THE ARTHROPOD *ODARAIA ALATA* WALCOTT, MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

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[Plates 1–9]

CONTENTS

This, the first detailed description, interpretation and reconstruction of *Odaraia alata*, is based on all 29 known specimens. These include material of *Eurysaces pielus* Simonetta and Delle Cave, 1975, which is synonymized with *O. alata* herein. The head bore a pair of large eyes anteriorly and a paired mandible posteriorly. Features between these are poorly defined and the number of limb-bearing cephalic somites is unknown.

The carapace was bivalved and essentially tubular in configuration, enclosing most of the body anteriorly. The trunk included up to at least 45 uniform short wide limb-bearing somites. The trunk appendages were biramous (with the possible exception of the first two), with an outer lamellate branch projecting dorsad of a segmented, spinose and apparently sometimes bifurcate inner branch which shows some evidence of variation along the trunk. The telson bore three large flukes, two projecting laterally and one vertically. The evidence suggests that *O. alata* fed by employing the carapace as a filter chamber within which the appendages, which trapped small pelagic animals, were confined. The arthropod probably swam on its back, using the appendages. Although the flukes did not articulate proximally, the telson appears to have been well adapted as a stabilizing and steering organ. *O. alata* shows some similarities to the Crustacea, particularly the Branchiopoda, but the preservation of the features of the cephalon is inadequate to allow its affinities to be determined unequivocally. It is classified in the family Odaraidae Simonetta and Delle Cave, 1975, but assignment to a higher taxon within the arthropods is not considered to be justified.

1. INTRODUCTION

Odaraia alata has been, to date, one of the least known of the Burgess Shale arthropods in spite of its large size (up to 150 mm) and unusual morphology and mode of life, even by the standards of its bizarre associates. This is largely because Walcott's (1912) original description was based on a number of specimens of the valves all of which were 'more or less crushed and distorted', including the holotype (figures 2, 3, plate 1), the only specimen that he figured (1912, pl. 34, fig. 2). Additional specimens were used as a basis for the only extensive redescription published since, that by Simonetta & Delle Cave (1975), who erroneously described some as a separate new genus and species *Eurysaces pielus*, synonymized with *Odaraia alata* herein. The brief account, by Simonetta & Delle Cave, of the morphology was in error in a number of other ways and lacked the detail necessary to allow an adequate interpretation of the arthropod. The present study is based on all the previously described material together with an additional 14 specimens. Eleven of these were discovered in Walcott's collections in the National Museum of Natural History in Washington, and three were collected by the Royal Ontario Museum expedition of 1975 (Collins 1978). The Geological Survey of Canada (G.S.C.) expeditions of 1966 and 1967 (Whittington 1971*a*) found no specimens. The G.S.C. specimens mentioned were given to the Survey by the National Museum in Washington in Walcott's day. The total of 29 specimens now known emphasizes the rarity of *Odaraia alata* compared to *Marrella splendens* (estimated 12000 (Whittington 1971*b*)) and *Canadaspis perfecta* (about 5000 (Briggs 1978)), although it is more common than *Branchiocaris pretiosa* (5 (Briggs 1976)) and *Perspicaris dictynna* and *P. recondita* (about 12 each (Briggs 1977)). The present study included, for the first time, detailed preparation of specimens by means of a micro-drill, which revealed hitherto unknown features, particularly of the appendages. The results of the investigation of the morphology are illustrated by the reconstructions (figure 103). The combination of an essentially tubular carapace and a telson bearing three large flukes is unique among the arthropods. Poor preservation of the cephalic region leaves the affinities of *Odaraia* in doubt, although it shows greatest similarity to the branchiopod Crustacea. The erection of a separate family Odaraidae by Simonetta & Delle Cave (1975) is vindicated but its relation to higher taxa remains to be determined.

The institutions where specimens are held are represented as the following prefixes to specimen numbers: G.S.C., Geological Survey of Canada, Ottawa; R.O.M., Royal Ontario Museum, Toronto; U.S.N.M., National Museum of Natural History, Washington, D.C.

2. TERMINOLOGY AND METHODS

The morphological terms used in the description are those of Moore & McCormick (in Moore 1969) as far as possible. The telson is not considered to be a true somite; the three processes borne by it are referred to as flukes. 'Sagittal' refers to the direction parallel to the long axis of the body, 'transverse' to the direction normal to this.

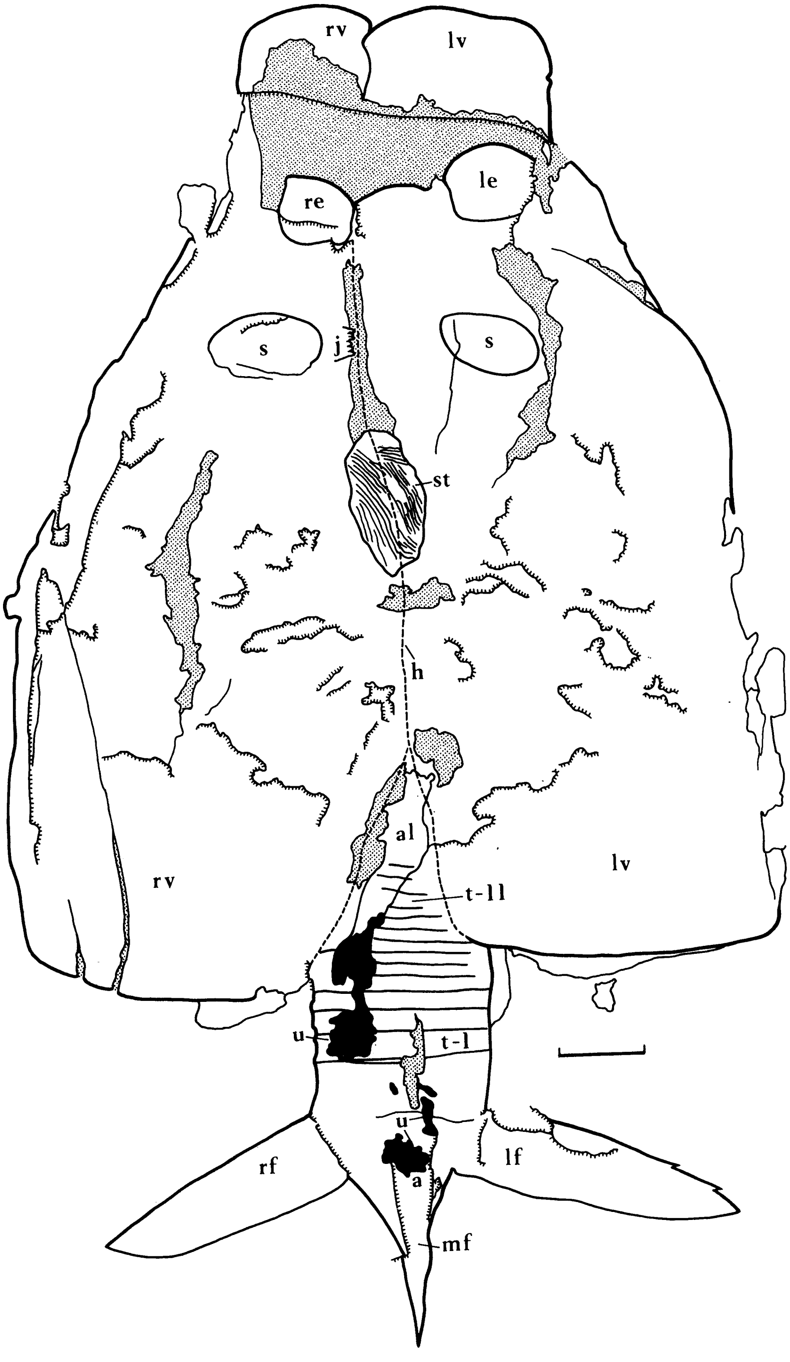
The evidence upon which the reconstructions are based is illustrated, as far as possible, by the plates. Differences in level on the fossils are expressed by a minute 'scarp' on the specimen that either casts a shadow, or reflects light, depending on the angle of illumination. The orientation of the specimen relative to the bedding is given as *parallel*, *lateral*, *oblique*, etc. (see § 3). The orientation of some specimens to the bedding was elucidated by means of a model (as explained in § 5*f*). The photographs, except where otherwise indicated in the plate descriptions, were taken on fine-grained 35 mm panchromatic film in ultraviolet radiation. This radiation was directed at approximately 30° to the horizontal, except where reflexion was desirable, when the angle was increased to about 65°. Some specimens were photographed under a film of water covered by a thin glass slip in ultraviolet light directed at a high angle (on 35 mm film), others immersed in alcohol under high-angle ordinary light (on fine-grained half-plate orthochromatic film). Some photographs of stages in the preparation of U.S.N.M. 189232 to reveal successive appendages were taken with a Wild MPS20 camera mounted on an M7S microscope (figures 69–72, plate 7; figures 73–75, plate 8). The use of these different photographic techniques is indicated in the descriptions of the plates.

The material was prepared by means of a needle inserted in a percussion hammer with an adjustable throw driven by a dental drill motor. An interpretation of the specimens is presented, where necessary, as a camera lucida drawing facing the plate. Different aspects of the morphology are revealed by varying the direction and angle of illumination, so that all the features on the drawings may not be evident on the photographs. A list of symbols used on the figures may be found at the end of the paper.

3. PRESERVATION

The effects of variation in orientation to the bedding before compaction on the appearance of bivalved arthropods has been discussed in relation to *Canadaspis perfecta* (Briggs 1978) and *Perspicaris* (Briggs 1977). The preservation of *Odaraia* appears to have been essentially similar and the same terminology is employed here. Where both part and counterpart of a specimen are known, the slab upon which most of the specimen remains is designated the part. The recognition of the orientation of specimens of *Odaraia* is more difficult than in other Burgess Shale arthropods, as the carapace was essentially tubular, the valves almost meeting ventrally, and the telson bore three nearly identical flat processes, or flukes, which projected from the telson at high angles to one another (figure 103).

Specimens orientated in exactly *parallel* aspect, the sagittal plane normal to the bedding, are compacted so that the hinge separating the valves coincides with the midline of the flattened arthropod. In this attitude the valves are approximately symmetrical about the hinge line, but in contrast to *Canadaspis* (Briggs 1978, pl. 7, figs 83, 84) no specimens are known with the valves preserved in outline showing the ventral margin; the valves are always folded beneath themselves. The telson is compacted with the two lateral flukes symmetrically arranged about the median one, the latter extending furthest posteriorly (figure 5, plate 1). The eyes, when



Description of plate 1 and figure 1

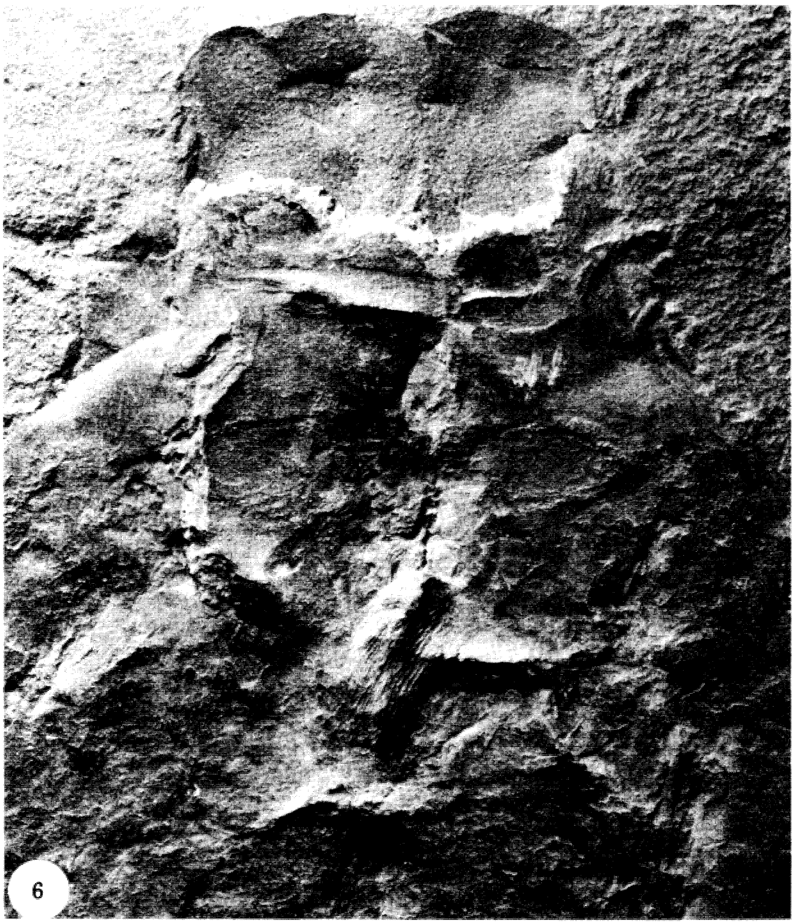
Odaraia alata Walcott, 1912

Figure 1. U.S.N.M. 213809, explanatory drawing. Scale bar 5 mm.

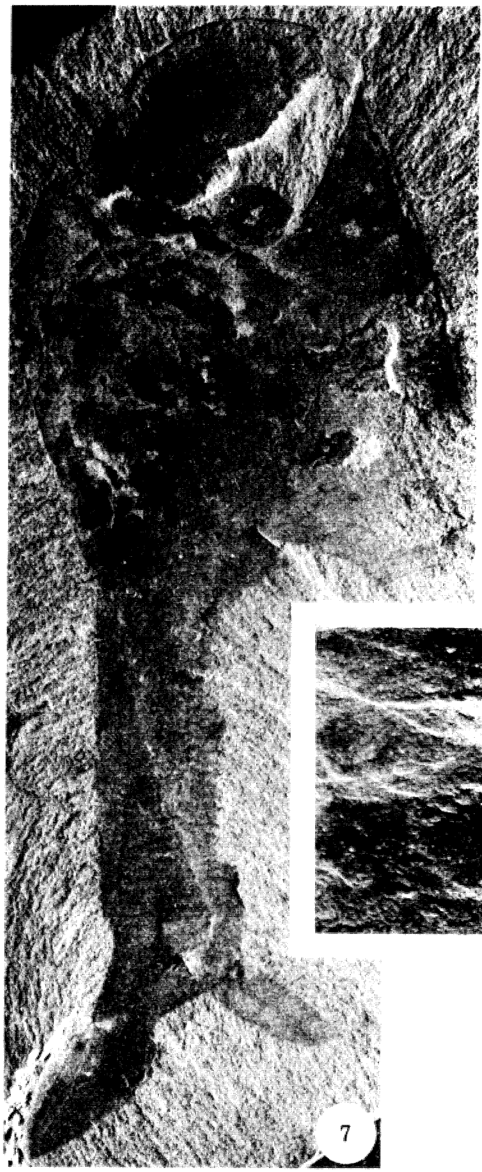
Figures 2 and 3. U.S.N.M. 57722, parallel–oblique. (2) Part, north, original of Walcott (1912, pl. 34, fig. 2). (3) Counterpart, reflected, west. (Both at natural size.)

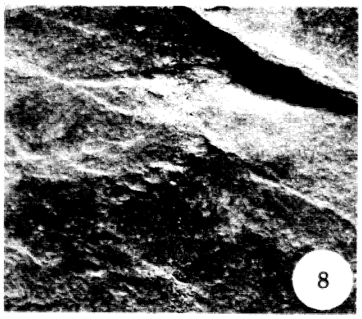
Figure 4. U.S.N.M. 189234, parallel, reflected, east. (Natural size.)

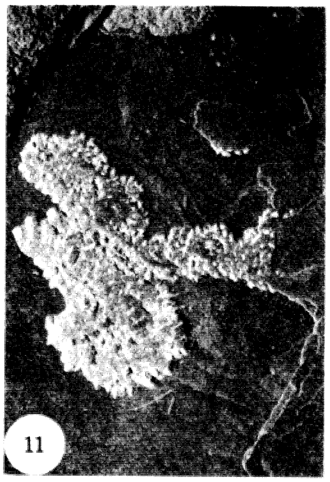
Figures 5 and 6. U.S.N.M. 213809, counterpart, and G.S.C. 11537 part, parallel. (5) Counterpart, east (Magn. × 1.5.) (6) Part, north, anterior of specimen. (Magn. × 3.)

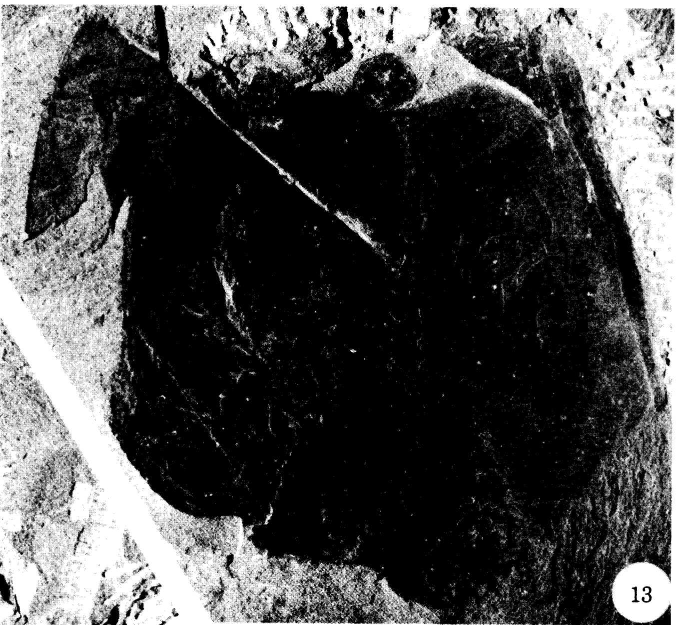


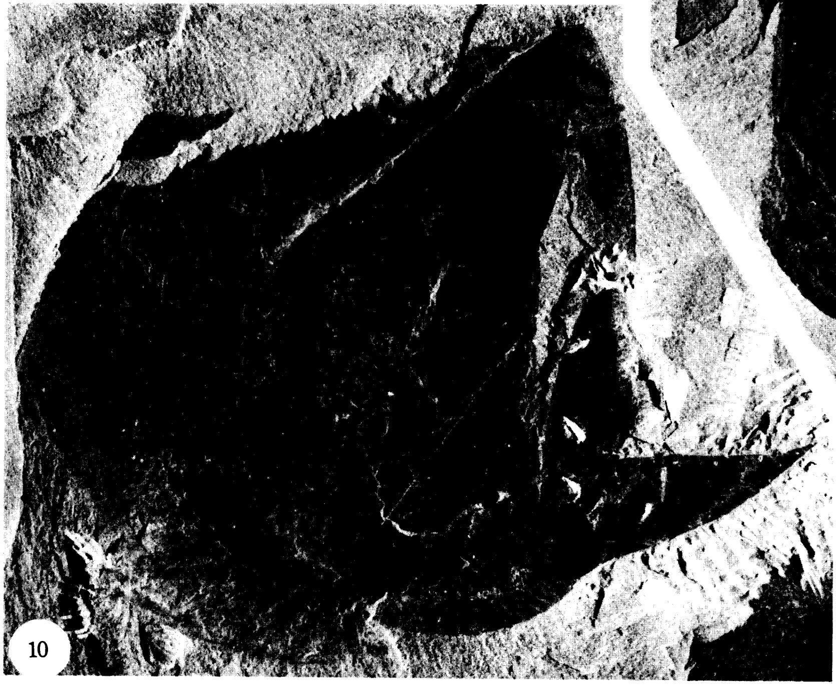
FIGURES 2–6. For description see opposite.



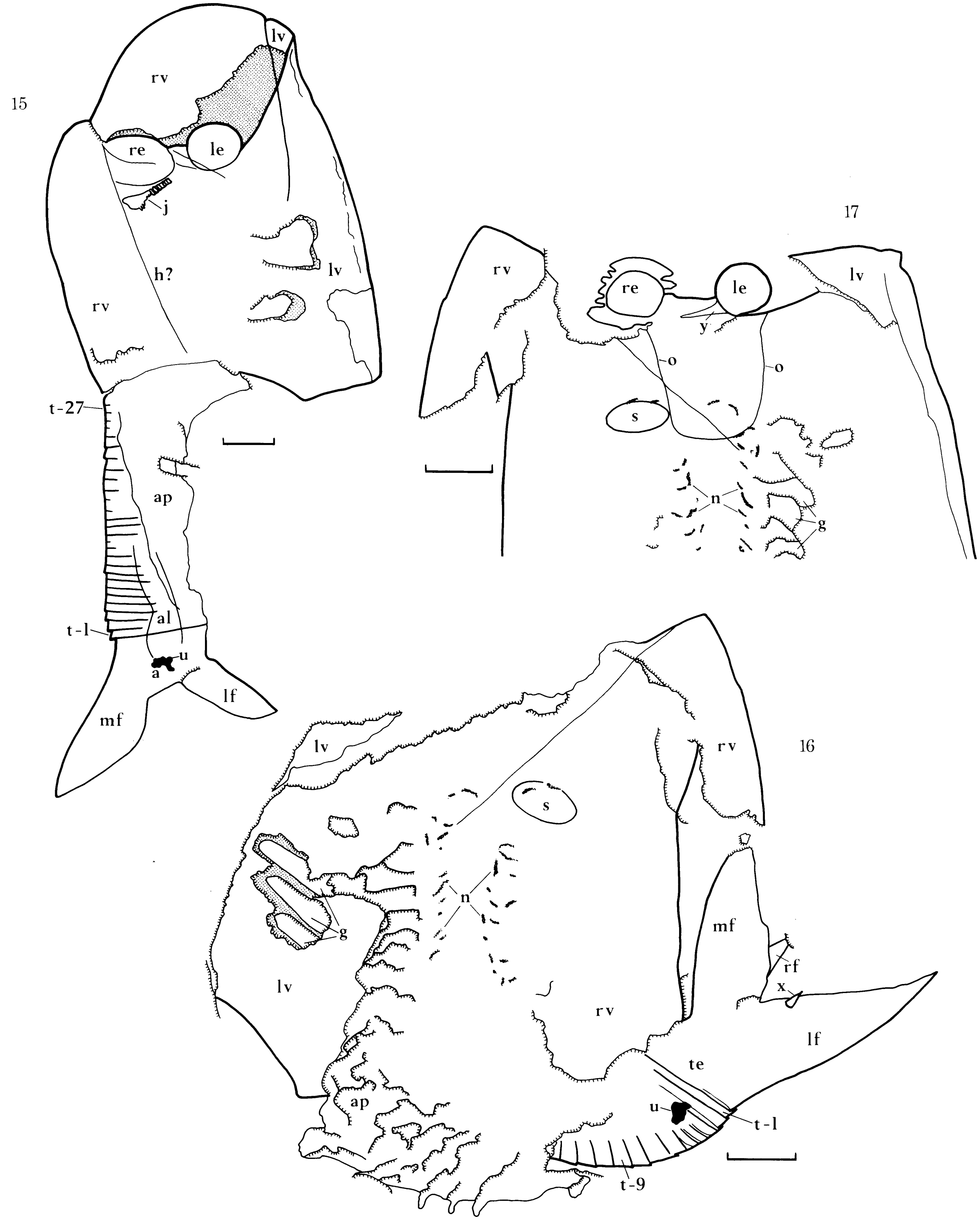








FIGURES 7–14. For description see opposite.



Description of plate 2 and figures 15–17

Odaraia alata Walcott, 1912

Figures 7–9. U.S.N.M. 189239, lateral–oblique. (7), (8) Counterpart, east. (7) Magn. ×2. (8) Mandible. (Magn. ×6.) (9) Part, north. (Magn. ×2.)

Figures 10–14. U.S.N.M. 189231. parallel, trunk twisted posteriorly through about 90°. (10), (11) Part. (10) Southwest. (Magn. ×2.) (11) East, appendages revealed by removal of left valve. (Magn. ×3.) (12)–(14) Counterpart. (12) Under glass, north, eyes and labrum after preparation of right eye. (Magn. ×3.) (13) Northwest. (Magn. ×2.) (14) North, eyes, after preparation of right. (Magn. ×3.)

Figures 15–17. Explanatory drawings. (15) U.S.N.M. 189239, counterpart, junction of valves ventrally (top right of figure) added from part. (16), (17) U.S.N.M. 189231. (16) Part, x indicates position of a tiny hyolithid. (17) Counterpart, anterior. Scale bars 5 mm.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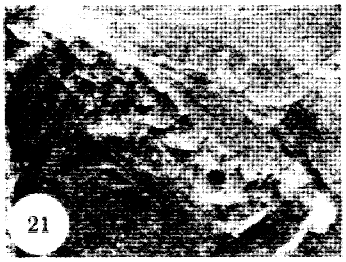
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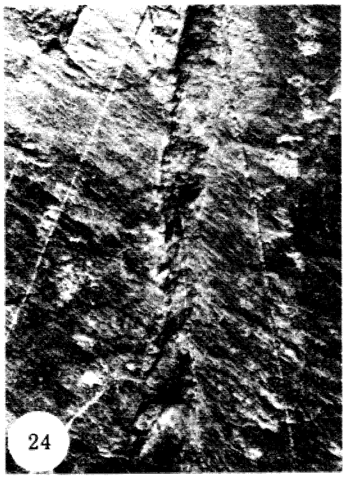
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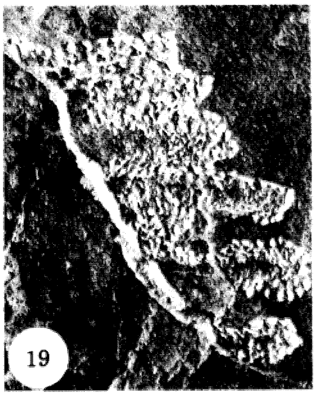
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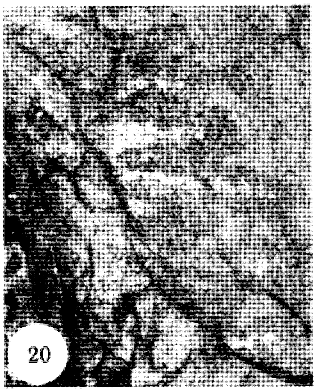
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FIGURES 18–23. For description see opposite.

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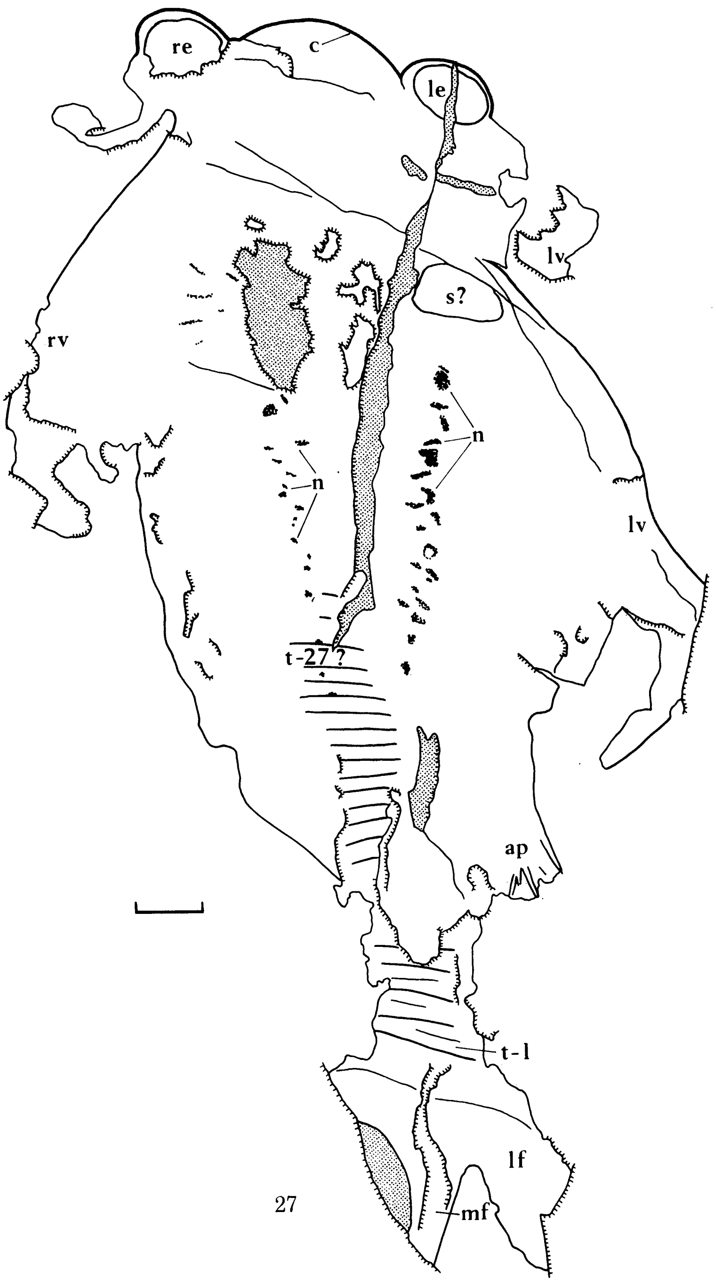

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Description of plate 3 and figures 26, 27

Odaraia alata Walcott, 1912

Figures 18–23. U.S.N.M. 202295, lateral–oblique. (18) North (magn. × 1.5). (19), (20) Appendages revealed by removal of right valve; west, and under glass, north respectively. (Magn. × 3.) (21) North, mandible, after removal of a fragment of overlying valve. (Magn. × 6.) (22), (23) Under alcohol, east. (22) Magn. × 1.5. (23) Inner rami of appendages. (Magn. × 3.)

Figures 24 and 25. R.O.M. 34306, parallel. (24) West, nodes in anterior of trunk. (Magn. × 3.) (25) Reflected, west. (Magn. × 1.5.)

Figures 26 and 27. Explanatory drawings. (26) U.S.N.M. 202295, after preparation to reveal appendages beneath right valve. (27) R.O.M. 34306. Scale bars 5 mm.

evident, are preserved in similar positions on either side of the midline (figure 4, plate 1; figures 66, 67, plate 7).

The hinge line in specimens in exactly *lateral* aspect coincides with the preserved margin of the carapace; the carapace is not folded about some other line. The lateral telson flukes are superimposed and the median one is preserved in outline, projecting dorsad of them (figures 37, 38, 41, plate 5). *Odaraia* is usually preserved in *oblique* aspect, intermediate between parallel and lateral. The configuration of the valves and position of the hinge allows a distinction to be made between lateral–oblique and parallel–oblique. Specimens approaching parallel aspect, the hinge line closer to the midline of the flattened arthropod than to the preserved margin of the carapace, are termed *parallel–oblique* (figures 31, 36, plate 4). Specimens with the hinge line closer to the preserved carapace margin are more nearly in lateral aspect and therefore termed *lateral–oblique* (figure 18, plate 3). The relative abundances of known specimens of *Odaraia* preserved in different orientations are tabulated below. Data for *Canadaspis perfecta* (Briggs 1978, p. 444) are included for comparison.

	Odaraia		*C. perfecta*	
parallel	46 %	26 specimens	32 %	301 specimens
lateral	8		51	
oblique	46		17	
lateral–oblique	19			
parallel–oblique	27			

The striking feature of the table is the preponderance of specimens of *Odaraia* preserved in parallel aspect compared to those of *C. perfecta*. This presumably reflects the oval cross section of the carapace in life, the long axis horizontal, and the configuration of the laterally directed telson flukes (figure 103). *Odaraia* is unknown in vertical aspect (cf. *Canadaspis perfecta* (Briggs 1978, pl. 1, figs 10, 11)). The carapace may, however, be detached from the trunk (figures 52, 53, plate 6) or at an unnatural attitude to it (figures 7, 9, plate 2), resulting in compaction at an angle to the bedding, and consequent foreshortening.

All the known specimens of *Odaraia* show some evidence of features in addition to the carapace. Of these 82 % were apparently complete when buried, but unfortunately over half (13 out of 23) are only partly known, due to breakage and non-collection or loss of part of the slab. In less than half of the total number of specimens are both part and counterpart known. Attempts to locate the missing fragments in the Walcott collection have met with no success. This exacerbates the problem of identifying orientation to bedding and distinguishing between dorsal and ventral sides. The lack of isolated carapaces (without 'soft' parts) is a feature *Odaraia* shares with *Marrella splendens* (Whittington 1971*b*, p. 18), *Yohoia tenuis* (Whittington 1974, p. 7) and *Burgessia bella* (Hughes 1975, p. 429), but in which it contrasts sharply with *Canadaspis perfecta* (Briggs 1978, p. 444), which is represented by as many carapaces as complete individuals, and *Naraoia compacta* (Whittington 1977, p. 418), of which a high proportion of specimens consist of the dorsal shield alone. This may reflect a greater robustness of the carapace of *C. perfecta* and *N. compacta*; the valves of *Odaraia*, and of the other examples mentioned, were presumably too thin to survive long as exuviae.

A number of specimens of *Odaraia* (about 25 % of the total) show an irregular crumpling of the carapace (figures 2, 3, plate 1; figure 90, plate 9), which is at least partly a reflection of an originally thin cuticle. In some cases this is associated with the growth of pyrite crystals (cf. Conway Morris, 1977, p. 5), presumably facilitated by anaerobic conditions implied by the lack of obvious decay (Conway Morris 1979, p. 236), which may have contributed to the crumpled appearance of the valves. The dark stain that 'is almost universally associated with specimens of *Marrella splendens*' (Whittington 1971*a*, p. 1188) and more rarely occurs in some other Burgess Shale animals (Briggs 1978, p. 445) has not been observed in specimens of *Odaraia*.

4. Systematic palaeontology

Class and Order uncertain

Family ODARAIDAE Simonetta and Delle Cave, 1975

Diagnosis (new herein). Carapace bivalved, tubular, extending posteriorly more than half of the total sagittal length; trunk elongate multi-segmented, with 25 to 50 short, wide divisions; telson bearing three large flat pointed processes.

Genus *Odaraia* Walcott, 1912

(= *Odaria* Fedotov, 1925; = *Odaria* Størmer, 1944; = *Odoraia* Roger in Piveteau, 1953; = *Odria* Krestovnikov, 1961)

Type species. *Odaraia alata* Walcott, 1912.

Diagnosis. Valves elongate, subrectangular in lateral outline, dorsal margin produced posteriorly into a short pointed process, ventral margins juxtaposed along most of their length. Biramous appendages borne by all the trunk somites posterior of the first two; inner ramus spiny, bifurcate, outer ramus lamellate. Telson processes elongate, curved and tapering, two paired projecting laterally, one median vertically.

Geological horizon. Middle Cambrian, Stephen Formation, Burgess Shale Section, *Bathyuriscus–Elrathina* zone, British Columbia.

