MIDDLE CAMBRIAN POLYCHAETES FROM THE BURGESS SHALE OF BRITISH COLUMBIA

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The Burgess Shale (Middle Cambrian) polychaetes *Canadia spinosa* Walcott, *Burgessochaeta setigera* (Walcott) gen. nov. and *Peronochaeta dubia* (Walcott) gen. nov. are redescribed on the basis of Walcott's type specimens and on much additional material. Two new polychaetes *Insolicorypha psygma* gen. et sp. nov. and *Stephenoscolex argutus* gen. et sp. nov. are described. A poorly preserved specimen of unknown generic affinity is described as type A. The polychaetes are preserved as thin films that adhere to both sides of the split in the rock so that part and counterpart may be available. In *C. spinosa*, *B. setigera* and *I. psygma*, parts of the bodies such as the fascicles of setae are separated by thin layers of sediment that apparently seeped in during turbulent transport in turbidites or mudflows. The bodies therefore lie on two or more planes of microbedding and the factors that control exposure across a specimen are discussed. Aspects of the palaeoecology of the Burgess Shale are reviewed, including the distance the biota was transported prior to burial, the reasons for the exquisite preservation, and the effects of sedimentary compaction.

C. spinosa was characterized by broad notosetae that extended across the dorsum, and large fascicles of neurosetae. Lobate branchiae were situated in the inter-ramal spaces. The prostomium bore a pair of elongate tentacles and the straight gut had an eversible unarmed proboscis. Several lines of evidence suggest that *C. spinosa* was an active benthonic swimmer. *B. setigera* was peculiar in possessing identical notosetae and neurosetae along the entire body. Long anterior tentacles, possibly of peristomial origin, may have been used in feeding. Indirect evidence indicates that *B. setigera* inhabited a burrow which it might have excavated with its proboscis. *P. dubia* may also have burrowed but it had uniramous parapodia bearing simple and acicular setae. The prostomium bore a pair of short appendages. *I. psygma* had extended neuropodia bearing cirri and elongate setae. The notopodia were reduced and cirri appear to have been wanting. The peculiar prostomium carried a pair of appendages. *I. psygma* is regarded as a pelagic polychaete. *S. argutus* possessed uniramous parapodia with simple stout setae. The bilobed prostomium bore at least one pair, and perhaps three pairs, of short appendages. Type A was the largest of the Burgess Shale polychaetes and had prominent setae on at least the anterior section of the body. Type A was a sediment eater but the feeding habits of the other polychaetes are uncertain. Particular attention is given to the influence of decay on the Burgess Shale polychaetes. To place the Burgess Shale polychaetes in some geological perspective other Cambrian worms, including a polychaete from the Spence Shale of Utah, are briefly redescribed and the late Precambrian (Ediacarian) worms *Dickinsonia*, *Spriggina* and *Marywadea* are assessed. Contrary to the findings of other workers, no convincing evidence for placing these latter worms in the polychaetes is forthcoming.

1. INTRODUCTION

Soft bodied polychaetes lack substantial hard parts which could resist decay and become fossilized. Their fossil record is thus almost non-existent. Not surprisingly the quality of preservation of the relatively few polychaete fossils known is indifferent and it is doubtful whether any fossil polychaetes show superior preservation to those from the celebrated Middle Cambrian Burgess Shale of British Columbia. The recognition and description of fossil polychaetes is of particular importance not only because of their rarity but because their early history and evolution are a matter of lively debate.

In common with nearly all the other fossil worms from the Burgess Shale the polychaetes have received little detailed attention. The Burgess Shale fauna is largely soft bodied and is so exquisitely preserved that even the gut and muscles may be identified in some species. This fauna postdates the major Precambrian radiation of the Metazoa (Cloud 1968, 1976) by geologically a comparatively short period of time. Thus, despite the localized nature of the fauna it has an enormous palaeontological significance because it illuminates aspects of metazoan evolution and diversification in the early Palaeozoic which otherwise are unknown or only represented by an extremely scanty fossil record. It has become apparent that numerous groups, perhaps entire phyla, with few or no hard parts were present in Cambrian times and probably formed a significant proportion of most marine faunas. The inevitable bias of fossilization in favour of animals with hard parts means that these soft bodied groups are not recognized in most deposits. It is tempting to speculate whether some of the relatively low faunal diversity in the Cambrian Period (see Valentine 1973) is simply a reflection of the rarity of groups possessing fossilizable hard parts.

At the end of the 1909 field season Charles Doolittle Walcott, Secretary of the Smithsonian Institution, discovered soft bodied fossils within a snow-slid block near Field, southern British Columbia. The following year he located the stratum from which the block was derived (see §2). The subsequent history of Walcott's excavations during the seasons 1910–13 and 1917 was summarized by Whittington (1971*a*). The large collections of fossils (over 40 000 specimens) were deposited by Walcott in the United States National Museum (U.S.N.M.) (now the National Museum of Natural History), Washington, D.C. Walcott issued a series of reports on about 75% of the biota which he himself regarded as preliminary (Walcott 1911*a*,*b*,*c*; 1912*a*, 1916, 1918*a*, *b*; 1919, 1920, 1931).

Only two units within the Burgess Shale have yielded abundant soft bodied fossils. The lower of these is the Phyllopod bed (Walcott 1912*a*) which is exposed in the Burgess or Walcott Quarry. Less than 21 m (68 ft) above this quarry another excavation, the Raymond Quarry (Raymond 1935), has yielded a generally less well preserved fauna of lower diversity in which polychaetes are almost unknown. Much of the faunal variation between the two quarries may be original rather than due to preservational factors (Conway Morris, in the press). In 1966 (Aitken, Fritz & Whittington 1967) and 1967 (Aitken & Fritz 1968) a Geological Survey of Canada (G.S.C.) team under the leadership of Dr J. D. Aitken reopened the quarries with the kind cooperation of the Parks Canada, Department of Indian and Northern Affairs, Ottawa and the authorities of the Yoho National Park. In 1975 a party from the Royal Ontario Museum (R.O.M.), Toronto collected material from the talus discarded by previous expeditions.

Walcott (1911*c*, 1931) allocated the majority of the worms that he described (*Miskoia*, *Aysheaia*, *Canadia*, *Selkirkia*, *Wiwaxia*, *Pollingeria*, *Worthenella*) to the polychaetes. It has become apparent, however, that with the exception of certain species of *Canadia* Walcott, none of them may be regarded as polychaetes or even annelids. Walcott recognized seven species of *Canadia*, the type species being *C. spinosa* Walcott, 1911. *C. irregularis* Walcott, 1911 and *C. grandis* Walcott, 1931 are junior synonyms of the type species (see §8*b*). *C. setigera* Walcott, 1911 and *C. dubia* Walcott, 1911 are assigned to new genera and are renamed herein *Burgessochaeta setigera* (Walcott) gen. nov. and *Peronochaeta dubia* (Walcott) gen. nov. respectively. *C. sparsa* Walcott, 1911 and *C. simplex* Walcott, 1931 are not polychaetes and they have been assigned elsewhere to *Hallucigenia* (Conway Morris 1977*a*) and *Lecythioscopa* (1977*b*). In addition two new polychaetes *Insolicorypha psygma* gen. et sp. nov. and *Stephenoscolex argutus* gen. et sp. nov. are described. A single specimen of a large worm is also regarded as a polychaete (figures 128, 129, plate 9). It is unlike any other Burgess Shale polychaete, but its incompleteness and poor preservation makes even a generic diagnosis impossible. It is, therefore, called type A. *C. spinosa* has marked similarities with modern palmyrid polychaetes, but the affinities of *B. setigera*, *P. dubia*, *I. psygma*, *S. argutus* and type A to modern families remain obscure.

As well as reillustrating all of Walcott's type material (figures 5–14, plate 1; figures 17–23, plate 2; figures 68–73, plate 5; figures 101–103, plate 7; figures 125, 126, plate 9 and figures 4, 15, 94, 121), a number of additional U.S.N.M. and R.O.M. specimens were selected from the hundreds available to portray additional features. This study provides considerable information on aspects of the external anatomy such as the parapodia and setae. With the exception of the gut few details of internal anatomy have, however, been preserved. To help place the findings reported here in context other worms described as polychaetes from the Ediacarian (late Precambrian) and Cambrian are reviewed.

2. STRATIGRAPHY

The Middle Cambrian Burgess Shale forms a unit composed predominantly (90%) of shale (125 m (410 ft) thick, Walcott 1928; incorrect sum of 128 m (420 ft) given by Walcott 1912*b*) and occurs within the Stephen Formation which is a basinal succession of shales and impure limestones (Fritz 1971). The Stephen Formation was deposited to the southwest of a steep carbonate bank (now forming part of the Cathedral Formation) which trended NNW. In the vicinity of Field the margin of the carbonate bank was interrupted by a prominent embayment. The Burgess Shale was deposited within this embayment and immediately in front of the bank (McIlreath 1974, 1975). Practically all the polychaetes were recovered from the 2.31 m (7 ft 7 in) thick Phyllopod bed which is within 9–12 m (30–40 ft) of the base of the Burgess Shale (Walcott 1912*b*, 1928). The Phyllopod bed is exposed in the Walcott Quarry (Walcott 1912*a*, *b*; U.S.N.M. locality number 35k). About 19.8 m (65 ft) above this quarry another soft bodied fauna, which includes a very few unidentifiable polychaetes, has been recovered from the Raymond Quarry. The Phyllopod bed lies within the *Pagetia bootes* faunule of the *Bathyuriscus-Elrathina* Zone. Fritz (1971) showed by using trilobite zonation that the Phyllopod bed was deposited at a depth of about 160 m (530 ft). The two quarries are situated on the west side of the ridge connecting Wapta Mountain and Mount Field at an elevation of about 2286 m (7500 ft). The quarries are 4.8 km (3 miles) north of Field, southern British Columbia.

3. TERMINOLOGY

(*a*) *Recent polychaetes*

The annelidan class Polychaeta forms, with a few exceptions such as the poeobiids (Robbins 1965), a coherent and well defined group. Its popular and long established subdivision into the Polychaeta Errantia and Sedentaria is artificial (Dales 1962, 1963; Day 1967), but attempts to cluster the seventy-five or more families (Fauchald 1977) into orders have proved difficult. A number of proposals relying on various characters are reviewed by Clark (1969), but no scheme has yet won widespread support.

A brief resumé of the polychaete body plan is given here to aid comprehension of the systematic descriptions in §8*b*–*g*. More extended accounts may be found in Fauvel (1953), Dales (1963), Day (1967) and Fauchald (1977). The body is divided into four units: *prostomium*, *peristomium*, metastomium or *trunk* which consists of a variable number of setigerous segments, and *pygidium*. The prostomium is a pre-oral and pre-segmental lobe that carries the brain; in certain species this unit carries the eyes. Primitively it apparently bore two *palps* and three *antennae*. The terminology of the prostomial appendages has been confused and homonymous structures are not necessarily homologous in all families (see e.g. Åkesson 1968), but it is now recognized that antennae are innervated via a single root from the brain, whereas palps are connected to either the brain or circumoesophageal ring by two roots (Fauchald 1974, 1977). Amongst the Burgess Shale polychaetes it is impossible to determine precisely the origin of prostomial outgrowths and they are non-committally referred to as *tentacles* (if long) or *appendages* (if short). The prostomium may also bear a dorsal lobe or *caruncle*. The peristomium surrounds the mouth and is often modified by reduction and fusion with adjacent parts of the body. The trunk bears *parapodia* which in the *biramous* state consist of a dorsal *notopodium* and a ventral *neuropodium*. The *uniramous* condition arises when one podium is suppressed. A podium is often supported internally by a rod or *aciculum*. Each podium normally bears one or more *fascicles* of chitinous *setae* (*notosetae* or *neurosetae*) which may be *simple* or *compound*. Setal morphology is variable: for instance thickened and flattened setae are termed *acicular setae* and *paleae* respectively. The setae arise from a *setal sac*. A slender or foliaceous extension of the podium is termed a *cirrus*. The post-segmental pygidium bears the anus. The gut is usually straight and the anterior section is frequently modified into an eversible *proboscis* which may be armed (Dales 1962). Polychaetes occupy a wide range of marine, and even freshwater, habitats. Burrowing, tubicolous, crawling and swimming varieties are all well represented.

(*b*) *Burgess Shale polychaetes*

In common with most members of the Burgess Shale fauna, the orientation of individual polychaete specimens varies with respect to the bedding. In discussing orientation the terminology of Whittington (1975*a*) is followed. The median dorsoventral plane is termed *sagittal*, whilst the vertical plane at right angles to it is called *transverse*. *Abaxial* and *adaxial* refer to directions away and towards the sagittal plane respectively. When the sagittal plane of a specimen is more or less at right angles to the bedding it is described as *dorsoventral* (e.g. figures 7 and 8, plate 1; figure 30, plate 3; figures 71 and 72, plate 5; figure 85, plate 6; figures 4 and 80); occasionally the axis of the body is inclined to the bedding (figures 38 and 39, plate 3). The attitude of the rock slabs was not usually recorded by collecting teams and it is impossible to determine whether a specimen was originally buried dorsal or ventral side up. Specimens with the sagittal plane approximately parallel to the bedding are termed *lateral* (e.g. figures 5 and 11, plate 1; figures 19, 20 and 22, plate 2; figure 51, plate 4; figures 15 and 44). *Oblique* specimens have the sagittal plane inclined to the bedding at an appreciable angle (e.g. figure 37, plate 3; figure 28). These simple definitions are sometimes complicated by the effects of turbulent transport on the soft bodied worms. Thus the body may be twisted along its axis (figure 96, plate 7). Sections may be also bent at sharp angles to the rest of the body. These specimens are referred to by a combination of orientation descriptions starting from the anterior, e.g. oblique-dorsoventral (figures 24 and 25, plate 2; figure 49, plate 4; figure 70, plate 5; figures 16 and 43); dorsoventral-(?)lateral (figure 125, plate 9). In all the polychaetes dorsoventral specimens predominate (*C. spinosa* 60 %; *B. setigera* 75 %, nearly all specimens of *P. dubia*, *I. psygma* and type A). Other orientations are less common (e.g. *C. spinosa* 25 % lateral, 15 % oblique and oblique-dorsoventral), presumably because of their instability during deposition.

Upon splitting open the rock, portions of the specimen lie on each side so that *part* and *counterpart* may be distinguished (figures 7 and 8, plate 1; figures 19, 20, 24 and 25, plate 2; figures 31 and 32, plate 3; figures 4, 15, 16 and 27). Their definition in *C. spinosa* and *I. psygma* follows Whittington (1975*a*, *b*). In dorsoventral and oblique specimens the side which has the original life orientation with the notosetae overlying the neurosetae is defined as the part. In the counterpart, of course, the neurosetae overlie the notosetae. Moreover, in *C. spinosa* the fascicles of notosetae formed an imbricate series. In the part therefore, the imbrication is in the life position with anterior fascicle overlapping posterior, whereas it is reversed in the counterpart. In lateral specimens the side which has the prostomium to the left is taken as the part. In the other polychaete species distinction between part and counterpart cannot be made in the same manner. This is because in *B. setigera* the notosetae cannot be distinguished from the neurosetae, while the remaining polychaetes (*P. dubia*, *S. argutus*, type A) are uniramous and the parapodia lie on a single bedding plane. Dorsal and ventral aspects cannot, therefore, be differentiated. The part is chosen on the basis of completeness and superior preservation. The counterpart is usually represented by a fainter and more residual film. Among these latter polychaetes, if only one side is known it is automatically regarded as the part.

4. Methods of study

Specimens were examined under a microscope and where necessary drawn with a camera lucida attachment. A microdrill was used to excavate parts of the body hidden by overlying sediment or other parts of the body (cf. figures 49 and 50, plate 4; figure 43). With the exception of figures 128–131, plate 9, which were photographed in ordinary white light, all the photographs were taken in either high or low angle u.v. radiation from a directional lamp. In high angle, the lamp was inclined to the specimen table at about 65°. The specimen was then tilted towards the lamp through about 10° until maximum reflectivity, as observed down the focusing tube, was obtained. In low angle, the specimen was placed horizontally and the angle of incident light was about 30°. After the specimen had been orientated correctly focusing was undertaken in ordinary white light. The differences in the angle of incident light accentuate different features of a specimen (cf. figures 7 and 8, plate 1; figures 56 and 57, plate 4; figures 116 and 117, plate 8). The explanation of the plate-figures is as follows: depository and specimen number; part or counterpart; orientation of specimen; brief description; nature and direction of the light, the top of the page being north; magnification and finally, any additional comments. For the sake of brevity depository numbers are not used in the text itself.

Some specimens were immersed in distilled water (figure 130, plate 9) or alcohol (figures 128 and 129, plate 9). This procedure was adopted because some features of a specimen which are obscure when dry become obvious upon wetting. With the exception of figures 128 and 129, plate 9, which were taken on Ilford N5–31 film, panchromatic film was used for all plate figures. By way of explanation, some of the plate figures have corresponding camera lucida figures placed opposite to show the author's interpretation. Where necessary, features restricted to the counterpart have been combined by reversal with the drawing of the part (figures 16, 27 and 111). In these camera lucida figures and figures 1 and 3, lines with hachures indicate definite breaks in slope between adjacent parts of the specimen or the surrounding matrix, the hachures being directed downslope. Stippled areas represent rock.

5. PRESERVATION AND BURIAL

(a) *Style of preservation*

The great majority of the soft bodied Burgess Shale fossils, including the polychaetes, are apparently preserved as very thin aluminosilicate films (Conway Morris 1977*b*). Areas within the film that are darker than the surrounding matrix in low angle light and are non-reflective in high angle light, may be distinguished from areas that are reflective, especially in high angle light. There is apparently no correlation between original body composition and type of preservation. Body parts which presumably had widely differing compositions – gut, muscles, eyes, setae and cuticular spines – are all preserved as reflective films in unrelated members of the fauna. The single specimen of type A is on a slightly weathered surface, but the other polychaetes are notable for their reflective preservation.

In the apodous priapulid worms from the Burgess Shale the specimens lie on a single bedding plane (Conway Morris 1977*b*). In the appendiculate forms, however, such as the arthropods, adjacent appendages or the sections of a biramous appendage are often separated by a thin layer of sediment which presumably seeped in during transport in the mudflows (Whittington 1971*a*, *b*, 1974, 1975*a*, *b*; Hughes 1975). This type of preservation with the various parts of the specimen preserved on two or more levels of microbedding, which upon splitting open are connected by steep scarps, also characterizes *C. spinosa*, *I. psygma* and most specimens of *B. setigera*. The notosetae and neurosetae of each parapodium, and often the fascicles of adjacent segments, are separated by a thin layer of sediment. The amount of sediment separating fascicles is variable and the notosetae and neurosetae can be closely adpressed. This variation in sediment infill is ascribed to the degree of turbulence during transport. Specimens of *P. dubia* are small enough to be effectively preserved on a single bed, although the fascicles of simple and acicular setae are sometimes separated by extremely fine sediment partings. The few specimens of *S. argutus* and type A are each preserved on a single bed.

Whittington (1975*a*, figure 3) demonstrated how slight variations in the plane of splitting through specimens of the enigmatic creature *Opabinia regalis* controlled which parts of the animal were exposed and which parts remained concealed from view in either the part or counterpart. The plane of splitting through a specimen is a matter of 'competition' between different parts of the body and it is dictated by three interdependent factors: (*a*) the surface area of a structure (e.g. a seta), (*b*) its thickness and (*c*) its angle to the bedding. The effect of these controlling factors may be recognized in most Burgess Shale fossils. They help to explain, for example, why the gills are so rarely exposed in lateral and oblique-lateral specimens of *O. regalis* (see Whittington 1975*a*, pp. 8–10, 38).

The influence of these controls is illustrated here by reference to dorsoventral specimens of *C. spinosa* (figure 1). The trunk occupies the axis of the specimen and is flanked by notosetae, while along the edges of the body the distal sections of the neurosetae are exposed. The trunk, notosetae and neurosetae each occupies different bedding planes connected by steep scarps. Even after some rotting the trunk, which presumably housed the relatively massive longitudinal muscles and gut, formed a thicker layer than the overlying proximal notosetae and so determined the split. The proximal notosetae are, therefore, often obscured by the trunk although they may be revealed by excavation (figure 60, plate 4). Where the proximal notosetae are exposed by the original split, as in the anterior and posterior of 198722 (figure 30, plate 3), the trunk had probably undergone considerable decay. The setae, which were presumably more

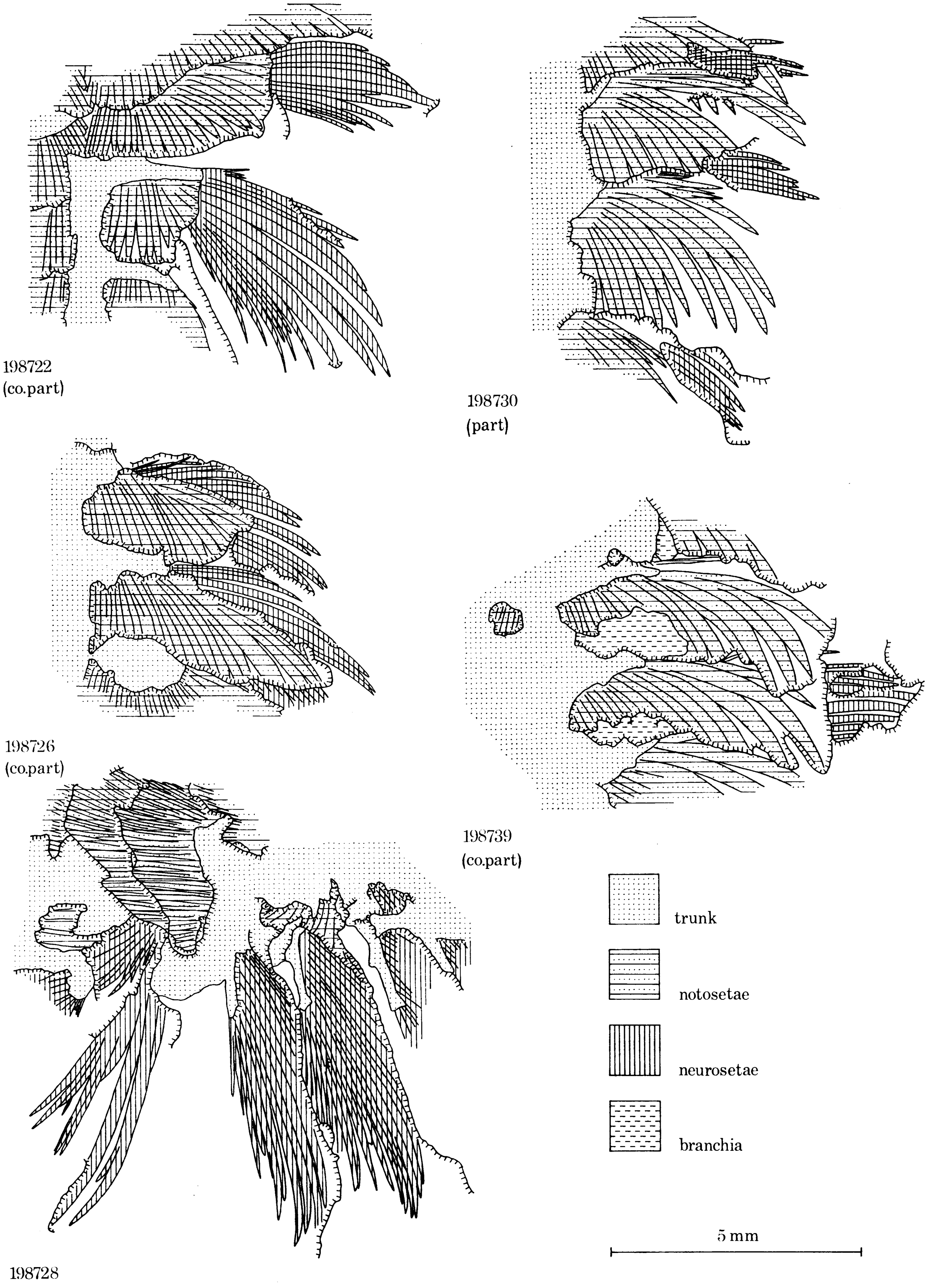


FIGURE 1. Camera lucida drawings of dorsoventrally (U.S.N.M. 198722, see figure 30, plate 3; 198726, see figure 47, plate 4; 198730; 198739) and laterally (U.S.N.M. 198728, see figure 51, plate 4) preserved specimens of *Canadia spinosa* Walcott. Each part of the body (trunk, notosetae, neurosetae and branchia) is preserved on a different level and the figure shows their distributional pattern as a result of splitting. The factors controlling the level at which the split passed through the specimens are discussed in §5*a*.

resistant to decay (see Schäfer 1972, pp. 176–177), could then control splitting. In contracted specimens the trunk was greatly thickened and it exerted an influence on splitting far beyond its usual limits (figure 23, plate 2). In uncontracted specimens the trunk projected abaxially into the parapodia; the broad notosetae, which are preserved parallel to the bedding, influence the split so that the parapodia are only indifferently exposed. The scarp connecting the trunk and notosetae is sometimes interrupted by an intermediate level exposing the branchia (198739, figure 1). Only the midlength of the adaxial notosetae is normally revealed. The proximal and distal sections are buried beneath the imbricating notosetae of the anterior (in the part) and posterior (in the counterpart) of the adjacent segments. By excavating these hidden sections and superimposing part and counterpart the entire fascicle of notosetae can be reconstructed (figure 27). The large abaxial notosetae extended away from the body and are completely exposed in some specimens. The fascicles of narrower neurosetae are not preserved parallel to the bedding and it is only where they protrude beyond the rest of the body that they can govern the split. In consequence the proximal sections of the neurosetae are usually hidden. However, the neurosetae of some of the posterior segments are enlarged and exert more control on the splitting than the reduced notosetae.

This overall pattern of splitting in a dorsoventral specimen of *C. spinosa* is complicated by local circumstances and no two segments are exposed exactly alike (figure 1). Exposure of the trunk and neurosetae is particularly variable. Burial of a dorsoventral specimen at a slight angle to the bedding, for instance, may result in the neurosetae being best exposed along one side of the body (figures 7 and 8, plate 1; figure 47, plate 4; figures 4 and 42). Curvature of the body may also cause a fascicle to be completely exposed (figure 9, plate 1; figure 39, plate 3). Changes in the orientation of the body along its length with respect to the bedding also determine exposure: in 198727 (figure 49, plate 4; figure 43) the posterior segments have been bent towards the observer so that the neurosetae are parallel to the bedding and dictate the splitting. In lateral specimens the notosetae are usually indifferently exposed (but see figure 5, plate 1) and the trunk often governs the split over wide areas of the body (figure 11, plate 1; figures 19 and 20, plate 2; figure 51, plate 4; figures 15 and 44).

In *B. setigera* the pattern of splitting is less complex. The body and fascicle, e.g. the notosetae, lie on one plane. If the other fascicle, i.e. the neurosetae, underlies the notosetae of the same parapodium, they are separated by a scarp (figure 71, plate 5). However, when the two fascicles of a parapodium diverge widely, the slope connecting them is usually continuous without a sharp break (figure 74, plate 5; figure 85, plate 6; figures 66 and 80). Scarps may separate the fascicles of adjacent segments, although it is only in contracted (figures 84 and 85, plate 6; figure 80) and curved (figure 74, plate 5; figure 97, plate 7; figure 66) specimens that the fascicles of adjacent segments actually overlap. The facing direction of the scarps is constant for each side of a specimen. Typically the scarp between the two fascicles of a parapodium is in the opposite sense to the scarp connecting the fascicles of adjacent segments.

(*b*) *History of transport and burial*

The variable orientation of specimens of *Marrella splendens* (Arthropoda) to the bedding and the separation of adjacent appendages from each other and the cephalic shield by thin layers of matrix, led Whittington (1971 *a*, *b*) to postulate that sediment clouds or mudflows catastrophically overwhelmed and transported the specimens downslope for a short but unspecified distance prior to deposition. Subsequent investigations on the sedimentology (Piper 1972) and other members of the Burgess Shale fauna (Whittington 1974, 1975*a*, *b*, 1977; Hughes 1975; Briggs 1976; Conway Morris 1976*b*, 1977*a*, *b*) have confirmed that most, if not all, benthonic forms underwent this history of burial. The epifaunal and nektobenthonic elements of the fauna could have been caught up at any point along the path of the mudflows. The presence, however, of a large number of priapulid worms, which were burrowers (Conway Morris 1977*b*), suggests that they were present from the inception of the mudflows and inhabited the muddy sediments that subsequently became unstable and slid downslope. The possibility that these and other infaunal species were eroded out by the mudflows is considered to be slight. With the exception of pelagic species it seems likely that the entire biota probably lived in the same area because certain species, e.g. *Ottoia prolifica* (Priapulida) and *M. splendens* (Arthropoda) extend through most or all of the Phyllopod bed (Whittington 1971*a*, *b*; Conway Morris 1977*b*, 1979). The fluctuations in abundance of many species through the Phyllopod bed (see Whittington 1971*a*, figure 5, 1971*b*, figure 1; Hughes 1975, figure 1; Conway Morris 1977*b*, figures 3, 18, herein figure 2) may reflect original abundances on the sea floor.

An indication of the distance the fauna was transported may be ascertained. The biota of the Burgess Shale includes apparently benthonic algae which presumably coexisted with the fauna (Walcott 1919). The depth of deposition of the Phyllopod bed was about 160 m (530 ft) (see Fritz 1971) and it is assumed here that the photic zone extended to a depth of about 91 m (300 ft) in keeping with values for clear oceanic water today. The minimum vertical distance of transport was therefore about 70 m (230 ft). Taking values of 1°, 10°, 25°, 50° and 80° for a slope of constant angle, the minimum distance of transport would have been about 4017 m (13180 ft), 404 m (1325 ft), 166 m (545 ft), 91 m (300 ft) and 71 m (235 ft) respectively.

The lack of bioturbation and scavenging and the exquisite preservation with only limited decay suggest that conditions in the Phyllopod bed were anaerobic (Whittington 1971*a*). Such a state may have arisen from the presence of hydrogen sulphide (H_2S) and it is supposed that the H_2S/O_2 boundary lay above the sediment-water interface. The Phyllopod bed where the mudflows were deposited formed the poisoned *post-slide environment*. Prior to transport and burial, the biota occupied an oxygenated *pre-slide environment*. Some modern polychaetes coil tightly during prolonged periods of anaerobiosis (Dean, Ronkin & Hoffman 1964); coiling, especially closely, of the Burgess Shale polychaetes is rare (less than 5%; figures 31 and 32, plate 3; figure 74, plate 5; figure 97, plate 7; figure 112, plate 8; figures 27 and 66) and there is no evidence of escape trails. The specimens therefore appear to have been killed during or shortly after burial. Reasons for this rapid death remain obscure. Cisne (1973) postulated that the thermal shock of a relatively warm mudflow overwhelming a coldwater fauna could account for the preservation of trilobite soft parts in the Ordovician Frankfort Shale ('Beecher's Trilobite Bed') of Rome, New York. Since at least the infaunal component of the Burgess Shale fauna was presumably present at the inception of the mudflows and therefore acclimatized exactly the same explanation seems unlikely. An analogous situation, however, may have arisen if the post- and pre-slide environments were separated by a thermocline. As the mudflows crossed the thermocline the fauna may have perished owing to temperature shock, although Cisne (1973) proposed that thermal shock only stunned the trilobites.

After burial and death anaerobic decay commenced. Anaerobic decay, especially at low temperatures, is much slower than aerobic decay (Hecht 1933; Zangerl & Richardson 1963). Nevertheless the first stages of fossilization must have included the relatively rapid removal of the specimens from the effects of decay. Decay was usually slight (see §9) and the reasons for the exquisite preservation remain uncertain. The fineness of the sediment, rapid burial, anaerobic conditions and protection from the subsequent stresses of tectonic deformation by the surrounding massive carbonates (Whittington 1971*a*, Piper 1972, McIlreath 1975) were all undoubtedly contributory factors. Nevertheless such conditions have surely been established often enough in the geological record to make the occurrence of soft bodied fossils more common than has been observed. Some additional factor must be invoked. One possibility is that a mineralizing solution, perhaps of a siliceous nature, influxed the Burgess Shale shortly after deposition and impregnated the soft tissues. The source of this solution remains obscure. Hecht (1933) noted that the flesh of a fish left to decay anaerobically became waterlogged after about a year, although the slightest disturbance resulted in its collapse. He commented that in such a state, the soft parts were in a condition suitable for impregnation by mineral solutions.

(*c*) *The effects of decay versus sedimentary compaction*

Zangerl & Richardson (1963) and Zangerl (1971) discussed factors involved in extraordinarily perfect preservation of fossils, principally fish from Carboniferous sediments of Illinois. They presented various lines of evidence that showed that although the fish appear to have been squashed flat, very little sedimentary compaction had occurred. In particular they noted that air filled bone cavities, sometimes containing uncrushed denticles, had persisted. Zangerl (1971) deduced that decay, which would have proceeded to completion long before sufficient sedimentary overburden had accumulated, was responsible for the collapse of the fish bodies. Whittington (1975*a*) did not support an application of Zangerl's observations to the Burgess Shale fossils on the grounds that unlike the fossil fish they do not lie on a single bedding plane. Such a distinction is, however, merely a reflection of the different modes of burial; the fish simply falling to the bottom whereas the Burgess Shale fossils were transported in mudflows. The author agrees, therefore, with Zangerl (1971) that as decay rates so far exceed the highest observed sedimentation rates, the former mechanism must be particularly relevant to an understanding of the preservation of soft parts in the Burgess Shale.

In his reinvestigations of members of the Burgess Shale fauna Whittington (1971*a*, *b*, 1974, 1975*a*, *b*) invoked, however, the mechanism of vertical compaction by sedimentary overburden as an important factor in the following preservational features:

(*a*) Some members of the fauna, including many of the polychaetes, have a dark stain associated with them. The earlier view that the stain represents body material squeezed out by superincumbent strata (Whittington 1971*a*, *b*, 1974; Hughes 1975) is considered unlikely. In §9 and elsewhere (Conway Morris 1976*b*, 1977*a*, *b*) the dark stain is reinterpreted as resulting from the leakage of body contents during decay.

(*b*) Whittington (1975*a*, pp. 10 and 11) also attributed the vertical flattening of the fossils without lateral spread in part to sedimentary compaction. He drew attention to Walton (1936) who reached similar conclusions when studying the flattening of fossil plants. Walton discussed, however, the effects of compaction on waterlogged (up to 90 %) and often rotten plant material that was flattened by simple expulsion of the interstitial water. Moreover, in a study of a well preserved Carboniferous biota Zangerl & Richardson (1963) attributed the flattening of logs and sticks to decay because the associated vertebrate remains showed no evidence of crushing. Strong evidence that some decay almost invariably occurred in the Burgess Shale priapulids (Conway Morris 1977*b*) suggests that in all the soft bodied animals some collapse took place prior to sedimentary compaction. A similar conclusion was reached by Johnson & Richardson

(1969) and Richardson & Johnson (1971) in their examination of the soft bodied fauna from the Francis Creek Shale (Carboniferous) of Illinois. Sedimentary compaction presumably completed the flattening of the soft parts (Whittington 1975*a*, figure 2) and its significance with respect to body parts which were decay resistant was considerable. For example, Whittington (1975*b*) documented a pronounced reduction in the convexity without notable cracking of the exoskeleton of *Olenoides serratus* (Trilobita).

(*c*) The walking legs and coxae of *O. serratus* (Whittington 1975*b*) and the walking legs of *Burgessia bella* (Arthropoda) (Hughes 1975) are rotated from their life position either forwards or backwards through 90° so that the broad faces lie parallel to the bedding. Whittington proposed that this rotation had the dual origin of sedimentary compaction (see also Hughes 1975) facilitated by decay loosening the muscles and ligaments which supported the legs.

The absence of the gut and muscles in all specimens of *O. serratus* which possess appendages indicates that these specimens suffered considerable decay (Whittington 1975*b*). Whittington noted that in addition to being rotated, the appendages were also displaced as a single unit from their life position and he suggested that detachment from the exoskeleton arose during decay. Whittington (1975*b*) was aware of the possible effects of turbulent transport in *O. serratus* and he suggested (p. 104) that 'The way the appendages of one side of *O. serratus* were swept under the body...presumably reflects the effects of transportation'. The author would propose further that the greater part of the displacement and rotation of the appendages also took place during turbulent transport rather than during sedimentary compaction. One objection to the latter mechanism with respect to rotation is that in dorsal specimens the exoskeleton overlies the proximal section of the leg and would presumably have acted as a protective shield during compaction. Nevertheless, equal rotation occurred along the entire length of the leg. If displacement and rotation took place during transport the specimens of *O. serratus* presumably were dead and had begun to rot in the pre-slide environment. Other members of the Burgess Shale fauna, however, appear to have been transported alive (Conway Morris 1977*b*). It is possible that owing to their large size the specimens of *O. serratus* were transported and deposited several times by mudflows and were only finally entombed after decay was advanced. In his restudy of *Naraoia compacta*, Whittington (1977) suggested that turbulence may have modified the position of the limbs, but he continued to emphasize the importance of compaction.

Examination of *C. spinosa* appears to support the suggestion that rotation of the legs of *O. serratus* and *B. bella* probably occurred during transport. In *C. spinosa* the neurosetae apparently projected ventrally at about 45° to the sagittal plane in fascicles that were shallowly inclined to the transverse plane of the body. Rotation in dorsoventral and lateral specimens of the fascicle of neurosetae by compaction of superincumbent strata has not been noted and the neurosetae are almost invariable clumped. The amount of clumping presumably depends upon the angle of burial of the fascicle and the body itself to the bedding. Whittington (1977, figure 1, *c–e*) documented a similar feature amongst the limbs of *N. compacta* and noted how their shape varies according to the angle of burial, with respect to the bedding. In extreme cases the fascicle forms a narrow reflective mass in which it is not easy to trace individual setae (figure 37, plate 3, figure 28). Using suitably orientated specimens of average length (3 cm) the width of the fascicle of neurosetae is measured as about 3.5 mm. By assuming that the fascicle underwent no lateral distortion, its angle of burial can be estimated by comparing the observed fascicle width with the original value of 3.5 mm. The angle of burial can reach about 80° and in any specimen the exact angle varies along the length of the animal. No vertically orientated fascicle has been observed, presumably because the neurosetae did not lie in a single plane and the fascicle was always preserved at least slightly obliquely to the bedding. It is concluded that the life orientation of the neurosetae has been effectively maintained and little or no rotation has occurred as a result of sedimentary compaction, although their subsequent crushing together may be attributed to compaction. The absence of rotation of the neurosetae in *C. spinosa* is probably because there are, unlike *O. serratus*, no anatomical features that would have allowed the neurosetae to become largely detached from the rest of the body by decay and rotated during transport.

6. Association of polychaetes with other Burgess Shale species

In both the G.S.C. and U.S.N.M. collections the majority of specimens are isolated on small sawn blocks and association with other species is uncommon. *C. spinosa* occurs with the ubiquitous *Marrella splendens* (Arthropoda), and also *Yohoia tenuis* (Arthropoda), *Pikaia gracilens* (Chordata), *Ottoia prolifica* (Priapulida) and *Scenella* (Mollusca). *B. setigera* is often associated with the alga *Morania confluens* (Walcott 1919). It is probable that these two species co-existed in the pre-slide environment although it is unknown whether *B. setigera* directly benefitted from the alga. This polychaete is also associated with *Y. tenuis* (Whittington 1974), *M. splendens*, *Burgessia bella* (Arthropoda), *Naraoia compacta* (Trilobita, Whittington 1977) and *Selkirkia columbia* (Priapulida). *P. dubia* is associated with *M. splendens* as well as scattered scales of *Wiwaxia corrugata* and algal fragments. Type A is associated with agnostid trilobites. *I. psygma* is on an isolated slab.

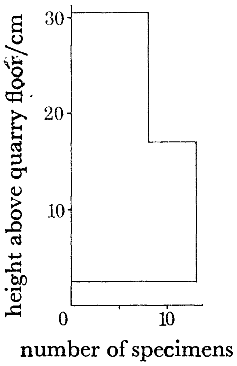


FIGURE 2. Vertical distribution of 21 G.S.C. specimens of *Burgessochaeta setigera* (Walcott) gen. nov. from the Phyllopod bed (Burgess Shale) which is exposed in the Walcott Quarry. The base of the quarry is defined as 0 cm.

7. Vertical distribution of polychaetes within the Phyllopod bed

Walcott (1912*a*, *b*) divided the 2.31 m (7 ft 7 in) thick Phyllopod bed into twelve levels of varying fossil content and thickness. His comments on the vertical distribution of species were unfortunately brief. The G.S.C. expeditions, however, noted the vertical height of each specimen, the base of the quarry being at 0 cm. Walcott (1912*a*) stated that *C. spinosa* and *B. setigera* were found in level 10 (7.6–48.3 cm (0 ft 3 in–1 ft 7 in)), whilst the former species of polychaete was also recovered from the basal level 12 (0–3.8 cm (0 ft 0 in–0 ft 1.5 in)). The three G.S.C. specimens of *C. spinosa* are from 45.7–61 cm (1 ft 6 in –2 ft 0 in), 58.4–61 cm

(1 ft 11 in–2 ft 0 in) and 91.4–109.2 cm (3 ft 0 in–3 ft 7 in) respectively. The known range of *C. spinosa* is, therefore, 0–109.2 cm (0 ft 0 in–3 ft 7 in). Walcott (1912*a*) indicated that this species was commonest in the basal 3.8 cm (1.5 in). The vertical distribution of the G.S.C. specimens of *B. setigera* is shown in figure 2. The known range of *B. setigera* is 2.5–48.3 cm (0 ft 1 in–1 ft 7 in). All the U.S.N.M. specimens of *P. dubia*, *I. psygma*, *S. argutus* and type A are labelled '35k' and so presumably originate from the Walcott quarry. Nothing is known, however, about their vertical distribution.

8. SYSTEMATIC DESCRIPTIONS

(*a*) *Problems of nomenclature*

Walcott's (1911*c*) description of *C. irregularis* as 'A small slender species not over 20 mm. in length. The setae are irregular in size and appearance and suggest partially worn macerated specimens of the slender forms of *C. setigera*', clearly does not correspond with the specimens illustrated as *C. irregularis* by Walcott (1931) and these particular specimens (figures 21 and 22, plate 2) are referred as junior synonyms to *C. spinosa* (see §8*b*, i). This description of *C. irregularis* does, however, closely apply to the specimens of *C. dubia* (now *Peronochaeta dubia* (Walcott) gen. nov.) that were illustrated by Walcott in 1931 (herein figures 101–103, plate 7; figure 94). The description by Walcott (1911*c*) of *C. dubia* as 'a small chaetiferous annelid not over 10 mm. in length. One specimen shows a bundle of very fine setae on each side near the head', is an accurate description of *C. simplex* (now *Lecythioscopa simplex* (Walcott), (see Conway Morris 1977*b*, plate 28, figures 5 and 6)) which was illustrated in 1931. The trivial name *dubia* suggests, furthermore, that Walcott was uncertain about placing the species in *Canadia*. It seems likely, but is impossible to prove, that the illustrations of *C. dubia* (Walcott 1931) should apply to the description of *C. irregularis* (Walcott 1911*c*), and the illustration of *C. simplex* (Walcott 1931) to the description of *C. dubia* (Walcott 1911*c*). This confusion may have arisen as Resser worked from unfinished notes whilst preparing the posthumous paper by Walcott (1931).

(*b*) Canadia spinosa *Walcott*

Phylum ANNELIDA Lamarck, 1802
Class POLYCHAETA Grube, 1850
Family CANADIIDAE Walcott, 1911; nom. correct Howell 1962

Diagnosis. Prostomium with tentacles. Segment 1 with uniramous parapodia, all other segments with biramous parapodia bearing flattened notosetae which cover the dorsum and fan shaped ascicles of simple neurosetae. Branchiae present.

Genus *CANADIA* Walcott, 1911

Type (*and only known*) *species*. *Canadia spinosa* Walcott, 1911. Original designation pp. 118–119.

Diagnosis. Body about 3 cm long, slightly dorsoventrally flattened. Quadrate prostomium with pair of long, usually recurved, tentacles arising from anterior (? dorsal) corners. Trunk of between twenty and twenty-two segments. Segment 1 with parapodia lacking neurosetae, remainder biramous. Notosetae arise from transversely elongate notopodium and cover the entire dorsum, slightly overlapping along the midline. Adaxial notosetae symmetrical, but abaxially they become longer, broader and curved towards midline. Largest notosetae with serrated abaxial edge. Most abaxial notosetae imperfectly formed. Notosetae of parapodia of two posteriormost segments reduced and lack asymmetrical setae. From about segment 4 to penultimate segment branchiae arise beneath notopodia. Neurosetae arise from lobate podium in a fan shaped fascicle. Neurosetae of parapodium of about four posterior segments more elongate and broader than normal, with serrated abaxial margin. Neurosetae of parapodia of posteriormost segments reduced. Straight gut with eversible unarmed proboscis.

