THE ENIGMATIC ANIMAL *OPABINIA REGALIS*, MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

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Ten almost complete specimens have been studied in detail; nine coming from C. D. Walcott's original collection, one from the recent re-investigation. The cuticle is preserved as a thin, dark layer; the external surface was apparently smooth, except for striations on the frontal process and adjacent to the mouth. Dorsally on the short cephalon were five eyes, thought to have been compound, the inner and outer pairs pedunculate, the median not stalked. From the anteroventral slope of the cephalon arose a long, flexible frontal process, divisible into a longer, cylindrical proximal portion, and a shorter, broad distal portion. The latter was divided longitudinally, each half bearing a group of long spines, directed inward and forward. The process probably contained a median, fluid-filled canal. The mouth was situated on the vertical, posteroventral wall of the cephalon, the alimentary canal U-shaped. The cylindrical axial region of the trunk tapered slightly backward, the alimentary canal situated ventrally and extending to the tip. The trunk was divided into a main portion of 15 segments, subequal in length, and a short posterior portion lacking segmentation. The junctions between segments gave a limited flexibility to the body. Each segment of the main portion of the trunk bore a pair of thin lateral lobes, directed downward and outward, overlapping, of maximum width medially, the lobes progressively more strongly prolonged backward. Dorsal to lobes 2-15, a paddle-shaped gill was attached near the base of the lobe. The ventral surface of the gill was flat, the outer, dorsal surface bearing imbricated, thin lamellae. The gills lay between adjacent, overlapping lateral lobes. Internally, in the main portion of the trunk what may have been diverticula of the gut are preserved, extending into the proximal portions of the lateral lobes. The posterior portion of the trunk bore three pairs of thin, lobate blades, directed upward and outward, overlapping in the opposite sense to the lateral lobes, the entire structure forming a tail fan. The dorsal margin of the tip of the axial region of the fan appears to have borne a pair of spines.

The body is preserved with thin layers of rock between such parts as left and right eyes of a pair, adjacent lateral lobes, between gills and lobes, and between gill lamellae. The parts of the bodies are shown to have been entombed at varied angles to the horizontal bedding planes, and are greatly compressed. It is therefore considered that individuals were trapped in a cloud of sediment in suspension, moving along the sea bottom, and buried as it settled out. If so, the animal was benthonic in habit. *Opabinia regalis* may have ploughed shallowly in the bottom mud, propelled by movement of the lateral lobes. The eyes are presumed to have been capable of detecting movements in the surrounding waters, and the frontal process to have been used to explore the mud for food and bring it to the backward-facing mouth. The posterior region of the trunk may have aided in producing water currents over the dorsal surface of the body, or have aided in steering if the animal was capable of swimming. No structures that appear to have been antennae, and no other jointed appendages, have been observed, and the gills are not trilobite-like. *O. regalis* is not considered to have been a trilobitomorph arthropod, nor is it regarded as an annelid. It may be descended from segmented animals from which arthropod phyla and/or annelids were derived.

1. INTRODUCTION

When an earlier version of figure 82 was shown at a meeting of the Palaeontological Association in Oxford, it was greeted with loud laughter, presumably a tribute to the strangeness of this animal. Walcott's original description in 1912 included photographs of the part of one specimen and the counterpart of another, the latter mistakenly described as showing the dorsal aspect of the animal. Hutchinson (1930) gave new drawings of portions of these specimens, and photographs of the counterparts of two additional individuals. Raymond (1935) studied the specimens illustrated by Walcott, followed his upside-down interpretation of one specimen, and concluded that it showed trilobite-like gill appendages lying ventral to lateral lobes of the trunk. Størmer's (1944) acceptance of Raymond's conclusion led to placing *Opabinia* in his Trilobitomorpha group of arthropods. Sharov's (1965, pp. 963–965, fig. 2; 1966, pp. 26–28, fig. 16) interpretation of *Opabinia* has fanciful additions to earlier views, and Simonetta (1970, Pl. 2, figs 2*a*, *b*, *c*) despite study of Walcott's collection, went even further to give *Opabinia* antennae, jaws, and biramous arthropodan appendages. Thus, continuous interest in *Opabinia* has not been accompanied by critical study of the specimens, so that fancy has not been inhibited by facts. The present work aims to provide a sounder basis upon which to speculate. The unusual way in which the fossils are preserved requires consideration, and authors have not realized how much information may be obtained from examining together part and counterpart of a single specimen. The orientation of the body in the rock is revealed, and the relative positions – dorsal or ventral, left or right – of portions of the body may be determined, and portions preserved only in part or counterpart recognized. Further, the bodies have been compressed in orientations relative to the horizontal bedding planes varying from dorsoventral to lateral. From these an original form of the body is deduced, so that there is an inseparable relationship between deductions regarding preservation and interpretation of morphology. The ten most complete specimens of *O. regalis* were selected for study, nine from Walcott's collection, and one showing unique features obtained during the recent re-investigation of the locality. The reconstruction of the animal (figure 82) is a compromise consistent with these specimens and their mode of preservation. My findings are explained by camera lucida drawings, those of entire specimens combining features of part and counterpart when available. Appropriate photographs face the drawings. The preservation is such that particular morphological details are emphasized by ultraviolet radiation directed in a specific manner, or by submergence of the specimen in liquid, so that several photographs of each specimen are needed. My conclusions on morphology have led to a reconstruction which differs in many important respects from all earlier ones. There was not one pair of eyes, but two pairs on short stalks and a median eye. The frontal process was not an eversible proboscis, the anterior part of the alimentary canal was U-shaped, and the mouth backward facing. The gill appendage was not trilobite-like, and was situated dorsally to the lateral lobe of the trunk. Therefore I reject the view, maintained since Walcott's work, that *O. regalis* was an arthropod, either an anostracan branchiopod or a trilobitoid. It was a segmented animal perhaps descended from a group ancestral to some arthropod phyla and/or annelids, a reminder of how little we know of the evolution of such creatures.

The Geological Survey of Canada, with the cooperation of authorities of the Yoho National Park and the Parks Canada, Department of Indian and Northern Affairs, Ottawa, undertook in 1966 and 1967 a re-investigation of the Burgess Shale (Whittington 1971*a*; Fritz 1971). 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 the U.S. National Museum), Washington, D.C., was afforded by Dr Porter M. Kier and Dr Richard E. Grant. Professor K. M. Waagé, Peabody Museum of Natural History, Yale University, kindly loaned a specimen which came from Walcott's original collection. My photographs have been enlarged by Mr David Bursill, who also made photographs of specimens submerged in alcohol. 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., for discussion on the mode of life and affinities of *Opabinia*, and to my colleagues Dr C. P. Hughes and Dr D. W. T. Crompton for discussions of matters palaeontological and biological.

2. TERMINOLOGY AND METHODS

Since the affinities of *Opabinia regalis* are open to question, it seems best to use terms that are widely applied, rather than terms such as 'thorax' or 'telson' which may suggest that the animal is believed to be an arthropod. The body is therefore divided into the *cephalon* and *trunk*, the latter having a *main portion* and a *posterior portion*. The cephalon bore on short stalks structures which appear to have been *eyes*, and extending forward from the ventral side was a tubular *frontal process* terminating in two groups of spines. The trunk consisted of an *axial region*, the main portion of which was divided into fifteen segments, each segment bearing a pair of *lateral lobes*. In addition, each segment except the first bore a second pair of lateral extensions of the body, situated outside (dorsal to) the lateral lobes. Each of these extensions was paddle shaped, and bore on its outer, dorsal surface a series of narrow *lamellae*; its form suggests that it may have acted as a *gill*. The posterior region of the trunk does not show axial segmentation, but bore three pairs of dorsally directed, lobe-like extensions, each termed a *blade*, the six forming a *tail fan*.

Following Walton (1936, p.221) the fossils are termed *compressions*, since they are preserved as thin sheets of carbonaceous matter, the original relief having been profoundly modified. When the rock was split to reveal a specimen, portions of the specimen adhere to each side of the split, and are termed *part* and *counterpart*. For clarity, it is arbitrarily decided that in *dorsoventral compressions* the *part* is the side which shows the specimen in *dorsal* aspect; in *lateral compressions* the *part* is the side which shows the *cephalon* to the *left*. It is convenient in designating directions in the specimen to denote the median line as *sagittal* (abbreviation, sag.), a line parallel to, but outside the sagittal line as *exsagittal* (abbreviation, exs.), and a direction at right angles to these as *transverse* (abbreviation, tr.). *Abaxial* denotes a position away from the dorsoventral plane in the sagittal line, *adaxial* a position towards this plane.

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, northwest, *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, by using orthochromatic film. Facing many of the plates are camera-lucida drawings intended to explain how a particular specimen has been interpreted. As explained in § 3 (*a*), thin layers of rock separate parts of the body, so that, for example, lateral lobes and gills, and blades of the tail fan, form an imbricated series. The changes of level between such parts 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 reveal different parts of the body, for example, lobes of left and right side, they are brought together in a single drawing.

It is the superposition of parts which enables the recognition of whether an eye, lateral lobe, or blade of tail fan belonged to the left or right side, so prefixes that indicate left (L) and right (R) are used in labelling the drawings. Abbreviations are listed which indicate the institutions in which a particular specimen is kept. These abbreviations are placed before the catalogue numbers in headings and plate explanations but omitted in the text for brevity.

3. PRESERVATION AND MANNER OF BURIAL

(*a*) *Interpretation of preservation*

The photographs show that the external cuticle of *Opabinia regalis* is preserved as an exceedingly thin layer which appears, in low angle radiation, darker than the surrounding rock. The cuticle of the entire body does not lie in a single plane, but parts lie in different planes, or in an imbricated fashion at a slight angle to the bedding. Thin layers of rock thus separate parts of the body, and §2 explains the methods used to portray these layers in the drawings. This manner of preservation is common to other fossils in the Burgess Shale (Hughes, 1975; Whittington, 1971 *a*, *b*; 1974, 1975), and drawings of them have been made in the same way. After burial the bodies were compressed as the sediment was compacted, and figure 1 shows, by means of transverse cross sections, stages in this compression of portions of the body, oriented at various angles. Figure 1 is diagrammatic, showing a supposed original cross section of the body from which a particular compressed specimen may have been derived. At compression 8 : 1 (probably less than the final amount), it may be seen how parts of the body will lie in different planes, in a manner like that displayed by particular specimens. The photographs show that some specimens have been buried with the sagittal dorsoventral plane approximately vertical to the bedding, and are compacted to an approximately bilaterally symmetrical form (figures 1*a*, *b*, *c*; figures 9–11, plate II). Other specimens have been compacted with the sagittal dorsoventral plane approximately parallel to the bedding (figures 1*d*, *e*), and show the animal in lateral aspect (figures 5, 6, plate I; figures 36, 37, plate VII). Yet other specimens (figures 25, 27, plate V; figures 68–70, plate XIV) are neither bilaterally symmetrical nor exactly lateral in aspect, but oblique, and the amount of obliquity varies along the length. To explain such specimens it is suggested that not only was the axial region of the body oriented obliquely at burial, but the lateral lobes and blades of the fan were inclined at various angles or flexed in different ways (figures 1*f*, *g*, *h*). Change in orientation of different parts of the body along the length (figure 2) are invoked to explain the appearance of particular specimens. These matters are discussed in more detail in the descriptions of individual specimens, but, for example, if the lateral lobes and gills were buried at what is thought to be the original angle of inclination to the body (figure 1*b*), the maximum width after compaction would be about one-third the sagittal length of the body. In 57684 (figures 9–11, plate II) the maximum width is about one-quarter the length, implying burial of the lateral lobes at a steeper angle. Again, in the anterior portion of the body of 131217 (figures 25–28, plate V), the very different width of the lateral lobes on each side is explained by burial of the lobes of one side in a horizontal position, the other side bent down at a steep angle (figure 1*f*). The above considerations indicate how the appearance of different specimens may be accounted for by assumptions as to the manner of burial and subsequent compression of the body. After figures 1 and 2 were complete, I came upon the similar ideas expressed by Walton (1936, pp. 219–225) in attempting to account for the form of certain fossil plants. In this account Walton introduced the term compression, and gave reasons why compression was in the vertical direction without any lateral spread (cf. figure 1).

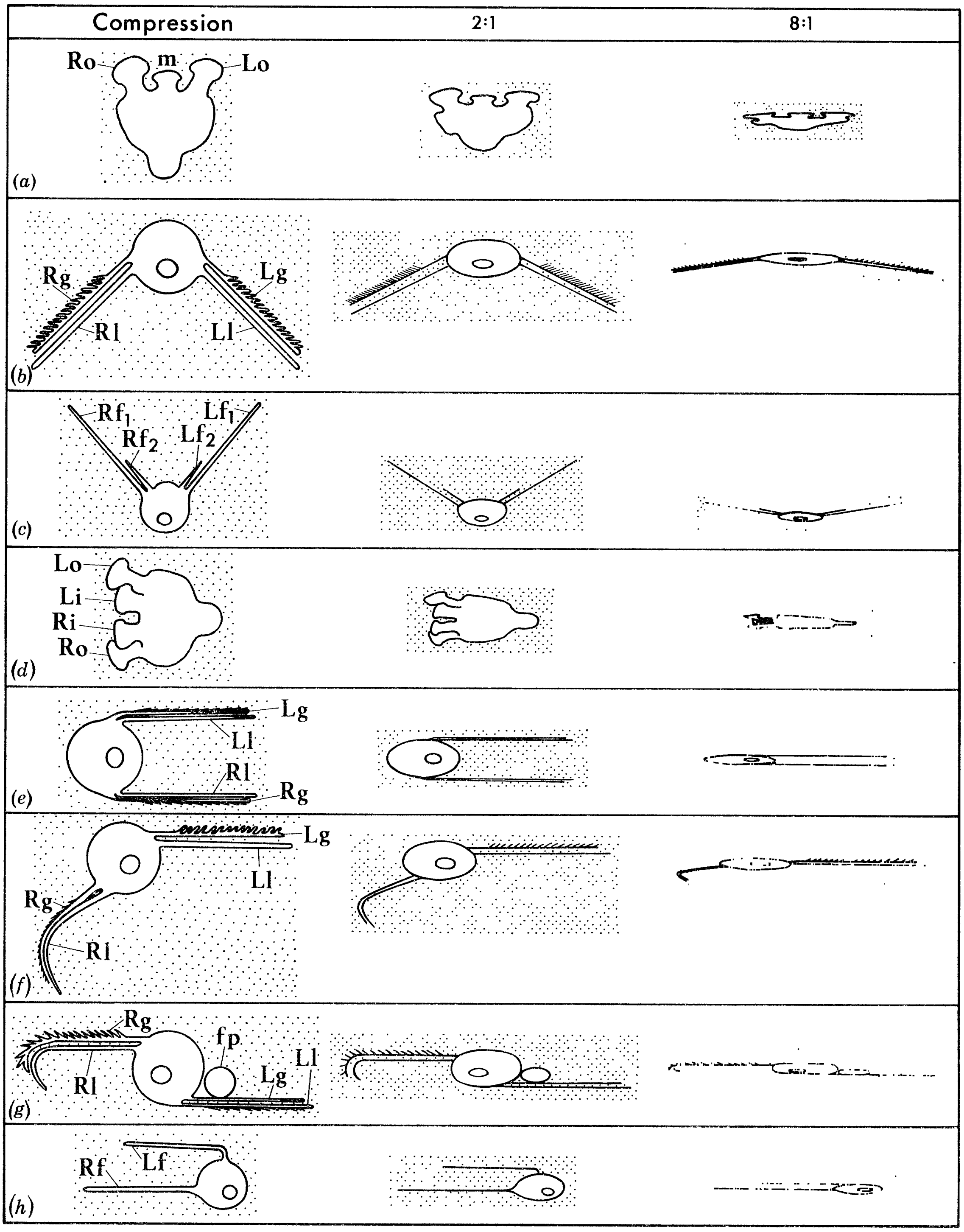


FIGURE 1. Cross sections of the body of *Opabinia regalis* showing the effects of post-burial compression in the ratios indicated. Cross sections before compression are those of figure 82 *b*, *c*, *d*, bedding planes are horizontal. (*a*, *b*, *c*) body oriented with sagittal dorsoventral plane at right angles to bedding; (*d*, *e*) same plane parallel to bedding; (*f*, *g*) sections of main portion of trunk obliquely oriented relative to bedding; *h*, section of obliquely oriented posterior portion of trunk. Gills in (*b*), left side of (*f*), right side of (*g*) shown with sediment between lamellae. In (*e*), right side of (*f*) left side of (*g*), sediment does not penetrate between lamellae, so that they lie against basal layer of gill. In (*e*), sediment does not penetrate between gills and lateral lobes, so that these structures are compressed into a single layer.

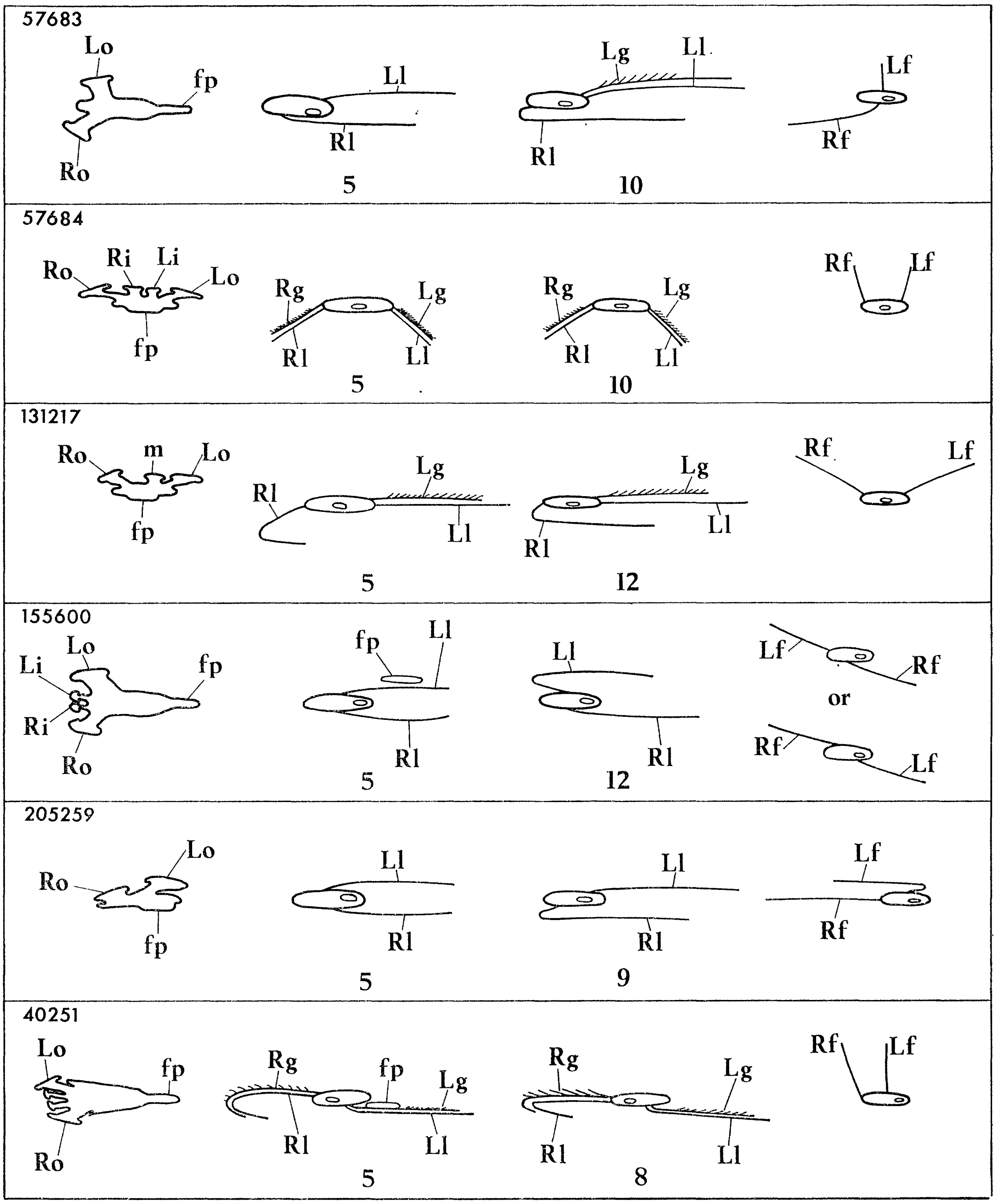


FIGURE 2. Diagrammatic cross sections through the specimens of *Opabinia regalis* indicated by the catalogue number, at a partially compressed stage, to elucidate the attitude in which each is preserved. Sections viewed from the anterior; from left to right through the cephalon, two through the main portion of the trunk at the segment indicated by number, on the right through the posterior portion of the trunk. Gills shown only in specimens in which they have been recognized. For further discussion see §3 and descriptions of individual specimens.

In the photographs taken in low-angle radiation, the cuticle is not uniform in appearance, but shows more or less clearly defined areas or strips which are relatively darker. This difference is accentuated in photographs (figures 68, 70, plate XIV) taken in ordinary light of the specimen submerged in alcohol. Reflected photographs show that the cuticle is more strongly reflective in some areas than others. Darker and strongly reflective areas may be wholly or partially coincident (e.g. figures 71, 72, plate XIV). Most conspicuous of such dark, strongly reflective areas are those considered to be the eye surfaces (e.g. figures 30, 33 plate VI). The body is extended straight or slightly curved, and the axial region may show a central darker strip, which is reflective. This strip may be vaguely (figures 5–8, plate I) or quite clearly (figures 25–28, plate V) outlined, and extends to the posterior tip. Oval, faintly biconvex areas may occur along the strip (figure 28, plate V; figure 71, plate XIV), or there may be an irregular series of blobs (figures 31, 32, plate VI). In 205259 (figures 56–59, plate XI) the anterior, U-shaped part of the strip is clearly outlined and gently biconvex. Certain specimens (figure 43, plate VIII) show an irregular dark stain in the rock adjacent to the posterior end of the body. In 5809 (figures 60–62, plate XII) the central strip is stained by weathering, and shows lobate, paired lateral extensions in each segment. In other specimens (figures 41, 42, plate VIII; figures 45–50, plate IX) similar extensions are sub-triangular in outline, dark in low angle radiation and reflective, best seen in the latter example.

The outline of the lateral lobes may be broadly ovate, as in the posterior part of 205259 (figure 58, plate XI), or narrow and lanceolate as in the anterior portion of the same specimen, or in 57683 (figures 5–8, plate I). These lobes overlap one another, each going below the one in front. Not only is the outline variable, but the width (tr.) relative to the axial region varies, as is well seen in 131217 (figures 25–28, plate V). As explained above, I consider this variation is dependent in part upon the attitude in which the animal has been buried, and in part on the thinness and consequent compressibility of the cuticle of these lateral lobes. In dorsoventral compressions, but less clearly or not at all in oblique-lateral compressions, a second type of lateral extension from the body is visible. As 57684 (figures 15, 16, plate III) and 205258 (figures 49, 50, plate IX) show, each area lies dorsal to a lateral lobe, separated from it by a thin layer of rock. The area itself is stepped, the steps running in an exsagittal or oblique direction. The steps are formed by thin strips of cuticle, obliquely disposed to the bedding, separated one from another by a thin rock layer, so that on splitting the rock parallel to the bedding a series of steps is produced. Each strip merges proximally into a basal sheet (figure 80, plate XVI). The structure is interpreted as a sheet to which were attached obliquely a series of narrow, folded strips, disposed like a partially opened venetian blind. The structure is considered to have been a gill, and since it is separated from the underlying lateral lobe by a thin rock layer (i.e. during burial sediment penetrated between them) it is considered to be a separate structure. The gill is best revealed by the dorsoventral compressions referred to, but is difficult to see (figure 65, plate XIII; figure 31, plate VI) in other such compressions. In lateral compressions (figures 5–8, plate I; figures 36–39, plate VII; figures 56–58, plate XI) little of the gill is visible. Such variations may depend upon the position of the split between part and counterpart (figure 3). For example, the split along one or both sides of a dorsoventral compression may pass through the compressed cuticle of successive lateral lobes, with a step between each, the gill being concealed in the counterpart (figure 3*a*, *b*). An example of this is the left side of 40251 (figure 71, plate XIV), where excavation has shown the presence of gills 4–9 in the counterpart (figure 75, plate XV). In specimens such as 57684 (figures 15, 16, plate III) and 205258 (figures 49, 50, plate IX), the split appears to have passed through successive lateral lobes and gills (figure 3*a*, *c*), with steps between each. The exact position of the step determines how much of the lobe or gill is visible, and whether a large or small area of either is exposed. In lateral compressions (figure 3*d*, *e*), if the split passes through successive lateral lobes the gills will not be visible, as in 155600 (figures 36–39, plate VII) and 205259 (figures 56–58, plate XI). The split may pass from one side to the other along the length (figure 3*d*, *e*) and where the change occurs there is a change in direction of facing of the steps, as shown between lateral lobes left 4 and right 5 in 155600.

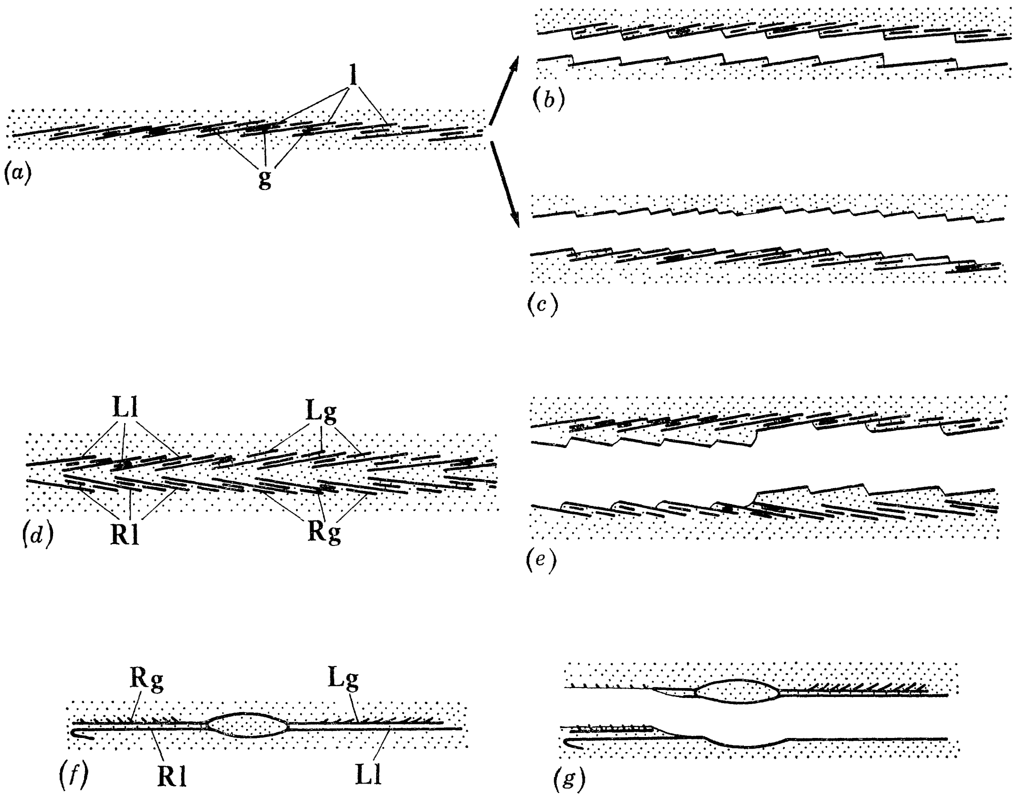


FIGURE 3. Diagrammatic sections, vertical to the bedding planes, through the partially-compressed body of *Opabinia regalis*, showing on the right ways in which the rock has split to give part and counterpart. On the right the portion above the split is the counterpart. (*a*) Section along exsagittal plane of a dorsoventral compression, showing (*b*) split which exposes successive lateral lobes only, and (*c*) split which exposes portions of successive lateral lobes and gills. (*d*) Section through left and right series of lateral lobes and gills of a lateral compression, showing (*e*) split which exposes successive lobes only on partly the right, and partly the left, side. (*f*) Transverse section through dorsoventral compression showing (*g*) split which reveals parts of gill and lateral lobe of right side, ventral cuticle of axial region, and lateral lobe only of left side. Compare figures 1*g* and 74.

The position of the split may vary over the area of the specimen, so that as in 57683 (figure 4; figures 5–8, plate I) it may be along left lateral lobes near their tips (as in lobes 1–7), but adaxially the right lateral lobes are revealed at a deeper level. As figure 3*e* shows, excavation at the original split may reveal concealed lateral lobes, and preparation of the counterpart of 205259 (figure 58, plate XI) revealed the tips of left lateral lobes 8? and 9?. The rock layer between gill and lateral lobe of one segment is extremely thin (figures 15, 16, plate III). If little or no sediment penetrated between them during burial, and did not penetrate between the gill lamellae, then the cuticle of gill and lateral lobe may have been compacted as a single layer.

This possibility, in a lateral compression, is suggested in figure 1*e*, and may help to account for the non-appearance of gills in certain specimens.

The posterior region of the body forms what is here called a tail fan, the three blades of each side overlapping, the overlap being in the opposite sense to the overlap of the lateral lobes of the trunk (figures 25, 27, plate V). In the oblique lateral compressions the blades project dorsally, upwards from the body, in the opposite direction to the lateral lobes (figures 36, 37, plate VII). In 205259 the split between part and counterpart has passed between the pairs, so that those of the right side are seen on the part (figure 56, plate XI), those of the left on the counterpart (figure 58, plate XI). In dorsoventral compressions the size and outline of the blades appears to depend on the angle at which they were buried – whether partially spread out on each side (figures 31, 33, plate VI) or crushed down vertically (figure 2; figures 9–11, plate II) so that little of them is visible.

(*b*) *Processes involved in preservation*

As has been deduced for other fossils in the Phyllopod bed of the Burgess Shale (Hughes 1975, Whittington 1971*a*, *b*, 1974, 1975), the animals were trapped alive by a moving cloud of suspended sediment, and buried as it settled out. This deduction is supported by Piper's (1972) investigation of the sediments. Such a catastrophic mode of burial accounts for the varied orientation of the bodies, or of parts of a body, relative to the horizontal plane. It also accounts for the penetration of sediment between adjacent lateral lobes, between lobes and gills, and between blades of the fan. A moving cloud of sediment may well have been turbulent, which would account not only for the way the sediment penetrated between parts of the body, but also for the twisting along the length (figure 2), variations in orientation of lateral lobes, and occasional reversals of the normal overlap relations between adjacent lobes. Likewise, it may help to account for the frontal process being preserved extended, curved back beside the body, or apparently broken off. However, apart from this presumed occasional breakage, individual animals are complete, so that the amount of transportation may not have been great, and the turbulence was probably weak.

In this manner the carcasses were buried in fine-grained mud, which must have contained a high proportion of water. As further sediments accumulated, the underlying layers, including those containing the carcasses, would have been compacted as the space between sediment particles was reduced by displacement of interstitial water, and the particles were rearranged and packed to form a progressively denser fabric. In figure 1 I have depicted a simple model of compression accompanying this compaction. Zangerl (1971, pp. 1218–1221) has discussed the role of compaction in the preservation of certain fossil fish, essentially in two dimensions, commonly referred to as 'crushed flat'. He points out that bacterial decomposition of the fish took place in a matter of a few years at most, causing the bones and scales to settle into a plane, while compaction was a process effective over a far longer time scale, of hundreds or thousands of years. Thus these fossil fish were not 'crushed flat' as a result of compaction of sediment. The specimens of *O. regalis* and other organisms in the Burgess Shale are not 'crushed flat', i.e. do not lie in one plane (§3(*a*)), and I consider that compression resulting from compaction has been an important process in preservation. However, it appears reasonable to suppose that decomposition of soft parts of *O. regalis*, and chemical changes that resulted in preservation of the cuticle, alimentary canal and possible gut diverticula, took place in a far shorter time than the compression. Thus figure 1 is a simple model in that it shows reduction in volume of the axial region and frontal process taking place in the compression time scale, whereas it may have taken place on a shorter time scale. On the other hand the specimens do not show features such as wrinkling or rupture that suggest that the axial region collapsed rapidly as a result of decomposition. Anaerobic conditions in the sediment are suggested by the perfection of preservation, by the occurrence of finely divided pyrite scattered over the surface of the fossils, and the absence of signs of burrowing animals in the fossiliferous layers. In these conditions decomposition may have been relatively slow, and reduction in volume of the axial region gradual rather than sudden. A dark stain in the rock, posterior to the body, is faintly recognizable in specimens of *O. regalis*. Similar, but far more conspicuous stains have been recognized in specimens of the arthropod *Marrella splendens* (Whittington 1971*a*, Fig. 24). I have suggested (Whittington 1971*b*, p. 16; 1974, p. 13) that such dark stains were made by organic matter squeezed out of the body. Such squeezing out implies lateral spread during preservation, as has also been inferred for parts of the body of the trilobite *Olenoides serratus* (Whittington, 1975). If some lateral spread did occur, it may have been before compaction had begun, when the processes of decay had affected the soft parts and the water content was high. The final amount of compression is difficult to estimate, but figure 1 suggests that it may have been considerably greater than 8 :1.

4. DESCRIPTIONS OF SPECIMENS OF *OPABINIA REGALIS* WALCOTT, 1912

(*a*) *Systematics*

The original description by Walcott (1912, pp. 166–169, Pl. 27, Fig. 6, Pl. 28, Fig. 1) was illustrated by one photograph of the part of 57683 and one of the counterpart of 57684, and the description included mention of other specimens, identified herein as probably those now numbered 131217, 155598, 155599 and 205258. As lectotype I select herein specimen number U.S.N.M. 57683, of which part and counterpart are known (figures 5-8, plate I). Walcott designated *O. regalis* as the type of his new genus *Opabinia*, and placed it in the family Opabinidae.

Walcott (1912, p. 170) described, but did not illustrate, a second species, *Opabinia* ? *media*, from the Burgess Shale at the level of the Raymond quarry (Whittington 1971*a*, pp. 1172–1173). No material so labelled has been traced in the U.S. National Museum collections, though included with the material of *O. regalis* were three specimens labelled 35k/10 (i.e. from the Raymond quarry level). Two of these were not identifiable, and the third may represent a species of *Leanchoilia*. I therefore conclude (cf. Simonetta 1970, p. 40) that this species cannot be recognized. A new species attributed to *Opabinia*, *O. norilica* has been described by Miroschnikov & Krawzov (1960, pp. 31–32, Figs 1, 3) from Upper Cambrian (Franconian) strata of the Norilsky region of the northwest Siberian platform. The single specimen is a mould in argillaceous limestone and admittedly poorly preserved. It is restored as an arthropod having a cephalon bearing eyes and a frontal process, a trunk of 11 segments, each bearing a pair of biramous appendages, and a short, terminal, furcate abdomen. This restoration appears from the photograph to be somewhat conjectural, and I do not consider that this species should be referred to *Opabinia*.

The genus *Opabinia* thus includes only the type species, unique to the Burgess Shale section.

(*b*) *Locality, stratigraphical horizon, numbers of specimens*

All known specimens of *Opabinia regalis* come from what Walcott (1912, pp. 151–153) called the 'Phyllopod bed', 2.3 m (7 ft 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).

The base of the 'Phyllopod bed' is at level 1.5 m (5 ft) in the Geological Survey of Canada party's measured section (Whittington 1971 *a*, Fig. 3). Walcott's specimens from this quarry (including Y.P.M. 5809) are labelled '35k', with no indication of the exact level from which they came, but Walcott (1912, p. 152) states that *O. regalis* came from a layer 3.8 cm (1½ in) thick at the base of the bed. The single specimen (G.S.C. 40251) collected by the Geological Survey of Canada party in 1967 came from level 1.68 m (5 ft 6 in).

In addition to the ten specimens described below, Walcott's collection in the U.S. National Museum contains eighteen less well-preserved specimens, seven having all or part of the counterpart. On the slabs of rock containing these specimens are also specimens of *Morania* sp. and other algae, the arthropods *Burgessia bella* Walcott, 1912, *Marrella splendens* Walcott, 1912, *Molaria spinifera* Walcott, 1912, and *Waptia fieldensis* Walcott, 1912, and an unidentified worm. The specimen G.S.C. 40251 came from the basal part of the 'Phyllopod bed' at a level at which *Marrella splendens* (Whittington 1971 *a*, Fig. 5; 1971 *b*, Fig. 1), *Burgessia bella* (Hughes, 1975) and *Yohoia tenuis* (Whittington 1974, Fig. 1) were collected.

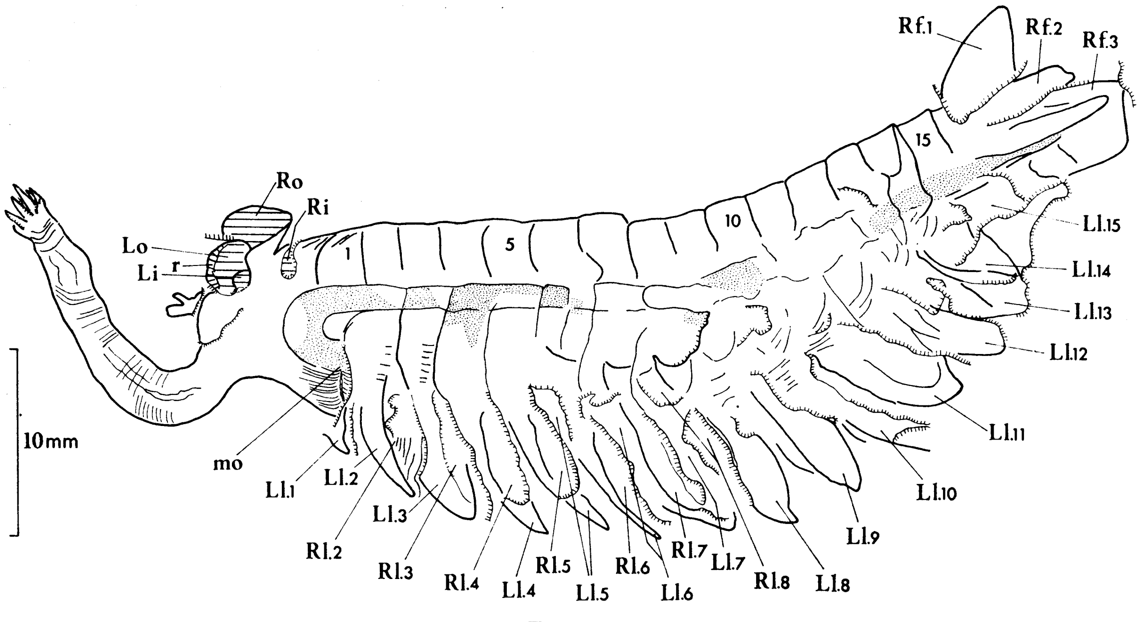


FIGURE 4

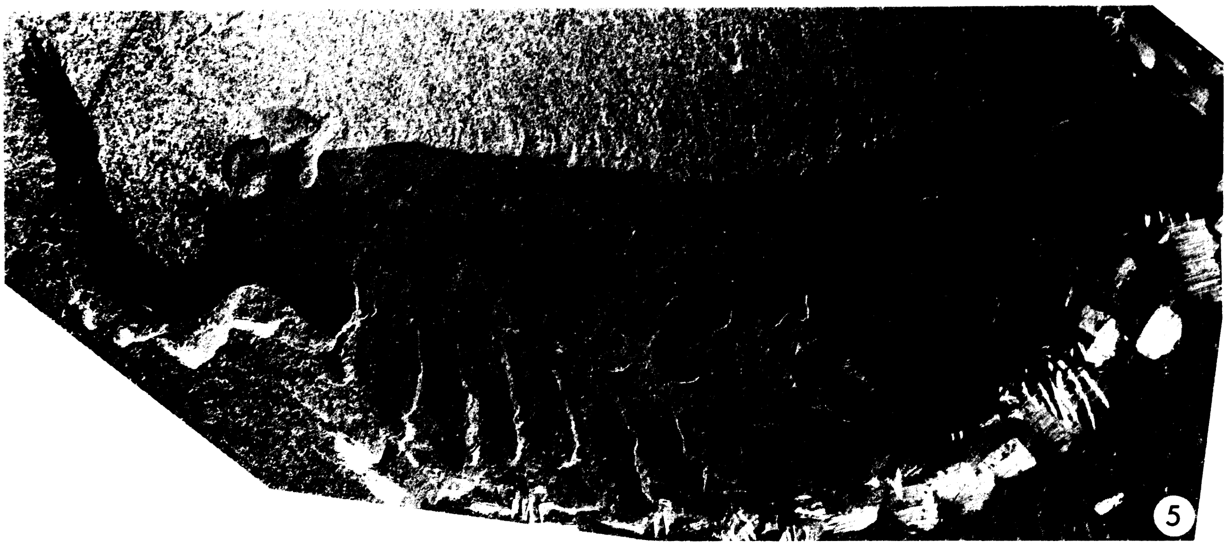
DESCRIPTION OF PLATE I AND FIGURE 4

Opabinia regalis Walcott, 1912. U.S.N.M. 57683, lectotype, Phyllopod bed, Walcott quarry

FIGURE 4. Composite explanatory drawing of part and counterpart.

FIGURES 5, 7, 8, Part, respectively, northwest (magn. x 2.5); cephalon and anterior portion of trunk, northwest (magn. x 5); cephalon and anterior portion of trunk, reflected (magn. x 2.5).

FIGURE 6. Counterpart, northwest (magn. x 2.5).



Figures 5–8. For description see opposite.

9

10

11

Figures 9–11. For description see opposite.

