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## The Silurian–Devonian fossil record of the Myriapoda

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[Plate 1]

The oldest recorded terrestrial invertebrates are various small Diplopods (millepedes) from the Lower Old Red Sandstone of Britain which were probably preserved preferentially due to their robust calcified exoskeleton. While the myriapod affinities and terrestrial habits of the earliest, pre-Prídolí, claims are highly questionable, true diplopods are known from the latest Silurian (Stonehaven Group) and Lower Devonian of Scotland. In addition, a variety of enigmatic myriapod-like arthropods occur sporadically in the late Silurian–Lower Devonian freshwater facies of the Midland Valley of Scotland and Welsh Borderlands. Among these, the kampecarids ss. constitute a discrete group of short-bodied, diplopodous uniramian arthropods, possibly with myriapod affinities and aquatic habits. In contrast to the diversity of chelicerate groups represented in the later terrestrial invertebrate faunas of Rhynie, Alken and Gilboa, the Middle to Upper Devonian fossil record of the Myriapoda is very sparse. While true diplopods are notably absent, a variety of fragmentary chilopods (centipedes) are now known from the Gilboa Fauna (Givetian) of New York State.

The fossil record of the earliest animals currently accepted as fully terrestrial comprises several isolated occurrences of pre-Siegenian arthropods which have been assigned to the Myriapoda (millepedes, centipedes and others) largely on the basis of their elongate, multisegmented trunk showing little regional differentiation into tagmata and, occasionally, a series of similar uniramous limbs.

More specifically, all the Silurian and most of the Devonian records have been assigned to the Diplopoda (millepedes), a predominantly herbivorous group of cryptozoic land arthropods. This accords well with Rolfe's (1980) suggestion that the land was invaded sequentially by independent groups of invertebrates occupying successively higher levels in the trophic web, commencing with the herbivores which accompanied or closely followed the earliest terrestrial plants.

However, the material upon which these critical early records are based is generally poorly preserved and, apart from a brief account by Rolfe (1980), has not been re-examined since the original descriptions (for example, Page 1856; Peach 1882, 1899; Brade-Birks 1923; Størmer 1935; Clarke 1951), which were erroneous in several important respects. Consequently, a number of misconceptions have become established in the secondary literature (for example, Pompeckj 1912; Verhoeff 1928; Sharov 1966; Hoffman 1969). In addition, several informative supplementary specimens have since been collected which remain undescribed.

In view of its relevance as the fossil evidence for the earliest known land animals, and in particular for the initial diversification of the terrestrial Uniramia (Myriapoda and their close relatives, the Hexapoda), a detailed revision of this critical material, which now comprises some

30 specimens, is therefore badly needed (see Bergström 1979, 1980; Hoffman 1969). Such a study is currently in progress, the preliminary results of which are outlined in the present paper.

Of the four extant Classes of Myriapoda, the Chilopoda (centipedes) are known sporadically as fossils from the Middle Devonian onwards (Shear *et al.* 1984), the Symphyla are only recorded from the Eocene Baltic amber (Larsson 1978), while the Pauropoda have as yet no known fossil record at all (Hoffman 1969). These last two groups comprise minute, soil-living forms with very low chances of preservation and may well be as ancient in origin as their larger relatives.

The Diplopoda (millepedes) have by far the longest (late Silurian onwards) and richest fossil record of all the myriapods, but this is probably more due to their higher preservation potential, by virtue of their robust calcified cuticle and burrowing-aestivating habits (Rolfe 1980) than a reflection of a greater age and past diversity of the group. Among living forms the exuvium is decalcified, papery-thin and usually eaten after ecdysis; most fossils are therefore believed to represent corpses of dead individuals rather than discarded moults.

The assignation of fossil forms to the Myriapoda in the literature is frequently questionable, especially in the case of this incompletely known early material, because it is largely based on the absence of features characteristic of other arthropod groups. In particular, an elongate homonomously-segmented trunk is probably primitive for a number of unrelated arthropod lineages and cannot be taken in isolation to indicate true myriapod status, unless the Myriapoda are redefined as a polyphyletic grade of organization.

Similarly, the presence of trunk diplosegments is not diagnostic of the Diplopoda alone; this feature has also been demonstrated in the late Carboniferous to Triassic Euthycarinoidea, though these may actually represent aquatic uniramians (Bergström 1979; Schram & Rolfe 1982), and possibly in the late Carboniferous Arthropleurida as well (Almond 1985), whose myriapod status remains controversial (Manton 1977; Størmer 1976; Rolfe 1969). Manton's interpretation of diplosomy as a fundamental burrowing adaptation of the Diplopoda may therefore need to be reassessed in the light of this new evidence for the same feature in aquatic and epigeal arthropods.

The modern Diplopoda constitute a well-defined monophyletic group (Enghoff 1984) with a remarkably uniform basic structure which is already well-developed as far back as the late Carboniferous, when a wide variety of unambiguous millepede taxa can be recognized (Scudder 1882, 1890; Fritsch 1899; Pompeckj 1912; Verhoeff 1928; Kraus 1974). The Subclass Chilognatha, which includes the vast majority of fossil and recent forms characterized by a calcified cuticle and the possession of repugnatorial glands, show a large number of skeletal features in common, many of which are potentially preservable and recognizable in fossil material.

