RARE ARTHROPODS FROM THE BURGESS SHALE, MIDDLE CAMBRIAN, BRITISH COLUMBIA

By H. B. WHITTINGTON, F.R.S.
Department of Geology, University of Cambridge, Sedgwick Museum, Downing Street, Cambridge CB2 3EQ, U.K.

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[Plates 1–14]

CONTENTS

Six species of arthropods from the Walcott Collection, U.S. National Museum, are described. *Molaria spinifera* Walcott is known from over 100 specimens, a sample that reveals the morphology fairly fully. Between one and 12 specimens of the other species are known, and yield limited information. *M. spinifera* had a smooth, convex exoskeleton, not trilobed, the cephalic shield being a quarter-sphere in shape, eight trunk tergites diminishing in size posteriorly and the cylindrical telson having a short ventral spine and a long, jointed posterior spine. The cephalon bore a pair of short, slim antennae and three pairs of biramous appendages. There were eight pairs of similar biramous appendages on the trunk. The biramous appendage had a large basal podomere, a segmented inner walking branch, and a lobate outer branch arising from the basal podomere and bearing marginal lamellae. The sagittal length of cephalon, trunk and telson ranged from 8 to 26 mm, the posterior spine slightly exceeding this length; the smallest specimens are similar to the largest. The animal lacked eyes, and was probably benthic and may have been a scavenger and deposit feeder. *Habelia optata* Walcott was superficially similar to *M. spinifera*, the trunk being of 12 tergites; there was no cylindrical telson, but a ridged and barbed spine inserted into the 12th tergite, the spine having a joint at about two-thirds its length. The external surface of the exoskeleton was tuberculate; the pleurae of the tergites curved back increasingly strongly posteriorly, the tips being spinose. The cephalon appears to have borne a slim, short pair of antennae and two pairs of biramous appendages; the proximal portions of the jointed inner branches may have been adapted for grinding food. The first six trunk somites bore biramous limbs, the inner branch being a relatively long walking leg, the outer a lobe having marginal lamellae; on the posterior trunk somites there is no trace of the inner branch, but the outer was present. *H. optata* lacked eyes and was probably a benthic animal. Only the smooth exoskeleton of a possible second species, *H? brevicauda* Simonetta, is known, of which the posterior spine is short and bluntly rounded. The new genus and species *Sarotrocercus oblita* is erected for a few specimens, in which the body is about 1 cm in length, and behind which is a slim spine having a group of spines at the tip. From beneath the anterolateral margin of the cephalic shield a large eye projected, and the cephalon bore also one pair of large, jointed appendages. Behind these were pairs of lobed appendages bearing marginal lamellae, one on the cephalon and one on each of the nine trunk somites. This small species may have drifted and swum in the higher water layers, the occasional carcass lying on the sea bottom having been preserved. The single specimen of *Actaeus armatus* Simonetta is over 6 cm in length. The exoskeleton of this specimen is divided into cephalic shield with marginal eye lobe, 11 trunk tergites and a triangular terminal plate. The anterior cephalic appendage was *Leanchoilia*-like, the stout proximal portion being curved and ending in a group of claws, the next two podomeres bearing long, slim extensions. The head shield also bore three pairs of biramous appendages, consisting of a small jointed inner branch and a large lobed outer branch with marginal lamellae; appendages like these outer branches are preserved beneath the trunk tergites. Only two specimens are identified as *Alalcomenaeus cambricus* Simonetta (length 3–4 cm). The exoskeleton is divisible into cephalic shield, trunk of probably 12 tergites, and an ovate terminal plate which has lateral bands. The cephalon has a marginal eye lobe and an anterior appendage which is broad proximally, the long distal portion being slim. The holotype shows a series of lobed appendages, the first three cephalic. Between them project the curved, pointed terminations of inner branches. The second specimen suggests that these lobed appendages bore marginal filaments, and reveals the inner branches as blade-shaped, and spinose on the inward-facing margin. These biramous appendages were present on all the trunk somites, being largest anteriorly. These remarkable appendages suggest a benthic scavenger, able to hold on to, and tear up, a carcass.

'*Leanchoilia protogonia*' Simonetta is most probably a composite, a poorly preserved *Leanchoilia superlata* lying on an unidentified, branching organism.

The five species showing appendages extend greatly the known range of variation in morphology of the Burgess Shale arthropods. Affinities are discussed, but familial and higher classification is postponed, pending completion of work on all the arthropods from the shale.

1. Introduction

Six species of arthropods are described and discussed in the following pages, and their characteristics are summarized in the abstract. Five are the type species of genera, one of which is new. All the specimens were obtained by C. D. Walcott, Secretary of the Smithsonian Institution, Washington, D.C., U.S.A., in his original excavations of the Burgess Shale made between 1909 and 1917. None of the species was found in the excavations by the Geological Survey of Canada (Whittington 1971*a*), and only the relatively abundant *Molaria spinifera* may be present in the collections made by P. E. Raymond (Rolfe 1962), but was not obtained by the party from the Royal Ontario Museum (Collins 1978). Two of these species, *M. spinifera* and *Habelia optata*, were briefly described by Walcott in 1912, but little attention has been paid to them because no additional information was available until Simonetta's work (1964). In 1970 Simonetta also described, from specimens that Walcott had picked out in his unfinished studies, two new species, each made the type of a new genus. Unfortunately Simonetta's photographic illustrations are of a poor standard, and his descriptions include statements for which no evidence is brought forward. His attractive-appearing restorations (repeated in: Simonetta & Delle Cave 1975; Simonetta 1976) show features for which evidence is lacking, or omit structures shown by the specimens. The present work provides photographs, faced by drawings showing how a particular specimen has been interpreted, as part of the evidence upon which the morphology and affinities of these species are redescribed and assessed.

The sample of *Molaria spinifera* is large enough to provide a range of specimens preserved in attitudes between dorsoventral and lateral, so that the exoskeletal form is evident. Preparation has shown details of the exoskeleton, as well as the complete posterior spine, and particularly the form of the appendage series and how it was related to cephalic shield and trunk (figures 33–35, plate 3; figure 41, plate 4; figures 52, 53 plate 5). I have reasonable confidence, therefore, in the restoration of this distinctive species (figure 73). The specimens of the other five species are so few that, for example, the lack of both dorsal and lateral compressions means that the convexity and other aspects of exoskeletal morphology are in doubt. Appendages of all or parts of the body are inadequately revealed, and in *Alalcomenaeus cambricus*, for example, while the two specimens appear to be of the same species, each reveals different details of appendages. The restorations given in figures 130–133 are therefore tentative compromises, far more dubious than that of *M. spinifera*.

This work is part of a comprehensive restudy of the Burgess Shale arthropods, or supposed arthropods (Briggs 1976, 1977, 1978, 1979; Bruton 1977; Hughes 1975, 1977; Whittington 1971*a*, *b*, 1974, 1975*a*, *b*, 1977, 1978, 1980*a*). Many new and unexpected features have been revealed, and the morphological gaps between species greatly enlarged. Each, with rare exceptions, shows a most distinctive combination of characters. The selection dealt with here adds further to the range of morphological characters in the non-trilobite arthropods, and to the variety of distinctive combinations of characters. For example, *Molaria spinifera* is shown to have an aglaspidid-like exoskeleton and a trilobite-like series of appendages; *Habelia optata* has a tuberculate and spinose exoskeleton, and a barbed posterior spine with a distal joint; *Sarotrocercus oblita* gen.nov., sp.nov., appears quite unlike any other arthropod in the shale; and, while there may be a superficial resemblance in lateral view between *Actaeus armatus* and *Alalcomenaeus cambricus*, the spinose inner branches of the appendages give the latter species a unique armature. Another example might have been provided by the spinose termination of '*Leanchoilia protogonia*', but I am convinced that this is a composite fossil, a specimen of *Leanchoilia superlata* lying upon an unidentified organism. The branches of the latter are shown to be strongly curved. How to group together the genera of these arthropods into higher taxonomic categories will be assessed when the revision is more complete; here such categories are not used.

2. Locality, stratigraphical horizon, associated fauna

All the specimens mentioned herein come from what Walcott (1912, pp. 151–153) called the 'Phyllopod bed', 2.3 m thick, in which he excavated his quarry. The quarry 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, 4.8 km north of Field, southern British Columbia (see Whittington (1980*b*) for an account of the age, occurrence and environment of deposition of the shale).

All the specimens used here are from the U.S. National Museum collections and labelled '35 k'. This label gives no indication of the level in the Phyllopod bed from which the specimen came. Walcott (1912, pp. 152–153) remarks that the specimens of *Molaria spinifera* came only from his layer 12, the basal 1.5 in (*ca.* 3.8 cm) of the bed, and lists the accompanying fauna. Whether this species was discovered at a different level in his subsequent quarrying in the 1912, 1913, and 1917 seasons we do not know. The specimens of the new genus and species were picked out from among those segregated as '*M. spinifera*' in the U.S.N.M. collections; it is uncertain whether this means that they came from the same level in the shale. Almost all specimens in these collections are isolated in small, sawn blocks of the shale, on which other species occur rarely; the fauna accompanying any one species cannot therefore be determined from the collection.

3. Terminology and methods

The divisions of the dorsal exoskeleton of these arthropods have been referred to as *cephalic shield*, tergites of the *trunk*, and either a *terminal plate* (in *Alalcomenaeus* and *Actaeus*) or a *telson*. The latter term is used for the cylindrical posterior portion of the exoskeleton of *Molaria* since it appears to bear the anus. Inserted into it is the long *posterior spine*. Other terms are defined in the list of abbreviations and symbols used on the drawings. To avoid ambiguity when referring to directions, the median longitudinal line in the body is termed *sagittal* (abbreviation, sag.), a line parallel to, but outside the sagittal line as *exsagittal* (abbreviation, exs.), and a direction at right angles to these as *transverse* (abbreviation, tr.). The dorsal exoskeleton and cuticle of the appendages are preserved as extremely thin layers in the shale, the original relief having been profoundly modified. The bodies were not buried with the horizontal plane parallel to the bedding planes, but all or parts of the body were entombed in a variety of attitudes. I have previously (Whittington 1971*a*, pp. 1182–1187, fig. 24) described these attitudes (of the horizontal plane of the body relative to the bedding) as *parallel*, *oblique*, *lateral* and *vertical*. These terms are used in the explanations of the plates, qualified as parallel oblique, lateral oblique, etc., to indicate that the specimen is approximately or partly parallel, lateral, etc. When the rock was split to reveal a specimen, portions of the specimen adhered to each side of the split, the *part* and *counterpart*. The former is the side that has the dorsal side of the animal toward the observer. This means that in a lateral, as in a dorsal, compression the part has the exoskeleton nearer to the observer than are the underlying appendages. 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. The direction from which such low-angle radiation comes is critical in revealing particular details. For example, three photographs of 272105 are used (figures 55–57, plate 6), in each the radiation in a different direction, to reveal articulating ridges, margins of tergites, joints in the posterior spine, and other slight changes in level. 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. Particular details (figure 128, plate 14), or subtle differences in reflectivity (figure 89, plate 10; figure 103, plate 11) may be most clearly shown in such photographs. 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 downslope 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. 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 for brevity.

4. Preservation

Recent general accounts of the Burgess Shale fauna (Conway Morris & Whittington 1979; Conway Morris 1979; Whittington 1980*b*) have summarized ideas on the environment in which the animals lived, and that in which they were buried and preserved. The former environment was at the foot of a submarine cliff, in lighted, oxygenated waters of perhaps 80 m depth, the animals living above, on and in the fine-grained, muddy sediment. These wet muds were unstable, and periodically a portion of them slumped downslope, as a turbulent cloud of sediment in suspension, which carried with it live or dead animals, empty shells or exoskeletons, that were on or in that particular portion of mud. The suspension slowed down as the slope was reduced, presumably in a small basin. Here the sediment settled out, burying the randomly orientated carcasses in what Conway Morris called the post-slide environment. Such a process explains the varied orientations of the specimens in the rock (figures 5, 8, plate 1; figures 47, 50, 53, plate 5). Specimens of all except one species (*H. ? brevicauda*) described here have the appendages preserved and not markedly displaced relative to the dorsal exoskeleton; the majority of the animals were probably alive when trapped in the suspension and killed during transport and burial. The dark stain adjacent to the posterior, and in some examples anterior, end of the alimentary canal may be the remains of organic matter that seeped from the carcass after burial. An implication of this mode of burial is that a numerically abundant species such as *Molaria spinifera* was probably benthic in habit, whereas a rare species such as *Sarotrocercus oblita* gen.nov., sp.nov., might have been planktic and represented in the original, benthic habitat by the occasional little-decayed carcass lying on the sea bottom. In such a mode of transport and burial it might well happen that two different organisms, or parts of them, were deposited in juxtaposition. This might have been an accidental association, or original if one animal lived attached to the other. An example of accidental association is figure 88, plate 10, in which the exoskeleton of *Habelia? brevicauda* lies on a portion of a sponge. Another example, originally thought to be a single organism, has been shown to be composite by Conway Morris (1978). A third example dealt with here is the supposed new species of *Leanchoilia*, '*L. protogonia*' of Simonetta (1970), which I consider is probably a poor specimen of the type species of *Leanchoilia* lying on a strange, unidentified organism.

Specimens that have appendages preserved almost invariably show some trace of the alimentary canal, as an infilling (figure 8, plate 1; figure 58, plate 6), a dark band in low angle radiation (figure 10, plate 1; figure 54, plate 6; figure 67, plate 8), or a more strongly reflective band (figure 7, plate 1); in some examples the latter two features are partly coincident (figures 5, 7, 9, plate 1; figures 67, 68, plate 8). Irregular blobs of mineral matter may also be scattered along the alimentary canal (figures 69–71, plate 8; figure 111, plate 12), and fine-grained pyrite in and adjacent to the axial region (figure 8, plate 1; figures 15, 19, plate 2). Fine-grained pyrite may also have been deposited in the narrow space between doublure and dorsal exoskeleton (figures 37, 42, plate 4), and pyrite as minute spheres may be associated with the fossils (see, for example: figure 55, plate 6, left side; figures 123, 124, plate 14). The presence of pyrite suggests that burial was in an oxygen-poor environment. In certain specimens of *Molaria spinifera* the fine-grained pyrite may extend out beyond the axial region of cephalic shield and trunk (figures 3, 26), and in others reflective bands and patches extend out in a similar manner (figure 12, plate 1; figure 39, plate 4; figure 49, plate 5). These patterns are not consistent or frequent in occurrence, as are those of *Naraoia compacta* (Whittington 1977, figs 16, 19, pl. 3, etc.), which reveal the lateral diverticula, and I doubt that such diverticula are revealed in *M. spinifera*. In specimens in which appendages are absent there is no trace of such soft parts as the alimentary canal (figures 84–88, plate 10).

The bodies of the arthropods with appendages do not lie in one plane in the rock, because of the mode of burial. Appendages are separated by a thin layer of rock from the dorsal exoskeleton, and the two branches of an individual appendage, as well as the members of a series, are imbricated with a thin layer of rock separating them. This mode of preservation enables appendages to be revealed beneath the exoskeleton by preparation (see, for example, figures 52, 53, plate 5), or the inner branch to be revealed by excavation beneath the outer branch (figures 33, 35, plate 3). In such specimens it is most valuable to have part and counterpart, so that the mutual relationship of exoskeleton and appendage branches may be seen and summarized in a composite drawing (figure 29). The split between part and counterpart of a specimen may pass through the dorsal exoskeleton (e.g. figures 6, 8, plate 1), or below the exoskeleton of the trunk (figures 10, 14, plate 1; figure 38, plate 4) giving a very different appearance by passing through parts of the successive branches of the imbricated appendages. In lateral and oblique specimens (figures 5, 9, plate 1; figures 31–35, plate 3) the level of the split may move from dorsal exoskeleton to appendages in different areas.

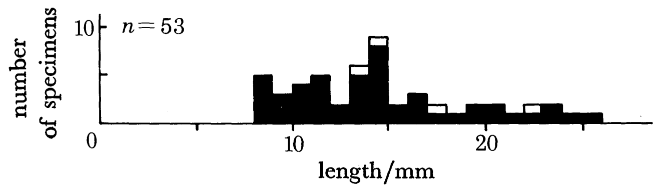


FIGURE 1. *Molaria spinifera* Walcott, 1912. Size-frequency histogram of measurements of sagittal length of body (excluding posterior spine) of 53 specimens. Blank rectangles are lengths of lectotype (the largest) and U.S.N.M. 57689, 57691, 57692.

After burial the mud enclosing the animal suffered compaction, a process operating over a much longer term than that of decay. During compaction the cephalic shield, for example, of *Molaria spinifera*, originally a quarter-sphere in shape, was compressed. The eventual outline seen in the rock is subsemicircular in a near-parallel specimen (figures 31, 32, plate 3; figure 37, plate 4), quarter-circle in a lateral specimen (figures 5, 7, plate 1), and various asymmetrical shapes in oblique specimens, e.g. ovoid (figures 16, 17, plate 2), broadly triangular (figures 10, 12, plate 1), or trapezoidal (figures 6, 11, plate 1). These outlines are dependent upon the original angle of burial, and the original shape and convexity is deduced from them (cf. discussion of form of the cephalic shield of *Naraoia compacta* in Whittington 1977, p. 420, fig. 3). A large sample of specimens entombed in a variety of attitudes facilitates such deductions, in other species discussed here the sample is small and hence the original form is much less clearly known.

5. *Molaria spinifera* Walcott, 1912

Figures 1–4; figures 5–14, plate 1; figures 15–20, 24, plate 2; figures 25–30; figures 31–36, plate 3; figures 37–42, plate 4; figures 43–46; figures 47–53, plate 5; figures 54–58, plate 6; figures 59, 60, 73, 74.

1912 Walcott, pp. 200–201, pl. 29, figs 1–5.
1920 Raymond, pp. 120–121, 149.
1944 Størmer, p. 86.
1959 Størmer *in* Moore, p. O 31, fig. 19, 1, 2 (copy of Walcott, figs 1, 2).
1964 Simonetta, pp. 216–219, fig. 1, pl. XXXIV (*non* figs of U.S.N.M. 144888), pl. XXXV.
1975 Simonetta & Delle Cave, pp. 21, 27, 32; pl. III, figs 3*a*, *b*, *c*; pl. XVIII, figs 1–7; pl. XIX, figs 1–8, 10, 11, (*non* fig. 9); pl. XX, figs 2, 5–8, 10, 11 (*non* figs 1, 3, 4, 9, 12); copies of Simonetta (1964) with additions.

(*a*) *Material*

Lectotype, U.S.N.M. 57688, selected Simonetta (1964, p. 216). Other material: U.S.N.M. 57689–57692 (originals of Walcott (1912)); U.S.N.M. 139208, 144885–144887, 144889, 144891, 144892, 144894–144906 (studied by Simonetta and Simonetta & Delle Cave). An additional

FIGURE 2

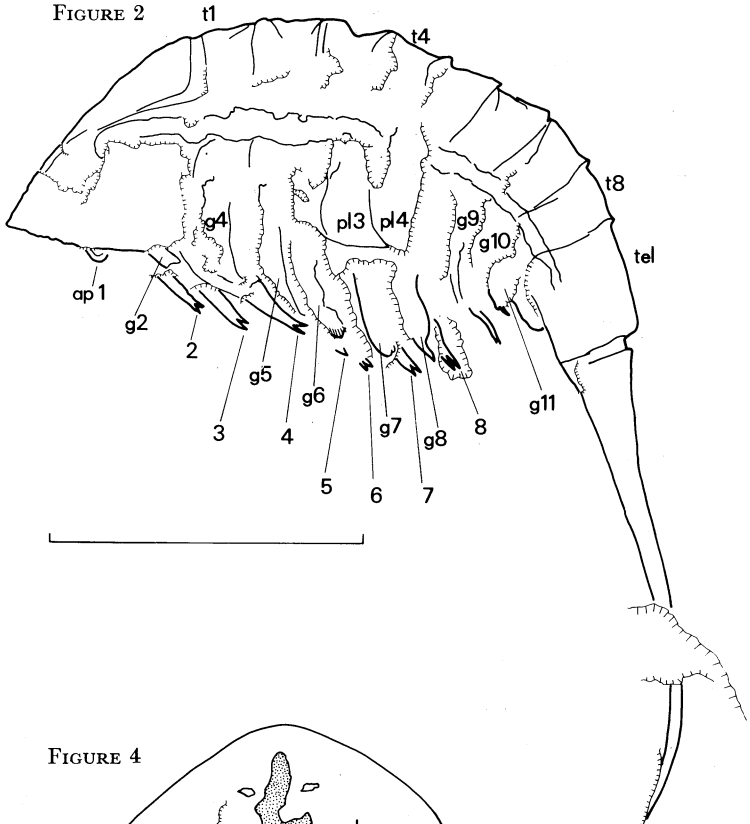


FIGURE 3

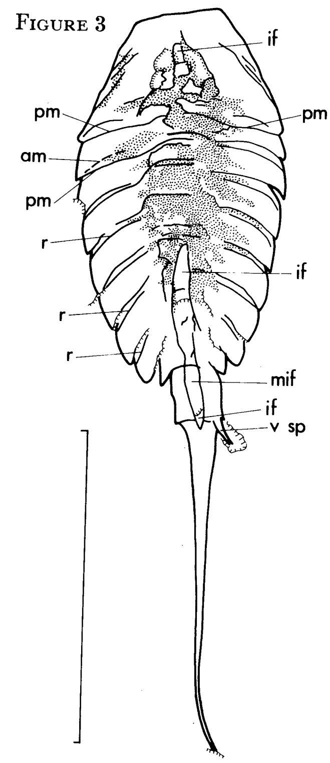
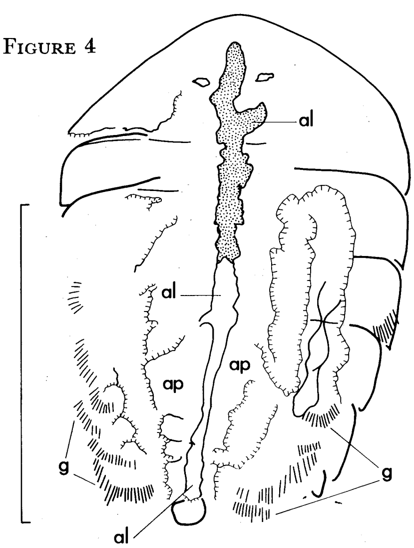


FIGURE 4



DESCRIPTION OF PLATE 1 AND FIGURES 2–4

Molaria spinifera Walcott, 1912, Phyllopod bed, Walcott quarry.

FIGURES 2–4. Respectively, composite explanatory drawings of U.S.N.M. 57688, 57689, 57690.

FIGURES 5, 7 AND 9. U.S.N.M. 57688, lectotype, lateral, part respectively northwest, reflected; counterpart west (magn. × 3.3).

FIGURES 6, 8 AND 11. U.S.N.M. 57689, parallel, respectively counterpart (excavated to show posterior margin of cephalic shield and of left side of first tergite) northeast, part north, counterpart reflected (magn. × 5).

FIGURES 10, 12, 13 AND 14. U.S.N.M. 57690, parallel, respectively part, west (magn. × 5), counterpart, reflected (magn. × 5), counterpart, posterior portion, reflected (magn. × 10), counterpart, west (magn. × 5).

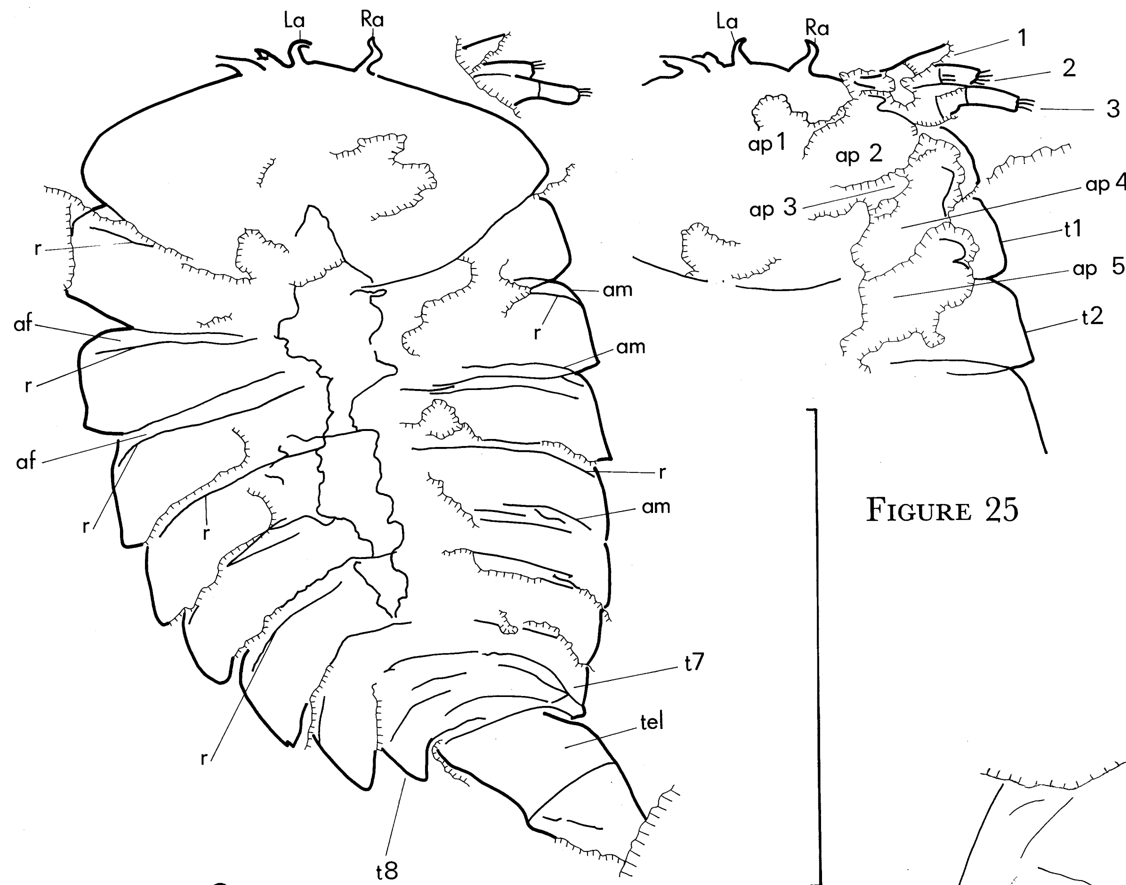


FIGURE 25

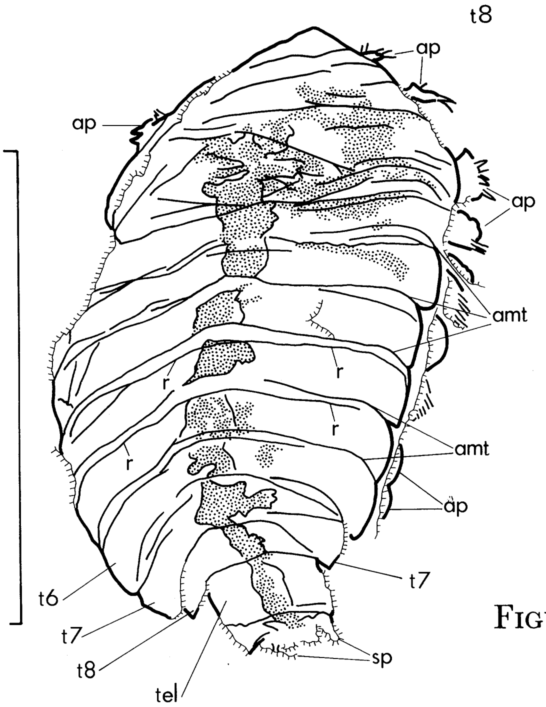


FIGURE 26

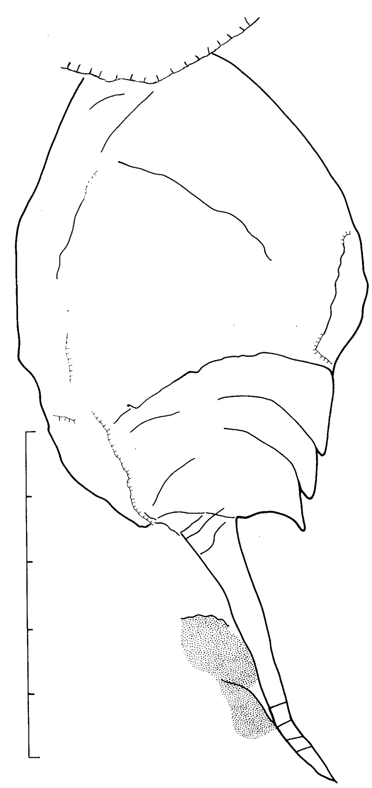


FIGURE 27

DESCRIPTION OF PLATE 2 AND FIGURES 25–27

FIGURES 15 AND 19. *Molaria spinifera* Walcott, 1912, Phyllopod bed, Walcott quarry. U.S.N.M. 57691, parallel oblique, part only, west, reflected (magn. ×5).

FIGURES 16–18, 20 AND 24. *Molaria spinifera* Walcott, 1912, Phyllopod bed, Walcott quarry. U.S.N.M. 57692, parallel, respectively part northeast, reflected (magn. ×5), right portion of cephalic shield and first two trunk tergites of part reflected (magn. ×10), counterpart reflected (magn. ×5), right portion of cephalic shield and first two trunk tergites of part after preparation, west northwest (magn. ×10).

FIGURES 21–23. U.S.N.M. 144888, undetermined organism, Phyllopod bed, Walcott quarry. Respectively 'part', north, reflected, 'counterpart' reflected (magn. ×6).

FIGURE 25. Composite explanatory drawing of U.S.N.M. 57692, at right is right anterior portion after preparation (compare figure 24).

FIGURES 26 AND 27. Explanatory drawings of U.S.N.M. 57691 and 144888 (composite).

