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# THE ARTHROPOD *SIDNEYIA INEXPECTANS*, MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

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[Plates 1–15]

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Old and new specimens of *Sidneyia inexpectans* have been studied and are accompanied by explanatory drawings and photographs. New reconstructions of the animal are given together with a three-dimensional model. The body consisted of a cephalon with a long backwardly directed doublure, a thorax of nine articulating somites, abdomen with cylindrical exoskeleton of two or three somites and a telson. A caudal fan was formed by a pair of uropods articulating at the posterior margin of the last abdominal somite. The cephalon had stalked eyes and preoral antennae but no walking or grasping appendages. The first four somites of the thorax had paired uniramous, prehensile walking legs attached to the body by broad coxae with spiny gnathobases. The coxae were smaller on the five posterior thoracic somites and the paired appendages were biramous, each bearing a gill supported on a flap attached at its proximal end to the first podomere of the leg. The coxa–body attachment resembles that of modern merostomes and is in advance of trilobites. Evidence suggests that *Sidneyia* was a bottom-living, carnivorous animal eating larger and harder food than trilobites. Gut contents include ostracodes, hyolithids, small trilobites and phosphatic debris.

*Sidneyia* is the earliest known form which could be an ancestor to merostomes, but its body plan and absence of chelicera distinguishes *Sidneyia* from this group.

The holotype of *Amiella ornata* Walcott, 1911 is reinterpreted and its synonomy with *S. inexpectans* is confirmed.

## 1. INTRODUCTION

The present account is of one of the larger fossil arthropods known from the Middle Cambrian Burgess Shale and the first to be described by Charles D. Walcott in the year following his discovery of the famous locality in 1910. It was named after his eldest son Sidney S. Walcott who, together with his family, had helped find the locality and collect the specimens illustrated (Walcott 1911). Among these, however, were specimens later shown to belong to another genus, specimens of isolated appendages since thought to belong to *Anomalocaris* Whiteaves, 1892, and one specimen considered by Walcott to be sufficiently distinct from *Sidneyia* as to represent a second genus, *Amiella*. The type species of *Amiella* (*A. ornata*) is described below and following Simonetta (1963) the genus is considered to be a subjective synonym of *Sidneyia*. Walcott's mixing of specimens has led to a series of subsequent misinterpretations of what *Sidneyia* is like, isolated appendages having been identified as belonging to the animal despite evidence to the contrary, and for this reason any discussion on the morphology of the animal and hence its classification must be critically examined and questioned.

It is surprising that, since Walcott (1911), only Størmer (1944) and Simonetta (1963) have actually studied specimens and the latter produced the first attempted reconstruction of the animal. My conclusions differ considerably from these as a result of detailed preparation, study and interpretation of specimens, summarized in the form of figures and plates.

Material of *Sidneyia* was studied by me during a visit to the U.S. National Museum in 1972 following which material was borrowed for further study in Oslo. A 6 month sabbatical leave at the Sedgwick Museum, Cambridge, U.K., from April to September 1976, enabled me to complete much of this work while benefiting from the advice and guidance of H. B. Whittington, F.R.S., C. P. Hughes, S. Conway Morris and D. E. G. Briggs, all of whom have studied and are still studying other Burgess Shale fossils. I had the added and unique experience in 1967 of joining H. B. Whittington, J. D. Aitken and W. H. Fritz (see Aitken *et al.* 1967; Aitken & Fritz 1968) on an expedition to the Burgess Shale quarry locality (Fritz 1971) where new and accurately located collections were made. Among these were specimens of *Sidneyia* that have been included here and some of these illustrate features not seen in such detail on specimens collected by Walcott and since figured by Simonetta (1963, 1975). Preparation of specimens, including types in some cases, with the aid of a vibro-drill, has revealed many hidden details of the limbs, while photographic methods including the immersion of specimens in liquids before photographing in white light, and the use of ultraviolet radiation, have allowed these new discoveries to be illustrated with some success. Camera lucida drawings of the specimens have afforded a graphic interpretation of each, and from the cumulative evidence an attempt has been made to construct a three-dimensional model. It is this model (plates 14, 15) that forms the basis for the reconstructions shown (figures 106, 107). In this model a number of assumptions had to be made as to the original convexity of the animal since the specimens are all compressed outlines in shale. Nevertheless the model puts constraints on such things as 'angle of swing' of a leg or, since no one specimen shows everything preserved, the relative sizes of appendages down the length of an animal. It also allows one to produce reconstructions of an animal that could have functioned as it either swam over or crawled on the bottom, rather than just a picture based more on fantasy than fact. In doing this I have been particularly influenced by the work of the late Dr Sidnie M. Manton, F.R.S., British Museum (Natural History), who states (Manton 1973, p. 111) with regard to arthropod relationships, 'Unless the functions of the various parts of an animal are understood in some detail and that means gaining and understanding as to how the whole animal works, no sound conclusions can be reached'. In this respect a study of the Middle Cambrian Burgess Shale fossils is essential not only because of their antiquity but because of their unique preservation which, as the present material shows, extends to details of hairs on limbs and antennae and internal soft parts not normally fossilized, plus an amount of detail that far exceeds that usually available to a palaeontologist.

## 2. TERMINOLOGY

Descriptive terminology of dorsal features includes the use of *cephalon* for the most anterior tagma and *thorax* and *abdomen* (including *telson*) for the main divisions of the body divided into individual *somites*. The term *antenna* for the first uniramous, multiannulated head appendage would appear suitable for descriptive purposes. Walking legs are described as consisting of individual components (*podomeres*) distal to the *coxa* which was joined to the ventral surface. Where biramous an outer ramus or gill is recognized and its function therefore implied. The following symbols and abbreviations used in the text and on text figures are defined thus:

| | | | |
|---|---|---|---|
| a | antenna | cb | coxal bar |
| ab | abdomen; suffix indicates number of somite | cc | coxal cavity |
| | | cef | cephalic flange |
| af | articulating fold | cdb | cephalic doublure |
| al | alimentary canal | ce | cephalon |
| am | anterior margin | cox | coxa |
| an | anus | coxb | coxal bar |
| antsp | anterior spine | coxsp | coxal spine |
| anpl | anal plate | d | dorsal; prefix |
| ar | articulation | dbl | doublure |
| arc | articulating cavity | dbpm | doublure posterior margin |
| arint | articulating integument | dcl | distal claw |

| | | | |
|---|---|---|---|
| ded | dorsal endite | messp | mesial spine |
| dex | dorsal exoskeleton | *N* | *Naraoia* |
| df | distal flange | O | ostracode |
| dsp | dorsal spine | pm | posterior margin |
| e | eye | re | reflective area of eye |
| ed | endite | R | right; prefix |
| es | eye socle | sag. | sagittal |
| ex | exoskeleton | s | somite; suffix indicates number from anterior |
| ens | endosternite | | |
| fil | filament | som | somite |
| fr | fracture | sp | spine |
| g | gill | t | telson |
| gf | gill flap | tam | telson anterior margin |
| gfil | gill filament | trans, tr. | transverse |
| gff | gill flap fold | u | uropod |
| gnl | gnathobasic lobe | v | ventral; prefix |
| L | left; prefix | vex | ventral exoskeleton |
| l | leg; suffix indicates number from anterior | vint | ventral integument |
| | | vsp | ventral spine |
| *L* | *Leanchoilia* | *W* | *Waptia* |
| ms | muscles | wr | wrinkle |

*Subscript numbers* are used to denote somites of thorax ($s_1$, $s_2$, etc.) and abdomen ($ab_1$, $ab_2$) from anterior backwards, and also corresponding legs ($l_1$, $l_2$, etc.) and gills ($g_1$, $g_2$, etc.) where recognized with reasonable certainty. They are also used to identify podomeres of a leg numbered from the coxa outwards, and for identifying divisions of the antenna.

## 3. EXPLANATION OF PHOTOGRAPHS AND DRAWINGS

Except when photographed under alcohol specimens were first focused in ordinary light and then photographed in ultraviolet radiation with use of panchromatic 35 mm film. Directions such as west, northwest, etc., refer to the origin of the radiation from a light source positioned at 30° to the horizontal. Reflected photographs are the result of the radiation coming from a light source approximately 60° to the horizontal and falling on a tilted specimen. The angle of tilt was varied to give the maximum reflexion but seldom exceeded 10–12°. Specimens were photographed under alcohol with use of a high-angled all-round light source. Each method has its advantages as the photographic results show, but reflected and alcohol-immersion methods tend to produce the best detail especially of the highly reflective areas.

Except where stated all specimens are from the Phyllopod Bed, Walcott Quarry, and belong to either the United States National Museum (abbreviated U.S.N.M.), now the National Museum of Natural History, Washington, D.C., or the Geological Survey of Canada, Ottawa (G.S.C.). For exoskeletons the convention is adopted that the part is the block showing a specimen in dorsal view, and the counterpart, in ventral view.

Explanatory drawings of specimens are positioned opposite photographs. Symbols used are explained above and explanations are given where necessary.

## 4. PRESERVATION

The majority of specimens figured here from the Walcott Collections were obtained by Walcott on later visits to the Burgess Quarry and after the type material was first figured. Two states of appearance of fossils are common, one in which the fossil occurs on a brown surface, a bedding plane along which weathering took place, the other on a fresh unweathered slate-black to blue-grey bedding surface. Fossils of the first type are numerous among Walcott's earlier collections and those commonly figured in his publications. Thus the lectotype (figure 65, plate 9) is of this category and only gross details such as the outline of the exoskeleton and poorly preserved appendages are visible. In some cases traces of the silver film (see below) are present, especially in the region of the alimentary canal, and are brought out when the specimen is photographed under alcohol or water, or if it is tilted and photographed by reflected ultraviolet radiation. Specimens of the second category of preservation include slightly more than half those studied and occur as well defined dark grey to black outlines against the slightly lighter matrix background. Details of both minute and large setal spines, segmented joints of limbs, alimentary canal and outlines of distal tips of pleurae are often accentuated by areas that are more intensely reflected than others especially when the specimen is photographed at varying angles to a low-angled (30–50°) light source. In this position the reflective areas appear as a silvery film which both under high magnification and under liquids appears to be made up of minute reflective particles. Recently Conway Morris (1977, p. 5) has shown that it may be a calcium aluminosilicate. Whittington (1971 *a*, *b*) interpreted similar highly reflective areas in *Marrella* as sites of originally fluid-filled canals, a possibility in regions of the alimentary canal, but more difficult to accept in such cases as tips of the pleurae or at joints between podomeres of limbs. While some reflective areas are blob-like and apparently structureless, others have regularly defined outlines which are sometimes strand-like or bundle-like (figure 25, plate 4). These have been interpreted as being muscles in some of the soft-bodied worms from the Burgess Shale (Conway Morris 1977) and in *Canadaspis* (Briggs 1978), and look convincing in the material that I have since examined. It is less convincing in the present material although the arrangement of the areas of silver film in the leg (figure 88, plate 12) and that associated with coxal attachment (figure 25, plate 4) are similar. Reflective areas arranged symmetrically each side of the axis on the specimen (figure 37, plate 5) are thought to be the less sclerotized ventral integument. The highly reflective outer rim of the eye (figure 25, plate 4; figure 37, plate 5) is similar to that of the enigmatic *Opabinia* (Whittington 1975 *a*, p. 23; plates 9, 10).

While pyrite is found in some specimens, it occurs as finely disseminated particles patchily distributed and Simonetta (1962) was wrong in thinking that the reflective areas were pyrite. Whittington (1971 *a*, *b*, 1975 *a*, 1980) has given a thorough account of the mode of preservation of other Burgess Shale fossils and their attitude in the rock, and many of his remarks apply equally well here. Nearly all specimens of *Sidneyia* lie morphologically parallel to the bedding but a few specimens show oblique (figure 41, plate 5; plate 6) and vertical attitudes (figures 25–27, 29, plate 4). Preparation of specimens shows features such as antennae and other appendages to occur at successive levels within the rock and these can be revealed by carefully removing one from above the other, or by removing the thin layer of sediment that separates them. With the specimen in dorsoventral aspect (figure 67, plate 9; figure 64) the method of approach has been to remove successively first the dorsal exoskeleton of the cephalon to reveal the doublure beneath and then parts of the thorax to reveal the filaments of the gills, and then these to expose the leg. Adjacent to the midline where the limb is attached, all three successive layers, dorsal exoskeleton – gill – leg, lie directly upon each other and it is a matter of hopefully removing an infinitely thin layer of material with the aid of a vibro-chisel. Laterally, however, the distance of separation increases so that each level is separated from another by a greater thickness of sediment. Only unweathered specimens lend themselves to this type of preparation which relies on the fact that structures to be prepared differ slightly in colour from the matrix, allowing them to be recognized when reached at depth, and that there is a natural line of separation between them and the matrix.

On the series of explanatory camera lucida drawings that appear opposite corresponding photographs of a particular specimen, these changes in level, and thus relative levels of adjacent structures, are illustrated by hachured lines, the hachures being directed downslope. These breaks in slope are minute scarps produced either naturally when the rock split or artificially during preparation. They are revealed by shadows on the photographs and become accentuated depending upon the direction of the light source used when the specimen is photographed. In many cases splitting of the rock has produced 'part' and 'counterpart' specimens though these are not the same as the conventionally used internal and external mould since, because parts of the body lie at different levels in the rock, different parts will come to lie on either side of the plane along which the rock has split. In structures that lie morphologically parallel to the bedding, however, the split appears to take place roughly through the middle so that the same structure occurs on both 'part' and 'counterpart'. However, when a specimen is preserved at an angle to the bedding the split can be step-like so that portions of the animal in both dorsal and ventral aspect face the observer (figure 7, plate 1; figure 41, plate 5). Some features of the Burgess Shale fossil preservation still remain to be explained, though Whittington's (1971*a*) idea that the animals must have been caught up in a turbulent cloud of sediment in suspension and then entombed in a variety of orientations as the sediment settled is gaining more and more support from other studies (Whittington 1980). Thus this method is a plausible way of explaining the peculiar attitude of the fossils in the rock, because it is difficult to believe that a specimen (figure 29, plate 4) with a cephalon 60 mm wide (tr.) could be buried in a vertical position simply by having died and then dropped to the sea floor to be buried by fine mud. Likewise the overwhelming by sediment is a method by which sediment can be forced between dorsal exoskeleton and appendages, but it does not explain the regularity of preservation of appendages. Compaction after burial has often had the effect of rotating the legs so that their anterior or posterior faces lie parallel to the bedding. This rotation (§7 (*h*)) is such that either the posterior face of the limb faces the ventral surface of the exoskeleton (figure 67, plate 9) or the anterior face does (figure 82, plate 11). This feature of limb rotation has been shown in such diverse forms as *Marrella* (Whittington 1971*b*), *Burgessia* (Hughes 1975), *Olenoides* (Whittington 1975*b*) and *Naraoia* (Whittington 1977) where appendages of different size, shape and even mode of attachment are involved. This then suggests the cause to be a *post mortem* one whereby early decay of the flexible point of articulation between the ambulatory branch and the ventral integument allowed the limb to rotate during subsequent compression of the rock.

Some early decay of specimens seems to have taken place and in a few cases very likely before burial. Where part and counterpart exist, some exoskeletons have no traces of appendages preserved (figure 24, plate 3). Some lack all but the antenna (figure 10, plate 2), while others lack this but retain the highly reflective areas that are part of the eye (figure 37, plate 5). The missing parts could have been lost during transportation but there is evidence to suggest that some of the empty exoskeletons represent moult stages in that they lack any sign of gut infilling and the cephalic doublure is either missing or displaced along the line of the marginal suture. A few isolated legs and a number of gill filaments can be recognized as belonging to *Sidneyia* but nothing like the number attributed to the genus by Walcott (1911) or Simonetta (1963) (see synonomy (§6)). As shown recently by Briggs (1979) some of these appendages probably belong to the arthropod *Anomalocaris*.

## 5. MEASUREMENTS

A total of 16 specimens chosen for study because of their completeness have been measured, the parameters taken being transverse width of cephalon, total length of exoskeleton and length of cephalon plus thorax. Measurements were made by means of a transparent rule placed on the specimen in a transverse or sagittal direction as the case may be. Where the abdomen has been twisted at an angle to the sagittal line, the sum of both straight directions measured is used. Figures 1 and 2 show plots of length of cephalon and thorax against transverse width of cephalon and total length of exoskeleton against length of abdomen respectively. A line of best fit calculated by means of a reduced major axis regression corresponds to the line of growth of an average animal over the range available.

Both graphs show that the ratio of length to width changes with an increase in size, large individuals being relatively narrower. Thus on figure 1 a specimen at the lower end of the observed size range (30 mm) has a length : width ratio of 0.70, while at the higher (90 mm), the ratio length : width is 0.57. Similarly on figure 2 the ratio total length of exoskeleton : length of abdomen is 0.29 for a specimen 50 mm long and 0.38 for one with a length of 140 mm. The higher ratio for larger specimens no doubt reflects a relatively longer abdomen (very often composed of two elongate somites) which in turn also explains the narrower appearance of the larger individuals.

Of interest from the study of both graphs is the fact that specimens from the Raymond Quarry (8, 9, 10) are not significantly different from the remainder collected at the stratigraphically lower Walcott Quarry.

## 6. SYSTEMATIC PALAEONTOLOGY

### Genus *Sidneyia* Walcott, 1911

*Type species. Sidneyia inexpectans* Walcott, 1911.

*Diagnosis.* Body divided into cephalon with long (sag.) ventral doublure, thorax of nine articulating somites and abdomen of two or three somites and telson. Cephalon with stalked lateral eyes and antenna. Appendages on all thoracic somites, the first four uniramous walking legs, posterior five biramous with outer ramus bearing filamentous gills carried on supporting flap. Legs attached to body by broad-based coxa; latter with well developed gnathobasic lobes. Abdomen with cylindrical exoskeleton, last somite bearing paired uropods which together with telson form caudal fan.

*Geological range.* Only the type species is known from the Middle Cambrian Burgess Shale, British Columbia, Canada. '*Sidneyia* sp.' Resser & Howell (1938, p. 232, pl. 13, fig. 3), from the Lower Cambrian Kinzers Formation, Pennsylvania, is based on two incomplete pleurae which I have examined. These are not like *S. inexpectans* and probably are not *Sidneyia*.

### *Sidneyia inexpectans* Walcott, 1911

1911 *Sidneyia inexpectans* sp.nov. Walcott, p. 24, pl. 2, fig. 1; pl. 3, figs 2, 3, 4; pl. 5, figs 1–4; pl. 6, fig. 3; pl. 7, fig. 1 non pl. 2, figs 2, 3 = *Emeraldella brocki* Walcott, 1912; non pl. 3, fig. 1 = *Ottoia prolofica*; non pl. 4, figs 1–4 = ?*Anomalocaris*.

non 1912 *Sidneyia inexpectans*; Walcott, p. 206, fig. 10 = *Emeraldella brocki*.

1944 *Sidneyia inexpectans*; Størmer, p. 88, fig. 17, pl. 9, 10 non 11, 12.

1949 *Sidneyia inexpectans*; Størmer, p. 199, fig. 25; p. 208, figs 9–10.

1959 *Sidneyia inexpectans*; Størmer, p. O27, fig. 16.

1963 *Sidneyia inexpectans*; Simonetta, pl. 7; pl. 8; pl. 9 (139704); pl. 10 (139702, 139705, 139718); pl. 11 (139713, 139720); pl. 12; non pl. 9 (139726, 139710, 139709, 139711, 139717, 139719, 139721, 139707); pl. 10 (57490, 139724, 57492); p. 11 (57493) = *Anomalocaris*.

1975 *Sidneyia inexpectans*; Simonetta, pl. 10, figs 1 a, b, 2 a, b, 5; pl. 11, figs 1 a, b, 2 a, b, 3, 4, 6, 7; pl. 12, figs 1–5; pl. 13, figs 1–3, 5–8; pl. 15, figs 2, 8; non pl. 10, figs 3, 4; pl. 11, fig. 5; pl. 12, figs 6, 7; pl. 13, fig. 4; pl. 14, figs 2–6; pl. 15, figs 3–7 = *Anomalocaris*.

1980 *Sidneyia inexpectans*; Whittington, pl. 3, fig. 4.

*Lectotype*. Here selected, U.S.N.M. 57487 (Walcott 1911, pl. 2, fig. 1, part and counterpart). The specimen is shown in figure 65, plate 9.

#### *Locality, stratigraphical horizon, number of specimens and associated fauna*

All specimens of *Sidneyia* collected by Walcott come from what he (Walcott 1912, pp. 151–153) later called the 'Phyllopod Bed', 2.3 m (7 ft 7 in) thick in which he excavated his quarry. The quarry is in the Middle Cambrian Burgess Shale Member of the Stephen Formation, and is situated on the ridge between Mount Wapta and Mount Field approximately 2286 m (7500 ft) a.s.l., 4.8 km north of Field, southern British Columbia, Canada. Associated with the fauna are trilobites of the *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* zone (Fritz 1971).

Specimens identified as *Sidneyia* and studied in detail number 55 and include eight figured by Walcott (1911) (U.S.N.M. 57487, 57489, 57494, 57495, 57496, 57497, 57498, 57499, type specimen of *Amiella ornata*, counterpart found subsequently and numbered 139701), one specimen, 65510, on same block as *Olenoides serratus* figured by Walcott (1918, p. 126, pl. 14, fig. 1; see Whittington 1975*b*, p. 111), and 13 topotype specimens figured by Simonetta (1963) (U.S.N.M. 139702, 139704, 139705, 139708, 139712, 139713, 139714, 139715, 139718, 139720, 139722, 139723 and 65057). All but two of these were figured by Simonetta (1975) together with a specimen, pl. 13, fig. 5, wrongly numbered 57494. This number is that of the isolated leg (Walcott 1911, pl. 5, fig. 4; Simonetta 1975, pl. 10, fig. 2 A, B, pl. 12, fig. 5). The following seven topotypes identified by Simonetta but not figured by him have been prepared and are figured herein, U.S.N.M. 139676, 139679, 139680, 139681, 139683, 139686, 139689, counterpart subsequently found and numbered 199895. Further topotypes figured herein and identified in 1972 are U.S.N.M. 250206, 250207, 250208, 250209, 250211, 250214, 250215, 250216, 250217, 250218. Unfigured topotypes are U.S.N.M. 139677, 139678, 139682, 139685, 139693, 139706, 139716. All specimens are labelled '35K' with no indication of where in the Phyllopod Bed they were collected. In the Geological Survey of Canada party's measured section (Whittington 1971*a*, fig. 3) the base of the bed was at 1.5 m (5 ft) and two specimens (G.S.C. 49740, 49746) were collected from intervals 2.43–2.62 m (8 ft–8 ft 7 in). In addition six specimens (G.S.C. 49739, 49741, 49742, 49743, 49744, 49745) were collected from level 22.55–23.14 m (74–76 ft) in the section from what is known as the Raymond Quarry (Whittington 1971*a*: 1172, 1174). Specimens of other genera from this level carry the label 35K/10 (Walcott 1912, p. 175) but my examination of many *Sidneyia* specimens in Washington and elsewhere has produced only one specimen (figure 10, plate 2) bearing this notation.

In addition to the numbered specimens listed above I have attempted to make approximate counts of other *Sidneyia* material in drawers at the U.S. National Museum, Washington, D.C. Among this are 20 more or less complete exoskeletons, 15 isolated coxae and numerous incomplete specimens including many 'parts' and 'counterparts' numbering over 120. There is clearly more, not to mention possible counterparts of specimens which may have found their way to other museum collections via exchange from Walcott himself. Specimens in Oslo (P.M.O. A5143) and Lund (L.O. 5267) that I have examined are of this category.

The estimated number of *Sidneyia* specimens in the U.S. National Museum is a little over 200, a figure considerably less than the 450 quoted by Simonetta (1963, p. 98).

Walcott (1912, p. 153) has listed the fauna from the Phyllopod Bed. A spectacular slab (U.S.N.M. 189800) figured by Walcott (1916, pl. 9) illustrates a specimen of *Sidneyia* surrounded by nine specimens of the trilobite *Olenoides serratus*, six of which have appendages, specimens of an agnostid, the peculiar trilobite *Naraoia compacta*, *Waptia fieldensis* and *Canadaspis perfecta* and various remains of a sponge and a hyolithid. Other specimens are associated with the monoplacophoran *Scenella*, the non-trilobite arthropod *Marrella splendens*, the worm *Ottoia prolifica*, the sponge *Choia*, a possible bradoriid ostracode and various algae. Specimens from the Raymond Quarry are associated with the non-trilobite arthropod *Leanchoilia superlata* and the sponge *Vauxia*.

The holotype of *Amiella ornata* (Walcott 1911, pl. 5, fig. 4) and type species of the genus *Amiella* is based on an extremely poorly preserved specimen said to differ from *Sidneyia* on account of narrower (tr.) somites and surface ornament, features considered here to be artefacts of preservation. Only the part was figured by Walcott but recently H. B. Whittington has found the counterpart and together they allow one possible interpretation. The part (figure 38, plate 5) consists basically of five plate-like structures lettered for convenience A–E, which overlap each other successively. Beneath E is a fragment, F, which is roughly on the same level as structures X and Y. A–E are separated by the breaks of slope indicated on the explanatory drawing (figure 34). Other smaller breaks of slope can be seen on the specimen but these are probably a result of step-like folds and minor faults in the material caused by the same oblique lateral compression that produced the more regular parallel wrinkles seen on the surface of X, A and C. These were regarded as being surface ornament by Walcott. No ventral structures or appendages are present and as it stands the specimen is indeterminate. However, there is a certain resemblance between this specimen and the oblique laterally compressed *Sidneyia* (figure 41, plate 5). If this is correct, then D and E are equivalent to the two somites of the abdomen (respectively $ab_1$ and $ab_2$), while F is the ventral surface of the abdomen. A, B, and C represent respectively somites 7, 8 and 9. Telescoping of the specimen has caused some underthrusting which accounts for structures X and Y below A, and these have been rotated and aligned more or less at right angles to A. Walcott (1911, pp. 27–28) was inclined to regard structure X as the epistome (= cephalic doublure), the dorsal cephalon having been detached and lost, and Y a possible detached body somite. I regard them as part of two or more anterior body somites. It has been suggested to me that they may even be parts of a separate fossil, but they are similar in colour to the other structures.

In considering *Amiella* to be a synonym of *Sidneyia*, Simonetta (1963, pp. 97, 104) saw similarities between the holotype of *Amiella ornata* and a second more complete specimen (Simonetta 1963, pl. 10; figure 8, plate 1, herein). The resemblance was based mainly on ornament but this, termed 'fine fan-shaped', is nothing more than parts of gill filaments ventral to somites 6–9 of the posterior thorax and like those of *Sidneyia inexpectans*. Differences between *S. inexpectans* and *S. ornata* were however shown to lie in the longer abdomen of the latter. While relatively long, the abdomen is no longer than those of several other specimens (cf. figures 6, 7, plate 1) and falls within the range of variation that I describe for *S. inexpectans*. Thus *A. ornata* is synonymous with *S. inexpectans*.

## 7. Description

### (*a*) *Cephalon*

Evidence for the shape and convexity of the cephalon comes from many specimens, the most important being U.S.N.M. 139713 (figure 27, plate 4) and U.S.N.M. 139723 (figure 29, plate 4) for the transverse convexity of the posterior margin, and specimens U.S.N.M. 139720, U.S.N.M. 139676, and U.S.N.M. 139680 (plate 6; figure 24, plate 3; figures 56, 57, plate 8) for the general outline of the cephalon as illustrated in the reconstruction (figures 106, 107). This shows the cephalon in dorsal view to be rectangular and approximately three times as wide (tr.) as long (sag.) with notched lateral borders for the antenna and eye stalk. The posterior margin is straight to gently curved convex forwards, the anterior more so. The shape in dorsal view is a foreshortened one because of the relatively long and steep downward drop of the cephalon to the anterior margin. Although there are no specimens preserved in lateral view to confirm this, specimen U.S.N.M. 139713 (figure 27, plate 4) preserved in vertical attitude and U.S.N.M. 139720 (plate 6) in oblique lateral attitude serve equally well in showing the height of the cephalon. Wrinkles in the exoskeleton of specimens suggest transverse convexity of the cephalon to have been greatest medially with a flattening out laterally towards the corners and anterior margin.

On the ventral side, the cephalon is underlain by what is here termed the *doublure* which is a ventral plate extending backwards to at least the junction between the back of the cephalon and the first thoracic somite or slightly farther. This is well shown on two new specimens G.S.C. 49742 and G.S.C. 49745 (figure 80, plate 10; plate 11) collected in 1966 and has also been prepared out in two specimens (figure 12, plate 2; figures 64, 93), from the Walcott Collection. A ventral structure, called an epistome by Walcott (1911, p. 24), is thus confirmed though it is difficult to understand fully the nature of this plate from the specimen U.S.N.M. 57496 figured by Walcott (1911, pl. 5, fig. 3; figure 66, plate 9, herein) exposed from the ventral side. The specimen (figure 80, plate 10) shows the doublure to cover the entire lower surface of the cephalon and has been partly prepared to show the ventral surface of the latter immediately beneath, and also the line of articulation of the head and the first thoracic somite. The back edge of the doublure extends even as far as the junction between the first and second thoracic somite but I believe this to be too far. Thus by allowing for compression and restoring the convexity of the cephalon, the back edge of the doublure would lie beneath or slightly in front of the cephalon – first thoracic somite articulation. This is supported by other specimens preserved more parallel to the bedding including the lectotype (figure 65, plate 9).

The curved to slightly sinuous posterior edge of the doublure is best seen on the specimen (figure 12, plate 2) where the dorsal exoskeleton of the cephalon has been removed to reveal the doublure beneath. Walcott (1911, p. 24) remarks that this doublure (= epistome) is attached to the ventral edge of the cephalon, and I believe this to be along a line that functioned as a marginal suture during moulting similar to that in the Recent *Limulus*. Evidence for this includes the recognition of empty skeletons or moults that lack this doublure (figure 24, plate 3) and specimens such as the lectotype (figure 65, plate 9; figure 27, plate 4) in which the dorsal part of the cephalon is displaced laterally in relation to the doublure. The latter specimen, preserved in approximately vertical aspect shows both surfaces and the frontal margin along which they join. This line of contact is a flattened flange (cephalic flange) along the border of the dorsal cephalon and the ventral doublure (figure 20). The clear line of separation between the latter further supports the fact that the doublure is a distinct plate and not, as interpreted by Simonetta (1963), the rolled continuation of the cephalon onto the ventral side. There is no evidence as to the original convexity of the doublure, but in the prepared specimen (figure 12, plate 2) it is still slightly concave as seen from above, suggesting that the ventral surface was not flat but convex. The position of the posterior margin of the doublure will depend on the way that the head has been compressed. Thus in the lectotype (see Walcott 1911, pl. 2, fig. 1; figure 65, plate 9), preserved in parallel aspect, the trace of the margin can be seen through the dorsal exoskeleton and is approximately in the correct position. In specimens squashed more obliquely, the plate appears shortened (figure 5, plate 1) or is not apparent at all, while a line of compression corresponding to the border flange is visible.

Walcott (1911, pp. 21–23) refers to the entire frontal tagma as a cephalothorax bearing five pairs of appendages. How these were supposed to be inserted is hard to imagine especially since he recognized correctly that the doublure (his epistome) was 'quite as long if not longer' than the tagma. However, as shown (§7(*d*)), apart from the antenna there is no evidence that the cephalon carried additional appendages. In fact, if my interpretation is correct, that the entire ventral part of the cephalon is covered by the doublure, then there is no room for ventral appendages as large as those identified by Walcott. Because of its position, the doublure or ventral plate cannot be called an epistome nor, in the absence of ventral appendages, can the term cephalothorax be used for the anterior tagma (for definition see Moore 1969, p. R93). I have used the term *cephalon* in a much broader sense than that defined by the latter.

Simonetta (1963, pp. 98–101, figs 1, 2) refers to the anterior tagma as head and included in this three segments, the most posterior being what Walcott (1911) and I regard as being part of the thorax. In all the specimens that I have examined, this somite is articulated directly to the cephalon without an intervening segment (no. 2 of Simonetta), and in my view there is no evidence for the latter. Two of the specimens figured by Simonetta and said to show this second segment, U.S.N.M. 65057, 57487 (figure 5, plate 1; figure 65, plate 9) are both exposed from the dorsal side and show the curved impression of the back edge of the doublure lying beneath the cephalon. It is this line that Simonetta has mistaken as the junction between his first and second segment. In other specimens where the doublure is not as evident, a similar line can be produced that is an impression of the thickened anterior edge of the first thoracic somite (figure 21, plate 3; figure 73, plate 10).

Simonetta inserted paired masticatory appendages on the two posterior segments of the cephalon, but there is no room for them on the cephalon, and evidence for appendages of this type on *Sidneyia* is not sound (§7(*d*)). There is no direct evidence for identifying other segments in the cephalon as attempted by Simonetta although the presence of an antenna must imply an antennal segment. The function of the doublure is interpreted as being a stiffening plate associated with a sharp marginal edge which would be used when the animal ploughed in the sediment (§9(*b*)).

### (i) *Mouth*

As shown in the reconstruction (figure 106B) the cephalon hangs downwards relative to the thorax and abdomen which when stretched out horizontally, lies some distance above a level surface on which in a feeding position the cephalic doublure would rest. Between the doublure and the cephalon there is a space and the mouth must have lain somewhere in this and dorsal to the doublure. No positive evidence for a mouth or any possible supporting structure such as a labrum has been found, nor is there evidence for the nature of the integument which closed the gap between the doublure and the cephalon. Presumably this was a thin, non-sclerotized membrane into which some form of suctorial mouth opened. (See § 9 (*b*).)

### (ii) *Antenna*

Many specimens have the antenna preserved even though other appendages may be missing. This attests to a firm point of attachment of this appendage although details of this are not clear. In specimens preserved in parallel attitude from the dorsal side, the antenna extends from the notch in the posterolateral margin of the cephalon, is directed laterally, then curved forwards, and is clearly flexible. The edge of the cephalon and rim of the notch always lies above the antenna and is compressed onto it. Because the doublure completely covers the ventral side of the cephalon below the antenna (figure 73, plate 10) the appendage must extend through an opening on the side of the cephalon and near the posterolateral corner. The antennular notch in dorsal view is thus the compressed rim of this opening in the exoskeleton. Subsequent flattening of the cephalon has the effect of 'clamping' the antenna between the cephalon and the doublure and this may explain why the antenna is so frequently preserved. This is well illustrated (figure 67, plate 9) where preparation and removal of the cephalon from the dorsal side has revealed the antenna lying above the doublure. In a second specimen (figure 24, plate 3), preserved from the ventral side and lacking the doublure, the base of the antenna lies on top of the cephalic flange but does not extend further inwards. While this does not necessarily mean that the antenna was attached to this flange, it does indicate the approximate depth of insertion of the appendage into the cephalon. At the base of the antenna (figure 69, plate 9) there is a highly reflective area which probably represents either some form of muscular attachment or part of the flexible integument surrounding the base. This area is not sufficiently thick to suggest that it is a basal segment. Thereafter follows a series of proximal segments, about four in number, approximately twice as wide (tr.) as long. The remaining segments are longer and slimmer distally, each segment widening distally from the point of articulation with the preceding segment. At each joint paired setae are inserted along both inner and outer surfaces but not on dorsal or ventral surfaces (cf. Simonetta 1963, figs 1, 2). The most distant segments seem to lack setae. The most complete specimen (figure 13, plate 2) has a total of at least 20 segments, probably more, if the distal joints were clear. Walcott (1911, p. 20) observed 30 segments but none of his specimens that I have seen confirms this.

### (iii) *Eye*

Present on almost all specimens, including two (figure 37, plate 5; figure 82, plate 11) in which the antenna is missing, are areas, often highly reflective, that extend from under the edge of the cephalon in the region of the antennal notch. Both Walcott (1911, p. 20) and Simonetta (1963, p. 101) identified these as eyes, the latter referring to them as 'semi-lunar blisters', which on his reconstruction are inserted on the side of the cephalon. Walcott thought the eye to be a distinct lobe and I agree with him and believe the eyes to have been hemispherical and stalked. Shapes vary, and while the right eye on the specimen in figure 37, plate 5, might be termed semilunar, the left eye is oval, while in figure 25, plate 4, it is rounded to semicircular and in figure 44, plate 6, it is truly pedunculate. The relationship of the eye to the antenna is important and where both are preserved it is clear that the eye is always above the antenna and posterior to it.

Parts of the eye are very highly reflective, the arrangement depending on how specimens have been compressed. Thus, when the eye is laterally compressed as it is on the right side of specimens preserved in parallel aspect (figure 21, plate 3; figure 67, plate 9), the reflective area forms a broad band parallel to the outer curved margin of the eye. In a more parallel compression from the dorsal surface, the reflective area covers most of the upper surface of the eye (figure 37, plate 5; right eye) or is restricted to parts such as the centre of the lobe or to the outer margins (figure 82, plate 11). In the latter specimen, which lacks the antenna, the eye lies alongside the edge of the cephalon and overlaps the first thoracic somite, onto which it is compressed, with a fairly thick layer of sediment separating the two. This suggests that unlike in Simonetta's reconstruction (1963, figs 1, 2) the eye was raised up and out from the cephalon. There is always a change in slope between the inner rim of the eye and a lower part that disappears beneath the notched border of the cephalon. This lower part, interpreted as a stalk that bore the eye, is best seen in figure 44, plate 6. In the reconstruction (figures 106, 107) the eye stalk and socle are shown, with the reflective area corresponding to the possible ommatidial layer, forming a hemispherical summit to the stalk. The reflective area is not pyrite as thought by Simonetta (1963, p. 101). The eye and stalk are thought to have protruded upwards and outwards from the same notch in the cephalon as the antenna, the latter being somewhat below the eye.

In the absence of a reflective area, some specimens (figure 16, plate 2; figure 17) carry structures that are less convincing as eyes. Thus the blade-like structure on the left side of the specimen (figure 21, plate 3) looks more like some form of appendage (endite or exite) from the base of the antenna than an eye. Evidence against this however is: (1) the arrangement of the reflective areas are similar to those in other Burgess fossils possessing undoubted eyes, such as *Opabinia* (Whittington 1975*a*, p. 23, pls 9, 10) and various Crustacea (Briggs 1978); (2) the occurrence of the 'eye' without an associated antenna, suggesting that they are independent structures; (3) the lack of a plumose margin. Thus the evidence for an eye being present in *Sidneyia* is strong but, apart from its attitude morphologically above the antenna, there is no evidence to suggest how both parts were arranged segmentally in the head. As shown above, Simonetta's recognition of segmentation in the head is not correct. Further, his reconstruction gives the impression of an eye attached close to the dorsal exoskeleton but this is not supported from my studies. On the contrary, the eye is clearly separated from the cephalon, which is not broken as one would expect if the eye was once attached and then detached during compression.

### (*b*) *Thorax*

The thoracic region, which consists of nine somites (1–9), is divided into two parts on the basis of the ventral appendages. The *anterior thorax*, corresponding to somites 1–4 and *posterior* thorax corresponding to somites 5–9. Study of numerous specimens shows that somite 1 articulates with the cephalon in exactly the same way as succeeding segments do with each other, and there is no reason for regarding somite 1 as a cephalic rather than a thoracic somite as Simonetta

(1963) did. The shapes of each are best seen in the specimen U.S.N.M. 139676 (figure 24, plate 3), the most complete individual preserved in near-parallel aspect. This specimen not only allows both the anterior and posterior margins of each somite to be traced, but also shows the extent to which the somites were imbricated from front to back along the line of articulation. That the extent of imbrication in this specimen is thought to approximate to the original, is shown by the narrow area of overlap at the distal part of each somite, which is a minimal one. Therefore the imbrication along the sagittal line of the thorax could not have been less than is shown, or the lateral parts of the somites would not overlap. Similar complete specimens confirm this type of imbrication, while others show somites that have parted either due to compression or, as seen in figure 21, plate 3, when the axis of the body has been bent. In this case opening between somites on one side of the body corresponds to telescoping of somites on the other. Other forms of telescoping occur, such as that between the 7th and 8th somite in the specimen (figure 73, plate 10), which presumably results from a shuffling of somites during compression and after decay of the articulating membrane.

When specimens are viewed from the dorsal side, it is the line of the anterior edge of each somite that is the most prominent, and usually this edge is pushed up through the overlying and preceding somite (figure 66, plate 9). Along this line the overlying somite is often broken, the line of break being represented by a change in slope, and all or parts of the somite behind this are lost (figure 6, plate 1). If compression is less severe (figure 37, plate 5), then the anterior edge is reflected as a groove in the overlying somite, which is thus entire, and its posterior edge is a line with or without a change of slope between it and the succeeding somite. The thin posterior margin indicates that the somite lacks a sclerotized intucked fold of the type illustrated for the diplopod *Siphonophora* (Manton 1961, p. 409, fig. 10) but is more like that shown for *Polyzonium* (Manton 1961, p. 414, fig. 14). The thickened anterior margin, however, is the result of a ventrally directed fold or flange. This structure, known as a *prophragma* in Diplopoda (see Manton 1961, figs 10, 17, 18), gives added strength to the joint and is also an area of attachment for longitudinal body muscles. Where shown on the explanatory drawings, it is referred to as the articulation fold (af).

On specimens viewed from the ventral side (figure 11) overlap of the somites is shown by a marked change of slope along the anterior margin of the succeeding somite lying above the preceding one. The posterior margin of the latter can be traced inwards from the distal part of the somite and followed either as a shadow through the overlying somite or as a highly reflective edge. The latter can be accentuated when the specimen is immersed in distilled water or alcohol. Using this method it is often possible to distinguish short setose spines along this margin or along the lateral edge of certain body and abdominal somites (figure 70, plate 10).

In ventral view the articulation fold forms a strip of varying width, most often approximately parallel to the anterior margin of the somite, and extends between points just inside the free distal tips of the somite. Along the ventral margin of the latter is a narrow doublure formed by a continuation onto the ventral side of the rolled pleural edge (figure 37, plate 5). Details of the articulation between the cephalon and the first thoracic somite are shown on this same specimen and the trace of the posterior margin of the cephalon and the anterior margin of somite 1 shows that there is considerable overlap of the latter. This area is not a somite of the cephalon, as believed by Simonetta (1963, p. 101), and the specimen in figure 73, plate 10, shows that there is an articulation fold along the anterior margin of the first somite similar to that on succeeding somites.

Presumably the arthrodial membrane at the different points of articulation was attached to the anterior and posterior margins of succeeding somites. In figure 37, plate 5, such a membrane could be the narrow area of highly reflective material that, in part, follows the anterior margin of the somites.