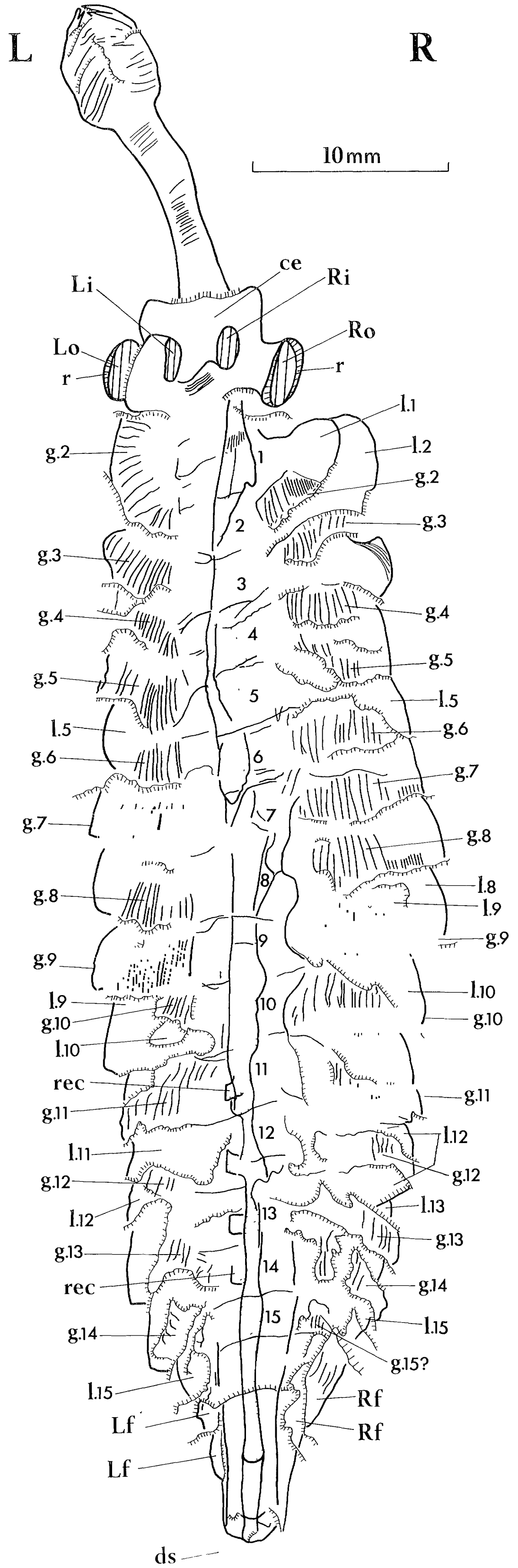


FIGURE 12

Opabinia regalis Walcott, 1912. U.S.N.M. 57684, Phyllopod bed, Walcott quarry.

FIGURES 9, 10. Part, respectively northwest (magn. × 2.7); reflected (magn. × 2.7).

FIGURE 11. Counterpart, northwest (magn. × 2.7).

FIGURE 12. Composite explanatory drawing of part and counterpart.

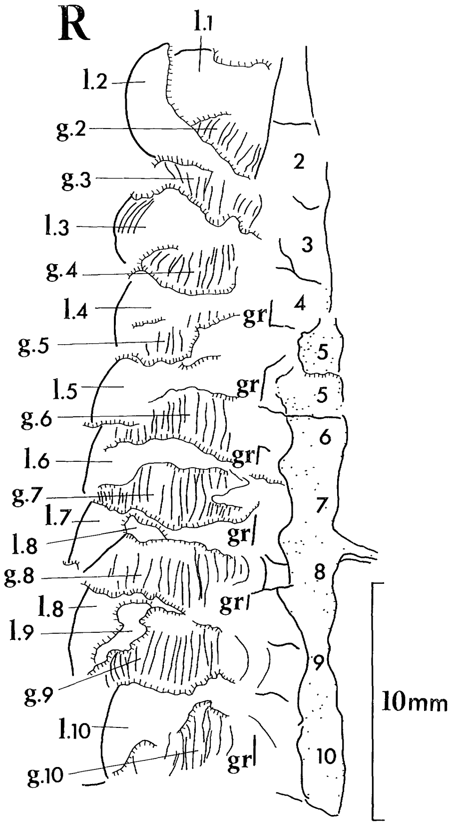


FIGURE 13

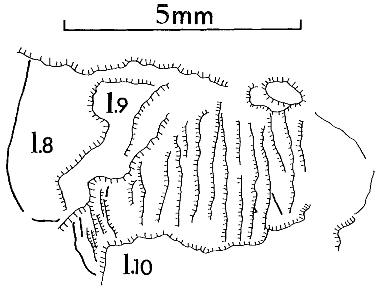


FIGURE 14

Opabinia regalis Walcott, 1912. U.S.N.M. 57684, Phyllopod bed, Walcott quarry.

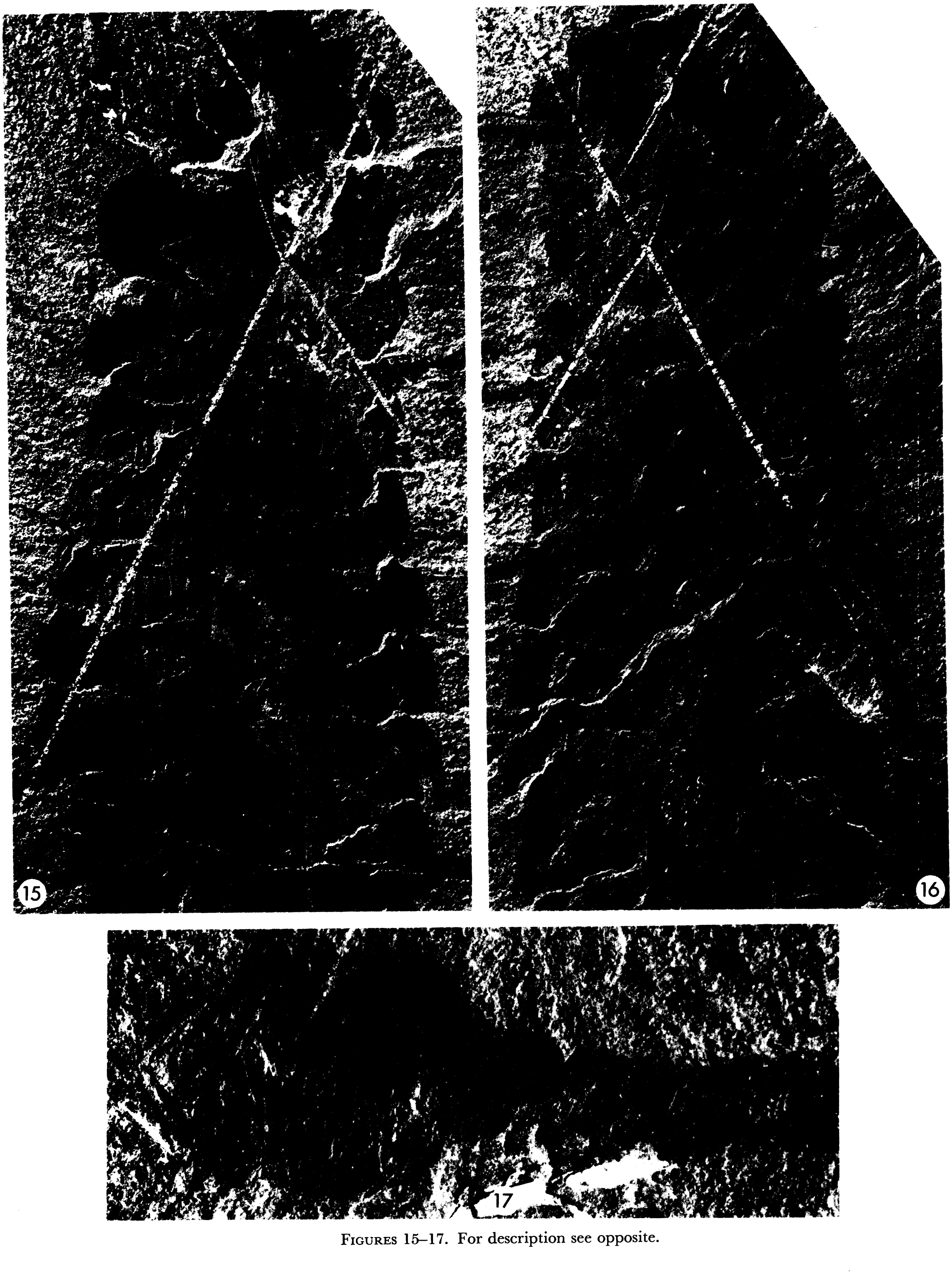
FIGURE 13. Explanatory drawing of portion of counterpart showing relation between lateral lobes and gills, ventral view. Compare figure 15.

FIGURE 14. Explanatory drawing of small portion of counterpart, showing relation between lamellae of gill 9, ventral view. Compare figures 13, 15.

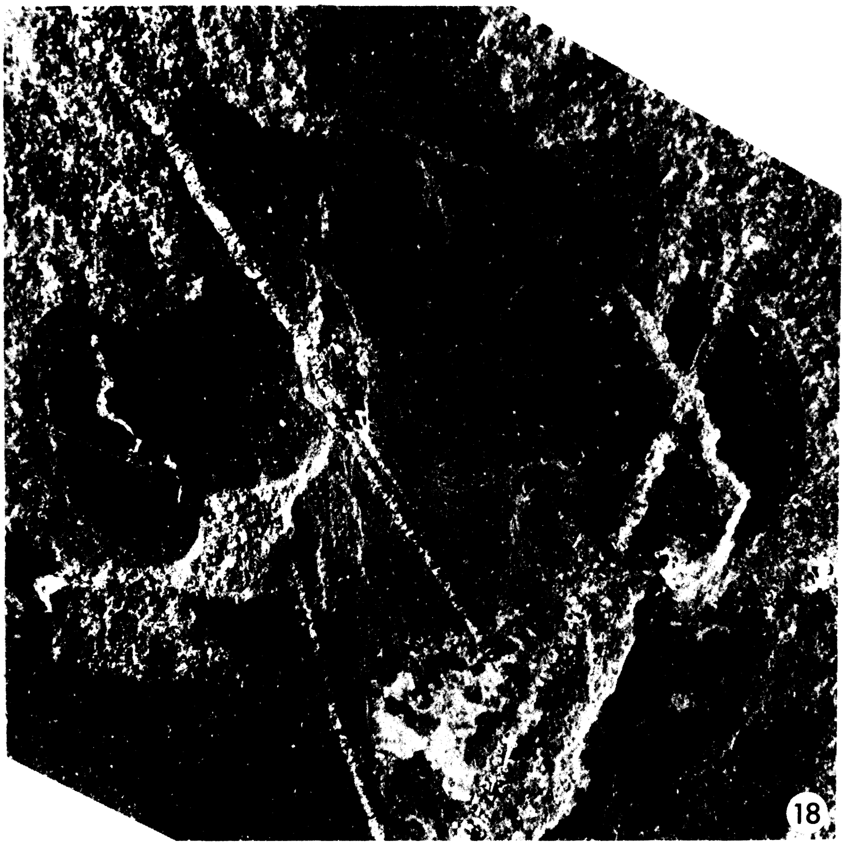
FIGURE 15. Counterpart, northwest (magn. × 4).

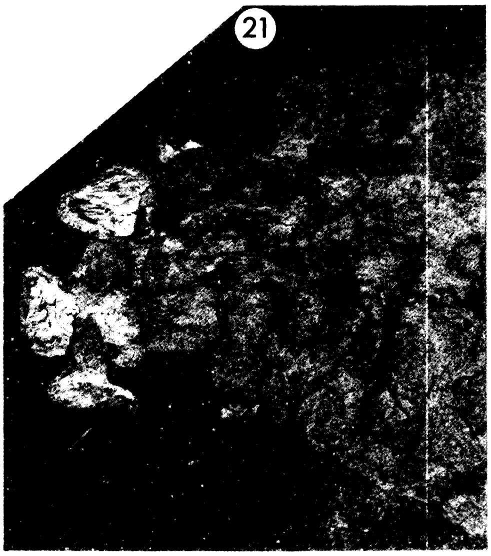
FIGURE 16. Part, northwest (magn. × 4).

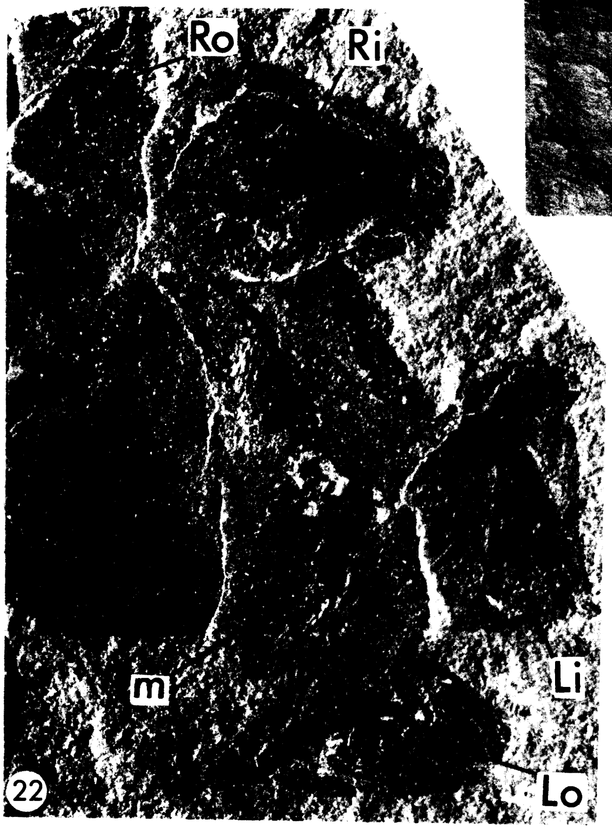
FIGURE 17. Counterpart, frontal process, west (magn. × 10).



Figures 15–17. For description see opposite.







FIGURES 18–23. For description see opposite.

(*c*) *U.S.N.M.* 57683

Figures 2, 4; figures 5–8, plate I

1912 Walcott, pp. 166–169, Pl. 27, fig. 6
1930 Hutchinson, pp. 3–7, Figs 1, 2*a*
1970 Simonetta, p. 40, Pl. IV, figs 7*a*, *b*

A slightly oblique lateral compression (figure 2), part and counterpart available. The part was illustrated by Walcott, considerably retouched, and sketches of the anterior and posterior portions of it were given by Hutchinson. This specimen is probably No. 3 in Walcott's (1912, p. 168) table of dimensions. At the upper, anterior margin of the cephalon are four areas at different levels (figure 4; figures 5–8, plate I). The anterior of these has a rim which slopes inward. The four areas do not appear darker in low angle radiation, but are reflective, and are considered to represent the left and right outer eyes, borne on short stalks, the inner pair of eyes being the smaller areas at their bases. Walcott and Hutchinson only recognized the stalked outer pair as eyes. Below the left pair is part of the cephalon, apparently the anterior slope, the margin curved convexly forward. Anterior to this portion is a fragment which does not appear to belong to this specimen. The frontal process projects downward and forward from below the anterior part of the cephalon, is curved and distally directed forward and upward. Striations run transversely across the proximal two-thirds of the process, and a narrow strip in the most curved portion (which appears slightly darker in low angle radiation and is reflective) may represent a median canal. The distal one-third of the process is not broader and subhexagonal in shape as in other specimens, but tapers slightly and ends in a group of longitudinally directed spines, which are at different levels and longest medially. This distal portion has transverse bands at the bases of the spines, proximal to this is a smooth portion with a suggestion of a darker median band (median canal?), and at the junction with the proximal portion the transverse striations swing forward on the lower (ventral) side. The ventral margin of the cephalon is directed backward and downward, forming a smooth curve with the lower margin of the frontal process. Posteriorly, inside this margin are fine, close-spaced striations (figure 7, plate I). This striated, posteroventral part of the cephalon was situated between the left and right first lateral lobes. Hutchinson (1930, Fig. 1) regarded this part of the cephalon as the antenna, but I cannot accept this interpretation. Dorsal to the striated portion, the gut is poorly preserved as a region appearing slightly darker in low angle radiation, and appears to run in a U-shaped curve, the mouth directed backward, presumably situated adjacent to the striated portion on the posterior wall of the cephalon (figure 4). The axial region of the trunk shows an indistinctly outlined darker band (stippled in figure 4, compare figures 5–8, plate I), which appears

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DESCRIPTION OF PLATE IV

Opabinia regalis Walcott, 1912. Phyllopod bed, Walcott quarry

FIGURES 18, 19. U.S.N.M. 57684, counterpart, cephalon and anterior portion of trunk, respectively west (magn. × 10); reflected (magn. × 5).

FIGURES 20, 22. U.S.N.M. 131217, counterpart, cephalon and most anterior portion of trunk, respectively reflected (magn. × 3.3); east (magn. × 10).

FIGURES 21, 23. U.S.N.M. 131217, part, cephalon and most anterior portion of trunk, respectively reflected (magn. × 3.3); west (magn. × 10).

to show the course of the alimentary canal. Dorsal to this band boundaries between segment are visible, those labelled between segments 4–15 (figure 4; compare figures 5–7, plate I) being clearest and extending inwards almost to the gut. The divisions between cephalon and segment 1, and segments 2 and 3, are faint and the interpretation tentative. Anteriorly boundaries between segments 2–6 are visible as grooves or changes in level across the darker band of the axial region, and can be traced into edges of the lateral lobes. Medially, such boundaries are hard to discern, but posteriorly those between 13 and 15 are clear. Ventral to the axial region, the body shows a series of overlapping, falcate lateral lobes, and those labelled 2 to 9 show on the part (figure 5, plate I) an anterior, gently convex portion, separated by a curving change of slope from a posterior, concave portion (convex on the counterpart, figure 6, plate I). From 10 onwards the lobes do not show this division, and are more rounded in outline. It is considered that the lobes of each side have been compressed against each other, and that the split between part and counterpart reveals, on the part, the convex surfaces of left lobes facing the observer, alternating with the concave faces of right lobes (figure 4). The lobes overlap each other, each passing inside the one in front, as revealed by changes in level and scarp faces of breaks. Thus a portion only of any lobe is visible, lanceolate in shape. Figure 4 shows this interpretation, and that parts of left-lobes 1–6, 8–15 and right lobes 2–8, may be recognized. The position of these lobes corresponds with that of segments 1–15 of the axial region, and lobe L1 must originally have lain beside the postero-dorsal part of the head. Walcott (1912, Pl. 27, fig. 6) recognized structures situated on the proximal parts of lateral lobes 8–15, adjacent to the trace of the gut, which he termed gills. They are indicated by faint, curved lines of fractures, the curves convex ventrally, as indicated in figure 4. These may indeed be traces of gills.

The posterior portion of the trunk, behind segment 15, is subrectangular in outline. The upper, posterior edge, towards which the trace of the gut runs, is broken. Attached to the dorsal edge are parts of what I regard as the three right blades of the tail fan. Each goes adaxially inside the one in front, so that Rf.1 is farthest from the observer in the part (figure 5, plate I). Hutchinson (1930, pp. 6–7, Fig. 2*a*) recognized this blade (as his appendage 15) and thought that it formed part of a tail fan. As figure 4 shows, I do not interpret lateral lobe 14 as having the outline portrayed by Hutchinson (1930, Fig. 2*a*) as his appendage 14.

(*d*) *U.S.N.M.* 57684

Figure 2; figures 9–11, plate II; figures 12, 13, 14;
figures 15–17, plate III; figures 18, 19, plate IV

1912 Walcott, pp. 167–168, Pl. 28, fig. 1 (counterpart)
1930 Hutchinson, pp. 3–7, Fig. 2*b* (counterpart)
1935 Raymond, pp. 217–218
1970 Simonetta, p. 40, Pl. V, figs 2*a*, *b* (part and counterpart)

A dorsoventral compression (figure 2), part and counterpart available; it is probably No. 2 in Walcott's (1912, p. 168) table of dimensions. The body is extended straight, the originally sloping lateral lobes and gills compressed on each side (figure 1*b*), the frontal process emerging from beneath the transverse anterior margin of the cephalon and curving forward and leftward. The process has an expanded anterior portion (figure 17, plate III), subhexagonal in outline, showing anteriorly a number of spines on each side, directed inward and forward with the tips closely opposed along the mid-line. Behind these spines are a number of ridges and grooves running subparallel to the spines and separated by a median change in level. This subhexagonal anterior portion thus appears to have been composed of two halves, that may have been able to move away from and toward each other, i.e. opening and closing. Behind this anterior portion the process is narrower, varies slightly in width, is crossed by striations, and in reflected light shows a suggestion of a median band (figure 10, plate II).

The cephalon appears subrectangular in outline, with an ovate area attached by a short, broad stalk to the right posterolateral margin (best seen on the counterpart, figure 18, plate IV). A paired ovate area is seen on the left side, overlain by an inner, left ovate area on a shorter stalk. The corresponding inner, right ovate area is incompletely preserved. These ovate areas appear dark in low angle illumination (figures 15–16, plate III) and are strongly reflective (figure 19, plate IV), the outer pair exhibiting a narrow external rim (figure 18, plate IV) which is less reflective and slopes downward and outward on the left side, upward and outward on the right. No subdivisions of the dark, reflective areas (which might represent facets of an eye surface) are visible, but they are interpreted as being eyes – an inner pair close together on short stalks, and an outer pair, each on a longer stalk which originates slightly behind and outside the inner one.

The axial region of the trunk exhibits a median band of irregular width, dark in low angle radiation and reflective, which commences just behind the base of the right, outer eye stalk and runs into the posterior portion (figures 9–11, plate II; figure 12). This band is the trace of the alimentary canal, and is crossed at intervals by slightly oblique ridges and grooves which extend into the surrounding region. These lines are indicated on figure 12 as the boundaries between segments 1–15 and the posterior portion, each segment being of approximately similar length. The zone outside the median dark band is smooth and featureless between the segment boundaries, except in the posterior half of the left side. Beside the dark band in each of segments 11–14 is a slightly darker, reflective rectangular area (rec, figure 12), the outer edge of which is sharply demarcated by a narrow ridge in the part. The lines of these outer edges is continued forward in segments 10–4 by a broken line of short ridges, and corresponding short, linear grooves are visible in the counterpart (figure 11, plate II; figure 15, plate III).

The main portion of the trunk (figures 9–11, plate II; figure 12) shows the relationship between the smooth lateral lobes and the gills, areas divided by steps into narrow bands running longitudinally. Figures 13, 14 (compare figures 15, 16, plate III) show these areas in ventral view in the counterpart. Hutchinson (1930, Fig. 2*b*) sketched the present right gill 8 and adjacent areas from the counterpart, but mistakenly considered this to be in dorsal aspect, an error perpetuated by Raymond (1935, p. 217). The banded gill areas have a structure like a closed venetian blind, each slat sloping beneath the one distal to it; this 'scarp and dip' structure is clear proximally, but distally in these regions the arrangement may be reversed (figure 14), possibly as a result of compression. Along each side the banded areas are irregular in outline, the smooth areas in most cases extending out beyond them and having a clearly bounded, straight or gently curved margin. Where the smooth areas (lateral lobes) extend out distally their arrangement is overlapping, each one going below the one in front. This arrangement is displayed by lobes 1–10 on the right side, and lobes 5–9 on the left (figure 12). Each banded area (gill) lies dorsal to the lobe having the same number (figures 12, 13), and there is no gill present on the dorsal side of lobe 1, so that gill 2 is the most anterior, and lies below (ventral to) lobe 1. Close to the axial region the gill appears to rest directly on the lobe, with little or no intervening rock layer, whereas distally the rock layer is thicker and clearly intervenes between gill and lobe. This relationship, evident from the photographs, is interpreted to mean that the gill was attached proximally to the outer surface of the lobe. This interpretation seems to fit the facts best, but the specimen has been compressed slightly obliquely, and not exactly dorsoventrally. Oblique compaction and some disturbance of the natural arrangement, is suggested to explain certain features shown in figure 12, for example, that the fragment of right lobe 13 seems to lie above, and not below right lobe 12. Similarly, left lobe 12 lies above 11. There is no sign of lobe 1 on the left side, but this presumably results from the position of the split between part and counterpart. The length of left gill 2, as exposed by this split, shows how far distally – close to the tip of the lobe – the gill extended. The segment boundaries of the axial region seem to show a relationship to gills and lobes, and have been numbered to correspond (figure 12). Lobe 15 can be identified on each side, but gill 15 is doubtfully identified because of the poor preservation.

Behind segment 15 is a subrectangular posterior portion of the trunk, of length (sag.) about that of three segments. There is no clear evidence of subdivisions of this portion, the conspicuous change in level crossing it at about one-quarter the length in the part being a change in slope that extends out into the matrix (figure 9, plate II). The alimentary canal extends back to about two-thirds the length, as a dark band gently concave in the part, and ends abruptly at a curved boundary. Beyond here it is difficult to trace but there is apparently a fragment at the posterior margin. The latter is curved convexly back, and there is a spine preserved at the right margin (figures 9, 10, plate II). Portions of at least 2 blades of the fan are preserved on each side, the anterior lying above lobe 15 and inside (adaxial to) the following blade. A faint, irregular dark stain is preserved in the matrix adjacent to the left posterior margin.

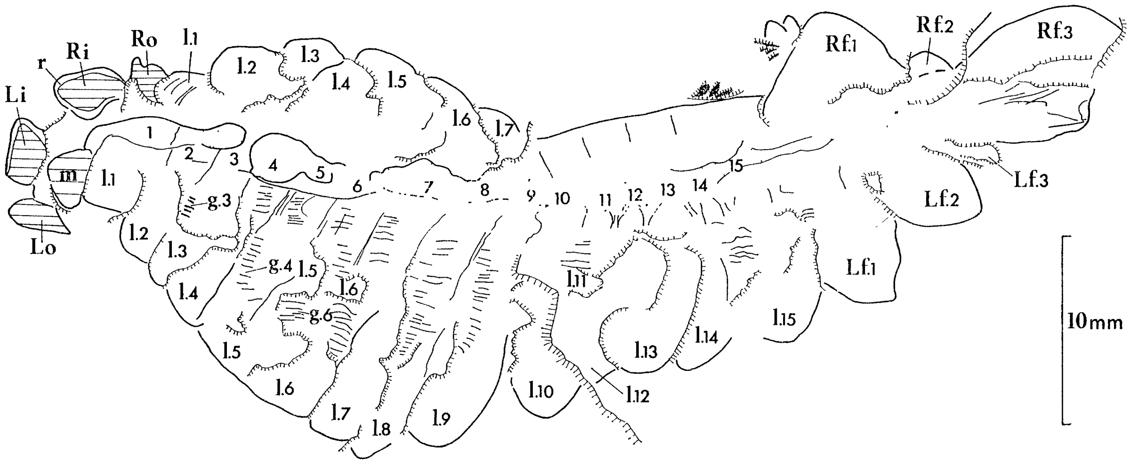


Figure 24

Description of plate V and figure 24

Opabinia regalis Walcott, 1912, U.S.N.M. 131217, Phyllopod bed, Walcott quarry

Figure 24. Composite explanatory drawing of part and counterpart.

Figures 25, 26. Part, respectively complete, west (magn. × 1.7); cephalon and main portion of trunk, northwest (magn. × 3.5).

Figures 27, 28. Counterpart, respectively complete, east (magn. × 1.7); complete except for most posterior portion of trunk, southeast (magn. × 3.5).

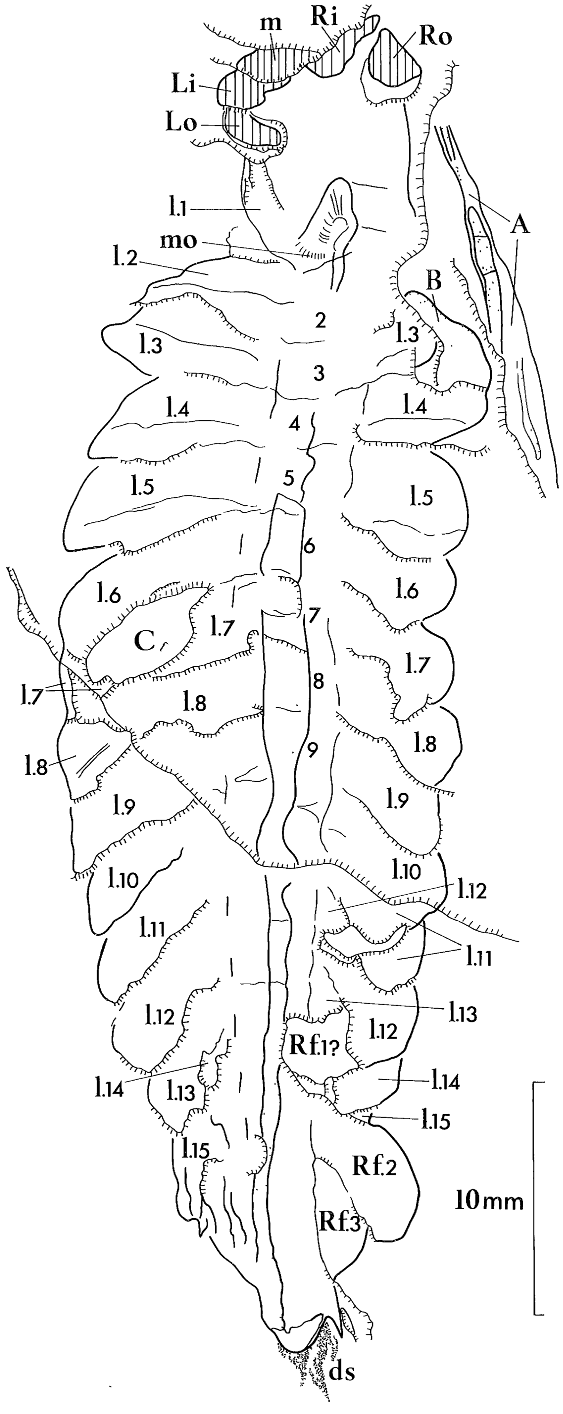


Figure 34

Opabinia regalis Walcott, 1912. Phyllopod bed, Walcott quarry.

Figures 29, 31. U.S.N.M. 155599, part, respectively reflected (magn. × 1.7); north (magn. × 2.7).

Figure 32. U.S.N.M. 155599, incomplete counterpart, north–northwest (magn. × 2.7).

Figures 30, 33. U.S.N.M. 155598, part, respectively reflected (magn. × 1.7); northwest (magn. × 2.5).

Figure 34. U.S.N.M. 155598, explanatory drawing of part.

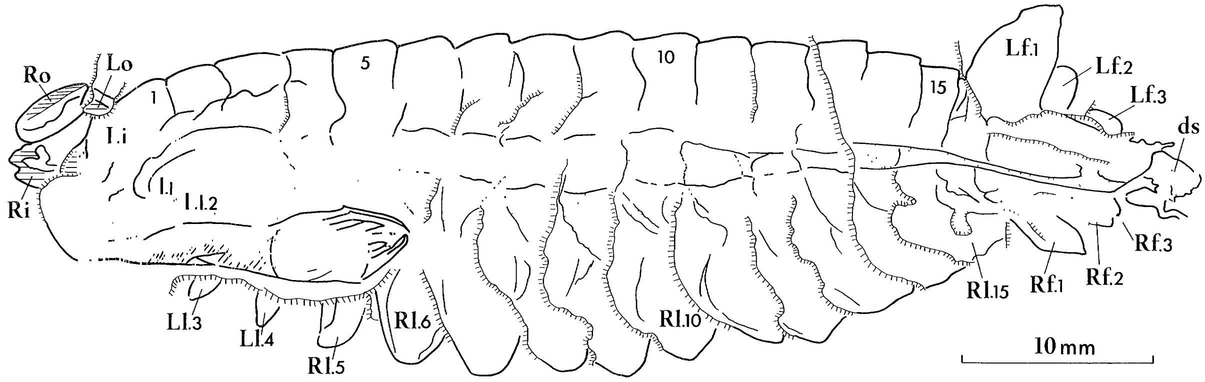


Figure 35

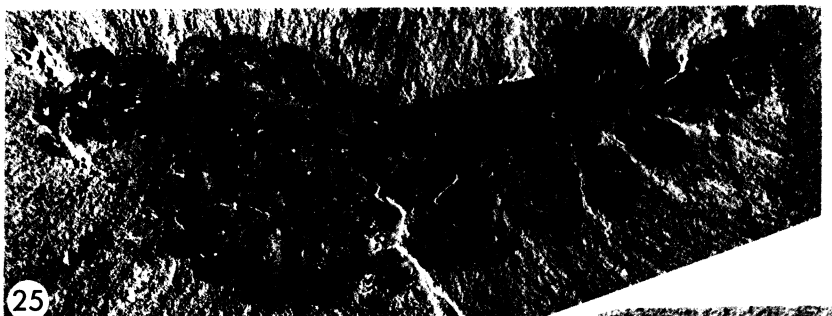
Opabinia regalis Walcott, 1912. U.S.N.M. 155600, Phyllopod bed, Walcott quarry.

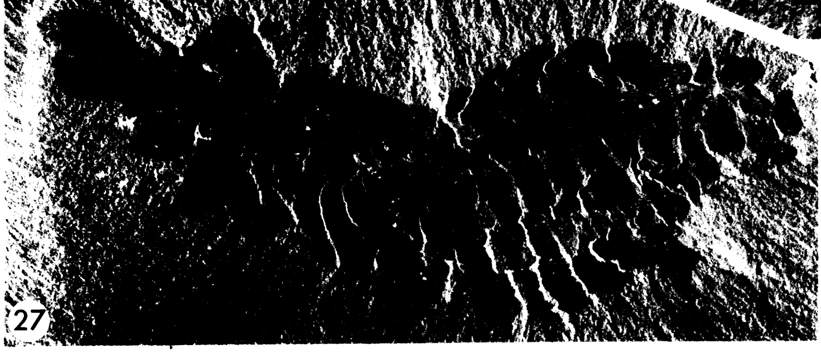
Figure 35. Composite explanatory drawing of part and counterpart.

Figures 36, 38, 39. Part, respectively complete, northwest (magn. × 1.7); complete, reflected (magn. × 1.7); cephalon and 12 trunk segments (magn. × 3.3).

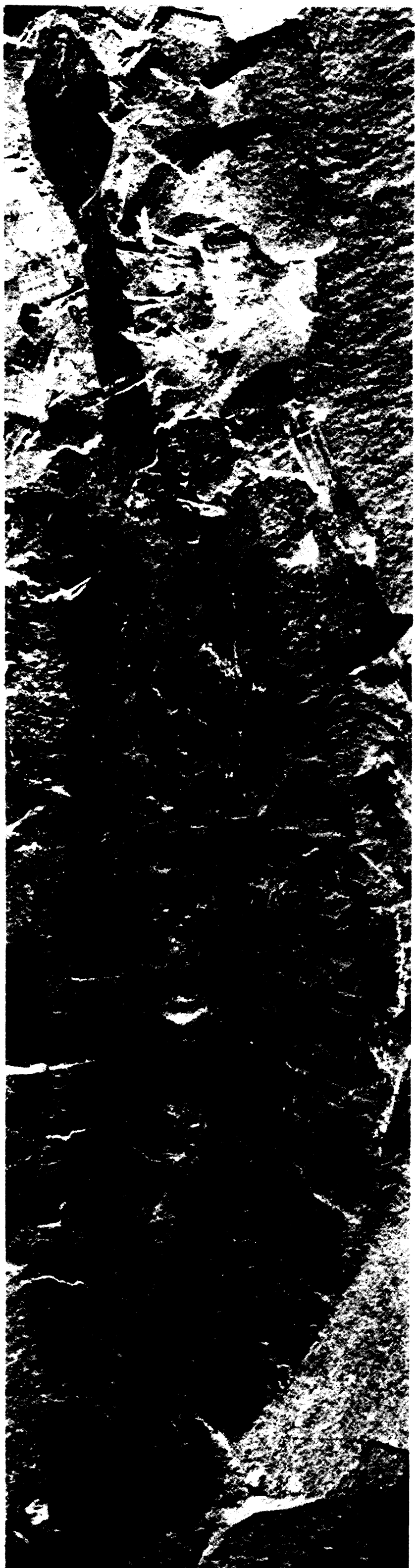
Figure 37. Counterpart, northwest (magn. × 1.7).

Figure 40. Frontal process of counterpart, west (magn. × 10).





Figures 25–28. For description see opposite.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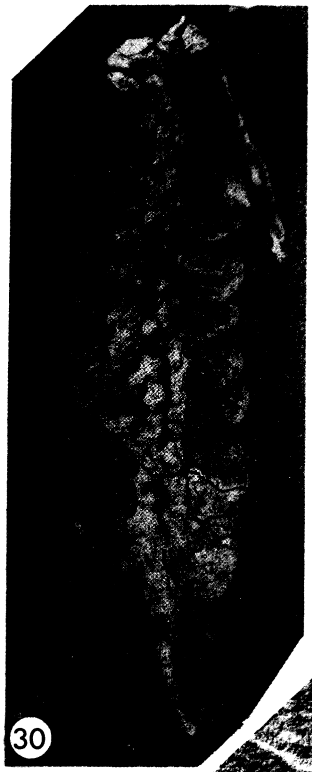
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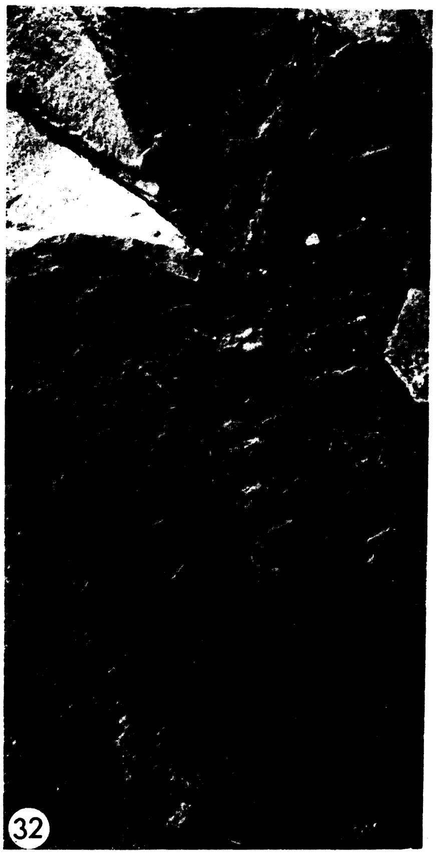
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33

FIGURES 29–33. For description see opposite.

Walcott (1912, Pl. 28, fig. 1) illustrated the counterpart, considering it to show the dorsal aspect of the animal. The levels of the eyes and frontal process, relative to the rest of the cephalon (figure 12; figures 9, 11, plate II), show that this cannot be correct; the counterpart shows the ventral aspect. I have been unable to find traces of the 'reticulated surface of the compound eye' (Walcott 1912, p. 167) that he claimed to see on the part. Simonetta (1970, p. 40) used this specimen as evidence of a 'pair of short conic appendages' on the cephalon, portrayed in his Plate II, figures 2*a b*, as segmented and regarded by him as reduced antennae. I suppose Simonetta was referring to what is here portrayed as the rounded anterolateral portions of the cephalon. The difference in outline on each side is the effect of slightly oblique compaction, but figure 18, plate IV provides no evidence for believing a segmented antenna was present. In Walcott's illustration (1912, Pl. 28, fig 1) the right anterolateral margin of the cephalon is labelled in error as an eye.

(*e*) *U.S.N.M.* 131217

Figure 2; figures 20–23, plate IV; figure 24;
figures 25–28, plate V

1912 Walcott, p. 169
1930 Hutchinson, p. 7, Pl. 1, fig. 3

An oblique compression, the right lateral lobes folded under the remainder of the body (figure 2). The cephalon exhibits five areas which are dark in low angle radiation and strongly reflective (figures 20–23, plate IV). Four of these are interpreted (figure 24) as the inner and outer pairs of eyes. The left outer eye can be seen to be supported on a stalk, the right outer is less completely preserved. A narrow marginal band or rim of the eye surface is best preserved in the inner eyes. No signs of facets are preserved. The fifth dark area, irregular in outline, is situated adaxial to the left outer eye; it appears to be like the other eye areas, and is interpreted as a median eye situated between the bases of the outer pair. A break in slope runs between the inner eyes (figures 22, 23, plate IV), so that the anterior margin of the cephalon is not preserved. Excavation in front of this break (figures 25, 26, plate V, the excavation having been made subsequent to the photographs forming figures 22, 23, plate IV) did not reveal any trace of the frontal process extending forward. The process may be bent back beneath the cephalon and trunk, but the broken edge does not support this view, it is a break rather than a fold. I regard it as likely that the frontal process has been broken off. Because the frontal process was not visible, Walcott regarded this specimen (probably that which he referred to as 61 mm in length, 1912, p. 169) as the female, differing 'from the male in having two slender caudal appendages or rami; and in having a slender bifid frontal appendage'. Hutchinson did not accept that a caudal cercus would characterize the female, but believed this specimen lacked the frontal process and was the female.

The trace of the alimentary canal extends from the head region to the posterior tip, as a dark, reflective band, broadest and tending to be beaded anteriorly, posteriorly narrow and of even width (figure 24; figures 25–28, plate V). Adjacent to the median eye (figure 23, figure 26), it appears to bend at right angles, and this is regarded as part of the U-shaped anterior portion flattened to one side in oblique compression. Traces of possible boundaries between segments of the main portion of the trunk cross the dark band, but such boundaries are best seen on the trunk extending between the dark band and the stepped margins of the lateral lobes. The tentative positions of segments 1–15 are indicated on figure 24.