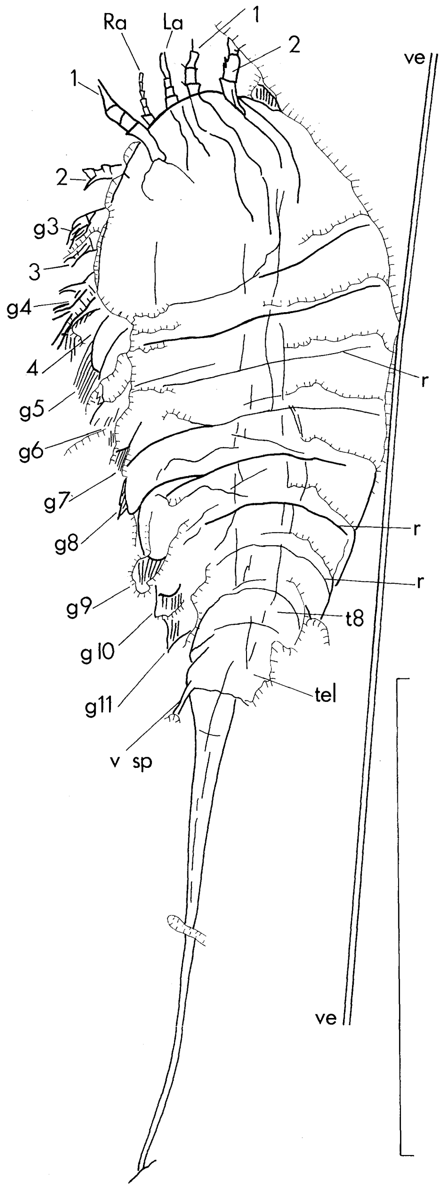


FIGURE 28

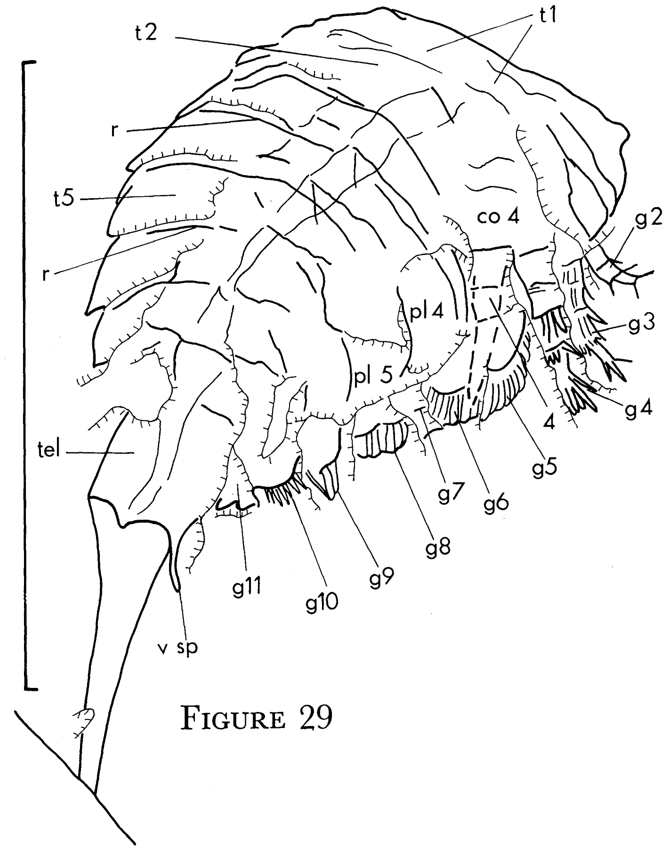


FIGURE 29

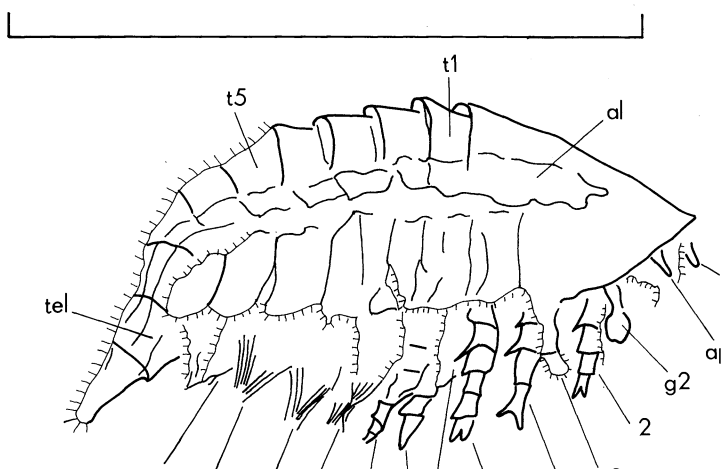


FIGURE 30

DESCRIPTION OF PLATE 3 AND FIGURES 28–30

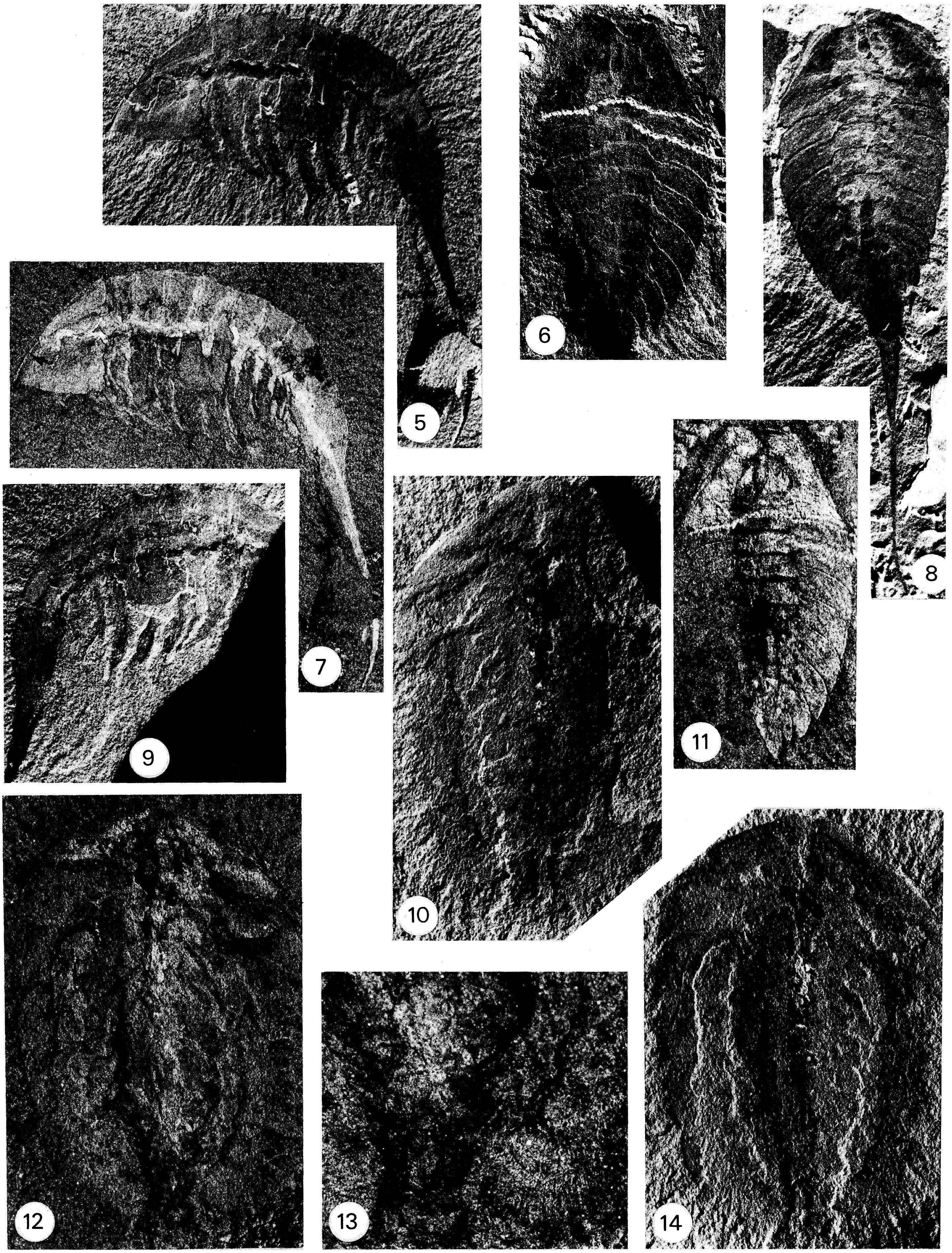
Molaria spinifera Walcott, 1912, Phyllopod bed, Walcott quarry

FIGURES 28–30. Respectively, explanatory drawings of U.S.N.M. 139208, 144885 (composite) from ventral, 144896.

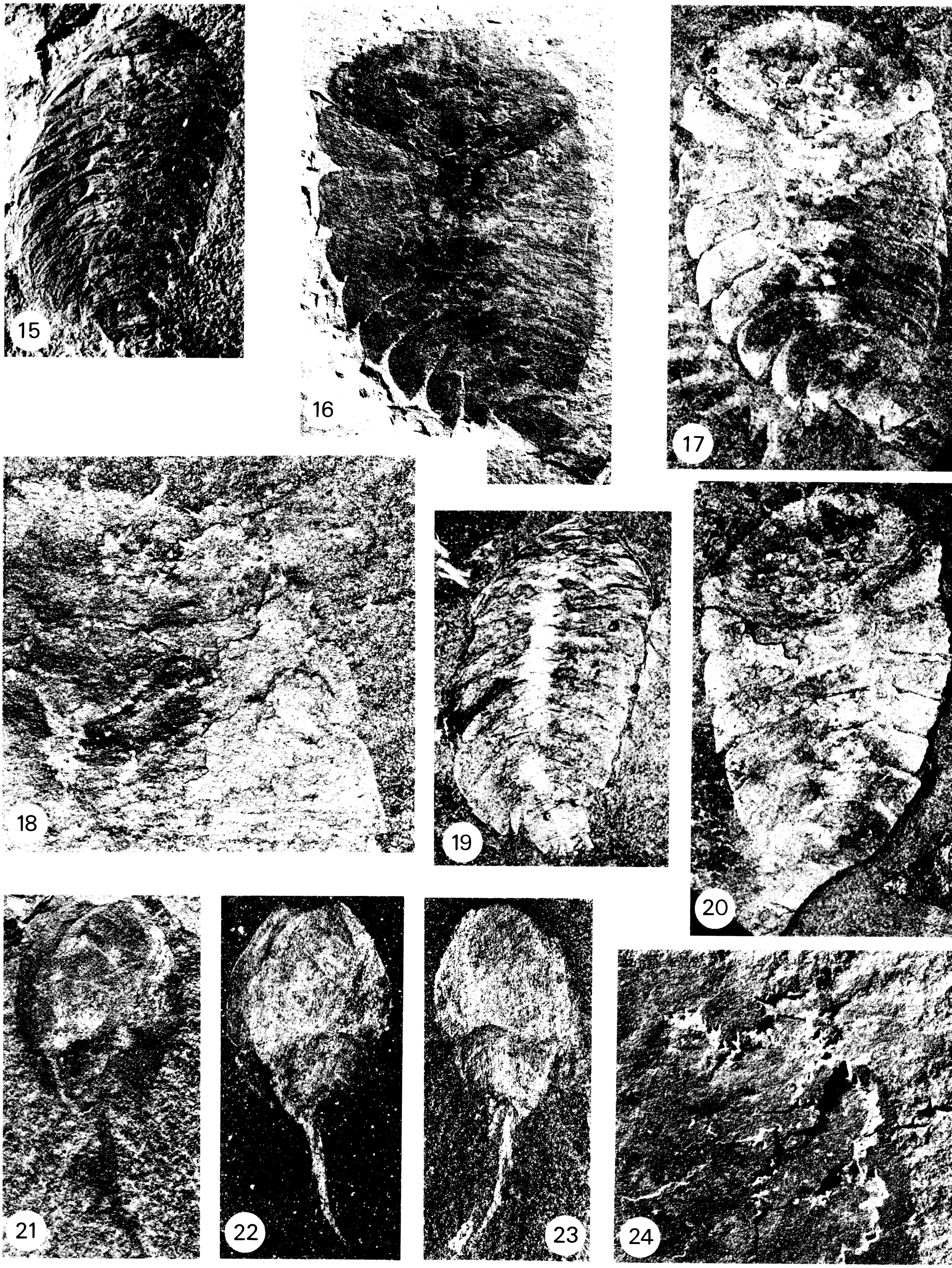
FIGURES 31 AND 32. U.S.N.M. 139208, parallel, counterpart only, anterior portion, north (magn. ×10); entire, northeast (magn. ×5).

FIGURES 33–35. U.S.N.M. 144885, oblique, respectively part, north, after excavation of leg branch 4; counterpart south southwest; part, northwest before excavation of leg branch 4, showing gill branches 2–11 (magn. ×10).

FIGURE 36. U.S.N.M. 144896, lateral oblique, part only, north (magn. ×10).

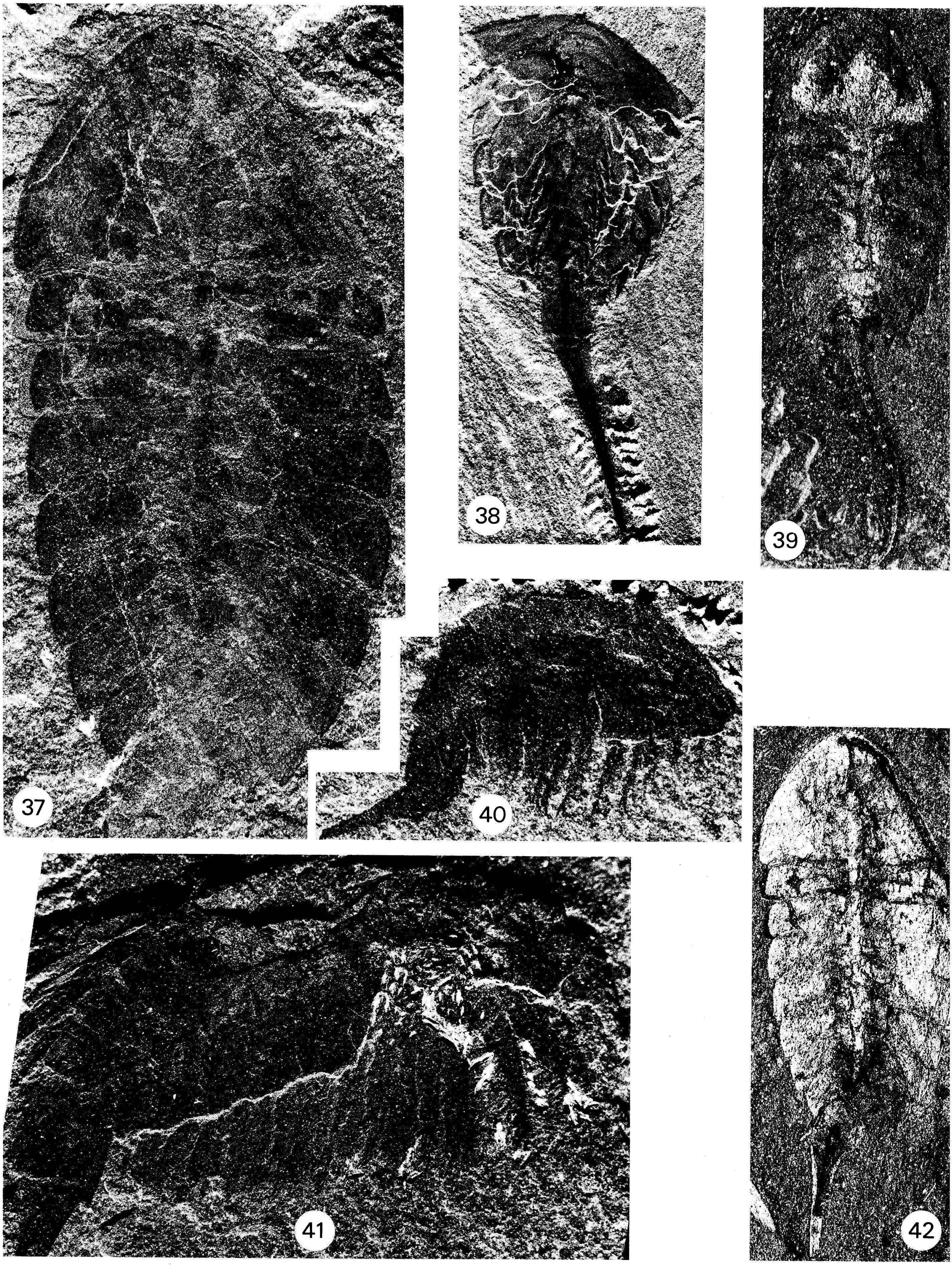


FIGURES 5–14. For description see opposite.



FIGURES 15–24. For description see opposite.

FIGURES 31–36. For description see opposite.



FIGURES 37–42. For description see opposite.

Description of plate 4 and figures 43–45

Molaria spinifera Walcott, 1912, Phyllopod bed, Walcott quarry

Figures 37 and 42. U.S.N.M. 144889, parallel, counterpart only, north (magn. ×10), entire reflected (magn. ×5).

Figure 38. U.S.N.M. 268936, parallel, part only, north (magn. ×3.3).

Figure 39. U.S.N.M. 272179, parallel, part only, reflected (magn. ×8).

Figure 40. U.S.N.M. 144905, lateral, counterpart only, north (magn. ×10).

Figure 41. U.S.N.M. 144892, lateral oblique, part only, after excavation of leg branch 3, south (magn. ×10).

Figures 43–45. Respectively, explanatory drawings of U.S.N.M. 144889, 144905, 144892 (before, at right after, excavation of leg branch 3).

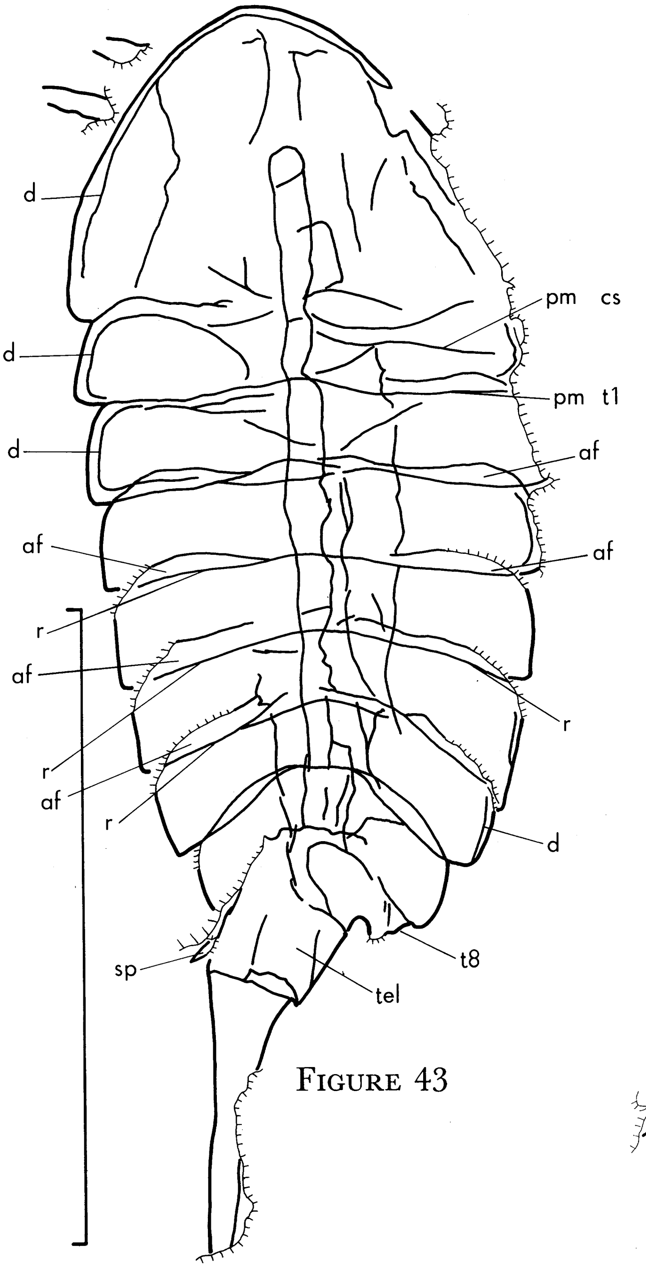
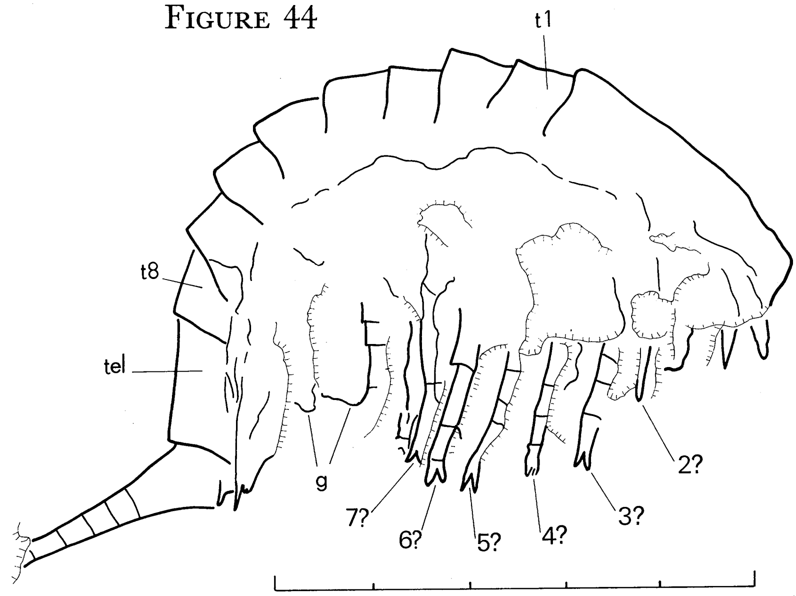


Figure 43

Figure 44



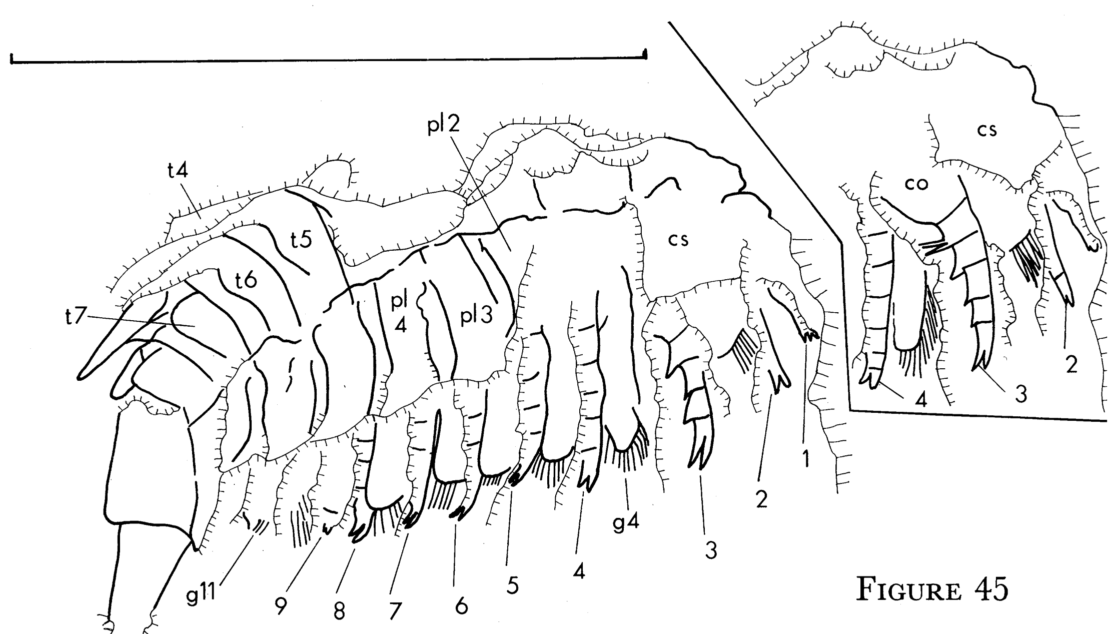


Figure 45

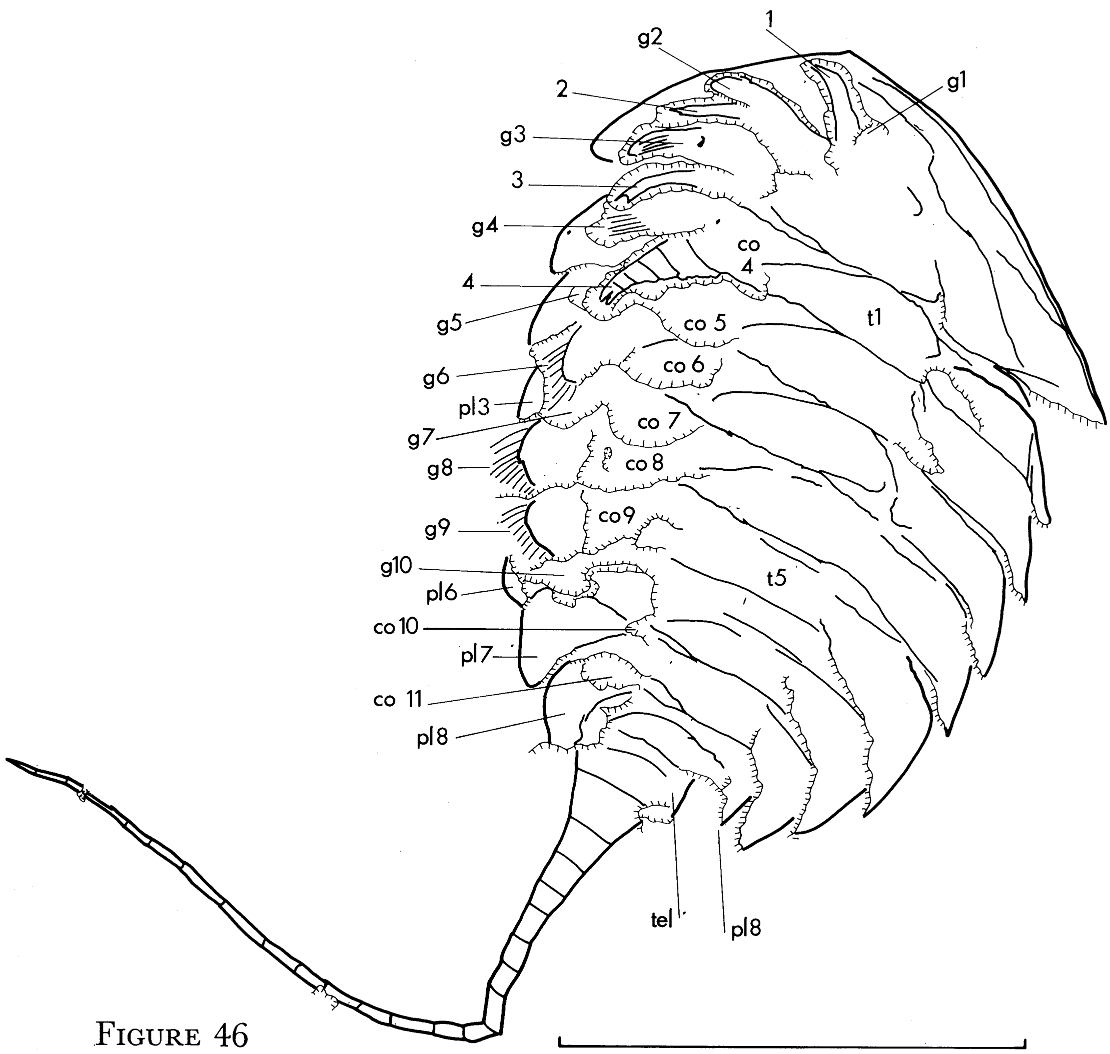


FIGURE 46

DESCRIPTION OF PLATE 5 AND FIGURE 46

Molaria spinifera Walcott, 1912, Phyllopod bed, Walcott quarry

FIGURE 46. Explanatory drawing of U.S.N.M. 268935.

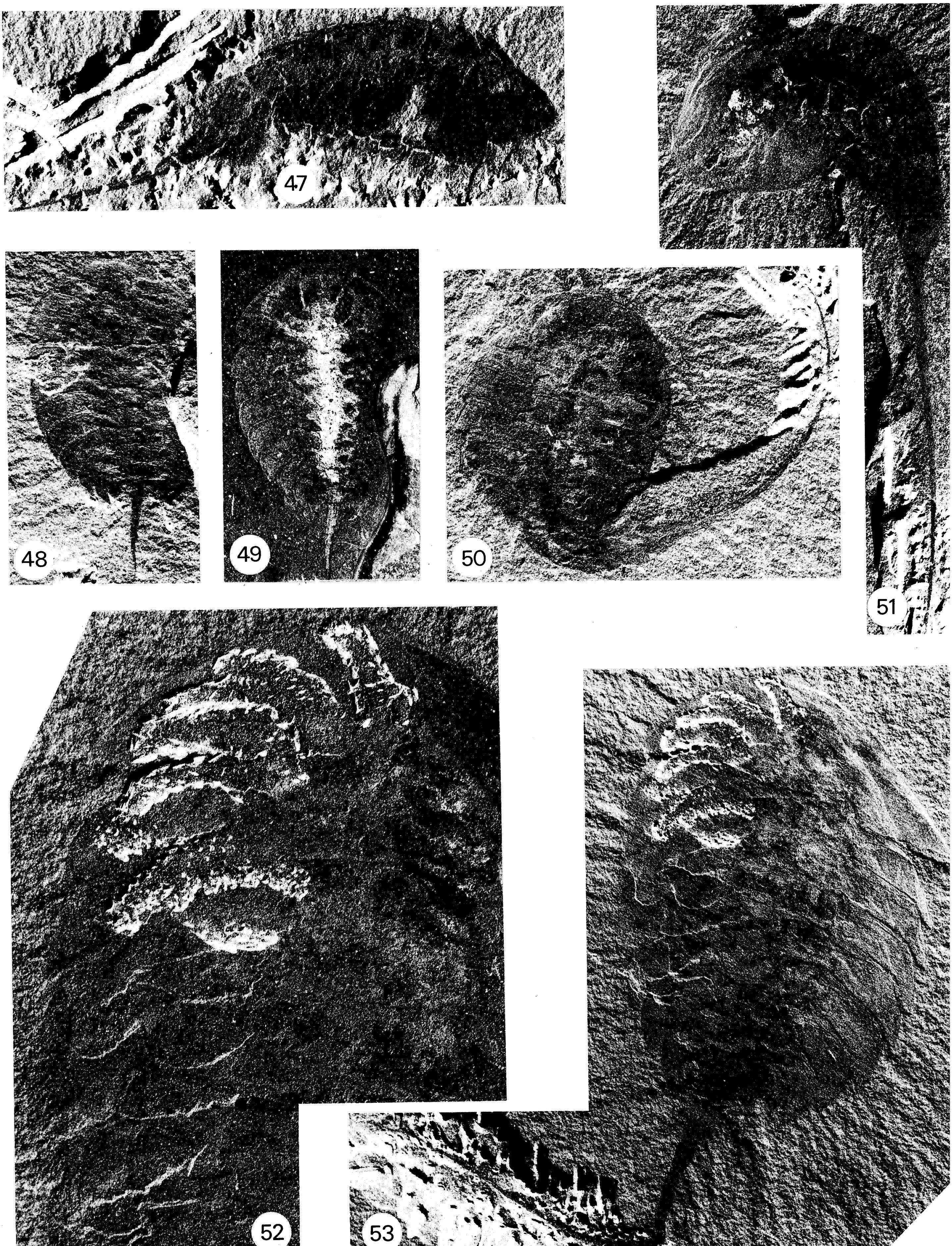
FIGURE 47. U.S.N.M. 268929; lateral oblique, part only, west (magn. ×5).

FIGURES 48 AND 49. U.S.N.M. 272094, parallel, part only, north, under water (magn. ×5).

FIGURE 50. U.S.N.M. 272103, oblique, part, north northwest (magn. ×5).

FIGURE 51. U.S.N.M. 272101, lateral oblique, part, northwest (magn. ×3.3).

FIGURES 52 AND 53. U.S.N.M. 268935, parallel oblique, part only, northwest (magn. ×10), entire, northeast (magn. ×5).



FIGURES 47–53. For description see opposite.

FIGURES 54–58. For description see opposite.

