THE LOBOPOD ANIMAL *AYSHEAIA PEDUNCULATA* WALCOTT, MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

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[Plates 1–14]

CONTENTS

Fifteen specimens of *A. pedunculata* have been prepared, photographed, and drawn to show how each specimen is interpreted and how portions preserved only in part or counterpart are related to the whole. The body was elongate, sub-cylindrical, bearing one pair of conical, branched anterior appendages inserted in the lateral wall, and ten pairs of short, uniramous limbs; anteriorly no distinct head region, posteriorly the body merged into the bases of the last pair of limbs. The cuticle was unmineralized, flexible, the body wall, anterior appendage and limbs, annulated. On the trunk the evenly spaced annulations were high, sharp-crested dorsally, changing to low and rounded laterally and faint or absent ventrally; dorsally the annulations appear to have borne a row of seven tubercles, each tubercle sharp and possibly spinose apically. One annulation opposite midline of anterior appendage and limbs 1–9, three in the space intervening between these limbs, five between anterior appendage and first limb; posteriorly annulations of trunk formed a continuous series with those of last pair of limbs. This arrangement implies that the body consisted of at least 12 somites.

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Annulations of the anterior appendage were sharp-crested, uniform in height; branches of the appendage were long, slim, pointed, three at the tip and three along the anterior side, each branch slightly flexible and movable about its base. About ten annulations on each limb, uniform in height, the cross-section varied from low, rounded, to high, sharp-crested, as the limb was extended, contracted or flexed. The tip of the limb was bluntly rounded, on the posterior wall of limbs 1–8, and the anterior wall of limbs 9, 10, was a group of seven curved claws. On limbs 2–8 a forwardly directed spine on the seventh annulation and a shorter spine on the distal annulation, on limbs 9 and 10 a prominent, backwardly directed spine. In front of the anterior appendage the one or two annulations were faint, the anterior end of the body bluntly rounded, the mouth, surrounded by a ring of six or so slim papillae, situated medially on the anterior wall. The alimentary canal is not preserved as a sediment fill, but as a reflective strip, widest adjacent to the mouth, extending back to end between the bases of the last pair of limbs. Sagittal length 1 to 6 cm, smallest similar to largest specimen.

Aysheaia pedunculata is one of the rarer animals in the Burgess Shale, occurring in association with arthropods and worms, and to an exceptional extent with sponge fragments. It was not a burrowing, mud-ingesting animal, and the soft body would seemingly make it vulnerable to predatory arthropods. It may have been protected by living amid sponge colonies, the claws having facilitated clinging to the sponge, the anterior appendage holding the suctorial mouth in position to feed on the soft parts. While it shows resemblances to both Onychophora and Tardigrada, it is not placed in either group, nor in any taxon of higher rank than Family Aysheaiidae. It may be regarded as the sole known example of the types of lobopod animals from which the arthropod phylum Uniramia, and the Tardigrada, may have been derived.

1. Introduction

The term 'lobopod' was used by R. E. Snodgrass (1938, p. 134), when propounding a phylogeny of Annelida, Onychophora and Arthropoda. He considered that the latter two groups were derived from elongate, worm-like animals with lobopods, lobe-like outgrowths of the soft body wall that served as limbs. These lobopod animals were contrasted with worm-like animals having segmental clusters of chaetae, primitive chaetopods, from which were evolved the annelid groups. Snodgrass (1938; 1958, fig. 1) proposed a monophyletic series leading from lobopods to Onychophora and the Arthropoda. S. M. Manton (1973*b*) has also used the hypothetical lobopod animal, but in the context of compelling arguments that the Arthropoda are polyphyletic, placing such an animal at the origin of the Phylum Uniramia. In their discussions both authors refer to *Aysheaia pedunculata*, because of its great interest as the best known example of an ancient, aquatic lobopodial animal. The reconstruction of this fossil published by G. E. Hutchinson has frequently been reproduced. Certain features of it have been challenged by Snodgrass and later authors, particularly the nature of the anterior end of the animal and its appendages. The latest contribution by L. Delle Cave and A. M. Simonetta gives another reconstruction, but the novel features shown are inadequately based on interpretations of poor photographs. The following pages are intended to provide the factual basis for a re-assessment of the morphology of *A. pedunculata*. All available specimens have been prepared for the first time, and are portrayed by photographs and interpreted in drawings which combine information from part and counterpart. My results are summarized in the abstract and a new reconstruction (figure 86), and I hazard a guess (figure 90) at how the animal may have lived. It is a rare fossil from a unique locality, which shows that one kind of lobopod animal was living in a particular niche within a Cambrian marine community (Conway Morris *in* Valentine 1977, pp. 31–33). The animals in this community include an

astonishing variety of arthropods as well as bizarre forms, such as those described by Whittington (1975*a*) and Conway Morris (1977*a*, *b*) which, like *Aysheaia*, are not readily placed in Recent higher taxa.

2. Terminology and methods

The body of *Aysheaia* consisted of an elongated, annulated *trunk*, which bore on the ventrolateral side ten pairs of *limbs*. The anterior portion of the trunk was not separated from the remainder as a head; this region bore a pair of branched *anterior appendages*, the terminal mouth was surrounded by slim *papillae*. To avoid ambiguity when referring to directions, the median

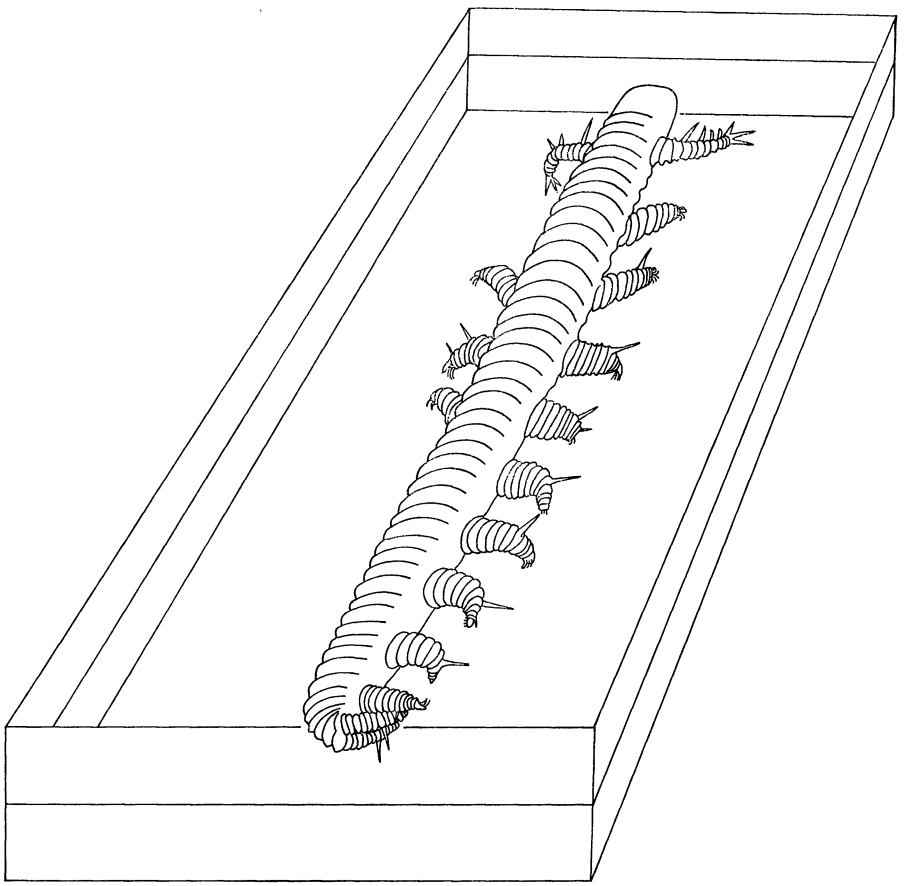

Figure 1. *Aysheaia pedunculata* Walcott, 1911. Representation of the attitude in which the original of U.S.N.M. 57655 (figure 4) lay immediately after burial. Bedding planes parallel to upper and lower surfaces of block.

longitudinal line in the body is termed *sagittal* (abbreviation, sag.), a line parallel to, but outside the sagittal line as *exsagittal* (abbreviation, exs.), and a direction at right angles to these as *transverse* (abbreviation, tr.). The trunk, limbs and anterior appendages are preserved (see § 3) as extremely thin layers, and the fossil is referred to as a *compression*. The orientation of the parts of the body at burial, relative to the horizontal bedding planes (figures 1, 2), varied. This orientation is referred to with reference to the trunk: *dorsoventral*, vertical plane in the sagittal line at right angles to the bedding (anterior portion of 57655, figure 1), and *lateral*, vertical plane parallel to bedding (posterior portion of 57655, figure 1). Divergence from these exact attitudes is denoted by the use of *oblique*. Thus in 83942*b* (figure 2) the orientation varies from

oblique lateral to lateral, from front to back of the body. When the rock was split to reveal a specimen, portions of it adhered to each side of the split (figure 3), the *part* and *counterpart*. Since no specimen is an exactly lateral compression, it is decided here to denote the part as that side which has some portion of the trunk in dorsal aspect facing the observer. Thus in 57655 the part would be formed by the lower half of the block portrayed in figure 1, whereas in 83942*b* (figure 2) it would be the upper half of the block. In the explanations of the plates the statement 'part only' or 'counterpart only' means that only one side of the specimen is known.

The photographs have been taken on panchromatic film, in ultraviolet radiation, after focusing in ordinary light. *Low angle radiation* has been directed at 30° to the horizontal, and the direction from which it came is given as west, northwest, etc. relative to north at the top of the page. Photographs referred to as *reflected* were taken in radiation coming from 65° to the horizontal, and the specimen was tilted about 12° so that the maximum amount of reflected radiation was directed into the camera. *Under water* photographs were taken in the same manner as reflected, except that the specimen was covered by a thin film of distilled water held under a cover glass. Camera-lucida drawings face the plates and show how a particular specimen has been interpreted. Minute scarps separate changes in level between one part of the body and another, and reveal their relationship. The scarps are delineated by a line along the upper edge, with hachures running down-slope from this line. The scarps were formed either when the rock was split, or by preparation, the changes in level resulting from the mode of preservation (§ 3). As figure 3 shows, limbs of one side of the body may be preserved only in either the part or counterpart. Drawings described as *explanatory* show part or counterpart, when only one or other is known. *Composite* drawings show the part and counterpart superimposed, to explain the relationships of parts of the body. The abbreviations listed include letters denoting the institution in which a particular specimen is housed. These letters are placed before the catalogue number in headings and plate and figure explanations, but omitted in the text; brevity is also served by using R 1, R 2, L 1–3, etc. in the text to refer to particular limbs.

3. Preservation

The body of *Aysheaia pedunculata* was presumably covered by a flexible cuticle, which is preserved as an extremely thin layer. There is no evidence of mineralization of the cuticle, such as there is in the trilobite *Olenoides serratus* (Whittington 1975*b*, p. 102). The layer may be composed of calcium aluminosilicates, as in the archaeopriapulid worms (Conway Morris 1977*c*, p. 5). In low angle radiation the layer appears darker than the surrounding rock. In high angle radiation it may be reflective, the trace of the alimentary canal (figure 35, plate 5) and the claws at the tips of the limbs (figure 52, plate 9) being more strongly reflective than the remainder of the layer. The layer is not planar, and hence in any one photograph the reflectivity may vary from one area to another, e.g. figure 35, plate 5, the right anterior appendage appears far more reflective than the adjacent parts of the body, but posteriorly the body becomes more strongly reflective as the orientation of the layer changes gradually but slightly. The darkness of the layer relative to that of the surrounding rock varies from specimen to specimen, in figures 9, 10, plate 1; figure 25, plate 4, it is marked, whereas in the original of figure 82, plate 14, it is so slight that the specimen is indistinguishable in a photograph in low angle radiation. Similarly, the strength of the reflectivity may be high, giving a striking

photograph (figure 23, plate 3; figure 48, plate 8), whereas in the originals of figure 77, plate 13; figure 81, plate 14, it is so low as to make it difficult to obtain a photograph by this method. Because of these differences in mode of preservation it is essential to use both methods in photography and in examination under the microscope. In using low angle radiation, the direction in which it crosses the fossil determines what details the photograph will reveal, e.g. figures 8, 9, plate 1; figures 19, 21, plate 3. Under water photographs enhance relative reflectivity and are particularly valuable in portraying details of morphology, e.g. the marginal outline in figure 13, plate 2, and tips of the limbs in figure 45, plate 7; figure 52, plate 9. The granularity of the surface of the fossil is evident in photographs at higher magnifications (figure 14, plate 2; figures 28, 29, plate 4; figure 38, plate 6) and minute spherical grains may be scattered over it. The granularity appears to be related to the grain-size of the rock, and the spheres are probably pyrite, for when broken they show the typical colour or the cubic habit. Extremely fine grains of pyrite (recognizable by their colour) may be scattered on the surface of the fossil, may form a patch (figure 85), may be associated with the trace of the alimentary canal, or as in 235880 (figure 79, plate 13) may form the dark lines just inside the margin of the trunk. These lines are dark because the pyrite is less reflective than the fossil. In 235883 (figures 65, 68, plate 11) both the scattered spheres and patches of minute grains of pyrite are present, the latter poorly reflective and hence dark (figures 67, 70, plate 11). In many specimens pyrite is present around the claws.

In addition to these features associated with preservation, there are those resulting from the compaction and subsequent history of the rock. These include the veins (shown in drawings to assist comparison with photographs) and folds (figures 41, 63), abrupt changes of level running across the fossil, as well as wrinkling. The latter is well seen in figures 5, 8, plate 1, crossing the fossil at about 10° to the sagittal line. Despite the wrinkling, annulations on trunk and limbs are preserved, enhanced if annulation and wrinkle happen to be parallel. In figure 19, plate 3, the wrinkling runs north to south in the photograph, and since the body is curved, the angle between the annulation and wrinkle varies from acute to zero. Thus in the anterior portion of the trunk wrinkles and annulations intersect obliquely, medially they are parallel and enhance each other. Posteriorly and in the limbs it may appear that wrinkling has obscured annulation, but in differently directed radiation this is seen not to be so (figure 21, plate 3). Despite the effects of wrinkling, and the occurrence of scattered spheres, tubercles may be faintly visible on the trunk annulations (figure 14, plate 2; figure 19, plate 3), though tubercle and sphere are similar in diameter. In 83942*a* (figures 25, 27, plate 4), in contrast, wrinkling is faint as are the annulations on the trunk, while stronger annulations are evident on the limbs. The granular, dark layer in which this specimen is preserved shows no trace of tuberculation. It is because of such variations in appearance that I am uncertain of the strength and frequency of tubercles on the annulations.

Each specimen has been revealed by a split along bedding planes in the rock, and this split has followed the parting formed by the flattened trunk and by such appendages as lay in approximately the same plane. Individual specimens so revealed are seen to be differently oriented, apparently dorsoventral (figures 5, 8, 9, plate 1), or lateral (figure 21, plate 3), but in reality only approximately so, the amount of obliquity varying. The body may be straight or gently curved as in these examples, sharply flexed (figure 51), or curved through more than 180° (figure 31). Detailed examination reveals further that there may be twisting along the longitudinal axis of the body, and that the appendages may not lie in the same plane as the

trunk, either within the series on one side, or on opposite sides. For example, figure 1 suggests the attitude in which the original of figures 5–9, plate 1, may have been buried, the body extended straight but rotated through about 90° along the axis. Thus the portion including anterior appendage and limbs 1–4 is oriented dorsoventral, behind here the progressive twist results in a lateral orientation so that L 5–9 are beneath the body and limb pair 10 lie one upon the other. As a result the anterior appendage, L 2–4 and 10, and R 1–10 lay in the same or closely adjacent bedding planes and the original split went through them. Figure 2 shows the attitude

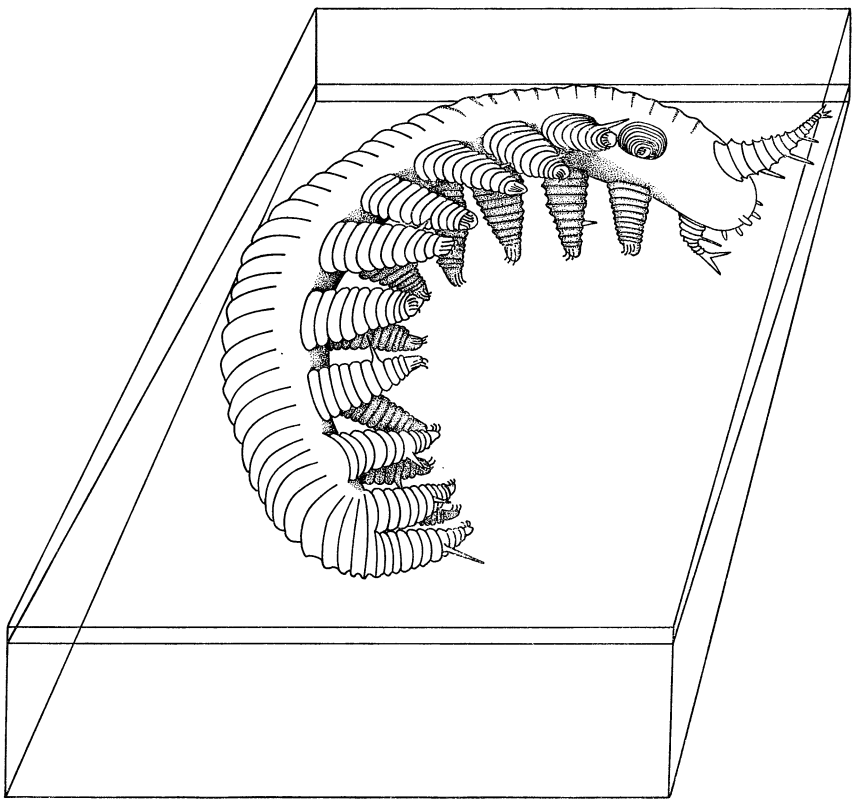

FIGURE 2. *Aysheaia pedunculata* Walcott, 1911. Representation of the attitude in which the original of U.S.N.M. 83942*b* (figure 31) lay immediately after burial. Bedding planes parallel to upper and lower surfaces of block. Animal is assumed to be lying on an imaginary surface which is not parallel to the bedding, but dips down, away from the observer.

in which the original of figure 31 may have lain immediately after burial. Not only was the body lying on its side, the longitudinal axis curved and slightly twisted along its length, but it appears to have sloped forward and downward relative to the horizontal bedding planes. Such inclination is invoked to explain why, in the compression (figure 31), R 5 overlies L 4 and R 9 overlies L 7. The original split was through the body, L 1–4, 10 and R 5–9. The alternation between opposing sides is because the longitudinal twisting brought them into approximately the same plane as the trunk. The anterior appendages were incompletely exposed in the part, and preparation has also revealed L 5–9. Twisting of the most anterior part of the body is invoked to explain the attitudes in which the anterior appendages are preserved as seen in figures 2, 31, the right nearer the observer than the body, the left curving down to emerge from beneath the body. In 83942*a* (figure 30) the body and R 1–10 were buried in the same plane,

through which the original split passed; since L 10 and R 10 were close together the split also partially reveals L 10. The bases of L 1–9 are visible (figures 25, 27, plate 4), and L 2 and L 6 have been prepared in the part, and are seen to diverge progressively distally from the plane in which the body lies. It is therefore deduced that this individual was buried lying on its side at an oblique angle, the right limb series parallel to the bedding planes, the left obliquely inclined. There was little longitudinal twisting of the axis, and preparation has shown that the left anterior appendage is inclined outward and upward (toward the observer in the counterpart, figure 28, plate 4) from the body, the right inclined in the opposite sense. Similar features are shown by other lateral oblique specimens, e.g. in 139206*b* (figure 18) the left series of limbs are in the same plane as the trunk, the right presumably preserved in the counterpart, which is missing. In 235882 (figure 62) and 35412 (figure 76) the left limb series is preserved, below and diverging distally from the right series. In several specimens a dark stain is associated with the anterior end of the body (figure 10, plate 1; figures 28, 29, plate 4; figure 42, plate 7; figures 65, 68, plate 11), in one with the posterior end (figure 19, plate 3), but in others (figures 32, 33, plate 5; figures 47, 50, plate 8; figure 71, plate 11; figure 77, plate 13) no such stain is in evidence. A dark stain is associated with many of the animals preserved in the Burgess Shale, and is considered to be the trace of decay products that seeped into the wet sediment at an early stage (Whittington 1977, p. 415; Conway Morris 1977*a*, p. 625). The size and intensity of the stain may be related to the amount of decay, and in § 5 (*a*) it is argued that some disruption of the anterior margin accompanied maximum development of the stain. The alimentary canal is not preserved as a filling showing relief, but only as a more strongly reflective strip, not sharply defined, discontinuous and variable in width (figures 34, 35, plate 5; figure 43, plate 7, figure 48, plate 8). The claws at the tips of the limbs are readily visible because they appear darker in low angle radiation than adjacent parts of the fossil, and are also more strongly reflective than any other part of the body (figure 52, plate 9).

The varied attitudes in which individuals of *A. pedunculata* were buried have been observed in other animals in the Burgess Shale (Whittington 1977, p. 413), and Conway Morris (1977*c*, p. 47) has observed longitudinal twisting in a fossil worm. It is concluded that these animals were caught up by a turbulent cloud of sediment in suspension which was moving down-slope, and the bodies were buried as the current slowed down and the suspension settled out. This stage of burial is depicted in figures 1 and 2. The individuals of *A. pedunculata* may well have been alive when engulfed by the suspension, so that at burial the trunk and appendages had their original convexity. Probably as a result of turbulence the appendages were twisted and flexed. Thus in 57655 (figure 1) the left anterior appendage was bent down distally, L 1, 5–9 swept under the body, R 8 bent down, etc. Thus one may account for the appearance of the fossil, i.e. the amount of flexure and outline of individual limbs, and directions of lateral spines. Between the stage shown in figure 1 and the preserved specimen a flattening of trunk and appendages has taken place, and the fossil is therefore called a compression (since it is not merely an impression in the rock). The use of this term is not intended to imply that flattening is solely the result of compaction of the sediment, i.e. that the body was 'squashed flat'. The processes of decay of the body, acting within a shorter time than compaction, must have played their part in preservation (Whittington 1975*a*, pp. 10, 11). However, if decay in *A. pedunculata* had been sufficiently rapid after burial to cause collapse of trunk and appendages, one would have expected to see evidence of such collapse. On the contrary, the annulations on trunk or appendages are subparallel, and the gradual change in direction of annulations in a flexed limb

is preserved. I thus conclude that decay was slowed and then inhibited by some factor or factors, so that not only was a soft-bodied animal preserved, but reduction of volume in the vertical direction (compaction) proceeded at much the same rate in the animal body as in the surrounding sediment. Only in this way am I able to account for the preservation of *Opabinia regalis* (Whittington 1975*a*, pp. 10–11) and *Naraoia compacta* (Whittington 1977, pp. 413–415), and the present species. In the latter (figure 3) the trunk is reduced to a flat film, lying in the same

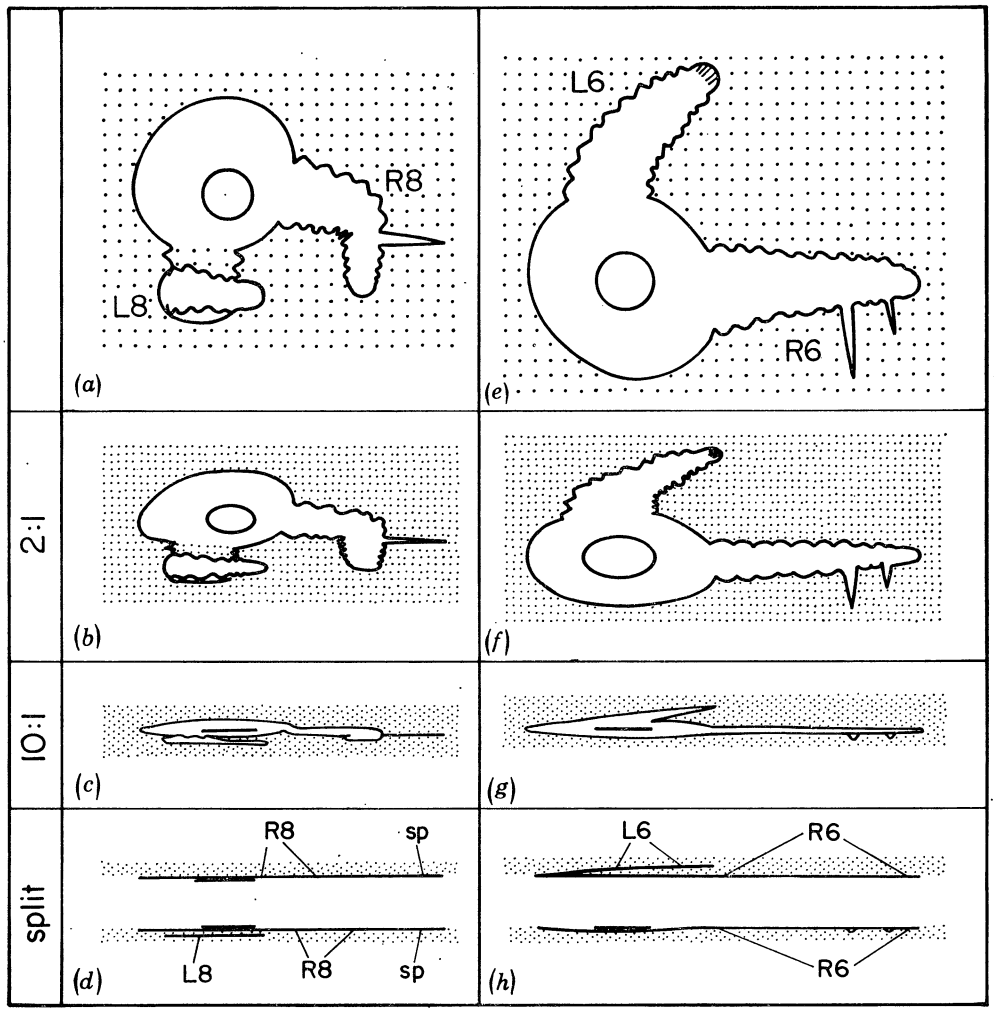

FIGURE 3. Cross sections through the body of two specimens of *Aysheaia pedunculata* to show the effects of post-burial compression and the way the rock has split to give part and counterpart. (*a*) Cross section through U.S.N.M. 57655 at limb pair 8 at burial; (*e*) cross section through U.S.N.M. 83942*a* at limb pair 6 at burial; (*b, c, f, g*) show effects of compression at ratios indicated; (*d, h*) show position of split. Part of 57655 (figure 8, plate 1) is lower half of (*d*), whereas part of 83942*a* (figure 27, plate 4) is upper half of (*h*).

bedding plane as the limbs of one side (also a flat film), while the limbs of the other side are reduced to a flat film which lies at a low angle to that of the trunk. Much of this reduction may have taken place relatively early, in a stage in which water was being expelled from the sediment and compaction proceeding relatively rapidly. Perhaps it was during such a stage that the dark stain was formed. The effect of this compression on a limb directed outward and upward or downward (i.e. obliquely across the bedding planes) is to reduce the apparent length but not the width, whereas there would be no such effect on a limb disposed parallel to the

bedding planes. Thus in R 8 of figures 3 (*a*), 4, or R 7–9 of figure 62, the outline is explained by the limbs having been bent down (away from observer), and the position of the claws in figure 62 supports this interpretation. On the other hand, the outline of the right limbs in figures 3 (*e*), 30, and the left limbs in figure 18, may most nearly reflect the original dimensions since they appear to have been compressed in one bedding plane.

4. Descriptions of specimens of *Aysheaia pedunculata* Walcott, 1911

(*a*) *Locality, stratigraphical horizon, number of specimens, associated fauna*

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

The U.S. National Museum collections include the 13 specimens described below, a poorly preserved complete individual 13 mm in length on the slab U.S.N.M. 57497, and two fragmentary specimens (U.S.N.M. 199911 and 202163). All are labelled '35k' with no indication of the level in the Phyllopod bed from which they came. However Walcott (1912, p. 153) states that *A. pedunculata* came from his layer no. 10, 7.6 cm (3 in) to 0.48 m (1 ft 7 in) above the base of the Phyllopod bed. In the Geological Survey of Canada party's measured section (Whittington 1971*a*, fig. 3) the base of the bed was at 1.5 m (5 ft) and a single fragment (G.S.C. 54851) of *A. pedunculata* was obtained in 1966 from shales between 1.5 m (5 ft) and 1.65 m (5 ft 5 in). The two specimens in the Royal Ontario Museum were obtained in 1975 from talus in Walcott's quarry. The total of 16 specimens in the Walcott collection, and the find of one fragmentary specimen in two seasons of quarrying by the Geological Survey of Canada parties, shows the great rarity of this species. Walcott (1912, p. 153) gave a list of the varied fauna in his layer no. 10. The worms *Ottoia prolifica*, *Wiwaxia corrugata*, and *Selkirkia columbia*, the arthropods *Marrella splendens*, *Naraoia compacta* and *Canadaspis perfecta*, the bivalved shell of a possible bradoriid ostracode, and the sponges referred to in § 5 (*b*), occur on the same pieces of rock as the specimens described herein.

(*b*) *U.S.N.M.* 57655

Figures 1, 3 (*a–d*), 4; figures 5–11, plate 1; figures 12–14, plate 2.

1911 Walcott, p. 117, pl. 23, figs, 8, 9 (counterpart).
1916 Walcott, pl. 12, figs. 8, 9 (counterpart).
1930 Hutchinson, p. 14.
1931 Walcott, p. 8.
1949 Cuénot, *in* Grassé pp. 34–35.
1953 Dechaseaux, *in* Piveteau, pp. 4–5, fig. 2 (counterpart).
1958 Snodgrass, pp. 2–4, fig. 2*d* (counterpart).
1959 Moore, p. O 18–19. fig. 12, 1*a*, 1*b* (counterpart).
1966 Sharov, pp. 21–22, fig. 13 (counterpart).
1969 Hutchinson, pp. 1062–1063.
1975 Cave & Simonetta, p. 69, figs. 2*a* (part), 2*b* (counterpart).

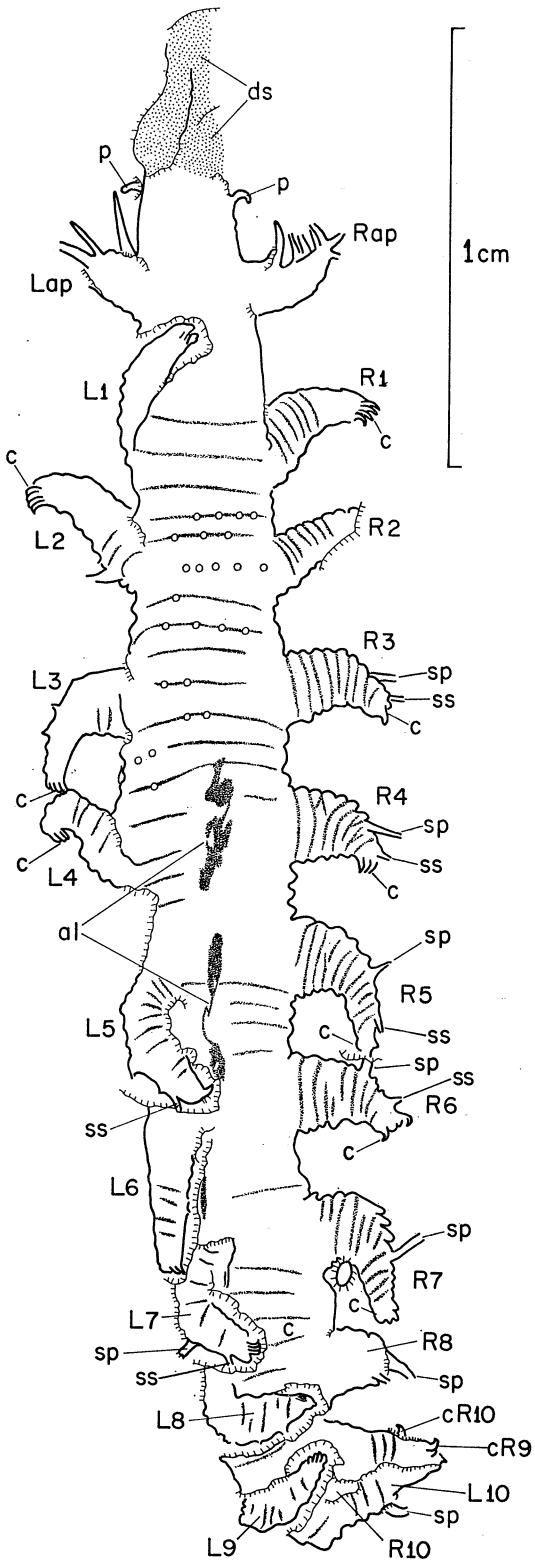

FIGURE 4

DESCRIPTION OF PLATE 1 AND FIGURE 4

Aysheaia pedunculata Walcott, 1911. U.S.N.M. 57655, holotype, oblique dorsoventral to lateral, Phyllopod bed, Walcott quarry.

FIGURE 4. Composite explanatory drawing of part and counterpart.

FIGURES 5, 6, 10, 11. Counterpart, respectively northwest (magn. × 3.5), reflected (magn. × 3·3), anterior portion north northwest and reflected (magn. × 10).

FIGURES 7, 8, 9. Part, respectively reflected, after preparation (magn. × 5), east (magn. × 3.5), northwest, before preparation (magn. × 3.5).


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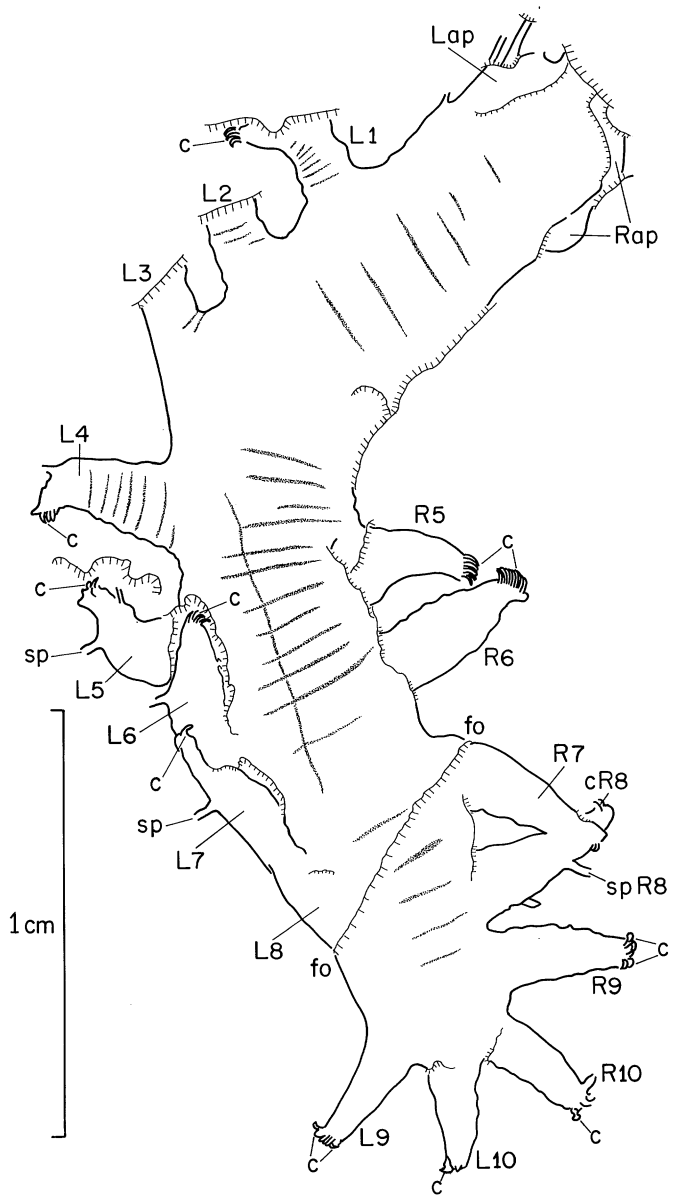


FIGURE 17

DESCRIPTION OF PLATE 2 AND FIGURE 17

Aysheaia pedunculata Walcott, 1911, Phyllopod bed, Walcott quarry

FIGURES 12, 13, 14. U.S.N.M. 57655, holotype, part, respectively R 4–6, west northwest (magn. × 12); R 2–6, under water (magn. × 10); anterior portion, southwest (magn. × 7).

