THE MIDDLE CAMBRIAN TRILOBITE *NARAOIA*, BURGESS SHALE, BRITISH COLUMBIA

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[Plates I–XVI]

CONTENTS

The type species of the genus, *N. compacta*, is described from new preparations and measurements of over 100 specimens from C. D. Walcott's original collection, and 5 from the recent re-investigation. Photographs and explanatory drawings provide the basis for considerations of mode of preservation, and lead to a new reconstruction. The dorsal exoskeleton was divided by a single articulation into two shields, each moderately convex with a raised axial region, the subcircular anterior shield overlapping for a short distance the longer posterior shield; narrow reflexed doublure on both shields. Dorsal surfaces of shields smooth, without transverse furrows, eyes absent. Axial region of anterior shield widest posteriorly, extending forward to three-quarters length of shield, labrum may have been present under anterior portion. Axial region of posterior shield tapered back, reaching close to posterior margin of shield. Alimentary canal may be preserved filled with sediment, and was probably U-shaped anteriorly, broadest beneath anterior portion of axial region, tapering back to tip of posterior shield. Two types of alimentary diverticula preserved as reflective bands on anterior shield; single trunk of lateral diverticula ran transversely at mid-length and ramified beneath lateral region of shield; three pairs of axial diverticula, one per segment, originated behind main trunk of lateral diverticula and ramified in posterior part of axial region. Axial diverticula, one per segment and not ramifying, appear to have been present beneath the axial region of the posterior shield. Paired areas of muscle attachment, preserved as reflective or pyritous areas, are segmentally arranged along the axial region, one pair close together at the anterior extremity. One pair of long, uniramous, multi-jointed antennae was attached beside anterior extremity of axial region, followed by a maximum of 19 pairs of similar biramous appendages, three pairs on the posterior part of the anterior shield, remainder beneath posterior shield. Large triangular coxa strongly spinose on adaxial margin; inner, leg branch of five podomeres and terminal, thorn-like spine; large, spinose endite on proximal podomere. Outer branch arose from abaxial, dorsal margin of coxa, and consisted of slim, tapering shaft with terminal lobe, dorsal margin of shaft bore many long, thin, upward and backwardly directed lamellae. Specimens range in length from 9 to 40 mm, some 40 % of the sample being cast dorsal exoskeletons, the remainder whole animals. About one-fifth of the sample bore a posterolateral spine on the anterior shield, rather than having a rounded angle. This difference was recently used to erect two new species, *Naraoia halia* and *N. pammon*; here it is taken as the sole evidence of dimorphism in the single species *N. compacta*.

A second species, *N. spinifer*, is recognized from two poorly-preserved specimens, characterized by seven pairs of lateral spines and a median posterior spine on the margins of the posterior shield; the axial region is poorly defined and appendages virtually unknown. *N. compacta* is considered to have been a benthonic predator and scavenger, walking, digging and raking in search of food much as did the trilobite *Olenoides serratus*, and to have had poor swimming powers. The lamellate outer branch of the appendage is regarded as a gill branch, aerated by currents produced when walking and swimming or drifting. There is no evidence of an abdomen or telson, so that *N. compacta* is a trilobite-like animal lacking the articulated thorax; it is regarded as representing a separate order of class Trilobita.

1. INTRODUCTION

The unique preservation of the Burgess Shale fossils reveals what arthropods were like at an early stage in their history, not only trilobites but some thirty-six genera of non-trilobites, the majority showing appendages and some soft parts. Despite their great importance, little more has been learned about the non-trilobites since Walcott (1912) first made them known, his early work supplemented only by a posthumously published (1931) paper on a few genera. This remains true despite the study of Walcott's collection by Simonetta (*in* Simonetta & Cave 1975, and references) because the photographs of specimens are of indifferent quality and because it is not explained how the evidence for the novel reconstructions is derived. In the course of a new investigation of the locality and the fossils (Whittington 1971 *a*) it became evident that although the arthropods were flattened in the shale, the process of preservation had resulted in thin layers of rock separating exoskeleton from appendage, and intervening between branches of appendages. This meant that a small mechanical chisel may be used to expose hitherto hidden appendages and to follow them beneath the exoskeleton. The wealth of new information so revealed has radically changed what were thought to be the characters of a particular species (Briggs 1976, 1977; Hughes 1975; Whittington 1971 *b*, 1974, 1975 *a*, *b*), and further work by these authors and Dr D. L. Bruton is in preparation. The present account of *Naraoia compacta* is another example of how such new information has been obtained and what it implies for affinities and mode of life. Walcott (1912) gave a photograph of the original of figures 5–8, plate I, which showed the two shields and what he interpreted as a telson. Hence the view has persisted that *Naraoia* displayed merostome characters. Neither this specimen nor any other gives evidence for the supposed telson. In 1931 Walcott figured additional specimens showing only the tips of the appendages projecting beyond the dorsal exoskeleton. Nevertheless he provided a restoration (1931, p. 14, fig. 1) in ventral view, showing the entire series of appendages, which seems to have been based to a great extent on limbs exposed in specimens of the other Burgess Shale genera *Burgessia* and *Marrella*. On this fragile foundation rested the view that the limbs of *Naraoia* were trilobite-like. A typical series of new preparations is shown in figures 31–34, plate VI, accompanied by drawings, figures 35–37, explaining how I interpret the specimen. It was both surprising and exciting to excavate for the first time (figure 37) the long point of the proximal endite of the leg branch and the large spinose coxa. These and other preparations demonstrate that these unexpected features are present consistently and in a series extending the length of the body, and have exposed the outer branch of the appendage for the first time. The shaft is not annulated, the lamellae are longer than Walcott thought, and the shaft bears a terminal, setiferous lobe. The outer branch is present on all appendages behind the antennae, the three pairs on the anterior shield being biramous and not uniramous as Walcott portrayed them. Thus the new reconstruction (figures 96, 97) shows a very different animal from Walcott's and other restorations, not merostome-like but far more trilobite-like than had been thought. Indeed I conclude *Naraoia* was a trilobite that lacked a thorax, and place it in a separate order of that class. In the following text discussion and conclusions (§4 (*a*, *i*), §5 (*c*), §6) are separated from the descriptions of what has been observed in the specimens. Terms applicable to other orders of trilobites (e.g. pygidium) are not used for *Naraoia* because of their implications and because the currently accepted definitions (Moore 1959) would require amendment.

2. TERMINOLOGY AND METHODS

The exoskeleton of *Naraoia* was dorsal, with a narrow, reflexed ventral portion or *doublure*; the exoskeleton was divided by a transverse articulation into an *anterior shield* and *posterior shield*, the former overlapping the latter for a short distance. The *axial region* of the exoskeleton was gently convex, and raised above the *lateral regions* of the shields. The *antenna* was the uniramous anterior appendage, and was followed by a series of biramous appendages, the proximal podomere of which was the *coxa*. The *inner* or *leg branch* was composed of five podomeres and a terminal spine. The *outer* or *gill branch* consisted of a *shaft* which bore an oval, *terminal lobe* fringed with *setae*; the shaft also bore many long *lamellae*. The adaxial margin of the coxa was spinose, and is termed the *gnathobase*, the prominent ventral spine of the proximal podomere of the leg branch is the *endite*. On the anterior shield traces are preserved of *lateral diverticula* of the alimentary canal, and on the axial region, behind the main trunk of the lateral diverticula, traces of *axial diverticula*. The latter appear to be present also on the axial region of the posterior shield. To avoid ambiguity when referring to directions, the median longitudinal line in the body is termed *sagittal* (abbreviation, sag.), a line parallel to, but outside the sagittal line as *exsagittal* (abbreviation, ex.) and a direction at right angles to these as *transverse* (abbreviation, tr.). *Abaxial* denotes a position away from the dorsoventral plane in the sagittal line, *adaxial* a position towards this plane. In describing appendages it is convenient to refer to directions which may be approximately transverse as *longitudinal* (abbreviation long.), referring to the longitudinal axis of the appendage and its branches.

The fossils are preserved as *compressions*, the original relief having been profoundly modified as the sediment was compacted at right angles to the bedding planes. 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. I have previously (Whittington 1971*a*, pp. 1182–1187, fig. 24) described these attitudes (of the horizontal plane of the body relative to the bedding) as *parallel*, *oblique*, *lateral* and *vertical*. These terms are used in the explanations of the plates, qualified as parallel oblique, lateral oblique, etc., to indicate that the specimen is approximately or partly parallel, lateral, etc. When the rock was split to reveal a specimen, portions of the specimen adhered to each side of the split, the *part* and *counterpart*. The former is the side which has the dorsal side of the animal toward the observer. In the explanations of the plates the statement 'part only' or 'counterpart only' means that only one side of the specimen is known.

The photographs have been taken on panchromatic film, in ultraviolet radiation, after focusing in ordinary light. *Low angle radiation* has been directed at 30° to the horizontal, and the direction from which it came is given as west, north-west, etc., relative to the margins of the plate. 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. The plates show that these two types of photographs reveal particular details more clearly than others, so that all or parts of a specimen may be illustrated by one or both methods. Two specimens have been photographed in ordinary light while submerged in alcohol. Facing many of the plates are camera-lucida drawings intended to explain how a particular specimen has been interpreted. As explained in § 3, thin layers of rock separate parts of the body, and the biramous appendages form an imbricated series. The changes of level between exoskeleton and appendages, and between an imbricated series of branches of an appendage, form minute scarps, which appear in the photographs as light or dark depending on the direction of radiation. In the drawings the scarps are represented by a line along the upper edge, and hachures running down-slope from this line. The scarps were formed when the rock was split, or by subsequent preparation, and their extent and course reveals the relationships between preserved parts of the body. When part and counterpart are available they reveal different portions of the body, and these are brought together in a composite drawing. The abbreviations listed include those for an institution in which a particular specimen is kept. These abbreviations are placed before the catalogue number in the plate and figure explanations, but omitted in the text for brevity.

3. PRESERVATION

The photographs show that the cuticle of the shields and appendages of *Naraoia compacta* are preserved as a thin layer which appears darker than the surrounding rock in low angle radiation; in high angle radiation the whole of this layer (e.g. figure 32, plate VI), or only certain areas of it, may be strongly reflective (e.g. figures 16, 19, plate III). The body does not lie in a single bedding plane, but portions (anterior shield, posterior shield, branches of appendages) lie in different planes, separated by thin layers of rock; the appendages thus show an imbricated arrangement. Individual specimens are compressions oriented at various angles to the observer, revealed by a split in the rock parallel to the bedding planes. This split has passed *through* portions of the exoskeleton, so that they are present on each side of the split, i.e. on part and counterpart. Portions of the exoskeleton through which the split did not pass are preserved in either part or counterpart, and the specimen can be prepared to reveal them. This manner of preservation is common to arthropods of the Burgess Shale, and the way in which it occurred has been discussed in detail previously (Hughes 1975, p. 416; Whittington 1971*a*, pp. 1180–1189; 1975*a*, pp. 5–11; 1975*b*, pp. 102–105). These arguments are not repeated here, it is assumed that the animals were caught in a moving cloud of sediment in suspension and buried as it settled out. Compression of the bodies in the compacted sediment was of the order of at least 10:1.

In *Naraoia compacta* the split between part and counterpart passed through the shields and the distal parts of the appendages (e.g. figures 5–8, plate I). Thus the proximal portions of the appendages are concealed beneath the shields in the part, and have been revealed by preparation of selected specimens (figures 14, 26, 37, 47, 57, 85, 86). In all cases (except gnathobases 2–4 in figure 86) the posterior face of the coxa and leg branch is revealed, sloping backward and slightly downward, away from the observer. The shaft and lamellae of successive gill branches are also imbricated, in some cases sloping backward and slightly upwards (toward the observer, figures 14, 26, 47, 57, 86) but in all or parts of strongly oblique specimens may be imbricated to slope forwards and slightly upward (appendage 2 in figure 37, figures 72, 85). These positions of the coxa and branches of the appendage are not those in the live animal (figure 96), but are the result of compression. Simple cases of the effects of compression are shown in figure 1, using outlines taken from the restoration (figure 96, 97). In figure 1*a* the thin films representing leg branch and terminal lobe after compression slope back and slightly down, the gill lamellae back and slightly upward, and a series of appendages would thus be imbricated as seen in figures 4, 14, etc. If an animal was buried in a vertical attitude, individual appendages would be affected by compression as in figure 1*b*, and a series would appear much as in figure 72. However, not only is the attitude of a branch modified by compression but the outline is altered, as shown in figure 1*c*, *d*, *e*. Thus in the coxa and leg branch, when buried at a steep angle, the coxa and podomere 2 are relatively narrowed, the endite brought closer to the big coxal spine, an effect like that seen in appendages, 5, 6 and 7 in figure 57. The distal part of the leg branch, after burial at a steep angle, is made relatively broader by compression when flexed (figure 1*c*, cf. appendages 4, 5, figure 57), or narrower when extended (figure 1*d*, cf. figures 26, 47). Compression after burial at a steep angle of the gill branch makes the branch relatively narrower and also directs the lamellae more strongly outward (figure 1*e*), an effect well shown in figures 4, 14, 57. These graphically simple cases are used as illustrations of effects in which there is wide variation, particularly in obliquely oriented specimens in which the appendage

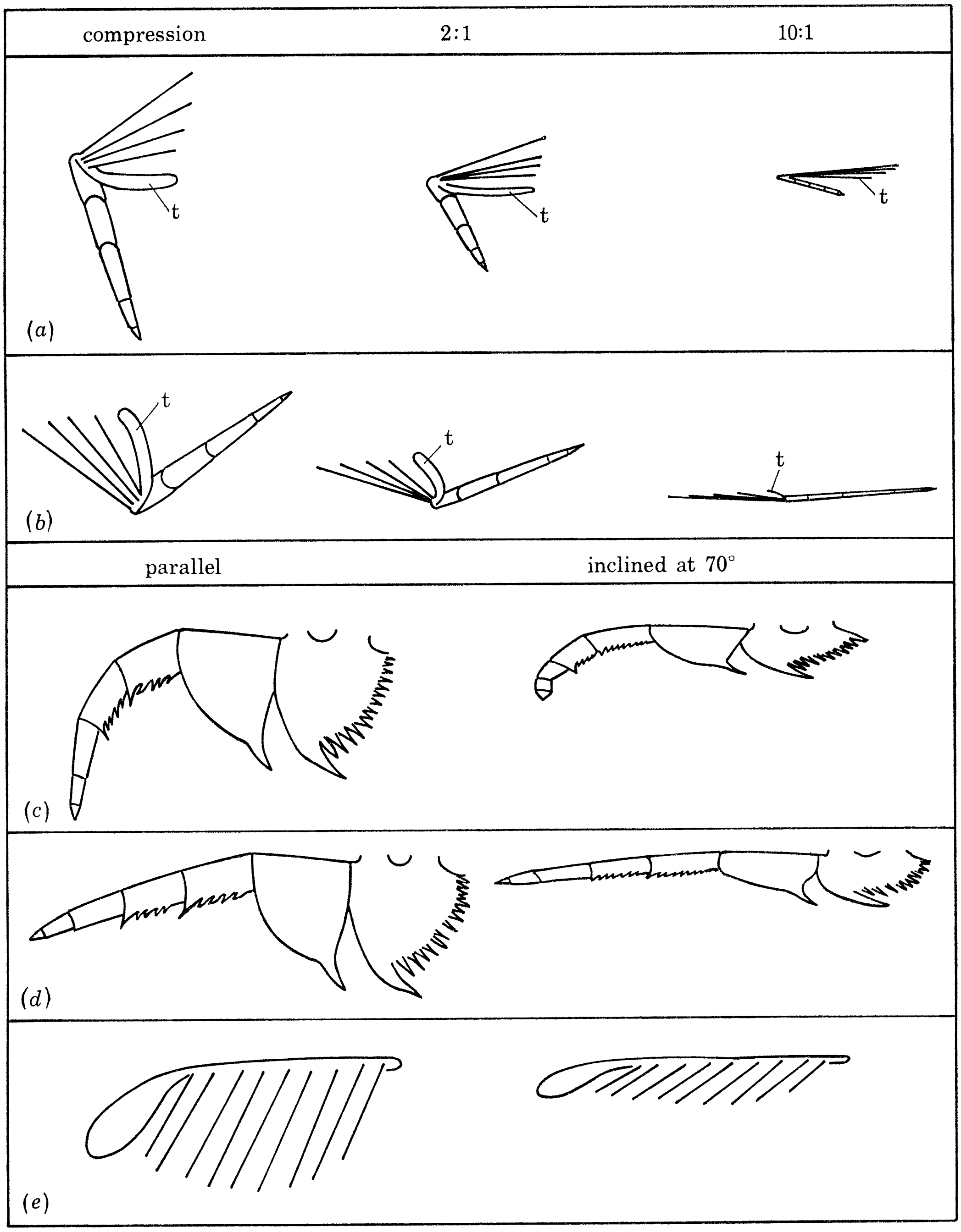


FIGURE 1. Diagrams to show the effects of post-burial compression on the appendages of *Naraoia compacta*. (*a*, *b*) left appendage in lateral view, buried at two different angles and compressed in the ratios indicated, bedding planes intersecting paper at right angles, parallel to lower edge of figure. (*c*, *d*) coxa and leg branch flexed and extended, compressed in plane of paper when oriented with antero-posterior surface parallel to, and inclined at 70° to, this plane. (*e*) gill branch compressed in plane of paper when oriented with dorsal surface parallel to, and inclined at 70° to, this plane. Outlines before compression taken from figures 96, 97.

series of each side is buried at widely differing angles (e.g. figures 14, 37). Similarly the outline of the anterior or posterior shield in any specimen has been modified by compression, and the effects are illustrated by graphically simple examples (figure 3) and discussed in more detail in §4(*d*).

Compression appears thus to have modified both the shape and the angle relative to the shield of the appendages, depending on the angle of burial. Compression may also have shifted the entire series of appendages longitudinally or laterally relative to the shields, for example in the originals of figures 14, 37, and 85. The gnathobases of the left side are preserved adjacent to the margin of the axial region, an effect of the obliquity of the orientation at burial, and in figure 37 the position of the right posterior gill branch shows that the right coxae must lie well within the axial region. In parallel compressions (figures 57, 86) the gnathobases of both sides are situated within the axial region. Crowding back of appendages by compression is discussed in §4(i), in relation to the number of pairs of appendages on the anterior shield. Such crowding has occurred particularly when the anterior shield has been preserved bent down at a steep angle, while the posterior shield was parallel (figure 57). A difficult problem is how post-mortem changes have affected the arrangement of the appendage series. In both oblique (figures 37, 85), lateral oblique (figures 26, 47) and vertical oblique (figure 72) compressions the series has a subparallel arrangement, and it is restored as such (figure 96), with a slight fanning of the anterior and posterior pairs. This appears to be a more natural arrangement than the strongly radial pattern seen in 57687 (figure 7, plate I), or the subparallel forward pattern in the originals of figures 48, 58, and 86. These modifications of the limb positions from those when the animal was walking (figure 96) may have been effected partly by turbulence during the process of burial, and partly by compression.

Similar problems to the above were encountered when interpreting the way in which the trilobite *Olenoides serratus* was preserved (Whittington 1975*b*, pp. 102–105, fig. 2). In *O. serratus* a far greater outward and backward displacement of the entire series of limbs has occurred in certain specimens. This may reflect the different behaviour during compression of a body with a more rigid, mineralized exoskeleton (*O. serratus*) and one with a thinner, less rigid exoskeleton.

My conclusions from these considerations is that, if allowance is made for the effects of turbulence in the moving cloud of suspended sediment that entrapped the animals, and for the post-mortem effects of compression, the animals were alive when entrapped. The sample (§4*c*, figure 2) consists of whole animals and cast exoskeletons, both showing a range in size, supporting the idea that a living community was sampled as a result of erosion by the density current. As the sediment settled out, some unknown distance away, the bodies were entombed at all angles. Cast exoskeletons are only known from parallel examples, perhaps because of their different behaviour in settling out. No partially dismembered individuals have been recognized, hence a corollary to this interpretation is that decay of whole animals began after burial. A dark stain in the adjacent rock is characteristic of many animals preserved in the Burgess Shale (Whittington, 1971*b*, pp. 16–17; 1975*a*, p. 11), and some examples from specimens of *N. compacta* are figures 9, 12, plate II; figures 31, 33, plate VI; figure 79, plate XIII; figures 87, 88, plate XV. The stain is typically situated posteriorly, but may be anterior (figure 49, plate IX). It appears to be the trace of decay products that seeped out into the wet sediment shortly after burial (Conway Morris 1976), and not of material squeezed out later, during compaction, as I earlier suggested. Pyrite, as minute grains or small spheres is commonly associated with fossils in the shale, and in *N. compacta* parts of the gill branches in some specimens are preserved in pyrite. Unusual concentrations of blobs of pyrite occur in the axial region in two specimens (figures 27, 28, plate V; figures 31, 33, plate VI), associated with the infilling of the alimentary canal in another (figure 49, plate IX), and apparently associated with areas of muscle attachment in 83945b (figures 9, 10, plate II). This pyrite appears to be related to decay products, and is indicative of anaerobic conditions in the sediment. As argued earlier (Whittington 1975*a*, pp. 10–11) decomposition presumably took place in a far shorter time than compression, so that some shift of the appendages relative to the shield would be possible during compression since they were no longer held in place by muscles and ligaments.

4. DESCRIPTION OF *NARAOIA COMPACTA* WALCOTT, 1912

(*a*) *Classification*

This study of *N. compacta* concludes (§6*c*) that the animal is best regarded as a trilobite, but such a conclusion requires a less restrictive definition of Class Trilobita than, for example, that of Moore (*in* Moore 1959, p. O 172) or of Hupé (*in* Piveteau 1953, p. 44):

Exoskeleton divided longitudinally by a convex median region or axial lobe; outline ovate; reflexed at margin and continued on ventral side for variable distance; divided transversely by one or more articulations. Alimentary diverticula particularly developed in anterior region of body. Anterior pair of uniramous antennae, followed by series of similar biramous appendages; large coxa with gnathobase, inner branch a jointed walking leg, outer branch bearing many long, narrow lamellae.

The Order Nektaspida may consequently be defined much as Raymond (1920, p. 148) originally proposed, and not as modified by Størmer (*in* Moore 1959, p. O 30), that is:

Trilobita with a single transverse articulation in the exoskeleton.

So defined the order includes the species *compacta* and *spinifer* accepted herein, which, following Walcott (1912, p. 175; 1931, pp. 9, 15), are placed in his genus *Naraoia* and family Naraoiidae. Two new species of arthropods, each considered the type of a new genus, were described by Repina & Okuneva (1969) from presumed Cambrian rocks of the Maritime Territory, U.S.S.R. The first of these forms was referred to the Naraoiidae, the second to a new family, and both placed in Nektaspida. The specimens are similar in size to the smallest illustrated herein (figures 40, 41, plate VII; figure 52, plate IX), are preserved with some relief in brown argillite, and show no traces of appendages. The first form, *Maritimella rara*, has the exoskeleton divided by a single articulation, the anterior shield the broader and bearing a pair of convex eye lobes situated far apart. It may belong in Nektaspida as here defined. The second form, *Orientella rotundata*, has the anterior shield without eye lobes, and the remaining part of the body divided into 1–3 articulated segments, followed by two shields of fused segments, the posterior the smaller. The present definition of Nektaspida would exclude this species. Implicit in this definition is the series of trilobite-like appendages, so that until appendages of the U.S.S.R. forms are known, their relationships will remain in doubt. In these circumstances a revised definition of family Naraoiidae is not possible, though that of Walcott (1912, p. 175), or Størmer's emendation (*in* Moore 1959, p. O 30) of it, are no longer acceptable. The present abstract provides a summary description of each of Walcott's species.

(*b*) *Lectotype, locality, stratigraphical horizon, numbers of specimens, associated fauna and flora*

Walcott's initial description (1912, pp. 175–177, pl. 28, figs. 3, 4) included photographs of two specimens, the original of figures 5–8, plate I, and that of figure 79, plate XIII. The former is the better preserved, and has the counterpart, so is here selected as lectotype.

All known specimens of *Naraoia compacta* come from what Walcott (1912, pp. 151–153) called the 'Phyllopod bed', 2.3 m (7ft 7 in) thick, in which he excavated his quarry. This excavation was in the Burgess Shale member, Stephen Formation, Middle Cambrian, *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone, situated on the ridge between Wapta Mountain and Mount Field at an elevation of approximately 2286 m (7500 ft), 4.8 km (3 miles) north of Field, southern British Columbia (Fritz (1971) gives an account of the stratigraphy and setting of the shale).

Walcott's collection in the U.S. National Museum includes 103 specimens (U.S.N.M. numbers 57686–7, originals of Walcott 1912; 83945a–e, originals of Walcott 1931, pp. 9–14, pl. 13, fig. 4; pl. 14, figs. 1–3, pl. 15, figs. 2, 3, 114257–8, 189202, 189210–222, 199815, 202684, 25822/826 (counterparts), 235842–878, 235885–89, 241027–049) which include those figured and measured herein; ten of these have counterparts. About 80 additional incomplete specimens were also examined in the Walcott collection. All these specimens are labelled '35k', implying that they came from the Phyllopod bed, but from a level unspecified. Walcott (1912, pp. 152–153) records *N. compacta* from his layers 12 and 10 only, i.e. from the basal 3.8 cm ($1\frac{1}{2}$ in), and a level 7.6 to 48.3 cm (3 in to 1 ft 7 in) above the base of the Phyllopod bed. In the Museum of Comparative Zoology, Rolfe (1962, p. 6) identified 3 specimens, one of which may be that of Raymond (1920, p. 140); in none of these are appendages well preserved. Other fragmentary specimens are among those listed as *Canadaspis* sp.ind. by Rolfe. The Geological Survey of Canada's collection, made in 1966 and 1967, yielded only 5 specimens (G.S.C. 47966 to 47970) from levels in the Phyllopod bed, two from 1.7 to 1.9 m (5 ft 5 in to 6 ft 2 in), two from 2.1 to 2.2 m (6 ft 11 in to 7 ft 2 in), and one from 2.9 to 3.0 m (9 ft 6 in to 10 ft 0 in; measurements as given in Whittington, 1971*a*, fig. 3, in which the base of the Phyllopod bed is at approximately 5 ft). These levels are those in which the arthropods *Marrella splendens* (Whittington, 1971*a*, fig. 5; 1971*b*, fig. 1), *Burgessia bella* (Hughes 1975, fig. 1), and *Yohoia tenuis* (Whittington 1974, fig. 1), and the trilobite *Olenoides serratus* (Whittington 1975*b*, fig. 1) are abundant. The numbers of specimens in the Walcott collection of the non-trilobite arthropods are respectively 12000, 1800, and 400, so that the 183 specimens of *N. compacta* indicate its relative rarity, as the Geological Survey of Canada's collection confirms. The trial excavation in disturbed beds at the south end of the quarry yielded a further 6 specimens of *N. compacta* and 12 of *Burgessia bella*, but the level relative to the Phyllopod bed is not known.

Walcott (1912, pp. 152–153) listed the fauna associated with *N. compacta*. The specimens in his collection confirm that it occurs in association with the arthropods *Burgessia bella*, *Canadaspis perfecta*, *Marrella splendens*, *Waptia fieldensis*, the trilobite *Olenoides serratus*, the worms *Ottoia prolifica* and *Canadia setigera*, and the alga *Morania* sp.

(*c*) *Range in size, dimorphism, whole animals and cast exoskeletons*

Measurements were made of 82 specimens, in 10 of which the sagittal length of the exoskeleton could not be measured; the remaining 72 specimens show a range from 9 to 41 mm (figure 2*a*). Specimens in the upper half of this range are more abundant, but there are no obvious breaks in the size range. Two types of specimens showing a similar size-range are included in this sample. The majority (39) are those which show traces of the appendages, alimentary canal and diverticula, specimens which thus appear to have been whole animals when buried. Thirty-three specimens are of the conjoined dorsal shields showing no such traces. These latter preservations may be of the most resistant part of the cuticle surviving after ecdysis, and the specimens characteristically show a narrow, thickened marginal band (figure 62, 63, plate XI). This suggests that the heavier dorsal cuticle of the shields was continued for a very short distance ventrally inside the margin, and that thinner cuticle covered the ventral side of the body and the appendages. After ecdysis the thinner cast cuticle decayed rapidly, leaving the heavier cuticle of the shields; indeed a line of splitting may have separated the two. The high percentage of cast exoskeletons in the sample is markedly different from that shown by other non-trilobite arthropods studied. In *Marrella splendens* (Whittington 1971 *b*, p. 18) about 0.1 % of the sample were cast exoskeletons, and in *Yohoia tenuis* (Whittington 1974, p. 7) and *Burgessia bella* (Hughes 1975, p. 429) the great majority of specimens are complete. Whether this difference reflects difficulty of recognition of cast exoskeletons, original resistance to decay, or other factors is uncertain.

Sixteen specimens ranging in sagittal length from 22 to 29 mm show the posterolateral corner of the anterior shield drawn out into a short spine (not broadly rounded). The majority are cast exoskeletons (figure 62, plate XI) in which presence or absence of these spines is readily visible. Thus of the thirty three cast exoskeletons studied (figure 2*b*) twelve show the spine while in the remainder it is absent. In whole animals it may be possible to show that the spine is (figure 50, plate IX; figures 60, 61, plate XI), or is not (figure 8, plate I; figure 76, plate XIII), present, but in many specimens (figure 28, plate V; figure 31, plate VI) this condition is uncertain. Thus of the forty nine whole animal specimens examined, in seventeen of them I could not be sure whether or not the spine was present, but in the majority (twenty eight) the spine was absent, being recognizable in four. The evidence suggests that perhaps one-fifth or one-quarter of the sample possessed the spine. Measurements taken from the sample (figure 2*c*–*f*) do not appear to provide further evidence of dimorphism. Simonetta & Cave (1975, p. 5, pl. V, figs. 11, 12, pl. XXXV, figs. 7, 8) observed the presence of the posterolateral spine in the original of figure 62, plate XI, and also the rounded outline of the anterior shield in 189212 (figure 63, plate XI), and based a new species on each of these cast exoskeletons. They did not observe the spine in specimens of entire animals, and as explained in §4(*d*) the outline of the anterior shield varies with the attitude of burial. The measured sample includes these two specimens, and I do not consider that these single characters are an adequate basis for distinct species.

(*d*) *Anterior shield*

Preparation of the counterpart of whole animal specimens (figure 8, plate I; figure 12, plate II; figure 50, plate IX) has exposed that portion of the anterior shield which overlapped the posterior shield. This preparation has consisted of removing parts of the thin layer of rock

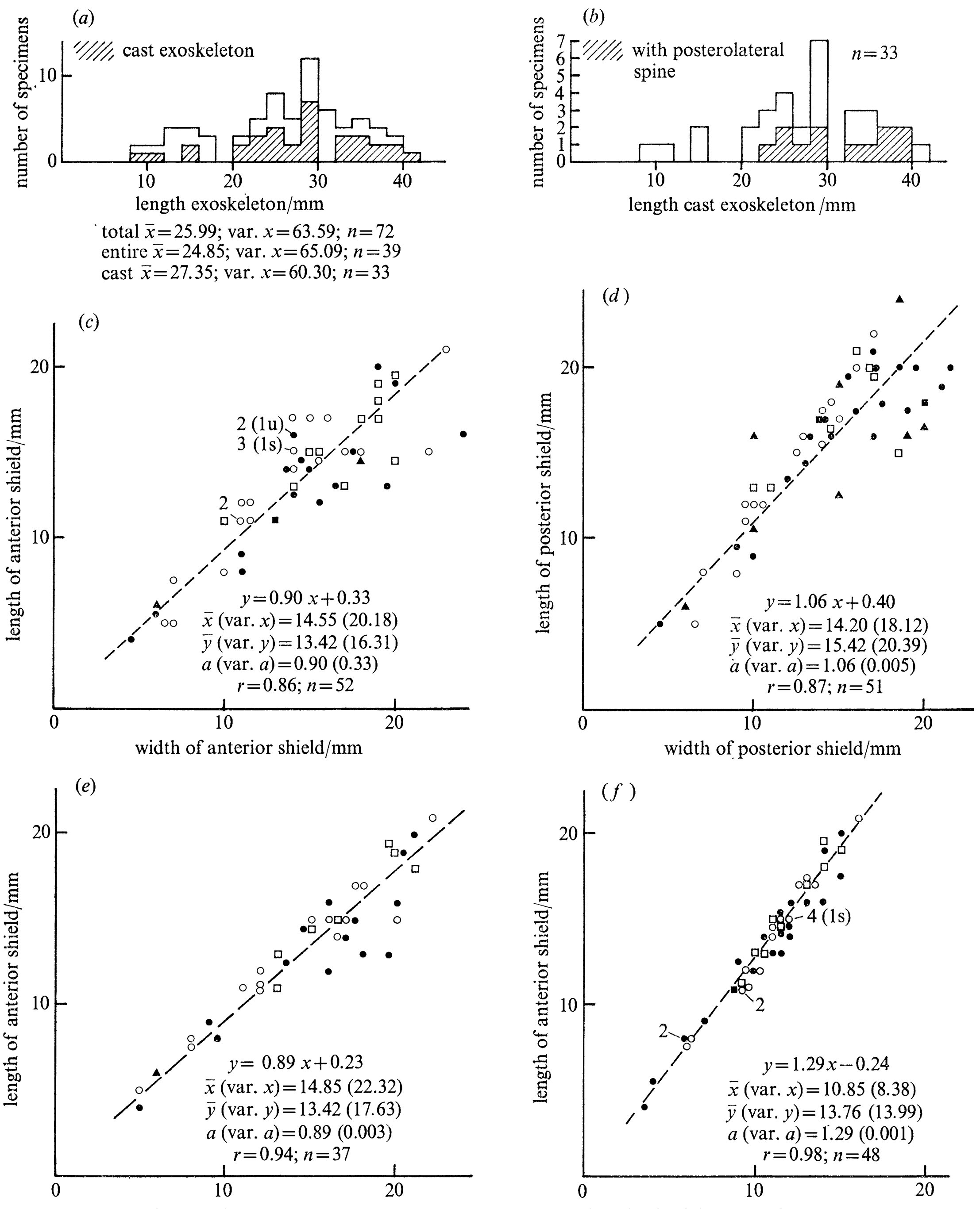


FIGURE 2. Size-frequency histograms (*a*, *b*) and graphs (*c*–*f*) of measurements in millimetres of entire individuals and cast exoskeletons of *Naraoia compacta*. Statistics by Dr C. P. Hughes. Entire individuals are U.S.N.M. 57686–87, 83945a–e, 25822/26 (counterparts), 114257–58, 189202/215 (counterparts), 189213–14, 189217, 189219, 235842–44, 235848, 235850–53, 235855, 235858–60, 235862–64, 235872, 235874–75, 241029–31, 241034–35, 241037–40, 241042, 241046, and G.S.C. 47966 to 67, 47969 to 70. Cast exoskeletons are U.S.N.M. 25822/26 (counterparts), 189210, 189212, 202684, 235847, 235849, 235854, 235856–57, 235865–871, 235873, 235876–78, 235885 (two specimens), 235887–88 (4 specimens), 241032–33, 241045, 241047–48, and GSC 47968. Explanation of symbols in (*c*)–(*f*): •, entire, without spine; ■, entire, with spine(s); ▲, entire, spine uncertain (u); ○, cast exoskeleton; □, cast exoskeleton with spine. The numeral is the sum of individuals of the same dimensions.

that intervened between the overlapping shields, far enough back to reveal the posterior margin of the anterior shield (figures 4, 14, 48, show the position of this margin). This layer of rock shows that sediment penetrated between the shields as far forward as their junction, which thus was at the anterior margin of the posterior shield. Presumably this margin was connected to the posterior margin of the anterior shield by arthrodial membrane. The effect of compression has been to imprint the curved trace of these margins on the shields. In the part of whole animal specimens (figure 5, plate I; figure 9, plate II; figure 49, plate IX) the impressed line curving convexly back on the posterior shield shows the position of the posterior margin of the anterior shield. The split between part and counterpart has passed through the junction between the two shields, resulting in a minute scarp which curves convexly forward (figures 4, 14, 48) and follows approximately the anterior margin of the posterior shield. Less commonly (figure 58; figure 60, plate XI) a minute scarp is not present, but impressed lines show the respective margins. As discussed in §4 (*c*), a small proportion of whole animal specimens bear a posterolateral spine on the margin of the anterior shield (figure 50, plate IX). Cast exoskeletons (figures 62, 63, plate XI) show the two impressed margins and may show the posterolateral spine.

Measurements of length (sag.) and maximum width (figure 2*c*) in parallel and parallel-oblique specimens show that the outline of the shield was subcircular. There is no justification for the selection of a single specimen of a cast exoskeleton (figure 63, plate XI) showing an 'almost perfectly round' outline of the anterior shield as the basis for a separate species (Simonetta & Cave 1975, p. 5, pl. V, fig. 11; pl. XXXV, fig. 12).

That the shield was originally convex is shown by lateral oblique (figure 22, plate IV; figure 28, plate V; figure 79, plate XIII) and the vertical oblique (figure 65, plate XII) specimens, but the amount of this convexity is difficult to judge. Figure 3 compares the outline of anterior shields of two different convexities after burial in different attitudes and compression. Comparisons between these outlines and the lateral oblique specimens, and between figures 3*d*, 3*h* and figures 49–51, plate IX, and figure 75, plate XIII, suggest that the more highly convex example may represent the original shape most closely. Thus it is considered (figures 96, 97) that the original height of the shield was approximately one quarter the maximum width.

Compressions in all attitudes (figures 17, 18, 20, plate III; figure 28, plate V; figure 49, plate IX; figure 65, plate XII; figure 76, plate XIII) show evidence of the axial region, the maximum width posterior and equal to about one third the maximum width of the shield. The bluntly-pointed anterior end is visible in most specimens and figure 2*f* shows the relative length. The convexity of the region, independent of the remainder of the shield, appears to have been low, and there is no evidence of a bounding furrow. Lateral oblique examples (figure 22, plate IV; figure 79, plate XIII) suggest that the shield was slightly flattened in front of the axial region.

Lateral oblique specimens (figure 22, plate IV; figure 28, plate V; figure 68, plate XII) show that the anterior shield could be flexed at up to 90° to the posterior shield, the articulation being along the line of junction so that the overlapping portion projected back behind it. It is because of such flexure that the anterior shield may be preserved parallel (figure 17, plate III) or inclined forward and downward (figure 20, plate III) relative to the parallel posterior shield. No special structures or heavier sclerotization is evident along the articulation, either in entire individuals or cast exoskeletons (figures 62, 63, plate XI). The occurrence of the latter points to the strength of the articulation; separate anterior or posterior shields have not been recognized.

A narrow, marginal band is evident on the anterior shield of both entire individuals (figures 16–18, plate III; figures 49–51, plate IX; figures 60, 64, plate XI) and cast exoskeletons (see §4*c*); this band is taken to indicate that there was a narrow, sclerotized doublure. The lateral diverticula (see §4*f*) are best seen in reflected photographs, being faintly visible as low ridges in certain specimens (compare figures 19 and 20, plate III; figures 66 and 68, plate XII; see also figure 87, plate XV). These ridges may be the result of compression, and not an original feature, since they are not present in cast exoskeletons (figures 62, 63, plate XI). Walcott (1912, p. 175) defined the family Naraoiidae (containing only the nominate genus) as having pedunculate eyes, but in his description of the species (1912, p. 177) stated that nothing was known of the eyes. Subsequently (Walcott 1931, p. 11, fig. 2) he portrayed a small, crescentic eye beside the anterior end of the stomach, describing the pair as 'bright spots'. A pair of crescentic, reflective areas (or a single such area on one side) may be present at the anterior end of the axial region of the anterior shield (figure 19, plate III; figure 77, plate XIII). These areas are not expressed in any way on the external surface, and I do not consider that they are eyes, but more probably areas of muscle attachment.

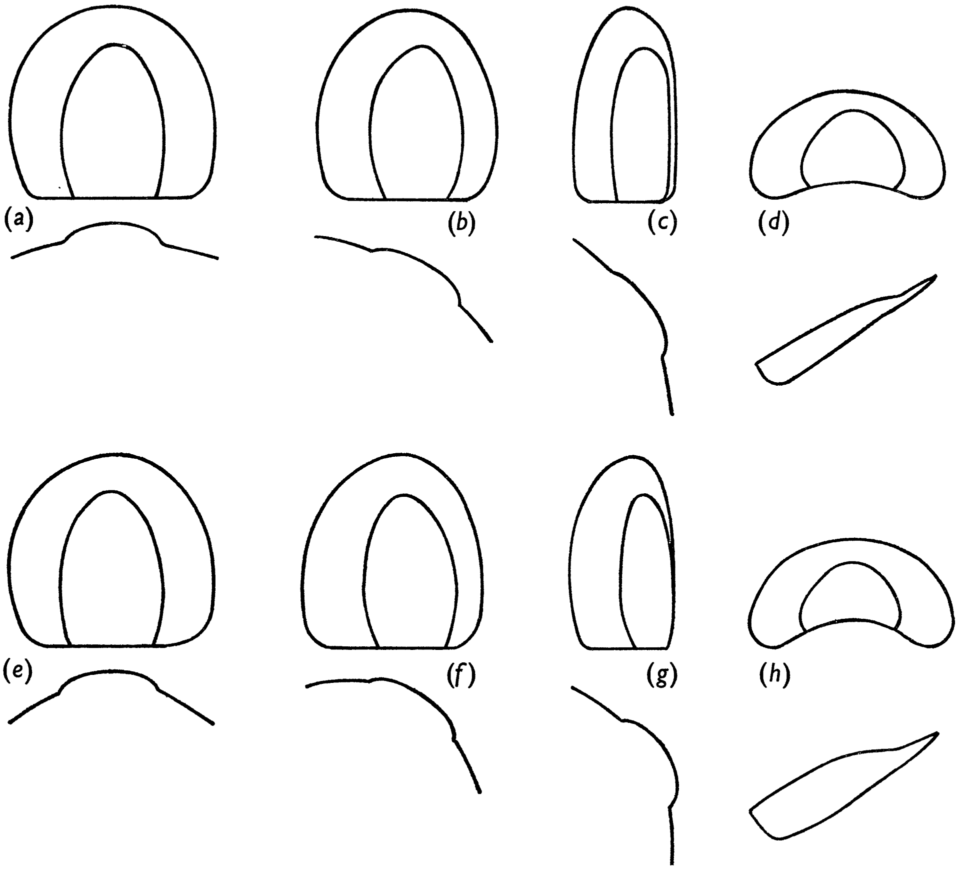


FIGURE 3. Diagrams to show the effects of post-burial compression on the outline of the anterior shield and axial region of *Naraoia compacta*. Diagrams in two series, *a–d* in low convexity, *e–h* in higher convexity; each series shown (upper row) compressed in plane of paper, and (lower row) with accompanying transverse sections (*a–c*, *e–g*) and sagittal sections (*d*, *h*). In *a*, *e*, parallel; *b*, *f*, tilted at 30° along sagittal line; *c*, *g*, tilted at 60° along sagittal line; *d*, *h*, tilted forward and downward at 55°.

(*e*) *Posterior shield*

Figures 2*d*, *e*, indicate that throughout the known size range the length (sag.) is slightly greater than the maximum width, and that the length is greater than that of the anterior shield. The axial region is visible in most specimens, the maximum width (tr.) about one third that of the shield; these maximum widths are attained at a point in front of the mid-length. The axial region tapers posteriorly, the rounded tip a short distance from the posterior margin of the shield. The convexity of the posterior shield (figure 28, plate V; figure 31, plate VI; figure 65, plate XII) conforms with that of the anterior, which has been discussed above; the axial region had a gentle independent convexity. Apart from the change in slope at the margin of the axial region, the external surface appears to have been smooth, without evidence of transverse or oblique furrows. The appearance of oblique or curving furrows on the lateral part of the shield (figures 5, 6, plate I; figure 17, plate III; figure 64, plate XI; figure 76, plate XIII) appears to be the result of compression of appendages against the shield and not original, because the position and curvature varies with that of the appendages, and the cast exoskeletons do not show them (figures 62, 63, plate XI). A narrow doublure, similar to that on the anterior shield, is visible on occasional specimens (figures 60, 62, 63, plate XI).