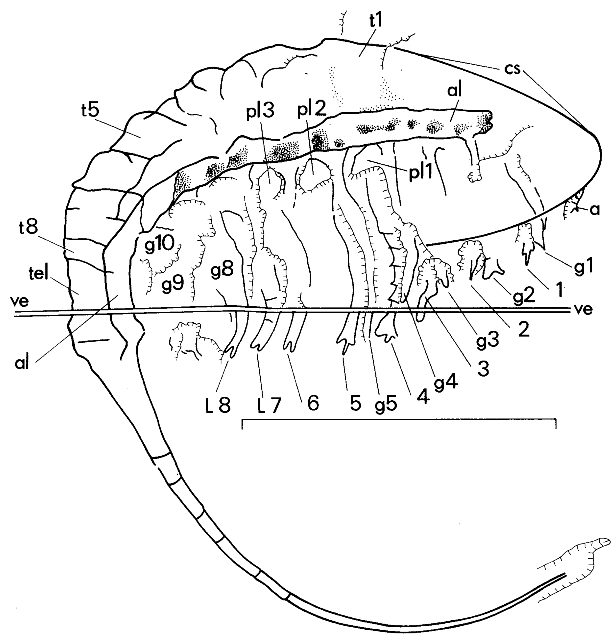


FIGURE 59

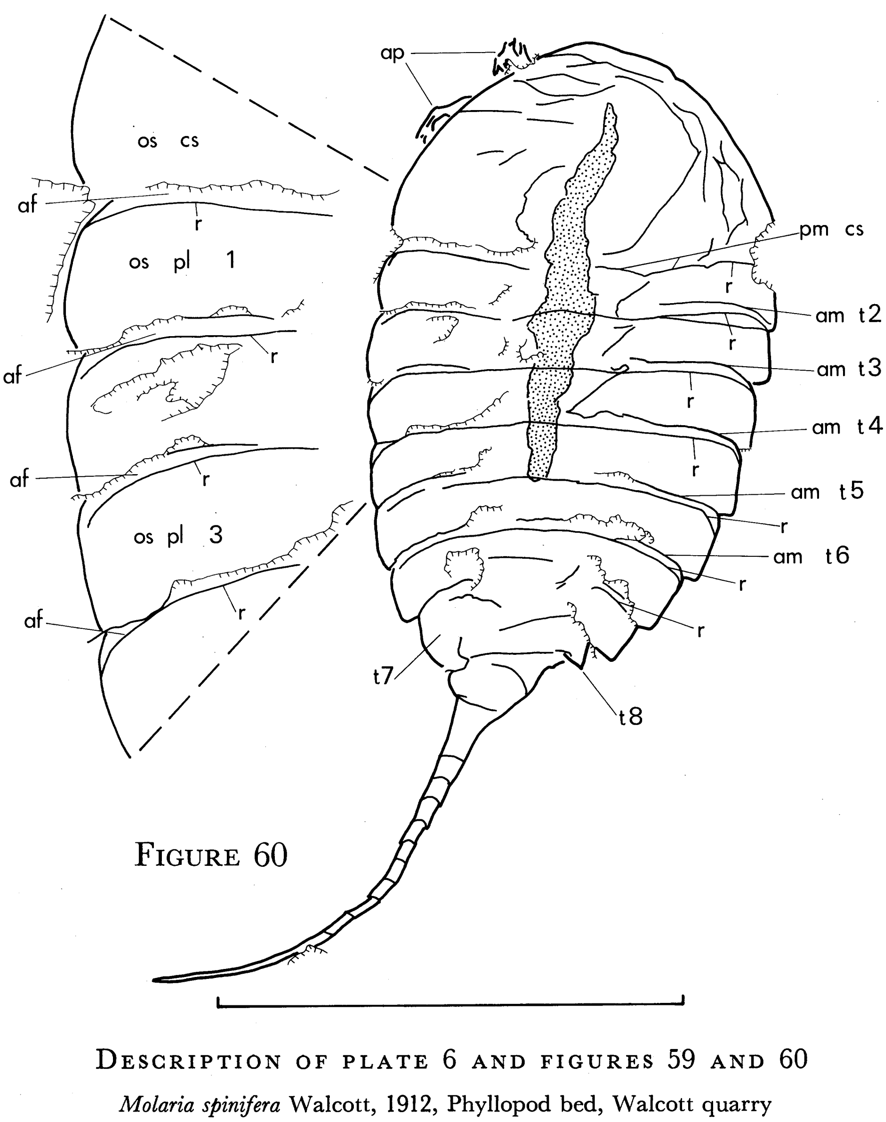


FIGURE 60

DESCRIPTION OF PLATE 6 AND FIGURES 59 AND 60

Molaria spinifera Walcott, 1912, Phyllopod bed, Walcott quarry

FIGURE 54. U.S.N.M. 144903, lateral, part only, south (magn. ×5).

FIGURES 55–57. U.S.N.M. 272105, parallel, part only, respectively north, northwest, northeast to show posterior spine (magn. ×10).

FIGURE 58. U.S.N.M. 272098, parallel, counterpart only, northwest (magn. ×5).

FIGURES 59 AND 60. Explanatory drawings of U.S.N.M. 144903, 272105 (with enlargement of portion of left side).

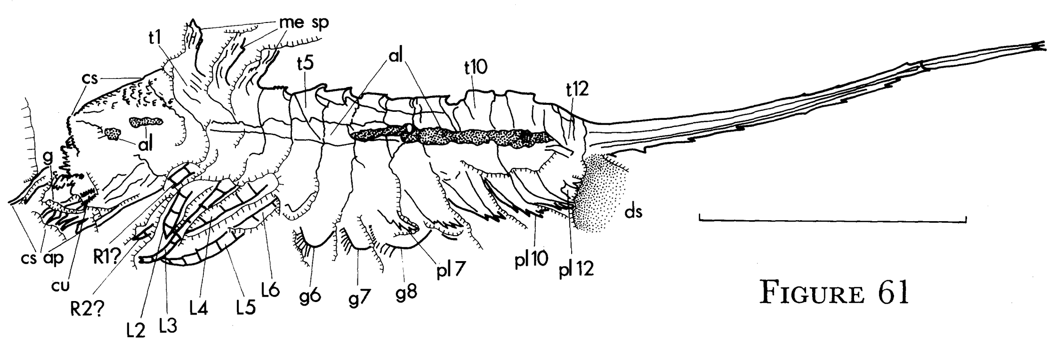


FIGURE 61

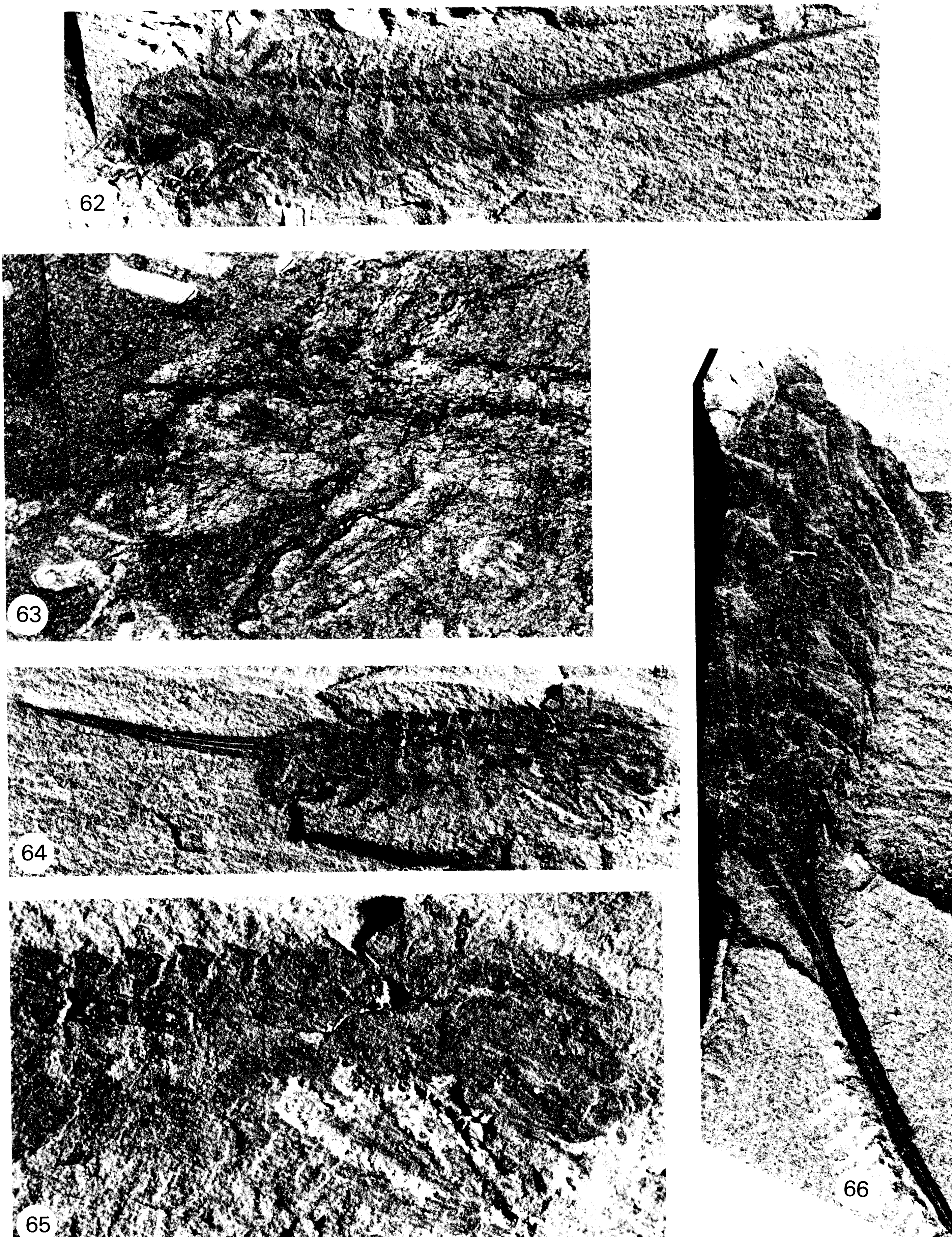
DESCRIPTION OF PLATE 7 AND FIGURE 61

Habelia optata Walcott, 1912, Phyllopod bed, Walcott quarry

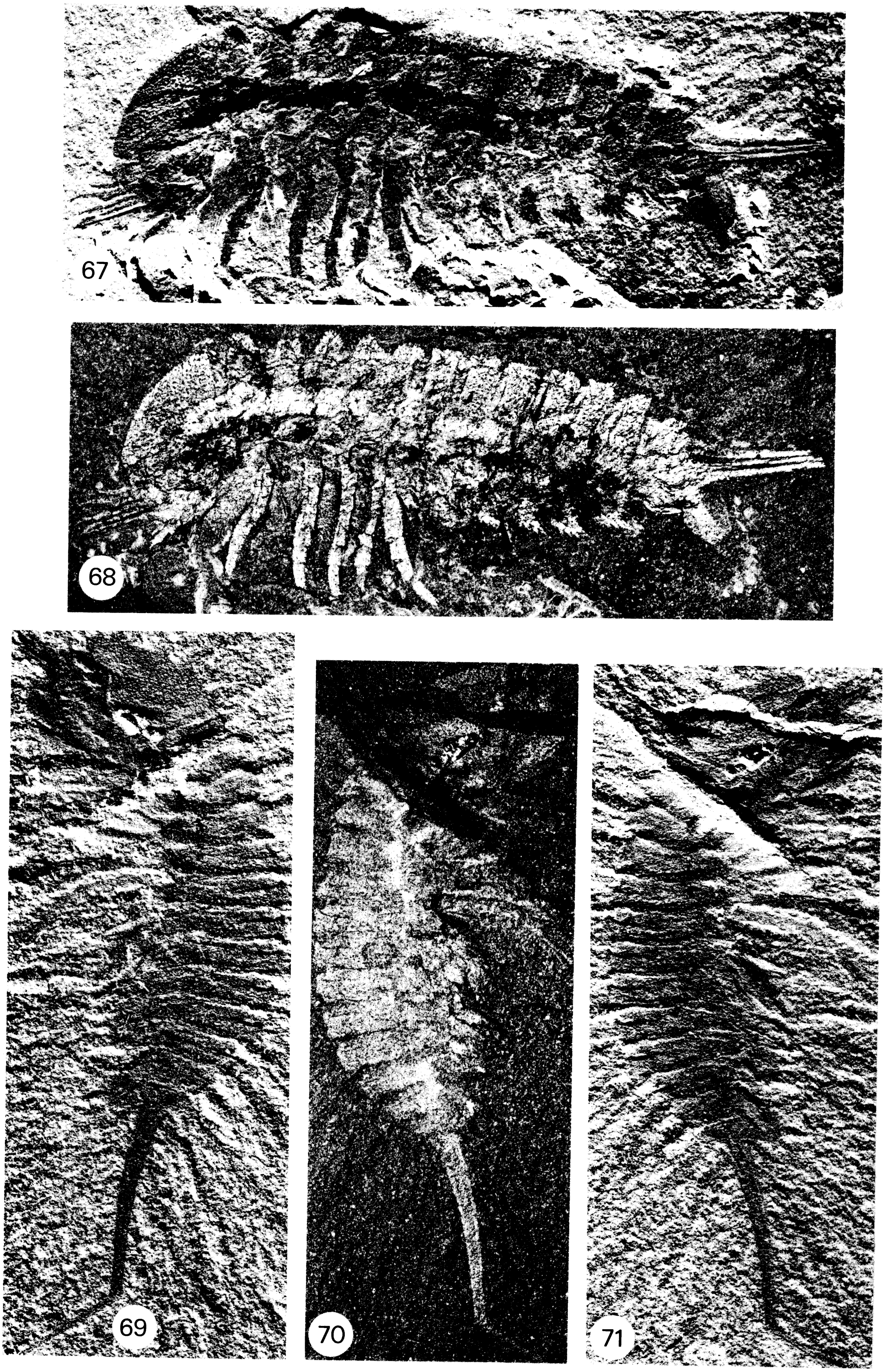
FIGURE 61. Composite explanatory drawing of U.S.N.M. 57693.

FIGURES 62–65. U.S.N.M. 57693, holotype, lateral, respectively counterpart northeast (magn. ×4.6), reflected (magn. ×10); part northeast (magn. ×4.6), anterior portion after preparation, east (magn. ×10).

FIGURE 66. U.S.N.M. 268938, oblique, counterpart only, north (magn. ×5).



FIGURES 62–66. For description see opposite.



Figures 67–71. For description see opposite.

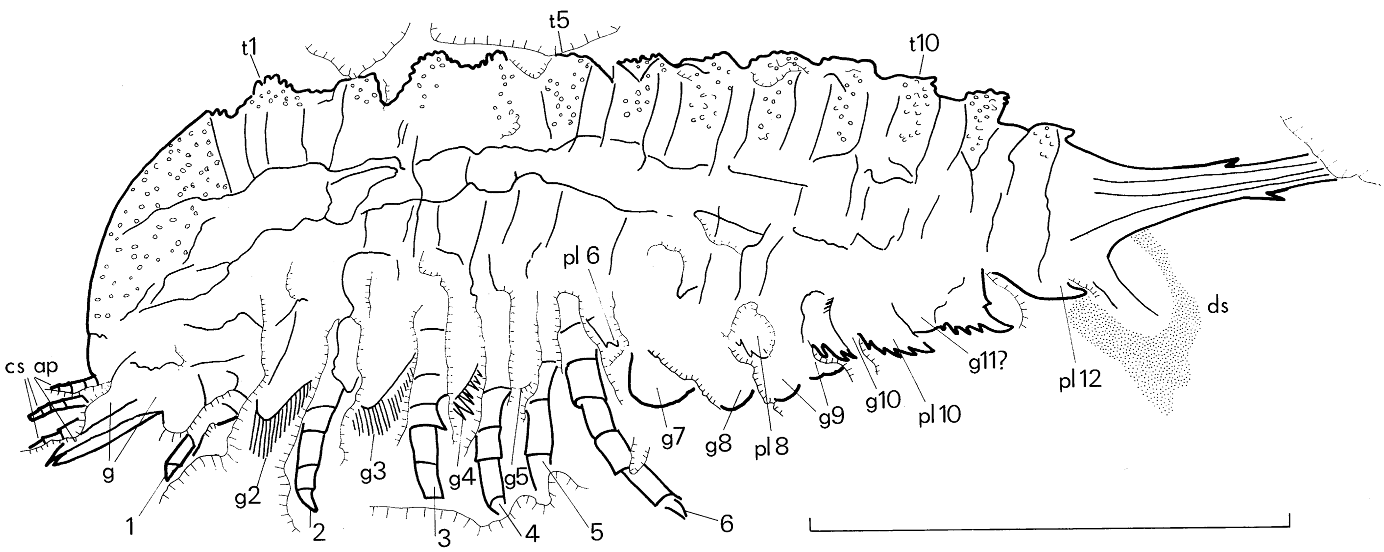


FIGURE 72

DESCRIPTION OF PLATE 8 AND FIGURE 72

Habelia optata Walcott, 1912, Phyllopod bed, Walcott quarry

FIGURES 67 AND 68. U.S.N.M. 139209, lateral, counterpart only, south, reflected (magn. ×4.6).

FIGURES 69–71. U.S.N.M. 144907, lateral, respectively counterpart (?) north northeast; part (?) reflected, south (magn. ×3.3).

FIGURE 72. Explanatory drawing of U.S.N.M. 139209.

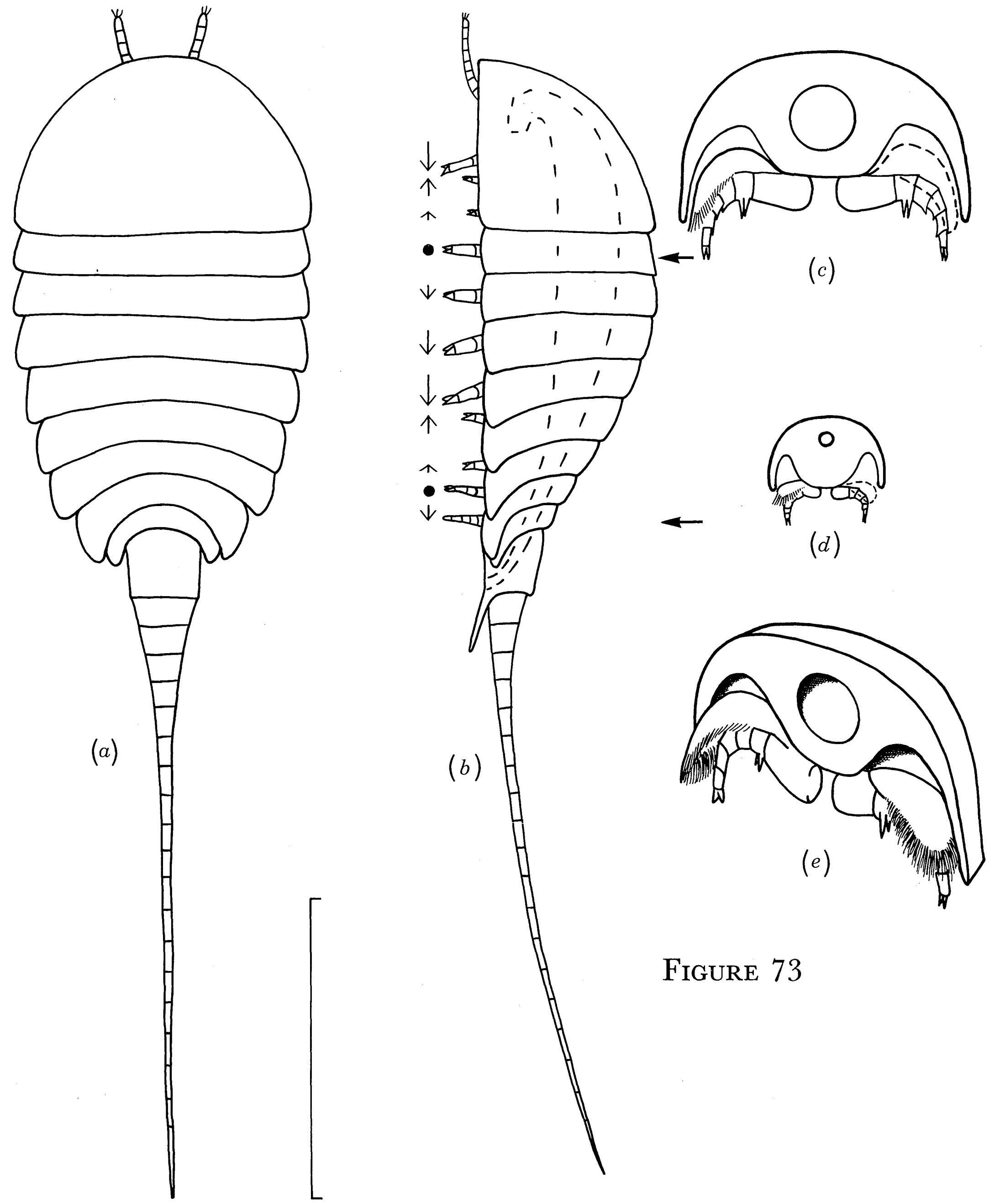


FIGURE 73

FIGURE 73. Reconstruction of *Molaria spinifera* Walcott, 1912. (*a*), (*b*) Dorsal and left lateral views, latter showing leg branches in 'still' position of gait discussed in the text. Beneath tips of leg branches are arrows showing direction and amount of promotor or remotor swing passed through; dot indicates beginning of remotor stroke. Dashed line is outline of alimentary canal, and suggests approximate position of backward-facing mouth. (*c*), (*d*) Cross-sections of body, with alimentary canal outlined, at first and eighth tergites, showing the pair of appendages in posterior view; gill branch outlined by dashed line on right side. (*e*) Oblique view of section of trunk showing the pair of appendages, to illustrate the form and position of attachment of the gill branch.

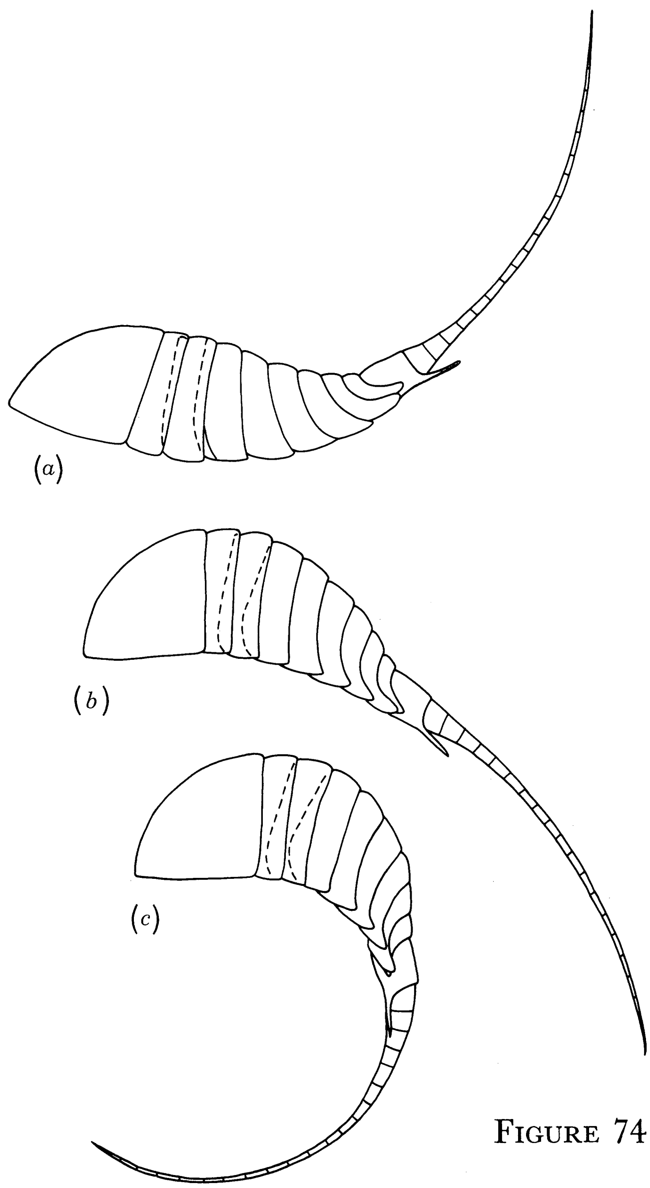


FIGURE 74

FIGURE 74. Left lateral views of restoration of *Molaria spinifera* Walcott, 1912, to illustrate suggested flexibility of body. Dashed lines show anterior margins of tergites 2 and 3 and thus the amounts of overlap between tergites in different positions. In (*a*) the overlap is at a minimum and the ridge (solid line) is visible laterally on tergite 3. In (*b*) the ridge is approximately coincident with the posterior margin of the preceding tergite; in (*c*) it lies beneath the posterior distal portion of the tergite.

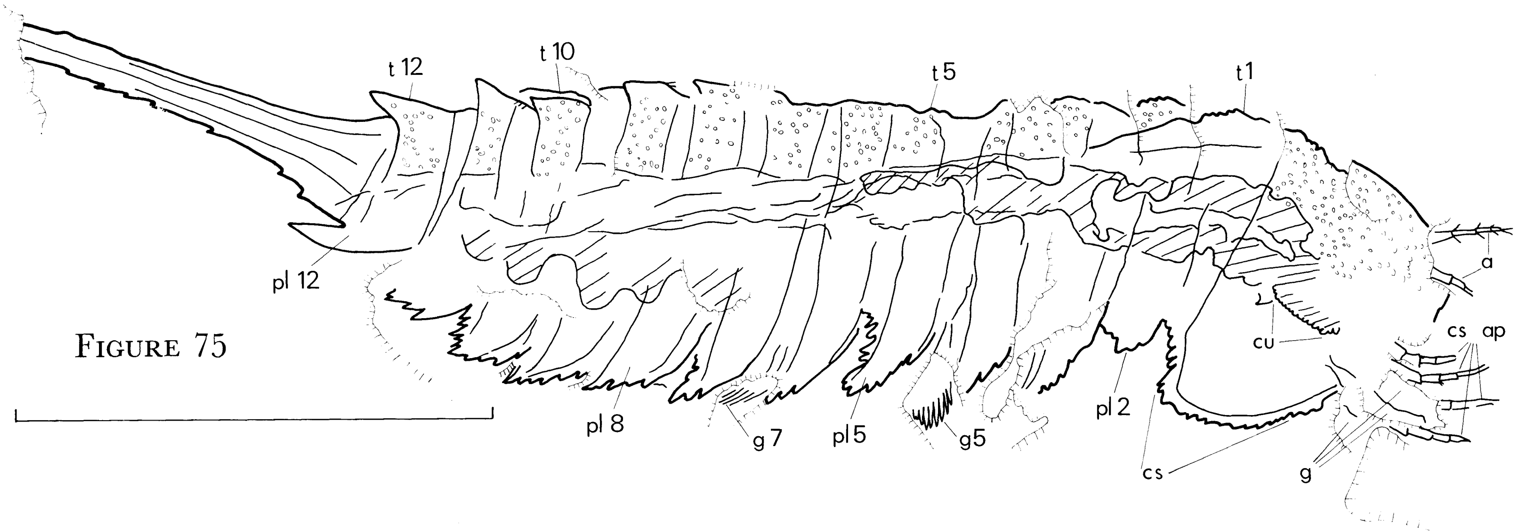


FIGURE 75

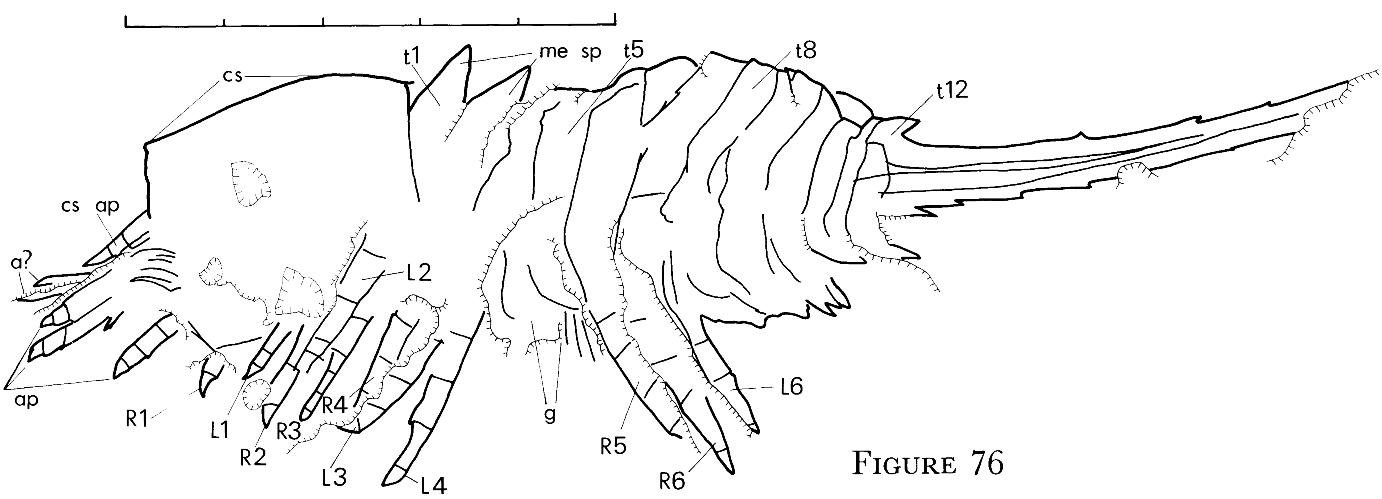


FIGURE 76

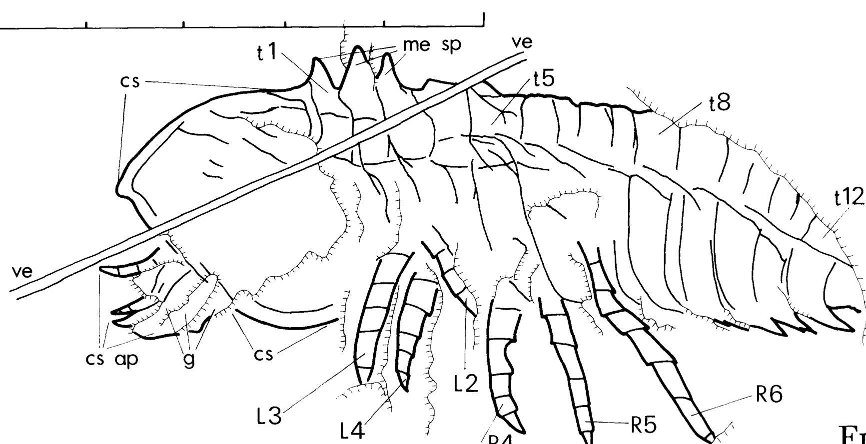


FIGURE 77

DESCRIPTION OF PLATE 9 AND FIGURES 75–77

Habelia optata Walcott, 1912, Phyllopod bed, Walcott quarry

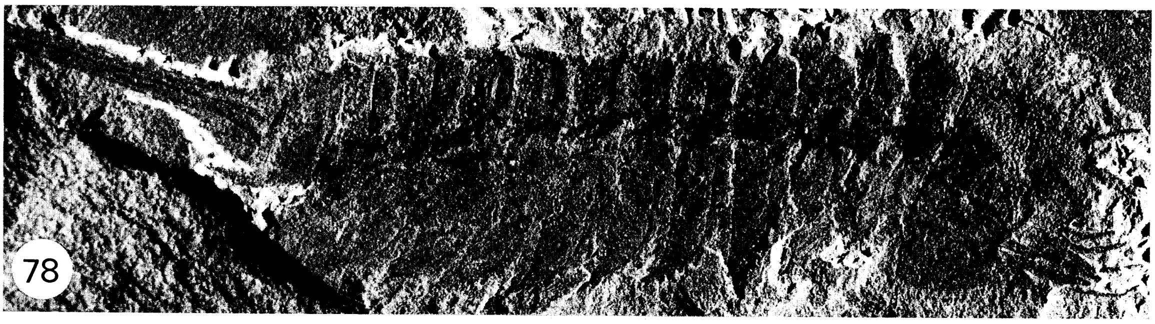
FIGURES 75–77. Respectively, explanatory drawings of U.S.N.M. 144908, 268931, 268927.

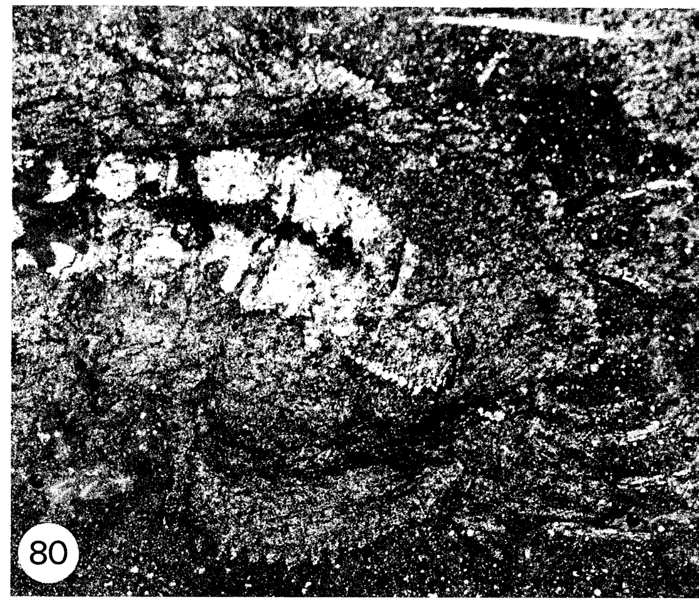
FIGURES 78–80. U.S.N.M. 144908, lateral, counterpart only, east (magn. ×4.7); anterior portion west, reflected (magn. ×10).

