THE MORPHOLOGY, MODE OF LIFE, AND AFFINITIES OF *CANADASPIS PERFECTA* (CRUSTACEA: PHYLLOCARIDA), MIDDLE CAMBRIAN, BURGESS SHALE, BRITISH COLUMBIA

By D. E. G. BRIGGS†
Sedgwick Museum, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, U.K.

(*Communicated by H. B. Whittington, F.R.S. – Received* 17 *January* 1977)

[Plates 1–13]

CONTENTS

A detailed description and reconstruction of *Canadaspis perfecta* demonstrates its status as the earliest well-preserved crustacean. The cephalon consisted of five somites (in addition to the eyes), the thorax eight, and the abdomen seven, excluding the telson. Two pairs of apparently uniramous antennae flanked a median cephalic spine. The mandible bore a massive incisor process posterior of a molar area made up of finer

---

† Present address: Department of Geology, Goldsmiths' College, University of London, New Cross, London SE 14 6NW.

spines, and apparently lacked a palp. The first and second maxillae were essentially similar to the eight pairs of thoracopods, with a multisegmented inner ramus, and foliaceous outer ramus made up of wide filaments attached to a proximal lobe. A bivalved carapace covered the thorax; no rostral plate was present. The abdomen lacked appendages, apart from a pair of spinose ventral projections of the pre-telson somite. There was no caudal furca. The evidence suggests that *C. perfecta* fed on coarse particles, possibly with the aid of currents set up by the biramous appendages. The erection of a new order Canadaspidida and family Canadaspididae Novozhilov (in Orlov 1960) to include *Canadaspis* is vindicated, and they are re-defined and the subclass Phyllocarida amended to include them.

1. INTRODUCTION

Walcott (1912) originally referred five species (two tentatively) from the Middle Cambrian Burgess Shale to *Hymenocaris* Salter, 1853. These were removed to a new genus, *Canadaspis*, by Novozhilov (in Orlov 1960), and two further species from the same locality were added by Simonetta & Delle Cave (1975).

The opposing slab of the only figured specimen of *Hymenocaris*? *circularis* (Walcott 1912, pl. 32, fig. 4), which was recently discovered in the National Museum of Natural History collection (figure 5, plate 1), shows the appendages and carapace in a more complete state than the original (figure 6, plate 1). It is clearly a poorly preserved example of *Burgessia bella*, compacted obliquely, with at least seven of the left? limbs extending ventrally from beneath the carapace (cf. Hughes 1975, pl. 6, figs. 2, 5, 7, 9). Walcott (1912, p. 185) mentioned a number of valves of *H.*? *circularis* averaging '5–8 mm. in length', but there is no way of identifying these now. *H.*? *parva* was represented by two specimens (Walcott 1912, p. 185), only one of which was figured (Walcott 1912, pl. 32, fig. 7), and there is insufficient information to identify the second. A reinterpretation of the known example (Briggs 1977) has revealed the spinose nature of the carapace border, and the specimen is referred with a query to *Tuzoia* Walcott, 1912.

Walcott (1912) described *Hymenocaris ovalis* on the basis of two specimens, U.S.N.M. 57714 (figure 7, plate 1) and U.S.N.M. 57715 (figures 8, 9, plate 1). Simonetta & Delle Cave (1975) identified the latter as *Canadaspis perfecta* and designated U.S.N.M. 57714, a single valve, as the lectotype of *C. ovalis*, reconstructing the species on the evidence of further material. An isolated valve is not, however, considered a reliable basis for a species and Simonetta & Delle Cave's additional specimens have been removed (Briggs 1977) to *C. dictynna* Simonetta & Delle Cave, 1975, leaving *C. ovalis* occupied by the indeterminate lectotype alone. *H. obliqua* Walcott, 1912, and *C. obesa* Simonetta & Delle Cave, 1975, are synonymized with *H. perfecta* herein, and its reference to a new genus, *Canadaspis*, by Novozhilov (in Orlov 1960) upheld, but some individual specimens have been removed to a new genus and species, *Perspicaris recondita* Briggs, 1977. *C. dictynna* is also referred to *Perspicaris* (Briggs 1977). *C. perfecta* thus remains the only completely known species of *Canadaspis*.

Respositories are abbreviated as follows in prefixes to catalogue numbers:

G.S.C.	Geological Survey of Canada, Ottawa
M.C.Z.	Museum of Comparative Zoology, Harvard
S.M.	Sedgwick Museum, Cambridge
U.S.N.M.	National Museum of Natural History, Washington D.C.
Y.P.M.	Peabody Museum of Natural History, Yale.

2. TERMINOLOGY AND METHODS

The morphological terms used in the description are those of Moore & McCormick (in Moore 1969) as far as possible; the telson is not considered to be a true somite. The terms first and second antenna, first and second maxilla are used in preference to antennule and antenna, maxillule and maxilla respectively. Sagittal refers to the direction parallel to the long axis of the body, transverse to the direction normal to this.

The evidence upon which the reconstructions are based is illustrated, as far as possible, by the plates. Differences in level on the fossils are expressed by a minute 'scarp' on the specimen which either casts a shadow, or reflects light, depending on the angle of illumination. The orientation of the specimen relative to the bedding is given as *parallel*, *lateral*, *oblique*, etc. (see § 3). The photographs, except where otherwise indicated in the plate descriptions, were taken on fine grained, 35 mm panchromatic film in ultraviolet radiation. This radiation was directed at approximately 30° to the horizontal except where reflection was desirable when the angle was increased to about 65°. Some specimens were photographed immersed in alcohol on fine grained, half-plate, orthochromatic film, in ordinary light directed at a high angle. The use of this, and other variations in photographic technique, is indicated in the plate descriptions.

An interpretation of the specimens is presented where necessary as an adjacent camera lucida drawing. The specimens were rotated in relation to a unidirectional light source during the preparation of these drawings. Different aspects of the morphology are revealed by varying the direction and angle of illumination, so that all the features on the drawings may not be evident on the photographs. A list of abbreviations used on the plates and figures will be found at the end of the paper.

The statistical data used in the preparation of figures 107, 163, 177, and 178 are tabulated in the author's Ph.D. thesis, held by the University Library, Cambridge.

3. PRESERVATION

Whittington (1971*a*, pp. 1180–1196, 1198, fig. 24) discussed the preservation of *Marrella splendens* in detail, explaining the effect of variations in orientation to the bedding before compaction on the appearance of the fossil. Recognition of the orientation of a specimen permits

---

DESCRIPTION OF PLATE 1

FIGURES 5, 6. *Burgessia bella* Walcott, 1912. U.S.N.M. 57713, lateral. 5. Part, north. 6. Counterpart, east, holotype of *Hymenocaris? circularis* Walcott, 1912, pl. 32, fig. 4. (Magns × 4.)

FIGURE 7. *Canadaspis ovalis* (Walcott, 1912). U.S.N.M. 57714, lateral, north, original of Walcott 1912, pl. 32, fig. 5 (magn. × 2).

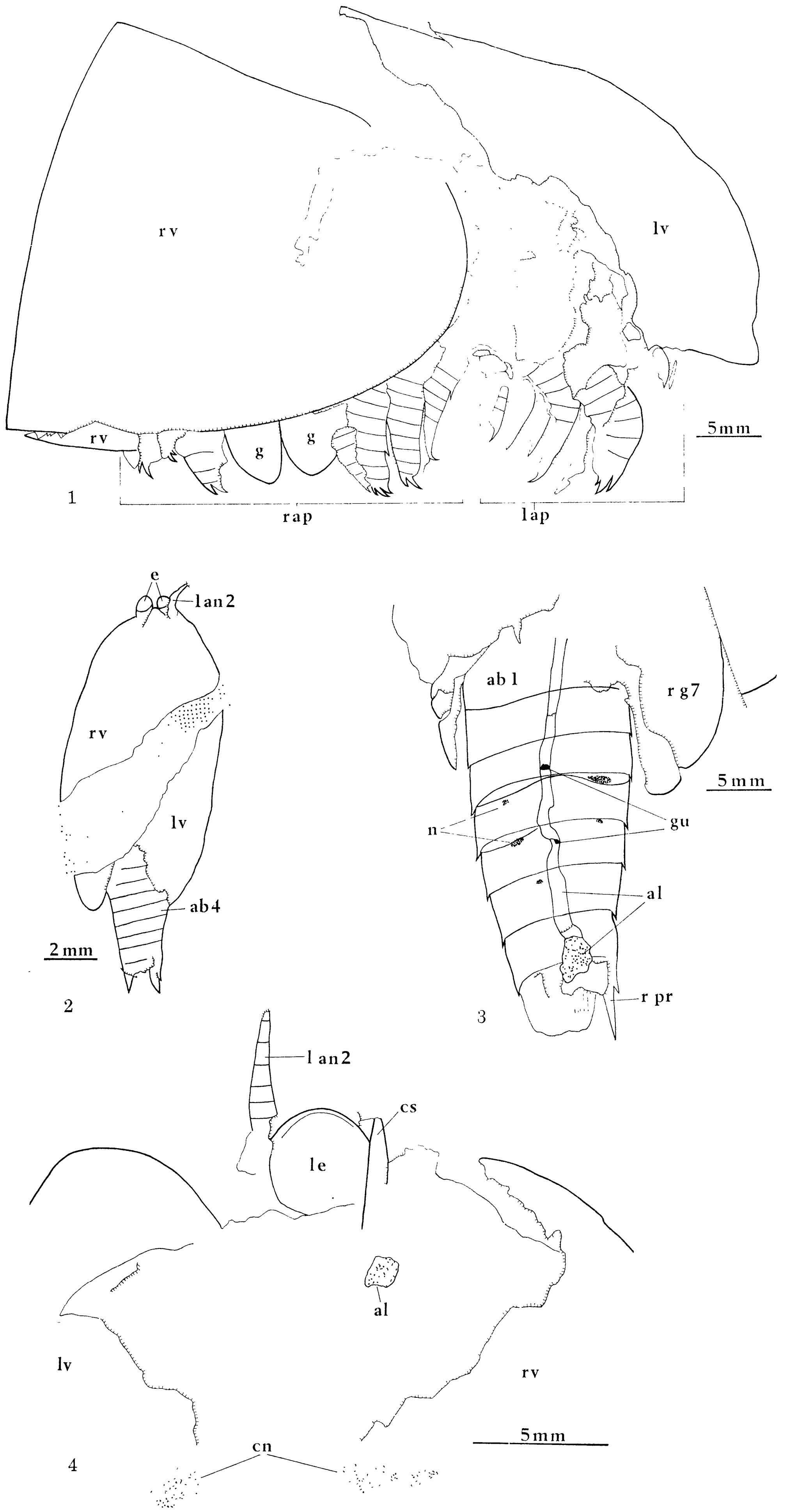
FIGURES 8, 9. *Canadaspis perfecta* (Walcott, 1912). U.S.N.M. 57715, parallel. 8. West. 9. Reflected, north. Original of Walcott 1912, pl. 32, fig. 6. (Magns × 4.)

FIGURES 10, 11. *Canadaspis perfecta* (Walcott, 1912). U.S.N.M. 189021, vertical-oblique. 10. Counterpart, reflected, south. 11. Part, east. (Magns × 1.5.)

FIGURE 12. *Canadaspis perfecta?* (Walcott, 1912). G.S.C. 45261, vertical, north (magn. × 1.5).

FIGURES 13–15. *Canadaspis perfecta* (Walcott, 1912). S.M. A1712, parallel. 13. North-east (magn. × 1). 14. Under alcohol, west, abdomen and dark stain (magn. × 1.5). 15. North-east, cephalic region (magn. × 3).

FIGURE 16. *Canadaspis perfecta* (Walcott, 1912). G.S.C. 45320, with electronic flash, surface wet with water (magn. × 0.15).



FIGURES 1–4. *Canadaspis perfecta* (Walcott, 1912). Explanatory drawings. 1. U.S.N.M. 189021, part. 2. U.S.N.M. 57715 3, 4. S.M. A1712, abdomen and cephalic region respectively.


5


6

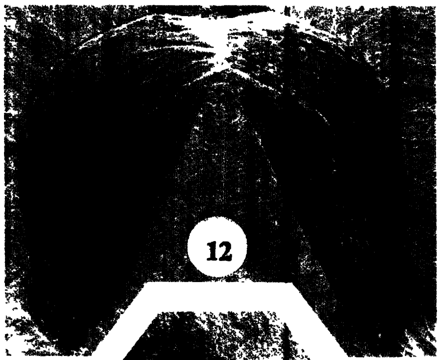

7


10


8

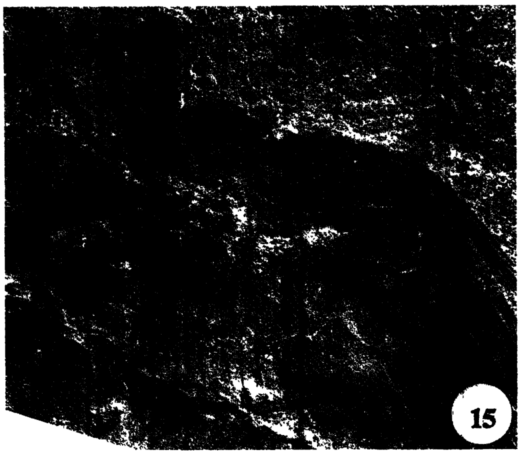

9

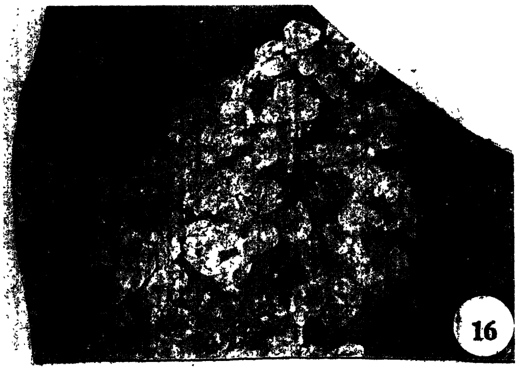

11


12


13


14


15


16

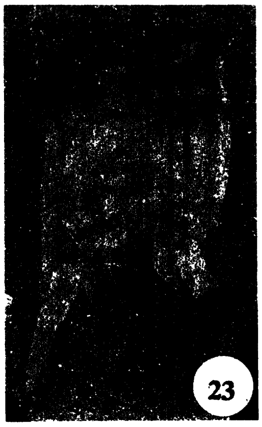

17


20


21


18


22


23


19


24


25

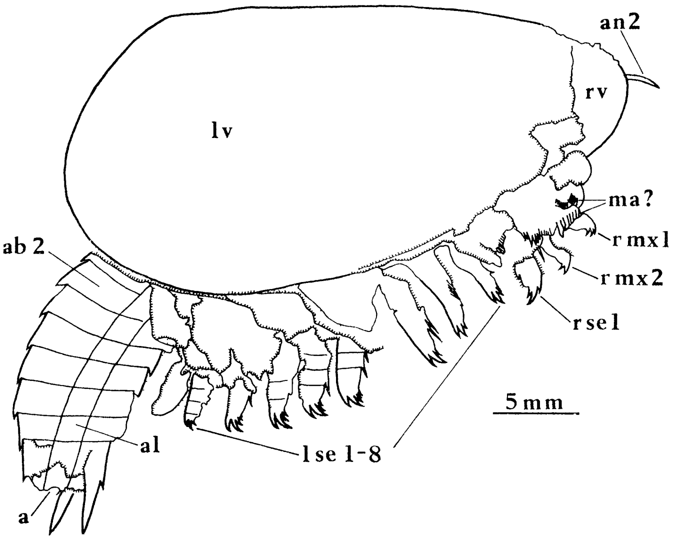


FIGURE 26. *Canadaspis perfecta* (Walcott, 1912). U.S.N.M. 57703, explanatory drawing of counterpart.

a differentiation between right and left, dorsal and ventral sides. The features exposed depend on the plane along which the fossil has split (Whittington 1975*a*, p. 9, fig. 3), but it is often possible to remove some of the specimen or matrix to reveal further information. The opposing slabs which have separated to expose the fossil are termed the *part* and *counterpart*. Specimens tend to split near the surface of one valve leaving the underlying trunk and appendages on one slab and an impression of the carapace on the other. The slab upon which most of the specimen remains is designated the *part*. Where the split is almost medial the distinction between *part* and *counterpart* is essentially arbitrary, but they are clearly identified in the plate descriptions.

Canadaspis perfecta shows a similar range of configurations to those described by Whittington (1971*a*) in *Marrella splendens*. Specimens which are orientated in *parallel* aspect, the sagittal plane normal to the bedding, preserve the cephalic appendages, carapace, and the trunk and telson arranged symmetrically about the mid-line along which runs the hinge or fold separating the valves. The preserved outline of the valves depends on the degree to which they are folded. This may be a function of the attitude or condition of the adductor muscles and consequent separation of the valves at burial; the greater the separation, the more complete the compacted outline of the carapace. The range of variation is illustrated by M.C.Z. 5977/70 (figure 40, plate 3) and U.S.N.M. 189018 (figures 74, 75, plate 6), for example, in which the valves are folded beneath themselves, and U.S.N.M. 189019 (figures 83, 84, plate 7) which shows the

---

DESCRIPTION OF PLATE 2

Canadaspis perfecta (Walcott, 1912)

FIGURE 17. U.S.N.M. 207310, north, specimen of *Naraoia* top left (magn. x 1.5).

FIGURES 18–20. U.S.N.M. 57703, lateral. 18. Part, north. 19. Counterpart, north, original of Walcott 1912, pl. 31, fig. 1. (Magns x 2.5.) 20. Counterpart, reflected, north, anterior appendages (magn. x 6).

FIGURE 21. U.S.N.M. 57705, parallel, reflected, east, original of Walcott 1912, pl. 31, fig. 3 (magn. x 4).

FIGURES 22, 23. U.S.N.M. 57707, parallel. 22. Part, reflected, north, original of Walcott 1912, pl. 31, fig. 5. 23. Counterpart, reflected, north. (Magns x 3.)

FIGURES 24, 25. U.S.N.M. 57708, parallel. 24. Counterpart, north, original of Walcott 1912, pl. 31, fig. 6, whereabouts of remainder unknown (magn. x 3). 25. Part, north (magn. x 1.5).

carapace border, although the valves display a considerable concentric folding peripherally to accommodate the original convexity. Specimens preserved in *lateral* aspect, the sagittal plane parallel to the bedding, preserve the valves and paired telson spines approximately superimposed (figures 18, 19, plate 2; figure 38, plate 3). *C. perfecta* also occurs in *oblique* aspect, intermediate between lateral and parallel, the outline of one valve approaching completeness, the other folded. U.S.N.M. 207295 (figure 141, plate 11), for example, preserves the outline of the left valve complete, and clearly demonstrates the compaction of the right valve beneath itself.

The relative abundances of specimens of *Canadaspis perfecta* preserved in the three main orientations outlined above which were collected by the Geological Survey of Canada in 1966 and 1967 (Whittington 1971 *a*) are tabulated below. The figures are based on specimens showing features in addition to the carapace, not on isolated valves. The percentages given by Whittington (1971 *a*, pp. 1182–1185) for *Marrella splendens* (the only other available data based on a sufficient sample) are included for comparison.

	C. perfecta	*M. splendens*
parallel	32 %	56–81 %
lateral	51 %	5–13 %
oblique	17 %	14–33 %
sample	301	318

The prevalent orientation of *C. perfecta* is lateral, in contrast to *M. splendens*, which is most frequently preserved in parallel aspect. This presumably reflects the difference in the gross morphology of the two arthropods. The carapace of *C. perfecta* affords a vertical planar dimension, whereas the cephalic shield of *M. splendens* is effectively horizontal.

A single positively identified specimen (showing features in addition to the carapace) is preserved with the saggital plane approaching a vertical orientation to the bedding (cf. *Marrella splendens*, Whittington 1971 *a*, p. 1187). U.S.N.M. 189021 (figures 10, 11, plate 1) is vertical-oblique in aspect with both valves folded about an axis normal to the hinge, and the appendages splayed in an unnatural attitude on either side of the trunk. A few specimens of isolated carapaces, probably *C. perfecta*, also occur in a near vertical orientation. G.S.C. 45261 (figure 12, plate 1), for example, illustrates how the carapace folded, concertina-fashion, when compacted along the hinge line. The relative positions of the cephalic shield and body in *M. splendens* tend to be fairly constant (Whittington 1971 *a*). Some complete individuals of *C. perfecta*, however, preserve the carapace thrown forward so that the hinge is at a high angle to the trunk. These are known in both lateral (figures 168, 171, 172, plate 13) and parallel aspect (figures 113, 114, plate 9) and some are interpreted as exuviae (§ 5*g*). Specimens of *Burgessia bella* with the carapace in a similar position were figured by Hughes (1975, pl. 3, fig. 8; pl. 4, fig. 1).

The Geological Survey of Canada collected as many examples of isolated valves and articulated carapaces (the vast majority presumably of *Canadaspis perfecta*) as they did complete individuals. This suggests that the carapace was strengthened relative to the rest of the cuticle, and was thus that part of both moults and dead individuals most commonly preserved. Isolated valves are abundant in the 'Fossil Beds' on Mount Stephen, for example, where more complete individuals are unknown. Analogies occur in the Recent Malacostraca (Schäfer 1972, p. 431); the elements of an exuvia are commonly not equally well preserved due to variations in the degree of calcification. A few complete exuviae of *C. perfecta* have, however, been recognized

(§ 5*g*), and fragmentary material other than the carapace is also known, including examples of the telson (figures 21–23, plate 2), abdomen (figures 118, 119, plate 10), and almost complete individuals with appendages (figure 89, plate 8). Whittington (1971 *b*, p. 19), on the other hand, noted that 'the overwhelming majority of specimens (of *Marrella splendens*) appear to have been whole animals when buried', and (Whittington 1971 *a*, p. 1188) that 'specimens showing only the cephalic shield are extremely rare (less than one per cent)'. The exuviae of *M. splendens*, and of *Yohoia tenuis* (Whittington 1974, p. 7) and *Burgessia bella* (Hughes 1975), which display a similar degree of completeness, were thus apparently not as robust as the carapace of *C. perfecta*, or the relatively common trilobite moults.

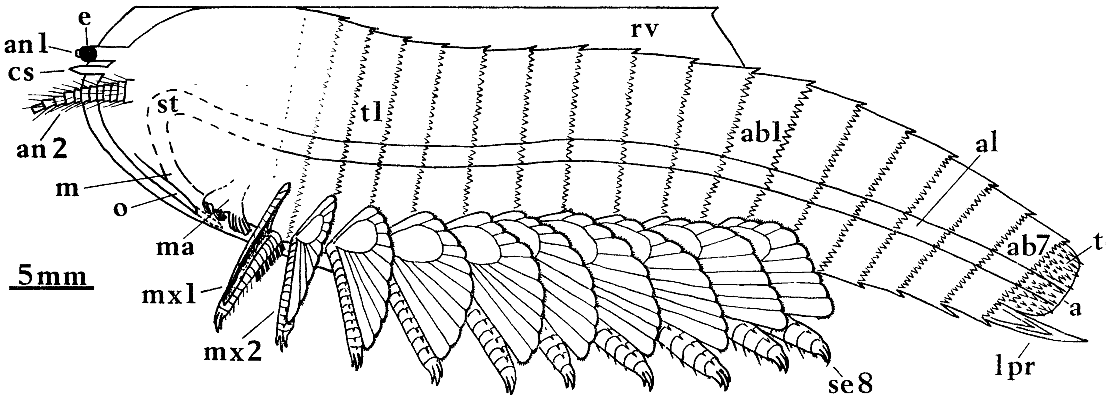


FIGURE 27. Diagrammatic reconstruction of *Canadaspis perfecta* (Walcott, 1912) in lateral view; left valve removed, and only left appendages shown.

Most specimens of *Canadaspis perfecta* which include features in addition to the carapace appear, however, to have been complete when buried. Variations in preservation are mainly due to subsequent, little understood processes. The majority of specimens composed of the dark, shiny film characteristic of the Burgess Shale fauna which the Geological Survey of Canada collected came from the quarry interval 2.18 m (7 ft 2 in) to 2.34 m (7 ft 8 in) (see Whittington 1971 *a*, p. 1176). Inferior preservation, which is more prevalent above and below this favourable horizon, is usually the result of the alteration of the dark film to a reddish material (due to oxidation?) with a corresponding loss of fine detail. A large proportion of the material of *C. perfecta* has been altered by this process, which is not confined to any particular level in the quarry. Only a few individuals on a slab bearing several may be affected, and specimens occur which are only partially altered (the posterior part of U.S.N.M. 189017, for example, figure 66, plate 5).

A 'dark stain' which 'is almost universally associated with specimens of *Marrella splendens*' (Whittington 1971 *a*, p. 1188), and has also been noted in *Yohoia tenuis* and *Opabinia regalis* (Whittington 1974, p. 13; 1975 *a*, p. 11), rarely occurs on specimens of *Canadaspis perfecta*. The only known extensive example is preserved in the vicinity of the telson of SM A1712 (figure 14, plate 1) and extends some distance posterior of it. More restricted stains are present just beyond the posterior border of the telson of a few specimens (figure 111, plate 9). Their position suggests that the stain may represent traces of organic matter exuded from the anus during decay.

Canadaspis perfecta shows a marked tendency to occur in clusters of a few to over 100 overlapping individuals (figure 16, plate 1). This phenomenon is not confined to particular levels in the quarry; clusters are present at the same horizons as numerous isolated individuals. The

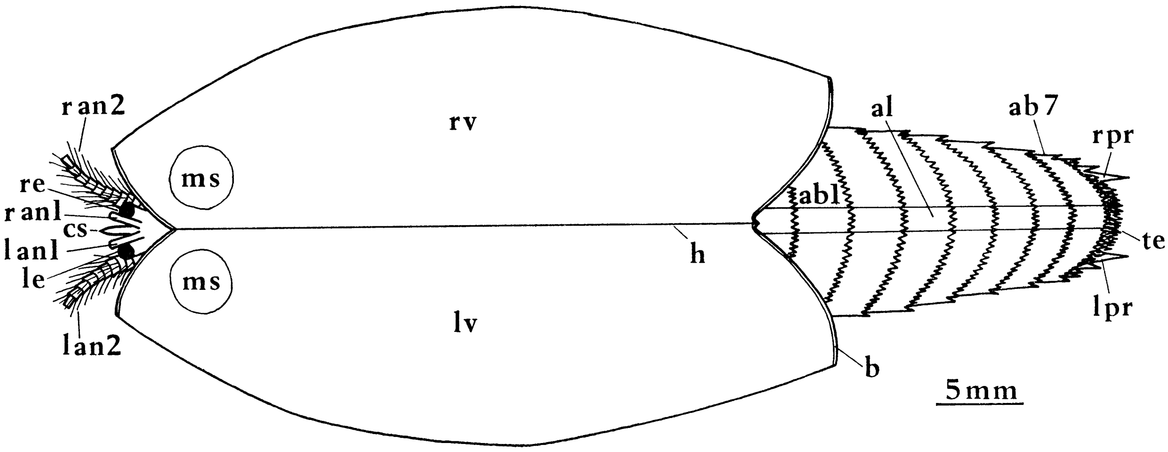


FIGURE 28. Reconstruction of *Canadaspis perfecta* (Walcott, 1912) in dorsal view.

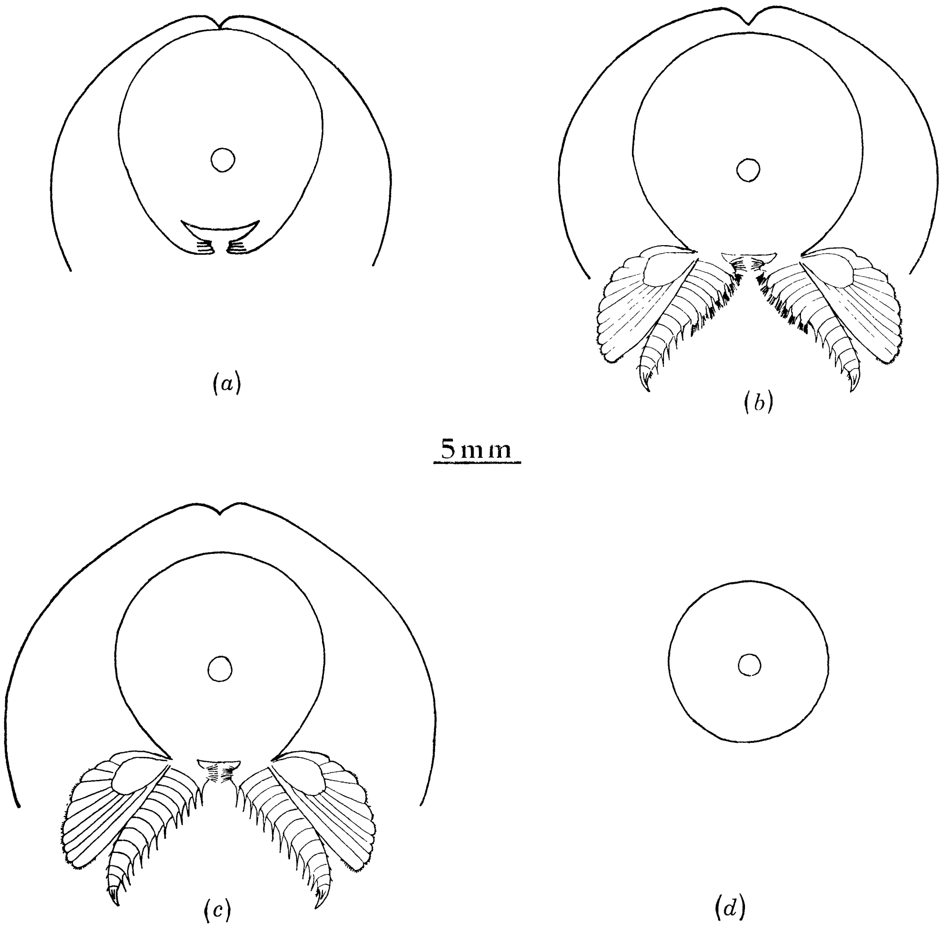


FIGURE 29. Diagrammatic cross-sections of *Canadaspis perfecta* (Walcott, 1912) through somites bearing (*a*) mandible (showing incisors only), (*b*) first maxilla, (*c*) second thoracic appendage, and (*d*) through fourth abdominal somite.

clusters appear to contain similar proportions of complete individuals and isolated carapaces as the collection as a whole, but this is difficult to verify as preservation is commonly poor, and specimens overlap. Other members of the fauna are also occasionally included (*Naraoia compacta* for example, figure 17, plate 2), but are rarely found in similar groupings themselves. The cause of clustering is not apparent. There is some indication of a preferred orientation, but sorting is confined to a gross level – the size distribution is bimodal (see §5*h*) and the two frequency groups do not tend to occur in association. Only one example of a cluster of smaller juveniles is known (figure 17, plate 2). Clustering may be due to sedimentary processes, but it is possible that *C. perfecta* tended to congregate in groups (the smaller juveniles separate) which were overcome, perhaps while feeding on the surface of the substrate, by the postulated slow-moving non-turbulent cloud of sediment (Whittington 1971*a*, p. 1197).

Fragments of the carapace of several specimens of *Canadaspis perfecta* were prepared and examined under the scanning electron microscope for primary microstructures. No evidence of canals or laminae was noted and it proved difficult to distinguish the carapace from either the matrix or the underlying layers of the body. The original structure of the cuticle thus appears to have been destroyed by alteration.

4. Systematic Palaeontology

Class *MALACOSTRACA* Latreille, 1806

Subclass *PHYLLOCARIDA* Packard, 1879

Diagnosis. Malacostraca with carapace of two valves, with or without dorsal hinge line, connected by adductor muscle. Thorax of eight short, free somites; abdomen of seven somites and telson.

Order CANADASPIDIDA Novozhilov (in Orlov), 1960

Diagnosis. Carapace with hinge line, rostral plate absent, first and second antennae uniramous; abdominal somites lacking pleopods.

Family Perspicarididae Briggs, new family

Diagnosis. Furca present.

Referred genus. *Perspicaris* Briggs, 1977.

Family Canadaspididae Novozhilov (in Orlov), 1960

Diagnosis. Furca absent.

Genus *Canadaspis* Novozhilov (in Orlov), 1960

Type species. *Hymenocaris perfecta* Walcott, 1912, designated Novozhilov (in Orlov), 1960.

Diagnosis. Eyes pedunculate, separated by median cephalic spine. First antenna reduced, second antenna small, multisegmented. First and second maxillae similar to thoracopods which are biramous, undifferentiated; inner ramus ambulatory, multisegmented; large, lamellate outer ramus divided into rays borne by a flattened proximal lobe. Pre-telson somite bearing spinose processes ventrally.

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

Canadaspis perfecta (Walcott, 1912)

1912 *Hymenocaris perfecta* Walcott, pp. 149, 151–153, 183–185, 222, pl. 31, figs. 1, 3, 5, 6, *non* figs. 2, 4.
1912 *Hymenocaris obliqua* Walcott, pp. 153, 185, pl. 32, figs. 1, 2? 3?
1912 *Hymenocaris ovalis* Walcott, pp. 153, 185, pl. 32, fig. 6.
1919 *Hymenocaris perfecta* Walcott, p. 219.
1920a *Hymenocaris*; Raymond, pp. 113–114, 142.
1920b *Hymenocaris*; Raymond, p. 405.
1923 *Hymenocaris ovalis*; Chapman, p. 41.
1925 *Hymenocaris perfecta*; Fedotov, pp. 386–387, 389.
1925 *Hymenocaris obliqua*; Fedotov, p. 386.
1925 *Hymenocaris ovalis*; Fedotov, p. 386.
1928 *Hymenocaris*; Broili, pp. 15, 18.
1928 *Hymenocaris perfectus*; Henriksen, p. 2.
1928 *Hymenocaris perfecta*; Henriksen, pp. 14–15.
1928 *Hymenocaris obliqua*; Henriksen, p. 14.
1928 *Hymenocaris ovalis*; Henriksen, p. 14.
1929 *Hymenocaris perfecta*; Gürich, pp. 41–42.
1929 '*Hymenocaris*' *perfecta*; Gürich, p. 39, fig. 2, nos. 1, 1*b*, *non* 1*a*.
1929 *Hymenocaris obliqua*; Gürich, p. 41.
1929 '*Hymenocaris*' *obliqua*; Gürich, p. 39, fig. 2, no. 2.
1929 *Hymenocaris ovalis*; Gürich, p. 41.
1930 *Hymenocaris perfecta*; Sherrard, pp. 136–137.
1934 ?*Hymenocaris perfecta*; Straelen & Schmitz, pp. 34, 199, 211, 232.
1934 ?*Hymenocaris obliqua*; Straelen & Schmitz, pp. 33–34, 199, 211, 232.
1934 ?*Hymenocaris ovalis*; Straelen & Schmitz, pp. 34, 199, 211, 232.
1935 *Hymenocaris perfecta*; Raymond, pp. 220–221, 224.
1936 *Hymenocaris obliqua*; Westergard, p. 61.
1939 *Hymenocaris*; Størmer, pp. 231–232, 237, 262.
1944 *Hymenocaris perfecta*; Størmer, p. 97, fig. 19, no. 9, pp. 100–101, 106–107, 109, 124, 130, 135.
1944 *Hymenocaris perfecta*; Shimer & Shrock, pl. 277, fig. 1, p. 655.
1945 *Hymenocaris*; Linder, pp. 20–21, 26.
1949 *Hymenocaris perfecta*; Størmer, p. 205, fig. 32, p. 209, fig. 36, no. 9.
1953 *Hymenocaris perfecta*; Dechaseaux, pp. 37–39, p. 38, fig. 12.
1958 *Hymenocaris perfecta*; Tiegs & Manton, p. 291, fig. 6d, p. 295.
1960 *Canadaspis perfecta*; Novozhilov (in Orlov), p. 198, fig. 442, p. 199.
1960 *Hymenocaris perfecta*; Novozhilov (in Orlov), p. 199.
1960 *Hymenocaris perfecta*; Jux, p. 1146.
1962 *Canadaspis perfecta*; Rolfe, pp. 2, 4, 7.
1962 *Canadaspis obliqua*; Rolfe, p. 7.
non 1962 *Canadaspis ovalis*; Rolfe, p. 7 (= *Naraoia compacta* Walcott, 1912).
1963a *Canadaspis perfecta*; Rolfe, p. 391.
1963*b* *Canadaspis*; Rolfe, p. 19.

1968 *Canadaspis perfecta*; Öpik, pp. 7, 9–13, 16–17.
1968 *Canadaspis obliqua*; Öpik, p. 9.
1969 *Canadaspis perfecta*; Rolfe (in Moore), pp. 299, 303–304, 310, 323–324, fig. 149, nos. 4*a*, 4*b*.
1971a *Canadaspis perfecta*; Whittington, p. 1175.
1975b *Canadaspis perfecta*; Whittington, p. 102.
1975 *Canadaspis perfecta*; Simonetta & Delle Cave *pars*, p. 11, pl. 5, fig. 1, pl. 38, figs. 1–5, 7–11, (*non* fig. 6), pl. 39, fig, 2, 4–6, pl. 40, figs, 1?, 3–5?
1975 *Canadaspis obesa* Simonetta & Delle Cave *pars*, p. 12, pl. 5, fig. 2, pl. 39, fig. 1, pl. 40, fig. 6?, 15?, (*non* fig. 10).
1975 *Canadaspis* sp. Simonetta & Delle Cave *pars*, pl. 39, figs. 3, 7.
?1975 *Protocaris pretiosa*; Simonetta & Delle Cave *pars*, pl. 53, fig. 8.
1976 *Canadaspis perfecta*; Simonetta, fig. 7, no. 34.
1976 *Canadaspis perfecta*; Briggs, pp. 9, 13.

Lectotype (designated herein). U.S.N.M. 57703 part, figure 18, plate 2, original of Simonetta & Delle Cave 1975, pl. 38, fig. 1*b*, and counterpart, figures 19, 20, plate 2, original of Walcott 1912, pl. 31, fig. 1; Shimer & Shrock 1944, pl. 277, fig. 1; Størmer 1949, p. 205, fig. 32; Dechaseaux 1953, p. 38, fig. 12; Simonetta & Delle Cave 1975, pl. 38, fig. 1*a*; and of line drawings of Gürich 1929, p. 39, fig. 2, no. 1; Størmer 1944, p. 97, fig. 19, no. 9, and 1949, p. 209 fig. 36, no. 9; Tiegs & Manton 1958, p. 291, fig. 6*d*; Novozhilov (in Orlov) 1960, p. 198, fig. 442; Rolfe (in Moore) 1969, fig. 149, 4*b*.

Other previously figured specimens. U.S.N.M. 57705, figure 21, plate 2, original of Walcott 1912, pl. 31, fig. 3; Simonetta & Delle Cave 1975, pl. 39, fig. 3: U.S.N.M. 57707 part, figure 22, plate 2, original of Walcott 1912, pl. 31, fig. 5; Gürich 1929, p. 39, fig. 2, no. 1*b* (line drawing); Simonetta & Delle Cave 1975, pl. 39, fig. 2, and counterpart, figure 23, plate 2: U.S.N.M. 57708 part, figure 25, plate 2, original of Simonetta & Delle Cave 1975, pl. 39, fig. 6, and counterpart, figure 24, plate 2, original of Walcott 1912, pl. 31, fig. 6 (whereabouts of a portion unknown): U.S.N.M. 57710, figure 38, plate 3, original of Walcott 1912, pl. 32, fig. 1; Gürich 1929, p. 39, fig. 2, no. 2 (line drawing); Simonetta & Delle Cave 1975, pl. 38, fig. 2: U.S.N.M. 57715, figures 8, 9, plate 1, original of Walcott 1912, pl. 32, fig. 6; Simonetta & Delle Cave 1975, pl. 38, fig. 8: M.C.Z. 5977/70, figures 40, 41, plate 3, original of Rolfe (in Moore) 1969, fig. 149, no. 4*a*, discussed by Raymond 1935, p. 221.

U.S.N.M. 189016, 189017 (cited by Simonetta & Della Cave 1975 as 189253 and 189252), 189254, 189255, 189023 (cited 189256), 189243, 189015 (cited 189257), originals of Simonetta & Delle Cave 1975, pl. 38, figs. 3, 4, 5, 7, 9, 10, 11 respectively: U.S.N.M. 189019 (cited 189258), 189182, 189018 (cited 189259), 189241, Simonetta & Delle Cave 1975, pl. 39, figs. 1, 4, 5, 7 respectively.

Additional material. U.S.N.M. 189021, 207262–207307, 207310–207311, 213825–213831, 213837, 213851–213861, 213863–213865, 240992, and over 4300 additional specimens collected by Walcott, many of which can not be unequivocally identified as *Canadaspis perfecta* due to inadequate preservation: G.S.C. 45261–45306, and some 870 additional specimens collected by the Geological Survey of Canada expeditions of 1966 and 1967 (of which only about 25% can be identified with certainty) including two large slabs with approximately 200 and 75 individuals respectively; earlier collections held by the G.S.C. include G.S.C. 45279 and about 100 further specimens (15 of which can be unequivocally referred to the species): M.C.Z. 5977/1–5977/74, 5978/1–5978/2, listed by Rolfe (1962, p. 7) as *C. perfecta*, and 5980/1–5980/7, listed as *C. obliqua*, which together include 35 specimens positively identified as *C. perfecta* (Rolfe 1963*b*, p. 19, gives a figure of 202 for the number of specimens held by the Museum of Comparative Zoology, but this refers to *Marrella splendens*, see Rolfe 1962, p. 6): Y.P.M. 5801, 5832–5835, and a slab with some 15 poorly preserved individuals: S.M. A1712: small collections held by the American Museum of Natural History, the New York State Museum, the Mineralogisk Museum, Copenhagen, the Paleontologisk Museum, Oslo and elsewhere, including about 700 specimens collected by a Royal Ontario Museum expedition in 1975, many too poorly preserved to be identified as *C. perfecta* with certainty, intended for distribution to various museums and universities in Canada.

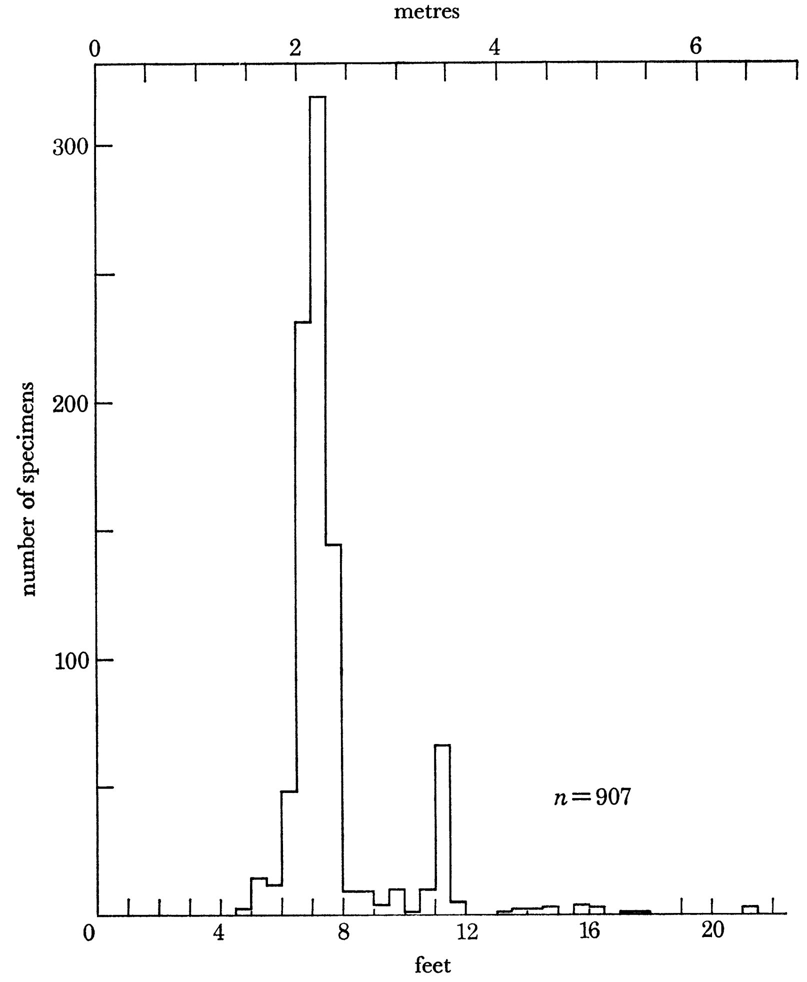


FIGURE 30. Numbers of specimens of *Canadaspis perfecta* collected from the Walcott Quarry by the G.S.C. expeditions of 1966 and 1967, counted in 6-inch intervals. Isolated carapaces, and other individuals too poorly preserved to be positively identified as *C. perfecta*, are included. Thus rare specimens of *Perspicaris* Briggs, 1977 may be represented, but this will not affect the distribution materially. The base of the Phyllopod Bed is at the level of 1.52 m (5 feet; see Whittington 1971*a*, fig. 3).

Locality and stratigraphical horizon. Middle Cambrian, Stephen Formation, Burgess Shale Section, *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone, situated on the ridge between

Wapta Mountain and Mount Field, at an elevation of approximately 2286 m (7500 feet), 4.8 km (3 miles) north of Field, southern British Columbia (see Fritz 1971, for an account of the stratigraphy).

Figure 30 shows the levels in the Walcott Quarry at which the specimens collected by the G.S.C. expeditions of 1966 and 1967, including those too poorly preserved to be positively identified as the species *Canadaspis perfecta*, occurred. The positions of these levels are indicated by Whittington (1971*a*, figs. 2, 3). Over 75% of the specimens were collected between 1.98 m (6 ft 6 in) and 2.44 m (8 feet), supporting Walcott's (1912, p. 152) observation that a 'great *Hymenocaris perfecta* bed' occurred from 2.26 m (7 ft 5 in) to 2.49 m (8 ft 2 in), correlating the base of Walcott's layer 12 with the G.S.C. level of 1.52 m (5 feet), as indicated by Whittington, 1971*a*, p. 1176). Walcott emphasized an abundance of *C. perfecta* at two additional horizons, layers 10, 1.60 m (5 ft 3 in) to 2.01 m (6 ft 7 in), and 5, 2.69 m (8 ft 10 in) to 2.74 m (9 feet), the latter also characterized by the presence of *Eldonia ludwigi*. The G.S.C. expeditions collected a significant number of specimens from the level of layer 10, but although Whittington (1971*a*, p. 1176) records the occurrence of a horizon similar to layer 5 between 2.62 m (8 ft 7 in) and 2.67 m (8 ft 9 in), yielding *E. ludwigi*, the numbers of *C. perfecta* obtained from about this level did not emulate Walcott's original observation. Walcott (1912, p. 153) recorded 'scattered valves' of *C. perfecta* above layer 5 but did not note a poorly preserved concentration exploited by the G.S.C. expeditions between 3.35 m (11 feet) and 3.51 m (11 ft 6 in). The distribution of *C. perfecta*, although it does not correspond in detail, is similar to that of *Marrella splendens* (Whittington 1971*a*, fig. 5; 1971*b*, text-fig. 1), *Yohoia tenuis* (Whittington 1974, text-fig. 1) and *Burgessia bella* (Hughes 1975, fig. 1) in that the majority of specimens occur around the level of 2.13 m (7 feet).

The precise levels from which the material of *Canadaspis perfecta* other than that collected by the G.S.C. in 1966 and 1967 was obtained are unknown. The specimens are associated with many other members of the fauna, notably *Ottoia prolifica*, *Scenella varians* and *Marrella splendens*, but this information is of little use in assigning them to particular levels in the quarry. All the labelled specimens in Walcott's collection in the National Museum of Natural History, except one, bear the locality number 35 k, indicating the 'Phyllopod bed' in the Walcott Quarry. The

---

DESCRIPTION OF PLATE 3 AND FIGURES 31–37

Canadaspis perfecta (Walcott, 1962)

FIGURES 31–37. Explanatory drawings of the cephalic region. 31. M.C.Z. 5977/70. 32. U.S.N.M. 207290. 33. G.S.C. 45266. 34. U.S.N.M. 207296. 35. Y.P.M. 5833. 36. M.C.Z. 5977/28. 37. U.S.N.M. 213860.

FIGURE 38. U.S.N.M. 57710, lateral, west, original of Walcott 1912, pl. 32, fig. 1 (magn. × 2).

FIGURE 39. U.S.N.M. 207286, lateral, east (magn. × 1.5).

FIGURES 40, 41. M.C.Z. 5977/70, parallel. 40. Reflected, north (magn. × 3). 41. South, cephalic region in dorsal aspect (magn. × 6). Original of Rolfe in Moore 1969, fig. 149, 4*a*.

FIGURE 42. U.S.N.M. 207290, parallel, north-west, cephalic region in ventral aspect (magn. × 4).

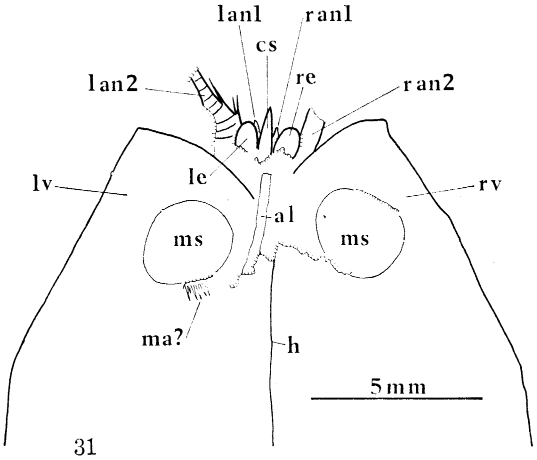
FIGURES 43, 44. G.S.C. 45266, lateral. 43. North-west (magn. × 1.5). 44. West, cephalic appendages (magn. × 6).

FIGURE 45. U.S.N.M. 207296, parallel, reflected, north, cephalic region in ventral aspect (magn. × 4).

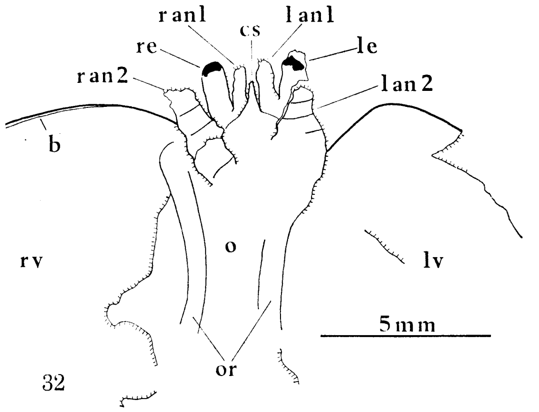
FIGURE 46. Y.P.M. 5833, lateral-oblique, north-east, cephalic appendages (magn. × 5).

FIGURE 47. M.C.Z. 5977/28, parallel, south-west, cephalic region in ventral aspect (magn. × 4).

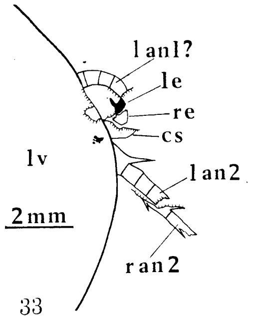
FIGURES 48, 49. U.S.N.M. 213860, parallel. 48. West. 49. Under alcohol, north-west. Cephalic region in ventral aspect. (Magns × 5.)



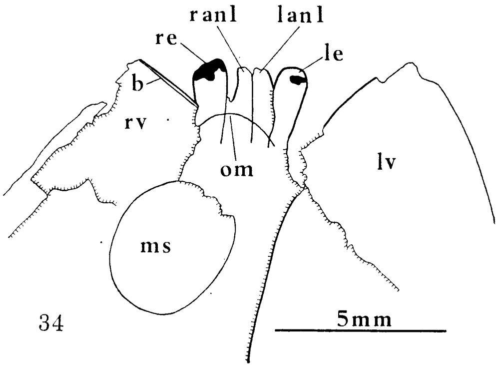
31



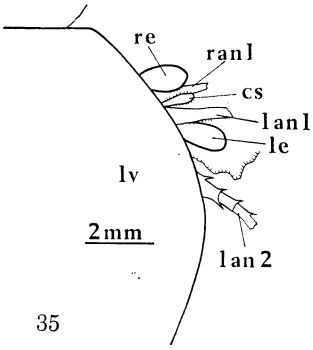
32



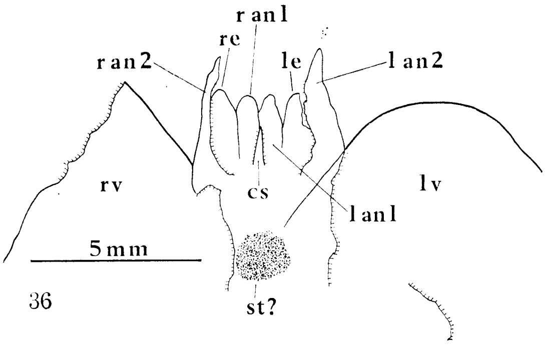
33



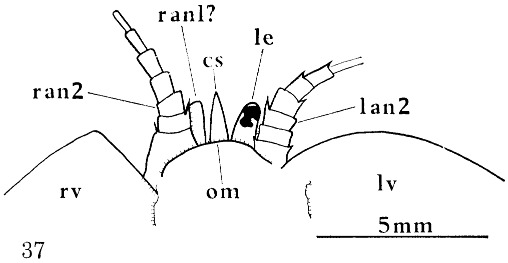
34



35

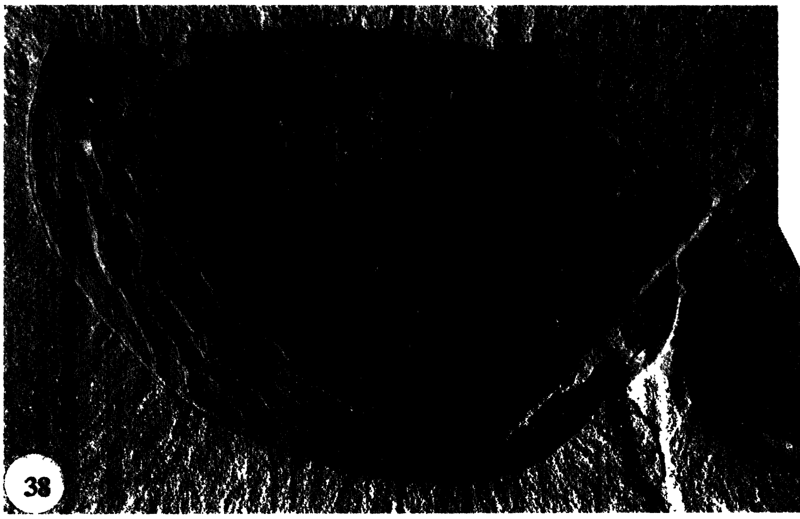


36



37

FIGURES 31-37. For description see p. 451.