In particular, emphasizing trunk characters since these alone are usually preserved in fragmentary fossil material, the simultaneous presence of posteriorly overlapping diplotergites transversely subdivided into pro- and metazonites (the latter usually bearing ozopores), and two pairs of sternites per tergite, each bearing a pair of spiracles and a pair of uniramous appendages with a single terminal claw, argues strongly for true diplopodan affinities, although details of cephalic structure are needed to establish this firmly.

The fragmentary and poorly preserved condition of much of the Siluro-Devonian material often precludes the recognition of these diagnostic features, even if they were originally present, and in some cases at least the specimens may have degenerated since their original description.

Despite this latter possibility, it is thought preferable to adopt a conservative policy in only considering features currently demonstrable in the specimens in the analysis of their structure and taxonomic affinities.

Consequently, on the basis of the criteria already outlined, few of the specimens can be confidently assigned to the Diplopoda, and sometimes not even to the Myriapoda; the latter are best left as Arthropoda *incertae sedis*. Certainly, in the absence of critical taxonomic features such as the mouthparts and gonopods, it is quite unrealistic to assign any of these early forms to modern diplopod Orders.

Since fossil myriapods are usually preserved in water-lain sediments in association with an aquatic fauna, the recognition of fully terrestrial habits presents a further difficulty, as highlighted by the recent re-interpretation of all pre-Upper Carboniferous scorpions as aquatic or amphibious, despite their close overall morphological resemblance to modern fully terrestrial forms (Størmer 1970, 1976). In the final analysis, the nature of the respiratory organs provides the most reliable criterion (and the locomotory appendages to a lesser extent), but in the case of myriapods sufficiently well preserved material demonstrating such features as spiracles is rarely found before the late Carboniferous.

A summary of all known published occurrences of claimed Silurian–Devonian myriapods is given in figure 1, with the exception of the following questionable records: undescribed Silurian myriapods from Australia mentioned by Bergström (1979); *Cariderpestes* Whidborne, 1896 from the marine Devonian of Devon, which is clearly not a myriapod; a Lower Silurian myriapod from Estonia mentioned by Koken (1893) which was later discounted by the same author (personal communication in Pompeckj 1912); taxa described as Devonian in age by

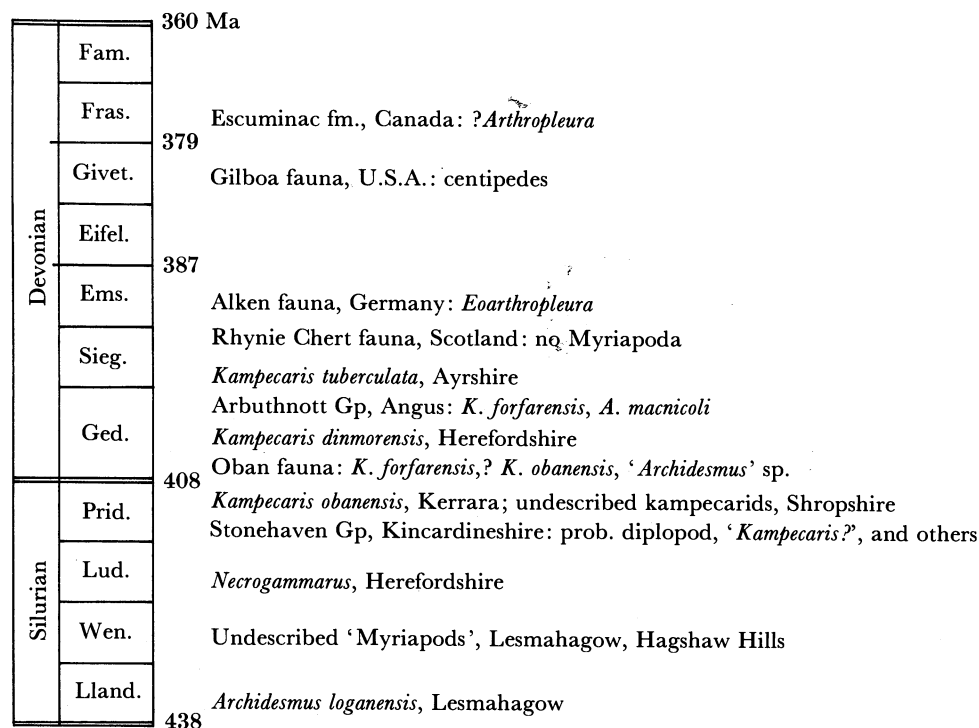


FIGURE 1. Summary of records of claimed Silurian–Devonian Myriapoda arranged according to stratigraphic occurrence. See text for discussion.

Matthew (1895) from the Little River Group, New Brunswick which actually belong to the Late Carboniferous, as discussed by Stopes (1914). (See also Mundel 1979; Rolfe 1982*a*.)

Of the earliest records from the Silurian inliers of the Midland Valley of Scotland, *Archidesmus loganensis* Peach, 1899 from the Llandovery shallow marine Patrick Burn Formation of the Lesmahagow Inlier was interpreted as a flat-backed millepede and as such would represent the oldest known land animal. The original specimen now only remains as a flaky carbonaceous film (Rolfe 1980, figure 4*b*) showing none of the specific millepede features described and illustrated by Peach. While it may since have deteriorated markedly, it has also been compared to associated algal remains (Ritchie 1963) and, in either case, is best disregarded as a valid record for the Myriapoda.