Odaraia alata Walcott, 1912

v* 1912 *Odaraia alata* Walcott, pp. 153–154, 159, 187–188, 228, pl. 34, fig. 2.
1913 *Odaraia*; Clarke in Zittel, p. 750.
1925 *Odaria*; Fedotov, p. 387.
1928 *Odaraia*; Henriksen, pp. 14–15.
1934 *Odaraia alata*; Straelen & Schmitz, pp. 171–172, 208, 227, 236.
1944 *Odaria*; Størmer, pp. 101, 135.
v. 1944 *Portalia*; Størmer, pp. 101, 135.
1969 *Odaraia alata*; Rolfe in Moore, pp. 299, 326–327, fig. 152, no. 5.
v. 1975 *Odaraia alata*; Simonetta & Delle Cave, pp. 13, 14, 24, 25, 26, 29, 35, pl. 3, fig. 6, pl. 51, figs 1, 2, pl. 52, figs 2–7.
v. 1975 Cfr. *Odaraia alata*; Simonetta & Delle Cave, pl. 52, fig. 1.
v. 1975 *Eurysaces pielus* Simonetta & Delle Cave, pp. 14, 35, pl. 3, fig. 7, pl. 51, fig. 3, pl. 52, figs 8, 9.
v. 1975 *Protocaris pretiosa*; Simonetta & Delle Cave *pars*, pl. 53, fig. 4.
1976 *Odaraia alata*; Simonetta, pp. 119, 126, fig. 7, no. 30 (cop. Simonetta & Delle Cave 1975, pl. 3, fig. 6).
1976 *Eurysaces pielus*; Simonetta, p. 126, fig. 7, no. 31 (cop. Simonetta & Delle Cave 1975, pl. 3, fig. 7).
1976 *Odaraia*; Briggs, p. 12, 16.

Holotype. USNM 57722 part (figure 2, plate 1), original of Walcott (1912, pl. 34, fig. 2);

Simonetta & Delle Cave (1975, pl. 51, fig. 1B) and counterpart (figure 3, plate 1), original of Simonetta & Delle Cave (1975, pl. 51, fig. 1A).

Other material. U.S.N.M. 189228–189239, originals of Simonetta & Delle Cave (1975, pl. 51, figs 2, 3; pl. 52, figs 1–9; pl. 53, fig. 4): U.S.N.M. 188630, 202295, 213807–213813, 213862, 241050: G.S.C. 11537, 12174: R.O.M. 34306, 34307, 38398.

Locality and stratigraphical horizon

Middle Cambrian, Stephen Formation, Burgess Shale Section, *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* zone, situated on the ridge between Wapta Mountain and Mount Field, at an elevation of approximately 2286 m, 4.8 km north of Field, southern British Columbia (see Fritz (1971) for an account of the stratigraphy). All the U.S. National Museum specimens, except U.S.N.M. 189235, which is not labelled, bear the locality number 35K, i.e. the 'Phyllopod Bed' in the Walcott Quarry. Walcott (1912, p. 153) records that 'several specimens' occurred in his layer 'No. 8', which is between 2.07 m (6 ft 9 in) and 2.26 m (7 ft 5 in), if one correlates the base of Walcott's layer 12 with the G.S.C. level of 1.52 m (5 ft) as indicated by Whittington (1971*a*, p. 1176) and extrapolates on the basis of Walcott's (1912, p. 152) measurements. None of the other material is localized; the G.S.C. expeditions of 1966 and 1967 did not collect any specimens of the genus, and so it is not known at precisely which horizon it occurs. The associated fauna includes (in order of decreasing abundance) *Canadaspis perfecta*, *Marrella splendens*, inarticulate branchiopods, *Waptia fieldensis*, agnostids, *Hyolithes*, *Ottoia prolifica*, *Scenella varians*, *Nisusia burgessensis*, *Burgessia bella*, *Takakkawia lineata*.

5. Description

(*a*) *Cephalic region*

The identification of dorsal and ventral sides of the arthropod, in both lateral and parallel aspect, is difficult but vital to an interpretation of the morphology. G.S.C. 12174 (figure 41, plate 5) appears to show the carapace in lateral aspect, one of the preserved margins is the straight hinge line, produced posteriorly into a small triangular projection. If it is assumed that the trunk and telson are not rotated with respect to the hinge, then it is evident that the median fluke extended dorsal rather than ventral of the lateral flukes. This observation is borne out by U.S.N.M. 189233 (figures 37, 38, plate 5), which preserves the straight posterior part of the hinge line and the median fluke extending dorsal and some distance posterior of the lateral ones. The dorsal position of the fluke thus established can be used to distinguish between dorsal and ventral in specimens in parallel aspect. Thus G.S.C. 11537/U.S.N.M. 213809 (figures 5, 6, plate 1) appears to have split through the dorsal part of the carapace and G.S.C. 11537, the part, represents an essentially dorsal view.

A pair of generally highly reflective subcircular projections of the cephalon (figure 34, plate 4) are interpreted as pedunculate eyes. They are evident in nine specimens and were borne on the anterior margin of the cephalon in a dorsal position (figures 5, 6, plate 1) projecting anterolaterally. In parallel aspect the eyes are usually preserved extending just beyond the anterodorsal margin of the carapace, but the carapace may extend beyond them anteroventrally (figure 6, plate 1; figures 33, 35, plate 4). The relative positions of the eyes and carapace margin clearly depend on the tilt of the specimen relative to the bedding; tilting downward posteriorly will displace the anteroventral margin of the carapace further beyond the eyes. The proximal part of the peduncle is usually obscured where it is compacted against the anterior margin of the cephalon (figures 66, 67, plate 7) or carapace (figure 7, plate 2), but it appears to taper gradually to its point of attachment. There is no evidence that it was segmented. In some specimens (figure 4, plate 1; figure 34, plate 4) there appears to be a ridge or groove connecting the peduncles, but this is probably the result of compaction of the cephalon against the anterodorsal margin of the carapace.

A clearly defined central area of the distal part of the eye stalk is highly reflective and is surrounded by a narrow, less reflective margin. The reflective area is usually subcircular in outline in specimens preserved in parallel aspect (figure 13, plate 2; figure 34, plate 4) but may, however, be oval (figure 36, plate 4; figure 66, plate 7), presumably as a result of slight tilting relative to the bedding. In the left eye of U.S.N.M. 189231 (figure 12, plate 2) it appears to continue as a narrow strand into the anterior part of the cephalon. This reflectivity is characteristic of the eyes of the Burgess Shale arthropods and has previously been interpreted as the visual surface (Briggs 1977, p. 602; 1978, p. 455). It seems likely, however, that the eye would compact into a plane of negligible thickness and therefore the retention of an impression on both part and counterpart implies that the split has passed through the eye. The result is a section, the visual surface including possibly the lenses represented by the darker outer margin, the inner photoreceptive tissue of the eye by the reflective central area. This would explain why *Odaraia*, in common with other Burgess Shale arthropods, shows no evidence of lenses on the surface of the presumably compound eyes, even though it bears the largest eyes of any of the arthropods of the fauna (over 6 mm in diameter in U.S.N.M. 189234, figure 4, plate 1). This interpretation is borne out by the eyes of *Opabinia* (Whittington 1975*a*, pp. 23, 32), the outer rim of which is sometimes preserved showing a series of radial steps which were interpreted by Whittington (1975*a*, p. 23) as ommatidia (cf. Calman 1909, p. 10, fig. 5). A similar preservation is evident in the right eye of U.S.N.M. 189231 (figure 14, plate 2), but there it appears to be the result of compaction.

The anterior margin of the cephalon, beyond which the eyes projected, was smooth and gently convex anteriorly; this is particularly evident in R.O.M. 34306 (figure 25, plate 3), where the eyes are widely spaced and possibly displaced laterally. No evidence of any appendages extending, like the eyes, beyond the anterior margin of the cephalon or carapace has been observed. Portions of the compacted valves occasionally project anteriorly and laterally beyond the cephalon (figure 5, plate 1; figure 25, plate 3), however, and may appear linear in specimens preserved in parallel aspect as a result of splitting. The carapace of U.S.N.M. 213809, for example, has been removed by splitting ventral to the eyes (it is present in this area in G.S.C. 11537, the part (figure 6, plate 1)) but the lateral margin of the right valve remains as an apparently linear feature (figure 5, plate 1) extending beyond the cephalon to the anterior carapace margin. Directly between the eyes of U.S.N.M. 189232 (preserved in parallel aspect) lies a group of three small subcircular reflective areas (figure 66, plate 7), two symmetrically flanking a smaller third, which lies immediately posterior of them. This feature is not evident in other specimens, apart from U.S.N.M. 213807, which shows a much less distinct reflective area just posterior of the eye peduncles (figure 34, plate 4), which appears to include three distinct spots. Both the position and symmetry of this feature suggest that it may represent a median eye. The median or nauplius eye of Recent Crustacea normally degenerates in the adult, but coexists with the pair of compound eyes in adult Branchiopoda, for example. 'When fully developed, it usually presents three divisions, each consisting of a cup-shaped mass of dark pigment, the cavity of which is filled with columnar retinal cells' (Calman 1909, p. 17).

At least five specimens preserve evidence of a row of regularly spaced tooth-like projections in the cephalic region. G.S.C. 11537/U.S.N.M. 213809 (figure 6, plate 1) preserves a row about 2 mm long extending parallel to the sagittal axis, just adaxial of the right adductor muscle scar. The teeth point adaxially and the row presumably represents the right member of a pair. The feature is best preserved in U.S.N.M. 202295 (figures 18, 21, plate 3); the row is about 4 mm long and inclined at about 60° to the sagittal axis, and the teeth appear to point normal to the bedding. The row is traversed by four obvious ridges and two additional ones less well defined. These ridges terminate in a small sharp projection on the anterior side of the feature and a larger blunter one on the posterior. The orientation of the specimen to the bedding, and the presence of ridges connecting the teeth on either side of the feature, suggest that it does not represent a pair of opposed rows, but rather one of a pair. In U.S.N.M. 189239 (figures 7, 8, plate 2) the feature is obscured to a greater extent by the overlying carapace. It extends for about 4 mm but curves through roughly 45° at about its midlength. The anterior section includes a series of about five blunt projections arranged in a line and separated by narrow grooves. The posterior section is less clear, but apparently negative in relief; it may represent the opposing appendage assuming that it was paired. This toothed structure is interpreted as a mandible because: (i) it was apparently denticulate and is preserved in relief suggesting that the cuticle was thickened or strengthened, a characteristic of arthropod jaws; (ii) it is preserved in the cephalic region in the expected vicinity of the mouth; and (iii) it is similar to the mandible of other arthropods. Rolfe (1962, p. 924, fig. 6B), for example, has demonstrated that the mandible of *Ceratiocaris papilio* bore two rows of opposing denticles, connected by a ridge in the case of the incisor process, an arrangement very similar to that evident in U.S.N.M. 202295.

There is no satisfactory evidence for the position of the mouth. U.S.N.M. 202295 (figure 22, plate 3) preserves a possible fragmentary trace of the gut as a dark stained area just posterior of the mandible. The preservation of the gut elsewhere in this specimen, however, suggests that the contents were scattered within the body cavity on either side of its original position due to decay and rupture of the canal wall. U.S.N.M. 189232 (figures 66, 67, plate 7) likewise preserves a possible fragment of the gut contents as a negative relief a short distance anterior of the carapace adductor muscle scars and mandible. It is reasonable to assume that the alimentary canal extended beyond the mandible and adductor muscles and curved ventrally to a posteriorly facing mouth. There is no unequivocal evidence of a labrum, which was presumably present. The preserved margin of the carapace in U.S.N.M. 189231 is followed by a concentration of very fine granular ?pyrite. A subrectangular outline, which is poorly defined in a similar manner (figure 12, plate 2), extends posteriorly from the anterior border of the cephalon to just beyond an apparent adductor muscle scar. It is essentially symmetrical about the midline and is similar in width to the distance between the midpoints of the eyes. This outline may represent the labrum.

Only two specimens, U.S.N.M. 189232 and 213807, preserve any indication of differentiated appendages other than the mandible anterior of the series of trunk appendages and the carapace adductor muscle scars. Both specimens show very faint equivocal traces of the mandible denticles in relief between the adductor scars. U.S.N.M. 189232 (figure 66, plate 7) preserves two short paired linear reflective traces of similar length just anterior of these scars, which are more evident on the right side. These extend anterolaterally almost the width of the scars and then curve posteriorly parallel to the sagittal axis of the trunk. They may represent appendages but comparison with the trunk limbs indicates that they are unlikely to have extended beyond the lateral margin of the cephalon. They could equally be any segmentally repeated structure, even muscles or inter-somite boundaries. Other, less clearly defined features, are preserved further anteriorly, including an indistinct reflective area apparently interpreted by Simonetta & Delle Cave (1975, pl. 3, fig. 6c, pl. 52, fig. 6) as the labrum. U.S.N.M. 213807 (figure 34, plate 4) preserves an ill defined reflective area anterior of the adductor muscle scars, which gives rise to two short lateral projections on the right side; no detail can be discerned.

The posterior margin of the cephalon is not well defined. The carapace in Crustacea develops as an extension of the posterior margin of the somite bearing the second maxilla (i.e. the posterior margin of the cephalon), and in bivalved forms is flexed by the adductor muscles, which are usually derived from this somite (Hessler & Newman 1975, p. 443; Rolfe in Moore 1969, p. 300). Thus the carapace and adductor muscles were presumably features of the cephalon of *Odaraia*, even though it may not have been a true crustacean. U.S.N.M. 189232 (affording a dorsal view in parallel aspect) shows the cephalon apparently in contact laterally with the right valve (figure 67, plate 7) to a point just level with the posterior margin of the adductor muscle scars. Beyond this point, which may represent the posterior margin of the cephalon, the overlapping appendages of the trunk are evident. Faint reflective traces in U.S.N.M. 213807 (figure 33, plate 4) also indicate the presence of the first of a series of longer appendages lying just posterior of the adductor muscle scars. U.S.N.M. 189231 (figures 10, 12, 13, plate 2) preserves linear nodular features, similar to those in *Canadaspis* (Briggs 1978, p. 457, 459), which occur in pairs along the axis of the trunk. The anteriormost of these are preserved level with the anterior margin of a probable adductor muscle scar and coincide with the most anterior indication of trunk appendages on this specimen. These nodes therefore may coincide with the posterior margin of the cephalon, although they occur inside the area covered by the possible outline of the labrum. The position of the adductor muscle scars relative to other features of the cephalon shows a slight variability. U.S.N.M. 202295 (figure 18, plate 3) preserves the mandible in its expected position just anterior of a possible adductor muscle scar. In G.S.C. 11537/U.S.N.M. 213809 (figures 5, 6, plate 1), however, the mandible lies level with the anterior part of the scars. This is presumably a function of small variations in orientation to the bedding. Compaction of the muscles at angles other than normal to the bedding would offset the carapace scars relative to the origin of the muscles in the posterior part of the cephalon. The adductor scars in *Canadaspis*, for example, (the muscles presumably maxillary in origin) occur in the anterodorsal apices of the valves, anterior of the usual preserved position of the mandible (Briggs 1978, p. 452, 453, figs 31, 34, 40, 45, 52, 55, 59, 61).

(*b*) *Carapace*

The carapace was smooth and, although bivalved, essentially tubular in configuration due to the juxtaposition of the margins ventrally. The preserved dorsal margin in G.S.C. 12174 (figure 41, plate 5) appears to correspond to the hinge. It is essentially straight, showing only a slight dorsal convexity, in contrast to the margin in specimens folded along other lines, which tends to slope adaxially toward the anterior of the specimen (figures 31, 35, plate 4). The dorsal margin is clearly produced posteriorly into a small triangular projection, a characteristic of the hinge of other bivalved arthropods (e.g. *Canadaspis* (Briggs 1978, p. 457), *Perspicaris* (Briggs 1977, p. 607)). There is no similar projection at the anterior end such as that occurring in *Branchiocaris* (Briggs 1976, p. 8). U.S.N.M. 189233 (figure 38, plate 5) shows a similar configuration of the telson and hinge line in lateral aspect, but unfortunately the anterior part of the specimen is unknown. The posterior extremity of the hinge does not appear to be produced into a triangular area as in G.S.C. 12174, but this may be a function of preservation. Relatively few specimens of *Canadaspis* (Briggs 1978) show this projection either. The hinge line is rarely well preserved in parallel aspect. The posterodorsal margin of G.S.C. 11537/U.S.N.M. 213809 (figure 5, plate 1) shows a clear V-shaped indentation medially, which leads to a lineation along the axis, presumably representing the hinge line. The line is also evident in U.S.N.M. 189236 (figures 31, 32, plate 4) in parallel–oblique aspect at the posterior end of the left valve. In parallel aspect the valves are folded beneath the cephalon and trunk and their ventral juxtaposition may be confused with the hinge. The median line separating the valves of U.S.N.M. 189228 (figure 40, plate 5), for example, appears superficially like the hinge, but the overlap posteriorly and tenuous trace of the carapace border suggests that it is the junction of the ventral margins. Compaction of the highly convex carapace resulted in small scale folding of the valves, naturally concentrated along the preserved margin of the carapace, where most of the convexity was accommodated (figure 36, plate 4; figure 43, plate 5).

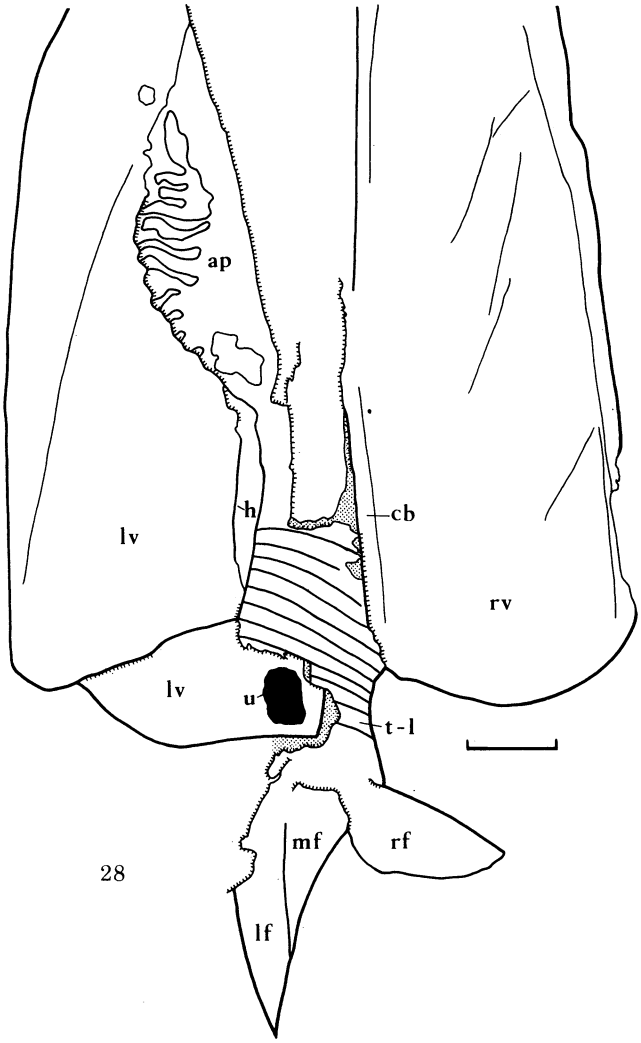
The presence of a pair of well defined anterodorsal adductor muscle scars provides additional evidence that the carapace was bivalved. *Hutchinsoniella* 'is the only known crustacean in which such a muscle is well developed and yet in which the carapace is not subdivided into two opposable valves' (Hessler 1964, p. 41). These scars are elongate oval in outline, trending normal to the hinge line. They are preserved in negative relief on U.S.N.M. 189232 (figures 66, 67, plate 7) and 213807 (figure 35, plate 4), both of which afford essentially dorsal views in parallel aspect with the carapace exfoliated. This implies that the scars were positive features on the internal surface of the valves, an observation borne out by their preservation in U.S.N.M. 213809 (figure 5, plate 1). Associated with the impression of the scars on U.S.N.M. 189232 and 213807 (figure 66, plate 7; figure 34, plate 4) are reflective areas that might represent traces of the actual adductor muscles. The muscle scars are not evident features on the external surface of the carapace (figure 41, plate 5).

An indication of the outline of the valves in lateral aspect is given by G.S.C. 12174 (figure 41, plate 5), but unfortunately the anterior extremity is missing. The left (uppermost) valve is evidently folded beneath itself, distorting the outline but at the same time giving an indication of the convexity of the carapace. The ventral margin of the less convex carapace of *Canadaspis* is not known in lateral aspect folded beneath itself in this manner (Briggs 1978, pl. 3, fig. 38, pl. 4, fig. 51). If expansion parallel to the bedding did not take place during compaction (Whittington 1975*a*, pp. 5, 6, fig. 1) G.S.C. 12174 gives an indication of the appearance of *Odaraia* in lateral view. The valves appear rectangular in this aspect with a blunt convex anterior margin (which is also evident in parallel aspect in U.S.N.M. 189236 (figure 31, plate 4) and U.S.N.M. 189228 (figure 40, plate 5) for example) roughly normal to the hinge, and a more rounded posterior margin diverging from the hinge at about 110°. The valves are also folded beneath themselves in parallel aspect (figure 5, plate 1), the preserved lateral margin diverging posteriorly from the hinge line and following a near-straight course to a point just anterior of the midlength, where it curves through 15° to 20° to run subparallel to the hinge line to the posterior margin of the valve. The indentation between the values is slight at the anterior margin but pronounced posteriorly, where it extends about 29% of the total length of the carapace.

The carapace was apparently attached to the cephalon only, as indicated by the merging of valves and body in this region and the position of the adductor muscle scars (figures 66, 67, plate 7); the trunk was thus free to move within the carapace. The number of somites (in addition to the telson) extending beyond the posterior extremity of the carapace varies from none (figures 2, 3, plate 1) to about 29 (figure 7, plate 2). Six of the 13 specimens in which this relation can be observed, however, show less than five somites beyond the valves, and the other seven specimens show a scatter through the remaining interval up to 29. Thus it appears that the carapace usually covered all but a few somites and the telson. Specimens with large numbers of somites extending beyond the carapace presumably represent distortion due to decay and compaction, but it is likely that the arthropod could vary the degree to which the telson projected beyond the valves, even perhaps by telescoping (cf. *Canadaspis*, Briggs 1978, p. 473). A similar variation occurs in specimens of *Branchiocaris* (Briggs 1976, p. 9), in which the number of somites extending beyond the carapace varies from 1 or 2 to 19. Due to the convexity and folding of the carapace, the true margins of the valves are not usually evident. There is no unequivocal evidence of a carapace border or marginal sculpture, but there are tenuous indications of a low narrow ridge running parallel to the ventral margin of U.S.N.M. 189228 (figure 40, plate 5) and to the anterodorsal margin of U.S.N.M. 213807, for example. There is no evidence of a rostrum, nor of articulating processes along the hinge line (figure 41, plate 5); the hinge may have consisted of a narrow strip of flexible cuticle.

(*c*) *Trunk*

The divisions of the trunk are assumed to represent somites rather than body annulations (the appendages and 'nodes' show a serial repetition, which would support this assumption). Due to incompleteness, poor preservation and concealment by the overlying carapace, the number of specimens giving some indication of the total number of trunk somites is limited. Further, the intersomite boundaries are not so clearly defined as they are in *Branchiocaris* (Briggs 1976). The trunk, for the purpose of this assessment, is deemed to extend from the anterior margin of the telson (which is not considered to be a somite) to the posterior margin of the adductor muscle scars or mandible. The intersomite boundaries may be evident posteriorly (figures 7, 10, plate 2; figures 33, 35, plate 4). Anteriorly the number of somites may be estimated on the basis of the limbs (assuming an approximate one-to-one correspondence between somites and paired appendages) or on the nodes, which may be preserved near the axis and appear to correspond in their spacing to the appendages. It has, however, proved necessary to extrapolate on the basis of somite length where evidence is lacking in parts of otherwise relatively well preserved sequences of trunk somites. The maximum observed number of somites was 45, evident in R.O.M. 34306 (figure 25, plate 3) as intersomite boundaries posteriorly and nodes anteriorly with extrapolation on the basis of length over only ten somites; U.S.N.M. 189239 (figures 7, 9, plate 2) shows evidence of 28 somites anterior of the telson and extrapolation as far as the mandible suggests a total of about 47. The minimum number of somites observed is 28 in U.S.N.M. 189235 (figure 36, plate 4), based on boundaries for five somites anterior of the telson and appendages otherwise. The trunk of U.S.N.M. 213807 (figures 33, 35, plate 4) appears to have borne 32 somites based on distinct boundaries for the posterior 22 and nodes for those anterior to them;.more equivocal evidence, essentially that of poorly preserved appendages, indicates about 31 in U.S.N.M. 189231 (figures 10, 13, plate 2). Traces of limbs borne by all the trunk somites are evident in U.S.N.M. 213807 (figure 35, plate 4); compaction in parallel–oblique aspect has preserved the right appendages in outline extending beyond the margin of the trunk. U.S.N.M. 189239, (figures 7, 9, plate 2), 213812a (figure 43,



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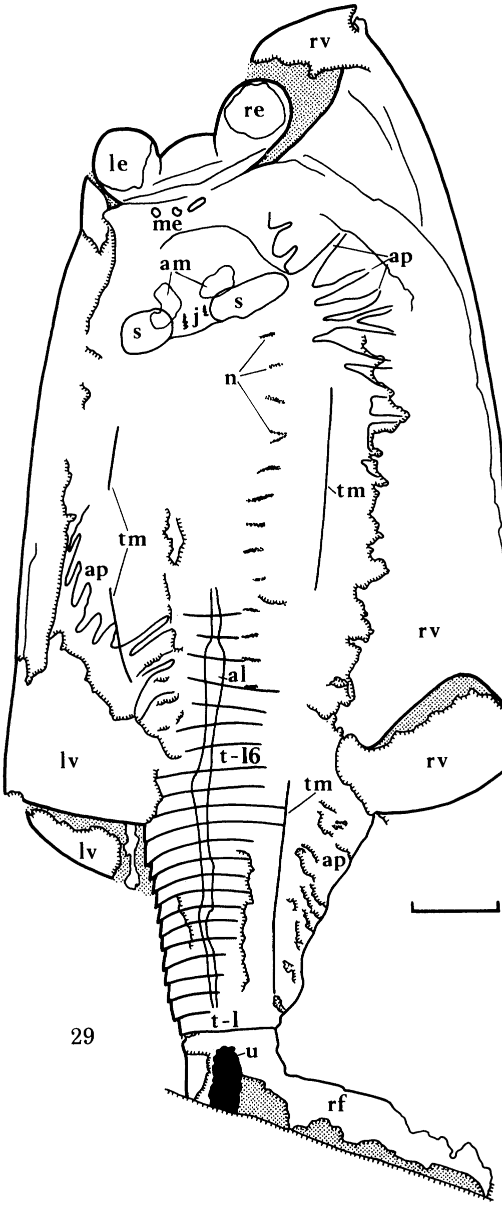

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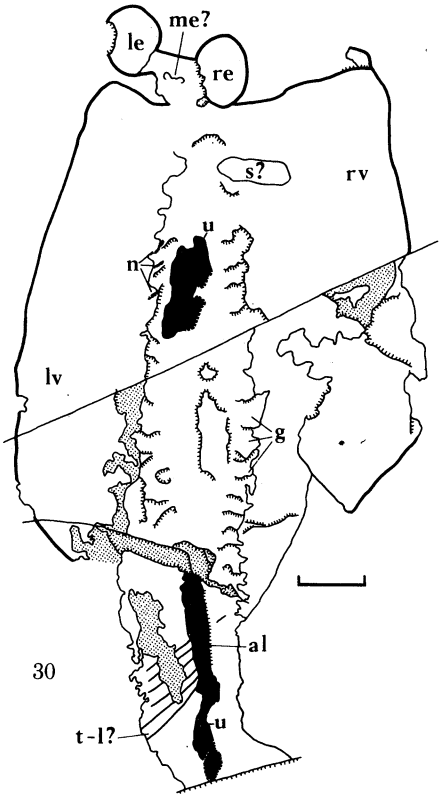

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DESCRIPTION OF PLATE 4 AND FIGURES 28–30

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FIGURES 28–30. Explanatory drawings. (28) U.S.N.M. 189236, posterior part. (29) U.S.N.M. 213807. (30) U.S.N.M. 189235. Scale bars 5 mm.

FIGURES 31 AND 32. U.S.N.M. 189236, parallel–oblique. (31) West. (Magn. × 1.5.) (32) Under alcohol, west, reflective traces of appendages. (Magn. × 3.)

FIGURES 33–35. U.S.N.M. 213807, parallel–oblique. (33) Reflected, west. (Magn. × 2.) (34) Reflected, north, cephalic region. (Magn. × 3.) (35) North. (Magn. × 2.)

FIGURE 36. U.S.N.M. 189235, parallel–oblique, reflected, west. (Magn. × 2.)


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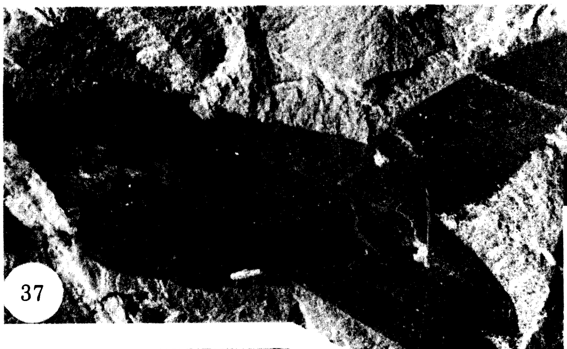
FIGURES 31–36. For description see opposite.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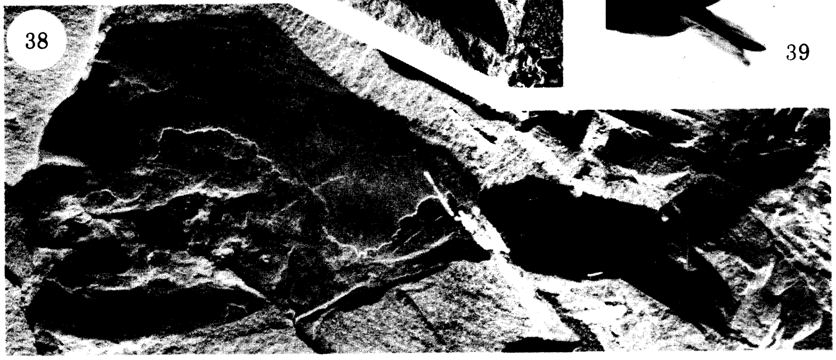
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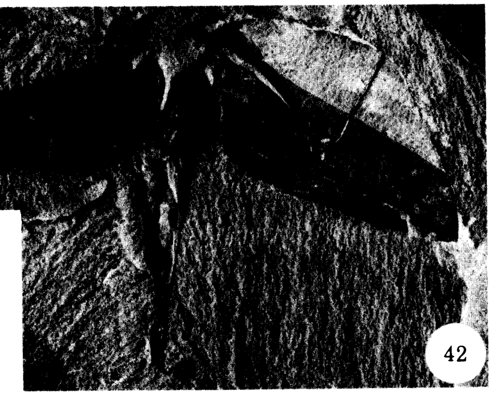
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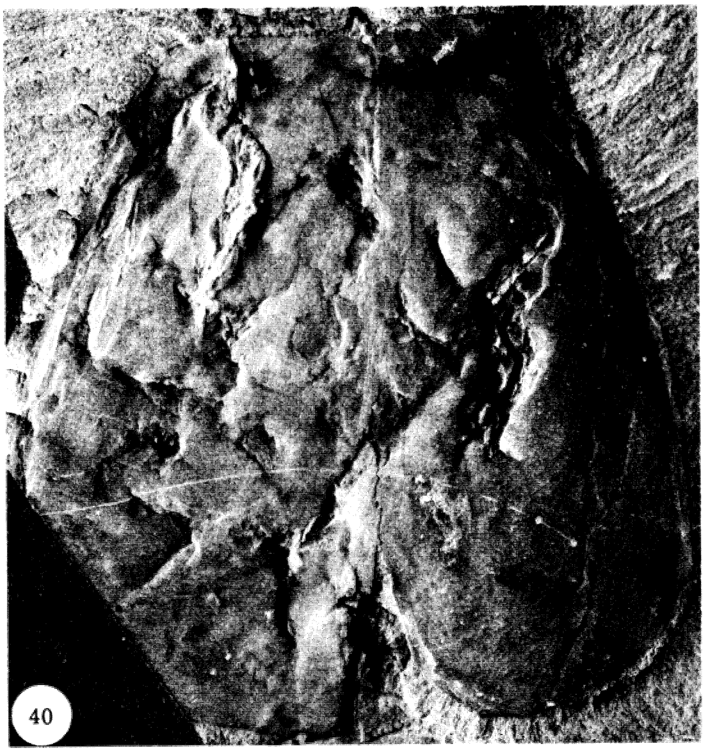
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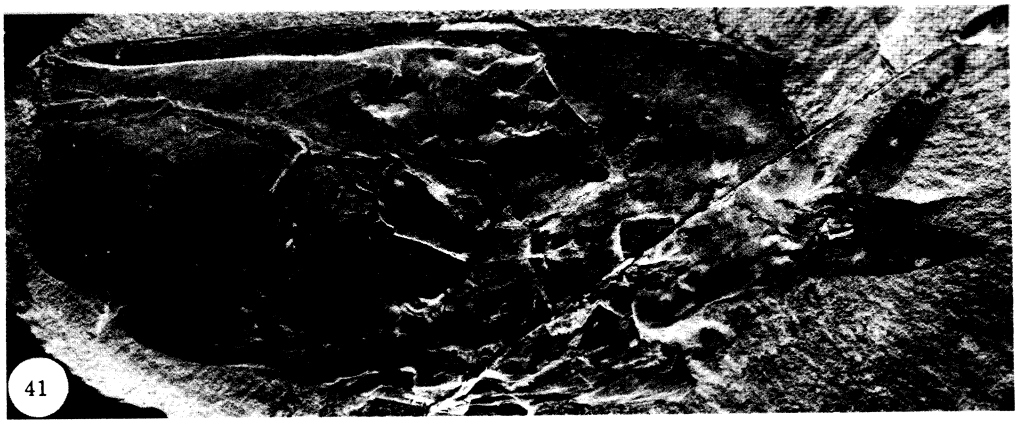
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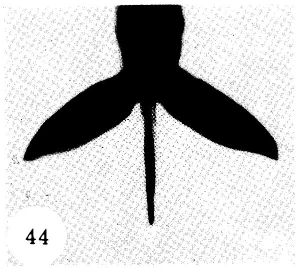
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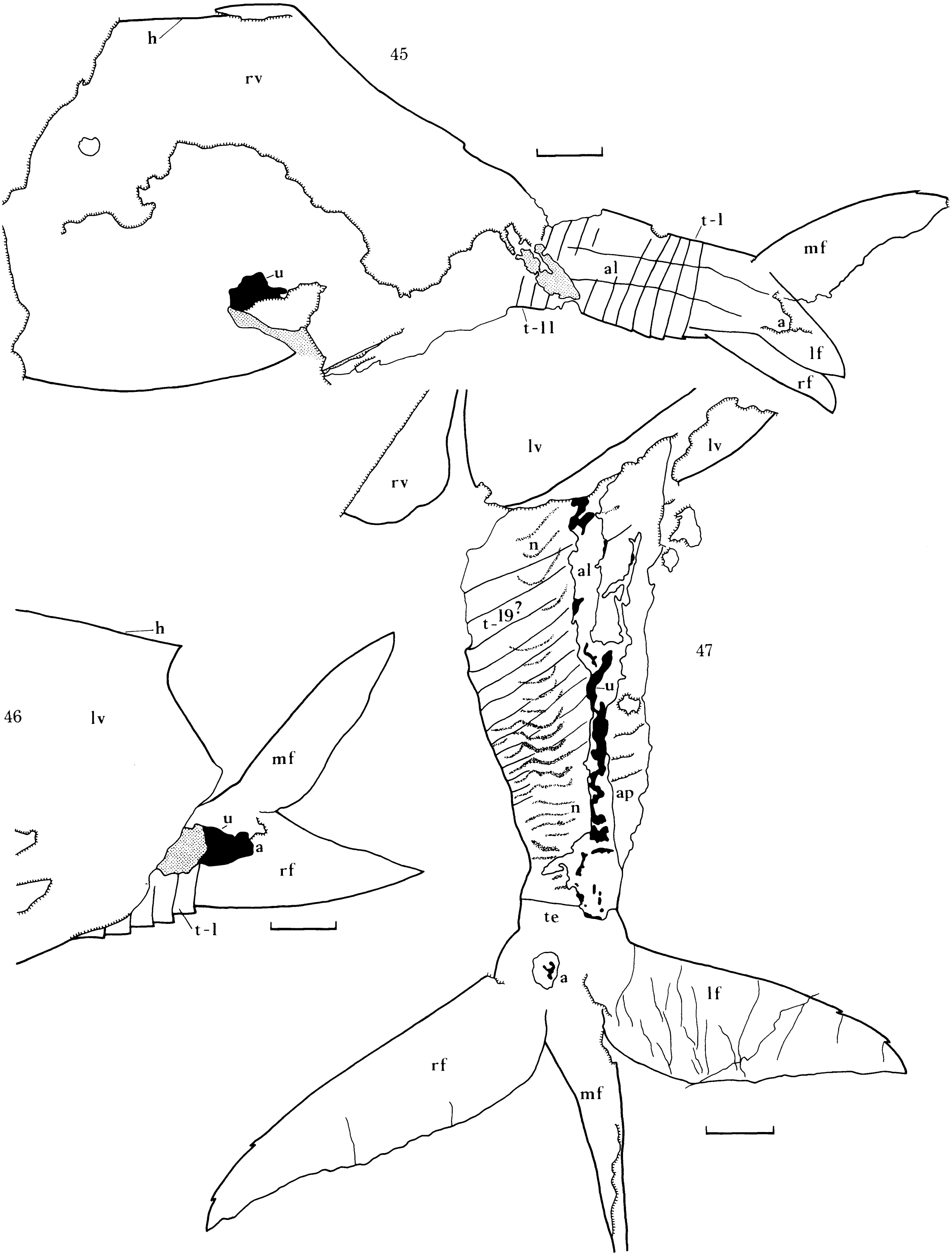
FIGURES 37–44. For description see opposite.



