

THE MIDDLE CAMBRIAN METAZOAN *WIWAXIA*  
*CORRUGATA* (MATTHEW) FROM THE BURGESS  
SHALE AND *OGYGOPSIS* SHALE, BRITISH  
COLUMBIA, CANADA

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A detailed redescription of the Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) is given with the aid of photographs, mostly taken under ultraviolet radiation, and explanatory camera lucida drawings. *Wiwaxia* is known only from the Stephen Formation with four localities within the *Bathyriscus-Elrathina* Zone, the celebrated Burgess Shale (Phyllopod bed) and *Ogygopsis* Shale and two localities that appear to expose strata relatively high in the Formation, and a new locality in the underlying *Glossopleura* Zone. Specimens from the *Ogygopsis* Shale consist almost entirely of isolated sclerites, whereas in the Phyllopod bed the species is also known from entire specimens, semi-isolated assemblages and isolated soft-parts. The description here is based almost entirely on Phyllopod bed material.

*Wiwaxia* was originally largely covered by sclerites. On the basis of shape and arrangement five distinct zones are recognizable: dorsal, upper lateral, lower lateral, anterior and ventro-lateral. In addition, there was a row of elongate dorso-lateral spinose sclerites running along either side of the body. Each sclerite was inserted separately via a root-like structure. Growth of the animal appears to have occurred by moulting of the sclerites; one unique juvenile specimen appears to be preserved in the act of moulting. The ventral surface was apparently an area of soft tissue devoid of sclerites. Little is known of the internal anatomy, although anteriorly there was a feeding apparatus consisting of two rows of posteriorly directed teeth. Most stages of growth are known varying from presumed juveniles, which at their smallest may have lacked spines, to adults over 50 mm long. *Wiwaxia* appears to have been an epifaunal deposit feeder that crawled across the sea-bed, although smaller juveniles may have been infaunal. The dorso-lateral spines may have provided protection against predators and the existence of broken spines suggests the successful deterrence of attack.

The affinities of *Wiwaxia* do not appear to lie with the polychaetous annelids. While the possibilities of convergence cannot be eliminated, there appears to be a significant similarity between *Wiwaxia* and molluscs that suggests a related derivation from a turbellarian ancestor. Nevertheless, *Wiwaxia* has a distinctive bodyplan and as such cannot be accommodated in any known phylum. While *Wiwaxia* is unique to the Stephen Formation isolated sclerites from Lower Cambrian rocks appear to represent earlier wiwaxiids, although these sclerites show differences in their size and composition as compared with *Wiwaxia*.

*Wiwaxia* enhances knowledge of early metazoan evolution and ecology in the Cambrian. In particular, it gives fresh insights into the origin and relative success of certain metazoan bodyplans, the origin of trace fossils, and the importance of predation in Cambrian communities.

## 1. INTRODUCTION

In this paper a detailed description of the sclerite-covered metazoan *Wiwaxia corrugata* (Matthew) is given with the aid of photographs taken under ultraviolet radiation and detailed explanatory camera lucida drawings. This monospecific metazoan presently is known only from

five localities within the Middle Cambrian of British Columbia, although such a restricted range could be due more to its demonstrably low fossilization potential than an original geographical and possibly stratigraphical restriction. *Wiwaxia* was first described from the *Ogygopsis* Shale which is a richly fossiliferous horizon within the Stephen Formation (§3). At this locality the species is known almost entirely from isolated sclerites. As entire specimens with the original complement and disposition of sclerites preserved, it is best known from the Phyllopod bed of the Burgess Shale, another fossiliferous horizon within the Stephen Formation which is located about 5.7 km north of the *Ogygopsis* Shale. Recently, however, a newly discovered locality on Mount Stephen in the *Glossopleura* Zone of the Stephen Formation has yielded entire specimens of *Wiwaxia* (D. Collins, personal communication). My description is based almost entirely on some of the material from the Phyllopod bed, and only passing reference is made to specimens from the *Ogygopsis* Shale.

The Middle Cambrian Burgess Shale fauna, most of which is either soft-bodied or lightly skeletized, has been known for over 70 years, since its discovery in 1910 by Charles Doolittle Walcott who was then secretary of the Smithsonian Institution. In a series of papers published between 1910 and 1931 Walcott described a very large proportion of the fauna (and flora) but most of his descriptions, including that of *Wiwaxia* were of a preliminary nature and in some cases issued before his collections from the two quarries within the Burgess Shale were completed (Walcott's last season's excavation was 1917, together with some material collected in July 1919 (Walcott 1920, p. 364)). A much greater understanding of the diversity and importance of the fauna has become apparent during a series of systematic redescriptions that followed excavations of the Burgess Shale by the Geological Survey of Canada (G.S.C.) in 1966 and 1967 (Whittington 1971a). More recently (1975, 1981–84) collecting by the Royal Ontario Museum, Toronto, both from the talus beneath the quarries discarded by previous expeditions and from a number of other localities in the general vicinity, including the *Ogygopsis* Shale, has added further to our knowledge (Collins 1978; Collins *et al.* 1983).

In comparison with the wealth of soft-bodied and lightly skeletized forms, a relatively small fraction of the Burgess Shale fauna consists of 'typical' Cambrian animals with hard parts of either calcium carbonate or calcium phosphate. These animals include trilobites, hyolithids, monoplacophorans, brachiopods and rare echinoderms. Some of these well-skeletized species, such as certain trilobites (Whittington 1975a, 1980a) and brachiopods (Walcott 1924), have associated soft-parts, while the hyolithids may occur as articulated specimens with operculum and helens in place (Yochelson 1961; Runnegar 1981). Unlike the soft-bodied species, most of which are unique either to the Burgess Shale or immediately adjacent localities, those with hard-parts generally have a wide geographical distribution and sometimes substantial stratigraphic ranges in the Cambrian. It is surely significant that had the extraordinary conditions of fossilization been absent within the Burgess Shale, the surviving assemblage composed of animals with robust hard parts would be very similar in overall character to many other Cambrian faunas (Conway Morris 1981; Conway Morris & Robison 1982); indeed the impoverished assemblage of Burgess Shale shelly fossils bears a marked general resemblance to a reconstruction of a Cambrian community in a recent palaeoecological textbook (Cocks 1978, figure 2). It seems plausible that like the Burgess Shale many Cambrian faunas originally possessed a substantial and possibly dominant component of soft-bodied organisms, but the less favourable taphonomic conditions generally have made only a very impoverished cross-section of Cambrian life available to palaeontologists. The Burgess Shale fauna thus provides a special insight into the original diversity of Cambrian marine life. There are, however, a number of

other U.S. Cambrian deposits, such as Kinzers Formation (Resser & Howell 1938; Conway Morris 1977; Briggs 1978*a*, 1979); Spence Shale (Resser 1939; Robison 1969; Willoughby & Robison 1979; Conway Morris & Robison 1982); Wheeler Formation (Brooks & Caster 1956; Robison & Richards 1981; Conway Morris & Robison 1982) that have yielded compression fossils of soft-bodied and lightly skeletized animals. In no case does the diversity of these deposits rival the Burgess Shale, but systematic re-excavations (especially in the Kinzers Formation) may yield important new information. Significantly, some of the species present in both these American localities and other Cambrian units exposed in areas such as China, Spain and Australia are also known from the Burgess Shale. It seems plausible that the isolated sclerites, and possibly even articulated specimens, of *Wiwaxia* will be recognized eventually in other Cambrian rocks.

Advances in our understanding of the Burgess Shale mean that this remarkable fossil community is able to provide a unique cornerstone to study on the evolution of metazoans during the early Phanerozoic. In particular, the scientific importance of *Wiwaxia* extends into at least four areas, which are summarized here and dealt with more fully in §§11 and 12.

(i) The proposal that *Wiwaxia* was a polychaetous annelid (Walcott 1911, 1931; see also Jell 1981) is not consistent with its known anatomy. Earlier I mentioned briefly that *Wiwaxia* may be related to the molluscs (Conway Morris 1979*a*; Conway Morris & Whittington 1979); an idea based chiefly on the apparent similarity between its feeding apparatus and the molluscan radula (§9*g*). The relationships of *Wiwaxia* are discussed in §11, and it will suffice to note here that although *Wiwaxia* was not a mollusc it shows certain similarities that could indicate an evolutionary relation. If the resemblance between *Wiwaxia* and molluscs are of any significance then this may throw new light on the origin of the major bodyplans or phyla, most of which probably arose in the late Precambrian. A number of other enigmatic species within the Burgess Shale (Conway Morris 1979*a*; Conway Morris & Whittington 1979; Whittington 1980*b*) appear to represent novel, and even bizarre, bodyplans. The presently available information can only hint at the variety of forms, many of them apparently geologically short-lived, that must have evolved during the first great wave of metazoan diversification during the early Phanerozoic.

(ii) Bengtson & Missarzhevsky (1981) and Jell (1981) have suggested independently that a number of isolated Lower Cambrian sclerites (for example, *Halkieria*, *Sachites*, *Thambetolepis*) are related to *Wiwaxia*. Despite certain differences a relationship seems likely and is discussed briefly in §11*b* and at greater length elsewhere (Bengtson & Conway Morris 1984). Without the whole body specimens of *Wiwaxia* any reconstruction of the possible sclerite distribution in Lower Cambrian forms would be extremely difficult. Moreover, information on the soft-part anatomy in *Wiwaxia* greatly aids attempts to uncover the wider relationships of this group. Conversely, the uncompressed sclerites from the Lower Cambrian contain details of internal anatomy that are not readily apparent in the compression fossils of *Wiwaxia*.

The sclerites of *Halkieria* and its relatives are part of a distinctive assemblage of phosphatic and phosphatized microfossils that occur in the Lower Cambrian, especially the Tommotian stage (Matthews & Missarzhevsky 1975; Bengtson 1977). This assemblage, best known from richly fossiliferous sequences in Siberia, Mongolia and China, has attracted much attention because it represents the first abundant remains of hard-parts within the fossil record. The evolution of hard-parts is the most obvious aspect of a dramatic metazoan radiation that was initiated in the late Precambrian and rose exponentially until reaching a plateau of diversity

in the Middle Cambrian (Sepkoski 1978, 1979). Other Lower Cambrian fossils were also probably derived from the break-up of larger skeletons composed of sclerites (Bengtson 1970, 1977). Soft-bodied faunas within the Lower and Middle Cambrian may well contain articulated equivalents of some of these forms and so provide important evidence into their palaeobiology, palaeoecology and phylogenetic relations.

(iii) Although there is no direct evidence of what sort of trace *Wiwaxia* may have made while moving over the sediment, general considerations of its anatomy suggest that a crawling trace would be similar to certain late Precambrian and Cambrian trace fossils that have been ascribed to the activity of molluscs. Notwithstanding a possible relationship between *Wiwaxia* and molluscs, this reiterates the problem attendant upon attributing a trace fossil to a particular animal group.

(iv) *Wiwaxia* possessed elongate spines that probably acted to deter predators, a view supported by the existence of broken and damaged spines. Cambrian communities have traditionally been regarded as experiencing low or even negligible levels of predation. Such a view presumably has arisen because of the available evidence from species with hard parts, most of which appear to have been either deposit or suspension feeders. While early Cambrian communities may have possessed few predators, the Burgess Shale fauna, however, suggests that predation was significant and the indication of attack on specimens of *Wiwaxia* is only one of several lines of evidence, that otherwise include gut contents and the type of feeding apparatus.

## 2. HISTORY OF RESEARCH

*Wiwaxia corrugata* was originally described from an isolated spine by Matthew (1899) from the *Ogygopsis* Shale, the specimen being part of a collection made available to him by Byron E. Walker. In passing, it should be noted that in the earliest description of the *Ogygopsis* Shale fauna Rominger (1888, p. 19) mentioned 'the occurrence of a form of *Theca* or *Hyolithes* [*sic*], of the same appearance as *Theca primordialis*'. Hall's (1861, 1866) description of *Hyolithes primordialis* (see Sinclair 1946) does not show a striking resemblance to a spine of *Wiwaxia*. *Hyolithes* is, however, rare in the *Ogygopsis* Shale, and while Rominger may have had before him '*Selkirkia fragilis*' (Walcott 1908, 1911; Conway Morris 1977) it is conceivable that he was referring to *W. corrugata*. In his very brief description Matthew (1899) identified the holotype (figure 14, plate 1) as a new species of the hyolithid *Orthotheca* Novak 1886, *O. corrugata*, and he provided a line drawing that poorly represents the original specimen. The holotype had been missing for many years and requests by Walcott (letters 13 February and 3 March 1908) to W. A. Parks (University of Toronto) to borrow it were unsuccessful. In 1977, however, D. M. Rudkin (R.O.M.) relocated the holotype on a slab of shale in association with various trilobites. Walcott (1908, plate 1, figure 21) illustrated another specimen (figure 79, plate 7) from the *Ogygopsis* Shale, but it was his later collecting from the adjacent Burgess Shale that unequivocally demonstrated how the specimens previously identified as hyolithid tubes were in fact the elongate spines belonging to an animal with numerous additional sclerites. Walcott (1911) illustrated four specimens which are refigured here (figures 11–13, 15, plate 1; figures 24–26, plate 2; figures 145 and 146, plate 14; figures 6, 150) and placed this metazoan in the new genus *Wiwaxia*. With this discovery it was clear that no direct relation existed between *Wiwaxia* and *Orthotheca* or any other hyolithid. In his last and posthumous paper Walcott (1931) illustrated another specimen of *Wiwaxia* (figures 137–141, plate 14; figure 147), but added

nothing material to his original short description. During my restudy, which has stretched over several years, a number of preliminary statements have been made, in particular refuting the idea of a relation with the annelids and drawing attention to the possibility of an affinity with the Mollusca (Conway Morris 1979*a*; Conway Morris & Whittington 1979). A very brief description of this worm (Conway Morris 1982*a*) contains an error in that ventral sclerites were identified. This was based on a misinterpretation of 83938 (figures 137–140, plate 14; figure 147), to which further reference is made below. The ventral area appears to have been devoid of sclerites and exposed soft-tissue.

### 3. STRATIGRAPHY

Specimens of *Wiwaxia corrugata* are known from the Phyllopod bed of the Burgess Shale, the *Ogygopsis* Shale, and new localities on Mount Stephen (D. Collins, personal communication), Odaray Mountain and Park Mountain (Collins *et al.* 1983). The Phyllopod bed is exposed in the Walcott Quarry (U.S.N.M. locality 35k, Rasetti (1951) locality S11f), a small artificial excavation at an elevation of about 2286 m (7500 feet) on the west-facing slope of the ridge (Fossil Ridge) that runs between Mount Field and Wapta Mountain. The quarry is located about 5 km (3.1 miles) NNE of the town of Field. Walcott (1912*a*, 1928) gave a measured section of the Burgess Shale, the 2.31 m (7 feet, 7 inches) thick Phyllopod bed being located in unit h (or 6c) of the Burgess Shale, some 9–12 m (30–40 feet) above its base. The Phyllopod bed is located in the *Pagetia bootes* faunule of the *Bathyriscus–Elrathina* Zone (in part equivalent to *Ptychagnostus praecurrens* Zone, see Robison (1982), Middle Cambrian (Fritz 1971)). The *Ogygopsis* Shale (U.S.N.M. locality 14s, Rasetti (1951) locality S8d) is exposed over a relatively extensive area of the western shoulder of Mount Stephen at an elevation of about 2073 m (6800 feet), 2.5 km (1.6 miles) SE of Field. Exposures of bed-rock are uncommon and much of the mountain-side of this locality is covered with talus material (Walcott 1908; Rasetti 1951). Although a local stratigraphy of the dip-slope beds has been recognized (Deiss 1940), practically all the material collected from the *Ogygopsis* Shale comes from the highly fossiliferous loose blocks and no precise stratigraphic horizon can be identified. The *Ogygopsis* Shale is located in the *O. klotzi* faunule of the *Bathyriscus–Elrathina* Zone and is thus somewhat older than the Phyllopod bed (Fritz 1971). The new locality containing *Wiwaxia* (D. Collins, personal communication) was discovered on the western slopes of Mount Stephen by a R.O.M. expedition in 1981 (locality 9; Collins *et al.* 1983). *Wiwaxia* is a recent addition to the faunal list which already included a variety of soft-bodied and skeletized fossils. This fauna was originally believed to be more or less equivalent in age to those in the Burgess Shale (Collins *et al.* 1983), but the discovery of *in situ* *Glossopleura* (Trilobita) now indicates that this fauna belongs to the underlying and older *Glossopleura* Zone (D. Collins, personal communication). Other newly discovered sites with soft-part preservation include outcrops on Odaray and Park Mountains that have yielded thus far only isolated sclerites of *Wiwaxia* (localities 12 and 14; Collins *et al.* 1983). The strata at these localities appear to be younger than the Phyllopod bed.

Both the Burgess Shale and *Ogygopsis* Shale are informal stratigraphic units within the 'thick' Stephen Formation, and are recognized on account of their richly fossiliferous nature. Precise correlations within the 'thick' Stephen Formation are usually not possible, and the available biostratigraphy presently depends on trilobite zonation (Fritz 1971). The 'thick' Stephen Formation is composed of shales, silts and some limestones that were originally deposited as

a basal succession adjacent to a large algal reef. Debris flows were derived from the reef margin at various times of basinal infilling and adjacent to the Escarpment intertongue with the clastics. The source of the clastics is more speculative, but it is almost certain that they were not derived from the reef top (Aitken 1971).

The reef has been dolomitized and forms the 'thick' Cathedral Formation (McIlreath 1974, 1975, 1977; Aitken & McIlreath 1981). This reef had a precipitous scarp, now identified as the Cathedral Escarpment, that initially rose up to several hundred metres above the basin floor. Both the Burgess and *Ogygopsis* shales were deposited during a fairly early stage of basin infilling. By using trilobite zonation Fritz (1971) was able to demonstrate that the Burgess Shale accumulated in water approximately 150 m (490 feet) deep. It seems likely that the *Ogygopsis* Shale was deposited at a comparable or slightly greater depth, while the locality in the *Glossopleura* Zone represents an earlier stage of basin filling and presumably accumulated in yet deeper water. The localities in the higher section of the Stephen Formation exposed on Odaray and Park Mountains, however, presumably were deposited in somewhat shallower water. Sediments of the 'thick' Stephen Formation eventually smothered the reef so that clastic sedimentation spread over the reef top forming the 'thin' Stephen Formation (Fritz 1971). By connecting scattered outcrops of the reef-basin margin, now separated by tectonic faulting and erosion, it is possible to trace the Cathedral Escarpment over many kilometres in a northwesterly direction, although in the Middle Cambrian the low latitude scarp was probably aligned more east-west (Scotese *et al.* 1979).

#### 4. TERMINOLOGY

The terminology of Whittington (1975*b*) is used in discussing orientation. *Wiwaxia* was bilaterally symmetrical. The median dorso-ventral plane is *sagittal* and this plane contains the *longitudinal* axis. Planes parallel to, but outside, the sagittal plane are termed *exsagittal*. A direction away from the sagittal plane is *abaxial*, while towards this plane is *adaxial*. A vertical plane at right angles to the sagittal plane is *transverse*. *Ventral* and *dorsal* surfaces of the animal are identified on the reasonable assumption that the spines projected dorsally and were protective rather than being ventral and locomotory. The *anterior* is identified by the presence of the *feeding apparatus*. The body of *Wiwaxia* was largely covered with ribbed sclerites, each sclerite was inserted into the body wall by a single *root*. Two basic types of sclerite are distinguishable: elongate *spines* and more flattened *body sclerites*. Five zones or regions of imbricated sclerites have been recognized over the surface of the body according to their characteristic shapes; *dorsal*, *upper lateral*, *lower lateral*, *anterior* and *ventro-lateral*. The *dorso-lateral* spines arose from a narrow zone along either side of the body and curved dorsally and adaxially.

Specimens of *Wiwaxia* occur in four different ways: as *entire* individuals (for example, figures 11 and 12, plate 1; figure 6), *semi-isolated assemblages* (for example, figure 21, plate 2; figure 77, plate 7; figure 2), *isolated sclerites* (for example, figure 23, plate 2; figure 96, plate 9; figures 31 and 91), and very rare *isolated soft-parts* (figures 157–159, plate 15; figure 153) that are only identifiable by the possession of the feeding apparatus. Semi-isolated assemblages represent varying proportions of the original animal, from substantially intact to examples consisting of sclerites scattered over an area of shale and showing differing degrees of separation. The gradation in completeness between entire specimens and isolated sclerites appears to reflect both a history of moulting during individual growth and decay of corpses or disaggregation of exuviae (§6, 9*b*).

Entire specimens of *Wiwaxia* are preserved in a variety of orientations with respect to the plane of bedding (figure 1), such variation apparently resulting from the effects of turbulent transport and catastrophic burial in turbid mudflows (Whittington 1971a; Piper 1972). Specimens with the sagittal plane more or less at right angles to the bedding are termed *parallel* (for example, figures 11 and 12, plate 1; figure 44, plate 3; figures 93 and 94, plate 9; figures 115 and 116, plate 11; figure 134, plate 13; figures 137–140, plate 14; figures 6, 90, and 147) and in such cases the bilateral symmetry of the animal is most obvious. When the sagittal

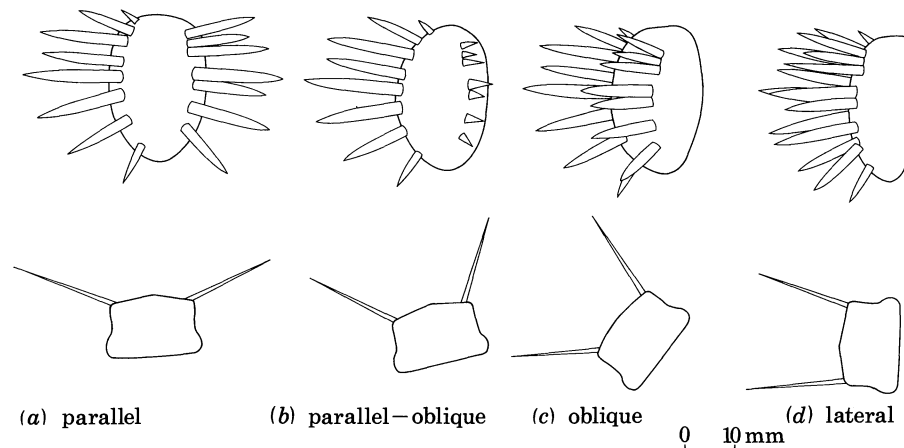


FIGURE 1. Diagrammatic illustration of the variable orientation of *Wiwaxia corrugata* (Matthew) in plan view (upper row) and uncompact transverse section (lower row) according to the angle of deposition with respect to the bedding plane. (a) Parallel, cf. figures 11 and 12, plate 1; figures 93 and 94, plate 9; figures 6 and 90; (b) parallel-oblique, cf. figures 74 and 75, plate 7; figures 110 and 111, plate 11; figures 72 and 108; (c) oblique, cf. figures 34, 35 and 37, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129; (d) lateral, cf. figures 64 and 65, plate 6; figures 82 and 83, plate 8; figures 70 and 88.

plane is effectively parallel to the bedding plane the specimen has a *lateral* orientation (for example, figures 64 and 65, plate 6; figures 82 and 83, plate 8; figures 70 and 88). *Oblique* specimens refer to intermediate cases where the sagittal plane is inclined at an appreciable angle to the bedding (for example, figure 16, plate 1; figures 34, 35 and 37, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129). Intermediate orientations of *parallel-oblique* (for example, figures 74 and 75, plate 7; figures 110 and 111, plate 11; figures 72 and 108) and *lateral-oblique* (figures 45–48, plate 4; figure 53) are also recognized. In these orientations the longitudinal axis is effectively parallel to the plane of bedding. More rarely the longitudinal axis lies at an angle to the bedding. A gentle inclination is apparent in *parallel-inclined* (figures 68 and 69, plate 6; figures 118–121, plate 12; figures 71 and 126) and *lateral-inclined* (figures 45–48, plate 4; figure 53) specimens. More steeply inclined specimens would be referred to as *subvertical*; 198668 appears to be sub-vertical (figures 8 and 9, plate 1; figure 5) but detailed examination reveals a more complex orientation with the longitudinal axis strongly curved so that the specimen is folded about an approximately median transverse plane more or less parallel to the bedding. No vertical specimens, that is longitudinal axis at right angles to the bedding, have been recognized. The scarcity of steeply inclined specimens is presumably due to their relative instability during transport and subsequent settling of the surrounding sediment. Overall, the shape of the body approximated to a flattened ellipsoid and together with the projecting spines ensured that in most cases burial was either



in an oblique or parallel orientation. Lateral specimens are less frequent, presumably because in this orientation stability was somewhat reduced. This lack of preference for a given orientation is in marked contrast to some species such as the arthropods *Marrella splendens* (Whittington 1971a) and *Sidneyia inexpectans* (Bruton 1981) where the anatomy favours a parallel disposition. Information on relative frequency of different orientations in other Burgess Shale species is given by Briggs (1978b, 1981a) and Conway Morris (1979b).

In common with other Burgess Shale organisms portions of a specimen adhere to either side of the split-open rock so that *part* and *counterpart* may be distinguished. The convention of recognizing part from counterpart in complete specimens follows Whittington (1975b). In parallel, oblique, inclined and subvertical specimens the side with the dorsal sclerites uppermost and the sclerite rows showing the original sense of imbrication is designated as the part. In lateral specimens the side with the anterior facing left is recognized as the part. In a number of cases only one side of a specimen is known and either the part (for example, figures 68 and 69, plate 6; figures 74 and 75, plate 7; figures 82 and 83, plate 8; figures 71, 72 and 88) or counterpart (for example, figures 64 and 65, plate 6; figures 93 and 94, plate 9; figures 110 and 111, plate 11; figures 79, 90 and 108) is missing. Among specimens of semi-isolated assemblages and isolated sclerites the part is chosen on the basis of completeness or superior preservation; if only one side is known it is automatically taken as the part. During collecting by the G.S.C. an effort was made to keep part and counterpart together as both are needed for a complete understanding of a specimen. Walcott, however, rarely kept the two halves together and sometimes they are found in different parts of the U.S.N.M. collection or even in other museums to which Walcott had sent material. In some cases one side of a specimen may never have been collected. The counterpart of a specimen of *Branchiocaris* was collected by the R.O.M. in loose scree below the quarries 45 years after the part was collected by Raymond's party (Collins 1978).

## 5. METHODS OF STUDY

From the available specimens, most of which are housed in the U.S.N.M., a selection were chosen for more detailed study. Specimens were examined under a binocular microscope. A percussion-hammer microdrill with an inserted needle was used to excavate either matrix or overlying parts of a specimen to reveal formerly concealed areas. On occasion thin films of calcite which obscured parts of a specimen were removed with dilute (*ca.* 3–5%) hydrochloric acid. This technique leaves the fossil unaffected, but as a precautionary measure the specimen was well rinsed. Where necessary specimens were drawn with the aid of a camera lucida attachment and these drawings are placed opposite the photographs of the specimens to show my interpretation. In some cases details of the counterpart (or part) have been transferred to the drawing of the part (or counterpart) by reversal so as to give a composite drawing. In most cases the drawings show more detail than is readily apparent in the photographs. This is because the specimens were photographed in directional radiation that inevitably fails to enhance some features. The drawings, however, were prepared by examining the specimens from several angles and under variable lighting conditions. In the drawings definite breaks in slope, which may be either natural or artificially produced by micro-drill excavation, are indicated by a line with hachures. The line proceeds along the top of the scarp and the hachures are directed downslope. Stippled areas represent matrix.

The holotype (figure 14, plate 1; figure 7) was photographed by D. M. Rudkin in ordinary

white light. The stereoscan electron micrographs of pyrite framboids (figures 39–41, plate 3) were taken from chips of fossil, coated with gold and examined on a Jeol TSM35. All other specimens were photographed in ultraviolet radiation from a directional lamp using panchromatic film. In the recent restudy of the Burgess Shale fauna ultraviolet radiation has been used routinely to photograph specimens, but it is interesting to note that over 50 years ago Ruedemann (1931) commented that ‘a study of the large quantity of [Burgess Shale] material now made available, with the new ultraviolet method, is most desirable’, although it is not clear whether Ruedemann ever pursued this suggestion. The specimens were photographed in either high- or low-angle radiation, the incidence accentuating different features (cf. figures 18 and 19, plate 2; figures 34 and 35, plate 3; figures 45–48, plate 4; figures 36–39, plate 5; figures 64, 65, 68 and 69, plate 6; figures 74 and 75, plate 7; figures 82 and 83, plate 8; figures 93 and 94, plate 9; figures 98–101, plate 10; figures 110 and 111, plate 11; figures 118–121, plate 12; figures 130 and 131, plate 13; figures 137–140, 145 and 146, plate 14; figures 154, 155, 157 and 158, plate 15). High-angle radiation reveals most clearly reflective areas within the fossil film. The steep scarps that connect different levels of a specimen appear as narrow dark (in shadow) or bright (reflective) lines according to direction of radiation. Low-angle radiation tends to accentuate the specimen as a whole against the matrix and generally less internal detail is visible.

In high-angle radiation the lamp was inclined to the specimen table at about 65° to the horizontal and centred on the specimen, which was then tilted through about 15° towards the lamp until maximum reflectivity (seen as a purplish glow) was observed through the focusing tube. In low-angle radiation the lamp was set at about 30° to the horizontal and the specimen placed level. Before exposure focusing was undertaken in white light. Explanation of plate-figures is as follows: depository and specimen number; part or counterpart; orientation of specimen; brief description; nature and direction of radiation, the top of the page being north; magnification and any additional comments. For the sake of brevity depository abbreviations are not used in the text itself.

## 6. PRESERVATION

### (a) *Setting of the Burgess and Ogygopsis shales*

Evidence presented below suggests that *Wiwaxia* was a benthic organism for most, and perhaps all of, its life. The benthic component of the Burgess Shale fauna appears to have inhabited the silts and muds, now forming part of the ‘thick’ Stephen Formation, that accumulated in relatively deep water immediately beside the foot of the large algal reef, now part of the ‘thick’ Cathedral Formation. Features of both the sediments, such as graded bedding (Piper 1972), and the enclosed fossils, for example, their variable orientation with respect to the bedding plane and seepage of sediment between the various parts of appendiculate species (Whittington 1971a) indicate that the sea floor on which *Wiwaxia* and other Burgess Shale organisms lived periodically slumped down-slope to be re-deposited as a sequence of turbidites which are exposed in the Walcott Quarry as the Phyllopod bed. Each turbidite is thus interpreted as a separate event that involved the slumping of a discrete area of sea-bed. The Phyllopod bed may contain in excess of 50 turbidite layers, implying an equivalent number of sediment influxes. The frequency of turbidite deposition is not known, but the Phyllopod bed may have accumulated in a relatively short period, perhaps a few hundred years. Such

a history of transport makes it necessary to distinguish a pre-slide environment, where the fauna lived and evidently flourished, and downslope a deeper post-slide environment (the Phyllopod bed) where the fauna was buried under more inimical conditions (Conway Morris 1979*a, b*). While the location of the post-slide environment is thus obvious, the exact position of the pre-slide environment is not certain, although almost certainly it was beside the base of the reef. The principal reason for identifying such a position is that other richly fossiliferous faunas, including the *Ogygopsis* Shale, invariably occur adjacent to the reef front at various other localities along the Cathedral Escarpment (McIlreath 1975; Aitken & McIlreath 1981). It appears that the sea-bed sloped downwards away from the reef, and at each of these localities an abundance of fossils does not extend for any appreciable distance away from the reef. This marked decline in fossil content means that most of the off-reef basinal sediments are unfossiliferous. The restriction of prolific faunas to a zone along the reef front argues for a favourable environment allowing benthic faunas to flourish, whereas more hostile conditions prevailing in the deeper water generally discouraged or even excluded benthic metazoan life. Such a contrast could have arisen if the deeper waters of the basin were anoxic and poisoned with H<sub>2</sub>S that extended for some distance above the sediment–water interface. Perhaps the sediments adjacent to the reef were piled up so as to project into slightly shallower water where oxygenated conditions above the zone of H<sub>2</sub>S permitted metazoan life. In this model the pre-slide environment of the Burgess Shale (Phyllopod bed) would have occupied some area within the oxygenated environment, whereas the post-slide environment lay in the deeper, anoxic water. It appears therefore, that both the pre-slide and post-slide environments were located beside the reef. This implies that the turbidity currents must have flowed parallel to the reef front, rather than following the general palaeoslope of the sea-bed away from the reef. Meagre palaeocurrent indicators within the Phyllopod bed (Piper 1972) support this interpretation.

There is reason to believe that the turbidity currents arose in the pre-slide environment itself, rather than originating elsewhere and sweeping up the fauna during their progress downslope. One piece of evidence to support this notion is the presence of numerous priapulid worms which are interpreted as infaunal burrowers (Conway Morris 1977). Their mode of life indicates that the turbidity currents would have had to have been exceptionally vigorous to erode significantly the sea-floor and incorporate these worms into the flows. Although the turbidity currents were evidently turbulent (see below), the lack of abrasion and dismemberment points to a relatively gentle flow. It is thus supposed that *in situ* slumping carried both the infaunal worms and a wide array of epifaunal and nektobenthic species to the post-slide environment. No detailed sedimentological study of the *Ogygopsis* Shale has been undertaken, so it is not clear whether it too owes its origin in part or completely to a series of turbidity flows. cursory examination of this deposit indicates that transport of the fossils may have been more restricted, with burial arising from a combination of weak traction currents and vertical hemipelagic fall-out, although Briggs & Mount (1982) indicated that the fauna may have been transported. Unlike the Burgess Shale the prolific nature of this fauna is largely due to shelly fossils, especially the exuviae of trilobites together with less abundant brachiopods, hyolithids and monoplacophorans, whereas soft-part preservation is generally more restricted. One explanation for this could be that the original *Ogygopsis* Shale community was dominated by shelly species, unlike the Burgess Shale where they appear to have formed a very low proportion of the standing crop of the living community (Conway Morris 1981). There are indications, however, that this is at best only a partial explanation and that some soft-bodied species were originally present. For example,

the arthropod *Marrella splendens* is known from an estimated 15000 specimens in the Burgess Shale, whereas only two examples are known from the *Ogygopsis* Shale (Whittington 1971b; Collins *et al.* 1983). Such scarcity might be more a result of selective preservation rather than original rarity. More significantly, the tubicolous priapulid *Selkirkia columbia* has been recorded from both localities (Conway Morris 1977), but only in the Burgess Shale are the soft parts known, whereas in the *Ogygopsis* Shale the species invariably occurs as vacated tubes that were evidently more resistant to rotting. The occurrence of *Wiwaxia* in the *Ogygopsis* Shale as isolated sclerites, with only one example of a semi-isolated assemblage and no entire specimens known, is also suggestive of unfavourable conditions for soft-part preservation, which may have included an absence of episodes of rapid and catastrophic burial. The more drastic taphonomic history in the *Ogygopsis* Shale inevitably places a bias on any comparison with the Burgess Shale fauna. There would appear to be both significant differences, as well as an intriguing similarity arising from the joint occurrence of *Wiwaxia*. In terms of a comparison between shelly components the absence of the trilobite *Ogygopsis klotzi* from the Burgess Shale stands in contrast with its great abundance in the *Ogygopsis* Shale (Rasetti 1951; Briggs & Mount 1982). This contrast in the trilobite assemblages extends to other species, with about eight unique to the *Ogygopsis* Shale, nine unique to the Burgess Shale, and only seven in common (see Rasetti 1951). The genus *Ogygopsis*, however, is of particular interest as it has a long stratigraphic range from the Lower to Middle Cambrian, combined with a localized and sporadic distribution that would appear to indicate a preference for a specific set of environmental conditions (Rasetti 1951; Nelson 1963; Fritz 1970; Palmer & Halley 1979; Briggs & Mount 1982). Exactly what these conditions were remains speculative, but some authors (Nelson 1963; Palmer & Halley 1979) regard either proximity to the open ocean or bathymetric control, or both, as being significant. Nevertheless, the presence of *Wiwaxia* (and certain other species) in both the *Ogygopsis* Shale and Burgess Shale indicates that whatever environmental differences existed between these two deposits appear not to have influenced this animal. It may also be significant that *Wiwaxia* has neither been recorded from the Burgess Shale beds exposed in the higher Raymond Quarry, which yields a largely soft-bodied fauna of different aspect to that of the Phyllopod bed (Conway Morris 1979c) nor in most of the other soft-bodied localities recently discovered adjacent to the Cathedral Escarpment (Collins *et al.* 1983). Virtually no palaeoecological information is available yet on the three new localities that have yielded *Wiwaxia* (Collins *et al.* 1983; D. Collins, personal communication).

(b) *Preservation of Wiwaxia*

As noted in §4 fossils of *Wiwaxia* may occur as entire specimens, semi-isolated assemblages, isolated sclerites and isolated soft-parts. The estimated numbers of specimens in the Burgess Shale (Phyllopod bed) of these four modes of preservation are given in table 1. In the *Ogygopsis*

TABLE 1. ESTIMATES OF THE NUMBER OF SPECIMENS OF *WIWAXIA CORRUGATA* IN DIFFERENT TYPES OF PRESERVATION

entire specimens	138
semi-isolated assemblages	20
isolated sclerites	718
isolated soft-parts	2

Practically all specimens are in the U.S.N.M. and G.S.C. These figures have been corrected for probable disassociation of parts from counterparts, see Conway Morris (1981) for further details.

Shale *Wiwaxia* occurs almost entirely as isolated sclerites, with only one example of a semi-isolated assemblage known (Collins *et al.* 1983). The absence of entire specimens was discussed above and was linked to the conditions for soft-part fossilization being relatively less conducive than in the Burgess Shale. Although no accurate count exist for the *Ogygopsis* Shale specimens, my impression is that spinose sclerites predominate and the first two specimens to be illustrated (Matthew 1899, plate 1, figure 3; Walcott 1908, plate 1, figure 12) both fall into this category. The bias towards the spines has several possible explanations, but it is suggested that as the spines were somewhat more massive and robust than the other sclerites they were more resistant to decay and so favoured during the processes of fossilization. In contrast the numbers of different types of isolated sclerites in the Burgess Shale seem to be roughly in proportion to their original values.

The rest of this section considers only the Burgess Shale (Phyllopod bed) specimens. The variation in preservational style is interpreted as a reflection of both moulting during the life of the animal, its subsequent death, whether by predation or natural causes, and any decay and scavenging that took place in either the pre- or post-slide environment. It seems reasonable to suppose that the pre-slide environment differed little from most other sea-beds with a benthic community, in that processes of microbial decay were reasonably rapid. In addition, a number of species within the Burgess Shale (Phyllopod bed) have been identified with varying degrees of certainty as scavengers, and they too would have contributed to the destruction of organic material, especially soft-tissues. The net result of these processes would have been the continued accumulation of the more resistant, generally shelly, remains in the sediments of the pre-slide environment. It seems reasonable to conclude, therefore, that entire specimens of *Wiwaxia*, together with complete specimens with soft-parts of other species, must have been alive at the time of slumping because any animal that died in the pre-slide environment would have quickly disintegrated. Hence, the specimens of isolated sclerites, isolated soft-parts and most of the semi-isolated assemblages appear to have formed in the pre-slide environment, but their mode of origin is not certain. Evidence given in §9*b* suggests that as *Wiwaxia* moulted its sclerites several times during its ontogeny it is likely that some of the semi-isolated assemblages and isolated sclerites represent exuviae discarded by the growing animal. In other cases, however, death of the individual may have been responsible for such specimens. Upon death the body of *Wiwaxia*, which may already have been dismembered by a predator, would quickly disintegrate to give semi-isolated assemblages and ultimately a large number of scattered, isolated sclerites. On occasion intact fragments of the soft-parts also drifted free, although such specimens are only now recognizable when the feeding apparatus is attached. Isolated soft-parts presumably only formed by disintegration of a corpse, but among the majority of semi-isolated assemblages (for example, figure 21, plate 2; figure 77, plate 7; figure 87, plate 8; figure 117, plate 11; figures 145 and 146, plate 14; figures 154 and 155, plate 15; figures 29, 150 and 151) and isolated sclerites there appear to be no reliable criteria to distinguish specimens produced by moulting as against death.

The survival time of isolated soft-parts in the pre-slide environment was probably short, and the rare examples (table 1) presumably were released during rotting and came to lie on an area of sea-bed that soon slumped into the post-slide environment. The sclerites do not appear to have been mineralized (§9*b*), but were presumably composed of a relatively tough material that rendered them moderately resistant to decay and so prolonged their residence time in the pre-slide environment sediments, although presumably not to the same extent as the more

robust and durable shelly remains of the trilobites, brachiopods, monoplacophorans and hyolithids. Evidence that the sclerites were not entirely immune to destruction comes from several sources: (i) most of the isolated sclerites are complete and often have the root present (figure 23, plate 2; figure 78, plate 7; figure 96, plate 9; figure 104, plate 10; figure 114, plate 11; figure 125, plate 12; figure 143, plate 14; figures 31, 73, 91, 107, 109, 128 and 147), while the few incomplete examples may show a tattered and frayed proximal margin (figure 38, plate 3; figure 50, plate 4; figure 97, plate 9; figure 124, plate 12; figures 33 and 92) that appears to have resulted from decay; (ii) disintegration or moulting of an entire, average-sized specimen of *Wiwaxia* would release over 150 sclerites. In view of the relative abundance of entire specimens (table 1), the comparatively low numbers of isolated sclerites is consistent with only a moderate residence time in the sediment. This conclusion is tentative because there may have been some collector bias in favour of entire specimens as against isolated sclerites. Some support for this latter view comes from the relative proportions between entire specimens and isolated sclerites in the U.S.N.M. and G.S.C. collections; estimated ratios are approximately 1:4 and 1:19 respectively. G.S.C. collecting may have been more thorough, and the U.S.N.M. collection could be biased against isolated sclerites. (iii) The lack of *Wiwaxia* sclerites in some other Middle Cambrian rocks, while in part original, may also be attributed to generally less favourable conditions of preservation. Nevertheless, scattered records of soft-bodied and lightly skeletized Cambrian fossils, including species otherwise known from the Burgess Shale (§1) suggest that at least the isolated sclerites of *Wiwaxia* may ultimately be recognized. Lower Cambrian sclerites with mineralized walls that appear to be related to *Wiwaxia* are discussed in §11*b*.

The turbidites that swept towards the post-slide environment are envisaged as carrying live individuals of *Wiwaxia* and incomplete material that probably arose both by moulting and post-mortem disintegration. There is reason to think that death of the entire specimens occurred either during transport or very shortly after burial; had the fauna arrived alive in the post-slide environment it seems that some species, especially the burrowing infaunal priapulids (Conway Morris 1977), would have produced the beginnings of an escape trace. No such traces have been observed and the absence of bioturbation is reflected in the unbroken sedimentary laminations of the Phyllopod bed. Although the post-slide environment was apparently anoxic, experiments with modern crustaceans and polychaetes stored in anoxic sediment for almost two months (Dean *et al.* 1964) demonstrate that they coil tightly and enter metabolic stasis. Such coiling is not a feature of the Burgess Shale organisms and is additional evidence that death may have occurred at an early stage, but the reason for mortality is not clear. Transport in a turbidity current may not have been responsible because although evidently turbulent there is a general lack of abrasion or disarticulation in the specimens. The estimated vertical displacement between the pre- and post-slide environments (*ca.* 90 m, Conway Morris 1979*b*) suggests that the slight change in water pressure (*ca.* 9 atmospheres, 912 kPa) would not have been instrumental in killing the organisms. Another suggestion is that a difference in water temperature, perhaps in the form of a thermocline, was responsible for the demise of the animals by thermal shock (Conway Morris 1979*b*). Upon settling from the turbulent suspension entire specimens came to lie at a variety of angles (figure 1), although the smaller isolated sclerites and semi-isolated assemblages generally adopted a more or less stable position parallel to the bedding.

The inimical conditions of the post-slide environment evidently excluded metazoan scavengers,

but evidence for limited decay has been documented for many Burgess Shale species (see Conway Morris 1979*a-c*), and is attributed to the activities of anaerobic bacteria. Evidence for slight decay is seen in some entire specimens of *Wiwaxia*. For example, in 198669 (figures 118–121, plate 12; figure 126) a gap in the sclerite covering on the anterior left-hand side together with rotation of an adjacent ventrolateral sclerite through approximately 180° may have been caused by rotting. Rotation of ventro-lateral sclerites so that they are directed ventrally in 198681 (figures 82 and 83, plate 8; figure 88) could also be due to decay loosening the tissues of basal attachment; a similar feature has been observed in a number of other specimens. Entire specimens practically never show any scattering of sclerites around the body, and the isolated sclerite beside 198680 (figure 47, plate 4; figure 53) is regarded as a fortuitous association. This style of preservation is in contrast to the polychaete worms *Canadia spinosa* and *Burgessochaeta setigera* where a number of specimens show detached setae, sometimes strewn around the body (Walcott 1931; Conway Morris 1979*b*). With few exceptions (figures 68 and 69, plate 6; figure 71) entire specimens lack a dark stain that characterizes a number of species, especially *Marrella splendens* (Whittington 1971*a, b*), other arthropods such as *Naraoia compacta* (Whittington 1977), and the polychaetes (Conway Morris 1979*b*). This stain has been interpreted as a decay product with body contents oozing into the surrounding sediment.

As noted above, the semi-isolated assemblages, isolated sclerites and isolated soft-parts are believed to represent moulted exuviae or post-mortem breakdown of entire specimens in the pre-slide environment. If entire specimens are a reliable guide then these types of specimen probably were subject to at most limited decay in the post-slide environment. There are, however, a few semi-isolated assemblages that consist of separated sclerites scattered over a small area of bedding plane (figure 21, plate 2; figures 145 and 146, plate 14; figures 29 and 150). Unless these sclerites were linked with tenuous strands of tissue or cuticle it is difficult to imagine that turbulent transport would not have scattered the sclerites more widely. These rare examples may represent further disintegration of a semi-isolated assemblage on the sea-floor of the post-slide environment under the influence of weak currents.

For reasons that remain obscure decay evidently ceased shortly after burial. This implies that one or more factors rendered the anaerobic bacteria inoperative, because even if rates of decay were hindered by low temperatures in the relatively deep water of the post-slide environment ultimately macroscopic destruction of the soft-parts would be expected. Clues for soft-part preservation could come from the survival of cellular structures for several thousand years in both deep (for example, Degens 1974; Degens *et al.* 1970) and shallow water environments (Golubic 1976; Knoll & Golubic 1979). Cessation of bacterial activity could be attributed to early dewatering of the sediment (see Brock 1976) or changes in the salinity (see Rolfe & Brett 1969; Knoll & Golubic 1979) of the interstitial waters, as both processes would interfere with bacterial metabolism. A further clue to the extraordinary preservation in the Phyllopod bed may, however, come from its history of deposition as a series of turbidites. In modern sediments bacterial concentrations decline markedly with depth (for example, Marty 1981). It is possible that with continued accumulation of graded beds the number of bacteria below the sediment surface fell to such low values that decay effectively ceased.

The fossils are preserved as thin films composed of aluminosilicates (Conway Morris 1977; Whittington 1980*a*). The stages by which the original carbon-rich fossils were converted into siliceous films are not known. Evidence of organic material providing templates for silicates in natural (Leone *et al.* 1975) and artificial (Ward & Benerito 1978) environments, however,

could provide clues on this transition in the Burgess Shale. The sediment of the Phyllopod bed contains a substantial proportion of chlorite (Piper 1972), and the rock is also traversed by narrow veins of this mineral (Larsen (in Walcott 1912*b*)). These veins, some of which are evident in the illustrations (for example, figures 8–10, 15 and 16, plate 1; figures 17–19, plate 2; figures 34 and 35, plate 3), run at a steep angle to the bedding plane. On some slabs set of veins running in two directions have been noted, and in these cases one set is often off-set relative to the other. The veins may also show an *en echelon* arrangement. The formation of these veins may conceivably be linked to the history of preservation.

Flattening of the soft-parts probably began with decay-induced collapse, followed by sedimentary compaction. The films that now form *Wiwaxia* are not entirely flat, but show some residual relief in the ribbing of the sclerites and the feeding apparatus, relief of the latter is especially apparent in some oblique specimens (figure 103, plate 10; figure 132, plate 13; figure 106). In common with other soft-bodied organisms from the Burgess Shale, the silicate films of *Wiwaxia* appear darker than the surrounding shale matrix when viewed in light set at a low incidence, whereas in high angle illumination certain areas become highly reflective while the remaining portions are darker. Analysis of the reflective parts of the film show them to be composed of muscovite mica (K. M. Towe, personal communication; see also Whittington 1971*a*, p. 1180). Reflective areas commonly include structures interpreted in various species as setae, spines, eyes, alimentary canal and muscles, although the delimitation between dark and reflective areas is not necessarily sharp. In *Wiwaxia* the distribution of reflective and non-reflective films, however, is often notably less regular than in many other species. Juvenile specimens frequently have prominent reflective preservation, covering much or all of the body (figures 42–44, plate 3; figure 49, plate 4; figure 81, plate 7; figure 123, plate 12; figure 134, plate 13; figure 127). In adult specimens ribs and marginal areas of some sclerites are highlighted in reflective strips, but reflective areas also may extend over a sclerite in a more irregular fashion. The soft-parts typically are composed of a dark film of rather uniform appearance, although some reflective patches of variable and inconsistent shape may occur (for example, figures 98–101, plate 10; figure 105). In the rare examples of isolated soft-parts, however, the film has areas of varying reflectivity whose outlines may be correlated with various internal organs (figures 157–159, plate 15; figure 153). The teeth of the feeding apparatus may also be preserved as reflective areas (figure 122, plate 12; figure 156, plate 15).

A number of specimens occur on weathered bedding planes where the grey-black colour of the original matrix has changed to a lighter grey to grey-yellow. The contrast between reflective and non-reflective areas of the unweathered fossil film tends to be subdued so that the specimen has a more uniform appearance that is conspicuously darker than the surrounding matrix in low angle light (for example, figures 84 and 85, plate 8; figures 99 and 101, plate 10), and faintly reflective in high-angle illumination. In other specimens parts of the body have a yellowish colour, while more rarely *Wiwaxia* (for example, 199993) is associated with a rust-red coloration that occurs particularly frequently with the crustacean *Canadaspis perfecta* (Briggs 1978*b*). Both the yellow and red compounds appear to represent oxidized iron compounds, perhaps derived from pyrite or iron silicates and presumably formed during weathering. Patches of calcium carbonate found on some weathered surfaces were probably deposited by ground water.

Pyrite has been reported in association with a number of Burgess Shale species (for example, Whittington 1974, 1977, 1981; Conway Morris 1977; Briggs 1981*a*; Bruton 1981; Bruton & Whittington 1983), and is sometimes present in specimens of *Wiwaxia*. In 198681 minute



yellowish spherules of pyrite thickly encrust some of the folded and crushed dorsal sclerites, while in 199894 irregular patches of pyrite spheres powder a number of sclerites. Examination of pyritiferous areas of *Wiwaxia* under the stereoscan electron microscope confirms that the minute spheres are framboidal pyrite (figures 39–41, plate 3). In general it appears that framboidal pyrite may be synthesized inorganically (for example, Berner 1969; Rickard 1970; Sweeney & Kaplan 1973; Hudson 1982), so that the frambooids on *Wiwaxia* cannot be interpreted as literally representing colonies of anaerobic bacteria inhabiting the sclerite surfaces. Nevertheless, such bacteria may have had some role in the pyrite synthesis. On occasion, however, the pyrite is seen to form thicker crusts of cubic crystals that are not arranged in obvious frambooids. In other specimens, for example, 198677 (figure 110, plate 11; figure 108), the fossil film is dimpled with widely scattered spherules that appear to have a pyritic composition (cf. Whittington 1974). The presence of pyrite is consistent with conditions of very low oxygen (Whittington 1971*a*, 1977) postulated to exist in the post-slide environment (Conway Morris 1979*b*, *c*). An interesting point of comparison in terms of preservation lies between fossils of the Burgess Shale and certain other Lagerstätten, such as the Ordovician Beecher's Trilobite Bed (Cisne 1973, 1981) and Devonian Hunsrückschiefer (Stürmer 1980), which appear to have been deposited in a broadly similar environment of muddy sediments under moderately deep water. In these latter Lagerstätten soft-part preservation is as pyritic films, whereas such preservation is sporadic in the Burgess Shale and practically all the fossils are composed of various aluminosilicates. The reasons for this contrast in preservation are not known, but might conceivably have been controlled by variations in the ambient Eh and pH.

As with other Burgess Shale fossils the split that exposes a specimen of *Wiwaxia* passes within the silicate films so that portions adhere to either side of rock giving part and counterpart. The path taken by the split through the fossil is of varying complexity, and depending upon its precise level will expose certain areas and conceal others within the specimen; these latter portions may be exposed by mechanical preparation. The style of splitting and the resultant exposure are apparent from the redescrptions of various Burgess Shale species, but the most detailed discussions are given by Whittington in his redescrptions of the enigmatic *Opabina regalis* (1975*b*) and the lobopod *Aysheaia pedunculata* (1978). In appendiculate species such as *Opabina*, the arthropods and polychaetes, the appendages (and carapace or other exoskeleton where present) are usually separated by thin layers of rock that evidently represent the lithified equivalent of the wet sediment that seeped in during turbulent transport. Appendiculate forms, therefore, tend to consist of two or more distinct levels of fossil films. The split usually jumps in a regular fashion via localized and steep scarps from one level to another, especially along a series of imbricated appendages, as it traverses the specimen (Whittington 1975*b*, figure 3). Three interdependent factors that determine which level the split will follow in the case of superimposed or otherwise adjacent films were identified by Conway Morris (1979*b*), which although illustrated with reference to the polychaete *Canadia spinosa*, are equally applicable to other Burgess Shale specimens and other examples of compression fossil (Schopf 1975; see Rex 1983; Rex & Chaloner 1983). In brief, these controlling factors are: (i) the thickness of the film, which in the soft tissues, and perhaps lightly skeletized remains, may be controlled by the extent of decay; (ii) its surface area; and (iii) its angle of burial with respect to the bedding plane. This third factor was also indicated by Whittington (1978) when discussing how variation in inclination of limbs of *Aysheaia* relative to the bedding plane influences their degree of exposure upon splitting.

The compact body of *Wiwaxia*, with its close covering of sclerites, usually did not permit

extensive access of seeping sediment during the turbulent transport, and thus in entire specimens a combination of decay followed by sedimentary compaction has reduced the body to a series of stacked films which represent various layers of sclerites and soft-tissues. As the sclerites covered more than half the surface area of the body, it is inevitable that superposition of sclerite layers will result. The adpression of the film layers results in a complex pattern of splitting and in nearly all specimens several layers of film being exposed. The multiple jumps of the split between these principal layers as well as across imbricated series of sclerites produces an intricate series of scarps (for example, figures 32, 53, 55, 70–72, 88, 90, 105, 108, 126, 129 and 147). In principle, the split has the ‘option’ of travelling through one of the several stacked films. Generally, the sclerites provide a preferred route for the split, as against the soft-parts and except in certain oblique specimens the soft-parts are usually either poorly exposed or hidden beneath other parts of the fossil.

In a number of Burgess Shale species the arrangement of anatomical features is such that most specimens in a given orientation to the bedding plane have a similar appearance because of exposure of the same areas of fossil film. The nature of *Wiwaxia* specimens, however, means that the route taken by the split through similarly oriented specimens is inconstant, so giving them a variety of appearances according to which layers of sclerites (and soft-parts) happen to be exposed. Nevertheless, with respect to the principal orientations adopted by specimens with their longitudinal axes more or less parallel to the bedding plane, a number of broad categories of exposure-type are recognizable. More precise details of the varying extent and appearance of the exposed sclerites and soft-parts, and the inferred distribution of concealed layers of the fossil film are given in §9c–g.

(i) *Parallel specimens* (for example, figures 11 and 12, plate 1; figures 93 and 94, plate 9; figures 6 and 90). Over much of the body the split is controlled by the sheet of dorsal sclerites, although sometimes a relatively narrow area of the more ventral soft-parts is exposed in the region of the anterior mid-line where presumably thickening due to organs such as the alimentary canal and musculature was sufficient to deflect the level of splitting. The dorsal sclerites are flanked by the upper lateral sclerites and the bases of the elongate spines; the latter extending across the bedding plane. The distal tapering ends of the spines commonly are buried within the matrix because increased separation combined with their diminishing surface area and thickness were unable to control the level of splitting; which moves to a new bedding plane via a fairly well defined scarp. To reveal the terminal portions of the spines in parallel (and other orientations) thus generally requires mechanical excavation.

(ii) *Parallel-oblique* (for example, figures 74, 75, plate 7; figures 110, 111, plate 11; figures 72, 108). Across much of the body the sclerites have a similar arrangement to parallel specimens, but along one side the ventro-lateral and lower lateral sclerites are so oriented to influence the level of splitting. The spines on this side are usually steeply inclined to the bedding plane and therefore, exert less control on splitting.

(iii) *Oblique* (for example, figure 16, plate 1; figures 34, 35 and 37, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129). In this position different sets of sclerites are subparallel to each other and the bedding plane, so that the split may take one of two alternative routes, either tending towards the ventral side and exposing some of the soft-parts or travelling more dorsally.

(iv) *Lateral and lateral-oblique* (for example, figures 45–48, plate 4; figures 64 and 65, plate 6; figures 82 and 83, plate 8; figures 53, 70 and 88). As with oblique specimens subparallelism of sclerite layers results in the split following several alternative paths. In 198681 the split

appears to have travelled along the left-hand side of the body, exposing the ventro-lateral and upper and lower lateral sclerites and concealing most of the rest of the body. In other specimens the split traversed a deeper level so that the fossil is more or less split in half, although jumps in the level of splitting in certain areas towards either side of the body result in the bulk of the fossil film residing on either the part or counterpart.

7. VERTICAL DISTRIBUTION IN THE PHYLLOPOD BED

Walcott (1912a, b, 1928) measured the Phyllopod bed as 2.31 m thick and divided it into 12 units of varying thickness which differed in lithology and fossil content. Walcott (1912b) noted that *Wiwaxia* occurred most commonly in the basal layer 12 (0–3.8 cm) and also in layer 10 (7.6–48.3 cm), but regrettably gave no further information on their vertical distribution. Most of the material of *Wiwaxia* in the U.S.N.M. is labelled 35k (locality number for the Phyllopod bed), but the exact horizons from which this material was derived are speculative and the associated fauna (§10) gives few reliable clues. The G.S.C. collecting teams made a note of the vertical distribution of specimens, but in most cases the information available on species occurring with *Wiwaxia* (see Whittington 1971a, figure 5, 1971b, text-figure 1, 1974, text-figure 1, 1975a, figure 1, 1977, p. 417; Hughes 1975, figure 1; Conway Morris 1977, text-figures 3 and 18, 1979b, figure 2; Briggs 1978b, figure 30) only narrow the potential choice

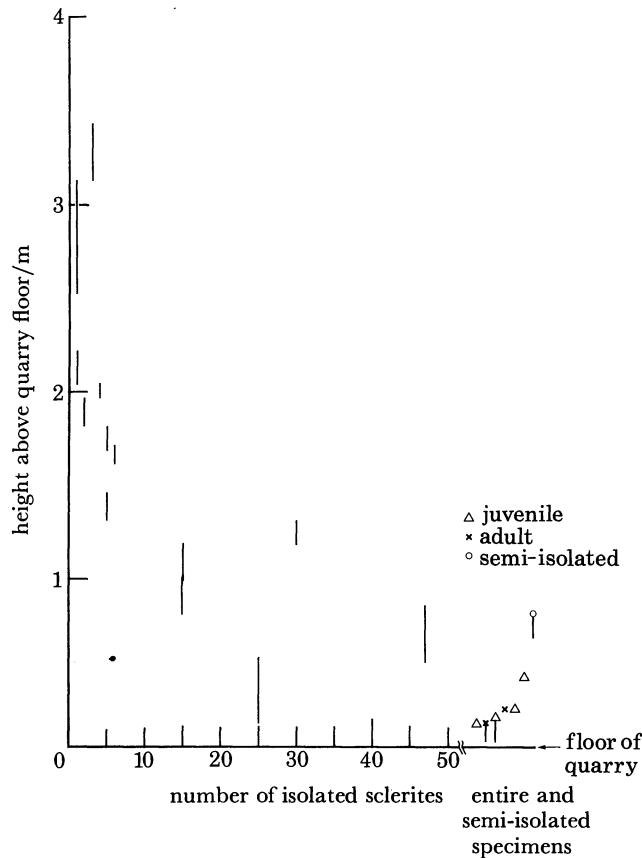


FIGURE 2. Vertical distribution of G.S.C. specimens of *Wiwaxia corrugata* (Matthew) from the Phyllopod bed (Burgess Shale). Left side of graph refers to 200 isolated sclerites (seven omitted from consideration), right side of graph to one semi-isolated assemblage and six entire specimens.

slightly as most occur at several levels. One species, *Eldonia ludwigi*, that is apparently restricted to a single horizon (Walcott 1912*b*; Conway Morris 1976) unfortunately is only known to occur with a few isolated sclerites of *Wiwaxia*.

The distribution of specimens of *Wiwaxia* collected by the G.S.C. is shown in figure 2. Isolated sclerites are relatively abundant and occur from the basal level of the quarry (0–15.2 cm) up to a level of 304.8–335.3 cm. The vertical distribution shows fluctuations with a maximum at 45.7–76.2 cm and a marked decline above about 121.9 cm. The data portrayed can only give a general indication as the interval thicknesses used by the G.S.C. are not constant, show some overlap, and thicker intervals could contain proportionally more sclerites. Moreover, the measured thicknesses bear no direct relation to individual turbidites and in the majority of cases probably encompass several beds so giving a time-averaged total. It is also uncertain to what extent the distribution of sclerites reflects original abundances of entire individuals. In the tubicolous priapulid *Selkirka columbia* a plot of relative vertical abundance of specimens with soft-parts (assumed to be alive at time of burial) and empty tubes showed a moderately good correlation (Conway Morris 1977, figure 18). The variations in sclerite abundance could also reflect very approximately original numbers of animals, although with a moderate residence time in the sediment (§6*b*) sclerites could be reworked. Moreover the small sample of entire G.S.C. specimens is restricted to the basal 71.1 cm, and their absence from higher strata is presumably due to limited sampling. The upper limit of *Wiwaxia* more or less coincides with the general disappearance of soft-part preservation in the section (for example, Whittington 1971*b*, text-figure 1; Conway Morris 1977, text-figure 18; Briggs 1978*b*, figure 30) and presumably reflects a cessation of suitable conditions, such as rapid burial.

## 8. SYSTEMATIC PALAEOLOGY

### *Phylum uncertain*

? *Class* Thambetolepidea Jell, 1981

? *Order* Sachitida He, 1980

*Family* Wiwaxiidae Walcott 1911; nom. correct Howell 1962

*Diagnosis.* (Modified from Walcott 1911.) Ovoid body bearing unmineralized ribbed sclerites on dorsal, lateral and ventro-lateral areas and elongate ribbed spines along dorso-lateral edges. Ventral area unarmed. Internal anatomy includes toothed feeding apparatus.

Genus *Wiwaxia* Walcott, 1911

*Type (and only known) species* *Wiwaxia corrugata* (Matthew, 1899).

Original designation p. 42.

*Diagnosis.* Bilaterally symmetrical, lepidote metazoan, average length about 25 mm. Body compact and ovoid, not demarcated into head or trunk, no tail. No eyes. External surface largely covered by ribbed, imbricated sclerites. Each sclerite attached to body wall by proximal root. Growth of sclerites apparently by moulting. Dorsal surface with about eight transverse rows of sclerites, six to eight sclerites per row, median asymmetrical sclerites overlap along mid-line, abaxially sclerites more elongate and less asymmetrical. Lateral surfaces with symmetrical sclerites on upper and lower regions. Upper region with approximately two rows, sclerites directed dorsally but inclined backwards towards posterior. Lower region bears about nine sclerite rows, two to three per row, adaxial sclerite somewhat shorter than remainder. Anterior face of body covered with symmetrical sclerites, continuation of lateral sclerites. Ventro-lateral regions bear single rows of crescentic sclerites, anteriorly arising either side of

mid-line. Elongate spines arise from dorso-lateral edges, extend dorsally, distal ends curve adaxially. Unequal number and spacing of spines either side of body, maximum length generally around mid-point, spines possibly absent in juveniles. Feeding apparatus of two, rarely three, rows of posteriorly directed teeth, located in anterior gut. Gut straight, probably terminal.