FIGURE 81. U.S.N.M. 268931, lateral, counterpart only, north (magn. ×10).

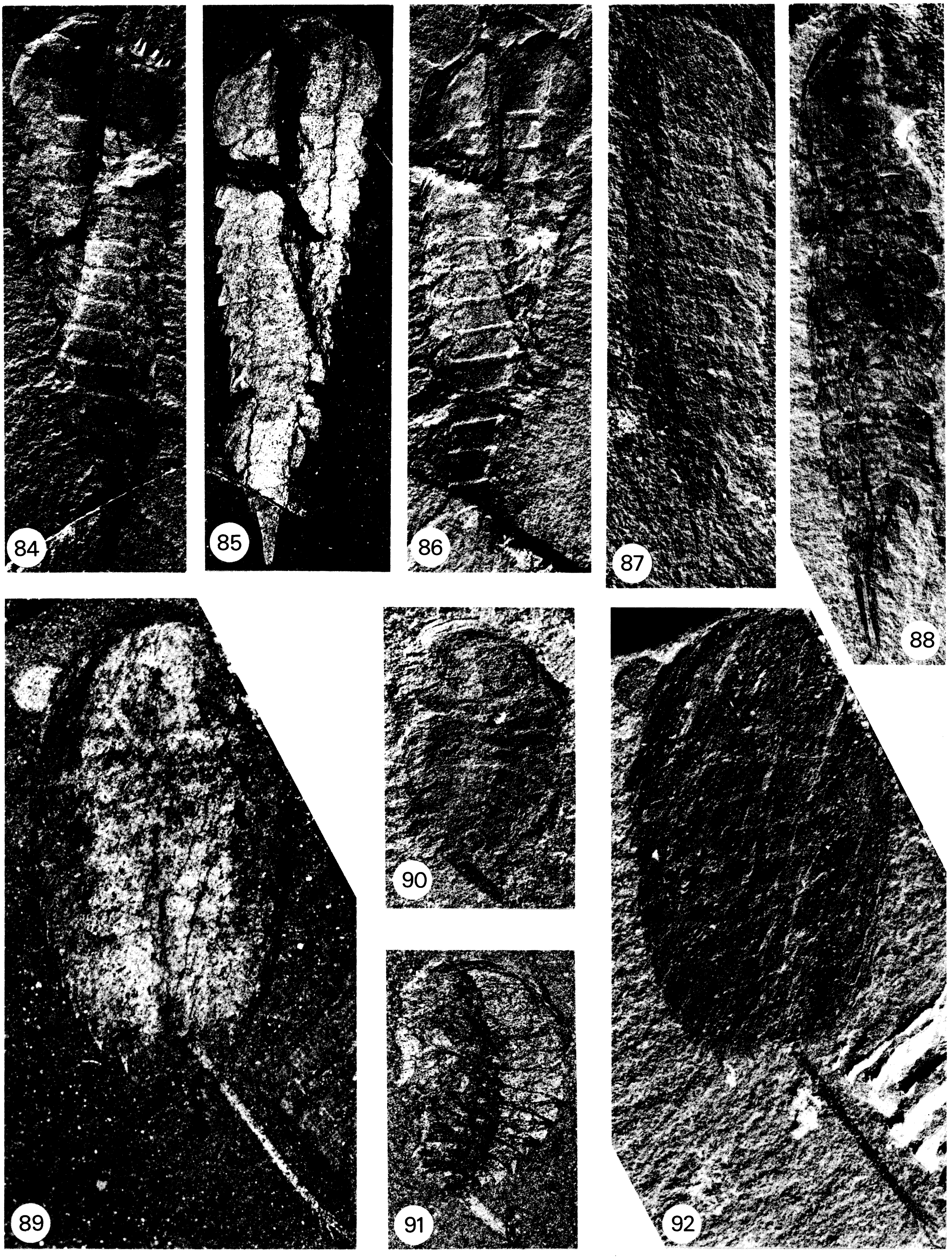
FIGURE 82. U.S.N.M. 268927, lateral, counterpart only, north (magn. ×10).

FIGURE 83. U.S.N.M. 144909, lateral, counterpart only, reflected (magn. ×3.3).





FIGURES 78–83. For description see opposite.



Figures 84–92. For description see opposite.

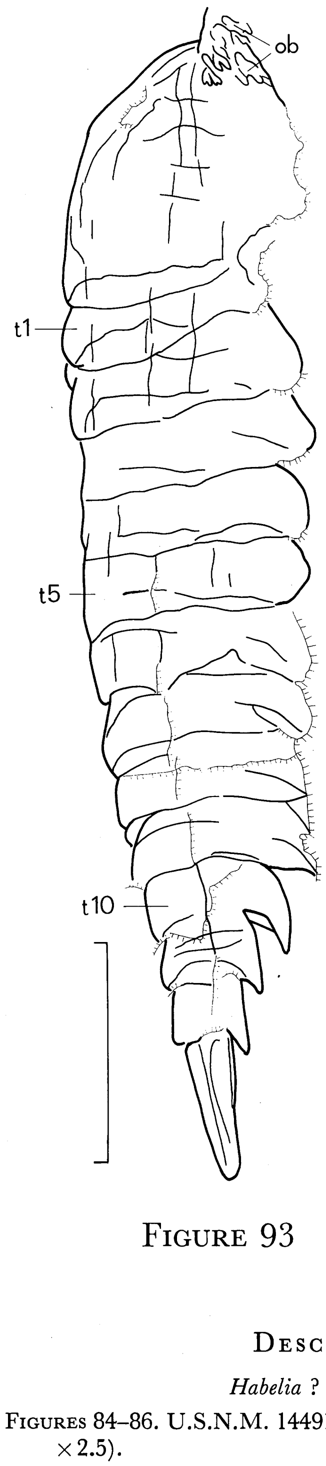


FIGURE 93

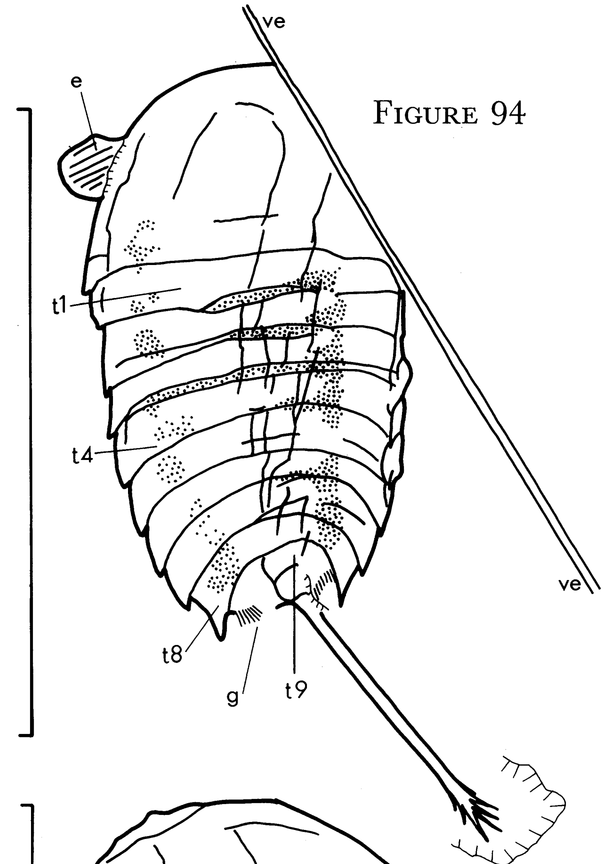


FIGURE 94

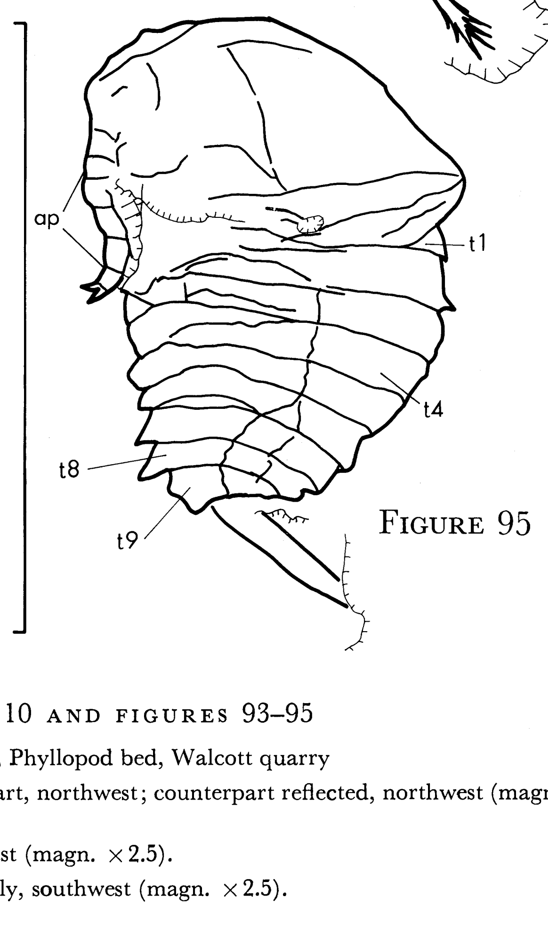


FIGURE 95

DESCRIPTION OF PLATE 10 AND FIGURES 93–95

Habelia ? brevicauda Simonetta, 1964, Phyllopod bed, Walcott quarry

FIGURES 84–86. U.S.N.M. 144912, parallel, respectively part, northwest; counterpart reflected, northwest (magn. ×2.5).

FIGURE 87. U.S.N.M. 275533, parallel, part only, northeast (magn. ×2.5).

FIGURE 88. U.S.N.M. 144910, holotype, lateral, part ? only, southwest (magn. ×2.5).

FIGURE 93. Explanatory drawing of U.S.N.M. 144910.

Sarotrocercus oblita gen. nov., sp. nov., Phyllopod bed, Walcott quarry

FIGURES 89 AND 92. U.S.N.M. 144893, counterpart only, parallel, under water, northwest (magn. ×10).

FIGURES 90 AND 91. U.S.N.M. 272151, part only, northwest, reflected (magn. ×6).

FIGURE 94. Explanatory drawing of U.S.N.M. 144893.

FIGURE 95. Explanatory drawing of U.S.N.M. 272151.

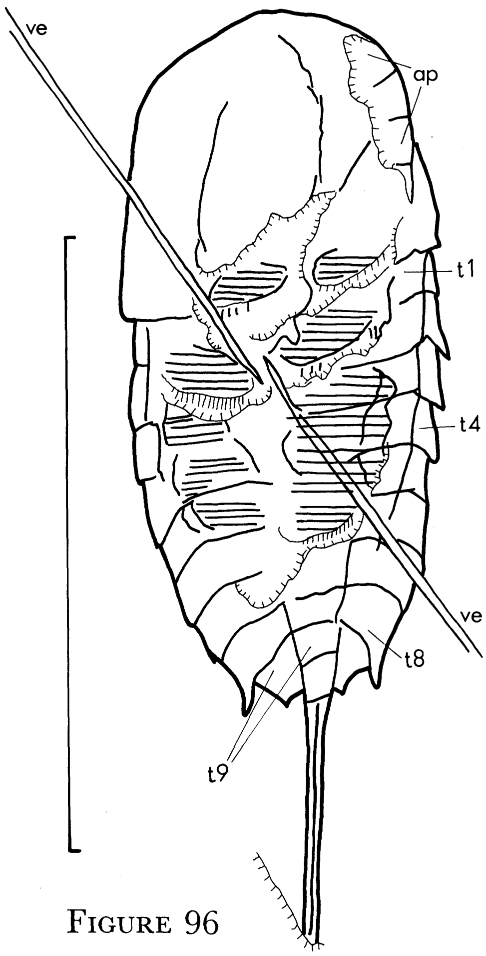


FIGURE 96

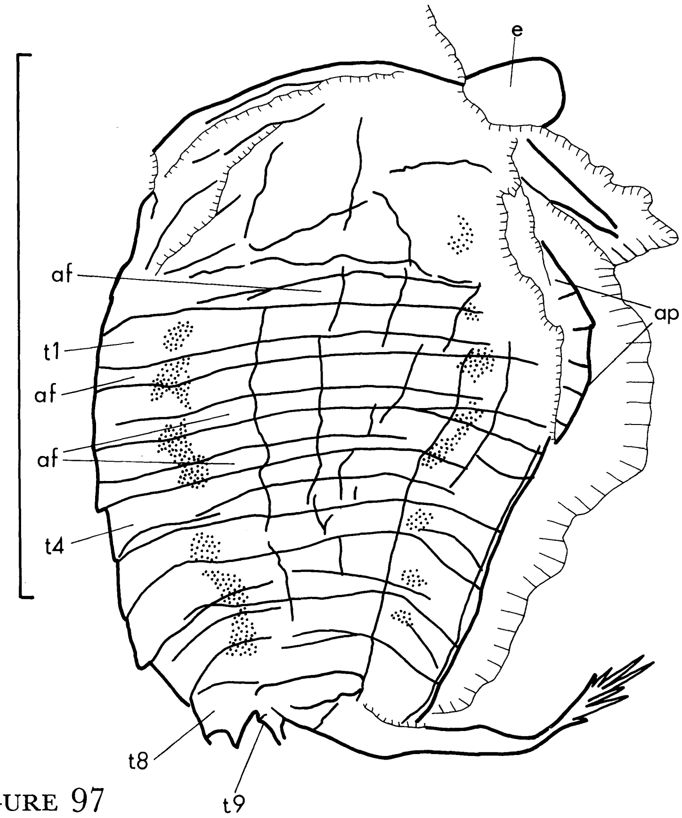


FIGURE 97

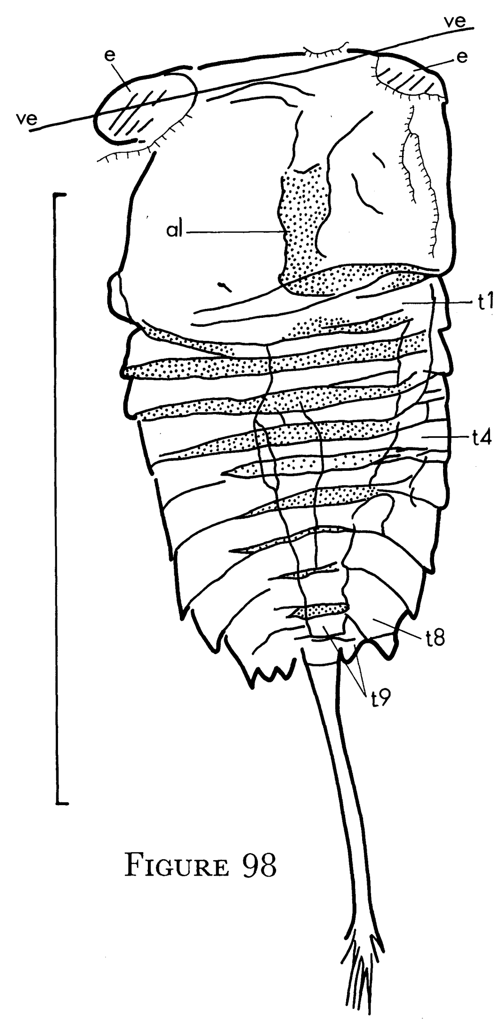


FIGURE 98

DESCRIPTION OF PLATE 11 AND FIGURES 96–98

Sarotrocercus oblita gen. nov., sp. nov., Phyllopod bed, Walcott quarry

FIGURES 96 AND 98. Respectively, composite explanatory drawing of U.S.N.M. 275539 (counterpart 272143) and 144890 (counterpart 272171).

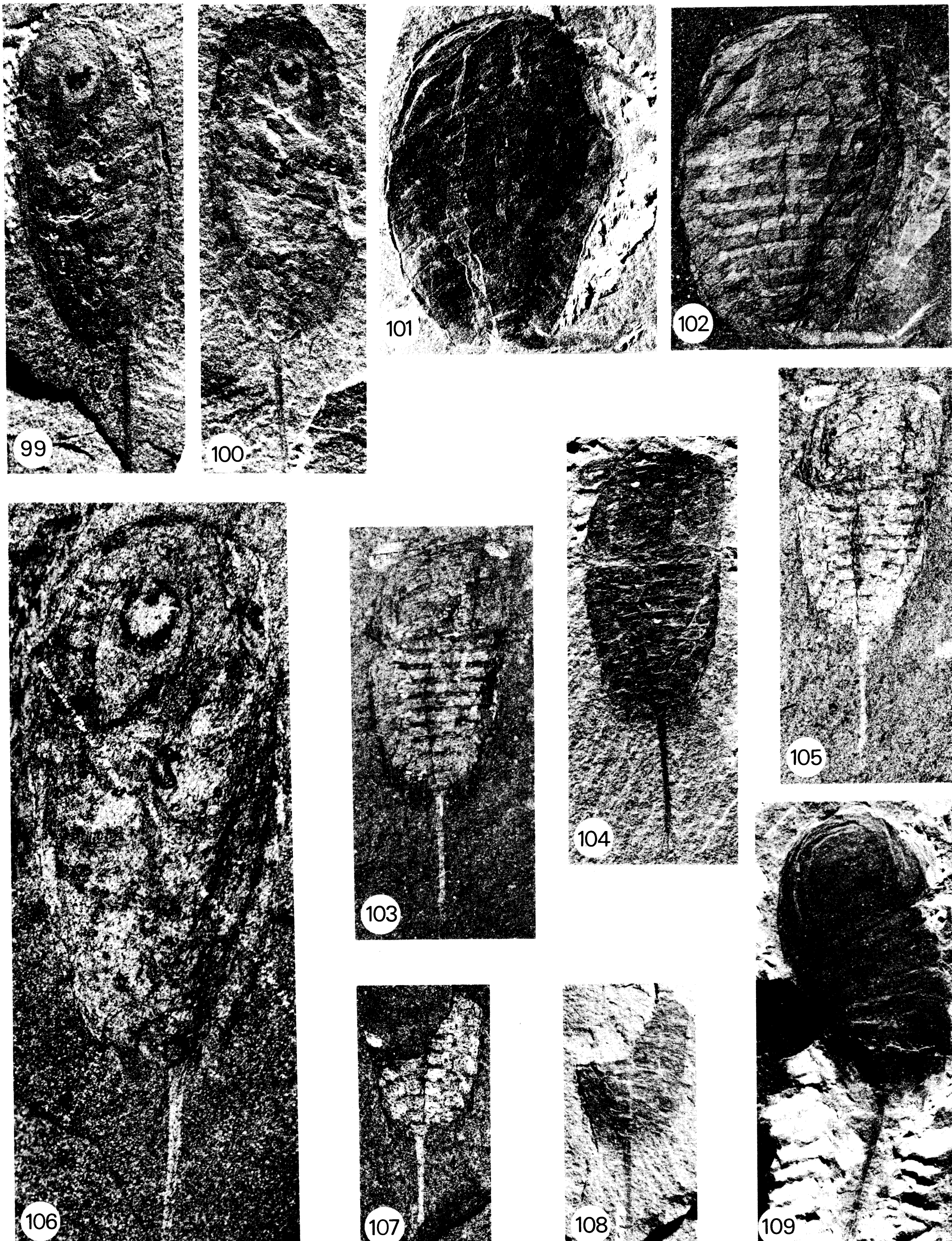
FIGURE 97. Explanatory drawing of U.S.N.M. 272194.

FIGURES 99, 100 AND 106. Parallel, part (U.S.N.M. 275539), northeast (magn. ×6); counterpart (U.S.N.M. 272143), north (magn. ×6); part, reflected (magn. ×10).

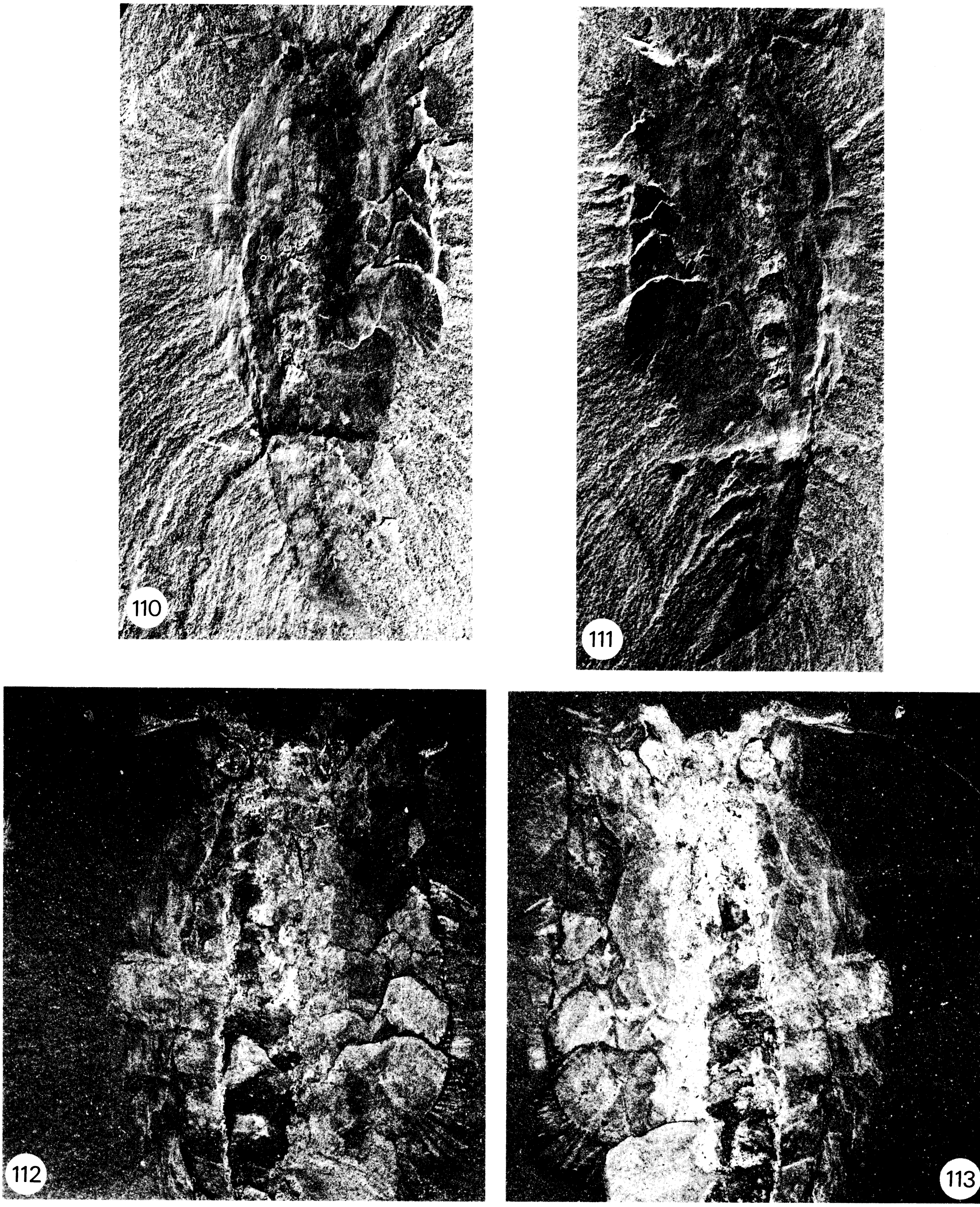
FIGURES 101 AND 102. U.S.N.M. 272194, parallel, counterpart only, east, under water (magn. ×6).

FIGURES 103–105, 107 AND 108. Holotype, parallel, counterpart (U.S.N.M. 272171), under water, north, reflected; part (U.S.N.M. 144890), reflected, northeast (magn. ×5).

FIGURE 109. U.S.N.M. 272099, parallel, part only, northeast (magn. ×5).



Figures 99–109. For description see opposite.



Figures 110–113. For description see opposite.

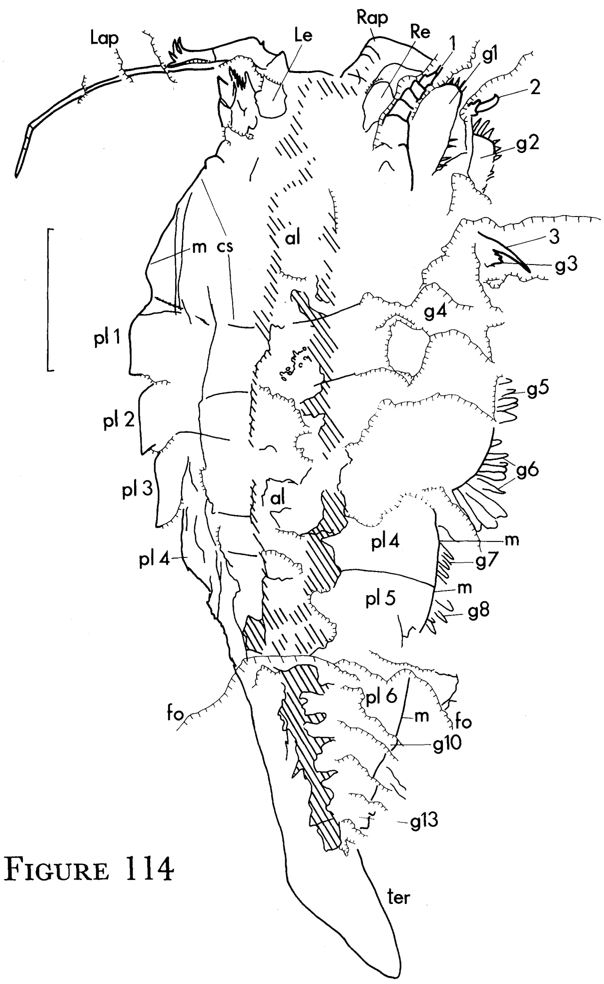


Figure 114

Description of plate 12 and figure 114

Actaeus armatus Simonetta, 1970, Phyllopod bed, Walcott quarry

Figures 110–113. U.S.N.M. 155597, holotype, parallel oblique, respectively part, northwest, counterpart, north (magn. ×1.7); anterior portion of part, under water, anterior portion of counterpart, under water (magn. ×2.5).

Figure 114. Composite explanatory drawing of U.S.N.M. 155597.

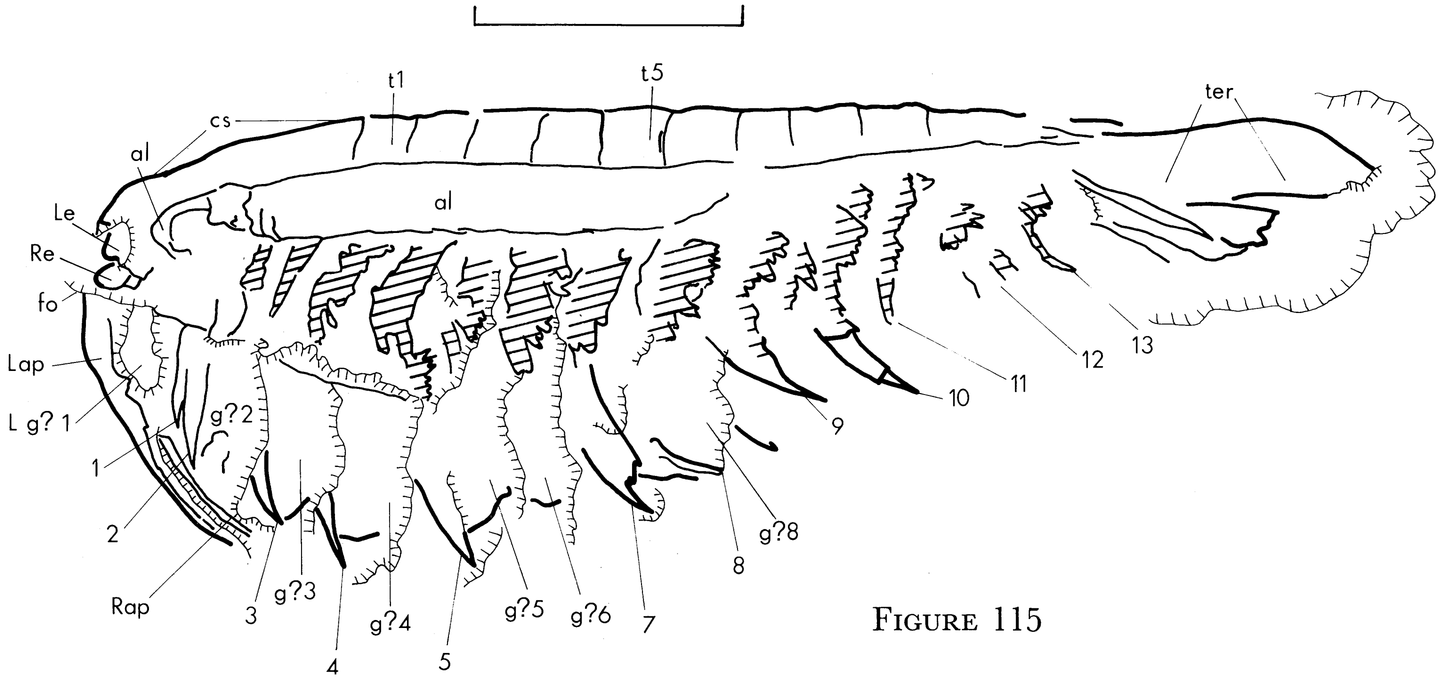


FIGURE 115

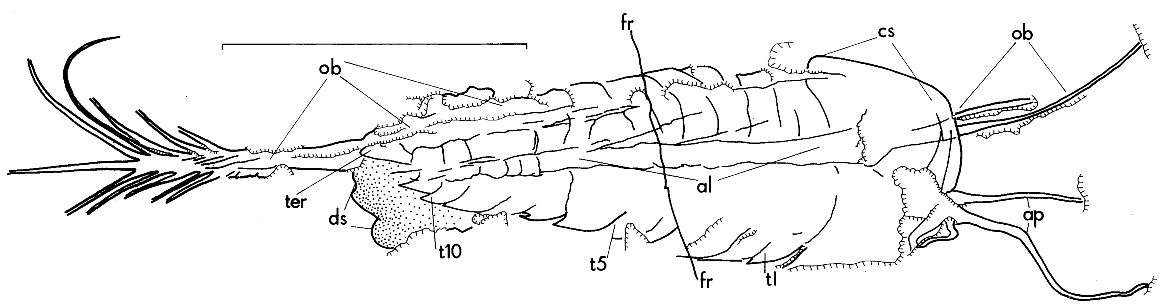


FIGURE 116

DESCRIPTION OF PLATE 13 AND FIGURES 115 AND 116

Alalcomenaeus cambricus Simonetta, 1970, Phyllopod bed, Walcott quarry

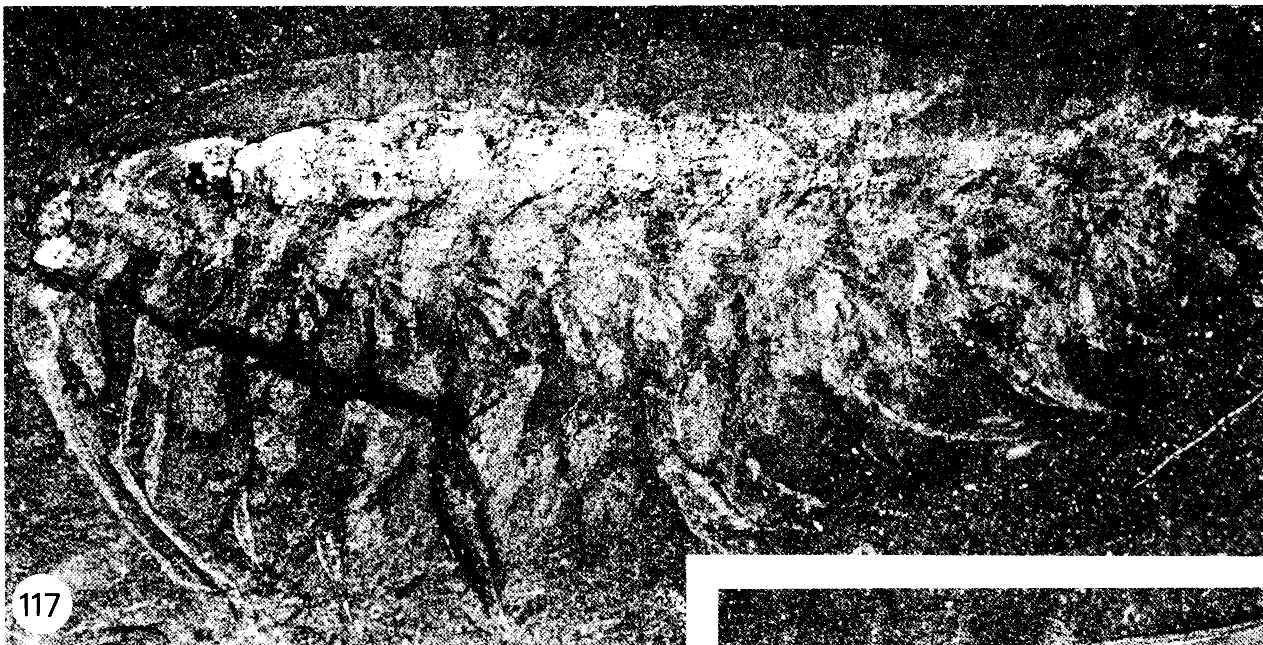
FIGURE 115. Explanatory drawing of U.S.N.M. 155658.