(*f*) *Internal anatomy and supposed telson*

Traces of the soft parts of the body in the axial region, and in the lateral area of the anterior shield are preserved in various ways in entire individuals. Cast exoskeletons (figures 62, 63, plate XI) show none of these features. Most conspicuous in low-angle illumination is the sediment-filled alimentary canal (figure 74, plate XIII), flattened elliptical in cross section so that the external surface is slightly convex, and where the fill is stripped off a concave impression remains (figure 64, plate XI). The fill is clavate in outline in the anterior shield, and extends back, maintaining a constant width for over half the length of the posterior shield. Only in the posterior part of the shield does it begin to taper gradually, and it extends back to the tip. The width is about one-fifth that of the axial region (figures 5, 7, plate I) but in some specimens (figure 87, plate XV) it appears relatively narrower, and may be merely a darker, narrower strip lacking in relief (figure 76, plate XIII). A particular fill may show constrictions and variations in width, and may show posteriorly (figure 49, plate IX; figure 54, plate X) what appear to be segmental divisions; these are best defined in the latter example. These variations presumably reflect the amount of fill at the time of death, the effects of compression, and possibly also the segmentation of the body. There may be no trace of a sediment fill (figure 28, plate V; figure 31, plate VI), and in these examples part of the axial region is crowded with small grains of pyrite. Removal of the shield posteriorly in 189221 (figure 38, plate VII) has shown a reflective strip at a deeper level representing the alimentary canal; in 114258 (figures 49, 50, plate IX) small pyrite grains are associated with the sediment-filling. In 189202 (figures 21–23, plate IV) the gut filling is poorly preserved but shows suggestions of segmentation though the specimen is obliquely wrinkled by compression. A deep fold traverses both shields, perhaps reflecting the left margin of the axial region. Between the fold and the trace of the alimentary canal in the anterior shield is the outline of a tubular structure (figure 24; figure 23, plate IV), passing forwards into striated, crumpled sections of the alimentary canal in the fold. It is possible that this structure represents the U-shaped anterior section of the alimentary canal, obliquely compressed, the tubular structure ending in the backward-facing mouth.

If the anterior section of the alimentary canal was U-shaped, then a labrum may have been present. In 241030 (figure 54, plate X; figure 64, plate XI) the ventral impression of the gut filling is preserved, anteriorly expanding, and showing a curved impression which may be of the posterolateral margin of the labrum. Removal of the anterior part of the filling in 47967 showed (compare figures 75 and 78, plate XIII) a similarly situated, backwardly convex series of wrinkles, which may indicate the position of the posterolateral margin of the labrum, and be associated with the forward expansion of the filling. The lack of any clearly outlined plate suggests that a labrum, if present, was lightly sclerotized.

When photographed in reflected illumination a conspicuous branching pattern of canals on the lateral area of the anterior shield (figure 19, plate III: figures 75, 78, plate XIII) is revealed. These lateral diverticula (hepatic caeca of Walcott 1931, pp. 13–14, fig. 2) originate from the alimentary canal by a transversely directed trunk situated in advance of the midlength of the shield; this trunk bifurcates into a branch which runs forward and one directed backward; from these main divisions others originate on the outer side and subdivide. The subdivisions terminate well within the margin of the shield, and end blindly, not being connected by a marginal canal. The lateral diverticula are preserved in specimens of length (sag.) 10 mm upwards (figure 40, plate VII; figure 52, plate IX) in compressions at all angles (figure 66, plate XII), and are limited to the area of the shield in front of the articulation.

Reflective strips and patches also occur on the axial region of both shields, and may be irregular or display bilateral symmetry or evidence of segmental arrangement. In dorsal aspect a subtriangular area, bluntly rounded anteriorly, divided sagittally by a trace of the gut, may occupy much of the axial region of the anterior shield (figure 16, plate III; figure 40, plate VII; figures 75, 78, plate XIII). The paired crescentic areas (supposed eyes of Walcott, 1931, see §4(*d*)) form the rounded apex of this triangle. Behind the main trunk of the lateral diverticula is the major portion of the triangular area (figure 7, plate I), which shows some subdivisions (figure 78, plate XIII) into a ramifying pattern, most clearly in 83945c (figure 19, plate III). The base of the triangular area ends abruptly at the line of the articulation between the shields, and the pattern appears to consist of three pairs of branching trunks, the axial diverticula, each radiating out from the alimentary canal. The reflective patches lie dorsal to the filling of the alimentary canal as preparation has shown (compare figures 75 and 78, plate XIII).

On the posterior shield segmentally arranged reflective patches extend the length of the axial region, from the junction of the two shields to the tip. They may be transversely subrectangular, extending partly or completely over the filling of the alimentary canal (figures 75, 78, plate XIII), or in irregular blocks on each side of the trace of the alimentary canal (figures 16, 19, plate III; figure 40, plate VII; figure 77, plate XIII). A narrower strip may extend out beyond each rectangular block (figure 7, plate I; figure 19, plate III). In 83945*b* (figures 9, 10, 12, plate II), in which no reflective areas are preserved in the axial region, there are paired areas of blobs of pyrite, lying just outside the alimentary canal in both shields. It is suggested that the rectangular reflective patches, and the areas with pyrite, are traces of muscle insertions in the axial region of the shields, one pair in each segment bearing biramous appendages. The narrow reflective strips that extend transversely from the margin of the rectangular patch to the edge of the axial region (figure 19, plate III) may represent axial diverticula of the posterior shield, single canals that do not branch like those of the anterior shield. The original of figure 19, plate III, suggests that up to fifteen pairs of muscle insertions and axial diverticula may have been present in the posterior shield.

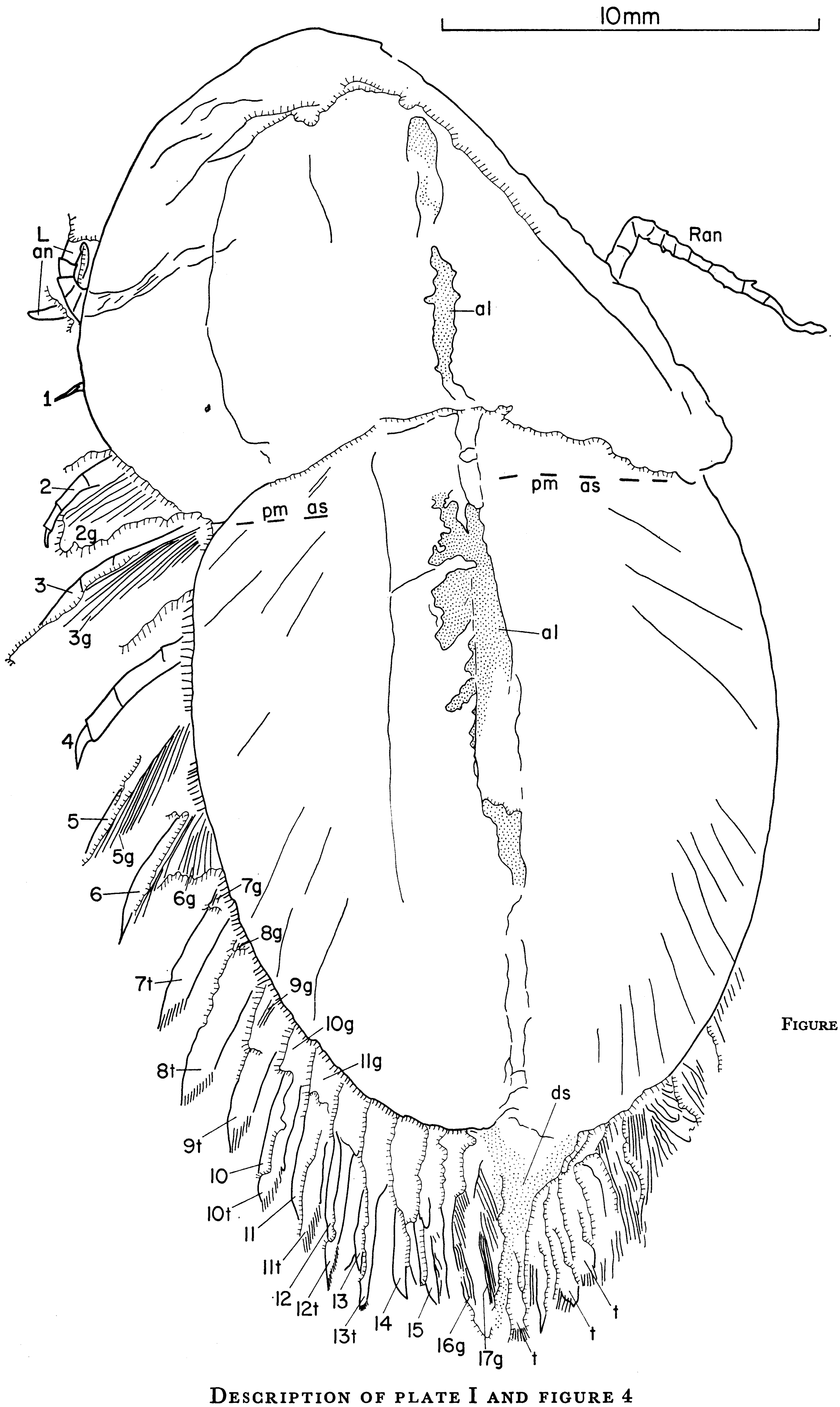


FIGURE 4

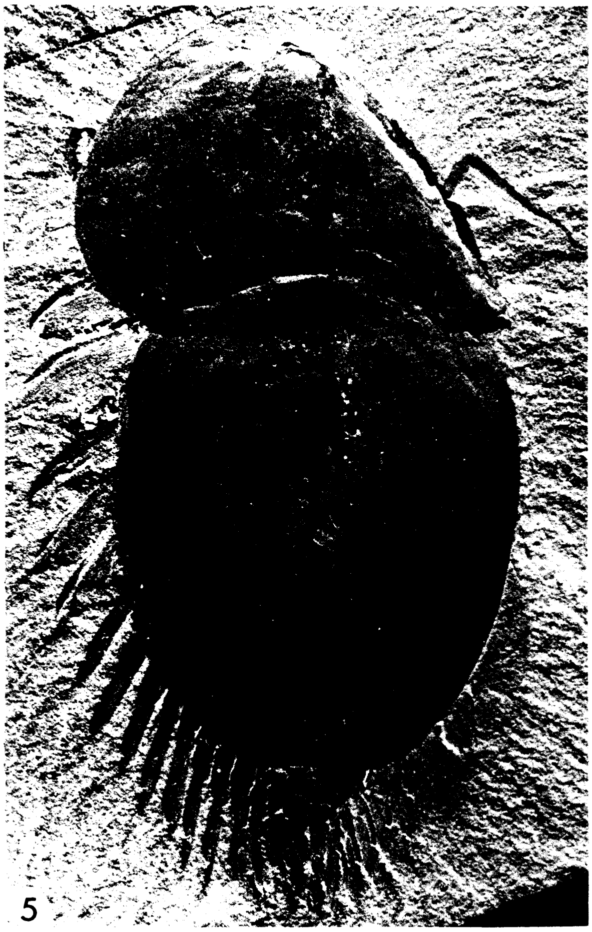
DESCRIPTION OF PLATE I AND FIGURE 4

Naraoia compacta Walcott, 1912. U.S.N.M. 57687, lectotype, parallel oblique, Phyllopod bed, Walcott quarry

FIGURE 4. Composite explanatory drawing of part and counterpart.

FIGURES 5, 6, 7. Part, respectively, north (magn. × 3.3); posterior portion, west (magn. × 6); in ordinary light under alcohol (magn. × 3.3). Original of Walcott 1912, pl. 28, fig. 4 and Simonetta & Cave 1975, pl. XXXIV, figs. 2*a*, 2*b*.

FIGURE 8. Counterpart, prepared to show posterior margin of anterior shield, northeast (magn. × 4). Original of Simonetta & Cave 1975, pl. XXXIV, figs. 2*c*, 2*d*.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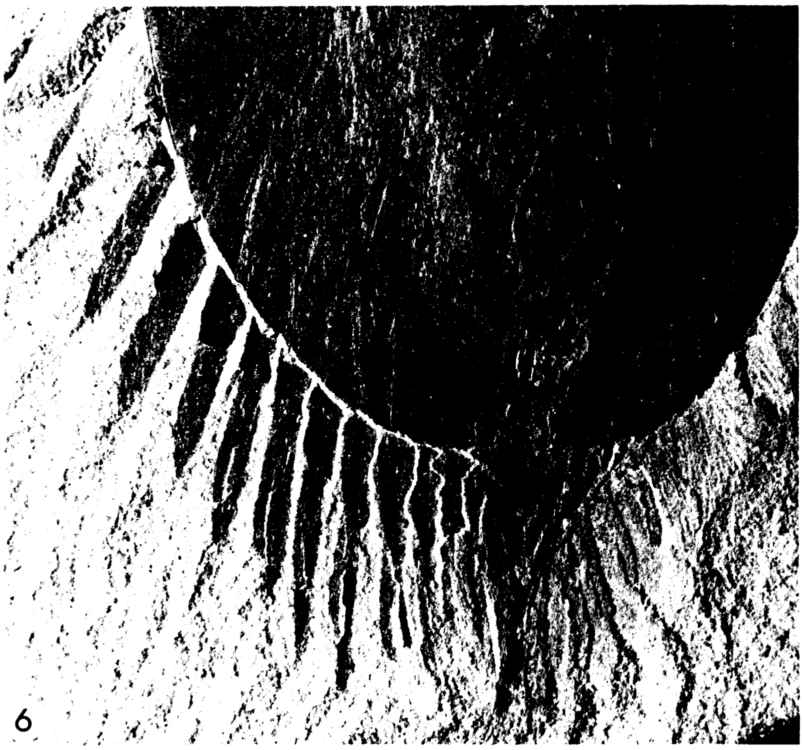
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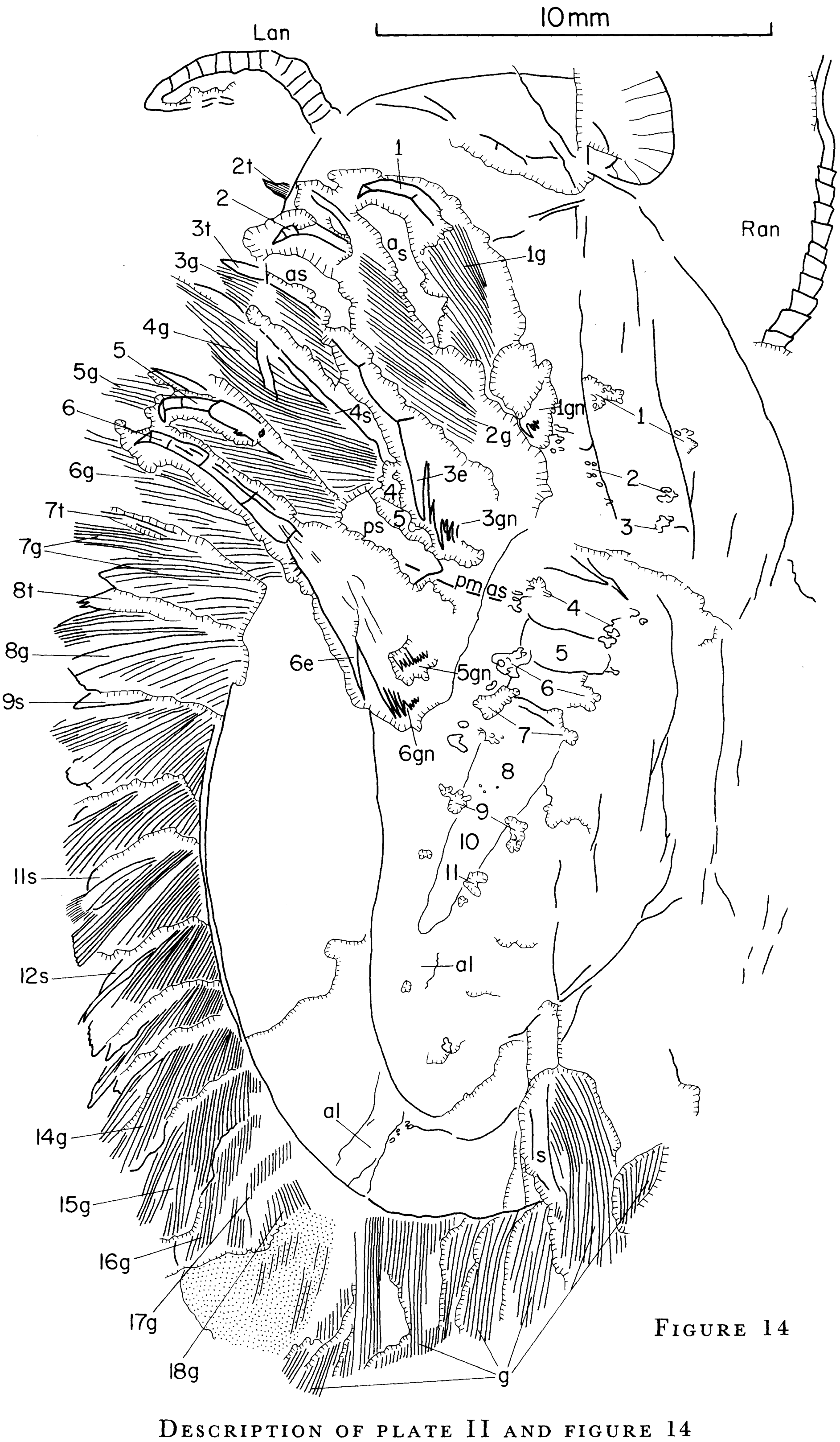

FIGURE 14

DESCRIPTION OF PLATE II AND FIGURE 14

Naraoia compacta Walcott, 1912. U.S.N.M. 83945b, parallel oblique, Phyllopod bed, Walcott quarry

FIGURES 9, 10, 11. Part, figured Walcott 1931, pl. 14, fig. 1, and Simonetta & Cave 1975, pl. XXXIV, fig. 3b. Respectively before preparation, north (magn. × 5); after preparation of appendages, north (magn. × 5); at early stage of preparation of gill branches 4–6, north (magn. × 3.3).

FIGURES 12, 13. Counterpart, figured Simonetta & Cave 1975, pl. XXXIV, fig. 3a. Respectively prepared to show posterior margin of anterior shield, north (magn. × 3.3); anterior portion to show right antenna, north (magn. × 5).

FIGURE 14. Composite explanatory drawing of part and counterpart after preparation. Axial segments 1–11 suggested by paired areas of pyrite granules.

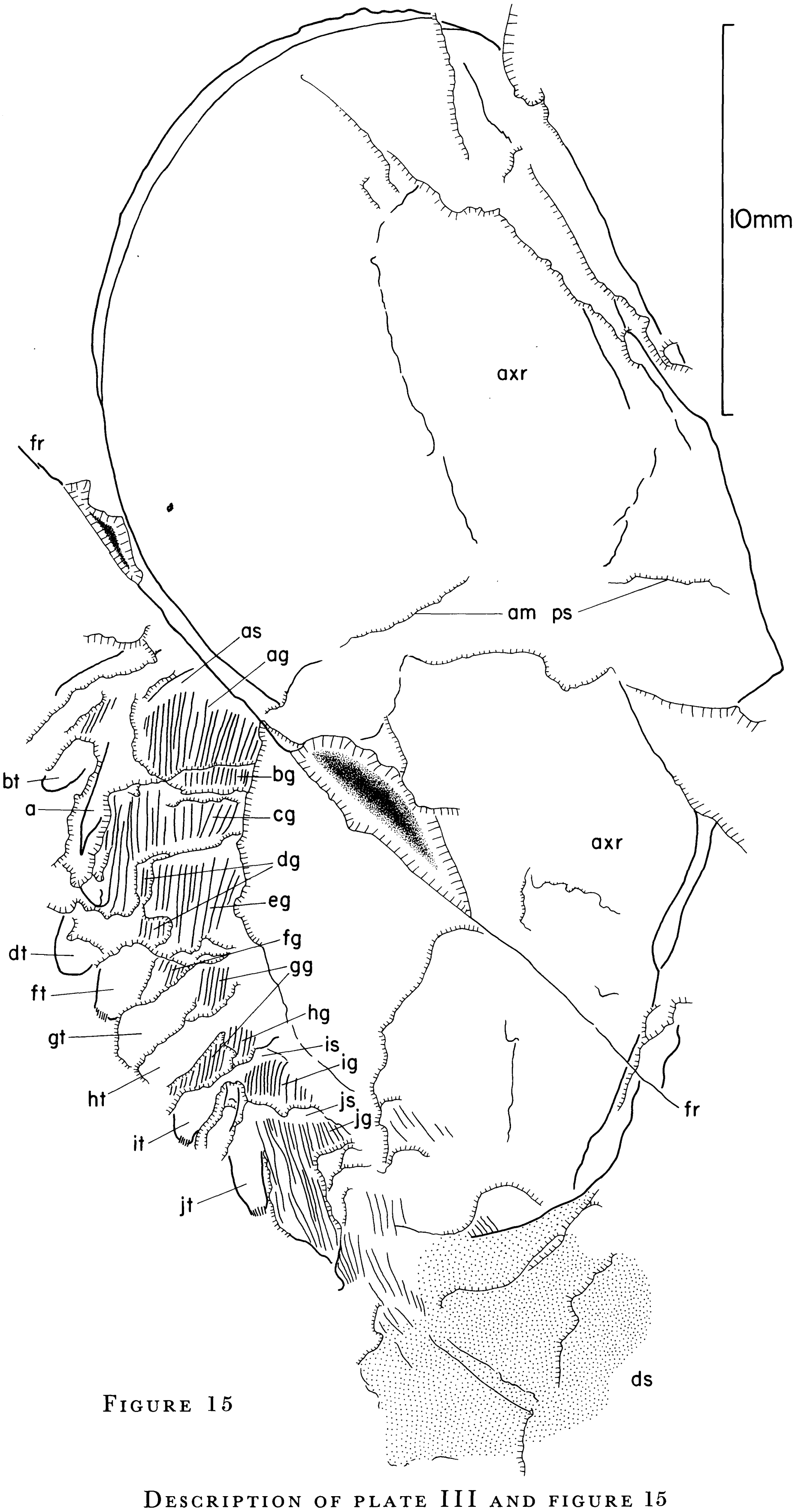

FIGURE 15

DESCRIPTION OF PLATE III AND FIGURE 15

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURE 15. U.S.N.M. 241038, explanatory drawing, series of appendages arbitrarily labelled a to j.

FIGURES 16, 17. U.S.N.M. 83945a, parallel, original of Walcott 1931, pl. 13, fig. 4; pl. 15, fig. 3, part only, respectively reflected, northeast (magn. × 3.3).

FIGURE 18. U.S.N.M. 241038, oblique, original of Simonetta & Cave 1975, pl. XXXIV, fig. 7, counterpart only, northwest (magn. × 3.3).

FIGURES 19, 20. U.S.N.M. 83945c, part only, parallel, original of Walcott 1931, pl. 14, fig. 2, and Simonetta & Cave 1975, pl. XXXV, fig. 5; respectively reflected (magn. × 4); northwest (magn. × 3.3).


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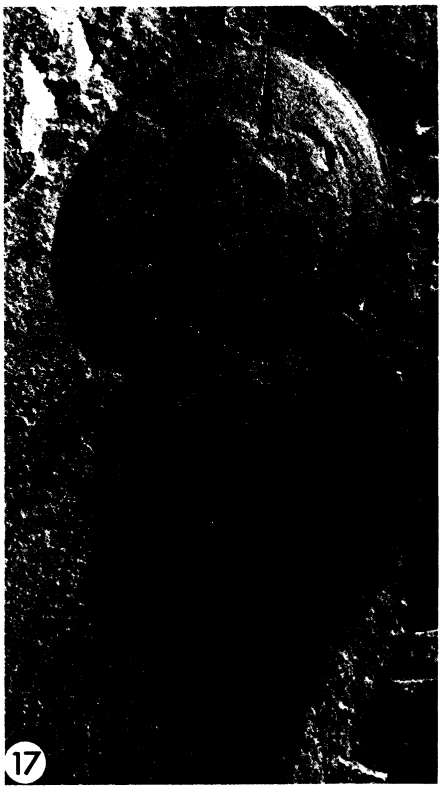
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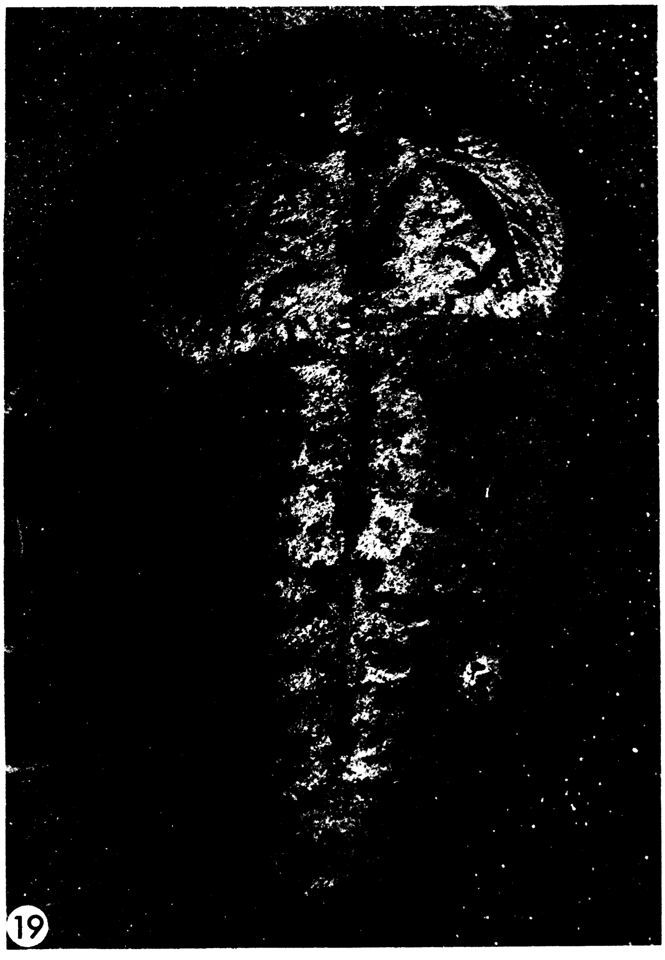
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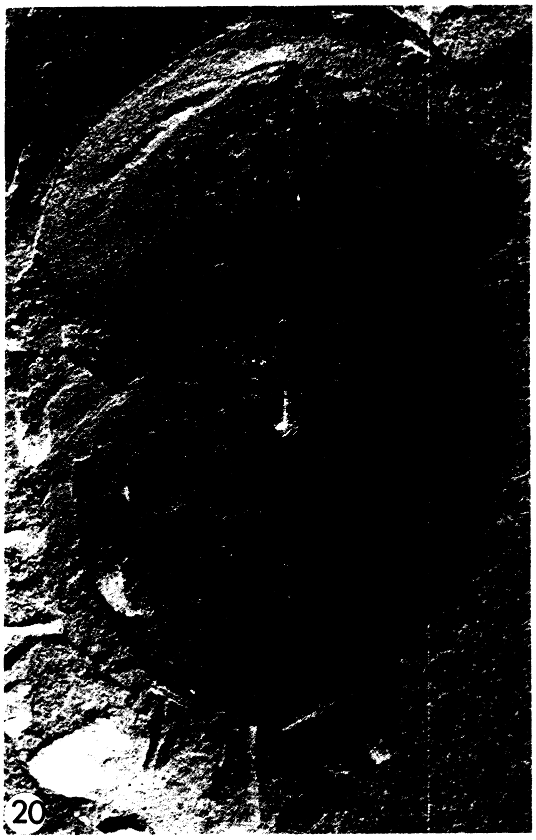
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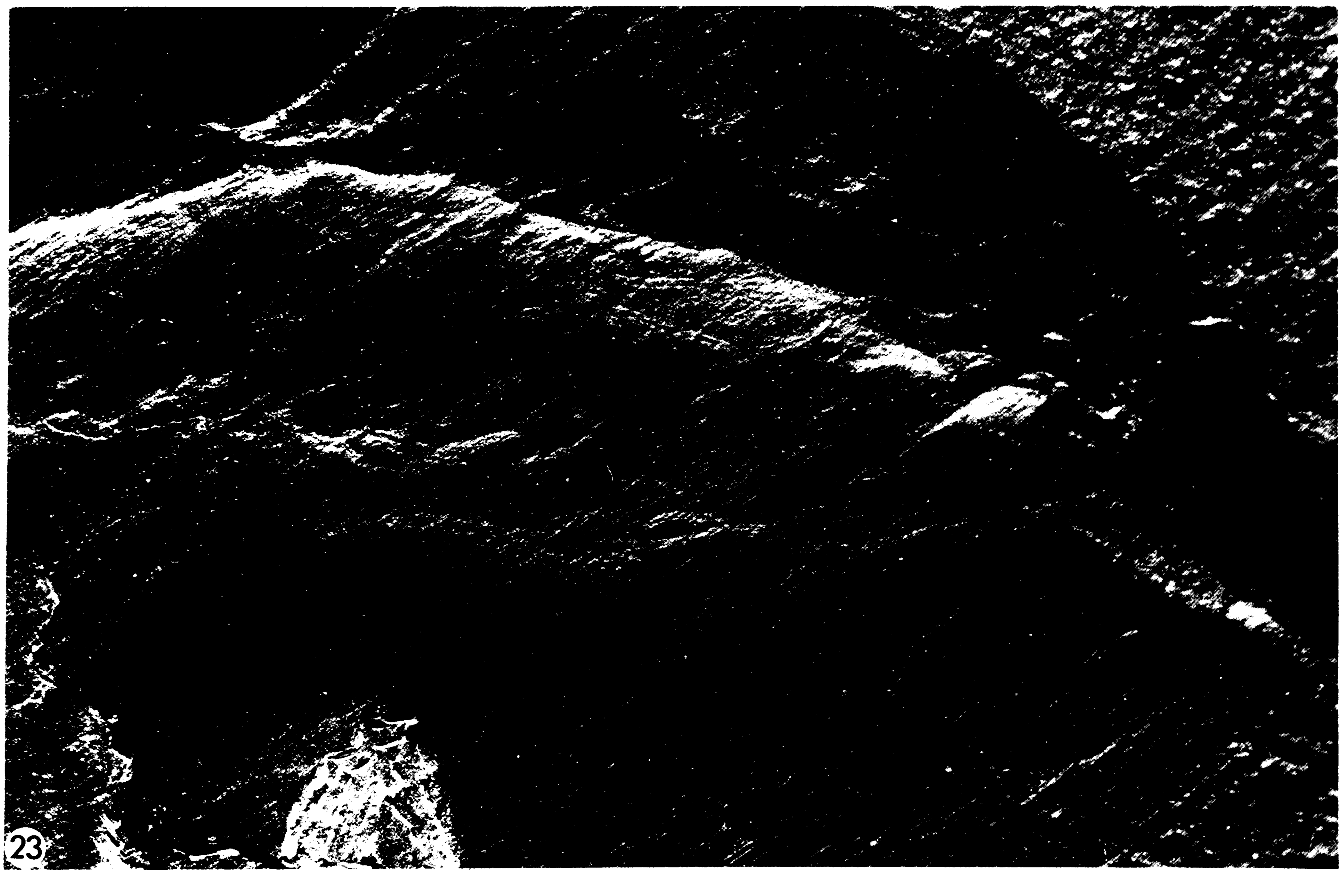

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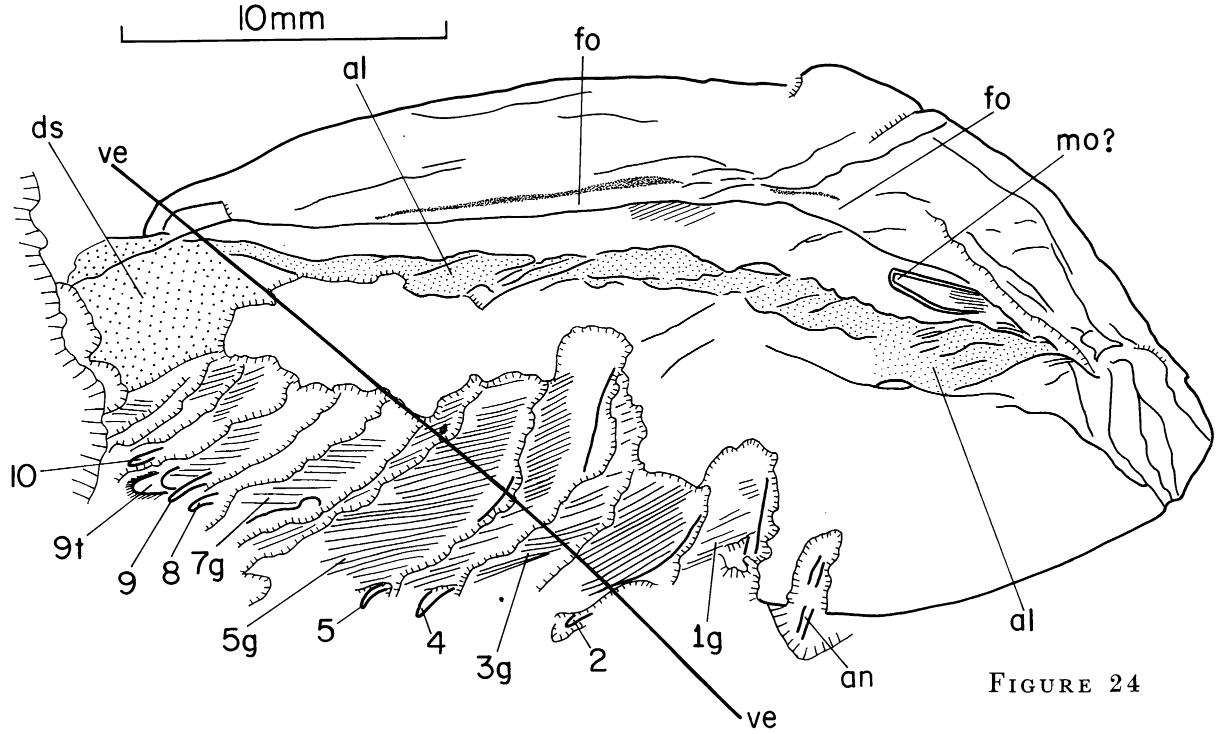

FIGURE 24

DESCRIPTION OF PLATE IV AND FIGURE 24

Naraoia compacta Walcott, 1912. Part (U.S.N.M. 189202) and counterpart (U.S.N.M. 189215), lateral oblique, Phyllopod bed, Walcott quarry

FIGURE 21. Counterpart, northwest (magn. × 3.3).

FIGURES 22, 23. Part, original of Simonetta & Cave 1975, pl. XXXIV, fig. 5, respectively northwest (magn. × 3.3); anterior portion, north (magn. × 10).

FIGURE 24. Composite explanatory drawing.

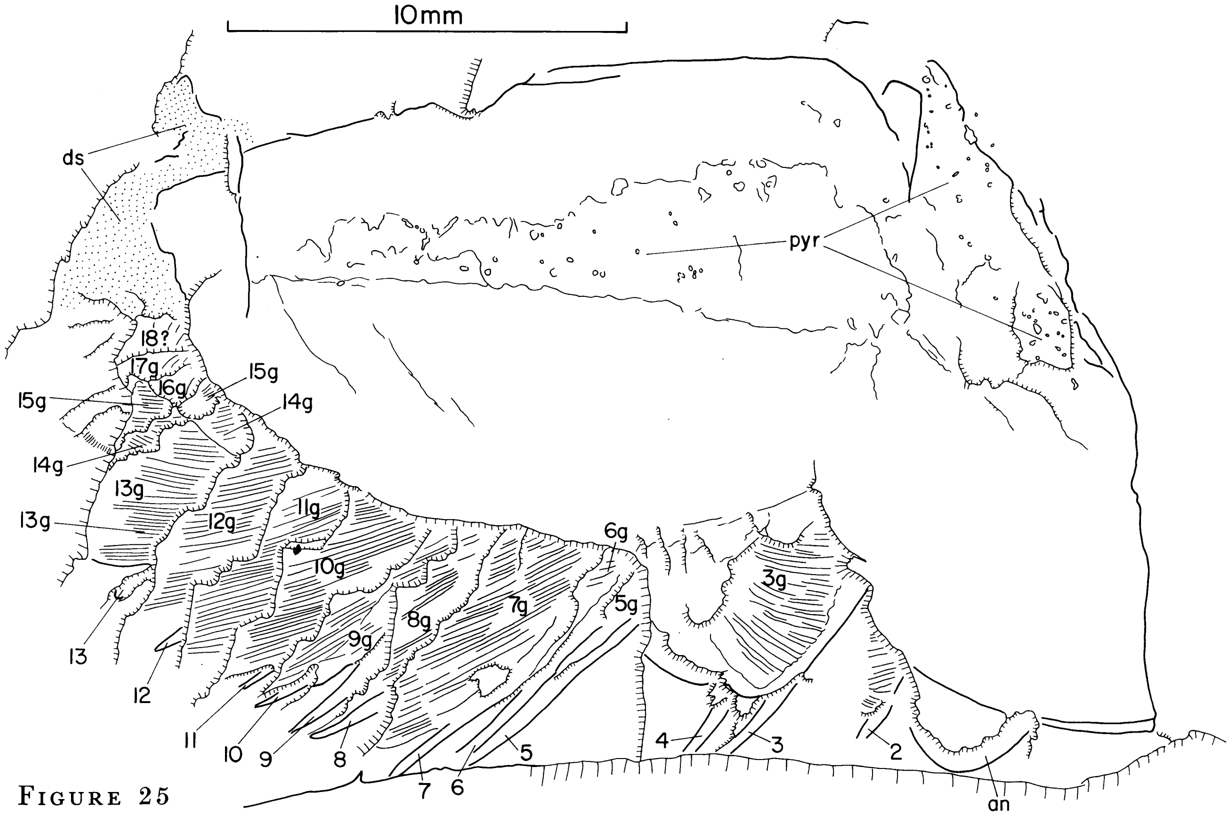

FIGURE 25

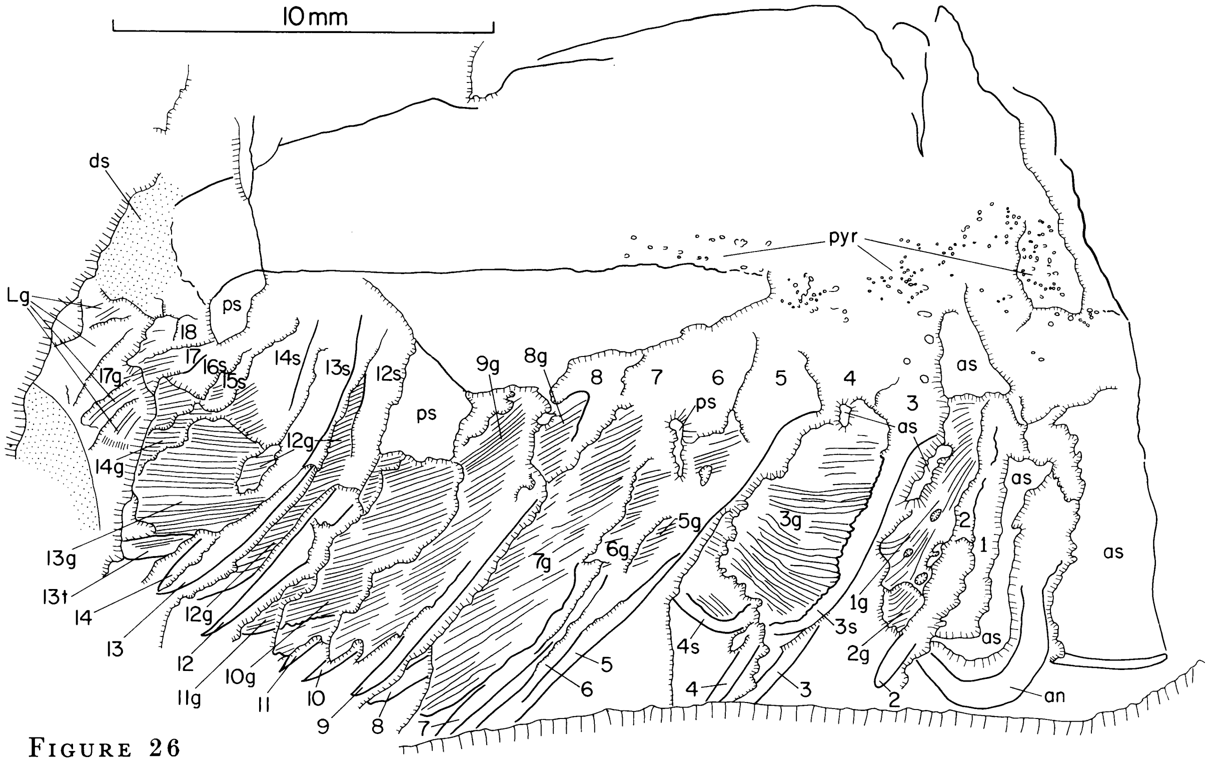

FIGURE 26

DESCRIPTION OF PLATE V AND FIGURES 25, 26

Naraoia compacta Walcott, 1912. U.S.N.M. 189216, lateral oblique, part only, Phyllopod bed, Walcott quarry. Original of Simonetta & Cave 1975, pl. XXXV, fig. 4

FIGURE 25. Explanatory drawing before preparation; compare figure 28.

FIGURE 26. Explanatory drawing after preparation; compare figures 27, 29, 30.

FIGURES 27–30. Respectively after preparation, north (magn. × 2.8); before preparation, north (magn. × 3.3); posterior portion after preparation, south (magn. × 10); anterolateral portion after preparation, north (magn. × 10).