Description of plate 5 and figures 45–47

Odaraia alata Walcott, 1912

Figures 37 and 38. U.S.N.M. 189233, lateral. (37) East, trunk extending beyond carapace, and telson. (Magn. × 3.) (38) North. (Magn. × 1.5.)

Figures 39 and 44. Model of telson, left lateral and dorsal views respectively.

Figure 40. U.S.N.M. 189228, parallel, west, carapace. (Magn. × 1.5.)

Figure 41. G.S.C. 12174, lateral, north. (Magn. × 1.5.)

Figures 42 and 43. U.S.N.M. 213812a, parallel, east, counterpart and part respectively. (Magn. × 1.5.)

Figures 45–47. Explanatory drawings. (45) U.S.N.M. 189233. (46) G.S.C. 12174, posterior. (47) U.S.N.M. 213812a. Scale bars 5 mm.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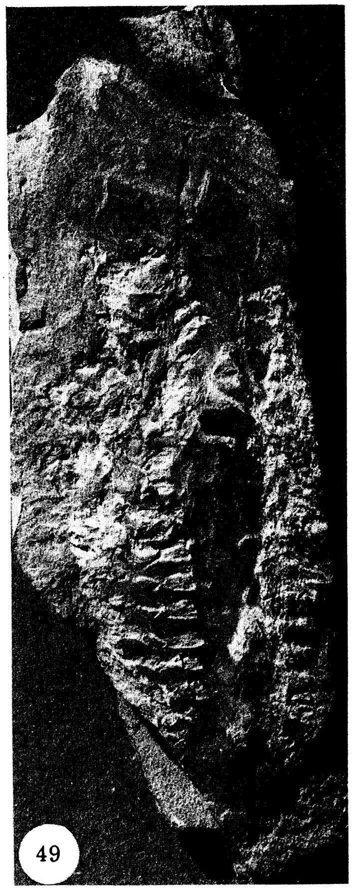
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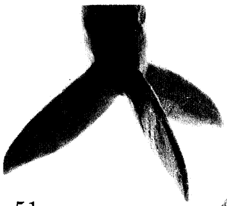
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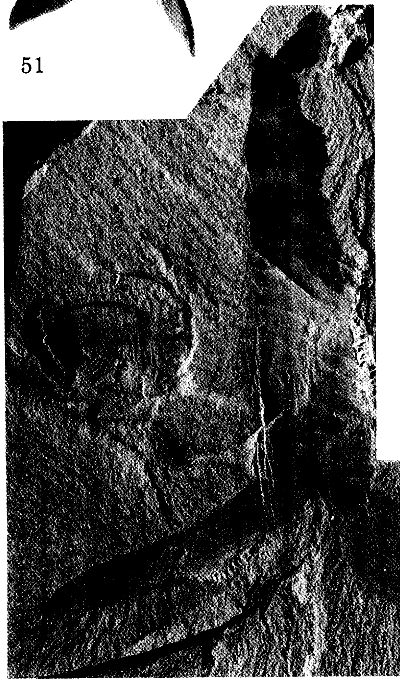
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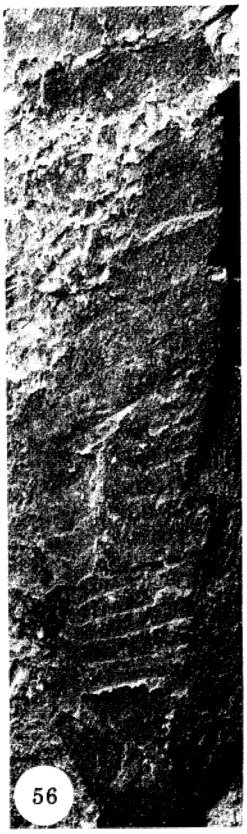
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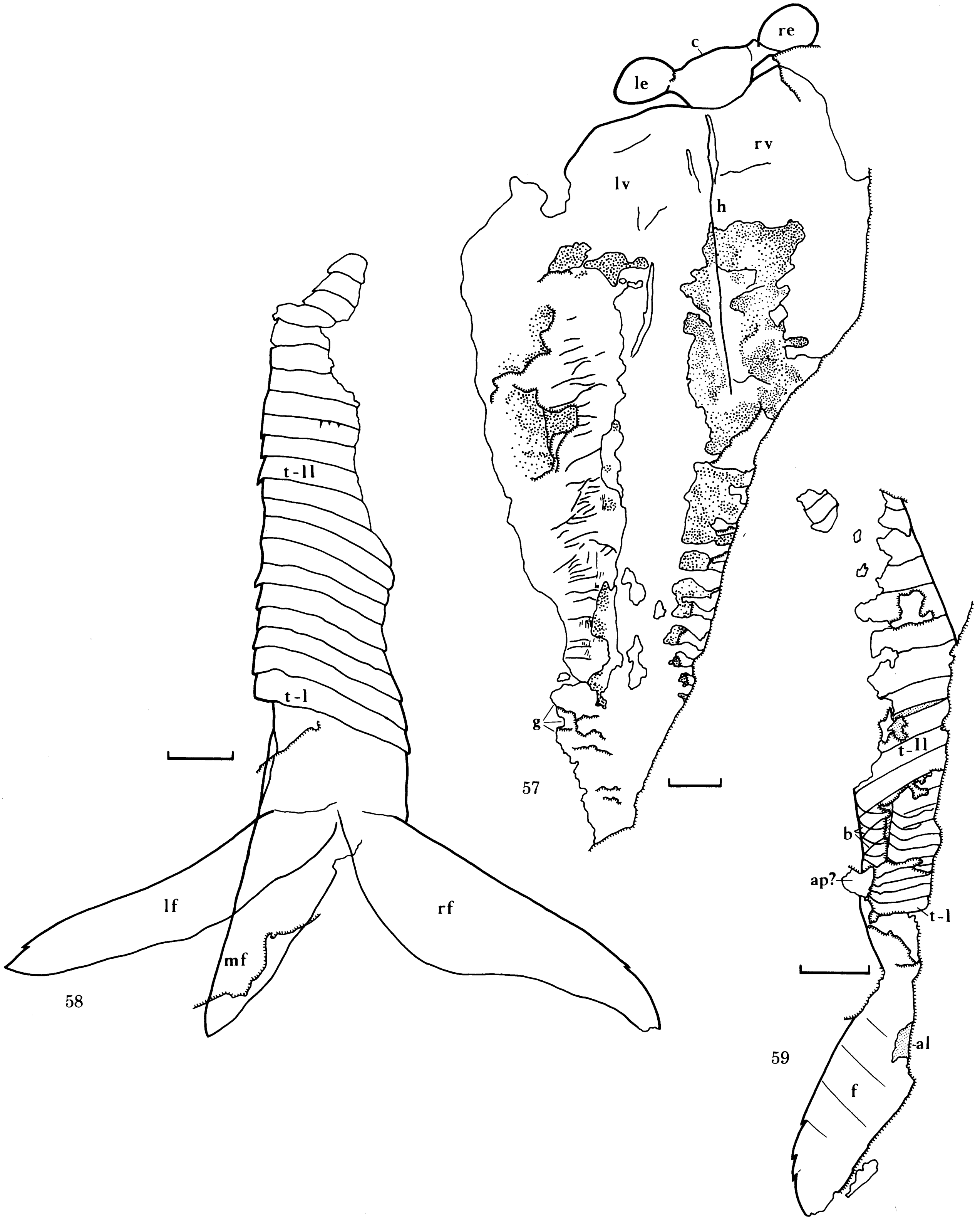
FIGURES 48–56. For description see opposite.



Description of plate 6 and figures 57–59

Odaraia alata Walcott, 1912

Figures 48–50. R.O.M. 38398, parallel. (48), (50) Part; north, and reflected east, respectively. (49) Counterpart, northwest. (Magn. × 1.5.)

Figure 51. Model of telson, 'group 1' orientation; see text.

Figures 52 and 53. U.S.N.M. 189238, parallel–oblique. (52) Part, east. (53) Counterpart, north. (Magn. × 1.5.)

Figures 54–56. U.S.N.M. 188630, orientation unknown. (54), (55). Reflected east, and northwest, respectively. (Magn. × 1.5.) (56) Northwest, trunk showing intersomite boundaries. (Magn. × 4.)

Figures 57–59. Explanatory drawings. (57) R.O.M. 38398, part. (58) U.S.N.M. 189238, part, outline of median fluke added from counterpart. (59) U.S.N.M. 188630. Scale bars 5 mm.

plate 5) and 213813 (figure 81, plate 8) preserve less obvious evidence that appendages were borne by all the trunk somites. The limbs were apparently borne on the ventrolateral margin of the trunk (figure 35, plate 4; figure 67, plate 7). They may appear to be absent posteriorly in some specimens due to (i) concealment beneath the overlying trunk, particularly in dorsal aspect (figure 5, plate 1), (ii) compaction against the trunk somites obscuring the outline of the limbs (figure 36, plate 4), and (iii) preservation on the counterpart. This latter is exemplified by the appendages of U.S.N.M. 189239, which are only present on the part (figure 9, plate 2). The counterpart (figure 7, plate 2) shows a depression in relief corresponding to their position, but, apart from a lack of obvious boundaries, the impression of the limbs is almost indistinguishable from the surface of the trunk. There is no evidence to suggest that some somites without appendages were added once a certain complement of limb-bearing trunk somites had been reached in ontogeny. U.S.N.M. 189239 (figure 7, plate 2), which had up to 47 somites in the trunk, the greatest number known, appears to bear appendages on all of them.

The dimensions of the small number of somites preserved extending beyond the carapace of U.S.N.M. 189233 (figure 37, plate 5) in lateral aspect suggest that the height of the somites increased toward the anterior of the specimen. A similar increase in width is evident in parallel aspect in the few somites posterior of the valves of U.S.N.M. 213809 (figure 5, plate 1). Anteriorly the margins of the trunk are obscured by the overlying carapace or appendages (figure 36, plate 4). They are evident, however, in U.S.N.M. 213807 (figures 33, 35, plate 4) as a shallow linear depression apparently caused by compaction of the edge of the trunk against the underlying appendages. The trunk shows a gradual increase in width anteriorly to a point about eight somites posterior of the adductor muscle scars. Anterior of this the margins appear subparallel, possibly converging slightly anteriorly. A line of nodes runs parallel and adaxial to the right margin anteriorly in U.S.N.M. 213807, presumably reflecting the configuration of the appendage attachments. R.O.M. 34306 (figure 25, plate 3), U.S.N.M. 189231 (figures 10, 13, plate 2) and U.S.N.M. 189232 (figure 66, plate 7) show a similar increase in the width of the trunk toward the anterior, based on the position of the nodes. The reflective traces of appendages and position of nodes in the anterior part of the trunk of U.S.N.M. 189232 indicate that the margins were parallel as in U.S.N.M. 213807, possibly tapering toward the cephalon.

The cross section of the trunk of Burgess Shale arthropods may be estimated by comparing specimens of similar size preserved in different orientations to the bedding, particularly in lateral and parallel aspect (e.g. Briggs 1978, p. 473). Such an assessment cannot readily be made for *Odaraia* due to the small number of specimens that preserve the trunk in outline extending beyond the carapace, and the difficulty of accurately determining orientation to the bedding. The trunk of one of the two specimens reasonably preserved in lateral aspect is concealed by the overlying carapace (figure 41, plate 5); about ten somites extend beyond the valves of the other (figure 38, plate 5), but the specimen is incomplete and no accurate determination of its overall size is possible. The trunk of the latter, however, is narrower than that of specimens similar in size preserved in lateral–oblique (figure 18, plate 3) and parallel (figure 5, plate 1) aspect. This crude comparison, which is all that is possible on the basis of the known material, suggests that the trunk was oval in cross section, flattened dorsoventrally (in contrast to *Branchiocaris*; Briggs 1976, p. 9).

The inter-somite boundaries of *Odaraia* are usually straight (figure 7, plate 2) or gently convex anteriorly (figures 33, 35, plate 4). Variation is produced by flexing of the trunk and differences in orientation to the bedding; irregular boundaries are presumably the result of uneven compaction. The trunk somites overlap, each inserting into the one anterior to it to which it was presumably joined by a band of flexible cuticle. Thus the inter-somite boundaries may appear double, made up of the posterior margin of one somite and the anterior of the next (figure 10, plate 2). The posterior margin of each somite was fringed with spines. These are often obvious in outline at the margins of the trunk (figure 35, plate 4) but are more rarely evident along the length of the inter-somite boundaries, where they are compacted against the cuticle of the succeeding somite (figures 52, 53, plate 6). Due to the short length of the somites and the generally poor preservation, traces of the inter-somite boundaries on both sides of the trunk are rarely evident as separate arcs converging at the margins (as in the abdomen of *Canadaspis perfecta*; Briggs 1978, p. 466). The anterior boundaries of the sixth to ninth somites anterior of the telson of the trunk fragment U.S.N.M. 188630 (figures 54–56, plate 6) are, however, preserved in this manner, but they are obscured by overlying fragments of the appendages or trunk cuticle.

Due to poor preservation anteriorly and variation within specimens due to flexing of the trunk and overlap of somites, it is impossible to give a quantitative indication of the relative lengths of individual somites. It appears, however, that there was a general but very gradual increase in sagittal length anteriorly (figure 35, plate 4; figure 43, plate 5; figures 52, 53, plate 6). The majority of specimens provide no evidence that the trunk was flexible. This is probably because most movement took place in the dorsoventral plane, and few specimens are preserved in lateral aspect. The trunk in U.S.N.M. 189231 (figure 10, plate 2), however, is curved through an angle of about 130°. This flexure, which is achieved by overlap of the somites on the concave side of the trunk, may have been exaggerated by the mode of deposition and preservation. The carapace is preserved in parallel aspect, but the trunk is twisted so that the left lateral and dorsal flukes are compacted in outline, suggesting some distortion during burial. The specimen indicates, however, that the trunk somites could overlap by up to half of their length.

The boundaries between the posteriormost somites of U.S.N.M. 213812a (figure 43, plate 5) are obscured by the presence of irregular granular bands of varying width which are presumably impressions of an aggregate of pyrite. These linear features are regularly arranged roughly normal to the trunk axis, but do not correspond exactly in their spacing to the somites. Within eight of the posterior somites with well defined boundaries, for example, there are ten such granular bands or nodes. They may have been associated with the musculature or attachment of the appendages, in which case there was not a one-to-one correspondence between paired limbs and somites, but a larger number of appendages, as in *Branchiocaris* (Briggs 1976, p. 11). The linear nodes in the posterior somites of U.S.N.M. 213812a presumably represent the right-hand members of a paired set. Although they exceed the somites in number this does not preclude a one-to-one correspondence between such nodes and the more anterior somites beneath the carapace. An excess of appendages over somites in *Branchiocaris* (Briggs 1976), for example, occurs only in the posterior part of the trunk.

Serially arranged linear 'nodes' of pyrite are an obvious feature in only three specimens of *Odaraia* in addition to U.S.N.M. 213812a and in all three the nodes are paired and occur near the lateral margins of the anterior part of the trunk, adaxial to the appendages. The maximum number preserved is about 13 (in R.O.M. 34306; figures 24, 25, plate 3), presumably corresponding to 13 somites. Preservation within the specimens is variable; the nodes in U.S.N.M. 189232 (figure 66, plate 7) and R.O.M. 34306, for example, are more fully developed on one side of the body than the other. In U.S.N.M. 189232 the nodes consist of a large subcircular mass of pyrite flanked anterolaterally (abaxially) by a smaller subrectangular mass which is divided transversely into two more or less equal sections. They thus differ from the linear nodes in the posterior part of the trunk of U.S.N.M. 213812a (figure 43, plate 5). A sequence of six of these dual nodes is preserved on the left side of U.S.N.M. 189232 (figure 66, plate 7), but only one is distinct on the right, the side upon which individual appendages can be distinguished. However, the left nodes appear to correspond in number and spacing to these right limbs. Similar dual nodes are preserved on the right side of the trunk of R.O.M. 34306 (figures 24, 25, plate 3). The distinction between a larger roughly circular area and a smaller linear one is less clear, however, particularly posteriorly, and the smaller element tends to be adaxial rather than abaxial of the other. The nodes in U.S.N.M. 189231 (figures 10, 12, 13, plate 2) also appear to be dual, but the difference between the elements is even less pronounced. The nodes, however, appear to correspond individually in position to traces of the adjacent appendages. Very faint traces of nodes are preserved on the anterior part of the trunk of U.S.N.M. 213807 (figure 35, plate 4). In this specimen relief traces of the inter-somite boundaries are also evident posteriorly and where the two overlap the nodes appear to coincide with the boundaries.

The nodes clearly represent structures that have afforded a locus for pyrite growth. The rare occurrence and variable preservation of nodes presumably reflect the conditions controlling the formation of the mineral rather than the presence or absence of the structure providing a growth site. Thus it is probable that all the nodes discussed represent similar morphological features. Their regular paired arrangement along the margins of the trunk, corresponding to the somites in number at least anteriorly, suggests that the nodes were associated with the appendages and that they may represent points of muscle attachment as suggested by Briggs (1978, p. 460) and Whittington (1977, p. 423) for similar features in *Canadaspis* and *Naraoia* respectively. The configuration of the nodes in U.S.N.M. 213812a is not inconsistent with this interpretation; their greater linear extension may represent part of the trunk muscles.

(*d*) *Trunk appendages*

Biramous appendages, consisting of a segmented branch, the inner ramus, extending ventral to a lamellate branch, the outer ramus, were borne by all the trunk somites (as demonstrated in § 5*c*) with the possible exception of the first two. A number of specimens preserve evidence of the outer rami overlapping posteriorly (figure 36, plate 4), but these are often compacted against one another so that individual lamellae are almost indistinguishable (figure 35, plate 4). The lamellae provide a plane along which splitting commonly takes place, and thus the segmented rami that lie ventral to them are usually concealed within the matrix. These inner rami are exposed, however, in the vicinity of the posterior margin of the carapace of U.S.N.M. 202295 (figures 22, 23, plate 3) which affords a lateral–oblique view of the left appendages, but the posteriormost limbs (which would be present on the unknown counterpart) are not evident. The appendages are best preserved in U.S.N.M. 189232, which affords a dorsal view in parallel aspect (figure 67, plate 7) and shows that they decreased gradually in size posteriorly. In the anterior part of the trunk each outer ramus is seen to overlap that immediately succeeding it. The inner rami are also preserved and have been further revealed by preparation (figure 68, plate 7). They overlap in the opposite sense to the lamellae, each ramus overlying that preceding it. This contrast in the overlapping direction of the two rami also occurs in the trilobite *Olenoides serratus*, for example (Whittington 1975*b*, pl. 20). It implies that the outer rami lay dorsad of the inner; they do not appear to have extended laterally beyond them or to have been interleaved between them. In the posterior part of the trunk of U.S.N.M. 189232 the rami appear to overlap anteriorly rather than posteriorly (figure 67, plate 7; figure 77, plate 8). It is evident, however, from the relative levels of the large spines, which project laterally beyond the appendages, that posterior to appendage 9 the inner rami rapidly approach the level of the outer. The level of splitting then shifts from the outer to the inner rami (cf. *Opabinia*: Whittington 1975*a*, fig. 3*d*, *e*), causing the apparent change in direction of overlap (figure 60).

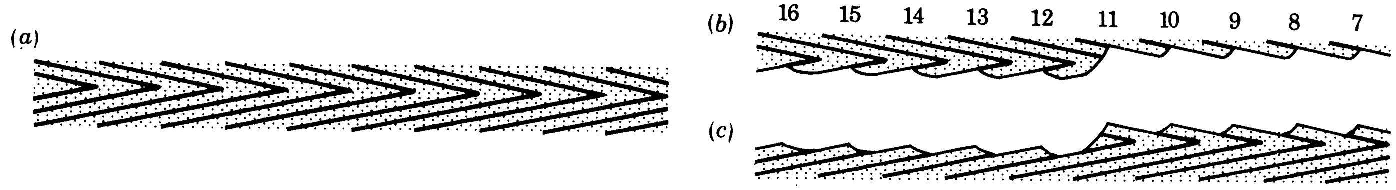
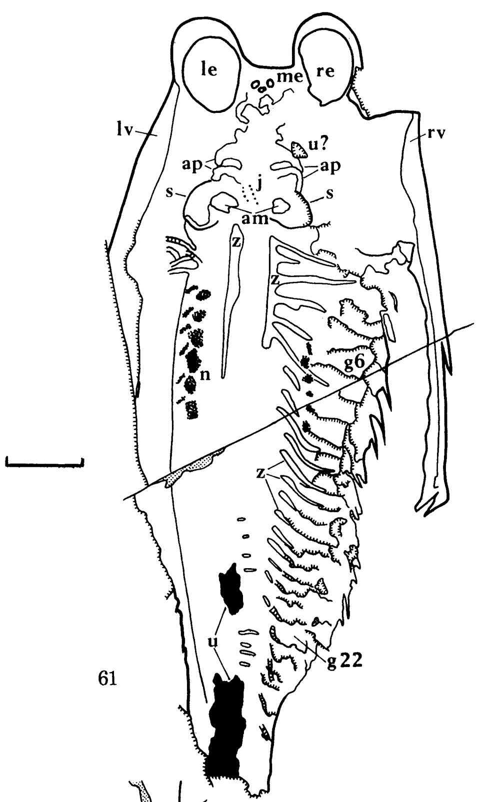


FIGURE 60. Diagrammatic exsagittal section to explain the preserved configuration of the right appendages of U.S.N.M. 189232 (figure 67, plate 7; cf. Whittington 1975*a*, fig 3). The numbers refer to the appendages (figure 61); anterior is to the right. The outer rami lie above and overlap posteriorly, the inner rami below and anteriorly. (*a*) The specimen before splitting to give (*b*) the unknown counterpart and (*c*) the figured part. For further explanation see text.

The outer lamellate rami of U.S.N.M. 189232 are superimposed on the majority of the inner rami, obscuring the details of at least the proximal part. The first ten appendages of the trunk were sufficiently separated by matrix, however, to allow individual rami to be prepared out in succession (figure 68, plate 7). Posterior of appendage 10 the rami are compacted together so as to be almost indistinguishable. This serial preparation of the appendages involved some loss by destruction, but the detail was recorded in camera lucida drawings and photographs (figures 69–72, plate 7; figures 73–78, plate 8). Only the distal parts of the inner rami could be exposed. Proximally they are compacted against their corresponding outer rami, obscuring the segmentation and attachment to the trunk. The most prominent feature of the inner rami is a large spine that extends laterally beyond the appendages and projects posteriorly at an angle of about 25° to the axis of the ramus. Some of these spines were exposed (by splitting of the slab) before preparation (figure 67, plate 7). The detailed preservation of the rami is poor in contrast to the preservation of the specimen as a whole; it seems likely that the inner rami were not strongly sclerotized. They are described in the order in which they were exposed by preparation.

The inner rami of appendages 7 to 10 (figures 69–72, plate 7), which appear to have been essentially similar, evidently extended laterally (normal to the sagittal axis) over half their length, parallel to the anterior margin of the outer ramus, which obscures them proximally. The outer and inner rami appear to be compacted together along this length (as in some specimens of *Canadaspis perfecta*; Briggs 1978, p. 463), but a break of slope parallel to their anterior margin in some appendages suggests that they were separate in life, both presumably attached to a basal segment. Details of the proximal segmentation and attachment are unknown. Preparation of the more posterior appendages (16, 19 and 22) proximally, however, revealed a convex posterior margin to the inner ramus (figures 77, 78, plate 8), which corresponds to the ventral margin in life, if one assumes that the appendages have been rotated during burial (cf. *Olenoides*; Whittington 1975*b*, 1980). The inner ramus curves posteriorly through 90° at about its midlength to be roughly parallel with the sagittal axis. At this pronounced geniculation the ramus increases in width and a large spine projects from it posteriorly beyond the outer (abaxial) margin of the



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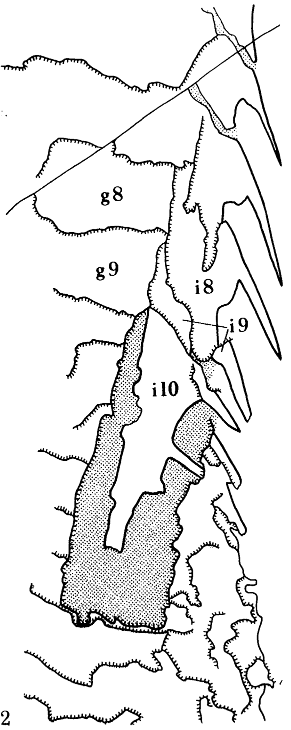

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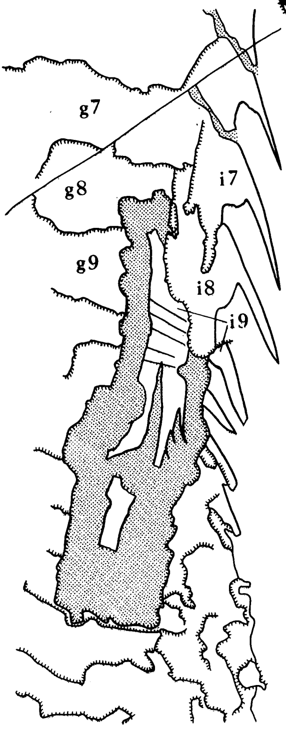

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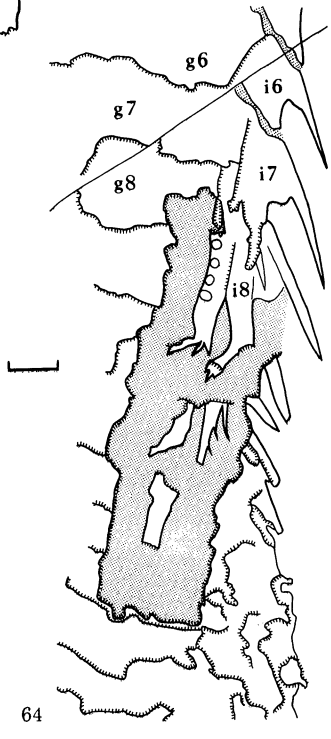

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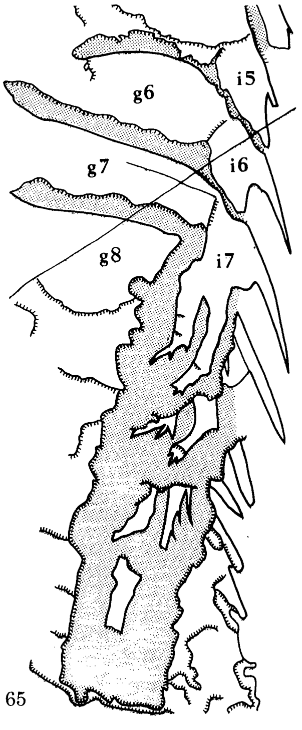

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DESCRIPTION OF PLATE 7 AND FIGURES 61–65

Odaraia alata Walcott, 1912

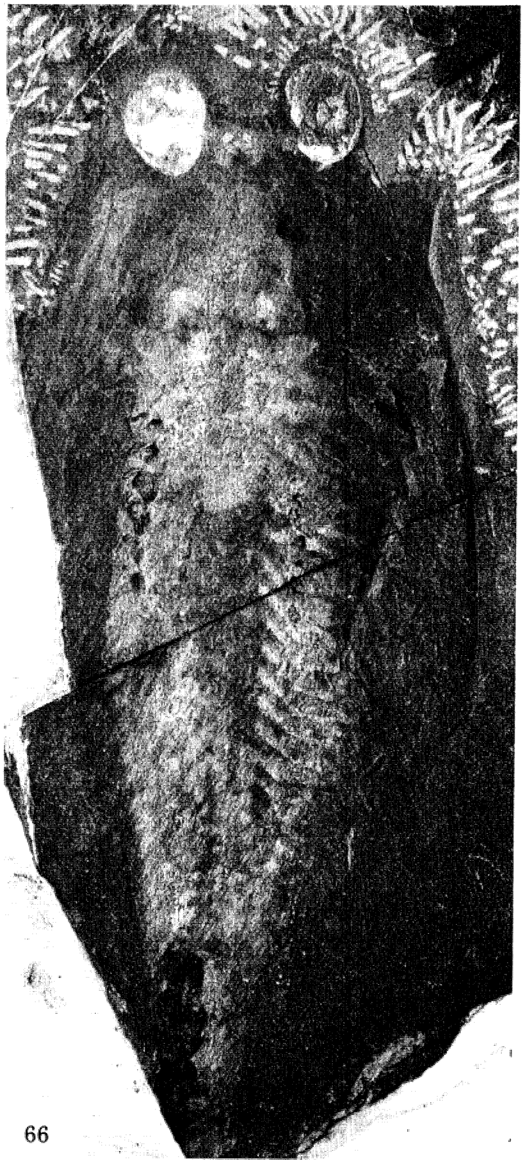
U.S.N.M. 189232, parallel

FIGURES 61–65. Explanatory drawings. (61) Specimen before preparation. Scale bar 5 mm. (62)–(65) Stages in preparation to reveal successive appendages anteriorly corresponding to figures 69–72. Scale bar 1 mm.

FIGURES 66 AND 67. Before preparation; reflected west, and north respectively. (Magn. × 3.)

FIGURE 68. On completion of preparation, northeast, right side of specimen. (Magn. × 3.)

FIGURES 69–72. North, stages in preparation to reveal successive appendages anteriorly, photographed under microscope; corresponding to explanatory figures 62–65. (Magn. × 6.)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FIGURES 66–72. For description see opposite.


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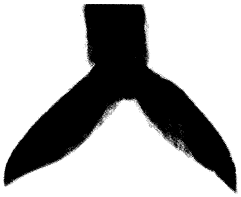
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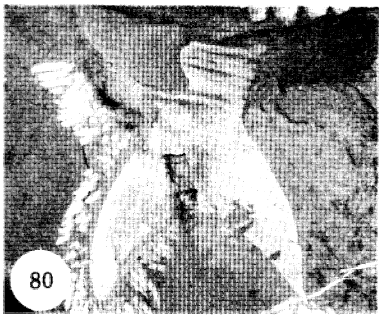
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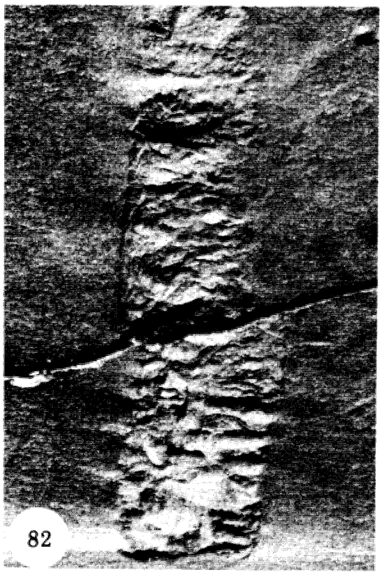
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Figures 73–82. For description see opposite.