The small 'millepedes' collected by Ritchie from the Wenlock fish beds of the Slot Burn Formation, Lesmahagow, and the Fish Bed Formation, Hagshaw Hills, are preserved respectively as a relatively featureless, faintly segmented external mould, and as a small (6 mm long) tapering trunk composed of *ca.* 18 similar overlapping segments (Rolfe 1980, figure 4*a*). The latter retains its original brown cuticle ornamented with delicate ridges or terrace lines. However, both specimens lack diagnostic Myriapod features and are best regarded as *Arthropoda incertae sedis*.

*Necrogammarus salweyi* Woodward, 1870 from the marine Ludlow of Herefordshire is based on a fragment of a large arthropod trunk showing three articulated segments, the middle one of which (5 × 2.5 cm) appears to be a diplo-segment in that it is subdivided by a transverse groove and bears two adjacent limb bases ventrally (Rolfe 1980, figure 1). In addition, one of the outer segments bears a uniramian-type limb, and so *Necrogammarus* was assigned to the Diplopoda by Peach (1899). The outer segments, if complete, do not appear to be double, however, nor is there any evidence for segmental overlap or terrestrial habits. As Rolfe tentatively suggests, *Necrogammarus* may possibly represent at most an aquatic relative of the early Uniramia.

The lacustrine *Dictyocaris* Member of the Cowie Formation, Stonehaven Group (Přídolí) at Cowie Harbour near Stonehaven has yielded a number of purported myriapods, mostly undescribed and in very poor condition, in association with a fauna of phyllocarids, eurypterids and agnathan fish (Armstrong & Paterson 1970). These include a new genus of arthropod with a tapering trunk of 12 or more similar overlapping segments showing a distinctive tuberculate ornament and possible postero-lateral spines (figure 3, plate 1). This form was originally described as *Kampecaris* (?) sp. by Størmer (1935) but clearly does not belong here; its affinities within the Arthropoda remain unclear.

The most interesting specimen from this fauna is BM(NH). In. 43574 (figure 2) which, though small and incomplete, shows an overall similarity in habitus to younger fossil millepedes as well as several characteristic diplopodan features such as a compact, recurved head, abbreviated anterior trunk tergites, and posterior trunk tergites with lateral swellings on the metazonite, each covering two (or more) large quadrangular sternites. The latter may be a primitive feature for the Diplopoda and are also seen in the Archipolypoda, an important group of spiny late Carboniferous millepedes. On this basis, the specimen can be placed with some confidence within the Diplopoda and thereby constitutes the first reliable record for the Class, and hence the Myriapoda as well. It is insufficiently well preserved to determine whether it was terrestrial or aquatic in habits.

The majority of claimed fossil millepedes of Devonian age come from the predominantly alluvial Lower Old Red Sandstone of the Strathmore region (Northeastern Midland Valley

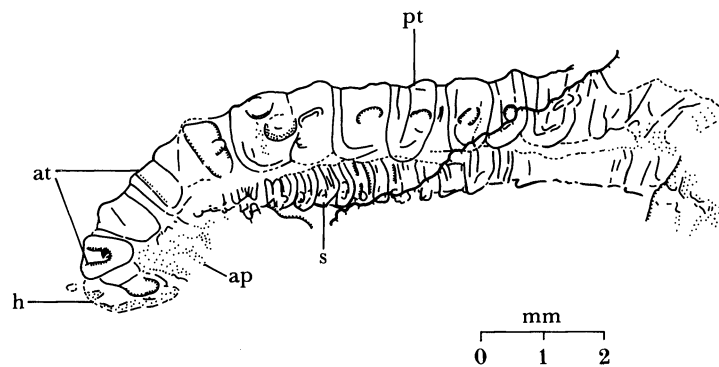


FIGURE 2. Camera lucida drawing of BM (NH). In 43574, possibly the oldest known Diplopod, from the Stonehaven Group (Pfidoli) of Cowie, Scotland. Abbreviations: ap, appendage; at, anterior tergite; h, head; pt, posterior diplotergite; s, sternite.

of Scotland), especially the Arbutnott Group and its lateral equivalents (Gedinnian, or possibly Siegenian; Mykura 1983) in Forfarshire (Angus) and Kincardineshire. These include *Kampecaris forfarensis* Peach, 1882 and *Archidesmus macnicoli* Peach, 1882 which occur in finely laminated lacustrine horizons ('fish beds') in association with a fauna of agnathan and Acanthodian fish and plant debris (Armstrong & Paterson 1970; Armstrong *et al.* 1978; Mykura 1983).

Peach (1882, 1899) interpreted both these forms as flat-backed 'chilognath myriapods' (that is, millepedes), although he believed (incorrectly) that they lacked diplosegments, the pro- and metazonites retaining their purported ancestral condition as clearly differentiated but unfused tergal rings. Despite their obvious differences, both genera were placed within a new taxon, the Archidesmidae, which was subsequently elevated to Family rank by Scudder (1886) and, mainly on the basis of their Palaeozoic age and metazonal expansions, placed within the Archipolypoda, not then regarded as true Diplopods by Scudder and now recognized as a quite different and distinctive group of late Palaeozoic millepedes. Consequently, the Archipolypoda are frequently regarded as the earliest millepedes in the later literature and, furthermore, Scudder's mistaken belief that the Carboniferous Archipolypods were aquatic has also been invalidly extended to the unrelated Devonian forms (for example, Bergström 1979; Little 1983).