Canadia spinosa Walcott, 1911

Figures 1 and 3; figures 5–14, plate 1; figures 17–26, plate 2; figures 29–41, plate 3; figures 47–63, plate 4; figures, 4, 15, 16, 27, 28, 42–46 and 64.

1911*c*	*Canadia spinosa*	Walcott pp. 118–119, plate 23, figures 4–7.
?1911*c*	*Canadia irregularis*	Walcott pp. 118 and 120.
1912*a*	*Canadia spinosa*	Walcott pp. 152, 153 and 162.
1912*b*	*Canadia spinosa*	Walcott p. 190.
?1912*b*	*Canadia irregularis*	Walcott p. 190.
1912	*Canadia spinosa*	Steinmann fig. 4B (copied Walcott 1911*c*, anterior of plate 23, figure 7).
1916	*Canadia spinosa*	Walcott plate 12, figures 4–7 (copied Walcott 1911*c*, plate 23, figures 4–7).
1931	*Canadia spinosa*	Walcott p. 4, plate 4, figures 1–3; plate 5, figures 1 and 2; plate 6, figures 1 and 2.
1931	*Canadia irregularis*	Walcott p. 5, plate 6, figures 4–6; plate 7, figure 3.
1931	*Canadia grandis*	Walcott p. 5, plate 9, figure 10.
1944	*Canadia spinosa*	Størmer p. 140, figure 27 (copied Walcott 1931, plate 4, figure 3).
1958	*Canadia spinosa*	Müller p. 388, figure 460.
1962	*Canadia spinosa*	Bock p. 112, figure 52 (copied Walcott 1911*c*, plate 23, figure 7).
1962	*Canadia spinosa*	Howell p. W165, 167, figure 106.2 (copied Walcott 1911*c*, plate 23, figure 7).
1969	*Canadia spinosa*	Robison p. 1170.

Material. Lectotype U.S.N.M. 57654. Walcott 1911*c*, plate 23, figure 7. Designated herein (figure 9, plate 1).

Paralectotypes U.S.N.M. 57651–57653, 83929*a–e*.

Other material U.S.N.M. 83932, 83933 (counterpart numbered 83934*a*), 83934*b*, 198719–198730, 198732, 198738–198742, 199655, 199758. There are about 40 other U.S.N.M. specimens. G.S.C. 8232, 45334–45336, an unnumbered specimen. B.M.N.H. A1950. R.O.M. 25871, 32571, and three unnumbered specimens. U.M. 1504.

(i) *Morphology*

The range in length (prostomium to pygidium, excluding elongate posterior neurosetae) is about 2.0–4.5 cm (average 3 cm). As *C. spinosa* and the other polychaetes were contractile (cf. figure 23, plate 2 with figure 30, plate 3; figure 84, plate 6 with figure 96, plate 7; figure 113 with figure 114, plate 8; figures 109, 110) these values are only indicative. Specimen 198742 is abnormally long (about 7.5 cm) but its attenuated nature may be due to decay

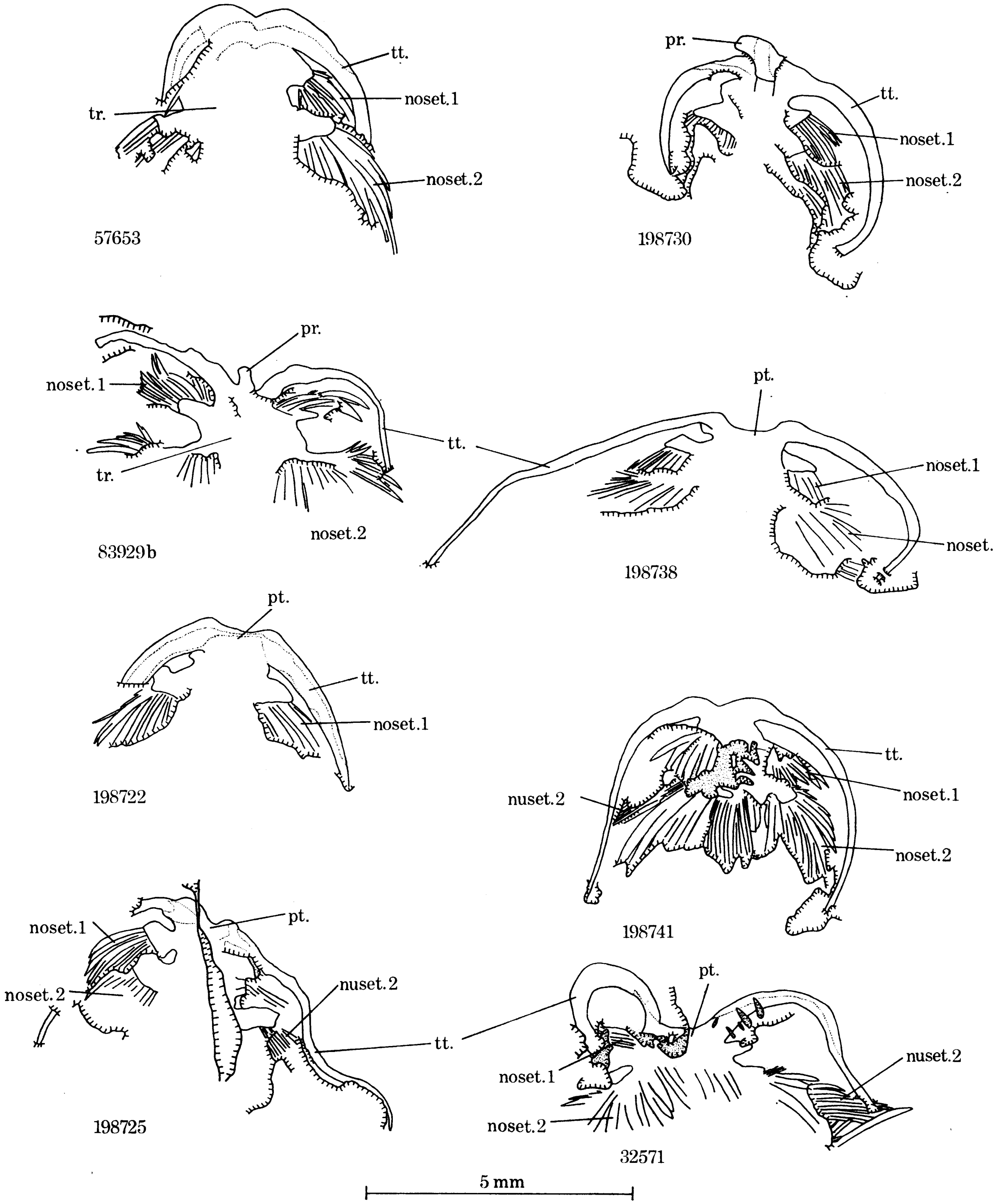
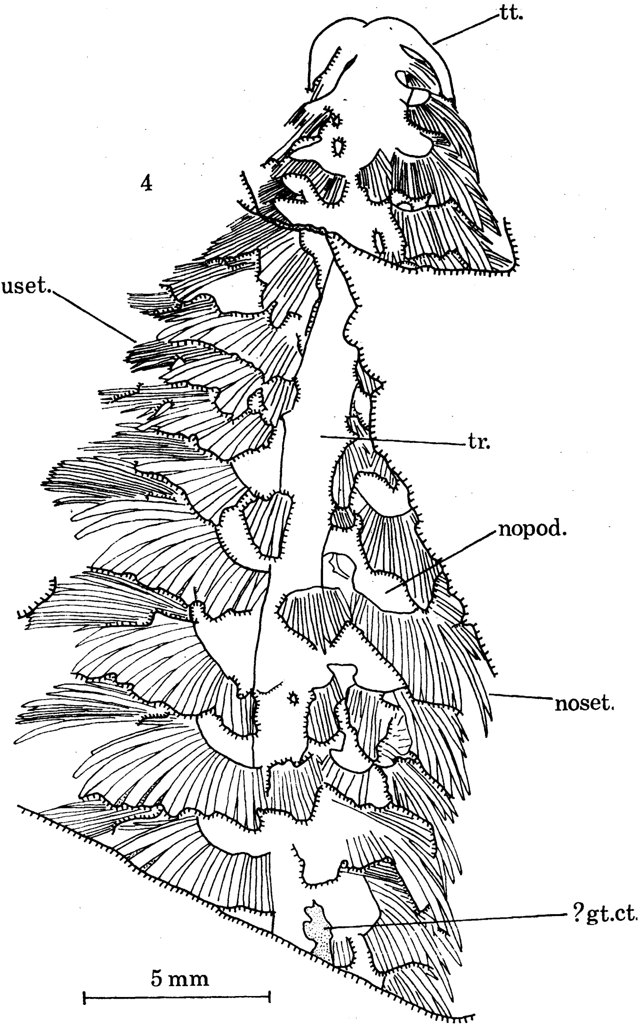


Figure 3. Camera lucida drawings of the anterior ends of dorsoventrally preserved specimens of *Canadia spinosa* Walcott (U.S.N.M. 57653, see figure 8, plate 1; 83929*b*, see figure 13, plate 1; 198722, see figure 29, plate 3; 198725, see figure 34, plate 3; 198730, see figure 52, plate 4; 198738, see figure 59, plate 4; 198741, see figure 60, plate 4; R.O.M. 32571, see figures 56 and 57, plate 4). The drawings show the variation in tentacle shape as well as the proboscis, prostomium and anterior segments in some specimens. The areas enclosed by dotted lines in 57653, 198722, 198725, 198730 and posterior to the dotted lines in 32571 represent particularly reflective areas.

(figures 53, 54, plate 4; figure 45). The absence of juvenile specimens is surprising. Whittington (1971*b*, 1974) proposed that the lack of specimens of the arthropods *Marrella splendens* and *Yohoia tenuis* less than 2.5 and 6 mm long respectively was because they were planktonic and escaped the benthonic mudflows. *C. spinosa* appears to have been well adapted for swimming and the juveniles may have had a prolonged nektonic stage that persisted until they reached about 2 cm in length. Alternatively the juvenile stages may have inhabited parts of the sea floor, such as the adjacent carbonate bank, which were not crossed by the mudflows.

The prostomium (1.5 mm wide, 0.6 mm long) is quadrate when viewed dorsoventrally (figure 29, plate 3; figure 59, plate 4; figure 3). Viewed laterally the prostomium is slender and may have been dorsoventrally compressed (figure 51, plate 4; figure 44). The overall shape of the prostomium may, therefore, have been tabloid. From the anterior corners (figure 59, plate 4; figure 3) of the prostomium two long and smooth tentacles (5–6 mm long) arose, perhaps from the dorsal side (figure 22, plate 2). Among the specimens the tentacles typically trail posteriorly but their curvature is variable. Most commonly they are arcuate with the distal tips directed adaxially (figures 6–8, plate 1; figures 29, 32 and 41, plate 3; figures 49, 52, 59, 60 and 61, plate 4; figures 3, 4, 27 and 43). In some specimens the tentacles extend laterally (figures 9 and 13, plate 1; figure 21, plate 2; figure 3) or even anteriorly before turning posteriorly (figures 56 and 57, plate 4; figure 3). In decayed specimens they project forwards (figure 17, plate 2; figures 53 and 54, plate 4; figure 45). These variations show that they they were not rigid, but although one tentacle in 198725 (figure 34, plate 3; figure 3) is flexed such an occurrence is unusual and they were probably fairly stiff in life. A marked diminution in width of the distal tip of the tentacle of specimen 198739 (figure 61, plate 4) is ascribed to the initial effects of decay. The width of the tentacles, especially of their proximal portions, varies. The slender, elongate tentacles (figure 59, plate 4; figure 3) may have been capable of contracting in life into shorter, stout tentacles (figure 29, plate 3; figure 3) that brought their bases together and gave the anterior edge of the prostomium a bilobate appearance (figures 6 and 8, plate 1; figures 60 and 61, plate 4; figures 3 and 4). The prostomial appendages of modern polychaetes do not appear to be as contractile (D. J. George, personal communication), and the proximity of the tentacle bases may also be partially controlled by the angle of burial of the prostomium in a similar manner to the variation in the anterior cephalic outline of *M. splendens* noted by Whittington (1971*a*, figure 24). In specimen 198740 the anteriormost part of the body has been bent downwards. The dorsal surface so revealed has a median protrusion (figure 62, plate 4; figure 46) which may represent part of the proboscis or even a prostomial caruncle.

The trunk consisted of about twenty to twenty-two setigerous segments. It is difficult to determine their exact number because of the smallness of the posterior segments with their reduced setae. When the ventral surface is exposed by folding back of part of the body it appears flat and featureless (figures 24 and 25, plate 2; figure 16). In specimens that have a portion of trunk flexed downwards the dorsum appears to have been gently convex (figure 23, plate 2; figure 47, plate 4; figure 42). The width of the animal increased to about segment 6 and tapered for about the five posteriormost segments. The width of the intervening segments was more or less constant: values of about 1.0–1.5 cm are typical (Walcott 1911*c*; his reading is misprinted in mm). In laterally preserved specimens the height of the body is about 4 mm. The posteriormost trunk apparently could project as a semi-naked lobe (figures 19 and 20, plate 2; figure 51, plate 4; figures 15 and 44).



Description of plate 1 and figure 4

Canadia spinosa Walcott, 1911. Phyllopod bed, Walcott Quarry.

Figure 4. U.S.N.M. 57653, explanatory drawing of part, see figures 7 and 8.

Figure 5. U.S.N.M. 57651, part; lateral, complete, high angle light from north. Portion of original of Walcott 1911*c*, (plate 23, figure 4) (magn. × 3).

Figure 6. U.S.N.M. 57652, counterpart; dorsoventral, folded over, low angle light from north. Original of Walcott 1911*c* (plate 23, figure 5) (magn. × 3).

Figures 7 and 8. U.S.N.M. 57653, dorsoventral, anterior half. Figure 7, counterpart; low angle light from southwest (magn. × 4.3) original of Walcott 1911*c* (plate 23, figure 6); figure 8, part; high angle light from northeast (magn. × 4); see also figure 3.

Figure 9. U.S.N.M. 57654, part; dorsoventral, complete, high angle light from east, lectotype (magn. × 3). Original of Walcott 1911*c* (plate 23, figure 7).

Figure 10. U.S.N.M. 83929*a*, part; oblique, complete with posterior over-lying shell of *Scenella* sp., low angle light from northeast (magn. × 2.2). Original of Walcott 1931 (plate 4, figure 1).

Figure 11. U.S.N.M. 83929*d*, counterpart; lateral, complete with proboscis everted, high angle light from north (magn. × 4.2). This is the counterpart of original of Walcott 1931 (plate 6, figure 1).

Figures 12, 13 and 14. U.S.N.M. 83929*b*, dorsoventral-oblique. Figure 12, part; complete, low angle light from north (magn. × 3.4), original of Walcott 1931 (plate 4, figures 1 and 2); figure 13, counterpart; anterior segments and prostomium with tentacles and proboscis, high angle light from northeast (magn. × 11.5), see also figure 3; figure 14, counterpart; abaxial notosetae, high angle light from east (magn. × 8).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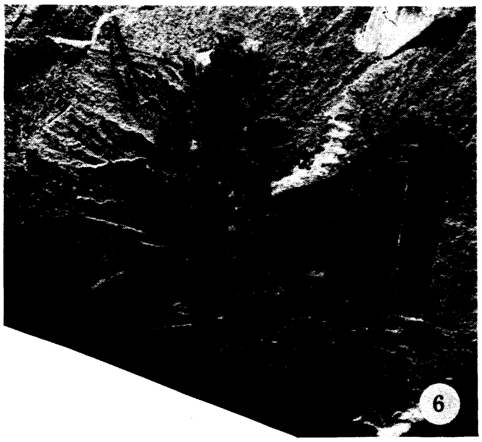
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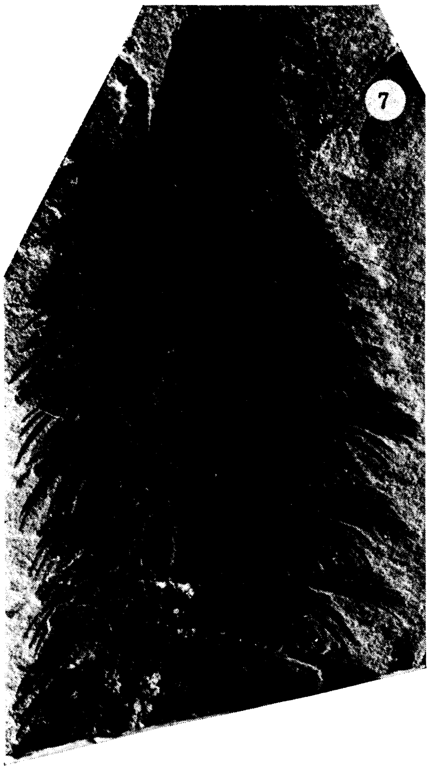
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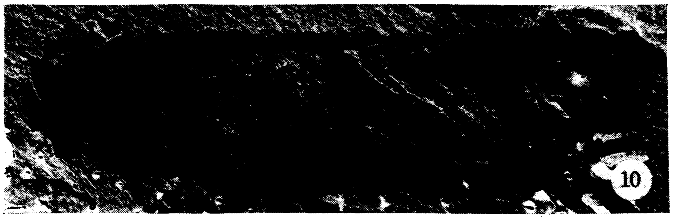
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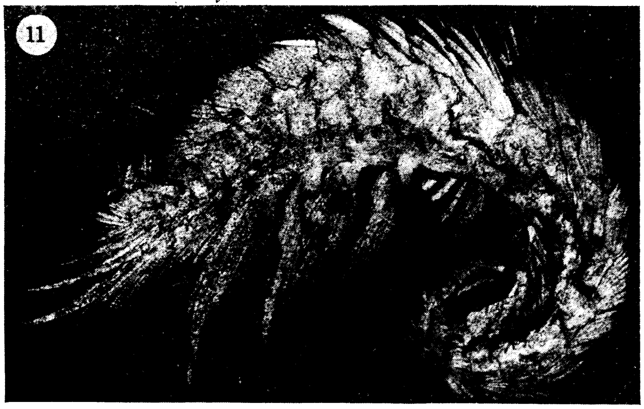
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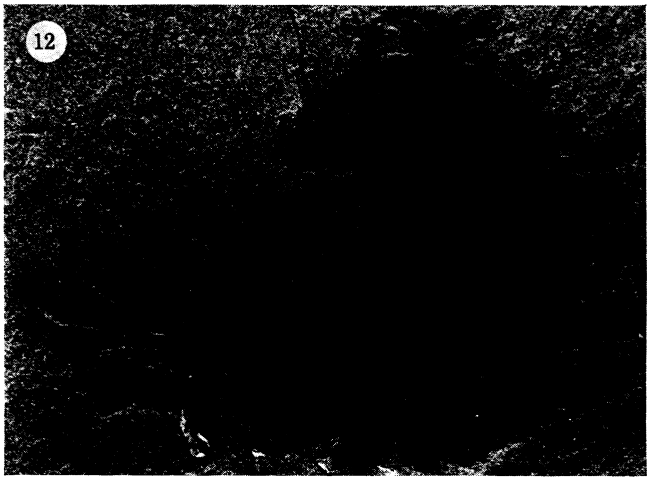
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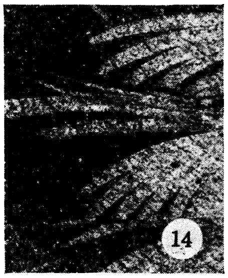
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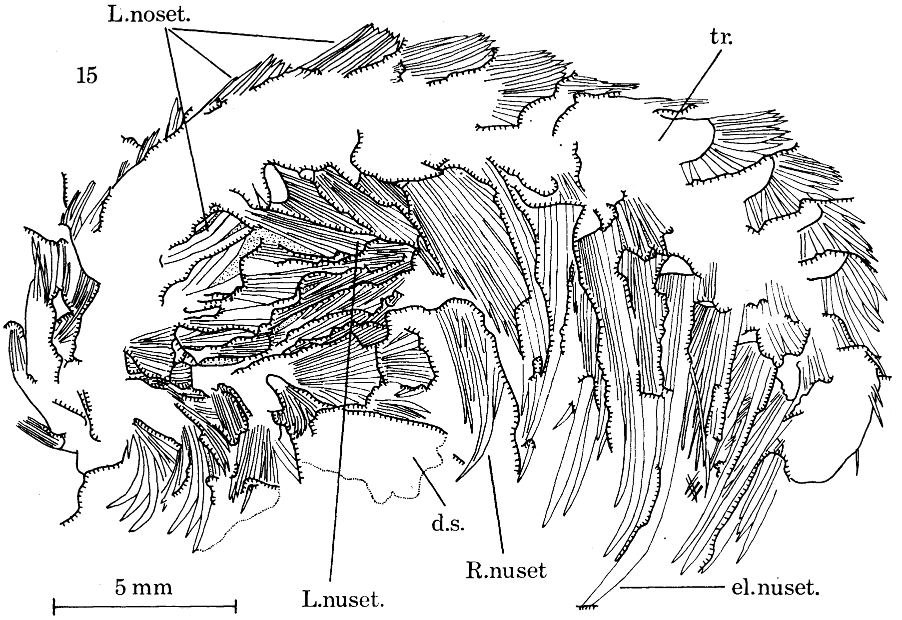
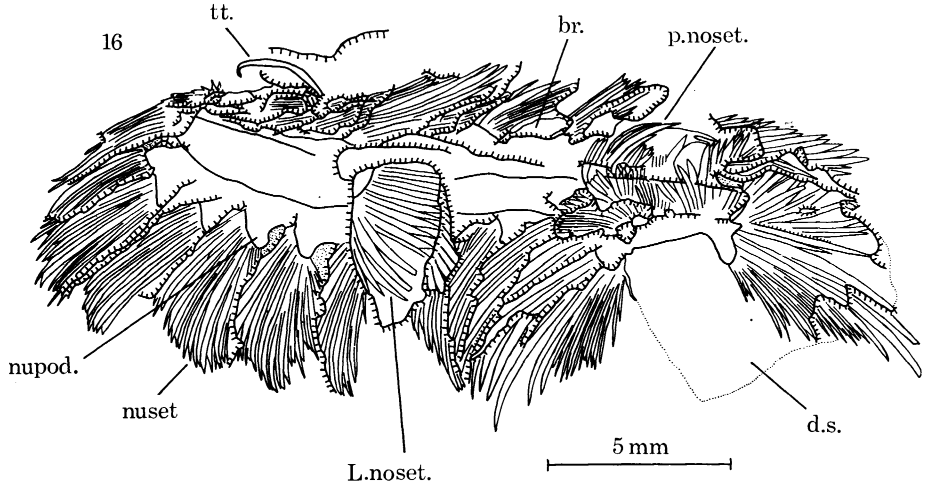
FIGURES 5–14. For description see opposite.





DESCRIPTION OF PLATE 2 AND FIGURES 15 AND 16

Canadia spinosa Walcott, 1911. Phyllopod bed, Walcott Quarry.

FIGURE 15. U.S.N.M. 83929*e*, explanatory drawing of part, see figure 20.

FIGURE 16. U.S.N.M. 198720, composite explanatory drawing of part and counterpart, see figures 24 and 25.

FIGURES 17 AND 18. U.S.N.M. 83929*c* part; dorsoventral. Figure 17, partially decayed; low angle light from west (magn. × 2.6), original of Walcott 1931 (plate 5, figures 1 and 2); figure 18, branchia, high angle light from west (magn. × 9).

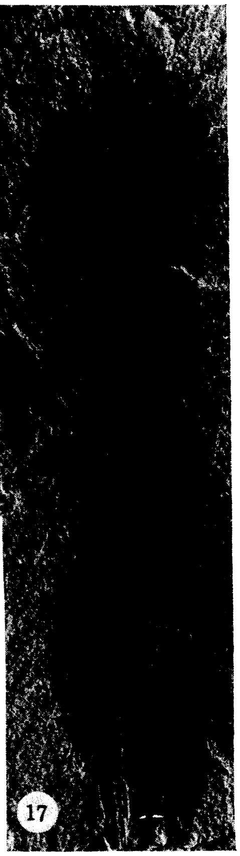
FIGURES 19 and 20. U.S.N.M. 83929*e*, complete; lateral (magn. × 3.2). Figure 19, counterpart; low angle light from south, original of Walcott 1931 (plate 6, figure 2); figure 20, part; high angle light from north.

FIGURE 21. U.S.N.M. 83934*a*, counterpart; dorsoventral, complete except for posterior tip, low angle light from east (magn. × 2.5). Original of Walcott 1931 (plate 6, figure 5).

FIGURE 22. U.S.N.M. 83934*b*, counterpart; lateral, complete with proboscis everted, high angle light from west (magn. × 3.7). Original of Walcott 1931 (plate 6, figure 6).

FIGURE 23. U.S.N.M. 83932, part; dorsoventral, anterior folded downwards, low angle light from northwest (magn. × 2). Original of Walcott 1931 (plate 9, figure 10).

FIGURES 24, 25 AND 26. U.S.N.M. 198720, oblique-dorsoventral. Figure 24, part; complete, high angle light from north (magn. × 4); figure 25, counterpart, fascicle of notosetae and posterior segments exposed by excavation, high angle light from north (magn. × 4.4); figure 26, counterpart, neurosetae arising from neuropodia, high angle light from northwest (magn. × 11).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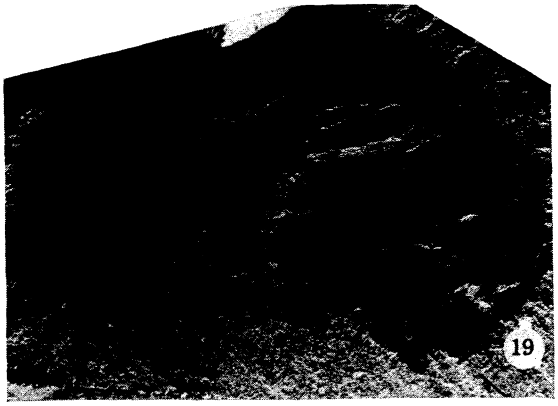
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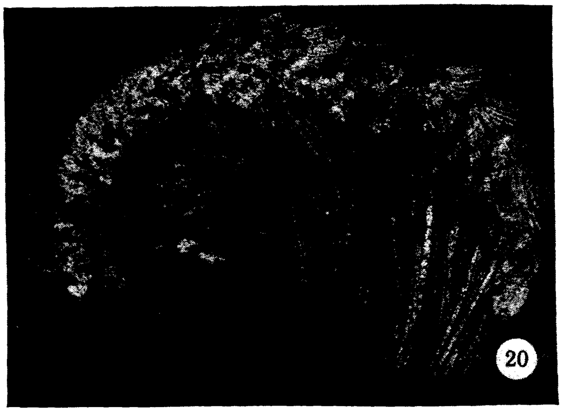
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FIGURES 17–26. For description see opposite.

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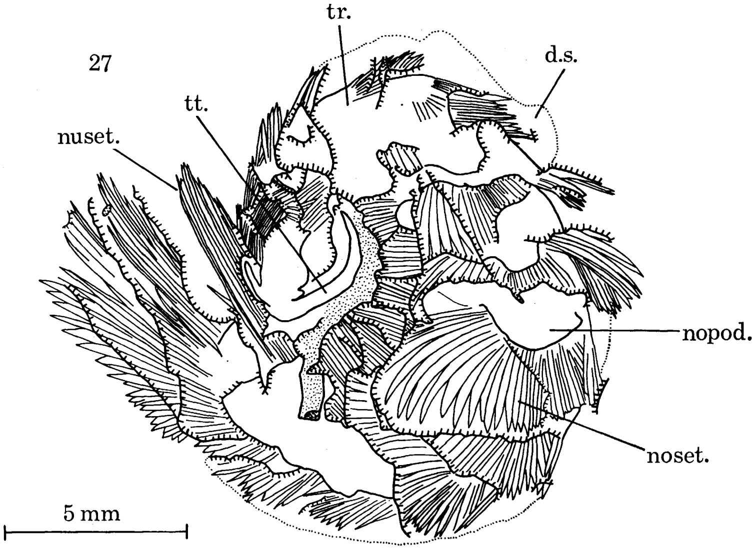

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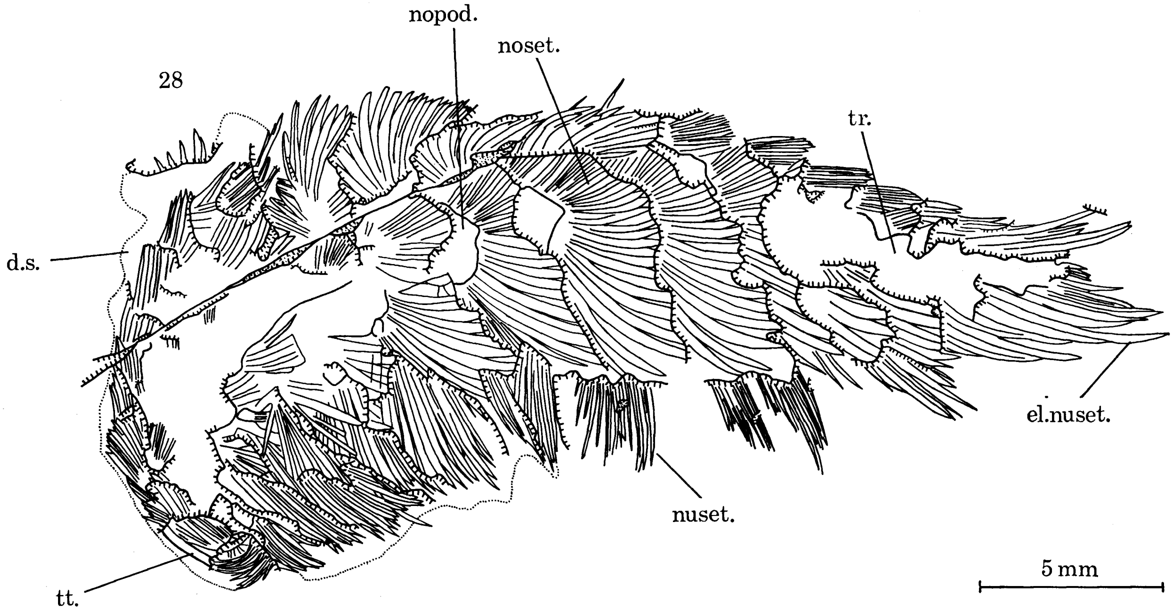


DESCRIPTION OF PLATE 3 AND FIGURES 27 AND 28

Canadia spinosa Walcott, 1911. Phyllopod bed, Walcott Quarry.

FIGURE 27. U.S.N.M. 198721, composite explanatory drawing of part and counterpart, see figures 31 and 32.

FIGURE 28. U.S.N.M. 198724, explanatory drawing of part, see figure 37.

FIGURES 29 AND 30. U.S.N.M. 198722, counterpart; dorsoventral. Figure 29, first segment and prostomium with tentacles, high angle light from northwest (magn. × 10), see also figure 3; figure 30, complete; high angle light from west (magn. × 3), see also figure 1.

FIGURES 31, 32 AND 33. U.S.N.M. 198721, lateral. Figure 31, part; tightly coiled, high angle light from east (magn. × 4); figure 32, counterpart; high angle light from east (magn. × 3.5); figure 33, part; fascicle of notosetae, high angle light from north (magn. × 15).

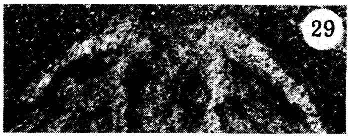
FIGURES 34, 35 AND 36. U.S.N.M. 198725, counterpart; dorsoventral. Figure 34, anterior segments and flexed prostomial tentacle, high angle light from southeast (magn. × 12), see also figure 3; figure 35, abaxial notosetae, high angle light from west (magn. × 19); figure 36, twisted neurosetae, high angle light from east (magn. × 16).

FIGURE 37. U.S.N.M. 198724, part; oblique, complete with anterior folded downwards, high angle light from south (magn. × 3).

FIGURE 38. U.S.N.M. 198723, counterpart; dorsoventral, complete with attenuated (?) proboscis extending across released decay products, high angle light from northwest (magn. × 4.8).

FIGURES 39 AND 40. U.S.N.M. 199758, counterpart; dorsoventral. Figure 39, complete except for anterior tip and posterior body semi-detached; high angle light from southwest (magn. × 3.2); figure 40, curved branchia, high angle light from south (magn. × 15).

FIGURE 41. U.S.N.M. 198729, counterpart; dorsoventral, anterior with proboscis everted and prostomial tentacle, high angle light from east (magn. × 10).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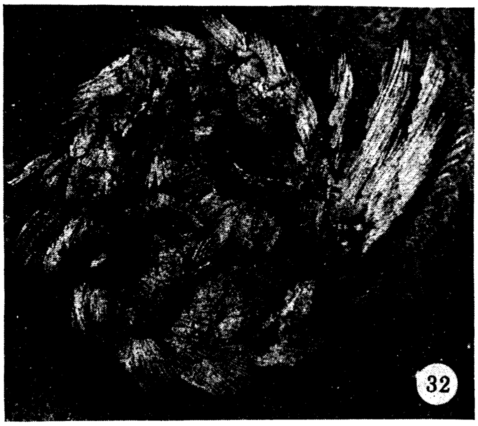
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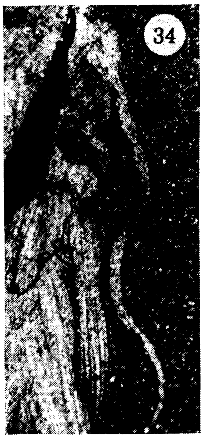
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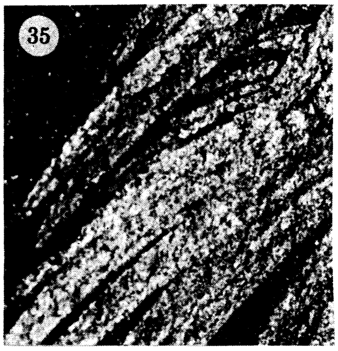
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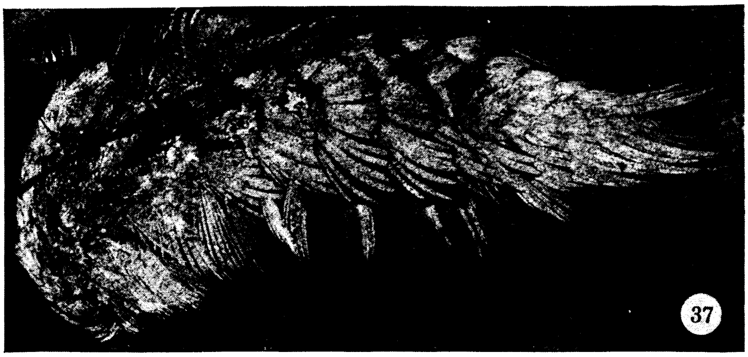
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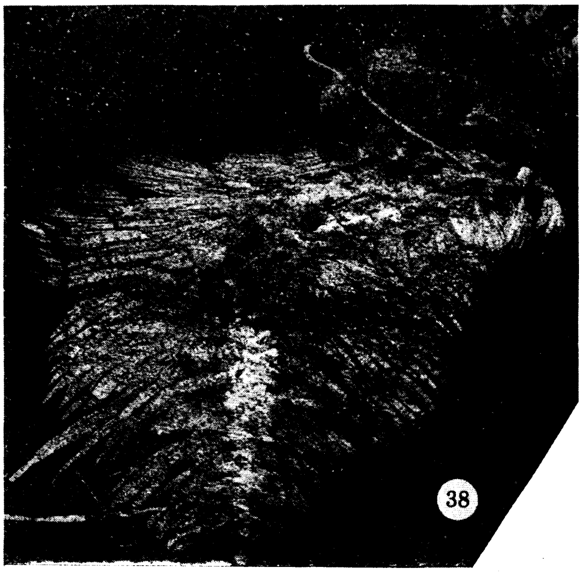
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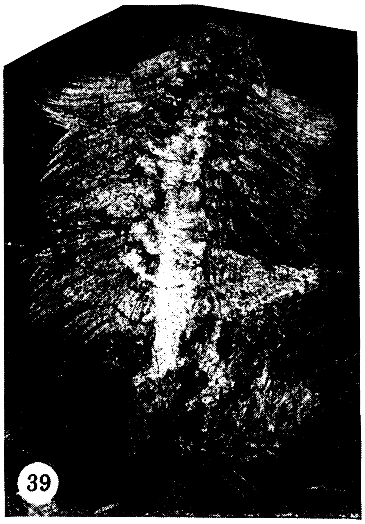
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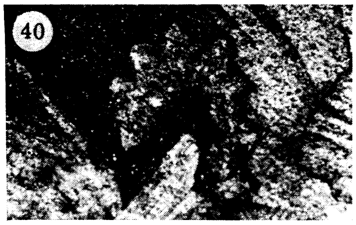
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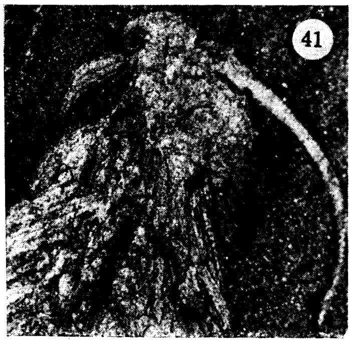
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FIGURES 29–41. For description see opposite.

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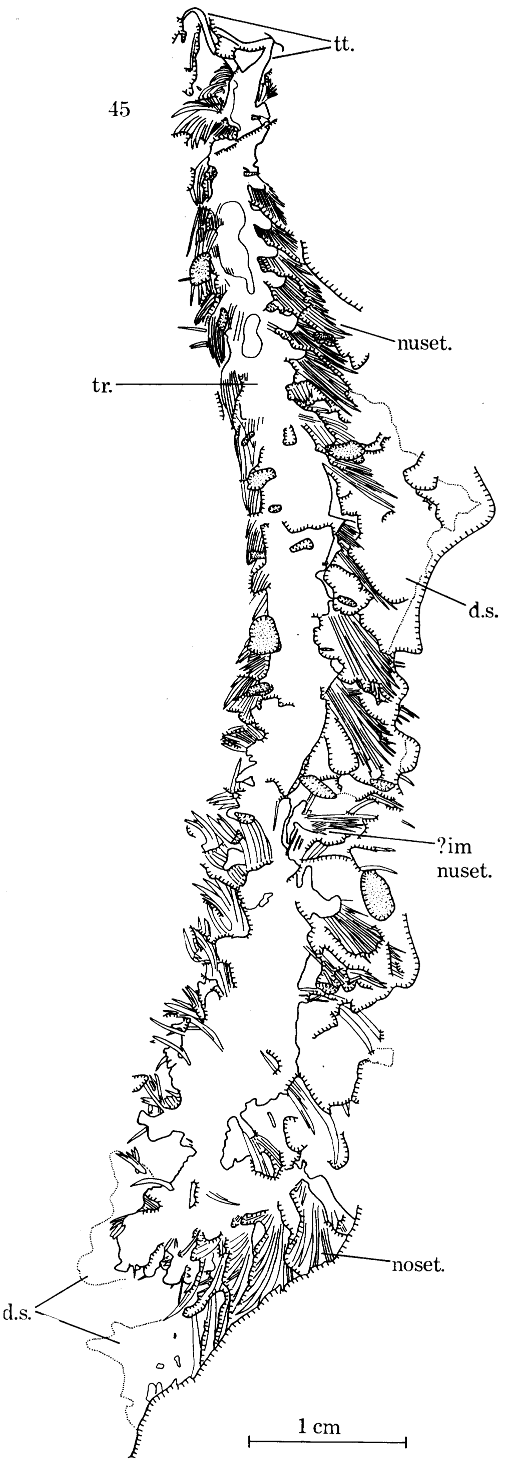

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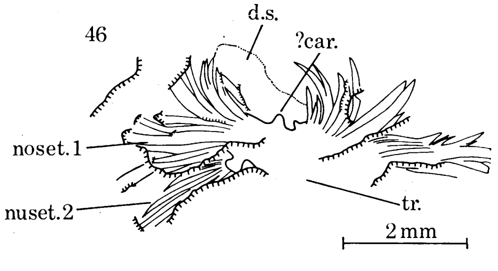


DESCRIPTION OF PLATE 4 AND FIGURES 45 AND 46

Canadia spinosa Walcott, 1911. Phyllopod bed, Walcott Quarry.

FIGURE 45. U.S.N.M. 198742, explanatory drawing of counterpart, see figures 53 and 54.

FIGURE 46. U.S.N.M. 198740, explanatory drawing of anterior of counterpart, see figure 62.

FIGURES 47 AND 48. U.S.N.M. 198726, counterpart; dorsoventral. Figure 47, anterior folded beneath posterior body, high angle light from east (magn. × 3.4); figure 48, distal section of elongate neurosetae with serrated abaxial edge, high angle light from west (magn. × 14).

FIGURES 49 AND 50. U.S.N.M. 198727, part; oblique-dorsoventral. Figure 49, complete, high angle light from north (magn. × 3.5), prior to excavation of neurosetae illustrated in figure 50; figure 50, complete parapodium with fascicles of notosetae and neurosetae separated by branchia, high angle light from east (magn. × 5.6).

FIGURE 51. U.S.N.M. 198728, counterpart; lateral, complete, high angle light from north (magn. × 3.6), see also figure 1.

FIGURE 52. U.S.N.M. 198730, counterpart; dorsoventral, anterior segments with prostomial tentacles and proboscis everted, high angle light from west (magn. × 6.6), see also figure 3.

FIGURES 53, 54 AND 55. U.S.N.M. 198742, counterpart; oblique. Figure 53, decayed with posteriormost trunk almost detached, high angle light from southwest (magn. × 1.3); figure 54, low angle light from west (magn. × 1.3); figure 55, possible imperfect neurosetae, high angle light from southeast (magn. × 9).

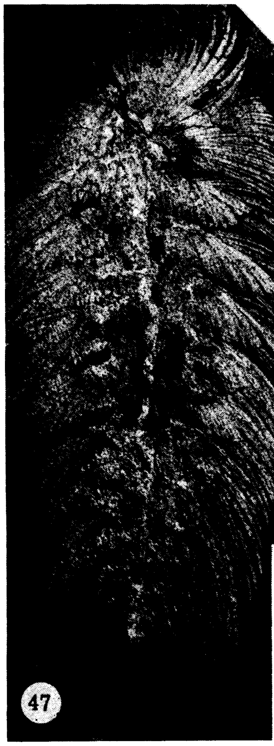
FIGURES 56, 57 AND 58. R.O.M. 32571, part; dorsoventral. Figure 56, folded over with some fascicles of setae detached by decay, low angle light from west (magn. × 2); figure 57, high angle light from west (magn. × 2), see also figure 3; figure 58, possible imperfect neurosetae, high angle light from south (magn. × 9).

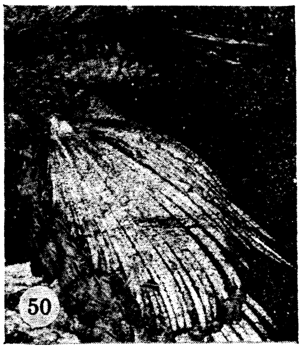
FIGURE 59. U.S.N.M. 198738, part; dorsoventral, anterior segments and prostomium with tentacles, low angle light from northeast (magn. × 4), see also figure 3.

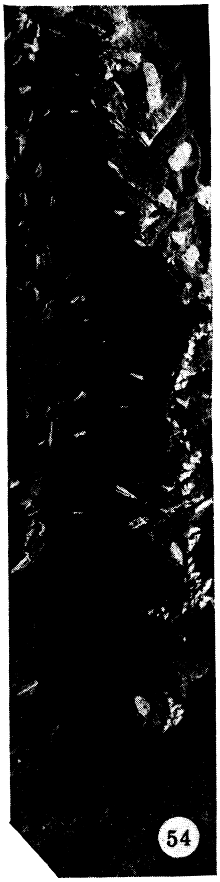
FIGURE 60. U.S.N.M. 198741, counterpart; dorsoventral, anterior segments and prostomial tentacles, high angle light from east (magn. × 8), see also figure 3.

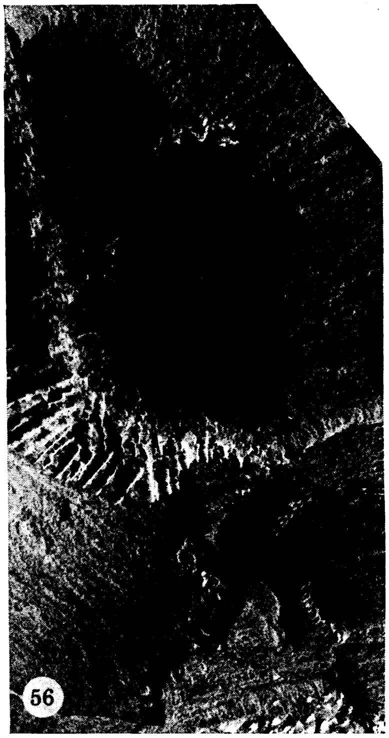
FIGURE 61. U.S.N.M. 198739, counterpart; dorsoventral, anterior segments and prostomial tentacle with pronounced distal kink, high angle light from west (magn. × 7).