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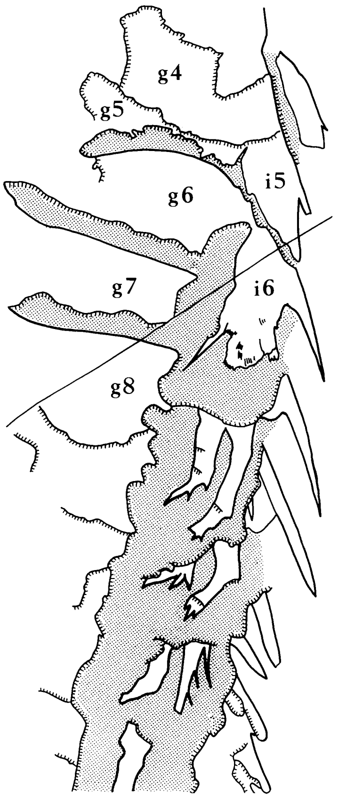

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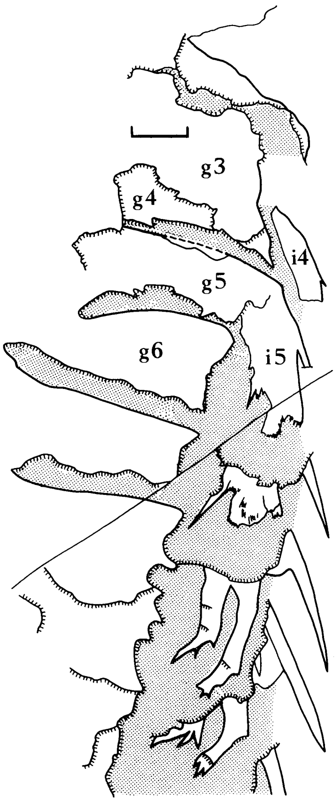

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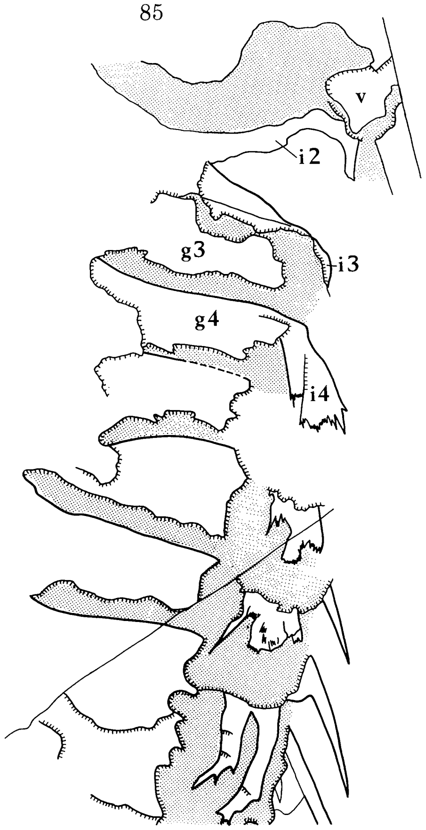

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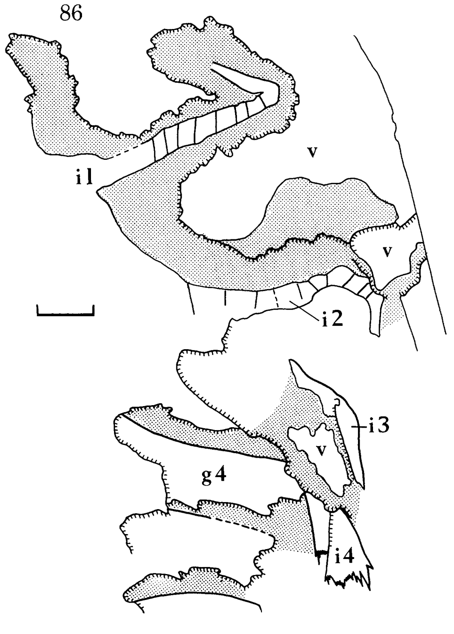

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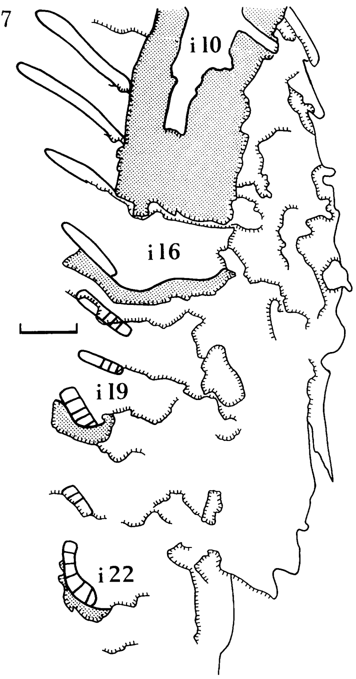

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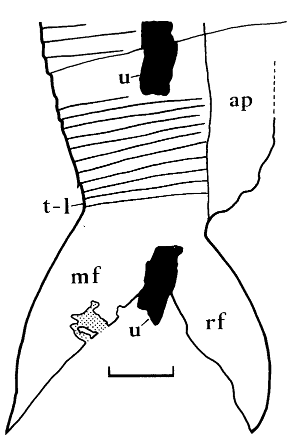

Description of plate 8 and figures 83–88

Odaraia alata Walcott, 1912

Figures 73–78. U.S.N.M. 189232, parallel. (73)–(76) Stages in preparation to reveal successive appendages anteriorly, corresponding to explanatory figures 83–86. (73)–(75) Photographed under microscope, north. (76) North-east. (77), (78) Preparation to reveal posterior (ventral) margin of inner rammi of posterior appendages proximally; northeast, and under glass, west, respectively, corresponding to explanatory figure 87. (Magn. ×6.)

Figure 79. Model of telson, 'group 3' orientation, see text.

Figures 80–82. U.S.N.M. 213813, parallel–oblique. (80) Counterpart, reflected west. (81) Part, reflected east, the carapace to the left is that of an overlying specimen of *Canadaspis perfecta*. (Magn. ×1.5.) (82) Part, north, gut contents. (Magn. ×8.)

Figures 83–88. Explanatory drawings. (83)–(87) U.S.N.M. 189232 stages in preparation to reveal appendages corresponding to figures 73–78. Scale bars 1 mm. (88) U.S.N.M. 213813, part, outline of right fluke added from counterpart. Scale bar 5 mm.


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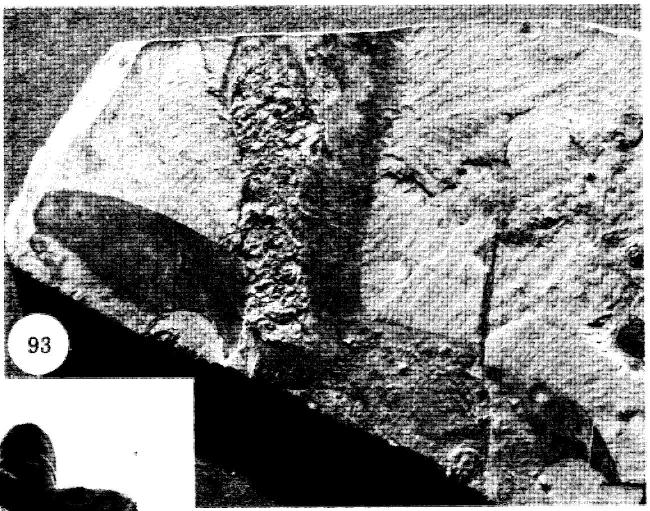
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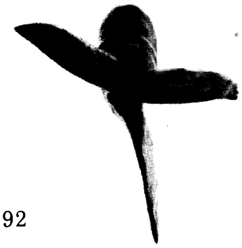
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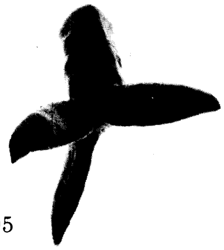
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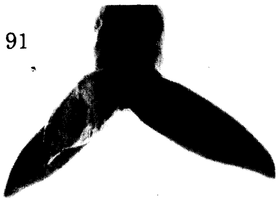
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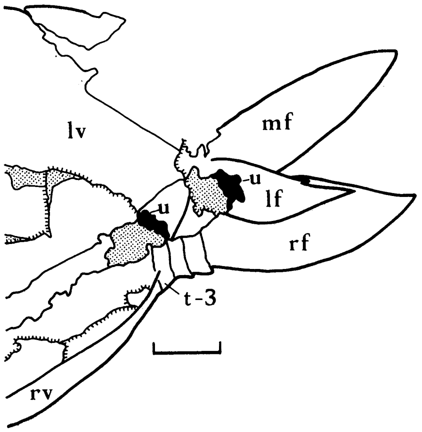
FIGURES 89–96. For description see opposite.



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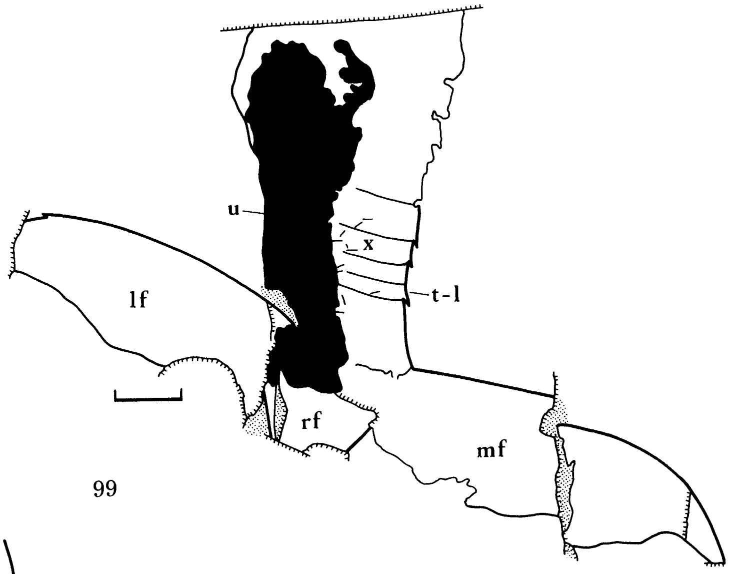

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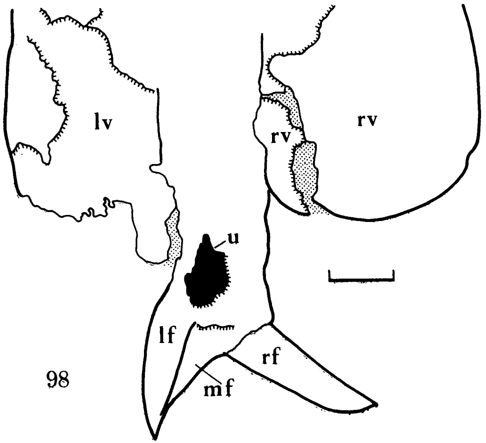

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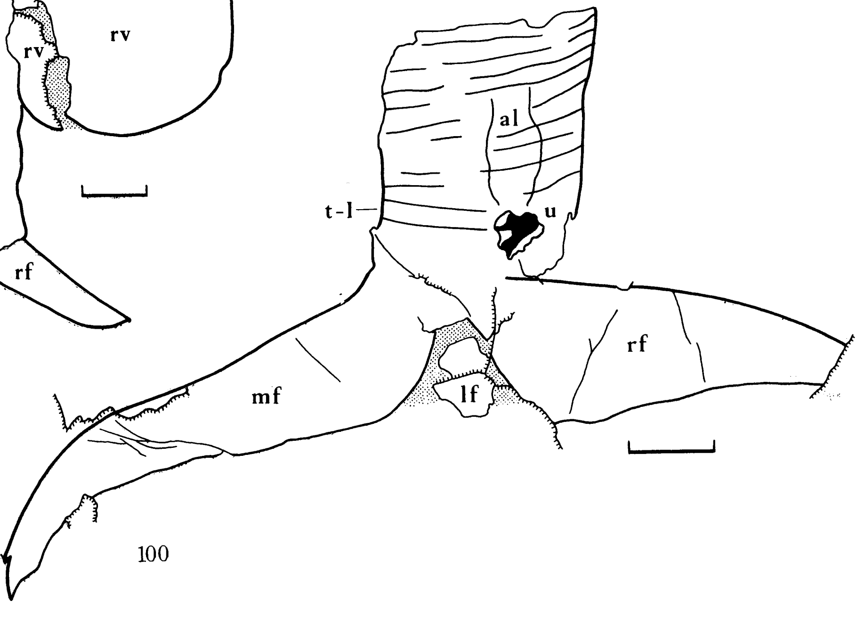

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Description of plate 9 and figures 97–100

Odaraia alata Walcott, 1912

Figure 89. U.S.N.M. 189229, lateral–oblique, reflected north. (Magn. × 1.5.)

Figure 90. U.S.N.M. 189237, parallel–oblique, northwest. (Magn. × 1.5.)

Figures 91, 92 and 95. Model of telson. (91) 'Group 2' orientation. (92), (95) 'Group 4' orientation. See text.

Figures 93 and 94. U.S.N.M. 241050, oblique. (93) Northwest. (Magn. × 1.5.) (94) Under alcohol, north, gut contents. (Magn. × 3.)

Figure 96. U.S.N.M. 213812b, oblique, northeast. (Magn. × 1.5.)

Figures 97–100. Explanatory drawings. (97) U.S.N.M. 189229, posterior. (98) U.S.N.M. 189237, posterior. (99) U.S.N.M. 241050, 'x' indicates ? sponge spicules. (100) U.S.N.M. 213812b. Scale bars 5 mm.

appendages at an angle of about 25° to the distal segments. This spine represents the maximum extension of the appendages laterally. It is clearly evident in appendages 5 to 12 and in 17, and ill defined traces may represent such spines as far posteriorly as appendage 21 or 22 (figure 67, plate 7). Distal to the attachment of this large spine, the inner ramus divides into two. This bifurcation is clearly preserved in appendages 7, 8 and 9 (figures 70–72, plate 7); the two branches diverge little, but are separated by matrix distally. More proximally the divide may be represented by a break of slope or scarp. Evidence for segmentation of the inner ramus is not clear. The part exposed proximal of the bifurcation in appendage 9 appears to be segmented. Reflective circular areas on the adaxial margin of appendage 8 may indicate segmentation beyond the bifurcation. The ramus is assumed to have been segmented throughout, but there is no indication of the nature of articulations between the joints. A graded series of smaller spines is preserved in appendage 9 (and less clearly 8) distal to the large spine at the geniculation and projecting posteriorly in a similar direction from the abaxial margin of the outer branch. Both branches of the inner ramus curve adaxially through 30 to 40° near their distal extremity, the outer extending a short distance further than the inner. The extremity is not well preserved, but one or two spines were evidently borne at the point of curvature, and both branches appear to have terminated in spines. The bifurcation is not evident in appendage 10, but the outline of the ramus is not very distinct and the division may be obscured by poor preservation.

The inner rami of appendages 3 to 6 (figures 73–76, plate 8) differ from those of 7 to 10 in that they terminate abruptly just distal of the large spine at the geniculation. Two factors suggest that this termination is real and not simply a result of poor preservation: (i) it is evident in at least three successive appendages; and (ii) the appendages appear to terminate in fine spines or setae. Some of these fine spines may be apparent rather than real, the result of a closely spaced lineation running obliquely across the specimen, but there is little doubt about the presence of a number of the most distal ones at least. Appendages 5 and 6 preserve evidence of a large posteriorly directed spine on the outer margin of the geniculum. There is no unequivocal evidence that the inner rami of these anterior appendages bifurcated, although a division may be represented by a break of slope on appendage 3.

Two appendages exposed anterior of the rest (figure 76, plate 8) lack any obvious trace of an outer lamellate ramus. The inner segmented rami project approximately normal to the margin of the body and extend laterally a similar distance to the appendages immediately succeeding them before flexing through over 90°, one anteriorly and the other posteriorly. It has not proved possible to prepare out the distal extremity of either, but the boundaries of at least 11 segments are just evident in reflected light and extrapolation suggests a total of about 15. The rami do not increase in width beyond the point of flexure in the manner of the more posterior appendages. There is no evidence that the segments bore spines. If these appendages bore similar outer rami to those of the succeeding limbs the rami should overlap them proximally. An ill defined area near the base of the second appendage might represent such a lamella, which could equally be preserved on the unknown counterpart. No outer lamella appears to have been associated with the first appendage, however, as removal of the overlying carapace failed to reveal it. This appendage originates about the posterior margin of the adductor muscle scars, and posterior of the impression of the mandible, the attachment thus coinciding with the suggested position of the boundary between the cephalon and trunk. Although the first two appendages are described with those of the trunk they could equally have belonged to the cephalon.

Only U.S.N.M. 202295, in addition to U.S.N.M. 189232, gives some indication of the morphology of the inner rami, but it is difficult to interpret in the absence of the counterpart. The configuration of the valves indicates a lateral–oblique orientation. The preservation of the inner rami above the outer near the posterior margin of the carapace (figures 18, 22, 23, plate 3) suggests that they represent the left series of limbs. The directions in which the rami overlap are consistent with this interpretation. Poorly preserved rami exposed anteriorly by removal of the carapace (figures 19, 20, plate 3) occur immediately beneath the valve and presumably represent the right outer rami. The appendages are poorly preserved; segmentation is only evident in reflected light (figure 23, plate 3) and the articulations between segments are not clear. The inner rami were similar in length to the width of the trunk and tapered gradually distally. The distal extremity is not sufficiently well preserved to permit description. There is evidence of at least eleven segments, but the proximal part of the appendages is obscured and extrapolation as far as a likely point of attachment to the body suggests that there may have been as many as six more, giving a total number similar to that in the inner rami of U.S.N.M. 189232. Each segment appears to have borne at least one pair of spines projecting normal to the axis a distance similar to the width of the ramus. The inner rami exposed in U.S.N.M. 202295 are clearly more posterior than those revealed by preparation of U.S.N.M. 189232. There is no unequivocal evidence that they bore the large lateral spines evident on the inner rami of U.S.N.M. 189232, nor that they were bifurcate. This may be a function of poor preservation or the result of compaction in a different orientation. Equally, there might be further differentiation of the inner rami posterior of those exposed in U.S.N.M. 189232. There is insufficient evidence to allow the cross section of the inner rami to be estimated.

The outer rami are also best preserved in U.S.N.M. 189232. Preparation of a number revealed the anterior margin (figures 73–75, plate 8) extending posterolaterally beyond the trunk at an angle of 70–80° to the body axis. This margin tends to be slightly concave proximally and convex distally. Neither the lateral nor posterior margins are preserved complete in U.S.N.M. 189232, and irregular splitting due to the compaction of successive rami together tends to obscure them in other specimens. The lateral margin appears to run roughly parallel to that of the trunk and the broken posterior margins preserved in U.S.N.M. 189232 suggest, like the poorly preserved outline of the outer rami revealed by removal of part of the carapace of U.S.N.M. 189231 (figure 11, plate 2), that the posterior margin of the ramus was convex. The rami thus appear to have been roughly semicircular in outline, the width (transverse to the trunk axis) exceeding the length (parallel to the axis) by a factor of about 2. This factor (2) may be slightly exaggerated by foreshortening due to compaction at an angle to the bedding. No indication of the detailed morphology of the outer rami has been observed, but there is no evidence that they changed in character posteriorly along the trunk.

An unusual preservation of the appendages in R.O.M. 38398 (figures 48–50, plate 6; in parallel aspect) merits specific comment. Most of the appendages are obscured by an irregular mass of dark material which consists of apatite with a trace of quartz (apatite is absent from other areas of the specimen and matrix). On splitting of the slab, some of this mineral has been retained on the part, some on the counterpart. The mineral is apparently identical to that associated with the alimentary canal of many Burgess Shale arthropods (see § 5*g*). It may not follow the original course of the canal precisely; the walls often ruptured, the released organic material leading to mineralization in an irregular area flanking the gut (figure 22, plate 3). In R.O.M. 38398, however, the mineralization does not follow any obvious gut trace, and occurs in two separate longitudinal bands rather than a single one. Although the bands do not flank the midline (the body seems to be displaced to the left of the carapace hinge line) they are apparently associated with the overlapping outer rami, traces of which are evident posteriorly. A regular arrangement of mineralized strips transverse to the axis is well displayed on the right side of the trunk, particularly on the counterpart. This regularity is apparently reflected in similarly spaced transverse ridges on the left, although the mineralization is more continuous longitudinally. The normal association of the mineral obscuring the outer rami of R.O.M. 38398 with the gut in other specimens is presumably due to a local concentration of organic material. Its formation in the vicinity of the appendages in this specimen suggests that the arthropod was buried while actively feeding and that organic material trapped between the appendages and confined by the tubular carapace gave rise to a similar concentration.

The contrasting directions of overlap of the two rami and the flexure of the inner ramus posteriorly in U.S.N.M. 189232 (figures 66–68, plate 7) suggest that the appendages were buried in a similar attitude to that illustrated by Whittington (1980, p. 190, text fig. 7) in *Olenoides*, although the inner rami of *Odaraia* show a pronounced geniculation. The outer rami were borne dorsal of the inner and therefore did not hang vertically as in *Branchiocaris* (Briggs 1976, fig. 2a). The contrast between the preservation of the inner rami of U.S.N.M. 202295 (figures 22, 23, plate 3), in lateral–oblique aspect, which project at an angle of about 60° to the axis, and those in U.S.N.M. 189232, in parallel aspect, which curve through 90° to extend parallel to the trunk, suggests that the appendages of the latter were rotated posteriorly before burial just as they commonly are in *Olenoides* (Whittington 1975*b*, p. 104, 1980, text fig. 7, pl. 20, figs 1–4). Thus the outer rami of U.S.N.M. 189232 may be foreshortened, but the relative positions of the margins (anterior, lateral and posterior) probably correspond to those in life. The inner rami presumably originally extended laterally and then curved ventrally normal to the trunk. The appendages are not sufficiently well preserved to provide any indication of the nature of movement about the appendage–body junction (cf. *Canadaspis perfecta*; Briggs 1978, p. 463). They presumably moved in a metachronal rhythm, but their preserved relative positions do not provide evidence to confirm this.

(*e*) *Reflective traces in the trunk*

A series of reflective traces is preserved in association with the appendages of U.S.N.M. 189232 (figure 66, plate 7). The traces are most obvious on the right of the trunk in somites 7–16. They originate on a line running along the trunk parallel to the lateral margin and adaxial of the appendages. They extend posteriorly at an angle of about 30° to this line before curving more normal to it to traverse the outer rami of the appendages. These serially repeated reflective traces correspond in number and spacing to the limbs. Anteriorly they are less clearly defined in somites 1–5, but the line along which they originate is preserved as a continuous reflective lineation. This feature, which originates just posterior of the adductor muscle scars, is much less obvious between somites 6 and about 16. The reflective traces are evidently paired; similar poorly preserved features are evident on the left side. In the posterior part of the trunk the lineations merge medially to some extent and details are difficult to distinguish (this merging tends to be more obvious in ultraviolet than in ordinary reflective light). Posterior to appendage 16 the traces appear segmented where they cross the proximal part of the appendages. Selective removal of overlapping appendages (where there was sufficient matrix between them to allow this) to reveal the posterior margin of the inner rami of 16, 19 and 22 (figures 77, 78, plate 8) indicates that the reflective traces follow the posterior (i.e. ventral) margin of these rami. Anterior of appendage 6 the inner rami are overlain by the outer rami. The reflective traces are preserved, however, traversing the outer rami medially along a line normal to the trunk axis which would coincide with the posterior margin of the inner ramus beneath. The traces tend to coincide with a slight linear depression, but this is presumably the result of compaction along the margin of the inner ramus which is followed by the trace.

Reflective traces also occur associated with the appendages of a number of other specimens, but the preservation is poor and details cannot be discerned. It is probable that poorly defined segmentally arranged traces in U.S.N.M. 213807 (figure 33, plate 4) indicate the position of the appendages, but what features are reflective is unknown. Reflective traces in the small area of appendages remaining in U.S.N.M. 189236 (figures 31, 32, plate 4) appear to be segmentally arranged, but they merge axially and their relation to the limbs is not clear. In U.S.N.M. 189235 (figure 36, plate 4) some of the surface of the outer rami is completely reflective and any internal details would thus be obscured. The nature of ill defined traces running transverse to the axis at about the midlength of U.S.N.M. 213809 (figure 5, plate 1) is not clear; small patches of reflective material occur across the entire specimen. Reflective traces do, however, appear to be associated with 'nodes' in U.S.N.M. 189231 (figures 10, 12, 13, plate 2), particularly on the left side of the anterior part of the trunk, and also possibly in U.S.N.M. 213812a (figure 43, plate 5), although in this specimen it is difficult to distinguish them from somite boundaries. This may not imply any direct association with the 'nodes', however, as both features were segmentally arranged.

The nature of the reflective traces is unknown. They are dissimilar in their position and lack of relief to the segmented 'proximal element' associated with the lamellate appendages of *Branchiocaris pretiosa* (Briggs 1977, p. 10). In other arthropods similar reflective traces to those in *Odaraia* have been interpreted as evidence of muscles (*Canadaspis perfecta*; Briggs 1978, p. 460, 470). Segmentally arranged nodes also occur in *C. perfecta*, but although it was suggested that 'they may represent points of muscle attachment' (Briggs 1978, p. 460) no relation between them and the reflective traces was observed. Other organ systems seem less likely candidates for preservation as reflective traces of this nature. The nervous system might have been ladder-like as in some Branchiopoda, accounting for the pair of longitudinal traces flanking the trunk adaxial to the appendages (figure 66, plate 7). It would, however, be expected to show an obvious expansion in the cephalic region, where only tenuous traces are preserved, and the nerves connecting to the appendages would hardly be as substantial as the traces suggest. The blood system would also presumably have taken the form of a longitudinal structure with lateral extensions into the appendages, but the heart is unlikely to have been paired as the traces suggest. If the reflective traces do indeed represent muscles, and this is by no means certain, the longitudinal strands may indicate the position of the dorsal or ventral longitudinal muscles, and the traces extending to the appendages the extrinsic limb muscles (cf. *Hutchinsoniella*; Hessler 1963, fig. 3).

(*f*) *Telson*

The anterior margin of the telson in the only well preserved specimen in lateral aspect, U.S.N.M. 189233 (figures 37, 38, plate 5), clearly inserts into the posteriormost trunk somite, the dorsal and ventral margins of the telson anterior of the flukes forming an extension of the gradually tapering outline of the trunk. The lateral flukes are preserved each extending almost exactly the same distance posteriorly (measured along the axis of the trunk). The preservation of the right fluke, underlying and ventral to the left, indicates a slightly oblique compaction; the specimen affords a 'ventrolateral' view. The lateral flukes are clearly foreshortened compared to their configuration in parallel aspect. The ventral margin of each is essentially straight proximally with a slight concavity at the distal extremity. This serves to identify it as the posterior margin in parallel aspect (cf. figure 43, plate 5). The dorsal margin (seen only on the left fluke) is also straight proximally, making an angle of about 17° to the trunk axis, but convex distally, where it curves to meet the ventral margin in a point; this confirms that it is the anterior margin in parallel aspect. It is not possible to determine with confidence the angle at which the lateral flukes were inclined to the horizontal due to the lack of specimens preserved in precisely lateral aspect. The high inclination suggested by the left fluke of U.S.N.M. 189233 (about 75°) is at least partly a function of the oblique compaction, which gives the telson a 'ventrolateral' aspect, and also of the attachment of the flukes along a line converging posteriorly with the sagittal axis (figure 5, plate 1). The flukes may have projected in a plane horizontal relative to the axis or tilted slightly posteriorly.

The median dorsal fluke of U.S.N.M. 189233 (figures 37, 38, plate 5) extends some 40% further posteriorly along the axis (measured from the anterior margin of the telson) than do the lateral flukes. The anterior margin is a smooth gently convex curve broken only by a small spine, an extension of the margin, near the distal extremity. The posterior margin is poorly preserved. The fluke projects a distance vertically, similar to the height of the telson anteriorly, and is directed posterodorsally at an angle of about 40° to the axis of the trunk. A small irregular positive feature at the base of the flukes appears to be continuous with the gut trace and may represent the anus. The flukes of U.S.N.M. 189229 (figure 89, plate 9) are preserved in a similar configuration to those of U.S.N.M. 189233, but most of the carapace is lacking and the near lateral orientation cannot be confirmed. The dorsal margin of the left fluke preserves a small spine projecting from it distally which identifies it as the anterior margin in parallel aspect. This margin is slightly concave distally rather than convex and the ventral (posterior) margin is gently convex throughout, lacking the slight concavity at the extremity preserved in U.S.N.M. 189233. These differences can be explained by a slight flexure of the tips of the flukes. The gut trace in U.S.N.M. 189229 extends to the base of the flukes.

The telson is preserved, in part at least, in 79% of the known specimens, but only two give a clear indication of its configuration in parallel aspect. U.S.N.M. 213812a (figures 42, 43, plate 5) affords a ventral view. The anterior margin of the lateral flukes is slightly concave at the proximal extremity but becomes straight for about half its length, inclined to the axis at 63° and 67° in the left and right flukes respectively, and then curves gently convexly to the distal point. Near the distal end two short spines project from the margin. The posterior margin of the flukes is more irregular and less clearly defined. At the proximal end it extends a short distance posteriorly, making an angle of about 18° to the axis, but then curves through about 55° to form a gently convex margin throughout most of its length. Toward the distal end it becomes irregularly concave. The median fluke projects dorsally in the vertical sagittal plane, extending 48% further posteriorly along the axis (measured from the anterior margin of the telson) than the lateral flukes. The configuration of the dorsal fluke in parallel aspect gives an indication of the outline of the flukes in cross section. The fluke is widest at the proximal end and tapers rapidly and then more gradually to a point. The slight asymmetry of the trunk and telson in U.S.N.M. 213812a is due to a downward tilt toward the left of the slab (as viewed), which presumably slightly exaggerates the apparent width of the median fluke in cross section. The incomplete counterpart shows the effect of this tilt on the left fluke, which is foreshortened, and shows crumpling transverse to the fluke axis. An isolated trace of the gut fill in the central part of the telson may represent the approximate position of the anus. U.S.N.M. 213809 (figure 5, plate 1) is also preserved in parallel aspect. The convexity of the anterior margin of the flukes is less pronounced distally than in U.S.N.M. 213812a and that of the posterior margin is more so. The slight distal concavity of the posterior margin is, however, less obvious. The anterior margin of the lateral flukes is inclined to the axis at 63° and 69° respectively. The median fluke extends only 34 % further beyond the anterior margin of the telson than do the lateral flukes. These slight differences are presumably a reflection of exact orientation bedding, except for the configuration of the tips of the flukes, which appears to indicate a degree of distal flexibility.

The preservation of the anterior and posterior margins of the flukes differs in most specimens. The anterior margin is continuous, smooth and clearly defined whereas the posterior is uneven (on a fine scale) and less distinct. This suggests that the flukes thinned posteriorly, and it facilitates the recognition of the anterior and posterior margins in specimens preserved in intermediate orientations where the distinction may not be clear.

The specimens preserved in lateral and parallel aspects provide a basis for a reconstruction of the telson. Difficulties arise, however, in interpreting specimens preserved in other orientations: is the variation simply a function of orientation to the bedding or does it reflect changes in the attitude of the flukes to the trunk, implying that they articulated proximally? The morphological evidence for the presence or absence of articulations at the base of the flukes is inconclusive. The obvious approach to this problem is to make a three-dimensional reconstruction, and to compare the result of compacting it in a variety of orientations to the bedding with the preserved specimens. This was achieved by modelling the telson and photographing it in different orientations to the plane of the camera. The three-dimensional model is thus projected onto a two-dimensional surface and the configuration produced is comparable with that resulting from flattening within sediment, on the assumption, as demonstrated by Whittington (1975*a*, pp. 5–7), that no lateral expansion occurred. In addition to those preserved in parallel and lateral aspects (figures 44, 39, plate 5), the specimens fall into four groups on the basis of orientation to the bedding.

(i) U.S.N.M. 189238, 189239 (figures 52, 53, plate 6; figure 7, plate 2)

These specimens preserve two flukes in outline, their anterior margins making an angle not exceeding 63° with the axis. One fluke expands considerably before tapering distally, the other is more parallel sided. The counterpart of U.S.N.M. 189238 preserves the third fluke projecting between the other two at a slightly different level. This fluke is preserved in outline, the convex margin displaced to one side, more or less in line with the margin of the trunk. It is presumably buried in the matrix of the incomplete counterpart of U.S.N.M. 189239. This configuration is achieved by considering the model in parallel aspect, dorsal view, and rotating it slightly to one side or other about the sagittal axis. A slight rotation about an axis normal to the sagittal is then necessary to adjust the degree to which the dorsal fluke extends posteriorly beyond the lateral (figure 51, plate 6). The angles between the flukes and the axis are most nearly approached if the dorsal fluke is that preserved between the other two. The normal relation of trunk (and telson) and carapace has obviously been distorted in U.S.N.M. 189239 during burial and compaction. The carapace is clearly folded around the body, but the position of the hinge line and ventral margin of the valves is not clear.

(ii) U.S.N.M. 189236, 189237 (figure 31, plate 4; figure 90, plate 9)

In these specimens, of which U.S.N.M. 189236 is the best preserved, one fluke projects laterally from the telson. Its anterior margin, which is gently convex, makes an angle of about 63° with the trunk axis; the posterior margin shows a more pronounced convexity. The other lateral fluke projects posteriorly to one side of the midline, extending further than the dorsal fluke, which is superimposed upon it. The convex anterior margin is preserved abaxial of the concave posterior one; the latter is approximately coincident with the margin of the dorsal fluke, from which it cannot readily be distinguished. Where the carapace is preserved the hinge line is displaced to the same side of the midline as the dorsal fluke. This configuration is achieved by considering the model in dorsal view, and rotating the trunk to one side about the sagittal axis through an angle greater than in group 1 so that the dorsal and left flukes overlap. To reach the configuration of U.S.N.M. 189236 the model must then be tilted down anteriorly so that the left fluke appears to extend further posteriorly than the dorsal (figure 91, plate 9). This downward tilt is borne out by the preservation of the anteroventral margin of the right valve slightly anterior to that of the left valve.

(iii) U.S.N.M. 189231, 213813 (figure 10, plate 2; figures 80, 81, plate 8)

These specimens are characterized by a symmetrical arrangement of two flukes about the midline, their anterior margins making angles of less than 50° with the axis of the trunk. This low angle indicates that one of the flukes is the dorsal; in specimens that preserve the lateral flukes arranged symmetrically about the midline (in parallel aspect) their anterior margins are inclined to the axis at angles in excess of 60° (figure 5, plate 1). U.S.N.M. 189231 preserves the right fluke projecting between the dorsal and left at a slightly lower level. This configuration is achieved by considering the model in dorsal view and rotating it about the sagittal axis through an angle intermediate between that in group 2 (above) and 90° (lateral aspect) so that the dorsal and one lateral fluke are symmetrically arranged about the midline (figure 79, plate 8). The third fluke is not evident in U.S.N.M. 213813 and is presumably concealed within the matrix of the part.