Parts of lobes 1–7 are visible on each side, lobes 8–15 being visible only on the left. The outline of left lobes 1–9 appears long (tr.) and narrow (exs.), whereas right 1–7 and left 10–15 are lobate in outline. These variations in shape appear to reflect the effects of oblique compression (figure 2). Each lobe passes beneath the one in front, except that right lobe 2 lies above 1, possibly an effect of modification of original position during burial. Traces of the longitudinally banded gills are faintly seen on the left side (figures 26, 28, plate V). They appear to lie on the lobes, and each seems to pass beneath the lobe in front. The posterior portion of the trunk appears relatively long (sag.), about half that of the main portion, the dark band running along it medially and extending close to the transverse posterior edge. Parts of each of the three blades of the fan are preserved on each side, each fan passing inside (adaxially to) the one in front, the anterior left blade lying upon lobe 15. This arrangement of the blades of the fan is the reverse of the overlap of the lateral lobes, so that while the first and second left blades are similar in outline to lobes 14 and 15, they are considered to be part of the tail fan. Between the anterior edge of the first right blade and the dorsolateral margin of the trunk are some isolated small, overlapping fragments (figure 28, plate V). Whether these are bits of a detached gill, or fragments of another organism, is uncertain.

(*f*) *U.S.N.M.* 155598

Figures 30, 33, plate VI; figure 34

1970 Simonetta, p. 40, Pl. V, fig. 4

An extended specimen, only the part available, obliquely compressed in approximately the dorsoventral direction so that lateral lobes are spread out to a different width on each side. The size suggests that it is probably the original of one of the two supposed females of Walcott (1912, p. 169) who recorded the length as 52 mm. Walcott described the frontal process as 'slender, bifid' in the female, noting that its character was 'more or less doubtful as it turned under and back on the side of the body'. He probably was referring to this specimen, which has the fragments marked A and B (figure 34) lying at a level above it, behind the cephalon on the right side. I regard these two fragments as not belonging to the specimen, but as being parts of some other fossil or fossils. The long, slim fragment (A) shows median strips which are dark in low angle radiation and are reflective (figure 30, plate VI). It is probably an unidentifiable worm, and the appearance in reflected light may have led Walcott to describe it as 'bifid'.

The cephalon is subrectangular in outline, displaying at the anterior and anterolateral margins five areas which are suboval or irregular in outline, highly reflective, dark in low angle radiation. Four of these areas overlap, but are separated one from another by a distinct change in level. These areas are interpreted (figure 34) as representing the inner and outer pairs (the latter behind and outside the inner pair) of eyes, and the median eye. There is evidence of a rim around the outer eyes. The anterior edge of the cephalon is broken along a line running through the right inner and median eye areas, and a portion of a specimen of *Waptia fieldensis* lies at a lower level adjacent to the line of breakage (figure 33, plate VI). Thus the frontal process, if it was preserved extending forward, is missing by breakage.

The axial region of the trunk appears slightly darker than the lateral regions, and is also more reflective (figures 30, 33, plate VI). Along this axial region runs an ill-defined, discontinuous still darker strip, of irregular width, indicated by stippling in figure 34. It appears to represent the alimentary canal, and the anterior end curves through 180°, the backward-facing termination (the mouth) crossed by fine striations. Posteriorly the darker strip is narrowest, and extends to the tip of the posterior portion of the trunk. Boundaries between segments 2–9 are visible in low angle radiation crossing the axial region, and in some cases run into the change in level which separates adjacent lateral lobes. Left lobes 2–13, and possible portions of left lobes 14 and 15, are long (tr.) and relatively broad (exs.), leaf-shaped to lobate in outline, longest medially, each passing inside the one in front. A forwardly bent fragment lying beside the cephalon may represent left lobe 1. No signs of gills are preserved. Left lobes 2–5 have the posterior half gently convex and standing above the anterior half, possibly as the result of compaction of overlapping portions of adjacent lobes enclosing the gills between them. The fragment of a lateral lobe labelled C (figure 34) resting on left lobes 6 and 7, has been glued on to the specimen, and its original relationship to it is by no means clear. Right lobes 3–10 appear shorter (tr.) than those of the left side, because of the oblique compaction. Each lobe passes beneath the one in front of it, and right 4 and 5 show the convex posterior half like those of left 2–5. Behind the fracture that traverses the specimen, portions of right lobes (11–15?) are preserved, passing one below the other, but difficult to identify. The posterior portion of the trunk is rectangular in outline, having one terminal spine and a rounded tip. Behind this tip are ill-defined, wispy carbonaceous areas. On the right side two blades of the tail fan are preserved, and in front of these is a third fragment, lying partly across the axial region (Rf.1? in figure 34), which may be the anterior blade. Some twisting has taken place posteriorly, since Rf.2 lies below both supposed Rf.1 and right lobes 14 and 15, rather than above them, i.e. adaxially to them. Further evidence of twisting is that Rf.3 lies partly above, and partly below, Rf.2. Left blades of the tail fan cannot be recognized, perhaps because they are crushed down vertically adjacent to the left margin of the posterior portion.

(*g*) *U.S.N.M.* 155599

Figures 29, 31, 32, plate VI

1912 Walcott, p. 168
1930 Hutchinson, p. 3
1970 Simonetta, p. 40, Pl. V (given in error as Pl. VII on p. 40), figs 3*a*, *b*.

A poorly-preserved dorsoventral compression, the part complete but only the posterior portion of the counterpart available. Its size suggests that it was No. 1 in Walcott's table of measured specimens, and it was probably referred to by Hutchinson as 'a dorso-ventrally compressed specimen very similar to specimen 57683' (the number should have been 57684). The frontal process is extended in front of the head region, the expanded distal portion lozenge-shaped, a change in level running in from the tip to half the length, and separating the two spine-bearing sides. The cephalon, including the frontal process, has suffered from rough preparation. The left anterolateral margin of the cephalon, beside the base of the frontal process, is acutely angulate, enclosing a highly reflective area having a narrow rim. This may represent the left inner eye, and immediately behind it, at a higher level, is a subcircular reflective area also having a narrow rim, which may represent the left outer eye. An irregular fragment at the right base of the frontal process is also reflective, as is a tiny strip outside it at a lower level. These may well be fragments of two other eyes (median and right inner?), but the evidence is unsatisfactory. The remainder of the right anterolateral part of the cephalon is broken away, leaving a small, irregularly shaped strip overlying the right proximal margin of the frontal process (figure 31, plate VI). Simonetta (1970, p. 40, Pl. V, fig. 3*b*) considered that 'at the base of the proboscis' there was a pair of small, faintly denticulated structures which he interpreted as a pair of jaws. Possibly he was referring to this small strip, which is not paired, and hardly evidence for such an interpretation. Better preserved specimens compressed in various directions do not reveal such structures.

The wide axial region shows anteriorly and posteriorly a darker strip, between the strips are irregular blebs which have relief; these blebs are probably mineral matter deposited along the original course of the gut. Faint lines crossing the axial region appear to be boundaries between segments. Some 12 or 13 lateral lobes are present on each side of the trunk, those of the right side having the margin curved convexly outward. Each of the first 6–7 lobes on each side passes below the one in front, but posteriorly on each side the arrangement is reversed, each sloping below the one following. Traces of gills, as longitudinal lines on the lobes, are faint. The posterior portion of the trunk shows a spine at the left tip, and blades of the tail fan. These blades appear narrow, presumably because they were inclined at a high angle at burial, before compression.

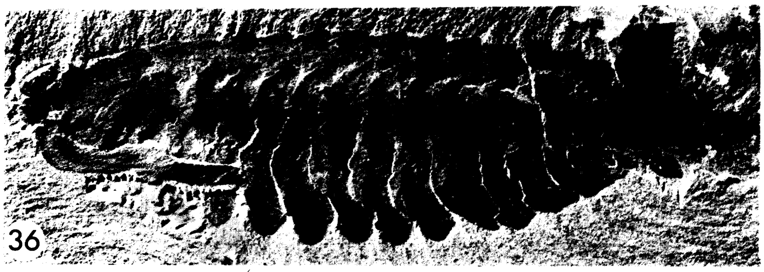
(*h*) *U.S.N.M.* 155600

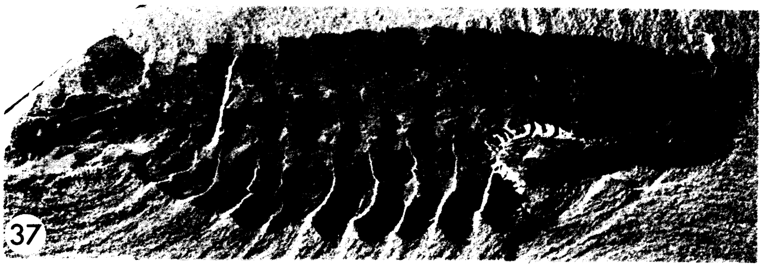
Figures 2, 35; figures 36–40, plate VII;
figures 41–43, plate VIII

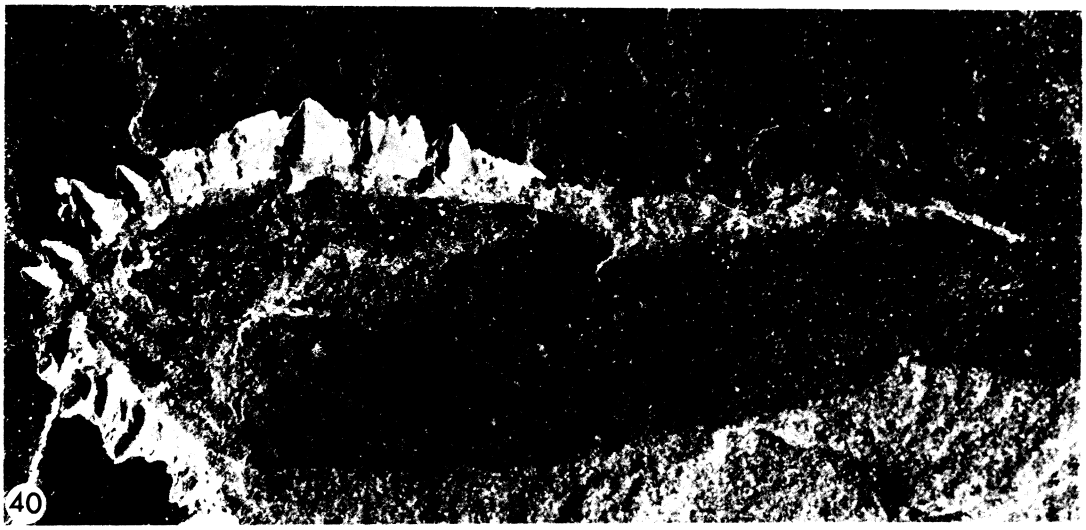
1930 Hutchinson, p. 3
1970 Simonetta, p. 40, Pl. V (given
in error on p. 40 as Pl. VII), figs 5*a*, *b*

A lateral compression, the posterior portion rotated to an oblique position (figure 2), part and counterpart available. The frontal process is curved back to lie over the lateral lobes of the left side, so that this may be the 'unfigured laterally compressed specimen' referred to by Hutchinson.

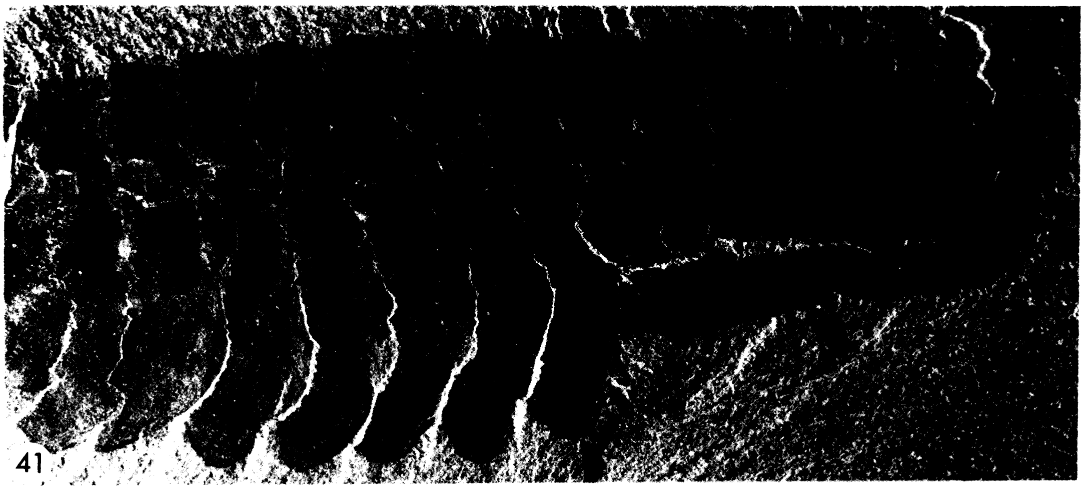
At the upper, anterior margin of the cephalon, and projecting beyond it, are four areas which appear dark in low angle radiation and are highly reflective – the eyes (figure 35; figures 36–39, plate VII; figures 41, 42, plate VIII). The two which are most dorsally situated, and appear to be borne on short stalks, are considered the left and right outer eyes, and are at sharply different levels. Two additional areas ventral to these, also at different levels, appear to represent the inner eyes. Below the eyes is the base of the frontal process, directed at first ventrally, then curved through 90° to run horizontally outside the left lateral lobes. It bears transverse striations, shows a central smooth, reflective band in the proximal half (figure 42, plate VIII), and has the expanded termination (figure 40, plate VII). Proximally this terminal portion appears expanded in both depth and width, and is crossed by subparallel diagonal ridges. A change in level runs inward from the tip, separating two groups of spines which converge distally. The dorsal margin of the main portion of the trunk is scalloped increasingly strongly posteriorly, where the outline of the margin becomes stepped. Intersegmental divisions run inward from the junctions between scallops or steps, and there appear to be fifteen segments in this portion (figure 35). Many of these divisions are continued by an irregular line of flexure across the axial region, and these in turn run into the changes in level between lateral lobes. The axial region appears dark in low angle radiation, irregular darker patches being visible adjacent to the boundaries







FIGURES 36–40. For description see opposite.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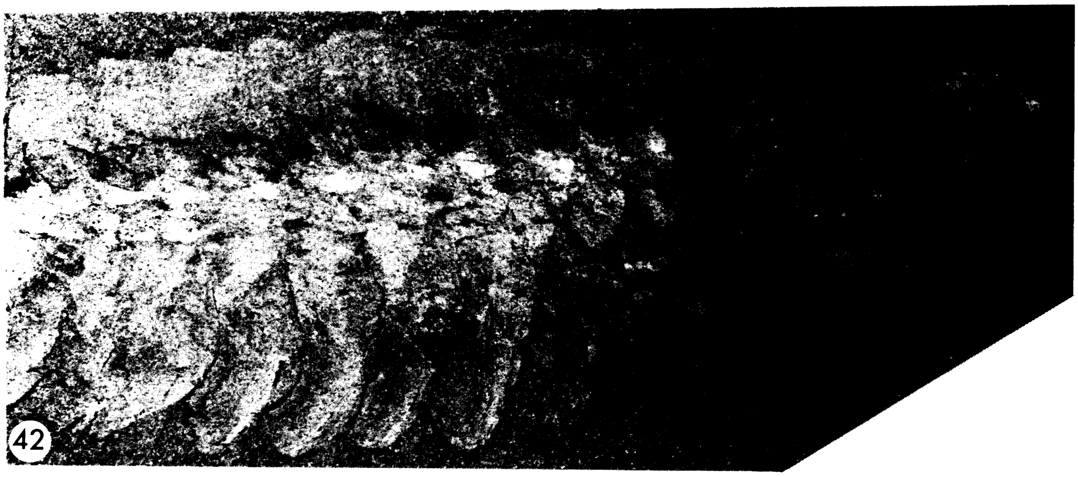
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43

Opabinia regalis Walcott, 1912. U.S.N.M. 155600, Phyllopod bed, Walcott quarry (magn. × 3.3).

FIGURES 41–43. Counterpart before preparation of frontal process, respectively cephalon and first 12 trunk segments, west; same, reflected; segments 7–15 of trunk and posterior portion, east.

between segments 5–10. A median darker strip extends through segments 11–15, narrowing posteriorly, and is continued as a narrow band through the posterior portion of the trunk. These patches and strip may represent an irregular deposition in the alimentary canal, and are more strongly reflective than adjacent areas. Lateral lobes are leaf-shaped, narrow anteriorly and becoming broader (exs.) posteriorly, maximum length (tr.) being median. There is a wide area of overlap of one lobe upon another. The anterior four lobes recognized (tips of 3 and 4 having been revealed by excavation below the margin of the frontal process, figure 39, plate VII) appear to belong to the left side, for when viewed from that side (figure 35) each goes below the one in front. Left lobe 1 lies on the posteroventral part of the cephalon, and the most anterior part of of the alimentary canal curves adaxially to it. Lateral lobes 5–15 appear to belong to the right side, since each lies above the one in front when viewed from the left side (figure 35). On the proximal portions of the inner surfaces of right lateral lobes 5–11 (figure 39, plate VII) are darker, subtriangular areas extending down from the axial region. These areas are reflective like the axial region (figure 38, plate VII; figure 42, plate VIII), and are stippled in figure 35. They are like similar areas in 205258, 5809, and 40251, and possibly represent diverticula from the alimentary canal. The posterior region of the trunk is subrectangular in outline, a spine situated at the upper, posterior edge (figure 43, plate VIII). A large blade of the tail fan lies upon its upper, anterior edge, and since it is nearest the observer in the part (figure 36, plate VII), is considered to belong to the left side. Parts of the second and third blades, lying one inside the other, may be recognized. Beside the lower margin of the posterior portion, and at a lower level, are parts of three further blades (figure 35; figure 43, plate VIII). If it is supposed that the posterior portion has been rotated so that the ventral side faces the observer in figure 35, these would be blades of the right fan. Against this interpretation is their overlapping relationship – if it were the outer surface of these blades facing the observer, the second should lie inside the first, and the third inside the second. The reverse arrangement is shown, so that if these are the fan blades of the right side, their original overlapping arrangement has been reversed during rotation and compaction. A second possibility (not adopted in figure 35, but shown in figure 2), is to assume that the posterior portion has been rotated so that the dorsal side is toward the observer in figure 35. The upper blades of the figure would then be right side (with the original overlapping arrangement reversed), the lower three the left side, showing the expected overlapping arrangement. On this interpretation, rotation would have been strong enough to carry the left fan to a lower level than right lateral lobe 15. The alimentary canal runs along the axial region close to the lower, ventral margin, in the first interpretation, and has been displaced to lie close to the dorsal margin in the second. Thus the evidence for rotation of the posterior region from a lateral position is equivocal, and interpretation of the fan problematical. An irregular dark area is visible at the posterior edge of the region, having a coiled form adjacent to the end of the alimentary canal.

(*i*) *U.S.N.M.* 205258

Figure 44; figures 45–51, plate IX; figures 52–54, plate X

1912 Walcott, p. 168
1930 Hutchinson, pp. 3, 7, Pl. 1, fig 4

A dorsoventral compression, extended straight, incomplete posteriorly, part and counterpart available. It is probably the original of No. 4 in Walcott's table of dimensions, and the counter-

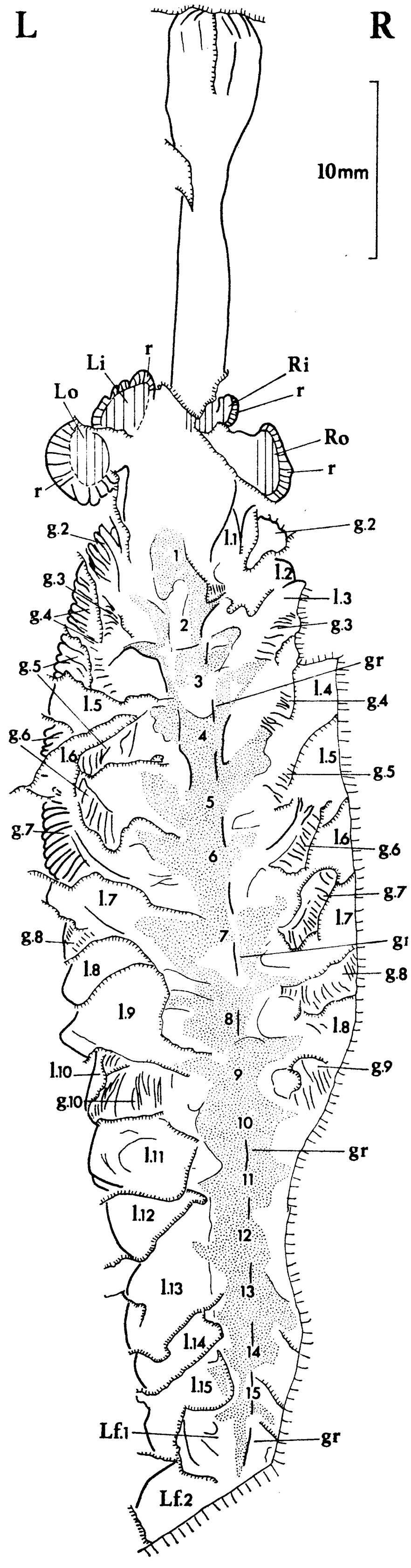

Figure 44

Description of plate IX and figure 44

Opabinia regalis Walcott, 1912. U.S.N.M. 205258, Phyllopod bed, Walcott quarry

Figure 44. Composite explanatory drawing of part and counterpart.

Figures 45, 46, 49, 51. Part, respectively north-northwest (magn. × 1.7); reflected (magn. × 1.7); cephalon and first 8 trunk segments, northwest (magn. × 3.3); trunk segments 8-15, northwest (magn. × 3.3).

Figures 47, 48, 50. Counterpart, respectively north-northwest (magn. × 1.7); reflected (magn. × 1.7); cephalon and first 6 trunk segments, northwest (magn. × 3.3).


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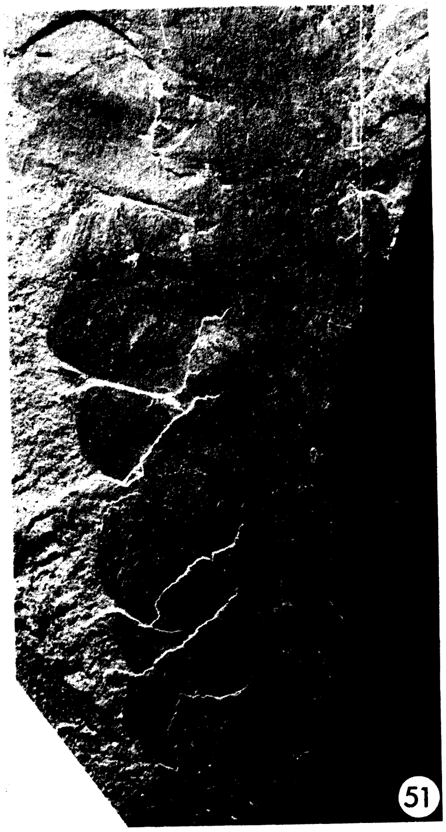
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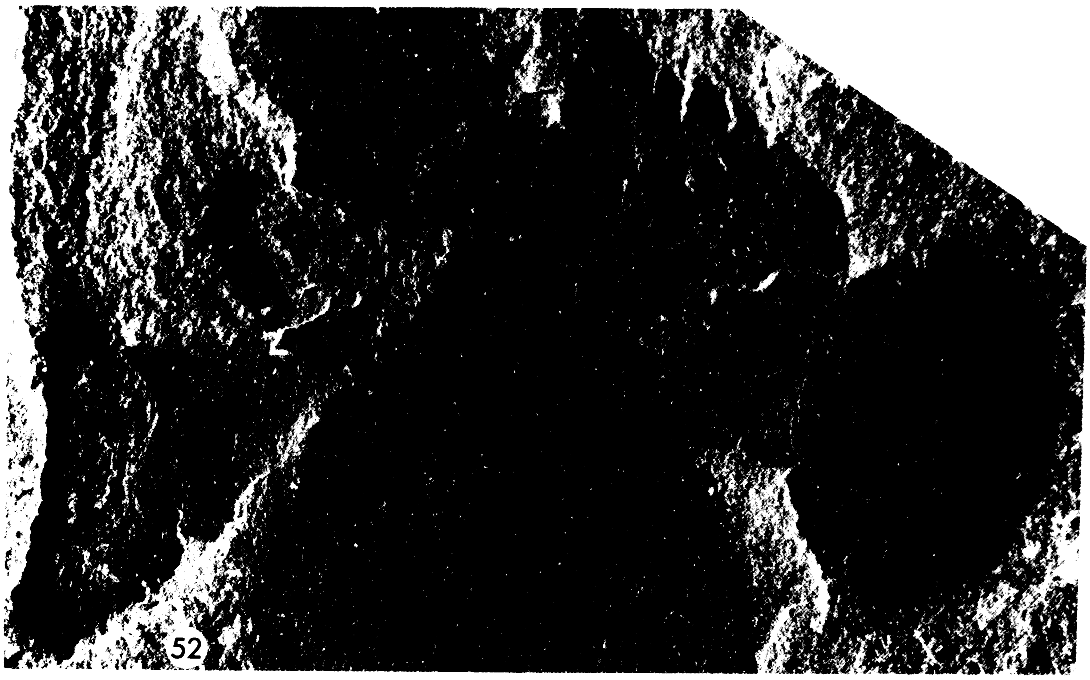
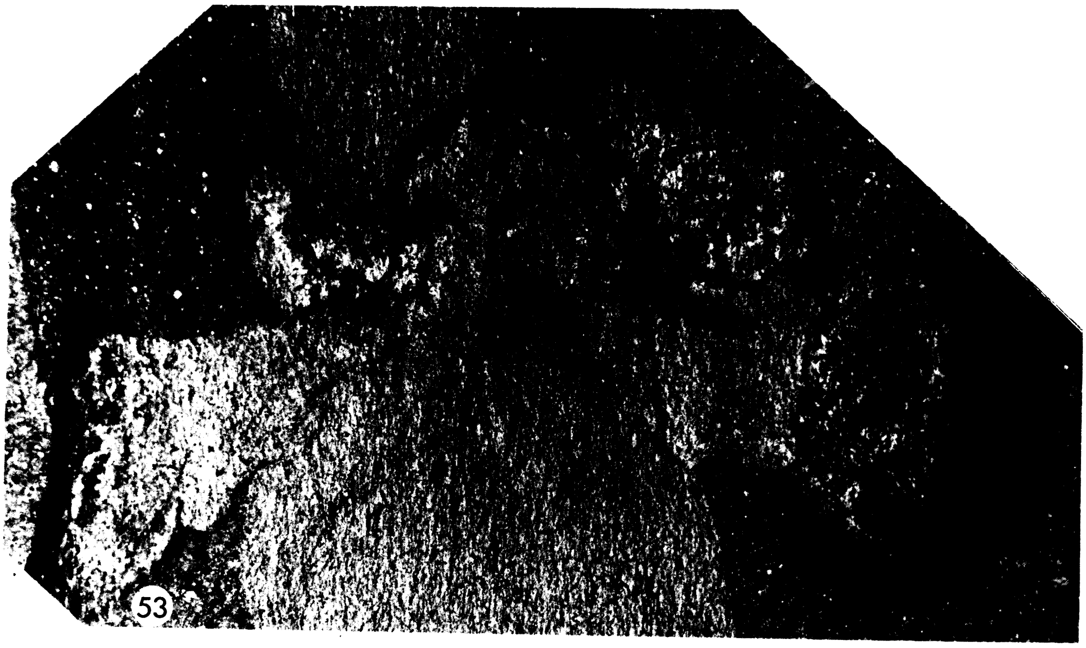
Figures 45–51. For description see opposite.





FIGURES 52–54. For description see opposite.

part was figured, using a 'retouched photograph left by Walcott' by Hutchinson (1930, p. 3). The manner of preservation is like that of 57684 and 155599, and many similar features are shown.

The frontal process is expanded anteriorly, this portion lozenge-shaped and showing a difference in level anteriorly between left and right sides, only the bases of the inwardly directed, distal spines preserved. Hutchinson noted the median reflective strip, faintly visible anteriorly in the counterpart (figure 48, plate IX), and regarded it as indicating the presence of an internal, fluid-filled cavity. Hutchinson also commented on what are here labelled (figure 44) as left and right outer eyes, borne on short, broad stalks, displaying a marginal, darker band which slopes outward and upward in the left eye, outward and downward in the right (figures 52–54, plate X). This band Hutchinson considered to be the ommatidial portion of the eye. He did not remark on the areas here labelled (figure 44) left and right inner eyes, situated at the anterior edge of the base of the stalk of the outer eye and at a higher level, and displaying a downward and outward-sloping, darker marginal band. Both the central, oval eye area (parallel ruled in figure 44) and the marginal band are strongly reflective (figures 46, 48, plate IX), though because of the angle between them the central area may be reflective in a particular photograph (figure 53, plate X) while the marginal rim appears dark. The enlarged photographs (figures 52–54, plate X) show the distinctive, irregular (patchily reflective) appearance of the central eye area, and that the rim is divided by radially arranged, minute steps in level. These steps may result from compression of ommatidia, and this specimen affords the best evidence for the presence of two pairs of compound eyes. The most anterior part of the cephalon is concealed in the counterpart (figure 50, plate IX) by the proximal part of the frontal process, but the convexly-curved lateral margins are well shown behind the outer eyes.

The axial region of the body shows in low angle radiation a darker strip (stippled in figure 44), which is impressed near its right margin by a series of short lines which are ridges in the part (figures 49, 51, plate IX). From this median strip paired irregular darker areas run outward and forward (stippled in figure 44). These darker areas are reflective (figures 46, 48, plate IX). The pattern is clearly related to segmentation, the lateral areas running out into the basal parts of the lobes. Comparable patterns appear on other specimens (57684, 155600, 5809), including the line of short ridges. Hutchinson (1930, p. 7) considered that the darker, reflective areas represented the alimentary canal and oblique segmental musculature.

Parts of lateral lobes are preserved on each side, those of the left more complete and showing curved or bluntly rounded tips. Lobes 1–10 are arranged so that each passes below the one in front, but this arrangement is reversed in left lobes 11–15 (figure 51, plate IX). Fragments of gills 1–10 are preserved as areas traversed obliquely by stepped changes in level. The narrow strips between each change of level appear to be rounded at the outer end in left gills 2–7 (figure 49, plate IX). The gills alternate with smooth lateral lobes, and the interpretation of figure 44 is that each gill lay upon the corresponding lobe, and was concealed by the overlap of the lobe in front. Gill 2 is the most anterior on each side, lying on lobe 2. This relation is clear on the

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DESCRIPTION OF PLATE X

Opabinia regalis Walcott, 1912. U.S.N.M. 205258, Phyllopod bed, Walcott quarry.

FIGURES 52, 53. Counterpart, portion of cephalon, showing eyes, respectively west; reflected (magn. × 10).

FIGURE 54. Part, portion of cephalon, showing eyes, northwest (magn. × 10).

right side (figure 49, plate IX), where a fragment of lobe 1 lies inside lobe 2. A similar interpretation is made of 57684, in which specimen the gills are preserved directed outward rather than curved forward distally.

The posterior portion is broken in this specimen, but assuming there are 15 lobes on the left side, they appear to be followed by parts of two left blades of the fan, the first lying adaxial to the second (figure 51, plate XI).

(*j*) *U.S.N.M.* 205259

Figures 2, 55; figures 56–59, plate XI

An oblique lateral compression (figure 2), incomplete part and counterpart available. The poorly preserved frontal process (figure 56, plate XI) curves downward and forward from the anteroventral side of the cephalon, expands distally but is incomplete, the anterior spinose portion being broken away. The cephalon juts forward, parts of four eyes being preserved at the anterior margin, the part (figure 59, plate XI) showing the left and right inner, and behind the latter at a much lower level, the right outer. Faintly defined steps cross the rim of the right inner and outer eyes. The counterpart (figure 58, plate XI) shows the right and left inner eyes, and at a lower level, behind the latter, the left outer eye. These eye areas are strongly reflective (figure 57, plate XI), appearing dark in low angle radiation, and having a broad reflective, raised rim. The gut is both reflective and visible as a darker band in low angle radiation. The anterior portion is bent into a ‘ U ’, exceptionally clearly outlined (figure 59, plate XI), the anterior end expanded slightly, backward-facing, and bearing short, fine, longitudinal striations. Posteriorly the gut narrows and extends as far as the trunk is preserved. The portion of the trunk dorsal to the gut is narrowest (tr.) anteriorly, becoming wider posteriorly as a result of the

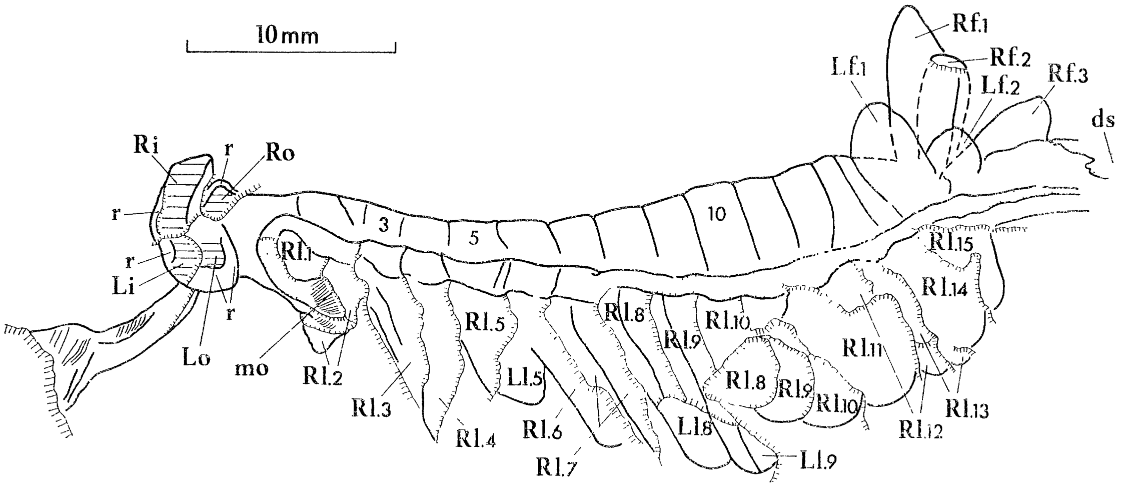


FIGURE 55

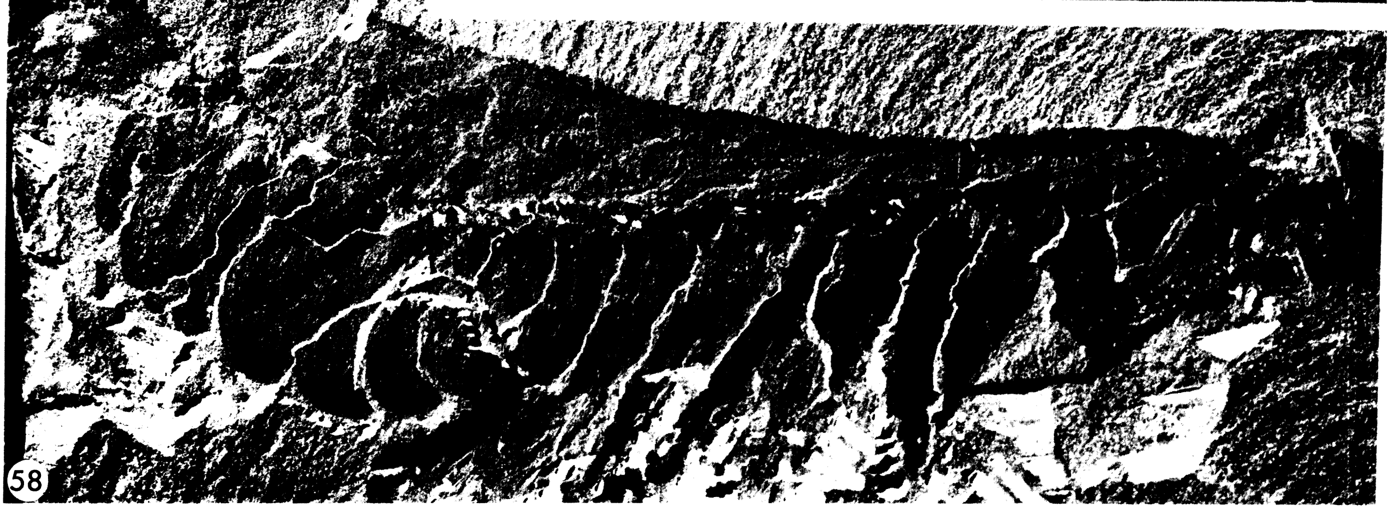
DESCRIPTION OF PLATE XI AND FIGURE 55

Opabinia regalis Walcott, 1912. U.S.N.M. 205259, Phyllopod bed, Walcott quarry.

FIGURE 55. Composite explanatory drawing of part and counterpart.

FIGURES 56, 57, 59. Part, respectively west (magn. × 3); reflected (magn. × 2.5); cephalon and most anterior portion of trunk, northwest (magn. × 10).

FIGURE 58. Counterpart, northwest (magn. × 4).



FIGURES 56–59. For description see opposite.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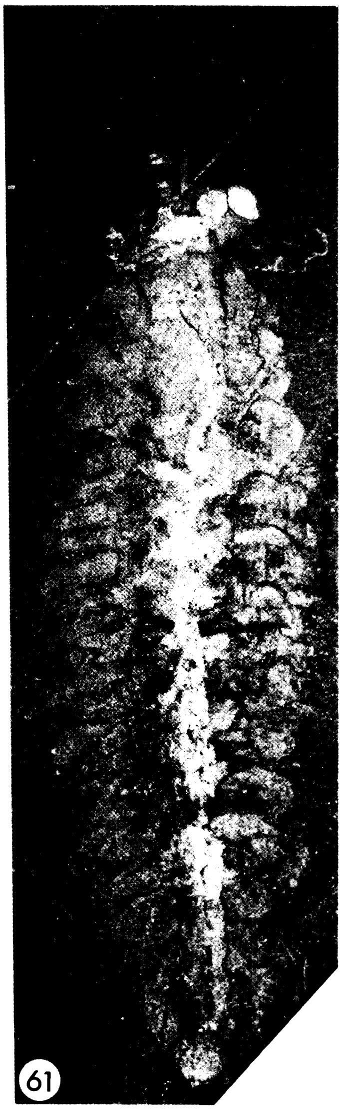
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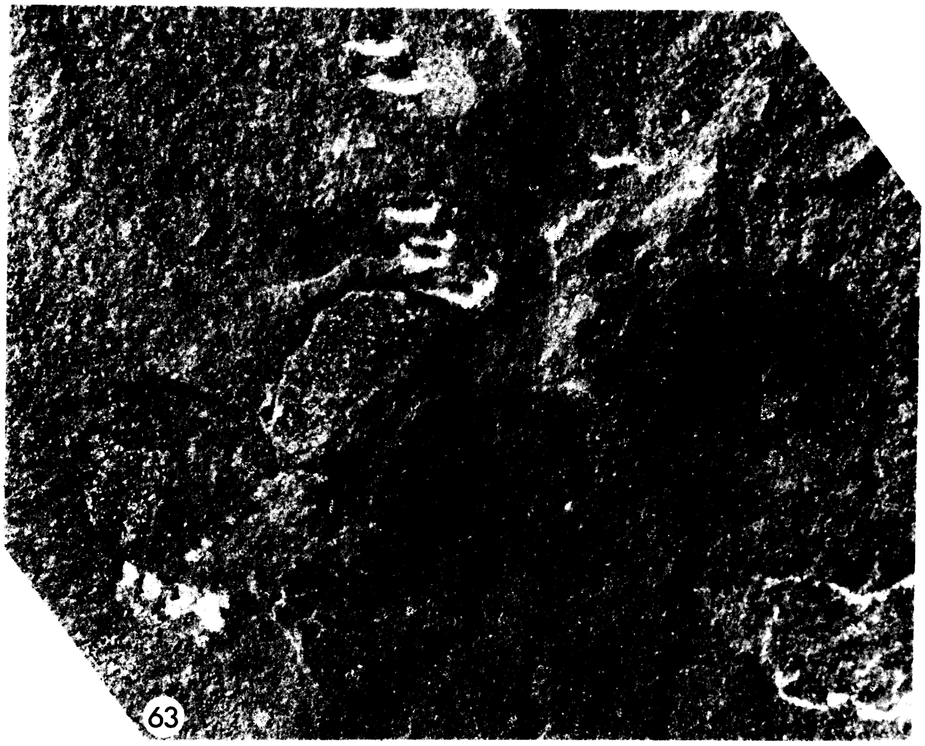
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FIGURES 60–63. For description see opposite.


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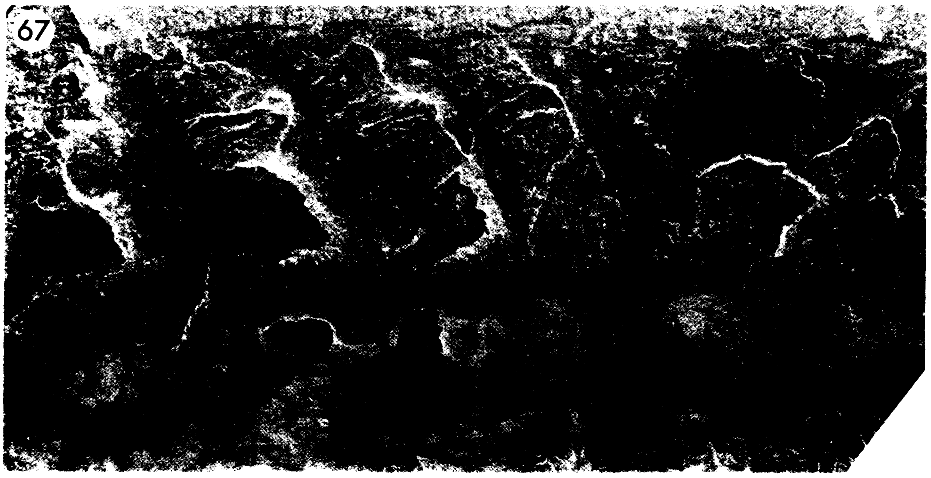
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Opabinia regalis Walcott, 1912.