*Archidesmus macnicoli* Peach, 1882 (figure 4) is almost certainly a true flat-backed millepede with a typical broad diplopodan head and a long trunk (*ca.* 5 cm long) with about 30 similar diplotergites, each of which bears quadrangular paranota on the metazonite. Each tergite covered more than one pair of limbs which did not project beyond the lateral margins of the paranota. While there is still no direct evidence for terrestrial habits, *Archidesmus sensu stricto* (that is, excluding the doubtful *A. loganensis* discussed above) probably 'split' a passage through contemporary leaf litter in a similar manner to modern flat-backed millepedes (Manton 1977).

The Genus *Kampecaris* was originally established by Page (1856) for a 'small phyllopod, or the larval stage of some larger crustacean' from the Lower Old Red Sandstone of Forfarshire. It was later reinterpreted as a (flat-backed!) millepede by Peach (1882) who described and illustrated as *K. forfarensis* a number of specimens showing characteristic diplopod features, most of which are no longer visible in the material and are therefore discounted. This applies in particular to details of head structures which were actually based on the *tails* of specimens incorrectly oriented back-to-front by Peach, in which he was followed by later authors such as Scudder (1886).

A number of specimens of *Kampecaris forfarensis* (figures 5 and 7), the commonest L. O.R.S.

'millepede', and similar forms from the Gedinnian of Herefordshire (*K. dinmorensis* Clarke, 1951) and the Přídolí of Shropshire (undescribed) allow a model, albeit incomplete, of kampecarid morphology to be formulated. They constitute a distinctive group of small (*ca.* 20–30 mm long), short-bodied uniramian Arthropods subdivided into three recognizable tagmata. The compact oval head is subdivided transversely into two equal subunits; the latter may, however, alternatively represent a head shield or modified anterior trunk tergite (compare the euthycarcinoid *Sottyxerxes*, Schram & Rolfe 1982). Immediately following the head is (?) a short, wide first trunk segment, possibly a haplosomite. The remainder of the more or less cylindrical trunk, tapering slightly towards the anterior, comprises nine similar posteriorly overlapping diplotergites, each with a ring-like prozonite sharply demarcated by a transverse groove from a posteriorly expanding metazonite. The body ends in a very characteristic swollen tail unit composed of a final (tenth) modified diplosomite whose metazonite tapers posteriorly into a terminal anal segment with which it is fused and which may be horizontally subdivided into dorsal and ventral anal valves. (A broadly similar 'pleotelson' is seen in late Palaeozoic phreatoicid isopods: Hesser (1969); Schram (1974). The tenth diplosegment is apodous, whereas more anterior trunk segments each bear two pairs of similar long uniramous limbs. These are rarely seen and may lack a fully mineralized cuticle. The nature of their attachment to the ventral sternites and the structure of the latter are poorly known. Where present, the cuticle is substantial, heavily calcified and composed of two discrete layers, the outer of which is perforated by closely spaced canals.

The kampecarids as defined here thus show a number of millepede features but are only questionably referred to the Diplopoda because of their very reduced number of body segments (albeit a character of dubious taxonomic significance), unusual head and tail morphology, and the uncertainty concerning the homologies of these various units and the detailed structure of the sternites. Pending further data on their cephalic appendages and other ventral structures, they are best considered for the time being as a discrete group of early uniramian arthropods of uncertain affinity, but possibly most closely related to the Diplopoda.

Rather than simply representing an early group of cylindrical burrowing millepedes (Rolfe 1980), their restriction to and comparative local abundance in fresh water facies (Page 1856; Peach 1882) as well as their lack of obvious terrestrial adaptations might be seen to favour

#### DESCRIPTION OF PLATE 1

FIGURES 3–8. Myriapod-like Arthropods from the Lower Old Red Sandstone of Scotland.

FIGURE 3. Arthropod *incertae sedis* (*Kampecaris* (?) sp. of Størmer, 1935). Grant Institute, Edinburgh GI. 1594. (Whitened latex of external mould; magn.  $\times 4$ .) Stonehaven Group (Přídolí), Cowie near Stonehaven, Kincardineshire.