*Wiwaxia corrugata* (Matthew 1899)

1899	<i>Orthotheca corrugata</i>	Matthew, p. 42, plate 1, fig. 3
1908	<i>Orthotheca corrugata</i>	Walcott, pp. 243 and 246, plate 1, fig. 12
1911	<i>Wiwaxia</i>	Walcott, p. 111
1911	<i>Wiwaxia corrugata</i>	Walcott, pp. 123–124, 125, plate 21, figs 1–4
1912a	<i>Wiwaxia corrugata</i>	Walcott, p. 190
1912b	<i>Wiwaxia corrugata</i>	Walcott, pp. 152 and 153
1912c	<i>Orthotheca corrugata</i>	Walcott, pp. 127 and 185
1912	<i>Wiwaxia corrugata</i>	Steinmann, fig. 3 (copied Walcott 1911, plate 21, fig. 2)
1915	<i>Orthotheca corrugata</i>	Walcott, p. 212
1928	<i>Orthotheca corrugata</i>	Walcott, p. 319
1931	<i>Wiwaxia corrugata</i>	Walcott, p. 6, plate 3, fig. 1
1931	<i>Wiwaxia</i>	Richter, p. 340
1946	<i>Orthotheca corrugata</i>	Sinclair, p. 81
1951	<i>Orthotheca corrugata</i>	Rasetti, p. 101
1952	<i>Wiwaxia corrugata</i>	Roger, p. 169, fig. 2 (copied Walcott 1911, plate 21, fig. 2)
1958	<i>Wiwaxia corrugata</i>	Walliser, p. 179
1959	<i>Wiwaxia corrugata</i>	Roger, p. 689, fig. 511 (copied Walcott 1911, plate 21, fig. 2)
1960	<i>Wiwaxia corrugata</i>	Termier & Termier, p. 36, fig. 82
1962	<i>Fieldia lanceolata</i>	Rolfe, p. 7
1962	<i>Wiwaxia corrugata</i>	Howell, p. W167, fig. 106.3 (copied Walcott 1911, plate 21, fig. 2)
1964	<i>Wiwaxia corrugata</i>	Termier & Termier, p. 164, fig. 141.2
1968	<i>Wiwaxia</i>	Termier & Termier, p. 93
1969	<i>Wiwaxia</i>	Clark, p. 3
1970	<i>Wiwaxia corrugata</i>	Bengtson, p. 382
1972	<i>Wiwaxia corrugata</i>	Mintz, fig. 16.43c
1974	<i>Wiwaxia corrugata</i>	Whittington, p. 5
1975	<i>Wiwaxia</i>	Hughes, p. 419
1976	<i>Wiwaxia corrugata</i>	Conway Morris, p. 200
1977	<i>Wiwaxia corrugata</i>	Conway Morris, p. 45
1978	<i>Wiwaxia corrugata</i>	Whittington, p. 173
1978	<i>Wiwaxia</i>	Collins, p. 19
1979a	<i>Wiwaxia corrugata</i>	Conway Morris, pp. 332, 342
1979b	<i>Wiwaxia corrugata</i>	Conway Morris, p. 239
1979	<i>Wiwaxia corrugata</i>	Conway Morris & Whittington, pp. 126, 127, 130–131
1979	<i>Wiwaxia</i>	Brasier, p. 120

1979	<i>Wiwaxia corrugata</i>	Runnegar <i>et al.</i> , p. 1382
1981	<i>Wiwaxia corrugata</i>	Jell, pp. 85, 87, 89, 92, 93
1981	<i>Wiwaxia corrugata</i>	Bengtson & Missarzhevsky, p. 19
1981 <i>b</i>	<i>Wiwaxia corrugata</i>	Briggs, p. 36
1981	<i>Wiwaxia corrugata</i>	Pojeta, p. 163
1981	<i>Wiwaxia</i>	Sepkoski, p. 38
1982 <i>a</i>	<i>Wiwaxia corrugata</i>	Conway Morris, pp. 93–97, plate 1
1982 <i>b</i>	<i>Wiwaxia corrugata</i>	Conway Morris, p. 6
1982 <i>c</i>	<i>Wiwaxia corrugata</i>	Conway Morris, pp. 1, 7, 30, 31, plate W. (Copied Walcott 1911, plate 21, fig. 3.)
1982	<i>Wiwaxia corrugata</i>	Simonetta & Cave, p. 107
1983	<i>Wiwaxia corrugata</i>	Runnegar, p. 124
1983	<i>Wiwaxia</i>	Collins <i>et al.</i> , pp. 164, 165

*Holotype*. R.O.M. 966 CM (figure 14, plate 1), original of Matthew (1899, plate 1, figure 3); Conway Morris (1982*a*, plate 1, figure 1).

*Other material*. U.S.N.M. 57633–57636, 83938, 194724, 194776, 195208, 195490, 195635 (counterpart is 195638), 195995, 198668, 198669, 198671–198681, 198745–198748, 199077, 199181, 199727, 199883 (two specimens), 199884, 199885, 199887–199890, 199892–199894, 199897–199899, 199905 (counterpart is 199910), 199906, 199908, 199911, 199912, 199914, 199915, 199919, 199920, 199922, 199932, 199944, 199946, 199954, 199960 (counterpart is 200035), 199962, 199981, 199984, 199989, 199991, 199993 (three specimens), 199996, 200012, 200045, 200047, 200048 (two specimens), 200051, 200062, 200066, 200078, 200091, 200094, 200095 (two specimens), 200096, 200097, 200101 (part is 233149), 200116, 200140 (*Ogygopsis* Shale), 229901, 271947, 277889, 277890. U.S.N.M. collections total: entire specimens 119 part only (estimated to be equivalent to 104 specimens assuming some to represent disassociated parts and counterparts) and 24 part and counterpart; semi-isolated assemblages 14 part only (estimate) and three part and counterpart; isolated sclerites 492 part only (estimate) and 38 part and counterpart; isolated soft-parts 1 (part only), see Conway Morris (1981), G.S.C. 8331a, 45344–45355. R.O.M. 25870, 32569, 32570, 38607, 38626, 38627, 40280, 43200. M.C.Z. 1024, 5981 (attributed to *Fieldia lanceolata* by Rolfe 1962, see also Conway Morris (1977)). Peabody Museum, Yale 3493. Bristol University, Geology Department Museum 13384. University of Montana 1320. University of Cincinnati, Geology Museum 8422. Cincinnati Museum of Natural History 850/3. University of Oslo, Palaeontology Museum A 5140 (two specimens). McGill University, Redpath Museum, one unnumbered specimen.

## 9. DESCRIPTION

### (a) Overall appearance and dimensions

The anterior of *Wiwaxia* is recognized by the location of the toothed feeding apparatus and its assumed proximity to the mouth; the latter, however, has not been precisely located. In addition, most of the sclerites that mantled the body have a posteriorly directed imbrication with the distal margin of an anterior sclerite overlapping part of the sclerite posterior to it. The dorsum of this animal is identified on the assumption that the spines projected upwards and not ventrally. The lower surface appears to have been a naked area, devoid of sclerites except

around its margins. The bilateral symmetry is most readily apparent in parallel specimens, where the sagittal plane is more or less perpendicular to the bedding plane. Recognition of bilateral symmetry in *Wiwaxia* generally depends on the similar disposition of the various sclerite types on each side of the body. In no specimen, however, are the lateral (lower and upper) and ventro-lateral sclerites sufficiently clearly preserved to determine whether their symmetry was precise, while in the rows of dorsal sclerites minor departures from a mirror image appear to have occurred. It is also clear from the relative spacing and size of the spines that there was not a one-for-one correspondence along either side. With the exception of the feeding apparatus practically nothing is known of internal organs (§9g), although it seems reasonable to suppose that like the feeding apparatus they too had a bilaterally symmetrical arrangement.

In parallel aspect specimens have an elongate oval outline, with a broadly rounded anterior edge and slightly convex lateral margins that taper to a blunt posterior termination (figures 24–26, plate 2; figure 44, plate 3; figures 93 and 94, plate 9; figures 115 and 116, plate 11; figure 134, plate 13; figures 137–140, plate 14; figures 90 and 147). The outline shape in non-flexed lateral specimens (figures 64 and 65, plate 6; figure 70) consists of a more or less straight ventral edge and an approximately convex dorsal margin comprising steeper anterior and posterior sections connecting a flatter median portion. The shape of parallel and lateral specimens indicates that the body of *Wiwaxia* approximated to a cabochon or one half of an elongate dome with a flat ventral area rising via steep sides to a dorsal region that was gently arched transversely and longitudinally. The outline shapes of oblique (figure 16, plate 1; figures 34 and 35, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129), parallel-oblique (figures 74 and 75, plate 7; figures 110 and 111, plate 11; figures 72 and 108), lateral-oblique (figures 45–48, plate 4; figure 53), and inclined (figures 68 and 69, plate 6; figures 118–121, plate 12; figures 71 and 126) specimens are consistent with this reconstruction. Unfortunately, no vertical specimens have been recognized as such an orientation gives a good approximation to the transverse section of the species (see Whittington (1971a), p. 1187, (1971b), plate 4, figures 2 and 3, plate 13, figures 2 and 3; Briggs (1978b), p. 444; Bruton (1981), plate 4, figure 29). The specimen 198668 (figures 8 and 9, plate 1; figure 5) is steeply inclined to the bedding but its interpretation is complicated by the body being transversely folded parallel to the bedding plane so rendering this specimen an unreliable guide to the original transverse appearance of *Wiwaxia*.

The cabochon-like shape of the body is only a first approximation, and more specific details of a reconstruction that includes a precipitous anterior margin and notched lateral margins are given below. Among adults the transverse section of the body appears to have been roughly rectangular (figure 172). The relative abundance of juvenile specimens preserved in parallel orientation (figure 20, plate 2; figure 44, plate 3; figure 81, plate 7; figures 115 and 116, plate 11; figures 133 and 134, plate 13; figure 28) suggests, however, that they may have been more dorso-ventrally compressed as such a shape would presumably represent the most stable mode during deposition. Some variation in shape is also to be expected because *Wiwaxia* was soft-bodied, lacking a rigid skeleton and presumably capable of muscular contractions. A size–frequency histogram of sagittal length (figure 3), therefore can be only indicative, and the approximately bimodal distribution may be due to the relatively small sample size ( $n = 44$ , many entire specimens are either incomplete or unsuitably oriented). Alternatively, the absence of specimens in the size range 15–20 mm could indicate an original biological feature such as a moulting stage, (§9b) or less plausibly sexual dimorphism. Any interpretations based on this and other size–frequency histograms presented for some of the other Burgess Shale species

(Whittington (1974), text-figure 3, (1977), figures 2*a, b*; (1981), figure 1; Hughes (1975), figure 2; Briggs (1978*b*), figure 177, (1981*a*), figure 102; Conway Morris (1977), text-figures 5, 19 and 31) must be treated with some caution as they represent time-averaged samples culled from many of the turbidite layers that accumulated over an unspecified length of time to form the Phyllopod bed. Even Whittington's (1971*a*, figure 23) portrayal of size-frequency histograms of the abundant arthropod *Marrella splendens* through five intervals of the lower part (121.9 cm) of the Phyllopod bed may each represent sampling from more than one turbidite and thus not necessarily single populations, although their overall statistical similarity suggests that the data are representative (cf. Whittington 1971*a*, p. 1196).

Specimens with a sagittal length of 15 mm or less, coinciding with the marked break in the size frequency histogram, are regarded as juveniles, although there is no available evidence to mark the onset of sexual maturity. The specimen 229901 (figure 123, plate 12; figure 127) is approximately 2.5 mm long, but it may be incomplete. The smallest unequivocally complete specimen is about 3.4 mm long (figure 134, plate 13). Other juvenile specimens (figures 17–20, plate 2; figures 42–44, plate 3; figure 49, plate 4; figures 80 and 81, plate 7; figures 115 and 116, plate 11; figure 133, plate 13; figures 27 and 28) are somewhat larger. Juvenile specimens are similar to adults, but show certain differences that include an apparent absence of spines in the smallest specimens (§9*c*).

The largest recorded individual is about 52 mm long (figures 84 and 85, plate 8) and this is probably near the upper size range judging by the comparable size of the largest sclerites in isolated specimens and semi-isolated assemblages. The mean sagittal length of *Wiwaxia* was about 26 mm (figure 3). Figure 4 depicts graphically the observed relation between the maximum body width and sagittal length in 15 parallel and parallel-oblique specimens. The scatter of points around the line of best fit must be due in part to variations in the angle of burial and slight inaccuracies in measurement, but this spread may also partly be attributed to varying degrees of muscular contraction. The parallel outline of the animal presumably would become subcircular in a contracted state (for example, figures 24–26, plate 2), while in relaxed individuals it would be more elliptical. The distribution of points in figure 4 should define some of the field of extensibility in *Wiwaxia*, as more extreme contraction would have been prevented by interference between the attachment points in adjacent rows of sclerites, and excess extension would have separated the sclerites to expose underlying soft-tissues, thereby jeopardizing their possibly protective function (§10). The height of the animal, which reached a maximum value about the midpoint, may be measured in lateral specimens: in 198678 (length about 35 mm; figures 64 and 65, plate 6; figure 70) and 198681 (length about 42 mm; figures 82 and 83, plate 8; figure 88) the maximum height is 13 mm and 18 mm respectively. In the latter specimen, however, there appears to have been marked contraction, with concave folding of the ventral side, which has probably accentuated the height. In the subvertical and transversely folded 198668 (figures 8 and 9, plate 1; figure 5) the height was approximately 8 mm, while the observed width of *ca.* 13 mm suggests its original length (see figure 4) was of the order of 20 mm. Taken together these meagre data suggest that a specimen of average length (26 mm) had a height of about 10 mm (excluding spines).

#### (b) *Sclerites and their growth*

Much of the body of *Wiwaxia* was covered with scale-like sclerites, those mantling the body are divisible into various regions (dorsal, upper lateral, lower lateral, anterior, ventro-lateral)



and are collectively termed the body sclerites. In addition, there were elongate spinose sclerites that projected away from the body; these are known as the spines. Consistent relations between the relative proximity and respective levels occupied by the sclerites of each area of the body allow a reconstruction of their overall distribution (figure 171). To summarize, the ventral area of the body appears to have lacked sclerites consisting of soft-tissues, which was flanked by ventro-lateral sclerites with a distinctive crescentic shape. The lateral areas of the body appear to have consisted of a gently inclined lower region, bearing elongate oval sclerites (lower lateral) directed posteriorly, and a much steeper upper region which was covered with more rounded oval sclerites (upper lateral) pointing dorsally. Towards the front of the animal these latter sclerites swung around to cover the precipitous anterior region of the animal. From among the upper lateral sclerites elongate spines arose, extending away from either side of the animal in a dorsal to dorso-lateral direction. The dorsal surface was covered with a number of transverse rows of sclerites, each row consisting of a series of asymmetrical scales either side of the mid-line.

The smallest known specimens possess recognizable body sclerites (for example, figure 123, plate 12; figure 134, plate 13; figure 127), and it seems possible they developed during or shortly after the larval stage. The sclerites show a range in morphology, best seen in adult specimens, but share features that suggest derivation from the secretory activity of the same type of tissue. Each sclerite had a separate insertion into the body, and was composed of two units: a smooth proximal root and the ribbed sclerite (ss). The roots are apparent in some entire specimens extending into the body, where they show no obvious connection with any other feature of the poorly known internal anatomy (for example, figures 8 and 9, plate 1; figure 20, plate 2; figures 45–48, plate 4; figures 68 and 69, plate 6; figures 118–121, plate 12; figures 5, 28, 53, 71 and 126). Generally, however, the form of the root is more apparent in isolated sclerites (figure 23, plate 2; figure 78, plate 7; figure 96, plate 9; figure 114, plate 11; figure 125, plate 12; figure 143, plate 14; figures 31, 73, 92, 109, 128 and 149) and disaggregated semi-isolated assemblages (figure 21, plate 2; figures 145 and 146, plate 14; figures 29 and 150).

The root is shorter than the rest of the sclerite; in body sclerites the ribbed section is generally between two-and-a-half and three times longer, whereas in the spines it is over three-and-a-half times as long. In isolated sclerites the root is usually preserved as a dark film and less usually as parts of it reflective, whereas in entire specimens the root is often highly reflective. In no case, however, is there evidence of any organized internal structure within the root. The smooth margins of the root, including the rounded to pointed proximal section, suggests that it did not have any intimate connection with the surrounding tissues of the body wall, but rather was probably located in a pocket-like invagination of the outer surface, analogous to the pit associated with hair follicles in mammals or chitinous setae in annelids. The width of the root may taper towards the proximal end, but more usually there is a slight to pronounced expansion along its length with some tapering of width in either direction. The insertion of the root into the sclerite was either terminal or apparently slightly subterminal. In the body sclerites the root is considerably narrower than the maximum width of the sclerite (ss), whereas the root of a spine was more massive and had approximately the same width as the sclerite (ss) base. Examples of isolated sclerites lacking a root (figure 14, plate 1; figure 79, plate 7; figure 135, plate 13; figure 142; plate 14; figures 7 and 148) but otherwise complete suggest that it was composed of soft-tissues more vulnerable to decay, and in 45350 (figure 96, plate 9; figure 91) the root appears to have suffered incipient disintegration judging from its tattered appearance.

The boundary between the root and sclerite (ss) probably marks the point of emergence of the latter from the body wall. The soft-parts of the root probably extended into the sclerite and were presumably responsible for secreting the sclerite walls (§11*b*). Direct evidence for the enclosed soft-parts is, however, obscure unless diffuse reflective patches in some sclerites represent these tissues. The exact composition of the outer layer is uncertain. Comparison with the style of preservation in organisms with either a calcareous (trilobites, articulate brachiopods, echinoderms) or phosphatic skeleton (inarticulate brachiopods) does not suggest the sclerites had a comparable composition. Furthermore, a predominantly organic composition is indicated by incomplete specimens of isolated sclerites in which the transverse margin is apparently frayed by the processes of decay. In the majority of examples decay was evidently polarized with the proximal region of the sclerite now absent (figure 38, plate 3; figure 50, plate 4; figure 97, plate 9; figure 104, plate 10; figure 124, plate 12; figures 33, 54, 92 and 107). The isolated spine 199954 is exceptional, however, because the distal area is missing whereas the proximal end is intact with attached root. The frayed appearance of these incomplete examples may indicate that the sclerites originally had a fibrous structure. A chitinous composition appears less likely because in comparison with the setae of Burgess Shale polychaetes (Conway Morris 1979*b*), which are assumed to have been chitinous like those of modern polychaetes (Dales 1967), the sclerites are preserved as a much less reflective film. Another possibility is that the sclerites were composed of either tanned proteins or collagen. A composition in some such material could render the sclerites with a low preservation potential, with only a limited resistance to decay. This might explain their apparent restriction in Middle Cambrian sediments to certain favoured taphonomic environments in the Stephen Formation.

The surface of the sclerites was ribbed; the ribs appear to represent rounded thickenings of the sclerite wall. Evidence given below suggests that in some of the body sclerites the ribs were confined to the outer surface, although in other body sclerites and the spines they may have been present on other areas. The ribs paralleled the sclerite margins so that in the body sclerites they converged towards either end, although in at least the distalmost area the ribs die out before actually meeting. The ribs appear to have been narrow thickenings of the outer wall which did not bifurcate or otherwise branch. They are frequently preserved with residual relief, although in some specimens the ribs are represented by reflective lines. There is no convincing evidence that they represent some internal structure, such as a series of rods, impressed through the outer wall during sedimentary compaction. The primary function of the ribs is supposed to have been to offer structural support to the sclerite.

The ontogenetic growth of the sclerites involved size increase and for certain sclerite types some slight modification in relative shape. Comparisons between the number of sclerites in specimens of different sizes can only be approximate because in no case is an entire series exposed. Nevertheless, estimates of the totals of the crescentic ventro-lateral sclerites, chosen for their easy recognition, along one side of the body in specimens varying in length from 11 to 52 mm gave comparable totals (*ca.* 16–18). This suggests that the complement of sclerites was laid down at an early stage of ontogeny, and that subsequent addition of new sclerites was either limited or possibly non-existent. The manner in which the sclerites grew during ontogeny, however, is open to several different interpretations. Walcott (1911, p. 124) suggested that the root 'probably continued down into the sac from which the scale began its growth'. While each sclerite presumably originated within the invagination of body wall, the constricted proximal region in all the body sclerites indicates that growth cannot have been by simple basal accretion

from secretory cells located in the root. The uniformly tapering shape of the spines means that in principle they could have grown by basal accretion, but comparisons between the spines in juveniles and adults suggests that they were not simply extruded from the root region, but had their shape modified during growth. Furthermore, although the ribs parallel the sclerite margins they cannot be regarded as growth lines marking successive increases in size. This is because there is no evidence that the ribs were concentrically arranged with a series of distal closures; rather in any sclerite of whatever size the ribs converge and ultimately die out towards the distal tip.

Three alternative modes of growth appear possible: resorption, extension, or moulting. Changes in sclerite size and alteration in the number and spacing of the ribs during ontogeny suggests that resorption would have had to have been extensive to accommodate growth. Evidence of resorption would probably be difficult to detect in *Wiwaxia*, but it is significant that no signs of resorption have been noted in the mineralized sclerites of *Halkieria*, which appears to be a Lower Cambrian relative (§11*b*). Direct evidence of growth by cuticular extension, comparable to that documented in some insects and other arthropods (for example, Bocquet-Vedrine 1982; Bordereau 1982*a*), is not apparent. Such a mode of growth would be difficult to envisage in mineralized *Halkieria* and its relatives. It also seems an implausible mechanism to account for the overall increase of size during the ontogeny of *Wiwaxia*, especially if the cuticle extended by unfolding. Nevertheless, extended cuticular growth does occur in some insects, such as the termite queen (Bordereau 1982*b*). While growth by either resorption or extension remain unproven possibilities, a unique specimen (figures 17–19, plate 2; figure 27) suggests that growth was by moulting. Superficially, there appear to be two specimens of *Wiwaxia* superimposed more or less at right angles. This specimen is unlikely to represent an example of cannibalism as *Wiwaxia* probably was either a grazer or deposit feeder (§10). Although cases of superposition are known in the Burgess Shale (Whittington 1981; but not Conway Morris 1978; see Whittington & Briggs 1982), in this specimen juxtaposition appears to have arisen by a newly moulted individual preserved in the act of crawling out of the exuvia. The area interpreted as the exuvia has a somewhat shrunken and elongate appearance that would be consistent with a vacated husk. More significantly the sclerites of the newly emergent individual appear to have lacked the rigidity apparent in other specimens of *Wiwaxia*. Furthermore, in some of these sclerites the distal area is constricted and could represent the process of reinflation of the sclerite, perhaps by body fluids, before the secretion and hardening of the new wall. It may also be significant that some of the sclerites show faint, closely spaced transverse lines that could conceivably represent original wrinkling of the partly inflated sclerite. There is no clear evidence for ribbing and the ribs were presumably only secreted when the sclerite reached its final post-moult size. Although measurements are difficult to obtain the newly moulted individual appears to be approximately 20% longer than the vacated exuvia. Accurate calculation of the relative increase in volume between the two moult stages is impractical because of unsuitable preservation and the need to extrapolate dimensions such as body height from available measurements. A crude estimate, however, suggests that a volumetric increase of the order of 50–70% occurred.

If this specimen is accepted as representing a moulting individual rather than arising by chance superposition then it has the following ramifications. There is no evidence that the sclerites split open during moulting, and as all the body sclerites have a constricted proximal end withdrawal of the soft-tissues, presumably via the root, would have required a considerable

loss in volume so that the pre-moult cycle may have involved histolysis of the sclerite tissues. A useful analogy appears to exist with the lobster claw where the absence of a moulting suture necessitates the withdrawal of muscles and other tissues through the narrow basis during moulting. The ratio between the cross-sectional areas of the widest part of the claw and the basis in one specimen was measured as 17:1 (Bengtson & Conway Morris 1984), a figure broadly comparable to that inferred to have existed between the areas of maximum width and the proximal region of body sclerites (figure 23, plate 2; figure 78, plate 7; figure 143, plate 14; figures 31, 73 and 149). In the land-crab *Gecarcinus lateralis* up to 40% of the protein in the large chela muscle is lost and this combined with extensive histolysis presumably facilitates withdrawal through the basis (Skinner 1966). In the juvenile 233149 (length *ca.* 8mm) the exuvia evidently consists of an intact unit (figures 17–19, plate 2; figure 27) so that not only the sclerites but also intervening cuticle appears to have been moulted, even though each sclerite was inserted separately into the body wall via the root. In this specimen it seems probable that the newly moulted animal crawled out through a vent in the cuticle of the ventral area. In larger individuals, however, it is conceivable that moulting did not yield an entire exuvia but a series of fragments. Nevertheless, the available evidence suggests that moulting was synchronous as in no adult specimen are there interruptions in the sclerite covering that would be consistent with sporadic moulting of either isolated sclerites, or zones of sclerites. In 233149 traces of the feeding apparatus (§9g) also occur. Its somewhat disorganized appearance, with one half-row pointing anteriorly suggests that the apparatus may have also been moulted. Extension of ectodermal tissue into the foregut, a feature found in many triploblastic metazoans, could result in the lining of this region including the feeding apparatus being discarded at each moult. Among arthropods both the foregut and hindgut linings are moulted. The frequency of moulting in *Wiwaxia* is uncertain. The limited size–frequency data gives no indication of successive instars, unless the absence of individuals in the 15–20 mm size-range (figure 3) indicates a substantial size increase during a moult. Assuming, however, that moulting was a recurrent feature of ontogeny and involved a regular 20–25% length increase then an adult *Wiwaxia* would have moulted about ten times during its life. The existence of moulting in *Wiwaxia* invites comparisons with other metazoans that moult their cuticles, in particular nematodes and more especially the arthropods. An analogy with the lobster has been drawn above, and it may be speculated as to whether further physiological similarities existed with the well-documented arthropod ecdysis. Pre-moult activities in *Wiwaxia* could have involved withdrawal of secretory tissues from the existing sclerite wall, preliminary formation of the new wall and histolysis of the soft-parts. Moulting may conceivably have been under the control of hormones.

The evidence for moulting in *Wiwaxia* means that many of the semi-isolated assemblages and isolated sclerites may have arisen by this process rather than decay and rotting of corpses. For example, 198747 (figure 87, plate 8) could represent either a recently vacated exuvia or the initial decay stage of a corpse. Moulting was presumably a rapid process if the chances of predation were to be reduced (§10), and the presence of 233149 preserved in the very act of moulting is additional evidence for catastrophic burial of the Burgess Shale fauna. No newly moulted individuals independent of their exuviae have been noted, although comparable examples of moulted specimens of the trilobite *Olenoides serratus* have been documented (Whittington 1980a).

*(c) Spines*

The elongate spines are a prominent feature of nearly every adult specimen, and at almost any angle of burial at least one of the two rows is so oriented that some of the spines extend from the body across the surrounding bedding plane. The specimen 83938 is unusual in that, with the exception of one anterior spine of the left, the spines are unexposed (figures 137–140, plate 14; figure 147). Part and counterpart of 83938 have respectively a convex and concave surface; this stands in contrast to the normally more flattened nature of the specimens. This feature is attributed to an originally pronounced downward, transverse curvature of the body about its sagittal plane. Furthermore, the two rows of spines appear to have projected into the sediment at a steep angle where they were unable to influence the level of splitting (§6*b*).

The influence of the angle of burial of the body on spine exposure is summarized in figure 1. The arrangement of the spines in two rows is best seen in parallel specimens (figures 11 and 12, plate 1; figures 93 and 94, plate 9; figures 6 and 90). With increasing inclination of the body's longitudinal axis to the bedding plane the spines of each row show varying degrees of superposition (figures 68 and 69, plate 6; figures 118–121, plate 12; figures 71 and 126), and this process of overlap reaches a culmination in the subvertical and folded 198668 (figures 8 and 9, plate 1; figure 5). This sequence of inclined and subvertical specimens indicates that the spines originally extended upwards and away from the body. Variations in the exact attitude will be influenced in part by the angle of burial. Comparison, however, between the spines of the inclined 198679 (figures 68 and 69, plate 6; figure 71) and subvertical 198668 (figures 8 and 9, plate 1; figure 5), where they extend at steep and shallow angles respectively to the dorsal surface, suggests that the inclination of each spine in a transverse plane may have been controlled by the animal; perhaps by the action of antagonistic muscles or ligaments such as a set of paired depressors and extensors. Although convincing evidence of musculature exists in some of the other Burgess Shale species (Conway Morris 1977; Briggs 1978*a*; Bruton 1981), no trace of muscles have been noted in *Wiwaxia* (§9*g*) and their presence can only be inferred indirectly. Circumstantial evidence for variation in spine attitude comes from other specimens. In the parallel 198672 (figures 93 and 94, plate 9; figure 90) the extension of the spines on the bedding plane suggests that originally they lay at a low angle to the dorsal surface and during compaction only slight crushing occurred with occasional formation of crease lines across the spines. The slight difference in length between the spines of either side is not thought to be original, but to stem from slightly oblique burial. Relative foreshortening (cf. Whittington 1977, figures 1 and 3) of the left row is largely due to slight inclination to the bedding, while the original angle to the body of the right spine row more or less coincides with the bedding. In 83938 (figures 137–140, plate 14; figure 147) on the other hand, evidence presented above suggests an originally steep angle of spine inclination.

In parallel-oblique specimens the spine row more nearly parallel to the bedding lies on the bedding surface, whereas the other row is more steeply inclined. In 199894 (figures 74 and 75, plate 7; figure 72), for example, at least one of the spines of the inclined left-hand row can be followed upwards in the part from the proximal section (via a missing portion) to the distal termination on a higher level of matrix. Other inclined proximal sections of the left spines are also evident. The right row in 199894 is somewhat foreshortened with distal breakage of two of the spines. This indicates that the right row was also inclined quite steeply to the dorsal surface

of the body, and obliquity of burial has only oriented the right row subparallel to the bedding. In 198677 (figures 110 and 111, plate 11; figure 108) a greater degree of obliqueness, to judge in particular from the relative exposure of the dorsal and crescentic ventro-lateral sclerites, has brought the spines of the left row effectively parallel to the bedding. Spines of the right row are inclined into a lower level of sediment and are mostly exposed as the distal portions at the anterior and posterior of the body, although the path of one spine can be traced downwards from its proximal portion.

In oblique specimens (for example, figure 16, plate 1; figures 34, 35 and 37, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129) the traces of the two spine rows show partial overlap, with one row extending away from the body and reasonably well exposed, while the other is largely buried beneath the body so that only the distal sections extend clear. These latter spines lie at a deeper level, usually separated from the opposite row of spines by a matrix 0.5–1 mm thick (determined by taking Plasticene moulds), and because of their narrowing surface area and declining width (§6*b*) are not always exposed by the split. Taking the thickness of rock separation between the spine rows as 1 mm, and comparing this with their separation as measured in inclined and subvertical specimens indicates that the original distance has undergone an approximately 20-fold reduction that is attributed to a combination of collapse by partial decay followed by sedimentary compaction. In 198676 (figures 130 and 131, plate 13; figure 129) one of the more deeply buried left-hand spines towards the anterior of the body has been mechanically excavated to reveal most of its length. Elsewhere in this specimen the proximal portion of at least one other left-hand spine is visible, with the more distal length disappearing beneath other sclerites. A comparable feature is shown by 199893 with the distal and proximal sections of two of the deeper series of right-hand spines visible, with their intervening section concealed below other sclerites (figures 34 and 35, plate 3; figure 32). In both 198676 and 199893 most of the spines of the deeper row appear to be almost entirely concealed.

The spine rows of oblique-lateral and lateral specimens are more nearly superimposed and the distal sections extend away from the body across the sediment for approximately equal distances. In the majority of such specimens (for example, figures 45–48, plate 4; figures 64 and 65, plate 6; figures 53 and 70) the path taken by the split has resulted in spines of both left- and right-hand rows being partly exposed on different levels. The specimen 198681 (figures 82 and 83, plate 8; figure 88) is more unusual because in the part (slightly incomplete) only the lower spines of the right-hand side are clearly exposed, and those of the left are assumed to reside on the unlocated counterpart. This distribution appears to have arisen because the specimen is contracted and the close apposition of scales has influenced the level of splitting.

The spines arose between the upper lateral and abaxial dorsal sclerites. Their points of insertion appear to have been adjacent to those of the upper lateral sclerites so that in life the proximal portion of each spine was concealed, and it is comparatively unusual for the split to expose the entire length of the spine in either part or counterpart. The roots of the spines are best seen in isolated sclerites (figure 114, plate 11; figure 109), but in entire specimens they appear to have been inserted into the body adaxially set at an angle to the overall direction of the spine (figures 68 and 69, plate 6; figure 71). It is not clear whether the spines arose either from the same body surface as the lateral sclerites (figure 172) or occupied a distinct groove. Circumstantial evidence for the latter might include the distinctive linear impression, possibly accentuated by compaction, on the right side of 198679 (figures 68 and 69, plate 6; figure 71)

and on either side of 83938 (figures 137–140, plate 14; figure 147) coincident with the assumed trace of the spine rows. On the other hand, there is no convincing evidence of soft-tissues forming an outer wall of this groove and so separating the spines from the upper lateral sclerites. If the spines arose from the same area of body wall as the upper lateral sclerites, it is possible that the spines owe their origin to modification of the germinal bud of a developing lateral sclerite.

The number of spines along one side of a specimen appears to vary from about 7 to 11, but the exact total is often uncertain because the orientation of the specimen serves to conceal or obscure some spines and the total per side may not be equal. The spine total per side appears to be correlated positively with body length (figure 163), suggesting that spines were added as growth proceeded. The possibility that the original number varied in each individual appears less likely. In some specimens either an anterior (figures 8 and 9, plate 1; figures 98–101, plate 10; figures 118–121, plate 12; figures 130 and 131, plate 13; figures 5, 105, 126 and 129) or posterior (figures 68 and 69, plate 6; figure 71) spine may be conspicuously shorter than the remaining members of a row, while in others (figures 56 and 57, plate 5; figures 93 and 94, plate 9; figures 55 and 90) there are also a few much shorter lanceolate spines interspersed with the larger members. These latter spines have an inconstant appearance among the specimens that may be either original or owing to obscuration by other sclerites and a lack of exposure by the split. Within the main series of spines of a row there is sometimes an approximate size increase towards the midpoint, but in other cases many of the spines are subequal in size (for example, figure 15, plate 1; figures 45–48, plate 4; figures 84 and 85, plate 8; figures 93 and 94, plate 9; figures 98 and 99, plate 10; figures 110 and 111, plate 11; figures 118–121, plate 12; figures 130 and 131, plate 13; figures 53, 90, 105, 108, 126 and 129). In 198678 (figures 64 and 65, plate 6; figure 70), however, a spine of the left row (L.sp.) is conspicuously short despite its location near the midpoint of the body; information on the more anterior spines of this row is not available because they are assumed to be confined to the (unlocated) counterpart. Such examples of a shorter spine in a row of spines of otherwise normal length may represent a replacement growth following the destruction of an earlier spine (see below). The spacing of the spines along a row was not equal in any individual; in some cases two spines may arise close together and be separated by a thin layer of matrix (for example, figures 11, 12 and 15, plate 1; figures 34 and 35, plate 3; figures 45–48, 52, plate 4; figures 84 and 85, plate 8; figures 98–101, plate 10; figures 6, 32, 53 and 105) whereas elsewhere along a row spines are separated by variable amounts. The spines in parallel (figures 93 and 94, plate 9; figure 90) specimens and those belonging to the row of lower inclination in some parallel-oblique specimens (figures 110 and 111, plate 11; figure 108) extend from the body edge more or less at right angles. This gives them a roughly fan-shaped arrangement as they follow the convex margin of the body. Specimens in oblique and lateral aspects indicate that the anterior and median spines arose at a steep angle to the dorsal margin. The posterior spines were more inclined and lay at a lower angle to the dorsal surface, much of this inclination is probably a reflection of their position on the sloping posterior flanks of the animal. Variations in the angle of burial make it difficult to determine the possible extent of antero-posterior movements during life. The marked forward inclination of the anterior two spines of the right-hand row in 198678 (figures 64 and 65, plate 6; figure 70) appears to be due more to the downward flexure of the body in this region, as suggested by the arrangement of adjacent sclerites, than independent movements of the spines. The superposition of many of the spines of both rows in 198669 (figures 118–121, plate 12; figure 126) is attributed to the inclined angle of burial and subsequent

compaction rather than a posterior sweeping back, and a similar interpretation may apply to 198675 (figure 61, plate 5). Other specimens do not appear to show unequivocal evidence of a marked ability to move the spines in a plane parallel to the sagittal plane of the body.

In the parallel 198672 (figures 93 and 94, plate 9; figure 90) the two spine rows do not form an exact bilaterally symmetrical series. Relative differences in spine length on each side have been discussed above and attributed to slight obliquity in burial, but the variable spacing along each row means that the insertion points of the spines do not have an exact counterpart on either side. Furthermore, there is no evidence to suggest that an originally even spacing of insertion points has been rendered irregular by some spines being aborted. Although the posteriormost section is absent, the total number (ignoring the short spines) on the left and right-hand sides appears to be six and eight respectively. Comparison of spacing, size and number of spines on either side of other specimens is hindered by unfavourable angles of burial. The available evidence, however, strongly suggests that the spines had a comparable arrangement to those of 198672, with an absence of direct bilateral equivalence between the spines of either row. This uneven distribution of the spines in *Wiwaxia* points to a lack of precise guidance, presumably genetic, in their positioning, so that within certain fairly wide constraints almost any combination was viable for an effective function (see Seilacher 1974).

In the smaller juvenile specimens (figures 42–44, plate 3; figure 49, plate 4; figures 80 and 81, plate 7; figure 123, plate 12; figures 133 and 134, plate 13) spines are not apparent. In 277889 (figure 20, plate 2; figure 28), however, with a body length of about 7.5 mm, elongate structures (length *ca.* 1.1 mm, maximum width 0.1 mm) at the posterior are interpreted as spines. The nonlinear relation between maximum spine and body lengths is summarized in figure 164. Variation in the angle of burial of both the body and spines, the possibility that in some of the specimens the longest spine is obscured or incomplete, and the very small sample number, especially below 20 mm sagittal length, means that conclusions are tentative. It appears, however, that spine length increased much more rapidly (about 2.5 times) than body length in the earlier stages of growth, but with increased body size the relative length of the spines decreases although there is no clear sign of an asymptotic relation. Replotting the data of figure 164 on a logarithmic scale confirms that the relation between body and spine length is not one of simple allometry (Gould 1966). The absence or minute size of the spines in specimens smaller than about 7 mm, the apparently rapid increase in length in larger juvenile specimens and the more limited size increase in adults may be related to the ecology of *Wiwaxia* and its defence against predators (§10).

In inclined and subvertical specimens the spines are generally curved adaxially, the curvature usually being more pronounced along the distal half as compared with the straighter proximal length. Most of the spines of a row exhibit this curvature, but in some specimens the shorter anterior or posterior spines are straight and dagger-like (figures 8 and 9, plate 1; figures 68 and 69, plate 6; figures 118–121, plate 12; figures 5, 70 and 126). In parallel specimens (figures 93 and 94, plate 9; figure 92) all the spines are more or less straight, presumably because compaction was effectively at right angles to the line of curvature. In specimens of other orientations the appearance of the originally adaxially curved spines is apparently related by their attitude, and that of the body, to the bedding plane. In the lateral-oblique 198680 (figures 45–48, plate 4; figure 53) the spines of either side show a fairly uniform and opposed direction of adaxial curvature, whereas in the similarly oriented 198678 (figures 64 and 65, plate 6; figure 70) a wider variety of orientations is evident with both straight anterior and posteriorly curved spines present. Spines in oblique specimens (figures 98–101, plate 10; figures 130 and 131, plate



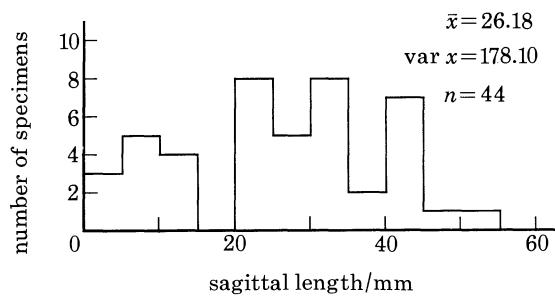


FIGURE 3. Size-frequency histogram of sagittal length of 44 specimens of *Wiwaxia corrugata* (Matthew).

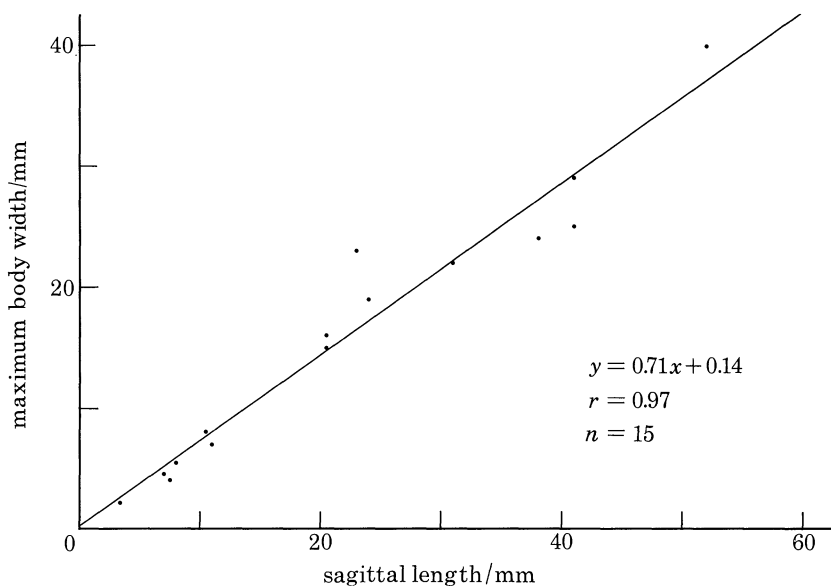
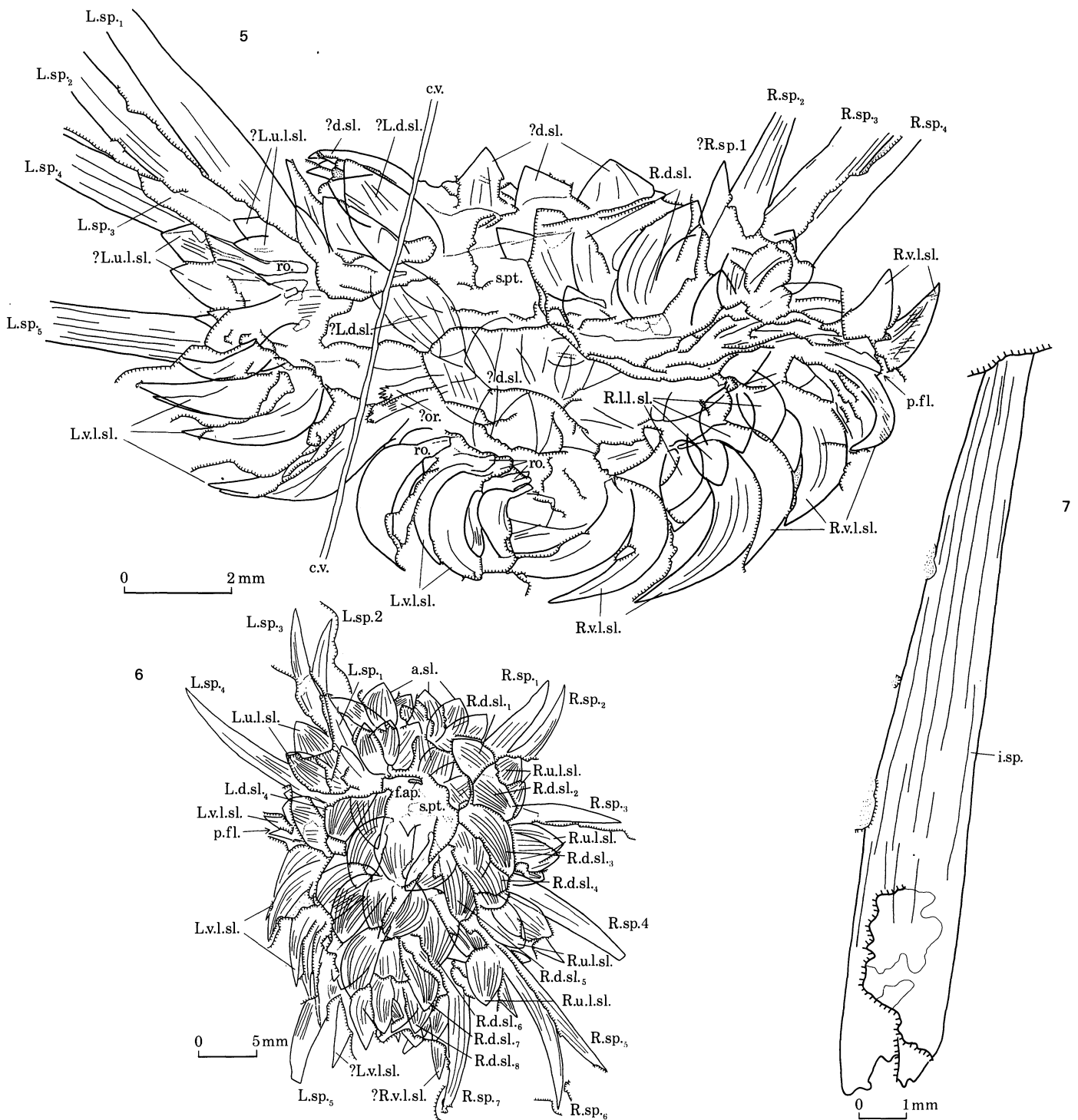


FIGURE 4. Bivariate plot of sagittal length against maximum body width in 15 specimens of *Wiwaxia corrugata* (Matthew).



DESCRIPTION OF PLATE 1 AND FIGURES 5-7

*Wiwaxia corrugata* (Matthew). Phyllopod bed  
(Walcott Quarry) and *Ogygopsis* Shale (Mt Stephen).

FIGURE 5. U.S.N.M. 198668, composite explanatory drawing of part and counterpart, see figures 8-10.

FIGURE 6. U.S.N.M. 57635, composite explanatory drawing of part and counterpart, see figures 11-13.

FIGURE 7. R.O.M. 996 CM, explanatory drawing of part, see figure 14.

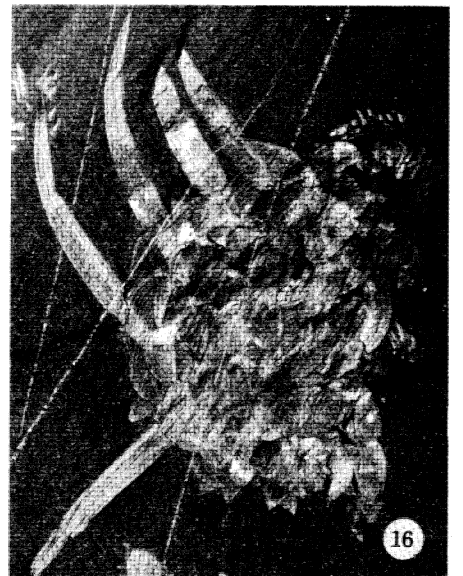
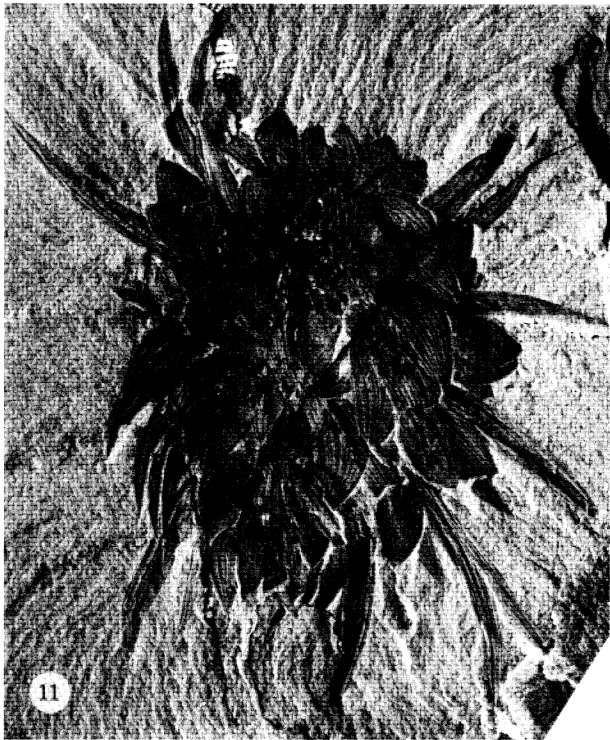
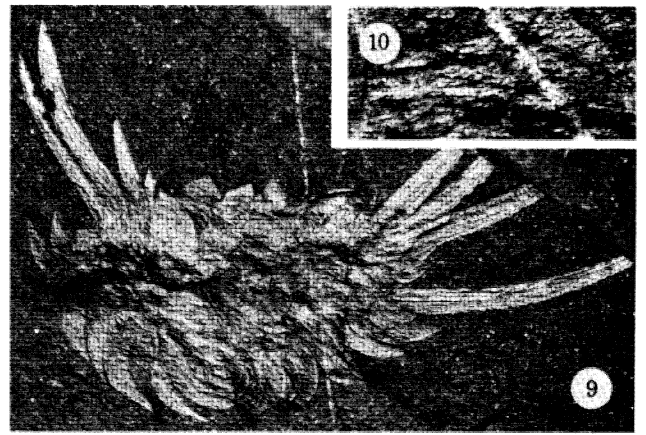
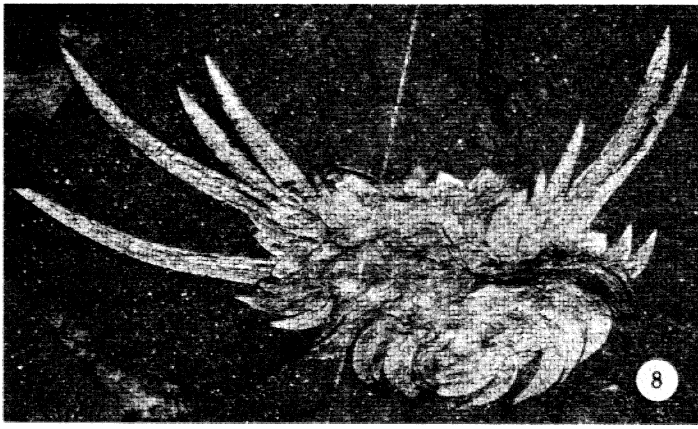
FIGURES 8, 9 AND 10. U.S.N.M. 198668, subvertical-folded. Figure 8, part, complete, high angle light from south (magn.  $\times 3.8$ ); figure 9, counterpart, complete, high angle light from northeast (magn.  $\times 3.8$ ); figure 10, counterpart, organ of uncertain affinities, high angle light from south (magn.  $\times 15$ ).

FIGURES 11, 12 AND 13. U.S.N.M. 57635, parallel, anterior folded downwards. Figure 11, part, complete, low angle light from southeast (magn.  $\times 2.1$ ), original of Walcott 1911 (plate 21, figure 3); figure 12, counterpart, complete, low angle light from east (magn.  $\times 2.1$ ); figure 13, part, detail of right anterior region, high angle light from northwest (magn.  $\times 4.3$ ).

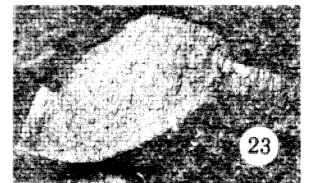
FIGURE 14. R.O.M. 996 CM, part, isolated spine, ordinary white light (magn.  $\times 6.5$ ), holotype. Original of Matthew (1899, plate 1, figure 3), specimen from *Ogygopsis* Shale.

FIGURE 15. U.S.N.M. 57633, counterpart, parallel, incomplete entire specimen, high angle light from south-east (magn.  $\times 2.4$ ). Original of Walcott 1911 (plate 21, figure 1).

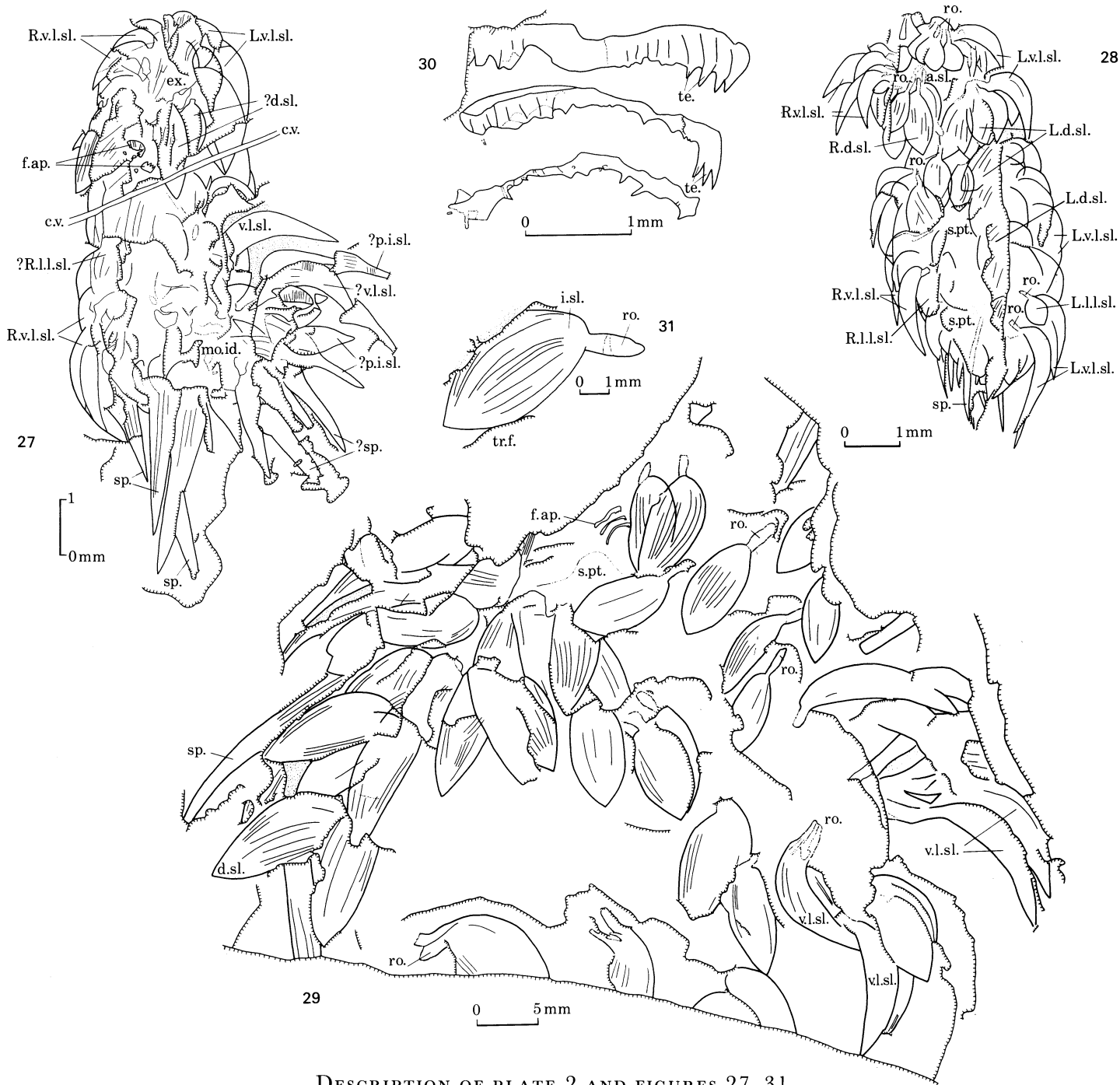
FIGURE 16. R.O.M. 32570, part, oblique, complete, high angle light from southeast (magn.  $\times 1.8$ ).



FIGURES 8-16. For description see opposite.



FIGURES 17-26. For description see opposite.



DESCRIPTION OF PLATE 2 AND FIGURES 27-31

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

FIGURES 17-19. U.S.N.M. 233149 (counterpart is 200101), parallel, complete individual preserved in act of moulting.

Figure 17, counterpart, high angle light from southwest (magn.  $\times 8$ ); figure 18, part, high angle light from northwest (magn.  $\times 9$ ); figure 19, part, low angle light from northeast (magn.  $\times 9$ ).

FIGURE 20. U.S.N.M. 277889, counterpart, parallel, complete juvenile, high angle light from west (magn.  $\times 8$ ).

FIGURES 21 AND 22. U.S.N.M. 199181, part, semi-isolated assemblage. Figure 21, complete, low angle light from southwest (magn.  $\times 1.4$ ); figure 22, feeding apparatus, high angle light from south (magn.  $\times 11$ ).

FIGURE 23. G.S.C. 45349, part, isolated dorsal sclerite, high angle light from north (magn.  $\times 5.5$ ).

FIGURES 24, 25 AND 26. U.S.N.M. 57634, parallel, complete. Figure 24, part, high angle light from southwest (magn.  $\times 2.3$ ); figure 25, part, low angle light from north (magn.  $\times 2.3$ ); original of Walcott 1911 (plate 21, figure 2); figure 26, counterpart, low angle light from northwest (magn.  $\times 2.2$ ).

FIGURE 27. U.S.N.M. 233149 (counterpart is 200101), composite explanatory drawing of part and counterpart, see figures 17-19.

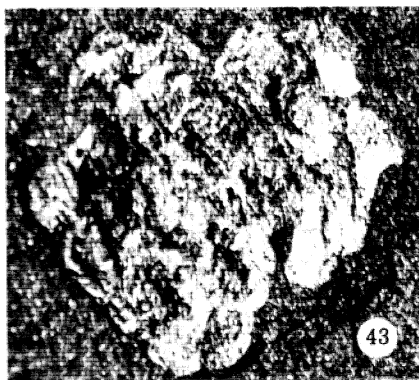
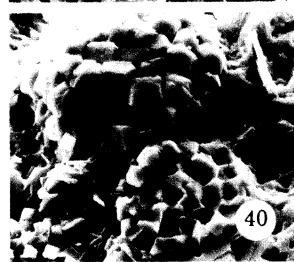
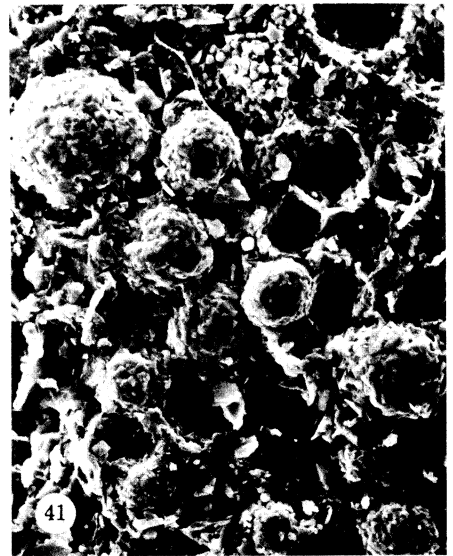
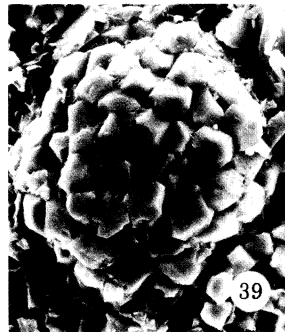
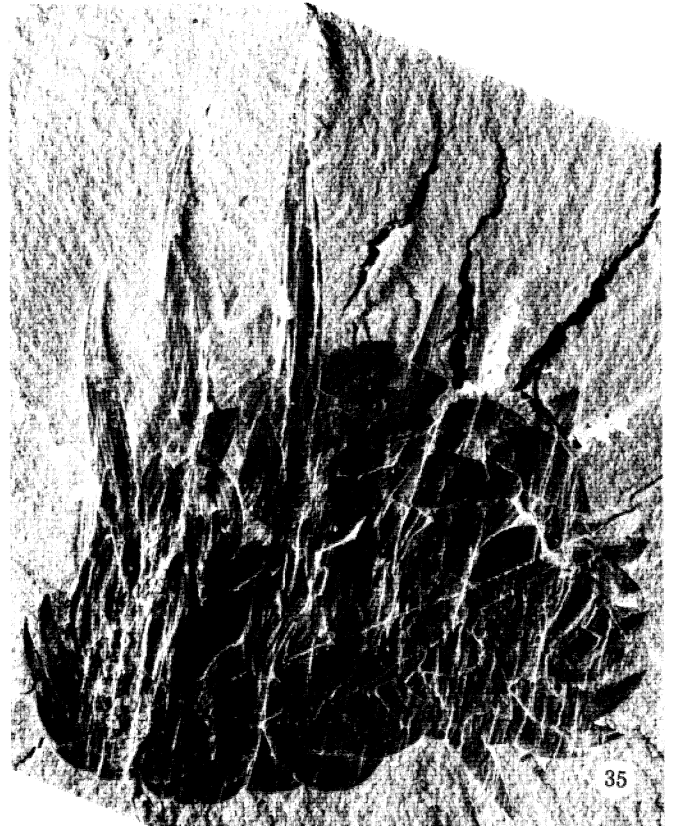
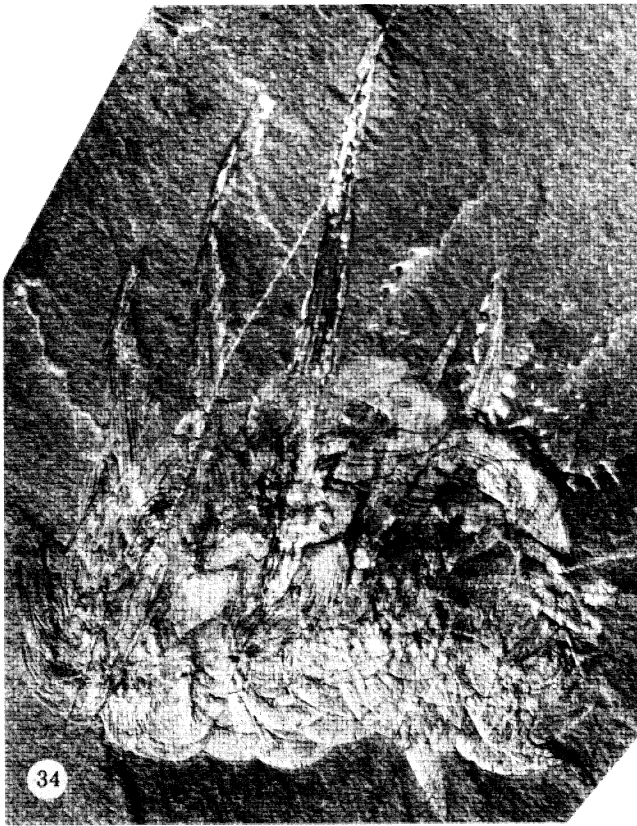
FIGURE 28. U.S.N.M. 277889, composite explanatory drawing of part and counterpart, see figure 20.

FIGURE 29. U.S.N.M. 199181, explanatory drawing of part, see figure 21.

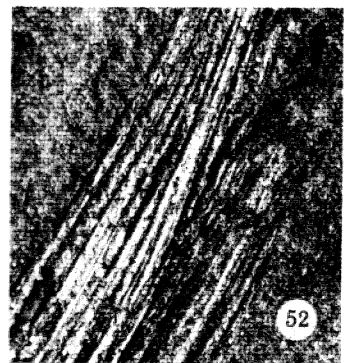
FIGURE 30. U.S.N.M. 199181, explanatory drawing of feeding apparatus, see figure 22.

FIGURE 31. G.S.C. 45349, explanatory drawing of sclerite, see figure 23.



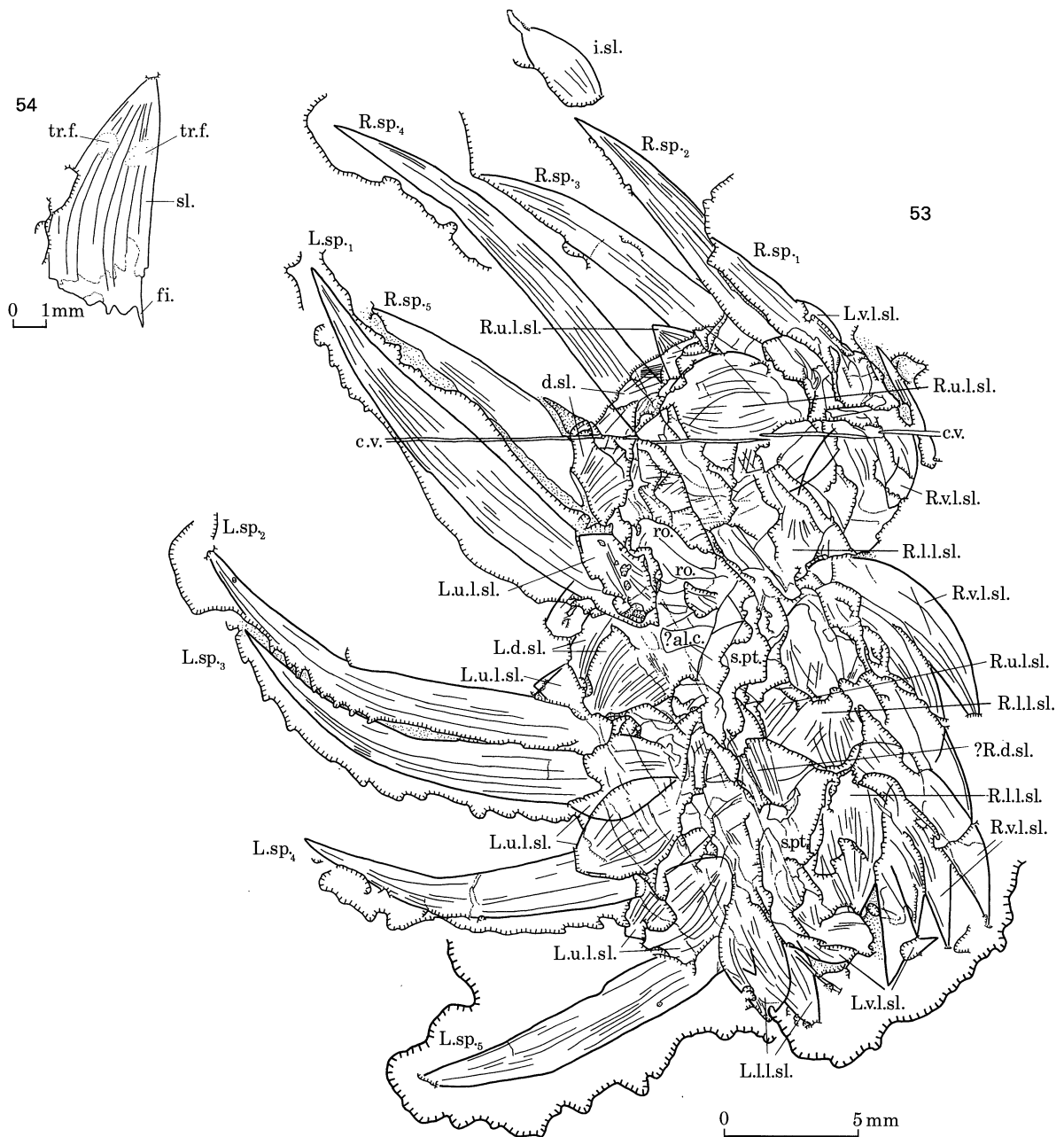


FIGURES 34-44. For description see opposite.