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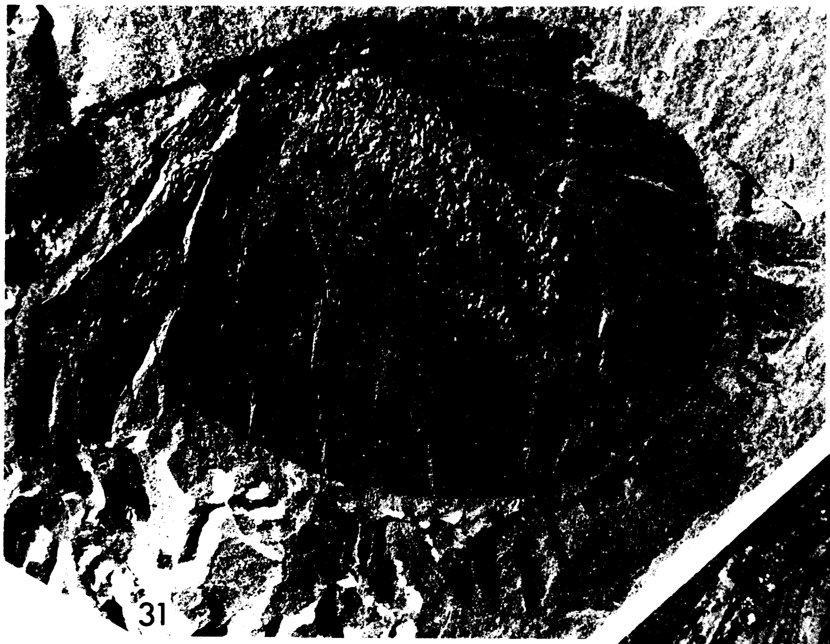

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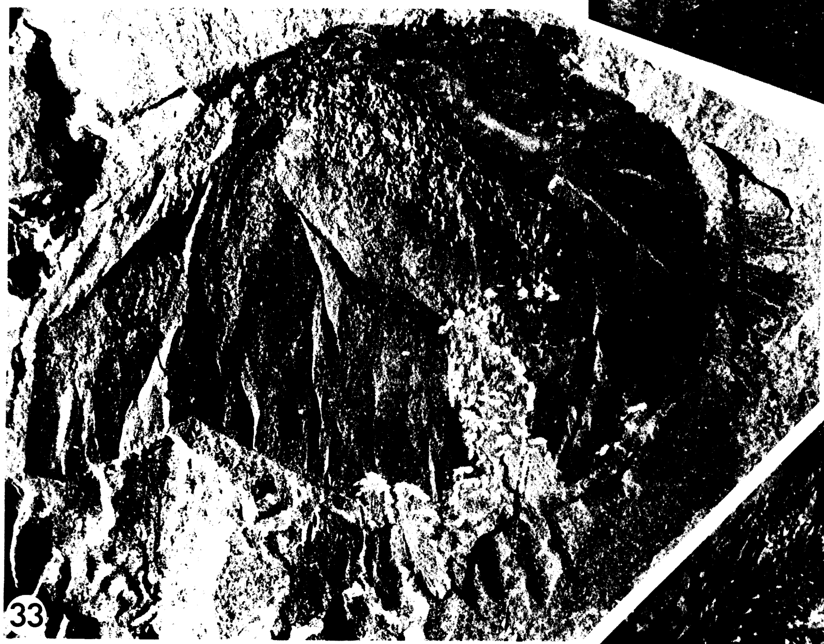

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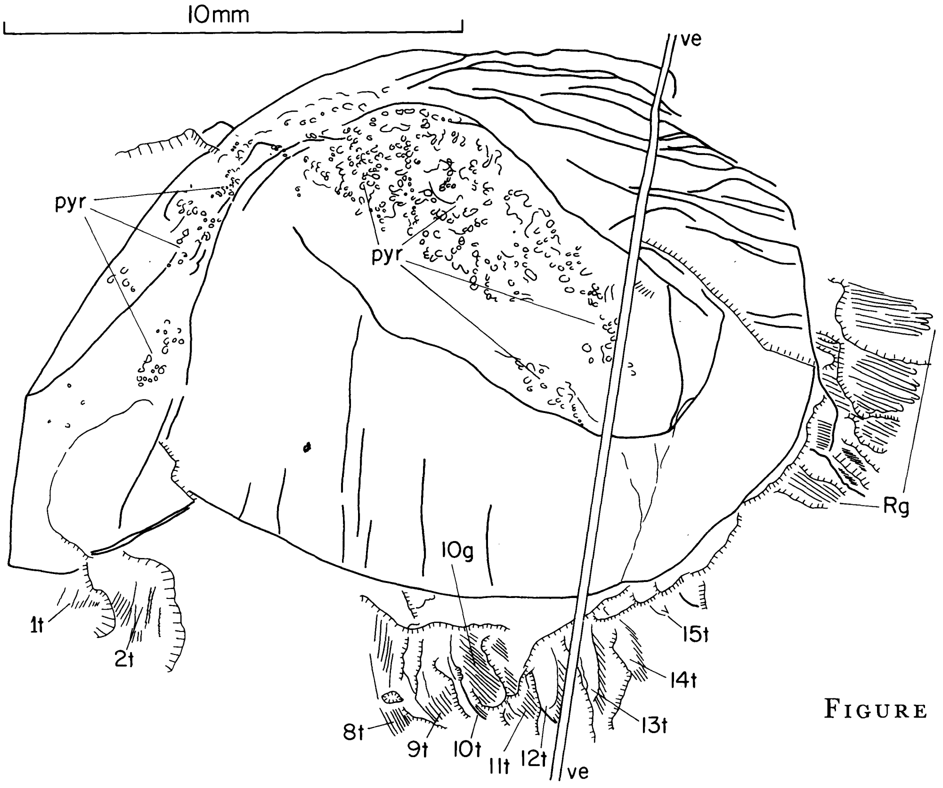

FIGURE 35

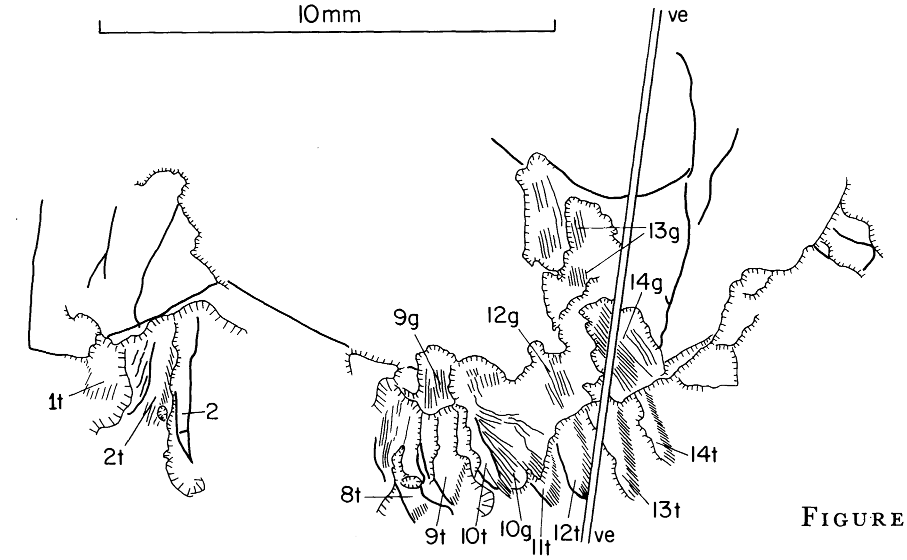

FIGURE 36

DESCRIPTION OF PLATE VI AND FIGURES 35, 36

Naraoia compacta Walcott, 1912. U.S.N.M. 189221, oblique, part only, Phyllopod bed, Walcott quarry. Original of Simonetta & Cave 1975, pl. XXXIV, fig. 6, before preparation

FIGURES 31–34. Respectively after initial preparation, northwest and reflected; after further preparation, west; after final stage of preparation, west (magn. × 5).

FIGURE 35. Explanatory drawing after initial preparation; compare figures 31, 32.

FIGURE 36. Explanatory drawing of portion of specimen after further preparation; compare figure 33.

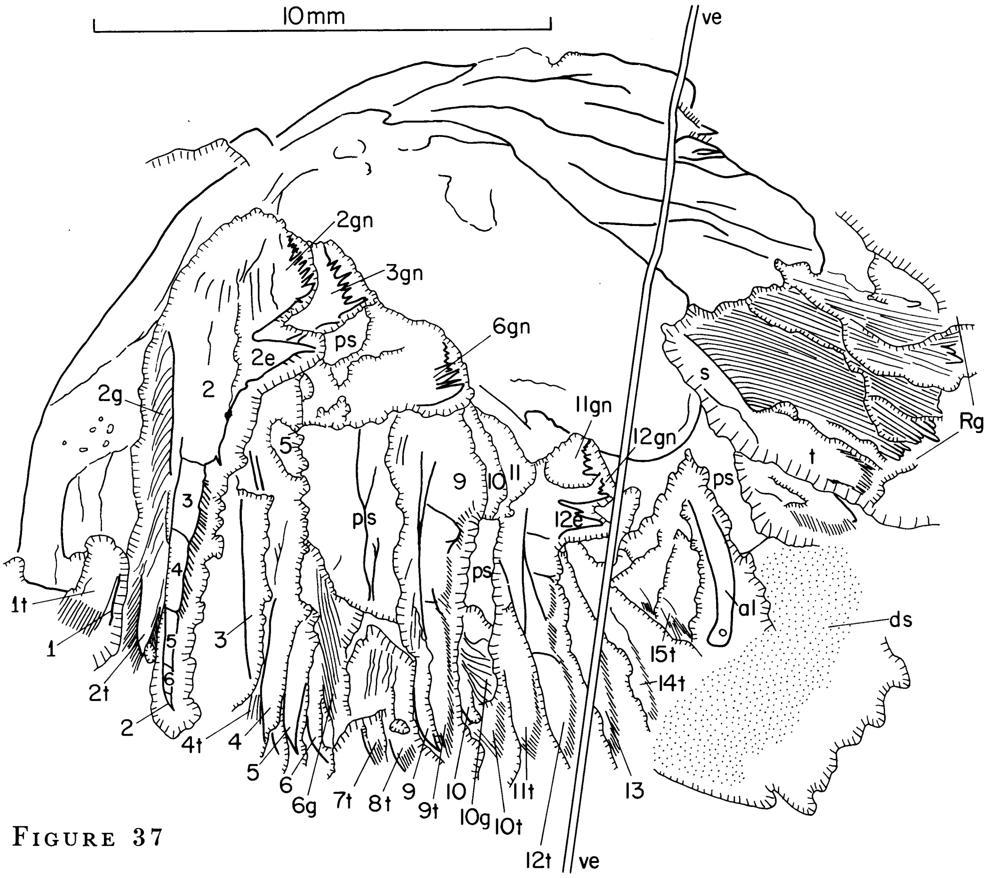

FIGURE 37

DESCRIPTION OF PLATE VII AND FIGURE 37

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURE 37. U.S.N.M. 189221, oblique, part only, explanatory drawing after final stage of preparation; compare figure 34, plate VI, and figures 38, 39, 42, plate VII.

FIGURES 38, 39, 42. U.S.N.M. 189221, oblique, part only, respectively detail of posterior portion, reflected and south, detail of appendages of left side, south (magn. × 10).

FIGURES 40, 41. U.S.N.M. 241029, parallel, part only, respectively reflected, west (magn. × 5).


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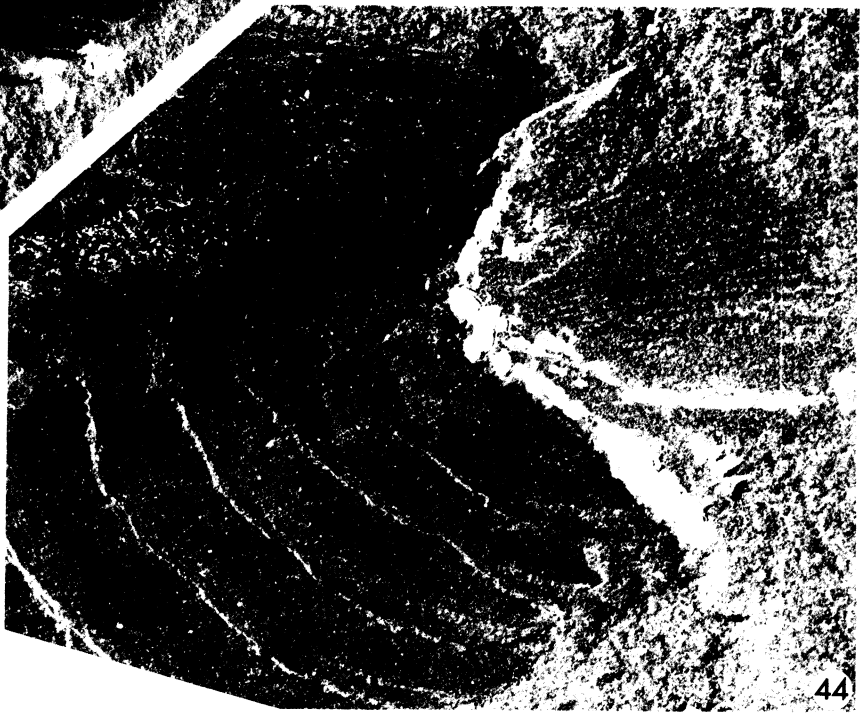
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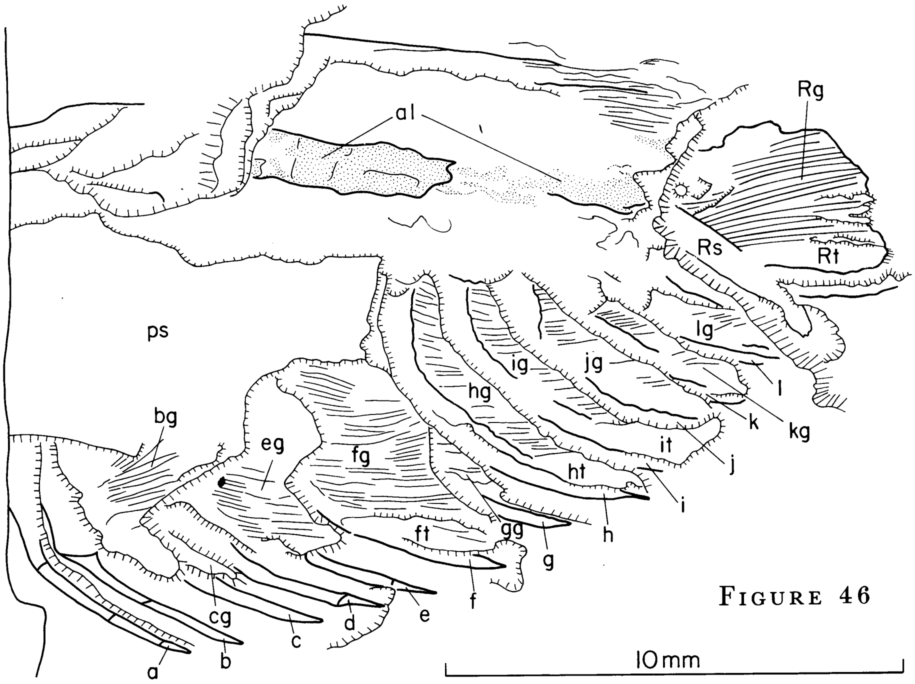

FIGURE 46

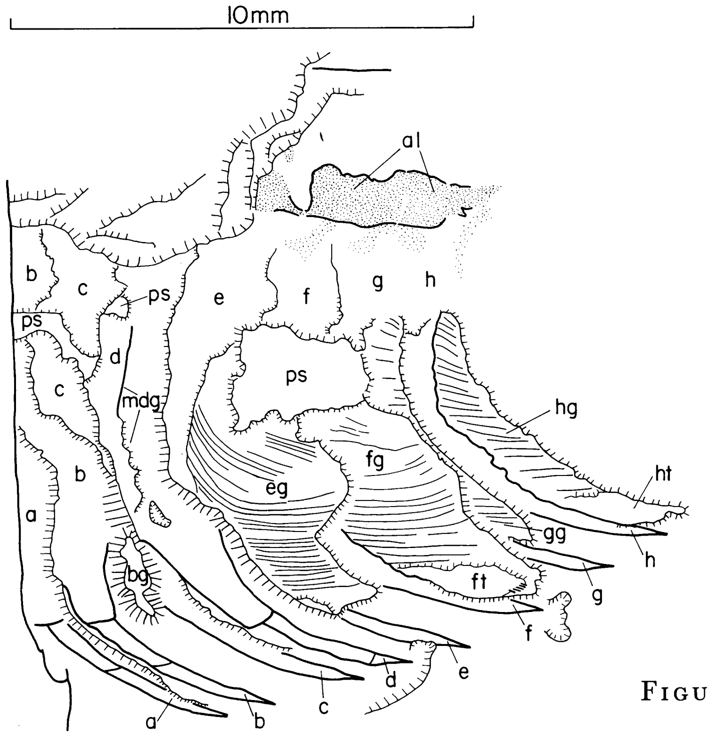

FIGURE 47

DESCRIPTION OF PLATE VIII AND FIGURES 46, 47

Naraoia compacta Walcott, 1912. U.S.N.M. 189222, incomplete lateral oblique, part only, Phyllopod bed, Walcott quarry. Original of Simonetta & Cave 1975, pl. XXXIV, fig. 4, before preparation

FIGURES 43–45. Respectively before preparation, west (magn. × 5); posterior portion after preparation, east (magn. × 10); anterior portion after preparation, west (magn. × 10).

FIGURE 46. Explanatory drawing before removal of posterior shield, compare figures 43, 44. Series of left appendages arbitrarily labelled a to l.

FIGURE 47. Explanatory drawing of anterior portion after removal of posterior shield, showing left appendages a to h; compare figure 45.

In his original description, Walcott (1912, p. 176, pl. 28, fig. 4) referred to 57687 as showing an abdomen including a 'telson-like extension', and later (1931, p. 12, fig. 1) portrayed an anal segment projecting behind the posterior shield and a spinose telson. Størmer (1944, p. 86, fig. 17, 4; 1959, p. O 30, fig. 18, 2) accepted this interpretation in his new restoration in dorsal view. Simonetta & Cave's restoration (1975, pl. V, figs. 9*a*, 9*b*) shows a telson as a thick spine without lateral barbs. They refer to it (Simonetta & Cave 1975, p. 4) as 'movable' but admit that it 'is not clearly preserved in any of the specimens studied'. I cannot see evidence of such a plate in any of the specimens figured herein, nor in the additional material, at whatever angle they are compressed. In the majority the overlapping gill branches project posteriorly beyond the shield, as they do in 57687 (figures 5–8, plate I). In this specimen the appendages on each side are directed backward, imbricated in the opposite sense on each side, and meet behind the axial region. It is the fortuitous way in which the two series of appendages overlap, and the position of the split between part and counterpart, which gives the appearance of a triangular projection behind the posterior shield. The presence of the dark stain (see §3 and figure 4) tends to accentuate this appearance. The similar conditions in 83945b (figure 9, plate II) give no such appearance, and there is no sign of a 'telson' in lateral (figures 21, 22, plate IV; figure 28, plate V), oblique (figures 31–34, plate VI) or vertical (figures 65, 67, plate XII) specimens. I conclude that there is no posterior spine, nor do I see evidence of an anal segment projecting behind the shield.

(*g*) *Antenna*

The antenna is preserved emerging from beneath the lateral margin of the anterior shield, in parallel or parallel oblique (figure 13, plate II; figures 60, 61, 64, plate XI) and lateral oblique (figure 28, plate V) compressions, at a point opposite the anterior part of the axial region. In figures 5, 7, plate I, it emerges farther back, presumably because of the oblique-forward tilt of the anterior shield. It tapers progressively, the segments (figure 51, plate IX) proximally shorter in length (long.) than width, becoming longer toward the slim tip (figure 13, plate II), which is poorly preserved. The right antenna in the latter example shows each segment narrowing proximally, apparently without setae at the junctions. The length of the projecting portion approaches the length (sag.) of the axial region of the anterior shield. In three specimens (figure 30, plate V; figure 54, plate X; figure 60, plate XI) it has been possible to follow the antenna inwards for some distance beneath the anterior shield. It appears to become slightly wider inwards, to be segmented, and to run towards the most anterior part of the axial region. A point of attachment to the body is suggested (figure 96), in agreement with these specimens. Walcott (1931, p. 12) stated that the antenna had a large proximal joint, which he showed by dotted lines in his restoration (1931, fig. 1), but offered no evidence.

(*h*) *Biramous appendages*

A series of specimens compressed in parallel oblique, oblique and lateral oblique attitudes, and one in a vertical oblique attitude, have been prepared to study these appendages. The explanatory drawings show my interpretation of an individual specimen, and the following notes draw attention to particular points. A summary of my conclusions is given in §4(*i*).

The proximal parts of the appendages have been revealed by excavation through the shields, and one of the best-displayed is appendage 6 of 199815 (figures 81, 84, plate XIV), which though incomplete has both branches compressed in the same plane. The coxa (podomere 1) is large, subtriangular in outline, flattened antero-posteriorly, the adaxial margin (the gnathobase) bearing many short spines overlapping at their bases and a long, curved spine at the ventral tip. The dorsal margin of the coxa is not defined in this or any other specimen, presumably because it was less heavily sclerotized than the gnathobase; the coxa-body junction is therefore unknown. Podomere 2 is shorter (long.), also subtriangular in outline and flattened antero-posteriorly, and bears a long, inward-curving, pointed endite. Podomeres 3–5 are subequal in length (long.) to 2, presumably sub-oval in cross-section, successively narrower and bearing small, outward and downwardly directed spines on the ventral edge; podomere 6 is the shortest (long.), articulated to it is the thorn-like terminal spine. In this specimen the coxa and leg branch are displayed posterior side toward the observer and were buried and compressed with the maximum cross-sectional dimension sloping backward and slightly downward. Adjacent to the dorsal margin of podomeres 2–4 of the leg branch is a smooth band, from the outer edge of which long, slim lamellae are directed forward and outward. Beside the most distal of these lamellae is an oval lobe, basally merging into the smooth band, marginally bearing fine setae. These structures constitute the gill branch of the appendage, the smooth shaft bearing lamellae and the terminal lobe. The proximal part of the branch is not preserved in this specimen, but the shaft and leg branch are parallel. As other specimens show, the gill branch is here ventral side toward the observer. In 199815 (figures 81–84, plate XIV) parts of the antenna and appendages 1–12 are visible on the left side, the leg branches imbricated to pass each below the one succeeding. Parts of gnathobases and endites of 5, 6, 11 and 12 have been exposed, all similar in form and imbrication; leg branches 11 and 12 smaller than 6. Gill lamellae and terminal lobes are preserved, sloping upward and forward and imbricated in the same way as the leg branches. The terminal lobe of appendage 3 (figures 82, 83, plate XIV) shows particularly clearly the marginal setae.

In 83945b (figures 9–12, plate II) parts of 18 gill branches are displayed on the left side, the shafts directed in a radial pattern, the lamellae directed outward and back from each shaft, sloping up toward the observer, an opposite arrangement to that in 199815. Parts of the shafts and terminal lobes are exposed at the anterior edges, beneath the broken distal parts of the lamellae of the preceding branch, e.g. terminal lobes 7, 8, and shafts 9, 11, 12. The overlap between successive gill branches is shown, and the dorsal face is toward the observer. The lamellae of gill branches 1 and 2 were exposed only after cutting through the overlying anterior shield, and no part of appendage 1 originally projected beyond the edge of the shield. Parts of coxae and leg branches 1–6 were revealed by cutting through the overlying gill filaments (compare figures 9 and 10, plate II). Both slope downward and backward, so that gnathobase 5 is exposed beneath 6, and the extremities of leg branches 1, 2, 5 and 6 lie deepest down. Compared to 199815 (figure 84, plate XIV) the endite and gnathobase of 3 and 6 lie closer together, overlapping at the junction and the endite directed more strongly inward. This suggests that the coxae and leg branches were buried with the antero-posterior faces directed more strongly downward than in 199815 (compare figure 1*c*, *d*). Posteriorly on the right side of 83945*b* (figures 9, 10, plate II) an imbricated series of sheets of lamellae is displayed outside the shield, the lamellae directed outward and backward. Partial excavation of one sheet shows the shaft and the lamellae curving out from it. If the appendages were symmetrically arranged, the lamellae should be on the inner side of the shaft, and directed inward and backward. Apparently on the right posterior side of this oblique compression the gill branches lie ventral side towards the observer, overturned relative to those on the left side.

The oblique compression 189221 was drawn and photographed at successive stages of preparation (figures 31–34, plate VI; figures 35–37; figures 38, 39, 42, plate VII). It shows coxae and leg branches of the left side arranged much as in 199815, subparallel to each other and imbricated to slope back and down below the one following. Parts of gnathobases and endites of 2, 3, 6, 11 and 12 have been exposed below the edge of the axial region, endite 2 showing small spines on the major spine. The distal part of leg branch 2 is exposed, gill branch 2 lying in front of it, the lamellae curving forward, outward and upward, ventral face toward observer. Only the distal tips of succeeding leg branches are exposed, beneath the overlying gill branches. In appendage 6, for example, the distal podomeres of the leg branch are overlain by the terminal lobe and the lamellae, the latter directed upward, outward and backward, i.e. dorsal face toward the observer. Terminal lobes 6–14 are imbricated in the same sense as the leg branches (figures 37 and 34, plate VI), fragments of lamellae lying at a higher level and arranged as in gill 6. I interpret this arrangement as showing each gill branch was directed out parallel to the leg branch, in 1 and 2 ventral side toward observer, but in 6–14 only the terminal lobe is ventral side toward observer, but the lamellae curve upward and outward through 180° so that they are dorsal side to the observer, and imbricated in an opposite sense to the lobes (figure 36 and figure 33, plate VI). In the three specimens described leg branch and gill shaft are aligned and close together along their length. Appendages 1 and 2 of 83945b (figure 14 and figure 10, plate II), and 2 of 189221 (figure 37 and figure 42, plate VII), show that shaft and gill lamellae extend far inward, to the level of the coxa-podomere 2 joint. This arrangement suggests that the gill branch arises from the dorsal side of the coxa, and that the shaft of the gill branch is rigidly attached and of limited flexibility.

In two parallel compressions the anterior appendages of the right side are directed forward and slightly outward. In 114258 (figures 49–51, 53, plate IX) the shafts (with which are associated reflective bands) of gill branches 1–7 are subparallel, the subparallel lamellae of successive branches showing a radial arrangement. In branch 7 the filaments appear exceedingly long, as they do in succeeding branches. This is explained as resulting from flexure of the shaft distally, i.e. that in branch 7 the shaft is proximally directed forward and outward, and distally curves back. The underlying coxae and leg branches in 114258 have not been excavated, but in 235844 some have. In this specimen (figures 87–90, plate XV; figure 94, plate XVI) there is a radial arrangement of appendages 1–7, and the coxa and leg branch were extended and curved down in a plane slightly oblique to the vertical. The gnathobases 2–4 are compressed dorso-ventrally (at right angles to the direction in 199815, figure 84, plate XIV) and appear as a mass of short spines, while the leg branch curves down progressively farther away from the observer. Coxae and leg branches 7 and 8 are directed more strongly outward, and the branch curves back and down beneath that following. The lamellae of each gill branch, in 114258 and 235844, slope upward and outward and are imbricated over those of the following branch. The overlap between successive lamellae in each branch is also displayed (figure 53, plate IX; figure 89, plate XV).

A remarkably symmetrical arrangement of the appendages is shown by 241030 (figure 54, plate X; figure 64, plate XI) a parallel compression with the anterior shield tilted down. The arrangement is radial, the gill branches curving back distally, the lamellae directed strongly outward and upward, overlying and thus concealing the shaft and terminal lobe, except where revealed by preparation. The distal parts of left leg branches 4, 5 and 6, and of right leg branch 5, curving backward and downward, have been revealed beneath the gill branches.

Preparation close to the infilling of the alimentary canal has also revealed the coxae and endites of right appendage 5 and left appendages 5–7 (figures 54, 56, plate X). The endites project back behind and below the coxa (the condition seen in 83945b, figure 10, plate II), an attitude which implies that the coxae and leg branches were buried inclined at a steep angle downward and backward (compare figure 1*c*, *d*). No attempt has been made to prepare 241030 in front of the appendage here labelled 1, but in 235844 (figures 88, 90, plate XV), in which the anterior shield is not tilted downward, the first appendage appears to lie relatively further forward. A crowding backward of anterior appendages in 241030 (and in 114258, figures 49–51, plate IX) may result from compression of the forward and downward-tilted anterior shield, so that the appendage labelled 1 may be the most anterior in these specimens.

The originals of figures 5–8, plate I, and figures 60, 61, plate XI, show arrangements of appendages analogous to those described – lamellae of gill branches sloping upward and backward, over those of the succeeding branch, the shaft and terminal lobe overlying the leg branch. The latter curves back and lies in a plane that passes down and backward below the plane in which the succeeding leg branch lies. In 57687 the most anterior left appendage emerging from beneath the anterior shield is labelled 1, although in the similarly preserved 83945b preparation revealed (compare figure 9 with figure 10, plate II) a hidden, more anterior appendage in front of the most anterior projecting beyond the shield. I have preferred not to prepare the lectotype, but the photograph taken under liquid (figure 7, plate I) does not suggest the presence of a more anterior appendage beneath the anterior shield. In the oblique compression 241037 the photograph under liquid (figure 61, plate XI) suggests that there is another appendage concealed beneath the anterior shield, between the right antenna and the gill branch labelled 2. In this specimen the appendages do appear to have been crowded back by compression. The oblique specimen 241038 (figure 18, plate III) shows appendages in ventral aspect, outside the shields, and particularly the relations between shaft, lamellae and terminal lobe.

Lateral oblique compressions show the sheets of gill lamellae imbricated each over that following, the length of the lamellae, and details of the proximal parts of the appendage. In 189202 (figures 21–23, plate IV) an attempt was made by preparing gill branch 5 in the counterpart to show the length of the lamellae, and consequent considerable overlap. This overlap is also shown by 189216 (figures 27–30, plate V), particularly by gill branches 7–12 in which the extremities of the lamellae reach to the second appendage following despite their strongly outward inclination. In gill branches 3 and 4 of 189216 the shafts are curved back distally, showing they are separate structures from the leg branches, which project from below them. It was not possible to prepare the antenna more than a limited distance adaxially in this specimen, and appendages 1 and 2 are not well preserved. The proximal parts of appendages 3 to 8 were exposed (figure 30, plate V), broad and imbricated in the opposite sense to the gill branches, and hence presumably coxae. On the other hand the proximal parts of appendages 12–16 (figure 29, plate V) are imbricated in the same sense as the gill branches, and so must be the shafts of these branches, lying on the coxae. The appearance of leg branches 12 and 13 from beneath the shafts distally supports this view. The fragments of gill branches of the left side, preserved posteriorly, show the obliquity of the compression. A third lateral oblique compression is 189222 (figures 43–45, plate VIII), which is unlike the other two in showing traces of three terminal lobes on the left side, and one has been exposed in ventral aspect on the right side; that these lobes are visible presumably reflects the different attitude of the gill branches in this specimen. Preparation of 189222 revealed the proximal parts of leg branches a–e, showing that while the distal portion of each branch (podomeres 5 and 6) is relatively long and slim, the proximal portion formed a broad, undivided strip. Successive strips are imbricated to slope adaxially and backward, rather than abaxially and backward as the gill branches. The innermost parts of appendages b–h (presumably the coxae) were also exposed adjacent to the axial region, and are imbricated in the same sense. Thus in 189222 and 189216 the two branches of the appendages lie in planes directed backward at an acute angle to each other, leg branches and coxae inclined adaxially, gill branches inclined abaxially. Both specimens show that the gill shaft with its lamellae originates close to the axial region, i.e. is probably attached to the dorsal edge of the coxa.

In an example of a vertical oblique compression (figures 65, 67, 69, 70, plate XII) the appendages are directed symmetrically downward and outward on each side, the two branches in the same plane. Appendage g on the right side has been most completely excavated, out of a series of thirteen (a–m) which lie in sheets one upon another. The posterior face of the leg branch and coxa, and ventral face of gill branch, are toward the observer. In appendage g the two branches lie side by side and lamellae arise from the gill branch in a series commencing opposite the coxa-podomere 2 joint, showing that the gill branch is attached to the dorsal margin of the coxa. The recognition of the endite of appendage h, and gnathobases of appendages j and k, show how far posteriorly in the appendage series these structures can be recognized. On the left side only parts of gill lamellae and terminal lobes have been prepared.

(*i*) *Conclusions on number, nature and attitude of appendages*

The interpretations given in figures 4, 14 and 26 show that there was one pair of uniramous antennae followed by 17, 18, or in a larger individual (figure 86), 19 pairs of biramous appendages. The originals of figures 14, 26, 48, 57 and 86 show unequivocally that the three pairs following the antennae were biramous. That of figure 14 provides the best evidence that these three biramous appendages belonged to the anterior shield in front of the articulation, since the dorsal edge of coxa 3 lies in front of the articulation and approximately in a transverse line with the third pair of muscle areas. In figure 48 the inner end of right gill shaft 3 is shown to lie just in front of the articulation, while in figure 86, gnathobases 3 and 4 are both in front of the articulation. In figure 57, the inner ends of appendages 3 are considered to lie behind the articulation, as in the original of figure 58. Crowding back of the appendages by compression, as a result of the attitude in which the body was buried, is invoked as an explanation. In the lectotype (figure 4 and figure 7, plate I) similar crowding back is suggested by the position of the antennae, and the anterior shield was compressed obliquely. I here accept the evidence of the most completely prepared specimen, shown in figure 14, which is not in conflict with that of other specimens if allowance is made for vagaries in preservation. The fourth pair of biramous appendages appears to have been attached to the body behind the articulation, in the area of overlap between the two shields (figures 14, 48), i.e. to have been the first pair of the posterior shield.

The biramous appendage (figures 37, 85) consists of a large coxa, subtriangular in outline with a proximal gnathobase, to which the leg branch was articulated on the abaxial side and the gill branch attached on the dorsal side. In all types of compressions – parallel (figures 4, 57), oblique (figures 14, 37, 85), lateral (figures 26, 46) and vertical (figure 72) – the two branches of the appendage are aligned, the shaft of the gill branch and the leg branch lying close together.

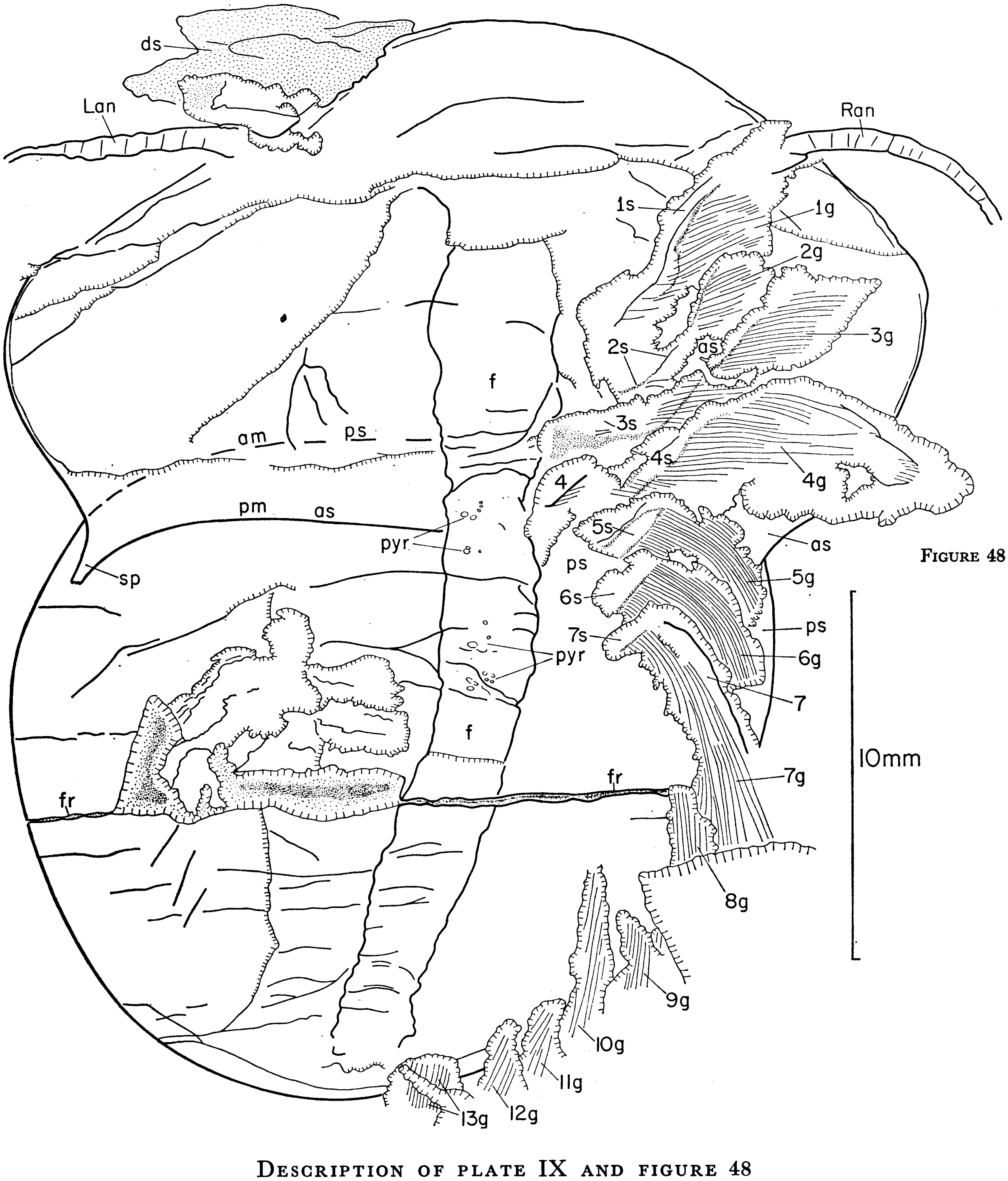

FIGURE 48

DESCRIPTION OF PLATE IX AND FIGURE 48

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURE 48. Composite explanatory drawing of U.S.N.M 114258. Stippled are fracture, dark stain, and reflective bands on shafts of gill branches.

FIGURES 49, 51, 53. U.S.N.M. 114258, parallel, part, after preparation, respectively northeast (magn. × 3.3); reflected (magn. × 2.5); portion of right side, north (magn. × 10). Original of Simonetta & Cave 1975, pl. XXXIII, fig. 1b, before re-arrangement of fragments and preparation.

FIGURE 50. U.S.N.M. 114258, parallel, counterpart, prepared to show posterior margin of anterior shield, north (magn. × 3.3). Original of Simonetta & Cave 1975, pl. XXXIII, fig. 1a, before preparation.

FIGURE 52. U.S.N.M. 189219, part, reflected (magn. × 5.0). Original of Simonetta & Cave 1975, pl. XXXV, fig. 1 (their pl. XXXIII, fig. 2, is of the counterpart, numbered 189249 in error).

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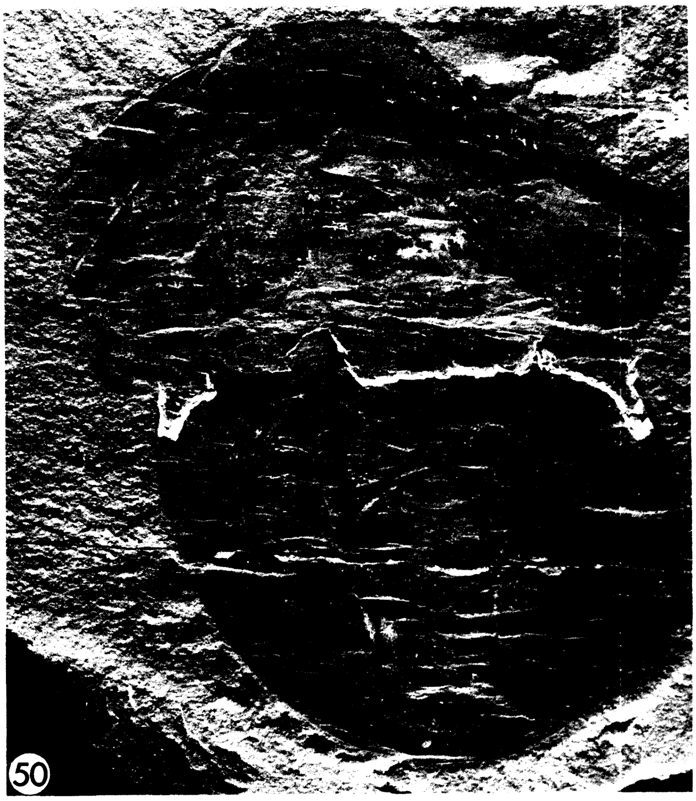

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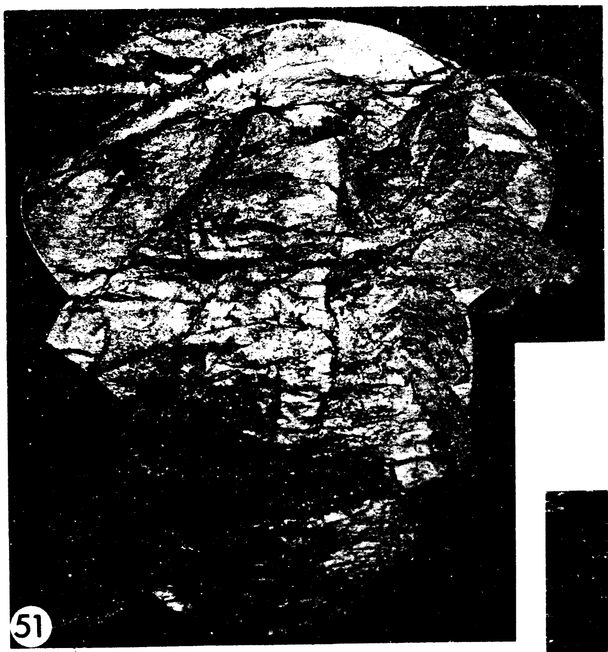

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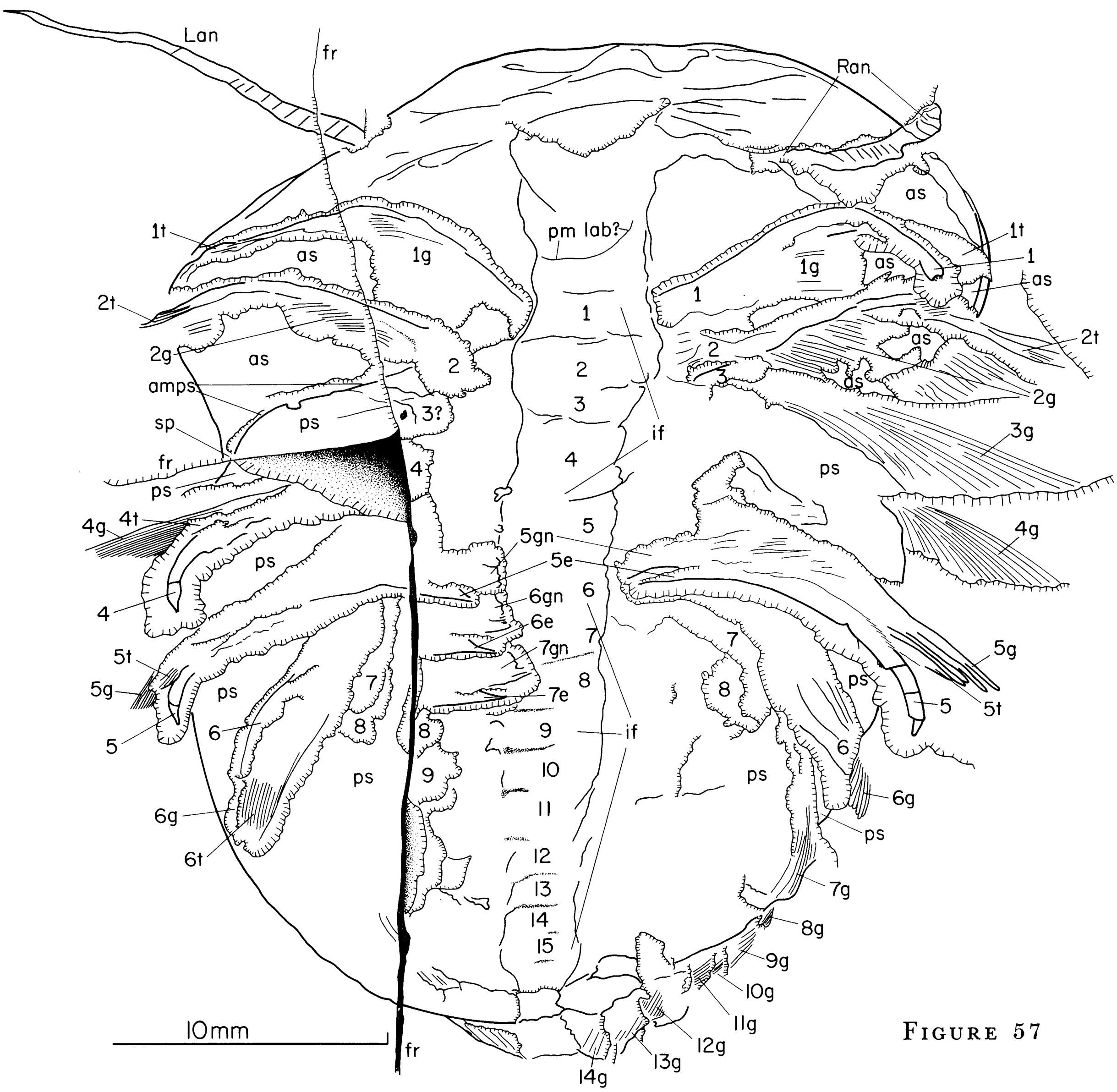

FIGURE 57

Description of plate X and figure 57

Naraoia compacta Walcott, 1912. U.S.N.M. 241030, parallel, part only, after preparation, Phyllopod bed, Walcott quarry

FIGURES 54–56. Respectively northwest (magn. × 4); parts of right appendages 2–5, north (magn. × 10); parts of left appendages 4–9, west (magn. × 10).