38


39


42


40

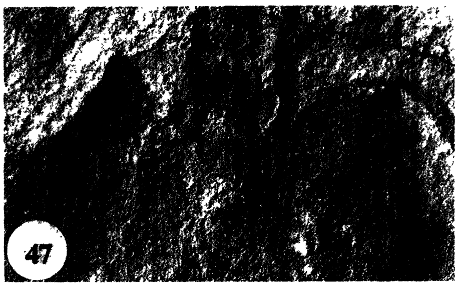

41


44


43


45


46

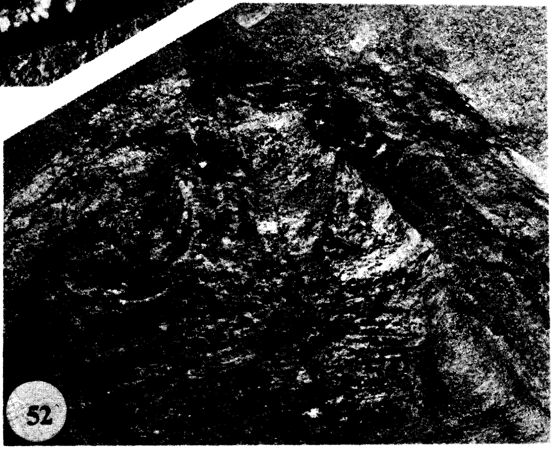

47

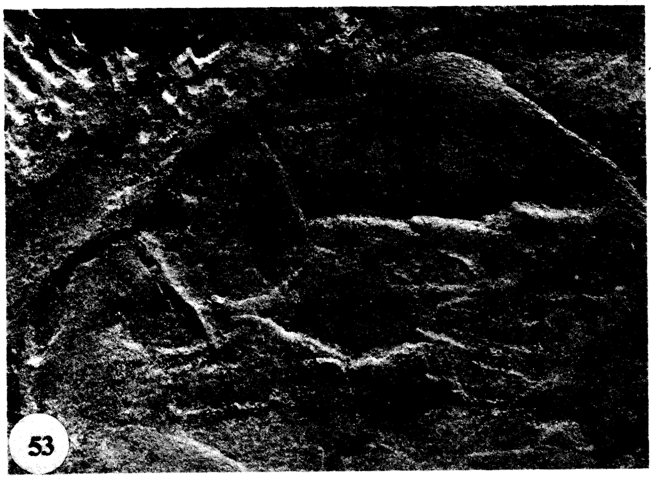

48

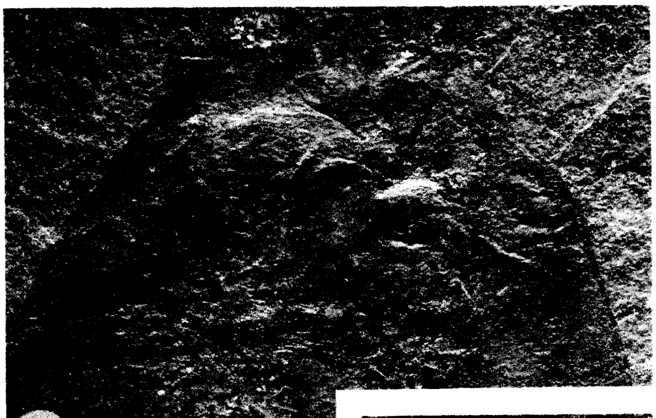

49

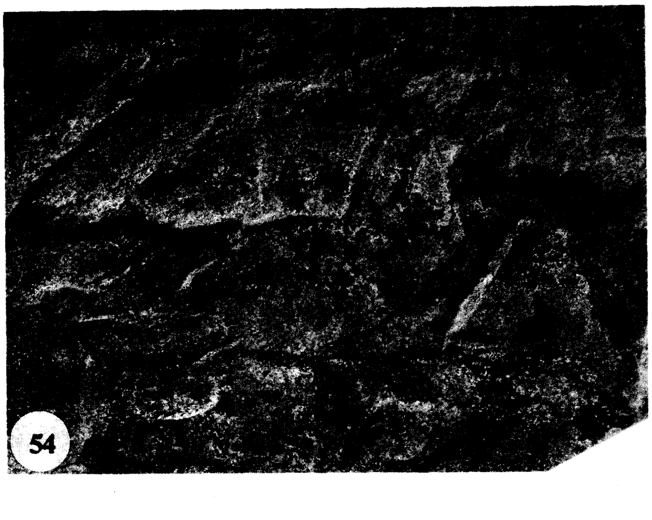

50


51

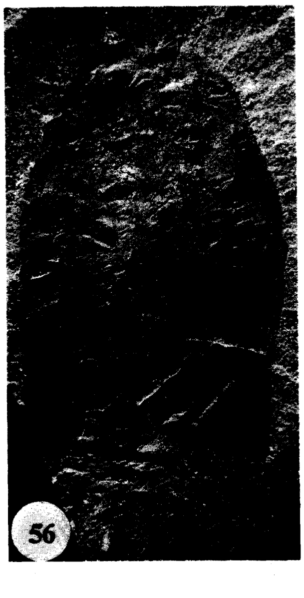

52

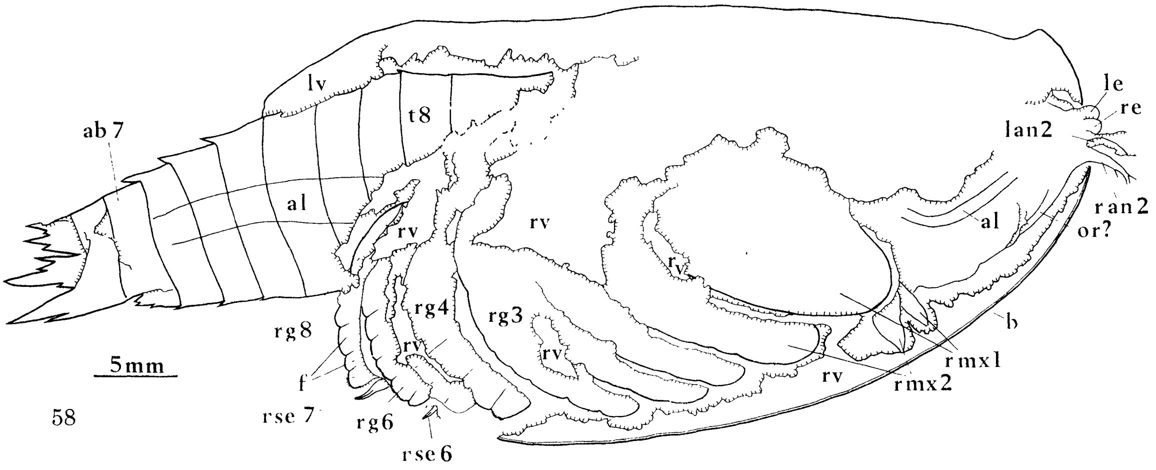

53


55

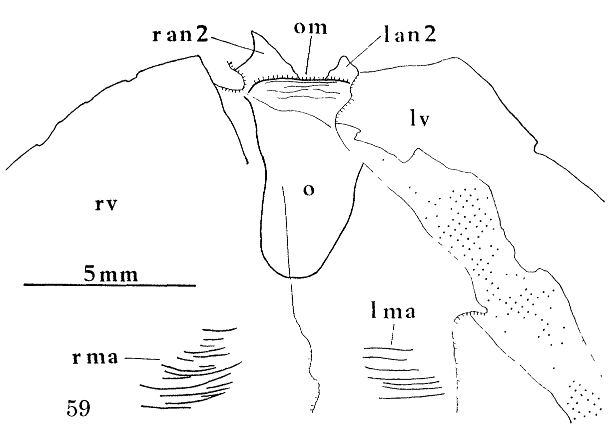

54


57

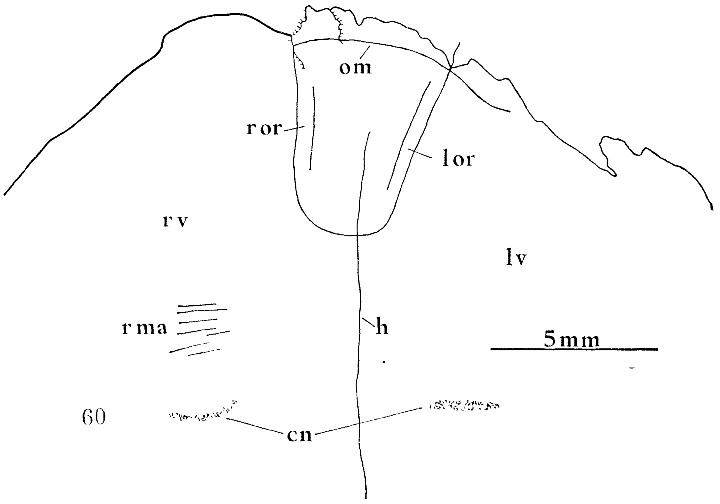

56



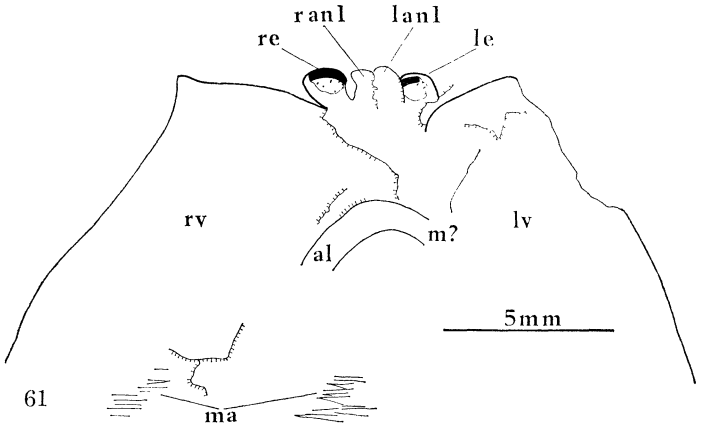
58



59



60



61

DESCRIPTION OF PLATE 4 AND FIGURES 58–61

Canadaspis perfecta (Walcott, 1912)

FIGURES 50, 51. U.S.N.M. 213856, lateral. 50. West, right valve removed to reveal cephalic region and right appendages (magn. x 2.5). 51. East (magn. x 1.5).

FIGURE 52. U.S.N.M. 213853, parallel, reflected, north, cephalic region in ventral aspect (magn. x 4).

FIGURES 53, 54. G.S.C. 45267, parallel. 53. Part, north-east. 54. Counterpart, north-west. Cephalic region in ventral aspect. (Magns x 4.)

FIGURES 55, 56. U.S.N.M. 207277, parallel. 55. North, cephalic region in ventral aspect (magn. x 4). 56. North (magn. x 1.5).

FIGURE 57. G.S.C. 45272, parallel, north, cephalic region in ventral aspect (magn. x 4).

FIGURES 58–61. Explanatory drawings. 58. U.S.N.M. 213856, with right valve removed. 59. U.S.N.M. 213853, cephalic region. 60. G.S.C. 45267, cephalic region of counterpart. 61. U.S.N.M. 207277, cephalic region.

single exception, U.S.N.M. 207286 (figure 39, plate 3), is labelled 35k/10 and presumably came from the 'Raymond Quarry' 19.8–22.9 m (65–75 feet) above the base of the main section (Whittington 1971*a*, pp. 1172–1173, fig. 1). Early collections held by the G.S.C. include some Walcott specimens (labelled 35k) and material obtained from the 'Burgess shale' by L. D. Burling and others. The examples in the Museum of Comparative Zoology are labelled 'Burgess shale, Middle Cambrian, Field, B.C. – Raymond collection, 1930'. The slab bearing M.C.Z. 5978/1 and 5978/2 carries the number 35k in addition, and was evidently one of Walcott's specimens. The specimens held by the Yale Peabody Museum and the Sedgwick Museum are labelled 35k and were also presumably collected by Walcott. The collection made by the Royal Ontario Museum in 1975 was based on the debris left by earlier expeditions and nothing in situ was removed.

Isolated carapaces, possibly of *Canadaspis perfecta*, are known from other Middle Cambrian localities in North America. These include specimens which Walcott considered to represent the carapace of *Anomalocaris* (Walcott 1908*a*, *A.? whiteavesi*, p. 15, pl. 2, figs. 2, 2*a*, *non* 4, 6, 6*a*; *A. canadensis*, p. 15, pl. 2, fig. 3, *non* 3*a*) from U.S.N.M. locality 14s (Walcott 1908*b*, p. 211; Rasetti 1951, p. 101). The National Museum of Natural History holds some 35 additional specimens from this locality which is in the Stephen Formation, Mount Stephen Section, *Ogygopsis klotzi* faunule of the *Bathyuriscus–Elrathina* Zone, situated on the south-west slope of Mount Stephen at an elevation of approximately 2073 m (6800 feet), 2.4 km (1½ miles) east 30° south of Field, southern British Columbia. A carapace has also been collected by Fritz (1971, p. 1167, fig. 6) from the *Pagetia bootes* faunule on Mouth Stephen. *Anomalocaris* is reinterpreted as the walking appendage of a large arthropod. Robison (1971, p. 797) recorded *Canadaspis*? sp. from the late Middle Cambrian Wheeler Shale of the House Range, western Utah.

5. Description

(*a*) *Cephalic region*

The carapace usually obscures most of the cephalon, which only extended a short distance beyond the anterior extremity of the hinge line. The anterior appendages are evident symmetrically arranged about the mid-line in parallel aspect (figures 41, 42, plate 3). A median pointed projection or 'cephalic spine' separated a pair of pedunculate eyes, each of which was flanked by a short 'first antenna' on the inner margin, and a longer, stouter 'second antenna' on the outer. The cephalic spine was subparallel sided proximally, but tapered rapidly beyond the anterior margin of the eyes (figures 40, 41, plate 3). It is difficult to distinguish the spine in lateral aspect, but it is assumed to have been sub-circular in cross-section (figures 27, 28). There is no evidence that it was segmented. It is preserved in parallel aspect at the level of the ventral surface of the eyes (figure 41, plate 3) or slightly below them (figure 42, plate 3), and has not been observed lying dorsal of the cephalic appendages. M.C.Z. 5977/70 (figure 40, plate 3) shows the maximum known extent of the spine anteriorly; it appears to be incomplete distally on other specimens which show it clearly (figure 15, plate 1; figure 42, plate 3). The nature of the spine is unknown, but there is no indication that it was an extension of the carapace, and it is unlikely to represent a displaced rostral plate.

A pair of supposed eyes was borne on short, blunt, apparently unsegmented stalks flanking the cephalic spine (figures 40, 41, plate 3), and may be exposed beyond the carapace in lateral aspect some distance ventral of the hinge line (figure 43, plate 3). The eye stalk expanded slightly distally in parallel aspect to a width approximately half its length (figure 45, plate 3). It is assumed to have been sub-circular in cross-section and was probably flexible. The stalk is darker in low angle illumination and more reflective in high angle distally (figures 40, 41, plate 3), and this area may represent the visual surface (cf. *Opabinia*, Whittington 1975*a*; *Perspicaris* Briggs, 1977). It was apparently sub-circular in outline, convex anteriorly (figures 41, 44, plate 3).

A pair of small, narrow, discrete projections is preserved between the eyes of several specimens in parallel aspect, divided by the cephalic spine where it is evident (figures 42, 45, plate 3). The nature of this projection is unknown, but it is assumed to have been a sensory appendage, and is therefore referred to as the 'first antenna'. It was not as wide as the eye stalk, and although similar in length in many specimens due to a fracture incurred in the splitting of the slab (figure 45, plate 3), it extended further anteriorly (figure 46, plate 3). The first antenna was presumably sub-circular in cross-section. The level at which it is preserved varies in parallel aspect from just below the eye, where it is barely visible in dorsal aspect (figure 41, plate 3), to above it (figures 42, 47, plate 3). A degree of flexibility is further evidenced by a slight lateral flexure in some specimens (figure 45, plate 3). There is no unequivocal evidence that the first antenna was either segmented or spinose, but this may be a function of its small size. A feature on G.S.C. 45266, which may be this appendage, appears to be segmented (figure 44, plate 3).

A pair of stout, elongate, segmented 'second antennae' was attached ventral and abaxial of the other anterior appendages. The segmentation is generally indistinct, but seven divisions are evident in U.S.N.M. 213860 (figures 48, 49, plate 3), and indications of at least nine on the incomplete left antenna of M.C.Z. 5977/70 (figure 41, plate 3); the total was probably in excess of twelve. The segments were progressively more elongate towards the extremity of the appendage; individually they increased in diameter distally, each inserting into the anterior margin of that proximal to it (figures 48, 49, plate 3). They were apparently sub-circular in cross-section. The anterior margin of the segments bore long, slender spines extending anteriorly the length of several divisions (figures 41, 44, plate 3). The second antenna was apparently flexible. In parallel aspect it is usually curved abaxially (figures 48, 49, plate 3), but may more rarely be straight (figure 47, plate 3), or curved slightly adaxially (figure 15, plate 1). In lateral aspect it is directed ventrally, and may point anteriorly (figure 44, plate 3) or posteriorly (figures 68, 70, plate 5).

Removal of the right valve of U.S.N.M. 213856 (figures 50, 51, plate 4) exposed evidence of the outline of the cephalic region in lateral aspect. The dorsal margin appears to extend posteriorly at a low angle to the hinge line from the attachment of the eye stalk. Below the second antenna the outline slopes gently postero-ventrally about half the height of the valve before curving posteriorly into the ventral margin of the trunk. In parallel aspect the outline of the cephalic region is obscured by the anterior appendages on specimens which afford a dorsal view (figure 41, plate 3), but may be exposed in ventral aspect between the valves as a gently curved outline, convex anteriorly (figures 48, 49, plate 3). The second antenna extends antero-dorsal to this convex margin, which may represent the anterior extent of the labrum. Traces of the labrum are rarely evident. It is approximately triangular in outline in parallel aspect, the lateral margins, which are defined by a narrow ridge, converging into a gently convex posterior border (figures 52–54, plate 4). A series of closely spaced, transverse folds parallel to the anterior margin of the labrum on specimens preserved in parallel aspect (figure 52, plate 4) probably accommodates the original convexity, which is suggested by the ventral outline of the cephalic region in lateral aspect (figure 50, plate 4).

Evidence for the position of the mouth is rarely preserved. Traces of the alimentary canal extend almost to the base of the anterior appendages on some specimens (figure 15, plate 1; figure 41, plate 3), and a nodular protuberance which occurs in about this position on M.C.Z. 5977/28 (figure 47, plate 3) may represent the stomach contents. The canal is preserved curving gently posteriorly in the area of the labrum on U.S.N.M. 207277 (figures 55, 56, plate 4) suggesting that the mouth was positioned postero-ventral to the anterior extremity of the gut. A pair of small, nodular protuberances is occasionally preserved near the lateral margins of the labrum in parallel aspect (figure 57, plate 4), just behind the extremity of the hinge line. These presumably represent traces of a paired organ such as the antennal nephridium.

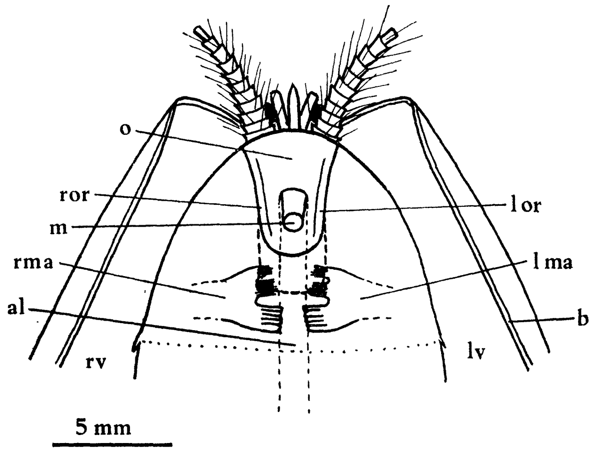


Figure 62. Diagrammatic reconstruction of the anterior of the cephalon of *Canadaspis perfecta* (Walcott, 1912) in ventral view. The position of the mouth is indicated above the labrum. The preserved outline of the labrum is represented by a solid line; its possible extent posteriorly ventral of the molar process of the mandible is dashed.

A series of spines borne between the second antenna and the most anterior biramous appendage is rarely evident in lateral aspect. Removal of the right anterior appendages of the counterpart of U.S.N.M 189017 (figures 68, 70, plate 5) revealed two bunches of at least six ventrally directed, fine, short spines, followed by a group of five, stouter and longer, borne on a slight projection of the ventral margin of the cephalic region. These features are presumed to represent the molar and incisor processes of the mandible respectively. They are preserved as closely opposed paired bunches of spines in parallel aspect on U.S.N.M. 189018 (figures 73–75, plate 6) in a similar arrangement to that shown in lateral aspect by U.S.N.M. 189017. Two bunches of adaxially directed, fine spines are evident on the right side lying anterior to a group of at least four stouter spines. The preservation of the mandible spines in sharp relief on several specimens in parallel aspect (figures 52, 55, plate 4) suggests that the cuticle was preferentially strengthened. U.S.N.M. 213853 (figure 52, plate 4) shows the mandible processes situated just beyond the apparent outline of the labrum. The margin of the labrum, however, may have extended posteriorly to underlie the anterior (molar) process as an area of flexible, unsclerotized tissue (figure 62).

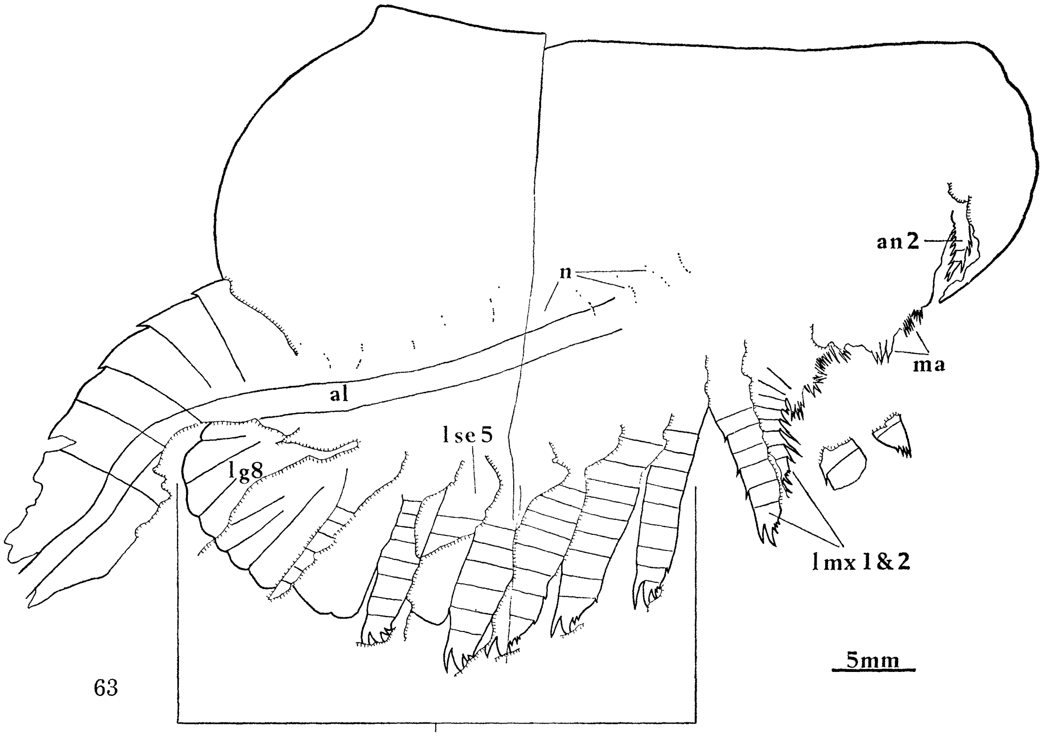
A series of ten pairs of biramous appendages was borne posterior of the mandible. The anterior two are interpreted as 1st and 2nd maxillae, but although assigned to the cephalic region, they are described with the other biramous appendages (§ 5*d*), to which they are essentially similar. The posterior margin of the cephalon is not an obvious feature. Traces of the inter-somite boundaries in this region are confined to infrequently preserved, linear nodular features normal to the sagittal axis (figures 13, 15, plate 1). These also occur in the thorax and probably represent points of muscle attachment (§ 5*c*). They are strongly developed immediately posterior of the position of the mandible in some specimens (figures 53, 54, plate 4), perhaps indicating the presence of powerful muscles employed in feeding.

(*b*) *Carapace*

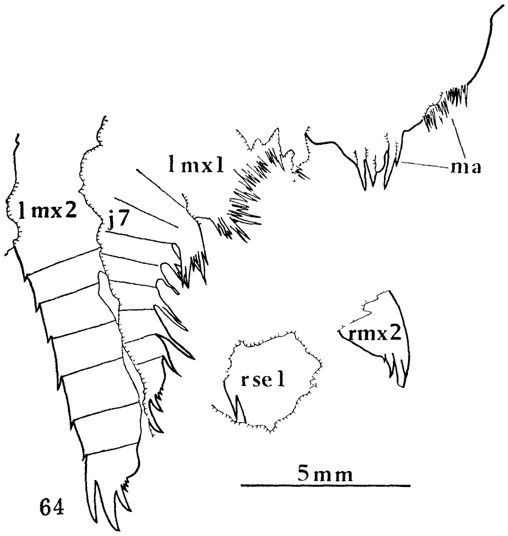
The carapace valves were sub-oval in outline, tapering anteriorly, and expanding slightly postero-ventrally (figure 51, plate 4). The hinge line is straight in parallel aspect (figure 40, plate 3), but may be slightly convex (figure 38, plate 3), concave (figure 112, plate 9), or both (figure 100, plate 8) in lateral aspect, presumably due to compaction. It terminated in an oblique angle with the anterior margin of the valve (figures 111, 112, plate 9), but was produced posteriorly into a small, blunt, triangular area (figure 100, plate 8; figures 111, 112, plate 9). There was no rostral plate. The anterior and posterior margins of the valve were angled at about 125° and 130° to the hinge line respectively, but the posterior embayment of the carapace was deeper due to the expansion of the valves in this direction (figure 40, plate 3). The carapace covered the body loosely posterior of the cephalic region (figures 50, 51, plate 4; figure 74, plate 6), permitting movement of the appendages beneath it. Only the seven abdominal somites and telson normally protruded beyond the hinge line (figure 51, plate 4).

Specimens in parallel aspect preserving the valves adjacent to the body, and consequently folded beneath themselves (figure 40, plate 3), provide an indication of the original convexity of the carapace. The maximum width occurs about the mid-length of the hinge line. The lateral margins converge posteriorly at an angle of less than 10°; anteriorly the angle may be up to 30°. The hinge line forms a groove on the dorsal surface. The concentric folding which accommodates the original convexity in parallel aspect where the valves are preserved in outline, is concentrated adjacent to the ventral margin (figures 83, 84, plate 7). U.S.N.M. 189021 (figures 10, 11, plate 1), in vertical-oblique aspect, also indicates that the downward curvature was most pronounced in this region. Specimens in parallel aspect which preserve the carapace folded beneath the trunk (figure 56, plate 4) suggest that the ventral margin of the valves could be directed adaxially. The carapace was bounded by a narrow border (figure 42, plate 3; figure 111, plate 9) defined by a shallow groove on its inner margin.

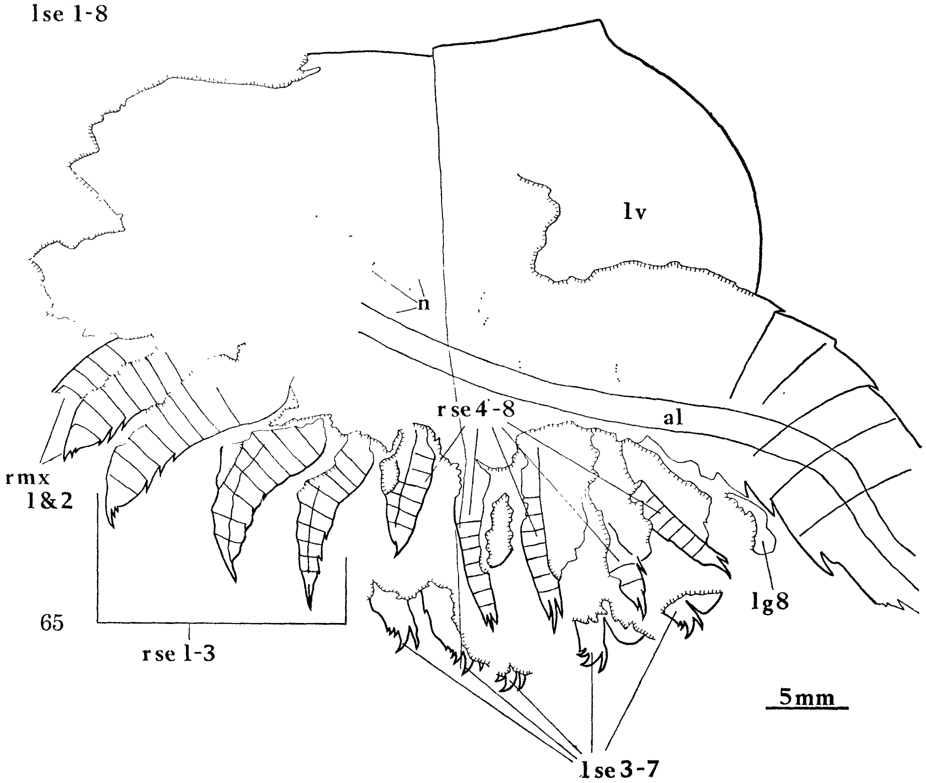
The carapace appears to have been attached to the posterior part of the cephalic region. In lateral aspect the anterior cephalic appendages extend beyond the valves some distance ventral of the hinge line (figure 43, plate 3), the anterior extremity of which does not appear to be in contact with the cephalon. The anterior thoracic somites are concave dorsally in lateral aspect, the trunk and hinge line converging to meet in the cephalic region (figure 100, plate 8). The carapace could tilt forward, probably in the course of moulting (figures 168, 171, 172, plate 13; § 5*g*) exposing most of the thorax while remaining attached to the cephalon anteriorly. Sub-circular areas, which are interpreted as traces of adductor muscle scars, are occasionally evident in the antero-dorsal apices of the otherwise smooth valves (figures 40, 41, plate 3). These provide further evidence for the attachment of the carapace in the cephalic region. The scars have little apparent relief, but are darker than the surrounding areas in low angle illumination and more reflective in high angle. The area of the carapace upon which they occur is commonly



63



64



65

DESCRIPTION OF PLATE 5 AND FIGURES 63–65

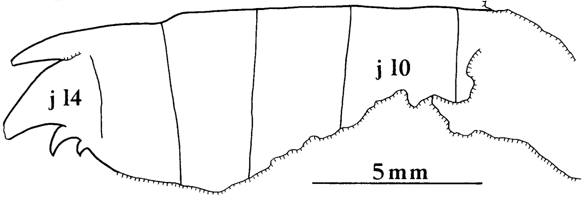
Canadaspis perfecta (Walcott, 1912), U.S.N.M. 189017

FIGURES 63–65. Explanatory drawings, after preparation. 63, 64. Counterpart; left appendages, and detail of left mandible and first and second maxilla, respectively. 65. Part, right appendages.

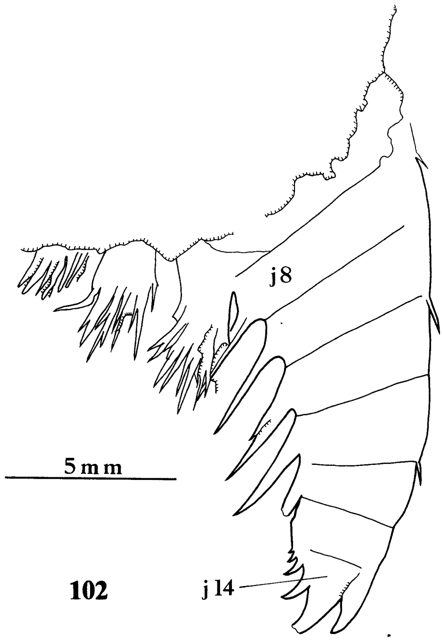
FIGURES 66, 68, 70, 72. Counterpart. 66, 68. North-west, before and after preparation to reveal all left appendages. (Magns × 1.5.) 70. North-west, left anterior appendages (magn. × 5). 72. Reflected, north, left appendages (magn. × 2).

FIGURES 67, 69, 71. Part. 67, 69. North, before and after preparation to reveal all right appendages. (Magns × 1.5.) 71. North-west, right anterior appendages (magn. × 3).

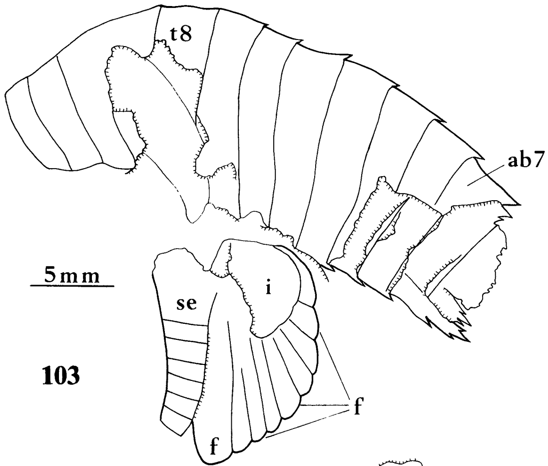
CANADASPIS PERFECTA



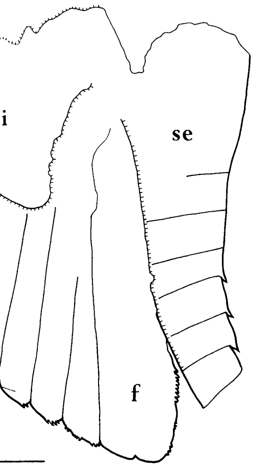
101



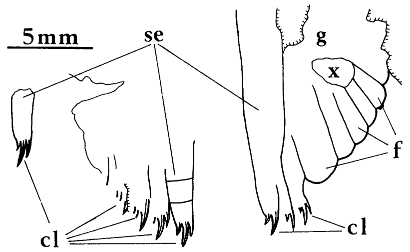
102



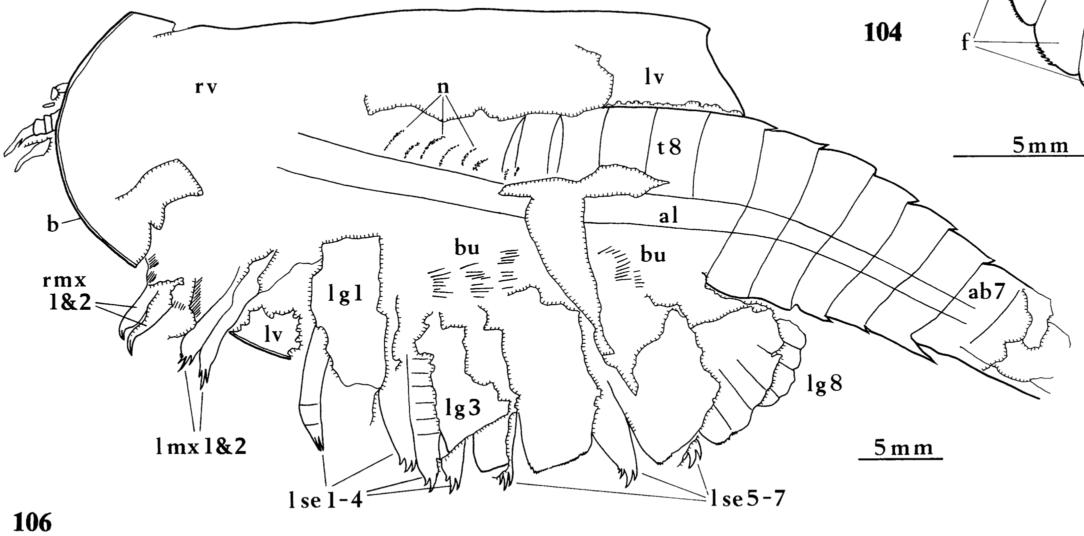
103



104



105



106

DESCRIPTION OF PLATE 8 AND FIGURES 101–106

Canadaspis perfecta (Walcott, 1912)

FIGURES 89–93. G.S.C. 45263, trunk lateral-oblique. 89. West (magn. × 1.5). 90. North-west, appendage dorsal of specimen (magn. × 6). 91. South-east, appendage ventral of specimen (magn. × 6). 92, 93. Isolated appendage anterior of specimen; south, and reflected, west, respectively (magns × 8).

FIGURES 94–98. U.S.N.M. 189015, trunk lateral. 94. Part, north-west (magn. × 2). 95, 97. Part, appendage; north-west, and reflected, north, respectively. 96, 98. Counterpart, appendage; north-east, and reflected, north, respectively. (Magns × 4.)

FIGURE 99. U.S.N.M. 207281, west, fragmentary appendages; a specimen of the sponge *Choia* overlies the outer ramus on the right (magn. × 3).

FIGURE 100. U.S.N.M. 213855, lateral, north-west (magn. × 1.5).

FIGURES 101–106. Explanatory drawings. 101, 102. G.S.C. 45263, appendages dorsal and anterior of specimen, respectively. 103, 104. U.S.N.M. 189015, part, and counterpart appendage, respectively. 105. U.S.N.M. 207281, 'x' indicates position of *Choia* specimen. 106. U.S.N.M. 213855.

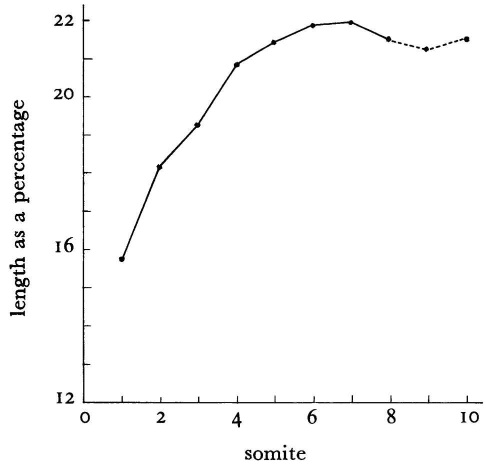


FIGURE 107. Relative lengths of thoracic somites of *Canadaspis perfecta*. Plot of lengths of thoracic somites of 14 specimens expressed as an average percentage of the total length of abdominal somites 3 to 7. Data for abdominal somites 1 and 2 included from figure 163 to permit comparison.

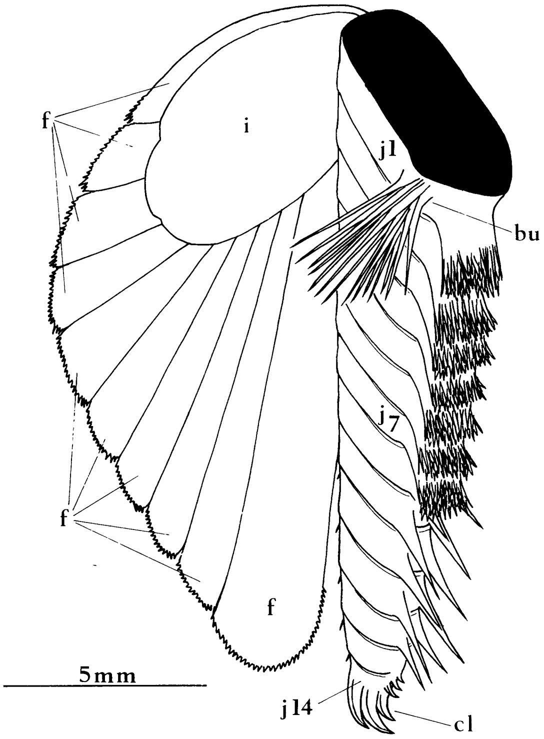
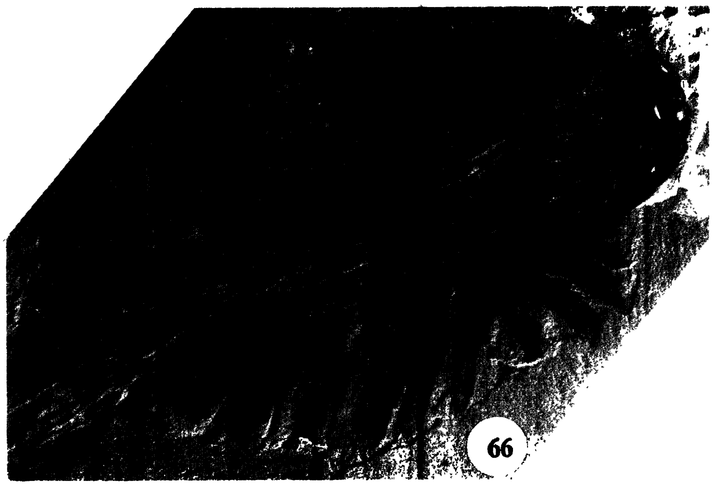


FIGURE 108. Reconstruction of left first maxilla of *Canadaspis perfecta* (Walcott, 1912). The interpretation of the proximal morphology of the segmented ramus is equivocal; the posteriorly directed bunch of spines ('bu') shown was borne proximally by the thoracic appendages but may not have been present on the first or second maxilla.


66


67

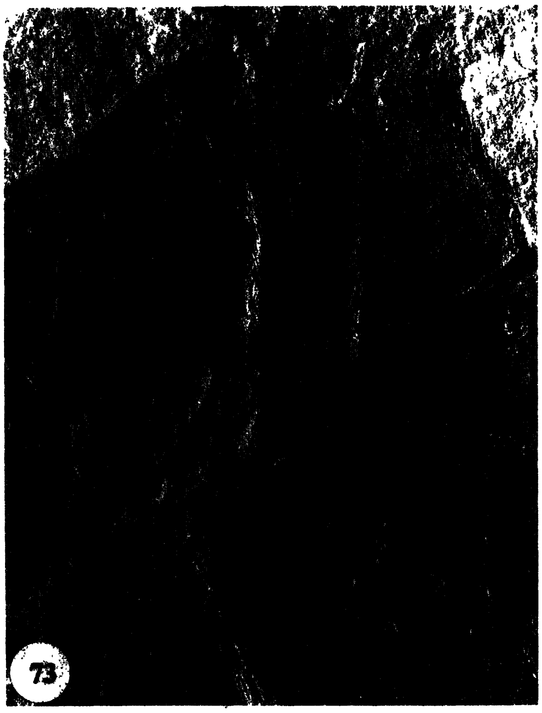

68

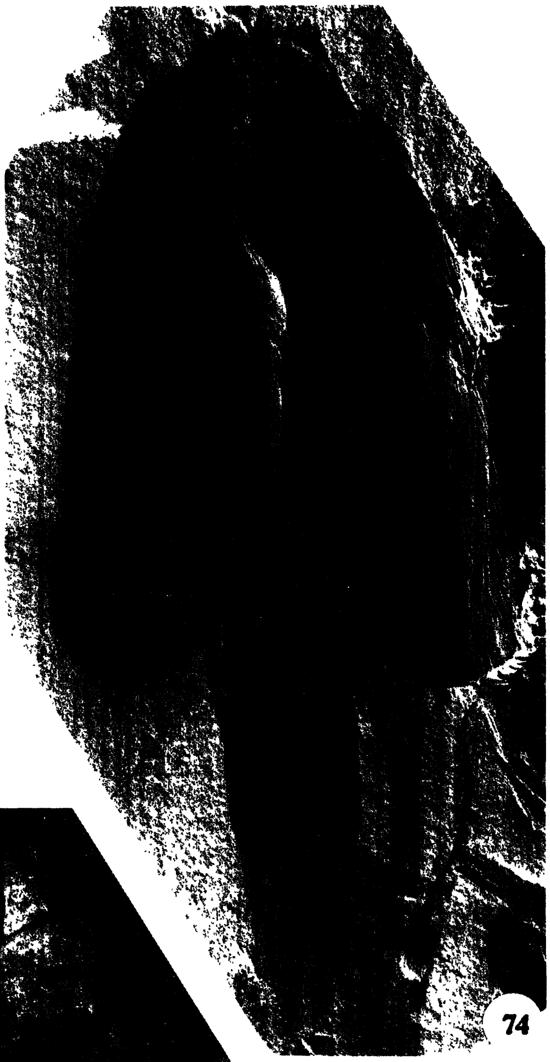

69

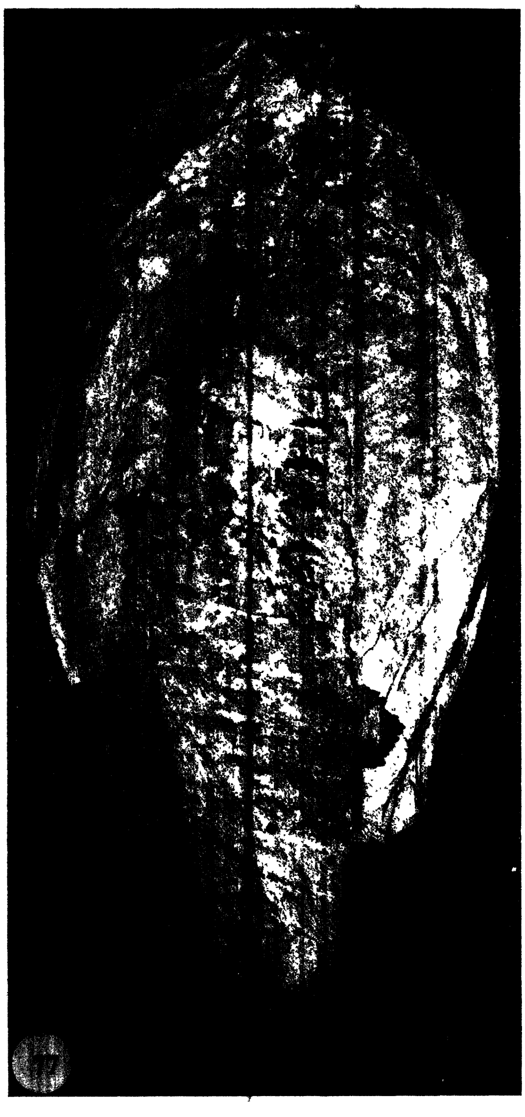

70

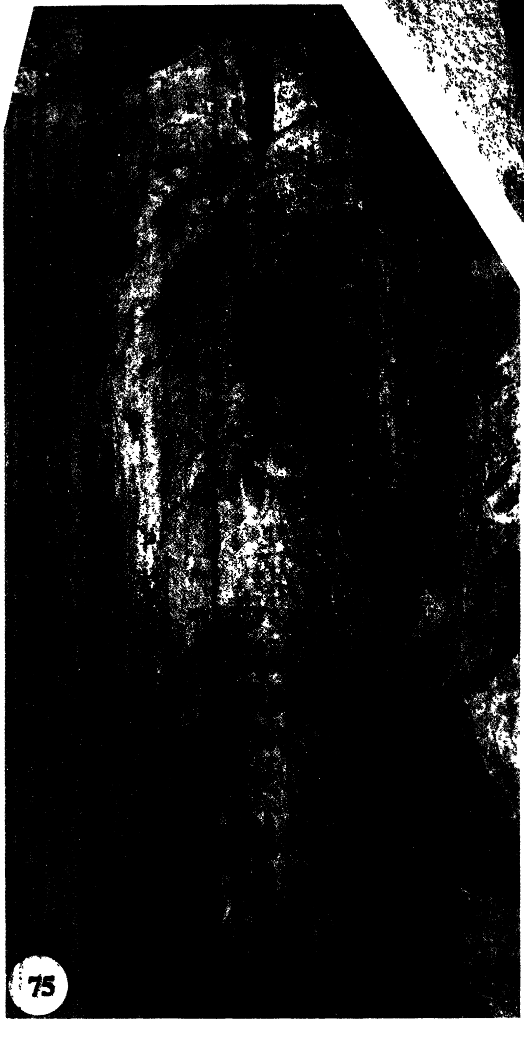

71


72


73

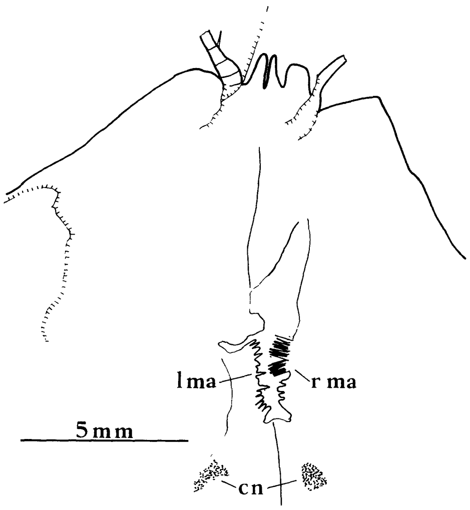

74


77

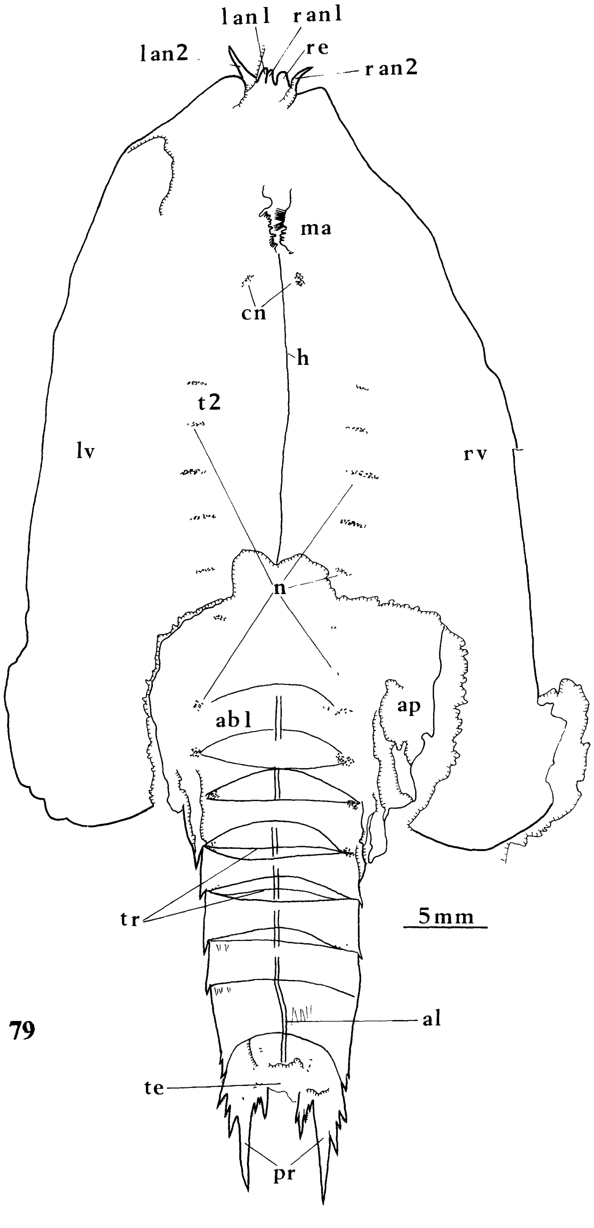

75


76

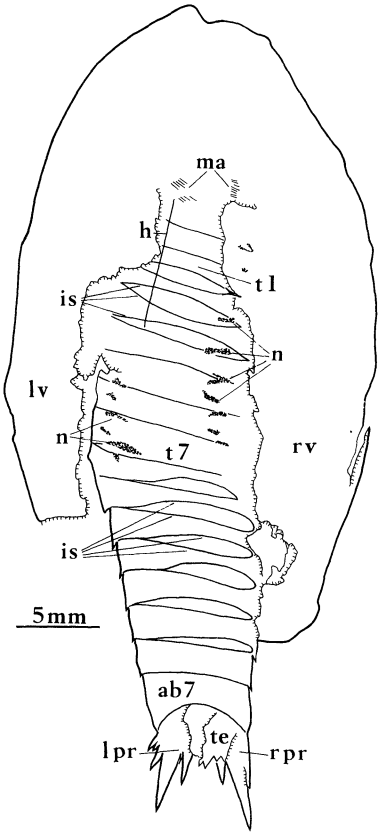
78



79



80



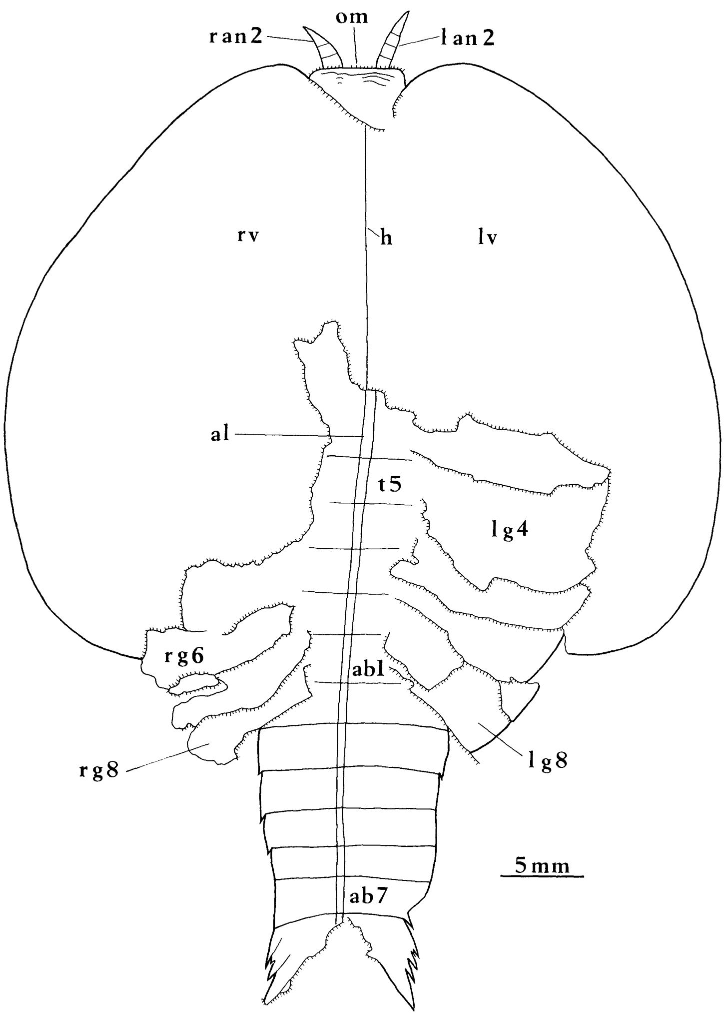
Description of plate 6 and figures 78–80

Canadaspis perfecta (Walcott, 1912)

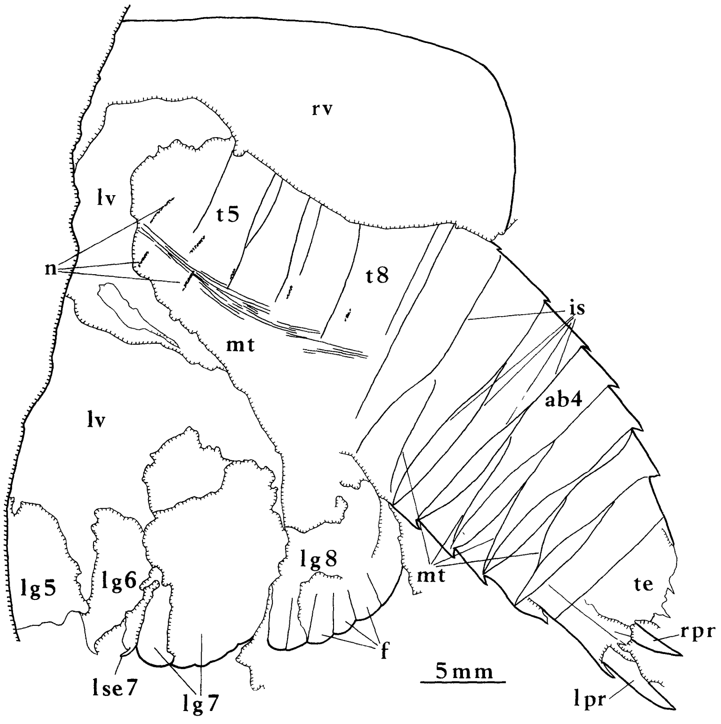
Figures 73–76. U.S.N.M. 189018, parallel. 73. East, cephalic region (magn. × 6). 74. North-west. 75. Reflected, east, carapace removed posteriorly. (Magns × 2.) 76. Reflected, east, telson (magn. × 4).

Figure 77. U.S.N.M. 207285, parallel, reflected, east (magn. × 3).

Figures 78–80. Explanatory drawings. 78, 79. U.S.N.M. 189018, cephalic region, and specimen after removal of carapace posteriorly, respectively. 80. U.S.N.M. 207285.



81



82

DESCRIPTION OF PLATE 7 AND FIGURES 81, 82

Canadaspis perfecta (Walcott, 1912)

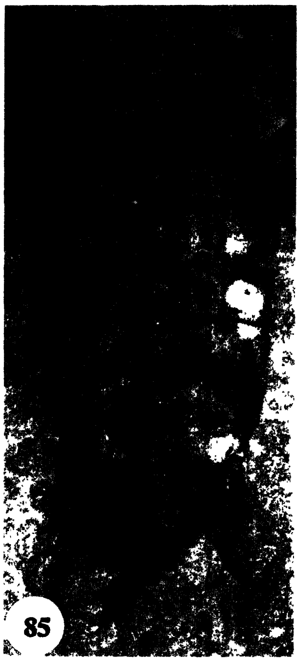
FIGURES 81, 82. Explanatory drawings. 81. U.S.N.M. 189019, counterpart. 82. U.S.N.M. 213859, part.

FIGURES 83–85. U.S.N.M. 189019, parallel. 83. Part, north-east (magn. × 1.5). 84, 85. Counterpart, under alcohol, north; complete, and abdomen and telson, respectively (magns × 1.5 and × 3).

FIGURES 86–88. U.S.N.M. 213859, lateral, under alcohol. 86, 88. Part, north-east; specimen after removal of part of carapace, and traces of thoracic muscles, respectively (magns × 2 and × 6). 87. Counterpart, south-west (magn. × 2).

