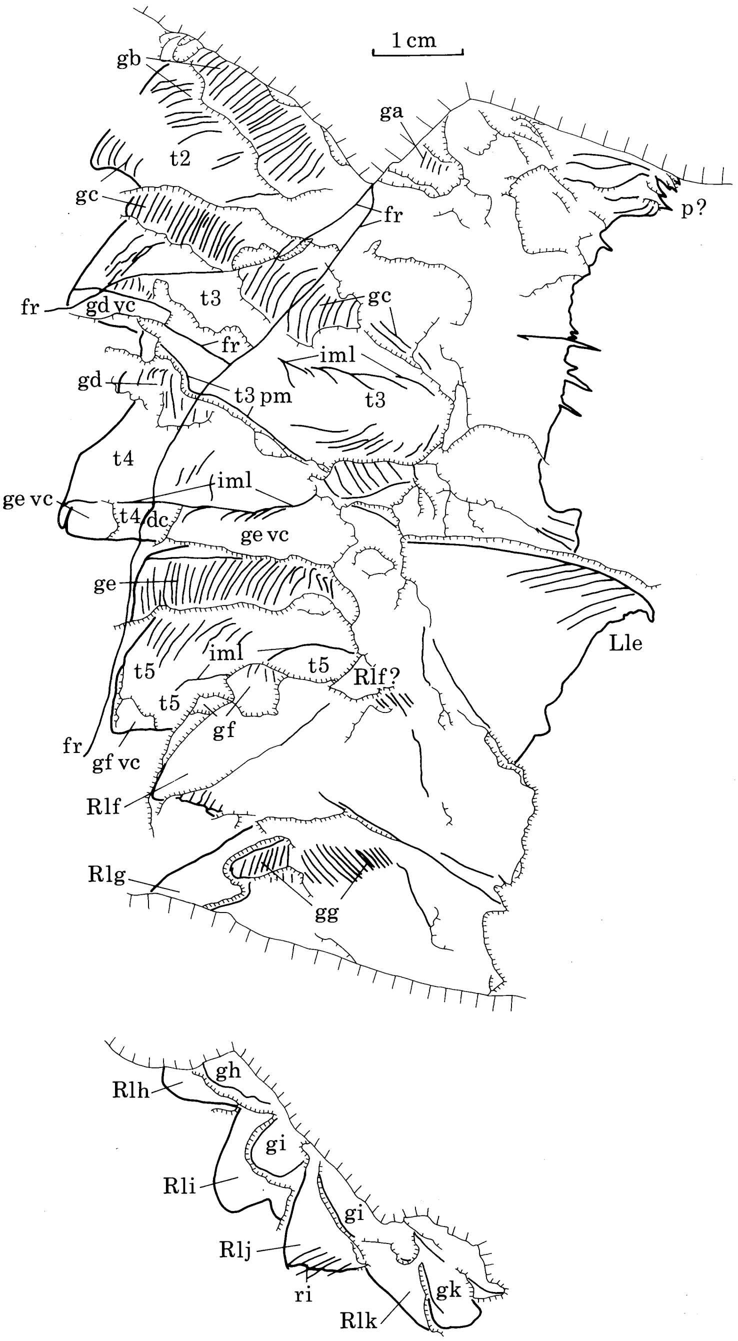
Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274154, the part of an oblique specimen (counterpart U.S.N.M. 274156, 274161, see figures 86–89).

FIGURES 81–83. Respectively entire, west (magn. × 1.0), anterior portion after preparation, north (magn. × 1.7), same before preparation (magn. × 1.7).

FIGURE 84. Explanatory drawing of entire specimen before preparation.

FIGURE 85. Explanatory drawing of anterior portion of specimen after preparation.



Description of figure 86 and plate 19

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 274156, 274161, joined together to form counterpart of U.S.N.M. 274154 (see figures 81–85).

Figure 86. Explanatory drawing of entire specimen.

Figures 87–89. Respectively entire, northwest (magn. × 1.0), anterior portion, northeast (magn. × 1.25), details of gills c, d, e before preparation, east (magn. × 2.5).

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Figures 87–89. For description see opposite.


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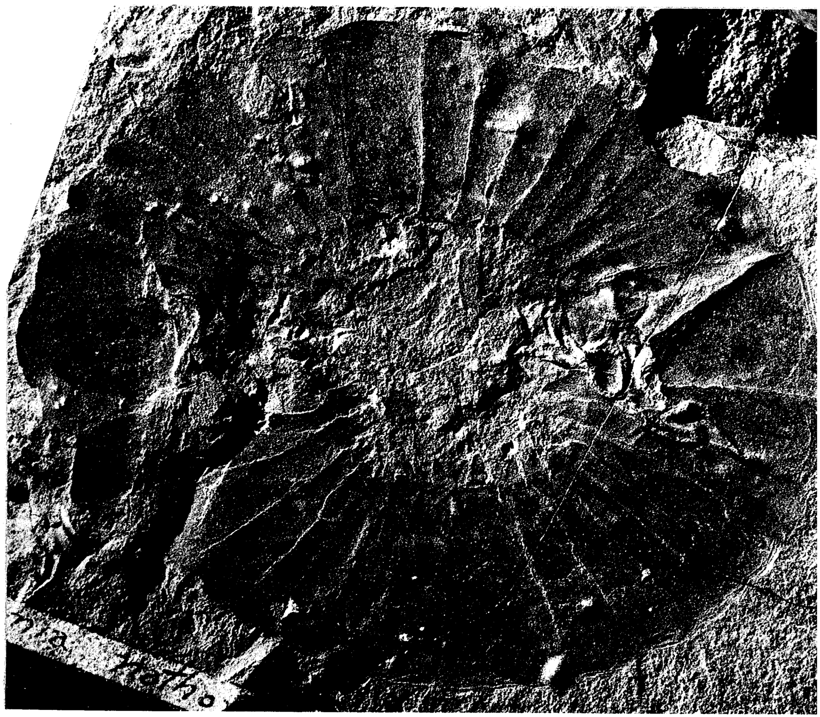
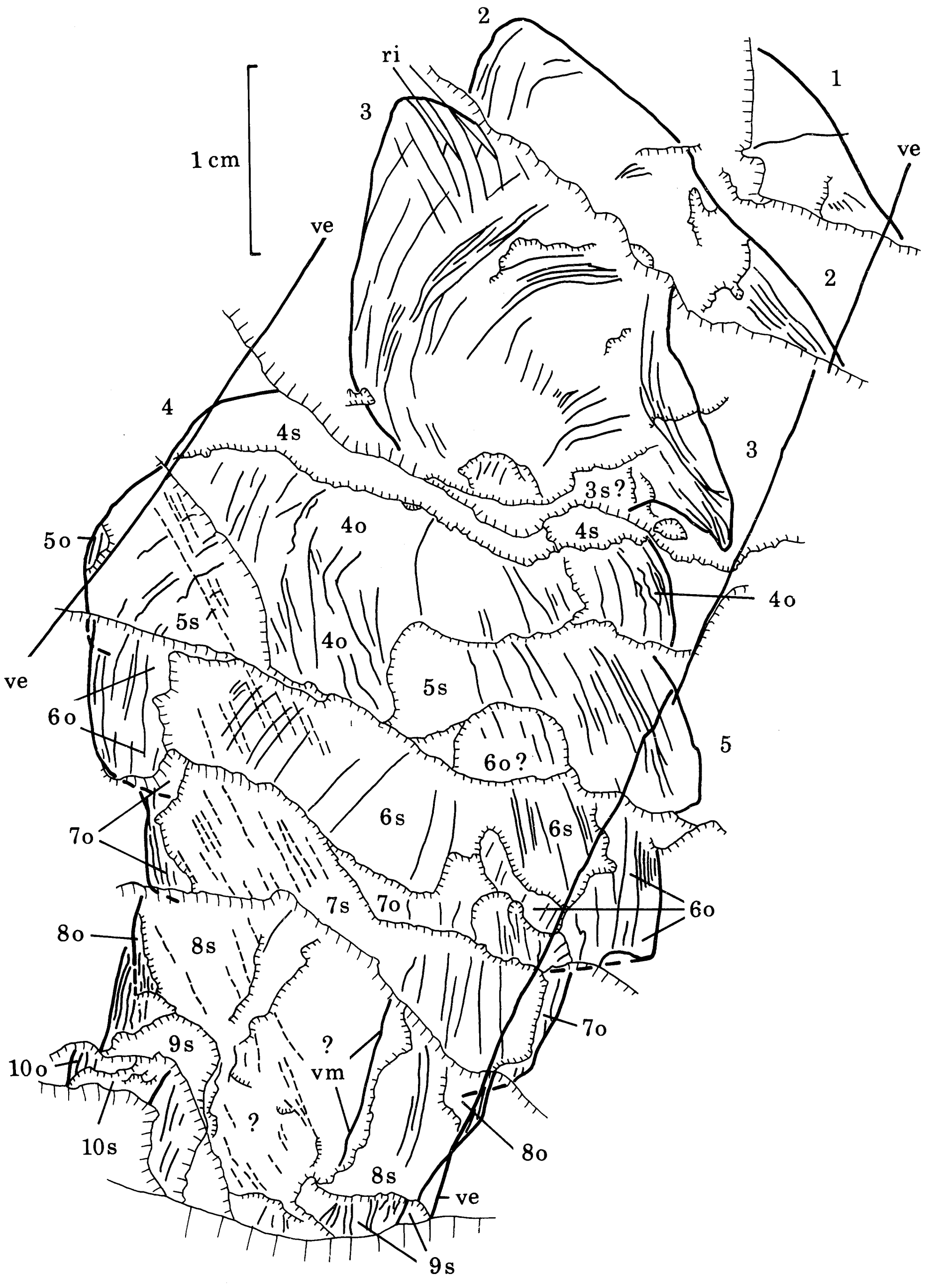

93

Figures 90–93. For description see opposite.

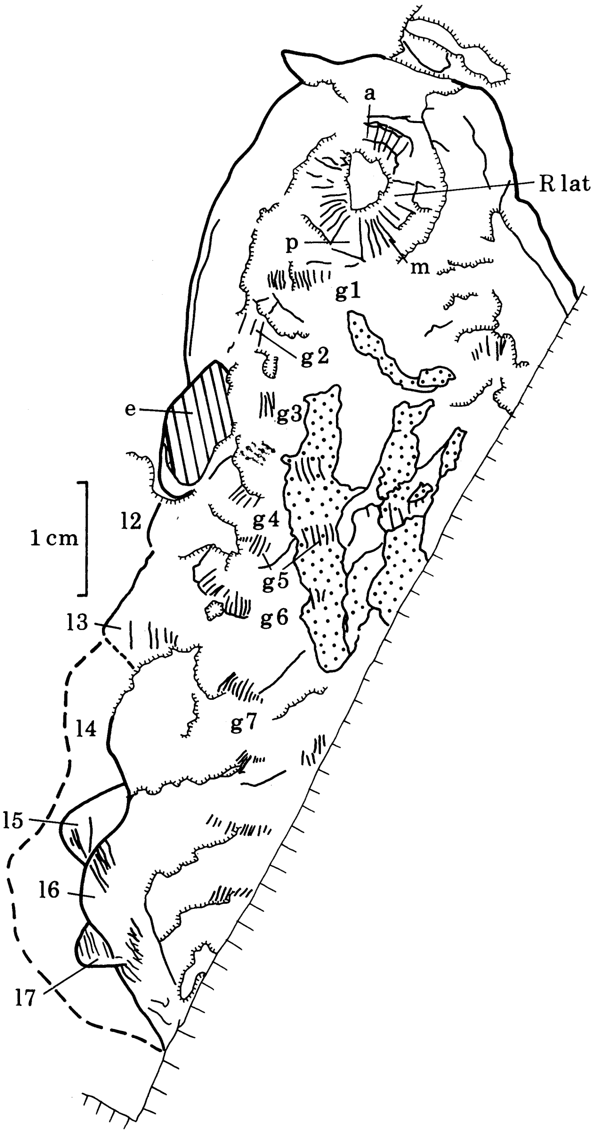


Description of plate 20 and figure 94

Figures 90–92. U.S.N.M. 57499, holotype of *Amiella ornata* Walcott, 1911*a*, respectively part, north–northwest and southwest, counterpart, west (magn. × 1.7).

Figure 93. *Anomalocaris nathorsti* (Walcott, 1911), U.S.N.M. 57539, counterpart of 'Peytoia' of Walcott, 1911*b*, plate 8, figure 2.

Figure 94. Composite explanatory drawing of U.S.N.M. 57499. Broken lines running north–northwest to south–southeast indicate a tectonic lineation. Hachures are longer and more widely spaced to indicate a greater step in level.



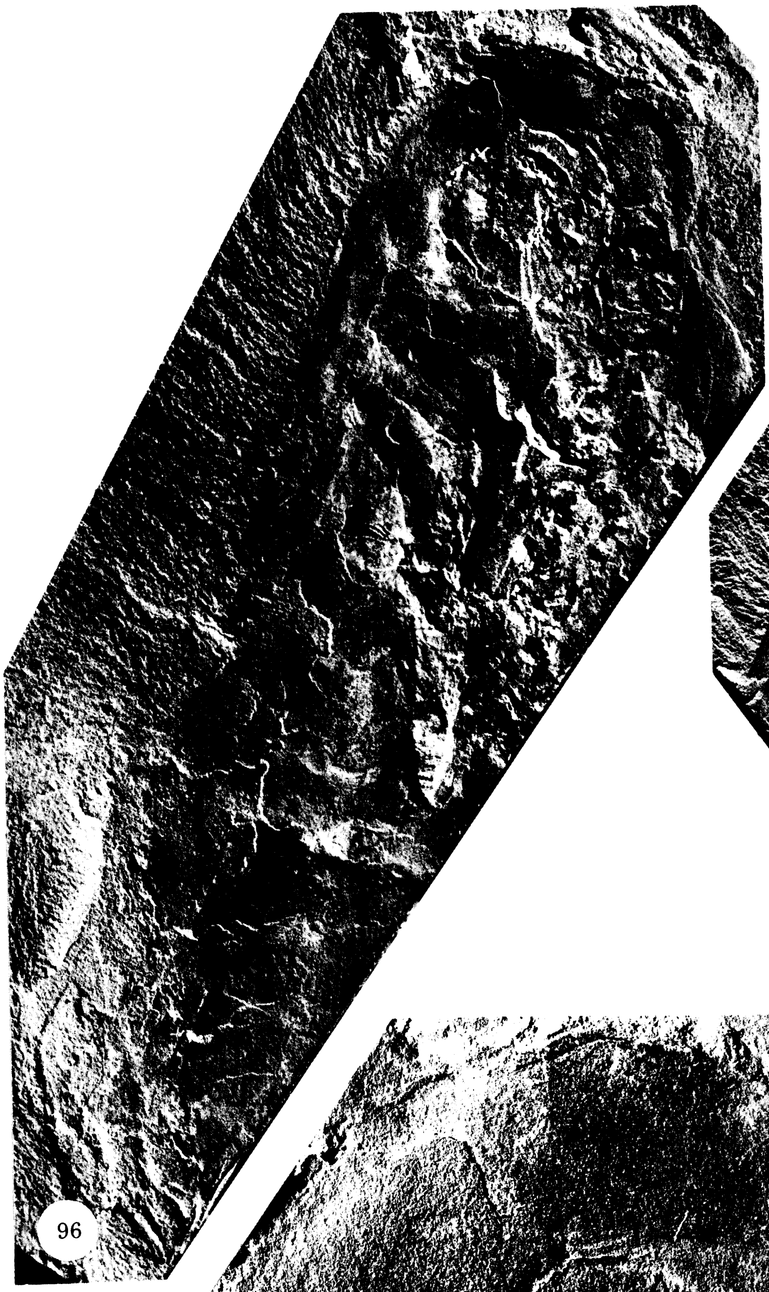
Description of figure 95 and plate 21

Anomalocaris nathorsti (Walcott, 1911)

U.S.N.M. 57555, holotype of *Laggania cambria* Walcott 1911*b*.

Figure 95. Explanatory drawing of part. Dashed line outside lateral lobes 4–7 marks margin of stained area beside lobes.

Figures 96–98. Respectively part, east–northeast, counterpart, northeast (magn. × 1.7), anterior area showing 'Peytoia', west (magn. × 5.0).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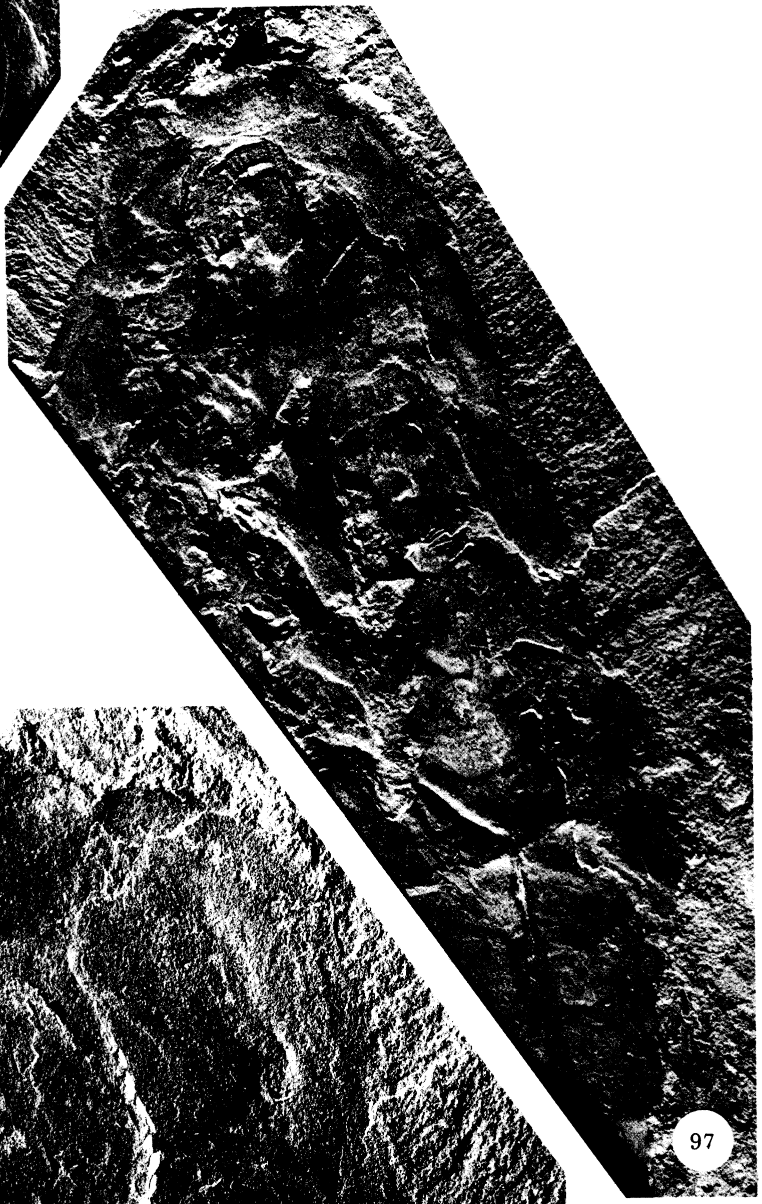
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FIGURES 96–98. For description see opposite.

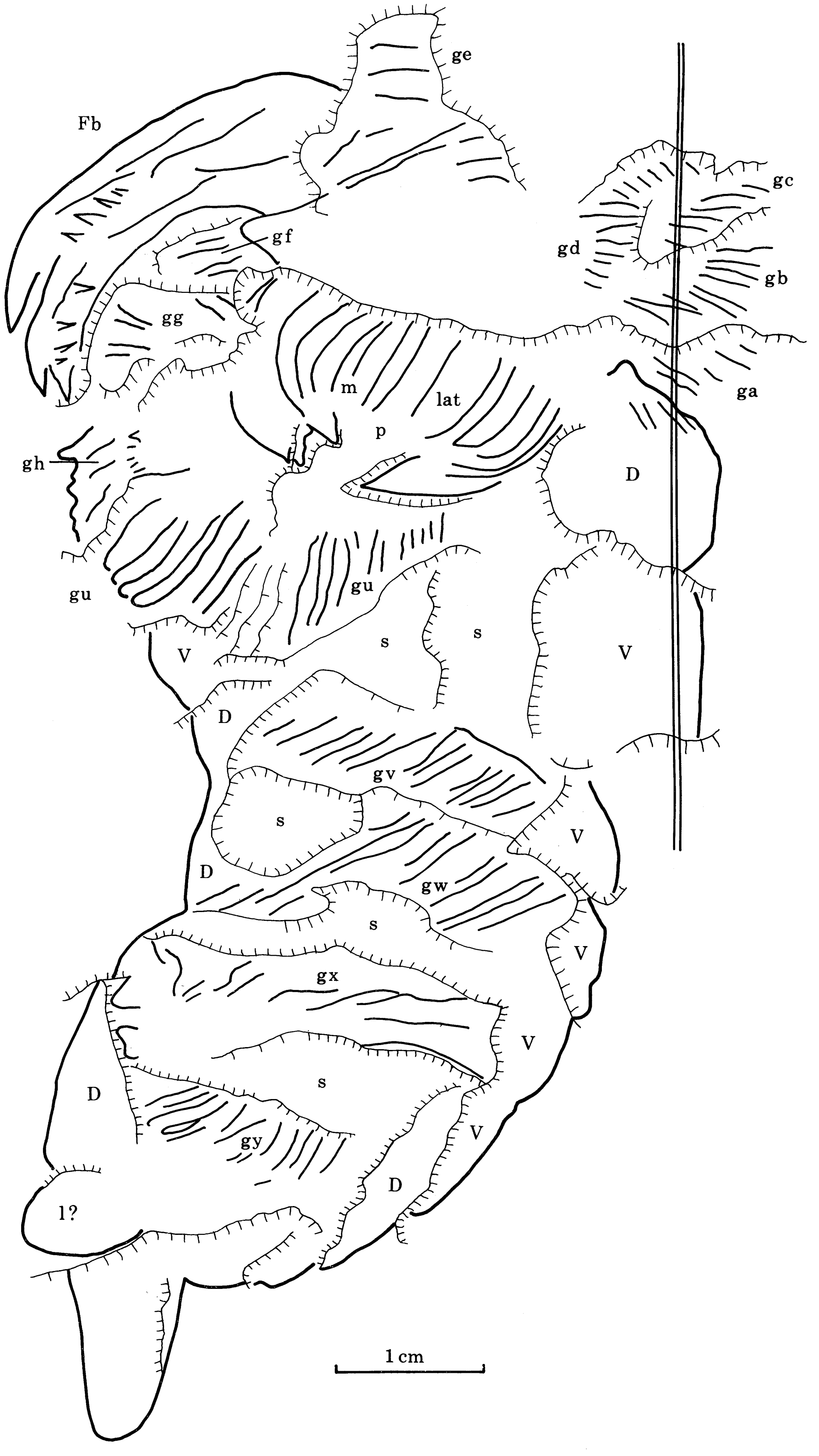

FIGURE 99. *Anomalocaris nathorsti* (Walcott, 1911). Composite explanatory drawing of U.S.N.M. 274155, 274158, 274159 (see figures 72–74, plate 16; figures 75, 76; figures 77, 78, plate 17).

Behind the maximum width (tr.) of the body the outline appears to have been evenly tapering. Up to 11 pairs of lobes may be discerned (figures 3, 5, 6), but their outline becomes progressively more difficult to decipher. The fragments of lobes 4–8 lying on the proximal portion of the succeeding lobes (figure 3) shows the considerable overlap between them. The trace of the alimentary canal can be followed to the limit of the specimen; and small patches of nodular mineralization are associated with it. There are suggestions of transverse divisions in the median posterior portion of the body, but these cannot be clearly linked to the lateral lobes. The only trace of lamellate structures is in the proximal portions of left lobes 5–8, where very faint, closely spaced changes of level running longitudinally may be discerned (shown as subparallel lines in figure 3). The margins of the lateral lobes are irregular and not sharply defined, and the margins of right lobes 6–11, and left lobes 8 and 9 are crumpled. A faint, narrow marginal band is visible on the anterolateral margins of right lobes 3 and 4, and left lobes 4 and 5 (figures 3, 4). These features may result from the oblique compaction of the specimen, and possibly from decay around the edges of the carcass.

(*c*) *Discussion*

The body of this animal had at least 11 pairs of strongly overlapping lateral lobes, was widest at lobes 4 or 5, and narrowed rapidly posteriorly, where the distal margins of the lobes were straight rather than curved. In form it was thus very like *Anomalocaris nathorsti*, but the anterior, cephalic portion appears relatively very short (sag.). This portion shows, like that of *A. nathorsti*, a probable pair of lateral eyes, and a fragment of 'Peytoia', but a distinctive type of anterior appendage. The fragment of 'Peytoia' lies above the proximal portion of the appendage, relatively much closer to the base of the appendage than in *A. nathorsti*. It is conceivable that the head region in this specimen was tilted to slope backward and downward on burial, so that compaction foreshortened it and pushed the 'Peytoia' circlet against the appendage. If so, the head region may have been of length (sag.) and form similar to that of *A. nathorsti*. The single specimen is an inadequate basis for a restoration of *A. canadensis*, but it seems that it may have looked like *A. nathorsti* (figures 101, 102), apart from the appendage. If the latter were attached in much the same position and orientation as in *A. nathorsti* (figure 106), the pairs of spines (see reconstruction in Briggs (1979), text-figure 1) would have pointed inward and backward, and not been opposed; the orientation may well have been different. Presumably on flexure the appendage of *A. canadensis* pierced and squeezed prey and brought it close to the mouth. These two animals probably swam in the same manner and were predators; they might have been dimorphs of one species, or separate species in which the appendage was specialized to deal with different types of prey.

The anterior appendage of *A. canadensis* has long been known in isolation, and was thought by Whiteaves (1892) to be the body of a phyllocarid crustacean. Briggs (1979) studied old and new material that comes from both Lower and Middle Cambrian rocks in North America, the distribution was reviewed by Briggs & Mount (1982), and new localities found by Collins *et al.* (1983). Briggs concluded that it was most probably the ambulatory limb of an arthropod, that (assuming a body of many somites each bearing one pair of appendages) might have been 1 m in length. The largest isolated appendages are of length about 20 cm, while the appendage of the present specimen is 6.3 cm (measured as in Briggs (1979), text-figure 14). This implies that entire animals may have attained a length (sag.) of some 40 cm. The present unique specimen shows for the first time the animal to which *A. canadensis* was attached, and demonstrates that there was a single anterior pair of appendages. They were not serially repeated along the body, as Briggs (1979, p. 653) suggested, based partly on the occurrence of two or three isolated appendages in approximately parallel arrangement. Isolated appendages randomly oriented are abundant on some bedding planes in the Ogygopsis Shale on Mount Stephen, so that the parallel arrangement seems to be chance, brought about by currents. The sharp outline and well-defined joints of the appendage (figures 8, 10), compared with the rest of the body, confirm the suggestion (Briggs 1979, p. 657) that it was more heavily sclerotized; hence after death it was more resistant to decay and disintegration, and so became isolated.

We have reconsidered (figures 7, 9, 11) the specimen described by Briggs (1979, pp. 634–635, plate 79, figures 1–3, text-figure 16) but it remains difficult to interpret because of its fragmentary nature. We tentatively orient it as in figure 11, part and counterpart as designated in the previous account. What was referred to by Briggs (1979) as a possible second ramus of the limb may be part of the 'Peytoia' circlet, including the wider posterior plate and some of the overlapping plates beside it. Behind this circlet, most complete on the counterpart (figure 9) is a portion of the body and a lateral lobe. The left limb is about 6 cm long and projects outward and backward, but if our orientation is correct curves forward distally, rather than backwards as in GSC 75535. Below its base (figure 7) a subcircular area has been excavated that may be an incomplete fragment of the right limb. Overlying this fragment and to the right of it are portions of the anterior end of the body. At the right extremity of the part, and excavated at the base of the left limb in the counterpart (figure 9) are areas that have a yellowish mineral coating and are reflective; these may be the supposed eyes. The assumed orientation (figure 11) brings the left of these areas on to the dorsal side, the right then being ventral. It will be seen in figure 11 (compare figure 7) that the left edge of the mouth plates then lies partly ventral to the base of the left appendage (not dorsal to it), a discrepancy we attribute to oblique compaction; much of the distorted mouth plate area lies dorsal to the appendage. Thus 189024, though fragmentary and probably compacted obliquely, may be reconciled with the new and more complete specimen.

7. *ANOMALOCARIS NATHORSTI* (WALCOTT, 1911)

(Figures 13–89, 93, 95–108, including plates 3–19; figure 93, plate 20; plate 21.)

1911*b*	Walcott, pp. 55–57, plate 8, figures 1, 2; original description of 'Peytoia'
1911*b*	Walcott, p. 52, plate 13, figure 1
1975	Simonetta & Delle Cave, plate xxvii, figure 5 (U.S.N.M. 274195, not 189248), identified as *Emeraldella brocki*
1978	Conway Morris, pp. 126–131, plate 1, figures 1–6
1979	Briggs, pp. 641–648, plate 80; plate 81, figures 1–8; text-figures 2, 20–32
1982	Whittington & Briggs, pp. 573–574, plate 1, figures 1, 2
1982	Simonetta & Delle Cave, plate 1, figure 1 (274142), figure 3 (274147); plate 2, figures 1, 2 (274142, 274141); plate 3, figure 1 (274164), figure 2 (274148)
1983	Collins *et al.*, table 1, occurrence of 'appendage F' in the Stephen Formation

(*a*) *Material*

Holotype: U.S.N.M. 57538, original of Walcott (1911*b*), plate 8, figure 1, from the Phyllopod bed, a large specimen of 'Peytoia'.

Other material: seven partial or almost complete parallel or parallel oblique compressions of the entire animal, all having counterparts: U.S.N.M. 57555 (original of Walcott (1911 *b*), plate 13, figure 1); 274143 and 274147; 274164; 274162 and 274145; 274148 and 274144; 274141 and 274142; 274146 and 274163, all from Walcott's locality 35k, that is, an unknown level in the Phyllopod bed. Two incomplete oblique compressions: U.S.N.M. 274154 (regarded as the part because each lateral lobe at the right posterior passes below that succeeding) with counterpart U.S.N.M. 247156, 274161; two fragments, U.S.N.M. 274155 and 274158, constituting the part and having the 'Peytoia' circlet lying ventrally, the counterpart U.S.N.M. 274159: both from Walcott's locality 35k. R.O.M. 42985 from an horizon 65 m above the Walcott quarry, and R.O.M. 42984 from the talus below the Walcott quarry, both poorly preserved specimens. R.O.M. 42983, a 'Peytoia' from the Burgess Shale section; the R.O.M. collections include 'appendage F' from other localities in the Stephen Formation (Collins *et al.* 1983). Twenty-six specimens, some with counterparts, of the 'Peytoia' mouth plates in the U.S.N.M. collection, numbered 57539, 193907 to 193926 inclusive, 193928, 194006, 253216, 368583, 368584, from the Phyllopod bed, labelled 35k. Seven specimens, G.S.C. 75528 to 75534, from the Phyllopod bed and the Raymond quarry at the levels shown in figure 1. Briggs (1979, p. 644) lists some 140 specimens of 'appendage F' from the Phyllopod bed, and gives the stratigraphical levels (figure 1) at which four of them occur. In the Walcott collection are two examples of 'appendage F' labelled respectively 35k/1 and 35k/10, and part of a complete specimen showing the appendages and mouth parts (U.S.N.M. 193912) is labelled 35k/1. The more or less complete specimens of *A. nathorsti* are associated with *Marrella splendens*, inarticulate and articulate brachiopods and hyolithids; while the more abundant mouth parts occur with a wider selection of species, similar to that associated with 'appendage F' (Briggs 1979, p. 644).

(*b*) *Description of parallel or parallel oblique compressions*

The cuticle appears to have been only lightly sclerotized, except for that of 'appendage F' and 'Peytoia'; the thinness of the distal portions of the lateral lobes may be shown by the irregular and vague outline. The original split that revealed the specimens followed the lateral lobes and the reflective eye areas, but did not follow either the ventral or dorsal cuticle in the anterior and axial regions of the body, passing instead through some level within it. In two specimens (figures 44, 45, 56) the split partly revealed the mouth parts and appendage, and in 57555 (figures 96–98) the mouth parts. In others, little of these features was evident originally, and they have been exposed by preparation. Because of their heavier sclerotization and consequently greater thickness, the rock parted relatively readily to reveal these portions of the body (figures 17, 26, 35–37). The rock parts with difficulty, or not at all, along the thinner cuticle, so that the lateral lobes are difficult to separate proximally (12, 13, figure 30; compare figure 28) and it has proved impossible to reveal the ventral or dorsal cuticle in the axial region. Whether or not there was any external evidence of segmentation in this region, for example, is not known.