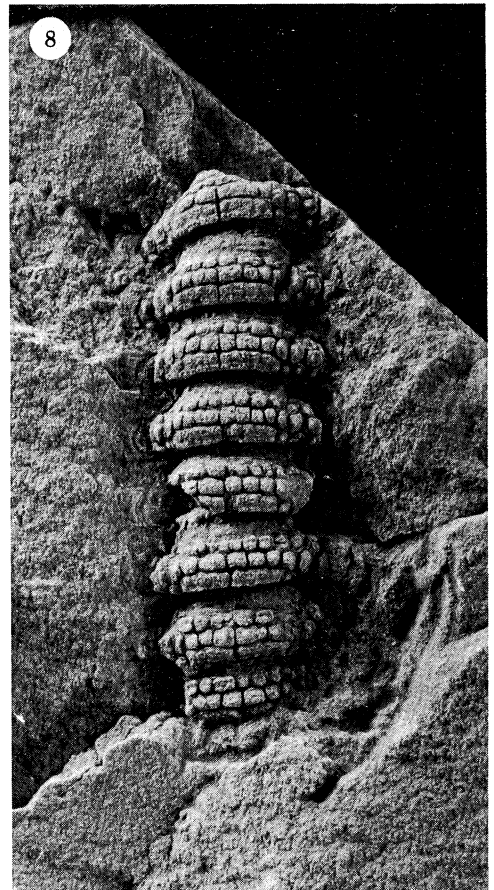
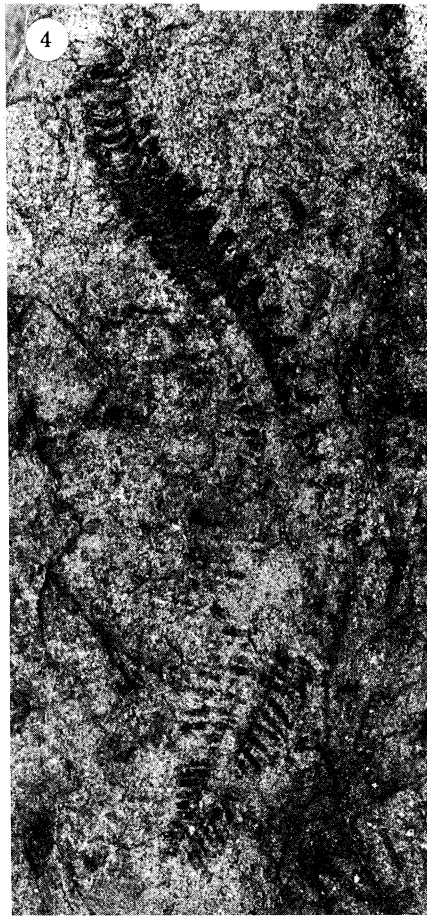
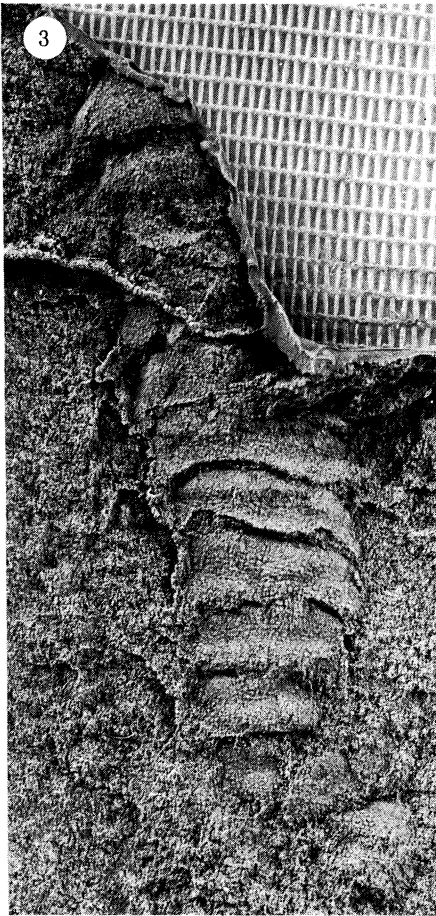
FIGURE 4. *Archidesmus macnicoli* Peach, 1882. Syntype. Royal Scottish Museum, Edinburgh 1953.7. (Photographed under alcohol; magn.  $\times 5$ .) Arbuthnott Group (Gedinnian), Carmyllie, near Arbroath, Angus.

FIGURE 5. *Kampecaris forfarensis* Peach, 1882. Flattened specimen in dorsal view, British Museum (Natural History) I.2940. (Whitened latex of external mould; magn.  $\times 4$ .) Arbuthnott Group (Gedinnian), Canterland Den, Kincardineshire.

FIGURE 6. *Kampecaris obanensis* Peach, 1899. Holotype. Institute of Geological Sciences, Edinburgh 10385. (Whitened specimen; magn.  $\times 6$ .) Přídolí, Island of Kerrera near Oban, Argyll.

FIGURE 7. *Kampecaris forfarensis* Peach, 1882. Royal Scottish Museum, Edinburgh 1969.16. (Whitened latex of external mould; magn.  $\times 5$ .) Carmyllie Group (Gedinnian), Mirestone Quarry, Angus.

FIGURE 8. *Kampecaris tuberculata* Brade-Birks, 1923. Holotype. British Museum (Natural History) In.23803. (Whitened specimen; magn.  $\times 4.5$ .) Lower Old Red Sandstone (Siegenian), Dunure, Ayrshire.



FIGURES 3–8. For description see opposite.

(Facing p. 232)



aquatic habits, in which case they might represent, as has already been suggested for the Euthycarcinoids (Bergström 1979; Schram & Rolfe 1982), products of an extensive early Palaeozoic aquatic Uniramian radiation. They may well have fed upon the abundant associated plant debris, and were possibly close to the ancestry of the longer-bodied early terrestrial millepedes.

A number of additional, and possibly quite unrelated, Silurian–Devonian Myriapod-like Arthropods which do not conform to this model as defined above have been placed in the genus *Kampecaris*, largely on the basis of their age and the mistaken original conception of the habitus of the latter as flat-backed millepedes.

In addition to *Kampecaris* (?) sp. Størmer, 1935 discussed already, *Kampecaris obanensis* Peach, 1899 (figure 6) from the Pridoli braided stream deposits of Kerrara near Oban, Argyll, is a (?decalcified) compression of a short-bodied arthropod with a compact head followed by a trunk of 14 tergites with lateral quadrangular plates (pleurites or paranota?) and terminal anal valves. Apart from possible ventral styli at the end of the body, appendages are lacking. However, it is probably Uniramian in affinities, but generically distinct from *Kampecaris* ss.