FIGURES 62 AND 63. U.S.N.M. 198740, counterpart; dorsoventral. Figure 62, anterior segments and possible caruncle, high angle light from west (magn. × 7); figure 63, fascicle of notosetae, high angle light from north (magn. × 6.4).









FIGURES 47–63. For description see opposite.

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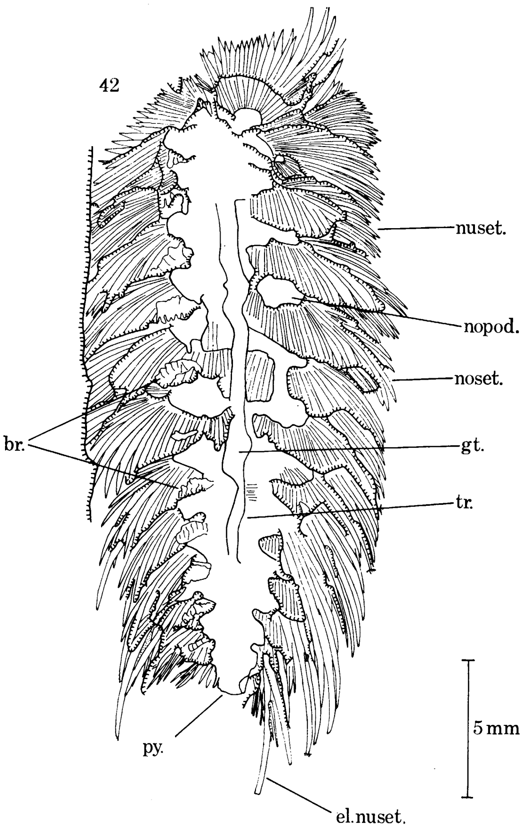

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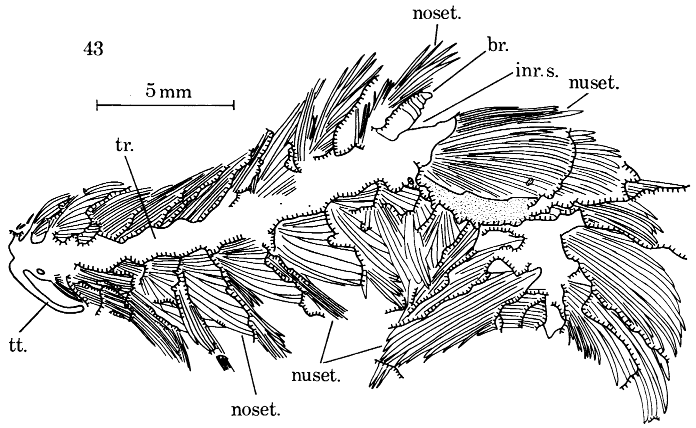

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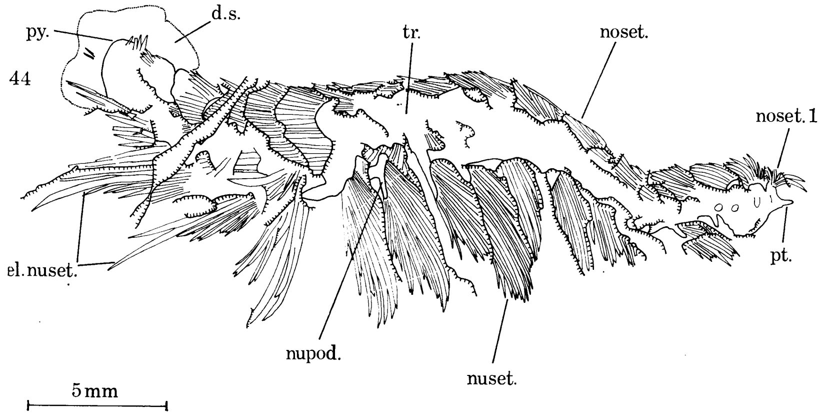


Canadia spinosa Walcott, 1911. Phyllopod bed, Walcott Quarry.

Figure 42. U.S.N.M. 198726, explanatory drawing of counterpart, see figure 47.

Figure 43. U.S.N.M. 198727, explanatory drawing of part, see figures 49 and 50.

Figure 44. U.S.N.M. 198728, explanatory drawing of counterpart, see figure 51.

Segment 1 had uniramous parapodia, but the remaining segments all had biramous parapodia. The podia (2 mm long) of segment 1 carried about fifteen setae each (1.2–1.5 mm long) which have an overall similarity to the notosetae of succeeding segments (figures 7, 8, 12 and 13, plate 1; figures 29 and 41, plate 3; figures 52, 60 and 61, plate 4; figure 3). The neuropodium and its setae, therefore, have been lost. In common with the other segments the notosetae of segment 1 are usually directed posteriorly but they occasionally point slightly forwards (figure 13, plate 1; figure 3) which suggests that the notopodia of segment 1 may have been flexible in life. This contrasts with the remaining notopodia which extended across the dorsal trunk and were probably capable of only limited movement. The anterior attitude of the notosetae of segment 1 may, however, have only arisen during transport in the mudflows. Similar distortion was noted by Whittington (1975*b*) in *Olenoides serratus* (Trilobita) where the gills are occasionally pushed forwards.

The biramous parapodia (figure 64) of the succeeding segments appear to have lacked aciculae. The noto- and neurosetae are identified on the basis of their similarity to those of the modern Palmyridae where the flattened notosetae (paleae) extend across the dorsum (see §8*b*, iii). The notopodium of a mid-segment carried about thirty to thirty-five posteriorly directed simple, unidentate setae that covered the entire dorsum (figures 7, 8, plate 1; figure 25, plate 2; figures 30–33, and 37, plate 3; figure 47, plate 4; figures 4, 16, 27, 28 and 42). The setae arose from transversely elongated podia and not as a rosette from a common point. The four or five adaxial notosetae of each side of a segment overlapped along the sagittal line. Furthermore, each fascicle of notosetae covered the anterior half of the notosetae posterior to it so that they formed an imbricated series. The fifteen or so notosetae nearest the sagittal line were symmetrical (1.5 mm long, 0.1–0.15 mm wide). The ten to fifteen distal setae were, however, asymmetrical and they curved adaxially. Distally these setae increased in length and width so that the largest one was 3–5 mm long and up to 0.3 mm wide. The asymmetrical notosetae were separated for more of their length than the adaxial symmetrical setae which only had their distal extremities free (figure 33, plate 3; figure 63, plate 4). The largest asymmetrical setae have about fifteen longitudinal striations which presumably represent ribs. The apparent restriction of the striations to these setae and the largest posterior neurosetae (see below) of *C. spinosa* suggests that they do not represent the internal tubular structure that has been documented in modern polychaete setae (see George & Southward 1973), because otherwise they should be visible in the other setae of the Burgess Shale polychaetes. The distal 1 mm of these setae also possessed minute, posteriorly directed serrations along the abaxial edge (figure 33, plate 3). Abaxial to the largest and widest seta there was a slightly smaller one, which was in turn succeeded by about five shorter and much thinner imperfectly formed setae (up to 1.5 mm long, 0.04 mm wide) which lacked ribbing or serrated edges (figure 14, plate 1; figure 35, plate 3; figure 63, plate 4). It is supposed that the group of large abaxial notosetae projected more or less horizontally away from the trunk and did not mantle the sides of the animal because in dorsoventral specimens they extend away from the body without visible distortion. The two posteriormost segments apparently lacked asymmetrical notosetae and their complement was confined to a few small (1 mm long, 0.1 mm wide) symmetrical setae (figure 47, plate 4; figure 42).

Each lobate neuropodium was, in transverse section, markedly asymmetrical. It consisted of a gently sloping dorsal section and a more or less horizontal ventral section connected by a bluntly conical termination which bore a fan-shaped fascicle of about thirty simple unidentate setae (figure 11, plate 1; figures 24–26, plate 2; figure 16). The setae were straight except for the ends which curved ventrally. The longest neurosetae (4–6 mm long, 0.1 mm wide) were situated in the middle of the fascicle and at either end of the fascicle there were imperfect setae (0.5 mm long, 0.02 mm wide) (figures 7 and 8, plate 1; figure 37, plate 3; figures 49–51, plate 4; figures 4, 28, 43 and 44). In decayed specimens an additional fascicle of 8–10 imperfect setae (1–2 mm long, 0.05 mm wide) arises from the ventral part of the podium (figures 55 and 58, plate 4; figure 45). It is uncertain whether this minor fascicle derives from the disruption of the main fascicle by decay, or whether it is an original feature.

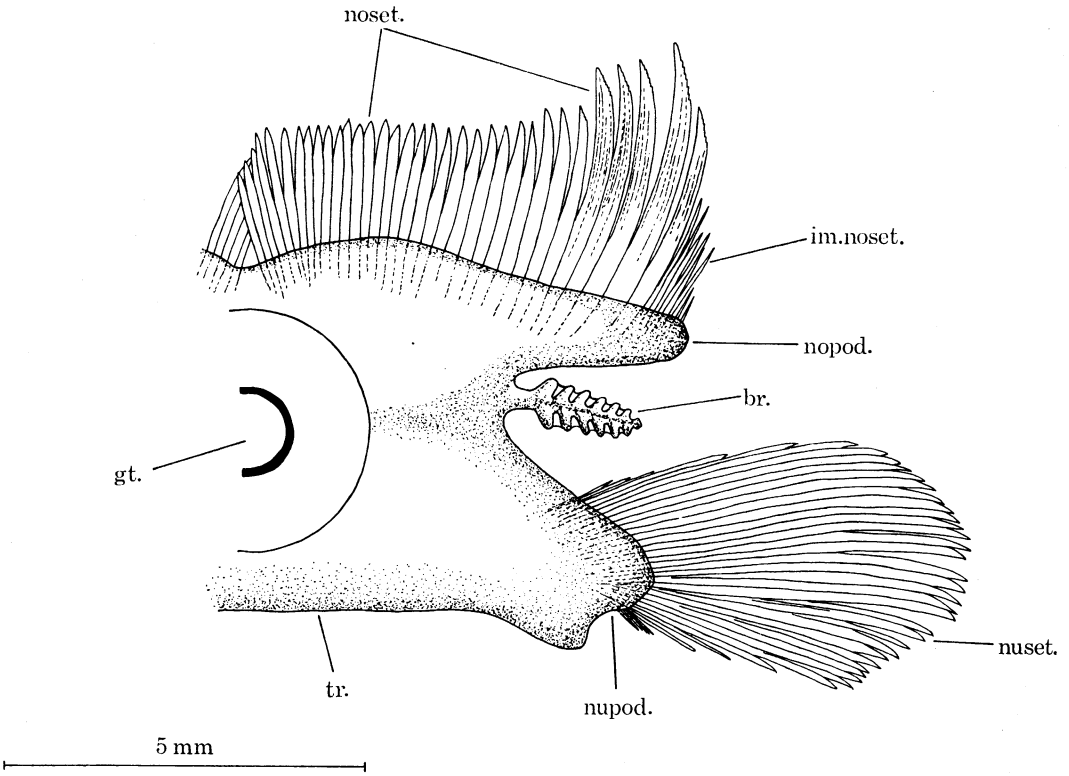


FIGURE 64. Reconstruction of a right parapodium from a mid-segment of *Canadia spinosa* Walcott. In accordance with reconstructions of modern palmyrid parapodia (see figure 65) the notosetae have been bent upwards from their originally horizontal position. The branchia has been twisted so as to reveal clearly its lobes.

The relationship between the orientation of the neurosetae and the bedding is discussed in §5*c*. Only in specimens which have part of the body axis inclined steeply to the bedding plane are the neurosetae exposed in what was presumably their life position (figures 24–26, plate 2; figure 49, plate 4; figures 16 and 43). Further examples of distortion include the twisting of neurosetae along their length so that the apparent width decreases distally (figure 36, plate 3). Such torsion presumably resulted from transport in a turbulent mudflow.

Two or three neurosetae of some of the posterior segments were greatly elongated (figures 19 and 20, plate 2; figures 30 and 37, plate 3; figures 47, 51, 56 and 57, plate 4; figures 15, 28, 42 and 44). Typically the longest setae (6–7 mm long, 0.2 mm wide) were situated on the fifth segment from the posterior end. They had longitudinal striations, interpreted as ribbing, and the abaxial edge of the distal 1 mm was serrated (figure 48, plate 4). They are thus markedly similar in shape to the largest asymmetrical notosetae and they may have had a similar function (see § 8*b*, ii). In dorsoventral and lateral specimens the elongate posterior neurosetae have not suffered the crushing that characterizes the normal neurosetae. In life they probably trailed behind the animal and only sloped ventrally at a modest angle.

Posterior to about segment 4 and extending to the penultimate segment each parapodium possessed an inter-ramal extension (1.5–2.5 mm long) which increased in length slightly towards the mid-segments. They are termed here branchiae because of the likelihood that they were used for respiratory purposes. They were attached to the parapodial wall by a broad stalk which continued as a central rachis bearing about twelve to fourteen lobes which alternated in position (figure 18, plate 2; figure 47, plate 4; figure 42). The lobes of the branchiae may overlap or be separated which indicates that they were extensible. The lobes apparently extended anteriorly and posteriorly from the rachis rather than vertically. Generally the branchiae extend straight out from the body, but more rarely they curved either forwards or backwards (figures 39 and 40, plate 3). The observations that the branchiae arise closer to the notosetae than the neurosetae (figure 50, plate 4; figure 43) is confirmed in other specimens where the thickness of sediment separating the branchiae from the neurosetae is about twice that separating it from the overlying notosetae. It is impossible to determine, however, whether the branchiae arose on the ventral section of the notopodium or the dorsal section of the inter-ramal area.

Walcott (1911*c*, p. 118) noted that 'A straight slender enteric canal is indicated on several specimens' of *C. spinosa* (figure 47, plate 4; figure 42), but unequivocal remains are fairly uncommon. This is perhaps due to the reflectively preserved body wall and setae obscuring the similarly preserved gut. Gut contents are almost unknown; one specimen (198739) has a bolus in the mid-segmental area of unidentifiable finely divided material. The anterior gut was apparently able to evert as a proboscis. It formed an unarmed lobe of variable size (0.3–5 mm long, typically 1 mm) (figures 11 and 13, plate 1; figure 22, plate 2; figure 41, plate 3; figure 52, plate 4; figure 3). The thin reflective strand (7 mm) extending from the anterior of specimen 198723 may represent an attenuated proboscis (figure 38, plate 3). The proboscis is visible in about 35 % of specimens. Its inconsistent appearance and variable length show that it is unlikely to have been a median prostomial tentacle. The anus was presumably located on the pygidium as in other polychaetes.

The parapodia of the specimens used by Walcott (1931) to illustrate *C. irregularis* and *C. grandis* are identical in appearance to those of *C. spinosa*. Although the preservation of these specimens is indifferent the distinctive setae are recognizable. The branchiae and prostomial tentacles are clearly preserved in one specimen (83933, counterpart 83934*a*; figure 21, plate 2) of *C. irregularis*, whilst the other specimen (83934*b*) apparently also has the proboscis everted (figure 22, plate 2). The abnormally broad trunk of the only specimen of *C. grandis* (figure 23, plate 2) is due to muscular contraction. The anterior has been folded beneath the rest of the body in a manner reminiscent of other specimens of *C. spinosa* (figure 47, plate 4; figure 42). *C. irregularis* and *C. grandis* are, therefore, taken to be junior synonyms of *C. spinosa*.

(ii) *Mode of life*

C. spinosa probably could walk across the sea floor on its neurosetal fascicles, but their extensive fan shape suggests they might have also been suitable for swimming. In general modern polychaetes swim by undulating the body aided to varying degrees by parapodial movements. The low width : length ratio (*ca.* 1 : 3) of the body of *C. spinosa* in comparison with many modern polychaetes that can swim suggests that body waves were of limited importance and the neurosetae were instrumental in propelling *C. spinosa*. The fascicles had sufficient freedom of movement for those of adjacent segments to overlap, although there is no preferential direction of overlap in the specimens. It is likely that the power stroke was delivered with the fascicle outspread, while during the recovery stroke frictional resistance was presumably reduced by clumping the setae and inclining them at a low angle to the body. The dorsal surface was streamlined by the imbricating notosetae. The large splayed asymmetrical notosetae may have acted as horizontal stabilizers. The degree of separation of these setae varies slightly and it is conceivable that the animal could exercise some control over their spacing.

The significance of the elongate posterior neurosetae is uncertain, especially as no counterpart appears to exist in modern polychaetes. Their restriction to the posterior segments indicates that they were only fully developed in the post-15 segment stage of the animal. They may, therefore, have been only necessary when the animal exceeded a certain size. Their posterior location makes it unlikely that they were primarily sensory. Their use as defensive spines would seem to have been limited. As they trailed behind the animal they presumably were ineffective during the locomotory power strokes of the neurosetae. It may be significant, however, that as the posterior segments taper the notosetae undergo a corresponding reduction (figures 30 and 37, plate 3; figure 47, plate 4; figures 28 and 42). It is proposed, therefore, that the elongate neurosetae could have replaced the stabilizing role held by the large notosetae more anteriorly.

The prostomial tentacles may have been sensory. Food could have been gathered by the proboscis, but its nature is not known. *C. spinosa* almost certainly was not a sediment eater and either a carnivorous or scavenging mode of life is considered likely. The branchiae were very probably used for respiration. The notosetal covering of the dorsum may have impeded gas exchange, especially during swimming. The branchiae probably helped to correct this. The location of the branchiae in a 'tunnel' formed by the rami and their setae (figure 64) suggests that water may have been channelled to flow past the branchiae during swimming. The Burgess Shale fauna does not appear to be unusually well endowed with species with marked adaptations to conditions of low O_2 concentrations and it is proposed that the presence of branchiae is because the respiratory demands of the animal were high.

(iii) *Systematic position*

Walcott (1911*c*) compared *C. spinosa* with the modern polychaetes *Palmyra aurifera* (Palmyridae) and *Chloeia euglochis* (Amphinomidae), and he noted (p. 119) that the latter species 'has almost the same grouping of setae on the parapodia'. The setae of *C. euglochis*, and all the other amphinomids, are tubular and never flattened as paleae, unlike the notosetae of *C. spinosa* (see Ehlers 1887; Day 1967). Moreover, although the bundles of notosetae are often luxuriant, they never extend across the dorsum. The branchiae are different in structure and they are located on the dorsal surface of the trunk, whereas the branchiae of *C. spinosa* are located more ventrally (figure 64). The structure of the head also differs, and *C. spinosa* apparently has no counterpart to the distinctive caruncle extending behind the prostomium in the amphinomids.

Comparison with the family Palmyridae is more fruitful. This small family comprises the genera *Palmyra*, *Paleanotus* (= *Chrysopetalum*, see Day 1962), *Bhawania*, *Heteropale* and *Dysponetus*. *Heteropale* is considered by some authors (e.g. Hartman 1959, 1961, 1968; Fauchald 1977) to be synonymous with *Paleanotus*. The last four genera are sometimes included separately in the Chrysopetalidae (e.g. Racovitza 1896; Fauchald 1977), but other authors (e.g. Gravier 1901;

Potts 1910; Day 1962, 1967) place all the genera in the Palmyridae and in this paper all the genera are collectively referred to as palmyrids. Most of the Palmyridae have distinctive flattened notosetae or paleae extending across most or all of the dorsal surface and fascicles of narrower neurosetae (figure 65). *C. spinosa* is, therefore, at least superficially similar to the palmyrids.

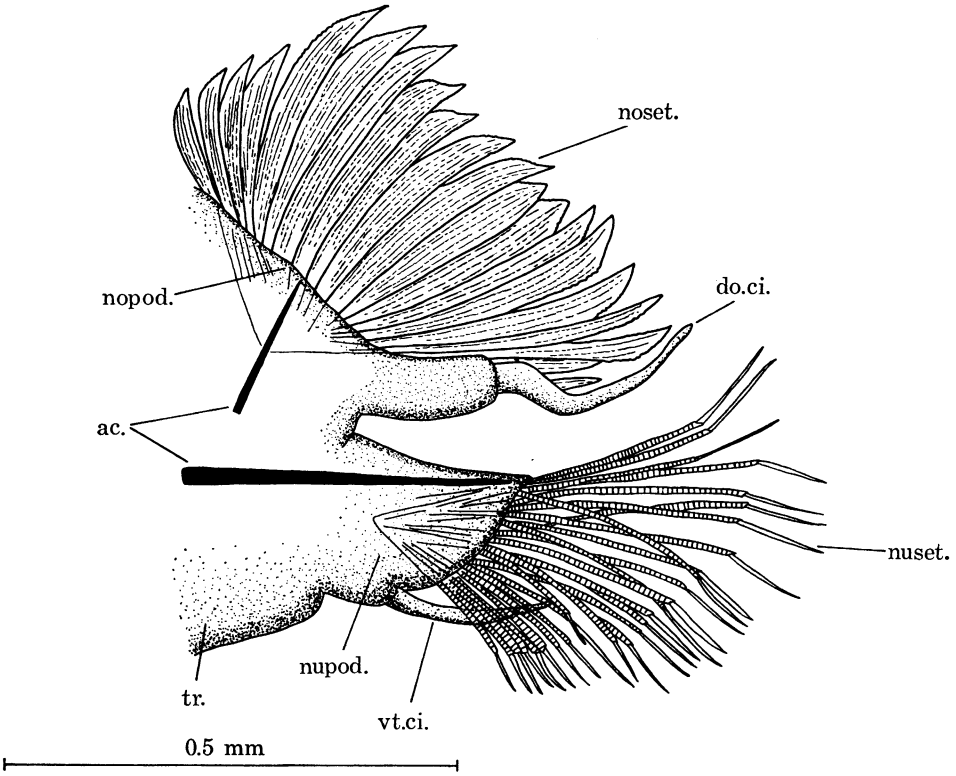


FIGURE 65. Parapodium of the modern palmyrid *Paleanotus debilis* (Grube 1855). From Gravier 1901, figure 276.

Similarities and differences between *C. spinosa* and some of the representative palmyrids are given in table 1. Owing to its aberrant nature *Dysponetus* (see e.g. Ushakov 1965) is not considered further here. The prostomium of *C. spinosa* is most similar to that of *Palmyra* although it lacks the facial tubercle and median antenna of the latter genus. *Palmyra*, *Paleanotus*, *Bhawania* and *Heteropale* have a pair of palps but it is unclear whether the tentacles of *C. spinosa* are equivalent to these palps. Unlike nearly all modern palmyrids *C. spinosa* appears to lack eyes. *C. spinosa* almost certainly has no counterpart to the caruncle noted in some palmyrids. In modern palmyrids segment 1 is reduced. In *Palmyra* and some species of *Paleanotus* the neurosetae are wanting, while the paleae exist as a reduced fascicle. However, the dorsal and ventral cirri persist. This condition with respect to the setae is comparable to segment 1 of *C. spinosa*. Segment 2 is reduced in some species of *Paleanotus* but it is normally developed in other modern palmyrids and *C. spinosa*. The biramous parapodia are of similar appearance in *C. spinosa* and palmyrids (figures 64 and 65). However, *C. spinosa* lacks the dorsal and ventral cirri that characterize all modern species. The branchiae are unlikely to be homologous with the dorsal cirri of palmyrids because of their different structure and point of insertion. The notosetae of *C. spinosa* are most similar to those of *Paleanotus*. In both groups the proximal setae are symmetrical and the distal ones asymmetrical being curved adaxially. The paleae of *P. chrysolepis* are serrated on the

Table 1. Comparisons of anatomy and mode of life between *Canadia spinosa* Walcott and modern palmyrids

Authorities consulted on palmyrids are given as numbers in brackets beneath each species name. 1, 2 Banse & Hobson (1968, 1974); 3–6 Day (1934, 1953, 1962 and 1967); 7 Fauvel (1953); 8 Gravier (1901); 9–11 Hartman (1954, 1961 and 1968); 12 Imajima & Hartman (1964); 13 Johnson (1897); 14 Katzmann, Laubier & Ramos (1974); 15 Laubier (1968); 16 Monro (1933); 17 Potts (1910); 18 Reish (1968); 19 Webster (1884).

feature	*Canadia spinosa*	*Palmyra aurifera* (2, 9, 17)	*Paleanotus chrysolepis* (6)	*Paleanotus debilis* (5, 7, 8, 14, 15, 18)	*Bhawania goodei* (3–8, 12, 16–19)	*Heteropale bellis* (1, 10–13)
length/mm	20–46	34	12–15	6–15	10–100	3
number of segments	19–22	30	*ca* 40	36–40	110–300+	27–39
prostomium	quadrate	subrectangular lobe	oval	oval	small, rounded, concealed by first segments	quadrate
prostomial appendages	2 tentacles	median antenna, and 2 palps, conical facial tubercule	2 lateral antennae, shorter median antenna, 2 stout palps	2 annulated lateral antennae, median antenna, 2 stout palps	2 lateral antennae, median antenna, 2 palps	2 lateral antennae, median antennae, 2 globular palps
eyes	absent	2 pairs	2 pairs	4	4	4
caruncle	?absent	absent	doubtful	spherical	absent	large, glandular
parapodium of segment 1	uniramous, reduced notosetae, neurosetae absent	dorsal and ventral cirri adpressed to body, few paleae neurosetae absent	pair of tentacular cirri; paleae and neurosetae absent	pair of tentacular cirri, very few paleae, neurosetae absent	small, but normal	left pair of tentacular cirri, right ventral cirrus sometimes absent, 3–4 paleae and small fascicle of neurosetae
parapodium of segment 2	normal	normal	fused to segment 1, but cirri not elongate; paleae and neurosetae absent	fused at base to segment 1, but cirri not so elongate; few paleae, neurosetae absent	normal	normal
notosetae (paleae)	transverse rows overlapping along midline; *ca* 15 proximal symmetrical; 15–20 asymmetrical curved adaxially, and abaxial serrated edge; distal setae imperfect	semi-circle leaving midline uncovered; slightly curved, blunt, smooth margins; distal setae imperfect	transverse rows do not cover midline; proximal symmetrical, asymmetrical curved adaxially; with 16–20 beaded ribs, larger beads on rib of abaxial margin; distal setae imperfect	transverse rows, just meet over midline; same arrangement as in *P. chrysolepis* but paleae have 6–10 ribs and each edge serrated	transverse rows overlapping along midline *ca* 30 symmetrical paleae with 20 ribs, 3 ridges with knobs, adaxial margin serrated and rounded tips; distal imperfect setae	transverse rows overlapping along midline, 13–14 asymmetrical paleae with ribs 7–8 of which have discs; 3–4 distal setae imperfect
neurosetae	simple, some posterior setae elongated with abaxial serrated edge	compound	compound, falcigerous, with blades of varying length	compound, falcigerous, with blades of even length	compound, mostly falcigerous but dorsal ones have spinigerous blades	compound, spinigerous
cirri	lobate branchiae	dorsal and ventral cirrus	dorsal and ventral cirrus	dorsal (well developed) and ventral cirrus	dorsal cirrus small, digitiform and retractable; ventral cirrus	jointed dorsal and ventral cirrus
mode of life	benthonic or ?nektobenthonic	coral dwelling	kelp holdfasts and bryozoan tufts below tide marks	coral boulders and rocky substrate	rock and coral crevices among sponges	among tunicates, bryozoa, sponges and seaweeds

abaxial edge in a similar manner to the distal notosetae of *C. spinosa*. A group of distal imperfect notosetae is common to *C. spinosa* and the majority of palmyrids. The paleae of *Paleanotus*, *Bhawania* and *Heteropale* are ribbed although, unlike *C. spinosa*, some or all of the ribs are ornamented. With the exception of *Palmyra* the paleae arise in a transverse row in a similar manner to the notosetae of *C. spinosa*. The neurosetae of *C. spinosa* are simple and unidentate, whereas the palmyrids have compound setae. No palmyrid has elongated neurosetae comparable to the enlarged posterior ones of *C. spinosa*. *C. spinosa* has fewer segments than *Palymra*, *Paleanotus* and *Heteropale* and many less than *B. goodei*. With the exception of *B. pottsiana* (Gibbs 1971) which is up to 45 mm long, the palmyrids are shorter than *C. spinosa*. Unlike *C. spinosa* the muscular proboscis of most palmyrids is equipped with a pair of stylets (Pettibone 1963). The larval stages of palmyrids (Mileikovsky 1962; Cazaux 1968; Blake 1975) do not appear to throw much light on the evolution of this family or its affinity with *C. spinosa*. The mode of life of palmyrids is varied. The majority are associated with hard substrata (table 1), but *B. reyssi* lives on muddy sands (Katzmann, Laubier & Ramos 1974). *C. spinosa* probably lived on or above a mud bottom.

C. spinosa does not, therefore, correspond exactly with any of the Palmyridae. The similarity of the notosetae is striking but the fossil worm differs in having simple neurosetae, no ventral cirri and probably no dorsal cirri, and simpler prostomial appendages. Although some of the differences might be due to a more active mode of life it is not possible to prove that the similarity between the parapodia of *C. spinosa* and the recent palmyrids is not a product of parallel evolution. *C. spinosa* is, therefore, retained in the family Canadiidae rather than being transferred to the Palmyridae.

(*c*) Burgessochaeta setigera (*Walcott*) *gen. nov.*

Family BURGESSOCHAETIDAE fam. nov.

Diagnosis. Small prostomium. Elongate anterior tentacles. Segment 1 with uniramous parapodia, all other segments with biramous parapodia with identical simple notosetae and neurosetae. Cirri and branchiae absent.

Genus *BURGESSOCHAETA* gen. nov.

Type (*and only known*) *species*. *Burgessochaeta setigera* (Walcott, 1911). The derivation of the generic name is obvious.

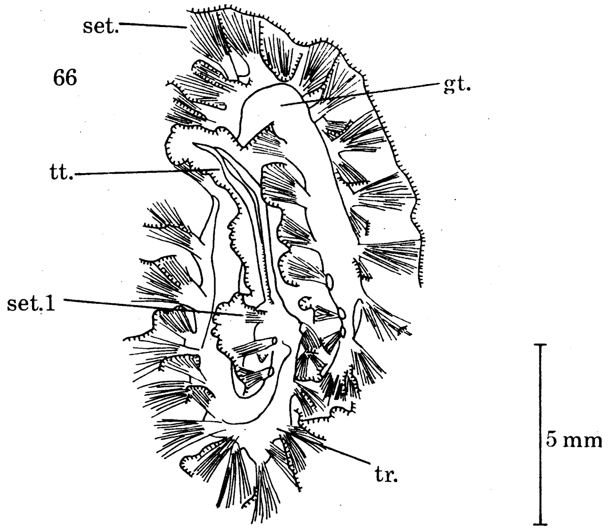
Diagnosis. Slender body, about 2.9 cm long. Pair of elongate tentacles probably arising from peristomium. Trunk of at least twenty four setigerous segments. Segment 1 has uniramous parapodia, remainder with biramous parapodia, all similar. Rami of each parapodium identical with about fifteen simple furcate setae each. Inter-ramal spacing moderate. Straight gut with eversible unarmed proboscis.

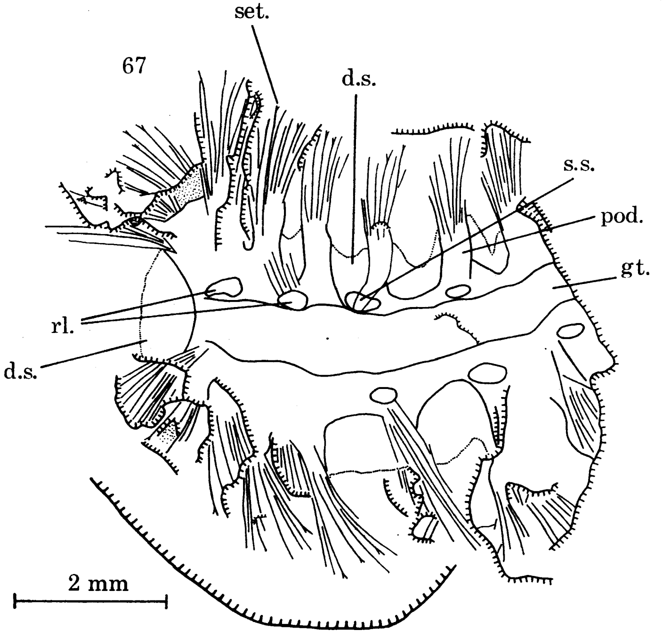
Burgessochaeta setigera (Walcott, 1911) gen. nov.

Figures 68–78, plate 5; figures 82–90, plate 6; figures 96–100, plate 7;
figures 66, 67, 79–81 and 91–93.

1911*c*	*Canadia setigera*	Walcott pp. 118–120, plate 23, figures 1–3.
1912*a*	*Canadia setigera*	Walcott p. 153.
1912*b*	*Canadia setigera*	Walcott p. 190.

1912	*Canadia setigera*	Steinmann figure 4A (copied Walcott 1911*c*, plate 23, figure 3).
1916	*Canadia setigera*	Walcott plate 12, figures 1–3 (copied Walcott 1911*c*, plate 23, figures 1–3).
1919	*Canadia setigera*	Walcott p. 220.
1931	*Canadia setigera*	Walcott p. 5, plate 7, figures 1 and 4; plate 8, figure 3.
1952	*Canadia setigera*	Roger figure 3 (copied Walcott 1911*c*, plate 23, figure 3).
1969	*Canadia setigera*	Robison p. 1170.





Description of plate 5 and figures 66 and 67

Burgessochaeta setigera (Walcott, 1911) gen. nov. Phyllopod bed, Walcott Quarry.

Figure 66. U.S.N.M. 198698, explanatory drawing of part, see figure 74.

Figure 67. U.S.N.M. 198695, explanatory drawing of part, see figure 77.

Figure 68. U.S.N.M. 57648, part; lateral, recurved, low angle light from southeast (magn. × 2.6). Original of Walcott 1911*c* (plate 23, figure 1).

Figure 69. U.S.N.M. 57650, part; dorsoventral, high angle light from north (magn. × 4), lectotype. Original of Walcott 1911*c* (plate 23, figure 3).

Figure 70. U.S.N.M. 83930*c*, part; oblique-dorsoventral, complete, low angle light from south (magn. × 1.8). Original of Walcott 1931 (plate 8, figure 3).

Figure 71. U.S.N.M. 83930*b*, part; dorsoventral, complete, high angle light from southwest (magn. × 3.2). Part of original of Walcott 1931 (plate 7, figure 4).

Figure 72. U.S.N.M. 57649, part; dorsoventral, posterior segments, high angle light from west (magn. × 7.2). Original of Walcott 1911*c* (plate 23, figure 2).

Figure 73. U.S.N.M. 83930*a*, part; oblique, strongly curved with prominent anterior dark stain, low angle light from north (magn. × 3.8). Part of original of Walcott 1931 (plate 7, figure 1).

Figure 74. U.S.N.M. 198698, part; dorsoventral, coiled, high angle light from west (magn. × 6.8).

Figures 75 and 76. U.S.N.M. 198697, part; oblique-dorsoventral, high angle light from north. Figure 75, complete with posterior segments folded downwards (magn. × 4.7); figure 76, anterior segments with everted proboscis (magn. × 12.8).

Figures 77 and 78. U.S.N.M. 198695, part; dorsoventral. Figure 77, incomplete with one end folded downwards, high angle light from northwest (magn. × 6.5); figure 78, setae with bifid tips, high angle light from southeast (magn. × 38).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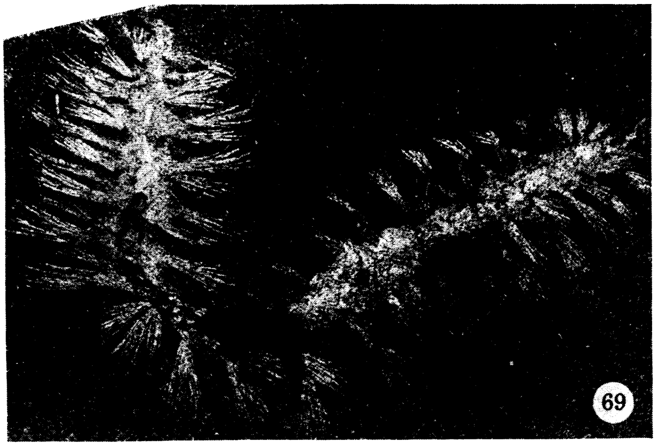
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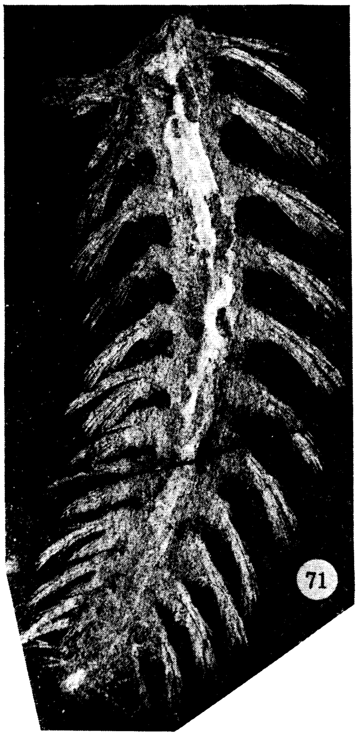
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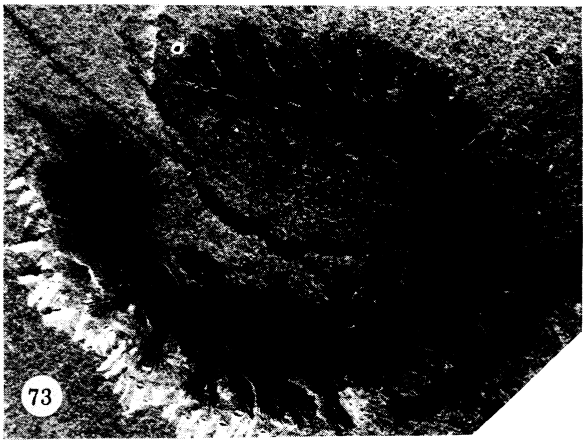
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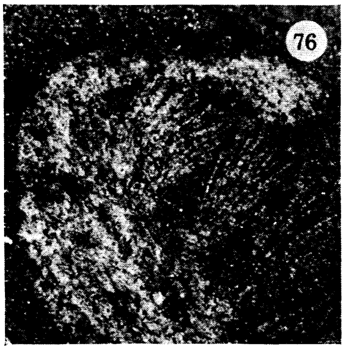
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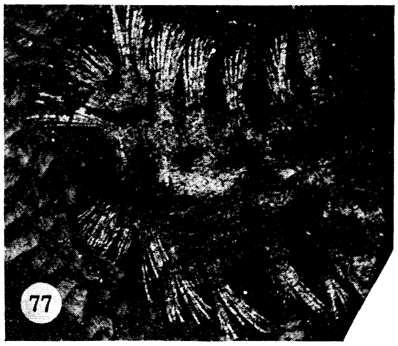
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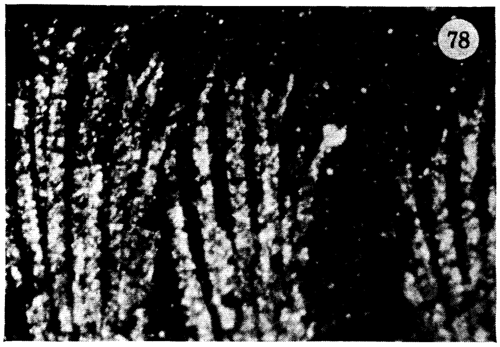
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FIGURES 68–78. For description see opposite.

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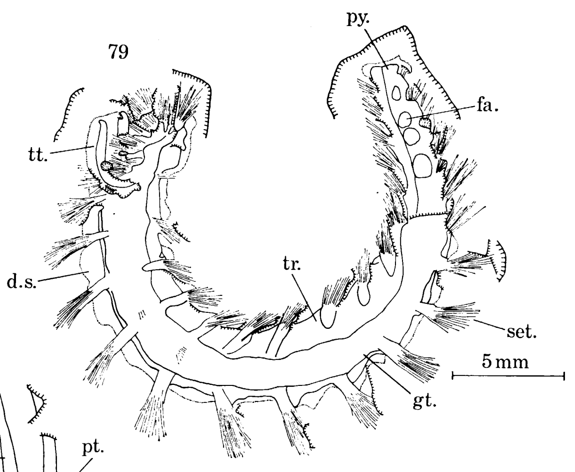

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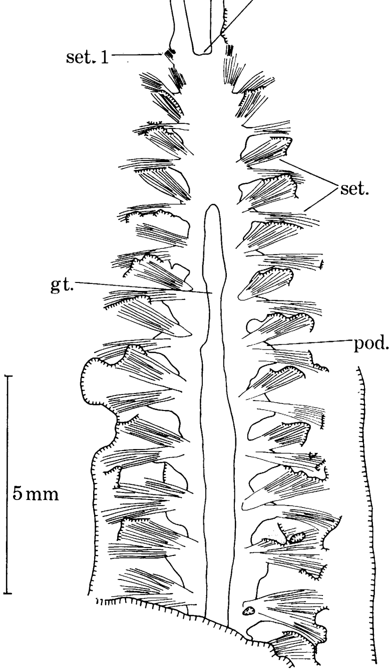

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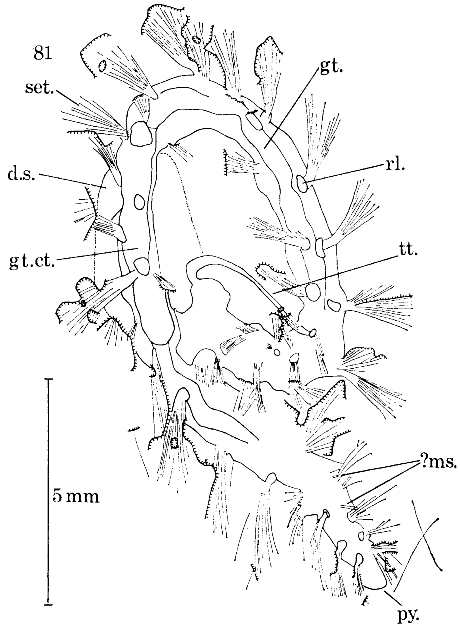


Description of plate 6 and figures 79–81

Burgessochaeta setigera (Walcott, 1911) gen. nov. Phyllopod bed, Walcott Quarry.

Figure 79. U.S.N.M. 198696, explanatory drawing of part, see figure 82.

Figure 80. U.S.N.M. 198699, explanatory drawing of part, see figure 85.

Figure 81. U.S.N.M. 198700, explanatory drawing of part, see figure 87.

Figures 82 and 83. U.S.N.M. 198696, part; lateral. Figure 82, curved with anteriormost segments folded beneath body, low angle light from south (magn. × 4.2); figure 83, posterior segments containing faecal pellets, high angle light from west (magn. × 11).

Figure 84. U.S.N.M. 198710, part; dorsoventral, posterior contracted half of body, high angle light from east (magn. × 3.5).

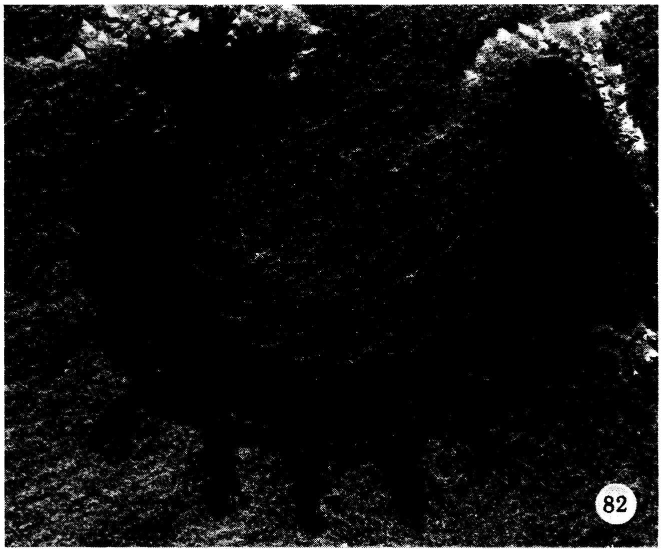
Figures 85 and 86. U.S.N.M. 198699, dorsoventral. Figure 85, part; anterior half of body, high angle light from west (magn. × 6.2); figure 86, counterpart; anterior segments and proximal section of (?) peristomial tentacles, high angle light from northeast (magn. × 25).