In front of the first lateral lobe the body tapered forward to a bluntly rounded anterior. In counterparts the lateral and frontal margins may form an evenly curved outline (figures 16, 44, 45) or may be irregular (figures 33, 58); where the dorsal cuticle is visible peripherally the surface appears smooth. It is assumed that an irregular outline is the result of folding of a thin cuticle combined with some obliquity of the specimen. A reflective oval area, which appears to be borne by a stalk, is usually preserved just in front of lateral lobe 1 (figures 16, 28, 29,

32) at a high level on the dorsal side of the body. This feature is interpreted as an eye, though no structure can be seen within it. In 274148 (figures 44, 45, 47, 50) the eye lies above lateral lobes 2 and 3, but the anterior region of the body is relatively short (sag.); the position of the eye this far posteriorly may be the result of the oblique orientation of the body to the bedding. In 274145 (figures 51, 52, 53) the right eye lies above lobe 2, the left just below the position of lobe 1, a configuration resulting from the oblique compaction.

In 274164 (figures 26, 29, 30) a pair of segmented features lies anteriorly just below the level of the dorsal cuticle, curving strongly backward ventral of the body. Spines project from the one on the right, and both features bear a series of elongate imbricated blades. These are a pair of 'appendage F' (cf. Briggs 1979, plate 80, plate 81, figures 1–8, and description), which when first described were known only in isolation. The spines projecting from the anterior margin of the specimen are either lateral or dorsal spines of the right appendage. A similar pair of anterior appendages has been partly exposed in 274143 (figures 21, 22, 23), where ventral blades of the left appendage lie ventral to the mouth plates. Preparation of the part of 274142 (figures 35–39) has revealed the curved spines at the tips of blades of opposing appendages, adjacent to the posterior portion of the 'Peytoia'. The spines are long and curved, like those of distal blades (blades 8–10 in Briggs (1979), text-figures 23, 30). Beside and in front of the 'Peytoia' are other portions of the appendages, and impressions of these are also preserved in the counterpart (figures 40, 41). In 274146 (figures 56, 58, 59) a jointed portion of the right appendage and overlapping ventral blades are poorly preserved. In 274148 (figures 44, 45, 50) traces of the right appendage are also seen, the ventral blades overlapping the mouth parts. It appears that this pair of appendages was attached anteriorly on the ventral side of the animal, and curved downward and backward. In some specimens they project in front of the anterior margin (figures 22, 26, 29) but they lie predominantly on the ventral side. In 274164 (figures 26, 29) oblique compression has resulted in both appendages curving towards the left side of the head rather than a symmetrical arrangement about the mid line.

Preparation of 274143 (figures 21, 22, 23) unexpectedly revealed a circlet of plates, divided into four quadrants by a narrower (tr.) anterior and posterior plate, and wider (exs.) lateral plates. Between these larger plates are seven narrower plates in each quadrant, the three on either side imbricated successively towards the median of the seven. At the inner tip of some of the plates blunt, triangular projections are evident, while the outer margin of each is curved, giving a scalloped outline to the circlet. The surface of each plate is gently concave on the inner, dorsal side and ridges mark the overlap between them. Thus on the outer, ventral side, the plates were gently convex. The right anterior portion of the circlet in 274143 is poorly preserved, apparently pressed against the right appendage. The margins of the circlet are not connected to the ventral cuticle, presumably because the more heavily sclerotized circlet became detached from the thinner surrounding cuticle during compression. This circlet of plates in 274143 is the best preserved *in situ* in any specimen, but portions of similar circlets are preserved in others (figures 36, 37, 48, 58, 96–98). Preparation of 274142 (figures 38, 39) revealed some of the plates and the inner projections; both this specimen and 274146 (figure 59) show the same configuration of plates within the circlet as 274143. This circlet is identical in the arrangement and symmetry of plates, and the inner projections, with the isolated specimens described by Walcott (1911*b*) as *Peytoia nathorsti* (figures 61–63). His type is over twice the size of that preserved in 274143. It, and other specimens (figures 64–66, 79, 80, 93) show the same relative size, outline, convexity and direction of overlap between individual plates, and are here (figures 60, 67) oriented with the narrower pair of major plates along the anterior–posterior axis. The projections surrounding the rectangular central opening (figures 63, 66) are here called teeth, on the assumption that it represents the mouth, because of its anterior, ventral position in the animal. The teeth on the four major plates are larger than the rest. The anterior and posterior major plates each bear a large median tooth flanked by two smaller ones; there appear to be at least two, probably three, large teeth on the major lateral plates. At each corner of the rectangular opening lies the median of the seven smaller plates in each quadrant. Each of the three plates on either side of the median one bears two teeth that curve towards it, the median plate bore at least two teeth. The teeth of the four major plates project farthest into the central opening, those of the minor plates successively less far, and those of the median plates least far. This arrangement gives a notch in each corner of the rectangular opening (figure 108*a*). The outer margin of each plate was curved, giving the circlet a scalloped outline. Fine wrinkles parallel the outer edge of each plate (figure 93); if these wrinkles resulted from compaction, then presumably the outer portion of a plate was more convex than the inner.

The split follows the convex outer surfaces of the plates peripherally, but a change in level to the inner surfaces may take place, and such steps in level are greatest near the inner ends of the plates. This suggests that the upper and lower surfaces are separated by a layer of sediment which thins toward the periphery of the circlet, where the two surfaces meet along the margin. The teeth borne by individual plates may show evidence of overlapping near the base (for example, the lateral plates in figure 67), indicating that they were set at different levels. The specimen 368583 (figures 69–71) shows teeth additional to those normally evident. They are more elongate than the teeth attached to the inner margins of the plates, and appear to have been aligned with the sides of the rectangular opening in at least three layers stacked one above the other, roughly parallel to the plane of the circlet. The overlapping rows are more exposed to one side of the aperture than the other, because of a slightly oblique compaction of the circlet, evidenced by the differences in length of the plates of the quadrants. How these additional teeth may have been related to the circlet cannot be investigated without damage to this unique example. They may not have been attached to plates of the circlet, but to the walls of a buccal cavity. Dark bands (figures 79, 80), in some examples reflective, are characteristic of the overlapping margins of the plates (cf. the specimens from Utah illustrated by Conway Morris & Robison 1982). These bands may be the remains of membranes between plates, which would have given the circlet a flexibility. Similar dark bands are occasionally preserved at the articulations between the segments of 'appendage F' (Briggs 1979, plate 81, figure 2). The rectangular shape and relative size of the mouth opening is, however, similar in all the specimens, both isolated and *in situ*, which suggests that horizontal movement between adjacent plates was limited; changes in the vertical configuration of the plates would not, however, be evident in compacted specimens.

The subtriangular outline and relative size of lateral lobes 2–6 is evident in the parallel specimen (figures 17, 20) and in parallel oblique specimens, particularly after preparations of part and counterpart to reveal the margins (figures 44–46, 50–55). The original of figure 50 has a fragment of left lobe 1 preserved on the part, and this lobe has been partly exhumed in 274143 (figure 17), and may also be seen in figure 32. The overlap between successive lobes is extensive, each lying dorsal to the lobe in front. Each lobe is longest (exs.) proximally, and this broad base merges into the trunk (for example, lobes left 1 and 2 and right 2 in figure 20; left 3–5 and right 3–8 in figure 51). Compared with more posterior lobes, 1–6 are more clearly outlined, the edges rarely ragged or crumpled (right lobes in 274164, figures 25, 30 are an exception). The maximum width (tr.) is across the extremities of lateral lobes 4, behind here the outline is triangular, tapering rapidly. Only in 274146 (figures 56, 57, 59) is there some doubt in identification of the right lateral lobes. An imaginary line joining the distal tips of lobes 4 in figure 59 is approximately parallel to a similar line through the centres of the eye lobes. The identification of g4 (as a gill because of its high, dorsal level in this counterpart) and mineralized areas 2–7 (figure 59) fits in, and suggests an oblique compression similar to the original of figure 50. If the posterior portion of 274146 (figure 59) is considered, and the course of the curved mineralized bands 8–12 noted, re-numbering of the right lateral lobes as 3–11 (rather than 2–10) gives a reasonable fit and a less distorted specimen. This re-numbering fits in less well with the anterior part of the body, so that neither numbering is entirely satisfactory. The explanation may lie in a change of obliquity along the length of the body; without the part to reveal whether one or more lobes lay in front of that here labelled 12 in figure 59, uncertainty remains.

Many specimens (figures 20, 30, 50) show evenly spaced, reflective, transverse lines curving forward and outward on the distal portions on the lateral lobes as far as the margin. These lines have negligible relief and therefore may be barely visible in low angle radiation (for example, figure 17). The enlargements of figures 42, 43 (see also figures 52–55, 57) reveal them, and how in this specimen the lines continue across a reflective inner portion of the lobe. The tips of the lobes may have been thinner and more flexible than the thicker, proximal portion, and the lines may represent strengthening rays. Only in 274145 (figures 42, 43) are the lines also seen on lateral lobes 7 and 8. Behind lateral lobe 6, the outline of the body becomes subtriangular, the lateral margins crumpled and irregular (right side in figures 52, 53) or almost straight (figures 25, 27, 28, 44–47, 56, 57). It appears from figures 32–34, and the left side in figures 52–55, that the posterior lateral lobes are subtriangular in outline and rounded at the distal tip. In this region the edges are difficult to prepare, but the overlap between lobes 6–10 is great (see figures 51, 59). There appear to be 11 pairs of lobes, and the blunt termination of the body is poorly preserved and shows no distinctive feature.

Irregular patches and strings of nodular mineralization are characteristic of the median region of the body. Anteriorly such patches lie behind the mouth plates, as far back as between the 2nd or 3rd lateral lobes (figures 20, 30, 50) and in 274145 (figure 51) there is also a large area adjacent to the termination of the body. These axial patches are probably related to the gut, and electron probe analysis of a sample (S in figure 20) shows it to be apatite. Similar apatite fillings are known in *Odaraia* (Briggs 1981, p. 570) and *Leanchoilia* (Bruton & Whittington 1983, p. 571). Other nodular patches of mineralization lie outside the axial region at about the midlength of the base of each lateral lobe, and are elongated forward and outward (figures 31, 59). In these two examples the paired patches numbered 6–12 in the figures are linked by a mineralized band across the axial region. In 274141 (figure 34) these elongate bands and patches are annulated, and three pairs of elongate, outward and forwardly directed patches (numbered 1–3 in figure 31), evenly spaced from each other and the pair associated with the first lateral lobe, occur on the anterior portion of the body behind the mouth plates (figures 32, 33). The second and third of these areas may be recognized in 274146 (figures 56, 57, 59). These bands and patches of mineralization are related to somites of the body, and numbered in series 1–12, the 4th related to lateral lobe 1, the 12th to lobe 9. In 274164 (figure 30) the paired mineralized areas are only slightly developed, but the posterior half of the axial region is light in colour with associated pyrite (figure 25). In 274144 and 274148 there are paired reflective areas (figure 47) on the mid-proximal portions of the lateral lobes, and these areas are finely striated (figure 49). Striations are present on similar areas of another specimen (figures 52–55). In 274143 (figures 17, 20) the nodular patches 1–10 are small, and situated at the adaxial end of the lamellar areas. Extremely faint darker lines and striations (figure 19) cross the axial region between the pairs 6–10.

The anterior portion of 274143 and 274147, between the mouth parts and lateral lobe 1, is exceptionally well preserved. In the part (figures 18, 20), extending out from the mid-region below the smooth dorsal cuticle seen on the left side of the counterpart, are areas that show the ragged sub-concentric broken margins of thin layers of matrix between lamellae. Three such areas are evident on the left side, the dorsal-most lamellae overlying the area following and succeeded by a fourth that overlies the anterior portion of left lateral lobe 1. On the right side of the part (before preparation, figures 20, 23) three similar areas were visible in front of lateral lobe 1, each passing *below* that following. The concentric broken edges of the lamellae on the right side are stepped in the reverse order, ascending outward. This contrast in stepping directions on left and right sides reflects the direction and inclination of the split between part and counterpart (see §4 and figure 2). In the counterpart (figures 13, 15) some of the dorsal-most lamellae of the four areas on the left side are preserved, and those of each area go above (below in the counterpart) those of the following area. Subsequent preparation of the first three areas and lateral lobe 1 of the right side (figures 21, 22, 24) revealed a large flap, semi-oval in outline, on the ventral side of the first area (fl 1 in figure 21). Similar flaps and lamellae of the second and third areas had to be largely removed to reveal the posterolateral margin of the first flap. The overlap between these flaps was great, like that between the succeeding lobes, and in the same sense; flap 3 goes back below lateral lobe 1 (figures 20, 22). The overlying lamellar areas had to be largely removed to reveal flap 1, but distal fragments of lamellae were left outside flaps 1–3 (figures 21, 24). These lamellae terminate just inside and above the ventral cuticle that has been exposed. At the lateral margins of flaps 1–3 each flap appears to merge into a lamella. That the lamellae were attached to the outer edge of the flap appears doubtful, if one assumes flaps and lateral lobes were homologous structures, because lamellar areas lie entirely above lateral lobes (see below). The appearance of the flap merging into lamellae may be misleading, the result of compaction of these thin structures one upon another; whether or not this is so is debatable. As seen in the counterpart (figures 13–16) lamellar areas 1–4 each slope down and back below the area following, that is, overlie it dorsally. The same relation is evident in the part on the left side (figures 17, 18, 20), less so in the distal fragments of right areas 1–3. We conclude that each lamellar area sloped backward and upward over the area following. Lamellae of the left first area immediately below the dorsal cuticle were partly stripped off to show their extent (lettered m to s in figure 21, compare figure 22). The lamellae were presumably attached proximally close to the axial region, and extended outward and forward; the exact position of the outer margin is uncertain, but there appear to have been many thin, extensive lamellae. Left area 2 (figure 21) has been prepared to show these lamellae and what may be the margin of the underlying flap.

Preparation of the anterior portion of the part of 274143 revealed also ventral cuticle (vc in figure 21; compare figures 22, 24) that has a clearly defined inner edge, situated outside right flaps 1–3 and the lamellar structures g1–3. In front of area 1 the ventral cuticle extends towards the mouth plates, the inner edge revealed on the left side (vm in figure 21). The inner edge of a similar lateral ventral doublure has been revealed on the right side of the part of 274164 (figures 26, 30). The form of the doublure may have been modified in this case by compaction of the specimen at a slightly oblique orientation to the bedding. Preparation of 274142 (figures 37, 39) has also revealed the doublure between the mouth plates and eye. No clear inner margin is evident, but it may coincide with the limits of the excavation beyond which the rock does not part along any plane. On the right side an outer margin appears to be present, but it may be a break resulting from folding of the cuticle. A subtriangular, posteriorly pointing outline is picked out by an impressed line approximately coincident with the exposed margin of the right and left doublures. Thus the doublure in 274142 appears similar in outline to that in 274143, narrowest in front of the eye, and widening forward towards the mouth parts. This outline may, on the other hand, represent the large first segment of 'appendage F' (Briggs 1979, p. 644, text-figure 20). In either case there was no median doublure, so that the flaps and overlying lamellar structures were not enclosed on the ventral side of the animal. The dorsal cuticle covered them dorsolaterally.

Excavation through the inner portions of lateral lobes 2–6 on each side of 274147 (figures 13–16) has revealed portions of a series of lamellar areas (g4 to g9) like those (g1 to g3) described in the anterior portion of the specimen. Each area slopes downward and backward beneath the one following (that is, slopes up dorsally backward), an opposite overlapping relationship to that between the lateral lobes. The series of lamellar areas lies wholly above that of the lateral lobes, but is related to them in position, area 4 overlying the inner, anterior portion of lateral lobe 1, area 5 that of lobe 2, etc. The preparation shows, for example, the relation between left area g8 and l5. Area g4 on the right side has been partly removed (figures 13, 14) to show a small area of the smooth, overlying dorsal cuticle. Whether or not such cuticle extended back over the trunk, covering the lamellar structures, is uncertain but is suggested in the reconstruction. No other specimen shows comparable details of the lamellar structures, only in 274142 (figures 37, 39) and 274146 (figure 59) are there indications of these structures anteriorly, g4 overlying l1.

The series of 12 pairs of nodular mineralized areas (numbered serially), has been described above, and they are clearly related not only to the flaps and lateral lobes, but to the overlying lamellar areas (figures 20, 31, 59). Each mineralized area, or the distal portion of a curved, transverse mineral band, lies in the proximal portion of a lamellar structure.

(*c*) *Description of oblique compressions*

Each of the two specimens described below shows characters of *A. nathorsti*, the first exhibits the typical 'appendage F' and 'Peytoia', while in the second there are pairs of lateral lobes. Each, however, shows other characters peculiar to it, such as the lateral plates and terminal piece of the first, and the supposed tergites of the second. Neither shows an axial region or associated nodular mineralized patches typical of the parallel compressions. The balance of the evidence favours placing them in *A. nathorsti*.

(i) *U.S.N.M.* 274155, 274158, *the part, and* 274159, *the counterpart*

Only the counterpart has previously been figured (Simonetta & Delle Cave 1975, plate xxvii, figure 5, numbered 189248) and incorrectly attributed to *Emeraldella brocki*.

Anteromedially in the part (figures 72, 73) is a structure of overlapping plates, which are curved so that the pointed ends are directed inward towards each other. The plates vary in width, two wide ones being separated by seven narrow plates, the median of these the narrowest. This arrangement of plates with inner prongs is thus like one half of 'Peytoia' seen from the side, so that a lateral plate lies subcentral. This structure is considered to be a lateral compression of the originally convex circlet of plates. The large prong at a low level on the right side in the part may be that of an anterior (or posterior) plate. In front and to the left of the circlet are a series of overlapping strips, seen in the counterpart (figure 77) to be curved inward distally and pointed, and having spines along the inner edges. These are the blades on the ventral side of 'appendage F' (cf. Briggs 1979, text-figures 29, 30), but the remainder of the appendage has been foreshortened by compaction at a high angle to the bedding and is difficult to recognize. The 'Peytoia' and 'appendage F' structures are on the ventral side of the part. Between them, and in front and to the sides of the 'Peytoia' (nearer to the observer), are at least eight tapering, lamellar areas in a radial arrangement (figures 72, 77; labelled ga to gh in figures 75, 76). These areas are of thinner (less sclerotized) cuticle than the remainder of the specimen, and so less easily visible in the photographs.

Behind this anterior portion is a subparallel-sided region (figures 74, 78) consisting of a series of plates, each wider (tr.) than long, some showing many layers. This region narrows abruptly posteriorly and has a blunt termination (figures 72, 77). The plates overlap each other, but not in the same sense. Certain of the many layers that go across the middle of the specimen are lamellar (gu to gy, figures 75, 76, 99). Area gu (best seen in the counterpart, figures 77, 78) immediately behind the 'Peytoia', shows that the lamellae have rounded tips and overlap markedly posteriorly. Areas gv, gw and gy on the counterpart (figures 76, 78) are clearly lamellar, but area gx less so, perhaps merely wrinkled parallel to the tectonic lineation; a portion of the posterior margin of area gx has been revealed in the counterpart. In between these lamellar areas, there are layers at many other levels, some separated by a considerable thickness of rock, others by a slight thickness, some merging as they are traced laterally. These areas are smooth (s in figures 75, 76), and intervene (at a lower level) between the lamellar areas, and extend also beneath them, for example, the smooth area behind lamellar area gv (figures 74, 75) lies below lamellar area gw (figures 76, 78). Immediately in front of area gx, smooth areas at six slightly different levels may be distinguished (figures 75, 76), some of them merging as they are traced inward. Along either side of the lamellar and smooth plates are the edges of other areas, which go under or over (respectively V and D in figures 75, 76, 99) both the lamellar and smooth areas. Anastomosing lines run subparallel to the margins of these plates, presumably resulting from folding of cuticle buried at a high angle to the bedding. The plates D and V curve towards each other and join at the right margin (as seen on the left of the counterpart, figure 78) but whether they extend completely across the specimen is unknown – to attempt to expose one would be too destructive. It appears, from matching of levels in part and counterpart, that such an area may go across the specimen beneath lamellar areas gv and gw, and the plates labelled D on either side of area gy (figure 99) may well have joined. Along the right side there were a series of perhaps six such external plates (two labelled D and four labelled V, figure 99), and the anterior plate D went over the 'Peytoia'. There may have been considerable overlap between these marginal plates. Posteriorly, there is a blunt, tapering, short projecting section, which shows some five overlapping layers. In front of it, at a markedly more dorsal level, is a single isolated lobe (figures 76, 77; l? in figure 99) and the tips of two smaller lobes project at the left edge of area gx (figures 74, 75).

Figure 99 summarizes our interpretation of the specimen. The presence of an 'appendage F', adjacent to a toothed circlet of 'Peytoia' type, indicates that this specimen is an example of *A. nathorsti*. The trunk region behind is very different in appearance, however, from specimens described in §7 *b* or the oblique compression next described, because it shows no series of lateral lobes. It does, however, show lamellar areas alternating with smooth areas, recalling the anterior portion of 274154 (figures 81–83, 100). The 'Peytoia' circlet is the only recognizable example of a lateral compression, the fragment on the counterpart of 274154 (figures 87, 100) being most doubtfully attributable. If an individual of *A. nathorsti* was laterally compressed, one would expect to find at a particular level of split a single 'appendage F', and the 'Peytoia' circlet (if it were convex ventrally) to be flattened as in this specimen. The trunk region would be relatively narrower than in dorso-ventral compressions, and complexly layered if the two sides were compressed one on another. One might expect (as the right side of this specimen shows, figure 99) to see many layers converging at the folded dorsal edge. An oblique lateral compression, with the axis of the animal oblique to the bedding, and perhaps also rotation of the body along the axis, would provide a most difficult problem in interpretation. We suggest, for example, that oblique compaction of the downwardly directed cephalic region may have splayed out the gills on each side (ga to gd on one side, ge to gh on the other, figure 99), brought one appendage out on one side, and turned the 'Peytoia' circlet to face backward at a lower level. The trunk, one side folded under the other (suggested by the convergent lateral areas V and D on the right side), may have been foreshortened, and because of the steep angle at which the lateral lobes were buried, their characteristic distal outline was modified (except in one or two cases), and the surface wrinkled. Some lamellar areas are preserved subparallel to the bedding, alternating with smoother areas which may be individual gill lamellae (especially those showing layers that are very close together or that merge), tergites (if such were present) or lateral lobes. To attempt any more detailed analysis of the complexities seems unprofitable, especially as any further preparation would destroy unique evidence.

(ii) *U.S.N.M.* 274154, *the part, and counterpart composed of two fragments* (*U.S.N.M.* 274156, 274161) *now joined*

The right side of this specimen shows a series of dark lamellar areas, lettered ga to gk (figures 81, 84, 86, 87). In the right anterior half of the specimen the conspicuous areas ga to ge are elongate, extend out to the margin, and each passes posteriorly beneath a layer of cuticle (t1 to t5, figures 84, 86) which is lighter in colour, not lamellar, but traversed by irregular, anastomosing longitudinal (exs.) lines (figures 82, 89). Behind t5 there is a fragment of a lamellar area (gf in figures 84, 86), and then in the right posterior side of the specimen a series of bluntly pointed lateral lobes, each going below the one following. These are lettered lf to lk (figures 84, 86), and a more anterior lobe le has been excavated in the part below ge, t4 and t5 (figures 82, 85). The distal portion of each lobe is crossed by subparallel lines, directed outward and curving gently back distally before meeting the margin. These lines are darker in low angle radiation (figures 81, 84) and reflective. In right lobes j and k the margin of the lobe is ragged, probably the result of decay, the lines projecting from the irregular edge. On the inner, anterior portions of lobes f to i of the part are darker, lamellar areas, labelled gf to gj. Excavation of the counterpart (figure 87) has revealed lobate areas (figure 86, labelled gg to gk) lying above the lateral lobes, each going posteriorly above that following (the reverse of the condition in the lateral lobes). Comparison of part and counterpart (figure 100) shows that these lobate areas are the distal portions of the lamellar areas. The next anterior of these areas, gf, is seen in the counterpart (figures 86, 88) to project out in front of lateral lobe f, beneath the posterior margin of t5. The areas (labelled t) on the right anterior side of the specimen (figures 82, 85) are unusual in that they lie above both lateral lobes and lamellar areas, have an angulate outline posterolaterally, and are crossed posteriorly by an impressed line that is transversely directed (i m l in t2 to t5, figures 84, 85). Behind this line is dorsal cuticle (t3 and t4 dc, figures 84, 86) overlying the lamellar area; the posterior margin of this cuticle has been excavated in t3 in the counterpart (t3 p m in figure 86, compare figures 88, 89). Behind the impressed line, below the dorsal surface, is the lamellar area, which the counterpart (figure 89) shows to be multi-layered, flattened beneath the posterior portion of t and projecting out behind it. In the part (figure 82) the slightly concave, most ventral surface of the lamellar area (gc to gf vc in figure 85) appears as an extension of t behind the impressed line. The posterior margin of this ventral cuticle (gc vc in figure 85) has been excavated in the part (figure 82) below more dorsal portions of lamellar area gc.

The entire specimen (figures 81, 87) is curved convexly to the right, the left side considerably narrower (tr.) than the right. In the posterior portion the left side is not symmetrical with the right side, and shows a series of seven lobes (lettered le to lk in figure 84, the anterior margin of le exposed by excavation of the counterpart, and that of lf in the part) of different outline, each of which lies with a slight change of level on that following. The anterior margin of lobe e (figure 88) is curved outward and backward, and shows the darker, reflective, subparallel lines curving to meet it; the tip may have been bluntly rounded, the posterolateral margin is irregular. This left lobe (le) thus resembles those of the right side. The following three lobes on the left side (lf to h, figures 84, 85) are much narrower (exs.), the margins rounded. The last three (li to k), though damaged, show a change to a fusiform outline, particularly the last. Lettering these lobes in the fashion adopted here gives a series e to k on each side, and emphasizes a twist to the left of the posterior portion of the specimen. The lack of symmetry may be ascribed to this twisting, which may have had the effect, after compression, of altering the outline of left lobes f to k, and obscuring any darker lines and lamellar areas, if such were originally present. Such twisting and compression may have given the prominent transverse wrinkles (figure 81) and have pressed the lobes together so that the difference in level between them is only evident distally, where it is slight and the overlap reversed compared with the right side. In front of the lateral lobe e (figures 81, 82) the left margin is ragged, with projecting spines, and most anterior is a lobe at a lower (more ventral) level. This portion of the specimen may be the remains of perhaps four lateral lobes, the spines resulting from decay of the edges leaving projecting strengthening rays. The specimen is incomplete anteriorly, but at the right anterolateral corner of the counterpart (figure 87; labelled P? in figure 86) is a dark area from which projects a group of blunt spines. This structure shows some curving divisions emphasized by colour or changes in level; regrettably it is not represented in the part, but must have lain on the left of the body, dorsal to the most anterior lobed area preserved on the left of the part.

Our interpretation of this specimen is summarized in figure 100. Preparation has been limited so that features revealed in the initial split are preserved in either part or counterpart. Further preparation, which would remove such features, seems undesirable. Hence two central areas labelled A, B, in figure 85 (compare figure 82), successively farther ventral than right lateral lobe e exposed in the part, have not been further prepared. Area B might be a portion of an additional lateral lobe. In front of area B is a multilayered area that may be the proximal portion of lamellar area d.

The right lateral lobes e to k, and accompanying lamellar areas ge to gk appear unquestionably to be approximately dorsoventral compressions of the posterior portion of *A. nathorsti.* The curvature of the body, and outlines of the corresponding left lobes, suggest that left lobes f to k were steeply inclined before compression, lobe e less so. Some decay of distal portions of more anterior left lateral lobes, and the last two right lobes, appears to have occurred, leaving the (presumably more sclerotized) rays projecting. At the extreme left anterior of the specimen is the projecting structure (P? in figure 86); the blunt spines and curving divisions suggest, by comparison with the far better-preserved example in 274159 (figures 72, 73) that this structure may be a small portion of an obliquely crushed 'Peytoia'. Unique to this specimen are the areas labelled 't'. These five areas appear to overlap proximally, but diverge radially, so that the posterolateral corners are separated. This arrangement is consistent with their having been overlapping, transversely rectangular plates, splayed out by curvature of the body to the left. Their position is dorsal to both lateral lobes and lamellar areas, hence they may have been tergites, somatic divisions of the dorsal cover of the gills. The supposed tergites and underlying lamellar structures are presumed to lie approximately parallel to the bedding, the lateral lobes inclined below them. Twisting along the axis of the body, as well as curvature, may have occurred, and would be necessary to bring the supposed 'Peytoia' around on to the left side. The peculiar double-layered structure along the posterior edges of tergites 2–5 may be explained by oblique compaction of gills gc to gf as the tergites were spread apart, each gill having been pressed up into the posterior portion of the corresponding tergite during compaction. Such compaction would explain the thickness of the lamellar area immediately behind the impressed line (iml in figure 100) that runs across the tergite, a thickness that causes a posterior marginal zone of the tergite to bulge slightly upward. Beneath this zone of the tergite the compacted gill was impressed into the matrix to form a concave transverse band, labelled gc vc to gf vc in figure 85. More dorsal layers of the lamellar area form separate structures that project behind this band and the tergite (the outer, posterior portions of gc, gd and ge, figure 85). It is the thickness and the layers of the lamellar areas that suggest oblique compaction.

If this interpretation is accepted, it would seem from the seven or eight lateral lobes recognized that the cephalic region was largely in the missing anterior portion of the specimen. Thus the supposed tergites 2–5 may have belonged to the anterior portion of the trunk, and appear to have been no more heavily sclerotized than the remainder of the exoskeleton. No evidence of such tergites has been recognized in the parallel compressions. This may be because the split has followed the lateral lobes, below the tergites, and the latter are thus concealed in the counterpart.

(*d*) *Discussion and restoration*

In the light of the specimens described in §7*b*, it is obvious that 57555 (figures 96–98) is not a composite (Conway Morris 1978), but an incomplete specimen of the whole animal, broken across diagonally. The anterior portion of the body shows the characteristic forwardly narrowing outline, the left reflective eye area, and nodular patches of a black mineral in the axial region; the projection beyond the margin on the left side may be part of the anterior appendage. The counterpart shows the smooth dorsal cuticle peripherally, and the rounded anterior outline. The circlet of mouth plates is typical of 'Peytoia', the anterior and posterior plates slightly skewed from the sagittal line. Portions of the left lateral lobes are preserved, the distal outline vague, and outside them is a bleached, yellow-weathered area (the limit of this

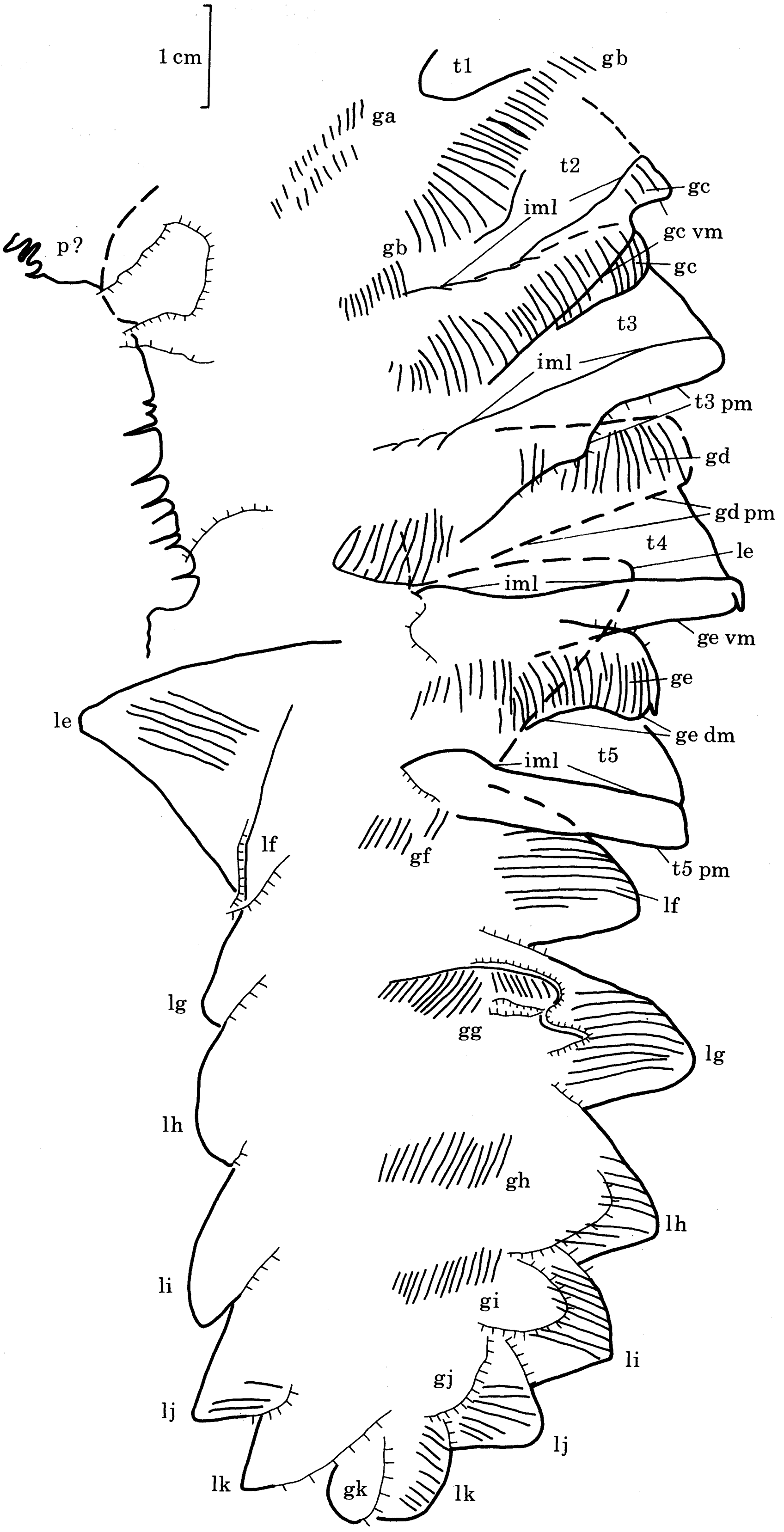

FIGURE 100. *Anomalocaris nathorsti* (Walcott, 1911). Composite explanatory drawing of U.S.N.M. 274154, 274156, 274161 (see figures 81–83, plate 18; figures 84–86; figures 87–89, plate 19).

area shown by a dashed line, figure 95). The thin distal portions of the lobes may have been crumpled. Extremely faint reflective lines on them run forward and outward, and probably represent the rays. In describing this specimen Conway Morris (1978, pp. 127–130, text-figure 1) noted the prong visible on one plate of the circlet, a branching network (the present nodular patches) and groups of 'vertical strands'. These latter extend over patches situated proximally and near the anterior edges of the lateral lobes, and are slight, subparallel changes of level; they represent the lamellar structures (labelled g1 to g7, figure 95). Four narrow, transverse ridges proximal to the reflective area may be equivalent to the outward and forwardly directed mineralized areas of other specimens.