83

84



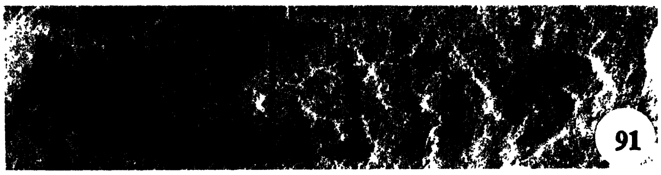
85

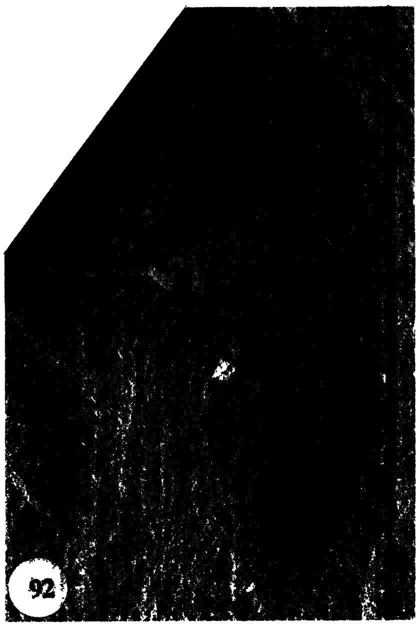
86

87

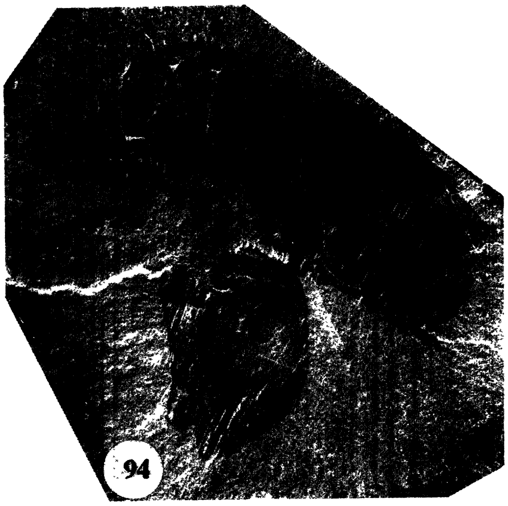

89


90

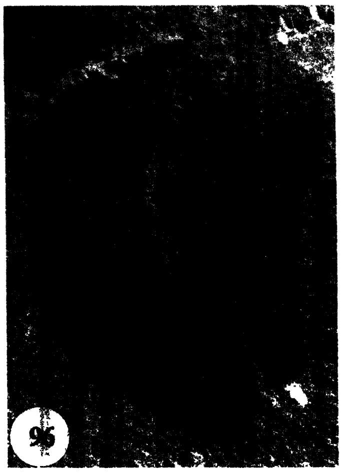

91


92


93

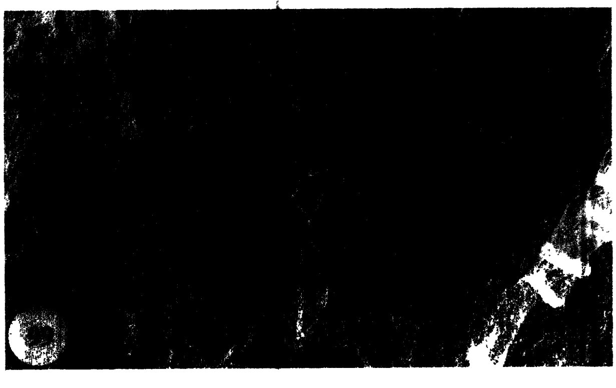

94

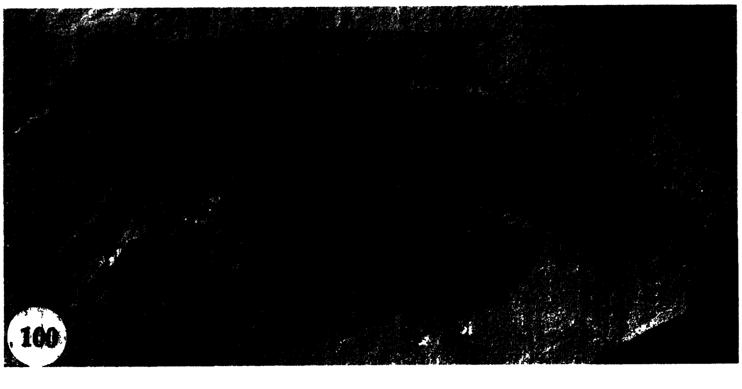

95


96


97


98




100

deformed or unexposed due to orientation to the bedding or the level of splitting. Most specimens which preserve traces afford a view of the inner surface of the valve (figure 45, plate 3). There is no evidence of articulating processes along the hinge line. The valves were presumably joined by a narrow strip of flexible cuticle which allowed them to be approximated to varying degrees by the adductor muscles.

(*c*) *Thorax*

Preparation of the part and counterpart of U.S.N.M. 189017 (figures 68, 69, plate 5) has exposed ten pairs of biramous appendages – the left and right limbs displayed separately in different attitudes on the opposing slabs. The anterior two pairs are interpreted as the first and second maxillae, the posterior eight as the appendages of the thorax. Preservation of the inter-somite boundaries in the thorax is similar in nature to that in the abdomen (§ 5*e*), but they are more rarely evident. The boundaries are commonly represented by poorly defined reflective traces, the course on opposite sides of the trunk usually offset due to the orientation of the specimen to the bedding (figure 77, plate 6; figures 144, 145, plate 12). The posterior margin of each somite was fringed by small spines which extended about one quarter the length of the succeeding somite, but these tend to be more obvious in the abdomen. A series of small, elongate, paired nodular features present in the thorax may be apparent impressed in relief through the overlying valves (figure 74, plate 6). Removal of part of the carapace of U.S.N.M. 189018 (figure 75, plate 6) revealed these nodes (which are also present in the anterior somites of the abdomen) where they occur at the convergence of the offset dorsal and ventral traces of individual inter-somite boundaries on the lateral margins of the trunk. The nodes can be used in the absence of other evidence for the position of the boundaries. They are rarely preserved anteriorly, but are present throughout the thorax of U.S.N.M. 207285 (figure 77, plate 6), for example, and also indicate the boundary of the somite bearing the second maxilla.

It is difficult to demonstrate unequivocally that each pair of appendages was borne by an individual somite without the overlap which occurs in some Recent notostracan branchiopods, and *Branchiocaris pretiosa* (Briggs 1976). The number of paired thoracic appendages, however, corresponds to that of somites based on traces of the boundaries alone. U.S.N.M. 189019 (figures 83, 84, plate 7) affords a ventral view of the posterior six appendages and, although the points of attachment are obscured by the overlapping outer rami, there appears to be a spatial correspondence between individual appendages and somites. Most of the evidence for such an arrangement, however, is provided by specimens preserved in lateral aspect. A rough correlation between the points of attachment of the appendages and the position of the boundaries (largely extrapolated from the nodes) is evident on U.S.N.M. 189017 (figure 72, plate 5), and is emphasized on U.S.N.M. 207263 (figures 111, 112, plate 9) by a series of discrete groups of spines borne proximally by the appendages (§ 5*d*).

The nature of the paired nodes is problematical. They are commonly elongate normal to the sagittal line, slightly convex anteriorly, and tend to follow the inter-somite boundaries (figure 72, plate 5; figure 77, plate 6). Nodular features appear to lie within the somites in some specimens (figure 77, plate 6; figure 116, plate 10), but they probably coincide with sections of the boundaries which are not visibly preserved (cf. examples in the abdomen, § 5*e*). The nodes are mainly confined to the thorax; rare examples occur on the most anterior somites of the abdomen (figures 13, 14, plate 1; figures 75, 76, plate 6). The nodes were mid-lateral in position and are preserved near the margin of the trunk in parallel aspect (figures 75, 77, plate 6). They may be offset, like the traces of the boundaries on opposite sides of the trunk, due to a slightly oblique orientation (figure 115, plate 10; figure 170, plate 13). The composition of the nodes is unknown, but they may be the result of a nucleation of pyrite (see Whittington 1971 *a*, p. 1180) about morphologically defined points in the trunk. The nodular features and minute pits which coincide with the abdominal inter-somite boundaries in some specimens may be similar in origin (figures 167, 169, plate 13). The arrangement of the nodes, one pair per thoracic somite, together with their mid-lateral position on the trace of the inter-somite boundaries along the body wall or cuticle, suggests that they may represent points of muscle attachment, perhaps associated with the appendages.

The muscles of the thorax are rarely evident, even when the carapace is removed from specimens which show traces of the more commonly preserved abdominal muscles (§ 5*e*). A series of groups of up to five, very fine, closely spaced, reflective strands is evident in lateral aspect on U.S.N.M. 213859 (figures 86, 88, plate 7), for example, extending anteriorly from the posterior margin of somite 8 through the thorax just ventral of the mid-line. These groups appear to insert at the posterior margin of each somite and extend anteriorly through at least two somites. They may represent traces of longitudinal muscle.

The ventral margin of the thorax appears to have been gently convex, assuming that it is reflected in the points of attachment of the appendages which normally obscure it (figure 112, plate 9; figure 115, plate 10). The dorsal margin was convex posteriorly but became concave anteriorly, curving dorsally towards the hinge line (figure 115, plate 10). The lateral margins are poorly defined in parallel aspect, but the nodes provide additional evidence that the thorax widened gradually anteriorly (figures 74, 75, plate 6). The transverse section is assumed to have been similar to that of the abdomen (§ 5*e*), approximately circular. The length of the thoracic somites (figure 107) increased markedly posteriorly to somite 4 and more gradually to somite 7, followed by a slight decrease in somite 8. Limited flexing of the thorax in the vertical plane appears to have been achieved by telescoping along the inter-somite boundaries (cf. abdomen, § 5*e*), causing a differential between the effective length of a somite along the dorsal and ventral margins. There is no unequivocal evidence for lateral flexing, which was presumably undesirable.

(*d*) *Biramous appendages*

The 1st and 2nd maxillae and all 8 thoracic appendages were biramous, with an inner multisegmented ramus, and a large lamellate, outer ramus divided into rays which were borne by a thickened proximal lobe. The joints in the inner ramus are usually poorly preserved, or obscured by compaction against other features. The total number of segments remains unknown. There appears to be a joint at the base of the terminal claws, but this is rarely evident (figures 90, 93, plate 8). The largest number of joints observed in any limb is 11 but the most proximal are consistently obscured and extrapolation toward the apparent attachment to the trunk suggests that a total number of 13 or 14 segments was present throughout (figures 66–72, plate 5). These are enumerated 1–14 distally. The segmented ramus tapered gradually, but appears wider when flattened with the claws curved in the plane of bedding, than with the claws directed adaxially normal to the bedding (compare anterior and posterior appendages in figure 66, plate 5). The cross-section was thus sub-oval, flattened antero-posteriorly. Individually the segments widened slightly distally, and bore elongate spines where they overlapped at the joints. Evidence for the morphology and distribution of these spines is lacking on the majority of specimens due to inadequate preservation.

The spines on the first maxilla are most favourably preserved on U.S.N.M. 189017 (figure 70, plate 5), but are also evident on the isolated limb of G.S.C. 45263, which is assumed to be the same appendage on the basis of similarity (figures 92, 93, plate 8). The spines on the outer margin were short and slender, and extended distally about half the length of the succeeding segment. They are reconstructed singly (figure 108) in the absence of unequivocal evidence to the contrary. The spines borne on the inner margin of the 7 most proximal segments differed from those on the more distal. They were grouped in bunches borne on a slight adaxial projection of the segment, and were directed distally at an acute angle to the ramus. Bunches are reconstructed (figure 108) on the segments nearest to the point of attachment to the trunk, but the evidence for the exact configuration of the spines in this area is equivocal. The inner spines on the distal segments appear to have been paired (figure 70, plate 5; figures 92, 93, plate 8). They were elongate, extending beyond the boundary of the succeeding segment, and varied in length. It is not possible to determine whether they alternated in length on successive segments as in *Anomalocaris*, or formed a graded sequence. They appear to have been flexible to a degree, and may have articulated proximally.

The spines on the second maxilla were similar in nature and distribution to those on the first, except for an apparent lack of bunches on the inner margin of the more proximal segments. The spines on the outer margin, and those on the inner margin of the distal segments, were shorter than those on the first maxilla (figures 70, 71, plate 5). A conglomeration of spines is poorly preserved adjacent to the anterior appendages of U.S.N.M. 57703 (figure 20, plate 2) but it is not clear to which appendage they belong. No trace of bunches of spines on the appendages posterior of the first maxilla, however, was revealed by removal of the right anterior appendages of U.S.N.M. 189017 (figures 68, 70, plate 5) to reveal the left. The second maxilla and the 8 paired appendages of the thorax appear to have been all essentially similar, the spines on the inner margin of the segments paired, and those on the outer single. The spines are rarely well preserved, but examples are evident on U.S.N.M. 57703 (figures 18–20, plate 2) and U.S.N.M. 189017 (figures 68, 69, 72, plate 5). Any variation in the length or attitude of spines on different specimens is probably largely the result of differences in the orientation of the appendages to the bedding. The segmented ramus bore a number of spines or 'claws' distally which curved adaxially away from the outer ramus (figures 10, 11, plate 1). There were 3 larger claws, the middle one extending farthest distally, followed by that posterior and anterior of it (figure 70, plate 5; figures 92, 93, plate 8). Three smaller spines were borne antero-dorsal to the most anterior claw. The relative levels of the claws vary with the orientation of the flattened appendage in the rock, as does their apparent curvature, which reaches a minimum when the claws are directed exactly normal to the bedding. The claws are occasionally preserved in obvious relief (figure 99, plate 8) suggesting that the cuticle may have been strengthened relative to that of the rest of the appendage. The convex margin of the larger claws and of at least one of the smaller spines formed a distinct ridge, flanking a blade-like inner area.

The evidence for the nature of the articulations in the segmented ramus provided by their preserved characteristics is inconclusive. The joints may be evident in slight relief, and are occasionally darker (figures 91, 92, plate 8), or more reflective (figure 93, plate 8) than the intervening areas, suggesting a resistance to decay possibly due to an overlap of cuticle. The joints thus delineated usually widen slightly towards the inner margin of the appendage (the direction in which the distal claws curve). Some are preserved in negative relief on U.S.N.M.

207276 (figure 169, plate 13), however, which appear to widen towards the outer margin, but this may be the result of moulting if the specimen is correctly interpreted as an exuvia (§ 5*g*). The attitude of the appendages commonly varies from approximately straight to curved strongly inwards. The successive joints of those which are preserved straight are approximately parallel (posterior appendages in figure 72, plate 5), the opposite side of each segment equal in length. Inward flexing was achieved by telescoping along the joint to decrease the effective length of the segment on the adaxial side of the appendage (figure 71, plate 5; figures, 92, 93, plate 8). Slight outward flexing is also occasionally evident (left anterior appendages in figures 18–20, plate 2). The segments appear to have been separated by short links of flexible cuticle or arthrodial membrane. The direction of movement at the joints may have been constrained by the precise configuration of the membrane and the antero-posteriorly flattened cross-section of the appendage to prevent excessive outward flexure. Segments 9, 10 and 11 appear to have been the longest (figures 70–72, plate 5; figures 92, 93, plate 8), the length of the remainder decreasing very gradually both distally and proximally. Differences in the apparent relative lengths which occur even within some individual specimens are probably the result of telescoping at the joints, or a lack of evidence for their precise position.

The outer ramus consisted of a thickened inner lobe from which radiated 9 or 10 defined rays forming convex arcuate divisions on the outer margin of the lamella. The rays are generally indistinct on complete specimens, but evidence for the detailed morphology is provided by isolated appendages orientated parallel to the bedding and undistorted by other features (figures 94–98, plate 8). The outer ramus was roughly trapezoidal in outline, the outer and inner margins sub-parallel and approximately normal to the blunt, slightly convex dorsal margin. The outer margin curved inwards through about 50° near the mid-length to converge with the inner in a rounded distal apex. The innermost ray, which was longer and wider than the others, was almost parallel sided and formed the inner margin of the ramus. The rays became progressively shorter away from the segmented ramus, and tapered proximally towards their apparent attachment to the inner lobe. Variations in the apparent dimensions of the rays in several examples suggest that they may have moved independently to a degree and are thus preserved overlapping slightly in a configuration depending on the orientation of the appendage to the bedding. The rays bore minute, closely spaced spines around the margin of the outer ramus (figures 95–98, plate 8). These were stoutest on the distal extremity of the innermost ray where they were directed ventrally. Elsewhere the spines were directed roughly horizontally at an oblique angle to the margin of the ramus, except on the most ventral part of the distal margin of each ray, where they pointed ventrally. No unequivocal evidence that the lateral margins of the rays were also spinose has been observed. There is no apparent difference in the outer rami of the maxillae and thoracic appendages, except for a slight reduction in size anteriorly (figure 50, plate 4).

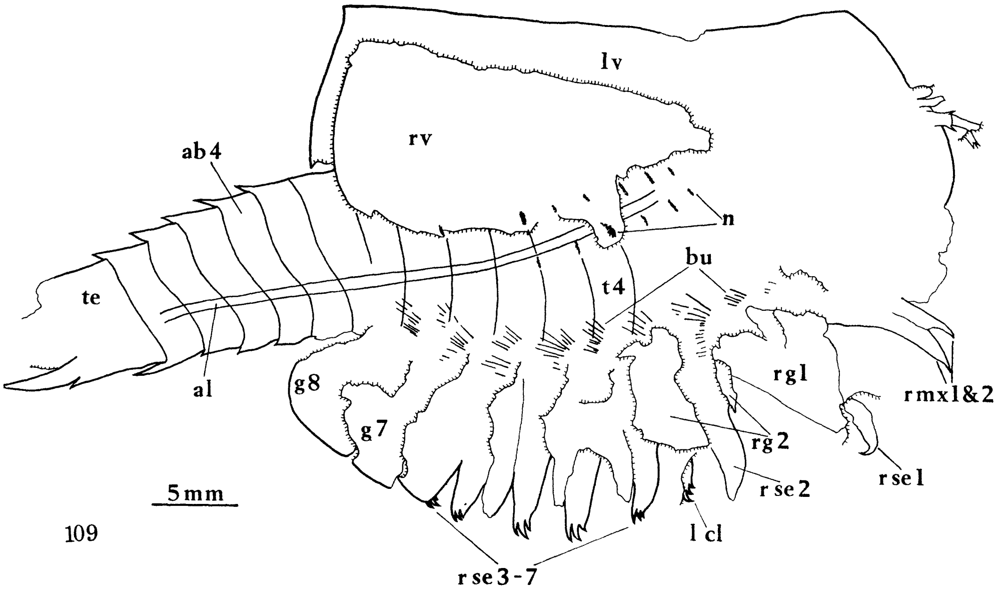
The exact nature of the attachment of the biramous appendages to the trunk is unknown. A series of paired groups of spines, one per somite, is evident along the ventral margin of the thorax near the base of the appendages in some specimens (figure 111, 112, plate 9; figure 167, plate 13). These features are slightly darker than the surrounding area and may have been resistant to weathering, which has affected the specimens upon which they are most obvious. Only very tenuous traces have been observed on finely preserved specimens in the dark film which is characteristic of the Burgess Shale (figure 116, plate 10). The groups consisted of at least 10 diverging, elongate spines which are preserved directed postero-dorsally and are not equivalent to the spines on the more proximal segments of the first maxilla (which are also evident on U.S.N.M. 213855, figure 100, plate 8). The groups of spines appear to have been borne on the inner margin of the first segment of the appendage, and directed posteriorly and adaxially (figure 111, plate 9). They are evident on G.S.C. 45267 in parallel aspect directed into the inter-limb space from a triangular projection of the basal segment, and could apparently meet medially (figures 113, 114, plate 9). The groups of spines have only been observed in association with the 8 thoracic appendages; it is not known whether they were also present on the first and second maxillae.

The morphology of the proximal articulation of the rami is unknown. The outer ramus is usually compacted against the other, which it overlaps to a degree depending on the orientation of the limb to the bedding (figures 115, 116, plate 10). Examples occur, however, of the rami diverging distally, and distinguished proximally by a boundary which extends almost to the apparent attachment of the appendages to the thorax (figure 115, plate 10). There is no evidence of divisions of the inner ramus proximal of the attachment of the outer, and both are assumed to have been borne by a basal segment. The biramous appendages were similar in length to the height of the trunk, the distal claws extending just ventral of the outer ramus (figure 115, plate 10). Their relative lengths appear to vary between individuals, but this is due to differences in attitude and orientation to the bedding. The appendages did not differ greatly in length, but may have decreased slightly anteriorly.

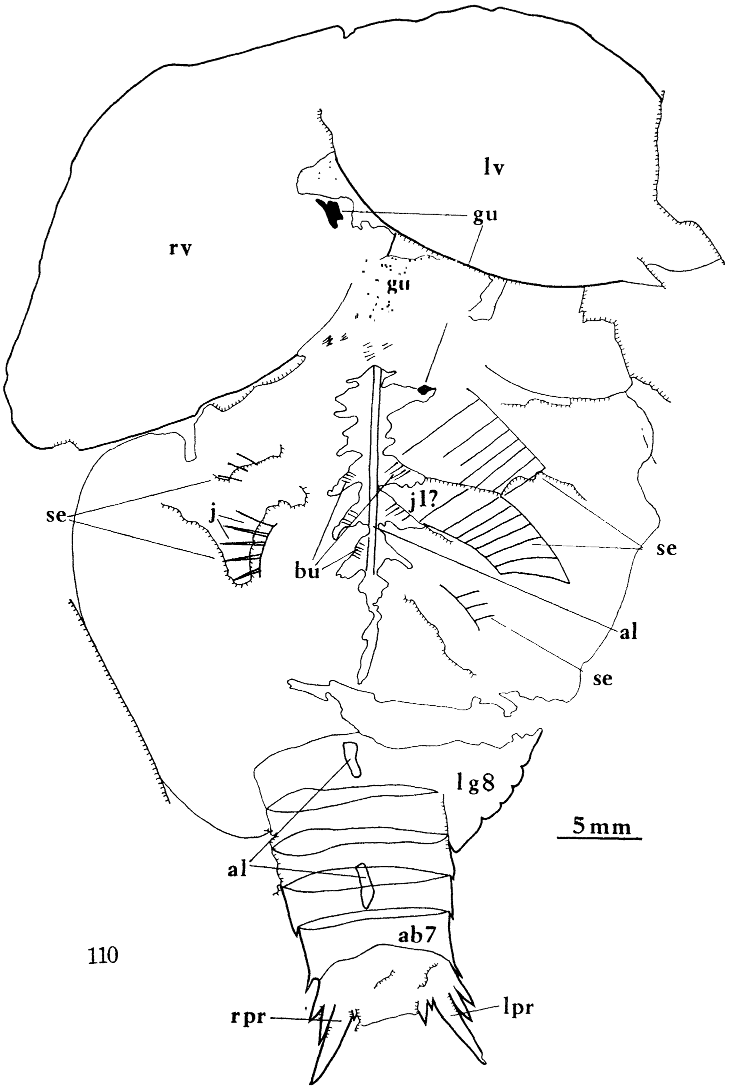
The attitude in which the appendages are preserved depends to an extent on the orientation of the specimen as a whole, but also on their arrangement at the time of burial. It is difficult to assess how far this reflects their relative positions during normal movement, as the arthropod may have employed unusual motions while struggling in the cloud of sediment, and changes in the configuration of the limbs may have taken place due to subsequent turbulence. Movement of the appendages apparently resulted in a slight rotation about a vertical axis. The posterior appendages of U.S.N.M. 207270 (figure 115, plate 10), for example, are directed backwards and apparently rotated so that the inner margin and distal claws face anteriorly and the outer ramus lies behind the segmented ramus and is orientated approximately in the plane of bedding. The appendages swing forward anteriorly through an arc of about 115° and rotate gradually in this direction so that the inner margin and claws face posteriorly and the outer ramus is superimposed on the other and extends slightly beyond its anterior margin. The lack of excessive overlap in this direction indicates that the outer ramus was directed postero-lateral of the segmented ramus in natural attitude. The outer rami of the anterior appendages are commonly orientated near normal to the direction of compression in lateral aspect and are obscured by foreshortening (figure 71, plate 5), but they are evident in outline when they overlap posteriorly (figure 50, plate 4). A similar effect may be observed in oblique aspect in U.S.N.M. 207293 (figure 116, plate 10) but, in this case, the posterior rami show the greatest foreshortening. Some specimens preserve the segmented rami overlapping posteriorly in lateral aspect at a low angle to the trunk (figures 168, 171, plate 13), but these are probably exuviae.

(*e*) *Abdomen*

The seven somites of the abdomen, apart from the most posterior, lacked appendages and, together with the telson, are usually preserved extending beyond the hinge line (figure 100, plate 8; figure 120, plate 10). Any considerable variation in the number of somites exposed beyond the carapace is probably the result of moulting, decay, or distortion in the course of



109



110

Description of plate 9 and figures 109, 110

Canadaspis perfecta (Walcott, 1912)

Figures 109, 110. Explanatory drawings. 109. U.S.N.M. 207263. 110. G.S.C. 45267, part.

Figures 111, 112. U.S.N.M. 207263, lateral. 111. Under alcohol, east (magn. × 2.5). 112. East (magn. × 2).

Figures 113, 114. G.S.C. 45267, parallel, under alcohol, north, counterpart and part respectively. (Magns × 2.)

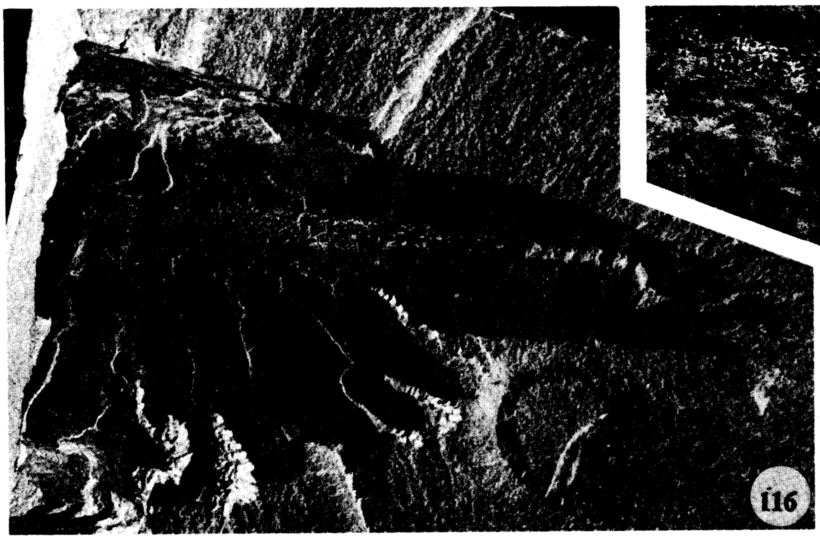
111

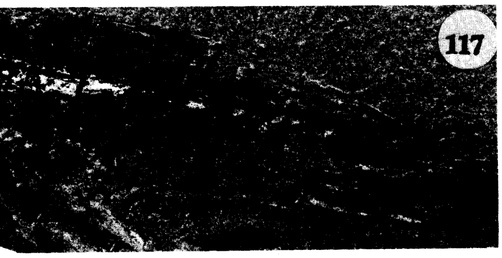
112

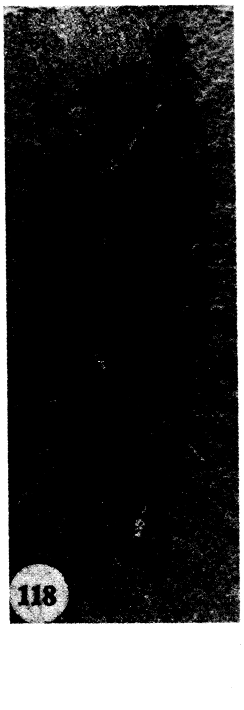
113

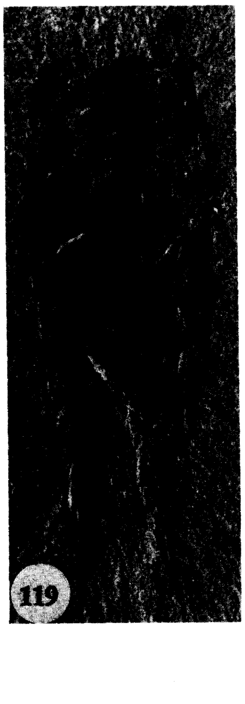
114


115

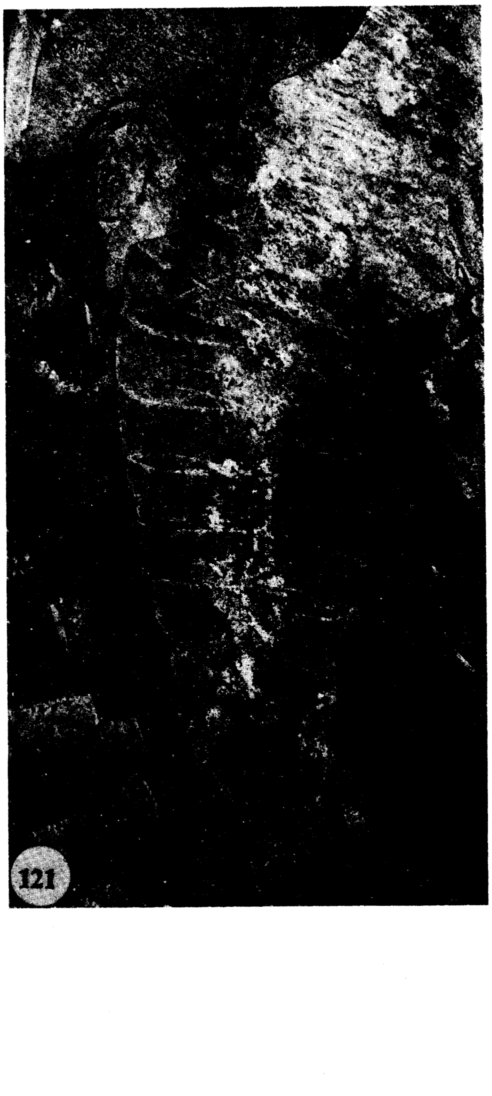

116

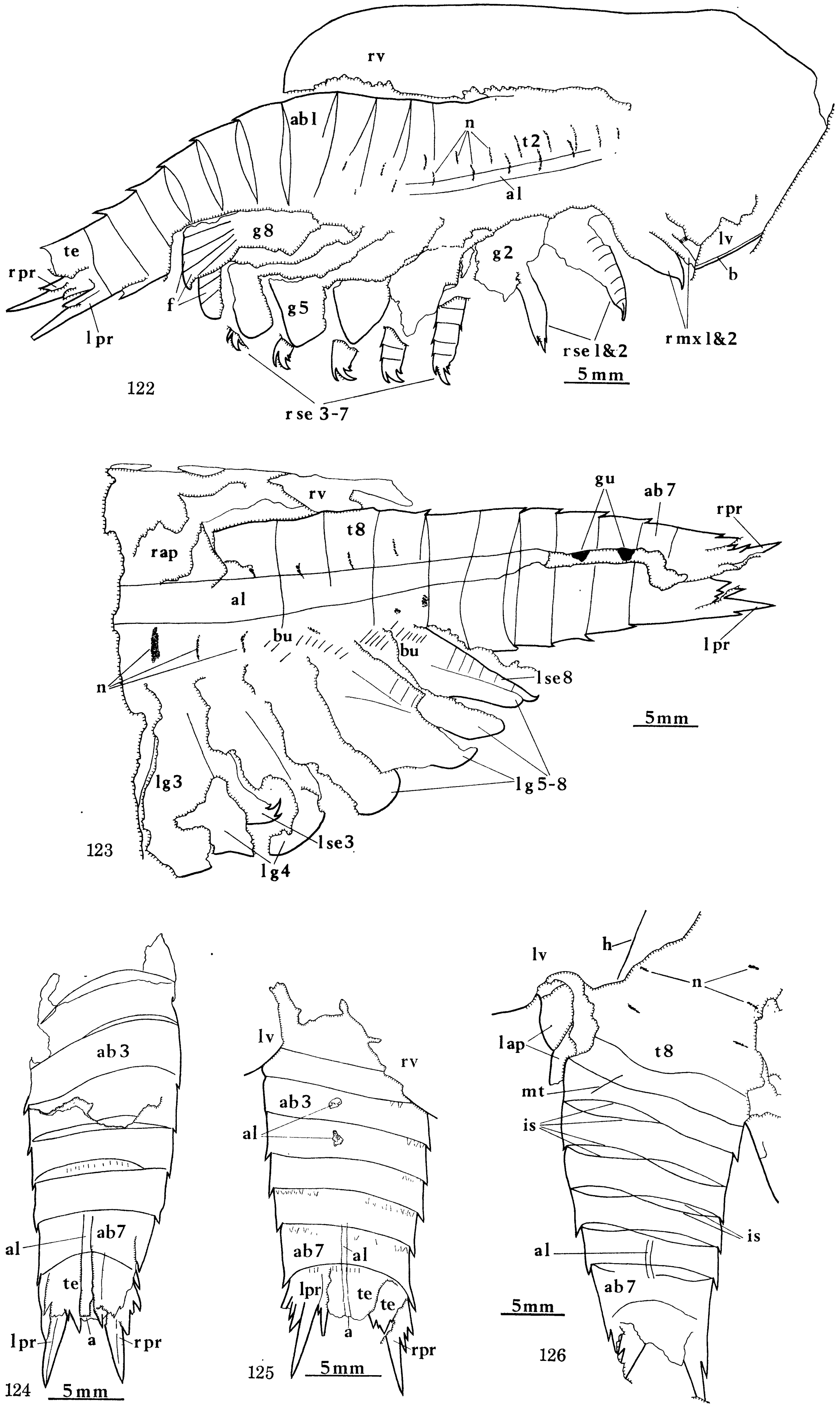

117


118


119


120

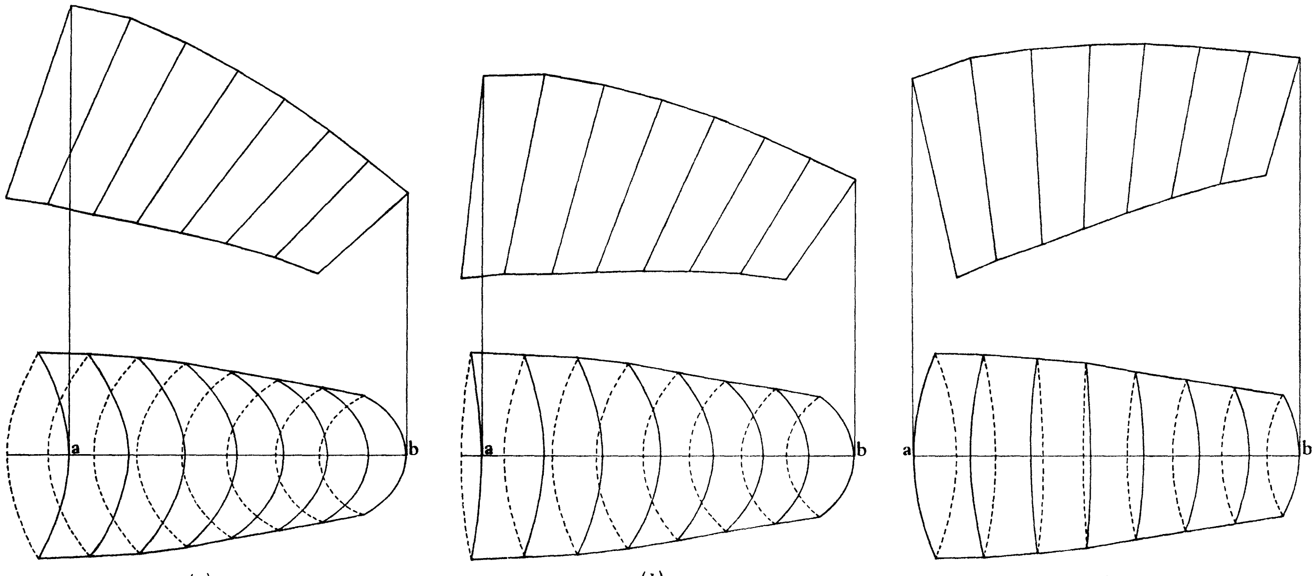

121



FIGURES 122–126. For description see p. 466.

burial or compaction (figures 168, 171, 172, plate 13; figures 149, 150, plate 12). A few incomplete specimens preserve the cuticle of both sides of the abdomen separated by a layer of matrix due to infilling of the abdominal cavity after it became disarticulated from the rest of the trunk. Traces of the inter-somite boundaries are evident offset on opposite sides of the abdomen of U.S.N.M. 189015 (figure 94, plate 8), for example, which is tilted slightly in lateral aspect. The boundaries in U.S.N.M. 207294 are partly outlined in darker material which also occurs elsewhere on the abdomen (figures 118, 119, plate 10). This may represent softer tissue adhering to the cuticle and facilitating movement between successive somites. The posterior margin of each somite bore 55–70 short, posteriorly directed spines which are usually evident in outline where they extend beyond the margin of the abdomen, but are rarely apparent across the width of the trunk (figure 120, plate 10).

The opposing sides of the abdomen in the vast majority of specimens are compacted together and indistinguishable. Traces of the inter-somite boundaries on both sides, however, are



(*a*) (*b*) (*c*)

Figure 127. Projections of the abdomen (excluding the telson) of *Canadaspis perfecta* from lateral to parallel aspect (assuming a circular cross-section) to show the effect of compaction at different attitudes to the bedding (horizontal) on the configuration of the inter-somite boundaries. The dorsal section of the boundaries in parallel aspect is represented by a solid line, the ventral section dashed. For further discussion see text.

Description of plate 10 and figures 122–126

Canadaspis perfecta (Walcott, 1912)

Figure 115. U.S.N.M. 207270, lateral, west (magn. × 2.5).

Figures 116, 117. U.S.N.M. 207293, oblique. 116. West. 117. Under alcohol, north-west, abdomen. (Magns × 2.)

Figures 118, 119. U.S.N.M. 207294, parallel, north and east respectively. (Magns × 2.5.)

Figure 120. U.S.N.M. 207284, parallel, north-west, abdomen (magn. × 3).

Figure 121. U.S.N.M. 207289, parallel-oblique, under alcohol, west, abdomen (magn. × 3).

Figures 122–126. Explanatory drawings. 122. U.S.N.M. 207270. 123. U.S.N.M. 207293. 124. U.S.N.M. 207294. 125. U.S.N.M. 207284, abdomen. 126. U.S.N.M. 207289, abdomen.

frequently evident as separate arcs converging at the margins; the trunk is rarely flattened so that the section of the boundary on one side precisely overlies that on the other. The boundaries are usually preserved in slight relief, but are also traced out by reflective bands. They appear to have been straight and approximately normal to the long axis of the trunk, but their preserved configuration depends on the attitude of the abdomen, and its orientation to the bedding; the trace on opposite sides may even cross over medially (figure 121, plate 10). The abdomen appears to have been naturally curved ventrally, as this is the usual configuration in lateral aspect. The ventral section of the inter-somite boundaries is thus usually preserved anterior of the dorsal (figure 100, plate 8).

Figure 127 illustrates the possible variation in the configuration of the boundaries and apparent length of the abdomen in parallel aspect caused by changes in orientation to the bedding. When the abdomen is compacted with the ventral margin at an angle of 15° or 20° below the bedding (figure 127*a*), the inter-somite boundaries overlap throughout most of its length (figure 135, plate 11). As the ventral margin approaches an orientation parallel to the bedding (figure 127*b*) the anterior boundaries cease to overlap (figure 136, plate 11), and become further separated when the ventral margin reaches an angle of 15–20° above the bedding (figure 127*c*; figures 137, 138, plate 11). Traces of the inter-somite boundaries on both sides of the abdomen are also evident in lateral and oblique aspect. U.S.N.M. 213858, for example, appears to have split through the abdomen to the right of the alimentary canal, which separates the traces of the boundaries on the opposing sides. The trace on the left side, which is convex anteriorly and prominent on the part (figure 139, plate 11), is interrupted by the canal, behind which it passes. The trace on the right side, however, is continuous across the canal and more highly reflective on the counterpart (figure 140, plate 11).

Recognition of possible configurations of the inter-somite boundaries draws attention to additional, rarely preserved, reflective features in the abdomen. Traces of the boundaries on both sides of the abdomen are evident on U.S.N.M. 207295 (figures 141, 142, plate 11), for example; the relief indicates that the anterior arcs (convex forwards) are ventral and the posterior (concave forwards) dorsal. The anterior arc separating somites 4 and 5, however, is doubled, the traces converging at the lateral margins. This may be due to overlap or to remnants of flexible cuticle at the boundary. The opposing arcs of the boundaries between somites 4, 5 and 6 are separated by a less reflective transverse median line, which converges with the

---

Description of plate 11 and figures 128–134

Canadaspis perfecta (Walcott, 1912)

Figures 128–134. Explanatory drawings of the abdomen. 128. U.S.N.M. 207301. 129. U.S.N.M. 207267. 130. G.S.C. 45275, part. 131, 132. U.S.N.M. 213858, part and counterpart respectively. 133. U.S.N.M. 207295. 134. U.S.N.M. 207288.

Figure 135. U.S.N.M. 207301, parallel, under alcohol, north, abdomen (magn. × 3).

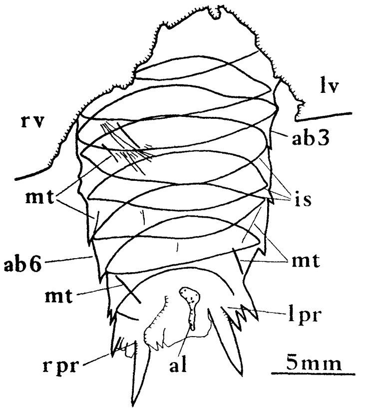
Figure 136 U.S.N.M. 207267, parallel, under alcohol, west, abdomen (magn. × 3).

Figures 137, 138. G.S.C. 45275, parallel, part and counterpart respectively, under alcohol, south-west, abdomen. (Magns × 3.)

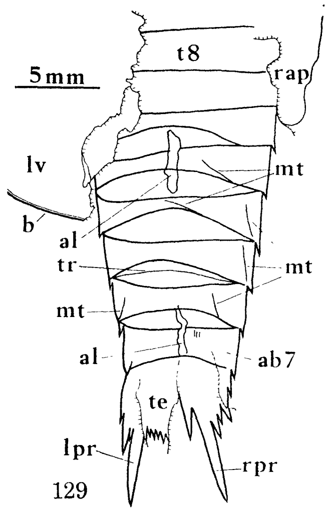
Figures 139, 140. U.S.N.M. 213858, oblique, under alcohol, abdomen. 139. Part, east. 140. Counterpart, north. (Magns × 3.)

Figures 141, 142. U.S.N.M. 207295, oblique. 141. East (magn. × 1.5). 142. Under alcohol, south-east, abdomen (magn. × 4).

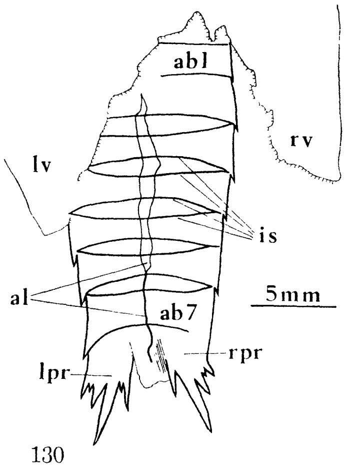
Figure 143. U.S.N.M. 207288, lateral, under alcohol, north-west, abdomen (magn. × 3).



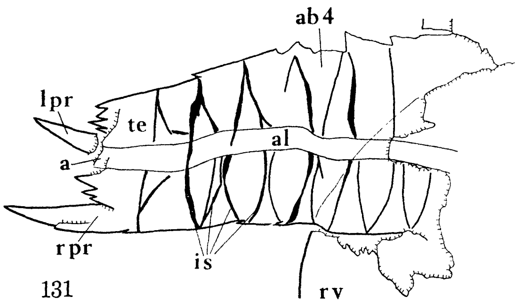
128



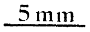
129

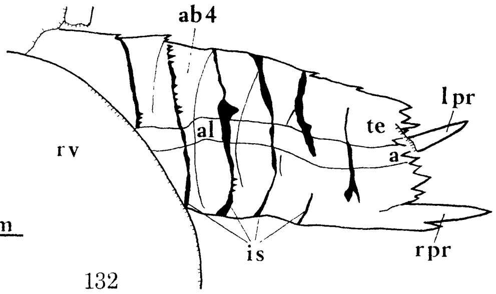


130

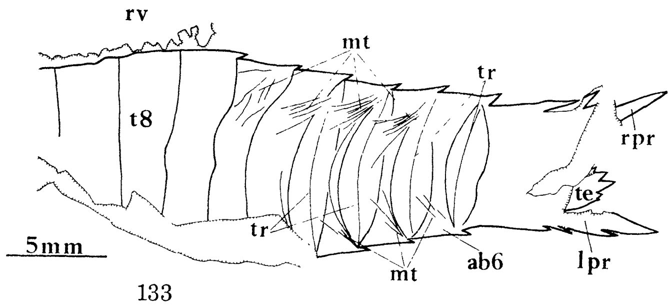


131

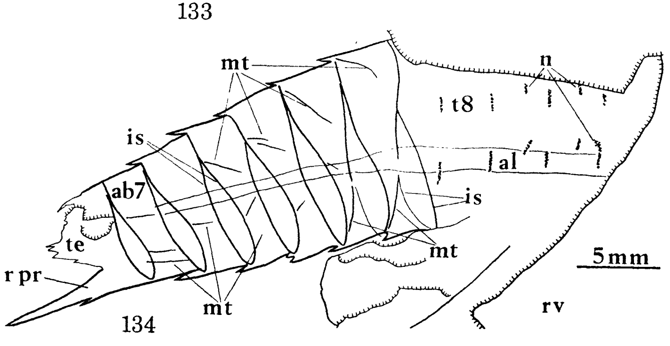




132



133



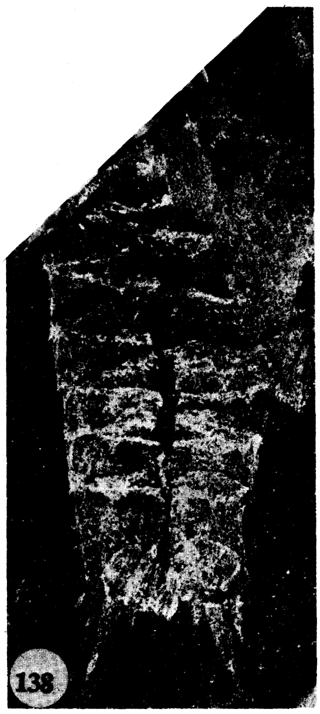
134

Figures 128–134. For description see p. 467.

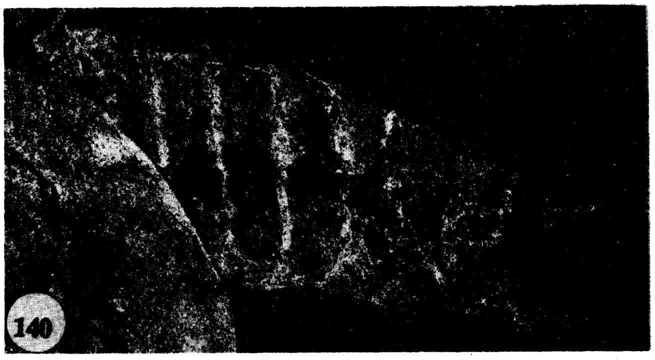

135

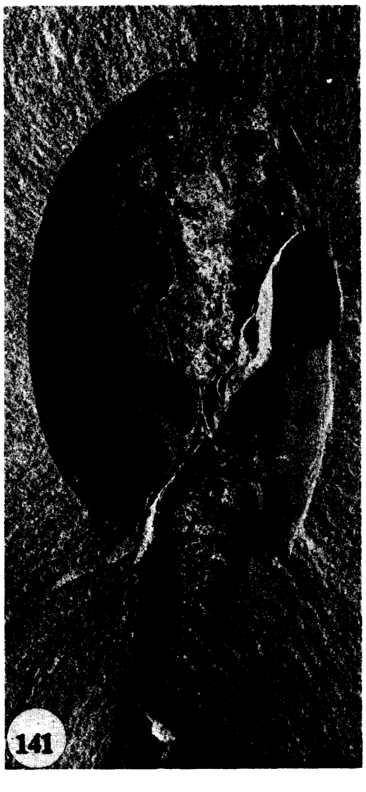

136


137

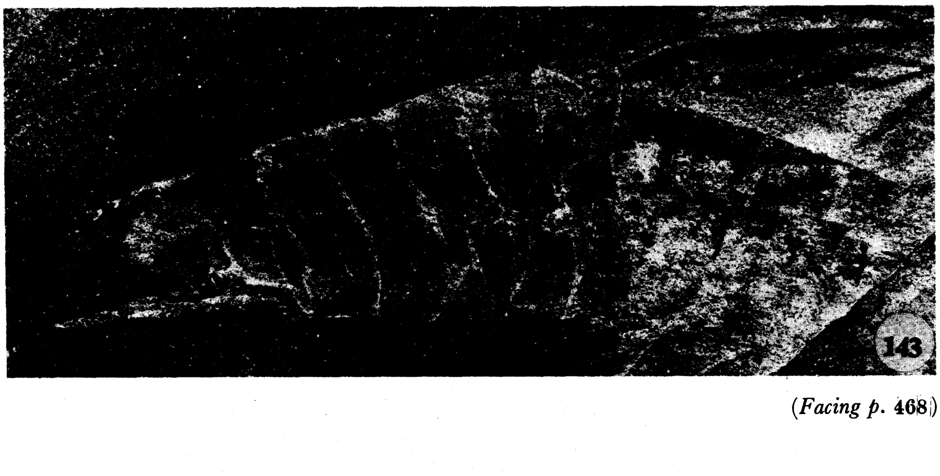

138

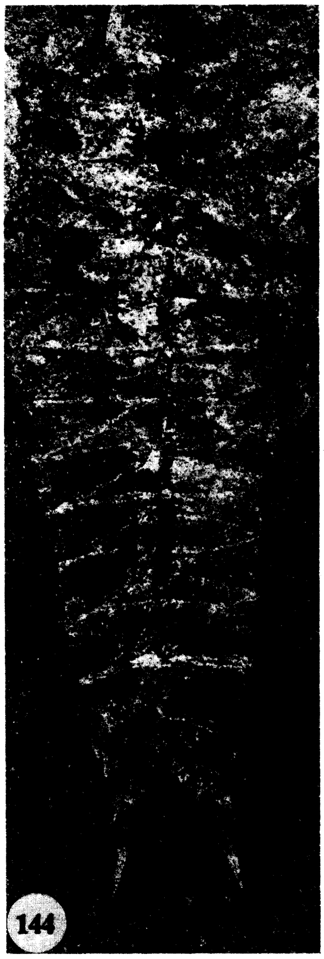

139


140

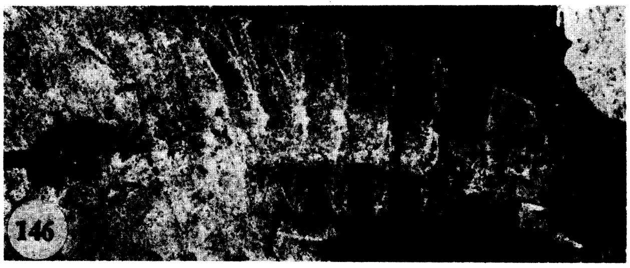

141


142

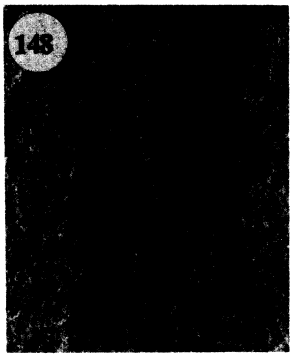

143

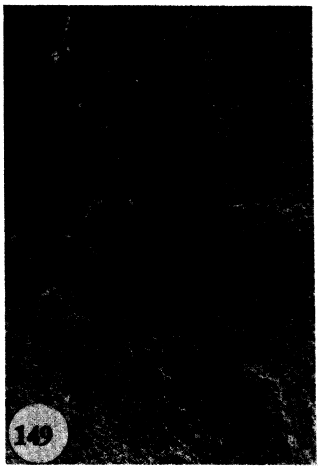

144


145

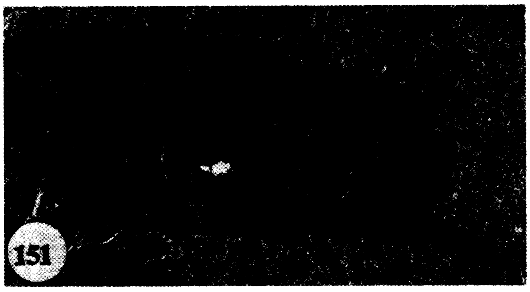

146


147


148

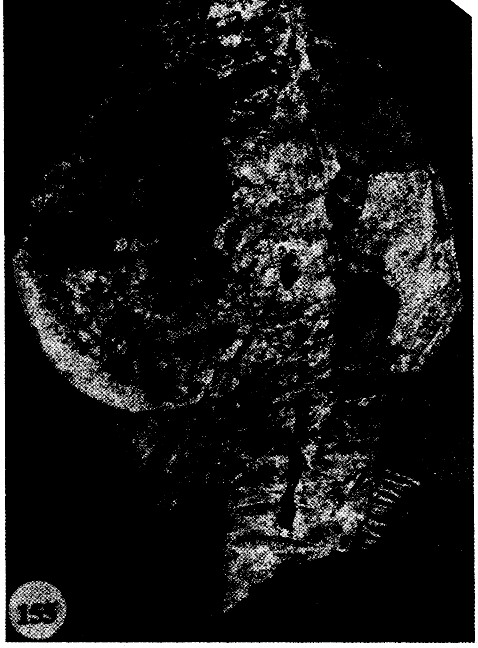

149


150


151

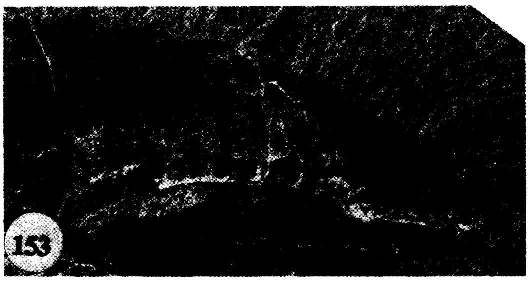

154

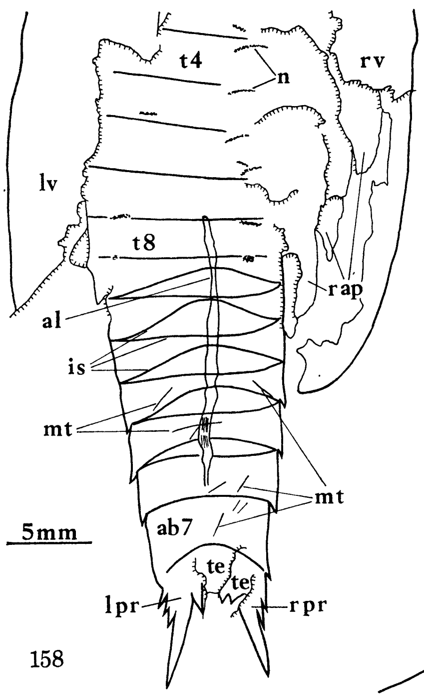

152


155

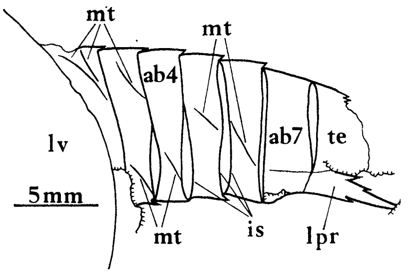

156


157

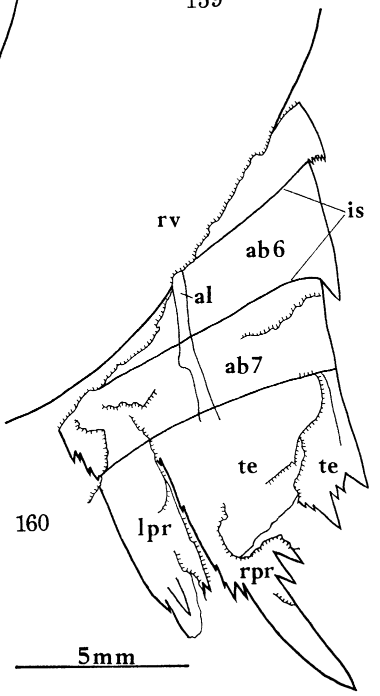

153



158



159



160

Description of plate 12 and figures 158–160

Canadaspis perfecta (Walcott, 1912)

Figures 144, 145. U.S.N.M. 213864, parallel, under alcohol, abdomen. 144. Part, north. 145. Counterpart, south. (Magns x 3.)