FIGURE 57. Explanatory drawing.

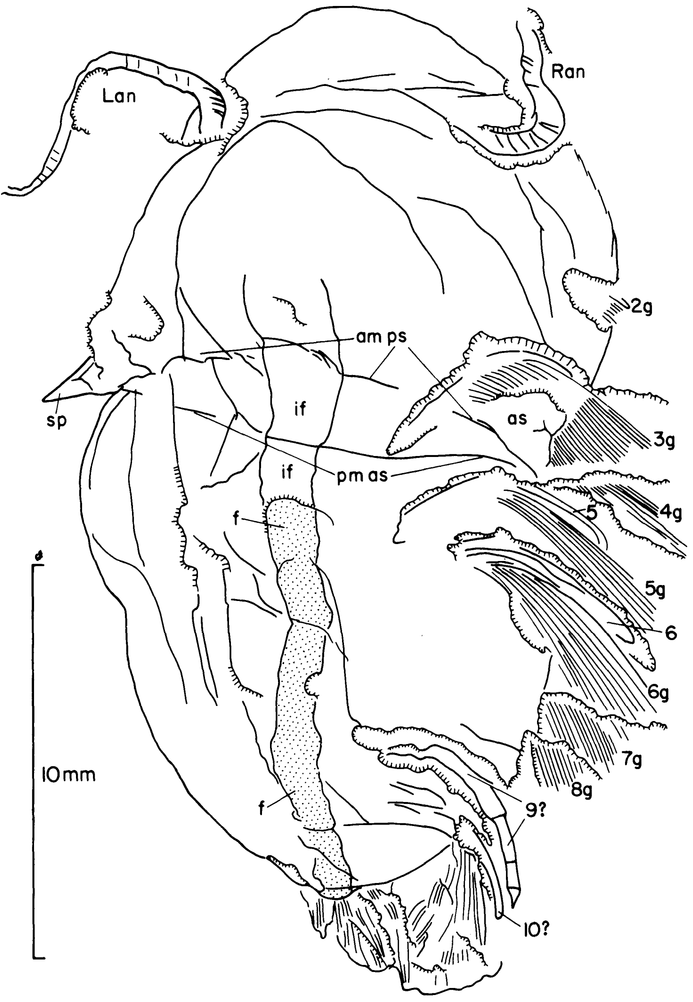

FIGURE 58

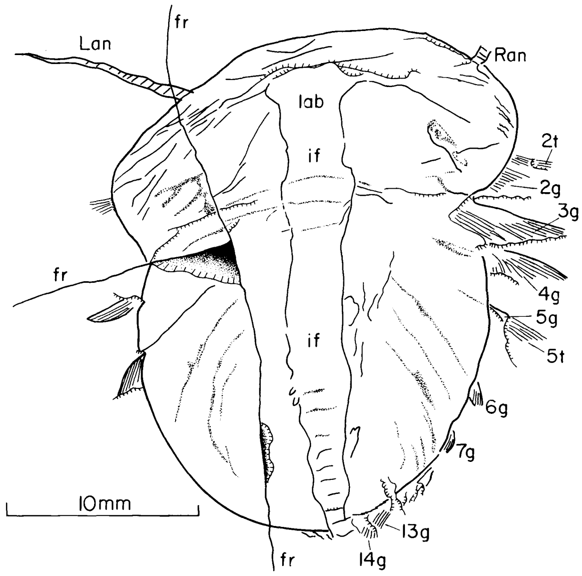

FIGURE 59

DESCRIPTION OF PLATE XI AND FIGURES 58, 59

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURE 58. Explanatory drawing of U.S.N.M. 241037.

FIGURE 59. Explanatory drawing of U.S.N.M. 241030, compare figure 57.

FIGURES 60, 61. U.S.N.M. 241037, oblique, part only, after preparation, respectively north (magn. × 5); photographed under alcohol (magn. × 5).

FIGURE 62. U.S.N.M. 189210, parallel, part only, cast exoskeleton, reflected (magn. × 3.3). Original of Simonetta & Cave 1975, pl. XXXV, fig. 7, as type of *Naraoia halia*.

FIGURE 63. U.S.N.M. 189212, parallel, counterpart only, cast exoskeleton, reflected (magn. × 3.3). Original of Simonetta & Cave 1975, pl. XXXV, fig. 8, as type of *Naraoia pammon*.

FIGURE 64. U.S.N.M. 241030, parallel, part only, before preparation, northwest, compare figures 54–56, plate X


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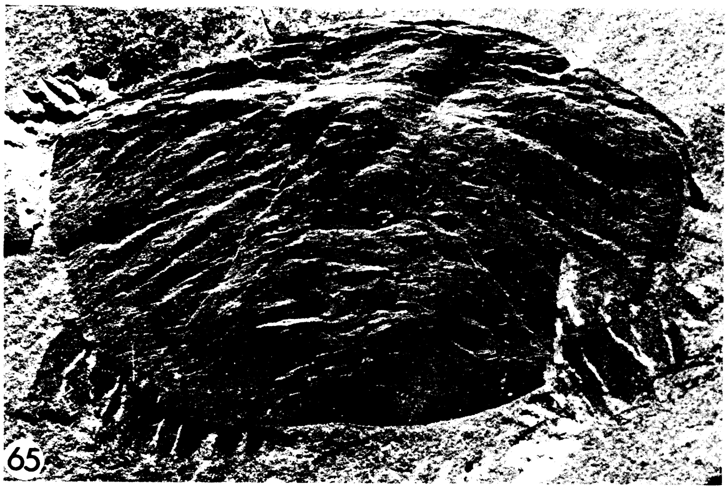
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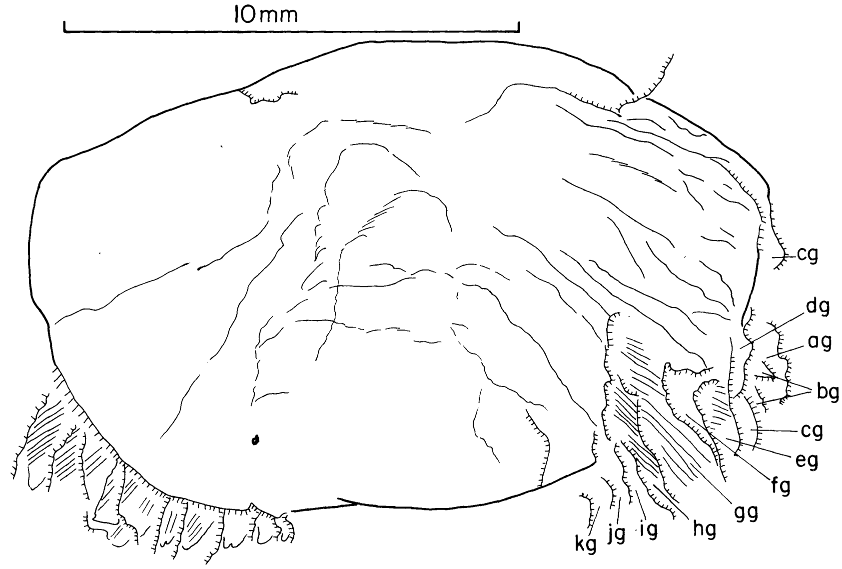


FIGURE 71

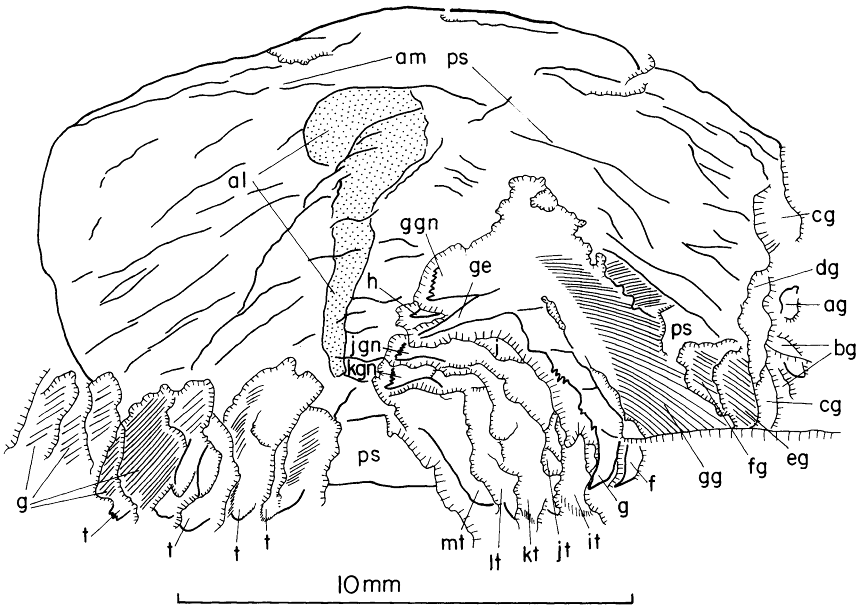


FIGURE 72

DESCRIPTION OF PLATE XII AND FIGURES 71, 72

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURES 65, 67, 69, 70. U.S.N.M. 241041, vertical oblique, part only, respectively at early stage of preparation, north (magn. × 5); completed preparation, north (magn. × 5); appendages of left side, south (magn. × 10); appendages of right side, northeast (magn. × 10).

FIGURES 66, 68. U.S.N.M. 235890, lateral oblique, the two shields flexed at right angles, part only, respectively reflected, southwest (magn. × 4).

FIGURES 71, 72. Explanatory drawings of U.S.N.M. 241041, respectively at early stage, and after, preparation. Series of appendages arbitrarily labelled a to m.

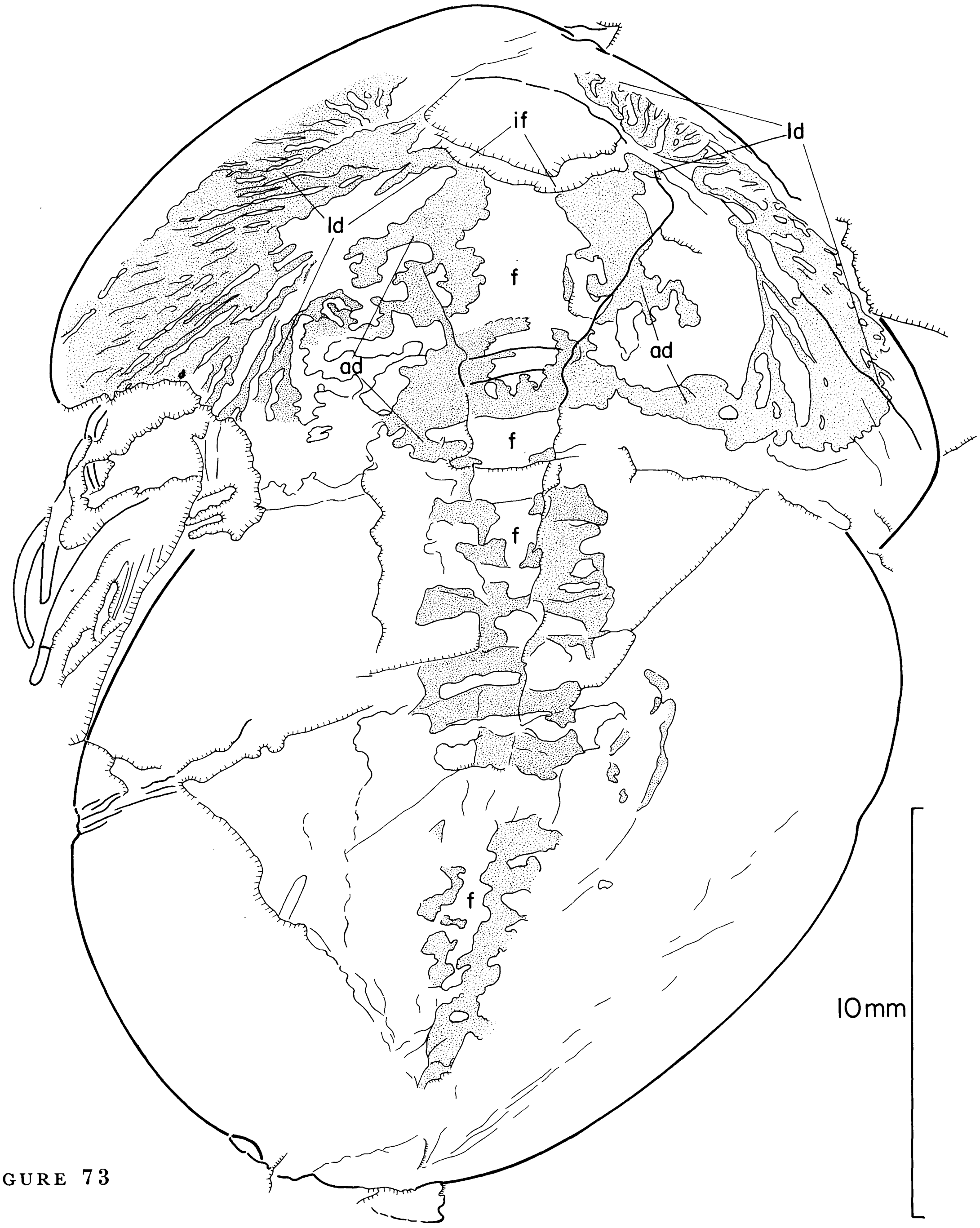


Figure 73

Description of plate XIII and figure 73

Naraoia compacta Walcott, 1912

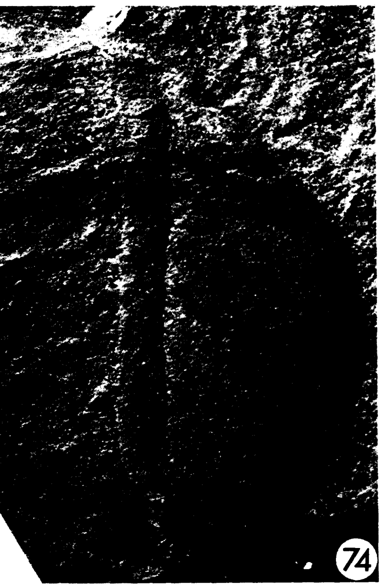
Figure 73. Explanatory drawing of G.S.C. 47967, fine stipple shows strongly reflective areas, compare figure 75.

Figure 74. U.S.N.M. 83945e, original of Walcott 1931, pl. 15, fig. 2, parallel oblique, part only, northwest (magn. × 3.3), Phyllopod bed, Walcott quarry.

Figures 75, 78. G.S.C. 47967, parallel oblique, part, respectively reflected (magn. × 3.3); reflected after removal of infilling of alimentary canal (magn. × 5); Walcott quarry, level 6 ft 11 in to 7 ft 2 in (2.1 m to 2.2 m).

Figures 76, 77. U.S.N.M. 241046, parallel oblique, counterpart, respectively northwest, reflected (magn. × 3.3), Phyllopod bed, Walcott quarry.

Figure 79. U.S.N.M. 57686, original of Walcott 1912, pl. 28, fig. 3, and Simonetta & Cave 1975, pl. XXXIV, fig. 1. Lateral oblique, part only, northwest (magn. × 5), Phyllopod bed, Walcott quarry. Extensive dark stain posteriorly.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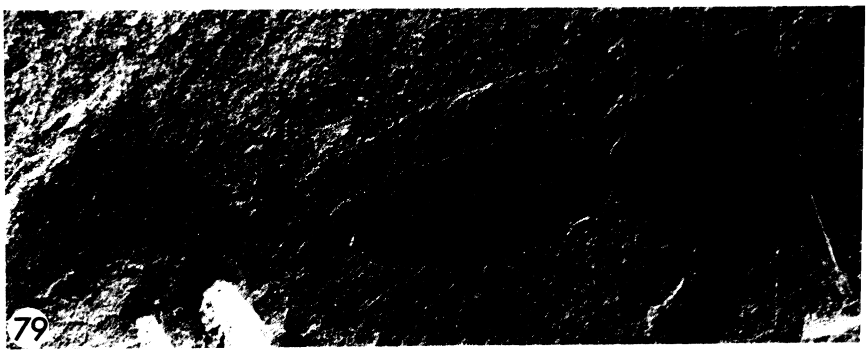
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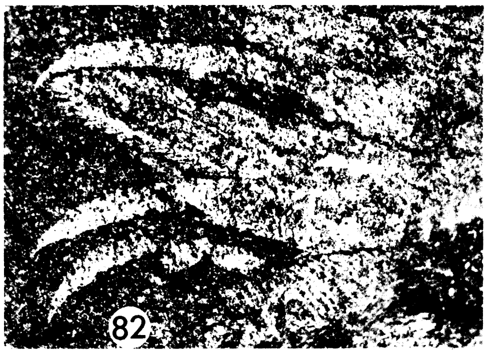
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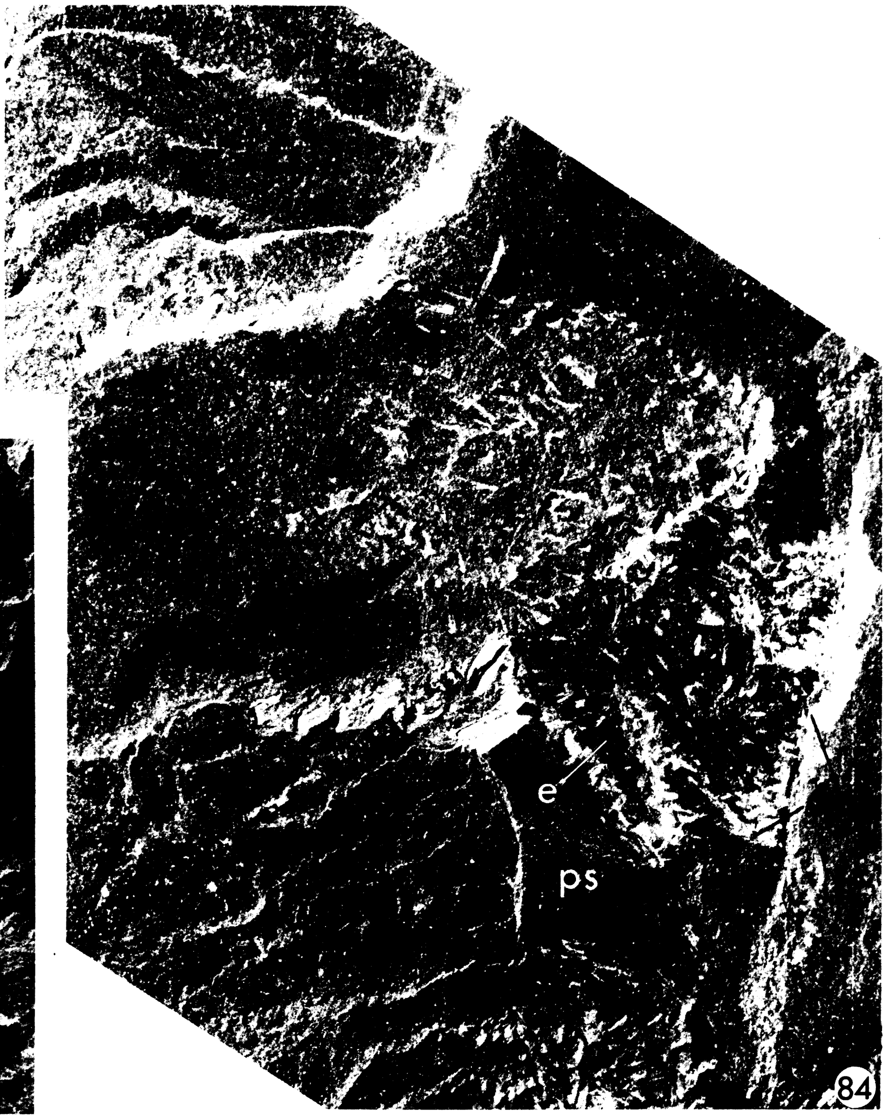

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FIGURE 85

DESCRIPTION OF PLATE XIV AND FIGURE 85

Naraoia compacta Walcott, 1912. U.S.N.M. 199815, oblique, Phyllopod bed, Walcott quarry

FIGURE 80. Counterpart, north–northwest (magn. × 3.3).

FIGURES 81–84. Part, respectively proximal parts of appendages 6–12, reflected (magn. × 10); distal parts of leg branches 2–4, and terminal lobe 3, reflected (magn. × 10); northwest (magn. × 3.3); left appendages 2–12, northwest (magn. × 10).

FIGURE 85. Explanatory drawing of part and counterpart.

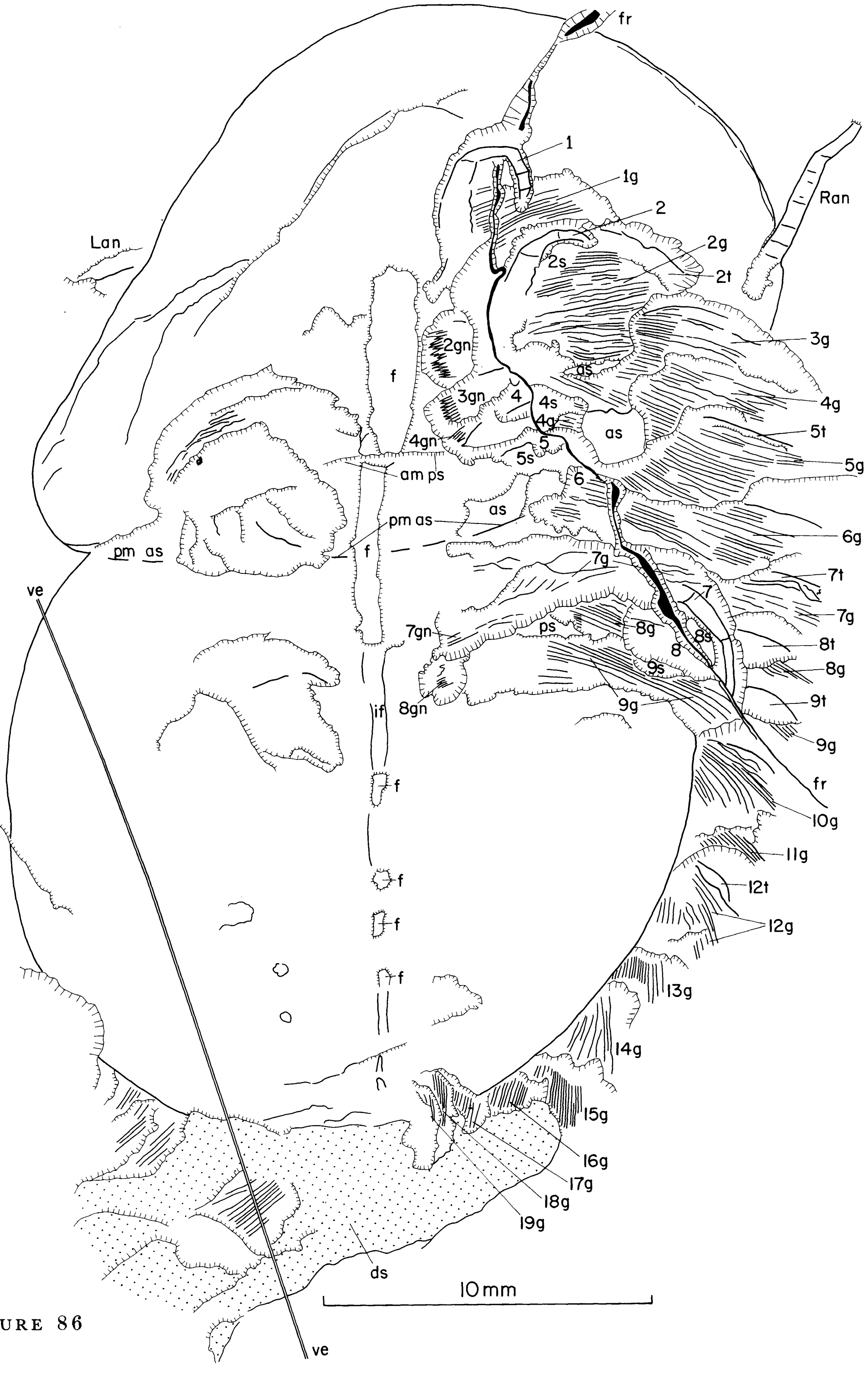

FIGURE 86

DESCRIPTION OF PLATE XV AND FIGURE 86

Naraoia compacta Walcott, 1912. U.S.N.M. 235844, parallel oblique, part only, Phyllopod bed, Walcott quarry

FIGURE 86. Explanatory drawing after preparation.

FIGURES 87–90. Respectively before preparation, north (magn. × 3.3); after preparation, north–northwest (magn. × 3.3); median right lateral portion, north–northwest (magn. × 10); right anterior portion, fragment to right of fracture removed to show leg branch 1, northeast (magn. × 10).


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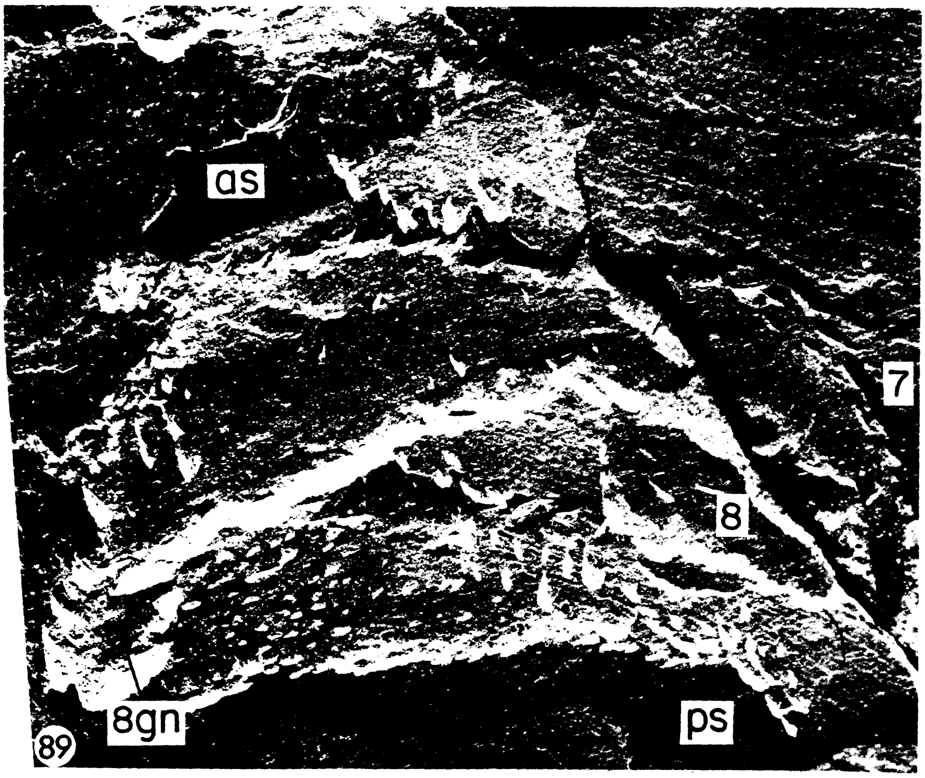
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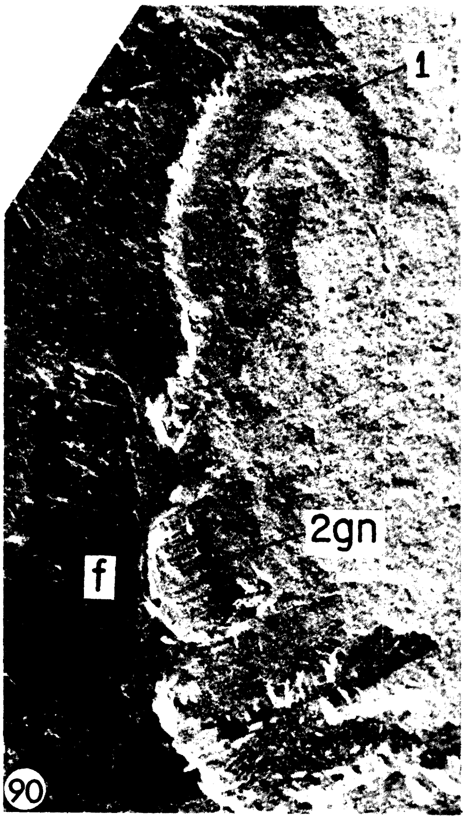
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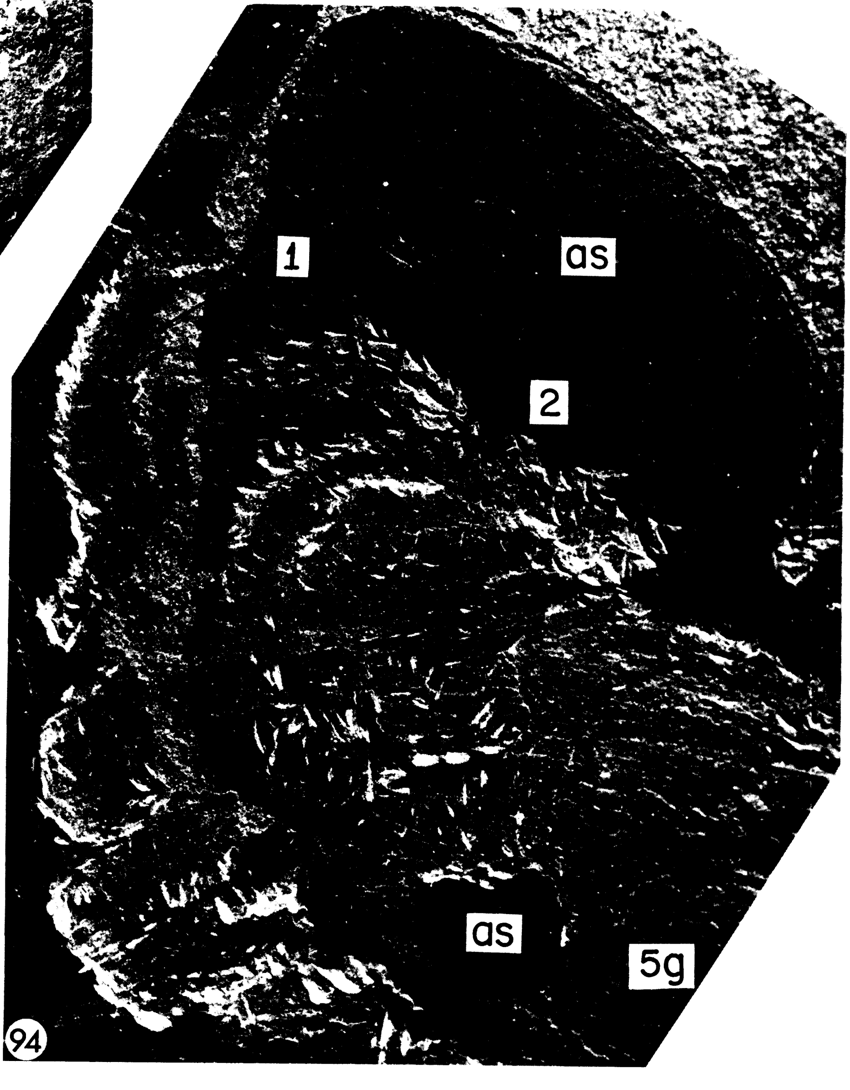
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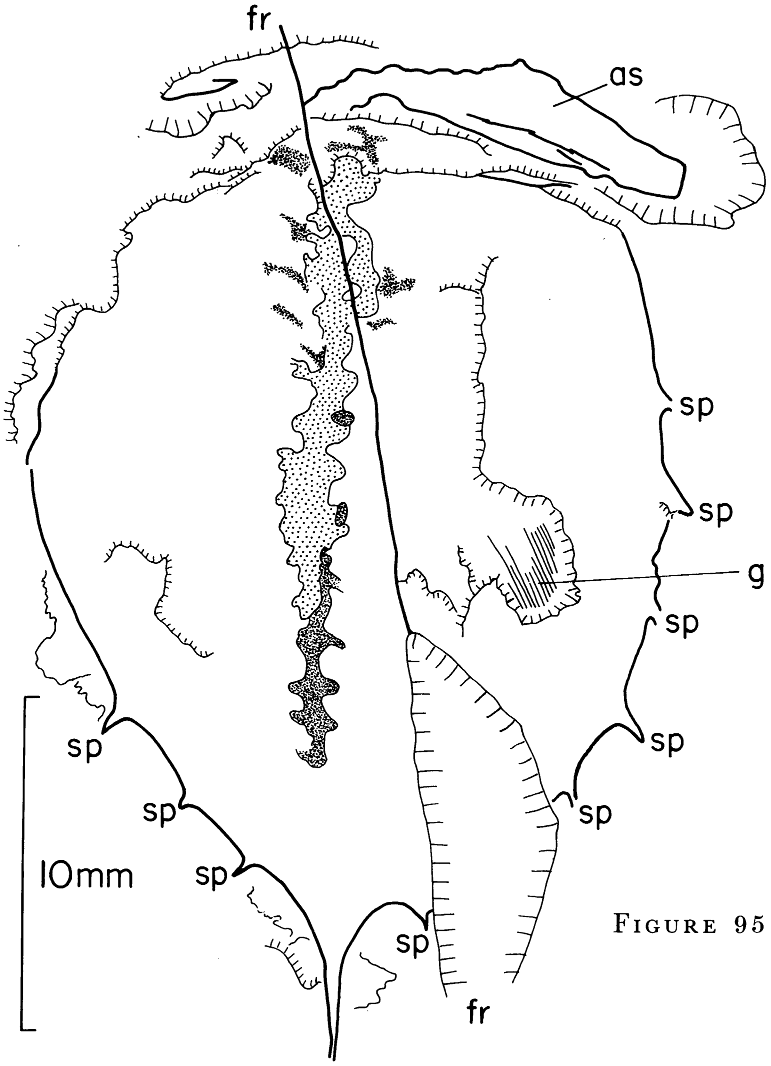

FIGURE 95

DESCRIPTION OF PLATE XVI AND FIGURE 95

Naraoia spinifer Walcott, 1931. Phyllopod bed, Walcott quarry

FIGURE 91. U.S.N.M. 131216, parallel, part only, northwest (magn. × 3.3).

FIGURES 92, 93. U.S.N.M. 83946, holotype, parallel, part only, respectively northwest, reflected (magn. × 3.3). Original of Walcott 1931, pl. 15, fig. 1, and Simonetta & Cave pl. XXXV, fig. 10.

FIGURE 95. U.S.N.M. 83946, explanatory drawing, coarse stipple shows areas which are dark in low angle illumination (fig. 92), darker stipple shows reflective areas (fig. 93) outside darker areas.

Naraoia compacta Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURE 94. U.S.N.M. 235844 (compare figures 87–90, plate XV, figure 86), right anterior portion, northeast (magn. × 10).

Only distally may they separate, for example in the originals of figures 57, 85 and 86, where the leg branch curves down and backward. This relationship implies that:

(i) there is no articulation at the attachment of gill shaft to coxa, so that no forward and backward swing of the branch independent of the coxa, was possible;

(ii) the shaft of the gill branch was relatively stiff. It may show flexure distally, as in right gill branches 3 and 4, figure 26, and right branches 5–7, figure 48, though this may be in part post mortem.

In all compressions studied the coxa and leg branches slope backward and downward (i.e. ventrally, or in the case of lateral compressions, adaxially) and pass each below the one following. The only exception noted is the slope of gnathobases 2–4 in 235844 (figure 86) but the usual relationship obtains farther posteriorly. In the majority of these examples the sheet of lamellae of the gill branch slope backward and upward (i.e. dorsally or in lateral compressions abaxially); and extend back over those of the following branch. The lamellae are subparallel, straight, gently curved or slightly radially arranged, suggesting that like the shaft they were relatively stiff. The angle at which they lie with respect to the shaft may vary, and in § 3 the preservational factors affecting this angle are discussed. In the reconstruction (figures 96–99) it is assumed that the gill branches were imbricated, the sheet of lamellae sloping backward and upward over the one following – the characteristic way in which they are preserved. However, on the left side of 199815 (figure 85) the gill branches slope *forward* and upward relative to the exoskeleton, as they do on both sides of 241041 (figure 72), and the right posterior side of 83945b (figure 14). This is considered to be a post mortem effect, resulting from the strong obliquity of these compressions (see §3).

No annulations or joints have been observed in the shaft of the gill branch, which terminated in a lobe bearing marginal setae, and to which the row of lamellae was attached along the dorsal margin. The lamellae were close-spaced, some 8–12 in 1 mm, appearing as narrow, imbricated flat bands, the exposed margin of each band irregular presumably because of fracture along it as the rock was split. The exposed margin may be on the abaxial side, the shaft inclined downward and outward (figure 53, plate IX; figure 89, plate XV; figure 94, plate XVI), or on the adaxial side (figure 30, plate V). The lamellae were longest medially, decreasing slightly in length abaxially and adaxially. Although preserved as flat strips, the lamellae may have been oval or circular in cross section, a form which would account for the imbrication. Attachment of the lamellae to the dorsal margin of the shaft is shown by left appendage 6 of 199815 (figure 85), and left appendage 2 of 189221 (figure 37). Further, both shaft and terminal lobe may be partly or wholly concealed by the lamellae in parallel (figures 4, 57), oblique (figure 14) and lateral (figures 24, 26) compressions, confirming that they projected upward and backward from the shaft. The terminal lobes are preserved directed backward and slightly downward in various types of preservation (figures 4, 37, 86) at a level below the lamellae, and show that no rotation of the shaft took place. In the course of burial and compression this relationship was occasionally reversed, as for example in the lateral compression 189222 (figure 46) and the oblique compression 241038 (figure 15), in both of which terminal lobes lie dorsal to the lamellae.

The outline in posterior view and relative lengths of the five podomeres of the leg branch, and the thorn-like terminal spine is shown by left appendage 6 of 199815 (figure 85) and left appendage 2 of 189221 (figure 37). In 189221 podomeres 3–6 appear narrower than in 199815, and in 83945b (figure 14) these podomeres appear of intermediate width in left appendage 6, although in this specimen the coxa and leg branches were buried sloping more steeply downward. Thus while the coxa and podomere 2 were antero-posteriorly flattened, podomeres 3–6 appear to have been sub-circular or oval in cross-section. Leg branches a–d of 189222 (figure 47) and 9? of 241037 (figure 58) become broader proximally at the podomere 4–5 joint, suggesting that podomeres 3 and 4 may have been deeper dorsoventrally than the distal podomeres. Small lateral spines were present on the endite of podomere 2, and ventral spines on podomeres 3 and 4. The joints in the leg branch are not well preserved, but while the dorsal margin is a continuous line, the ventral margin shows a step at each joint, the podomere narrower on the distal side. It is thus presumed that there were hinge joints at the dorsal margin between podomeres 2–6, and the way the branch is flexed supports this view. The nature of the coxa–podomere 2 joint is uncertain, but is here presumed to be a hinge joint, the hinge at the dorsal margin. The endite of podomere 2 is close beside and below the coxa in left appendage 3 and 6 of 83945b (figure 14), and in appendages 5–7 of 241030 (figure 57). This position is ascribed in part to burial at a steep downward angle (figure 1*c*, *d*) but may also result from flexure at such a hinge joint.

The length (long.) of each branch of the appendage is similar, the first appendage (figures 14, 57, 86) shorter (long.) than the similar sized series of appendages 2–12. From 12 onwards (figures 14, 26) the appendages become successively shorter (long.), but similar in construction, as 241041 (figure 72) shows. Thus pairs of coxae, and endites of podomere 2, are present in the first to the posterior appendages. In life (figure 97) the plane of maximum dimension of the coxa and basal podomere of the leg branch must have been approximately dorso-ventral in position, the gnathobases of a pair opposed. The position of the coxa–body junction must have been such that the gnathobases could be closely opposed and able to tear food and pass it forward to the mouth. If the gill branch was attached to the distal part of the dorsal margin of the coxa, the junction with the body was at the proximal part of this margin. As figure 97 makes clear, the coxa–body junction must have lain well within the margin of the axial region.

5. Description of *Naraoia spinifer* Walcott, 1931

(*a*) *Holotype, other material, locality*

The holotype, 83946 (Walcott 1931, p. 15, pl. 15, fig. 1), and a second specimen 131216, from the 'Phyllopod bed' (see §4 (*b*)), labelled '35k', but with no information on the level from which they were obtained. No further specimens have been collected, and the third specimen mentioned by Walcott (1931, p. 15) has not been traced.

(*b*) *Morphology*

In the holotype (figure 92, plate XVI) the anterior shield is steeply inclined relative to the bedding, and crushed so that only fragments are preserved. In 131216 (figure 91, plate XVI) this shield is wider than long (sag.), lacks a clearly defined axial region, and on the right side is extended posterolaterally suggesting a spine, at the base of which is a curved, impressed line. In both specimens the posterior shield is longer (sag.) than wide, the axial region not defined, the margin showing a stout median posterior spine and seven pairs of lateral spines, the second (at the maximum width) the largest, similar in size to the posterior spine. In 83946 probable traces of appendages are visible at the left lateral margin of the posterior shield; an excavated area at the right midlength (figure 95) shows parallel strips which are probably gill lamellae matted together. In the anterior shield of 131216 are two pairs of slight depressions, curving convexly forward and outward from the axial region (figure 91, plate XVI), which may represent traces of appendages, but no details are preserved. A longitudinal strip, dark in low angle illumination and reflective (compare figures 92 and 93, plate XVI), represents the alimentary canal in the posterior shield of 83946. The strip has irregular, paired lobate projections, presumably diverticula, and is extended by areas which are reflective only, and may represent muscle attachment areas. In 131216 the body appears disrupted by a fold crossing the posterior shield just in front of the midlength. In front of this fold irregular, carbonaceous, reflective patches are present and continued on to the anterior shield; a well-defined, dark and reflective strip runs obliquely through these patches and is the infilling of the alimentary canal. Behind the fold a further section of the canal, similarly preserved, is present to the left of the midline; it ends abruptly some distance from the posterior margin.

(*c*) *Discussion*

The two specimens appear to represent a species of *Naraoia* differing from *N. compacta* in having a poorly defined axial region, and in that the posterior shield bore seven lateral and a median posterior marginal spine. The length (sag., to base posterior spine) of 131216 is 39 mm, and the length of the posterior shield of the holotype suggests it was of similar size; these lengths are in the upper range of these of *N. compacta* (figure 2*a*). Simonetta & Cave (1975, p. 4, pl. V, fig. 10, pl. XXXV, fig. 10) briefly discussed the holotype, and apparently considered that the median posterior spine was analogous to the supposed 'telson' in *N. compacta*.

6. DISCUSSION AND CONCLUSIONS ON *NARAOIA COMPACTA*

(*a*) *The reconstruction*

The reconstruction (figures 96–98) summarizes the evidence discussed above and shows how the animal may have looked when walking on the sea bottom. Outlines in dorsal view and relative sizes of the shields are derived from averages of the measurements (figure 2). The original convexity of the shields, and of the axial region relative to the rest, cannot be derived from measurements because of the obliquity of the compressions. They are conjectural, designed to give a cross section that will allow a hanging stance (Manton 1952, p. 97, fig. 1) of the walking legs and space for the gill branch and its lamellae. Walcott (1931, pp. 11–12) considered the axial region to be present only on the posterior shield, Raymond (1920, p. 140) was followed by Størmer (1944, p. 86) in considering that both shields showed the axial region, while Simonetta & Cave (1975, pl. V, fig. 9*a*, *b*) do not show any such region. I consider there is evidence for an axial region, defined from the remainder of the shields by its independent convexity but not by a marginal furrow. Although there is evidence for segmentation of the body (§4(*f*)), there is no evidence for segmental furrows on the shields. In lateral view (figure 96*b*) the anterior shield is drawn as inclined downward and forward relative to the posterior shield. Any lesser inclination raises the mouth above the ranks of gnathobases; some inclination is implied by lateral specimens (figure 22, plate IV; figure 28, plate V) and those (figure 49, plate IX; figure 64, plate XI) in which the posterior shield is parallel to the bedding and the anterior inclined down. There is slim evidence of a labrum, but the outline and position of such a lobe is suggested.