### (*c*) *Abdomen*

Reference to figure 40, plate 5, and the reconstructions (figures 106, 107) shows that the abdomen consists of three somites ($ab_{1-3}$) which form simple articulated rings, and a fourth terminal plate or telson. Paired uropods articulate with the posteriormost abdominal ring and together with the telson form a caudal fan. The reconstruction was based on specimen U.S.N.M. 139676 in which the three somite rings can be easily recognized and others (figure 7, plate 1; figure 10, plate 2; figure 70, plate 10) also show this to be the case. Some specimens, however, clearly do not, and when the telson is present there are only two rings in front of it (figure 22, plate 3), $ab_2$ being relatively long and presumably incorporating a fused third ring. The proportionately longer abdomen that results seems to be a real one, though abdominal shape and differences in the shape of the telson can be partly explained by angle of burial and subsequent compression. The two types of abdomen recognized here are considered to fall within the limits of variation shown by other structures though the possibility that they represent dimorphs cannot be excluded. Walcott (1911, p. 24) considered the posterior region of the abdomen to consist of three segments, including the terminal structure, while Simonetta (1963, p. 106) included three abdominal segments plus this structure. Both authors made no remarks about the anus, a point of reference necessary in defining the terminal portion of the animal. As described (§ 7 (*e*)) the anus opens on the anteroventral surface of the terminal somite, which is thus a telson. The best specimen (figure 40, plate 5) shows the telson to be triangular, widest (tr.) posteriorly. Dorsally there is a gently raised rectangular central area separated by a conspicuous line from lateral areas defined posteriorly by a cuspate margin. Various wrinkles in the exoskeleton along the length of these lateral areas suggest that they are much thinner and more flexible than the median area. There is certainly no evidence from the material studied to suggest that these wrinkles are the imbricated margins of several lamellae (Simonetta 1963, figs 1A, B). The posterior border of the telson was also thinner and more flexible than elsewhere, which accounts for the varying shape of the margin when compressed (plate 1). On the ventral surface, the true nature of the anal opening is unknown, though on many specimens a roughly circular area marks where the alimentary canal ends. Covering this area is a raised level, the anal plate (figure 40, plate 5), and compression of the telson often causes this to be reflected on the dorsal surface (figure 6, plate 1; figure 23, plate 3). Presumably the anus lay within this plate, perhaps in the form of a slit surrounded by flexible membrane. The gently curved anterior margin of the telson articulates with the preceding abdominal somite and the degree of overlap can be judged by tracing the posterior margins of the latter on the dorsal and ventral sides. Highly reflective areas occur in some specimens and may be traces of muscles. When the telson is pulled away from the abdomen (figure 23, plate 3) or is missing altogether (figure 44, plate 6), some idea of the articulation can be seen. Thus on the former specimen the abdominal somite is compressed and shows dorsal and ventral surfaces and respective posterior margins. Projections or spines occur medially and laterally, the latter surrounding the sockets into which the uropods articulate.

Walcott (1911, p. 24) believed the 'swimmerets' (uropods) to be attached to the telson and in the specimens figured by him it is difficult to interpret this otherwise. In specimen G.S.C. 49744 (figure 23, plate 3) both telson and uropods have been detached from the abdomen together. However, when the margins of the preceding somite are traced and a well defined overlapping arrangement is obvious as it is in specimens figured as figure 10, plate 2, and figure 22, plate 3, the uropods clearly articulate independently of the telson in lateral sockets. I therefore agree with Simonetta (1963, p. 106) that the uropods belong to the abdomen and not the telson. How much freedom of movement the uropods had is difficult to demonstrate and none shows any angular displacement sideways from the telson. The specimen illustrated as figure 40, plate 5, shows the best undistorted shape of the uropods, which are broad and lobe-like with an indented and plumose posterior margin. This was probably equally as thin and flexible as the lateral and posterior parts of the telson, but the anterior edge is thickened, and thus stiffer, with a curved distal spine. This thickening is more apparent in figure 10, plate 2, but this is probably a more oblique compression. Walcott (1911, p. 24) believed the abdominal somites to be simple annular rings, and when specimens have been suitably compressed dorsal or ventral and internal surfaces can be exposed. The diameter of the rings decreases posteriorly and the preceding ring overlaps the succeeding one, but the type of articulation is not known. The amount of overlap between $ab_2$ and $ab_3$ suggests that articulation was probably fairly rigid and that the abdomen could only have been flexed slightly and not curled round under the thorax. Various spines and projections are seen along the margins of abdominal somites on suitably preserved specimens.

### (*d*) *Thoracic appendages*

Previous views of the number and type of thoracic appendages have led to confusion mainly because poorly preserved appendages *in situ* have been wrongly interpreted by means of more complete but isolated specimens. Further, Walcott (1911, pl. 2, figs 2, 3) wrongly identified as *Sidneyia* two specimens later shown (Walcott 1918, p. 118) to be *Emeraldella*. These two specimens were the reason for Walcott (1911, pp. 21–25) identifying five pairs of appendages on the cephalothorax of *Sidneyia*, a number later accepted by Størmer (1944, p. 89).

Among the isolated appendages was one, U.S.N.M. 57494 (Walcott 1911, pl. 5, fig. 1; figures 49–50, plate 7, herein), interpreted (figure 46) as being a posterior thoracic appendage consisting of a broad based coxa, gill branch and leg. Walcott's interpretation was that this appendage was three separate head appendages (his 3rd, 4th and 5th) compressed together. Details of each appendage, greatly enhanced by retouching of his figure, were thought to be recognizable on specimens *in situ* and were also seen to share features of a large number of isolated appendages (Walcott 1911, pl. 4). Thus the distal part of his supposed appendage 3 (cb, figure 46) was conveniently retouched to show segments, and this part compared with a more complete isolated appendage (Walcott 1911, pl. 4, fig. 4) showing a segmented main shaft bearing long blade-like scales and with chelate-like terminal section.

Additional specimens (Walcott, pl. 4, figs 1–3) showed further details. The supposed 4th appendage (podomere 1 of leg with gill attached, figure 46) was also retouched to show a slim elongated distal shaft said to have three small spines. These are not evident on Walcott's figure (pl. 5, fig. 1) nor are they present on the specimen. The supposed 5th appendage (leg, figure 46) was correctly interpreted as a leg but the setal spines on the inner side of each segment were thought by Walcott to be branchial filaments as in the specimens (Walcott 1911, pl. 2, figs 2, 3) then included in *Sidneyia* but subsequently shown to be *Emeraldella*.

Only two entire exoskeletons figured by Walcott (1911, pl. 2, fig. 1, lectotype; pl. 6, fig. 3) show details of what he interpreted as being the 2nd head appendage (the first being the antenna). On the lectotype (figure 65, plate 9; figure 62) a poorly preserved leg has been squeezed up between the back of the head and the first thoracic somite, and could well belong to the latter. Appendages behind the left antenna are similar but not well preserved. On the right side, the segmented appendage with slightly expanded distal end coming out from beneath the third segment is the trunk and tail of a *Waptia*. This was considerably retouched on Walcott's figure, but was nevertheless subsequently included in Størmer's (1944, p. 90, fig. 17, 9–10; 1959, p. O27, fig. 16) drawing of the counterpart and photograph of the part. What is of interest on the lectotype is the way in which the cephalon is slightly tilted backwards and is compressed onto the underlying doublure. The region between the back edge of this and the posterior margin of the cephalon is where Walcott believed the last four pairs of head appendages were attached, including the large masticatory organs of the type only known isolated and figured (Walcott 1911, pl. 4).

Simonetta (1963, p. 101) likewise included a pair of large masticatory appendages on the same area of the cephalon which he erroneously interpreted as being the second segment (§7(*a*)) and another pair on what I interpret as being the first thoracic somite (Simonetta's third segment of the head). Not one specimen of *Sidneyia* that I have studied shows appendages of this type *in situ*, nor as expressed (§7(*a*)) is there any room on the head for an appendage of this size behind the back edge of the doublure. Simonetta (1975, p. 20) maintains that there is evidence but fails to produce any. It is wrong to maintain as he does that Walcott (1911) and Størmer (1944) illustrated one of the types with the big grasping leg *in situ*. Although not named specifically, this specimen is presumably the lectotype, the only specimen that Størmer figures, and this does not show any appendage that can be recognized as being grasping or masticatory, a view also shared by Størmer (1944, p. 89). Nevertheless Størmer, following Walcott, accepted that such an appendage existed and that it was likely to be the first postoral.

Isolated appendages can only be unequivocally assigned to a particular animal if examples are also known *in situ*. For this reason the numerous isolated appendages described by Walcott (1911, 1912, 1916) and Simonetta (1963, 1975; see synonomy, §6), must be excluded from *Sidneyia*. I have examined them and believe them to belong to a much larger and hitherto unknown animal while Briggs (1979) believes that some may belong to the same arthropod that bore the walking appendage *Anomalocaris*.

As the following discussion will show, I believe the cephalon of *Sidneyia* to have borne the eyes and antenna but no legs.

### (i) *Anterior thorax*

Three specimens (figures 25–27, 29, plate 4) preserved in vertical attitude provide unique cross sections of *Sidneyia* in the region of the head and succeeding anterior thorax. Present in all are paired structures which meet along the midline with a series of closely interlocking spines extending from the inner edge. Lateral to this spinose margin the structure tapers outwards and curves upwards reaching the inner surface of the somite immediately above. The original of figure 27, plate 4, shows at least two of these spinose edges which are imbricated over each other from front to back and thus represent a succession of structures that hung down from beneath the body in a vertical plane. Associated with these are a series of jointed appendages which are curved upwards under the dorsal exoskeleton, their distal tips being held just inside the outer extension of the pleurae. These appendages, or legs, can be traced inwards towards the midline and on the specimen (figure 29, plate 4) two of these legs are each attached to the ventral face of a vertical structure on the same level. One isolated leg preserved alongside the specimen (figure 25, plate 4; figure 88, plate 12) shows in detail how the leg is attached to an enlarged basal segment (coxa) consisting of a mesially directed lobe fringed with spines forming a gnathobase, and a lateral coxal bar which extends upwards and terminates with a curved distal flange.

Coxa and legs are also visible on numerous specimens preserved in parallel aspect and four collected in 1966 show a series of coxa partly imbricated and lying with either posterior or anterior face facing the ventral surface of the exoskeleton. Four coxa with spines of the gnathobase are present down the right side of the specimen (figures 82, 83, plate 11), and although difficult to relate to their thoracic somites are thought to belong only to numbers 1–4 respectively. Reasons for believing this are numerous and rely mainly on the fact that, where the distal flange of the coxal bar can be identified, this always lies approximately beneath its corresponding somite and never extends to the cephalon (Simonetta (1975, p. 20) maintains that they do but he included in the head what is here considered to be the first thoracic somite). Thus in specimen U.S.N.M. 139713, preserved in vertical attitude, the highest coxal bar and flange immediately below the cephalon (cox$_1$, figure 32) lies approximately below somite 1 and coxa 2 beneath its somite. This is further substantiated by a new specimen exposed from the ventral side (figure 73, plate 10) where the first coxal bar (cb$_1$, figure 80) reaches to somite 1 and the curved distal flange lies on top of it. Whether this was the natural position of the flange is not known with certainty, but it seems likely. The position of the gnathobase however is not a natural one. On the specimen illustrated as figure 82, plate 11, the anterior face of each coxa is uppermost, indicating by direct comparison with specimens preserved in vertical attitude (plate 4) that the coxal lobe and bar has been rotated through 90°. Restoring the coxa to the vertical position and swinging the coxal bar so that it lies more or less transversely, will bring the gnathobases in line, that of the first coxa being directly behind the back edge of the cephalic doublure and near the assumed position of the mouth. Recognition of anterior and posterior faces of the coxa is simple if the coxal bar is present since this is always dorsal, or if corresponding legs are present, since these are ventral in natural position. In specimens preserved in parallel aspect, the rotation of the coxa and legs is such that the latter always lie parallel to the bedding and are curved backwards when the posterior face of the limb is uppermost (figure 67, plate 9) or forward when the reverse is the case as it is in figure 82, plate 11. This specimen shows superbly how four coxal lobes (cox 1–4, figure 81) with gnathobasic spines, are imbricated from the anterior backwards, while laterally the distal spine-bearing podomeres of four legs (R $l_{1-4}$) are similarly imbricated in the same order. It seems inescapable that these are legs of the corresponding coxae. All four coxae have been displaced in relation to the overlying thoracic somites, the legs more so, and they lie bunched up and protrude from beneath the posterolateral corner of the cephalon. A similar situation occurs in specimen U.S.N.M. 139713 (figure 27, plate 4), in which legs extend from beneath the cephalon in the region of the antennal–ocular notch and on the right side (as viewed) even overlie the antenna. Likewise specimen U.S.N.M. 139720, preserved in oblique lateral attitude (plate 6), shows the distal podomeres of anterior thoracic appendages telescoped and imbricated under the cephalon and extending beyond it, those on the right side (as viewed) being below the antenna. In this specimen Simonetta (1963) believed these to be the lamellae (segmental scales) of two pairs of grasping head appendages of the type illustrated on his reconstructions. He repeats this again (Simonetta 1975, p. 20) in reply to my explanation given at an international meeting held in Oslo in 1973. However, he has produced no new and convincing evidence in support of his claim.

### (ii) *Coxa*

The coxa, which forms the enlarged basal podomere of the leg, consists of two parts referred to above as the gnathobase and the coxal bar with flange. Details of this podomere, seen *in situ* on a number of specimens, can also be obtained from several isolated specimens, among which are two (figure 55, plate 7; figure 88, plate 12) thought to belong to the anterior thorax because they lack the gill branch (§7(*b*)). The coxa is widest at the gnathobase, becoming narrower distally along the length of the curved bar, which ends distally (dorsally) in a blade-like flange. The latter forms an acute angle with the bar, the junction being marked by a deep groove (figure 28, plate 4). This is not a joint nor is there any reason to believe that movement could have taken place along the groove. It is assumed that the coxal bar was flattened antero-posteriorly, with a rounded ventral surface and a dorsal coxal cavity. Evidence for the latter is $\text{cox}_4$ (figures 70, 71, plate 10; figure 75), which has the cavity partly infilled with sediment between the inside wall of the anterior face and the dorsal edge of the posterior face of the bar. The inner margin of the gnathobase appears to be straight and bears a double row of spines, which would be directed towards the midline in natural position. These rows occur on the anterior and mesial edges of the gnathobase (figure 71, plate 10; plate 11) though because of compression it is not always easy to decide from which edge they extend. Spines on coxae 3 and 4 of specimen G.S.C. 49745 (figure 83, plate 11) are all short, blunt and solid, and when immersed in alcohol show highly reflective tips. Spines on coxae 1 and 2, however, are longer and thinner, both rows giving a more 'bushy' appearance to the gnathobase. For this reason the isolated leg U.S.N.M. 139708 (figure 55, plate 7) is considered to be one of the first three anterior thoracic appendages. This specimen has a stout spine at the ventral corner of the gnathobase and similar spines situated on the lower half of the mesial edge. The stout ventral corner spine seems to be common to gnathobases of all anterior thoracic appendages.

On the isolated appendage (figures 49, 50, plate 7) a lobe-like structure with fringing spines lies directly above the dorsal corner of the gnathobasic lobe and could well be a type of movable endite contained in the dorsal cavity. However, no other coxa has this structure.

### (iii) *Legs*

All complete examples of legs (figure 55, plate 7; figure 58, plate 8; figure 88, plate 12) show, in addition to the coxa, seven podomeres, or eight if one regards the distal claws as a separate podomere. For the purpose of this description I do not consider the distal claw to be a podomere, nor do I follow Simonetta (1963) in naming each podomere. Podomere 1 is short and on the inside margin has a lobed extension bearing long stout spines. In natural position these extend inwards below the ventral spine of the gnathobase (figure 107*b*). During abduction and adduction of the limb these spines would probably interlock. Specimen U.S.N.M. 139705 (figure 55, plate 7) shows that there is a change of slope between the main part of the podomere and the lobe, indicating that the latter is an endite of podomere 1. Whether this endite projected from the anterior face of the podomere in natural position, as suggested in Simonetta's (1963, fig. 20) reconstruction, or from the inner face, is difficult to decide. Study of the isolated right leg (figure 88, plate 12) supports Simonetta's conclusion since the ventral edge of the gnathobasic lobe overlaps the endite, and trace of the dorsal margin of the latter can be seen lying beneath. However, the reverse is the case on leg 4 of specimen U.S.N.M. 139723 (figure 31). I have concluded that the endite was attached to the mesial (inner) face of the podomere and explain the apparent contradiction noted above by the fact that, following decay of the arthrodial membrane between the first podomere and the coxa, the latter has overridden the podomere, which thus either lies under the coxa or is telescoped into the articulating area. In the isolated appendage U.S.N.M. 139708 (figure 55, plate 7) the first podomere and endite lies above the coxa, which has a broken dorsal edge and bar. Simonetta (1963, p. 103) refers to this specimen and states that it shows a peduncle of the coxa (to which, in his interpretation the gill was attached) and gill filaments. I interpret the 'peduncle' to be the broken and truncated coxal bar and cannot identify any filaments. Simonetta's remarks probably refer to specimen U.S.N.M. 57494 (figures 49, 50, plate 7), which I interpret as being a posterior thoracic appendage in which the gill is attached, not to the coxa, but to the first podomere of the leg (figure 46). The type of articulation between the first podomere and the coxa is not clear, though the junction between the two suggests that this is a mesial pivotal articulation. A contrast in reflective area behind the pivotal point might be the thick arthrodial membrane necessary for leg 'rocking' or promotor–remotor swing. Podomeres 2 and 3 of all legs are of approximately the same size, longer from dorsal to ventral surface than wide (tr.), and have a series of tufts of strong spines from the lower anterior and posterior surfaces. Podomere 3 is characteristically wider (tr.) than long but equally spiny on the ventral surface. The relative sizes of these three podomeres can be recognized on all specimens whether isolated or *in situ*. In the latter case they can be identified and numbered even if the limb is incomplete (figure 31). When the leg is compressed in parallel aspect, as it is in specimen U.S.N.M. 131703 (figure 55, plate 7), podomeres 2, 3 and 4 have a dorsal spine which extends from the margin in the direction of the length of the leg.

Articulation between podomeres 1 and 2, 2 and 3 and 3 and 4 is thought to have been pivotal, that between 1 and 2 and 2 and 3 taking place medially with movement being greatest ventrally as shown by the large expanse of arthrodial membrane. Movement between podomere 3 and 4 was apparently less as the trace of the inner edge of podomere 4 shows that this pivotal joint was a simple cuticular imbrication between the edges of overlapping podomeres from front to back. Podomeres 5, 6 and 7 become progressively slimmer distally, there being stout incurved spines from the base of podomeres 6 and 7 in the region of the articulation (figure 48). The arrangement of these spines much depends on the way that the limb has been compressed. Thus in parallel anterior–posterior compression they appear to be single (figures 49, 50, 55, plate 7), but on a leg compressed slightly obliquely (figure 58, plate 8) the spines are paired and arise from the base of the podomere and project inwards from the ventrolateral faces. In describing leg U.S.N.M. 139708, Simonetta (1963, p. 103, fig. 20) believed the spines to arise at the distal end of the podomere (his tarsus) while on his reconstruction it is correctly shown. His reconstruction however shows only seven podomeres including the coxa and he fails to recognize an additional podomere (podomere 6, figure 48) between the tarsus and the pretarsus. It is correct that the specimen figured by him (Simonetta 1963, pl. 12) is incomplete in this region, but the counterpart (figure 53, plate 7) is complete and my interpretive drawing combines details from study of both part and counterpart.

Additional spines occur between the basal spines of podomere 7 and the distal claw. This long incurved claw appears to articulate with podomere 7 and is flanked by shorter paired spines at the articulation. These are seen well on specimen U.S.N.M. 65057, in which the distal part of the leg has not been rotated and the dorsal surface is seen in parallel compression (figure 6, plate 1).

Articulation between podomere 4 and 5 is thought to have been a hinge joint (Manton 1973, p. 272, fig. 11*e*; 1969, p. R17, fig. 1E) on account of the angular flexure seen at this point (figure 29, plate 4; figure 55, plate 7), the difference in diameter between podomere 4 and 5, and the enlargement of what is interpreted as arthrodial membrane on the inside of the joint (figure 58, plate 8), where movement would be greatest. Articulation between podomeres 5 and 6 and 6 and 7 is less obvious but, since in all specimens this part of the leg is always held aligned, it is thought that the articulations were simpler and perhaps separated by a short limiting area of sclerotized cuticle allowing only slight flexure.

Anterior thoracic legs of the type described above can also be recognized *in situ* though they are seldom as complete or in natural position. Nevertheless specimens such as those illustrated in figure 11, plate 2, plate 6, figures 67, 68, plate 9, and figure 98, plate 13, show complete legs in natural succession, and all sufficiently near the back edge of the cephalon and doublure to cast added doubt on Walcott's and Simonetta's claim that there were appendages anterior to them. Preparation of specimen U.S.N.M. 139681 (figure 64) has revealed part of a leg lying above the antenna in the head region and apparently between the dorsal exoskeleton of the cephalon and the inner face of the doublure. However, in this specimen considerable foreshortening and compression of the cephalon has resulted in the doublure being pushed backwards relative to the overlying dorsal surface with the leg displaced so that it lies between the two. Otherwise a forward rotation of legs beneath the cephalon will account for their unnatural position in this region and explains the basal part of leg 1 seen lying below the cephalon as shown in figure 81. Nevertheless unless the distal part of the leg can be traced with some certainty to its corresponding coxa proximally, as in $l_4$, figure 31, it is not possible to assign the appendage to its body somite. This specimen shows four legs in succession down the length of the animal and these are interpreted as being legs of the first four thoracic somites. Size of podomeres and the total length of each limb is remarkably constant and there is little increase in size from front to back. Likewise these limbs correspond well with those of isolated specimens of similar size preserved in parallel compression, and are used as the basis for the reconstructions (figures 106, 107). Only in the specimen U.S.N.M. 139679 (figure 98, plate 13), preserved in oblique dorsal view, has the right anterior limb been distorted and the unusually large podomeres are thought to be a result of compression. Distortion of the left side coxa, however, seems to be less and they correspond well with the coxae *in situ* on exoskeletons of comparable size.

No specimens that I have studied display gills on the anterior thorax. There are however traces on weathered specimens of numerous parallel depressions beneath the exoskeleton, some of which appear to be associated with parts of limbs and coxal bars. Their relationship to these, however, is not clear and in some cases they can be bunches of gill filaments which seem to have been detached from more posterior somites and lie in an unnatural anterior position. Some impressions are almost certainly those of setal spines from the ventral (inside) of the legs. Thus in specimen U.S.N.M. 65510 (figure 11, plate 2) these are considerably longer and more bushy than those seen on isolated specimens and it could well be that these were an additional and effective means of aiding food capture and movement towards the mouth.

Gills are therefore not thought to have been present on anterior thoracic appendages and the fact that isolated appendages of *Sidneyia* type lack the gill branch, confirms this. Evidence for the number of somites that did not have gills is however equivocal, but as shown in §7 (*d*) (iv) I conclude that gills were not present on the first four thoracic somites.

### (iv) *Posterior thorax*

Numerous specimens preserved in parallel aspect show parts of legs and associated filamentous appendages mainly on the posterior half of the thorax, but all are incomplete and not one specimen shows the appendages in succession.

Walcott (1911, p. 26) identified only gills on all nine somites, yet despite heavy retouching of his figure of the lectotype (Walcott 1911, pl. 2, fig. 1) only seems to portray them on the last six somites. My study of the lectotype shows that lamellar structures can only be recognized with certainty on the last four somites of the thorax. Størmer (1944, p. 90, fig. 17(12)) believed that evidence for legs on the posterior part of the thorax was also lacking and this is not surprising since none of Walcott's type specimens shows these. Nevertheless Størmer's interpretation of the gill being attached to a jointed shaft is not supported by specimens, while Sharov's (1966, p. 33, fig. 19*c*) interpretation of a modified posterior walking limb is fanciful. This was based on the isolated specimen U.S.N.M. 57486, which Walcott (1911, pl. 3, fig. 1) thought to be part of a gill. I have studied this specimen together with its counterpart which Dr D. E. G. Briggs observantly found among uncatalogued material in the Walcott Collection. Study of this confirms the opinion of Simonetta (1963, p. 105) that it is not a gill of *Sidneyia*. Dr S. Conway Morris has since recognized it as being a decayed and folded specimen of the worm *Ottoia prolifica* (Conway Morris 1977, pp. 7–8).

Simonetta (1963, fig. 1*b*) includes lamellar structures that he interpreted as gills, and legs, on eight thoracic somites, but presents no evidence for this number nor does he illustrate specimens showing gills and legs *in situ*. Not listed among specimens studied by Simonetta is U.S.N.M. 139681, part and counterpart, which have been prepared to show the relationship between legs and gills *in situ*. Careful removal of the dorsal exoskeleton on the right side of the part (figure 67, plate 9; figure 64) shows the silver reflective outline of a series of legs which have been rotated through 90° so that their posterior faces lie uppermost and the distal podomeres are curved backwards. Disruption of the specimen along the midline has unfortunately destroyed details of the proximal part of the posteriormost legs which abut clumps of infilling of the alimentary canal. Anteriorly, however, two imbricated gnathobasic lobes of coxae are preserved, these also having their posterior faces uppermost. All legs have been slightly displaced from corresponding somites but only insofar as they have swung backwards distally and six legs ($l_4$–$l_9$) (figure 64) can be recognized. Associated with five of these legs ($l_5$–$l_9$) are a series of pad-like flaps, best seen on the counterpart (figure 68, plate 9), each with a finely plumose semicircular margin. These flaps are imbricated but, unlike the tiles on a roof, overlap each other from back to front when viewed from the dorsal side, and also lie morphologically above the legs. In some cases the legs have been partly pushed up through the flaps but study of the counterpart leaves no doubt as to the relationship between the two. Morphologically above the pad is a series of broad blade-like filaments, interpreted as being gills, which are imbricated and apparently attached in some way to the uppermost (dorsal) surface of the flap. These are best seen on the left side, where, although filaments and flap have been displaced forwards relative to the overlying somites, there is no doubt as to the succession of levels below the carapace which is: filaments, flap, leg. These filaments are sometimes visible on the ventral side of the flap, but only as a reflective outline showing through what must have been a fairly thin membrane.

A specimen preserved in vertical attitude (figure 25, plate 4) with the cephalon obliquely compressed shows the relationship between more posterior legs and a gill flap in what is assumed to be one of several possible natural positions. On the left side (as viewed) a flap lies above a series of successive legs, its lower curved plumose margin therefore being posterior and the nearest face being ventral. No filaments are visible, nor would one expect to see them if they were attached to the reverse or dorsal face of the flap. In this position it would appear that the gill flap could hang down ventrally at an angle between successive legs. This is the position shown on the reconstructions (figures 106, 107).

On no specimen are complete coxae, legs and gills preserved *in situ* on the posterior thorax, and at best only parts of the latter are present. Coxae with associated gills and legs are known as isolated specimens (figure 58, plate 8) and are thus shown on the reconstruction. Why coxae are not preserved *in situ* on the posterior thorax is difficult to explain, especially since they are present on the anterior thorax. Two reasons may be suggested, first that the anterior thoracic coxae being involved in transverse biting and shredding of food (§8(*b*)) were more highly sclerotized and robust, and secondly (as a corollary of the first) that the heavier musculature needed for these movements means that the coxa was more firmly attached and therefore not easily lost during transport and burial. Certainly isolated specimens such as U.S.N.M. 250211 (figure 54, plate 7) and U.S.N.M. 13970B (figure 86, plate 12) have a much simpler form of gnathobase which one would expect the farther away from the mouth they are placed. Examples of this type, such as the gill-bearing appendages illustrated in figure 58, plate 8, are therefore considered to be more posterior. In this specimen two legs (A and B), belonging to left and right sides, are preserved back to back with the anterior faces of opposing coxae uppermost. The coxal bars are incomplete, that on B being broken and truncated. Parts of the gill flaps bearing gill filaments on the upper (dorsal) surface lie above the leg and between the dorsal surface of this and the ventral edge of the coxal bar. Rotation of leg B in relation to its coxa is shown by the anterior and posterior edges of podomere 2, which are not aligned, and the way in which the dorsal edge is visible as a line beneath the overlying gill. Of interest is the way in which the gill flap appears to be attached to the dorsal surface of podomere 1 in a manner similar to that shown in U.S.N.M. 57494, the specimen figured by Walcott (1911, pl. 5, fig. 1), which was wrongly interpreted by him as being three successive appendages (§7(*g*)). This specimen (figures 49, 50, plate 7) is not as poorly preserved as Simonetta (1963, p. 103) maintains and shows the coxal bar obliquely compressed to reveal both anterior and posterior rims of the dorsal coxal cavity, parts of the gill flap and a leg. The anterior margin of the gill flap is a distinct line between the ventral edge of the coxal bar and the upper surface of the leg, while the plumose posterior margin is seen along the inner edge of the leg. A series of gill filaments attached to the anterior margin of the gill flap clearly overlie the leg of the part and are thought to be on the dorsal surface of the flap, yet the plumose margin on the counterpart appears beneath the leg. This apparent contradiction is explained by the fact that during compression the leg has been pushed up through the thin membranous flap and thus lies unnaturally above it. The part of this specimen (figure 49, plate 7) is thus a left side appendage. The gill flap is attached at the proximal end of the dorsal surface of podomere 1 of the leg, the area of attachment being a slim triangular area widest at the contact and tapering distally along the anterior edge. This area is delimited behind the anterior edge by a line interpreted as being a hinge along which the gill flap could be moved upwards and downwards. This hinge line, here called the gill flap fold (gff), is present on the incomplete right side appendage (figure 54, plate 7), where parts of a gill flap overlie the leg and there is a notch in the posterior border at the hinge. Behind this notch, part of the curved plumose posterior margin of the flap is visible. Characteristic of both this specimen and U.S.N.M. 57494 is the way that the mesial edge of the gnathobasic lobe of the coxa is gently curved, not straight as in appendages from the anterior thorax; but they do have the spinose endite from the inner face of podomere 1.

On the counterpart of U.S.N.M. 57494 (figure 50, plate 7; figure 46) a sinuous line crosses the base of the coxal bar but although merely a fold in the exoskeleton it may also reflect a natural change of slope caused by different convexities of lobe and bar. Interestingly enough this corresponds approximately to the line of fracture of the coxa of specimen U.S.N.M. 139708 (figure 55, plate 7), but less so than that of the broken fragment of a gnathobasic lobe, U.S.N.M. 139704, illustrated by Simonetta (1963, pl. 9). It was this specimen that Simonetta (1963, fig. 2D) used in his reconstructions of the gill–coxa attachment, referring to the broken edge as a peduncle to which the gill was attached. Specimens described above clearly show that the coxal bar and gnathobasic lobe are part of the same structure and that the gill branch was attached to the first podomere of the leg.

The posterior appendage (figure 54, plate 7) shows that the reflective area outlining the parts of the appendage are patchily arranged, podomere 1 being highly reflective, while only the outline and spines are reflective on the succeeding podomeres. Wisps of reflective material also occur between the anterior edge of the gill flap and the coxal bar as they do in specimen U.S.N.M. 57494, but this is thought to be a preservational effect and there is no definite proof that the gill flap and coxal bar were in any way joined to each other.

Yet another modified appendage type is shown in figure 72, plate 10. This exhibits an almost complete gill flap lying beneath a leg attached to a coxal bar. The thickened plumose posterior margin can be followed inwards beneath the base of the leg, where the gill flap fold arises from the first podomere. The gill flap widens distally, the outer curved margin being thickened and bearing a tuft of fringing spines at the posterolateral corner. A similar ending to the flap can be recognized on the 9th gill of U.S.N.M. 139681 (figure 64) and both specimens explain similar structures occurring on somites 5–9 on U.S.N.M. 65510 (figure 11, plate 2). The flaps overlie each somite when viewed from the ventral side but only the distal part and part of the anterior margin are preserved. The latter is raised and thickened and interpreted as being the stiffening edge to which the gill filaments were attached. The fact that these structures occur on the last five somites is additional evidence for suggesting that the four anterior thoracic somites did not carry gill-bearing appendages. Although incomplete, the gnathobasic lobes on U.S.N.M. 139722 (figure 78) carries a series of long setose spines which also form thick tufts along the inner surface of the leg. Only six podomeres (one less than the anterior limbs) can be recognized on the leg, the distal podomere 6 bearing a long claw-like spine which appears to articulate at the joint and opposes a smaller spine on the inside of the podomere. Whether the distal spine could close against the latter and function as a form of chela is impossible to decide and this is the only specimen known showing this. There seems little doubt that this type of appendage belongs to *Sidneyia* since the gill flap is identical to those found *in situ* on complete individuals. The shortened leg is also similar to those found *in situ* on the posterior thorax of complete individuals, indicating that the appendage belongs here and in all probability to the 8th or 9th somite. If this is correct, then the spinose inner surface of the leg indicates that all thoracic appendages had a prehensile function and were involved with the movement of food from the posterior forwards, the anterior appendages being the most powerful. These possess strong spinose endites and such structures are missing on the posterior legs.

The gill flap with plumose margin on specimen U.S.N.M. 139722 was interpreted by Simonetta (1963, p. 102) as being the external margin of the exoskeleton, but clearly the size and shape of the gill flap does not correspond to a thoracic somite nor do similar structures preserved *in situ* show that they were, as Walcott (1911, p. 26) believed, attached to the ventral surface of the body. They are always associated with legs to which they are attached, and gill filaments, and are interpreted as being the ventral membranous cover to these dorsally arranged structures.

### (v) *Gill filaments*

When found *in situ* on specimens preserved in parallel aspect, filaments of the gills always lie directly beneath the dorsal exoskeleton and consist of a series of broad, blade-like imbricated structures. The way in which they are imbricated may vary on the same specimen but rarely on the same gill, suggesting that these filaments lay at right angles to the gill flap to which they were attached, and have been flattened during compression so that either flat face lies uppermost. In all cases, the proximal part of each filament seems to extend backwards from the region of the anterior margin of the gill flap and is thought to be attached here in some way. Specimens preserved in parallel aspect from the dorsal side also show filaments belonging to the same gill to consist of two sets, one above the other, though the relationship is never clear. It is clear, however, on numerous isolated specimens that show both sets of filaments to be joined along a common axis as recognized by Simonetta (1963, fig. 2D; Bergström 1979, fig. 1, 3G), but, unlike this interpretation, mine implies that the axis is not a shaft but part of the proximal margin of the gill flap to which the filaments are attached. The structures can be likened to a book where the proximal margin corresponds to the spine of the book and the gill flap to the lower cover and the two sets of gills are the top cover and first page which have been cut into strips across their width.

Opening the book by folding back the top cover would correspond to what is seen in specimen U.S.N.M. 139718 (figure 74, plate 10), in which one set of filaments opens outwards along the proximal margin, the other set lying imbricated but flat on the gill flap. Both unfolding and tearing away of the gill filaments from the anterior margin of the gill flap occurs, and filaments do not always necessarily belong to their corresponding flap. Almost certainly some gill filaments, such as those below leg B (figure 60) belong to other appendages, and stray filaments centred way above the gill flap (figure 78) either have become detached from it or belong elsewhere. A remarkable but isolated specimen is U.S.N.M. 139708 (figure 86, plate 12), which shows both sets of gill filaments opened out along the line of common axis of the gill. Opening has not been entirely symmetrical along the axis, some filaments of one side having been folded onto the other, while others interlock and one has even been folded back on itself. Both sets have been detached from the gill flap, which is not present although some wisps of reflective material lateral to the filaments might represent all that is left of it, and the filaments lie above an incomplete gnathobasic lobe and parts of the first two podomeres of a leg (figure 89).

The opening of both filaments sets along the axis explains the 'bush'-like or 'Christmas tree' effect of the gill filaments as in figure 84, plate 12, which is thought to be the result of parallel compression of gills formerly held in a downward (ventral) hanging position at the time of burial. Subsequent compression and probable decay appears to have separated the filaments from the gill flap since this is not recognizable. It is however seen, albeit rarely, when rotation of the gills to a more horizontal position at the time of burial causes the filaments to remain attached to the flap, or simply to be compressed onto it (figure 87, plate 12).

### (*e*) *Alimentary canal*

One specimen (figure 96, plate 13) shows the continuous course of the alimentary canal from mouth to anus but because of flattening its original size is not known with certainty. On the other specimens parts of the canal with relief infilling are present at various intervals down the length of the animal, most commonly in the abdominal region, where the contents extend to the anus on the telson. Presumably the abdominal section of the canal together with contents is more likely to be preserved during fossilization since it is housed within the tubular abdomen, while the thoracic section, lying within the softer body wall, is more easily destroyed, together with the appendages and ventral integument. Compaction of the abdominal region causes the contents to be pushed through dorsal (figure 10, plate 2) or ventral (figure 24, plate 3) surfaces, or alternatively is revealed when the rock is split and exoskeletal material is removed. On specimen G.S.C. 49739 (figure 22, plate 3) part of the wall of the canal with contents adhering to it has been squeezed out so as to lie on the ventral surface and a reflective trace of the wall of the alimentary cavity can be followed down the length of the abdomen to the telson. Width of the cavity varies and on figure 96, plate 13, a wide relief trace is revealed on the first abdominal somite and presumably this is the result of flattening within the body. In this specimen the relief infilling occurs inside a highly reflective area arranged symmetrically about the midline. This area is considered to be the gut wall and the undulating outlines corresponding approximately to segmental boundaries to be the muscles supporting it. In the head region the relief infilling is finer grained than that nearer the anus and occurs laterally in areas that also follow the segmentation. It is tempting to suggest that these are gut diverticulae but this is the only specimen showing such a feature.

X-ray diffraction studies of gut content show this to be almost entirely calcium phosphate (apatite), while under the microscope it consists of a mass of irregular, often striated, clumps. Pyrite is rare though present in small amounts. Simonetta (1963, p. 104) believed the gut contents to contain unidentifiable arthropod fragments and specimen U.S.N.M. 139679 (figures 97, 98, plate 13) exhibits a small but complete ptychopariid trilobite lying within the alimentary canal and specimen U.S.N.M. 250216 (figure 99, plate 13), viewed from the ventral surface, shows a group of five agnostid trilobites lying partly beneath the doublure and in the region of the mouth. The arrangement of these trilobites seems to be more than fortuitous and it is unlikely that they were compressed onto the specimen during subsequent burial and compaction. More definite shapes occur within the gut of specimen U.S.N.M. 57489 (figures 94, 95, plate 13), which contains a hyolithid mollusc surrounded by fragments that may be bradoriid ostracode valves.

## 8. THE COXA–BODY ARTICULATION

Comparison of specimens preserved in vertical attitude with those of the model in vertical aspect (figure 103, plate 15) and the reconstruction (figure 107) shows that the coxa was attached to the body along a broad area. Attachment was presumably by muscles that were inserted in the coxal cavity and attached dorsally to the ventral side of the exoskeleton. The highly reflective material dorsal to the coxae illustrated on figure 25, plate 4, might well be such muscles. Stability of the coxa was probably enhanced by the dorsal flange, which is bent inwards as if to fit some form of lateral articulation. What this articulation was, if present, or what the connection was between the flange and the dorsal exoskeleton, is not known. Presumably large muscles would be needed to support the coxa, but there are no signs of where these were inserted nor is there a longitudinal furrow or rachis to provide rigidity to the exoskeleton.

When specimen U.S.N.M. 250214 (figure 37, plate 5) is immersed in alcohol or examined in angled light from the dorsal side, areas of highly reflective material are seen arranged symmetrically on either side of a non-reflective central area. These are shaded on the explanatory drawing (figure 33). Laterally this reflected area follows the line of the doublure of each somite, fills the width (exs.) of the somite and extends inwards to a distinct line marking the boundary with the unreflective area. The reflective area thus outlined is interpreted as being the ventral integument, the non-reflective area as a space corresponding in life to the median ventral area housing the food groove at the base of the coxa. It was presumably this space into which the coxal flange was inserted. The inner line of the integument is so well defined as to suggest that this is a natural edge which surrounded part of the coxal bar.

### (*a*) *Legs and walking*

Construction of the leg in *Sidneyia* with a hinge knee joint between podomeres 4 and 5 allows flexure at this point and would enable the animal to attain the typical hanging stance (Manton 1952, fig. 1; 1973, pp. 320, 325). In this position the legs would be held up under the body, the knee joint being pushed dorsally; raising and lowering of the leg would take place at the joint between the coxa and podomere 1. Leg movement consisting of a promotor–remotor swing leads to a series of stepping movements, the simplest being a short forward stroke followed by a longer backstroke consisting first of progressive flexure followed by progressive extension. A variation of this pattern during acceleration and digging is accomplished by an increase in the angle of swing of the leg coupled with a decrease in the relative duration of the backstroke. Relative duration of forward and backward strokes of arthropod legs during walking produces what is known as the gait pattern (Manton 1952, 1958, 1973). Any attempt at producing a sound gait pattern for *Sidneyia* must be speculative and the system chosen arbitrary. Nevertheless such a pattern is shown (figure 105*a*) and has been constructed assuming that one cycle of movement involved six legs, i.e. with a total of nine legs on the animal, paired legs 1–6 partake in the cycle, legs 7–9 repeat it. To portray the gait graphically the whole cycle of leg movement is taken as 10 units and the relative duration of forward and backward stroke as 2 : 8 (figure 104 *a*). Using graph paper the movement for leg 1 is drawn showing a steep-angled line equivalent to 2 units (forward duration) and a lower-angled line equivalent to 8 units (backward duration). Similar patterns are drawn for successive legs which are shown out of phase with each other. This phase difference, arbitrarily selected as 0.2, is derived on graph paper (figure 104*b*) by making a lateral shift of each leg pattern to the left, equivalent to 2 units. The phase difference number (0.2) means that each leg is 0.2 of a pace in advance of the leg in front. This number is small and is necessary for long legs situated close behind one another (Manton 1964, p. 33). Any vertical line (L–L, figure 105*a*) drawn through the gait patterns of legs 1–9 will give at the point of intersection, the position of each leg at a given moment of time. Thus $l_1$ (figure 105*b*) is halfway through its forward swing with tip off the ground, $l_2$ has just started its backward swing but with tip on the ground (i.e. 0.2 of a pace in front of $l_1$) while $l_4$ is over halfway ($\frac{5}{8}$) through the backward duration also with the tip on the ground. The complete pattern produced is one in which four pairs of legs partake in the propulsive phase at any one moment. Figure 105*b* shows the leg positions diagrammatically in dorsal view while figure 105*c* shows the cycle ($l_1$–$l_6$) in lateral view. Such positions are those used in the reconstructions (figures 106, 107). The pattern shown for *Sidneyia* is similar to that used by *Limulus*, which walks slowly and burrows using 'bottom gear gaits' (Manton 1952, 1954, 1964, p. 33).