The alimentary canal in *A. nathorsti* is not as clearly outlined as in the single specimen of *A. canadensis* (figure 3). In *A. nathorsti* nodular patches of apatite occurring anteriorly in the mid-region (figures 20, 30), or also posteriorly (figure 51), are thought to indicate the canal; only in one specimen is there an extensive anterior infilling by sediment (figure 59). The lateral, paired nodular areas, numbered serially in figures 20, 31 and 59, and the similarly placed reflective patches shown in figure 50, are situated in the proximal portions of lateral lobes and lamellar areas (gills). Electron probe analyses of samples from the points indicated in figures 30 and 59 showed the mineral matter to be carbonate–apatite (confirmed by X-ray diffraction analysis). Mineralized strips (figures 31, 59) may connect these areas, and correspond in position with the darker, striped bands in 274143 (figure 20); the annulation of the bands in 274142 (figure 34) is striking. These areas and strips are preserved in various ways, and may be absent (figures 30, 51). They represent some serially repeated structure, associated in position with the gills and lateral lobes, of uncertain nature, perhaps endoskeletal or related to intersomite boundaries. That the lamellar areas are gills is suggested by the extent and number of thin sheets revealed by preparation (figure 21), that recall the gill lamellae of living *Limulus*.

The restoration of *Anomalocaris nathorsti* (figures 101, 102) is based on averages of measurements of the specimens described in §7*b*, of which only 274143 (figure 20) is approximately parallel, the remainder being parallel oblique. The specimens described in §7*c* give no clear guidance on the possible lateral aspect and original convexity, so that given is conjectural. Preservation is such that the 'Peytoia', appendages and lateral lobes may be restored with fair confidence, but the external appearance of the axial region of the body is unknown, and evidence of the form of the gill structures limited. A dorsal cuticle covered gills 1–3 in 274143 (figures 20, 21), and in the counterpart (figure 13) a small area above the fourth gill and lateral lobes 1 and 2 has been excavated on the right side. We therefore show this cuticle covering the cephalic and trunk regions, with a conjectural division between these regions. The ventral cuticle in the cephalic region is based on that revealed by excavation (figures 21, 30, 39). Such specimens as the originals of figures 20 and 31 show that the eye was borne on a short stalk at a high level relative to the first lateral lobe. The cephalic region bore the distinctive three pairs of flaps, smaller structures than the lateral lobes of the trunk region. The specimen shown in figure 100 is interpreted as showing tergites, divisions of the dorsal trunk covering. Such divisions are omitted from the restoration (figure 101), because no parallel or parallel oblique specimen shows evidence of tergites. The suggestion of divisions between 14 somites in the axial region (figure 102*b*) is again conjecture; the middle of each division is transversely in line with the maximum width of flap or lateral lobe. The total number of such divisions in the body is unknown. Each gill is related to a somite, and hence the gill extends outward and forward over the anterior portion of the flap, or inner, anterior portion of each lobe. This arrangement is consistent with the positions of numbered nodular mineralized areas, or reflective patches, and the lamellar gill areas as best preserved in 274143 and 274147 (figures 13, 20). The size and form of each gill in the series (figures 101*b*, 102*a*, *c–f*) is based on the latter specimen, which shows the opposite directions of overlap of successive gills and lateral lobes. For simplicity, only four lamellae are shown in each gill, the actual number having been much greater. To provide space for the gills in a chamber beneath the dorsal covering, the flaps and lateral lobes cannot have been inclined backwards more steeply than shown in figure 102*a*. This angle of inclination is 6° to the horizontal (figure 103*a*), and could only be increased if the depth of the body (figures 102*c–f*; figure 104) were increased in the restoration. Hence as seen in cross section (figure 102*d*, *e*, *f*) the strongly overlapping lobes must have been thin, close together, and presumably were inclined outward at a moderate angle. Considerable flexure of the outer portions of the lateral lobes (the portion outside the dorsal exoskeleton) of the trunk would have been possible, and this is the portion crossed by reflective lines. These lines may be the remains of strengthening rays, because in the left anterior lateral lobes of 274154 (figure 84), and the right lobes 2–4 of 274164 (figure 30), they project from the decayed margin.

The relative size and position of the 'Peytoia' is shown unequivocally by 274143 (figure 20) and 57555 (figure 95), but of 'appendage F' less clearly because of the compaction. In all the parallel or parallel oblique specimens (figures 20, 30, 39, 40, 59) the shaft and blades of the appendage lie in front of, beside and just behind the 'Peytoia', and in front of the eye. This bespeaks an attachment far forward, anterolateral to the mouth plates, the shaft curved downward and backward (figure 106). The lateral and dorsal spines of the appendage, and those on the blades, are simplified in figures 101, 102. The mouth plates are given a moderate convexity, consistent with the wrinkling around the margin (figure 68) resulting from compaction, and the laterally compressed example (figure 75).

The scale given in the restoration (figures 101, 102) is for an individual the size of the original of figure 20. Isolated specimens of the appendage (Briggs 1979, text-figure 26) are twice the size shown, and the holotype of 'Peytoia' (figure 60) is three times the size of the circlet of mouth plates in the restoration. Thus the animal may have attained a length of 0.5 m.

(*e*) *Functional morphology*

(i) *Locomotion*

As restored, the body of *Anomalocaris nathorsti* is dorsoventrally flattened and streamlined, and this form, combined with the large eye and spinose anterior appendage, suggests that it was an actively swimming predator, probably moving forward close to the sea bottom in search of food. Lacking segmented appendages, apart from the pair in the head region, *A. nathorsti* cannot have progressed by walking. Propulsion was by swimming, either by dorsoventral flexure of the trunk, or by movements of the lateral lobes.

Most fish with a body outline similar to that in *A. nathorsti* swim in the carangiform mode (Webb 1975, p. 34), in which the amplitude of a propulsive wave increases significantly toward the posterior of the body, which generally accommodates less than one half-wavelength; these fish are characterized, however, by a caudal fin. The supposed divisions of the body in *A. nathorsti* were relatively long (figure 102*b*), which does not suggest great flexibility, and there was no tail 'fin'. We conclude that trunk flexure is unlikely to have played a significant role in propulsion.

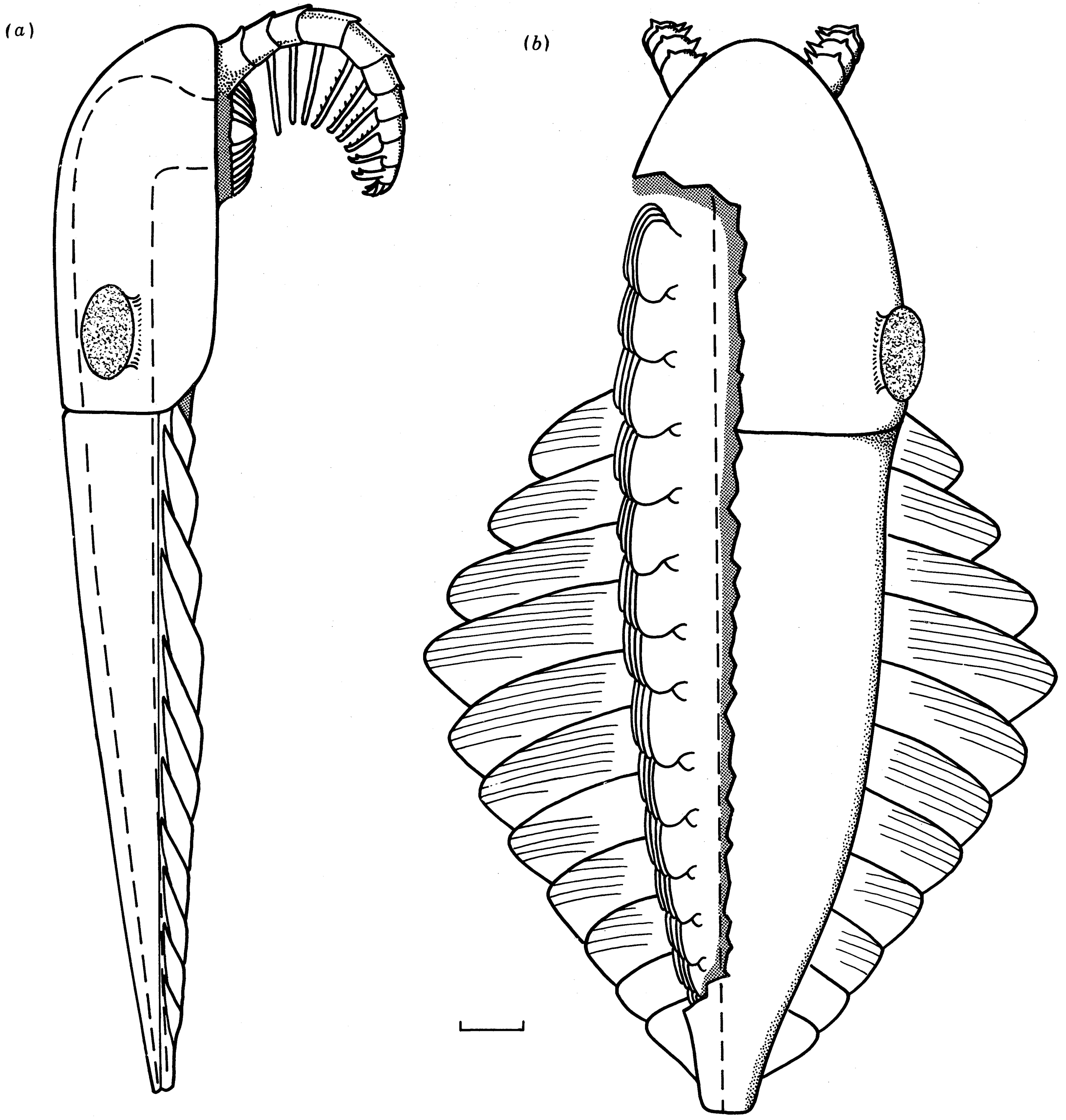

FIGURE 101. Reconstruction of *Anomalocaris nathorsti*, appendage partly flexed, lateral lobes in still position. (*a*) Right lateral view, outline of alimentary canal dashed; (*b*) dorsal view, portion of external cuticle on left side cut away to show gills (diagrammatic) below, left margin of alimentary canal dashed. Scale bar, 1 cm.

The movement of appendages (lobes in the case of *A. nathorsti*) in swimming corresponds to either rowing or 'subaqueous flying' (for example, Robinson 1975; Alexander 1982), both involving movement of a flat projection – limb or fin – through the water. In rowing the oar moves parallel to the direction of progress and propels the animal by means of a drag force. An oar operates as a lever and characteristically the shaft has a narrow base, expanding distally

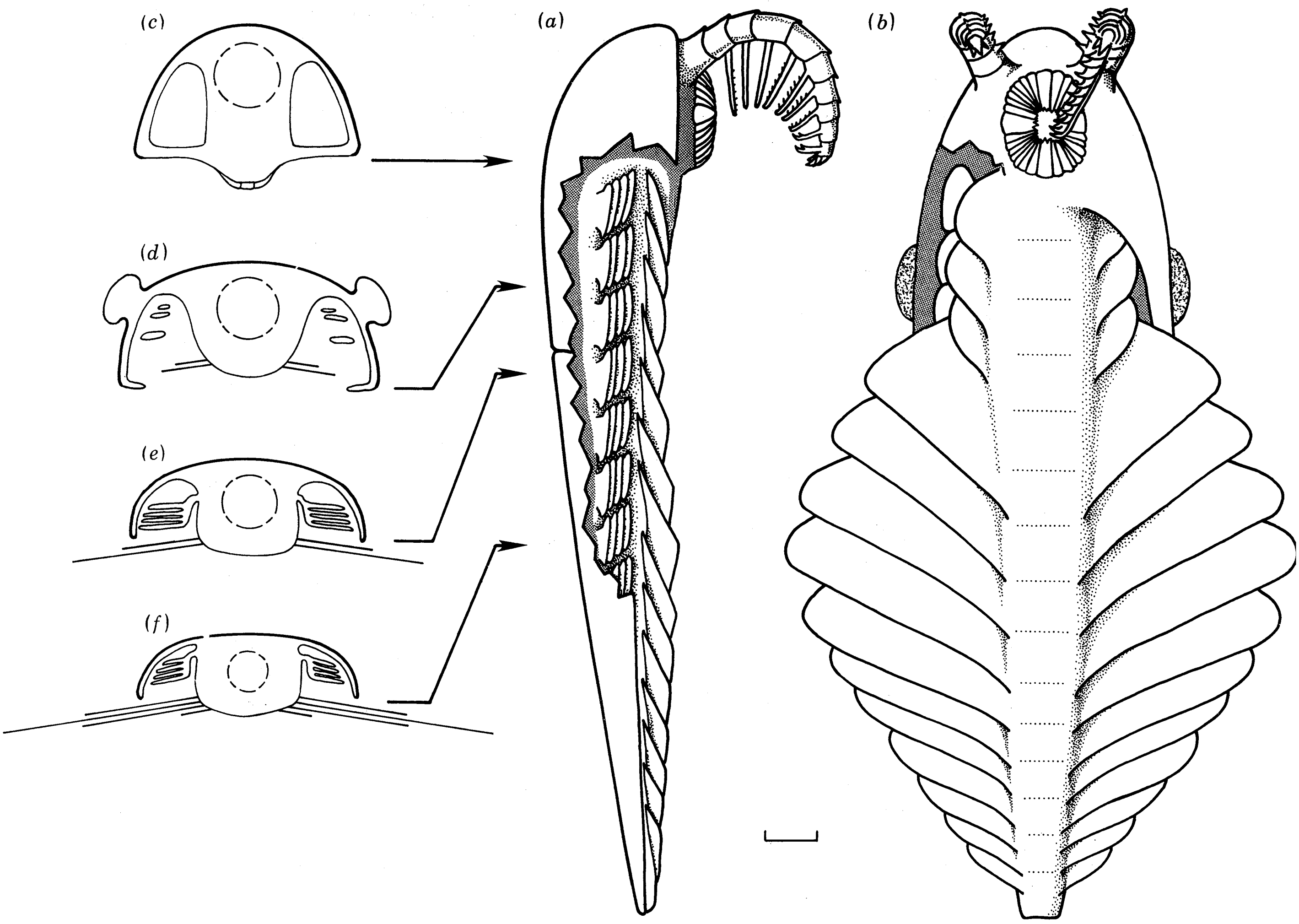

FIGURE 102. Reconstruction of *Anomalocaris nathorsti*, appendage partly flexed, lateral lobes in still position. (*a*) Right lateral view, portion of external cuticle cut away to show arrangement of gills; latter are diagrammatic, being shown as consisting of only four lamellae. (*b*) Ventral view, part of ventral cuticle of head region cut away on right side of animal to show flaps and gills. Blades omitted from right appendage so that circlet of mouth plates is visible. Segmental divisions of body, shown by a dotted line, are conjectural. (*c–f*) Transverse sections through the body as indicated, alimentary canal dashed. Scale bar, 1 cm.

into the blade which is blunt-ended to maximize drag. The propulsive stroke is followed by a recovery stroke during which the oar must present the minimum resistance to progress (by rotation, folding, collapse). The triangular lateral lobes of *A. nathorsti* were attached to the body wall (figure 103*a*) close together with a large overlap, and gently inclined downward both backward and outward (figures 101*a*, 102, 104). Neither their shape nor manner of attachment would have permitted them to act as oars. In 'subaqueous flying' the appendage or fin moves at right angles to the direction of progress and the propulsive force is the result of lift rather than drag. Rotation of the appendage ensures that the angle of attack remains favourable and that propulsive forces are generated during both the up and down stroke (see, for example, Robinson 1975, pp. 292–294). Subaqueous flying is more efficient than rowing, particularly for large animals, because there is no requirement for a recovery stroke. The appendage tends to have a characteristic hydrofoil cross-section, rounded at the front and thinning posteriorly.

It is also flexible, and tapers distally; a broad base concentrates the lift forces close to the centre of mass and reduces any tendency to roll (Webb 1975, p. 27). The lateral lobes of *A. nathorsti*, in shape and attitude, seem well suited to have acted as hydrofoils. There was very little space between the proximal portions of successive lobes, as shown by the inward diminution in thickness of the layer of rock separating them (figures 17, 19, 32–34), and the consequent difficulty of tracing them proximally into the body wall. Thus only that part of each lobe extending beyond the dorsal cuticle (figure 104) could have moved up and down to any extent. The required change in the angle of attack between up and down strokes could have been achieved, however, by a flexible outer portion. This portion displays rays (figures 42, 43, 101) which may have had a strengthening function similar to fin rays in fishes where 'individual segments are capable of fairly extensive independent movement because muscular forces are transmitted to stiff fin rays supporting a thin, highly flexible finweb' (Webb 1975, p. 47). The direction of overlap of the lobes, and their slight tilt posteriorly, would have presented a suitable attitude for a propulsive upward stroke. A similar attitude for a propulsive downward stroke would have required the anterolateral portion of the lobe to be curved downward, and held so, against the passive tendency to curve upward. The strengthening rays in the lateral lobe are most prominent in this region, and their function may have been to assist in maintaining the most advantageous form of the lobe during the downstroke. This form is suggested in figure 103*b*. Limbs or fins used in 'subaqueous flying', however, normally occur in one or two pairs, as in the tail fins of fish, 'wings' of penguins, paddles of sea-turtles, and limbs of plesiosaurs (Robinson 1975), rather than in an overlapping series. It is plausible, however, that the lobes in *A. nathorsti* could have acted as a series of hydrofoils, moving in a metachronal rhythm, and

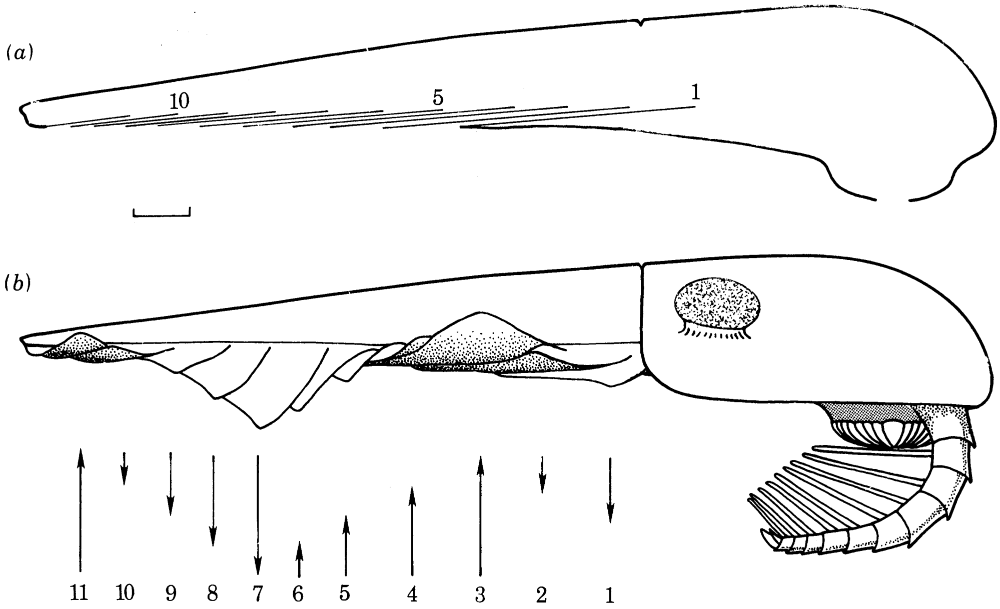

FIGURE 103. Reconstruction of *Anomalocaris nathorsti*. (*a*) Outline of body in right lateral view, on which are shown lines of attachment of lateral lobes 1–11 to wall of axial region of body. (*b*) Right lateral view of animal swimming, the lateral lobes moving in the metachronal rhythm shown. Length of arrows proportional to length of up or down stroke that each successive lobe has gone through. Right appendage shown in 'feathered' position, that is, median plane of shaft in a vertical exsagittal plane. Scale bar, 1 cm.

thus functioned rather like a single lateral fin running the length of the trunk. A number of fish swim by passing waves along the fins, rather than by undulating the body. 'Generally, a propulsive wave is propagated anteroposteriorly for forward motion' (Webb 1975, p. 47). There is a functional gradation from propulsion with a short fin acting like a simple hydrofoil, to long fins, in *Raja*, for example, where several half-wavelengths occur within the fin length (Webb 1975, p. 47). Figure 103*b* shows a possible configuration of the 11 lobes of *A. nathorsti* moving in a metachronal rhythm, a wave embracing eight lobes. Such waves would be propulsive in a manner similar to those in the long lateral fin of fish like the ray or even the cuttle-fish (Webb 1975, figure 26; Alexander 1982, figure 2.8). The portion of the lobe outside the dorsal cuticle of the trunk would tend to become slightly concave dorsally during the downstroke, and convex dorsally in the upstroke (figure 104). As suggested above, this form may have been mofified along the anterolateral margin during the downstroke to give the most effective angle of attack, as shown in figure 103*b*. The widening of the lobes near the mid-length of the body would have concentrated the lift forces near the probable centre of gravity. The anterior three flaps, concealed beneath the cephalic region, may have moved in sequence with the lobes. The movement of these flaps, and the inner portions of the lobes beneath the dorsal cuticle, may have acted to force water in and out of the gill chamber.

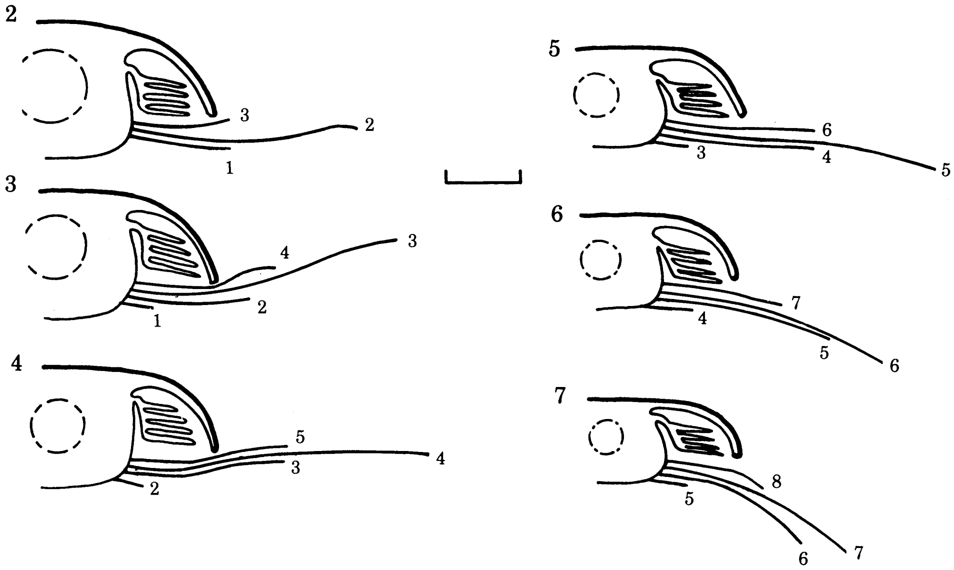

FIGURE 104. A series of transverse sections through the trunk of the restored *Anomalocaris nathorsti*, while swimming as postulated in figure 103*b*. Sections are through the tips of lateral lobes 2–7 (large numerals), and in each are shown sections of lobes as indicated in smaller numerals. Outline of alimentary canal dashed, gill is diagrammatic as in figures 101, 102. Scale bar, 1 cm.

If *A. nathorsti* swam in the manner proposed, the morphological convergence with the cuttle-fish is striking; not only in swimming by the undulation of a laterally projecting fin or lobes, but in the elaborate anterior appendages for prey capture, and in the position of the eye on the side of the head. These similarities are no more than a response to similar hydrodynamic requirements, however; cuttle-fish are fundamentally different in using jet propulsion as their normal mode of swimming, both forward and rapidly in reverse, for escape. The analogy prompts consideration of whether *A. nathorsti* swam mainly backwards or forwards. The position of the eyes and configuration of the anterior appendages (figure 106) suggests that prey would have been more readily captured by moving forward; it is unlikely that *A. nathorsti* required to escape from predators. The overlap and posterior tilt of the lobes are such that lift would be created when moving in this direction. Reversal of the metachronal wave so that it passed forwards, rather than backwards along the lobes, however, would have allowed swimming in reverse. Movement of the lobes in opposing directions on opposite sides of the trunk would have given the ability to turn and manoeuvre, and slow speed undulations the ability to hover.

The large overlap between the lateral lobes of *A. nathorsti* prompts consideration of an alternative, hydraulic means of generating thrust similar to that used by some branchiopods (Cannon 1933; Barlow & Sleigh 1980). Figure 105 shows diagrammatically how water might have been drawn in and forced out from between the lobes as they moved up and down. Thus, as lobes 1 and 2 move down (and 3 completes the upstroke) water would be drawn into the intervening spaces; conversely as lobes 3–6 move upwards (while 7 completes the downstroke) water would have been forced out. La Barbera (personal communication) has used such a mechanism in extending Whittington's (1975, p. 40) interpretation of swimming in *Opabinia regalis*. While this model remains a possibility for locomotion in *A. nathorsti*, we consider it less likely than the propulsive wave discussed above for the following reasons:

(i) while a considerable degree of overlap between lobes is an apparent advantage in allowing larger volumes of water to be set in motion, the close proximity and wide extent of the lobes limits the degree to which they could have been moved apart (figure 104);

(ii) a greater degree of coordination and flexibility is required to ensure that the posterior and anterior margins of each lobe successively approach the adjacent lobes to enclose a volume of water and push it out;

(iii) there is no obvious means of channelling jets of water, emerging from between the lobes in a posterior, as opposed to a lateral, direction;

(iv) the hydraulic mode of locomotion would work more efficiently with a greater phase difference between the lobes than that depicted in figure 103*b*, as this would yield a greater total thrust: but this would require even more flexibility of the lobes, a flexibility constrained by overlap;

(v) the hydraulic mode of locomotion allows more limited manoeuvrability than a propulsive wave – in a forward direction only.

FIGURE 105. Reconstruction of *Anomalocaris nathorsti*. Outline of body in right lateral view, on which are superimposed exsagittal sections through successive lateral lobes when swimming. These sections are cut a short distance outside the edge of the dorsal cuticle, and show the angle of attack of each lobe. The arrows suggest how water may have been drawn in between lobes in the downstroke, and particularly between lobe 2 moving down and lobe 3 completing the upstroke. Conversely water is expelled from between lobes in the upstroke, and particularly from between lobe 6 moving up and lobe 7 completing the downstroke. Scale bar, 1 cm.

So far as we are aware the mode of swimming postulated here for *A. nathorsti*, the use of a series of overlapping closely spaced lobes in an undulatory mode to create a propulsive wave, is unique. If the muscular coordination of the outer rayed portion of the lobes was adequate, some hydraulic thrust may also have been created. This might in some degree compensate for the loss of efficiency due to drag created between the lobes, drag which would have been eliminated in a continuous lateral fin.

(ii) *Capture and maceration of prey*

Briggs (1979, pp. 655–656) discussed the functional morphology of 'appendage F', and noted that the graduation in length of the blades is such that the tips lay in a straight line when the appendage was extended (figure 106*a*). The position shown appears to be the maximum extension; the shaft is always found curved, never straight. Now that the entire animal is known, we suggest that the pair of limbs was attached to the ventral cuticle with the blades directed inward and backward (figure 106*a*, *b*, *c*). In anterior view the appendages with their blades and spines may be seen to form a formidable apparatus for catching prey as the animal advances on it. On capture, flexure of the appendages (figure 106*d*, *e*, *f*) would have torn and squeezed prey impaled by the spines, and brought it to the mouth. The position of attachment of the appendage, and angle of the blades to the sagittal line (figure 106*c*, *f*) are optimal for functioning in this way, given our reconstruction. The basal attachment of the appendages was probably not rigid, but limited movement was possible. Thus appropriate musculature may have enabled the pair of appendages to be swung slightly outward or inward, to assist in capture and holding of prey. Limited rotation of the shaft at the base would have permitted the appendage to be turned so that the plane passing through shaft and blades lay in an exsagittal direction; combined with flexure this would have brought the appendage into a streamlined position for swimming (figure 103*b*).

'Peytoia', the circlet of plates, because of its position and relationship to the alimentary canal (figures 30, 59) must have surrounded the mouth (as Walcott 1911*b*, p. 68, indicated in his original description of 57555, figure 95). The rectangular opening, the long axis of which runs sagittally (figure 21) and the teeth (figure 67), were observed by Walcott. The overlapping arrangement of the plates has not been commented on previously; the difference in level between adjacent plates is minimal peripherally and increases inward. Our reconstruction (figure 107) shows this arrangement, the probable convexity, the increase in thickness of the plates inward, and the slightly different levels of the teeth in each plate. Some specimens (figures 69, 70, 79, 80) show darker, reflective bands at the margins of adjacent plates. We regard these bands as the remains of membranes between adjacent plates, which would have allowed movement at the junctions. As far as we are aware no living animal has a jaw similar to that of *A. nathorsti*, to provide a possible functional analogy. A number of groups have radial jaws, including cnidarians, ctenophores, aschelminth phyla (such as the nematodes), echinoderms, and lampreys among the chordates. Such radial jaws usually reflect the overall body symmetry or occur in organisms that feed as parasites. The irregularly convex outer surface of the circlet and the different levels at which the teeth project negate the possibility that the jaw of *A. nathorsti* was primarily suctorial.