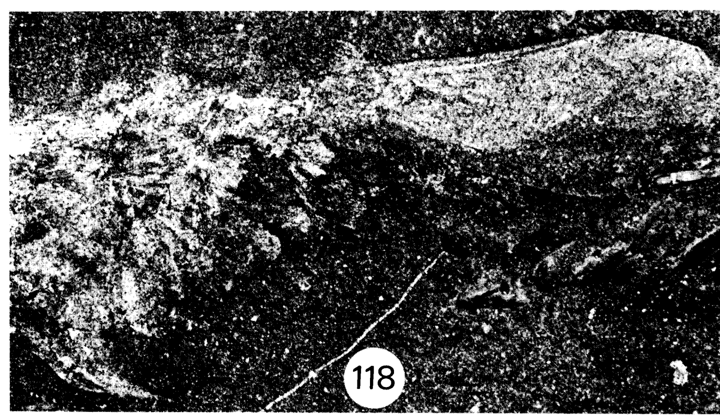
FIGURES 117–119. U.S.N.M. 155658, holotype, lateral, part only, respectively cephalic shield and anterior portion of trunk, posterior portion of trunk and terminal plate (overlapping with figure 117) under water (magn. ×5); entire, west southwest (magn. ×2.5).

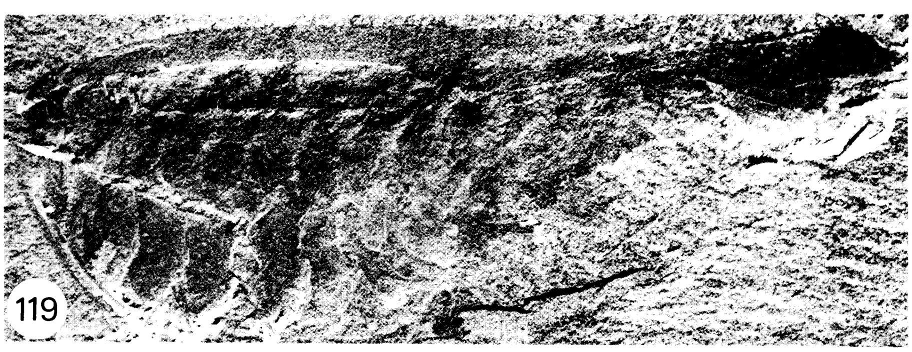
Leanchoilia superlata Walcott, 1912, associated with an unidentified organism, Phyllopod bed, Walcott quarry.

FIGURES 120–122. U.S.N.M. 155648, parallel, part only, entire specimen, reflected, east (magn. ×3.3); posterior portion and branching organism, northwest (magn. ×5).

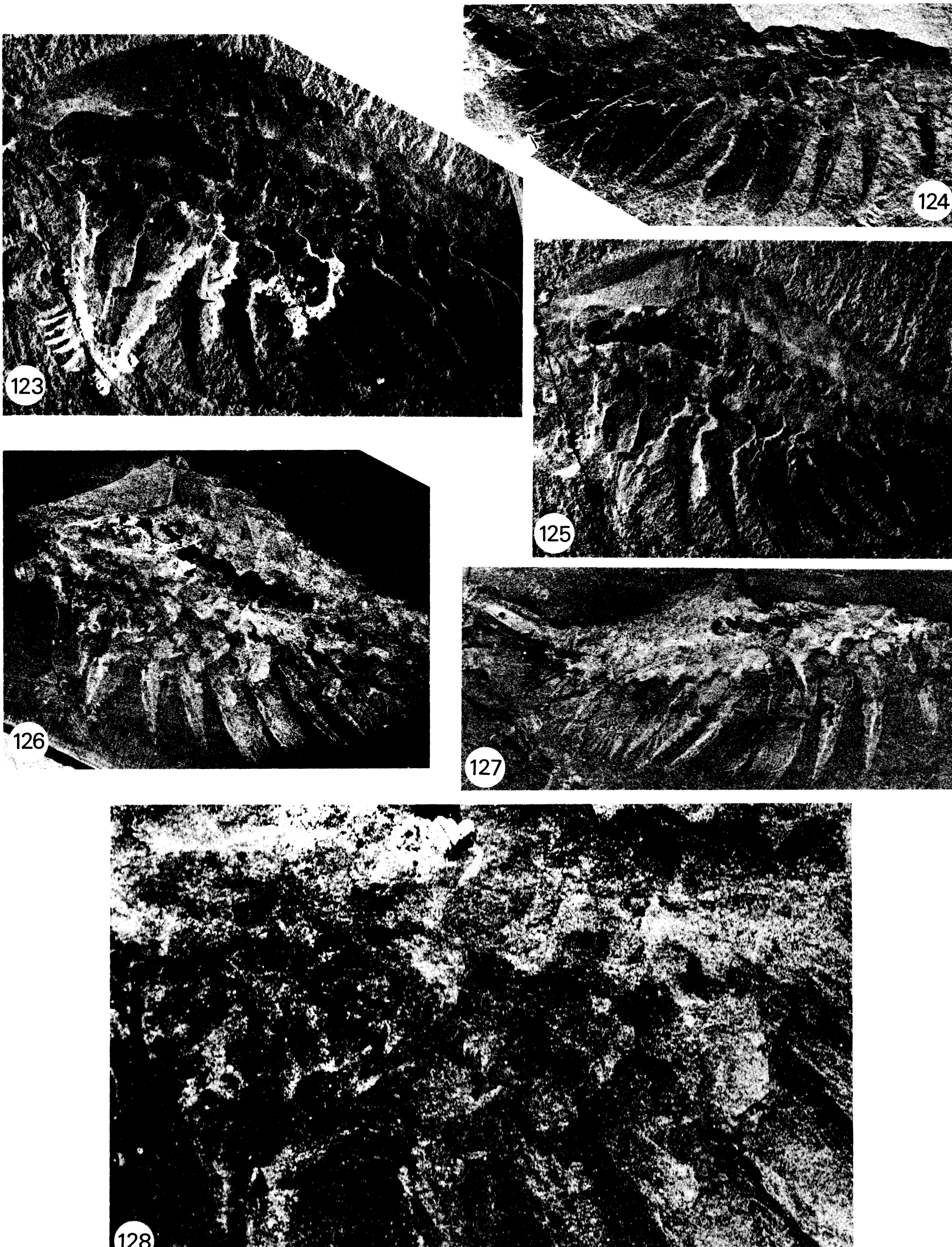
FIGURE 116. Explanatory drawing of U.S.N.M. 155648.







FIGURES 117–122. For description see opposite.



Figures 123–128. For description see opposite.

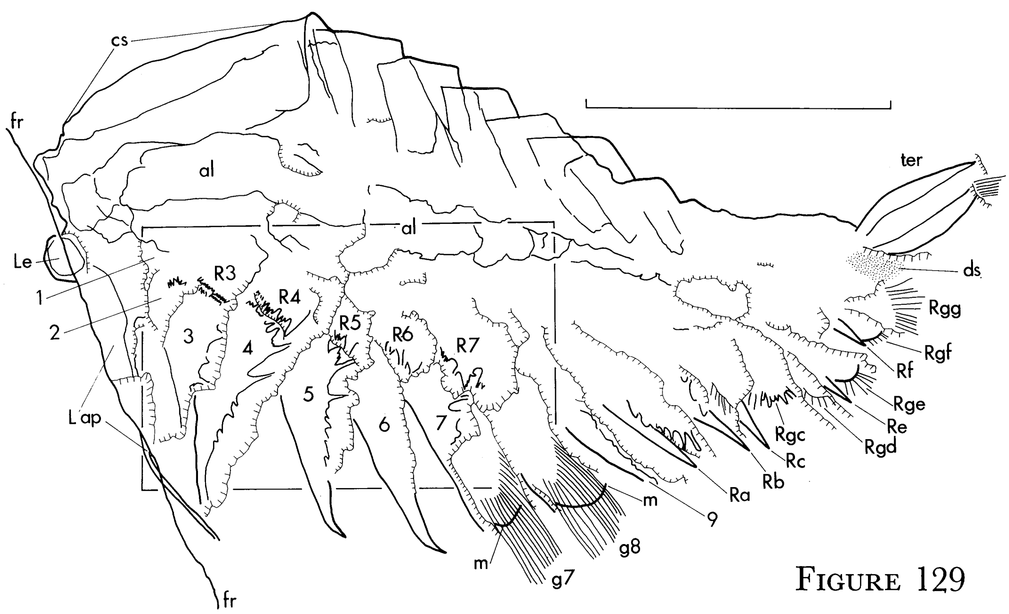


FIGURE 129

DESCRIPTION OF PLATE 14 AND FIGURE 129

Alalcomenaeus cambricus Simonetta, 1970, Phyllopod bed, Walcott quarry

FIGURES 123, 125, 126 AND 128. U.S.N.M. 155659, lateral oblique, part, west (magn. ×4); west northwest, before preparation to show proximal edges of inner branches 4–7; reflected, after preparation (magn. ×3.3); under water, enlargement of proximal edges of left and right inner branches 3–7 (magn. ×10).

FIGURES 124 AND 127. U.S.N.M. 155659, lateral oblique, counterpart, north, under water (magn. ×3.3).

FIGURE 129. Composite explanatory drawing of U.S.N.M. 155659. Rectangle encloses area shown in figure 128, plate 14.

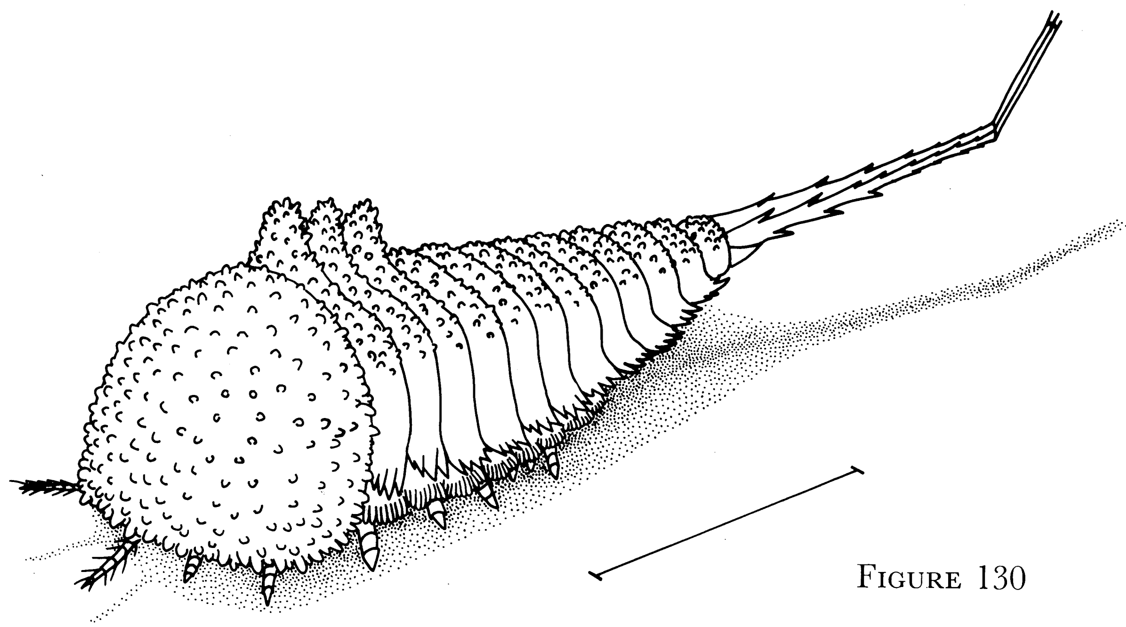


Figure 130

Figure 130. *Habelia optata* Walcott, 1912. Reconstruction in oblique anterior view, suggesting the animal walking on the sea bottom.

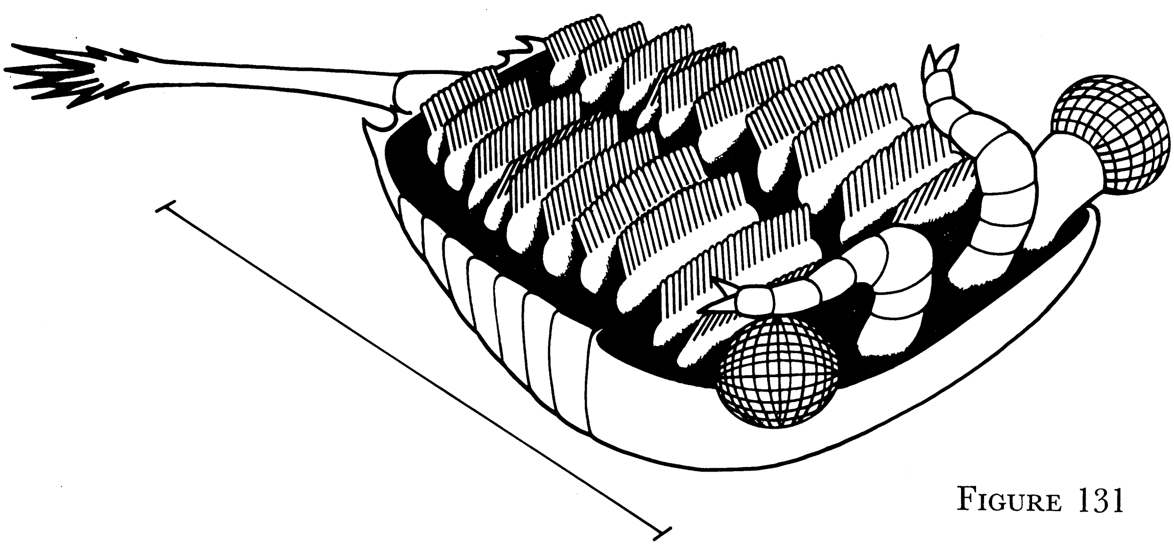


FIGURE 131

FIGURE 131. *Sarotrocercus oblita* gen. nov., sp. nov. Reconstruction in oblique ventral view, suggesting how the eye lobe was attached to the body and showing what is known of appendages. The animal is portrayed as swimming by movements of the gill lobes in a metachronal rhythm.

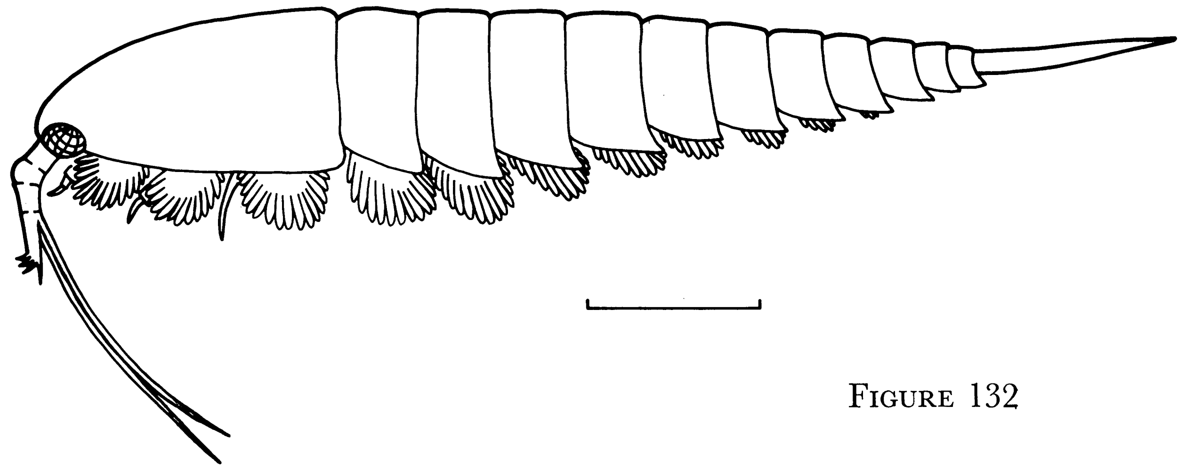


FIGURE 132

FIGURE 132. *Actaeus armatus* Simonetta, 1970. Reconstruction in lateral view showing what is known of appendages. Dashed lines on proximal portion of anterior appendage suggest possible joints, based on similarity to *Leanchoilia superlata* Walcott, 1912.

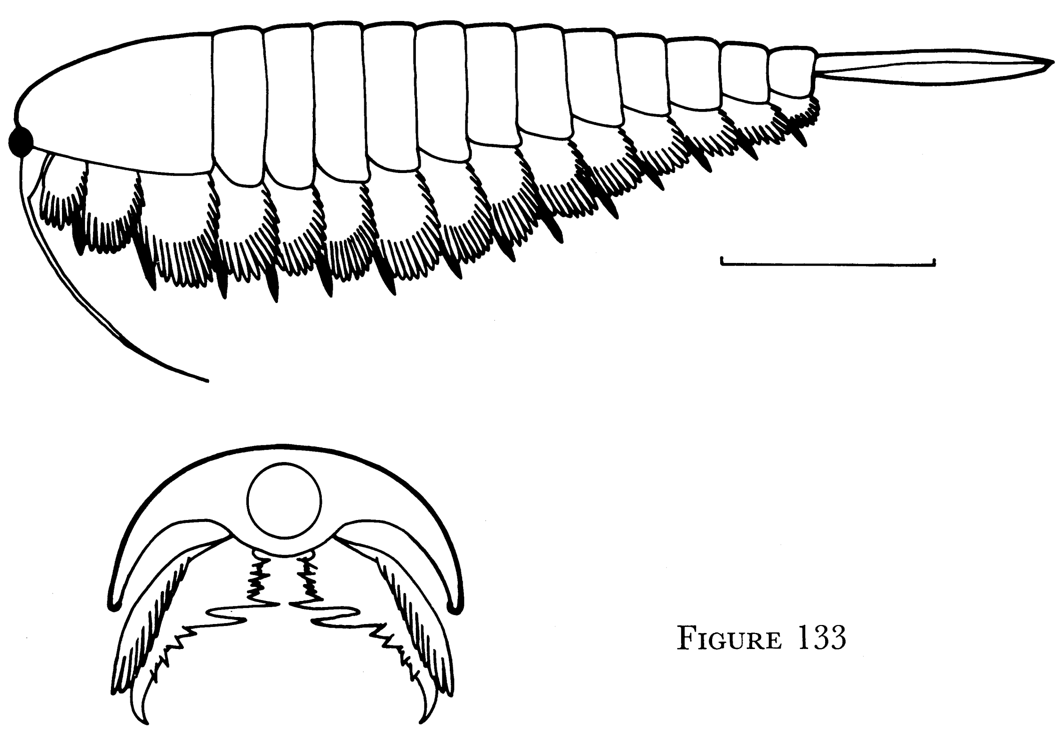


FIGURE 133

FIGURE 133. *Alalcomenaeus cambricus* Simonetta, 1970. Reconstruction in left lateral view with cross-section of body at trunk tergite 2, suggesting form of appendages and positions of mesial spines of inner branch.

86 specimens, as follows: 195009, 195386, 268920, 268922–268924, 268928–268930, 268932–268937, 268939, 268940 (counterpart of 268933), 272093–272098, 272100–272112 (272101 and 272104, 272106 and 272107, counterparts), 272115–272120 (272119 is counterpart of 272103), 272123 (counterpart is 272125 and 272126), 272128–272130, 272132, 272134, 272136 (counterpart is 268925), 272141, 272142, 272144, 272148–272150 (272148 is counterpart of 272100), 272153, 272157, 272158, 272162–272167 (272163, 272164, counterparts), 272170, 272174–272179, 272184, 272185, 272187–272193, 272195, 275537, 275541–275545, 275662, 305085–305089.

(*b*) *Occurrence, size*

The 111 specimens listed are all from Walcott's collection, and he (1912, p. 152) noted that this species was found only in the basal $1\frac{1}{2}$ in (*ca.* 3.8 cm) of the Phyllopod bed. No specimen of length 40 mm (Walcott 1912, p. 201) has been seen, the size range of the sample (figure 1) showing a maximum little more than half of this size.

(*c*) *Description*

The reconstruction (figure 73) summarizes my conclusions on the outline, convexity, and size of parts of the exoskeleton relative to one another, and is based on averages of measurements of 50 specimens. The cephalic shield is considered to have been subsemicircular in outline in dorsal aspect, the posterolateral angle rounded (figures 6, 11, plate 1; figure 31, plate 3; figures 37, 42, plate 4; figures 55, 56, plate 6), the convexity even and the maximum depth (at the posterior margin) almost equal to the sagittal length (figures 5, 7, plate 1; figure 54, plate 6). The external surface was apparently smooth, the sclerotized exoskeleton reflexed around the margin to form a narrow doublure (figures 37, 42, plate 4; figure 55, plate 6), which may appear as a reflective band. Depending on the original orientation of the cephalic shield, the outline after compaction may vary from subsemicircular to triangular (figure 38, plate 4), oval (figures 16, 17, plate 2) or trapezoidal (figures 6, 11, plate 1). Walcott (1912, p. 200) referred to a central area like the trilobite glabella, having lateral lobes, based apparently on his retouched illustration of 57689. The irregular lobe-like structures shown by this specimen (figures 6, 8, 11, plate 1) are the result of compression, and a structure like the trilobite glabella is not seen in any specimen. The remainder of the body may be divided into a trunk of eight somites, and the subcylindrical telson, which bears a long, tapering posterior spine. The outline and convexity of successive trunk tergites shown is based on little-distorted specimens (figures 37, 42, plate 4; figures 55, 56, plate 6), and confirmed by partly oblique specimens (figures 16, 17, plate 2; figure 32, plate 3; figure 53, plate 5). A narrow doublure on the lateral margin may be reflective, or may be emphasized by finely granular pyrite laid down in the space between the two layers (figure 37, in which it appears as a light band, and figure 42, as a dark band, plate 4). Across the anterior portion of each tergite a narrow ridge (on the dorsal surface, groove in the ventral) runs transversely without any marked forward swing medially (r in figures 25, 26, 43, 60); distally it curves back and dies out above the doublure. In these parallel compressions the ridge lies close to the posterior margin of the preceding tergite, the anteriormost portion of each tergite extending beneath the preceding one (or posterior edge of the cephalic shield) as an articulating flange. Distally the flange has a characteristically convex-forwardly curved margin; it appears to have been continuous across the axial region. Because the split was through the exoskeleton, the posterior margin of the tergite may be broken in the part (figures 25, 60), whereas in the counterpart the anterior edge of the articulating flange is broken (figures 28, 43).

Behind the curved eighth tergite is the subcylindrical telson, longer (sag.) than any tergite. In oblique (figure 8, plate 1; figures 32, 34, plate 3) and lateral specimens (figure 5, plate 1) a single spine projects from the posterior portion of the telson; it is not seen in dorsoventral specimens and appears to have been ventral in position. Inserted into the end of the telson was the long, tapering posterior spine. In specimens showing almost the entire length (figures 50, 51, 53, plate 5; figure 54, plate 6), it was longer than the sagittal length of the remainder of the animal, and may be preserved slightly or strongly and evenly curved. Some specimens (figures 5, 7, 8, plate 1) show no evidence of segmentation in the spine, in others (figure 39, plate 4; figure 57, plate 6) it is clear. In 272105 (figure 57, plate 6) the joints appear curved because the spine was inclined when buried; in 268935 (figure 53, plate 5) the spine is flexed to varying degrees at joints in the proximal portion. It appears that the spine was segmented and that in life flexibility at the joints was limited, giving the evenly curved appearance.

Traces of appendages are preserved in almost all specimens, revealed beneath the exoskeleton by the level of the split (figure 38, plate 4), or projecting beyond it (figure 34, plate 3). The series of appendages is not markedly displaced relative to the exoskeleton, the attitude in which any one is preserved, swung forwards, curved back, etc., depending on events during burial. The most important specimen showing the relationship between exoskeleton and biramous series is 268935 (figure 46; figures 52, 53, plate 5). It shows three pairs beneath the cephalic shield, increasing in size posteriorly, the jointed leg branch arising from a large coxa. The tongue-shaped outer branch arose from the coxa, and bore a fringe of lamellae. A similar biramous appendage lies beneath each trunk tergite; those beneath the first three or four tergites are largest, the series diminishing rapidly in size posteriorly. In 57692 (figures 16–18, plate 2) a tiny pair of appendages projects from beneath the anterior margin of the cephalic shield, but other appendages are poorly preserved. In this specimen the body is curved concavely dorsally, so that the cephalic shield is directed forwards and upwards; the antennae were evidently short and attached far forward, in front of the first pair of biramous appendages. They are also preserved in 139208 (figures 31, 32, plate 3), and appear composed of many podomeres. Possibly minute hairs projected from the junctions of the podomeres, but these tiny antennae are not well preserved in any specimen. In 268935 the first four leg branches (figure 52, plate 5) have been exposed, but junctions between podomeres are not well preserved. Leg branch 3 has been exposed in 144892 (figure 41, plate 4), revealing the large coxa, five distal podomeres, and a pair of curved terminal claws. On the inner side of the proximal podomere inwardly directed spines are poorly preserved, but their disposition and number cannot be made out. The terminal claws may be seen at the tips of the succeeding leg branches 4–8; leg branches belonging to the last three trunk somites have not been seen in any specimen. The structure of the leg branch is also revealed in 144885 (figures 33–35, plate 3), and on both these oblique dorsal specimens the gill branch lies outside the leg branch, and passes below the one following (cf. figures 52, 53, plate 5). This same imbricated relationship between gill branches is also revealed in lateral compressions (figure 5, plate 1; figure 54, plate 6), only being reversed in gill branches 1–4 of 57692 (figure 24, plate 2) because the cephalon is directed upward and forward. In dorsoventral (figures 12–14, plate 1) or oblique dorsoventral (figures 52, 53, plate 5) compressions the lamellae of the gill branch lie below the tips of the pleurae or outer portion of the cephalic shield, the position in life; only in lateral (figures 5, 7, plate 1) and oblique lateral compressions (figures 34, 35, plate 3; figure 41, plate 4) do they project well outside the pleurae. In 268935 and 139208 (figures 46, 28, respectively) the succession of biramous appendages may be numbered with some confidence, the former showing that the largest leg branches are 3 and 4, the posterior of the cephalon and first of the trunk. Numbering of the biramous series in the lectotype (figure 2) and the other lateral and oblique compressions is consistent with this arrangement, and appears to support it. In the smallest specimen (figure 40, plate 4) identification of particular limbs is not possible. The majority of, if not all, specimens thus show that the gill branch, in life, must have curved upwards, downwards and outwards over the leg branch, and hung down on the posterolateral side between successive leg branches. The fringing lamellae do not appear to have projected beyond the lateral margin of the tergite. Whenever the two branches of the appendage are visible (e.g. figures 5, 7, 9, plate 1; figures 33, 35, plate 3; figures 52, 53, plate 5) their axes diverge at a small angle. This implies that the gill branch was rigidly attached to the coxa, and consequently that in life the appendage moved as a unit.

Along the axial region of the body there may be a band (figures 5, 7, plate 1) or series of patches (figures 16, 17 plate 2), dark in low-angle radiation but reflective; the reflective area may extend outside the dark area. Part or all of this band may be preserved as a flattened-biconvex filling of extremely fine-grained material (figure 58, plate 6, shows a portion of the filling beneath the cephalic shield, behind is the mould of the infilling). Fine-grained pyrite (figures 8, 11, plate 1; figures 15, 19, plate 2) may overlie this axial band and extend out beyond it as fingers on the lateral regions. The band is broadest anteriorly, the tip rounded, in 57688 (figures 5, 7, plate 1) the shape suggesting that it may have curved forward, downward and backward. It appears to be the trace of the alimentary canal, and to have ended close to the posterior margin of the telson (e.g. figure 38, plate 4; figure 54, plate 6); the appearance that it extended farther (figure 7, plate 1) may be the result of compression. Walcott (1912, pp. 160, 201, pl. 29, fig. 3) claimed that intestinal diverticulae were visible on the posterolateral portion of the cephalic shield of 57690; his figure appears to have been retouched (compare with figure 12, plate 1). A consistent pattern of branching canals is not revealed on the cephalic shield in reflective radiation; only an occasional specimen shows obscure branches from the alimentary canal on cephalic shield and trunk (figure 39, plate 4; figures 48, 49, plate 5). Patches and strings of fine-grained pyrite may extend out from the axial region (figures 8, 11, plate 1; figures 15, 19, plate 2) but are not consistent in occurrence or pattern. The darker areas along the alimentary canal unique to 144903 (figure 54, plate 6) appear to have been emphasized by weathering; their significance is uncertain. A dark stain (presumably formed by decay products seeping out from the soft parts) is rarely visible, and may occur anteriorly as well as posteriorly (figure 47, plate 5).

(*d*) *Discussion*

The only earlier restoration was by Simonetta (1964, fig. 1), who considered that the cephalic shield bore five pairs of biramous appendages. The evidence of 268935 (figures 52, 53, plate 5), supported by that from the lectotype and other specimens (figures 5, 7, plate 1; figures 31, 32, plate 3; figure 41, plate 4; figure 54, plate 6), shows that the fourth biramous pair belongs to the first trunk somite, and that the first pair were uniramous. I regard the first pair as antennae: though minute they appear distinctive and were attached far forward on the cephalon. The profile in lateral specimens does not suggest that the cephalic shield was flattened peripherally, and there is no evidence of a lateral eye lobe. Eight trunk tergites are present in all specimens and show a progressive decrease in length (sag.) and increase in backward curvature; the eighth tergite may be difficult to see in telescoped specimens or in those in which the telson is flexed laterally or downward. One pair of biramous appendages was present on each trunk somite. Neither cephalon nor trunk shows evidence of a convex, axial region. The posterior margin of the telson bore only a single, ventrally directed spine, situated immediately behind the anus. The posterior spine was of length (sag.) greater than the rest of the body, jointed and flexible. The new reconstruction (figure 73) shows these features, and the cross sections portray the large basal podomere of the appendage, the five of the leg branch, and the large gill lobe which hung down outside as well as behind the leg branch. Simonetta (1964, pp. 217–218) described the leg branch as having a fringe of setae at the junction between podomeres, and a tarsus provided with two claws. Two terminal claws are visible in several specimens (figure 36, plate 3; figures 40, 41, plate 4), but the leg branch does not show a fringe of setae at each joint. This appearance of the first three appendages in 144885 (figures 34, 35, plate 3), and of R3 and R4 of 139208 (figure 31, plate 3), is misleading, the appendages in question being obliquely compressed gill lobes, lying farther from the observer than does the leg branch in 139208. The lamellae around the margins of the lobe give the appearance of fringes of spines, and both part (before excavation) and counterpart of 144885 show that these appendages were part of the series of gill lobes, and not leg branches. The leg branch of the first trunk somite of 144885 was revealed by excavation of the part (figure 33, plate 3), and runs backward and outward ventral to the gill lobes. The unexplained circular patches along the alimentary canal in Simonetta's restoration may be based on the dark patches in 144903 (figure 54, plate 6), but their significance is uncertain. No evidence of a ventral nerve chord, as claimed by Simonetta (1964, p. 218), is shown by the lectotype (figures 5, 7, 9, plate 1).