Figures 65, 66. Y.P.M. 5809, part, respectively segments 1–10 of trunk, northeast (magn. × 5); cephalon and segments 1–7 of trunk, north–northwest (magn. × 3.3). Phyllopod bed, Walcott quarry.

Figure 67. G.S.C. 40251, part, axial region and right side of trunk segments 4–9, northeast (magn. × 5). Walcott quarry, level 1.68 m (5 ft 6 in).

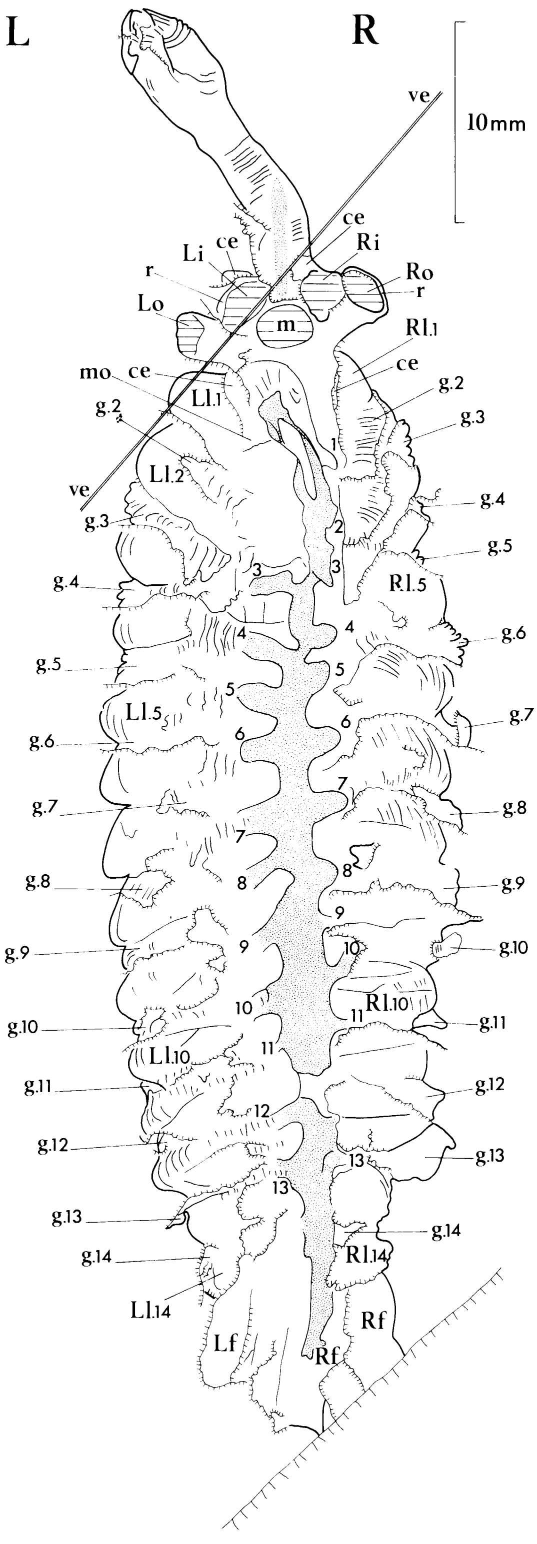


Figure 64

Opabinia regalis Walcott, 1912. Y.P.M. 5809, Phyllopod bed, Walcott quarry.

Figures 60, 61, 62. Part, respectively in ordinary light under alcohol; reflected; northwest (magn. × 2).

Figure 63. Part, portion of cephalon showing eyes, north (magn. × 10).

Figure 64. Explanatory drawing of part.

increasingly oblique orientation of the body (figure 2). Divisions between segments 5–14 are visible as faint, darker lines which are slightly reflective, those between segments 1-5 difficult to discern and only tentatively indicated on figure 55. Ventrally to the gut portions of fifteen imbricated lateral lobes are preserved, the first lying within the 'U'-shaped anterior portion of the gut. The first seven lobes vary from triangular to blade-like in outline, but right lobes 8–15 are broad (exs.) and rounded in outline (figure 58, plate XI). Only the proximal portions of the lobes are preserved in the part (figure 56, plate XI), so that the lobes shown in figure 55 are based largely on the counterpart. In the latter the majority of the lobes are imbricated to pass below the one in front, i.e. they must belong to the right side. In confirmation of this, excavation distally has shown (figure 58, plate XI) the presence of portions of three left lobes, presumed to be 5, 8, and 9, at a deeper level. These fragments are shown in figure 55, the left lobes appearing at a higher level in this reconstruction of the left-hand aspect of the specimen. The interpretation of the outline of right lobes 8–10, 12, is in conformity with the outline of the most completely exposed lobe, lateral lobe 11. These lobes are remarkably long (exs.), with an extensive overlap, even greater than that shown, for example, by the corresponding lateral lobes in 155600.

The tip of the posterior region of the trunk is not preserved, exactly where it ends being difficult to determine, and there is an adjacent irregular dark patch in the rock. However, parts of the three right, and first two left, blades of the posterior fan have been excavated (lying below the adjacent part of the trunk) in the part (figure 56, plate XI) and counterpart (figure 58, plate XI) respectively. Each blade passes inside (adaxial to) the one in front, and the left and right sides lie at quite different levels, so that the structure of the fan is well demonstrated. Further, the blades of the right side (preserved in the part) extend higher above the preserved dorsal edge of the trunk than those of the left side (preserved in the counterpart). This implies that the posterior part of the trunk was obliquely orientated in the rock before compression (figure 2), the right side lying higher than the left. Such an orientation is confirmed by right lobes 8–10 lying higher than left lobes 8 and 9, and in the anterior part of the trunk by the position of the eyes on the left and right sides. It may also be observed that in the part (figure 59, plate XI), the anterior portion of the gut and the mouth region lie at a level below (i.e. outside) what is considered to be right lobe I. The natural position would be between the left and right first lobes, and this displacement may have occurred during transportation, immediately prior to burial.

As in other lateral or lateral-oblique specimens, no sign of the gill structures is visible. The counterpart shows the right lobes from the outer side, but the split between part and counterpart may have passed through the lobes (figure 3*e*). If so, the outer layers of the right lobes, and the overlying gill structures, may not be visible because of the incompleteness of the counterpart.

(*k*) *Y.P.M.* 5809

Figures 60–63, plate XII; figure 64; figures 65, 66, plate XIII

An extended dorsoventral compression, counterpart unknown. The frontal process (figure 66, plate XIII) extends forward a short distance and then is bent to the left through an angle of about 25°. The expanded distal portion is divided by a longitudinal change in level, and parts of spines, directed inward and forward, are present on each side at the tip. Transverse striations cross the proximal portion, and a darker, reflective, median band is visible in the most proximal part. The cephalon lies at a higher level than the frontal process, and displays five oval reflective areas which are dark in low angle radiation (figure 64; figures 60–63, plate XII). The median area is adjacent to the base of the frontal process, in front and on either side of it are the two areas which stand highest, the left showing a distinct rim. Outside, and slightly behind and below these areas, are the outer pair, each borne on a broad stalk which is directed outward and forward from a point behind the inner, posterior margin of the median area. The right hand of these areas has a distinct, narrow raised rim. A mineral vein cuts the specimen diagonally, crossing the base of the frontal process and the left inner area. Anterolaterally to this vein the fossil is preserved as a dark film, on the other side of the vein the fossil is stained yellowish. In association with this difference, the median and two right eye areas appear dark in low angle illumination but are strongly reflective, whereas the two left areas are dark, but adhering crystalline deposits reduce the reflectivity. As in other specimens, these areas are considered to be eyes. The abaxial margin of the stalk bearing the outer eye is defined by a change in level. On the right side this change in level is most marked, down to a barely visible level (ce, figure 64) and down further to the first right lateral lobe. The relationship is the same on the left side, but a larger area of the presumed dorsal region of the cephalon (ce, figure 64) is visible. A small area also projects in front of and below the inner eye on each side, and presumably represents part of the compressed frontal slope of the cephalon.

Behind the cephalon the axial region of the trunk extends straight back. It displays a broad central band, dark and highly reflective, partially covered by a yellowish film; paired, irregular branches from this central band are present along its length (figure 60, plate XII). This band and its branches are stippled in figure 64, and it extends almost to the tip of the posterior region of the trunk. At the anterior end the band is irregularly lobate. Beside and in front of this lobate portion, between it and the median eye, is a curving impressed line, the area it encloses crossed by a few faint striations. This region may represent the U-shaped curve of the anterior end of the gut, and a faint transverse line on the left side, beside the anterior portion of the gut, may represent the approximate position of the mouth. On each side of the axial region of the trunk the lateral lobes extend out to a similar distance, and alternate in position with traces of the gills. Anteriorly gills and lobes 1–4 on each side are partly forwardly directed, changing to transverse in 5–10, those behind this point slightly backwardly directed. The lateral lobes have an evenly curved or bluntly pointed distal margin, and some display curving, impressed lines directed subparallel to the distal margin. Each lobe passes below the one in front, lobes 1–6 on the right side appearing flat (figure 65, plate XIII), whereas in the following lobes 7–12, a transverse line divides the lobe into an anterior, faintly concave portion, and a posterior, flat portion. On the left side lobes 9–13 show this subdivision. The gill areas stand above (nearer the observer than) the lobes, are irregular in shape, and the surface appears roughened and may bear irregular, transversely or obliquely directed lines or slight changes in slope or level (figure 66, plate XIII). In, for example, right gills 8 and 12, left gills 8, 10, 13 (figure 62, plate XII), the gill appears to have been partially stripped off when the rock was split, leaving a slightly concave area floored by the lateral lobe. It is possible that the slightly concave portions of the lobes, separated from the remainder by a change in slope, may result from compaction upon the lobe of the overlying gill. As noted above, the arrangement of gills and lobes is alternating, lobe 1 on each side is that at a level below the stalk of the outer eye and lateral part of the cephalon (figure 66, plate XIII). At the posterior margin of lobe 1, and appearing below it, is a gill. This gill lies on lobe 2 with a sharp change of slope at the margin. Each succeeding gill has a similar relative position, emerging from beneath the lobe in front and resting at a higher (nearer the observer) level on the succeeding lobe, so that there is a conspicuous break in slope at the posterior margin of the gill. I have interpreted this specimen in the same way as 57684, i.e. that there is no gill structure associated with lobe 1, but that the first gill visible belongs to the second segment, and rests on the anterior portion of the lobe of the same segment. The same relationship extends along the length of the trunk in this specimen, to gill and lobe 13 on each side. Behind lobe 13 on the left side is what appears to be a small lobe 14, with a possible fragment of gill 14 at the anterior edge; similarly preserved areas on the right side may represent gill and lobe 14. Attention was drawn above to the paired branches of the dark, irregularly yellow-stained, reflective median band, stippled in figure 64. Each branch appears to project toward the proximal portion of a lateral lobe, with some irregularity presumably related to compression. Branches 3–13 have been recognized on each side, branches 1 and 2 only on the right. The central band and branches may represent the alimentary canal and paired diverticula, each pair related to a trunk segment. As in other specimens, segment 1 of the trunk includes the portion of the alimentary canal immediately following the U-shaped anterior portion which is in the cephalon.

The posterior portion of the trunk is not well preserved, but includes the subrectangular axial portion into which the dark band runs; the right posterior corner is bluntly pointed. Parts of blades of the tail fan are present, on each side lying above the last lateral lobe; possibly parts of two right blades are visible, and one left blade.

(*l*) *G.S.C.* 40251

Figure 2; figure 67, plate XIII; figures 68–72,
plate XIV; figure 73; figure 74; figures 75–78,
plate XV; figures 79–81, plate XVI

An oblique dorsoventral compression, the cephalon twisted to an almost lateral position (figure 2), part and counterpart available. The frontal process, crossed by fine, transverse striations (figure 81, plate XVI), originates at the most anteroventral part of the cephalon, and is curved back through 90° to lie on lateral lobes 1–5 of the left side. The expanded distal portion (figures 75, 76, plate XV; figure 79, plate XVI) lacks the striations and the tip is divided longitudinally into two equal portions which lie at different levels. Each portion terminates in at least four curved, broad-based spines, the largest distal, the shorter proximal ones having smaller spines at their bases. The spines are imbricated proximally, and curve inward and forward to form two opposed sets. A group of five structures (figures 77, 78, plate XV; figure 79, plate XVI), lying at different levels, project from the anterior and anterodorsal margins of the cephalon. Each has a strongly reflective central area, ovate in outline, the surface irregular, and a darker, smooth, narrow rim which lies at a slight angle to the central area. These structures are considered to be the eyes, the stalk bearing the left outer eye clearly outlined. The greatest difference of level separates the left and right outer eyes. Projecting below these, at an intermediate level, are the left and right inner eyes. The circular, strongly reflective area of the median eye is situated behind the base of the left outer eye.

The trunk extends almost straight back behind the cephalon (figures 68–72, plate XIV; figure 73), on one side of the main portion a series of overlapping lateral lobes, each passing below the one in front so that this is assumed to be the left side. On the right side the margin forms a smooth curve for about half the length, beyond here it is scalloped and stepped.

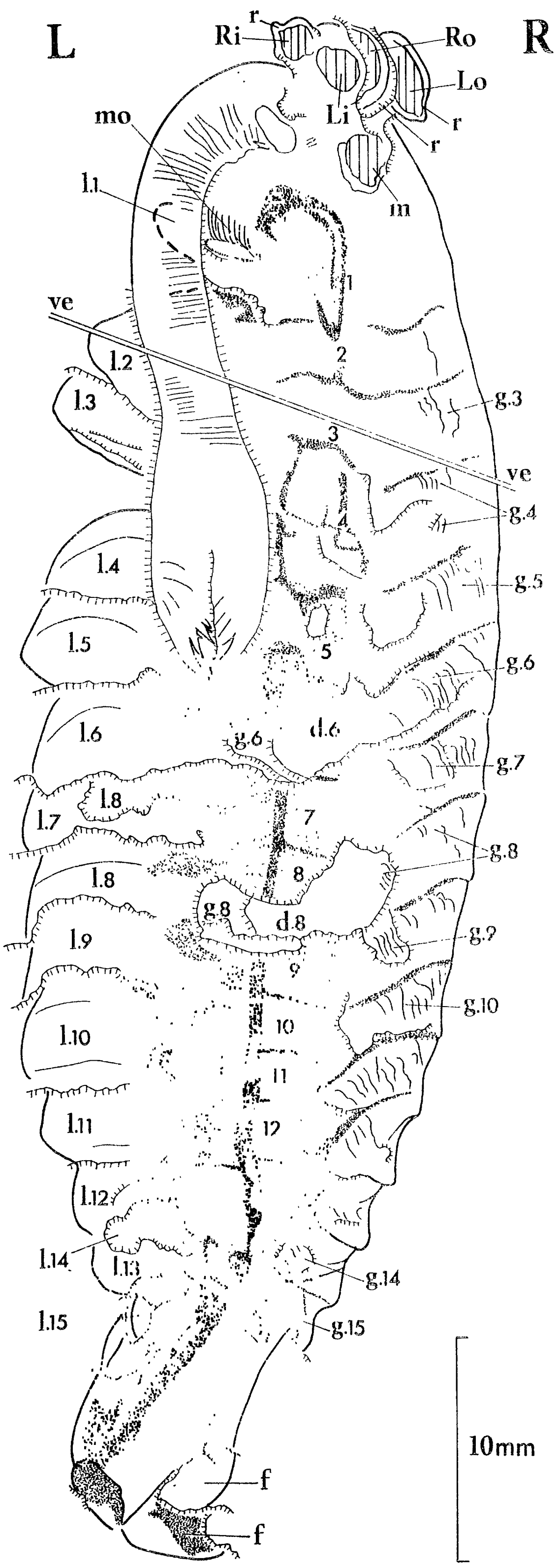


FIGURE 73

DESCRIPTION OF PLATE XIV AND FIGURE 73

Opabinia regalis Walcott, 1912. G.S.C. 40251, Walcott quarry, level 1.68 m (5 ft 6 ins).
FIGURES 68, 71, 72. Part, respectively ordinary light under alcohol; northwest; reflected (magn. × 2).
FIGURES 69, 70. Counterpart, respectively northwest; ordinary light under alcohol (magn. × 2).
FIGURE 73. Composite explanatory drawing of part and counterpart.


68


69


70


71


72

FIGURES 68–72. For description see opposite.

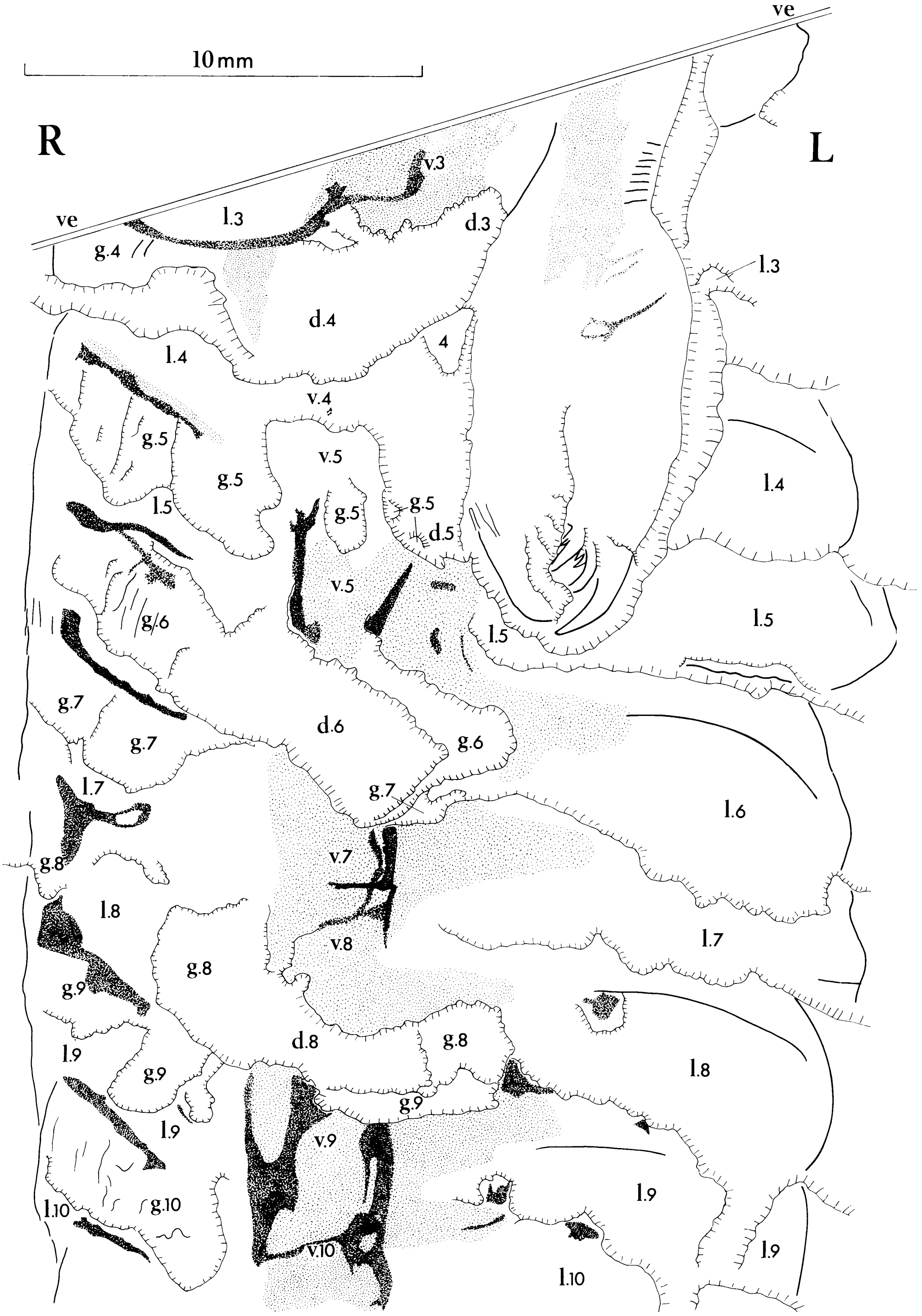


FIGURE 74

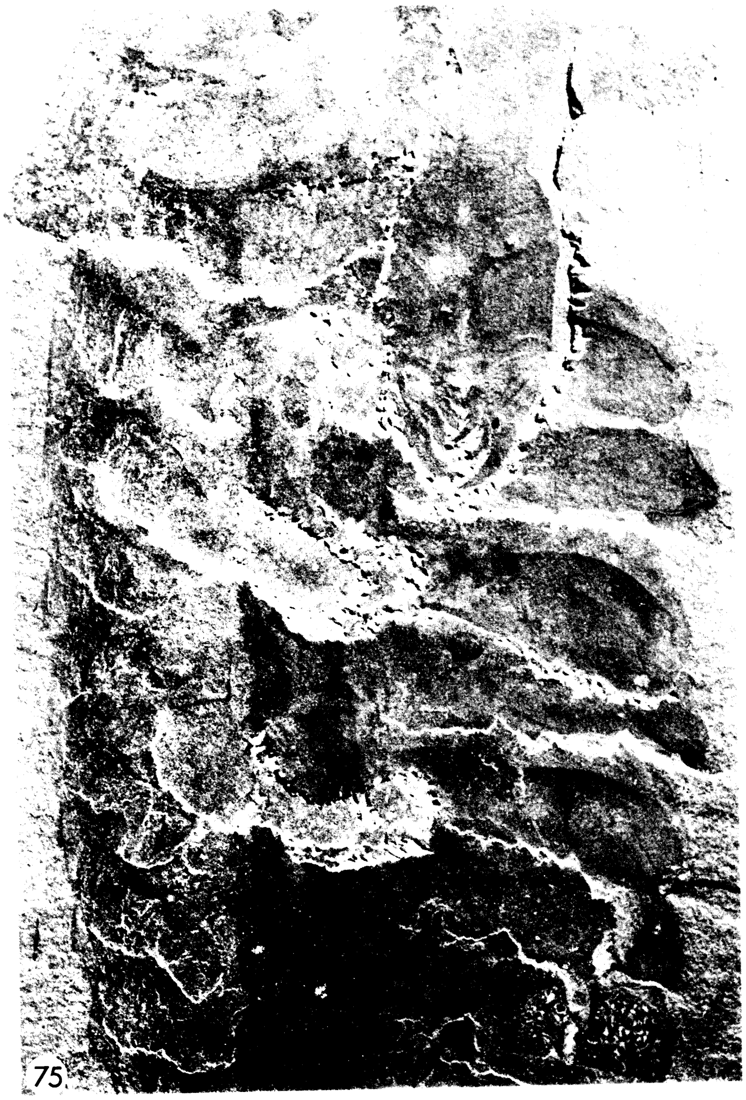
Opabinia regalis Walcott, 1912. G.S.C. 40251, Walcott quarry, level 1.68 m (5 ft 6 in).

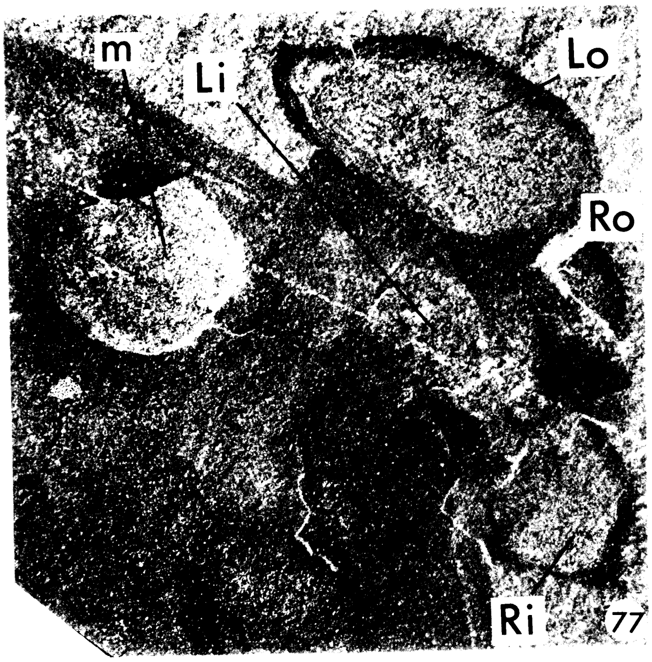
FIGURE 74. Explanatory drawing of counterpart.

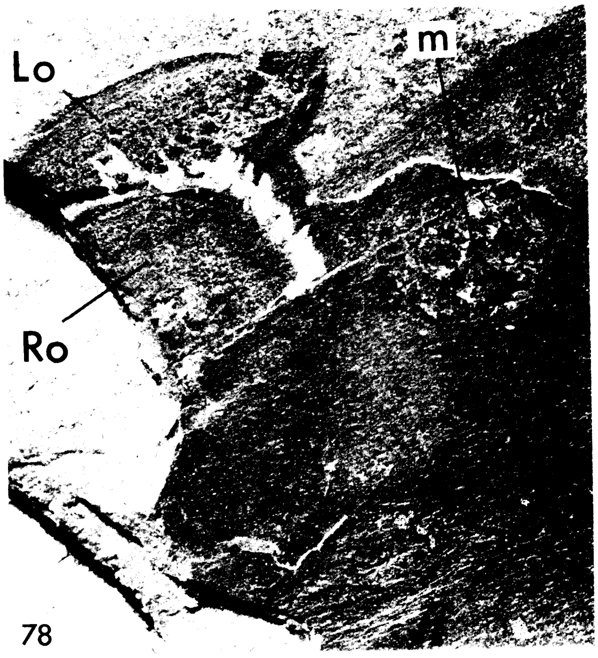
FIGURES 75, 76. Counterpart, respectively portion shown in figure 74, north–northeast (magn. × 4); reflected (magn. × 2).

FIGURE 77. Counterpart, portion of cephalon showing eyes, northwest (magn. × 10).

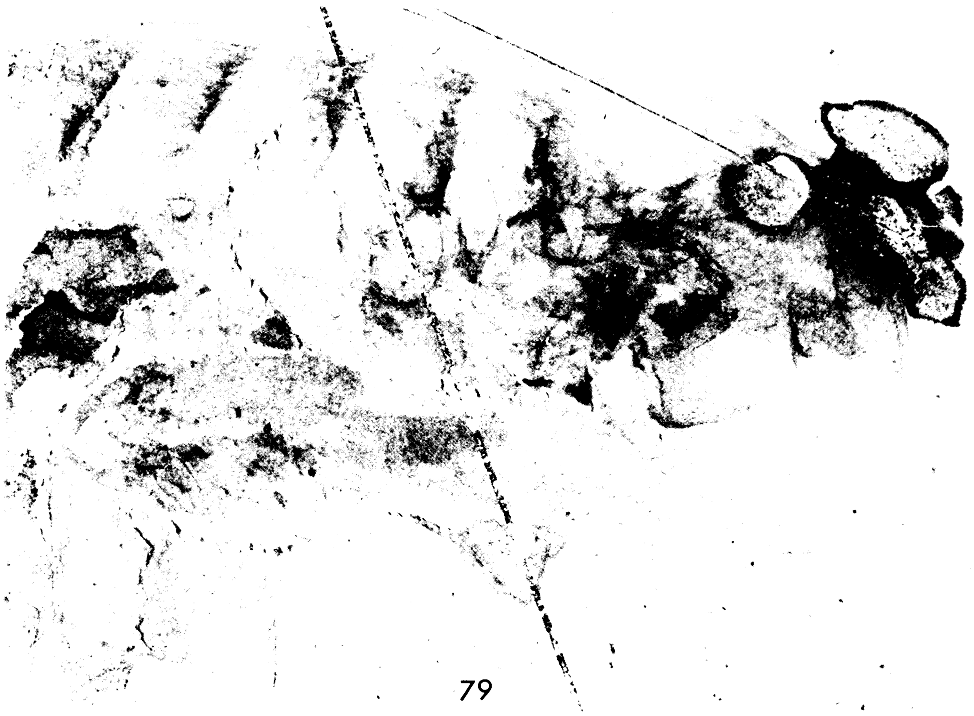
FIGURE 78. Part, portion of cephalon showing eyes, northwest (magn. × 10).

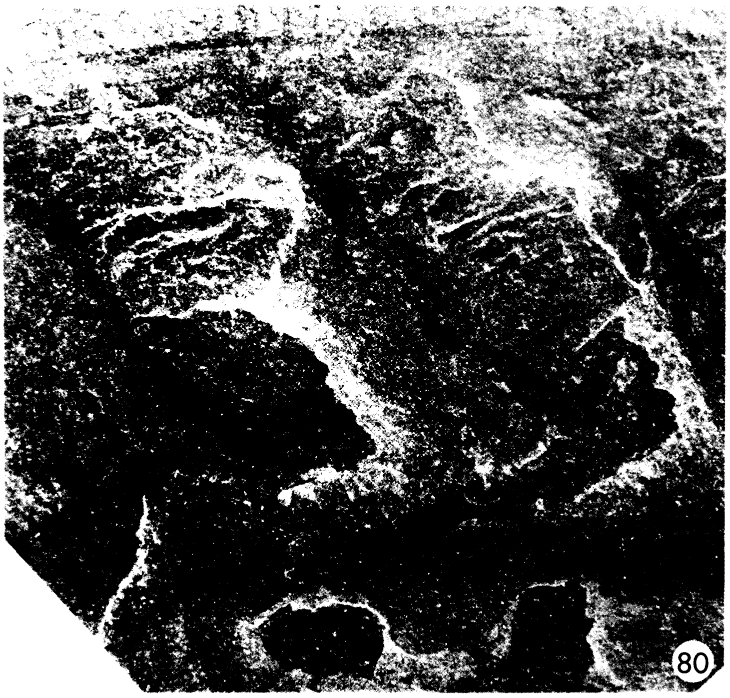






FIGURES 75–78. For description see opposite.





Opabinia regalis Walcott, 1912. G.S.C. 40251, Walcott quarry, level 1.68 m (5 ft 6 in).

FIGURE 79. Counterpart, cephalon and segments 1–6 of trunk, ordinary light under alcohol (magn. × 4).

FIGURE 80. Part, right gill areas 5 and 6, northeast (magn. × 10).

FIGURE 81. Counterpart, portion of cephalon showing median eye and mouth area adjacent to proximal portion of frontal process, northeast (magn. × 10).

A series of oblique dark bands cross the right side and suggest divisions between successive lobes; transverse breaks in slope such as separate lobes of the left side are not seen. The axial region of the main portion of the trunk is visible as a broad zone which is dark in low angle radiation and under alcohol, and is also reflective. This zone shows darker, incomplete and irregular transverse lines, certain of which (for example those between 4–12) appear, since they are in line with boundaries between lateral lobes, to correspond to boundaries between segments. A narrow, darker strip lies along the axial region from segments 3–13, expanding into oval areas in segments 4 and 5 to 6 (figure 68, plate XIV). Its definition is variable, and beyond segment 13 it merges into the dark, axial region. This narrower band, with its occasional expansions, may represent the alimentary canal. Anteriorly, in segment 1 and the cephalon, the most anterior part of the band is sharply defined and curved into a U-shape (figure 79, plate XVI), widening toward the anterior end. This band lies on the inner side of a U-shaped structure that lies on the inside of, and adaxial to, the proximal part of the frontal process (figure 81, plate XVI). At its backward-facing end this latter structure is as wide as the frontal process, and bears fine longitudinal striations which merge into the dark band around its margins. The outer structure with the longitudinal striations may be the ventral part of the cephalon, the dark band inside it being the alimentary canal, curving to the backward facing mouth. The ventral part of the cephalon appears to lie at a level, as seen in the part (figure 71, plate XIV), below the frontal process, but above the first lateral lobe. The natural position would appear to have been between the first pair of lateral lobes (i.e. below the left first lobe), but this displacement may reflect twisting of the body during burial and compaction.

The left lateral lobes are rounded or bluntly pointed in outline, 4–12 showing a curved line (a fine groove in the part) running subparallel to the anterior margin and dividing a flat anterior portion from a faintly convex or forwardly inclined, longer (exs.) posterior portion. No one lobe is entirely exposed on part and/or counterpart, so that the complete outline is not revealed; this is particulary true of lobe 1, which has been partially exposed by excavation of the frontal process (figure 71, plate XIV). Lobes 1–3 have been curved forward, and 3 apparently folded, so that a gap separates 3 and 4 distally. At about segment 15 the trunk is flexed, so that the posterior portion lies at an angle to the remainder. This appears to have resulted in a crowding together of lobes 12–15, leading to the suggestion (figure 73) that 14 lies partly below 13, and that the fragment preserved in the counterpart outside and behind 14 is part of lobe 15. This interpretation offers an explanation for the areas lying below (adaxial to) the proximal parts of lobes 12 and 13 as being displaced lobe 14, but I am uncertain of its validity. The broad, darker axial region has subtriangular lateral extensions on to the proximal parts of the lobes. These areas are best seen on left lobes 5–11, appearing dark and being reflective like the axial region (figures 71, 72, plate XIV). They extend on to the median portion of each lobe, each is clearly related to a segment and they are on the ventral side of the lobe. Gills of the left side are not visible because the split between part and counterpart lies on this side at the level of the lobes.

The right side of the main portion of the trunk presents a different appearance, crossed by diagonal lines which are darker in low angle radiation and reflective (figures 68–72, plate XIV). These lines do not appear to connect with supposed segmental boundaries in the axial region, but they are associated with gill fragments, which also appear dark under alcohol. The gill fragments are preserved as patches clinging to the part (figure 67, plate XIII), because the split on the right side is at the level of the gills. These gill fragments merge, at the dark line along the anterior edge, with the underlying surface of the lateral lobe (figure 80, plate XVI).

Posterior to this line, the gill fragment is separated from the lateral lobe by a wedge-shaped rock layer which reaches its maximum thickness at the posterior edge of the fragment. The gill fragment appears as a single, dark layer proximally, adjacent to the axial region. Distally the surface is stepped as it becomes a series of imbricated lamellae, with an extremely thin rock layer between each lamella. Presumably these lamellae were attached proximally to a continuous sheet of cuticle, which is separated by the underlying wedge-shaped rock layer from a continuous surface, which as noted above must be formed by the lateral lobes. However, unlike the left side, these lobes are not imbricated, separated one from another by a thin rock layer, but apparently compacted together and preserved as a single sheet. Sediment intervened during burial only between gill and lateral lobe, and the gill lamellae, but not between adjacent lobes. The margin of the compacted lateral lobes forms a smooth curve with that of the cephalon to segment 6, beyond here it is stepped increasingly strongly and the margin between each step is concave outwards. It is assumed that this appearance results from the twisting of the body along the axis during burial, so that while the cephalon appears to have been compressed laterally, the trunk was oriented oblique-dorsoventrally, with consequent folding-under of the right lateral lobes and probably the right gills also (figure 2). In an attempt to elucidate the structures displayed by the part, the counterpart was partially excavated medially (figure 74; figures 75, 76, plate XV). Not only is the frontal process best preserved, but beside and behind it features of the median region are uniquely displayed. Certain of these features, associated with segments 6, 8 and 9, have been transferred to figure 73, but all are shown at a larger scale in figure 74. On the left side of figure 74 (right in the animal) are visible the depressions corresponding to the fragments of gills 4–10 which adhere to the part, and distal to the depressions are imbricated gill fragments. Two of these depressions, g.6 and g.8, have been followed by excavation and extend across the mid-region at the lowest (i.e. most dorsal) level. Medially these areas are no longer gills, but presumably are the inner surfaces of the dorsal cuticle of each segment. As these layers were excavated further, various carbonaceous layers, separated one from another by thin sheets of rock, were revealed on the left side (right in figure 74). These layers are interpreted as being the inner surfaces of gills of the left side. Proximal parts of gills 5, 6, 7, 8, and 9 are labelled, and show the sheet-like form of the gill. This interpretation implies that the inner and outer cuticle of lateral lobe and gill were compressed together to form a single carbonaceous layer, and that during burial sediment penetrated between these structures and formed the thin intervening rock layer. Along the axial region, between the dorsal cuticle of 5, 6 and 8, at a level nearer the observer (i.e. farthest ventrally), is visible the same surface as in the mid-region of the part. On this surface are the darker areas (stippled in figure 74), and these presumably represent the ventral cuticle of the axial region, and are labelled V.5, V.7, V.8, etc. On the left side (right in figure 74) a thin layer of rock intervenes not only between lobe and gill, but also between gill and dorsal cuticle. However, this layer thins towards the axial region and dies out, as at the inner extremity of g.5, g.6, and g.8. On the right side no layer of sediment intervenes between dorsal cuticle and gill, but one passes into the other. I interpret this effect as the result of overfolding of the thin dorsal cuticle toward the left side during burial (figure 2), trapping a thin layer of sediment between overfold and gill. Features shown in the axial region of segments 3–5, beside the frontal process, also appear to result from this overfolding of dorsal cuticle. In the part (figure 71, plate XIV) the ventral axial cuticle, showing the darker bands, lies adjacent to, and at a lower level than, the distal part of the frontal process. In the counterpart (figure 74), however, cuticle lying at a lower level than the distal part of the frontal process is preserved. This cuticle must be dorsal, and is interpreted as belonging to segments 3, 4, and 5. It must be overfolded dorsal to the frontal process, while lateral lobes and gills of 3–5 are extended beneath the opposite (ventral) side of the frontal process (figure 2).

The above interpretation suggests that the cuticle was thin and relatively flexible, and readily folded during burial. Another example of such folding appears to be afforded by the left lobes (figure 73). An anterior portion of what appears to be lobe 8 has been excavated, lying below lobe 7. There appears to be a change in level between the main part of lobe 8 and this supposed portion of it. Comparable structures are not seen on other lobes, except adjacent to 12 and 13, which have been explained as displaced lobe 14.

The posterior portion of the trunk is subrectangular in outline and has a median darker band (figure 70, plate XIV) which appears to be the trace of the alimentary canal. There is a blunt spine at the right, posterior corner, and the posterior margin is ill-defined. The posterior portion has been flexed relative to the rest of the trunk, and its orientation is obscure. There are parts of two blades of the tail fan on the right, and since the anterior lies adaxially to the posterior they are assumed to belong to the right side. Below the fragment of what is assumed to be the left lateral lobe 15 is part of another structure. It lies at a level below the posterior portion (as seen in the part) and can hardly therefore be part of the left side of the tail fan. Its nature is problematical.

TABLE 1. APPROXIMATE LENGTH/mm OF SPECIMENS ALONG THE SAGITTAL LINE (IN EXTENDED SPECIMENS IN STRAIGHT LINE, IN FLEXED SPECIMENS ALONG ARC), FROM ANTERIOR MARGIN OF CEPHALON TO POSTERIOR MARGIN OF TRUNK

205259	43
57683	52
155600	54
131217	56
155598	56
155599	57
5809	58
57684	62
40251	67
205258	70

5. DISCUSSION AND CONCLUSIONS

The preceding §4 has given in detail the evidence presented by the specimens. This evidence has been interpreted as resulting from processes of burial and compression of the bodies as deduced in §3. In this section the reasons for my conclusions on morphology (embodied in figures 82–84) are discussed, taking account of earlier views. Table 1 gives an approximation to the known size range of animals which are presumed to have been adults. The cuticle is preserved as an extremely thin, black layer which shows no sign of having been impregnated with mineral salts. The external surface appears to have been smooth, except for the fine ridges on the proximal part of the frontal process, and adjacent to the mouth. The cuticle appears to have been sufficiently rigid in life to have maintained the shape of the lateral lobes, gills and blades of the tail fan.

(*a*) *Morphology of cephalon*

The anterior margin of the first trunk segment is poorly preserved in all specimens, so that the posterior margin of the head region is ill-defined. The cephalon appears to be of length (sag.)

equal to approximately 2–2½ trunk segments, but shows no subdivisions; it bore the eyes and frontal process, the mouth opened on the posterior wall and led into the U-shaped anterior part of the gut. Lateral compressions (figure 7, plate I; figure 59, plate XI) show the cephalon diminishing in depth forward, the frontal slope rounded, to give a subsemicircular profile. Dorsoventral compressions (figures 18, 19, plate IV) may show a subrectangular outline of the cephalon, the anterolateral corner rounded, projecting in front of the eyes, or (figures 30, 33, plate VI) gently convex lateral margins giving a forward taper to the outline. In both oblique and dorsoventral compressions (figures 26, 28, plate V; figures 49, 50, plate IX) the eyes may project beyond the anterior margin of the cephalon. The restoration (figure 82*a*, *e*) embodies my view that the cephalon shallowed forward to a bluntly rounded anterior slope, that the eyes were borne high on the anterodorsal slope, and that the frontal process was situated on the ventral side at the base of this anteroventrally directed slope. The appearance of the cephalon in different dorsoventral compressions may have resulted from tilting during burial – tilted slightly forward the eyes project in front of the anterior margin (figures 49, 50, plate IX), whereas tilted slightly backward the frontal slope juts out in front of the eyes and is flattened to give a transverse anterior margin with rounded corners (figures 9–11, plate II).

Only one pair of eyes has previously been claimed to be present, Walcott (1912, p. 167; Pl. 27, fig. 6; Pl. 28, fig. 1) having noted what is here termed the outer pair, carried on a short, broad stalk, in the two specimens he figured. Simonetta (1970, p. 40; Pl. II, figs 2*a*, *b*) accepted the single pair, but regarded them as 'sessile', i.e. not carried on a stalk. The eye areas in many specimens show a narrow rim which may slope up or down from the main area. In Walcott's originals (figures 4, 12) there are four eye areas, lying at different levels, the outer pair borne on a short, thick stalk. The two pairs are seen, in the same relation, in other specimens (figures 24, 44, 55), the different levels well shown in the lateral compression (figure 55). The inner pair were borne on a much shorter base, situated inside and in front of the outer pair. A fifth eye area (a median eye situated slightly behind the inner pair) is displayed by 131217 (figures 22, 23, plate IV), 5809 (figures 60–63, plate XII; figure 64) and 40251 (figures 77, 78, plate XV). Walcott (1912, p. 167) considered that 'traces of the reticulated surface' of the eye remained in 57684, but this is not evident in the present photographs (figures 18, 19, plate IV). In 205258 (figures 52–54, plate X) it is the rim, not the central area, which appears dark in low angle radiation (though it is reflective), and this rim shows radially arranged steps (changes in level) or faint ridges. In 205259 (figure 59, plate XI) similar steps are less clearly visible, while in 40251 (figures 77, 78, plate XV) the rim appears smooth. The central area in all the specimens is an irregular, highly reflective surface. I have assumed that each eye was compound, and it appears that the visual surface was greater than a hemisphere. The rim may then be explained as resulting from the compression of the overhanging sides as the eye is crushed down on the stalk (figure 1*a*), which was of a lesser diameter than the eye.