The circlet was attached peripherally to the ventral cuticle. Horizontal movement (in the plane of the circlet) between adjacent plates would be required to arrange them so that the teeth of the lateral plates (figure 108*c*) could oppose each other to bite, the opening becoming

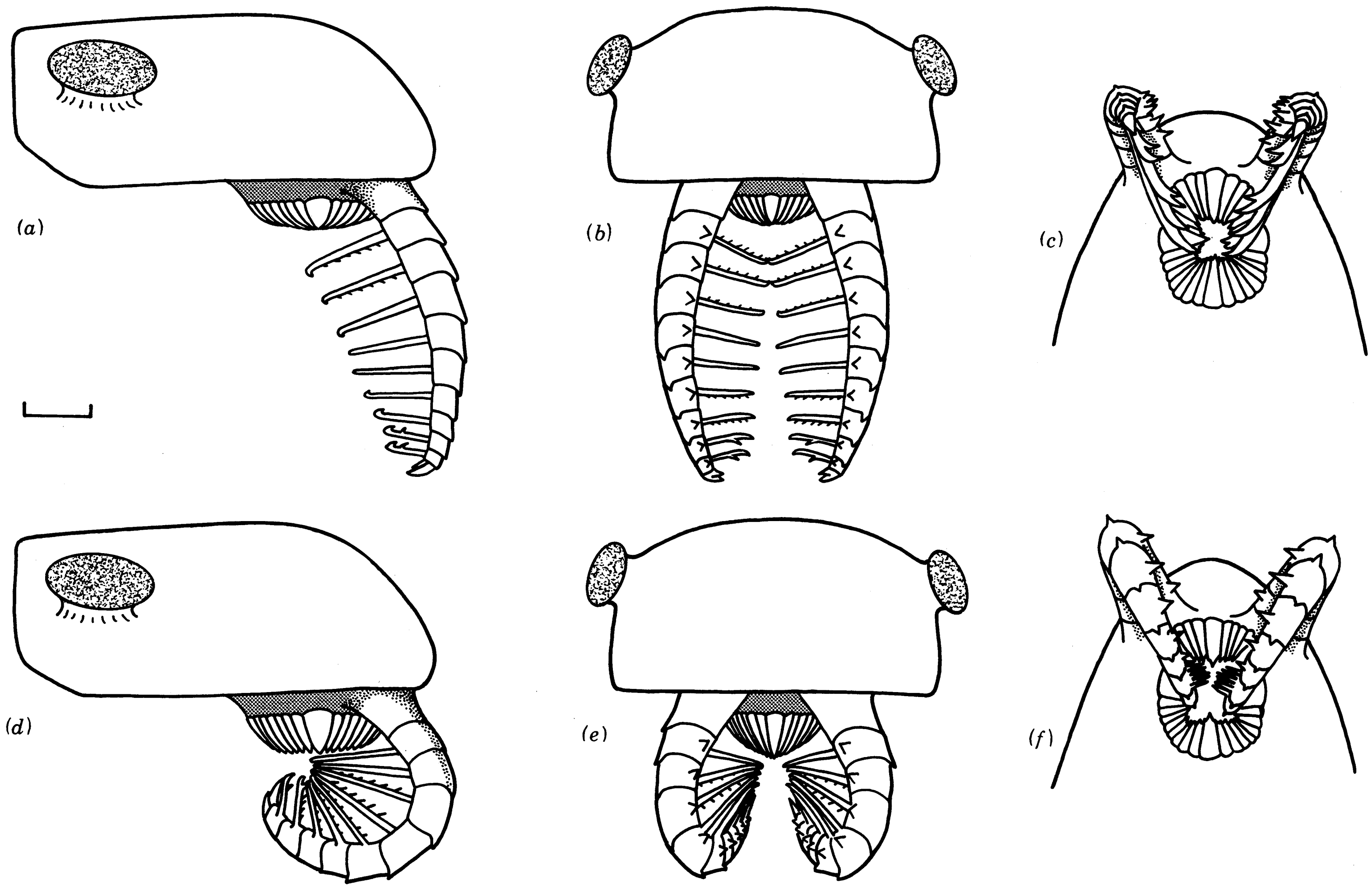

Figure 106. Restoration of head of *Anomalocaris nathorsti* to show movements of the appendages and mouth plates in the capture and ingestion of prey. (*a*, *b*, *c*) Right lateral, anterior, ventral views, appendages fully extended in position for capturing prey, mouth plates withdrawn and aperture minimum. (*d*, *e*, *f*) Similar views, appendages flexed to hold prey between the opposing shafts and blades, and bring it to mouth. Circlet of mouth plates swung down and aperture of mouth enlarged. Scale bar, 1 cm.

a narrow slit. Such movements (and similar movements to bring the anterior and posterior plates into opposition) would have required great flexibility in both the membranes and the ventral cuticle, and have disrupted the circlet. The curvature of the teeth of the minor plates toward the median plate does not appear to fit with such a mode of operation; no specimen suggests that it took place and we regard it as unlikely.

In some isolated specimens (figure 67) the opening is a parallelogram rather than a rectangle. We regard this as the result of oblique burial and compaction, and not as representing a stage in another possible way in which opposing teeth could be brought together by horizontal movements between the plates. Although it would bring the curved teeth at the acute angle of the opening into opposition (figure 108*b*) any further closure would be open to the same objections as those levelled against the arrangement shown in figure 108*c*.

It appears to us more likely that the mode of operation of the jaw plates was as shown in figure 107. That is, the circlet was inserted in the ventral cuticle and no significant horizontal movement between adjacent plates occurred. The membranes between the plates, and appropriate musculature, would have allowed the inner ends to swing down about the outer margin, a rotation in a radial plane vertical to the plate. Such movements would have enlarged the opening and increased the differences in level between the teeth at the inner ends of the plates. Retraction of the plates would have squeezed and cut prey, and possibly torn in opposition to a pull given by extension of the appendages. A firm anchorage, to provide a fulcrum at the jaw perimeter, would have been necessary to gain the mechanical advantage of using the plates as levers to increase the force exerted by the jaw in gripping prey. That entire specimens of 'Peytoia' occur suggests that the circlet was firmly held together. If movement of the plates had been predominantly horizontal one might not expect such specimens, and the mechanical advantage referred to would not have been possible. The larger teeth of the major plates projected beyond the others (figure 107), the pairs at 90° to each other. Possibly each pair could have been lowered and raised alternately to grasp prey and pull it into the mouth as they were retracted. The additional rows of teeth in the buccal cavity (figure 68) assisted in macerating the food.

Does the suggestion that *Anomalocaris* could have inflicted wounds on trilobites (Rudkin 1979; Briggs & Mount 1982; Vorwald 1982) remain plausible now that the jaw apparatus is known? Could a jaw of sclerotized plates, acting as suggested, have been powerful enough to wound an animal that had a mineralized exoskeleton? The answer is uncertain, and no fragments of such exoskeletons occur in the gut. Because the teeth did not meet, the exoskeleton of trilobites too large to be ingested whole would have to have been broken (the jaws acting like nutcrackers) rather than bitten through. The prey could have been held on edge by the appendages, diagonally across the jaw, accommodated in the depressed groove across the circlet at the median plates. The outline of a bite, inflicted as the circlet retracted, might then have been shaped like an asymmetric W. It is impossible to assess the depth of the bite with confidence, but it was probably not less than one quarter the length (sagittal) of the aperture. The size of isolated circlets suggests that *A. nathorsti* could have inflicted bites up to 20 mm across and 5 mm deep. Although the injuries to *Ogygopsis klotzi* from the Stephen Formation on Mount Stephen illustrated by Rudkin (1979) show evidence of cicatrization which may obscure their original outline, those in his figures 1 B and 1 F could have been inflicted by *Anomalocaris*, and both show a hint of the predicted asymmetric W. The wounds in his figures 1 D and 1 H would require the trilobite pleura to have broken beyond the teeth, but this is quite possible, assuming that

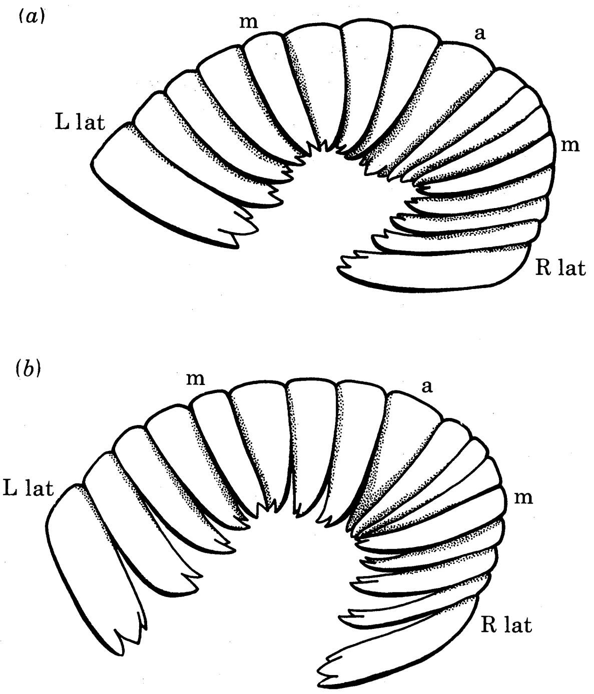

FIGURE 107. Half of 'Peytoia', the circlet of mouth plates of *Anomalocaris nathorsti*, viewed obliquely from the inner dorsal side, membranes between plates omitted. (*a*) Retracted position, aperture of minimum size; (*b*) extended position, plates pivoted downward about the periphery, median plates moved the least amount, anterior and lateral plates swung farthest downward, aperture enlarged.

the exoskeleton was brittle. The scars on pygidia of *Asaphiscus wheeleri* from the Middle Cambrian Wheeler Formation of Utah (Vorwald 1982) also show an indication of an asymmetric W, and occur in association with isolated specimens of the jaw of *A. nathorsti* (Conway Morris & Robison 1982). The injury to *Olenellus robsonensis* figured by Rudkin (1979, figure 2B), on the other hand, is almost certainly too deep to have been inflicted by the jaw of *A. nathorsti* (particularly as it is partly enclosed by a surviving pleural spine). *Anomalocaris*, however, is not known from the same locality; the origin of this injury is unknown. Thus, certain injuries to trilobites may represent unsuccessful attacks by *A. nathorsti*, but do not show that trilobites were necessarily the preferred prey. Arthropods lacking a mineralized exoskeleton were far more abundant (68 % of the total arthropods in the Burgess Shale) and probably easier prey.

Our reconstruction of *A. nathorsti* includes various conjectures, so that the interpretations of mode of locomotion, aeration of the gills, and feeding are speculative. We regard the animal as having been primarily a predator, cruising at no great speed over the sea bottom in search of food. The proximity of the blades to the tip of the appendage does not suggest that the terminal spines were used to dig into the bottom, rather the armature of blades and spines were used to trap unwary animals on the bottom surface. *A. nathorsti* is the largest known Cambrian animal, and the appendages and jaw apparatus must have made it a formidable enemy of the lightly skeletonized and soft-bodied, vagrant benthos.

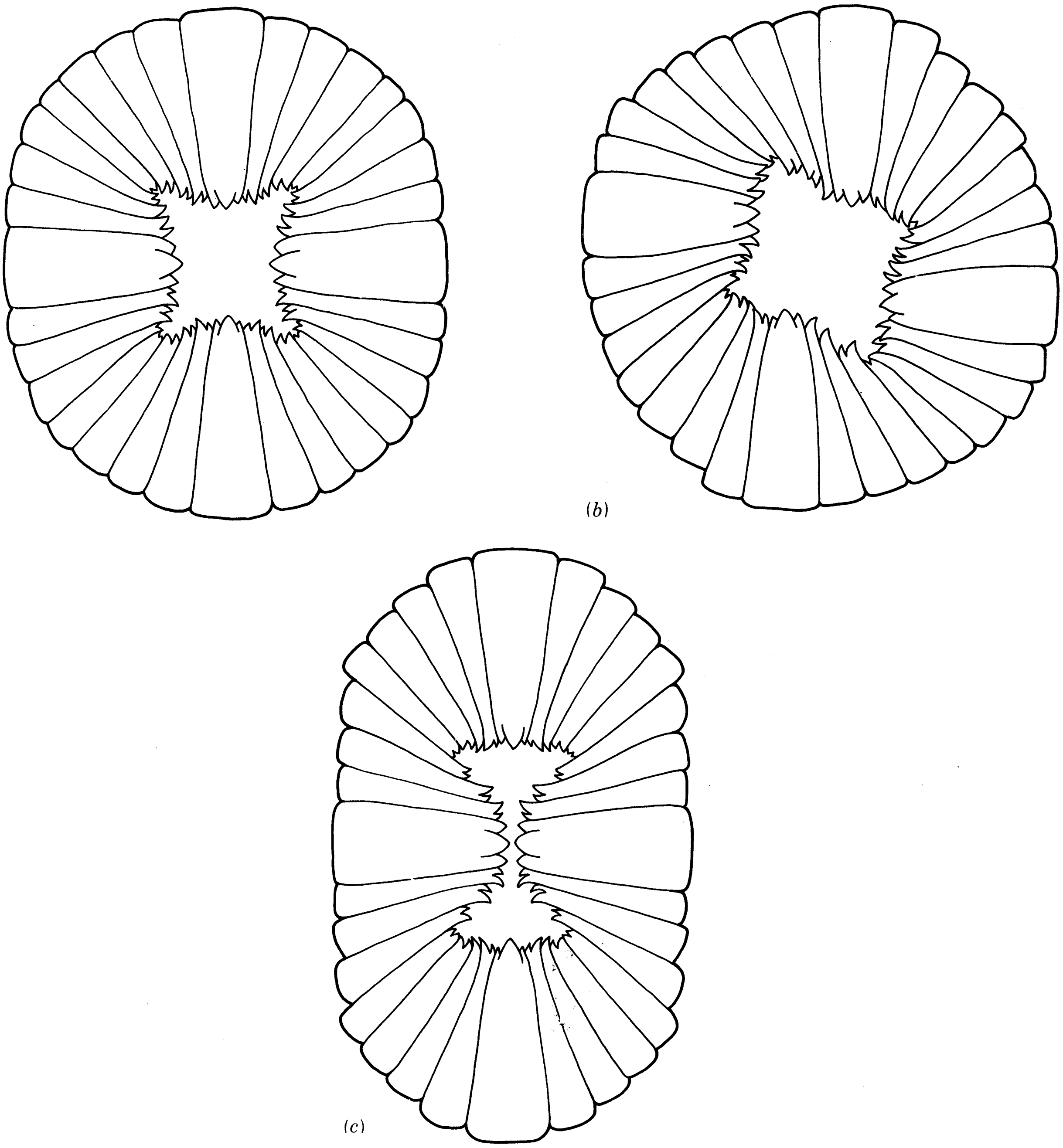

FIGURE 108. Ventral views of the circlet of mouth plates, 'Peytoia', of *Anomalocaris nathorsti*. (*a*) Symmetrical arrangement, as seen in parallel specimens (figures 61–63, plate 13; figures 79, 80, plate 17). (*b*) Asymmetrical arrangement as seen in oblique specimens (figures 64–66, plate 14). (*c*) An imaginary arrangement, devised by moving the outlines of the plates in the plane of the paper, that brings the lateral plates in apposition.

8. AFFINITIES OF *ANOMALOCARIS*

The view has persisted (Rolfe, p. R323, in Moore 1969) that *Anomalocaris* may be the body of a phyllocarid, but Briggs (1979) and Bergström (1979, pp. 10–11; 1980, pp. 12–14) suggested that it was more probably the limb of a myriapod-like arthropod. Bergström thought that the body might be like *A. lineata*, but in his redescription of this latter species Briggs (1978) placed it in a new genus, *Serracaris*, and considered it unlikely to be related to *Anomalocaris*. As the new material shows, this appears to be the case. Although *Anomalocaris* bears a single pair of arthropod-like limbs, and the body is metameric, it is unlike any known arthropod, particularly in the nature of the jaw apparatus and the close-spaced, strongly overlapping lateral lobes. It shows some similarities to *Opabinia* (Whittington 1975) in the thin cuticle of the cylindrical axial trunk region and lateral lobes, dorsal to which were lamellar gill structures; the head and terminal regions are very different in the two animals. Neither can be referred to any known group, both may be descended from segmented animals from which arthropod phyla or annelids, or both, were derived, but each appears to represent a quite separate such line of descent. If Arthropoda were considered to constitute a single phylum, it would be difficult to include *Anomalocaris* within it. If arthropods are regarded as embracing at least three phyla (Manton 1977) then *Anomalocaris* must be regarded as a Cambrian representative of a new phylum of metazoan animals. The implication is that the arthropod-like pair of anterior limbs were evolved independently. We do not propose any name for a taxon higher in rank than Anomalocarididae (Raymond 1935).

9. *AMIELLA ORNATA* WALCOTT, 1911

(Figures 90–92, 94)

1911*a*	Walcott, p. 27–28, plate 5, figure 4
1944	Størmer, p. 91
1959	Størmer, in Moore, p. O 30
1963	Simonetta, pp. 97, 104
1975	Simonetta & Delle Cave, plate 13, figure 7
1982	Bruton, pp. 627–628, figure 34; figure 38, plate 5

(*a*) *Holotype*

U.S.N.M. 57499, part and incomplete counterpart, from locality 35k.

(*b*) *Description*

We orient this specimen as did Walcott, with the narrowest (tr.) portion posterior, the part (figures 90, 91) convex and more complete than the counterpart (figure 92). Anteriorly are three areas of cuticle (1–3, figure 94), each appearing below the one in front, the first a triangular fragment, the second and third each having a bluntly rounded outline at the left anterolateral margin, the third showing a bluntly pointed outline at the right posterolateral margin. In the left anterolateral portion of the third area, faint subparallel lines are discernible, that run forward and curve into the anterior margin (ri in figure 94). There is evidence of more than one layer in each area of cuticle, and of lines or wrinkles subparallel to the margins. The third area passes posteriorly into the matrix at a prominent change in level (up posteriorly, and greatest to the left) across the specimen. Behind this change in level are a series of gently convex plates (4–10, figure 94), wider than long, each overlapping that following, the maximum width across plates 5 and 6, diminishing posteriorly. The counterpart (figure 92) is of this portion of the specimen. The conspicuous changes in level between plates 4 and 5, 5 and 6, and 6 and 7 are least medially, and increase laterally. Behind plate 7 is a step down (ventrally), prominent medially as well as laterally. Medially, in this posterior portion of the specimen, features are exposed that lie further ventrally, while laterally are portions of plates 8–10. As interpreted here, each of plates 4–7 shows two layers. The outer layer (o in figure 94), has a wrinkled appearance that is strongest at the margins (figures 91, 92), the wrinkles running subparallel to the lateral margins. The inner layer (s in figure 94) lacks such conspicuous wrinkles, and is separated by a layer of matrix from the outer layer, the two layers coming closer distally to join along the lateral margins. The entire specimen also shows faint, subparallel diagonal striations (dashed lines in figure 94, compare figure 91) which may be tectonic in origin. There is a very great overlap between plates 4–7, the outer layer of plate 4, for example, reaching back towards the posterior margin of plate 5s. The posterior margins of these plates are only seen laterally, the rounded posterolateral corners of plates 5–7 having been exposed in the counterpart (figure 92); it may be that the posterior margin ran between these corners in a curve that was gently convex posteriorly. In plates 8–10 the wrinkled outer and smooth inner layers may be distinguished, the last two plates being fragmentary. In the median region of plate 8, an additional sheet of cuticle lies below the smooth layer, and slopes down toward the right side to end in a straight margin (vm in figure 94). Other additional, problematical layers occur behind this one.

(*c*) *Discussion*

Walcott (1911*a*, plate 5, figure 4) illustrated only the part of this specimen, apparently with some retouching to emphasize striations in what are here called the smooth layers of plates 6 and 7; he regarded it as quite distinct from any specimen of *Sidneyia inexpectans*. Simonetta (1963, p. 104, figure, plate X) illustrated a different specimen which he regarded as an example of *A. ornata*, and concluded that the species should be placed in *Sidneyia*. As Bruton (1981, p. 628, plate 1, figure 8) showed, this specimen belongs within the type species *Sidneyia inexpectans*. Bruton (1981, p. 627, figure 34; plate 5, figure 38) described the holotype of *A. ornata*, and argued that it was an oblique and telescoped example of *S. inexpectans*. We do not find this argument convincing. The areas of cuticle 2 and 3 (figure 94) have a lobate outline on the left anterolateral side, and there are faint rays on 3, combining to suggest lateral lobes of *Anomalocaris nathorsti*. From their overlapping relation to each other they would appear to be right lateral lobes exposed from the inner side. Plates 4–10 would then presumably represent succeeding portions of the trunk, the cephalic region (including 'Peytoia' and 'appendage F') missing from the specimen. Plates 4–10 show some superficial resemblances to the transverse smooth and lamellar areas of one of the oblique compressions (figures 74, 78), but in that specimen successive areas do not step down (ventrally) one behind the other. The marginal plates (V and D in figure 99) are, like those of 57499, wrinkled parallel to the margins, but appear to lie above or below the smooth and lamellar areas. The original of figure 99 is thought to be an oblique lateral compression. However, plates 4–10 of 57499 show an approximately bilateral symmetry, in the way the outer and smooth layers of each plate join distally, and in the way the layer of matrix between successive plates thickens distally. May this portion of the trunk be regarded as a dorsoventral compression, buried with the lateral lobes (and tergites) steeply sloping or curved inwards distally to give a tube-like form? The obstacle to this interpretation is that the layers of matrix extend across the supposed dorsal mid-region. If one regards the layer of matrix observed below the posterior margin of successive plates as separating the posterior edges of overlapping tergites, then why are there outer and smooth layers in each supposed tergite? If, on the other hand, one regards each plate as representing the left and right gill of a pair (and suggests layering and wrinkling as resulting from compressed lamellar structures), why does the matrix layer extend across the midline? Thus, while we are not persuaded by Bruton that 57499 is an example of *Sidneyia inexpectans*, the evidence it affords leaves us in doubt that it is an unusually orientated compression of *A. nathorsti*. This specimen is isolated by the combination of characters peculiar to it.

In 1966 and 1967 a re-investigation of the Burgess Shale (Whittington 1971; 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.E.G.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 Richard E. Grant, Dr M. A. Buzas and Mr F. C. Collier. D.E.G.B.'s research was financed by a Royal Society Scientific Investigations Grant and Goldsmiths' College Research Fund, and was continued at the Field Museum of Natural History, Chicago, Illinois, under the auspices of the Visiting Scientists' Program. We are grateful to M. C. La Barbera (University of Chicago) for discussion of the hydrodynamics of swimming animals, and to Dr D. H. Collins for the loan of specimens from the Royal Ontario Museum. We are indebted to Dr J. V. P. Long and Dr A. Buckley for analyses using the Natural Environment Research Council electron probe at the University of Cambridge. In Cambridge H.B.W. made the photographs, which were enlarged by Mr D. Bursill, and pencil drawings which were converted into the figures by Miss Adele Prouse.

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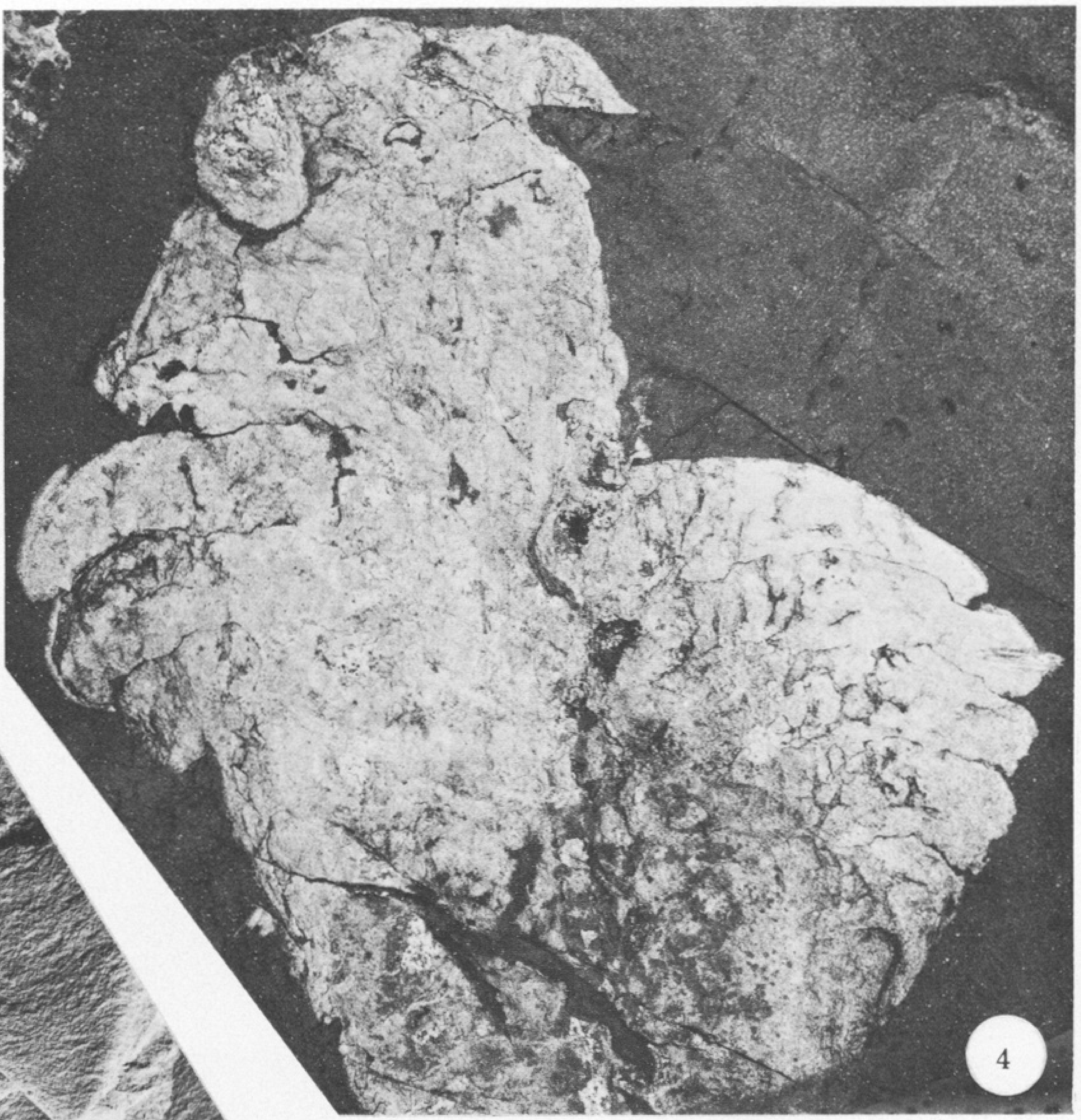
LIST OF ABBREVIATIONS AND SYMBOLS

a	large anterior plate of 'Peytoia'
A, B	indeterminate areas (figure 85)
a–z	serial lettering of gills (ga, gb, etc.), lateral lobes (la, lb, etc.) when most anterior in body cannot be identified, and gill lamellae (figure 21)
al	alimentary canal
am	anterior margin
ap	appendage
Br	brachiopod
Bur	specimen of *Burgessia bella* (figure 75)
D	marginal plates that pass over the trunk, and are dorsal in position
dc	dorsal cuticle
dm	dorsal margin
e	eye
F	'appendage F'
fl	semicircular flap, on anterior, ventral side of body
fo	fold in specimen
fr	fracture in specimen
Fb	blade of 'appendage F' (spine of Briggs 1979)
Fl	lateral spines on segment of 'appendage F'
F sp	spines on blade of 'appendage F' (auxiliary spines of Briggs 1979)
g	gill or lamellar area, numbered in series corresponding with nodular mineralized areas, lettered in series where anterior in body not known
G.S.C.	Geological Survey of Canada
iml	impressed line in tergite when compacted on to gill
inf	infilling of alimentary canal
j	podomere of appendage of *A. canadensis* or 'F' type, numbered distally from j1, that was attached to the body
l	lateral lobe, numbered serially or lettered where anterior in body not known
L	left side of animal, as prefix
lat	large lateral plate in 'Peytoia'
lm	lateral margin
m	median plate in 'Peytoia'
o	outer layer of plate in U.S.N.M. 57499 (figure 94)
p	large posterior plate of 'Peytoia'
P	'Peytoia' circlet of plates, see a, lat, m and p for individual plates
pm	posterior margin
R	right side of animal, as prefix
ri	reflective lines on lateral lobes
R.O.M.	Royal Ontario Museum
s	smooth plates running across trunk (figures 75, 76, 99); smooth layer of plate in U.S.N.M. 57499 (figure 94)
S	where sample taken for analysis from nodular mineralized area
t	possible tergite

U.S.N.M.	United States National Museum of Natural History
V	marginal plates that pass beneath the trunk and are ventral in position
vc	ventral cuticle
ve	vein in rock
vm	ventral margin
vpm	ventral posterior margin
1–n	serial numbering of lateral lobes, gills, nodular mineralized areas, divisions of body, podomeres of appendage (Briggs 1979, text figures 1, 20)
hachures	run down-slope from a line along the upper edge of an abrupt change in level; unless otherwise noted the hachures are drawn widely spaced and short to indicate a slight change in level, more closely spaced or longer hachures, or both, indicate a greater change in level
	horizontal lines in figure 30 denote lighter areas with which pyrite is associated
	vertical lines denote a strongly reflective area, such as the eye lobe
	stipple denotes nodular mineralized areas, which are numbered serially from the anterior when paired
	broken line denotes edge of lateral lobe, eye, or body, drawn from the part and shown on the counterpart, or vice versa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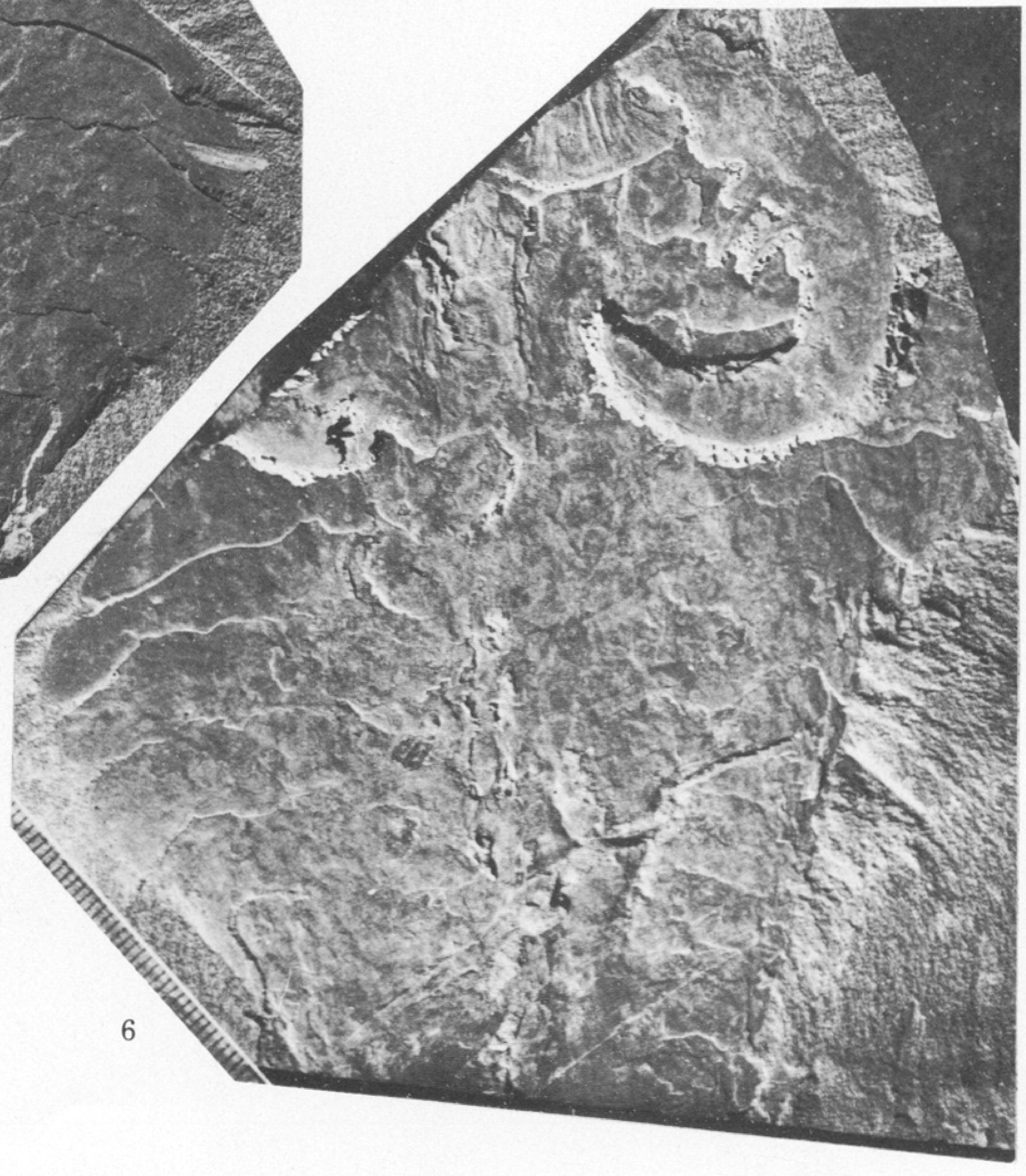
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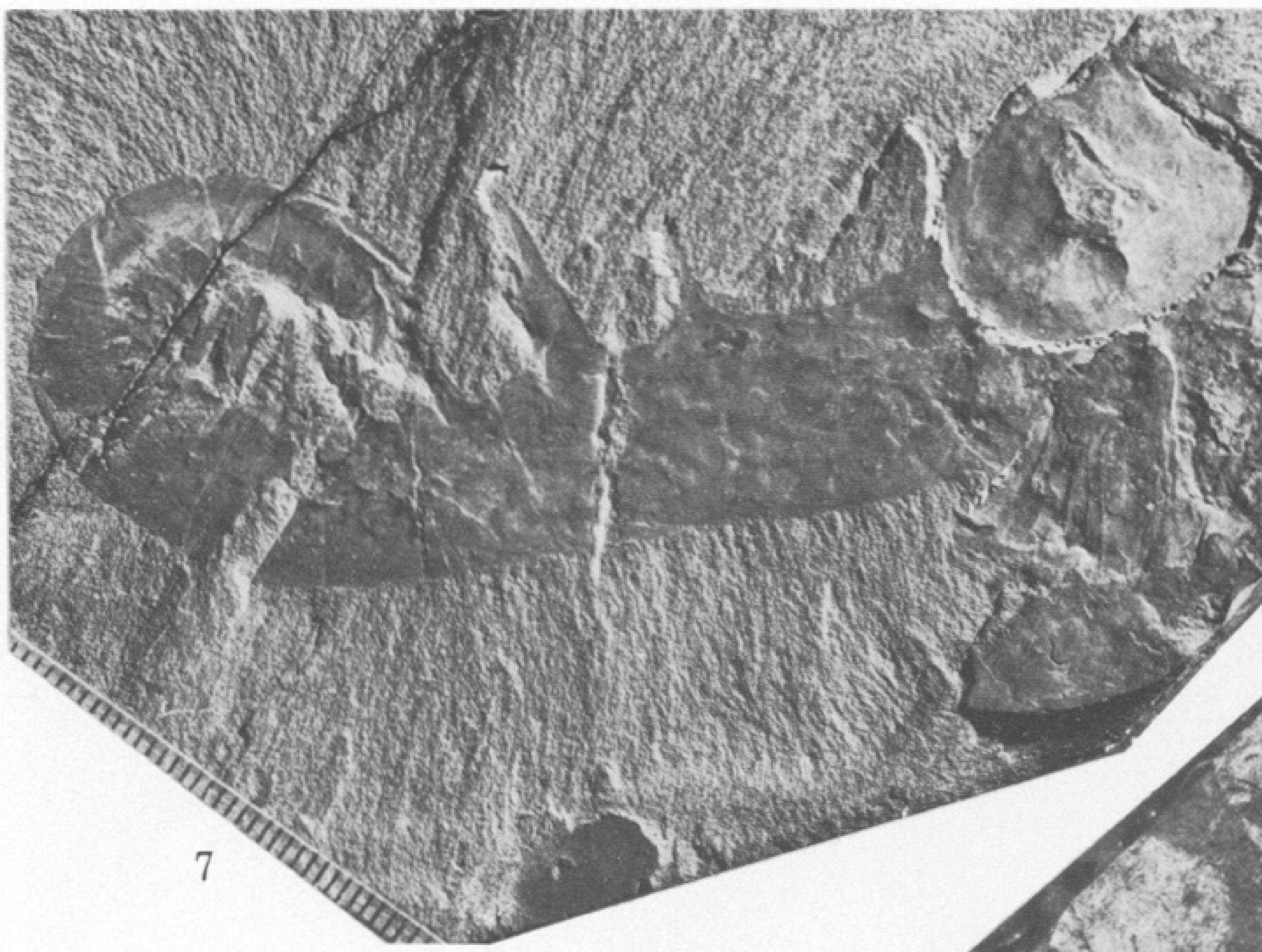