Odaraia tends to be preserved with the long axis parallel to the bedding. In view of this, and the tubular nature of the carapace, it is not surprising that most of the preserved configurations of the telson can be explained by differing rotations about the sagittal axis. Thus groups 1 to 3 above represent rotation about this axis from a parallel orientation through 5–10° (figure 51, plate 6), about 25° (figure 91, plate 9) and about 55° (figure 79, plate 8) respectively, the spectrum being completed by specimens in lateral aspect (a rotation of 90° from parallel). Tilting of the long axis must also be taken into account in explaining some of these configurations, but it is of secondary importance.

(iv) U.S.N.M. 213812b, 241050 (figures 96, 93, plate 9)

These specimens are characterized both by a high angle between the anterior margin of the two flukes preserved in outline and the sagittal axis and by a large difference in the value of these two angles. In U.S.N.M. 213812b the angles are 57° and 89° respectively; in U.S.N.M. 241050, 77° and 128°. In specimens preserved in parallel aspect these angles do not exceed 70°, nor does the difference between them exceed 6°. High values occur at orientations approaching vertical to the bedding. Such configurations are achieved if the model is viewed from the posterior in vertical aspect and tilted upwards anteriorly and rotated to the left for U.S.N.M. 213812b (figure 95, plate 9) and to the right for U.S.N.M. 241050 (figure 92, plate 9). In both the gut contents are preserved as expected on the opposite side of the trunk to the dorsal fluke. It is probable that such a near vertical orientation was more easily achieved by incomplete specimens like U.S.N.M. 213812b, which includes only the telson and a small number of somites.

The investigation of the preservation of the telson has shown that differences between specimens can be explained, in general at least, by simple variations in orientation to the bedding rather than by movement of the flukes about a proximal articulation. There is no unequivocal evidence of articulations at the base of the flukes, nor is there any indication that their relative attitudes altered significantly in life. Slight variation in the attitude of the tip of the lateral flukes is indicated by the curvature of the margins of the fluke distally (contrast figure 5, plate 1 and figures 42 and 43, plate 5, for example). This is probably the result of a slight flexibility of the fluke, particularly distally, which is borne out by crumpling in some specimens (figures 42, 43, plate 5) of what was evidently thin cuticle. U.S.N.M. 188630 (figures 54, 55, plate 6) preserves a number of apparently evenly spaced faint relief traces that are suggestive of segmentation, traversing a fluke roughly normal to its axis. Similar traces, however, are clearly the result of folding due to compaction at an angle to the bedding in other specimens (left fluke of U.S.N.M. 213812a, figures 42, 43, plate 5, for example). No specimens are known where the flukes clearly articulate along their length or are broken transversely, and it is therefore considered unlikely that they were segmented.

(*g*) *Alimentary canal*

The gut is preserved in a variety of ways, but only the narrow relief trace, preserved through part of the length of U.S.N.M. 213813 (figures 80–82, plate 8), is likely to reflect its true diameter as the canal walls appear to be intact. It reaches a maximum width of 2.5 mm in this specimen, about 26 % of that of the trunk (excluding the appendages that extend beyond it). The lack of evidence of the posterior course of the gut in U.S.N.M. 213813 is presumably due to the absence of any content in this section. The gut is more usually preserved as a discontinuous inhomogeneous relief trace of relatively greater but variable width, implying that the canal walls have decayed and the contents migrated laterally into the body cavity (figure 22, plate 3; figures 93, 94, plate 9). The course of the gut may also be indicated by a tenuous, reflective trace (figure 33, plate 4) which may be continuous with an incomplete relief trace (figure 36, plate 4; figures 37, 38, plate 5).

A number of specimens show evidence of the gut within the telson, indicating the position of the anus in the midline near the posterior end of the base of the flukes (figures 37, 41, 43, plate 5). Only U.S.N.M. 189233 (figures 37, 38, plate 5) shows the course of the alimentary canal in lateral aspect and the evidence is confined to the posterior part of the trunk. The canal runs more or less along the axis of the trunk, but is directed slightly dorsally from the anus to the anterior margin of the telson and then slightly ventrally in the posterior ten preserved trunk somites. The most complete evidence for the course of the canal in parallel aspect is provided by U.S.N.M. 189235 (figure 36, plate 4) in which an incomplete relief trace, supplemented by reflective sections, indicates that it extends along the midline throughout the length of the trunk. There is no evidence of diverticula, unless the dark features extending laterally in the central part of the trunk of U.S.N.M. 213809 (figure 5, plate 1) represent extensions of the gut rather than appendages. The position of the mouth and the course of the alimentary canal in the head are discussed in § 5*a*.

The posterior part of the preserved relief trace in U.S.N.M. 213813 (figure 82, plate 8) shows regular transverse annulations on the upper and lower sides of the canal wall (as compacted) which are more closely spaced than the inter-somite boundaries. These may represent circular muscle fibres. Similar, but slightly more closely spaced annulations, are present in the fragments of the gut scattered in the anterior part of the trunk of U.S.N.M. 202295 (figures 18, 22, plate 3).

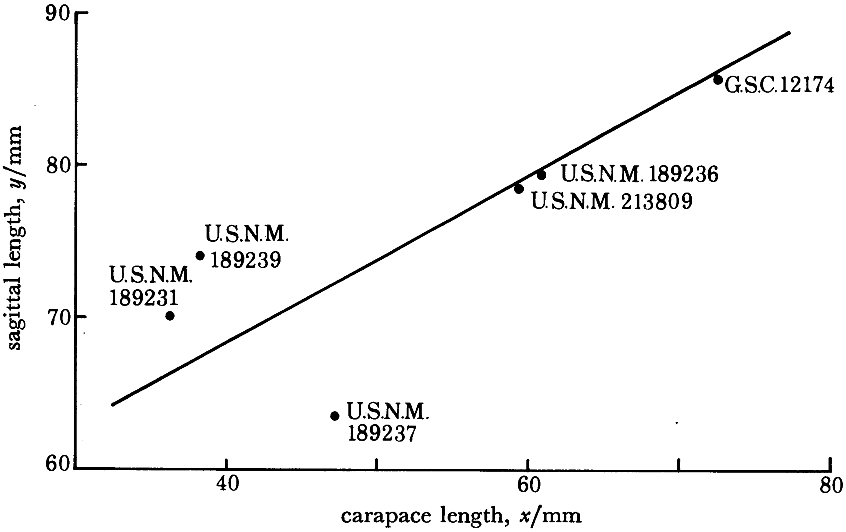

Figure 101. Plot of carapace length of *Odaraia alata* against total sagittal length. Solid line represents reduced major axis. Specimens identified by catalogue numbers. Bivariate statistics, x/y: mean x (var. x) = 52.45 (170.14); mean y (var. y) = 75.2 (51.08); a (var. a) = 0.55 (0.02); r = 0.78; N = 6; axis $y = 0.55x + 46.35$.

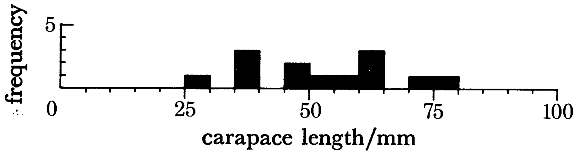

Figure 102. Size-frequency histogram of carapace length of specimens of *Odaraia alata* from the Walcott Quarry plotted in 5 mm intervals (mean 52.6, var. 248.0, N = 13).

Similar annulations were figured by Simonetta (1970, pl. 15, fig. 2*c*) and Simonetta & Delle Cave (1975, pl. 29, fig. 1*c*) in the gut of *Leanchoilia superlata*, but were erroneously interpreted (Simonetta 1970, p. 38) as features of an ingested polychaete. Posterior of the adductor muscle scars in U.S.N.M. 213809/G.S.C. 11537 (figures 5, 6, plate 1) a structure with substantial relief is preserved in the midline continuous with the dark, reflective gut trace. The surface is covered with regularly spaced ridges separated by narrow grooves similar in scale to the annulations on the alimentary canal of other specimens, but traversing the feature oblique to the long axis. A similar swollen part of the gut occurs in about the same position in U.S.N.M. 202295 (figures 18, 22, plate 3), suggesting that it may represent a distinct section of the alimentary canal, possibly the stomach. The ridges may represent a masticatory apparatus similar to that in the Leptostraca (Cannon 1960).

The core of the 'stomach' in U.S.N.M. 213809/G.S.C. 11537 (figures 5, 6, plate 1) is composed of the hard, black apatite characteristic of the gut contents of *Odaraia* (cf. Conway Morris 1977, p. 26). The mineral is soft in U.S.N.M. 202295 (figures 18, 22, plate 3) and has a fibrous appearance possibly due to weathering. Sediment may be preserved adhering to it in some specimens (U.S.N.M. 213813, figures 81, 82, plate 8) but is part of the layer above. Part of the gut trace of U.S.N.M. 213813 includes a smoother area traversed by irregular, closely spaced ridges running mainly transverse to the axis. These appear to differ in character from the annulations and ridges described above and may reflect the gut contents. A small number of mainly straight linear structures up to 1 mm long are evident, scattered within an otherwise unidentifiable mass of black granular material in the gut of U.S.N.M. 241050 (figures 93, 94, plate 9), which has expanded laterally, presumably due to the decay of the canal walls. Similar features, which may represent sponge spicules, are preserved in negative relief outside the gut, suggesting that they were superimposed onto the cuticle rather than compacted through it. It is therefore probable that their association with the gut contents is fortuitous and they were not part of the arthropod's diet.

(*h*) *Morphometrics*

The maximum length of the carapace parallel to the hinge is considered the most reliable indication of the overall size of *Odaraia*; distortions are readily recognized and measurements, which are made in a straight line, approach the true dimension in the usual orientations to the bedding. It is rarely possible to measure total sagittal length as a high proportion of specimens are incomplete, and this dimension may be distorted by flexing or telescoping of the trunk (cf. *Canadaspis*; Briggs 1978, p. 475). The six specimens in which both carapace length and total sagittal length can be measured, however, show a significant correlation between these dimensions (figure 101; $r = 0.78$, significant at the 5% level) as expected. Only 13 of the specimens are suitably preserved to provide data for a size–frequency histogram of carapace length (figure 102). The data show a scatter between 25 and 80 mm, but the sample is insufficiently large to determine whether or not the distribution is bimodal (cf. *Canadaspis perfecta* (Briggs 1978, fig. 177) and *Marrella splendens* (Whittington 1971*a*, p. 1195), for example). The plot of the reduced major axis (figure 101) implies a total sagittal length of about 90 mm in specimens with a carapace approaching 80 mm long (U.S.N.M. 213810). The preserved section of the incomplete specimen U.S.N.M. 213812a (figure 43, plate 5), however, is 98 mm long and a comparison of the dimensions of the telson flukes with those of U.S.N.M. 213809 (figure 5, plate 1) indicates a total sagittal length of about 150 mm. The fragmentary specimens U.S.N.M. 241050 (figures 93, 94, plate 9) and R.O.M. 34307 may also have approached this length. Thus *Odaraia* is one of the largest Burgess Shale arthropods, approaching the sizes reached by *Sidneyia* and *Helmetia* (Briggs 1979, p. 656).

The slope of the reduced major axis implies a relative increase of the length of the carapace with growth, but this cannot be considered a reliable inference in view of the very small number of readings available.

6. DISCUSSION

(*a*) *Previous research*

Walcott's (1912, p. 188) original description of *Odaraia alata* was based on 'several specimens of the valves' collected in the field seasons of 1910 and 1911, but he reported that 'unfortunately all of them are more or less crushed and distorted' and this is borne out by the poor preservation of the holotype (figures 2, 3, plate 1), the only specimen that he figured (1912, pl. 34, fig. 2). Walcott noted that *Odaraia* had 'several cercopods attached to the last abdominal segment' (1912, p. 159) and correctly observed the presence of two exposed on the holotype (p. 188).

Størmer (1944, p. 101) added nothing to Walcott's account except to suggest that *Odaraia* 'might yet have had trilobitan appendages'. He mentioned, however, examining a specimen of the genus *Portalia* in Walcott's collections 'which has indications of gill-blades on the appendages'. A number of specimens of *Odaraia* in the U.S.N.M. collections were labelled *Portalia alata* and it was one of these, probably U.S.N.M. 189232 (figures 66, 67, plate 7), to which Størmer was referring. These specimens bear no relation to the species *Portalia mira*, which Walcott figured in 1918 (Briggs 1976, p. 12). Rolfe (in Moore 1969, p. 327) figured a line drawing of the holotype of *Odaraia*. The 'oblique posterior truncation' of the carapace noted in his descriptive diagnosis of the genus is the result of the orientation of that specimen to the bedding; the true outline is convex posteriorly.

The only study of *Odaraia* based on an extensive examination of additional specimens published since Walcott's (1912) original description is that of Simonetta & Delle Cave (1975). The present investigation, however, has shown that Simonetta & Delle Cave's account is in error in a number of ways. These, taken in the order in which they appear in their brief description (1975, pp. 13, 14), are enumerated below. In each case the evidence for the new interpretation is discussed in detail in the appropriate section of the description above.

(i) Simonetta & Delle Cave observed that 'the margins of the carapace touch each other ventrally for a considerable length', but incorrectly stated that 'the carapace appears to have no dorsal hinge'.

(ii) They noted the presence of two of the 'flat, unsegmented cerci' attached to the telson, but failed to include the median third one in their reconstruction (Simonetta & Delle Cave 1975, pl. 3, fig. 6a, b).

(iii) They recorded '30 to 35 postoral body segments', whereas the evidence suggests a variation between about 28 and 47.

(iv) They stated that only the first 25 of these body segments bore appendages, whereas it is clear that all of them did.

Simonetta & Delle Cave (1975, p. 13, pl. 53, fig. 4) figured U.S.N.M. 189228 (figure 40, plate 5) as *Protocaris pretiosa*, but the counterpart clearly preserves one of the flat broad flukes characteristic of *Odaraia alata* (Briggs 1976, p. 16).

In addition, Simonetta & Delle Cave (1975, p. 14) described five specimens identified herein as *Odaraia alata* as a separate genus and species *Eurysaces pielus*. This is said to be similar to *Protocaris* (i.e. *Branchiocaris* Briggs, 1976) and differs from *Odaraia* in the presence of a dorsal hinge, a much shorter carapace and rather broader laterally projecting 'cerci'. It is also considered to lack appendages on the somites extending beyond the valves. Simonetta & Delle Cave (1975, p. 14) noted that '5 specimens referable to this new taxon have been identified'. Their list of plate and specimen numbers, however, indicates that two counterparts are included in this number and only three different specimens, U.S.N.M. 189239 (figures 7–9, plate 2), 189233 (figures 37, 38, plate 5) and 189238, (figures 52, 53, plate 6) are concerned. The reconstruction of the telson was apparently based on the part of U.S.N.M. 189238 (figure 52, plate 6) that, like U.S.N.M. 189239, belongs to telson 'group 1' above. The configuration of the 'cerci' differs from other specimens referred to *Odaraia* by Simonetta & Delle Cave as a result of orientation to the bedding. The third (median) fluke is omitted from their reconstruction (Simonetta & Delle Cave 1975, pl. 3, fig. 7) although it is evident in addition to the lateral fluke in their figure of the counterpart of U.S.N.M. 189238 (figure 53, plate 6; Simonetta & Delle Cave 1975, pl. 52, fig. 9*a*). The presence of a hinge line in *Eurysaces* is not disputed herein, but it does not differ in this respect from *Odaraia* as asserted by Simonetta & Delle Cave. U.S.N.M. 189233 (figures 37, 38, plate 5) is incomplete anteriorly and the relative length of the carapace cannot be assessed. Only ten somites extend posteriorly beyond the valves, however, compared to 15 reconstructed in *Eurysaces* (Simonetta & Delle Cave 1975, pl. 3, fig. 7).

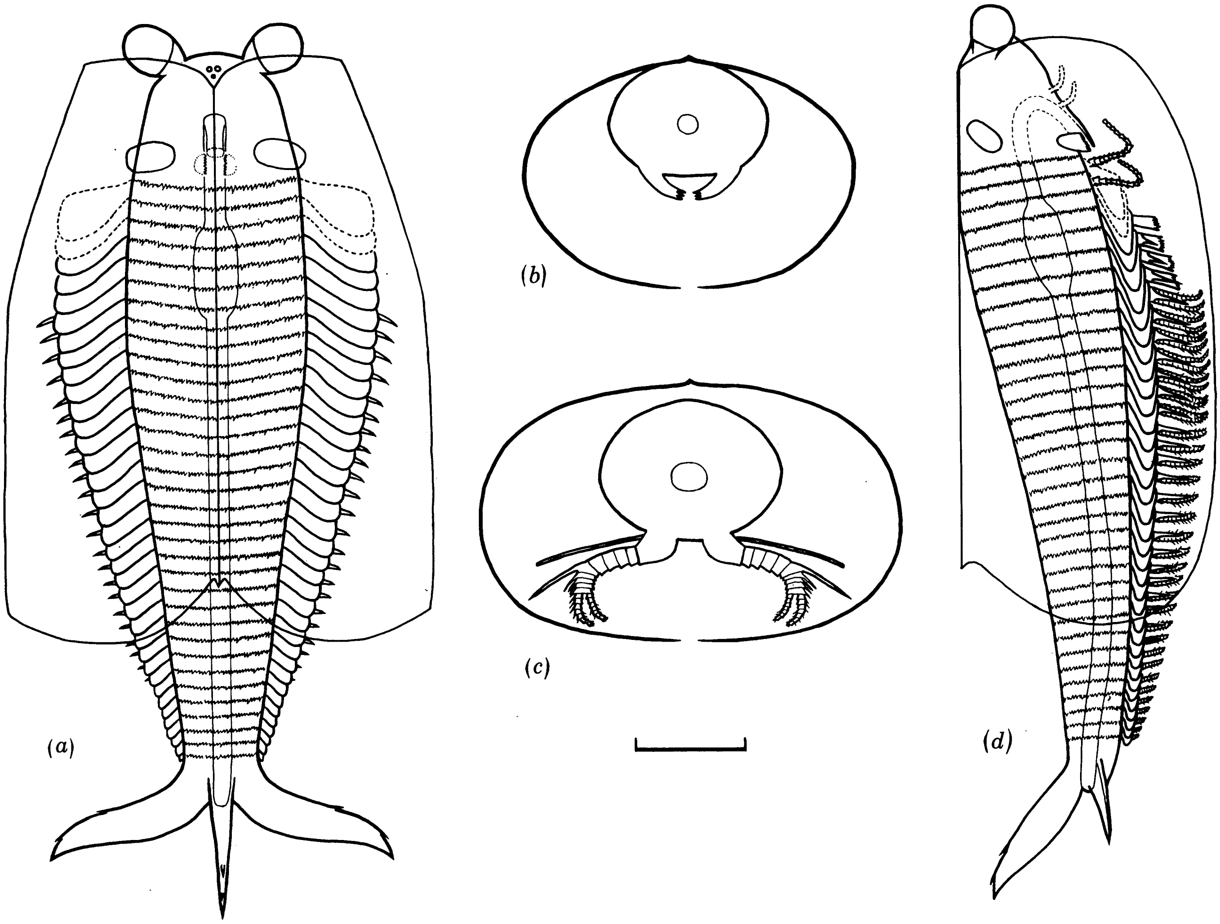

FIGURE 103. Diagrammatic reconstructions of *Odaraia alata* Walcott, 1912. Scale bar 10 mm.

(*a*) Dorsal view, carapace and adductor muscle scars outlined. The three elements of the median eye are shown between the eye peduncles. The gut trace, ?stomach, mandible and mouth are depicted in faint outline. The lamellae of the first two outer rami are dotted as there is some uncertainty about whether they exist. Only the large spines of the inner rami extend beyond the outer.

(*b*), (*c*) Cross sections through the somites bearing the mandible, and seventh pair of trunk appendages, respectively. The details of the appendages proximally are largely hypothetical.

(*d*) Lateral view, right valve and adductor muscle scar outlined, only right appendages shown. Two cephalic appendages anterior of the labrum and mandible are dotted as they are very poorly known. The first twelve trunk appendages are rotated slightly laterally to give an indication of their outline anteriorly, including the distal bifurcation posterior of appendage 6. Beyond this they are depicted normal to the sagittal axis and the detailed morphology, which is unknown, thereby omitted. The configuration of the appendages is generalized; no attempt has been made to reconstruct their positions during a metachronal wave.

U.S.N.M. 189238 is also incomplete, consisting only of the telson and some trunk segments. The evidence for a shorter carapace therefore rests on U.S.N.M. 189239 (figures 7, 9, plate 2) alone. In this specimen 29 somites are preserved beyond the posterior margin of the carapace. This number varies in *Odaraia*, however, from a concentration below five through a scatter up to 29 (in U.S.N.M. 189239), and at least three other specimens, presumably unknown to

Simonetta & Delle Cave, preserve over 15 (U.S.N.M. 213812a (24) (figure 43, plate 5), 213813 (about 17) (figure 81, plate 8) and 202295 (about 16) (figures 18, 22, plate 3)). These higher numbers are mainly a function of orientation, although flexure and telescoping of the trunk may also play a part. A distortion of the normal relation of the carapace to the trunk in U.S.N.M. 189239 (figures 7, 9, plate 2) is indicated by the unusual preserved configuration of the valves. In addition, a plot of carapace length against total sagittal length (figure 101) for specimens identified as *Odaraia* in this paper (based on the only six specimens suitable for measurement) shows that U.S.N.M. 189239 does not depart significantly (at the 5% level) from the reduced major axis, and indeed lies closer to it than U.S.N.M. 189237 (figure 90, plate 9), which Simonetta & Delle Cave correctly identified as *Odaraia alata.* U.S.N.M. 189239 also preserves evidence of appendages compacted against the trunk posteriorly as far as the telson. There is no justification for retaining the genus and species *Eurysaces pielus* and it is synonymized with *Odaraia alata* herein.

(*b*) *Functional morphology*

The morphology of *Odaraia* (figure 103) suggests an actively swimming, filter-feeding, nektonic mode of life. The arthropod clearly spent little or no time on the substrate, as the appendages were apparently completely enclosed by the carapace except for those borne by the short length of trunk that extended beyond the valves posteriorly. It is not clear whether the valves of the carapace could separate ventrally to expose the appendages, but this seems unlikely, and the specimens provide no evidence that it was so. The arthropod may have spent some time resting on the substrate, using the telson flukes to lever the body clear of the sediment when swimming recommenced. The trunk appendages were biramous, but neither ramus appears to have been solely adapted for swimming. The directions in which the preserved rami overlap (see §5*d*) suggest that the outer extended parallel to the ventral surface of the trunk and were presumably restricted in their movement to a small vertical displacement that allowed a current of water to pass over them, but did not create significant thrust. They therefore probably functioned mainly in respiration. The segmented inner rami, however, extended unimpeded ventrally within the chamber formed by the valves and were subdivided distally into two apparently spinose lobes. Movement of these rami would have propelled the arthropod along. The preservation of a toothed mandible in *Odaraia* indicates that it did not primarily filter fine particles (cf. Rolfe in Moore 1969, p. 309). The apparent lack of other well developed specialized cephalic appendages for catching and manipulating food directly to the mouth, however, suggests that an essentially filtering mode of feeding was employed. The spiny lobes of the inner rami of the trunk appendages presumably captured larger particles, which were transferred to a food groove and then transported anteriorly to the mouth. It is reasonable to assume that the feeding and respiratory currents were set up during locomotion by moving the appendages in a metachronal fashion. Suction created by the appendages acting as valves (as in *Nebalia*, for example) would have been limited because movement of the flap-like outer rami was restricted. *Odaraia* apparently used the carapace as a filter chamber instead, within which the appendages were confined. Movement of the appendages in swimming would have drawn water bearing food particles into this chamber anteriorly and expelled it posteriorly. A large arthropod like *Odaraia* would probably have been more dense than water and in that case the generation of lift during swimming would have been important to prevent sinking. It is therefore likely that *Odaraia* swam on its back (like Recent notostracan branchiopods and *Limulus*, for example) with the hinge line inclined to the trunk axis and the latter parallel to the direction of locomotion.

The dorsal surface of the flattened carapace would have contributed considerable lift in this attitude. The same effect would not have been achieved by swimming on the ventral surface. Although the valves met ventrally they were not fused and slight differences of pressure would have been set up, causing a tendency to roll and increasing drag at the expense of lift.

The eyes of *Odaraia* are the largest borne by any Burgess Shale arthropod. If the vision was correspondingly well developed it is possible that *Odaraia* actively pursued small animals which swam in shoals perhaps, rather than as individuals, drawing them into the carapace chamber, where they were captured. In this sense it may have been a predator rather than filtering in a more random fashion. The function of the median eye is problematical. Fortey & Clarkson (1976) demonstrated that the median glabellar 'tubercle' of the benthic trilobite *Nileus* was light-sensitive and that it complemented the visual field of the lateral eyes. They suggested that it monitored illumination from above independently of the visual function of the eyes. The visual field of the eyes of *Odaraia* cannot be determined; it is not clear to what extent they faced ventrally or dorsally rather than anteriorly, but they appear to have been borne on short peduncles, implying some degree of flexibility. It therefore seems unlikely that the median eye could have functioned in determining light intensity independently. In addition, it appears to be situated on the dorsal side of the head and therefore of limited use in detecting light from above if the arthropod swam on its back. It seems more likely that it simply represents the nauplius eye (which is also retained in some adult Branchiopoda) and had no specific function in the adult.

The morphology of the telson of *Odaraia* is unique among the arthropods. It appears that the projecting flukes did not articulate proximally and therefore could not have been employed as swimming appendages in the manner of the furca of the Recent phyllocarid *Nebaliopsis*, for example. Some decapods (shrimps and prawns, for example), however, swim rapidly backwards by suddenly flexing the abdomen and tail to escape from predators. It is unlikely that the telson of *Odaraia* propelled the arthropod backwards as, in contrast to those of Recent decapods, the body was not at all streamlined in a reverse direction. The large posteriorly facing gape of the carapace would presumably have caused sufficient drag to seriously impede backward progression. The telson flukes would, however, have provided an effective brake if the trunk were flexed ventrally during forward movement.

A large arthropod with an essentially tubular carapace would have required a well developed stabilizing and steering organ, and the telson was adapted to fulfil this role. It was similar in structure to the tail of aircraft and submarines, for example. In Crustacea 'the most usual method of controlling rotations around the transverse axis is by the action of flattened structures at the end of the abdomen' (Lochhead 1961). Steering, however, is usually accomplished by the swimming appendages, either moving in different directions or at different speeds. Some Crustacea nevertheless use rudders, which may, as in *Odaraia*, be associated with the telson (the third uropods of the amphipods *Bathyporeia* and *Urothoe*, for example; Lochhead 1961). *Odaraia* lacked any equivalent on the carapace to the median and paired fins of fish and cetaceans that control stability (Webb 1975, p. 47), and the flukes presumably fulfilled this role (which was perhaps the function of the lateral projection of the valves of the ?phyllocarid *Pseudoarctolepis sharpi* Brooks and Caster, 1956). Lateral steering would have been achieved by flexing the trunk laterally, the dorsal fluke acting as a rudder. Little advantage would have been gained by having two flukes in the dorsoventral plane; only one could extend beyond the margin of the carapace, where it was most effective.

The design requirements for steering and stabilizing are, to an extent, similar to those for swimming. In either case the telson moved through the water and morphological adaptations to reduce drag and increase lift are to be expected. The outline of the trunk and particularly of the telson of *Odaraia* is flattened posteriorly because, as in fish, this eliminates the 'large hydromechanical resistance that would be associated with any blunt backward-facing base' (Lighthill 1970, p. 268). The preservation of the flukes suggests that the leading edge was stouter than the trailing edge and that the flukes thinned posteriorly. Assuming that the leading edge was rounded, the cross section would have approximated the streamlined profile for a hydrofoil. The outline of the telson flukes was also influenced by hydrodynamic considerations. Webb (1975, p. 27) pointed out that a hydrofoil tapered in outline produces the highest lift forces 'close to the centre of mass, reducing the magnitude of rolling forces acting on the body in the event of any asymmetry of flow'. *Odaraia* would have been particularly susceptible to roll, due to the subcircular cross section of the carapace. The tapered outline requires 'less heavy support per unit of lifting area than rectangular hydrofoils of the same area' (Webb 1975, p. 27). It also reduces cross flow and thus inhibits the formation of vortices at the tips (the small spines toward the distal extremity of the leading edge of the flukes in *Odaraia* probably also functioned in this respect). The outline of a fin (or hydrofoil) can be expressed as an aspect ratio (Webb 1975, p. 27), which is basically the ratio of width to length. Lift tends to be greatest for a hydrofoil of given area when the aspect ratio is highest. A high ratio also reduces induced drag and concentrates lift forces near the body (Webb 1975, p. 29). In addition, reduction of the length (exsagittal) of the lobes of the caudal fin may prevent separation of the boundary layer (which can only occur a certain distance from the leading edge) on the tail surface as opposed to beyond the trailing edge, where it contributes less drag (Aleyev 1977, pp. 117–122). The aspect ratio of the lateral flukes of *Odaraia* (considered together as a single hydrofoil) lies between 11 and 14 (span^2/total area of both lateral flukes (Webb 1975, p. 27), calculated on the basis of U.S.N.M. 213809 (figure 5, plate 1) and 213812 (figures 42, 43, plate 5)). This is in contrast to a maximum of 6.1 observed in fish by Nursall (1958, p. 118), who stated that 'as a general rule aerodynamic efficiency improves as the aspect ratio increases, to about AR values of 8 to 10. Beyond this efficiency is sharply reduced as bulky structural members are required to support the wide span'. Such structural constraints would have been less significant in *Odaraia*, where the flukes were apparently rigid proximally and only slightly flexible at the tips. In addition, the forces acting on the flukes would have been much less in steering and stabilizing than in swimming.

Optimization to reduce drag and increase lift is thus considered the most likely explanation for the convergence between the outline of the paired lateral flukes in *Odaraia* and that of the semi-lunate tail used in the propulsion of fast-swimming fish, sharks and cetacean mammals (Lighthill 1970). The possibility that *Odaraia* might have swum with an oscillating movement of the trunk in addition to using the appendages must, however, be considered. In view of the restriction imposed on trunk movement by the carapace, the only likely method is one similar to the carangiform mode used in some fish (Webb 1975), in which only the posterior part of the body is thrown into a wave, the amplitude of which increases rapidly toward the tail. The large number of short trunk somites, which inserted one into another and were apparently connected by a band of flexible cuticle, would have permitted flexure through a sufficiently wide arc and their apparent decrease in sagittal length posteriorly would have increased the flexibility of the trunk in this direction. Although it appears that, in theory at least, *Odaraia* could have used the trunk and telson in swimming, it is considered unlikely that this was an important mode of locomotion. There is no evidence of an abrupt change in the length or character of the somites at any point along the trunk which might delimit a posterior part adapted for swimming. Nor is there any evidence that the trunk flexed more readily dorsoventrally than laterally, as would be expected if the paired lateral flukes were employed in propulsion. More importantly, the attitude of the median dorsal fluke would have inhibited swimming in this manner. Lying in the plane in which the telson would have moved up and down in swimming, it would have been deflected to one side or the other during each stroke, producing a tendency to roll and contributing additional drag particularly at the flexible tip. Swimming with the trunk and tail would have caused up and down yawing with little to combat it. The closest analogy to the telson of *Odaraia* within the arthropods is provided by the flat paddle-like telson with a median dorsal keel of some eurypterids (Størmer 1955). Similar functional considerations apply to these arthropods, although they are diverse morphologically and details clearly vary (see for example, Waterston 1979); it seems likely that the eurypterid telson was primarily a stabilizing and steering organ and did not usually function as a swimming paddle, locomotion (swimming and walking) being carried out by the appendages.

Swimming with the appendages in *Odaraia* would have been part of a unified process also involving feeding and respiration. Filtering is inhibited by too rapid locomotion. With one adequate mode of swimming there would normally be no need for an additional one. The trunk and telson may, however, have provided additional power when needed for rising off the bottom, vertical climbing and even forward escape, just as it does in a number of crustacean groups (Lochhead 1961).

(*c*) *Classification and affinities*

Walcott (1912) classified *Odaraia* in the order Hymenocarina Clark (in Zittel), 1900 of the sub-class Malacostraca. He did not assign it to a family. Fedotov (1925, p. 387) considered that Walcott (1912, p. 154) had united *Odaraia* with *Hurdia*, *Tuzoia*, *Fieldia* and *Carnarvonia* into a single, undetermined family, although this was not Walcott's intention, and pointed out that, on the basis of Walcott's description, it can only be stated that *Odaraia* may have belonged to the Crustacea. Henriksen (1928, pp. 14, 15) supported Walcott's classification of *Odaraia* in the Hymenocarina, but cautioned that 'it cannot be definitely proved from the carapace alone'. Størmer (1944) assigned all arthropods with what he considered to be 'trilobitan' limbs to a new sub-phylum Trilobitomorpha and included the order Hymenocarina in a new class Pseudocrustacea. He considered that *Odaraia* (1944, p. 101) had 'apparently an archaeostracan carapace, but might yet have had trilobitan appendages'. *Odaraia* was tentatively assigned to the Hymenocarina. Thus Størmer removed *Odaraia* from the Crustacea, but for the wrong reasons. The reinvestigation of the Burgess Shale arthropods has shown that there is little justification for retaining the 'trilobitan limb' as a diagnostic character at least outside the trilobites. *Odaraia* was subsequently rejected from the Trilobitomorpha by Størmer (1959) and Rolfe (in Moore 1969) treated it with the Phyllocarida 'Order and Family uncertain'. Simonetta & Delle Cave (1975, p. 35) were the first authors to assign *Odaraia* to a family, erecting the new family Odaraidae and order Odaraida, without diagnoses, to include it. However, they erected in addition a new family Eurysacidae for their new genus and species *Eurysaces pielus*, which has no validity as the species is synonymized with *Odaraia alata* herein.

Of the major arthropod taxa (phyla of Manton (1977)) *Odaraia* shows the most striking similarity to the Crustacea. Clearly neither the embryology or nervous system of the cephalic region can be studied, and hence an interpretation of the cephalic segmentation must rest essentially on the presence or absence of appendages. Unfortunately the cephalic region is not well preserved. No antennae extend anteriorly beyond the carapace, but two paired reflective features anterior of the position of the mandible may represent limbs. Posterior to the adductor muscle scars and mandible the trunk bears a series of appendages. The anterior two pairs (described in §5*c*) appear to differ from those following and might represent maxillae. The segmented ramus exposed may represent a palp-like structure such as that on the first maxilla of *Nebalia* (Calman 1909, p. 153). Thus *Odaraia* may have been a crustacean in spite of the extraordinary morphology of the telson, but it is not possible to state this unequivocally.