Figure 146. G.S.C. 45268, lateral, under alcohol, west, abdomen (magn. x 3).

Figure 147. G.S.C. 45274, lateral, east, showing large ventral spine on sixth abdominal somite (magn. x 3).

Figure 148. U.S.N.M. 207269, parallel, east, ventral projections of pre-telson somite in ventral aspect (magn. x 4).

Figures 149, 150. U.S.N.M. 207266, lateral. 149. North-east, posterior abdominal somites and telson (magn. x 3). 150. North (magn. x 1).

Figure 151. G.S.C. 45264, lateral, east, showing attitude of ventral projection of pre-telson somite (magn. x 3).

Figure 152. G.S.C. 45269, lateral, north-east, showing attitude of ventral projection of pre-telson somite (magn. x 3).

Figure 153. G.S.C. 45273, lateral, north-west, showing course of alimentary canal in abdomen. (magn. x 3).

Figure 154. U.S.N.M. 207299, lateral, south, showing dorsal flexure of abdomen (magn. x 1).

Figures 155–157. U.S.N.M. 207297, parallel-oblique. 155. Under alcohol, north (magn. x 1.5). 156, 157. Alimentary canal; under alcohol, north, and west, respectively. (Magns x 3.)

Figures 158–160. Explanatory drawings. 158. U.S.N.M. 213864, part. 159. G.S.C. 45268, abdomen. 160. U.S.N.M. 207266, posterior abdominal somites and telson.

boundary at the margin of the trunk. This feature is convex forwards, indicating that it was situated in the ventral part of the abdominal cavity; it may represent an intersegmental tendon. Groups of about six strands of reflective material with very faint relief are also evident in the abdomen, particularly on the right side of somites 4 and 5. Traces also occur on the left side, indicating that the features were paired. The strands, which are stoutest at the margins of the groups, appear to have been attached laterally at the inter-somite boundaries and diverge anteriorly, extending obliquely across the abdomen. The posterior attachment of the group of strands near the right hand margin of somite 5 appears to extend adaxially along the transverse median line. There is no evidence of the nature or position of the attachment anteriorly, but the strands appear to terminate along a line approximately normal to the longitudinal axis, the innermost extending almost to the mid-line, and may thus have been attached to the preceding inter-somite boundary. These features are interpreted as traces of muscles.

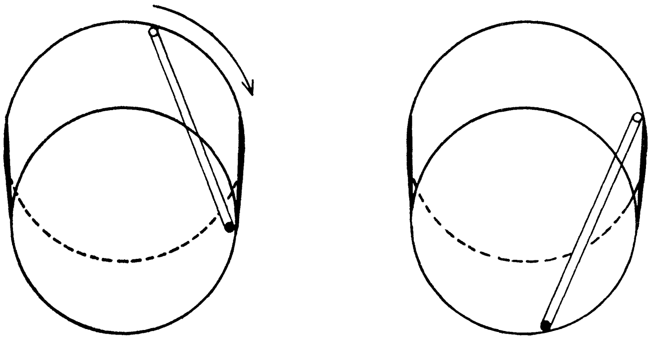


FIGURE 161. Diagrammatic representation of a single somite of *Canadaspis perfecta* demonstrating the effect of a slight rotation of the trunk relative to the bedding on the preserved configuration of a muscle strand traversing the body cavity obliquely. For further discussion see text.

The abdominal muscles are rarely apparent, and often only individual strands are preserved. Additional specimens compacted in parallel aspect (figure 136, plate 11; figures 144, 145, plate 12) confirm that groups of strands extended from the postero-lateral margin of the somites towards the mid-point of the anterior margin. Occasional examples (figure 135, plate 11) appear, on the other hand, to traverse the somite from about the mid-point of the posterior boundary to the lateral extremity of the anterior margin. Figure 161 shows how this difference in attitude may be the result of a slight rotation of the abdomen relative to the direction of compaction. Single strands are preserved in lateral aspect (figure 143, plate 11; figures 86, 87, plate 7) traversing the somites obliquely from about the ventral and dorsal extremities of the posterior margin; those in the ventral part of the abdomen are more prominent. Occasional departures from this configuration (figure 146, plate 12) are probably also the result of differences in orientation. A large muscle extended from the proximal end of the major paired spines which projected beneath the telson, to the anterior margin of the last abdominal somite (figure 135, plate 11). Evidence of longitudinal muscles similar to those observed in the thorax is lacking. An even layer of reflective material on the counterpart of U.S.N.M. 213864 (figure 145, plate 12), however, partly obscures the inter-somite boundaries and traces of individual muscle strands which are evident on the part (figure 144, plate 12) and may represent the ventral half of a sheath of longitudinal muscle, or the body wall. This layer is evident on many specimens but the plane of splitting rarely ensures so obvious a contrast in reflectivity between the opposing slabs. There is no satisfactory basis for a reconstruction of the abdominal musculature. Some of the reflective traces interpreted as muscles may represent other features.

The sixth abdominal somite bore a fringe of spines posteriorly (figure 120, plate 10) similar to that on the others, but this included a number of larger spines ventrally which are occasionally evident in specimens preserved in lateral aspect (figure 147, plate 12; figure 100, plate 8).

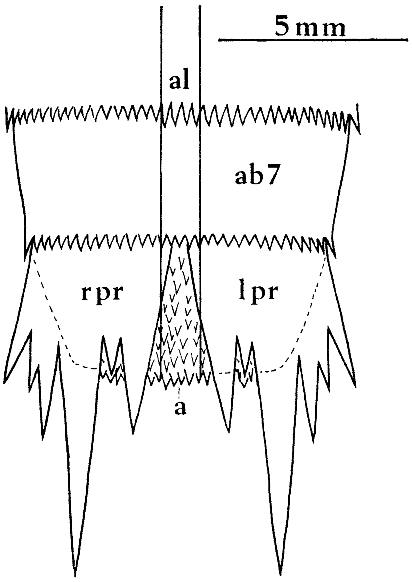


FIGURE 162. Reconstruction of seventh abdominal somite and telson of *Canadaspis perfecta* (Walcott, 1912) in ventral view.

These enlarged spines have not been observed on the more anterior somites. The seventh, or pre-telson somite, bore a pair of deeply divided spinose projections which extended posteriorly ventral of the telson (figures 136–138, plate 11; figures 74–76, plate 6). The longest spine on these projections was broader proximally and over twice as long as the others. It was flanked on the outer margin by three smaller spines, the middle shortest, and on the inner by two, the longer adaxial. Small additional spines are occasionally evident separating these six (figure 76, plate 6), but it is not clear whether their occurrence is variable, or they are normally obscured. The median spines tend to be preserved ventral of those flanking them (although their relative levels vary with slight differences in orientation to the bedding) indicating that together the spines formed a curve in transverse section, concave dorsally (figure 146, plate 12). The longest spine is usually curved slightly dorsally at its distal extremity (figure 139, plate 11). It is similar in dimension in lateral and parallel aspect and was therefore sub-circular in transverse section, as were, presumably, the other spines. The longitudinal grooves or ridges on the spines of U.S.N.M. 207294 (figure 119, plate 10) are probably the result of compaction; they have not been observed on other specimens.

The ventral projections occupy the entire width of the pre-telson somite in parallel aspect (figure 162; figure 148, plate 12) but only about one fifth of the height in lateral aspect (figures 146, 151, plate 12), and were therefore flattened proximally in transverse section. The posterior margin of the somite is evident traversing the projections as a reflective or relief trace in some specimens (figure 136, plate 11; figures 144, 145, plate 12), and the spines which fringe it are also occasionally apparent in outline ventral of the projections (figure 149, plate 12).

Further evidence that the projections inserted into the pre-telson somite is provided by a defined ridge along its ventral margin in lateral aspect. They do not, however, appear to have articulated proximally. Their attitude varies from almost parallel (figure 118, plate 10) to slightly divergent (figures 136–138, plate 11) in parallel aspect, but this is probably due to slight variations in orientation or morphology. The longest spine is usually directed posteriorly parallel to the ventral margin of the abdomen in lateral aspect (figure 147, plate 12), but a degree of flexibility, or malformation, is suggested by examples flexed dorsally (figure 38, plate 3) or slightly ventrally (figure 151, plate 12), or more obliquely in this direction (figure 152, plate 12).

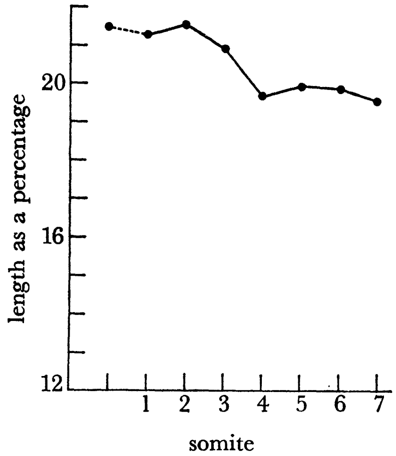


FIGURE 163. Relative lengths of abdominal somites of *Canadaspis perfecta*. Plot of lengths of abdominal somites of five specimens, preserved in lateral aspect, expressed as an average percentage of the total length of abdominal somites 3–7 (somite length calculated as the average of that measured along dorsal and ventral margins). Data for thoracic somite 8 included from figure 107 to permit comparison.

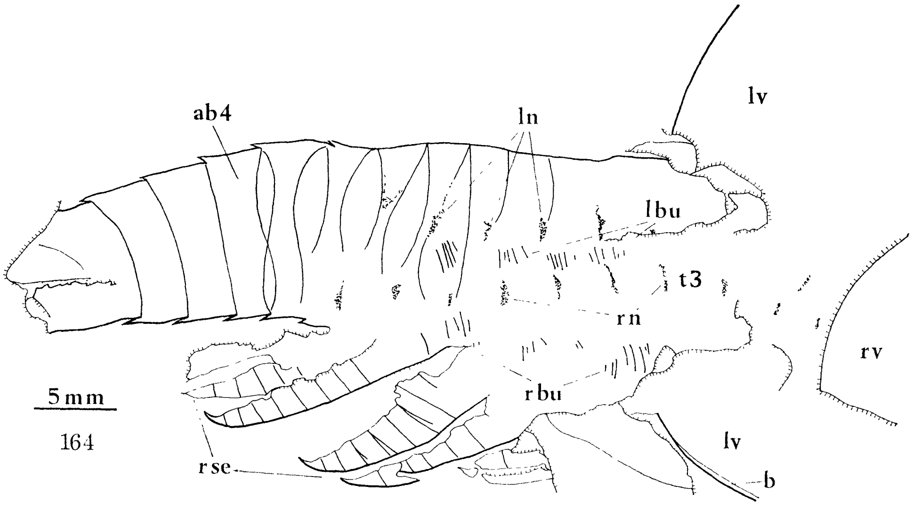
The anterior margin of the telson shows a more pronounced curvature in parallel aspect than the abdominal inter-somite boundaries anterior of it (figures 137, 138, plate 11; figures 144, 145, plate 12). This is not apparent, however, in lateral aspect (figure 146, plate 12), and is presumably an effect of orientation (cf. figure 127). The telson was similar in length to the posterior abdominal somites. It is compacted against the ventral projections in parallel aspect, obscuring the lateral margins, which taper more rapidly posteriorly than those of the abdomen (figure 120, plate 10). The dorsal margin was parallel to that of the abdomen, the telson terminating in a blunt spinose border (figure 143, plate 11); the ventral margin is usually compacted against the underlying projections. No regular arrangement of the small spines on the posterior margin is apparent; the outline differs in detail on every specimen, although this is presumably partly the result of slight variations in orientation. They appear to have covered the entire posterior surface and are occasionally evident as a series of closely spaced lineations parallel to the longitudinal axis of the telson (figures 137, 138, plate 11; figure 86, plate 7). The anus is situated at the mid-point of the posterior margin in parallel aspect flanked by the ventral projections of the pre-telson somite (figures 118–120, plate 10), but lies slightly ventral of the mid-point in lateral aspect (figures 18, 19, plate 2). It is occasionally displaced ventrally due to decay or distortion (figure 153, plate 12).

The abdomen tapers gradually posteriorly in parallel aspect (figures 144, 145, plate 12). The dorsal margin is curved and converges with the ventral, which is usually straight (figure 143, plate 11) or slightly concave (figures 111, 112, plate 9), posterior of the second somite. The relative lengths of the somites are probably distorted in parallel aspect due to the ventral curvature of the abdomen (cf. figure 127). In lateral aspect there is a gradual decrease in length posterior of the second somite, interrupted by the shorter fourth somite (figure 163). A comparison of the height of individual somites preserved in lateral aspect with their width in parallel aspect (the values expressed as a fraction of the total length of a number of somites) indicates that the transverse section was approximately circular. The abdomen was capable of a degree of flexing, particularly ventrally (figure 154, plate 12, shows dorsal flexure, but this may be the result of decay). A comparison of the dorsal and ventral lengths of individual somites in several specimens suggests that this was achieved by differential telescoping along the boundaries between the somites, which were presumably joined by a band of flexible cuticle. Slight lateral flexing also occurred. The height of the somites in U.S.N.M. 213859 (figures 86, 87, plate 7) greatly exceeds those of U.S.N.M. 213855 (figure 100, plate 8), although the lengths are similar, and this, together with the wide reflective traces along the inter-somite boundaries in the former, suggests that the overall length of the abdomen could also be reduced by telescoping.

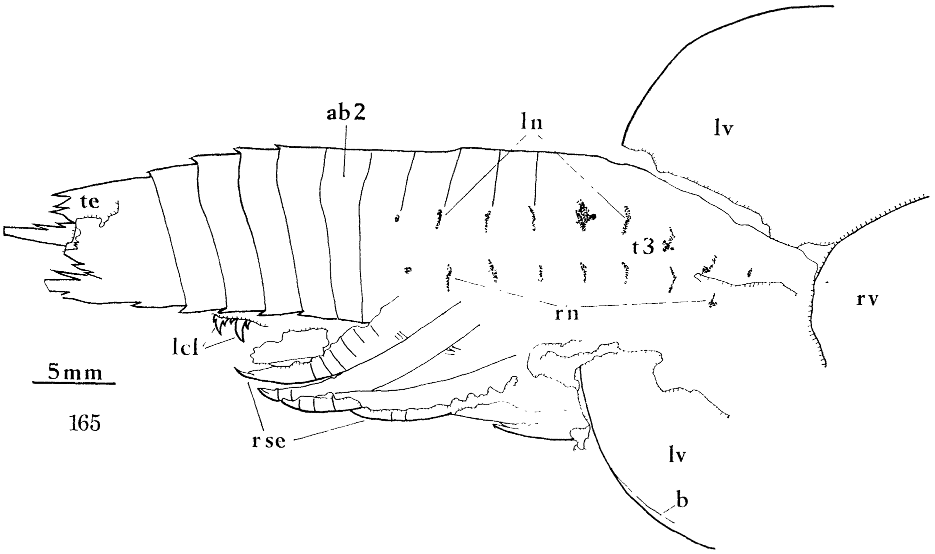
(*f*) *Alimentary canal*

The preservation of the canal is highly variable, and may even change markedly within an individual specimen. Examples preserving no evidence of its course are, however, rare. The canal is frequently evident in relief, presumably due to the presence of ingested material, the trace ranging from a shallow, continuous band of uniform width (figures 139, 140, plate 11) to a discontinuous series of almost nodular areas of sediment of varying diameter (figures 155–157, plate 12). An incomplete trace is probably the product of a degree of decay and the retention of the contents where the wall survives. The occasional occurrence of an uncharacteristically wide relief trace (figures 18, 19, plate 2; figure 39, plate 3) may be the result of flattening within the body cavity unimpeded by confining sediment, or the adherence of surrounding material to the canal when the fossil was split. The contents consist of a darker material (figures 156, 157, plate 12) which is only visible where the 'core' of the gut is exposed, and appears to have been finer in texture than the surrounding features and enclosed by a highly reflective wall. A series of closely spaced, transverse lineations on the canal wall, which become coarser posteriorly on U.S.N.M. 207297 (figure 156, plate 12), may represent muscle bands, or be merely an effect of contraction due to fragmentation of the canal during decay. Longitudinal lineations also occur (figures 144, 145, plate 12), but do not appear to be confined to the wall itself, and may be a feature of the contents. Relief traces are commonly flanked by a dark, reflective band which is apparently continuous in places with the wall. This band may parallel the relief trace (figure 166, plate 13) or widen slightly anteriorly (figure 155, plate 12), but usually bears no relation to its actual width. In the absence of a relief trace, reflective traces of 'normal' width rarely occur, but wider bands, which may be due to seepage of the contents laterally into the body cavity, are not uncommon (figure 146, plate 12). Discontinuous relief traces may be connected by a much wider reflective band (figure 117, plate 10), or more rarely one of similar width (figure 14, plate 1) which may represent remnants of the canal walls.

The canal is preserved in the mid-line in parallel aspect (figures 137, 138, plate 11) and, although it tends to be obscured anteriorly, is assumed to maintain an undivided course from a point anterior of the mouth, where it curves postero-ventrally (§ 5*a*). In lateral aspect the canal usually lies just ventral of the mid-line (figure 100, plate 8) and approximately parallels



164



165

Description of plate 13 and figures 164, 165

Canadaspis perfecta (Walcott, 1912)

Figures 164, 165. Explanatory drawings omitting carapace; U.S.N.M. 207276 and 207287 respectively.

Figure 166. Y.P.M. 5801, parallel, reflected, west, abdomen (magn. × 3).

Figures 167–169. U.S.N.M. 207276, lateral. 167. Under alcohol, north, trunk and appendages (magn. × 3). 168. East (magn. × 1). 169. East, appendages (magn. × 3).

Figures 170, 171. U.S.N.M. 207287, lateral. 170. Under alcohol, north, trunk and appendages (magn. × 3). 171. East (magn. × 1).

Figure 172. U.S.N.M. 207305, lateral, north (magn. × 3).

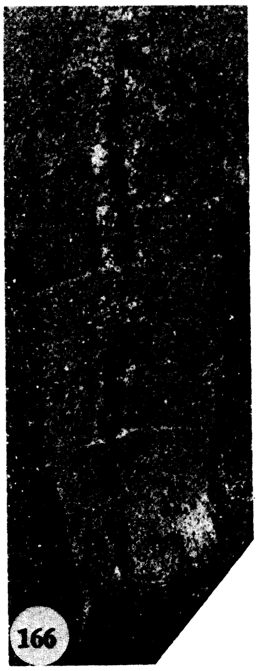
Figure 173. U.S.N.M. 213837, lateral, north-west (magn. × 3).

Figure 174. G.S.C. 45279, parallel, north-east (magn. × 3).

Canadaspis perfecta? (Walcott, 1912)

Figure 175. U.S.N.M. 57711, lateral, west, original of Walcott 1912, pl. 32, fig. 2 (magn. × 1.5).

Figure 176. U.S.N.M. 57712, lateral, north-west, original of Walcott 1912, pl. 32, fig. 3 (magn. × 1.5).


166

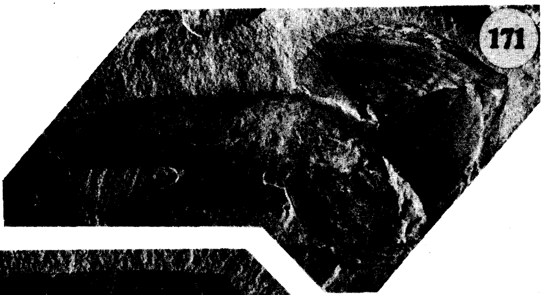

167

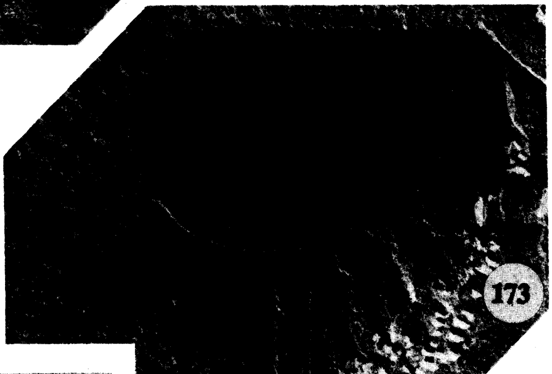

168

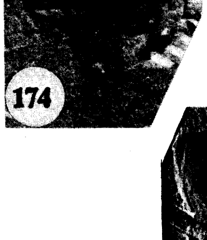

169

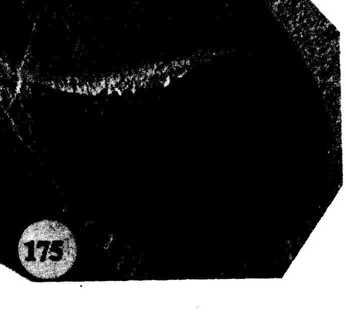

170

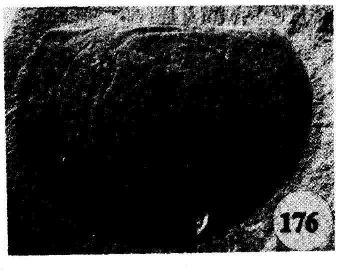

172


171


173


174


175


176

the ventral margin of the trunk. A slight ventral flexure is evident in some specimens in the somites immediately anterior of the telson (figures 116, 117, plate 10). No evidence of diverticula has been observed. The gut trace in several individuals deviates from its normal course (figures 66–69, plate 5) perhaps due to decay of the support within the body cavity. The canal probably did not alter in diameter along its length, except perhaps in the cephalic region (§ 5*a*), but is appearance varies with the nature of the preservation and, presumably, the amount of ingested material. Examples with a prominent, uniform relief trace probably provide the most accurate indication of the size (figures 139, 140, plate 11), as the retention of the contents implies that the wall has remained intact.

(*g*) *Exuviae*

Individuals which can be identified as intact exuviae are rare; they probably broke up rapidly and may be represented by fragments of the cuticle or more frequently by isolated carapaces. A few specimens, however, preserve the carapace at an uncharacteristic angle to the trunk. U.S.N.M. 207276 (figures 167–169, plate 13) and 207287 (figures 170, 171, plate 13) also lack traces of the alimentary canal, and the trunk is unusually straight as a result of an upward flexure of the abdomen near the boundary with the thorax, reflected in a slight concavity of the dorsal margin in this region. A pronounced downward flexure occurs about the mid-thorax but is insufficient to account for the attitude of the valves, which appears to be due to a dislocation near the posterior margin of the cephalon. The thoracic appendages overlap unnaturally and are directed posteriorly at a low angle to the trunk. These specimens exhibit many features associated with moulting in Recent Malacostraca, and probably represent exuviae. The evidence suggests that the process was initiated by rupture of the flexible cuticle joining the thorax and cephalon. The latter was then withdrawn posteriorly and as the unsupported carapace swung forward ventrally the trunk and appendages emerged anteriorly from the rest of the discarded cuticle, possibly aided by tearing of the dorsal margin of the anterior thoracic somites.

Traces of the alimentary canal are evident along most of the length of G.S.C. 45267 (figures 113, 114, plate 9) and U.S.N.M. 207305 (figure 172, plate 13), although the carapace is thrown forward. These specimens are therefore unlikely to represent exuviae, but may have been beginning to moult when buried.

(*h*) *Morphometrics*

Total sagittal length is considered an unreliable indication of size, as the dimensions of the abdomen are susceptible to variation with orientation (figure 127), and a degree of telescoping and flexing. Carapace length, however, has advantages; distortions are easily recognized, and measurements, which are made in a straight line, approach the true dimension in both lateral, parallel and some oblique aspects. In addition the relationship between the length of the carapace and that of the abdominal somites appears to be isometric, like most bivariate relationships in arthropods (Andrews, Brower, Gould & Reyment 1974, p. 83). The number of specimens suitable for measurement is, however, limited. Only those showing features in addition to the carapace can be positively identified as *Canadaspis perfecta*, and additional examples are eliminated by orientation to the bedding and poor or incomplete preservation. This leaves about 10 % of the material collected by the Geological Survey of Canada in 1966 and 1967, for example.

A size-frequency histogram based on carapace length (figure 177) shows a clearly bimodal distribution (cf. *Marrella splendens*, Whittington 1971*a*). The increase in length between the two means is much greater than that expected between successive instars, assuming that moulting occurs when the body mass doubles (Andrews *et al.* 1974). Each group thus presumably represents several stages. There is little apparent difference between the smallest examples of *Canadaspis perfecta* and those which fall into the group of larger individuals; they are unlikely to represent sexual dimorphs. Ten pairs of biramous appendages are evident, and seven abdominal somites and the telson extend beyond the carapace (figure 173, plate 13). A graph of the length of the hinge against both the length and height of the valves (figure 178) demonstrates an isometric relation between these variables. The eye and second antenna, however, appear to have been proportionally larger in the smaller individuals (figure 174, plate 13). Negative differential growth of the eyes occurs in many arthropods (Andrews *et al.* 1974, p. 83).

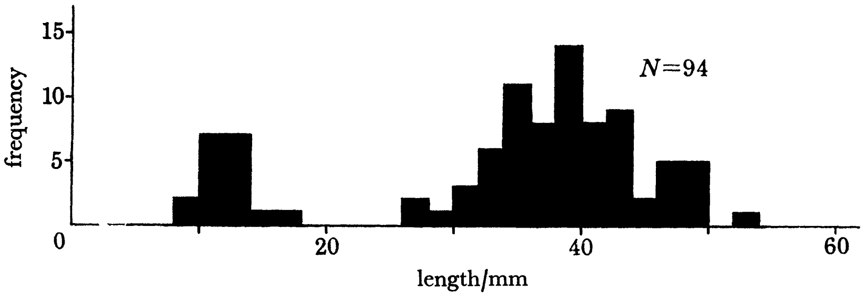


FIGURE 177. Size-frequency histogram of carapace length of specimens of *Canadaspis perfecta* from the Walcott Quarry plotted in 2 mm intervals. The material falls into two groups: mean 11.87, var. 4.31, $N = 18$ and mean 39.42, var. 32.86, $N = 76$.

6. DISCUSSION

(*a*) *Previous research*

Canadaspis perfecta is the type species of the genus erected by Novozhilov (in Orlov 1960) to include Burgess Shale arthropods referred by Walcott (1912) to *Hymenocaris*. The fate of all previously referred species is tabulated below.

original designation	current status
Hymenocaris perfecta Walcott, 1912	Retained as type species. Some individual specimens removed to *Perspicaris recondita* Briggs, 1977.
Hymenocaris? circularis Walcott, 1912	Identified as *Burgessia bella* Walcott, 1912 (§ 1).
Hymenocaris obliqua Walcott, 1912	Synonymized with *Canadaspis perfecta* by Simonetta & Delle Cave 1975.
Hymenocaris ovalis Walcott, 1912	Occupied by the indeterminate lectotype alone (Briggs 1977).
Hymenocaris? parva Walcott, 1912	Removed to *Tuzoia?* Walcott, 1912 (Briggs 1977).
Canadaspis obesa Simonetta & Delle Cave, 1975	Synonymized with *Canadaspis perfecta* herein.
Canadaspis dictynna Simonetta & Delle Cave, 1975	Removed to *Perspicaris* Briggs, 1977.

Simonetta & Delle Cave (1975, p. 11) found insufficient evidence to separate *Canadaspis obliqua* from *C. perfecta*, although Walcott (1912) considered that 'they differ in the form of the carapace'. The specimens of *C. obliqua* figured by Walcott (1912, pl. 32, figs. 1–3: figure 38, plate 3; figures 175, 176, plate 13) appear to differ from the lectotype of *C. perfecta* (1912, pl. 31, fig. 1: figures 18, 19, plate 2) in the angularity of the extremities of the hinge and the ratio of height to length of the valves (although Walcott 1912, p. 224, states that two of the examples of *C. obliqua* are shortened due to compression). The outline of the valves may, however, vary considerably with orientation to the bedding (§ 3). U.S.N.M. 57703 (figures 18, 19, plate 2) is incomplete antero-dorsally, giving the valve a rounded appearance (cf. figures 111, 112, plate 9). In addition, U.S.N.M. 57710 and 57711 (figure 38, plate 3; figure 175, plate 13) are tilted downward anteriorly in relation to the bedding (the posterior margin of the left valve of U.S.N.M. 57710 is preserved anterior of the right) resulting in shortening of the carapace, reflected in concentric folds along the anterior margin, and a distortion of the antero-dorsal outline. A plot of hinge length against valve height for a variety of specimens of *C. perfecta* (figure 178) shows a high degree of correlation. The large scatter is predictable as the dimensions are at right angles, and variations in orientation will therefore tend to alter one

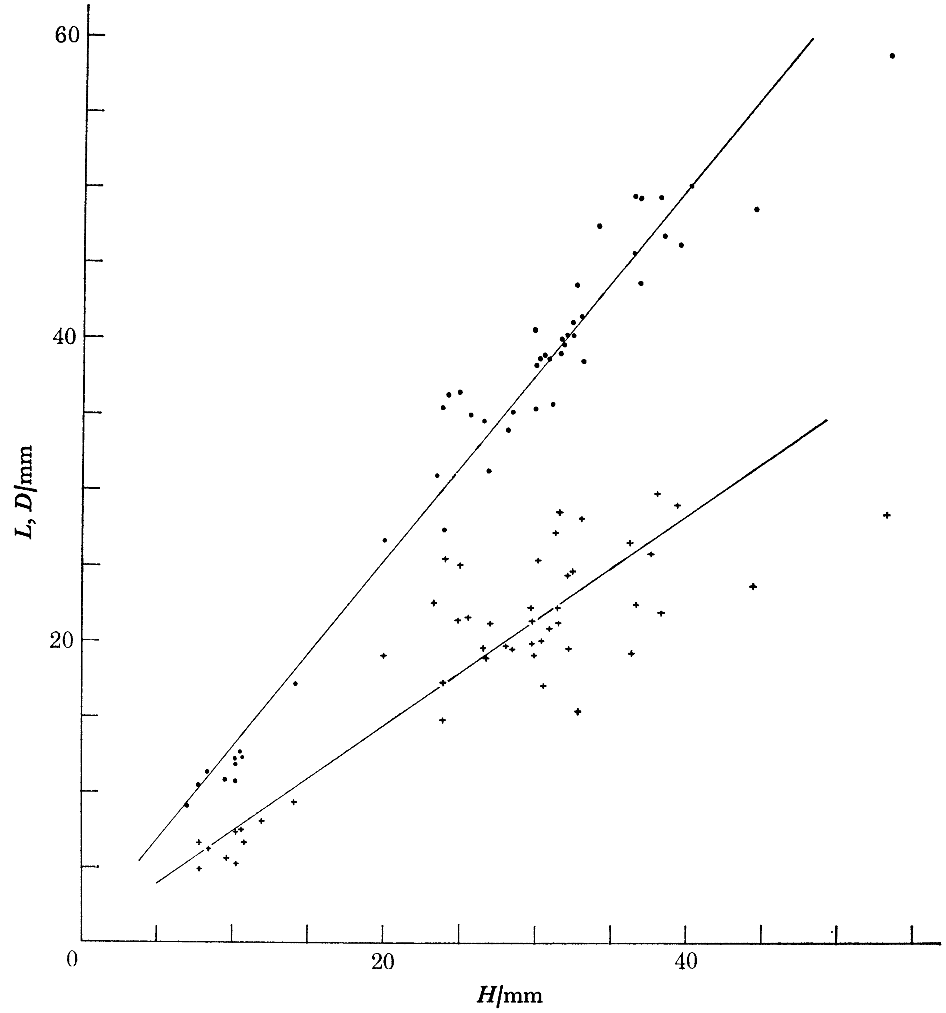


FIGURE 178. Graph of hinge length (H) of *Canadaspis perfecta* against both maximum length of carapace parallel to hinge (L), plotted in dots, and maximum valve height normal to hinge (D), plotted in crosses. Solid lines represent reduced major axes (Imbrie 1956). Measurements in millimetres. Bivariate statistics, H/L: mean H (var. H) = 27.11 (110.67); mean L (var. L) = 34.01 (168.48); α (var. α) = 0.98 (0.00087); a (var. a) = 1.23 (0.0013); r (r_e) = 0.98 (0.98); N = 48. H/D: mean H (var. H) = 27.01 (106.50); mean D (var. D) = 19.11 (52.13); α (var. α) = 1.00 (0.0051); a (var. a) = 0.70 (0.0025); r (r_e) = 0.87 (0.87); N = 49.

value independently of the other. Walcott's (1912) specimens of *C. obliqua* lie on the perimeter of the points plotted, but the gradation towards the reduced major axis, in addition to the considerations outlined above, vindicates Simonetta & Delle Cave's (1975) suppression of the species.

Simonetta & Delle Cave (1975, p. 12) erected *Canadaspis obesa* on the basis of 'the much more rounded and bulging carapace' and the caudal 'furca' 'which is made up by only two rather short and almost leaf-shaped spines'. The 'furca' of U.S.N.M. 189019, the only complete specimen (cited by Simonetta & Delle Cave 1975, pl. 39, fig. 1, as U.S.N.M. 189258) has been misinterpreted; although it is poorly preserved posteriorly several of the spines characteristic of the projections of the pre-telson somite of *C. perfecta* are evident on both sides (figure 85, plate 7). The additional examples of the telson, which are referred to as *Canadaspis* cfr. *obesa* (pl. 39, figs. 9, 10), belong to a different genus, *Perspicaris* Briggs, 1977. The unreliability of carapace outline as a diagnostic character has been demonstrated above. The inflated appearance of the valves in U.S.N.M. 189019 (figures 83, 84, plate 7), for example, is due to their preservation in outline, in contrast to those of most specimens of *C. perfecta* in parallel aspect, which are folded beneath themselves (figure 40, plate 3). In addition, both the outline and projections of the hinge of the isolated valve U.S.N.M. 189020 (cited as U.S.N.M. 189260 and 189261, pl. 40, fig. 10) suggest that it is a specimen of *Branchiocaris pretiosa* (Briggs 1976, p. 6). There is no justification for retaining the species *C. obesa*, and it is therefore suppressed.

The cephalic spine of *Canadaspis perfecta* was first observed by Raymond (1935, p. 221), who interpreted it as a rostrum, in two specimens collected by the Museum of Comparative Zoology expedition of 1930 (Whittington 1971*a*, pp. 1172, 1173). One of these was M.C.Z. 5977/70 (Rolfe 1963*a*, p. 391; figures 40, 41, plate 3); a study of the M.C.Z. collection suggests that M.C.Z. 5977/28 (figure 47, plate 3) was most likely the second. Rolfe (in Moore 1969, p. 324) figured M.C.Z. 5977/70 and interpreted the spine as a rostral plate. The evidence (§ 5*a*) suggests, however, that it is a feature with no exact counterpart in Recent arthropods. Simonetta & Delle Cave (1975, p. 11) noted the lack of a positively identified rostral plate, but made no reference to the cephalic spine.

Walcott (1912, p. 184) noted that 'a pair of small pedunculated eyes project in front of the carapace' but did not figure a specimen which showed them, 'as they were not observed until after the plates were made up'. The only previously published figure showing the eyes is that of Rolfe (in Moore 1969, p. 324, fig 4*a*; M.C.Z. 5977/70, figures 40, 41, plate 3). Walcott (1912, p. 184) also recorded the appendages described as first antennae (§ 5*a*) as 'minute jointed antennules', but he did not illustrate them. Størmer (1944, p. 100) considered it more probable that they represent 'distorted cephalic telopodites', but the evidence (§ 5*a*) does not support this view. The first antenna was not mentioned by Rolfe (in Moore 1969, p. 324) or Simonetta & Delle Cave (1975, p. 11). Walcott (1912, p. 184) described the second antenna on the basis of U.S.N.M. 57704 (pl. 31, fig. 2), but the discovery of the counterpart of this specimen has shown that it belongs to a new genus and species *Perspicaris recondita* Briggs, 1977. The existence of a second antenna in *Canadaspis perfecta* has not been disputed by subsequent authors, although Linder (1945, p. 26) remarked that 'the presence of preoral antennae is very uncertain'. The expansion of the alimentary canal in the cephalic region (§ 5*a*) was recorded by Walcott (1912, p. 184), but the specimen was not illustrated and has not been identified.

Raymond (1935, p. 221), in contrast to Walcott (1912), regarded the carapace as univalved, but he noted several specimens showing 'a deep, narrow furrow along the middle of the back which may indicate the beginning of a hinge'. One of these was undoubtedly M.C.Z. 5977/70 (figure 40, plate 3), the hinge of which is obscured anteriorly by exfoliation. Rolfe (1962, p. 2), however, considered the valves to be joined by 'a membranous hinge along the dorsal border', an interpretation supported by the present study (§ 5*b*). Öpik (1968, p. 10), in a comparison with the Bradoriida, suggested that 'the articulation of the valves was implemented by the flexibility and elasticity of the connective matter and by adductor muscles'. Walcott (1912) cited U.S.N.M. 57703 and 57704 (pl. 31, figs. 1, 2) as evidence of a 'strong adductor muscle scar'. U.S.N.M. 57704 has, however, been identified as *Perspicaris recondita* Briggs, 1977. The scars in *Canadaspis perfecta* are usually very tenuous and Walcott's figure of U.S.N.M. 57703 has almost certainly been retouched in this respect (cf. figures 18, 19, plate 2).

Walcott (1912, p. 158) considered that there were six cephalic (the eye representing one) and eight thoracic segments. His account of the appendages (p. 184) is complicated by reference to an unidentified specimen 'which was found...after the plates were finished and before this description was written' and which 'shows three cephalic legs' in addition to the first and second antennae. 'The two anterior are slender (mandible and maxillula) and the posterior maxilla is large and formed of short strong joints.' Walcott stated (p. 184) that 'there are eight pairs of thoracic legs'. It seems probable that his interpretation was influenced by the differentiation between cephalic and thoracic limbs characteristic of Recent Crustacea. Both maxillae were, in fact, essentially similar to the appendages of the thorax, and only the mandible was specialized (§ 5*a*). Raymond (1920*a*, p. 113) compared *Canadaspis perfecta* with the Nebaliidae on the basis of Walcott's description, but Rolfe (in Moore 1969, p. 299) considered the number of thoracic somites equivocal, and suggested (p. 324) that a mandible might have been absent. Simonetta & Delle Cave (1975, p. 11) found it 'impossible to say whether there were specialized mouthparts', but nevertheless postulated (p. 25) that there were 'two postoral somites at most' in the cephalon. They considered that 'ten to eleven pairs of legs are present'.

Walcott (1912, p. 184) used U.S.N.M. 57703 (pl. 31, fig. 1) to illustrate the thoracic appendages. 'The broad, setiferous joints of the exopodite' which he maintained were evident near the carapace, probably referred to the obvious spines on the inner margin of the segmented ramus of the anterior appendages (figure 20, plate 2). Walcott also noted 'traces of oval gills (epipodites)', which are the lamellate outer rami of the posterior appendages, but there is no evidence that they were positioned 'on the outer side of what appears to be the second joint of the leg'. Raymond (1920*a*, pp. 113, 114) based a comparison of the appendages with those of the Nebaliidae on Walcott's description, and concluded that the greatest similarity occurred in *Nebaliella antarctica* (which he erroneously referred to *Nebalia*) 'in which the endopodite consists of short flattened segments, and the exopodite is a long setiferous plate'. He considered, however, that epipodites were present in both arthropods (perhaps due to a confusion with *Nebalia*) whereas the appendages of *Canadaspis perfecta* resemble those of *Nebaliella*, rather than the other nebaliids, mainly because both lack epipodites. Raymond (1920*a*, 1935, p. 220) asserted that 'the strongly developed endopodites and exopodites...are distinctly trilobitan, not at all malacostracan', an opinion reiterated by Størmer (1939, 1944, 1949) and Dechaseaux (1953), and echoed by Simonetta & Delle Cave (1975, p. 23). Rolfe (1963*b*, p. 19), however, cast doubt on this interpretation, pointing out that 'the basal lamella is not filamentous as it is in the trilobitan limb'. He considered that the outer ramus was 'presumably pre-epipodial' but underestimated the number of segments (§ 5*d*) as 'up to eight' in concluding that the appendage 'could be a normal crustacean limb minus exopod'. The evidence does not support

Rolfe's (in Moore 1969, p. 324) contention that 'four distal, anteriorly curved claws' were present, or that of Simonetta & Delle Cave (1975, p. 11) who claimed to show that there are 'not four, but two, followed on each side by three minute claws or spines'. Simonetta & Delle Cave also underestimated the number of segments, and although they offered the first reconstruction of an isolated appendage (Simonetta & Delle Cave 1975, pl. 5, fig. 1*c*), it lacks most of the detailed morphology.

Walcott did not actually refer to the lack of appendages on the posterior trunk somites, but it is obvious from his figure of U.S.N.M. 57703 (1912, pl. 31, fig. 1; figures 18, 19, plate 2). Raymond (1920*a*, p. 113), however, was reluctant to acknowledge their absence, presumably in the light of the other similarities between *Canadaspis perfecta* and the Nebaliidae. He continued to express doubts (1935, p. 220), even after examining the material collected under his leadership by the Museum of Comparative Zoology expedition of 1930, being 'inclined to believe that further study...will show that this animal had appendages on all segments of the trunk'. The lack of abdominal appendages (apart from those on the pre-telson somite) was not, however, disputed by Fedotov (1925), or later authors; Størmer (1944, p. 124) considered that it was the result of 'a complete reduction'.

Walcott (1912, p. 183) noted that 'several specimens show seven abdominal segments extending beyond the carapace' (including the telson), but listed (p. 158) the number as six, with a query. The presence of seven was assumed by Fedotov (1925), Tiegs & Manton (1958), and by Rolfe (in Moore 1969, p. 299) with a query, but this figure, except perhaps in the case of Fedotov, probably did not include the telson. Simonetta & Delle Cave (1975) did not attempt to enumerate the somites. Rolfe's (in Moore 1969, p. 324) statement 'pleomeres of same length as thoracomeres' is misleading (figures 107, 163). Walcott's (1912) interpretation of the telson and pre-telson somite was confused by reference to U.S.N.M. 57706 (pl 31, fig. 4) which has been identified as *Perspicaris recondita* Briggs, 1977. Henriksen (1928, p. 14), however, pointed out that Walcott's observation of 'two to six cercopods' was the result of 'a varying shape of the edge of a single pair of cerci'. Størmer (1939, p. 262) considered that *Canadaspis perfecta* differed from the Phyllocarida in the structure of the telson. He observed (1944, p. 100) that 'only two cerci are present' but misinterpreted the remaining spines as 'the serrate hind margin of the last segment'. Rolfe (in Moore 1969, p. 324) recognized that the spines were projections of the pre-telson somite, and his outline of the morphology is largely confirmed by the present study. Simonetta & Delle Cave (1975, p. 11), however, reverted to the ill-founded notion that there were three pairs of 'true cerci'.

Walcott (1912, p. 184) overestimated the average length of the carapace as '40 to 60 mm' (figure 177), but Størmer's (1939, p. 231) indication of the overall? sagittal length (45 mm) is slightly low. Simonetta & Delle Cave (1975) gave no indication of the size apart from an undefined scale bar on the photographs.

(*b*) *Habitat, mode of life, functional morphology*

The preservation of the Burgess Shale arthropods (Whittington 1971*a*, 1974, 1975*b*; Hughes 1975; Briggs 1976) has been interpreted as evidence that a living population was overwhelmed and buried by a slow moving cloud of sediment (*Anomalocaris canadensis*, which appears to be represented by fragments of exuviae, may be an exception). This appears to have been the fate of *Canadaspis perfecta* also, and allied to the morphology of the appendages, suggests that it was benthonic in habitat, although Størmer (1944, p. 106) considered it nectonic.

The antennae were sensory rather than locomotory in function. The cephalic spine was much smaller than the rostral plate in the Nebaliidae, and is unlikely to have functioned in directing or controlling currents employed in feeding; it may have afforded some protection to the eyes.

It is reasonable to assume that the biramous appendages moved in a metachronal fashion. The nature of the segmented ramus suggests that it was ambulatory, and the arthropod could probably vary the attitude and gape of the carapace to allow unimpeded movement of the appendages during locomotion on the surface of the substrate. Movement of the flattened appendages presumably set up respiratory currents which may have assisted in feeding. The outer rami could overlap posteriorly (§ 5*d*) and may have acted as valves, as in some branchiopods and *Nebalia* (Cannon 1927) for example, which directed these currents. The carapace may have also facilitated suction by enveloping the trunk to protect the respiratory outer rami during feeding in a soft substrate. The strengthened distal claws on the segmented rami (§ 5*d*) presumably equipped them for raking the sediment into suspension, or scraping material off the substrate. The nature of the inwardly directed spines on the appendages, and the massive processes on the mandibles, incidate that *Canadaspis* did not filter fine particles. Coarse particles would, however, have been retained by these spines, and passed dorsally toward the ventral surface of the trunk.

The evidence suggests that each appendage moved through an arc as it swung forward (§ 5*d*). This would have allowed the group of posteriorly facing spines borne proximally by the segmented ramus to interact with that posterior of it, forming a type of conveyor belt system. These spines were elongate and slender, and though apparently strengthened, probably served mainly to propel rather than comminute the food. The bunches of inwardly-facing spines on the more proximal segments of the anteriormost pair of biramous appendages (the first maxilla) may have been used to grip large particles of debris, or to capture smaller particles sucked posteriorly into the median space. Large food particles were broken up by the massive posterior incisor processes of the mandible, apparently unhindered by the labrum which did not extend this far posteriorly. The food was further comminuted by the finer spines of the anterior molar processes before being sucked anteriorly dorsal of the labrum into the mouth.

The paired ventral processes of the pre-telson somite do not appear to have been adapted for swimming. They were not large and flattened like the furcal rami of *Perspicaris recondita* Briggs, 1977 or the Recent *Nebaliopsis* (Rolfe in Moore 1969), and the evidence of a proximal articulation is inconclusive. This supports the supposed benthonic habitat, and ambulatory function of the segmented rami of the appendages. The ventral processes may have assisted in pushing the arthropod out of a soft substrate, aided by the flexible abdomen.

There is no satisfactory basis for a reconstruction of the trunk musculature. Individual traces in the thorax (§ 5*c*) extend through at least two somites and presumably represent ventral longitudinal muscles which functioned in maintaining rigidity. The obvious traces in the abdomen (§ 5*e*) are probably superficial oblique muscles which kept the somites aligned and facilitated flexure (cf. Manton 1973, p. 362).

(*c*) *Classification and affinities*

Walcott (1912) originally referred *Canadaspis perfecta* to *Hymenocaris* Salter, 1853 and while this was disputed by subsequent authors (Gürich 1929; Straelen & Schmitz 1934; Raymond 1935; Størmer 1944, 1949; Dechaseaux 1953), it was not until 1960 that Novozhilov erected the new genus to include it. Jones & Woodward (1892, p. 75) found difficulty in defining the 'original outline of the ends of the carapace' of *Hymenocaris vermicauda*, but a study of the type material confirms that it lacked a hinge (Rolfe in Moore 1969, p. 314), the dorsal margin curving ventrally anteriorly (Jones & Woodward 1892, pl. 13), in contrast to the straight hinge of *C. perfecta*. The telson, which bore three pairs of spinose processes along the distal margin (Rolfe in Moore 1969, p. 315, fig. 135), was also fundamentally different to that of *C. perfecta*, and was cited by Rolfe (in Moore 1969) as a basis for the 'tentative erection' of a new order, the Hymenostraca, to include *Hymenocaris* alone. There is thus no justification for referring the Burgess Shale species to *Hymenocaris* and the genus *Canadaspis* Novozhilov (in Orlov), 1960, is upheld (Rolfe in Moore 1969).

Walcott (1912) considered that *Canadaspis perfecta* was a crustacean and classified it in the order Hymenocarina Clarke (in Zittel), 1900. Raymond (1920*a*) and Henriksen (1928) noted the similarity to the nebaliids and most subsequent authors agreed with a phyllocarid designation. Raymond (1935), however, maintained that the appendages were trilobitan, and erected a new subclass, the Homopoda, to include such Crustacea, emending the order Hymenocarina accordingly. Størmer (1944) assigned all arthropods with trilobitan limbs to a new subphylum Trilobitomorpha, and included Raymond's emended order Hymenocarina in a new class Pseudocrustacea. The appendages of *C. perfecta* resemble those of the trilobites to the extent that both bore a single outer ramus. Analogies may be drawn between the rays of this ramus in *C. perfecta* and the filaments of the trilobite exite, but this is most likely a functional convergence. There is little justification for retaining the 'trilobitan limb' as a diagnostic character outside the trilobites. Størmer (1959) did not retain the bivalved forms in the class Trilobitoidea when he reclassified many of the Burgess Shale arthropods, and Rolfe (in Moore 1969) included *C. perfecta* in Phyllocarida 'order and family uncertain'.

Fedotov (1925) considered that the Burgess Shale species referred by Walcott (1912) to *Hymenocaris* were not Malacostraca, but might belong to the Ostracoda, Phyllopoda, or even Cirripedia. Linder (1945) shared the doubts of previous authors (Størmer 1944, for example) that the Burgess Shale forms were Crustacea, but suggested that, if they were, analogies should be sought in the Branchiopoda. He deemed 'the presence of preoral antennae' in *Canadaspis perfecta* 'very uncertain', a valid observation on the basis of Walcott's (1912) description, but not borne out by the present study (§ 5*a*). Apart from the bivalved carapace, reduced first antenna, and apparent lack of a mandibular palp, *C. perfecta* does not share the characters of the Branchiopoda.

Öpik (1968, p. 9) considered that 'without the body, empty shells (moults) of *Canadaspis* would be placed in the Bradoriida' (= Bradorina Raymond, 1935) in the family Indianidae. He admitted (p. 10), however, that the eyes differed 'being stalked in *Canadaspis* and enclosed in eye tubercles in *Bradoria*' and noted that a posterior gap was rarely present in the bradoriids; hence few if any had an exposed abdomen. Sylvester-Bradley (1961) discussed the arguments for classifying the Bradoriida as Ostracoda rather than Conchostraca (Ulrich & Bassler 1931) or Archaeostraca (Raymond 1935) and erected a new order, Archaeocopida, to include them. Rolfe (in Moore 1969, p. 312) considered that 'carapace shape and the nature of surface ornament' in the Archaeostraca 'might be expected to be the most variable of characters' and pointed out that a classification on this basis might conceal convergences. A comparison of *Canadaspis perfecta* with *Branchiocaris pretiosa* (Briggs 1976) confirms that very different arthropods may occupy similar carapaces. It seems unlikely that the Bradoriida were phyllocarids but without further evidence of their morphology this possibility can not be ruled out.

The morphology of *Canadaspis* is strikingly crustacean, and it shows a marked similarity to the Recent Leptostraca. The main differences lie in the lack of a defined boundary between the cephalon and thorax, and the absence of abdominal appendages.

The cephalon bore a pair of stalked eyes and two pairs of antennae anteriorly. Posterior of the labrum the incisor processes of the mandible are evident. The outline of the appendage bearing them is obscured, and while no evidence of a palp has been observed its presence can not be entirely ruled out. A palp may have been borne by a juvenile stage (although such detail can not be distinguished in the smallest specimens) and subsequently lost in the adult (as in some branchiopods and the Cephalocarida).

The boundaries separating the somites bearing the biramous appendages are ill-defined, particularly immediately posterior of the mandible, but their position is indicated by paired nodular features which may represent points of muscle attachment. There is thus no direct evidence for the posterior margin of the head. The biramous appendages were essentially similar throughout, but the anteriormost pair differed in bearing an inwardly facing bunch of spines on the seven proximal segments. These bunches of spines were apparently absent from the second and successive pairs of biramous appendages. The position of the anterior two pairs of biramous appendages immediately posterior of the mandible, and the differentiation of at least the first pair from those posterior to it, prompts their interpretation as first and second maxillae. An equal similarity between the second maxilla and thoracic appendages is found in the Cephalocarida (Sanders 1963). Furthermore, the designation of the anterior two pairs of biramous appendages as first and second maxillae leaves eight pairs in the thorax – the number of somites characteristic of the Malacostraca.

The biramous appendages of *Canadaspis* differed from those of Recent Crustacea in two main respects, neither of which are considered to be of fundamental significance. Firstly the segmented ramus included up to 14 divisions, but the large number may have compensated for constraints on the flexibility of the appendages imposed by their uniformity and the lack of specialization at the joints (Manton 1973). Secondly the limbs bore only one exite, but a similar condition is displayed, for example, in the abdominal appendages of the Malacostraca, and an epipod may also be absent from the thoracic appendages of the Nebaliidae (*Nebaliella antarctica*).

The abdomen of *Canadaspis* consisted of seven somites and a telson, the arrangement characteristic of the Leptostraca, but lacked appendages, apart from a pair of postero-ventral projections of the pre-telson somite. Manton (in Moore 1969, p. 52) suggested that the differentiation of the malacostracan thorax and abdomen occurred in benthonic forms, as a response to a walking as opposed to swimming mode of locomotion; the abdominal appendages 'might have disappeared had the Malacostraca remained entirely bottom-living'. This may explain their absence in *C. perfecta*, together with the lack of a caudal furca, which also functions primarily in swimming.

The number of somites in the tagmata of *Canadaspis* as interpreted above, and the bivalved nature of the carapace, indicate a strong affinity with the Phyllocarida Packard, 1879 (Rolfe in Moore 1969). The similarity of the appendages interpreted as first and second maxillae to those posterior of them may represent a condition prior to the complete differentiation of the posterior cephalic somites from the thorax. The lack of a rostral plate, and the adaptation of the abdomen to a presumed benthonic mode of life, are not considered sufficient justification for the erection of a new subclass, and the diagnosis of the Phyllocarida is emended accordingly.

The order Canadaspidida (= Prophyllocarida Simonetta & Delle Cave, 1975), and family Canadaspididae Novozhilov (in Orlov), 1960 are upheld, but redefined. *Persipicaris* Briggs, 1977, which also lacks pleopods and a rostral plate, is made the type of a new family Perspicarididae, of the order Canadaspidida, as unlike *Canadaspis*, it bears a true caudal furca.

The classification of the phyllocarids (Rolfe in Moore 1969) is thus modified as follows:

Class **MALACOSTRACA** Latreille, 1806
  Sublass *PHYLLOCARIDA* Packard, 1879
    Order LEPTOSTRACA Claus, 1880
    Order CANADASPIDIDA Novozhilov (in Orlov), 1960
    Order HYMENOSTRACA Rolfe (in Moore), 1969
    Order HOPLOSTRACA Schram, 1973
    Order ARCHAEOSTRACA Claus, 1888

It must be emphasized, however, that only the Canadaspidida of the four fossil orders can be diagnosed in terms comparable with the Recent Leptostraca. The less completely known Hymenostraca, Hoplostraca and Archaeostraca, which are based on telson and carapace morphology and the configuration of the somites, must be considered tentative.

An alternative classification would elevate the orders Leptostraca and Canadaspidida to subclass status, leaving the remaining poorly known fossil orders within the subclass Phyllocarida. This would imply, however, differences between these three divisions of equal rank to those separating them from the Eumalacostraca. The classification above, on the other hand, emphasizes the similarity between the Leptostraca and the fossil forms, as far as they are known, in the presence of a bivalved carapace and seven abdominal somites. Future discoveries and research on the Archaeostraca may provide further evidence of their position, but the classification adopted herein is considered the most satisfactory on the present evidence.