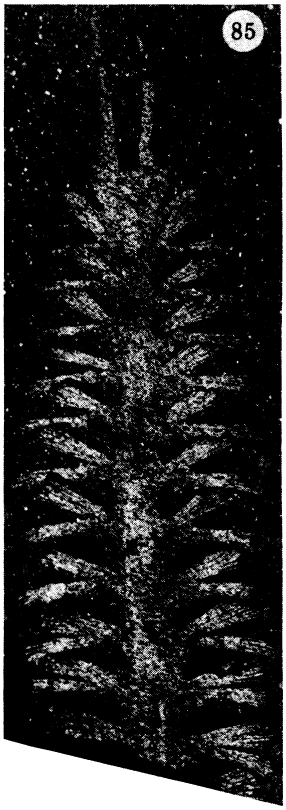
Figure 87. U.S.N.M. 198700, part; lateral, coiled, high angle light from east (magn. × 8.4).

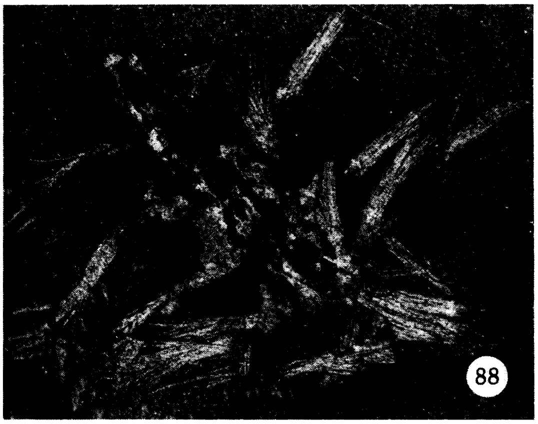
Figure 88. U.S.N.M. 198707, part; dorsoventral, decayed fragment with gut projecting from trunk, high angle light from north (magn. × 3.4).

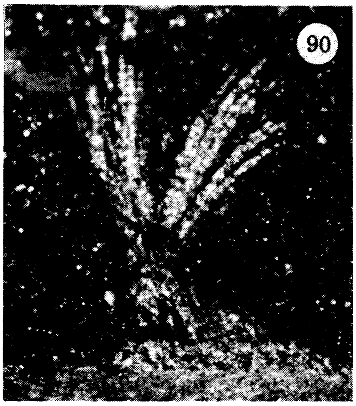
Figure 89. U.S.N.M. 198711, part; dorsoventral, complete parapodium with neurosetae and notosetae separated by moderate inter-ramal space, high angle light from northwest (magn. × 16.2).

Figure 90. U.S.N.M. 198704, part; dorsoventral, parapodium of posterior trunk bearing setae and with radiating reflective lines interpreted as musculature, high angle from north (magn. × 29).









FIGURES 82–90. For description see opposite.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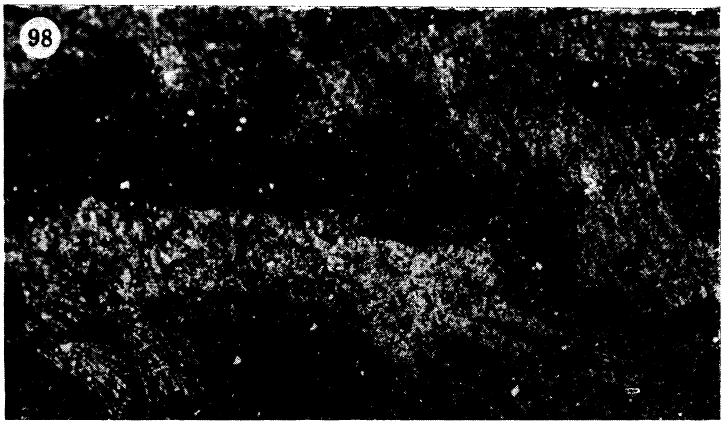
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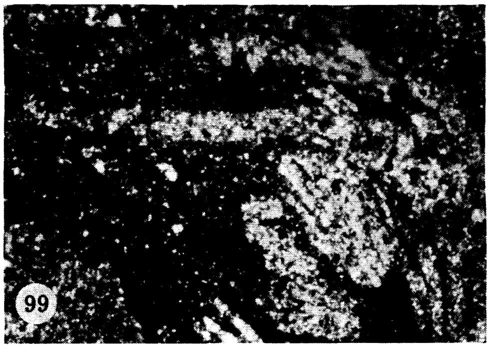
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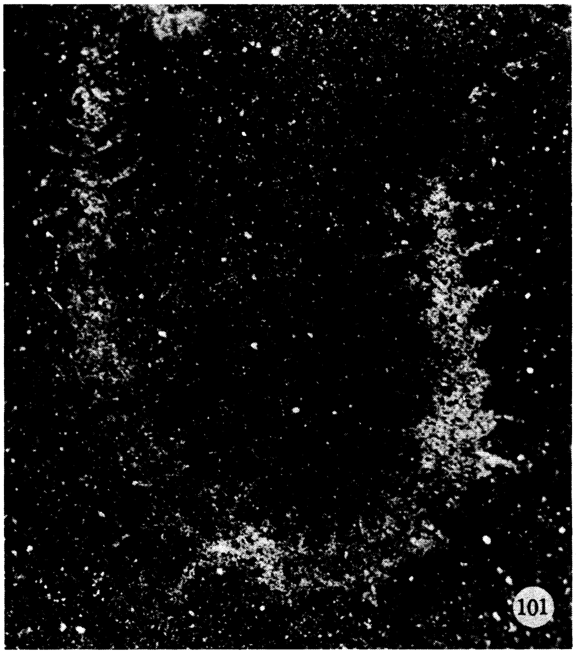
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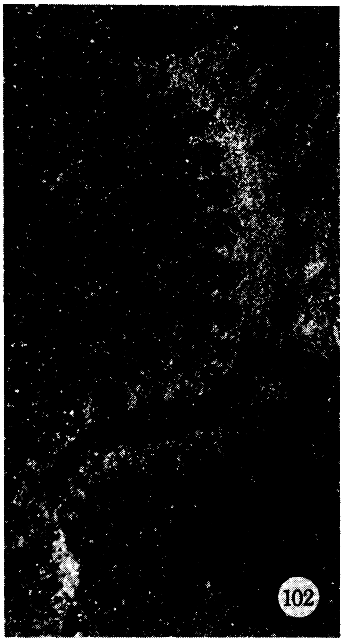
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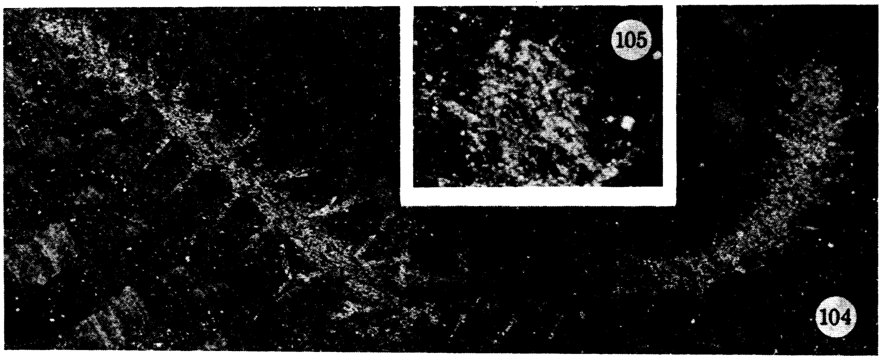
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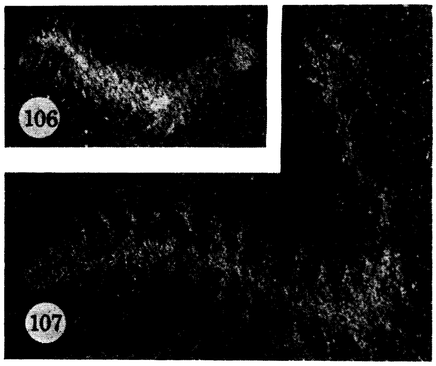
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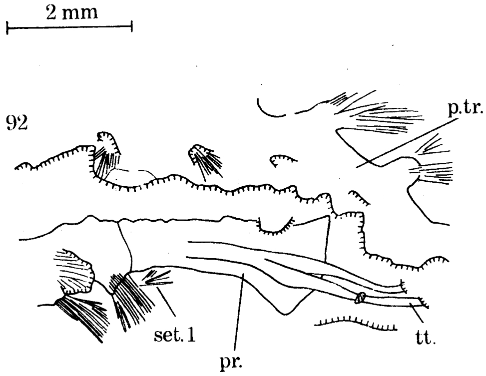
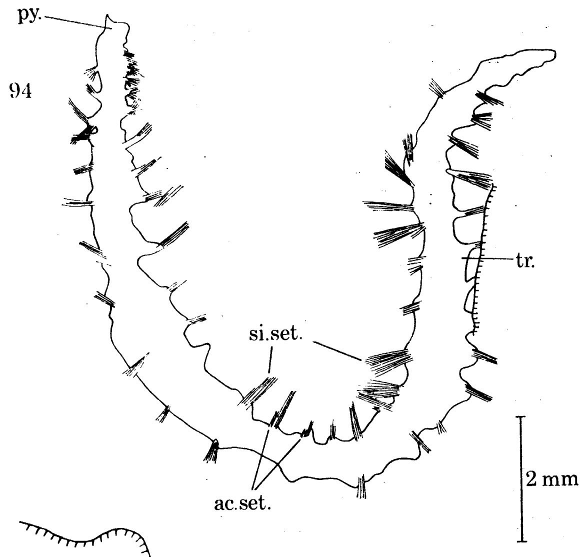
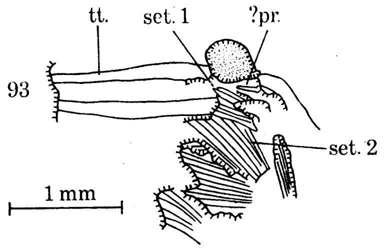
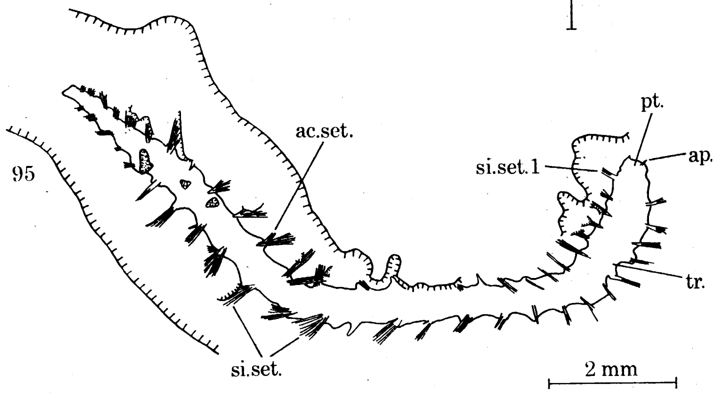
Figures 96–107. For description see opposite.









Description of plate 7 and figures 92–95

Burgessochaeta setigera (Walcott, 1911) gen. nov. Figures 92, 93 and 96–100.
Peronochaeta dubia (Walcott, 1911) gen. nov, Figures 94, 95, 101 and 103–107.
Polychaete gen. et sp. indet. Figure 102. Phyllopod bed, Walcott Quarry.

Figure 92. U.S.N.M. 198705, explanatory drawing of anterior body and section of posterior trunk of part, see figure 98.

Figure 93. U.S.N.M. 198702, explanatory drawing of anterior of part, see figure 99.

Figure 94. U.S.N.M. 83936*a*, explanatory drawing of part, see figure 101.

Figure 95. U.S.N.M. 198718, explanatory drawing of part, see figure 104.

Figure 96. U.S.N.M. 198703, part; oblique-dorsoventral, complete, high angle light from northeast (magn. × 5.3).

Figure 97. U.S.N.M. 198701, part; oblique-dorsoventral, looped, high angle light from east (magn. × 5.2).

Figure 98. U.S.N.M. 198705, part; lateral, everted proboscis overlying (?) peristomial tentacles, high angle light from northwest (magn. × 16).

Figure 99. U.S.N.M. 198702, part; oblique, anterior segments and (?) peristomial tentacles, high angle light from north (magn. × 34).

Figure 100. U.S.N.M. 198708, part; dorsoventral, anterior segments and everted proboscis, high angle light from east (magn. × 16.4).

Figure 101. U.S.N.M. 83936*a*, part; dorsoventral, curved, high angle light from south (magn. × 9), lectotype. Original of Walcott 1931 (plate 7, figure 2).

Figure 102. U.S.N.M. 83936*c*, part; dorsoventral, decayed specimen of an unidentified polychaete, high angle light from west (magn. × 7.6). Original of Walcott 1931 (plate 8, figure 2).

Figure 103. U.S.N.M. 83936*d*, part; dorsoventral, strongly recurved, high angle light from west (magn. × 16). Original of Walcott 1931 (plate 9, figure 8).

Figures 104 and 105. U.S.N.M. 198718, part; dorsoventral, high angle light from northeast. Figure 104, complete (magn. × 11); figure 105, anterior segments and prostomium with pair of short appendages (magn. × 32).

Figure 106. U.S.N.M. 198736, part; dorsoventral-oblique, complete, high angle light from south (magn. × 6.8).

Figure 107. U.S.N.M. 198737, part; dorsoventral, complete but posterior trunk considerably decayed, high angle light from east (magn. × 8.4).

1970 *Canadia setigera* Black figure 142.
1974 *Canadia setigera* Whittington p. 5.
1977 *Canadia setigera* Whittington p. 417.

Material. Lectotype U.S.N.M. 57650. Walcott 1911*c*, plate 23, figure 3. Designated herein (figure 69, plate 5).

Paralectotypes U.S.N.M. 57648–49, 83930*a–c*.

Other material U.S.N.M. 198695–198711, 199680, 199741. There are about 150 other U.S.N.M. specimens. G.S.C. 8316, 8316*a–c*, 45337, and 20 unnumbered specimens. U.M. 1503.

(i) *Morphology*

The length ranges from 1.8–4.9 cm (average 2.9 cm), but despite this range there is no other evidence to support Resser's suggestion (*in* Walcott 1931, p. 5) that 'several distinct forms are included in the species as now constituted'. The anterior end bore two unsegmented and smooth tentacles (up to 6 mm long). Their variable length and width suggest that in life they were contractile. Considerable flexibility is also indicated because in about half the specimens the tentacles extend in front of the body (figures 73 and 74, plate 5; figures 85 and 86, plate 6; figures 97 and 98, plate 7; figures 66, 80 and 92), whereas in the other half they are recurved (figure 68, plate 5; figure 87, plate 6; figure 96, plate 7; figure 81). It is impossible to determine whether they arose from the prostomium or segment 1, i.e. the peristomium, but their proximity to the setae of segment 1 (figures 85 and 86, plate 6; figure 99, plate 7; figures 80 and 93) strongly suggests that they were of peristomial origin. It is not known whether the tentacles arose dorsally or ventrally. The prostomium was apparently a minute structure situated between the tentacle bases (figures 85 and 86, plate 6; figure 80). The reflective mass to one side of the tentacles in specimen 198701 (figure 97, plate 7) is not believed to represent a prostomial extension because of its absence in other specimens, and it may be the proboscis.

The trunk tapered at either end but otherwise was of fairly constant width (*ca.* 2 mm). In specimens where a section of the body has been folded beneath the remainder, the trunk surface appears flat and featureless (figures 75 and 77, plate 5; figure 89, plate 6; figure 67) which suggests that in transverse section the trunk may have been sub-rectangular. The number of setigerous segments was not constant and varied from about twenty-one to at least twenty-four. The trunk ended in a small smooth pygidium (figures 82 and 83, plate 6; figure 79).

The parapodia on about the four anterior and posteriormost segments decreased in size towards the ends of the animal. Those of the intervening segments were of more or less equal size. The rami of the parapodia consisted of bluntly conical setigerous extensions of the body separated by a moderate inter-ramal space (figures 71, 75 and 77, plate 5; figure 90, plate 6; figure 67). The parapodia of segment 1 were uniramous (figure 74, plate 5; figures 85 and 86, plate 6; figures 98 and 99, plate 7, figures 66, 80, 92 and 93), but the remainder were biramous (figures 72 and 74, plate 5; figures 84, 85 and 89, plate 6; figures 66 and 80). Other than differences in size along the length of the body, the biramous parapodia (figure 91) were identical. Each ramus carried between eleven and seventeen smooth setae (1.5–2 mm long, 0.09 mm wide) which were apparently disposed in a single plane steeply inclined to the trunk (figure 85, plate 6; figure 80). The tips of the setae were unequally bifid with one prong about half the length (i.e. 0.1 mm) of the other (figure 78, plate 5). There is no evidence that the setae were originally compound with the bifid tip representing the socket in which a now detached distal section lay. Within the parapodium the setae enter an adaxially tapering reflectively preserved bundle which presumably represents the setal sac (figure 77, plate 5; figures 86 and 89, plate 6; figure 67). Aciculae appear to have been absent. The notosetae and neurosetae of each ramus were identical. The dorsal and ventral sides of the animal, therefore, cannot be distinguished and it is not known which ramus is absent from segment 1. The parapodia lacked branchiae and cirri. One parapodium of specimen 198704 has about twelve reflective strands radiating adaxially from the distal end (figure 90, plate 6). These strands are interpreted as muscles which upon contraction would have withdrawn the setae. Similar muscles, but acting as protractors, were reported in the modern polychaete *Nephtys* (Clark & Clark 1960, but see Mettam 1967, p. 264). Reflective strands in two of the posterior parapodia of specimen 198700 may represent other muscles (figure 87, plate 6; figure 81).

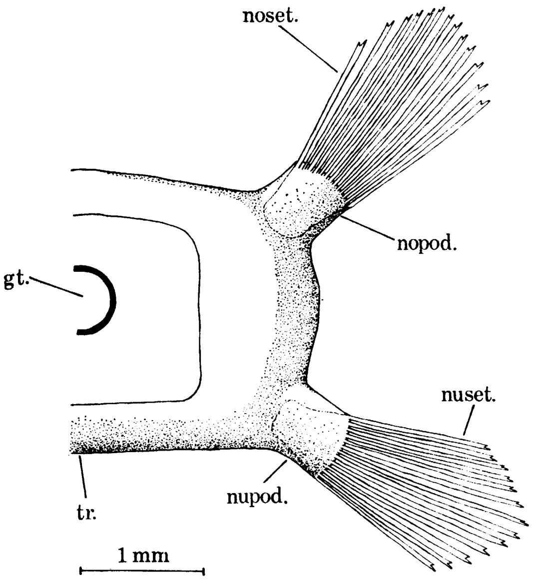


FIGURE 91. Reconstruction of a right parapodium from a mid-segment of *Burgessochaeta setigera* Walcott) gen. nov.

About 35% of the specimens have up to six roughly circular areas with prominent relief beside or upon the proximal ends of setal sacs (figures 74 and 77, plate 5; figure 87, plate 6; figures 66, 67 and 81). These areas generally occur only on one side of the animal, but they may be found anywhere along the trunk. Their significance is uncertain. Interpretations that they are local distensions of a lateral blood vessel or food filled gut caeca are considered unlikely. The areas may result from the extreme contraction of parapodial muscles during death.

A longitudinal strip, often reflectively preserved, within the trunk of most specimens is regarded as the gut (figures 70, 71, 74 and 77, plate 5; figures 82, 84 and 85, plate 6; figures 66, 67, 79 and 80.) The anterior gut could evert as an unarmed proboscis (figures 75 and 76, plate 5; figure 100, plate 7). When fully everted its anterior end was flared (figure 98, plate 7; figure 92). The rest of the gut was externally undifferentiated as a simple tube. The anus opened on the pygidium (figure 84, plate 6). Gut contents occur in about 25% of specimens and always consist of unidentifiable shreds and fine granular material (figure 69, plate 5; figures 87 and 88, plate 6; figure 81). The posterior gut of specimen 198696 contains four rounded faecal pellets (figure 83, plate 6; figure 79).

(ii) *Mode of life*

B. setigera presumably propelled itself with its setae. The similarity of the notosetae and neurosetae is not regarded as primitive and may derive from their having similar functions. It is tentatively suggested that *B. setigera* inhabited burrows which it progressed along by pushing both fascicles of setae against the burrow wall. The method of feeding is speculative. In overall appearance this worm is not dissimilar to members of the modern Spionidae, Magelonidae and Heterospionidae which all possess elongate peristomial palps that have usurped the role of the proboscis in feeding. The proboscis is now used for constructing burrows of varying permanence. The proboscis of *B. setigera* was probably instrumental in burrowing. The tentacle: body ratio of *B. setigera* (1:5) is only slightly less than typical spionids (about 1:6) and it seems likely that the tentacles were used to collect food. Unlike the peristomial tentacles of modern forms which are often ornamented (e.g. grooved, papillate), those of *B. setigera* appear to have been smooth. The modern spionids and related polychaetes are generally deposit feeders and the gut is often filled with sediment and food particles (Day 1967). Such a feature has not been observed in *B. setigera.*

(iii) *Systematic position*

Walcott (1911*c*) placed this worm in *Canadia* but numerous differences exist with the type species, *C. spinosa.* They include furcate notosetae which are not paleae, do not cover the dorsum and are identical to the neurosetae. Branchiae are also wanting. *Burgessochaeta* gen. nov. is therefore proposed.

A number of modern polychaete families such as the Amphinomidae and Nephtyidae have representatives with closely similar notosetae and neurosetae. The presence, however, of additional prostomial appendages, parapodial branchiae and cirri shows that no close affinity exists between these families and *B. setigera.*

Despite the proposed parallels between the mode of life of *B. setigera* and the modern Spionidae, Magelonidae and Heterospionidae important anatomical differences remain. The spionids, for instance, have gills and the simple setae are dissimilar to those of *B. setigera.* Furthermore, the setae of the two rami of each parapodium are not identical. To avoid further laborious comparisons it should suffice to note that no close relationship can be demonstrated between *B. setigera* and these families. As this fossil worm cannot be placed in any modern or fossil polychaete family Burgessochaetidae fam. nov. is proposed herein.

The polychaetes are often cited as a group that has maintained primitive metamerism with many more or less identical segments and little tagmatization. It might be argued that *B. setigera* shows primitive features, especially in having similar segments with notosetae and neurosetae of the same type. A more critical assessment of *B. setigera* indicates, however, that its apparent simplicity arose by reduction from a more complex condition. If *B. setigera* was primitive the absence of cirri is particularly surprising. The proposed primitive arrangement of prostomial appendages of three antennae and two palps (Day 1967) would also appear to have undergone reduction.

(*d*) Peronochaeta dubia (*Walcott*) *gen. nov.*

Family PERONOCHAETIDAE fam. nov.

Diagnosis. Prostomium with short appendages. All segments with uniramous parapodia bearing simple and acicular setae. Cirri and branchiae absent.

Genus *PERONOCHAETA* gen. nov.

Type (and only known) species. *Peronochaeta dubia* (Walcott, 1911).

Derivation of name. From perone (Gr. needle) and chaeta.

Diagnosis. Slender body, about 11 mm long. Bilobed prostomium with pair of short conical appendages arising from anterior corners. Trunk of over twenty-five segments. All segments similar with uniramous parapodia. Each parapodium carries about twenty simple straight setae and two to four flexed acicular setae. Parapodia of posteriormost segments more closely spaced than anterior segments. Straight gut apparently without proboscis.

Peronochaeta dubia (Walcott, 1911) gen. nov.

Figures 101 and 103–107, plate 7; figures 112–115, plate 8; figures 94, 95 and 108–110.

1911*c* *Canadia dubia* Walcott p. 118, 119.
1912*b* *Canadia dubia* Walcott p. 190.
1931 *Canadia dubia* Walcott p. 6, plate 7, figure 2; plate 9, figure 8. (non plate 8, figures 1 and 2).
1969 *Canadia dubia* Robison p. 1170.

Material. Lectotype U.S.N.M. 83936*a*. Walcott 1931, plate 7, figure 2. Designated herein (figure 101, plate 7; figure 94).

Paralectotype U.S.N.M. 83936*d*.

Other material U.S.N.M. 195204, 198715–198718, 198736, 198737, 202155, (counterpart is 202168), 202157. There are 4 other U.S.N.M. specimens. G.S.C. 12174.

(i) *History of research*

Four specimens were used by Walcott to illustrate this worm but only two (83936*a*, *d*) can now be referred to *P. dubia* (figures 101 and 103, plate 7; figure 94). 83936*c* (figure 102, plate 7) is probably a polychaete, but it is too poorly preserved to be identified to even generic level. 83936*b* (figure 125, plate 9) has uniramous parapodia but it lacks the diagnostic acicular setae and is larger than *P. dubia*. It is the holotype of *Stephenoscolex argutus* gen. et sp. nov. which is described below (see §8*f*).

(ii) *Morphology*

Only one G.S.C. and fifteen U.S.N.M. specimens have been located and the total may not exceed twenty. Its rarity must be due in part to the likelihood of poorly preserved specimens being unidentifiable but it probably was originally an uncommon component of the Burgess Shale fauna. Of the sixteen known specimens, eleven are complete and have a length ranging from 10–20 mm (average 11 mm).

The prostomium was apparently bilobate (0.45 mm long, 0.2 mm wide) with a pair of short (0.01 mm long) conical papillae that arose from its anterior corners (figures 104 and 105, plate 7; figure 95). The trunk was composed of up to thirty-four segments. It is not known whether segment number was constant in the adults, but nearly all the specimens have more than twenty-five segments. Apparently all the segments had similar, uniramous parapodia which arose on opposite sides of the trunk (figure 108). Each parapodium bore two types of setae which probably lay in a plane more or less parallel to the transverse plane of the body (figures 101, 104, 106 and 107, plate 7; figures 112–115, plate 8, figures 94, 95, 109 and 110). One type consisted of thin (0.005–0.008 mm), moderately long (0.5–0.7 mm) simple setae without ornamentation. They totalled fifteen to twenty per parapodium. Within the podium these setae coalesce into a reflectively preserved unit which probably represents a setal sac rather than an aciculum. The other type were flexed acicular setae (0.2–0.4 mm long, 0.02–0.03 mm wide) which numbered between two and four per parapodium. The simple and acicular setae were derived from the same ramus, but whether from the notopodium or neuropodium is not known. The acicular setae arose close to one margin of the fascicle of simple setae. It is assumed to have been ventral and there is some evidence that the acicular setae were inserted anterior to the main fascicle. The flexure of the acicular setae two thirds of the way along their length resulted in their extending below the simple setae. No branchiae or cirri have been identified. The parapodial spacing was about 1 per 0.5 mm, the exact amount presumably depending on the state of contraction. The spacing of approximately the ten posteriormost parapodia was, however, reduced to about 1 per 0.2 mm (figures 101 and 104, plate 7; figure 113, plate 8; figures 94, 95 and 109).

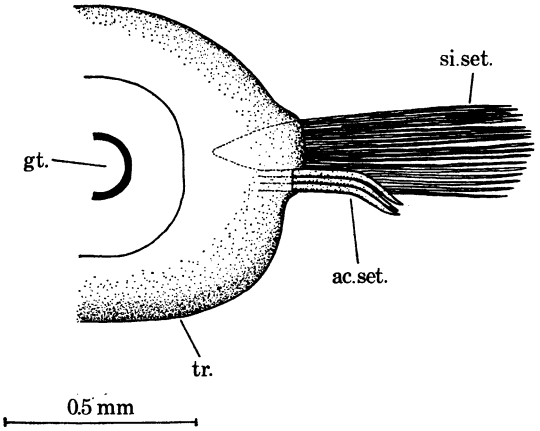


FIGURE 108. Reconstruction of a left parapodium from a mid-segment of *Peronochaeta dubia* (Walcott) gen. nov.

(iii) *Mode of life*

This worm does not appear to have been a deposit feeder and it may have scavenged. The simple setae were presumably used for locomotion. The function of the stout acicular setae is speculative; if *P. dubia* was a burrower they may have been used as anchors during the burrowing cycle.

(iv) *Systematic position*

Although Walcott (1911*c*) placed this worm in *Canadia* it differs in many respects from the type species. It is much smaller, but has more segments. The parapodia are uniramous with acicular setae. *P. dubia* cannot be compared directly with any other fossil or recent polychaete genus. Accordingly *Peronochaeta* gen. nov. is proposed.

P. dubia cannot be accommodated in any known family of polychaetes. The uniramous parapodia are markedly similar to some of the posterior neuropodia of certain members of the

Paraonidae (e.g. *Paraonis uncinatus* Hartman 1965, plate 26, figure C), but among other differences this modern family also possesses notosetae and the acicular setae are confined to the posterior end. Peronochaetidae fam. nov. is proposed to hold this monospecific genus.

(*e*) Insolicorypha psygma *gen. et sp. nov.*

Family INSOLICORYPHIDAE fam. nov.

Diagnosis. Prostomium with bifid organ. Segments 1 and 2 possibly with uniramous parapodia, remaining segments with biramous parapodia, neuropodium with cirri and long simple setae, notopodium with shorter setae.

Genus *INSOLICORYPHA* gen. nov.

Type (*and only known*) *species. Insolicorypha psygma* sp. nov.

Derivation of name. The generic name refers to the curious head: Latin insolitus (odd, unusual) and greek koryphe (head). Greek psygma (fan) refers to the arrangement of the neurosetae.

Diagnosis. Short (12 mm) and broad (1.3 mm) body. Elongate prostomium bearing two massive appendages. Trunk of at least nineteen segments. Parapodia of segments 1 and 2 probably uniramous, segment 1 possibly also achaetous. Other segments have biramous elongate parapodia. Neuropodium bears prominent fascicle of about forty simple setae and three (two dorsal, one ventral) cirri. Notopodium smaller, bears shorter setae, no cirri.

Insolicorypha psygma gen. et sp. nov.

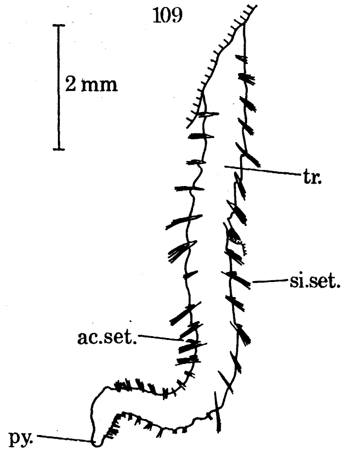
Figures 116–119, plate 8; figures 123 and 124, plate 9; figures 111, 120.

Material. Holotype and only known specimen. U.S.N.M. 198712 (figures 116–119, plate 8; figures 123 and 124, plate 9; figure 111).

(i) *Morphology*

The body (12 mm long) can be divided into a bifid structure and a setigerous trunk (figures 116 and 117, plate 8; figures 123 and 124, plate 9; figure 111). The bifid structure consisted of a stalk (0.6 mm long, 0.4 mm wide) which terminated in two blunt prongs (0.6 mm long) which flared distally (figure 118, plate 8). A number of interpretations on this structure are possible. In modern polychaetes the setae of preserved specimens usually point posteriorly and the bifid structure of *I. psygma* should perhaps be regarded as posterior. As preserved the bifid structure is not completely bilaterally symmetrical. This is due to the slightly oblique burial of the body as may be noted by comparing the distribution of the setae along each side of the body. The abrupt termination of the trunk below the bifid structure could be interpreted as resulting from the rotting or breaking away of the posteriormost trunk leaving the gut projecting freely. This feature has been noted in modern polychaetes (J. D. George, personal communication) as well as in a decayed specimen of *B. setigera* (figure 88, plate 6). It is difficult to understand, however, why the projecting gut should be bilaterally symmetrical. Alternatively the bifid structure could conceivably represent anal cirri. No exact counterpart appears to exist amongst modern polychaetes although some of the alciopids have prominent foliaceous anal cirri. If the bifid structure is posterior, the significance of the three spines at the other end is uncertain.

109



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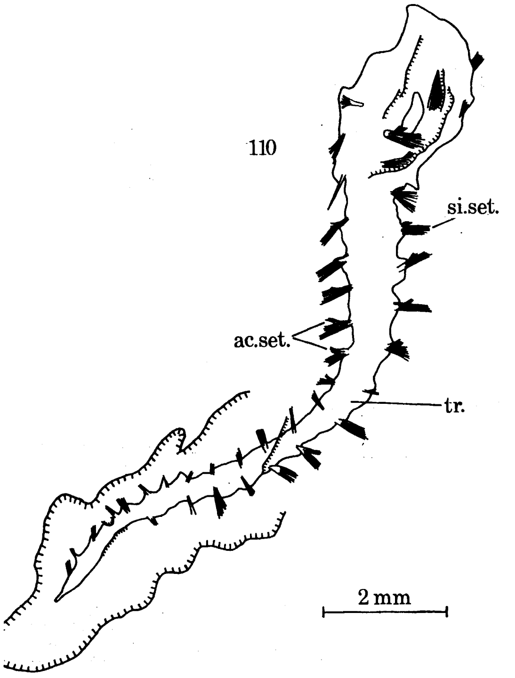

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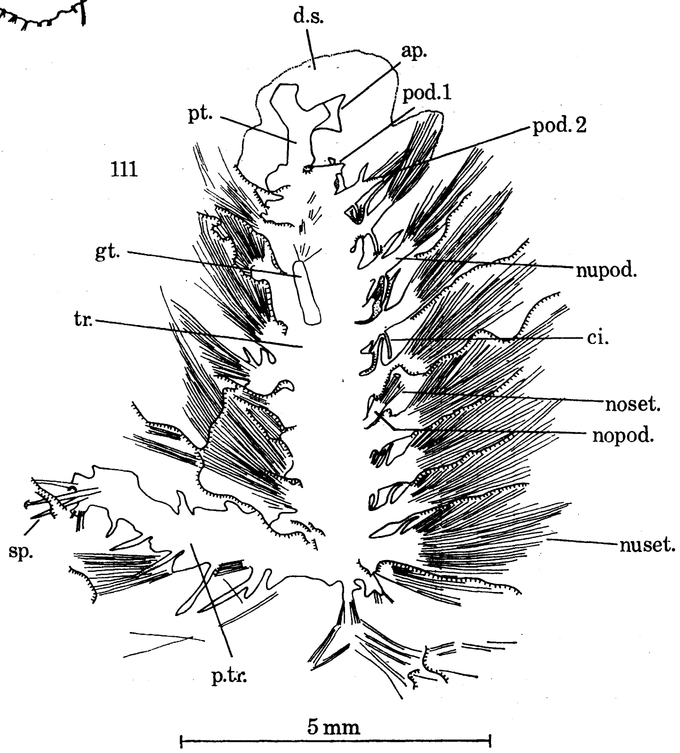

Description of plate 8 and figures 109, 110, and 111

Peronochaeta dubia (Walcott, 1911) gen. nov. Figures 109, 110 and 112–115.
Insolicorypha psygma gen. et sp. nov. Figures 111 and 116–119.
Phyllopod bed, Walcott Quarry.

Figure 109. U.S.N.M. 198717, explanatory drawing of part, see figure 113.

Figure 110. U.S.N.M. 198716, explanatory drawing of part, see figure 114.

Figure 111. U.S.N.M. 198712, composite explanatory drawing of part and counterpart, see figures 116, 117, 123 and 124.

Figure 112. U.S.N.M. 198715, part; dorsoventral, coiled, high angle light from south (magn. × 17).

Figure 113. U.S.N.M. 198717, part; dorsoventral, posterior trunk and pygidium, high angle light from west (magn. × 14).

Figures 114 and 115. U.S.N.M. 198716, part; dorsoventral. Figure 114, anterior looped upon itself, high angle light from west (magn. × 9.2); figure 115, simple and acicular setae arising from trunk, high angle light from southwest (magn. × 33).

Figures 116, 117, 118 and 119. U.S.N.M. 198712, dorsoventral. Figure 116, part; complete, high angle light from southwest (magn. × 14); figure 117, part; low angle light from northeast (magn. × 13); figure 118, part; prostomium with two prong-like appendages, high angle light from west (magn. × 25); figure 119, counterpart; neurosetae and cirri arising from neuropodia and shorter notosetae, high angle light from northeast (magn. × 25.2), holotype.


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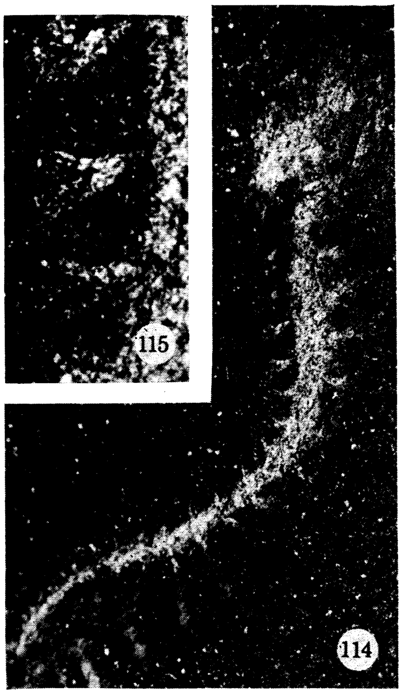
113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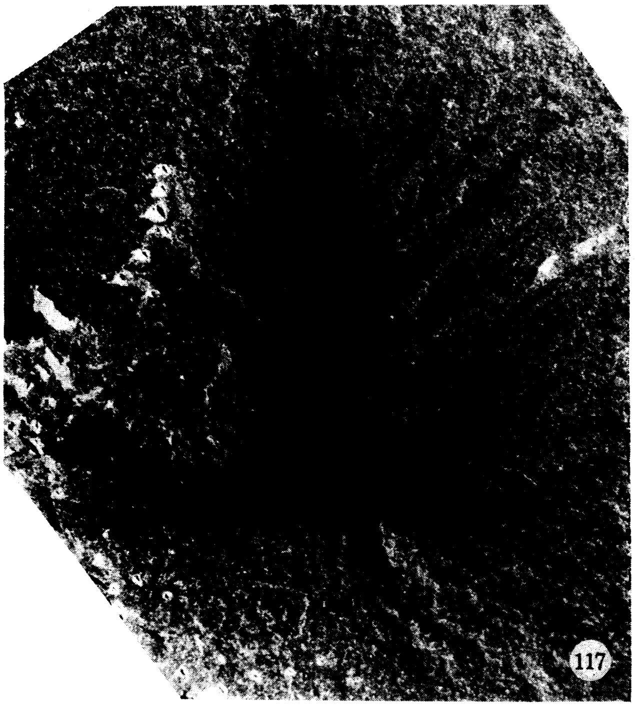
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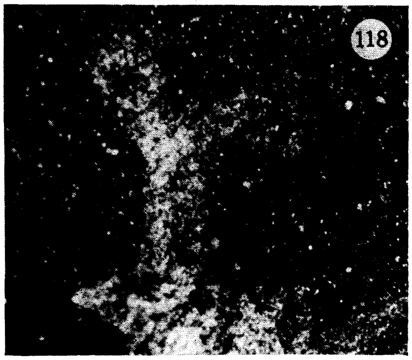
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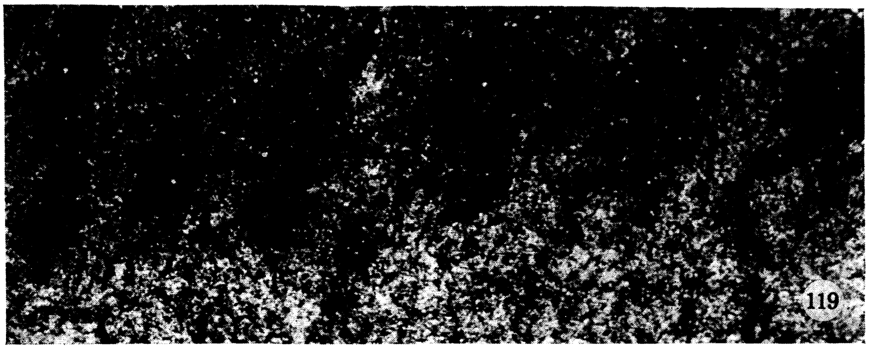
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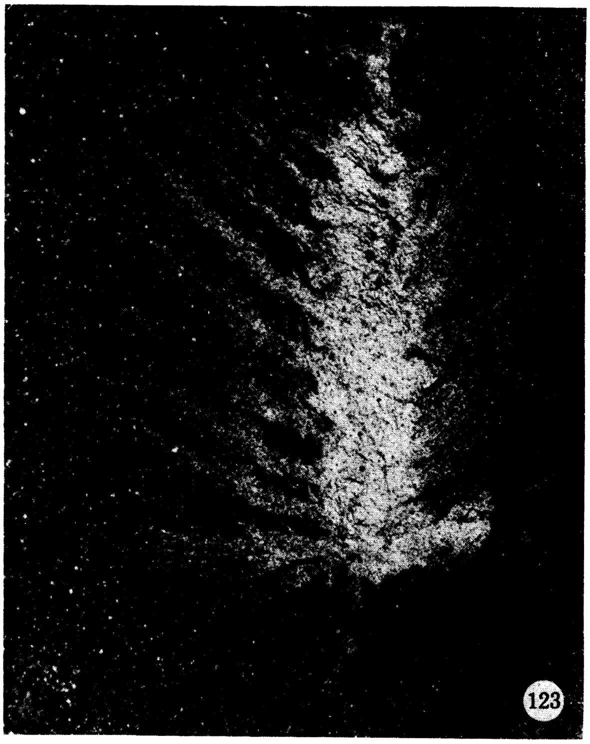
FIGURES 112–119. For description see opposite.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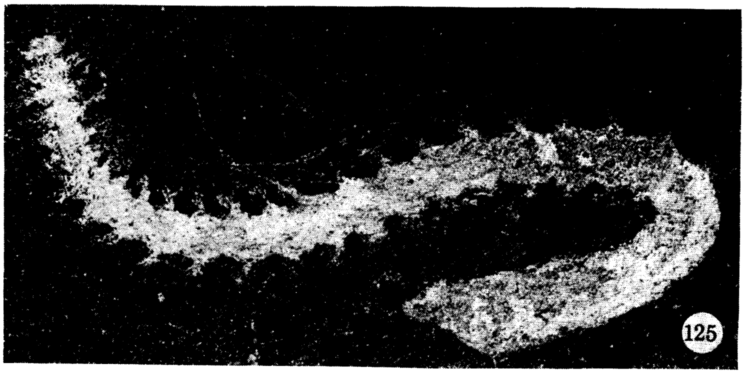
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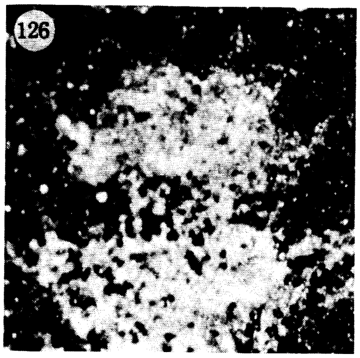
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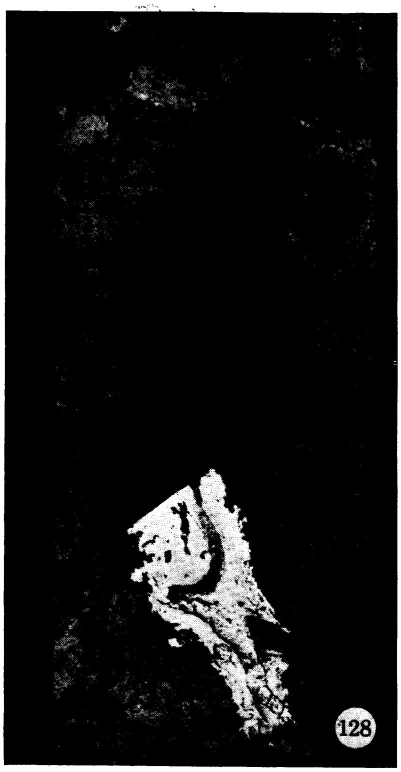
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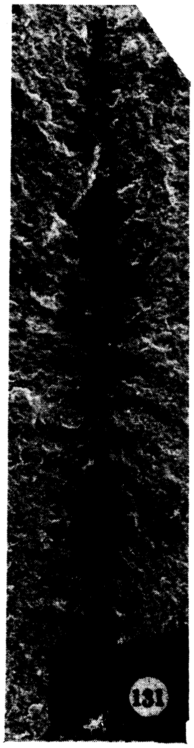
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Figures 123–131. For description see opposite.