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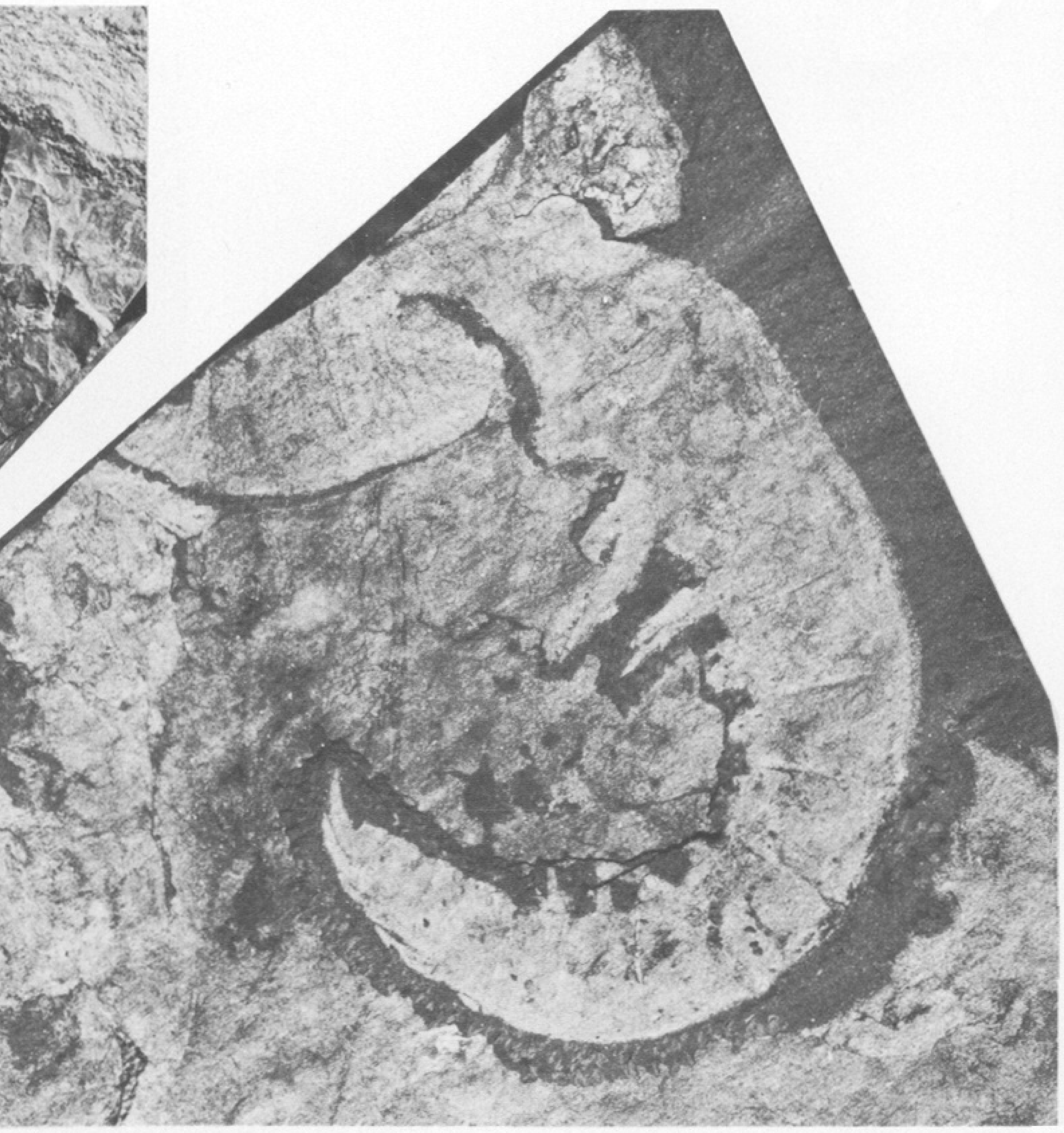

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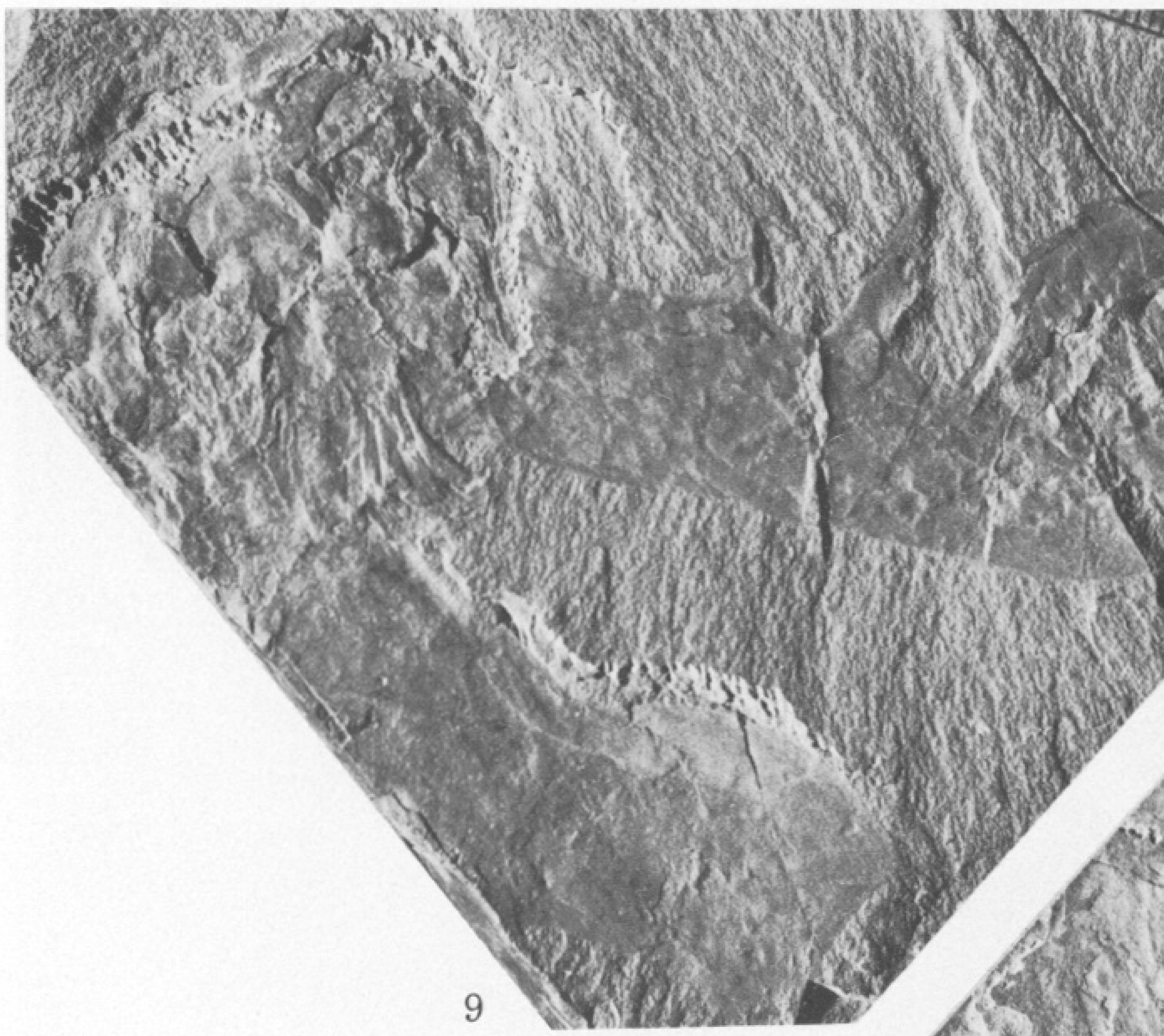

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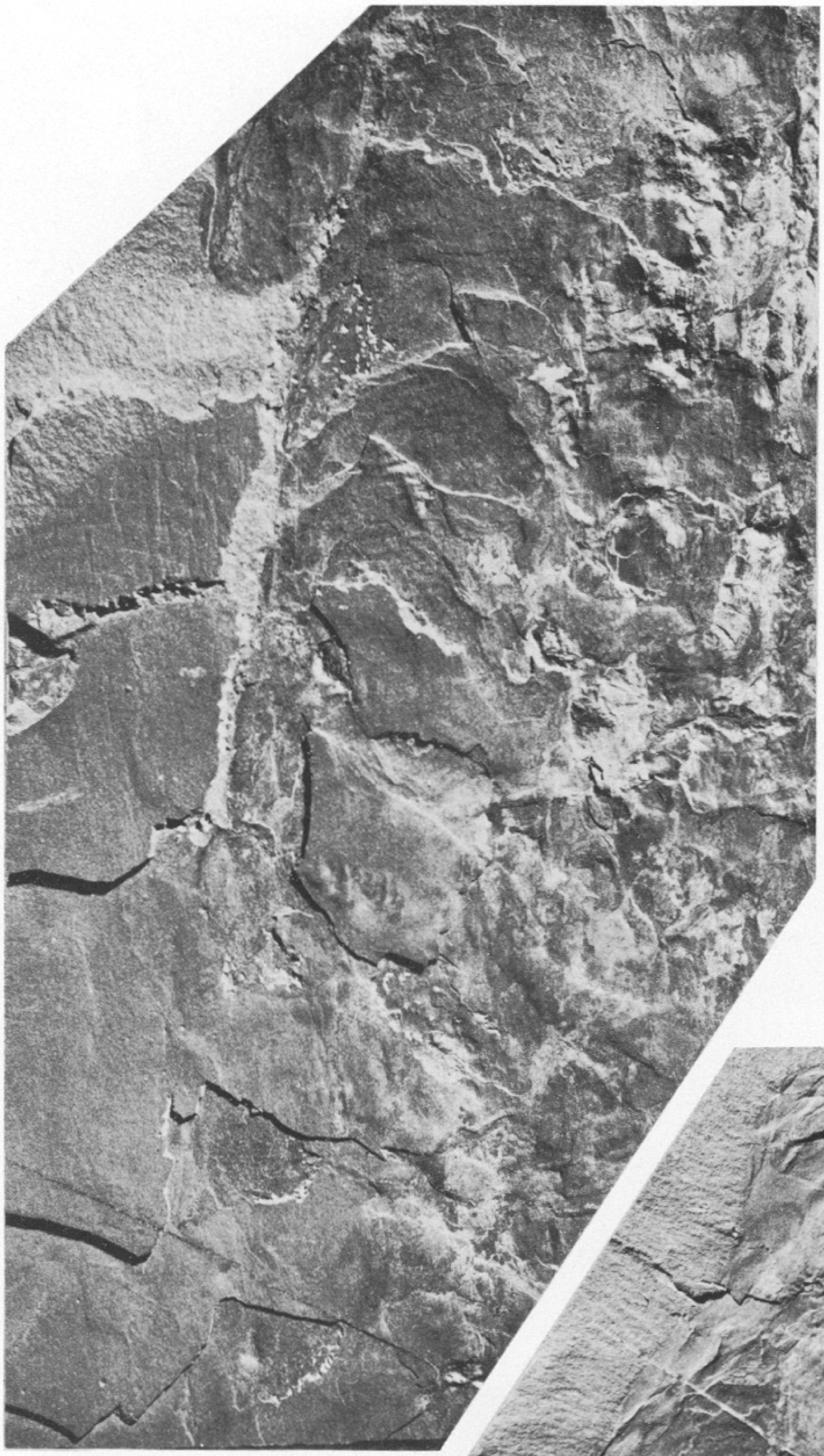
FIGURES 7–10. For description see opposite.



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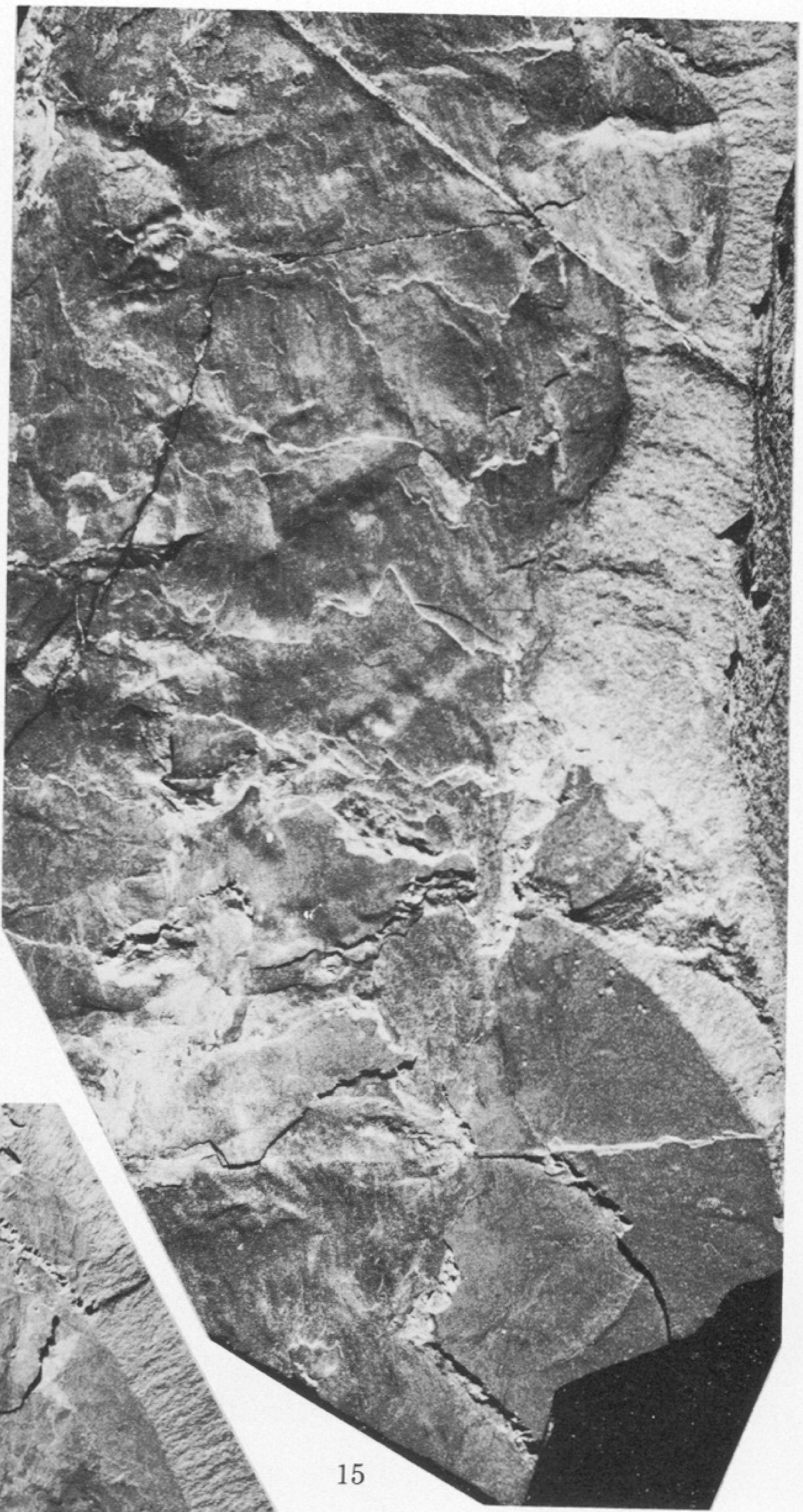

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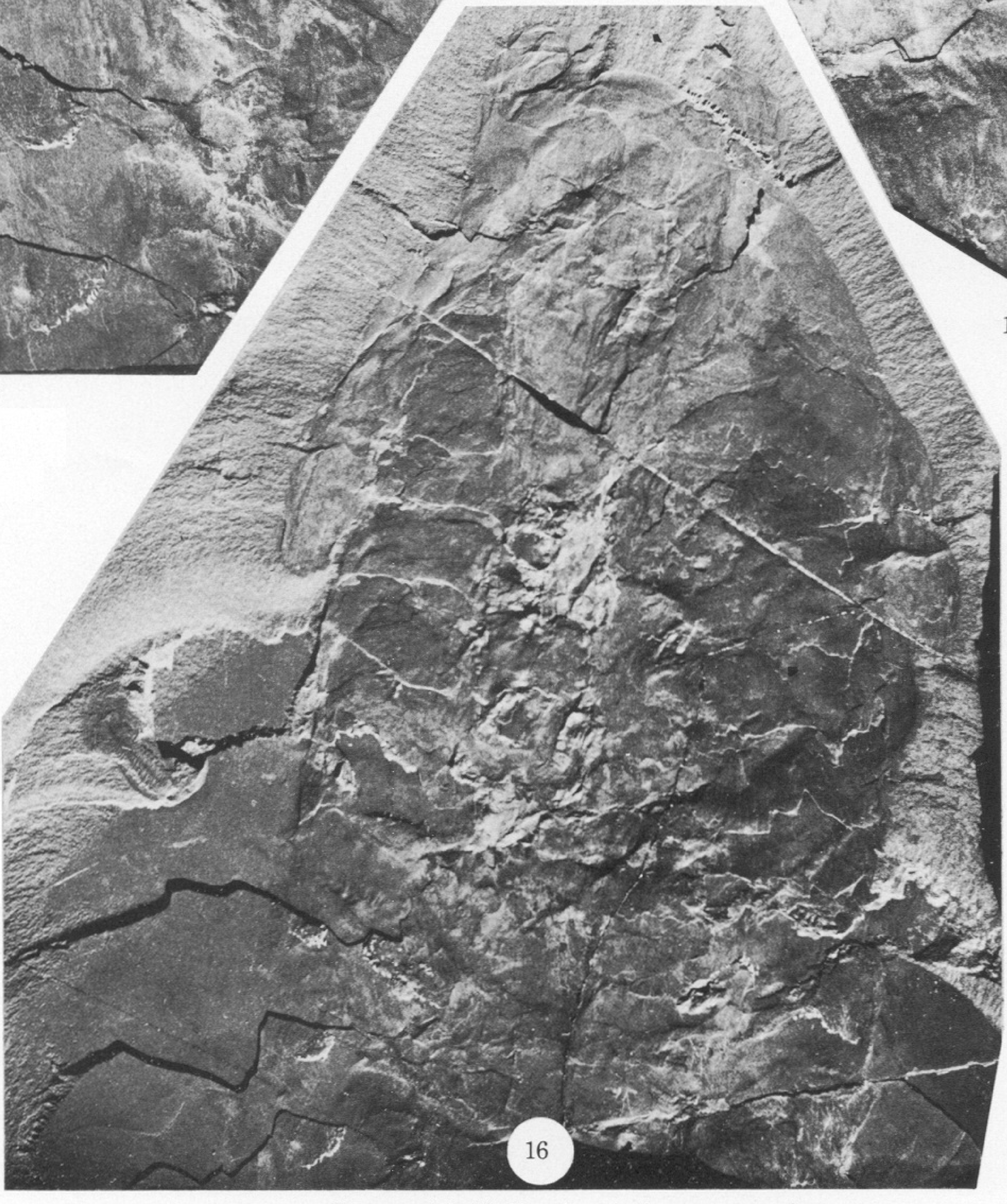

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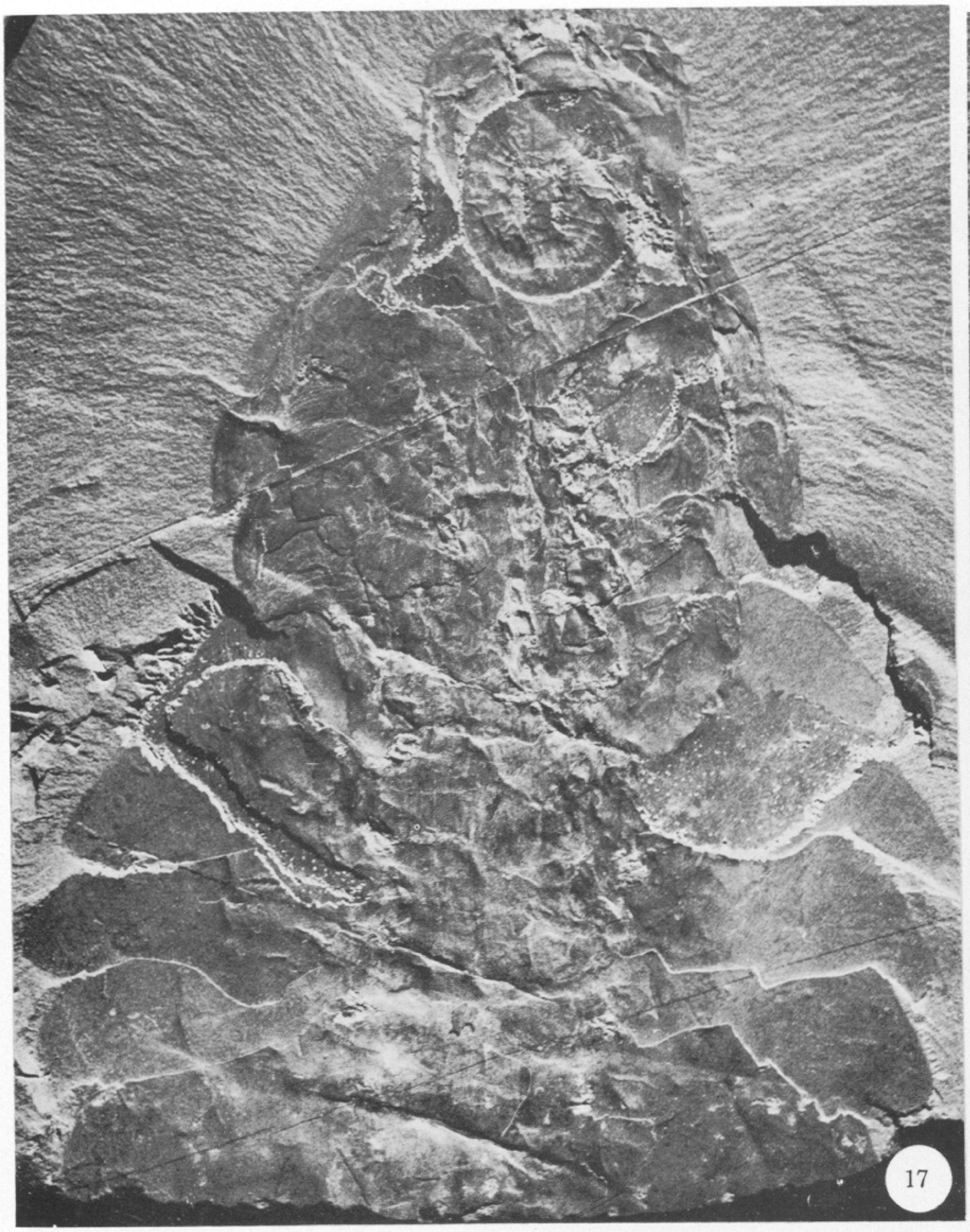

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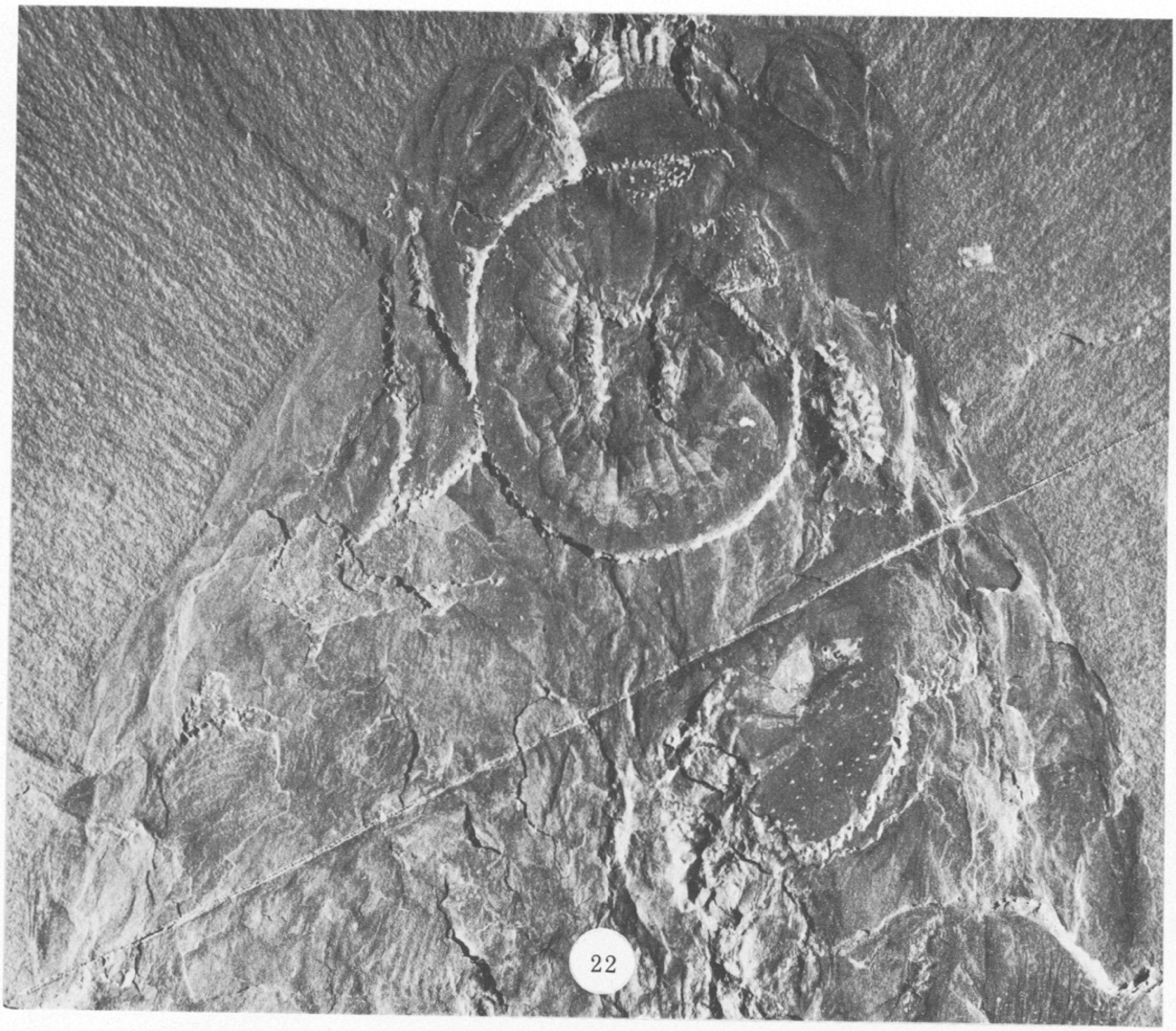

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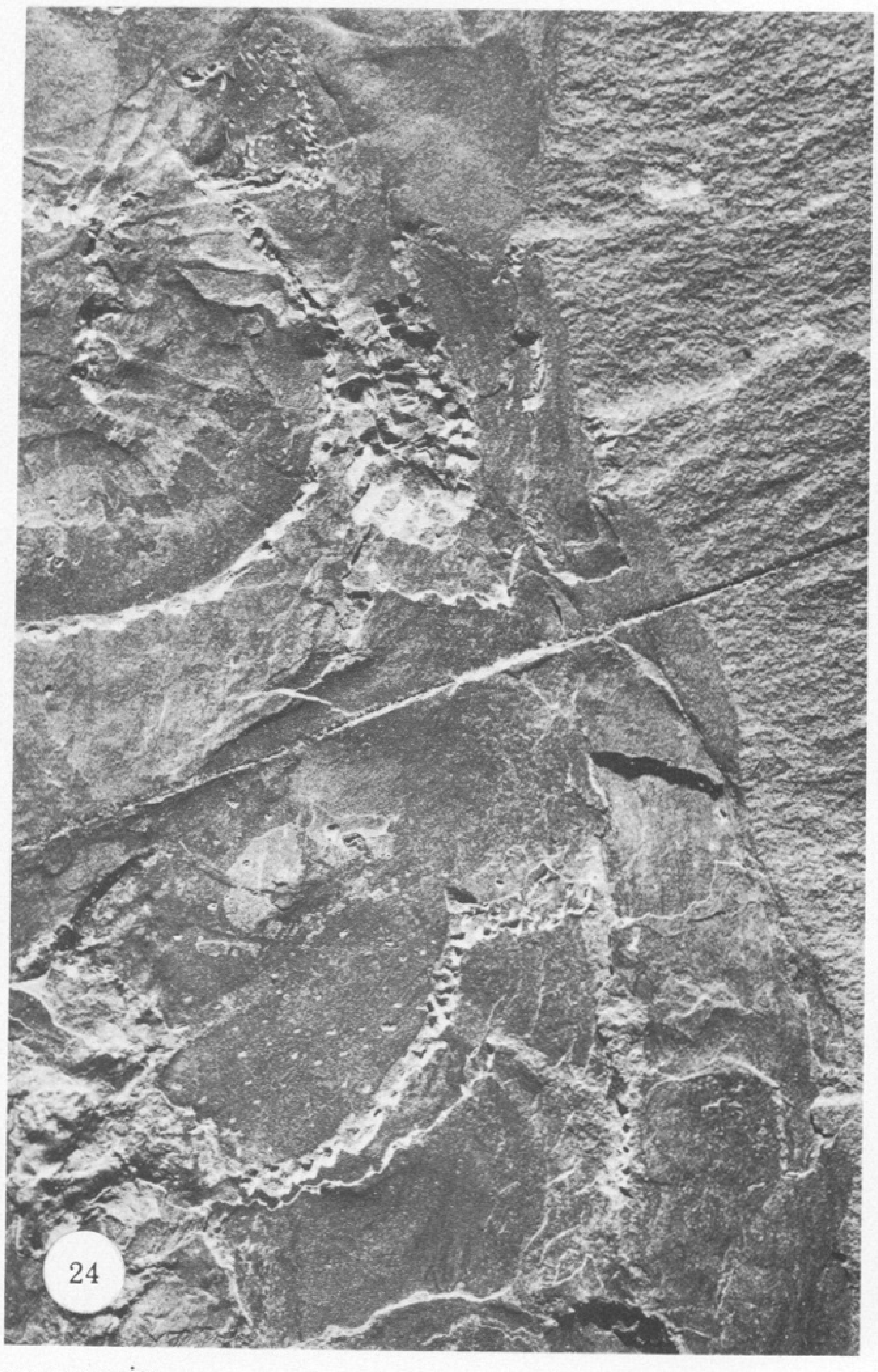