In the gait pattern constructed for *Sidneyia* the phase difference chosen is the same between all legs but factors such as length of leg and shape and number of body somites are among those that can cause a change in phase difference between successive legs. Thus with long legs fields of movement overlap and in *Limulus* (Manton 1964, p. 33, fig. 18*c*) walking legs 2–5 step inside each other to avoid interference. Likewise in the isopod *Ligia* (Manton 1952, fig. 3) the fields of movement of the seven pairs of legs overlap considerably. Of interest here is the way that the smaller posterior pair step inside the pair in front and how in the middle region of the body there is an anterior and posterior spread of the field of movement to minimize interference. This spread means in effect that the posterior legs swing farther posterior to the leg base than anterior, and one result of this is the need for a progressive backward fanning of the somites, which afford cover and protection to the appendage during the more posterior swing. In *Sidneyia* a similar progressive pleural fanning is present from somites 5–9, which together form the posterior thorax (plate 14) covering the gill-bearing appendages. Thus protection of the gills is afforded by such fanning whether or not it is associated with posterior swing of the associated legs.

With use of all information from various specimens of *Sidneyia* where legs are preserved, it is possible to recognize a slight progressive lengthening of the leg from front to back on the first four somites of the anterior thorax and an overlap during the gait seems reasonable. These four legs are assumed to have been the main walking legs. A progressive shortening of the leg occurs on the remaining somites and whether the posteriormost was always in contact with the ground during walking is difficult to decide. In the gait pattern constructed for *Sidneyia* and in the reconstructions (figures 106, 107) it is assumed that it reached the ground.

### (*b*) *Legs and feeding*

The likeness of the coxal segment in *Sidneyia* to that of Recent xiphosurans such as *Tachypleus* (Manton 1973, fig. 11) is great, as is true for details of the broad coxa–body attachment and type of gnathobase. This suggests that in *Sidneyia* movement of the gnathobases during feeding could have been by adduction and abduction in the transverse plane of the body with a chewing action between paired gnathobases taking place at right angle to the promotor–remotor swing of the coxa on the body. Use of the latter during walking enables the shredded food to be moved forwards between the gnathobases.

The anterior legs of *Sidneyia* are well suited for this method of feeding, are typically prehensile (figure 48) and show a differentiation in the type of gnathobase from front to back, the 4th pair from the mouth having the strongest cuspate spines capable of 'crushing' food (figure 83, plate 11; figure 81).

### (*c*) *Gills during walking and swimming*

Experiments with the model (plate 15) have shown that during the promotor–remotor movement of the legs during walking, movement of the gills would be possible depending on the roll of the coxal bar along the junction with the body, and movement at the joint between the first podomere of the leg and the coxa. Otherwise the attitude of the gill in the transverse plane would be fixed above the sediment surface and be independent of leg flexure. Space between succeeding legs would be sufficient to allow some movement of the gill flap in a dorsal–ventral direction along the line of the gill flap fold, but in the assumed pattern of gait this movement would be slight. Movement could be accentuated during swimming especially if the

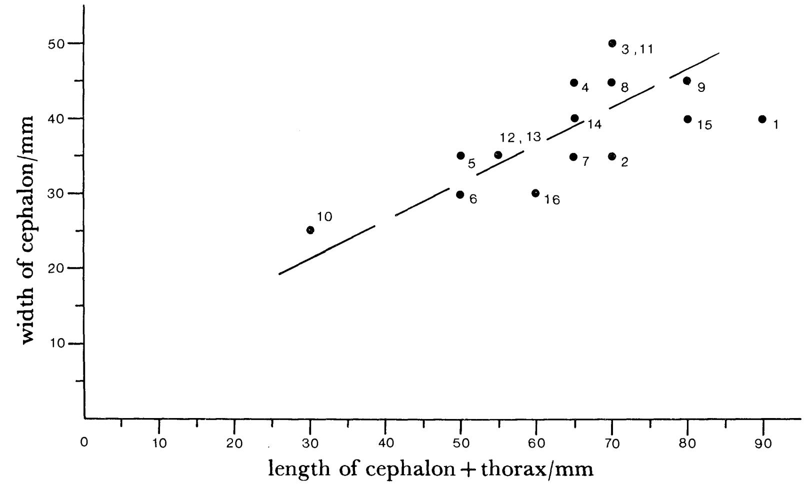


FIGURE 1. *Sidneyia inexpectans* Walcott. Plot of length of cephalon and thorax against transverse width of cephalon. Measurements, in millimetres, of extended specimens in straight line. Numbers correspond to following specimens used:

1, U.S.N.M. 250215; 2, U.S.N.M. 65057; 3, U.S.N.M. 250208; 4, L.O. 5267; 5, U.S.N.M. 250207; 6, U.S.N.M. 250214; 7, U.S.N.M. 139676; 8, G.S.C. 49739; 9, G.S.C. 49744; 10, U.S.N.M. 250209; 11, U.S.N.M. 57487; 12, U.S.N.M. 57489; 13, U.S.N.M. 57495; 14, U.S.N.M. 57497; 15, U.S.N.M. 139682; 16, U.S.N.M. 65510.

Bivariate statistics by Dr C. P. Hughes: $y = 0.51x + 5.8$, $\bar{x}$ (var $x$) $= 64.06$ (204.20), $\bar{y}$ (var $y$) $= 38.44$ (52.42), $a$ (var $a$) $= 0.51$ (0.01), $r = 0.68$, $n = 16$. Best fit lines calculated by means of a reduced major axis regression.

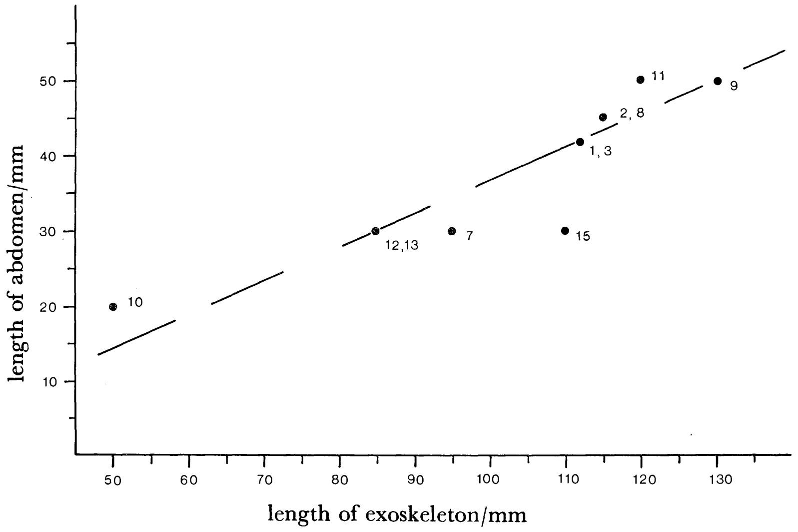
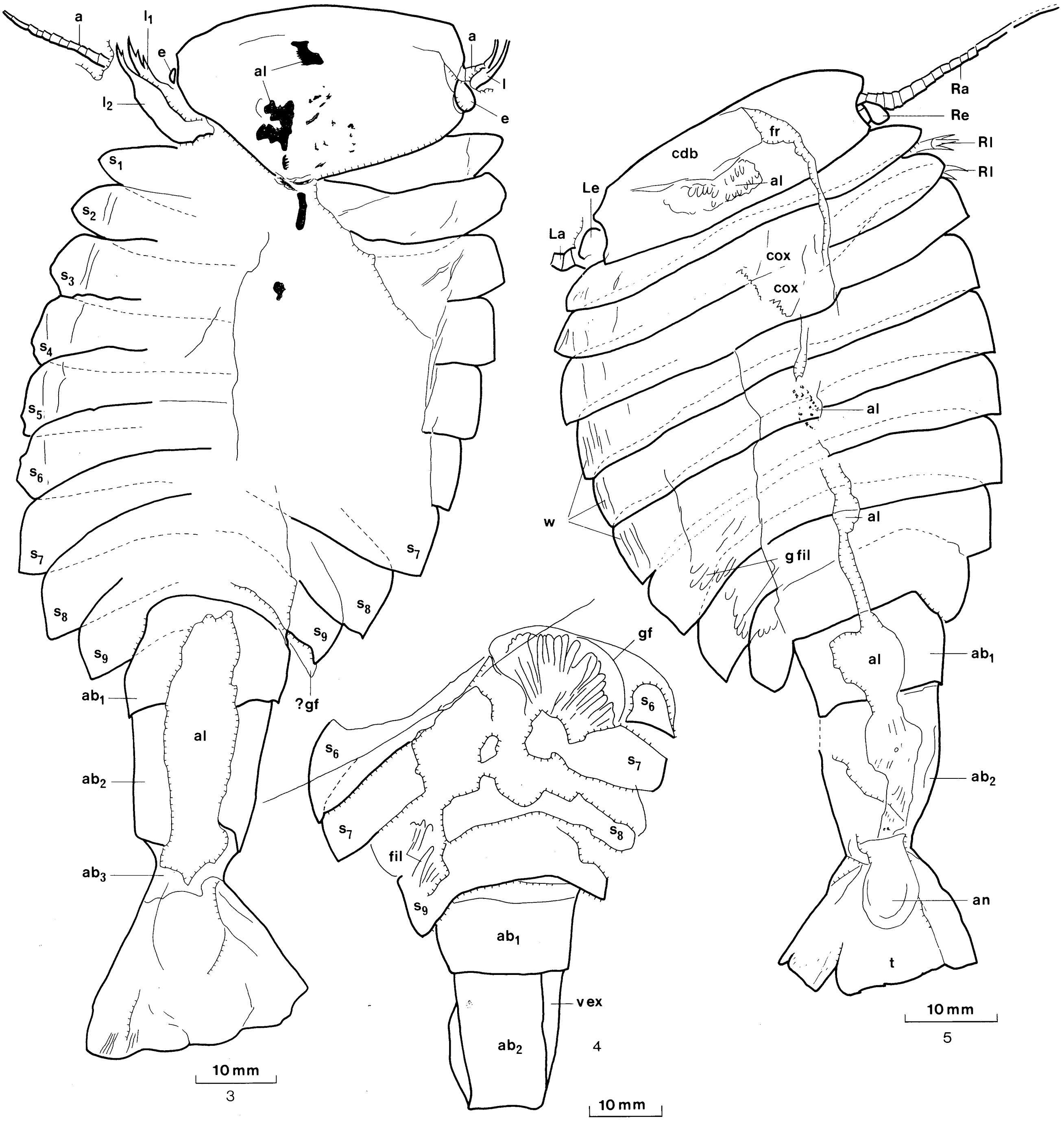


FIGURE 2. *Sidneyia inexpectans* Walcott. Plot of total length of exoskeleton against length of abdomen. Bivariate statistics: $y = 0.44x - 7.7$, $\bar{x}$ (var $x$) $= 105.64$ (664.61), $\bar{y}$ (var $y$) $= 38.82$ (126.34), $a$ (var $a$) $= 0.44$ (0.003), $r = 0.92$, $n = 11$. Specimen numbers the same as in figure 1.



## Description of figures 3–5 and plate 1

Figure 3. U.S.N.M. 250215, explanatory drawing of figure 7. Specimen lies oblique to bedding so that left side (as viewed) is counterpart, right side is part.

Figure 4. U.S.N.M. 139702, explanatory drawing of figure 8, posterior thorax and abdomen.

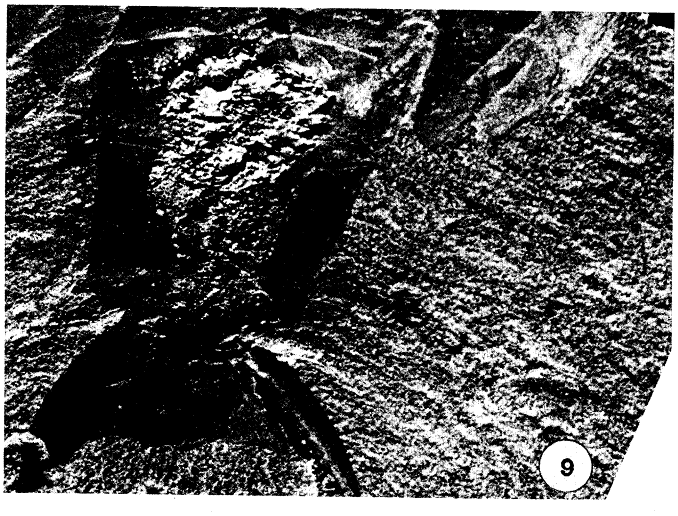
Figure 5. U.S.N.M. 65057, explanatory drawing of figure 6.

Figure 6. U.S.N.M. 65057, part; northwest. (Magn. × 1.75.)

Figure 7. U.S.N.M. 250215, counterpart; northwest. (Magn. × 1.25.)

Figure 8. U.S.N.M. 139702, part; northwest; note elongate abdomen. (Magn. × 1.)

Figure 9. U.S.N.M. 269164 ~~250217~~; counterpart; northwest, showing details of abdomen and alimentary contents. (Magn. × 1.)



Figures 6–9. For description see opposite.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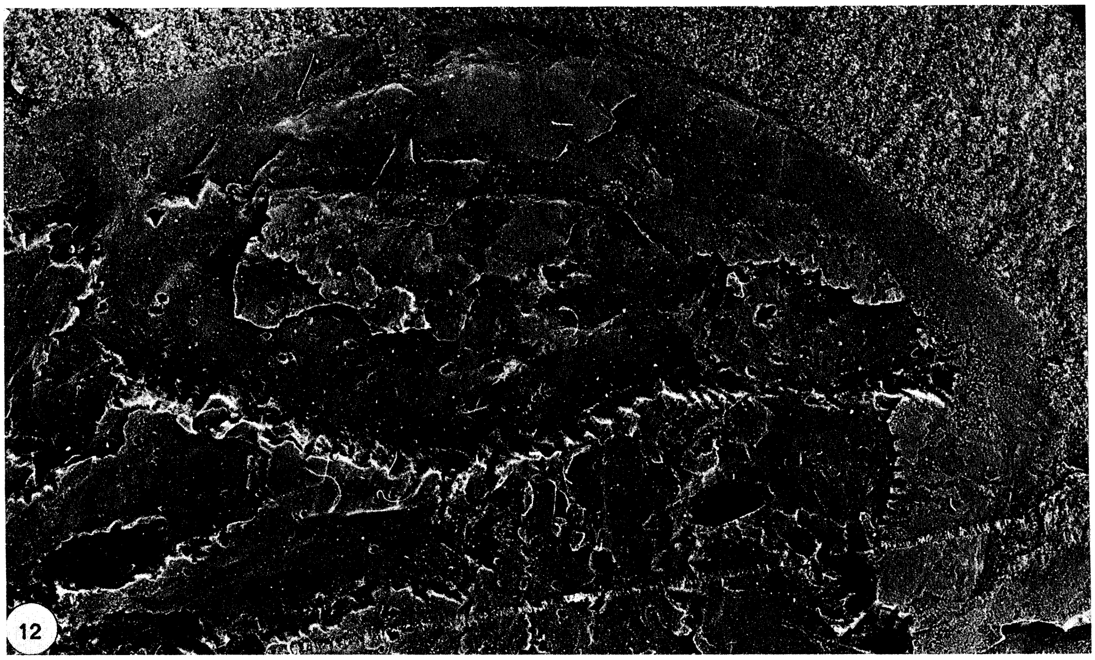
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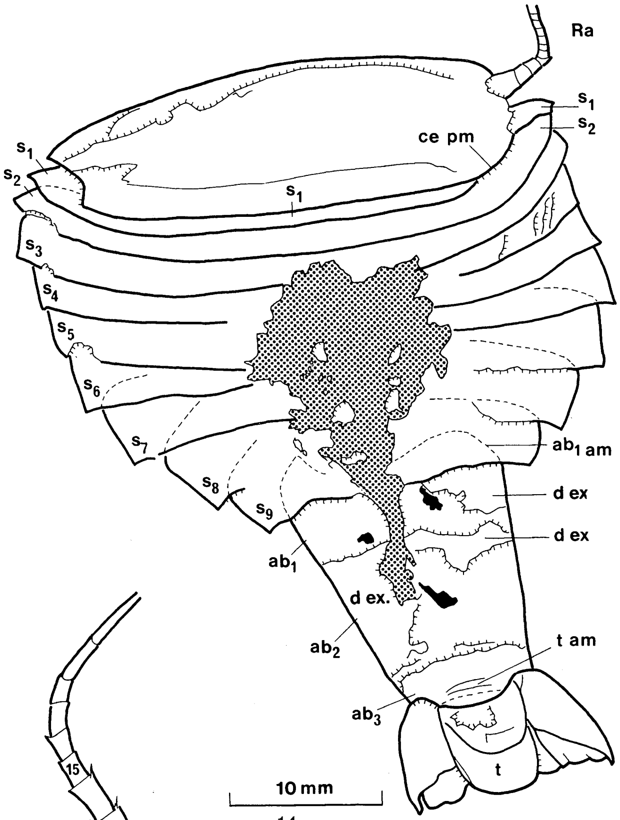
Figures 10–13. For description see opposite.



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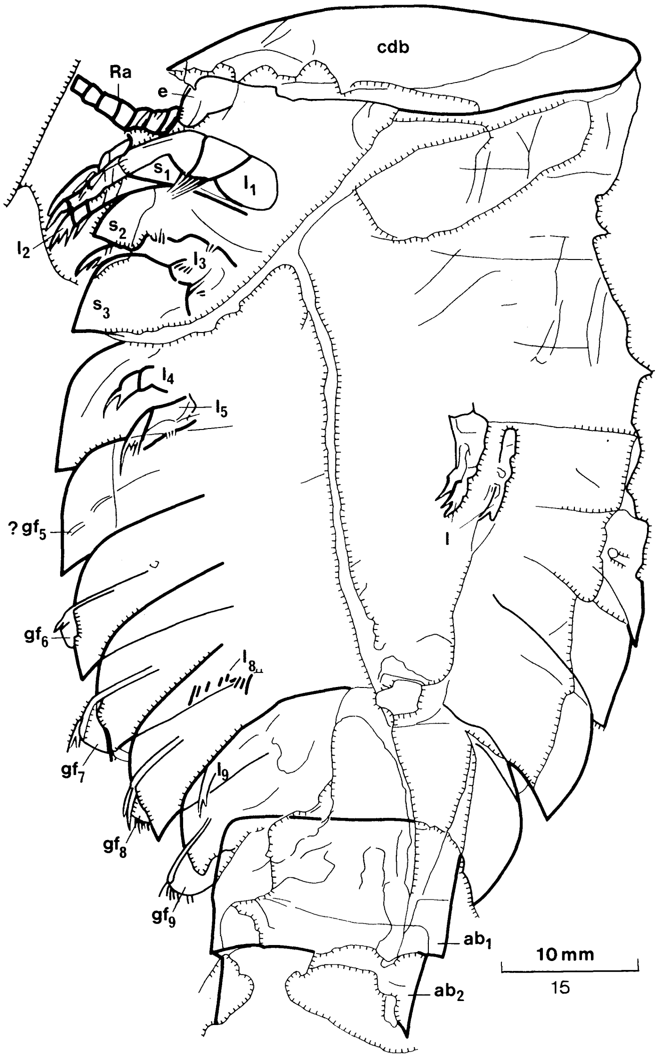

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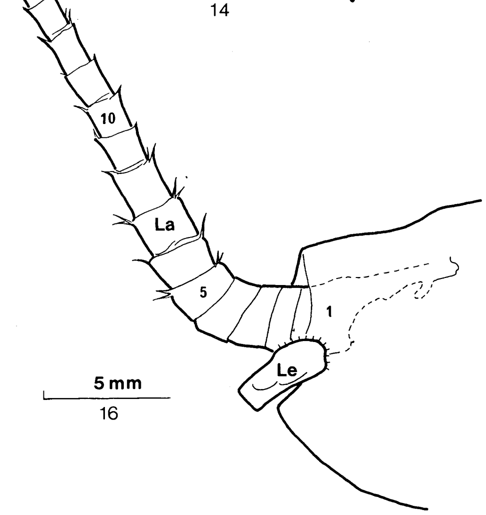

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## DESCRIPTION OF PLATE 2 AND FIGURES 14–16

FIGURE 10. U.S.N.M. 250209, part; northwest. (Magn. ×3.) Walcott's locality 39k/10 = Raymond Quarry, level unknown.

FIGURE 11. U.S.N.M. 65510, counterpart; northwest. (Magn. ×1.5.) Specimen on same block as *Olenoides serratus* (Rominger, 1887). Original of Walcott (1918, pl. 4, fig. 1), Whittington (1975, pl. 9, fig. 1).

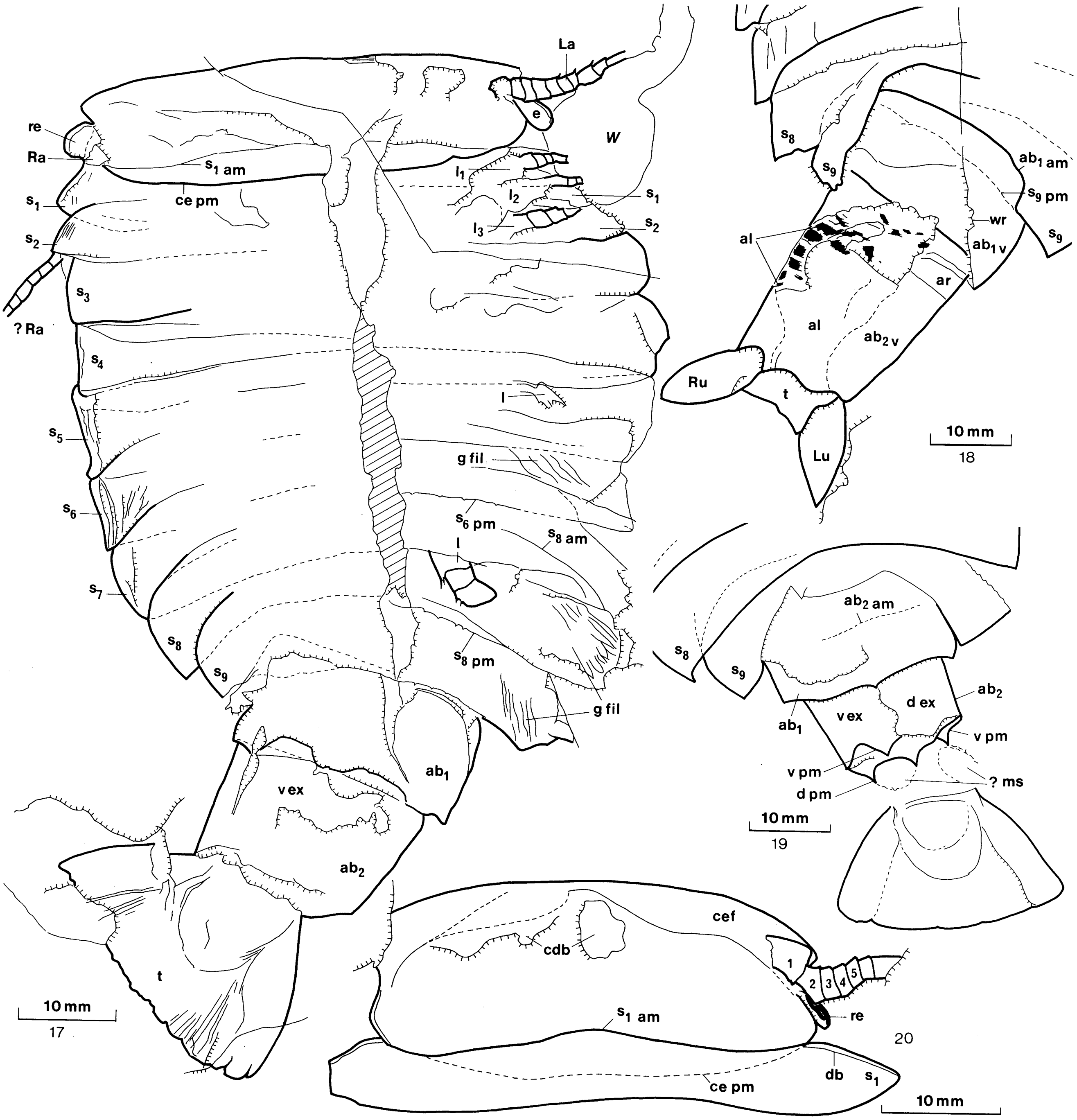
FIGURE 12. U.S.N.M. 139679a, part after preparation to show posterior margin of cephalic doublure, whitened with ammonium chloride and photographed in normal light. (Magn. ×4.) See figure 98.

FIGURE 13. U.S.N.M. 250207, part; antenna and left eye, north. (Magn. ×4.5.)

FIGURE 14. U.S.N.M. 250209, explanatory drawing of figure 10. Stippled area is alimentary canal which has opened and contents have been compressed through dorsal exoskeleton. Black areas are phosphate.

FIGURE 15. U.S.N.M. 65510, explanatory drawing of figure 11. Note gill flaps on posterior thorax.

FIGURE 16. U.S.N.M. 250207, explanatory drawing of figure 13.



## DESCRIPTION OF FIGURES 17–20 AND PLATE 3

FIGURE 17. U.S.N.M. 250208, explanatory drawing of figure 21.

FIGURE 18. G.S.C. 49739, explanatory drawing of figure 22. Note how alimentary canal has been squeezed out on abdomen.

FIGURE 19. G.S.C. 49744, explanatory drawing of figure 23. Note how caudal fan has been detached from abdomen. Compression of latter allows recognition of dorsal and ventral posterior margins.

FIGURE 20. U.S.N.M. 139676B, explanatory drawing of cephalon of figure 24.

FIGURE 21. U.S.N.M. 250208, counterpart, photographed under alcohol. (Magn. × 1.5.)

FIGURE 22. G.S.C. 49739, counterpart; northwest. (Magn. × 1.5.) Raymond Quarry, level 74–76 ft.

FIGURE 23. G.S.C. 49744, part; northwest. (Magn. × 1.5.) Raymond Quarry, level 74–76 ft.

FIGURE 24. U.S.N.M. 139676B, counterpart; northwest. (Magn. × 1.75.)

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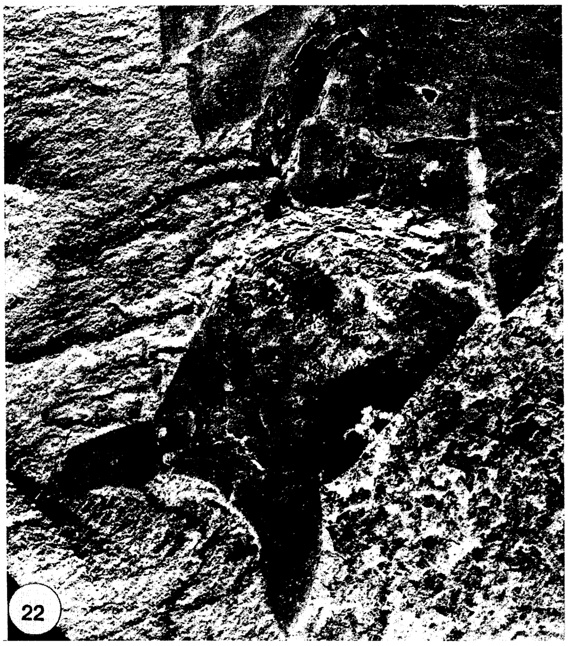

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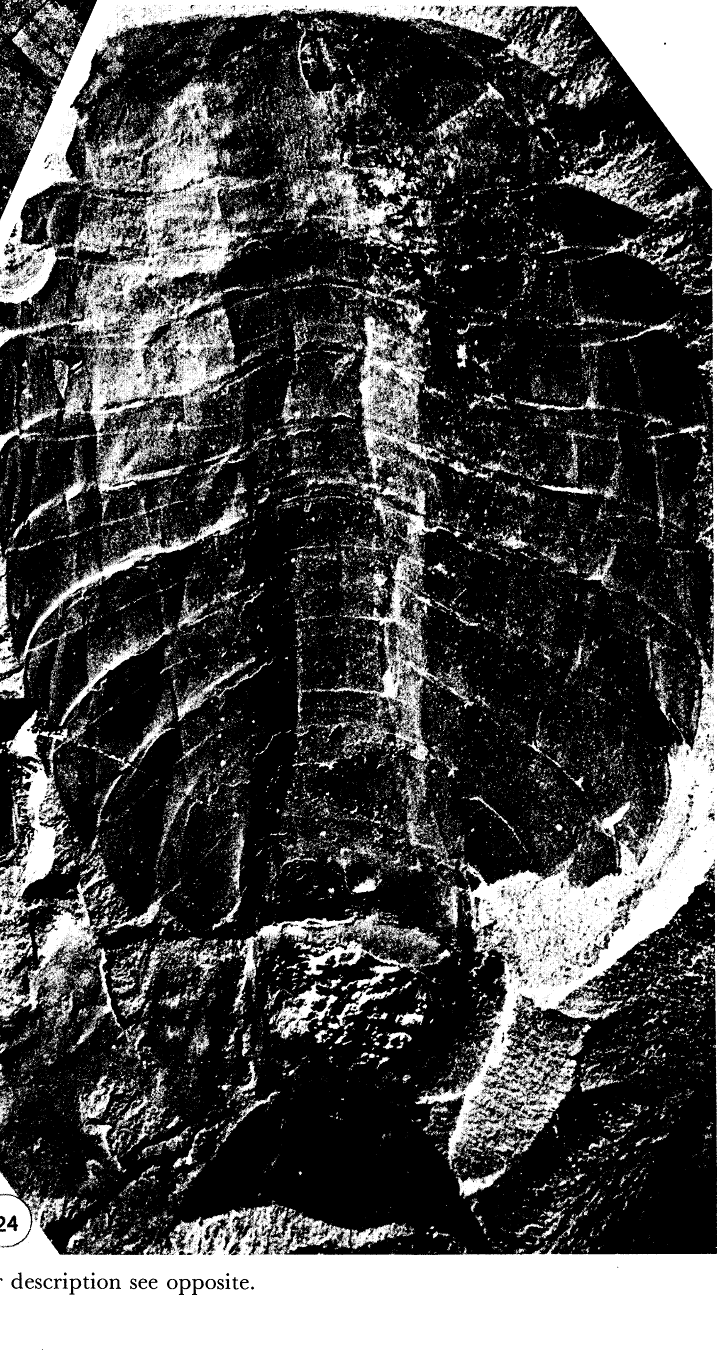

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FIGURES 21–24. For description see opposite.


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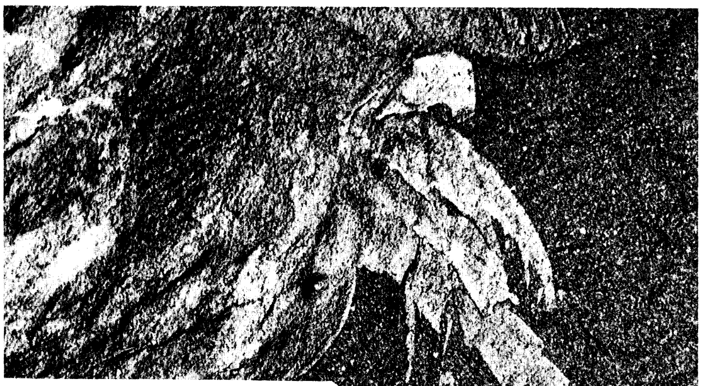
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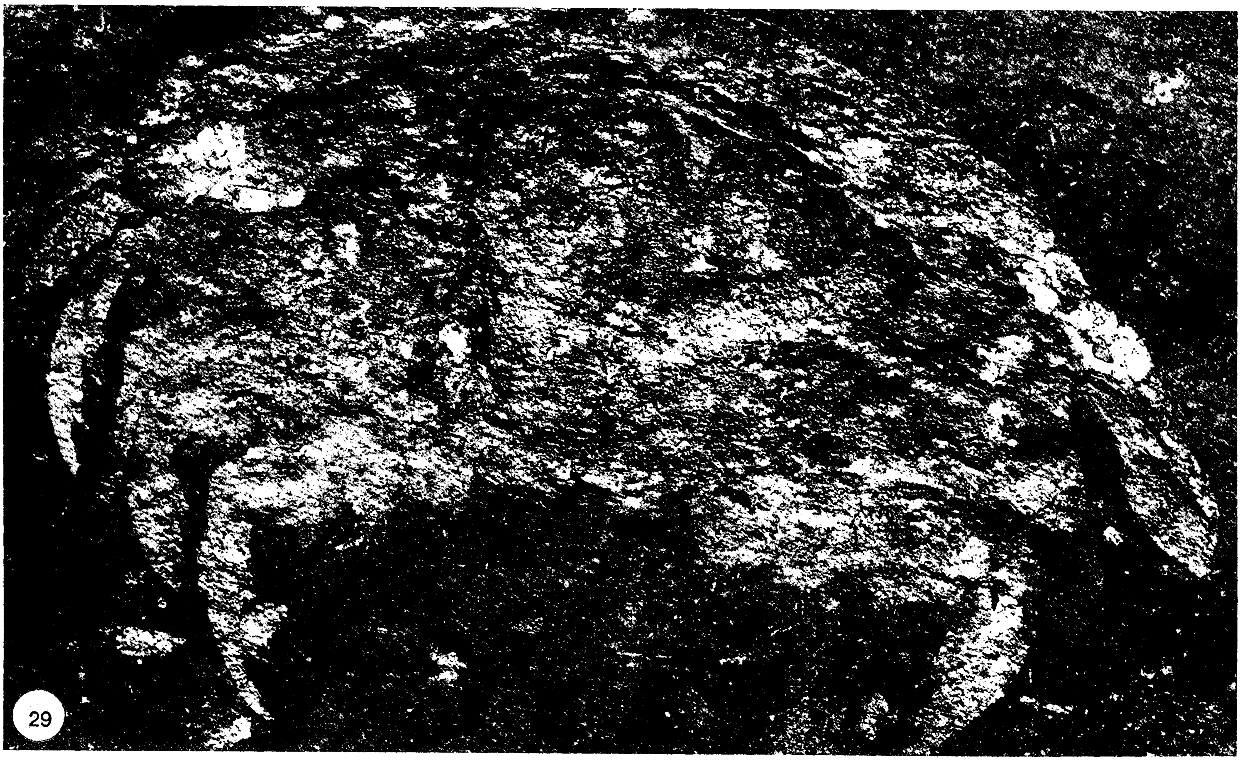
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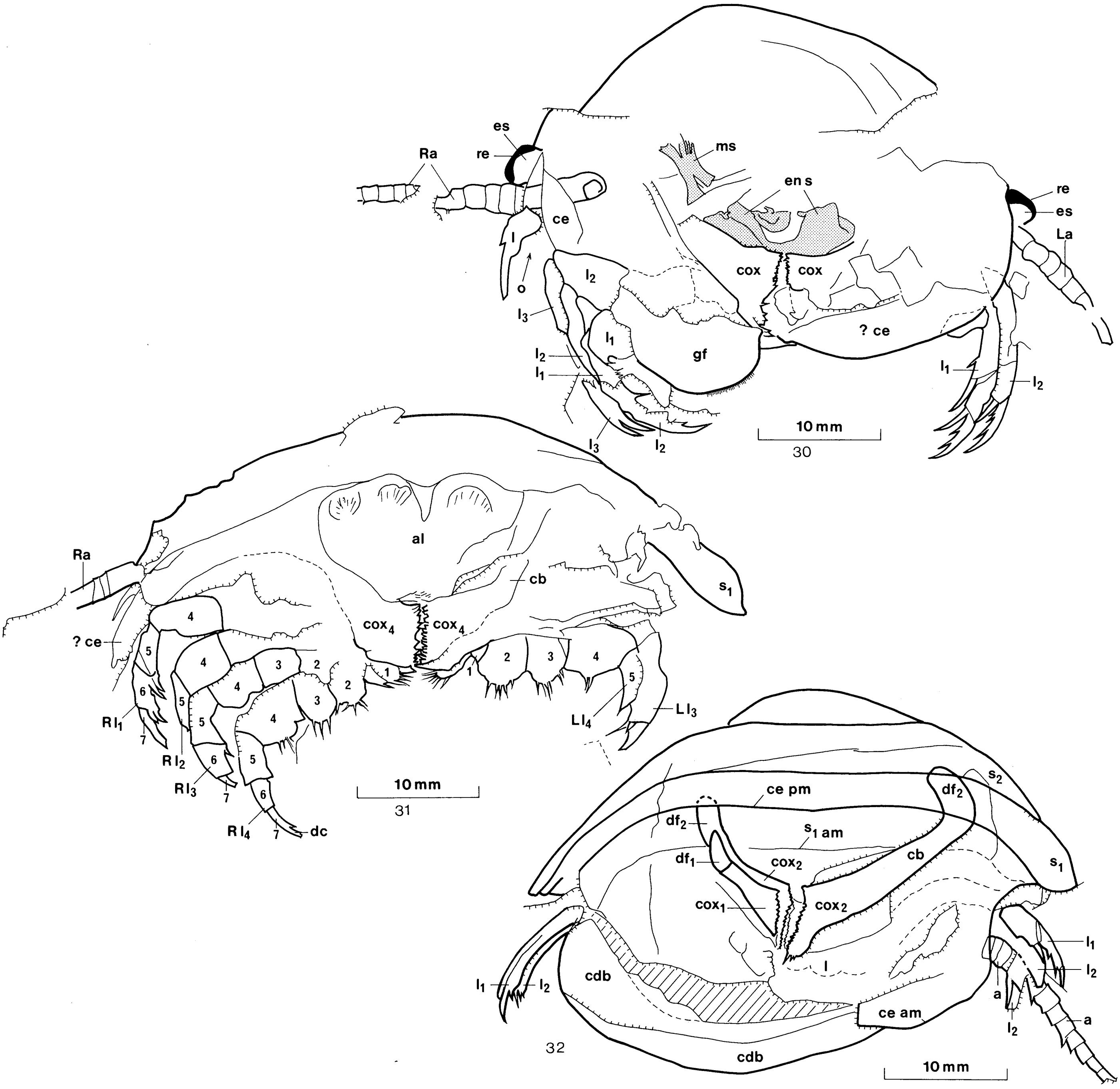
Figures 25–29. For description see opposite.



## Description of plate 4 and figures 30–32

Figure 25. G.S.C. 49740, part; anterior view under alcohol. (Magn. × 1.4.) Phyllopod Bed, Walcott Quarry, level 8 ft–8 ft. 7 in.

Figure 26. U.S.N.M. 139713, part; anterior view reflected, detail of antenna and appendages. (Magn. × 3.5.)

Figure 27. U.S.N.M. 139713, part; anterior view west. (Magn. × 3.5.)

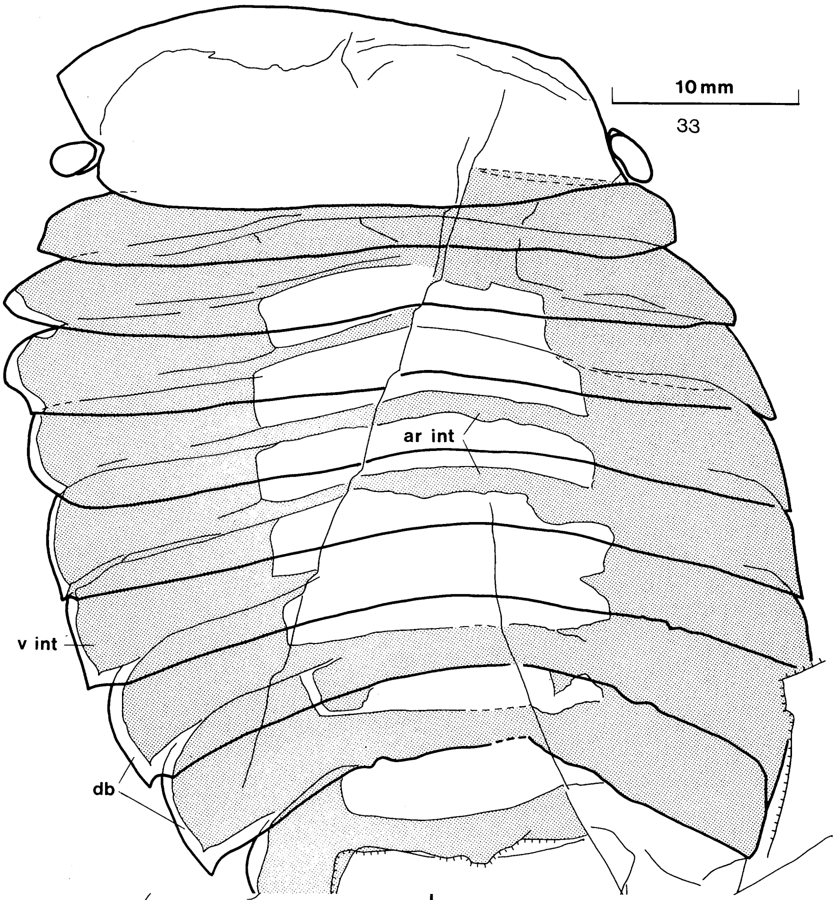
Figure 28. U.S.N.M. 139688, reflected; detail of coxal bar and distal flange. (Magn. × 5.)

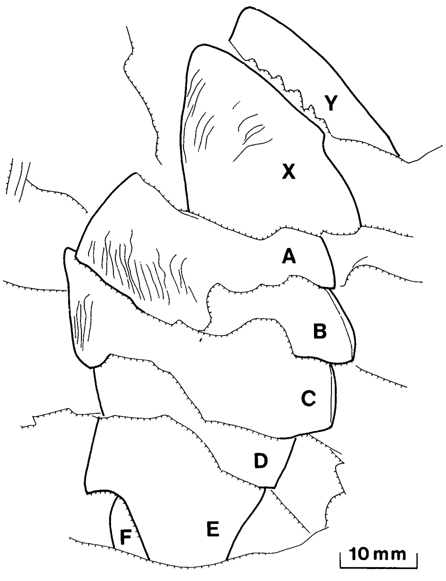
Figure 29. U.S.N.M. 139723, anterior view, under alcohol. (Magn. × 2.4.)

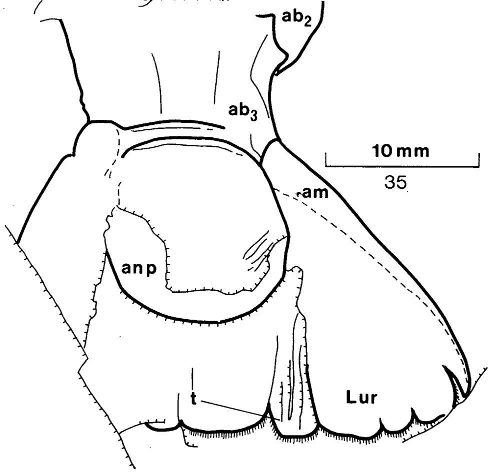
Figure 30. G.S.C. 49740, explanatory drawing of figure 25. Legs numbered in order of succession on specimen. Presence of gill flap suggests legs of posterior thorax.