The frontal process, from its base on the anteroventral slope of the cephalon to the tip, is of length (sag.) about four times that of the cephalon. The proximal two-thirds is of similar width in all compressions, so presumably was cylindrical, the distal portion expanded in most specimens. That this distal portion is not expanded in the lectotype (figure 7, plate I) is unusual, but in this and all other specimens showing the process, the distal spines are present. The proximal, cylindrical two-thirds or more of the process bore fine transverse striations and was clearly flexible. A narrow central band, reflective or slightly darker in low angle radiation, may be visible along parts of this portion. I see no evidence for Simonetta's claim (1970, p. 40) that the upper surface was grooved along the length. Possibly Simonetta derived his idea from Størmer's (1944, Fig. 19, 10) drawing, which presumably depicts a section along the frontal process showing the supposed median canal. No specimen shows clear evidence of such a canal along the entire length of the frontal process, but in 205258 (figure 48, plate IX) there is a median band in the distal portion. At about two-thirds of its length from the base the process expands into a subhexagonal distal portion of maximum width at least twice that of the proximal portion. This expansion is evident in lateral (figure 40, plate VII), dorsoventral (figures 9–11, plate II; figure 50, plate IX), and oblique (figures 69, 70, plate XIV) compressions, in all of which there is a longitudinal change of level dividing the distal portion, each side bearing opposed spines. Some 5 or 6 spines (with small spines at their bases) on each side are directed forward and inward, and behind them are strips (separated by a ridge or change in level) running parallel to the spines. The most proximal part, adjoining the striated cylindrical portion of the process, may be smooth and lacks the longitudinal change in level. The tip of the process in 57683 (figure 7, plate I) does not show two halves, nor is it expanded, and the 7 spines, at different levels, are directed longitudinally. It is presumed that this distal portion of the process is compressed in a direction at right angles to that obtaining in the other specimens, and shows only one side and hence no expansion. The different modes of preservation imply that the striated proximal part of the process was not only flexible but capable of limited rotation. The two halves of the distal part are not preserved widely 'open' or separated, but it seems reasonable to assume that movement between them was possible and that the opposing spines could be used for grasping or entangling. The reconstruction (figure 82*a*, *e*) shows the two halves oriented to move in the vertical plane, so that in dorsal aspect the process has the appearance shown by 57683. It may be that the normal position was at right angles to this, but one cannot tell.

In 205259 (figure 59, plate XI) the anterior part of the gut is visible as a sharply bounded dark strip, curved into a U-shape so that the anterior end faces backward. Fine striations running longitudinally are visible at and near the anterior end. In 40251 (figure 79, plate XVI) the U-shaped dark band is well displayed, lying at the inner margin of an apparently tubular structure bearing striations, the mouth of this tube backward facing. In 57683 (figure 7, plate I) the U-shaped dark band is preserved, and the most ventral part of the cephalon lies below the anterior part of the gut and shows the striations. These specimens are taken to indicate that the mouth opened on a posterior-facing wall on the striated ventral part of the cephalon (figure 83). Hutchinson (1930, Fig. 1) observed this ventral part of the cephalon, interpreting it as probably the antenna, but I cannot subscribe to this view.

Walcott (1912, p. 169) referred to two specimens which he considered to be the female of the species, having a slender, bifid frontal appendage. His originals were 131217 (figures 25–28, plate V) and 155598 (figures 30, 33, plate VI), the two specimens described herein that do not show the frontal process. As explained in § 4 (*e*), (*f*), in the former the process may have been broken off before burial, and in the latter it is not preserved because the specimen is incomplete anteriorly. There is thus no evidence for Walcott's view, and I do not accept Hutchinson's (1930, p. 7) belief that 131217 truly lacked the frontal process and represented the female. In the remaining eight specimens described above the frontal process is either extended forward or curled back beside the body. In the 18 additional, undescribed specimens, the frontal process is present in half of them (extended or curled back) and in the remainder either broken off, concealed, or the specimen lacks the anterior end. Since in those specimens lacking the frontal process there appears to be a break at the anterior margin of the cephalon, I do not consider the

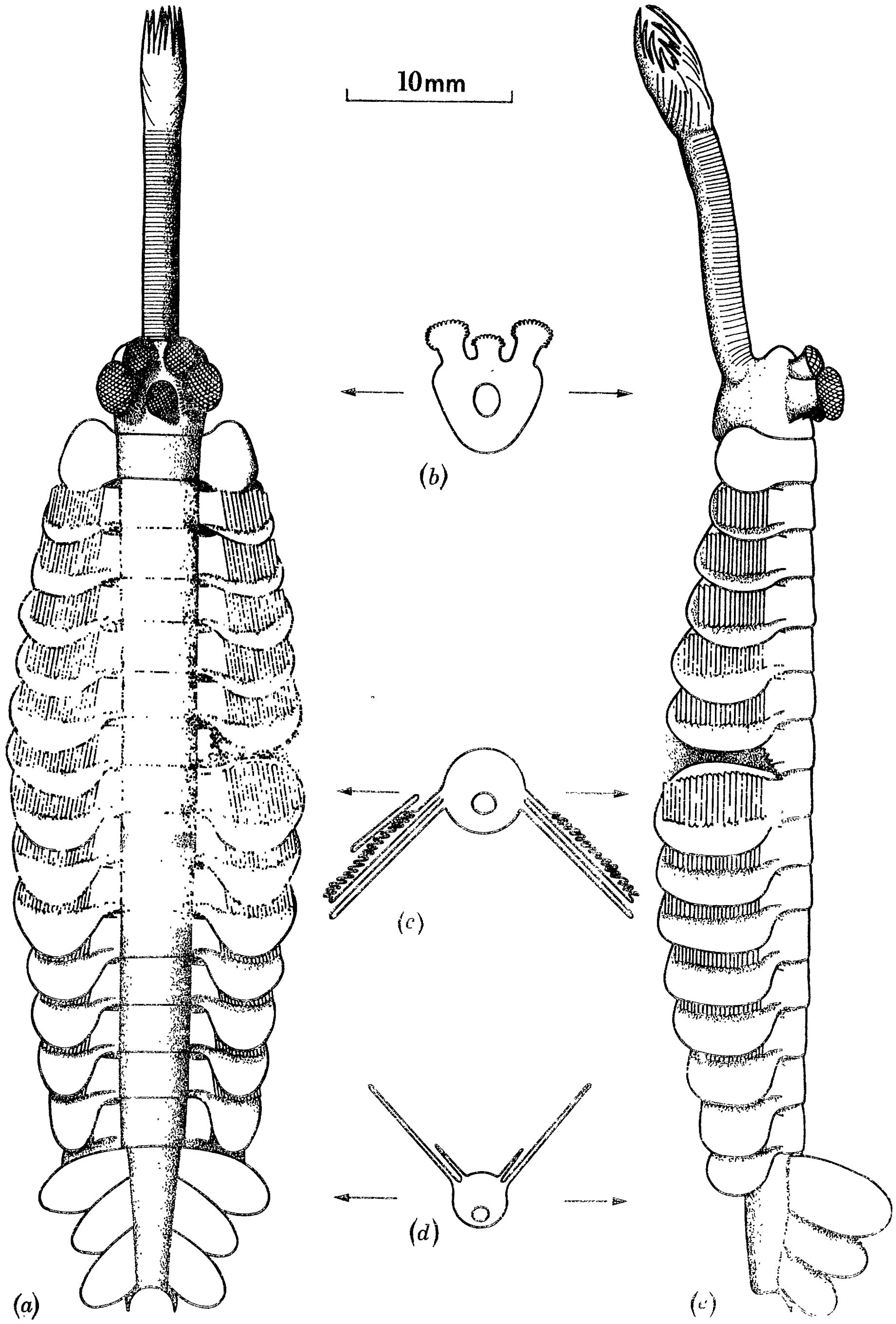


FIGURE 82. Reconstruction of *Opabinia regalis* Walcott, 1912.

(*a*) Dorsal view, light from northwest, right lateral lobe and gill of segment 7 cut off proximally to show lateral lobe and gill of segment 8. (*b*, *c*, *d*) Cross sections of body at the levels indicated by the arrows, position of alimentary canal indicated. (*e*) Left lateral view, light from northeast, left lateral lobe and gill of segment 7 cut off proximally to show lateral lobe and gill of segment 8.

evidence to be satisfactory for two groups of individuals, one with, and one truly lacking, the frontal process. Sharov (1965, p. 964, fig. 2; 1966, pp. 26–27) considered the frontal process of *Opabinia* to be an eversible proboscis, explained the specimens apparently lacking the proboscis as having been buried when it was withdrawn, and considered that there was an 'upper lip' at the anterior margin of the cephalon, which served to close the mouth opening when the proboscis was withdrawn. The present interpretation makes these views untenable, in that the process is a structure independent of the alimentary canal, and there is no evidence that it was eversible. The anterior portion of the alimentary canal is U-shaped, the mouth opening on the posterior face of the ventral side of the cephalon. In the part of 57683 (figure 7, plate I) the anterior slope of the cephalon is nearer the observer than the proximal part of the frontal process, and separated from it by a change in level. This appearance is probably the result of oblique compression, which folded the most anterior part of the cephalon over the proximal part of the frontal process. It is presumably this appearance that led Sharov to postulate an 'upper lip'.

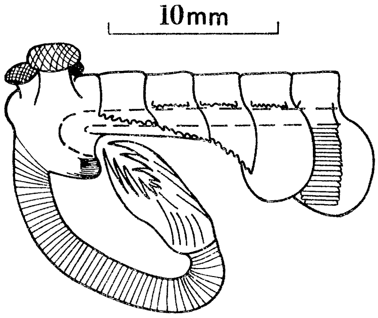


FIGURE 83. *Opabinia regalis* Walcott, 1912. Lateral view of cephalon and first five segments of trunk, lateral lobes 1–3 and gills 2, 3, 4 cut off proximally to show mouth and normal wall of axial portion of trunk. Frontal process curved around to mouth, course of alimentary canal shown by dashed lines.

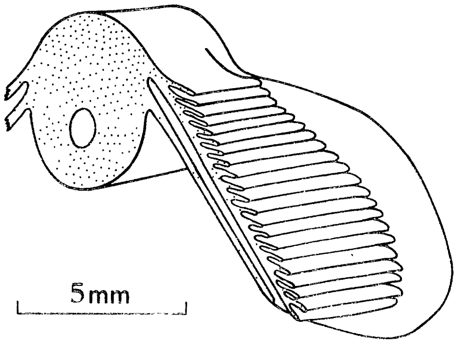


FIGURE 84. *Opabinia regalis* Walcott, 1912. One segment of main portion of trunk, oblique view, shaded area is transverse section near anterior end, showing (unshaded) alimentary canal. Left lateral lobe and gill cut anteriorly by transverse section, right lobe and gill cut off proximally.

In 57684 the anterolateral margin of the cephalon appears as a rounded corner, in my view as a result of compression of the backwardly tilted head. Simonetta (1970, p. 40) observed these projections and considered they represented the antennae, showing them (Simonetta 1970, Pl. II, figs 2*a*, *b*,) as conical, short, with a number of segments. I do not consider the specimen (figures 18, 19, plate IV) affords the evidence for such an interpretation. Simonetta (1970, p. 40, Pl. V, fig. 3*b*) also claimed that 'at the base of the proboscis' in 155599 (figures 29, 31, plate VI) there was a pair of small structures which appeared similar in outline to the antennae and were faintly denticulated. The specimen is poorly preserved in this region and has suffered from crude preparation, and neither this nor other specimens provide evidence for such supposed structures, which Simonetta (1970, Pl. II, figs 2*a*, *b*) restored as projecting forward beneath the cephalon.

(*b*) *Morphology of trunk*

Behind the cephalon a broad axial region of the body, crossed by darker or impressed lines, but not by changes in level, extends to the posterior tip. The axial region is divided into 15 segments of similar length, and an undivided posterior portion equal in length to about 3 segments. The axial region is of similar width in specimens compressed in various directions, a feature well shown by the posterior portion. It is thus concluded that the axial region was subcylindrical in form, and the slight step in the profile at segmental boundaries (e.g. figures 5, 6, plate I) suggests a joint between segments, first trunk segment and cephalon, and last segment of main portion of trunk and undivided posterior portion. These joints seem to have given a limited (25° in 57683, figures 5, 6, plate I) flexibility to the body. A darker, reflective band runs back, in continuation of the U-shaped cephalic part of the alimentary canal, to the tip of the trunk (figures 5, 6, plate I; figures 9–11, plate II; figures 25–28, plate V; figures 56–58, plate XI). This band becomes narrower beyond about segment 9. There may be blobs of mineral matter along it (figures 31, 32, plate VI), or oval, faintly convex areas (figure 67, plate XIII), suggesting gut filling. However, the band is not a continuous sediment-filled strip, flattened-ovate in cross section, with clearly defined margins, as in some specimens of *Yohoia tenuis* (Whittington 1974, Pl. 12, figs 4, 5). On the contrary it may be ill-defined, without any relief (figures 36-38, plate VII). Because the band is situated at the lower edge of the axial region in lateral compressions (figures 5, 6, plate I; figures 56-58, plate XI), and is visible only on the ventral surface of 40251 (figures 68–70, plate XIV; the band is absent where the counterpart has been excavated to show the dorsal cuticle), it is assumed that the alimentary canal ran along the ventral side of the trunk. A unique feature shown by 40251 (figure 67, plate XIII; figures 68–72, plate XIV; figure 73) is that the broad, dark band of the axial region shows a narrow, darker band running along to the left of the sagittal line. The band (figure 73, darker stipple) runs from the cephalon into segment 2, is continuous from segment 7 to the posterior tip, and preserved on the ventral side. This band appears to represent the alimentary canal, within the axial region of the trunk. Thus in less well-preserved specimens the dark band, which seems in the main to represent the alimentary canal, may also represent adjacent parts of the axial region. In 5809 paired, lobate extensions of the axial dark band, one pair in each segment, project out toward the proximal parts of the lateral lobes (figures 60–62, plate XII; figure 64). In other specimens (figures 41,42, plate VIII; figures 45–48, plate IX; figures 71, 72, plate XIV) similar extensions are faintly defined, darker or reflective patches, sub-triangular in outline. In 40251 these patches are preserved on the ventral surface of the trunk, as is the alimentary canal. Hutchinson (1930, p. 7) referred to these structures in 205258 as 'obliquely arranged segmental musculature'. The preservation in 5809 and 40251 suggests the possiblity that they are diverticula of the gut, or that they may be connected with circulation associated with the supposed gills. In 57684 (figures 9–11, plate II; figure 12) analogous areas on the left side of segments 11–14 are rectangular in outline and sharply defined, a feature not seen in any other specimen. Impressed lines at the positions of the outer edge of these areas are seen in more anterior segments, and similar impressed lines are visible along the right side in 205258 (figures 49-51, plate IX). The significance of these features is not clear.

Each of the fifteen segments of the main portion of the trunk bears a pair of lateral lobes, successive lobes overlapping, each passing inside the one in front. In dorsoventral compressions (figures 9–11, plate II; figures 31, 32, plate VI; figures 45–51, plate IX; figures 60–62, plate XII) the lobes appear subrectangular in outline, wider (tr.) than long, the tip rounded or bluntly pointed, the lobes and boundaries between them showing a slightly radial rather than transverse-parallel arrangement. Considerable overlap of one lobe on its successor is evident, particularly in the longer (exs.), backwardly-curved posterior lobes. Fine ridges subparallel to the margins may be developed. In slightly oblique-lateral compressions (figures 5, 6, plate I; figures 56, 58, plate XI) the first six lobes may not show a forward-outward direction (as they do in 155600, figures 36–39, plate VII), but outward to outward-backward, and have a lanceolate outline. The more posterior lobes, 8–15, appear longest (exs.) and most broadly rounded in 155600 and 205259 (figure 58, plate XI), and show the greatest overlap. Such more strongly oblique compressions as 131217 (figure 24), 155598 (figure 34), and 40251 (figure 73) show the maximum difference in appearance of the lateral lobes on each side. For example, on the right side of 131217 and 155598 the lobes appear narow (tr.) and rounded, strongly overlapping, but on the left side wider (tr.), and rectangular or falcate in outline. The right side of 40251 is unique in that there are no steps in level at the boundaries between adjacent lobes, possibly because the lobes were pressed together during burial without sediment penetrating between them. In explanation of these varied appearances after compression, I consider that each lobe was thin and flexible, so that a rounded lobe could be wrinkled parallel to the distal margin, or crushed in an exsagittal direction to give a lanceolate form. Lobes of opposite sides were also apparently matted together (figure 4). Further, each lobe did not project out so that a horizontal line along the external surface was parallel to the exsagittal line, but must have been turned inward to permit overlap and give space for the gill. This position is suggested in the restoration (figure 82*a*) by the inward and forwardly inclined margins of the gill lamellae. The amount of this inclination may have varied along the length. This variation, combined with the variation in width (tr., maximum at lobe 8), and length (exs., greatest posteriorly) of lobes along the trunk, may explain the slight radial appearance after compression. The junction between axial region of the trunk and lateral lobe is not clearly defined, the one passing into the other. In many examples the boundary between segments axially passes into the change in level between adjacent lateral lobes, which change becomes more marked distally. Because the most dorsal portion of the axial region projects above the proximal parts of the lobes in lateral compressions (figures 5, 6, plate I; figures 36–39, plate VII) it is considered that the lobes arose from the lateral margin of the axial region (figure 82*a*, *e*). Fifteen segments with lateral appendages and a posterior region of the trunk were recognized by Hutchinson (1930, p. 5) though he considered the fifteenth appendage to be what is here called the first right fan blade. Walcott (1912, p. 167) had earlier claimed 16 segments, counting the part of the posterior region in front of the first blade in 57683 (figure 4) as a sixteenth segment. Without reference to any specimen as evidence Simonetta (1970, p. 40) claimed 14 segments. It appears from the present study that most specimens show 15 segments with lateral lobes in the main portion of the trunk. The evidence for the fifteenth pair cannot be seen clearly in 5809 (figure 64) because of poor preservation, and in 40251 (figure 73) because of flexure, but all other specimens appear to show it.

As discussed in § 3 (*a*), dorsoventral compressions show the structure of the supposed gills and how they alternate in position with the lateral lobes. Unique evidence on the structure of the gills is preserved in 40251 (figure 74), where the basal sheet has been traced in the axial region. Figure 84 shows my interpretation of the structure as longitudinally arranged, narrow, imbricating lamellae projecting from a basal sheet. During burial, penetration by sediment between each lamella, and between basal sheet and lateral lobe, is held to account for the mode of preservation. The rock layer intervening between lateral lobe and gill diminishes in thickness proximally and the two structures merge, hence it is believed that the gill arose from the outer, proximal surface of the lateral lobe. No gill is present on the first pair of lateral lobes, and the gills appear to have lain between the overlapping portions of adjacent appendages. The forward curvature displayed by the anterior gills in 57684 (figure 12) and 205258 (figure 44) is held to attest to the thinness and flexibility of these structures. In this latter specimen, and 5809 (figure 64), where the lateral edge of the gill is preserved, the rounded ends of successive lamellae are revealed. In 5809, and the left side of 40251 (figure 73), a transverse subdivision of the lateral lobe is evident, into a faintly convex and faintly concave portion. The concavity is believed to result from compaction of gill and lateral lobe one upon another. In § 3 (*a*) I have discussed possible explanations of why there is little sign of the gill structure in lateral and oblique-lateral compressions. These explanations are incomplete, and do not show satisfactorily why the lamellate part of the gills should be well preserved only in dorsoventral compressions.

Walcott (1912, p. 168, Pl. 27, fig. 6) recognized the lateral lobes in 57683, but regarded them as legs, showing two or three basal joints and a lobe-like distal joint. I agree with Hutchinson (1930, p. 5) in seeing no trace of such joints, and in regarding them as unjointed lobes. Raymond (1935, p. 217), Størmer (1944, p. 92) and Simonetta (1970, p. 40) have called these appendages pleural lobes, Sharov (1965, p. 964; 1966, p. 28) using the term lateral plate or paratergal lobe. All have agreed they are unjointed, but the relative size and variation in outline of the series had not been investigated. I differ from all previous authors in my interpretation of the gill – of the shape and form, and that it originated from the axial region dorsally to the lateral lobe (figure 84). The evidence of 40251 (figure 74; figure 75, plate XV) is critical in this latter respect. Dorsoventral compressions such as 57684 (figures 12, 13), 205258 (figure 44; figures 45–51, plate IX), and 5809 (figures 60–63, plate XII; figure 64) show the overlapping relation between gills and lobes, and the form of the gill. The lamellate structure is shown by 57684 (figures 13, 14; figures 15, 16, plate III) and 40251 (figure 67, plate XIII; figure 80, plate XVI). Walcott (1912, p. 168) and Hutchinson (1930, p. 5) interpreted the gill lamellae of 57684 as setae, in Hutchinson's view setae attached to the internal edge of the lateral lobe. Hutchinson took this view because he thought the counterpart of 57684 (Hutchinson, 1930, Fig. 2*b*, portrayed present gill 8 and the adjacent area, compare figure 13 and figure 15, plate III) showed the animal in dorsal view, the lateral lobes having been broken off to expose the 'setae' below. To regard the original of figure 15, plate III (and figure 11, plate II) as showing the animal in dorsal aspect implies that the eyes were on the ventral side of the cephalon and the frontal process arose from the dorsal side, views incompatible with 57683 (figures 5–7, plate I) and other specimens. Raymond (1935, pp. 217–218) also considered the original of figure 15, plate III, as showing the animal in dorsal aspect, and went on to assume that most of a supposed 'test' is broken off to reveal underlying appendages. He then compared these appendages to the gill branch of the appendage of the trilobite *Olenoides serratus*. Such an interpretation compounds errors, and cannot be reconciled with this or other specimens of *Opabinia regalis*. My recent re-investigation of the appendages of the trilobite *Olenoides serratus* (Whittington 1975) shows no similarities between the gill branch and structures seen in *Opabinia regalis*. The more recent accounts of

O. regalis by Størmer (1944, p. 29, Fig. 19, 10; in Moore 1959, p. O32, Fig. 22) are erroneous since they are based on an acceptance of Raymond's views. Sharov (1965, pp. 964–965, Fig. 2*v*; 1966, p. 28, Fig. 16*c*) produced new variations on this theme, giving *O. regalis* a many-jointed limb bearing gill filaments, attached to the body below the base of the 'paratergal' lobe. Simonetta (1970, p. 40, Pl. II, Figs 2*a*, *b*, *c*,) has restored *Opabinia* as an arthropod, the trunk having narrow (tr.), outward and downwardly directed 'pleural lobes', and biramous appendages. The latter are portrayed as having a spinose basal joint, the inner branch being a seven-jointed leg, the outer a lobate branch bearing lamellae. No evidence from particular specimens is offered, and I fail to see the justification for what is a fanciful restoration, particularly since no specimen I have studied shows evidence of a jointed leg branch.

The axial region of the posterior portion of the trunk appears to have been cylindrical in form, not divided into segments, the alimentary canal ventral. The tip is not well preserved in any specimen, and the outline varies. A spine may be present at one edge, and it is assumed in figure 82*a*, *e*, that there may have been a pair of spines at the margins on the dorsal side. The manner in which the three pairs of blades of the tail fan are preserved (§(3*a*)) appears to account for the variation in form shown by different specimens. The structure is best demonstrated in 205259 (figure 55; figures 56–58, plate XI), and the overlap between blades, opposite in sense to that of lateral lobes, shown by 131217 (figure 24; figures 25, 27, plate V). These considerations have suggested the attitude of the blades adopted in the restoration (figure 82*a*, *d*, *e*,), and imply that the blades were thin, flexible and readily crushed. Such flexibility may have made possible a reversal of original overlap relations during burial, and so account for some difficulties in interpretation, for example of 155600 (figure 2 and §4(*h*)). The dark stain faintly visible at the posterior tip of some specimens (figures 34, 35, 55) may result from extrusion of body contents at some stage of preservation, and is like that seen in other Burgess Shale fossils (Whittington 1971*b*, p. 16; 1974, p. 13).

Walcott (1912, p. 169) refers to caudal appendages only in the supposed female, and he may have been referring to 131217 or 155598. Hutchinson (1930, pp. 6–7) recognized a tail fan, but not that there were three blades and that they were dorsally directed. Simonetta (1970, p. 40, Pl. II, figs 2*a*, *b*) considered that a caudal fan was formed by an enlarged outer, lamellate branch of the last segment in front of the posterior region. The blades recognized here are not lamellate, and such specimens as 131217 (figures 25–28, plate V) and 205259 (figures 56–58, plate XI) show that they are distinct and different structures from the lateral appendages of the fifteenth segment.

(*c*) *Mode of life*

The mode of burial of Burgess Shale fossils suggested in § 3 (*b*) implies that the animals were benthonic in habit, otherwise they were unlikely to be trapped by suspended sediment moving along the sea bottom. The nature and position of the compound eyes of *Opabinia regalis* indicates that they were well adapted to detect changes in intensity of light, and thus movements, in waters beside and above a benthonic animal. The frontal process is interpreted as having been muscular, adapted to exploring the sediment for food, trapping it, and conveying it to the mouth (figure 83; cf. Walcott 1912, p. 169). No jaw structures are known, so the food was presumably soft. Digestion may have been aided by diverticula of the gut, which extended into the lateral lobes of the trunk. These lateral lobes must have been moderately rigid (wrinkling and variations in outline in the fossils being attributed to post-burial compression), able to support the body on the soft substrate, and an up and down movement would both aerate the gills and propel the animal. It may be assumed that such movements were slow, enabling *Opabinia* to plough shallowly in the surface of the bottom mud as the frontal process explored for food. The eyes and the tail fan would have been just above the surface of the mud, and the blades of the fan may have helped to create currents over the dorsal surface of the body, aiding in aeration of the gills. Flapping movement of the lateral lobes may have also enabled the animal to have moved over the substrate, swimming feebly. If such movements were in the form of a metachronal wave along the body, the swimming powers would have been somewhat stronger, and the tail fan could have been used in steering. The fossils do not suggest more than a limited flexibility of the trunk, so that swimming by a body wave does not seem to have been possible.

(*d*) *Affinities*

Walcott (1912, pp. 154, 167–9) concluded that *Opabinia* was a branchiopod crustacean, belonging to the order Anostraca. He compared it to the Recent *Thamnocephalus* Packard (1883, pp. 352-355, fig. 23, Pl. 14, figs 1–7), an anostracan which has remarkable branched, biramous frontal appendages. The resemblance is superficial. Hutchinson (1930, pp. 7–12) accepted Walcott's ordinal classification, but recognized the peculiar characters of *Opabinia* by placing it in a separate sub-order. His comparison of *Opabinia* with the Carboniferous fossil *Rochdalia* is no longer useful, since Rolfe (1967) has shown *Rochdalia* to be an insect nymph. The view that *Opabinia* may be an anostracan has been referred to by Fedotov (1925, p. 389), Richter (1932, p. 855), Lindner (1946, pp. 25–26) and Tiegs & Manton (1958, p. 294; their figure 6*e* of *Opabinia* is from Hutchinson 1930, and not as stated from Størmer 1944). Raymond (1935, pp. 217–218, 226) placed *Opabinia* in a separate order ancestral to Anostraca, and interpreted the specimen as showing pleural lobes and having beneath these lobes an appendage like that of the outer branch of the appendage of the trilobite *Olenoides serratus*. In § 5 (*b*) I have shown why I cannot accept this view of the gill structures, but its acceptance by Størmer (1944, pp. 93, 135; 1949, in Grassé, pp. 205–206; in Moore 1959, p. O 32) led him to place *Opabinia* in his Trilobitomorpha, animals showing longitudinal trilobation, possessing antennae, and having a jointed walking leg with a lateral gill branch attached at the base. With differing emphasis on sub-groupings, these views have been followed by Dechaseaux (in Piveteau 1953, pp. 39–40) and Novojilov (in Orlov 1960, p. 197). Regrettably, more recent considerations of *Opabinia* have strayed into fantasy. Sharov (1965, pp. 964–965, Figs 2, 10; 1966, pp. 26–28, Figs 16, 84), relying on published accounts, considered the frontal process to be an eversible proboscis, and gave the animal an aboral complex on the dorsal surface of the head, and on the trunk many-segmented appendages bearing filaments. He placed *Opabinia* in a new class within his new superclass of Proboscifera, which embraces the 'most primitive living arthropods'. Other aspects of his claims for the Proboscifera have been heavily criticized (Manton 1967, and references), and the present study offers no support for his views on the morphology of *Opabinia*. Simonetta (1970, p. 40, Pl. II, figs 2*a*, *b*, *c*; Pl. IV, figs 7*a*, *b*; Pl. V, figs 2–5) has restudied the Walcott collection, but his illustrations and description of the specimens are unsatisfactory, and his restoration embodies features for which I find no evidence. These features include the supposed antennae and jaws, the single pair of sessile eyes, the nature of the supposed biramous appendages, and the structure of the caudal fan.

Opabinia is shown here to have been an animal having a head region on which were 5 eyes and a feeding organ, and a segmented trunk bearing serially repeated appendages and a differentiated posterior portion, the tail fan. The body was covered by a flexible cuticle, apparently infolded at the margins of segments in the axial region of the trunk. This enigmatic animal thus exhibits features common to arthropods and annelids (cf. Manton, in Florkin & Scheer 1970, pp. 2–3), but cannot be placed in any recognized group of either. The absence of antennae and jointed, trilobite-like limbs exclude it from Trilobitomorpha, and thus from the vaguely defined class Trilobitoidia (Størmer 1959, in Moore, pp. O 28–O 29). The lateral lobes of the main portion of the trunk have the gills dorsal to them, and might be likened to the parapodia of certain polychaetes. If they had borne chaetae, it is difficult to believe they would not have been preserved, as are those in the polychaete *Canadia* from the Burgess Shale (see, for example, Walcott 1931, Pls 4, 5; Pl. 8, fig. 3; Pl. 9, fig. 10). In a synthesis of arthropod phylogeny Manton (1973, p. 128) refers to segmented ancestors of annelids, from which arthropods may have been derived. I suggest that *Opabinia* is neither an arthropod nor an annelid, but may be a representative of such an ancestral group of segmented animals. The Burgess Shale fauna contains other, undescribed segmented animals of uncertain affinities, and a younger representative is *Tullimonstrum* (Johnson & Richardson 1969). This marine, Carboniferous animal was bilaterally symmetrical, segmented, the head bore a frontal process terminating in a jaw-like structure, and the tail region bore lateral fins. The trunk did not bear lateral lobes, the alimentary canal apparently ran the length of the animal from the jaws back, and it possessed the strange, transverse bar organ. Resemblances between *Opabinia* and *Tullimonstrum* may well be superficial, but they remind us how fragmentary is our knowledge of ancient segmented animals which lacked hard parts.

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Plates I-XVI have been printed at the University Press, Oxford.

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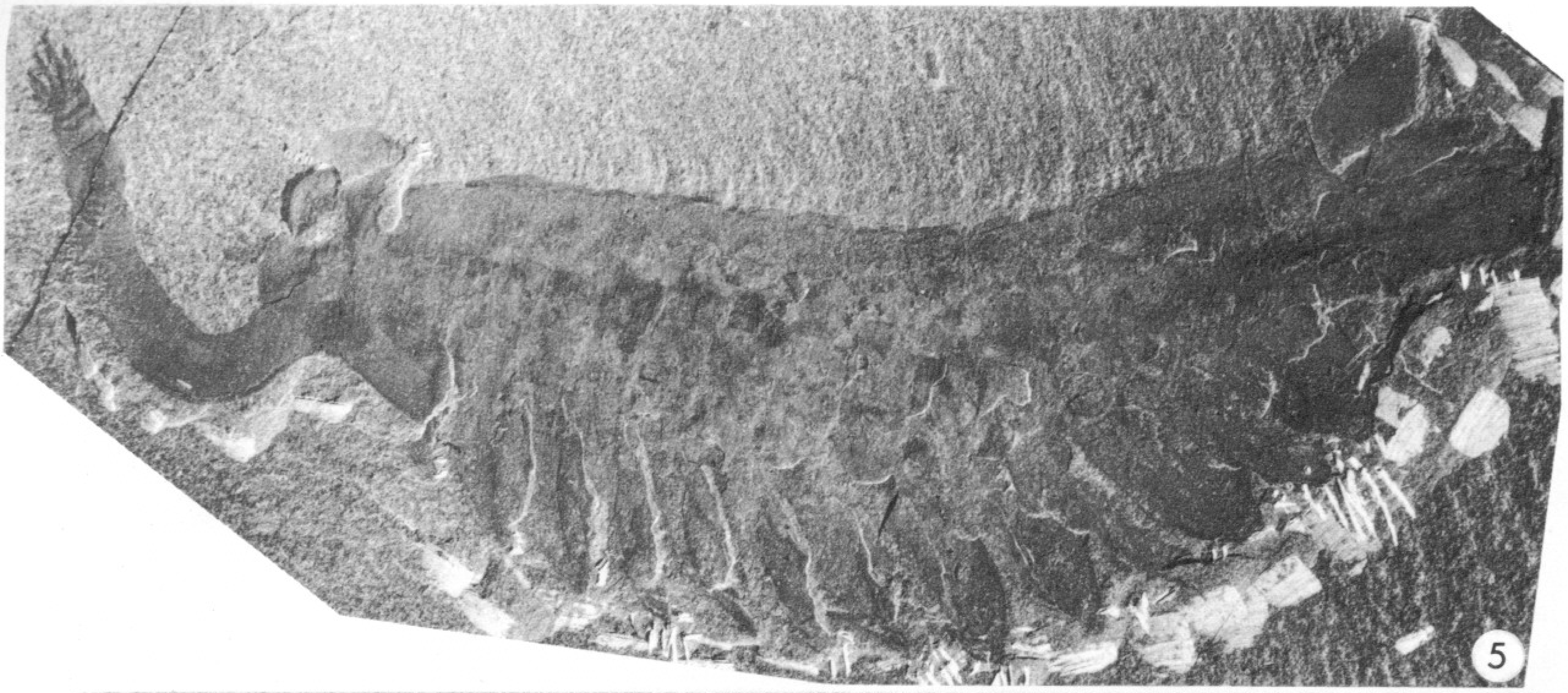
It is regretted that an incorrect volume number is shown at the head of plates I-XVI, which were printed in advance of the text. The correct volume number is 271 not 270.

LIST OF ABBREVIATIONS AND SYMBOLS

A,B,C	parts of other animals or uncertainly related fragments (figure 34)
G.S.C.	Geological Survey of Canada
L	Left, as prefix or to denote orientation of entire figure
R	Right, as prefix or to denote orientation of entire figure
U.S.N.M.	U.S. National Museum (now National Museum of Natural History)
Y.P.M.	Yale University, Peabody Museum of Natural History
ce	cephalon
d	dorsal cuticle
ds	dark stain
exs.	exsagittal, parallel to sagittal (median) line
f	blade of fan of posterior region of trunk
fp	frontal process
g	gill
gr	groove, corresponds to ridge at outer edge of rectangular area (rec)
i	inner eye
l	lateral lobe of main region of trunk
m	median eye
mo	mouth
o	outer eye
r	rim of eye
rec	rectangular area beside alimentary canal
sag.	sagittal (median) line
tr.	transverse, i.e. direction at right angle to sagittal or exsagittal line
v	ventral cuticle
ve	mineral vein in rock
1–*n*	number in series of segments, diverticula, lateral lobes, gills or blades of fan

stipple shows darker-appearing areas on fossil
parallel ruling shows highly reflective area of eye



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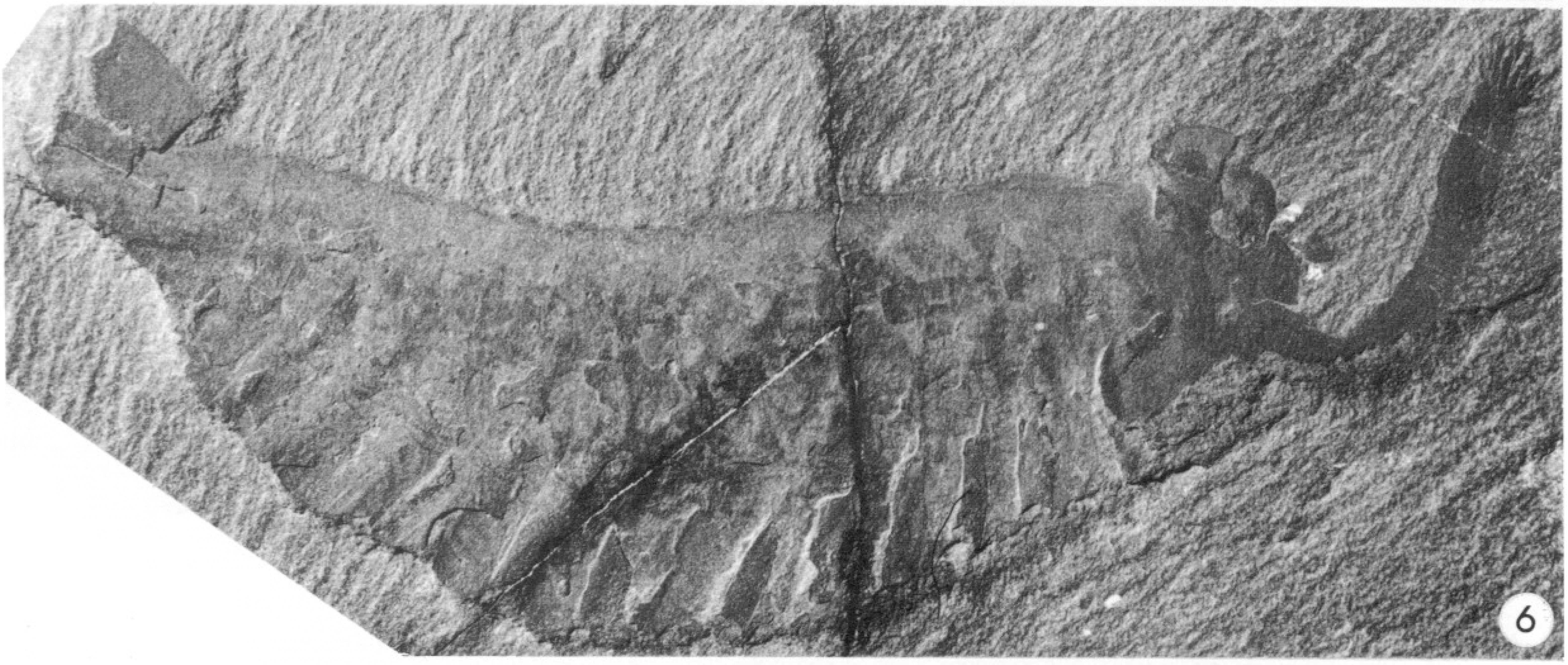

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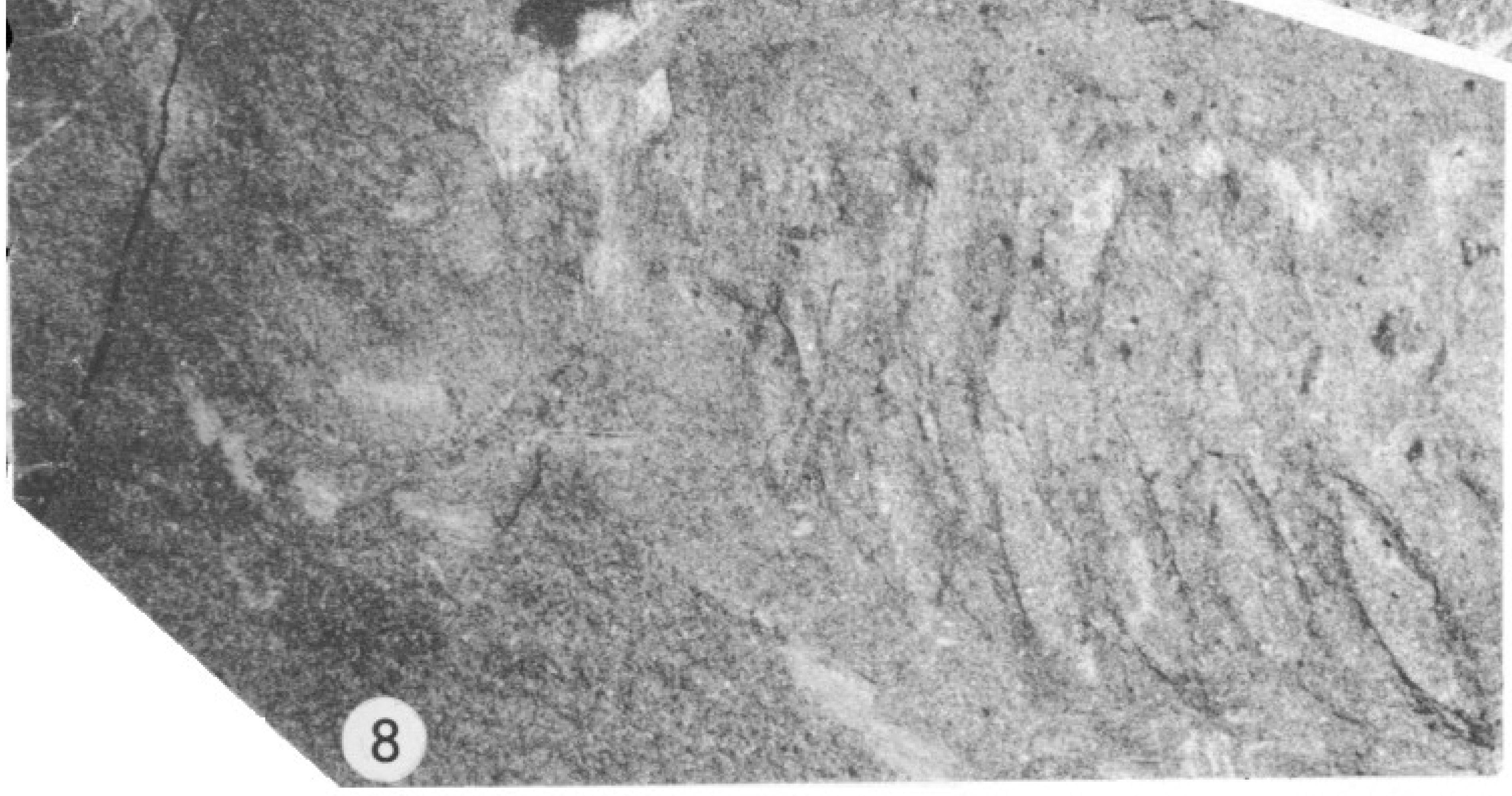
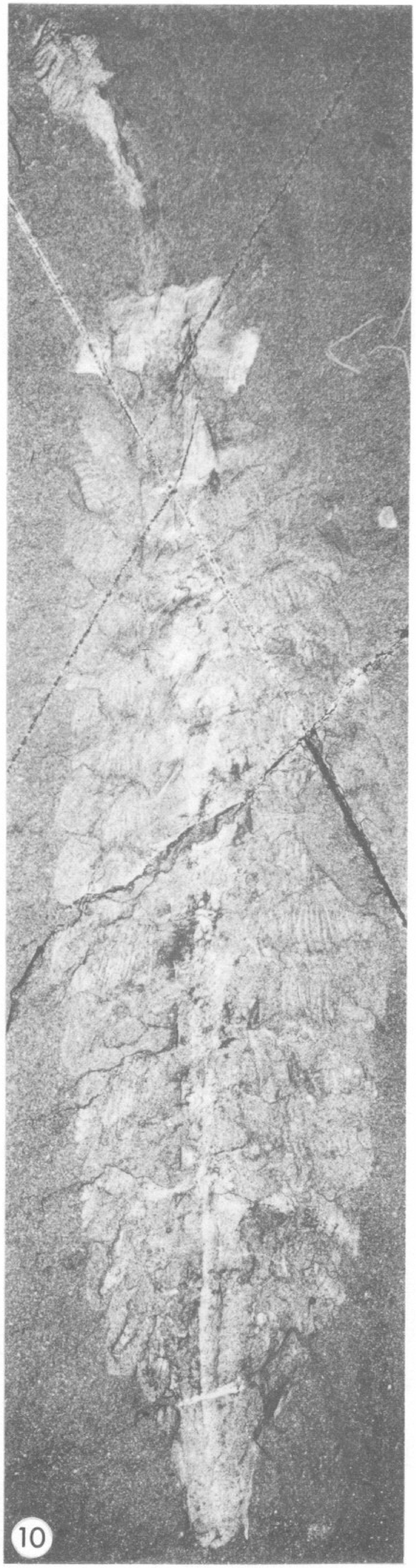


8

FIGURES 5–8. For description see opposite.