FIGURES 45-52. For description see opposite.





DESCRIPTION OF PLATE 4 AND FIGURES 53 AND 54

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

FIGURES 45-48. U.S.N.M. 198680, lateral-oblique, complete. Figure 45, part, high angle light from west (magn.  $\times 2.8$ ); figure 46, part, low angle light from northeast (magn.  $\times 2.7$ ); figure 47, counterpart, high angle light from north (magn.  $\times 3$ ); figure 48, counterpart, low angle light from south (magn.  $\times 3.2$ ).

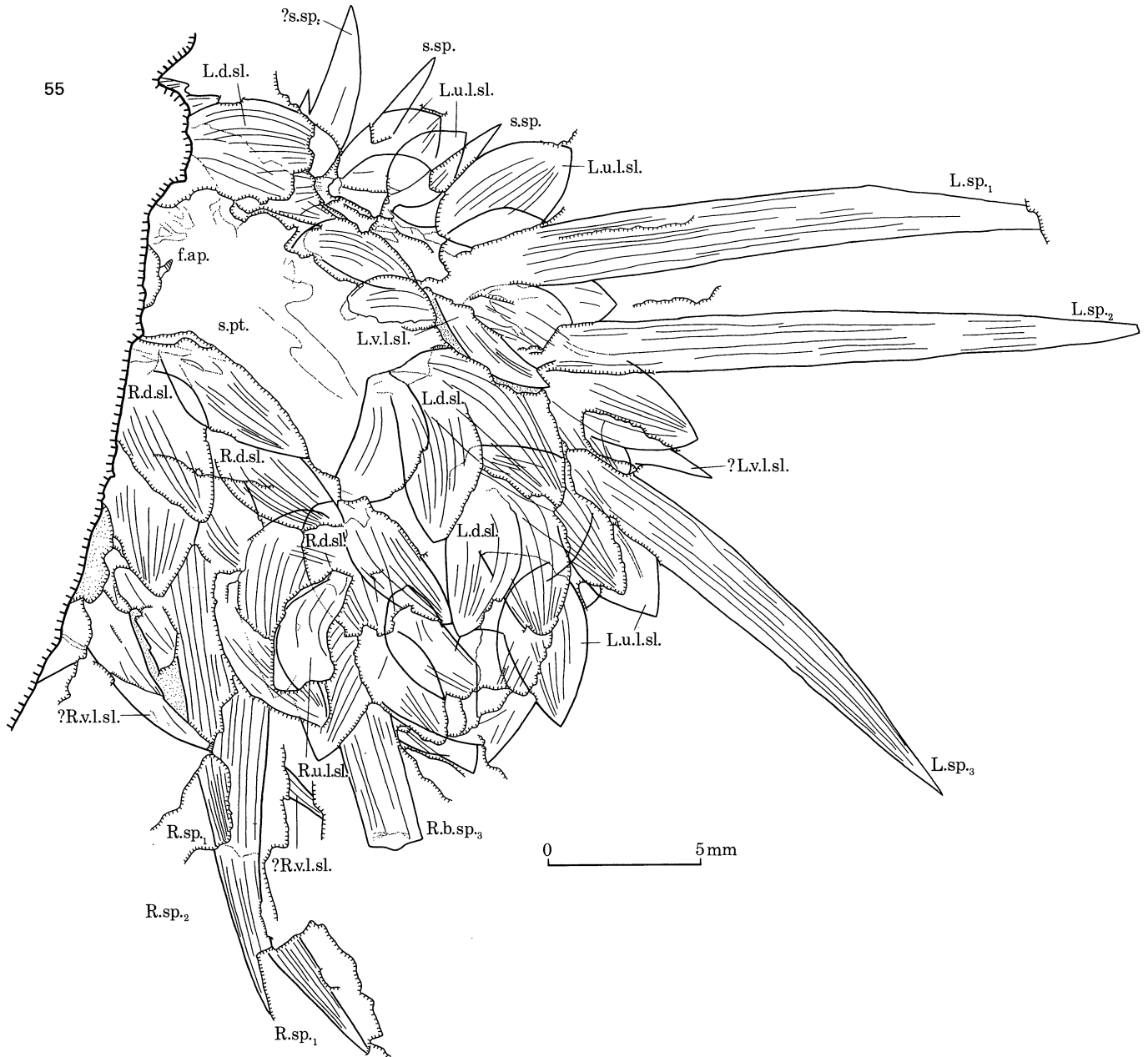
FIGURE 49. U.S.N.M. 198674, part, oblique, juvenile, high angle light from northeast (magn.  $\times 11$ ).

FIGURE 50. G.S.C. 45354, part, isolated sclerite showing evidence of decay, high angle light from north (magn.  $\times 6.1$ ).

FIGURES 51 AND 52. G.S.C. 45344, part, oblique. Figure 51, broken spine towards anterior, high angle light from north (magn.  $\times 8$ ); figure 52, two spines near midpoint with right spine broken and left spine entire, high angle light from southeast (magn.  $\times 9$ ).

FIGURE 53. U.S.N.M. 198680, composite explanatory drawing of part and counterpart, see figures 45-48.

FIGURE 54. G.S.C. 45354, explanatory drawing of part, see figure 50.



### DESCRIPTION OF PLATE 5 AND FIGURE 55

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry). Figures 55-61.

*Pollingeria grandis* Walcott. Phyllopod bed (Walcott Quarry). Figures 62 and 63.

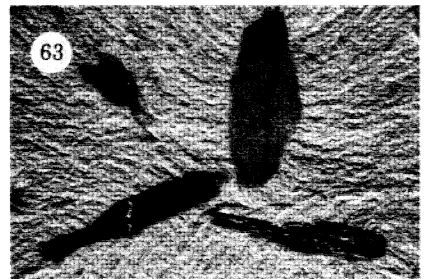
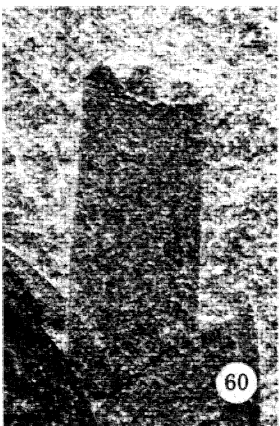
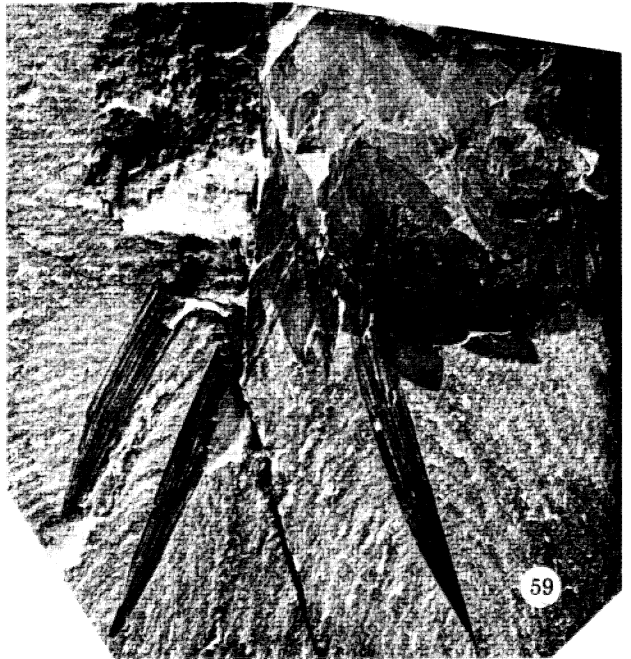
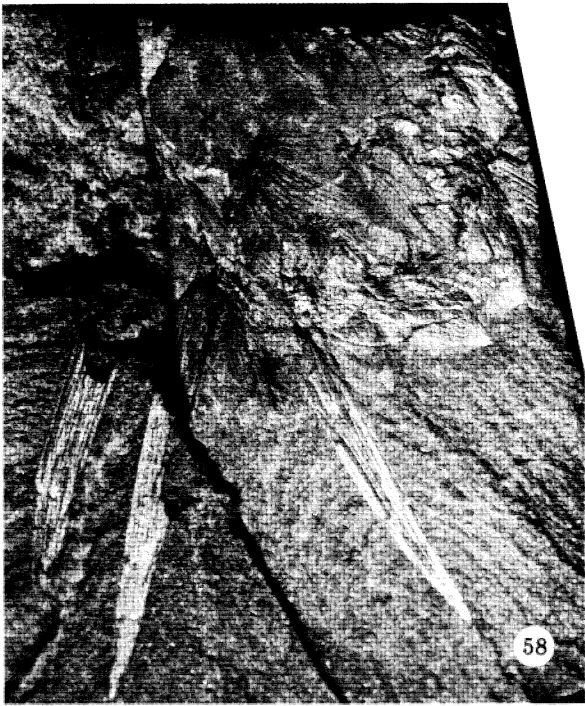
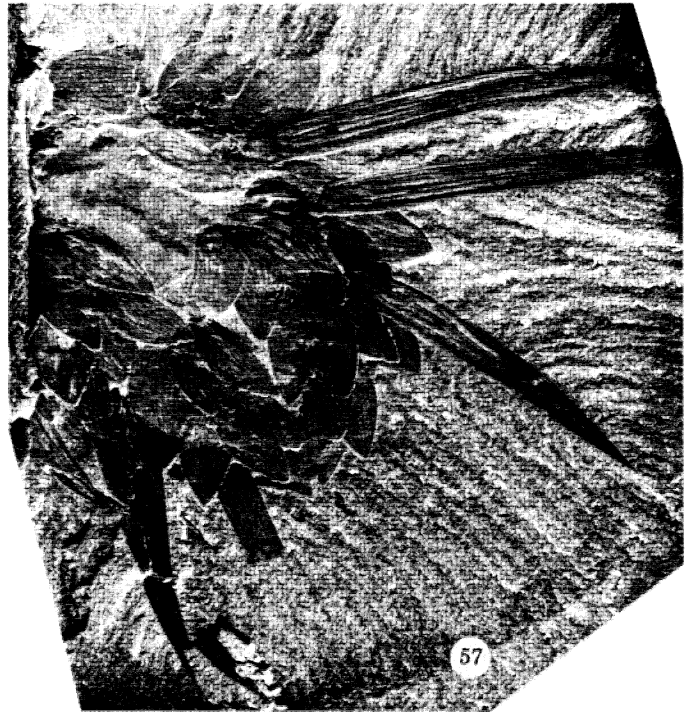
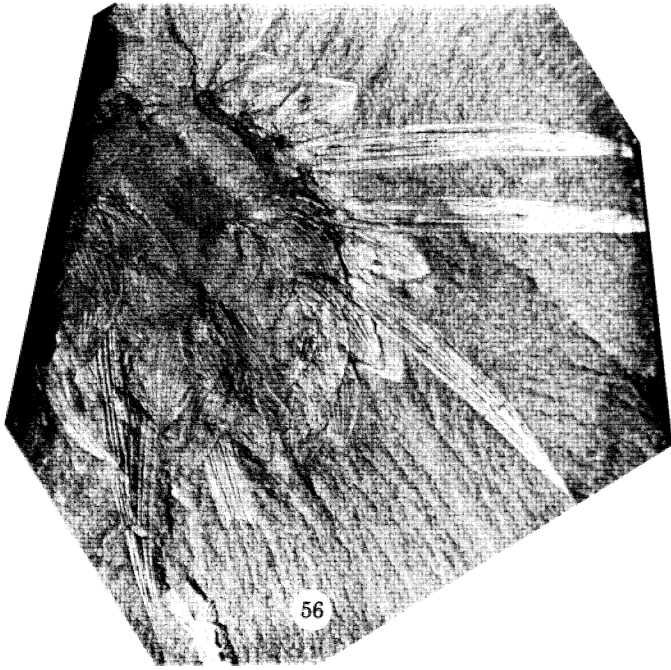
FIGURE 55. U.S.N.M. 199910 (part is 199905), composite explanatory drawing of part and counterpart, see figures 56-60.

FIGURE 56-60. U.S.N.M. 199910 (part is 199905), parallel. Figure 56, counterpart, complete, high angle light from east (magn.  $\times 2.4$ ); figure 57, counterpart, complete, low angle light from northwest (magn.  $\times 2.8$ ); figure 58, part, complete, high angle light from south (magn.  $\times 3.2$ ); figure 59, part, complete, low angle light from north (magn.  $\times 3$ ); figure 60, counterpart, broken spine, low angle light from north (magn.  $\times 10$ ).

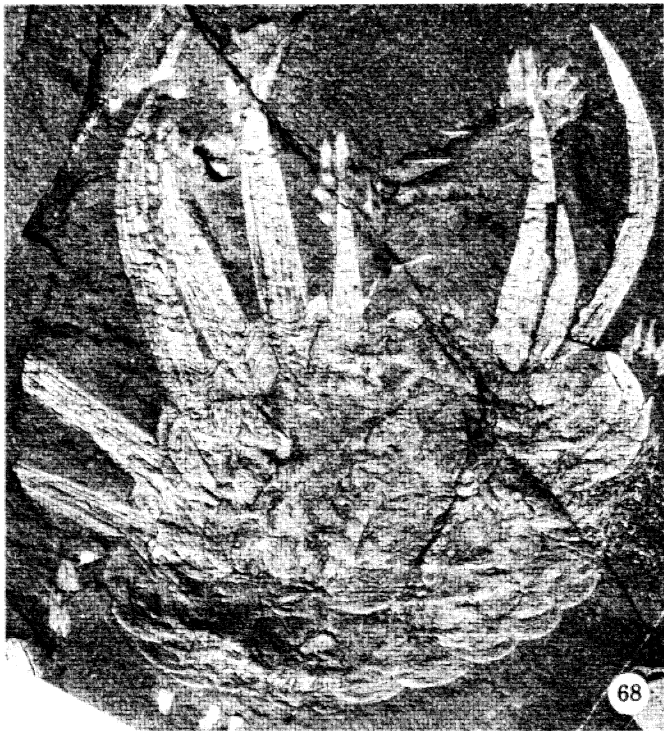
FIGURE 61. U.S.N.M. 198675, counterpart, parallel, complete, high angle light from north (magn.  $\times 4.8$ ).

FIGURE 62. U.S.N.M. 57640, part, complete, low angle light from northeast (magn.  $\times 4$ ). Original of Walcott 1911 (plate 21, figure 8).

FIGURE 63. U.S.N.M. 57641, part, complete, three specimens, low angle light from south (magn.  $\times 1.9$ ). Original of Walcott 1911 (plate 21, figure 9).

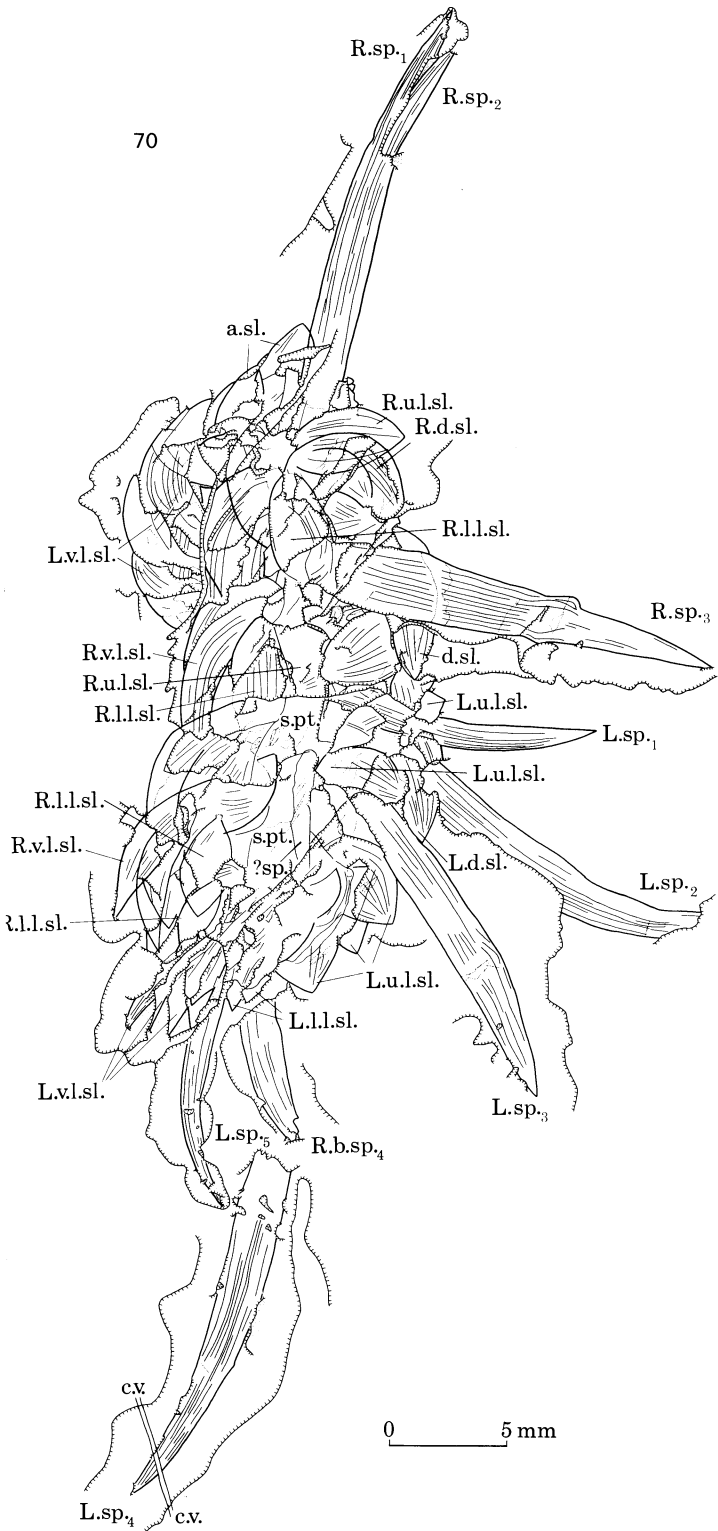


FIGURES 56-63. For description see opposite.

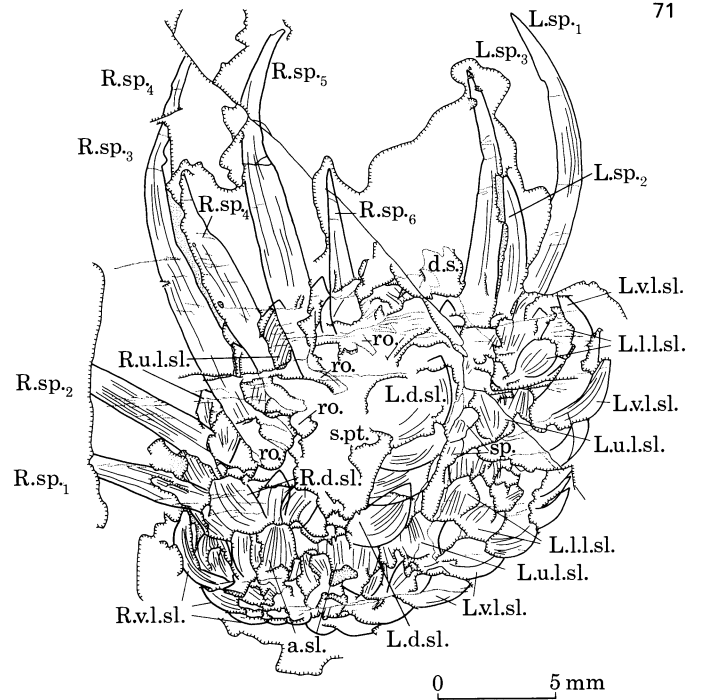


FIGURES 64-69. For description see opposite.

70



71



### DESCRIPTION OF PLATE 6 AND FIGURES 70-71

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

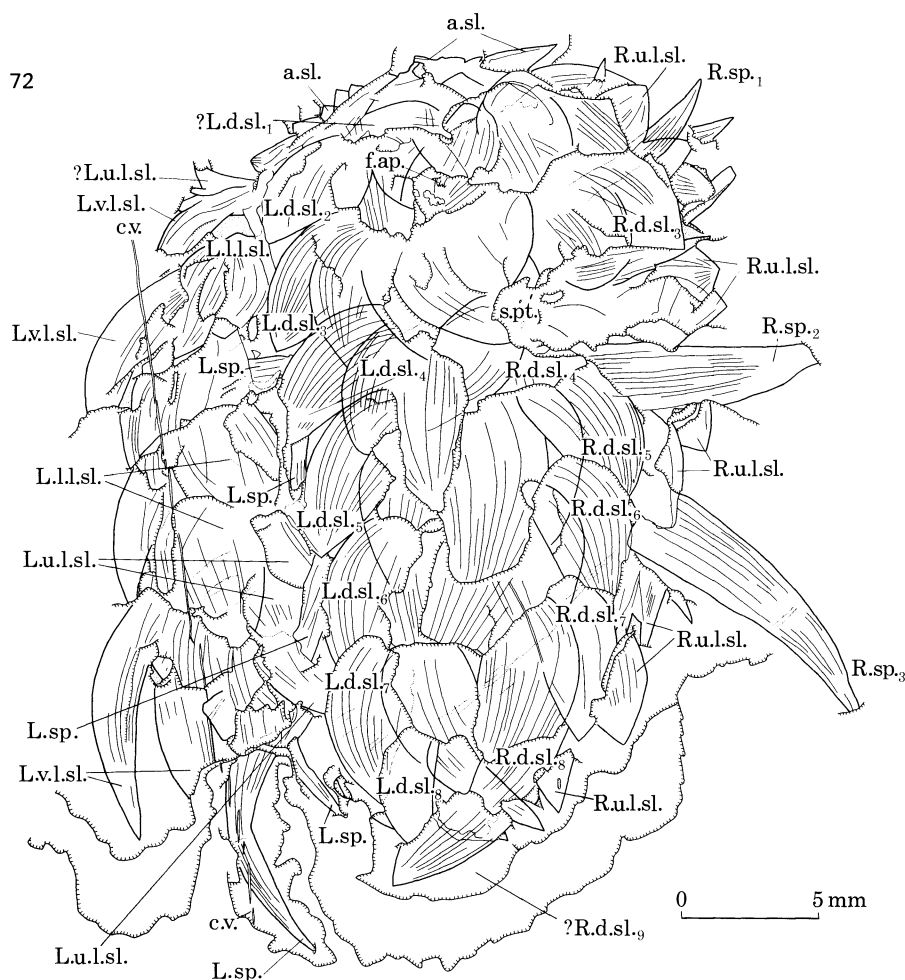
FIGURES 64-67. U.S.N.M. 198678, counterpart, lateral. Figure 64, complete, high angle light from east (magn.  $\times 2.3$ ); figure 65, complete, low angle light from west (magn.  $\times 2.2$ ); figure 66, spine with disruption, high angle light from south (magn.  $\times 9$ ); figure 67, broken spine to left, high angle light from east (magn.  $\times 9$ ).

FIGURES 68 AND 69. U.S.N.M. 198679, part, inclined, complete. Figure 68, high angle light from southeast (magn.  $\times 3.7$ ); figure 69, low angle light from east (magn.  $\times 3.8$ ).

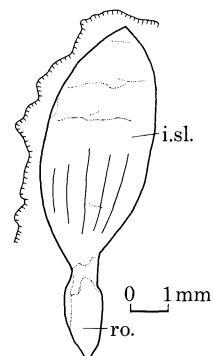
FIGURE 70. U.S.N.M. 198678, explanatory drawing of counterpart, see figures 64-67.

FIGURE 71. U.S.N.M. 198679, explanatory drawing of part, see figures 68 and 69.

72



73



### DESCRIPTION OF PLATE 7 AND FIGURES 72 AND 73

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

FIGURE 72. U.S.N.M. 199894, explanatory drawing of part, see figures 74–76.

FIGURE 73. U.S.N.M. 200012, explanatory drawing of part, see figure 78.

FIGURES 74–76. U.S.N.M. 199894, part, parallel-oblique. Figure 74, complete, high angle light from east (magn.  $\times 3.2$ ); figure 75, complete low angle light from west (magn.  $\times 3.2$ ); figure 76, detail of dorsal sclerites, low angle light from west (magn.  $\times 6.5$ ).

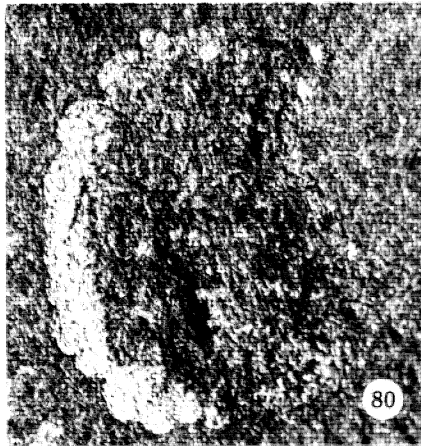
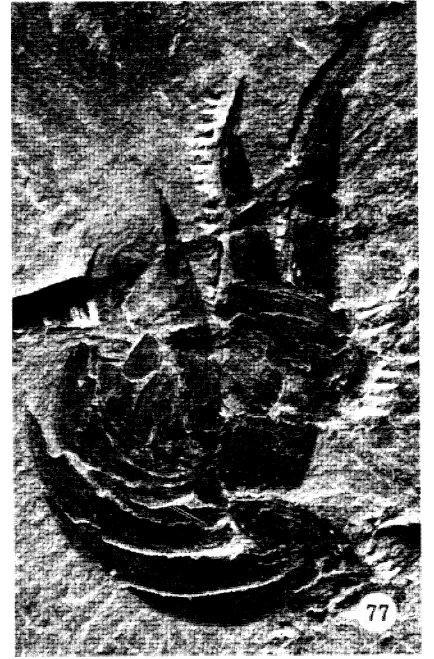
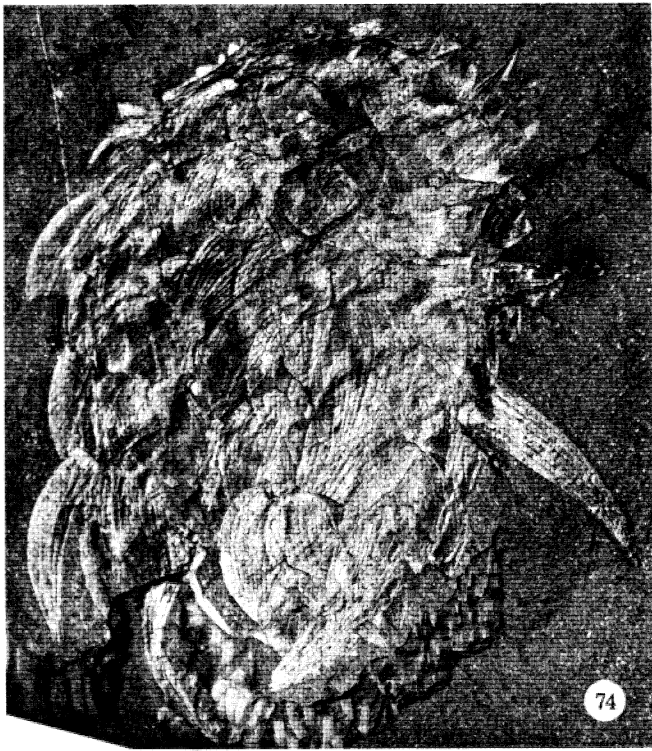
FIGURE 77. G.S.C. 45345, part, semi-isolated assemblage, low angle light from north (magn.  $\times 1.3$ ).

FIGURE 78. U.S.N.M. 200012, part, isolated ?lower lateral sclerite, high angle light from east (magn.  $\times 6.4$ ).

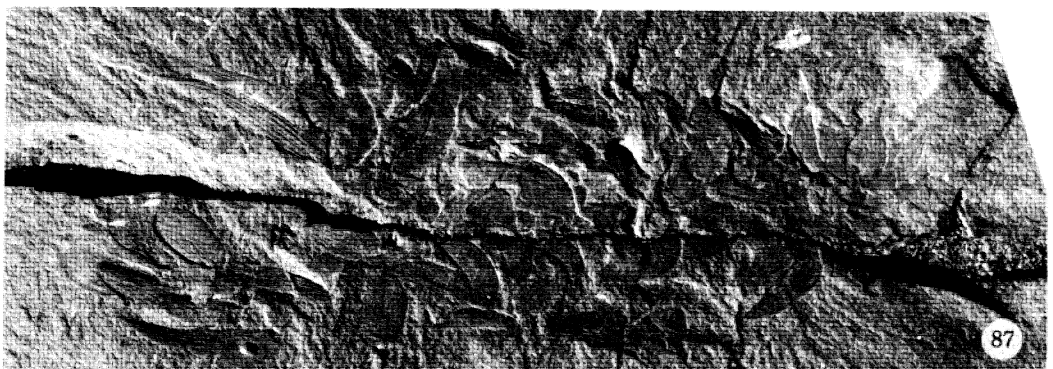
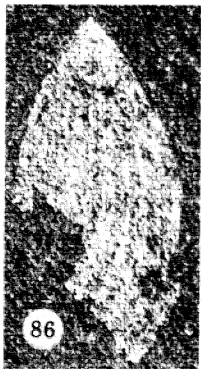
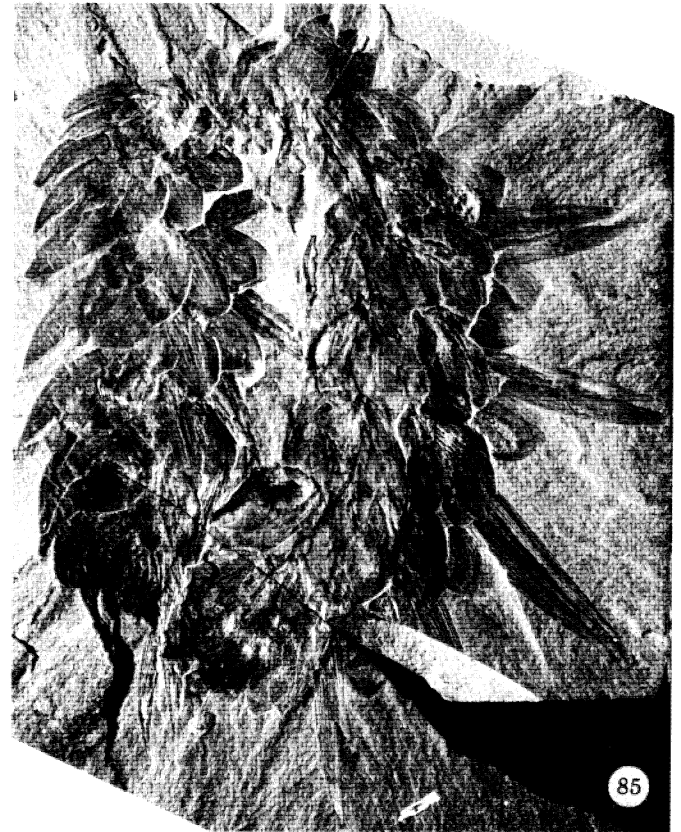
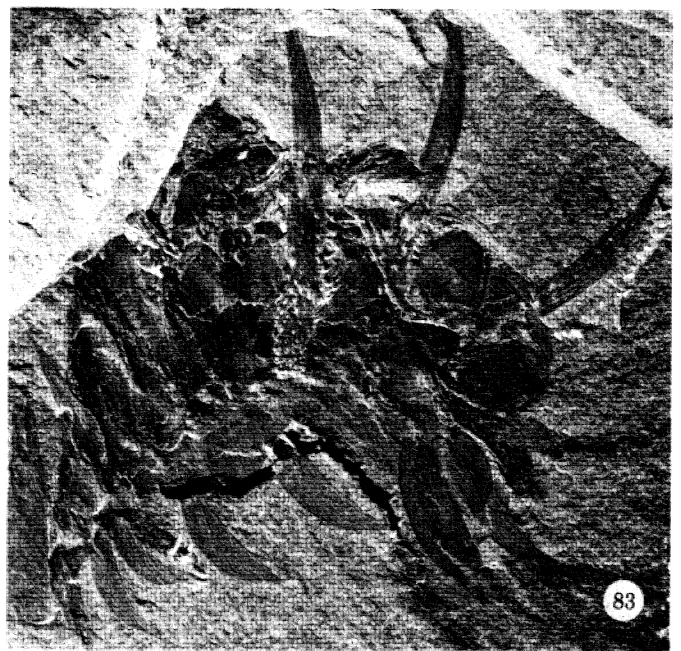
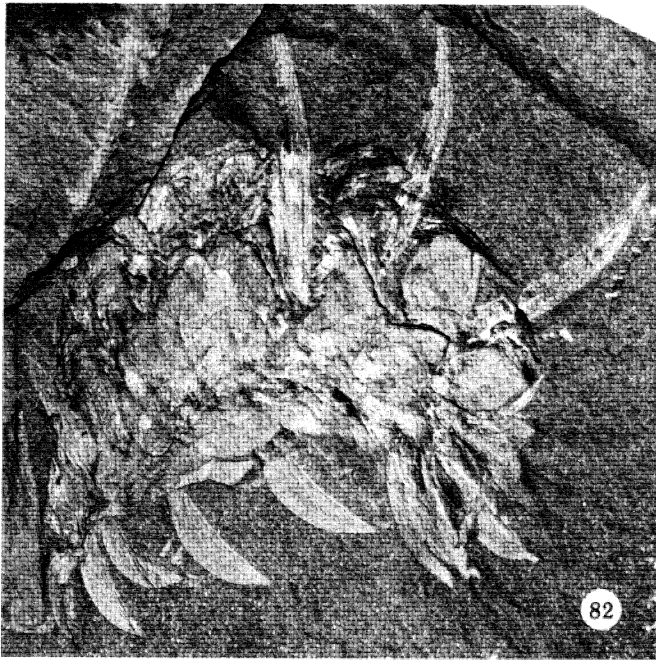
FIGURE 79. U.S.N.M. 200140, part, isolated spine, high angle light from northeast (magn.  $\times 1.9$ ). Original of Walcott 1908 (plate 1, figure 12).

FIGURE 80. G.S.C. 45346, part, ?oblique, juvenile, high angle light from east (magn.  $\times 9$ ).

FIGURE 81. G.S.C. 45347, part, ?parallel, juvenile, high angle light from southeast (magn.  $\times 8$ ).

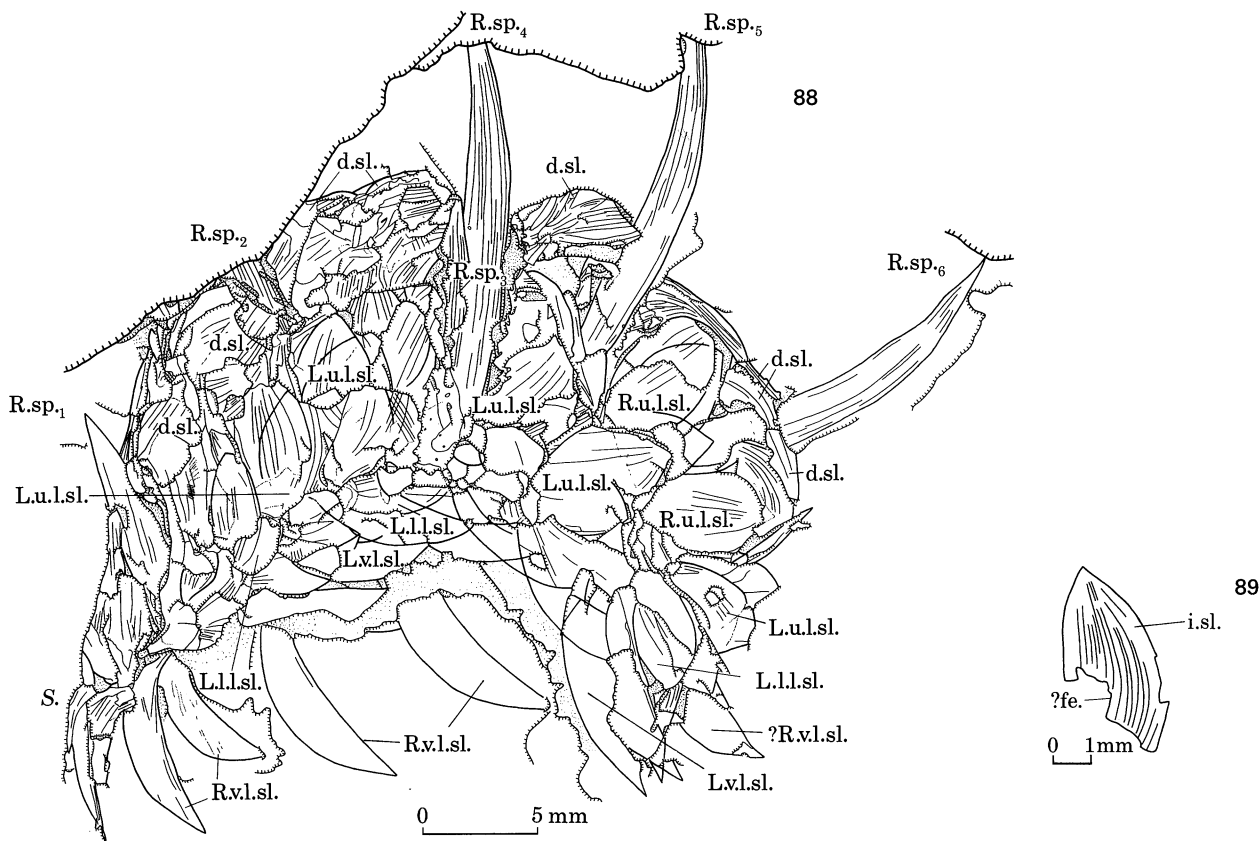


FIGURES 74-81. For description see opposite.



FIGURES 82-87. For description see opposite.





DESCRIPTION OF PLATE 8 AND FIGURES 88 AND 89

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

FIGURES 82 AND 83. U.S.N.M. 198681, part, lateral, complete (magn.  $\times 2.2$ ). Figure 82, high angle light from south; figure 83, low angle light from north.

FIGURES 84 AND 85. U.S.N.M. 198745, oblique, complete (magn.  $\times 1.7$ ). Figure 84, part, low angle light from northwest; figure 85, counterpart, low angle light from west.

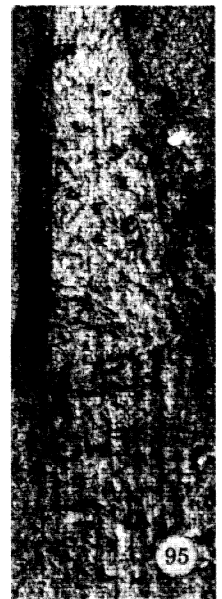
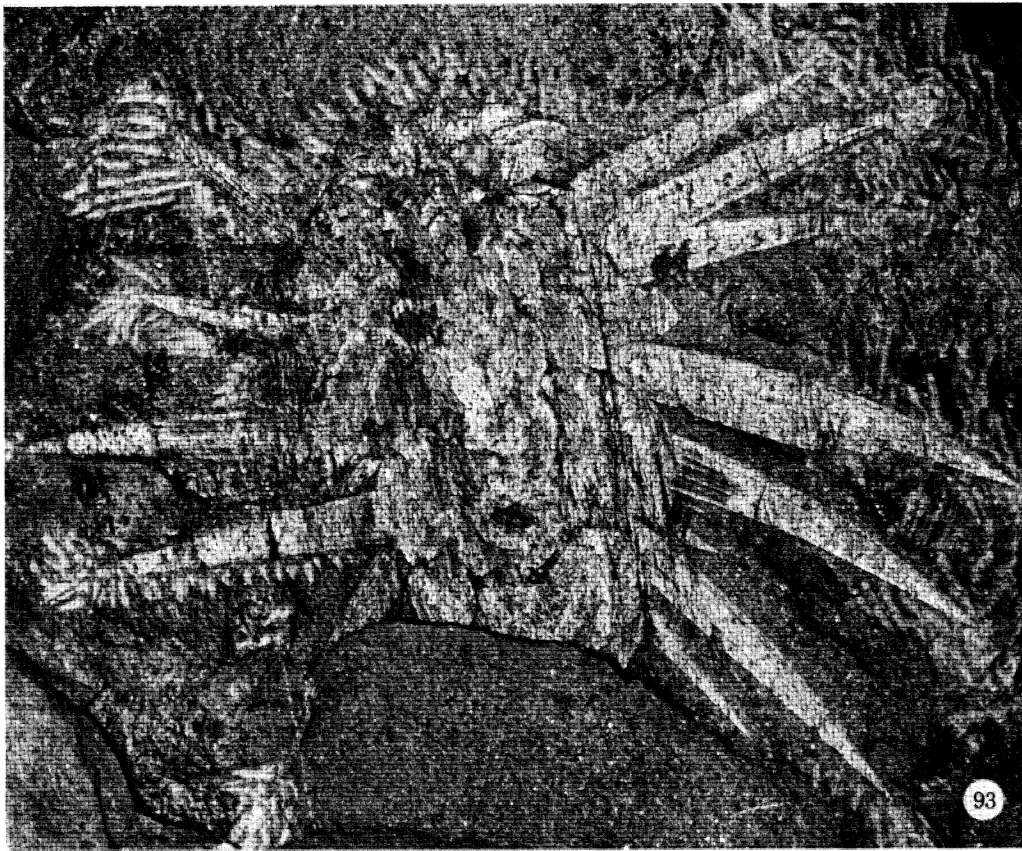
FIGURE 86. G.S.C. 45355, part, isolated sclerite incomplete owing to possible fracturing, high angle light from east (magn.  $\times 7.3$ ).

FIGURE 87. U.S.N.M. 198747, part, semi-isolated assemblage, low angle light from southwest (magn.  $\times 1.4$ ).

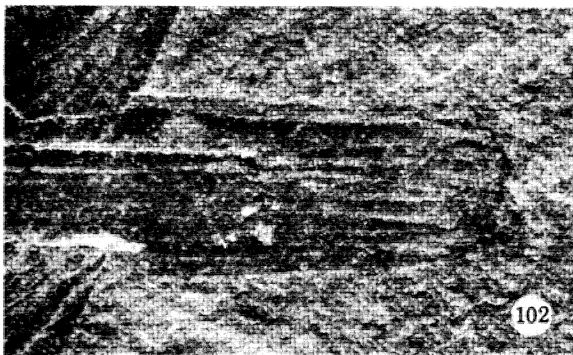
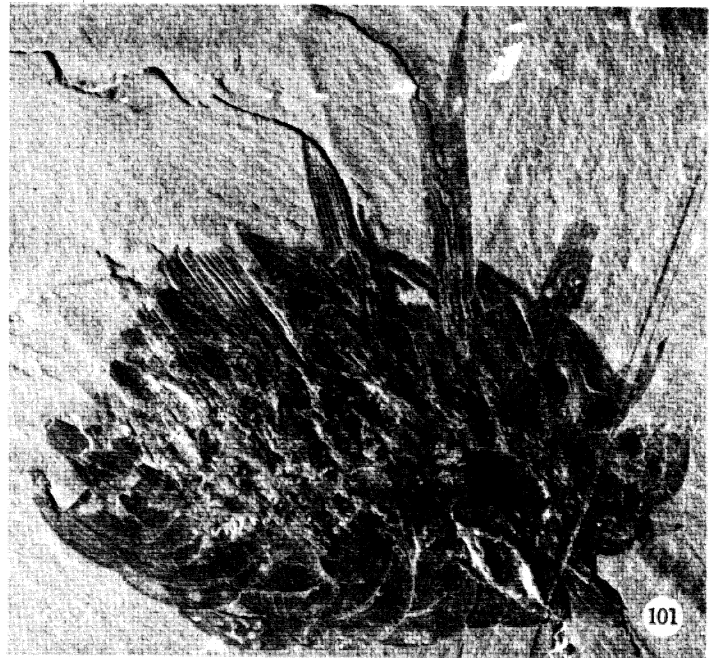
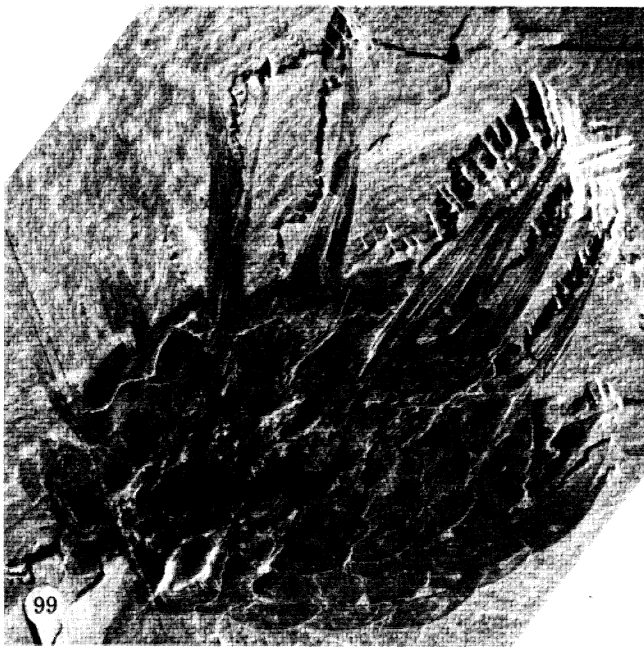
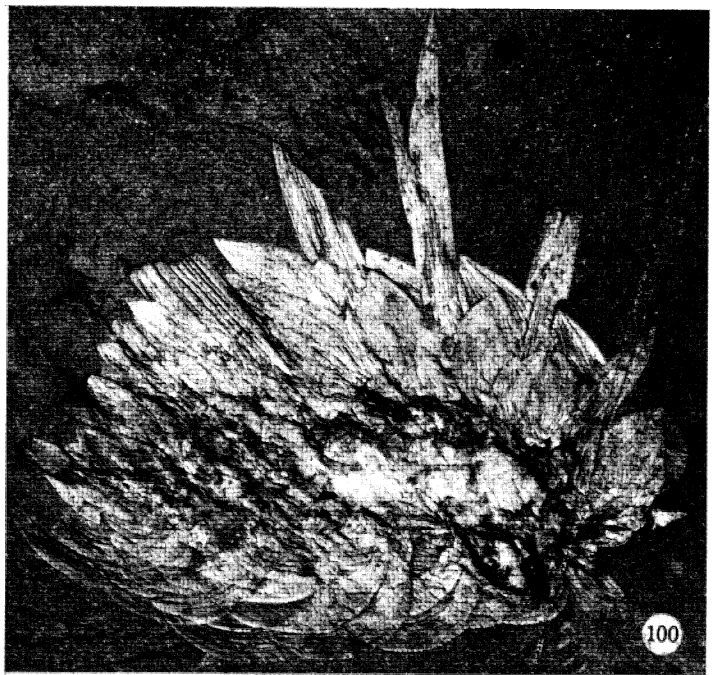
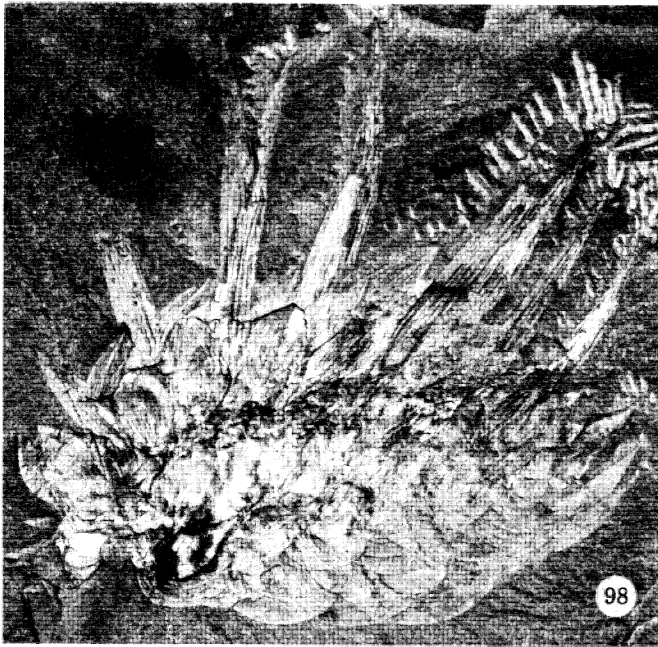
FIGURE 88. U.S.N.M. 198681, explanatory drawing of part, see figures 82 and 83.

FIGURE 89. G.S.C. 45355, explanatory drawing of part, see figure 86.



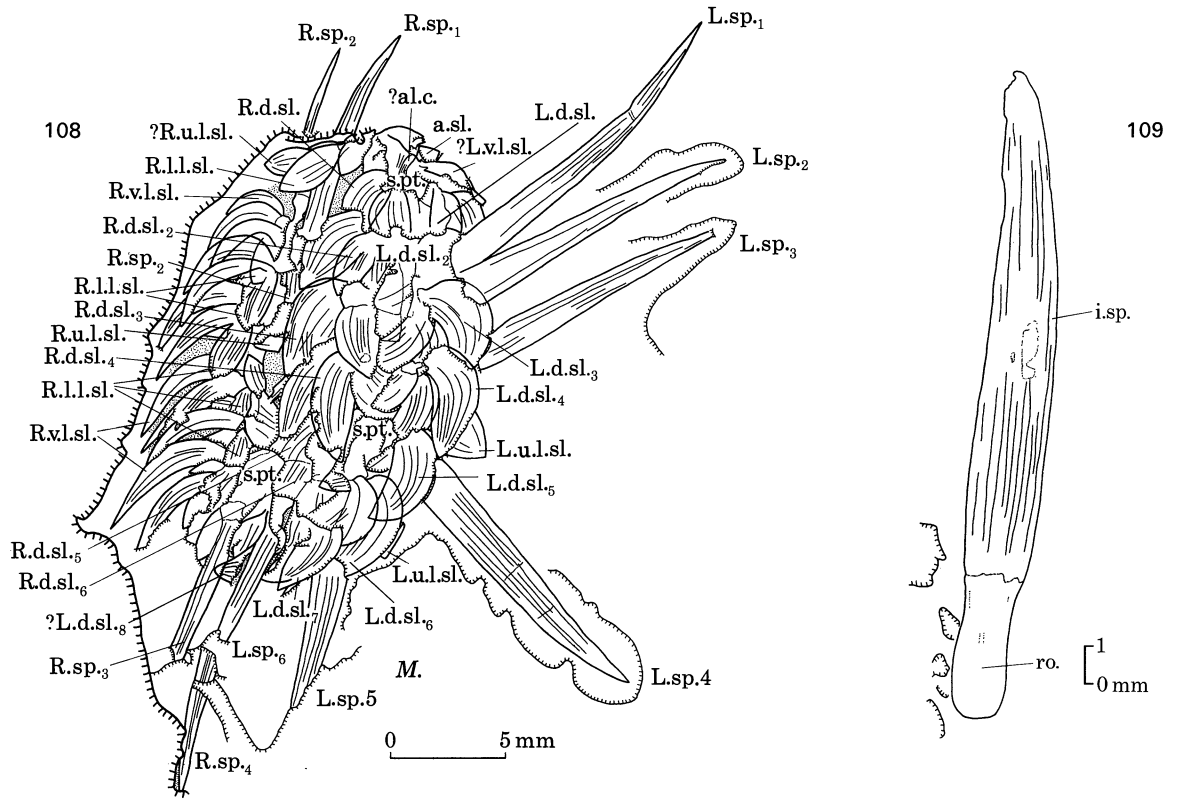


FIGURES 93-97. For description see opposite.



FIGURES 98-104. For description see opposite.

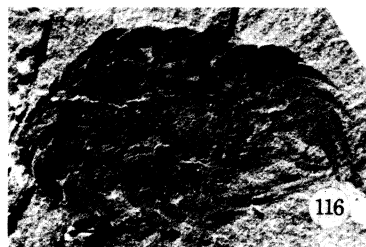
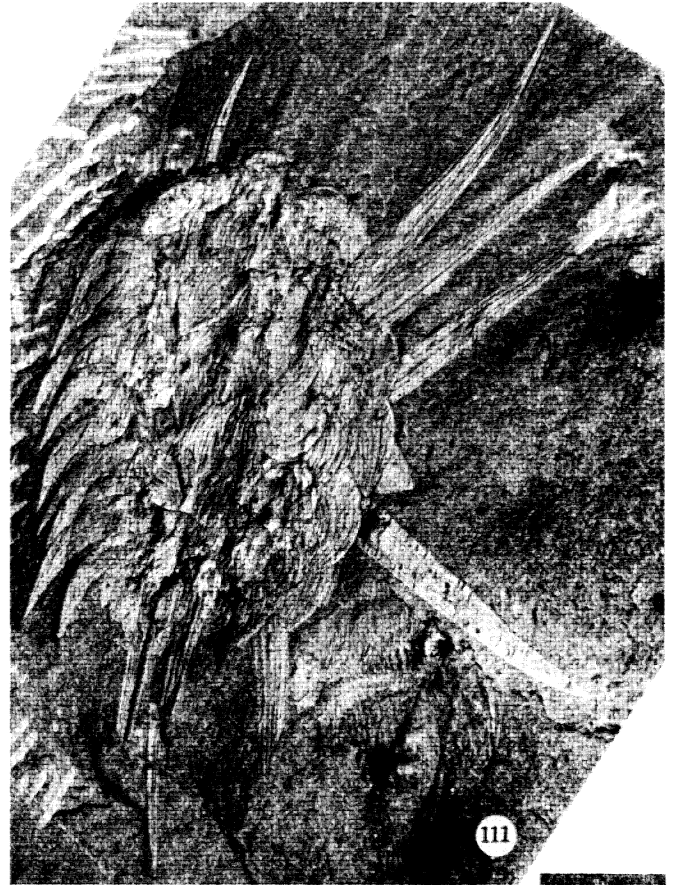




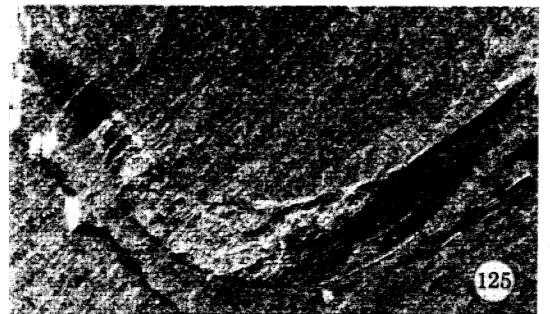
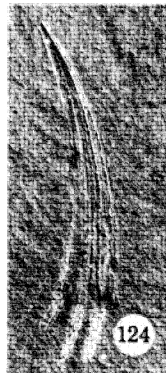
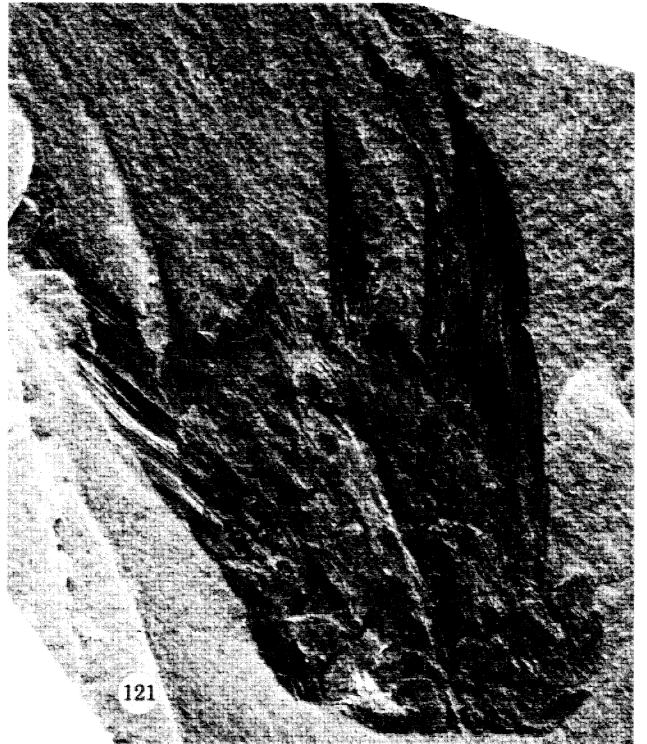
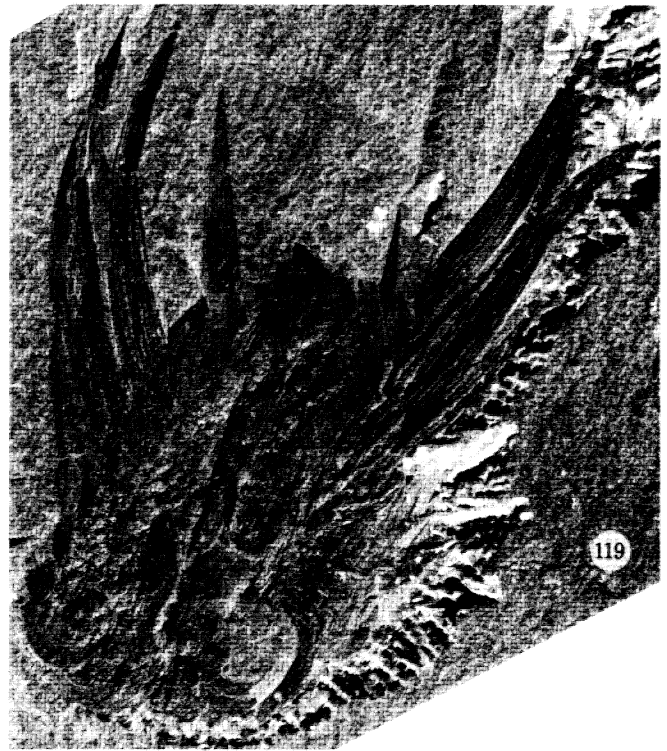
DESCRIPTION OF PLATE 11 AND FIGURES 108 AND 109

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

- FIGURE 108. U.S.N.M. 198677, explanatory drawing of counterpart, see figures 110–113.
- FIGURE 109. G.S.C. 45352, explanatory drawing of part, see figure 114.
- FIGURES 110–113. U.S.N.M. 198667, counterpart, parallel-oblique. Figure 110, complete, low angle light from north (magn.  $\times 3.3$ ); figure 111, complete, high angle light from southwest (magn.  $\times 3.3$ ); figure 112, detail of dorsal sclerites, high angle light from north (magn.  $\times 8$ ); figure 113, detail of right ventro-lateral and adjacent sclerites, high angle light from west (magn.  $\times 5$ ).
- FIGURE 114. G.S.C. 45352, part, isolated spine, high angle light from southwest (magn.  $\times 2.4$ ).
- FIGURES 115 AND 116. U.S.N.M. 198746, counterpart, parallel, complete (magn.  $\times 3.7$ ). Figure 115, high angle light from north; figure 116, low angle light from northwest.
- FIGURE 117. U.S.N.M. 199887, part, semi-isolated assemblage, high angle light from east (magn.  $\times 2.4$ ).

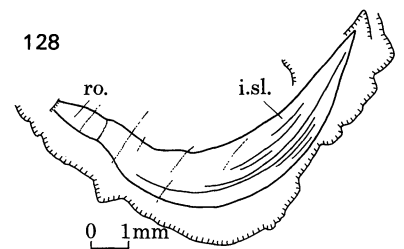
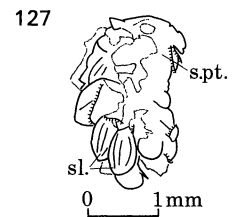
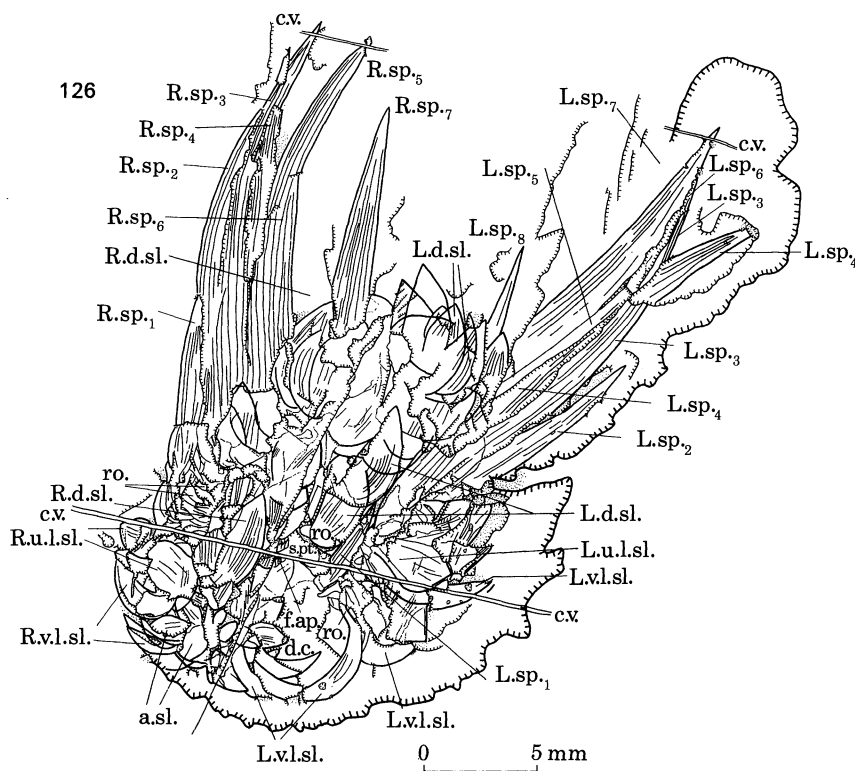


FIGURES 110-117. For description see opposite.



FIGURES 118-125. For description see opposite.





### DESCRIPTION OF PLATE 12 AND FIGURES 126-128

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

FIGURES 118-122. U.S.N.M. 198669, inclined-parallel. Figure 118, part, complete, high angle light from north (magn.  $\times 3.2$ ); figure 119, part, complete, low angle light from southwest (magn.  $\times 3.2$ ); figure 120, counterpart, complete, high angle light from north (magn.  $\times 3.3$ ); figure 121, counterpart, complete, low angle light from west (magn.  $\times 3.2$ ); figure 122, counterpart, feeding apparatus, high angle light from east (magn.  $\times 22.1$ ).

FIGURE 123. U.S.N.M. 229901, counterpart, oblique, juvenile, high angle light from southwest (magn.  $\times 19.6$ ).

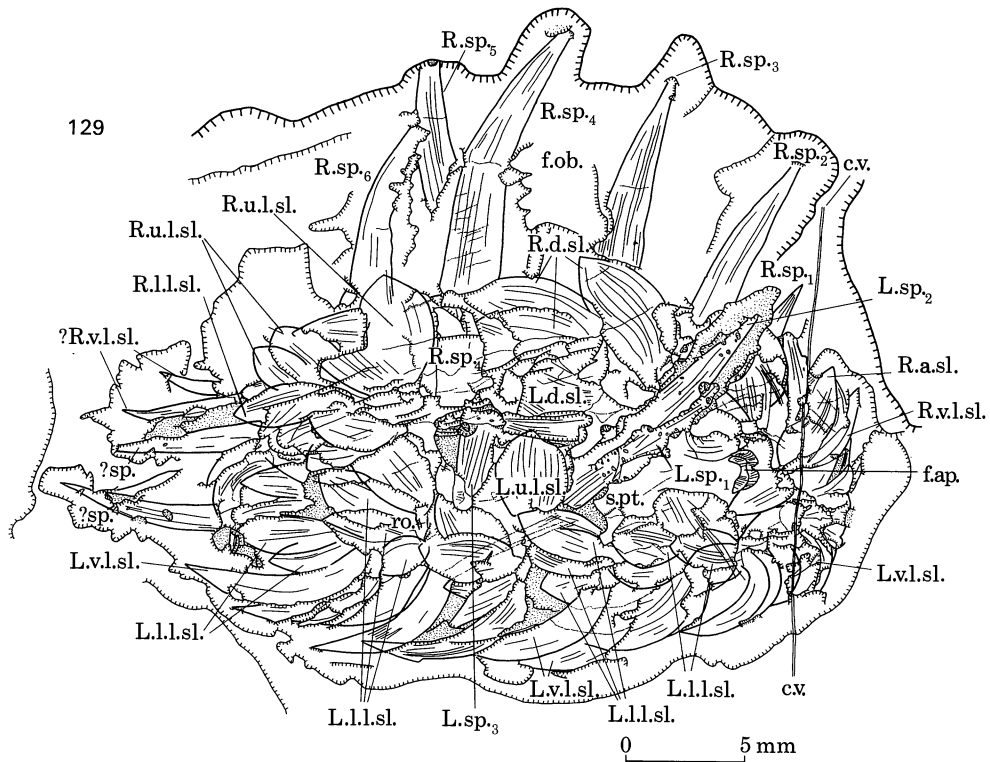
FIGURE 124. G.S.C. 45348, part, isolated spine showing evidence of decay, high angle light from east (magn.  $\times 2.7$ ).