*Kampecaris tuberculata* Brade-Birks, 1923 (figure 8) from the Siegenian inter-laval red beds of Dunure, Ayrshire is certainly not a kampecarid ss. and constitutes the youngest, largest (trunk 7 mm wide, including paranota) and most incontrovertible L. O.R.S. millepede. It occurs in association with a rich terrestrial ichnofauna, attributed to diplopods among others (Rolfe 1980; E. Walker, unpublished). In its strongly tuberculate tergites and quadrangular paranota it bears a striking resemblance to later flat-backed millepedes such as the Dinantian *Anthracodesmus* Peach, 1899 and the Recent *Polydesmus*, and may well have led an analogous litter-inhabiting existence. Details of the sternal morphology and robust laterally inserted limbs are well preserved beneath the dorsal surface, but require further investigation.

While the pre-Siegenian fossil record of terrestrial invertebrates is dominated by these isolated occurrences of presumably herbivorous or detritivorous diplopods and kampecarids, well-substantiated millepedes are, in contrast, notably absent from younger Devonian rocks. Even in the relatively well studied Middle and Upper Old Red Sandstone facies of Britain, lacustrine and fluvial faunas are composed almost entirely of a rich diversity of fish accompanied by very few arthropods, apart from the conchostracan '*Estheria*' (Mykura 1983).

The later Devonian record of terrestrial invertebrates comprises essentially three relatively rich arthropod faunas from the Rhynie Chert, Scotland (Siegenian), Alken an der Mosel, West Germany (Emsian) and Gilboa, New York State (Givetian), all of which are dominated by a diversity of carnivorous chelicerates accompanied by primitive hexapods (spore-feeders–detritivores) and, in the last case, predatory centipedes (Shear *et al.* 1984; Rolfe 1982 and personal communication, 1984).

Myriapods have not as yet been recorded from the Rhynie Chert, though G. Whaley (personal communication, 1984) has suggested tentatively that *Rhyniognatha* Tillyard, 1928 may be a myriapod mandible, and this fauna may well prove much richer than hitherto recorded on further investigation.

Størmer (1976) described *Eoarthropeura devonica* as an amphibious–terrestrial myriapod from Alken, representing the earliest record of the Arthropleurida. However, the myriapod status of the latter remains controversial (Manton 1977; Rolfe 1969) and Størmer's detailed interpretation of this extremely fragmentary material is open to question on a number of points; even its arthropleurid affinities cannot be regarded as well established.

Of the other Devonian aquatic arthropods which have been compared with the Arthropleurida, *Budenbachiellus* Broili, 1930 from the Siegenian Hunsrück Shale has been reassigned to the Genus *Cheloniellon* (Stürmer & Bergström 1978), while *Oxyuropoda* (Carpenter & Swain 1908) from the latest Devonian–earliest Carboniferous of Kilkenny, Eire is clearly quite unrelated to the Myriapoda and may be an isopod crustacean (Rolfe 1969). Thus, perhaps excepting an undescribed possible arthropleurid fragment from the Escuminac Formation (Frasnian) of Canada (Schultze 1972), the Devonian record for the Arthropleurida remains poorly established and the earliest fairly reliable occurrence is the material from the Namurian of Czechoslovakia described by Přibyl (1960).

The recently discovered Middle Devonian fauna from the black deltaic mudstones of Gilboa (Rolfe 1982; Shear *et al.* 1984) includes flattened cuticular fragments (isolated tergites, forcipules, podomeres) provisionally assigned to at least two extant Orders of Chilopoda (Craterostigmatomorpha and Scutigermomorpha), constituting the earliest records of the Class. Fossil centipedes remain unknown thereafter until the late Carboniferous of North America (Mundel 1971).

In view of the extremely sporadic temporal and spatial distribution of fossil Myriapoda throughout the Phanerozoic, few reliable conclusions can be drawn as yet concerning the relative ages of the various lineages or the geographical pattern of their initial colonization of the land and subsequent dispersal.

The appearance of the first fossil myriapods coincides with that of extensive continental sediments in the late Silurian–Devonian (Johnson 1980) and the predominance of diplopod-like forms over other land arthropods may similarly be merely a preservational artefact rather than a reflection of the true pattern of faunal invasion and evolution. Likewise, the geographical distribution of these early myriapod records probably largely reflects the differing intensity of palaeontological research between the various continents.

All substantiated Silurian–Devonian fossil records of myriapods are confined to the Laurasian supercontinent and within this landmass diplopods are known only from Europe before the late Carboniferous, while Palaeozoic Chilopoda have yet to be substantiated outside North America. (Several fossil centipedes were recently recorded by D. Sotty and G. Pacand in an unpublished preliminary inventory of the Stephanian B fauna of Montceau-les-Mines, France. However, until this material is described, its chilopod affinities must remain uncertain.) As the commonest known forms, the late Silurian–early Devonian kampecarids are recorded from fresh water facies of two quite separate British L. O.R.S. basins, the intramontane Midland Valley of Scotland and the marginal marine South Wales areas, and possibly a third isolated basin in the Lorne area of Eastern Scotland (Mykura 1983). However, in view of the uncertainty concerning their terrestrial or aquatic habits, little can usefully be said concerning possible migration routes.