9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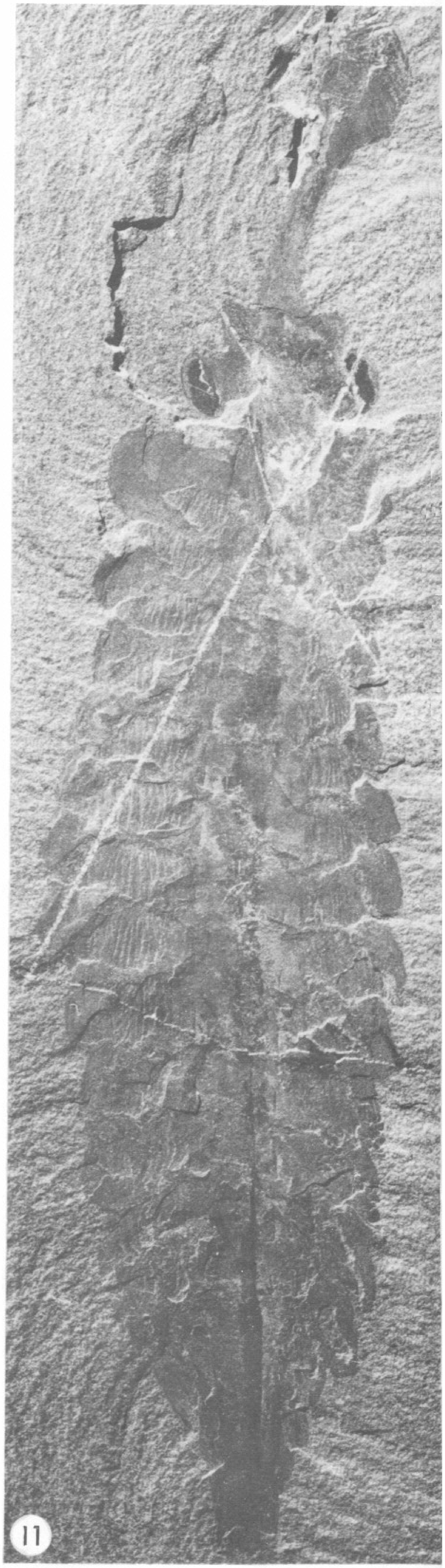
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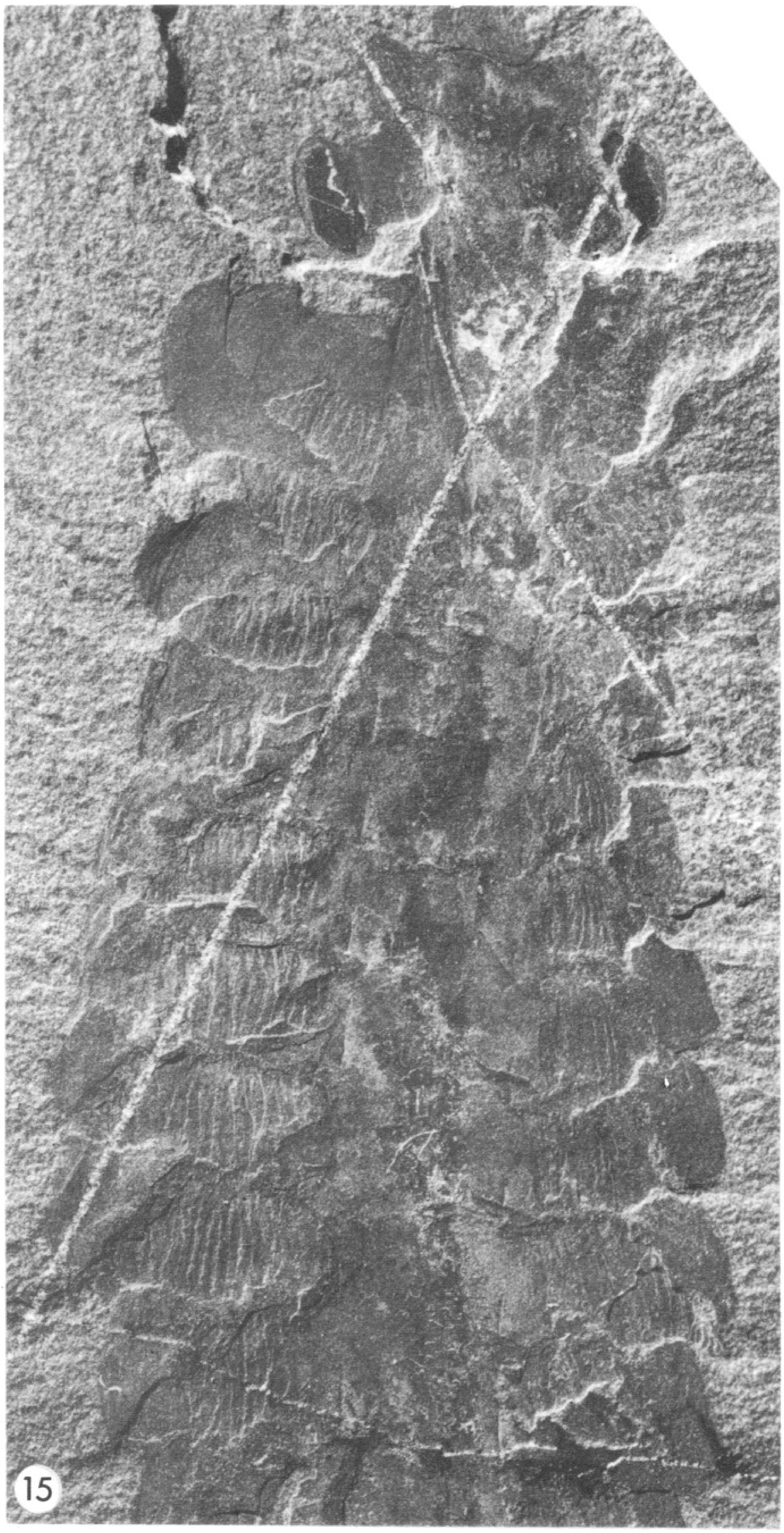
FIGURES 9–11. For description see opposite.



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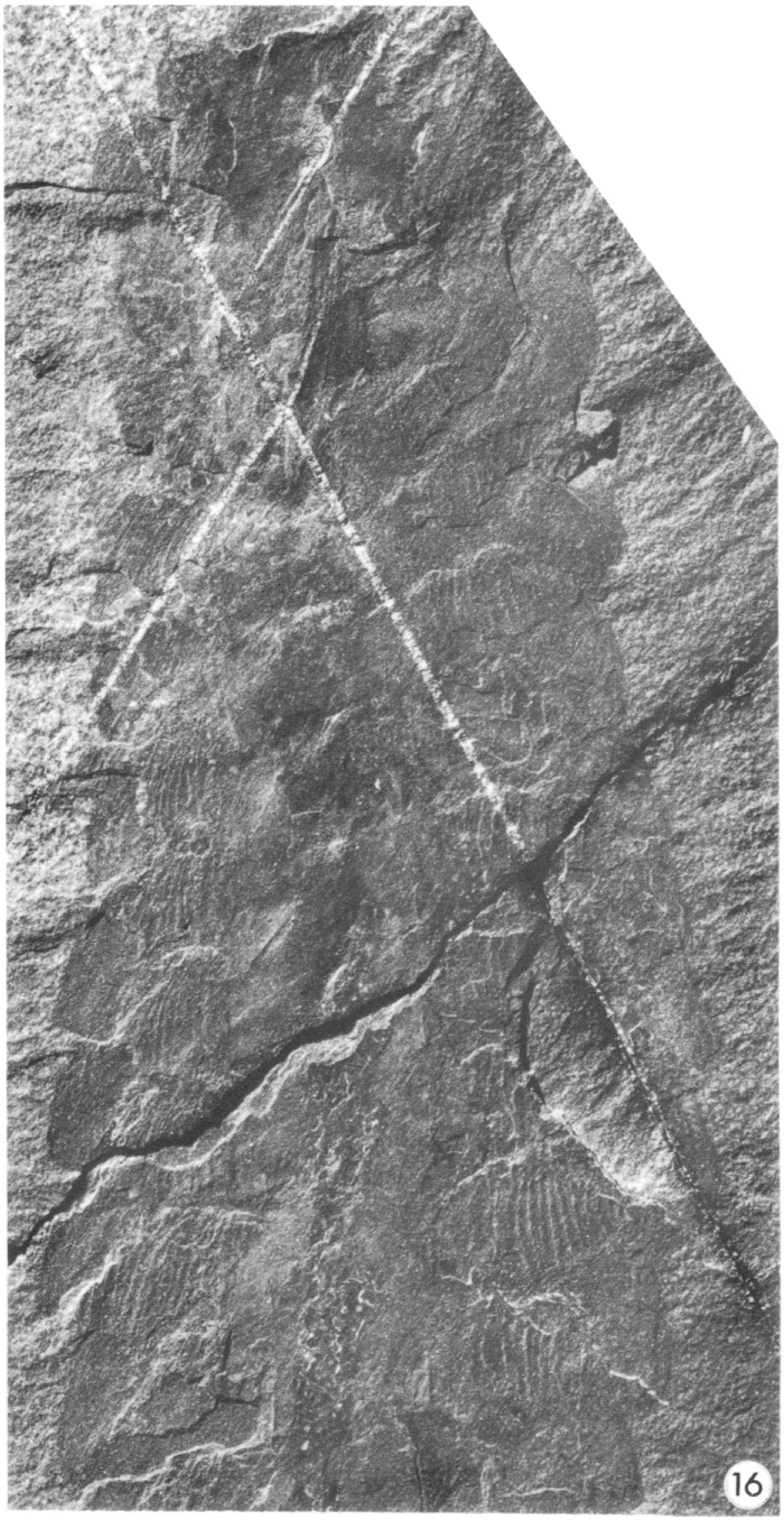

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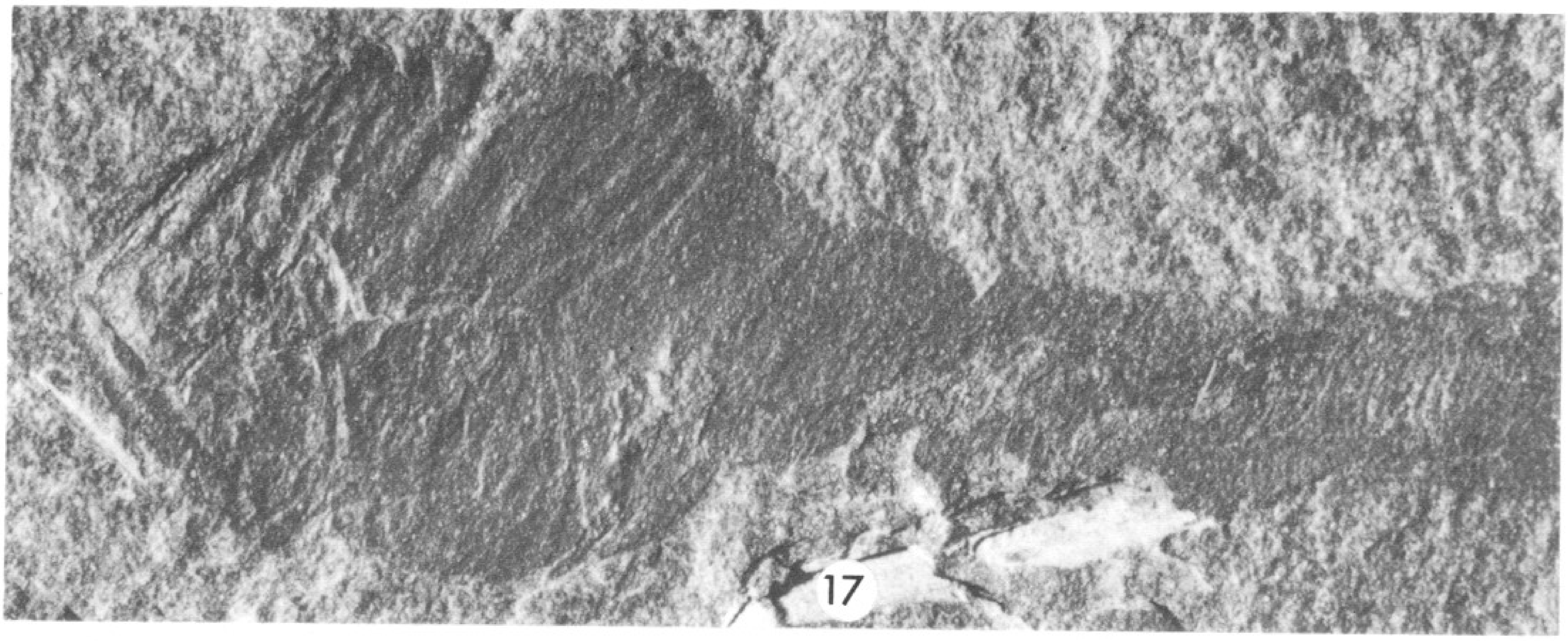
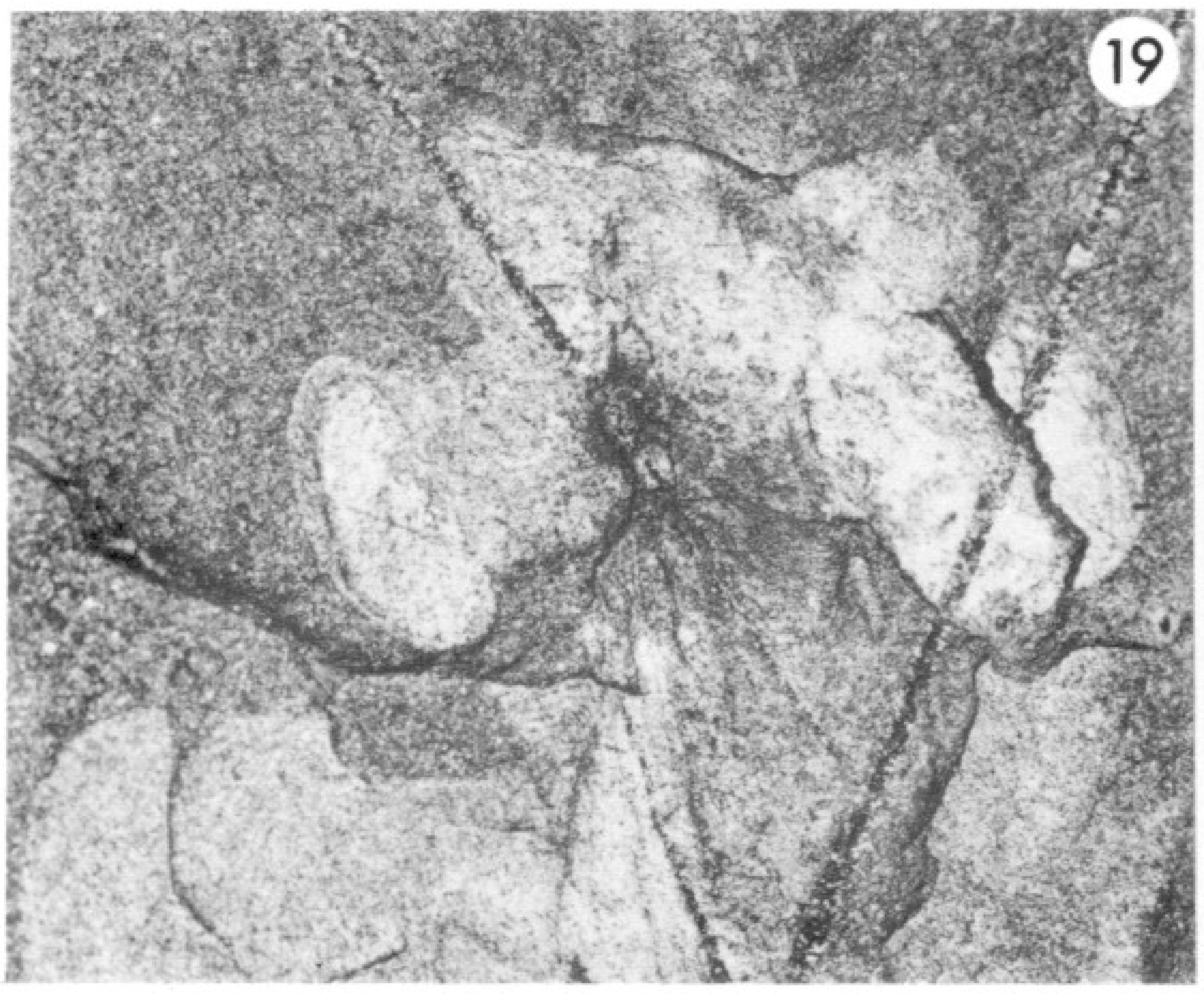
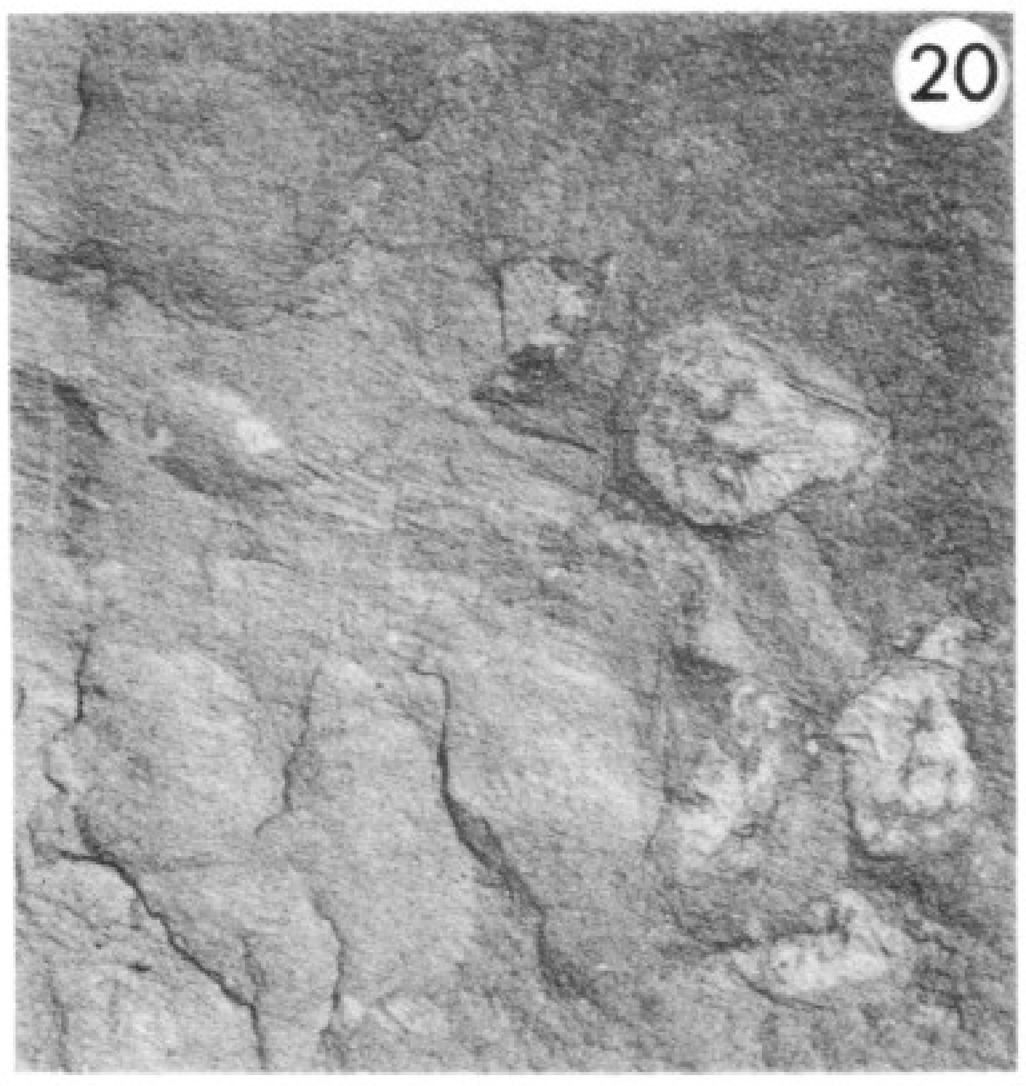
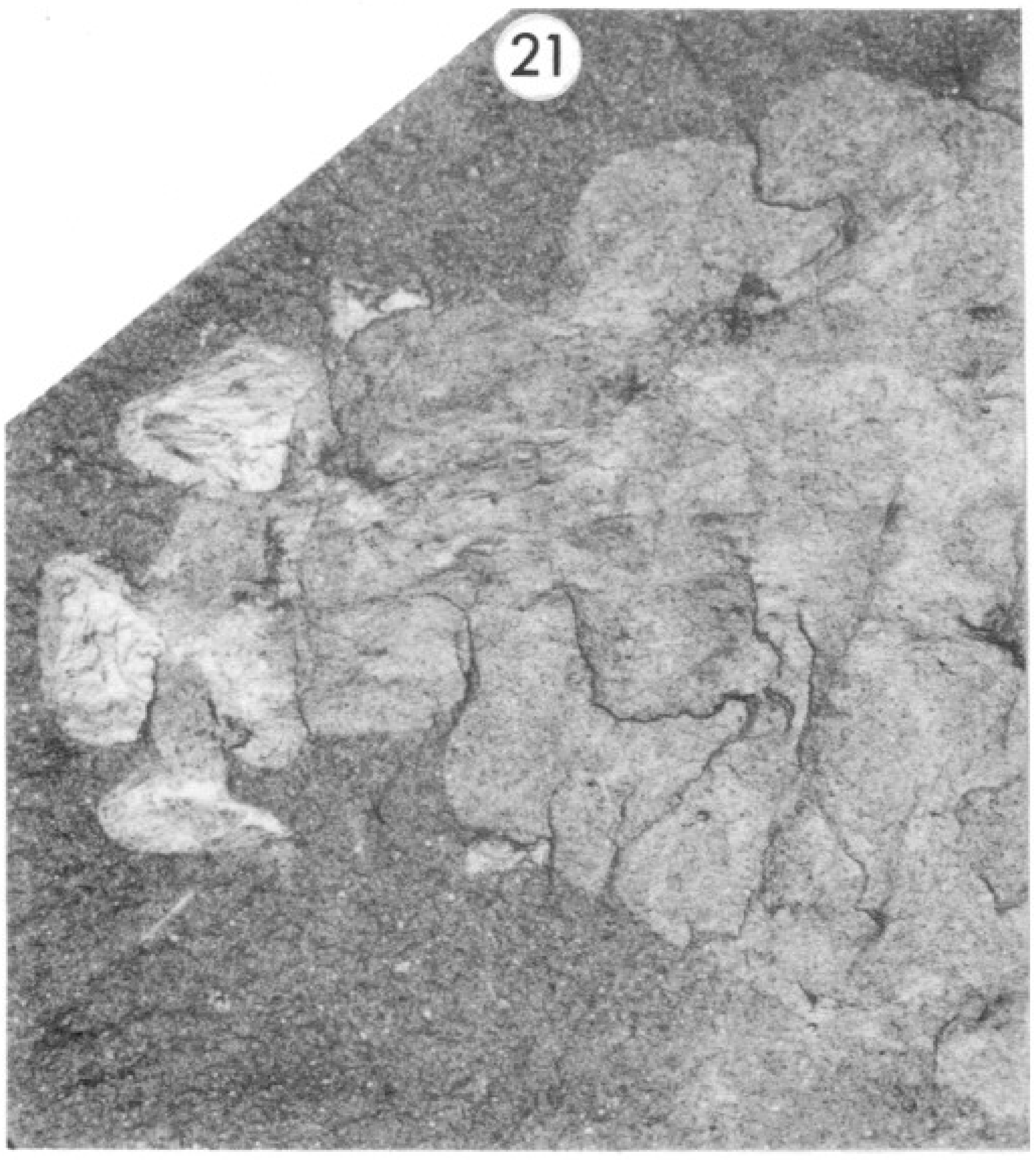


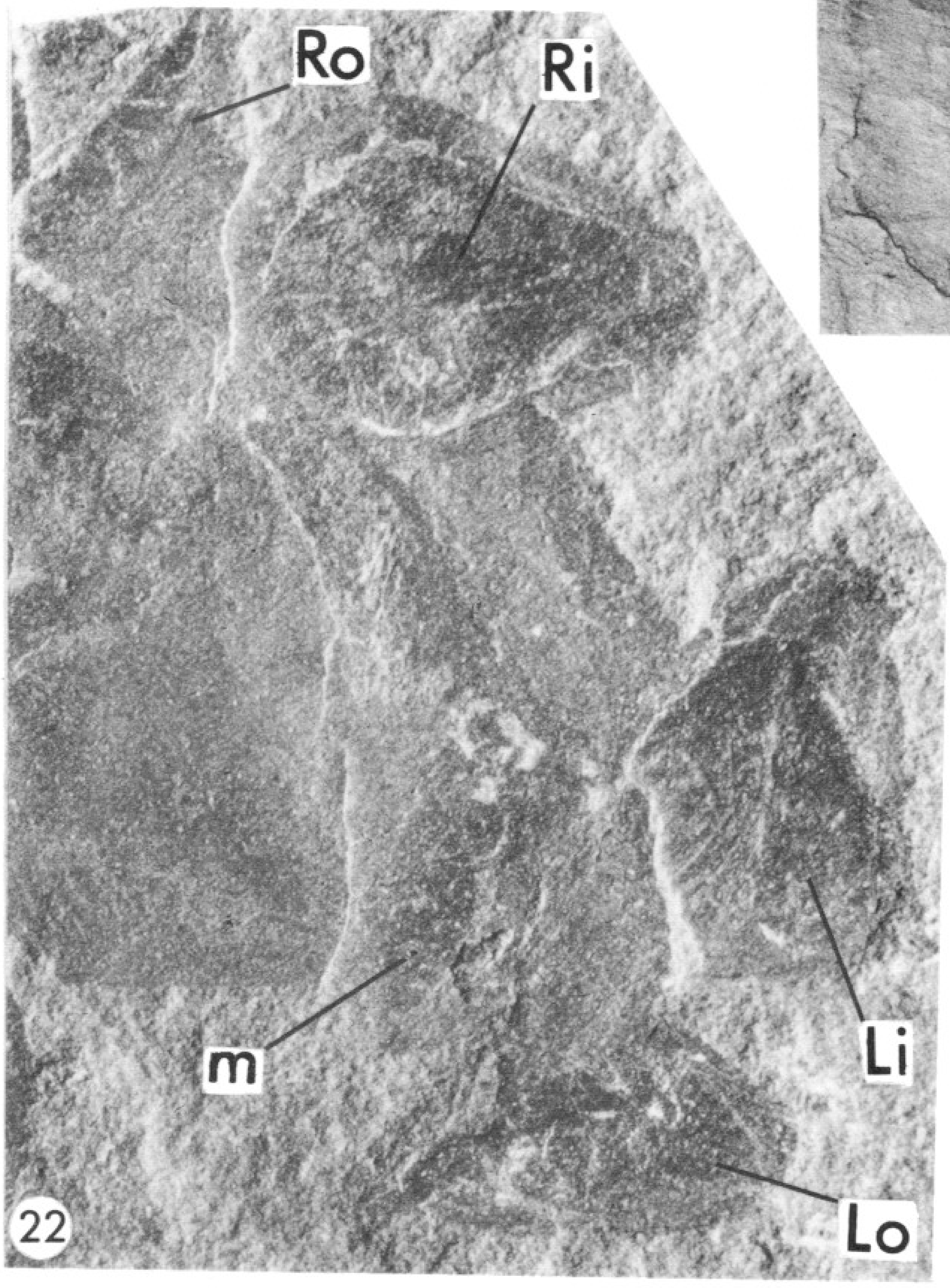
17

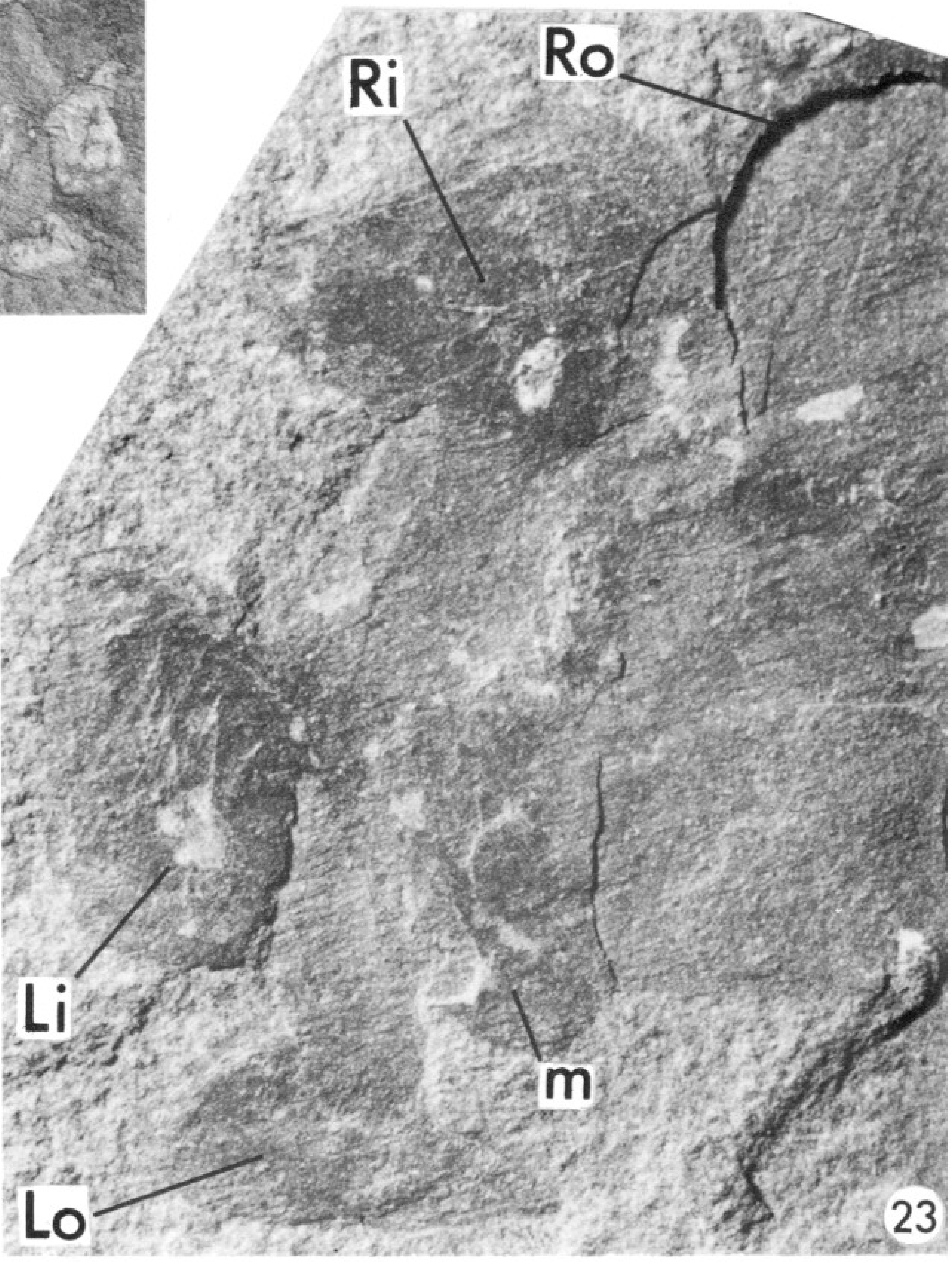
Figures 15–17. For description see opposite.





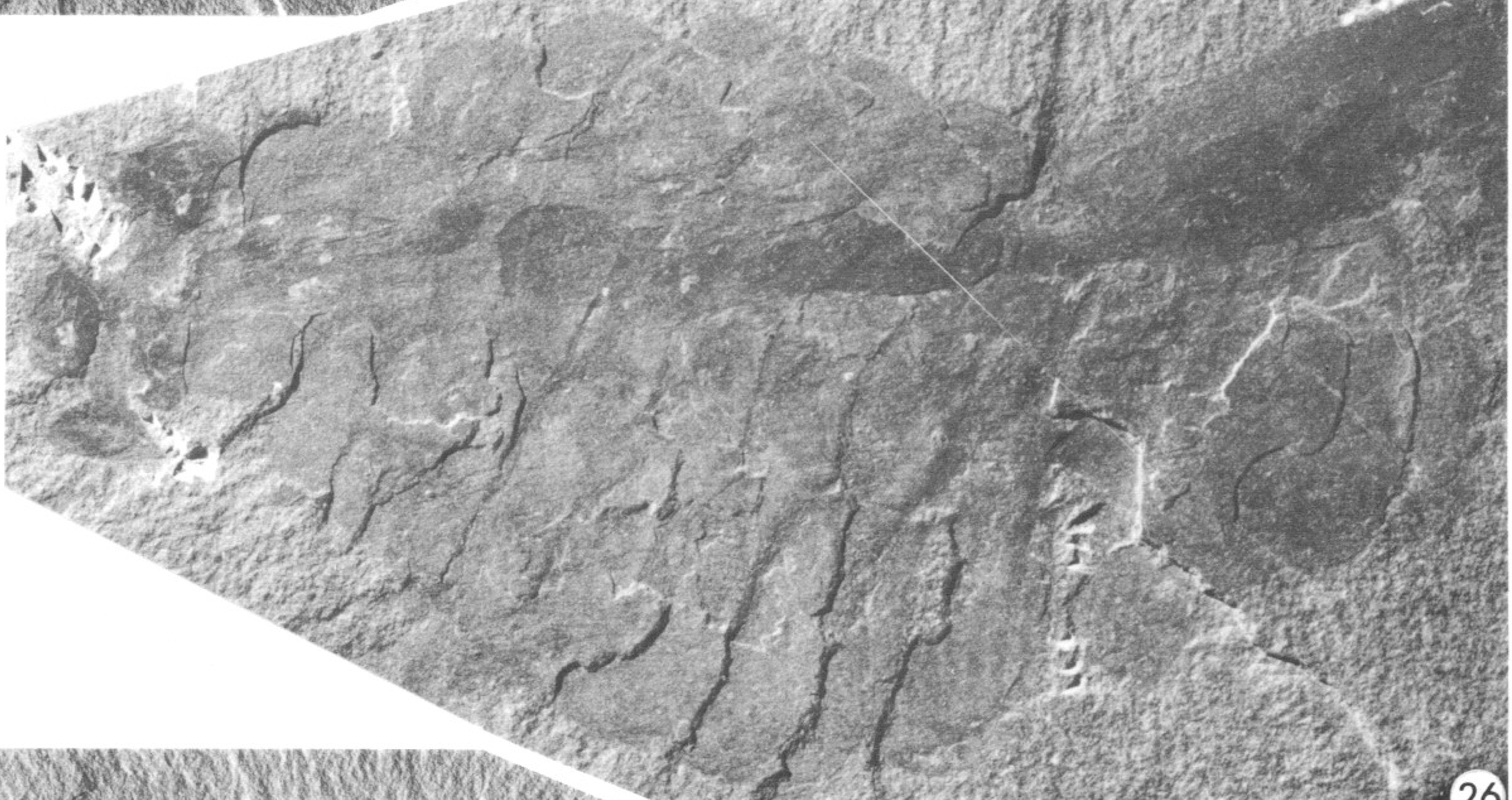






FIGURES 18–23. For description see opposite.