The antenna has been traced partially beneath the shield in three specimens (figures 26, 57,

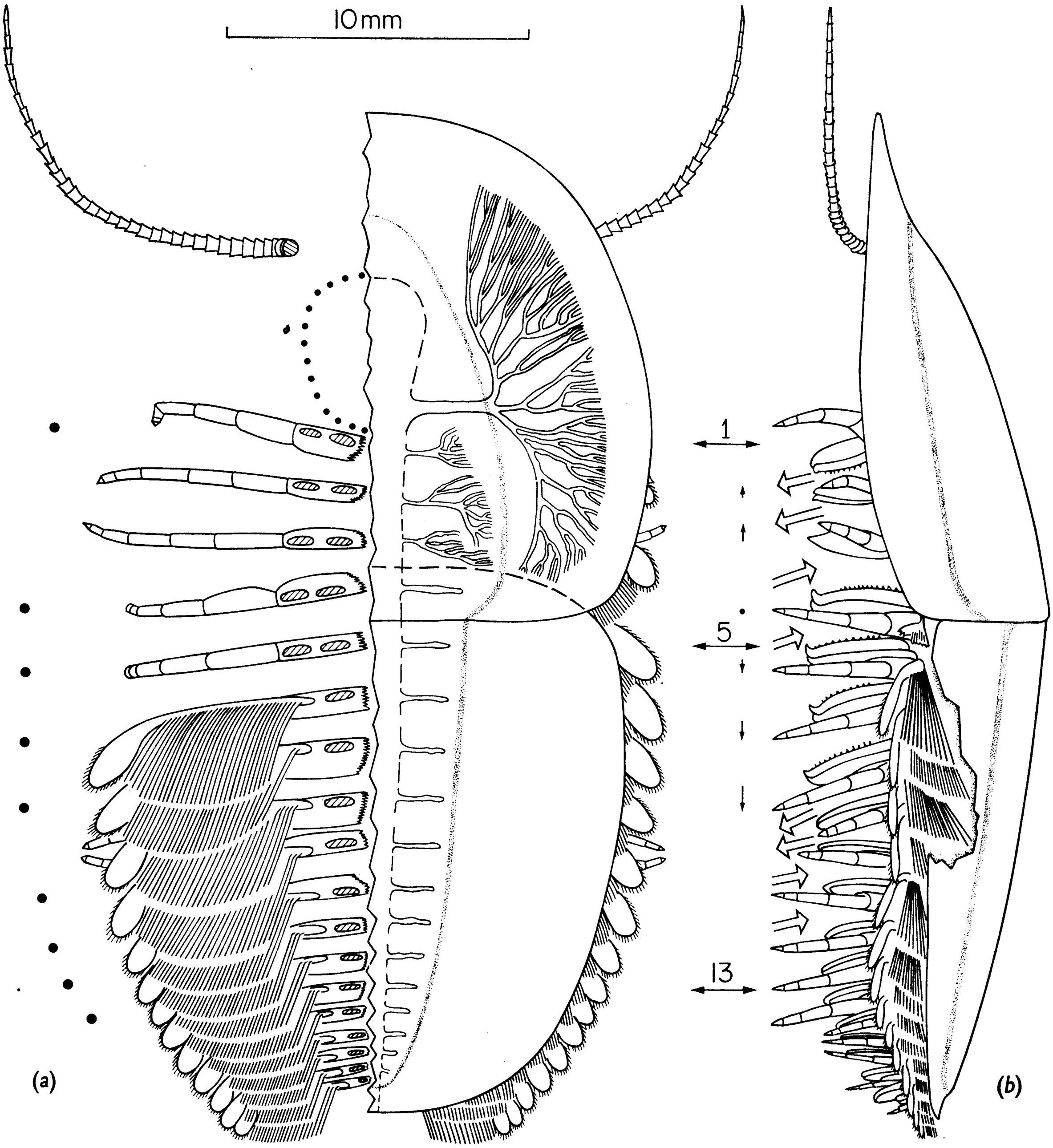

FIGURE 96. Reconstruction of *Naraoia compacta* Walcott, 1912, (*a*) Dorsal view of individual with 18 pairs of biramous appendages, lacking posterolateral spine on anterior shield; left half of body cut away to reveal appendages below insertion (diagonally shaded) in ventral cuticle, gill branches of first five biramous appendages removed (insertion in coxa diagonally shaded) to show leg branches. On right side position of margin of alimentary canal shown by dashed line, of axial and lateral diverticula by solid lines; on left side outline of labrum in solid dots. Biramous appendages shown in the 'still' position of a particular gait (see § 6 (*a*)), solid circles on left in transverse line with tips of leg branches which are stepping on sea floor, intervening branches are in recovery phase. (*b*) Left lateral view of same individual, gill branches 1–3 removed, branch 4 partially cut away, and part of posterior shield and ventral cuticle cut away to show gill branches 5–7 more completely. Appendages are in same 'still' position of gait shown in (*a*), beneath tips of leg branches 2–7 (in same metachronal wave) are arrows showing direction and amount of promotor or remotor swing passed through, dot under 4 indicates beginning of remotor stroke. Arrows with double shafts indicate directions of water currents caused by approach or separation of coxae and leg branches. Horizontal double-ended arrows indicate positions of cross sections of figure 97, number of segment with biramous appendage indicated.

58), suggesting that it was attached much farther forward than Walcott (1931, fig. 1) thought, adjacent to the anterior end of the axial region. Eighteen pairs of biramous appendages are shown, the maximum number observed (figure 86) being nineteen. The arguments for attributing three pairs to the anterior shield are given in §4 (*i*), and reliance placed on pairs of muscle areas (figure 14) and suggestions of segmentation (figure 57) for their position and spacing. The appendages are restored from the new evidence summarized in §4 (*i*) and consequently differ from Walcott's portrayal (1931, figs. 1, 2). I have seen no evidence that the shaft of the gill branch was annulated as Walcott claimed, and he did not observe the terminal lobe. Judging by their restoration Simonetta & Cave (1975, pl. V, fig. 9) observed these lobes projecting outside the shield, and appear to have concluded that the outer branch of the appendage consisted only of a 'lanceolate lamella fringed all around by subequal short hairs' (1975, p. 23). The original of figures 80–84, plate XIV, for example, shows that this conclusion

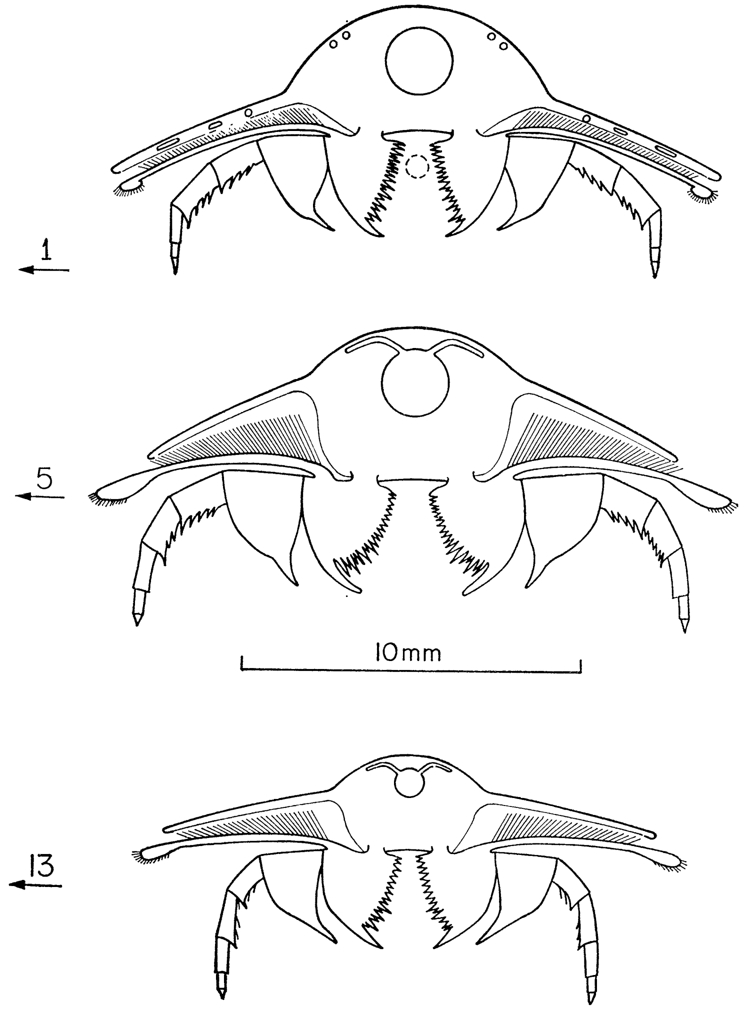

Figure 97. Reconstruction of *Naraoia compacta* Walcott, 1912. Three cross sections of the same individual as figure 96, each at the numbered segment bearing biramous appendages indicated. In each section the pair of appendages is shown in posterior view, and in the body the alimentary canal and diverticula are outlined. The circle in dashed line in section 1 indicates the position of the mouth (compare figure 98), situated a short distance in front of the line of section. Arrows correspond in position to double-ended arrows of figure 96.

is incorrect. Neither the ventral cuticle inside the doublure, nor the inner, dorsal portion of the coxa is preserved, so that the coxa–body junction is unknown. In suggesting a possible gait, I have used considerations based on Manton's (1973 and references) work on arthropod locomotory mechanisms, similar to those employed in considering the gait of the trilobite *Olenoides serratus* (Whittington 1975*b*, pp. 129–131). Each pair of legs moved in unison in a promotor-remotor swing about an approximately transverse, and slightly upward and outwardly directed, axis at the coxa–body junction. Legs 1–13 provided the locomotion, in a slow movement with a relative duration of forward and backward strokes of 3:5. Each metachronal wave included six legs, four on the ground at one time and two in the recovery phase, a phase difference of 0.17. Such an arrangement means that at any one time never less than one pair of legs of the anterior shield are on the ground (figure 96), so that the body is adequately supported. The angle of swing of the legs is shown as 4° in front, and 12° behind, the transverse plane. Because the gill branch was rigidly attached to the coxa, the promotor-remotor swing of the coxa would rotate the shaft of the gill branch. This rotation would tend to depress the sheet of filaments during the promotor movement, and elevate it during the remotor swing.

The alimentary canal is shown in figures 97, 98, though the evidence for the U-shaped anterior portion (§4 (*f*)) is slim. The lateral and axial diverticula are shown in the dorsal view (figure 96*a*) as if seen through the shields, there apparently being no trace of them on the exterior surface. In claiming the presence of eyes as 'crescent-shaped bright spots', Walcott (1931, p. 12) did not refer to a particular specimen, but he was referring presumably to the area at the left anterior end of the axial region seen in 83945c (figure 19, plate III) or the pair seen in 241046 (figure 77, plate XIII). The presence of eyes was accepted by Størmer (1944, p. 86), but not by Raymond (1920, p. 139) or Simonetta & Cave (1975, pl. V, fig. 9). No eye structure is preserved on the external surface of the anterior shield, and these reflective areas may well be areas of muscle attachment (see §4 (*f*)). A smaller, similarly situated pair of reflective spots in *Burgessia bella* (Hughes 1975, pp. 421, 429) are interpreted as points of muscle attachment. I find no evidence for the telson (see §4 (*f*)) so it is omitted. The posterolateral spine on the anterior shield was observed in a cast exoskeleton (figure 62, plate XI) by Simonetta & Cave (1975, p. 5) and taken by them to distinguish a separate species. It is present in about one fifth of both entire individuals and cast exoskeletons (§4 (*c*)), and is here taken as the only evidence of dimorphism in the sample of *N. compacta*.

(*b*) *Mode of life*

The most striking feature of *Naraoia* is the relatively enormous gnathobase, proportionally far larger than that of the trilobite *Olenoides serratus* (Whittington 1975*b*, figs. 25–27). In conjunction with the spinose endite of the first podomere of the leg branch, a powerful armoury for capturing, crushing and tearing up food was formed, extending from the posterior tip of the body to the mouth, flanking a median groove. Hence I assume that *Naraoia* was a benthonic predator and scavenger, walking, digging and raking much as did *O. serratus* (Whittington 1975*b*, p. 133). The coxa–body junction (figure 97) is restored so that opposing gnathobases were relatively close together. The axis of swing of the coxa in appendages 4–13 (figure 96*a*) is drawn directed outward and backward at about 8° to the transverse plane, a parallel arrangement which is modified anteriorly and posteriorly to suggest a fanning of the legs (cf. Manton 1952, figs. 2, 3). Directed inward and slightly forward, the gnathobases would be more closely opposed as the coxae swung back, enabling them to sieze and crush food. In the forward swing

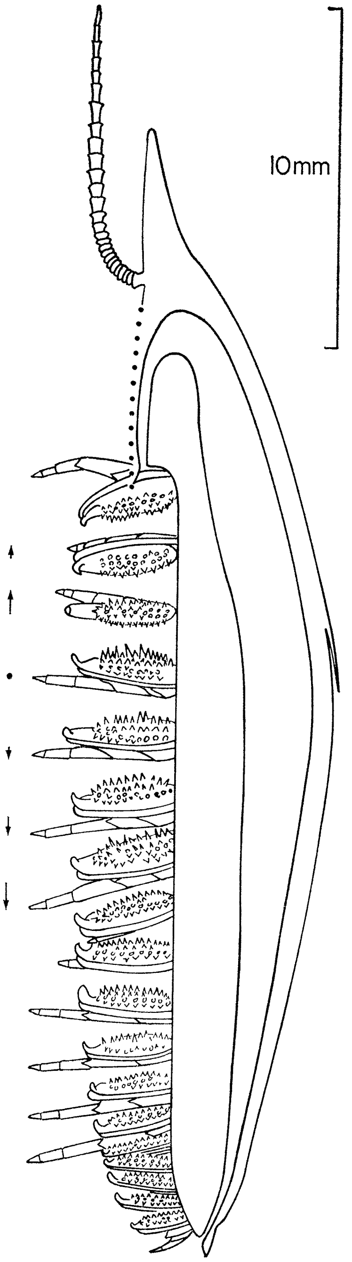

FIGURE 98. Reconstruction of *Naraoia compacta* Walcott, 1912. Sagittal section of same individual as figure 96, showing outline of alimentary canal and position of labrum (solid dots). Antenna, coxae and leg branches of right side only shown. Individual in same 'still' position of gait as in figure 96, arrows as in figure 96(*b*).

the gnathobases would have moved progressively farther apart, so releasing the crushed mass to be seized by the next pair in front. The insertion of the coxa in an apparently thin, flexible ventral body wall suggests that the food-grinding mechanism cannot have been powerful enough to crush hard food. But, as in *O. serratus*, adductor-abductor movements of the coxae, combined with a forward shift of gnathobases at the end of a backstroke, may have enabled soft food to have been grasped, squeezed and moved forward both while the animal was walking or digging, or while it was at rest. Figure 99 suggests possible abductor-adductor positions of the coxae as well as attitudes of the leg branches of the anterior half of the posterior shield when digging for prey and pushing it toward the mid-line. The body of *Naraoia* could be bent only at the hinge-line between the two shields, and this limited flexibility may have enabled the animal to cope with unevenness of the sea floor and also to push the anterior shield into the sediment in the search for food. *Naraoia* appears to have been particularly well adapted (in part by the rigidity of an undivided posterior shield as a support for musculature) to capture and feed on the varied, small, worm-like creatures that abounded in the Burgess Shale (Conway Morris 1976). In walking on the bottom it would have produced a trackway like that deduced for *Olenoides serratus* (Whittington 1975*b*, fig. 28), and as pairs of legs flexed inward, in combination with a remotor swing of the coxae, it would also have produced the V-shaped scratches of *Cruziana* type. The limited flexibility of the body provided by a single hinge may be viewed as a compromise adaptation which gave at the expense of body flexibility a more rigid support for muscle insertions. The presence of a sediment-filled gut, variable in width, in some but not all specimens of *N. compacta*, contrasts with the absence of such a fill in the trilobite *Olenoides serratus* (Whittington 1975*b*, p. 103). Both animals are considered to have been predators and scavengers, and not to have fed primarily by ingesting large quantities of mud. Both the lateral and axial diverticula in *Naraoia* aided in digestion.

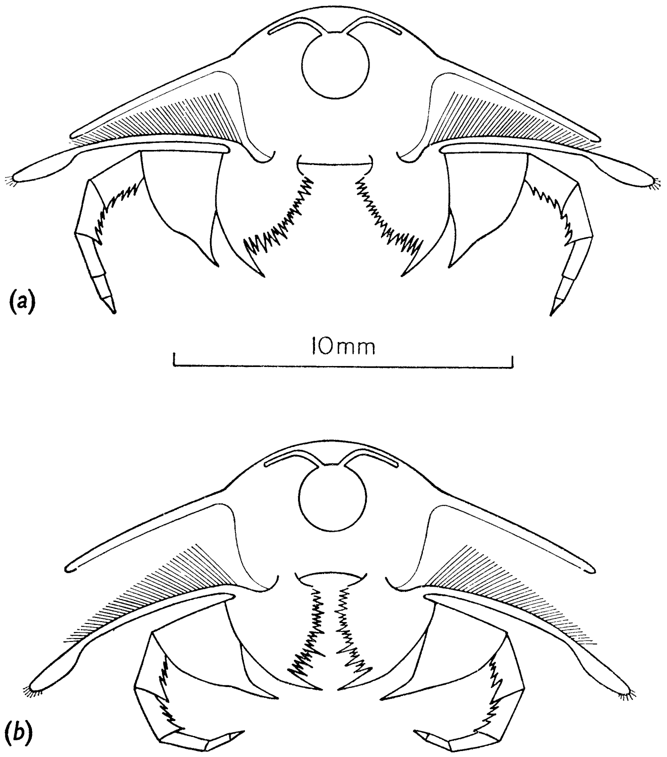

FIGURE 99. Reconstruction of *Naraoia compacta* Walcott, 1912. Two cross sections showing biramous appendages 5 in posterior view (compare figure 97) to suggest (*a*) maximum abduction of gnathobases, and (*b*) adduction of gnathobases and maximum flexure of leg branches. See § 6 (*b*) for discussion.

Each lamella of the gill branch had a diameter of about 0.1 mm, suggesting that the internal space was ample for blood circulation (Tiegs & Manton 1958, p. 282, footnote). The up and down movement of the gills resulting from the remotor-promotor swing of the appendage, and the water currents (figure 96*b*) sucked into the interlimb spaces as the leg branches moved away from each other (or expelled as the interlimb space contracts) during walking, would have aerated the gills, much as postulated in *O. serratus* (Whittington 1975*b*, p. 133). It was suggested that the latter animal swam with the coxa and leg branches swung back into a 'trailing' attitude, propelling itself by flexing the gill branches series up and down against the ventral cuticle in a metachronal rhythm (Whittington 1975*b*, p. 132, fig. 30). Such a mode of propulsion is conceivable in *N. compacta*, but as argued in §4(*i*) the shaft and lamellae were relatively stiff and there was no articulation or rotation at the junction of gill shaft and coxa. Thus the possible amount of flexure of the shaft appears to have been limited, and the swimming powers consequently low. There is no evidence of such flexibility that the terminal lobes were used as a series of paddles, and indeed the lobes were apparently far out relative to the posterior shield and so could not be used to direct water currents at the margin of the shield. Thus a backward push by a series of legs in unison may have launched *N. compacta* off the bottom to drift in a favourable current, and perhaps swim feebly before sinking down. Even feeble swimming activity of the kind envisaged would promote aeration of the gills.

(*c*) *Affinities*

Walcott, (1912, pp. 154, 158, 175) considered the cephalon of *Naraoia* to have had six segments (five? bearing appendages and one bearing eyes), the thorax 17–19, and the abdomen two segments and the telson. He concluded that it was a notostracan branchiopod. He maintained this view in 1931 (pp. 14, 20, 37), but remarked on the many characters in common with the trilobite. Raymond (1920, pp. 139–140, 145, 148, fig. 36) ignored the supposed abdomen and considered *Naraoia* as 'the most primitive of all trilobites', placing it in a new order, the Nektaspida. He regarded it as a trilobite without a thorax, one that grew to an adult while retaining the morphology of a degree 0 growth stage, i.e. an example of what we now call paedomorphosis. Fedotov (1925, pp. 385, 389–390) was unable to accept Raymond's ideas, since he accepted the abdomen, but did not consider *Naraoia* to be a phyllopodan or even a crustacean. Henriksen (1928, p. 11) interpreted the abdomen as an undivided telson, and made the new suggestion that *Naraoia* was a primitive xiphosuran. Størmer (1944, pp. 86–87, 134, fig. 17, 4–6) accepted the details of Walcott's 1931 description and amalgamated the Raymond–Henricksen views, regarding *Naraoia* as trilobite-like (trilobate dorsal shields, presence of antenna and trilobite-like appendages) but also showing xiphosuran characters (large thoracic-abdominal shield, postabdomen with telson, chelicerate-like intestinal diverticula). With some variation in names of higher taxa, this analysis has been maintained (Størmer *in* Grassé 1949, p. 201; *in* Moore 1959, pp. O 30–O 31; Dechaseaux *in* Piveteau 1953, pp. 30–31; Novojilov *in* Orlov 1960, p. 195; Sharov 1965, pp. 970–971; 1966, pp. 41–42), but the new information makes it no longer tenable. *Naraoia* is trilobite-like in the presence of a raised axial region on the two dorsal shields, in having one pair of antennae followed by a series of similar biramous appendages, and in having alimentary diverticula which ramify on the lateral area of the anterior shield. In trilobites diverticula are segmentally arranged and preserved on the lateral regions, not the axial region (Öpik 1961). The biramous appendages are like those of the contemporaneous trilobite *Olenoides serratus* (Whittington 1975*b*, figs. 25–27), differing in that there is one less podomere in the leg branch, a large endite rather than ventral spines on podomere 2, and the slim shaft rather than inner lobe of the gill branch. The gill branch in both is attached rigidly to the coxa, bears many slim lamellae and has a terminal lobe fringed with setae.

Further, both have one pair of antennae and three pairs of biramous appendages on the anterior shield. The younger trilobite *Triarthrus eatoni* (Cisne 1975) has biramous appendages which differ in the same way from those of *N. compacta*, except that the outer branch has an annulated shaft terminating in a small, non-setose lobe. The striking difference between *Naraoia* and these trilobites is the lack of a series of articulations in the exoskeleton, i.e. of the thorax. While holaspid trilobites have two to forty or more segments in the thorax, they all pass through a developmental stage, degree 0, when the exoskeleton is divided by a single articulation. Thus *Naraoia* has many characters in common with trilobites, and may be included in that class in the manner proposed in §4(*a*). Its combination of characters are not so peculiar as to justify placing it in an isolated order (Simonetta & Cave 1975, p. 32), nor do they justify any longer grouping it with *Sidneyia*, *Emeraldella*, or *Leanchoilia* (D. L. Bruton, personal communication) in Størmer's (1959, *in* Moore, pp. O 29–31)emended subclass Merostomoidea. The Class Trilobitoidea Størmer, 1959 (*in* Moore 1959, pp. O 28–29) was proposed as a convenient category in which to place various supposedly trilobite-like arthropods, mainly from the Burgess Shale, and regarded as of equal rank to the Class Trilobita. Studies recently published (Hughes 1975; Whittington 1971*a*, *b*, 1974, 1975*a*, *b*) and in progress (Briggs 1977) are providing abundant new information, particularly on appendages, as unexpected as those presented here. The reconstructions of Simonetta & Cave (1975, pls. I–IX), on which their re-assessment of systematics is based, all require considerable modification. The Class Trilobitoidea can no longer be regarded as a useful concept, and a new basis for assessment of relationships is emerging.

In 1966 and 1967 a re-investigation of the Burgess Shale (Whittington 1971*a*; Fritz 1971) was undertaken by the Geological Survey of Canada, with the cooperation of authorities of the Yoho National Park and Parks Canada, Department of Indian and Northern Affairs, Ottawa. The Geological Survey of Canada kindly invited me to be Chairman of the palaeobiological work, and I am indebted to the Natural Environment Research Council (grant GR3/285) for support of both field and laboratory work. 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 by Drs Porter M. Kier and Richard E. Grant. My photographs have been enlarged by Mr David Bursill and Mr John Lewis has skilfully converted my pencil drawings into the present figures. I am greatly indebted to Dr S. M. Manton, F.R.S., and Drs C. P. Hughes and D. L. Bruton for discussion and comments in the course of this work.

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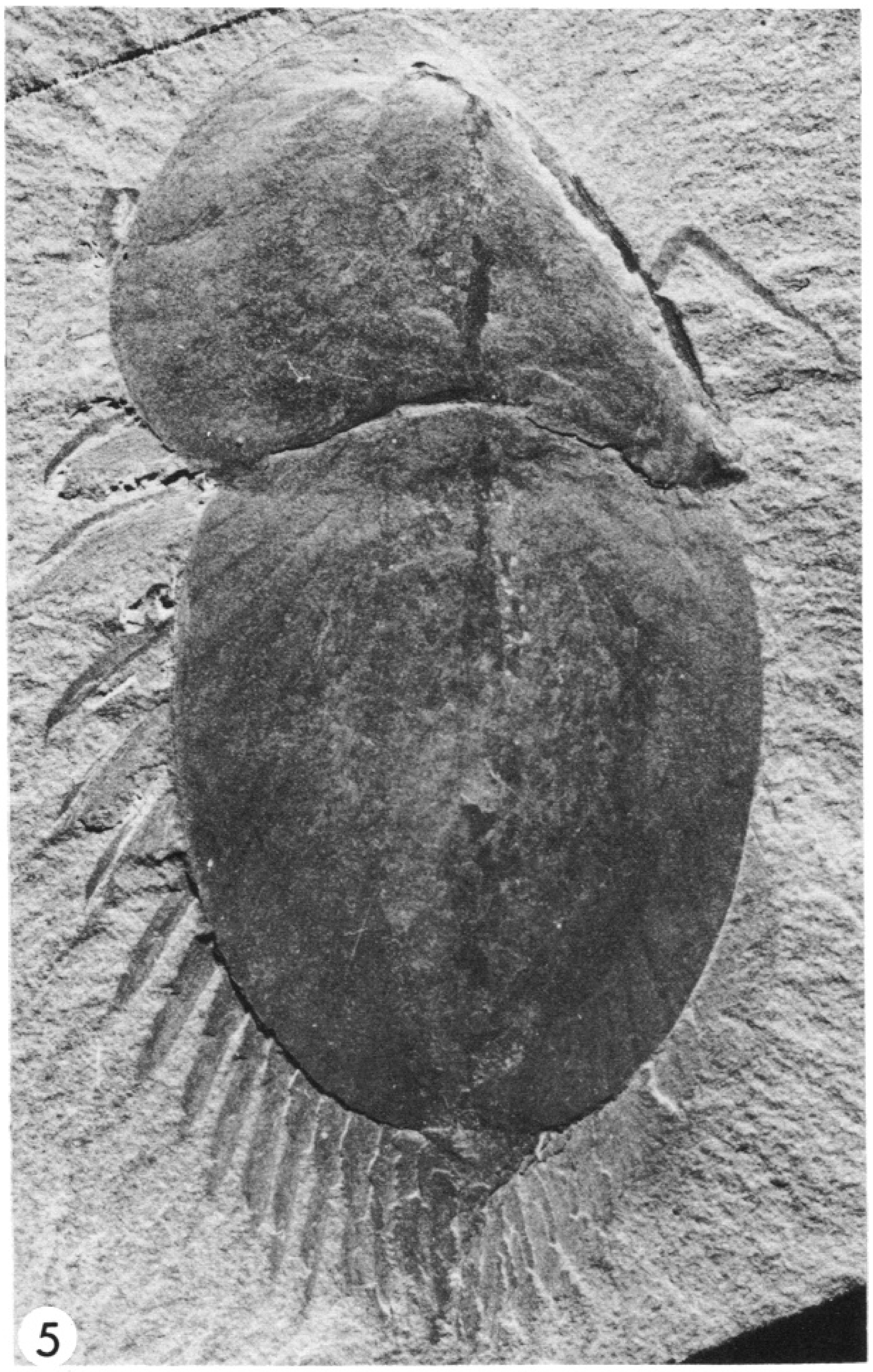
[Plates I–XVI have been printed at the University Press, Oxford.]

List of abbreviations and symbols

G.S.C.	Geological Survey of Canada
L	Left side of animal, as prefix
R	Right side of animal, as prefix
U.S.N.M.	United States National Museum (now National Museum of Natural History)
a–n	lettered series of biramous appendages in which the first is not known (figures 15, 46, 47, 71, 72); applied without additional letter to leg branch
ad	axial diverticula
al	alimentary canal
am	anterior margin
an	antenna
as	anterior shield; also in figure 15 for first gill shaft in series a to j
axr	axial region of shield
cox	coxa
ds	dark stain in rock
e	endite of podomere 2 of leg branch
f	filling of alimentary canal
fo	fold
fr	fracture
g	gill branch of biramous appendage
gn	gnathobase of coxa
if	concave impression of filling of alimentary canal
lab	labrum
ld	lateral diverticula
m	margin
mo	mouth
pm	posterior margin
ps	posterior shield
pyr	pyrite granules in axial region
s	shaft of gill branch of biramous appendage
sp	posterolateral spine of anterior or posterior shield
t	terminal lobe of gill branch of biramous appendage
ve	vein in rock
1–*n*	numbered series of biramous appendages, applied without additional letter to leg branch; also used for corresponding segments of axial region (figures 14, 57). In figures 37, 85, podomeres of leg branch also numbered in series
stipple	shows darker-appearing areas on fossil; used for reflective areas in figures 73, 85, 95



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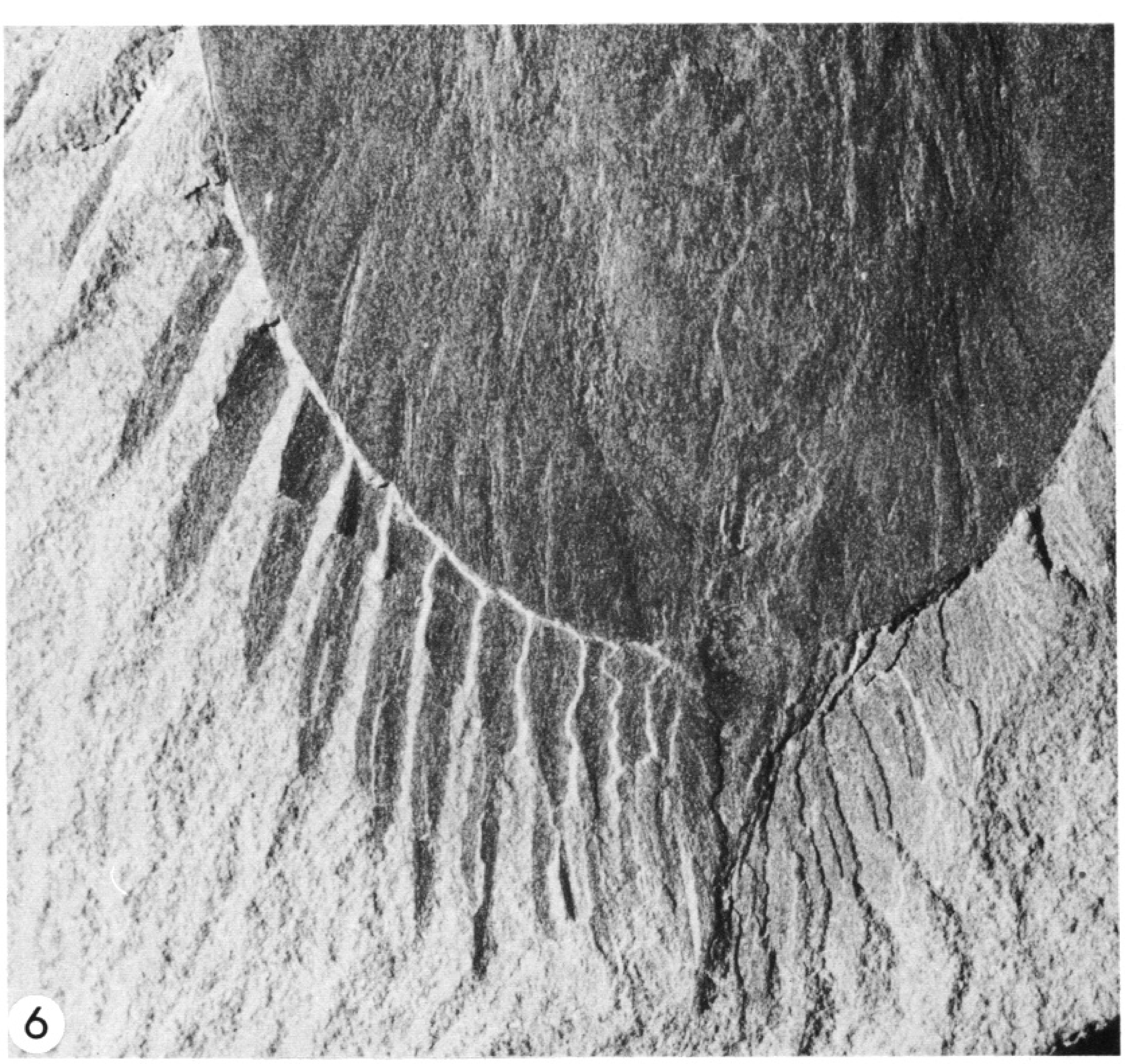

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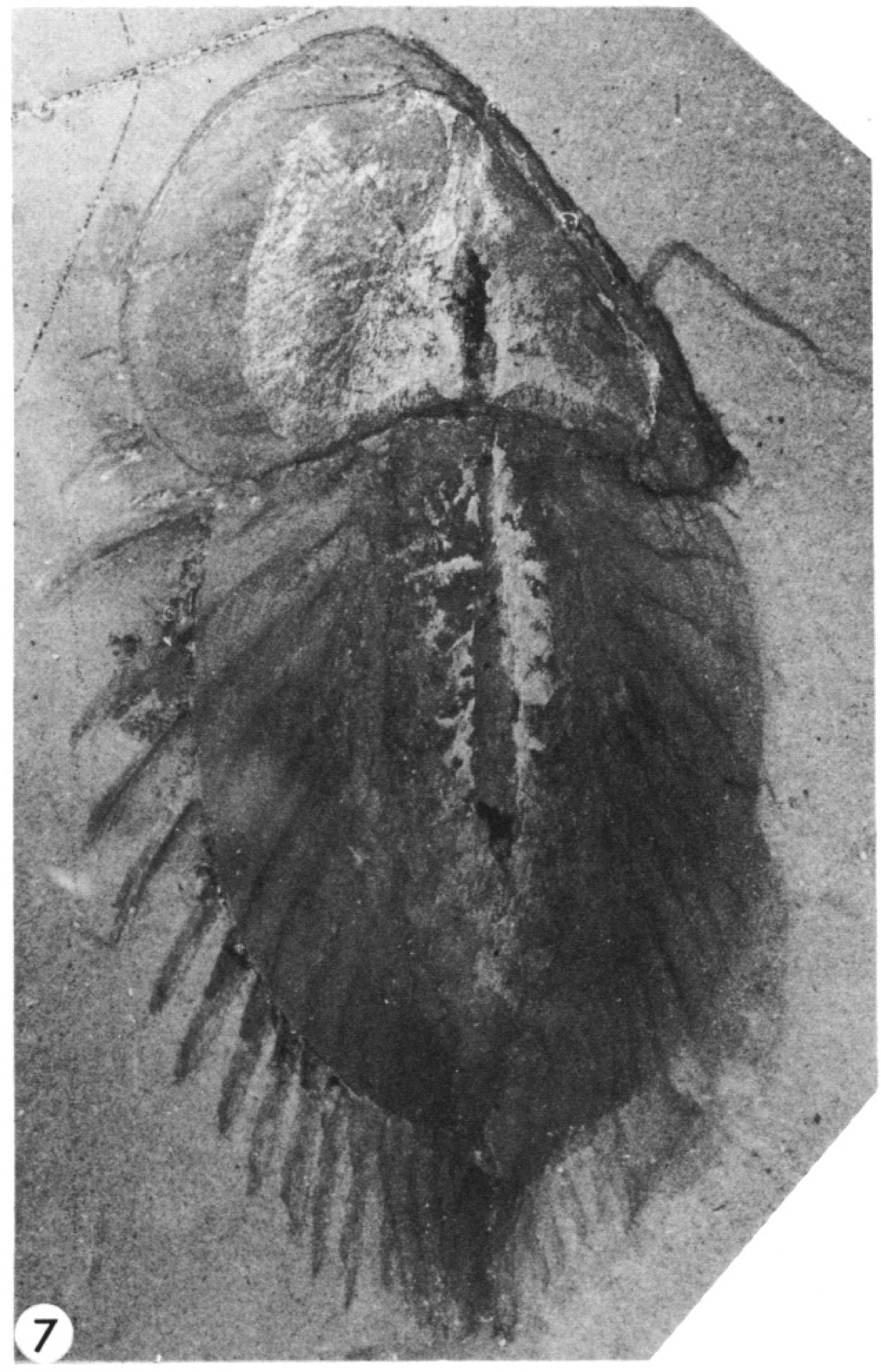

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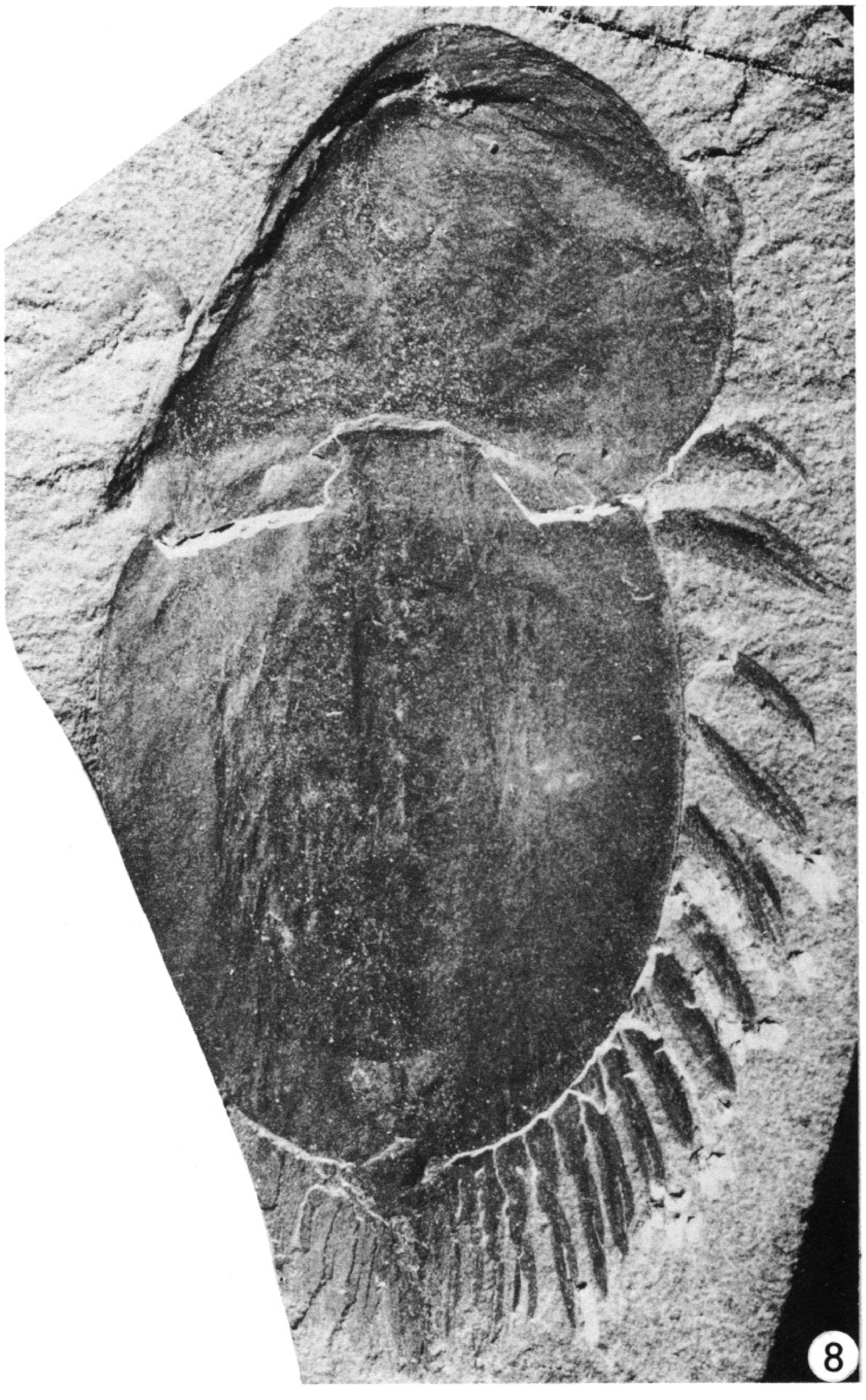