FIGURES 15, 16. U.S.N.M. 139206a, dorsoventral, respectively counterpart, northwest (magn. × 5); part, north northwest (magn. × 5).

FIGURE 17. U.S.N.M. 139206a, composite explanatory drawing of part and counterpart.

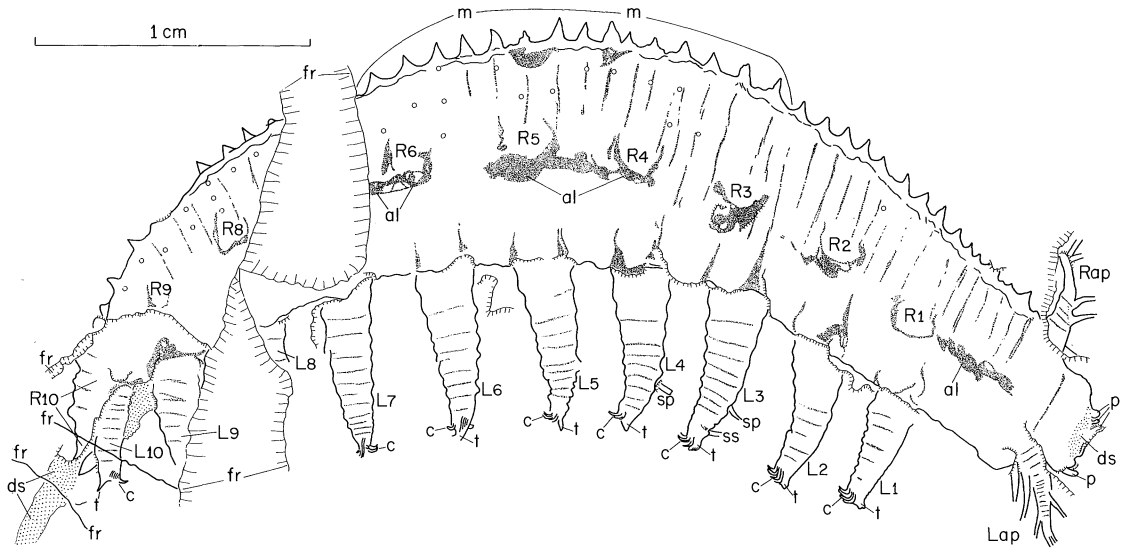


FIGURE 18

DESCRIPTION OF PLATE 3 AND FIGURE 18

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 139206b, oblique lateral, counterpart only, Phyllopod bed, Walcott quarry

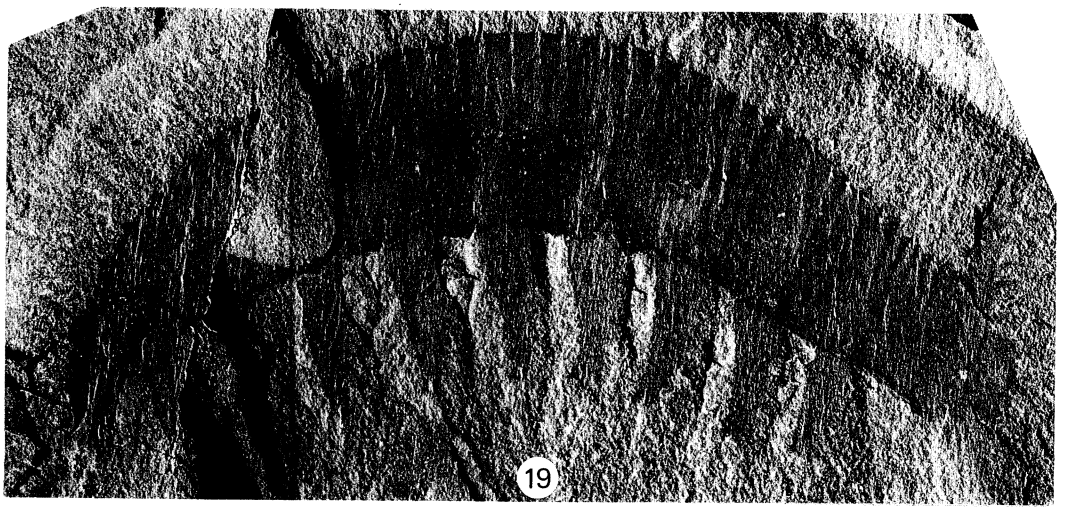
FIGURE 18. Explanatory drawing.

FIGURES 19, 21, 23. Entire, respectively east northeast, north northwest, reflected (magn. × 3.3).

FIGURE 20. First and second left limbs, northwest (magn. × 10).

FIGURE 22. Third and fourth left limbs, northwest (magn. × 10).

FIGURE 24. Anterior portion, showing anterior appendages and papillae, west southwest (magn. × 10).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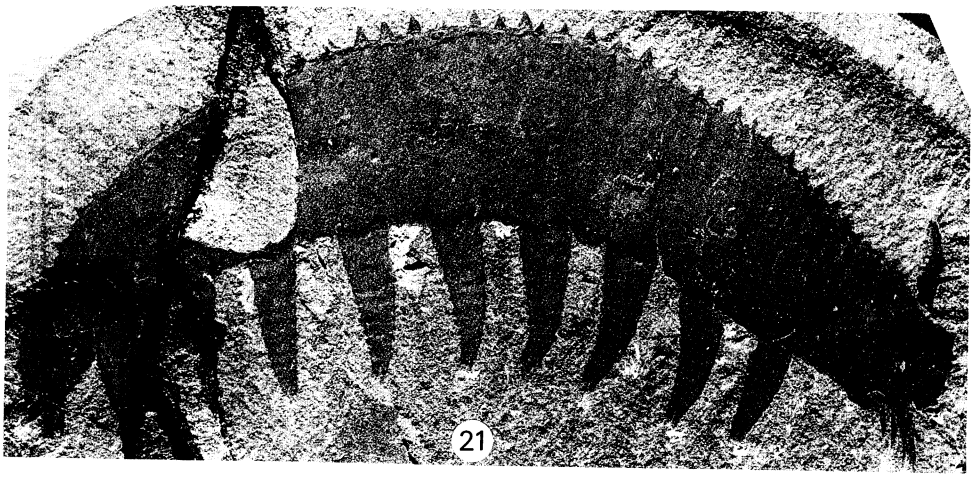
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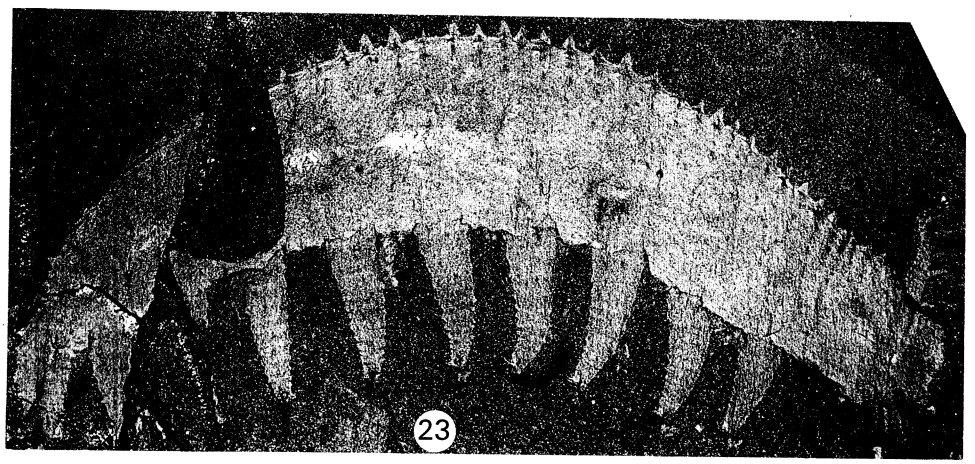
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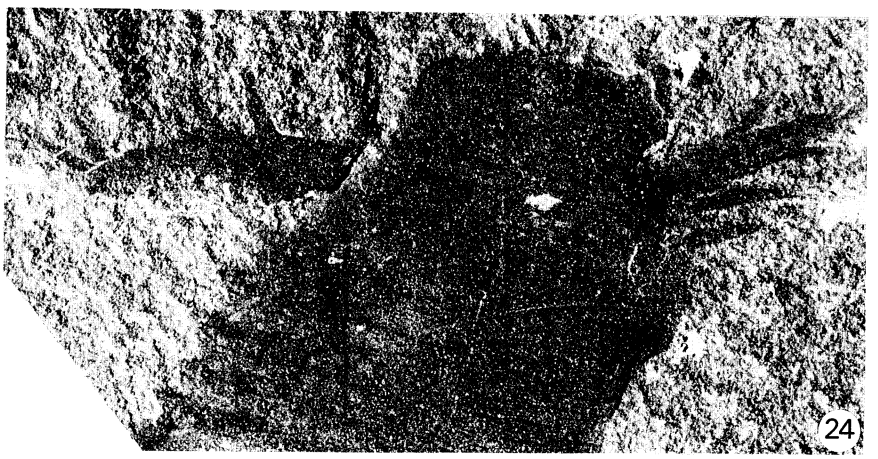
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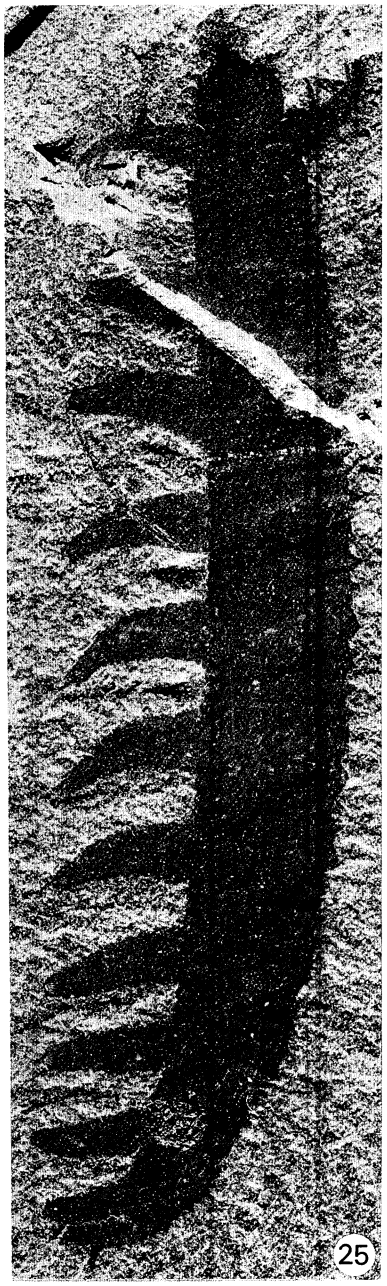
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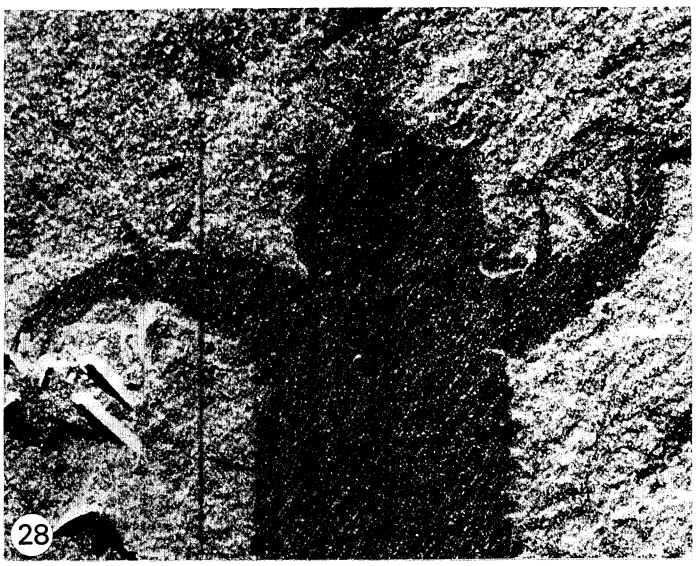
27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29

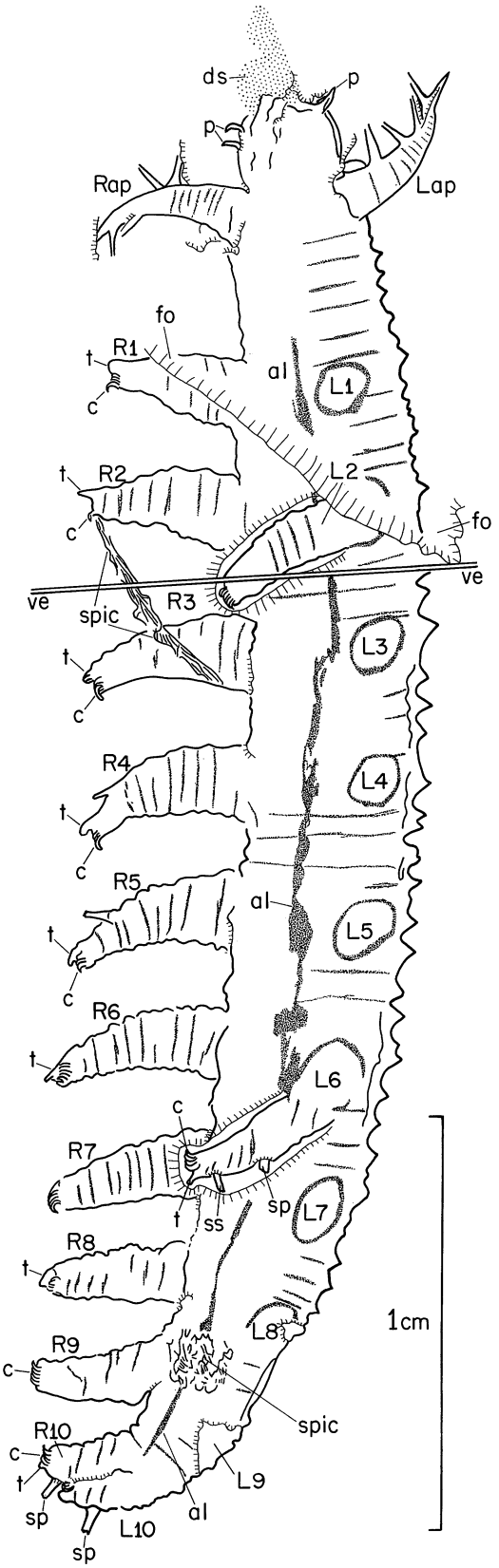


FIGURE 30

DESCRIPTION OF PLATE 4 AND FIGURE 30

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 83942a, oblique dorsoventral, Phyllopod bed, Walcott quarry

FIGURES 25, 26, 28. Counterpart, respectively north (magn. 3.3); reflected (magn. × 3.3); anterior portion, south (magn. × 10).

FIGURES 27, 29. Part, respectively southwest (magn. × 3.3); anterior portion, southwest (magn. × 10).

FIGURE 30. Composite explanatory drawing of part and counterpart, ventrolateral view.

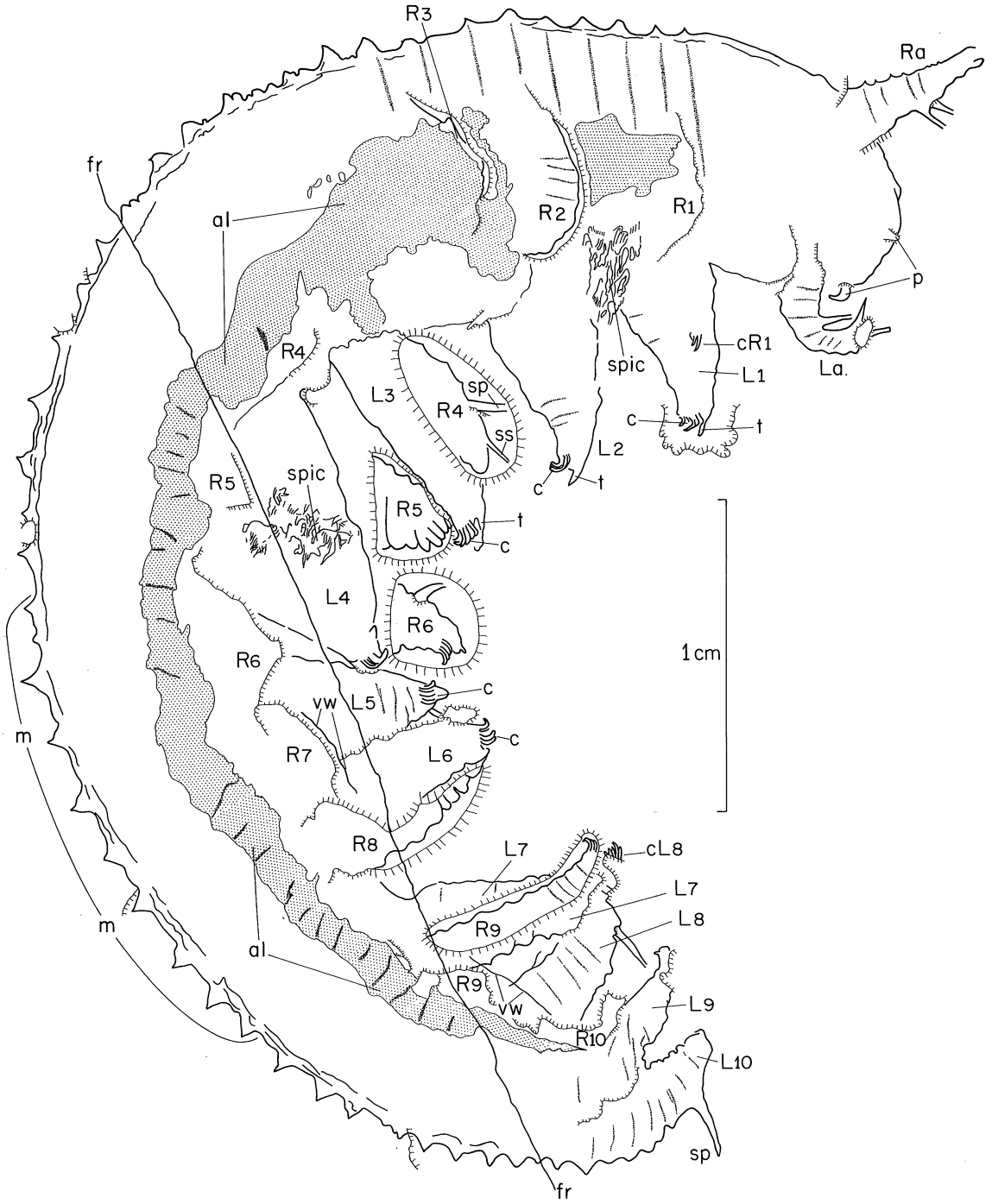


FIGURE 31

DESCRIPTION OF PLATE 5 AND FIGURE 31

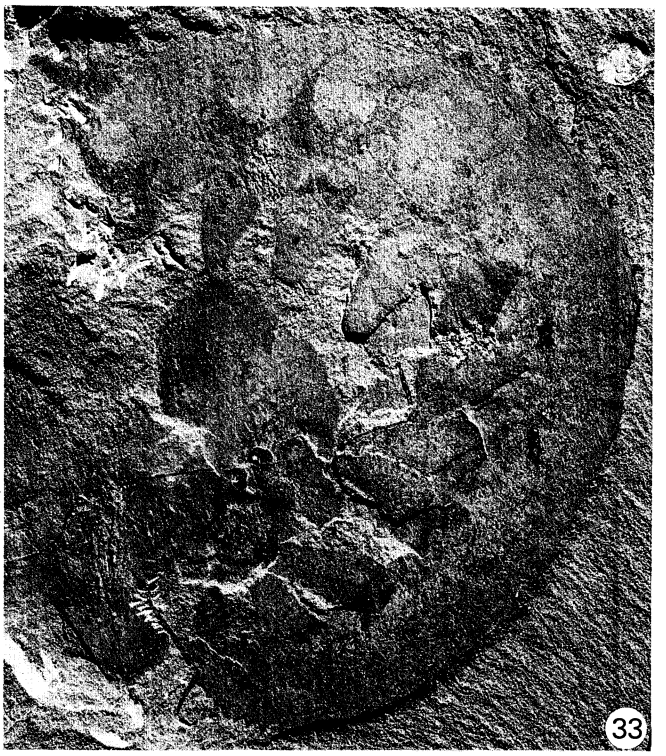
Aysheaia pedunculata Walcott, 1911, U.S.N.M. 83942b, oblique lateral, Phyllopod bed, Walcott quarry

FIGURE 31. Composite explanatory drawing of part and counterpart, ventrolateral view.

FIGURES 32, 34. Counterpart, respectively north, reflected (magn. × 2.5).

FIGURES 33, 35. Part, respectively north, reflected (magn. × 2.5).

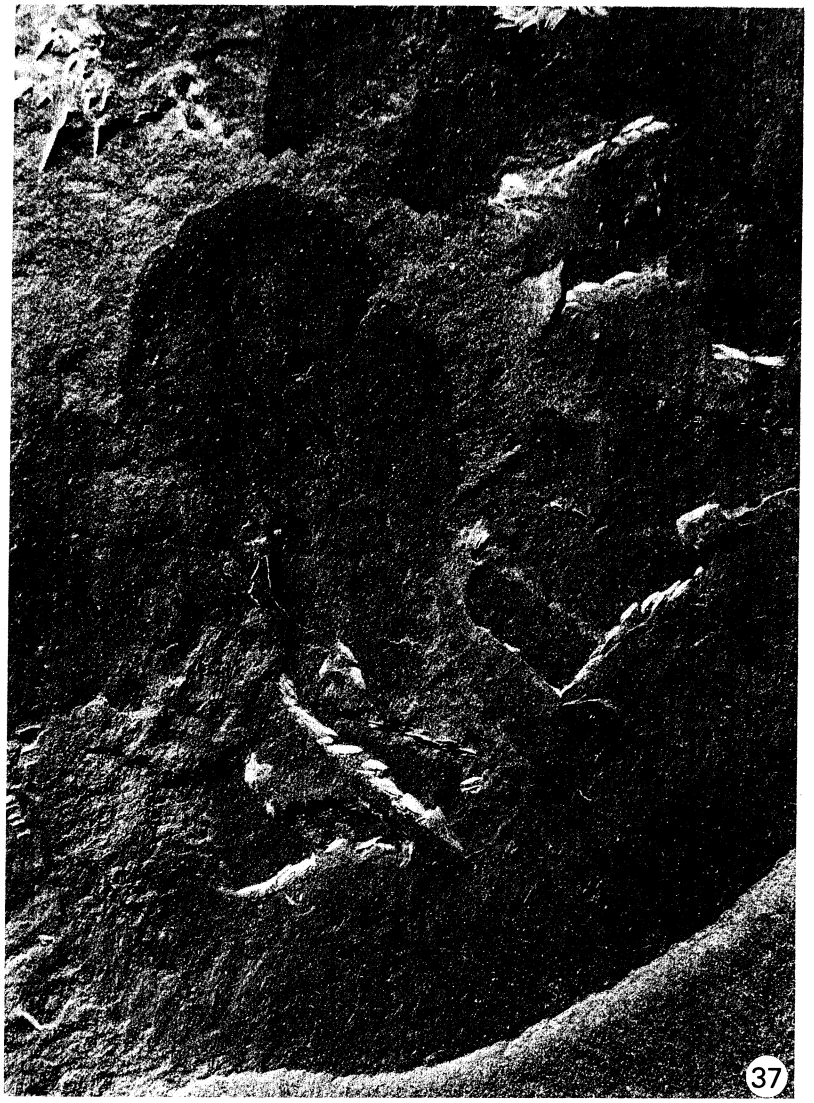

32


33


34


35


36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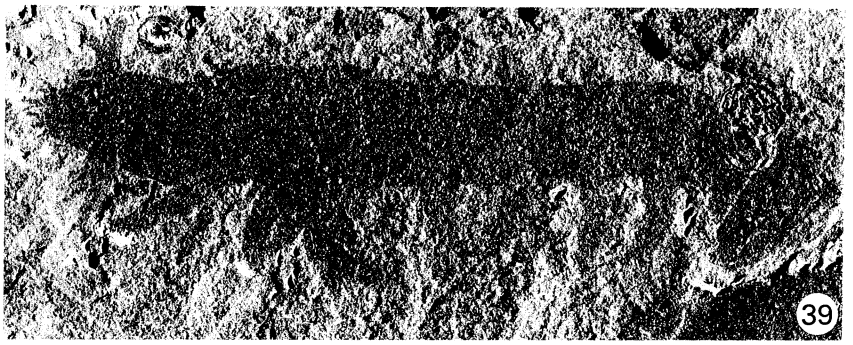
38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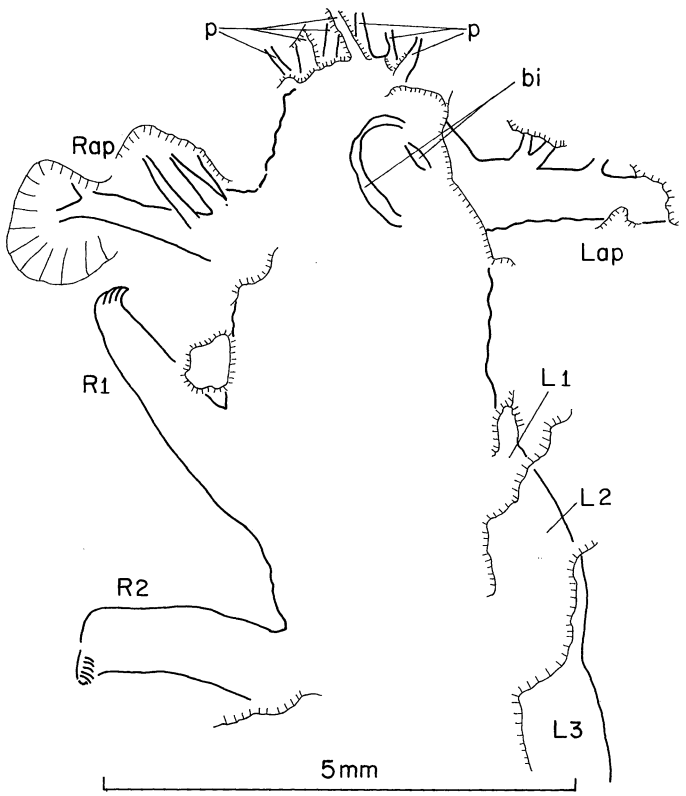


FIGURE 40

DESCRIPTION OF PLATE 6 AND FIGURE 40

Aysheaia pedunculata Walcott, 1911, Phyllopod bed, Walcott quarry

FIGURES 36, 37. U.S.N.M. 83942b, part, respectively anterior portion, south (magn. × 5); posterior portion after preparation, south (magn. × 5).

FIGURES 38, 39. U.S.N.M. 200331, oblique dorsoventral, counterpart only, respectively anterior portion, south (magn. × 10); entire, east (magn. × 5).

FIGURE 40. U.S.N.M. 200331, explanatory drawing of anterior portion.

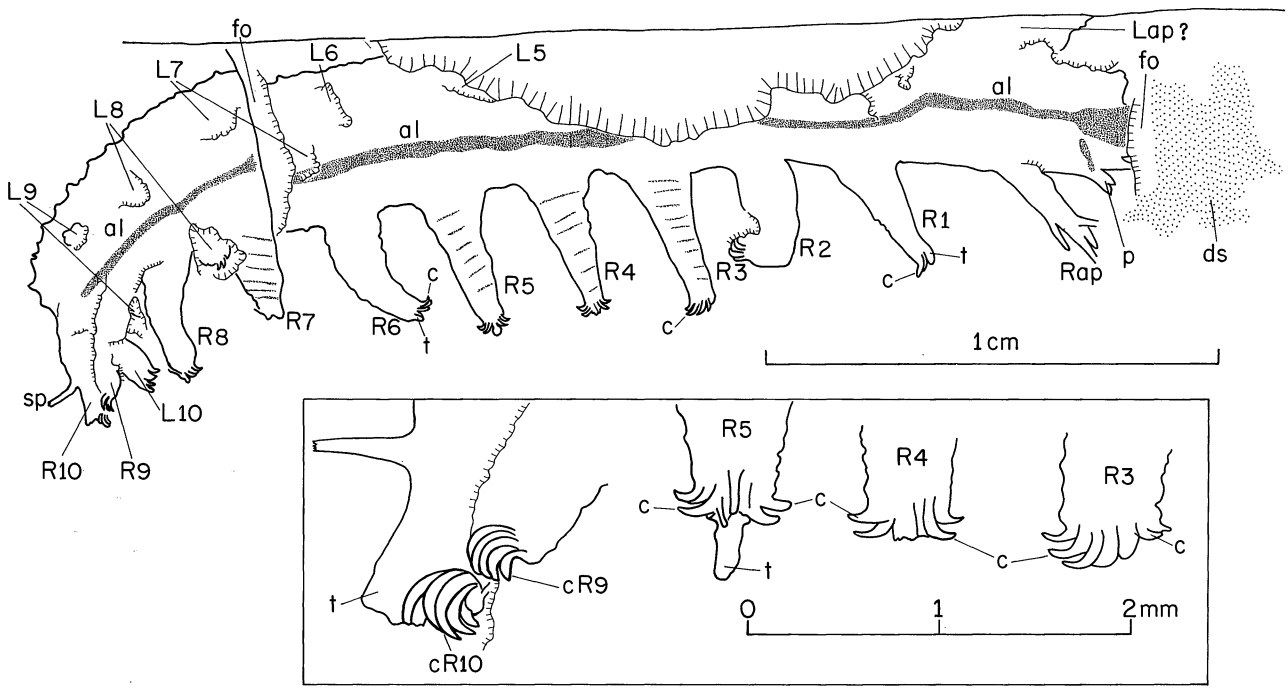


FIGURE 41

DESCRIPTION OF PLATE 7 AND FIGURE 41

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 235879, oblique dorsoventral to lateral, part only, Phyllopod bed, Walcott quarry

FIGURE 41. Explanatory drawing with (inset) details of tips of limbs.

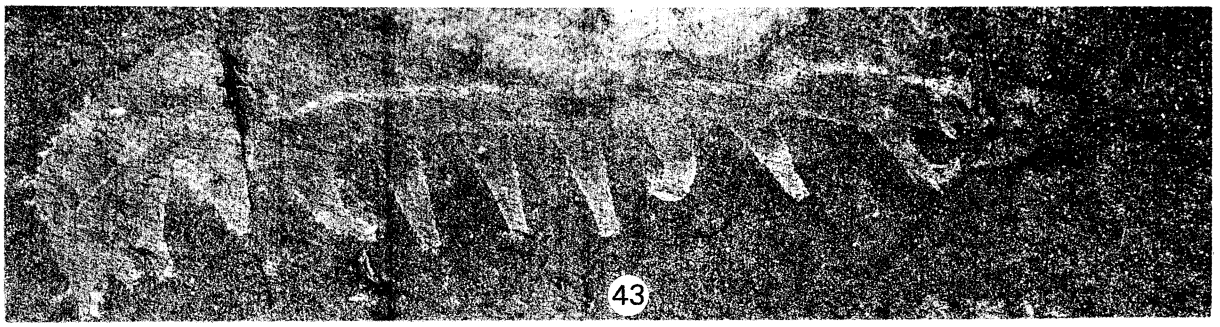
FIGURES 42, 43. Entire, respectively northwest, under water (magn. × 5).

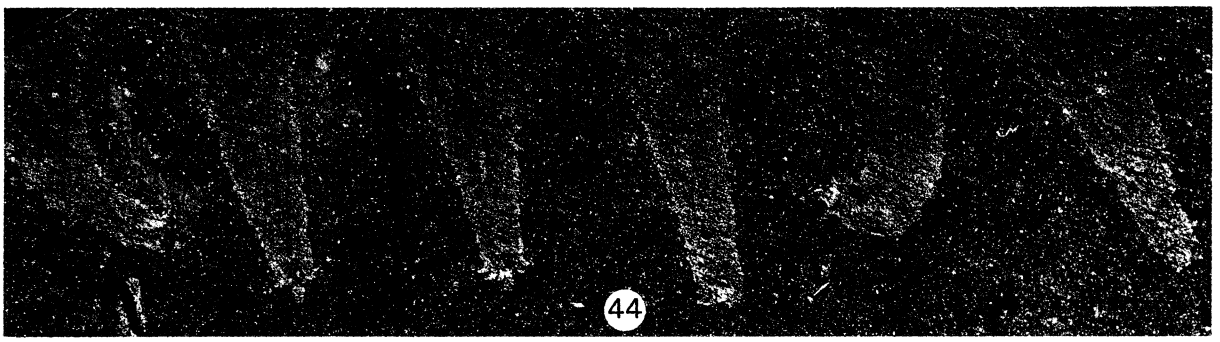
FIGURE 44. Right limbs 1–6, under water (magn. × 15).

FIGURE 45. Posterior portion, under water (magn. × 15).

FIGURE 46. Anterior portion, reflected (magn. × 10).