25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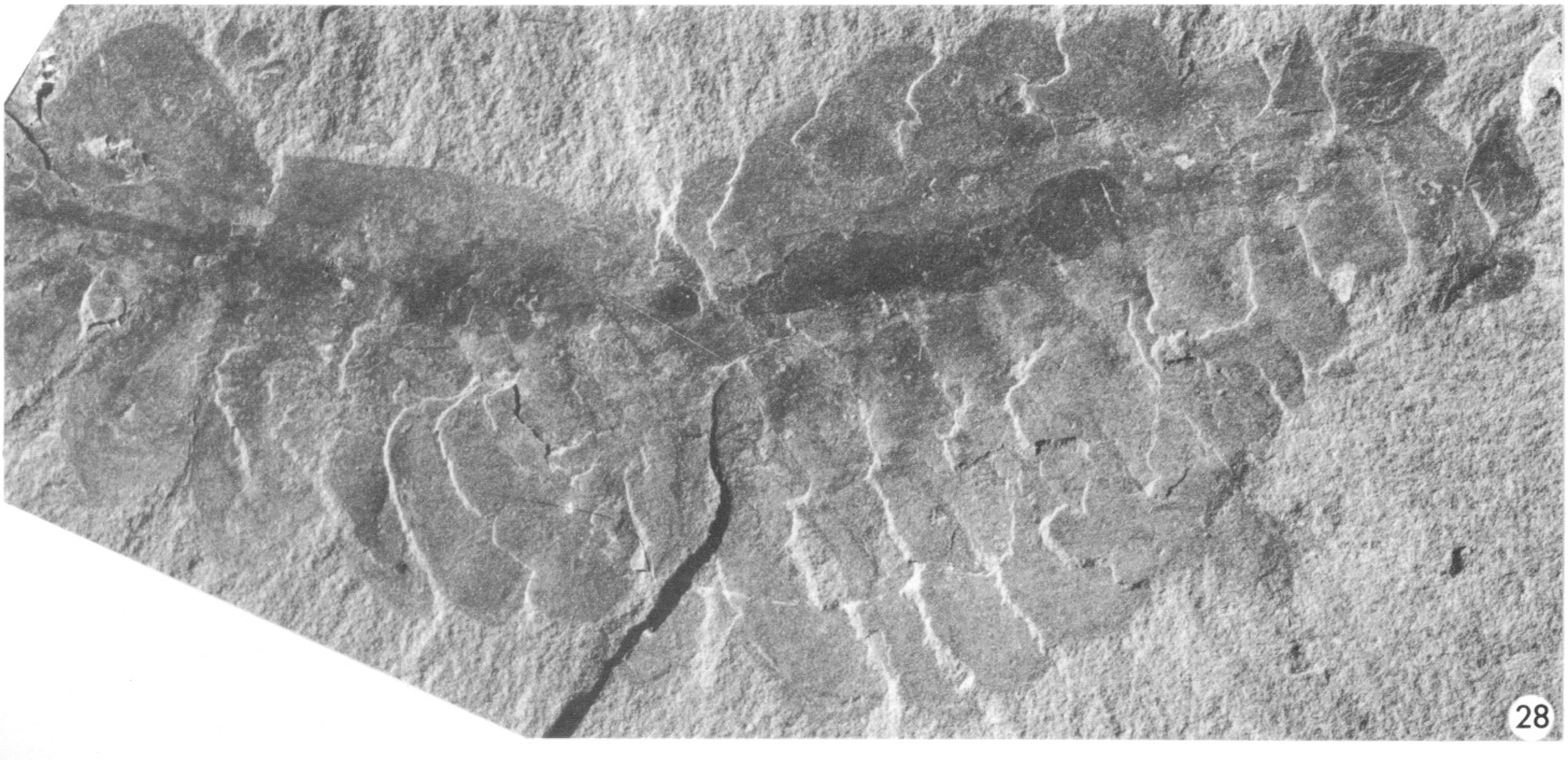
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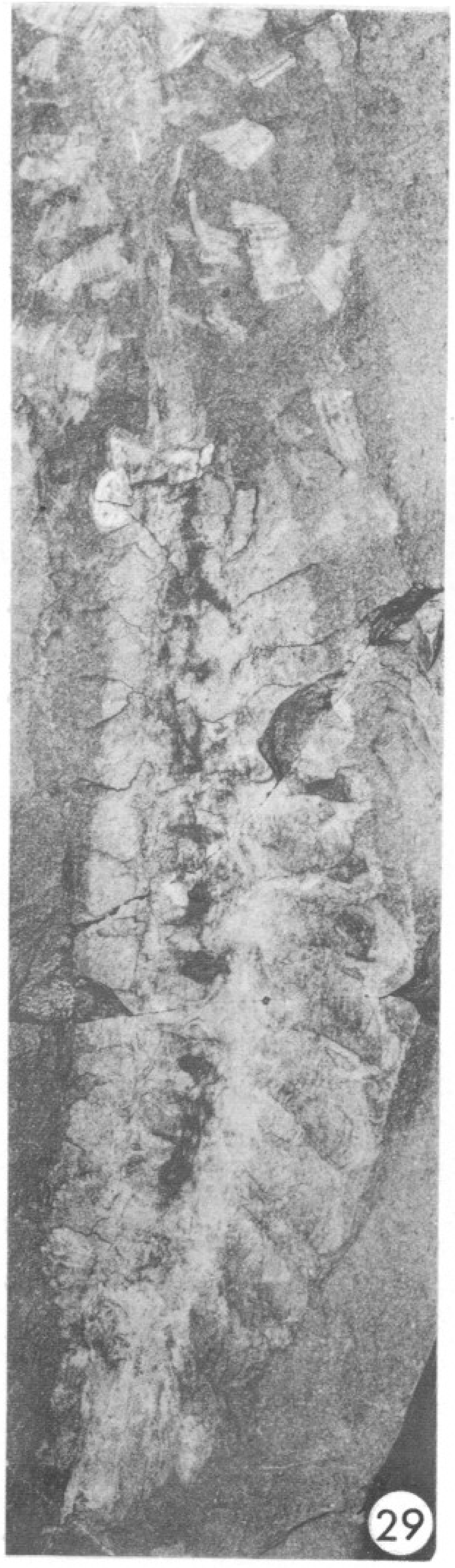
FIGURES 25–28. For description see opposite.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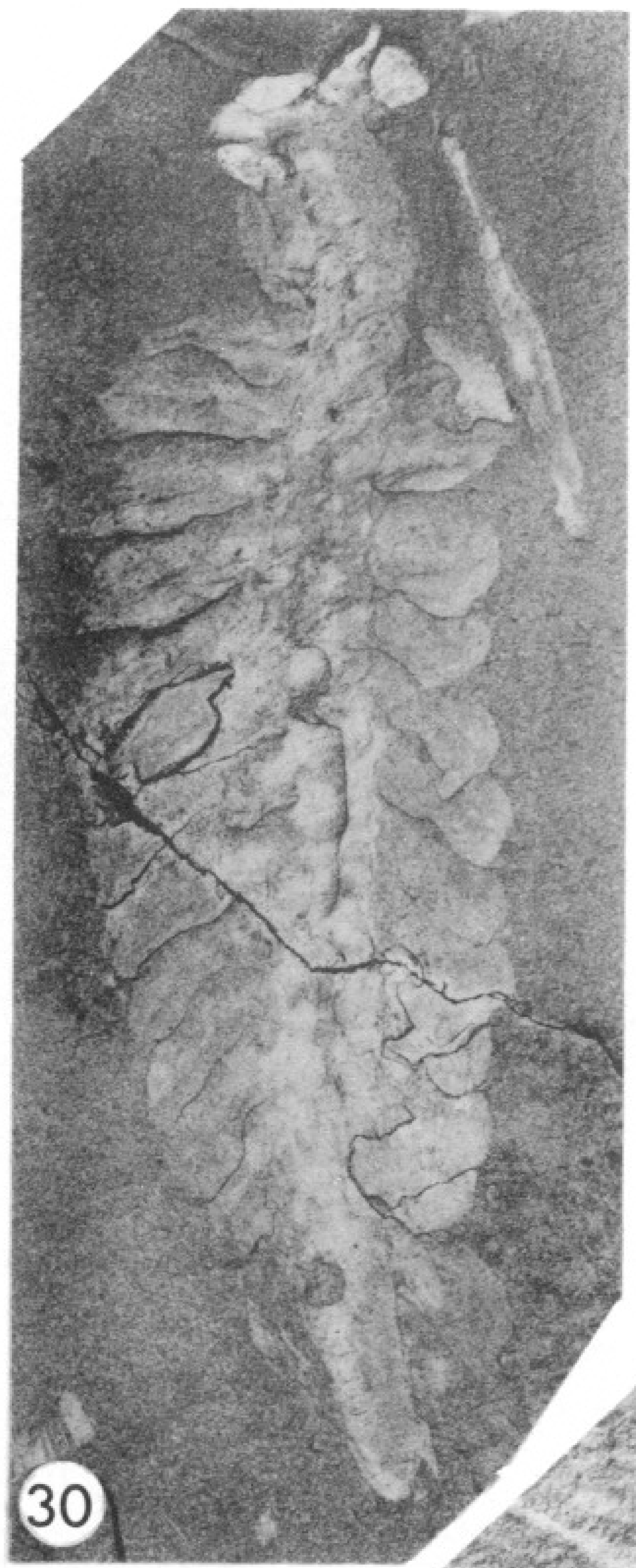
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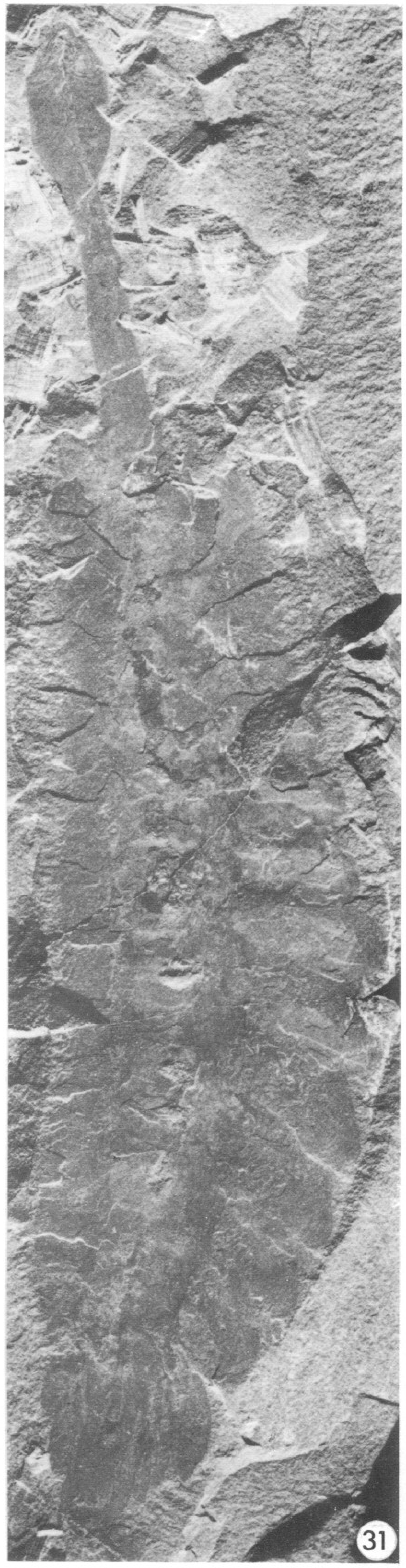
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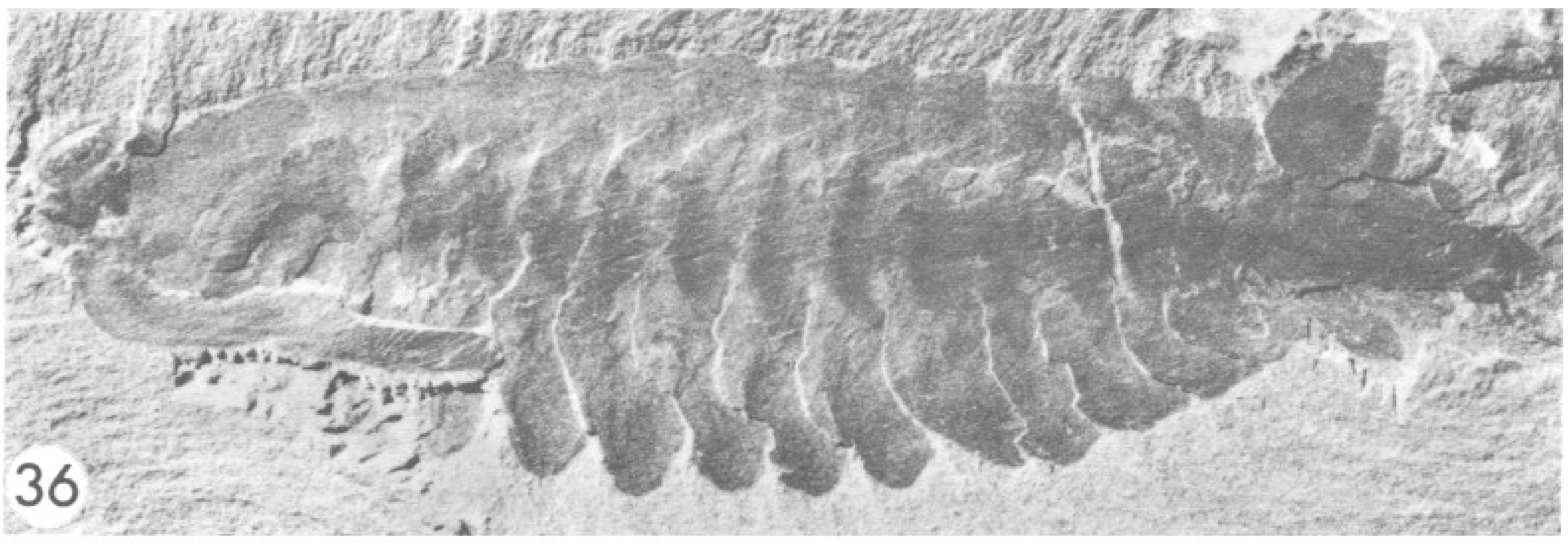
33

FIGURES 29–33. For description see opposite.



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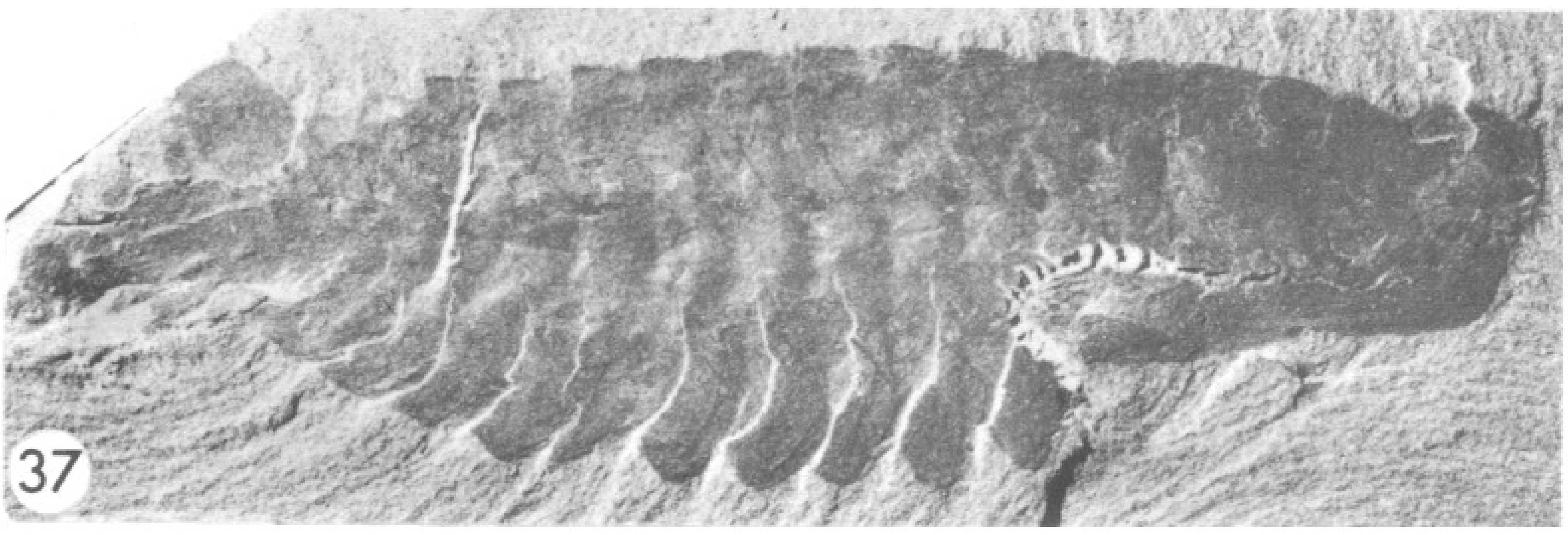

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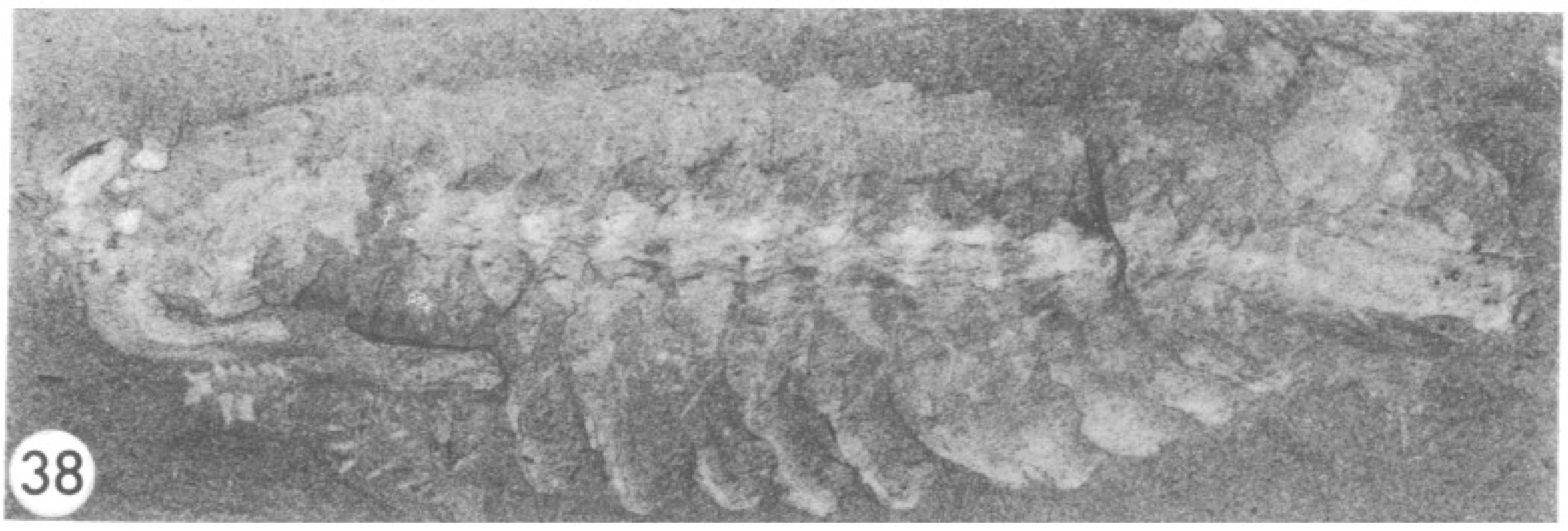

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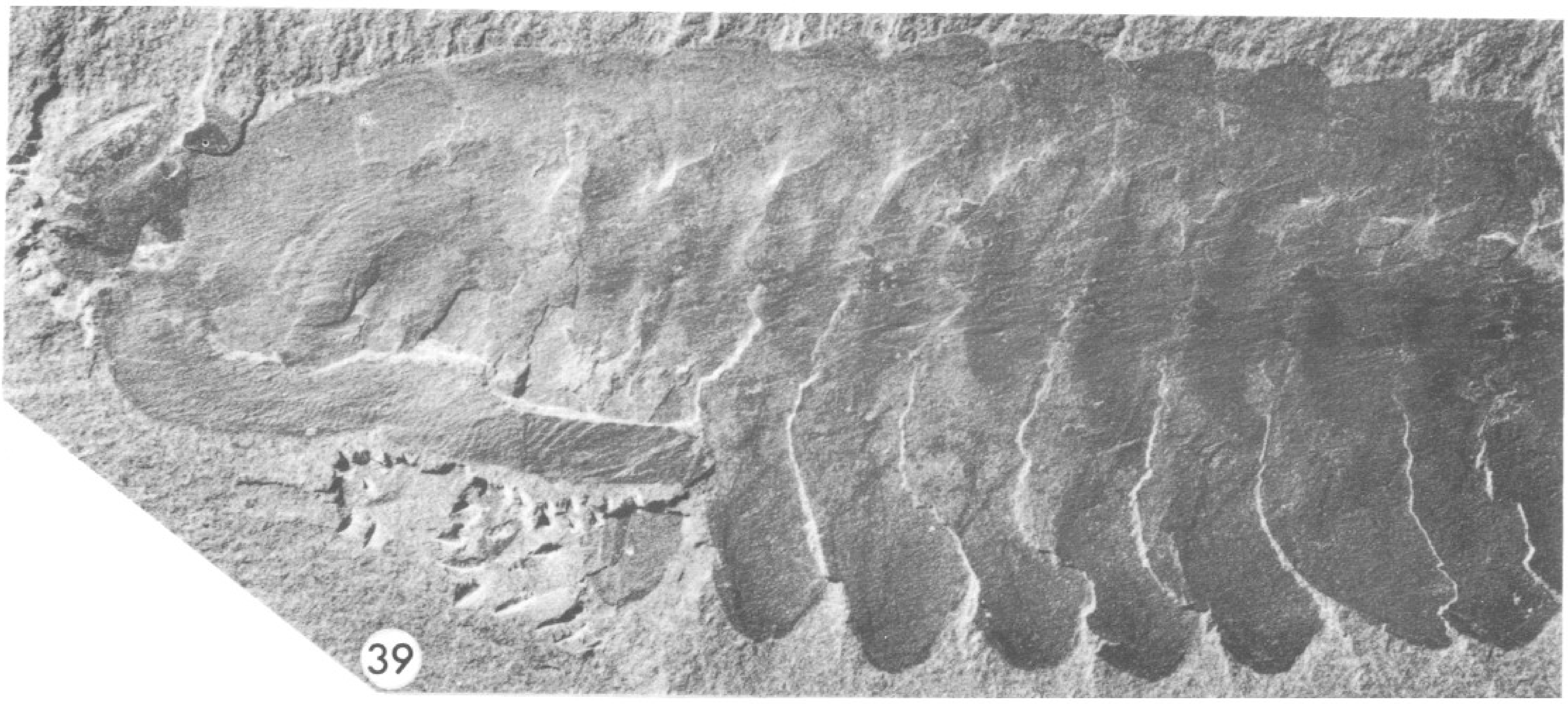

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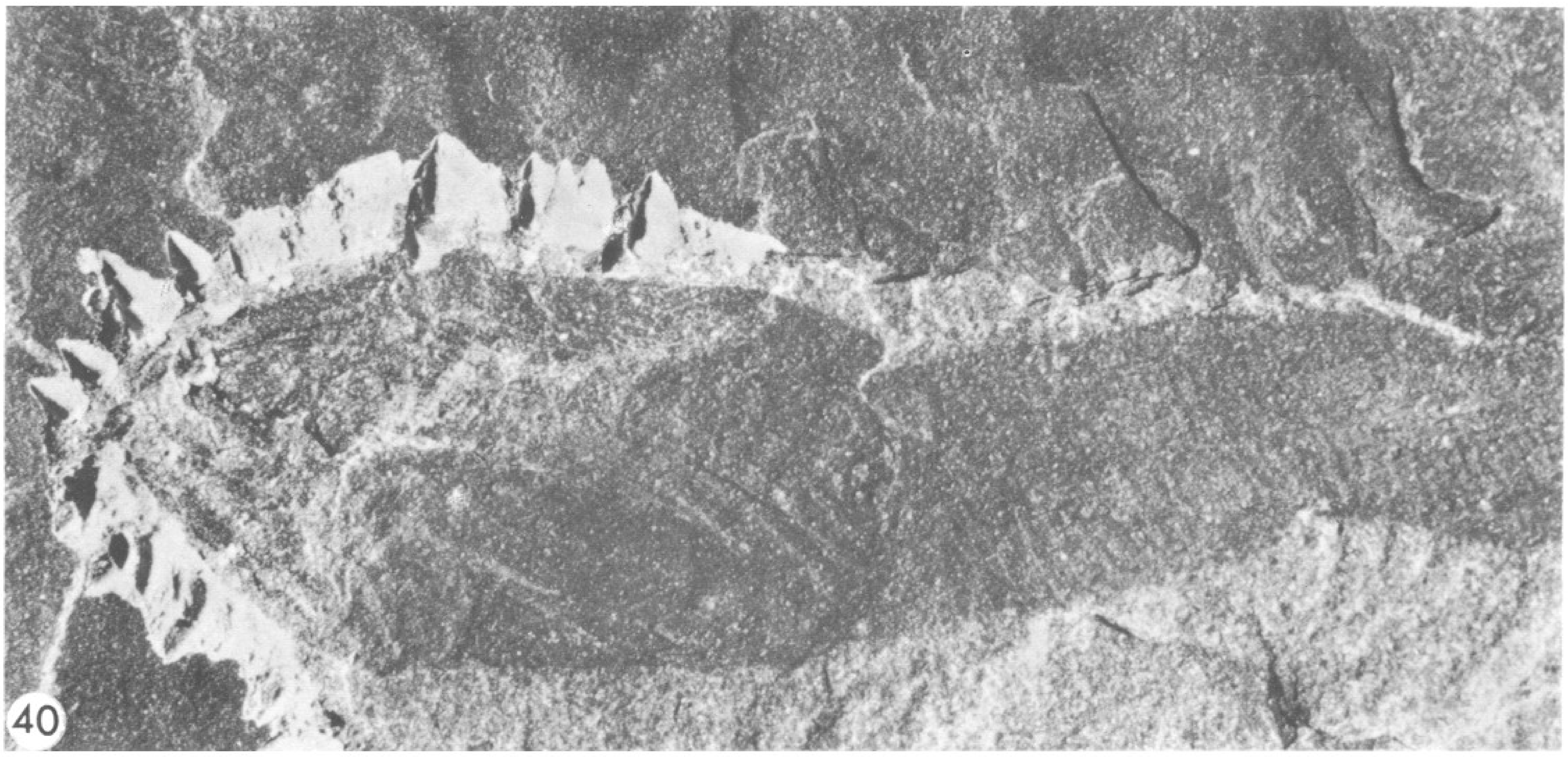


40

FIGURES 36–40. For description see opposite.

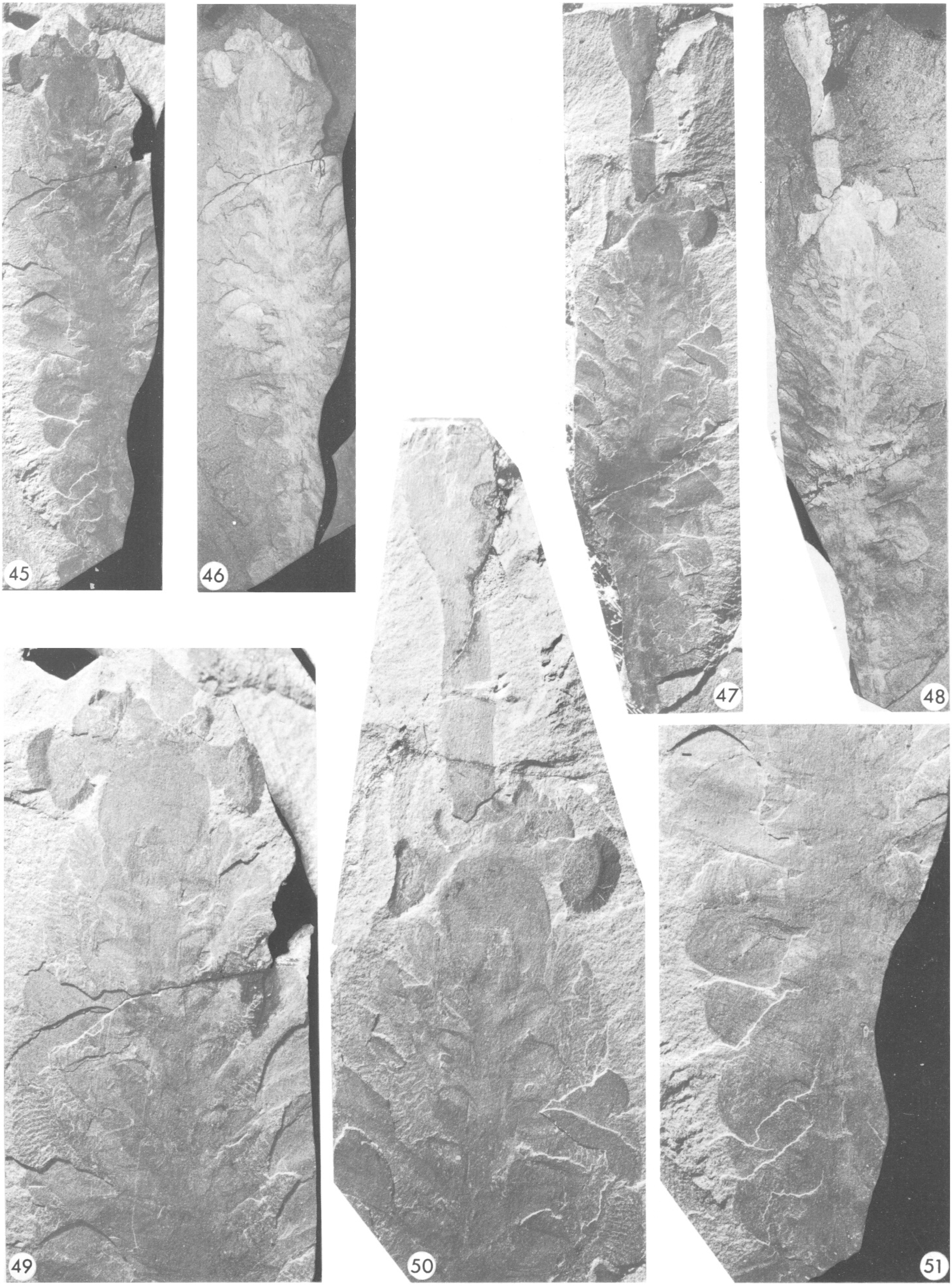

41


42

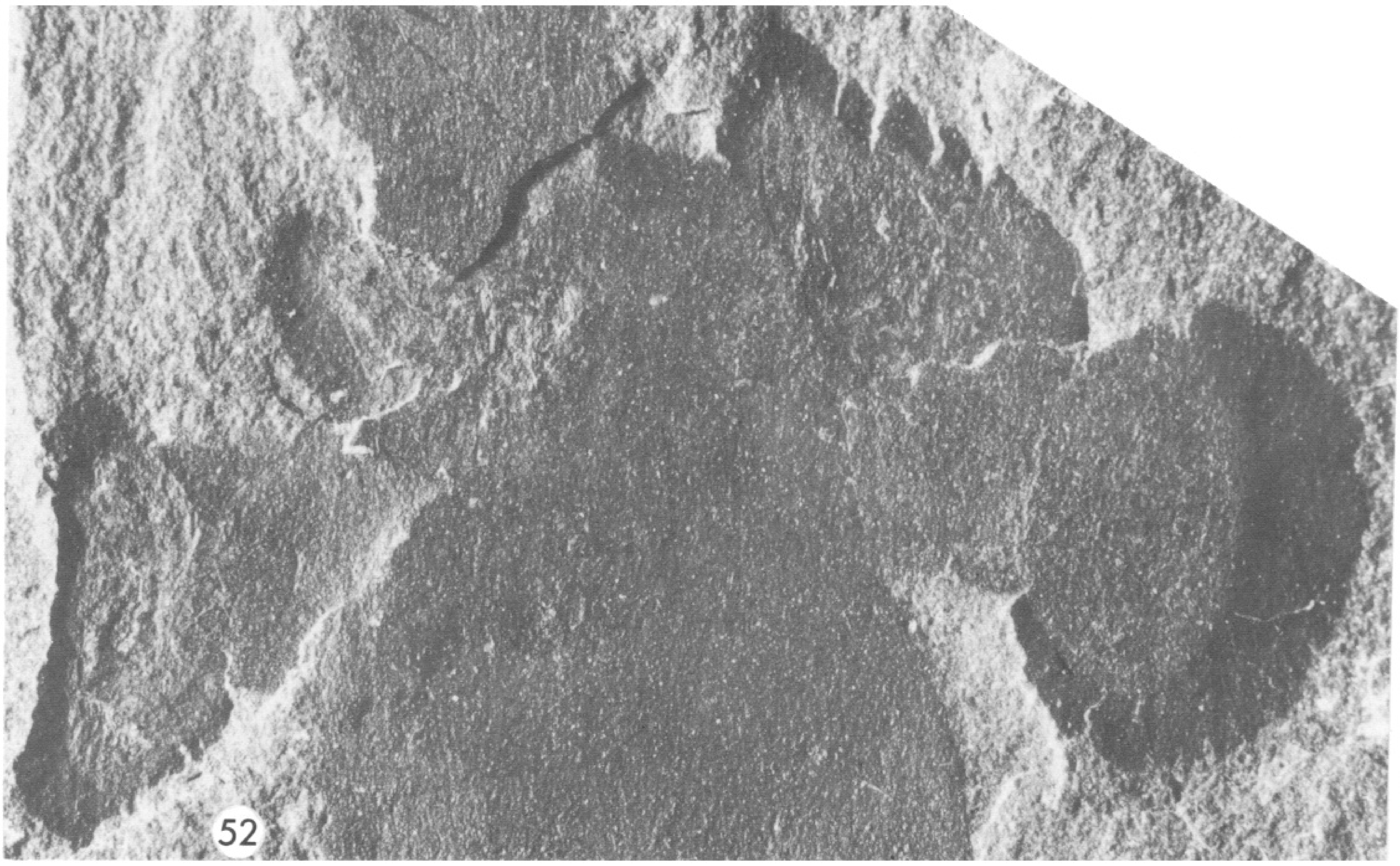

43

Opabinia regalis Walcott, 1912. U.S.N.M. 155600, Phyllopod bed, Walcott quarry (magn. ×3.3).

FIGURES 41–43. Counterpart before preparation of frontal process, respectively cephalon and first 12 trunk segments, west; same, reflected; segments 7–15 of trunk and posterior portion, east.



Figures 45–51. For description see opposite.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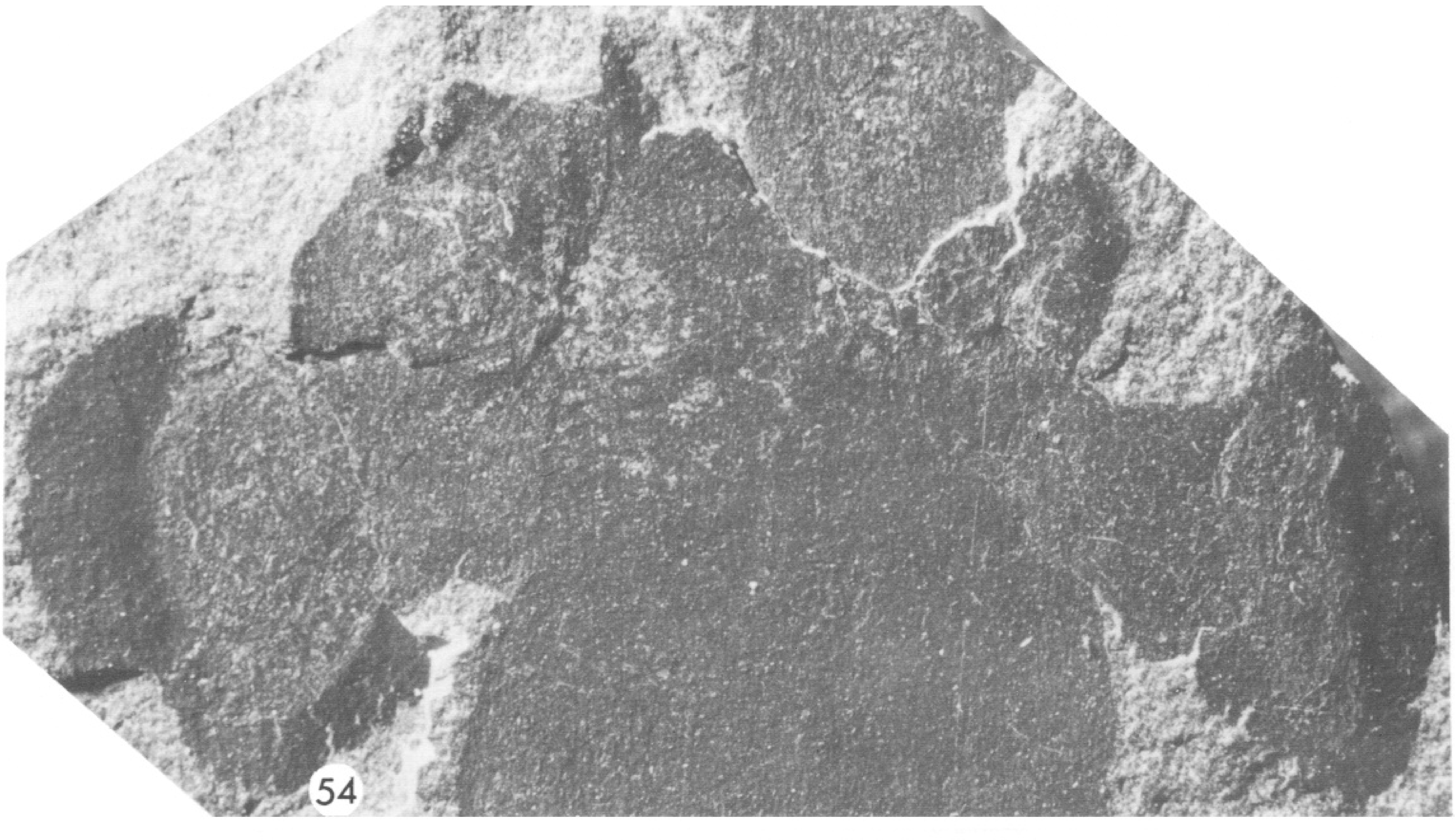
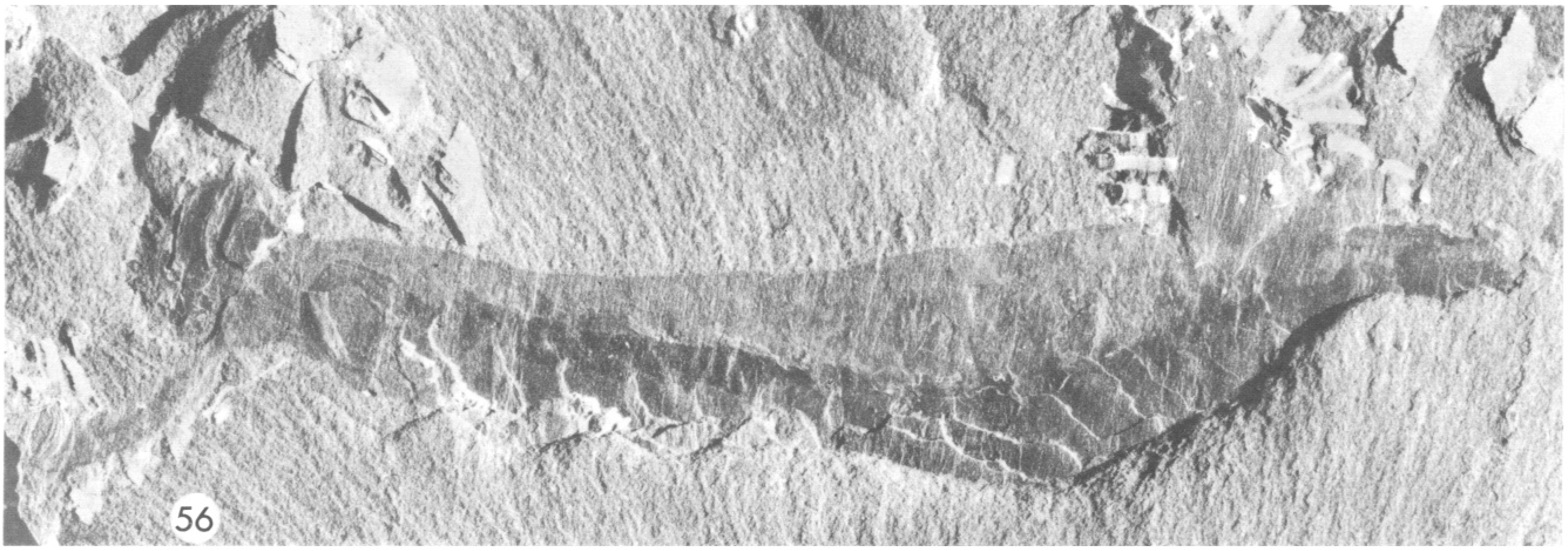