I am particularly grateful to Professor H. B. Whittington, F.R.S., for advice, assistance and encouragement throughout this study. Dr W. D. I. Rolfe, Dr S. M. Manton, F.R.S., Dr C. P. Hughes and Dr A. T. Thomas provided valuable discussion. I am indebted to Dr R. E. Grant and F. J. Collier of the National Museum of Natural History (formerly U.S. National Museum) for providing every facility for study of the Walcott collection, and to the following for allowing access to material in their care: Professor B. Kummel and Miss V. Kohler, Museum of Comparative Zoology, Harvard; Dr T. E. Bolton and Dr W. H. Fritz, Geological Survey of Canada, Ottawa; Professor K. Waagé and Mrs J. S. Lawless, Peabody Museum, Yale. Dr J. E. Dalingwater examined some material of *Canadaspis perfecta* under the scanning electron microscope. D. F. Bursill assisted with some aspects of the photography. The work was financed by a Research Fellowship held at Sidney Sussex College, Cambridge, and N.E.R.C. grant GR3/285 awarded to Professor H. B. Whittington.

REFERENCES

Andrews, H. E., Brower, J. C., Gould, S. J. & Reyment, R. A. 1974 Growth and variation in *Eurypterus remipes* De Kay. *Bull. geol. Instn Univ. Upsala* (n.s.) **4**, 81–114.

Briggs, D. E. G. 1976 The arthropod *Branchiocaris* n. gen., Middle Cambrian, Burgess Shale, British Columbia. *Bull. geol. Surv. Can.* **264**, 1–29.

Briggs, D. E. G. 1977 Bivalved arthropods from the Middle Cambrian Burgess Shale of British Columbia. *Palaeontology* **20**. (In the press.)

Broili, F. 1928 Beobachtungen an *Nahecaris*. *Sber. bayer. Akad. Wiss.* **1**, 1–18.

Cannon, H. G. 1927 On the feeding mechanism of *Nebalia bipes*. *Trans. R. Soc. Edinb.* **55**, 355–370.

Chapman, F. 1923 Report on fossils from an Upper Cambrian horizon at Loyola, near Mansfield. In A. M. Howitt: Phosphate deposits in the Mansfield district. *Bull. geol. Surv. Vict.* **46**, 34–45.

Claus, C. 1880 *Lehrbuch der zoologie.* Marburg and Leipzig: N. G. Elwert'sche Verlag.

Claus, C. 1888 Über den Organismus der Nebaliden und die systematische Stellung der Leptostraken. *Arb. zool. Inst. Univ. Wien* **8**, 1–148.

Dechaseaux, C. 1953 Classes des Mérostomoides, des Pseudocrustacés et des Marrellomorphes. In *Traité de Paléontologie* (ed. J. Piveteau) **3**, 27–43. Paris: Masson.

Fedotov, D. 1925 On the relations between the Crustacea, Trilobita, Merostomata and Arachnida. *Izv. ross. Akad. Nauk* 1924, 383–408.

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

Gürich, G. 1929 *Silesicaris* von Leipe und die Phyllokariden überhaupt. *Mitt. Miner.-geol. StInst. Hamb.* **11**, 21–90.

Henriksen, K. L. 1928 Critical notes upon some Cambrian arthropods described by Charles D. Walcott. *Vidensk. Meddr dan. naturh. Foren.* **86**, 1–20.

Hughes, C. P. 1975 Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. *Fossils and Strata* **4**, 415–435.

Imbrie, J. 1956 Biometrical methods in the study of invertebrate fossils. *Bull. Am. Mus. nat. Hist.* **108**, 211–252.

Jones, T. R. & Woodward, H. 1892 A monograph of the British Palaeozoic Phyllopoda (Phyllocarida, Packard). Part II. *Palaeontogr. Soc.* [*Monogr.*], 73–124.

Jux, U. 1960 *Montecaris lehmanni*, a new crustacean from the Rhenish Devonian and the problem of its systematic position. *J. Paleont.* **34**, 1129–1152.

Latreille, P. A. 1806 Histoire naturelle, générale et particulière, des Crustacés et des Insectes. In *Histoire naturelle* (L. de Buffon) vol. 80, pp. 1–408. Paris: Dufart.

Linder, F. 1945 Affinities within the Branchiopoda, with notes on some dubious fossils. *Ark. Zool.* **37**A (4), 1–28.

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

Moore, R. C. 1969 (ed.) *Treatise on invertebrate paleontology*, Part R, Arthropoda 4 (1), 1–398. Lawrence, Kansas: Geol. Soc. Am. & Univ. Kansas.

Öpik, A. A. 1968 Ordian (Cambrian) Crustacea Bradoriida of Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* **103**, 1–44.

Orlov, Yu. A. 1960 (ed.) *Osnovy Paleontologii*, Arthropoda, Trilobitomorpha and Crustacea. Moscow: Nedra.

Packard, A. S. 1879 The Nebaliad Crustacea as types of a new order. *Am. Nat.* **13**, 128.

Rasetti, F. 1951 Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithson. misc. Collns* **116** (5), 1–277.

Raymond, P. E. 1920*a* The appendages, anatomy and relationships of Trilobites. *Mem. Conn. Acad. Arts Sci.* **7**, 1–169.

Raymond, P. E. 1920*b* Phylogeny of the Arthropoda with especial reference to the trilobites. *Am. Nat.* **54**, 398–413.

Raymond, P. E. 1935 *Leanchoilia* and other Mid-Cambrian Arthropoda. *Bull. Mus. comp. Zool. Harv.* **76**, 205–230.

Robison, R. A. 1971 Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. *J. Paleont.* **45**, 796–804.

Rolfe, W. D. I. 1962 Two new arthropod carapaces from the Burgess Shale (Middle Cambrian) of Canada. *Breviora* **160**, 1–9.

Rolfe, W. D. I. 1963*a* Catalogue of type specimens in the invertebrate paleontological collections of the Museum of Comparative Zoology – Arthropoda (Trilobita, Arachnida and Insecta excluded). *Bull. Mus. comp. Zool. Harv.* **129**, 369–398.

Rolfe, W. D. I. 1963*b* Discussion following Dahl's paper. In H. B. Whittington & W. D. I. Rolfe (eds.): Phylogeny and evolution of Crustacea. *Spec. Publ. Mus. comp. Zool. Harv.* 19.

Salter, J. W. 1853 On the lowest fossiliferous beds of North Wales. *Rep. Br. Ass. Advmt Sci.* (1852), Trans. of the sections, 56–58.

Sanders, H. L. 1963 The Cephalocarida – functional morphology, larval development, comparative external anatomy. *Mem. Conn. Acad. Arts Sci.* **15**, 1–80.

Schäfer, W. 1972 *Ecology and palaeoecology of marine environments* (English edition, ed G. Y. Craig). Edinburgh: Oliver and Boyd.

Schram, F. R. 1973 On some phyllocarids and the origin of the Hoplocarida. *Fieldiana, Geol.* **26** (2), 77–94.

Sherrard, K. 1930 Notes on a phyllocarid and a brachiopod found in the Lancefield zone of the Lower Ordovician rocks of Victoria. *Proc. R. Soc. Vict.* (n.s.) **42** (2), 135–139.

Shimer, H. W. & Shrock, R. R. 1944 *Index fossils of North America.* New York & London: Wiley & Chapman and Hall.

Simonetta, A. M. 1976 Remarks on the origin of the Arthropoda. *Memie Soc. tosc. Sci. nat.* B **82**, 112–134.

Simonetta, A. M. & Delle Cave, L. 1975 The Cambrian non trilobite arthropods from the Burgess Shale of British Columbia. A study of their comparative morphology, taxonomy and evolutionary significance. *Palaeontogr. ital.* **69** (n.s. 39), 1–37.

Størmer, L. 1939 Studies on trilobite morphology – Part 1. The thoracic appendages and their phylogenetic significance. *Norsk. geol. Tidsskr.* **19**, 143–273.

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

Størmer, L. 1949 Classes des Merostomoidea, Marrellomorpha, et Pseudocrustacea. In *Traité de Zoologie* (ed. P. P. Grassé), vol. 6, pp. 198–210. Paris: Masson.

Størmer, L. 1959 Trilobitoidea. In *Treatise on invertebrate paleontology* (ed. R. C. Moore), Part O, Arthropoda 1, pp. 23–37. Lawrence, Kansas: Geol. Soc. Am. & Univ. Kansas.

Straelen, V. van & Schmitz, G. 1934 Crustacea Phyllocarida (= Archaeostraca). In *Fossilium Catalogus* 1, Animalia (ed. W. Quenstedt), vol. 64, pp. 1–246. Berlin: Junk.

Sylvester-Bradley, P. C. 1961 Order Archaeocopida Sylvester-Bradley, n. order. In *Treatise on invertebrate paleontology* (ed. R. C. Moore), Part Q, Arthropoda 3, pp. 100–103. Lawrence, Kansas: Geol. Soc. Am. & Univ. Kansas.

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

Ulrich, E. O. & Bassler, R. S. 1931 Cambrian bivalved Crustacea of the order Conchostraca. *Proc. U.S. natn. Mus.* **78** (4), 1–130.

Walcott, C. D. 1908*a* Mount Stephen rocks and fossils. *Can. alp. J.* **1**, 232–248.

Walcott, C. D. 1908*b* Cambrian sections of the Cordilleran area. In Cambrian geology and paleontology 1. *Smithson. misc. Collns* **53** (5), 167–230.

Walcott, C. D. 1912 Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. In Cambrian geology and paleontology, 2. *Smithson. misc. Collns* **57** (6), 145–228.

Walcott, C. D. 1919 Middle Cambrian algae. In Cambrian geology and paleontology, 4. *Smithson. misc. Collns* **67** (5), 217–261.

Westergard, A. H. 1936 *Paradoxides oelandicus* beds of Öland. *Sver. geol. Unders. Afh.* C (394) **30** (1), 1–66.

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

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

Whittington, H. B. 1974 *Yohoia* Walcott and *Plenocaris* n. gen., arthropods from the Burgess Shale, Middle Cambrian, British Columbia. *Bull. geol. Surv. Can.* **231**, 1–27.

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

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

Zittel, K. A. von 1900 (English edition, ed. C. R. Eastman). *Text-book of palaeontology*. London and New York: Macmillan.

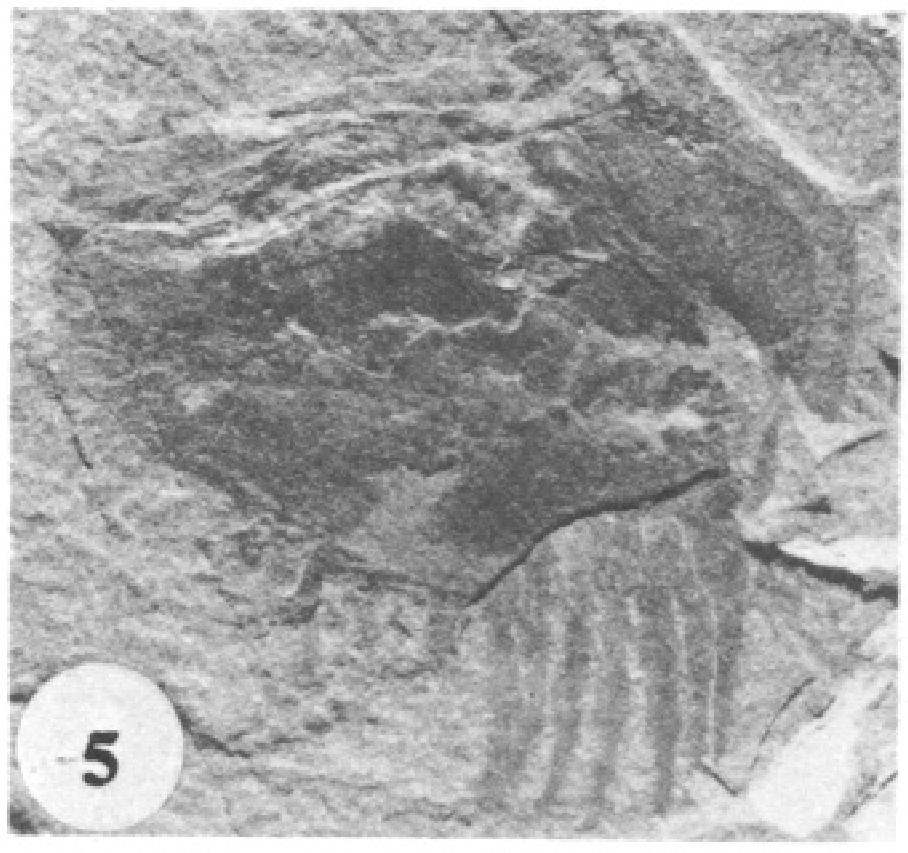
The plates in this issue have been printed at the University Press, Oxford.

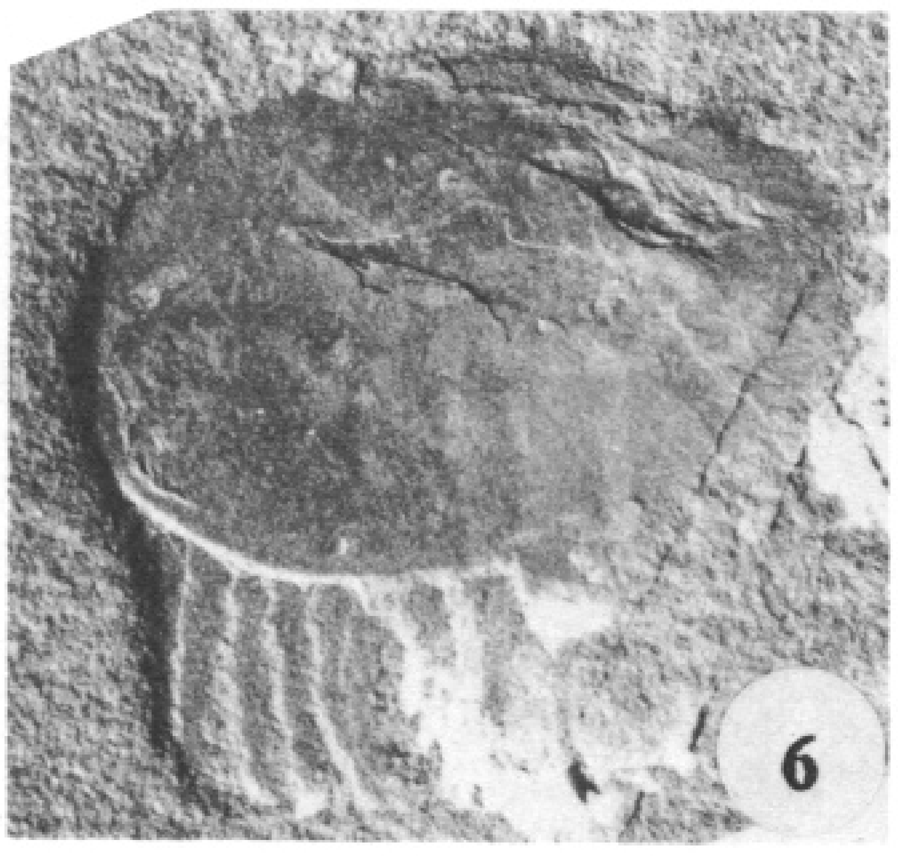
LIST OF ABBREVIATIONS USED ON FIGURES

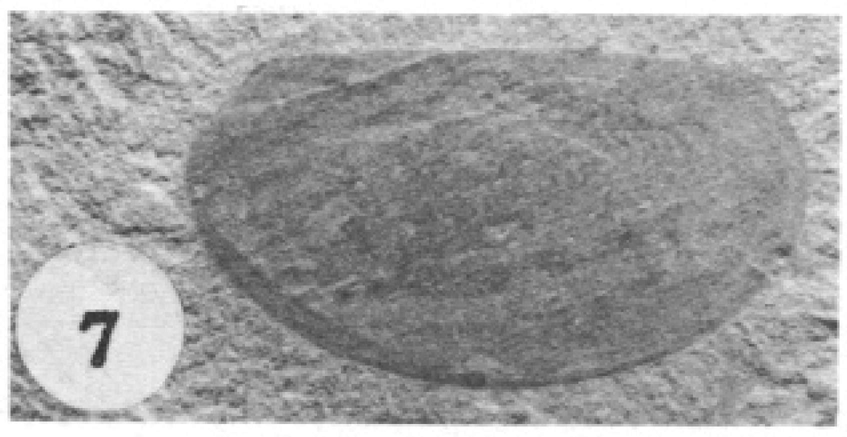
a	anus
ab1, ab2, etc.	abdominal somites
al	alimentary canal
an1	first antenna
an2	second antenna
ap	appendage
b	border of carapace
bu	bunch of spines borne proximally by segmented ramus of biramous appendage
cl	distal claws of segmented ramus of biramous appendage
cn	nodular features in posterior part of cephalic region
cs	cephalic spine
e	eye
f	ray of outer ramus of biramous appendage
g1, g2, etc.	outer ramus of thoracic appendage
gu	gut contents
h	hinge of carapace
i	inner lobe of outer ramus of biramous appendage
is	inter-somite boundary
j1, j2, etc.	segment of inner ramus of biramous appendage, assuming a total of 14
k	paired nodular features flanking labrum
l	prefix indicating left side
m	mouth
ma	mandible
ms	muscle scar on carapace
mt	trace of trunk muscle
mx1	first maxilla
mx2	second maxilla
n	nodular feature associated with inter-somite boundary
o	labrum
om	anterior margin of labrum
or	lateral ridge of labrum
pr	ventral projections of pre-telson somite
r	prefix indicating right side
se1, se2, etc.	segmented ramus of thoracic appendage
st	stomach
te	telson
t1, t2, etc.	thoracic somites
tr	transverse median line
v	valve of carapace
x	*see* plate description

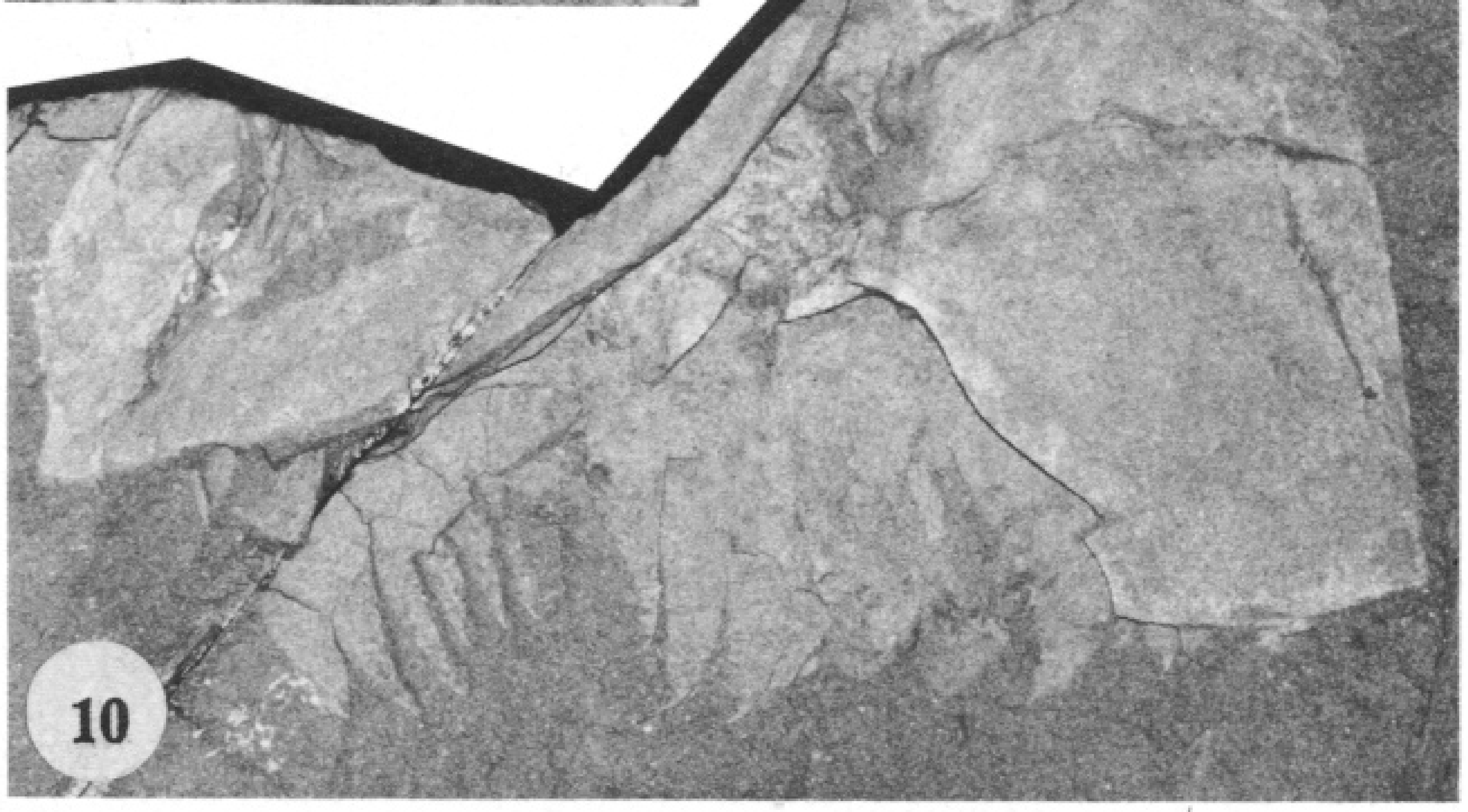
Breaks of slope are represented by hachures, the solid line at the upper edge of the break, the hachures directed downslope.

Stippled areas represent 'outcrops' of matrix within the outline of a specimen, unless otherwise indicated.