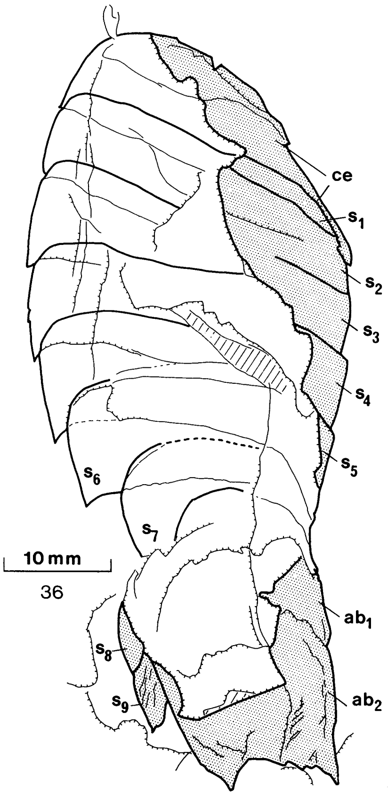
Figure 31. U.S.N.M. 139723, explanatory drawing of figure 29. Legs numbered in natural succession as those on anterior thorax.

Figure 32. U.S.N.M. 139713, explanatory drawing of figure 27. Anterior view showing coxa and legs compressed on underside of cephalon. Latter separated and broken along anterior margin to reveal cephalic doublure beneath.









## DESCRIPTION OF FIGURES 33–36 AND PLATE 5

FIGURE 33. U.S.N.M. 250214, explanatory drawing of figure 37. Shaded area shows trace of silver film interpreted as being ventral integument (vint) and articulating integument (arint).

FIGURE 34. U.S.N.M. 57499, explanatory drawing of figure 38.

FIGURE 35. U.S.N.M. 139714B, explanatory drawing of figure 40.

FIGURE 36. U.S.N.M. 139683, explanatory drawing of figure 41. Specimen lies oblique to bedding and splitting has resulted in dorsal (shaded) and ventral surfaces being preserved.

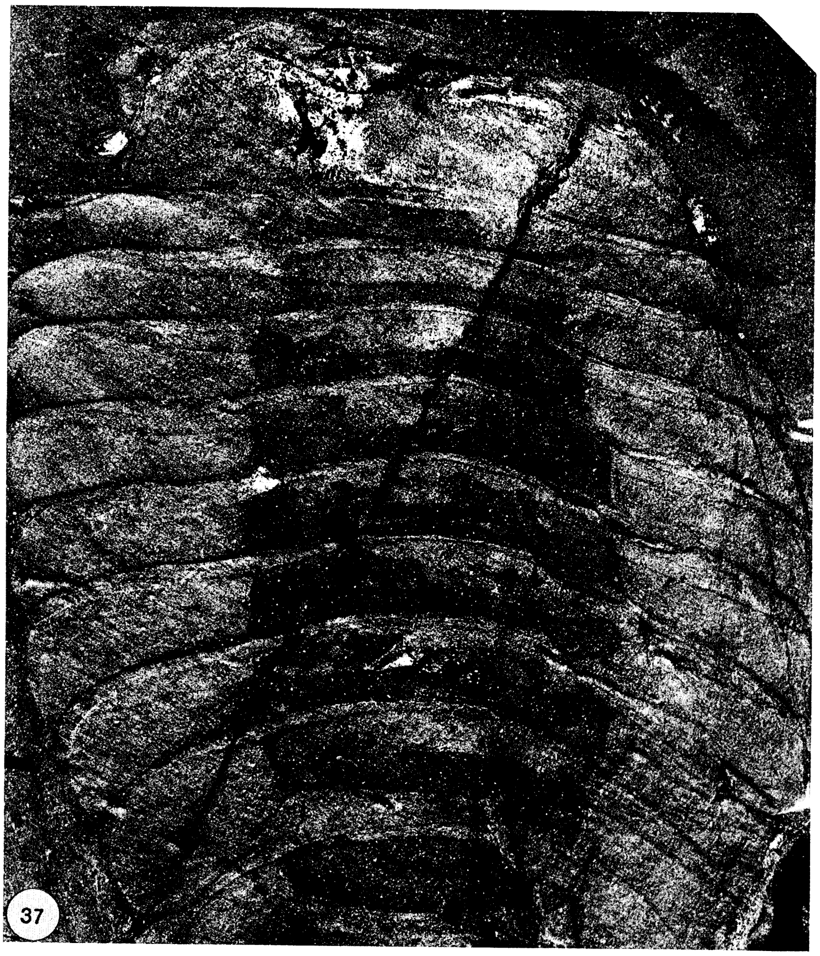
FIGURE 37. U.S.N.M. 250214, part, under alcohol. (Magn. × 2.3.)

FIGURE 38. U.S.N.M. 57499, part, west. (Magn. × 1.5.) Holotype of *Amiella ornata*. Original of Walcott (1911, pl. 5, fig. 4).

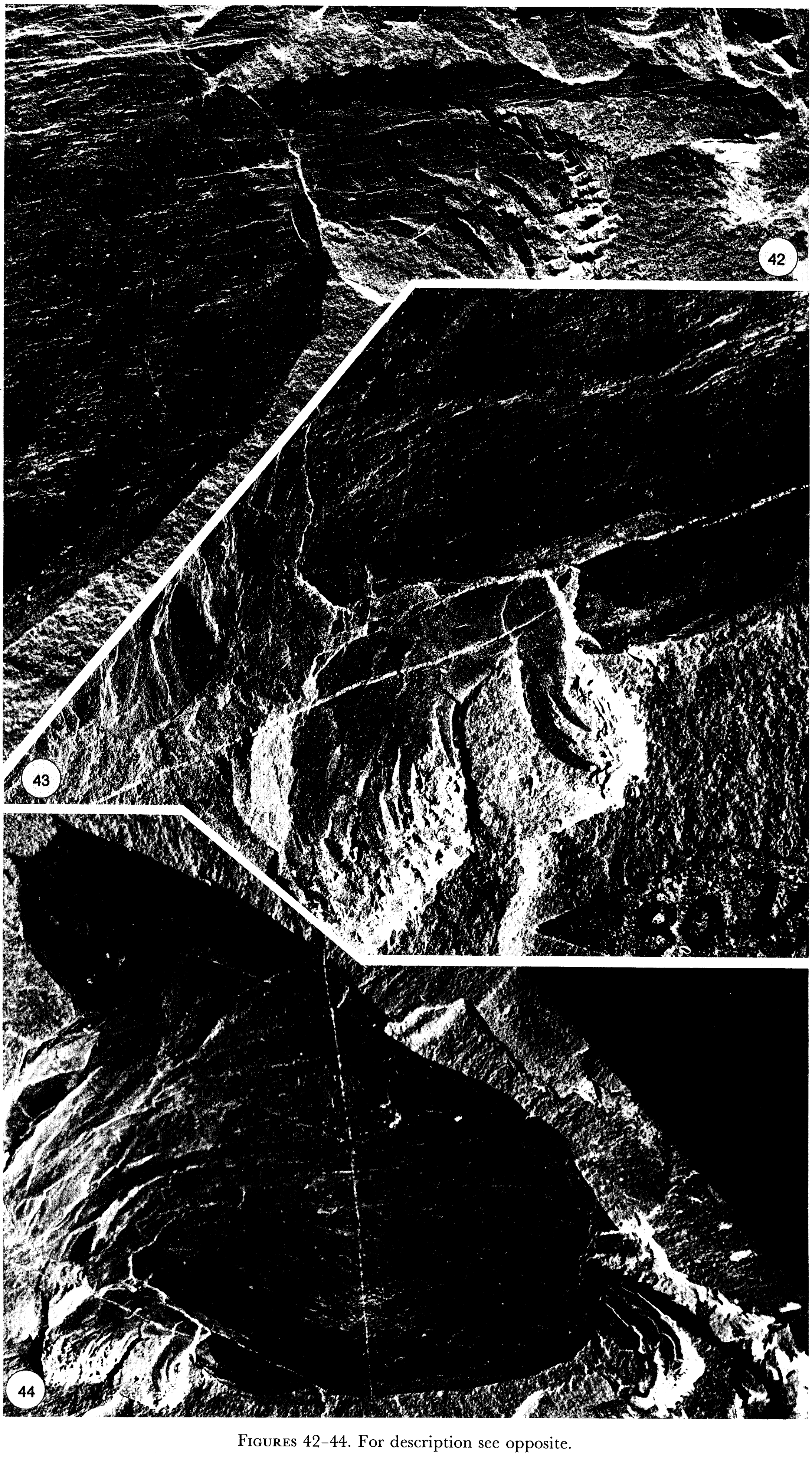
FIGURE 39. U.S.N.M. 250214, part, under alcohol, detail of left eye and reflective visual surface. (Magn. × 3.5.)

FIGURE 40. U.S.N.M. 139714, counterpart, west, detail of telson and uropods of abdomen. (Magn. × 4.5.)

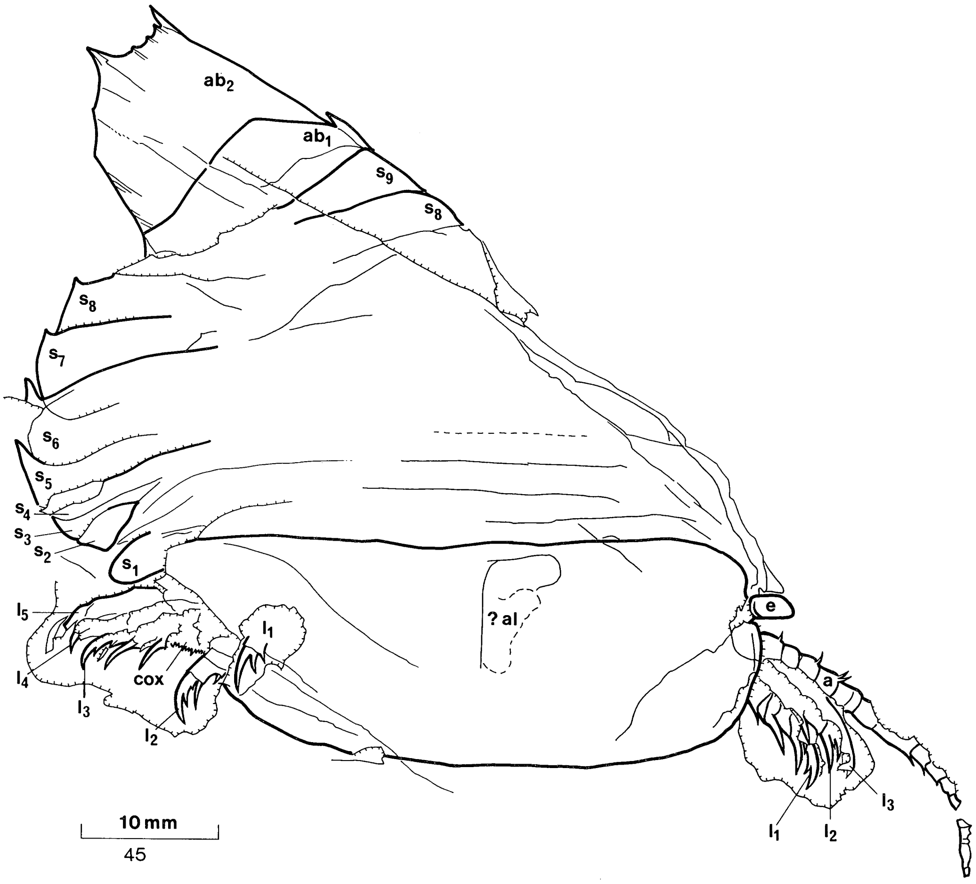
FIGURE 41. U.S.N.M. 139683, part, oblique lateral compression, northwest. (Magn. × 1.7.)



FIGURES 37–41. For description see opposite.



FIGURES 42–44. For description see opposite.



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## Description of plate 6 and figure 45

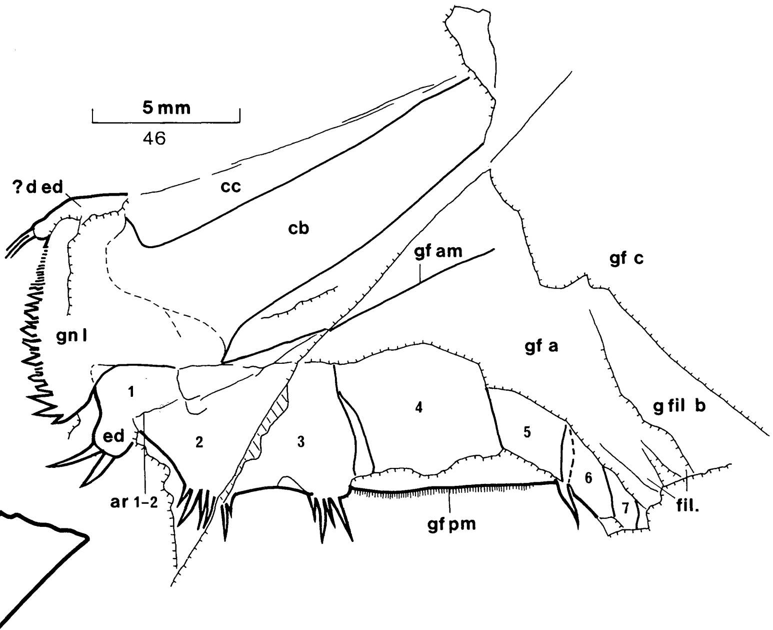
Figures 42–44. U.S.N.M. 139720, part, oblique anterior compression.

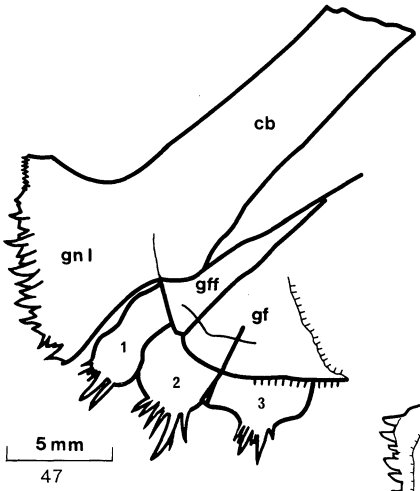
Figure 42. Detail, north, showing left eye, antenna and tips of anterior legs. (Magn. × 4.)

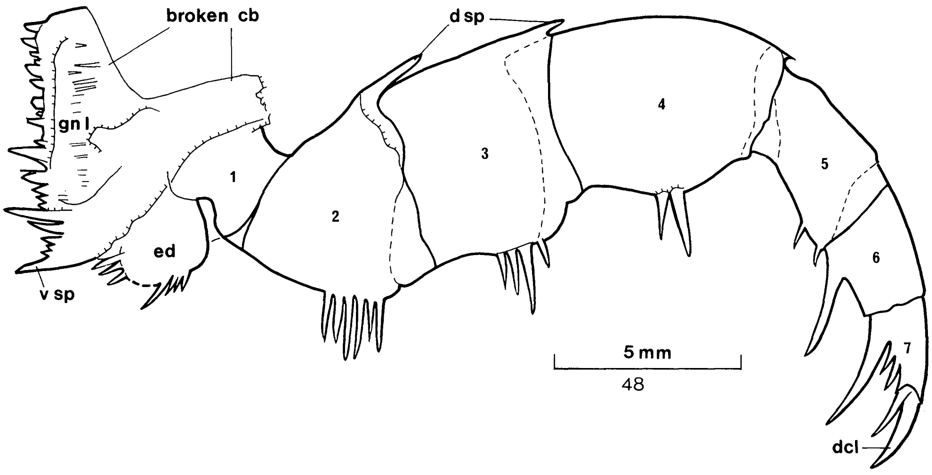
Figure 43. Detail, west, right side anterior appendages. (Magn. × 4.)

Figure 44. Complete exoskeleton lacking telson. (Magn. × 1.75.)

Figure 45. U.S.N.M. 139720, explanatory drawing of figure 44.







## Description of figures 46–48 and plate 7

Figure 46. U.S.N.M. 57494, explanatory drawing of figure 50, coxa, gill and leg. This is only specimen showing possible dorsal endite (? ded).

Figure 47. U.S.N.M. 250211, explanatory drawing of figure 54. Part of coxal bar and gnathobase with leg and attached gill flap.

Figure 48. U.S.N.M. 139708, explanatory drawing of figure 55.

Figure 49. U.S.N.M. 57494, part, reflected. (Magn. × 5.) Original of Walcott (1911, pl. 5, fig. 1).

Figure 50. U.S.N.M. 57494, counterpart, reflected. (Magn. × 5.)

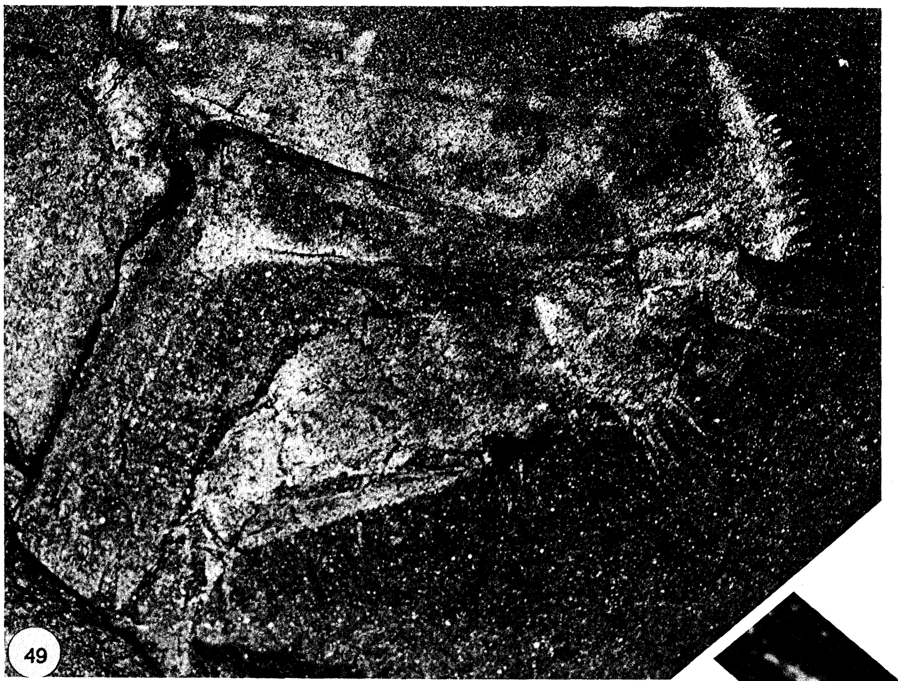
Figure 51. U.S.N.M. 250210, series of gill filaments attached to gill flap. Note top layer partly folded back, north. (Magn. × 4.)

Figure 52. U.S.N.M. 139708, counterpart, under alcohol. Detail of pivot joint between podomere 5 and 6. (Magn. × 3.)

Figure 53. U.S.N.M. 139708, counterpart, reflected. (Magn. × 6.)

Figure 54. U.S.N.M. 250211, part of coxal bar and gnathobase with leg and attached gill flap, reflected. (Magn. × 4.5.)

Figure 55. U.S.N.M. 139708, isolated leg, part, reflected. (Magn. × 4.5.)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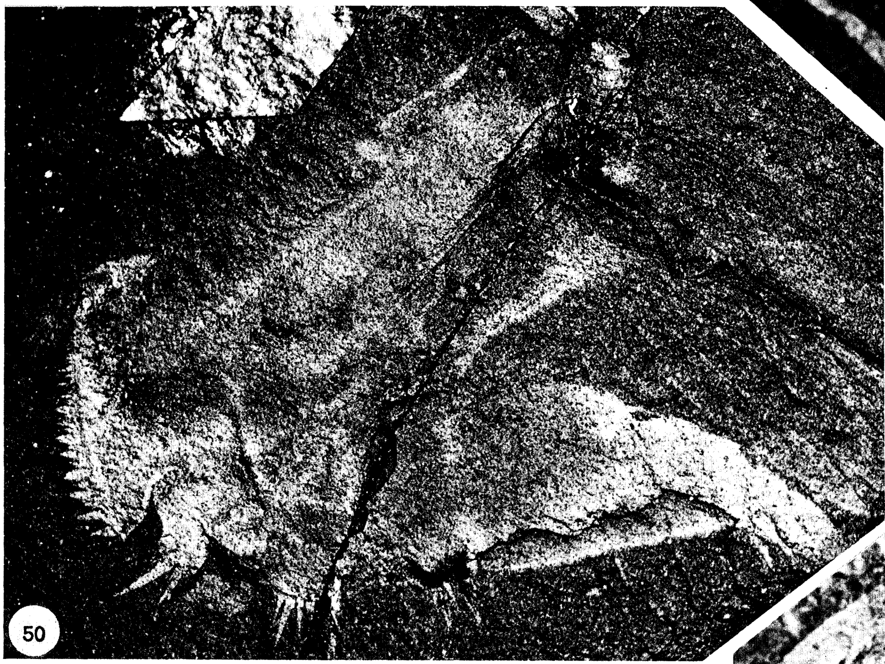
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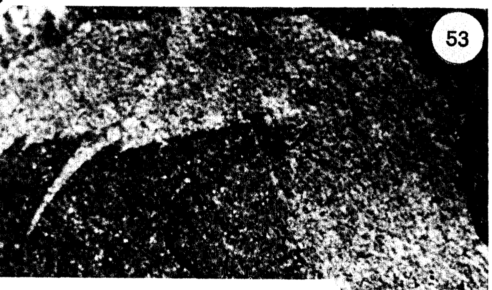
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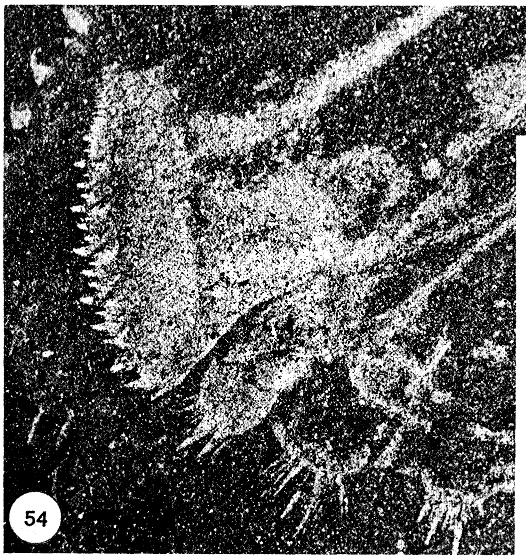
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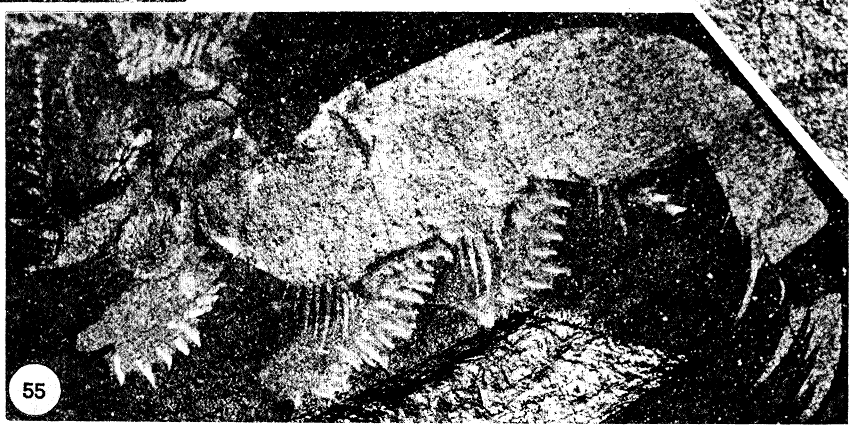
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FIGURES 49–55. For description see opposite.


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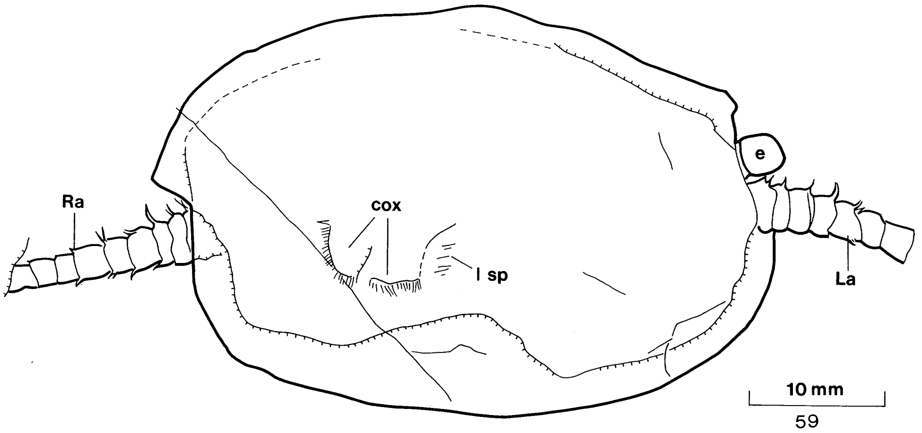
Figures 56–58. For description see opposite.



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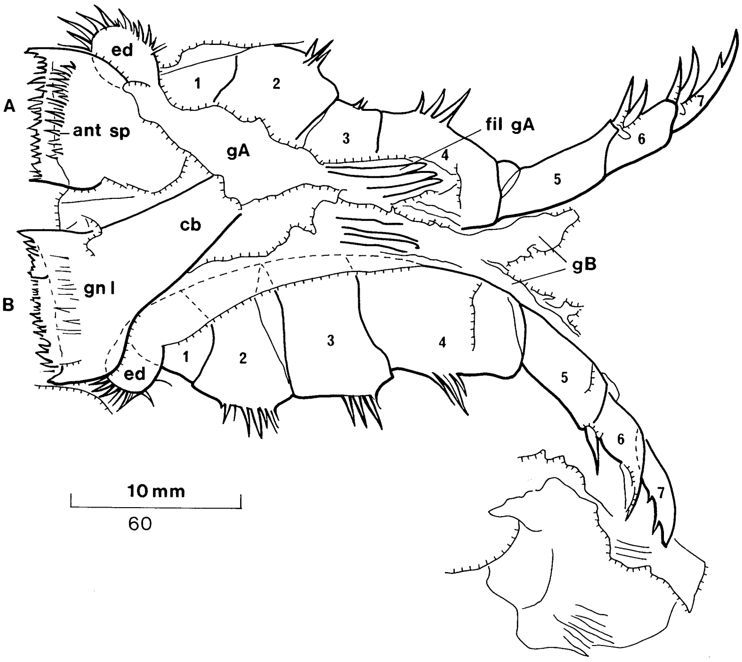


60

## DESCRIPTION OF PLATE 8 AND FIGURES 59 AND 60

FIGURES 56–57. U.S.N.M. 139680, anterior view of cephalon and antenna, counterpart reflected.

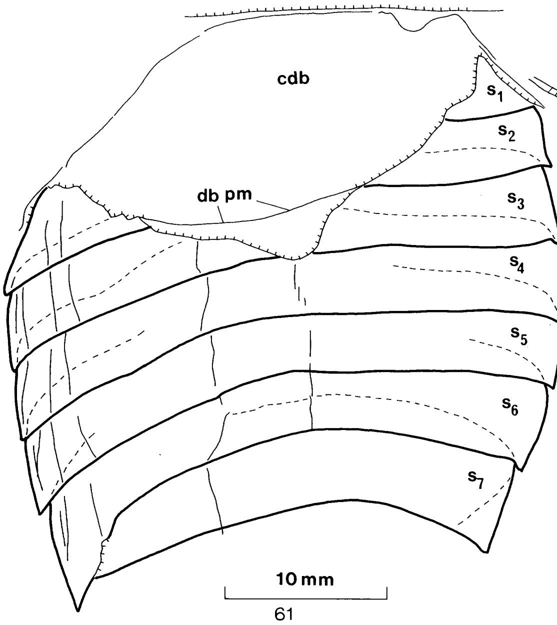
FIGURE 56. Left eye and antenna. (Magn. × 3.5.)

FIGURE 57. Right antenna. (Magn. × 3.5.)

FIGURE 58. U.S.N.M. 250206, paired legs preserved in an unusual fortuitous back-to-back position, part, west. (Magn. × 4.)

FIGURE 59. U.S.N.M. 139680, explanatory drawing of figures 56 and 57.

FIGURE 60. U.S.N.M. 250206, explanatory drawing of figure 58. Orientation of endite (ed) in relation to gnathobase and anterior spines on latter indicates that legs A and B represent right and left sides respectively.



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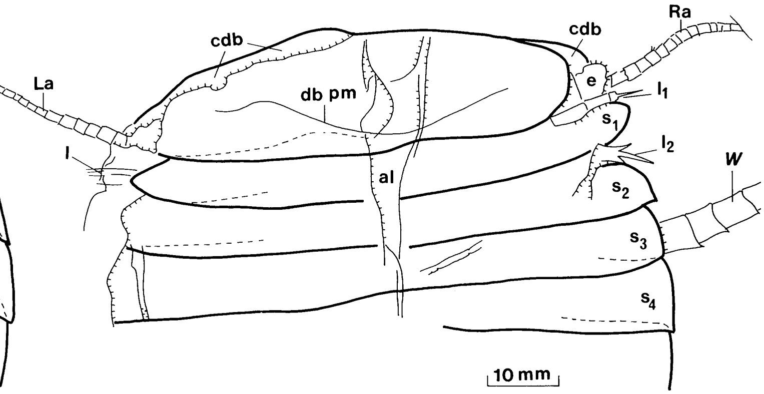

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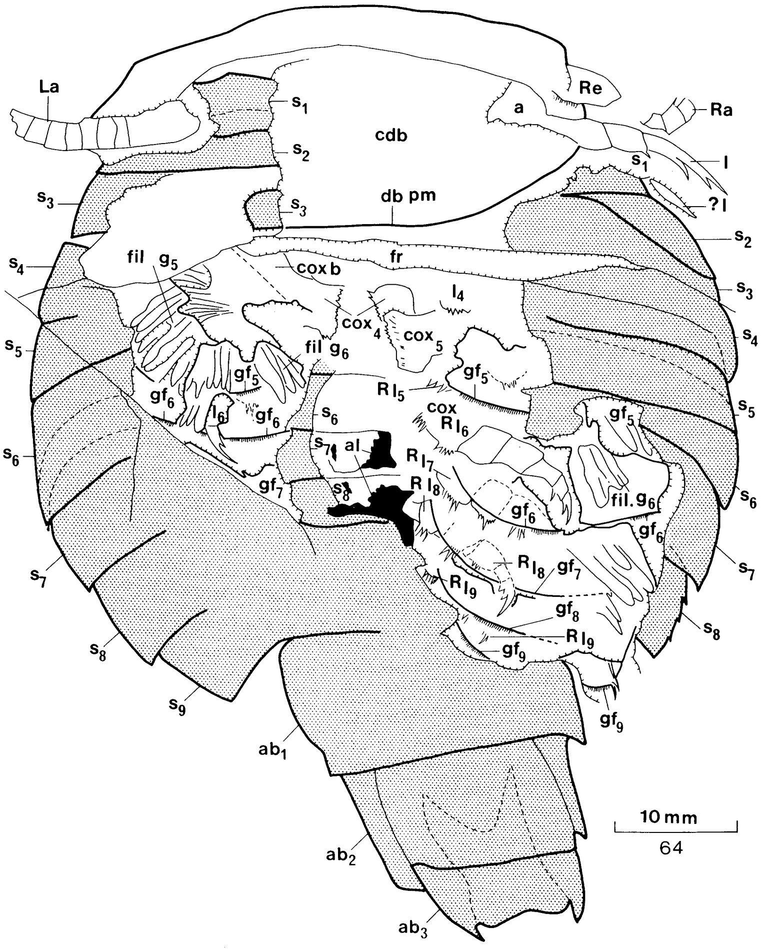

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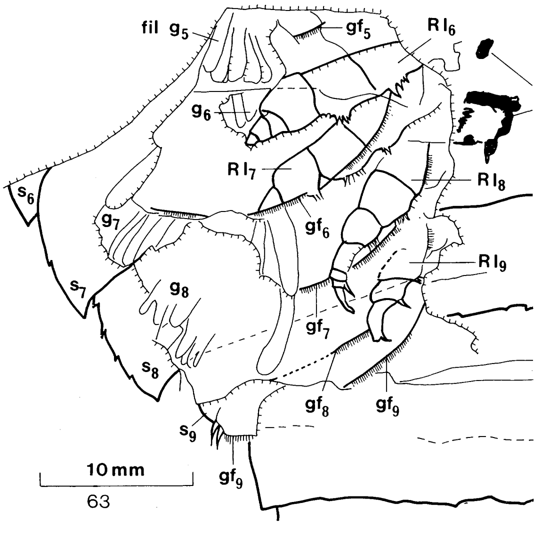

63

## Description of figures 61–64 and plate 9

Figure 61. U.S.N.M. 57496, explanatory drawing of figure 66, showing cephalic doublure.

Figure 62. U.S.N.M. 57487, lectotype. Explanatory drawing of figure 65. Anterior section of specimen to show anterior appendages and *Waptia* tail from under third segment of thorax.

Figure 63. U.S.N.M. 139681, explanatory drawing of figure 68. Detail of counterpart showing right side gills and legs.

Figure 64. U.S.N.M. 139681, explanatory drawing of figure 67 after preparation. In preparing the specimen, parts of the anterior thorax and the dorsal cephalon were removed to reveal gills, legs and cephalic doublure. The drawing combines evidence from study of part and counterpart. Dorsal exoskeleton stippled.

Figure 65. U.S.N.M. 57487, lectotype of *Sidneyia inexpectans* Walcott, 1911. Original of Walcott (1911, pl. 2, fig. 1). Part, north. (Magn. × 2.)

Figure 66. U.S.N.M. 57496, counterpart, north. (Magn. × 2.2.) Original of Walcott (1911, pl. 5, fig. 3).

Figure 67. U.S.N.M. 139681, specimen lacking telson, part, northwest. (Magn. × 1.75.)

Figure 68. U.S.N.M. 139681, detail of right side appendages, counterpart, reflected. (Magn. × 4.)

Figure 69. U.S.N.M. 250207, detail of antenna and lateral hairs, counterpart, reflected. (Magn. × 3.5.)


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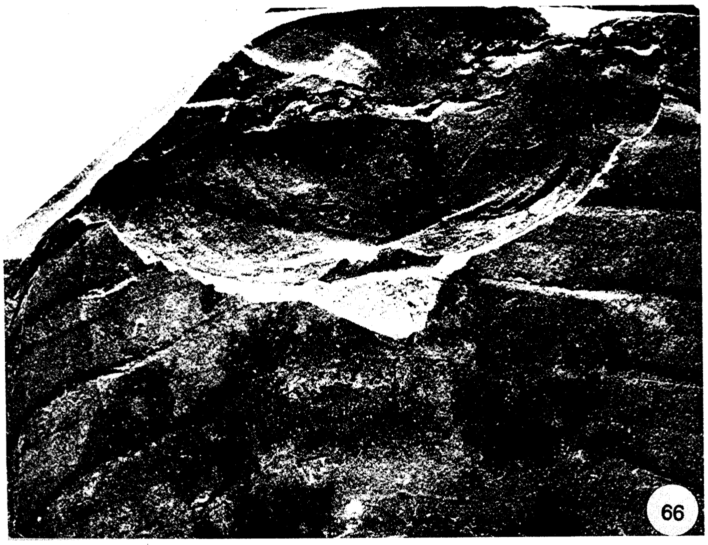
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FIGURES 65–69. For description see opposite.


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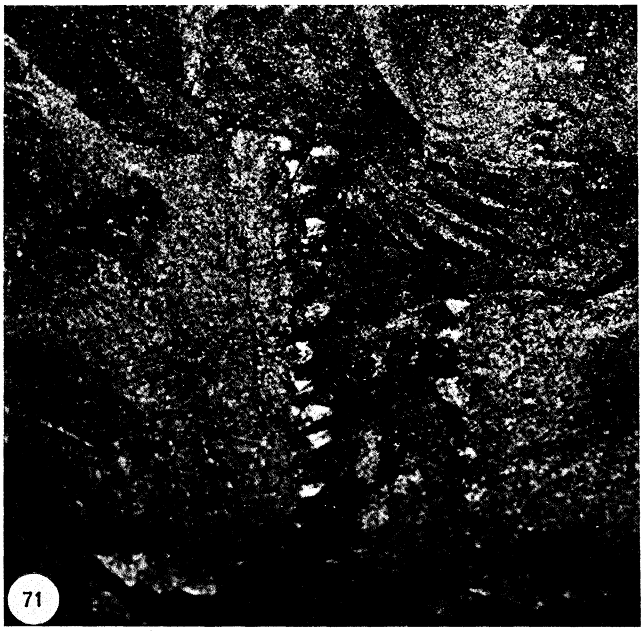
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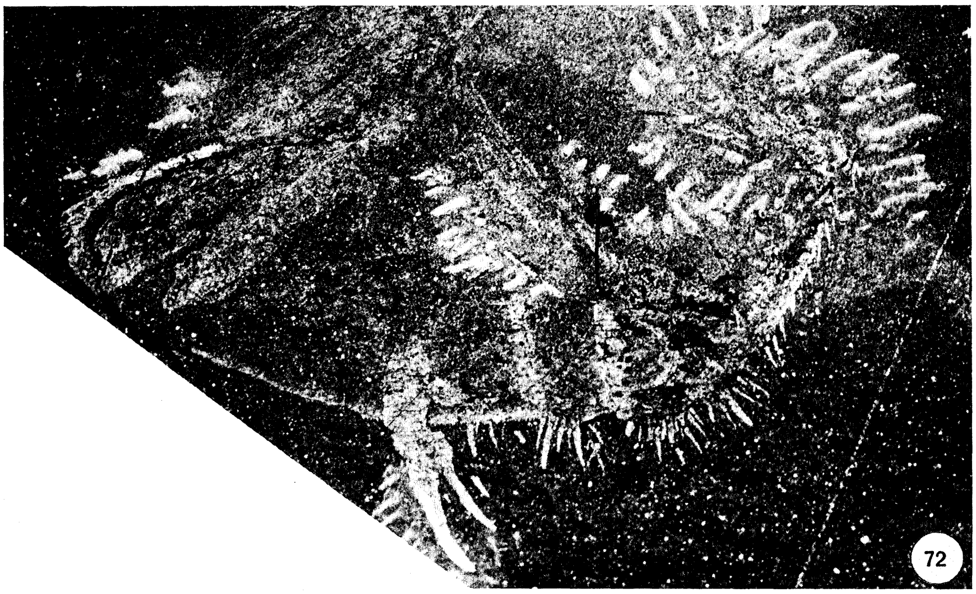
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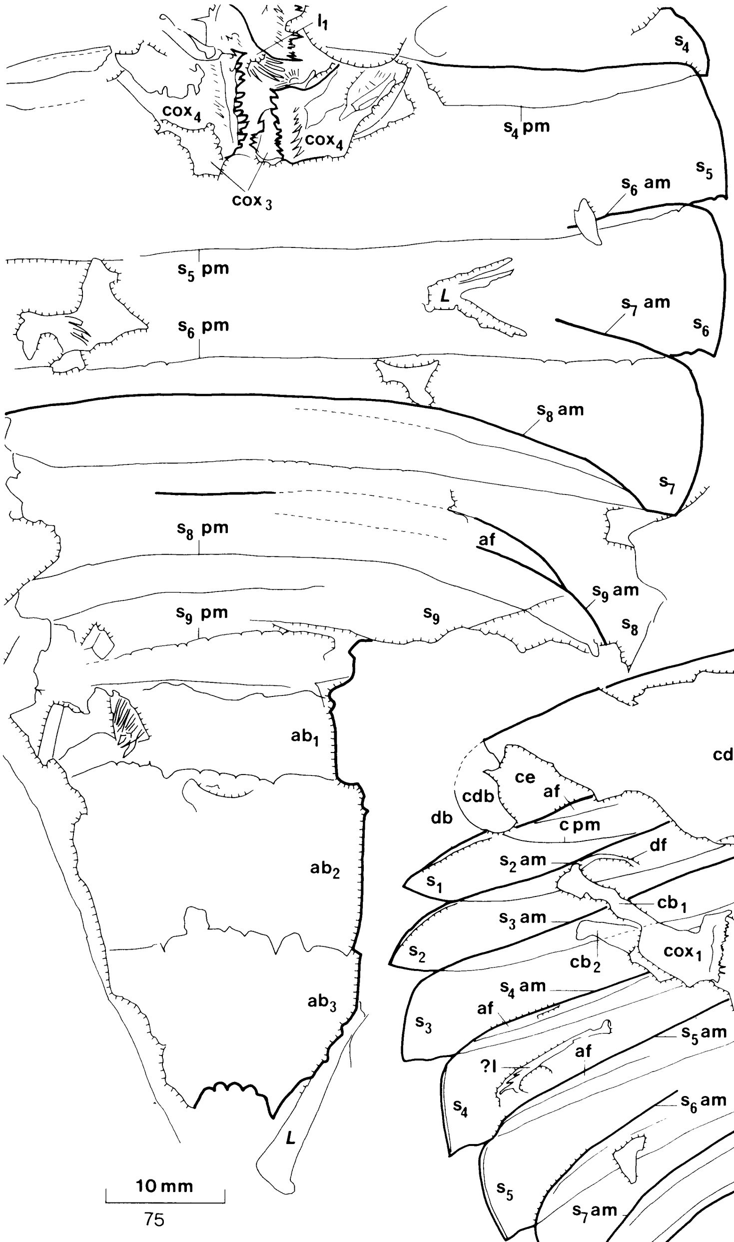
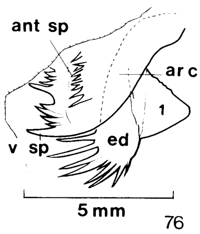
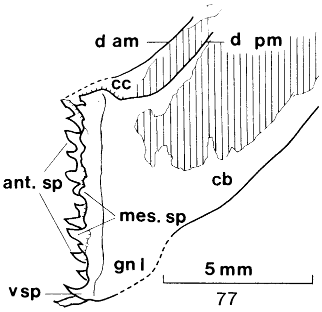
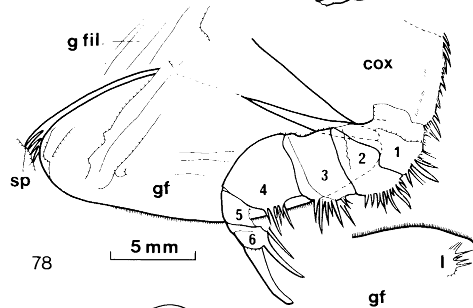
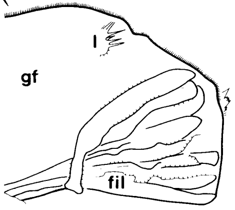
Figures 70–74. For description see opposite.