FIGURE 125. U.S.N.M. 200062, part, isolated ventro-lateral sclerite, high angle light from southeast (magn.  $\times 7.4$ ).

FIGURE 126. U.S.N.M. 198669, explanatory composite drawing of part and counterpart, see figures 118-122.

FIGURE 127. U.S.N.M. 229901, explanatory drawing of counterpart, see figure 123.

FIGURE 128. U.S.N.M. 200062, explanatory drawing of part, see figure 125.



DESCRIPTION OF PLATE 13 AND FIGURE 129

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry). Figures 130-135.  
*Pollingeria grandis* Walcott. Phyllopod bed (Walcott Quarry). Figure 136.

FIGURE 129. U.S.N.M. 198676, explanatory drawing of counterpart, see figures 130-132.

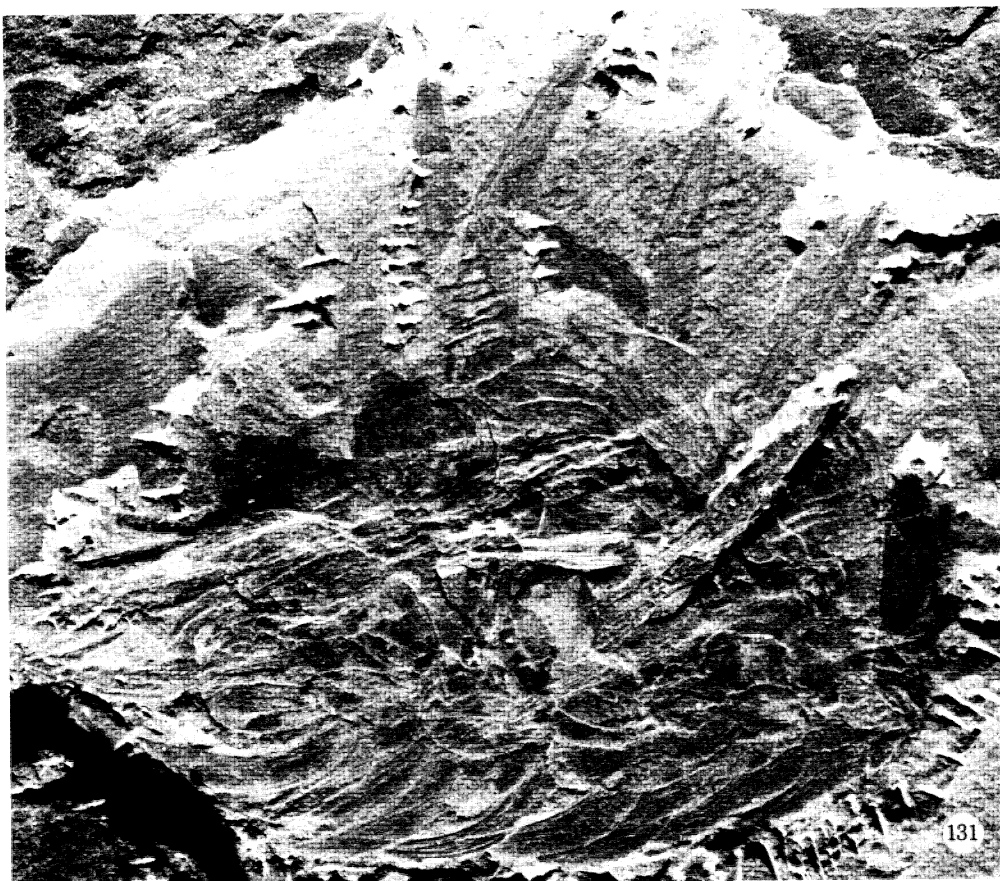
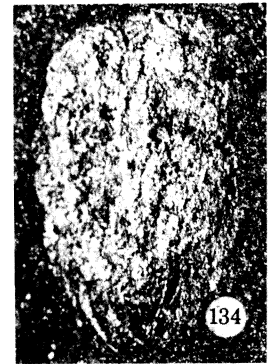
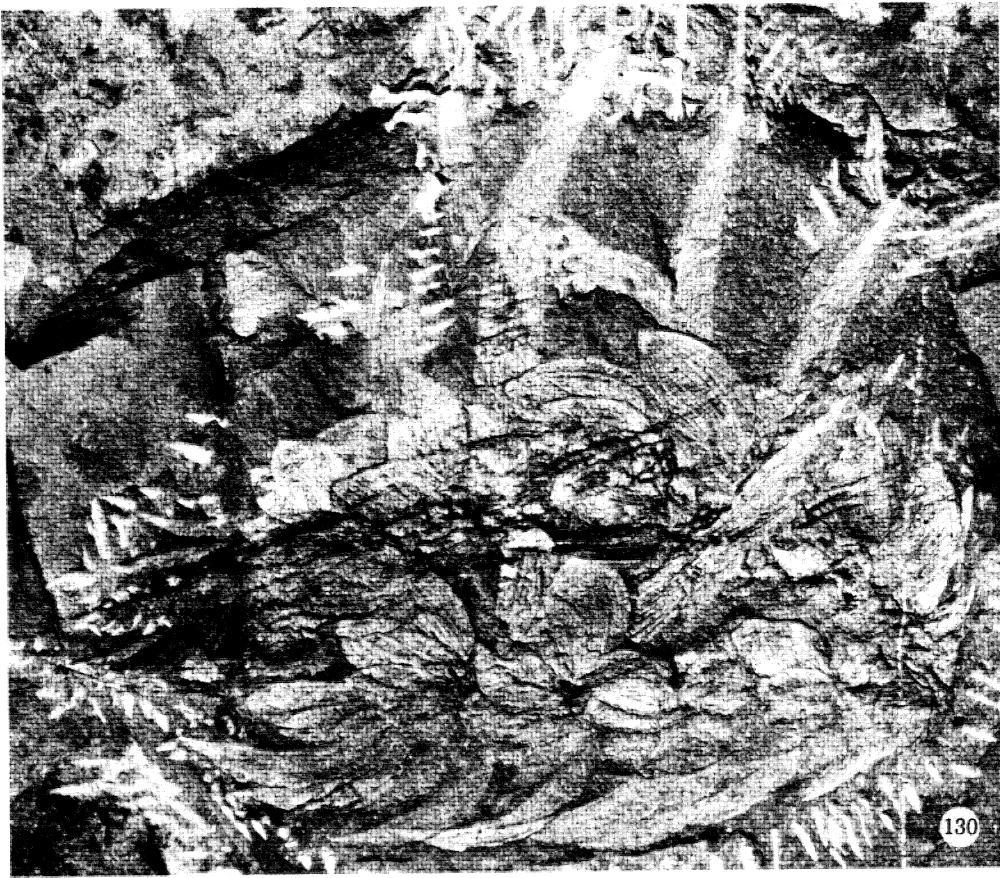
FIGURES 130-132. U.S.N.M. 198676, counterpart, oblique. Figure 130, complete, high angle light from east (magn.  $\times 3.7$ ); figure 131, complete, low angle light from west (magn.  $\times 3.7$ ); figure 132, feeding apparatus, low angle light from east (magn.  $\times 26.7$ ).

FIGURE 133. U.S.N.M. 277890, counterpart, parallel, juvenile, high angle light from northeast (magn.  $\times 6.2$ ).

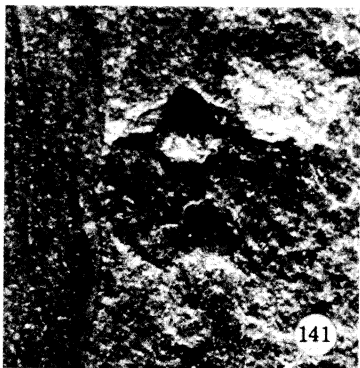
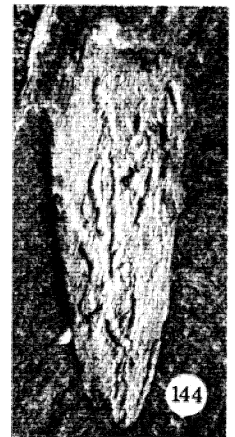
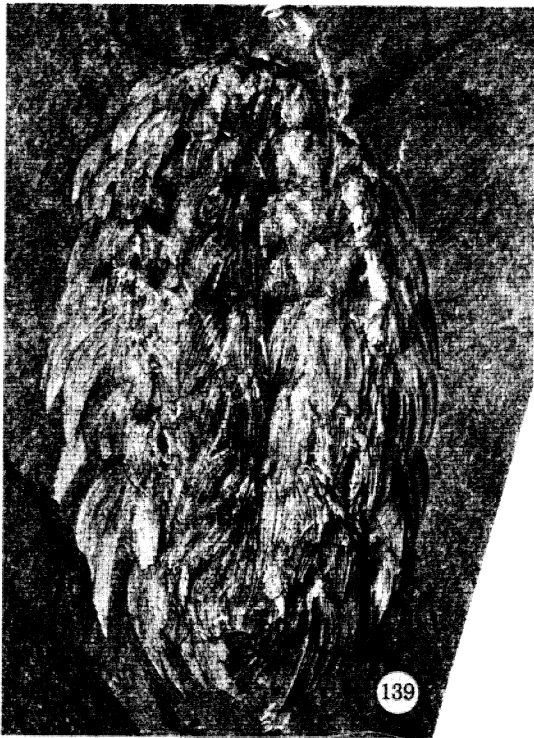
FIGURE 134. U.S.N.M. 271947, part, parallel, juvenile, high angle light from west (magn.  $\times 13.4$ ).

FIGURE 135. G.S.C. 45353, part, isolated upper lateral sclerite, high angle light from south (magn.  $\times 4.7$ ).

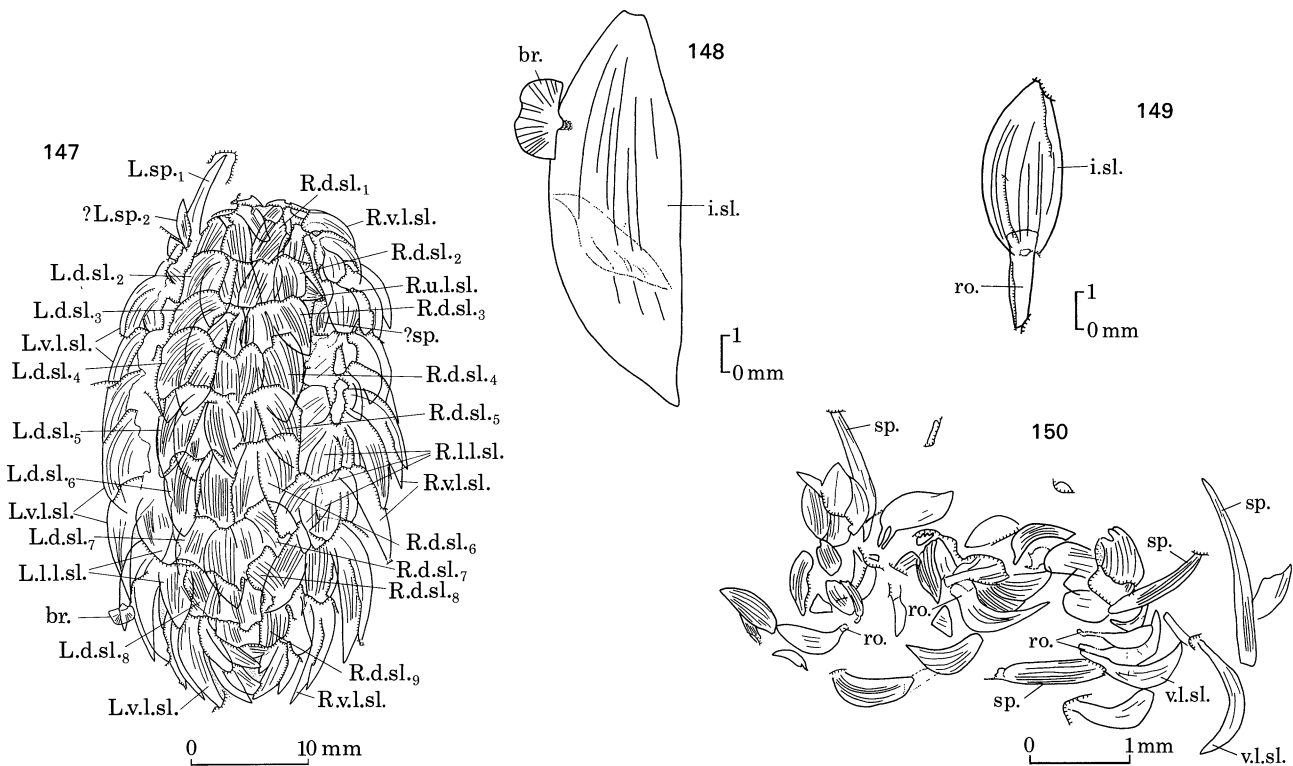
FIGURE 136. U.S.N.M. 277835, part, numerous individuals, low angle light from east (magn.  $\times 0.8$ ).



FIGURES 130-136. For description see opposite.



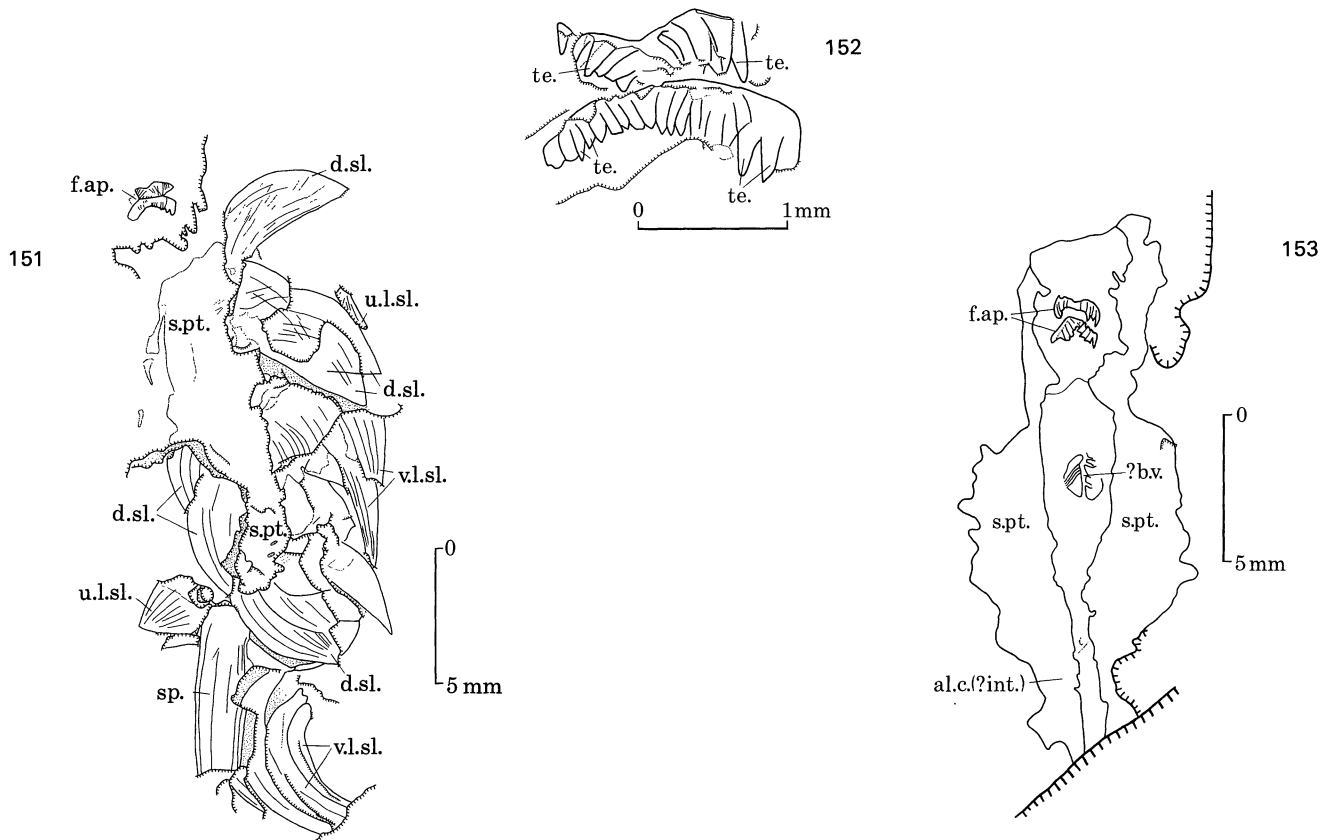
FIGURES 137-146. For description see opposite.



DESCRIPTION OF PLATE 14 AND FIGURES 147-150

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry). Figures 137-143, 145 and 146.  
*Pollingeria grandis* Walcott. Phyllopod bed (Walcott Quarry). Figure 144.

- FIGURES 137-141. U.S.N.M. 83938, parallel. Figure 137, part, complete, high angle light from east (magn.  $\times 2.2$ ); figure 138, part, complete, low angle light from southwest (magn.  $\times 2.2$ ); original of Walcott 1931 (plate 3, figure 1); figure 139, counterpart, complete, high angle light from southeast (magn.  $\times 2.1$ ); counterpart, complete, low angle light from northwest (magn.  $\times 2.1$ ); counterpart, articulate brachiopod attached to posterior left ventro-lateral sclerite, low angle light from north (magn.  $\times 16.9$ ).
- FIGURE 142. U.S.N.M. 199960, part, isolated dorsal sclerite with attached articulate brachiopod, high angle light from west (magn.  $\times 5$ ).
- FIGURE 143. U.S.N.M. 200051, part, isolated lower lateral sclerite, high angle light from west (magn.  $\times 8.3$ ).
- FIGURE 144. U.S.N.M. 57639, part, complete, high angle light from east (magn.  $\times 3.3$ ). Original of Walcott 1911 (plate 21, figure 7).
- FIGURES 145 AND 146. U.S.N.M. 57636, part, semi-isolated assemblage (magn.  $\times 1.2$ ). Figure 145, high angle light from southwest; figure 146, low angle light from northeast. Original of Walcott 1911 (plate 21, figure 4).
- FIGURE 147. U.S.N.M. 83938, explanatory composite drawing of part and counterpart, see figures 137-141.
- FIGURE 148. U.S.N.M. 199960, explanatory drawing of part, see figure 142.
- FIGURE 149. U.S.N.M. 200051, explanatory drawing of part, see figure 143.
- FIGURE 150. U.S.N.M. 57636, explanatory drawing of part, see figures 145 and 146.



DESCRIPTION OF PLATE 15 AND FIGURES 151-153

*Wiwaxia corrugata* (Matthew). Phyllopod bed (Walcott Quarry).

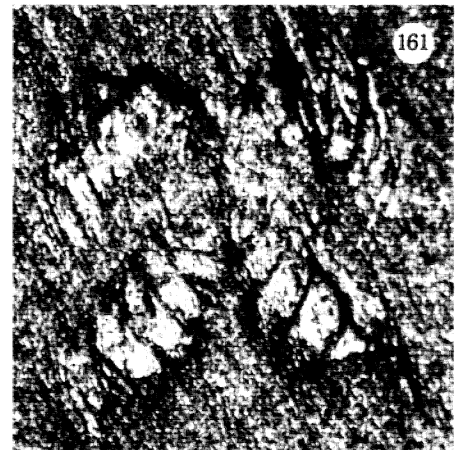
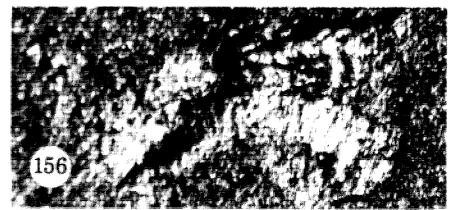
FIGURE 151. U.S.N.M. 199892, explanatory drawing of part, see figures 154-156.

FIGURE 152. U.S.N.M. 199892, explanatory drawing of feeding apparatus, see figure 156.

FIGURE 153. R.O.M. 32569, explanatory composite drawing of part and counterpart, see figures 157-161.

FIGURES 154-156. U.S.N.M. 199892, part, semi-isolated assemblage. Figure 154, complete, high angle light from west (magn.  $\times 4.3$ ); figure 155, complete, low angle light from northeast (magn.  $\times 4.3$ ); figure 156, feeding apparatus, high angle light from north (magn.  $\times 21$ ).

FIGURES 157-161. R.O.M. 32569, isolated soft-parts. Figure 157, part, complete, high angle light from northeast (magn.  $\times 7.8$ ); figure 158, part, complete, low angle light from northwest (magn.  $\times 7.8$ ); figure 159, counterpart, complete, high angle light from east (magn.  $\times 8.2$ ); figure 160, part; feeding apparatus, high angle light from southwest (magn.  $\times 14.1$ ); figure 161, counterpart, feeding apparatus, high angle light from northeast (magn.  $\times 30$ ).



FIGURES 154–161. For description see opposite.

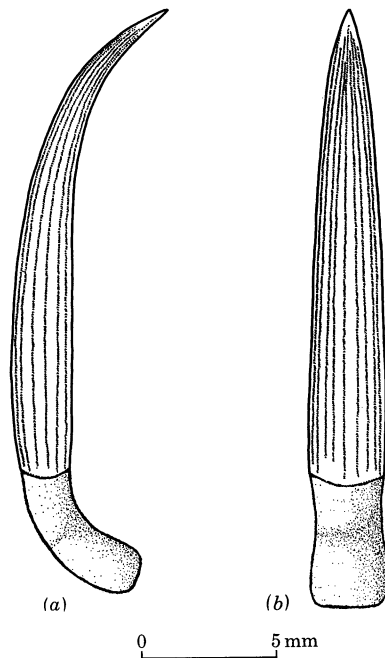


FIGURE 162. Reconstruction of a spine of *Wiwaxia corrugata* (Matthew). (a) Transverse view, (b) lateral view.

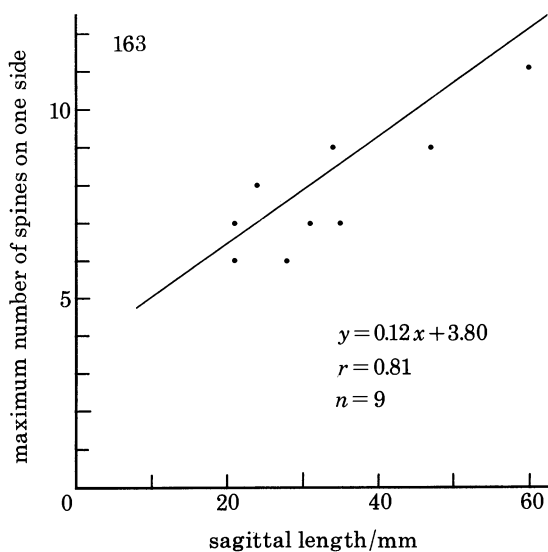


FIGURE 163. Bivariate plot of sagittal length against maximum number of spines along one side in nine specimens of *Wiwaxia corrugata* (Matthew).

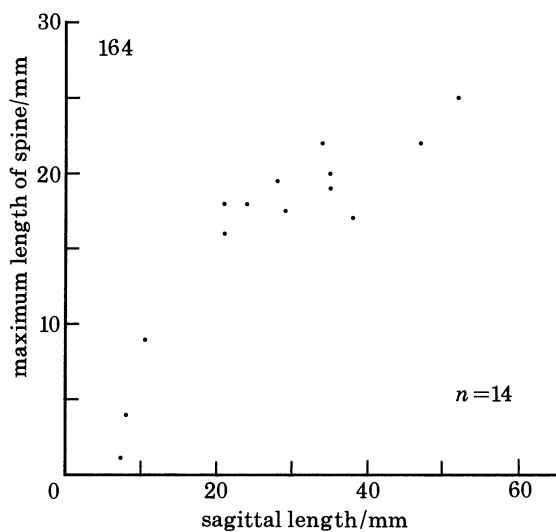


FIGURE 164. Bivariate plot showing nonlinear relation between sagittal length and maximum spine length in 14 specimens of *Wiwaxia corrugata* (Matthew).



13; figures 105 and 129) tend to show a fairly consistent sense of direction along one row. Variation in the attitude of the spines in these specimens, as determined by their degree and direction of curvature, was possibly controlled in part by muscular movements that could rotate the spine slightly. Rotation of the spines by subsequent sedimentary compaction appears to be less likely (cf. Whittington 1975 *a*). The original dorso-lateral extension of the spines means that in the majority of orientations at least one row has been compacted so as to lie effectively on the same bedding plane as the rest of the body. Narrow transverse zones of wrinkling distributed at irregular distances along many of the spines are interpreted as post-mortem creasing produced by compaction, but more extensive zones of wrinkles, best seen in low-angle radiation (for example, figure 35, plate 3; figure 69, plate 6; figure 94, plate 9; figures 32, 71 and 90), are presumably of tectonic origin.

The maximum widths of spines of similar length in a parallel (figures 93 and 94, plate 9; figure 90) and inclined (figures 68 and 69, plate 6; figure 71; spine length in 198679 measured as chord to be equivalent to direction of curvature in parallel specimen) specimens were measured as 2.2 mm and 1.8 mm respectively, suggesting that the spines originally had a slightly oval cross-section (ratio of diameters *ca.* 1:1.2) with the major axis of the ellipse parallel to the spine row. Examination of other specimens appears to support this reconstruction. In 198678 (figures 64 and 65, plate 6; figure 70) spines 1 and 3 of the right-hand side are approximately the same length, but are straight and curved posteriorly respectively so indicating burial at different angles. Comparison of the maximum widths (2.8 mm, 1.9 mm) suggests an elliptical cross-section with a ratio of about 1:1.4.

Whatever the orientation of the spines, longitudinal ribbing is apparent, and it appears that the ribs occupied the entire circumference. They consisted of unornamented linear ridges with a rounded cross-section that occupied almost the entire length of the sclerite above the root but appeared to have died out towards the distal tip. As with the body sclerites (see below) the width of the ribs is variable and this may be largely original rather than being due to compaction. A range in width of about 0.06–0.15 mm with a mean ( $n = 20$ ) of approximately 0.1 mm, has been noted. Spacing between the ribs, which decreases towards the narrowing distal end, is not constant for any transverse section and near the proximal end varies widely between about 0.03 and 0.23 mm, with an average spacing of 0.1 mm ( $n = 15$ ). This variation in rib width and more importantly spacing means that the visible rib total in spines of a similar size is not constant and varies from about 6 to 11 per spine, suggesting that the original total around the circumference was approximately 18–30 ribs. Apart from the ribbing there is no evidence that the rounded cross-section was interrupted by either carinae, keels or other angular projections.

Occasional evidence for spine malformations exists. In 198678 (figure 66, plate 6; figure 70) spine 3 of the right-hand row shows a local and irregular increase in width just over half way towards its distal end, associated with disruption and distortion of the ribbing. A similar but more subdued and symmetrical feature appears to exist at about the same relative position on spine 3 of the left-hand row in 198672 (figure 95, plate 9; figure 90). In both specimens the malformation is accompanied by compaction creases, but the absence of such distortion in association with numerous other creases suggests that the described features are not the result of sedimentary compaction. Their origin is not certain, such malformations may mark a growth anomaly or parasitism, but a preferred alternative is that they represent damage by a predator (§10).

In a number of specimens a spine is incomplete. Although the counterpart is not always

available, the continuity of the surrounding rock surface without adjacent changes of level suggests that this incompleteness is original. In some specimens the transverse termination is relatively smooth (figure 60, plate 5; figure 102, plate 10; figures 55 and 105), in others it is more irregular (figure 36, plate 3; figure 67, plate 6; figures 32 and 70), while one specimen shows both types of termination (figures 51 and 52, plate 4). These occurrences of broken spines are uncommon and with the exception of two broken spines in 45344 (figures 51 and 52, plate 4) are apparently confined to one per individual. The meagre sample indicates that breakage is more usually towards the posterior, rarely anteriorly and in only one example is known amongst the median spines. In these examples it generally appears that between a third and a half of the spine has been lost. It is unlikely that damage occurred during transport as numerous other delicate soft-bodied structures in a variety of species are well preserved. Loss may be by the action of predators, and although the abrupt terminations could indicate in principle excision by autonomy, the more jagged end of other broken spines may point to a more forceful removal (§ 10).

(d) *Dorsal sclerites*

The overall distribution of the dorsal sclerites (figure 165), seen most clearly in parallel (figures 11 and 12, plate 1; figures 24–26, plate 2; figures 93 and 94, plate 9; figures 137–140, plate 14; figures 6, 90 and 147) and parallel-oblique specimens, consists of a number of transverse, bilaterally symmetrical rows. Symmetry is most apparent in parallel specimens, whereas in those of parallel-oblique orientation the sagittal line along the dorsal surface has shifted so that one margin of the dorsal sclerite field lies very close to the specimen edge with some of the abaxial sclerites ‘silhouetted’ against the surrounding matrix (figures 74–76, plate

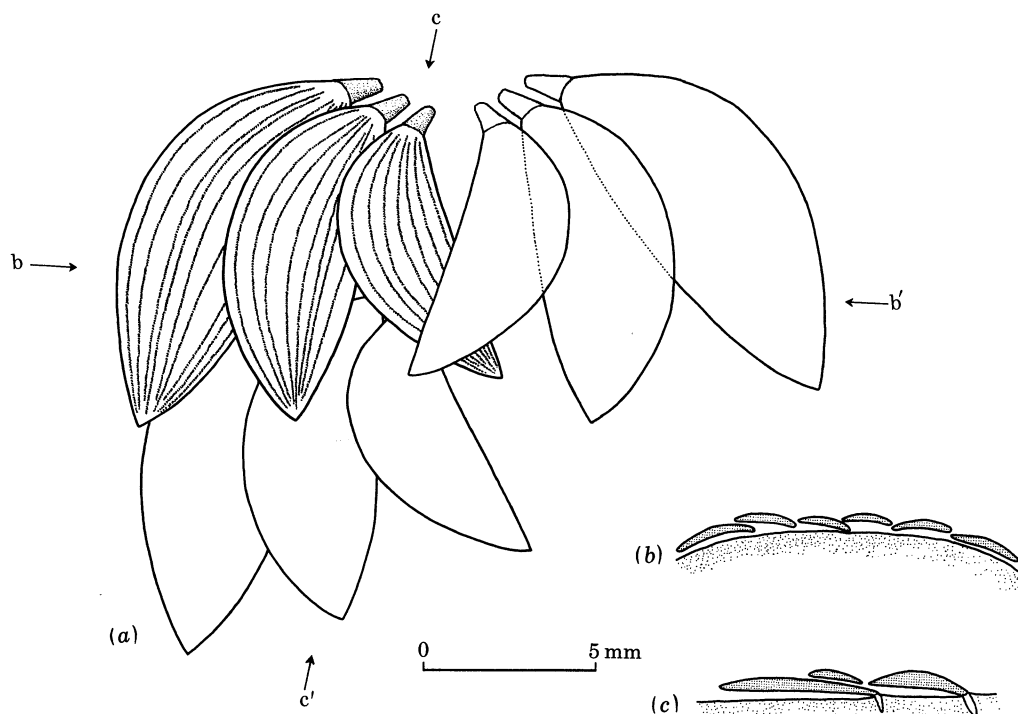


FIGURE 165. Reconstruction of dorsal sclerites in *Wiwaxia corrugata* (Matthew). (a) Transverse row and next posterior left-hand half-row, (b) hypothetical transverse section, (c) hypothetical longitudinal section.

7; figures 110–112, plate 11; figures 72 and 108). In 83938 (figures 137–140, plate 14; figure 147) nine transverse rows of dorsal sclerites are evident, but in the other parallel and parallel-oblique specimens the totals are slightly less (198672, seven or eight rows, but posterior tip missing (figures 93 and 94, plate 9; figure 90); 199894, eight or possibly nine rows (figures 74–76, plate 7; figure 72); 198677, 8 rows (figures 110, 112, plate 11; figure 108)). The specimens compared here are of fairly similar size, and there is little evidence to suggest that new rows were added during at least adult growth. Although variation in row number could be original, it may also be due to incomplete exposure of the dorsal surface and the related difficulty of matching the few dorsal sclerites at the posterior end of the body to the sequence of rows. The sclerites formed an imbricated roof to the dorsal soft-parts, which are assumed to have been gently curved in a transverse plane, and either very largely or entirely concealed them. The rows were posteriorly imbricated so that in general the distal sections of an anterior row overlap the insertion points and proximal region of the next posterior row. Exceptions to this pattern have been noted between the most abaxial sclerites of adjacent rows where the imbrication sometimes shows a reversal with part of the anterior sclerite wedged beneath the outer free margin of posterior one (figures 34–36, plate 3; figures 110–113, plate 11; figures 32 and 108). Such reversal is possible because of the direction and extent of projection of the abaxial sclerites from their more adaxial points of insertion. Whether this reversal of imbrication occurred in life is uncertain, and it may have arisen during the turbulent transport towards the post-slide environment. The imbrication directions within one side of a transverse row, termed here a half-row, show consistent relations, with the imbrication directed outwards from the median line so that outer sclerites were overlapped along their adaxial margins by inner sclerites. A consistency in the imbrication also exists across the sagittal line, with the median sclerite of the right-hand row overlying part of the median left sclerite (figures 11 and 12, plate 1; figure 76, plate 7; figures 93 and 94, plate 9; figure 112, plate 11; figures 137–141, plate 14; figures 6, 72, 90, 108 and 147).

In general, the dorsal sclerites are less well exposed in specimens with orientations other than parallel and parallel-oblique. In the gently inclined 198669 (figures 118–121, plate 12; figure 126) much of the dorsal area is visible, but with the exception of some of the left abaxial sclerites the details of sclerite form and distribution are not particularly clear and have been obscured further by a compaction crease running the length of the specimen close to the sagittal line. In the more steeply inclined 198679 (figures 68 and 69, plate 6; figure 71) the split has passed beneath most of the dorsal sclerites, exposing lower soft-parts across much of this region and restricting dorsal sclerites to the anterior and left-hand margin. This limited exposure of dorsal sclerites can be correlated with the orientation of the specimen, which in addition to being inclined appears to have been slightly tilted towards its right as judged from the distribution of the spines, lateral and ventro-lateral sclerites. The combination of an oblique component and the downward curvature of the antero-lateral margins means that the anterior and left-anterior region would be more nearly parallel to the bedding and so here the dorsal sclerites would be able to control the split. Elsewhere, the path taken by the split was presumably influenced by the relatively steep angle of the dorsal sclerites to the bedding (§6*b*). In the subvertical and transversely folded 198668 (figures 8 and 9, plate 1; figure 5) the dorsal sclerites are mostly obscured by crushing resulting from partial superposition and subsequent compaction. In obliquely preserved specimens some of the abaxial sclerites of one of the half rows are usually fairly well exposed, located in between the spines and upper lateral sclerites,

and are partially 'silhouetted' against the matrix (figures 98–101, plate 10; figures 130 and 131, plate 13; figures 105 and 129). The remainder of each transverse row normally is partly (figures 34–37, plate 3; figure 32), or more rarely completely, concealed beneath other regions of the body. The relative levels occupied by the dorsal sclerites and differences in the direction of curvature of the ribbing facilitate distinction between members of each half-row in these oblique specimens. Not surprisingly, the exposure of dorsal sclerites in lateral and lateral-inclined specimens is generally poor owing to the dorsum lying either steeply or vertically to the bedding (figure 1). In 198678 (figures 64 and 65, plate 6; figure 70) a few sclerites of the left- and right-hand sides are visible. They are assumed to have been abaxial, principally because the slight downward curvature of the dorsum adjacent to its lateral margins would set this region at an angle to the bedding plane suitable for the split to expose these sclerites. In 198680 (figures 45–48, plate 4; figure 53), some of the abaxial dorsal sclerites of the left half-rows are exposed, but the crushing and superposition of much of the body has almost entirely obscured those of the right. In 198681 (figures 82 and 83, plate 8; figure 88) crushing of the dorsum has been extensive with severe distortion of the dorsal sclerites.

As seen in parallel and parallel-oblique specimens a transverse row is composed typically of six sclerites, arranged as half rows of three sclerites on either side of the mid-line. More exceptionally, there appear to have been eight sclerites per row, as in row 4 of 198672 (figures 93 and 94, plate 9, figure 90) where the details of the median area are obscured by overlying (in counterpart) soft-parts. The insertion points of each half-row were closely spaced, and were located somewhat closer to the sagittal plane than the row of spines nearer the margin of the body. The points of insertion defined a short line that in most of the rows ran abaxially obliquely forward, the angle to the sagittal plane being most pronounced to the anterior. This angle of insertion presumably varied with the degree of contraction of the body, so that in relaxed individuals the line of insertion was subparallel to the transverse plane. In 198669 (figures 118 and 120, plate 12; figure 126) the reflectively preserved roots of some of the left abaxial sclerites of a consecutive ex-sagittal sequence are visible, running adaxially and slightly to the anterior. Their appearance in this inclined-parallel specimen suggests that the roots of these sclerites, and presumably those of the rest of the half-rows, were inserted into the dorsum at a steep angle that projected towards the midline. Their exposure presumably resulted from the inclination of this specimen bringing them sub-parallel to the bedding and plane of splitting. Independent evidence to support this reconstruction comes from 277860 (figure 37, plate 3; figure 32) where the root of a posterior dorsal sclerite, exposed by mechanical excavation, projects steeply downwards.

Typically, the sclerites of a half-row show some increase in symmetry and length abaxially. The sclerites are splayed across the dorsum, and slight variations in their disposition with respect to one another and to the sagittal plane must be due, in part, to the angle of burial, but may also be original with their arrangement under some degree of muscular control. The median sclerite is the most asymmetrical and appears to have had an almost straight to gently concave adaxial margin, while the opposite abaxial margin is convex (for example, figures 11 and 12, plate 1; figure 93, plate 9; figures 6 and 90). The orientation of the median sclerites of each half row appear to have varied, but most typically they were gently inclined towards the sagittal plane so that the posterior regions overlapped and the anterior sections adjacent to their insertion points were separated. In 198677 (figures 111 and 112, plate 11; figure 108) the angle of inclination of some of the median sclerites to the sagittal plane is greater than usual, but

this may stem largely from the obliquity of the body to the bedding. Areas of dorsal soft-tissue exposed between half-rows were covered almost entirely by the imbrication of the next anterior row of sclerites; the overlap of these sclerites sometimes combines to produce a distinctive cruciform pattern (figure 93, plate 9; figures 111 and 112, plate 11; figures 90 and 108). In 198672 (counterpart; figures 93 and 94, plate 9; figure 90) the median area of the dorsal sclerites in the central region of the body is obscured by soft-parts, which in the (unlocated) part would have lain below the sclerites. This narrow zone of soft-tissue may have been exposed between the median sclerites, such exposure perhaps arising by a transverse flexure of the dorsum upwards separating the half-rows by a greater than usual spacing. Such a flexure could also explain the spines coming to lie at a lower angle and extending across the bedding plane (§9*c*), although as noted above their inclination may have been under muscular control. The other abaxial sclerites of a half-row have more convex abaxial margins than those of the median sclerite, which together with convex abaxial edges give these sclerites a less asymmetrical shape. The form and distribution of these sclerites shows little change over much of the body, although there is some size increase in the anterior two or three rows. The posterior one or two rows appear to have a reduced number of sclerites which are more steeply inclined to each other and the longitudinal axis (for example, figures 74 and 75, plate 7; figure 72) as they match the posterior curvature.

In parallel-oblique specimens (for example, figures 110–112, plate 11; figure 108) the abaxial sclerites of the specimen may show a particularly convex, sometimes almost semi-circular, outer edge, while the inner margin is straighter or even concave. The contrast between this outline shape and that seen when these sclerites are viewed more perpendicularly, either in parallel specimens or in the opposite half-row of parallel-oblique specimens, is interpreted as resulting from a steeper angle of burial of the marginal half-row showing it in a more lateral aspect. The shape of the abaxial sclerites in such an orientation suggests that they were not flat, but had an arched upper surface and a flat or concave lower surface (figure 165). In some oblique specimens (for example, figures 34–36, plate 3; figures 130 and 131, plate 13; figures 32 and 129) the abaxial sclerites show comparable outlines that support this reconstruction, but in others (for example, figures 98–101, plate 10; figure 105) these sclerites have a more conical outline that is interpreted as resulting from partial crushing. The position of the more adaxial sclerites of a transverse row means that at the steeper angles of burial that pertain to oblique specimens they are usually obscured by superposition and compaction, and although they too are reconstructed with concavo-convex transverse sections (figure 165), little direct evidence is available.

In practically all the specimens the distribution of the dorsal sclerites is consistent with them concealing either all, or a very large proportion, of the underlying soft-parts. In 199910 (counterpart 199905), however, there appears to have been anomalous distribution of dorsal sclerites over the left side (figures 56–59, plate 5; figure 55). It is not easy to understand this specimen since it is broken with only the posterior half available. Distribution of the spines and other sclerites suggests that the orientation is parallel-oblique with the upper lateral sclerites (see below) well exposed on the left-hand side. The dorsal sclerites on the right-hand side appear to show the usual distribution, but the left-hand area is largely devoid of these sclerites, and shows instead an extensive area of soft-parts. However, more posteriorly and possibly along the abaxial margins, dorsal sclerites occur. Judging by differences in levels between the dorsal sclerites, the soft-parts, and ventro-lateral sclerites (some of which were revealed by mechanical

excavation in the part), the exposed soft-parts appear to have been dorsal. No evidence suggests that the dorsal sclerites have been concealed beneath the soft-parts by the split passing at a lower level than normal. Their exposure is conceivably a result of unusual flexure of the dorsum separating the dorsal sclerite half-rows, combined with an oblique burial of this region to the bedding plane. It is not easy to reconcile this hypothesis with the available evidence from the existing dorsal sclerites and a possible alternative is that the dorsal sclerites were partly absent over the left-hand side, conceivably owing to aborted development or perhaps non-lethal damage. There is no clear evidence that the sclerites of this region had been moulted recently, because if this was the case one might expect to see attachment areas and soft-bodied lobes that represent newly moulted sclerites.

With the exception of the ventro-lateral sclerites (see below) identification of the different sclerite types in juvenile specimens is often hindered by their small size and indifferent preservation. Sclerites identified as dorsal (for example, figures 17–20, plate 2; figure 44, plate 3; figure 61, plate 5; figures 115 and 116, plate 11; figures 27 and 28) appear to have been arranged in transverse rows, but there is some indication that the sclerites were more symmetrical in outline and possessed fewer ribs than the adults.

In the part of parallel and parallel-oblique specimens, where the imbrication of the dorsal sclerites corresponds to the original life-position, the ribs are preserved in positive relief. In the counterpart, with reversed imbrication, the ribbing is represented in negative relief as grooves. Assuming that the ribs are correctly interpreted as originally being linear welts of the sclerite wall, the association between normal imbrication of the sclerites and positive relief appears to be explicable only if the ribs lay on the dorsal surface (figure 166 *a–c*). The apparently invariable nature of this relation between imbrication and rib relief indicates that the split traversed the

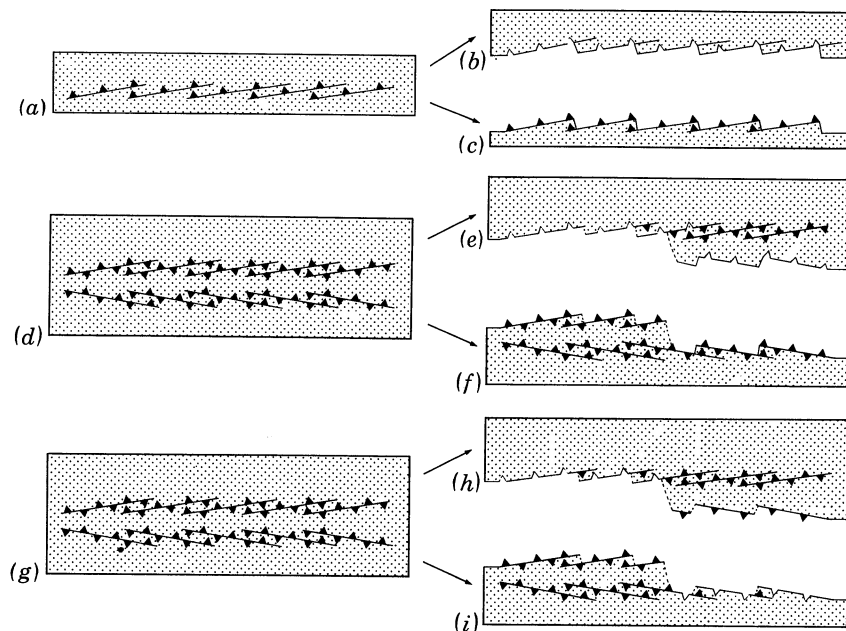


FIGURE 166. Diagrammatic illustration of the effect of splitting at different levels through imbricated series of sclerites of *Wiwaxia corrugata* (Matthew). Ribbing indicated by triangles, black showing positive relief and white showing negative relief. (*a*)–(*c*) Step-like splitting in a parallel specimen, (*d*)–(*f*) step-like splitting in a lateral specimen with uniform relief on part and counterpart of sclerite ribs, (*g*)–(*i*) step-like splitting in a lateral specimen with change in rib relief along length of part and counterpart.

outermost surface of the sclerites and any ornamentation of the lower ventral surface is obscured. In the oblique 277860 (figures 34, 35 and 37, plate 3; figure 32), however, abaxial dorsal sclerites of the left- and right-hand sides appear to have been juxtaposed by collapse and compaction. The sclerites of either side are distinguished on two criteria: opposite directions of the curvature of the ribs and imbrication between adjacent transverse rows. The ribbing of the left-hand sclerites is markedly convex towards the dorsal region, whereas the opposite curvature of the right sclerites is less pronounced, especially towards the posterior. This variation in curvature combined with the outline of these sclerites suggests that in this oblique specimen at least abaxial sections of left half-rows were subparallel to the bedding while the right half-rows were more steeply inclined. The direction of imbrication is opposite in left- and right-hand sclerites, thus in the counterpart the left sclerites show normal imbrication and the right reversed. One exception to this pattern lies between two left sclerites towards the posterior, and this is assumed to be an example (see above) of a reversal in overlap with the anterior sclerite wedged beneath the posterior one. In both sets of sclerites, however, the sclerite ribbing shows the same relief (negative in counterpart, positive in part). This arrangement appears to be explicable only by postulating the existence of ventral ribs, in addition to the dorsal set identified above (figure 166). The alternative possibility that the dorsal ribs were impressed onto the ventral surface during compaction seems less likely in view of the clarity of the ribs on the sclerites of both sides. In figure 166*d-f* the pattern of rib relief is shown as arising by the split following the outer surface of the right-hand sclerites and inner surface of the left-hand sclerites, but the same pattern would arise if the split was to take the alternative path, that is, inner surface of right-hand sclerites and outer surface of left-hand sclerites. There seems to be no method to distinguish which of these two paths was taken in 277860. In contrast to this arrangement, the ribbing of dorsal sclerites on opposite sides of 198678 (figures 64 and 65, plate 6; figure 70) shows negative (left) and positive (right) relief in the counterpart (part unlocated). This configuration of rib relief is explicable by assuming the split followed either the outer or inner surfaces of the sclerites; figure 166*g-i* depicts the former alternative.

The spacing and width of the ribs is seen best in parallel and parallel-oblique specimens. The number of ribs per sclerite varied in adult specimens from about 6 to 12, with most individuals having rib totals towards the larger number. As the ribbing ran subparallel to the sclerite margins, the spacing between the ribs diminished towards either end of the sclerite with the maximum values coinciding with the greatest width of the sclerite; at this point rib spacing varied from about 0.07 to 0.34 mm with an average of 0.16 mm ( $n = 37$ ). The ribs died out close to the distal tip of the sclerite, but otherwise had a more or less constant width along its length with values varying from about 0.03 to 0.14 mm, average width 0.08 mm ( $n = 44$ ). The ribs have rounded margins, and although they presumably have suffered some compaction there is no evidence to suggest that originally their profile was more angular.

(*e*) *Lateral and anterior sclerites*

The lateral regions of the body were mantled by two types of sclerite, referred to here as the upper lateral and lower lateral sclerites respectively. Although these sclerites had a similar symmetrical shape (figures 167 and 168) they are distinguished because of differences in (i) their orientation, most pronounced towards the anterior where they lay more or less at right angles to each other, and (ii) their attachment to areas of body wall of different inclination with the upper lateral area being almost vertical in contrast to the more gently sloping lower

lateral area. The stepped configuration of the lateral areas, seen as a dog-leg in transverse section (figure 172), has influenced the exposure of upper and lower lateral sclerites in different specimens according to their angle of burial with respect to the bedding (=splitting) plane. Towards the posterior of the body the upper lateral sclerites became backwardly inclined. The shift in orientation of these sclerites presumably reflects the tapering of the hindmost quarter, but their distinction as a zone separate from the lower lateral sclerites appears to be maintained. At the front of *Wiwaxia* the upper lateral sclerites evidently swung towards the sagittal plane so as to cover the steeply inclined anterior face of the body. The lower lateral sclerites, however, appear to have been confined to the sides of the animal.

Predictably, the upper lateral sclerites are seen best in lateral specimens. In 198681 (figures 82 and 83, plate 8; figure 88) the upper laterals of the left-hand side are well-exposed over a large area of the specimen while towards the posterior a downward jump in the level of splitting has revealed some of the right-hand sclerites. The exceptional extent of exposure of the upper lateral sclerites in 198681 even in contrast to other lateral specimens (see below), may be because of a strong degree of longitudinal contraction as manifested in the pronounced dorso-ventral curvature of the body. A greater than average superposition of the upper lateral sclerites promoted splitting at their level across an extensive area. In other lateral and lateral-inclined specimens (for example, figures 45–48, plate 4; figures 64 and 65, plate 6; figures 53 and 70) the split follows a more complex multi-level path, with upper lateral sclerites of

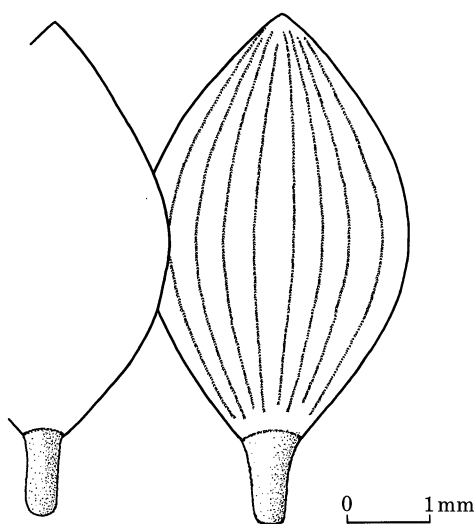


FIGURE 167. Reconstruction of upper lateral sclerites in *Wiwaxia corrugata* (Matthew).

both sides exposed owing to major changes of level. Overall, exposure of upper lateral sclerites in these latter specimens is less extensive; this may be attributed to their both being more relaxed and buried at slightly different angles to the bedding so that other regions of the body were so aligned to govern the level of splitting. In oblique specimens upper lateral sclerites of one side, and sometimes both, are usually visible. The extent and distribution of exposure varies between the specimens; this is presumably due to their exact attitude. In 198671 (figures 98–101, plate 10; figure 105) upper lateral sclerites of the left-hand side are well exposed, especially towards the anterior, whereas those on the right are largely obscured by other parts



of the body. A similar arrangement prevails in 277860 (figures 34, 35 and 37, plate 3; figure 32), albeit with the right-hand sclerites better exposed; mechanical excavation has revealed some of the upper lateral sclerites of the posterior left. Sclerites of both upper lateral sides are identifiable in 198676 (figures 130 and 131, plate 13; figure 129) but in neither case are they extensively revealed by the split. The upper lateral sclerites of either side in parallel-oblique specimens tend to show a marked contrast in their appearance. The lateral edge that is more steeply inclined to the bedding, and thus is closer to the mid-region of the specimen, shows poor exposure of the upper lateral sclerites with the few recognizable examples dipping into the matrix at a high angle (figures 74 and 75, plate 7; figures 110 and 111, plate 11; figures 72 and 108). The opposite side, set at a lower angle to the bedding, is located nearer one edge of the specimen and shows the distal sections of the more dorsally located upper lateral sclerites. In 199894 (figures 74 and 75, plate 7; figure 72) mechanical excavation in an anterior region has revealed some of these sclerites more completely by removal of overlying dorsal sclerites. In parallel specimens a number of upper lateral sclerites, evidently representing the more dorsal examples, are usually exposed (figures 93 and 94, plate 9; figure 90). A slight degree of obliquity in burial, however, will favour one side, and this may explain the better exposure of these sclerites on the right-hand side of 57635 (figures 11 and 12, plate 1; figure 6). Although 83938 is a parallel specimen it is exceptional in this regard by showing highly restricted exposure of the upper lateral sclerites with the few examples, especially on the right-hand side, barely recognizable owing to their steep inclination (figures 137–140, plate 14; figure 147). Other lines of evidence suggesting that 83938 shows a strong transverse curvature about the sagittal plane are discussed elsewhere, and such a configuration would appear to explain also the distribution of the upper lateral sclerites. In inclined specimens the steep attitude of the upper lateral sclerites to the bedding does not favour their clear preservation. In the relatively gently inclined 198669 (figures 118–121, plate 12; figure 126) a few such sclerites are visible towards the anterior, but they show evidence of distortion that presumably arose during compaction. In 198679 (figures 68 and 69, plate 6; figure 71) a few upper lateral sclerites of the left-hand side are recognizable, but downward tilting of the body towards the right (see above) has favoured exposure of the corresponding sclerites to a greater degree. Some examples of upper lateral sclerites are evident in the subvertical and transversely folded 198668 (figures 8 and 9, plate 1; figure 5), but extensive superposition and compaction has otherwise obscured them.

The distribution and appearance of the upper lateral sclerites appears to be consistent with their being attached to the sides of the animal and extending upwards at a very steep angle to the horizontal. Their precise angle is difficult to determine, and direct measurement in the only known subvertical specimen is suspect because of additional folding and extensive crushing. There is an indication from parallel-oblique specimens (figures 74 and 75, plate 7; figures 110 and 111, plate 11; figures 72 and 108), however, that in at least some cases these sclerites may have been inclined at an oblique angle so as to diverge slightly on either side of the body. Evidence for this lies in the contrast between the almost complete obliteration of the upper lateral sclerites along one side of the body and more extensive exposure, albeit with frequent evidence for compactional distortion, along the opposite side. With the sagittal plane of parallel-oblique specimens inclined to the bedding, slight divergence of these sclerites would result in those of one side coming to lie more or less at right angles to the bedding and inevitably suffering extensive crushing, whereas those of the opposite edge would be more inclined so that distortion would be less intense and at least the upper sclerites would be in a position to control

locally the level of splitting. The appearance of upper lateral sclerites in some parallel specimens (figures 11 and 12, plate 1; figures 93 and 94, plate 9; figures 6 and 90), where they extend abaxially, would also appear to be consistent with a moderate degree of outward divergence, whereas had they been disposed vertically their exposure presumably would have been very restricted. Oblique and lateral specimens do not appear to show additional evidence to resolve the problem of the exact inclination of these sclerites. It is also uncertain whether the underlying soft-parts showed a close degree of apposition with the upper lateral sclerites, and it seems possible that even if the sclerites diverged outwards the body wall had a more vertical disposition (figure 172).

The upper lateral sclerites appear to have consisted of about two horizontal and imbricated rows, with the lower row overlapping the upper. The top of the upper row was more or less level with the dorsum, and was separated from the abaxial dorsal sclerites by a space that housed the row of spines. Extensive overlap between sclerites of a row occurred in contracted specimens (figures 82 and 83, plate 8; figure 88), but more usually adjacent sclerites show a wider separation. The imbrication direction of sclerites within a row apparently did not show a consistent and invariable relation. Along the anterior half of the body the upper lateral sclerites were more or less vertically oriented with the distal tip directly above the point of attachment. Towards the posterior, however, the long axes of these sclerites were rotated so as to be inclined backwards at about 50–60° to the horizontal. Such a change in attitude is presumably a reflection of the tapering height of the posterior section of the body. The extension of upper lateral sclerites on to the anterior face of the animal is described below.

Viewed laterally the individual sclerites were symmetrical in outline, with an elliptical shape that tapered more or less equally towards the root and distal end. The degree of roundness varied (height:width ratio of sclerite *ca.* 1:1.4–1:1.7), with more globose and relatively slender forms being recognizable. Much of this variation appears to have been an original feature of the sclerites, rather than being due to compaction. Information on the thickness and possible degree of curvature is limited as sclerites in theoretically appropriate orientations are usually crushed or otherwise distorted. It appears, nevertheless, that the upper lateral sclerites were relatively compressed in cross-section and may have shown abaxially a gentle convex curvature. The root is generally not well preserved, presumably because it ran at a steep angle to the sclerite into the body wall (figure 172). In common with the other sclerites, those of the upper lateral sector were ribbed. Where sclerites of left- and right-hand sides are together exposed, as in some oblique and lateral specimens (for example, figures 64 and 65, plate 6; figure 70) invariably the ribbing has opposite relief on either side. Such a pattern of positive and negative relief is explicable by assuming that the split moved across the outer surfaces bearing ribs (figure 166*g–i*). In the parallel 198672 (figures 93 and 94, plate 9; figure 90) the ribs of the upper lateral sclerites of either side have positive relief, whereas those of the more median dorsal sclerites (reversed imbrication) are in negative relief. Consideration of the pattern of splitting in this specimen supports the notion that the ribs of the former sclerites occupied the outer surfaces. The inner surfaces may have been more or less smooth and devoid of ribs.

The ribs numbered about seven to nine per sclerite, and had a width that varied from about 0.05 to 0.12 mm (average 0.08 mm,  $n = 34$ ). They show an approximately symmetrical arrangement across the sclerite surface, with the maximum spacing between the ribs corresponding to the greatest width of the sclerites. Values of maximum spacing vary from about 0.12–0.32 mm (average 0.20 mm,  $n = 17$ ).

The upper lateral sclerites are rarely recognizable with certainty in juvenile specimens, although they are relatively clear in 45347 (figure 81, plate 7) where apart from their small size appear to have had a morphology similar to that of the adult. Their indifferent preservation in many other juveniles is probably because of a predominance towards parallel orientation in which the upper lateral region would have been set at a high angle to the bedding unfavourable to exposure.

The anterior face of the body was covered by symmetrical sclerites of a similar size and shape to those of the upper lateral zone, and they appear to have been formed simply by a forward extension of the upper lateral sclerites. The sclerites of the anterior face are well exposed in the inclined 198679 (figures 68 and 69, plate 6; figure 71), but are somewhat less so in 198669 (figures 118–121, plate 12; figure 126) where the degree of inclination appears to have been less pronounced. The much poorer preservation of this region in practically all specimens with their longitudinal axes more or less parallel to the bedding also suggests that the anterior face was steeply inclined to the horizontal at an angle comparable to that of the upper lateral sector. Exposure of the anterior sclerites is poor (figures 64 and 65, plate 6; figure 70) to almost non-existent (figures 45–48, plate 4; figure 53) in lateral specimens, with most of this area having suffered considerable compaction. In some oblique specimens (figures 34 and 35, plate 3; figures 98–101, plate 10; figures 32 and 105), however, restricted areas of the anterior face are exposed; such exposure apparently is favoured by the longitudinal axis being slightly inclined to the plane of bedding. It is in such specimens that the continuity between the upper lateral and anterior sclerites is most clearly seen. In parallel and parallel-oblique specimens the steep inclination of the anterior face to the bedding plane generally has resulted in extensive crushing and obliteration of most features, but in some such specimens (figures 74 and 75, plate 7; figures 93 and 94, plate 9; figures 72 and 90) the anterior margin has a distinctively serrated appearance which is due to the distal sections of some of the anterior sclerites projecting against the surrounding matrix. The specimen 57635 (figures 11 and 12, plate 1; figure 6) is exceptional among parallel specimens in displaying a very substantial proportion of the anterior sclerites. This arrangement appears to have arisen by a downward flexure of the front end of the body bringing the anterior sclerites subparallel to the bedding and into a position to control the level of splitting. Additional evidence for such a flexure appears to be evident from some of the ventro-lateral sclerites (see below). A comparable anterior flexure is apparent in the lateral 198678 (figures 64 and 65, plate 6; figure 70) and has also been documented in the Burgess Shale polychaete *Canadia spinosa* where the dorsal notosetae are splayed outwards along the transverse hinge line (Conway Morris 1979*b*, therein figure 6, plate 1; figure 47, plate 4; figure 42). The appearance of the anterior sclerites in appropriately oriented specimens suggests that their overall arrangement, imbrication, outline shape and ribbing were effectively the same as that noted for the upper lateral sclerites.

As is also the case with the upper lateral sclerites, and presumably for similar reasons, those of the anterior face are generally obscure in juvenile specimens, although such sclerites are identifiable in 277889 (figure 20, plate 2; figure 28). In this specimen apart from size differences, they appear to be similar to those of the adult.

The lower lateral sclerites occupied a zone along either side of the body, flanked adaxially and dorsally by the upper lateral sclerites. They are best exposed in parallel-oblique and more particularly oblique specimens, whereas in other orientations where the longitudinal axis is more or less parallel to the bedding the lower lateral sclerites are obscure and in some cases concealed.

Consideration of the relations between the angle of burial to the plane of splitting suggests that their appearance in oblique and parallel-oblique specimens is a consequence of the lower lateral sclerites of one side coming to lie subparallel to the bedding plane. Rotation of such specimens about their longitudinal axes places these sclerites at an inclination of approximately  $65^\circ$  to the horizontal. As the upper lateral regions were either steeply or vertically inclined, the sides of *Wiwaxia* are reconstructed so as to have a stepped profile in transverse section (figure 172).

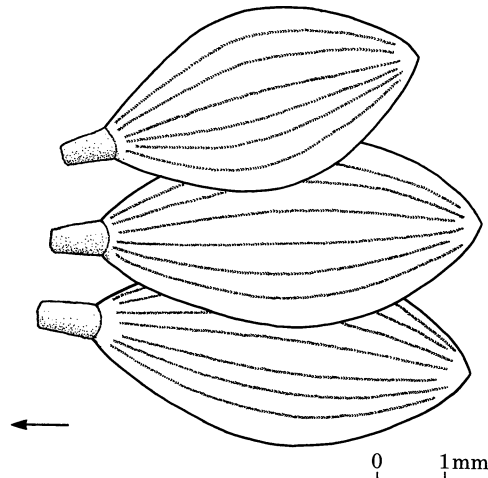


FIGURE 168. Reconstruction of left transverse row of lower lateral sclerites in *Wiwaxia corrugata* (Matthew). Arrow indicates anterior direction.

In oblique specimens lower lateral sclerites of either the left (figures 130 and 131, plate 13; figure 129) or right-hand sides (figures 34, 35 and 37, plate 3; figures 98–101, plate 10; figures 32 and 105) are well exposed, the attitude depending upon which way up the specimen was buried. The equivalent sclerites of the opposite side lay at a steeper angle to the bedding and so are at best poorly revealed by the split. In parallel-oblique specimens the degree of exposure of the more favourably oriented side is variable. In 198677 (figures 110 and 111, plate 11; figure 108) relatively few of the right lower lateral sclerites are visible, whereas in 199894 (figures 74 and 75, plate 7; figure 72) their exposure (left-hand side) is more extensive but has suffered some distortion that has rendered the details of the individual sclerites less clear. The relative superiority in appearance of the lower lateral sclerites in oblique as against parallel-oblique specimens suggests that it was in the former orientation that this zone was mostly nearly parallel to the bedding and thus best able to control the level of splitting. In parallel specimens the lower lateral sclerites are almost invariably obscured, presumably because of this region's angle relative to the bedding and concealment by other more favourably oriented parts of the body. However, 83938 (figures 137–140, plate 14; figure 147) is exceptional in showing lower lateral sclerites, especially along its right-hand side. This unusual occurrence is presumably a consequence of the pronounced transverse curvature (see above) that has brought the more marginal areas, including the lower lateral zones, into an orientation suitable for exposure. The position of the right lower lateral sclerites, however, is anomalous in that they override the dorsal sclerites, although the left-hand side shows the usual and consistent arrangement that prevails in other specimens. This peculiarity is tentatively attributed to extreme curvature along the right-hand side so that this marginal region lay above the dorsum, with local overlap accentuated during compactional crushing.

Unlike the sclerites of the upper lateral region, those of the lower lateral zone in lateral specimens are indifferently exposed (figures 45–48, plate 4; figures 64 and 65, plate 6; figures 82 and 83, plate 8; figures 53, 70 and 88), so supporting the notion that the latter sclerites lay at a lower angle and thus were inclined more steeply to the bedding plane. In the inclined 198669 (figures 118–121, plate 12; figure 126) the lower lateral sclerites are almost entirely obscured by other sclerites, especially the spines. In 198679 (figures 68 and 69, plate 6; figure 71) however, a slight leftward tilt in this inclined specimen has placed the lower lateral region of the right-hand side into a propitious orientation and those sclerites are moderately well exposed along much of this zone. In the subvertical and transversely folded 198668 (figures 8 and 9, plate 1; figure 5) the lower lateral sclerites of the posterior right region are visible, but elsewhere in this specimen overlap and crushing has almost entirely obscured them.