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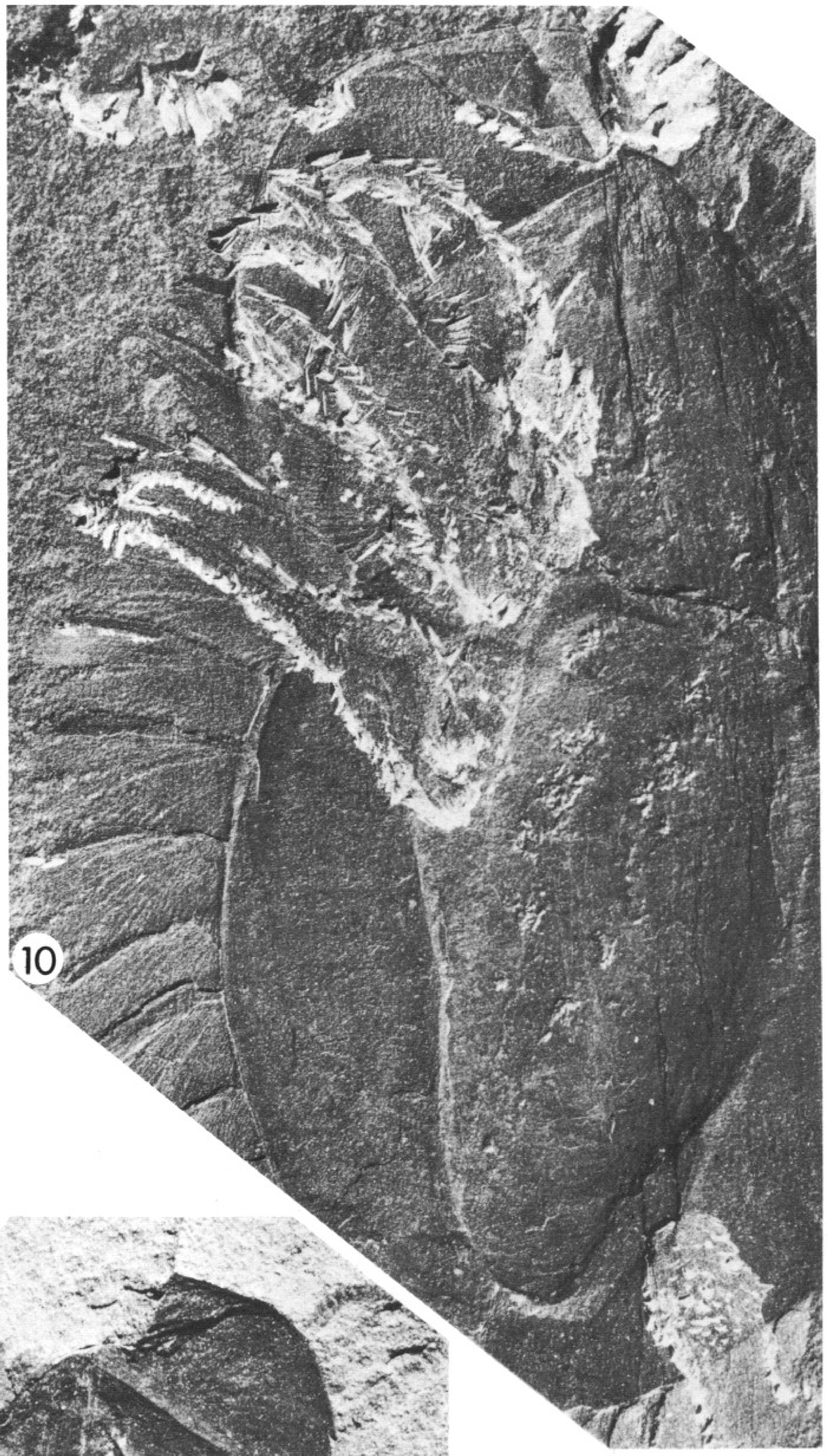
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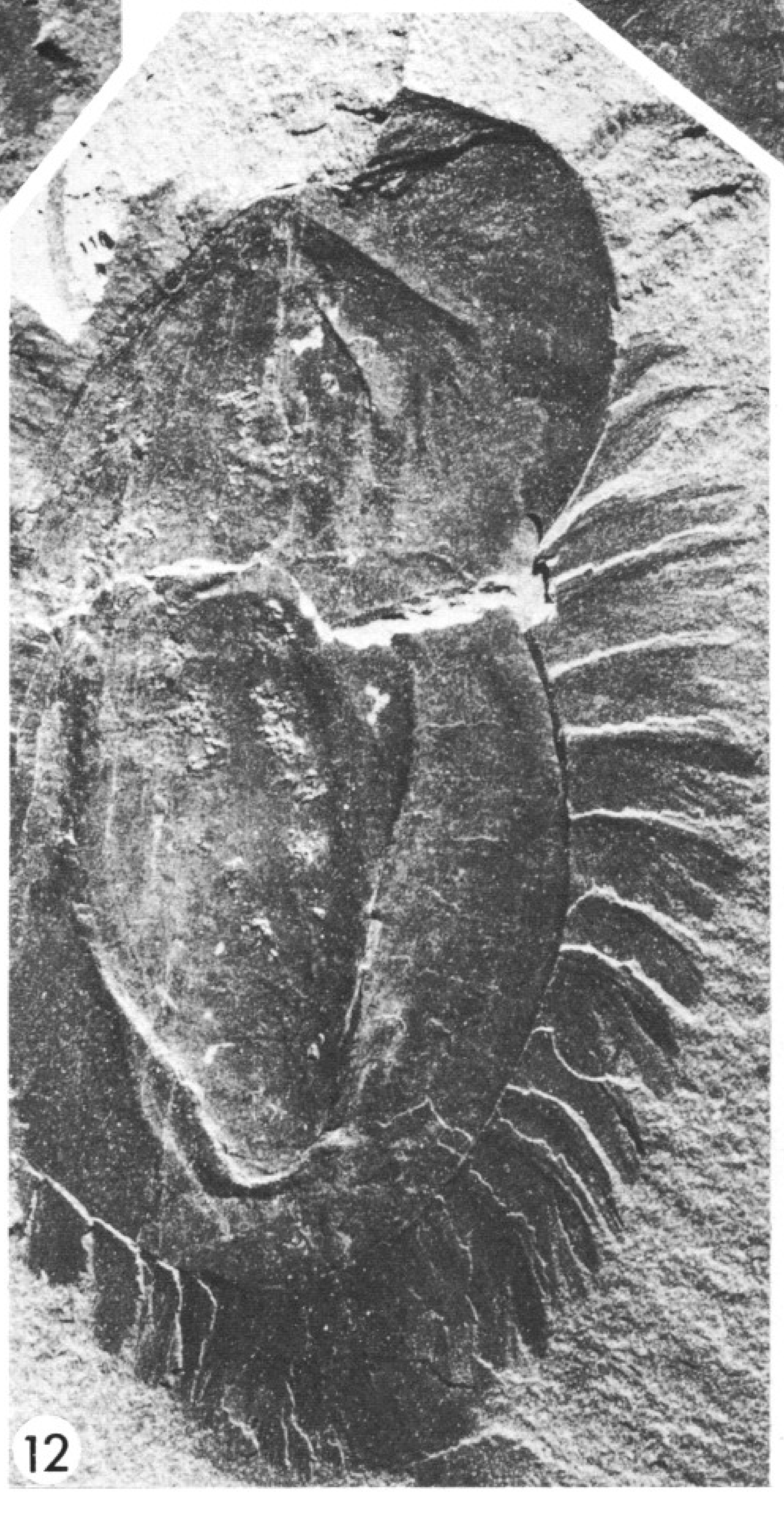
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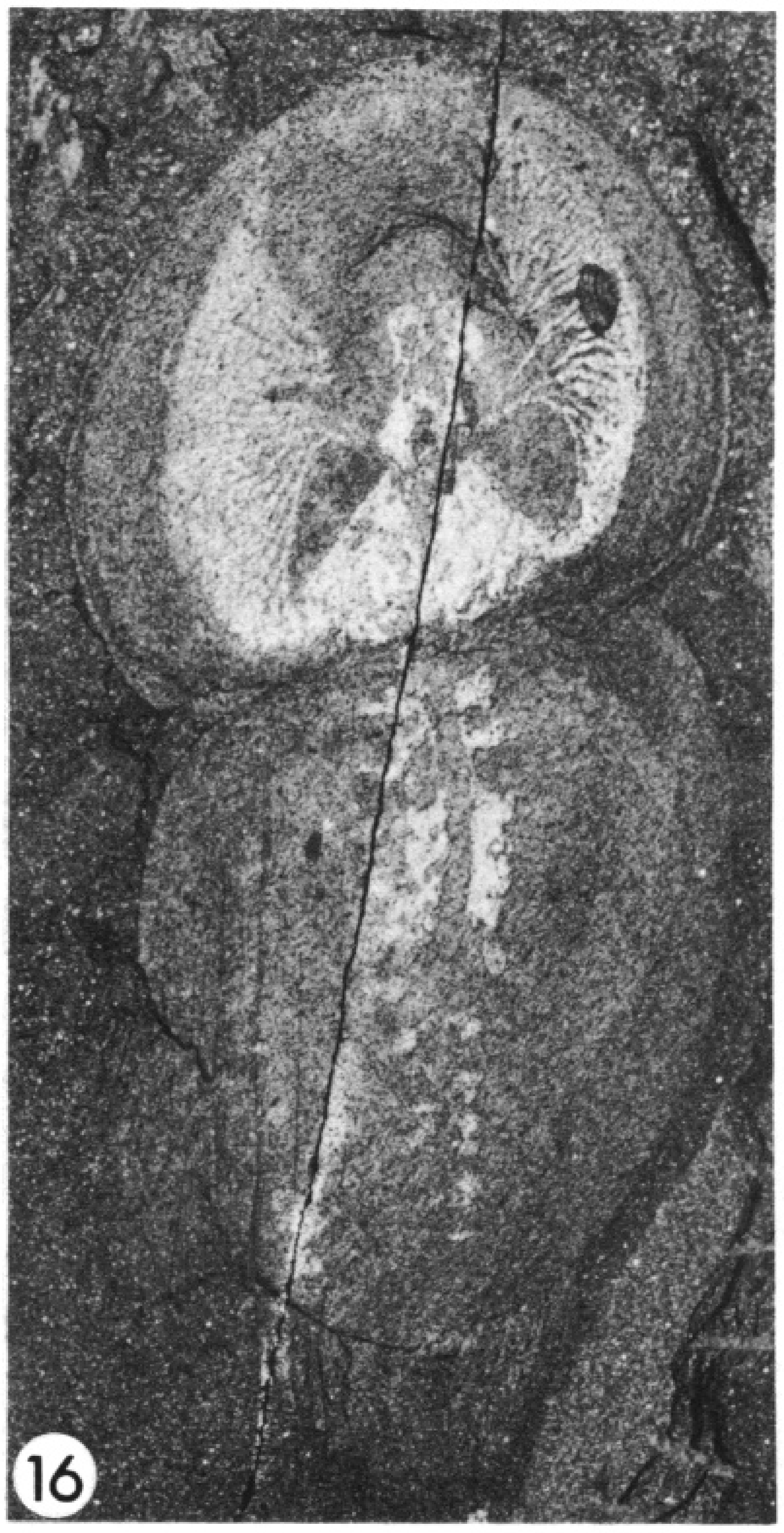
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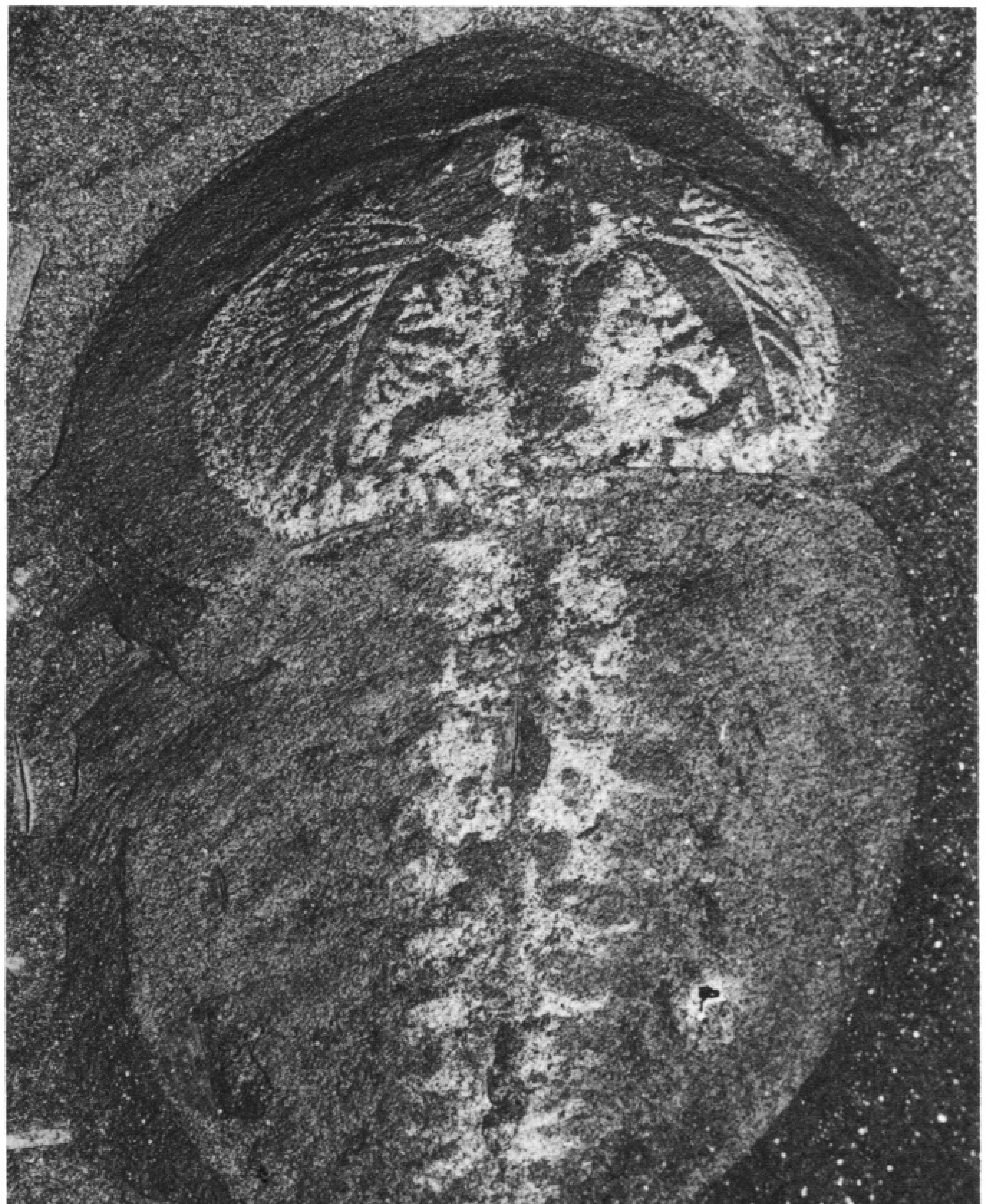
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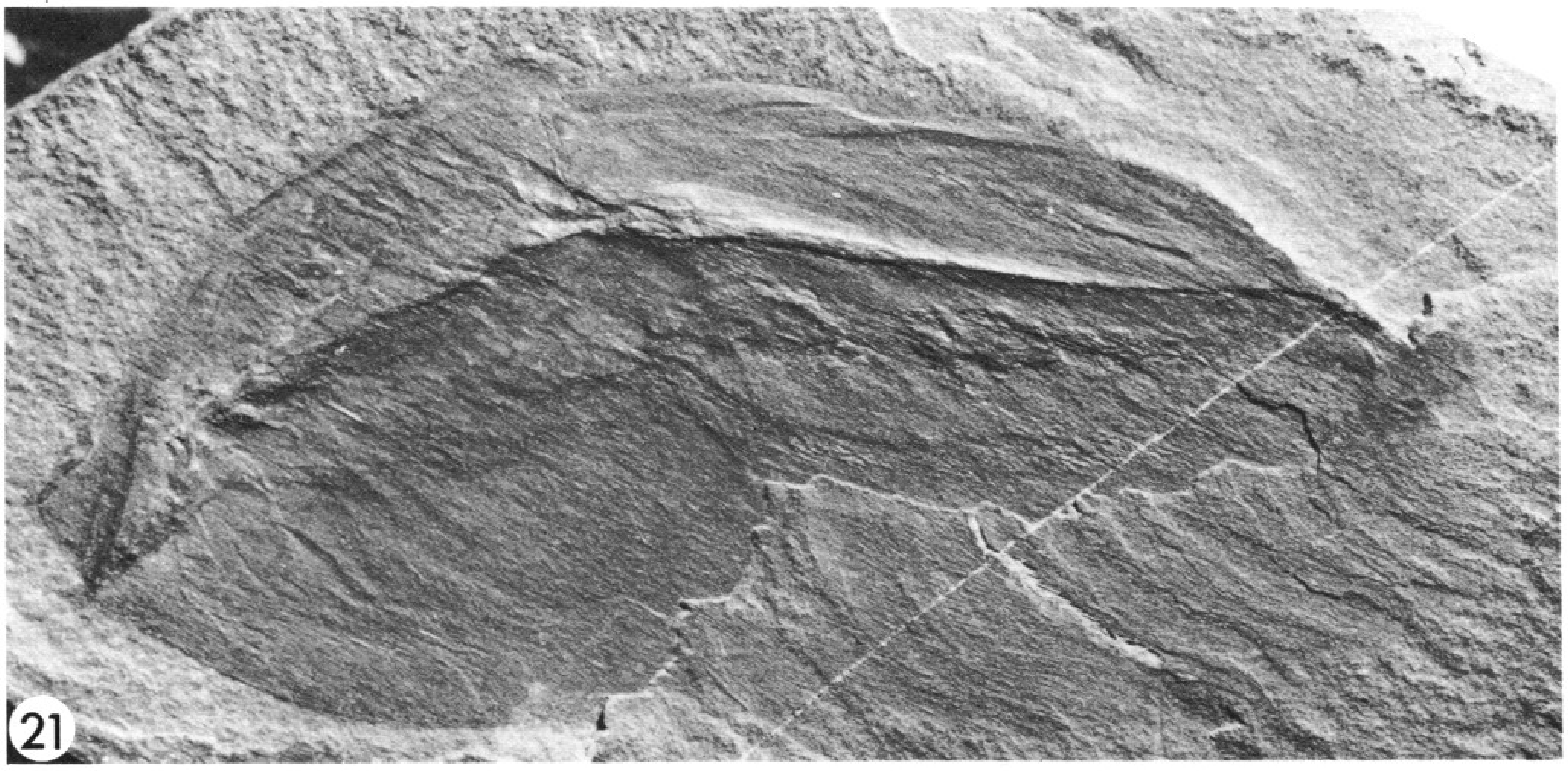

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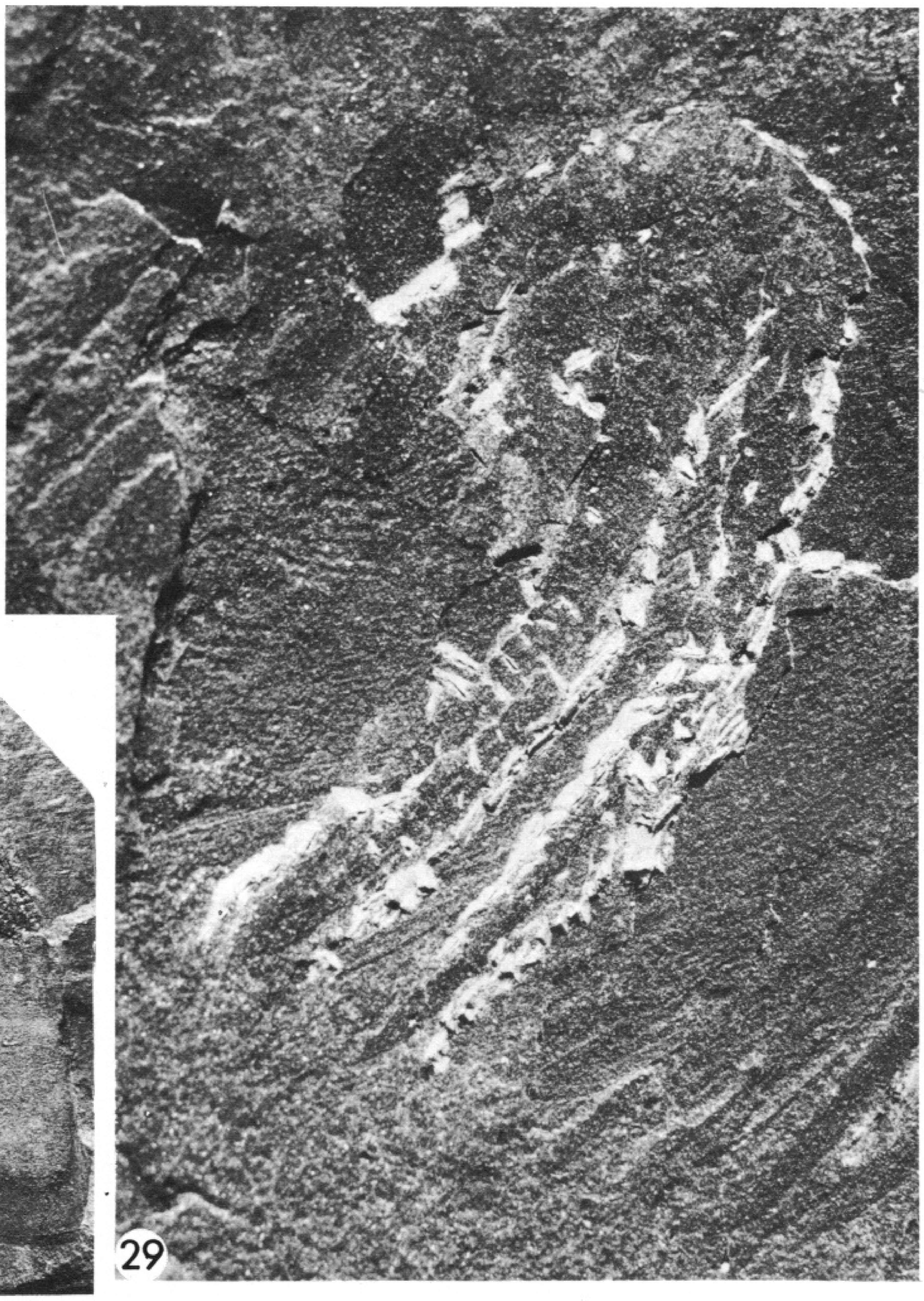

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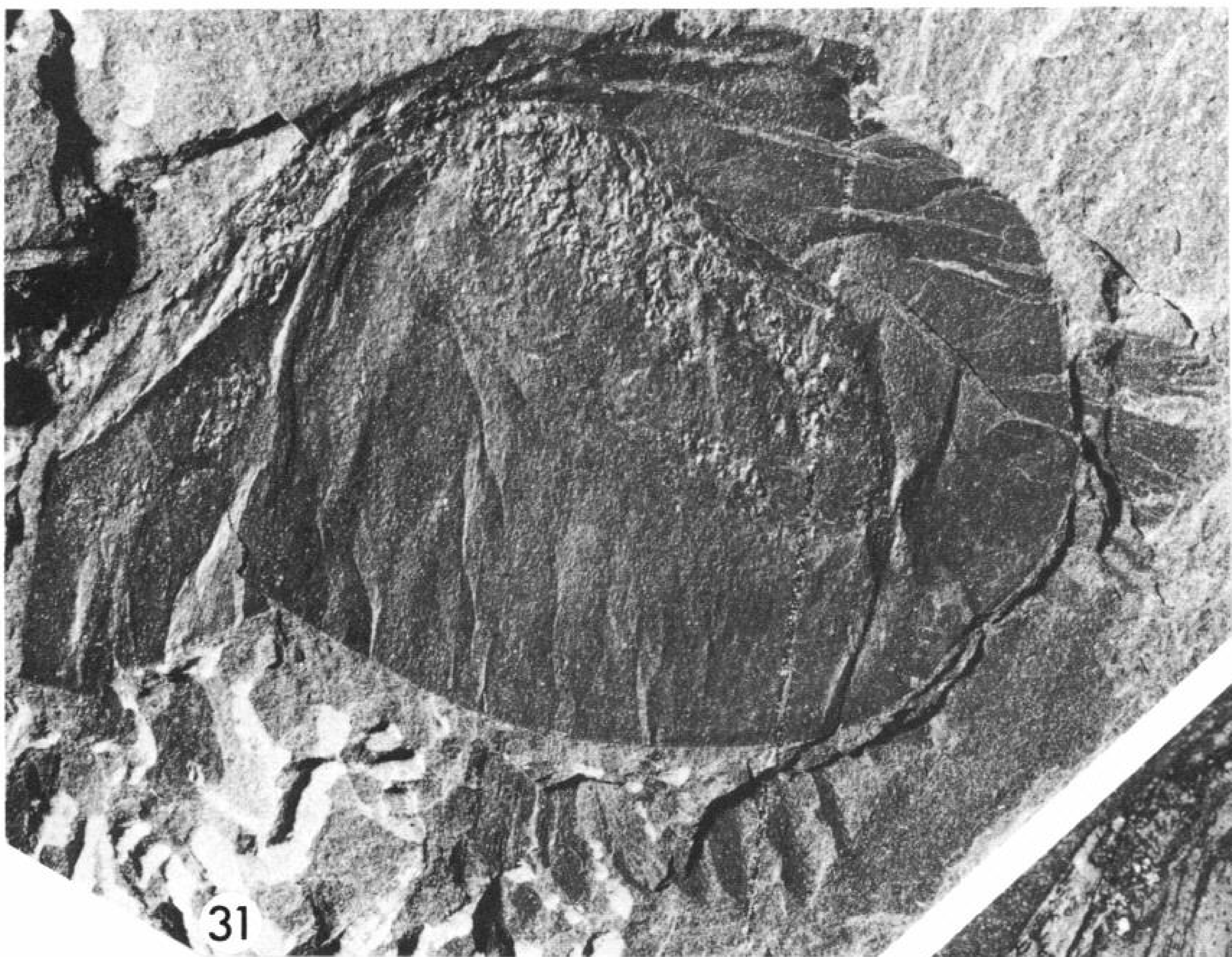

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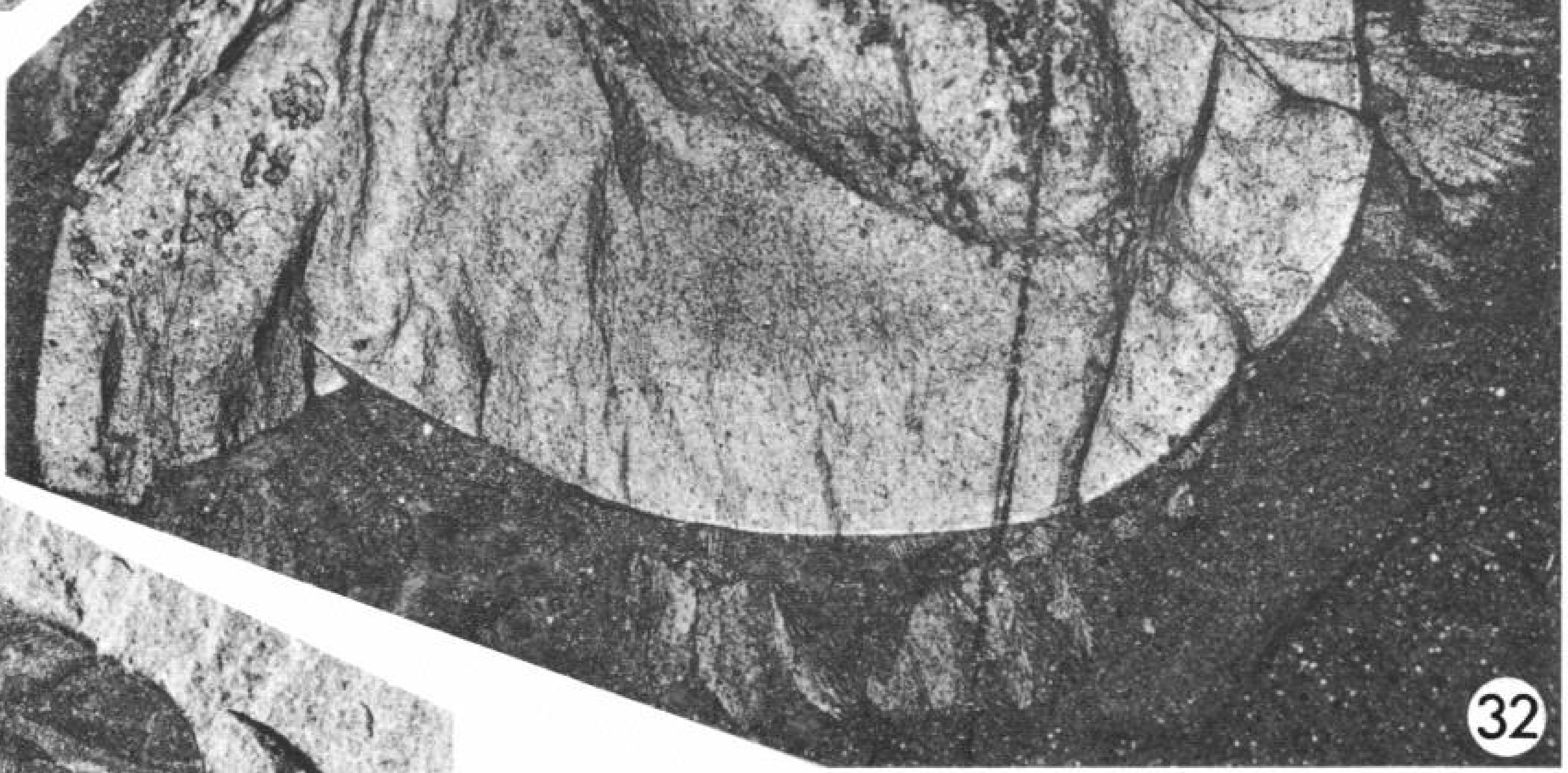