The crustacean class to which *Odaraia* shows greatest similarity is the Branchiopoda. A bivalved carapace occurs in the Conchostraca, a folded carapace encirling the body in the Cladocera, and branchiopod carapaces, like that of *Odaraia*, are not strongly calcified. The Notostraca have a large number of somites, numbers in excess of 40 in *Triops* approaching the maximum observed in *Odaraia*. The branchiopods are characterized by a long series of uniform trunk limbs which are usually lamellate and lobed, but in contrast to those in *Odaraia* these are absent on the posterior somites of the trunk. The number of appendages in the Notostraca exceeds that of somites and it is possible that this was also so, to a lesser extent, in *Odaraia*. The telson of the branchiopods, however, characteristically bears a caudal furca which consists of two movable appendages or claws, totally unlike the flukes of *Odaraia*, but this may have been absent in the Kazacharthra (Tasch in Moore 1969, p. 135). The first and second antennae in Notostraca are greatly reduced and this might also have been the case in *Odaraia*. The notostracans also have a wide-toothed mandible similar to that in *Odaraia*. It is not clear, however, whether or not *Odaraia* bore first and second maxillae between the mandible and the biramous trunk appendages. The eyes in branchiopods are usually sessile, but large stalked eyes like those of *Odaraia* occur in the Anostraca, and the median naupliar eye is also characteristically retained in adult Branchiopoda.

The similarities between *Odaraia* and the branchiopods, particularly the Notostraca, merit consideration as *Odaraia* could arguably represent a branchiopod, even though it may have lacked the characteristic crustacean head. It may have had a similar cephalic morphology to that of *Canadaspis* (Briggs 1978), in which the maxillae were similar to the trunk appendages, although the trunk had already acquired the diagnostic malacostracan tagmosis. The branchiopods are not united by a feature like the segmentation of the malacostracan trunk which allows the class to be readily identified in a fossil. Two obvious non-branchiopod features in *Odaraia*, however, the lack of both a caudal furca and an apodous posterior section of the trunk, are arguably sufficient to eliminate it from the Branchiopoda as presently defined (Tasch in Moore 1969, p. 131). In addition, *Odaraia* was marine whereas the branchiopods generally occur in brackish or fresh water and their fossil record only extends back as far as the Devonian. Further, many of the characters shared by *Odaraia* and the Branchiopoda are arguably symplesiomorphic and therefore not useful in determining relationships. The main difficulty is in identifying characters that are primitive (as opposed to derived), but this can be overcome to some extent by reviewing the occurrence of characters in related groups outside the taxa under discussion (Eldredge 1974, p. 32). Thus the following features common to *Odaraia* and the branchiopods may be considered primitive: (i) the bivalved carapace, as it also occurs in the phyllocarid Malacostraca, the Ostracoda and Cirripedia and other unrelated Cambrian arthropods such as *Plenocaris* (Whittington 1974), *Protocaris* and *Branchiocaris* (Briggs 1976);

(ii) the large number of serially homologous trunk somites all bearing similar appendages. The latter hardly needs to be defended as a primitive arthropod feature. It was justified by Hessler & Newman (1975) as a character of their ancestral crustacean and also occurs in the unrelated Cambrian arthropods *Marrella* (Whittington 1971*b*), *Protocaris* and *Branchiocaris* (Briggs 1976), the myriapodous Uniramia and probably the olenellid trilobites, although their appendages are unknown. The morphology of the Notostraca, however, is more complex; the number of appendages is variable and greatly exceeds that of somites (Longhurst 1955). Indeed, the large number of somites in the notostracans may be a derived feature (Calman 1909, p. 51). There may have been a few more appendages than trunk somites in *Odaraia*, but the large number of somites is almost certainly primitive. Whether the high number of somites in the Notostraca is primitive or derived, it is not a reliable indication of affinity with *Odaraia*. There is no compelling evidence that *Odaraia* was related to the branchiopods.

Were Simonetta & Delle Cave (1975, p. 35) justified in erecting a new family and order to include *Odaraia*? The higher taxonomy of the Palaeozoic bivalved arthropods is unsatisfactory due mainly to poor preservation (Rolfe in Moore 1969, pp. 311, 312). Only the Canadaspidida of the four orders of fossil Phyllocarida, for example, is sufficiently well known to permit a diagnosis in terms comparable with the Recent Leptostraca (Briggs 1978, p. 484). Higher taxa based solely on carapace morphology are unreliable and should be considered tentative compared to those founded on additional preserved features. They provide a convenient pigeon hole for carapaces of similar morphology but are unlikely to have any taxonomic validity. The family Isoxyidae Vogdes, 1893 (name corrected after Rolfe (in Moore 1969, p. 326)), which includes *Isoxys*, *Dioxycaris* and *Tuzoia*, is an example (see discussion in Briggs (1976, p. 14) and Glaessner (1979, p. 25)). New taxa above the genus should not be erected on carapace morphology alone; the designation 'order and family uncertain' is preferable if no taxon is already available. Genera like *Odaraia*, however, in which features in addition to the carapace are known, can be classified in one of three ways: (i) in a Recent taxon, or one based on comparably preserved fossil material; (ii) in a fossil taxon based on similar carapace morphology alone, which thus becomes more nearly comparable with Recent taxa; (iii) in a new taxon, as Simonetta & Delle Cave (1975, p. 35) have done, but with a diagnosis, which they omitted. The problem of determining which characters should be considered diagnostic at order and family level remains. In the phyllocarids, for example, 'ordinal classification is based essentially on the nature of the telson and furca. Such single character classification is obviously unsatisfactory, but few other morphological features observable in fossil material are as conservative or reliable' (Rolfe in Moore 1969, p. 311). Carapace shape and sculpture have been extensively used in familial classification, but, as Rolfe (in Moore 1969, p. 312) points out, these are likely to be extremely variable and commonly convergent. For well preserved material of bivalved arthropods it would seem more appropriate to base orders on the gross structure of the trunk tagmata and families on the details of the appendages.

The only existing fossil taxon based on comparable material to which *Odaraia* might belong is the order Protocarida, to which Simonetta & Delle Cave (1975, p. 35) assigned *Eurysaces*, their monospecific genus synonymized with *Odaraia* herein. Simonetta & Delle Cave did not diagnose their new order Protocarida, but it was based on the family Protocarididae Miller, 1889, which was discussed in detail by Briggs (1976). The Protocarididae also show similarities to the Notostraca, although they were neither branchiopods nor Crustacea. The family is diagnosed (Briggs 1976, p. 2) on the basis of a combination of characters; due to the largely primitive morphology no one character is sufficient. Those shared by the Protocarididae and *Odaraia*, however, are the large number of somites and bivalved carapace, and both are argued above to be symplesiomorphic. There would be a case for arguing relationship if it could be shown that the large number of trunk somites is a derived character in both cases, but this is clearly impossible. The differences in the structure of the cephalon (lack of eyes and very different appendages in *Branchiocaris*) and telson are sufficient to separate the arthropods at generic and familial level and thus the creation by Simonetta & Delle Cave (1975, p. 35) of a new family Odaraidae, in the absence of one based on a similar carapace morphology, is vindicated.

In view of the limited development of trunk tagmosis (a symplesiomorphic feature) in both *Protocaris* and *Branchiocaris* (Briggs 1976), and in *Odaraia*, it is not considered possible to assess relationships between them at ordinal level with any degree of confidence. Simonetta & Delle Cave (1975) give no justification for erecting the two new orders Protocarida and Odaraida; the publication of orders without diagnoses represents no progress in understanding, but may succeed in concealing a lack of it. The designation 'class and order uncertain' is preferred pending a synthesis of the Burgess Shale arthropod fauna as a whole (in preparation).

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LIST OF SYMBOLS USED IN FIGURES

a	anus
al	alimentary canal
am	reflective trace of adductor muscle
ap	appendages
b	intersomite boundary
cb	border of carapace
c	anterior margin of cephalic region
e	eye
f	telson fluke
g1, g2, etc.	outer ramus of trunk appendage
h	hinge of carapace
i1, i2, etc.	inner ramus of trunk appendage
j	mandible
l	prefix indicating left side
m	prefix indicating median
n	nodular feature
o	possible outline of labrum
r	prefix indicating right side
s	muscle scar on carapace
st	stomach
t1, t2, etc.	trunk somites numbered from the boundary with the cephalic region
t − 1, t − 2, etc.	trunk somites numbered from the anterior margin of the telson
te	telson
tm	trace of margin of trunk
u	gut contents
v	valve of carapace
x	see figure description
y	extension of reflective area in the eye
z	reflective traces in the trunk.

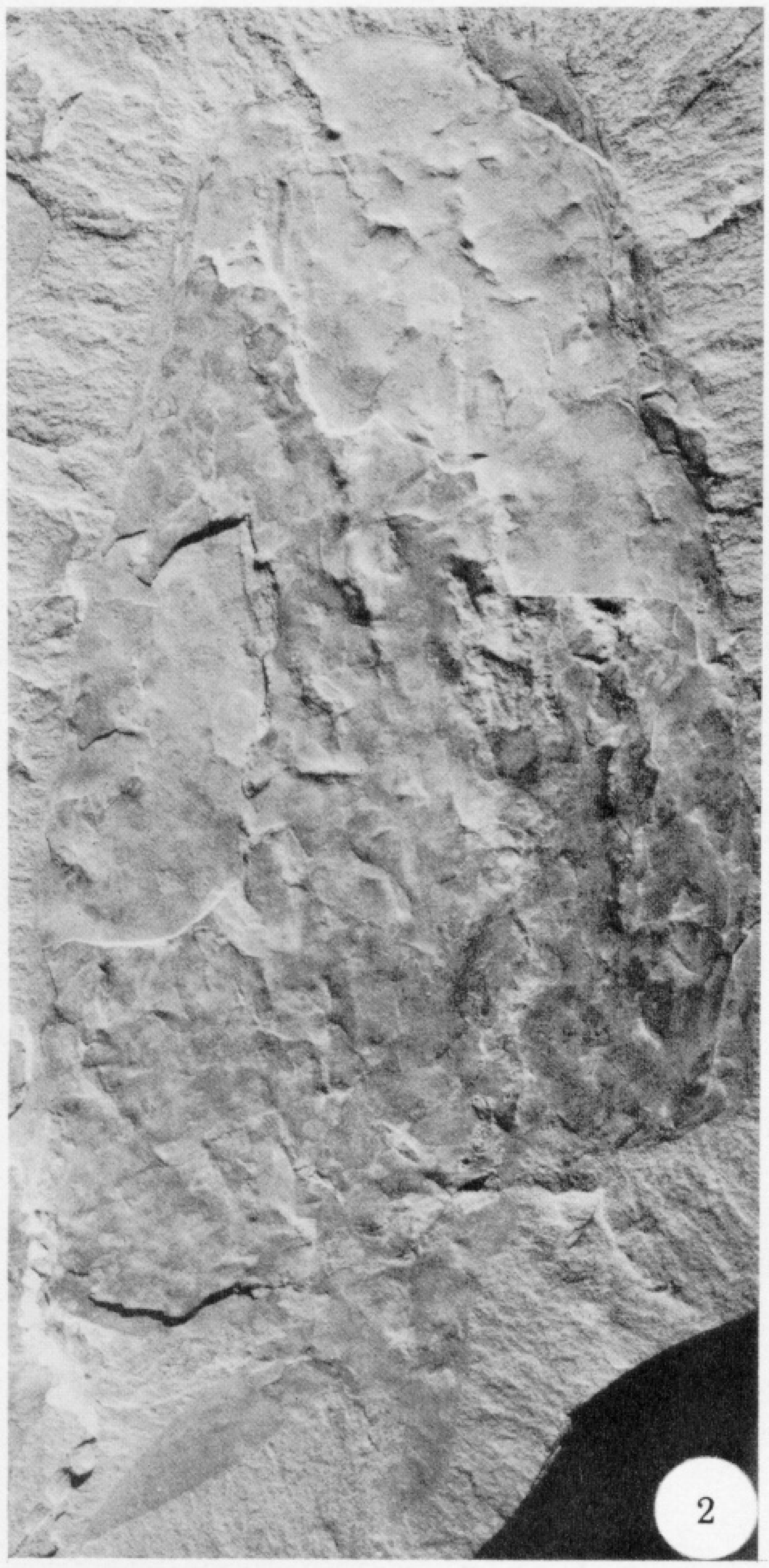
Solid black areas represent a dark material (mainly apatite) occurring in place of the gut contents.

Irregularly coarse stippled areas represent the occurrence of this same mineral elsewhere.

Regularly fine stippled areas represent 'outcrops' of matrix that might otherwise be confused with morphological features of a specimen.

Breaks of slope are represented by hachures, the solid line at the upper edge of the break, the hachures directed downslope.

[Plates 1–9 have been printed at the University Press, Oxford.]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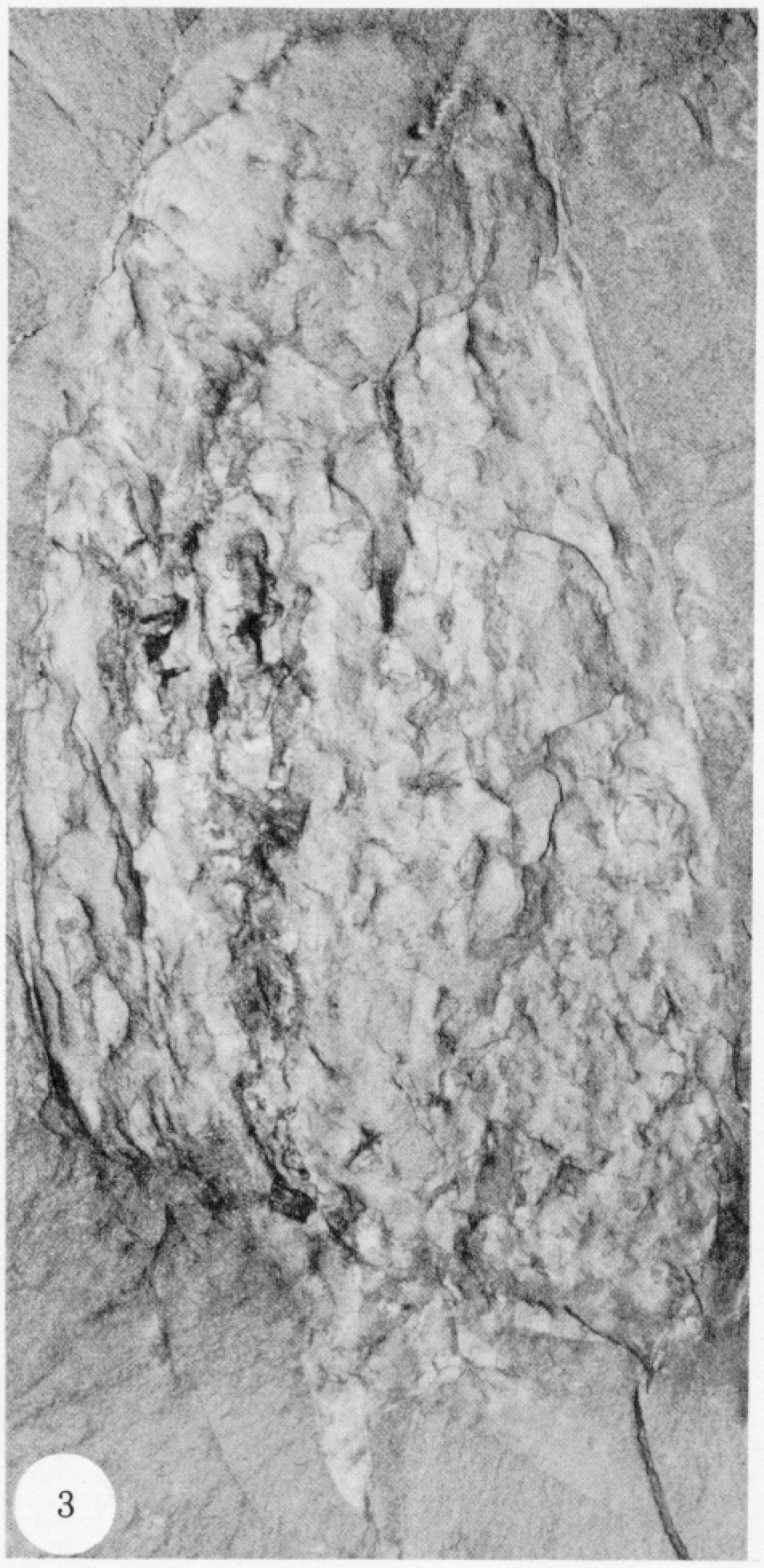
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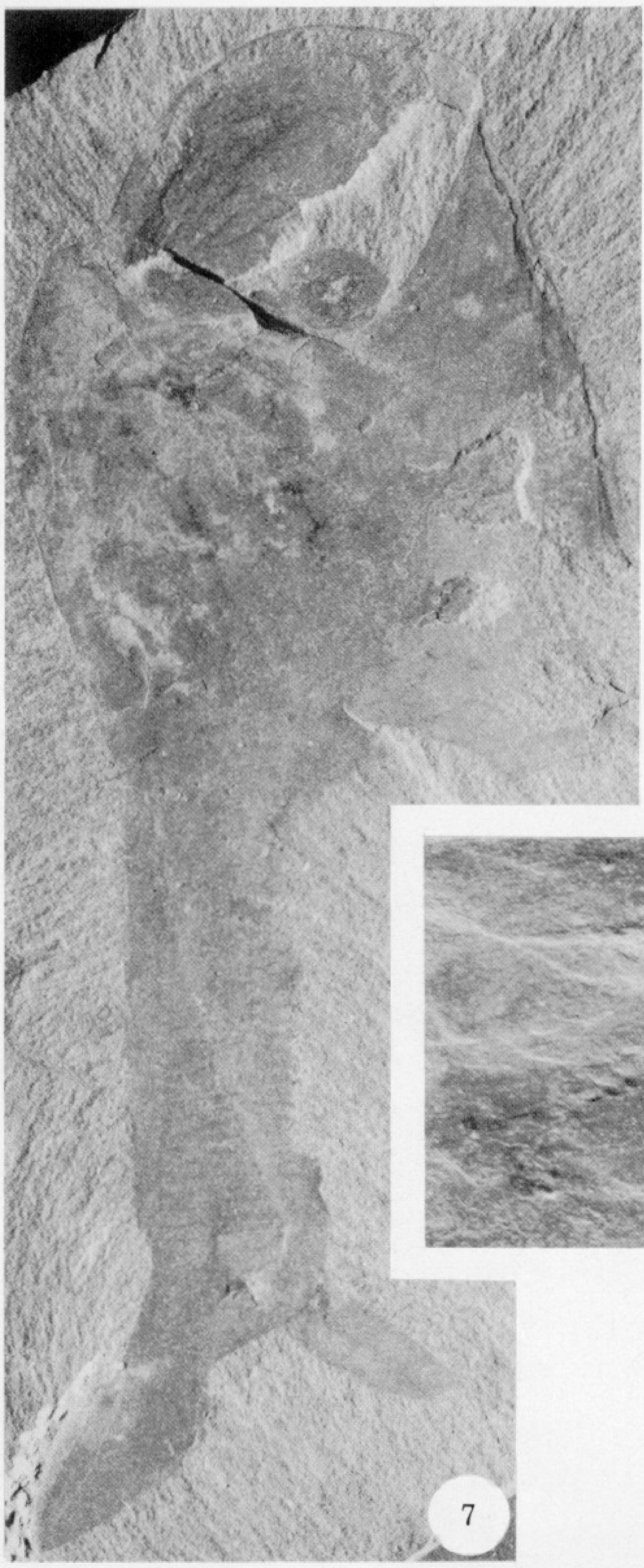
FIGURES 2–6. For description see opposite.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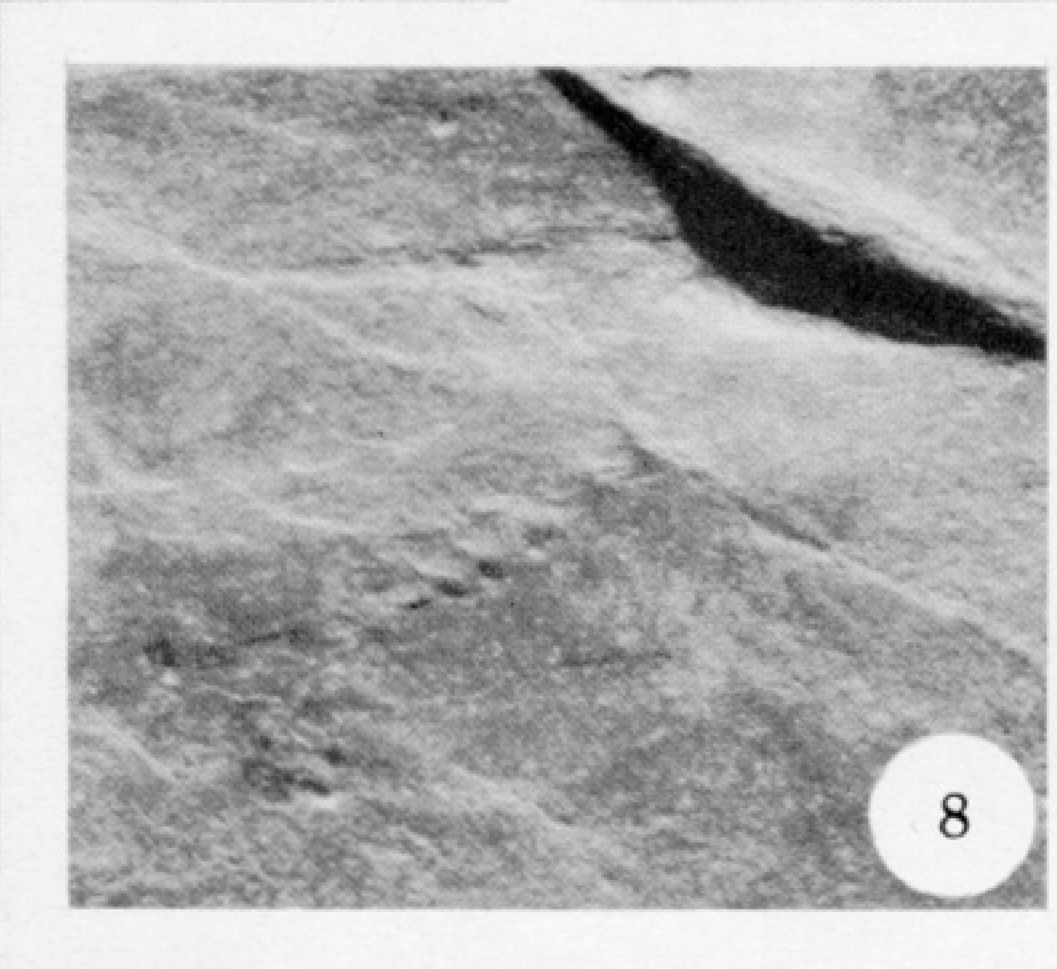
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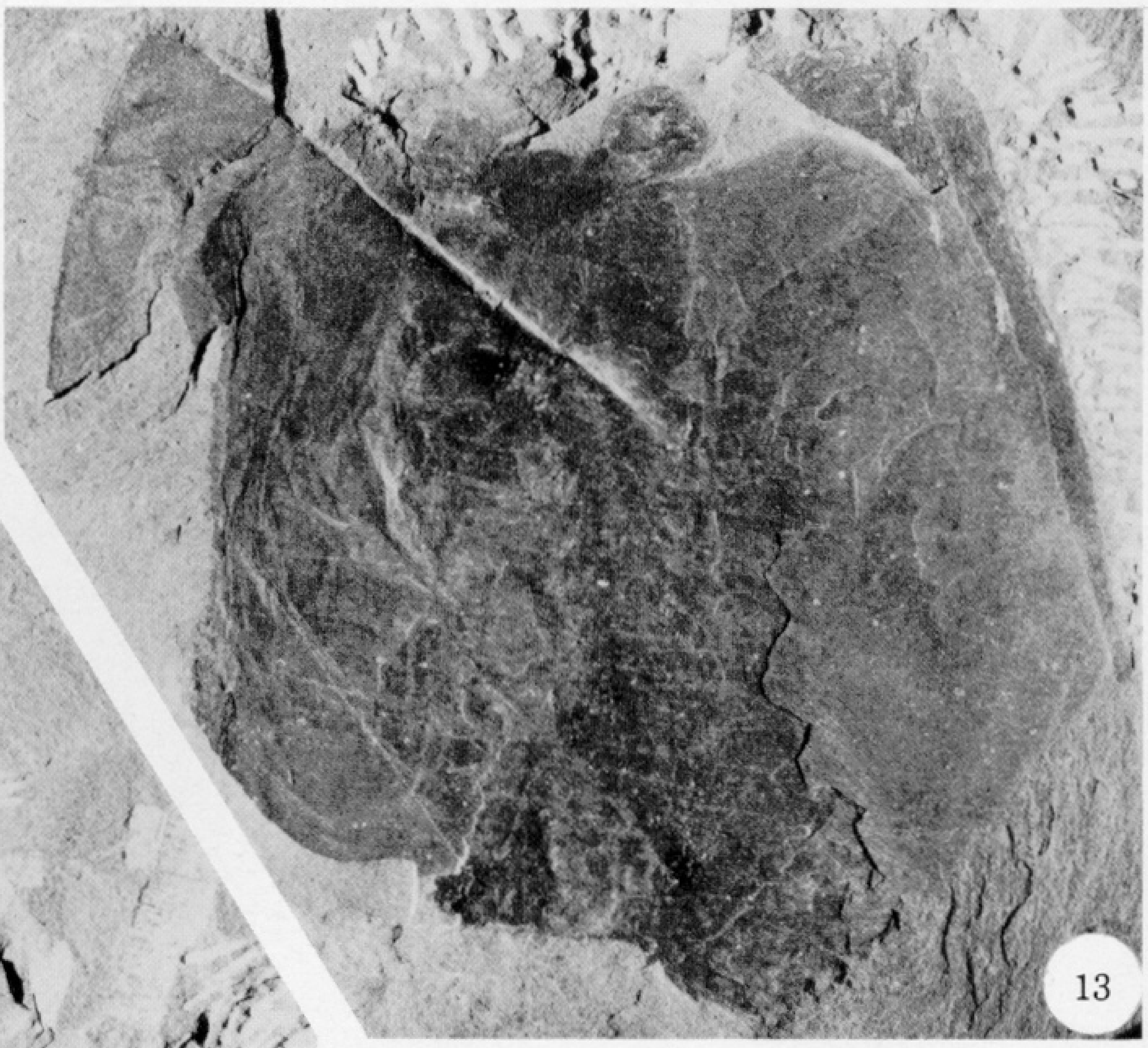
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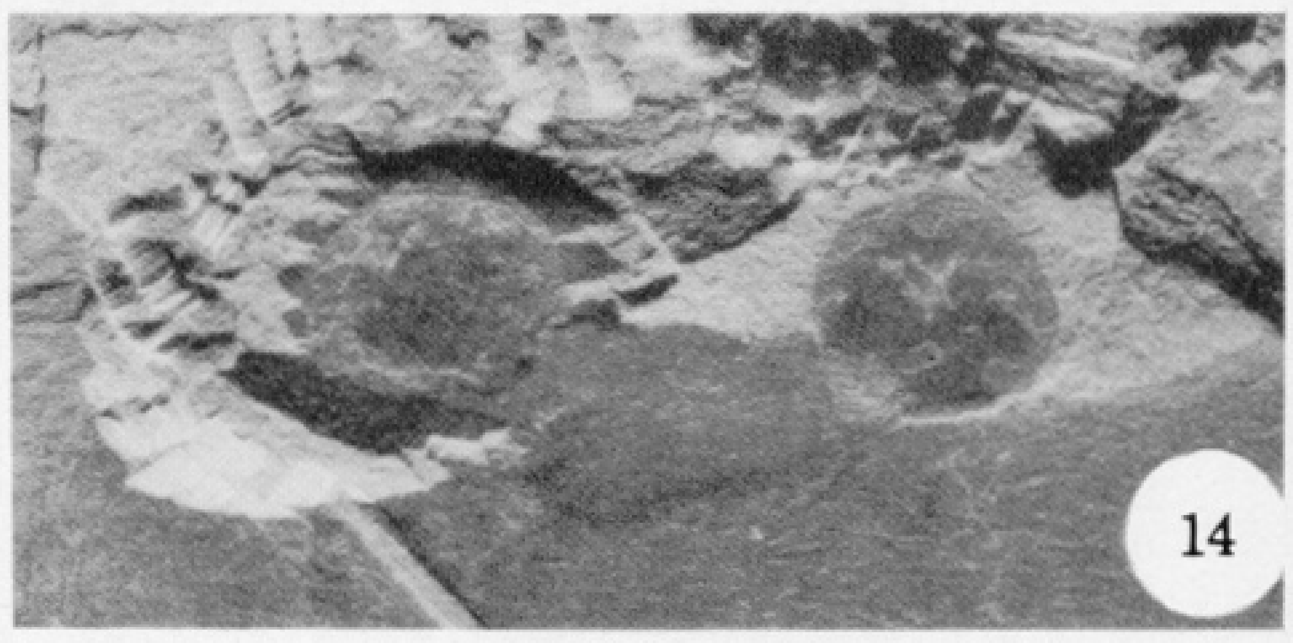
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FIGURES 7–14. For description see opposite.