The lower lateral sclerites extended along the entire length of each side, appearing to commence just behind the anterior face and running to the posterior of the body. Each zone consisted of about eight transverse rows, imbricated towards the posterior. The rows are assumed to have been bilaterally symmetrical, although in no specimen where the lower lateral sclerites of both sides are visible is this possible to confirm unequivocally. Furthermore, the transverse rows appear to have alternated, rather than coincided with the equivalent rows of dorsal sclerites. Each row consisted of three, or more, rarely two, sclerites, which appear to have had an imbrication in the opposite sense to the dorsal sclerites, with outer overlapping inner and the adaxial sclerite of a row abutting the proximal portions of the more ventral row of upper lateral sclerites. Within a transverse row the sclerites had a sub-radial pattern, with the median sclerite approximately parallel to the longitudinal axis and the outer and inner sclerites pointing at low angles abaxially and adaxially respectively. There is some evidence that the abaxial sclerite of a row (figures 84 and 85, plate 8; figures 130 and 131, plate 13; figure 129) was slightly shorter than the more median sclerites. In the first few rows the size of the sclerites increased posteriorly, but thereafter appears to have been fairly constant along the length of the body. The root of a sclerite is occasionally visible in an entire specimen, and is assumed to have entered the body wall at a similar angle to those roots anchoring the dorsal sclerites. Each sclerite was symmetrical, elliptical in outline and somewhat more elongate than the upper lateral sclerites. The sclerites are assumed to have been compressed with a concave–convex transverse section, although there is little direct evidence to support this reconstruction. The relief of the ribs shows an invariable relation to the direction of imbrication: positive relief in normal imbrication, negative in reverse. A comparable arrangement in upper lateral sclerites was used to suggest that the ribbing was confined to the outer surface, and the lower lateral sclerites are reconstructed here with ribbing only on their upper sides. The number of ribs per sclerite varies from about five to seven. The rib width varied from about 0.04 to 0.14 mm, average width 0.08 mm ( $n = 38$ ). The arrangement of the ribs was similar to that of the upper lateral sclerites, with the greatest spacing across the mid-point of the sclerite. Values for maximum spacing vary widely, from about 0.07 to 0.48 mm with an average of 0.21 mm ( $n = 26$ ).

Remains of lower lateral sclerites are identifiable in a number of juvenile specimens (for example, figure 20, plate 2; figure 61, plate 5; figures 115 and 116, plate 11; figure 28). Apart from size differences their arrangement and shape were similar to those of the adult. The relative frequency of appearance of these sclerites, in contrast to those of the upper lateral and anterior regions in juveniles may be a consequence of a more dorso-ventrally compressed body in comparison with adults (see above), combined with a tendency to adopt a parallel orientation.

*(f) Ventro-lateral sclerites*

The distinctive crescentic shape of the ventro-lateral sclerites (figure 169) facilitates their recognition, and at least some traces of this type of sclerite may be identified in every entire specimen. The sclerites formed an imbricating row along either margin of the body, extending from anterior to posterior extremities. Their exposure in parallel specimens is invariable, but in most cases is relatively poor. In 198672 (figures 93 and 94, plate 9; figure 90) visible remains of the ventro-lateral sclerites are confined to anterior regions either side of the median zone, and elsewhere along the margins the split has followed a higher level so restricting these sclerites to the (unavailable) part. In 57635 (figures 11 and 12, plate 1; figure 6) some ventro-lateral

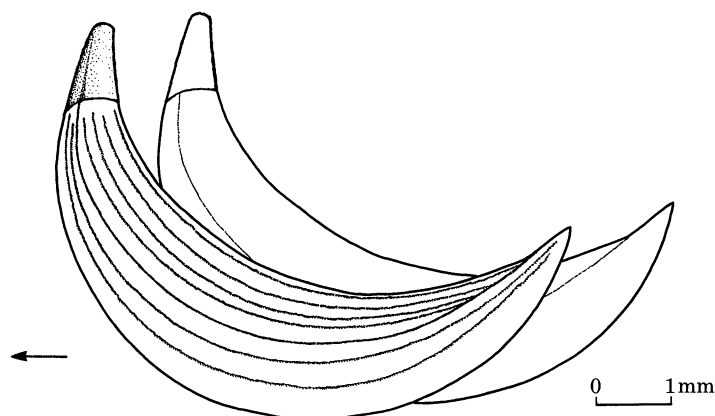


FIGURE 169. Reconstruction of left ventro-lateral sclerites in *Wiwaxia corrugata* (Matthew). Arrow indicates anterior direction.

sclerites are exposed along part of the left-hand side, the anteriormost of which project outwards rather than posteriorly and have a less arcuate shape. This configuration apparently has arisen by a transverse flexure of the body in this region, a feature which also controlled the distribution and unusually clear appearance of the anterior sclerites (§9*e*). Elsewhere in 57635 the ventro-lateral sclerites evidently are concealed beneath upper lateral and abaxial dorsal sclerites which are more favourably positioned to control the plane of splitting. Exposure of these sclerites in 199910 (figures 56–59, plate 5; figure 55) was originally indifferent, but mechanical excavation on the left-hand side exposed one hitherto entirely concealed sclerite and the proximal section of a more posterior sclerite, while on the right-hand side what appear to be the proximal sections of some ventro-lateral sclerites are now revealed. However, among the parallel specimens the ventro-lateral sclerites are most clearly preserved in 83938 (figures 137–140, plate 14; figure 147) where their bilaterally symmetrical arrangement along either side of the body is clear. Other aspects of sclerite arrangement in 83938 have been attributed to an abnormal transverse curvature of the body. The configuration and relative clarity of the ventro-lateral sclerites is also interpreted as resulting from a rotation from their more usual position adjacent to the ventral margin of the body. The right-hand row in 83938 is more clearly exposed and this matches both the distribution of the adjacent lower lateral sclerites and arguments for extreme curvature along the right margins (§9*e*). It is not obvious, however, either in 83938 or any other specimen whether the symmetry was exact, with each ventro-lateral sclerite of one side having a corresponding equivalent opposite.

In parallel-oblique specimens the ventro-lateral sclerites of one side are generally well exposed, especially in 198677 (figures 110, 111 and 115, plate 11; figure 108) where much of the right row is visible along the margin of the body, although neither anterior- nor posteriormost sections are present and presumably reside on the (unavailable) part. In 199894 (figures 74 and 75, plate 7; figure 72) the exposure of the ventro-lateral sclerites is less satisfactory, with evidence for crushing along the adaxial margins of some sclerites. The quality of exposure of the adjacent lower lateral sclerites in 198677 and 199894 shows a reciprocal relation to that of the ventro-lateral sclerites; this contrast is presumably a reflection of slight differences in the attitude of burial between these two parallel-oblique specimens. The ventro-lateral sclerites on the opposite side (right in 199894, left in 198677) are almost entirely obscured by other more favourably oriented sclerites, although in 198677 part of an anterior left sclerite appears to be visible. In oblique specimens (figures 34, 35 and 37, plate 3; figures 84 and 85, plate 8; figures 98–101, plate 13; figures 130 and 131, plate 13; figures 32, 105 and 129) the sclerites of one side are well exposed and the entire row, or a very large fraction thereof, can be traced along the length of the body. In 277860 the posterior section of the row is interrupted by an outwardly directed sclerite. Its position and relative imbrication suggests that it may be a ventro-lateral sclerite that has been rotated out of line and subsequently crushed to give it a more spinose appearance. The sclerites on the opposite side of these oblique specimens are inclined at a steeper angle to the bedding (figure 1) and are generally less apparent. In 277860 (figures 34 and 35, plate 3; figure 32), and to a considerably less extent in 198676 (figures 130 and 131, plate 13; figure 129), the anteriormost section of these sclerites are visible until obscured by changes in level that expose other regions of the body. Their relative clarity in 277860 is believed to be due to the longitudinal axis of the anterior body being inclined slightly to the bedding so as to bring the left ventral region more nearly parallel with the plane of splitting. Elsewhere in 277860 the left ventro-lateral sclerites are almost entirely concealed by other parts of the body, although a few of them have been revealed by mechanical excavation. In 198676 the sclerites along most of the right-hand side appear to have suffered severe crushing and such distortion is apparent in some of the posteriormost sclerites which extend clear of the body. A similar explanation appears to account for the almost total concealment of the left-hand row in 198671 (figures 98–101, plate 10; figure 105) and left-hand row in 198745 (figures 84 and 85, plate 8). In 198671 concealment is further compounded by an abrupt jump in this region from upper lateral sclerites to soft-parts, both of which are oriented to control the split.

The ventro-lateral sclerites of both sides are usually visible in lateral and lateral-inclined specimens, although those of one margin normally show markedly better exposure and may be traced along much of the length of the row (right in 198680, 198678 (figures 45–48, plate 4; figures 64 and 65, plate 6; figures 53 and 70); left in 198681 (figures 82 and 83, plate 8; figure 88)). Lack of exact superposition of the two ventro-lateral rows must indicate a slight obliquity in the angle of burial. In 198678 the left sclerites are exposed at the anterior, where downward curve of the front end appears to have been responsible for bringing them into a suitable orientation, and also posteriorly. In the latter area they show evidence for crushing and their distortion may be due to burial at a steeper angle than their better exposed counterparts on the right-hand side. The intervening length of left ventro-lateral sclerites is presumably attached to the (unlocated) counterpart. In 198681 superposition of the two sides of the animal appears to have been almost exact, with the sagittal plane parallel to the bedding.

The right ventro-lateral sclerites are only apparent where some of them have been rotated downwards. Such rotation may have been facilitated by early decay loosening the basal attachment which could have already been strained by the dorso-ventral curvature that reflects marked contraction of the body. Projection of these right sclerites beyond the rest of the body has enabled them to control the level of splitting, but adjacent to the body the split rises along a major scarp to expose mostly the left-hand side of the animal. The distribution of the ventro-lateral sclerites in 198680 is fairly similar to 198681.

Details of the anterior portion of the ventro-lateral sclerites, while visible in some oblique specimens, tend to be especially clear in certain inclined individuals, particularly 198679 (figures 68 and 69, plate 6; figure 71). In this specimen the exposure of the left row and concealment of much of the right row is attributable to a slight downward tilt in the latter direction (see above). In the inclined 198669 (figures 118–121, plate 12; figure 126), however, most of the ventro-lateral sclerites are either poorly exposed or hidden beneath other sclerites. The ventro-lateral sclerites of 198668 (figures 8 and 9, plate 1; figure 5), which is subvertical and transversely folded, exhibit a series of shape changes associated with the flexure of the body. The posteriormost sclerites are well exposed on either side of the body, while about the point of flexure the affected sclerites show signs of crushing and other distortion. More anteriorly the sclerites are overturned, show a reversal in imbrication direction in comparison with the set posterior to the fold, and have a similar shape to the ventro-lateral sclerites associated with the transverse flexure in 57635.

The row of ventro-lateral sclerites along either side of the body consisted of a single posteriorly imbricated file, and at no point does there appear to have been transverse duplication. The total of sclerites per row is estimated as about 16–17 although in no specimen is an entire complement unequivocally identifiable, and within small limits the total per individual may have varied. As noted above, however, there is no compelling evidence that the number of sclerites in this zone, or any other part of the body, increased from at least an early stage of ontogeny. Each row of ventro-lateral sclerites arose either side of the midline at the anterior and diverged posteriorly around the body margins. The few suitably oriented specimens (figures 34 and 35, plate 3; figures 68 and 69, plate 6; figures 32 and 71) indicate that the first sclerite of the right-hand side slightly overlapped that of the left, and this may have been an invariable relation. The tapering shape of the posterior body results in the ventro-lateral rows converging. In 83938 (figures 137–140, plate 14; figure 147) the posteriormost sclerites overlap, and although this could be attributed to the specimen's transverse curvature, a similar overlap in 198688 (figures 8 and 9, plate 1; figure 5) appears to be an original feature rather than accident of superposition caused by the angle of burial. In the juvenile 271947 (figure 134, plate 13) and 198746 (figures 115 and 116, plate 11) the tips of the last ventro-lateral sclerites of either side just meet.

The ventro-lateral sclerites were inserted beneath the abaxial section of the lower lateral sclerites on the sides of the body, while at the front they arose beneath the anterior sclerites. The root is obvious in some isolated sclerites, and although identifiable in some entire specimens, principally lateral and oblique, is usually indifferently preserved. In 198688 (figures 8 and 9, plate 1; figure 5), however, the roots of some of the left-hand ventro-lateral sclerites at the posterior are evident. Their position in this subvertical and folded specimen indicates that they were oriented transversely, lying at a steep angle to the body wall. Such an orientation would explain their obscurity in other entire specimens where they would tend to suffer extensive



crushing. The anterior three or four sclerites show an increase in size around the anterior margin from the mid-point. Thereafter, however, their size along the body margins appears to have been more or less constant.

The shape of an individual ventro-lateral sclerite varies according to the orientation of the specimen. In some parallel-oblique specimens (figures 110, 111 and 115, plate 11; figure 108) the sclerites have a pronounced arcuate shape with a strongly convex abaxial margin, while the angle between the proximal and distal sections is about 80°. In lateral specimens, however, the curvature of the sclerites is somewhat reduced and although the ventral margin has a pronounced convexity, the upper margin is less concave and in some cases may appear to be almost straight along part of its length (figures 64 and 65, plate 6; figures 82 and 83, plate 8; figures 70 and 88). Sclerites in oblique specimens (figure 16, plate 1; figures 34, 35 and 37, plate 3; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 32, 105 and 129) show an intermediate morphology between that in parallel-oblique and lateral specimens. The contrast in outline between the sclerites of parallel-oblique and lateral specimens, that is, a difference in angle of burial to the bedding plane of about 70°, is interpreted as a consequence of the ventro-lateral sclerites originally having an approximately semi-circular or perhaps sub-triangular cross-section, with the entire sclerite possessing a gently domed upper surface and strongly convex lower surface. The overall shape, therefore, is reconstructed as having a proximal length extending slightly abaxially and downward, while the more distal section curved so as to parallel the outer edge of the body with its overall direction changing from more or less horizontal to an upwardly directed terminus. Considering the possible degree of curvature in this body region, it seems plausible that slight torsion occurred along the length of the sclerite as it matched the configuration of underlying soft-parts. The evidence for crushing and other distortion in most parallel specimens (for example, figures 11 and 12, plate 1; figures 58 and 59, plate 5; figures 6 and 55), parallel-oblique specimens (for example, figures 74 and 75, plate 7; figure 72) which were buried at a low angle to the bedding, and in the more poorly exposed row of oblique specimens (for example, figure 37, plate 3; figures 130 and 131, plate 13; figures 32 and 129) appear to support this reconstruction.

The ribbing of the ventro-lateral sclerites shows the same relation to imbrication direction as the lower lateral sclerites, with positive relief of the ribs invariably associated with normal (posterior) imbrication. This suggests that ribbing may have been confined to the outer surfaces of the sclerite. The ribbing is most obvious on the area interpreted as the upper and flatter surface, and the sides of the sclerite generally have either subdued ribbing or may even appear smooth. This latter preservation could be due to the split passing through the middle of the sclerite, which unlike the other more flattened body sclerites would presumably have been reduced to a thicker film on account of its cross-sectional shape (figure 172). About five to six ribs are visible on a sclerite at a given orientation, suggesting that the total over the outer surface was in the order of seven to nine. The width of the ribs varied from about 0.05 to 0.14 mm, average 0.09 mm ( $n = 43$ ). The spacing of the ribs varied as they ran sub-parallel to the arcuate margins, converging at either end. The maximum spacing varied between about 0.07 and 0.44 mm, average 0.19 mm ( $n = 24$ ).

A small articulate brachiopod (width *ca.* 2.3 mm) (*Diraphora bellicostata*, see Walcott 1924; Bell 1941) is associated with one of the posterior, left ventro-lateral sclerites in 83938 (figure 141, plate 14; figure 147). While this could be a chance superposition arising as a result of turbulent transport (§6*a*), it may be significant that the brachiopod is located on the upper

surface of the sclerite with its pedicle centred on the mid-area. This unique occurrence, therefore, is tentatively considered to be a life association, where the normally sessile brachiopod would presumably benefit from increased possibilities of food supply. If this be accepted, it could give a very approximate minimum estimate of the interval in adult specimens between moults, as the brachiopod would presumably have been cast off had 83938 survived to its next moult. The size of the brachiopod suggests that it was a juvenile, and considerably larger specimens are known in the Burgess Shale (Walcott 1924). While growth rates of Cambrian brachiopods are largely speculative, it might be suggested on the basis of comparisons with growth rates in modern articulate brachiopods (for example, Paine 1969, figure 4; Doherty 1979, figure 7; Curry 1982, text-figure 7D) that this individual had been attached for at least a month and possibly longer. The location of this brachiopod on the lower margins of the body would support other lines of evidence that the adults did not normally burrow, and furthermore places a constraint on the depth of ploughing (§10). A comparable example may occur in another entire specimen (8422) where an articulate brachiopod of similar size (width *ca.* 2 mm) to that associated with 83938 appears to be attached to the adaxial margin of a posterior dorsal sclerite (right-hand side). The only other example of an attached brachiopod, also *D. bellicostata*, is a comparably sized specimen anchored to the margin of an isolated sclerite, apparently derived from the dorsal region (figure 142, plate 14; figure 148). It seems impossible to determine if this latter example is another example of pre-mortem attachment or whether the larval spat settled on the sclerite after its detachment by either moulting or death, although the former alternative seems plausible. Other examples of articulate and inarticulate brachiopods attached to other organisms such as priapulid worm tubes and sponges have been noted in the Burgess Shale (Conway Morris 1977; Whittington 1980*b*; Whittington in Conway Morris 1982*c*).

(*g*) *Soft-parts and internal anatomy*

With the exception of the feeding apparatus, described in more detail below, comparatively little information is available on the soft-part anatomy. As the systematic redescrptions of the Burgess Shale fauna have progressed it has become evident that in terms of detail of internal anatomy the priapulids, especially *Ottoia prolifica* (Conway Morris 1977), are exceptional, and in the majority of other forms such as most arthropods and polychaetes knowledge of the internal anatomy is confined to the gut trace and more occasional muscle strands. *Wiwaxia* falls into this latter category in terms of quality of preservation. In the majority of specimens the visible soft-parts appear as a rather featureless, relatively smooth area of dark film, sometimes containing irregularly shaped reflective patches that cannot, however, be readily resolved into recognizable organ systems (figures 11, 12, 13 and 15, plate 1; figures 45–48, plate 4; figures 56–59, plate 5; figures 64, 65, 68 and 69, plate 6; figures 74 and 75, plate 7; figures 84 and 85, plate 8; figures 93 and 94, plate 9; figures 98–101, plate 10; figures 110 and 111, plate 11; figure 118–121, plate 12; figures 130 and 131, plate 13; figures 154 and 155, plate 15; figures 6, 53, 55, 70, 71, 72, 90, 105, 108, 126, 129 and 151). Whereas the upper surfaces of the body were almost entirely obscured by sclerites, much of the ventral area appears to have been naked and unprotected by sclerites. This ventral area was rimmed by the crescentic ventro-lateral sclerites (figure 172) that normally appear only to have encroached onto the margins of the ventral area. The generally poor exposure of the soft-parts is presumably because the flattened and relatively rigid sclerites were better able to control the level of splitting, whereas the soft-parts would be reduced to thinner films, especially if slight decay occurred

to leave only the cuticle and some resistant organs. The soft-parts are best seen in some oblique specimens (figures 84 and 85, plate 8; figures 98–101, plate 10; figures 130 and 131, plate 13; figures 105 and 129) where some of the anterior region is evident, and could reflect a concentration of more massive organs such as the anterior gut (pharynx and stomach) and possibly associated musculature. In the part of 198671 (figures 100 and 101, plate 10) mechanical excavation has removed overlying sclerites to reveal the soft-parts along much of the median area of the body. Exposure of soft-parts in specimens other than obliquely buried is generally limited and of sporadic distribution. Occasional examples of more extensive distribution of soft-parts may usually be attributed to special circumstances. A considerable area of soft parts in the posterior region of 199910 (figures 56–59, plate 5; figure 55) has been ascribed tentatively to the failure of some dorsal sclerites to develop (§9*d*). Their exposure in the anterior of 57635 (figures 11–13, plate 1; figure 6) may be a reflection of the downward flexure of the body in this region, placing the overlying dorsal sclerites in an inopportune position at a steep angle to the bedding. Similarly, in the inclined 198679 (figures 68 and 69, plate 6; figure 71) the angle of burial appears to have favoured the split passing below the dorsal sclerites over much of the dorsum. Areas of soft-part are also preserved in some semi-isolated assemblages, particularly in 199892 (figures 154 and 155, plate 15; figure 151) which may represent either a decay remnant or moult fragment. In 199181 (figure 21, plate 2; figure 29) some faint patches of soft-parts, probably representing mostly cuticle, occur among the scattered sclerites. The very rare examples of isolated soft-parts are discussed below in more detail.

The most conspicuous feature within the area of soft-parts is a bilaterally symmetrical toothed structure, which is interpreted as a feeding apparatus. The apparatus is well preserved in some entire specimens, most notably in certain obliquely oriented individuals as well as some parallel and parallel-oblique examples (figures 11 and 12, plate 1; figures 17–19, plate 2; figures 74 and 75, plate 7; figures 84 and 85, plate 8; figures 93 and 94, plate 9; figures 98–101 and 103, plate 10; figures 118–122, plate 12; figures 130–133, plate 13; figures 6, 27, 72, 90, 105, 106, 126 and 129). In general, lateral specimens show practically no trace of the feeding apparatus. The apparatus occurs about 5 mm from the anterior end in an entire specimen of average size, and when viewed in parallel aspect is located beneath the second row of dorsal sclerites. The feeding apparatus is preserved with noticeable relief, most particularly in oblique specimens. Such relief may have been accentuated by folding of the retracted apparatus (see below), but it suggests that originally the teeth had a tough composition. The feeding apparatus is also preserved in a number of semi-isolated assemblages (figures 21 and 22, plate 2; figures 154–156, plate 15; figures 29, 30, 151 and 152) and isolated soft-parts (figures 157–161, plate 15; figure 153); in the latter their presence is the only key to the origin of the remains.

In most specimens the feeding apparatus consisted of two arcuate, anteriorly convex, bars of posteriorly directed teeth (for example, figure 103, plate 10; figure 132, plate 13; figure 106). The semi-isolated assemblage 199181 is exceptional, however, in showing three rows of teeth (figure 22, plate 2; figure 30). Preservation of the feeding apparatus in this specimen is indifferent and may be attributed to decay processes. The size of the sclerites in 199181 suggests that this was originally a very large specimen, near the upper size range of *Wiwaxia*. As other specimens appear to show invariably two rows of teeth, it is conceivable that a third posterior row was added at a late stage of ontogeny. However, in the largest known entire specimen (figures 84 and 85, plate 8) the feeding apparatus, although indifferently preserved, appears to consist only of two rows. Furthermore, while there is evidence that the two rows became closely

juxtaposed when withdrawn there is no obvious indication that a third row was actually concealed. In adult specimens the overall width of the apparatus varied from about 1.6 to 2.5 mm, and the length from about 1.1 to 1.7 mm, although some of this variation is due apparently to the relative angle of burial and extent of folding when retracted.

Remains of the feeding apparatus are also evident in juvenile specimens (for example, figures 17–19, plate 2; figures 115 and 116, plate 11; figure 27). In 277890 (figure 133, plate 13) for example, with a body length of about 8 mm, the feeding apparatus has a width of *ca.* 0.8 mm, while in the still smaller 271947 (length *ca.* 3.4 mm; figure 134, plate 13) traces of the feeding apparatus are also present. Apart from size differences the feeding apparatus of juveniles appears to be similar to that of adult specimens, consisting of two bars with a similar number of teeth. The presence of a feeding apparatus in some of the smallest known specimens suggests that the feeding habits of *Wiwaxia* (§10) were effectively unchanged during much of its ontogeny.

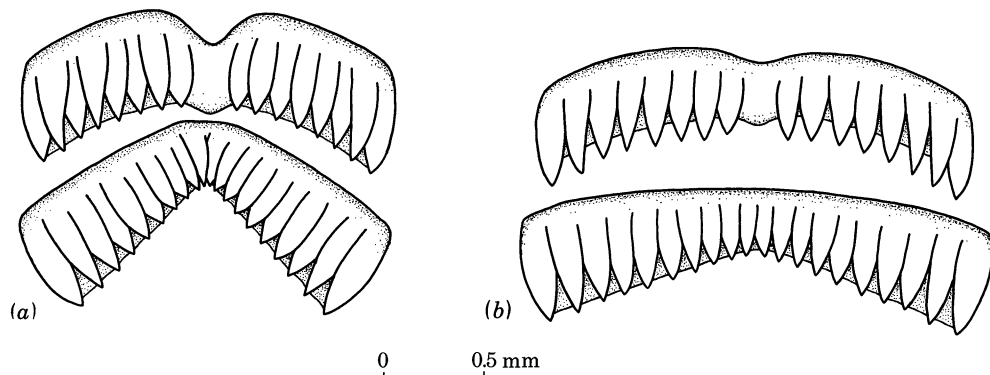


FIGURE 170. Reconstruction of feeding apparatus in *Wiwaxia corrugata* (Matthew). (a) Folded and retracted position, (b) expanded position suitable for feeding.

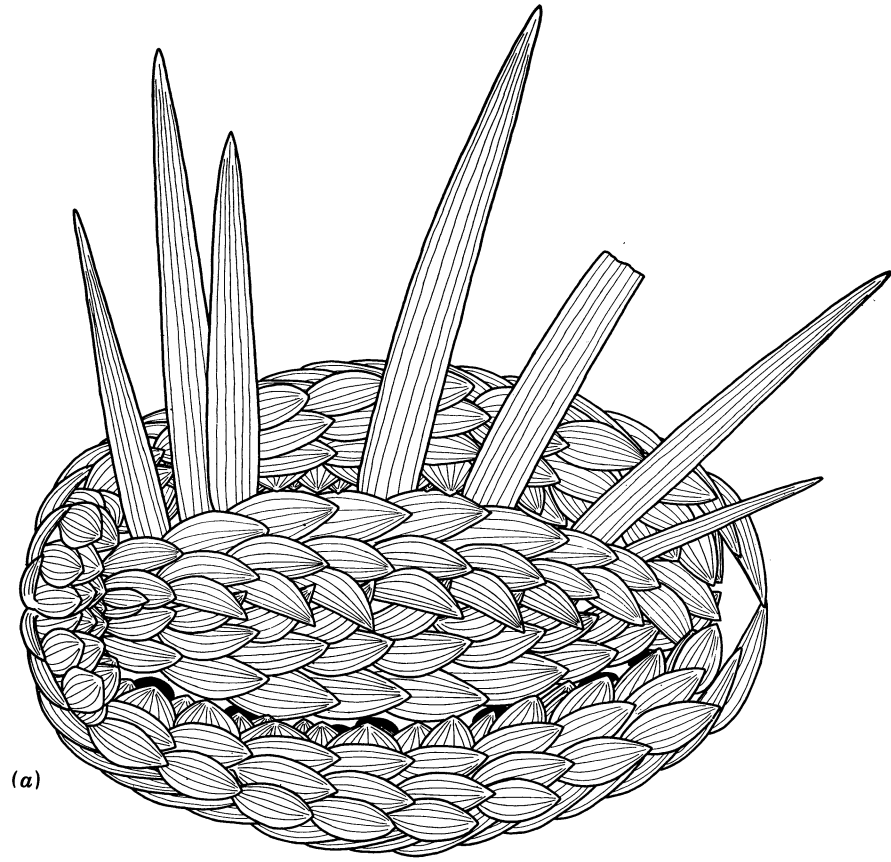
The bars of the feeding apparatus were transversely oriented about the sagittal plane. The symmetry and general appearance of the apparatus is not consistent with it having a location on the lateral walls of the gut with the two halves operating as an opposable jaw, and the apparatus was evidently attached to the floor of the gut. Each bar bore a series of simple teeth, apparently originally more or less conical in shape. The teeth appear to have been attached to a common base (figure 170). Their relative relief suggests that they were made of some tough substance, and although their exact composition is not known it does not appear to have incorporated phosphatic or carbonate material. Evidence for the shedding of teeth during moulting in 233149 (figures 17–19, plate 2; figure 27) is equivocal (§9*b*), unless certain semi-isolated assemblages with preserved feeding apparatuses (figures 21 and 22, plate 2; figures 154–156, plate 15; figures 27 and 151) represent exuviae. The postulated position of the apparatus within the foregut, which could have been of ectodermal derivation, means that any such discarding would find an analogy in the moulting of the foregut gizzard teeth and other masticatory equipment in crustaceans. Furthermore, if the teeth are of ectodermal derivation, they may have had a composition related to that of the sclerites. The apparent flexibility of the apparatus is also consistent with such a composition as against a strongly mineralized material.

The anterior bar of the feeding apparatus appears to have been somewhat shorter than the posterior bar, although this difference may have been largely dependent on the extent of folding.

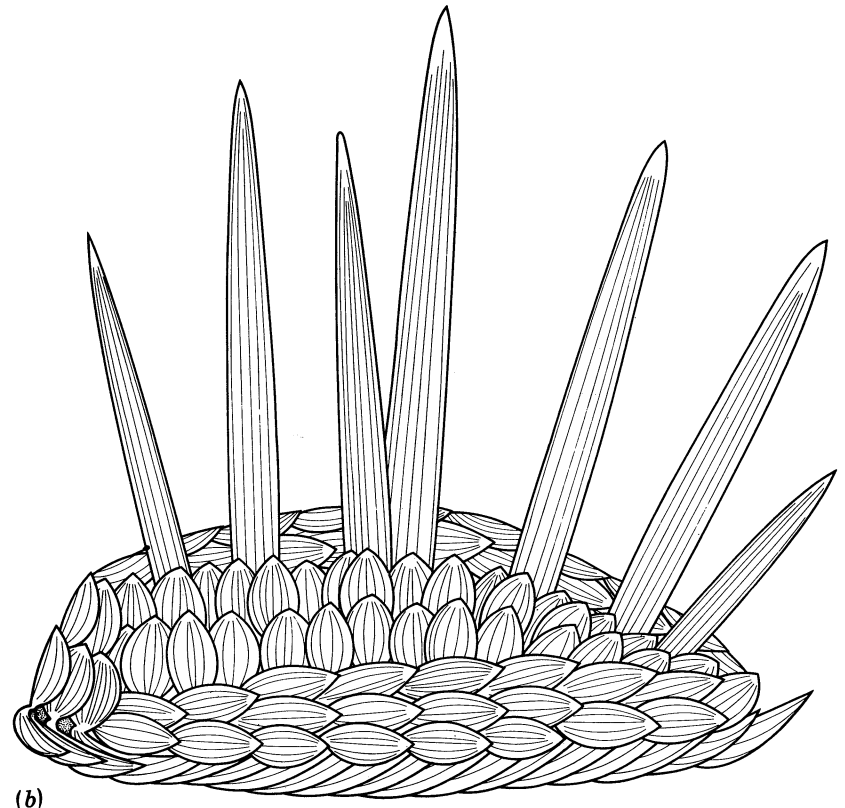
In entire specimens the shape of the anterior bar is a product of two arcuate units which, meeting about the mid-line, form a pronounced notch on the anterior edge and a corresponding deflection towards the posterior (for example, figure 132, plate 13; figure 156, plate 15; figures 129 and 152). Each half of the anterior bar bore about seven or eight teeth, although it is not possible to determine in either this bar or the posterior one whether the teeth showed an exact bilateral symmetry. In most specimens each half of the anterior bar appears to be separated by a narrow unarmed isthmus, whereas in 198671 (figure 103, plate 10; figure 106) this central region consists of a more square or rectangular area with a series of faint, paired structures along part of its anterior margin. The difference in appearance of the central region between 198671 and other specimens may be because in the former specimen the lower surface of the apparatus is exposed, whereas in the others the upper side is visible. The second posterior row appears to have lacked the notched margin of its anterior equivalent, and in general was more uniformly arcuate. The row contained about 20 teeth, which appear to have occupied the bar without inconspicuous interruption. The third bar, which may be unique to 199101 (figure 22, plate 2; figure 30), had a similar aspect to the second bar and although its preservation is indifferent the teeth may have been slightly shorter.

The structure of the feeding apparatus, with its posteriorly directed teeth, and its location within the anterior gut strongly suggests that to be effective it would have to have been protruded from the mouth to grasp food. In 198677 (figures 110 and 111, plate 11; figure 108) a small area of soft-parts at the anterior contains a lineated strand which, if representing the foregut would suggest that the mouth was located either at, or very close to the anterior of the animal. It seems unlikely that the roughly circular area immediately to the anterior of the feeding apparatus in 198671 (figure 103, plate 10; figure 106) represents the mouth, and this structure may represent either a depression within the foregut or some other organ. The location of the feeding apparatus in entire specimens is therefore taken to represent a retracted position within the foregut. It may be significant that in the semi-isolated 199181 (figure 22, plate 2; figure 30) the bars of the apparatus show minimal curvature, although the notch at the front of the anterior bar is still evident. In this partly disaggregated specimen such an arrangement could have been produced by unfolding of the soft-parts during decay. The more arcuate configuration seen in entire specimens may arise when the feeding apparatus is retracted and perhaps folded into a longitudinal trough. Such a suggestion of folding is particularly evident in the apparatus of 32569 (figures 157–161, plate 15; figure 153), although the observed configuration must be treated with caution on account of the specimen's unusual preservation. The differences in shape and evidence for retraction suggest that when the apparatus was protruded during feeding the ends of each bar rotated anteriorly, while the apparatus stretched slightly so that the separation between the teeth along a row and the adjacent bars increased (figure 170). The alteration in apparatus shape that is believed to have occurred during protrusion would result in the teeth adopting a more favourable attitude for feeding.

Other information on the soft-parts of *Wiwaxia* is largely dependent on 32569 (figures 157–159, plate 15; figure 153), a rare specimen of isolated soft-parts that presumably separated from a decaying corpse. The apparent clarity of preservation may be due in part to decay heightening the contrast of more resistant tissues. The feeding apparatus is surrounded by relatively reflective area with irregular margins. The anterior extension does not terminate in an obvious mouth, but possible evidence in 198677 for the location of a terminal mouth was given above. Behind the feeding apparatus in 32569 the presumed foregut joins a more reflective



(a)



(b)

0 5 mm

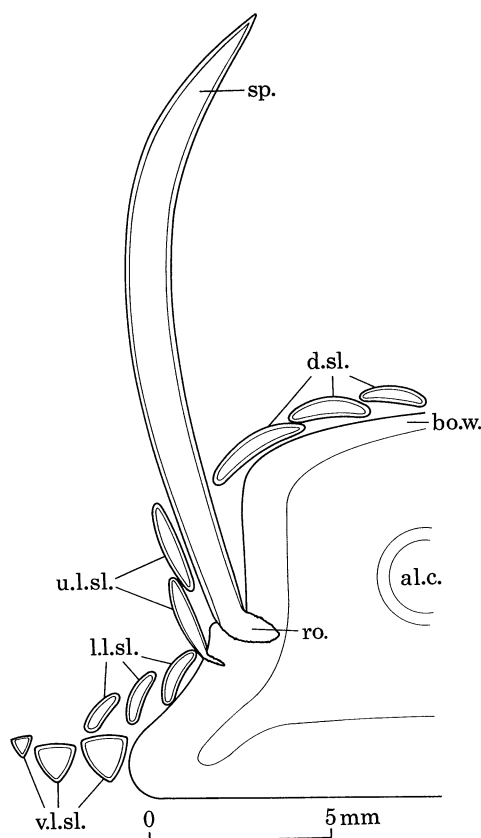


FIGURE 172. Hypothetical transverse section of the mid-region (left-hand side) showing arrangement of sclerites in relation to body wall.

strand that tapers posteriorly. The contrast in the degree of reflectivity in preservation between the two lengths of gut could reflect a histological difference and might support the notion that the foregut and enclosed feeding apparatus is of ectodermal derivation, while the tapering length could be part of the midgut. The reduction in width of the presumed midgut is relatively gradual and may have arisen during decay, but alternatively it could represent originally a broad stomach leading to a narrower intestine. No gut contents are evident, but possible remains of part of the intestine are present in 198680 (labelled ?al.c. in figure 53), and appear to contain a fine granular material that could represent detrital contents (figures 45–48, plate 4; figure 53). Available evidence on the configuration of the gut suggests that it ran towards the posterior with a terminal anus.

Within the area tentatively identified as part of the stomach in 32569 (figures 157–159, plate 15; figure 153) there is an elongate structure with branches arising on either side. Its apparent proximity to the gut means that it is less likely to be part of a nerve chord, and it is interpreted tentatively as a series of large blood vessels or sinuses, possibly running along either the top or bottom of the gut. The remains of soft-tissues surrounding the gut have irregular margins and contain no discernible detail. In 198668 (figure 10, plate 1; figure 5) two elongate structures

FIGURE 171. Reconstruction of the appearance of *Wiwaxia corrugata* (Matthew). (a) Dorsal view, spines of left-hand side have been omitted but relative positions are indicated by black ellipses. Spine 5 of the right-hand side is depicted as broken, following an encounter with a predator. (b) Lateral view, left-hand side.

with dentate ends occur on the left-hand side. Owing to transverse folding their original location is difficult to judge, but they do not appear to be part of the feeding apparatus. They could represent gills located beneath the sclerites, although no similar remains have been identified in other specimens and their nature remains obscure.

Other aspects of the soft-part anatomy of *Wiwaxia* are based on circumstantial evidence. Transverse folding in 198681 (figures 82 and 83, plate 8; figure 88) appears to have resulted from contraction of longitudinal muscles. The distribution of certain sclerites and the subdued concavo-convex relief of 83938 (figures 137–140, plate 14; figure 147) is inferred to indicate longitudinal folding, possibly produced by the action of transverse musculature. Muscles may have also been attached to at least the roots of the spines, enabling them to move in a transverse direction. If the hypothesis that the feeding apparatus was unfolded and protruded during feeding is correct, then this would suggest the action of the muscles around the anterior gut. However, despite the evidence for muscles in different parts of the body, no actual remains have been identified. The presence of a nerve cord, excretory organs and possibly a body cavity is also likely but direct evidence is wanting.

#### 10. ECOLOGY AND ASSOCIATION WITH OTHER SPECIES

It is difficult to imagine *Wiwaxia* swimming for any appreciable distance, if at all. The relative abundance of this creature, especially in comparison with rare soft-bodied pelagic organisms (Conway Morris 1976, 1979*a, b*; Whittington 1981), suggests that individuals were readily trapped and transported by benthic mudflows. Accordingly, *Wiwaxia* is regarded as a member of the vagrant benthos within the community of the pre-slide environment (Conway Morris 1979*c*, 1981). Among adults an entirely infaunal mode of life is considered unlikely. This is because although the body shape is not dissimilar to some infaunal animals such as Mesozoic and Cainozoic irregular echinoids, the resistance offered by the elongate spines would appear to place a prohibitive constraint on such a mode of life. Adult *Wiwaxia* is interpreted, therefore, as a member of the epifauna. Furthermore, if the attachment of an articulate brachiopod to a ventro-lateral sclerite of 83938 (figure 141, plate 14; figure 147) is accepted as a life association then *Wiwaxia* may have only ploughed shallowly over the sea-floor. In contrast to the adults, however, it is possible that the smaller juveniles (less than about 7 mm) could burrow. In addition to obvious size differences these juveniles may have had a more compressed dorso-ventral section (§9*a*) that may have facilitated infaunal movement. Moreover, the spines were either absent or very short and thus unlikely to impede progress. As the spines appear to have been primarily defensive such an infaunal habit among juveniles might also act as a substitute defence from predation.

Podia or other appendages appear to have been absent and locomotion presumably involved a series of muscular contractions as *Wiwaxia* may have been too large to have been propelled by ciliary gliding. Locomotory muscles may have been concentrated within the ventral area (figure 172), giving a style of locomotion highly reminiscent of the gastropod and chiton foot where waves of muscular contraction in association with secretion of mucus propel the animal (for example, Elves 1961; Trueman 1976; Denny 1980). There is, however, no unequivocal evidence that the ventral area formed a conspicuous raised mass that kept the rest of the animal clear of the sediment. The extent of involvement of the rest of the body in locomotory movements is speculative, and while the ventral area could have been largely decoupled from



other regions the imbricated nature of the body sclerites would allow latitude for movement. In the majority of sclerites locomotory movements would have simply involved antero-posterior movements, possible with some rotational movement especially among the dorsal sclerites where the distal tips may have swung abaxially. Outward rotation, however, would have presumably been more pronounced in each row of ventro-lateral sclerites with the sclerites becoming more transverse to the body during contraction.

Speculation on the feeding habits of *Wiwaxia* is based largely on the feeding apparatus, as the rare examples of preserved alimentary canal either contain unidentifiable fine granular debris or are evidently empty (§9g). The location of the feeding apparatus in an apparently folded condition within the foregut suggests that it was protruded from the mouth during feeding. The array of teeth appear to be well suited either to rasp or collect organic material. Thus, *Wiwaxia* may have rasped organic (?algal) substrates, but it is perhaps more likely that the animal collected organic grains and other organic detritus. The possibility that it was a scavenger or even a carnivore appears less likely. *Wiwaxia* is classified here as a deposit (collector) feeder, but how catholic the diet of this creature was remains uncertain.

In the apparent absence of eyes or elongate tentacles the sensory equipment of this animal is speculative and it may have relied largely on chemosensory devices. No unequivocal evidence for gills located among the sclerites is available. With the ventral area normally adpressed to the sediment gaseous diffusion probably mostly occurred through the cuticle beneath the sclerites. The extent of diffusion through the sclerites themselves would be largely dependent upon wall thickness and composition together with ease of access of gases to other parts of the body via the proximal opening and root. The relative robustness of the sclerites suggests that diffusion may have been limited. More theoretical considerations also cast doubt on whether the sclerites had an important respiratory function. Comparison of the length of ventro-lateral sclerites in six individuals (sagittal length *ca.* 3.5–52 mm) indicates that size increase was isometric with geometric similarity of ventro-lateral and other body sclerites being maintained during ontogeny. The well-known relationship between body area and volume suggests, however, that the sclerites would show positive allometry if they were to increase their area sufficiently to supply the respiratory requirements of volumetrically larger individuals. Circulation of seawater beneath the sclerites may have been effected by tracts of ciliated tissue, but a more effective method of promoting circulation may have been by elevating and depressing the sclerites so as to flush out interstitial spaces. In this context it is worth commenting on the respiratory mechanism of the modern marine polychaete *Aphrodita* (van Dam 1940) with which *Wiwaxia* shares certain generalized anatomical similarities although there is no close phyletic relation (§11a). Normally, *Aphrodita* is infaunal, although the respiratory mechanism remains unchanged if an individual is placed on the sea-bed in a position presumably comparable to the epifaunal *Wiwaxia*. In *Aphrodita* water is drawn from the posterior tip along the ventral surface, pumped laterally so as to enter the spaces between elytra and dorsum, and finally flushed backwards by an antero-posterior wave of closure between elytra and dorsum. The degree of similarity between the respiratory cycles of elytrous polychaetes and *Wiwaxia* is speculative. In particular, it seems questionable whether water could be pumped around the lateral sides of *Wiwaxia*, and it is possible that the respiratory cycle only involved the dorsal region of the animal.

The Burgess Shale community harboured a variety of predators (Conway Morris 1977, 1979a, 1981; Whittington 1975a, b, 1977, 1978, 1980a; Bruton 1981; Whittington & Briggs

1982) and as an epifaunal animal *Wiwaxia* presumably sought to deter attack. In particular, the elongate spines are interpreted as primarily defensive (Conway Morris & Whittington 1979) and have a distribution over the dorsum that is consistent with this function. The possibility that they could be moved by muscles would increase their potential as a defensive organ. Examples of broken spines are attributed to unsuccessful attack by predators, with jagged and smooth terminations possibly reflecting the style of cutting (§9c). Detachment of spines was evidently non-lethal and may not have been especially traumatic. The presence of broken and crushed spines in certain Carboniferous millipedes was attributed by Rolfe (1980) to encounters with would-be predators, while Gunter & Ward (1961) have documented extremely severe non-lethal injuries in a variety of fish, although the vulnerability of *Wiwaxia* in this respect is speculative.

Incomplete isolated spines consisting of the distal length with a frayed end (figure 38, plate 3; figure 97, plate 9; figure 124, plate 12; figures 33 and 92) could have been detached by predators and subsequently begun to decay on the sea-floor. Attributing broken spines to other causes such as difficulties in withdrawing soft-tissues during moulting seem less likely, because no comparable examples are known among body sclerites although, in principle, the withdrawal of soft-tissue would be more difficult in the latter sclerites owing to their more restricted proximal opening (compare figure 162 with figures 165, 167, 168 and 169). In addition to the broken spines, those with malformations could also be attributed to predation. The distortion in one spine of 198678 (figure 66, plate 6) may have arisen by crushing between feeding appendages. In other cases, however, *Wiwaxia* may not have been able to thwart its enemies. 45355 (figure 86, plate 8; figure 89) is an isolated sclerite with an incomplete margin that appears to be consistent with breakage by sudden fracturing. Some examples of semi-isolated assemblages and other isolated sclerites may have also arisen as a result of predation. The apparent absence of spines in smaller juveniles (§9c) may be correlated with a cryptic infaunal habitat, and the disproportionate increase in spine lengths of slightly larger specimens of *Wiwaxia* (figure 164) suggests that there was a premium on their defensive role. Once adult, however, the increasing size of the body may have complemented the spines for protection so that the largest individuals may have been largely immune from predators (see Paine 1976). Other evidence for defensive reactions could include the pronounced transverse curvature of 198681 (figures 82 and 83, plate 8; figure 88) which results in the spines forming a fan-like array. Similarly, downward folding of the anterior region (figures 11 and 12, plate 1; figures 64 and 65, plate 60; figures 6 and 70) could also serve as a protective measure. What measures *Wiwaxia* take to avoid predators immediately after moulting, when the sclerites apparently were being reinflated and hardened (§9b), is debatable. One possibility is that such individuals hid amongst sponges or algae.

*Wiwaxia* is interpreted, therefore, as spending much of life crawling over the muddy sediments of the pre-slide environment, possibly leaving a track behind it (§12c). The episodes of slumping, however, have destroyed any trails and other traces made by the Burgess Shale animals. Periodically the animal moulted, and although frequency of moulting remains speculative, the actual process was probably rapid (§9b). Direct interactions with other members of the fauna may have included rare epizoan attachments by articulate brachiopods and circumstantial evidence of predation, both attempted and successful. Most of the specimens of *Wiwaxia* occur on small sawn slabs that limit the opportunity to assess associations with other species. Furthermore, an individual turbidity flow may have brought together originally widely

separated individuals. The available data from the collections show that entire specimens of *Wiwaxia* are associated with the following forms (in decreasing order of abundance): *Canadaspis* sp. (arthropod, carapaces), *Canadaspis perfecta* (with appendages), *Morania* sp. (algae), *Scenella amii* (monoplacophoran), agnostoid trilobites, ostracodes, *Burgessochaeta setigera* (polychaete), *Marrella splendens* (arthropod), *Burgessia bella* (arthropod), polymeroid trilobites, articulate brachiopods, *Ottoia prolifica* (priapulid), inarticulate brachiopods, eodiscid trilobites, *Isoxys acutangulus* (arthropod), indeterminate arthropods, vacated tubes of *Selkirkia columbia* (priapulid), *Aysheaia pedunculata* (arthropod), *Hyolithes* sp. (hyolithid), *Vauxia gracilentia* (sponge), 'Ottoia' *tenuis* (?hemichordate), *Protospongia* sp. (sponge), and *Waptia fieldensis* (arthropod). Co-associations of entire specimens of *Wiwaxia* are uncommon with only about ten slabs known with either two or more rarely three specimens. Although separation of adjacent specimens may have occurred during sawing of the slabs the available data suggests that *Wiwaxia* was not particularly gregarious. Data on relative abundances of intra- and interspecific associations may throw more light on aspects of the ecology of the Phyllopod bed benthic community. For example, it may be significant that although *Marrella splendens* is the most abundant arthropod (ca. 15000 specimens) its degree of co-association with *Wiwaxia* is about seven times less than *Canadaspis perfecta*, although the latter arthropod is known only from approximately 4700 specimens. Similarly the degree of co-association of both *M. splendens* and *Burgessia bella* with *Wiwaxia* is about equal, although the latter arthropod is about seven times scarcer.

The relative toughness of the isolated sclerites and the potential for their reworking and transport means that data on their co-association with other Burgess Shale species are likely to be of little significance. Not surprisingly isolated sclerites have been recorded with practically all the species known to co-occur with entire specimens of *Wiwaxia*, one exception is *Protospongia* sp. which occurs with a single entire specimen. Furthermore, isolated sclerites occur with over thirty other Burgess Shale species as well as the occasional entire specimen of *Wiwaxia*.

## 11. SYSTEMATIC POSITION

### (a) *Phyletic position*

Walcott (1911) interpreted *Wiwaxia* as a polychaetous annelid and drew comparisons with the aphroditacean families Aphroditidae (*Laetmonice producta willemoesii*, *L. producta wyvilli*, *L. aphroditoides* (misspelt *aphroditis* by Walcott) and Polynoidae (*Iphione* (= *Iphionella* of Walcott, see Fauchald 1977) *cimex*). Walcott regarded his specimens as dorsally orientated and the ventral surface to be unknown at the time of his description. Accordingly, he compared the body sclerites of *Wiwaxia* with the scale-like elytra that cover the dorsum of aphroditacean polychaetes. While realizing that the spines probably were modified sclerites, Walcott also suggested a possible comparison with the prominent harpoon setae of *Laetmonice*. The available evidence, however, suggests that *Wiwaxia* can be neither a polychaete nor indeed any type of annelid (compare Jell 1981). The elytra of aphroditaceans are distributed segmentally along the dorsal surface and are interpreted as being homologous to the distal segment (cirrostyle) of the cirrus. In most aphroditaceans the elytra alternate with unmodified cirri, at least along the anterior of the body, although posteriorly elytra may occupy all segments. The distribution of the body sclerites in *Wiwaxia* is more complex than that of elytra, and the former organs do not show a regular metameric arrangement across different regions. Gross anatomical similarities between elytra and sclerites are not strong and there appears to be no direct

comparison between the sclerite root and subcentrally positioned stalk (elytrophore = basal cirrus) by which the elytron is attached to the body wall. Moreover, external details of elytra (Anton-Erxleben 1977) are not similar to the sclerites. Arguments given below (§11*b*) and elsewhere (Bengtson & Missarzhevsky 1981; Jell 1981; Bengtson & Conway Morris 1984) linking *Wiwaxia* with various Lower Cambrian genera have led to identification of a major group informally referred to as either wiwaxiids (Bengtson & Missarzhevsky 1981; Jell 1981; Landing & Brett 1982) or sachitids (Bengtson & Conway Morris 1984), terms that are regarded as synonymous. Jell (1981) discussed briefly the possible similarity between wiwaxiid sclerites, especially those of *Thambetolepis delicata* (§11*b*) which unlike *Wiwaxia* have preserved an internal structure of a central cavity and flanking lateral canals, and polychaete elytra. Jell referred to a brief and rather vague description of elytron structure by M'Intosh (1885), but more comprehensive accounts (for example, Jourdan 1855; Pflugfelder 1933; Bonhomme 1942; Nicolas 1977; Pavans de Ceccatty *et al.* 1977), while revealing a complex internal anatomy which includes an array of elongate 'pillars' or cellular fibrils, do not suggest any close comparison to the internal structure of *Thambetolepis* or other wiwaxiids.

A further difference between *Wiwaxia* and polychaetes is the apparent absence of setae in this Cambrian animal. Walcott's (1911) comparison of the elongate spines to harpoon setae is unconvincing and the spines show no evidence of either arising from parapodia or even showing a segmental arrangement; clearly they are homologous with the other sclerites and may even be modified upper lateral sclerites (§9*e*). In theory, setae could have been concealed beneath the sclerites, but they are also absent in well-dispersed semi-isolated assemblages (for example, figure 21, plate 2; figures 145 and 146, plate 14; figures 29 and 150). Although the Burgess Shale fauna possessed a considerable diversity of polychaetes (Walcott 1911, 1931; Conway Morris 1979*b*), it is concluded that *Wiwaxia* cannot be included in this group.

Earlier brief tentative mention was made of the possible relation of *Wiwaxia* to the Mollusca (Conway Morris 1979*a*; Conway Morris & Whittington 1979; see also Runnegar *et al.* 1979, p. 1382). Any such comparison would necessarily focus on the vermiform aplacophorans, rather than spiculose molluscs with secondarily lost shells such as the gastropod family Acochliidae and *Rhodope* (see Rieger & Sterrer 1975). The spiculose aplacophorans are divided into two major taxa, the Chaetodermomorpha (or Caudofoveata) and Neomeniomorpha (or Solenogastres). The position within the taxonomic hierarchy of these two groups and their interrelationships are not generally agreed. Scheltema (1978) regards these groups as equivalent subclasses of the Class Aplacophora. Salvini-Plawen (1969, 1972), however, interprets their similarities as merely representing a grade of organization that renders the Aplacophora a superfluous concept, and he has further proposed (Salvini-Plawen 1980, 1981*a*) that the Solenogastres and Polyplacophora (chitons) are more closely related to each other than the Caudofoveata. Whatever the exact relations between the two aplacophoran taxa, representatives of both groups are largely covered with small calcareous (aragonite) spicules (scales and spines) and thus have a superficial resemblance to *Wiwaxia* and more particularly its mineralized Lower Cambrian relatives (§11*b*). Aplacophorans are effectively soft-bodied and are not known as fossils. In principle, however, the spicules could be preserved and may yet be located in fine-grained sediments. Pojeta (1980) tentatively suggested that the enigmatic Ordovician microfossil *Ptiloncodus* (Ethington & Clark 1982) could be compared to certain aplacophoran spicules. *Ptiloncodus* has a phosphatic composition, although this could represent secondary replacement of an originally calcareous skeleton.

The apparent difference in composition between the sclerites of *Wiwaxia* (§9*b*) and the calcareous spicules of aplacophorans may not be significant because Lower Cambrian wiwaxiids appear to have had calcareous sclerites, although not necessarily aragonitic (Bengtson & Conway Morris 1984). Nevertheless, comparisons between the modes of formation of aplacophoran spicules (Hoffman 1949; Beedham & Trueman 1968; Haas 1981) and sclerites of wiwaxiids show no significant similarity. Spicules of the former group begin development as an intracellular secretion which continues growth through the cuticle by basal accretion, the spicule nestling in an organic 'cup' that maintains a connection with the underlying mantle epithelium. Although the spicules may be hollow, they do not contain organic material responsible for secretion. The mode of formation of these spicules is thus entirely different to the sclerites of *Wiwaxia* and its relatives. Further specific comparisons between *Wiwaxia* and aplacophorans are not profitable as no close relation can be demonstrated, although the supposed primitive status of aplacophorans within the Mollusca may be significant when assessing the broader mollusc-like characters of *Wiwaxia*.

Although *Wiwaxia* cannot be accommodated within the Mollusca, there exist similarities between their respective bodyplans that may suggest an evolutionary relation at some more fundamental level. In overall shape *Wiwaxia* (figures 171 and 172) resembles the relatively primitive polyplacophorans (chitons), which have a ventral expanse of soft-tissue forming the muscular foot and a dorsal secretory area. If the ventral area of *Wiwaxia* was muscular, as is plausible from the inferred demands of locomotion (§10), then it would have differed little from the molluscan foot of polyplacophorans and gastropods. In the aplacophorans, however, the foot has been greatly reduced and the spicular integument now covers most of the surface. As noted above the mode of formation of *Wiwaxia* sclerites is not comparable to that of aplacophoran spicules, nor indeed any other molluscan shell. However, if secretion of a dorsal exoskeleton was restricted to specific nodes as against deposition across a broad mantle epithelium, then an arrangement comparable to *Wiwaxia* could arise. Such a skeleton could not grow by lateral accretion along the mantle margins and any appreciable size increase would be achieved by moulting (§9*b*).

With so little known of the internal anatomy of *Wiwaxia* further comparisons with the molluscan bodyplan are necessarily tenuous. There is, however, a striking similarity between the feeding apparatus of *Wiwaxia* and the molluscan radula, the latter generally consisting of several to many transverse rows of teeth arranged in a ribbon-like strip that is attached to the ventral floor of the buccal cavity. Among the primitive aplacophorans the radula has a wide variety of shapes (for example, Salvini-Plawen 1969, 1972, 1981*a, b*; Scheltema 1972, 1981; Deimel 1982), of which some of the distichous varieties are broadly comparable to the feeding apparatus of *Wiwaxia*. Radulae of other molluscan groups such as polyplacophorans and gastropods also have a generalized resemblance to the feeding apparatus. Like the molluscan radula the feeding apparatus occupied a comparable position in the fore-gut, and when not in use appears to have adopted a folded configuration (§9*g*). Unfortunately, no information on the histology of the feeding apparatus or the presence of associated structures such as a radula sac are preserved. Primitive molluscs tend to show pseudometameric arrangement of some organs. This pseudometamery differs from the regular metameric segmentation of annelids in that the total number of each set of organs is not constant. In the virtual absence of information on the internal anatomy of *Wiwaxia* its supposed pseudometameric condition is speculative, but it may be significant that although the different types of sclerite show a regular arrangement

along the body there is no precise repetition that would suggest underlying metameric segmentation.

It is generally agreed that the origins of the Mollusca lie among either the turbellarians or their ancestors (for example, Vagvolgyi 1967; Salvini-Plawen 1969, 1972, 1981*a*; Stasek 1972; Trueman 1976; Pojeta 1980; Runnegar 1983). The hypothetical intermediate steps between turbellarian and mollusc appear to be functionally plausible and need not have involved radical re-organization of the body-plan via one or a few abrupt major steps. The evolutionary transition included the development of a muscular foot, radula and gills (ctenidia), but the key innovation appears to have been the formation of a cuticle beneath which calcareous spicules were later secreted (Stasek 1972). At a later stage the spicules coalesced to form a rigid shell secreted by underlying mantle tissue. The presence of calcareous spicules in some turbellarians (Rieger & Sterrer 1975) is regarded by some workers (for example, Runnegar *et al.* 1979; Pojeta 1980) as an important indicator of the evolutionary origins of molluscan hard-parts. It should be emphasized, however, that although some of these turbellarian spicules are epithelial, others occupy deeper body levels (Rieger & Sterrer 1975) that suggest no direct evolutionary connection with the development of spicules in molluscs (see also Haas 1981).

If the ultimate derivation of molluscs from turbellarians is accepted, it seems reasonable to suppose that they were only one such off-shoot and that during the Precambrian–Cambrian radiation a number of other mollusc-like forms evolved, including *Wiwaxia* and its relatives (figure 173). Another such off-shoot could be represented by the hyolithids which despite

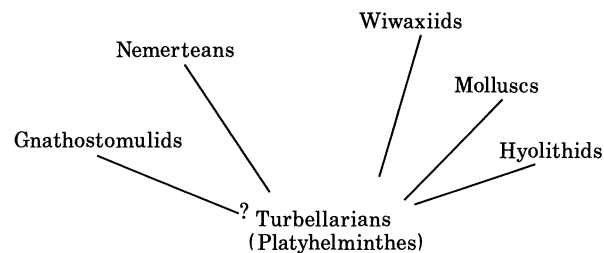


FIGURE 173. Tentative phylogenetic relationship of the wiwaxiids showing derivation from a turbellarian flatworm. This ancestral form was relatively close to the ancestors of the molluscs (Pojeta 1980) and hyolithids (Runnegar 1981). The nemerteans and possibly gnathostomulids also appear to have risen from the turbellarians, but no close relationship exists with the Molluscata.

similarities to molluscs are regarded as a distinct phylum (Pojeta 1980; Runnegar 1981). Taken together these phyla (Mollusca, Wiwaxiida, Hyolitha) could constitute part of the superphylum Molluscata (Valentine 1973), although the use of the term Molluscata is meant to imply neither agreement with Valentine's (1973) ideas of its derivation from a coelomate ancestor nor the validity of various other coelomate superphyla. The probable shared characters of the Molluscata are debateable, but Stasek's (1972) statement that 'The radula probably appeared prior to all other distinctly molluscan features' could accord with the similarity between the feeding apparatus of *Wiwaxia* and the molluscan radula. Unfortunately, no information exists as to whether hyolithids possessed a radula. Differentiation of molluscs, hyolithids and wiwaxiids may be traced to the differing modes of secretion of the exoskeleton.

While the derivation of wiwaxiids and molluscs from closely related turbellarian stocks is the preferred hypothesis, a realistic alternative must be that such similarities as exist are convergent so that wiwaxiids comprise a distinct phylum without any obvious close relatives (Conway

Morris 1982*a*; Bengtson & Conway Morris 1984). Many authors (for example, Vagvolgyi 1967; Anderson 1982) have stressed that among relatively simple phyla generalized similarities may have arisen from analogous responses to comparable adaptive requirements. Given the phyletic complexity of the turbellarians it is conceivable that the origins of wiwaxiids and molluscs were indeed distant.

(*b*) *Relations between Wiwaxia, Halkieria and other related genera*

The Lower Cambrian is well known for a wide variety of shelly microfossils, often phosphatized, many of which are of an enigmatic zoological position (Matthews & Missarzhevsky 1975; Bengtson 1977; Brasier 1979). Abundant in these faunas are small sclerites attributed to several genera, including *Sachites* Meshkova 1969, *Sinosachites* He 1980, *Dactyosachites* He 1980, *Microsachites* He 1981, *Thambetolepis* Jell 1981, and *Halkieria* Poulsen 1967. Bengtson & Missarzhevsky (1981) and Jell (1981) proposed independently that these sclerites were related to *Wiwaxia*, their comparisons being largely based on a general morphological similarity including overall shape and surface ornamentation. Despite certain differences, such as the smaller size of the Lower Cambrian sclerites and their mineralization with an apparently original composition of calcium carbonate, the resemblances appear to be significant. They are assessed elsewhere in detail by Bengtson & Conway Morris (1984), and only some brief remarks of direct relevance to the study of *Wiwaxia* are presented here.

Because of their differing modes of preservation, taken together the Lower and Middle Cambrian sclerites can give a series of reciprocal insights into the palaeobiology of the group. Lower Cambrian wiwaxiids occur almost invariably as isolated sclerites that were dispersed following the death and decay of the original organism. As they are etched from calcareous rocks they retain their three-dimensional form and may show details of an internally complex structure. The extensive flattening, on the other hand, experienced by specimens of *Wiwaxia* makes reconstruction of exact sclerite configurations difficult, while any traces of internal structure within the sclerites appear to have been obliterated. However, entire specimens of *Wiwaxia*, preserved under the unusual taphonomic conditions of the Burgess Shale, provide a useful guide or template to the disposition of sclerites in *Halkieria* and its relatives, although in no case are the Lower Cambrian sclerites identical in shape to those of *Wiwaxia*. The difference in composition with the inferred loss of calcium carbonate from the sclerites of *Wiwaxia*, is not believed to debar an evolutionary relation. This is because there is a fundamental similarity in the mode of secretion, and it is conceivable that a fibrous layer present in *Halkieria* (Bengtson & Conway Morris 1984) is homologous to the fibrous wall of *Wiwaxia* (§9*b*). The apparent loss of hard parts in *Wiwaxia* finds parallels in other groups where effectively soft-bodied organisms can be derived from well-mineralized ancestors, for example, nudibranch and some pulmonate (slugs) gastropods. Nevertheless, in view of the recurrent emphasis on the development of hard parts as part of the major metazoan diversification during the Cambrian, it is worth emphasizing that the evolutionary patterns must have been more complex with some groups effectively disappearing from the normal fossil record with a reduction in mineralized hard parts.

In describing isolated wiwaxiid sclerites (*Thambetolepis delicata*) from the Lower Cambrian of South Australia Jell (1981) discussed their possible function. His claim that 'The complex internal structure... indicates that the sclerites had a primary function associated with a vital organ of the body' may not be justified if the system of apparently fluid-filled canals that

occupied the sclerites could be related primarily to their secretion (Bengtson & Conway Morris 1984). Nevertheless, Jell (1981) proposed that the sclerites of *Thambetolepis*, and by implication those of *Wiwaxia*, were associated with respiration or extensions of the alimentary canal and in doing so he relegated the protective role of at least the spines to secondary importance. Jell's (1981) arguments, however, are not compelling. The sclerite wall in *Thambetolepis* and related Lower Cambrian genera was mineralized and must have provided some barrier to gaseous diffusion, especially in contrast to the surrounding cuticle and the possible existence of a flushing mechanism to drive seawater over the body surface (§10). Respiratory exchange across the unmineralized sclerite wall in *Wiwaxia* is in principle more feasible, but as is discussed in §10 the intervening areas of cuticle may have been the main sites of gas transfer. Although evidence on the nature of the alimentary canal in *Wiwaxia* is meagre (§9g), there is no evidence for extensive ramifications or branching, and it is surely unlikely that the massed array of sclerites in *Wiwaxia* was intimately connected with the process of digestion and assimilation. Jell's (1981) suggestion that the spines had a 'secondary [protective] function which may only have come into play when the animal rolled up' is considered less likely on the strength of the evidence given in §10 and the likelihood that the spines would have been effective in protection irrespective of whether *Wiwaxia* was enrolled. The protective nature of the spines therefore, is upheld, but the possible functions of the body sclerites are less certain. Presumably they contributed to the defence of the animal, and there is no firm evidence to suggest an intimate connection with one or more internal organs.