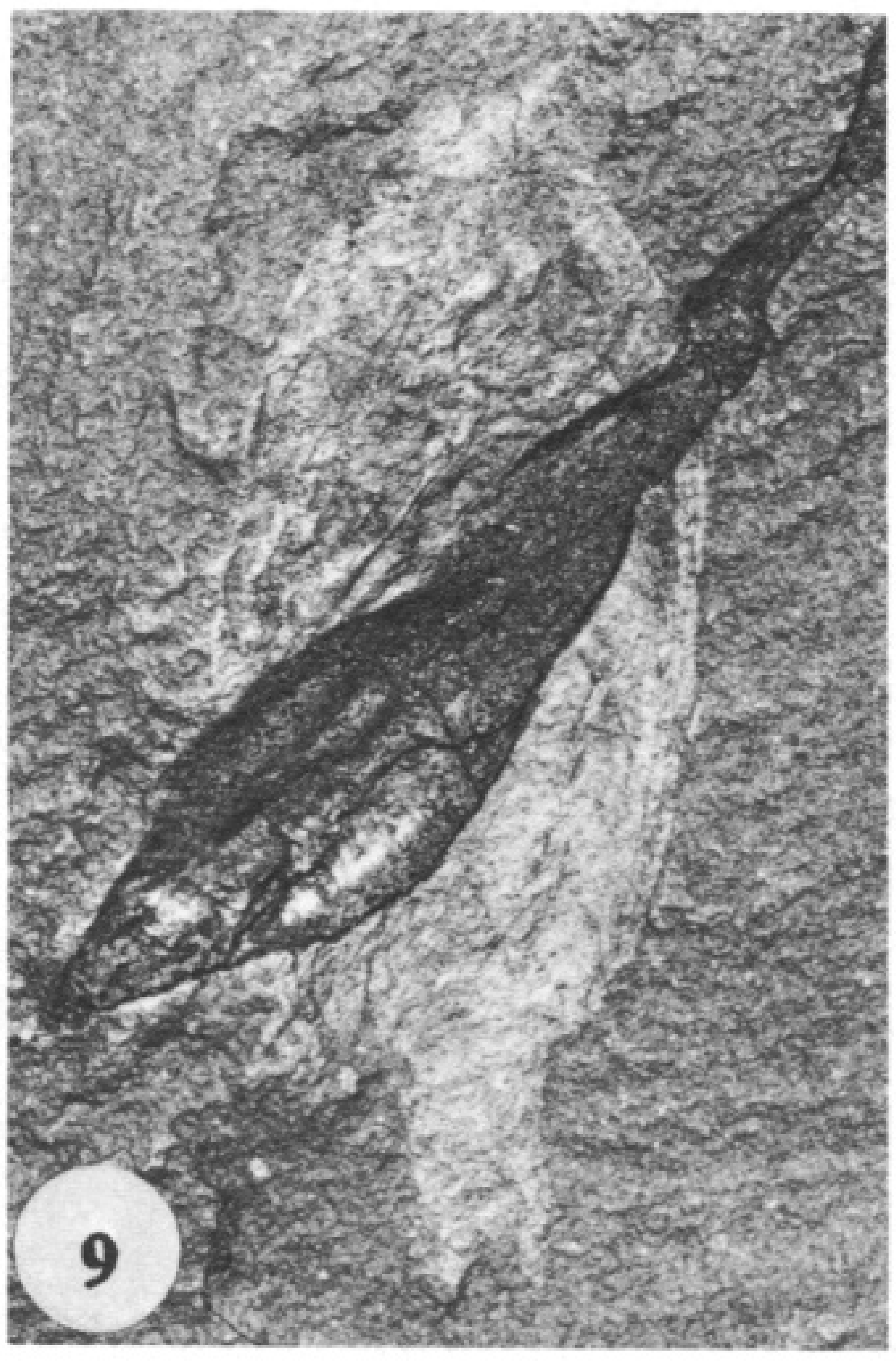

5

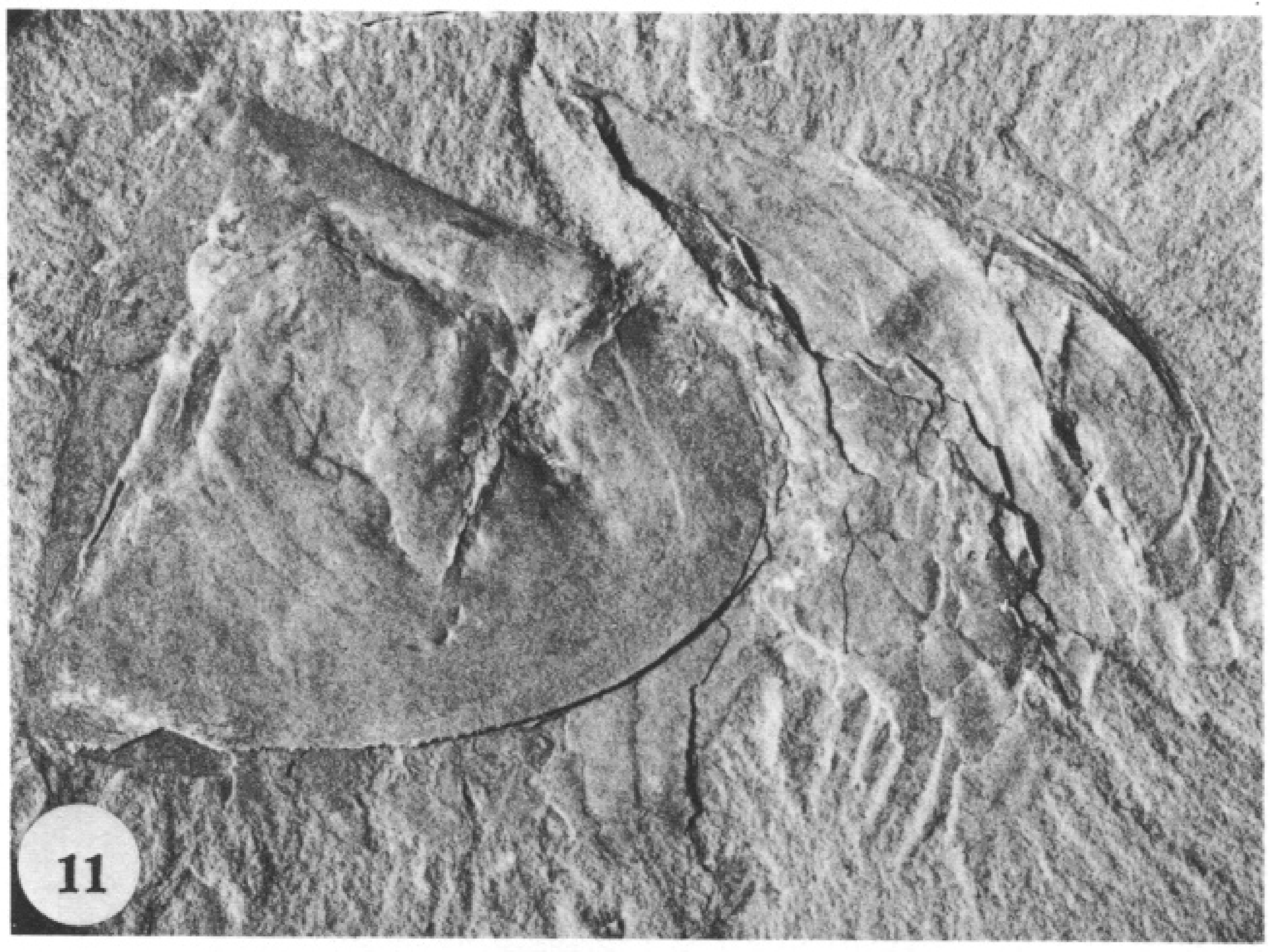

6

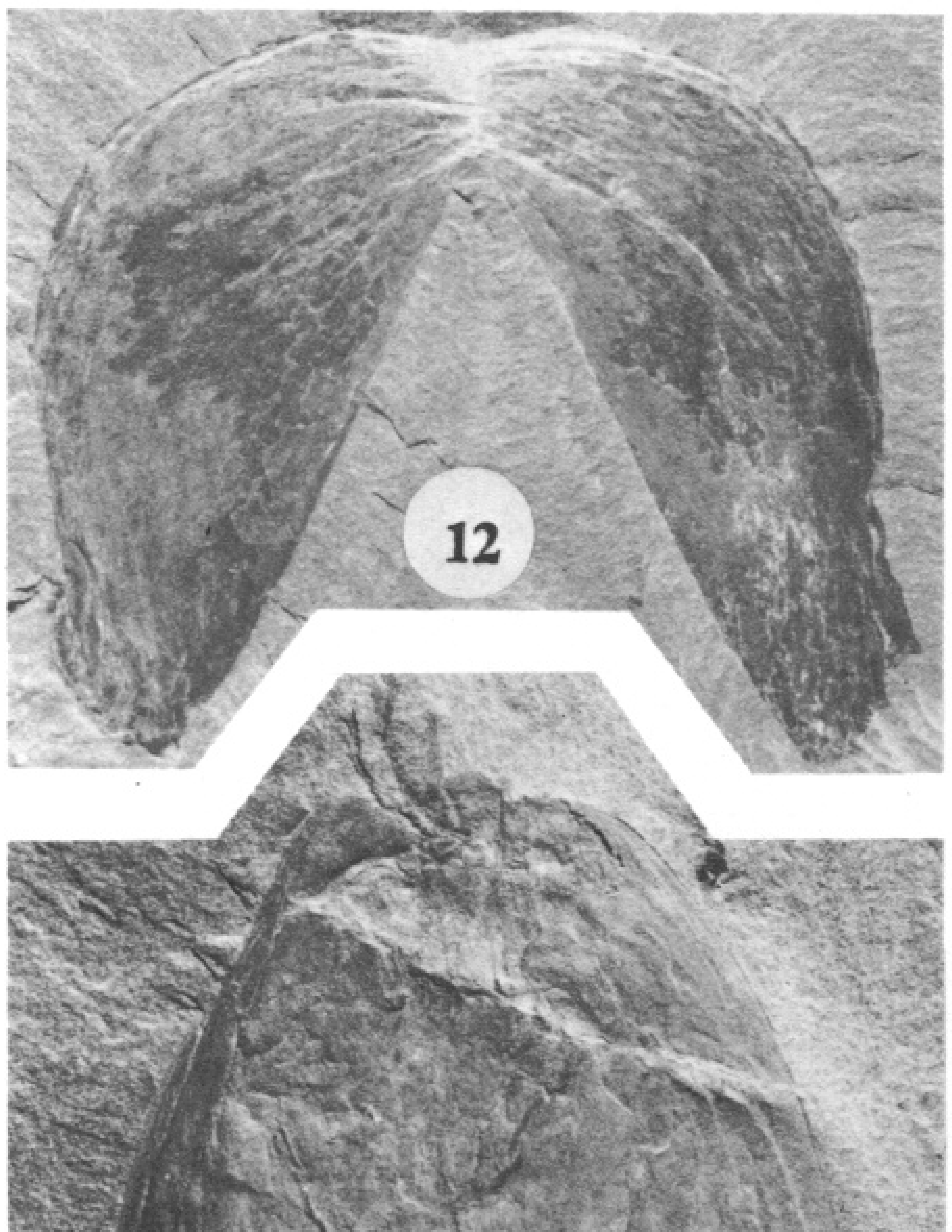

7

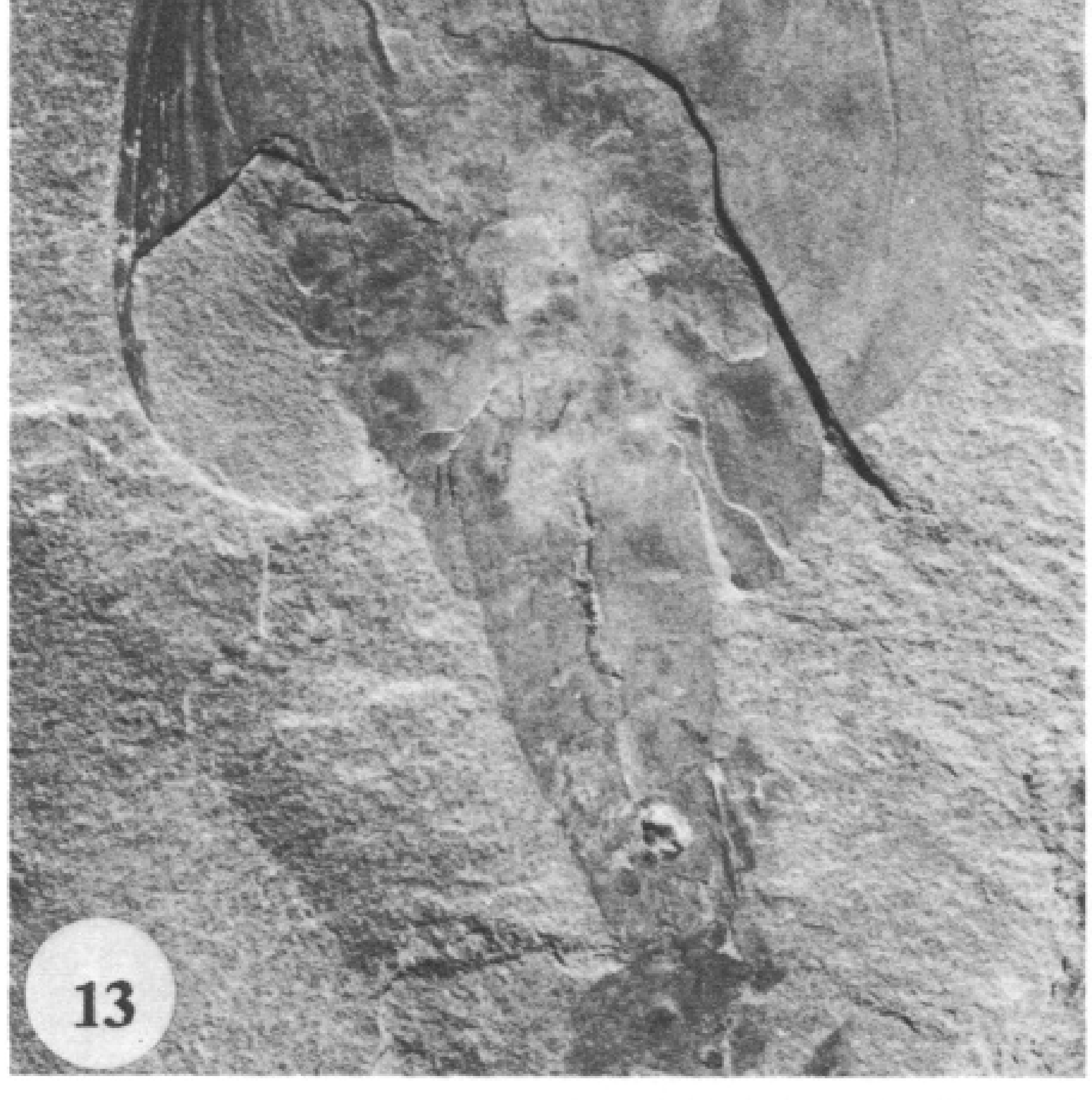

10

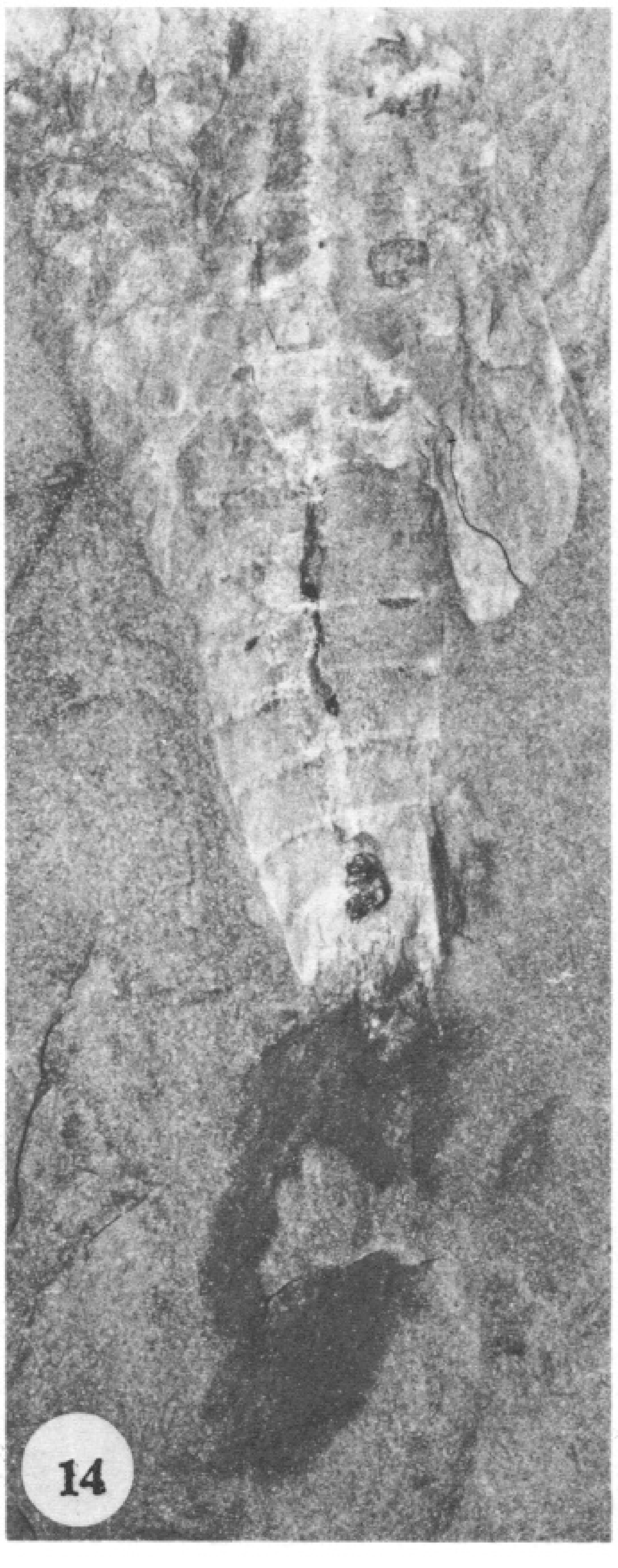

8


9

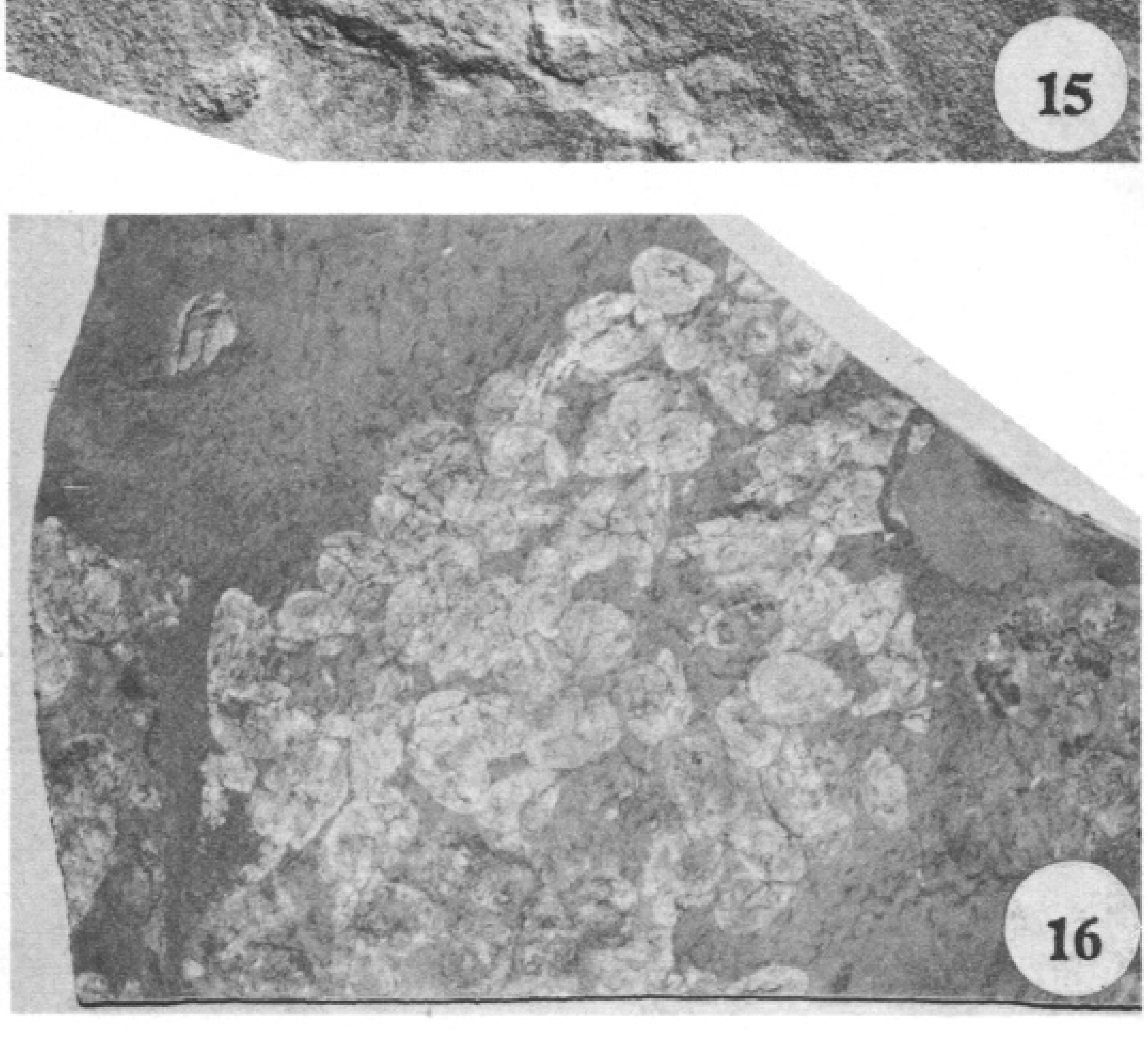

11

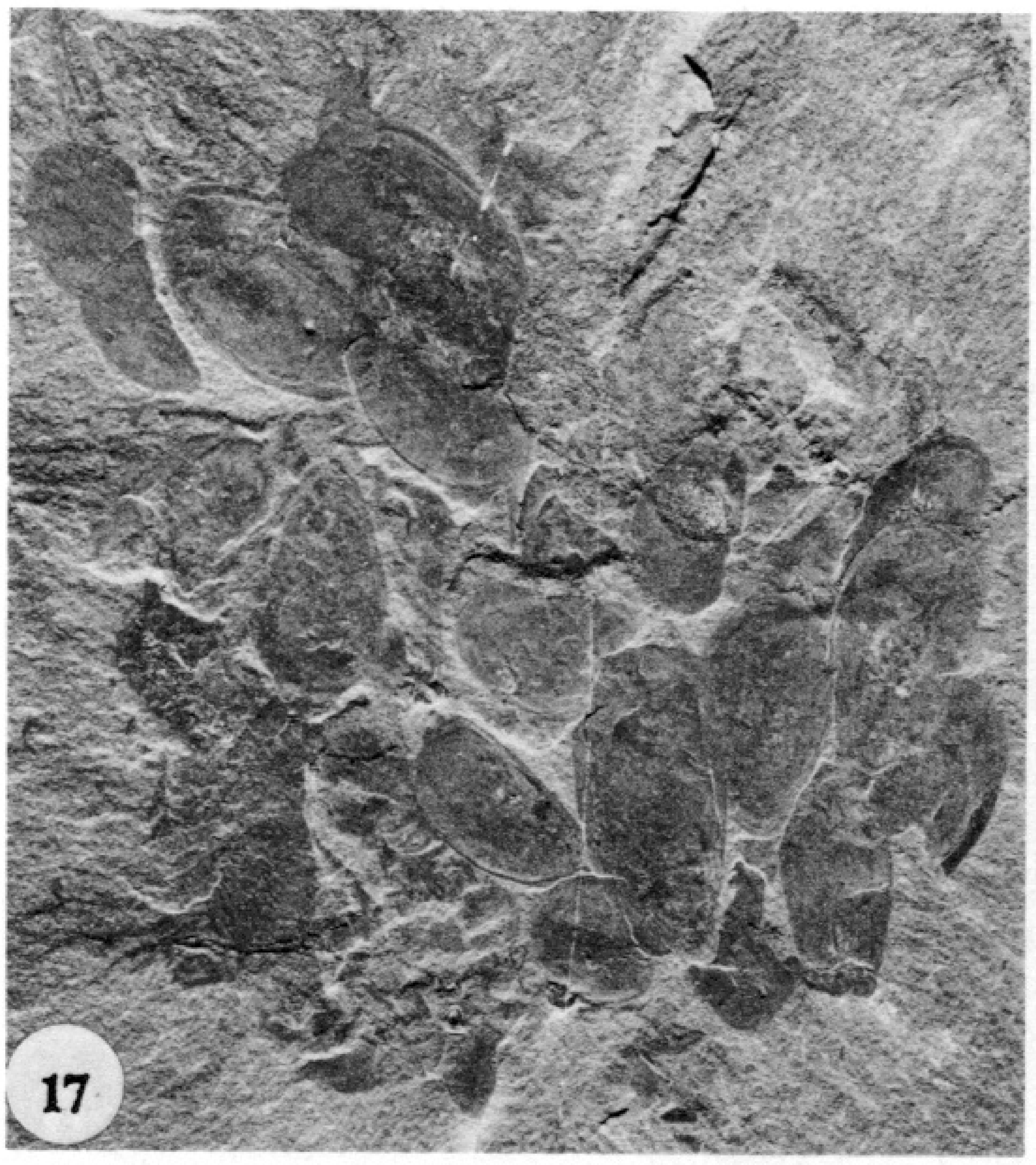

12


13


14

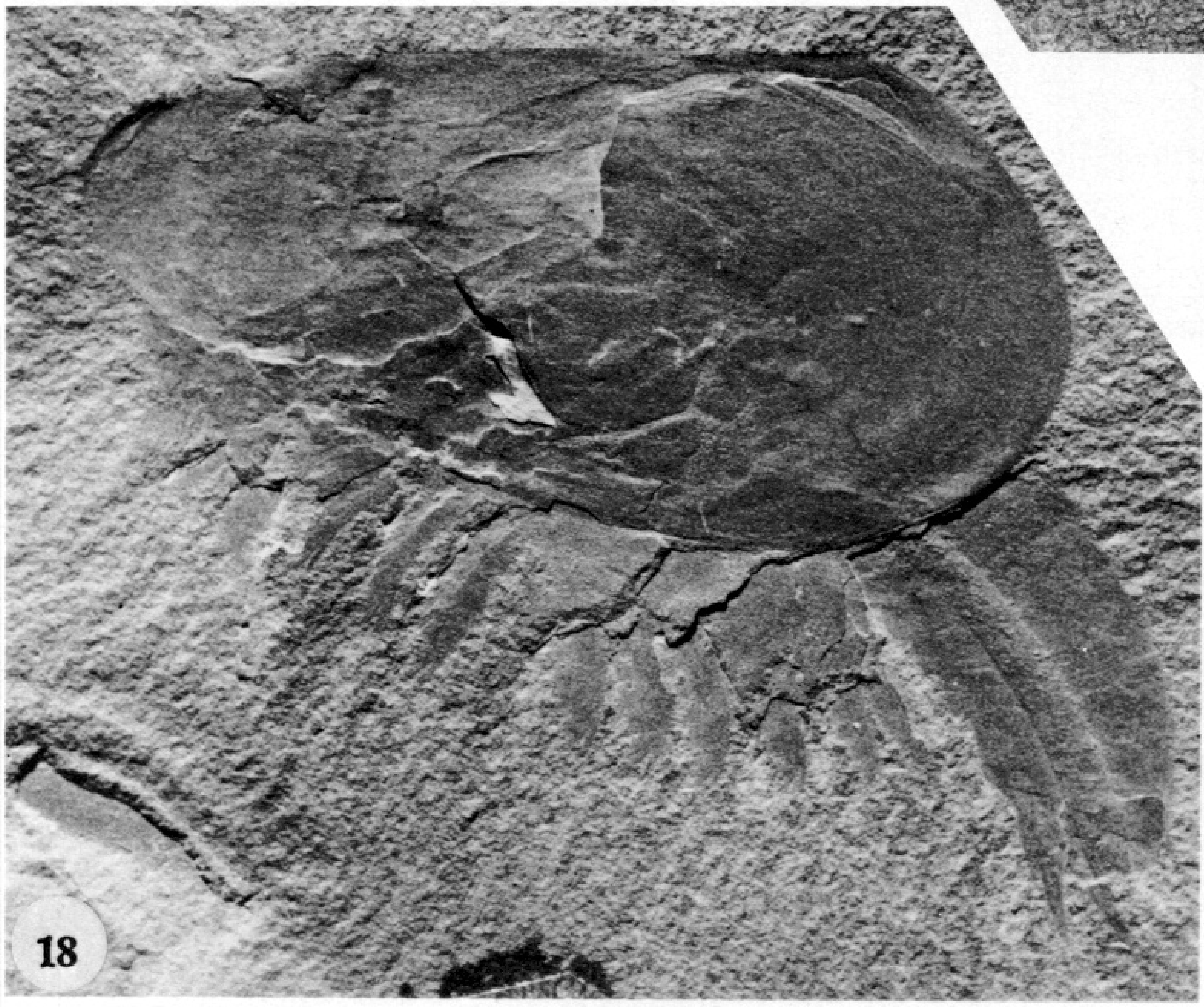

15


16


17

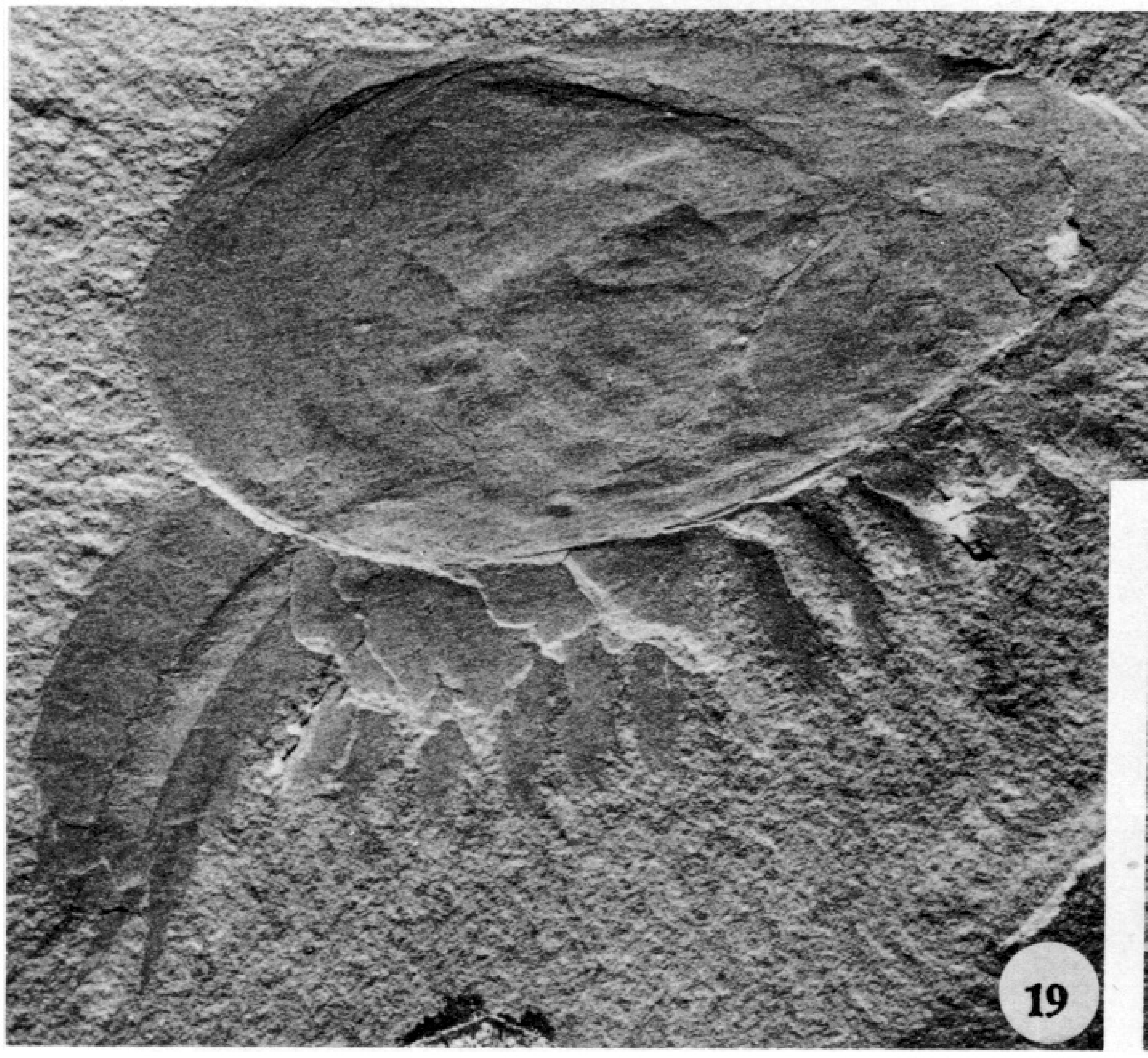

20


21


18

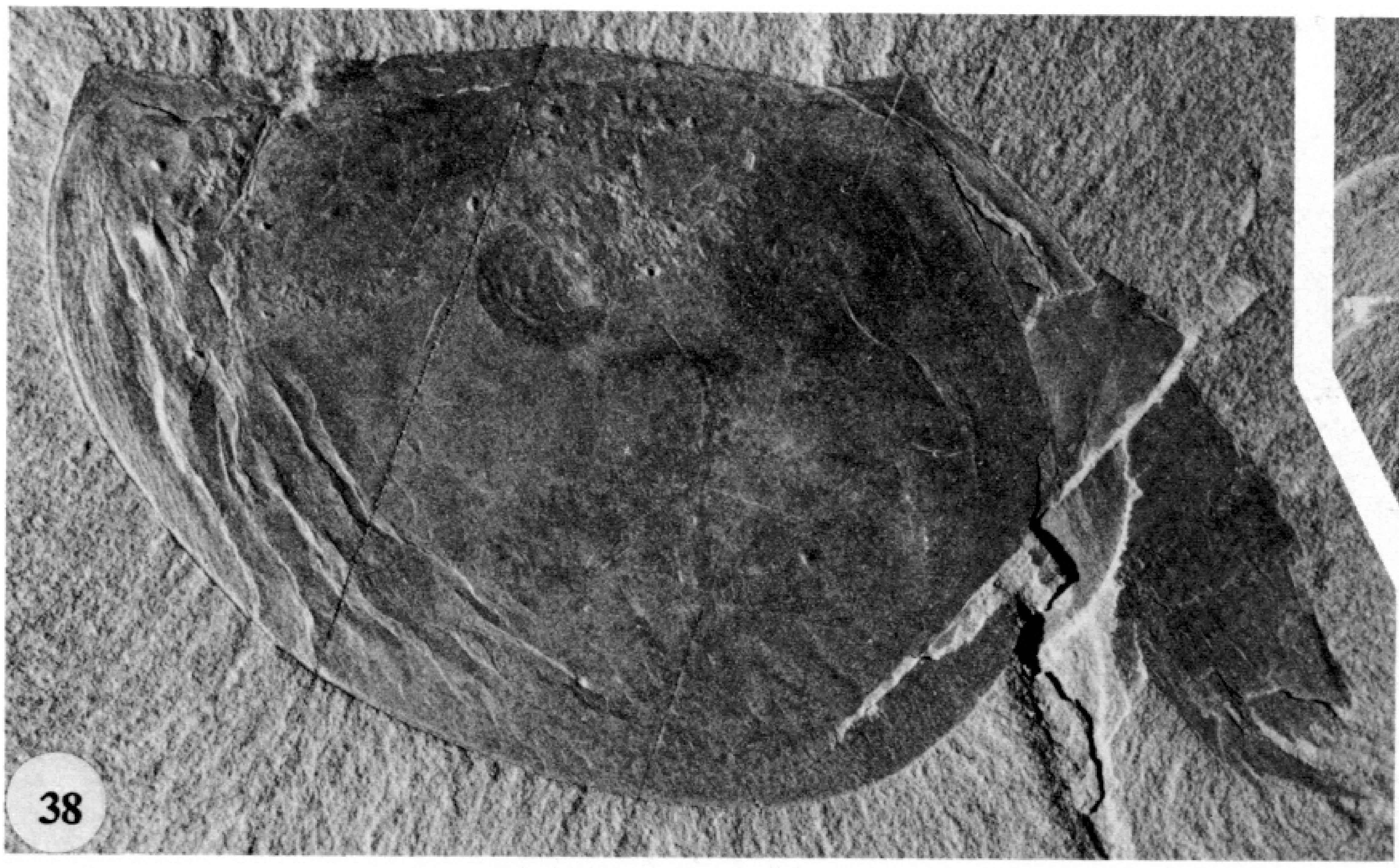

22

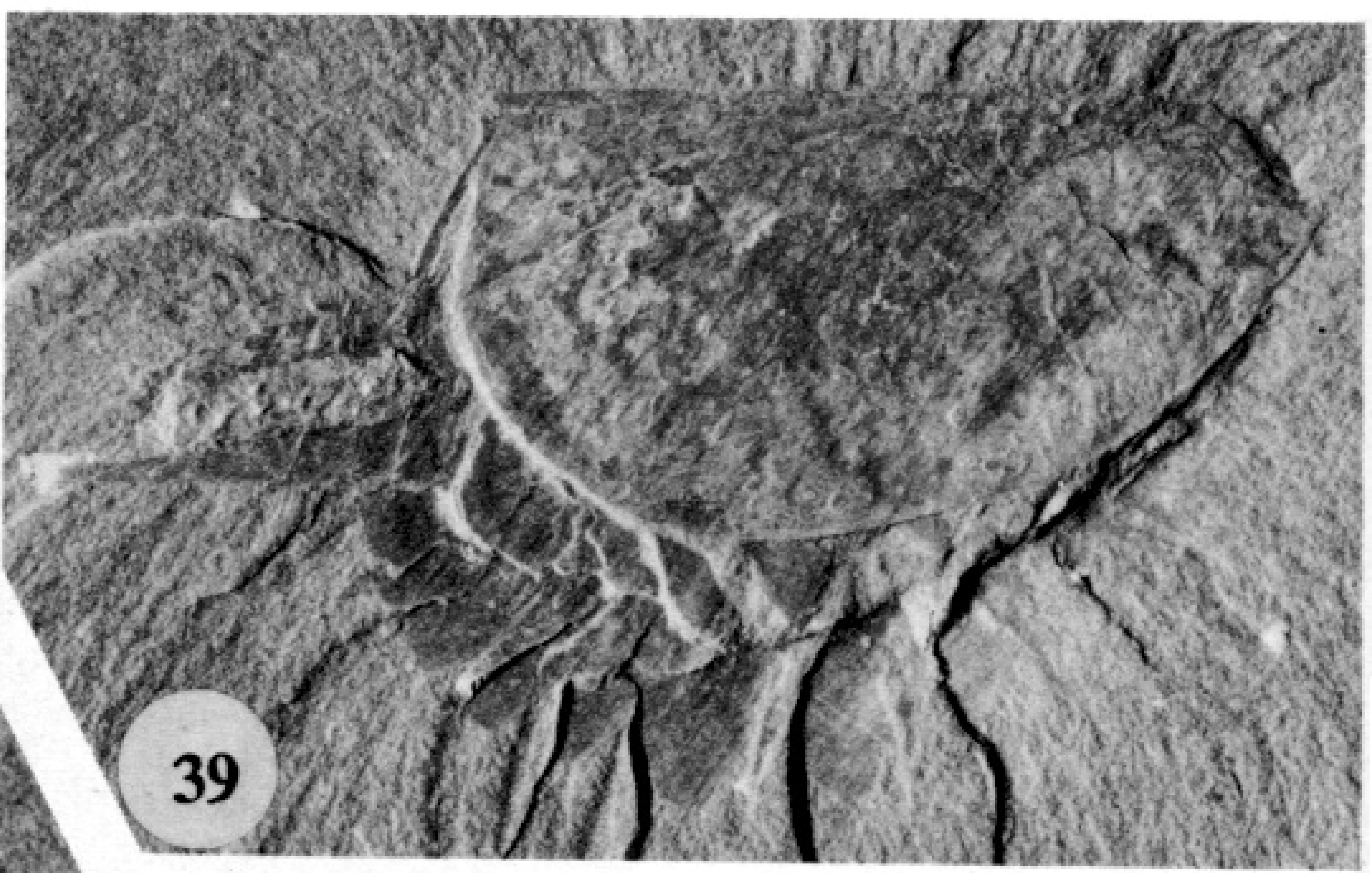

23

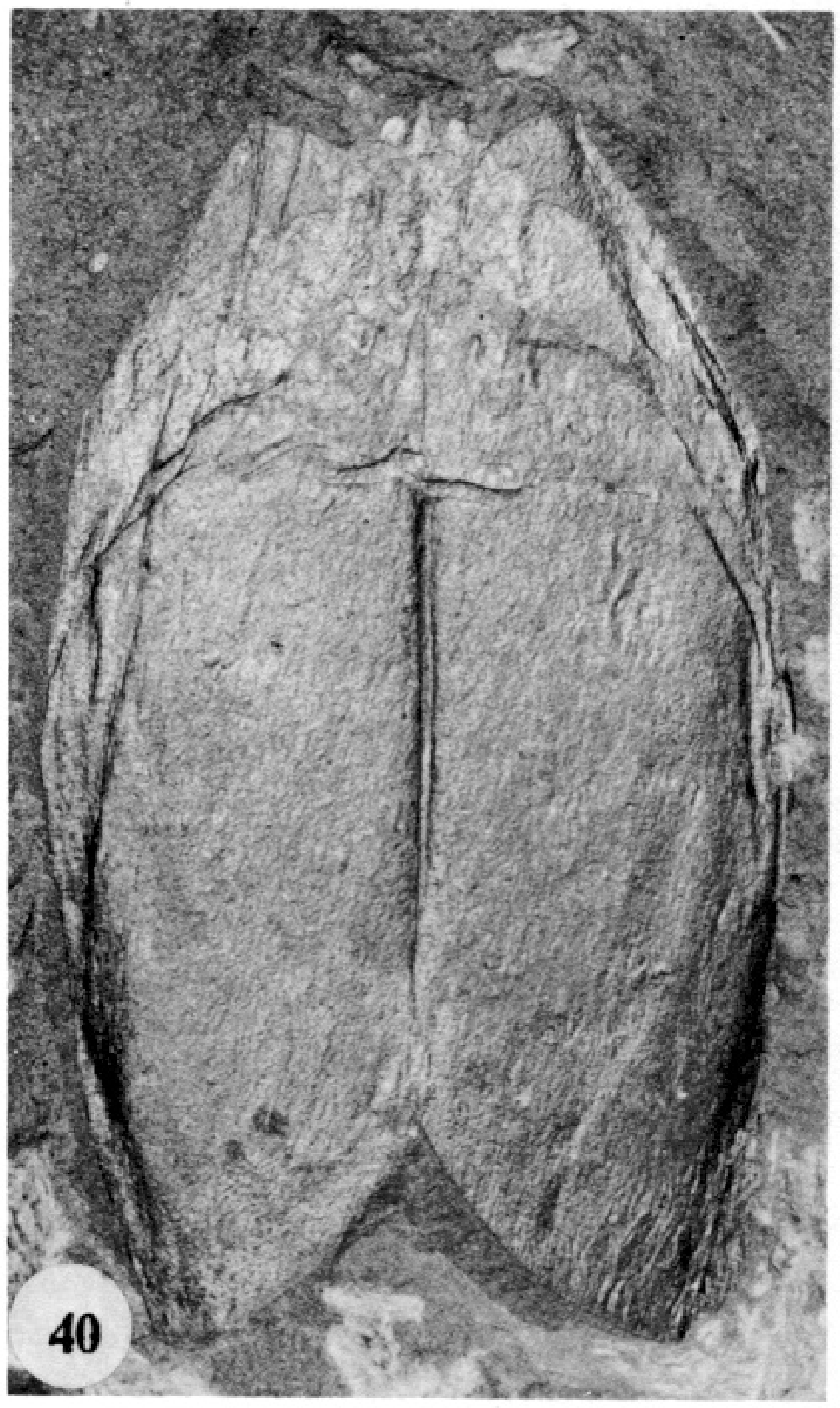

19

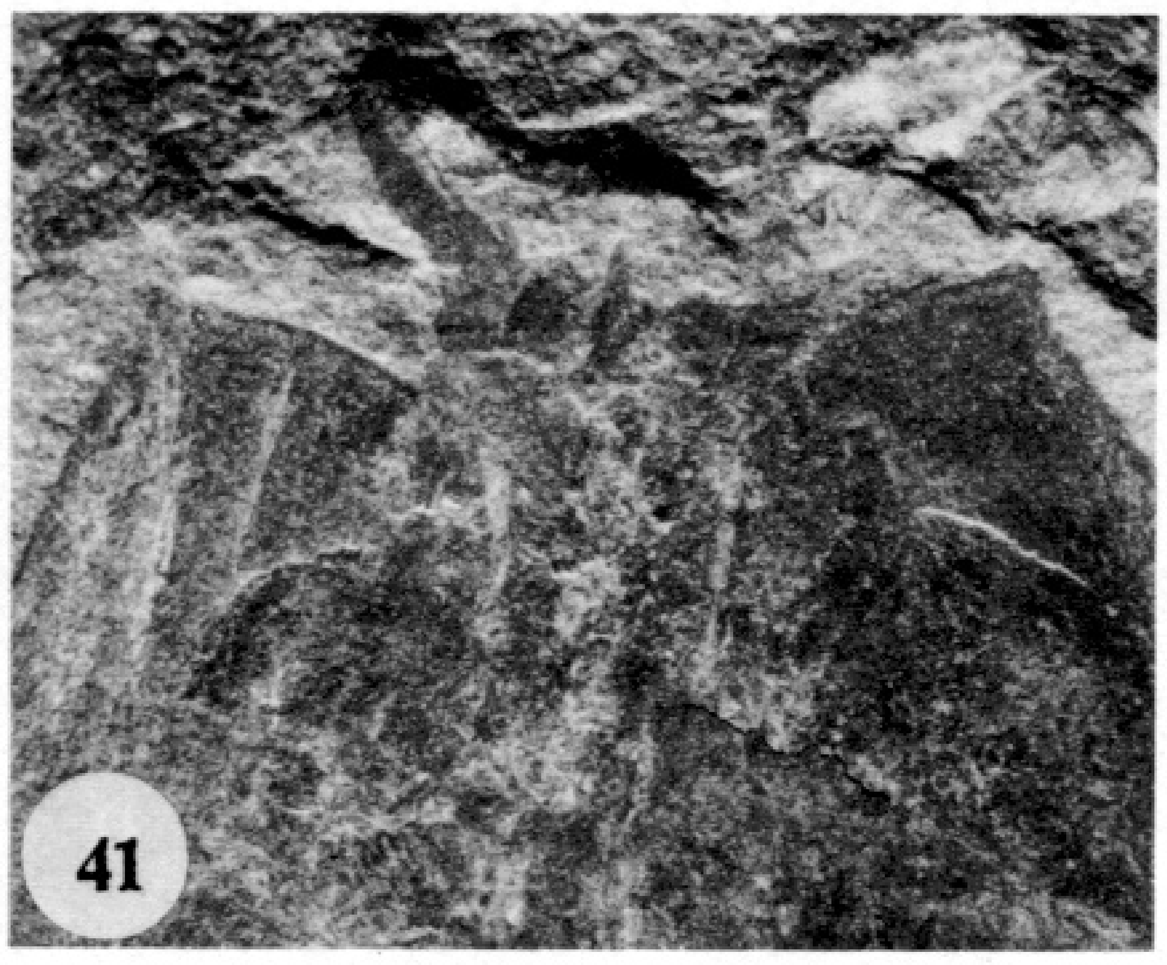

24

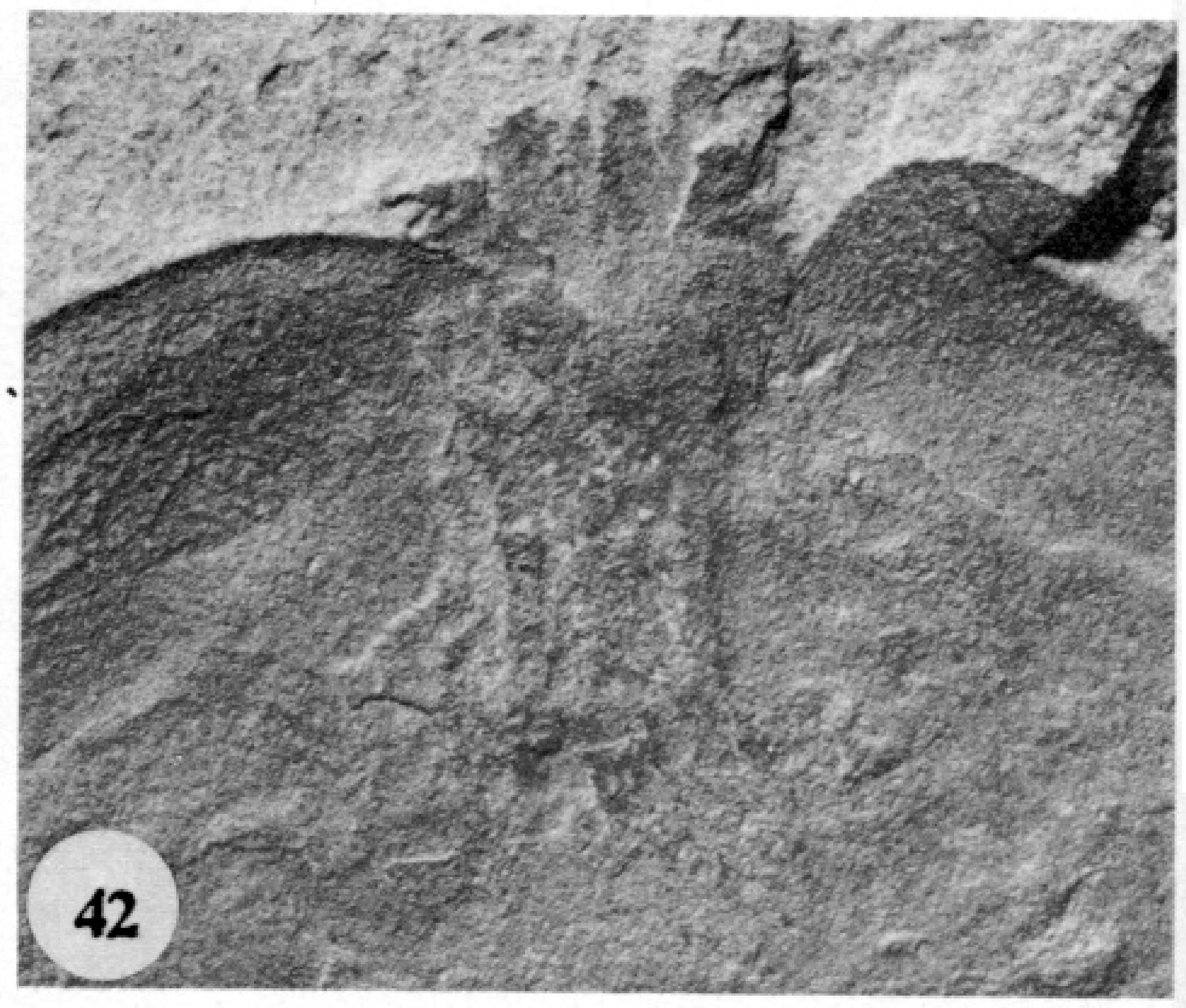

25


38


39


40


41


42

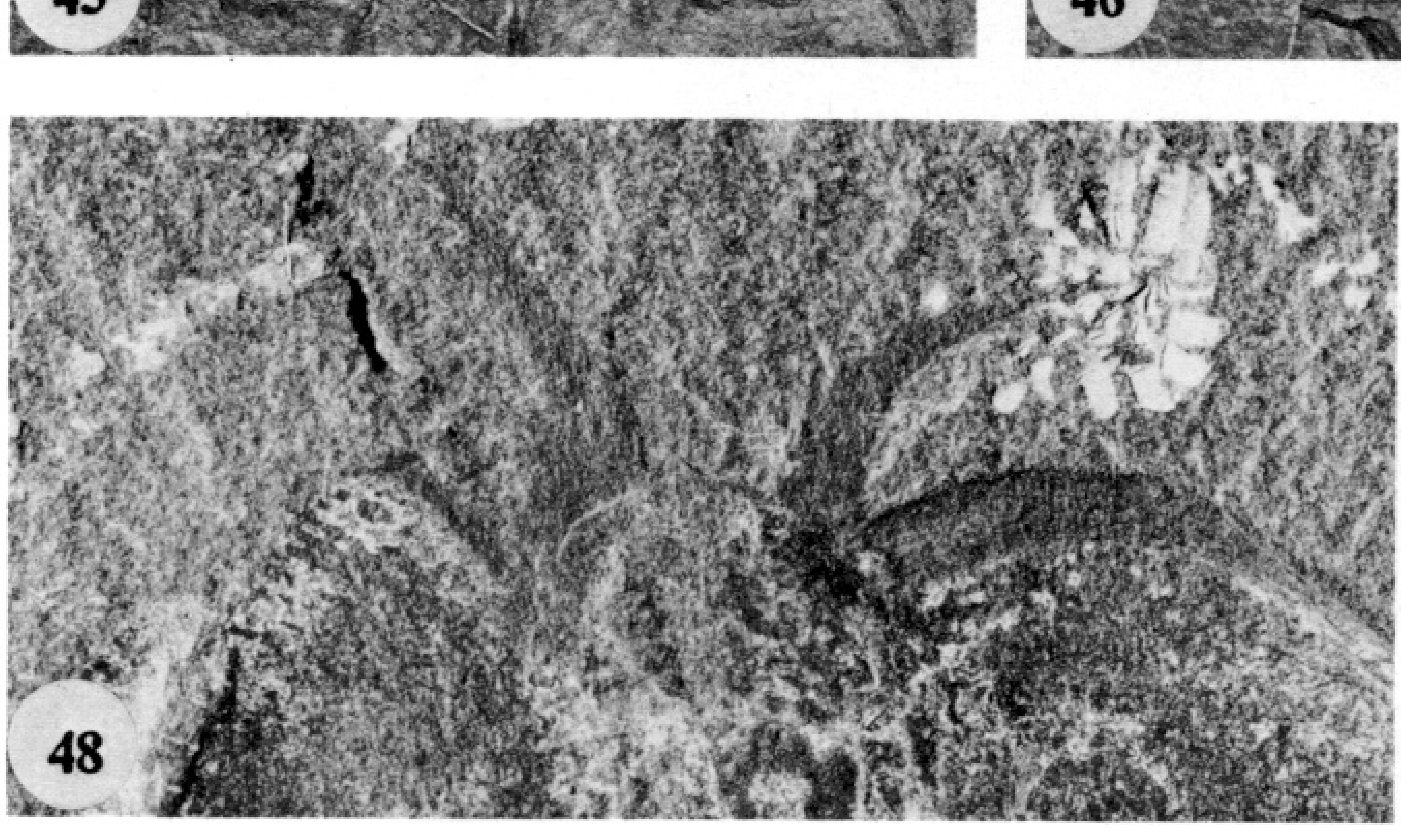

43


44

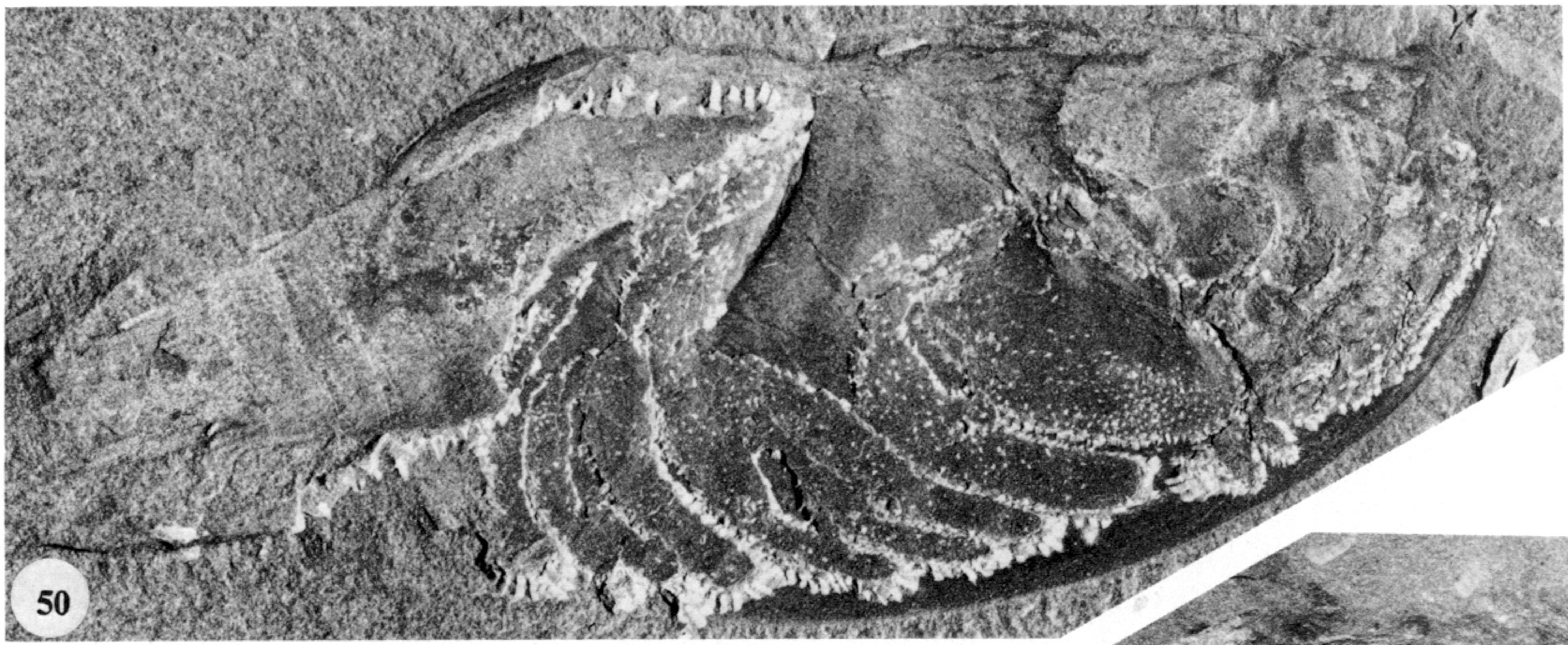

45

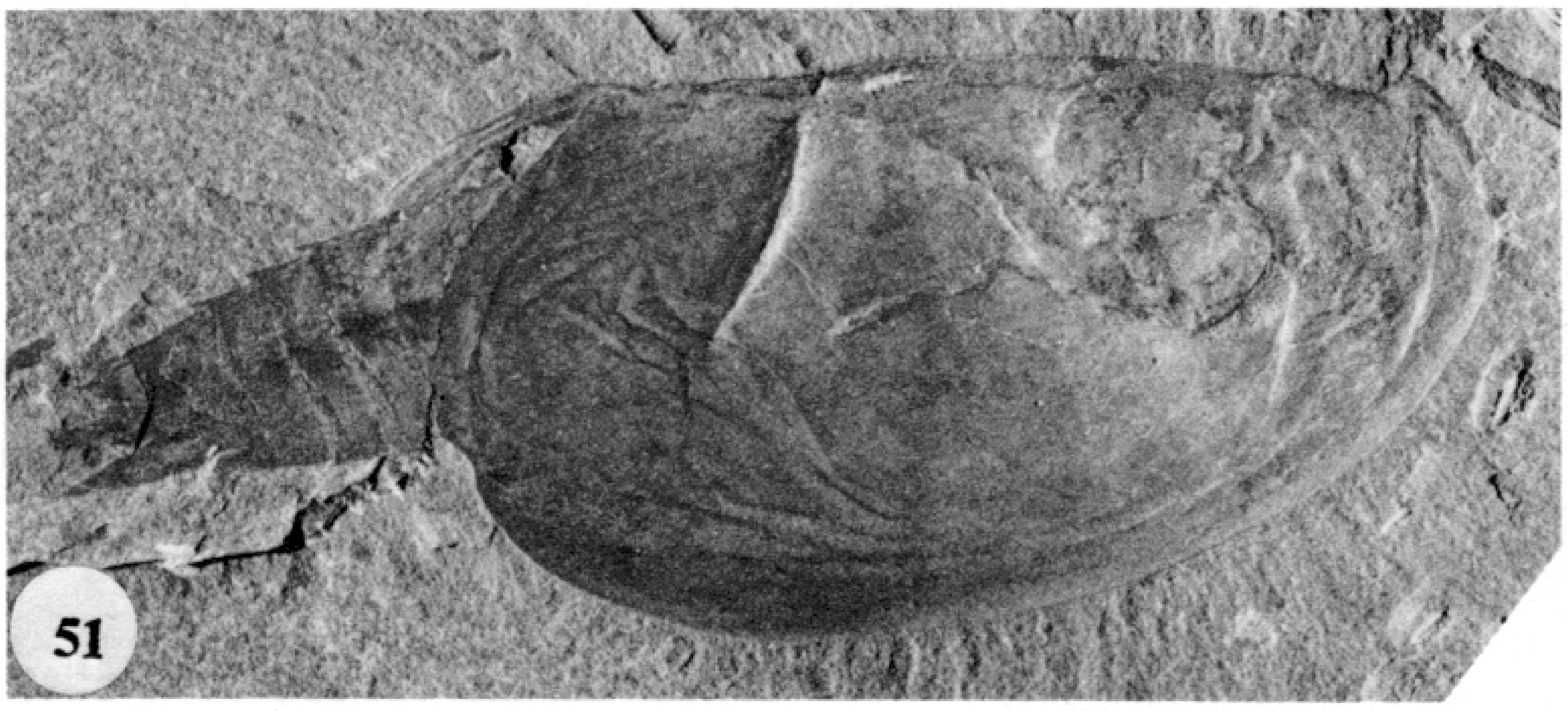

46

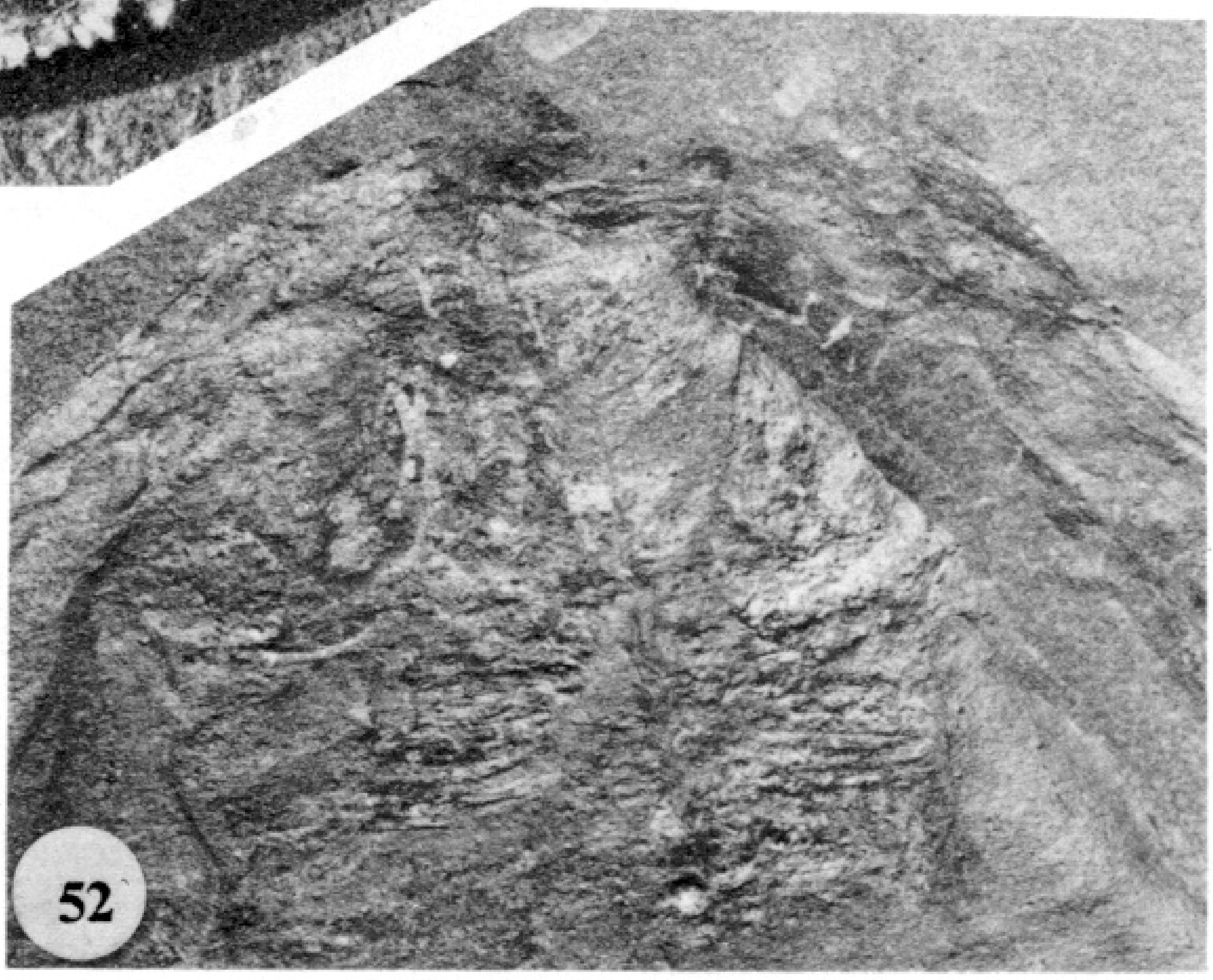

47


48

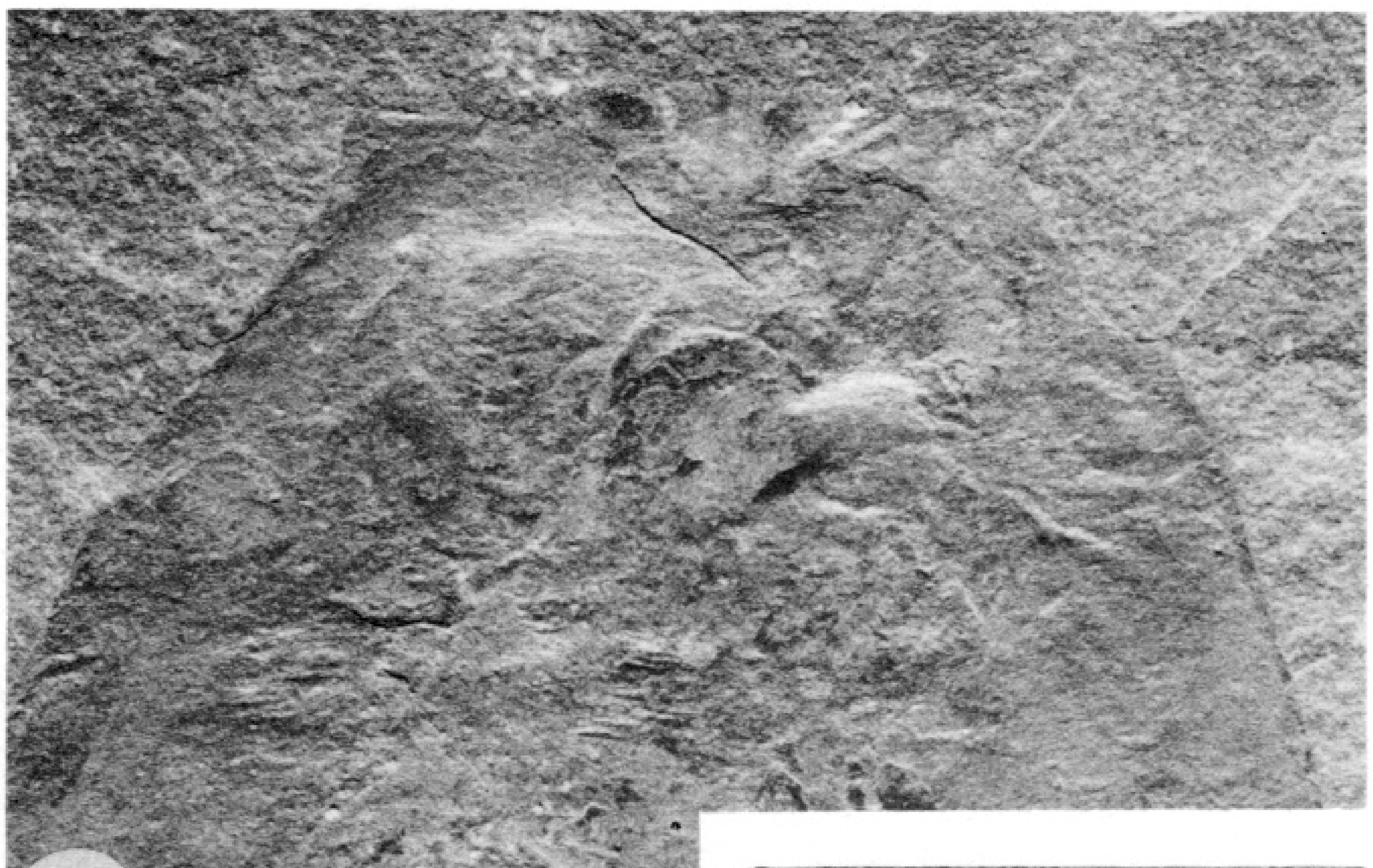

49


50

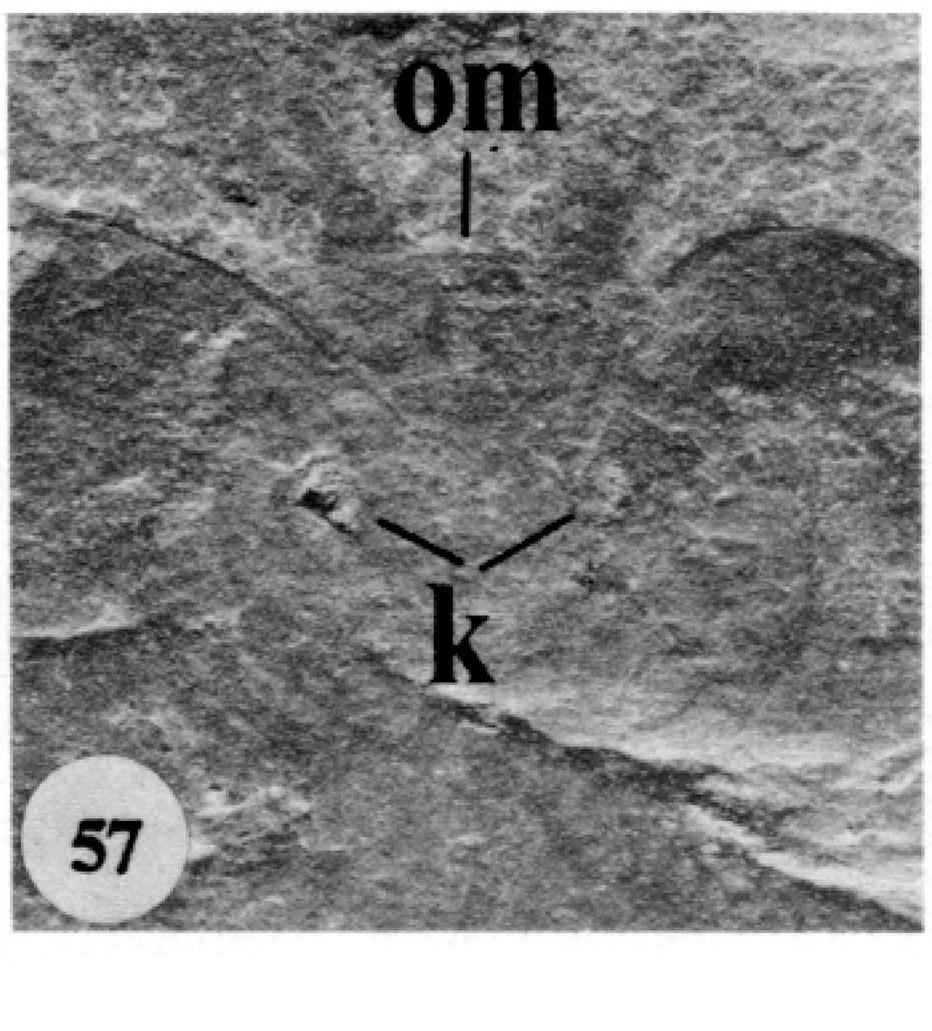

51


52

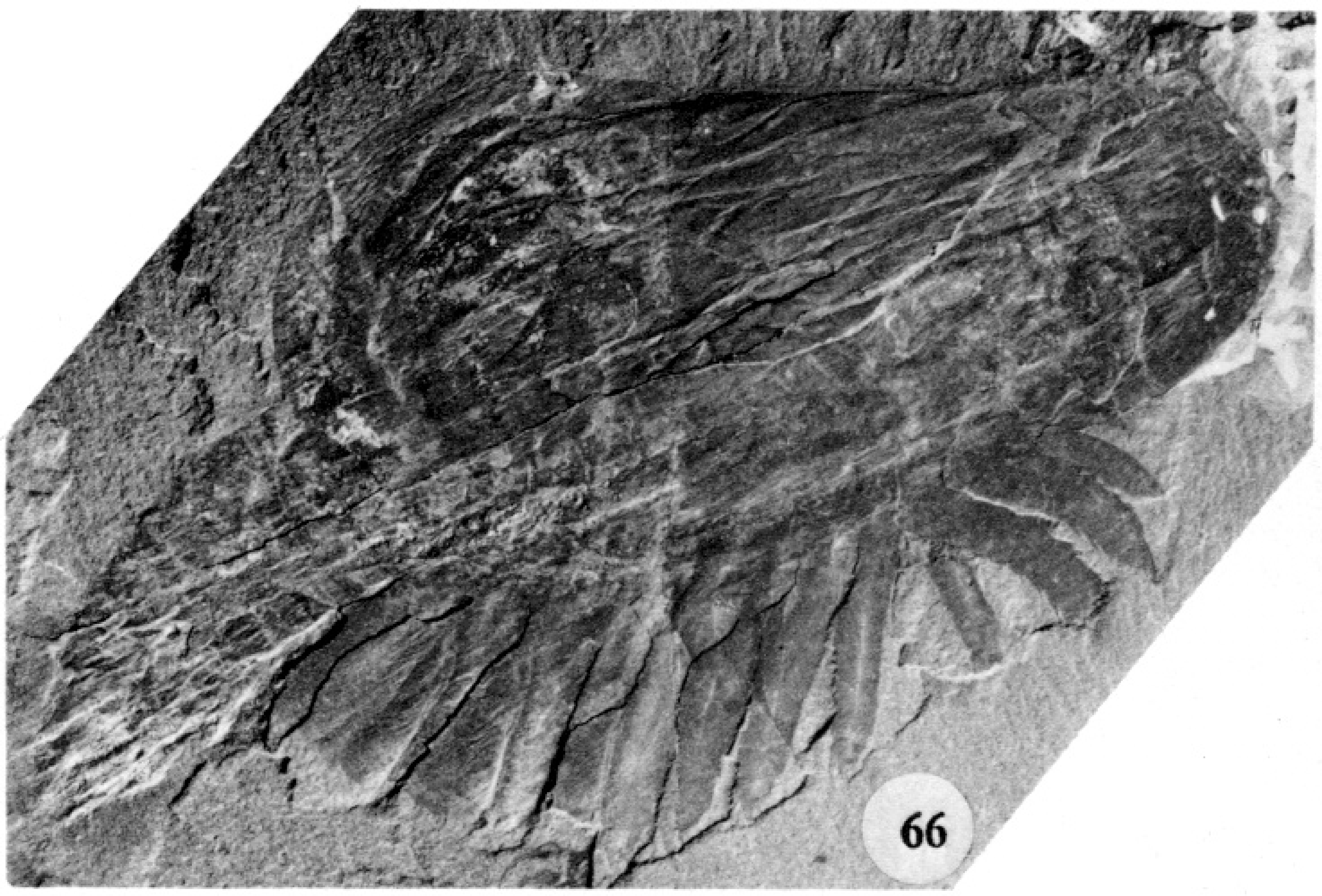