42


43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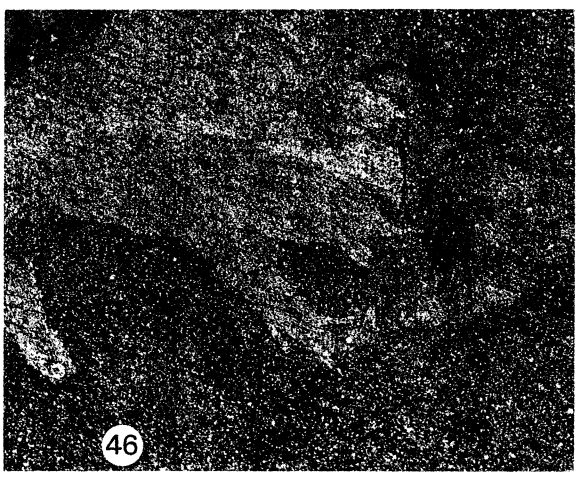
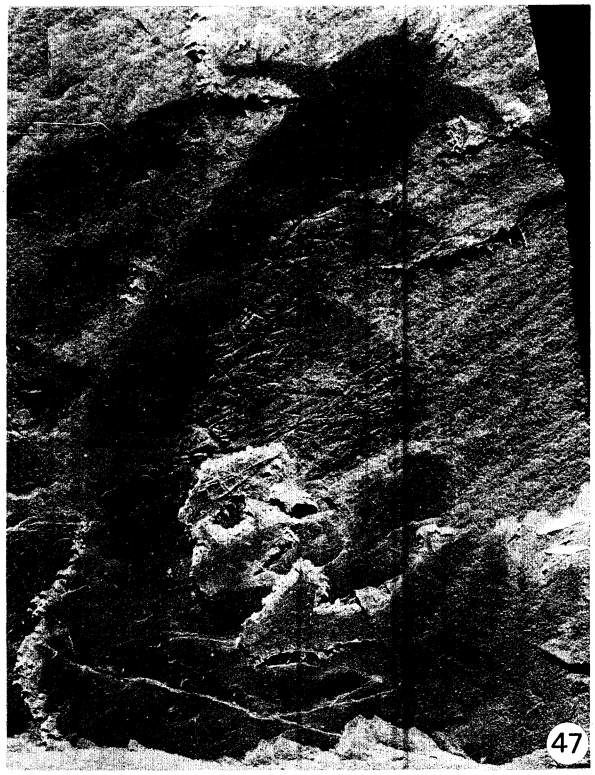
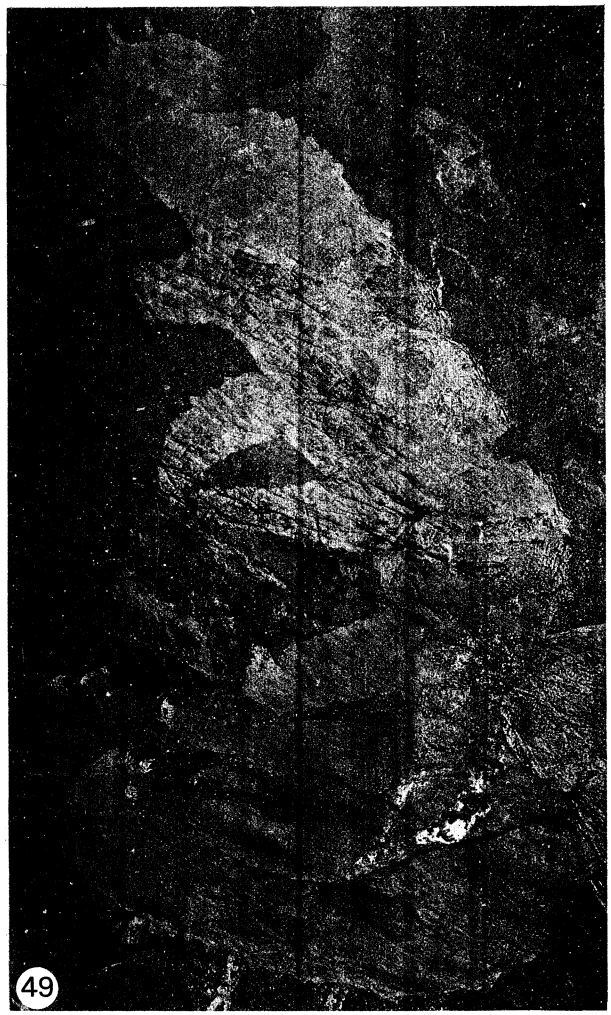
45


46


47


48


49


50

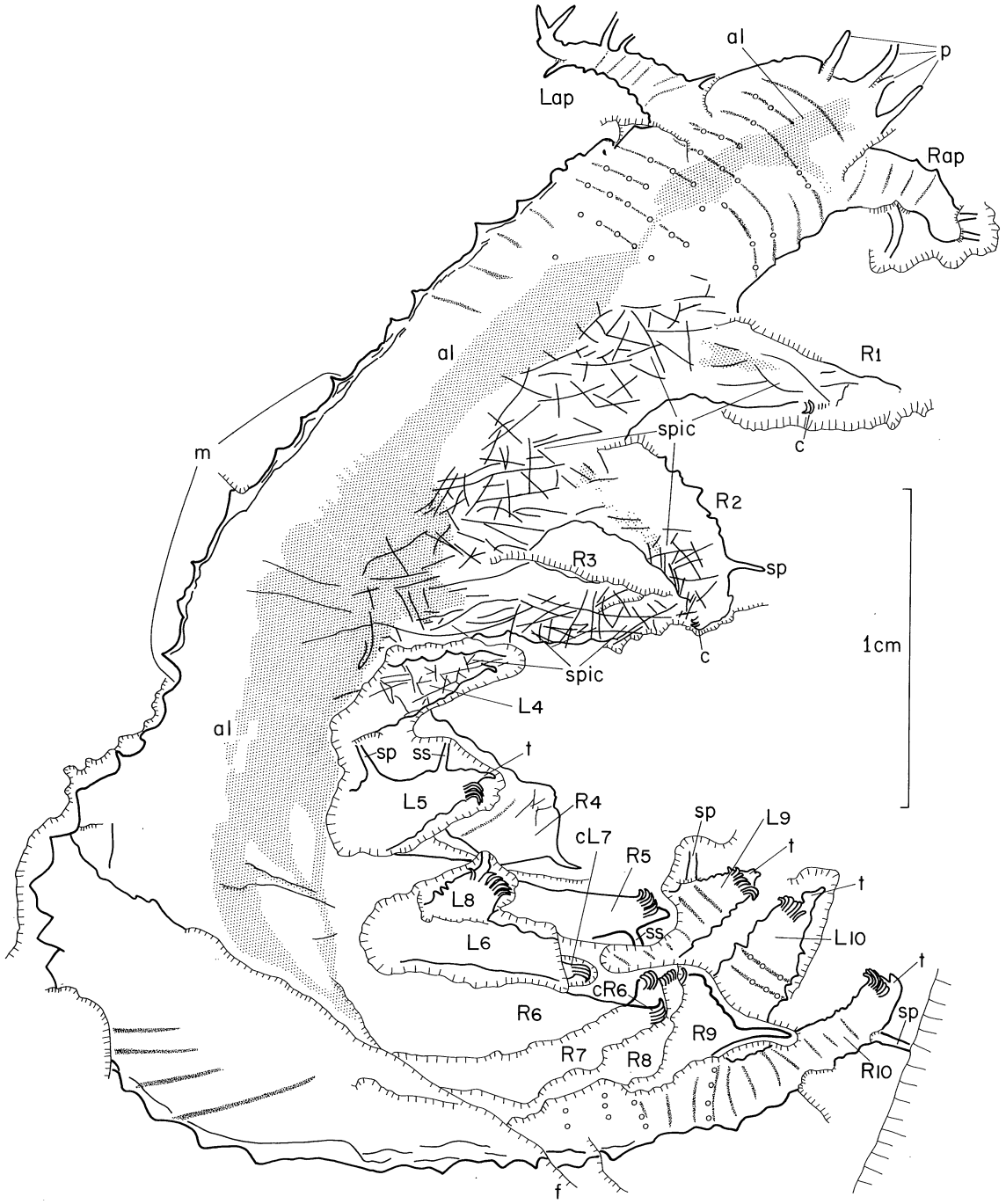


FIGURE 51

DESCRIPTION OF PLATE 8 AND FIGURE 51

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 235880, oblique lateral, Phyllopod bed. Walcott quarry

FIGURES 47, 48. Part, respectively south (magn. × 2.7), under water (magn. × 3.3).

FIGURES 49, 50. Counterpart, respectively under water (magn. × 3.3), northwest (magn. × 2.7).

FIGURE 51. Composite explanatory drawing of part and counterpart.

A slightly oblique dorsoventral compression anteriorly, the body twisted along the sagittal axis (figure 1), so that posteriorly the compression is lateral; part and counterpart available. As a result of twisting L 5–9 lie beneath the trunk, as has been shown by preparation (figures 7, 8, plate 1). Anteriorly the trunk merges into a vaguely-bounded dark area of the rock which diminishes in width and dies out. This area is preserved in the counterpart (figures 5, 6, 10, 11, plate 1) but largely broken off in the part (figure 14, plate 2). It shows no definite structures in low angle or reflected radiation. On each side of the trunk, adjacent to where it merges into the stain, is a small, curved projection, considered to be a papilla. Both anterior appendages are preserved, the undulating posterior margins suggesting annulations which are not visible as impressions crossing the appendage. The right appendage is curved, tapering, with three branches at the tip and 5 at different levels along the anterior margin. The left appendage is bluntly rounded, presumably because it was flexed down distally at burial (figure 1), and shows three branches, the innermost long, curved and pointed. Behind the anterior appendage the trunk continues to widen to a maximum at the 4th pair of limbs, maintains this width to the 7th pair, then diminishes and merges into the bases of the 10th pair. Between L 1–4 and R 1–6 the margin of the trunk undulates (figure 7, plate 1; figure 13, plate 2), the undulations rounded in outline or sharply pointed. There are three undulations between successive limbs. In low angle radiation the part (figure 14, plate 2) shows faint curved, transverse ridges crossing the trunk, one corresponding to each pair of limbs, three between each pair, corresponding in position to the marginal undulations. In the counterpart there are corresponding grooves. Behind the fourth pair of limbs the ridges are less evident (figures 7, 9, plate 1), and the margin of the trunk between R 6–8 is not scalloped. I interpret these ridges as the traces of annulations, which appeared in profile as rounded or sharp-crested ridges. Posteriorly, where the compression is lateral, the smooth ventral profile of the trunk suggests that the annulations were weak on the ventral side. On the annulations in front of the fourth pair of limbs there are faint indications of small tubercles (figure 4), as mounds (part) or pits (counterpart).

Ten pairs of limbs are present, pairs 1 to 8 evenly spaced from each other, 8 to 10 progressively closer together; limb 1 is separated by a wider gap from the anterior appendage. Limbs 2 to 7 are the longest, longer than the anterior appendage, tapering, the first and 8–10th pairs smaller, the latter diminishing progressively backward. The varied attitudes and curvature of the limbs show the twisting along the trunk and are presumably evidence of turbulence prior to burial. Each limb shows about ten annulations, preserved as transverse ridges and curved projections along the margins. In low angle radiation (figure 12, plate 2) it is evident that the ridges have been modified by the wrinkling that crosses the specimen at about 10° to the sagittal line. An under-water photograph (figure 13, plate 2) shows reflective lines curving across the limbs, each line following the crest of an annulation into the marginal projection. Their disposition and curvature is clearly related to the curvature of the limb, as is the shape of the marginal projections. Limbs 3–7 bear a large spine, apparently on the anterior side at about the 7th annulation, and a smaller spine near the tip is shown by some examples. Distally the limb has a blunt tip, bearing a group of small, curved claws; in L 1–8 the claws are on the posterior side. In limb 10 the lateral spine points backward, and in 9 and 10 the claws appear to curve forward and to be on the anterior tip of the limb. A faint median longitudinal reflective band between limb pairs 3 and 4 runs obliquely back to the left margin behind limb 6. This band may be a trace of a portion of the alimentary canal, the oblique course resulting from the twisting of the body.

Walcott's (1911, pl. 23, figs. 8, 9) original illustrations of the counterpart have been reproduced frequently. Instead of the dark stain merging into the ill-defined anterior end of the body (figure 10, plate 1), they show a definite curved boundary immediately in front of the papilla, and in front of this what Walcott called the 'head', a central narrow band with an anterior pair of tiny projections, and a pair of lobes at the base of the narrow band. Walcott's illustrations must be based on a reflected photograph, and comparison with the present one (figure 11, plate 1) shows no justification for Walcott's clearly defined 'head', portrayed as reflective on a black background. Hutchinson (1930, p. 14; 1969, pp. 1062–1063) has discussed this inaccuracy on two occasions. The originals of Walcott's plates are not preserved, but the present photographs make clear that Walcott's must have been retouched, not only in respect of the 'head' and dark stain, but also the tubercles on the annulations. The drawing by Snodgrass (1958, fig. 2*d*) omits the 'head' of Walcott, but introduces new inaccuracies in the form of a sharply defined anterior boundary to the body and many rows of dark spots (? tubercles) between the anterior margin and the first pair of limbs. Cave & Simonetta (1975, pp. 69, 70) interpreted the dark stain in the counterpart as the 'truncated and slightly enlarged head from which protrudes the "proboscis"'.

(*c*) *U.S.N.M.* 139206*a*

Figures 15, 16, plate 2; figure 17.

1930 Hutchinson, listed p. 16 as specimen *e*, pl. 1, fig. 1 (counterpart).

1975 Cave & Simonetta, figs. 6*a* (part), 6*b* (counterpart).

An approximately dorsoventral compression, the anterior and right antero-lateral margins of the trunk not preserved, the part less complete than the counterpart. This specimen is of length *ca.* 27 mm, and is the original of Hutchinson's specimen (*e*) rather than specimen (*c*) as he states in error (1930, p. 24). Only the counterpart shows the anterior portion of the body, the left and right anterior appendages directed forward, lying at a higher level than the trunk, two proximal branches preserved on the left appendage. The anterior margin of the body is not preserved, nor the distal portions of the anterior appendages. L 1–3 are incompletely preserved, equally spaced from each other but the first limb a longer distance from the base of the anterior appendage. The body is flexed at an oblique angle behind limb 3, the straight posterior portion showing limbs 4–10 (except R 4) variously arranged beside and under the body. The terminal pair are extended backward and outward, and radially arranged with pair 9 and right 8. Claws at the tips of many of the limbs, and lateral spines, are preserved, as well as faint traces of annulations on the trunk and the more anterior limbs.

(*d*) *U.S.N.M.* 139206*b*

Figure 18; figures 19–24, plate 3; figure 84, plate 14.

1930 Hutchinson, pp. 15–18, listed as specimen *b*; fig. 4*d*; pl. 1, fig. 2.

1953 Dechaseaux, *in* Piveteau, fig. 3.

1958 Snodgrass, fig. 2*b*.

1959 Moore, *in* Moore, fig. 12, 1*c*.

1969 Hutchinson, p. 1064.

1975 Cave & Simonetta, fig. 3.

An oblique lateral compression, counterpart only available. The series of limbs that project from one side of the trunk lie at a lower level (figure 18), and are therefore L 1–10. A fragment

of R 10 lies on L 10, and along the mid-region of the trunk are subcircular slightly raised areas, associated with darker patches which show the position of the bases of R 1–6, 8, 9. The right limbs were presumably preserved in the missing part. The subrounded anterior margin of the trunk is irregular, with small projections, the papillae, arising at different levels. A dark stain, slightly reflective, is present just inside the anterior margin. Behind this most anterior part of the trunk both anterior appendages are preserved, the left projecting forward and outward, lying below the adjacent trunk, the right projecting out and lying well above the trunk. Each anterior appendage has branches along its length and a pair at the tip; particularly the left shows faint annulations. The series of left limbs (figures 20–23, plate 3) taper, up to ten annulations are shown by the scalloped margins and faint, transverse ridges. In L 1–6 the tip is on the anterior side, bluntly pointed, and behind are attached the claws, curved to point backwards. The tip of L 7 has the claws curving out on each side, while in L 10 the orientation of point and claws is opposite to that of L 1–6. Left limbs 3 and 4 show the larger lateral spine at the 7th annulation and L 3 the smaller spine situated near the tip. The compressed latero-dorsal margin of the trunk, from just behind the right anterior appendage to the 10th limbs, shows a series of triangular projections, approximately evenly spaced, larger medially. The projections are at the same level along the margin, some sharply pointed, the edges broken and each projection lying above the surrounding rock, showing that the precise outline is a result of fracture and may not represent exactly the original outline. The projections are at the ends of faint ridges, the annulations, which cross the dorsal portion of the trunk (figure 19, plate 3). The annulations are absent on the ventral portion of the trunk, and the latero-ventral profile between the bases of the left limbs is gently scalloped. In low angle radiation (figure 21, plate 3) small raised areas are visible near the bases of some of the dorsal projections, associated with the slightly thickened, darker margin of the trunk. In addition, one or two pits or mounds are discernible on the annular ridges, indicated by small circles in figure 18. In reflected radiation (figure 84, plate 14) the raised areas and tubercles appear dark. Such is the evidence for tubercles on the annulations. Hutchinson (1930, p. 16) considered that four papillae (i.e. tubercles) in a row were shown by this specimen, suggesting at least eight on each annulus. He assumed also that the triangular projections along the margin were laterally compressed tubercles. I am not persuaded that this is a satisfactory interpretation. The diameter of the pits or mounds (traces of tubercles) is much less than the basal width of the triangular projections, and pits or mounds are few and irregular in disposition, and do not show a row of four on each annulus. My interpretation is discussed in § 5(*a*). Hutchinson also considered that there were four annulations per somite, one median to each limb and 3 intervening between any pair (1930, p. 16, fig. 5). His estimate was based on this specimen, and appears to be approximately correct. Along the mid-region of the body are traces of the alimentary canal, and a dark stain lies adjacent to the posterior end of the canal.

Hutchinson relied to a considerable extent on this specimen for his interpretation of morphology. He described both anterior appendages (though reversing left and right), and recognized that these appendages 'were inserted at a somewhat higher level on the body wall than were the following ten pair of legs' (1930, p. 17). That this view is correct is shown in figure 18, in which the left appendage is below the body and inside the margin, i.e. higher up the further (left) side than the left leg bases, and the right appendage is above the body, the proximal portion closer to the dorsolateral margin than the right leg bases. The sketch by Snodgrass (1958, p. 3, fig. 2*b*) of this specimen is not accurate. He considered the right anterior

appendage to have been displaced, because it is not connected to the trunk. This lack of connection is the result of the way the rock has split between part and counterpart, and there is no evidence of displacement of any part of the body. Cave & Simonetta (1975, fig. 3) misinterpreted this specimen as laterally flattened and showing the right side, and mistook shadows in their photograph (which was illuminated in a similar way to the present figure 19, plate 3) for portions of 'left legs' appearing beside L 6 and L 7. They also regarded the projections along the laterodorsal margin as flattened tubercles, and accepted Snodgrass's view that the anterior appendage was a 'modified leg'.

(*e*) *U.S.N.M.* 83942*a*

Figures 3 (*e–h*); figures 25–29, plate 4; figure 30.
1931 Walcott, pl. 11, fig. 1 (counterpart).
1958 Snodgrass, fig. 2*c*.
1975 Cave & Simonetta, figure 12 (counterpart).

An oblique dorsoventral compression, part and counterpart available. Low angle radiation shows the faint shadows across the trunk that outline the position of the left series of limbs (figures 25, 27, plate 4), and there is a darker ring at the base of each limb in the part. L 2 and L 6 have been prepared in the part, and fragments of L 8 and L 9 adhere to the counterpart. The anterior margin of the trunk shows papillae at different levels on each side, the median portion an irregular projection which merges into a dark stain (figures 28, 29, plate 4; figure 30). The anterior appendages are branched, each showing a pair of branches at the tip, and traces of annulations. The proximal portion of the left appendage (in ventral view, figure 30) lies nearer the observer than the left lateral wall of the trunk, to which it must have been attached at a higher level than the left series of limbs. Similarly, the proximal part of the right anterior appendage lies below the margin of the trunk, and was attached on the right lateral wall, while the first two limbs merged into the ventrolateral wall of the body. Some 10 annulations are shown by the scalloped profile of the limbs and faint transverse ridges. R 1–8 are straight or curved gently back, the blunt tip anterior, the claws situated on the posterior side, curved down and back, in R 9 and R 10 the claws are on the anterior side, the tip posterior. The tip of L 6 shows the opposite orientation to that of R 6, presumably the result of twisting before burial. The profile of the margin of the trunk opposite to the limbs (figure 26, plate 4) shows triangular projections which correspond in position with the low ridges of the annulations; these ridges are faint or absent on the ventral portion of the trunk. The profile between the right limb bases 4–8 is gently undulating, the convexities corresponding with the annulations. There appear to be 3 annulations between successive limbs, and probably one in line with each limb, i.e. 4 annulations per segment. A faint reflective strip, varying in width, shows the position of the alimentary canal. Athwart this strip, near the base of R 9, is a circular patch of sponge spicules; lying across R 2 and R 3 is a second sponge fragment which in arrangement of spicules resembles that of the outer wall of *Takakkawia lineata* Walcott 1920 (pl. 87, figs. 4*a*, 4*b*).

The counterpart of this specimen was illustrated by a reflected photograph in Walcott (1931, pl. 11, fig. 1), and by an inferior low angle photograph in Cave & Simonetta (1975, fig. 12). The latter authors interpreted the dark stain as the protruding 'tip of the proboscis'. Snodgrass (1958, fig. 2*c*) sketched the anterior end of the counterpart, but did not see the bases of the left limbs and consequently reversed the orientation.

(*f*) *U.S.N.M.* 83942*b*

Figures 2, 31; figures 32–35, plate 5; figures 36, 37, plate 6; figure 83, plate 14.

1931 Walcott, pp. 8, 41, pl. 11, fig. 2 (counterpart).

1958 Snodgrass, fig. 2*e* (counterpart).

1969 Hutchinson, p. 1063.

1975 Cave & Simonetta, figs. 8*a*, *b* (part and counterpart).

The largest known specimen, *c.* 59 mm in length, an oblique lateral compression (figure 2 and § 3), the body curved through 180°, part and counterpart available. The anterior margin of the body, the two papillae, and the branched anterior appendages are preserved only on the part (figures 33, 35, plate 5; figure 36, plate 6). The right anterior appendage lies below the level of the trunk in the part, and hence was attached on the right lateral wall above the level at which the limbs were attached. The left anterior appendage was attached in a corresponding position on the left wall, and lies above the trunk in the part (these relative positions are shown in reverse in figure 31). The trunk tapers posteriorly, and displays a reflective band along the course of the alimentary canal, this band having dark specks and blobs along its length and displaying faint transverse bands (corresponding to the annulations?). The dorsolateral margin of the trunk shows evenly-spaced triangular projections along its length (figure 83, plate 14). In the median region the projections are sharply pointed, the point slightly extended, proximally the margins convex to give a helmet-shaped outline. A narrow, raised, marginal strip at the base of the projections. Annulations are visible as faint ridges on the trunk anteriorly, where each ridge runs into a dorsal marginal projection. If each projection is taken as corresponding to an annulus there are approximately 4 annulations per segment. In the counterpart (figures 32, 34, plate 5) left limbs project from the margin of the trunk at the same level, farther from the observer than the proximal portions of the right limbs. Annulations are visible on some of these limbs, and L 1–3 show the blunt tip, behind which the claws curve backward. Lateral spines are shown by L 8 and 10. The basal portions of R 1–R 3 are preserved as low, curved platforms projecting from the mid-part of the trunk, those of R 4 to R 10 as subtriangular projections. Preparation of the part (figures 33, 35, plate 5; figure 37, plate 6) has revealed more distal portions of R 4–6, 8 and 9, farthest from the observer, beside and beneath portions of the left limbs. Preserved at an intermediate level between the proximal portions of the limbs is the profile of the compressed ventral body wall, revealed by preparation at two places. This profile shows little trace of annulations. The two limb series are superposed in figure 31, showing that in the posterior half of the body the tips of left and right limbs lie one above the other, whereas anteriorly the claws of R 1 lie on the midpart of L 1. This is the result of twisting along the axis during burial, as shown in figure 2 (see § 3). In addition to the patches of sponge spicules shown in figure 31, a similar patch lies on the left anterior appendage (figure 36, plate 6), a network of *Vauxia* sp. on and adjacent to L 7–10 (figure 35, plate 5), and fragments of long, isolated spicules occur (figures 34, 35, plate 5) nearby.

Walcott illustrated only the counterpart, and (perhaps because the anterior appendages are not shown) regarded it as possibly different from *A. pedunculata*. Snodgrass's sketch of the part is indifferent, and as Hutchinson (1969, p. 1063) pointed out, Snodgrass appears to have added an extra limb. Cave & Simonetta's photographs are poor, and features supposed to be indicated by arrows are difficult to see; they recognized the anterior appendage in the counterpart.

(*g*) *U.S.N.M.* 200331

Figures 38, 39, plate 6; figure 40.

Poorly preserved oblique dorsoventral compression, only what is considered to be the counterpart is available. In this counterpart R 1–10 are extended at the same level as the trunk, R 8–10 overlapping where the posterior end of the body is bent ventrally (towards observer). Parts of L 1–6 lie nearer the observer, partly on the trunk, hence the interpretation that the specimen is a counterpart, showing an oblique ventral view. On each side of the anterior portion of the trunk the branched anterior appendage extends outward, the branches on the anterior side. The rounded anterior end of the trunk has an irregular margin, from which project six or seven small tapering processes, the papillae. They project at slightly different levels and overlap one another at their bases.

This specimen lies adjacent to, and below, a specimen of *Selkirkia columbia* (Conway Morris 1977*c*). Lying across the posterior portion of the body is a small bivalved shell, crushed and wrinkled, the two valves lying in the same plane. Similar valves lie on the anterior part of the trunk and near the left anterior appendage. This shell may be of a bradoriid, and occurs in association with other animals (Whittington 1971*b*, plate 1, figures 1–3).

(*h*) *U.S.N.M.* 235879

Figures 41; 42–46, plate 7.

1930 Hutchinson, pp. 15–18, listed as specimen *a*, figs. 4*a*, *b*, *c*.

1969 Hutchinson, p. 1063.

1975 Cave & Simonetta, fig. 4.

Incomplete compression, apparently oblique dorsoventral anteriorly, body twisted to oblique-lateral posteriorly; part only, crossed by two folds. Hutchinson figured portions only of this specimen, stating in error that most of the right (not left) side was missing. The anterior end of the body (figure 46, plate 7) with a papilla and right anterior appendage having three or four branches, and the reflective trace of the alimentary canal (widest anteriorly), is as he portrayed it (Hutchinson 1930, figure 4*a*). The anterior margin is truncated by a fold, on the opposite side of which is the dark stain; it is uncertain whether or not the vague dark area on the left margin of the body represents the left anterior appendage. R 1–10 are extended straight, or flexed in various attitudes, at the same level as the margin of the trunk. Claws are preserved at the tip of all except R 7, and are variously oriented. Hutchinson (1930, p. 16, fig. 4*b*) gave a sketch of the tip of R 4, and stated that it showed 6 claws, 3 turned forward and 3 backward. I agree that there appear to be six claws, but only two pairs appear to point in opposite directions, the tips of the middle two claws obscure (figure 41; figure 44, plate 7). In R 5 the claws are similarly arranged, the bluntly-tapering tip of the limb projecting below. In R 1 all the claws are behind the tip and curved backward, while R 3 shows an intermediate arrangement, one claw curving forward, five backward. In R 6, R 8–10, and L 10 the tip is on the posterior side and the claws curved forward (figure 41; figure 45, plate 7). The orientation of the claws in life is discussed in § 5 (*a*), the varied positions in this specimen reflecting the effects of twisting during burial. Hutchinson (1930, p. 17) also remarked on a triangular dark spot at the tip of the limb adjacent to the base of the claws. This spot appears to me to be the dark area where the subparallel bases of the claws were inserted in the limb. Posteriorly both the bases of L 5–9, and distal portions of L 7–10 below or beyond the body, have been recognized.

I interpret L 10 as passing obliquely beneath R 9 and R 10, which are close together; this differs from Hutchinson's (1930, fig. 4*c*) view that my R 9 is R 10, and my R 10 is L 10. My interpretation is based on the relative levels of limbs, and on the evidence (figure 41) that L 7–10 were swung forward, subparallel to each other beneath the body, before compression. The spine of R 10, directed backward, is clearly preserved, and the blunt tip of the limb lies behind the forward-curving claws. Hutchinson identified a second dark area as a detached fragment of the spine of his left limb 10, but I do not recognise such a clearly defined fragment. The specimen is not well preserved and margins are sharply defined only when viewed under liquid (figures 43–45, plate 7); the posterior margin of the trunk is scalloped and shows some sharp peaks – traces of the annulations. The surface of the trunk and limbs, however, shows only faint traces of such annulations. The faint reflective band, presumably the trace of the alimentary canal, extends from the anterior margin to a point between the bases of the 10th pair of limbs, and indicates the position of the anus.

(*i*) *U.S.N.M.* 235880

Figures 47–50, plate 8; figure 51; figures 52–56, plate 9; figure 79, plate 13.
1930 Hutchinson, p. 16, specimen *c*.
1975 Cave & Simonetta, figs. 13*a*, *b*.

An oblique right lateral compression, trunk sharply flexed beyond fifth pair of limbs. The anterior margin (figure 56, plate 9) is rounded with occasional minute triangular projections, four papillae arising at different levels inside the margin and extending beyond it. These papillae are better-defined than in any other specimen, proximally broad based, long, the outline suggesting both stiffness and some flexibility distally. The right anterior appendage lies at the same level as, or slightly above, the margin of the trunk, is branched but apparently the tip is bent down and concealed. The left anterior appendage lies below the margin of the trunk, because of the obliquity, and has the branches well preserved. It also shows scallops along the margin and faint corresponding transverse divisions; similar structures are less well seen on the right appendage. In front of R 1 the trunk shows annulations as scallops on the margin (figure 48, plate 8) and faint ridges (figure 54, plate 9). The latter curve convexly forward and the scallops are asymmetrical, suggesting that the trunk was dipping down anteriorly when entombed. There appear to be perhaps three annulations in front of that in line with the anterior appendages. Tubercles on the annulations are small and difficult to see except in a particular direction of illumination; figure 51 (compare figure 54, plate 9) indicates those I recognize. The left (laterodorsal) margin of the trunk shows triangular projections, but the sponge spicules, and wrinkles associated with the flexure, combine to obscure further evidence of annulations. Patches and lines of extremely fine-grained pyrite are present over the surface of the trunk, and are particularly evident as dark lines along a portion of the left margin, following the shape of the projections or running straight beneath them (figure 79, plate 13). Some of these lines are minute ridges, others are grooves. A reflective band (figure 48, plate 8) which varies in width, narrow and well defined posteriorly where it terminates between the bases of the last pair of limbs, shows the position of the alimentary canal. Limbs have been exposed in part and counterpart (figures 47–50, plate 8), and are shown superposed in figure 51. The complete series has been identified on the right side, R 6–10 pressed closely one upon another in the counterpart. What appear to be L 4–10 are indicated in figure 51, and lie farther

from the observer than the right series. The position of L 8, pointing forward and lying beneath L 6, results from the sharp flexure of the trunk; the claws of L 7 are tentatively identified from a fragment on the counterpart. The dispositions of the limbs show that there was twisting along the axis of the body at burial, because anteriorly the right limbs extend out beyond the left, while posteriorly the reverse is the case. Limbs L 9, 10, and R 4, 10 show marginal scallops and corresponding faint transverse grooves, the annulations, as well as claws and lateral spines (figures 52, 53, plate 9). On L 9 and 10, and on the trunk near the base of R 10, there are small tubercles on the annulations (figure 51; figure 55, plate 9).

The spicules of a sponge, *Protospongia* sp., are impressed into the right side of the trunk, R 1–3 and L 4. In the part the impressions in L 4 are grooves, elsewhere they are ridges, suggesting that the spicules lay between the limbs and below the trunk.

This specimen was listed by Hutchinson and poorly figured by Cave & Simonetta. The latter authors described the structures here called papillae as 'pin-like reflecting filaments' (Cave & Simonetta 1975, p. 69), and alleged that they protruded from four supposed papillae surrounding the mouth (see § 4(*n*)).

(*j*) *U.S.N.M.* 235881

Figure 82, plate 14.

1930 Hutchinson, p. 16, specimen *d*.

1975 Cave & Simonetta, fig. 5.

A small, poorly preserved specimen, body curled through 150°, apparently a right oblique lateral compression. In front of the branched anterior appendages the trunk narrows, and from the transverse anterior margin there appear to be 4 or 5 small projections, the papillae. Portions of both left and right limbs, mainly right, project from the body, the reflective claws at the tip. Small blobs of some other material overlie the body at the 2nd to 4th limbs, and at the posterior end, making identification of particular limbs difficult. A zig-zag, reflective, presumed sponge spicule lies immediately behind the body. A faintly reflective median strip traverses the trunk, widest and clearest anteriorly. It is not a sediment filling of the gut, as suggested by Cave & Simonetta (1975, p. 70) and I see no justification in such poor preservation for interpreting the wider anterior portion as an 'introflexed proboscis'.

(*k*) *U.S.N.M.* 235882

Figures 57–61, plate 10; figure 62.

1930 Hutchinson, p. 16, probably listed as specimen *f*.

1975 Cave & Simonetta, fig. 11.

A poorly preserved, incomplete, right oblique lateral compression (counterpart not available), showing R 2–10, and the position of the bases of L 2–8, L 6 having been exposed below

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Description of plate 9

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 235880, Phyllopod bed, Walcott quarry.

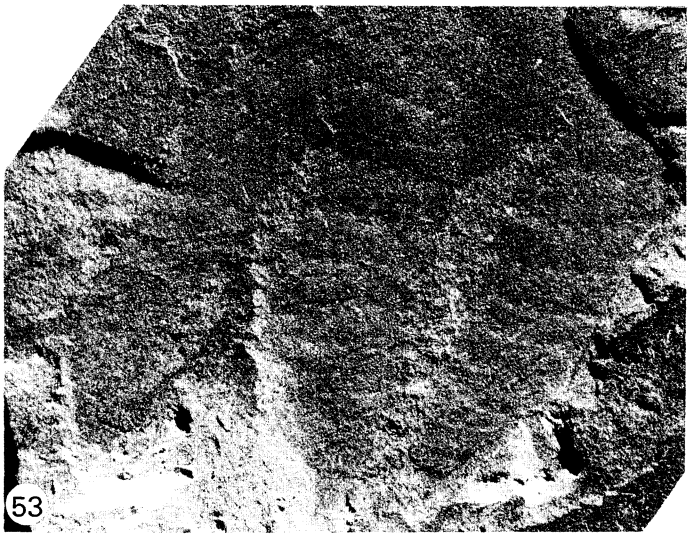
Figures 52, 53. Part, left limbs 9, 10, right limb 10, respectively under water, north (magn. × 8).

Figure 54. Part, anterior portion, north, to show tubercles on annulations (magn. × 5).

Figure 55. Counterpart, oriented as in figure 50, plate 8, posterior portion to show limbs, northwest (magn. × 8).

Figure 56. Part, anterior portion, under water (magn. × 10).