## 12. WIDER IMPLICATIONS OF *WIWAXIA*

### (a) *The origin and relative success of major metazoan bodyplans*

The fossil record of early metazoans convincingly shows that during the early Phanerozoic (late Precambrian to Cambrian) there was a series of major adaptive radiations (Sepkoski 1978, 1979; see also Runnegar 1982). Although the increase in diversity, as measured by number of families, was dwarfed by a subsequent rise caused by further adaptive radiations in the late Cambrian and Ordovician (Sepkoski 1979), it appears that most, and perhaps all the major bodyplans or phyla were established during the first wave of metazoan diversification (Brough 1958; Nicol *et al.* 1959; Valentine 1981). The magnitude of this radiation, which effectively provided the foundations of all subsequent metazoan history, is generally interpreted as arising from the progressive occupation of an effectively empty marine ecospace. Valentine (1975, and elsewhere) has further suggested that this diversification was linked to changes in environmental variability, especially as reflected in the degree of resource (trophic) stability and the extent of continental fragmentation following the apparent dispersal of a late Precambrian supercontinent. While such factors must have influenced early metazoan evolution, it may be that diversification is simply a reflection of the availability of an almost empty ecospace with low levels of competition permitting the evolution of a wide variety of bodyplans, only some of which survived in the increasingly competitive environments through geological time. Among the early bodyplans are a variety of bizarre forms, perhaps best known among many Tommotian species (Bengtson 1977), echinoderms (Sprinkle 1980), and a number of soft-bodied metazoans in the Burgess Shale (Conway Morris 1979a; Conway Morris & Whittington 1979), that with hind-sight may be interpreted as 'experiments' in metazoan design. With the increasing congestion of the marine environment the opportunities for the evolution of entirely new



bodyplans steadily diminished as existing groups radiated into the available habitats (Brough 1958; Nicol *et al.* 1959; Valentine 1975, 1981; Stanley 1976). At what point in geological time new phyla stopped evolving so that metazoan evolution became more a question of exploring variations on established themes is uncertain. General considerations suggest that if new bodyplans can only evolve in an ecological 'vacuum', then probably all phyla had evolved by the end of the Cambrian. The only other periods of geological history that would have provided particularly propitious conditions for the appearance of new bodyplans would be after a mass extinction (Raup & Sepkoski 1982; Sepkoski 1982) with the vacation of numerous ecological niches. However, even following the late Permian mass extinction, arguably the most severe of these events, the fossil record suggests that existing phyla exploited the available opportunities rather than any new phyla evolving. Certainly, the post-Cambrian first appearances of body fossils of many soft-bodied phyla, for example, ctenophores (Stanley & Stürmer 1983), nemerteans (Schram 1973), nematodes (Størmer 1963; Schram 1973), rotifers (Southcott & Lange 1971), may reasonably be attributed to the vagaries of the fossil record. There are also a number of bizarre soft-bodied forms apparently representing novel bodyplans from exceptional fossil deposits in the Silurian (Scourfield 1937) and Carboniferous (Nitecki & Schram 1976; Nitecki & Solem 1973; Johnson & Richardson 1969; Conway Morris 1979*d*) that may have evolved in the late Precambrian or Cambrian, although a later derivation is not necessarily excluded.

In §11*b* it was suggested that *Wiwaxia* evolved from a turbellarian-like ancestor, together with molluscs, and probably a variety of other groups such as hyolithids. Their evolution exemplified the scope of the Precambrian–Cambrian radiation with the establishment of at least three distinct bodyplans or phyla that could be accommodated in the superphylum Molluscata (Valentine 1973). *Wiwaxiids*, molluscs and hyolithids all occur in the lowest Tommotian stage of the Cambrian so that any common ancestor must have existed during or before the late Precambrian. If the descent of *wiwaxiids* and molluscs from similar turbellarian-like worms is accepted their common derivation should give additional insights into the origin and relative success of major bodyplans. Stasek (1972) noted 'that at least some of the very traits now held to be basic in defining the individual phyla were, in their incipient stages, nothing more than variable minor traits of specialization integrated into a single broad framework'. The suggested equivalence of the feeding apparatus of *Wiwaxia* to the molluscan radula is one such example (§11*a*), in that although the radula is now regarded as a hall-mark of molluscs its inferred presence in the very earliest members of the phylum (Stasek 1972) suggests that either a radula or its precursor was also present in the immediate turbellarian ancestors. Other examples of the evolution of characters that only subsequently proved to be of fundamental importance in the definition of a bodyplan appear to be known. Jollie (1982) has indicated that the 'callichordates' may be regarded as echinoderms that evolved before the development of the water vascular system, a character that otherwise is considered to be a cachet of the Echinodermata. Similarly, the enigmatic '*Peytoia* animal' (Whittington & Briggs 1982) possessed an anterior pair of jointed appendages that when found isolated would be readily interpreted as arthropodan (Briggs 1979). Thus in many cases a hypothetical Cambrian systematist confronted with a continuum of morphological features would probably erect a rather different classification (see also Bengtson 1977) because to a certain extent major bodyplans are only recognized in hind-sight. For example, regarding the origin of bivalves from rostroconchs Runnegar (1978) emphasized that had the lineage failed the earliest and only

representatives would have been probably classified simply as aberrant bivalved rostroconchs. Indeed a hypothetical observer in the Cambrian would presumably have had no means of predicting which of the early metazoans were destined for phylogenetic success as established bodyplans and which were doomed to extinction. The fossil record shows that the shallow waters of many Lower Cambrian seas were teeming with wiwaxiids and monoplacophorans, both with broadly comparable bodyplans and presumably similar modes of life as epifaunal grazers and deposit feeders. Wiwaxiids probably became extinct during the early Palaeozoic, perhaps before the end of the Cambrian and they evidently did not radiate widely. In contrast the molluscan radiation from monoplacophoran ancestors has been a story of unprecedented success with an immense variety of forms evolving that range from squids and nautilus to nudibranchs and predatory gastropods. Whether the relative success of wiwaxiids and molluscs from similar beginnings is a result of adaptive superiority is an interesting question (see also Stanley 1976). In discussing the disappearance of major taxa during geological time Strathmann (1978) speculated on whether certain adaptive types are favoured by local circumstances that might not otherwise prove competitively superior through time, or whether there are indeed unique features that provide a definitive advantage over co-existing bodyplans. Rigorous data to test this hypothesis are not easily available. However, in a study of the demise of one major Palaeozoic group, the trilobites, Raup (1981) suggested that the underlying cause for this decline may have been selective extinction, presumably due to relative inadaptiveness, rather than a series of random deleterious events that by chance tipped the balance against trilobites. As Raup (1981) put it their final extinction was more likely to be due to 'bad genes' as against 'bad luck', and more recently other applications of this principle have been explored with reference to the extinction of conodonts (Clark 1983) and the speculation that although life originated a number of times only one lineage survived (Raup & Valentine 1983). In comparing the adaptive potential of wiwaxiids and molluscs it might be argued that the continuous accretion of a shell was ultimately superior to the moulting cycle of wiwaxiids, given that other features such as a locomotory foot and radula, which are often cited as reasons for molluscan success, were present in both groups as either analogous and possibly homologous organs. Nevertheless, moulting as a mode of growth is widely used in a number of phyla including arthropods and nematodes, these latter two groups being arguably the most successful of all metazoan phyla. In conclusion, if the clock was turned back so metazoan diversification was allowed to re-run across the Precambrian–Cambrian boundary, it seems possible that the successful bodyplans emerging from this initial burst of evolution may have included wiwaxiids rather than molluscs.

(b) *Predation in the Cambrian*

Knowledge of the existence and extent of predation during the Cambrian is important both because of its inferred importance in the evolution of protective hardparts (Bengtson 1977) and its possible role in determining the diversity and trophic complexity of early metazoan communities. It has long been recognized, however, that evidence for either Cambrian predators or their effects is limited, especially in the lower part of the system. Some workers (for example, Glaessner 1972) have accepted the available fossil record as a reliable guide, whereas others have suggested that most Cambrian predators were soft-bodied with a low fossilization potential and so were normally incapable of preservation (Hutchinson 1961; Bengtson 1977; see also Matthew 1891). It is significant, therefore, that redescription of the

Burgess Shale fauna, where fossilization bias has probably been minimal, has shown that predators were an important component of at least this Middle Cambrian community. One of the clearest examples of predation in the Burgess Shale is the presence of hyolithids in the gut of the priapulid *Ottoia prolifica* (Conway Morris 1977) and arthropod *Sidneyia inexpectans* (Bruton 1981). This example is of significance in two ways. First, to judge from their appearance in the priapulid guts the hyolithid shells would show no evidence of having been predated; in principle many of the Cambrian hyolithids found as fossils could have suffered predation. Second, the number of Burgess Shale hyolithids in the gut trace of *Ottoia* is recorded as 48, being distributed among 31 specimens of the worm (Conway Morris 1977). Bruton (1981) only illustrated one specimen of *Sidneyia* with an intact hyolithid in the gut, and hyolithids may have formed a subsidiary part of this arthropod's diet. Alternatively, the hyolithid shells may have been rendered unrecognizable by crushing during feeding. The total of free-living hyolithids with attached helens and opercula, and thus judged to be alive at the time of burial (Conway Morris 1981), is about 54. Disarticulated hyolithids are far more abundant, but these individuals do not represent part of the standing crop, rather they persist in the fauna owing to a prolonged residence time in the sediment of the vacated shell. In the Burgess Shale the roughly equal total of hyolithids in the guts of *Ottoia* and *Sidneyia*, which presumably were alive when eaten, and as individuals living on the sea-floor suggest that predation levels among at least hyolithids were very significant.

As well as gut contents (see also Bruton 1981), indirect evidence for predation includes mouth parts or other appendages apparently suitable for grasping or shredding prey (Whittington 1975a, b, 1977, 1978, 1980a; Whittington & Briggs 1982; Briggs & Mount 1982). Significantly, the predators of the Burgess Shale are either soft-bodied or lightly skeletized, even the trilobite *Olenoides serratus* has appendages with a minimal fossilization potential. Other indirect evidence of predation occurs in *Wiwaxia* and includes the presence of broken (figures 51 and 52, plate 4; figure 60, plate 5; figure 67, plate 6; figure 102, plate 10; figures 55, 70 and 105) and crushed spines (figure 66, plate 6; figure 70), an apparently fractured sclerite (figure 86, plate 8), and perhaps some of the semi-isolated assemblages.

By counting the number of specimens of *Wiwaxia* with broken and damaged spines in comparison with entire individuals it should be possible, in principle, to measure the intensity of attempted predation. However, as both spine rows are rarely completely visible and there is uncertainty surrounding the ability of the animal to repair damage during succeeding moults, the recorded value of about 20% of individuals showing evidence of attack may be an underestimate. Moreover, if there was some method for determining successful predation events in *Wiwaxia* then it would be possible to assess what proportion of all attacks actually resulted in a kill (see Vermeij 1982); such information could indicate the relative efficiency and sophistication of some Cambrian predators. Although some semi-isolated assemblages probably represent the results of a successful attack, others appear to have resulted from moulting.

It seems likely, therefore, that our knowledge of Cambrian predators is controlled more by fossilization potential than original abundance. Nevertheless occasional examples of predation are known from other Cambrian faunas and deserve more systematic study. Available evidence includes damage to trilobites (Burling 1917; Lochman 1941; Öpik 1961; Alpert & Moore 1975; Rudkin 1979; Vorwald 1982) and certain trace fossils. The latter include coprolites sometimes with enclosed trilobite and other shelly fragments (Matthew 1891; Durham 1971), arthropod digging traces intersecting worm burrows (Bergström 1973), burrows attributed to sea

anemones or comparable cnidarians that contain trilobite and sometimes other debris (Alpert & Moore 1975; Birkenmajer 1977), and a variety of borings not all of which are necessarily indicative of predation (Bengtson 1968; Pelman 1973; Matthews & Missarzhevsky 1975; McBride 1977; S. Conway Morris and S. Bengtson, unpublished observations). Yet more circumstantial evidence is the apparent example of crypsis in the late Cambrian trilobite *Stenopilus pronus*, which closely resembles associated limestone intraclasts (Stitt 1976).

(c) *Cambrian trace fossils*

In addition to evidence from body fossils the Precambrian–Cambrian metazoan radiation is also reflected in the changing diversity of trace fossils (Alpert 1977). Notwithstanding reiterated warnings that in most cases it is impossible to match unequivocally a given trace fossil to a particular group of metazoans, a number of authors (for example, Glaessner 1969; Crimes *et al.* 1977) have attributed a variety of Cambrian trace fossils to the activities of ancestral molluscs, molluscs or even gastropods. Such identifications appear reasonable in as much as construction of the traces appears to have involved the movement of a large muscular foot, but as the anatomy of *Wiwaxia* suggests that it too could have produced directly comparable traces, non-committal identifications with regards to original makers are clearly preferable. Given the similarity between the molluscan radula and feeding apparatus of *Wiwaxia* even marks attributed to the rasping activities of a radula in Cambrian rocks may not necessarily be molluscan. Seilacher (1977) has described enormous radula markings from the Upper Cambrian of Saudi Arabia. While these trace fossils were most probably made by an animal similar to the Upper Cambrian genus *Matthevia* (Runnegar *et al.* 1979), there remains the possibility that a wiwaxiid was responsible.

13. COMMENTS ON THE SUPPOSED SCALE WORM *POLLINGERIA GRANDIS* WALCOTT

In his principal paper on the Burgess shale worms Walcott (1911) described *Pollingeria grandis* as isolated scales broadly similar to *Wiwaxia*. He illustrated five specimens (figures 62 and 63, plate 5; figure 144, plate 14) and stated that ‘in only one example are they [the scales] grouped together to indicate the size and form of the dorsal surface’, and his mention of an incomplete specimen measuring 12 cm long (later modified to 13 cm (Walcott 1912*d*)) and 7 cm wide presumably refers to this specimen. Walcott may have been referring to 277835 (figure 136, plate 13), but despite the scales being oriented in a broad linear tract there is no evidence to suggest that they represent the disaggregated remains of sclerite-covered worm. Although the scales of other specimens often occur in close proximity on the sawn slabs, they are always isolated and never show a coherent arrangement. The scales are extremely abundant, with an estimated total in the U.S.N.M. collections of over 5000 specimens.

The scales are leaf-like, evidently compressed in life, with smooth edges and a rather variable morphology (Walcott 1911). Generally one end of the scale is relatively slender, but there is no evidence for an attachment area or organ. The scale is traversed by irregularly meandering and narrow structures that tend to be preserved with noticeable relief. Walcott (1911) interpreted them as the trails made by some commensal worm as it grazed over the scale. Such an interpretation appears unlikely, and these narrow ridges are believed to be an integral part of the organism. In some specimens the ridges appear to have become partly detached and extend away from the specimen as silvery strands. This detachment may have occurred during decay and suggests that the ridges were superficial features.

The affinities of *Pollingeria* are enigmatic. There is no evidence to support the suggestion that they represent the now scattered scales of a worm. Indeed, it may be questioned whether they are even animals, and an alternative suggestion is that they represent some sort of algae with the leaf-like body representing a flattened thallus. The meandering strands might conceivably represent reproductive bodies. No close resemblance, however, appears to exist with either the Burgess Shale algae (Walcott 1919) or other algae.

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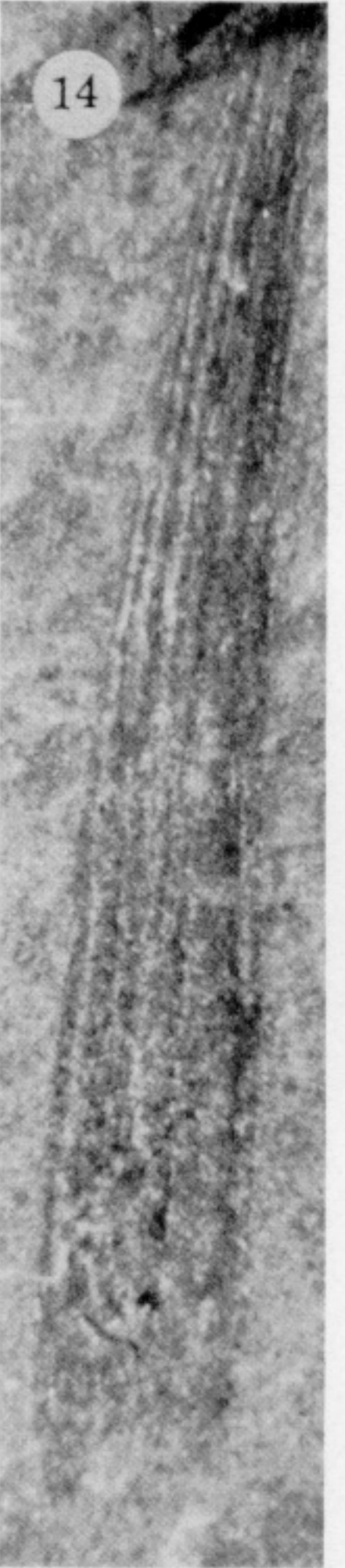
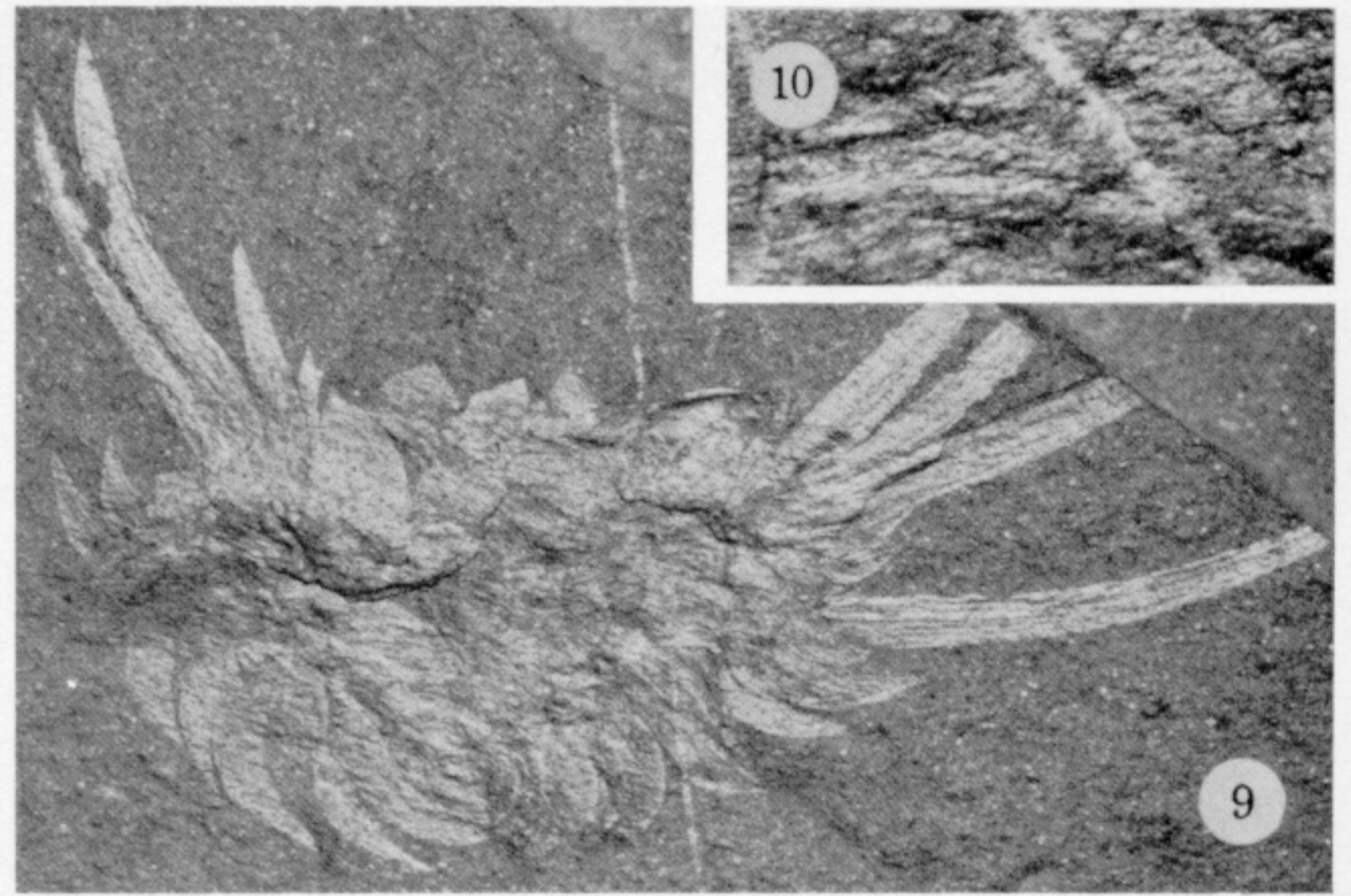
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## EXPLANATIONS OF ABBREVIATIONS

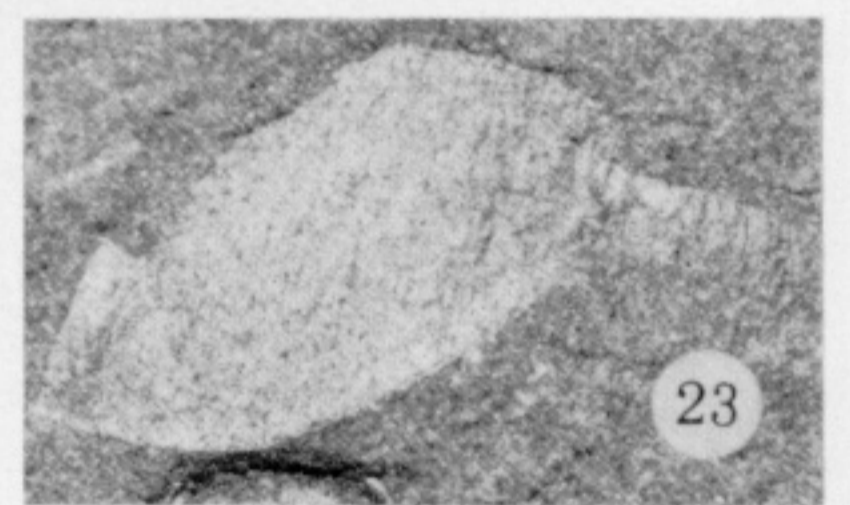
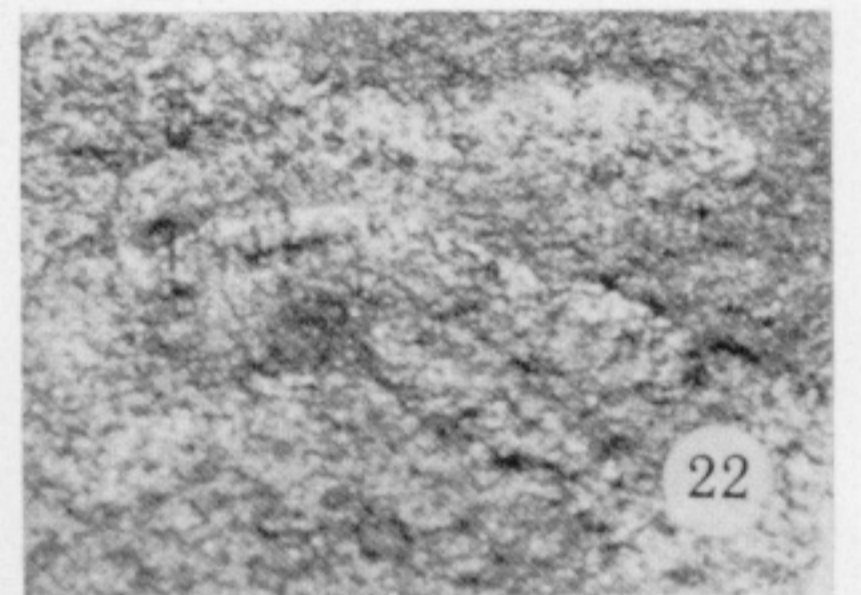
G.S.C.	Geological of Survey, Ottawa
M.C.Z.	Museum of Comparative Zoology, Harvard
R.O.M.	Royal Ontario Museum, Toronto
U.S.N.M.	United States National Museum (now National Museum of Natural History), Washington, D.C.
al.c.	alimentary canal
a.sl.	anterior sclerite
bo.w.	body wall
br.	brachiopod (articulate)
b.sp.	broken spine
?b.v.	possible blood vessel
cr.	crease
c.v.	chlorite vein
d.c.	possible area of decay
d.s.	dark stain
d.sl.	dorsal sclerite
ex.	exuvia
f.ap.	feeding apparatus
?fe.	possible fractured edge
fi.	fibres
fo.b.	foreign body
?int.	possible intestine
i.sl.	isolated sclerite
i.sp.	isolated spine
L.	left; prefix
l.l.sl.	lower lateral sclerite
<i>M.</i>	<i>Marrella splendens</i> (arthropod)
mo.id.	moulting individual

?or.	unidentified organ
p.fl.	point of flexure
?p.i.sl.	?partly inflated sclerite
?pt	pit, possibly associated with feeding apparatus
R.	right; prefix
ro.	root of sclerite
S.	<i>Selkirkia columbia</i> (priapulid)
sl.	sclerite, unspecified
sp.	spine
s.pt.	soft-parts
s.sp.	short spine
te.	teeth
tr.f.	trilobite fragments
u.l.sl.	upper lateral sclerite
v.l.sl.	ventro-lateral sclerite
1- <i>n</i>	As subscript numbers to denote transverse rows of sclerites, spines of either side, rows of feeding apparatus. In the case of the spines the numbering only refers to those visible in a specimen; other spines may be concealed or restricted to an unavailable counterpart.

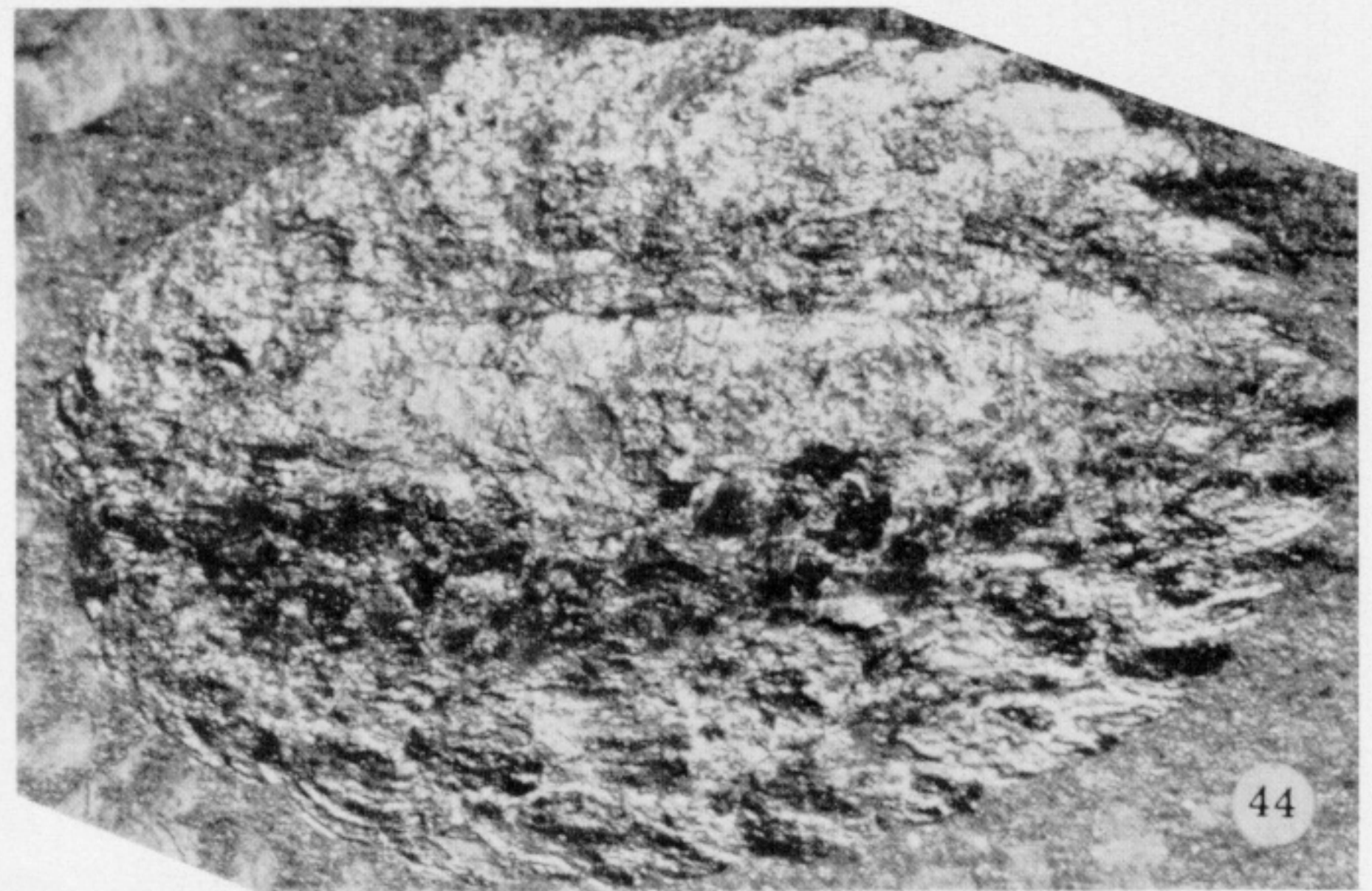
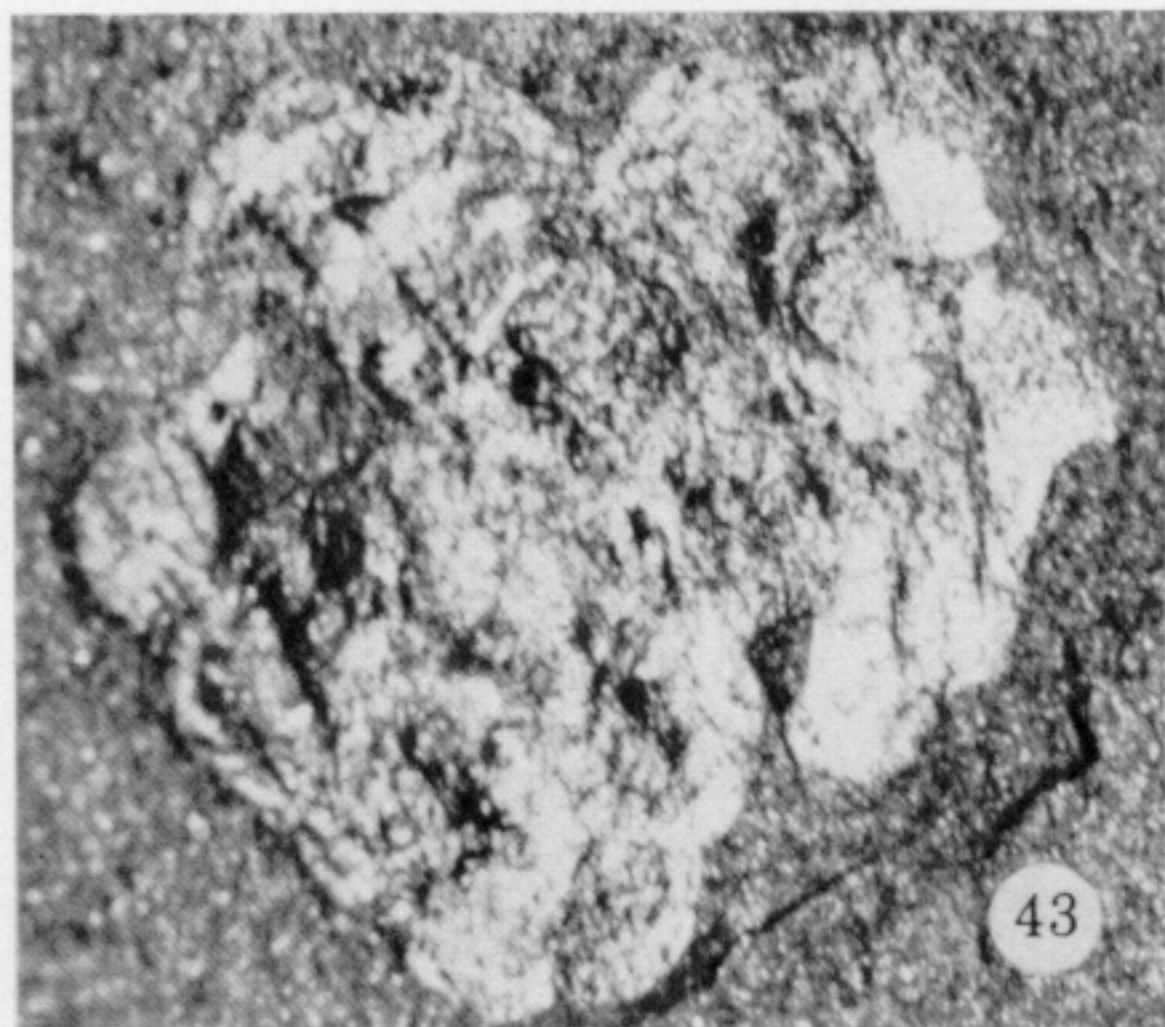
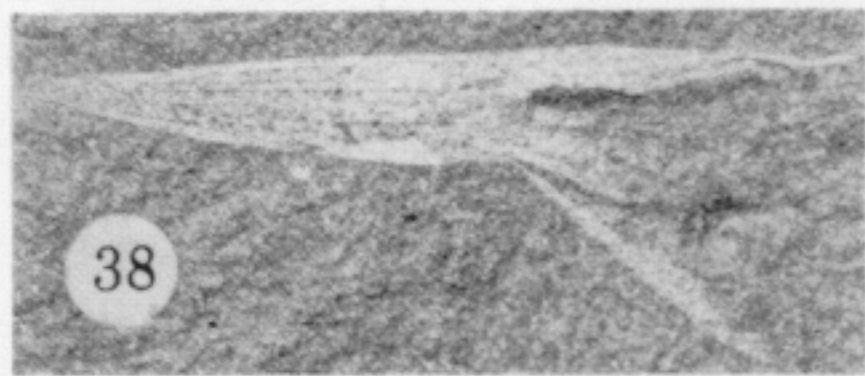
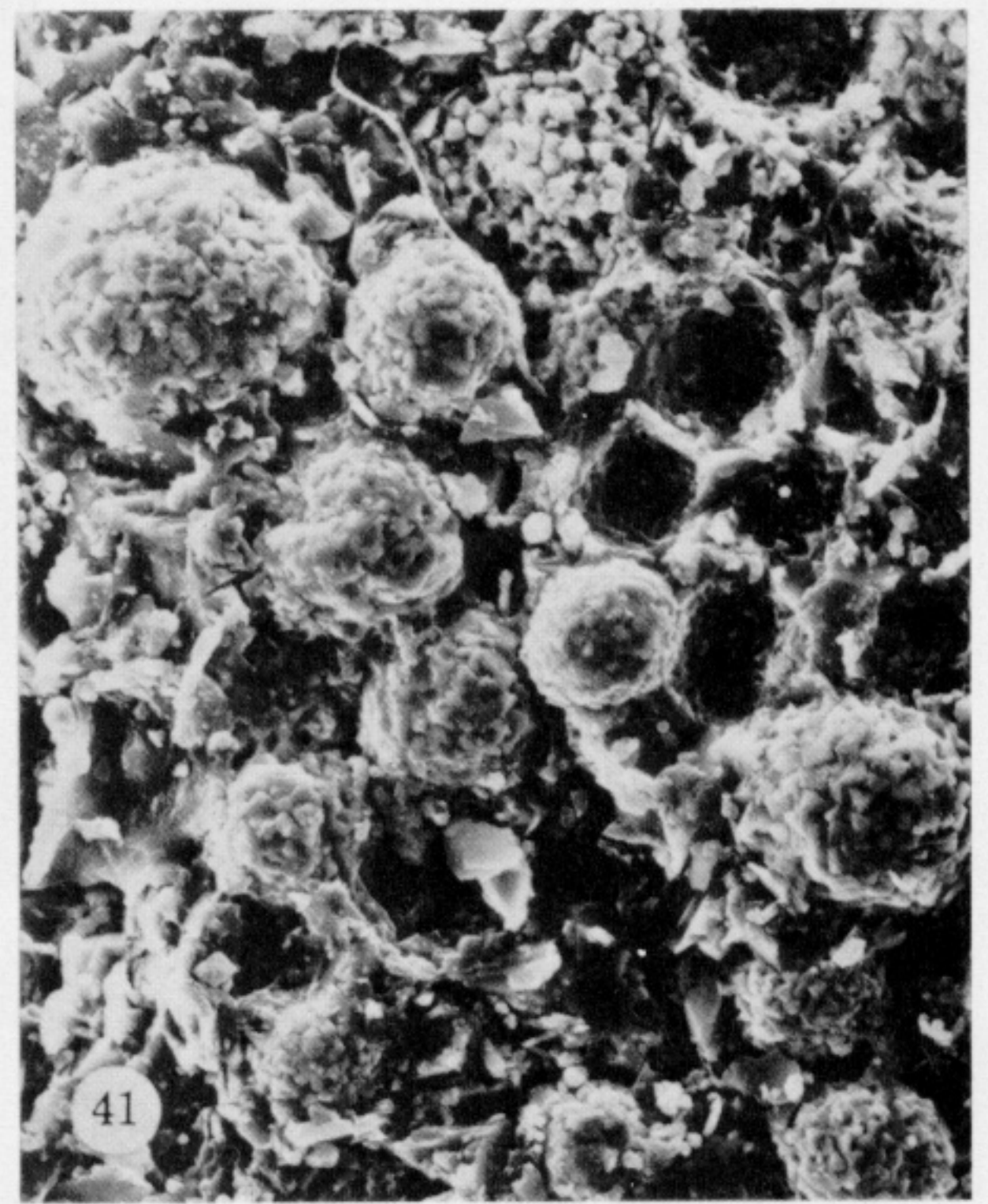
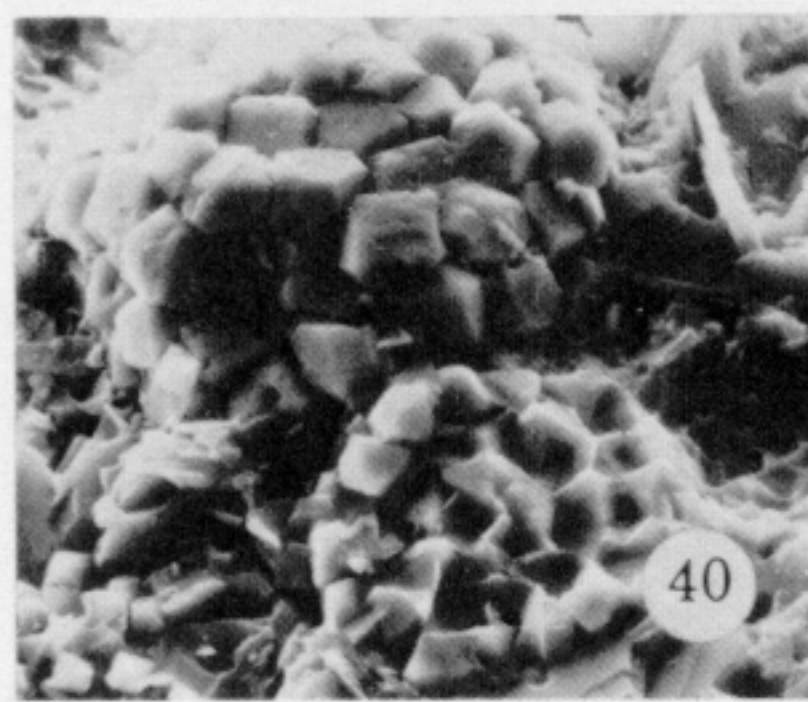
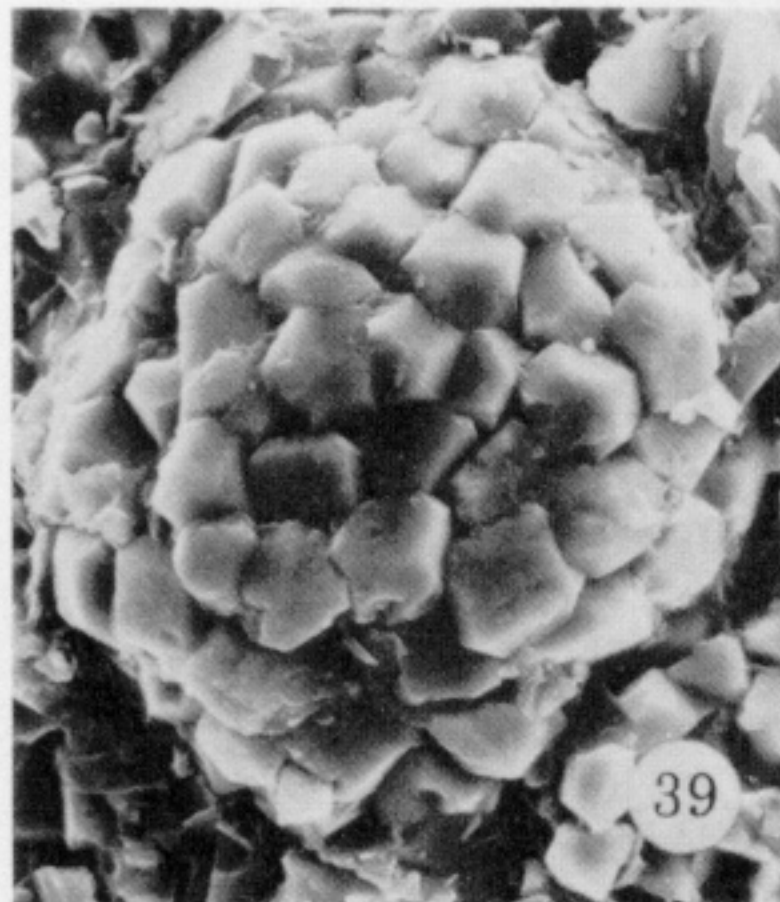
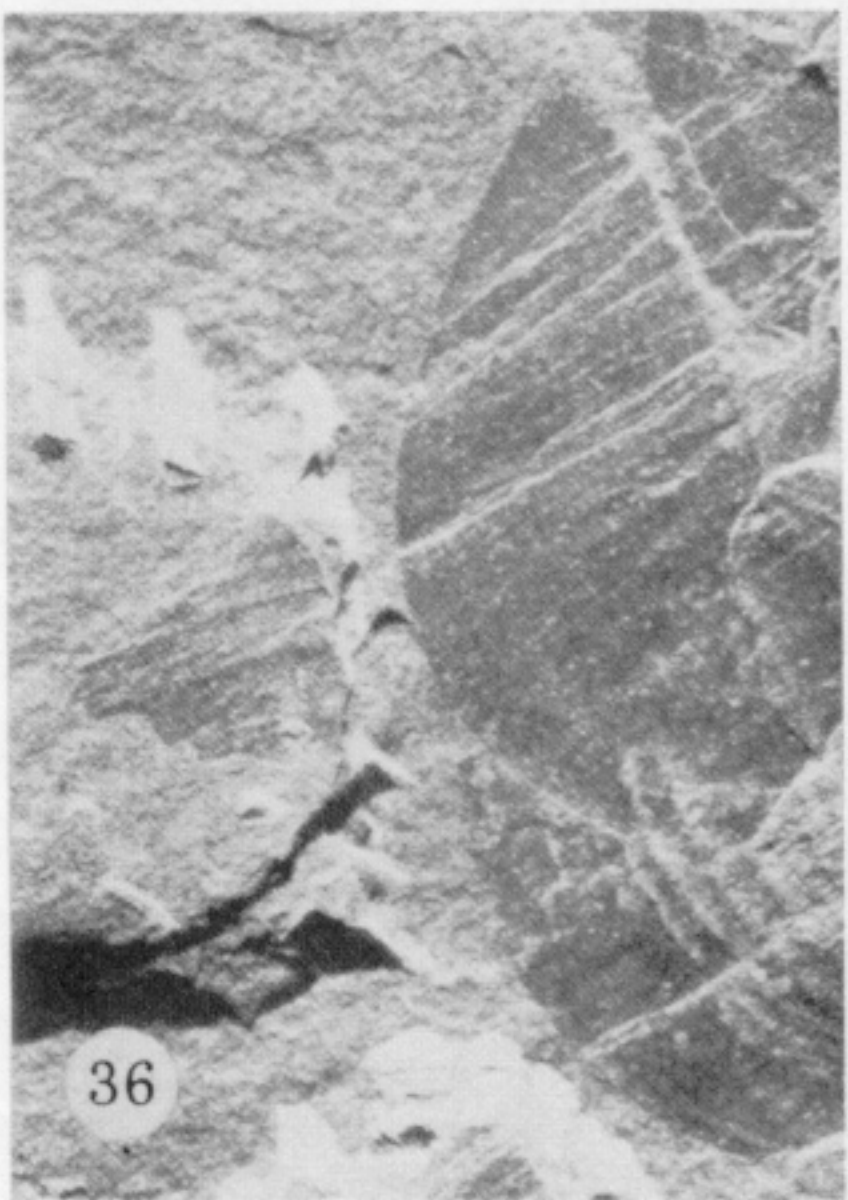
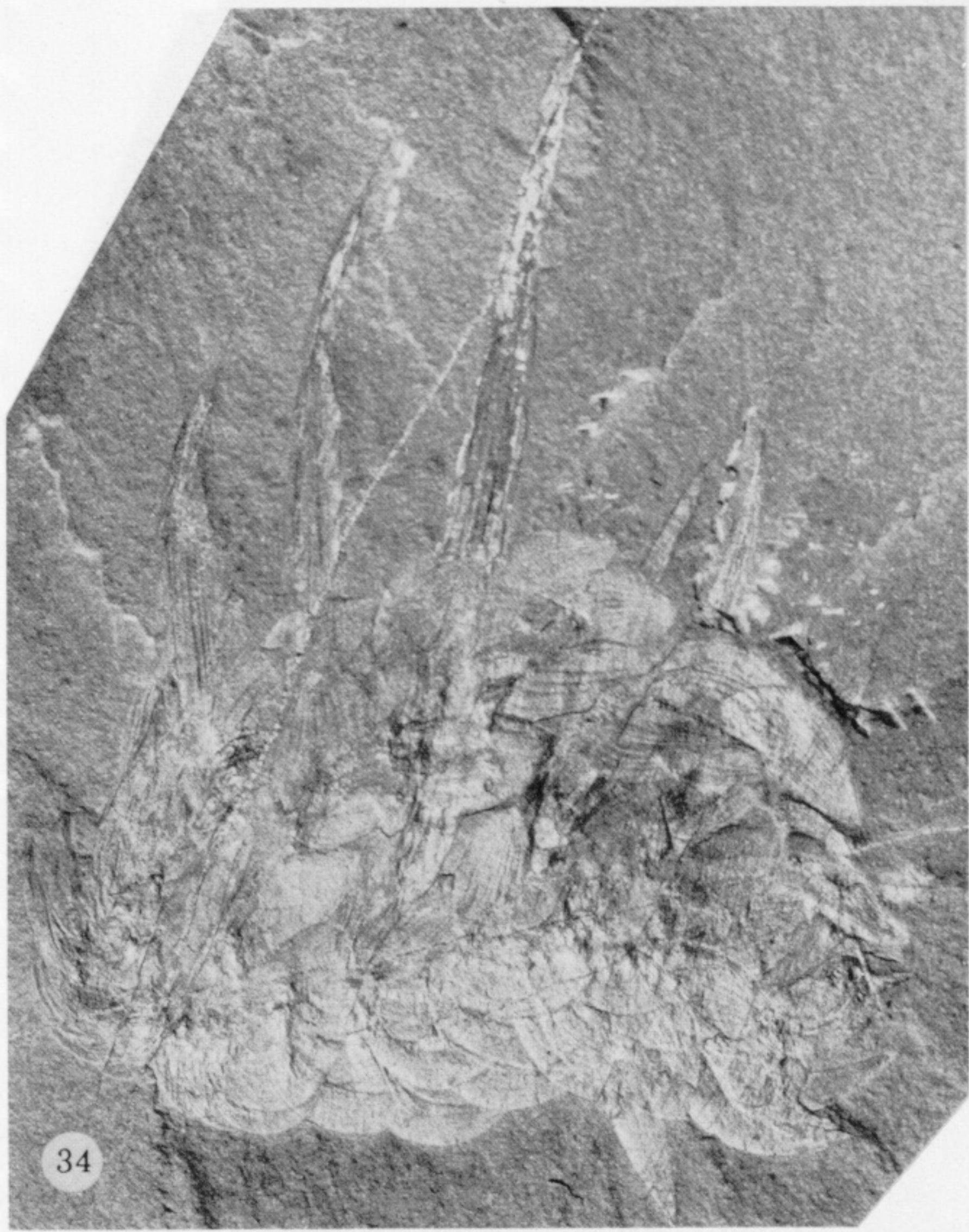
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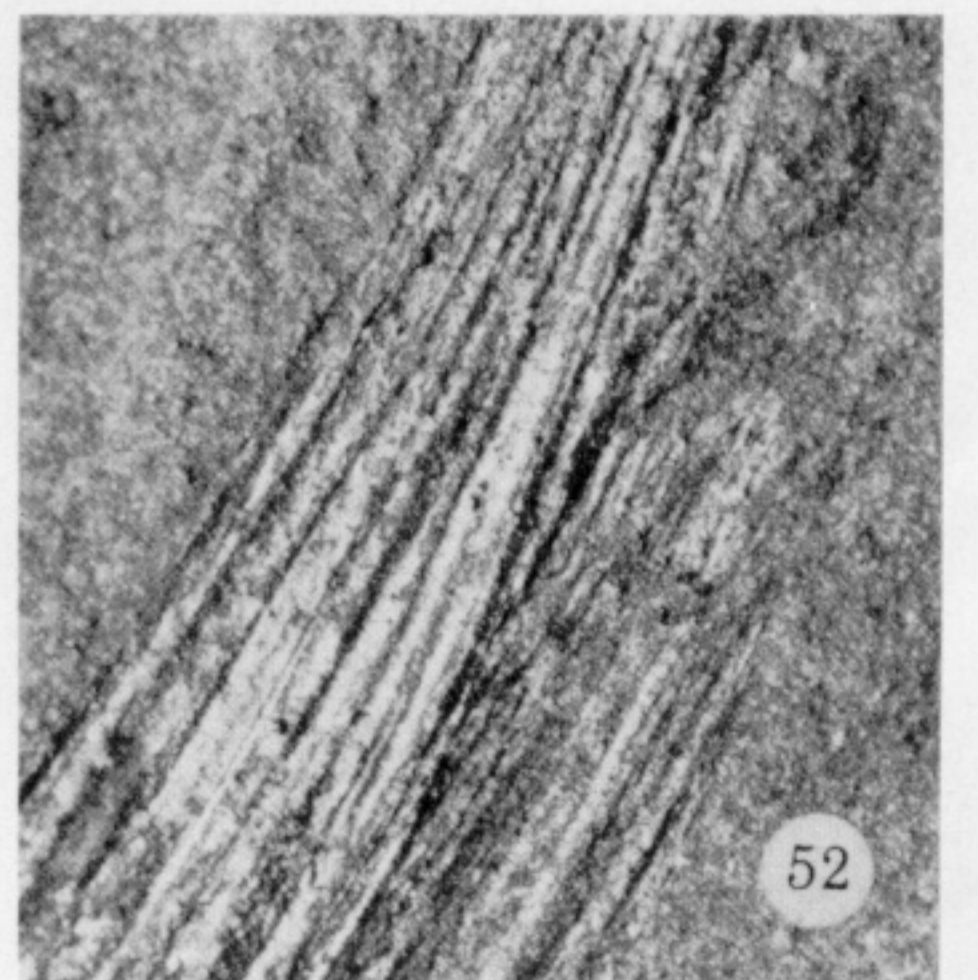
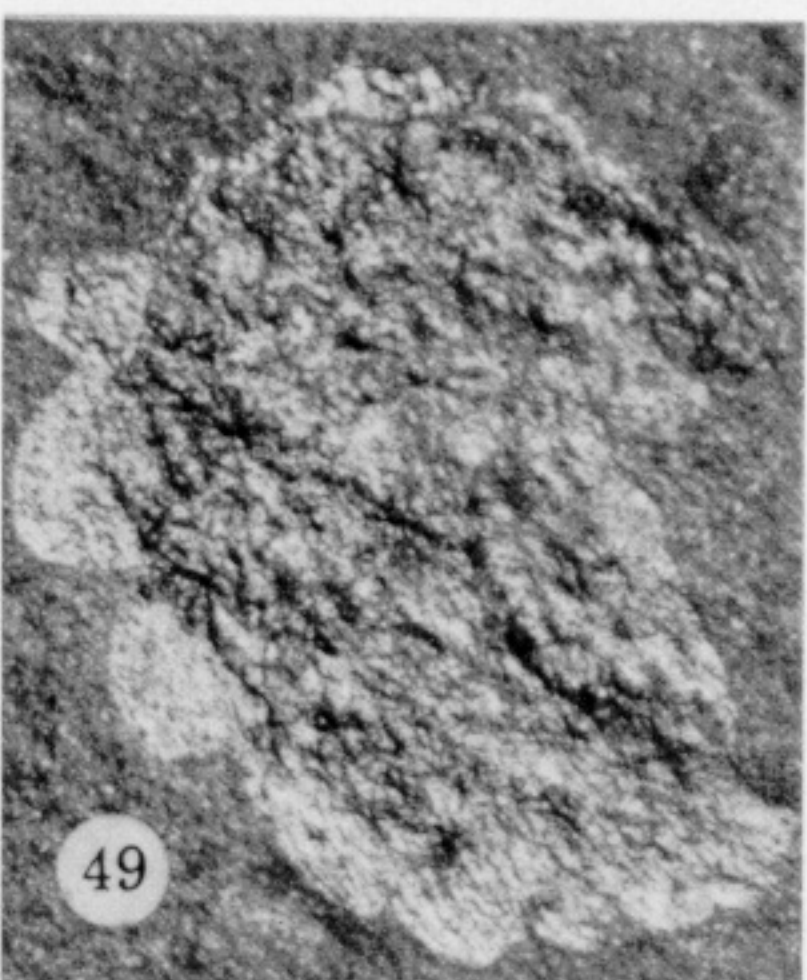
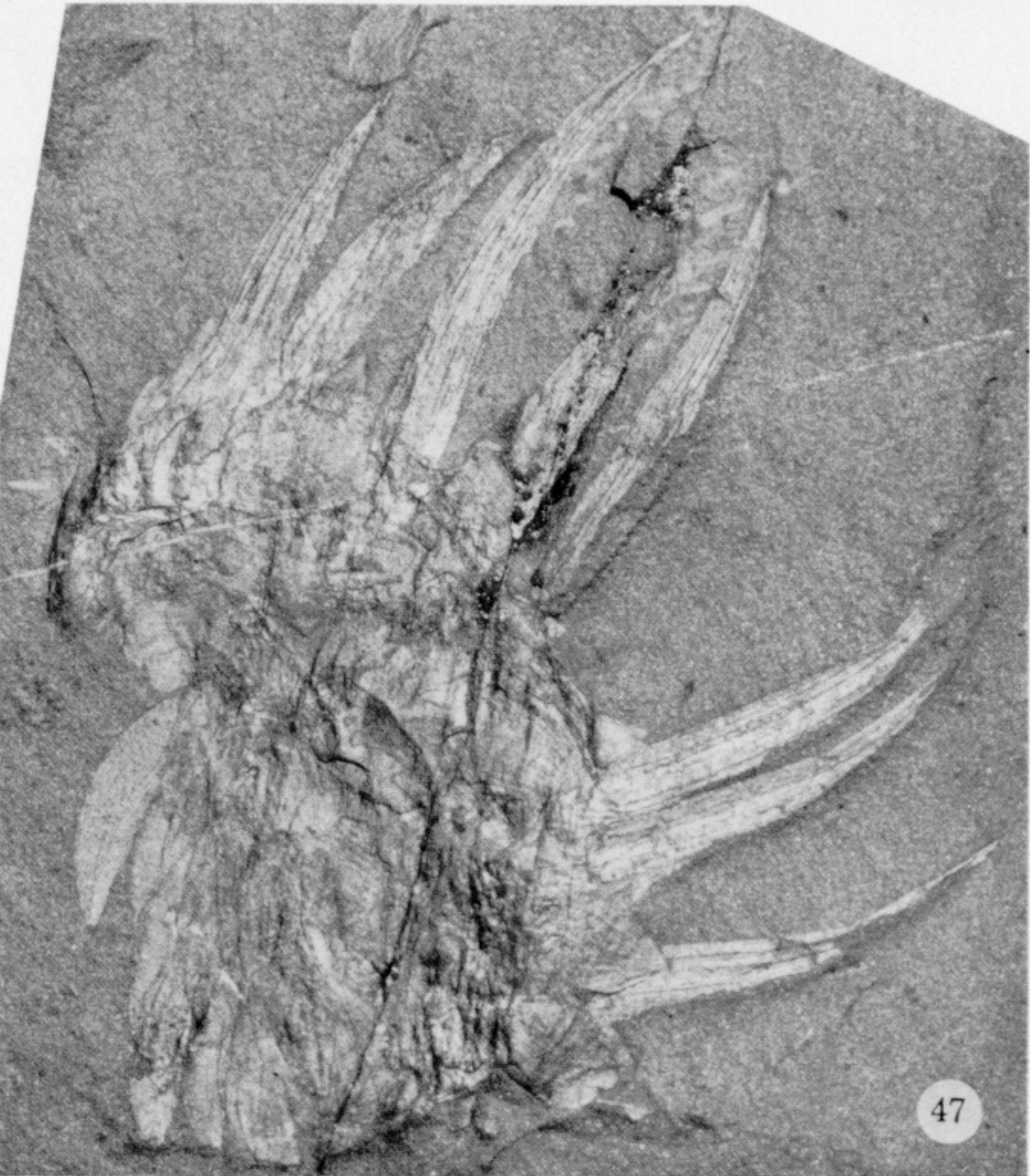
FIGURES 8-16. For description see opposite.



FIGURES 17-26. For description see opposite.

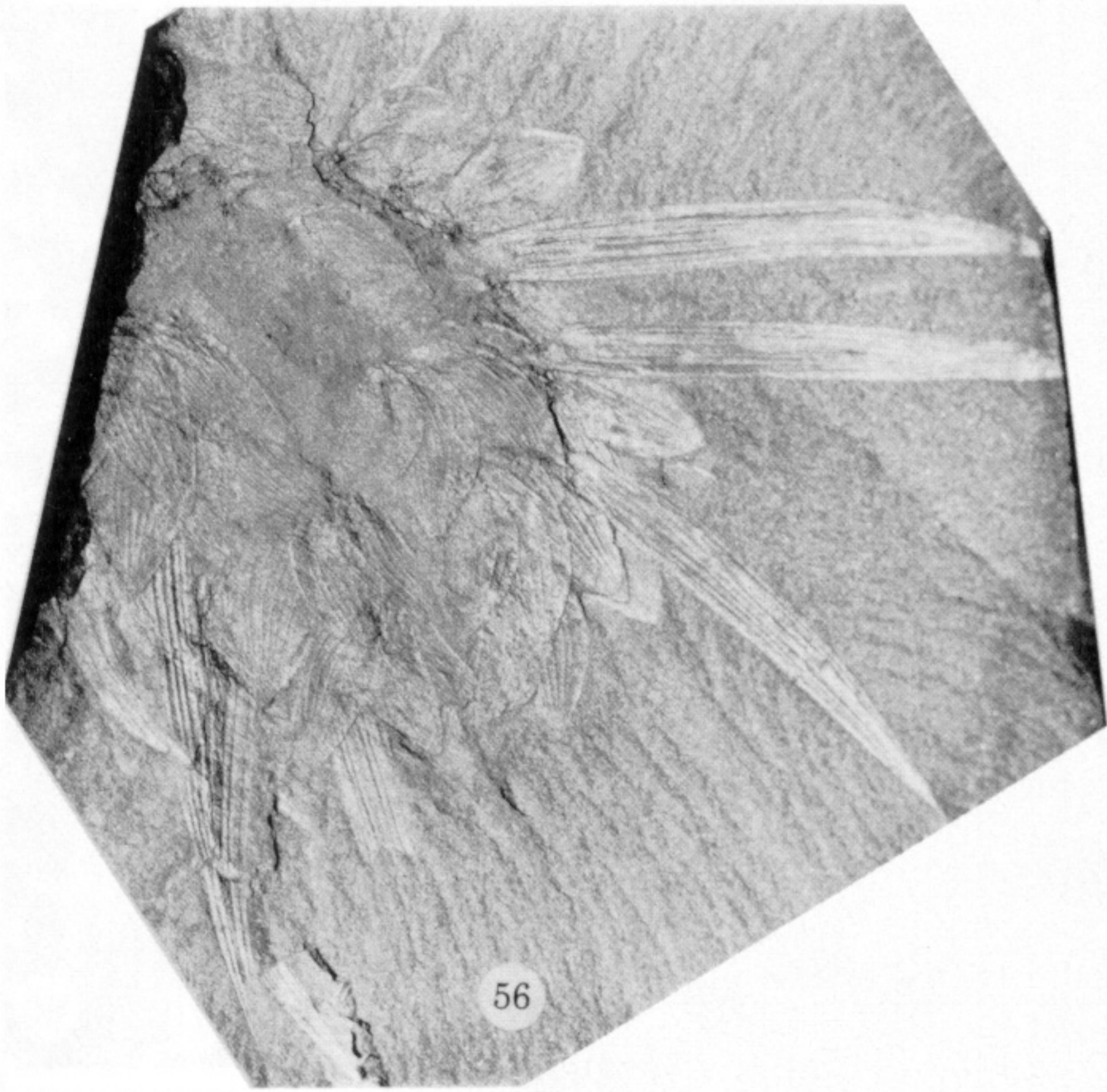


FIGURES 34-44. For description see opposite.



FIGURES 45-52. For description see opposite.