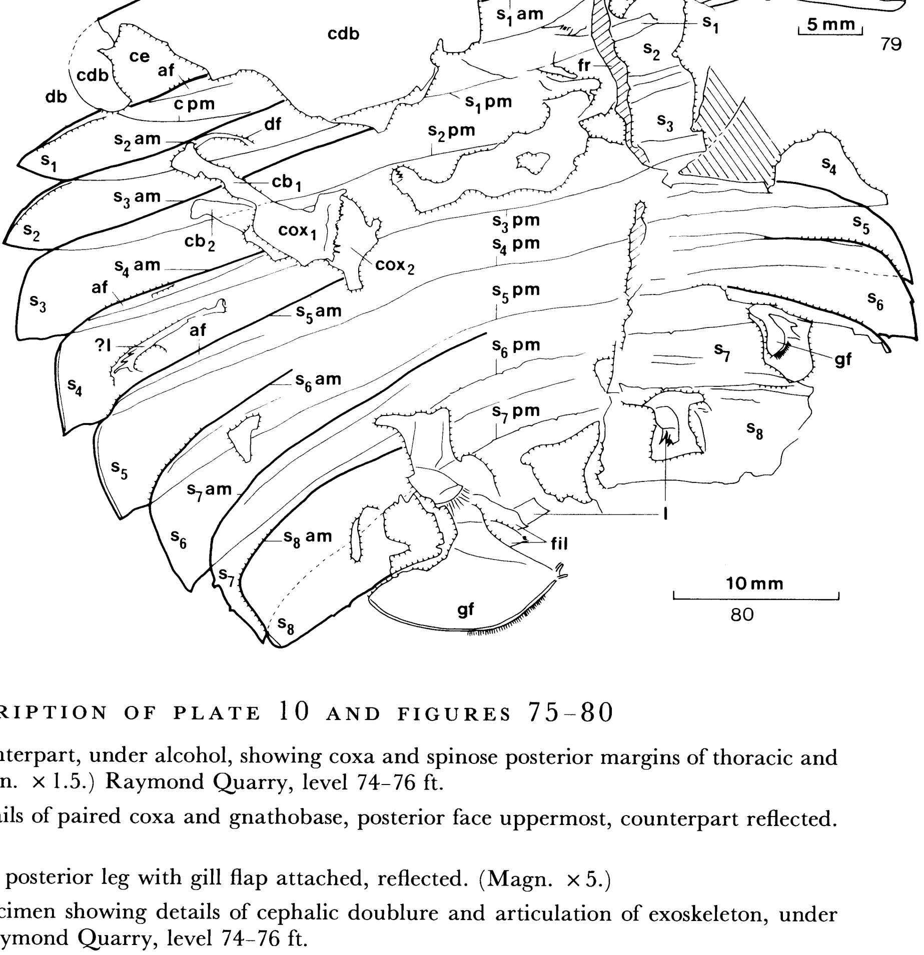












# Description of plate 10 and figures 75–80

Figure 70. G.S.C. 49743, counterpart, under alcohol, showing coxa and spinose posterior margins of thoracic and abdominal tergites. (Magn. × 1.5.) Raymond Quarry, level 74–76 ft.

Figure 71. G.S.C. 49743, details of paired coxa and gnathobase, posterior face uppermost, counterpart reflected. (Magn. × 6.)

Figure 72. U.S.N.M. 139722, posterior leg with gill flap attached, reflected. (Magn. × 5.)

Figure 73. G.S.C. 49742, specimen showing details of cephalic doublure and articulation of exoskeleton, under alcohol. (Magn. × 2.) Raymond Quarry, level 74–76 ft.

Figure 74. U.S.N.M. 139718, gill filaments attached to dorsal margin of gill flaps and partly folded back, west. (Magn. × 4.)

Figure 75. G.S.C. 49743, explanatory drawing of figure 70; *L*, appendage of *Leanchoilia superlata*.

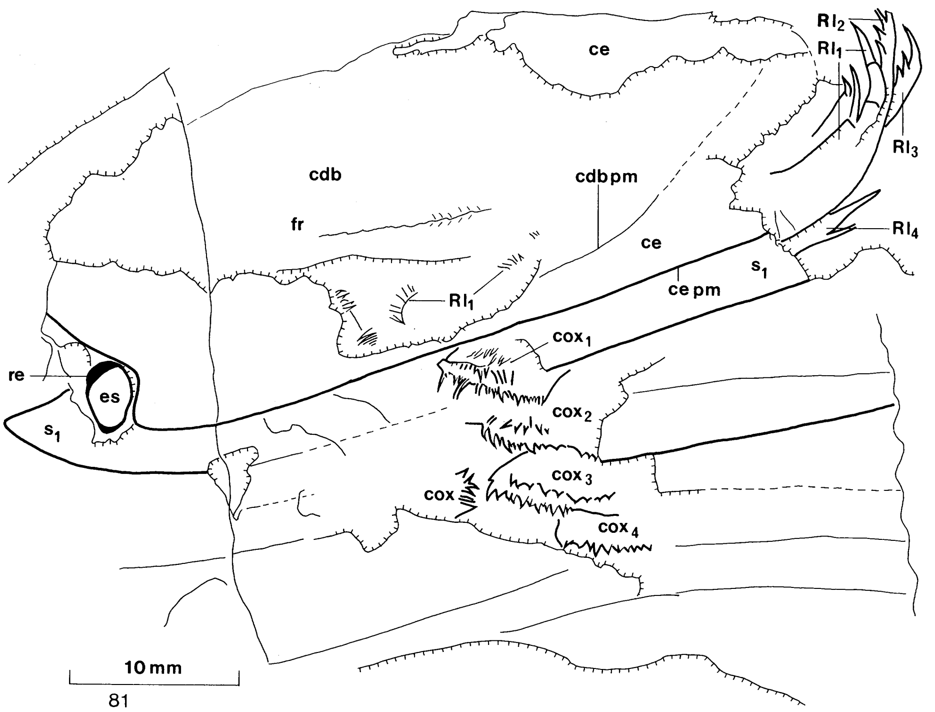
Figure 76. G.S.C. 49743, explanatory drawing of figure 70, coxa and endite, part.

Figure 77. G.S.C. 49743, explanatory drawing of $cox_4$, figure 71, showing mesial and anterior cuspate spines of gnathobase, part.

Figure 78. U.S.N.M. 139722, explanatory drawing of figure 72.

Figure 79. U.S.N.M. 139722, explanatory drawing of figure 74.

Figure 80. G.S.C. 49742, explanatory drawing of figure 73. Note that $cox_1$ and $cox_2$ have rotated posteriorly but are attached distally.



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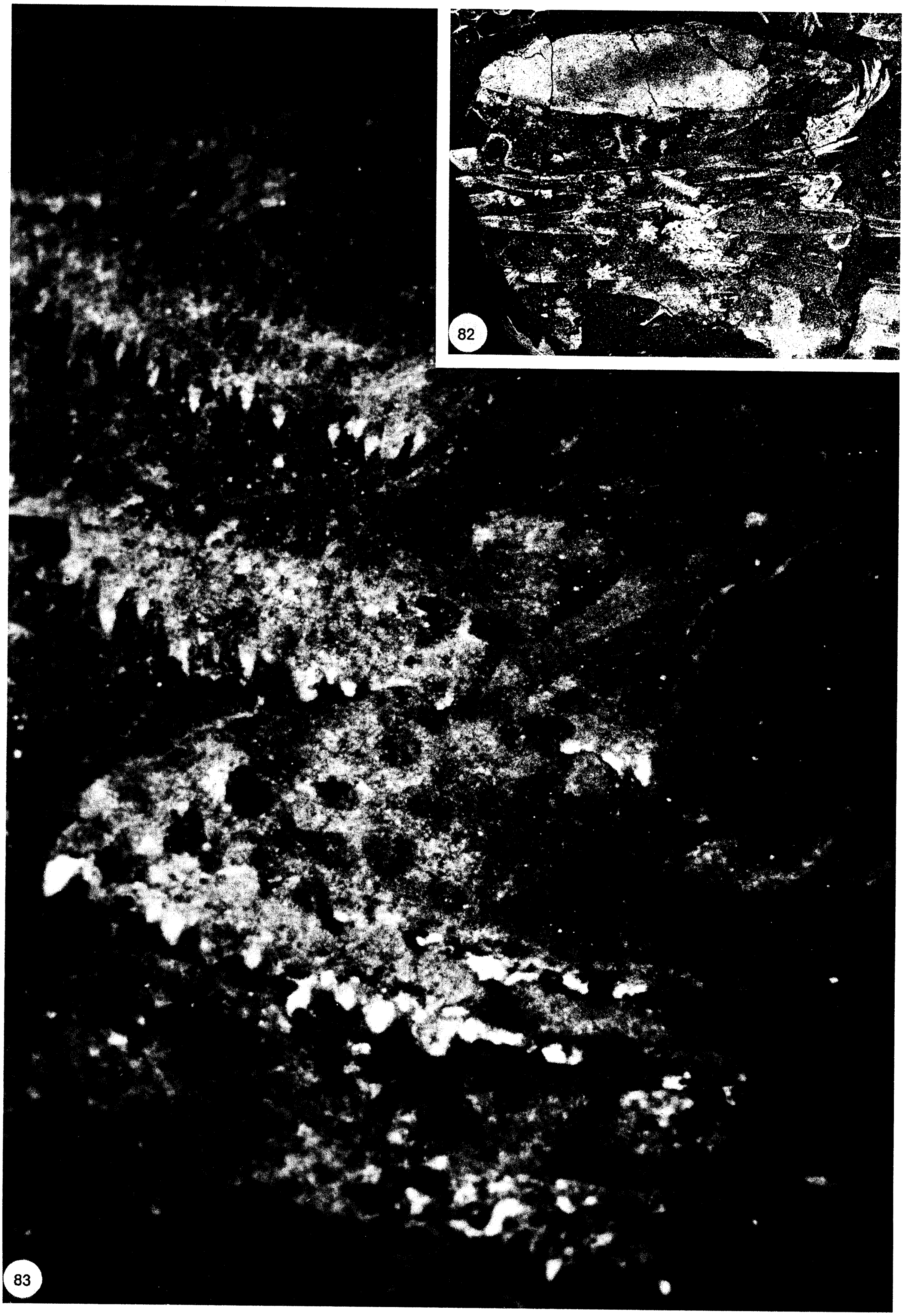
## Description of figure 81 and plate 11

Figure 81. G.S.C. 49745, explanatory drawing of figure 82.

Figure 82. G.S.C. 49745, part, under alcohol. (Magn. × 1.4.) Raymond Quarry, level 74–75 ft.

Figure 83. Detail of coxa. (Magn. × 12.) Note differentiation of gnathobases from front to back, the anteriormost with long feathery spines, the posteriormost with short cuspate spines. Recognition of the anterior row of spines shows that the coxa have rotated posteriorly and the associated legs have swung forwards to lie under the lateral edge of the cephalon.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Figures 82 and 83. For description see opposite.


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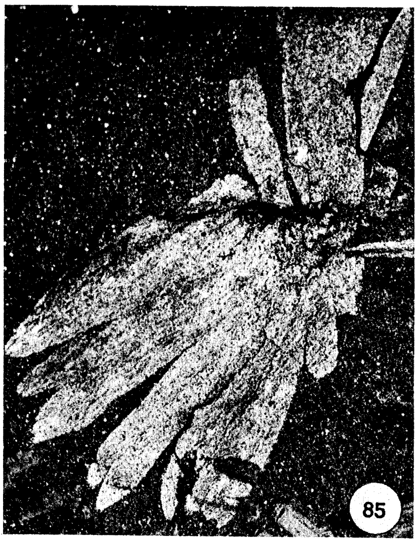
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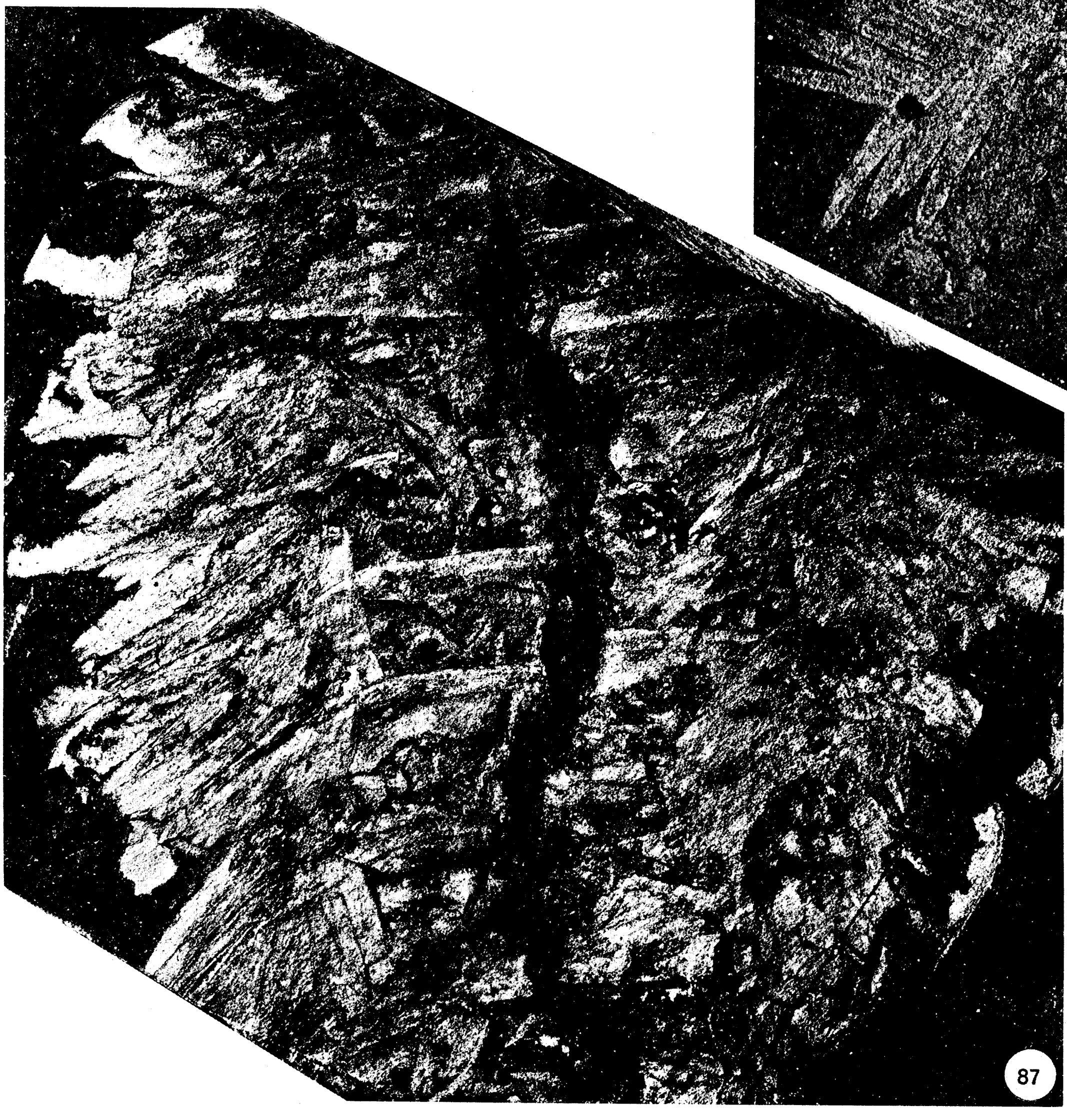
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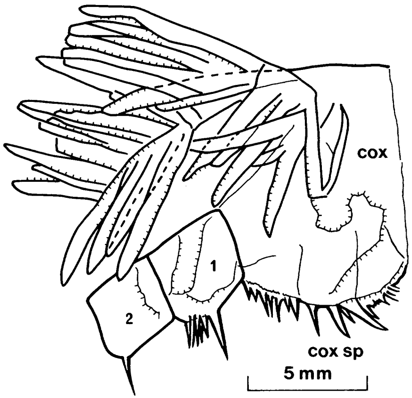
FIGURES 84–88. For description see opposite.



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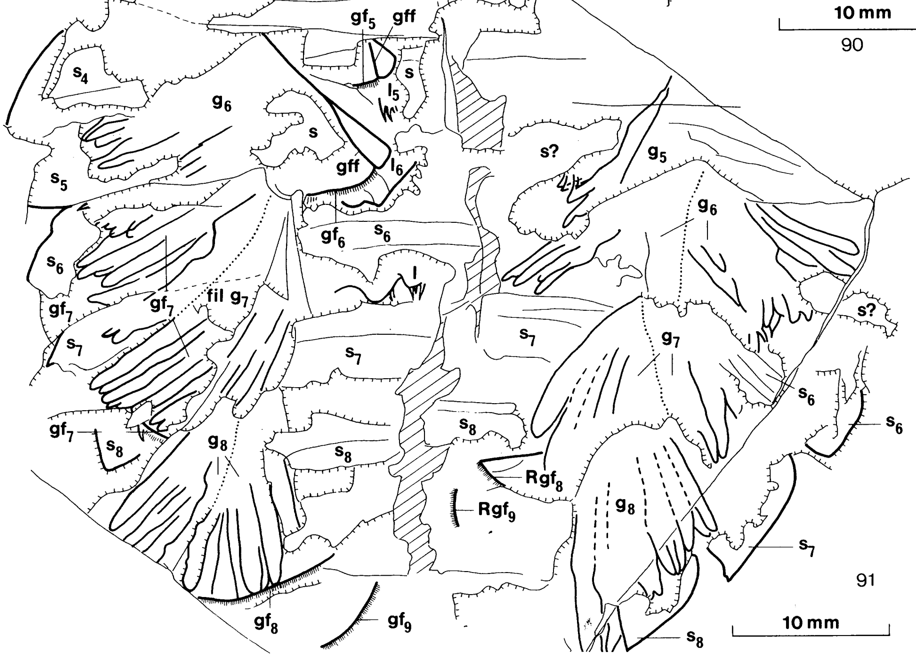

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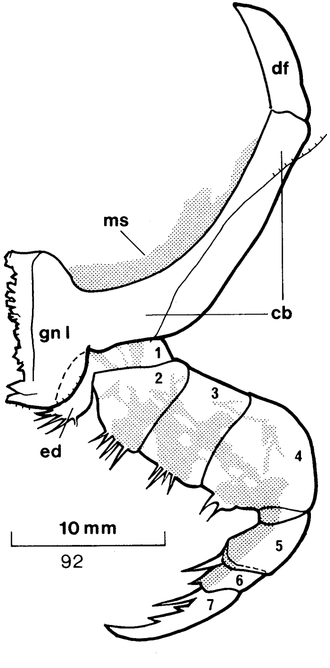

92

## DESCRIPTION OF PLATE 12 AND FIGURES 89–92

FIGURE 84. U.S.N.M. 139712, part, under alcohol. (Magn. ×2.5.) Right and left side gills beneath distal and medial parts of dorsal exoskeleton.

FIGURE 85. U.S.N.M. 250216, isolated gill filaments, reflected. (Magn. ×5.)

FIGURE 86. U.S.N.M. 13970~~8~~5, double row of gill filaments detached from gill flap and partly folded out to lie above leg, part, reflected. (Magn. ×4.)

FIGURE 87. U.S.N.M. 139686, right and left side gills lying beneath dorsal exoskeleton of posterior thorax, part, under alcohol. (Magn. ×2.5.)

FIGURE 88. G.S.C. 49746, isolated appendage, part, under alcohol. (Magn. ×1.4.) Phyllopod Bed, Walcott Quarry, level 8 ft–8 ft 7 in.

FIGURE 89. U.S.N.M. 13970~~8~~5, explanatory drawing of figure 86.

FIGURE 90. U.S.N.M. 139712, explanatory drawing of figure 84; gA and gB are gill filaments opened in direction of arrows.

FIGURE 91. U.S.N.M. 139686, explanatory drawing of figure 87.

FIGURE 92. G.S.C. 49746, explanatory drawing of figure 88. Shaded area shows outline of silver film corresponding either to muscle or contracted tissue.

93

## Description of figure 93 and plate 13

Figure 93. U.S.N.M. 139679, explanatory drawing of figure 98 after preparation of cephalic doublure.

Figure 94. U.S.N.M. 57489, detail of abdomen and contents of alimentary canal; h, hyolithid. (Magn. × *ca.* 4.) Original of Walcott (1911, pl. 3, fig. 2).

Figure 95. Same specimen as figure 94. (Magn. × 1.) Part, northwest.

Figure 96. U.S.N.M. 250218, counterpart, under alcohol. (Magn. × 2.) Note phosphatic contents (black) of alimentary canal in cephalic and abdominal regions, and specimen of *Ottoia prolifica* on left.

Figure 97. U.S.N.M. 139679, complete trilobite in alimentary canal of specimen figure 98. Specimen whitened with ammonium chloride. (Magn. × 10.)

Figure 98. U.S.N.M. 139679, part, oblique dorsal compression, prepared to show cephalic doublure (figure 12, plate 2). West. (Magn. × 1.75.)

Figure 99. U.S.N.M. ~~250217~~ 269164, counterpart detail of complete exoskeleton, northwest. (Magn. × 1.) Note group of agnostid trilobites lying beneath cephalic doublure in mouth region.

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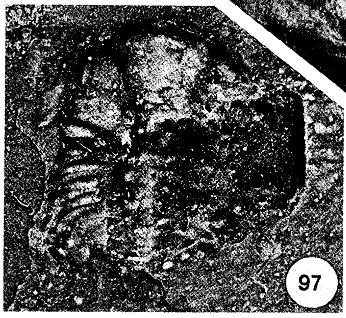

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FIGURES 94–99. For description see opposite.

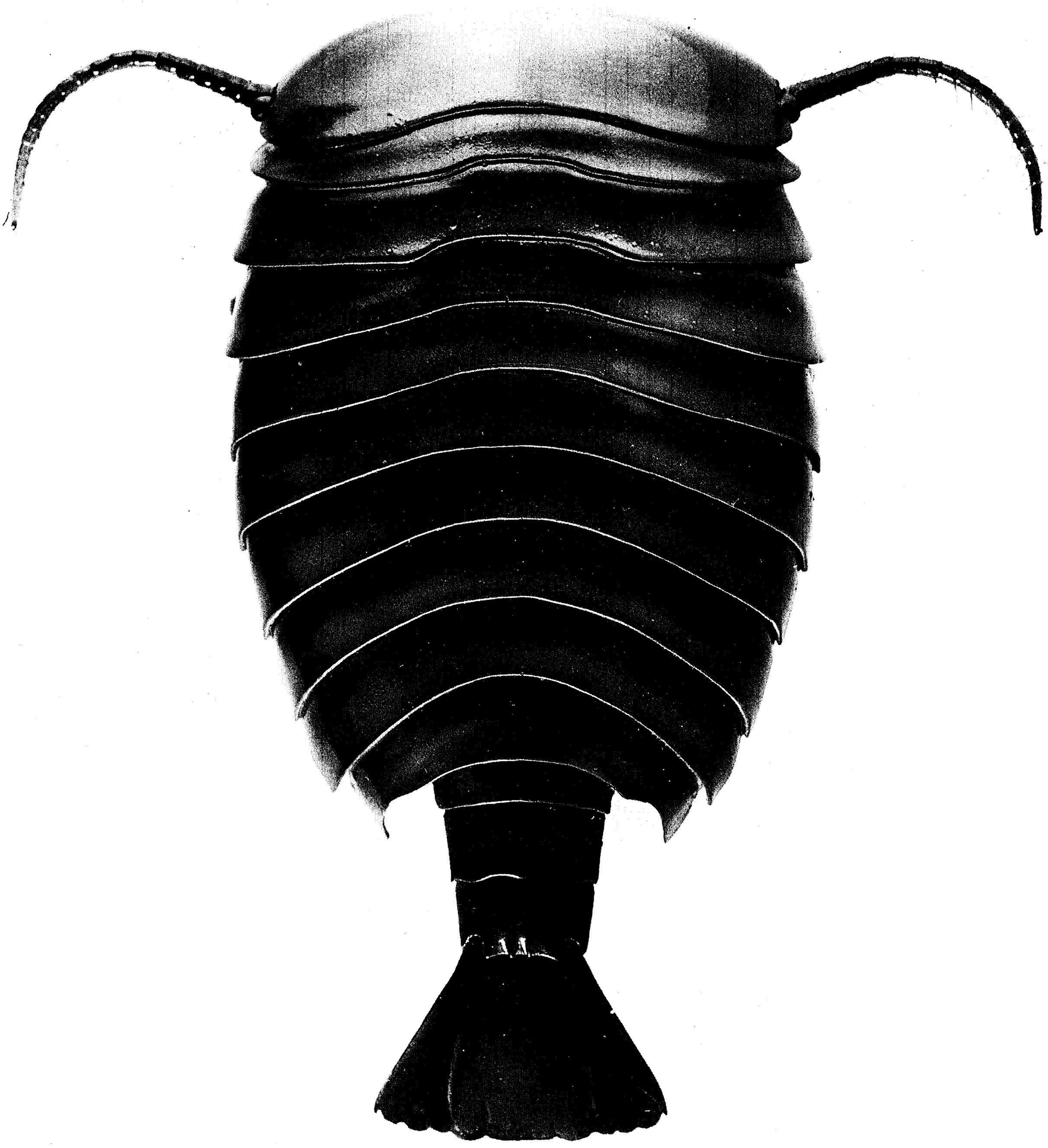

FIGURE 100. Model of *Sidneyia inexpectans*, dorsal view, approximately three times life size.

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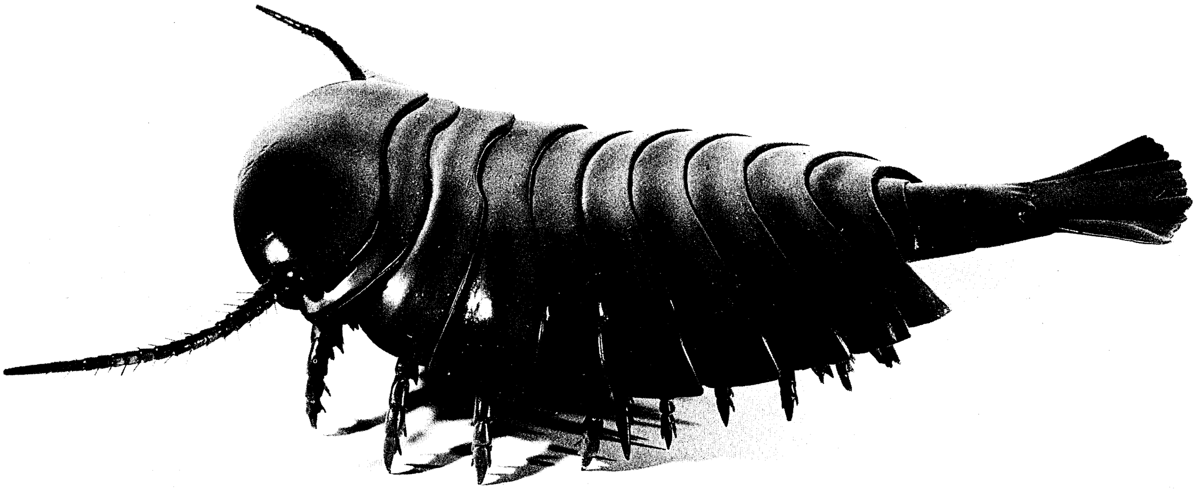
## DESCRIPTION OF PLATE 15

Model of *Sidneyia inexpectans*. Approximately life size.

FIGURE 101. Left lateral view with appendages in 'still' position of gait.

FIGURE 102. Left lateral view with appendages in 'still' swimming position.

FIGURE 103. Oblique anteroventral view showing anterior walking legs and posterior legs with gills.



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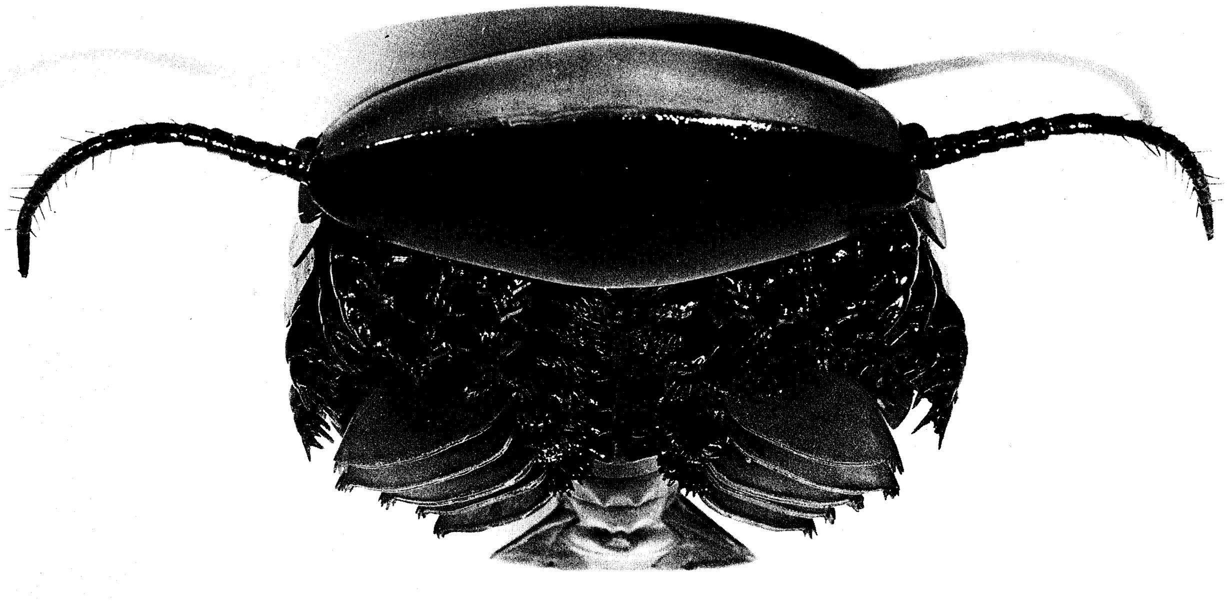

(103)

Figures 101–103. For description see opposite.

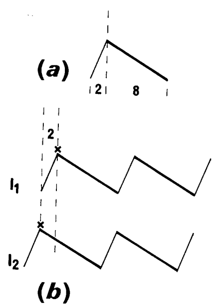

FIGURE 104. Method of constructing the gait pattern for *Sidneyia inexpectans* illustrated in figure 105.

(*a*) Relative duration of forward and backward stroke 2:8. This means that, from point of attachment ×, the total duration of leg movement, represented by ten units, includes a short forward stroke equal to two units, and a longer propulsive back stroke equal to eight units.

(*b*) Gait pattern for two successive legs $l_1$ and $l_2$ with a phase difference between them of 0.2. This means that $l_2$ is 0.2 of a step in advance of $l_1$ and the pattern is constructed by moving point × of $l_2$ two units to left.

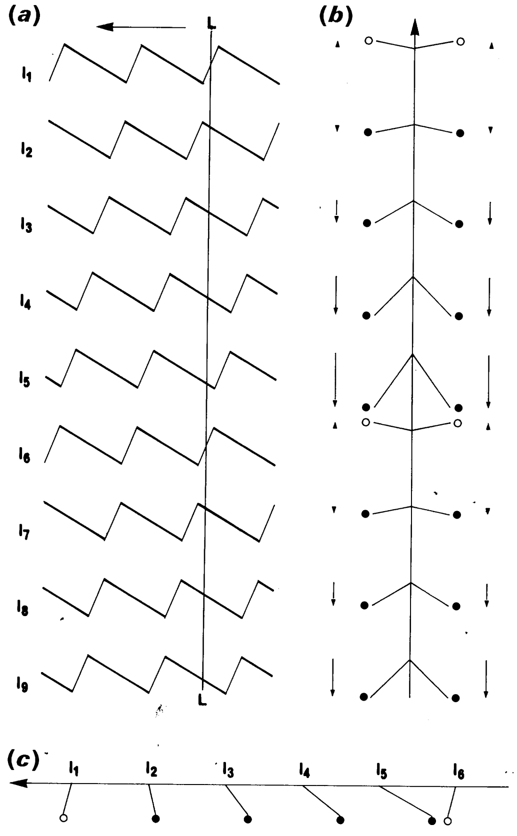

FIGURE 105. Gait pattern for *Sidneyia inexpectans*.

(*a*) Gait diagram showing the movements of nine successive legs ($l_1$–$l_9$); heavy lines denote the propulsive backstrokes 2:8. Phase difference between successive legs is 0.2. Arrow indicates forward movement of animal.

(*b*) The nine paired legs as seen from dorsal side performing assumed pace duration and gaits at a given moment in time indicated by line L–L in (*a*). Legs on ground indicated by closed circles; legs picked up from ground, by open circles. Arrows indicate direction of leg movement; length of arrow indicates duration of movement. Note that the pattern produced is one in which four pairs of legs in the propulsive phase are followed by one in the recovery phase and legs of a pair are again in the same phase.

(*c*) Lateral view showing one complete cycle of leg movement. For further explanation see text.

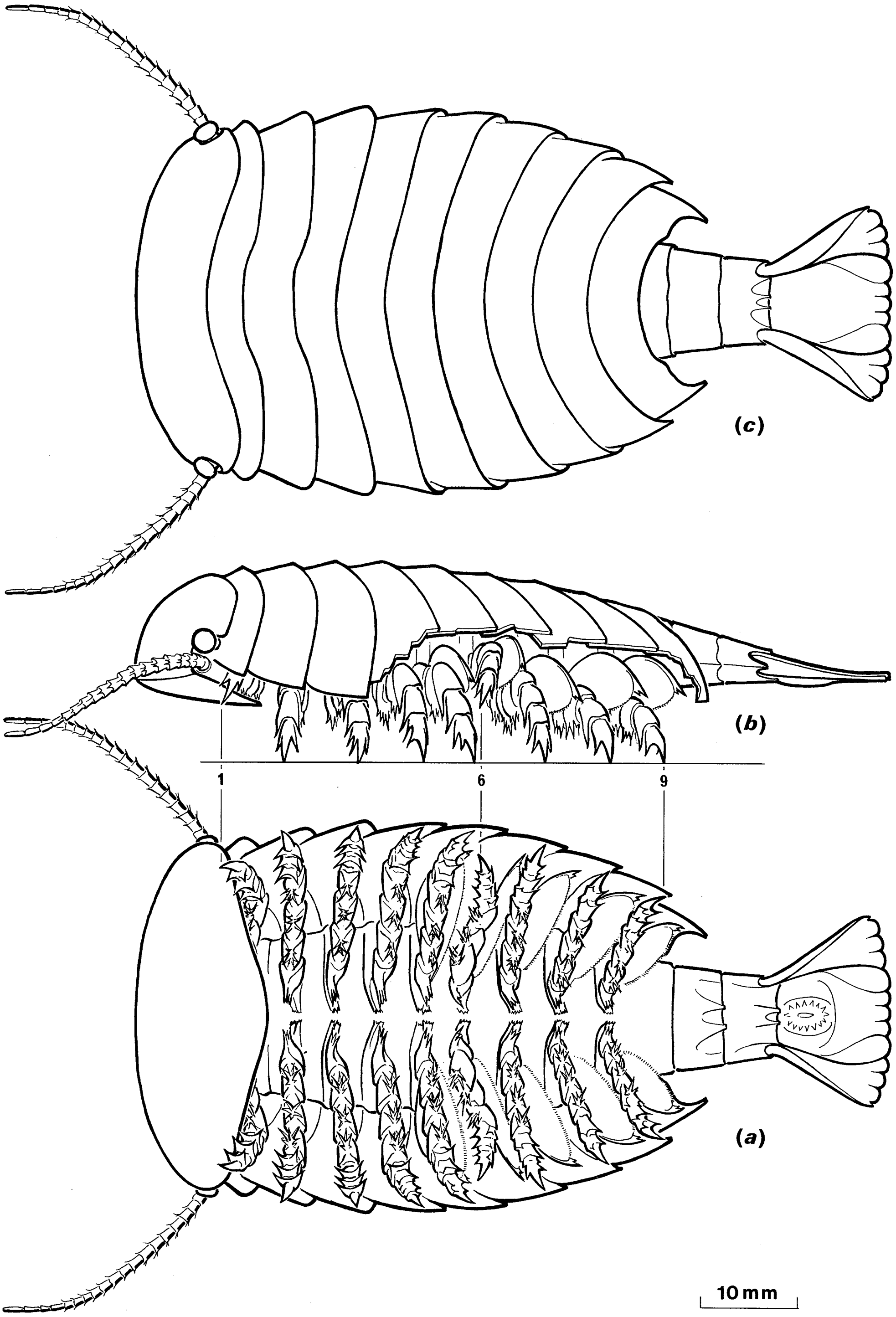

FIGURE 106. Reconstruction of *Sidneyia inexpectans* Walcott.

(*a*) Ventral view with appendages in 'still' position of gait.

(*b*) Left lateral view of same individual with parts of thorax cut away to reveal gills on appendages 5–9.

Appendages are in same 'still' position of gait shown in (*a*) with one cycle of movement involving six pairs of legs of which four pairs (2–5) partake in the propulsive phase while two pairs (1, 6) are in the recovery phase. The direction and amount of promotor–remotor swing passed through by the legs can be seen by comparing ventral and lateral views. Legs 1, 6 and 9 are indicated for ease of identification.

(*c*) Dorsal view.

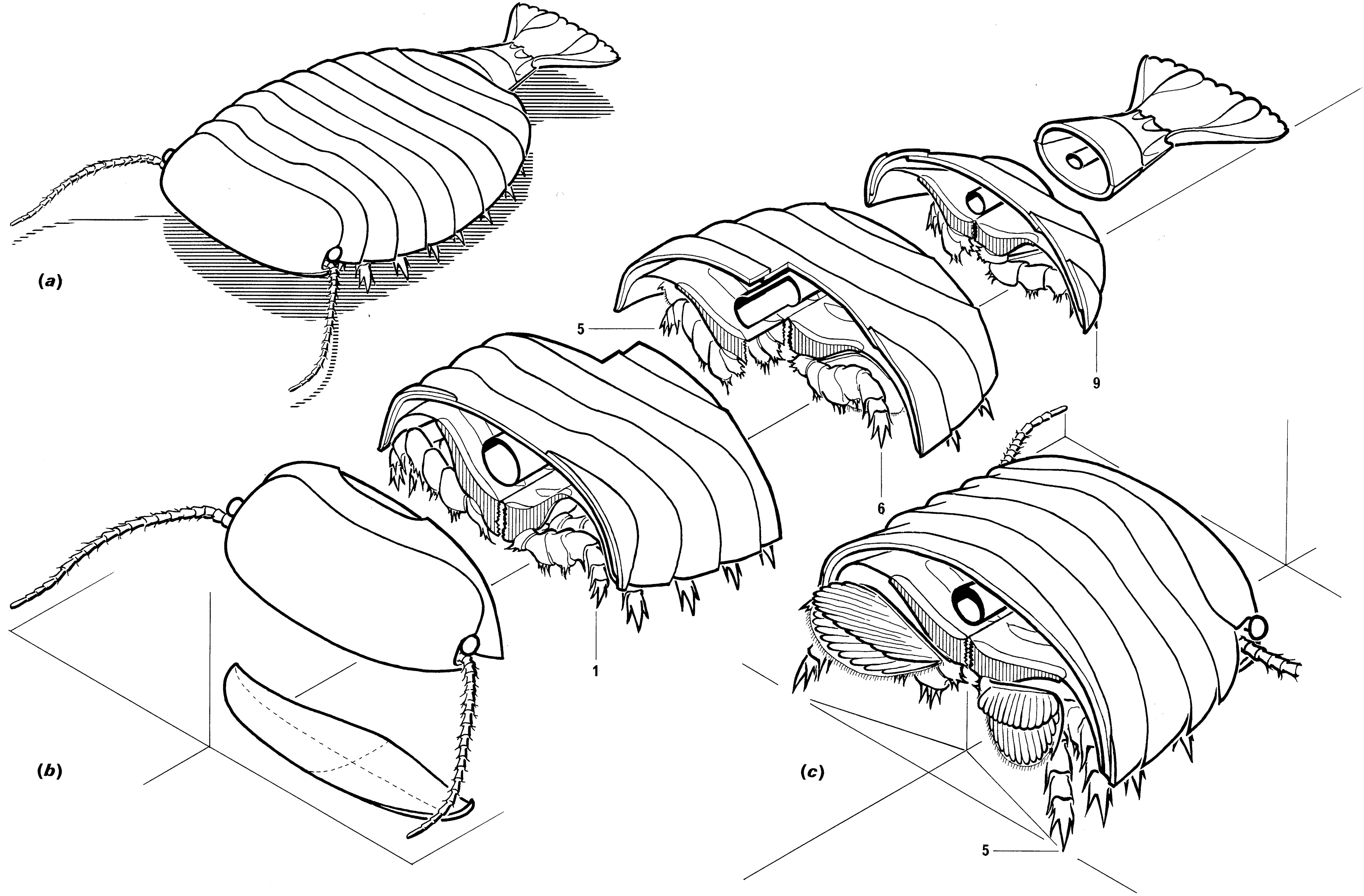

Figure 107. For description see opposite.

pattern of gait was exchanged for one in which the legs swung backwards and forwards in rhythm. In this way water movement would cause the double set of filaments to open in a manner similar to that shown on figure 107*c*, during a forward stroke, and close expelling water on the return stroke. Movement of water in this way would be through the filaments and across the entire gill flap.

## 9. Discussion and conclusions

### (*a*) *The model and reconstructions*

The model (plates 14, 15) and reconstructions based on this (figures 106, 107) summarize the evidence presented above and show how the animal may have looked when swimming or walking along the sea bottom. The convexities are derived from the unique cross sections described in §7 (*a*) and provide space for the walking legs and associated gills (§7 (*d*)(iv, v)).

Preparation of specimens from the dorsal side has confirmed Walcott's ideas that the cephalic doublure was attached to the ventral cephalon. I believe it to be a distinct plate and not, as interpreted by Simonetta (1963), the rolled continuation of the cephalon on the ventral side.

A posterolateral space between the doublure and cephalon allowed insertion of the antenna and also accommodated the eyes. These were stalked not, as thought by Simonetta, attached to the side of the cephalon.

The backward extension of the doublure allows no space for appendages of the size and type thought to exist on the cephalon by Walcott (1911), Størmer (1944) and Simonetta (1963). I conclude that the cephalon did not bear appendages apart from the uniramous antenna. There is no visible evidence for segmentation of the cephalon, Simonetta's segment 2 being the compressed impression of the posterior margin of the doublure, his segment 3 being the first thoracic somite, which is shown to articulate with the cephalon.

When the thorax is viewed from the dorsal side (figure 106*c*, plate 14) the first four somites have weakly curved margins, while the posterior five somites become shorter and progressively curved backwards. These cover the first four pairs of uniramous walking legs and the posterior five pairs of biramous appendages respectively. The latter consist of an inner ambulatory branch and an outer ramus bearing a gill consisting of two layers of filaments attached along the dorsal margin of a large flap (§7 (*d*) (iv, v)). There is no evidence that this flap was attached to the ventral surface of the animal in the manner described by Walcott (1911) or Simonetta (1963).