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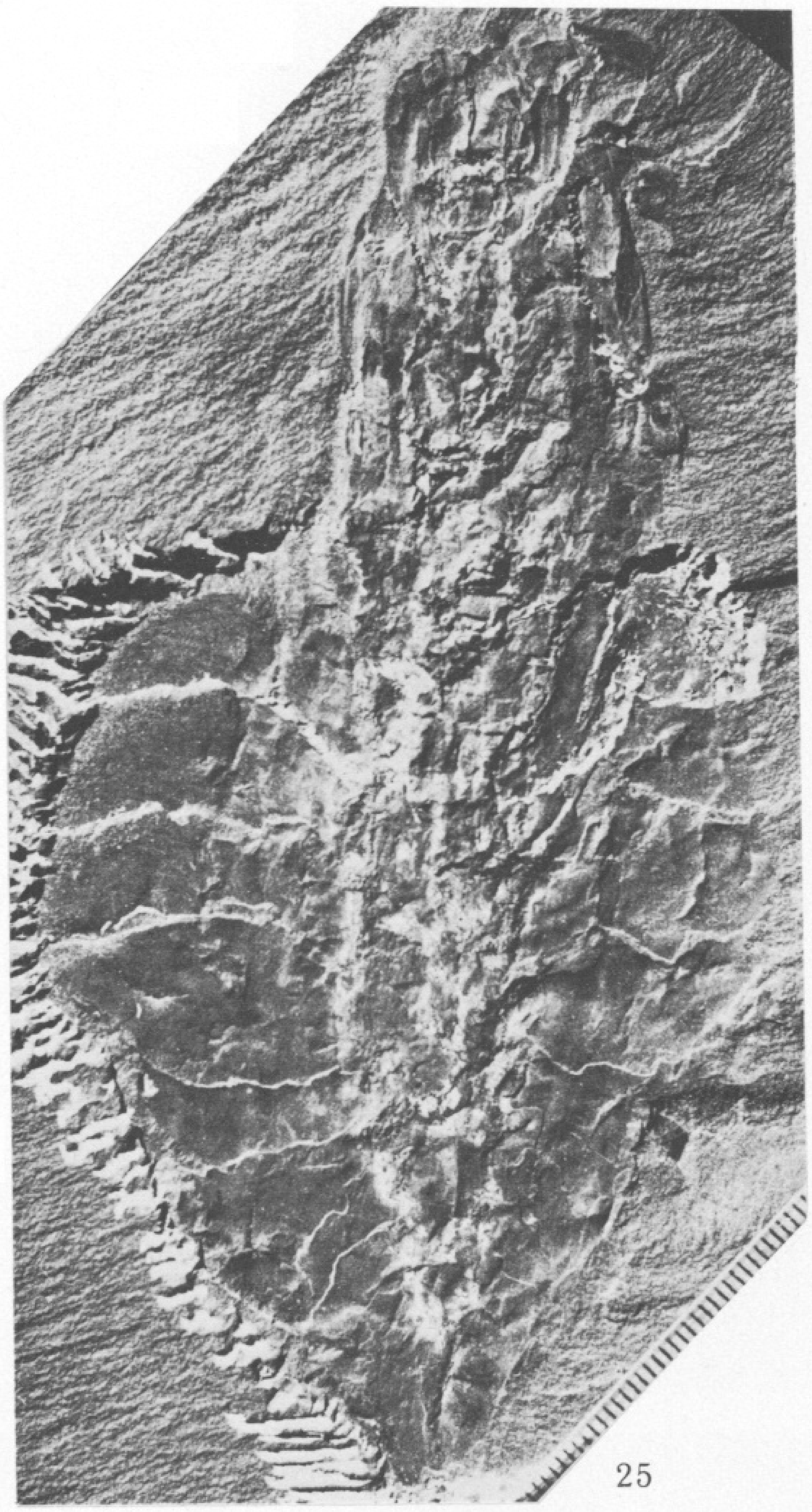
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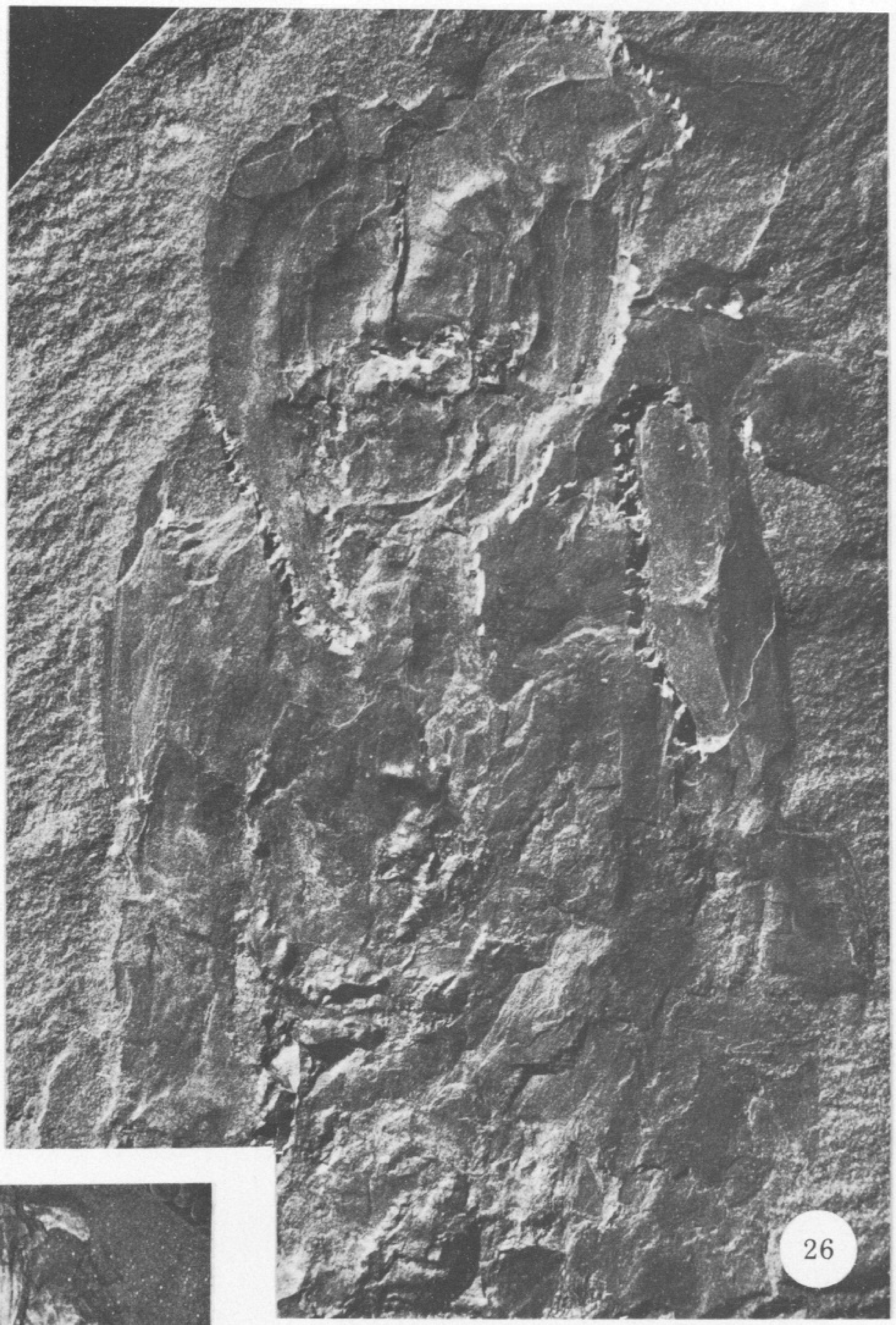
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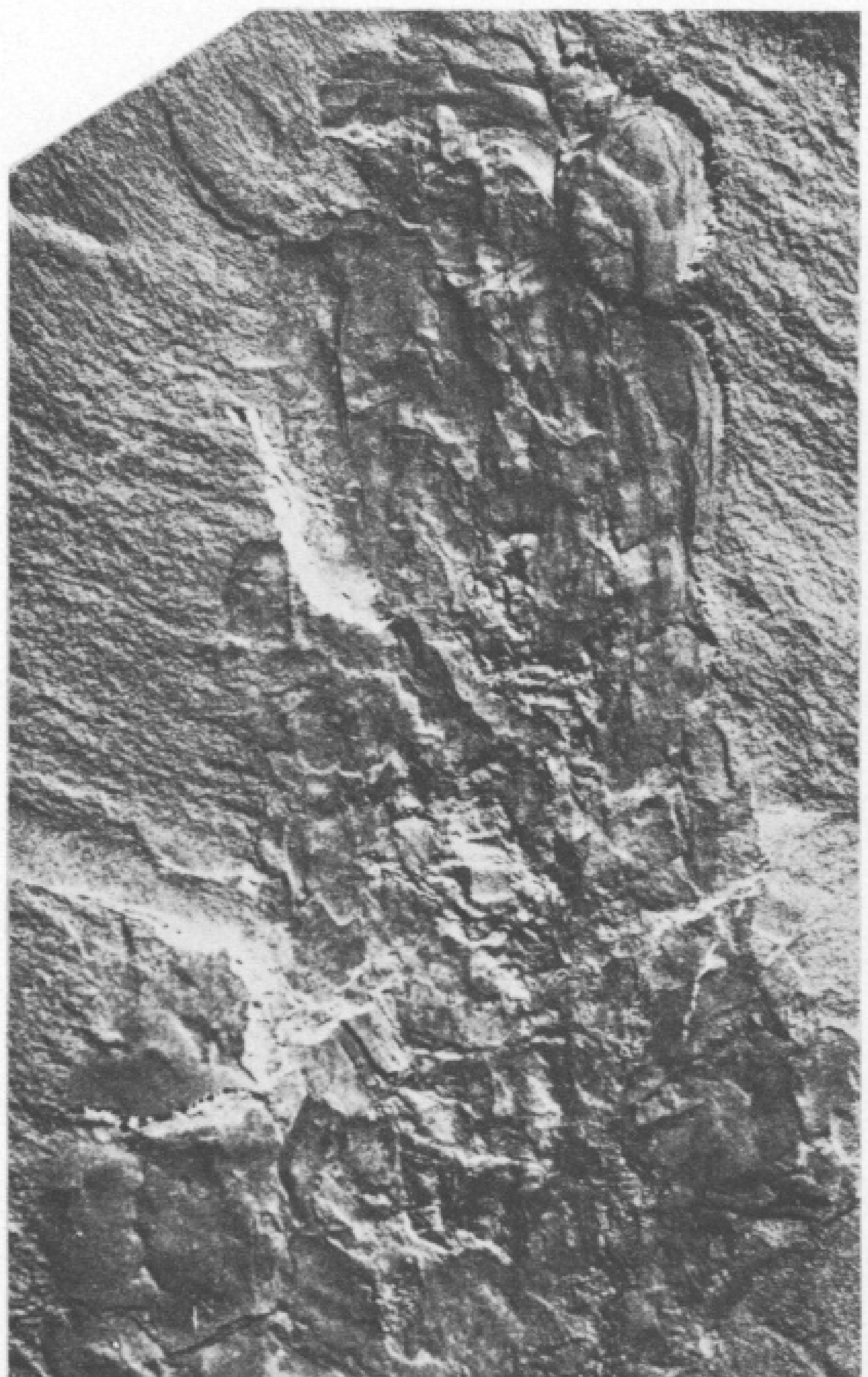
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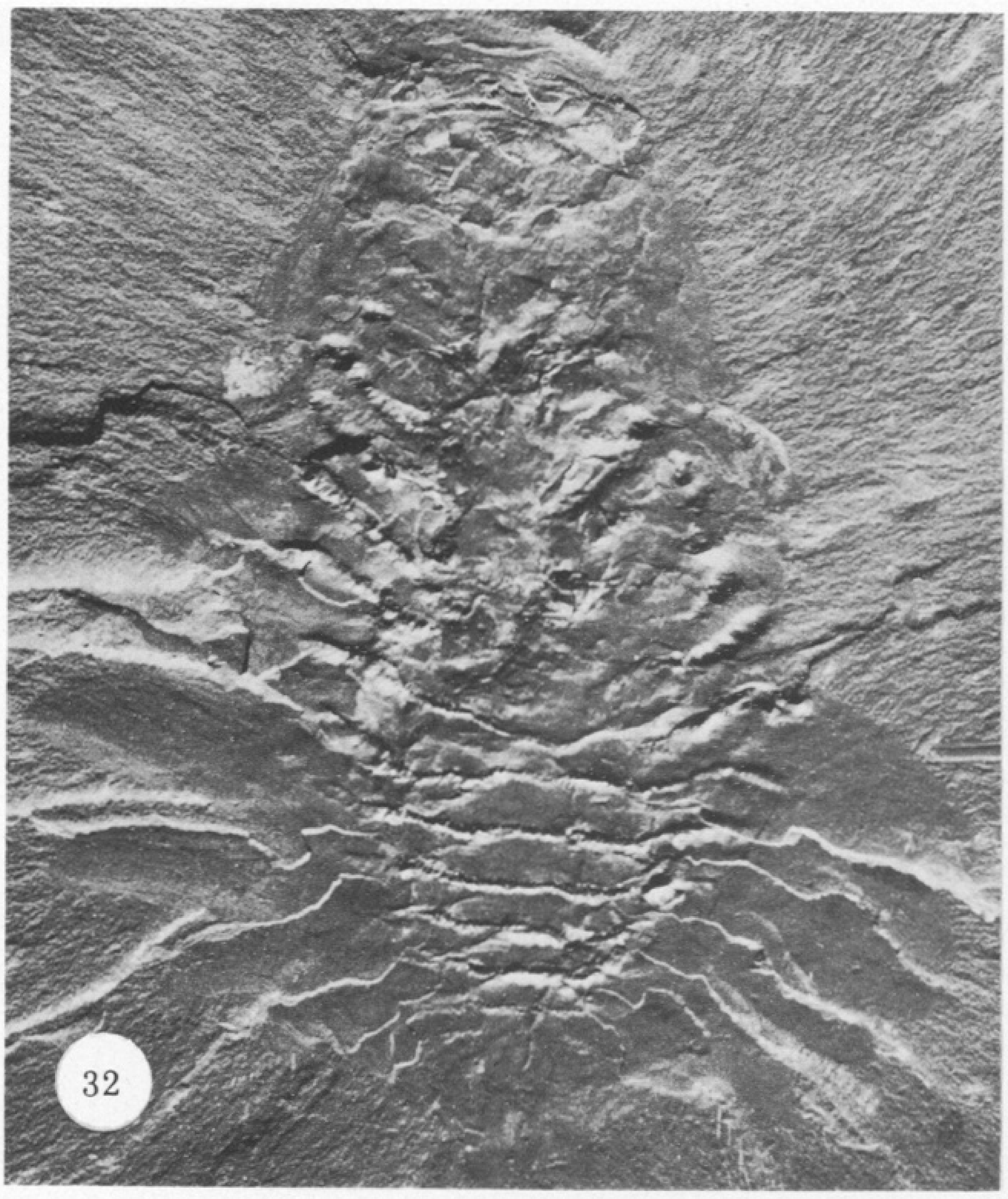
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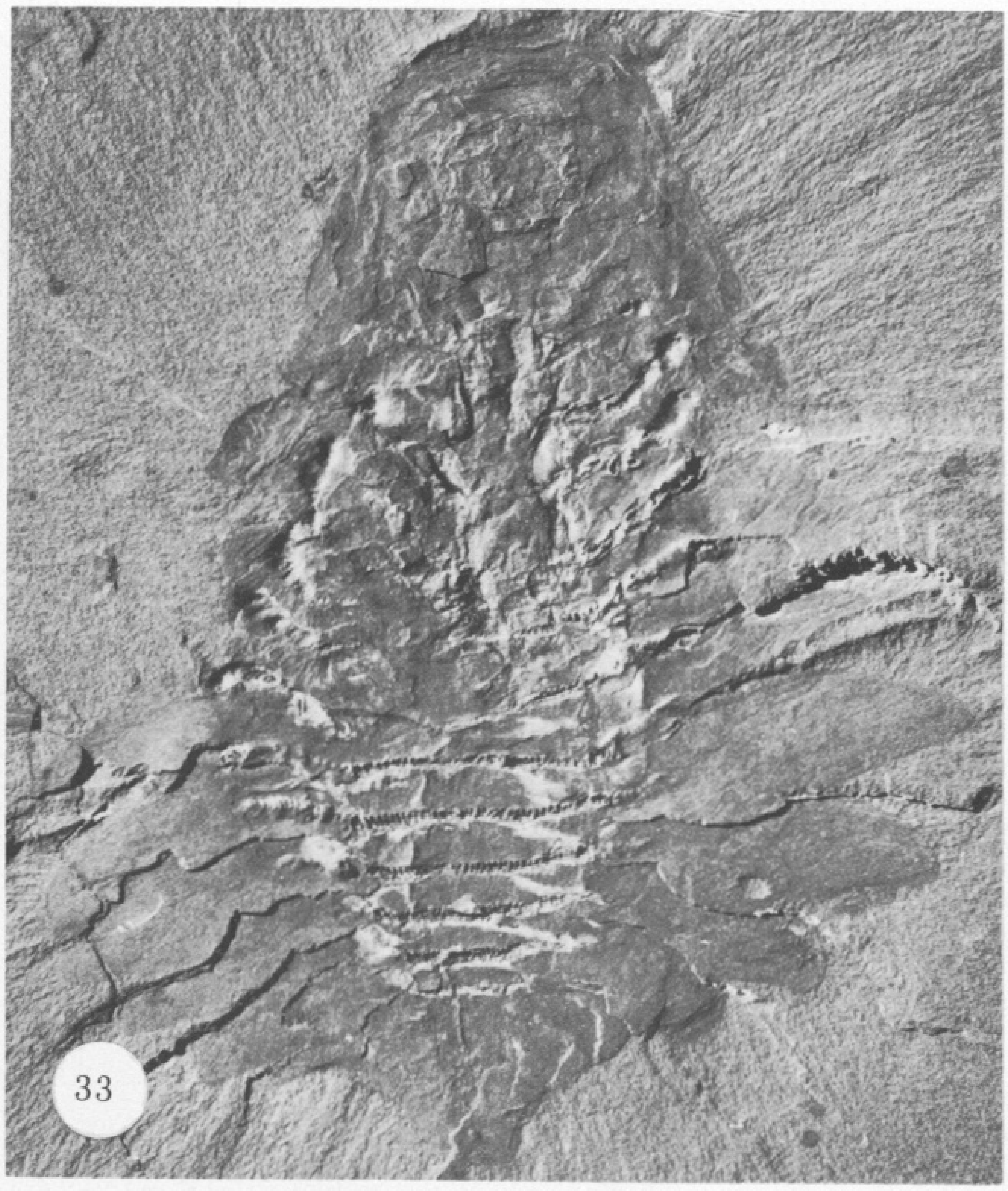
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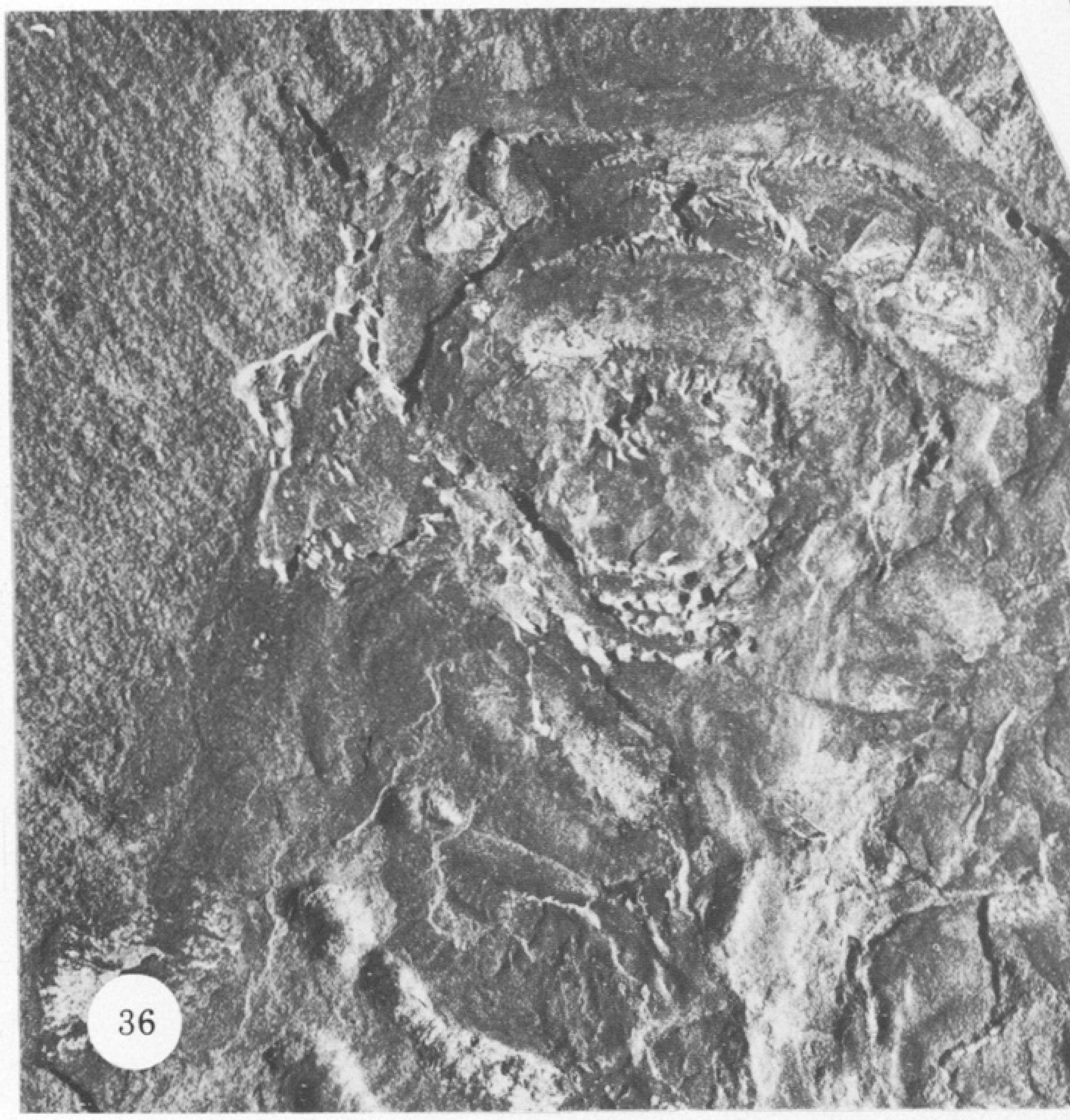
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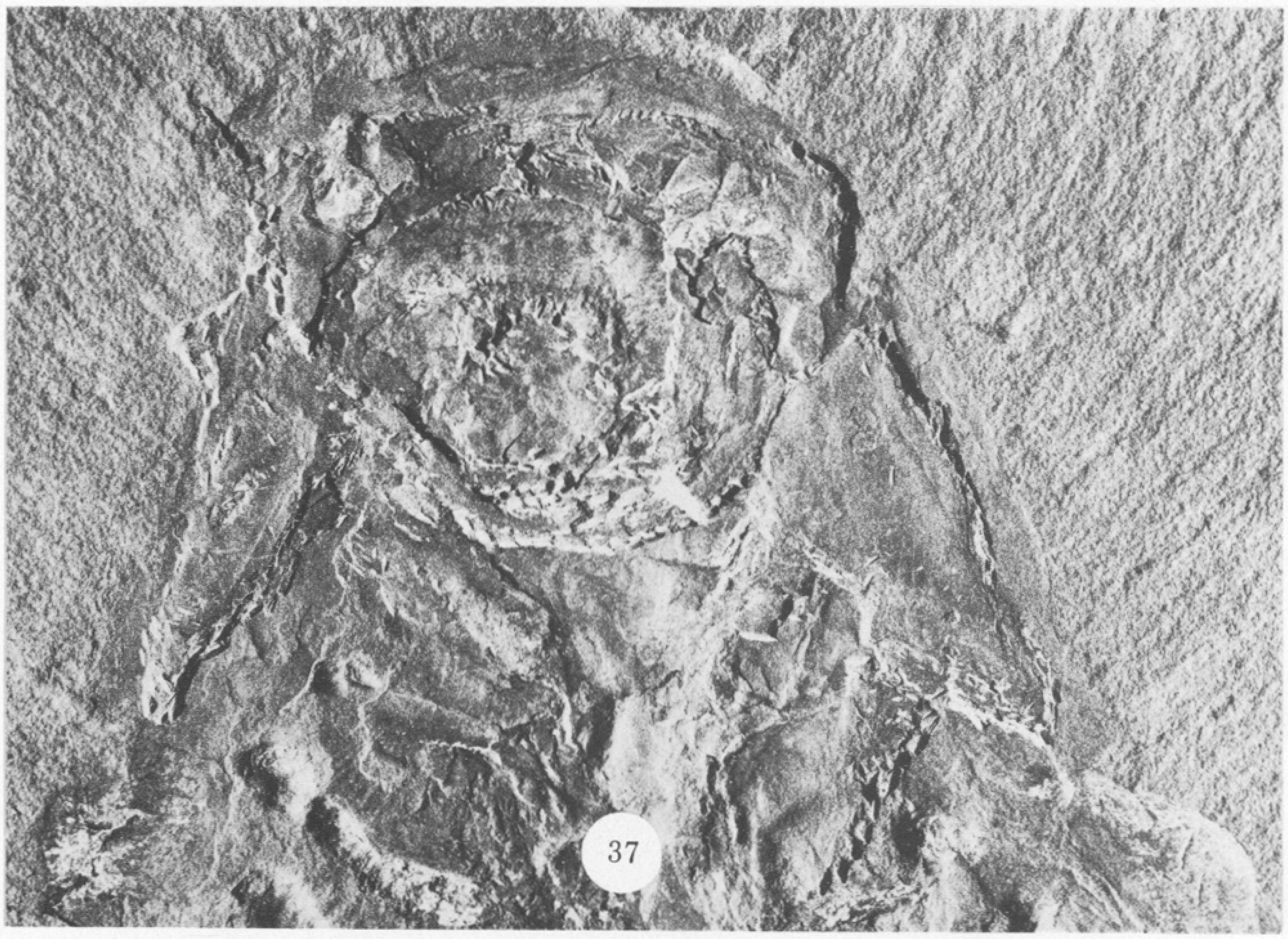
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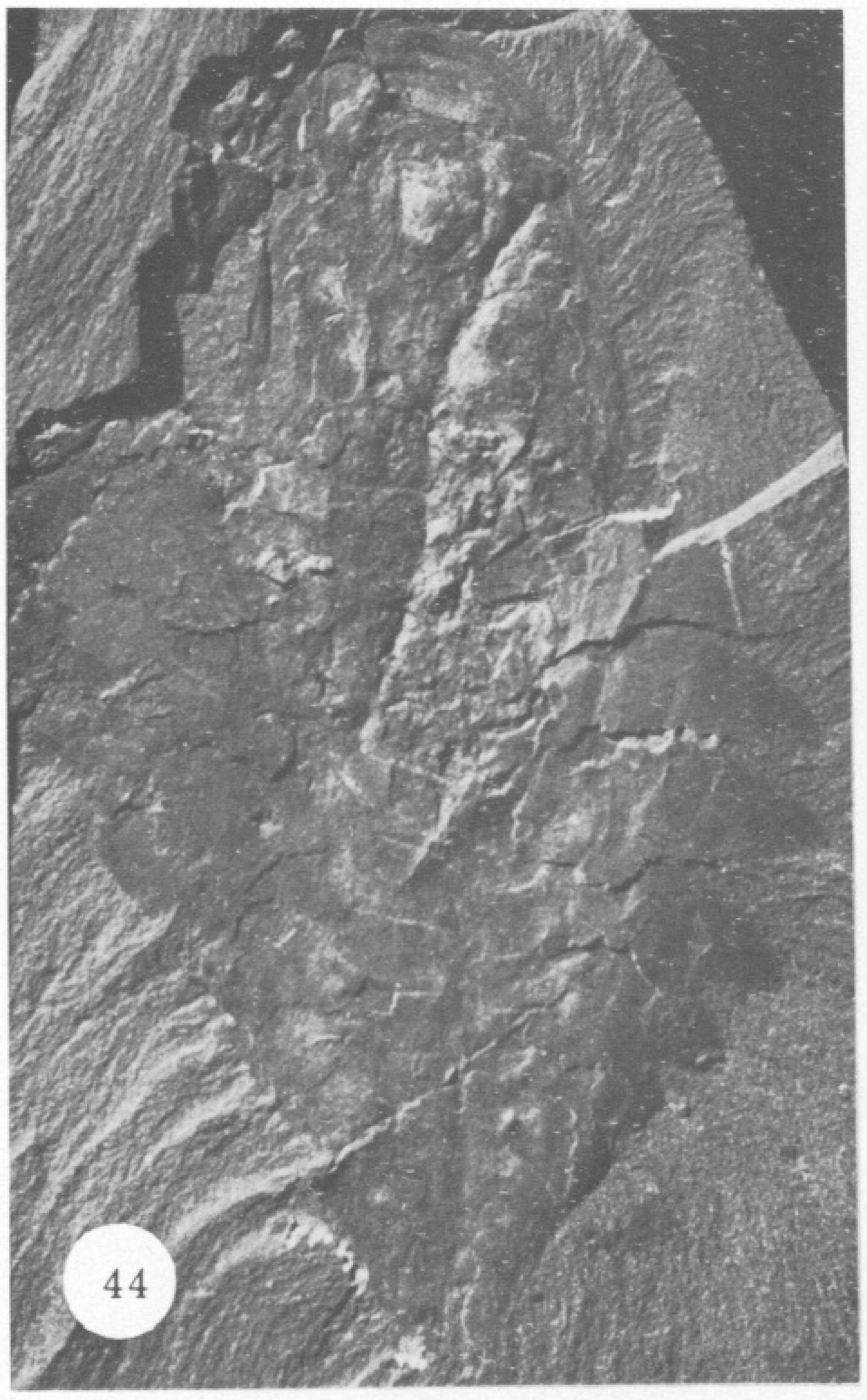
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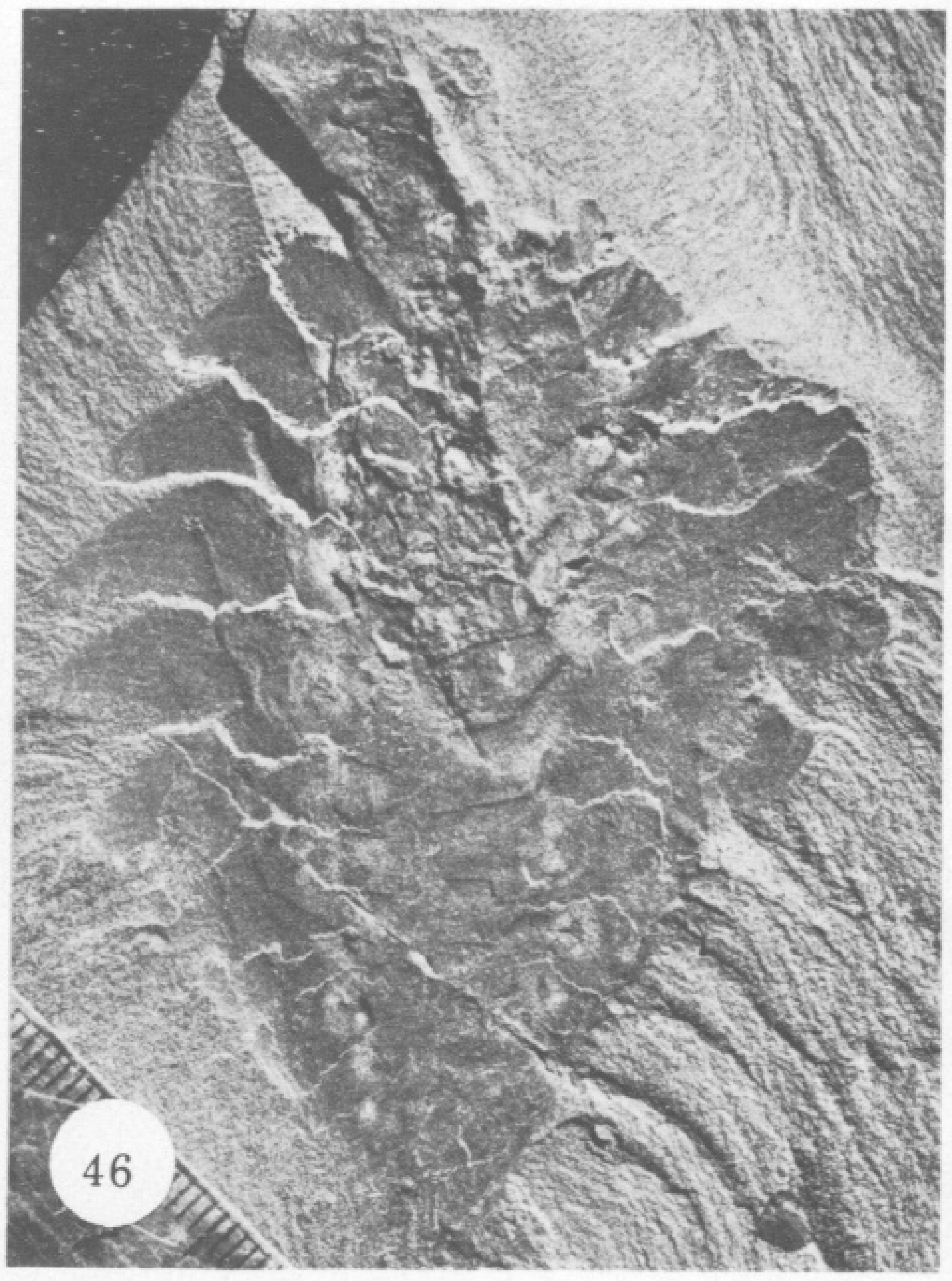
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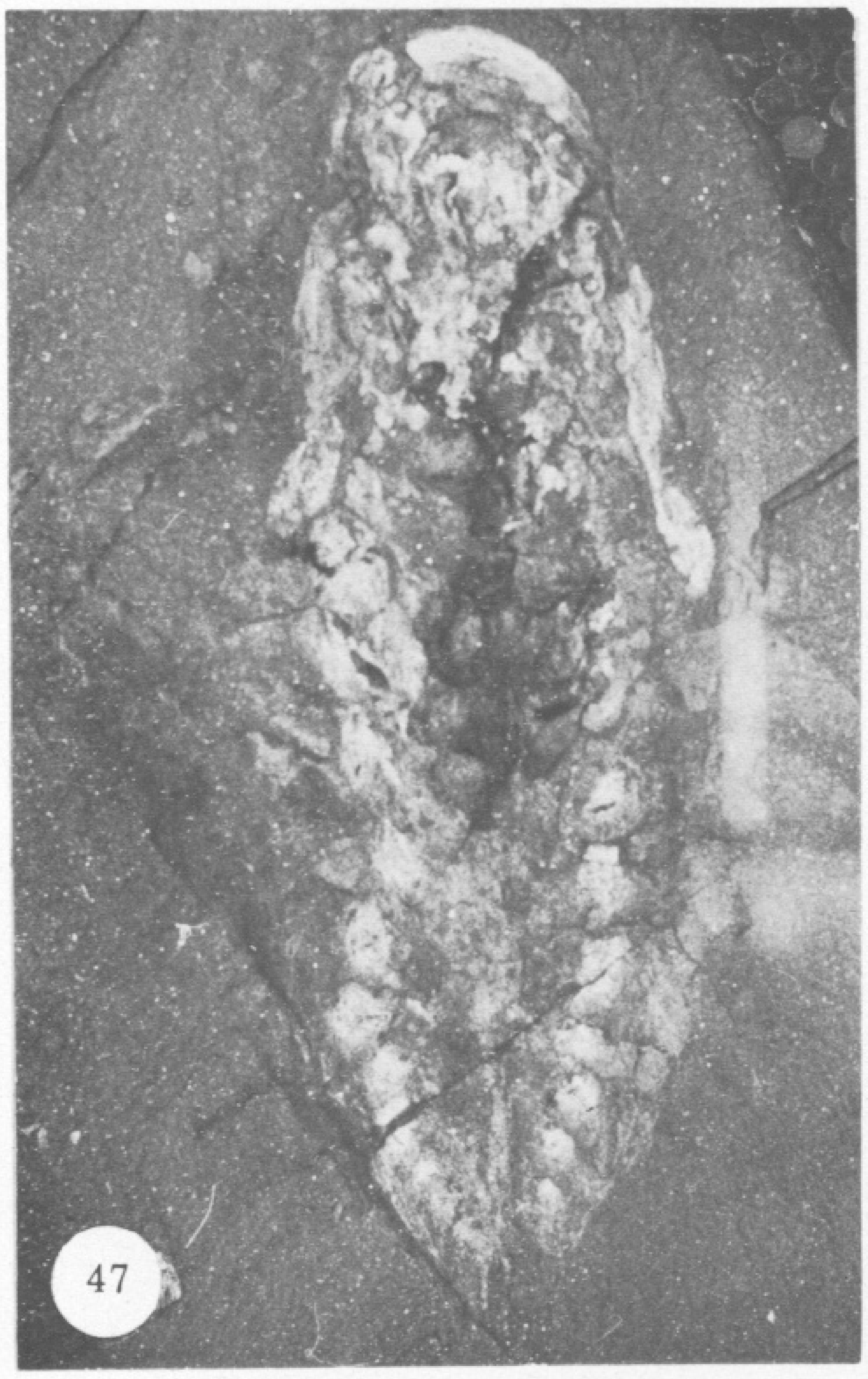
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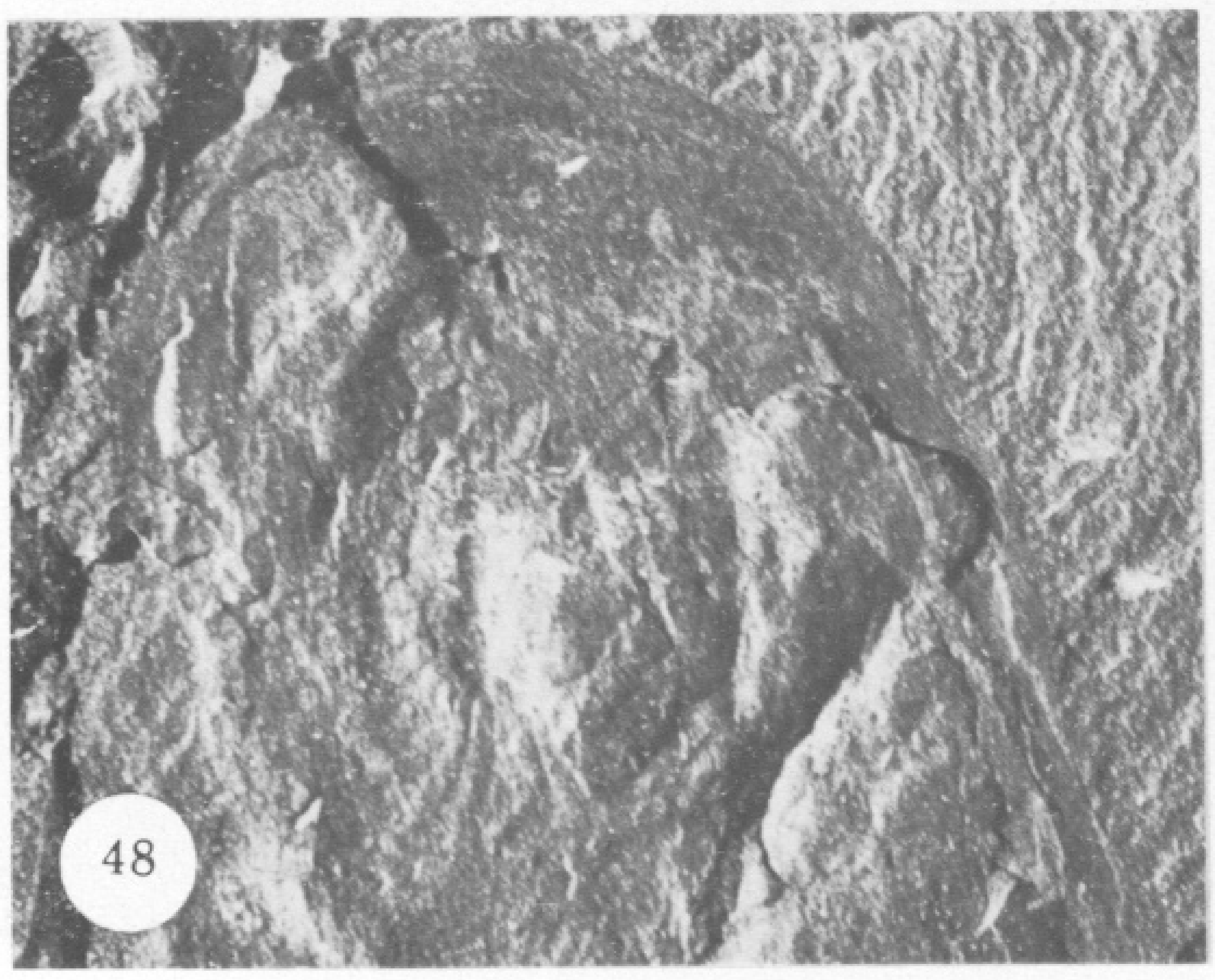
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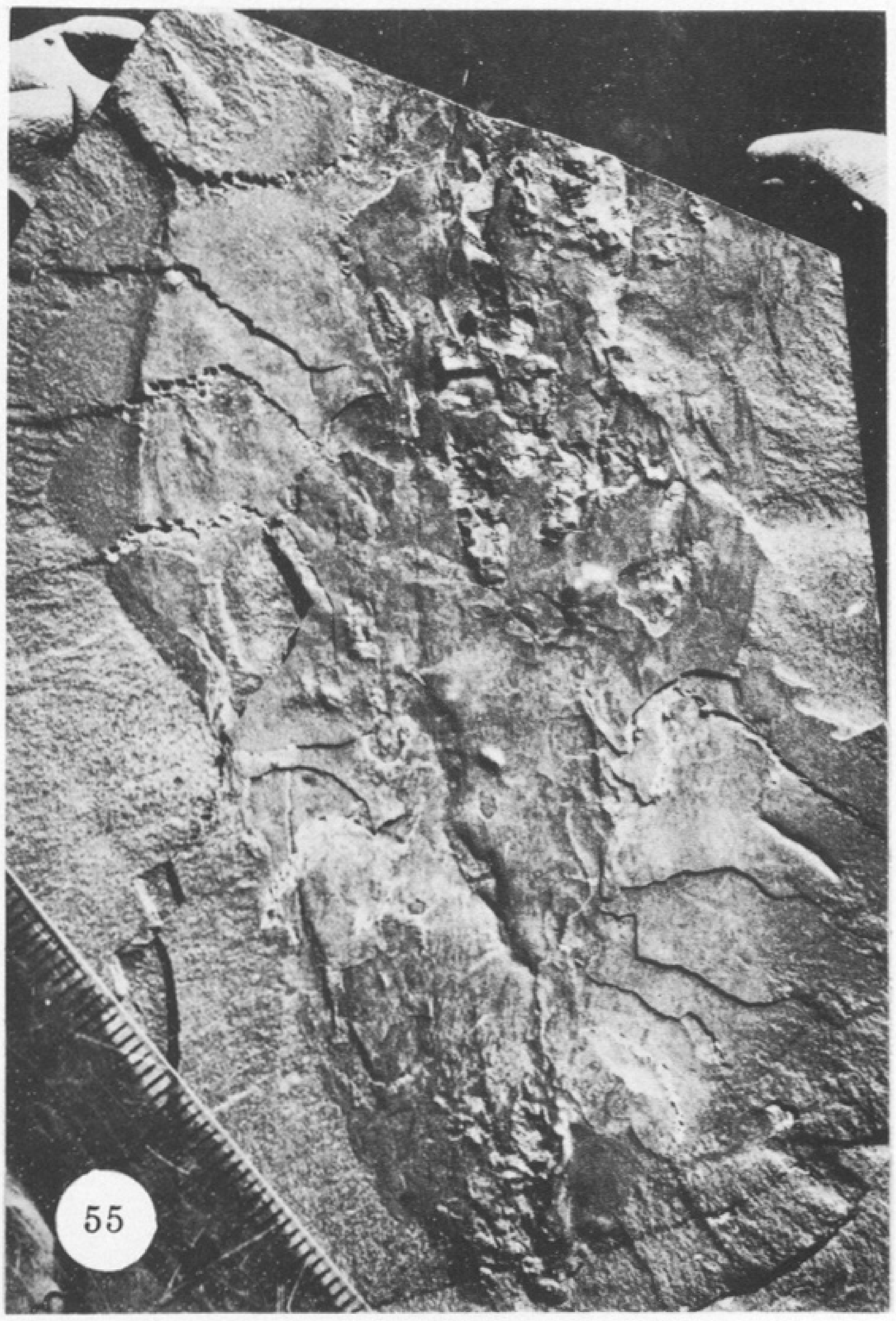
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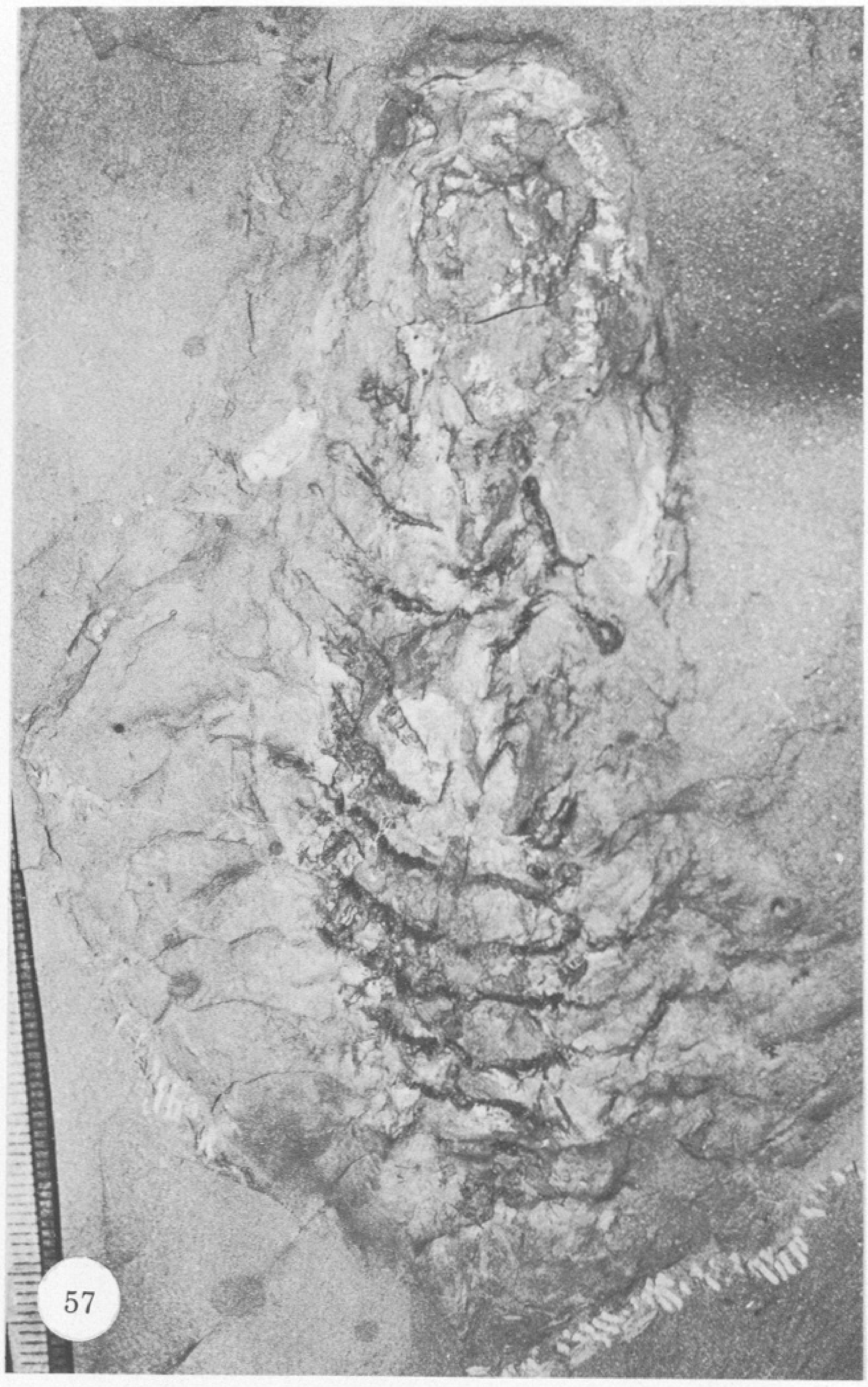
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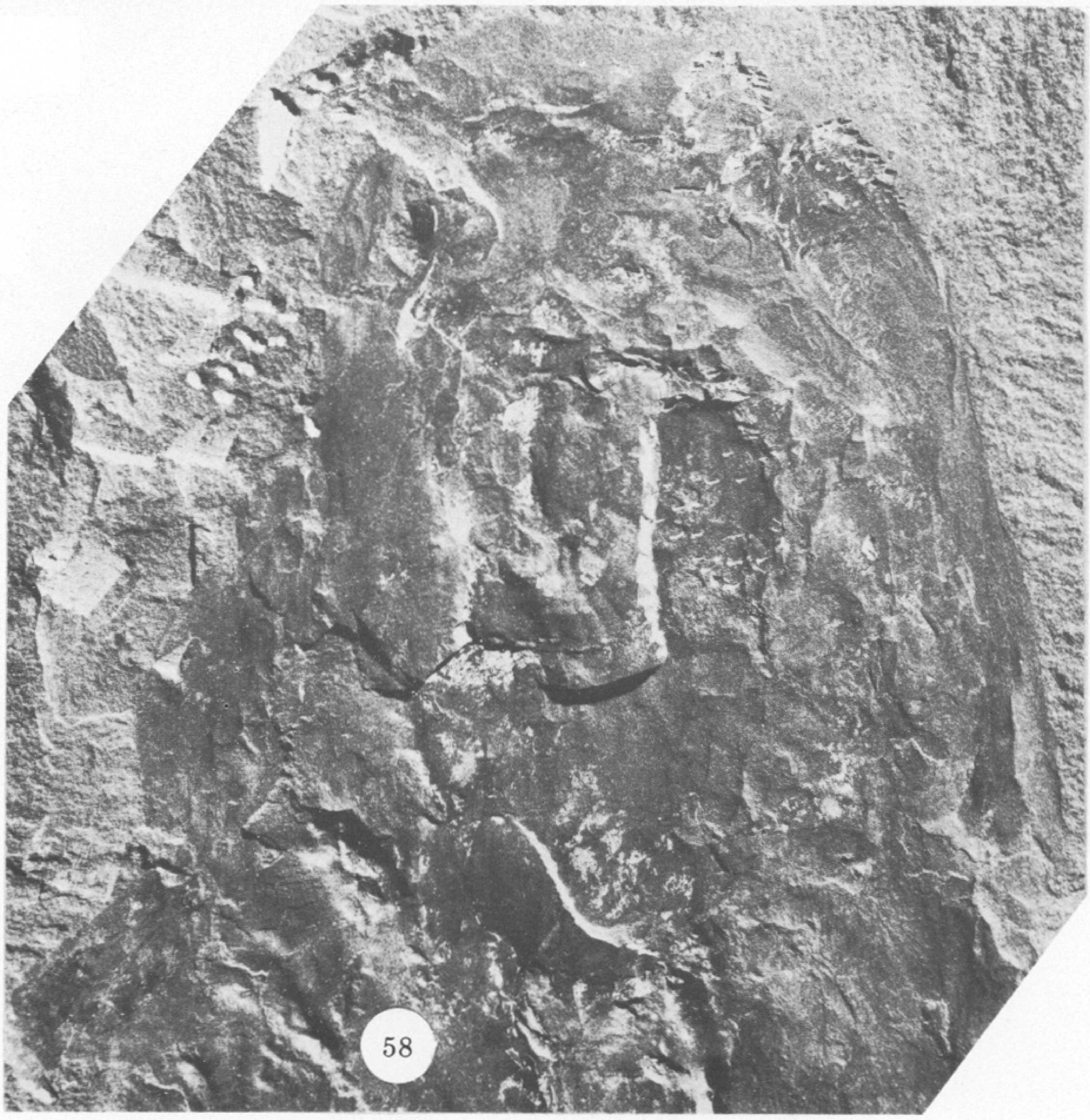
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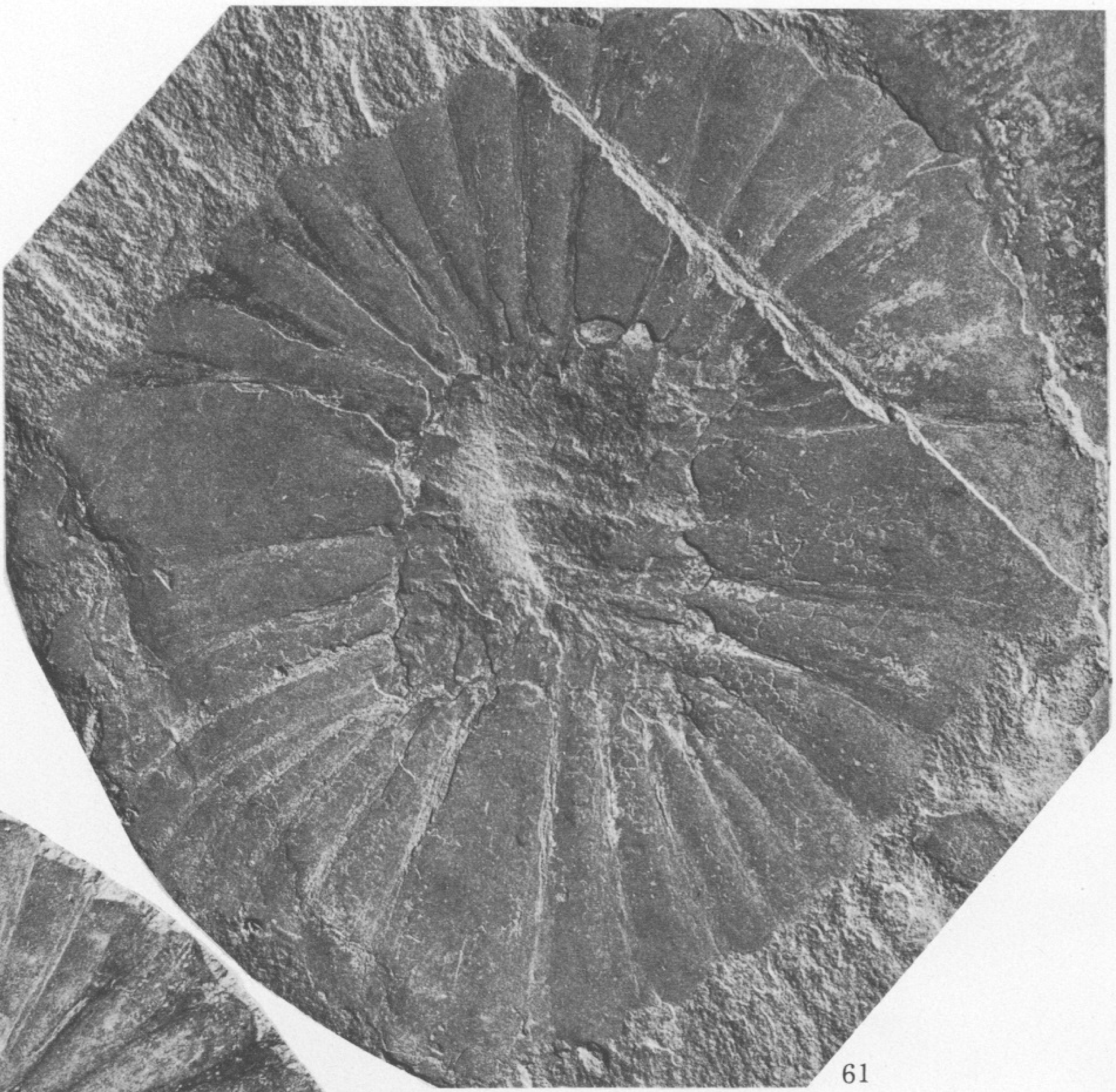