53


55

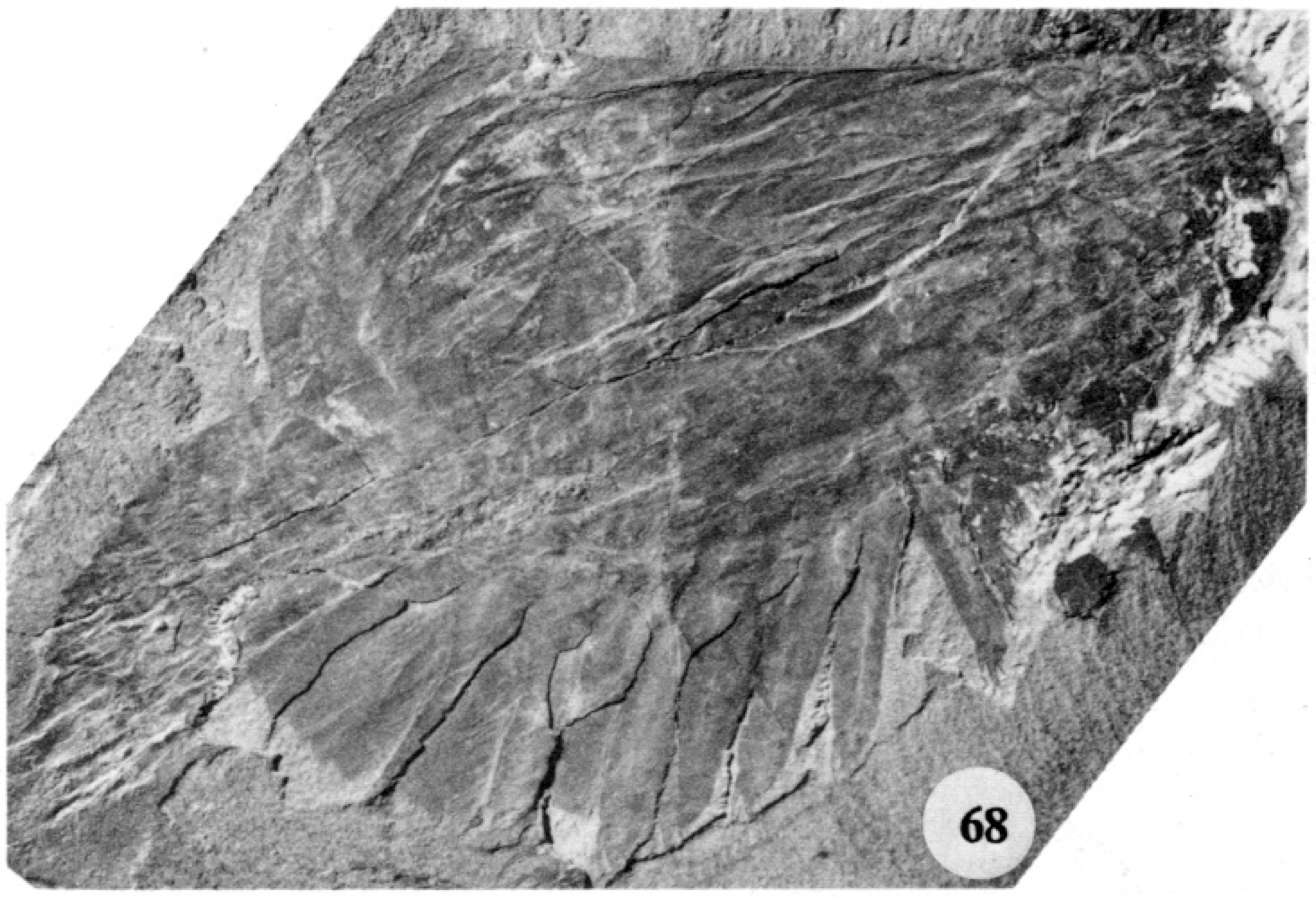

54


57


56


66


67


68


69

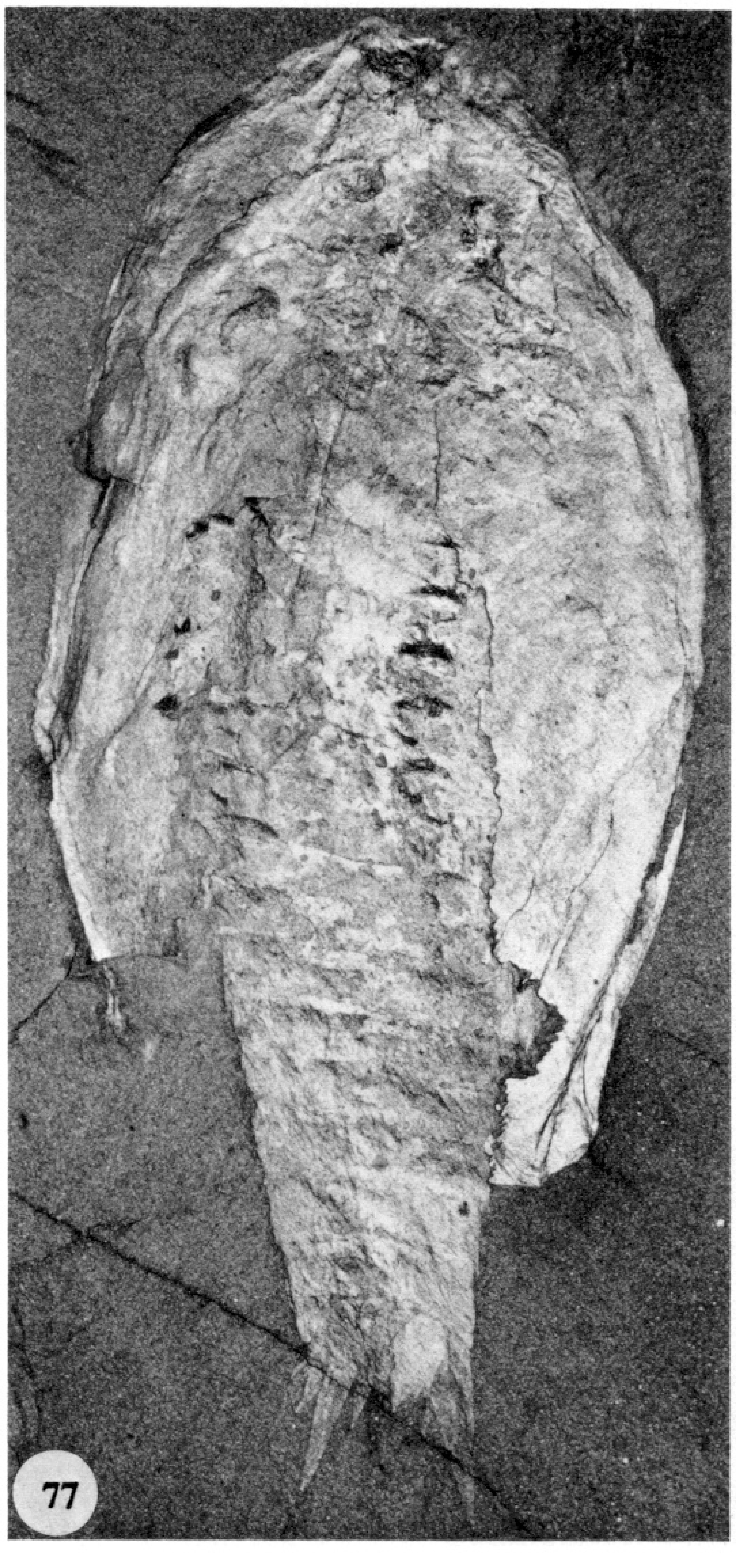

70

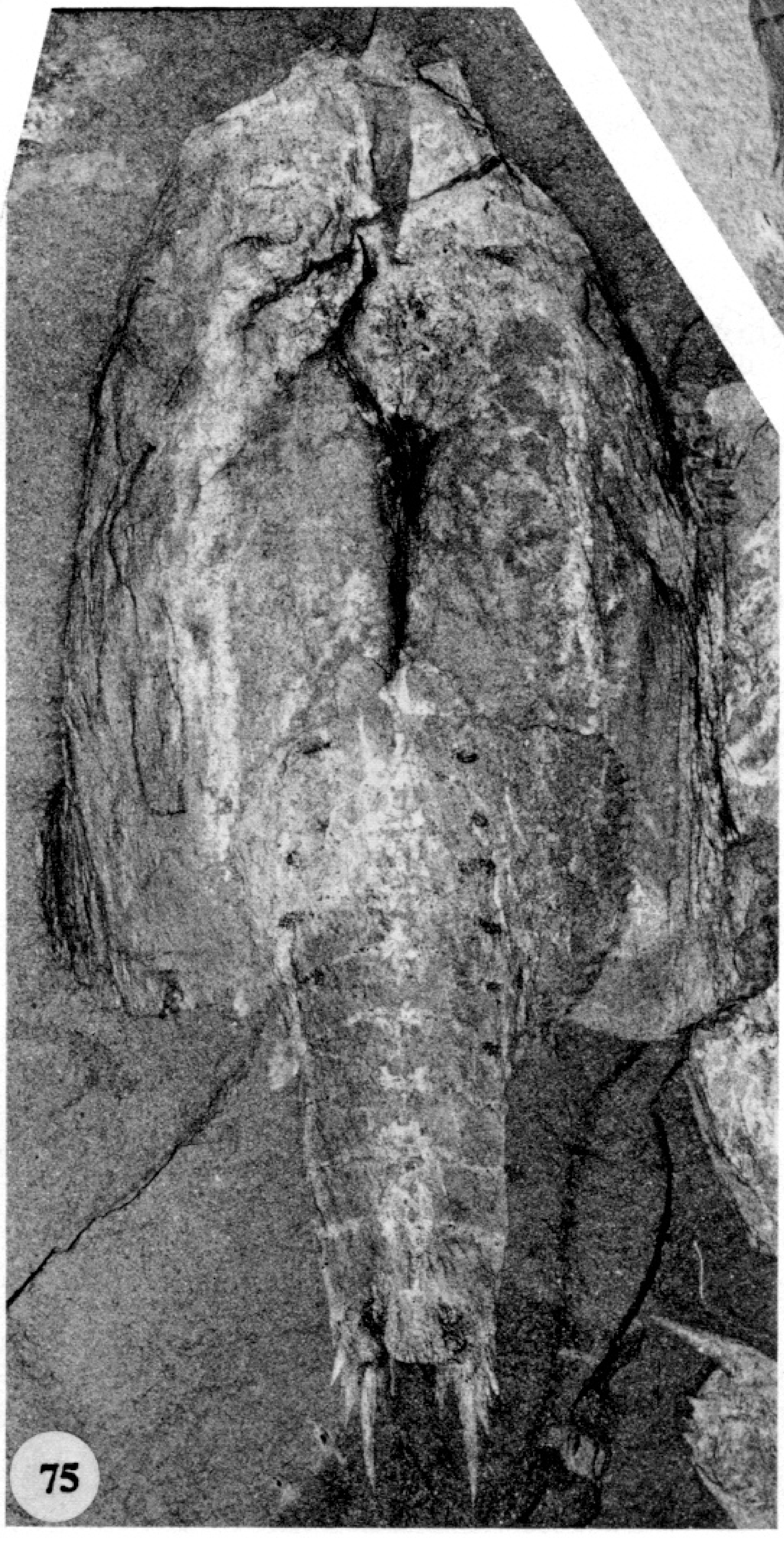

71


72

73

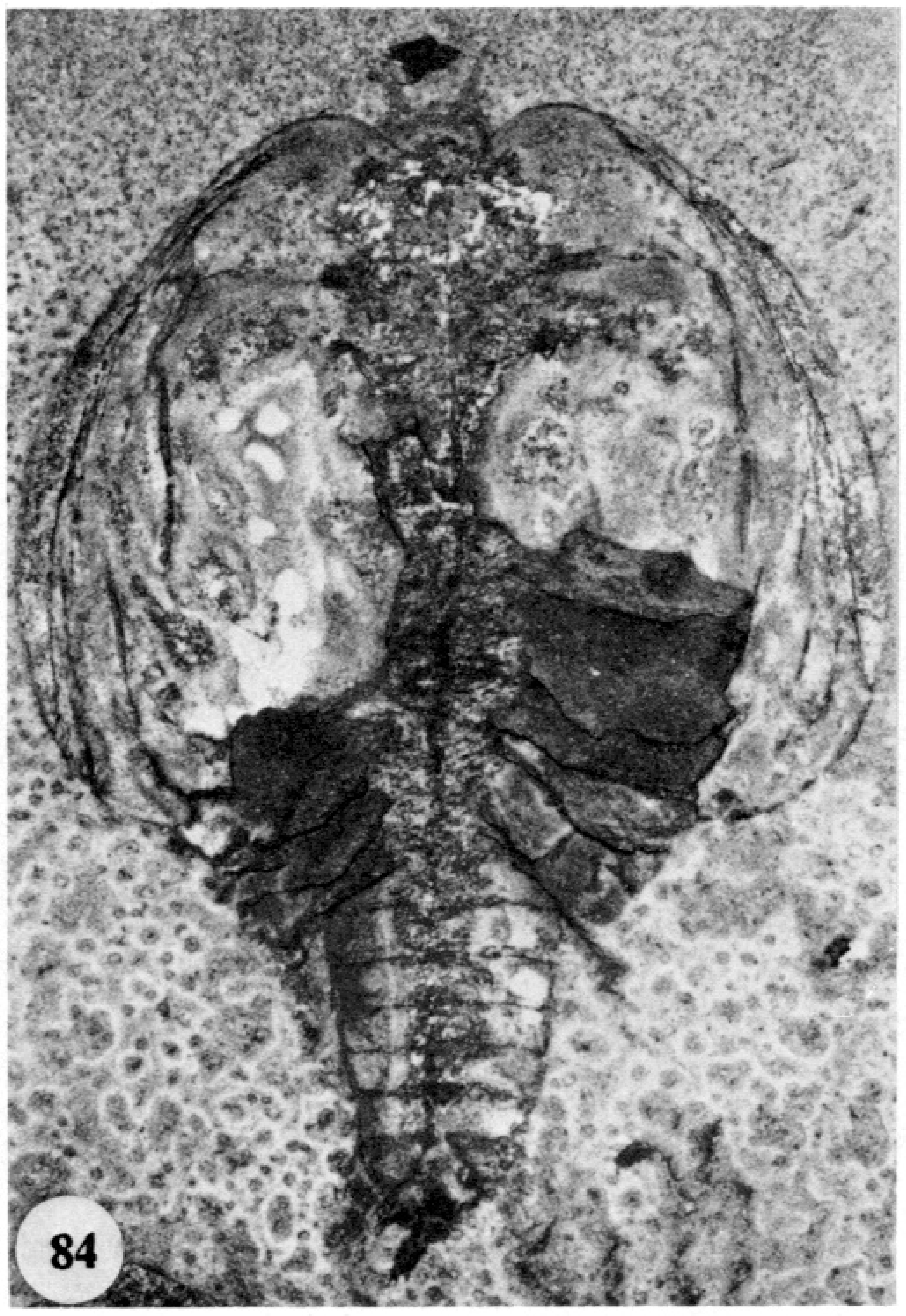

74

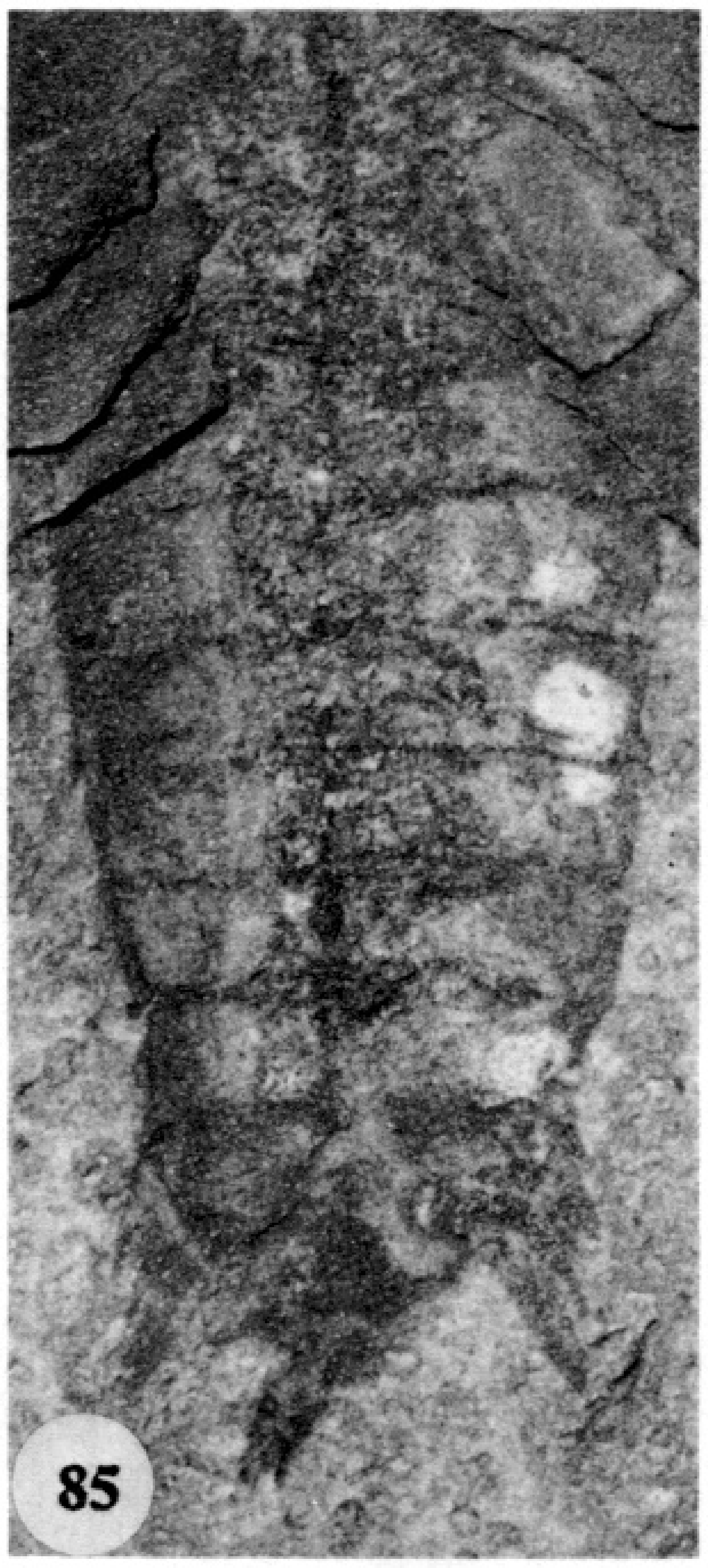

77

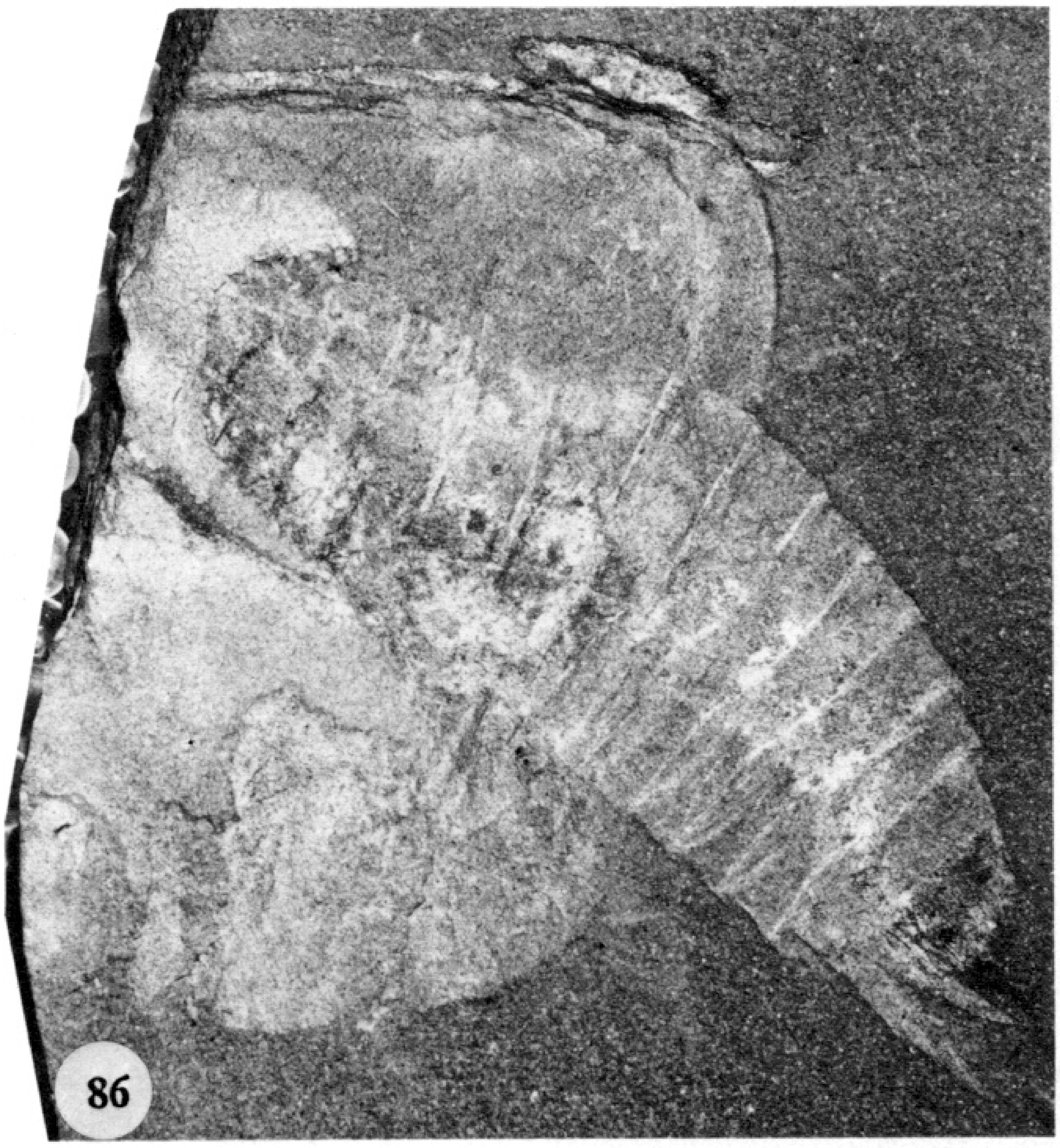

75

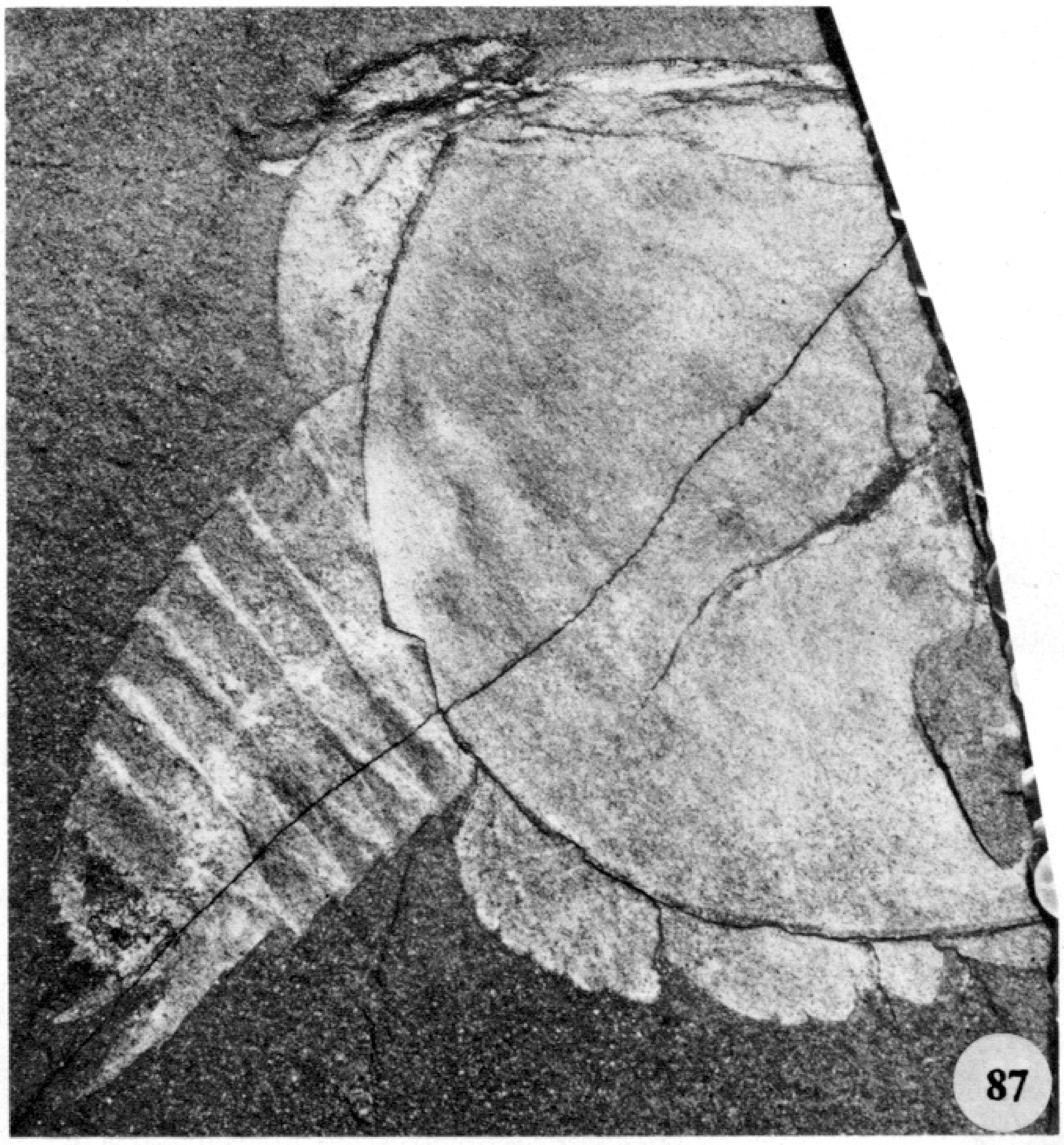

76

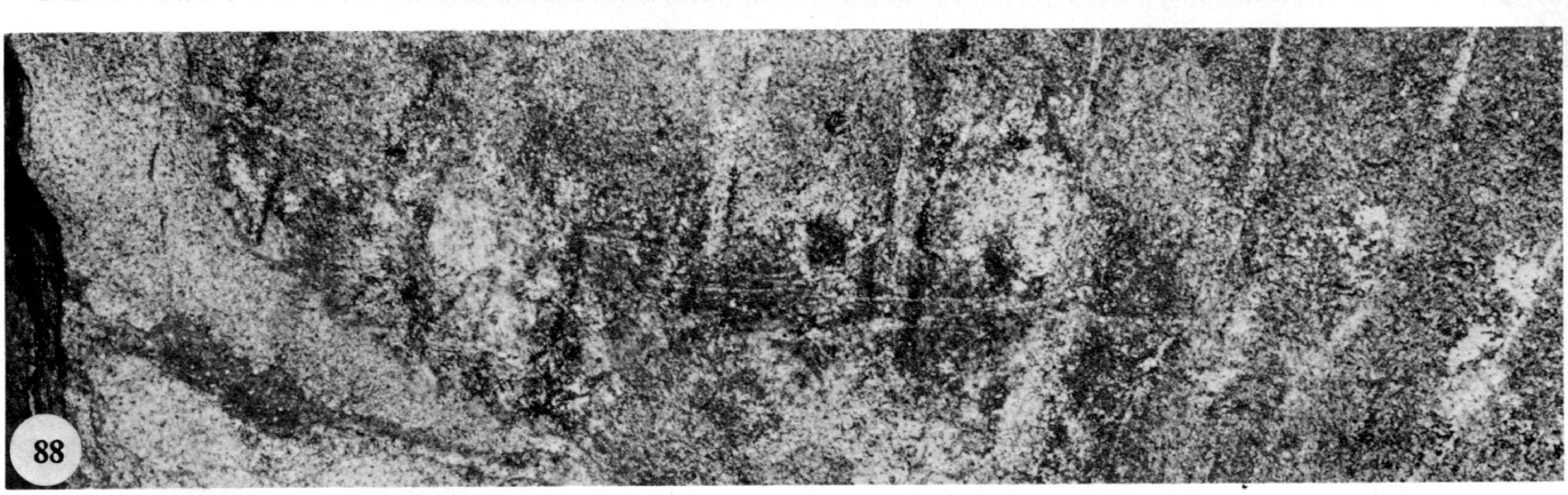

83

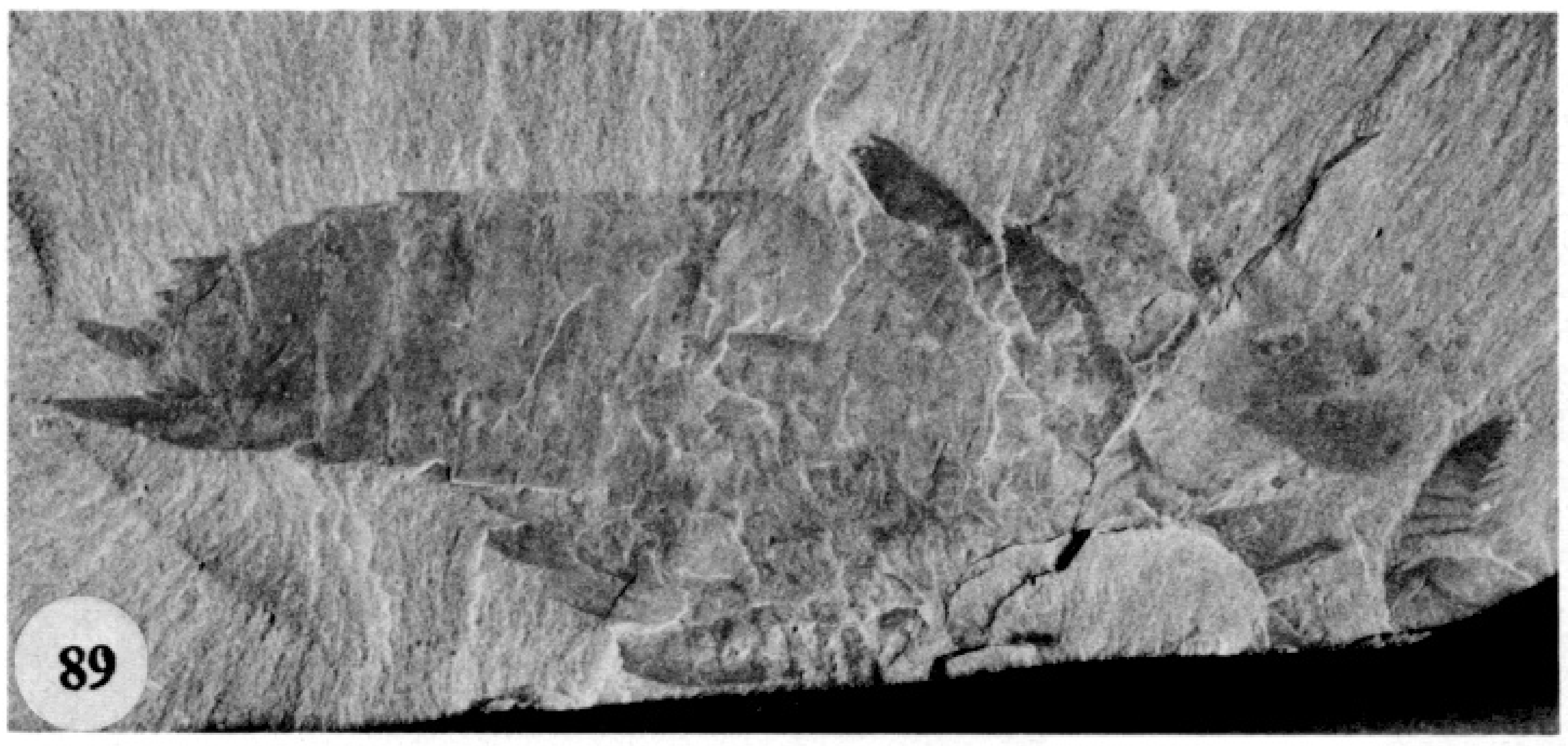

84

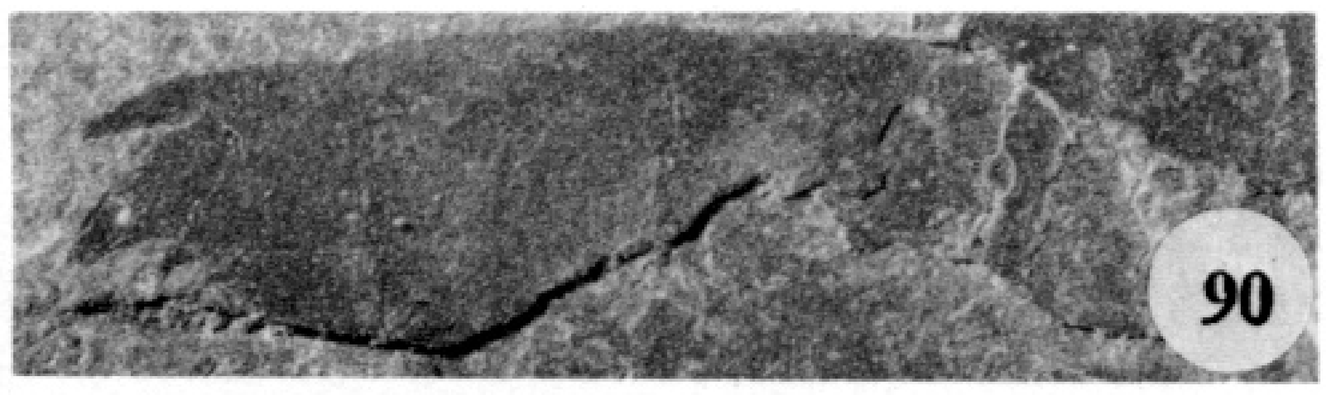

85

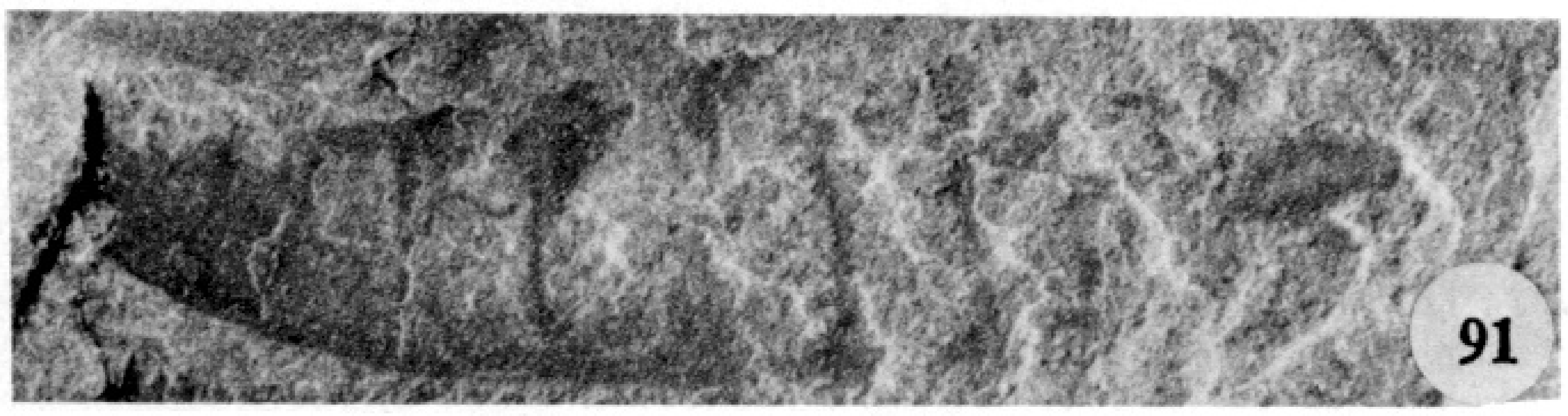

86


87


88


89


90

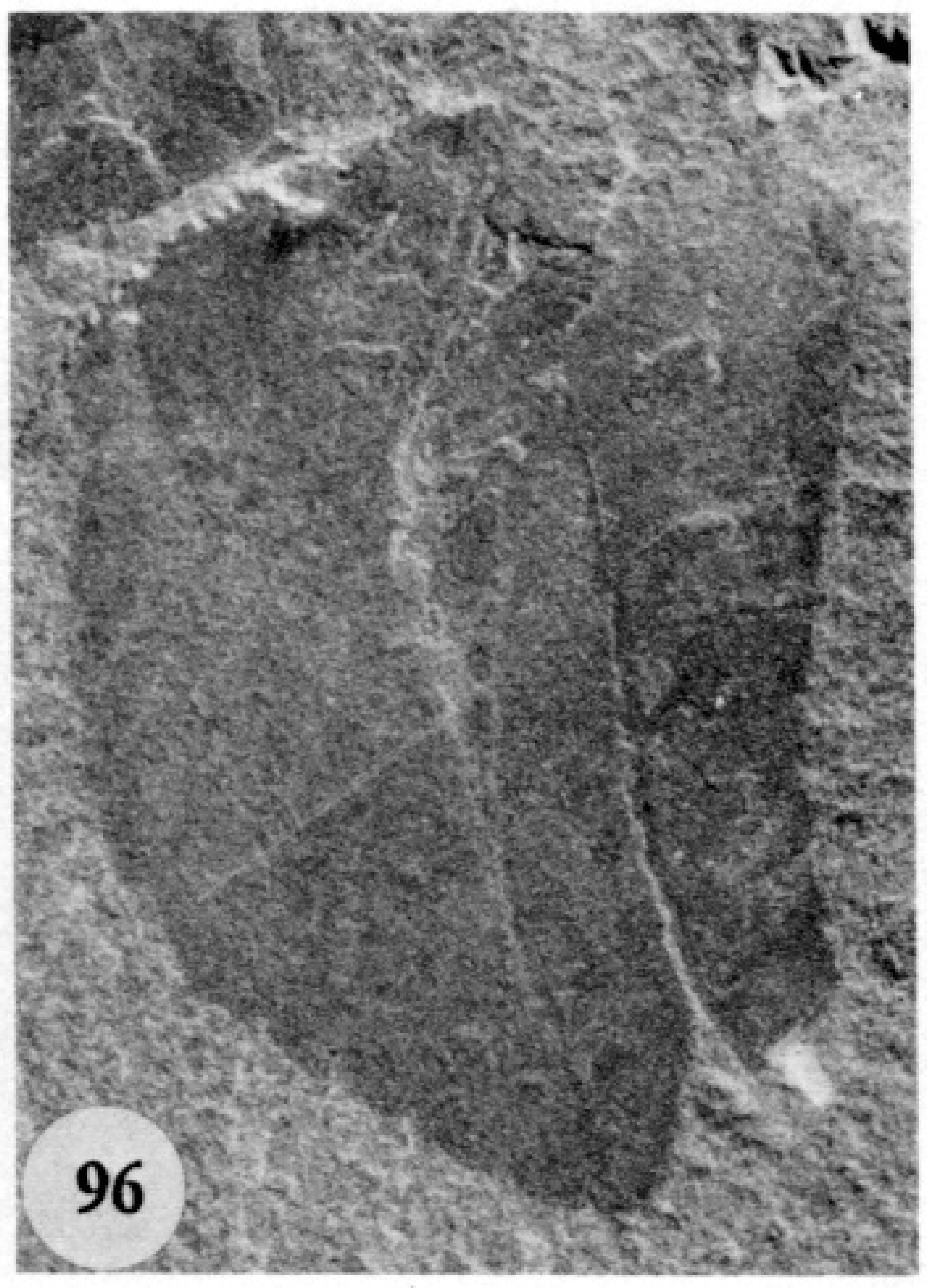

91


92


93


94


95

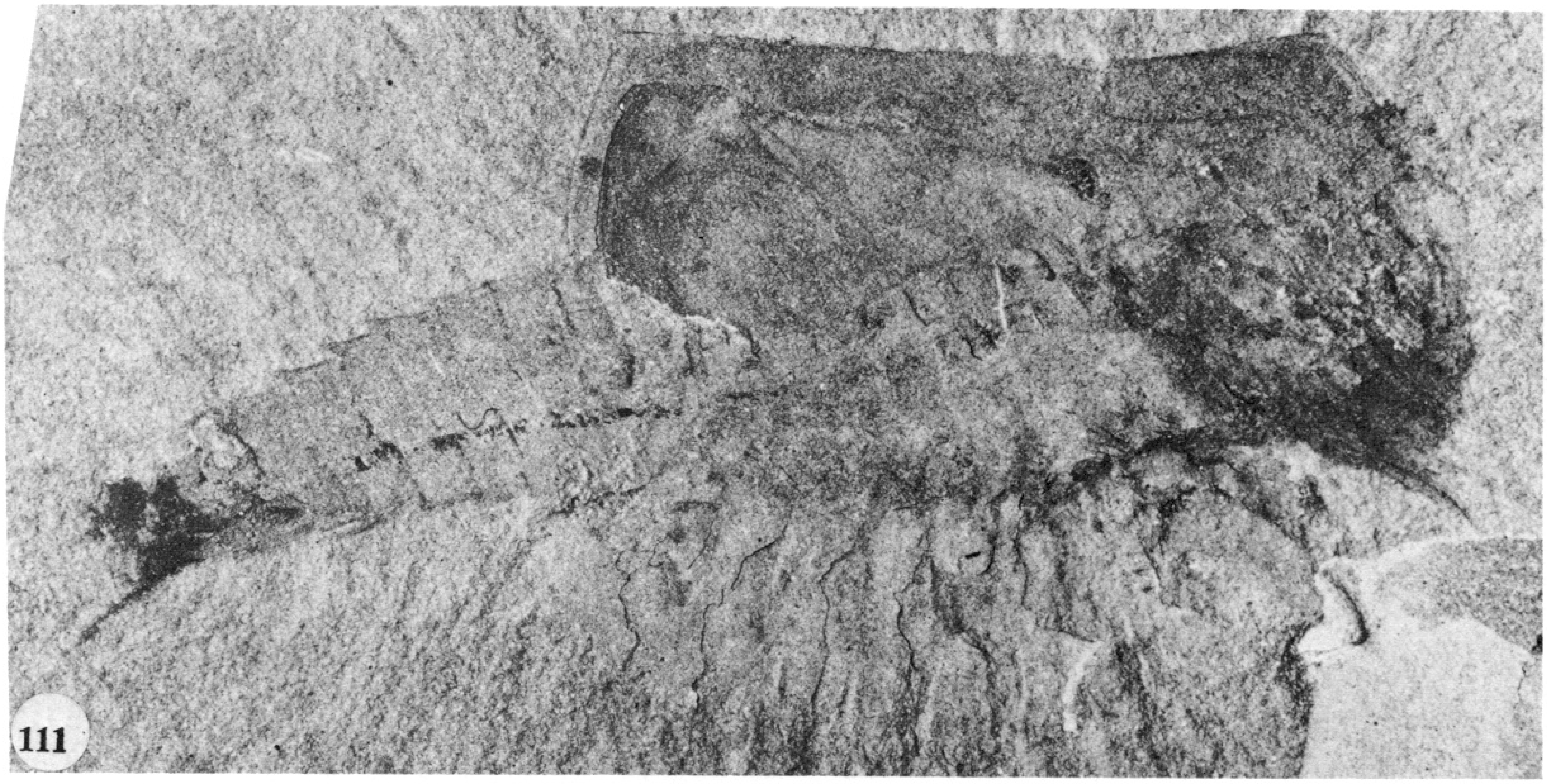

96

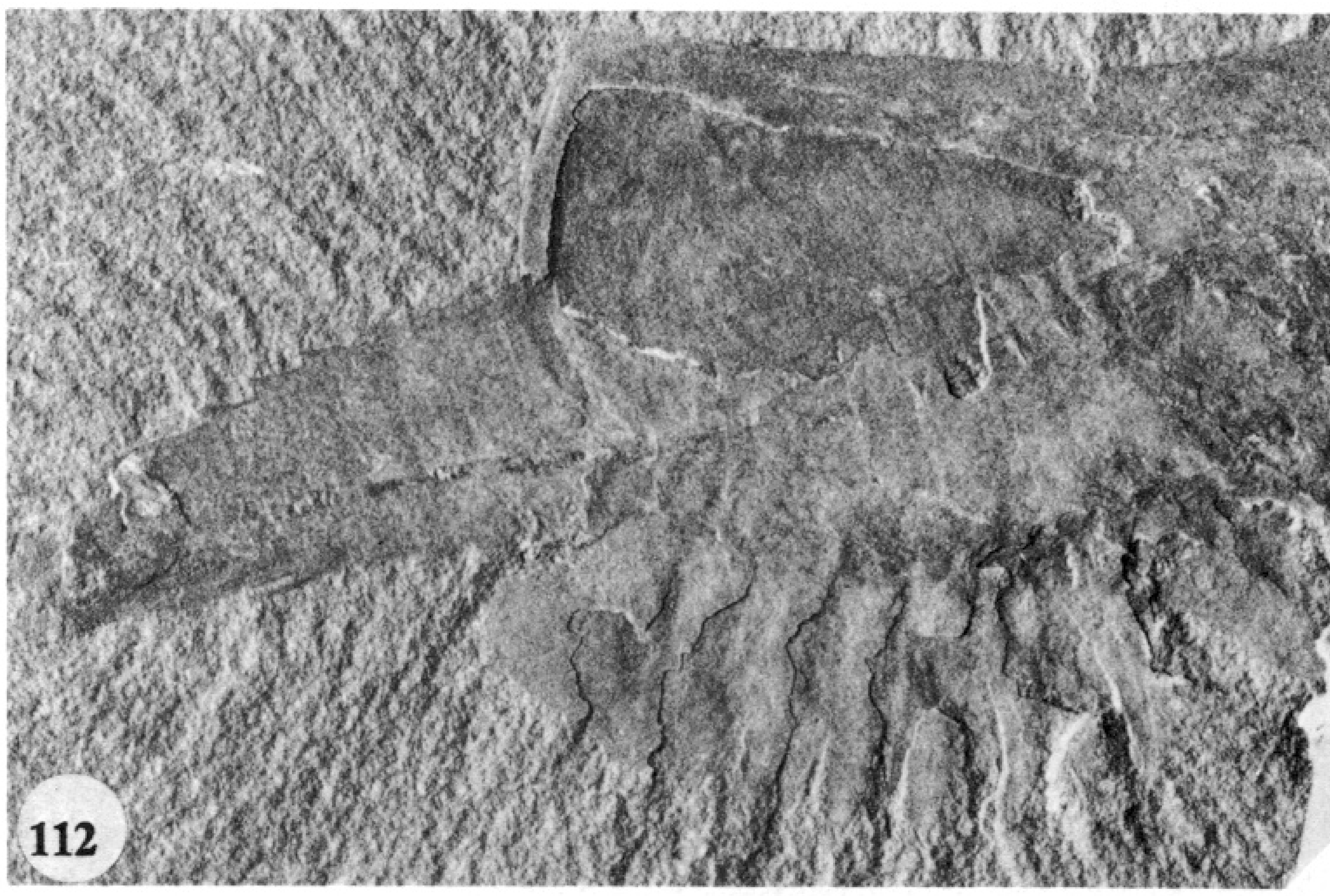

97

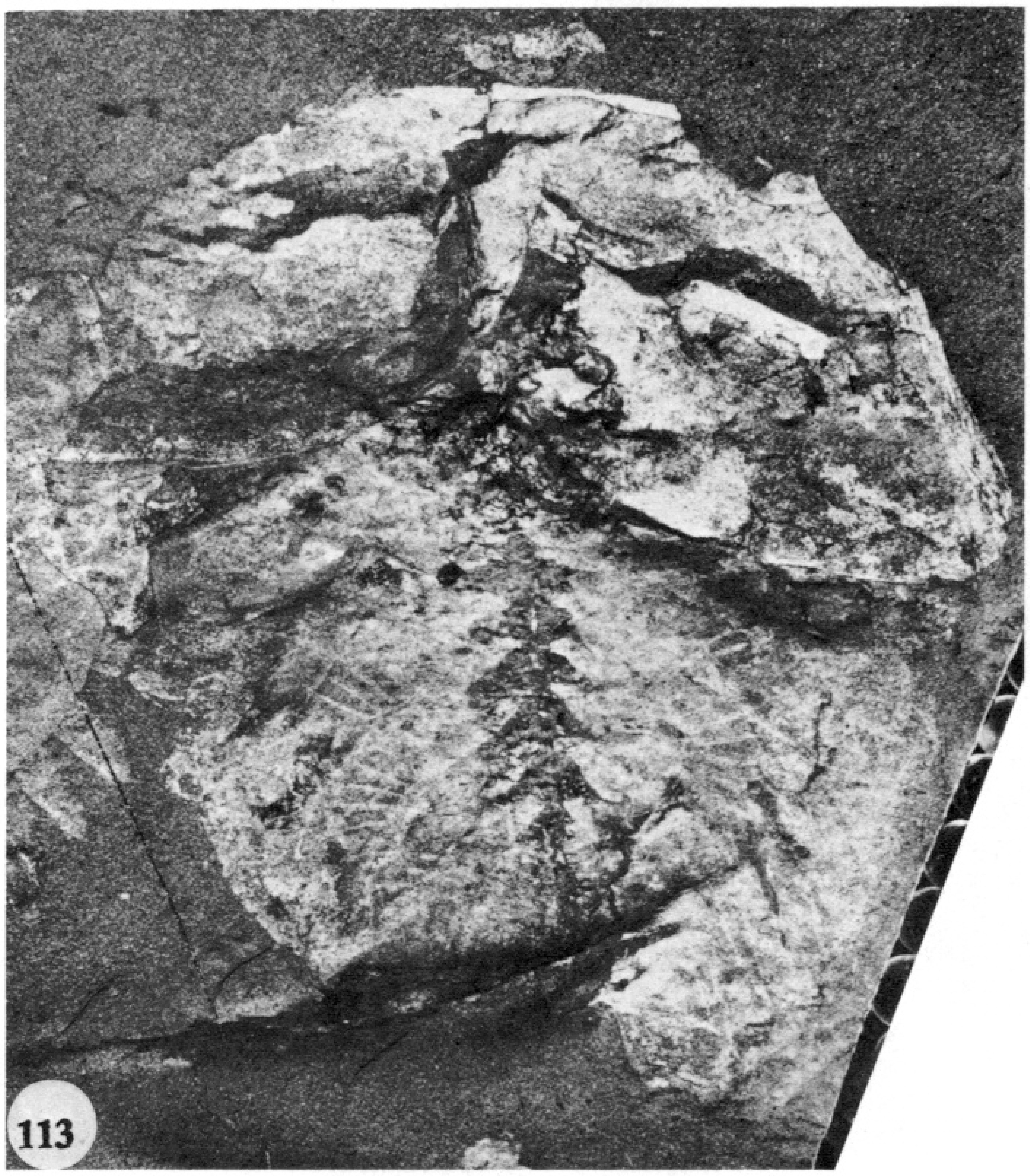

98


99


100

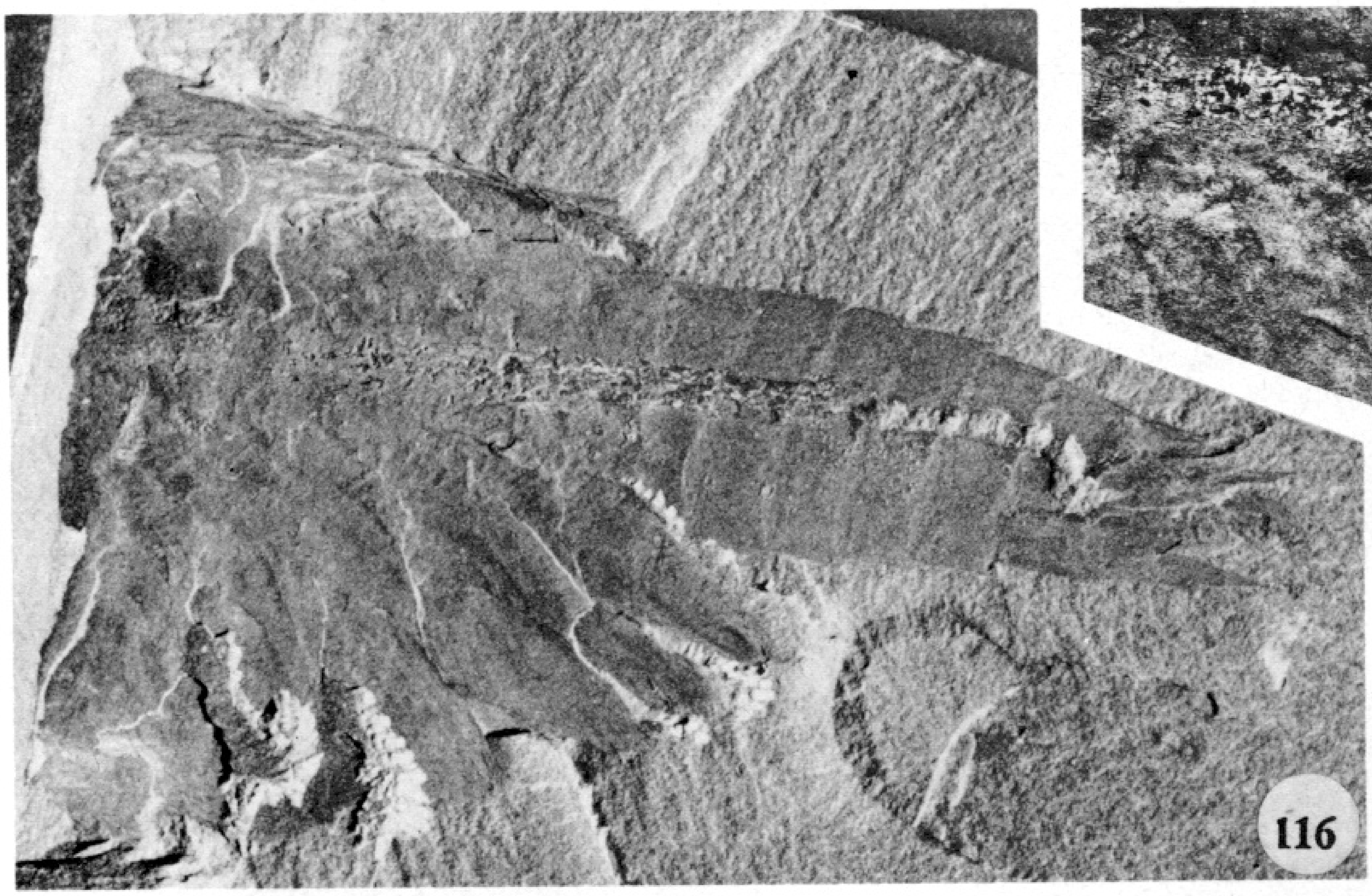

111

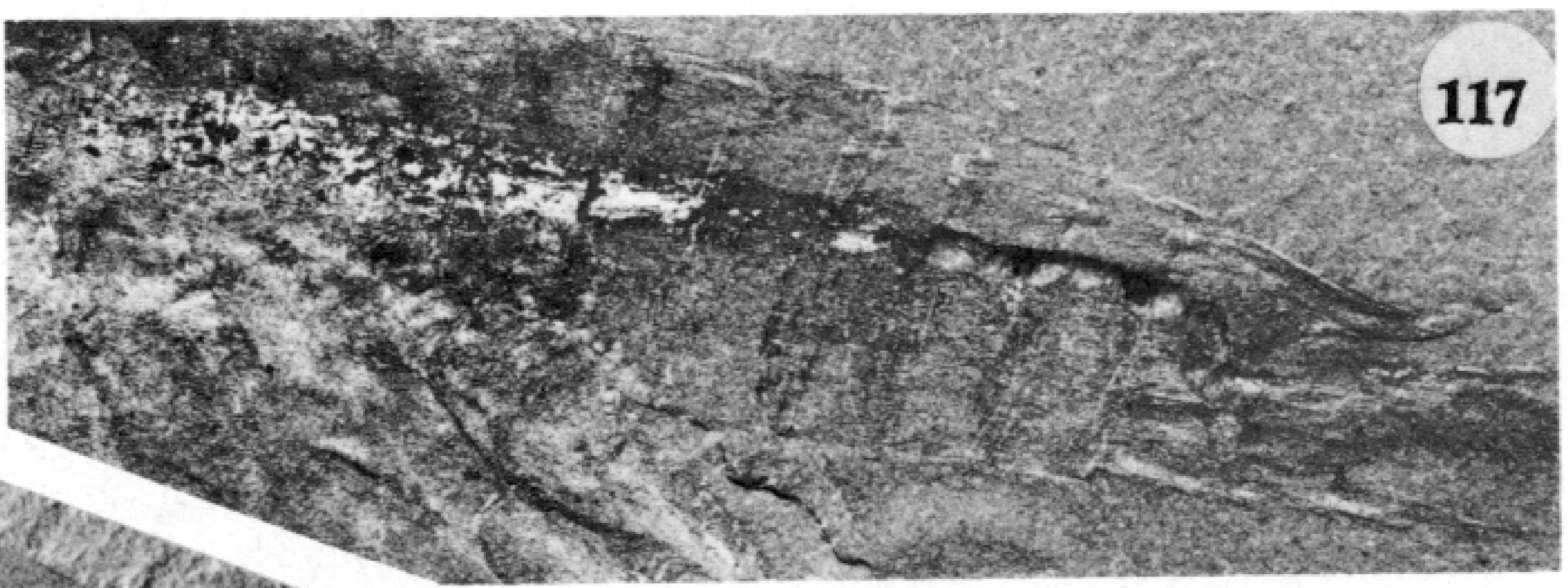

112


113


114

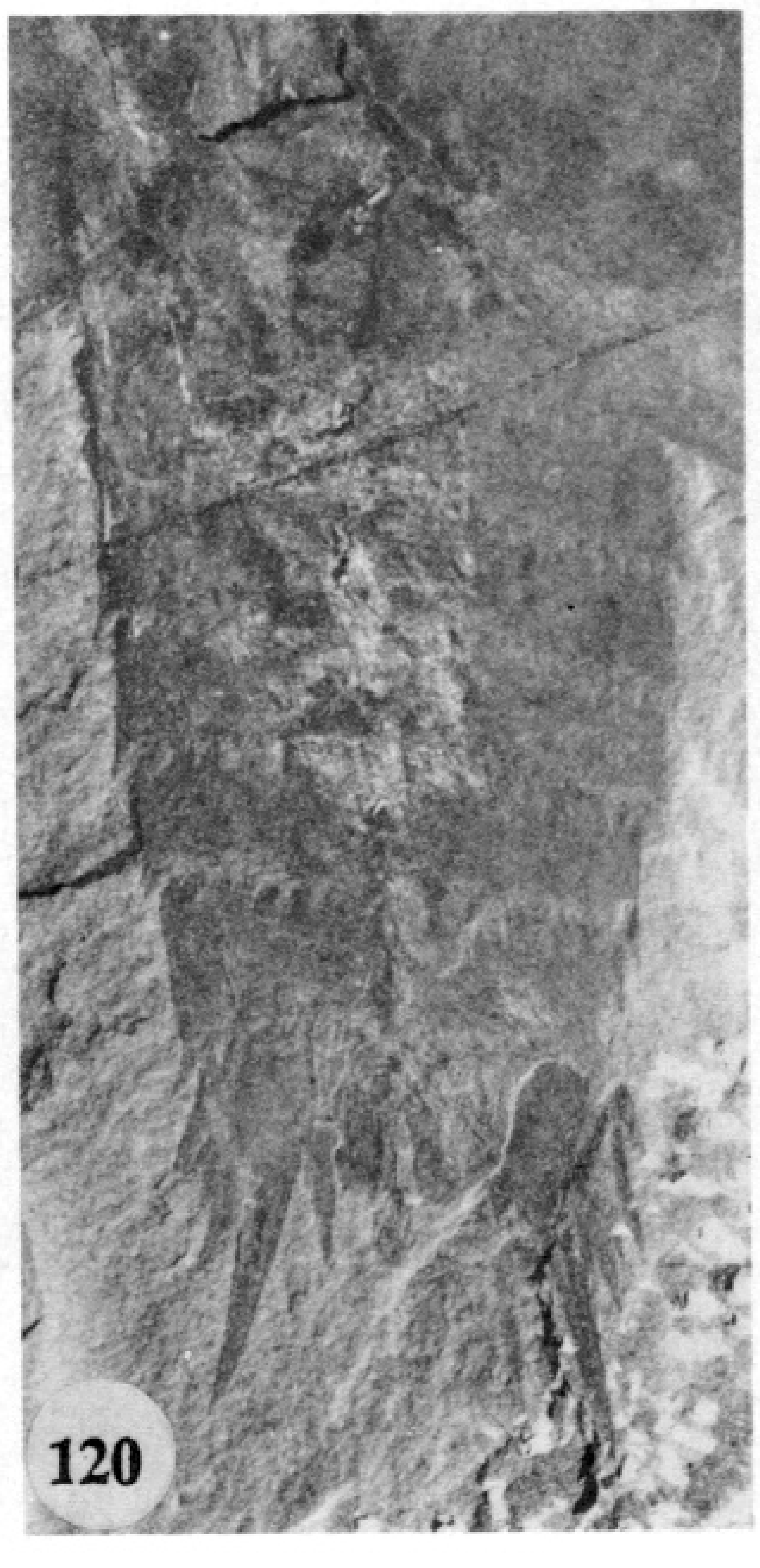

115


116

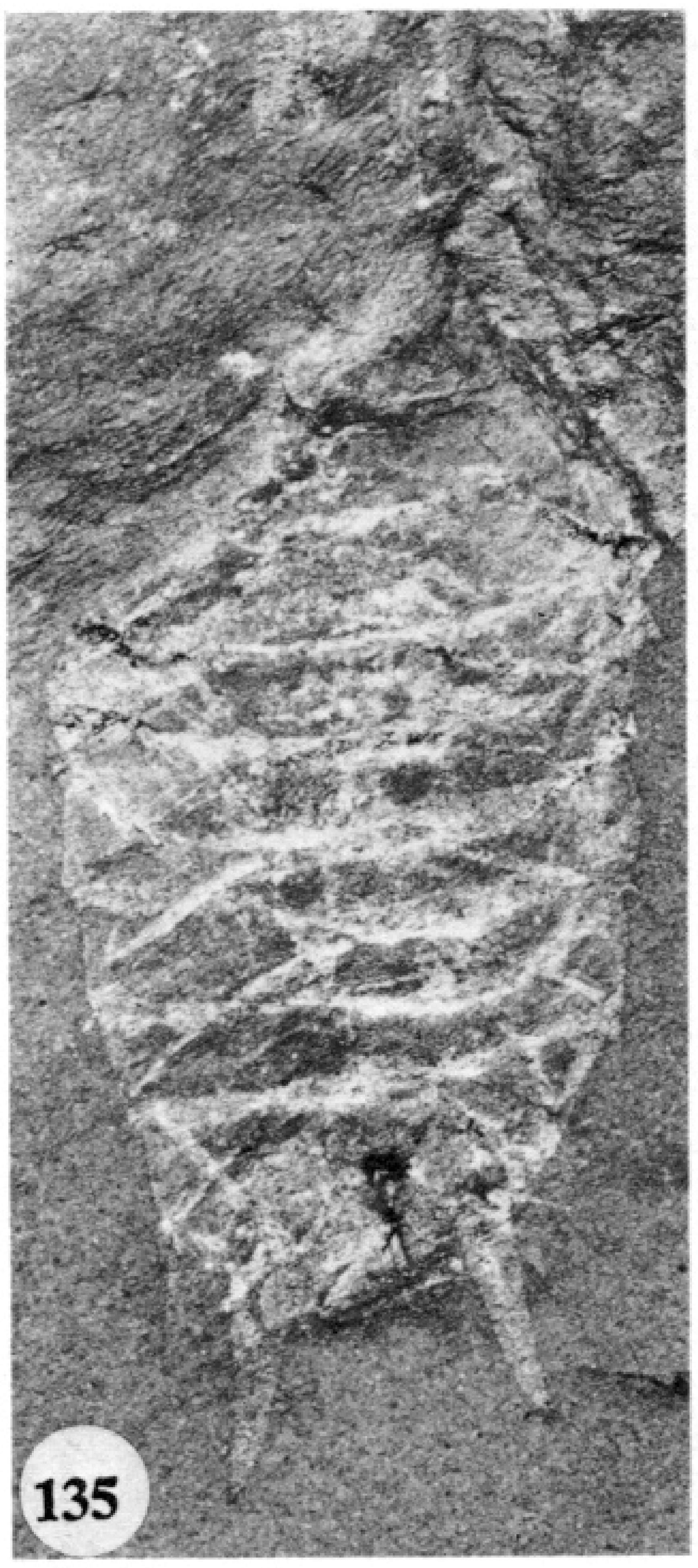

117