I conclude that the gill was attached to the first podomere of the leg and hung down between

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Figure 107. Reconstruction of *Sidneyia inexpectans* Walcott. Reconstruction of animal in same 'still' position of gait.

(*a*) Oblique lateral view of complete individual.

(*b*) Isometric projection of oblique lateral view from anterior with exoskeleton cut at four places and exploded to reveal legs and coxae. Cuts have been made through somites 1 and 2 to reveal the first pair of legs, through somites 5 and 6 to reveal fifth leg (right) and the succeeding sixth pair, and through somites 7, 8 and 9 to reveal the ninth pair of legs. Paired legs 1 and 6 are in the promotor recovery phase, leg 5 and pair 9 are in the remotor propulsive phase. Because of the promotor–remotor swing of the legs, cuts through the exoskeleton pass through the midline of the coxae which are thus seen in vertical section (shaded). The abdomen has been cut between its first and second somites to reveal the dorsal and ventral rings. The cephalic doublure has been detached from the cephalon along the marginal suture and is projected beneath the cephalon. Dotted transverse and sagittal lines are drawn to give some idea of convexities.

(*c*) Isometric projection of oblique lateral view from the posterior with exoskeleton cut through somite 5 to reveal the fifth pair of legs and those bearing the first gills. The gills hang obliquely down and the two layers of filaments are shown opening.

In (*b*) and (*c*) legs 1, 5, 6 and 9 are numbered for ease of identification. Transverse, sagittal and vertical construction lines are shown for ease of interpretation.

successive legs on the posterior thorax. Movement in a dorsal–ventral direction could have taken place along a fold in the gill flap membrane. This movement was probably greatest when the animal swam. Movement in a vertical plane was also possible due to the promotor–remotor swing of the large coxa. These bore strong gnathobases on the first four appendages and are considered to have been capable of capturing and crushing hard food. The appendages are restored from the new evidence summarized in §7(*d*), and differ considerably from previous interpretations.

A theoretical gait pattern (§8(*a*)) has been constructed for an animal such as *Sidneyia*, with a series of large legs positioned closely together, and a relative duration of forward and backward stroke of 2:8. Each metachronal wave included movement of six legs, i.e. with a total of nine legs. Paired legs 1–6 partake in the cycle, legs,7–9 repeat it. The reconstructions (figures 106*a*, *b*, 107*b*, *c*) show this and at any one time seven legs are on the ground and two are in the recovery phase.

The abdomen consists of two or three articulated rings (§7(*f*)) and a terminal plate or telson onto which the anus opened. Paired uropods articulate independently of the telson, in lateral sockets in the abdomen. This confirms the observation of Simonetta (1963, p. 106) but not that of Walcott (1911, p. 24). Both the lateral margins of the telson and uropods were thin and flexible and became folded or wrinkled during burial and compression. They are not the imbricated margins of several free lamellae as thought by Simonetta.

### (*b*) *Mode of life*

The well jointed walking limbs and type of gnathobase suggests that *Sidneyia* was an animal well suited to a bottom-living habit. The characteristic prehensile anterior limbs with large robust gnathobases certainly indicates a carnivorous animal capable of dealing with fairly large prey, which could be cut, ground or shredded before ingestion. Study of gut contents shows that ostracodes, hyolithids and small trilobites, some whole, were among the diet of *Sidneyia*, and gut filling contains a high percentage of phosphate presumably derived from other shell-bearing organisms, among which inarticulate brachiopods and monoplacophora are known in association. Such food could be obtained from the substrate surface by a scooping action of limb tips and spinose inner surfaces of leg podomeres, and brought to the gnathobases ventrally.

The first four somites forming the anterior thorax have weakly curved margins which, during articulation, probably allowed some dorsal and ventral movement of the body in this region. This flexibility may have enabled the animal to push the head into the sediment in search of food. Together with the stiffened lateral edge of the cephalon and the backwardly projecting doublure this seems to be an adaptation to 'ploughing' in the sediment.

It is thought that *Sidneyia* was primarily a bottom-living animal, although the telson with caudal fan must be considered a provision for swimming. Whether *Sidneyia* used the fan in active swimming as in the shrimps or for rapid 'jumps' as in the lobster is not known but the latter seems less likely because of the apparent rigidity of the abdomen.

Flexure of the anterior thorax might also help the animal to right itself if it became inverted. Such a situation is common in modern xiphosurans, which swim upside down and often land on the bottom in this position. Righting can be attained in one of several ways (Fisher 1977) but help is given by a dorsal jackknife bending of its prosoma and opisthosoma along the line of the hinge. A corresponding upward bend in *Sidneyia* would be possible in the anterior thorax and somites in this region are shaped to allow this.

### (*c*) *Affinities*

In a classification of arthropods based on the cephalic region, *Sidneyia* must rate as unusual if not unique. Apart from the dorsal shield, stalked eye, preoral antenna and ventral doublure which functions as a labrum, there are no feeding or walking limbs on the cephalon. Successive thoracic limbs show differentiation into those involved with walking and biting, and those that combine walking with food transport, breathing and presumably swimming. The arrangement and number of limbs is neither trilobite-like nor crustacean-like, though in form and function the walking legs are similar to those of living merostomes.

On the dorsal surface, however, construction of the body and abdomen bearing a caudal fan, is more a crustacean feature, showing that any assignment based on dorsal features of the exoskeleton alone would be suspect. One is therefore left to decide whether it is at all possible to classify *Sidneyia* into any extant or fossil arthropod group. Previous classifications have been based entirely on features of the limbs, and Walcott (1911), having confused specimens and wrongly assigned isolated appendages to the animal, provided the starting point from which subsequent authors could add further confusion. Thus we have the reconstructions of Burling (1917), Størmer (1944, 1959) and Simonetta (1963, 1975, 1976), which combine isolated appendages of disproportionate size and affinity to exoskeletons despite evidence to the contrary, and Sharov's (1966, fig. 19) 'theoretical' limbs. Other classifications are more philosophical, though have as a starting point Walcott's interpretation of morphology, and all concern discussions on the relationship between the Trilobita, Merostomata and Crustacea and the part, if any, that *Sidneyia* plays in this. Walcott believed *Sidneyia* to be a merostome and intermediate between trilobites and eurypterids, while Clarke & Ruedemann (1912), Raymond (1920) and Raasch (1939) interpreted the appendages as being crustacean and thus far removed from the merostomes. Walcott received support from Fedotov (1925) for the merostome affinity of *Sidneyia* but he based his arguments on Walcott's (1911, pl. 5, fig. 1) misinterpreted limb as indicating a closer relationship to the trilobites. Størmer (1944) erected the Trilobitoidea for those arthropods with a body plan different from trilobites but related to them on account of the so-called trilobite appendage. Thus among arguments used was the fact that a modified trilobite appendage could give rise to that of a merostome (*Limulus*) and that among the Trilobitoidea are forms that are Crustacea-like or that with little modification could conform to the crustacean organization.

Størmer's Merostomoidea (see Størmer 1944, p. 134; 1959, p. O29) was established to include *Sidneyia* and a number of other non-chelate genera, all from the Middle Cambrian Burgess Shale. Others from different stratigraphical horizons have subsequently been added to this group (Bergström 1971, 1979), and it has been recently shown that *Aglaspis* is also non-chelate and likewise presumably are other genera constituting the family Aglaspididae (Briggs *et al.* 1979). *Aglaspis* and *Sidneyia* are not related nor is *Sidneyia* like *Naraoia*, *Molaria*, *Emeraldella* and *Leanchoilia*, included by Størmer in the Merostomoidea because of the so-called similarity of the modified 'trilobite' appendage and the superficial resemblance of the dorsal shield. Common to all, however, is the fact that movement of food was, as in the trilobites, from posterior forwards, and a prehensile limb is characteristic, together with some form of spinose inner edge of the coxa. Gnathobasic lobes used in feeding have been shown to exist in the trilobites *Triarthrus* (see Cisne 1975), *Olenoides* and *Naraoia* (Whittington 1975*b*, 1977), in the non-chelate arthropod *Cheloniellon* (Stürmer & Bergström 1978) and in *Sidneyia*. In *Sidneyia*, however, the coxa–body articulation indicates that the mechanics of feeding and leg movement must have been fundamentally different, and is more like the condition in living merostomes, where biting and chewing takes place in the transverse plane. Biting and chewing in the transverse plane in merostomes is a primary feature which, according to Manton (1963, 1977), indicates a wide gap between the Merostomata and the Crustacea. In my view it also indicates a wide gap between

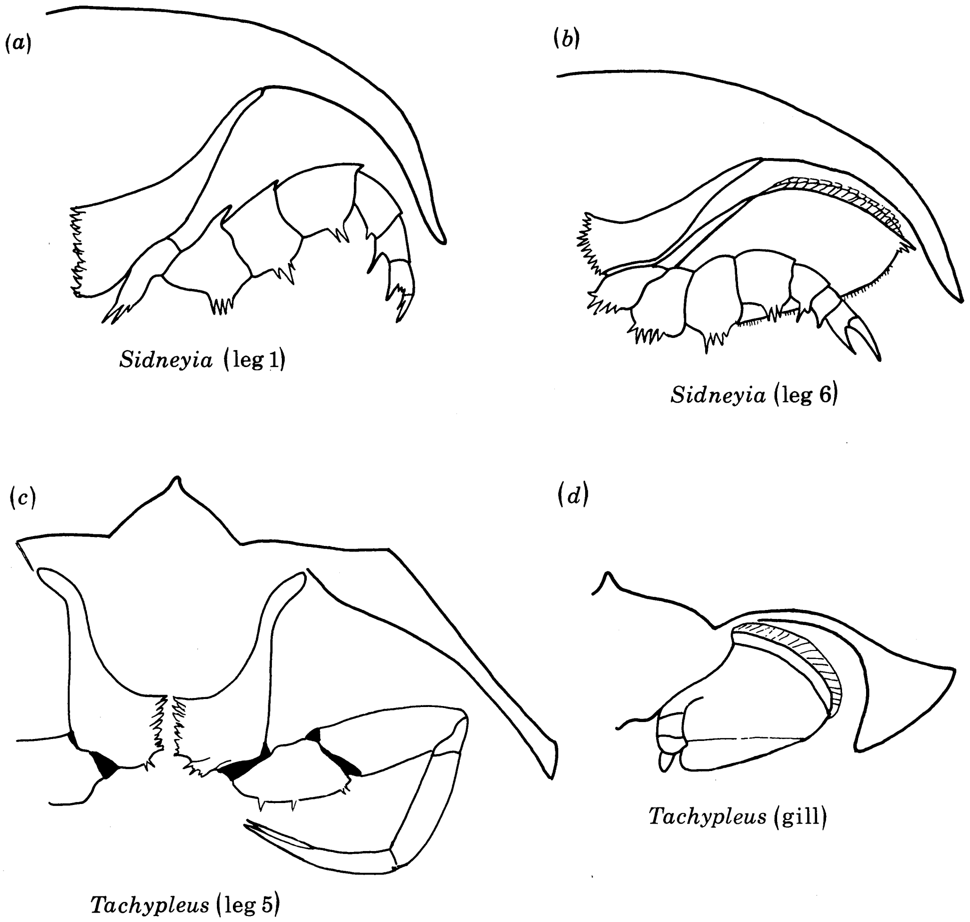

FIGURE 108. Comparison of legs and gills of *Sidneyia* with those of the merostome *Tachypleus*. (*a*) *Sidneyia*, leg 1; (*b*) *Sidneyia*, leg 6; (*c*) *Tachypleus*, leg 5; (*d*) *Tachypleus*, gill.

the trilobites and the Merostomata and, contrary to statements by Manton (1963, p. 132; 1977, p. 244), legs of the two do not exhibit a strong resemblance to each other. As described here, limbs of *Sidneyia* are a more likely prototype of the modern merostome limb than are the limbs of trilobites. Figure 108 shows the similarity between the coxa and walking legs of *Sidneyia* and the modern merostome *Tachypleus*. It takes little imagination to derive a modern merostome gill from a gill-bearing appendage of *Sidneyia* by enlarging the posterior point of attachment of the gill to the base of the walking leg, and reduction of the latter to give the condition in *Tachypleus*. In *Sidneyia* the gill (figure 107*c*, 108) is attached to the posterior–lateral face of the first podomere of the leg whereas it arises from a similar position on the coxa in trilobites. This suggests that the coxa is probably not a homologous structure in trilobites and in *Sidneyia*.

Thus *Sidneyia* shows that already in the Middle Cambrian a type of limb and feeding method similar to that used in living merostomes had been developed probably to meet the need for accommodating larger and harder food, a fact supported by study of the gut contents. This system of feeding is in advance of the trilobites with their serially arranged gnathobases and legs on a small coxa–body attachment (Whittington 1975*b*, 1977) and is in contrast to the Crustacea, in which the mandible lies directly behind the mouth (Briggs 1978).

Despite the resemblance between the limbs of *Sidneyia* and living merostomes, the former, because it lacks chelicerae, is still not a merostome though this gap is small if one accepts that the merostome chelicera is a modified preoral antenna. *Sidneyia* therefore is the earliest form known that could be a likely ancestor to the merostomes. It still defies group classification and I do not believe that anything would be gained by trying to modify a previously established group to accommodate it nor do I see the value in erecting a new one. Furthermore it shows that caution is needed when trying to classify less well preserved fossil material and even more so when trying to erect phylogenetic patterns within the arthropods at such an early stage in their history.

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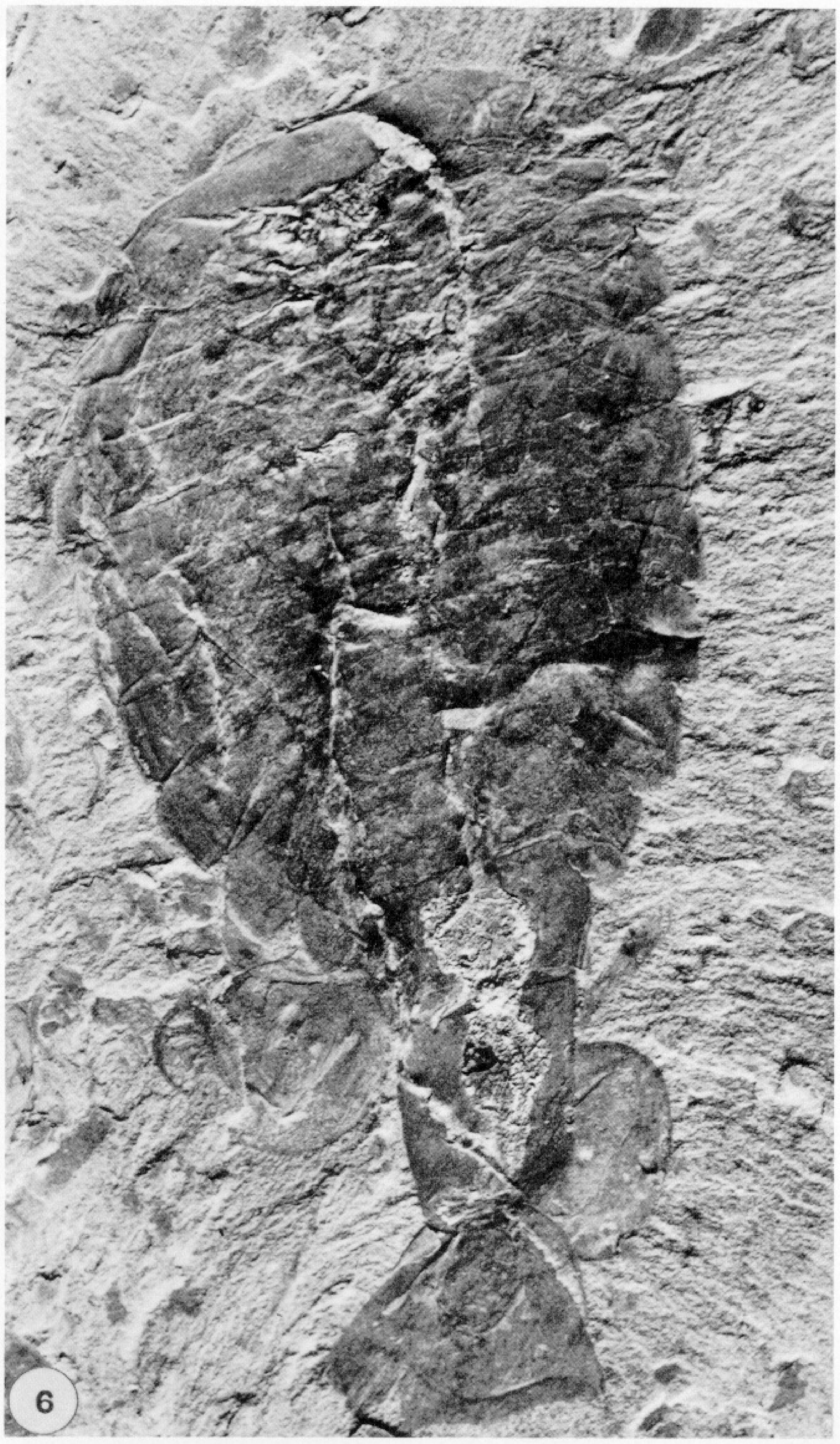

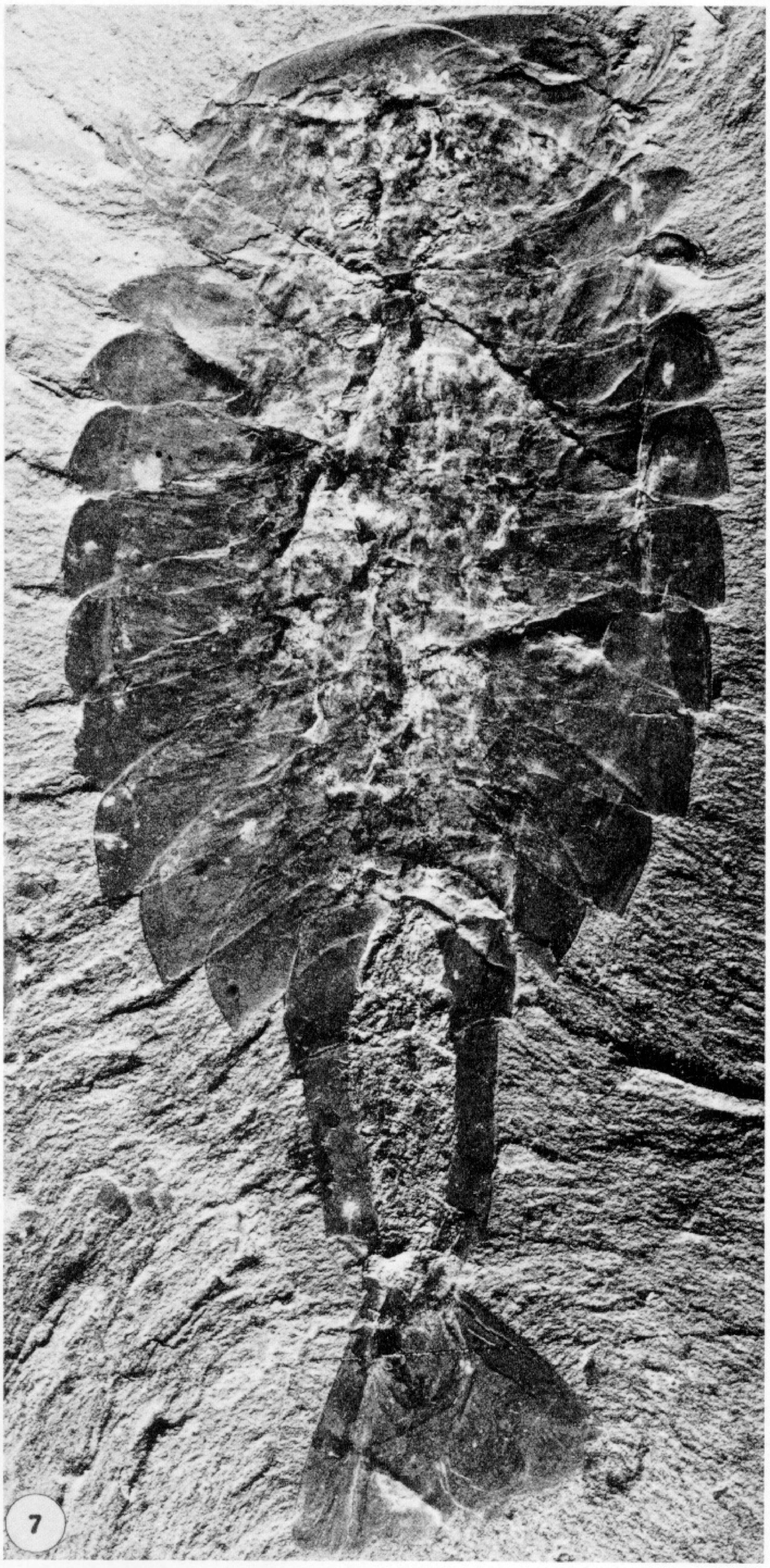

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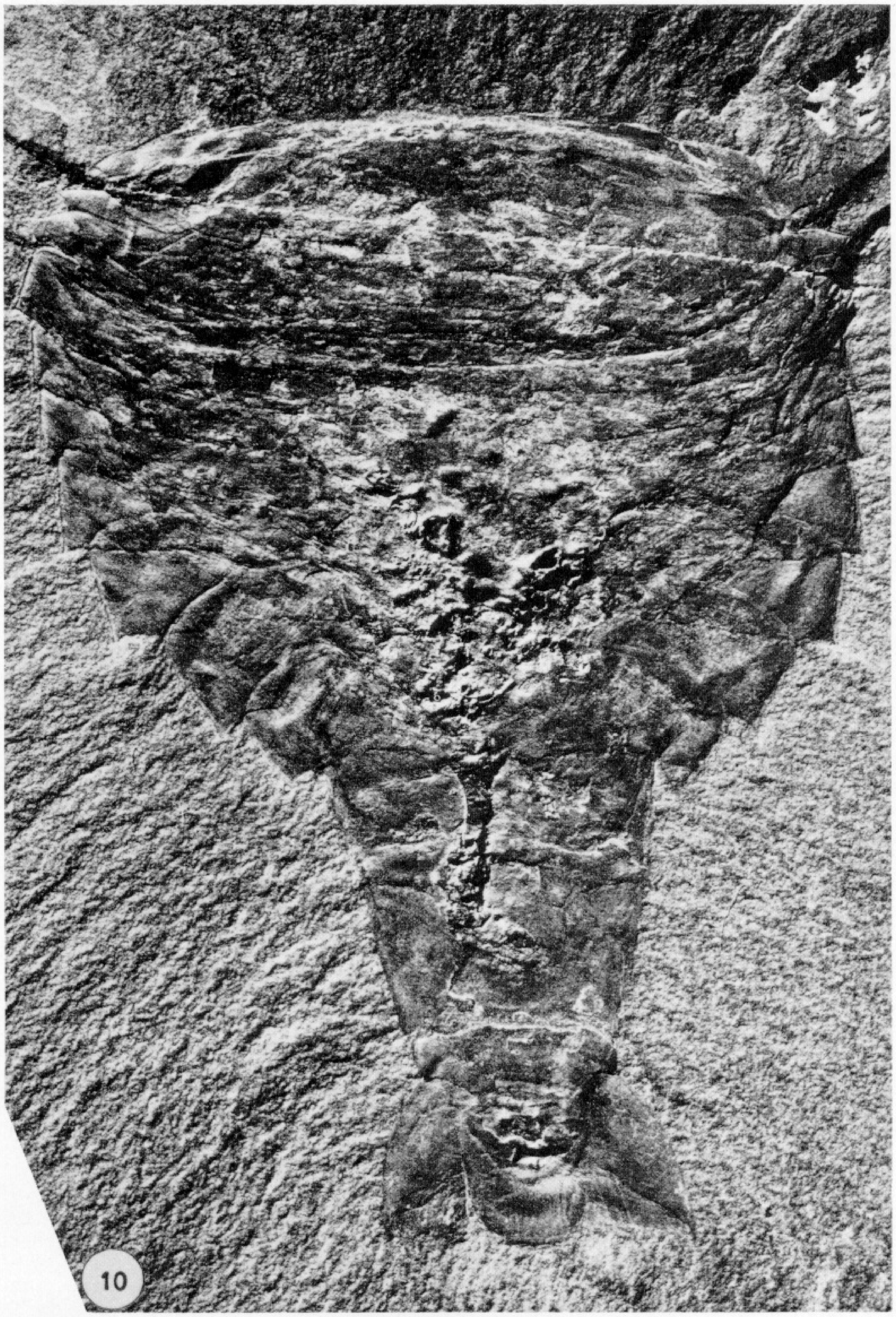

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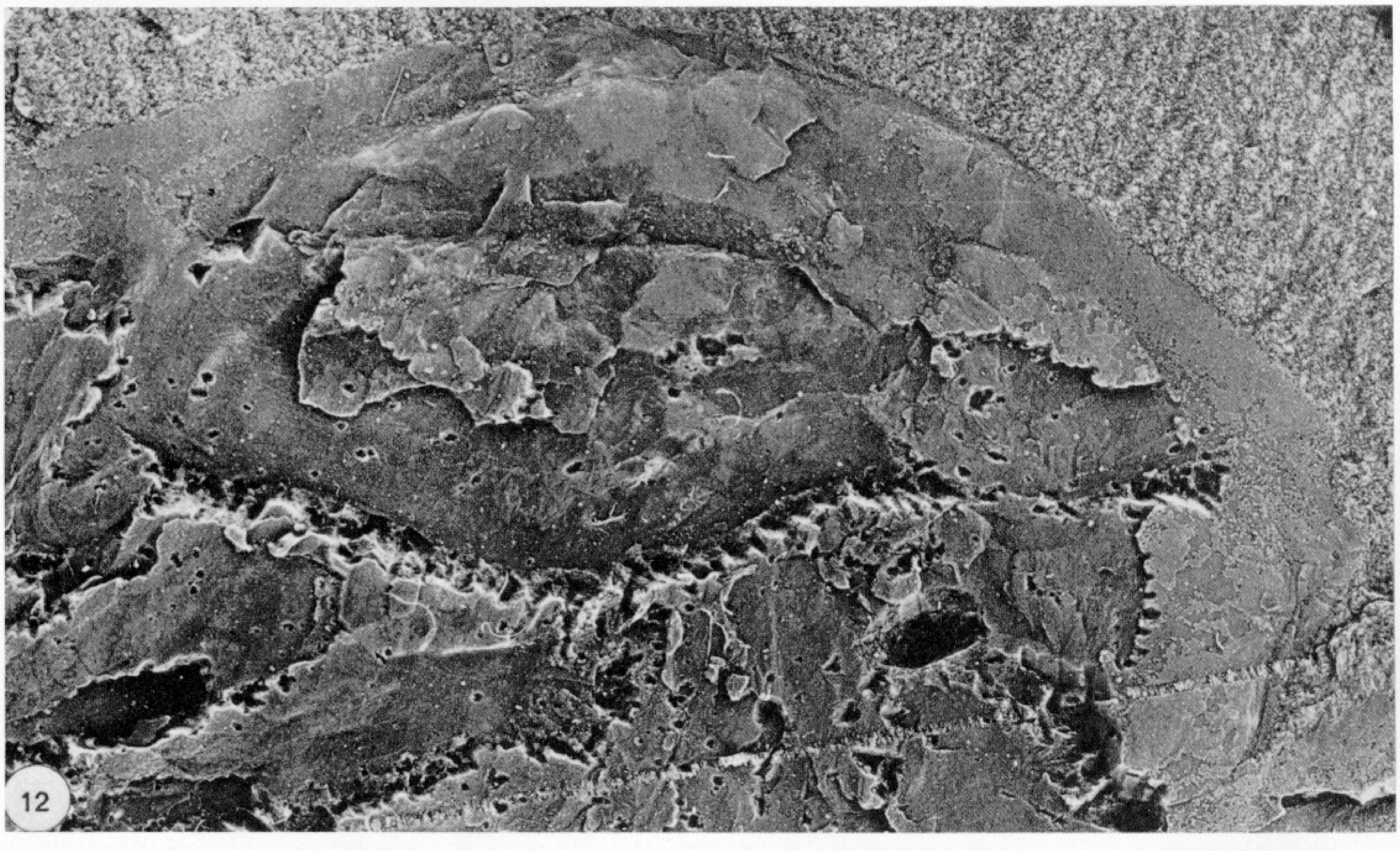

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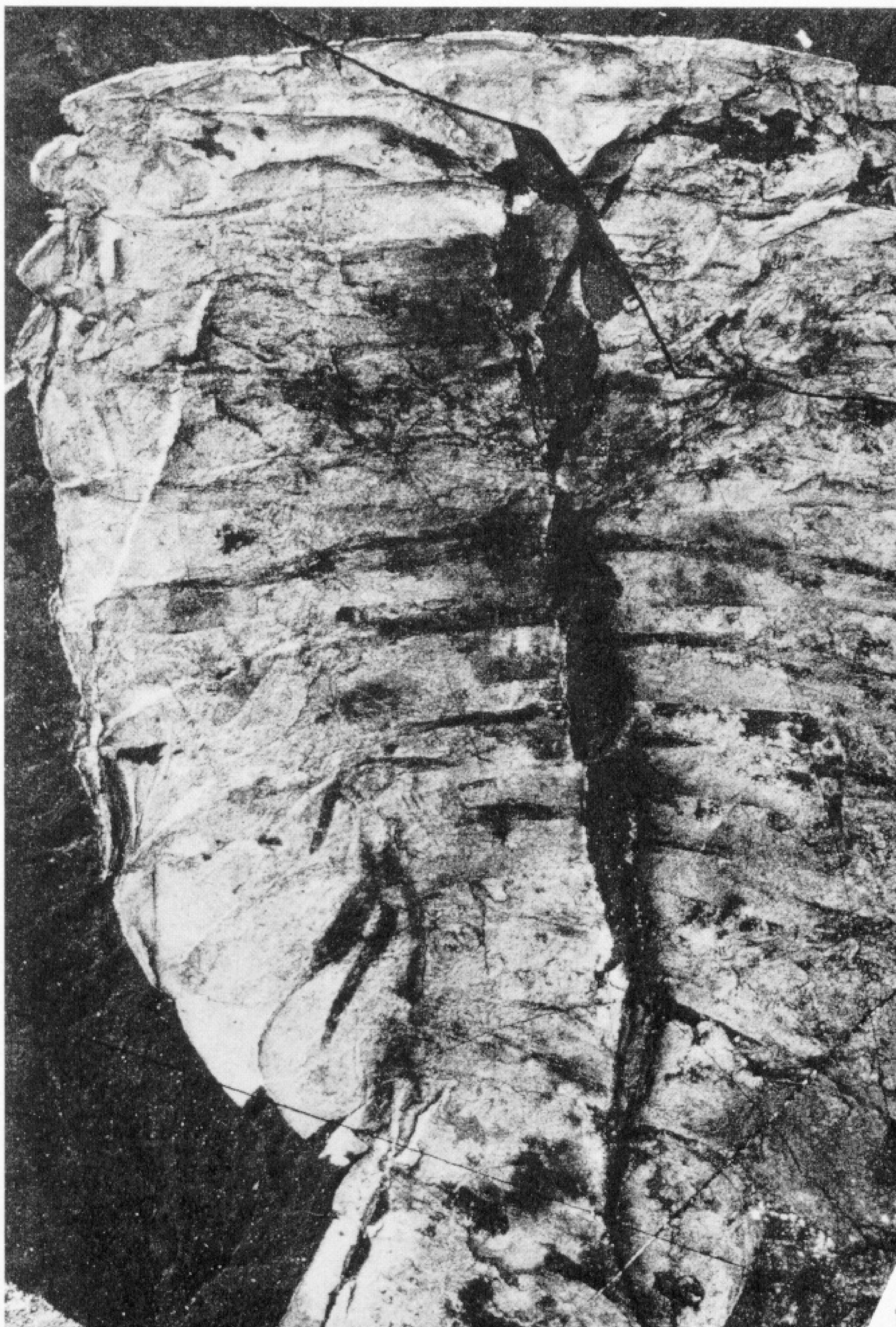
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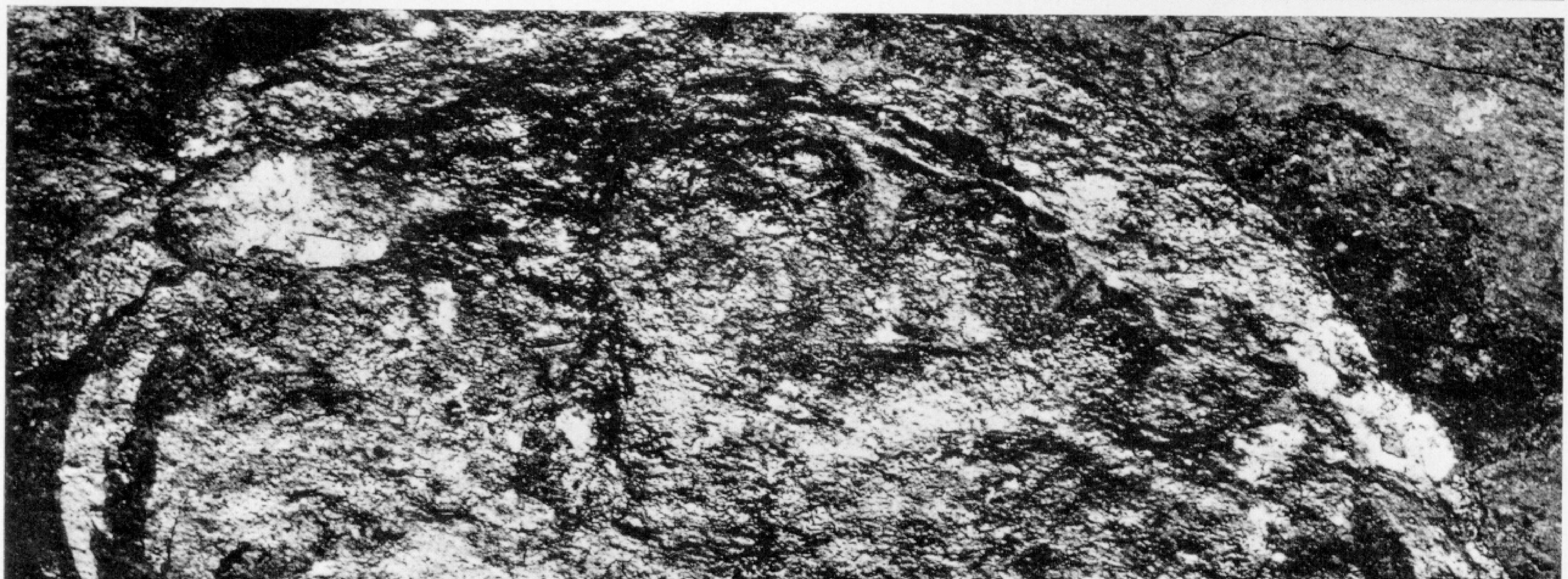
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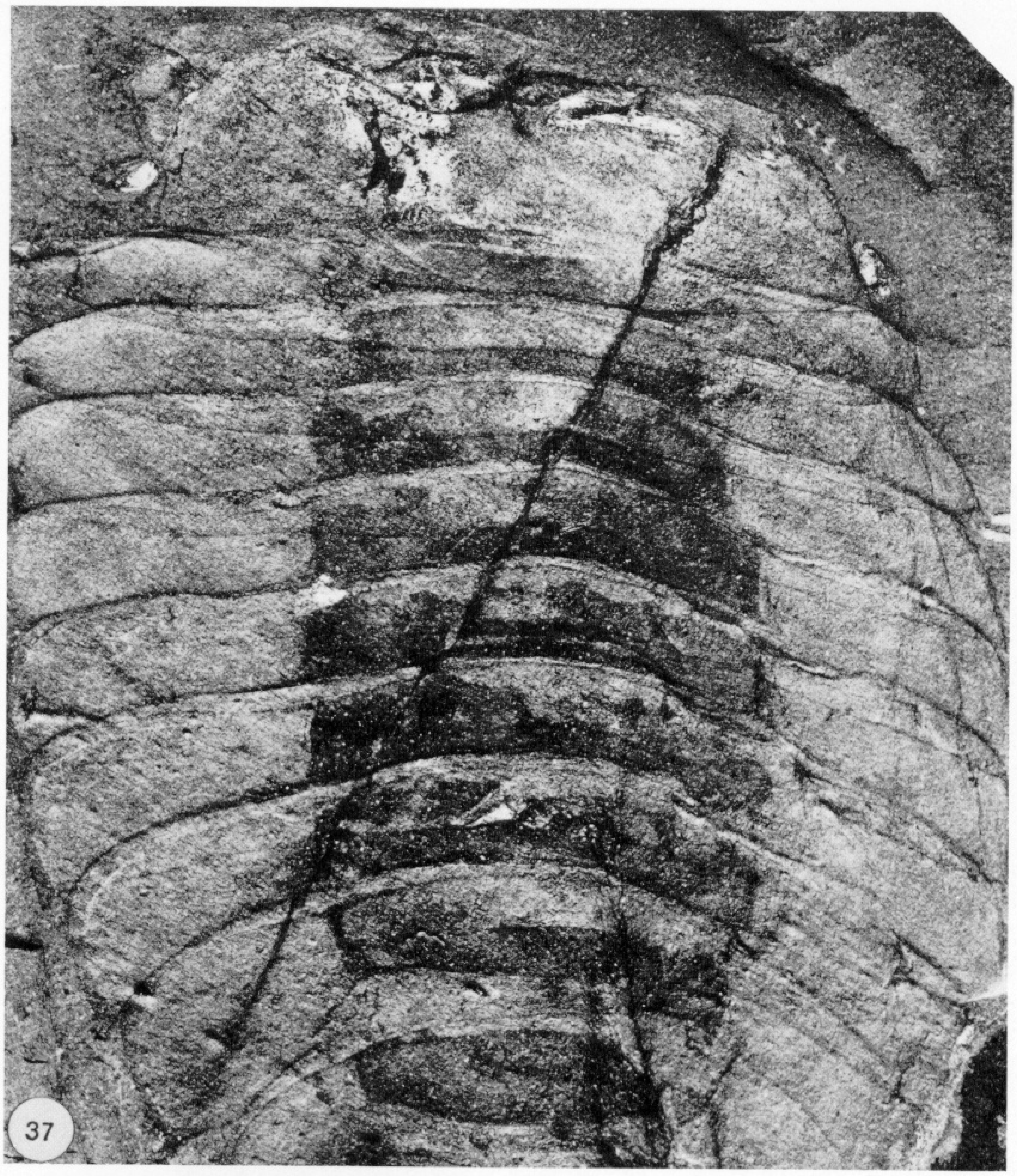
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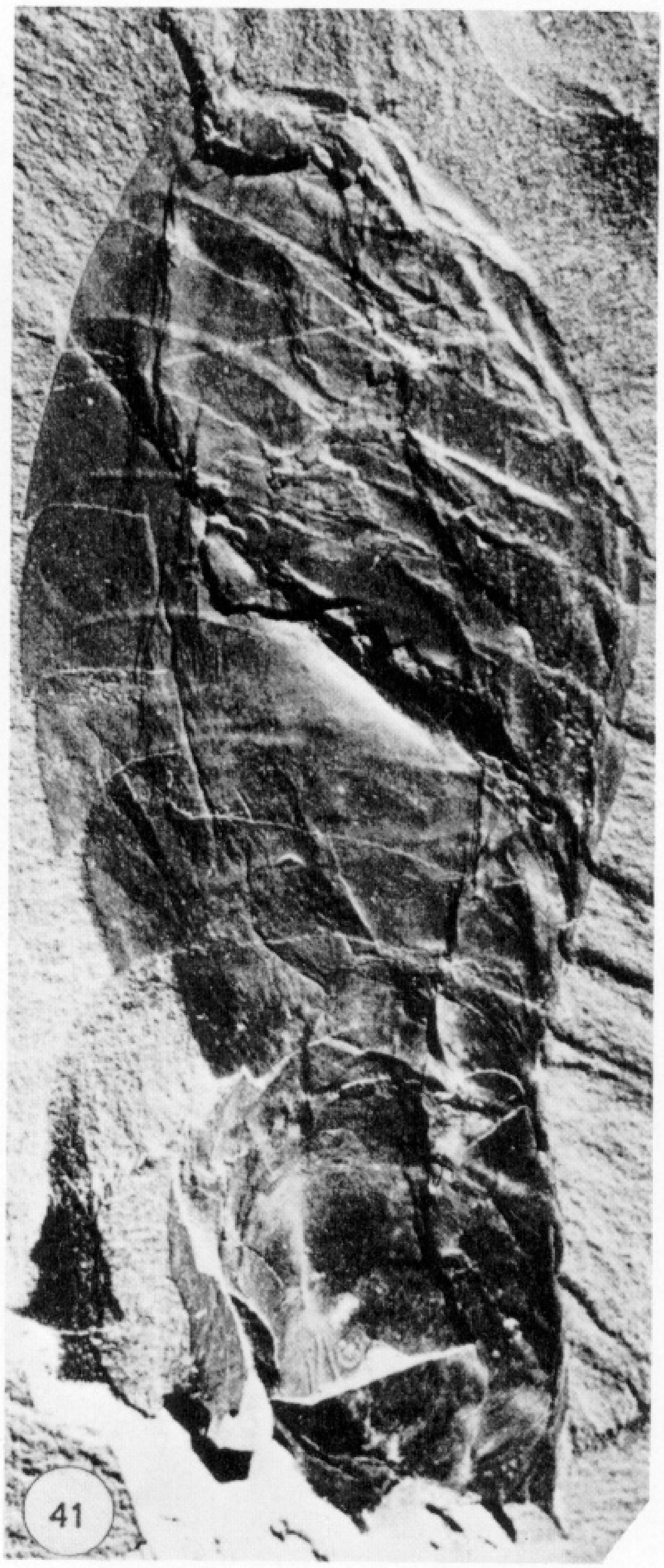
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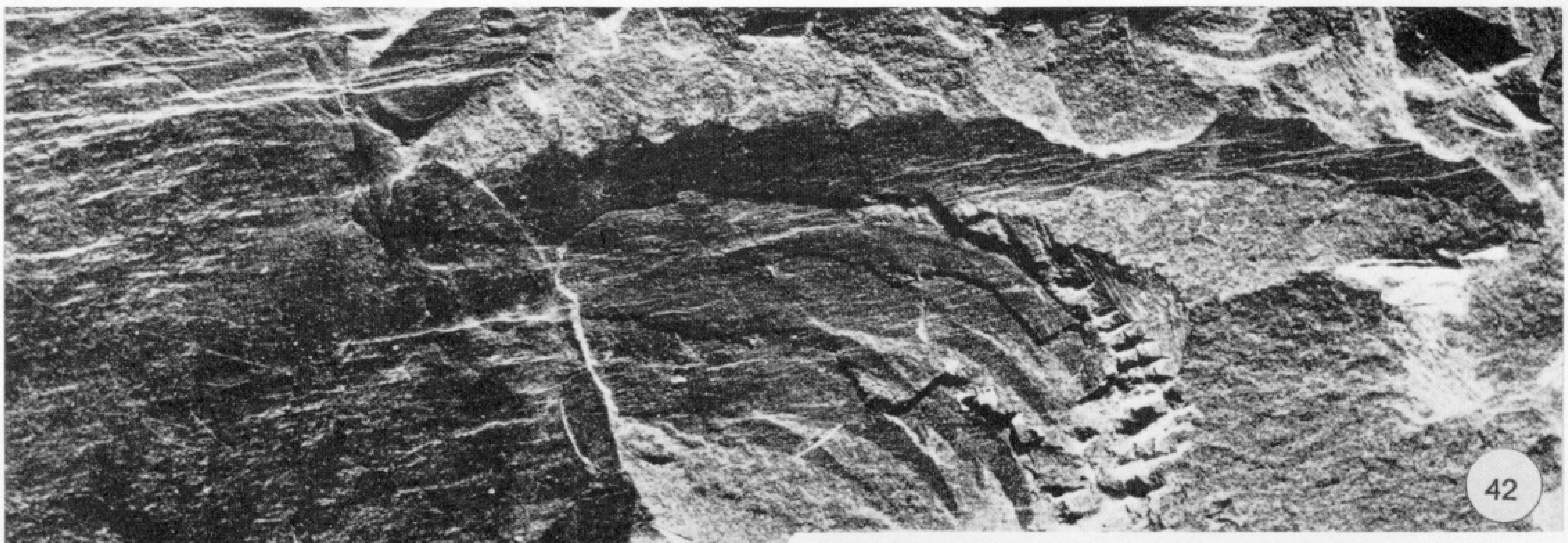