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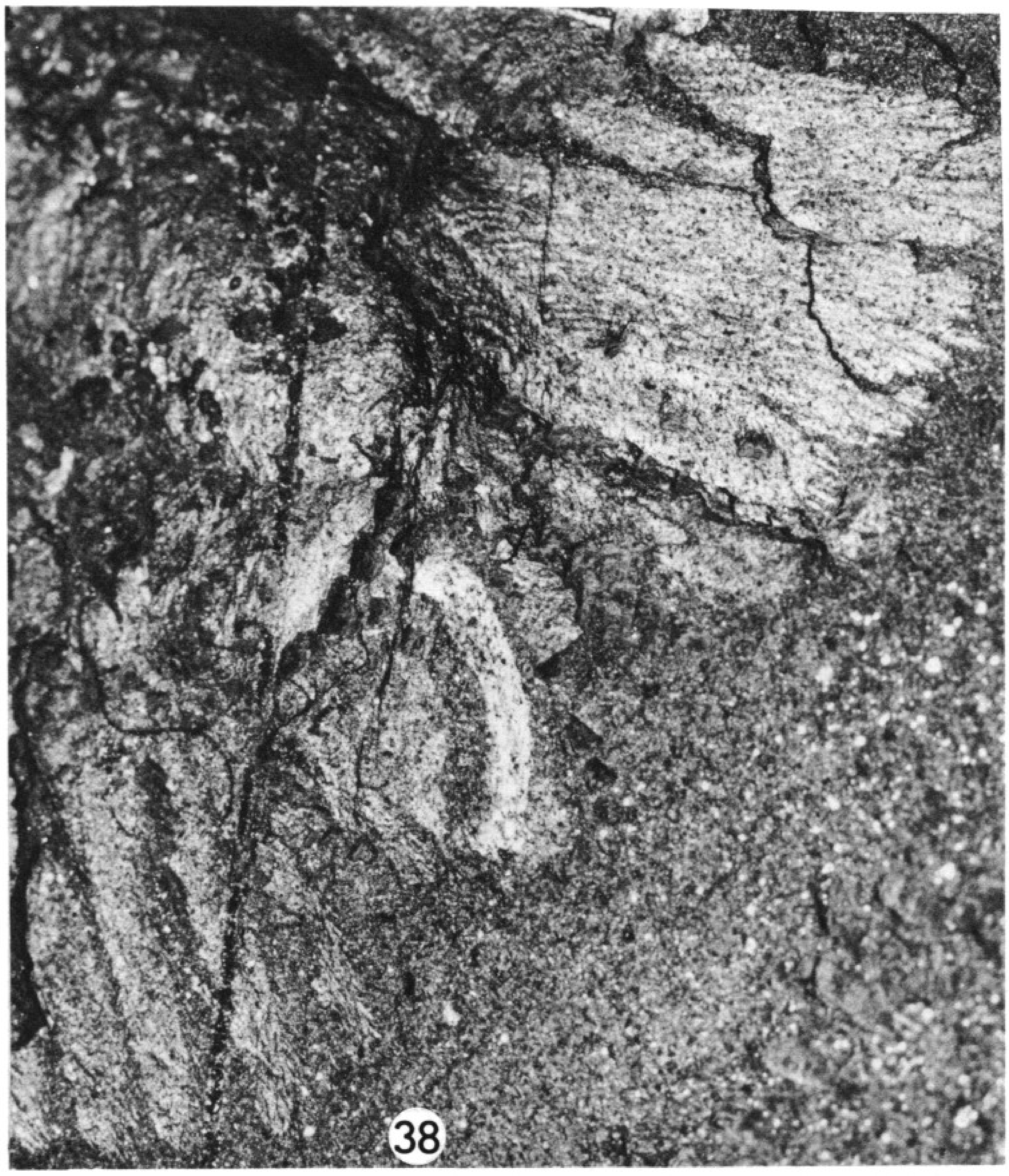
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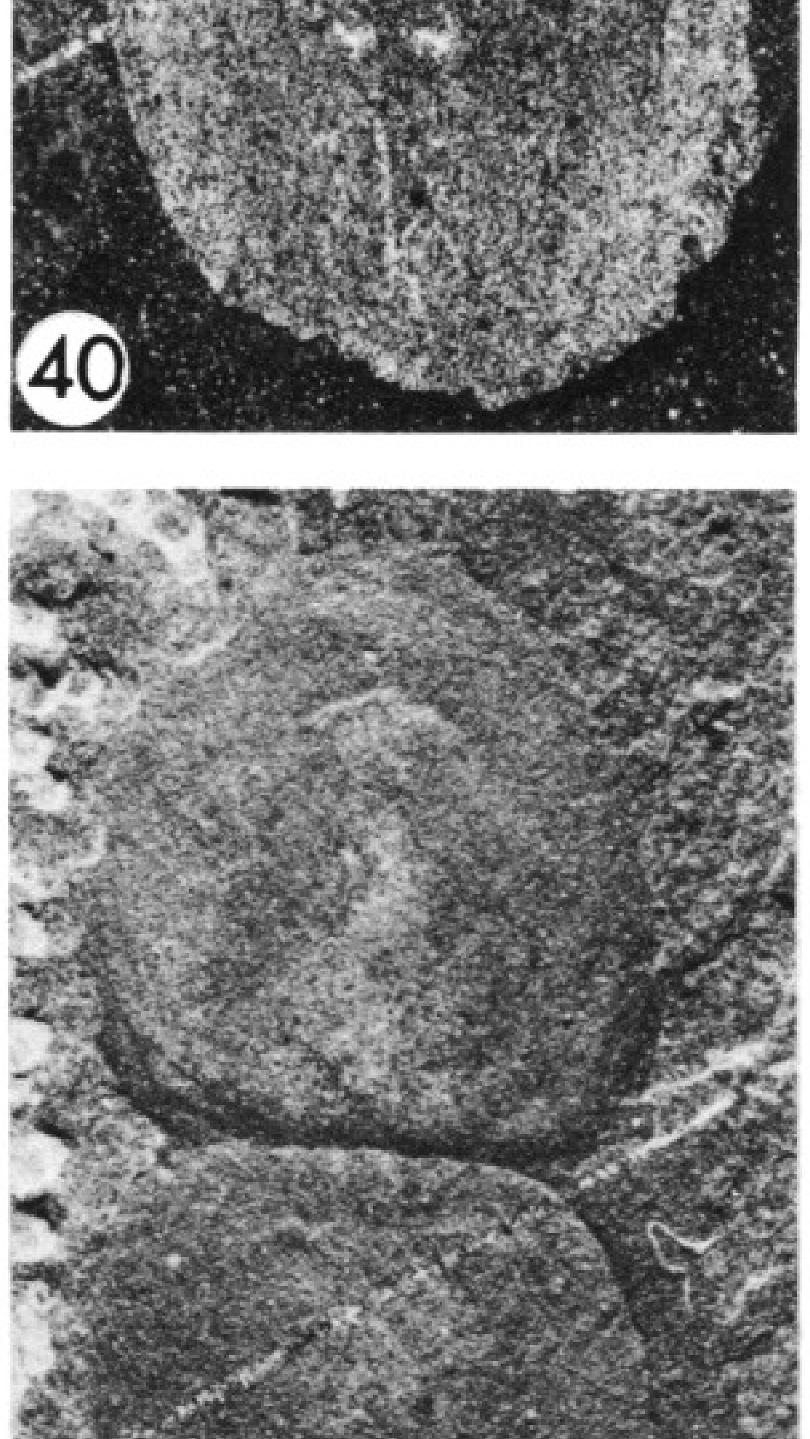
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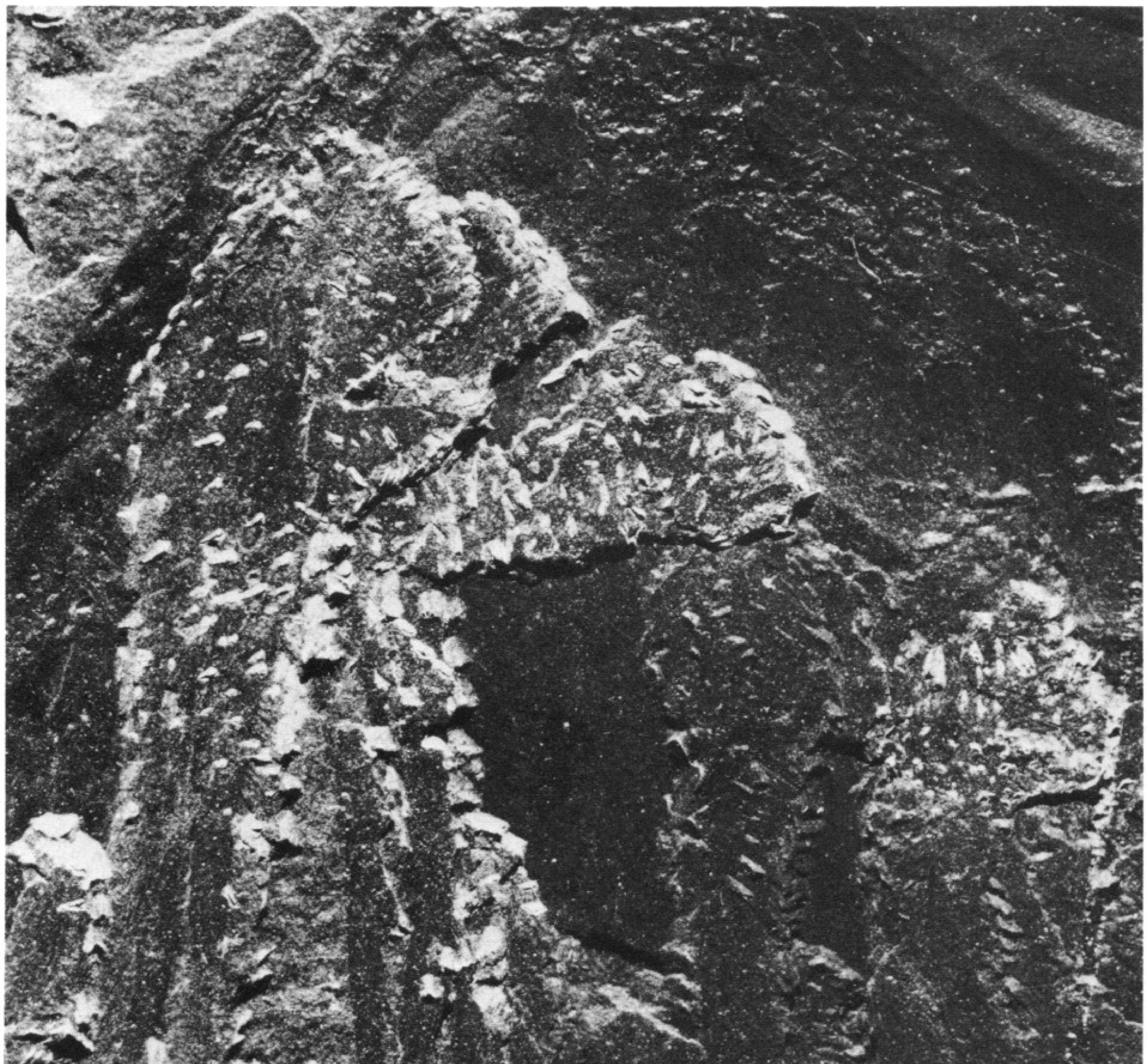
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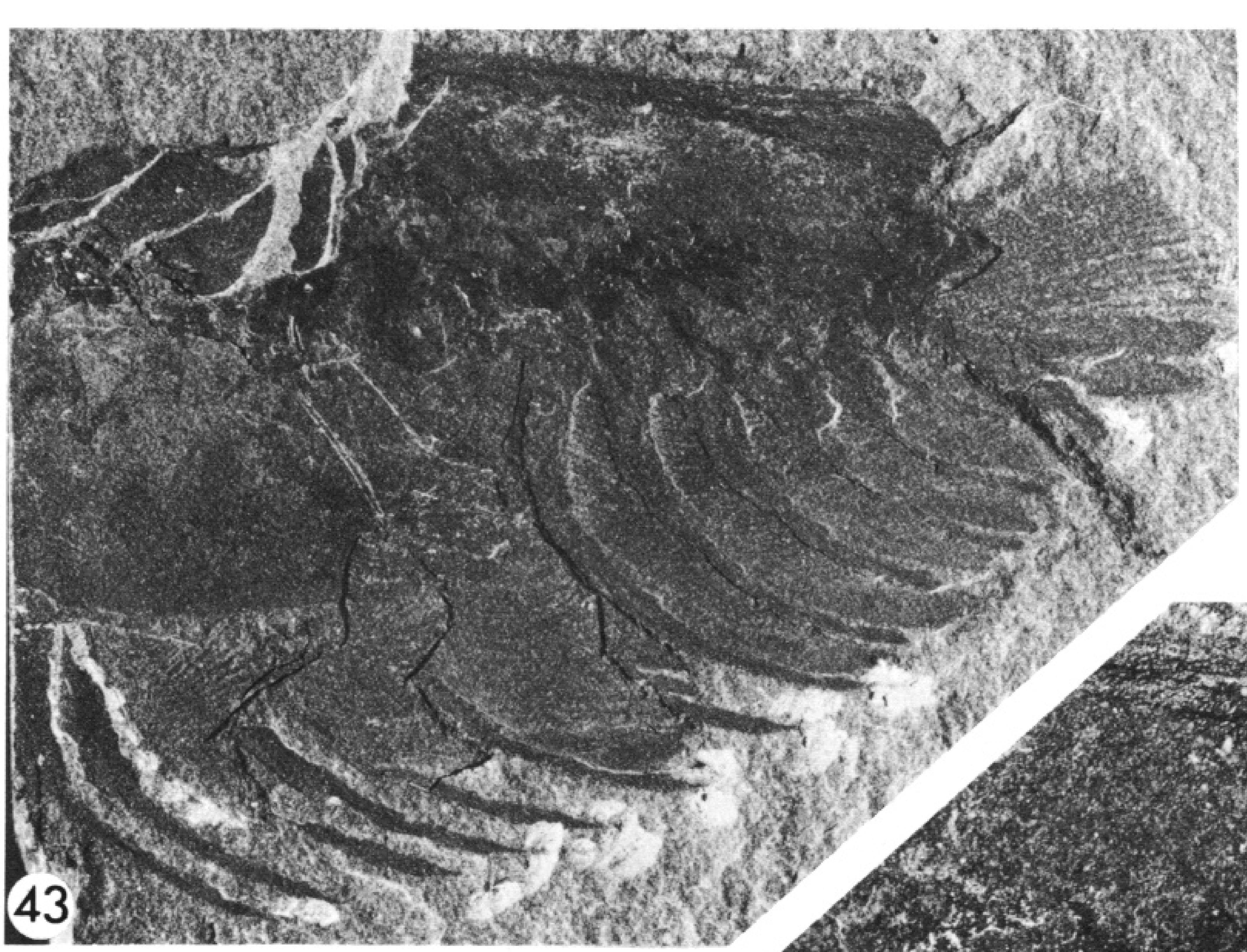
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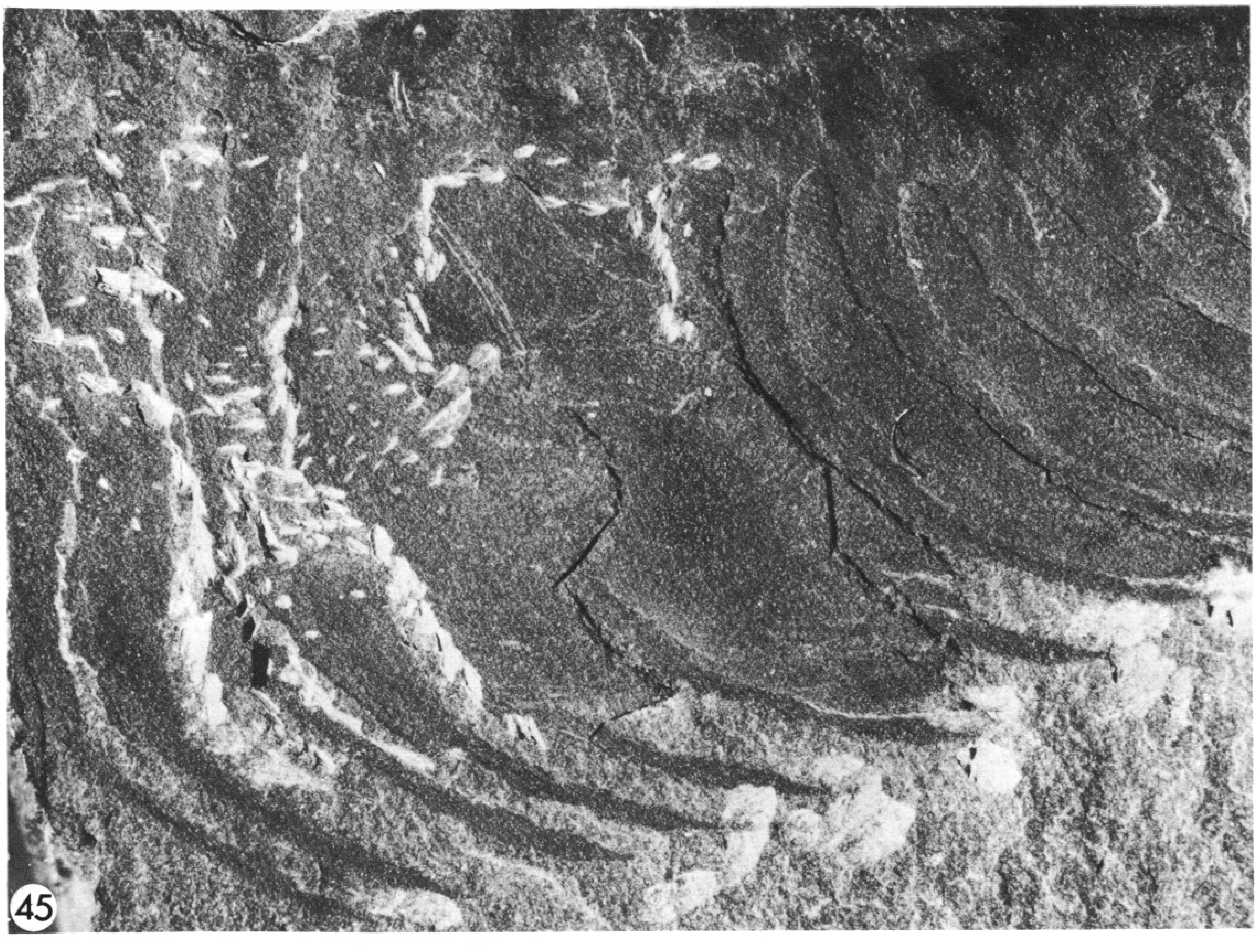
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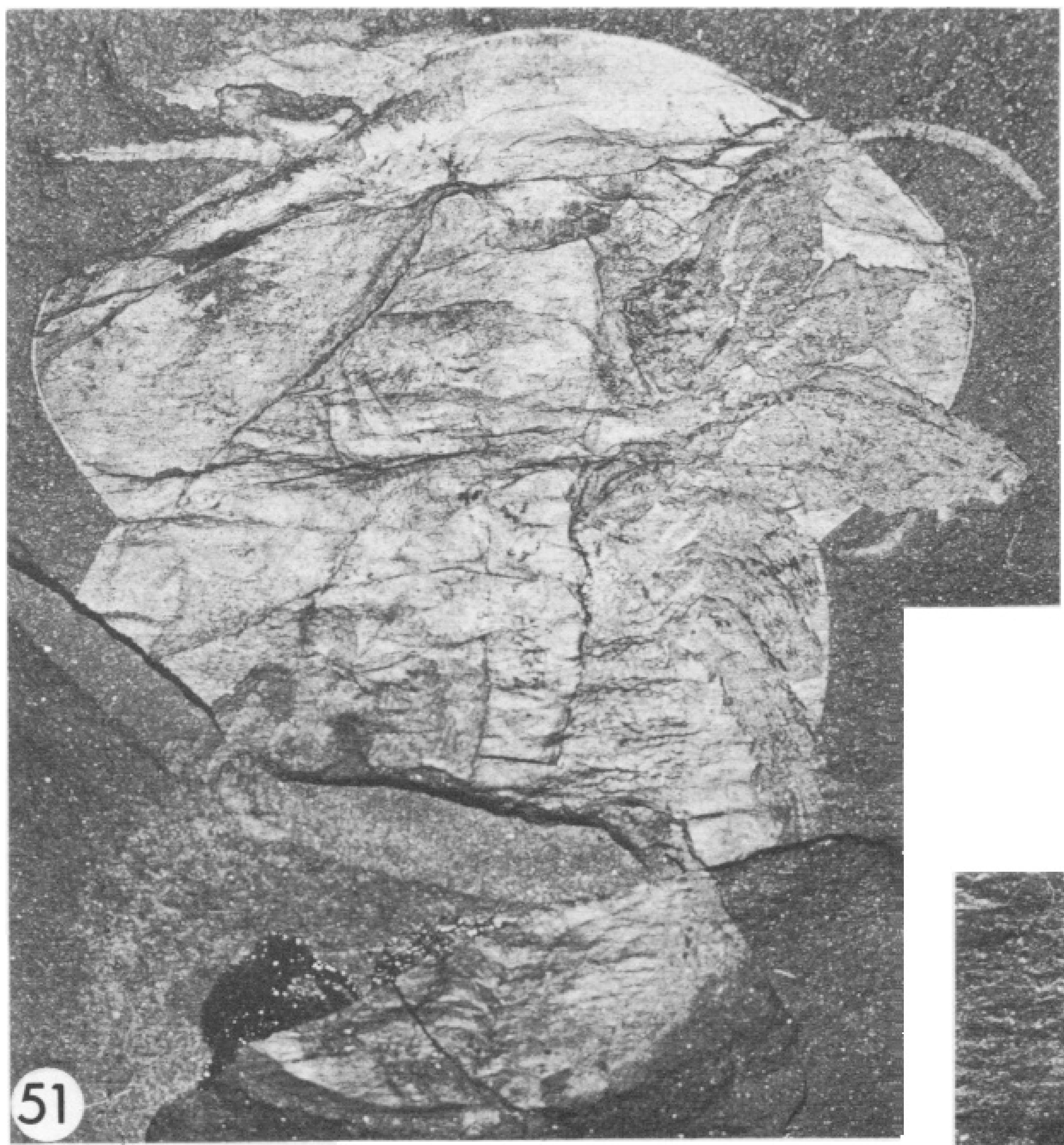
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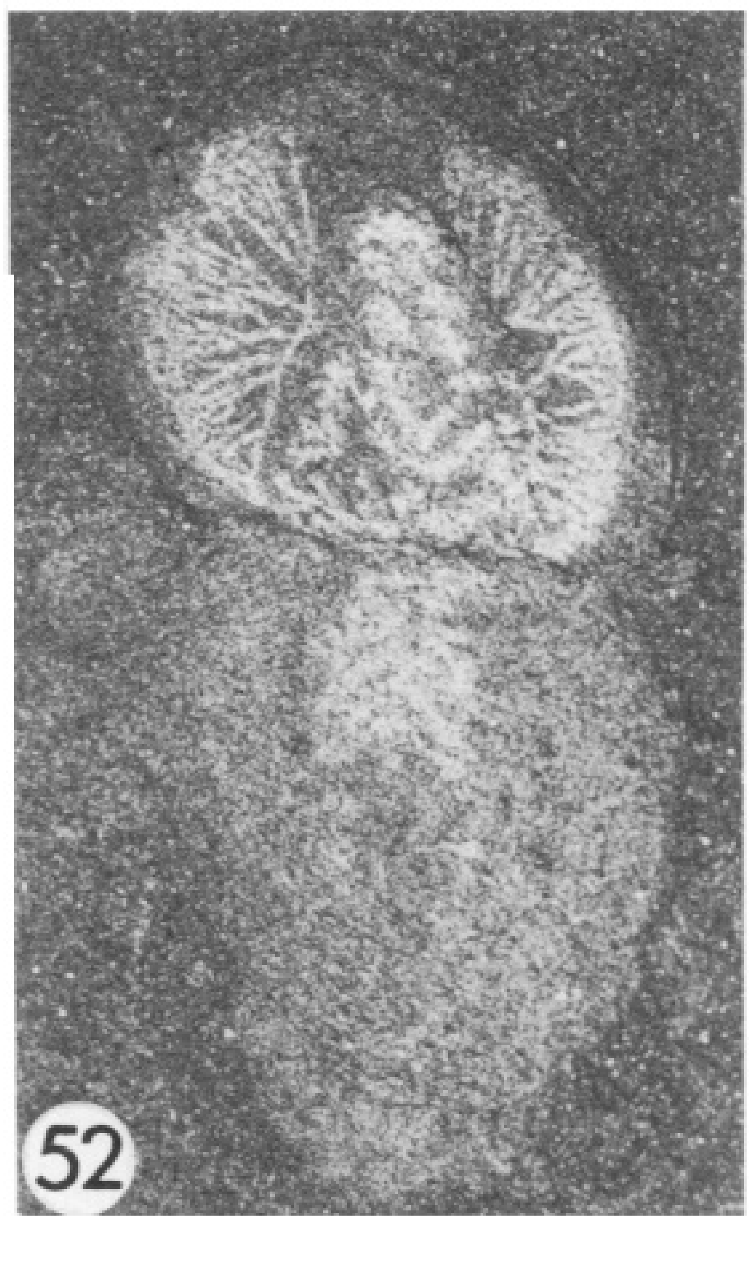
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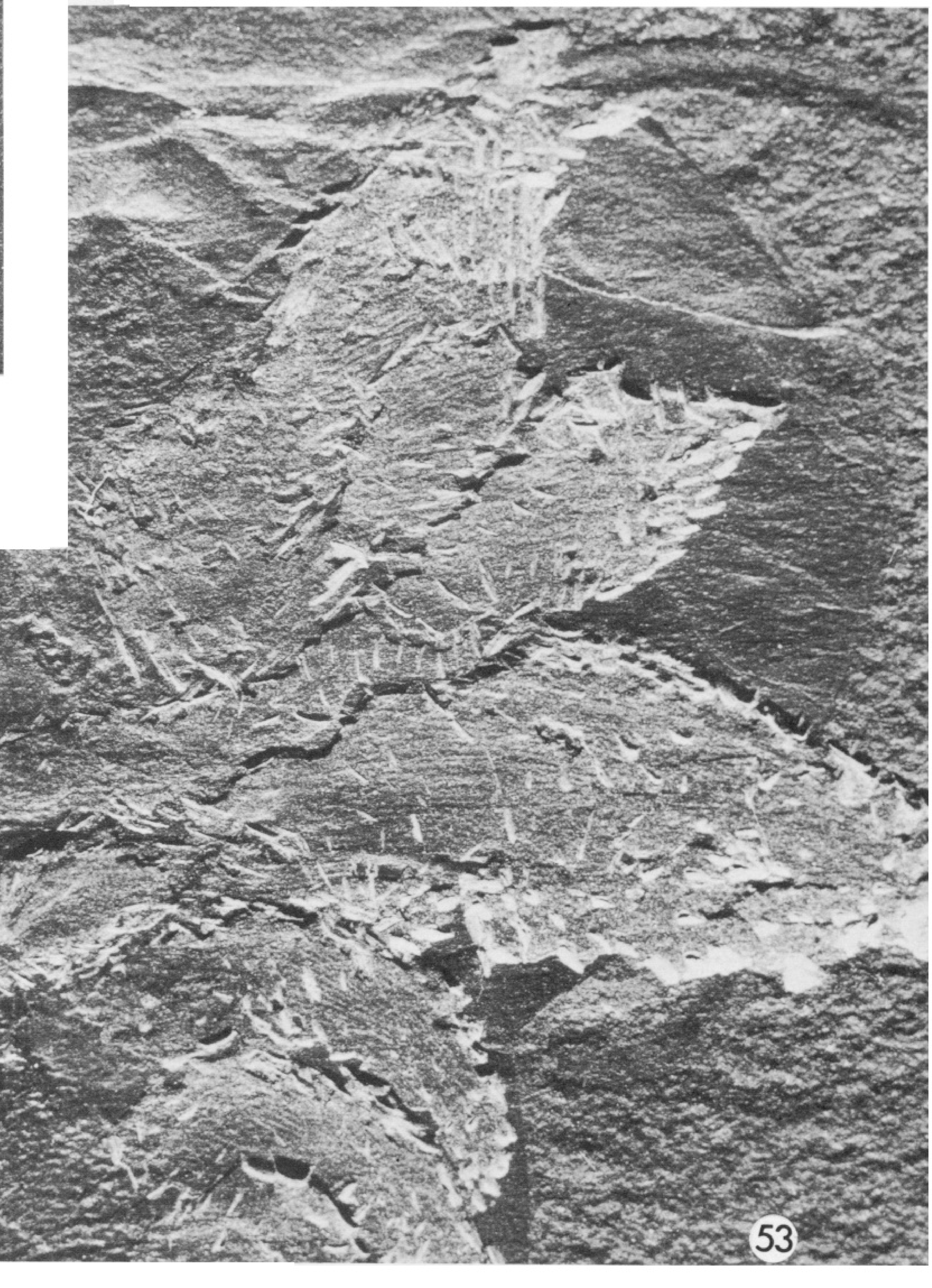
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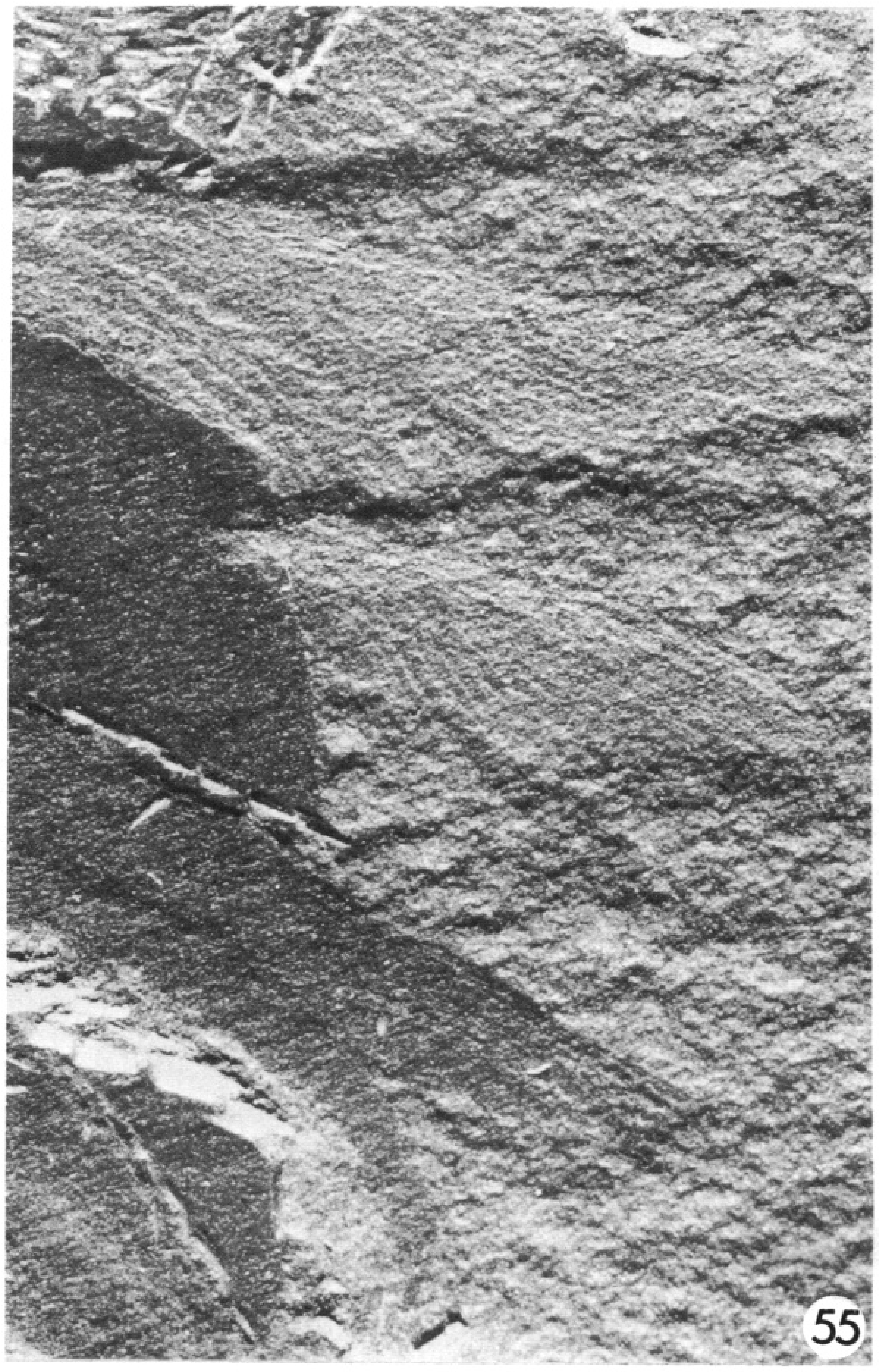
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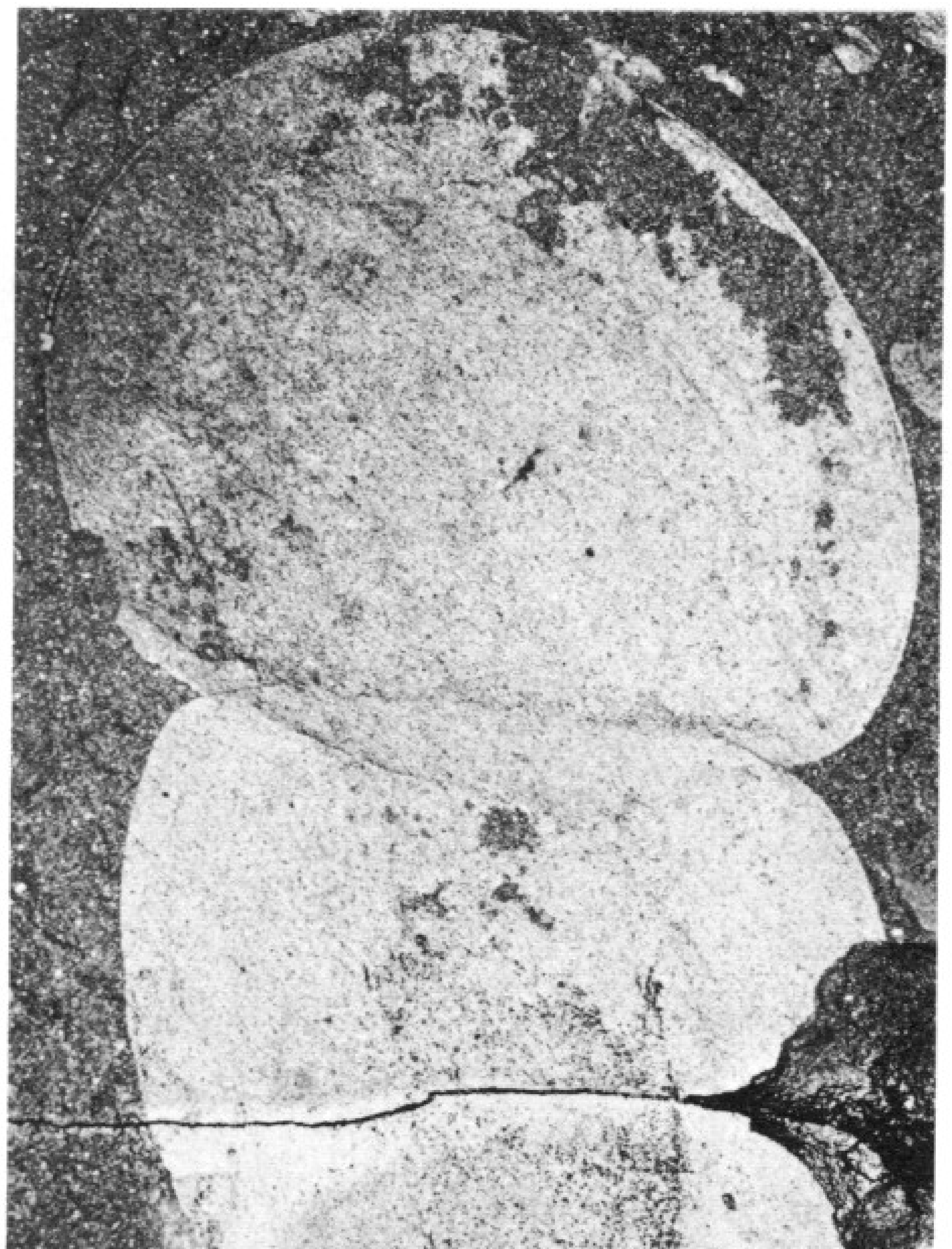
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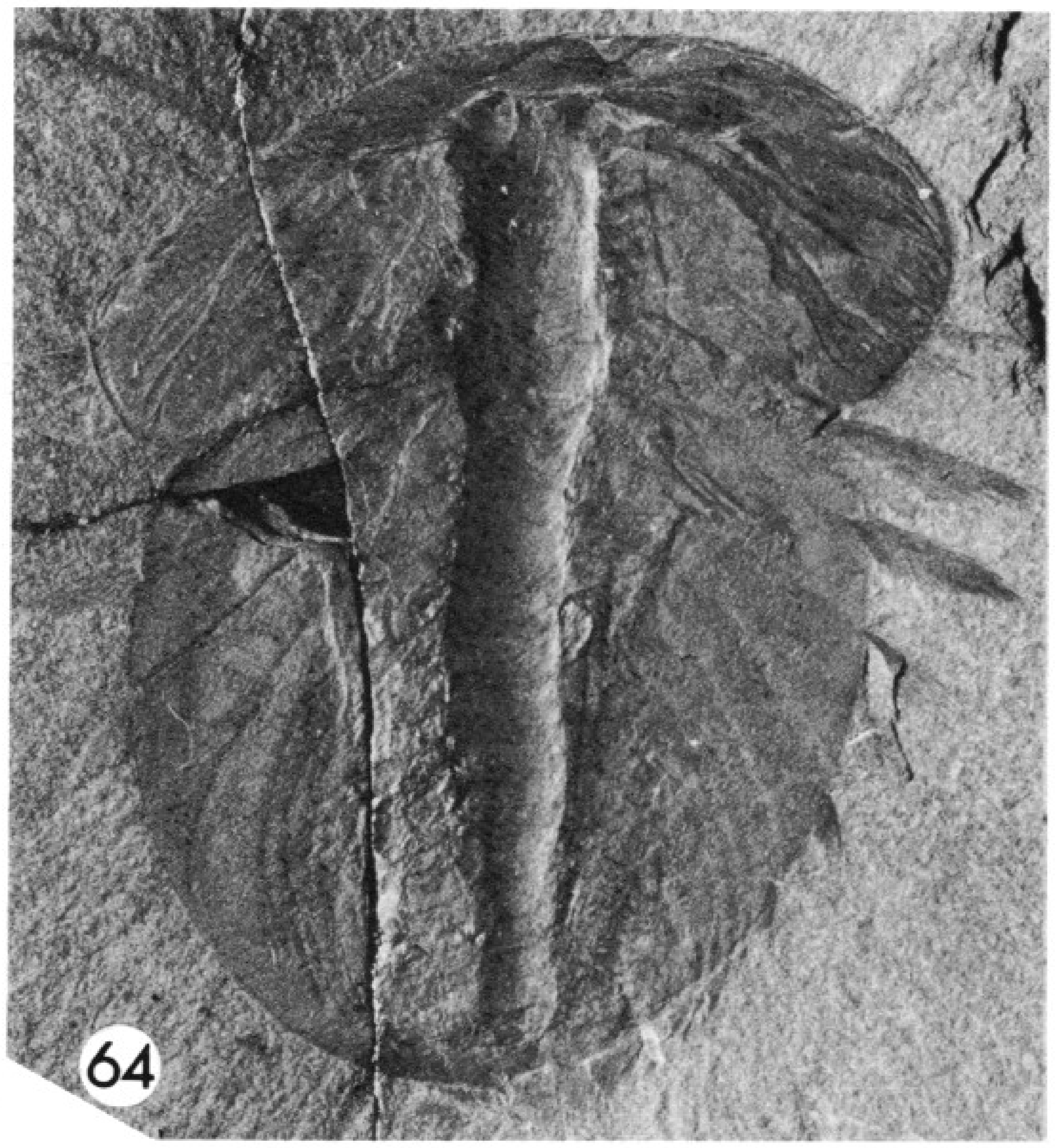
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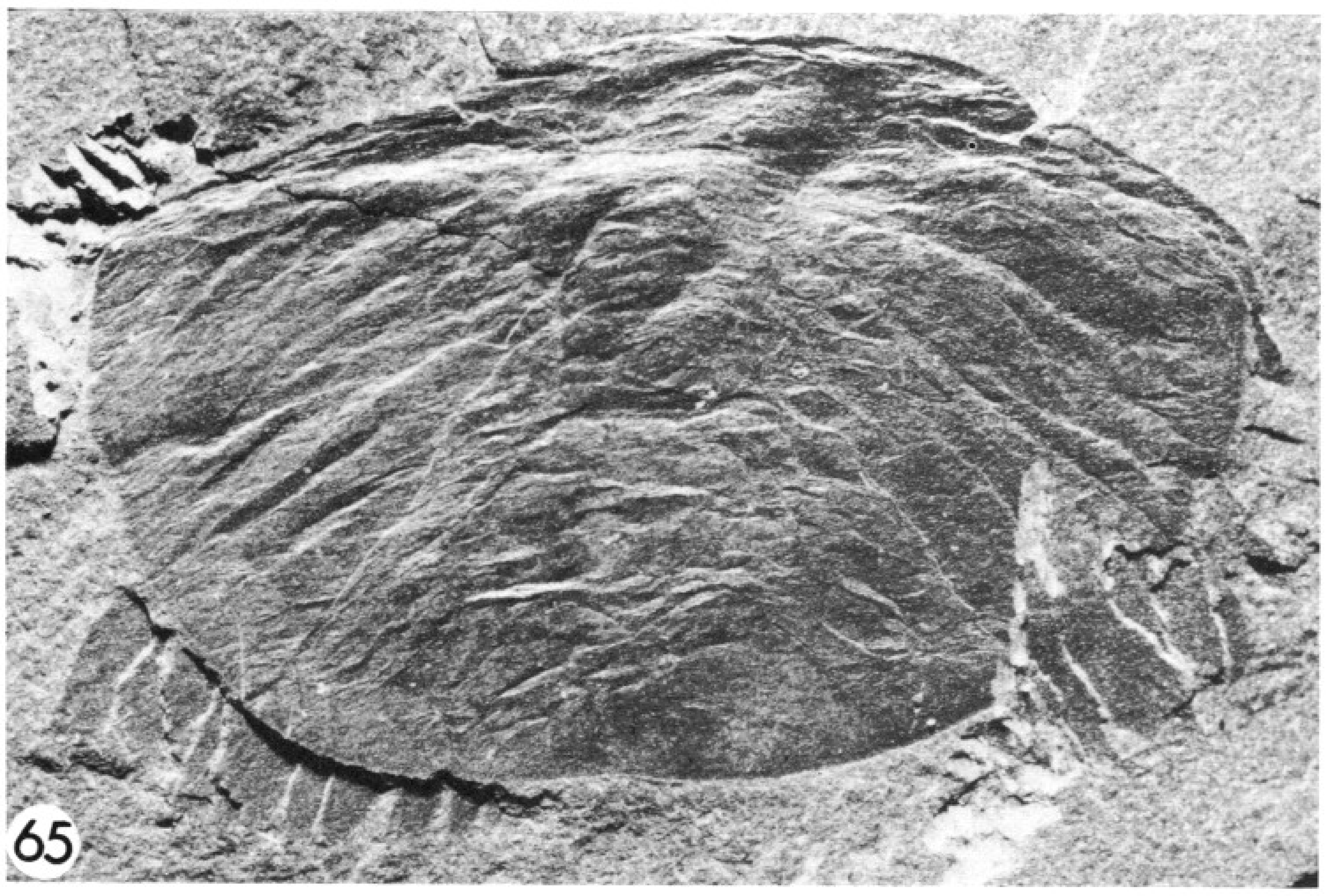
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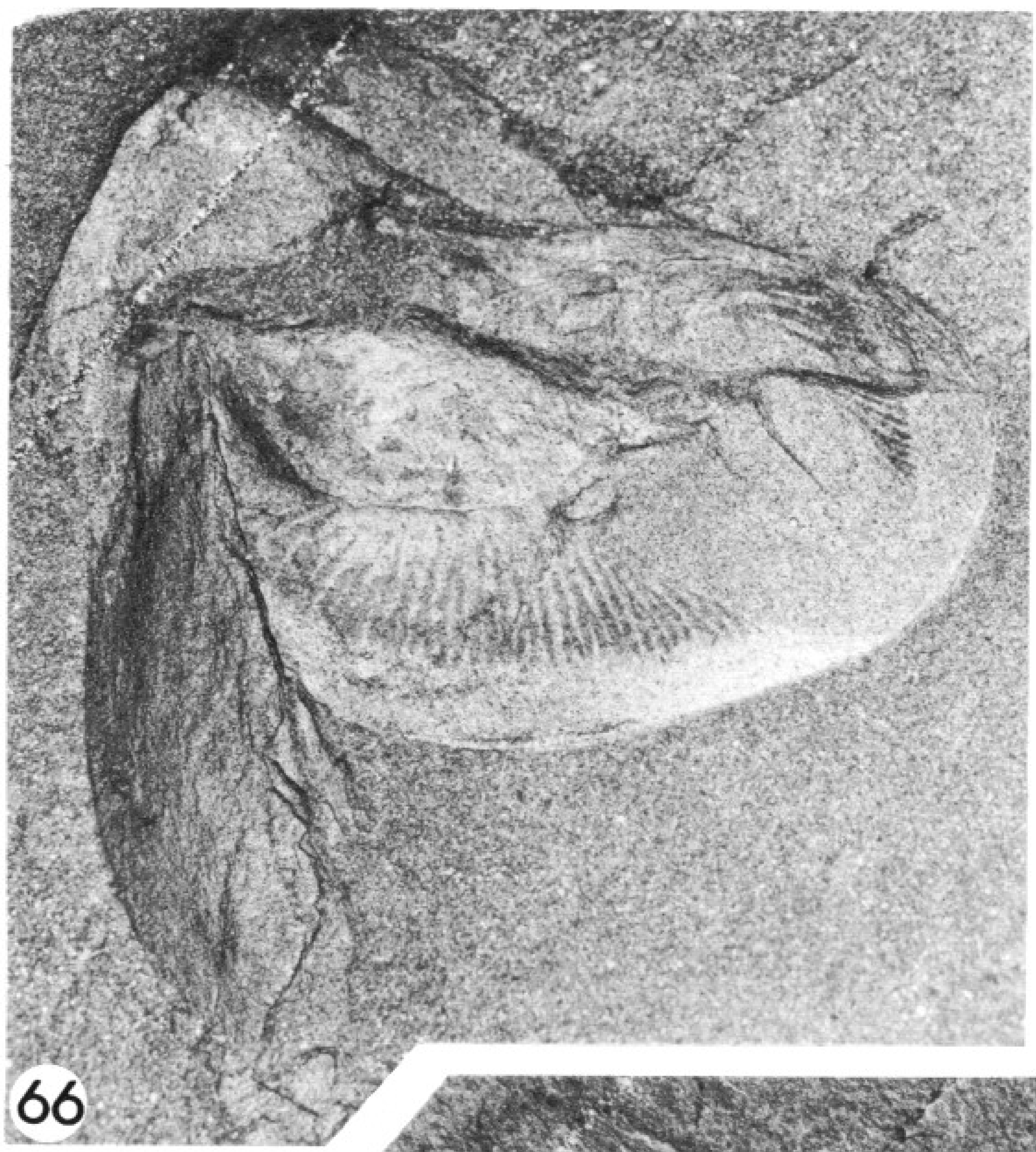
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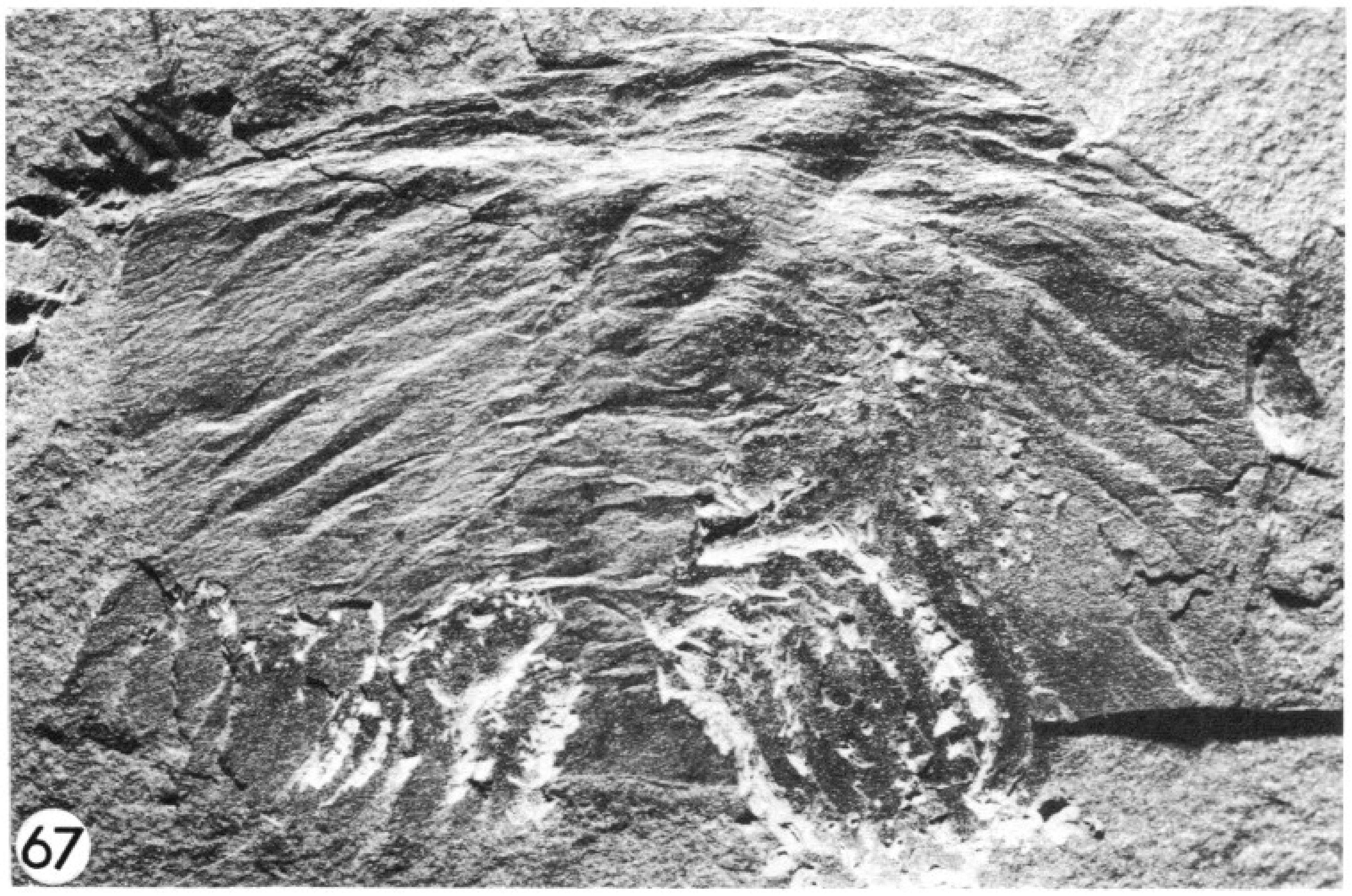
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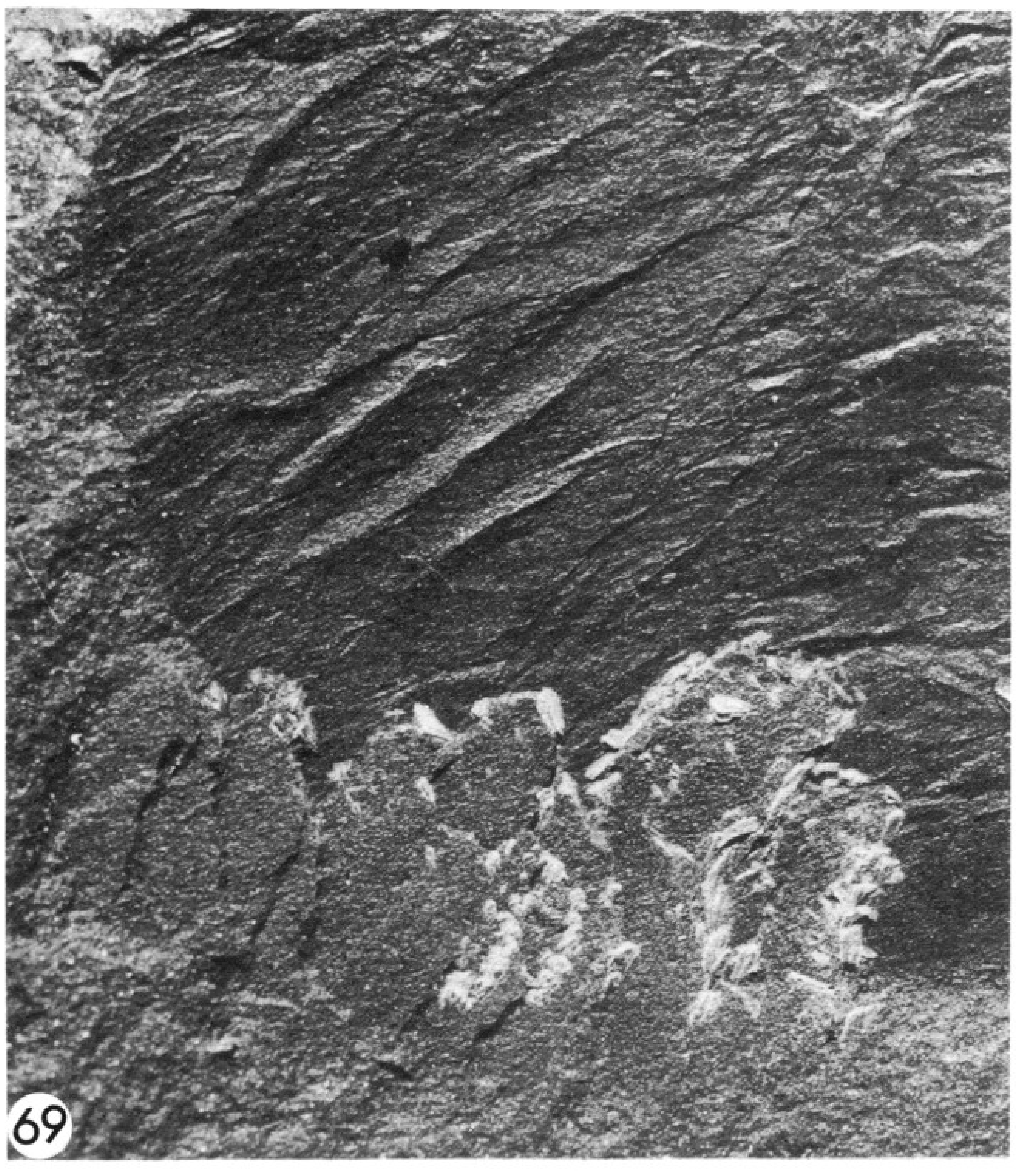
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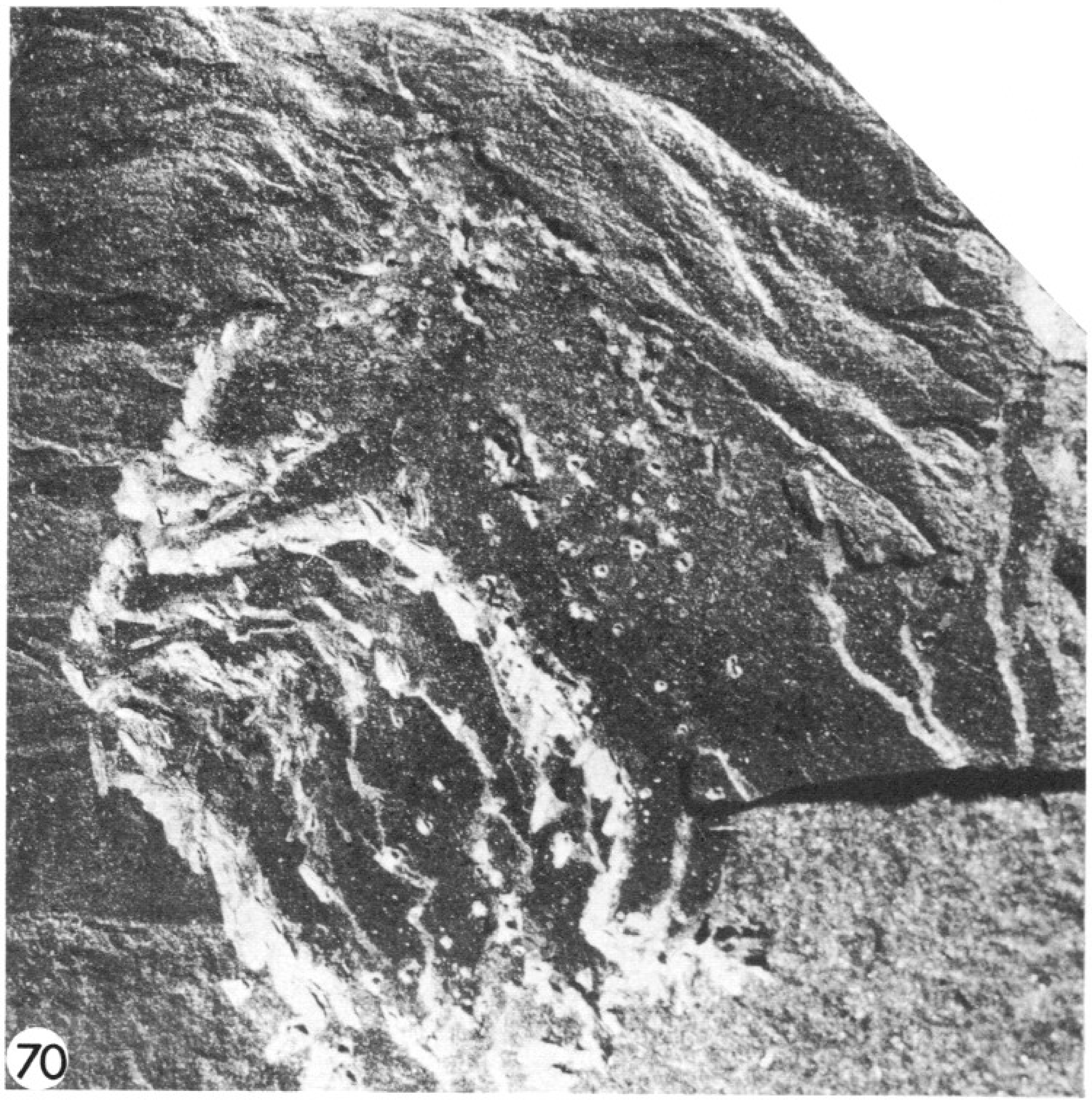
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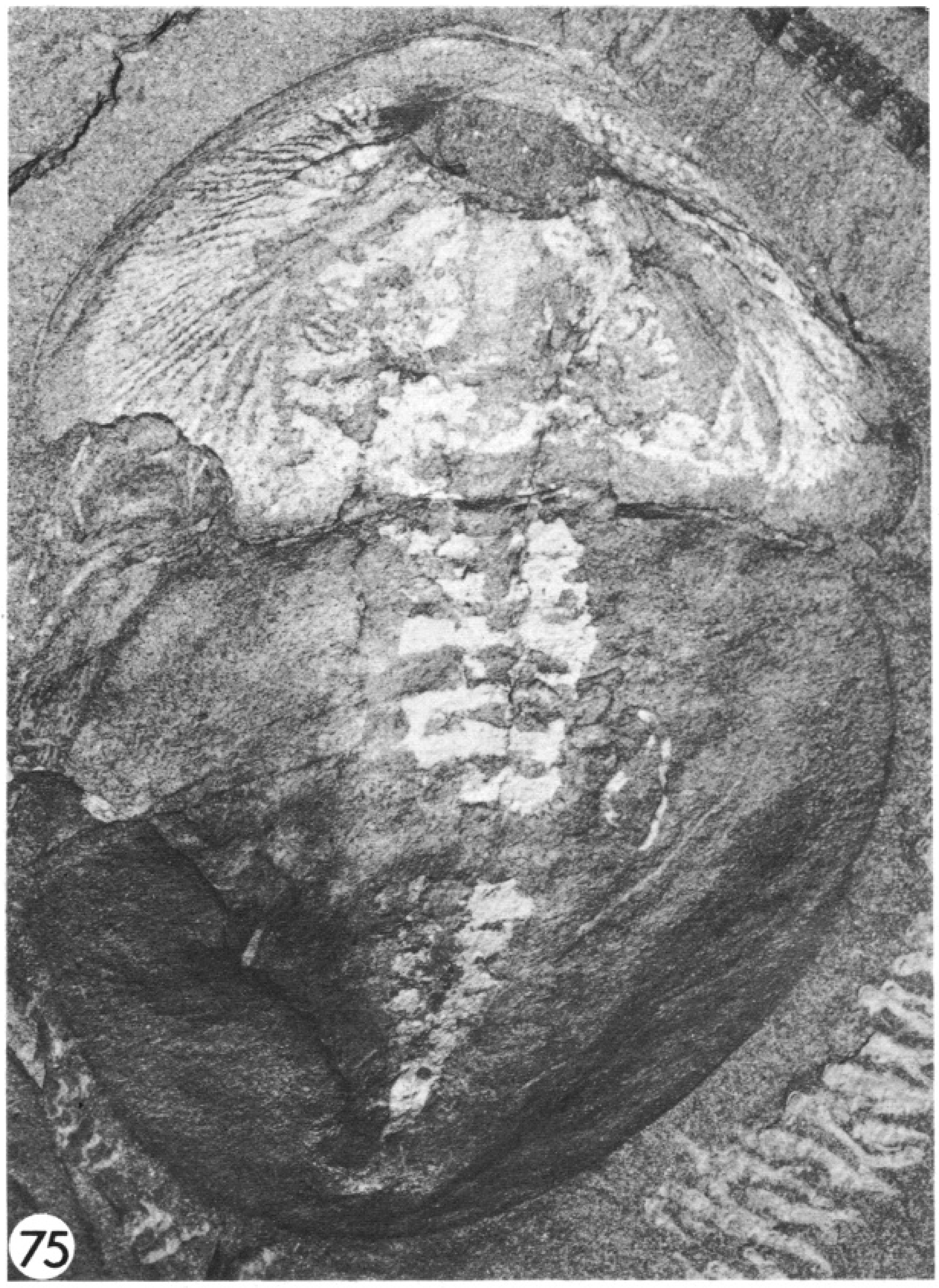
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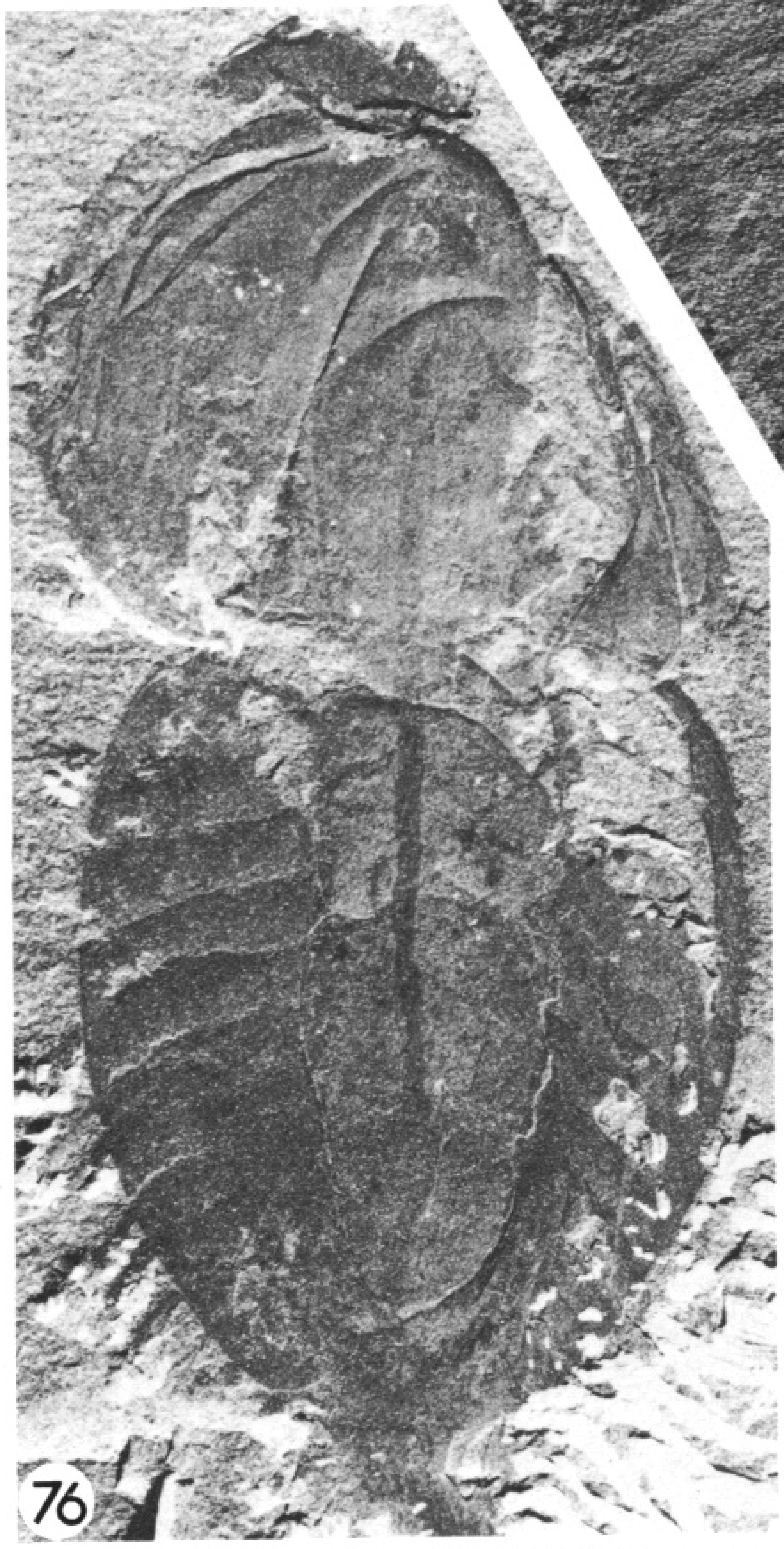
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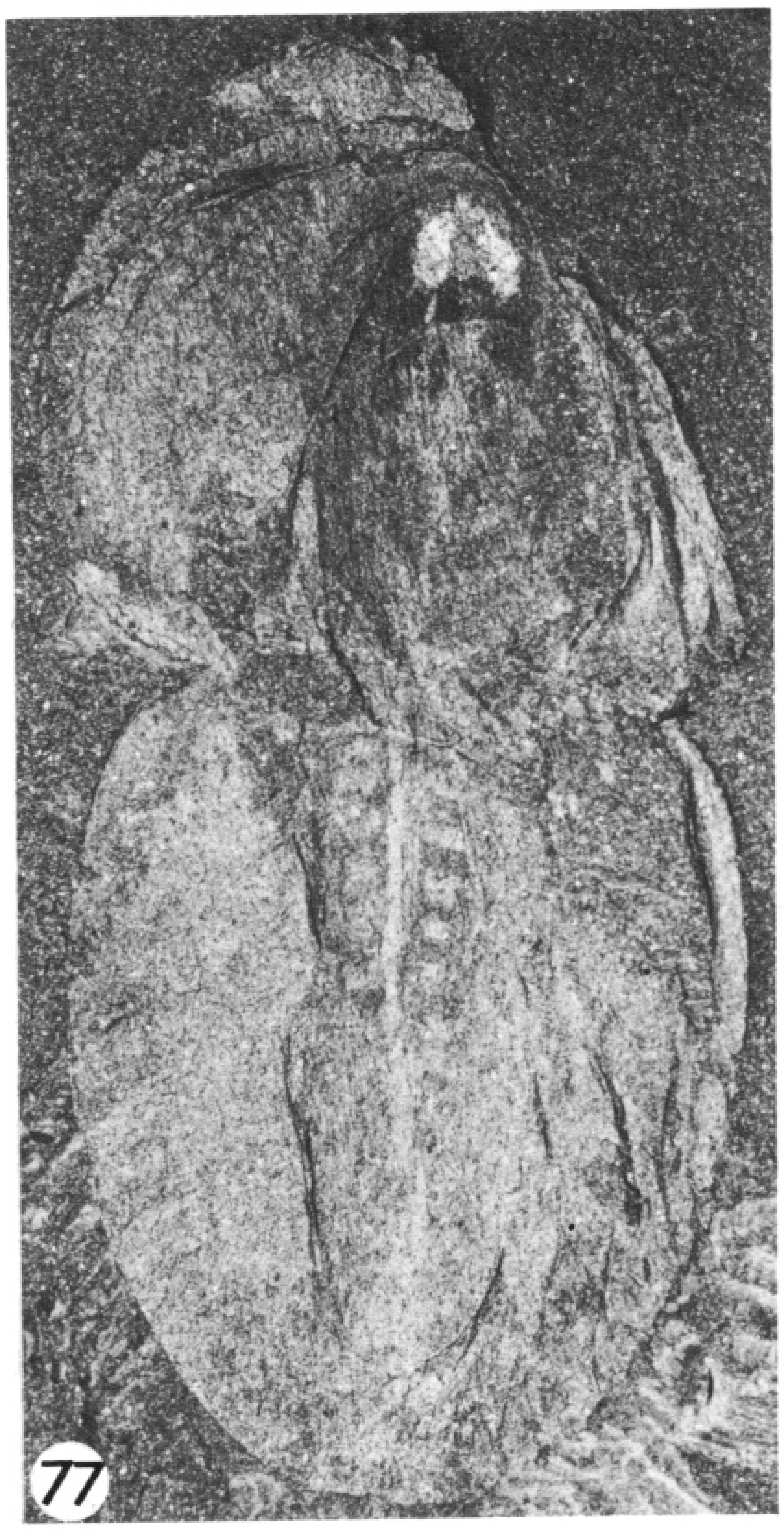
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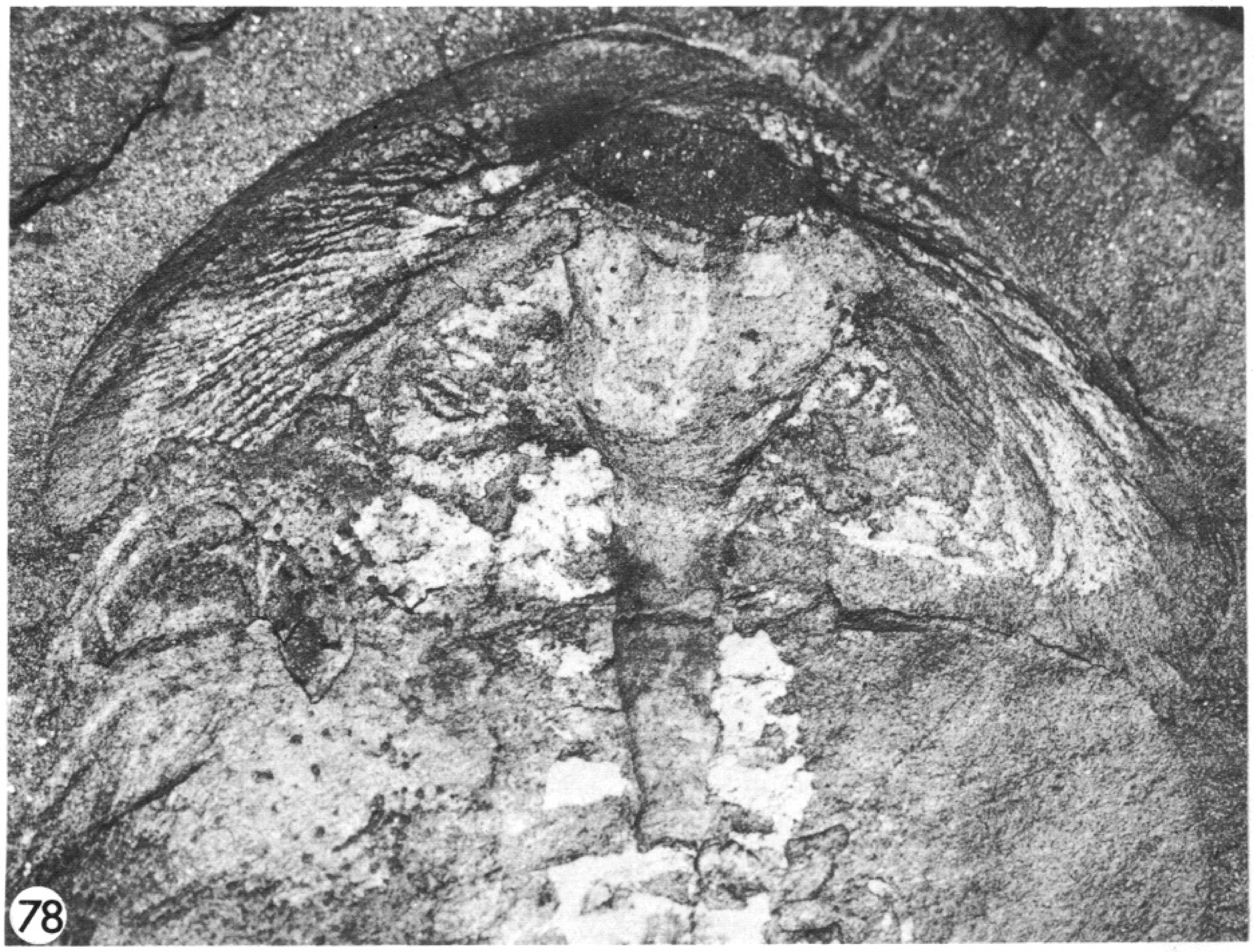
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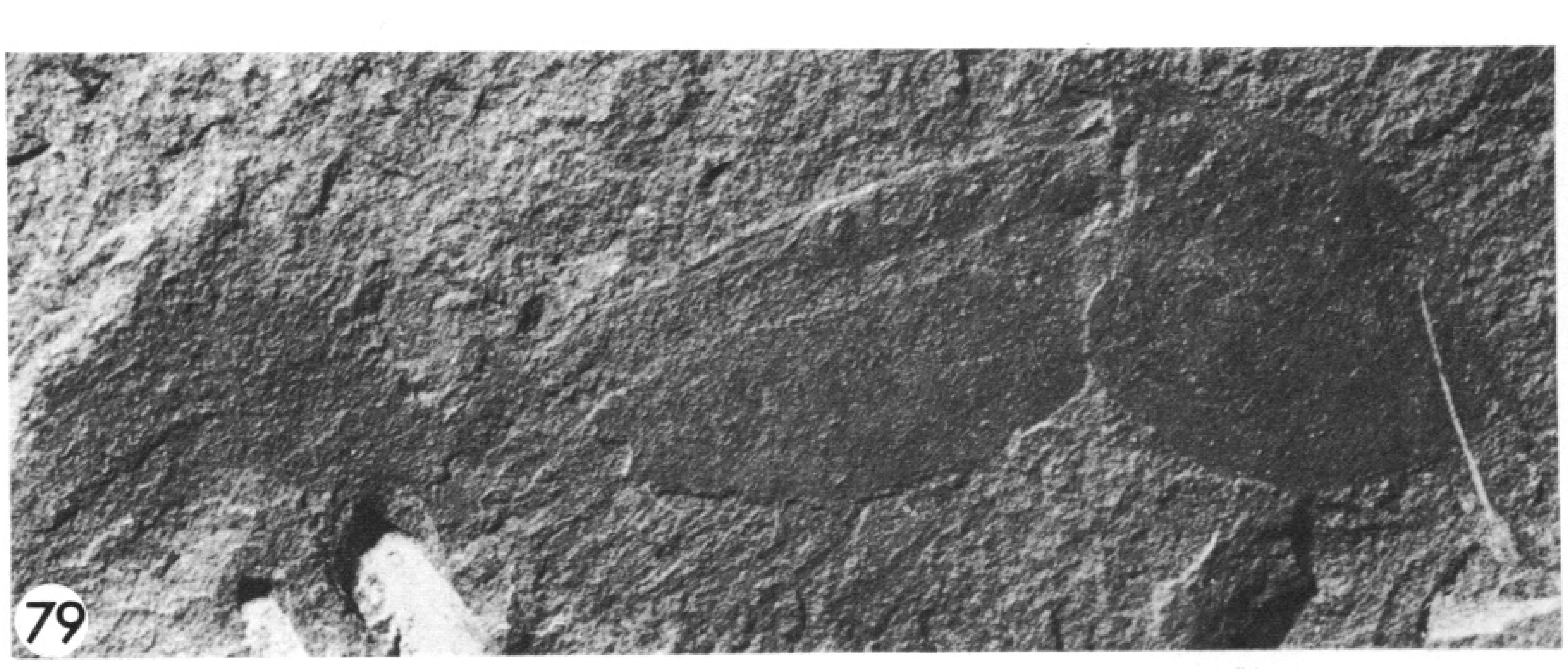
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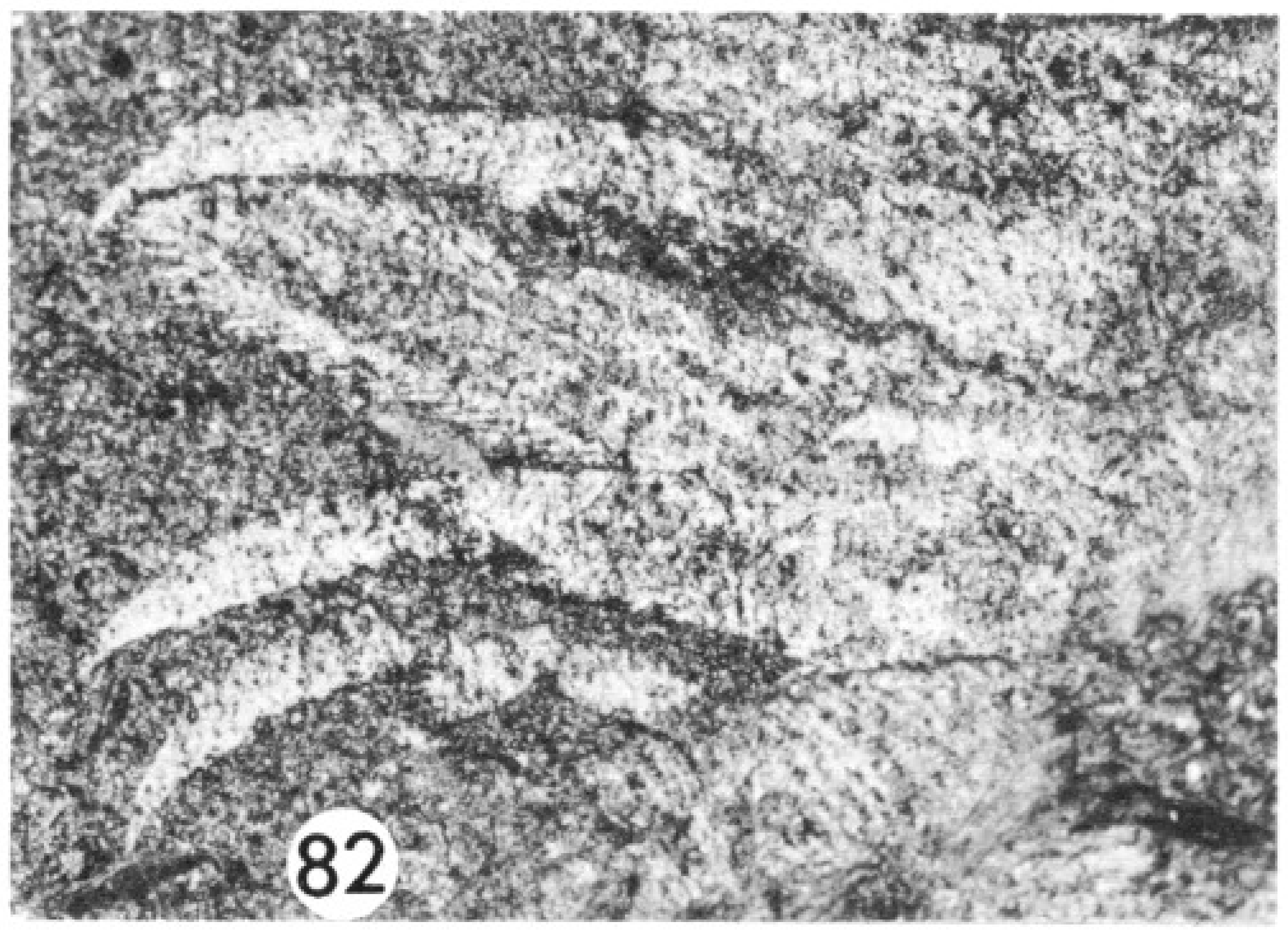
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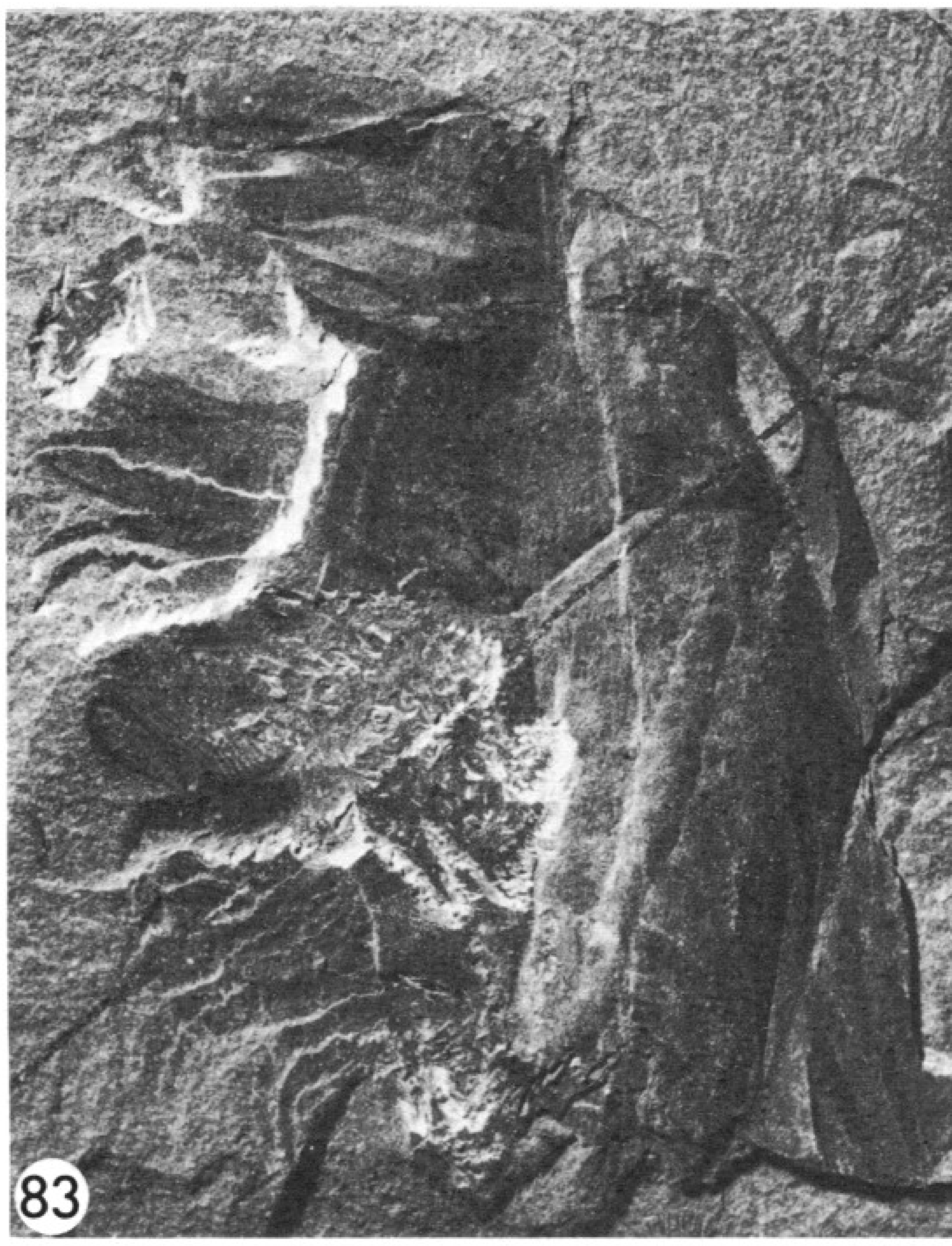
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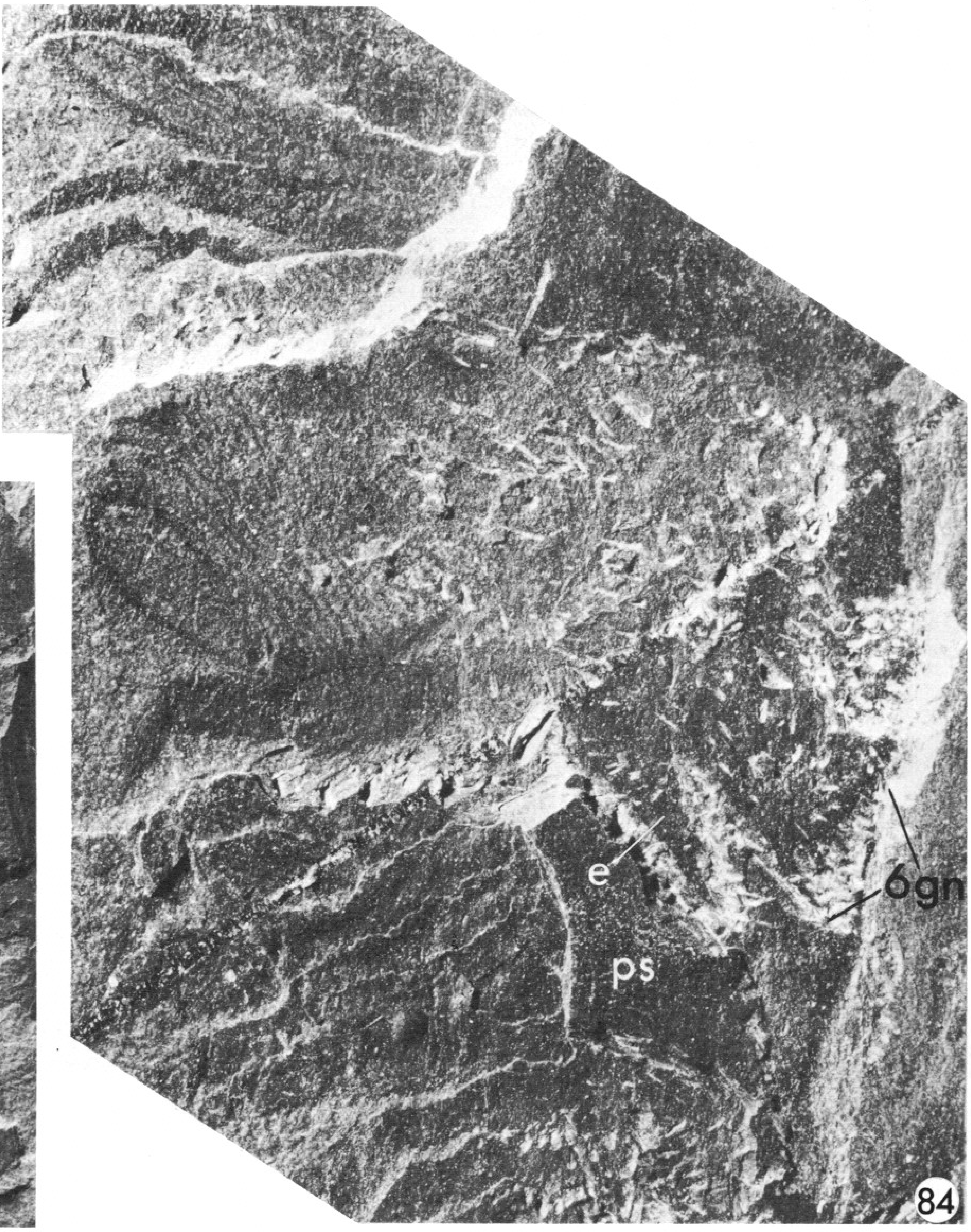
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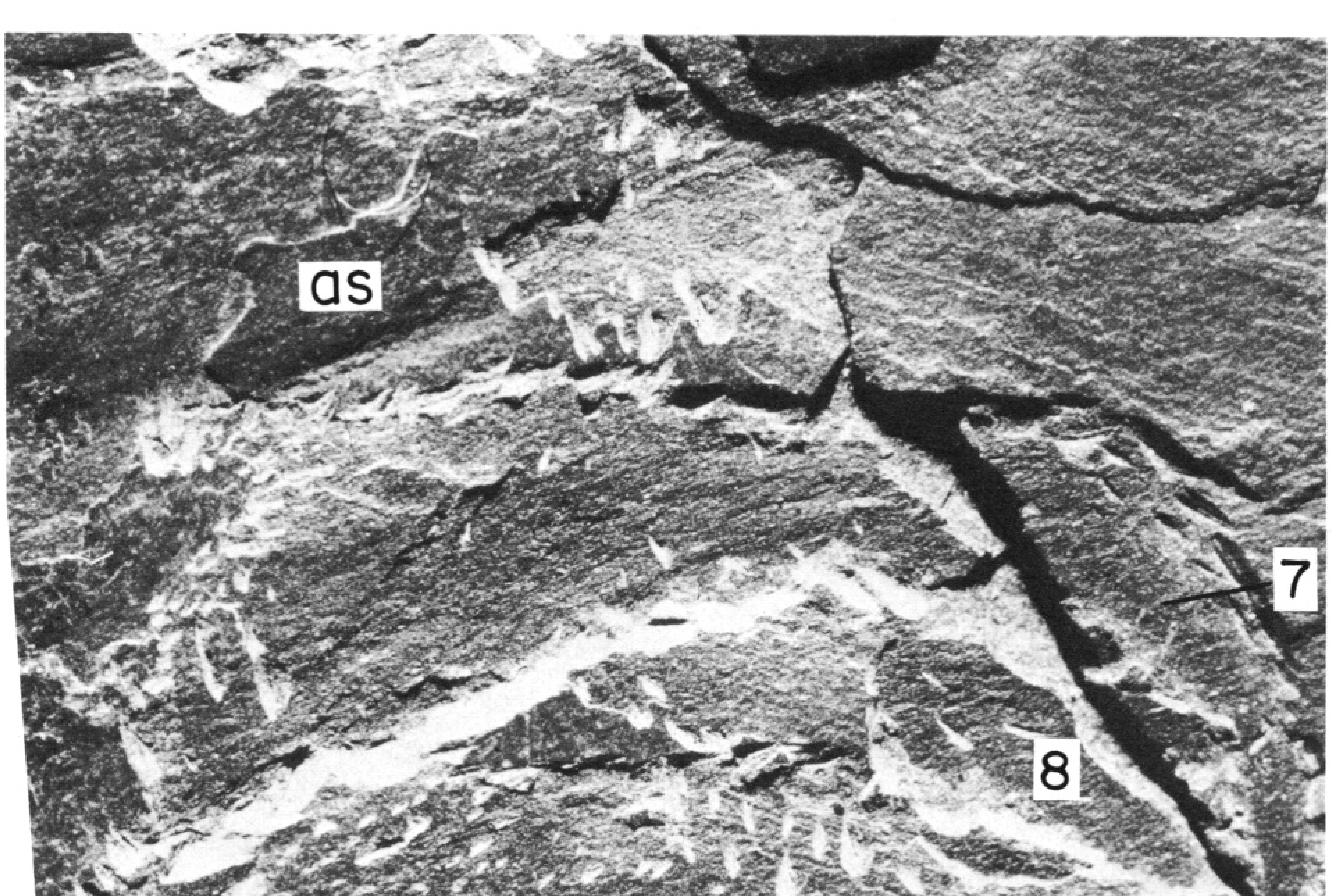
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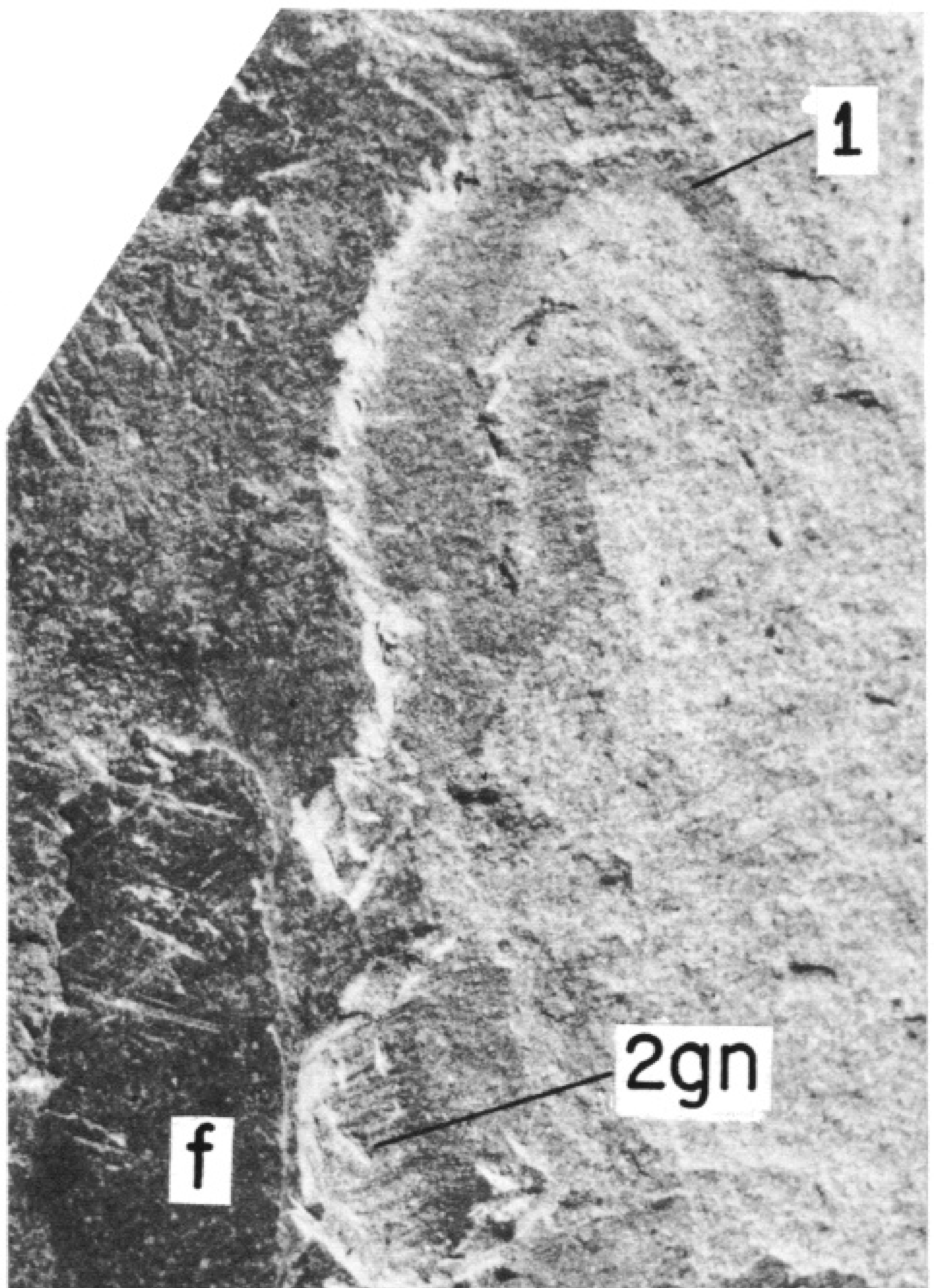
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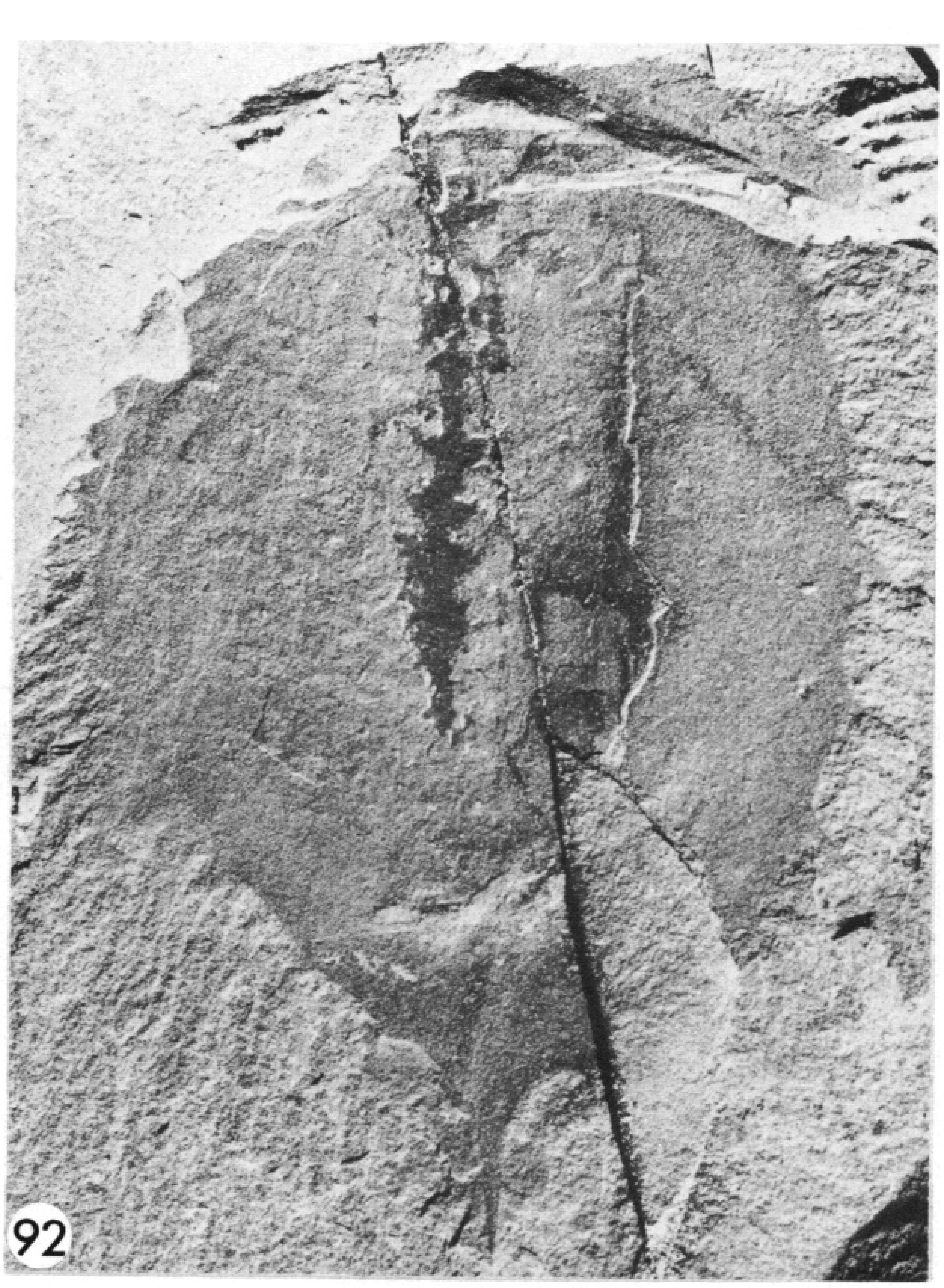