52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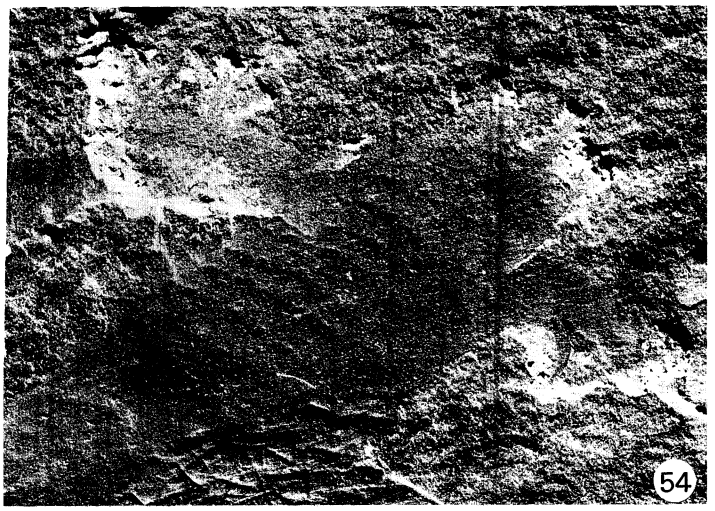
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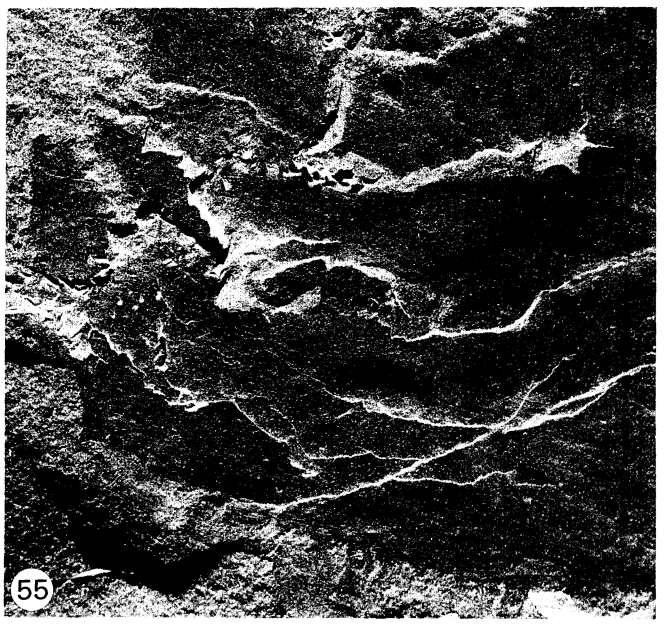
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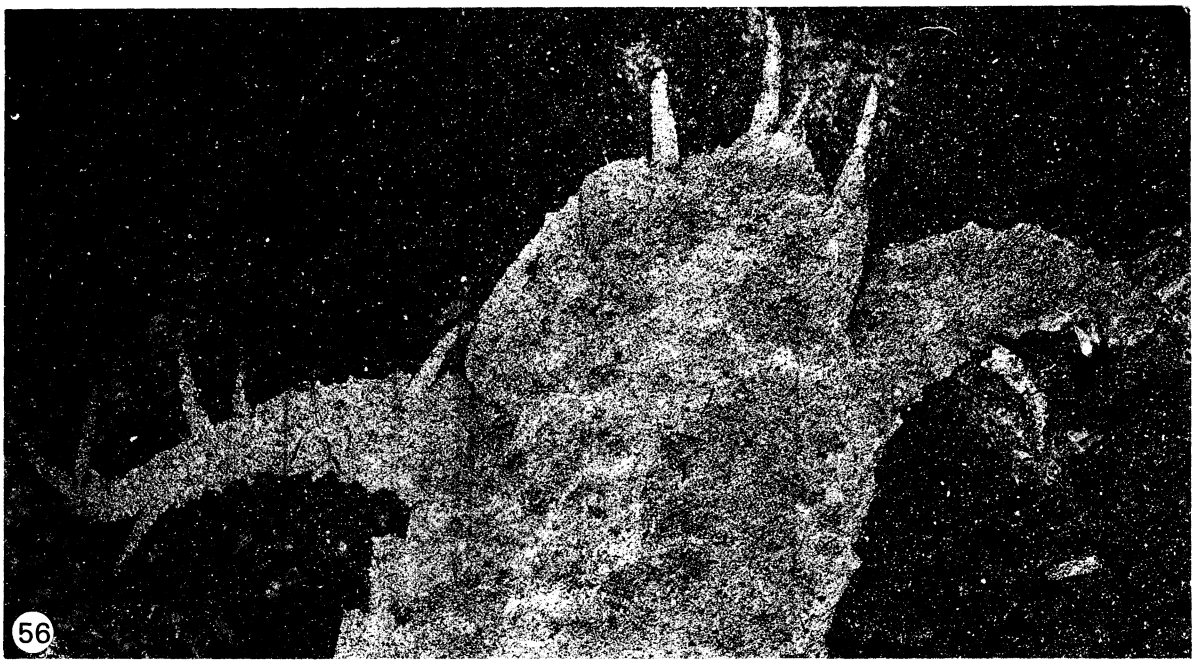
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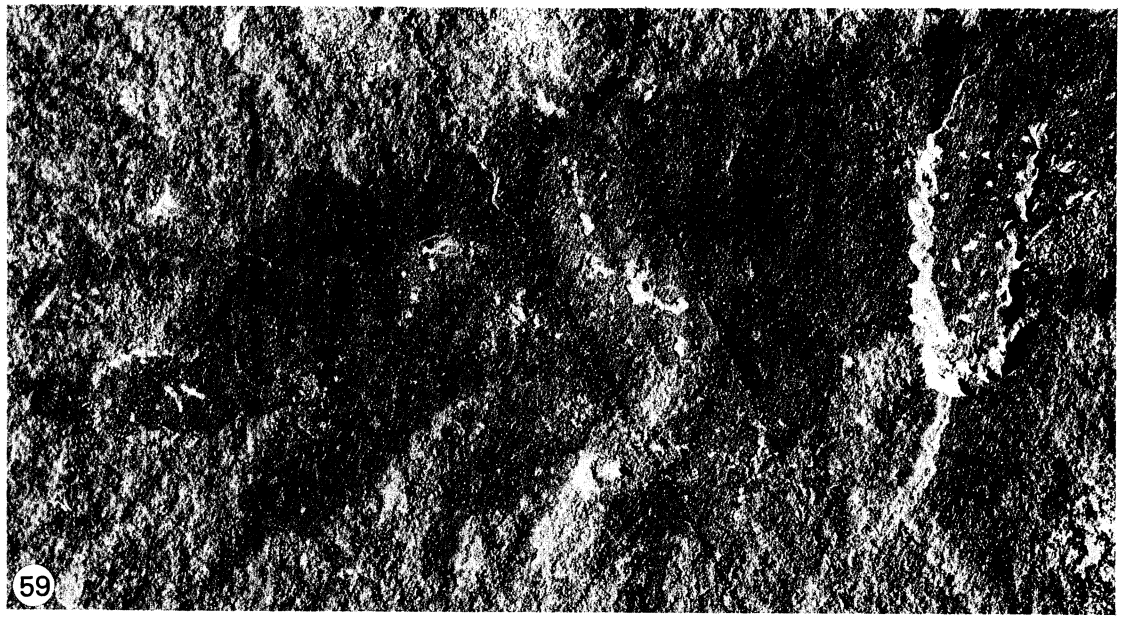
58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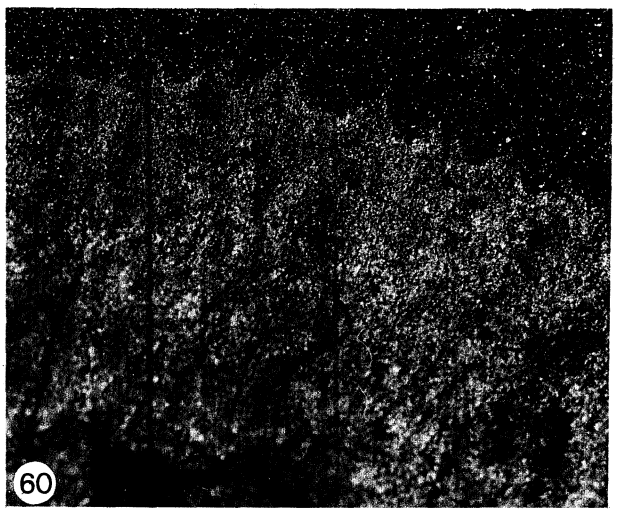
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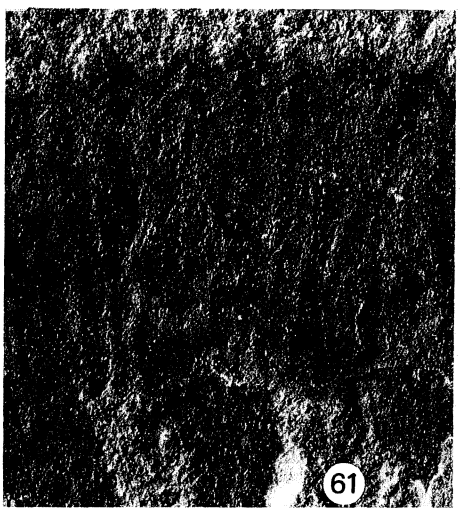
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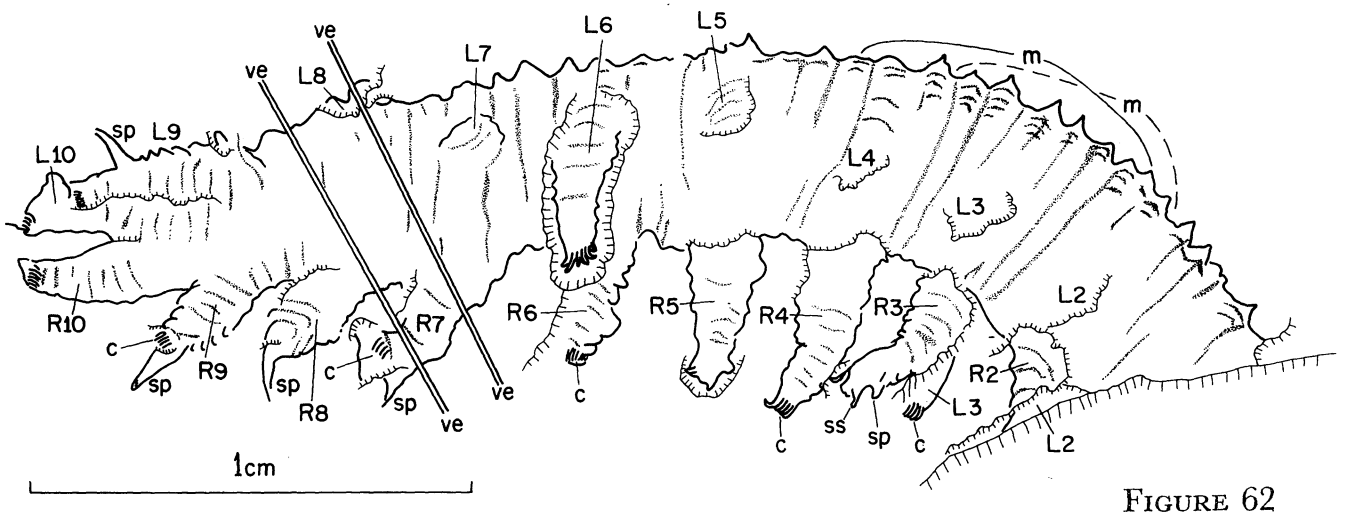
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ve
L8
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FIGURE 62

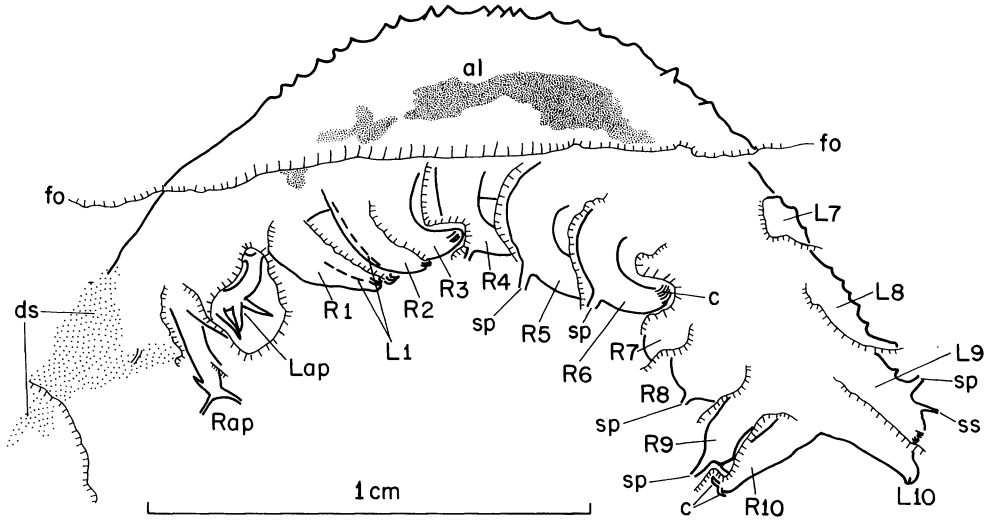


FIGURE 63

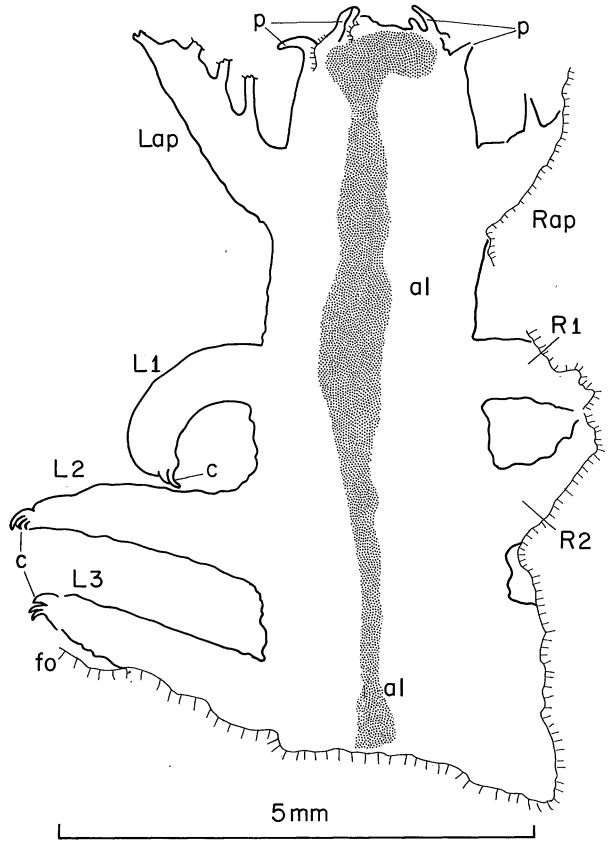


FIGURE 64

DESCRIPTION OF PLATE 11 AND FIGURES 63, 64

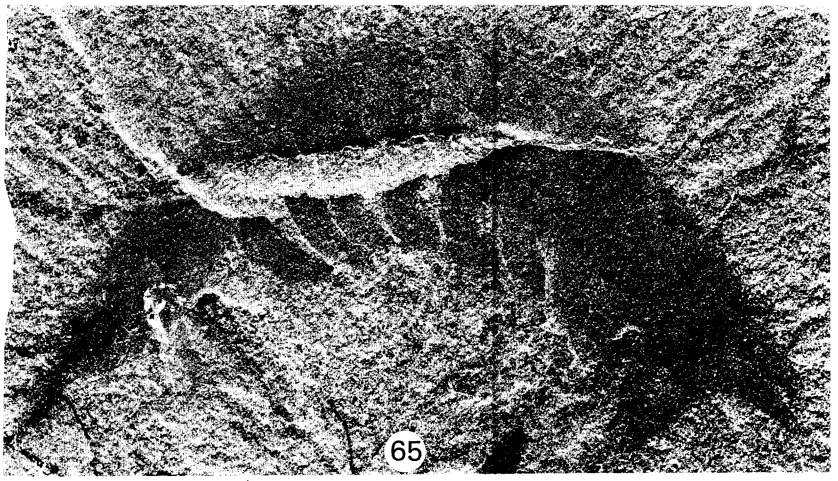
Aysheaia pedunculata Walcott, 1911, Phyllopod bed, Walcott quarry

FIGURE 63. U.S.N.M. 235883, composite explanatory drawing of part and counterpart.

FIGURE 64. U.S.N.M. 235884, explanatory drawing of anterior portion.

FIGURES 65, 67, 68, 70. U.S.N.M. 235883, lateral to ventral oblique, respectively counterpart, north, reflected; part, west, reflected (magn. × 5).

FIGURES 66, 69, 71. U.S.N.M. 235884, dorsoventral, part only, respectively entire, under water (magn. × 5); anterior portion, under water, south (magn. × 10).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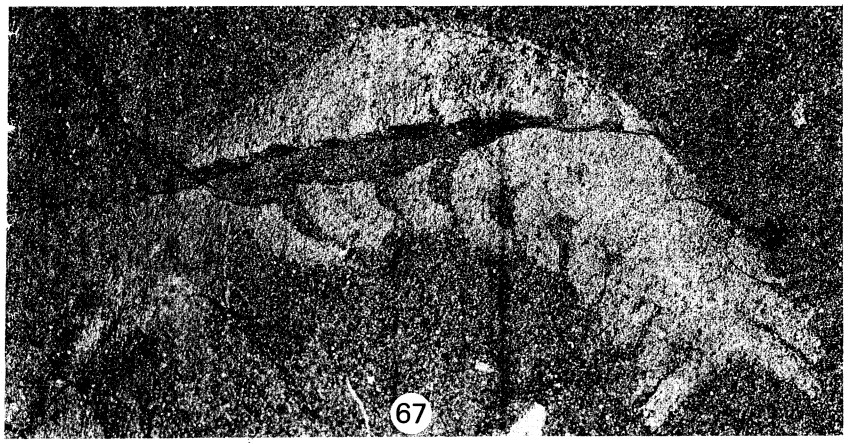
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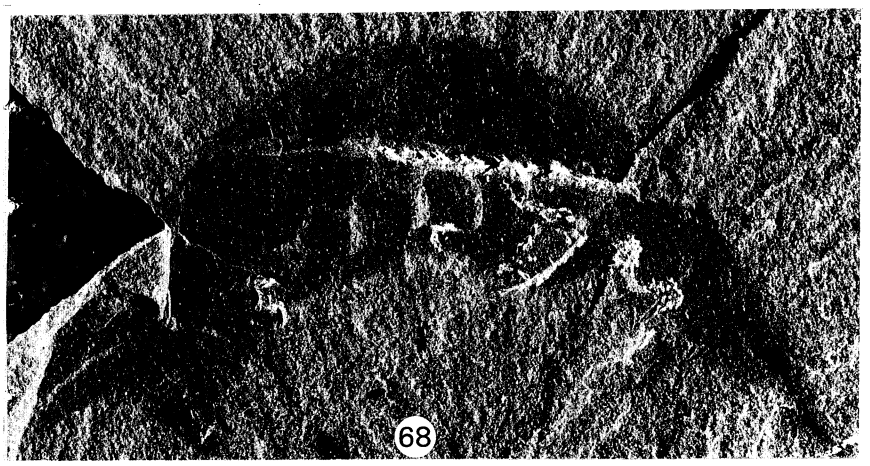
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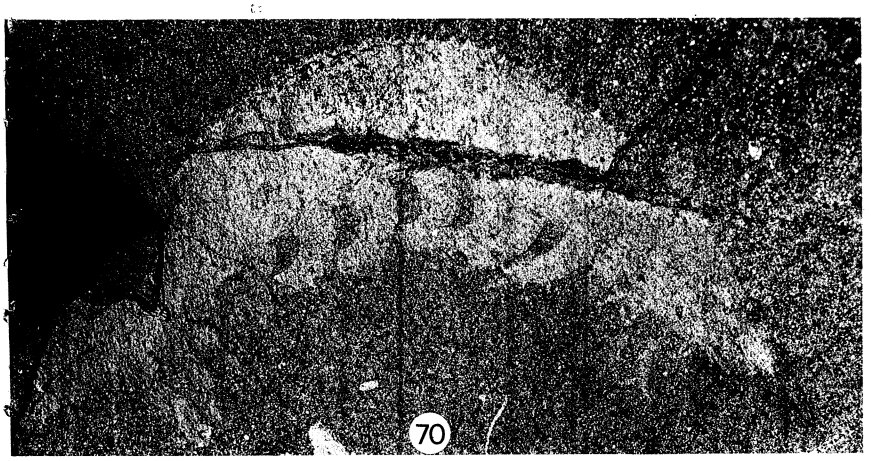
71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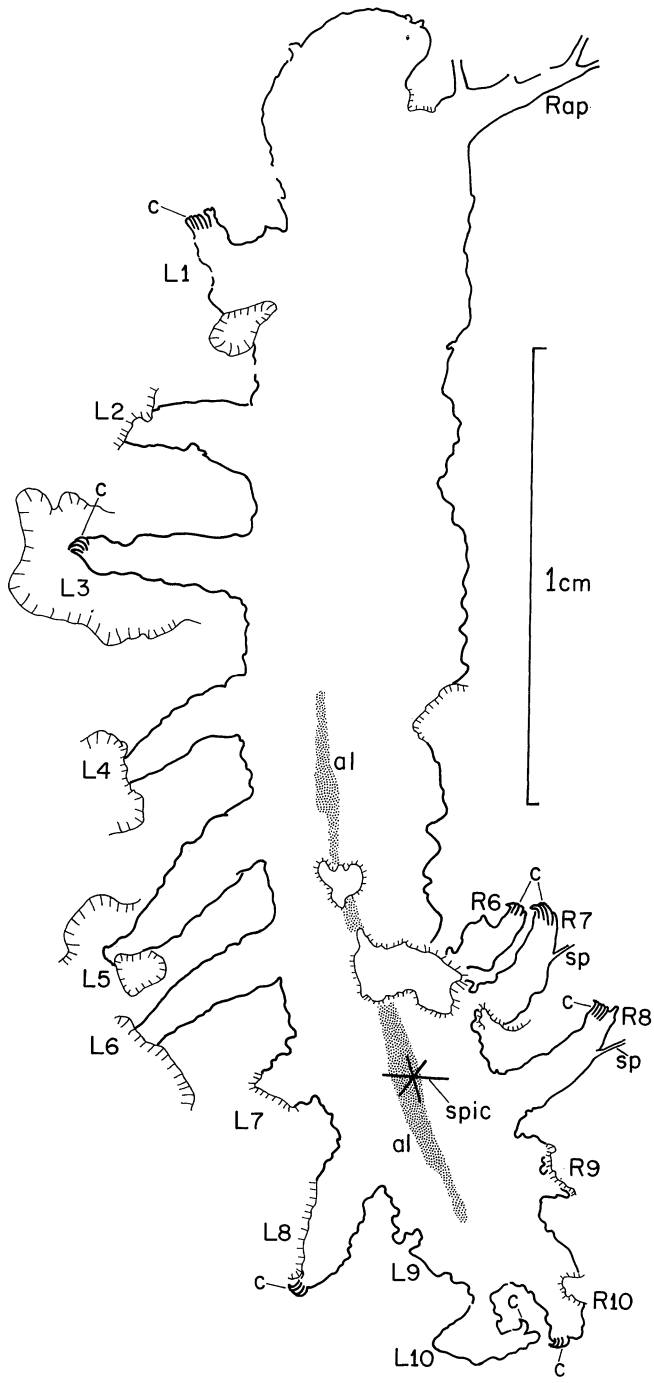


FIGURE 75

DESCRIPTION OF PLATE 12 AND FIGURE 75

Aysheaia pedunculata Walcott, 1911, U.S.N.M. 235885, dorsoventral, Phyllopod bed, Walcott quarry

FIGURE 72. Part, under water (magn. × 5).

FIGURES 73, 74. Counterpart, under water (magn. × 5); posterior portion, under water (magn. × 15).

FIGURE 75. Composite explanatory drawing of part and counterpart.

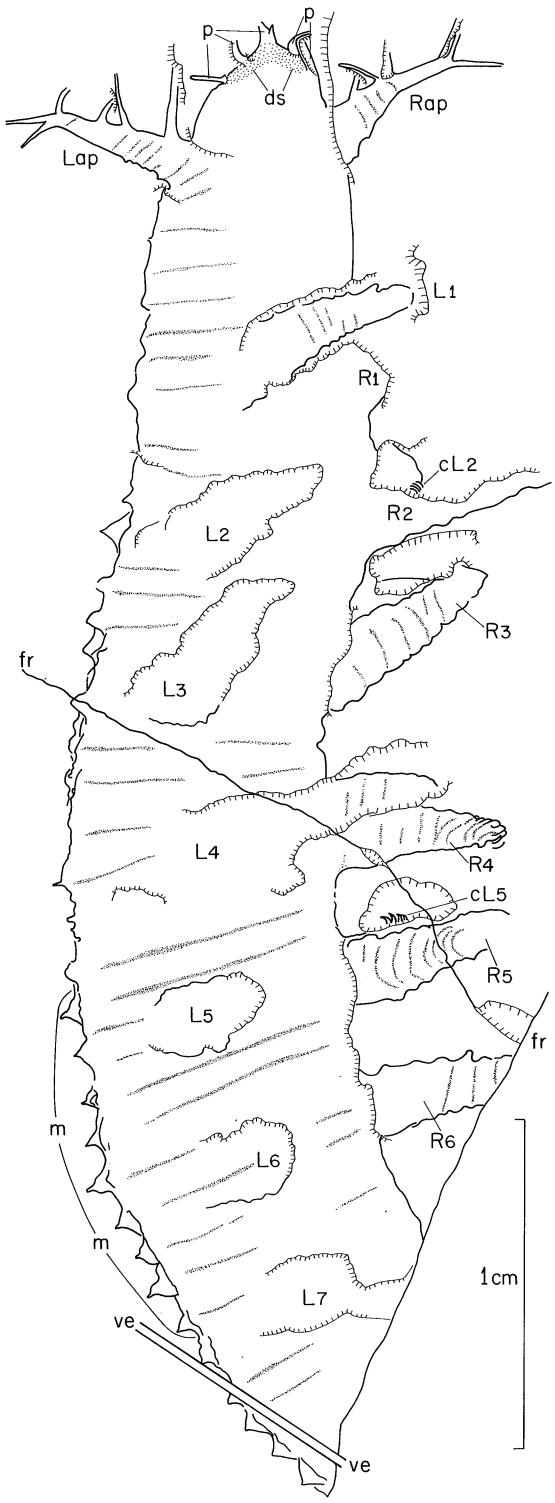


FIGURE 76

DESCRIPTION OF PLATE 13 AND FIGURE 76

Aysheaia pedunculata Walcott, 1911, Phyllopod bed, Walcott quarry

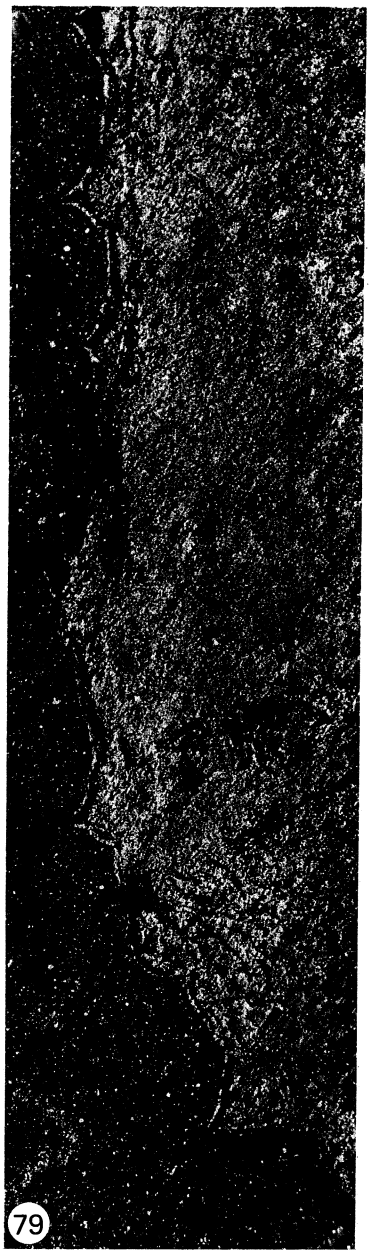
FIGURE 76. R.O.M. 35412, explanatory drawing.

FIGURES 77, 78, 80. R.O.M. 35412, oblique lateral, part only, respectively south (magn. × 3.3); portion of margin indicated by (m) in figure 76, under water (magn. × 15); anterior portion, west (magn. × 10).

FIGURE 79. U.S.N.M. 235880, portion of margin indicated by (m) in figure 51, under water (magn. × 15).


77


78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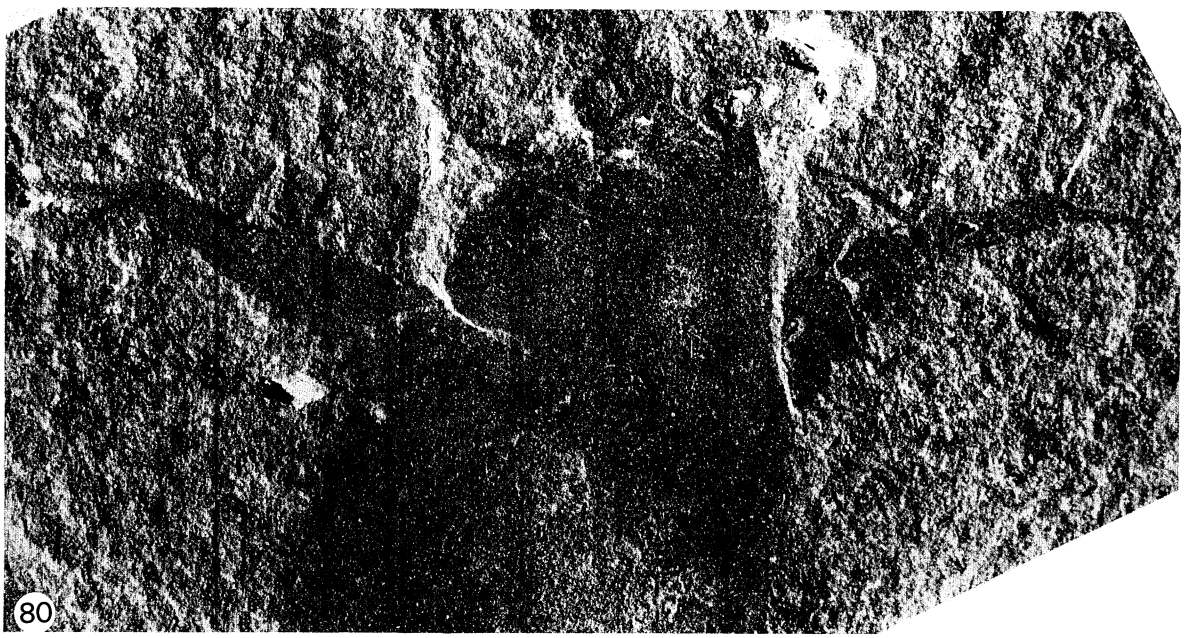
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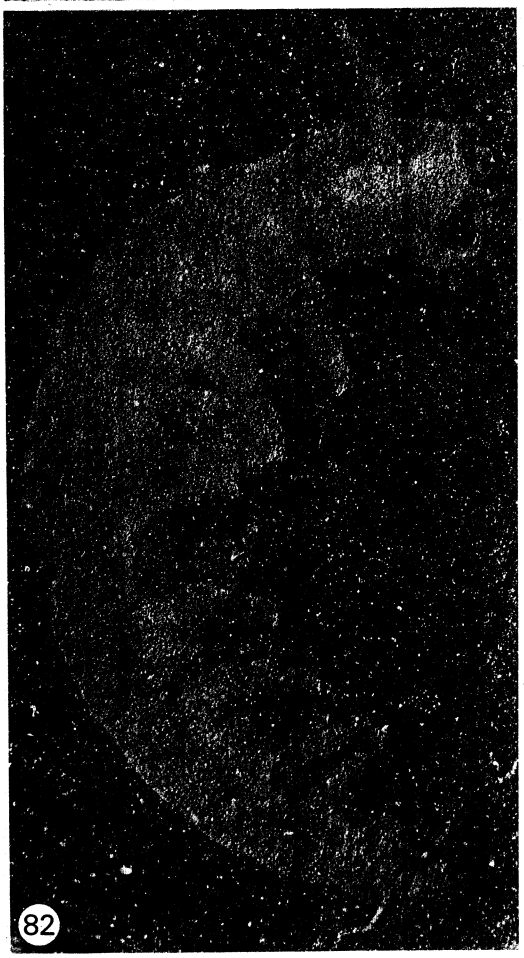
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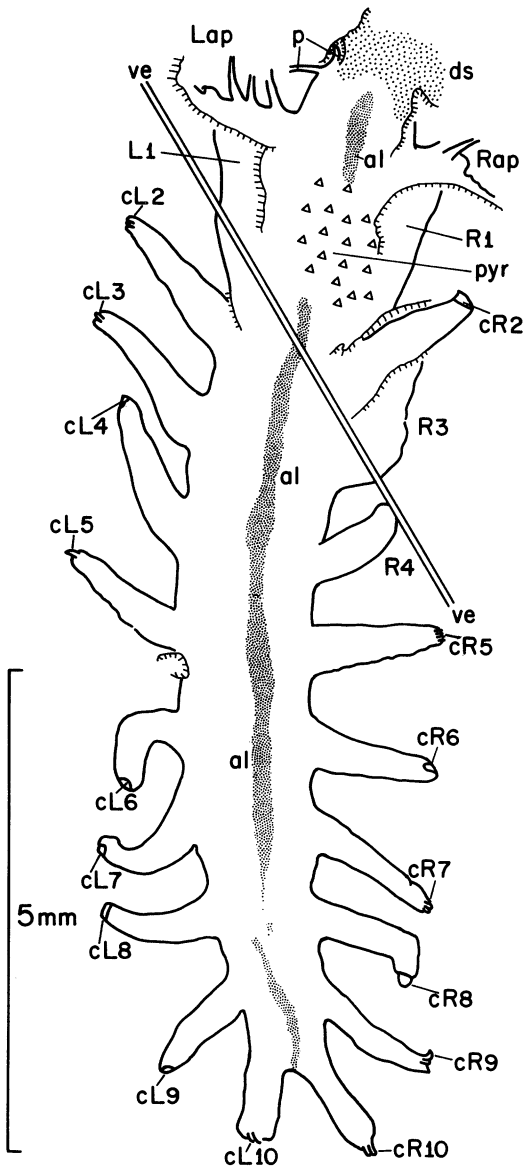

FIGURE 85

DESCRIPTION OF PLATE 14 AND FIGURE 85

Aysheaia pedunculata Walcott, 1911, Phyllopod bed, Walcott quarry

FIGURE 81. R.O.M. 35413, dorsoventral, part only, south southwest (magn. × 10).

FIGURE 82. U.S.N.M. 235881, oblique lateral, part only, under water (magn. × 10).

FIGURE 83. U.S.N.M. 83942b, portion of margin indicated by (m) in figure 31, west (magn. × 15).

FIGURE 84. U.S.N.M. 139206b, portion of margin indicated by (m) in figure 18, reflected (magn. × 15).

FIGURE 85. R.O.M. 35413, explanatory drawing.

the trunk. R 10 points directly backward, as does L 10 which lies partly below it, and in turn partially obscures the similarly-directed L 9. R 3–5 are extended, slightly curved, while R 7–9 appear short, because the distal portions were flexed sharply at burial to bring the claws directly below the base of the lateral spine; the claws are thus preserved at the base of this spine. As a result of the flexure the trace of the annulations is strongly curved (figure 58, plate 10). The trunk shows traces of annulations as ridges and grooves, each ridge corresponding in width and position with a triangular projection on the dorsolateral margin (figure 61, plate 10). I therefore interpret each projection as the profile of an annulation, and not as a tubercle (Cave & Simonetta 1975, p. 72). Close to the base of the projection each annulation is crossed by two or three circumflex-shaped ridges, which may be the remains, after compression, of tubercles on the annulations. In reflected radiation (figure 60, plate 10) the projections appear sharply pointed or bluntly rounded and in one or two the summit appears to bear a short spine. There appear to be four annulations per somite.

(*l*) *U.S.N.M.* 235883

Figure 63; figures 65, 67, 68, 70, plate 11.

1930 Hutchinson, p. 16, listed as specimen *g*.

1975 Cave & Simonetta, pp. 69, 72, 74, figs. 9*a*, *b*.

The body is curved and crossed by a fold. Anteriorly the compression is lateral (as shown by the position of the anterior appendages and limbs 1 and 2), changing to ventral oblique posteriorly, part and counterpart available. In front of the anterior appendages the trunk grades into a dark stain, which narrows forward and dies out. Immediately behind this portion the dorsal margin of the trunk adjacent to the fold is straight, while on the ventral side parts of the anterior appendages are preserved, the right projecting down, the left curved backward, each branched. The remainder of the trunk shows traces of the annulations only as irregularly-spaced triangular projections from the dorsolateral margin. Slightly more reflective patches on the trunk are probably traces of the alimentary canal. Small, dark patches between the fold and the dorsolateral margin are non-reflecting patches of very fine-grained pyrite on the surface of the fossil.