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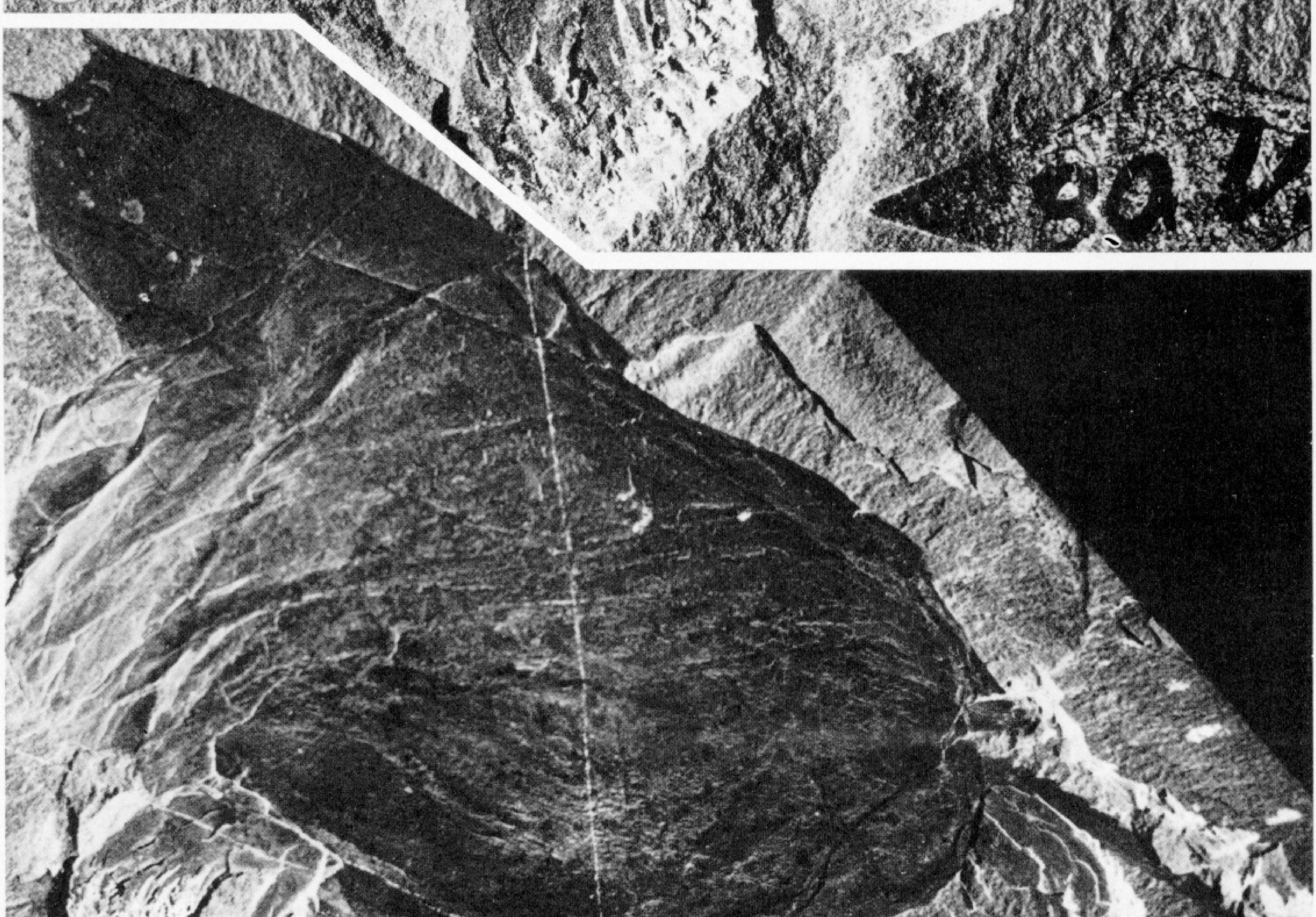

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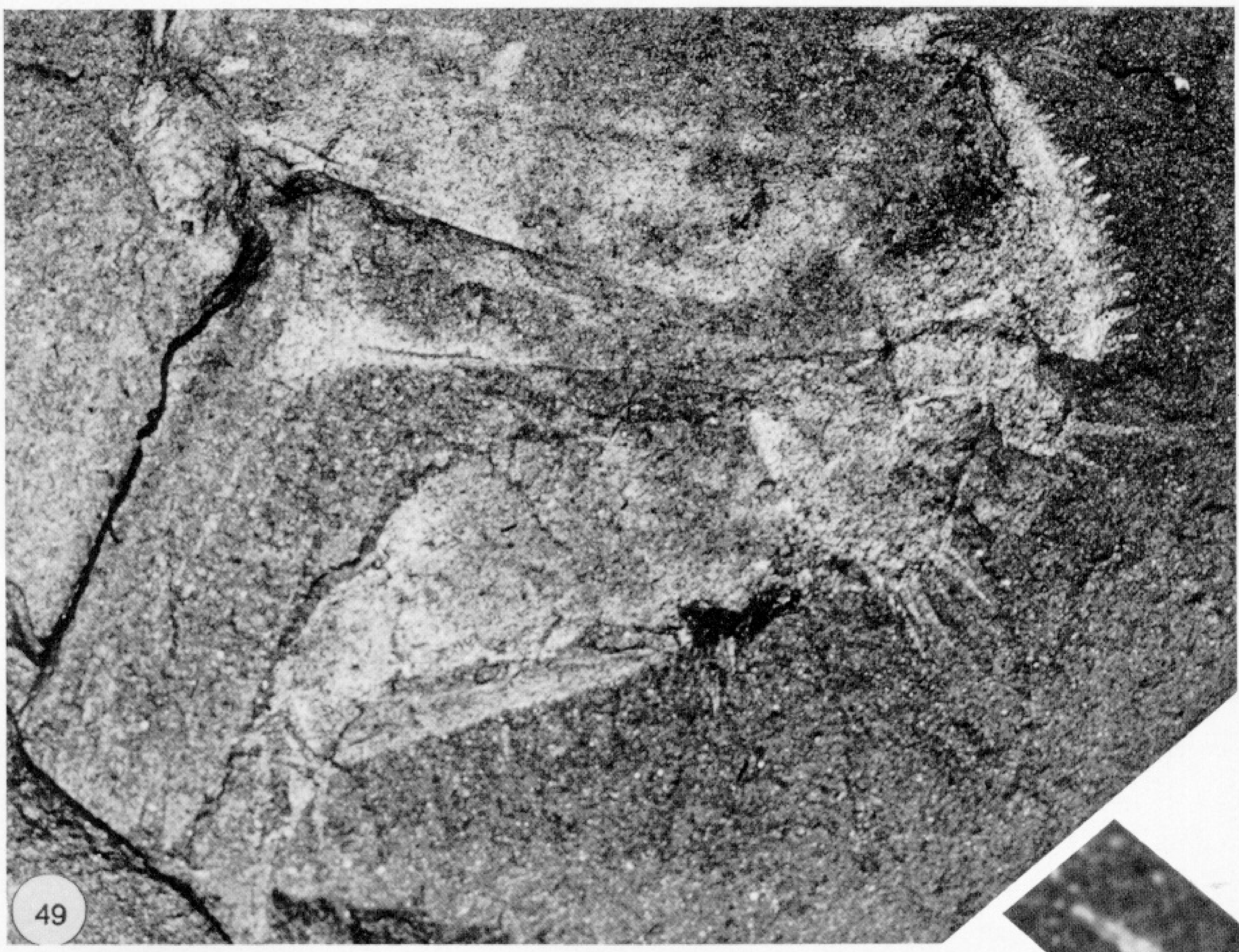
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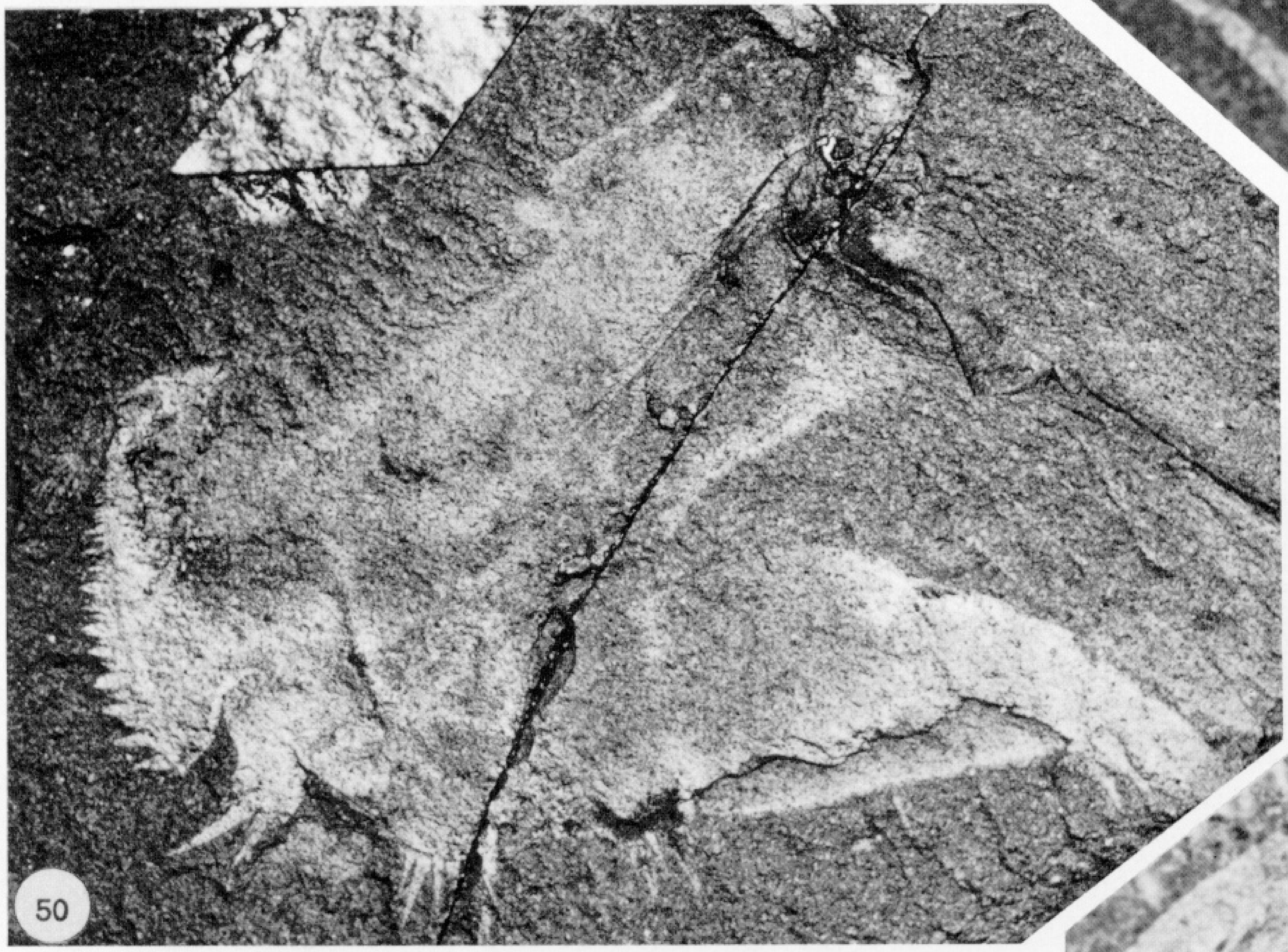
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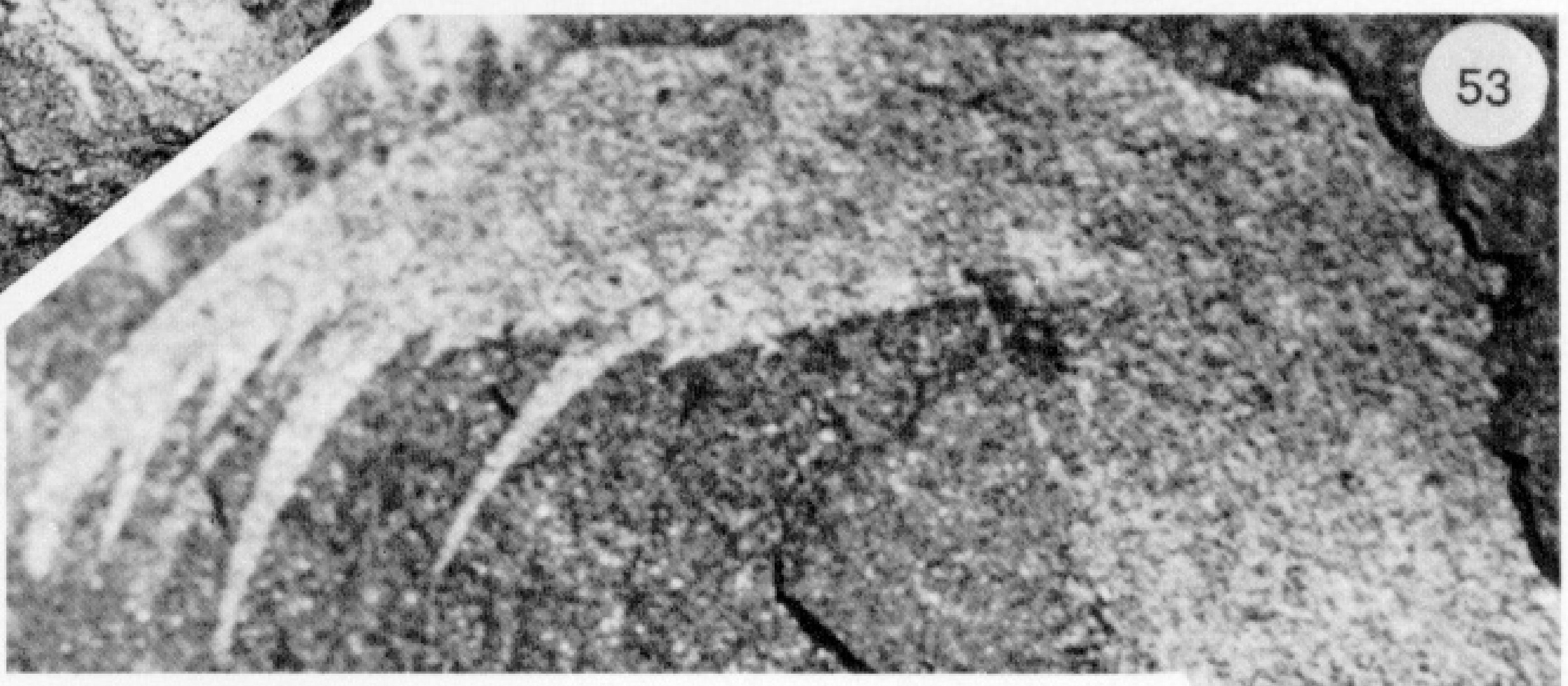
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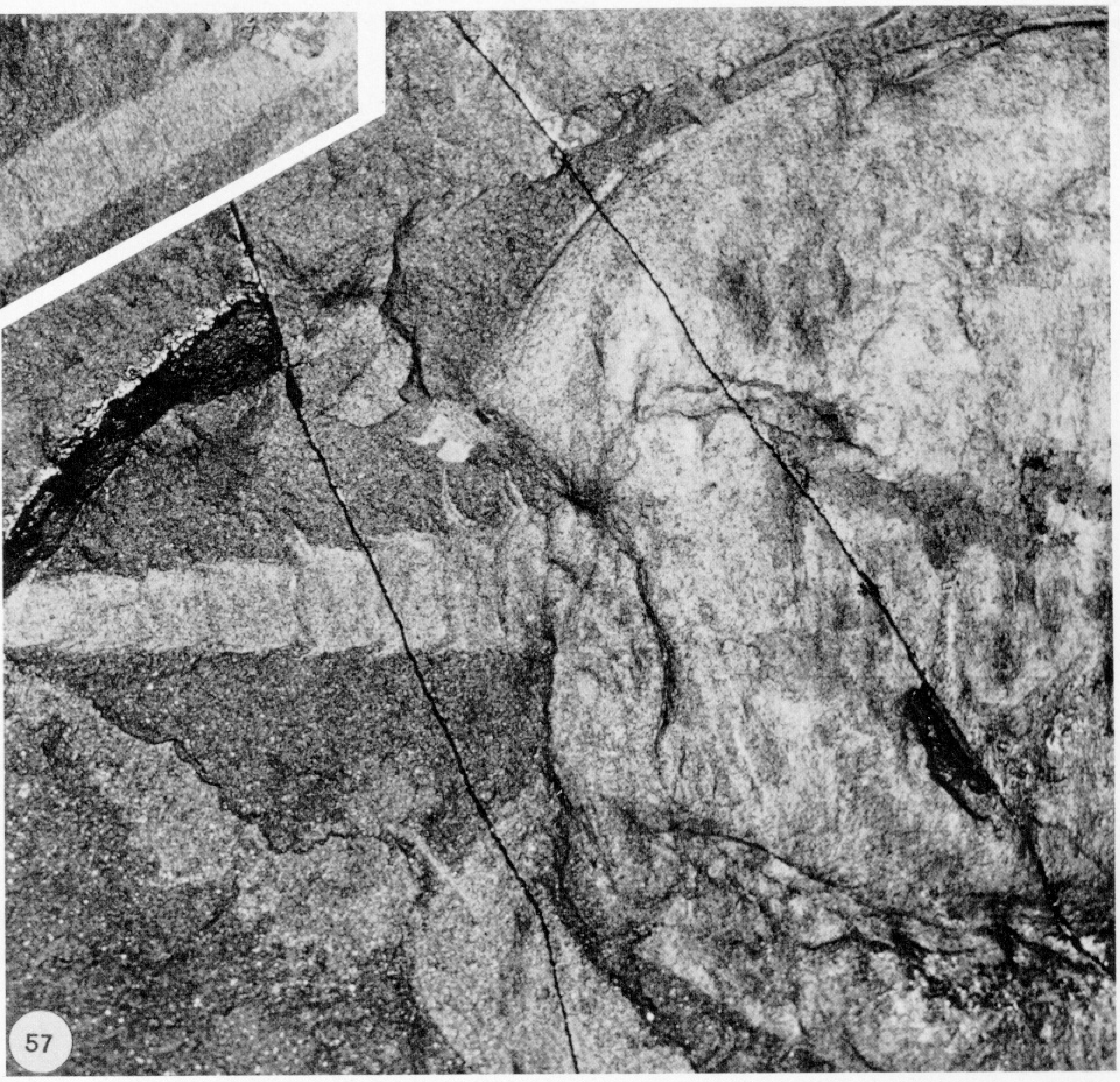
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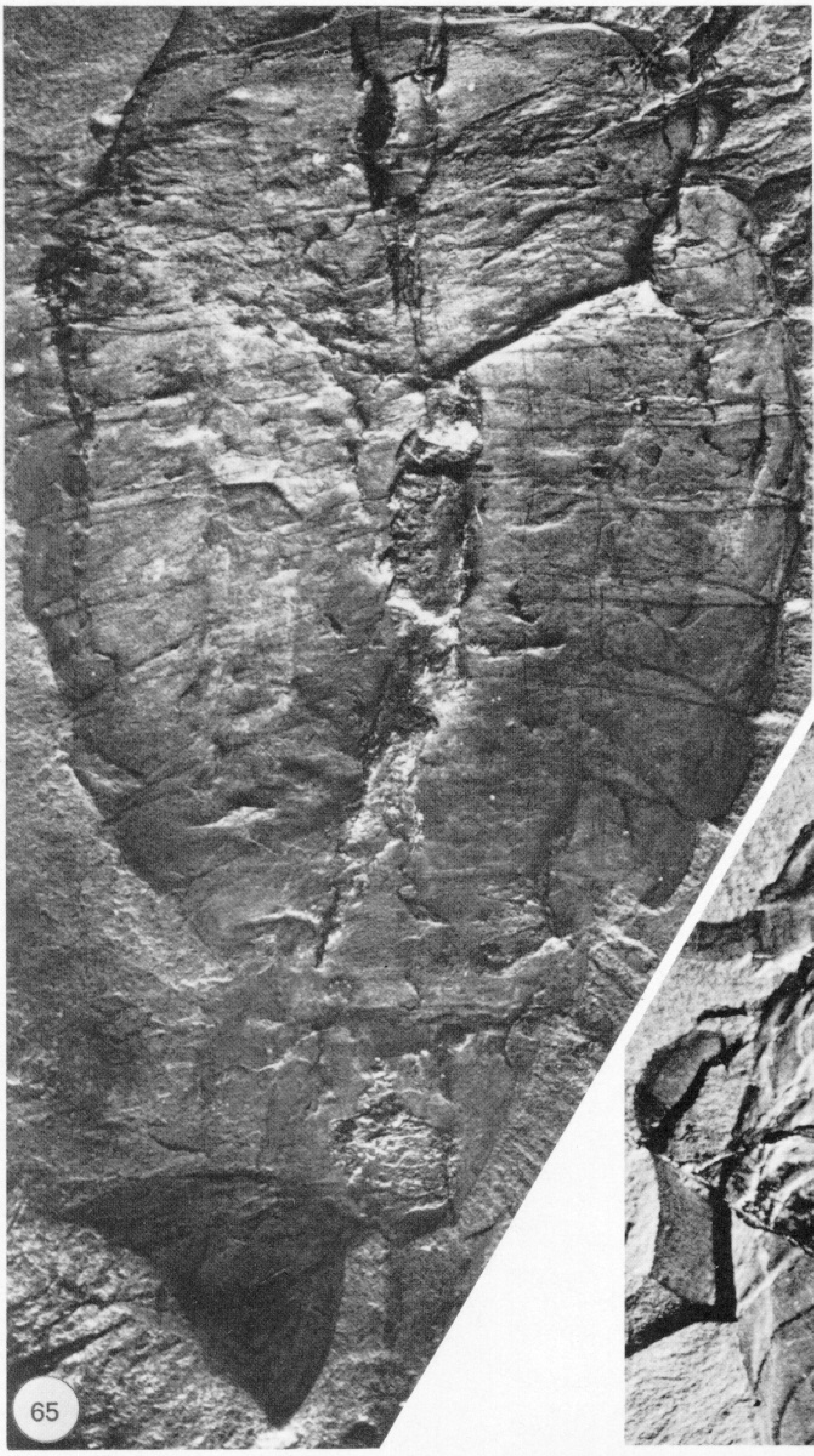
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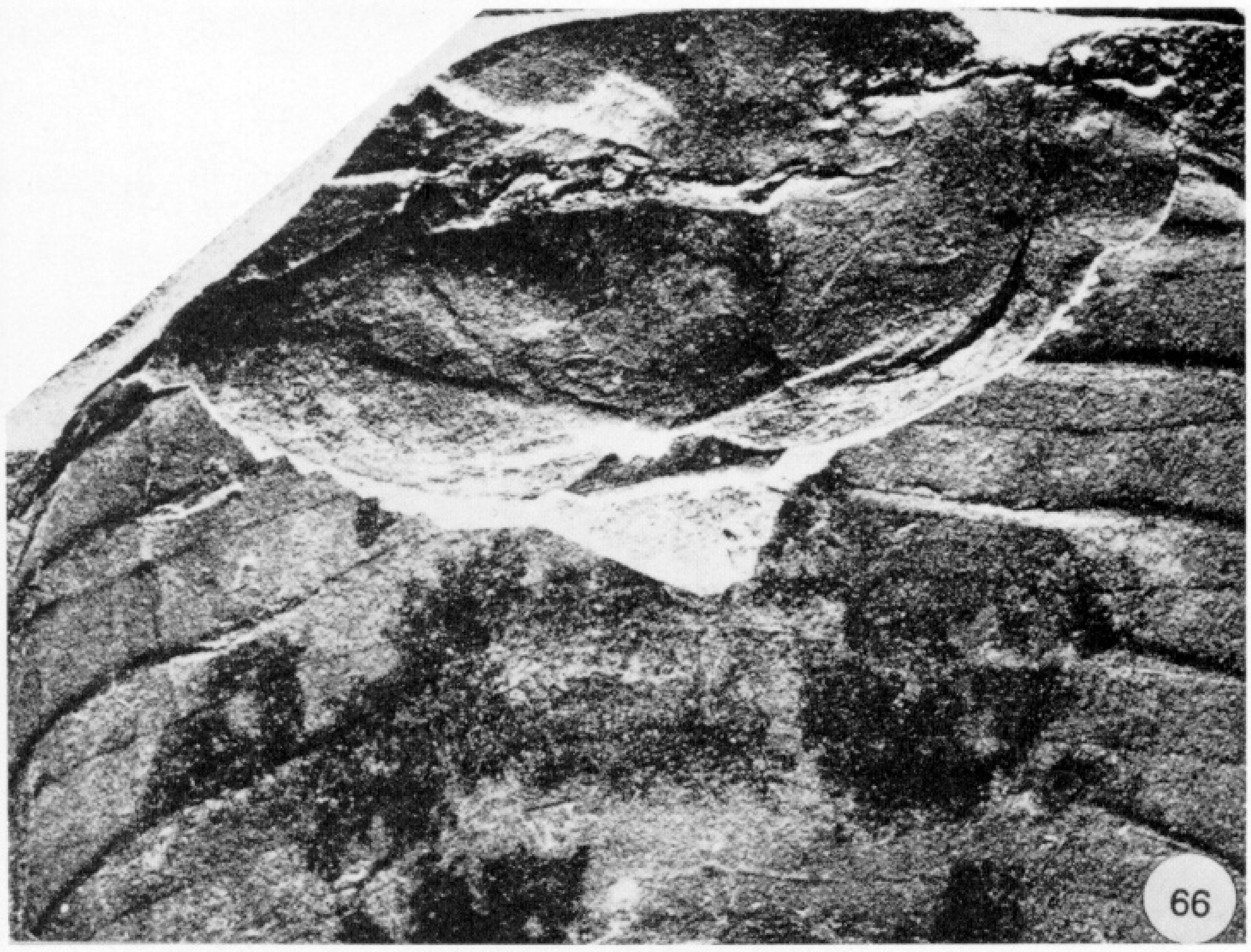
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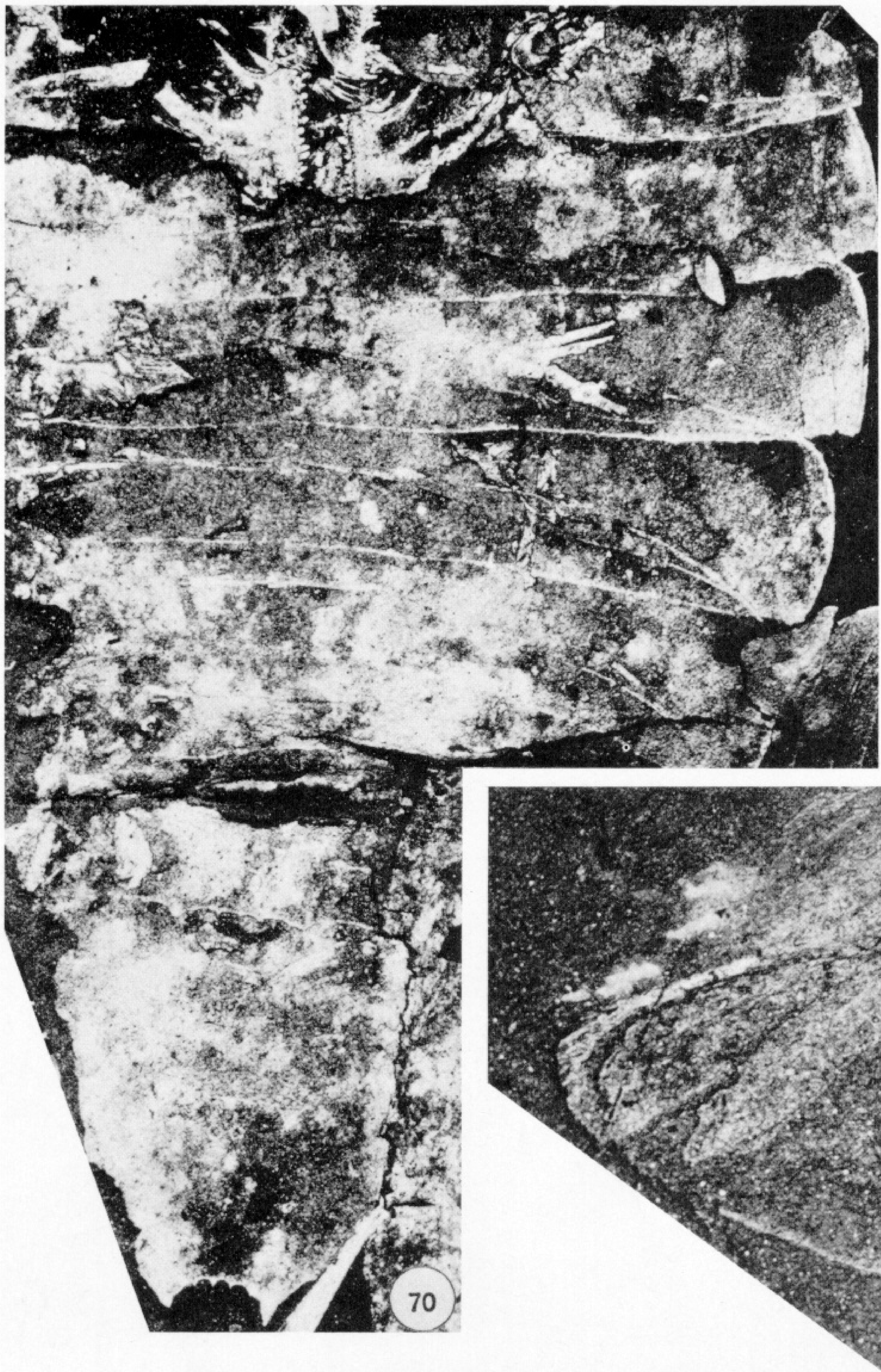
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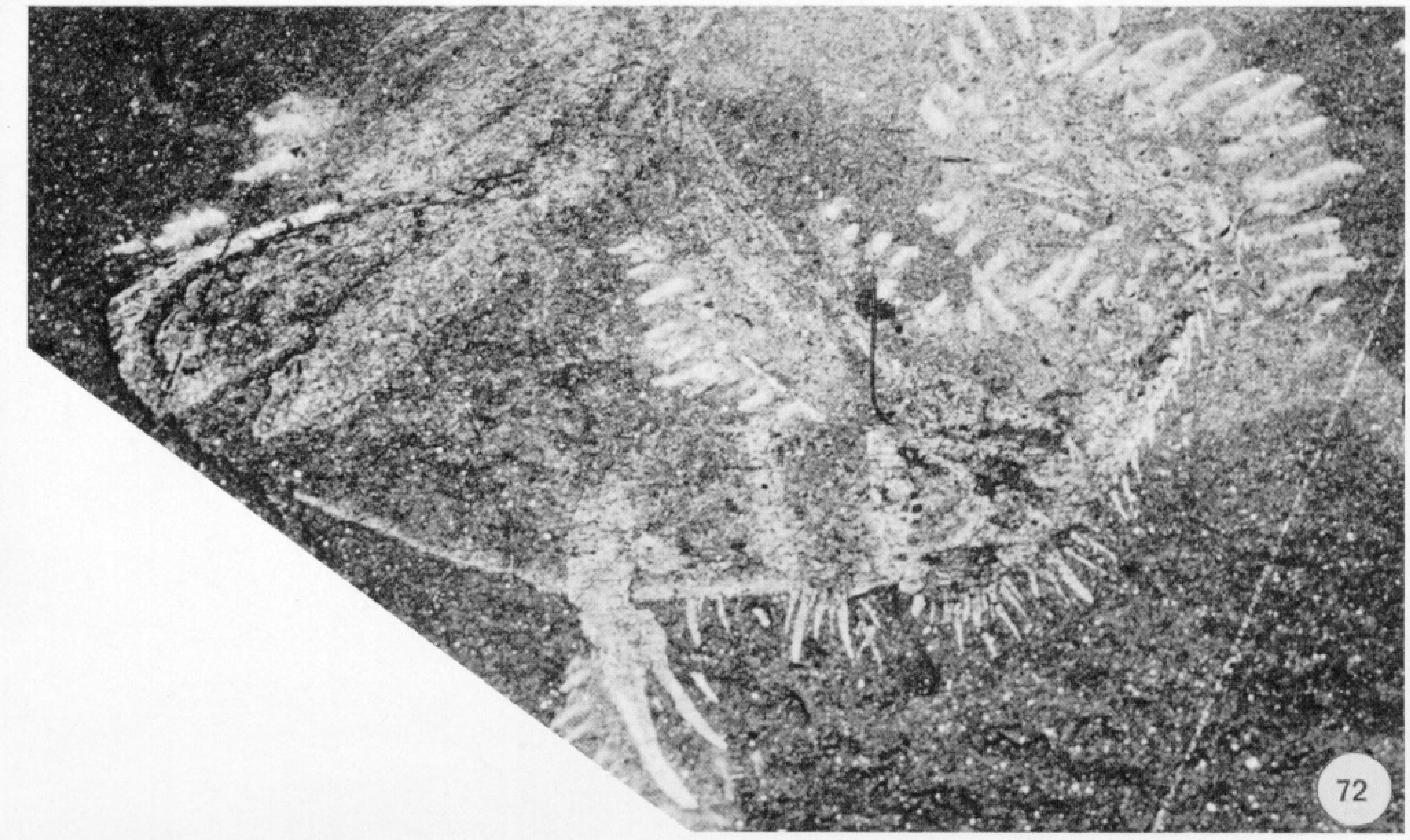
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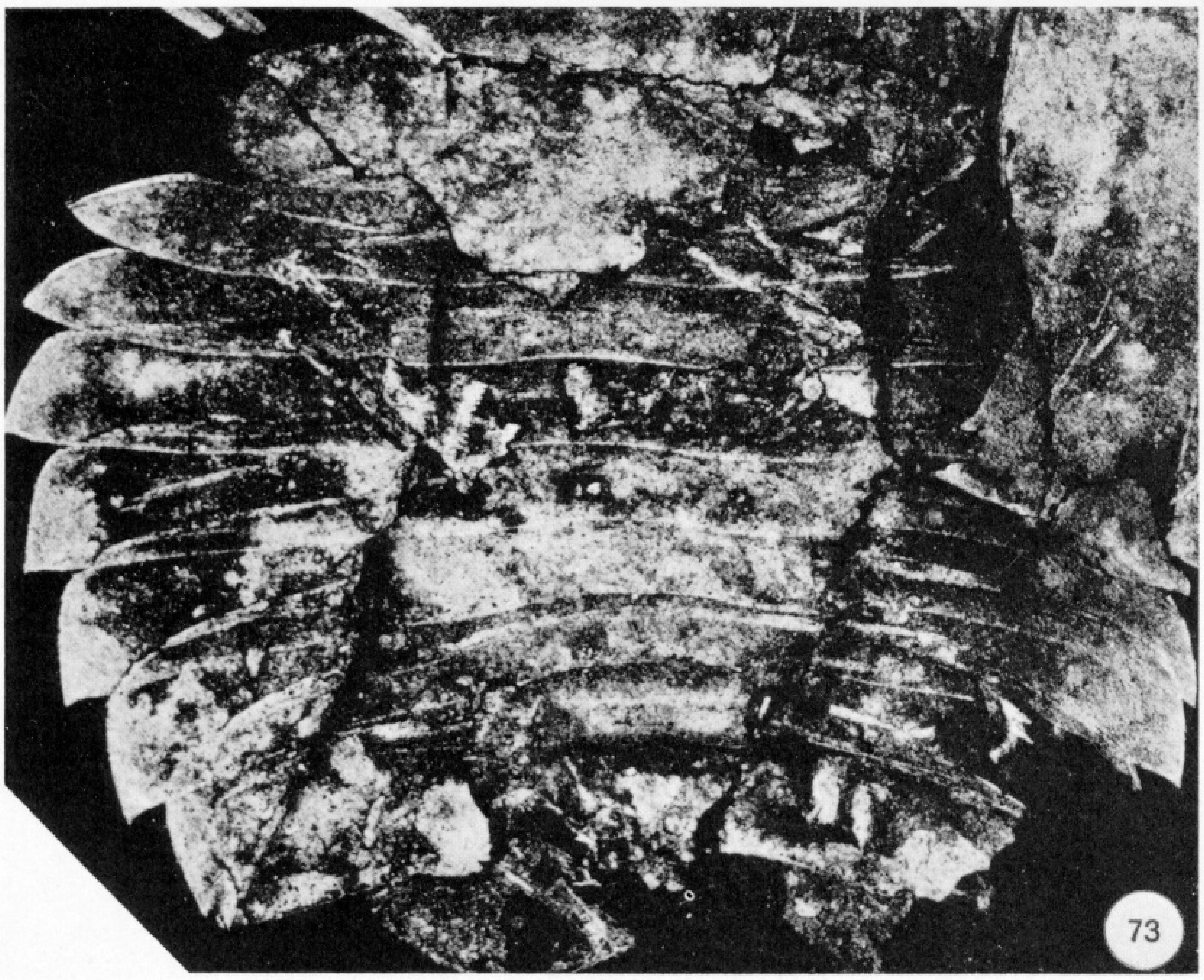
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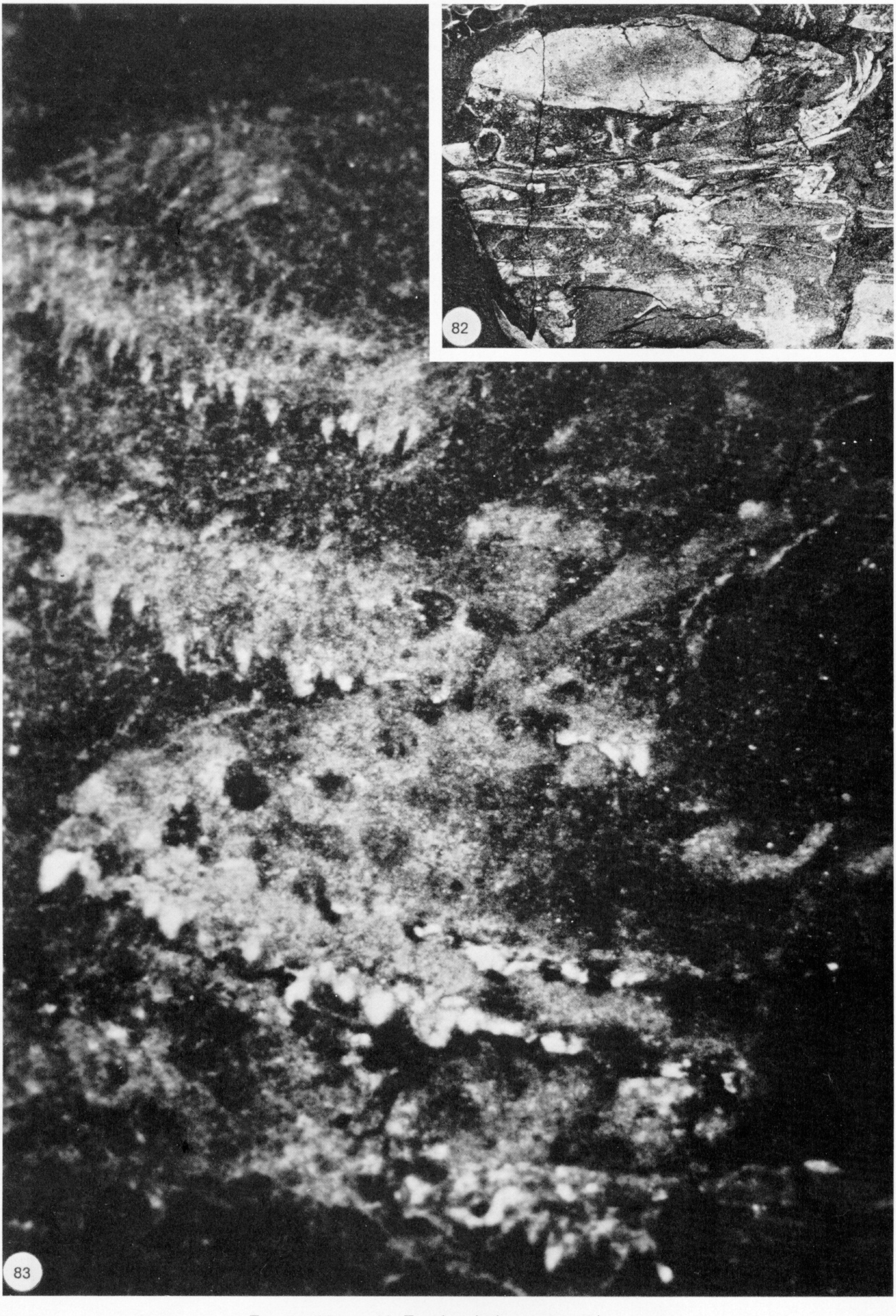
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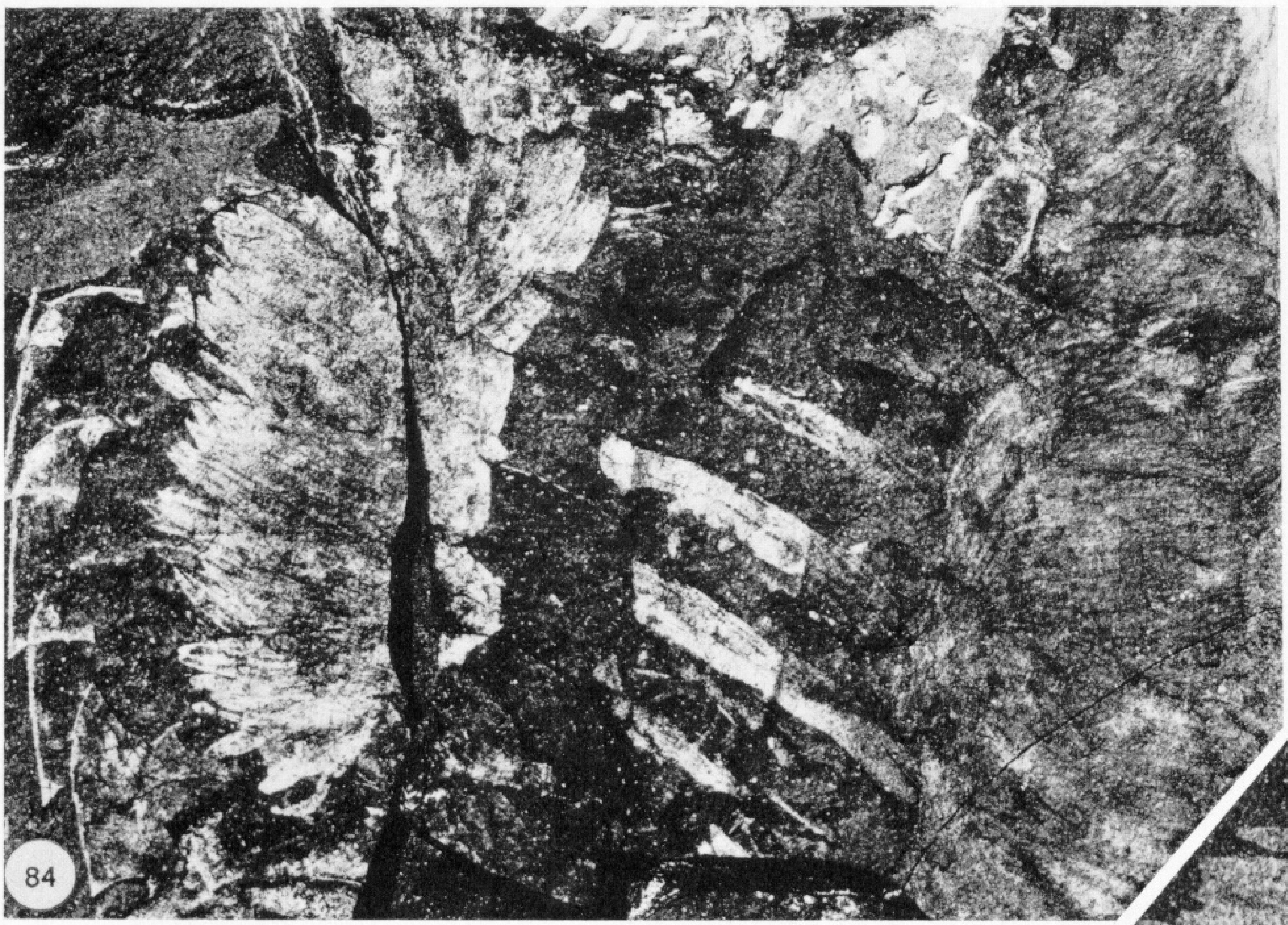
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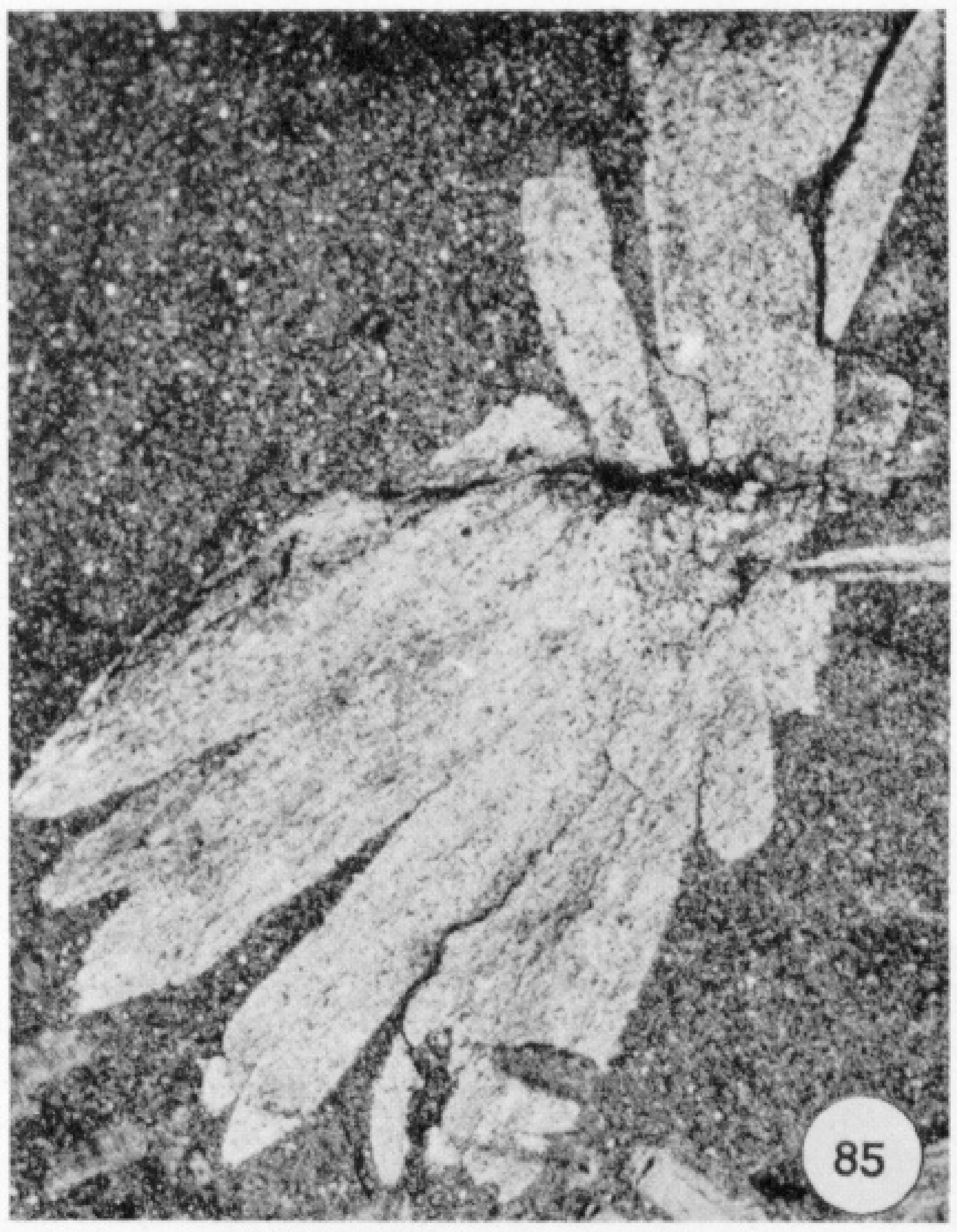
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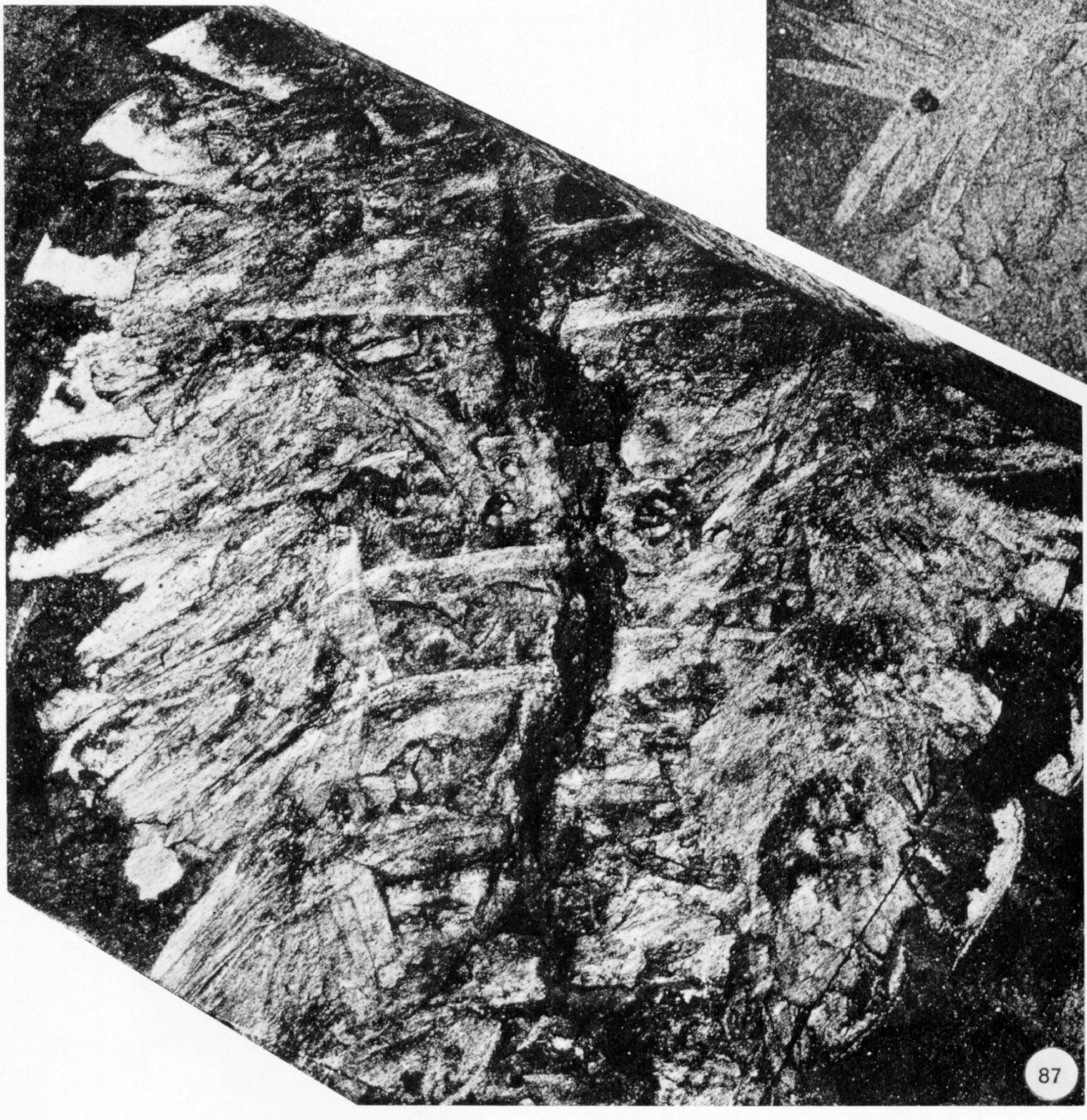
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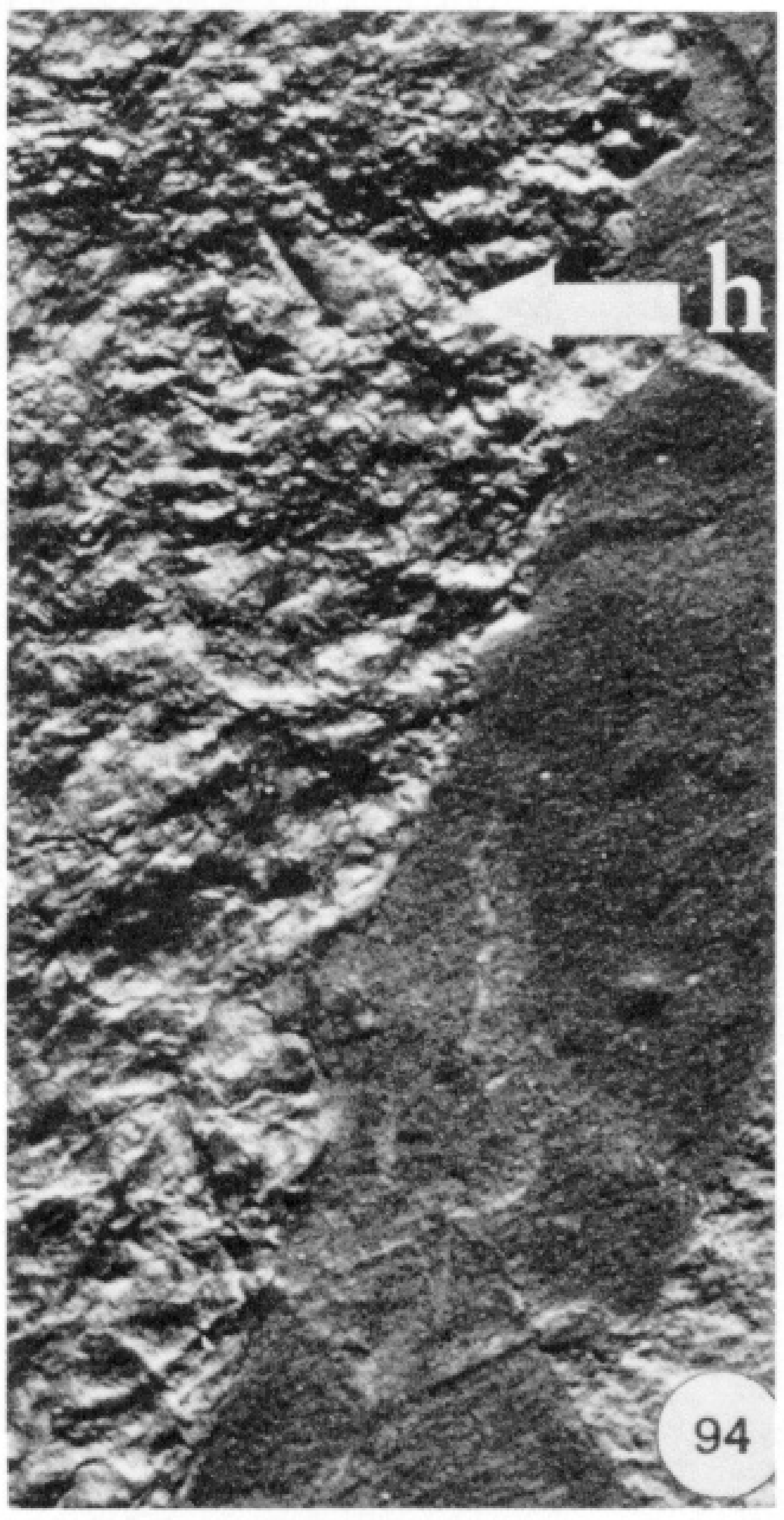