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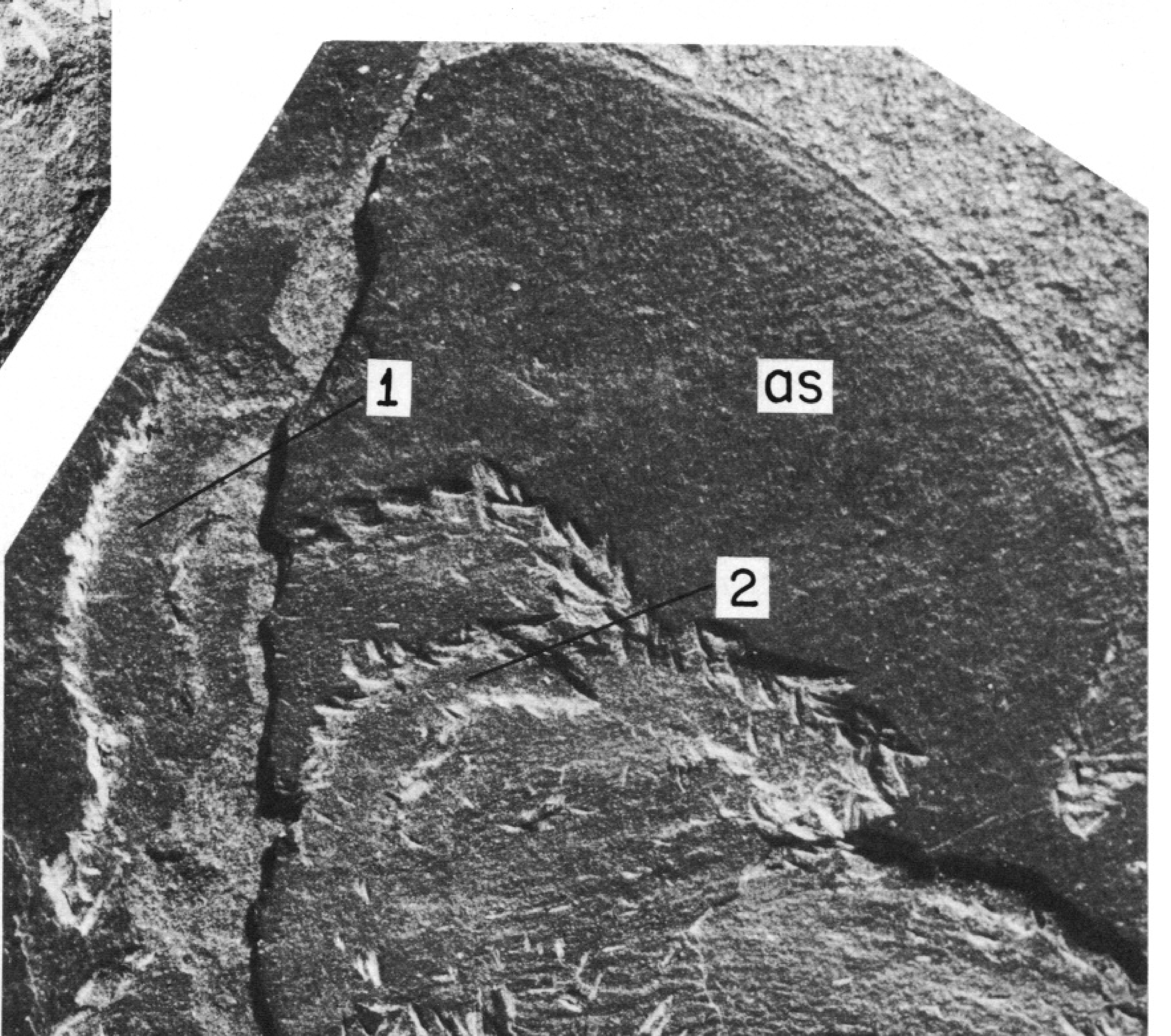

94