Portions of the complete series of right limbs are preserved, curved to extend one inside the next following, so that the tips of R 3, 6 and 9 could be exposed in the part (figure 68, plate 11); R 10 is straight. In the part L 1 has been exposed below R 1 and 2; portions of L 7 to 10 are preserved posteriorly on the opposite margin of the trunk. Lateral spines and claws are preserved, but not annulations.

Cave and Simonetta regarded this specimen as showing a 'bulbous structure at the fore part of the head', evidence of an 'evertible proboscis' or of a pharyngeal structure, which they thought had been forced out during compression. Their indifferent illustration of the part suggests that they were referring to a lozenge shaped reflective area at the anterior end. Comparison with the present illustrations shows that this area corresponds to the anterior portion of the trunk bearing the anterior appendages, and to part of the dark stain. The photographs in low angle radiation (figures 65, 68, plate 11) show that the most anterior part of the trunk merges into the dark stain, which has irregular and indefinite margins. No clearly outlined structures are visible, and my interpretation is that the anterior margin probably ruptured during decay, and that decay products seeped out into the adjacent mud.

(*m*) *U.S.N.M.* 235884

Figure 64; figures 66, 69, 71, plate 11.
1930 Hutchinson, p. 16, listed as specimen *h*.
1975 Cave & Simonetta, fig. 7.

An approximately dorsoventral compression, the appendages projecting outward on each side, posteriorly the body curves down into the rock so that the last three pairs of limbs lie successively one below the other. A line of displacement crosses the specimen obliquely; part only available. The anterior portion of the trunk, in front of the anterior appendages, is semicircular in outline, the most anterior part of the margin irregular and showing a number of small projections at slightly different levels. These projections are the compressed papillae, the outer ones directed outward, the inner group converging forward. No dark stain is associated with the anterior end of the body. The remainder of the trunk shows little trace of annulations. A faintly reflective median band, which represents the alimentary canal, is evident in front of the line of displacement (figure 64; figure 66, plate 11). The band widens in front of the second pair of limbs and extends to the anterior margin. The anterior pair of appendages is incompletely preserved, forward and outwardly directed, with branches from the anterior edge. The left series of limbs is complete, those of the right side not so; annulations are not preserved, the more intensely reflective claws show as a bright spot at the tip of several of the limbs (figure 66, plate 11).

(*n*) *U.S.N.M.* 235885

Figures 72–74, plate 12; figure 75.
1975 Cave & Simonetta, pp. 69, 72, fig. 10*a*, *b*.

In reflected radiation this specimen is clearly defined, in low angle radiation the distinction between fossil and matrix is slight. Part and incomplete counterpart available, which have been prepared subsequent to the photographs of Cave and Simonetta. Preparation was difficult because, unlike most specimens, this one did not part readily along the layer in which it is preserved. This layer has an unusual reticulate appearance in reflected radiation (figures 72–74, plate 12), the fine, dark lines, some of which intersect at 60° or 90°, being sponge spicules; the position of one such spicule of *Protospongia* is indicated in figure 75. Before preparation the part (original of Cave & Simonetta 1975, fig. 10*b*, in which photograph the anterior end is to the left), showed the body only as far forward as L 3. Not only have L 1 and L 2 been exposed (the former showing reflective claws at the tip), but also the poorly-defined anterior margin and the right, branched anterior appendage (figure 72, plate 12). No sign of the left anterior appendage was found, but L 1 is crumpled and perhaps it was bent beneath the body. The compression appears to have been oblique lateral anteriorly, changing to dorsoventral posteriorly. The ninth pair of limbs seem to have been bent beneath the body and so largely concealed; the part (figure 72, plate 12) is thus incomplete and does not show the remainder of the body. The counterpart (original of Cave & Simonetta 1975, fig. 10*a*, in which photograph the posterior end is to the left) shows (figures 73, 74, plate 12) the body as far forward as L 3, and the 10th pair of limbs, bent and posteriorly projecting, were prepared subsequent to Cave and Simonetta's photograph. That they are limbs is shown by the terminal claws. Thus, Cave & Simonetta's (1975, fig. 10*a*) interpretation that this end of the specimen is anterior is incorrect. An arrow on their photograph, pointing to what is now recognized as the basal portions of the

10th pair of limbs, purported to indicate the position of the 'circum-oral papillae'. There is thus no evidence from this specimen for such structures.

(*o*) *R.O.M.* 35412

Figure 76; figures 77, 78, 80, plate 13.

An oblique right lateral compression, part only available, incomplete, length probably similar to that of 235880. The specimen is weathered, the reflectivity similar to that of the matrix, the surface showing orange-brown patches. The anterior margin of the trunk (figure 80, plate 13) is bluntly pointed, five or six finger-like projections, the papillae, arising from it at different levels, straight or curved, randomly directed. The projection in the mid-line is relatively wide, the sides clearly defined, but it is difficult to decide whether it is one projection or two narrower projections close together. Inside the anterior margin, at the base of the papillae, is a faint dark stain. The pair of anterior appendages has the right markedly above (nearer the observer) the margin of the trunk, the left goes down below the margin; each tapers and shows faint annulations. Three long, slim branches on the anterior side of each, and three at the tip, each of those of the left differently directed, while at the tip of the right appendage two of the branches lie close together, one overlapping the other. The branches are straight or gently curved. Behind the anterior appendages the trunk is gently curved, the maximum width at about the fifth pair of limbs, the annulations preserved as faint, transverse ridges. Along the margin opposite to the limbs are triangular or rounded projections, between the limb bases the margin is faintly scalloped; the ridges correspond with these scallops and projections. This correspondence implies that each annulation was a sharp-crested ridge on the dorsum, and became a low, rounded ridge on the venter. No pits or mounds representing tubercles are preserved on the annulations. The projections preserved opposite limbs 5–7 (figure 78, plate 13) show features like those described in 235880 (figure 79, plate 13), i.e. lines or ridges following the margin or running straight beneath it, the surface stained orange-brown rather than covered by a film of fine-grained pyrite. The tips of certain projections are sharp, and in several the tip is extended as a short spine (cf. 235882, figure 60, plate 10).

The proximal portions of R 2–6 lie upon the margin of the trunk, whereas L 1–7 are inserted nearer to the left edge of the specimen than the right, and extend below the trunk to project on the right side. Left limb 1 has been completely exposed; both left and right limbs show faint annulations, and the claws are exposed in three. The positions of the left and right limb insertions show that the obliquity of the compression is the same between limbs 2–7, but the insertion of L 1 is more centrally placed, suggesting a change in obliquity anteriorly towards a more lateral compression. The left anterior appendage is inserted at a higher level on the left (farthest from the observer) than L 1, and may have projected upwards as well as outwards. The strong change in level between the right anterior appendage and the trunk shows that the insertion was on the right side of the body.

(*p*) *R.O.M.* 35413

Figure 81, plate 14; figure 85.

A dorsoventral compression, the smallest known specimen, part only available. At the anterior end the body passes into a pronounced dark stain, which obscures this end except on the left, where two slim papillae may be seen. Each anterior appendage projects straight outward,

proximally branched on the anterior side, distally the left is incomplete, the right fades away into the rock and is also incomplete. The trunk narrows progressively backwards and divides posteriorly into the 10th pair of limbs; no annulations are visible, but there is a narrow, faint, reflective median band, the trace of the alimentary canal. This trace is interrupted anteriorly where a patch of fine granules of pyrite lies on the specimen. The granules are piled up in the centre of the patch, more widely scattered peripherally; grains of pyrite of similar size are scattered sparsely over the remainder of the specimen. The 10 pairs of limbs are subradially arranged around the body, show no annulations or lateral spines, but traces of the claws as dark or reflective spots. The anterior pairs of limbs are strongly forwardly directed, so that the tip of each passes beneath the outstretched anterior appendage.

5. Discussion and conclusions

(*a*) *Morphology*

The evidence reviewed in § 4, interpreted in the light of the manner of preservation, is summarised in a reconstruction (figure 86). The length (sag.) of 14 specimens was measured (figure 87), and the range in length of the trunk is from 10.5 mm (35413) to 59 mm (83942*b*). Dimensions of parts of the body, positions relative to each other of anterior appendage and limbs, and dimensions of cross sections, are based on averages of measurements of the specimens, which are compressed in different directions; the scale in figure 86 suggests an intermediate size. The elongate trunk was thickest at about the fifth pair of limbs, reduced progressively behind here, not projecting behind the last pair of limbs but merging into their bases. About one-sixth of the length of the trunk lay in front of the first pair of limbs, and bore the anterior appendages. The anterior part of the trunk was bluntly rounded, no head region being clearly demarcated. The appearance in 83942*a* (figures 28, 29, plate 4) that there was a rounded 'head' region in front of the anterior appendages is unique to this specimen and is the fortuitous result of breakage where the proximal portion of the appendage overlies or underlies the trunk (figure 30).

Hutchinson (1930, p. 16, fig. 5) considered that the external surface of trunk and limbs was annulated, each annulus of the trunk formed by a close-spaced row of papillae, visible in the fossils either flattened along the dorsal margin or as small apical pits. He thought it probable (by analogy with modern Onychophora) that each apical pit bore a minute seta. Sharov (1966, figure 14) did not comment on this view, but showed annulations on trunk and limbs. Cave & Simonetta (1975, fig. 1), without discussion, show rings of close-spaced tubercles on trunk and limbs, but no setae. The present re-examination shows that trunk, limbs and anterior appendages of specimens 3 cm in length or larger are crossed by low ridges, evident in low angle radiation, but less so or not at all in high angle radiation. The marginal profile of the trunk shows on the dorsal side of the body evenly spaced triangular projections (figures 83, 84, plate 14); on the ventral side the profile is straight or gently undulating. These projections and undulations correspond in number with the ridges, and are at the end of them (figure 61, plate 10). Each margin of the anterior appendage (figure 56, plate 9) or limb (figure 52, plate 9) is scalloped, the scallops corresponding in position with the ridges. I interpret these features as showing that the external surface of *A. pedunculata* was annulated. On the trunk each annulus was a ridge, low on the ventral side but highest and sharp-crested on the dorsal side; possibly subsemicircular in profile laterally (figure 13, plate 2) as it changed in shape. On the anterior

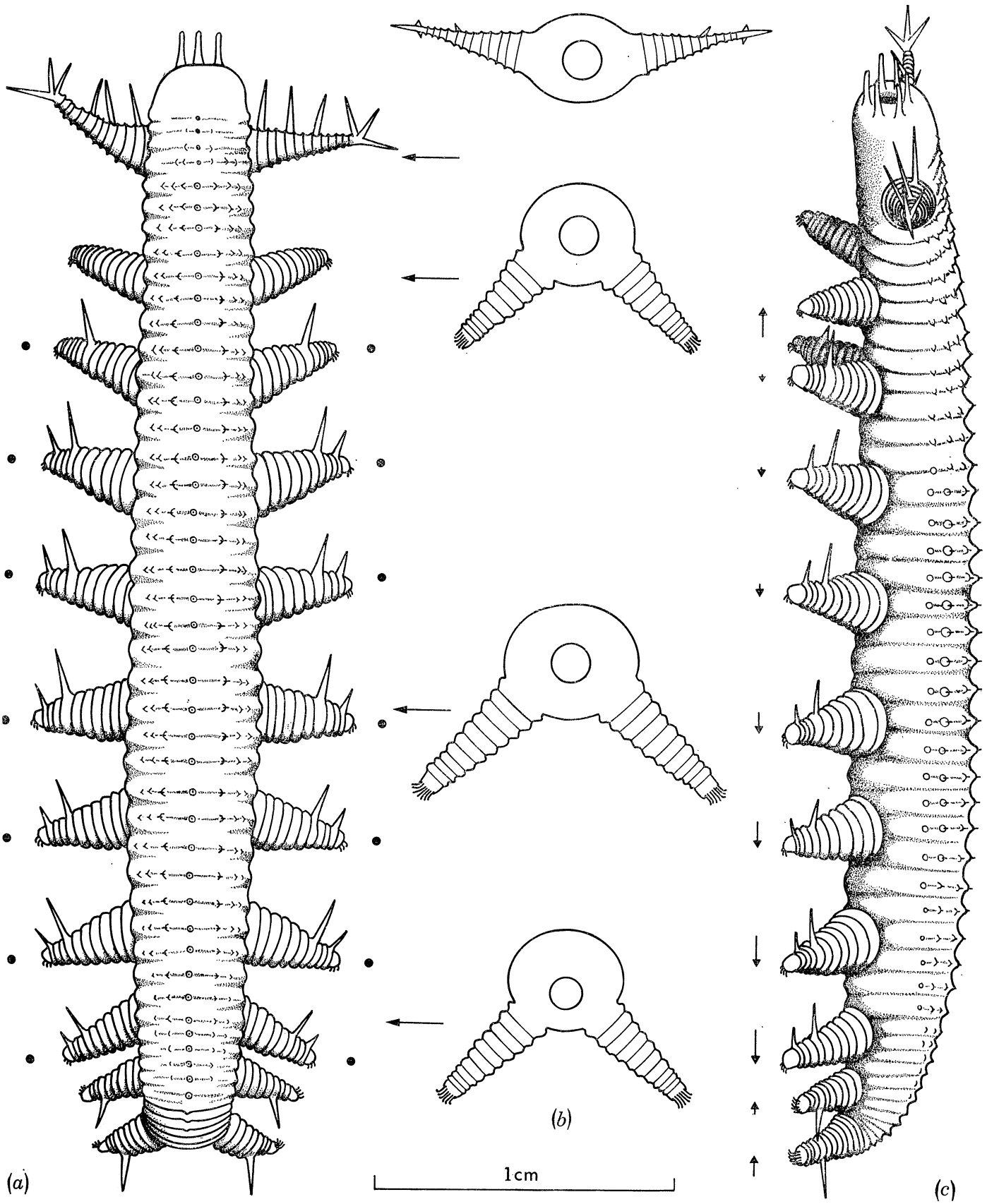

FIGURE 86. Reconstruction of *Aysheaia pedunculata* Walcott, 1911. (*a*) dorsal view, light from northwest. Limbs shown in 'still' position of a particular gait (see §5 (*b*)), solid circles in transverse line with tips of limbs stepping on sea floor. (*b*) Cross sections of body at the levels indicated by the arrows, position of alimentary canal shown. (*c*) left lateral view, light from northeast, anterior part of body turned slightly to left to give anterolateral view. Arrows beneath tips of limbs show direction and amount of promotor or remotor stroke passed through.

appendages the annulations appear to have been sharp-crested and of even height all round. In profile the annulations of the limbs may appear rounded or subtriangular, and they appear to be of similar height all round. That these ridges and marginal scallops represent raised annulations is strongly suggested by their shape and curvature in limbs that are flexed (figures 4, 62) as contrasted with extended limbs (figures 18, 30). The sharpness of the crest of the annulation may have varied as the limb was extended, contracted or flexed during burial. I agree with Hutchinson (1930, p. 16) that four annulations correspond to each limb in the trunk, one opposite the mid-line of each limb, and three in the intervening portion (figures 4, 18, 62). However, between the anterior appendage and first limb there are 5 to 6 annulations (figures 18, 30, 76), and 235880 (figure 51; figure 54, plate 9) shows not only one opposite the appendage but three in front of it. There is thus an implication that if each somite bore one

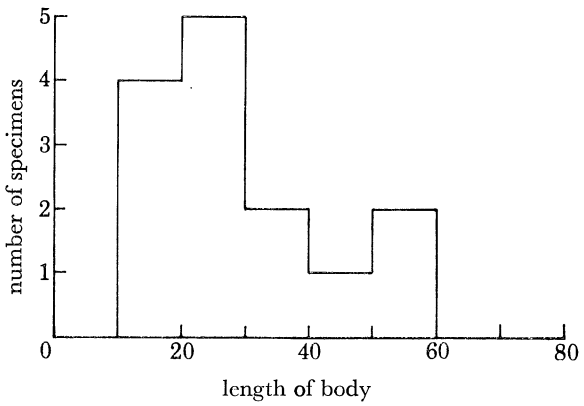

FIGURE 87. Size–frequency histogram. Length (sag.) measured from anterior margin of body, along arc of curvature to posterior margin at base of 10th pair of limbs. Specimens measured were U.S.N.M. 57497 and those described in § 4, except U.S.N.M. 235882 and R.O.M. 35412.

pair of limbs, the portion of the trunk in front of the first pair of limbs was composed of at least two somites. The arrangement of the annulations means that those of the anterior appendage and limbs 1–9 ran at right angles to those of the trunk. It is notable that the annulations of the most posterior part of the trunk form a continuous series with those of the 10th pair of limbs (figure 25, plate 4; figures 52, 53, plate 9). This latter arrangement was not shown by Hutchinson (1930, fig. 5) or Sharov (1966, fig. 14) but is by Cave & Simonetta (1975, fig. 1), who show, however, far more annulations on the trunk than is warranted by the evidence.

Walcott (1911, p. 117) considered that in the holotype (figure 4; figure 14, plate 2) there were 13 pits along the line of each annulation; since he was describing the counterpart these were presumably impressions of tubercles. There are faint, ill-defined mounds or pits along some of the annulations (figure 14, plate 2; figures 19, 21, 23, plate 3; figure 54, plate 9), but such structures do not seem to be present on other specimens (figures 25, 27, plate 4; figures 32, 35, plate 5; figure 77, plate 13). When visible they are less in diameter than the basal width of the triangular projections along the dorsal edge. These latter were taken by Hutchinson (1930, p. 16) and Cave & Simonetta (1975, figs. 3, 11) to be flattened tubercles, but the evidence reviewed above leads me to consider them as annulations in profile. The projections may be triangular in outline, the sides flat, steeply sloping, the tip an acute angle, in others the sides are rounded and the apex sharply pointed (figure 60, plate 10; figures 83, 84, plate 14). In 35412 (figure 78, plate 13) some of these points are long and slightly curved, spine-like. Each

apical point or spine may represent a flattened tubercle on the crest of the annulation, the spine at the apex of the tubercle. The exact position of the compressed, folded edge of the specimen presumably caused the variation in form of the projections. It thus appears that there is evidence of tubercles on the annulations on the crest of the ridge on the dorsal side of the trunk; these tubercles appear to have borne an apical spine. How many there were is uncertain; if the faint mounds or pits in the originals of figures 4, 18 and 51 are also traces of them, there may have been a row of 7 on the dorsal side (figure 86). The sharpness of the crests of the annulations, and their height on the dorsal side, may partly result from this row of tubercles. Perhaps because of the softness of the cuticle these tubercles, evident on the folded, flattened edge, are rarely visible on the ridges of the annulations. The circumflex-shaped ridges at the base of the projections in 235882 (figure 61, plate 10) may be the compressed remains of tubercles on the annulations. The only evidence that there may have been tubercles on the limb annulations is afforded by L 9 and 10 of 235880 (figure 51; figure 55, plate 9) and this evidence is slight.

Characteristic of the folded, flattened dorsal margin of the trunk, with the triangular projections, is a marginal zone beneath the projections. This zone may appear darker and bear discontinuous ridges or grooves subparallel to the edge (figure 78, plate 13; figures 83, 84, plate 14). Fine pyrite may be concentrated in lines along the zone (figure 79, plate 13), or there may be small raised areas (figures 57, 58, 61, plate 10) or circumflex-shaped ridges below the projections. Such a marginal zone is not apparent along the lateral (figure 13, plate 2) or ventral (figure 23, plate 3) margin, so that the zone does not appear to represent structures within the body wall, but rather properties of the dorsal cuticle. It has been argued that this cuticle is the most strongly annulated and that the ridges bore tubercles, and the zone may represent wrinkling and flattening of tubercles in an originally thicker dorsal cuticle.

The anterior end of the trunk appears well preserved in 235880 (figure 56, plate 9) and 35412 (figure 80, plate 13), and shows straight or curved projections, the papillae, arising along the margin, four to seven (figure 38, plate 6) in number. These papillae appear similar in size to the branches of the anterior appendage, or considerably smaller, as in the less well preserved original of figure 24, plate 3. In specimens in which the anterior margin is poorly preserved because it merges into a dark stain (figure 10, plate 1; figures 28, 29, plate 4; figure 42, plate 7), papillae are recognizable at the anterolateral margin. In specimens in which the reflective strip representing the alimentary canal extends anteriorly (figures 43, 46, plate 7; figure 48, plate 8; figure 66, plate 11), it appears to be wider and to reach the mid-part of the anterior margin. I therefore conclude that the mouth was situated centrally at the anterior end of the body and surrounded by a ring of six or seven papillae (cf. Hutchinson, 1930, p. 18). The holotype (figures 10, 11, plate 1; figure 14, plate 2) offers no evidence for the head described and portrayed by Walcott (1911, p. 117, pl. 23, figures 8, 9) and accepted by Sharov (1966, p. 22, figure 14). The anterior end of the animal portrayed by Cave & Simonetta (1975, figure 1) is based on misinterpretations of specimens (see § 4 (*i*) (*n*)). What are here described as papillae in 235880 (figure 56, plate 9) are called by them 'pin-like filaments', and shown protruding from four 'papillae' which were said to be seen on what has proved to be the incompletely exposed posterior end of the counterpart of 235885. The dark stain at the anterior end is here considered to be decay products, and not evidence of an 'evertible proboscis or pharynx' (Cave & Simonetta 1975, p. 69). In specimens in which the stain is largest and most intense (figures 65, 68, plate 11), it merges into the anterior margin and suggests that decay

may have proceeded farthest and been accompanied by disruption of the margin. In two other examples (figure 11, plate 1; figures 28, 29, plate 4) papillae are present only at the outer edge of the anterior margin, a position which may have resulted from folding back of the cuticle as decay products escaped. The 'short appendage or frontal papilla of uncertain structure' of Hutchinson (1930, p. 18, figure 5; but omitted in Hutchinson 1969), on the right side of 235879 (figure 46, plate 7), is also one such displaced oral papillae. Where there is little or no stain, and no disruption of the margin, the papillae are more nearly in their natural position (figure 24, plate 3; figure 56, plate 9).

Preparation of previously illustrated specimens (figures 28, 29, plate 4), and the excellent preservation of 235880 (figure 56, plate 9) and 35412 (figure 77, plate 13), have shown the anterior appendage in detail. It is as wide (exs.) at the base, and as long, as the first limb, but tapers more rapidly. The level of the proximal portion relative to the trunk shows that it was attached high on the side (cf. Hutchinson 1930, p. 17). The appendage bore slim, pointed branches which were apparently only slightly flexible, but movable about the base. There was a group of three at the tip (which may be preserved in different positions at the tip on either side, figure 76) and at least 3 along the anterior margin (figures 18, 30, 51, 76). In 57655 (figure 4) there appear to be four such branches, and they are at different levels along the edge. In most specimens these branches are forwardly directed, but occasionally are preserved on the opposite side (figures 18, 30, 51), suggesting either that the appendage could be twisted along its axis, or more likely showing the effect of turbulence in twisting the appendages before burial. I have discussed above why I consider that the anterior appendage was annulated, and that it did not bear long, pointed tubercles (Cave & Simonetta 1975, p. 74, figure 1). My restoration of these appendages thus differs considerably from that of the latter authors, Hutchinson's more recent sketch (1969, fig. 1) of this appendage being closer to his original observations (1930, pp. 17–18) than his earlier restoration (1930, fig. 5).

Preparations have shown that in early described specimens (figures 4, 17, 18, 30, 31) there were 10 (not 9) pairs of limbs terminating in claws, and additional specimens show this number in the smallest (figure 85) to largest (figure 31) individuals known. Limbs 1–3 show a gradational increase in size, 4–7 are similar, and 8–10 show a progressive decrease. Each limb is broad at the base, tapering, the diameter at the base greater than the gap between adjacent limbs, the gap between limbs 8–9 and 9–10 markedly narrower than the remainder. The nature of the annulations on the external surface of the body has been discussed above. Some ten such annulations, progressively narrower distally, are indicated on each limb by transverse ridges and grooves and scallops on the compressed margin. The fossils do not provide evidence for assuming that the annulations on the limbs were formed by rows of tubercles, as portrayed by Hutchinson (1930, fig. 5) and Cave & Simonetta (1975, fig. 1). At the blunt tip of the limb a group of curved claws are present in specimens of all sizes known; the maximum number observed on any limb is seven (figure 52, plate 9). Hutchinson (1930, figs. 4*b*, 4*c*) drew special attention to the claws in 235879 (figure 41) and in this specimen the claws may be in an imbricated row curved in the same direction (R 3, 9, 10), or symmetrically arranged (R 4). He did not mention or portray the tip of the limb, seen in R 5 extending beyond the claws. A similar tip is visible in various examples (figures 20, 22, plate 3; figure 26, plate 4; figure 52, plate 9). The claws always curve away from the blunt tip, in limbs 1–8 the tip is anterior and the claws point backward, in limbs 9, 10 the orientation is reversed. This arrangement is dominant, but an occasional limb may show a different orientation (for example, L 6 in figure 30;

R 5, 6 in figure 41), which I interpret as resulting from twisting during burial, turning the tip through 90° or 180°. A specimen such as 139206*a* (figure 17) shows the varied orientation of tips of limbs to be expected in a specimen so flexed. To satisfy these appearances after compression I reconstruct the tip of the limb (figure 88) as a blunt, fleshy point, which bore on the posterior (in limbs 1–8) face seven claws in a radial arrangement; in limbs 9 and 10 the claws were on the anterior face. The 'subapical triangular area' (Hutchinson, 1930, p. 17, fig. 4*b*) at the base of the claws, described as a 'dark, longitudinal elongate spot' appears to be the

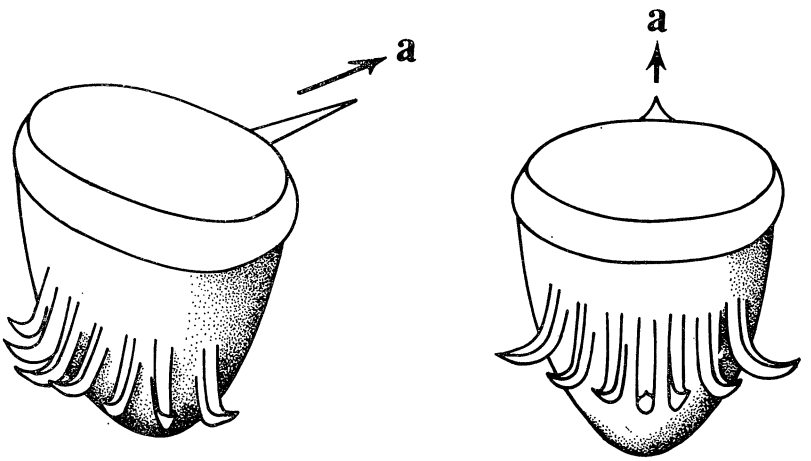

FIGURE 88. Reconstruction of the tip of limb 3–8 including distal annulation, small spine and claws. **a** indicates anterior side. In limbs 1 and 2 there was no small spine, and in limbs 9 and 10 the claws were on the opposite face of the tip.

proximal, longitudinal portions of the claws. Hutchinson (1930, p. 17, figs. 4*c*, 5) noted the spine on the right (not left) limb 3 of 57655, (figure 4), which shows similar spines on R 4–8, 10 and L 5, 7, 10, all arising from the seventh annulation. These spines point forward (when the limb is extended), except that on L 10 which is directed backward. Similar long spines are seen on other specimens, only on 235880 (figure 51) is there such a spine on the second, right, limb, and it has not been seen on the first limb. A small spine on approximately the tenth annulation is also visible in several examples (as in figures 4, 18, 30) on the third to eighth limbs. The large spine is present on the 9th limb (figures 62, 63) on the opposite side to the claws. Lateral spines have not been observed in specimens smaller than 235883 (figure 63, length 20 mm). In the reconstruction I portray these spines forward and outwardly directed, in the opposite direction to the claws, in limbs 2–8, and backwardly directed in limbs 9 and 10. The backward direction in 10 appears universal and real, not a result of twisting, and in 9 the claws point forward (figures 4, 41) and I assume this is real and direct the spine backward. I do not regard the spines as 'internal processes' (Hutchinson 1930, p. 17, and shown backwardly and inwardly directed in figure 5). There is no evidence for regarding all the limbs as bearing numerous 'filamentous processes', forwardly directed, as did Sharov (1966, p. 22, fig. 14).

Nothing of the internal anatomy appears to be preserved except the trace of the alimentary canal, extending part or all of the length of the trunk (figures 30, 31, 41), the anterior portion appearing wider in two examples (figures 41, 64). The posterior portion may be visible adjacent to the proximal parts of limbs 9 and 10 (figure 45, plate 7; figure 48, plate 8) and suggests that the anus was situated between the posterior pair. Specimens through the known size range (figure 87) show the branched anterior appendage and 10 pairs of limbs with claws, and the

proportional size and shape of parts of the body appears the same. In the two smallest specimens (figures 81, 82, plate 14) no trace of the annulations is apparent, but faint traces may be seen in the slightly larger 235884 (figures 66, 69, plate 11). No lateral spines are visible on the limbs of the two smallest specimens, but the larger spine on L 9, 10 (pointing backward) is visible in 235884, and in 235883 (figure 63) lateral spines are seen on several limbs. The differences between specimens of 1 cm length (figure 85) to the largest known (6 cm, figures 18, 31, 76) are therefore slight and those mentioned may have resulted from factors in preservation.

(*b*) *Mode of Life*

Aysheaia pedunculata must have been broadly similar to a Recent onychophoran (Snodgrass 1938; Manton 1973*a*, pp. 267–270, figs. 3, 4), in that muscles in the body wall worked against an internal hydrostatic pressure to maintain rigidity (or otherwise) of the trunk and limbs, to vary the length of the limb when walking, and to provide a promotor-remotor swing of the limb. Whether or not the body cavity was haemocoelic, divided by oblique muscle sheets, with vascular channels running within each annular ridge on the body wall, is uncertain, but the external morphology does not preclude such close similarity. In the reconstruction I have

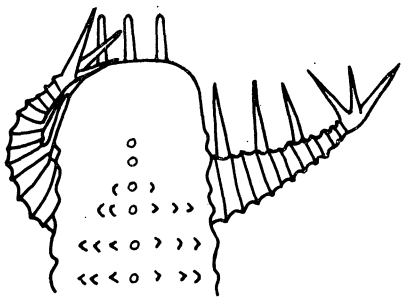

FIGURE 89. Anterior portion of body, dorsal view, taken from figure 86(*a*), but with left anterior appendage flexed forward as close to body as lateral spines permit. Note that only tips of terminal spines are near to mouth.

drawn the animal in a gait still of onychophoran type (Manton 1973*a*, pp. 261–266, 296) in which the relative duration of forward and backstrokes is 3.5:6.5, and a phase difference of 0.1 is chosen, to given 7 limbs on the substrate and two off in one metachronal wave. Such a slow walk, on the rounded tips of the limbs, would be suitable for traversing the muddy sea bottom. Limbs 9 and 10 were short, and it is argued, with forward-curving claws; whether or not either pair was used in normal walking is uncertain. The alimentary canal in *A. pedunculata* has not been found preserved as a mud-filling, suggesting that the animal did not ingest large quantities of mud, and that it was not burrowing in habit. No trace of jaws is preserved, and I agree with Hutchinson (1930, p. 18) that had sclerotized jaws of Recent onychophoran type been present, some trace would have been visible. The terminal mouth appears to have been ringed with papillae, the anterior appendage of a length that allowed, at the maximum curvature, only the tips of the three terminal processes to be brought near the mouth (figure 89). There is no evidence of eyes.

In the Burgess Shale sponge remains occur rarely on the same slab of rock as arthropods and other animals, but are associated to an exceptional degree with *A. pedunculata*. Of the 19 known specimens, at least 6 have sponge remains on or near them:

83942*a* (figure 30) has a fragment resembling the outer wall of *Takakkawia lineata* Walcott 1920 (p. 277) across limbs 2 and 3, and a further patch of fragments on the trunk posteriorly.

83942*b* (figure 31; figures 34, 35, plate 5) has long spicules and patches of fragments lying on or near it, and near the posterior end occurs a portion of wall similar to that of *Vauxia gracilenta*, Walcott, 1920.

235880 (figures 47–50, plate 8) has a spicular mass, possibly of *Protospongia*, lying apparently between limbs 1–4.

Less conspicuous are the spicules on 235885 (see § 4 (*n*)), the presumed spicule at the posterior end of 235881 (figure 82, plate 14) and scattered spicules on the same slab as 235883.

Particularly the large areas of sponge remains, as seen in the first three specimens, suggest an association between sponges and *Aysheaia*, preserved by the catastrophic burial. I put forward (figure 90) the notion that *A. pedunculata* may have preyed on sponges, the clumps of which

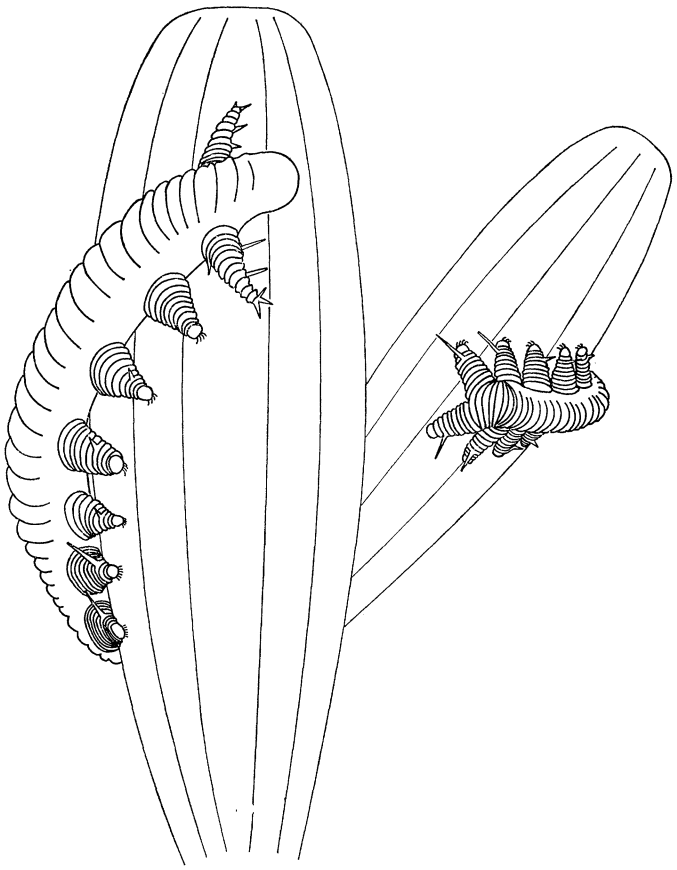

FIGURE 90. *Aysheaia pedunculata* Walcott, 1911, reconstruction suggesting that the animal preyed on sponges.

would afford concealment and protection from predators such as *Olenoides* (Whittington 1975*b*). The claws, not apparently useful on a muddy substrate, would have helped in climbing and holding on, and the backward-facing ones provided anchorage for the posterior part of the body perhaps while the anterior part was exploring. The anterior appendage, apparently not adapted for sweeping food into the mouth (fig. 89), was perhaps well suited to lacerate the sponge and hold the mouth in place while it was being ingested. The papillae may have helped to keep the mouth in position and to extend the wound, or aid in digestion. A diet of soft parts

of sponges would explain the lack of mud or other remains in the alimentary canal. The distal spines on the limbs, and the tubercles with apical spines on the dorsal part of the annulations of the trunk, may have been sensory, as the animal moved amid the sponges, and perhaps also defensive. Figure 90 is no more than a suggestion, and it may be objected that *A. pedunculata* is associated with a variety of sponges from the Burgess Shale (Walcott 1920). It is possible that the animal preyed also on algae, but no evidence of this is provided by association.