In Simonetta & Delle Cave (1975) the earlier reconstruction is reproduced, and the photographs of Simonetta (1964) with additions. These photographs are all of poor quality and give no new information. The originals of pl. xx, figs 4, 12, have not been traced in the U.S.N.M. collections, and the photographs are unrecognizable. The original of pl. xx, fig. 3 (155678), shows left and right limbs of a series curving down beneath an exoskeletal fragment; the limbs are not those of *M. spinifera* and have not been identified. The originals of pl. xix, fig. 9, and pl. xx, fig. 1, are described below under *Sarotrocercus oblita*, gen.nov., sp.nov.

Walcott (1912, p. 201, pl. 29, fig. 3) apparently considered the limb of *M. spinifera* to be triramous, but it is difficult to reconcile his text with his labelling of the retouched figure. The original (figures 10, 12–14, plate 1) shows the outer portions of the right tergites (in the counterpart), and the lamellae of the gill branches on both sides. The specimen is poorly preserved, the split in the trunk having apparently passed mainly through the alimentary canal and limbs below the tergites. The interpretation of the portions between the alimentary canal and gill lamellae is uncertain, but the reflective areas Walcott labelled as gills are probably proximal portions of leg branches. No specimen shows evidence of a triramous limb. A specimen (figure 38, plate 4) in which the split is similarly situated to that in 57690 shows the imbricated, backwardly and outwardly directed leg branches flanking the axial region. Outside them and nearer to the observer are the imbricated gill branches, the lamellae visible inside the pleural tips. In 57691 (figures 15, 19, plate 2) the posterior spine is irregularly broken adjacent to its junction with the telson. Walcott (1912, p. 201) regarded the irregular projections at the break as minute limbs.

(*e*) *Development*

An example of the smallest specimens known (figure 39, plate 4) is dorsoventrally compressed; the eighth tergite is not visible, probably because of telescoping, which also conceals much or all of the telson. The posterior spine is almost complete and jointed. A second example (figure 40, plate 4) is laterally compressed and shows traces of appendages. These smallest individuals do not appear to be different in number of somites or shapes and proportions to those of large ones. Simonetta (1964, p. 219) regarded 144905 as an early developmental stage, but associated with it a specimen (figures 21–23, plate 2) that bears no resemblance to one of *M. spinifera* of comparable size (figure 39, plate 4). No other specimen like 144888 has been found in the Walcott collection, and its identification remains problematical. Simonetta (1964, pp. 219, 228–229) remarked on the xiphosuran-like appearance of 144888, and, because he assumed it was an early growth stage of *M. spinifera*, regarded the development of *Molaria* as 'anamorphic', by which he presumably meant that the larva hatched with an incomplete number of segments. These assumptions about the development of *Molaria*, which I consider have no foundation, appear to have influenced his views on the affinities of the genus.

(*f*) *Functional morphology*

Almost all specimens show traces of appendages, which are not markedly displaced relative to the exoskeleton. Hence when entombed in the mud they were probably carcasses that had suffered little decay; in the pre-slide environment *Molaria* was thus most probably a benthic animal. Lateral (figure 51, plate 5; figure 54, plate 6) and oblique (figure 50, plate 5) specimens show the great flexibility of the body (including the posterior spine) in the vertical, sagittal plane. There is little evidence of much flexibility in the horizontal plane (the appearance of slight curvature of the trunk in oblique specimens is the result of compression), except perhaps in the distal portion of the posterior spine. Flexure in the vertical plane may have extended from a concave to strongly convex (figure 74) profile, the articulating flange of the tergite serving to close lateral or axial gaps in the exoskeleton. The ridge of the tergite does not appear to have served to limit articulation, particularly laterally, where it must have moved beneath the preceding tergite of the cephalic shield. Possibly the ridge was a site for apodemes for attachment of the longitudinal and diagonal musculature necessary to effect the movements. The specimens suggest that flexure between tergite 8 and the telson, and the telson and posterior spine, was very limited. In a number of examples the telson appears to have been telescoped into the body, and tergite 8 concealed, presumably by compaction.

The flexible body and form of the limbs may have enabled *Molaria* to walk on the bottom and to plough shallowly into the sediment by inclining the cephalic shield downwards, as suggested for the trilobite *Olenoides* (Whittington 1980*a*, pp. 193–4, 199, text-figs 10, 11, 15). The gait shown in figure 73*b* is based on the work of Manton (1977, pp. 39–49). Each pair of limbs is assumed to have moved in unison in a promotor–remotor swing about an approximately transverse, and slightly upwardly directed, axis at the coxa–body junction. An angle of swing of the legs is shown of about 5° in front, and 15° behind, the transverse plane. The relative duration of forward and backward strokes is 3.5:6.5, each metachronal wave including six legs moving with a phase difference of 0.17 between them. This would have enabled a slow walk with the body continually and adequately supported. The animal may have launched itself off the bottom by swinging a few successive pairs of limbs back in a wave (as suggested for the trilobite

Olenoides in Whittington (1980*a*, text-fig. 13)). Once launched, both branches of the limbs, moving in unison in a metachronal rhythm, may have aided in swimming, and the posterior spine may have been used in balance and steering. The length and flexibility of the posterior spine suggests, perhaps, that it was not used in digging but may have been used to right the animal. Possibly sudden flexure of body and spine may have been used as an escape mechanism, or to launch the animal for upside-down swimming. Presumably the animal was a benthic feeder on detritus (to account for the mud filling of the gut) or a scavenger. The large basal podomere of the limb, and the spines on the inner side of the leg branch, suggest that food was scraped up from the sea bottom by the legs and pushed forward along the midline to a presumably backward-facing mouth, i.e. a mode of feeding analagous to that in the trilobite *Olenoides* (Whittington 1980*a*). The primary function of the outer branch of the limb, with its fringe of lamellae, is thought to have been as a gill.

(*g*) *Affinities*

The view that *Molaria* (and *Habelia*, see below) is similar to *Emeraldella* continues to be put forward (Walcott 1912, pp. 155, 163–164; Størmer 1944, p. 86; 1959, pp. O 30–31; Simonetta & Delle Cave 1975, pp. 27, 32). The type species of *Emeraldella* was briefly described by Walcott (1912, pp. 203–205, fig. 8; pl. 30, fig. 2), who later (1918, p. 118) referred to it two additional specimens previously assigned to *Sidneyia inexpectans*. Further comments were made by Raymond (1920, pp. 119–120, 149) and by Størmer (1939, fig. 29*c*, pp. 234–235; 1944, pp. 84–85, fig. 17, 3), and in 1964 Simonetta redescribed the species based on additional specimens, and gave a new reconstruction. Simonetta & Delle Cave (1975, p. 19, pl. II, figs 1*a–i*, pl. XXIII, figs 2–4, pls XXIV–XXVII, pl. XXVIII, fig. 1) copied the 1964 photographs and figured additional specimens, and copied the restoration except for an obscurely explained modification of a cross section showing a limb (pl. II, fig. 1*d*). All this material will be redescribed by D. L. Bruton. Pending publication of this work I have examined some of the specimens of *E. brocki* and observed the resemblance of the exoskeleton to that of *Molaria spinifera*: the semicircular cephalon lacks eye lobes; the trunk tergites are progressively more strongly curved back distally; there is a cylindrical telson into which is articulated a long posterior spine. There are 11 tergites in the trunk of *Emeraldella*, not eight as in *Molaria*, but the overlap between them and presence of an articulating ridge is similar; longitudinal trilobation of the exoskeleton is not apparent in either species. The appendages of *Emeraldella* are quite different from those of *Molaria*, consisting of the long annulated antennae, the broad, spinose anterior cephalic limbs, the long, slim limbs immediately behind these, and the distinctive outer branch with marginal lamellae. The resemblances between *Emeraldella* and *Molaria* thus seem to be in the exoskeleton only and I leave open the question of whether they should be placed in separate families (Simonetta & Delle Cave 1975, p. 32) or in separate orders (Størmer 1959, p. O 30–31; Raymond 1920, pp. 119–121, 149). The view expressed by Walcott, Raymond and Simonetta & Delle Cave that these two genera are aglaspidid-like seems to be based on the broad similarity in the exoskeletons: in convexity, form and overlap of trunk tergites, and presence of a terminal spine. Appendages of only one specimen of *Aglaspis* are known, and the terminal spine and postventral plates (Briggs *et al.* 1979) are different in structure from the cylindrical telson and posterior spine of *Molaria*. Størmer (1944, pp. 84–86; 1959, pp. O 30–31) acknowledged the aglaspidid-like exoskeleton, but stressed the trilobite-like nature of the appendages. Those of *Molaria*, anterior antennae followed by a biramous series in which the coxa is large, the inner branch a jointed walking leg, the outer branch rigidly attached to it, a lobe having marginal lamellae, are unquestionably trilobite-like (Whittington 1977, p. 416; 1980*a*). How to assess these characters in classification, as opposed to those of the exoskeleton, is a question to be taken up in a general review of relationships of the Burgess Shale arthropods.

6. *Habelia optata* Walcott, 1912

Figure 61; figures 62–66, plate 7; figures 67–71, plate 8; figures 72, 75–77; figures 78–83, plate 9; figure 130.

1912 Walcott, pp. 202–203, pl. 29, fig. 6.
1920 Raymond, pp. 120–121.
1944 Størmer, p. 86.
1959 Størmer, *in* Moore, p. O 31, fig. 19, 3 (copy of Walcott (1912)).
1964 Simonetta, pp. 219–222, fig. 2, pl. XXXVI, unnumbered figures of U.S.N.M. 57693, 139209, 144907–909.
1975 Simonetta & Delle Cave, pp. 27, 32, pl. III, figs 2*a*, 2*b* (copied from Simonetta (1964)), pl. XXI, figures 1–3, figures of same specimens as Simonetta (1964).

(*a*) *Material*

Holotype, U.S.N.M. 57693, lateral compression, part and counterpart, latter the original of Walcott (1912). Other material; U.S.N.M. 139209, 144907–144909, 268927, 268931, 268938, 272169, 272180, 272202 and 272203 (counterparts), 305090–305092, which include the plesiotypes of Simonetta (1964). Length (sag.) of the body, excluding the posterior spine, ranges from 8 mm (268927) to 25.5 mm (144907).

(*b*) *Description*

Exoskeleton divided into a cephalic shield and trunk of 12 tergites, the posterior spine inserted into 12th and of length (sagittal) between that of the trunk and that of the cephalic shield and trunk. The specimens all appear to be lateral or slightly oblique and none is dorsoventral, so that the outline and convexity is difficult to judge. I have assumed (figure 130) that the cephalic shield was approximately quarter-sphere in form, because in lateral specimens (figures 67–71, plate 8) length is similar to depth. The external surface is not well preserved in any specimen, but the shield appears to have been evenly convex, with no sign of a raised axial region or posterior border, or of an eye lobe. Short, blunt spines projected from the border (figure 80, plate 9), and there was a narrow doublure; the external surface was elsewhere finely tuberculate. The posterior margin was not straight, but curved forward distally, the posterolateral angle rounded (figures 79, 80, plate 9).

Axial region of trunk tergites having a broad, raised tuberculate band and a narrow, depressed, smooth anterior band; medially tubercles elongated into blunt spines (figure 68, plate 8). Lateral portion of tergites (figure 78, plate 9) blade-shaped, the first short (tr.), the second longer and slightly curved backward, three to nine of similar length and backward curvature, 10–12 progressively shorter, more strongly curved, the 12th a backwardly directed point. The margins of the curved pleural tips bear close-spaced spines; external surface of pleura not well preserved, probably finely tuberculate, possibly coarser along posterior edge. In two specimens (figures 67, 68, plate 8; figure 78, plate 9) the crests of tergites 1–12 appear in lateral profile to be similar in height though varying from rounded anteriorly, to flattened posteriorly, with a backward projection of the last two. In all other specimens (figure 62, plate 7; figures 69–71, plate 8; figures 81–83, plate 9) showing this profile the first three tergites are blunt peaks. In figure 130 I show these tergites as having a blunt, thick median spine that bore elongate tubercles. The wrinkled appearance of these supposed spines in the holotype (figure 62, plate 7) is assumed to result from the flattening of the tuberculate surface. To explain the profiles of 139209 (figure 68, plate 8) and 144908 (figure 78, plate 9) one must assume either that these specimens are sufficiently oblique for the profile to be lateral to the spines, or that there were two forms, one without the spine. In such a small sample the latter assumption is questionable, and yet the former is also questionable, because the specimens are approximately lateral.

The base of the posterior spine is assumed to have been subcircular in cross section, because it is of similar breadth in all specimens; it was inserted into the posterior margin of the 12th tergite; no specimen shows evidence of flexure at this junction. The spine is traversed by ridges and grooves (figures 67, 68, plate 8), and the margin is barbed (figure 66, plate 7); it is suggested that external ridges bore these backwardly directed barbs. In large (figure 62, plate 7; figures 69–71, plate 8), as well as in a small, poorly preserved specimen (272202–272203), the spine shows an abrupt flexure at two-thirds or three-quarters of the length; this flexure is at a clearly defined line (figure 66, plate 7), and appears to have been a joint. I assume that this distal portion was movable, the tip in the holotype appears barbed, in 268938, rounded.

A band that is reflective along parts of its length and dark in low angle radiation (figures 67, 68, plate 8; figures 78–80, plate 9) marks the alimentary canal. It may be broadest anteriorly beneath the cephalic shield and first tergite, and extends into the 12th tergite and base of the posterior spine (figure 62, plate 7). Irregular, raised (mineralized?) blobs may occur along it (figures 69–71, plate 8), but there is no evidence of a sediment filling. There is no evidence, either, of the nature and position of the mouth beneath the cephalic shield. The anus may have opened on the ventral side of the base of the posterior spine. The dark stain (figures 62, 64, plate 7; figures 67–71, plate 8; figure 83, plate 9) is an indefinitely shaped and bounded area, reflective but dark in low angle radiation, adjacent to the anal opening. It is distinct from the pleurae and posterior spine, not part of the exoskeleton, and considered to have been made by organic matter seeping from the carcass after death.

Appendages are preserved in large and small specimens, conspicuous being the six pairs of jointed legs projecting from the anterior half of the trunk (figures 67, 68, plate 8). In the type (figures 62–65, plate 7) and other examples (figures 67, 68, plate 8; figures 81, 82, plate 9) the cephalic appendages are indifferently preserved and bunched together, projecting from beneath the anteroventral margin of the shield. Perhaps in part because of the obliquity of the compression, these appendages are separated and best preserved in 144908 (figure 79, plate 9). One pair, farthest forward, were uniramous, setose at the joints, and may have been the antennae. The other four (two pairs?) of appendages are stouter and longer, having irregular dark sheets associated with the proximal portions. These sheets may represent flattened gill lobes and indicate that these limbs were biramous. Dark sheets in a similar position in other examples (figure 67, plate 8; figures 81, 82, plate 9) reinforce this interpretation. In the holotype (figures 62–65, plate 7) an amorphous dark layer lies on the inner side of the cephalic shield and may represent these lobes. From between this layer and the shield the jointed inner branches project outward and downward. In reflected radiation two opposed rows of tiny cusps (cu in figure 61, compare with figure 63, plate 7) lie on the amorphous layer. A similar single row of cusps is also revealed in reflective radiation, adjacent to the ventral margin of the alimentary canal, on the cephalic shield of 144908 (cu in figure 75, compare figure 80, plate 9). These cusps may represent the grinding edge of a mandible, or perhaps more likely, since the rows are aligned with the appendages, the grinding surface of a proximal podomere or coxa.

The multi-jointed walking legs of the trunk are long and stout, and seem to belong to somites 1–6; there is no sign of any jointed limb posteriorly. At the tip is what appears in some specimens to be a single, blunt spine, in 305091 there is one large and two small spines. In 139209 (figures 67, 68, plate 8) a lobed outer branch, bearing lamellae around the margin, is associated with each walking leg. The two branches approach the same level proximally, and the lobe appears to have been attached near the base of the appendage, on the outer, anterior side (the limbs in 139209 are assumed to be the right-hand series, since they are directly underlain by right tergites). In this specimen and the holotype, lobed appendages are visible back to the eighth tergite, and the fragments in 139209 suggest the series goes back to the 11th or 12th somite. The appendages of the smallest specimens (figures 81, 82, plate 9) seem to be essentially the same as those in the largest.

(*c*) *Discussion*

Figure 130 shows the animal walking on the longer, stouter six pairs of trunk limbs, the shorter second and third cephalic limbs presumably having been used mainly in handling and cutting up food. The nature of the basal podomere of the trunk limbs is unknown, and it may be wrong to assume that maceration of food was only by the cephalic limbs. The lengths of the branches of the trunk limbs relative to the tergites is based on 139209, a lateral compression. The distal parts of these branches may have been held in approximately the position shown in figure 130, protected by the spinose tips of the tergites. The animal appears to have been a benthic scavenger, armoured against predators; the posterior spine would not have been a weapon but a device to make difficult approach and attack from behind. The shorter lateral portions of the first and second tergites, and the shape of the cephalic shield laterally, allowed considerable movement between cephalon and trunk. Examples such as the original of figure 83, plate 9, show this strong flexure without disruption. The down-bent cephalon may have been protective as well as allowing the animal to push and dig the cephalon into the substrate in search of food.

Walcott's (1912) description was hasty, and his illustration of the holotype so poor as to give little idea of the species. Størmer (*in* Moore 1959, p. O 31) speculated that it was of a specimen of *Burgessia bella* that had lost the carapace. Hughes's (1975) descriptions show that this is not so, particularly his illustrations (pl. 3, fig. 8; pl. 4, fig. 1) of specimens in which the carapace is pulled forward. Simonetta (1964) illustrated the holotype, 139209, and 144907–144909, probably the specimens Walcott had before him in 1912. Simonetta presumably followed Walcott in stating that there were five pairs of cephalic appendages, citing 139209 and 144908 in support of this view. Figures 72 and 75 show my interpretations, and I consider it likely, because of its size and position, that limb 1 in figure 72 belonged to the first trunk somite and not the cephalon. There appears to be evidence, on these and other specimens, for one pair of antennae and two pairs only of biramous limbs on the cephalon. Simonetta considered the presence of a compound eye 'probable', and showed it in his restoration, but offered no evidence. The lateral emargination of the cephalon that he portrayed is not seen in the originals of figures 79, 80, 82, 83, plate 9. While there is evidence for 11 pairs of gill branches on the trunk, there is none for the posterior five pairs of leg branches restored by Simonetta. He noted the dorsal spines on the first three tergites, and speculated that this form was the male. The feature that I regard as the dark stain is shown by Simonetta (1964, figure 2) as a plate projecting vertically downward from the base of the posterior spine; he considered it to have covered the ventral surface of the last postcephalic somite. I do not accept this interpretation of what is a variably developed and shaped area.

(*d*) *Affinities*

The type species of *Habelia* (figure 130) looks similar to *Molaria* (figure 73) in having a convex exoskeleton that is not trilobate, no trace of an eye on the cephalic shield, a trunk of 12 tergites (rather than 8), and a posterior spine. In both genera the appendages include antennae and a biramous series, at least in the anterior half of the trunk of *Habelia*. The cylindrical telson of *Molaria* is not seen in *Habelia*, and the resemblances between the type species of these two genera appear superficial. As for *Molaria* and *Emeraldella* (see § 5 (*g*)), the suggestion that *Habelia* is aglaspidid-like is based on general exoskeletal characters only. Simonetta (1964, p. 228), considering that there was a ventral plate beneath the base of the posterior spine in *Habelia*, likened this supposed plate to the postventral plates in *Aglaspis* (Briggs *et al.* 1979, pp. 175–178), and thus supported his view that *Habelia* was aglaspidid-like. I doubt that such a ventral plate was present in *Habelia*, and leave for future discussion the relationships of this genus.

7. *Habelia ? brevicauda* Simonetta, 1964

Figures 84–88, plate 10; figure 93.

1964 Simonetta, p. 222, pl. xxxvii.

1975 Simonetta & Delle Cave, pl. xxi, figs 4, 5; pl. xxii, fig. 1 (*non* fig. 2), copied from Simonetta (1964); reconstruction, pl. i, figs 3, 5.

(*a*) *Material*

Holotype; U.S.N.M. 144910, part, lateral compression, associated with the sponge *Hazelia* cf. *nodulifera* Walcott, 1920 and the carapace of *Canadaspis* sp. Other material: U.S.N.M. 144911, 144912, 275531 and 275532, dorsoventral compressions with counterparts; 275533, dorsoventral compression, part only. I exclude 144913, original of one figure on pl. xxxvii of Simonetta (1964) (copied as fig. 2, pl. xxii, of Simonetta & Delle Cave (1975)) because it is too poorly preserved to be identified. An additional specimen compared to this species (Simonetta & Delle Cave 1975, pl. xvi, fig. 3) is also excluded as unrecognizable.

(*b*) *Discussion*

Simonetta regarded these specimens as representing a second species of *Habelia*, distinguished by its larger size, short posterior spine, and lack of tuberculation on the exoskeleton and spines at the margins of the pleurae. These specimens are twice as large as the largest known of *H. optata*, and show no sign of the alimentary canal or of appendages; they are presumably moults. The posterolateral margins of the cephalic shield are incomplete in the type, where it is compressed over a sponge; in other specimens the right-angled corner is rounded. The trunk is composed of 12 tergites, and the specimens suggest that a longitudinal furrow or change in slope separated a broad, convex axial region from the blade-shaped pleura. The pleura of the first segment was short (tr.) and rounded, the series following wider (tr.), progressively developing a backward pointing tip, the last three shorter and becoming more strongly pointed and backwardly directed. A narrow (sag. and exs.), depressed band separates the axial regions of successive tergites, probably the site of a narrow articulating flange that extended beneath the tergite in front. A reflective band along the margin of the cephalic shield, and of the pleurae, suggests that there was a narrow doublure. The posterior spine was short and tapering, the tip bluntly rounded. The external surface of the exoskeleton appears to have been smooth; an appearance of fine granulation results from the texture of the matrix having been impressed into the thin exoskeleton.

These specimens presumably represent a distinct species, and do not appear to be moults of any other form in the shale. I have questioned the generic assignment because of the absence of appendages. In having a broad (tr.) axis and narrow pleurae, the trunk of *brevicauda* recalls the morphology of the first ten tergites of the trunk of *Yohoia tenuis* (Whittington 1974); this resemblance is superficial and other exoskeletal characters are quite different.

8. *Sarotrocercus* gen.nov.

Type species: *Sarotrocercus oblita* gen.nov., sp.nov.

(*a*) *Diagnosis*

Oval, convex body divided into a cephalic shield, nine trunk tergites and a narrow, cylindrical segment which bore a posterior spine terminating in a group of small spines; large stalked eye projected from beneath anterolateral margin of cephalic shield. Cephalon bore one pair of jointed appendages, followed by one pair of lobed appendages, which had marginal lamellae; one pair of similar lobed appendages on each of the nine trunk somites.

(*b*) *The type species* Sarotrocercus oblita *gen.nov.*, *sp.nov.*

Figures 89–92, plate 10; figures 94–98; figures 99–109, plate 11; figure 131.
1975 *Molaria spinifera*, Simonetta & Delle Cave, pl. XIX, fig. 9; pl. XX, fig. 1.

(*c*) *Material*

Holotype; U.S.N.M. 144890, incomplete part; counterpart 272171. Other material; U.S.N.M. 144893, 272099, 272133, 272143 (counterpart 275539), 272151, 272194.

(*d*) *Description and discussion*

Seven specimens were picked out from those originally brought together in the C. D. Walcott collection as probably representing *Molaria spinifera*. The length (sag.) of cephalic shield and trunk varies from 8.5 mm (figures 89, 92, plate 10) to 11 mm (figure 109, plate 11), a range like that of the smallest specimens of *M. spinifera*. They may be distinguished from that species by the following characters.

(i) A large, semicircular and highly reflective area that projects anterolaterally from beneath the cephalic shield (figures 89, 92, plate 10; figures 103–105, plate 11) is here presumed to be an eye lobe borne on a short stalk (figure 131), because it lies at a different level to the cephalic shield.

(ii) Each of the nine trunk tergites (and the posterior margin of the cephalic shield) shows a darker, posterior band (figure 103, plate 11), presumably where the articulating flange of the following tergite underlies it. This band extends across the width of the anterior tergites, but is less extensive posteriorly. There is no anterior ridge. The ninth tergite is short (sag.) and narrow (tr.).

(iii) Behind the ninth tergite is a short (sag.) and narrow (tr.), apparently cylindrical segment, markedly narrower, shorter and less conspicuous than the telson of *M. spinifera*.

(iv) The posterior spine is relatively short, narrow (tr.) at the base, terminating distally in a group of spines (figures 89, 92, plate 10; figures 102, 104, 109, plate 11).

(v) Appendages are poorly preserved, but the large anterior cephalic limb (figures 90, 91, plate 10) is distinctive. The posterior portion of the cephalic shield and trunk of 275539 (figures 99, 106, plate 11) is split below the level of the exoskeleton, and reveals lobed appendages, imbricated to slope one below the other, and bearing lamellae on the posterior edge; one pair appears to belong to the cephalon, and one pair is situated below each tergite. The lamellae of the pair below the ninth tergite are visible in figures 89 and 92, plate 10. The darker areas of the lateral parts of the tergites in this specimen and 272194 (stippled in figures 94 and 97) may be the remains of these lobes on the inner surface of the exoskeleton.

These differences seem to be sufficient to separate these specimens from *Molaria spinifera* at the generic as well as the specific level. The large, jointed, anterior limb is poorly preserved in 272194 (figures 101, 102, plate 11); no specimen suggests the presence of jointed legs behind this position. That is, the inner branch of succeeding appendages may have been reduced or even absent, the appendage being a lamellate lobe. Whether the anterior limb was biramous is unknown. A darker area apparently representing the anterior part of the alimentary canal (figure 104, plate 11) is present in one specimen; none shows evidence of a sediment filling. No example is compressed laterally, so that convexity is difficult to judge. The cephalic shield shows evidence of flattening (figures 101, 109, plate 11), suggesting that it may have been as strongly convex as that of *M. spinifera*. It is difficult to compare shape between the two species because of the small sample of the new species, but it may be that the body was broader (relative to its length) and the cephalic shield more quadrate in outline. Whether the body was as flexible as that of *M. spinifera* is uncertain, but 272194 (figures 101, 102, plate 11), in which the posterior spine is bent around at a different level from the rest of the body, suggests considerable flexibility. The posterior spine does not show evidence of jointing.

The large eye, absence of mud filling of the gut and perhaps of walking legs suggests that these rare specimens may have been carcasses of a pelagic animal. The tentative reconstruction (figure 131) shows the stalked eye and what is known of the appendages. It portrays the animal swimming in an inverted position by the lobes moving in a metachronal rhythm. The lamellate fringe borne by the lobes suggests that they may have functioned as gills.

This small animal is not only quite different from *Molaria spinifera*, but also unlike any other arthropod in the Burgess Shale; it does not appear to be the young stage of any larger species. This taxonomic isolation results in the generic diagnosis of § (*a*) being no more than a brief characterization of the only known species.

9. *Actaeus armatus* Simonetta, 1970

I take the correct original spelling of the generic name to be *Actaeus*, as used in the title and elsewhere in Simonetta (1970), except in the heading in which the genus is proposed, where the name is mis-spelt.

Figures 110–113, plate 12; figures 114, 132.

1970 Simonetta, p. 43, pl. VIII, fig. 4*a*, *b*; pl. IX, fig. 3.

1975 Simonetta & Delle Cave, pp. 27, 33; pl. IV, fig. 2; pl. XXXV, figs 11*a*, *b* (copies of Simonetta (1970)).

(*a*) *Description*

The single specimen, U.S.N.M. 155597 a, b, is a dorsal oblique compression with counterpart, ill preserved and crossed by a fold. The lateral and posterior margins of the cephalic shield are visible on the left side and medially, but not on the right side. The pleurae of the first four trunk tergites are visible on the left side, bent double by the oblique crushing, the outline suggesting that the tips were progressively prolonged backwards. The right side of figure 114 shows what I regard as the margins of pleurae 4–6. The posterior portion of the body is twisted beyond the fold, and the split seems to go below the tergites and shows what may be overlapping appendages. A triangular terminal plate is outlined. The trace of the alimentary canal extends from close to the anterior margin of the cephalic shield to the base of the terminal plate, and is partially reflective; it shows divisions corresponding to the trunk tergites.

At the ill defined anterior end of the cephalic shield is a pair of suboval, reflective areas, nearest to the observer on the part (figures 110, 112, plate 12). These are thought to be eye lobes, but the areas show no subdivisions or other features. Beneath and just inside the eye lobe the anterior appendage emerges, which is most completely preserved on the left side. The stout proximal portion is bent through about 70° at its mid-length, and obscurely jointed, the distal end bearing a group of four curved spines; from the inner side of this portion of the appendage arise two long, slim, flexible branches. These curved branches are incompletely preserved, but the fragments are at two levels and so seem to represent two branches lying one upon the other. Only the proximal portion of the right anterior appendage is preserved. On the right side of the cephalic shield are what appear to be three pairs of biramous appendages (figure 112, plate 12), exposed below the shield and outside it because of the oblique crushing and position of the split. The first of these consists of an elongate lobe showing fragments of lamellae around the margin; between and below it and the right eye lobe is a tapering, jointed, inner branch, which has been exposed by removing the edge of the lobe. The tip of the lobe and jointed branch of a similar, second appendage lie below and behind the first. Opposite the postero-lateral portion of the cephalic shield is a curved spine and obscure traces of lamellae, the tips of the third appendage. Traces of the first left biramous appendage are visible outside and below the left eye lobe. Along the right side of the trunk is a series of imbricated plates, each going below the one in front, interrupted by three (pl 4–6 in figure 114) plates that have a clearly defined lateral margin and are thought to be pleurae of tergites 4–6 of the trunk. The plates anterior to these pleurae are at a lower level, and may represent lobes of appendages 4–6; outside the margins of 5 and 6 project broad, overlapping lamellae arranged fan-wise. The tips of similar lamellae emerge from beneath the fourth and fifth pleurae. The imbricated plates posterior to pleura 6 are vaguely defined distally and show no marginal lamellae, but may represent lobes of appendages 10–14.

(*b*) *Morphology and affinities*

Figure 132 summarizes my interpretation of the morphology. The eye lobe may have been situated on the anterolateral margin of the cephalic shield, or it was pedunculate and emerged from beneath the margin. Simonetta's reconstruction (1970, pl. IX, fig. 3) shows what appears to be a single anterior appendage as two separate appendages, the first a long, slim antenna in which he portrays joints. This does not agree with the evidence (figures 112, 113, plate 12), in that the slim branches arise from the inner side of the broad, proximal portion of the appendage, and not separately from beneath the cephalic shield; the evidence suggests two, not one branch. The present jointed branches of the biramous cephalic appendages were not observed by Simonetta. He (1970, p. 43) 'positively' identifies three of five probable pairs of cephalic appendages, each a lobe fringed by lamellae, but why five are probable is not explained. He divides the remainder of the body into thorax and abdomen, considering that each segment of the former bore a 'pair of legs' having an outer branch of a rounded lobe fringed by lamellae. I do not consider that the specimen shows evidence of a subdivision of the trunk; segmented 'legs' are not visible on this portion of the body, but there do appear to have been lobate appendages with marginal lamellae on at least the anterior portion.