Faunal and floral evidence from the Old Red Sandstone facies of Laurasia (especially Greenland) and Australia suggests ease of migration between these two areas (Johnson 1980) and a possible connection between Laurasia and Gondwanaland in the Devonian is not precluded by available palaeomagnetic evidence (A. G. Smith, personal communication, 1984). However, incontrovertible terrestrial arthropods have yet to be recorded from Australia; the undescribed Silurian myriapod material mentioned by Bergström (1979) is actually Devonian in age and its myriapod status is highly questionable (H. B. Whittington, personal communication, 1984).

The fossil record of the Myriapoda similarly affords insufficient data to resolve such questions as the nature of the aquatic precursors of the terrestrial Uniramia (Myriapoda, Hexapoda, ?Onychophora) or whether or not the various groups all evolved on land from a single common terrestrial ancestor, as opposed to colonizing the land independently after an initial aquatic radiation.

On the evidence of a detailed structural and functional analysis of the extant groups as well as embryological studies, Manton (1977 and earlier papers) regards the Myriapoda as a monophyletic assemblage which evolved, as did the Hexapoda independently, from a hypothetical soft-bodied terrestrial lobopod. Dohle (1980 and earlier works), however, on the basis of a cladistic analysis of the living forms, derives the hexapods from among the Myriapoda, which therefore are regarded as a paraphyletic assemblage, both groups having ultimately evolved from a common terrestrial tracheate ancestor.

In complete contrast, Bergström (1979, 1980) envisages an extensive radiation of aquatic sclerotized uniramians in the Lower to Middle Palaeozoic, perhaps in marginal limnic environments poorly represented in the rock record. These included the ancestors of all the various Hexapod and myriapod lineages that subsequently colonized the land, independently acquiring terrestrial adaptations such as a tracheal system (see Meglitsch 1972, p. 615 onwards), as is now well accepted for the Arachnida (see, for example, Størmer 1976; Rolfe 1980). Although most of the fossil forms cited in support of such a hypothesis are either irrelevant (for example, *Anomalocaris*), poorly known (for example, *Xenusion*, *Tesnusocaris*) or mistakenly regarded as aquatic (for example, Arthropleurida, Archipolypoda), the late Carboniferous euthycarcinoids (Schram & Rolfe 1980), and perhaps even the kampecarids and the enigmatic *Necrogammarus*, might be seen to suggest the presence of a diversity of sclerotised aquatic Uniramian lineages in the middle Palaeozoic, one or several of which may have given rise to the terrestrial Uniramia by the late Silurian. Collection of further material from the well-localized Scottish localities (Armstrong & Patterson 1970) coupled with analysis of associated sedimentary facies and faunas and the detailed restudy of the available material should contribute to the amplification or disproof of this hypothesis.