(*c*) *Affinities*

Walcott (1911, pp. 116–117, pl. 23, figs. 8, 9) described the holotype of *Aysheaia pedunculata* as a polychaete worm, to which he added an imaginary head (cf. Hutchinson 1930, p. 18; 1969, pp. 1062–1063). This head has been accepted only by Sharov (1966, p. 22), who explained its absence in all other specimens as because it was retractile. Walcott's posthumous publication (1931, p. 8) shows that the onychophoran-like appearance of the fossil was drawn to his attention immediately after publication of his 1911 paper. Hutchinson (1930) studied the holotype and seven additional specimens of *Aysheaia*, and concluded that it belonged within the Onychophora, and showed what the oldest members of that group were like. Because of the differences between *Aysheaia* and Recent terrestrial forms, he subdivided the group into two new orders, Protonychophora (including only *Aysheaia*, in the family Aysheaiidae Walcott, 1911) and Euonychophora (all Recent forms). This view has been adhered to by Størmer (1944, p. 24), Cuénot and Vandel (*in* Grassé 1949, pp. 34–35, 100, 140), Dechaseaux (*in* Piveteau 1953, pp. 4–7), Tiegs & Manton (1958, p. 262), Moore (1959, pp. O 18–O 19) and Sharov (*in* Orlov 1962). It was re-affirmed by Hutchinson (1969), after a re-examination of specimens led him to reject observations and conclusions put forward by Snodgrass (1958) and Sharov (1966). Hutchinson's 1969, figure 1, lateral view of *Aysheaia* is modified from his 1930 version, omitting the 'frontal papilla' and setae on the tubercles, and showing an anterior appendage more like that shown here.

It is the merit of Cave & Simonetta (1975, pp. 74–75) and Simonetta (1976, pp. 114–115) to have drawn attention to similarities between *Aysheaia* and Tardigrada. These similarities include the terminal mouth surrounded by papillae (cf. Ramazotti's 1972, fig. 467, p. 689, of the mouth of *Milnesium tardigradum*), the presence of claws on the limbs, which on the last one or two pairs curve forward (opposite to those on more anterior limbs), and the shape of the posterior end of the body, which does not project behind the bases of the posterior pair of limbs, but merges into them. Cave and Simonetta also note as a similarity the lack of antennae, since they considered the present anterior appendage to be a leg. One Cretaceous species (Cooper, 1964) and several hundred Recent species of tardigrades are known, all no more than about 1 mm in length, aquatic, and having only four pairs of short uniramous limbs. They are thus very different animals from the macroscopic *Aysheaia*. The latter is also undoubtedly onychophoran-like, in size, in possessing an anterior pair of appendages and many pairs of short, uniramous limbs (those of onychophorans also bear claws), and having annulations of trunk and limbs. However, onychophorans are known only from the Recent, are terrestrial, possess a jaw apparatus, and the terminal part of the body projects behind the last pair of limbs. These similarities and differences (amended and added to here) led Cave & Simonetta (1975, pp. 75–76) and Simonetta (1976, p. 115) to suggest that *Aysheaia* was intermediate between Tardigrada and Onychophora, but does not belong in either group, and may merit inclusion

in a separate class. I prefer not to use any new or amended higher taxon, but to suggest that *A. pedunculata* may be regarded as the sole known representative of an early group of soft-bodied, metamerically segmented, lobopodial animals, a representative that appears to have been well adapted to a particular niche, in which it was preserved rarely in exceptional circumstances. From this hypothetical group may have been descended both the Tardigrada and the Onychophora. The latter suggestion is in harmony with the view of Manton (1972, fig. 40; 1973*a*, pp. 260–261; 1973*b*, p. 124, fig. 7) that the Arthropoda are polyphyletic and include at least three phyla, one of which is the Uniramia (Onychophora, Myriapoda, Hexapoda), descended from early lobopodial animals. Thus *Aysheaia*, like such other Burgess Shale animals as *Opabinia* (Whittington 1975*a*), *Hallucigenia* (Conway Morris 1977*a*); and *Dinomischus* (Conway Morris 1977*b*), does not fit readily into any extant higher taxon.

In discussion of *Aysheaia* reference has frequently been made (e.g. Moore 1959, p. O 17–20; Manton 1973*b*, p. 124; Cave & Simonetta 1975, p. 76) to *Xenusion auerswaldae*, based on a single external mould in quartzite from presumed Lower Cambrian rocks of Sweden (Jaeger & Martinsson 1967). These authors consider it to be a portion of a segmented animal (which was considerably larger than *Aysheaia*) which bore pairs of annulated lobopodial appendages. However, Tarlo (1967) compared *Xenusion* to fossils from quartzites in South West Africa, South Australia and Leicestershire, now referred to *Rangea*, *Glaessnerina* and *Charnia* (Germs 1973 and references). The nature and affinities of these fossils is a matter of debate (Glaessner & Walter 1975), and Tarlo's suggestion appears plausible in view of the mode of preservation of *Xenusion*. Further consideration of it in the present context does not appear to be warranted.

In 1966 and 1967 a re-investigation of the Burgess Shale (Whittington 1971*a*; Fritz 1971) was undertaken by the Geological Survey of Canada, with the cooperation of authorities of the Yoho National Park and Parks Canada, Department of Indian and Northern Affairs, Ottawa. The Geological Survey of Canada kindly invited me to be Chairman of the palaeobiological work, and I am indebted to the Natural Environment Research Council (grant GR3/285) for support of both field and laboratory work. Every facility for study of the Walcott collection in the National Museum of Natural History (formerly U.S. National Museum), Washington, D.C., was afforded by Dr Porter M. Kier and Dr Richard E. Grant. Dr D. H. Collins kindly arranged the loan of specimens collected by the Royal Ontario Museum, Toronto, party in 1975. My photographs have been enlarged by Mr David Bursill and Mr John Lewis has skilfully converted my pencil drawings into the present figures. I am greatly indebted to Dr S. M. Manton, F.R.S., and Dr D. E. G. Briggs, Dr S. Conway Morris and Dr C. P. Hughes for discussion and comments in the course of this work.

References

Cave, L. Delle & Simonetta, A. M. 1975 Notes on the morphology and taxonomic position of *Aysheaia* (Onycophora?) and of *Skania* (undetermined phylum). *Monitore Zool. Ital.* (N.S.) **9**, 67–81.

Conway Morris, S. 1977*a* A new metazoan from the Cambrian Burgess Shale, British Columbia. *Palaeontol.* **20**, 623–640.

Conway Morris, S. 1977*b* A new entoproct-like organism from the Burgess Shale of British Columbia. *Palaeontol.* **20**, 833–845.

Conway Morris, S. 1977*c* Fossil priapulid worms. *Spec. Pap. Palaeontology* **20**, iv + 95 pp., 30 pls.

Cooper, K. W. 1964 The first fossil Tardigrade: *Beorn leggi* Cooper, from Cretaceous amber. *Psyche* **71**, 41–48.

Fritz, W. H. 1971 Geological setting of the Burgess Shale. *North Am. Paleont. Convention, Chicago*, 1969, *Proc.* I, 1155–1170. Lawrence, Kansas: Allen.

Germs, G. J. B. 1973 A reinterpretation of *Rangea schneiderhoehni* and the discovery of a related new fossil from the Nama Group, South West Africa. *Lethaia* **6**, 1–9.

Glaessner, M. F. & Walter, M. R. 1975 New Precambrian fossils from the Arumbera Sandstone, Northern Territory, Australia. *Alcheringa* **1**, 59–69.

Grassé, P. P. 1949 (ed.) *Traité de Zoologie*, vol. 6. Paris: Masson.

Hutchinson, G. E. 1930 Restudy of some Burgess Shale fossils. *Proc. U.S. Natn. Mus.* **78** (11), 1–24.

Hutchinson, G. E. 1969 *Aysheaia* and the general morphology of the Onychophora. *Amer. Jour. Sci.* **267**, 1062–1066.

Jaeger, H. & Martinsson, A. 1967 Remarks on the problematic fossil *Xenusion auerswaldae*. *Geol. Fören. Stockholm Förhandl.* **88**, 435–452.

Manton, S. M. 1972 The evolution of arthropodan locomotory mechanisms. Part 10. Locomotory habits, morphology and evolution of the hexapod classes. *J. Linn. Soc., Zool.* **51**, 203–400.

Manton, S. M. 1973*a* The evolution of arthropodan locomotory mechanisms. Part 11. Habits, morphology and evolution of the Uniramia (Onychophora, Myriapoda, Hexapoda) and a comparison with the Arachnida, together with a functional review of uniramian musculature. *J. Linn. Soc., Zool.*, **53**, 257–375.

Manton, S. M. 1973*b* Arthropod phylogeny – a modern synthesis. *J. Zool., London* **171**, 111–130.

Moore, R. C. 1959 (ed.) Treatise on Invertebrate Paleontology, Part O, Arthropoda 1. Geol. Soc. Am. and Univ. Kansas, Lawrence, Kansas.

Orlov, Yu A. (ed.) 1962 *Oznovy Paleontologii*; *Arthropods tracheate and cheliferous*. Acad. Sci.U.S.S.R., Moscow.

Piveteau, J. 1953 (ed.) *Traité de Paléontologie*, vol. 3. Paris: Masson.

Ramazotti, G. 1972 Il phylum Tardigrada, 2nd edit. *Mem. Instit. Italiano di Idrobiologia* **28**, 1–732.

Sharov, A. G. 1966 *Basic arthropodan stock, with special reference to insects*. Oxford: Pergamon.

Simonetta, A. M. 1976 Remarks on the origin of the Arthropoda. *Atti. Soc. Tosc. Sci. Natur. Mem.* (1975) B, **82**, 112–134.

Snodgrass, R. E. 1938 Evolution of the Annelida, Onychophora, and Arthropoda. *Smithson. misc. Collns.* **97**(6), 1–159.

Snodgrass, R. E. 1958 Evolution of arthropod mechanisms. *Smithson. misc. Collns.* **138**(2), 1–77.

Størmer, L. 1944 On the relationships and phylogeny of fossil and Recent Arachnomorpha. *Skr. norske Vidensk. -Akad. Oslo, I Mat.-Nat. KI.* **5**, 1–158.

Tarlo, L. B. H. 1967 *Xenusion* – Onychophoran or coelenterate? *Mercian Geol.* **2**, 97–99.

Tiegs, O. W. & Manton, S. M. 1958 The evolution of the Arthropoda. *Biol. Rev.* **33**, 255–337.

Valentine, J. W. 1977 General patterns of metazoan evolution, *in* Hallam, A. (ed.), *Patterns of Evolution*. Amsterdam: Elsevier.

Walcott, C. D. 1911 Cambrian Geology and Paleontology. II. Middle Cambrian annelids. *Smithson. misc. Collns.* **57**(5), 109–144.

Walcott, C. D. 1912 Cambrian Geology and Paleontology. II. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Smithson. misc. Collns.* **57**(6), 145–228.

Walcott, C. D. 1916 Evidences of Primitive Life. *Ann. Rep. Smithson. Instit.*, 1915, 235–255.

Walcott, C. D. 1920 Cambrian Geology and Paleontology. IV. Middle Cambrian Spongiae. *Smithson. misc. Collns.* **67**(6), 261–364.

Walcott, C. D. 1931 Addenda to descriptions of Burgess Shale fossils. *Smithson. misc. Collns.* **85**, 1–46.

Whittington, H. B. 1971*a* The Burgess Shale: history of research and preservation of fossils. *North Am. Paleont. Convention, Chicago*, 1969, *Proc.* I, 1170–1201. Lawrence, Kansas: Allen.

Whittington, H. B. 1971*b* Redescription of *Marrella splendens* (Trilobitoidea) from the Burgess Shale, Middle Cambrian, British Columbia. *Geol. Surv. Can., Bull.* **209**, 1–24.

Whittington, H. B. 1974 *Yohoia* Walcott and *Plenocaris* n. gen., arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Geol. Surv. Can., Bull.* **231**, 1–21.

Whittington, H. B. 1975*a* The enigmatic animal *Opabinia regalis*, Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. R. Soc., Lond.* B **271**, 1–43.

Whittington, H. B. 1975*b* Trilobites with appendages from the Middle Cambrian, Burgess Shale, British Columbia. *Fossils and Strata* **4**, 97–136.

Whittington, H. B. 1977 The Middle Cambrian trilobite *Naraoia*, Burgess Shale, British Columbia. *Phil. Trans. R. Soc., Lond.* B **280**, 409–443.

[Plates 1–14 have been printed at the University Press, Oxford.]

List of abbreviations and symbols

G.S.C.	Geological Survey of Canada
L	Left side of animal, as prefix
R	Right side of animal, as prefix
R.O.M.	Royal Ontario Museum
U.S.N.M.	United States National Museum (now National Museum of Natural History)
al	reflective band, trace of alimentary canal
ap	anterior appendage of body
bi	bivalved shell, probably ostracod
c	claws
ds	dark stain
fo	fold
fr	fracture
m	portion of margin shown by enlarged photograph
p	papilla
pyr	pyrite granules
sp	large spine on limb
spic	isolated spicule or spicular meshwork of sponge
ss	small spine on limb
t	tip of limb
ve	vein in rock
vw	ventral wall of body
1–10	number in series of limbs
stipple	fine stipple shows annulations, particular darker areas, and is also used for reflective trace of alimentary canal; coarser stipple indicates dark stain
circle	small open circles in figures 4, 18, 51, show position of tubercles


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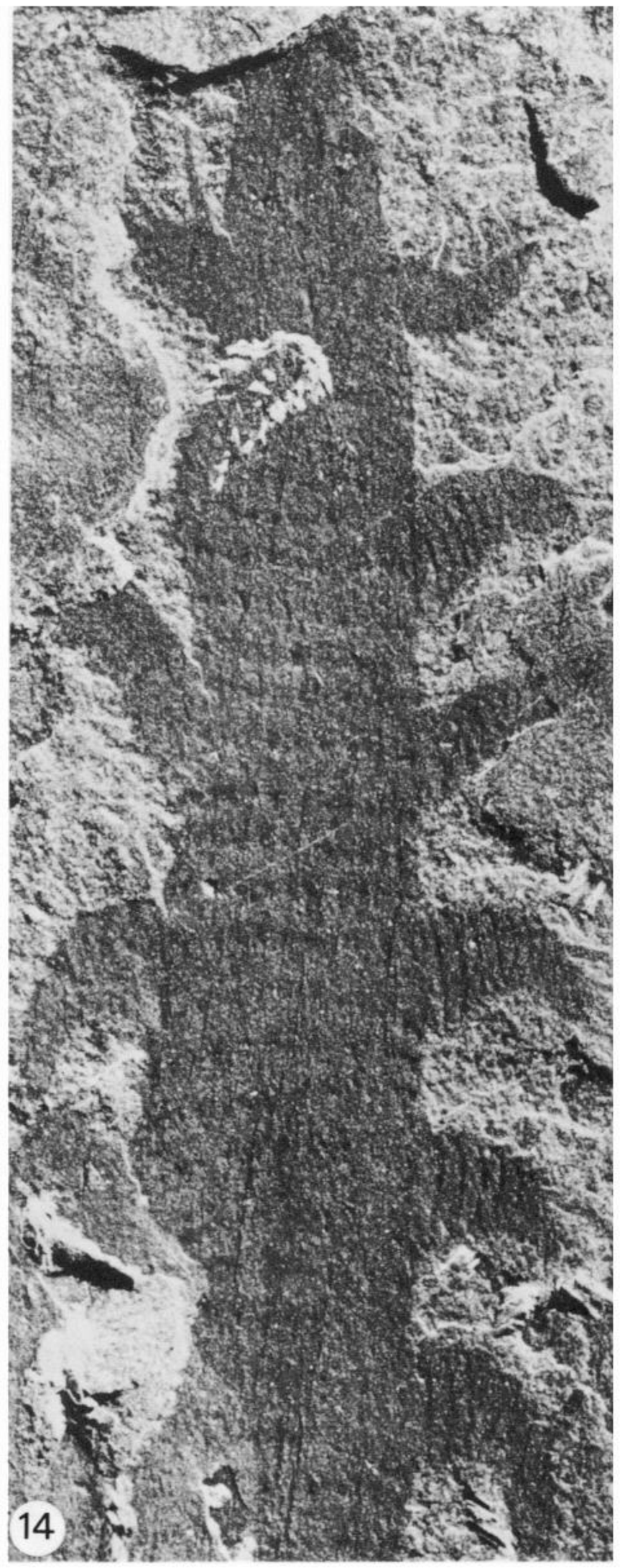
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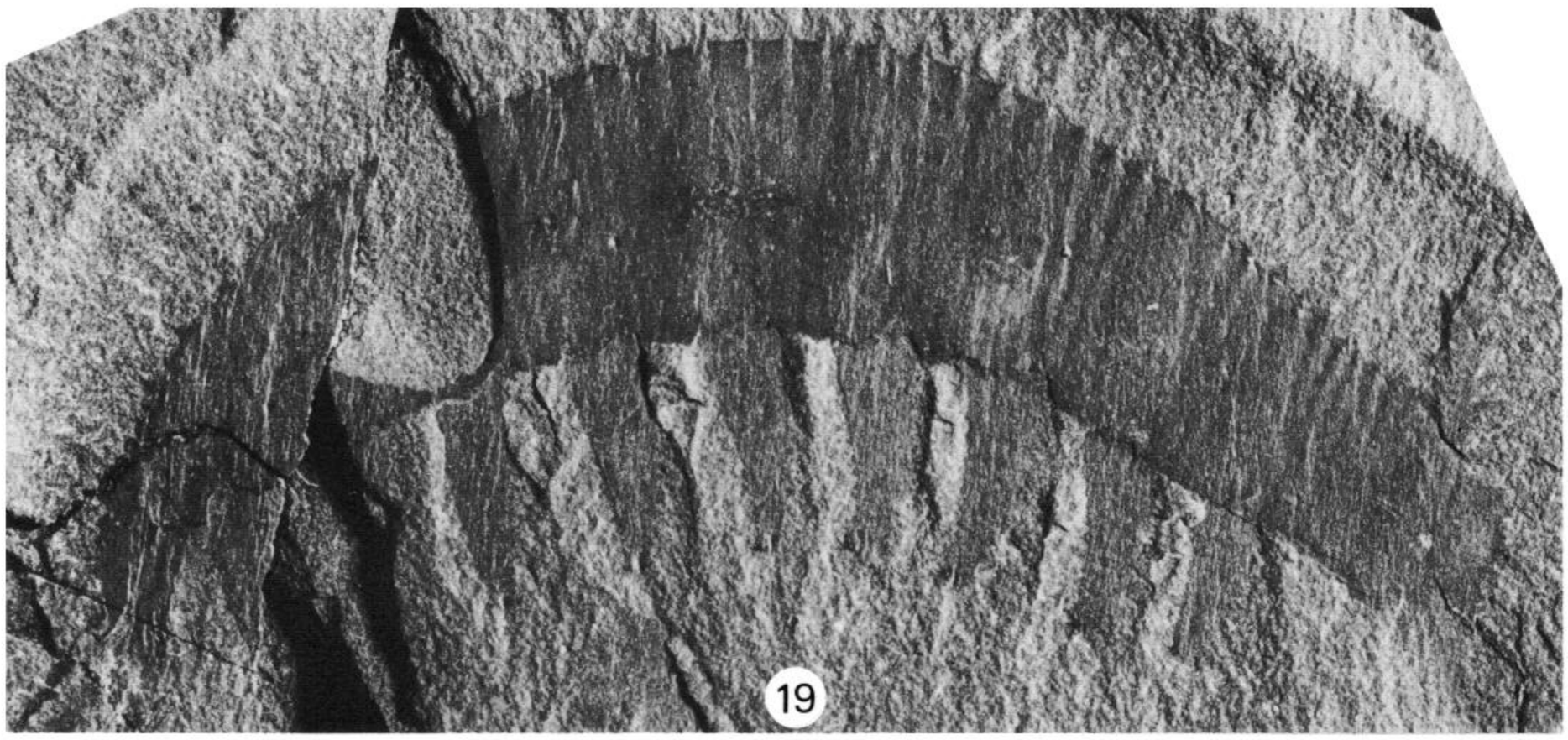
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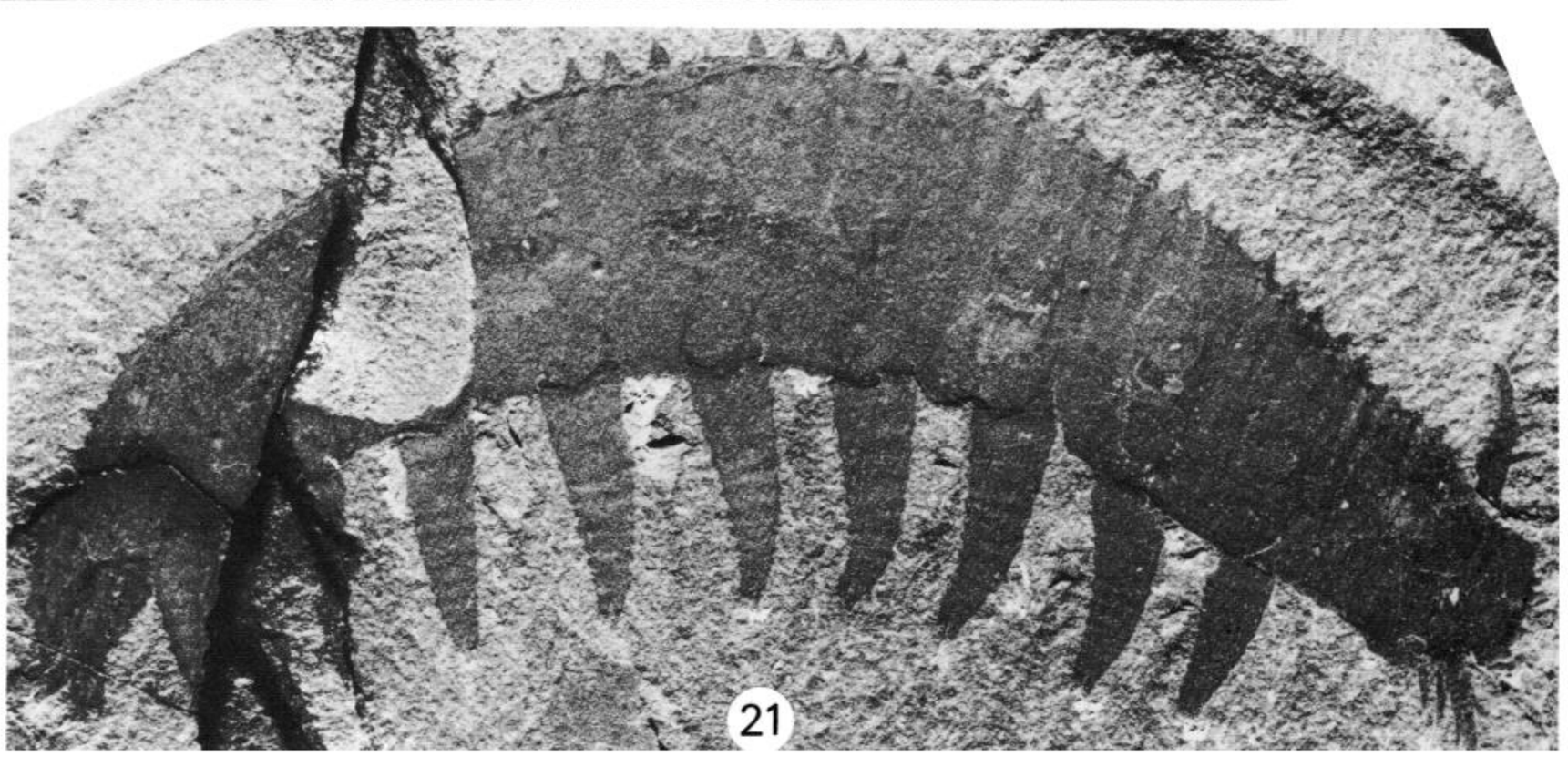
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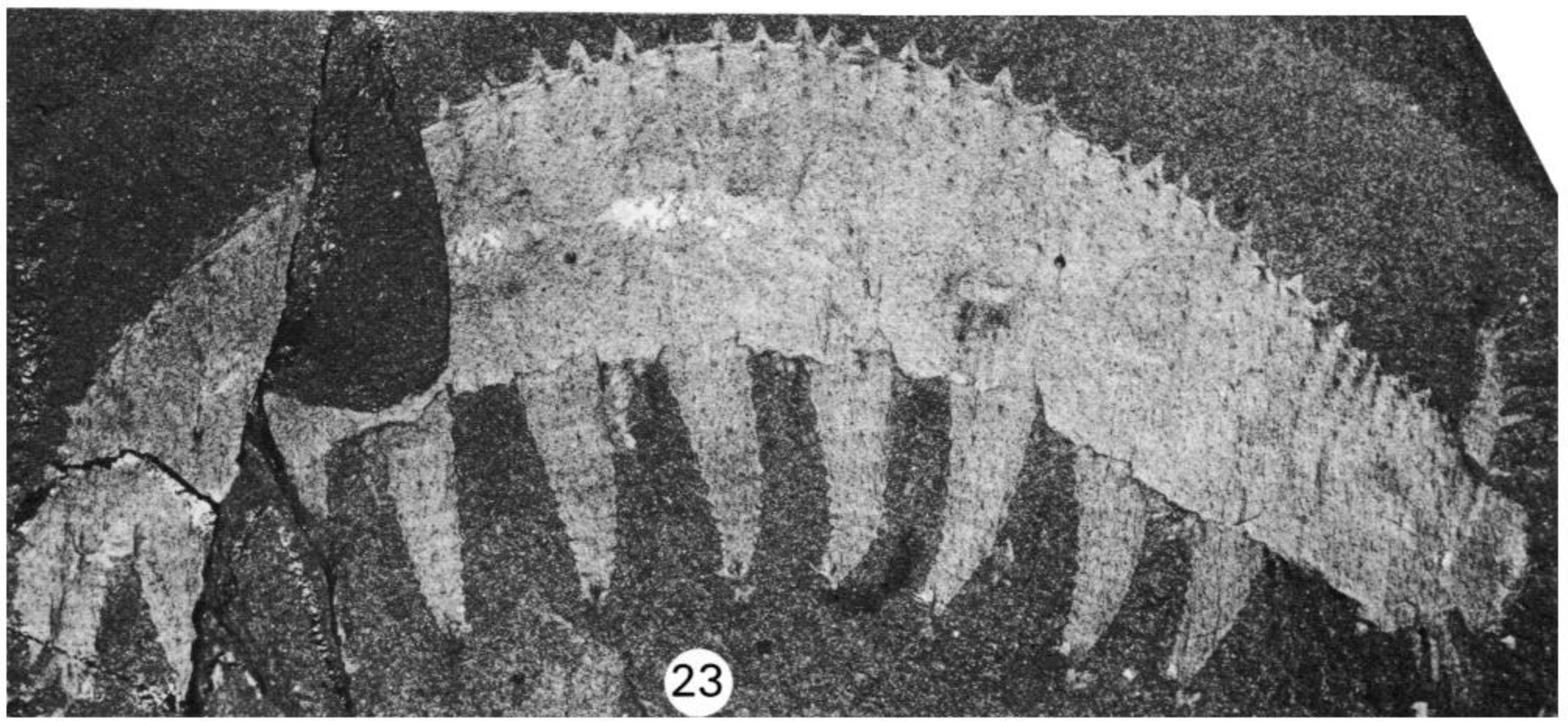
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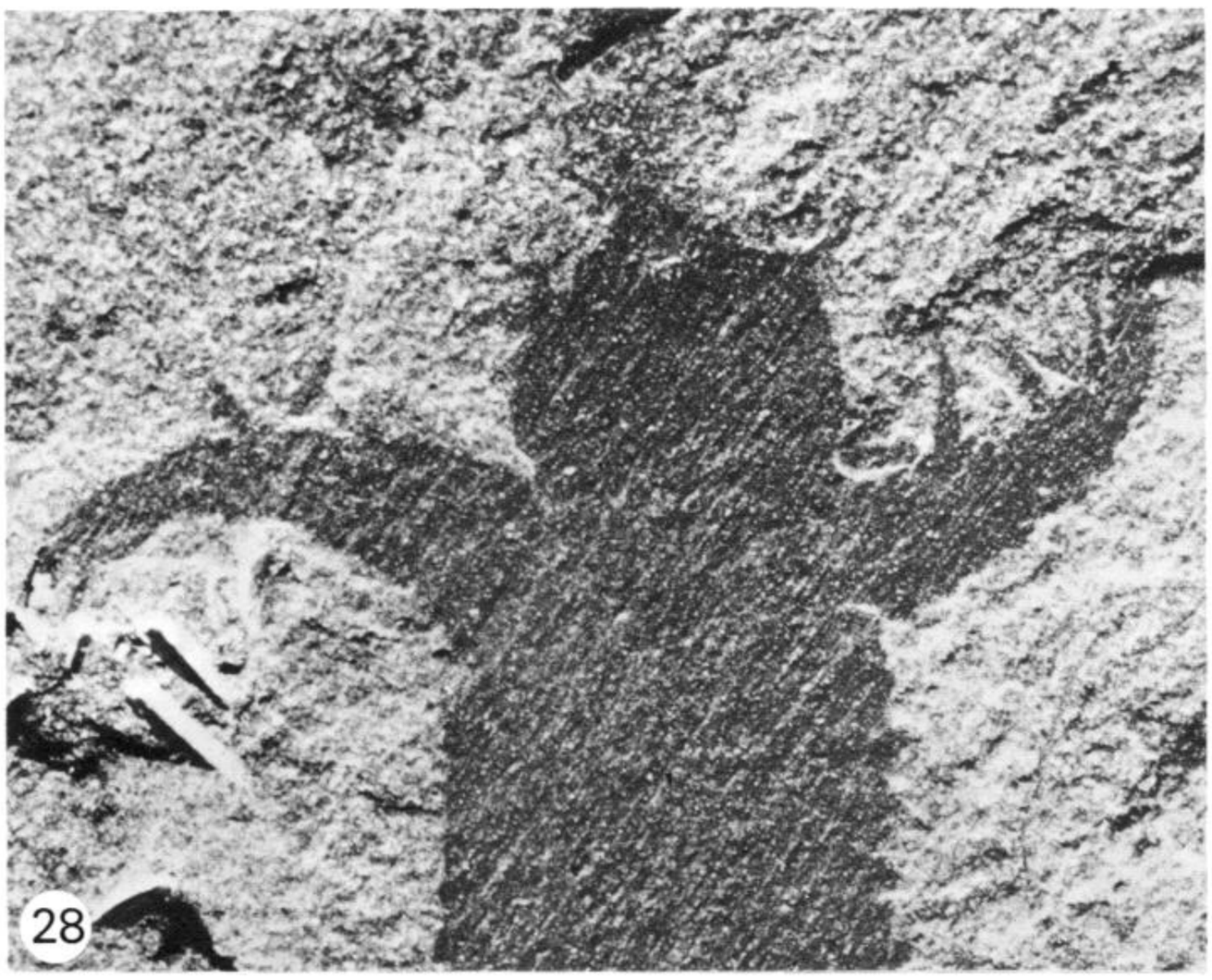
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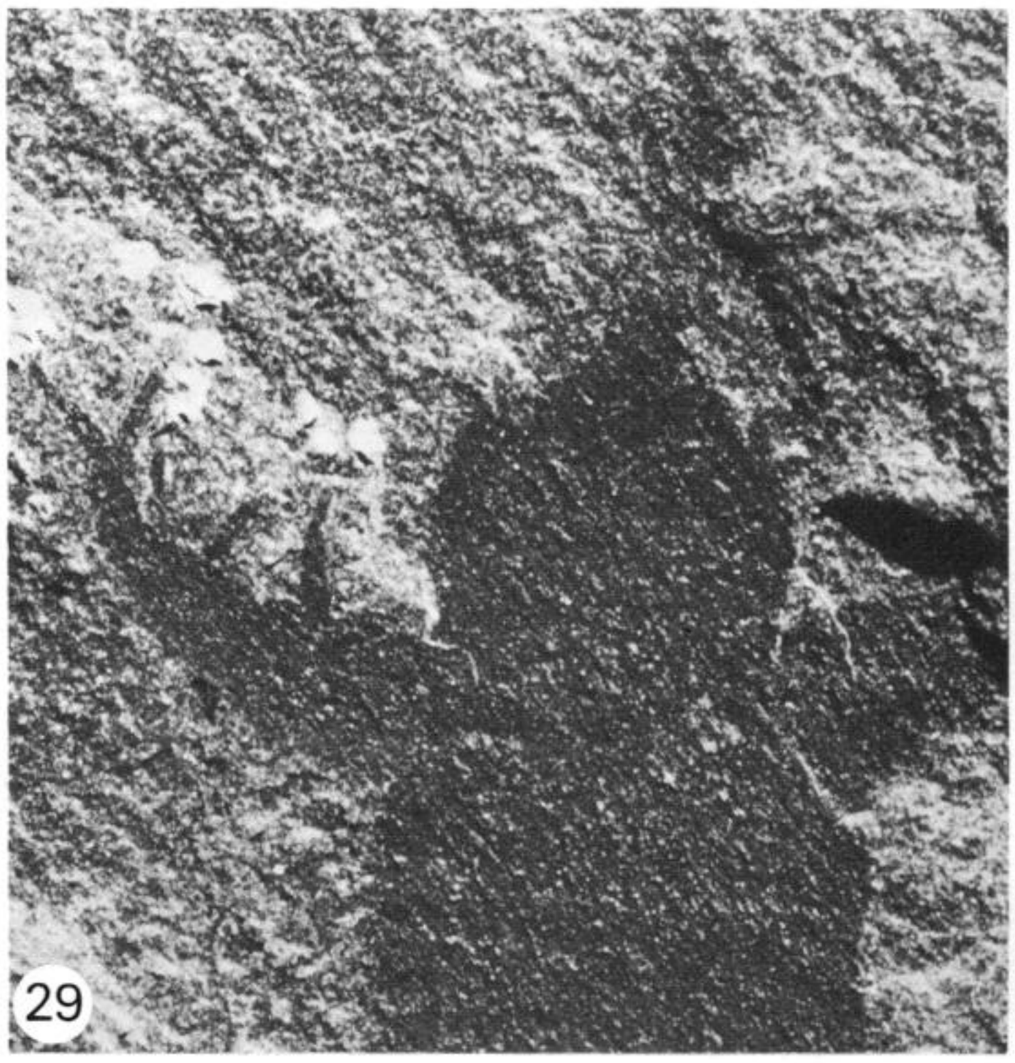
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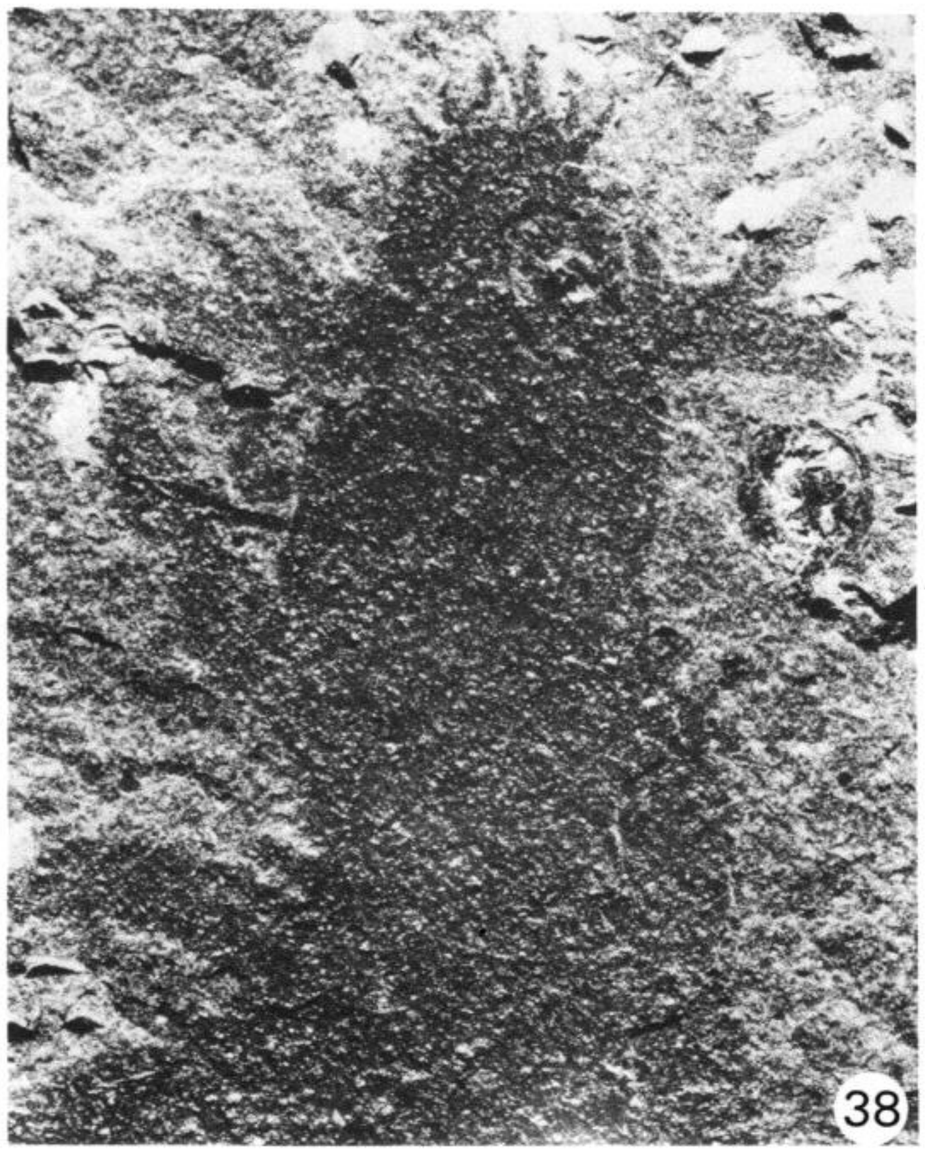