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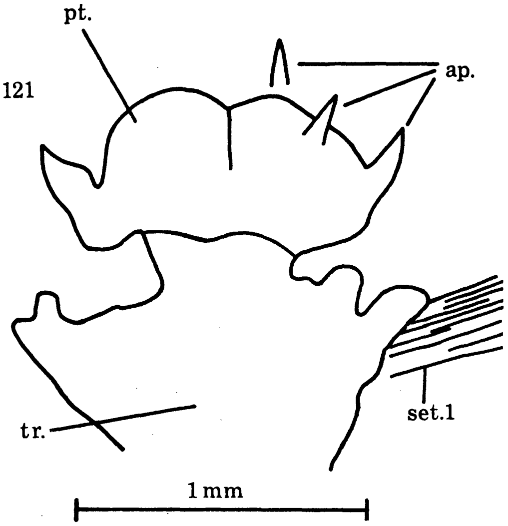

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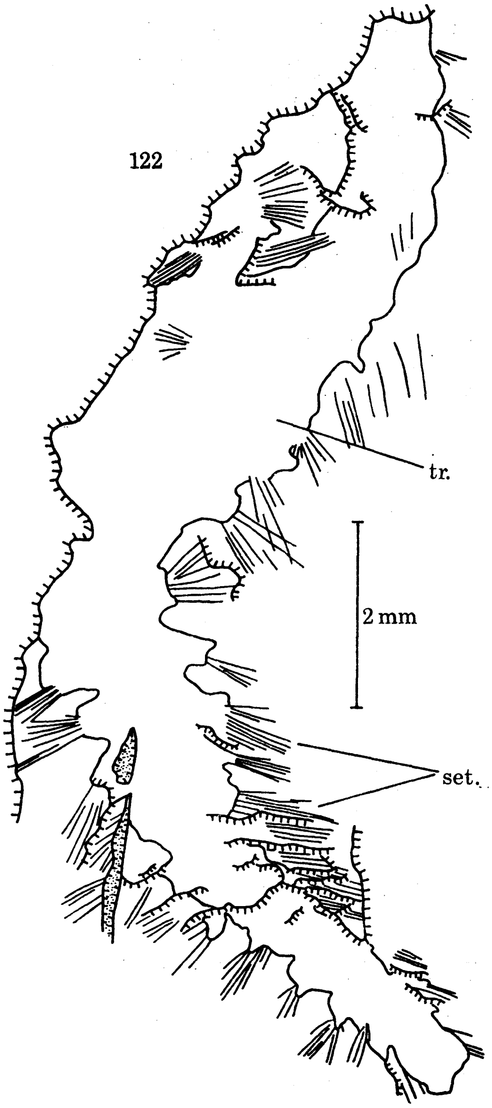

Description of plate 9 and figures 121 and 122

Insolicorypha psygma gen. et sp. nov. Figures 123 and 124.
Stephenoscolex argutus gen. et sp. nov. Figures 121, 122 and 125–127.
Polychaete gen. et sp. undetermined (type A polychaete). Figures 128 and 129.
Phyllopod bed, Walcott Quarry.
Polychaete gen. et sp. indet. Figures 130 and 131.
Spence Shale (Middle Cambrian), Utah.

Figure 121. U.S.N.M. 83936*b*, explanatory drawing of anterior of part, see figure 126.

Figure 122. R.O.M. 32574, explanatory drawing of part, see figure 127.

Figures 123 and 124. U.S.N.M. 198712, counterpart; dorsoventral. Figure 123, complete; high angle light from west (magn. × 10); figure 124, low angle light from southeast (magn. × 9.6), holotype.

Figures 125 and 126. U.S.N.M. 83936*b*, part; dorsoventral-(?)lateral, high angle light from northwest. Figure 125, complete (magn. × 3.8), original of Walcott 1931 (plate 8, figure 1); figure 126, first segment and prostomium with appendages (magn. × 28), holotype.

Figure 127. R.O.M. 32574, part; dorsoventral, posterior trunk, high angle light from east (magn. × 5), paratype.

Figures 128 and 129. U.S.N.M. 198743, oblique, complete, ordinary white light under alcohol. Figure 128, part (magn. × 0.6); figure 129, counterpart (magn. × 0.7).

Figures 130 and 131. UU 1021, part; dorsoventral, complete, ordinary white light (magn. × 3.4). Figure 130, under water; figure 131, in air. Original of Robison 1969 (plate 138, figure 3).

The author does not regard the above suggestions as feasible. The bifid structure is regarded as anterior, but it probably does not represent a proboscis. Although the probosces of some polychaetes, e.g. *Vanadis minuta* (see Day 1967, figure 7.2K) have bifid terminations, unlike the prongs they taper distally. The bifid structure is interpreted here as the prostomium (the proximal stalk) with appendages (distal prongs) which may have borne sensory organs. They probably were not eyes because amongst other groups from the Burgess Shale the eyes are almost invariably preserved as very reflective areas. The prostomium of some genera of the Scalibregmidae possess a pair of divergent frontal horns, although they do not appear to be as prominent as those of *I. psygma*.

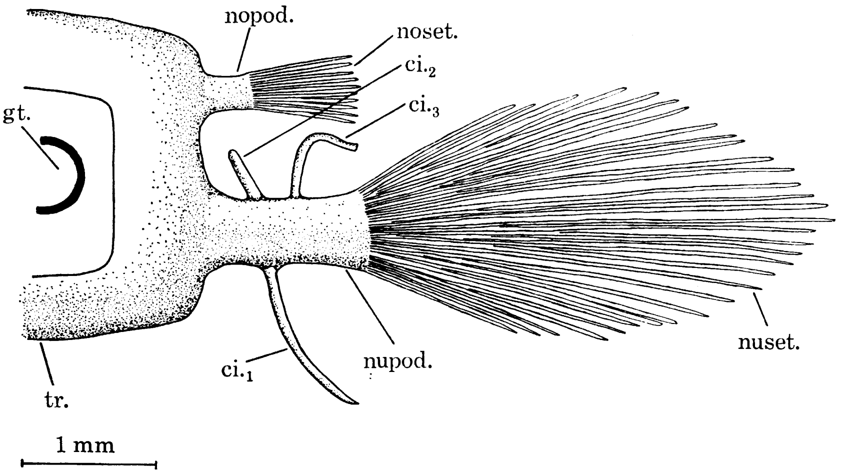

FIGURE 120. Reconstruction of a right parapodium from a mid-segment of *Insolicorypha psygma* gen. et sp. nov.

The trunk consists of approximately nineteen segments (figures 116 and 117, plate 8; figure 111). Whether this was the total is uncertain as portions of the body may have become detached during decay. Excavation of the rock beyond the decayed portion of the trunk failed to reveal additional traces of the worm. The trunk was broad (1.3 mm), although this may be partially a result of muscular contraction. The decrease in width posteriorly is probably principally due to decay, although twisting may also be a contributory factor especially if the trunk was dorsoventrally compressed.

Immediately behind the prostomium the lateral extensions of the trunk are interpreted as the short (*ca.* 3 mm) parapodia of segment 1. They were apparently uniramous and achaetous. The parapodia of segment 2 may also have been uniramous. As the rami carried cirri as well as setae they were probably the neuropodia (figure 116, plate 8; figure 123, plate 9; figure 111). All the other parapodia in the well preserved anterior trunk, and perhaps the posterior trunk, were biramous and consisted of a large and small ramus (figure 120). Apart from an increase in length up to segment 4 the parapodia had a constant structure. The majority of modern pelagic polychaetes, to which *I. psygma* is apparently comparable in mode of life, have uniramous parapodia, but among benthonic polychaetes if one ramus is reduced or absent it is usually the notopodium. The larger ramus is, therefore, assumed to be the neuropodium. Each neuropodium (figure 119, plate 8) was elongate (1 mm) and of more or less constant width (0.3 mm). It bore three unannulated cirri, one (Ci_1, 1.2 mm long) on the presumed ventral surface, and two on the dorsal surface (Ci_2 proximal, 0.2 mm long; Ci_3 distal, 0.6 mm long). The uniramous parapodia of segment 2 may have possessed another cirrus proximal to Ci_1, but preservation is too poor for unequivocal identification. Distally the neuropodium gave rise to a fascicle of between thirty and forty simple capillary setae (0.03 mm wide, up to 3 mm long) (figures 116 and 117, plate 8; figures 123 and 124, plate 9; figure 111).

The notopodia are obscured by the neuropodia, and generally only the proximal section of each podium is visible. Segments 5 and 7 in the counterpart show, however, that the small notopodia (0.4 mm long, 0.2 mm wide) bore about ten setae. Cirri appear to have been wanting (figure 119, plate 8; figure 111). From the posterior end three spines (1.2 mm long) arose (figures 116 and 117, plate 8; figure 111). They are unlikely to be aciculae exposed by decay because the more anterior parapodia apparently lack aciculae, but they might represent acicular setae. A short longitudinal area with slight relief (in the counterpart) within the anterior trunk is interpreted as a section of the gut, perhaps containing finely divided contents.

(ii) *Mode of life*

The large fan shaped fascicles of setae situated on elongate neuropodia appear to have been adapted for active swimming. The notosetae presumably had a more passive role. If the prostomial prongs bore terminal sensory organs this also indicates that *I. psygma* was an active nektonic animal. The rarity of *I. psygma* is in common with other Burgess Shale species which are believed to have been pelagic, e.g. *Odontogriphus omalus* (Conway Morris 1976*a*, 1 specimen), *Nectocaris pteryx* (Conway Morris 1976*c*, 1 specimen) and *Amiskwia sagittiformis* (Walcott 1911*c*; Conway Morris 1976*b*, 5 specimens).

(iii) *Systematic position*

I. psygma cannot be directly compared with any of the other Burgess Shale polychaetes and in particular the parapodia differ in being more elongate with cirri. The setae are longer and narrower than those of *B. setigera* and they differ even more markedly from the setae of *C. spinosa*. The uniramous parapodia of *P. dubia* or *S. argutus* are not closer in form. Although the setae were apparently natatory, *I. psygma* differs by too much from the other Burgess Shale polychaetes to be reasonably considered as an epitokic sexual stage equipped for swimming that characterizes some modern polychaetes, e.g. heteronereids (Clark 1961). For these reasons this worm is considered to represent a new genus and species.

The affinities of *I. psygma* to modern polychaete families would appear to be remote. Superficially *I. psygma* resembles certain pelagic families such as the Pontodoridae, Iospilidae, Lopadorhynchidae and Alciopidae which have elongate podia with cirri (often foliaceous) and long setae. However, in all these families the parapodia are uniramous and the setae are usually compound. The pelagic family Tomopteridae has biramous parapodia but the differences in anatomy are otherwise great. Moreover, the peculiar prostomium of *I. psygma* has no counterpart in these families. Amongst benthonic polychaetes the elongate prostomium of the Glyceridae with four distal antennae is not entirely dissimilar to the prostomium of *I. psygma* whilst the similarity of the scalibregmid prostomium with that of *I. psygma* has been noted above. However, neither the Glyceridae nor Scalibregmidae have any other features that suggest a close affinity with this fossil worm. The Syllidae have prominent cirri, but the parapodia are uniramous with compound setae. The parapodia of the Hesionidae are often biramous with cirri but the prostomium differs markedly. It is concluded that *I. psygma* cannot be placed in any extant or fossil family and Insolicoryphidae fam. nov. is therefore proposed.

(*f*) Stephenoscolex argutus *gen. et sp. nov.*

Family STEPHENOSCOLECIDAE fam. nov.

Diagnosis. Prostomium with at least one pair of appendages. All segments with uniramous parapodia bearing simple setae. Cirri and branchiae absent.

Genus *STEPHENOSCOLEX* gen. nov.

Type (and only known) species. Stephenoscolex argutus sp. nov.

Derivation of name. The generic name is derived from Mt Stephen which is close to the Burgess Shale and the latin word Scolex (worm). The trivial name *argutus* (bright, shiny) refers to the very reflective preservation of this species.

Diagnosis. Slender body, about 3 cm long. Bilobed prostomium with a prominent pair of short posterolateral appendages and possibly a pair of smaller anterolateral and anterior appendages. Trunk of about forty segments, all similar with uniramous parapodia each bearing about fifteen simple setae.

Stephenoscolex argutus gen. et sp. nov.

Figures 125–127, plate 9; figures 121 and 122.

1931 *Canadia dubia* Walcott plate 8, figure 1.

Material. Holotype U.S.N.M. 83936*b* (figures 125 and 126, plate 9; figure 121). Paratype R.O.M. 32574.

(i) *Morphology and mode of life*

Specimen 83936*b* (figure 125, plate 9) is complete (32 mm long), but specimen 32574 (figure 127, plate 9; figure 122) lacks the anterior part of the animal and only 15 mm is preserved. The reflective preservation of both specimens is noteworthy. No features of internal anatomy are preserved. The prostomium was bilobate (1.2 mm wide, 0.5 mm long). It had a prominent pair of short (0.25 mm long) posterolateral, non-jointed conical papillae. The right lobe also has preserved an anterolateral and an anterior appendage (both 0.2 mm long) (figure 126, plate 9; figure 121). Although these latter appendages are not duplicated on the other lobe they appear to be original features that are incompletely preserved.

In specimen 83936*b* (figure 125, plate 9) about twenty-one setigerous parapodia are visible. Their disappearance posteriorly may be due to the torsion of the trunk so that the reflectively preserved setae are superimposed on the reflective trunk. In specimen 32574 (figure 127, plate 9; figure 122) the setae extend to the posterior end. All the parapodia appear to have been similar and uniramous. Each supported a fascicle of between ten and fifteen simple straight setae (0.6 mm long). There were no cirri or branchiae. The spacing of the parapodia (6–8 per 5 mm) suggests that the 83936*b* possessed about forty. Little can be deduced about the mode of life of *S. argutus*, but it is conceivable that it moved either in or over the muddy sediment.

(ii) *Systematic position*

Although specimen 83936*b* was previously placed in *P. dubia* (Walcott 1931, Conway Morris 1976*b*) it differs from this polychaete in a number of features. It was up to three times as long as *P. dubia*, but despite its size it had only a few more parapodia because of their greater spacing.

The parapodia were uniramous in both worms, but in *S. argutus* they lacked acicular setae. The prostomium apparently had additional appendages. *S. argutus* cannot be compared more closely with any of the other Burgess Shale polychaetes.

S. argutus is not clearly related to any modern family. It has superficial similarities to the Iospilidae but this family is characterized by compound setae, cirri, and a simpler prostomium which suggest at best only a distant connection. Accordingly Stephenoscolecidae fam. nov. is proposed.

(*g*) *Burgess Shale polychaete type A* (*U.S.N.M.* 198743)

Figures 128 and 129, plate 9

(i) *Morphology and mode of life*

This polychaete is known only from a single specimen, which is poorly preserved and incomplete at either end owing to rock breakage (figures 128 and 129, plate 9). The author, therefore, has refrained from erecting a new genus and species although it obviously differs from the other Burgess Shale polychaetes. The bedding surface on which the specimen is exposed is weathered. The contrast of the specimen is slight, but it may be enhanced by immersion in water or alcohol. The specimen is cut obliquely by a chlorite vein and the posterior section of the fossil film is more reflective. A similar feature was noted by Whittington (1975*a*) and it occurs sporadically elsewhere amongst the Burgess Shale fossils.

Nothing is known of the prostomium or pygidium. The preserved length is 17.5 cm but the original length presumably exceeded 20 cm. The width of the trunk is about 17 mm. The body can be divided into two parts. One section (10 cm long) is taken to be the anterior and it possessed about twenty pairs of spinose appendages which are interpreted as setigerous parapodia. The remainder of the body was apparently apodous. It is unlikely that the parapodia have been obscured by decay or torsion and this feature may be original. The poor preservation of the parapodia makes their interpretation difficult, but they seem to have formed conical (7–8 mm long) projections of the body wall which housed a spine (16 mm long), or possibly a bundle of spines, which projected from the parapodium. The character of the appendages does not appear to change along the length of the anterior body. The parapodial spines could represent aciculae, but in modern polychaetes they rarely extend far beyond the distal tip of the parapodium. They might, therefore, be regarded as one or more massive setae.

The centre of the body is occupied by a longitudinal strip (3–4 mm wide) with prominent relief which is interpreted as the sediment filled gut. Except for a pronounced kink in its posterior section it is fairly straight. The sediment has a scalloped appearance which presumably results from its packing into the gut. Anteriorly the course of the gut is interrupted and it extends via an unfilled section away from the rest of the body as an adaxially tapering mass. If this anterior length represents the proboscis it is difficult to see why it should be sediment filled and situated so posteriorly. Alternatively the gut may have drifted from the body due to rupturing caused by decay.

The sediment filled gut indicates a benthonic existence, although it is not known whether type A was epifaunal or was a burrower. Its rarity must be due to factors such as original sparseness or extension beyond its normal range.

(ii) *Systematic position*

Although type A is clearly distinct from the other Burgess Shale polychaetes, incomplete and poor preservation make speculation on the affinities of this polychaete to other fossil and recent forms unwise.

9. PRESERVATION AND DECAY OF THE BURGESS SHALE POLYCHAETES

Despite the exquisite preservation, the Burgess Shale fossils underwent slight but recognizable decay (Conway Morris 1977*b*). The majority of the polychaetes are preserved complete. In some specimens, however, of *C. spinosa* (figure 17, plate 2; figures 56 and 57, plate 4), *B. setigera* and the only specimen of *I. psygma* (figures 116 and 117, plate 8; figure 111) some of the setae are dislodged: presumably by decay destroying parapodial muscles. In such specimens of *C. spinosa* and more especially *B. setigera*, one or more fascicles of setae are detached from the trunk. When the fascicle is adjacent to the body it usually remains intact. However, at a greater distance from the body the setae are more scattered, presumably because the tougher tissues which bound the fascicle rotted. Detachment of the setae may have occurred during transport in the mudflows but it is perhaps more likely that disassociation took place in the post-slide environment, when the specimens lay on the sediment surface so that the loosened setae were scattered by very weak currents. During burial the majority of specimens presumably came to lie in, rather than on, the sediment. Such entombment would have helped to prevent disassociation of the body. The partial disintegration of the trunk in *C. spinosa* is also attributed to decay. In specimen 199758 (figure 39, plate 3) the posterior trunk is bent at a sharp angle to the rest of the body and shows signs of detachment. In specimen 198742 (figures 53 and 54, plate 4; figure 45) the posterior trunk is almost completely detached from the remainder of the attenuated trunk. In an unnumbered R.O.M. specimen this process has proceeded slightly further and the two sections of the body have drifted apart and are now separated by sediment. A similar feature has also been noted in a few specimens of *B. setigera* (e.g. specimen 199741). With prolonged rotting in *C. spinosa* and *B. setigera* the body fragments are widely scattered. In specimen 199655 (*C. spinosa*), for instance, only the anterior third of the body is preserved. In specimen 198707 (*B. setigera*) much of the body seems to have vanished and in addition to the disorganized fascicles the gut projects beyond the surviving trunk (figure 88, plate 6). A similar feature has been noted in modern decomposing polychaetes (J. D. George, personal communication). Some of the polychaete specimens have patches of minute pyritic spherules which are interpreted as the product of anaerobic bacteria living on the surface of the corpse.

Rotting has hindered a clear understanding of *I. psygma* (see §8*e*, i). In the only known specimen, two thirds of the body is comparatively well preserved, whereas the remainder is less so; there has been considerable loss and scattering of setae (figures 116 and 117, plate 8; figure 111). Why rotting should have been so polarized is uncertain. The posterior body may have projected above the sediment into the overlying water where decay perhaps was more rapid facilitating scattering of the parts. Destruction of the posterior by the next incoming mudflow may have been averted by a protective blanket of hemipelagic mud (see Piper 1972). Alternatively in modern polychaetes it has been observed that as the animal dies the mid-segments start to rot before the anterior and posterior regions (J. D. George, personal communication). It is possible that this occurred in *I. psygma* and one end of the specimen has been entirely lost.

Polarized decay has also been observed in *B. setigera* (specimen 199680) and *P. dubia* (figure 107, plate 7).

The great majority of specimens of *C. spinosa* and *B. setigera*, a few specimens of *P. dubia* and the only specimen of *I. psygma* have a dark stain associated with them (figure 5, plate 1; figures 19, 20, 24 and 25, plate 2; figures 31, 32, 37, 38 and 39, plate 3; figures 51, 53, 54 and 62, plate 4; figures 73 and 77, plate 5; figures 82, 87 and 88, plate 6; figures 116 and 117, plate 8; figures 15, 16, 27, 28, 44–46, 67, 79, 81 and 111). This stain was first noted in detail by Whittington (1971 *a*, *b*) in his redescription of *M. splendens* (Arthropoda). Although the dark stain is characteristic of *M. splendens* and most of the polychaetes, its occurrence in other species is apparently sporadic. Whittington (1971 *a*, *b*, 1974) suggested that the dark stain was derived from body contents being squeezed out by sedimentary compaction; Conway Morris (1976 *b*, 1977 *a*, *b*), however, argued that the stain represents body contents that oozed out during decay. The dark stain associated with the polychaete specimens is very rarely as prominent or as extensive as that of *M. splendens*. In dry specimens it is usually inconspicuous but it becomes clear when they are immersed in water or alcohol. The stain is usually found around the anterior and/or posterior ends in the form of an irregular halo. Sometimes it extends along the sides of the specimen. This distribution suggests that fluids first escaped via the mouth and anus, but with prolonged decay the body wall also ruptured. The dark stain has also been noted on occasions to be adjacent to detached fascicles of setae in *B. setigera*, suggesting that at this point body contents leaked through the trunk. Specimen 198723 (figure 38, plate 3) has around its anterior a slightly reflective mass which is surrounded by a halo of dark stain material. This cloudy mass may represent more extensive release of decayed internal organs than usual. The reflective strand that traverses the cloudy mass was interpreted in §8 *b*, i, as an attenuated proboscis. It is not impossible, however, that it represents a detached portion of the intestine similar to the cases noted by Whittington (1971 *a*, figure 22; 1971 *b*, plate 16, figure 2) in *M. splendens* where the intestine extends from the posterior end. The areal extent of the stain is presumably, for specimens of an equal size, more or less proportional to the degree of decay. The extensive development of the stain in specimen 198742 (figures 53 and 54, plate 4; figure 45) which shows other evidences of relatively advanced decay cannot, therefore, be coincidental.

10. Concluding remarks on the Burgess Shale polychaetes

In comparison with the situation in many modern marine environments the Burgess Shale polychaetes had a relatively minor role. Although they account for about the same fraction (5% of the total number of genera) of the fauna as the priapulids, numerically they are far less important. The morphological diversity of the polychaetes is striking and all the families are monospecific. This variety suggests a long evolutionary history. The ancestral polychaete is generally regarded as being oligochaete-like (Fauchald 1974), if not actually derived from the oligochaetes themselves (Clark 1964, 1969). Unfortunately none of the Burgess Shale polychaetes appears to throw much light on the possible nature of the primitive polychaetes. With the possible exception of the Canadiidae none of the Burgess Shale families appear to be closely related to modern families. The absence of jawed forms is notable and the rise of the polychaetes may perhaps be traced from the Ordovician with the appearance of fossil jaws or scolecodonts which belonged to eunicid-like forms. By Carboniferous times polychaete diversity was considerable and many jawed forms existed (Thompson, in the press). The polychaetes appear to be an example of a group that has successfully occupied most marine niches. In comparison the descendants of other Cambrian groups, e.g. priapulids (Conway Morris 1977*b*) apparently only avoided extinction by largely adopting habitats in marginal environments which are physically and chemically less attractive to most metazoans.

11. Other cambrian and precambrian soft bodied fossils ascribed to the polychaetes

Robison (1969, plate 138, figure 3) described a poorly preserved fossil polychaete from the Spence Shale (Middle Cambrian) near Calls Fort, Utah (figures 130 and 131, plate 9) as *Canadia* sp. He believed that its strongest resemblance lay with *P. dubia.* The parapodia are uniramous and each gave rise to about eight stout, straight, simple setae. Its length is about 29 mm and it consists of approximately twenty-one segments. Neither prostomium (Robison 1969) nor pygidium are clearly preserved. The absence of acicular setae and its greater size show that it is not closely related to *P. dubia* as now defined (see §8*d*). It is, however, not dissimilar to *S. argutus* (figures 125 and 127, plate 9; figure 122). The parapodia and size are comparable although the Spence Shale polychaete has rather greater parapodial spacing than *S. argutus.* The absence of prostomial details makes it impossible to establish how closely related these two species were but a fairly close relationship may have existed.

Chapman (1928) described Cambrian fossils from Tasmania which he called *Tasmanadia twelvetreesi.* He believed that they represented setae and brief comparison was made with *Canadia. T. twelvetreesi* is, however, now interpreted as an arthropod track (Glaessner 1957). Similar remains described by Miroshnikov, Krawzov & Shcheylova (1959) and Miroshnikov & Krawzov (1960) from the Upper Cambrian of the River Chopko area in Siberia as *Canadia* also appear to be trace fossils. They cannot be compared with any Burgess Shale polychaete.

The late Precambrian Ediacarian soft bodied fauna includes three worms, *Dickinsonia*, *Spriggina* and *Marywadea*, which are generally ascribed to the polychaetes. Although the Ediacarian fauna has a worldwide distribution with the exception of a dickinsoniid from Russia (Sokolov 1976; Keller & Fedonkin 1977) and a possible sprigginid from SW Africa (Germs 1973) these worms have only been found in South Australia from the Pound Quartzite where they account for about 25 % of the specimens found (Glaessner 1971). Dickinsoniids reported from the Silurian of Pennsylvania (Johnson & Fox 1968) have been reinterpreted as pyritic pseudofossils (Cloud 1973).

Dickinsonia (*D. costata* (type species), *D. brachina*, *D. elongata*, *D. lissa* and *D. tenuis*) had an oval to elongate body (adults 17–60 cm long) which was composed of numerous segments. The anterior and posterior segments fanned forwards and backwards increasingly tightly and the leading edges of segment 1 were fused together and surrounded the head at the point of closure. Harrington & Moore (1956) placed *Dickinsonia* in the coelenterates, but the bilateral symmetry, prominent segmentation and gut caeca do not lend credence to their argument (Glaessner 1960; Glaessner & Wade 1966). *Dickinsonia* has, however, a striking resemblance to the modern aberrant polychaete *Spinther* (Glaessner 1959, figure 4; Glaessner & Wade 1966, plate 101, figure 4, plate 102, figure 3, plate 103, figure 1; Wade 1968, figures 17, 27 and 28; 1972, plates 5–7; Keller & Fedonkin 1977, plate 1, figure 5, plate 2, figures 1–3). The spintherids are a small (up to 5 cm in *S. arcticus*, Manton 1967) group of sluggish polychaetes semi-parasitic on sponges to which they efficiently attach themselves with hooked neurosetae. The quasi-radial symmetry of the body is highlighted by the elongate setigerous notopodia that radiate across the dorsum, but is also reflected in the segmentation, septa and gut caeca (Manton 1967).

The segments of *Dickinsonia* are equally prominent on the dorsal and ventral sides. The dorsal part of the segments of *D. costata* possess an additional ridge that Wade (1972) compared to the notopodial ridges of *Spinther*. The apparent absence of the notosetae themselves, which should be readily preservable, in all the dickinsoniids is surprising. An indistinct lobe at the base of segment 1 was cautiously interpreted by Wade (1972) as a prostomium or an appendage thereof. Wade argued that increase in size from spintherid ancestors led to the probable redundancy of the neurosetae as effective locomotory agents in favour of more general body contractions and undulations. She claimed that the dickinsoniids were active swimmers and crawlers. Wade's claim (p. 187) that quasiradial symmetry was maintained in the large *Dickinsonia* because 'For a mobile worm, there are advantages in not greatly diminishing (and weakening the musculature in) the anterior segments. . . The combination of selection for flatness and mobility seems enough to explain the encircling of the prostomium by the first body segment' does not find a parallel amongst modern animals. True and quasiradial symmetry is, however, characteristic of immobile or semi-sessile animals such as *Spinther* and the Myzostomaria and is seen in its initial stages in some slow moving amphinomid polychaetes, e.g. *Euphrosine* (Day 1967, figure 3.1*u*). In the dorsoventrally compressed bathypelagic nemerteans, for instance, radial symmetry is never closely approached – rather in advanced mobile forms (e.g. *Nectonemertes*) the bilateral symmetry is very pronounced. If *Dickinsonia* was active it is difficult to understand why the putative prostomium, which presumably had an attendant battery of sensory organs, should remain to the posterior. In all active polychaetes the principal sensory organs are anterior. The author would argue that *Dickinsonia* was semi-sessile. Its shape and flatness may be a response to factors such as stability, gaseous diffusion at low oxygen tensions, and even feeding if the dorsal ridges were used as food collectors. There is no definite evidence that *Dickinsonia* was a polychaete and its actual affinities remain uncertain. The similarity with the spintherids is probably a product of parallel evolution.

Similar difficulties arise with the interpretation of *Spriggina* (*S. floundersi*, see Glaessner 1958, plate 1, figures 1–3; 1959, figures 1 and 2; 1962, plate 1, figure 8; Glaessner & Daily 1959, plate 47, figures 1–4), *Marywadea* (*M. ovata*, see Glaessner & Wade 1966, plate 98, figure 4; Glaessner 1976, figure 1) and an unnamed possible sprigginid from SW Africa (Germs 1973, figures 1–3). The sprigginids are up to about 4.6 cm long and are bilaterally symmetrical. An unsegmented arcuate head with trailing corners precedes forty or more segments. Notwithstanding references to a possible affinity with the arthropods, Glaessner (1958, 1959, 1960, 1962, 1976) interpreted the sprigginids as polychaetes and compared them with the modern pelagic tomopterids. In comparison with the complex and specialized tomopterid anatomy that of the sprigginids is relatively simple and the resemblance between the two groups would seem to be completely superficial. Glaessner (1976) rejected suggestions that the head was an arthropodan headshield but it must also be admitted that it is unlike any known polychaete prostomium. He considered that each segment and possibly the corners of the supposed prostomium of *M. ovata* (Glaessner & Wade 1966) ended in acicular setae. In modern polychaetes the parapodia are usually fairly widely separated to enable freedom of movement during locomotion. In the sprigginids, however, the segments and supposed parapodia are tightly packed. Examination of photographs of specimens does not contradict the view that the sharp terminations of the segments have been misinterpreted as parapodia ending in acicular setae. Moreover, in no recent polychaete does the preoral prostomium give rise to setae. The apparent sclerotization of the spriggininds, especially of the head (Glaessner 1960, 1962) does not find a counterpart in recent polychaetes. The author concludes that there is no firm evidence that the sprigginids are polychaetes and that their affinities are unresolved. Thus, although it is most probable that the polychaetes had a long Precambrian history the first definite soft bodied remains only occur in the Middle Cambrian (Spence and Burgess Shales).

Lest it be thought that any segmented, soft bodied fossil must automatically be regarded as an annelid or primitive arthropod it is worth recalling that a number of segmented animals from the Burgess Shale which were previously placed in the arthropods or annelids have been shown to possess novel features which not only exclude them from these phyla but any other known phylum as well (Conway Morris 1976*b*, 1977*a*; Whittington 1975*a*). It seems likely that the late Precambrian and Cambrian were times of intense experimentation by the Metazoa. It appears that a number of groups with bizarre body plans ultimately failed in the competition for survival and became extinct early in the Palaeozoic.

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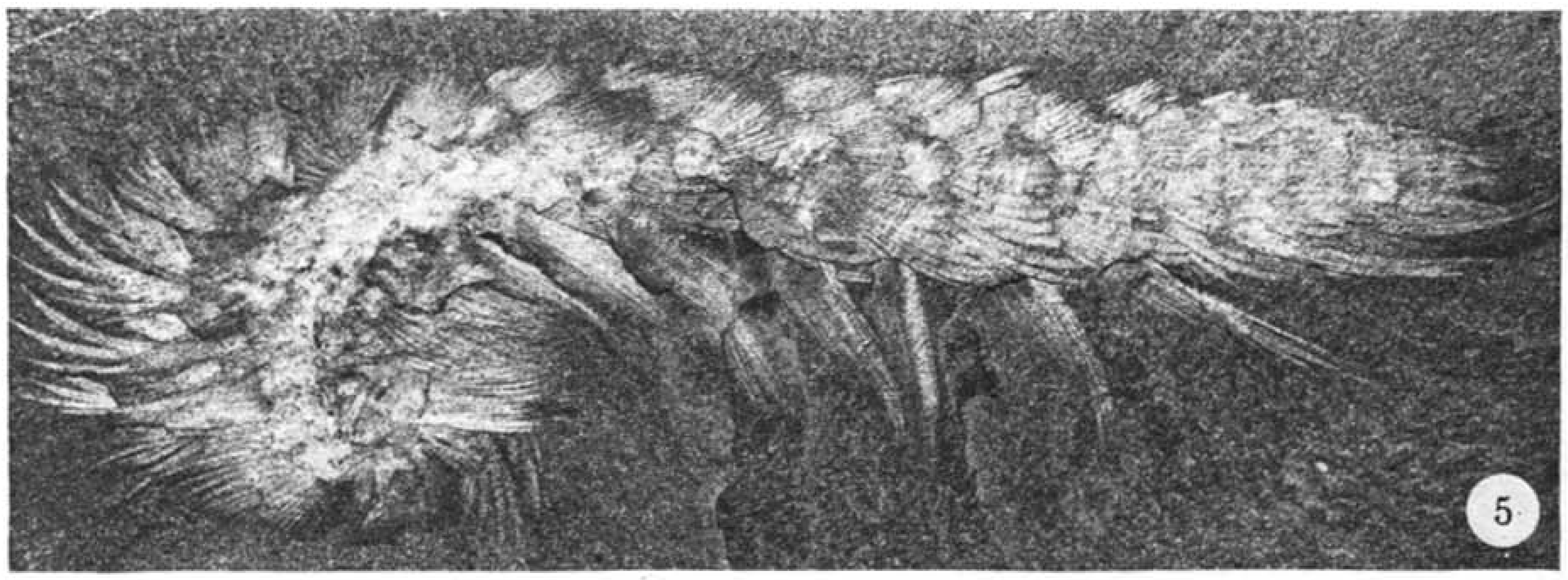
Explanation of abbreviations

(a) Institutions

B.M.N.H.	British Museum (Natural History), London
G.S.C.	Geological Survey of Canada, Ottawa
R.O.M.	Royal Ontario Museum, Toronto
U.S.N.M.	United States National Museum (now National Museum of Natural History), Washington, D.C.
U.M.	University of Montana, Missoula
U.U.	University of Utah, Salt Lake City

(b) Descriptive features of the fossil material

ac.	aciculum
ac. set.	acicular setae (in *P. dubia*)
ap.	appendage of prostomium
br.	branchia
?car.	possible caruncle
ci.	cirrus
co. part	counterpart
do. ci.	dorsal cirrus
d.s.	dark stain (delimited by dotted line)
fa.	faecal pellets (in *B. setigera*)
el. nuset.	elongate neurosetae (in *C. spinosa*)
gt.	gut
gt. ct.	gut contents
im. noset.	imperfect notosetae
im. nuset.	imperfect neurosetae
inr. s.	inter-ramal space
L.	left, as prefix
?ms.	possible muscle
nopod.	notopodium
noset.	notosetae
nupod.	neuropodium
nuset.	neurosetae
p. noset.	notosetae of posterior segments
p. tr.	posterior trunk
pod.	parapodium
pr.	proboscis
pt.	prostomium
py.	pygidium
R.	right, as prefix
rl.	area of localized relief
set.	setae
si. set.	simple setae (in *P. dubia*)
sp.	spine
s.s.	setal sac
tr.	trunk
tt.	tentacle
vt. ci.	ventral cirrus
1-n	number in series of notosetae, neurosetae, podia or cirri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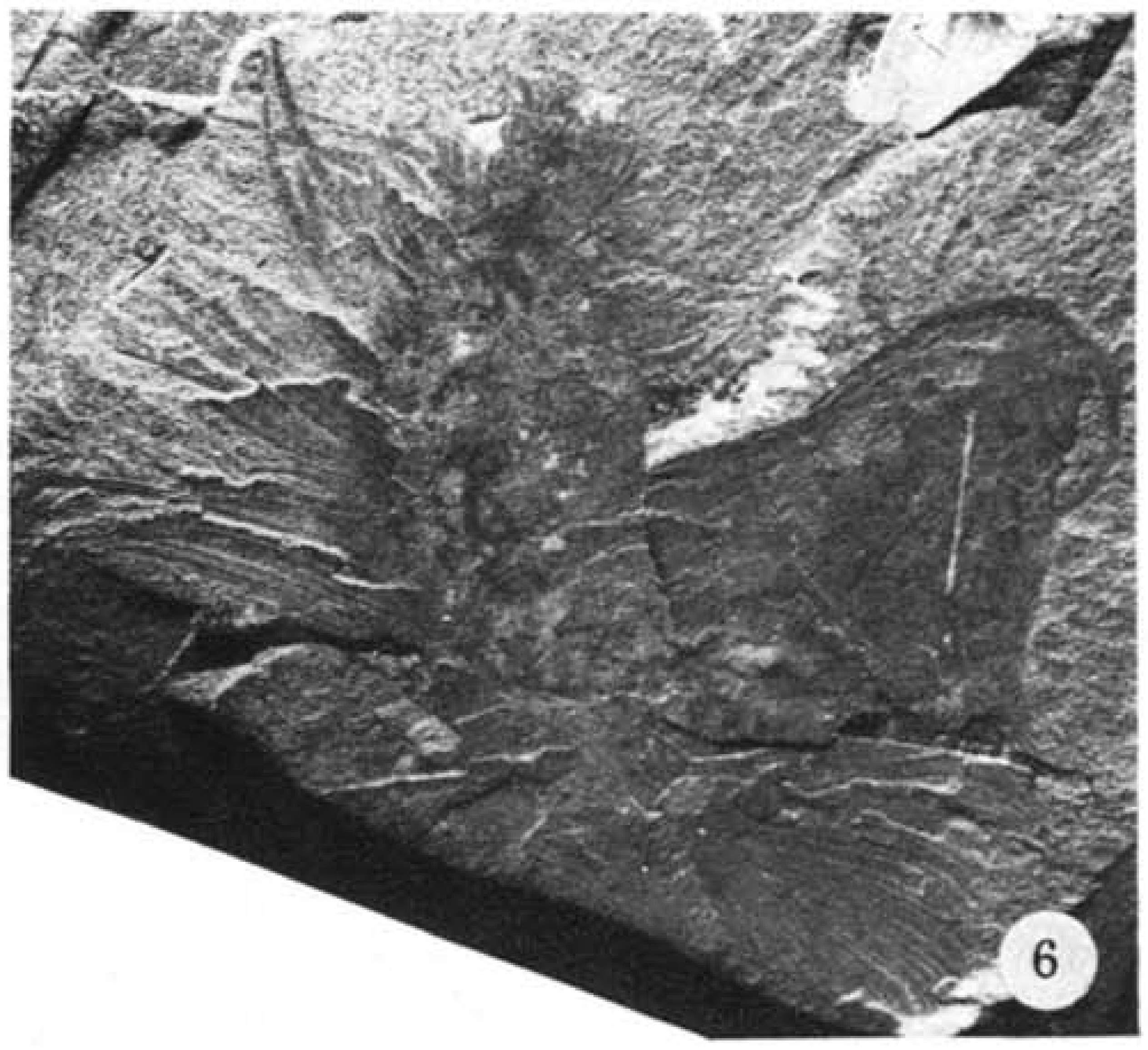
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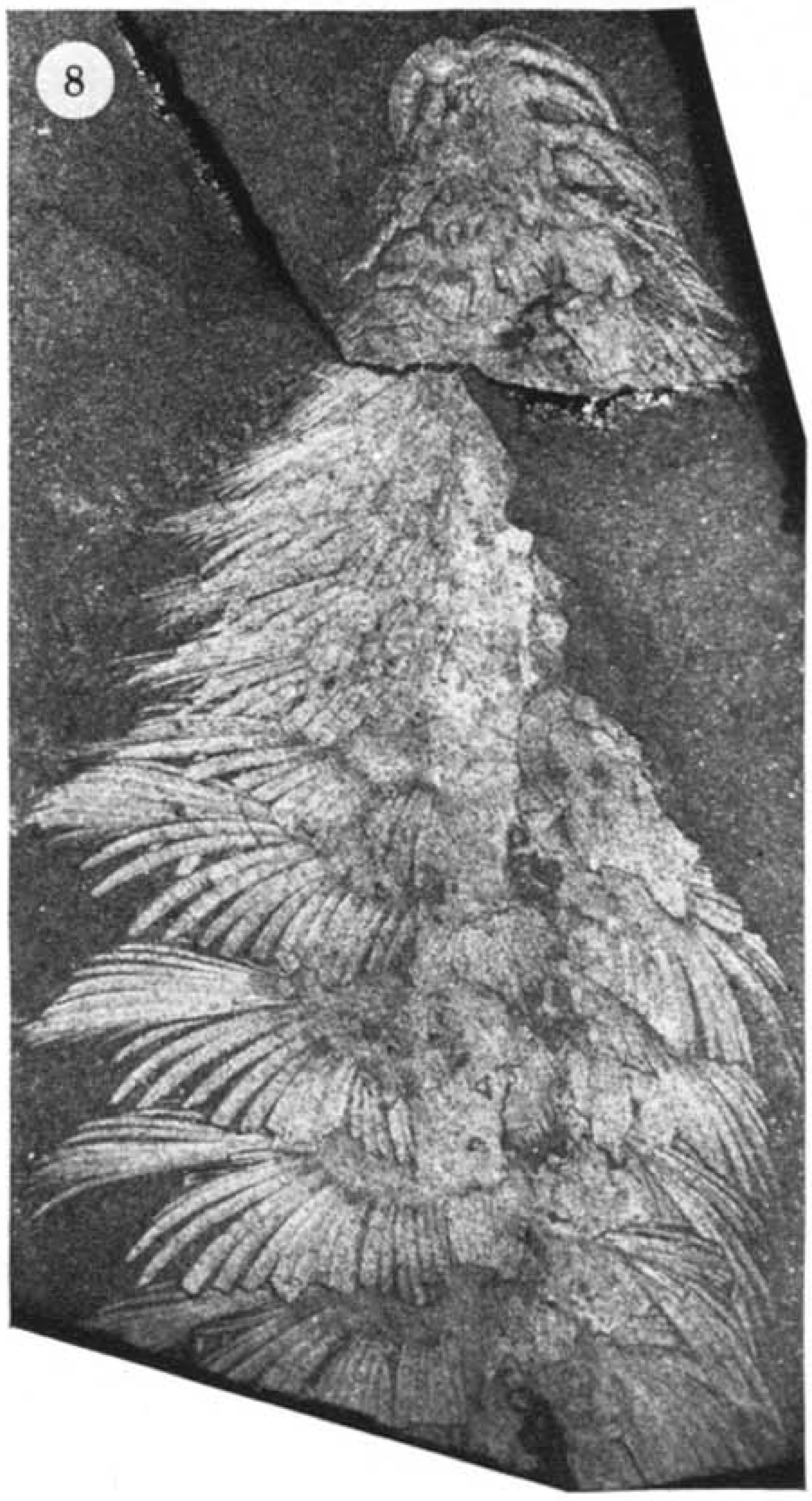
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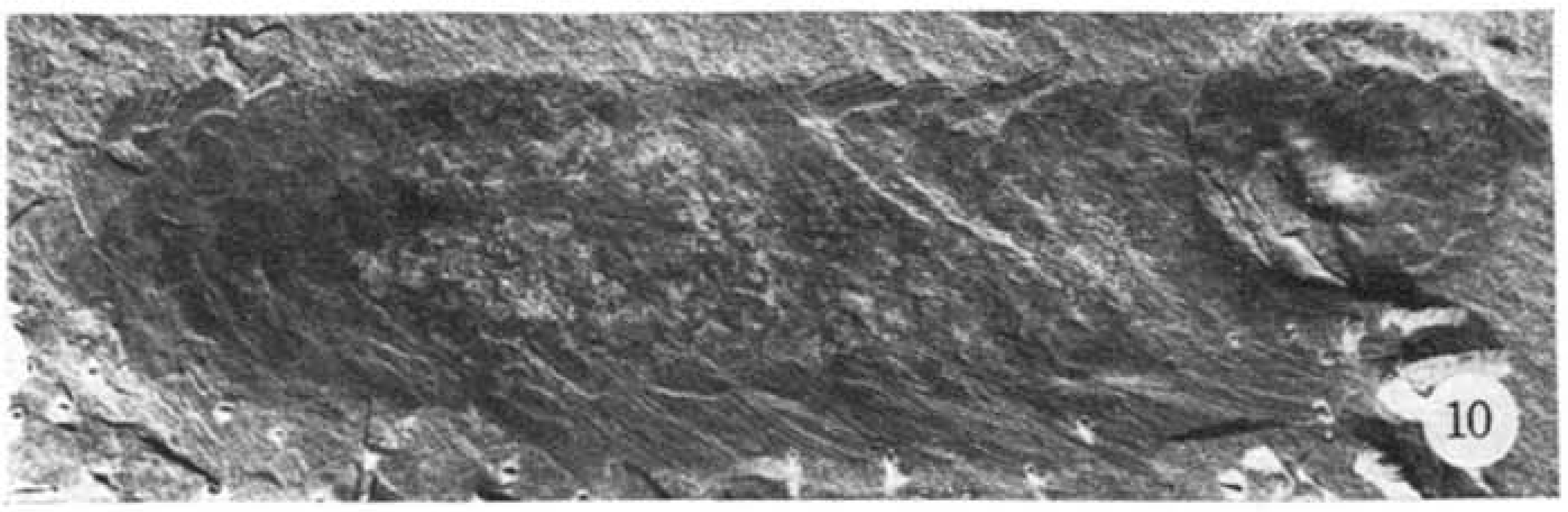
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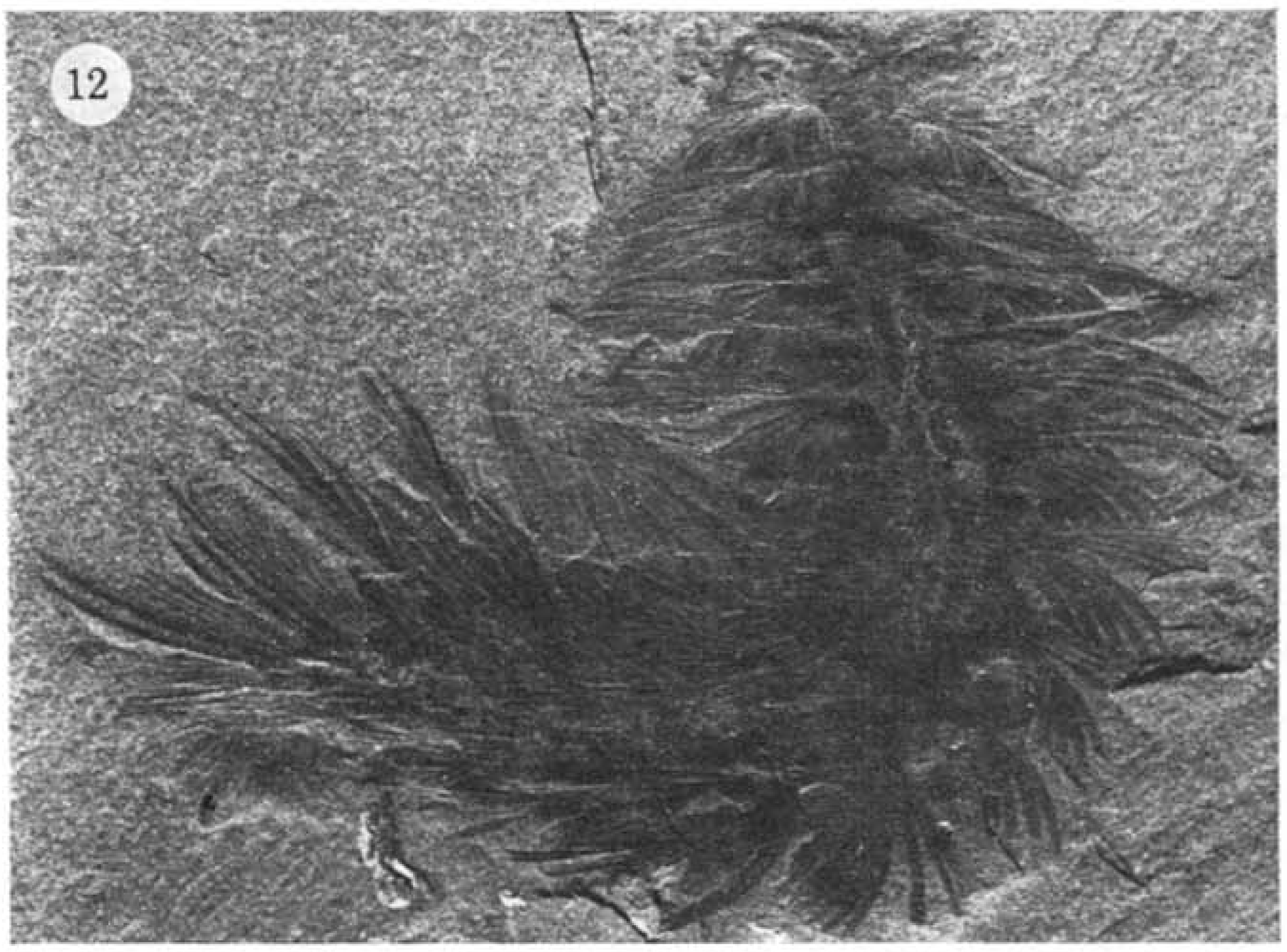
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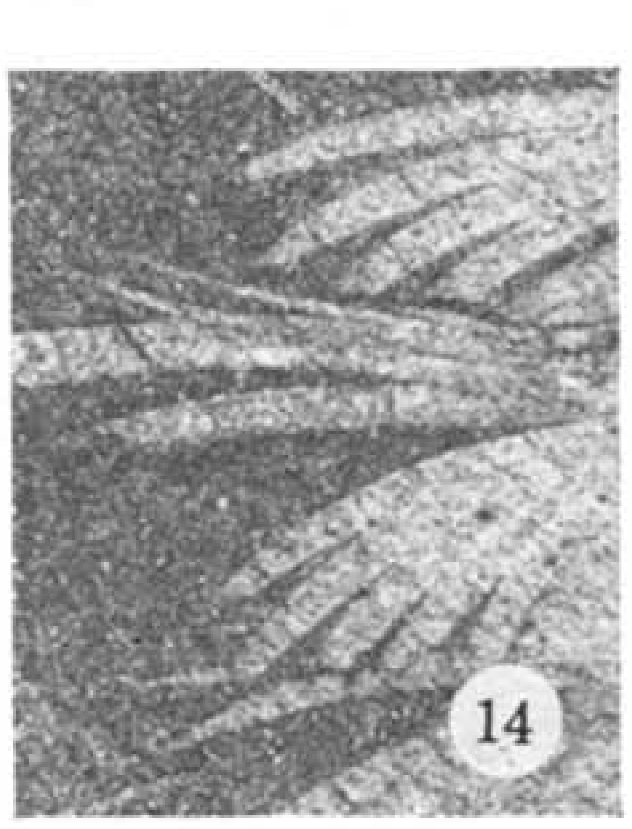
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Figures 5–14. For description see opposite.