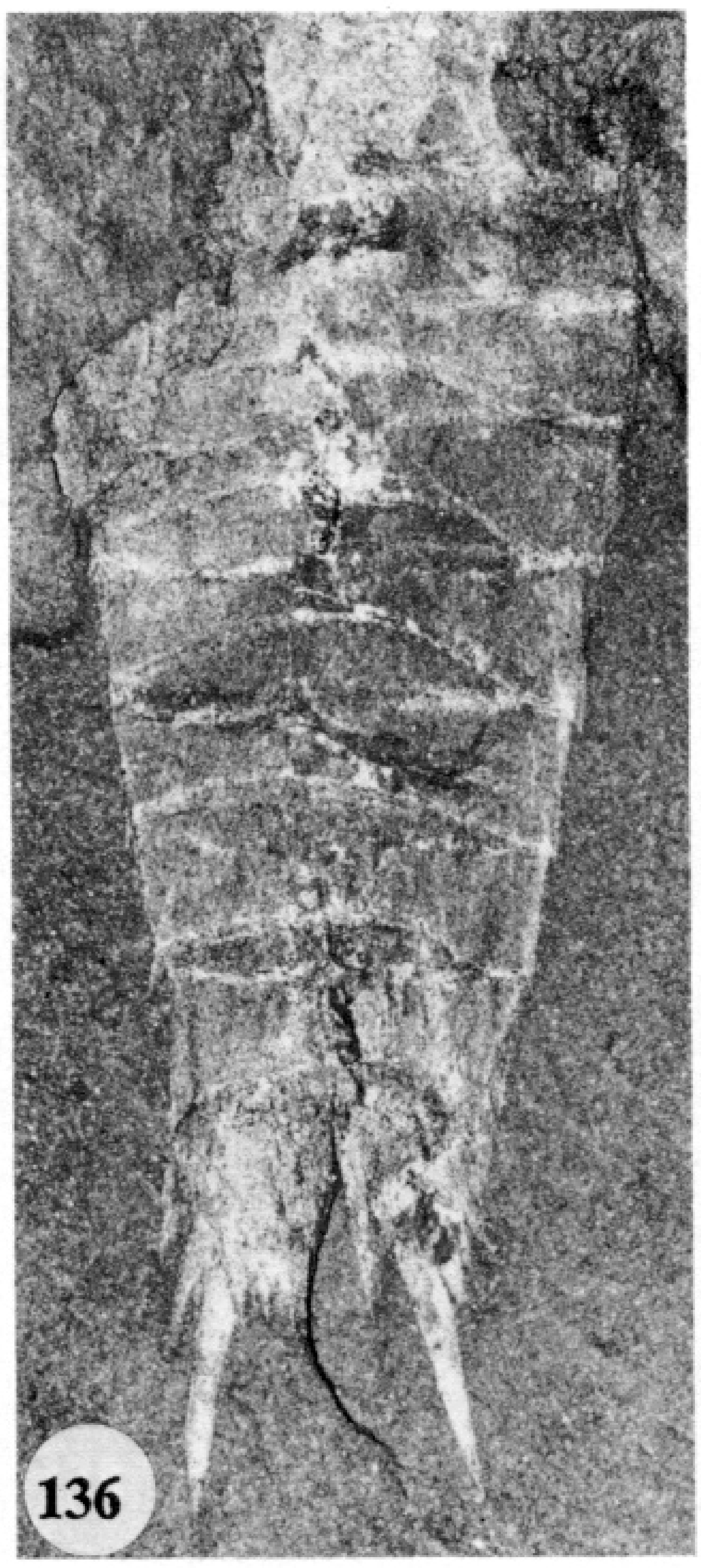

118


119

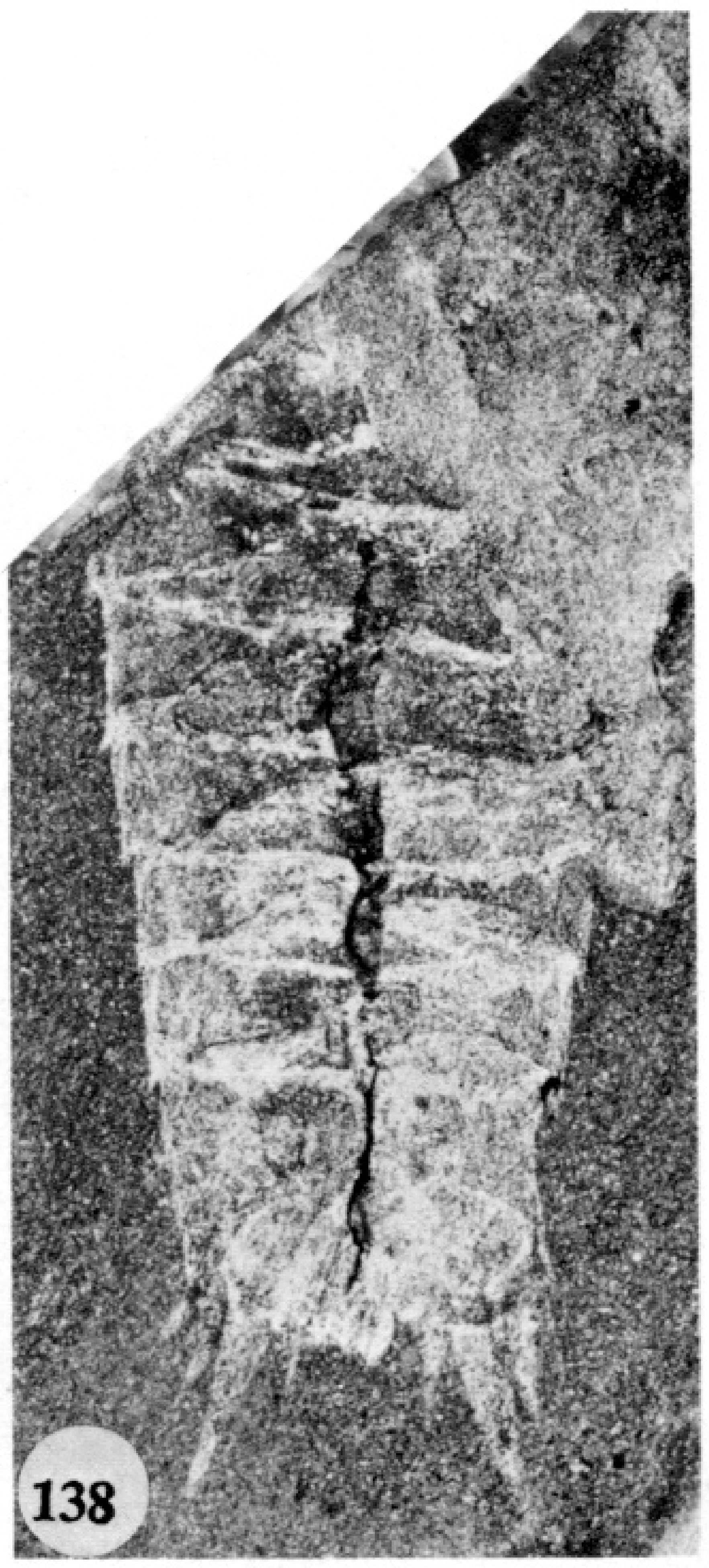

120

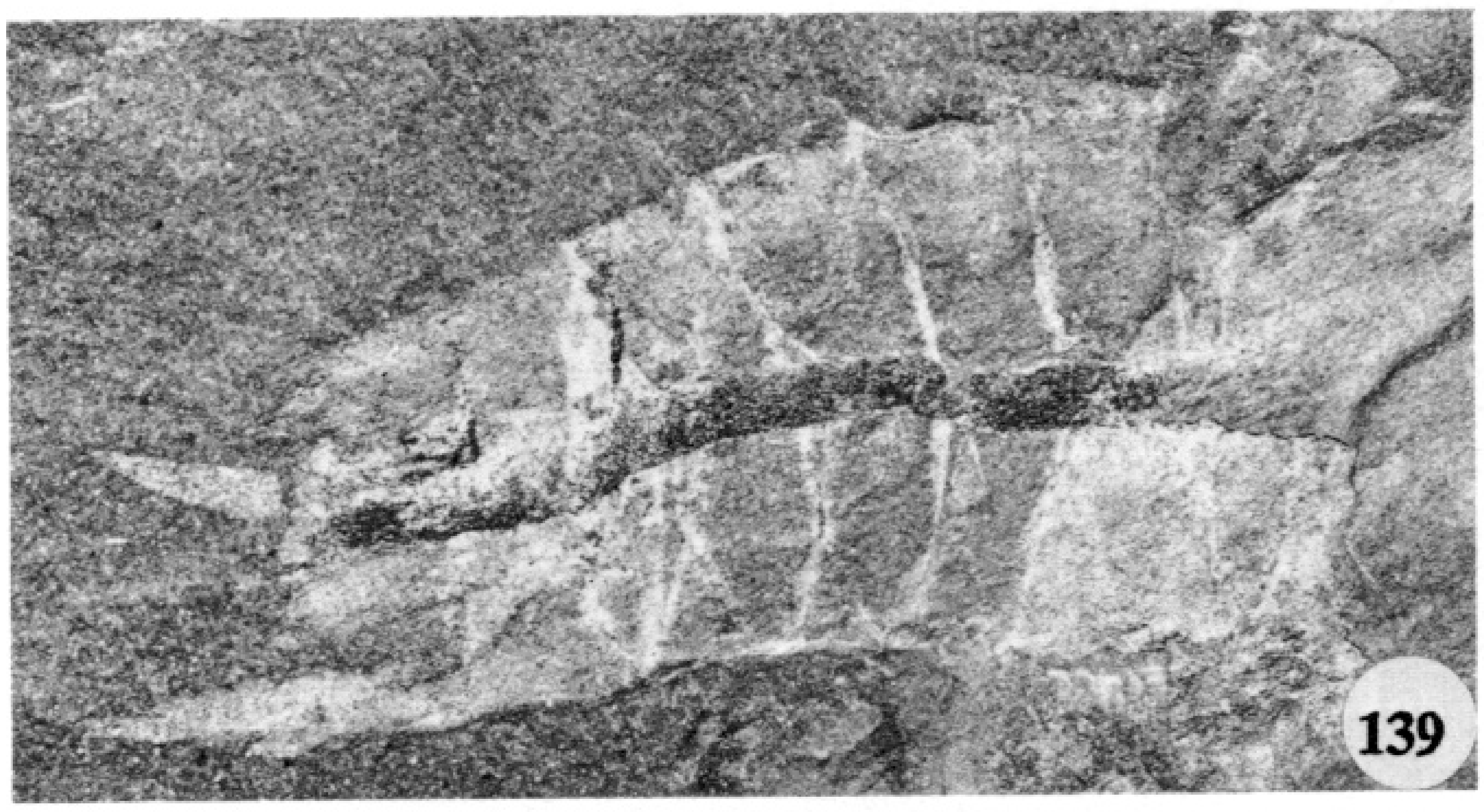

121


135

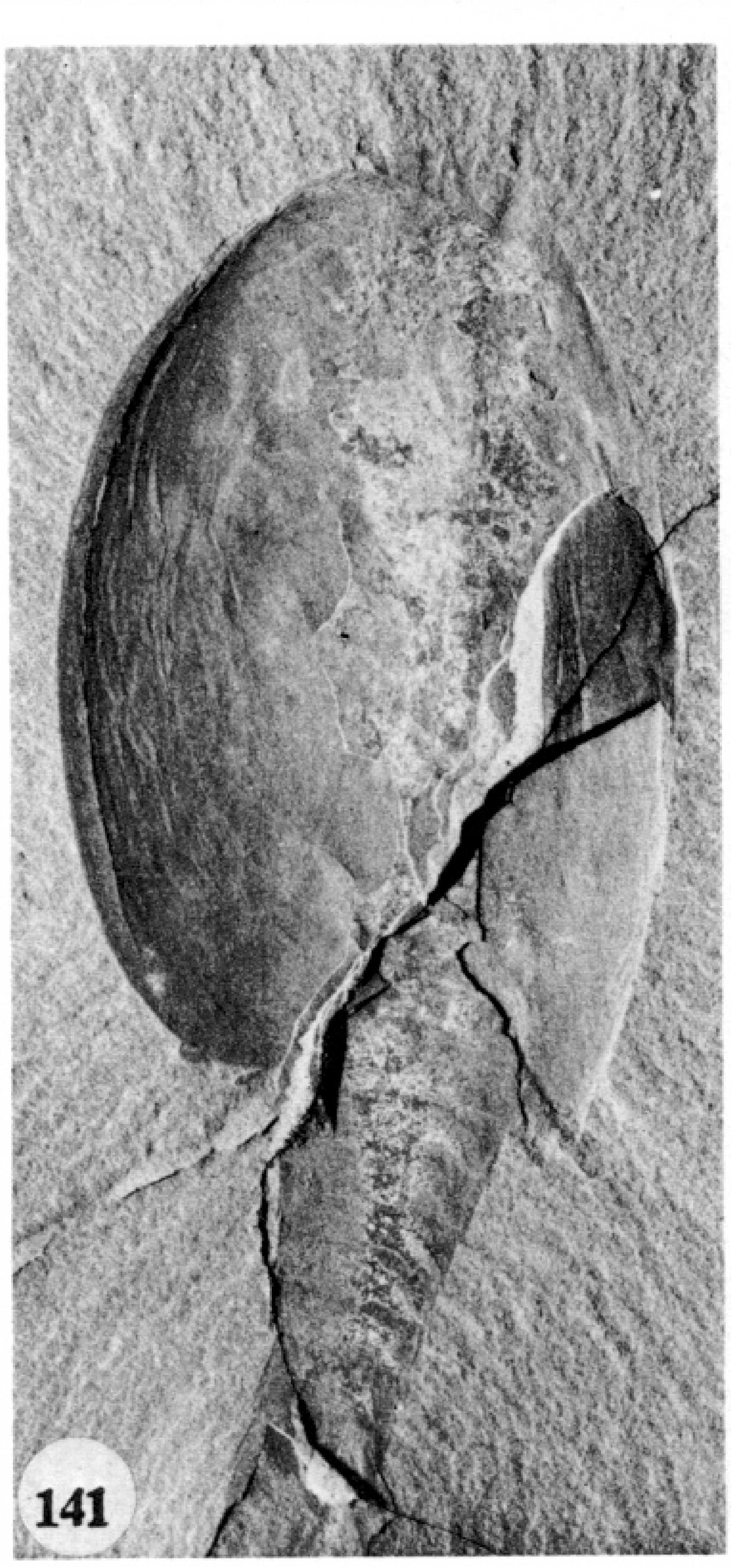

136


137


138

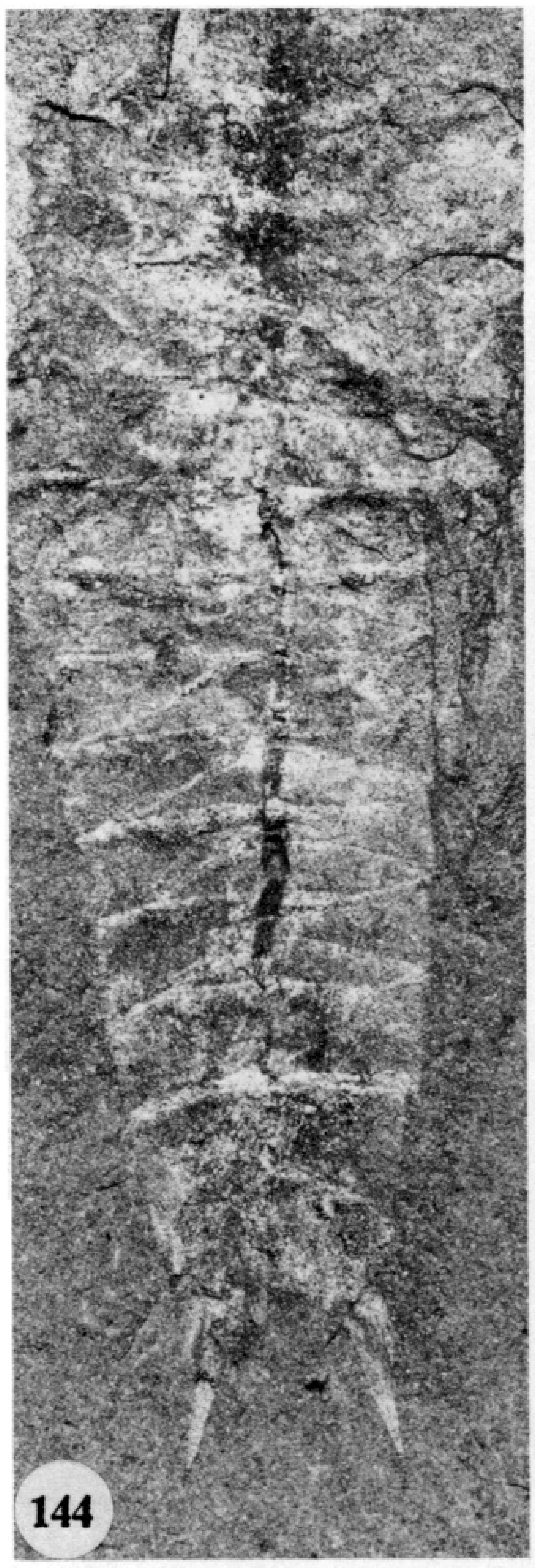

139

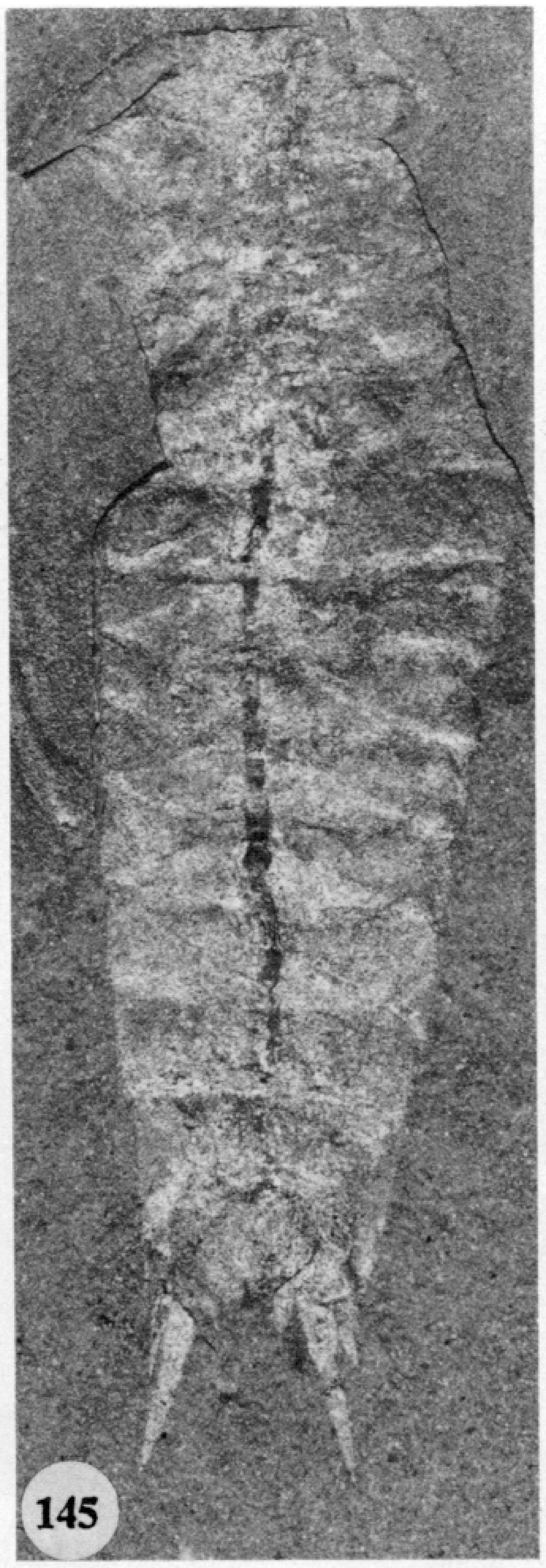

140

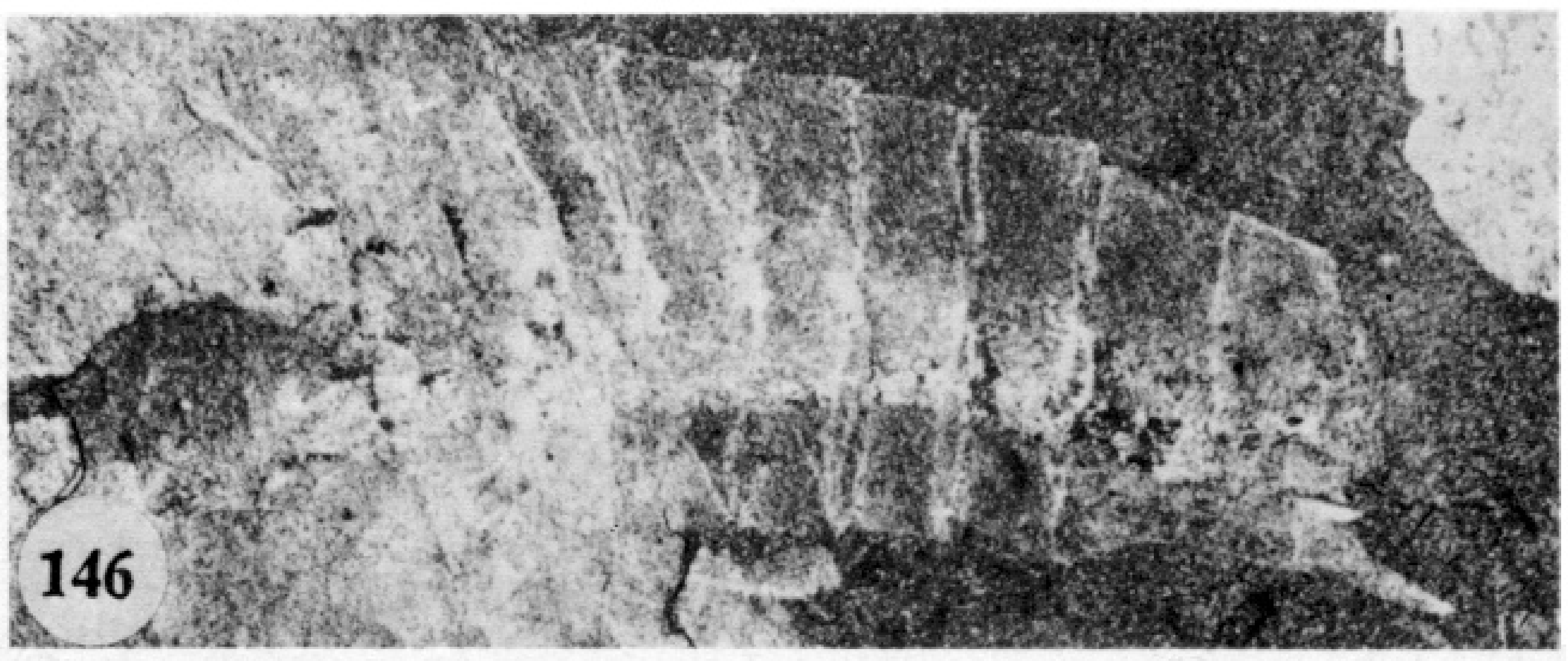

141


142

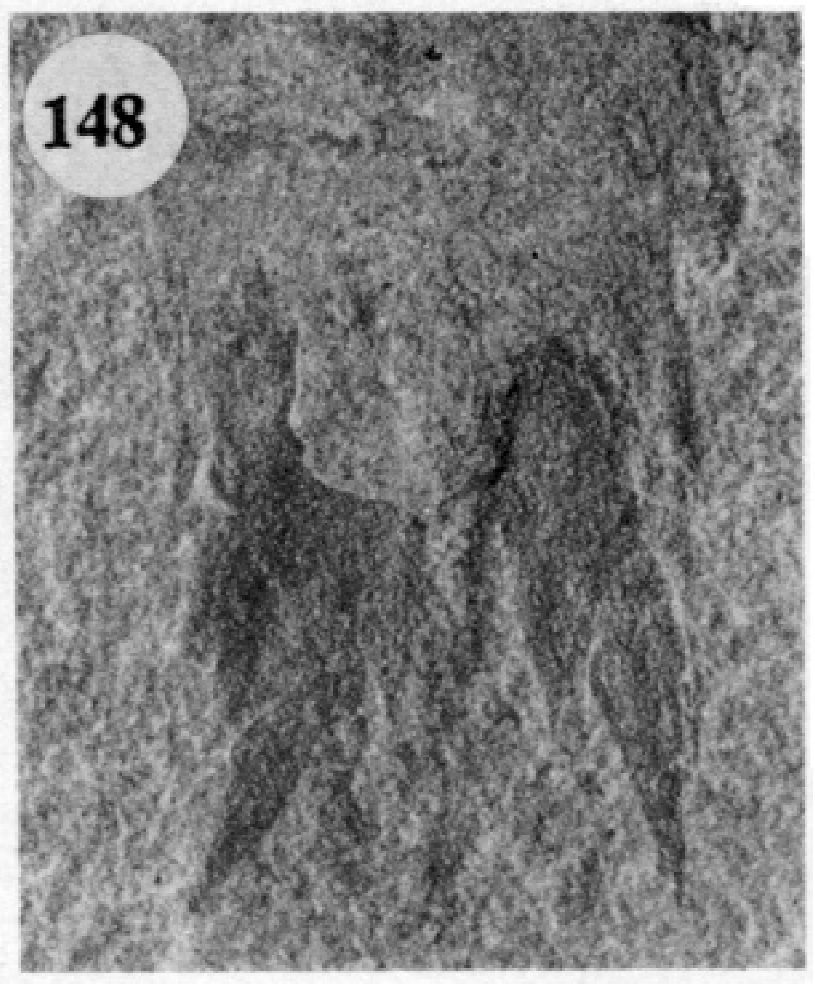

143

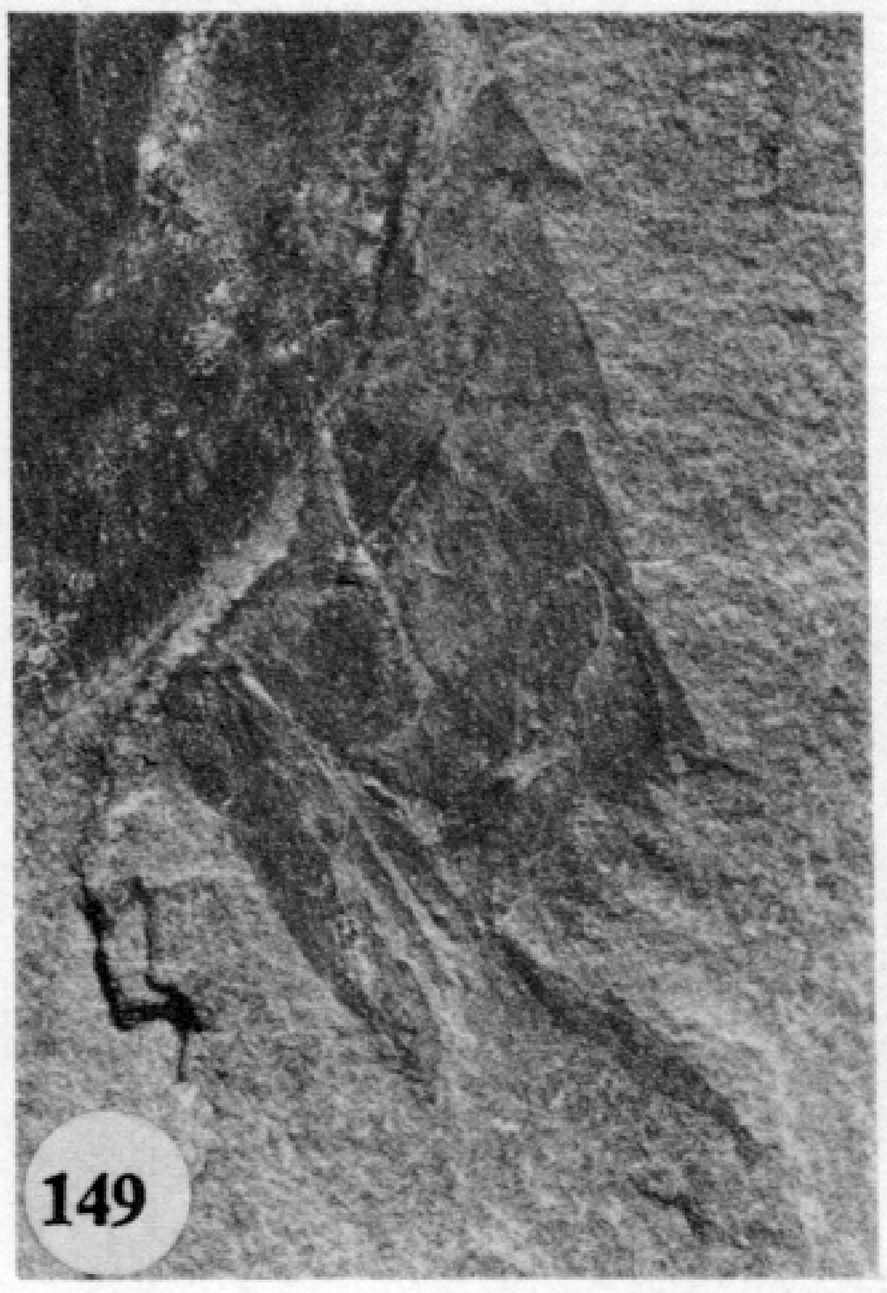

144

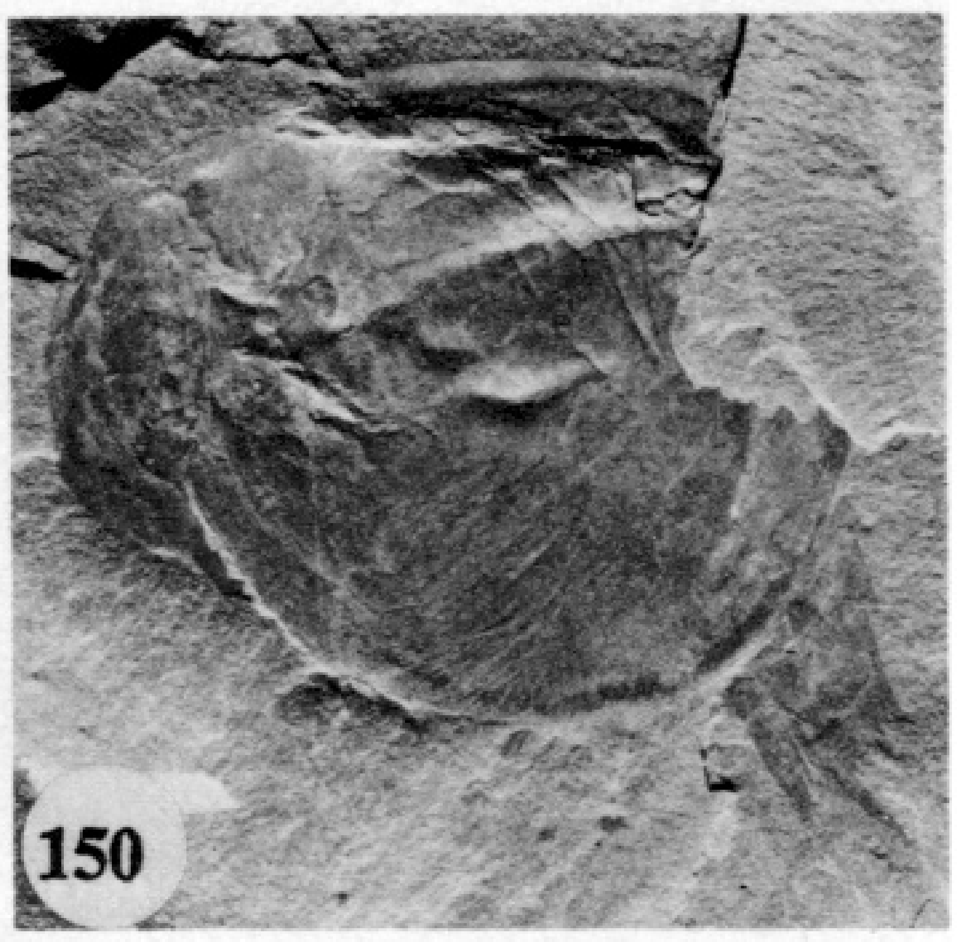

145


146

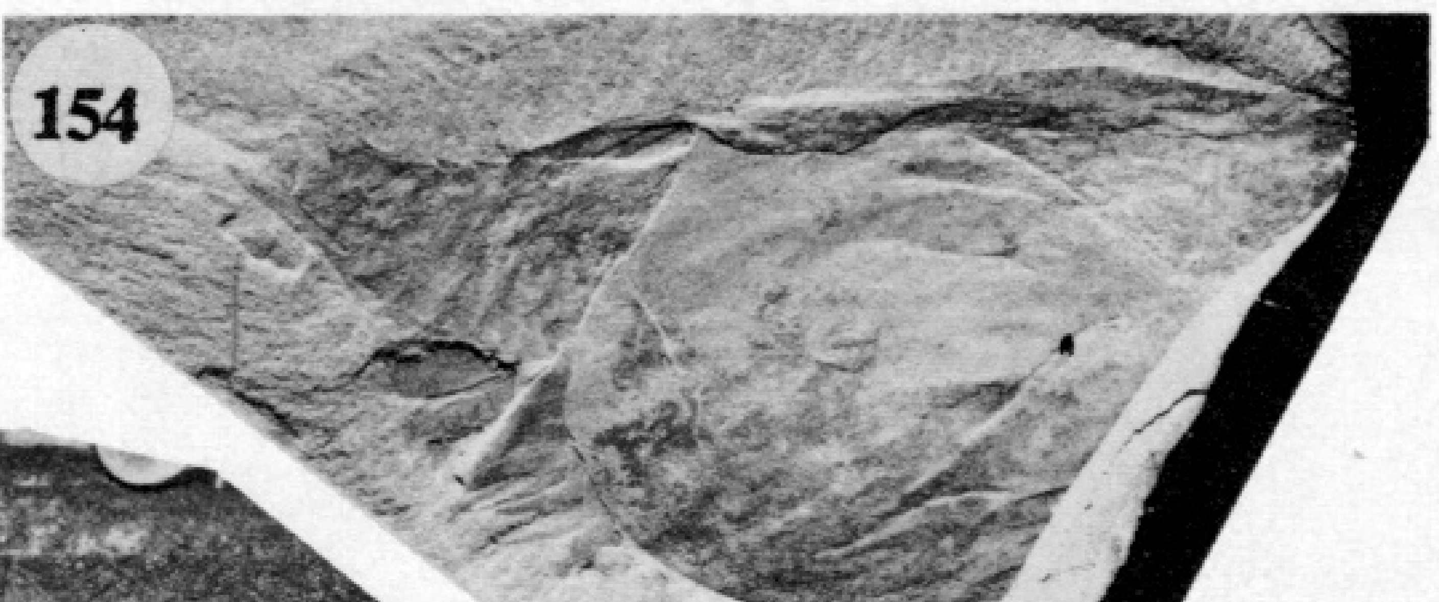

147


148


149

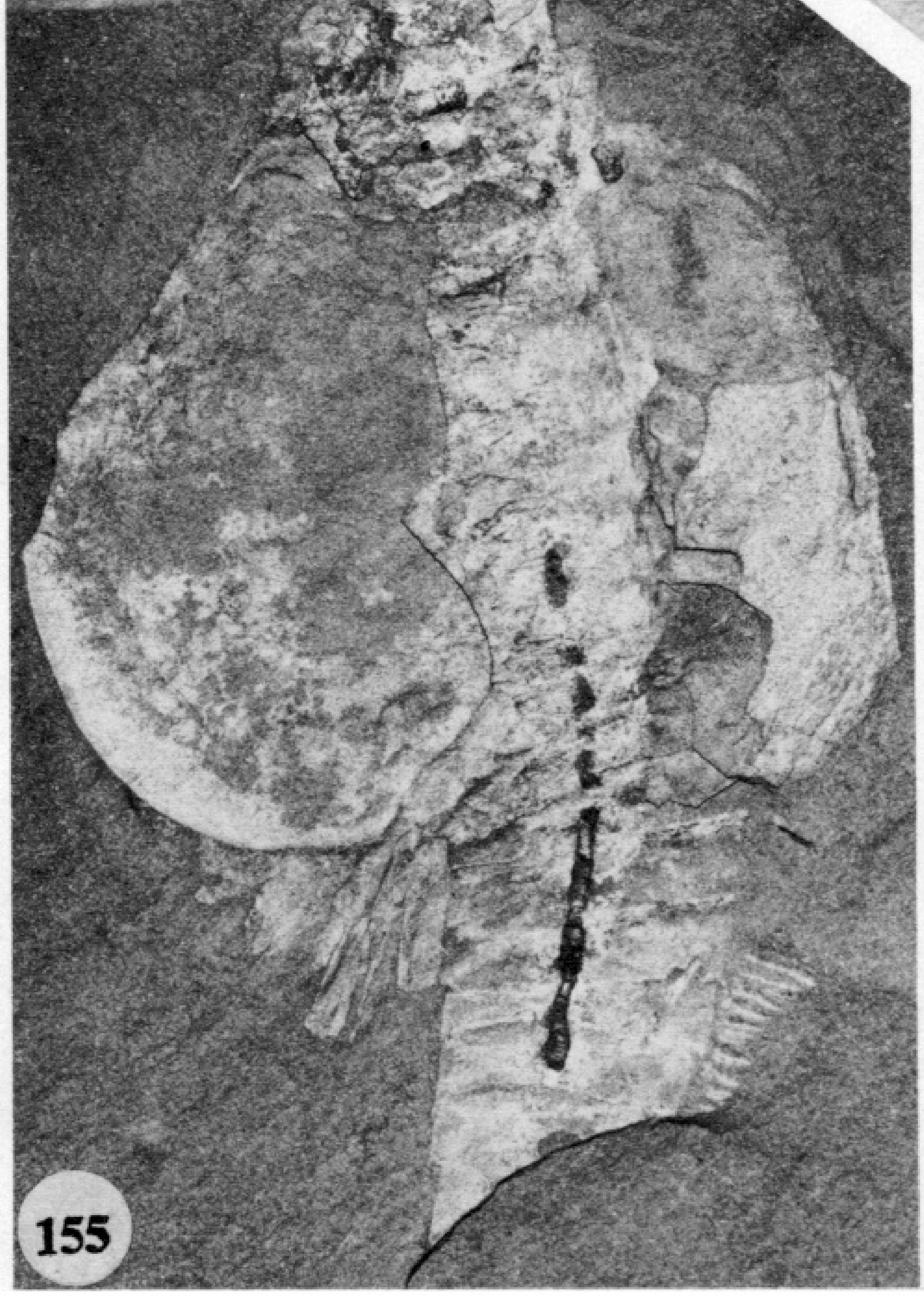

150

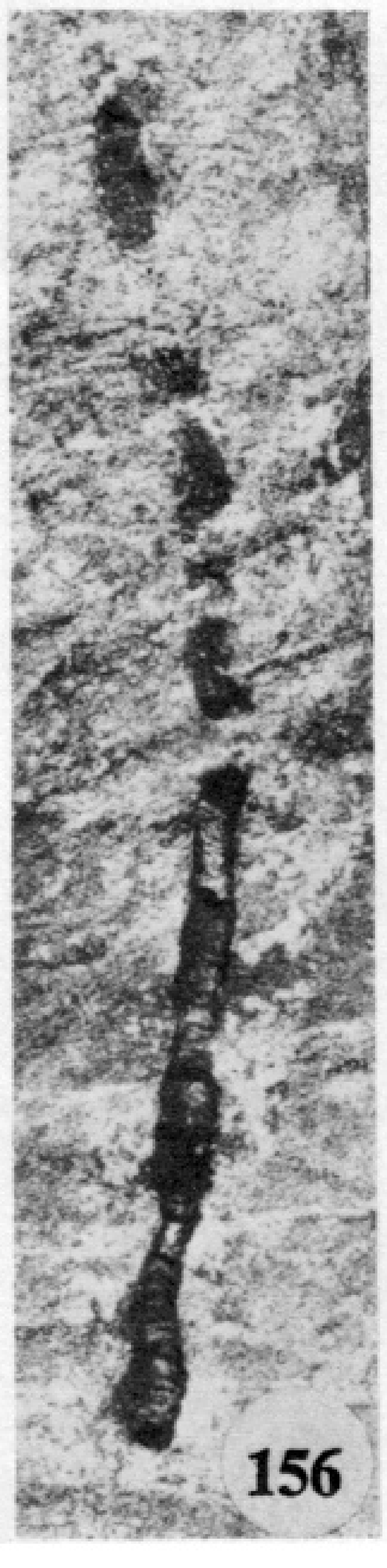

151

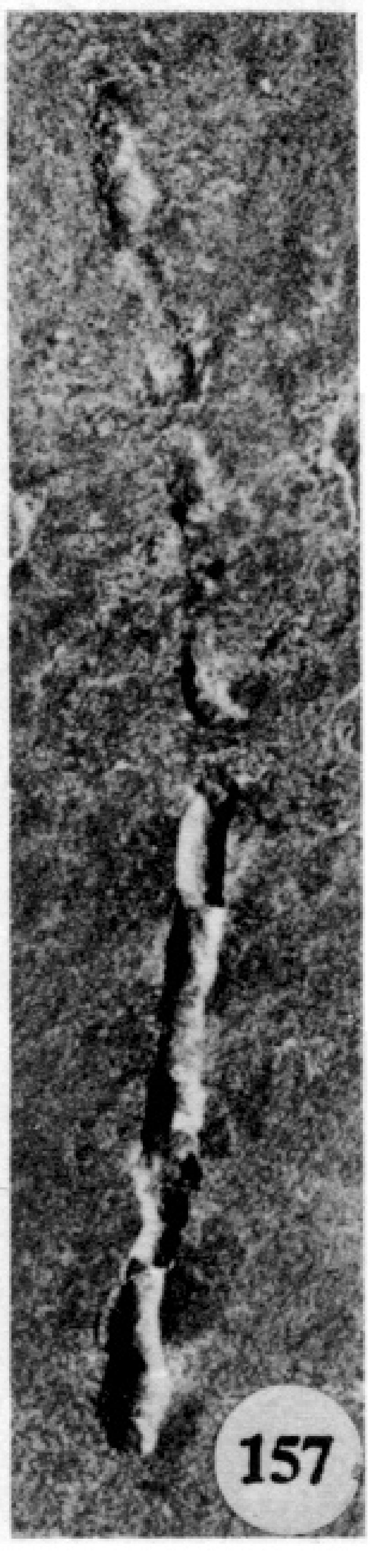

154


152


153


155


156

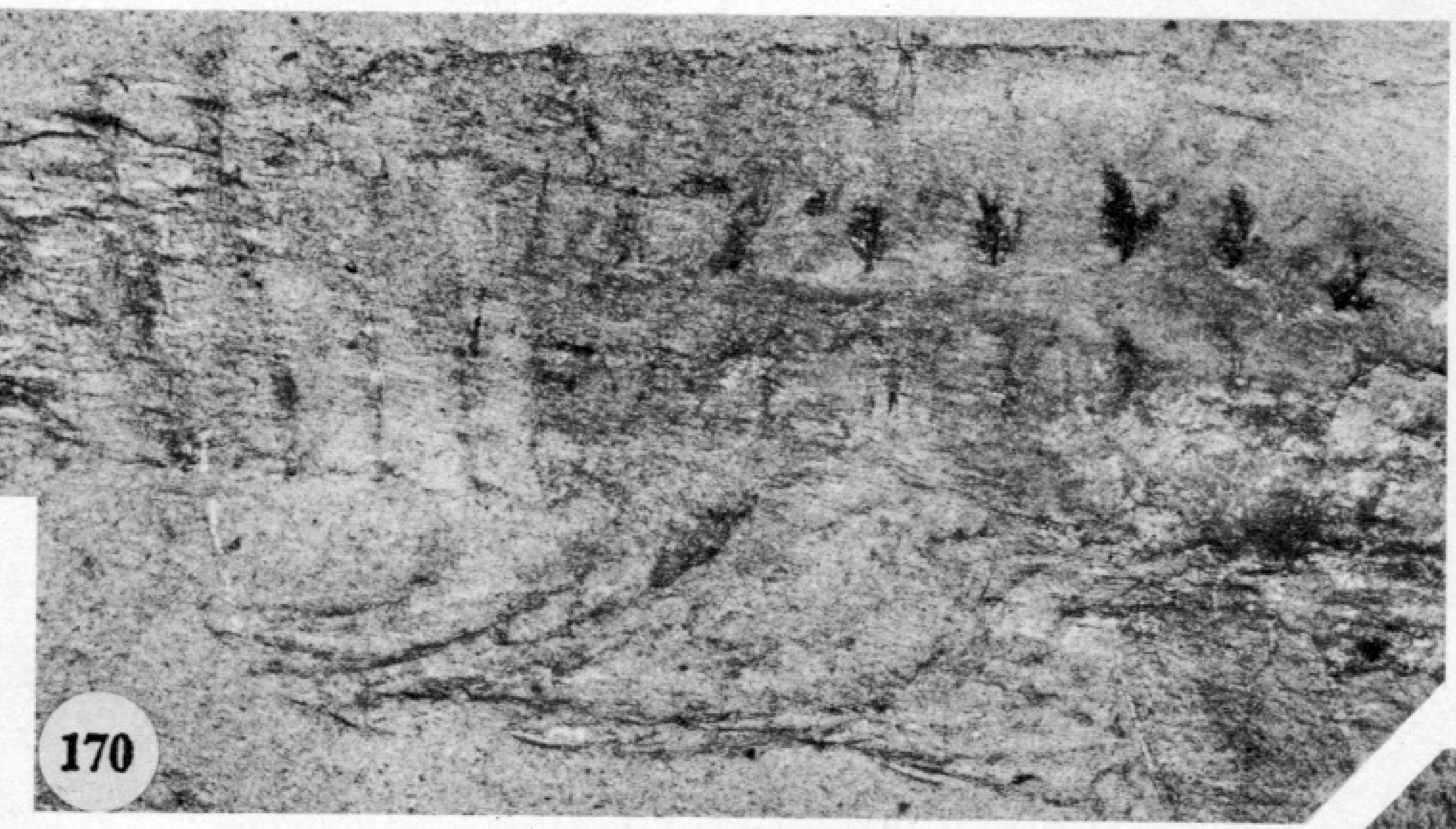

157

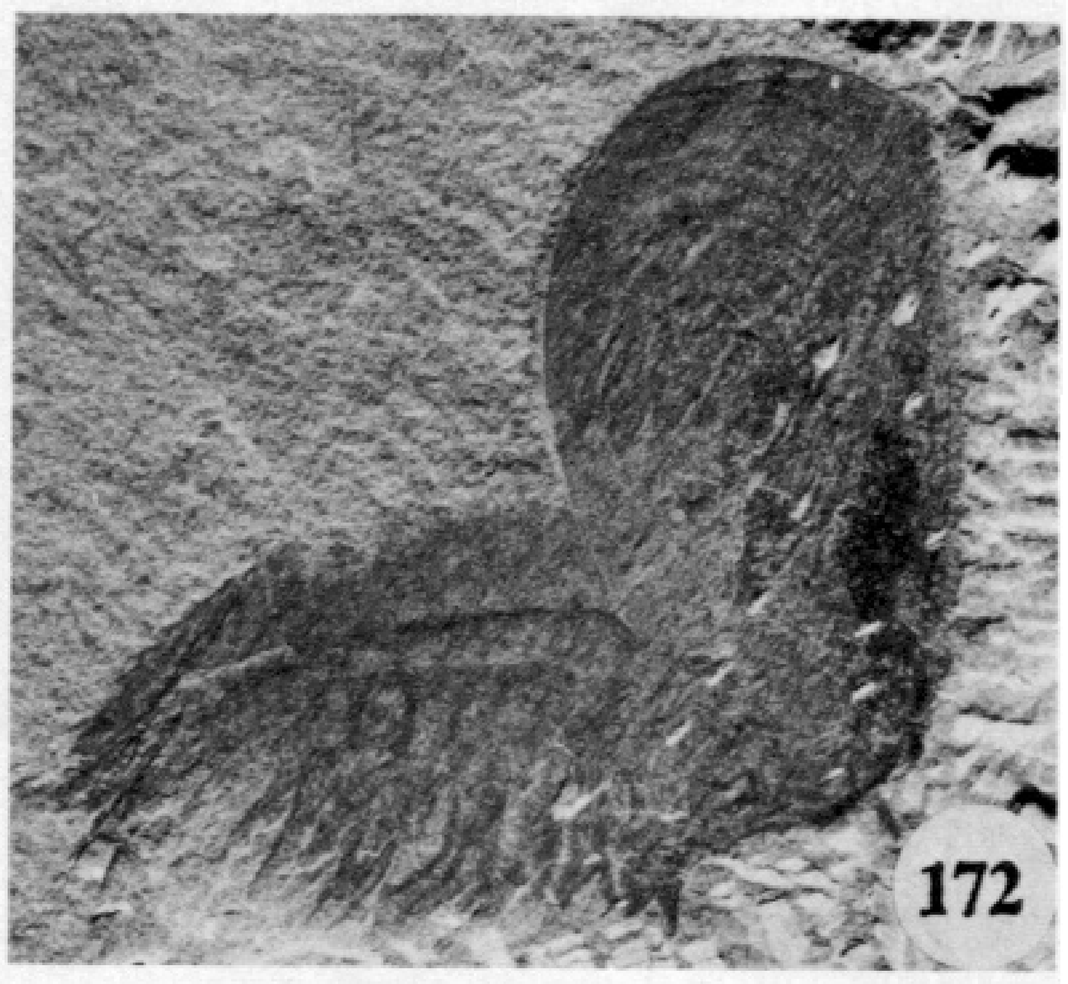

166


167

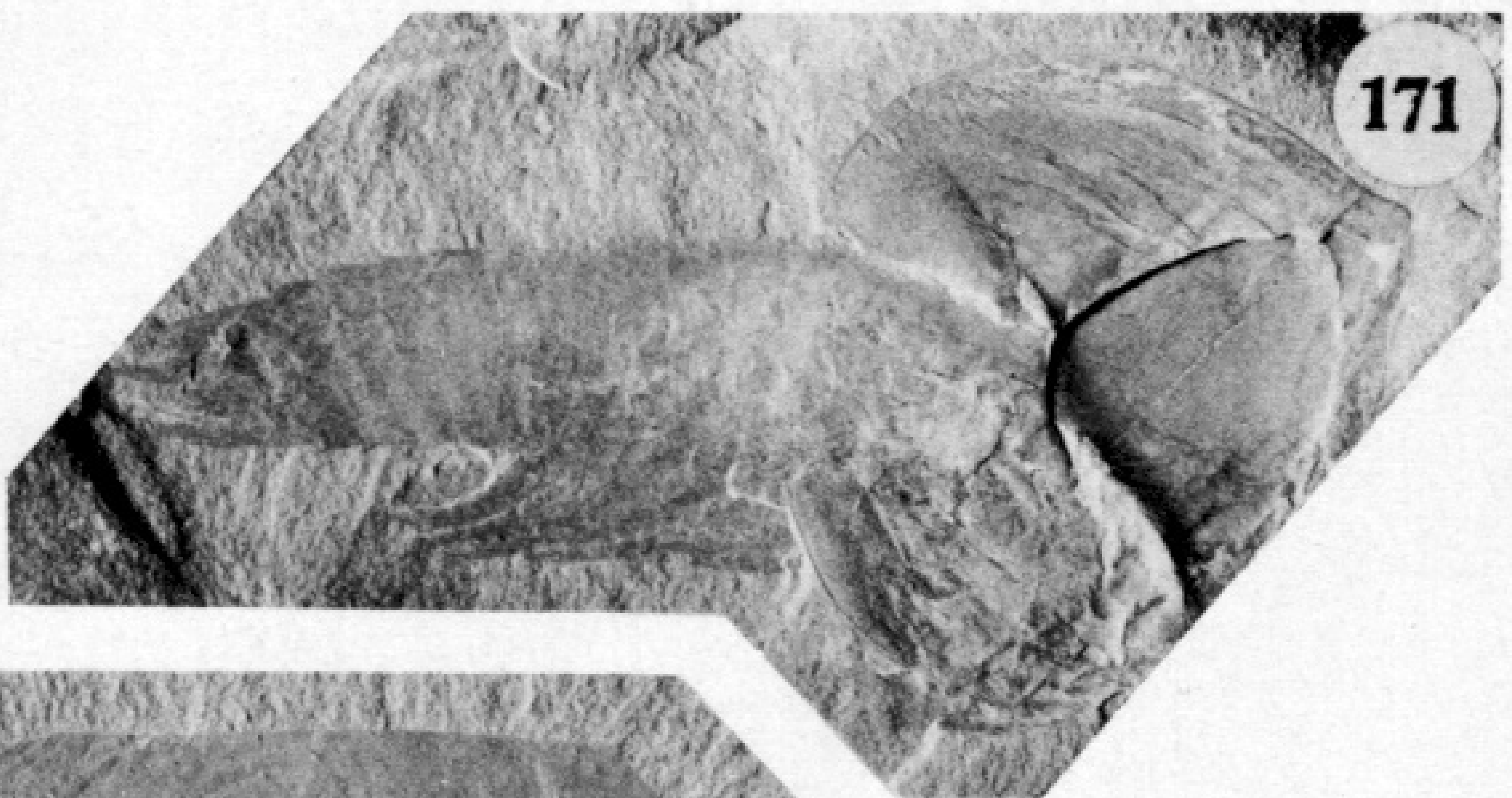

168

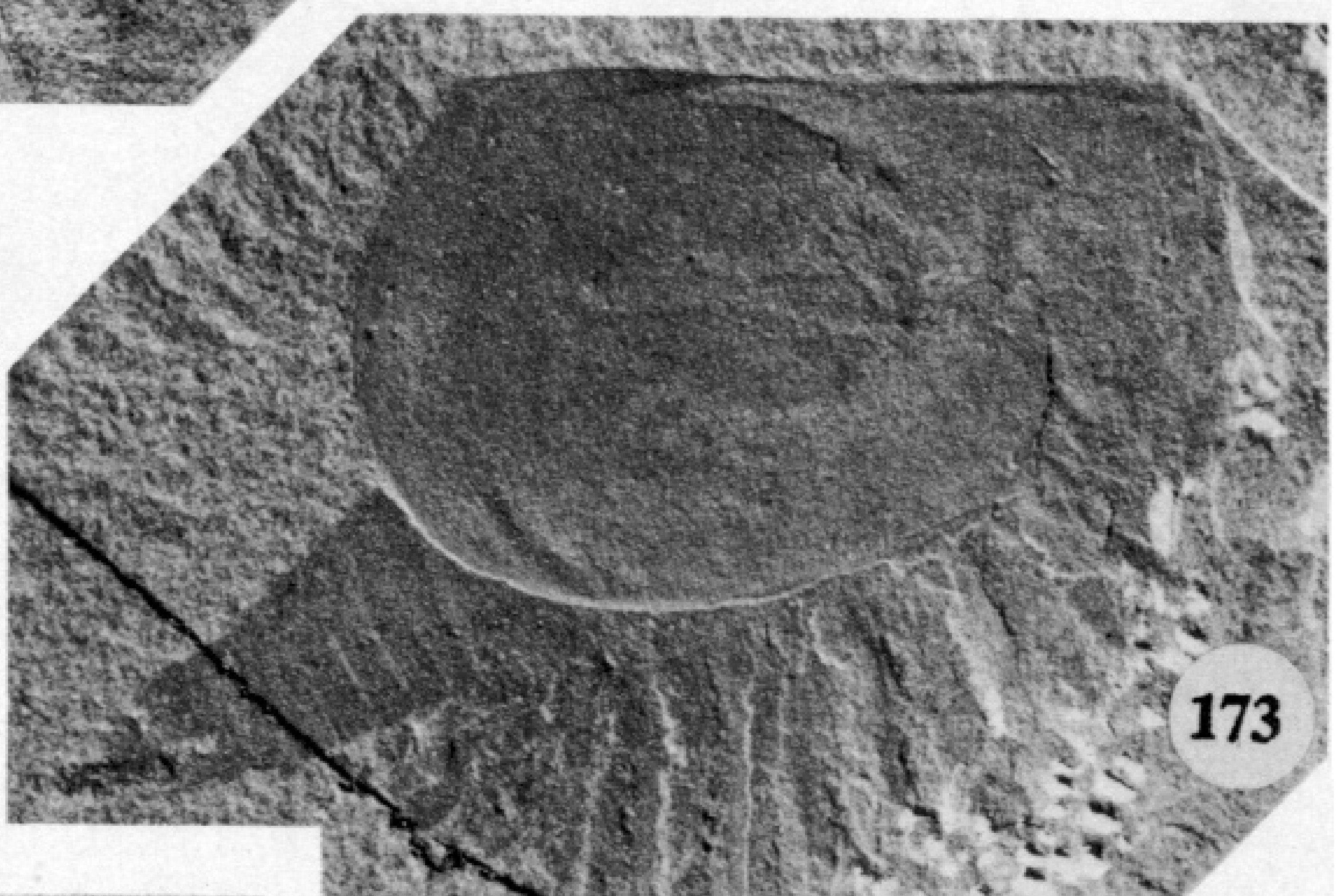

169

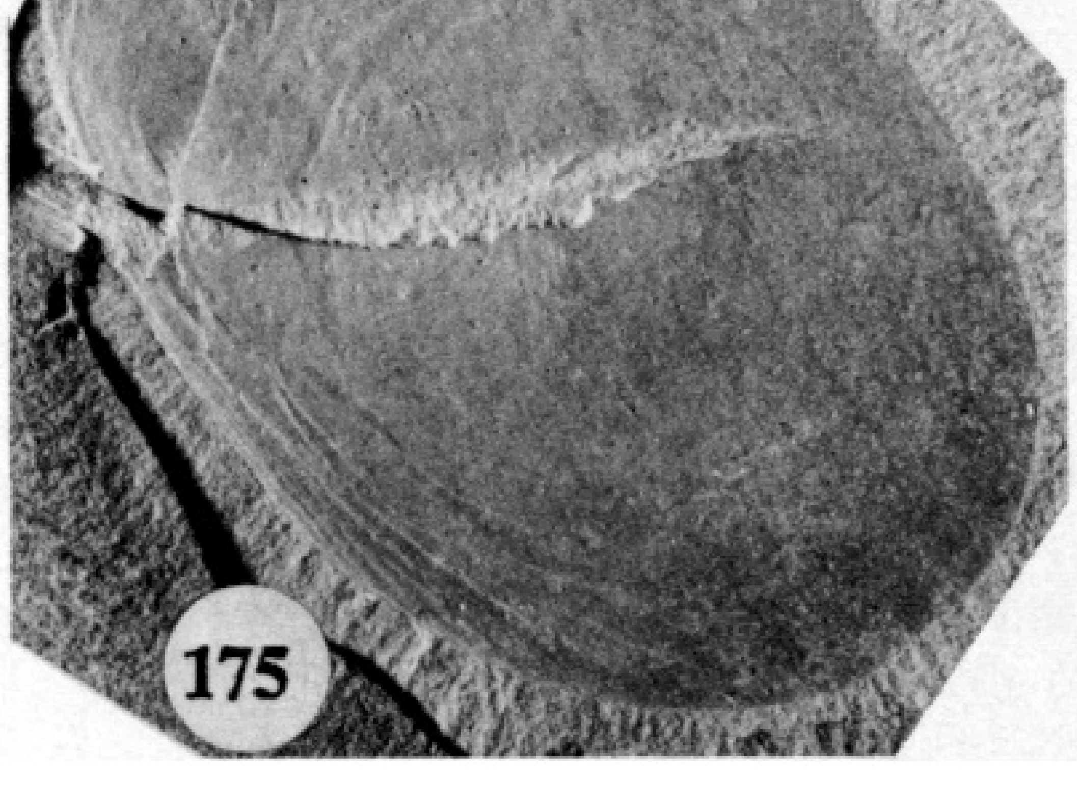

170

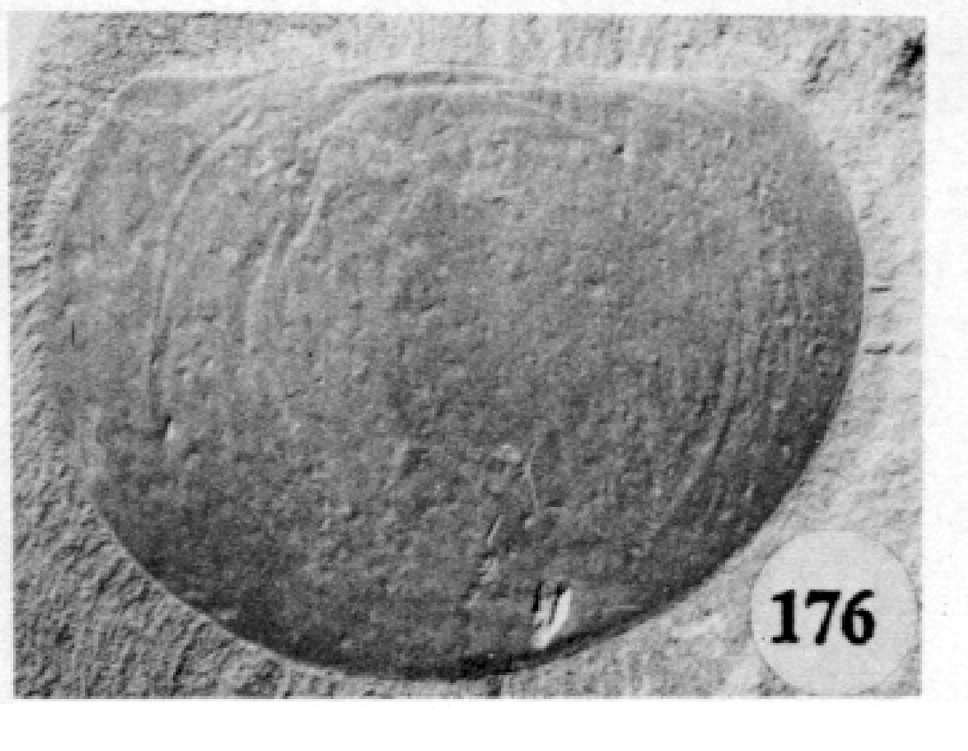

172


174


171


173


175


176