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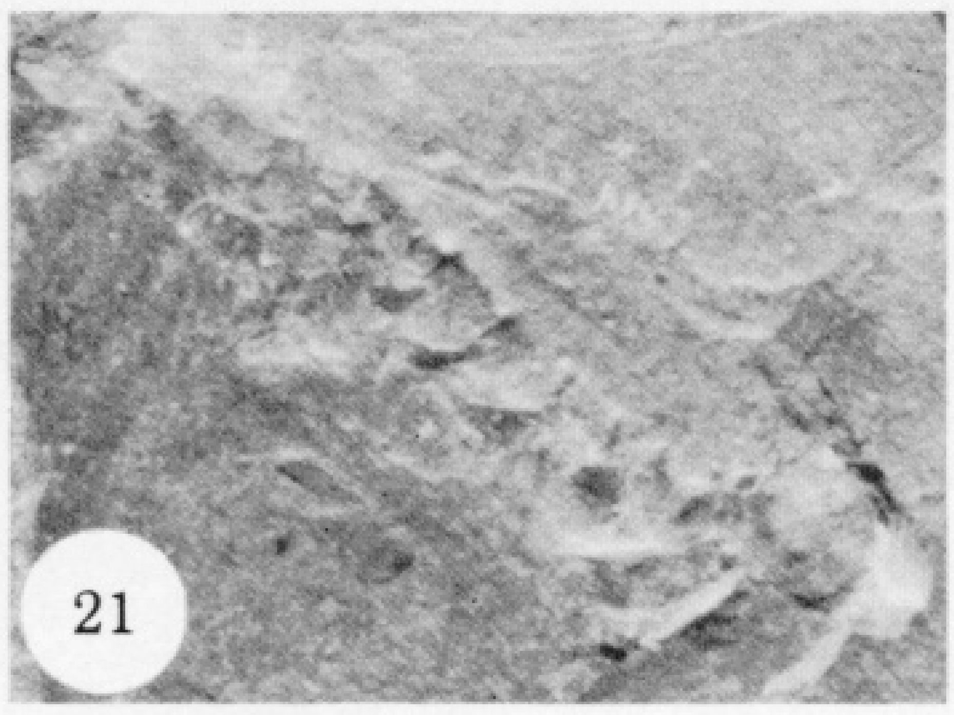
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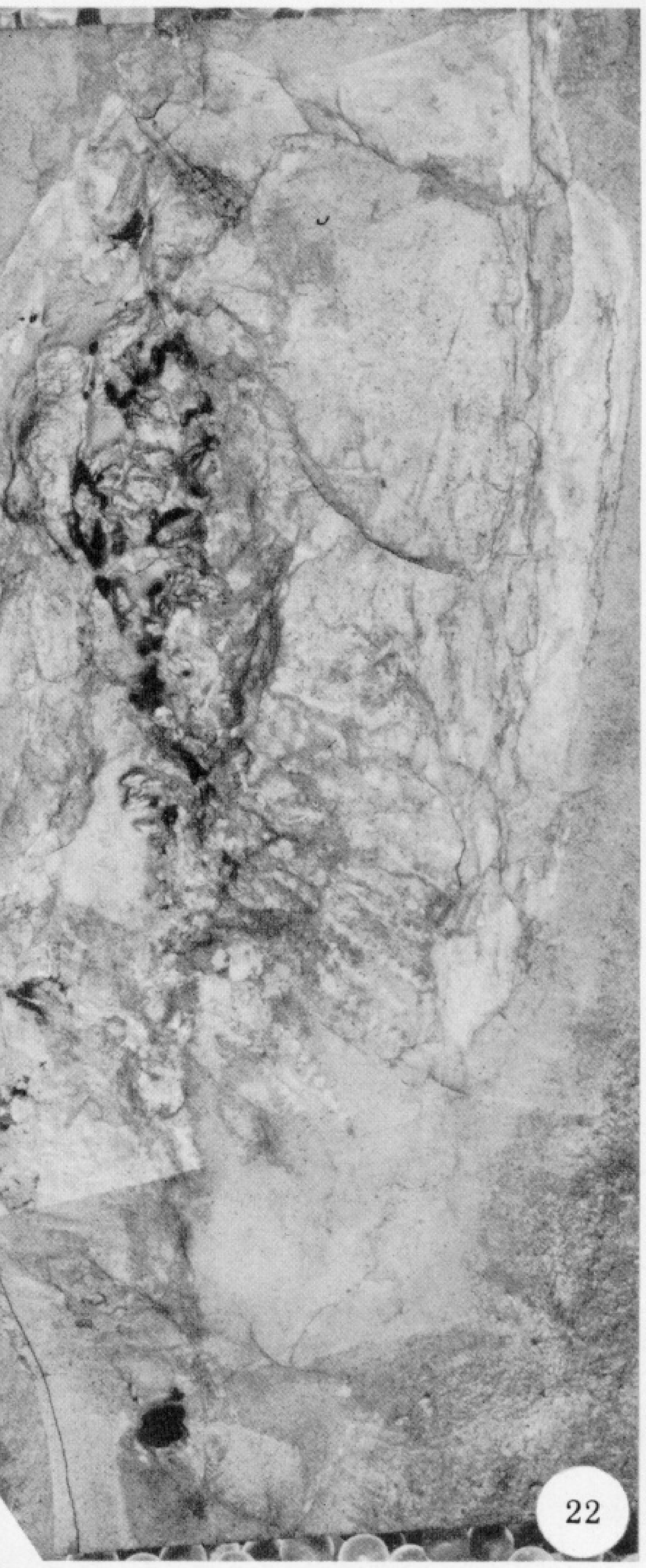
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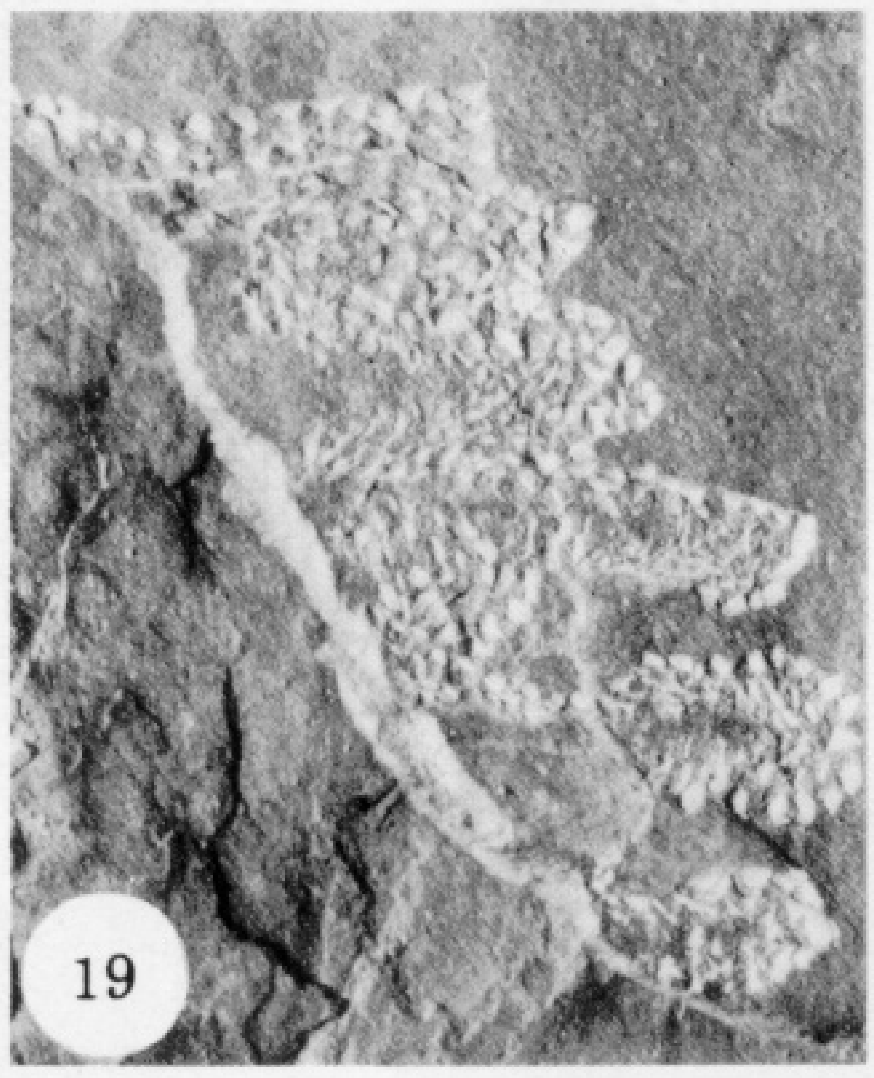
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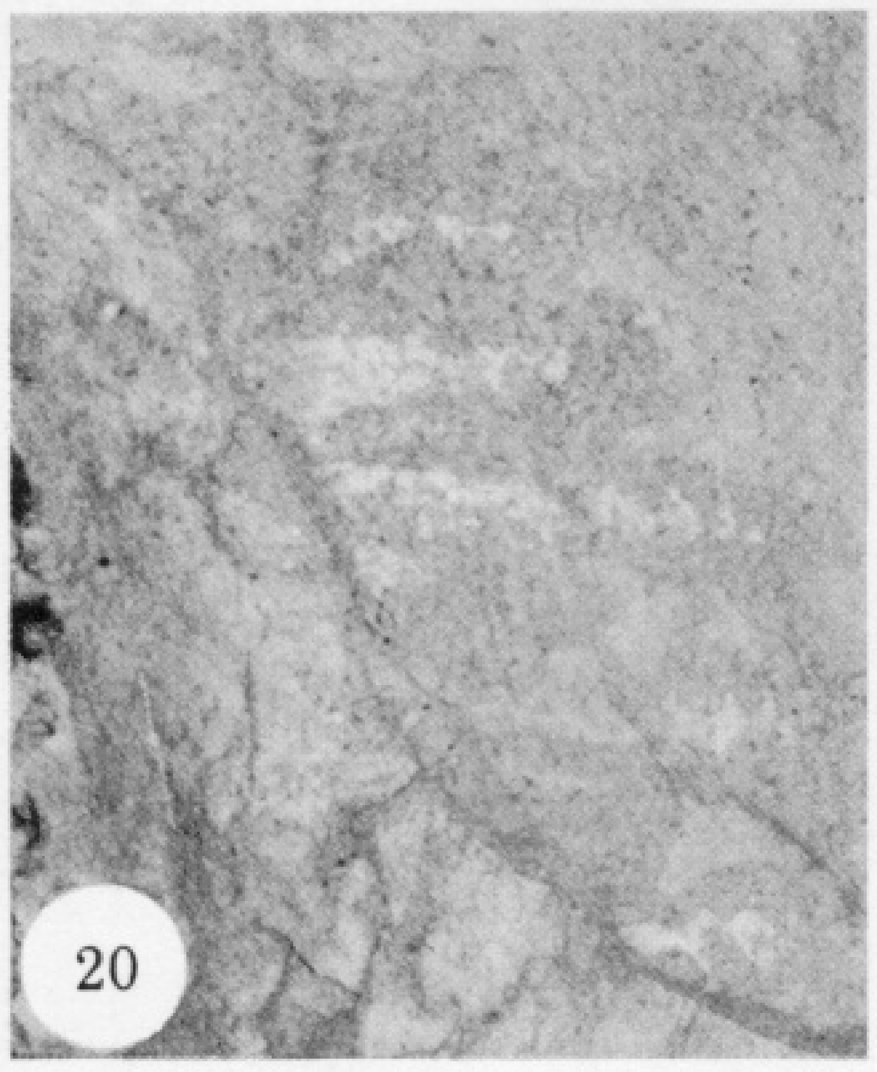
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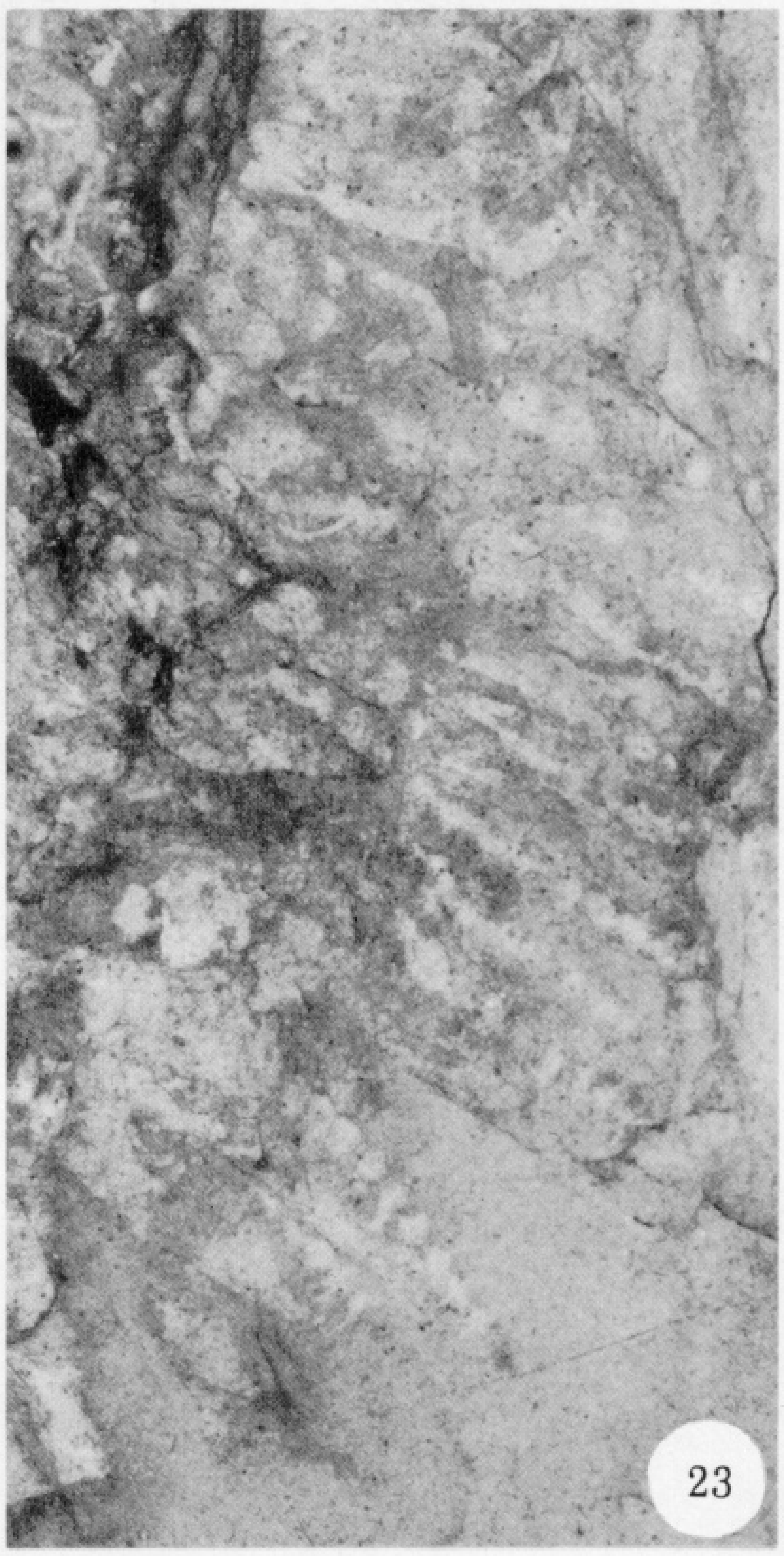
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FIGURES 18–23. For description see opposite.


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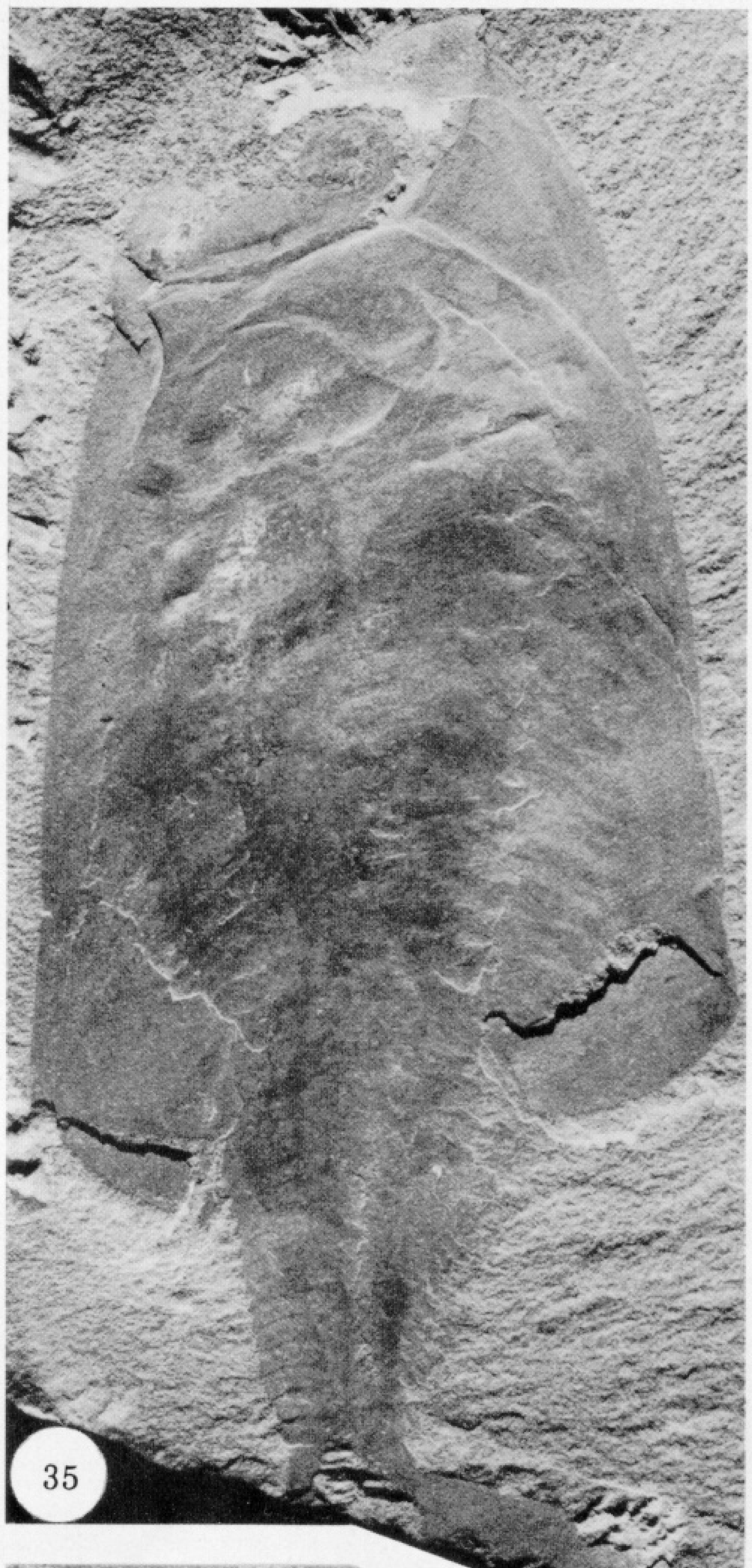
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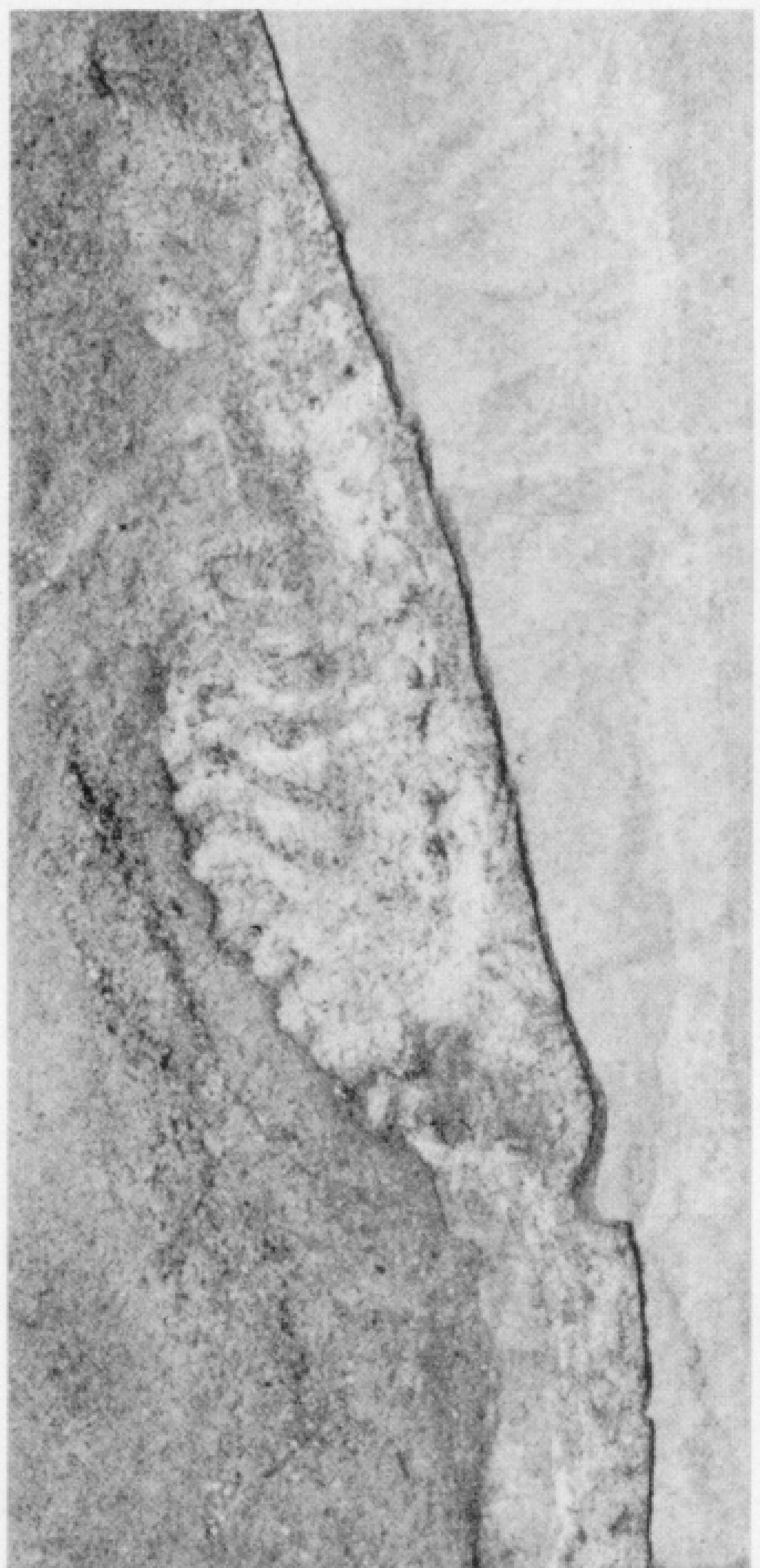
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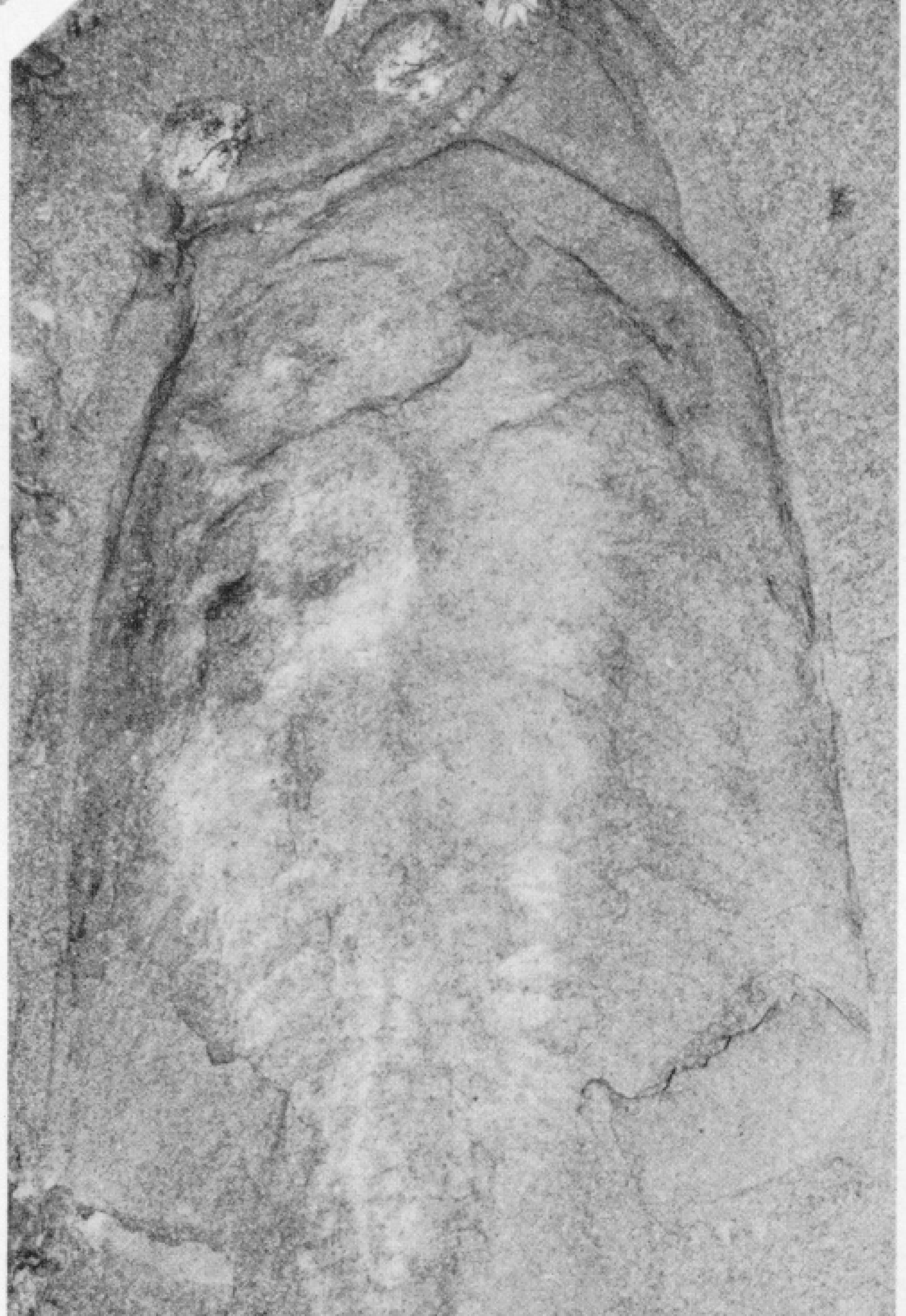
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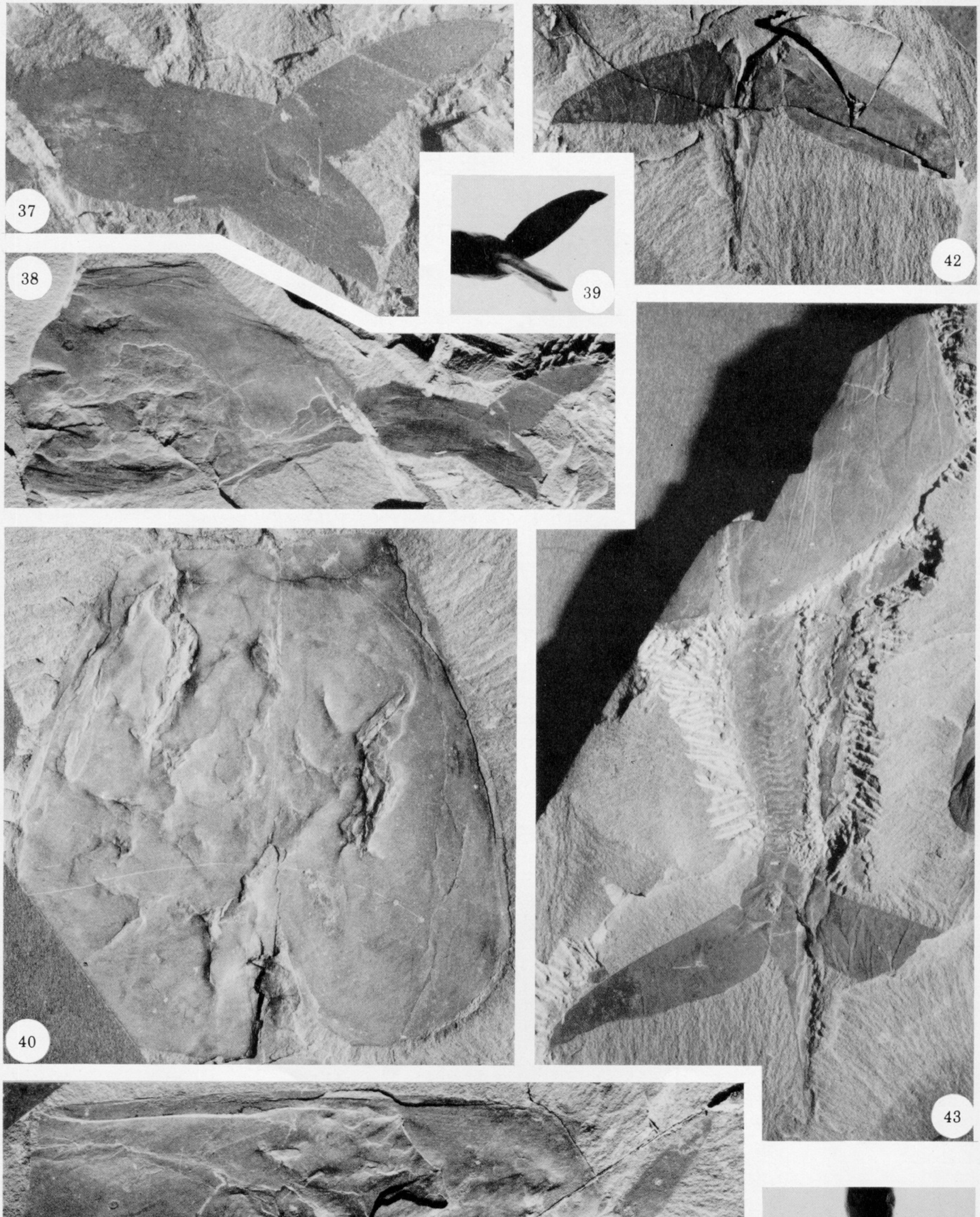
FIGURES 31–36. For description see opposite.



FIGURES 37–44. For description see opposite.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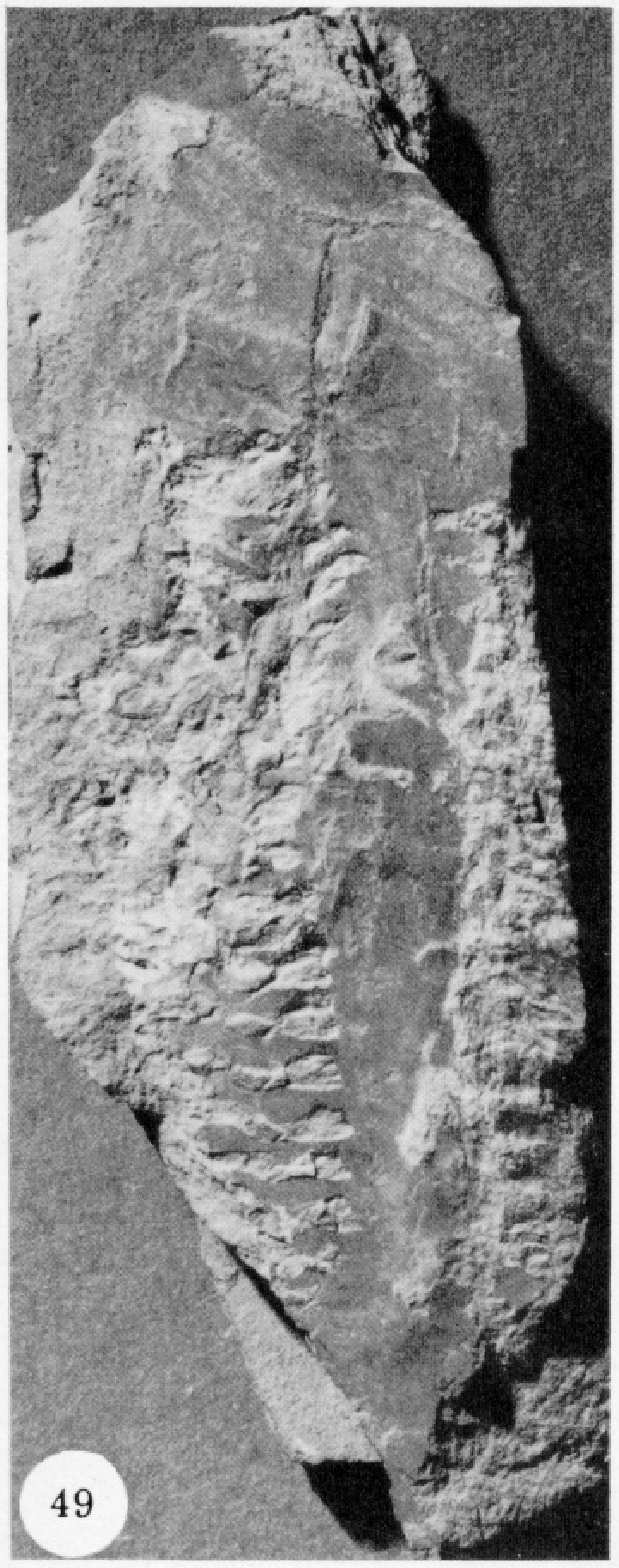
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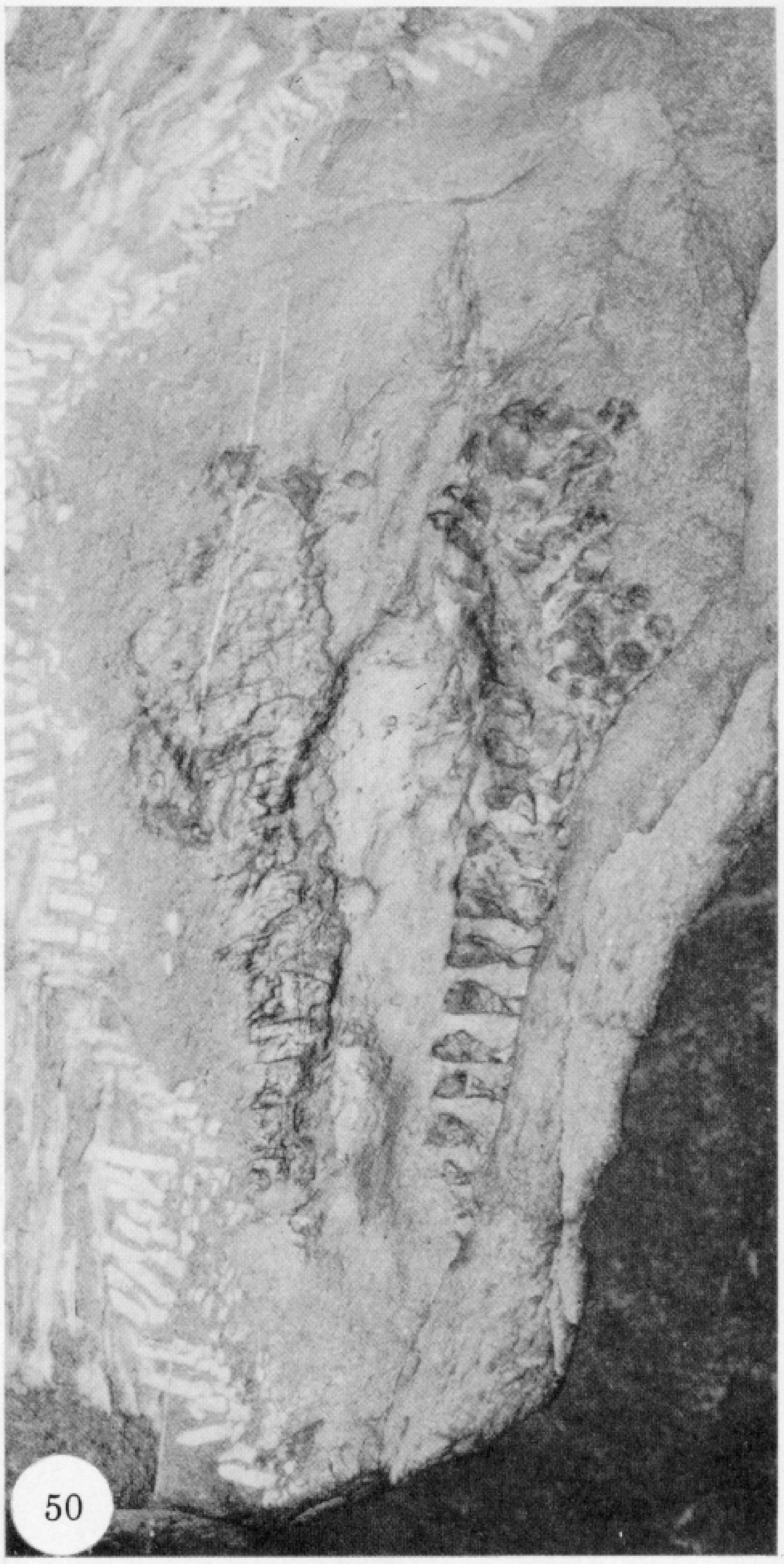
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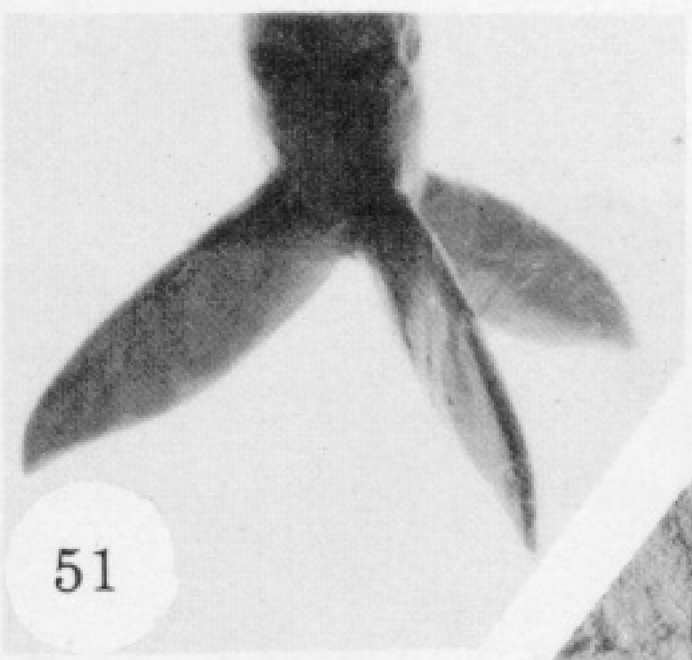
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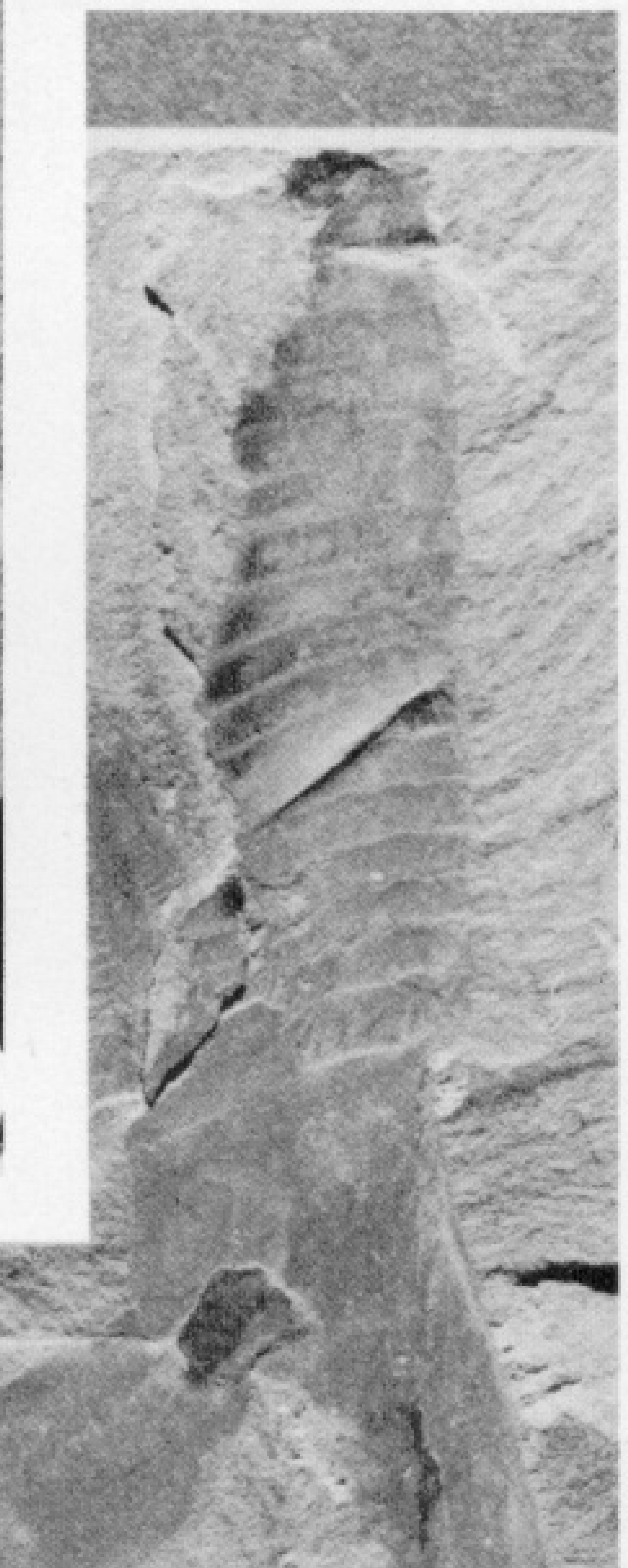
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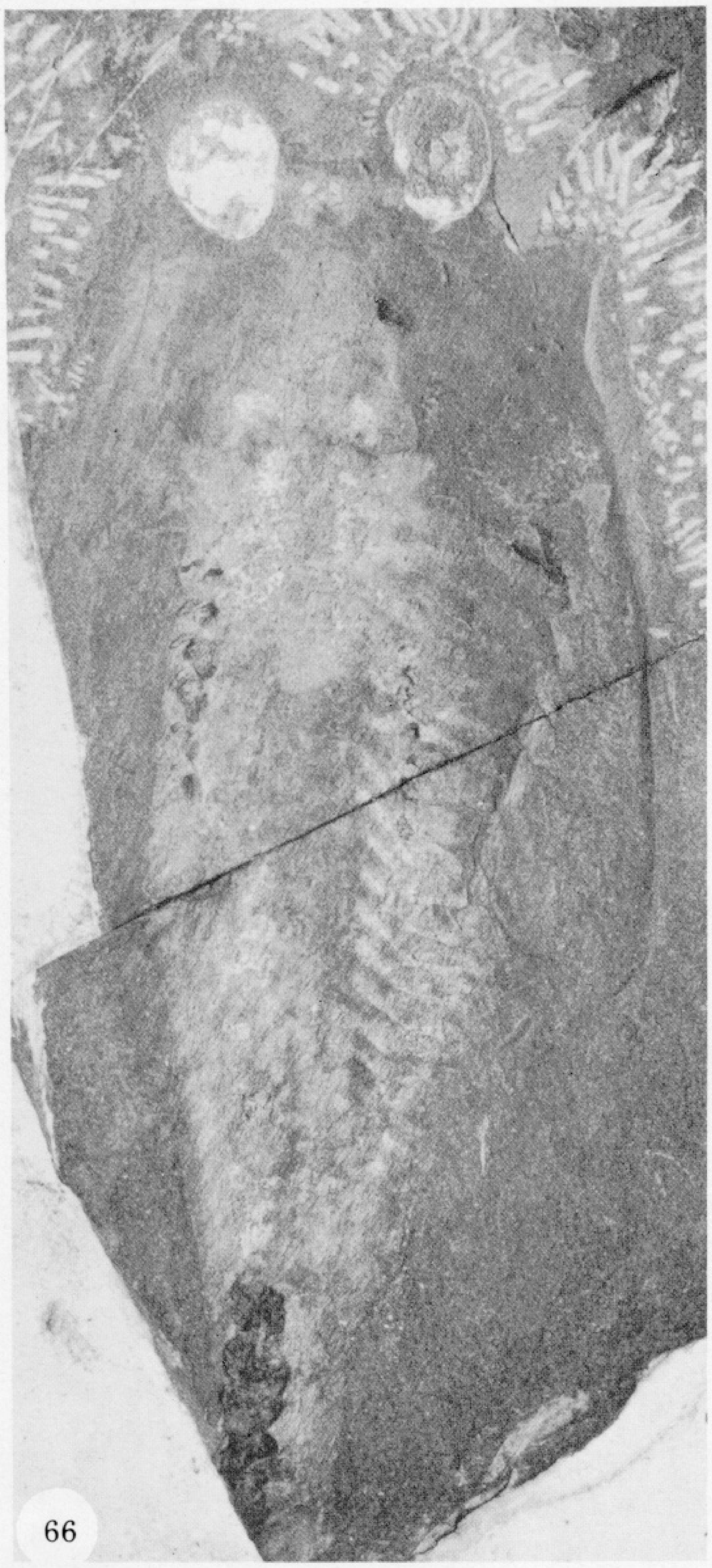
FIGURES 48–56. For description see opposite.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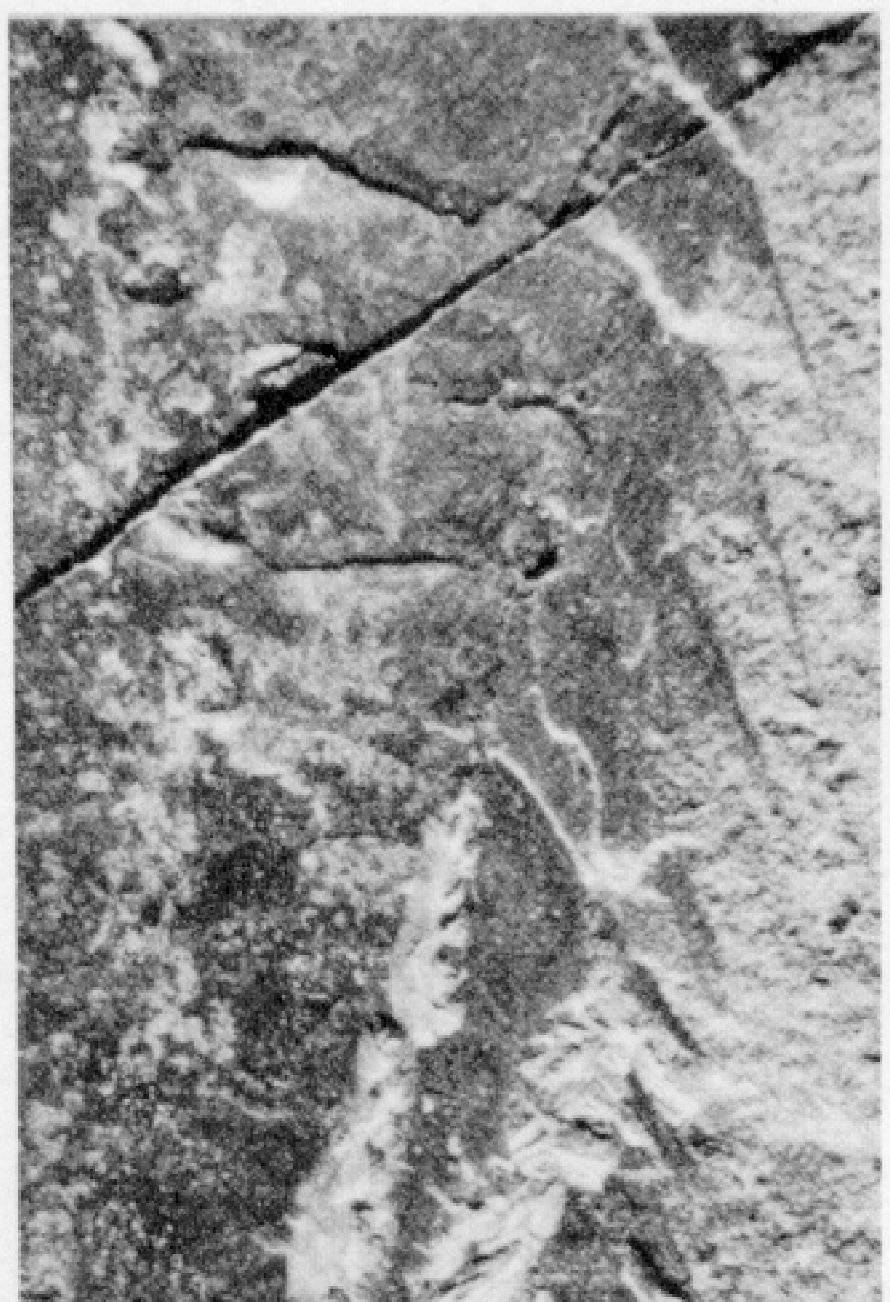
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FIGURES 66–72. For description see opposite.