Actaeus armatus as here interpreted shows a similarity to *Leanchoilia superlata* Walcott, 1912. In both the exoskeleton includes a cephalic shield, 11 tergites and a triangular plate. The large anterior appendage is similarly constructed: the proximal portion is broad and curved; the distal podomere has claws; and the next proximal podomeres bear the long extensions. In both species lobes fringed with lamellae are conspicuous on the trunk, but in *L. superlata* the eye lobe is absent and jointed appendages are not prominent on the cephalic shield. *L. superlata* is the type species of the genus *Leanchoilia,* and was described by Walcott (1912, pp. 170–171, pl. 31, fig. 6), who subsequently published photographs of additional specimens (Walcott 1931, pp. 8–9, pl. 12, figs 1–3; pl. 13, fig. 2, *non* fig. 1; pl. 14, figs 4, 5). Further material was described and illustrated by Raymond (1935, pp. 205–216, figs 1–3), who gave a restoration. Størmer (1939, pp. 235–236, pl. 12, fig. 3, text-fig. 30*e*; 1944, pp. 82–84, text-figs 16; 17, 1, 2; 24*c*; *in* Moore 1959, p. O 31, figs 13, 20) figured another specimen and gave another restoration. More specimens from the Walcott collection were figured by Simonetta (1970, pl. I, figs 1–8; pl. III, figs 1–4; pl. IV, figs 1–4), a new reconstruction of the type of species was offered (pl. II, fig. 1 *a*, *b*, *c*), and three additional species of *Leanchoilia* were distinguished. Simonetta (*in* Simonetta & Delle Cave 1975, p. 19, pl. XXVIII, figs 2–7; pl. XXIX, figs 1–6; pl. XXX, figs 1–6; pl. XXXI, figs 1–8) repeated his earlier illustrations and gave some additional ones, and offered reconstructions (pl. I, figs 2, 6) of two of the new species as well as repeating (pl. I, figs 1 *a*, *b*) the dorsal and lateral views, but not the cross section, of *L. superlata*. A revision of all this material is in preparation by D. L. Bruton, and will provide a new basis for assessing the relationship with *Actaeus*.

In their systematics Simonetta & Delle Cave (1975, pp. 27, 31, 33) place *Actaeus* in a separate family, and relate it to the monogeneric family containing *Yohoia*. No doubt this is based on their reconstruction of *Actaeus* as well as Simonetta's (1970, pl. IX, figs 1, 2) reconstruction of *Yohoia.* In 1975 Simonetta (*in* Simonetta & Delle Cave 1975, pp. 18–19, pl. IV, figs 1 a–e; pl. XXXII, figs 1–21) reproduced his reconstruction of *Yohoia tenuis* as well as the photographs, and added some of additional specimens. He also disputed the conclusions that I reached (Whittington 1974) in my study of all the specimens that he cited and many more. He maintained that particular specimens (the originals of Whittington (1974, pl. 2, figs 1–3; pl. 4, figs 1, 2; pl. 7, figs 3, 4)) show evidence for the presence of antennae and a labrum, and cited an additional specimen (155611) as showing the antennae. This specimen is of length (sag.) about 7 mm, an incomplete external mould, which shows fragments of the great appendage in front of the cephalic shield; I considered it too poorly preserved to be worth illustrating in 1974. Simonetta also repeated his claim that the inner branch of the thoracic appendage is revealed by particular specimens (originals of Whittington (1974, pl. 4, figs 1–5, pl. 5, figs 3, 4)). No new evidence was brought forward by Simonetta in support of his claims, and I see no reason to modify the conclusions that I reached (Whittington 1974, pp. 5–6); I failed to find evidence for antennules, a labrum as portrayed by Simonetta, or a distal branch from the walking leg of the trunk, and considered the structure of the anterior great appendage to have been misrepresented. The single specimen on which *Actaeus* is based (figure 132) is over three times as long as the largest known of *Yohoia* (Whittington 1974, figs 2, 3, 5). The exoskeleton of both is divided into cephalic shield, trunk and terminal plate, but the form of these parts and number of trunk tergites is different. The large anterior appendage is dissimilar in the two species, and whether or not there is an eye lobe in *Yohoia* is uncertain. Lobate appendages with marginal lamellae are present on cephalon and trunk of *Actaeus*; somewhat similar appendages are found on only the trunk of *Yohoia*. Generalized arthropod characters are common to these two species, but the special characters of each are different and do not suggest relationship.

(*c*) '*Leanchoilia protogonia*', *a composite fossil*

Of the three additional species of *Leanchoilia* distinguished by Simonetta (1970), two are regarded by D. L. Bruton (personal communication) as synonymous with *L. superlata*. The third, *L. protogonia* Simonetta, 1970 (Simonetta 1970, p. 38, pl. IV, fig. 2; Simonetta & Delle Cave 1975, pl. I, fig. 6; pl. XXXI, fig. 1) is based on a single example (figures 120–122, plate 13) interpreted as shown in figure 116. It appears to consist of a poorly preserved specimen of *L. superlata*, obliquely dorsally compressed upon an unidentified portion of a branched organism. The specimen of *L. superlata* shows the cephalic shield, 11 tergites and a poorly preserved terminal plate, obscured by the dark stain. The great anterior appendages project forward on the right side, lying one upon the other. The alimentary canal is conspicuous anteriorly, as in many specimens of *L. superlata*. The unknown organism is preserved in the same way as *L. superlata*, as a dark reflective film; pyrite is conspicuous along the centre of the strands, and is also present on the great appendages and margin of the cephalic shield of *L. superlata*. The organism projects from under the left side of the cephalic shield as two strands, presumably underlies the body, and emerges posteriorly as a broad, apparently bipartite strip, which then branches, some of the branches being curved (at least one curved through 180°), the central strand being tapering and prolonged. No other specimen of this organism is known. Simonetta (1970) did not observe the strands of the organism projecting in front of the cephalic shield, and regarded the portion behind *L. superlata* as a spinose terminal portion of the body. My drawing shows how it emerges posteriorly at a level below the poorly preserved terminal plate and is not continuous with any portion of the exoskeleton of *L. superlata*. In my opinion the species '*L. protogonia*' is based on a misinterpretation of a composite fossil; the only known species of *Leanchoilia* is the type species.

10. *Alalcomenaeus cambricus* Simonetta, 1970

I take this to be the correct original spelling of the generic name, as used in the title and heading in which the genus was proposed; several mis-spellings occur elsewhere in that publication and later ones.

Figure 115; figures 117–119, plate 13; figures 123–128, plate 14; figures 129, 133.

1970 Simonetta: p. 39, pl. IV, figs 5, 6*a*, *b*; pl. IX, fig. 4; *non* pl. V, fig. 1.

1975 Simonetta & Delle Cave: p. 27, pl. I, fig. 4; *non* pl. XV, fig. 1; pl. XVI, figs 2, 4*a*, *b* (copies of Simonetta (1970)).

(a) *Description*

The holotype by original designation is U.S.N.M. 155658, a lateral compression lacking the counterpart (figures 117–119, plate 13). In the anterior half of the body is an elongate-oval area, sharply bounded, slightly raised and reflective, which appears to be an infilling of the alimentary canal. It is extended forward by a clearly bounded, narrower portion, which runs in a U-shaped curve, suggesting that the alimentary canal curved to the backward-facing mouth. Beyond about half the length of the specimen the raised, elongate-oval area dies away, and its posterior continuation is vaguely suggested by an ill defined, darker, reflective strip. The narrow region dorsal to the alimentary canal is sharply bounded anteriorly and medially, but posteriorly the margin becomes irregular and ill defined. Traces of divisions cross this region and suggest a cephalic portion of the body and a trunk region of more than 10 somites; the body has an ovate terminal plate. Anteriorly the dorsal margin curves down, to end against a small sub-oval area lying at a higher level; this area is strongly reflective (figure 117, plate 13). A second oval, strongly reflective area lies between it and the fold; I regard these areas as representing left and right eye lobes. Below the trace of the alimentary canal the body shows a series of imbricating, elongate, leaf-shaped lobes (labelled g? in figure 115), changes in level between them dying out proximally. A series of eight lobes may be traced and lobes 2–8 are referred to the right side, on the assumption that each passed inside the one in front. This assumption implies that the left lobes may have been preserved in the (unknown) counterpart, except for the irregular fragment considered to be part of the left first lobe (labelled Lg? 1 in figure 115). Between successive lobes a backwardly curved spine projects, and a series of ten, perhaps 13, can be seen in reflected radiation. Between lobes 1 and 2 are two such spines, close together and lying at slightly different levels; these may be a pair but are here considered to be the first and second in the series. Only spine 10 shows a suggestion of segmental divisions. In reflected radiation (figures 117, 118, plate 13) an overlapping series of reflective areas lies between the trace of the alimentary canal and the lobes and spines. These reflective areas are spinose along the posterior margin and may be the proximal portions of the spines. Anterior to the series of lobes and spines is an anterior appendage, curved downward and backward, proximally broad and distally slim; the distal portion only of the right one is preserved.

The terminal plate is paddle-shaped; the posterior edge is poorly preserved and with an irregularly curved outline. Each lateral margin shows a narrow band, bent slightly up toward the observer on the upper side and down on the lower.

The second specimen referred to this species (figures 123–128, plate 14) is considered to be an oblique lateral compression, and only the counterpart shows the posterior portion. As in the holotype, there is a filling of the alimentary canal, most prominent in the anterior half of the body, and U-shaped anteriorly. Dorsal to the canal is part of the undivided cephalic shield, and an imbricated series of right pleurae, probably folded over by the oblique crushing; some six pleurae are visible (figure 123, plate 14); behind them the margin of the body becomes vaguely defined. The terminal plate is oval, with broad lateral bands, one sloping down and the other up, with respect to the median portion. The left eye lobe and anterior appendage are preserved, the latter having a short, broad base and a long, slim distal portion. The first seven of the left, curved, spine-like series of inner branches of the appendages are more completely preserved than in the holotype and are triangular, broad proximally and tapering rapidly, the mesial and inner margins being spinose (figures 126, 128, plate 14); each slopes to pass inside the one following, and excavation of the overlying lobes 4, 5 and 7 (compare figures 123 and 125, plate 14) revealed the inner spines more completely. Adjacent to the spines on the mesial margins of 2–7 are mirror-image spines, which are the rows on the mesial edges of the right-hand series (R 3–7, figure 129). These spines thus made a formidable armature along the midline. Lying outside left limbs 7 and 8 are the distal portions of pleural lobes 7 and 8, the margin outlined (m in figure 129), and lying on probably the inner side of each is a gill lobe bearing long, marginal lamellae. Pleura and gill 8 pass beneath pleura and gill 7, i.e. the opposite imbrication to inner branches 7 and 8; this means that there is an acute angle between inner branch and pleural lobe, the anterior margins close together, the two branches diverging posteriorly. This relationship may mean that in life the triangular blade of the limb was directed transversely, the spines of a pair being opposed, whereas the pleural lobes and gills were lateral in position. Behind left appendage 9 are a series of curved spines (tips of limbs) and lobes with marginal filaments (gills) the more posterior preserved only on the counterpart (figure 127, plate 14). Each gill passes inside the one in front, showing that this is a right-hand series of appendages, here labelled (figure 129) *a–g* because the true number in the whole series is unknown. As in the holotype, these posterior limbs and gill lobes diminish rapidly in size posteriorly, and the pleural lobes are ill defined. The dark stain suggests that the alimentary canal terminated at the base of the terminal plate.

(*b*) *Discussion*

Simonetta (1970, p. 39) referred to this species specimens numbered U.S.N.M. 155660–155663 inclusive. The first, 155660, is in error, since on the same page Simonetta made this specimen the holotype of his '*Leanchoilia amphiction*', probably a synonym of *L. superlata* (D. L. Bruton, personal communication). U.S.N.M. 155661 is poorly preserved and unidentifiable; 155662 is a specimen of *L. superlata* (D. L. Bruton, personal communication). In 1977 I discovered the counterpart (U.S.N.M. 199667) of 155663, which shows the cephalic region of the animal, apparently with a pair of eye lobes and an anterior appendage which is broad proximally, the distal portion long and slim. The remainder of the body is poorly preserved, and while as a whole the specimen resembles *A. cambricus*, I hesitate to identify it.

The two specimens here referred to *A. cambricus* show a division of the dorsal exoskeleton into cephalic shield, trunk tergites and a terminal plate, a prominent alimentary canal anteriorly, one pair of eye lobes, and an anterior appendage having a single long, slim distal portion. A series of biramous appendages follows the anterior appendage, and totals 13 or 14. The common characters suggest that these two specimens are of one species, but the differences between them are not readily reconciled. The holotype appears to be a lateral compression (not oblique as 155659), and shows lateral lobes 1–8 hanging down below the cephalic shield and first five trunk tergites (figure 115). Because they are below the cephalic shield they cannot be pleurae and are assumed to be gill lobes, though they show no trace of marginal lamellae. In 155659 these lamellae are preserved in the posterior portion of the specimen, while the anterior portion shows no such lobes, but does reveal the spinose inner branches. Only the tips of the latter are shown by the holotype; what the reflective areas represent (figure 115) is uncertain. Neither specimen shows the lateral margin of the cephalic shield or the margins of the pleural portions of the trunk tergites; it is uncertain that the faint line 'm' in figure 129 indicates the pleural margin. The reconstruction (figure 133) assumes that the two specimens are of the same species, and the gill lobes are shown hanging down well below the margins of the cephalic shield and pleurae. The tips of the inner branches project between these lobes. While these branches appear to have borne a formidable armature of opposed spines, running from behind the mouth along the trunk, joints are not seen in them in 155659, and only questionably on limb 10 of 155658; they are not shown in the restoration. A total of 12 tergites is shown, based on the assumption that left appendage 8 and right appendage 'a' of 155659 are a pair, giving a total of 15 pairs including the anterior. The first three pairs and the large anterior appendage appear to be cephalic. It is assumed that the eye was pedunculate, projecting below the margin of the cephalic shield. The posterior portion of the trunk is vaguely defined in both specimens, and the lateral bands of the terminal plate are broad in 155659 but narrow in the holotype. Perhaps the exoskeleton was thin posteriorly, and the angle of burial accounts for the differences in appearance of the terminal plate.

The bases for Simonetta's reconstruction (1970, p. 39, pl. IX, fig. 4) are difficult to discern, particularly since he referred a specimen of *Leanchoilia superlata* to this species. He shows the large anterior appendage as jointed, though admitting that no joints can be observed. He interpreted what are here called inner branches 1 and 2 (or possibly pair 2) of 155658 as two successive jointed cephalic appendages, each presumably uniramous. Specimen 155659 shows that the series of spinose inner branches (which Simonetta did not observe) of the biramous series is present from appendages 2–8; the nature of appendage 1 is obscure. I am only able to recognize the large anterior pair as uniramous and quite distinct from any following appendages.

(*c*) *Morphology and affinities*

As tentatively restored (figure 133) *A. cambricus* sensed the environment by the eye and the long flexible anterior appendage, the biramous series of limbs having the inner branch adapted to tearing food and passing it forward to the backward-facing mouth, the outer branch in part respiratory in function. The animal may have swum by moving these outer branches in a metachronal rhythm, the flexible trunk and terminal plate steering and perhaps assisting in swimming. The curved, sharp, inwardly directed points of the inner branches do not look to be adapted to walking, nor does the limb itself; perhaps this animal was a scavenger, alighting on carcasses, clinging to them and tearing them with the inner branches.

Simonetta & Delle Cave (1975, pp. 27, 33) placed *Alalcomenaeus* in a separate, monogeneric family, which they put in the same order as that containing *Leanchoilia*. In § 9*b* I have suggested that the similarities between *Leanchoilia* and *Actaeus* may imply a relationship. *Alalcomenaeus* (figure 133) shows a similarity to *Actaeus* in the relatively short (sag.) cephalic shield and graded series of trunk tergites, in the presence of an eye lobe, and in having a large anterior appendage followed by a biramous series, the outer branch of which was a lobe bearing marginal lamellae. The anterior appendage of *Alalcomenaeus* does not show the distal joint of the proximal portion, which bears curved spines, present in *Actaeus* and *Leanchoilia*, and the inner branches of the biramous appendages in *Alalcomenaeus* are distinctive and unlike any structures in the other two genera. When *Leanchoilia* is restudied the relationships between these three genera may be clarified; at present it appears that the appendages of *Alalcomenaeus* distinguish it sharply from the other two genera.

In 1966 and 1967 a reinvestigation 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. 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.

Enlargements from my negatives have been prepared by Mr David Bursill. Mr John Lewis and Miss Adele Prouse have skilfully converted my pencil drawings into the figures.

I am greatly indebted to Dr D. H. Collins, Royal Ontario Museum, Toronto, and to my colleagues Dr D. E. G. Briggs and Dr C. P. Hughes, for advice and discussion in the course of this work.

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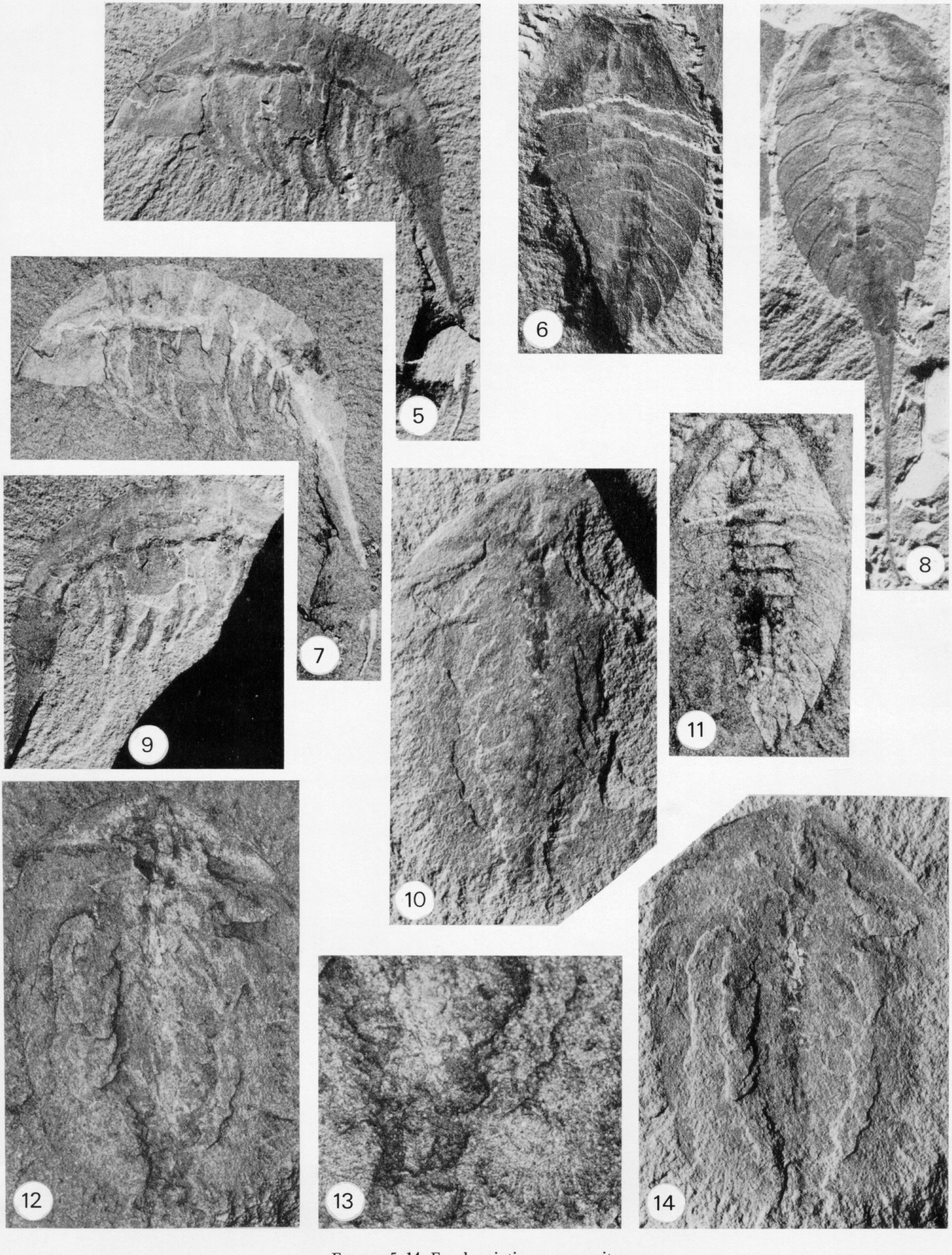
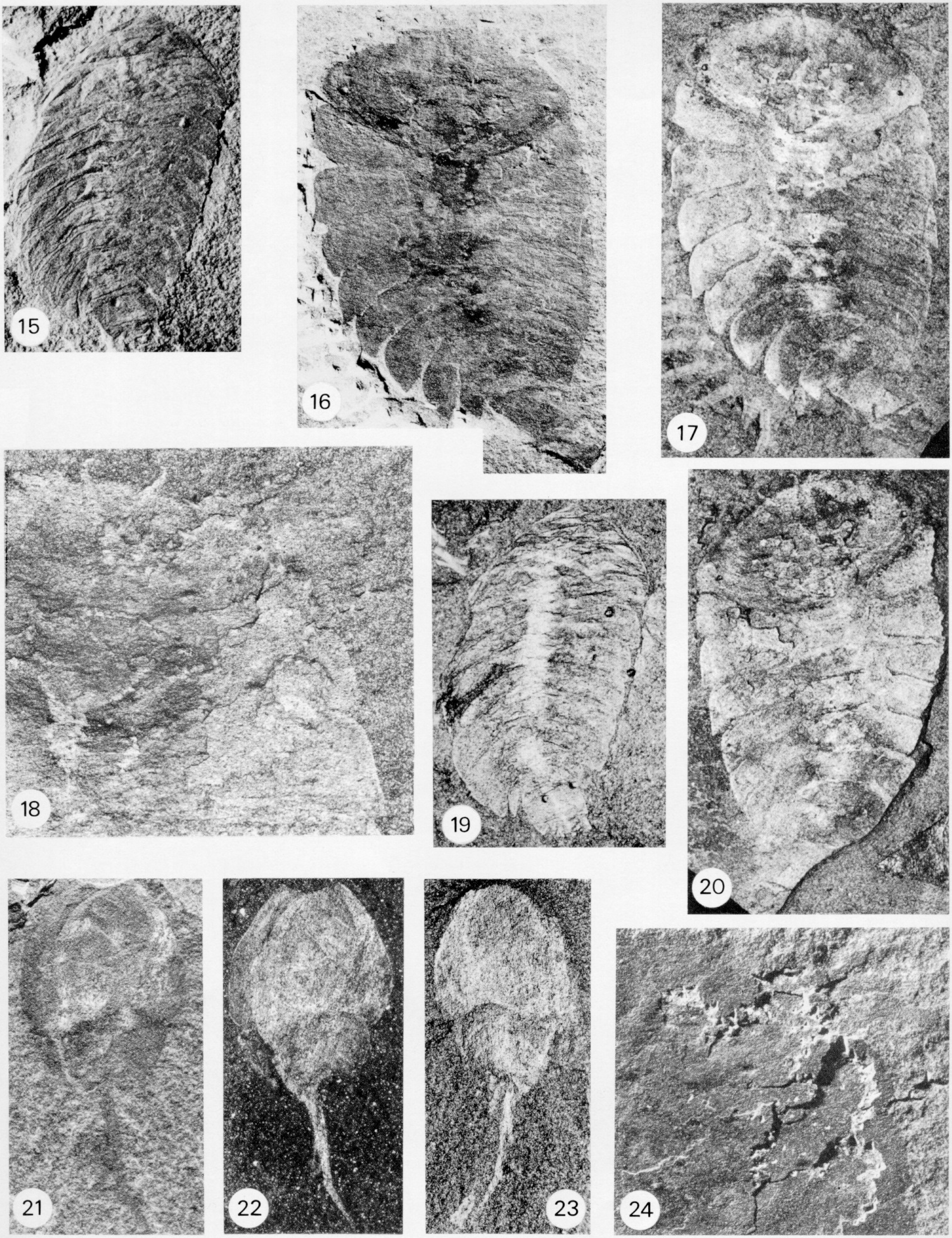
List of abbreviations and symbols used in figures

L	left side of animal, as prefix
R	right side of animal, as prefix
U.S.N.M.	United States National Museum, now the National Museum of Natural History
a	antenna
a–n	lettered series of biramous appendages used (figure 129) when most anterior on cephalic shield, on either right or left side, is not known
al	alimentary canal
am	anterior margin
ap	appendage, not necessarily complete
af	articulating flange of tergite, in front of ridge
co	coxa
cs	cephalic shield, exoskeleton of cephalic region
cu	cusp
d	doublure, reflected portion of exoskeleton
ds	dark stain
e	eye lobe
fo	fold
fr	fracture
g	gill or outer branch of appendage, consisting of a lobe with marginal lamellae
if	infilling of alimentary canal
m	margin
me	median
mif	mould of infilling
ob	unknown organism
os	outer surface
pl	pleura, lateral, down-curved portion of trunk tergite
pm	posterior margin
r	exterior ridge (groove on internal surface) on anterior portion of tergite
sp	spine
t	tergite, exoskeleton of dorsal surface of trunk somite
tel	telson
ter	terminal plate
v	ventral
ve	vein in rock, shown to help relate drawing to photograph

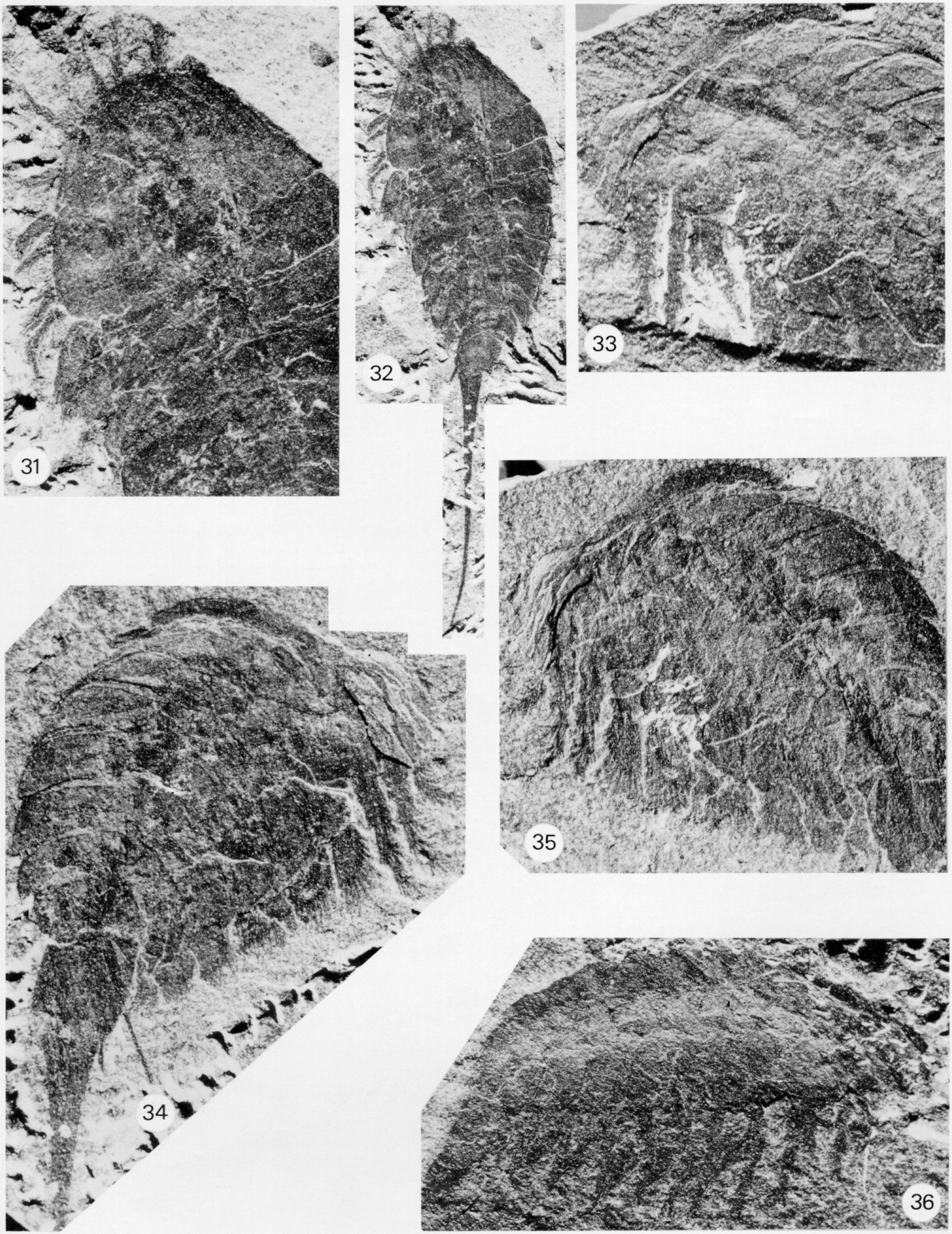
$1-n$	numbered series of biramous appendages, beginning with most anterior of cephalic region, (except in figures 61, 72, 76, 77, where cephalic appendages are not numbered); applied without prefix to inner or leg branch, with prefix g to gill or outer branch, and used with prefix t for tergites, pl for pleura of trunk.
stipple	used to denote fine-grained pyrite on surface (figures 3, 26), darker areas along alimentary canal (figures 4, 59–61) and anterior bands of tergites (figures 94, 98), and the dark stain (figures 61, 72)
shading	by diagonal or horizontal lines has been used to denote strongly reflective areas such as the alimentary canal (figures 75, 114), the eye lobes (figures 94, 98), or appendages (figures 96, 115)
scale bar	undivided bar is 1.0 cm; bar showing five divisions is 0.5 cm



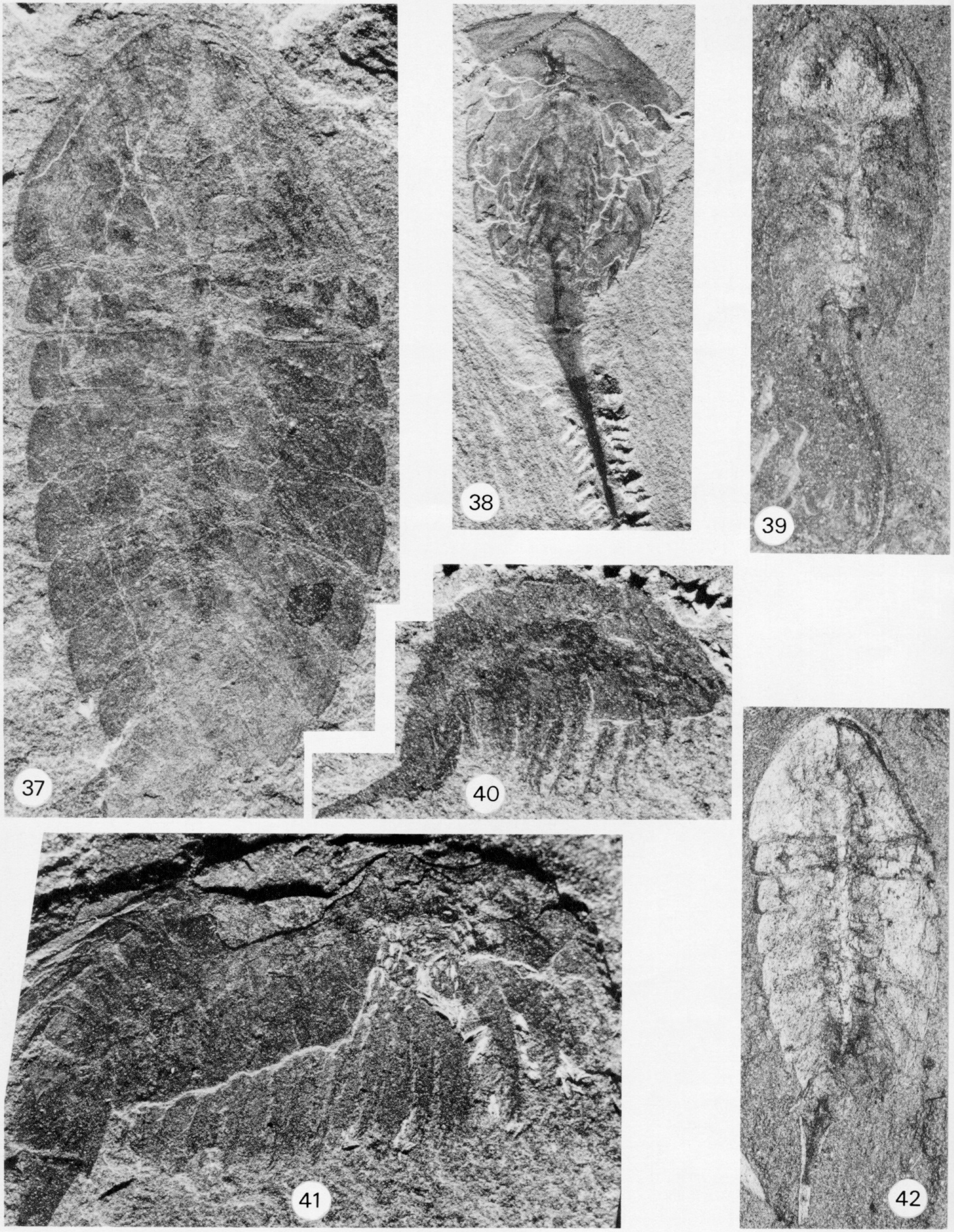
FIGURES 5–14. For description see opposite.