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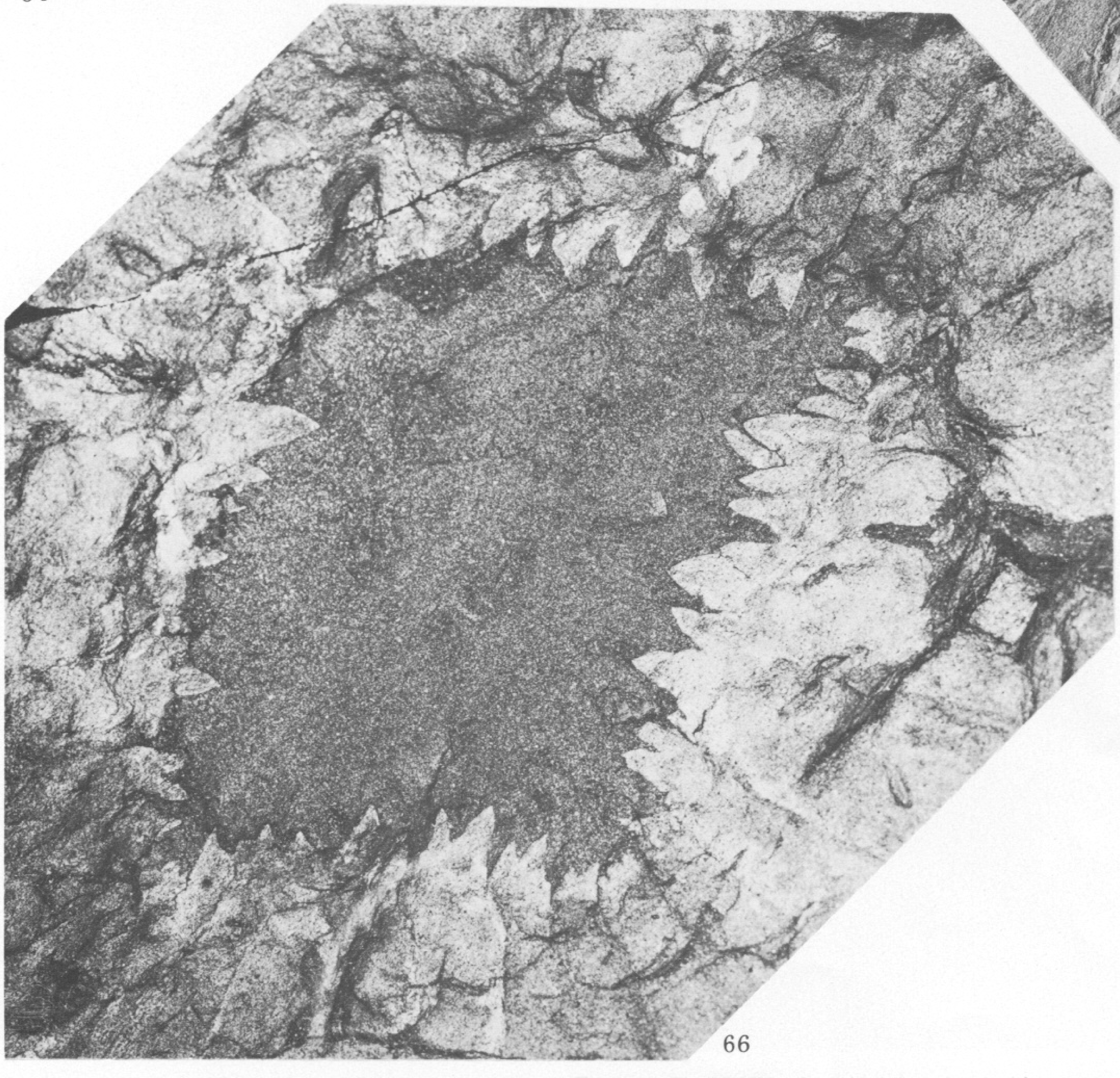