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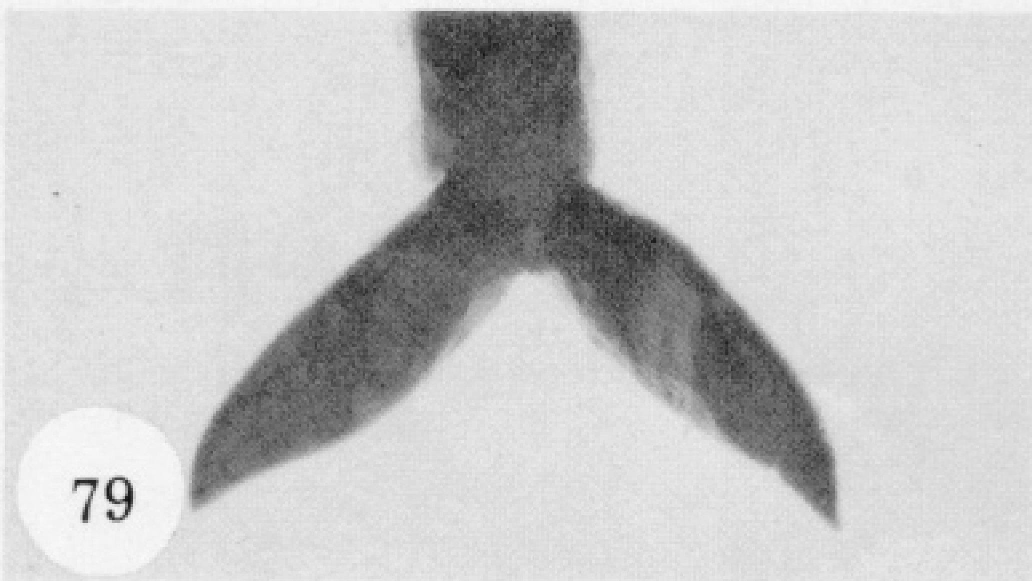
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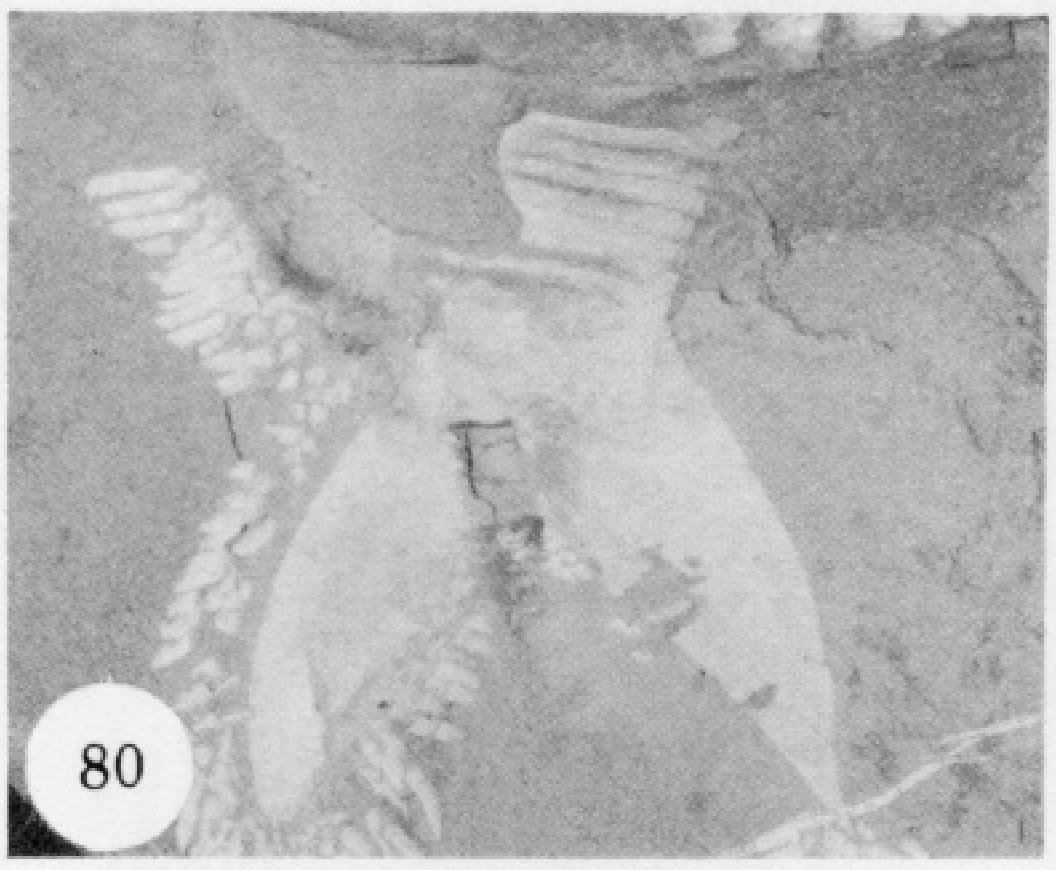
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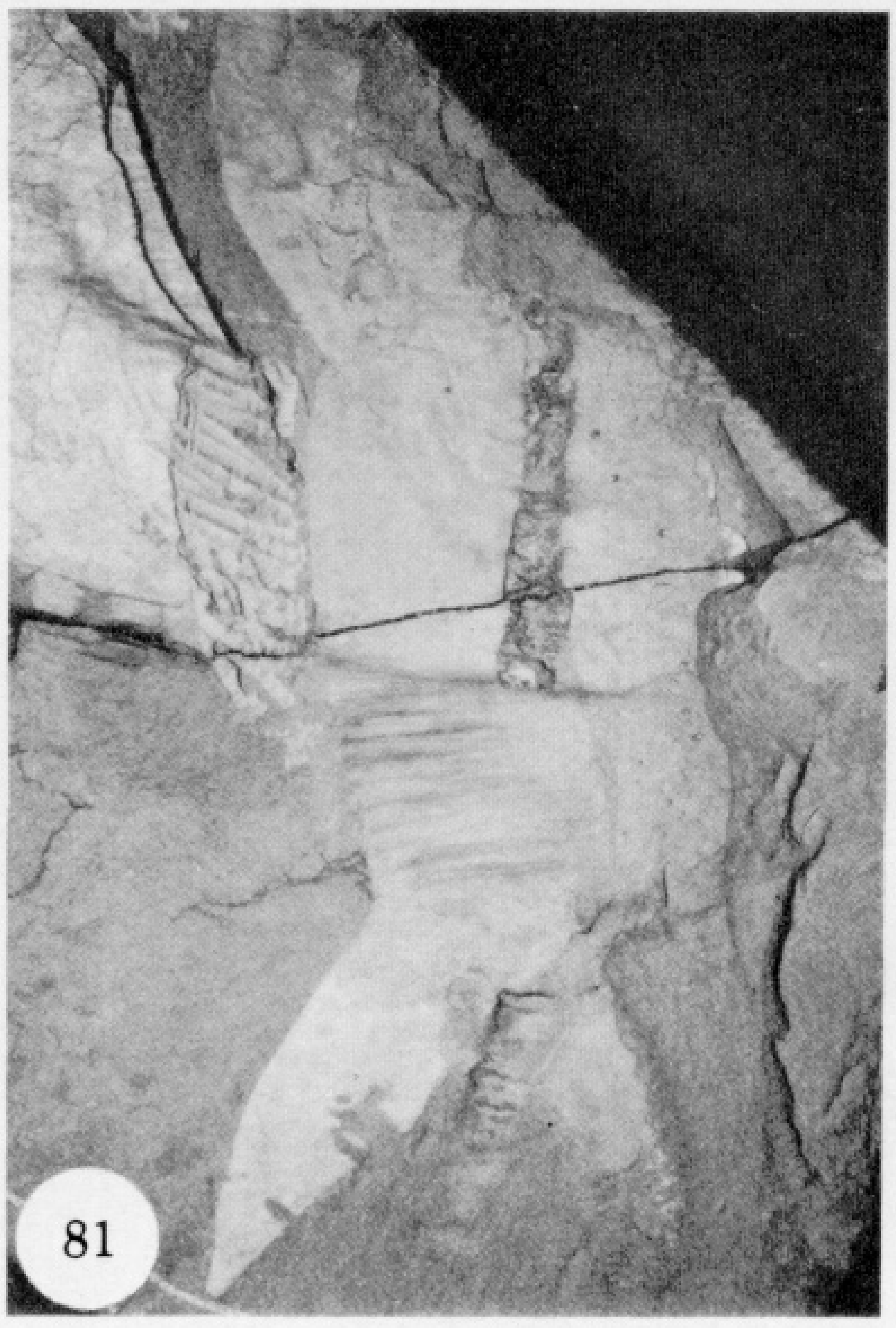
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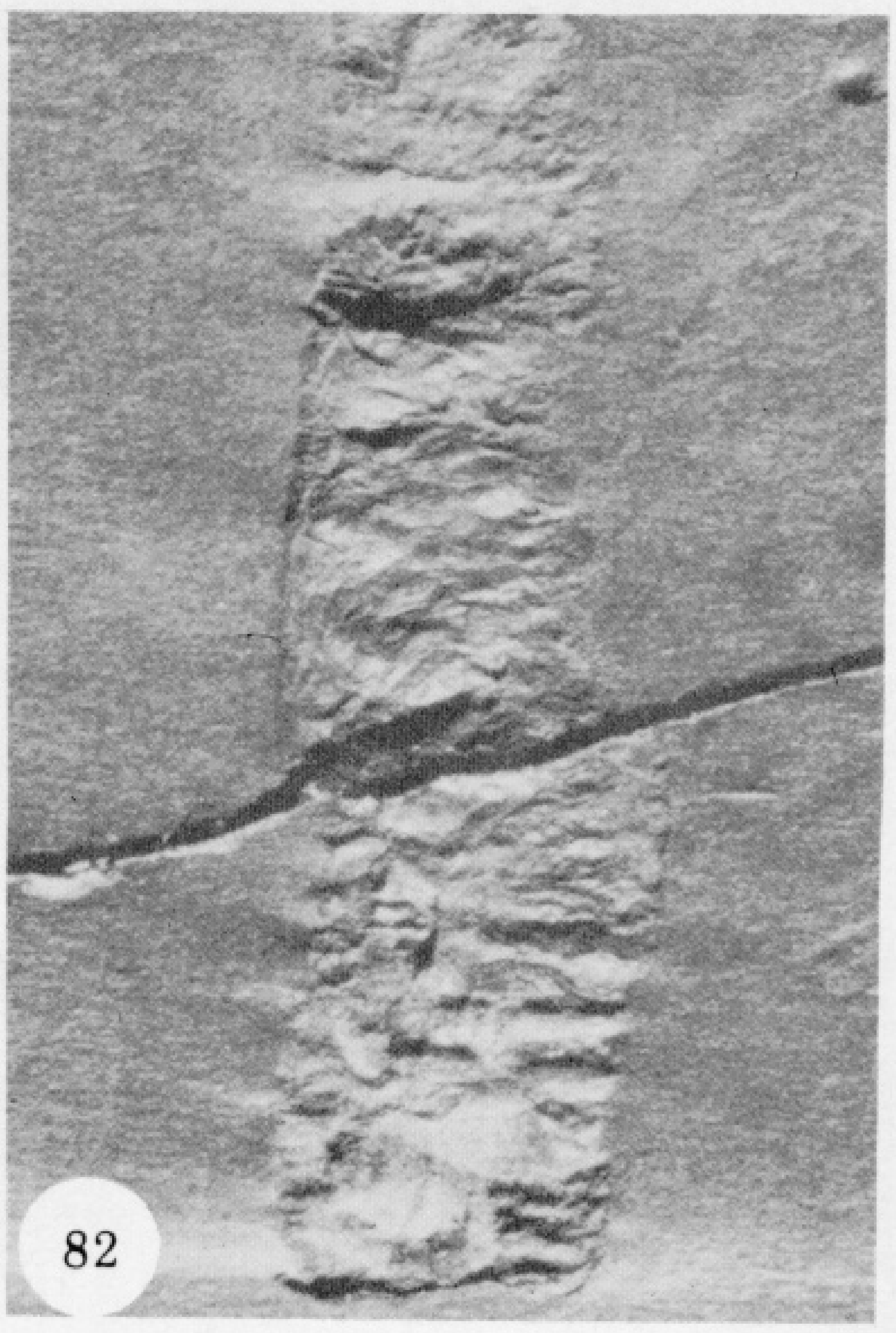
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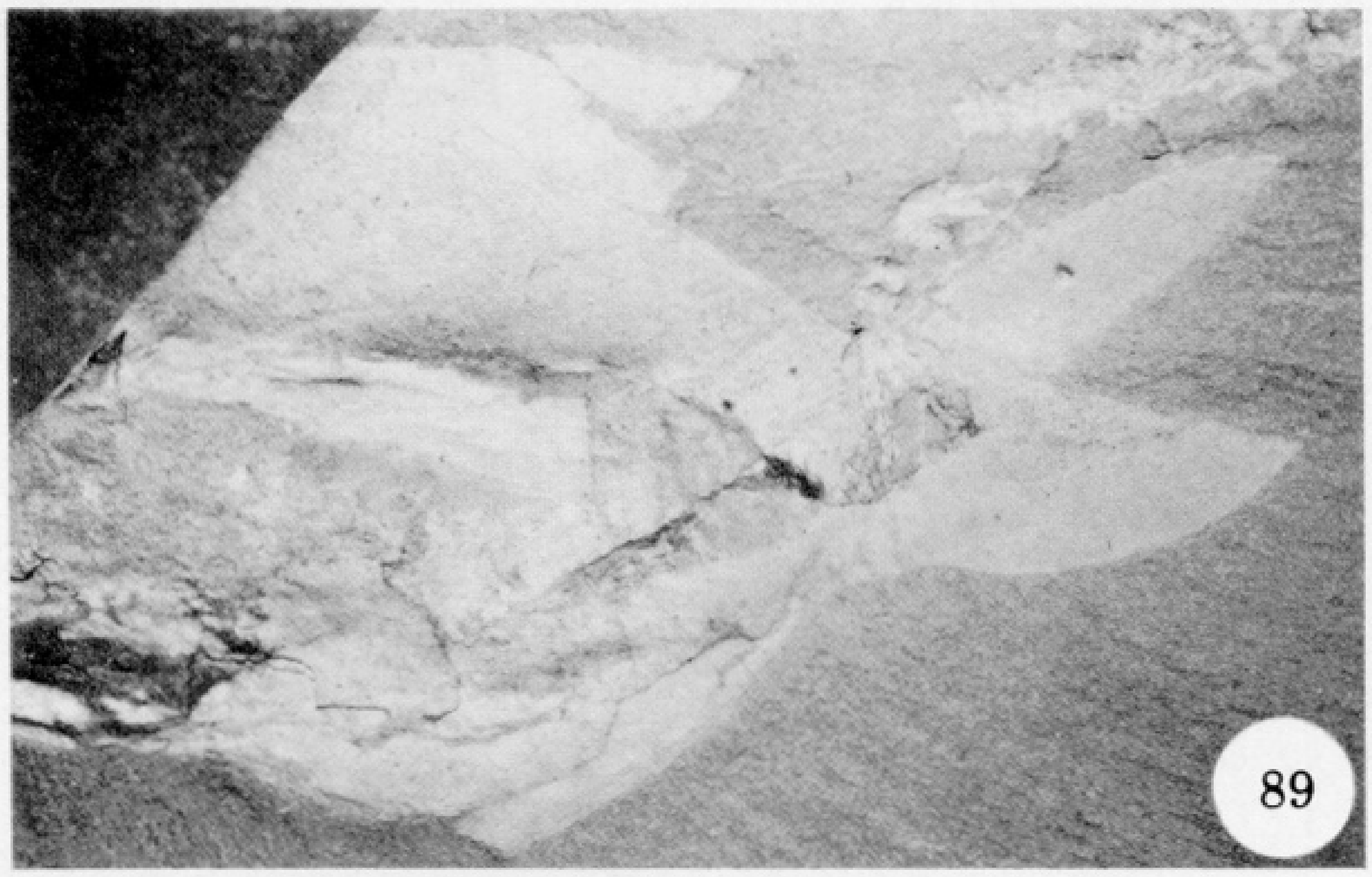
Figures 73–82. For description see opposite.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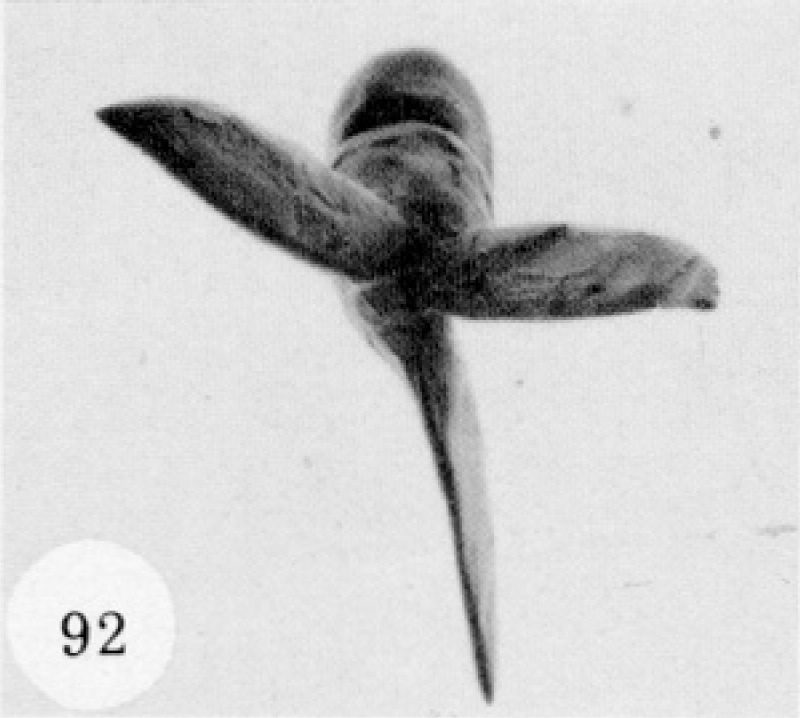
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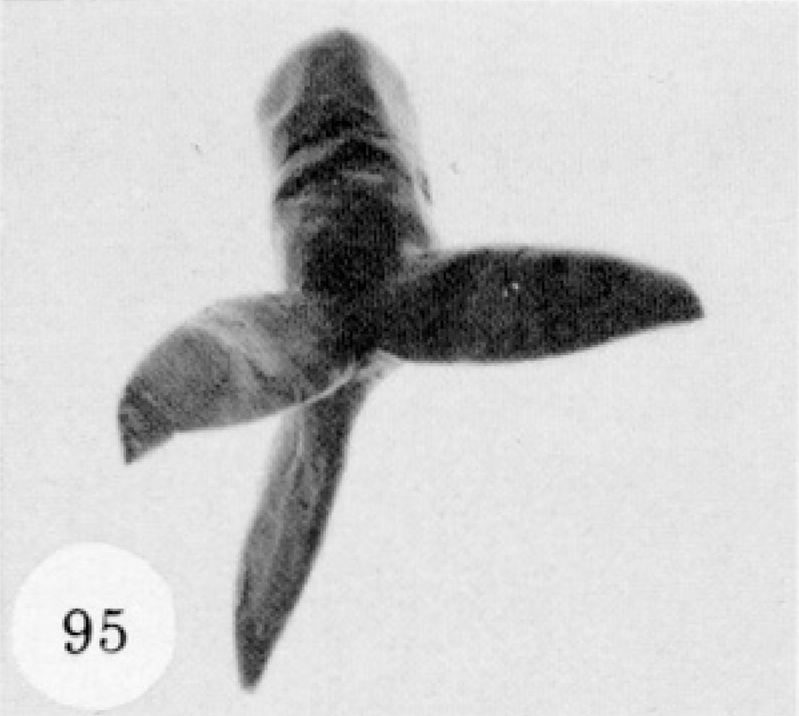
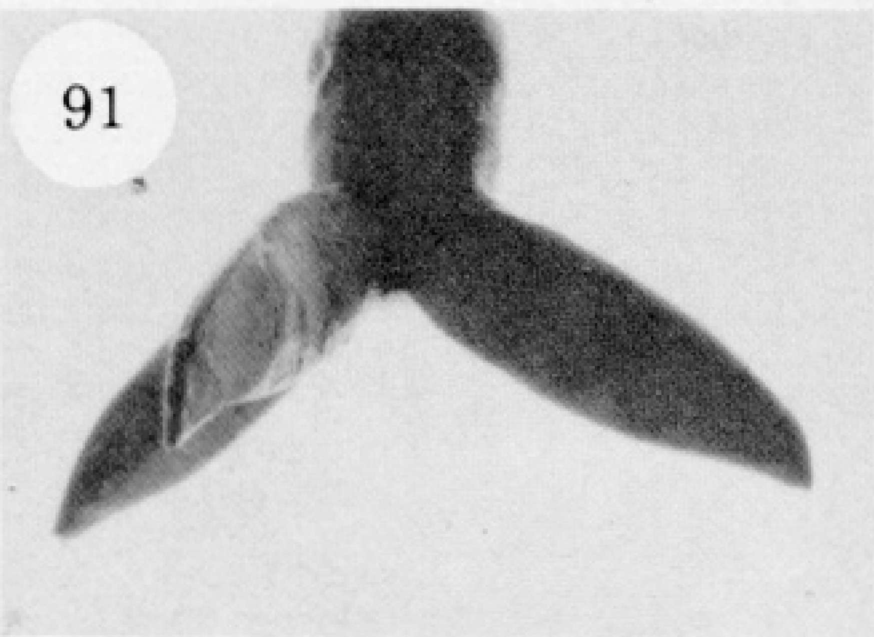

95


94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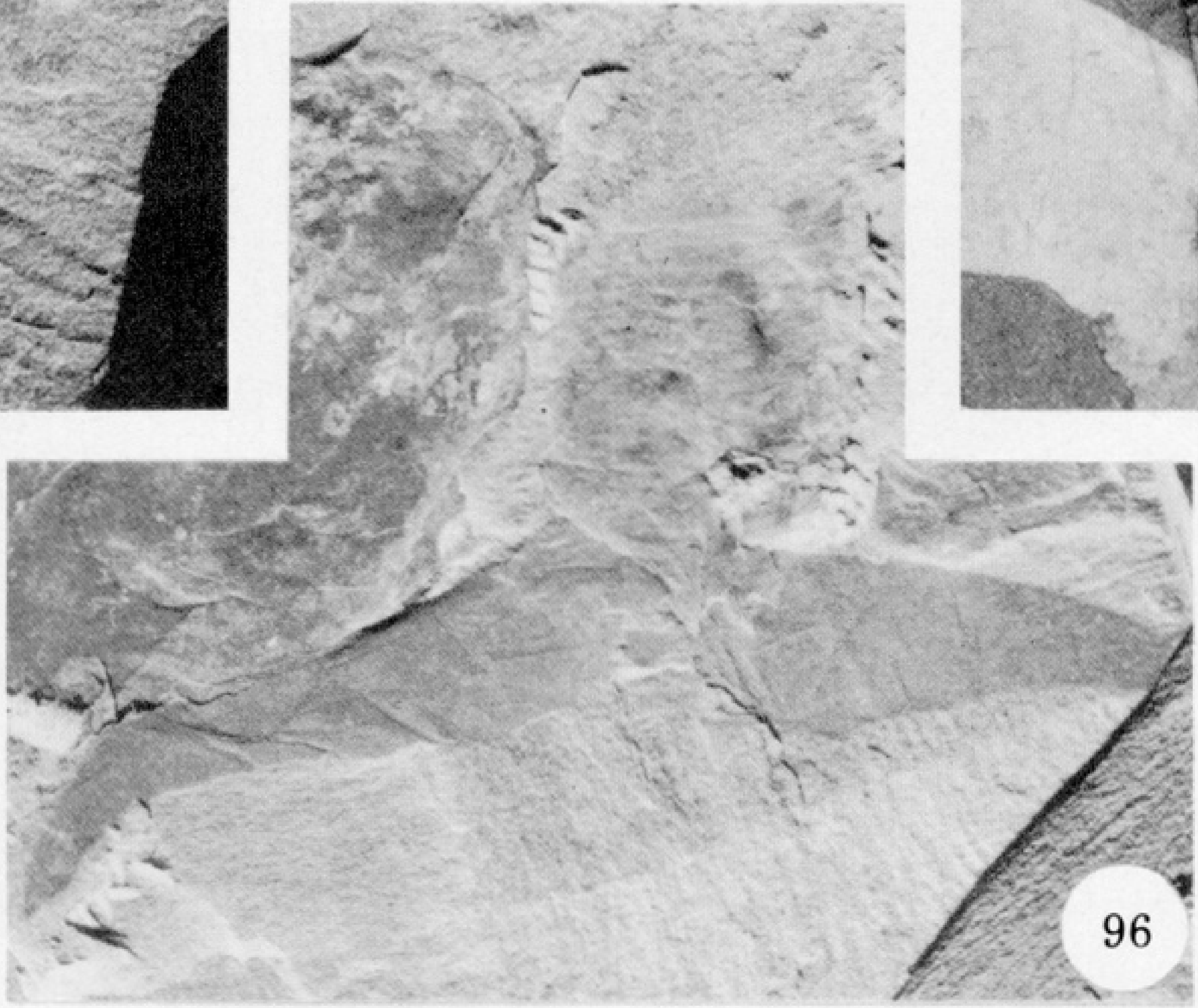
96

FIGURES 89–96. For description see opposite.