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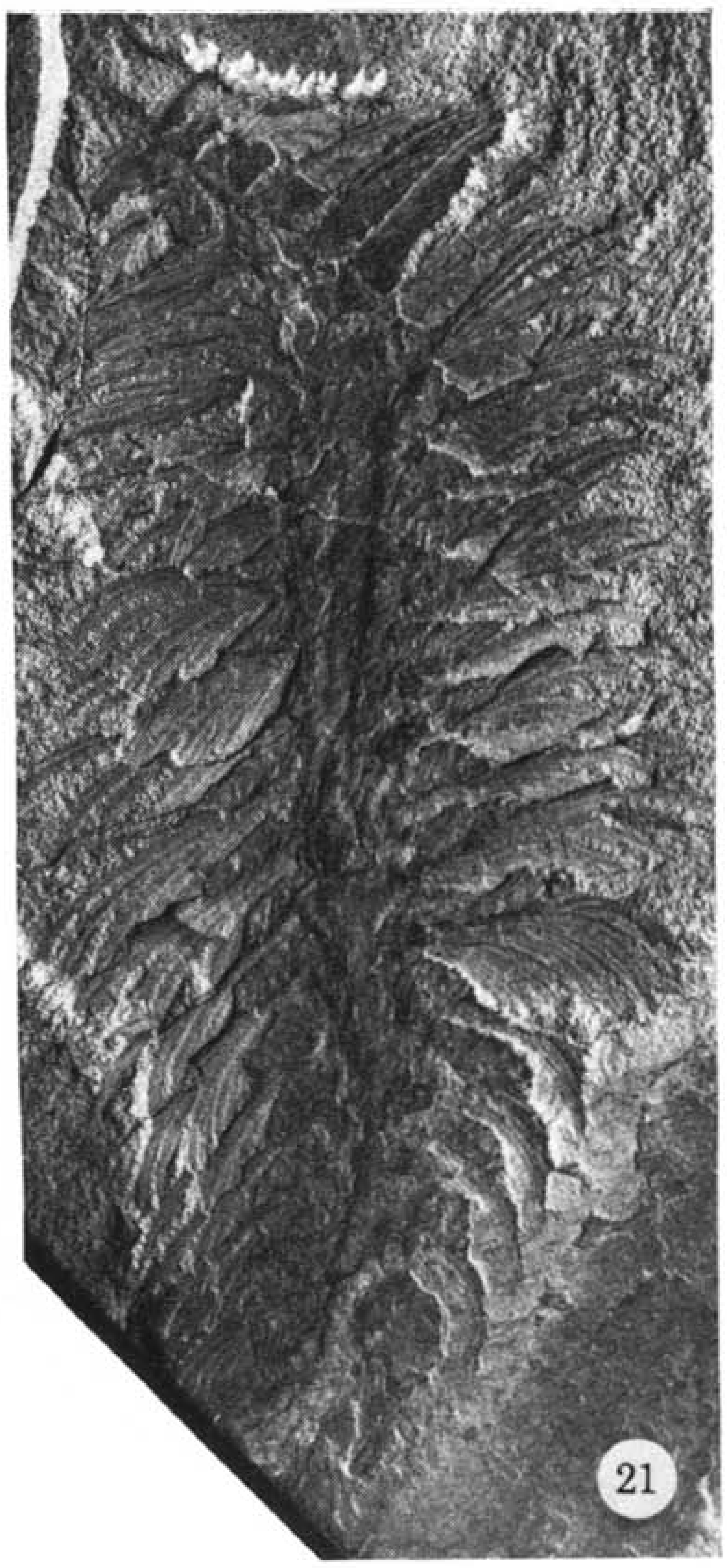
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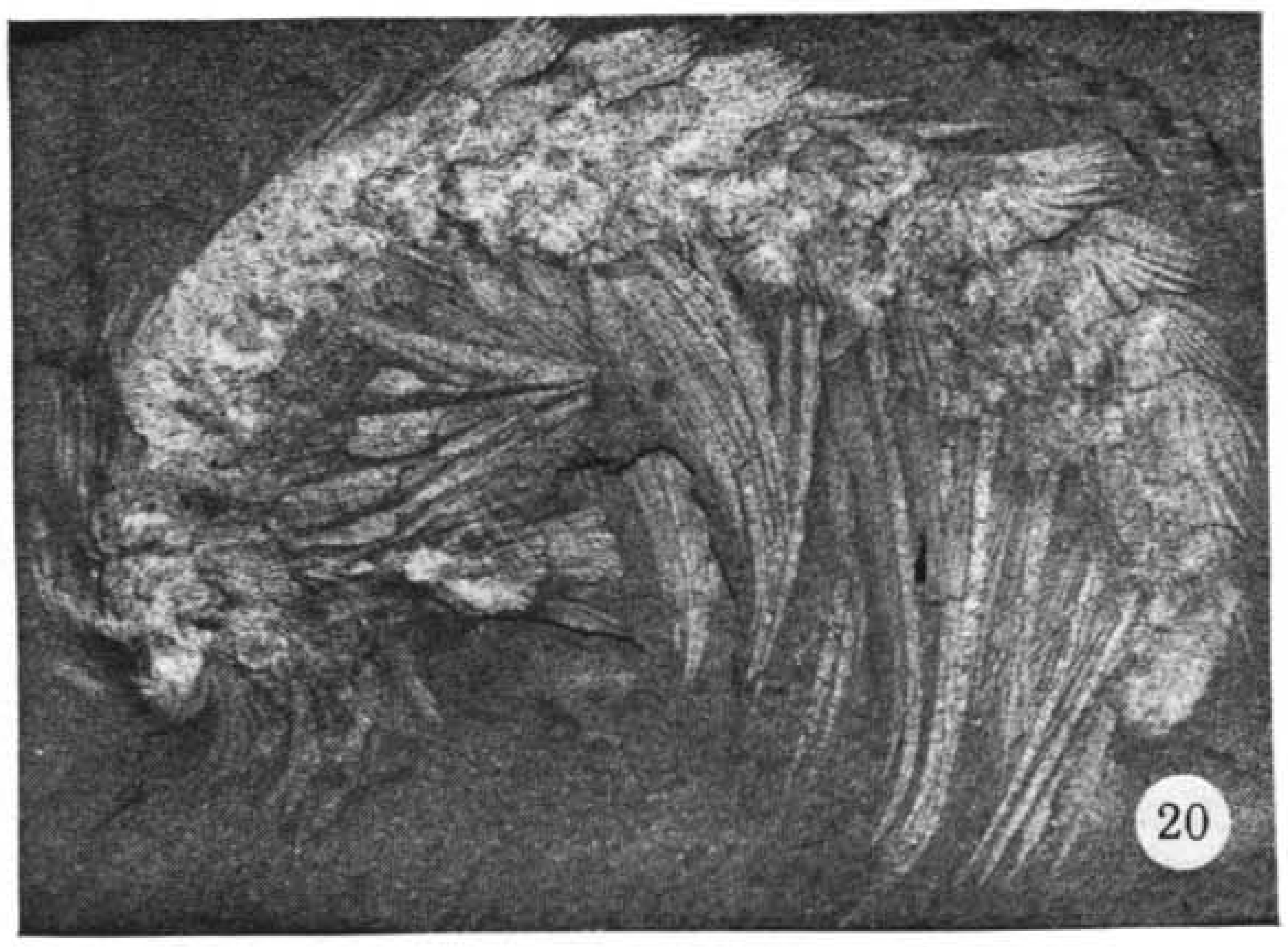
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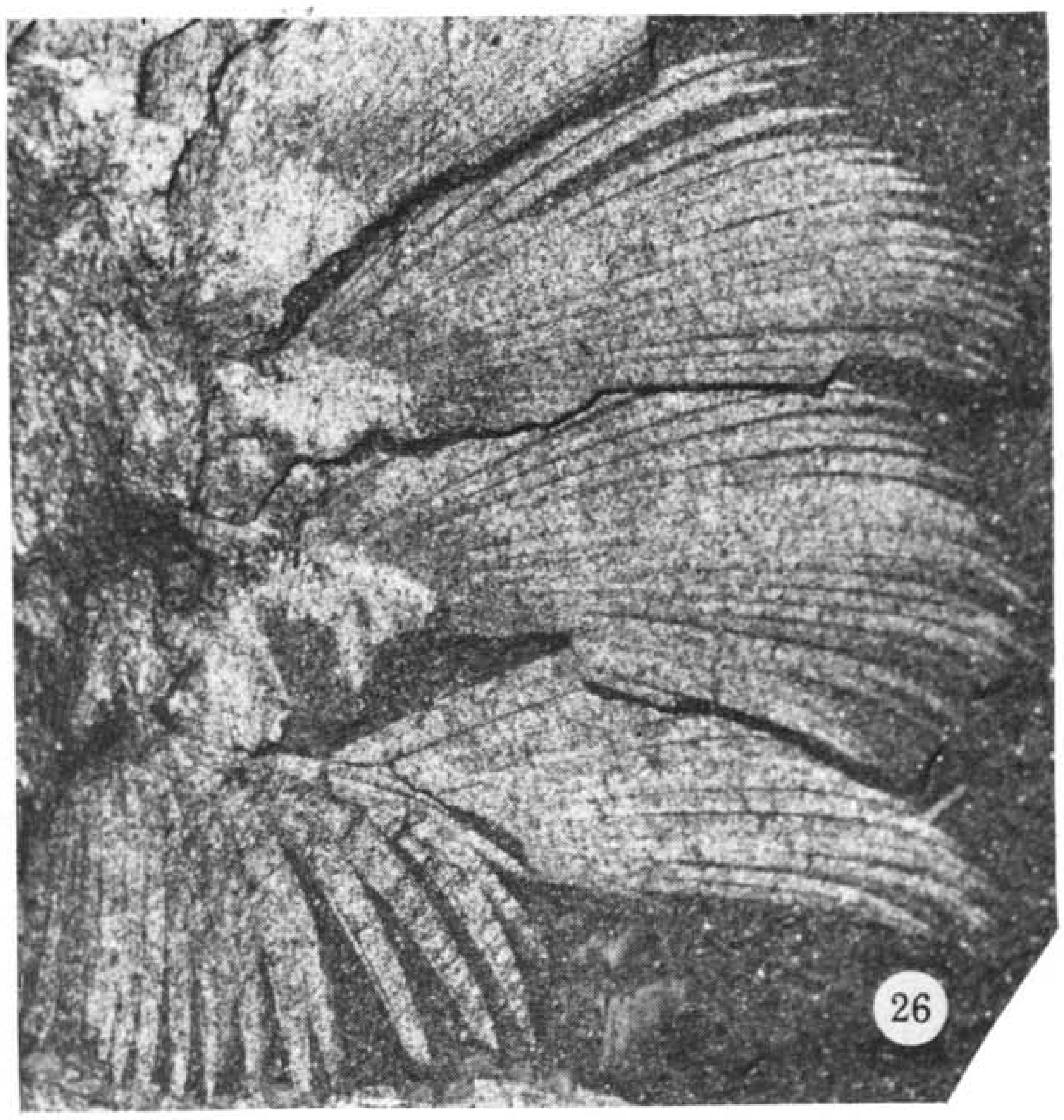
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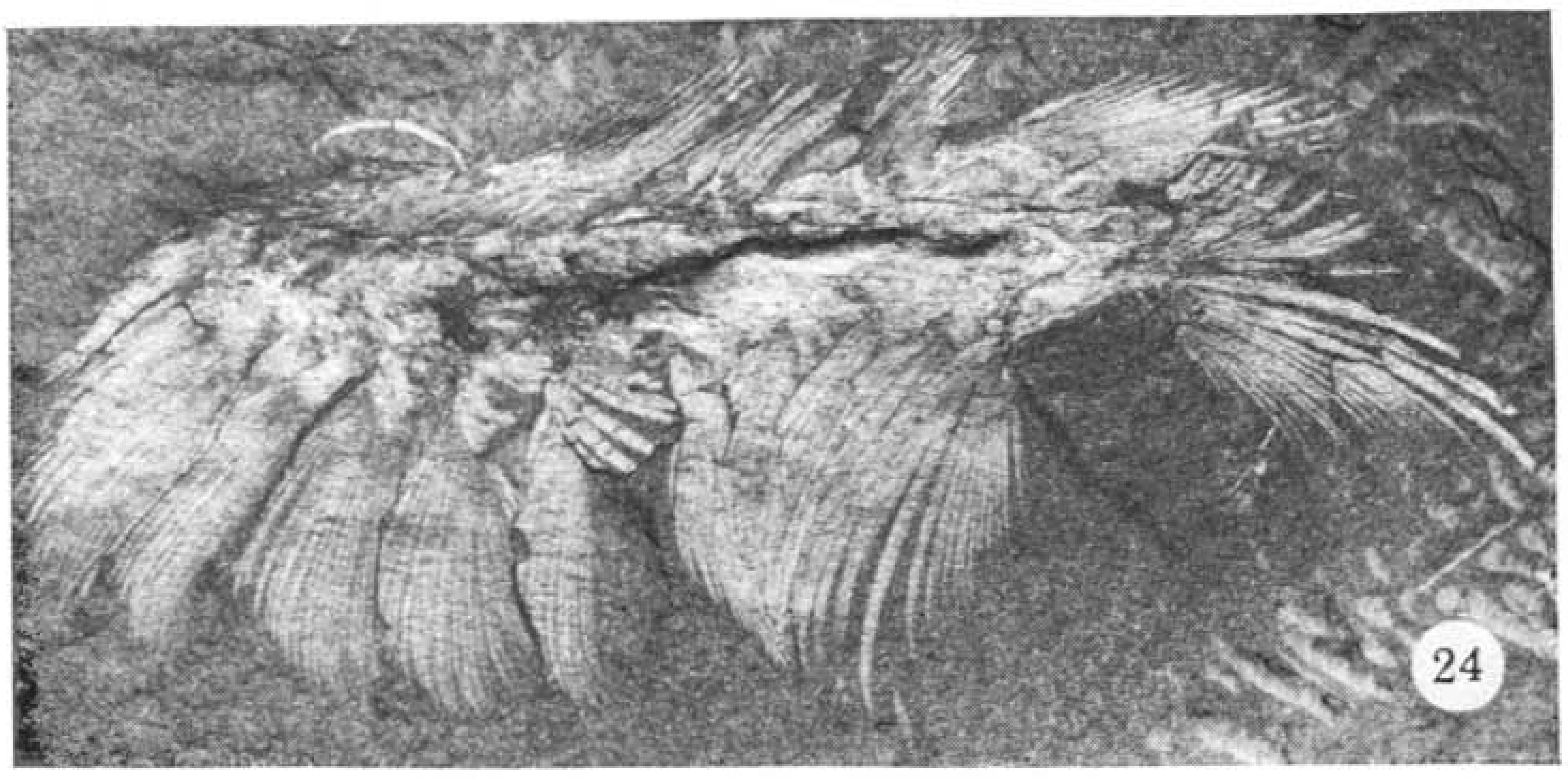
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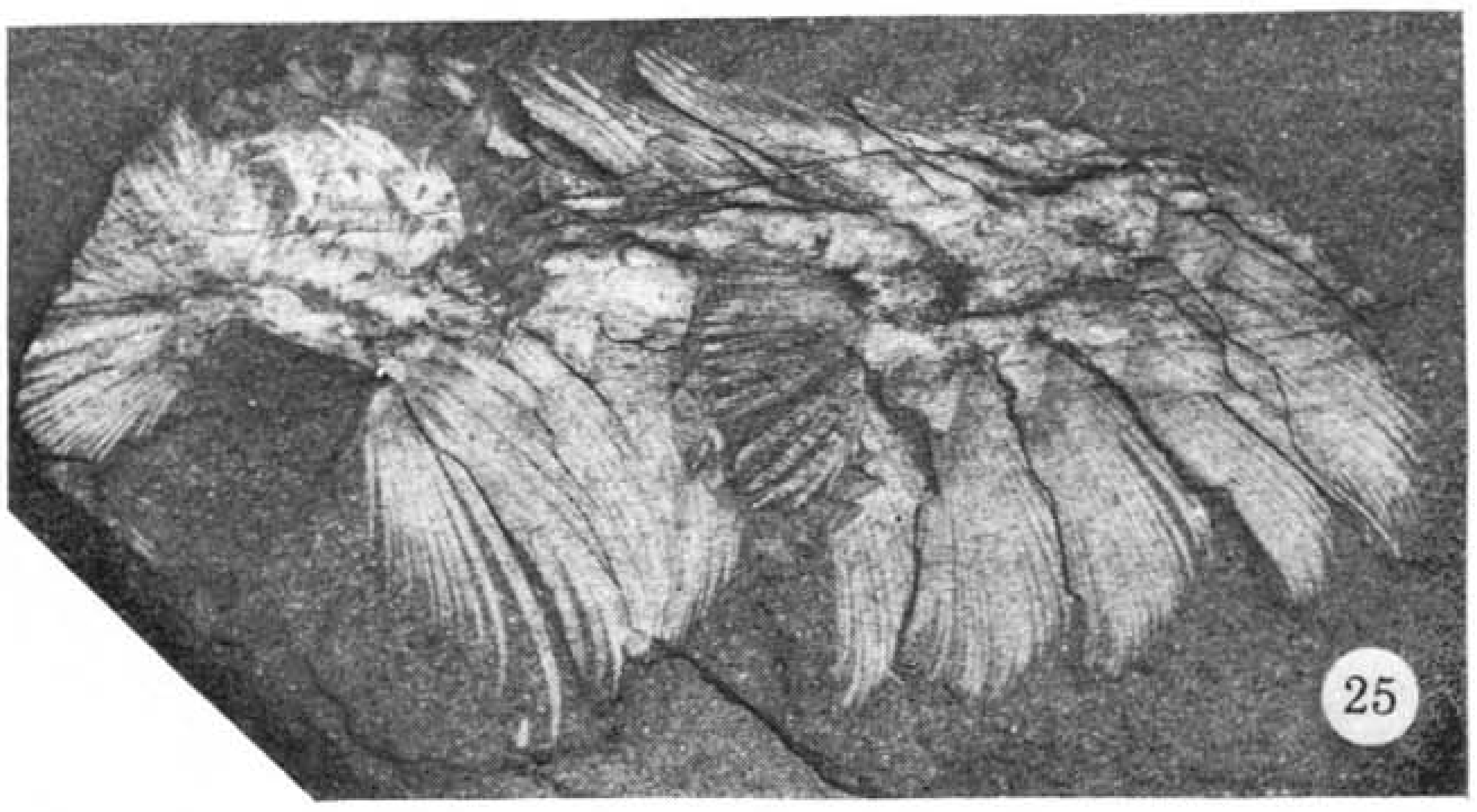
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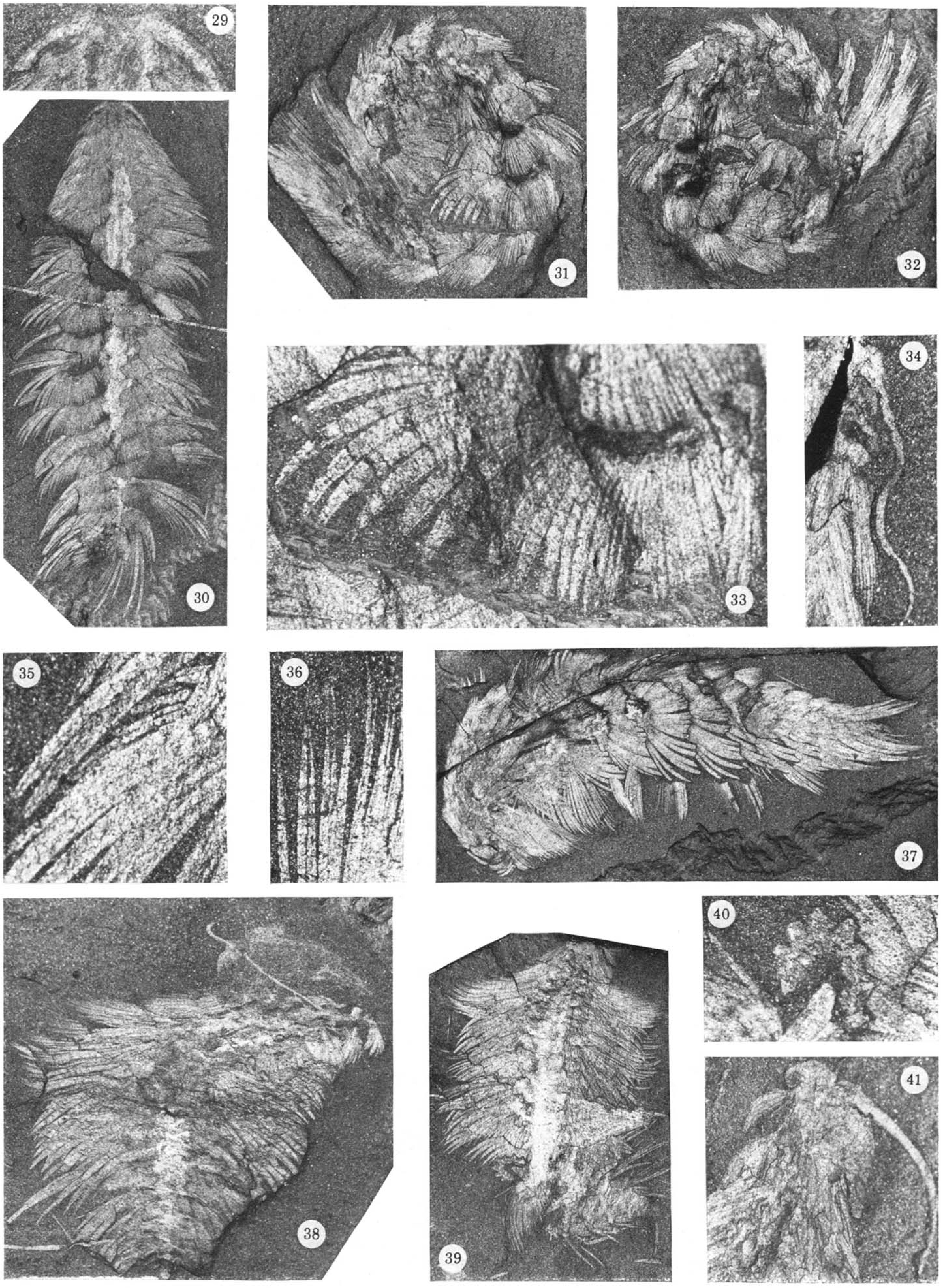
FIGURES 17–26. For description see opposite.



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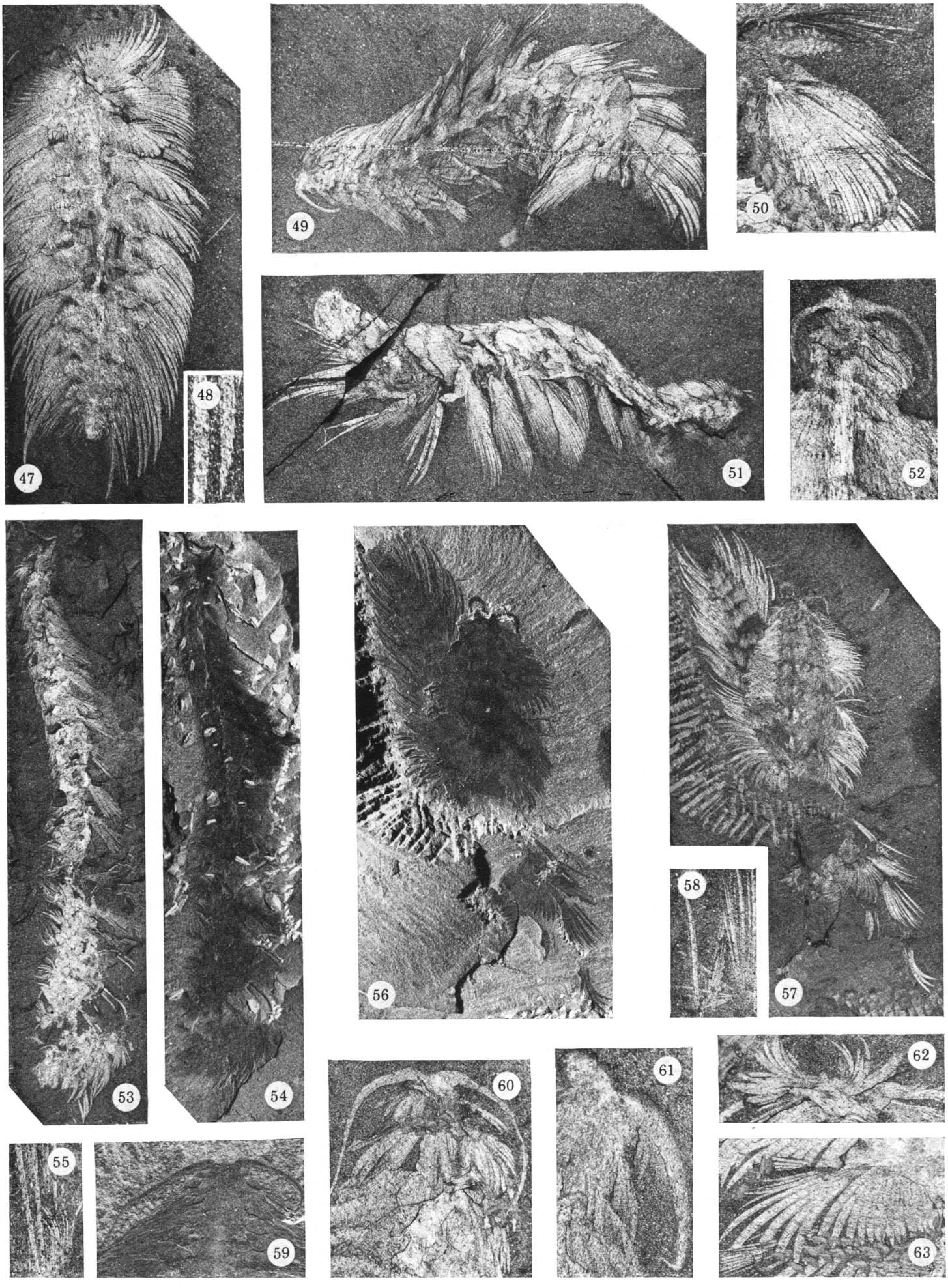

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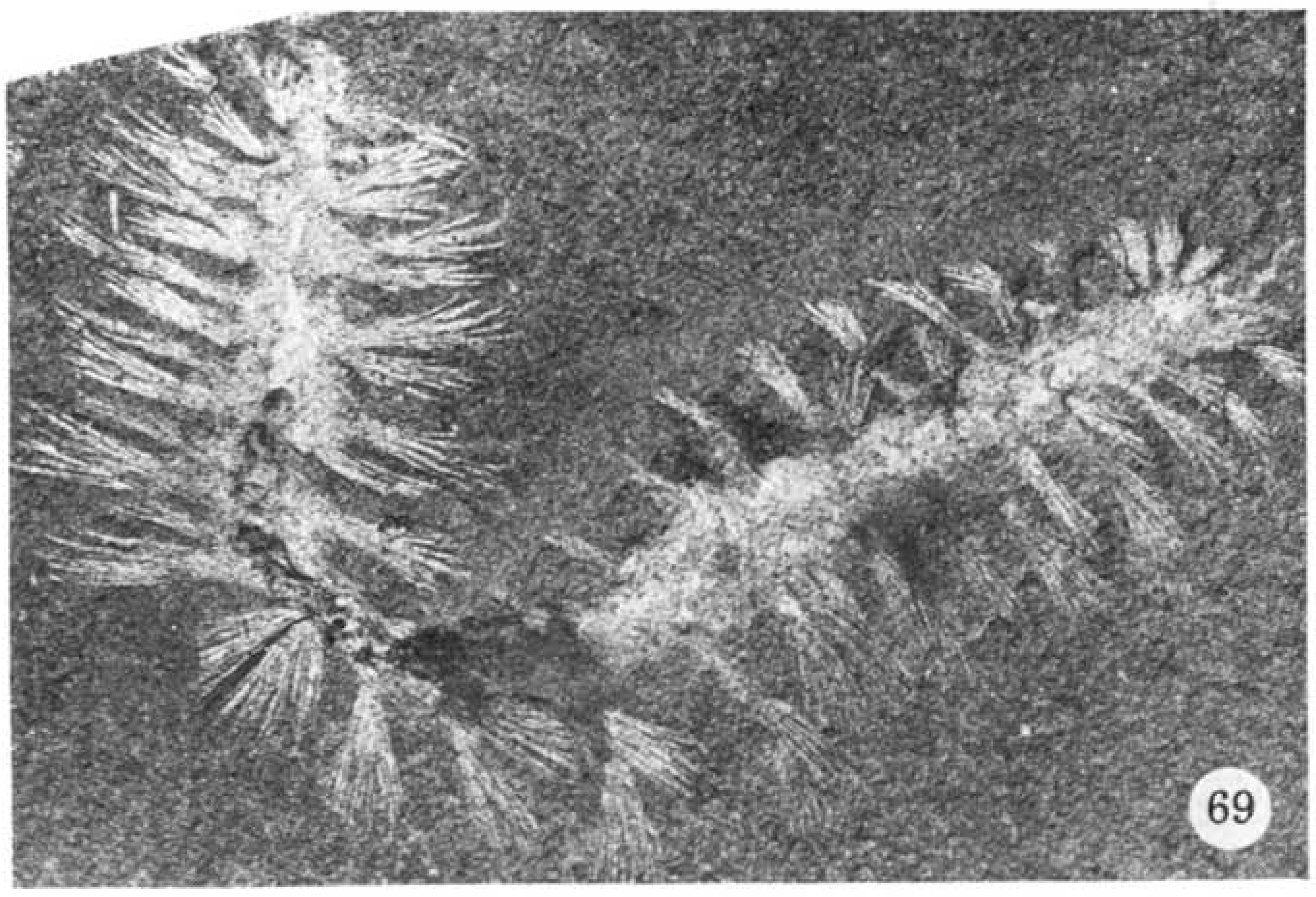