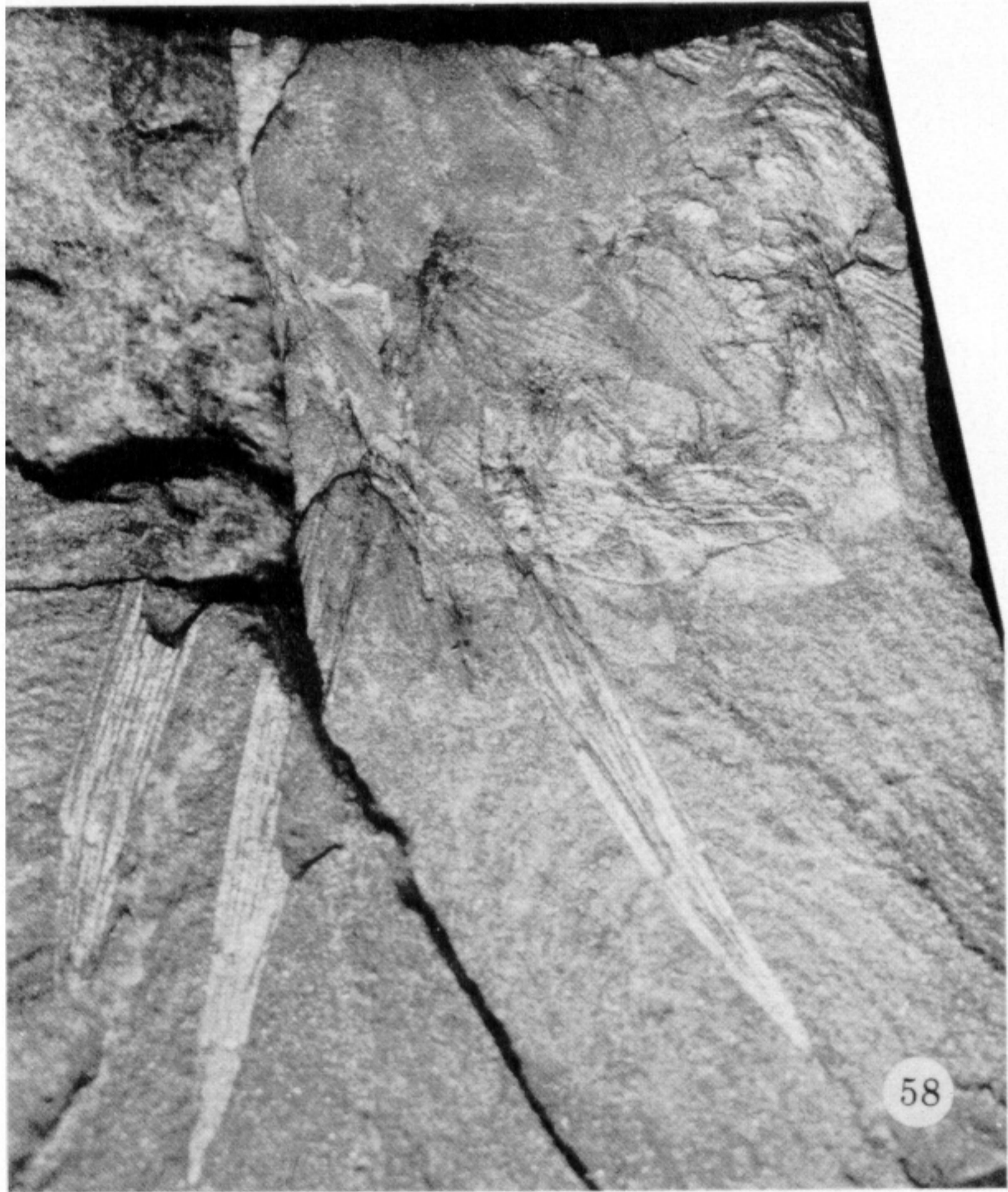




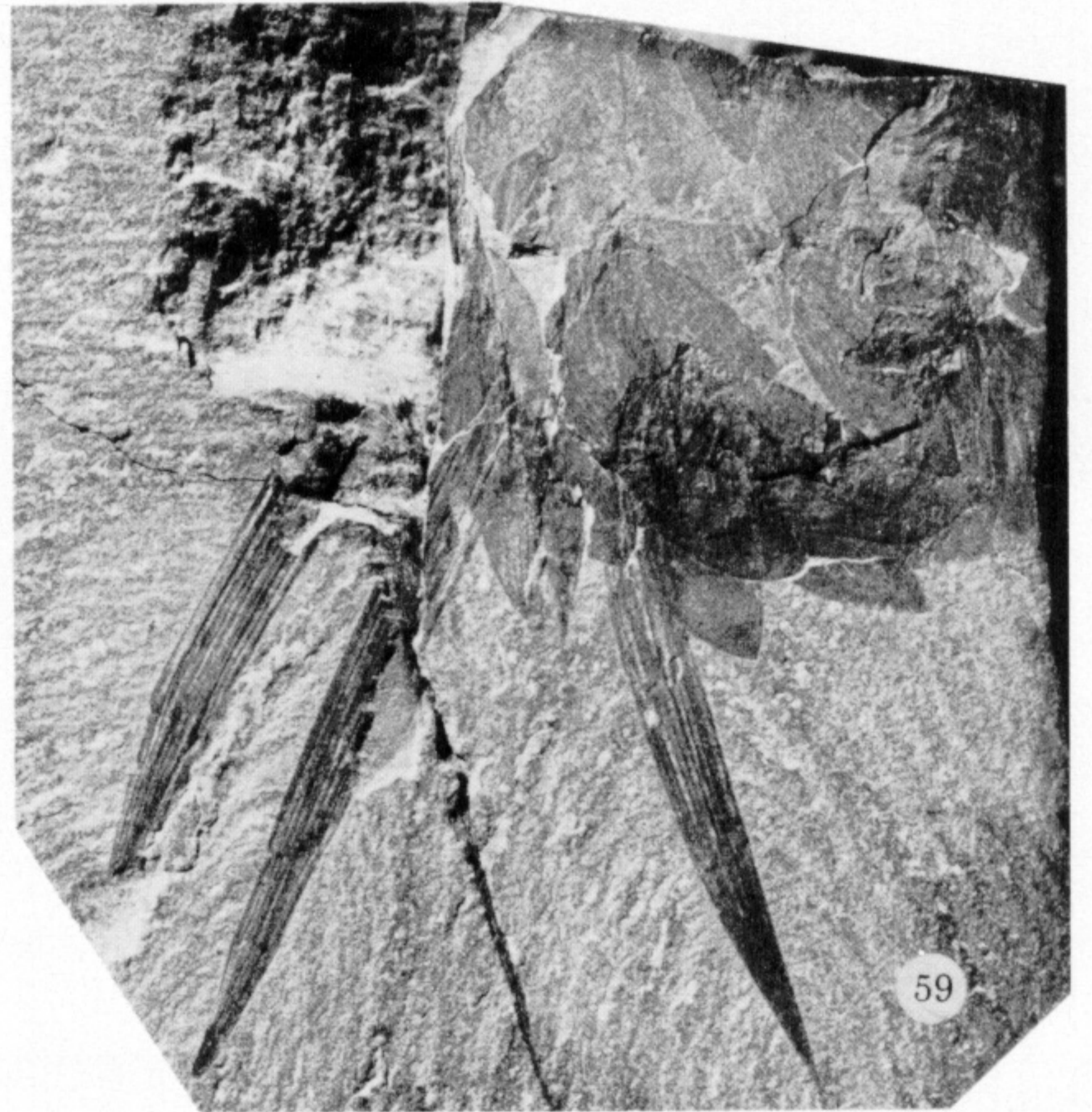
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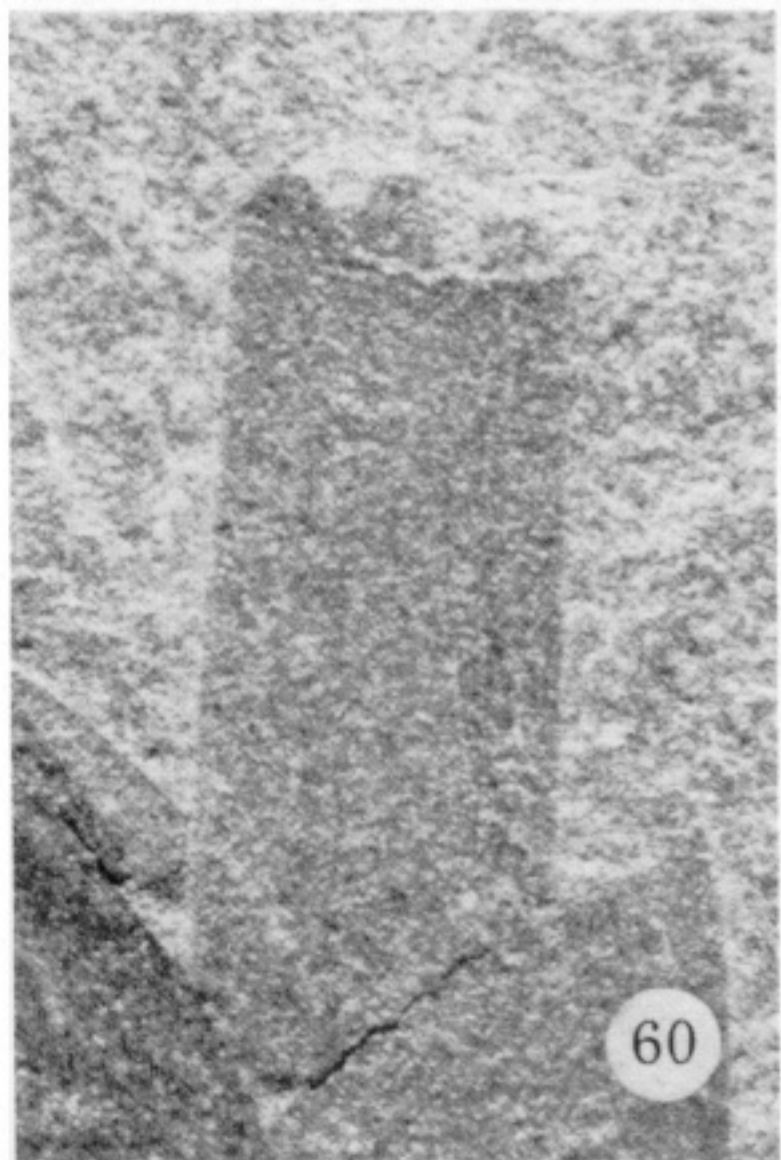
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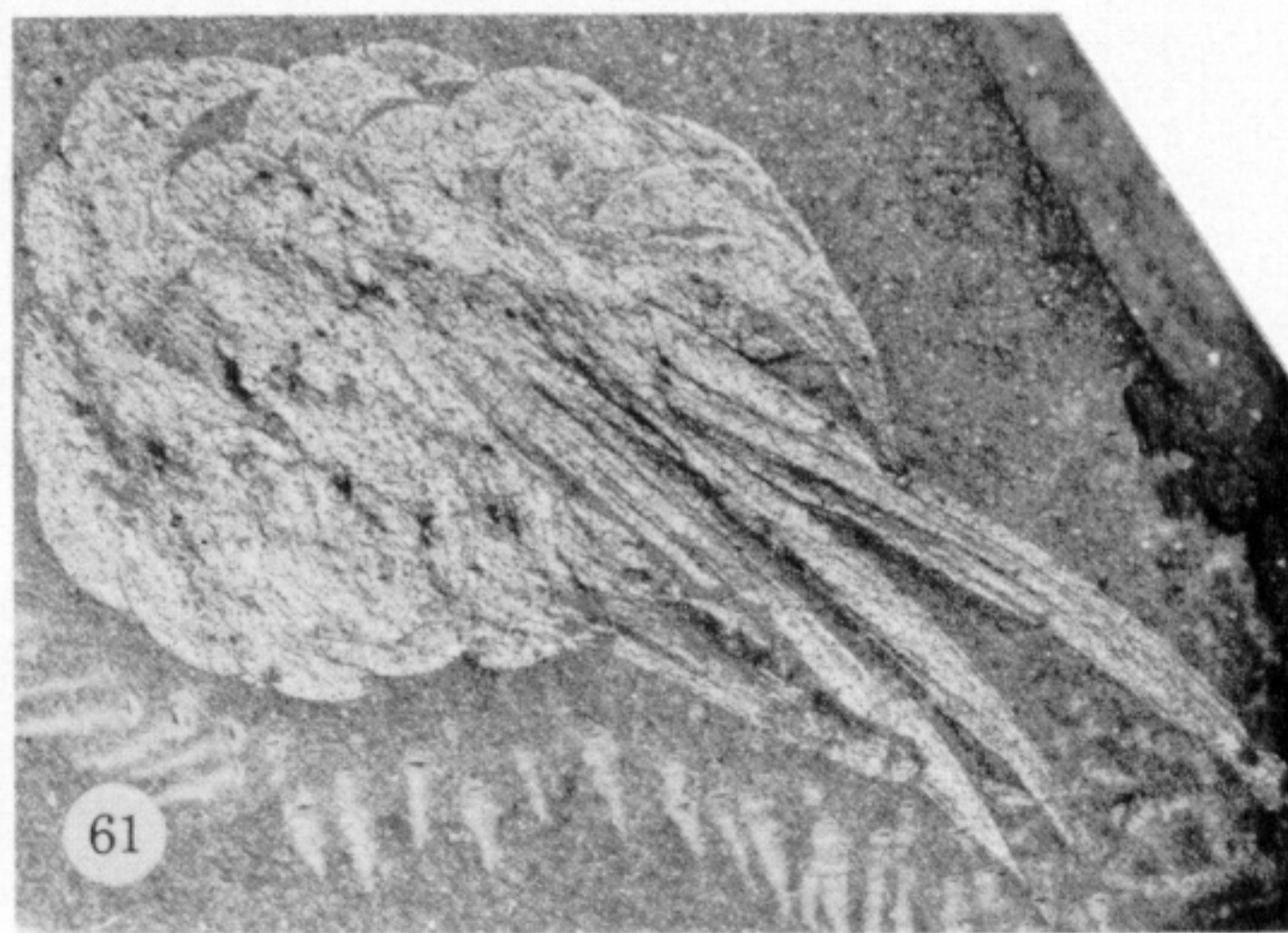
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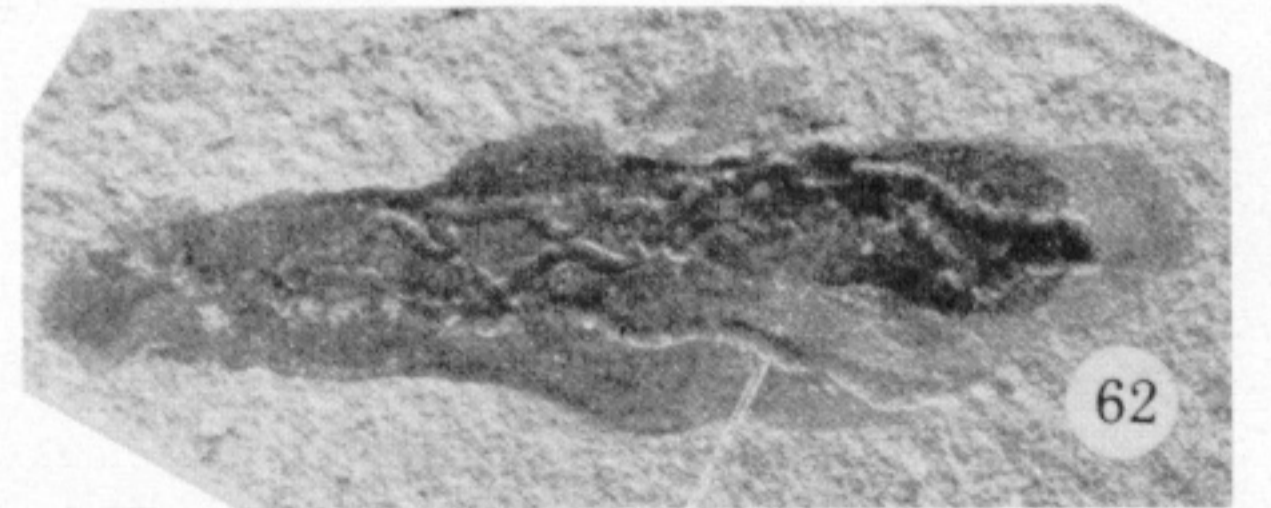
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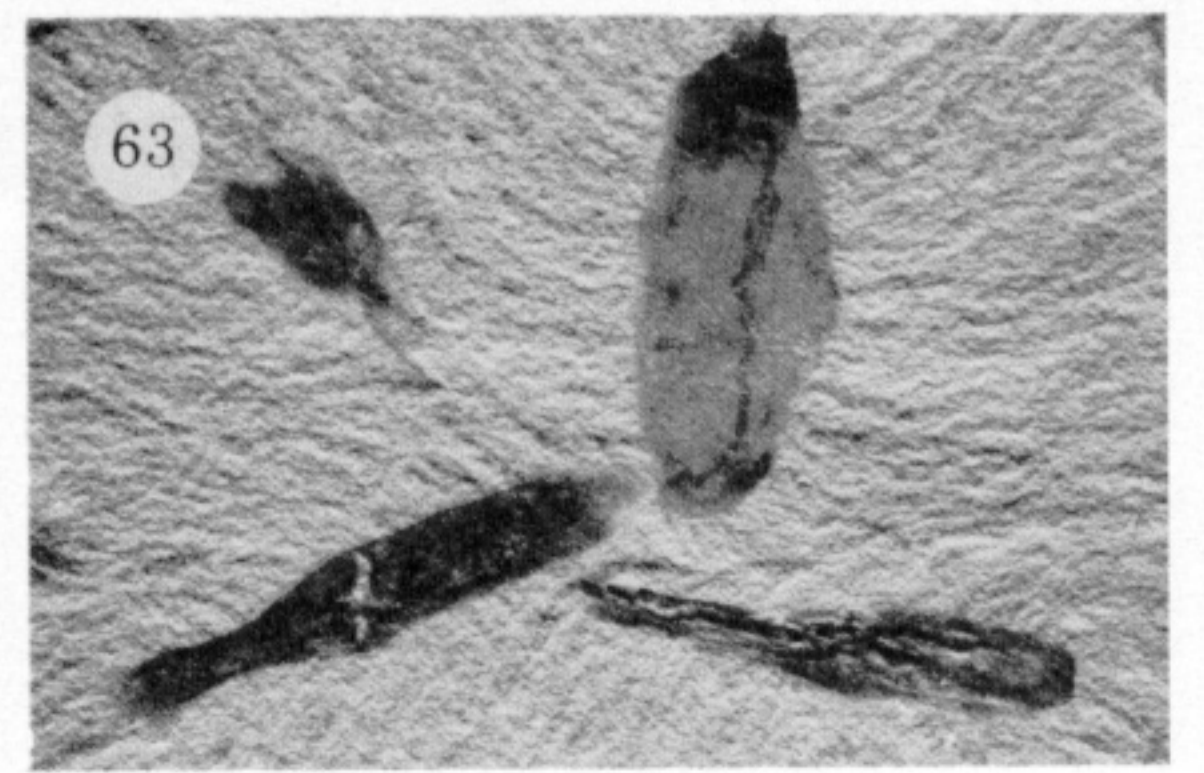
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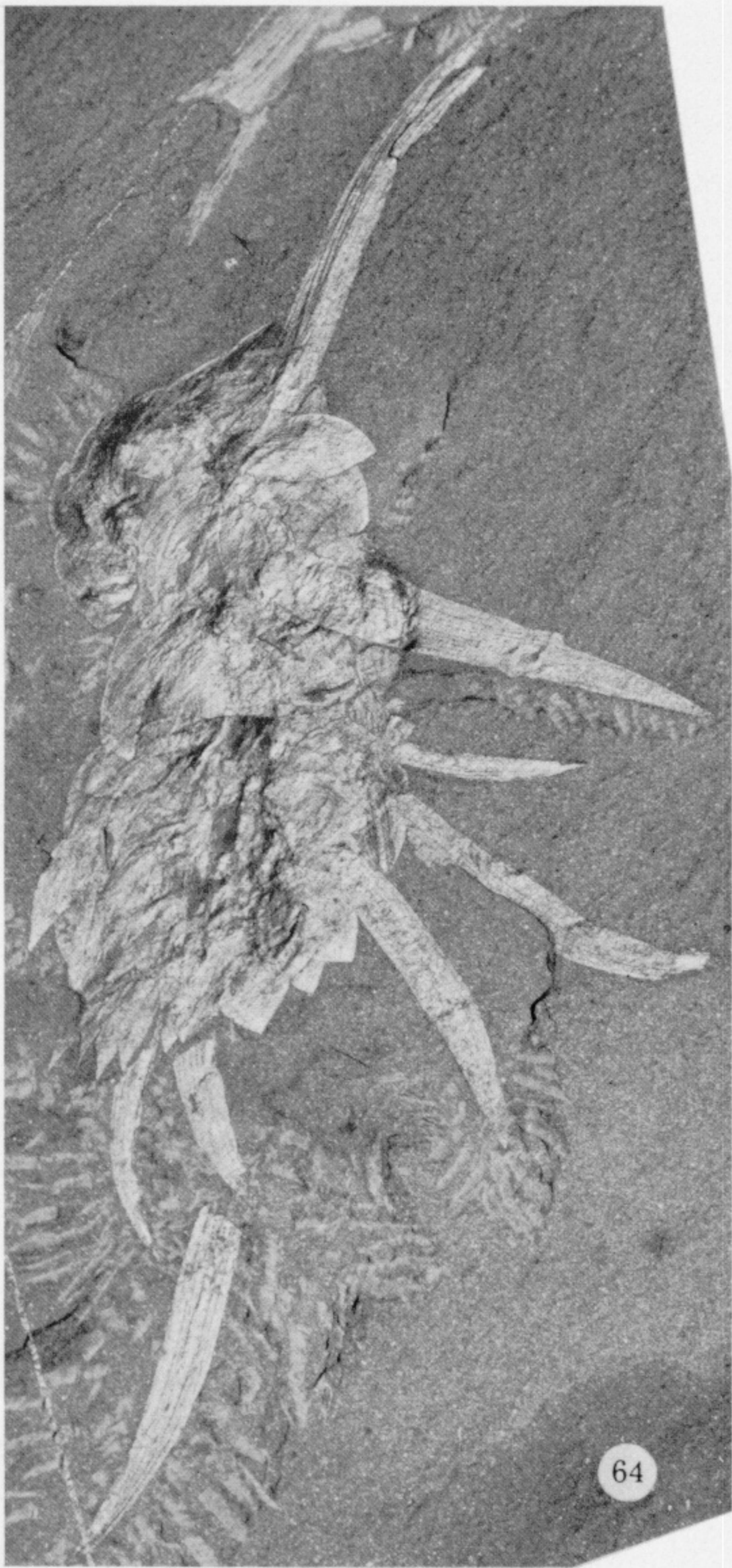


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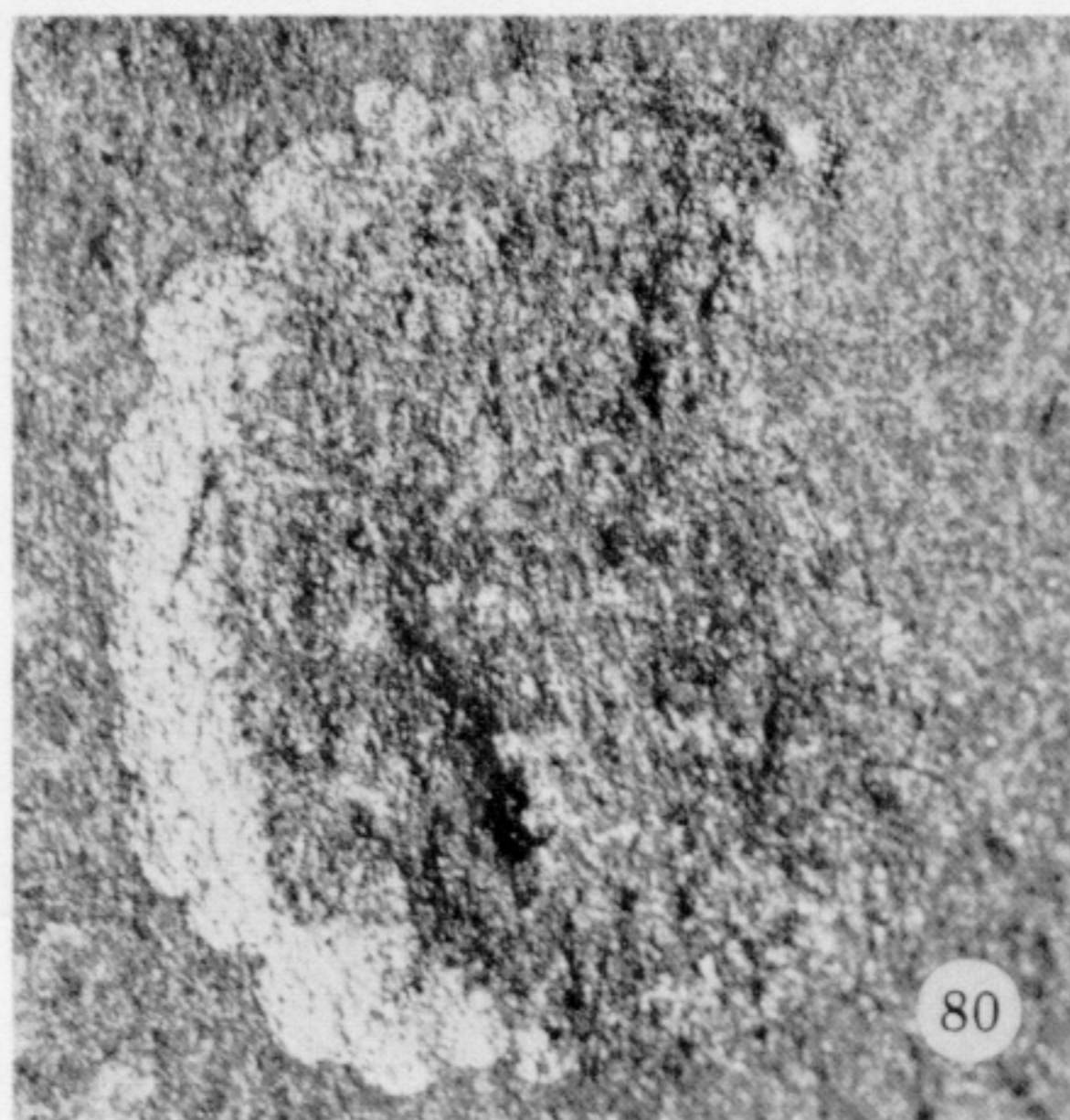
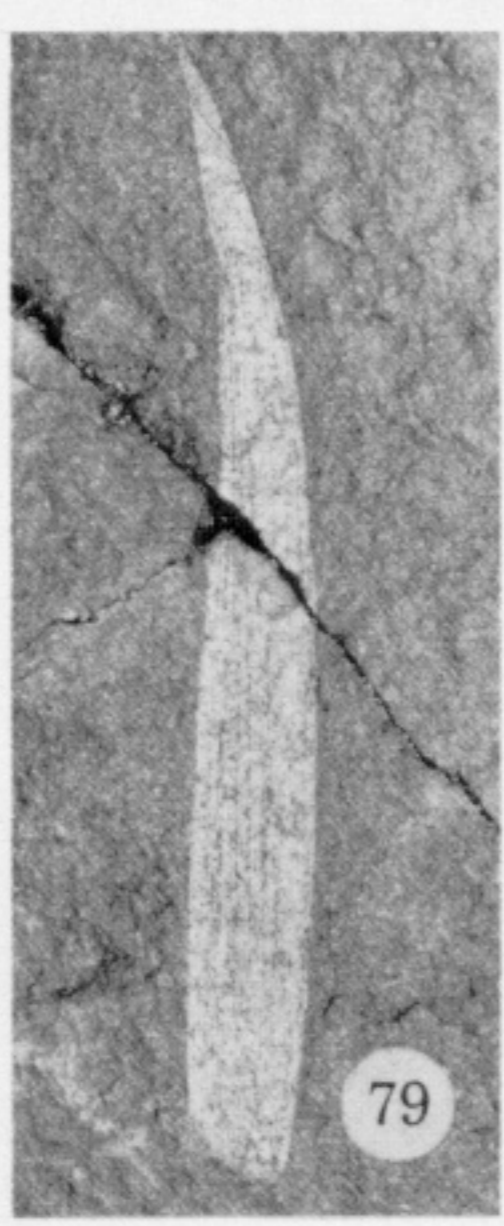
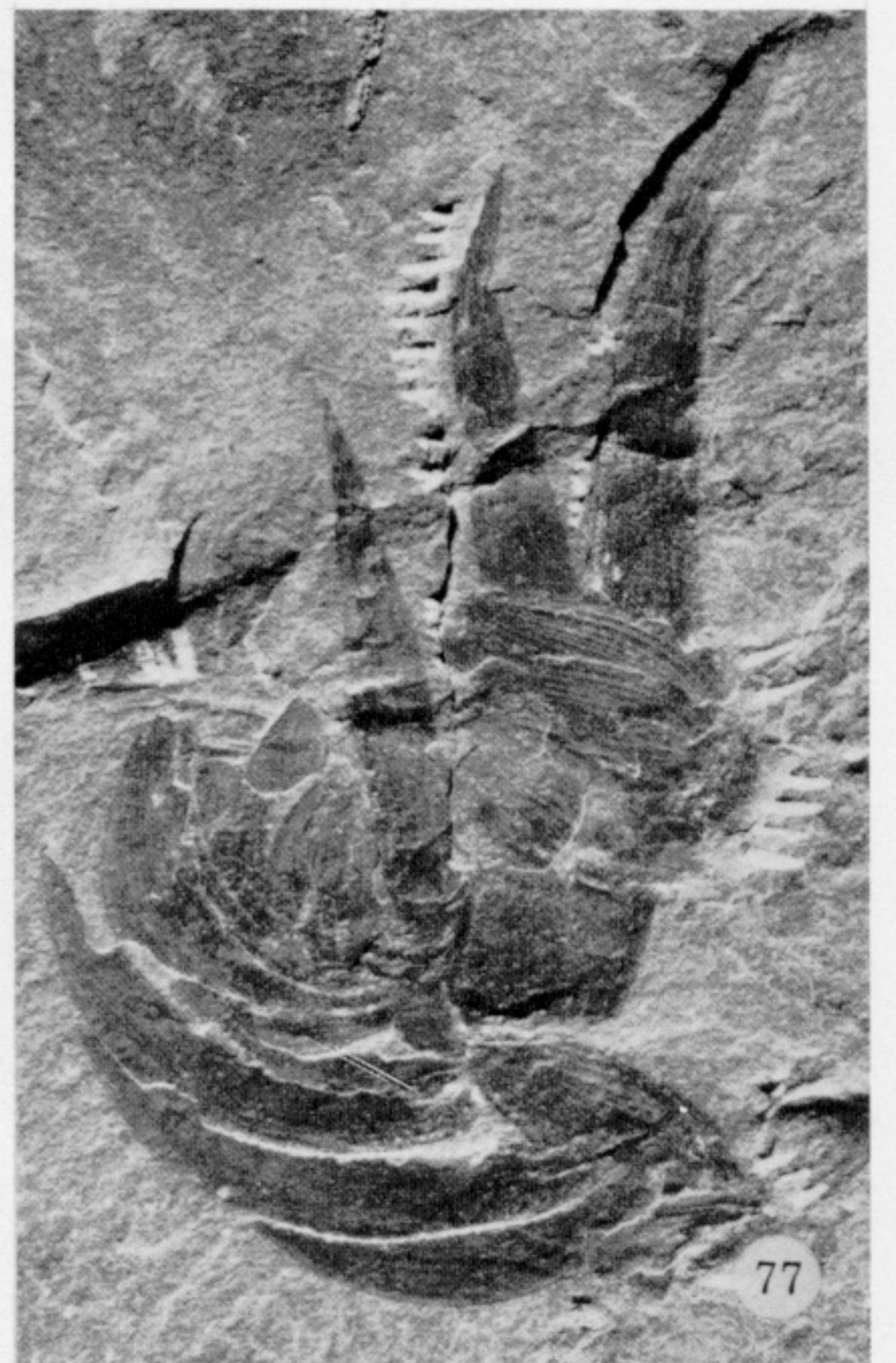


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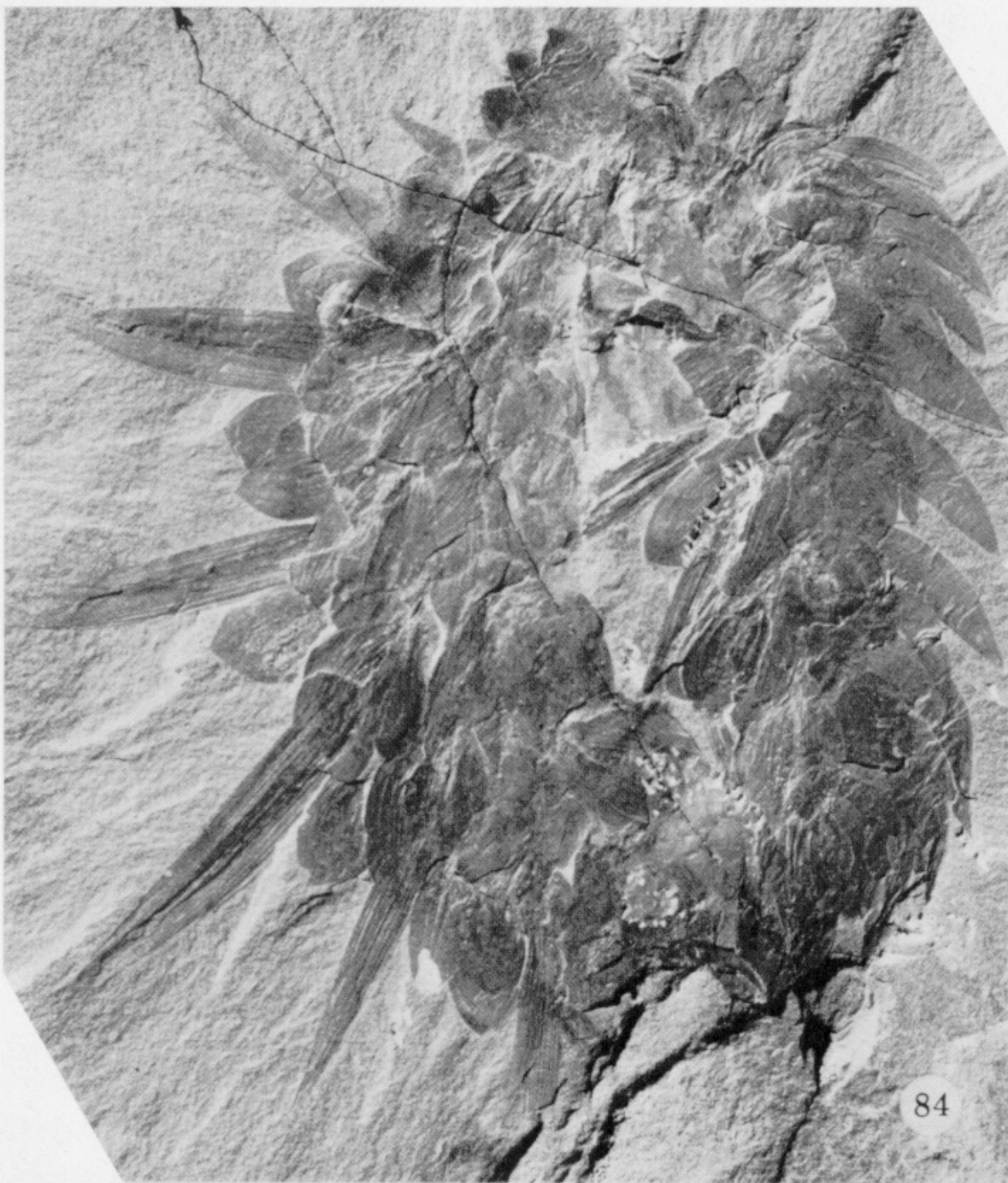
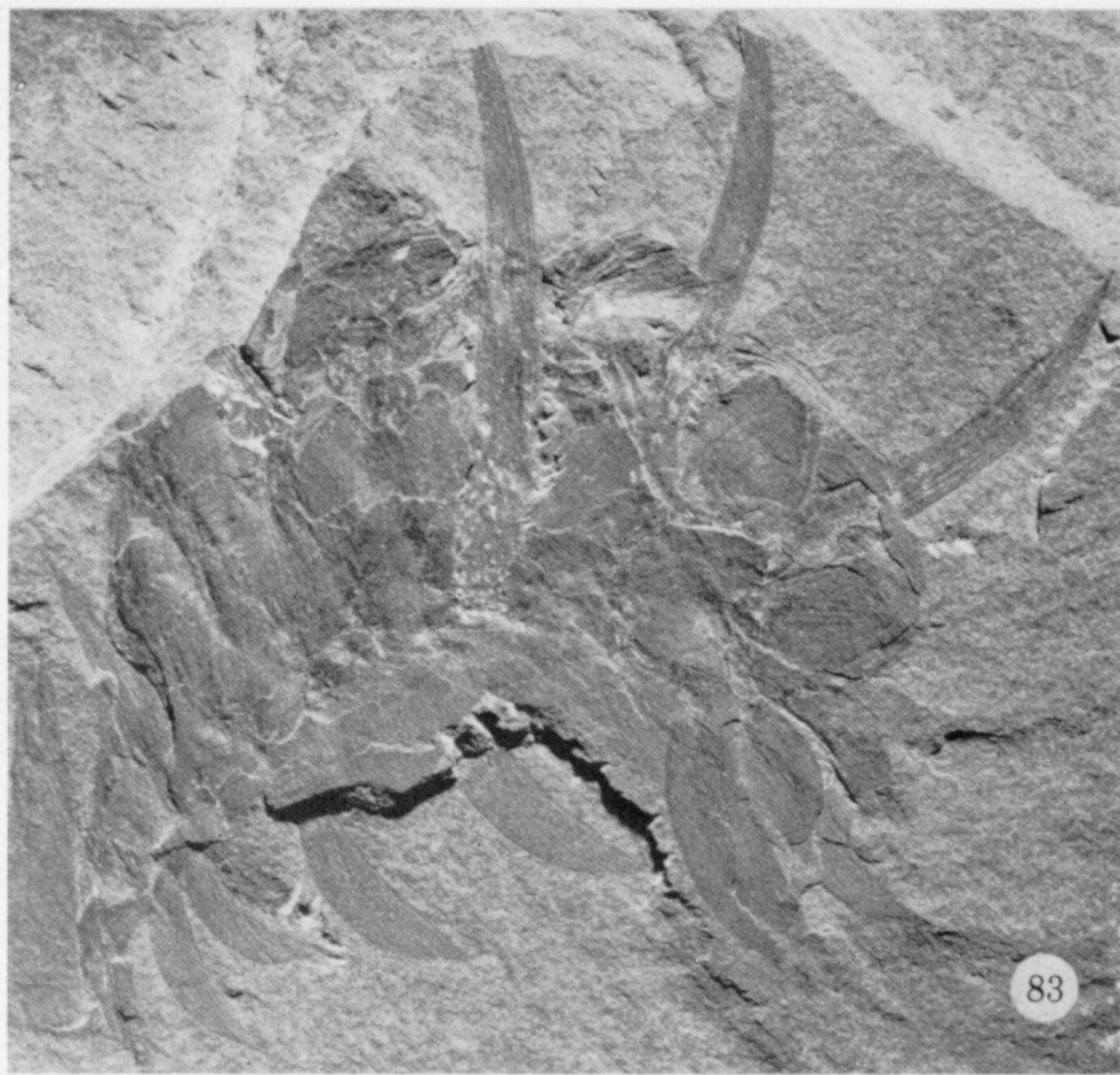
FIGURES 56-63. For description see opposite.



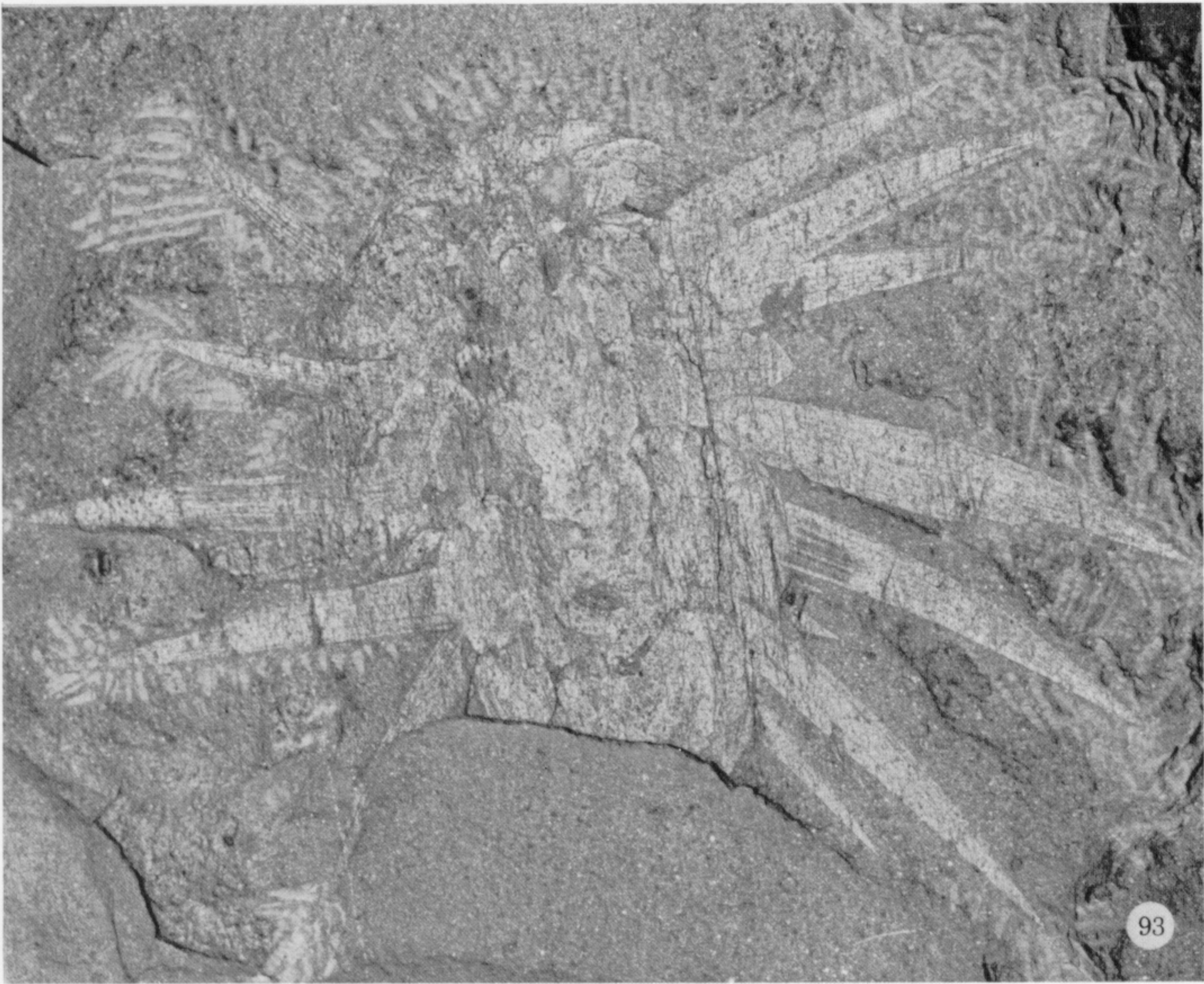
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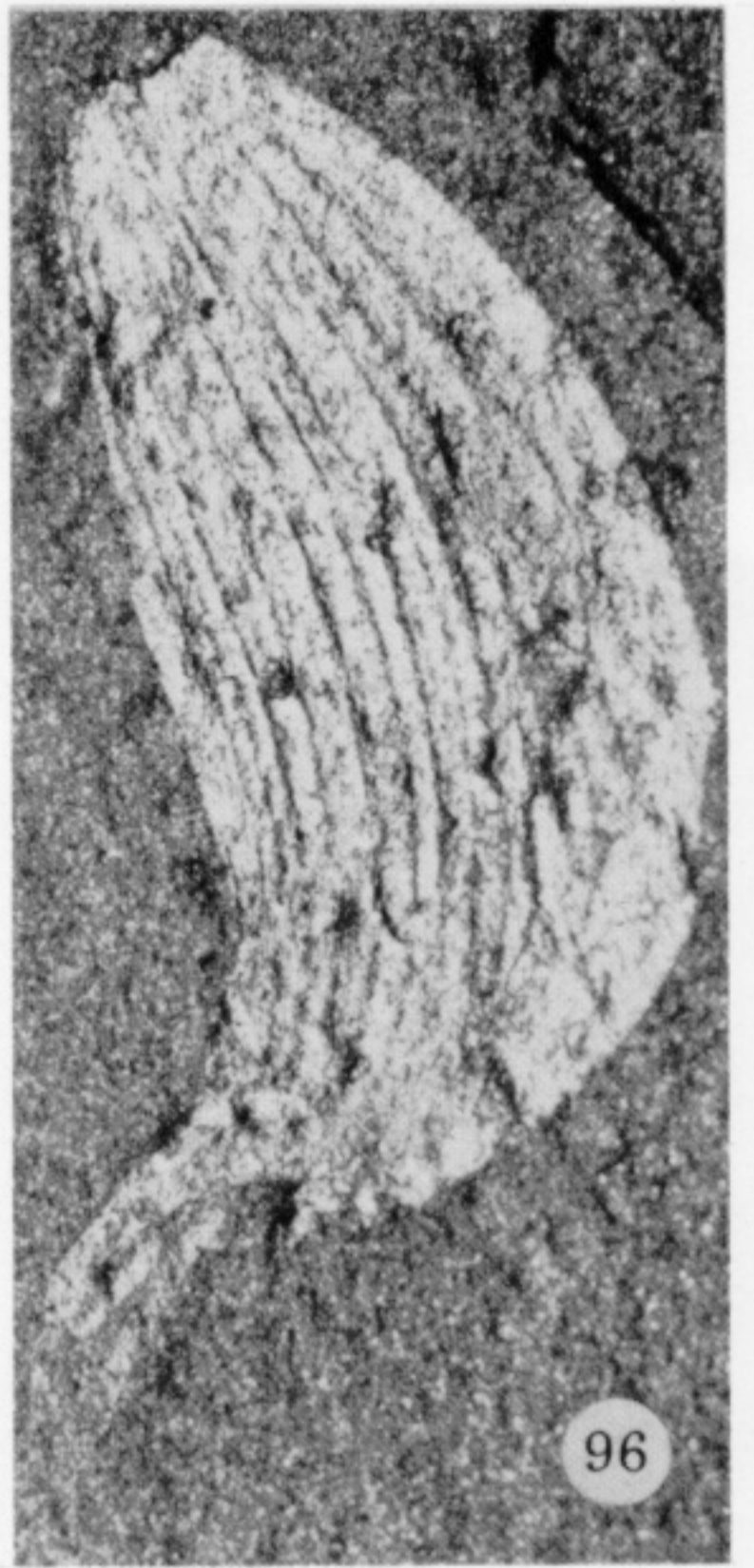
FIGURES 74-81. For description see opposite.



FIGURES 82-87. For description see opposite.



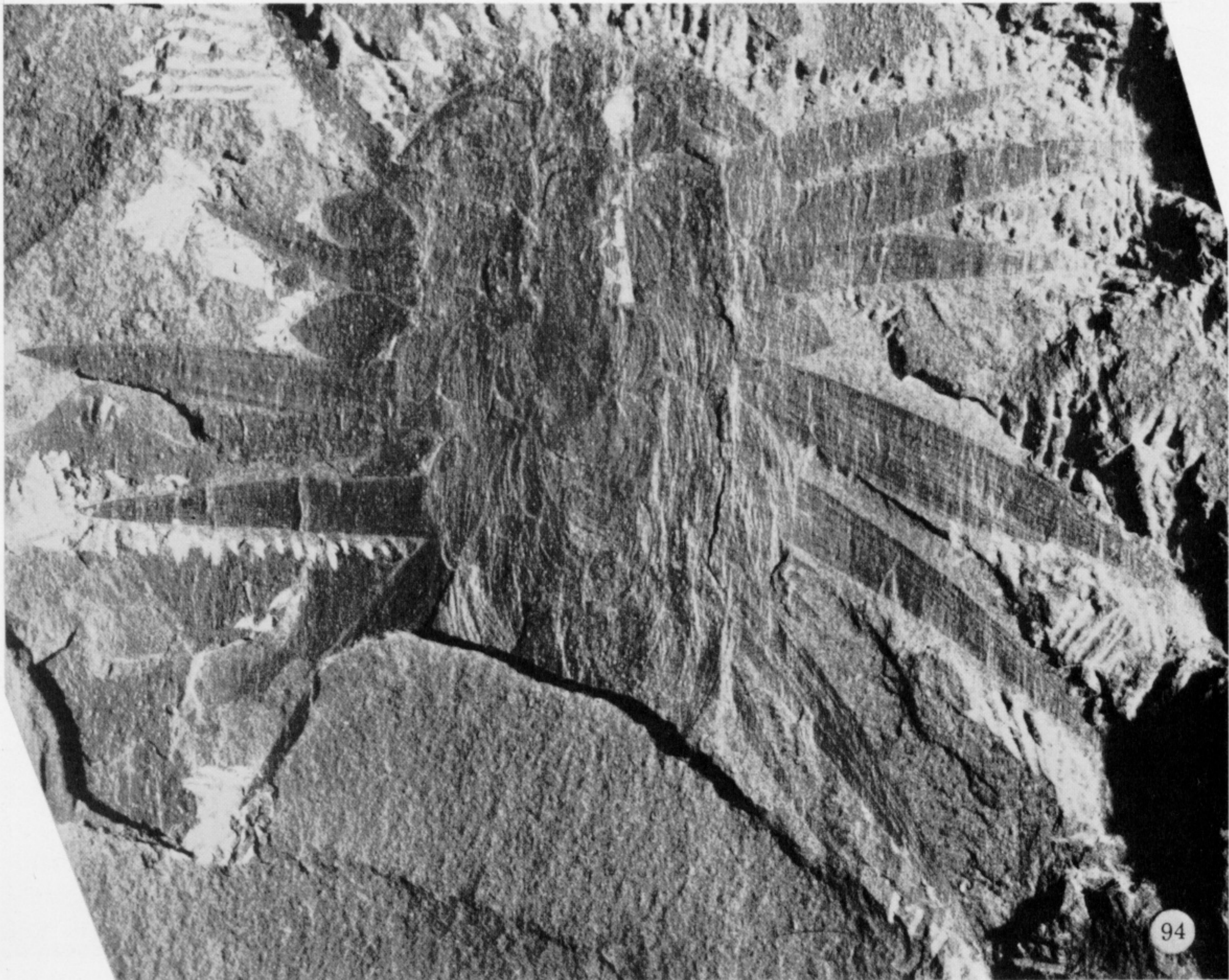
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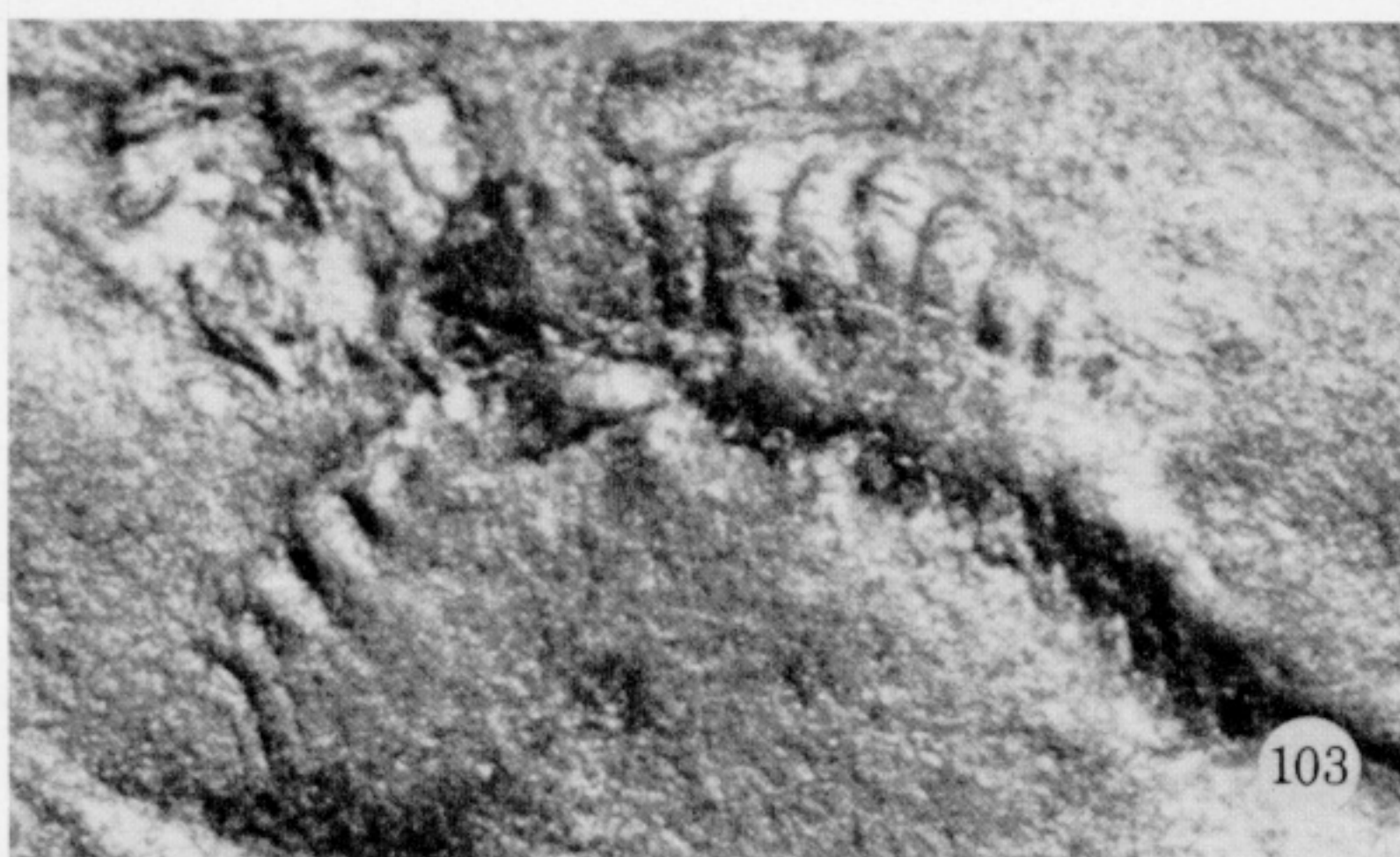
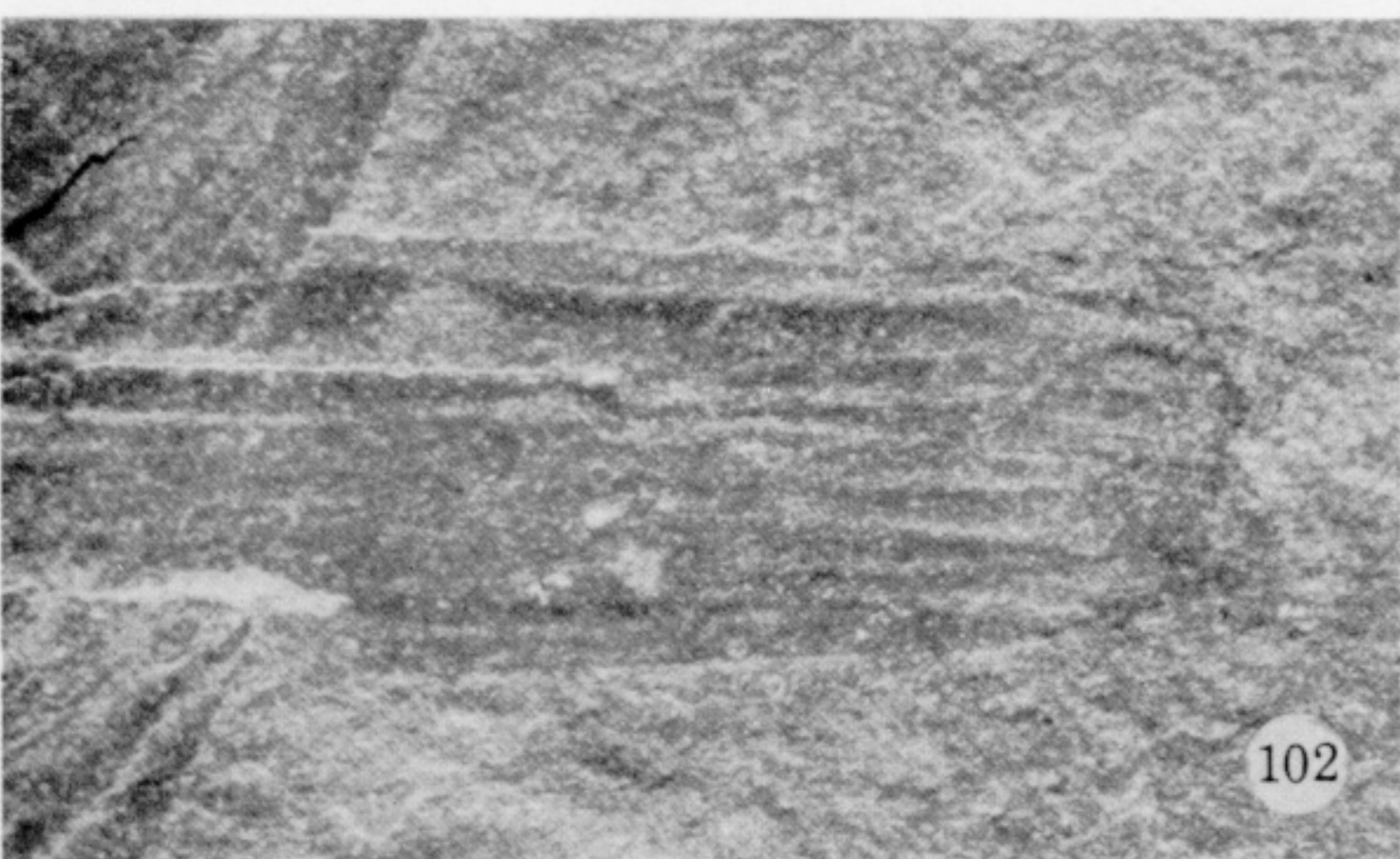
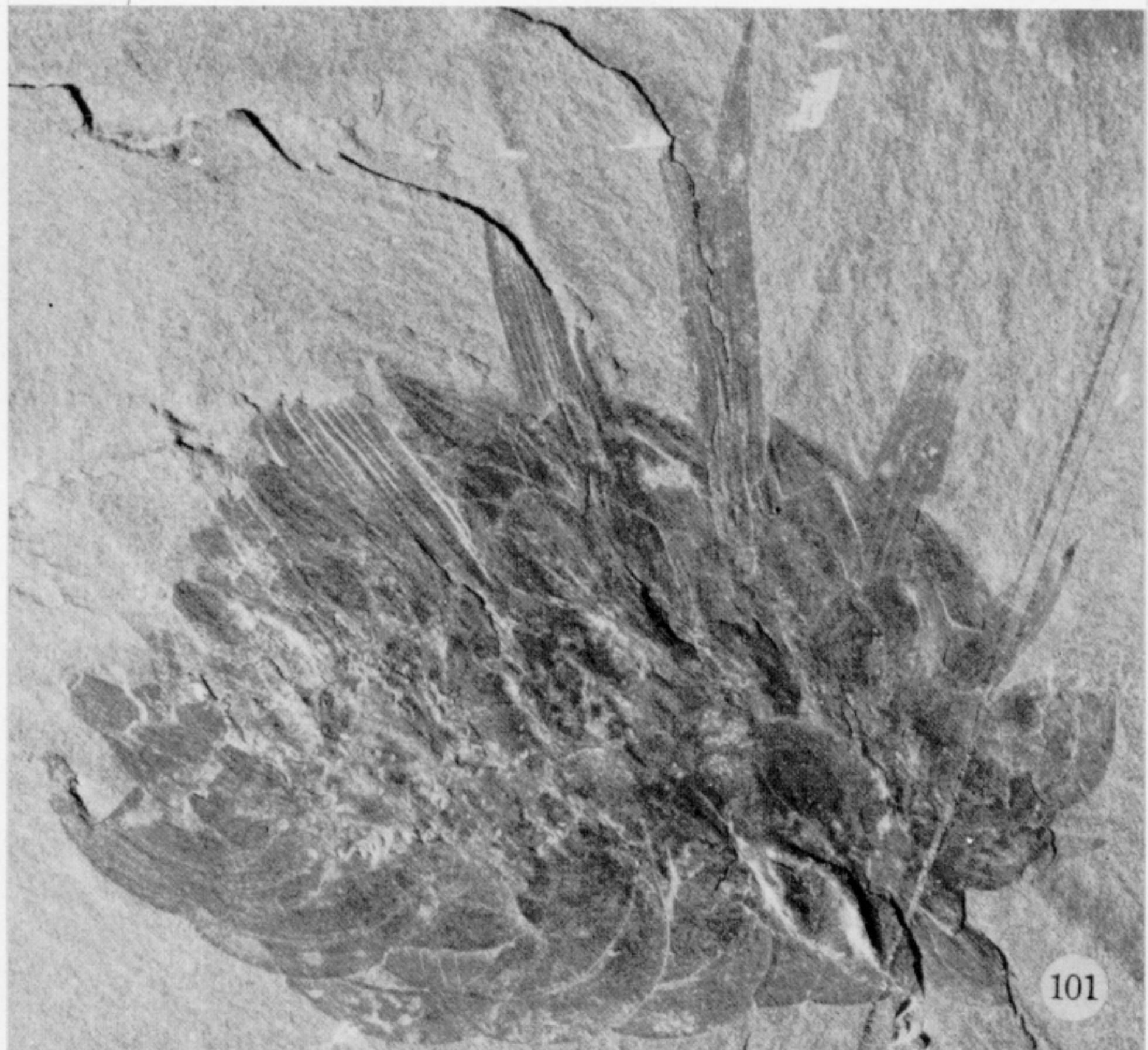
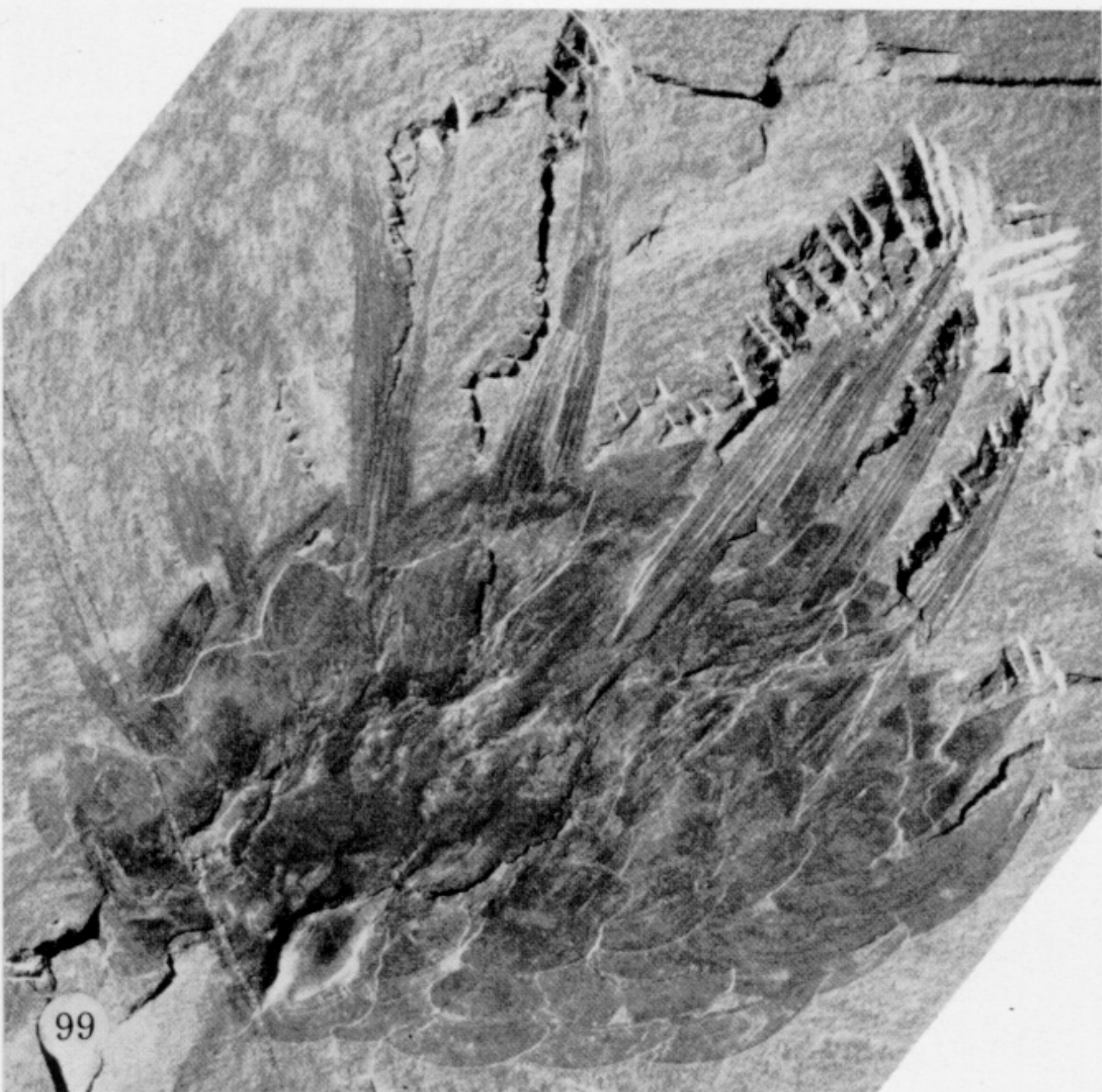
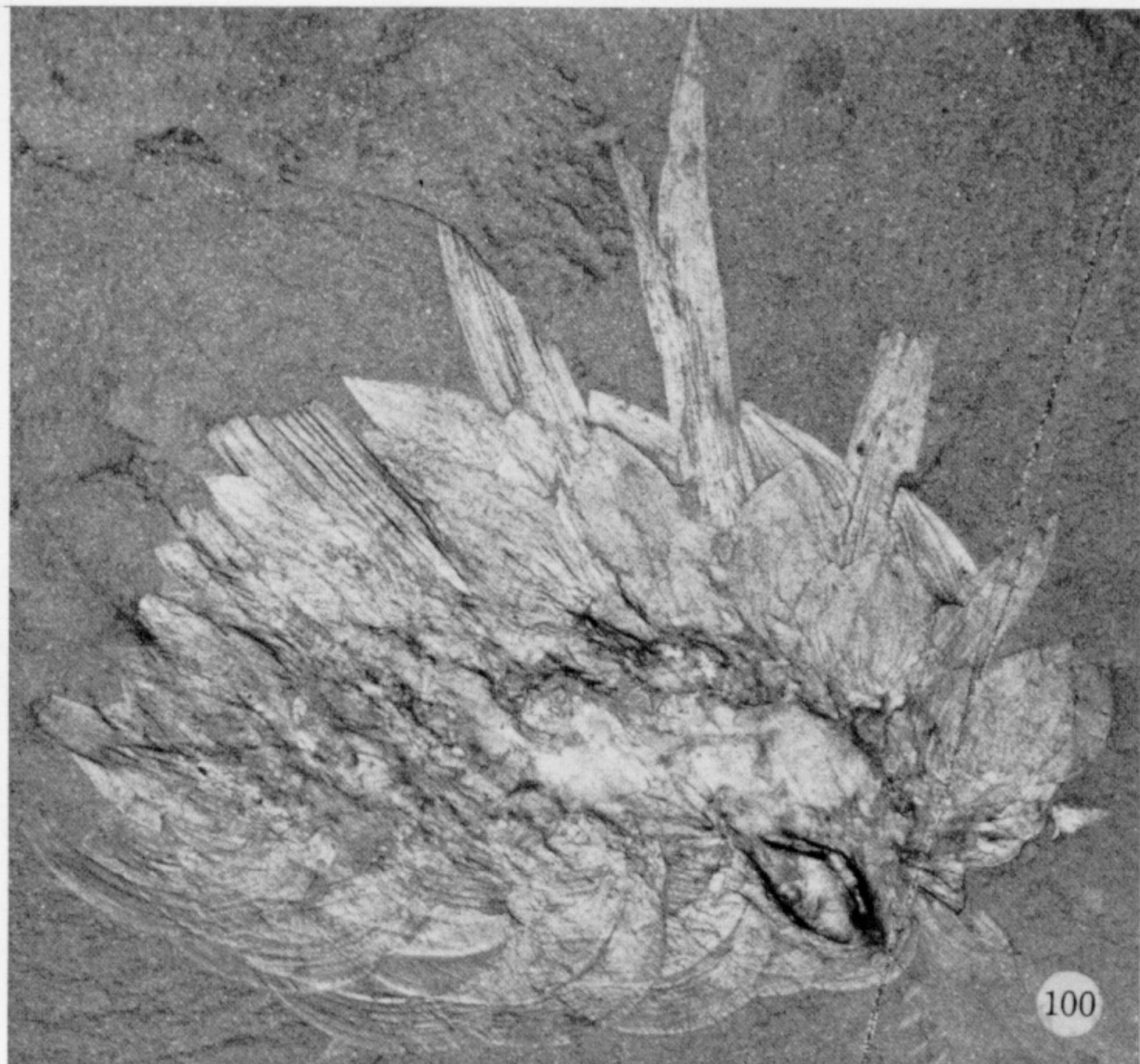