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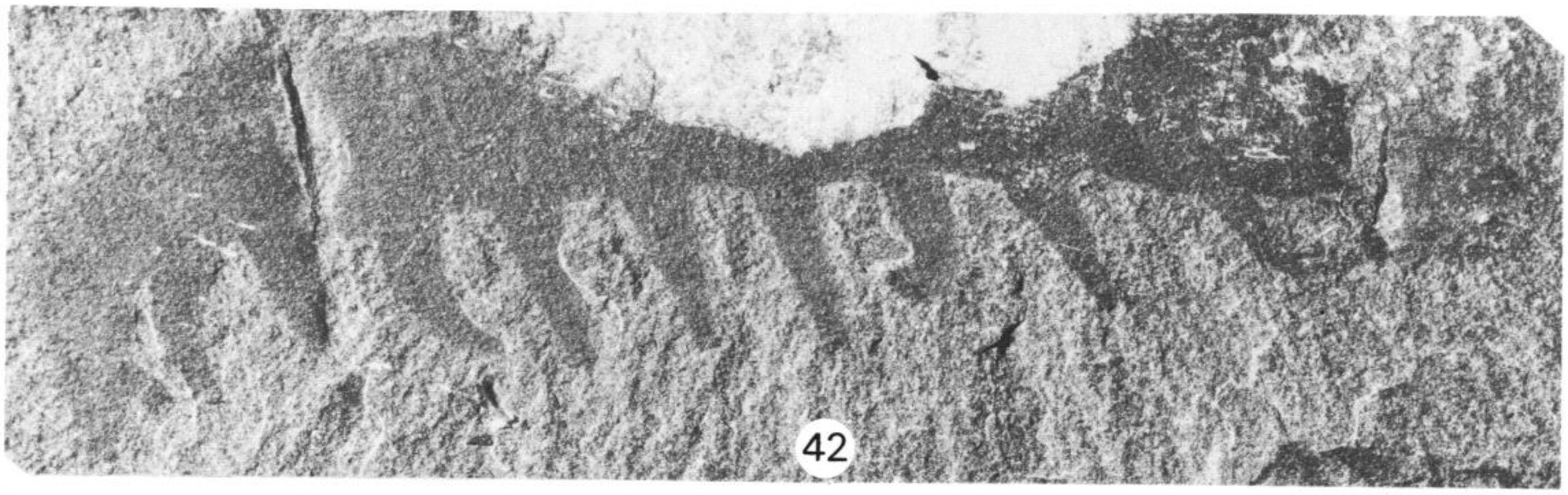
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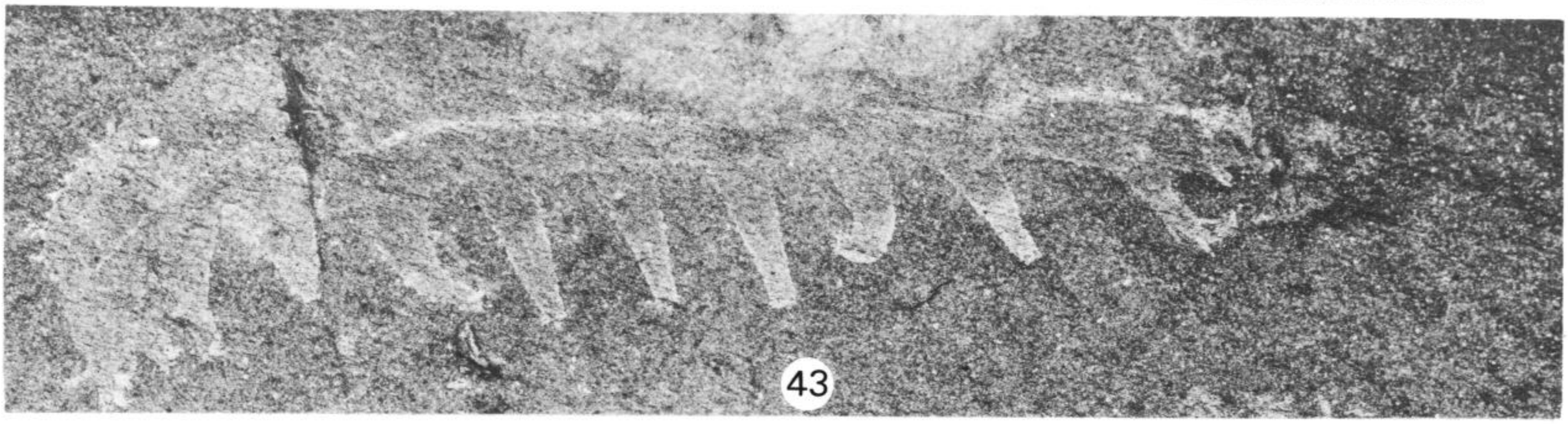
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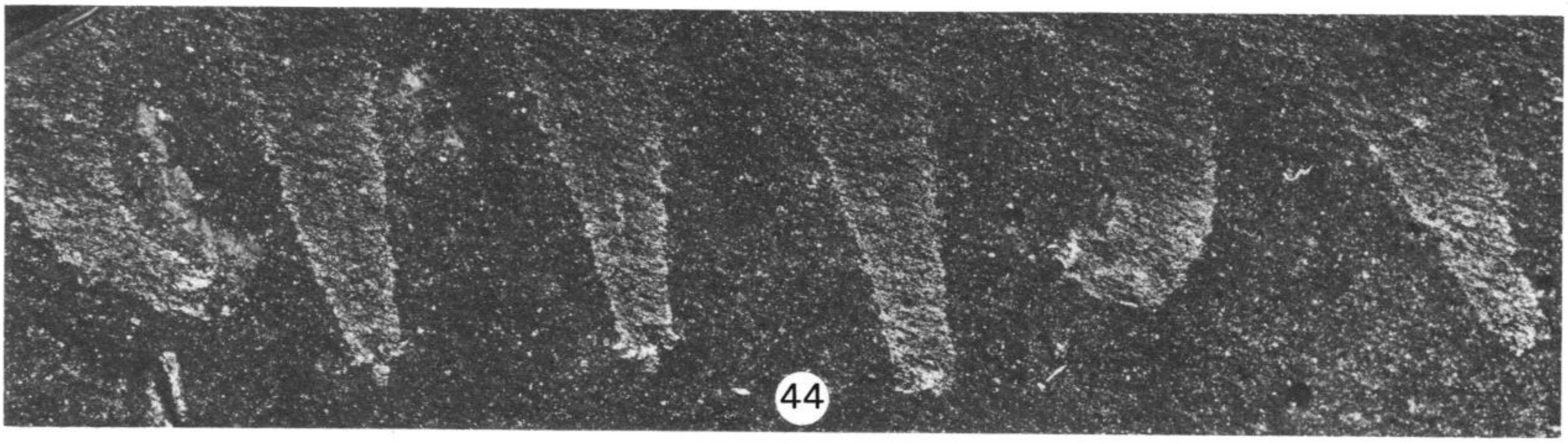
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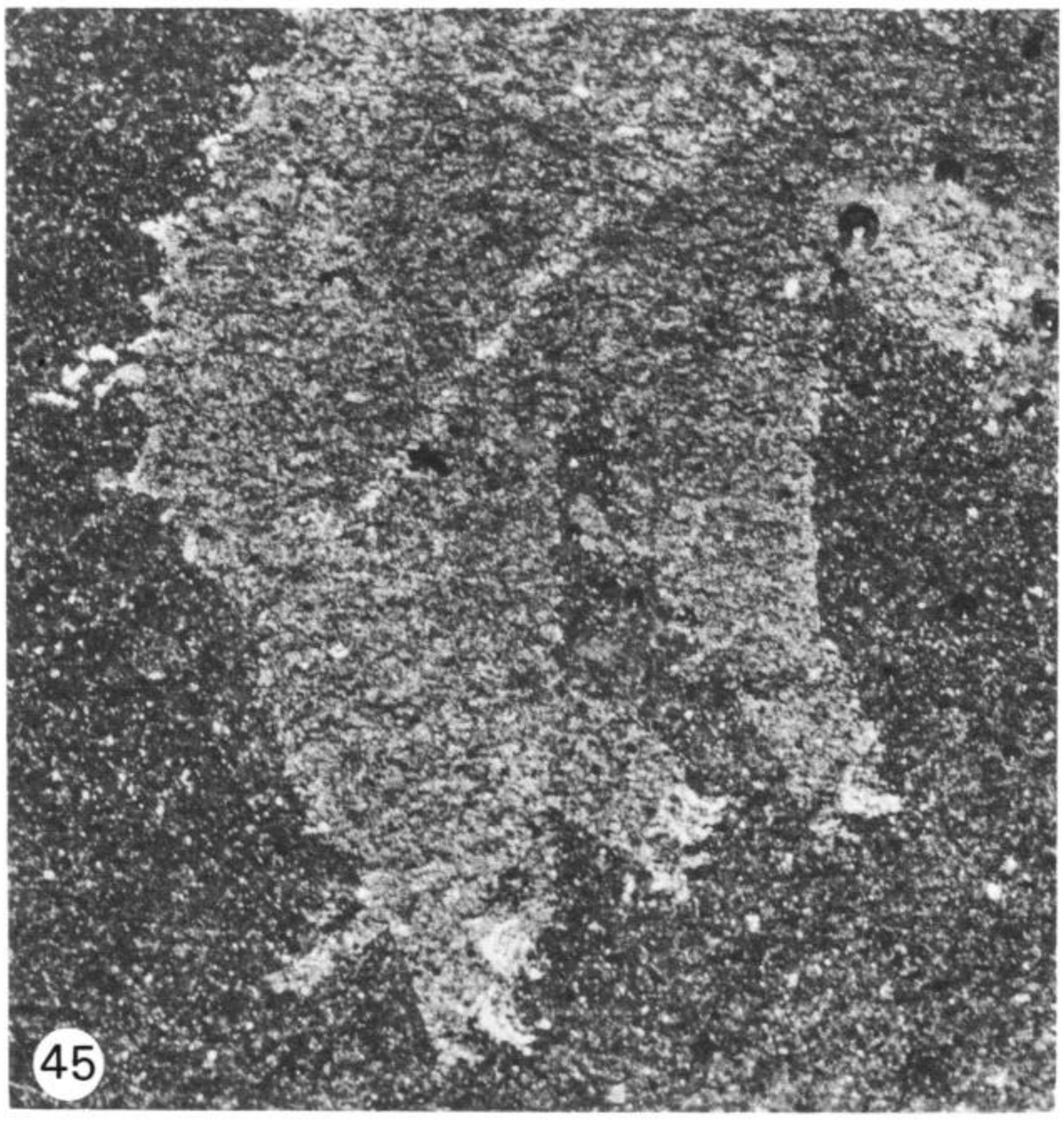
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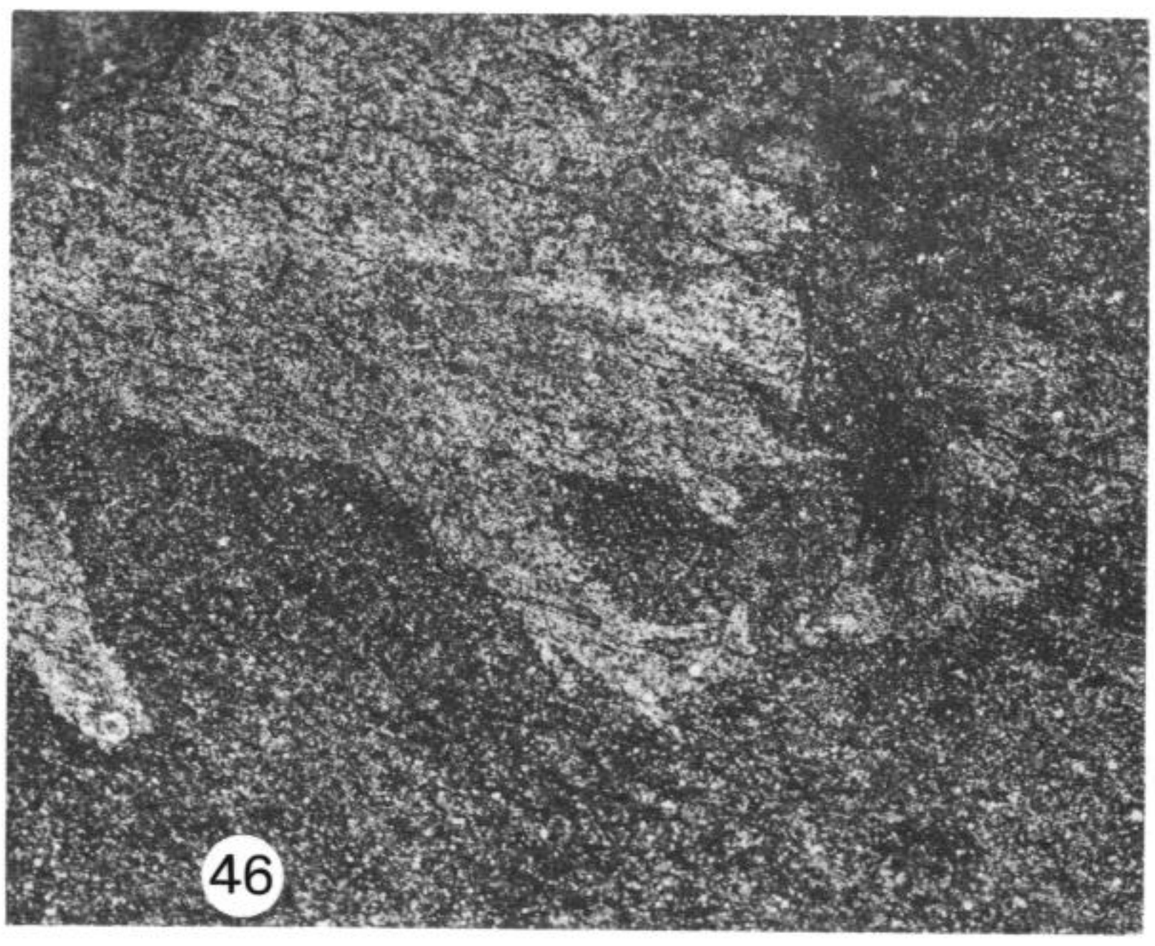
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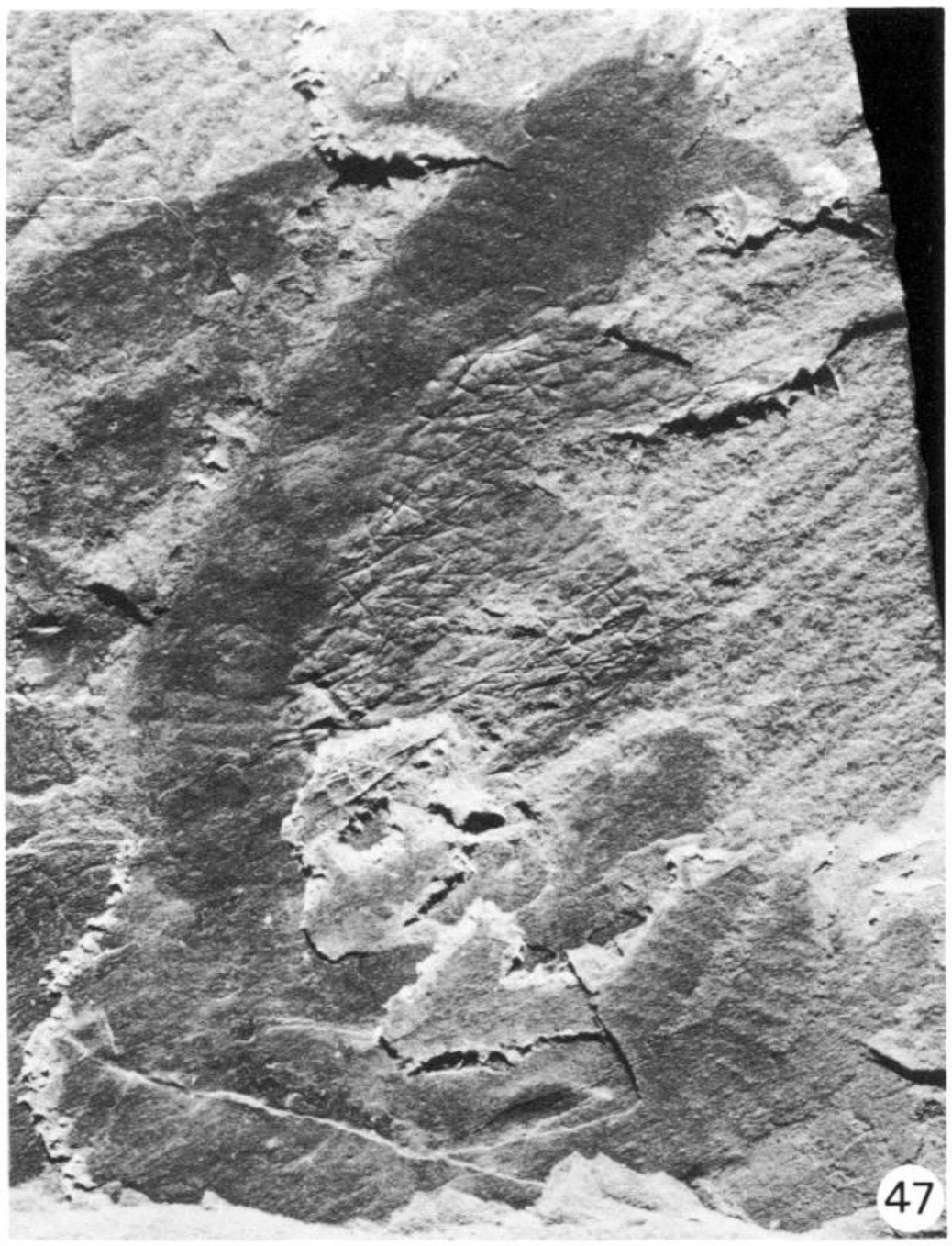