54

FIGURES 52–54. For description see opposite.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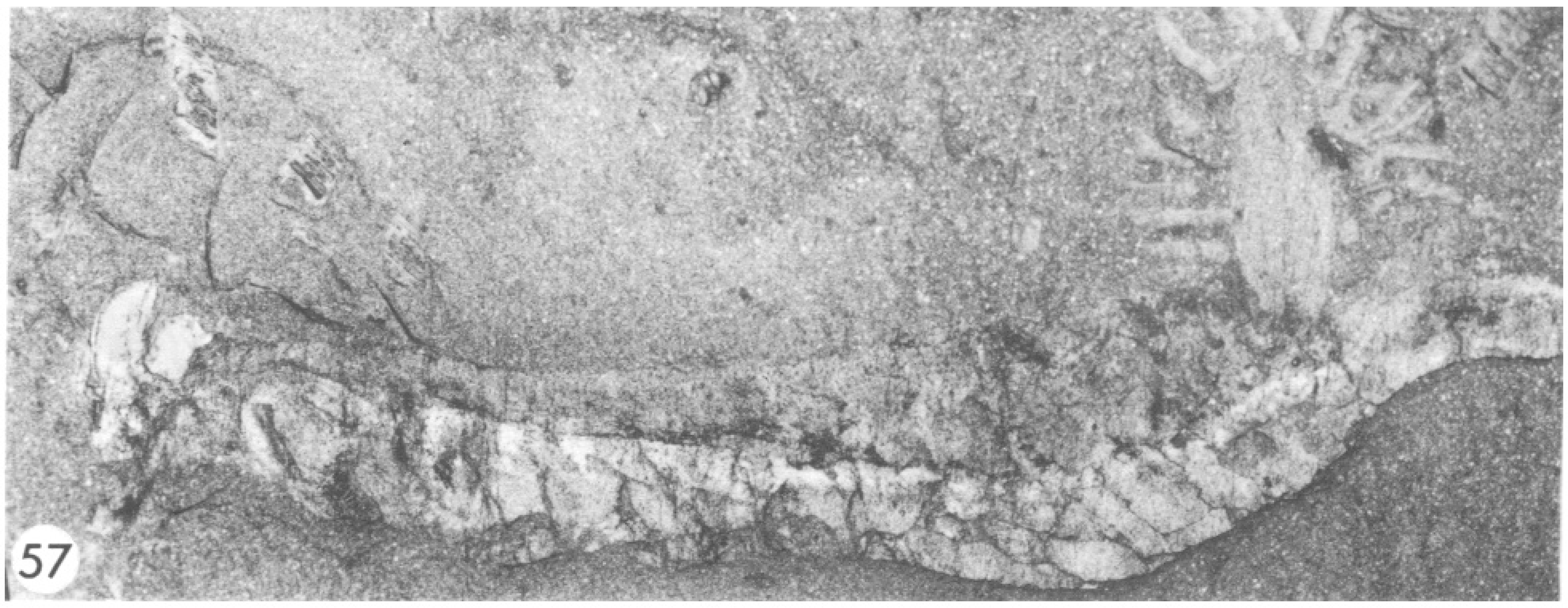
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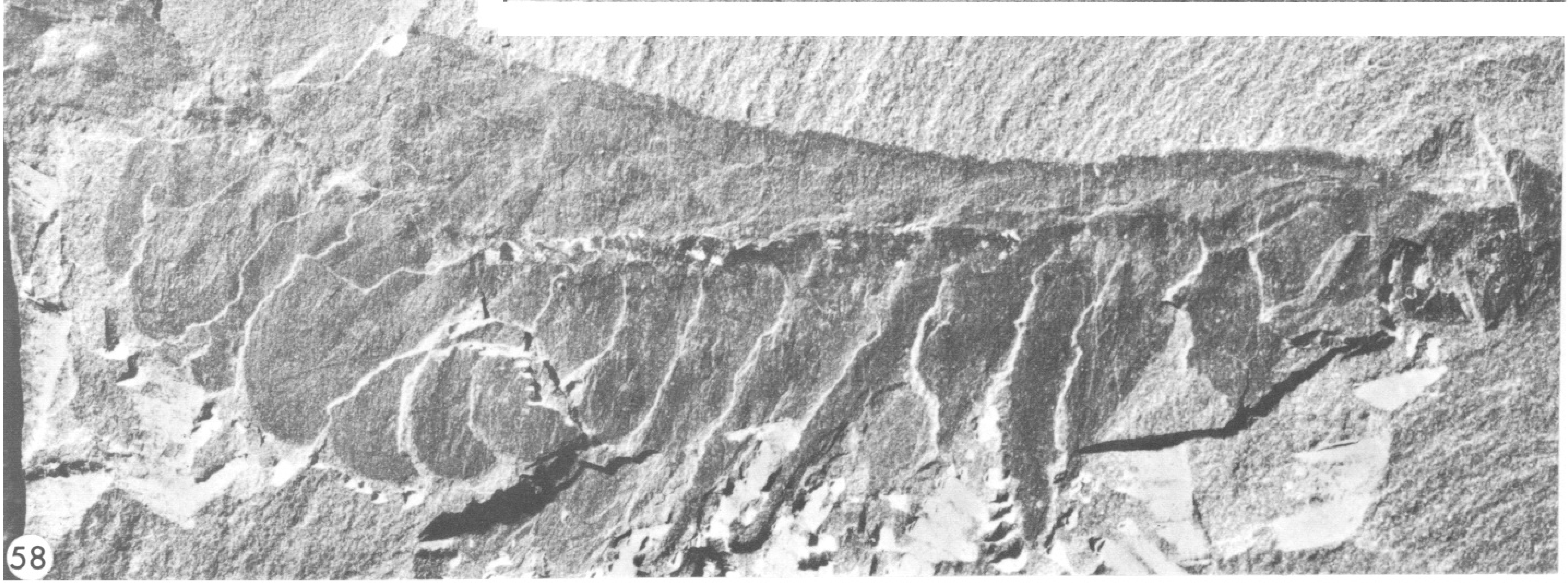
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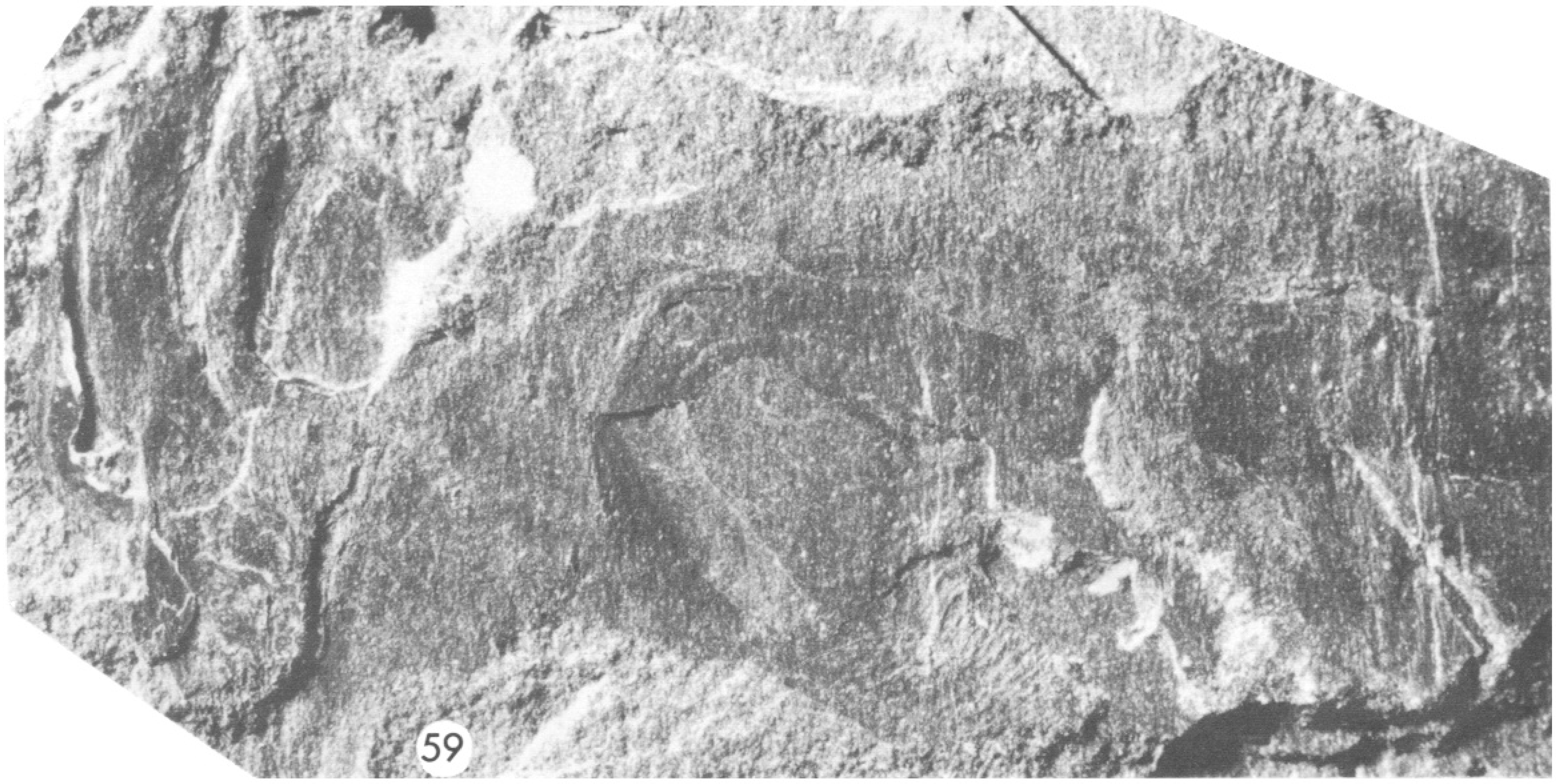
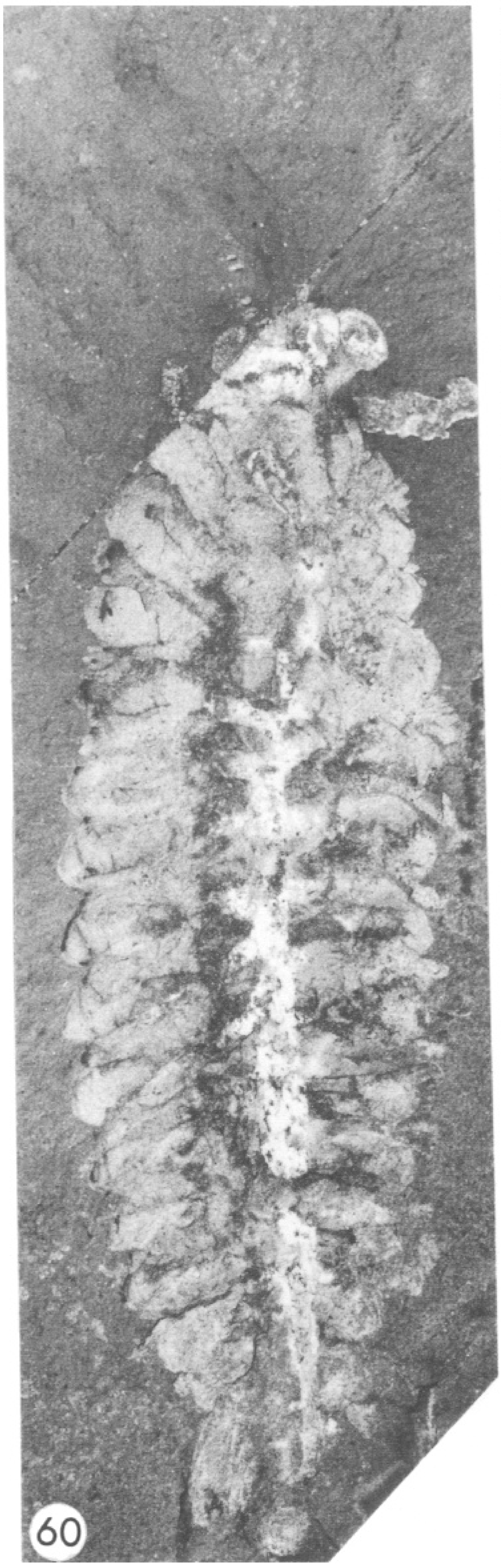

59

FIGURES 56–59. For description see opposite.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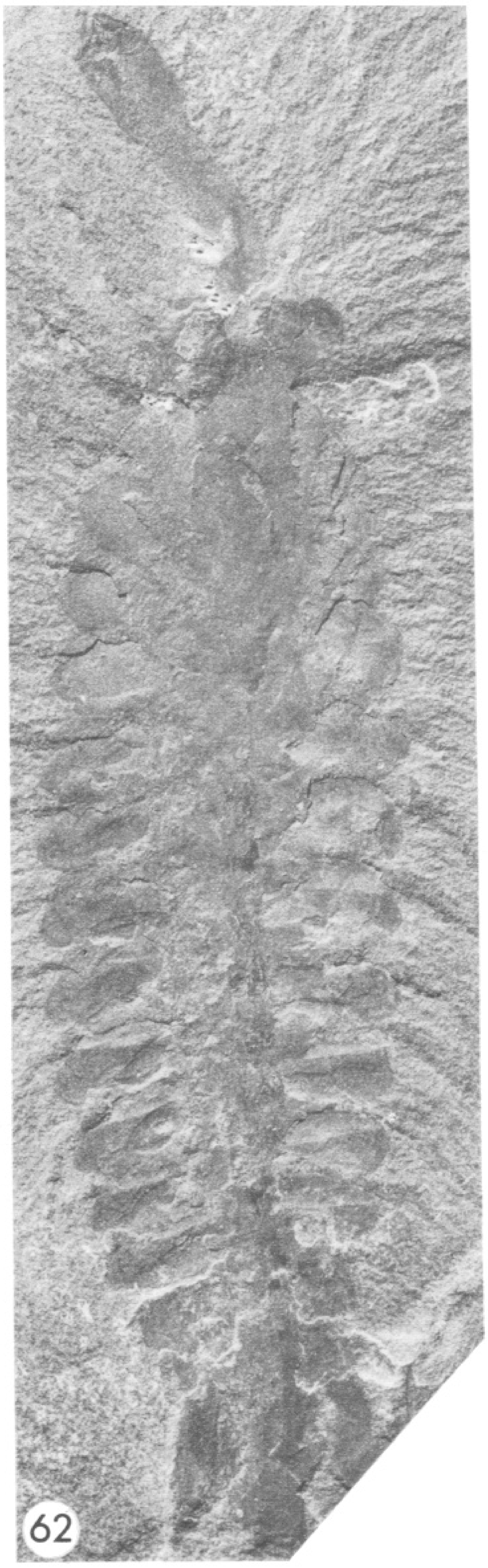
61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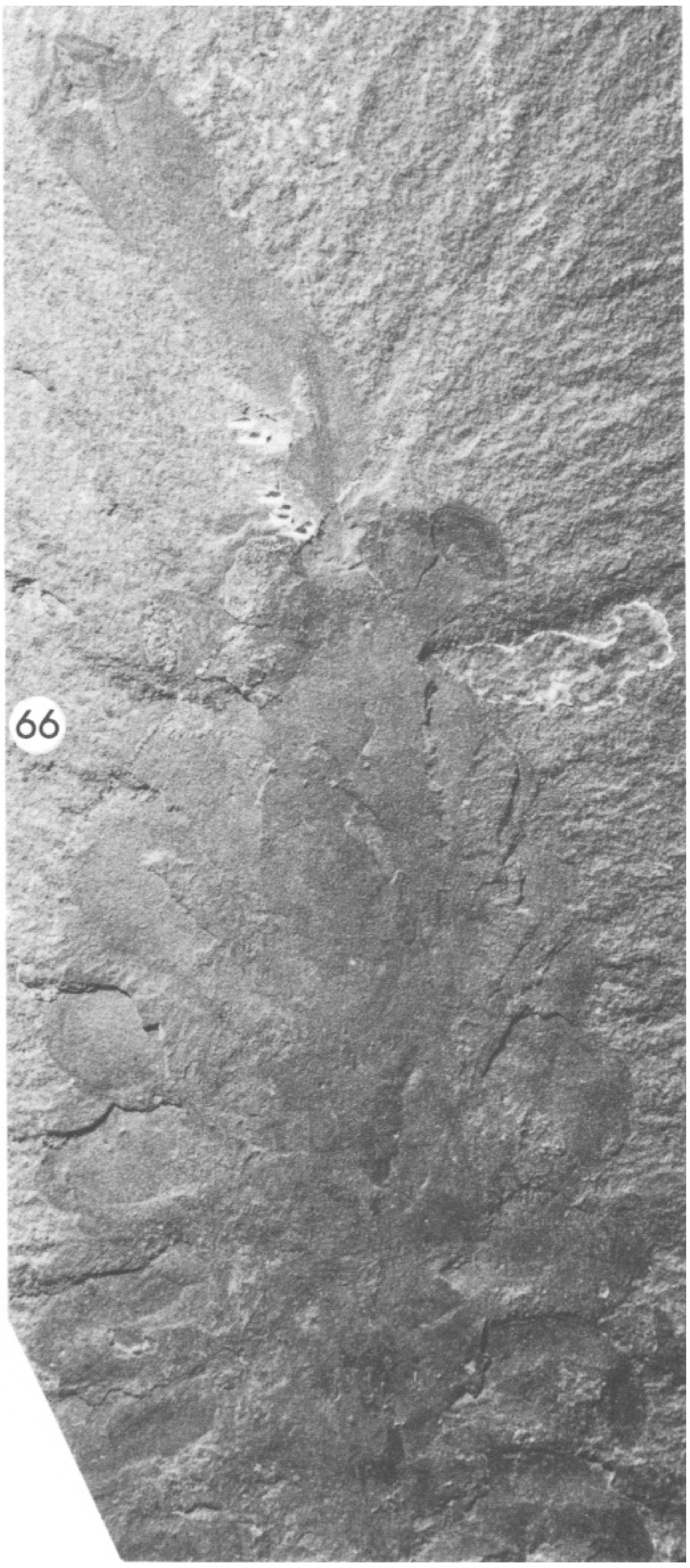
63

FIGURES 60–63. For description see opposite.


65

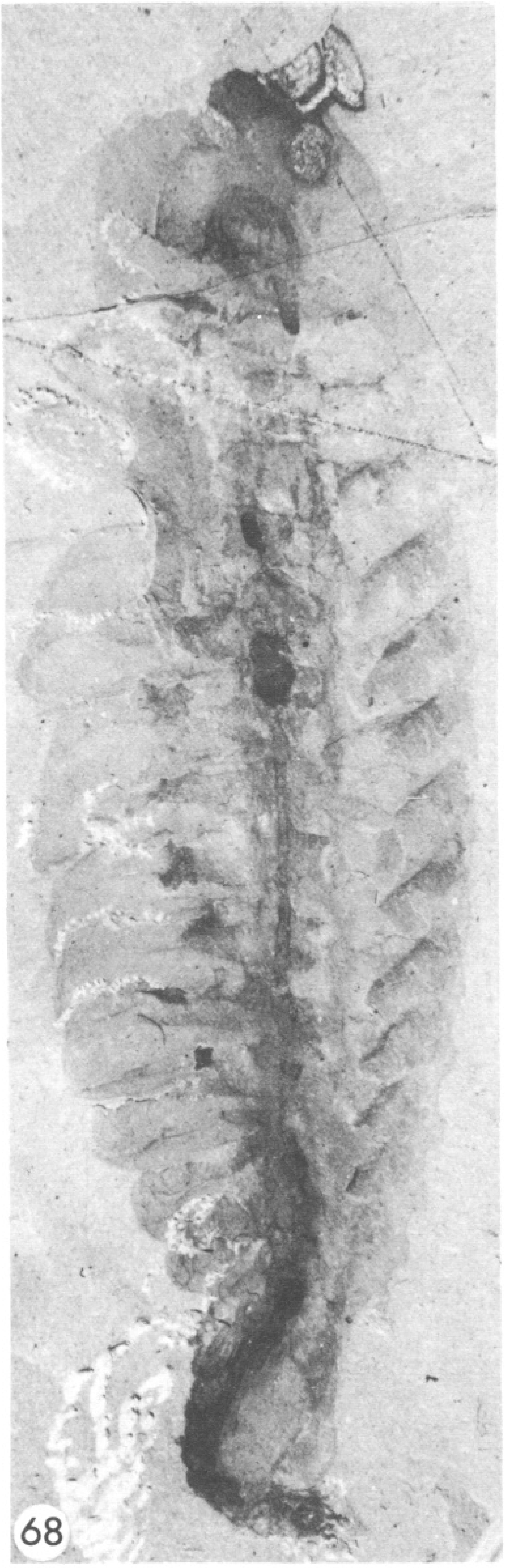

66


67

Opabinia regalis Walcott, 1912.

Figures 65, 66. Y.P.M. 5809, part, respectively segments 1–10 of trunk, northeast (magn. ×5); cephalon and segments 1–7 of trunk, north–northwest (magn. ×3.3). Phyllopod bed, Walcott quarry.

Figure 67. G.S.C. 40251, part, axial region and right side of trunk segments 4–9, northeast (magn. ×5). Walcott quarry, level 1.68 m (5 ft 6 in).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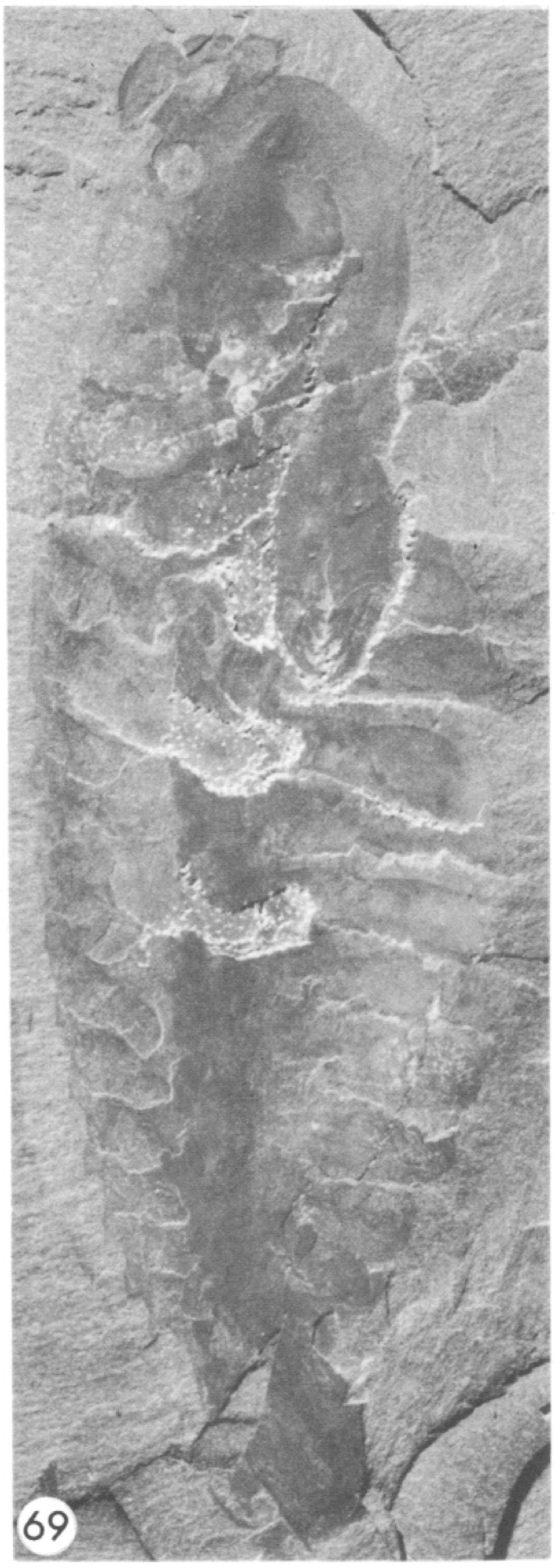
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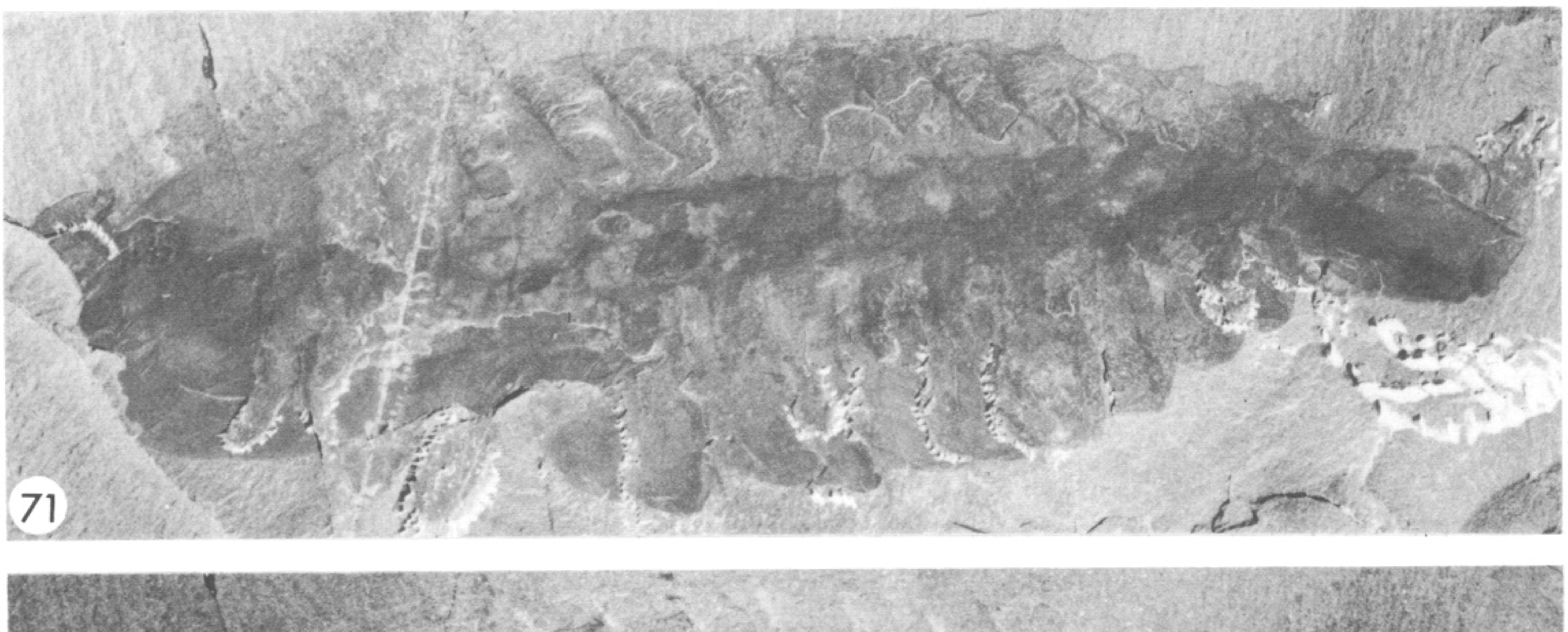
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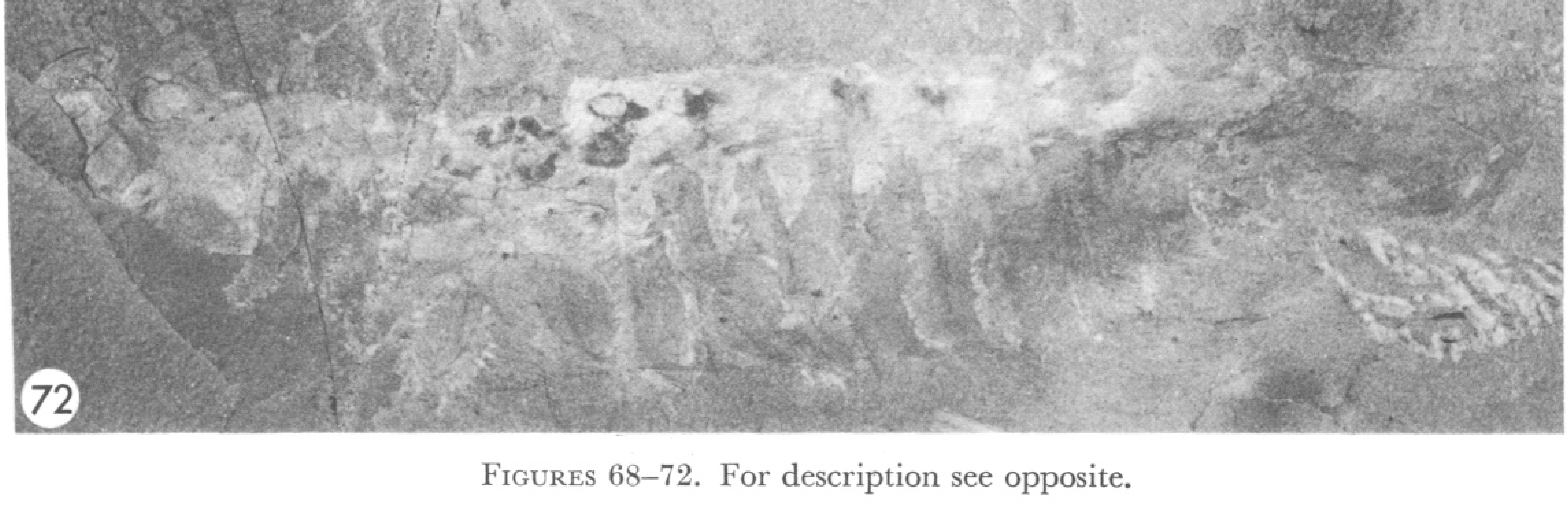
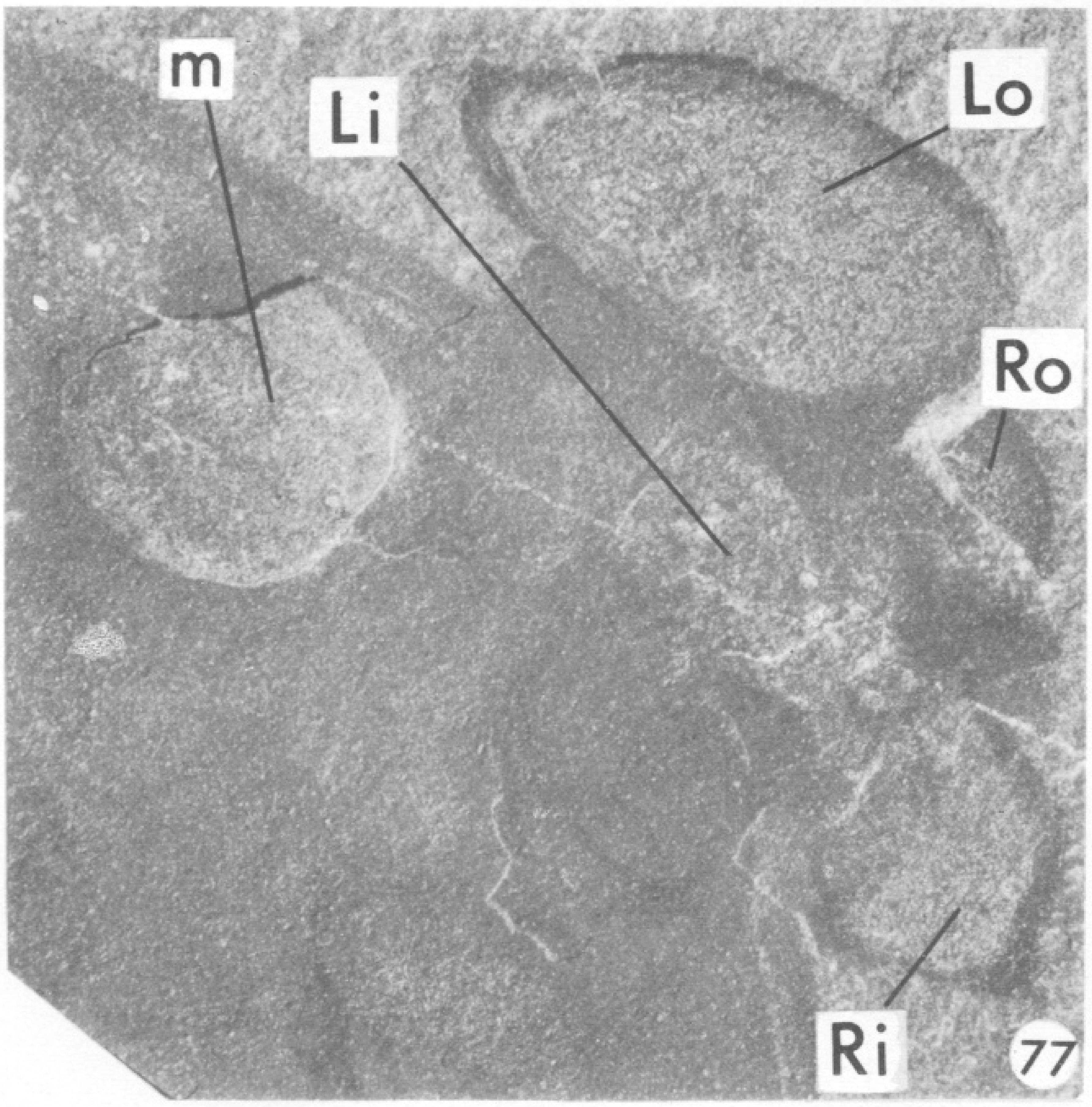
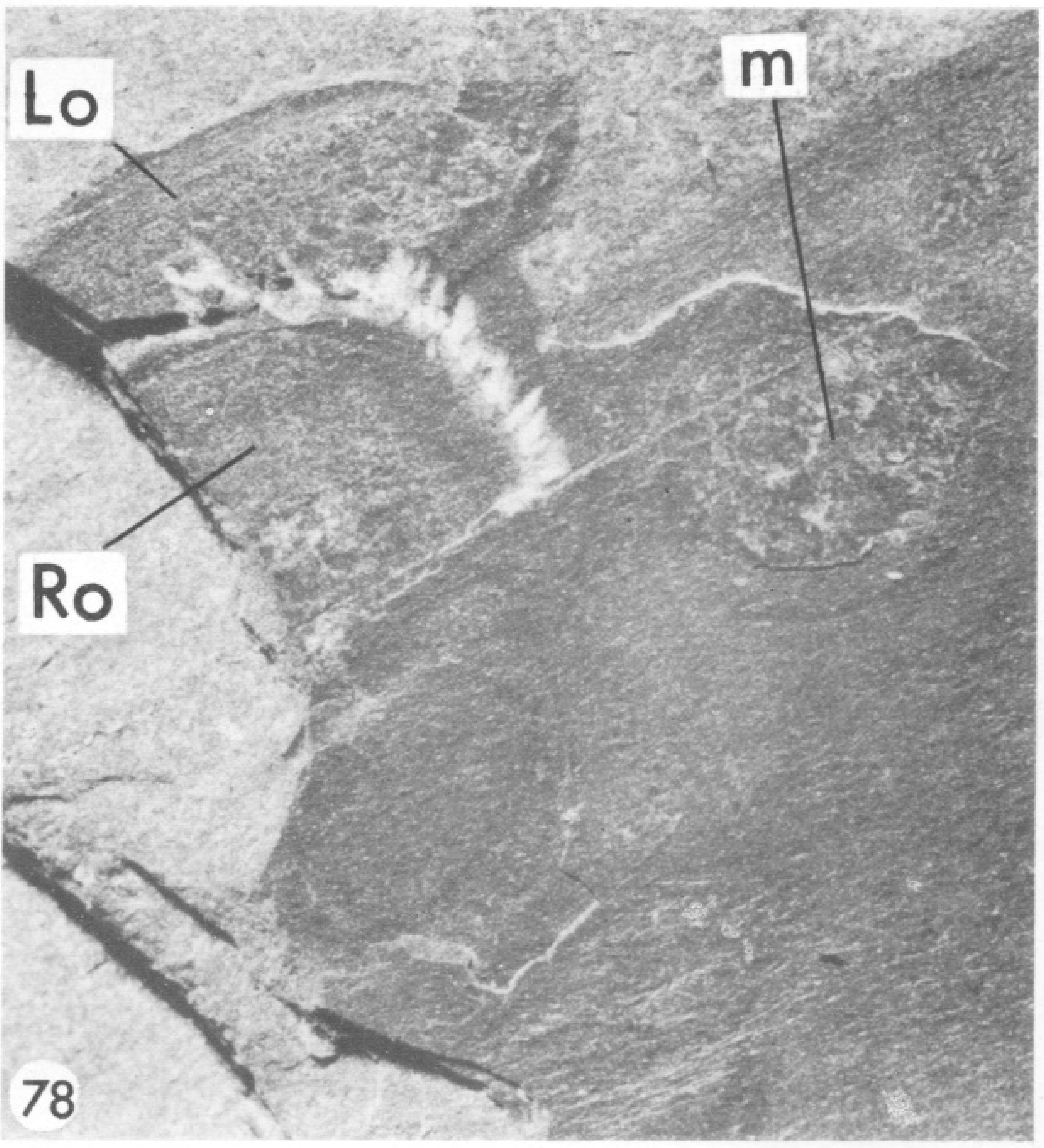
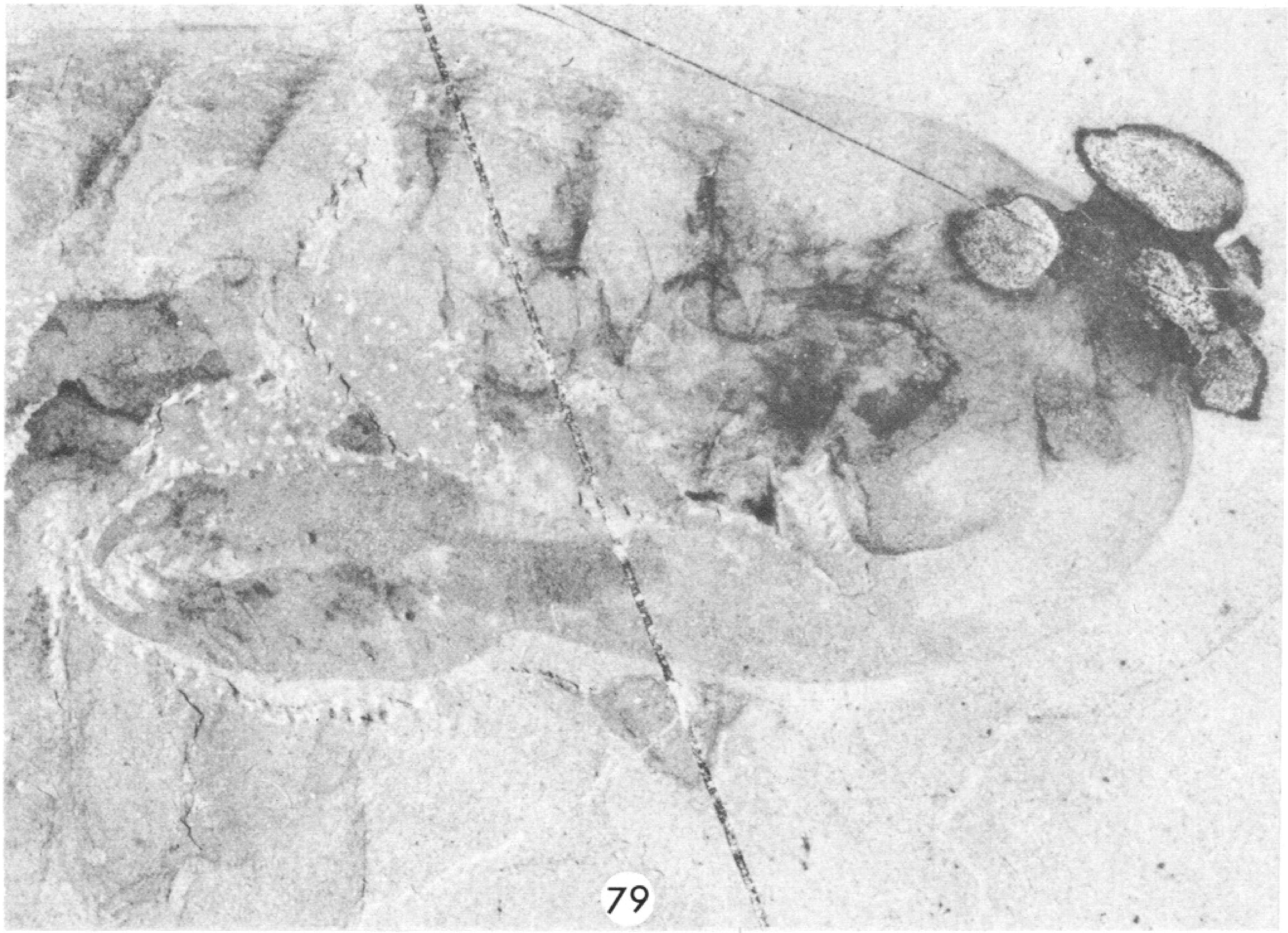

72

FIGURES 68–72. For description see opposite.





Figures 75–78. For description see opposite.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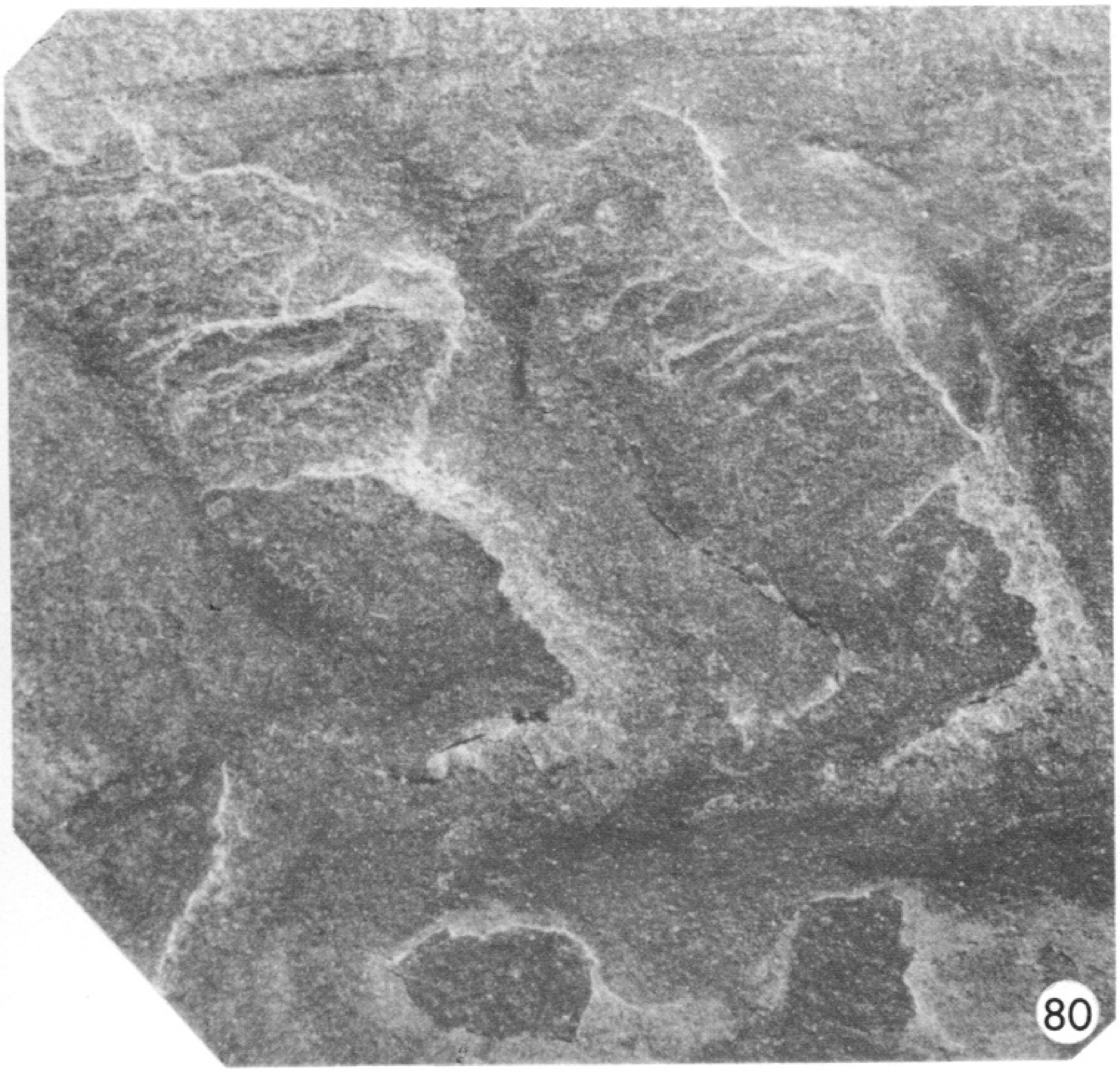
80


81

Opabinia regalis Walcott, 1912. G.S.C. 40251, Walcott quarry, level 1.68 m (5 ft 6 in).

FIGURE 79. Counterpart, cephalon and segments 1–6 of trunk, ordinary light under alcohol (magn. ×4).

FIGURE 80. Part, right gill areas 5 and 6, northeast (magn. ×10).

FIGURE 81. Counterpart, portion of cephalon showing median eye and mouth area adjacent to proximal portion of frontal process, northeast (magn. ×10).