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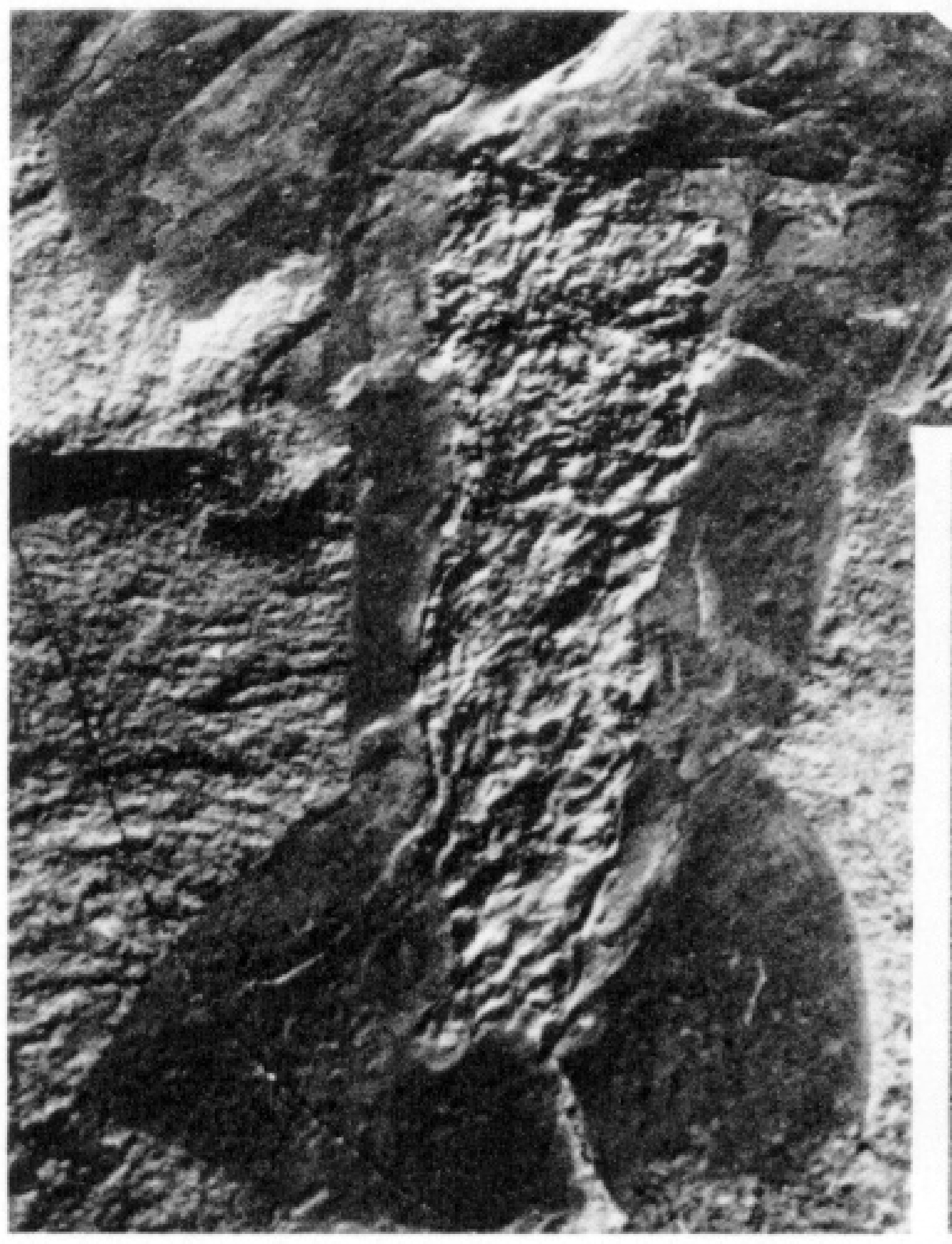
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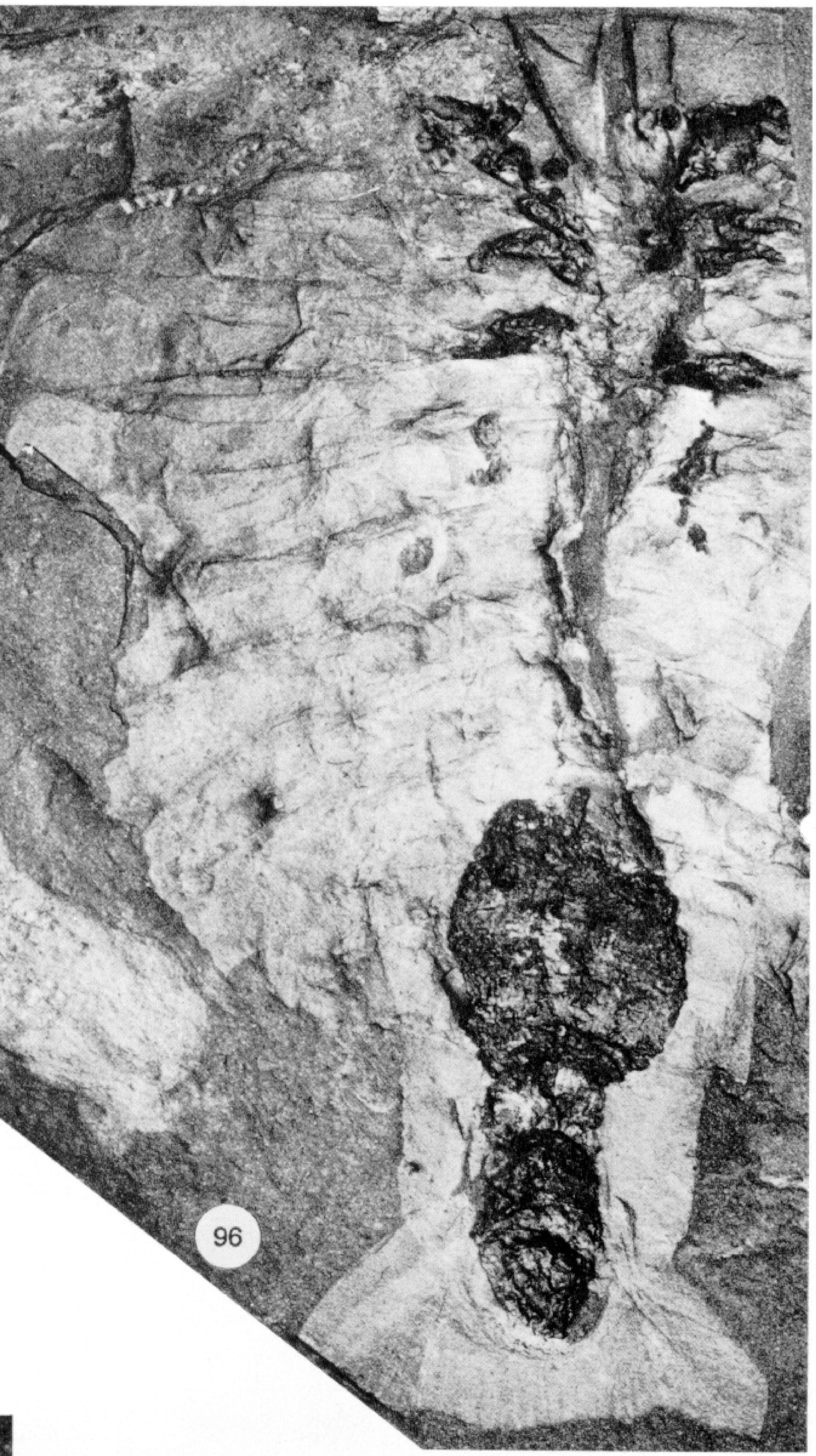
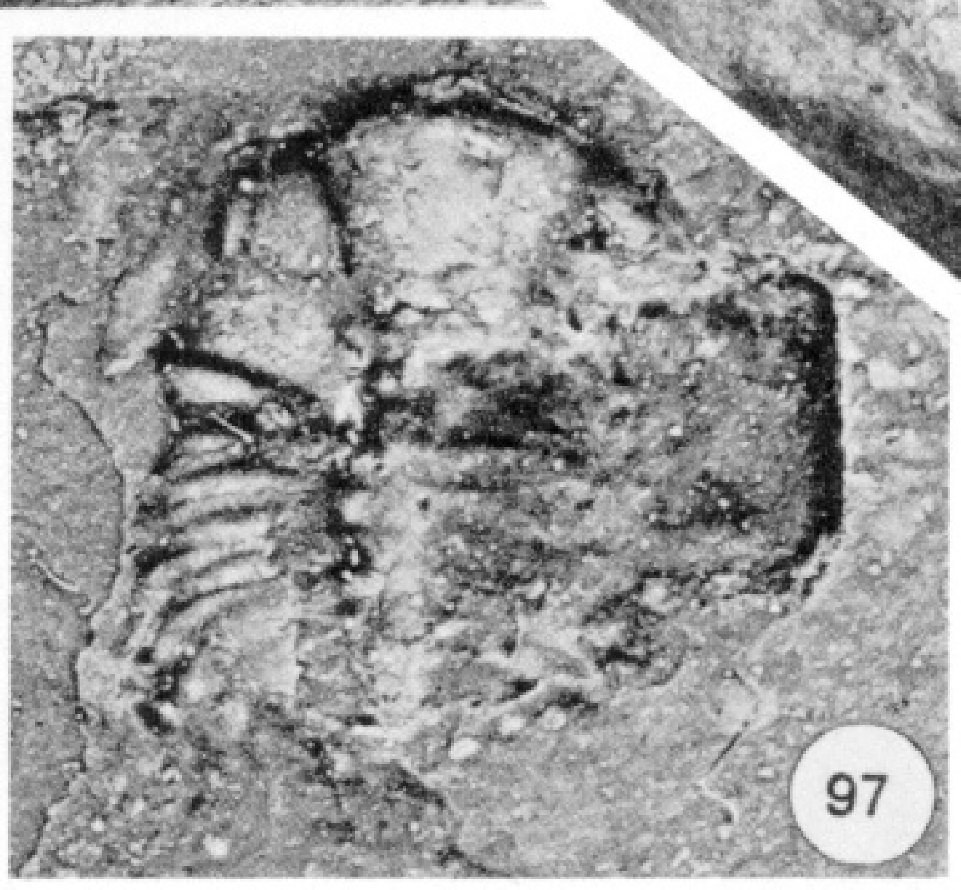
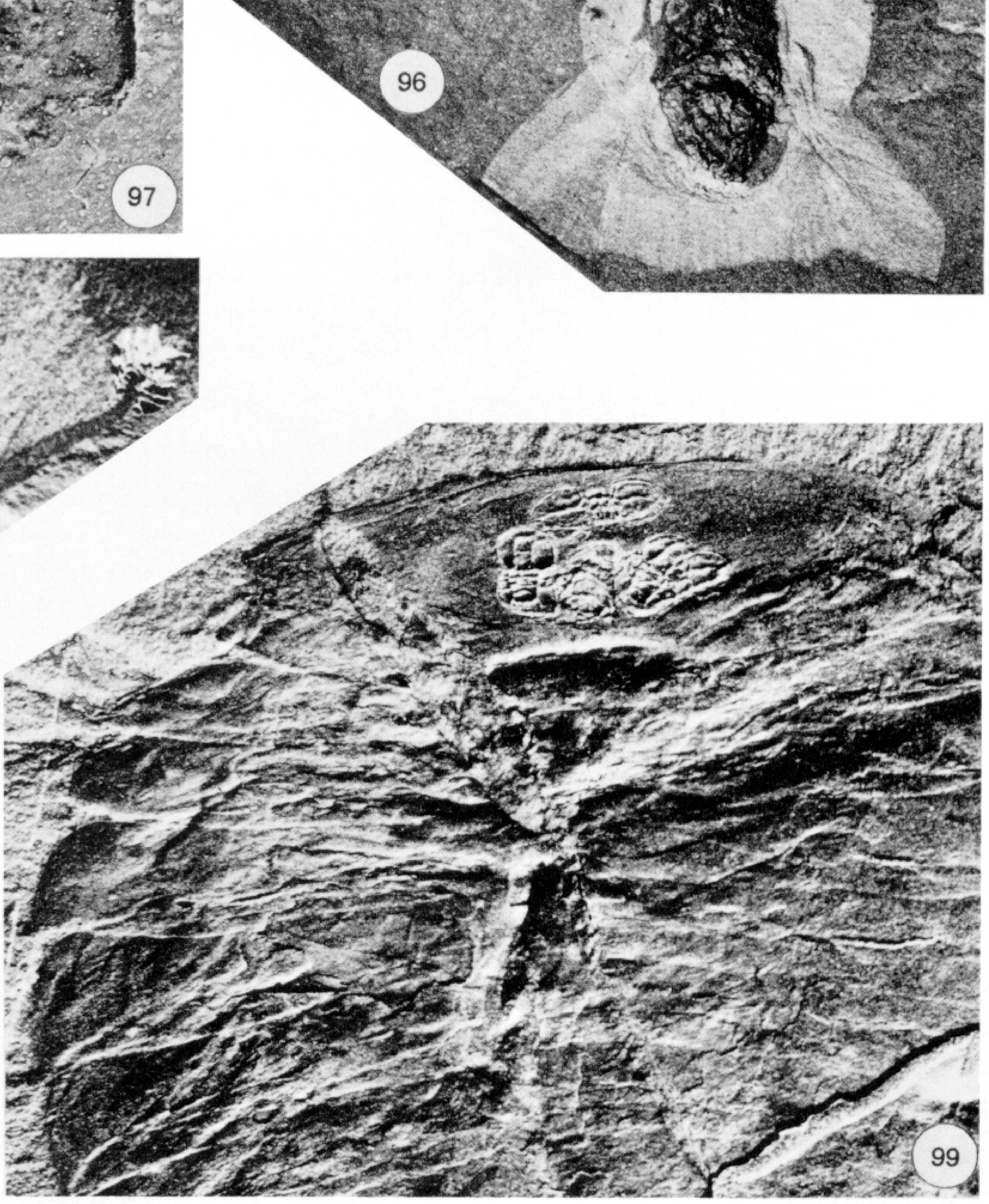

96


97


98


99

FIGURES 94–99. For description see opposite.

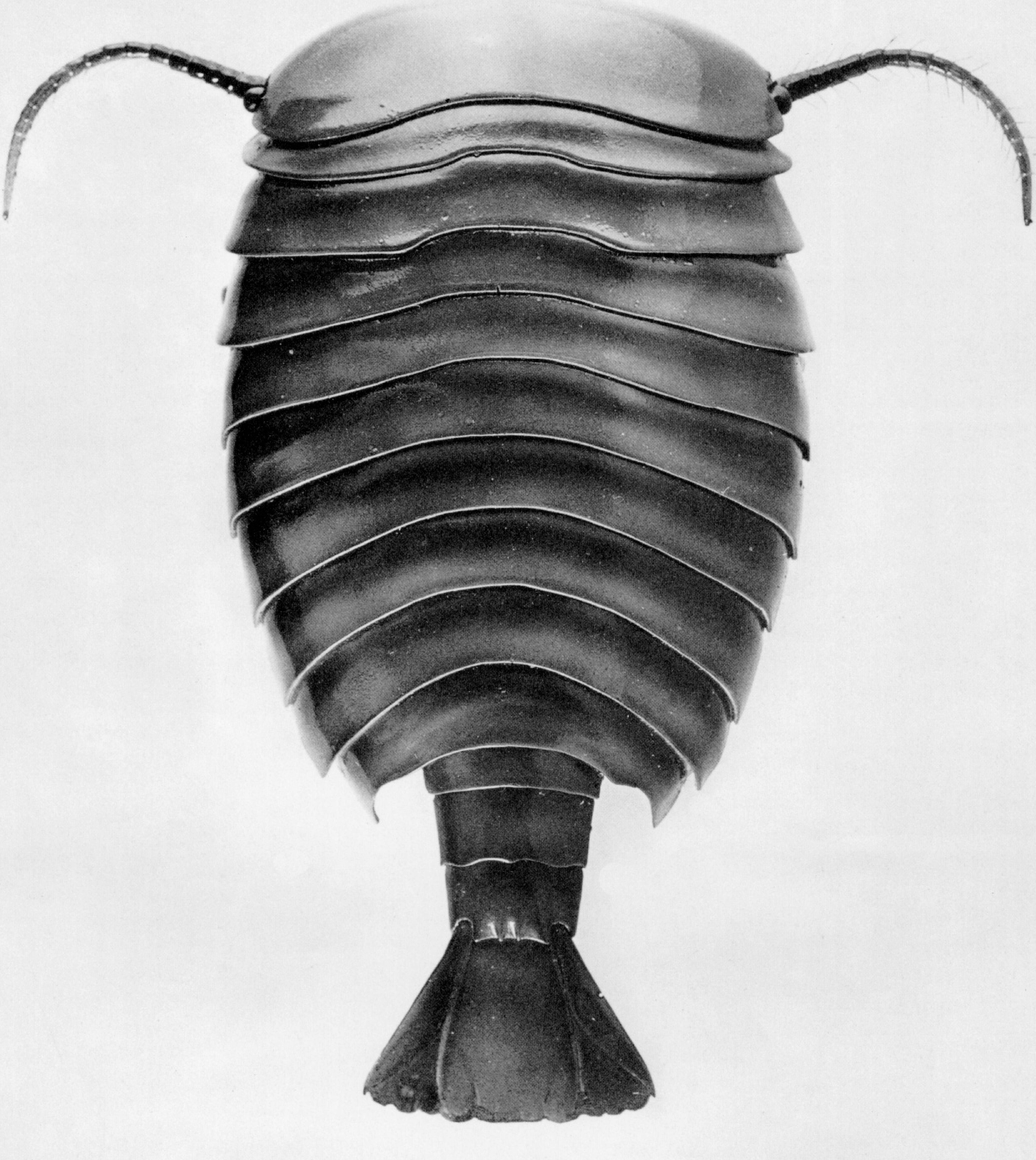
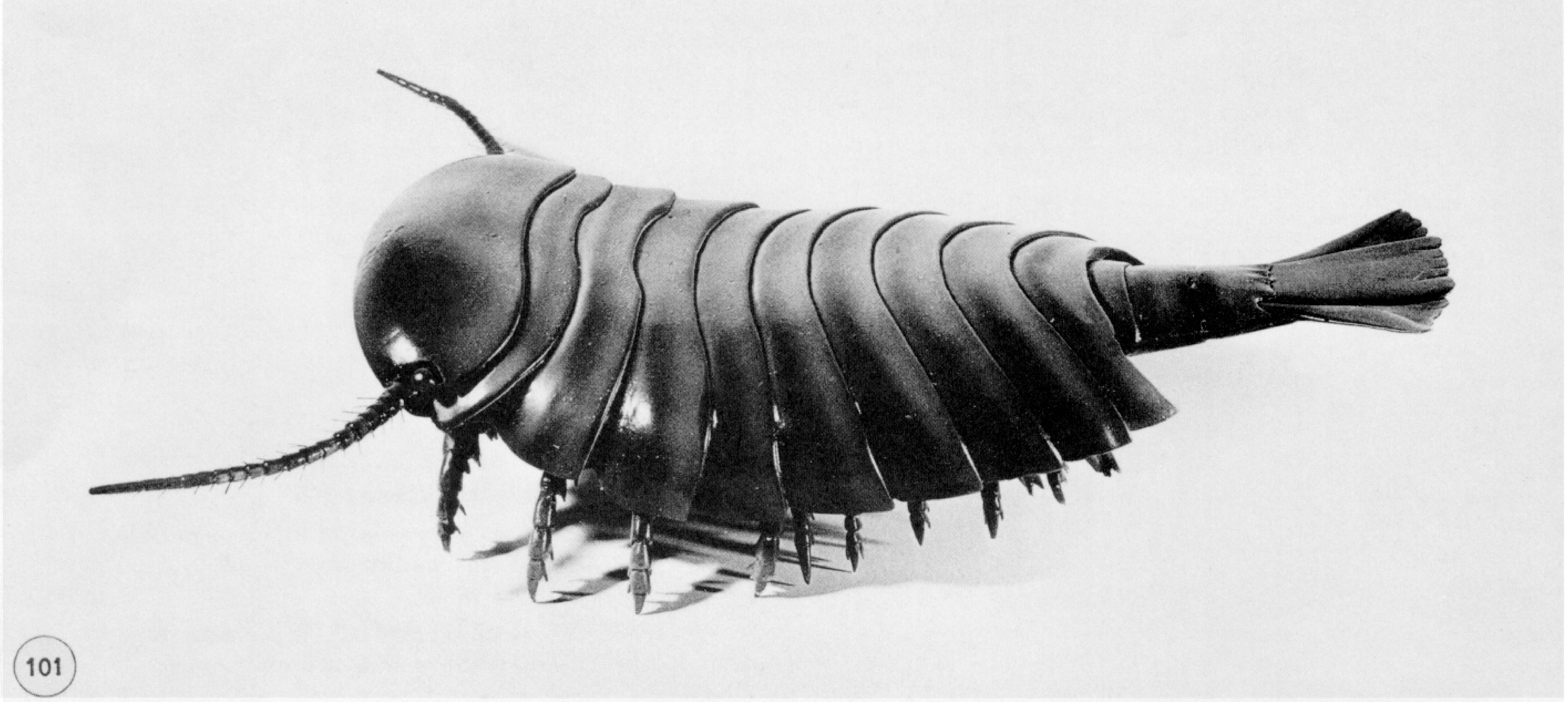
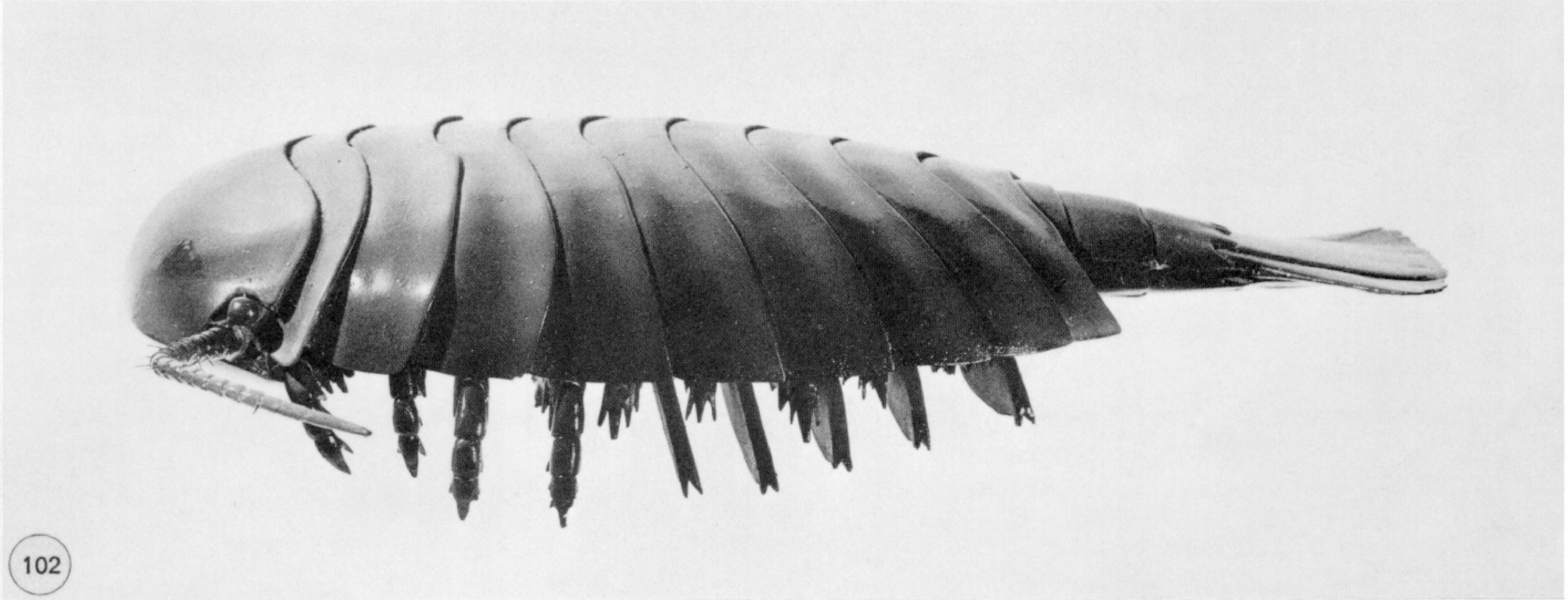
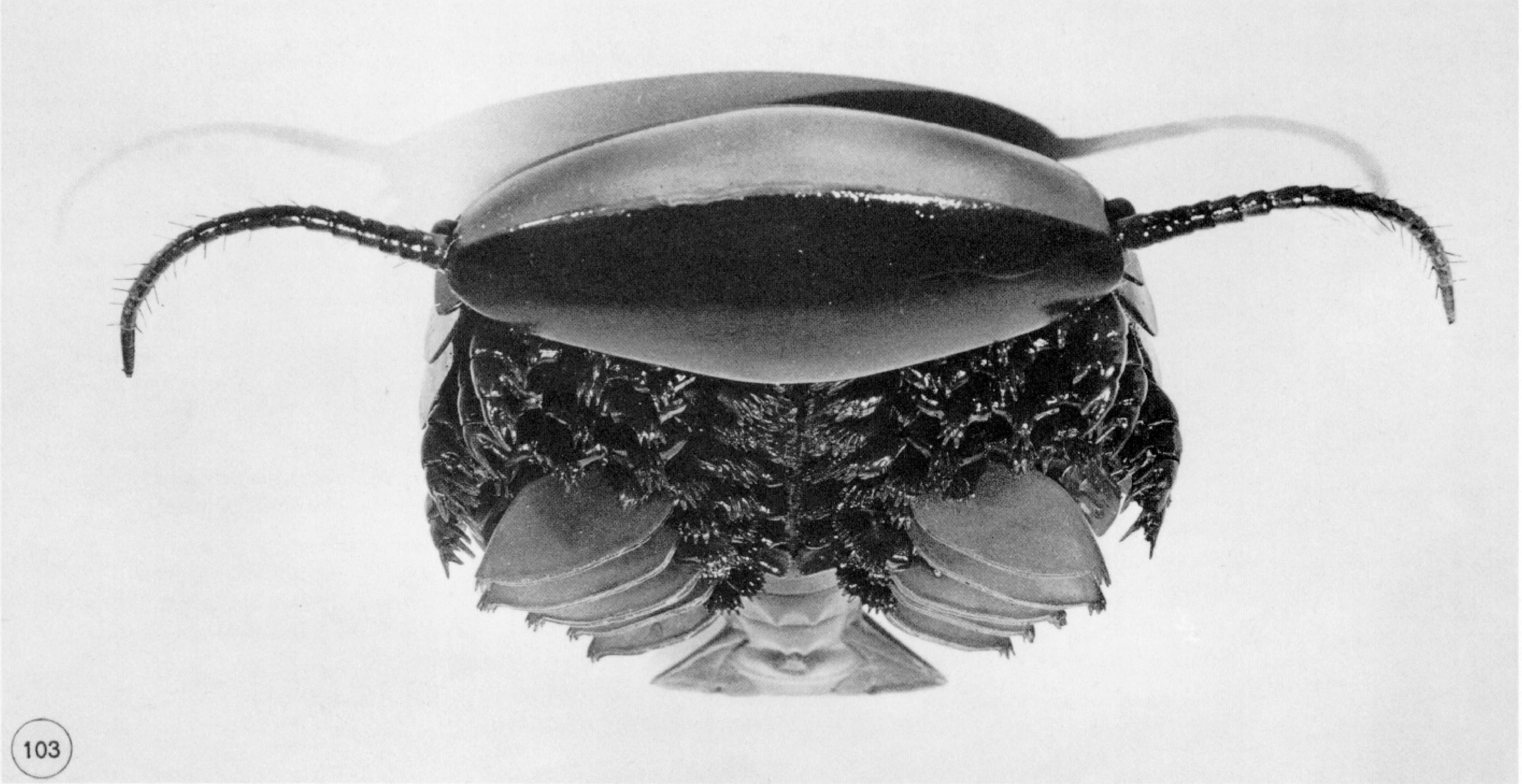


FIGURE 100. Model of *Sidneyia inexpectans*, dorsal view, approximately three times life size.


101


102


103

FIGURES 101–103. For description see opposite.