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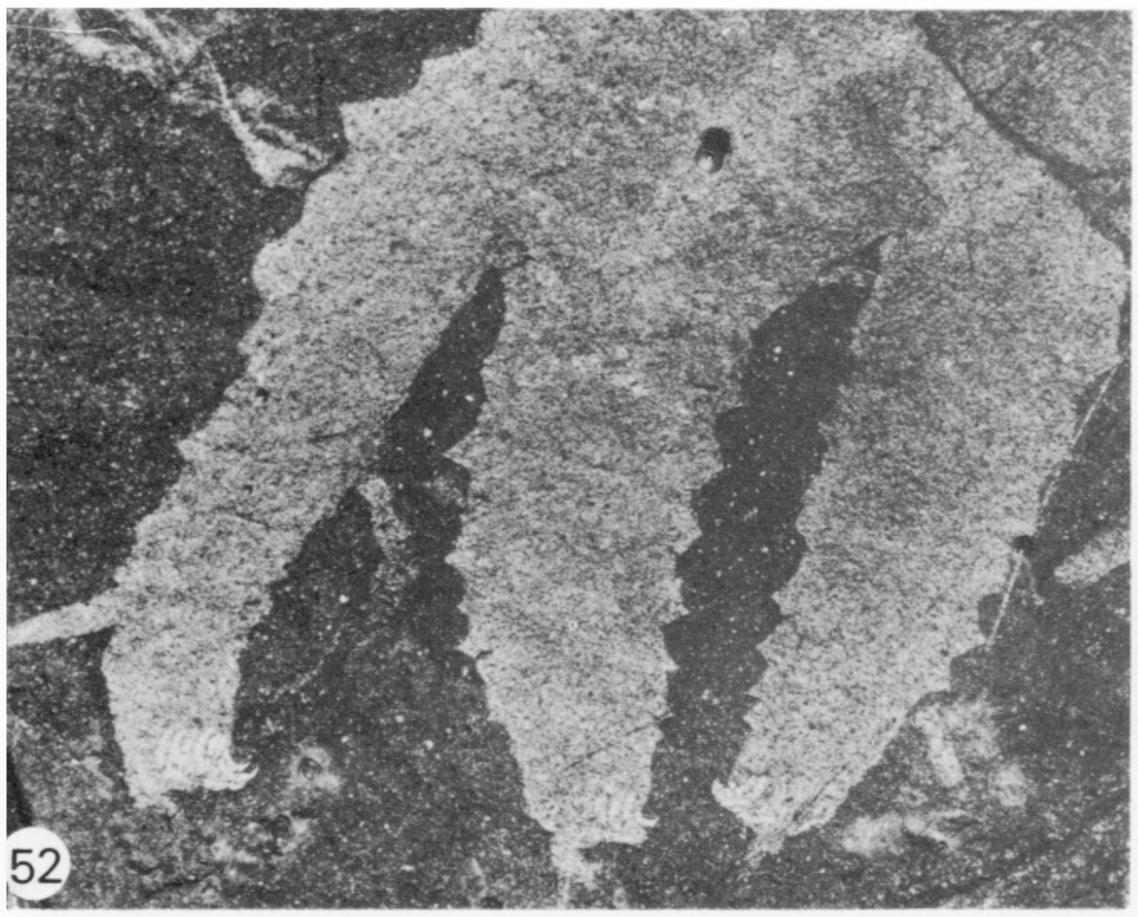
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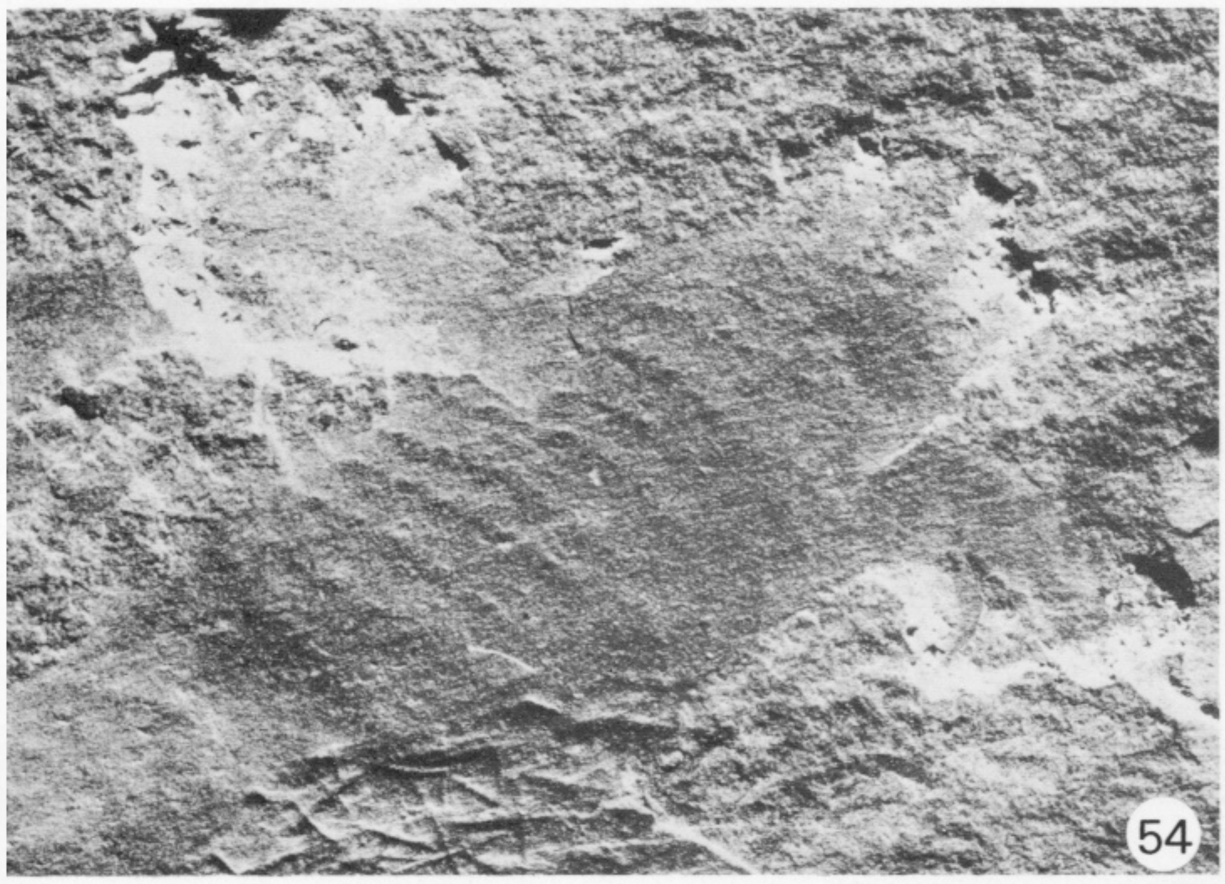
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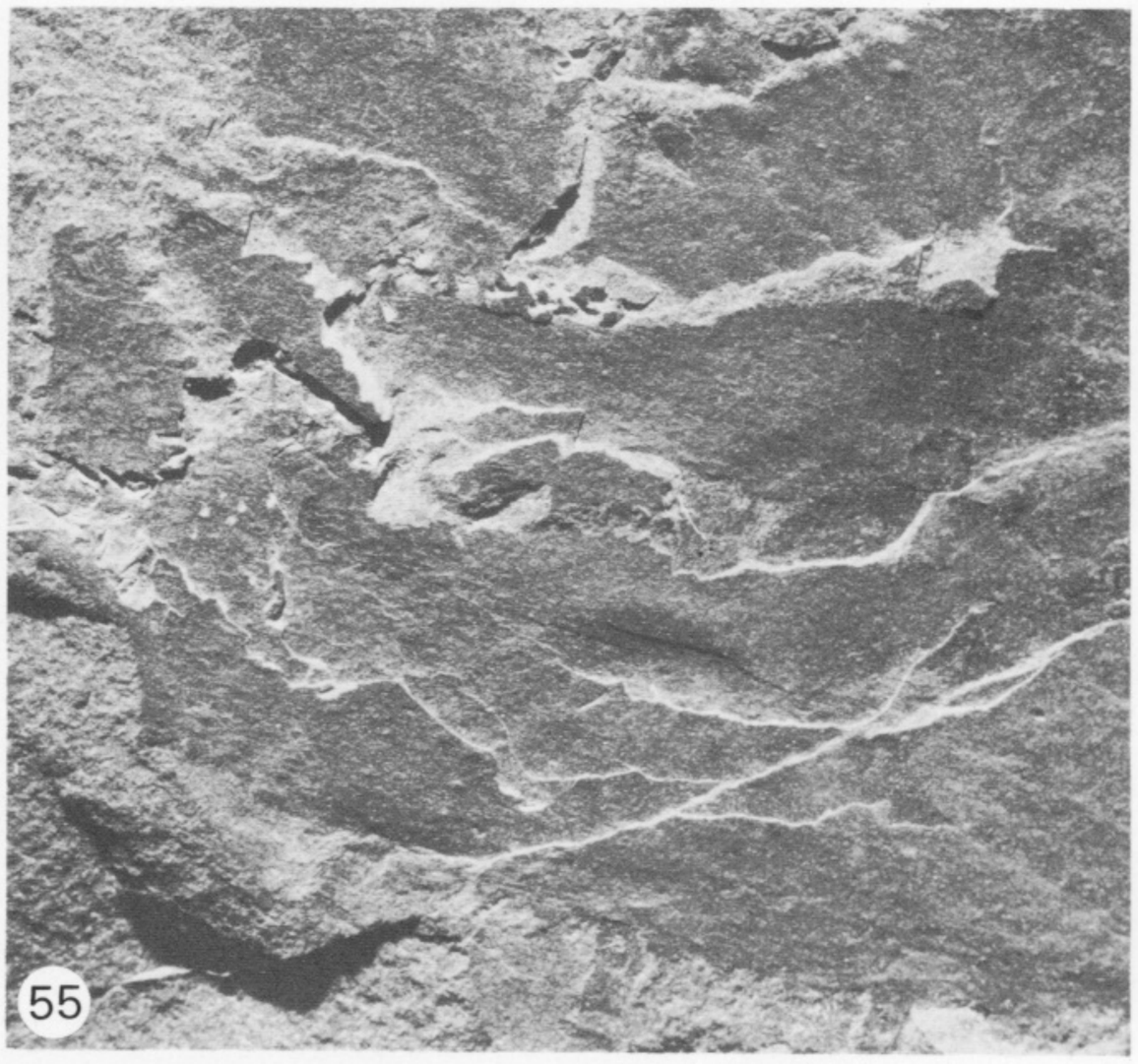
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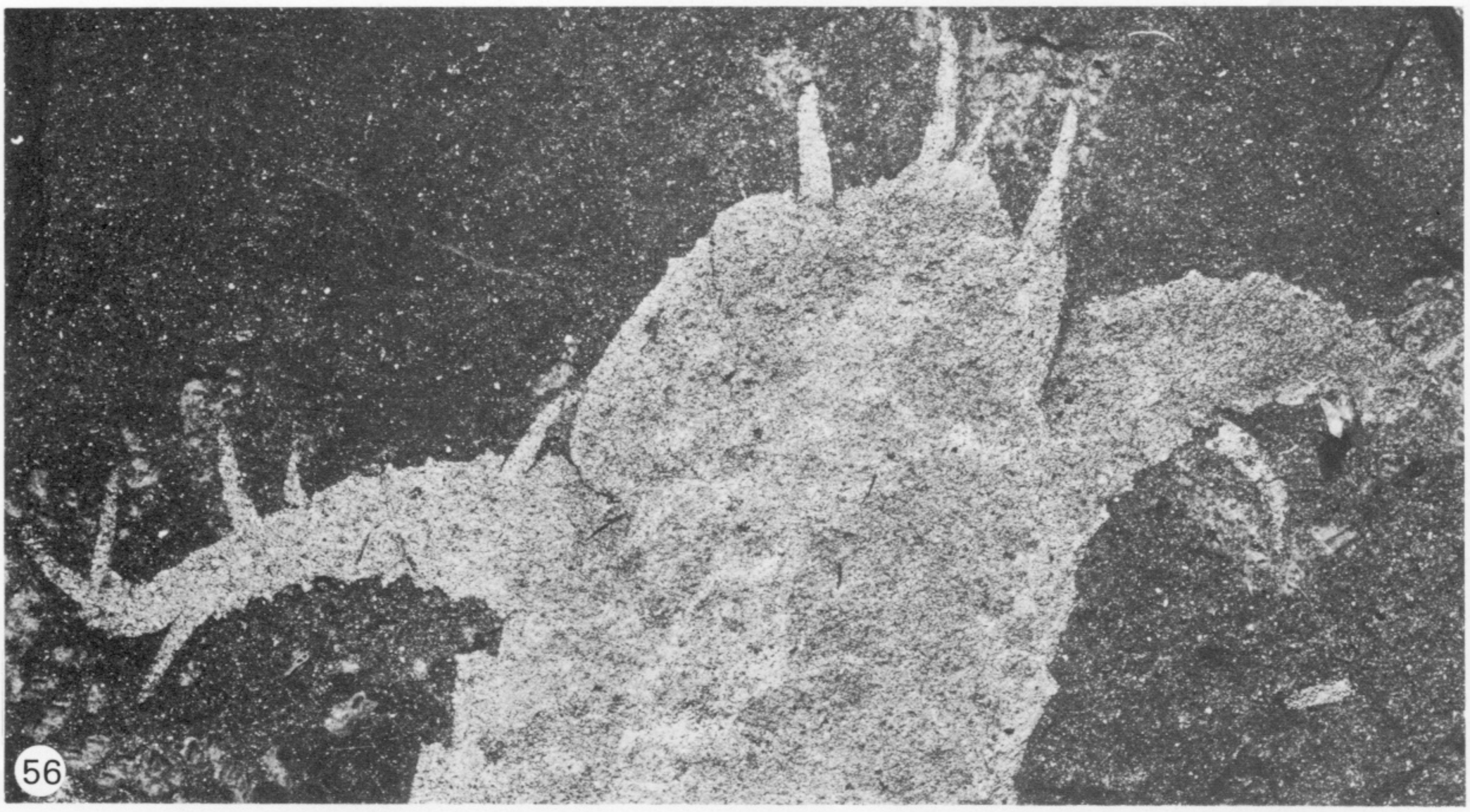
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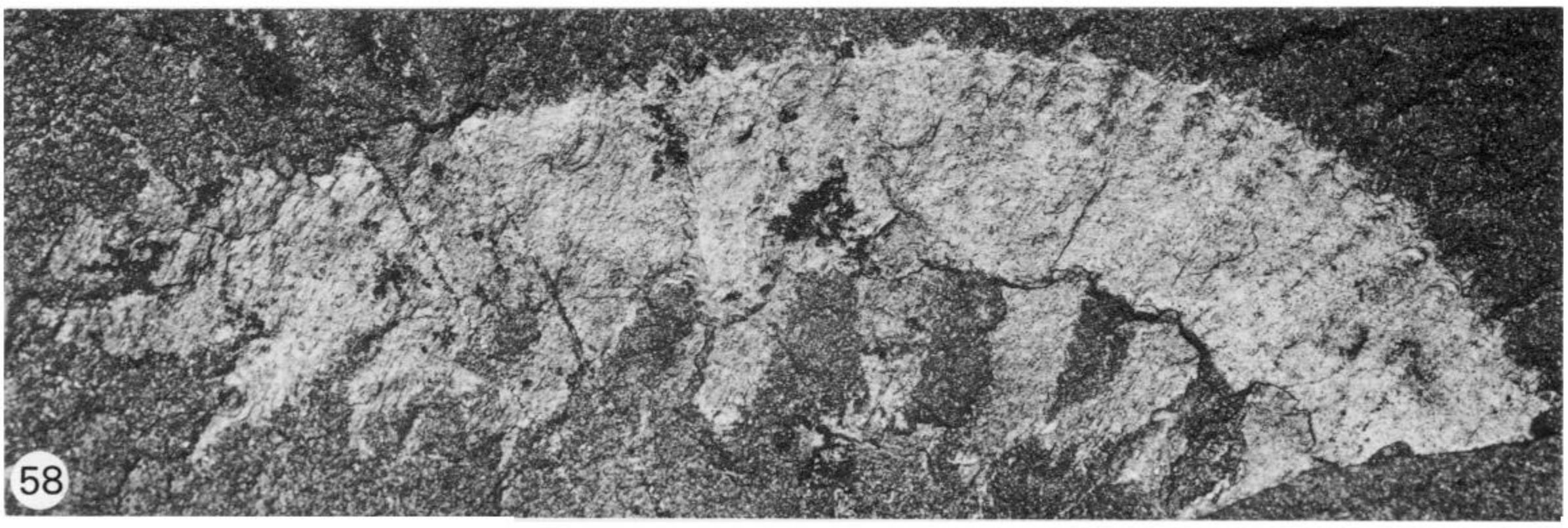
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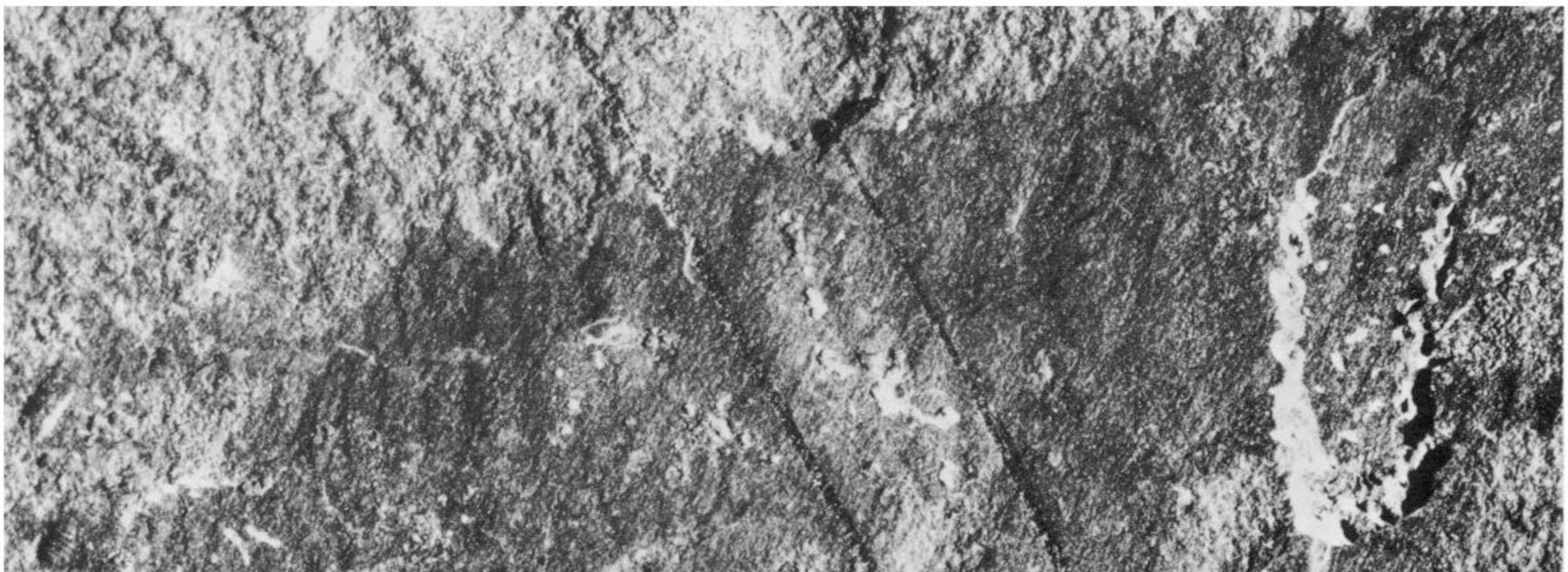
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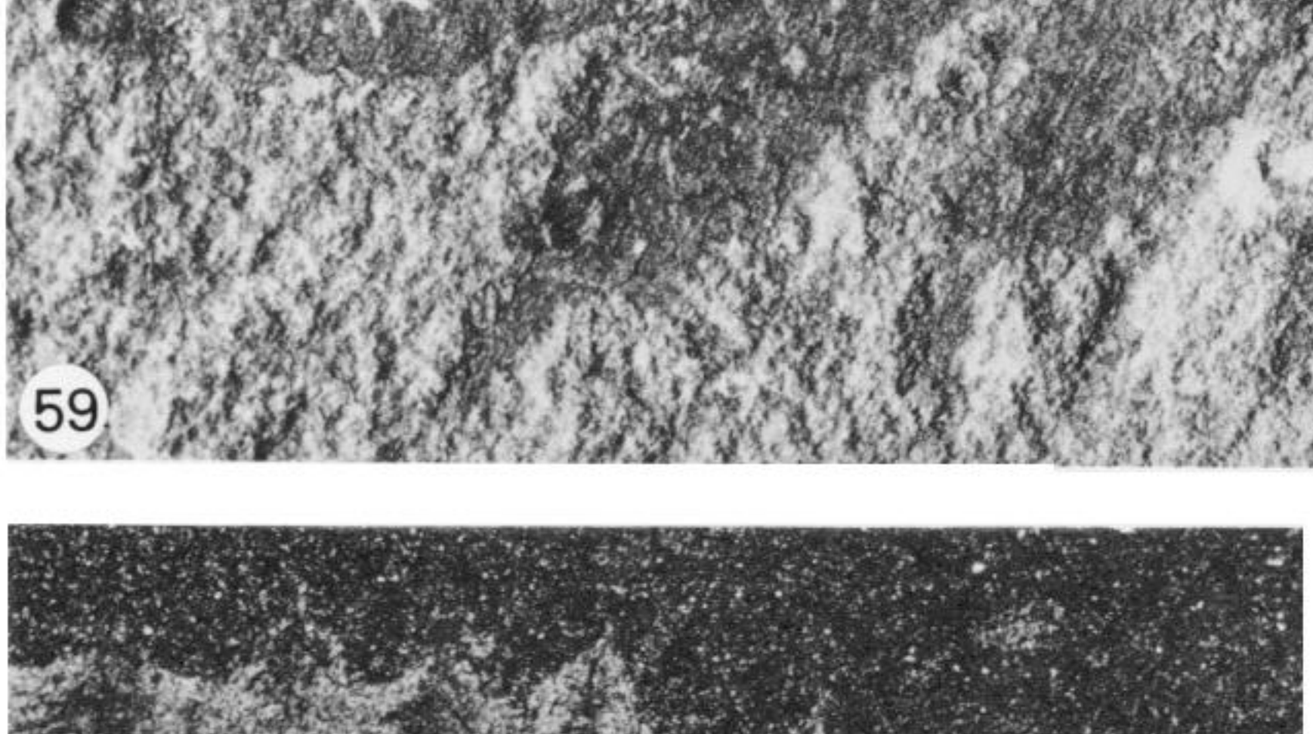
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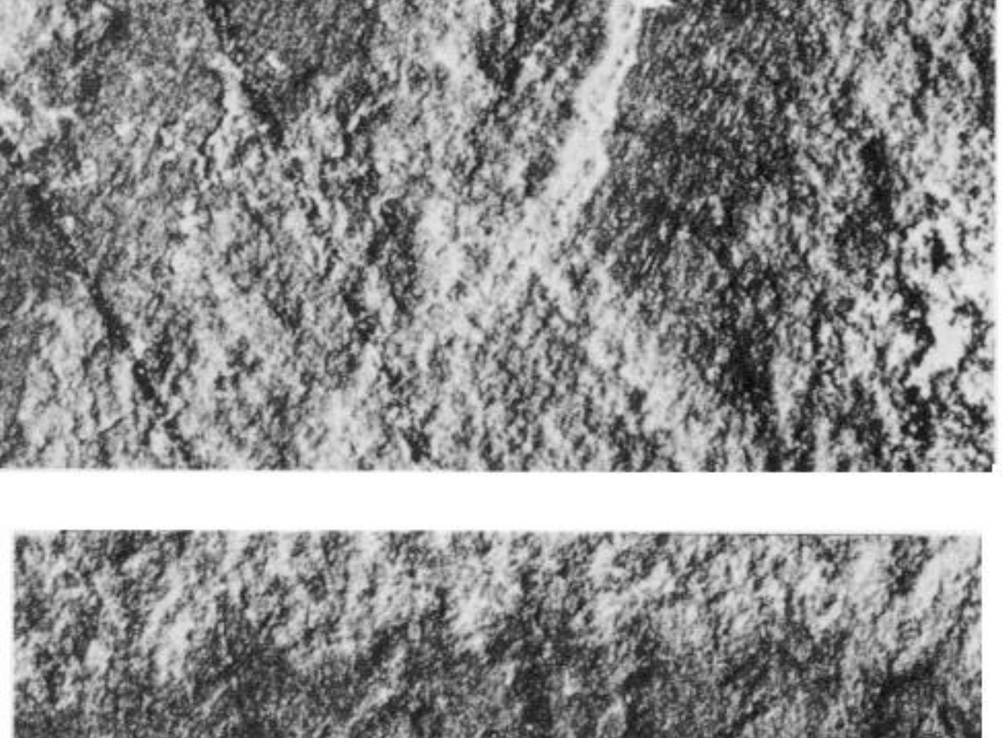
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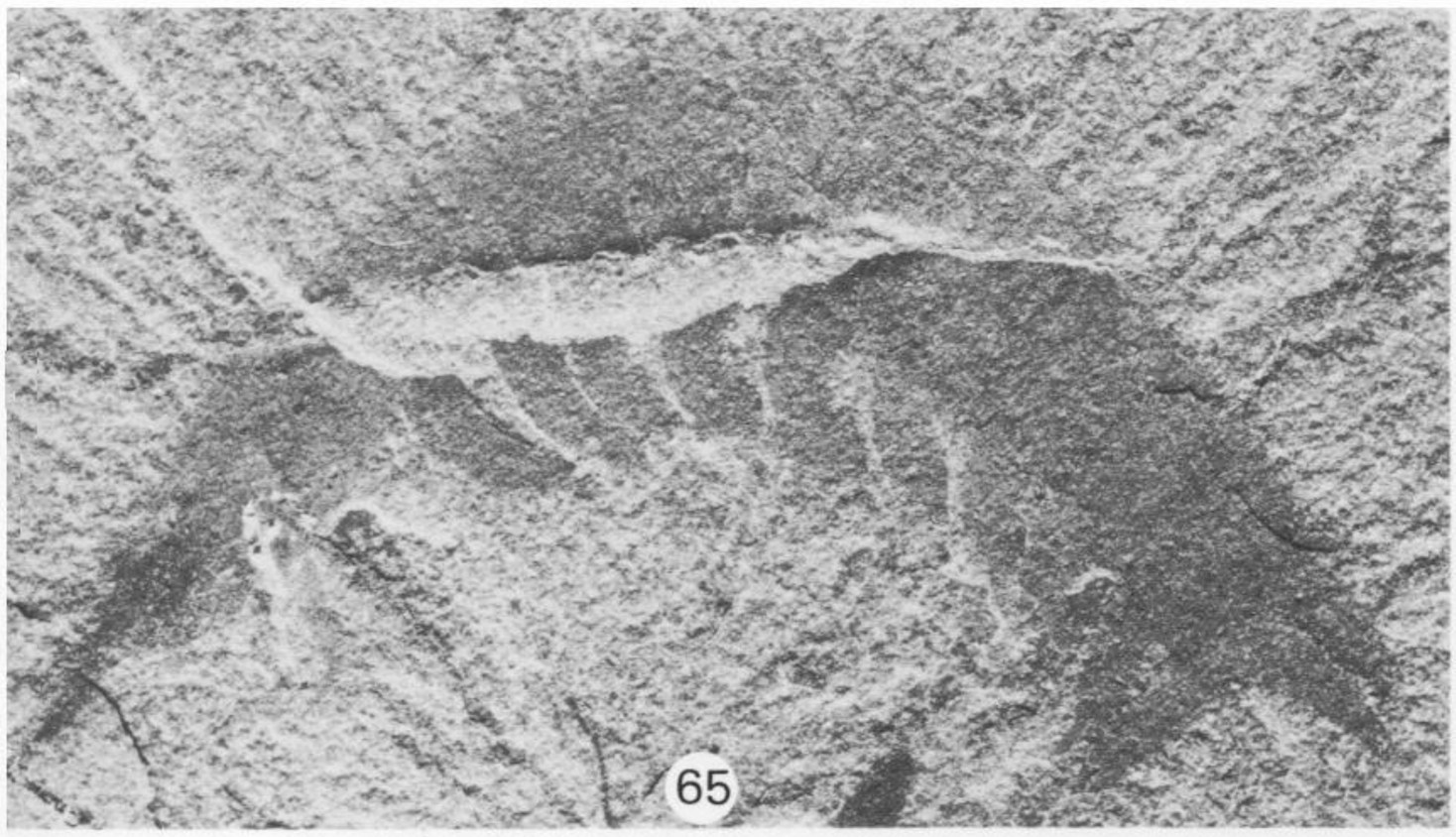
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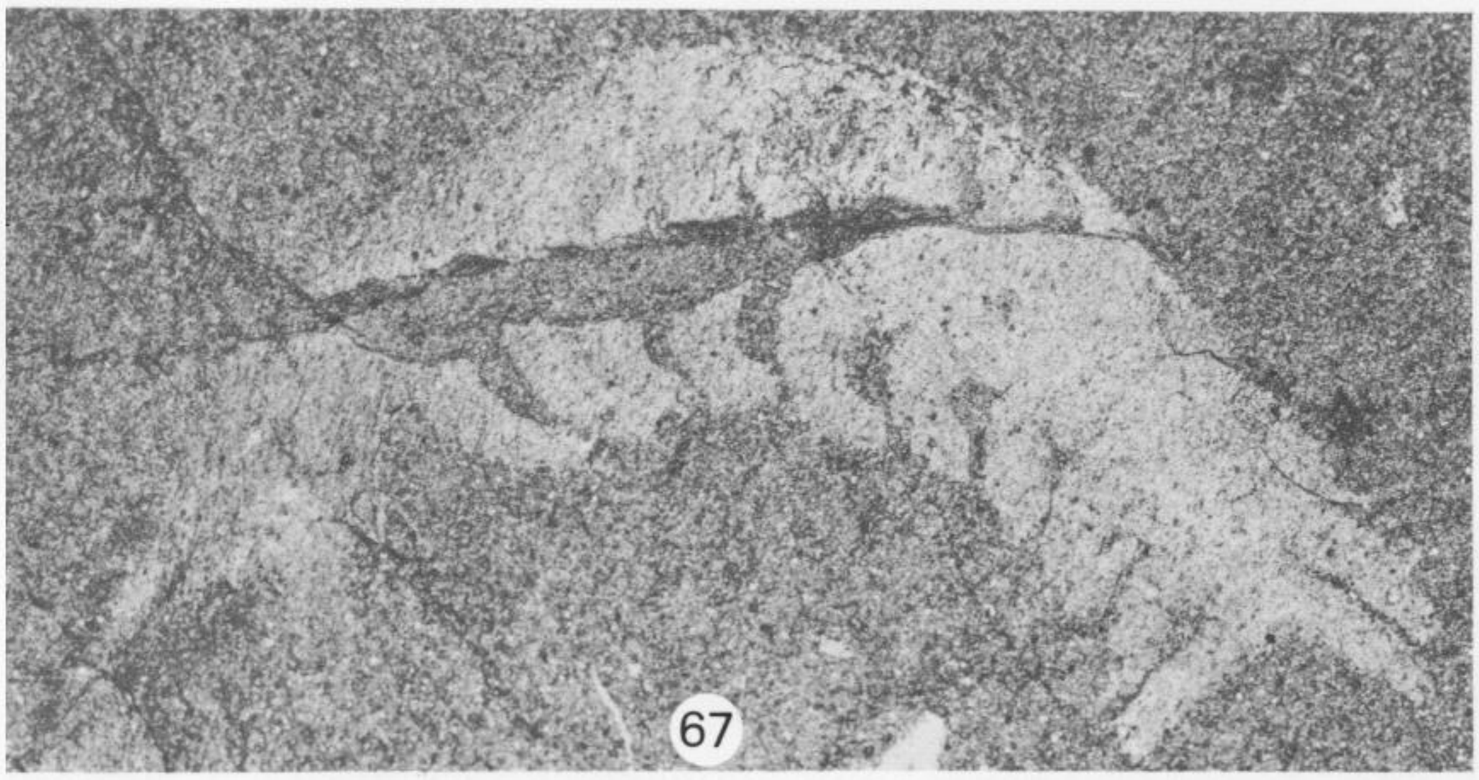
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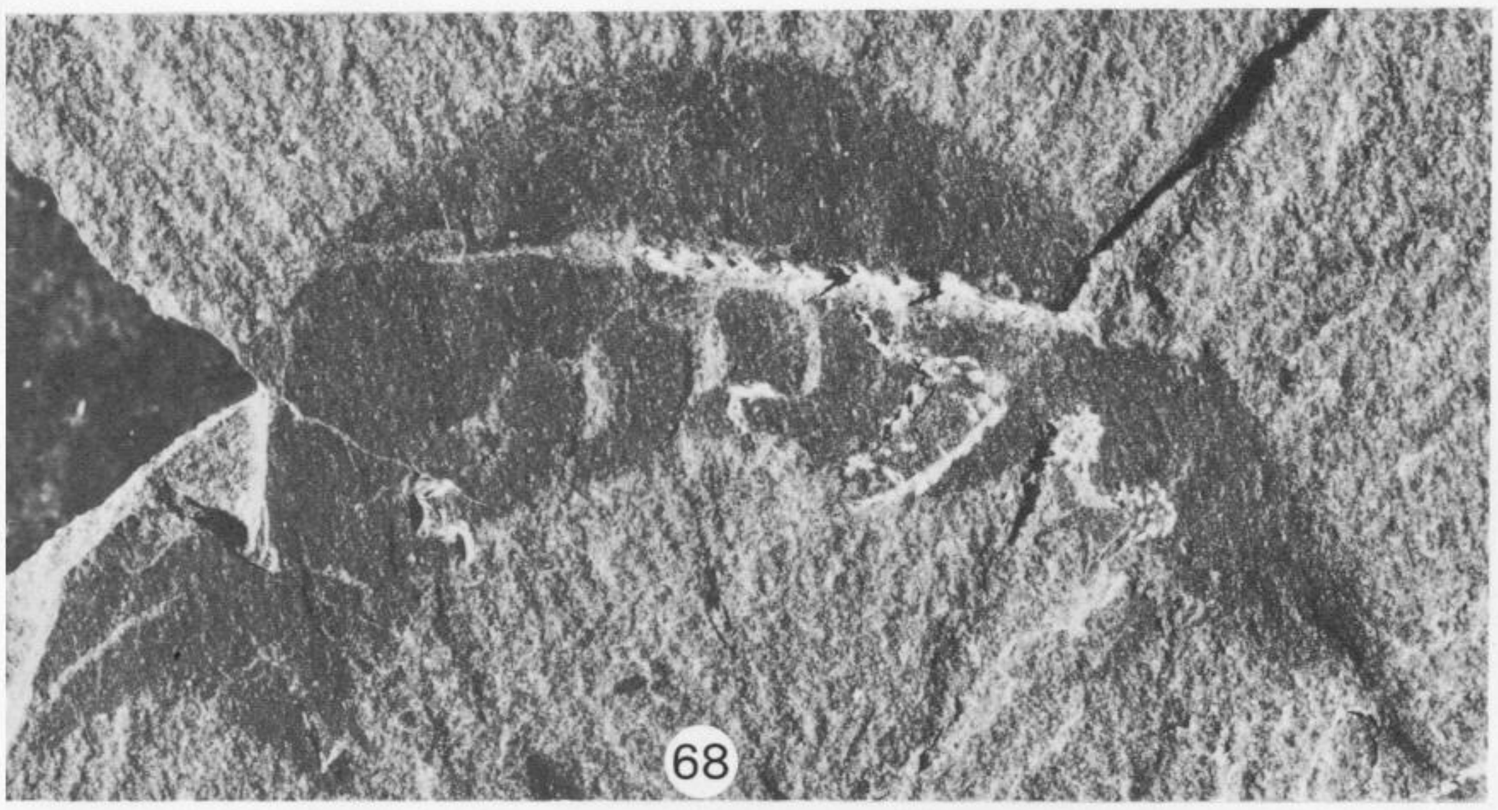
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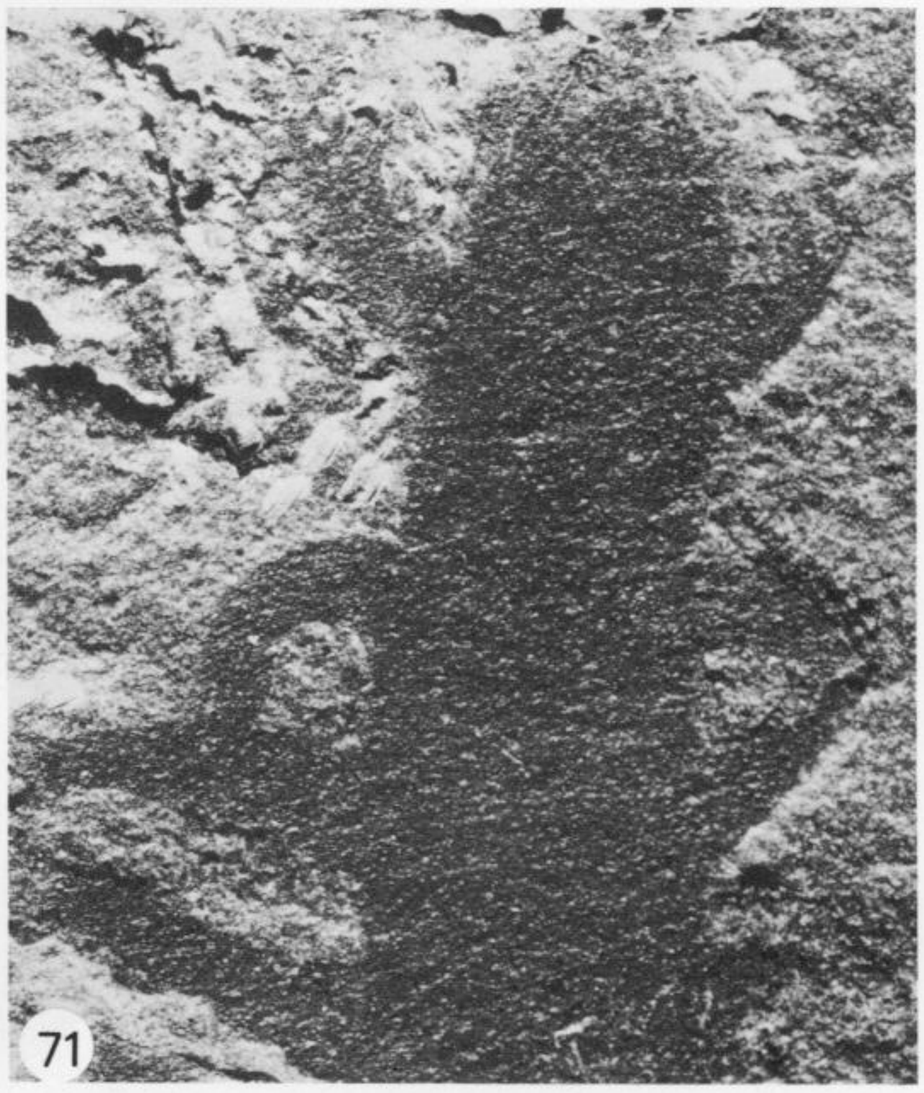
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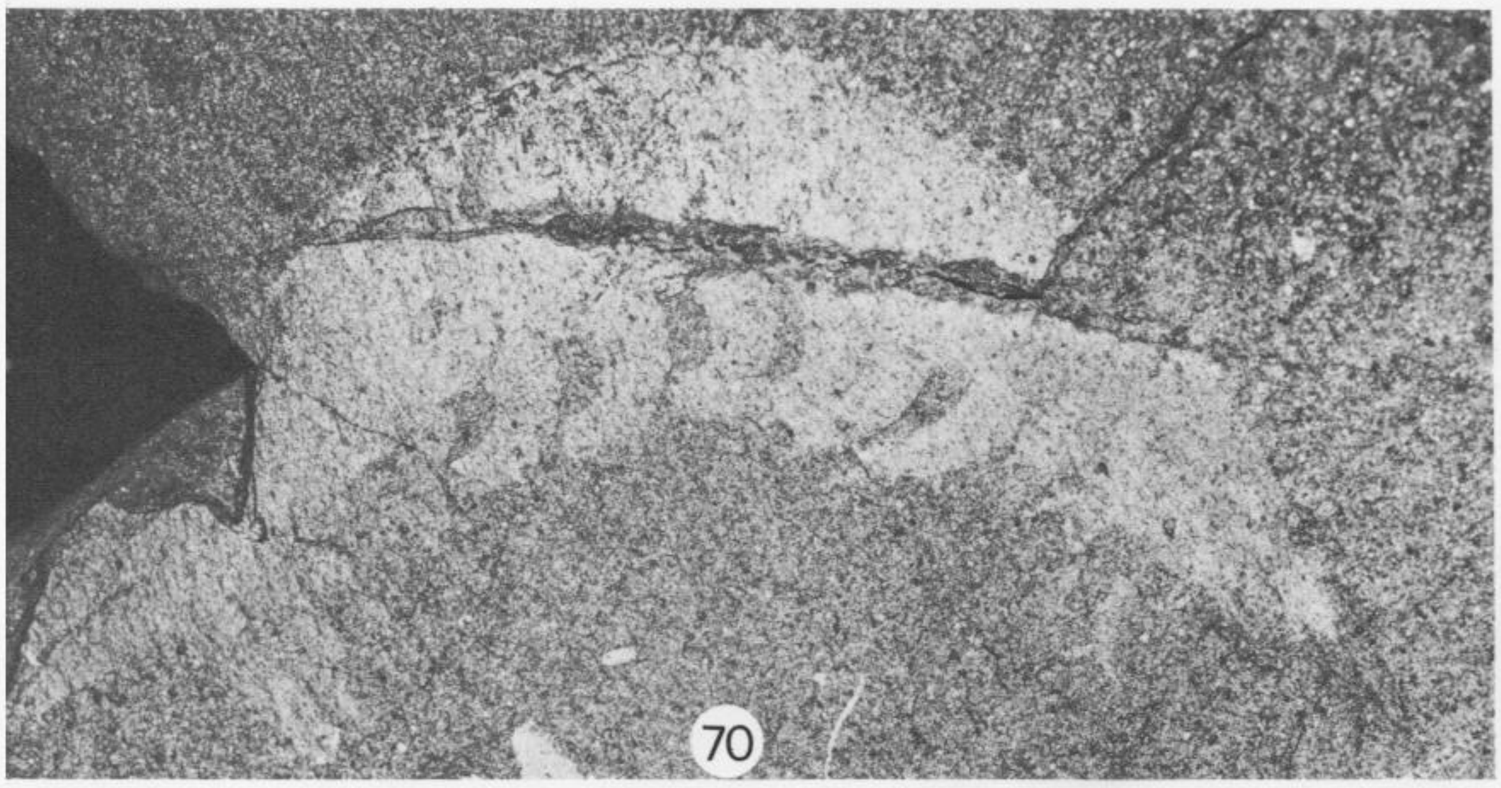
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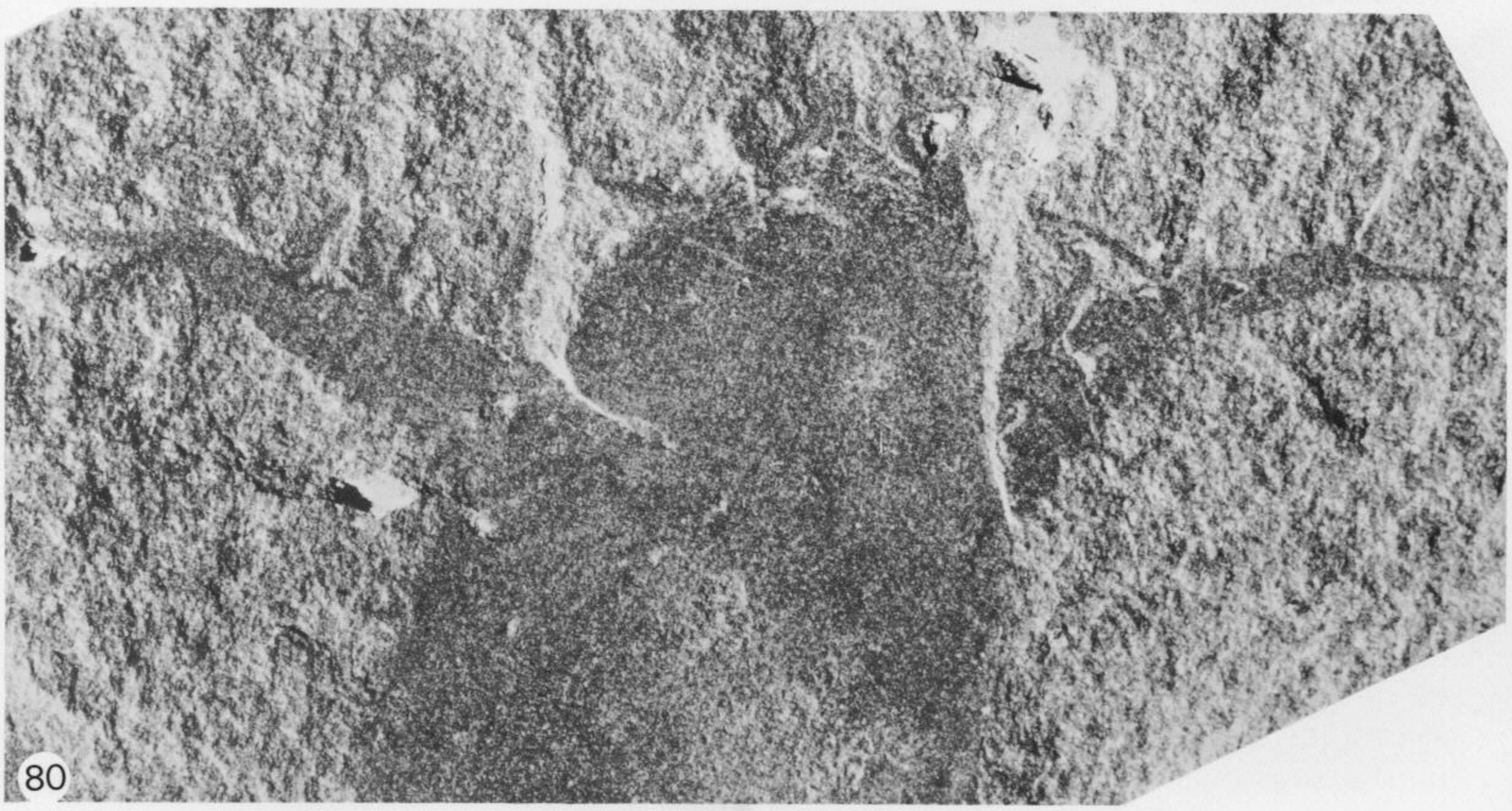
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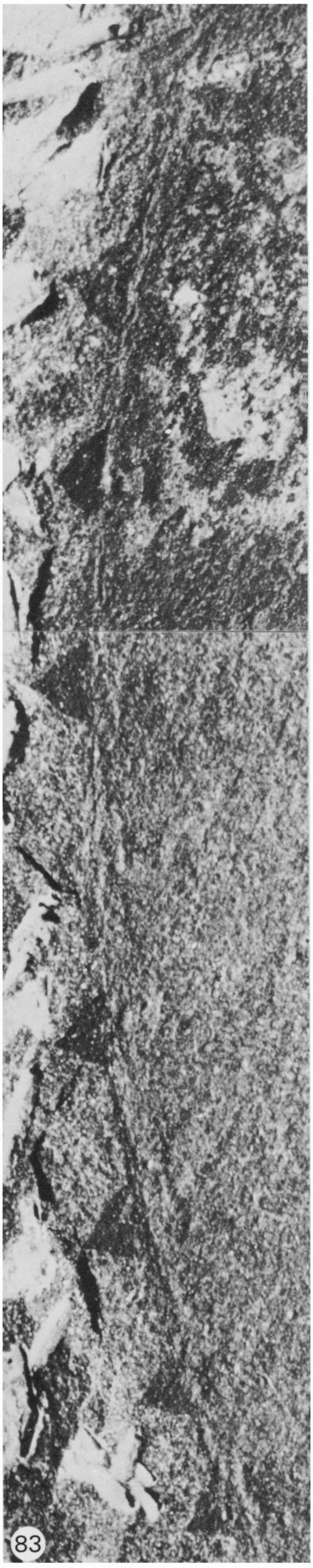
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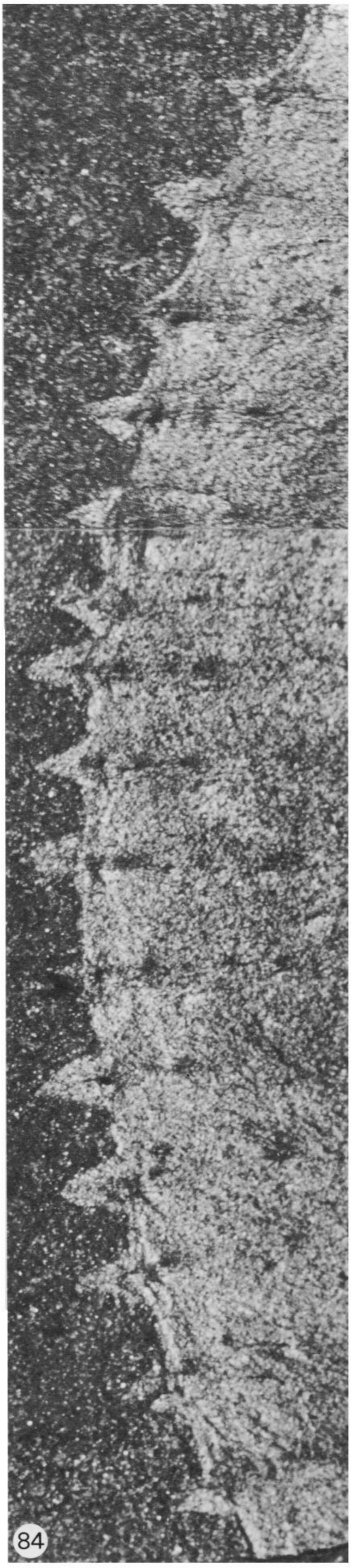
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