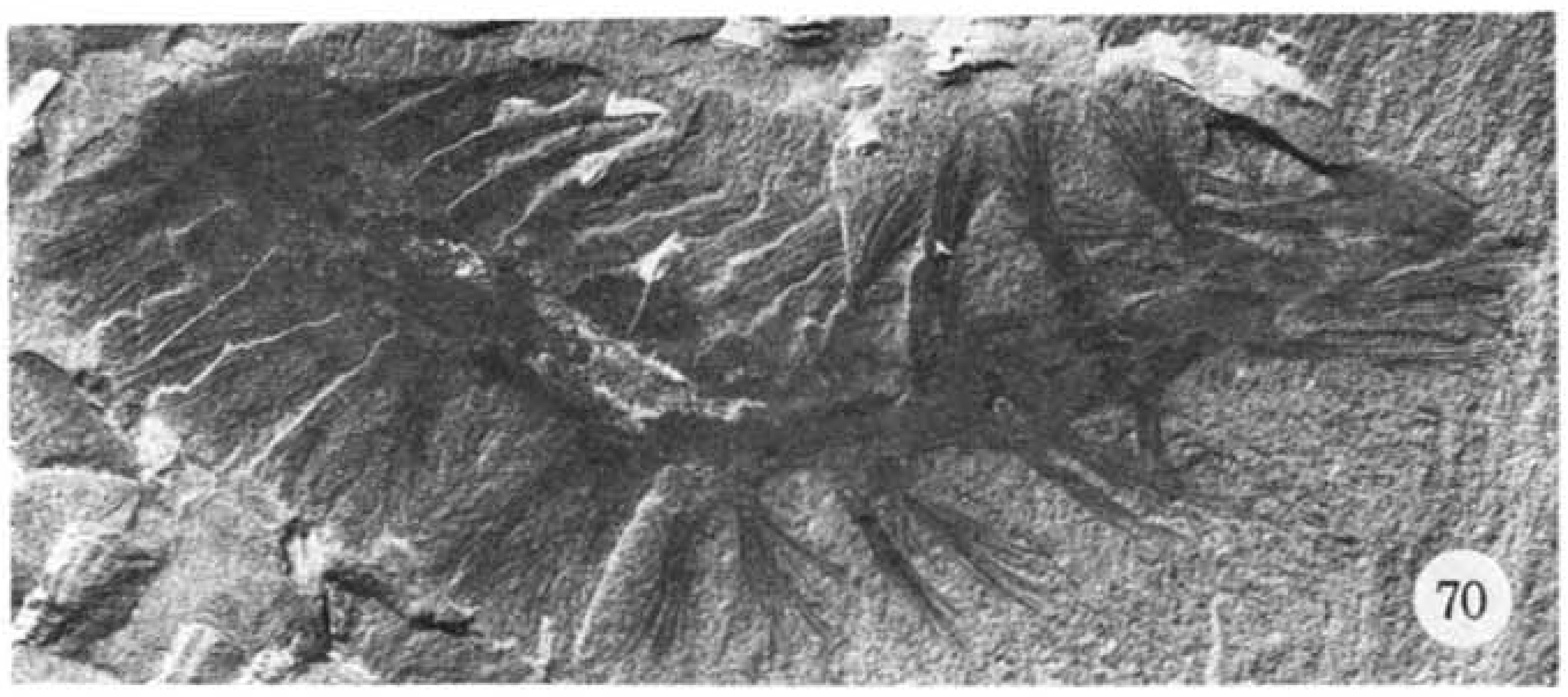

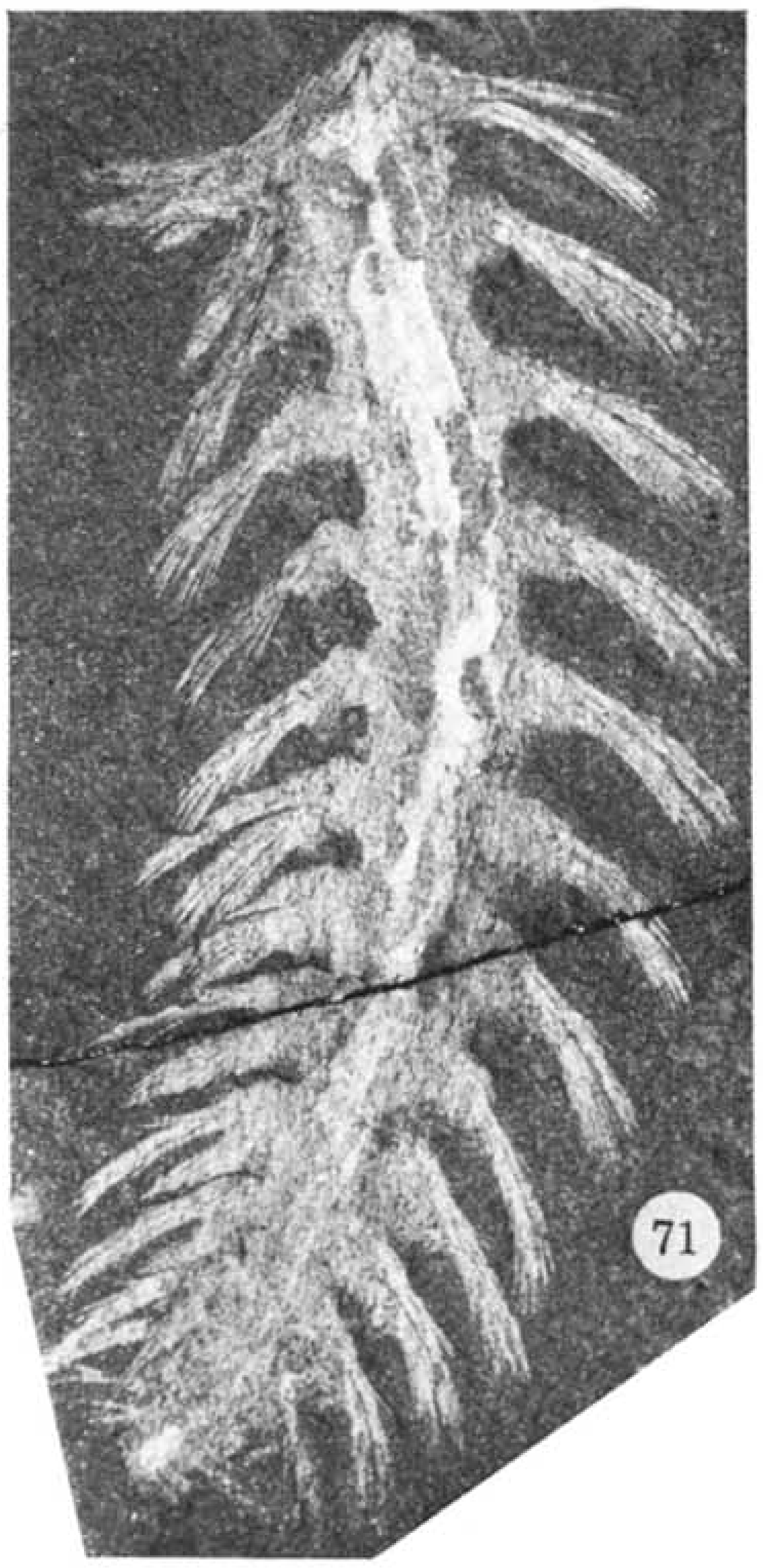

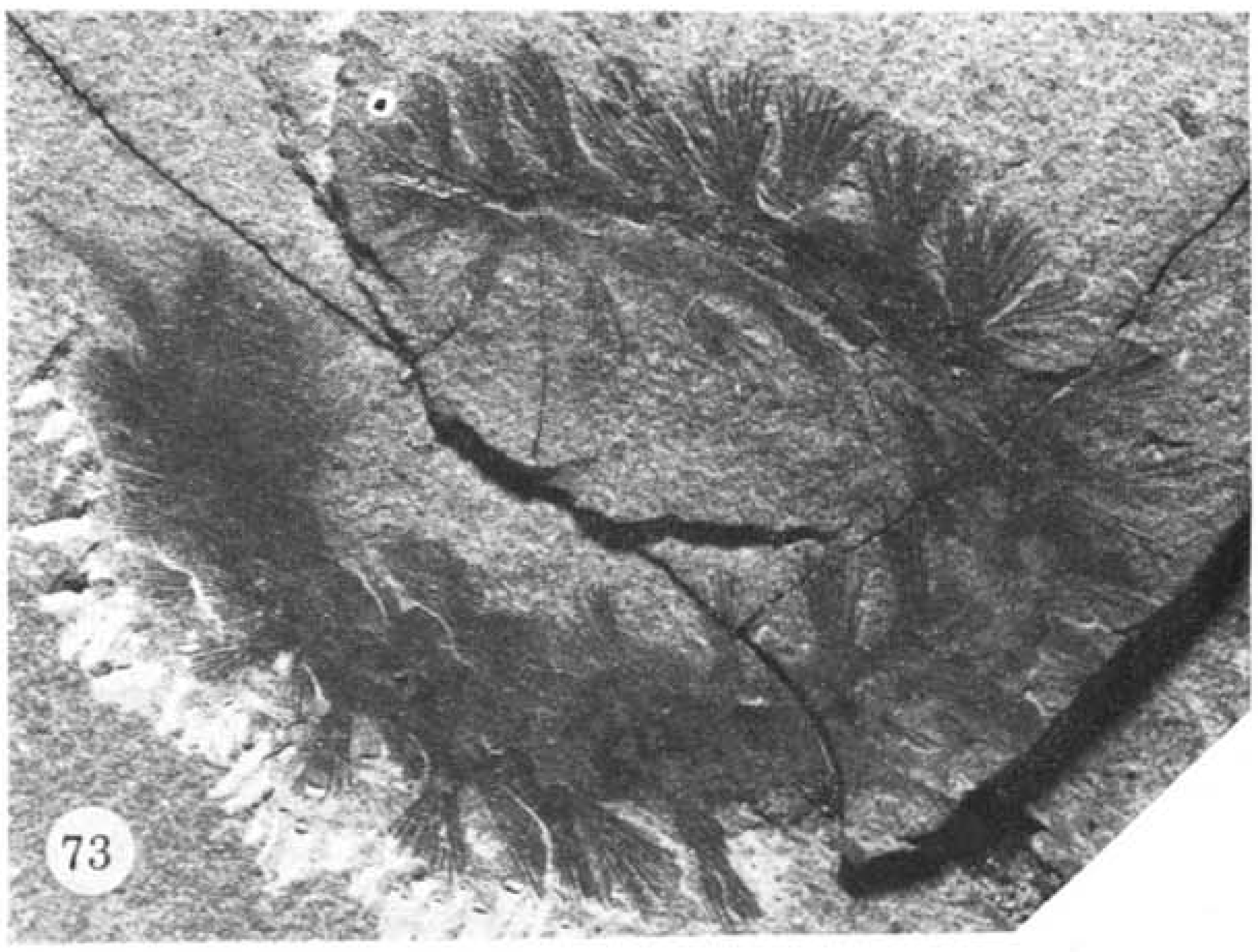

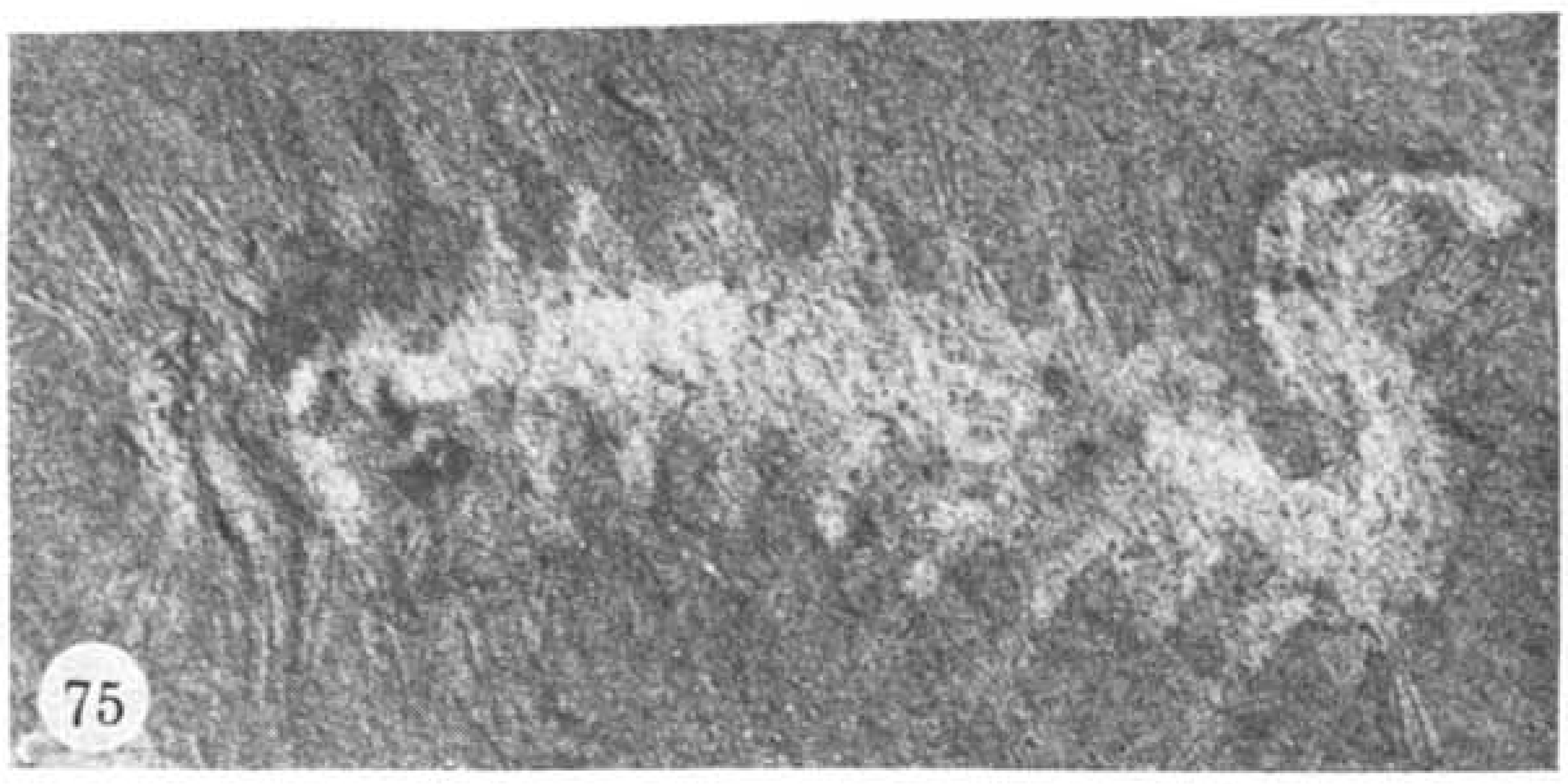

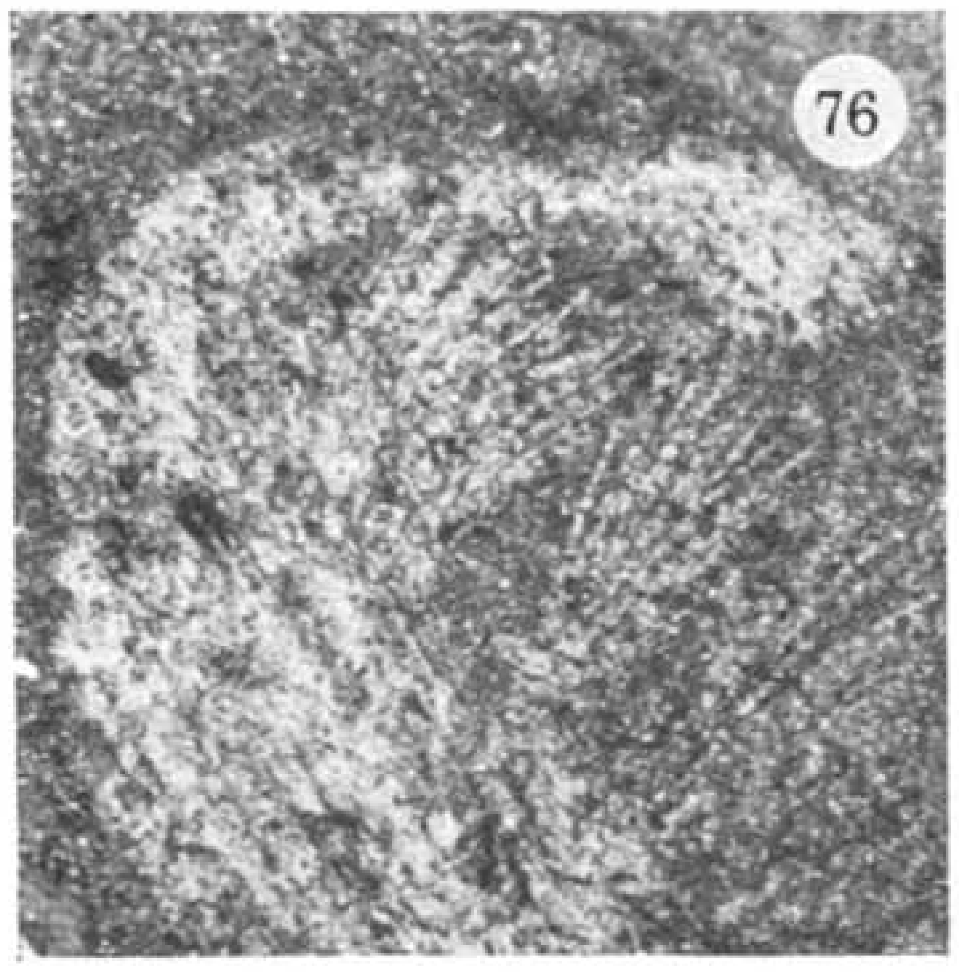

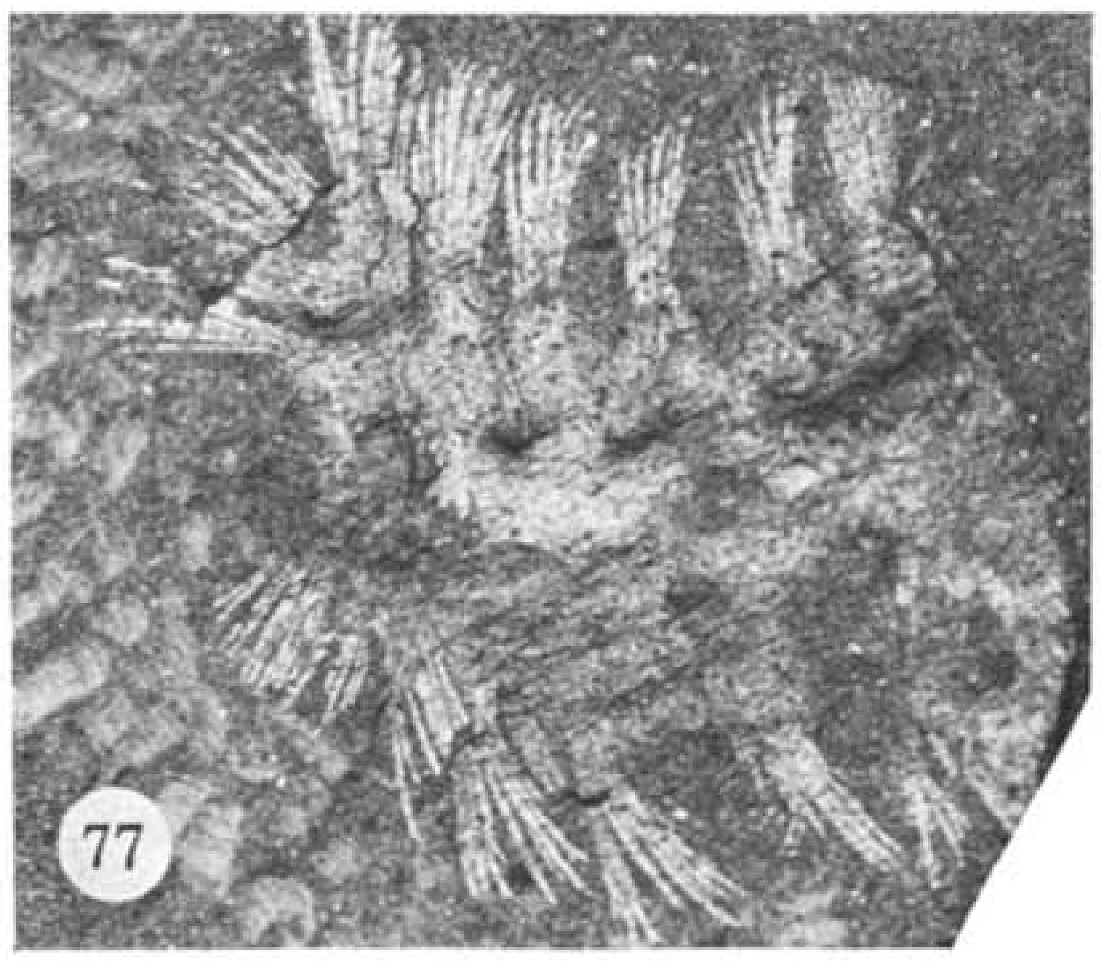

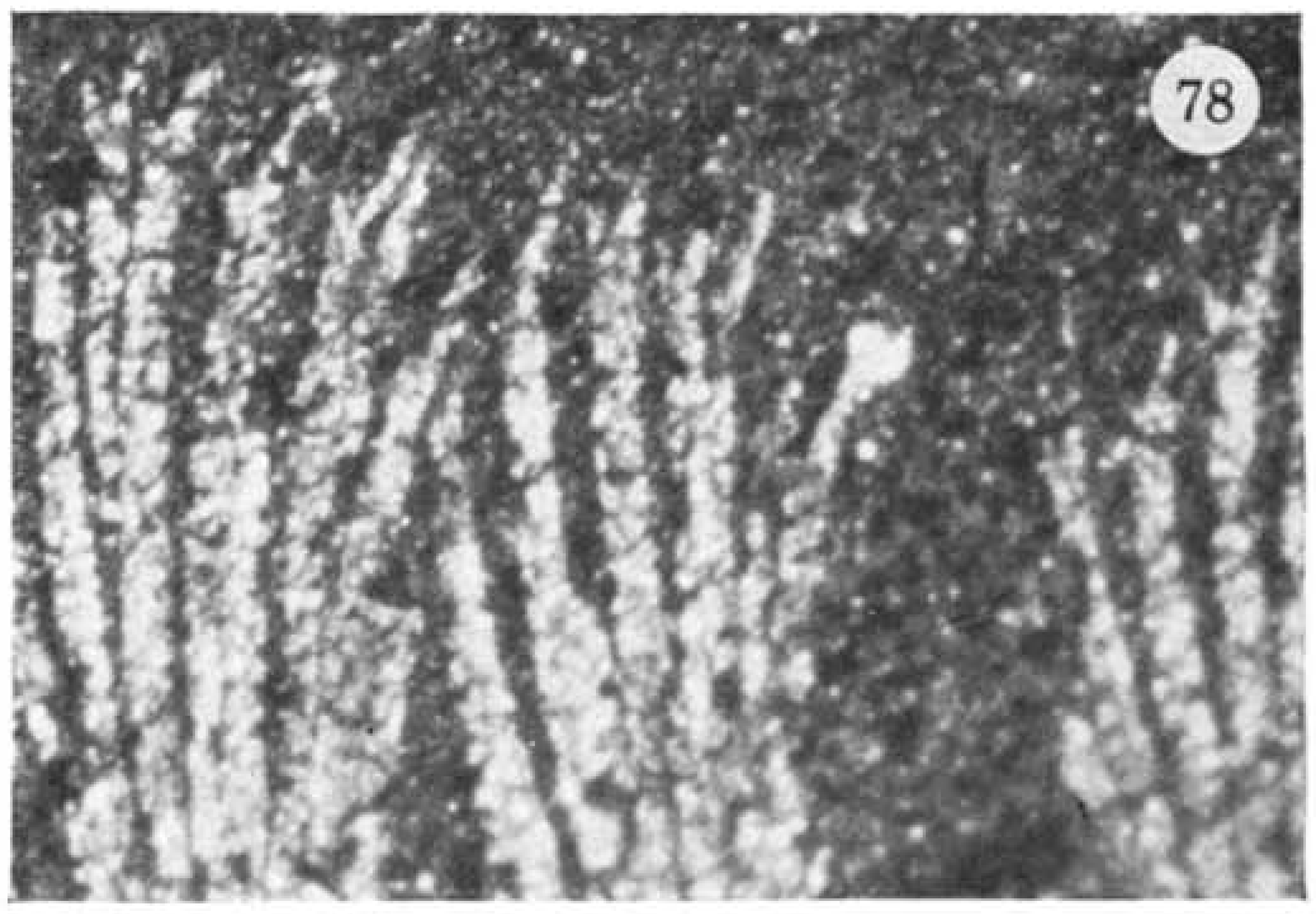

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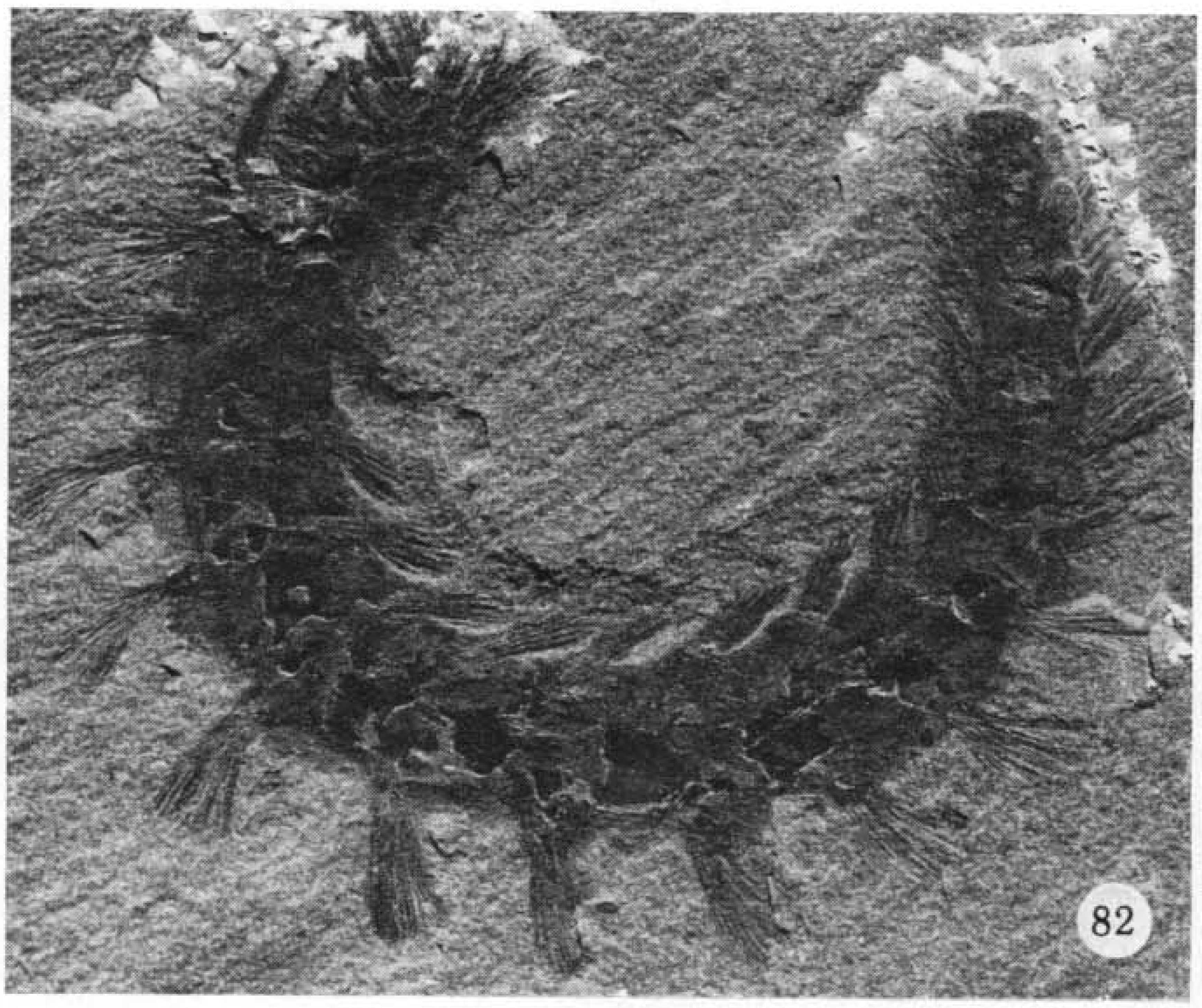
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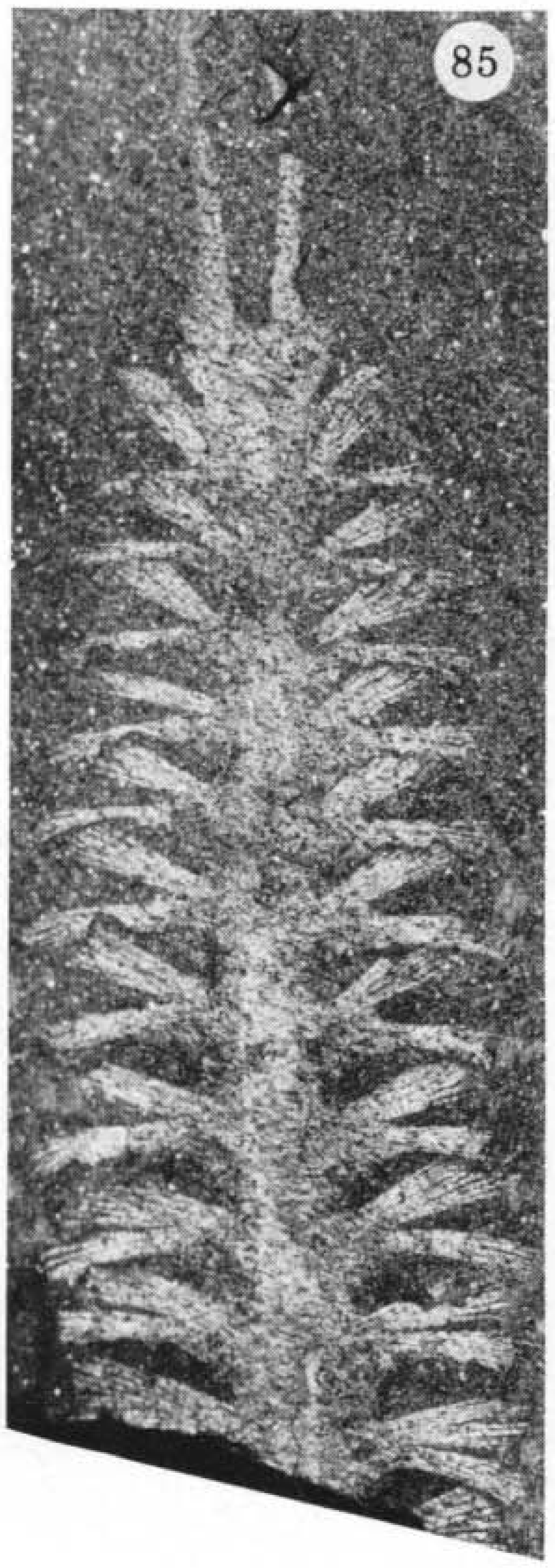
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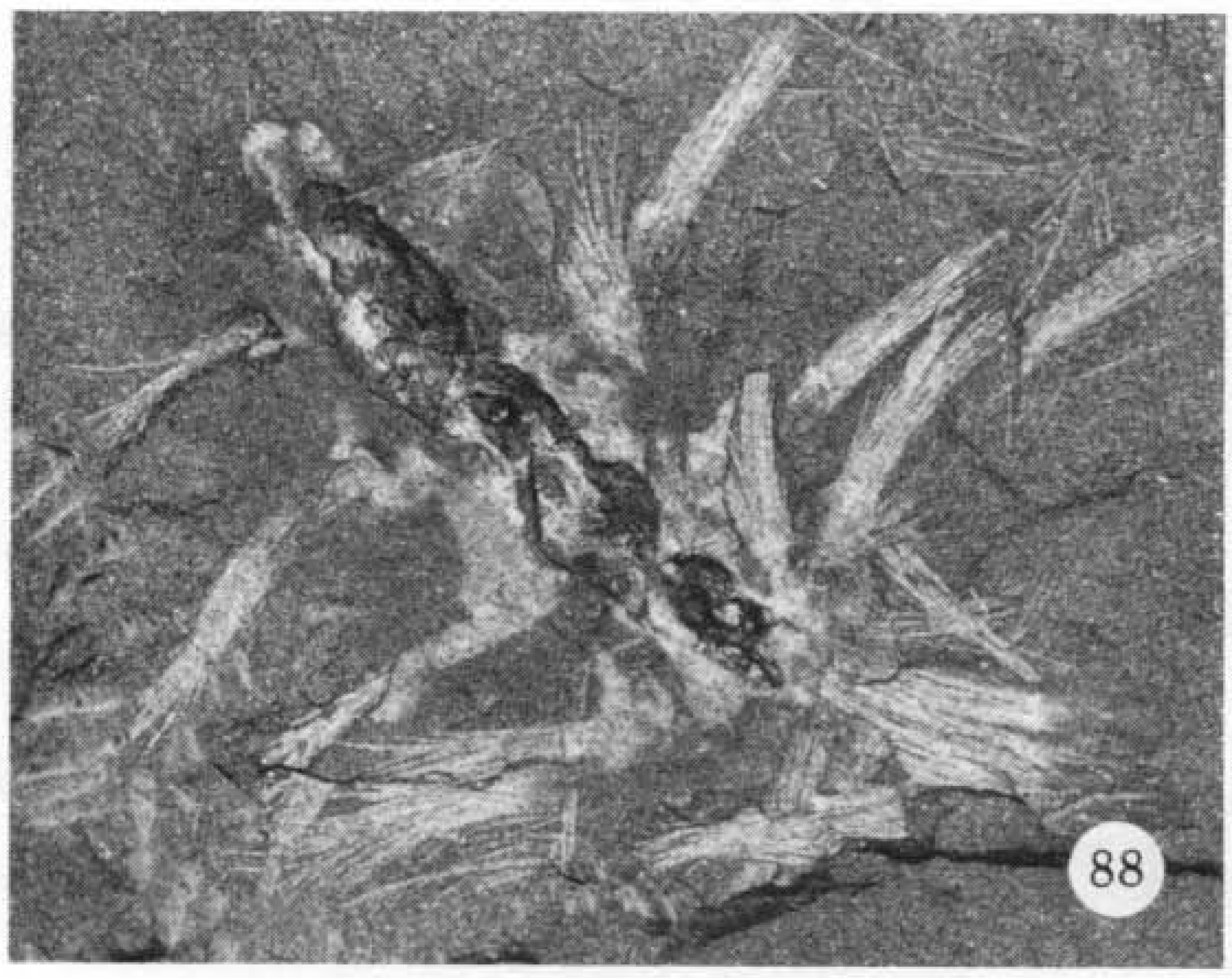
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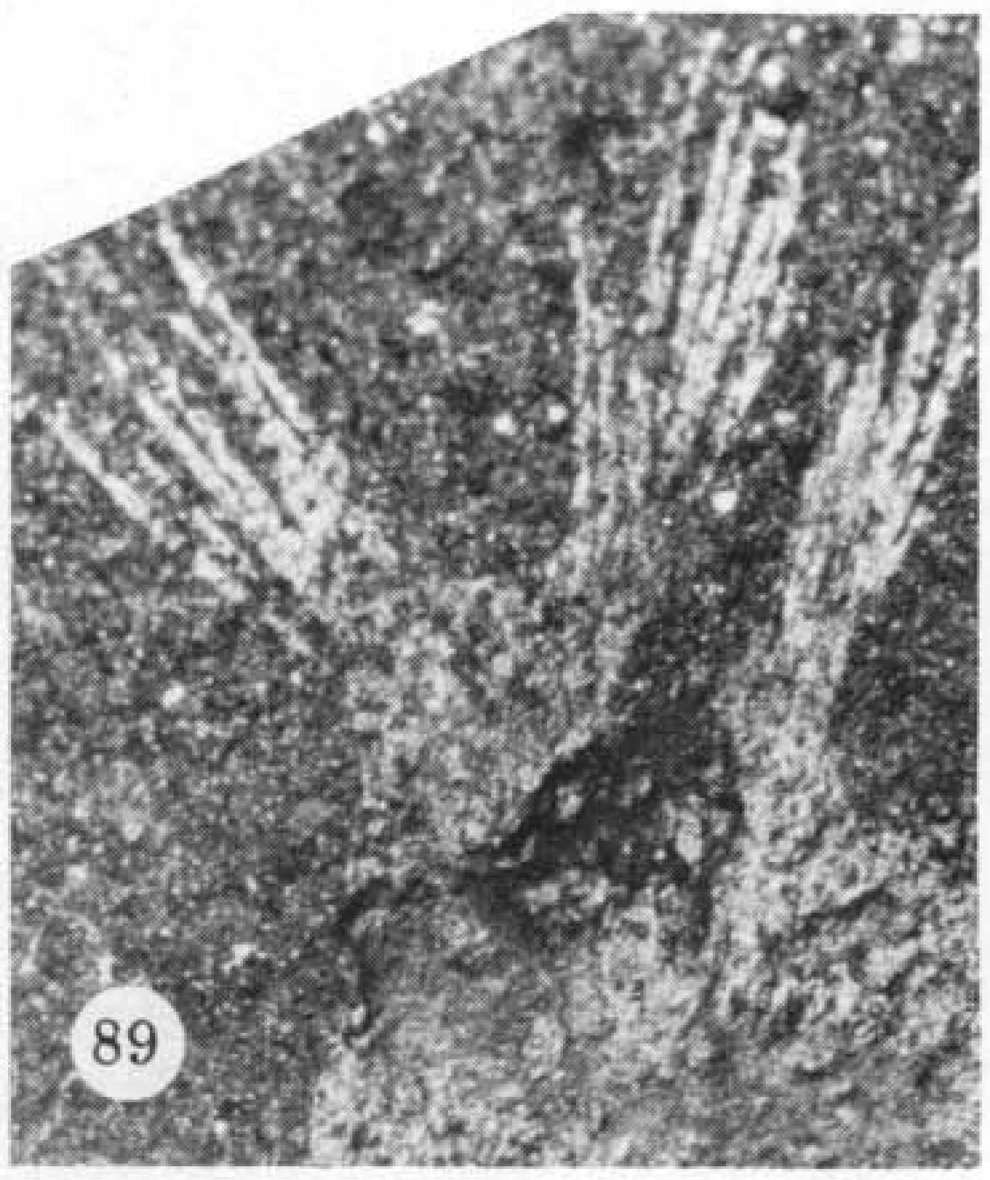
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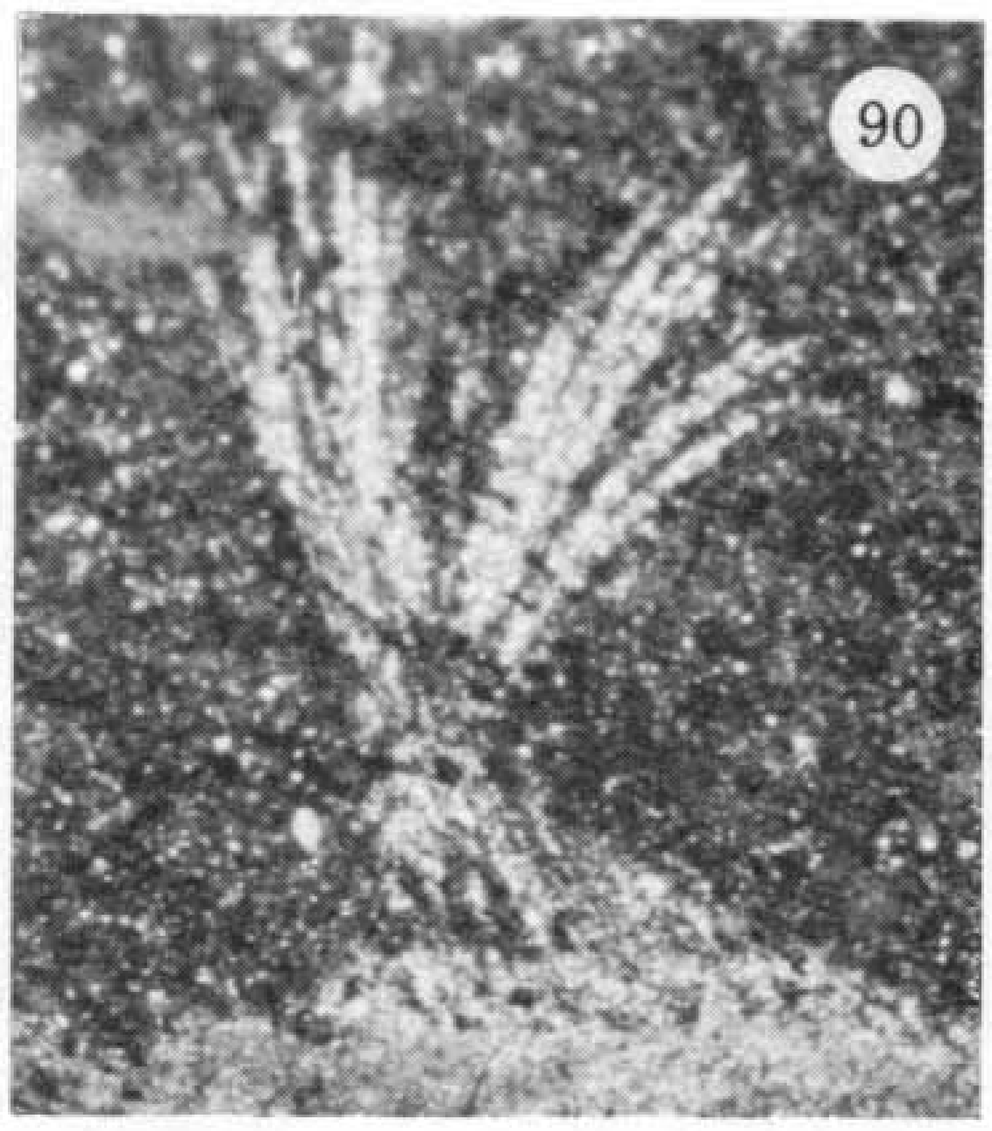
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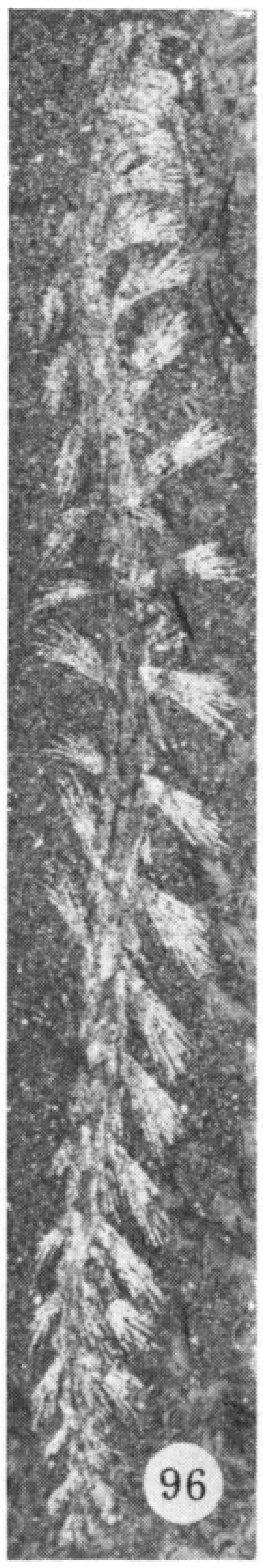
FIGURES 82–90. For description see opposite.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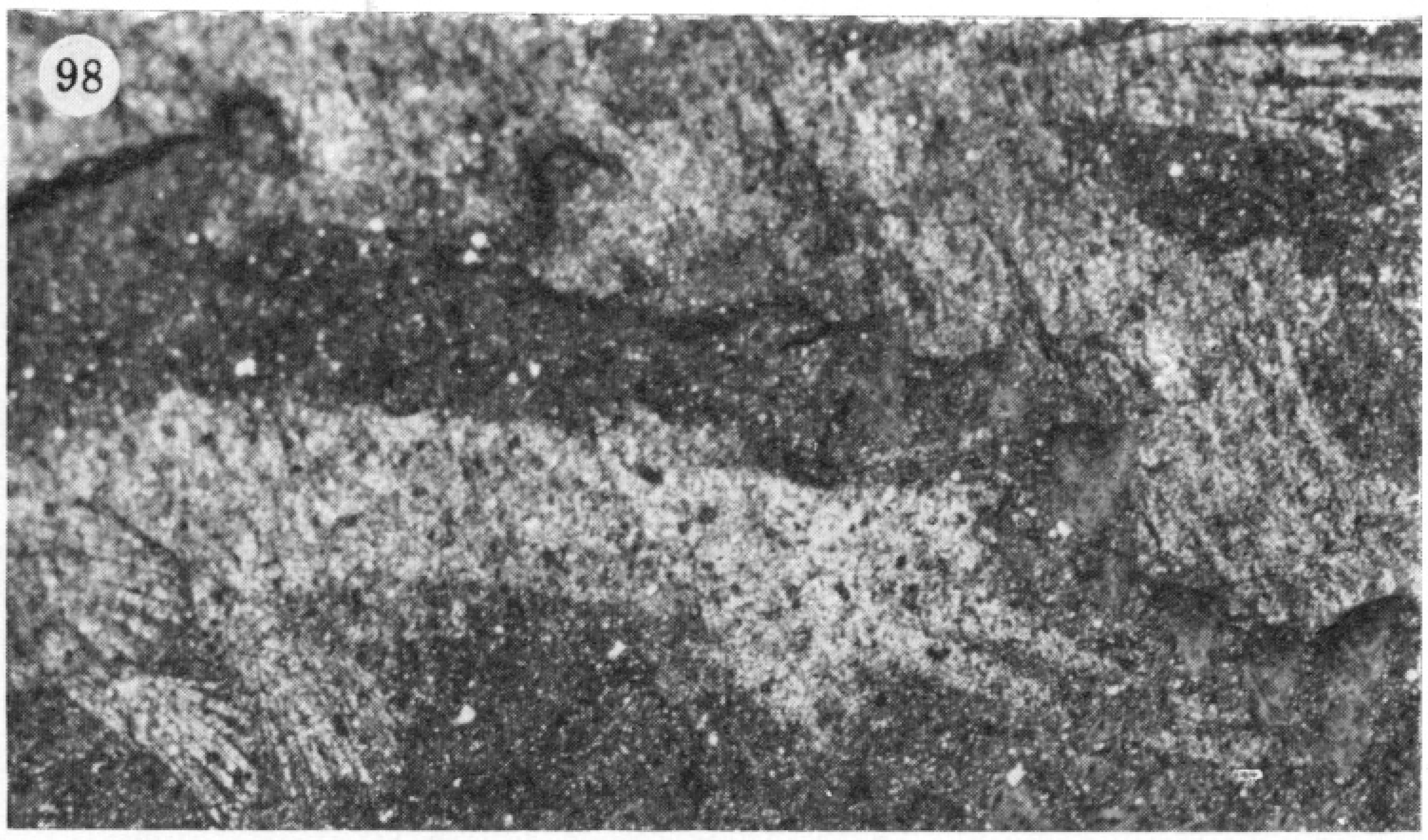
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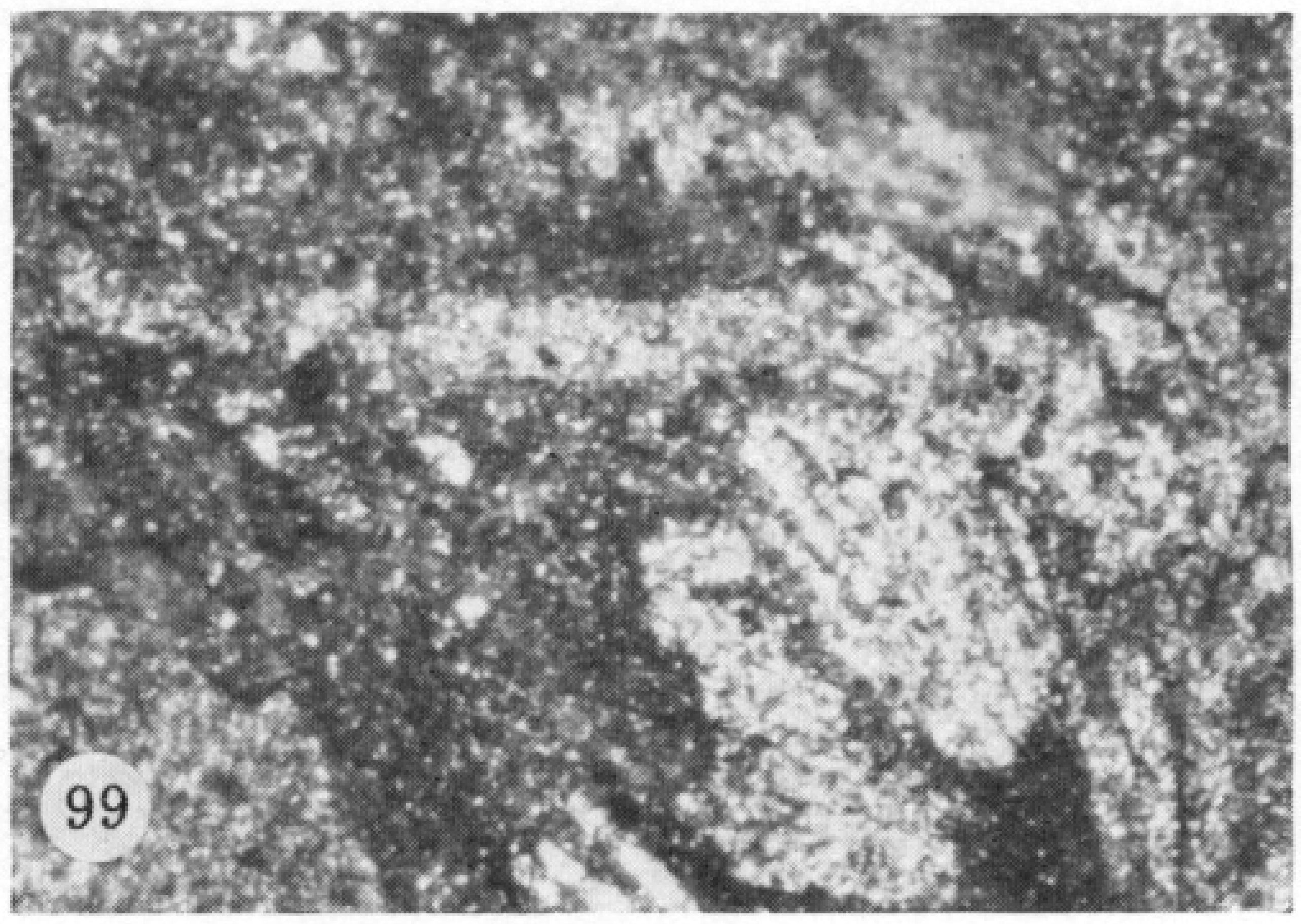
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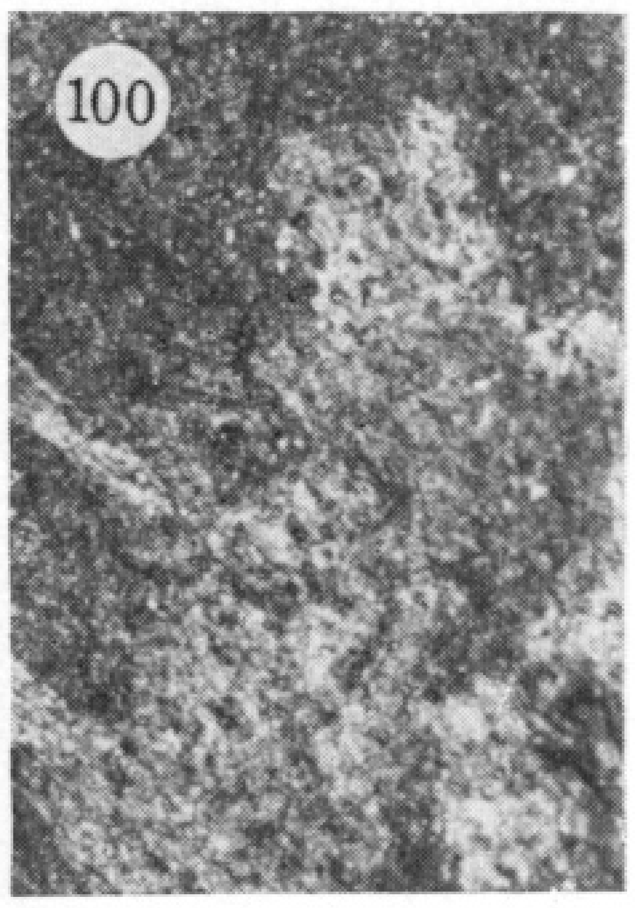
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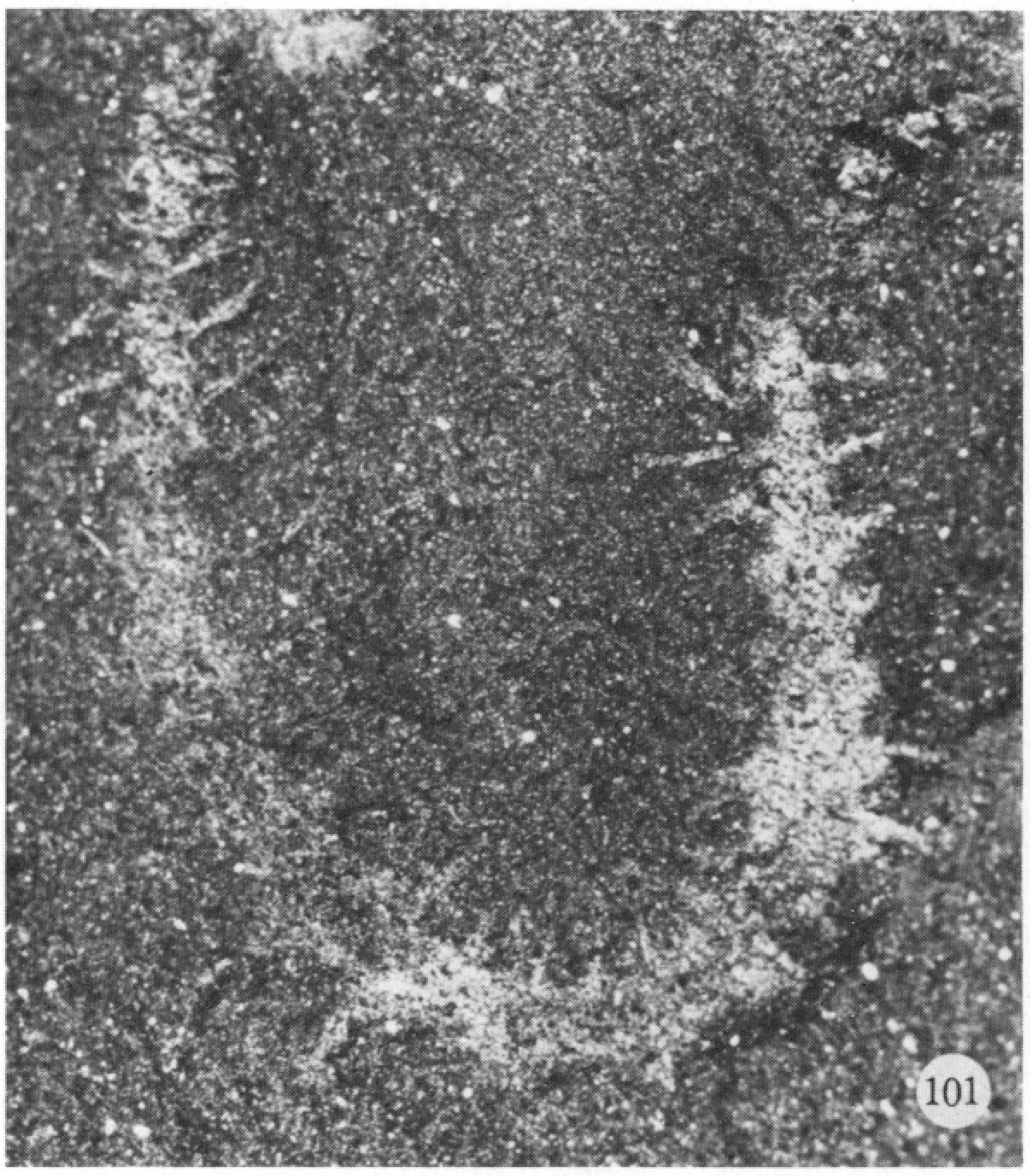
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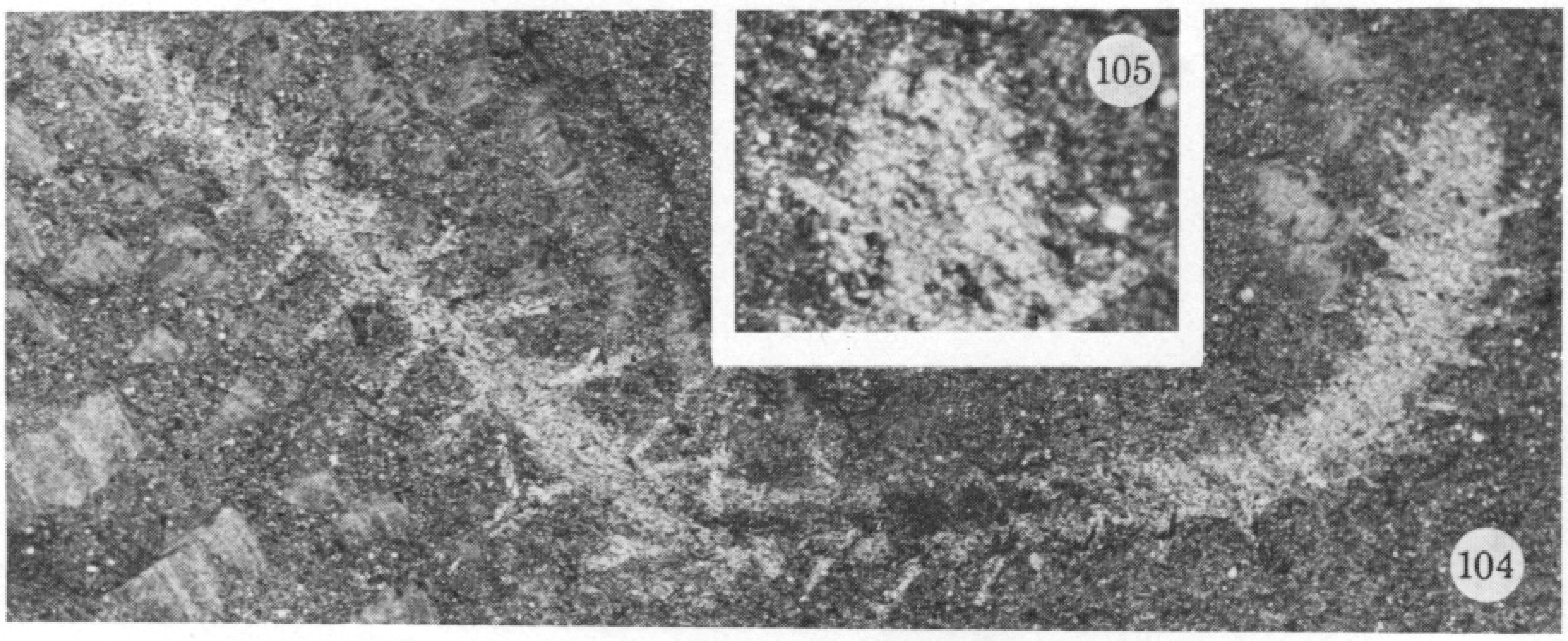
102