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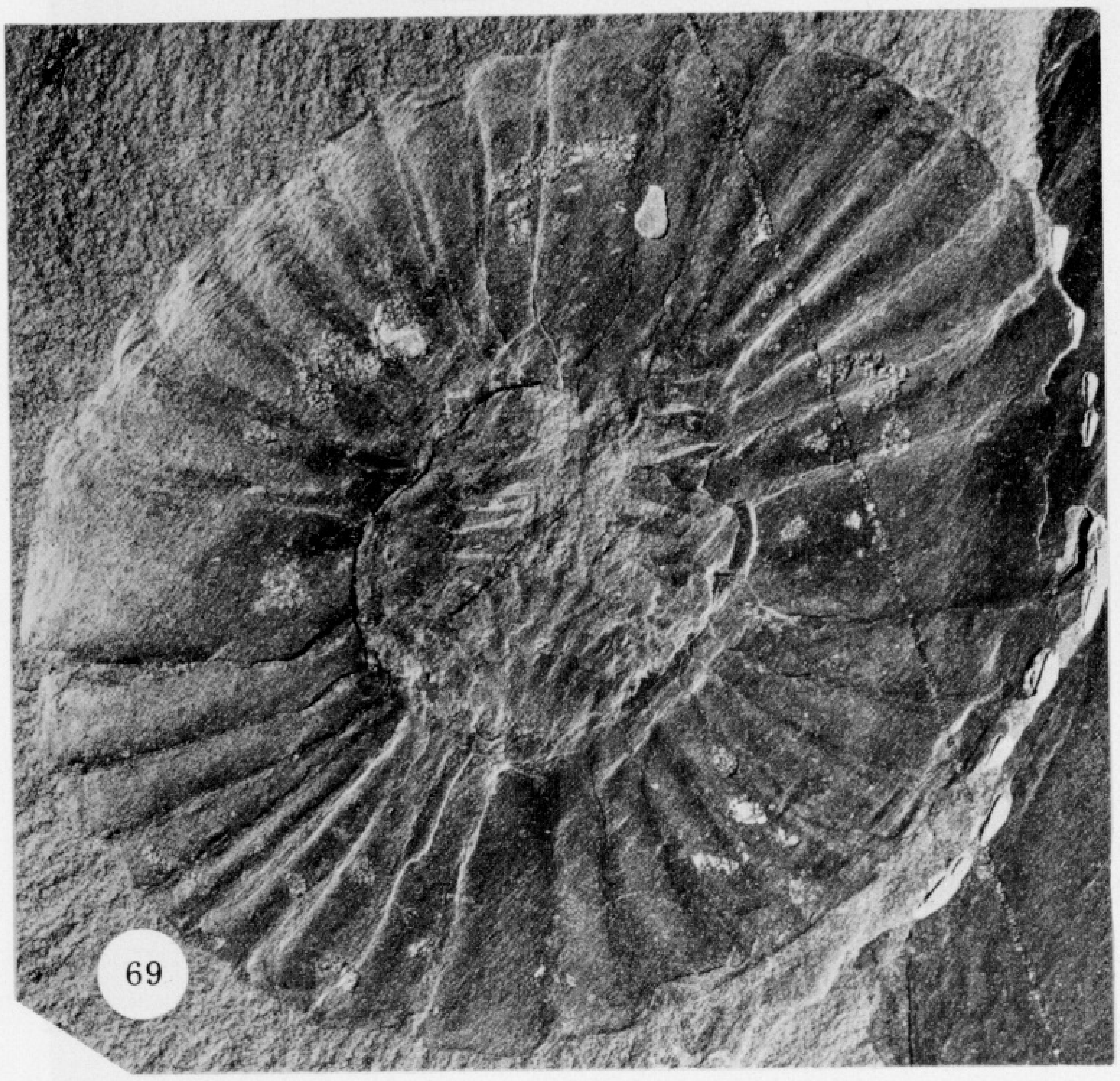
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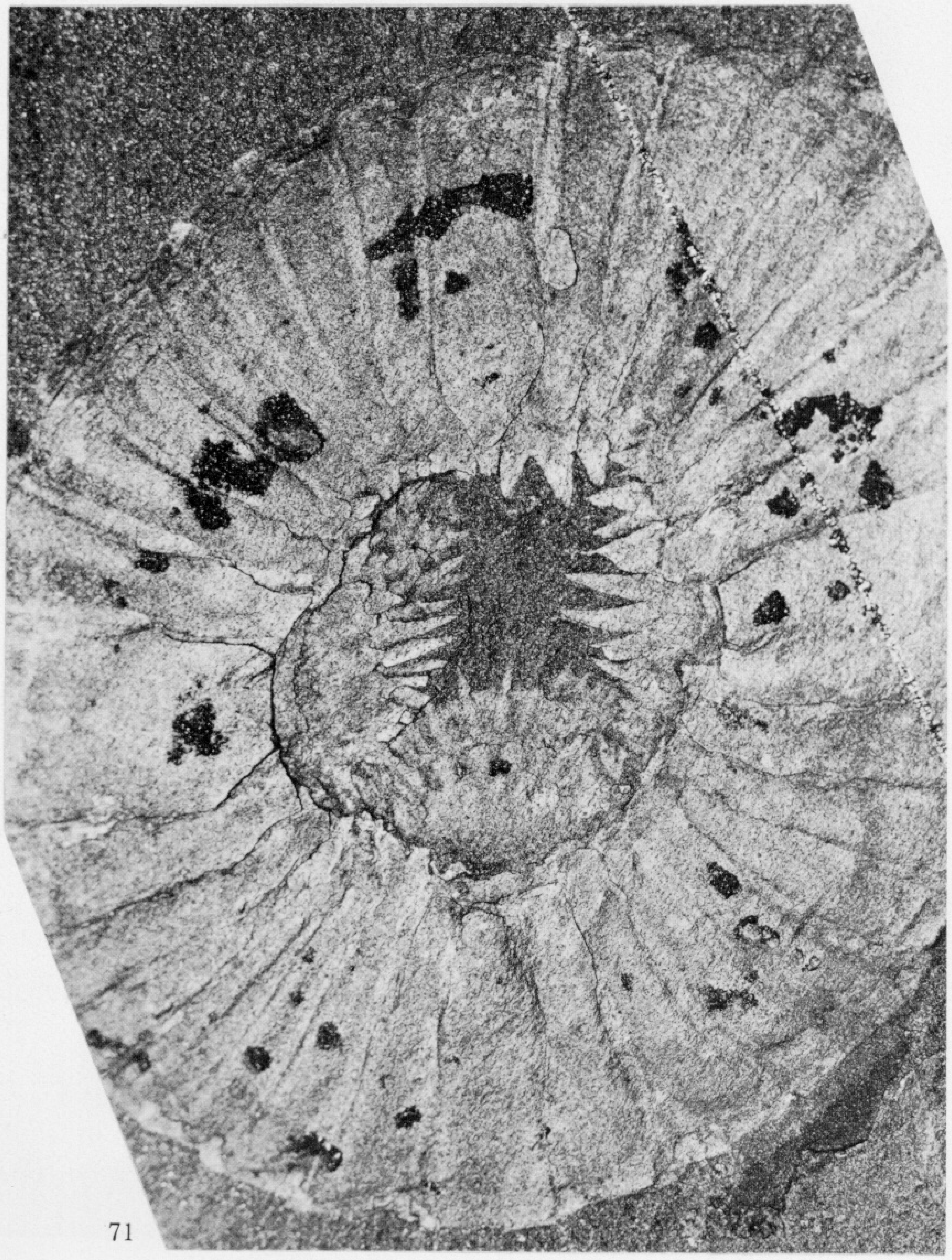
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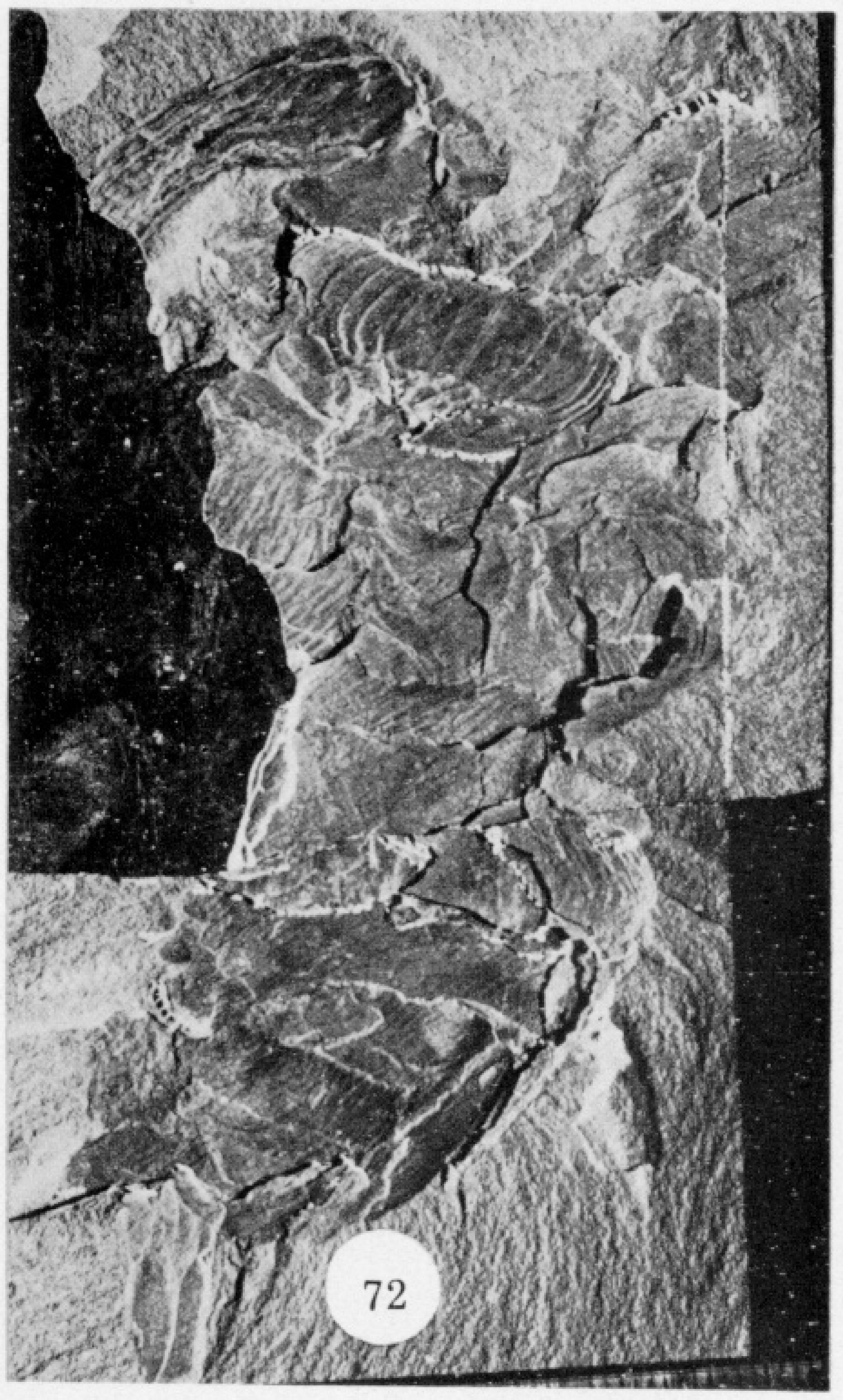
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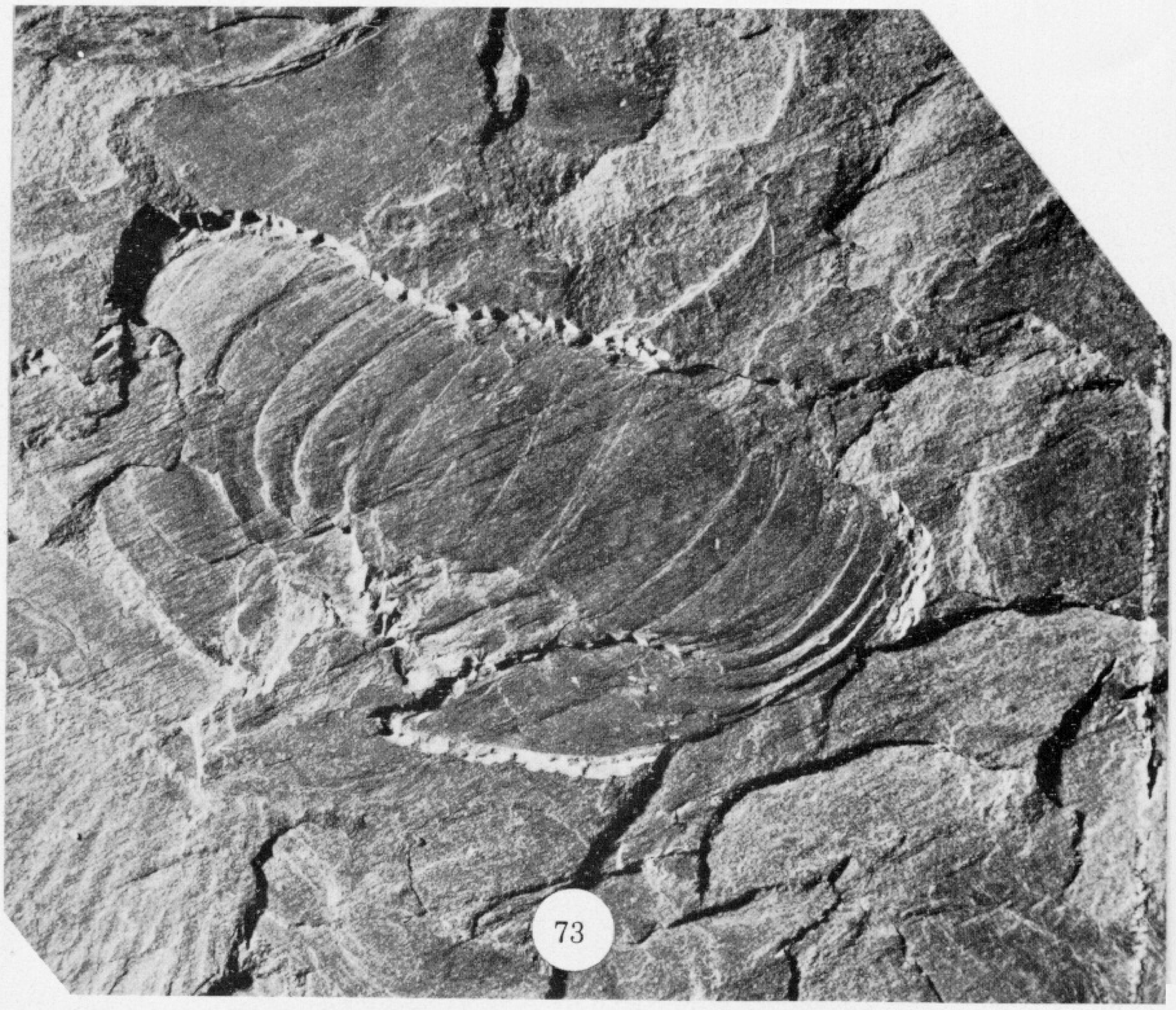
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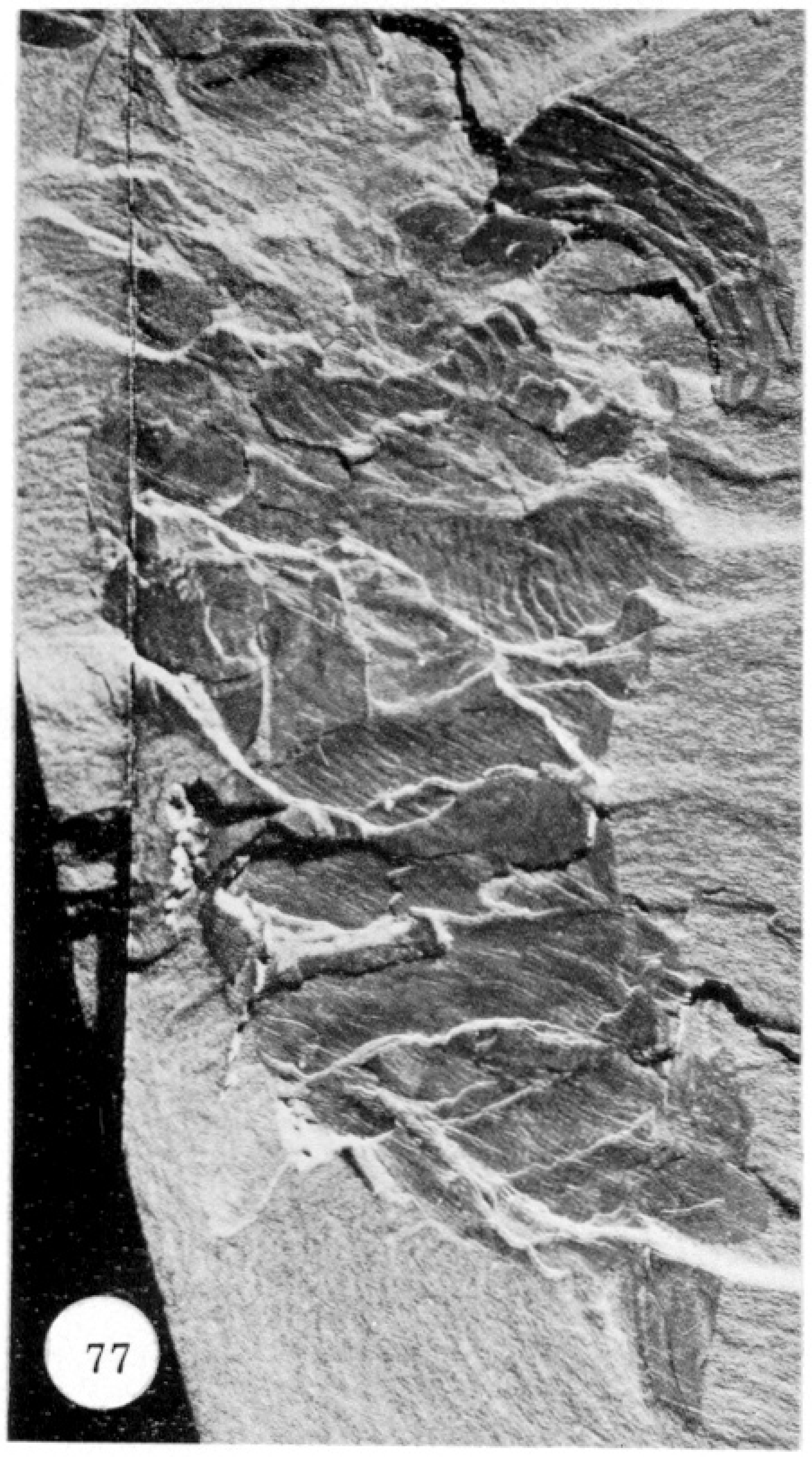

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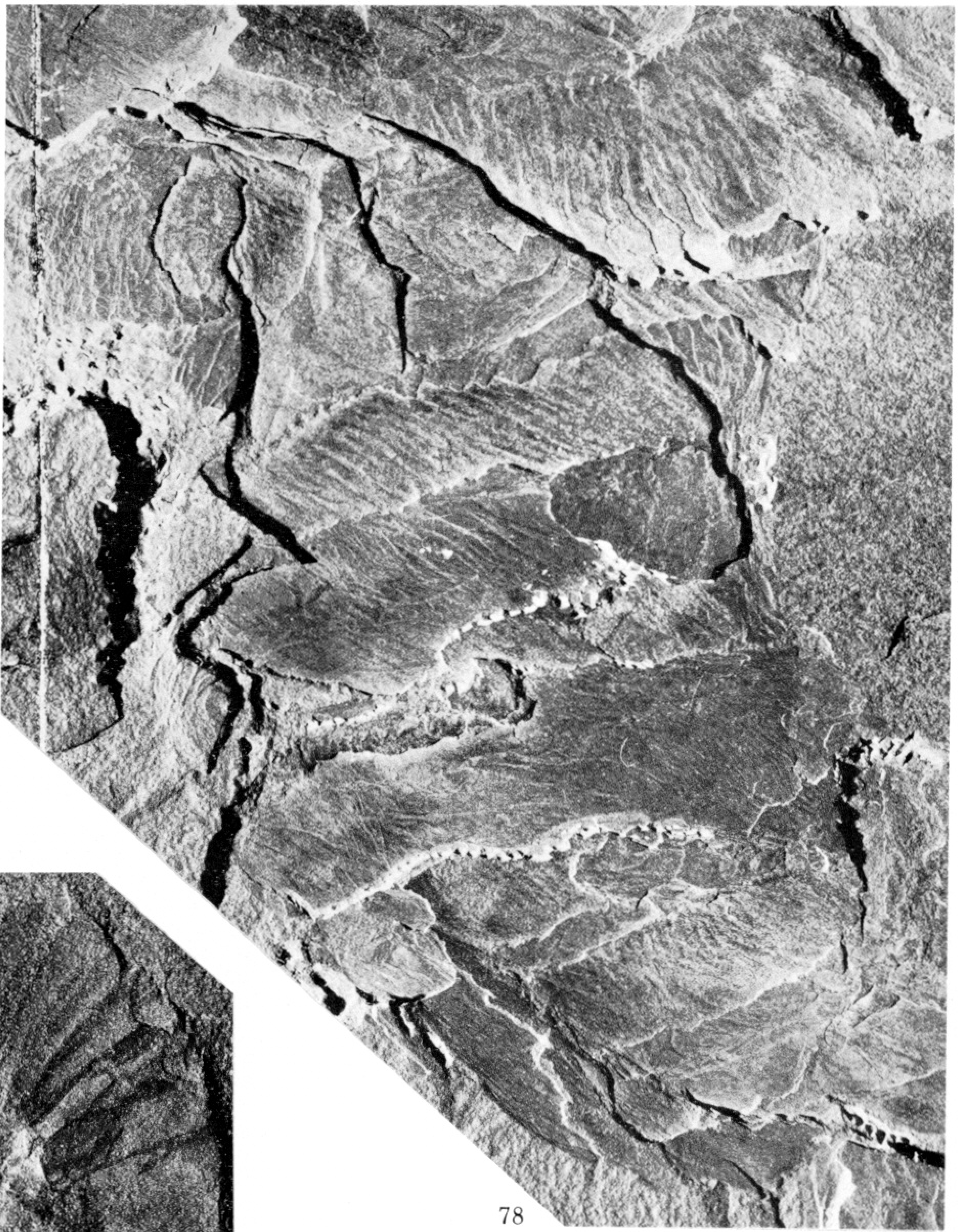

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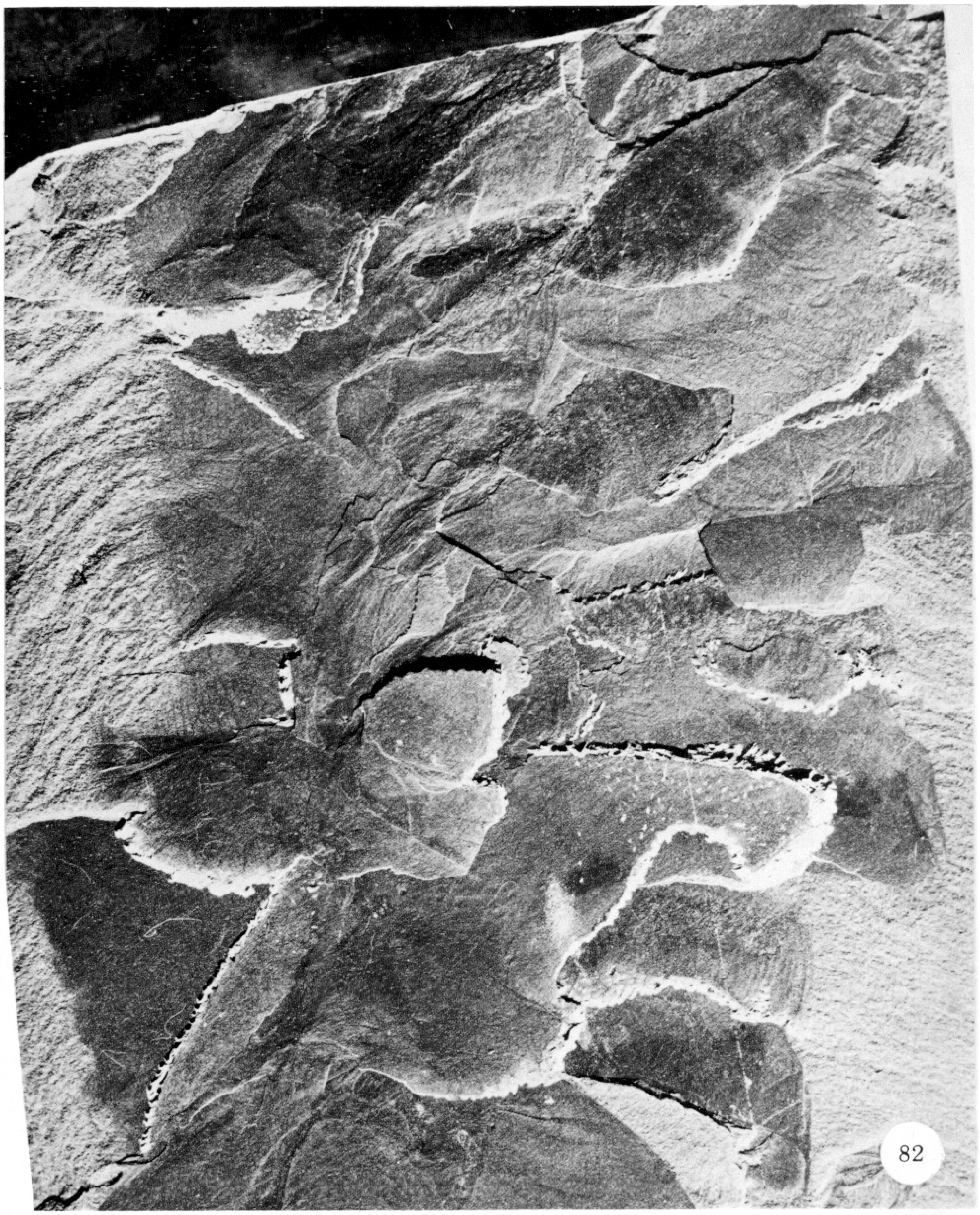

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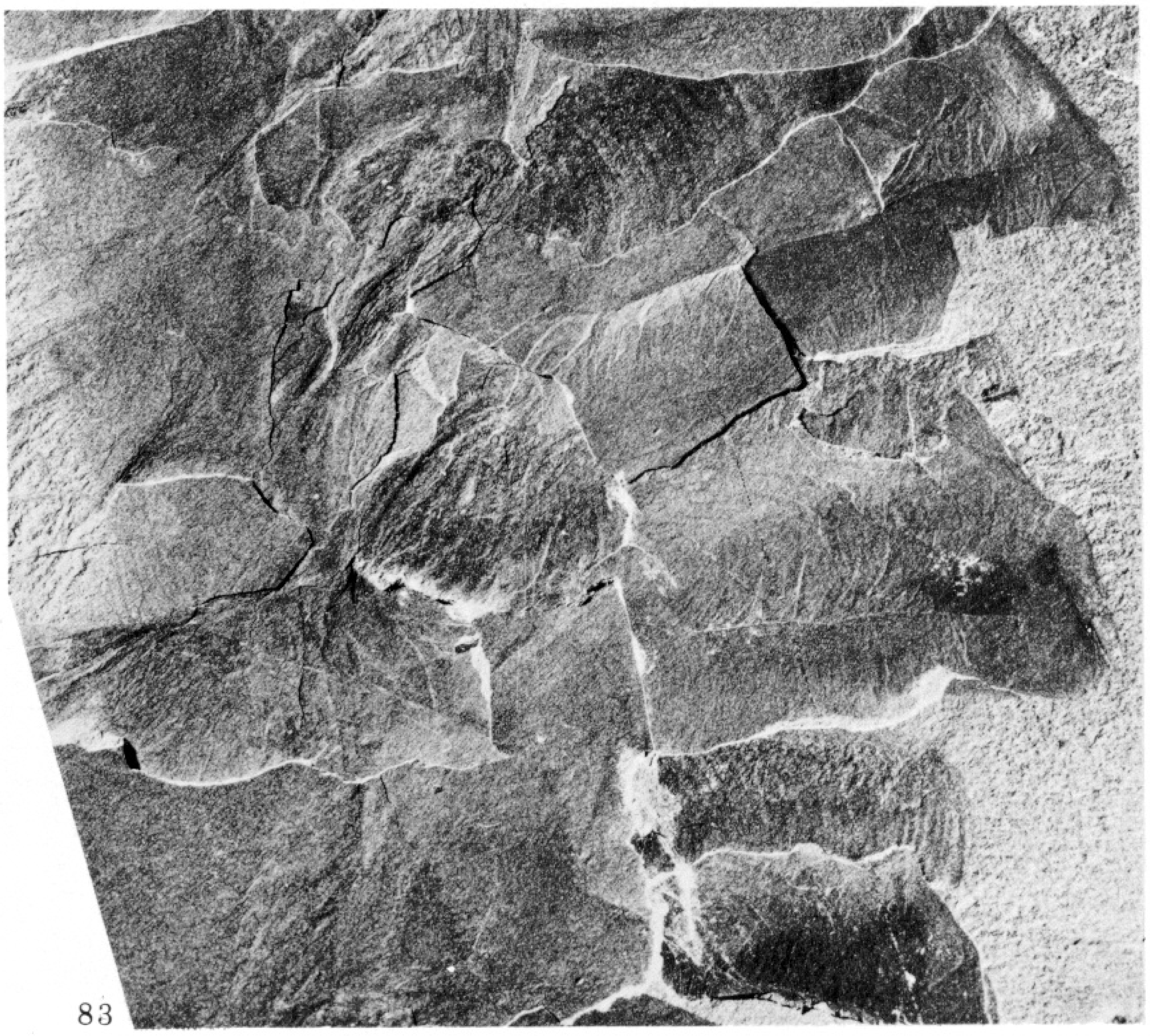

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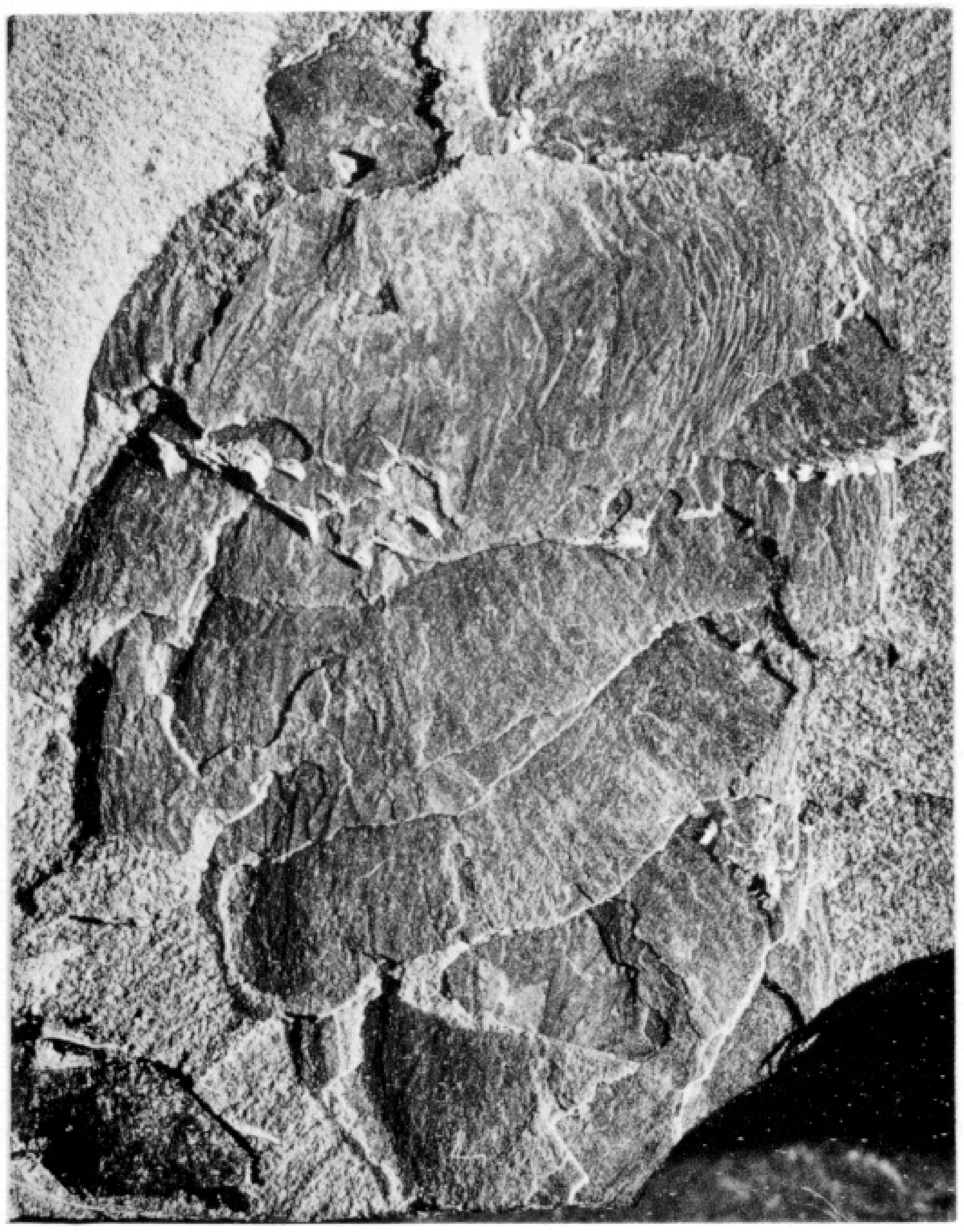

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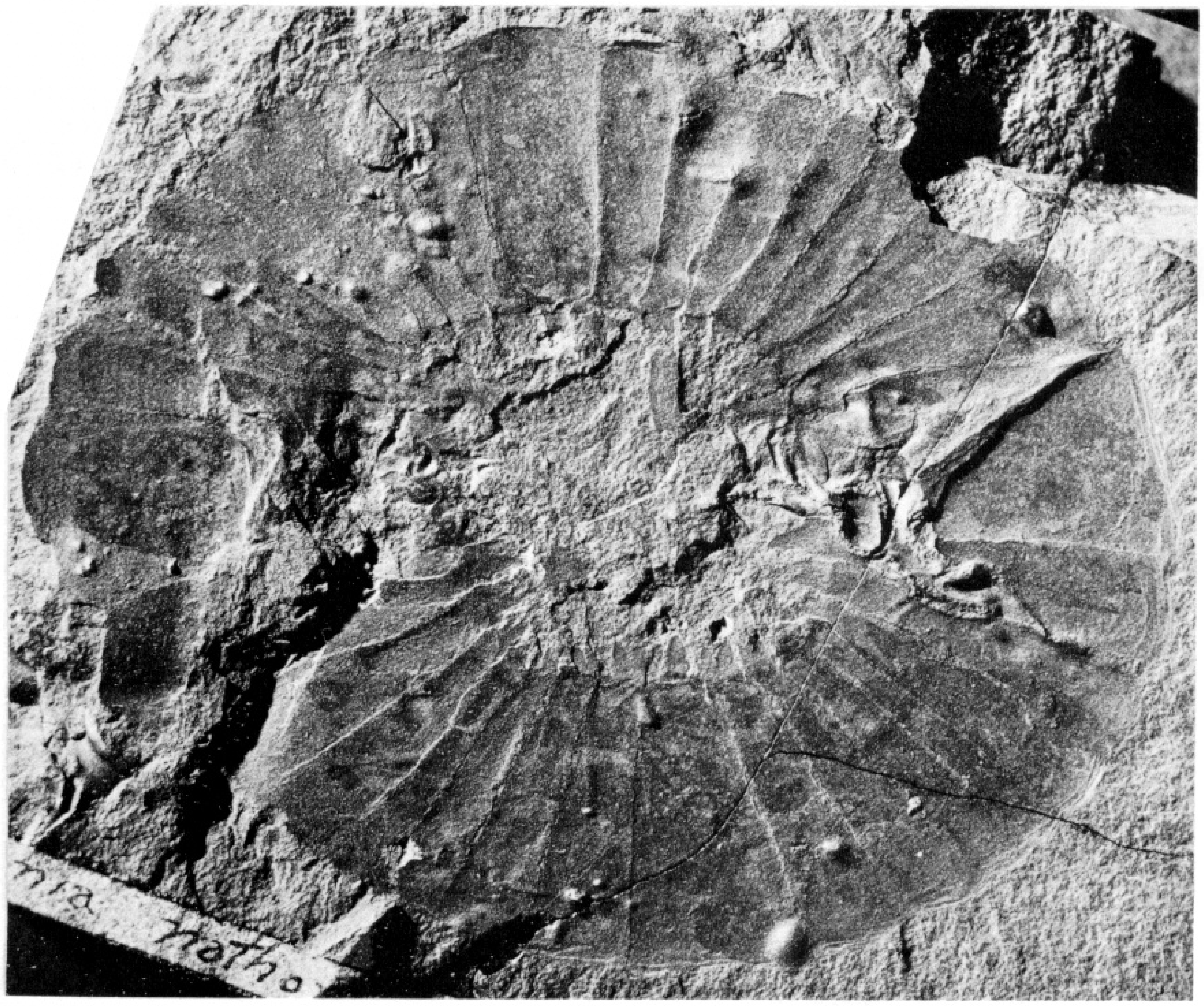

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FIGURES 90–93. For description see opposite.

FIGURES 96–98. For description see opposite.