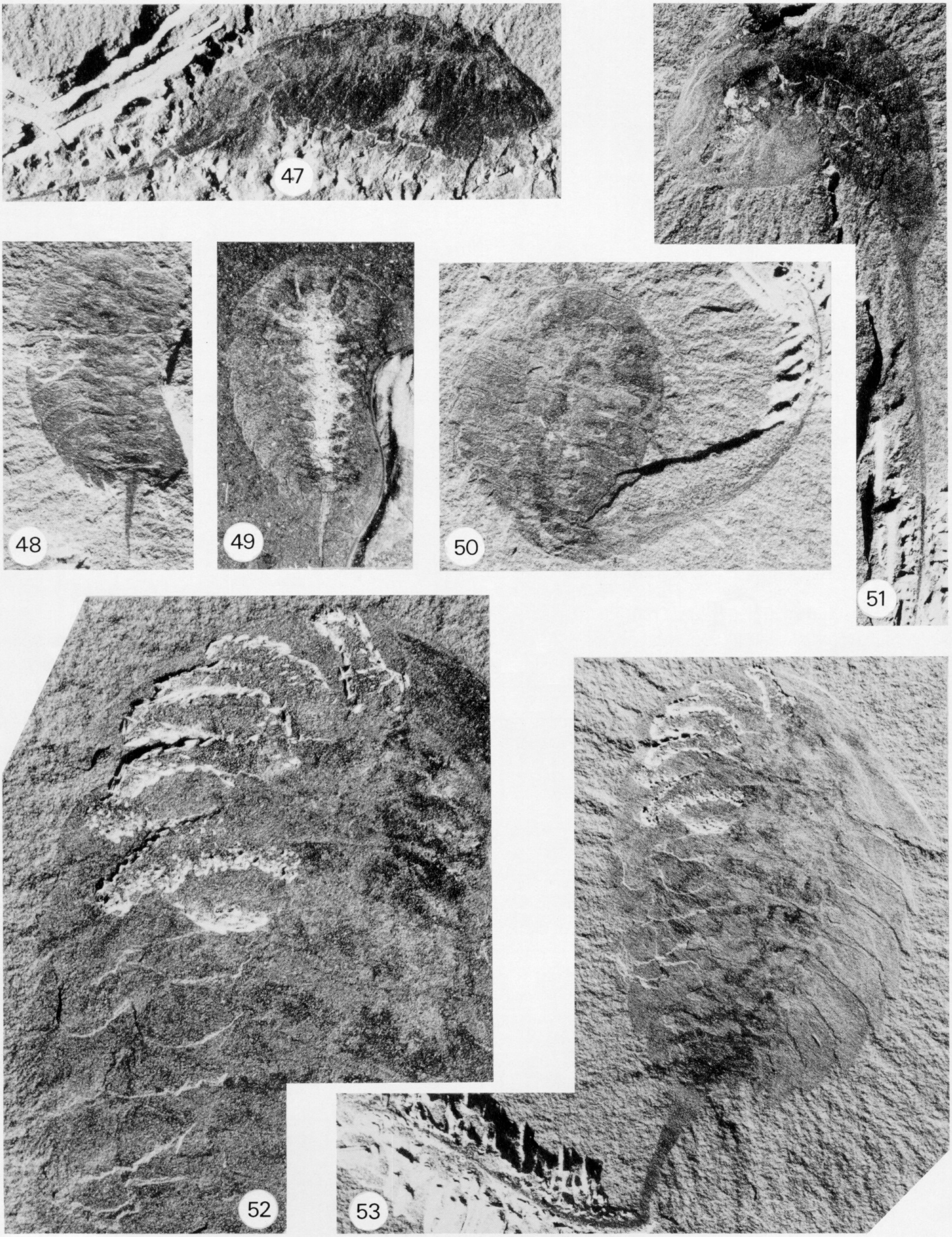
FIGURES 15–24. For description see opposite.



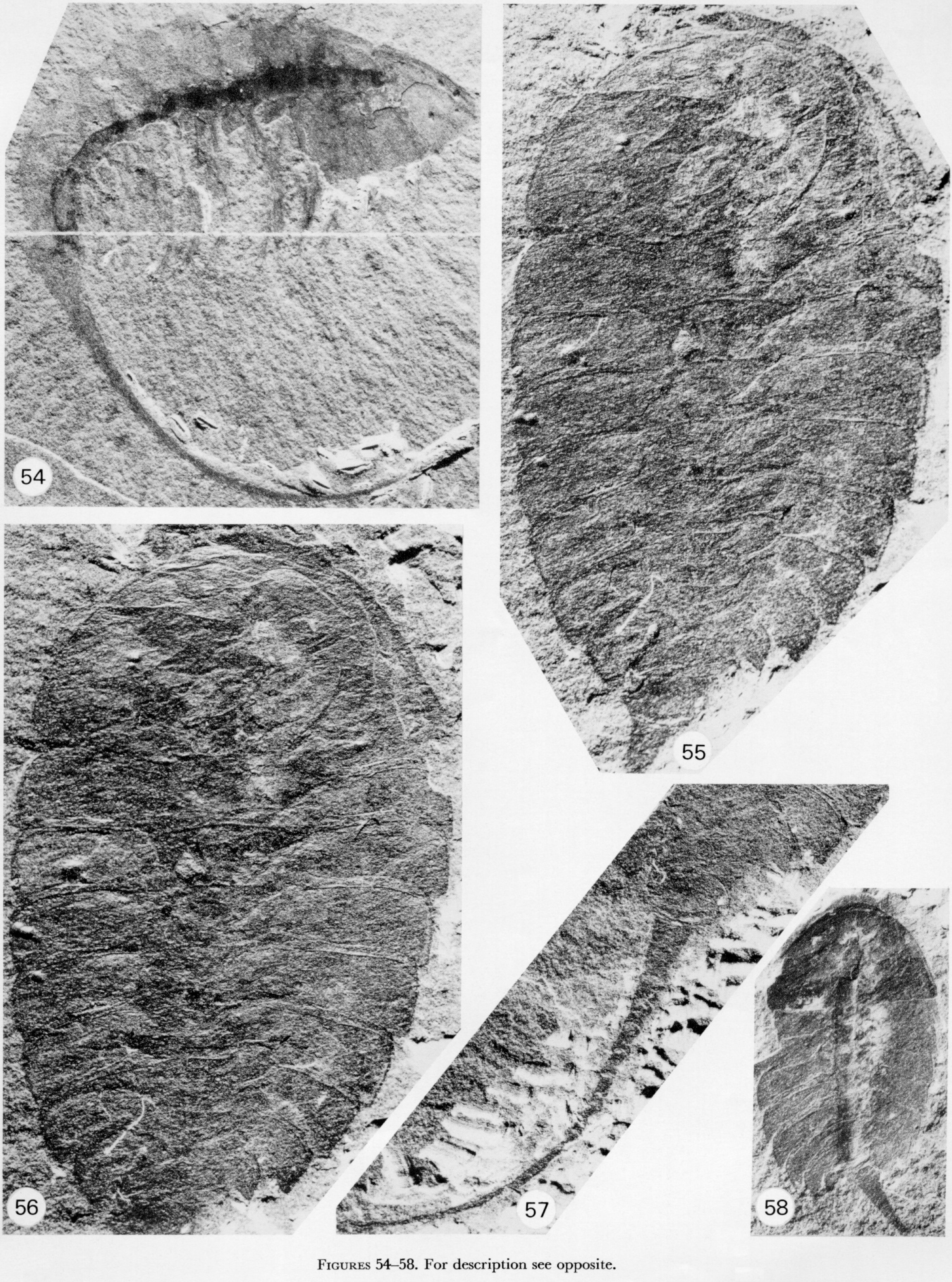
Figures 31–36. For description see opposite.



FIGURES 37–42. For description see opposite.



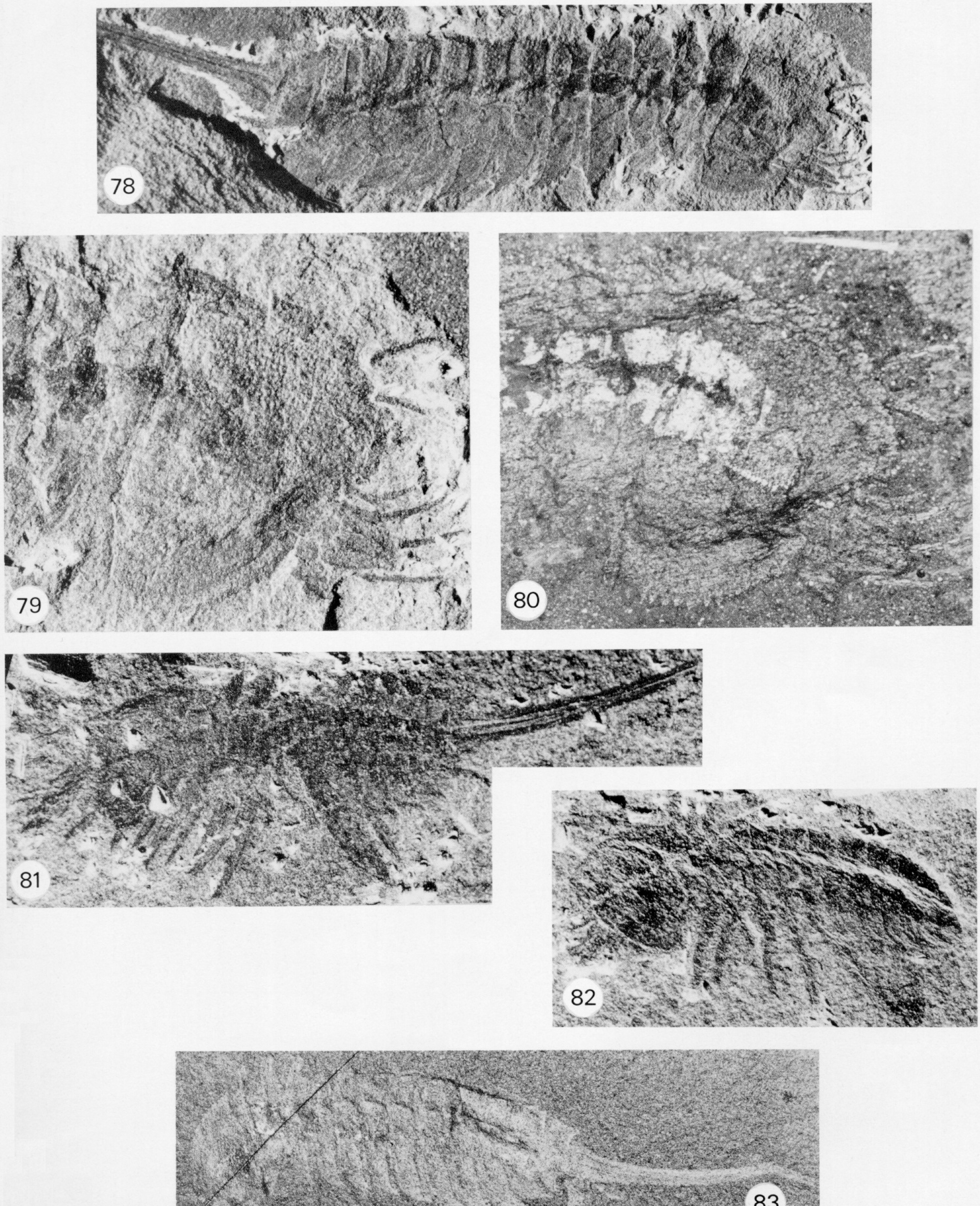
Figures 47–53. For description see opposite.



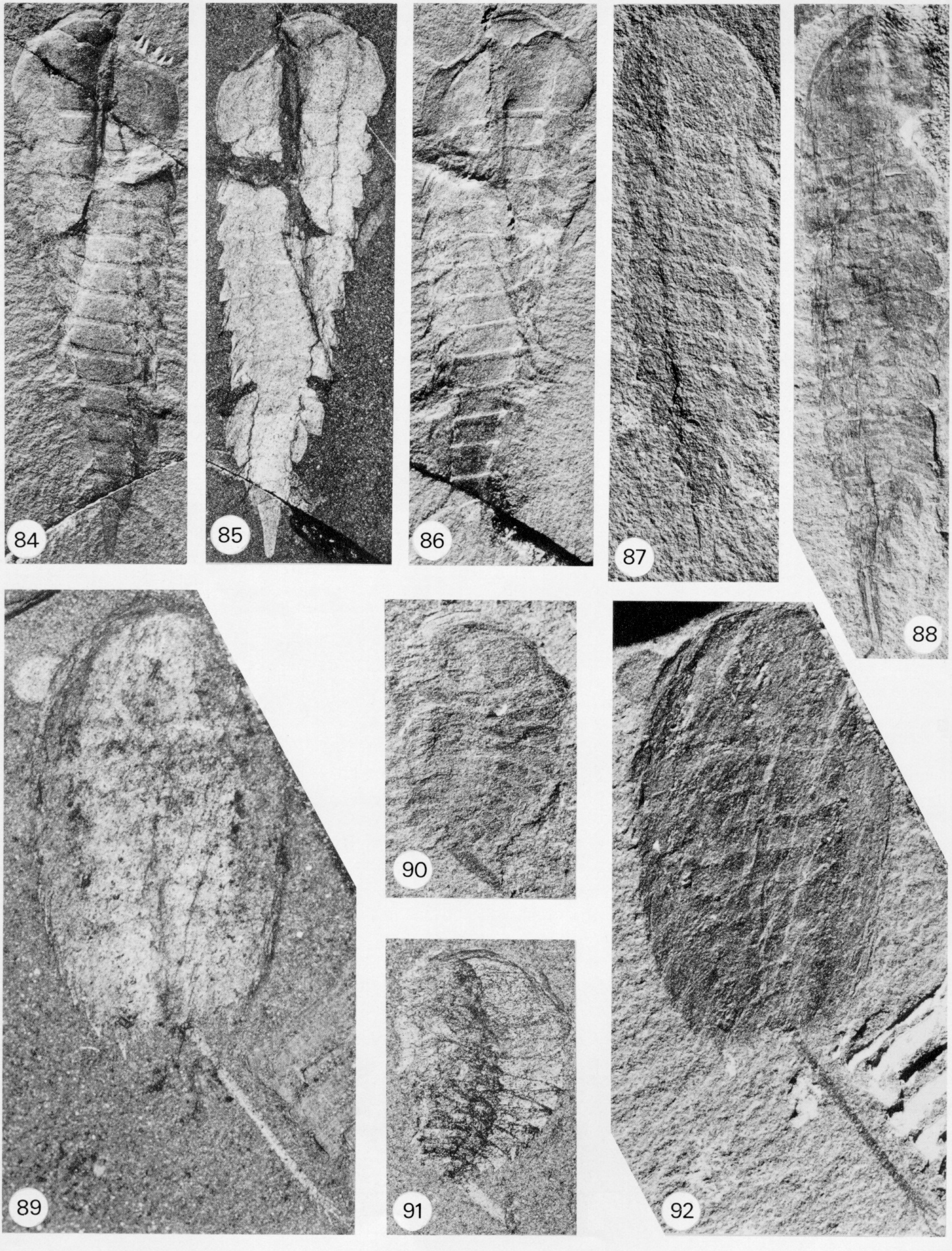
Figures 54–58. For description see opposite.

FIGURES 62–66. For description see opposite.

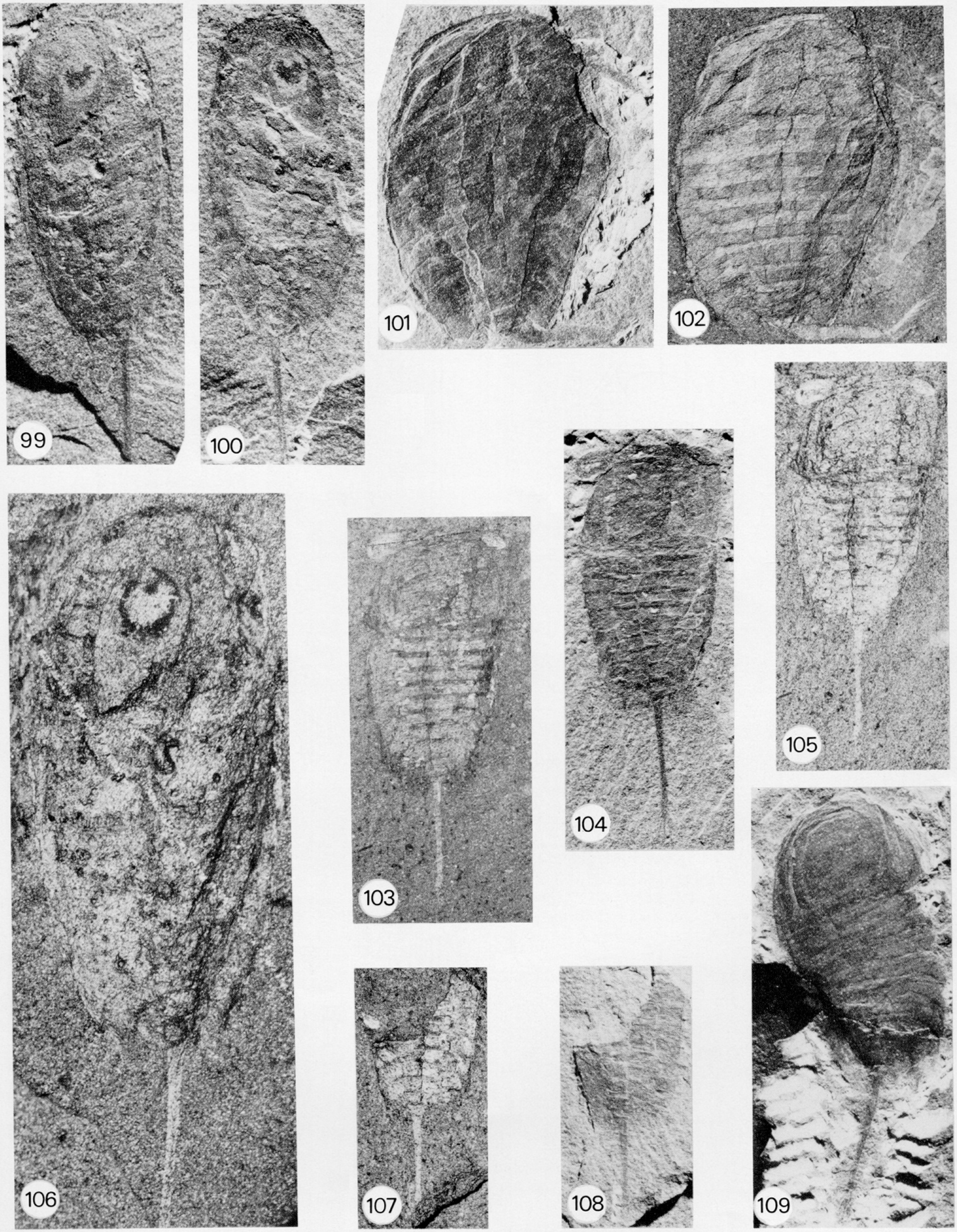
FIGURES 67–71. For description see opposite.



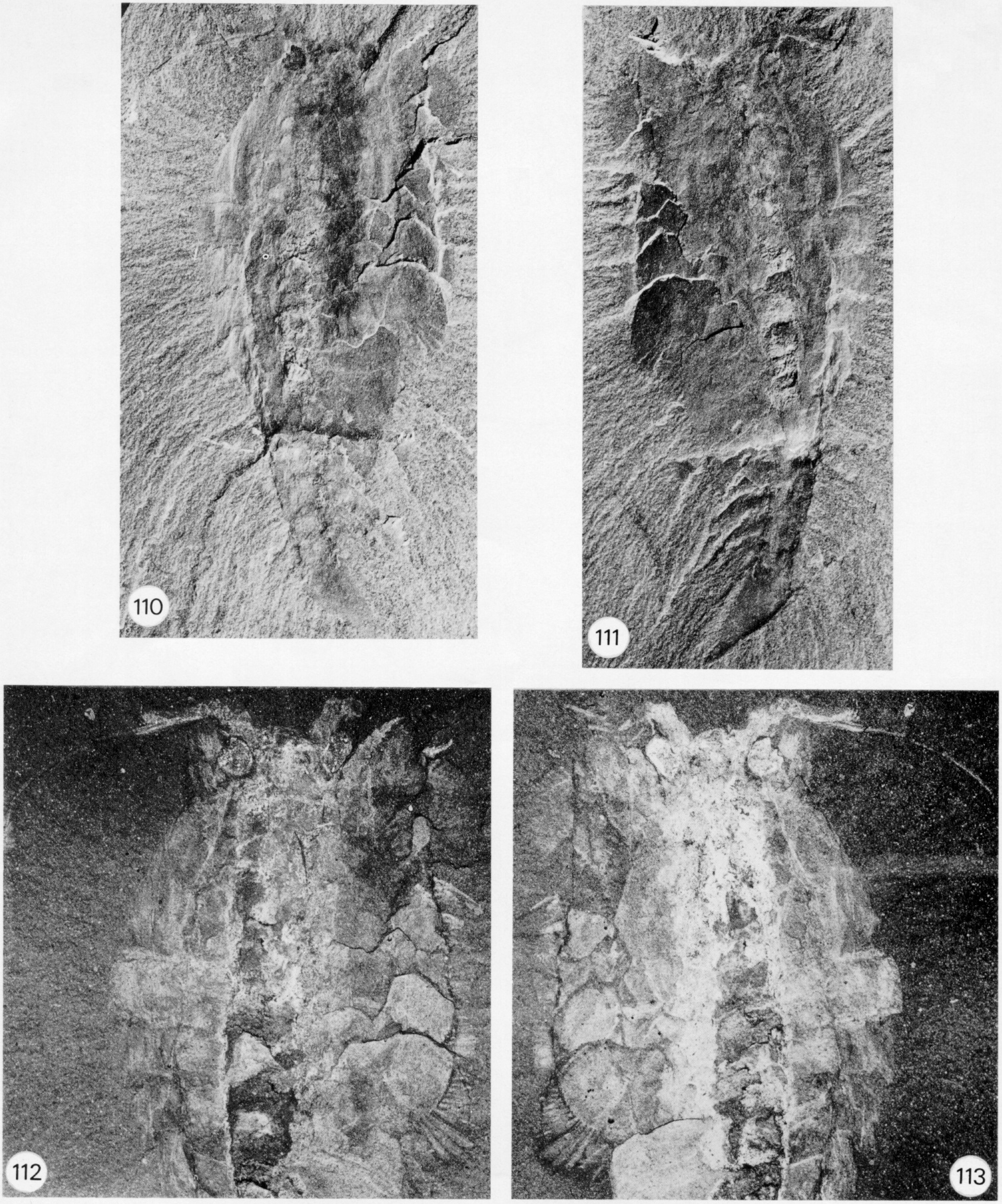
FIGURES 78–83. For description see opposite.



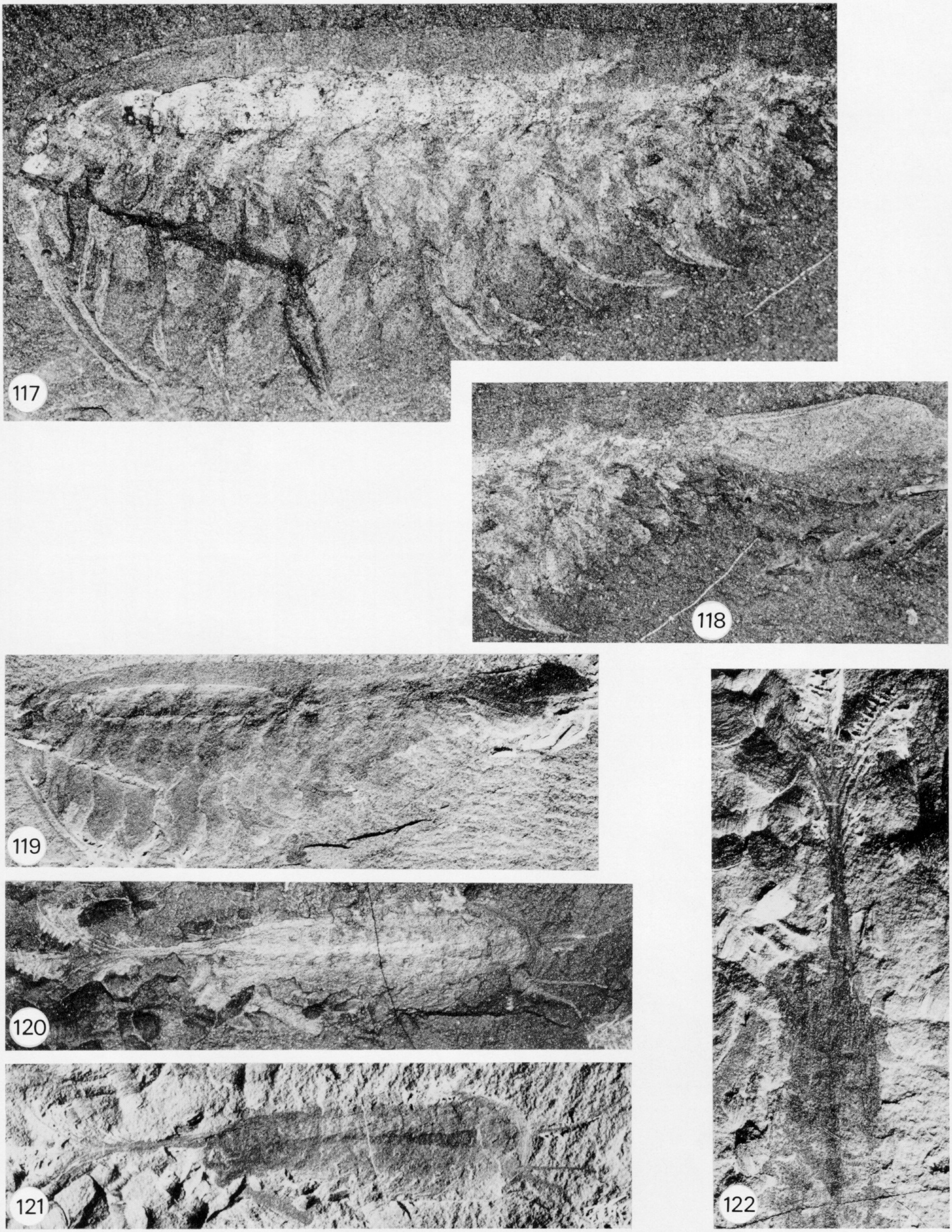
FIGURES 84–92. For description see opposite.



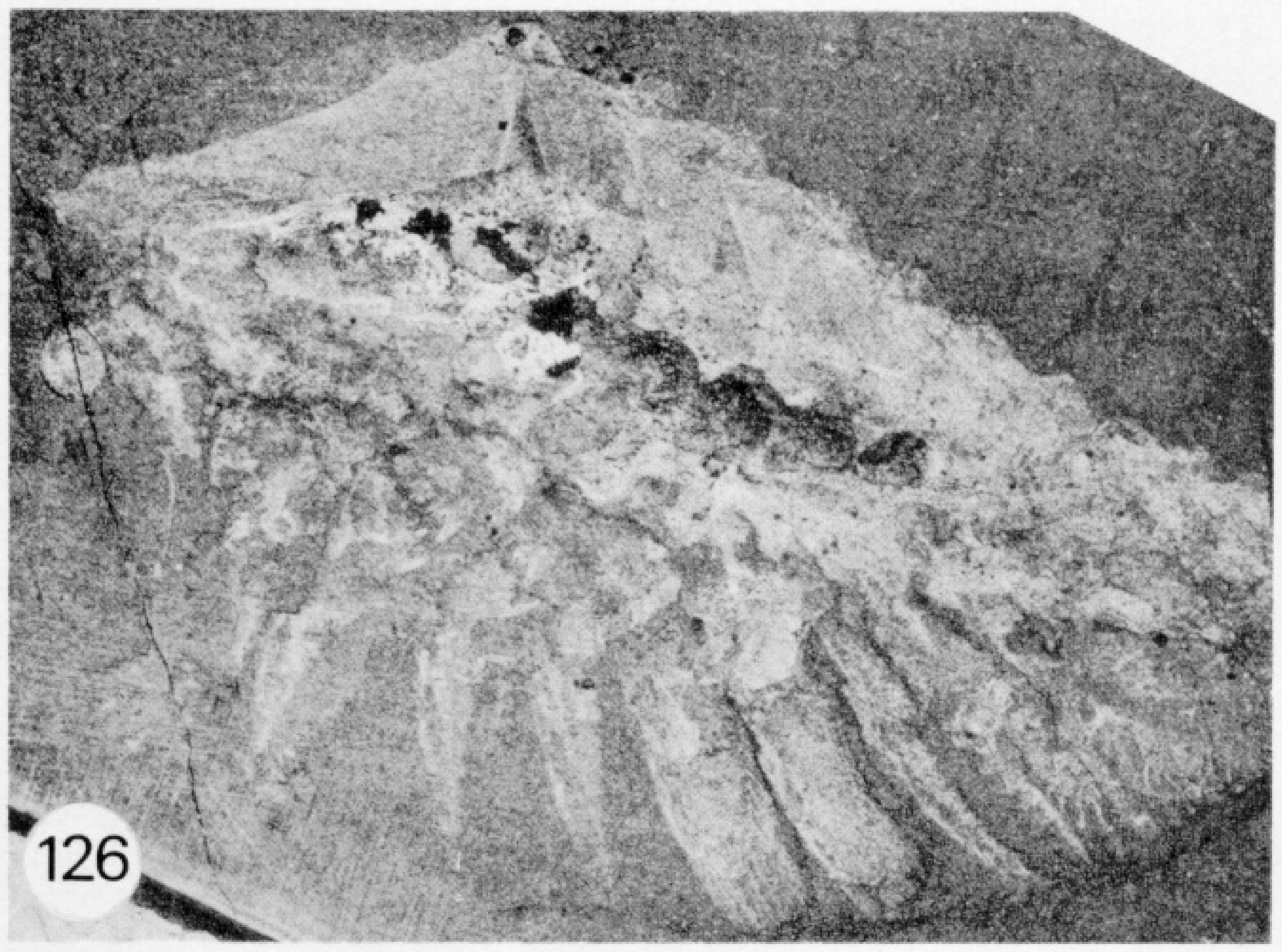
Figures 99–109. For description see opposite.



FIGURES 110–113. For description see opposite.



FIGURES 117–122. For description see opposite.



FIGURES 123–128. For description see opposite.