103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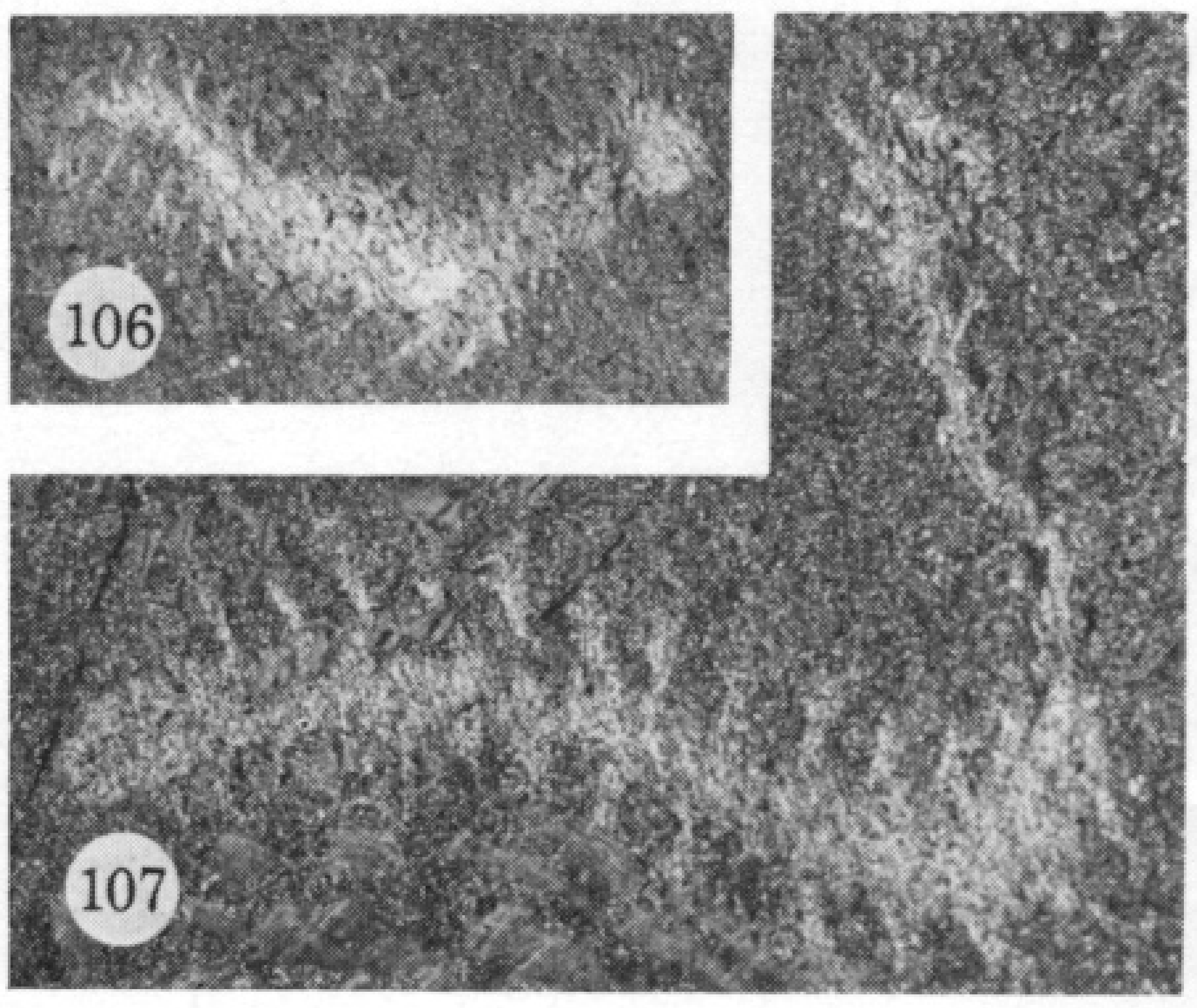
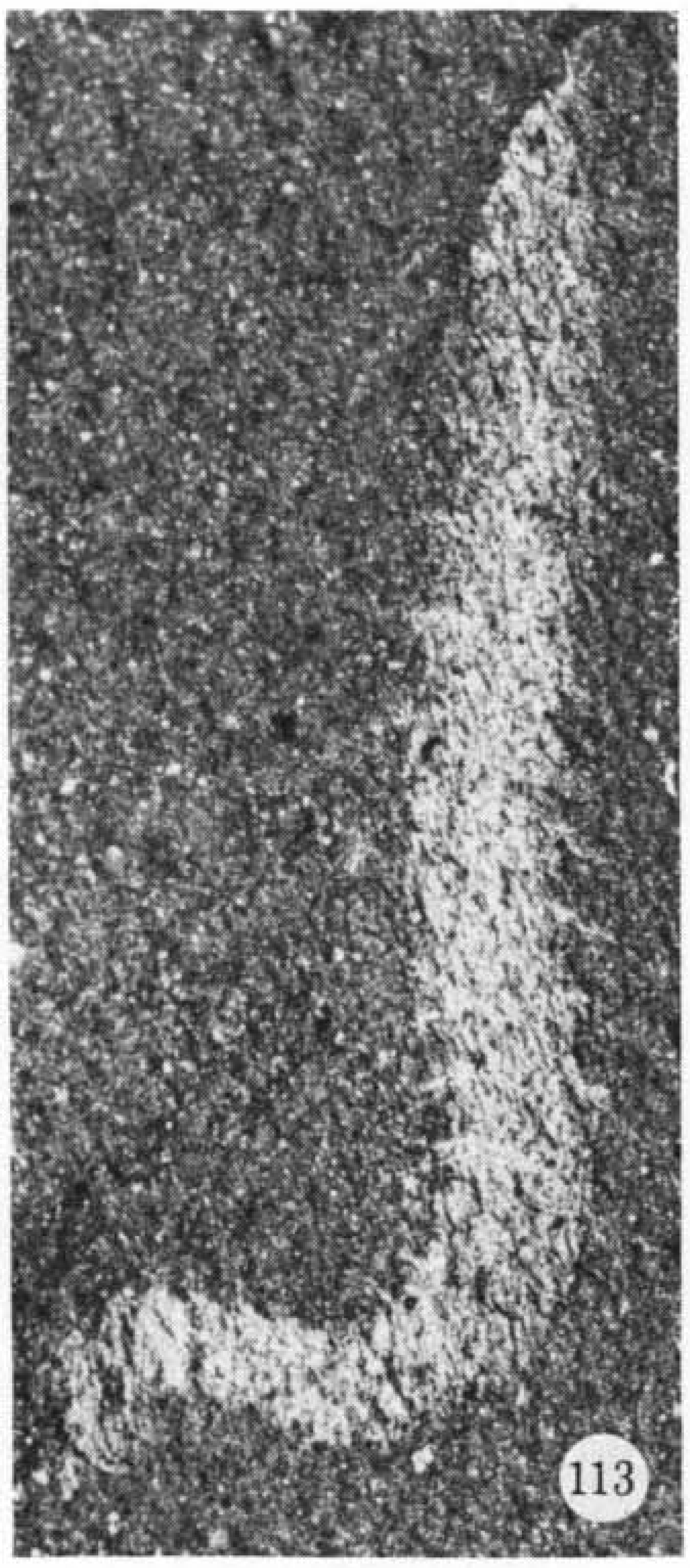
104


106

107

FIGURES 96–107. For description see opposite.


112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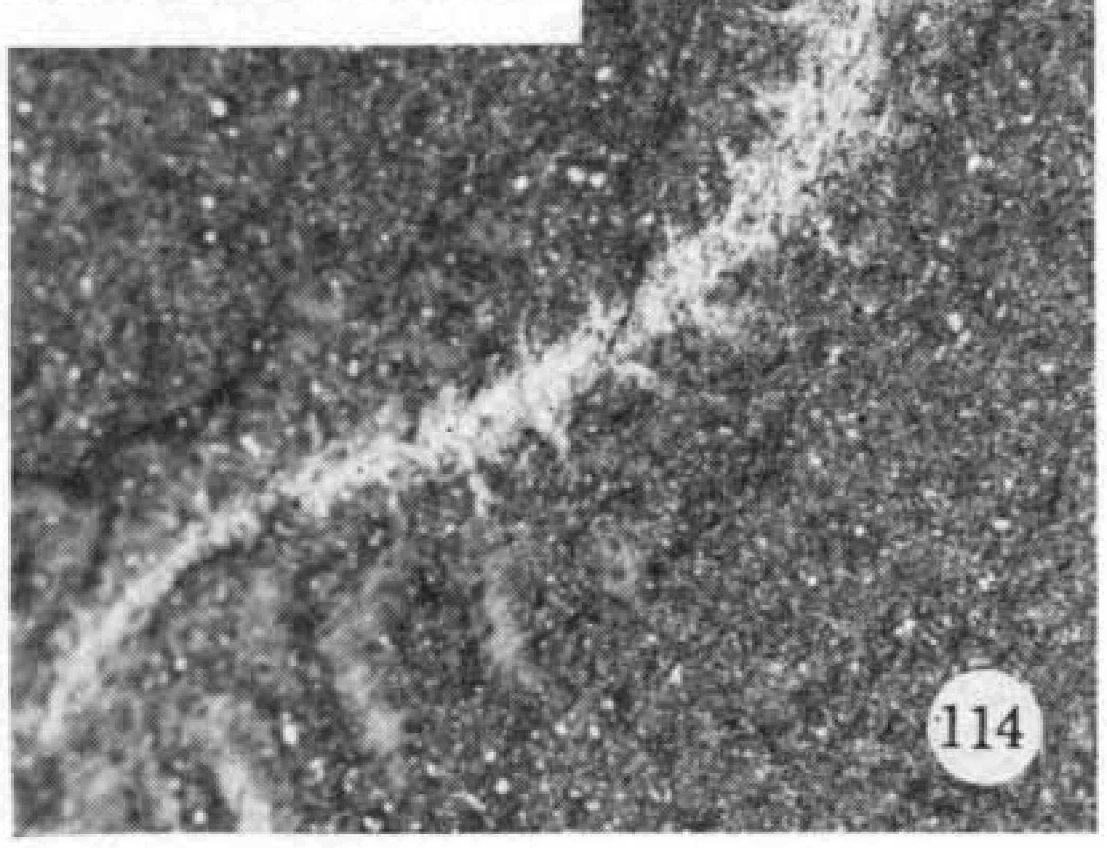
115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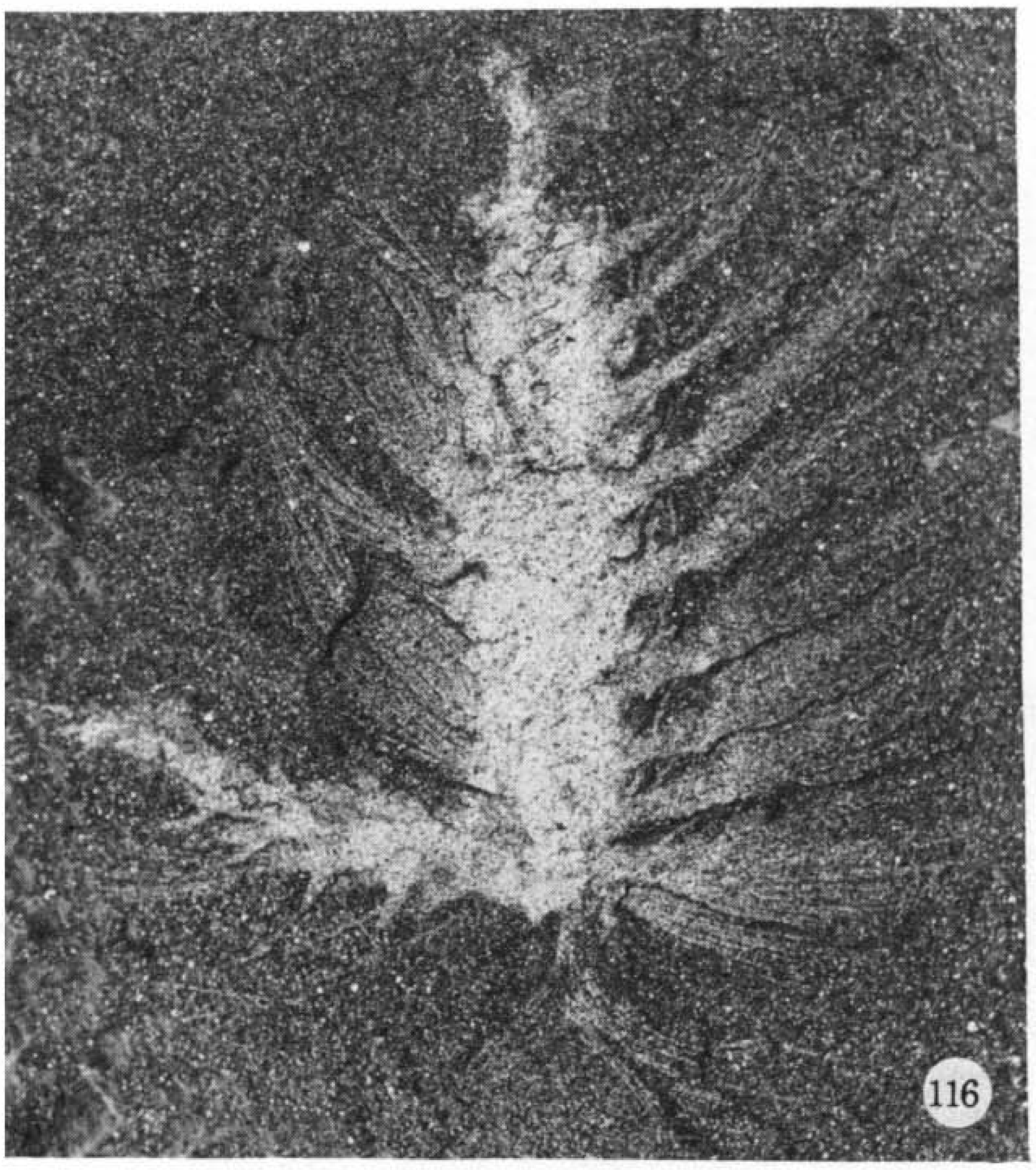
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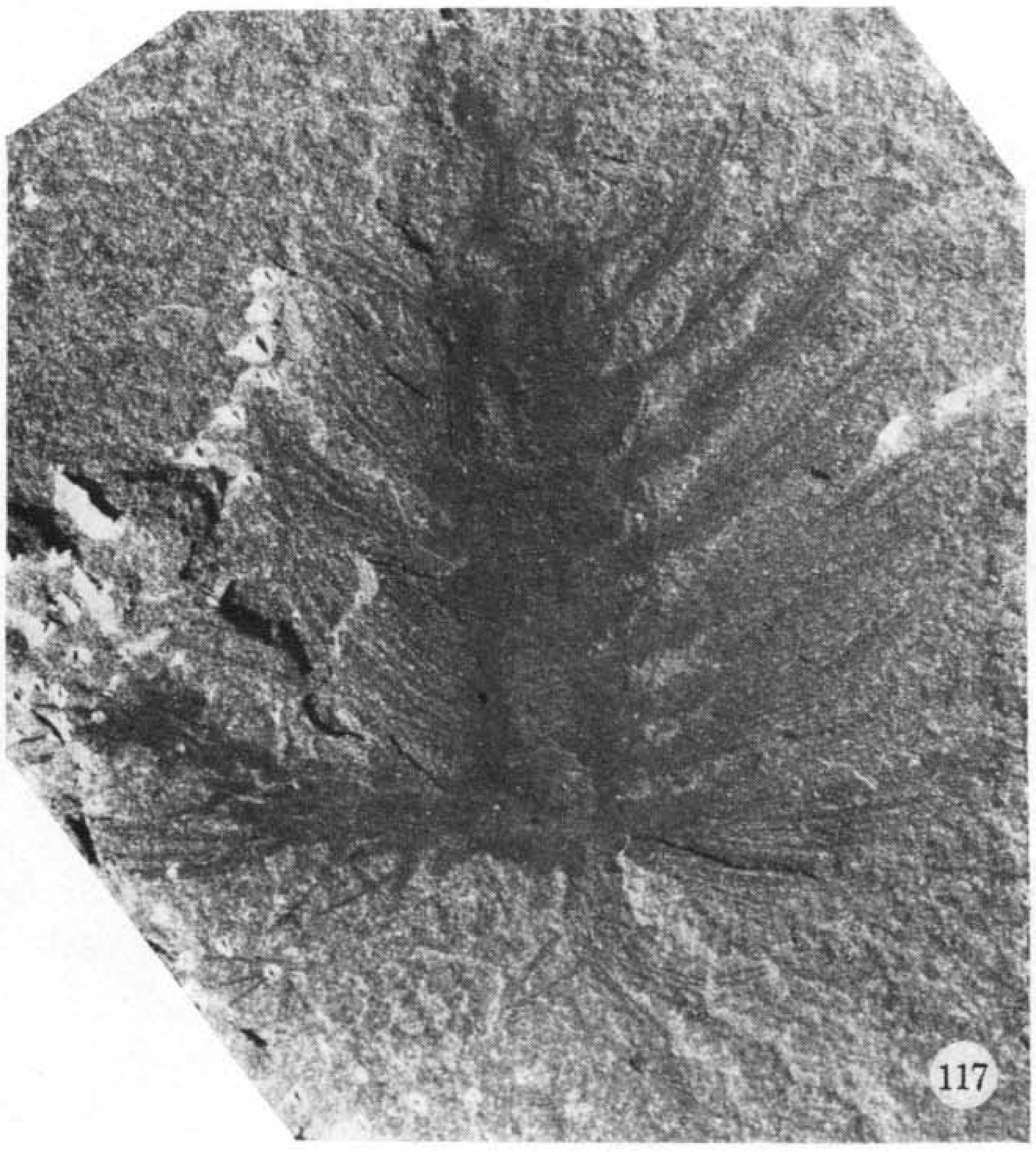
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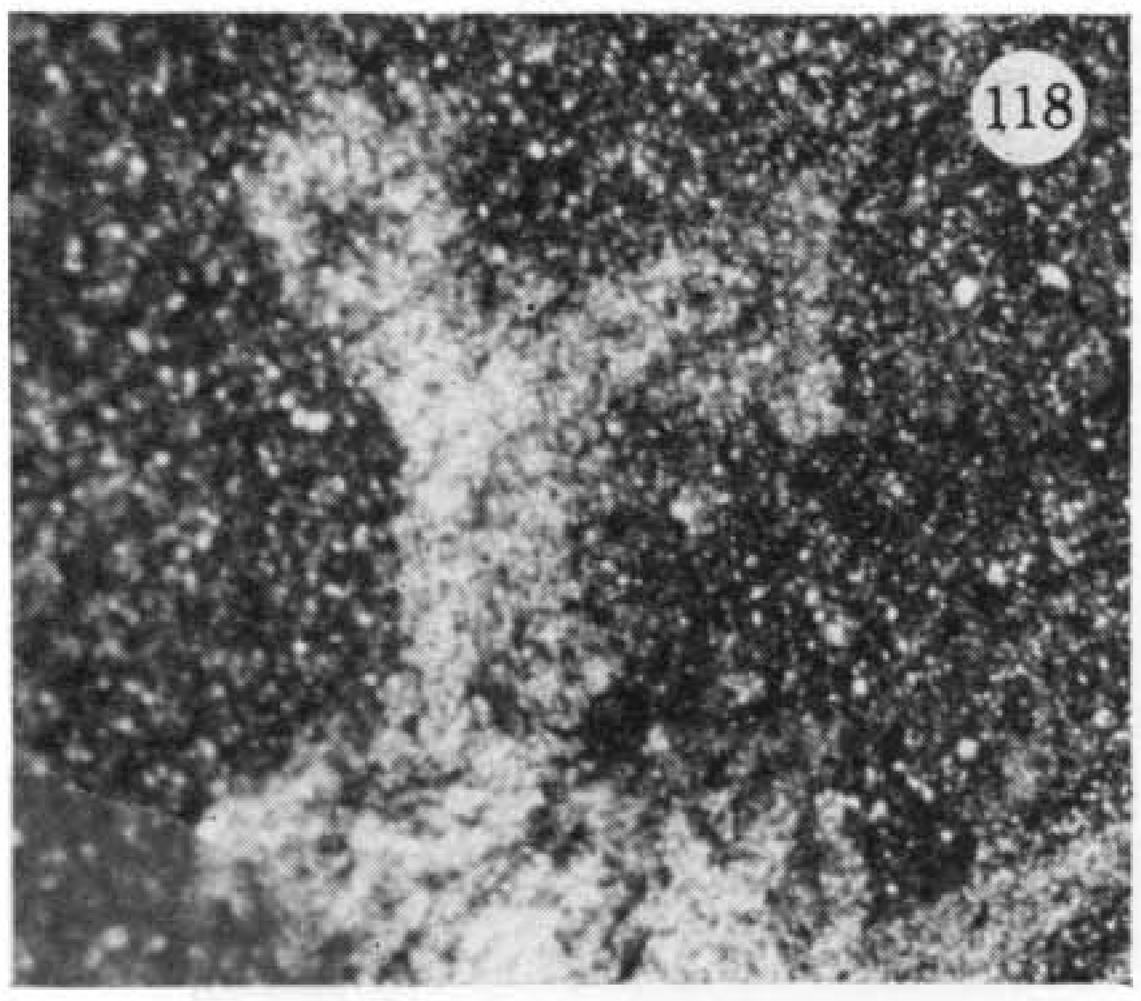
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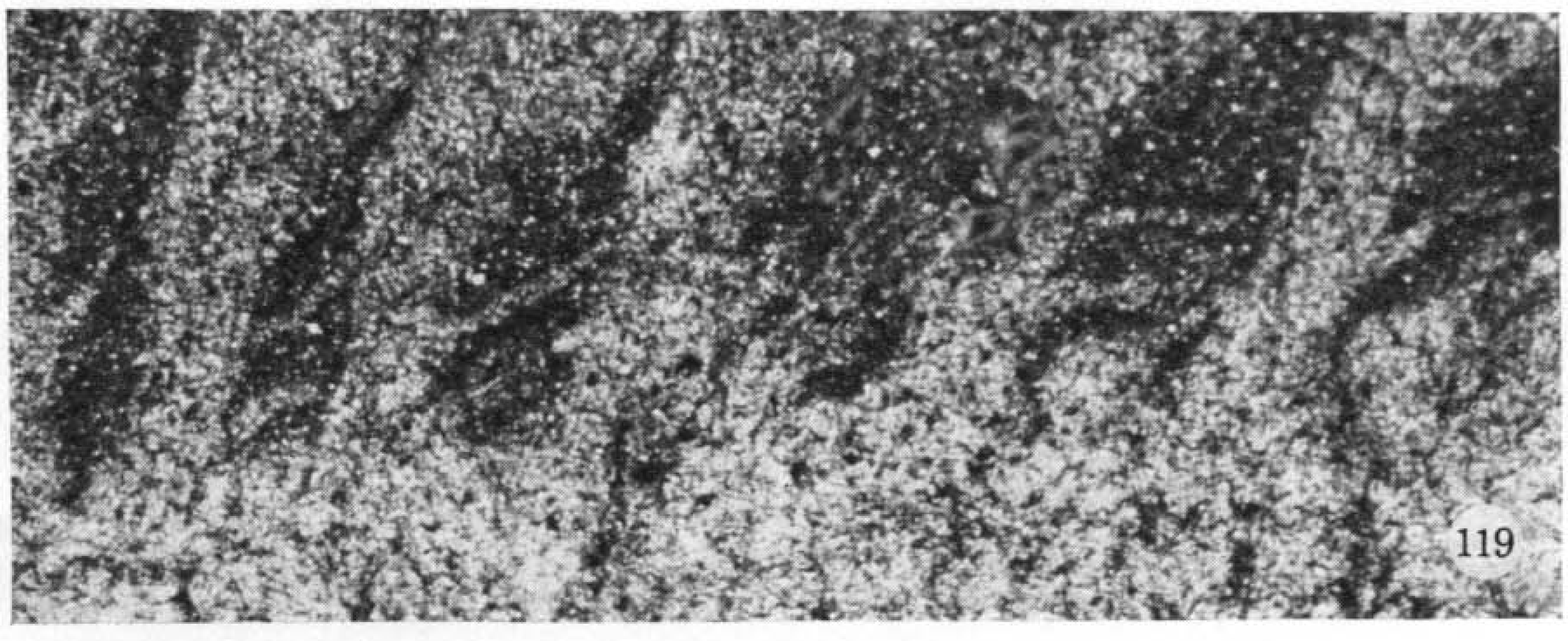
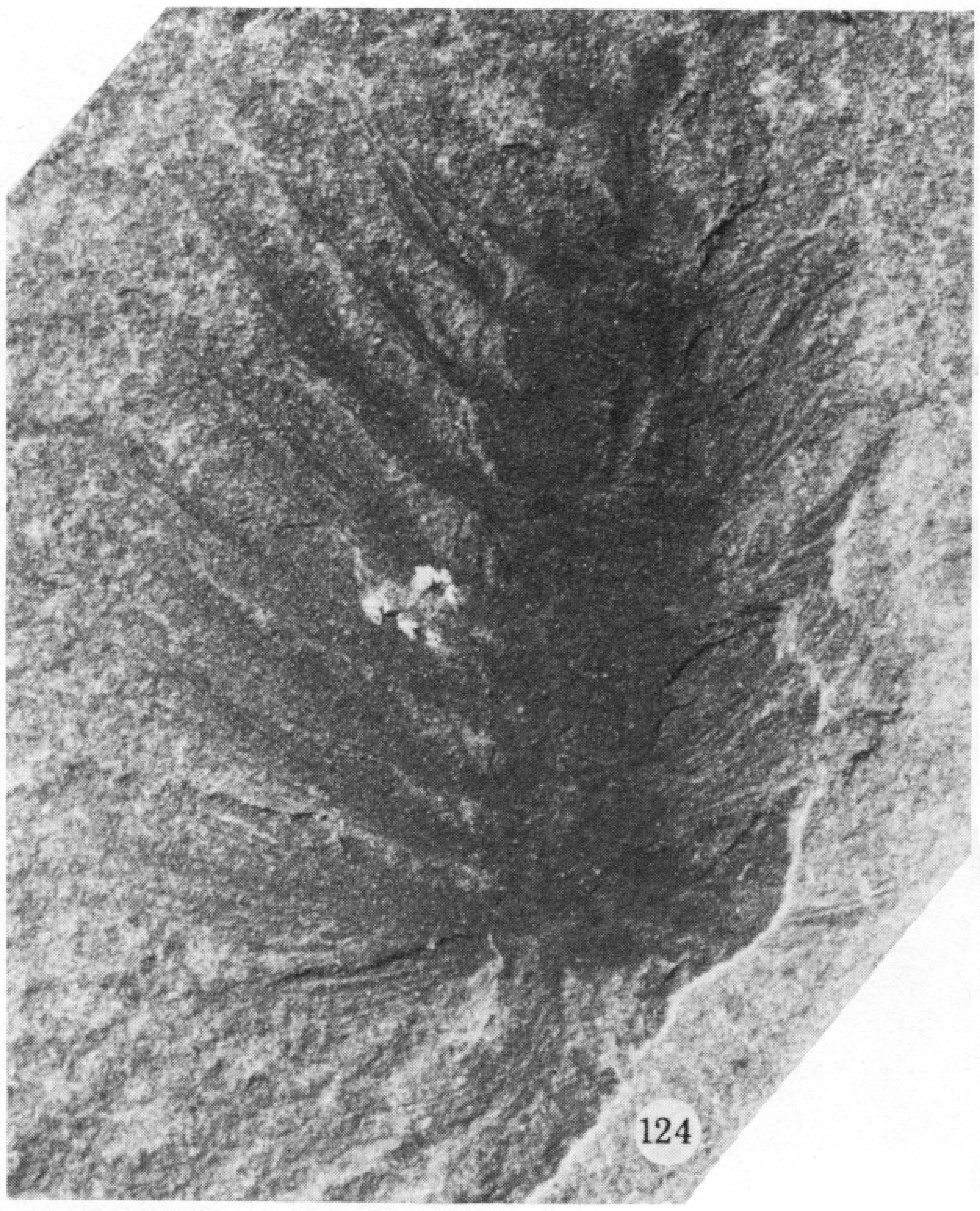

119

FIGURES 112–119. For description see opposite.


123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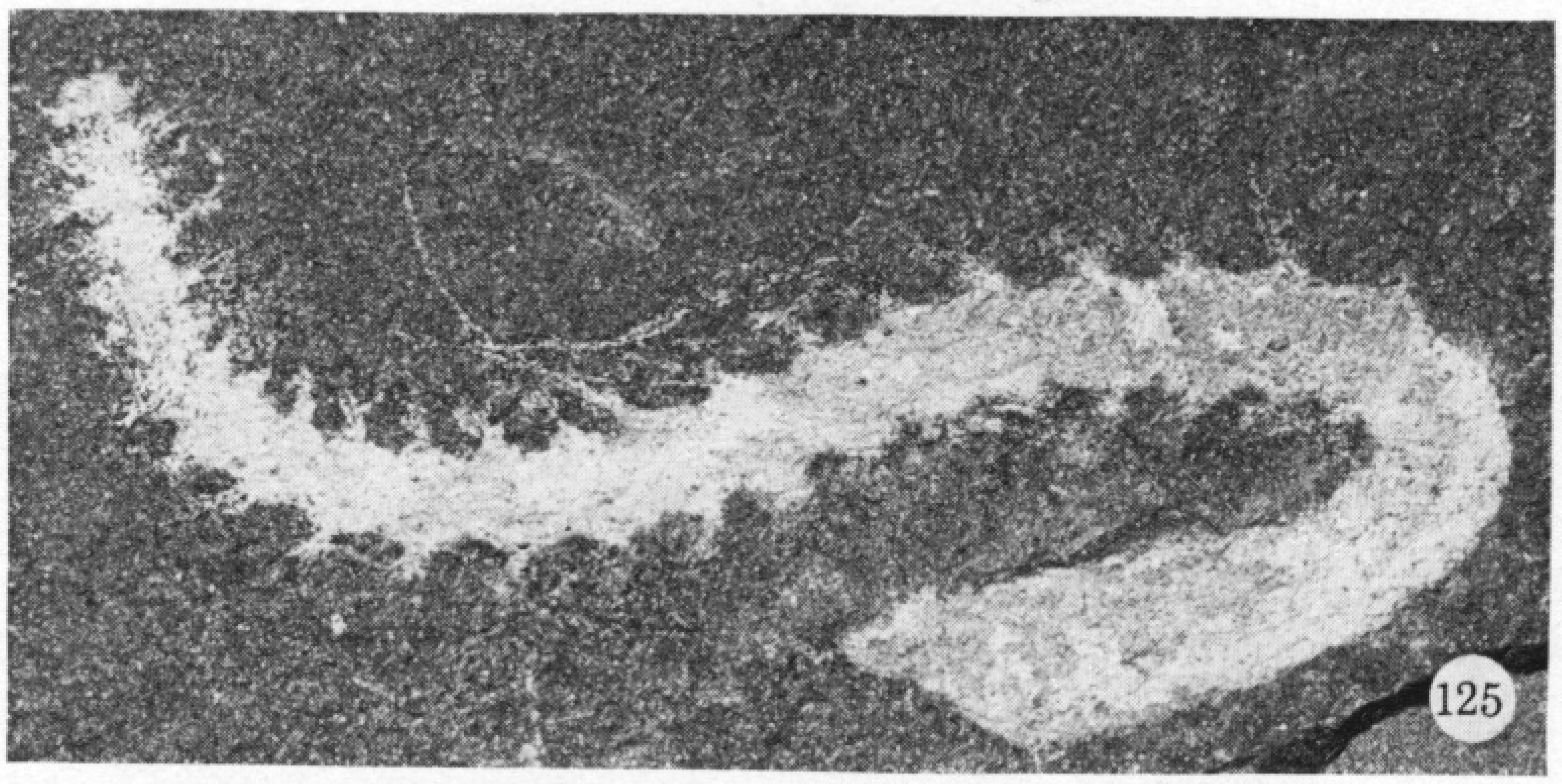
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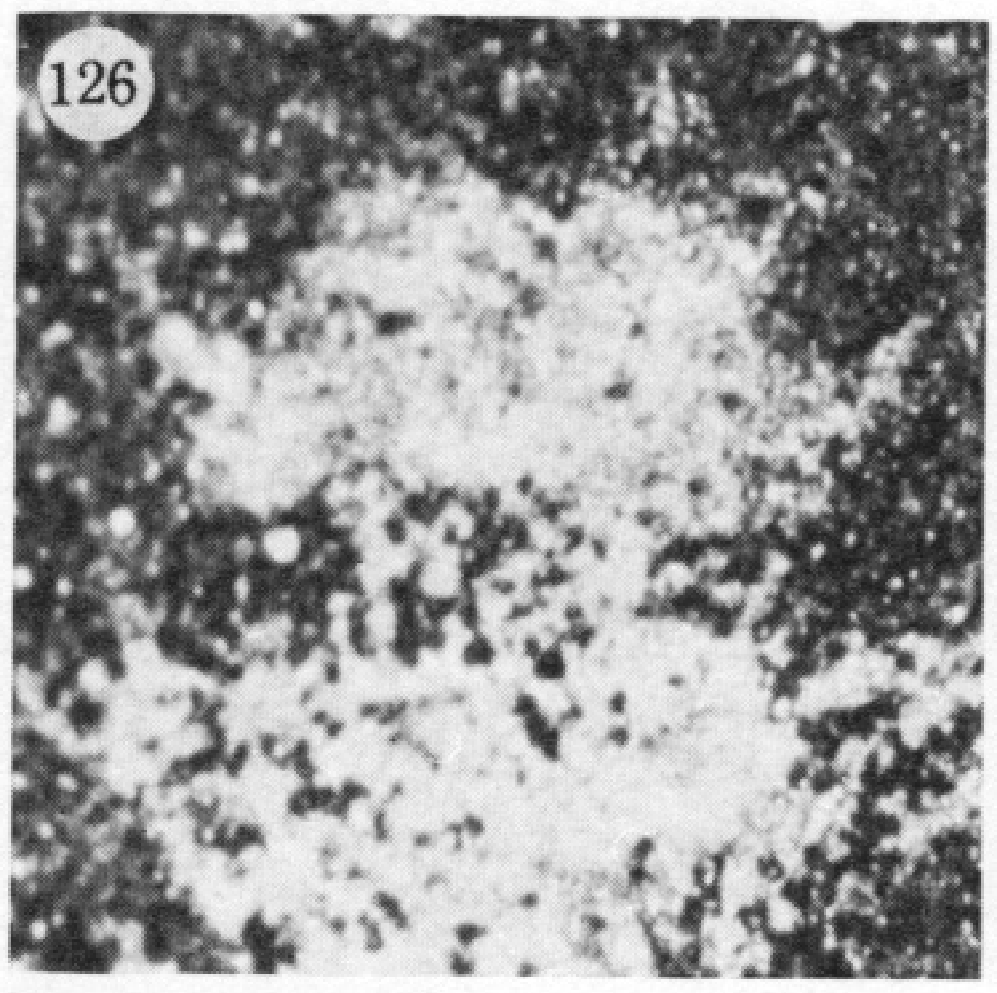
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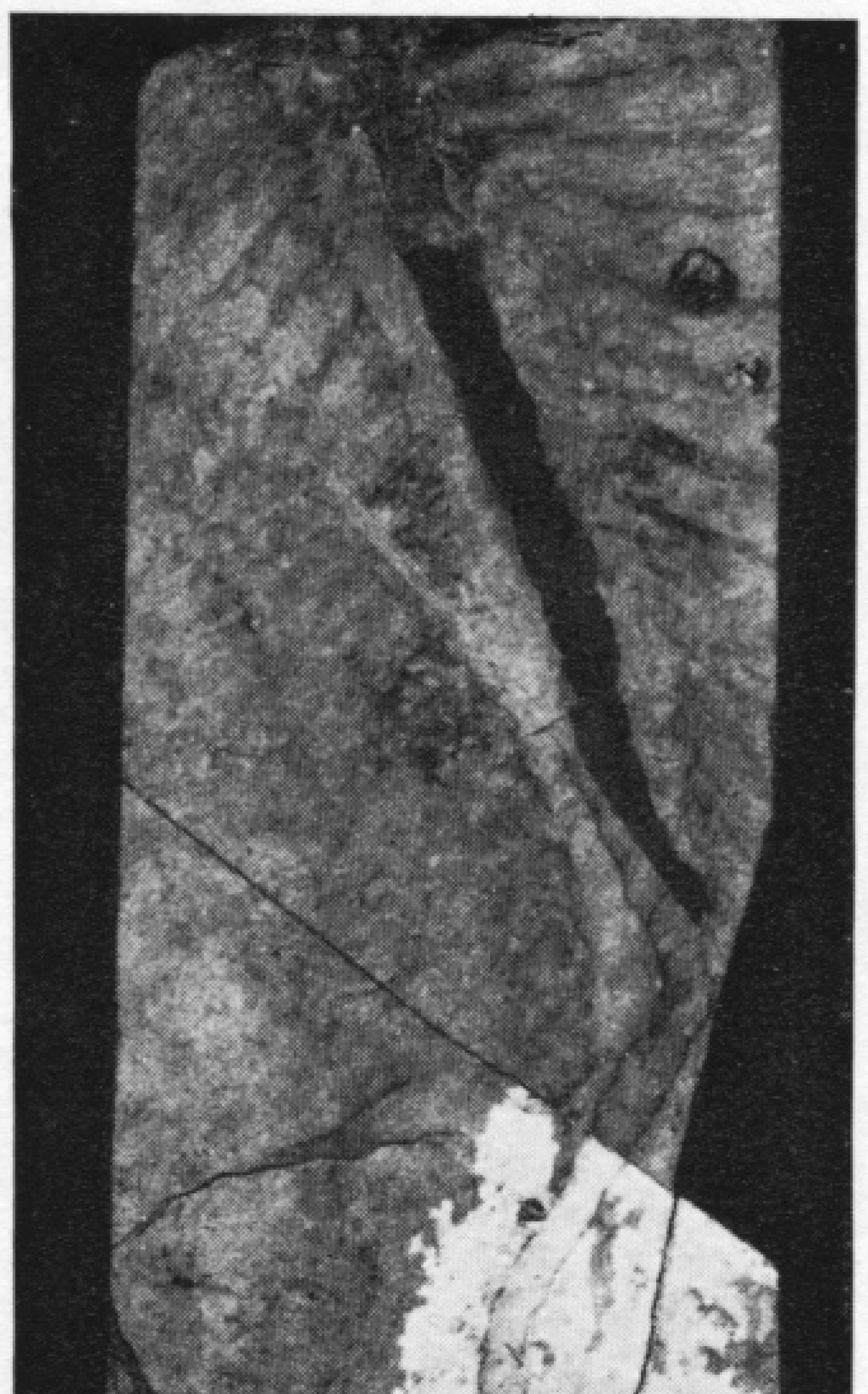
127


128


129


130


131

FIGURES 123–131. For description see opposite.