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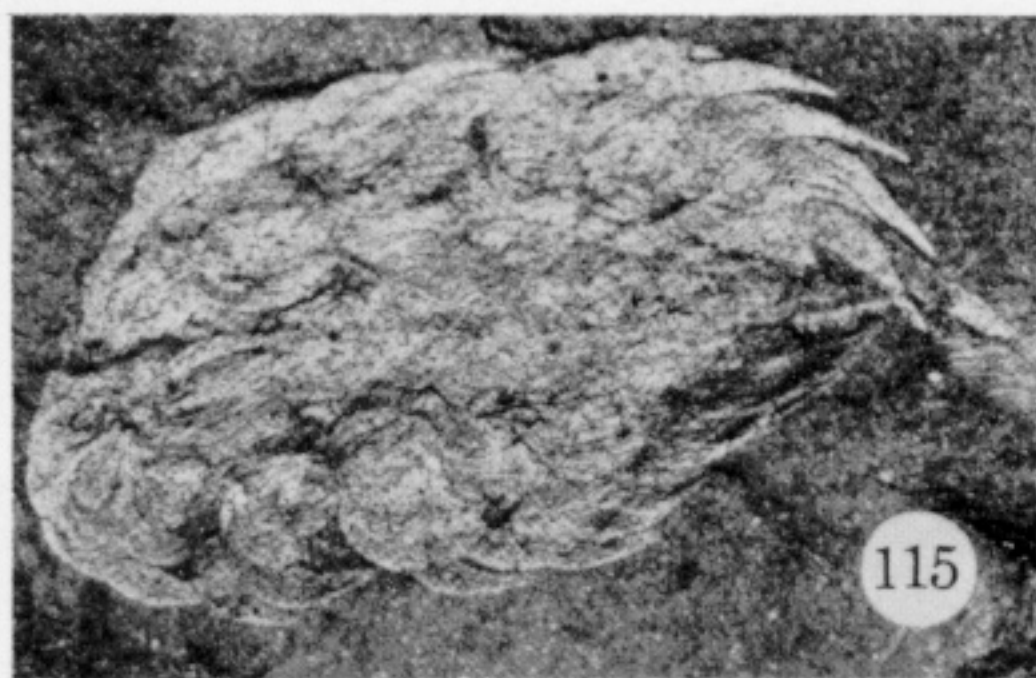
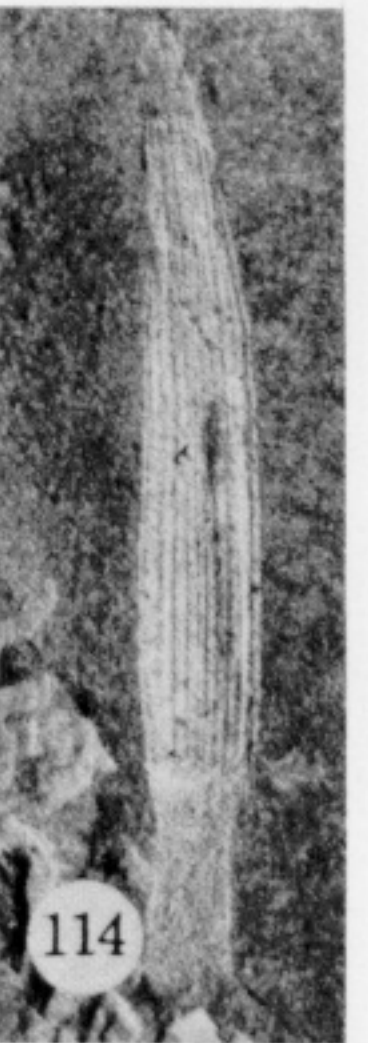
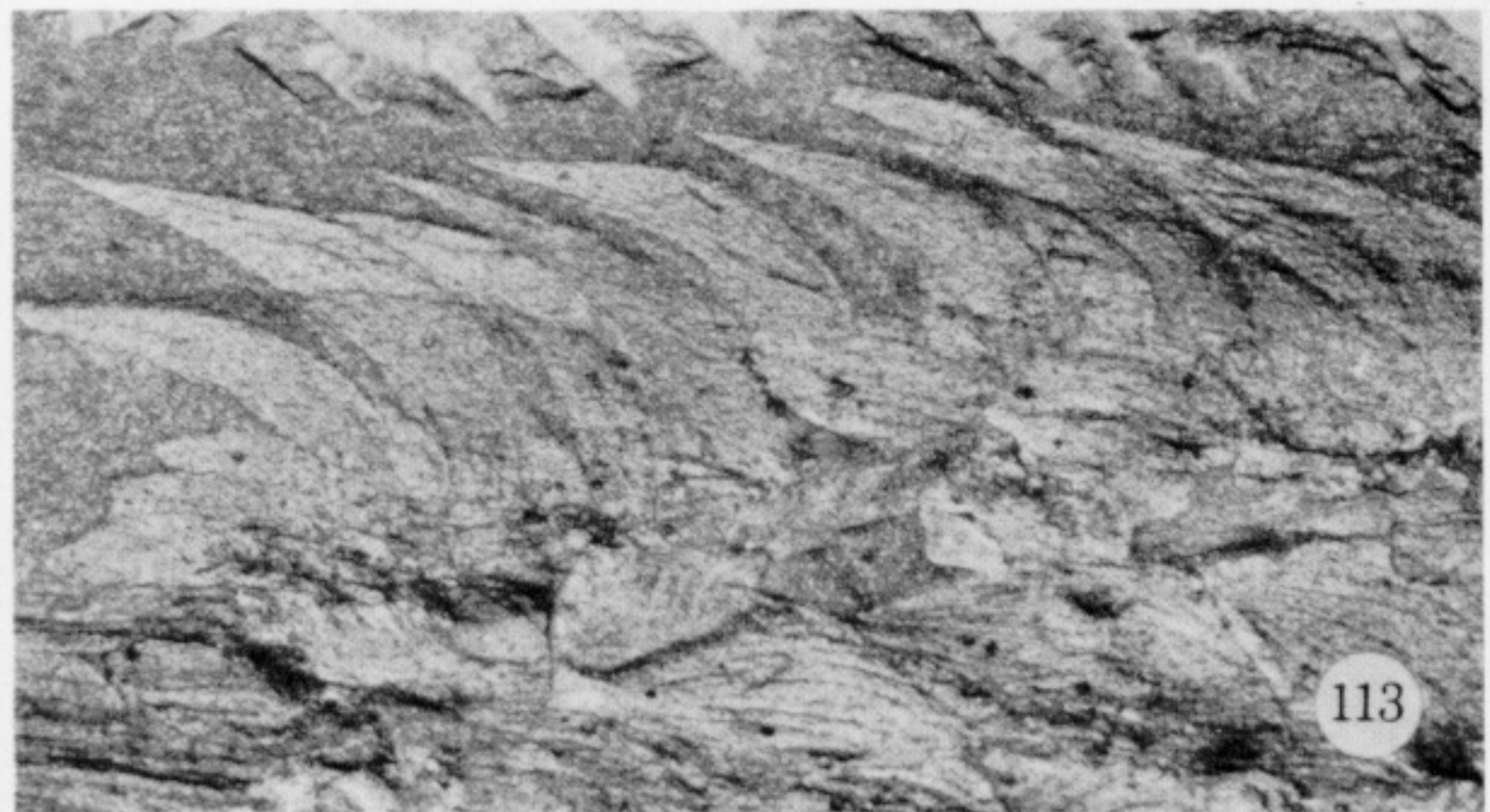


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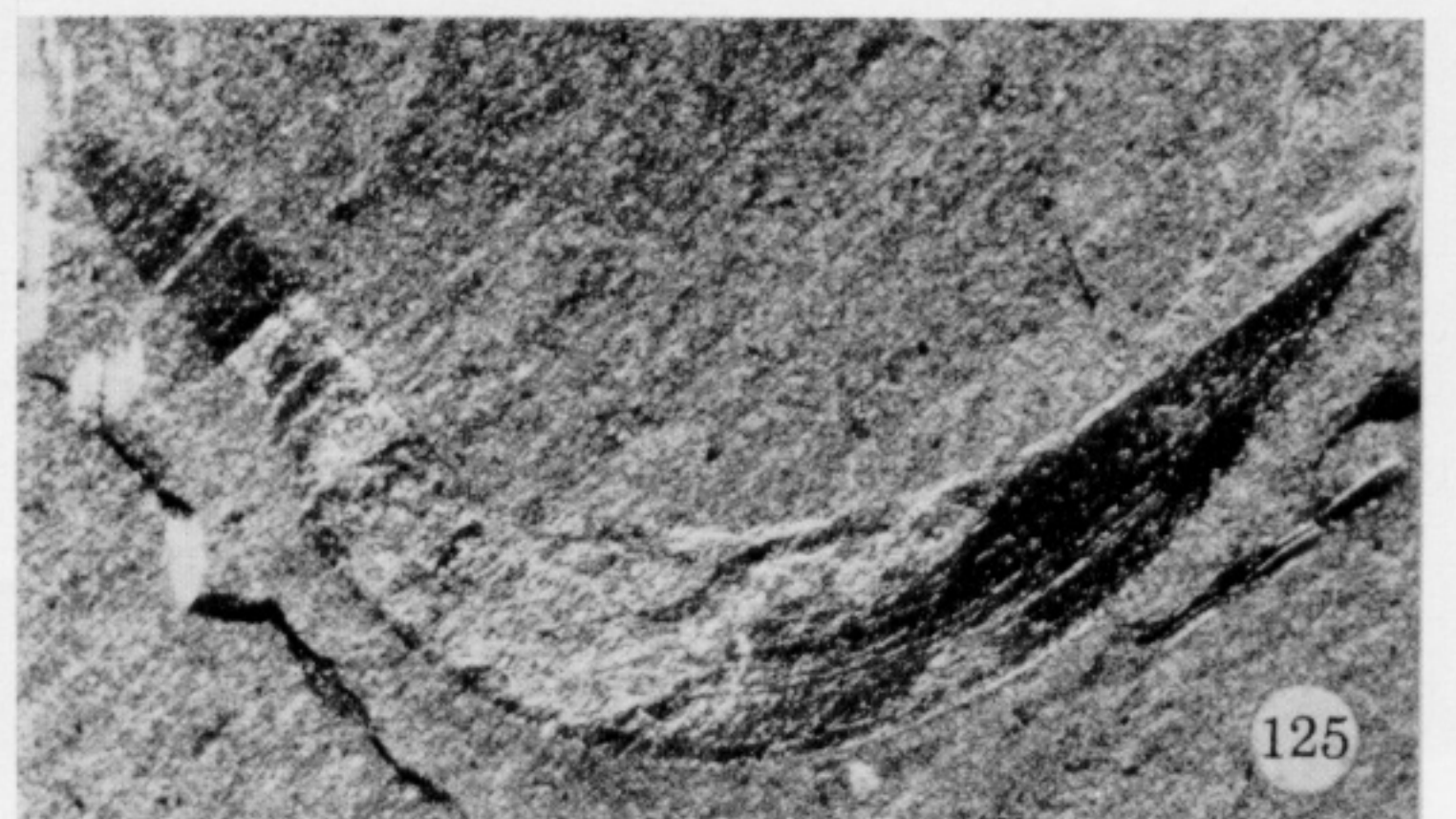
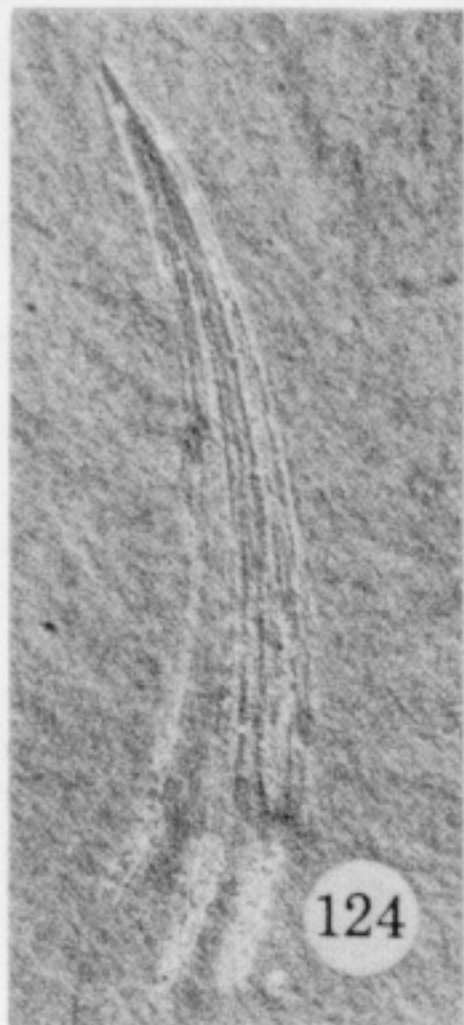
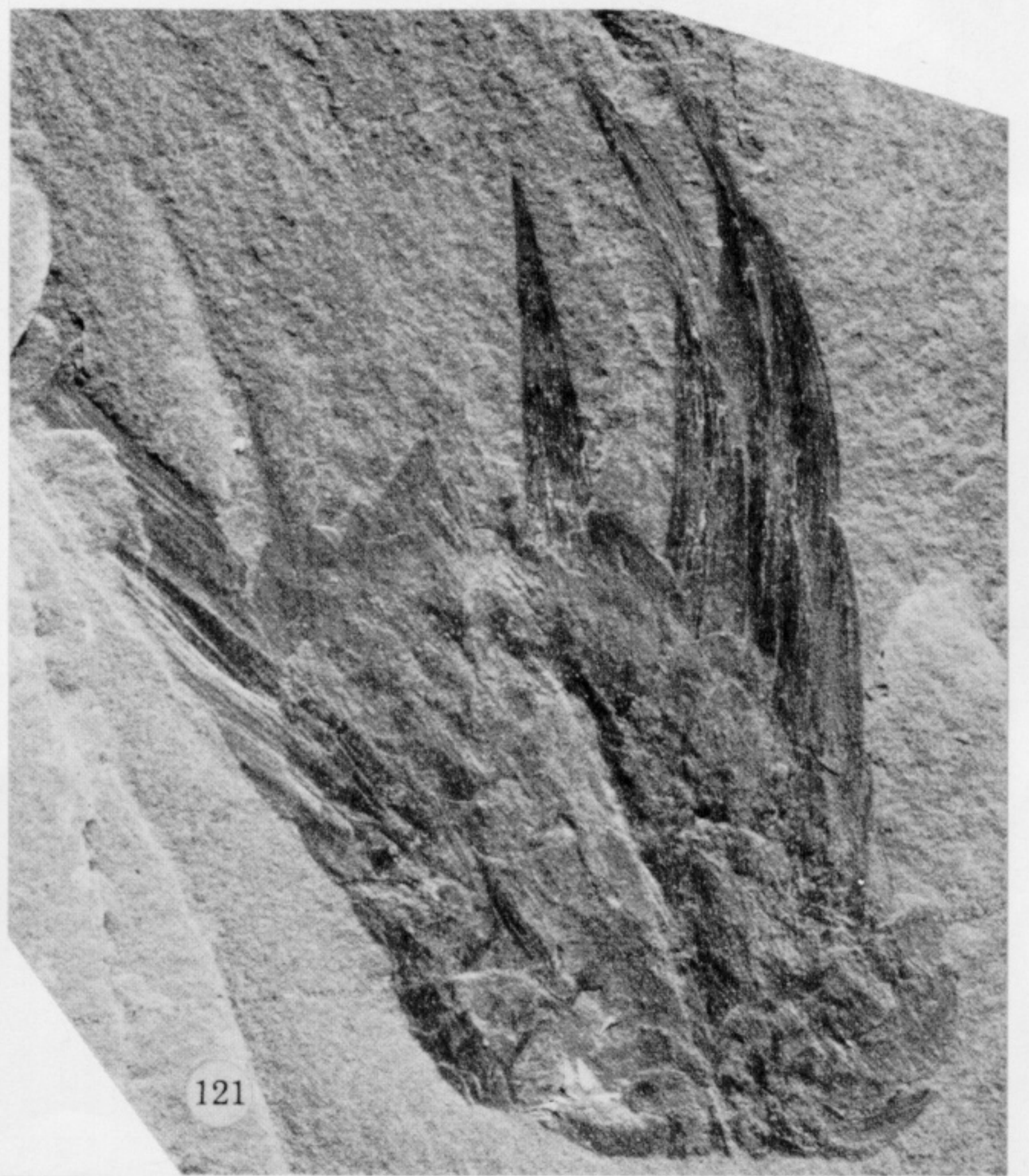
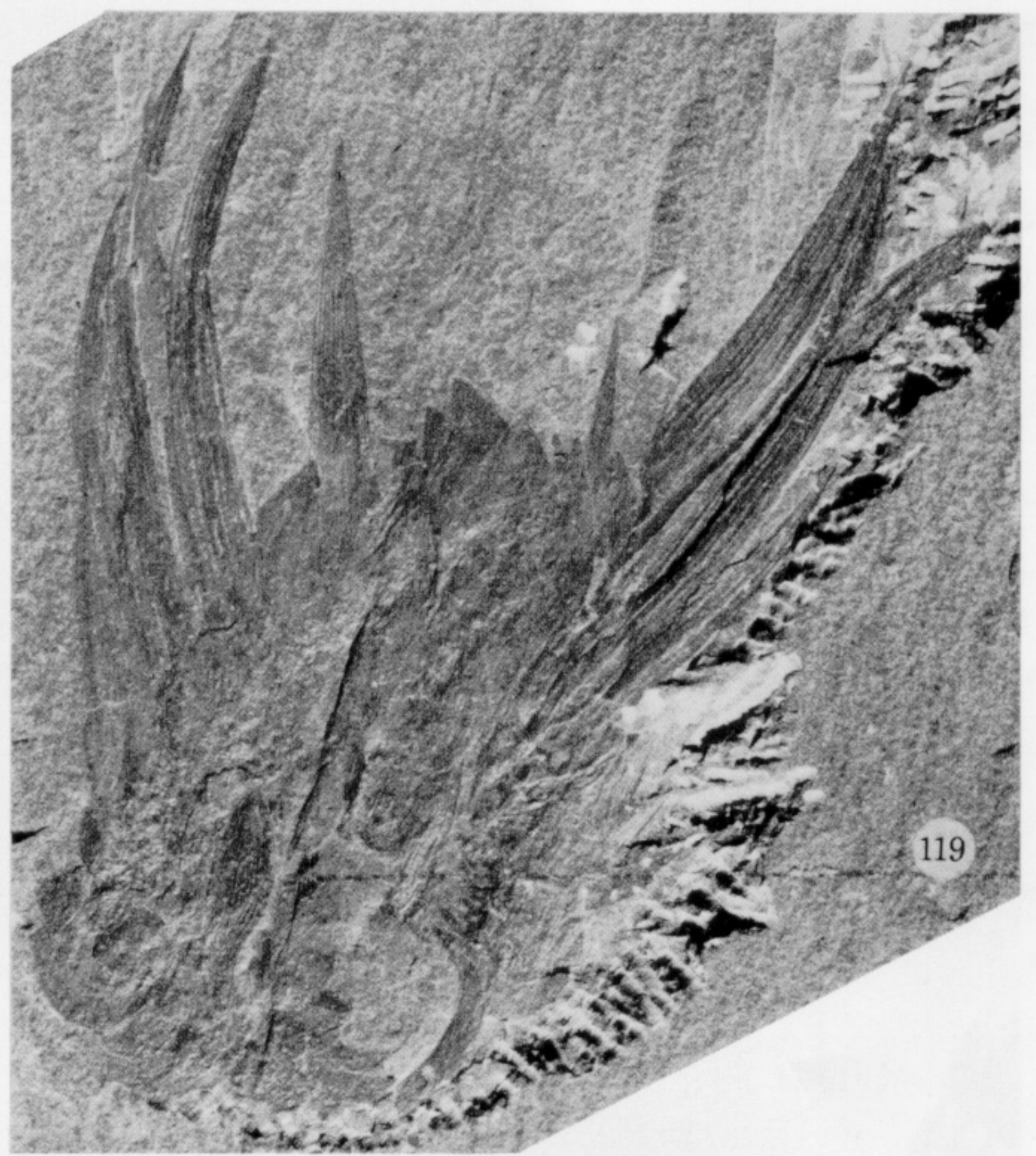
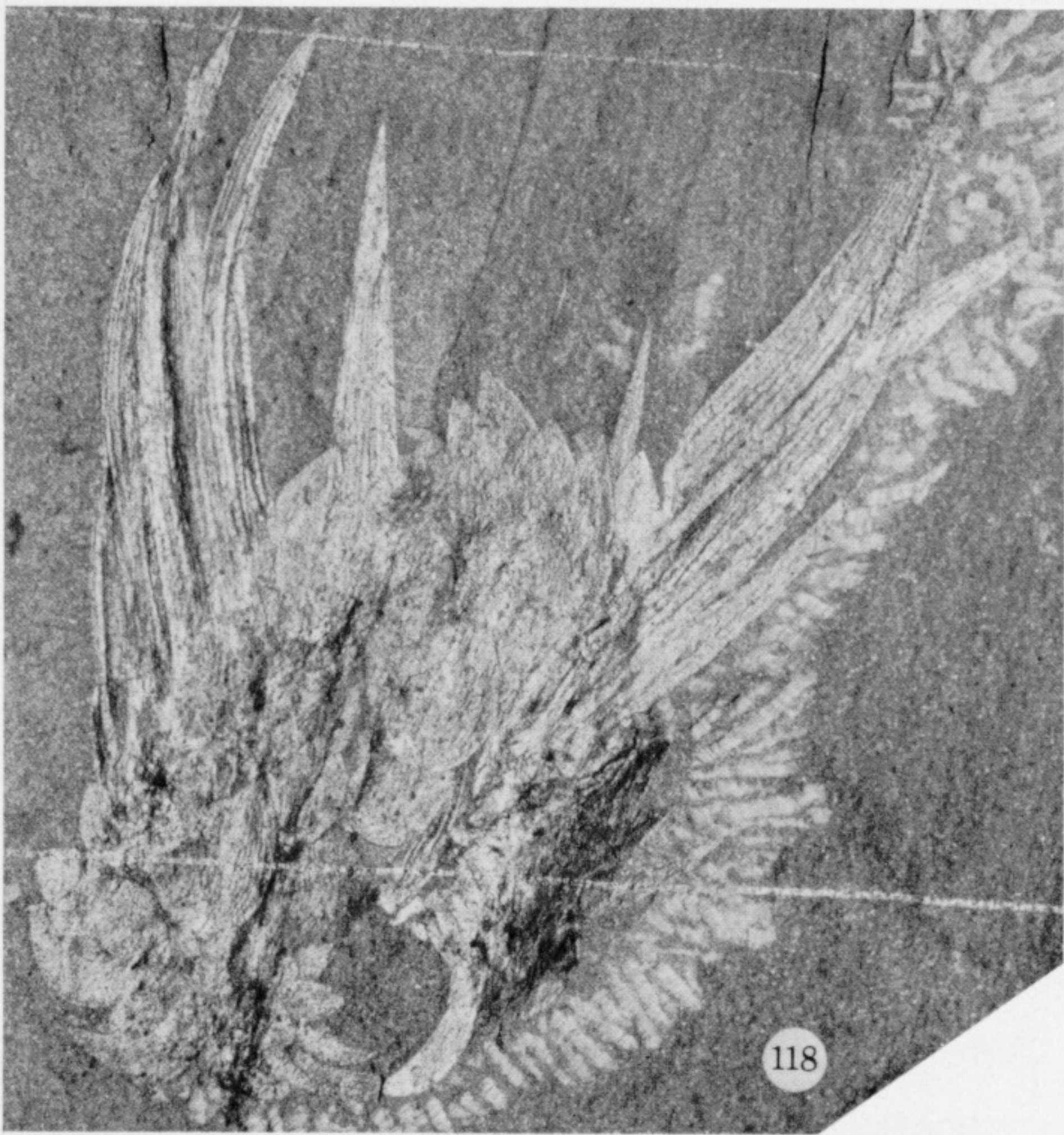
FIGURES 93-97. For description see opposite.



FIGURES 98-104. For description see opposite.

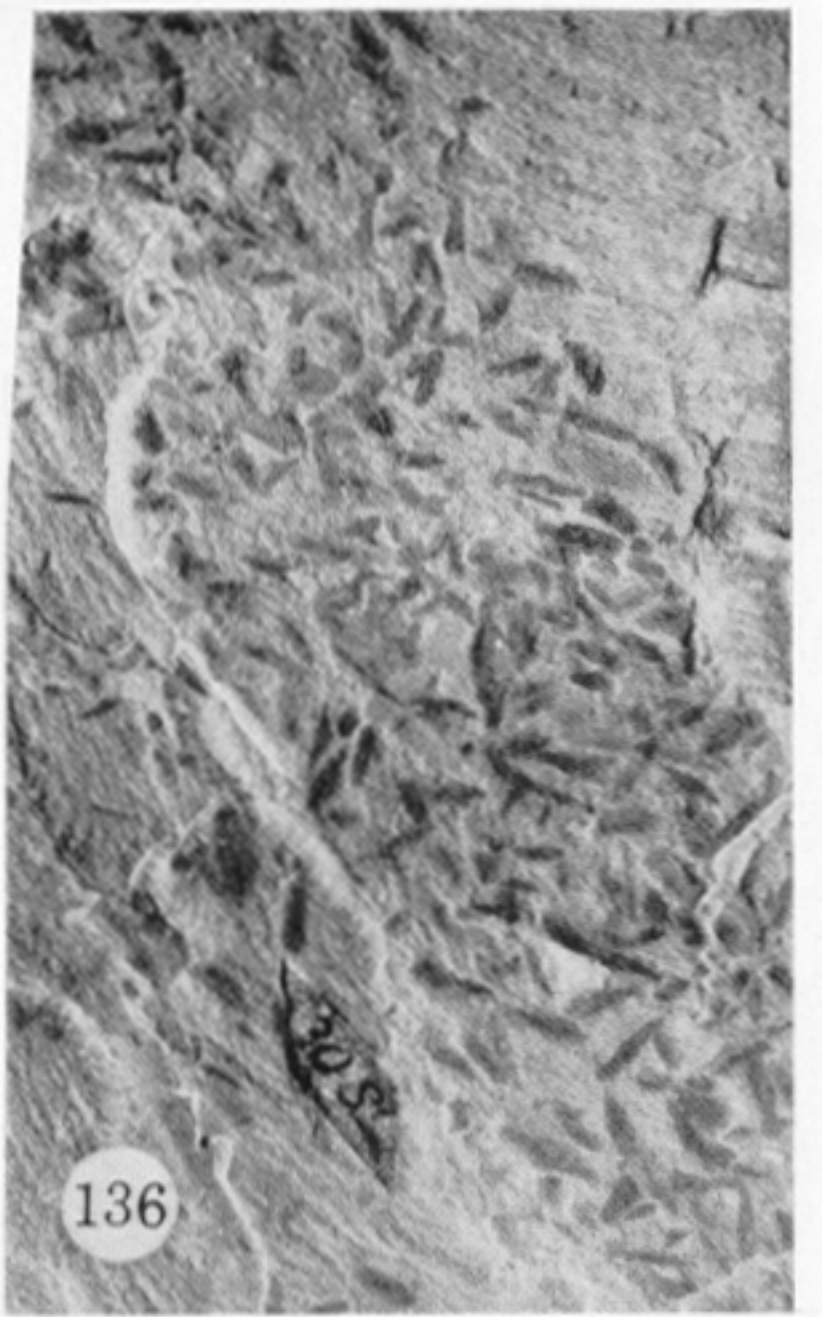
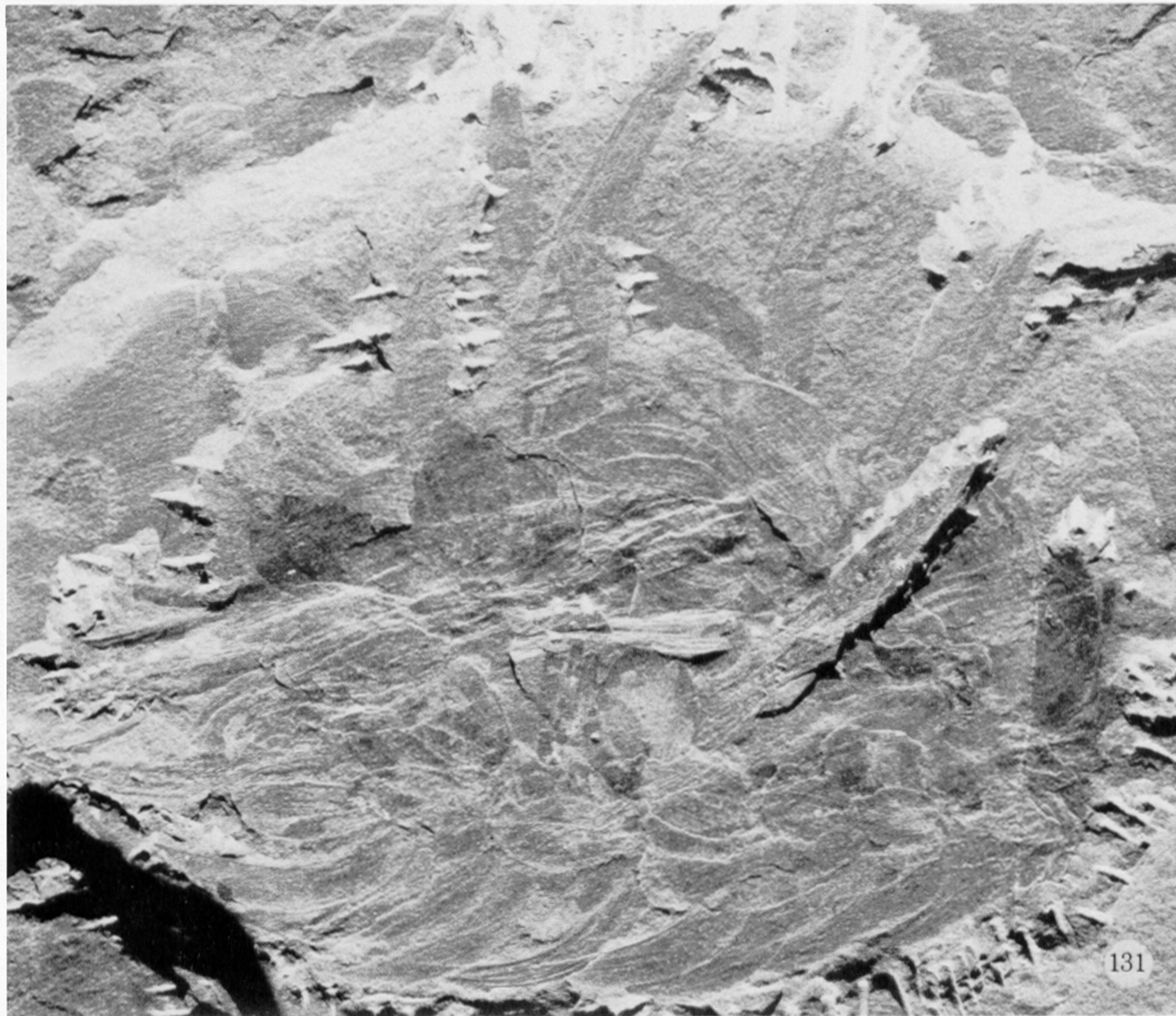
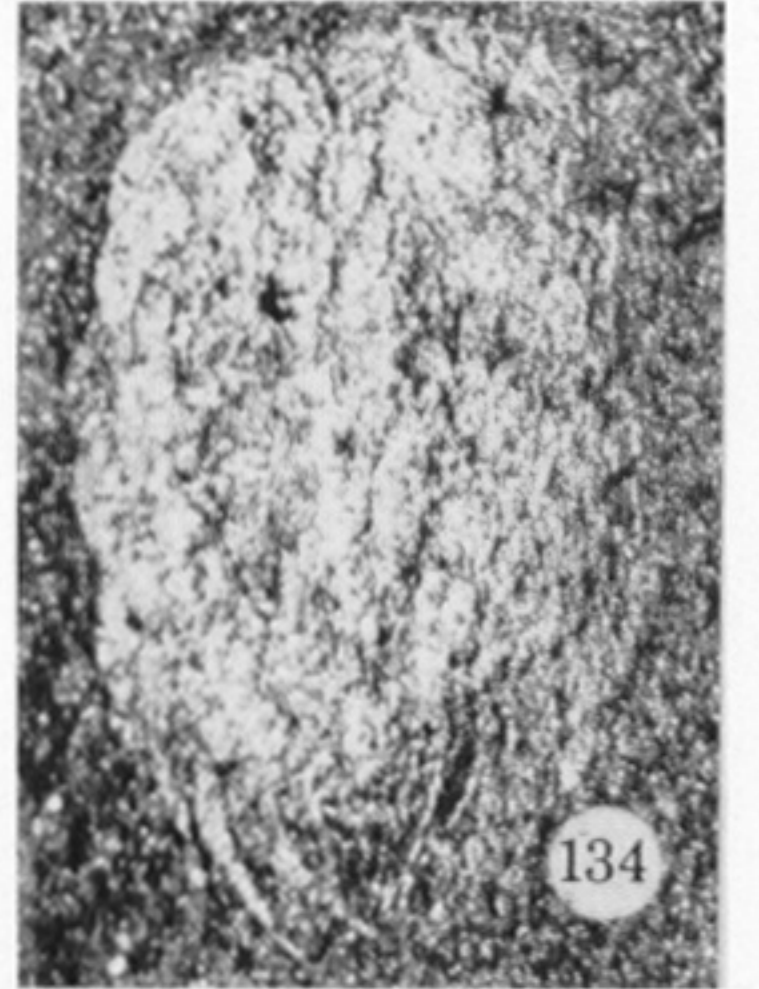


FIGURES 110-117. For description see opposite.

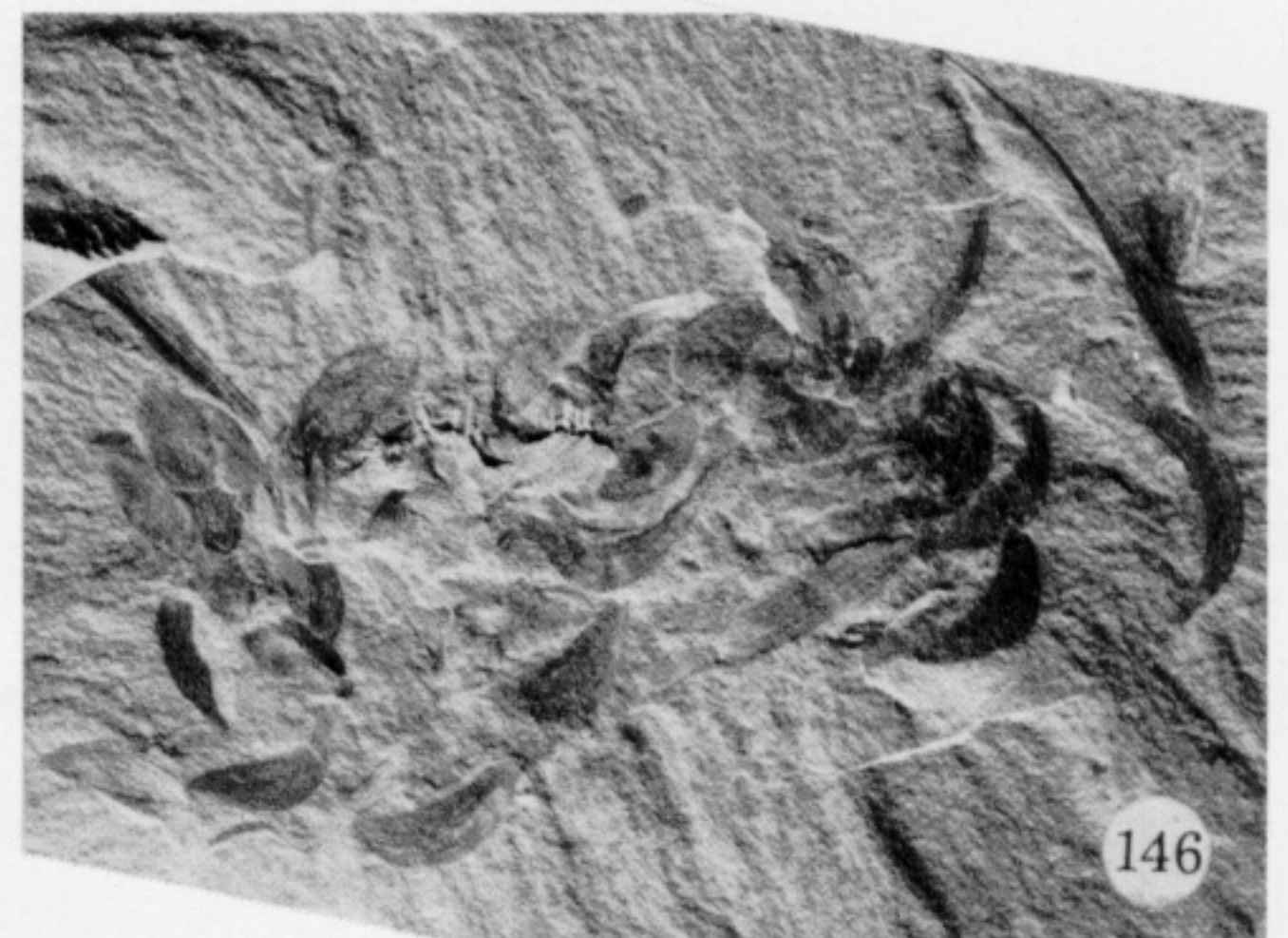
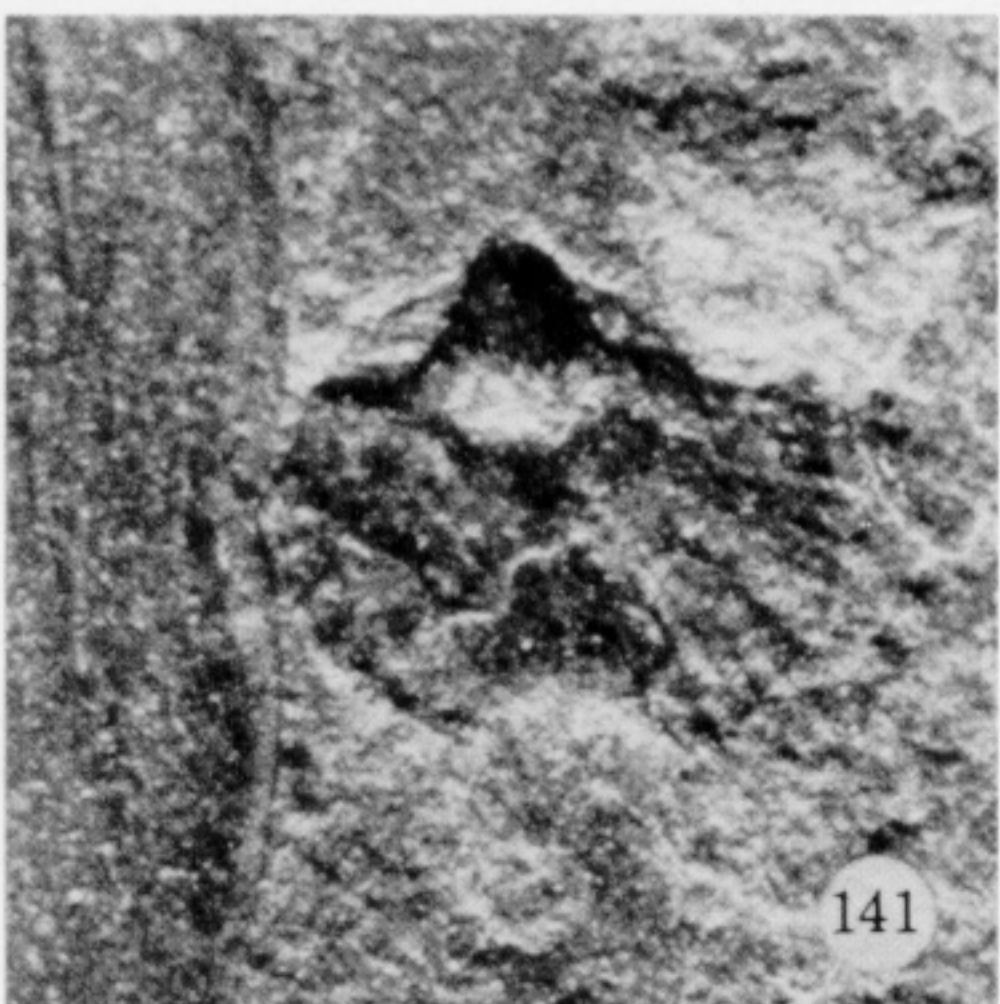
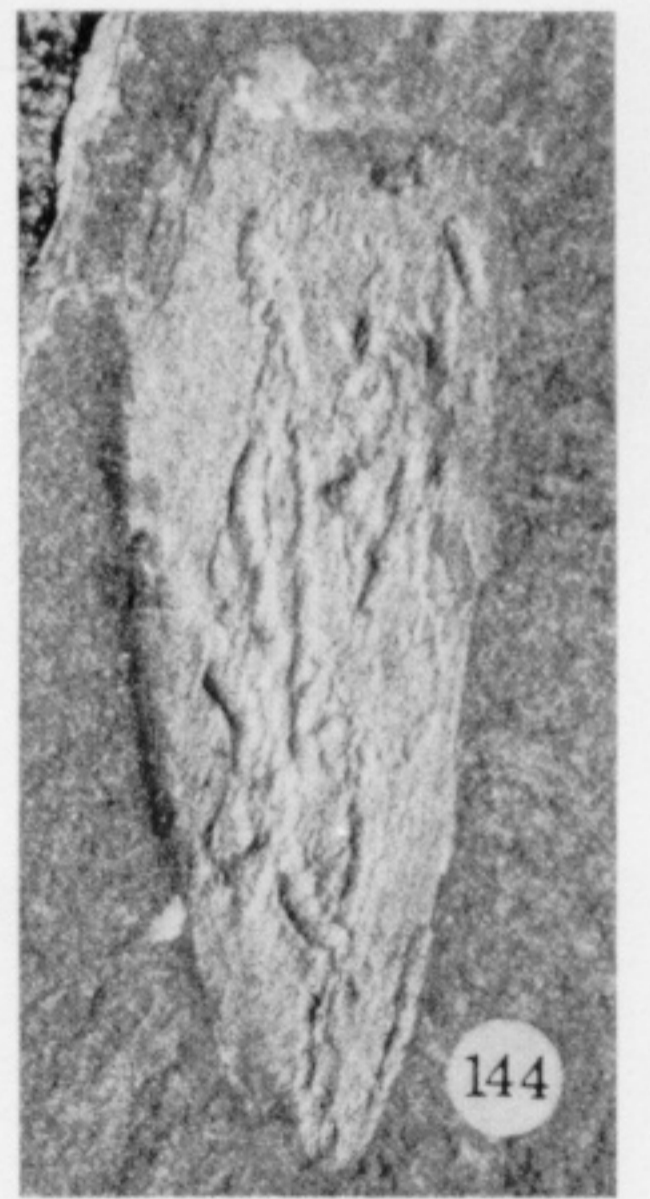
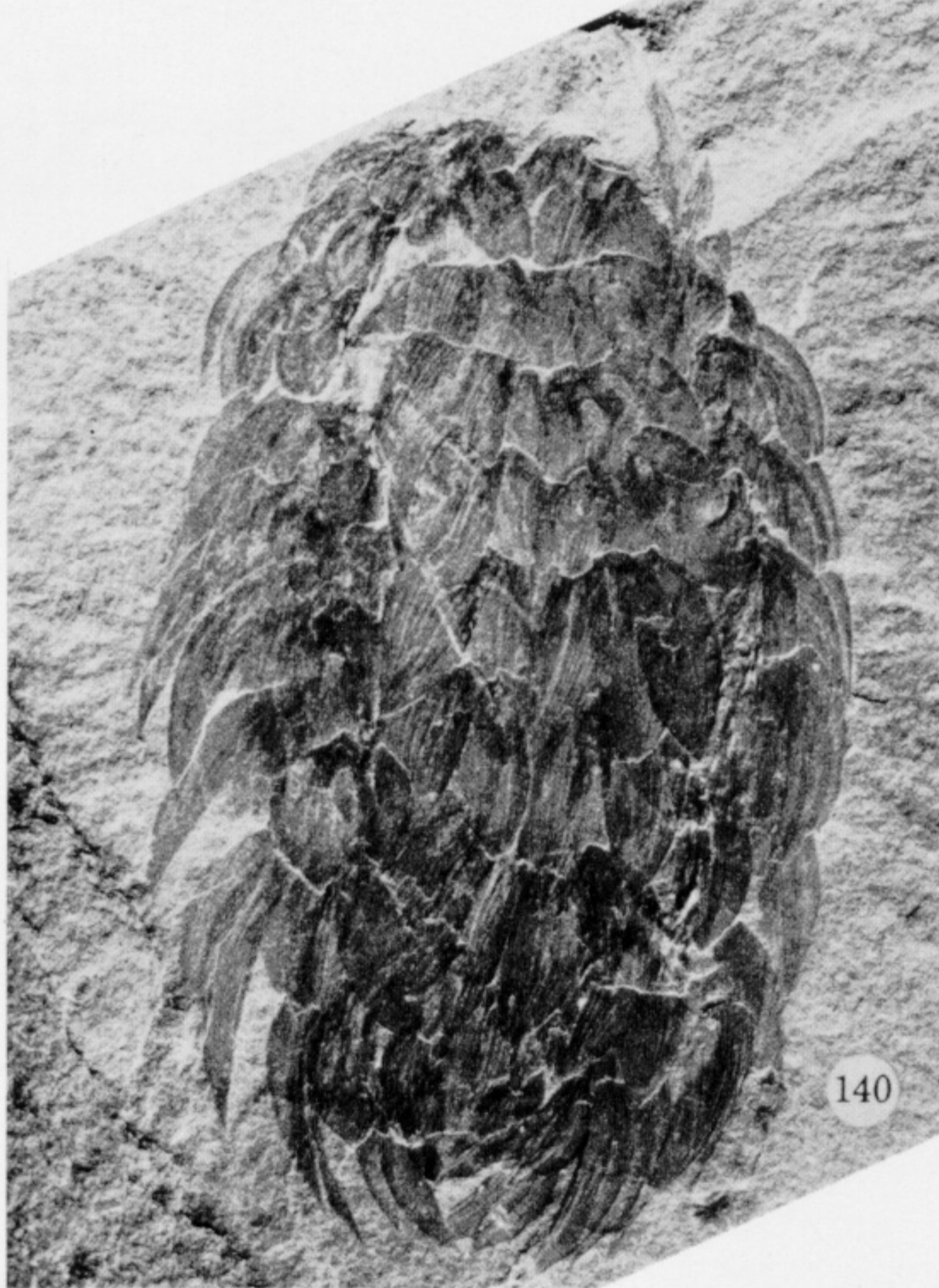
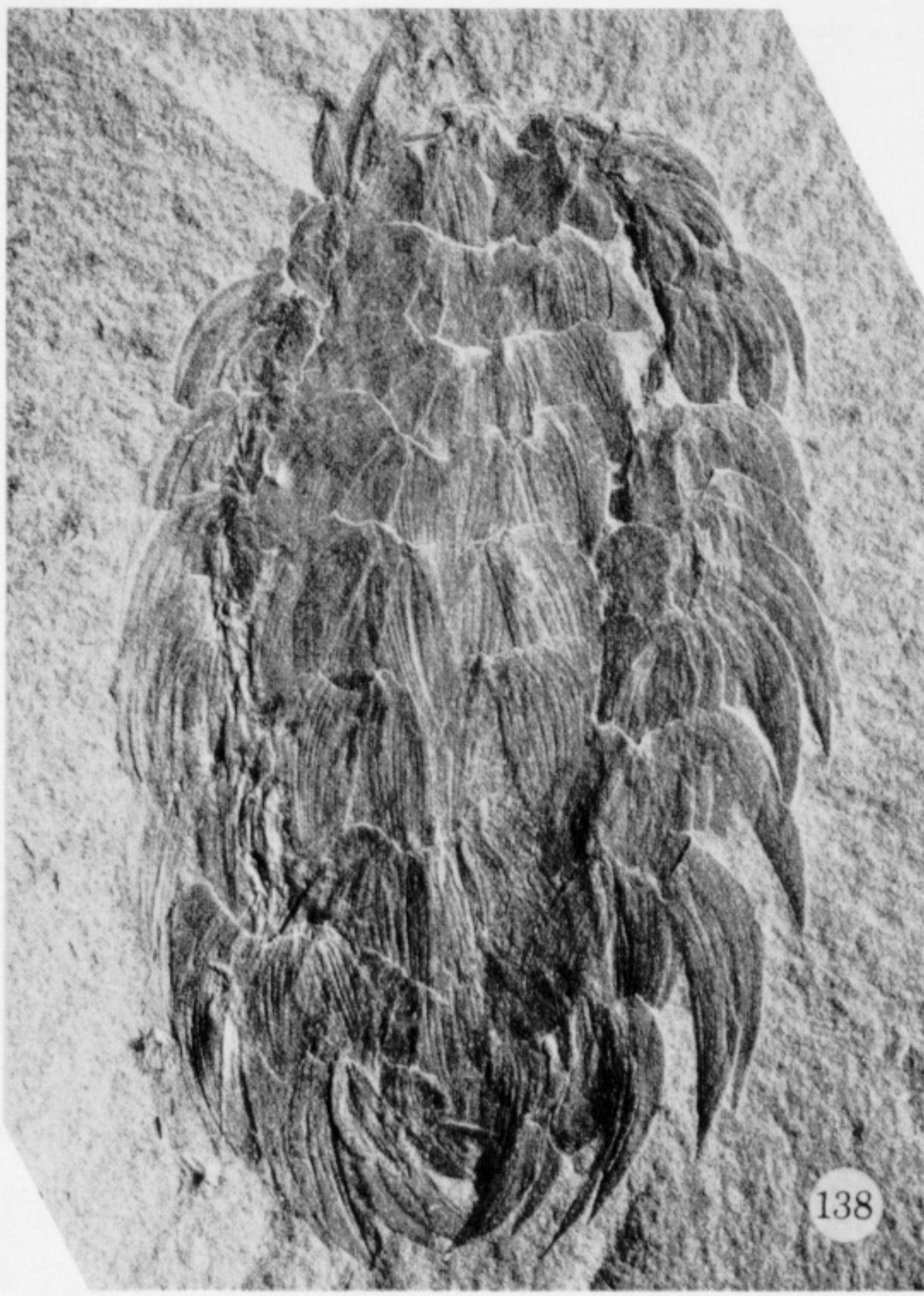


FIGURES 118-125. For description see opposite.

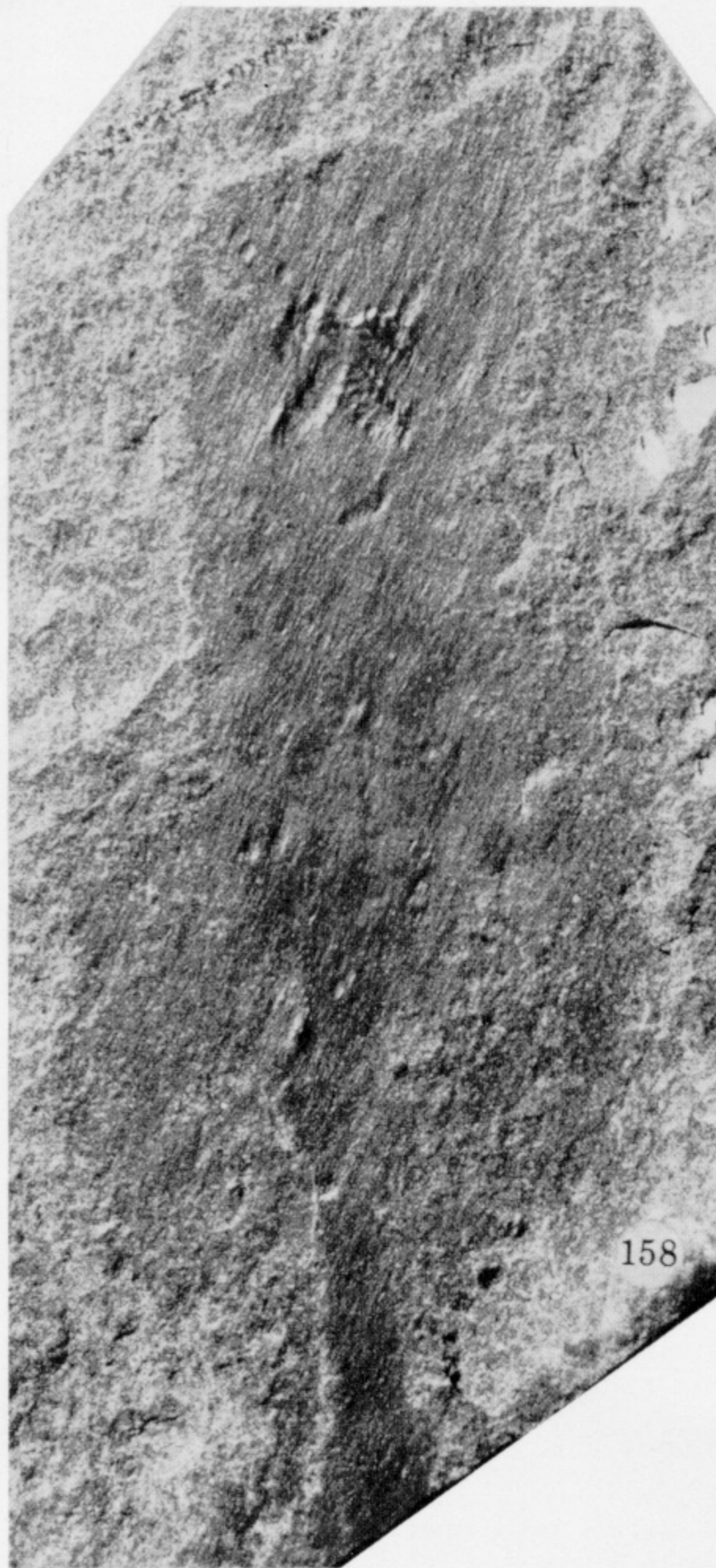
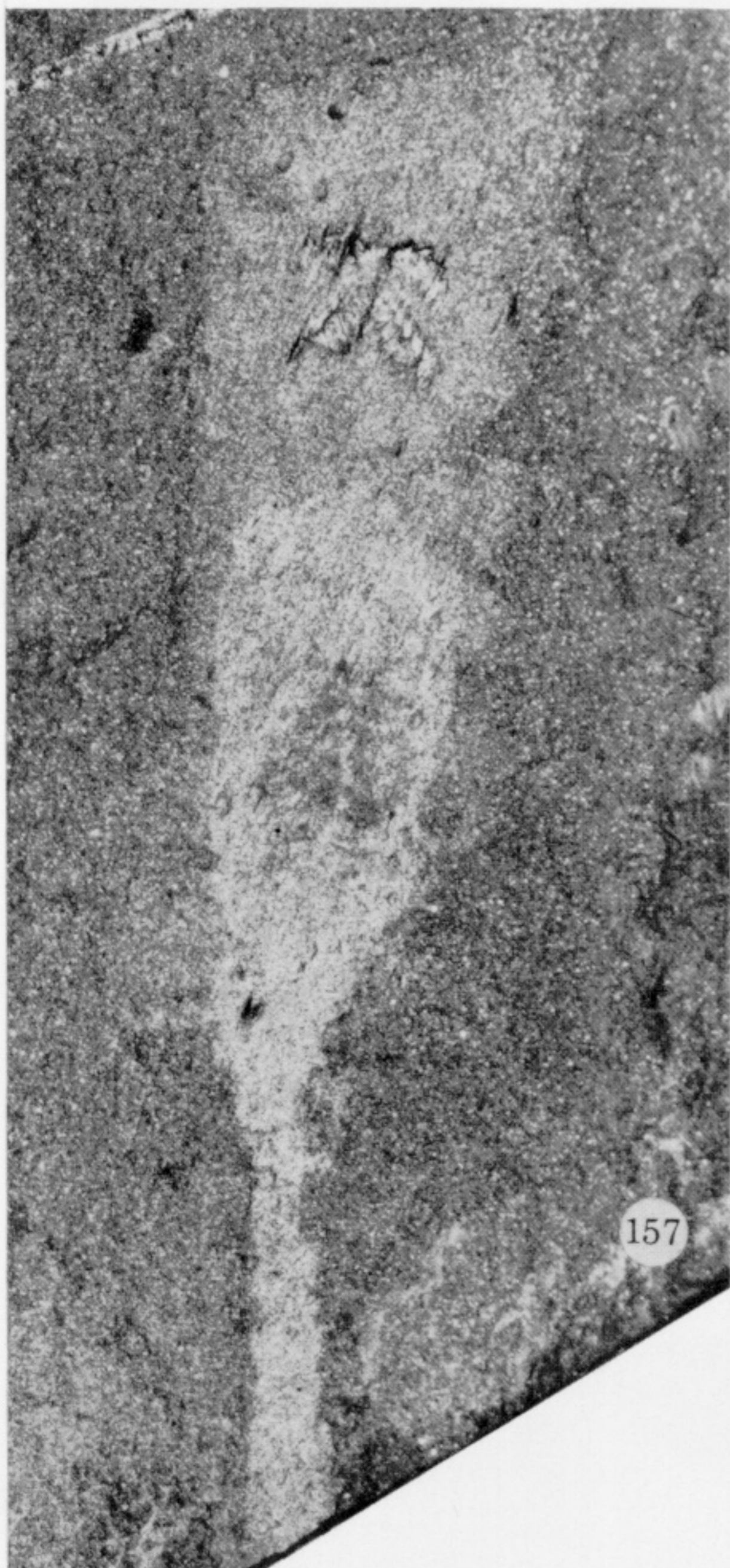
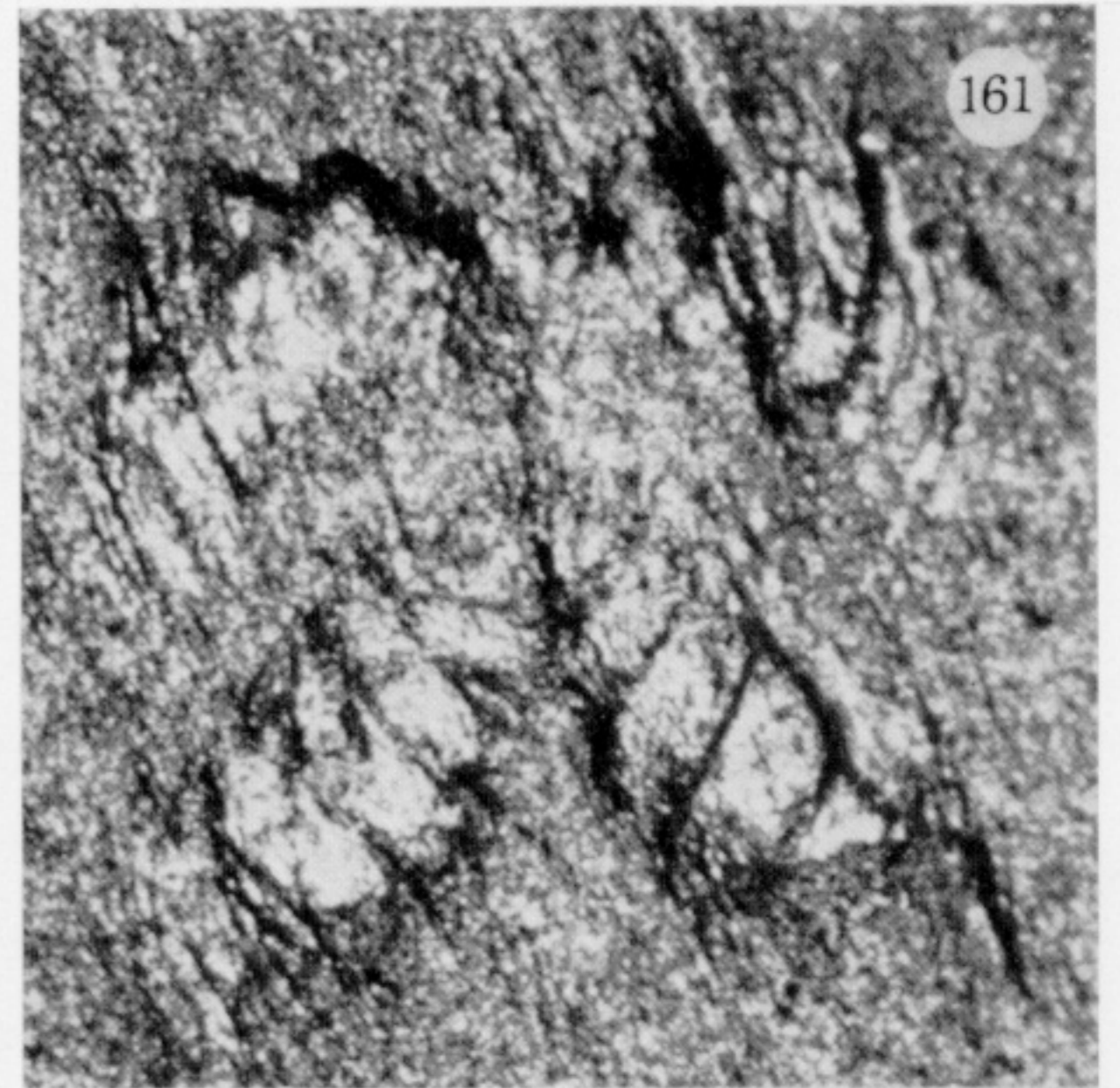
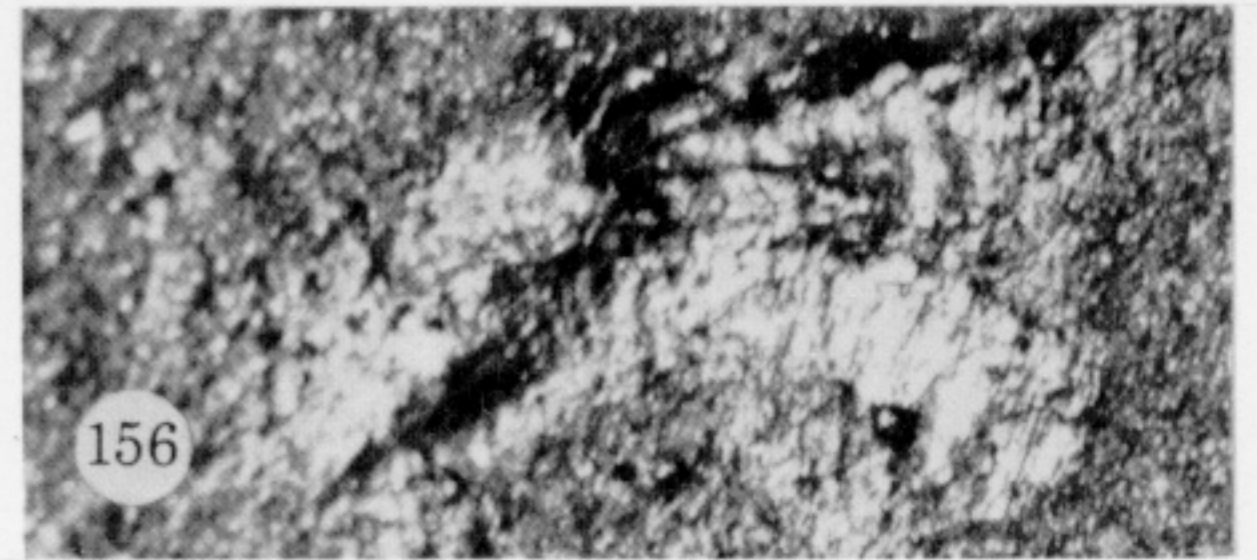




FIGURES 130-136. For description see opposite.



FIGURES 137-146. For description see opposite.



FIGURES 154-161. For description see opposite.