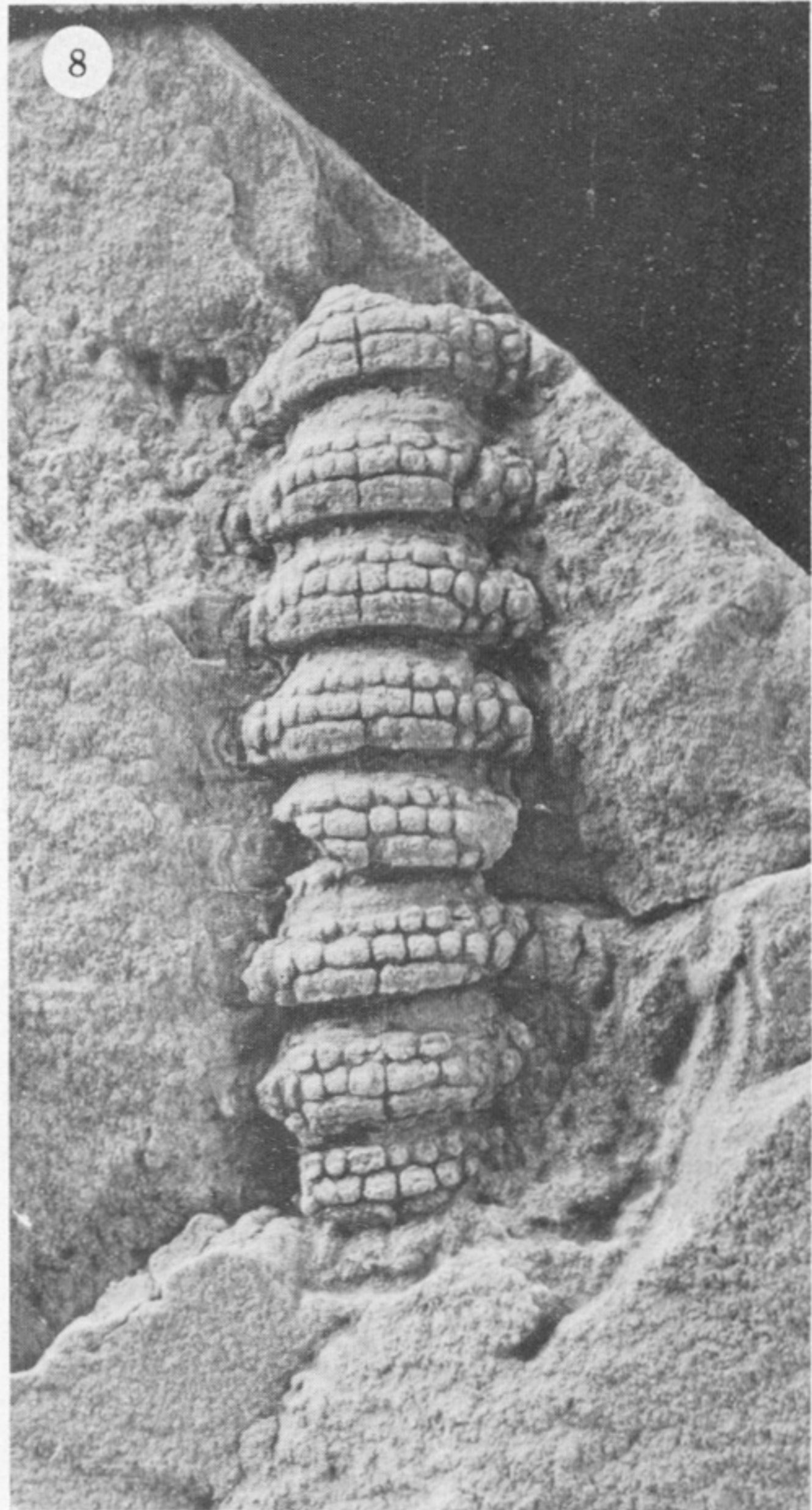
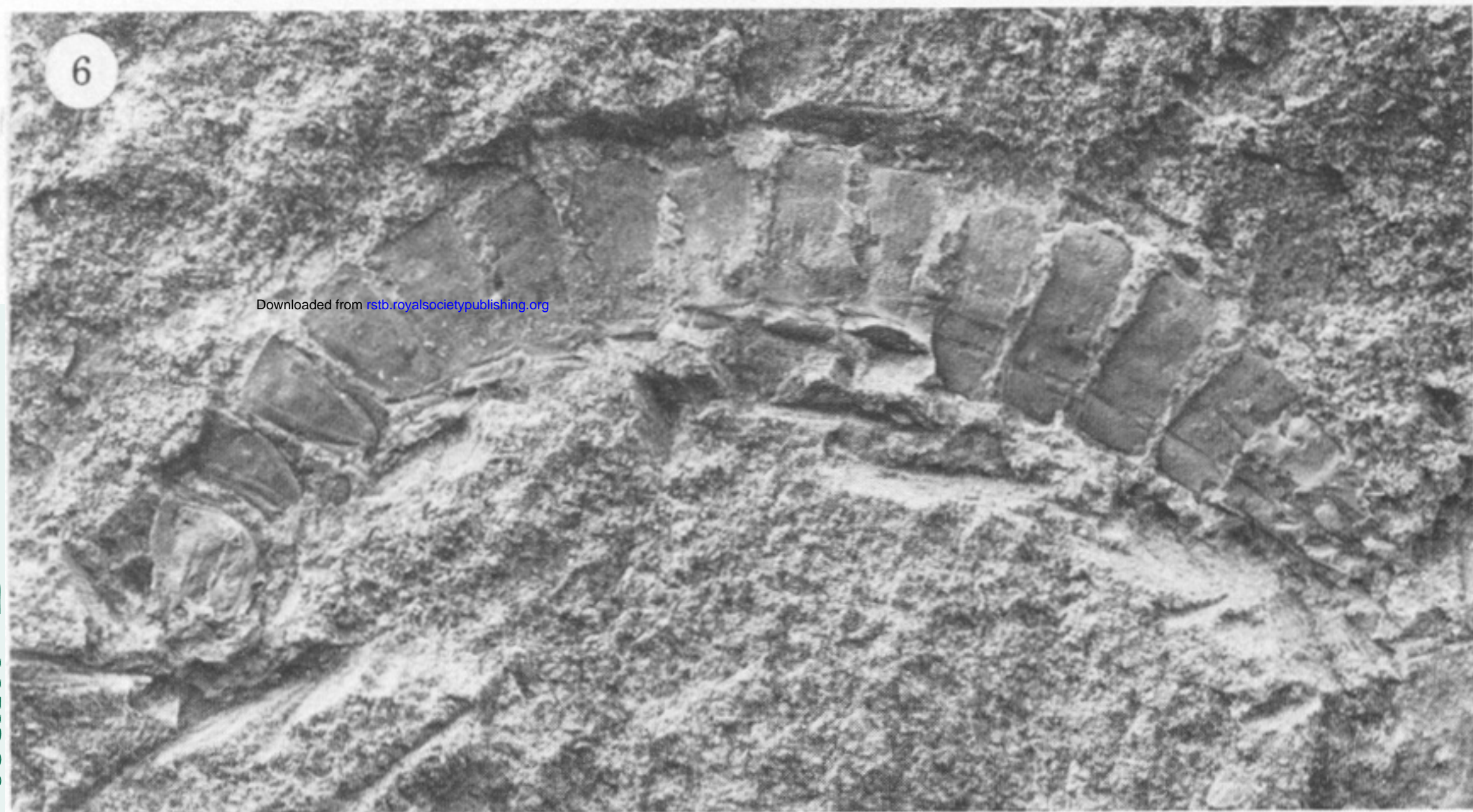
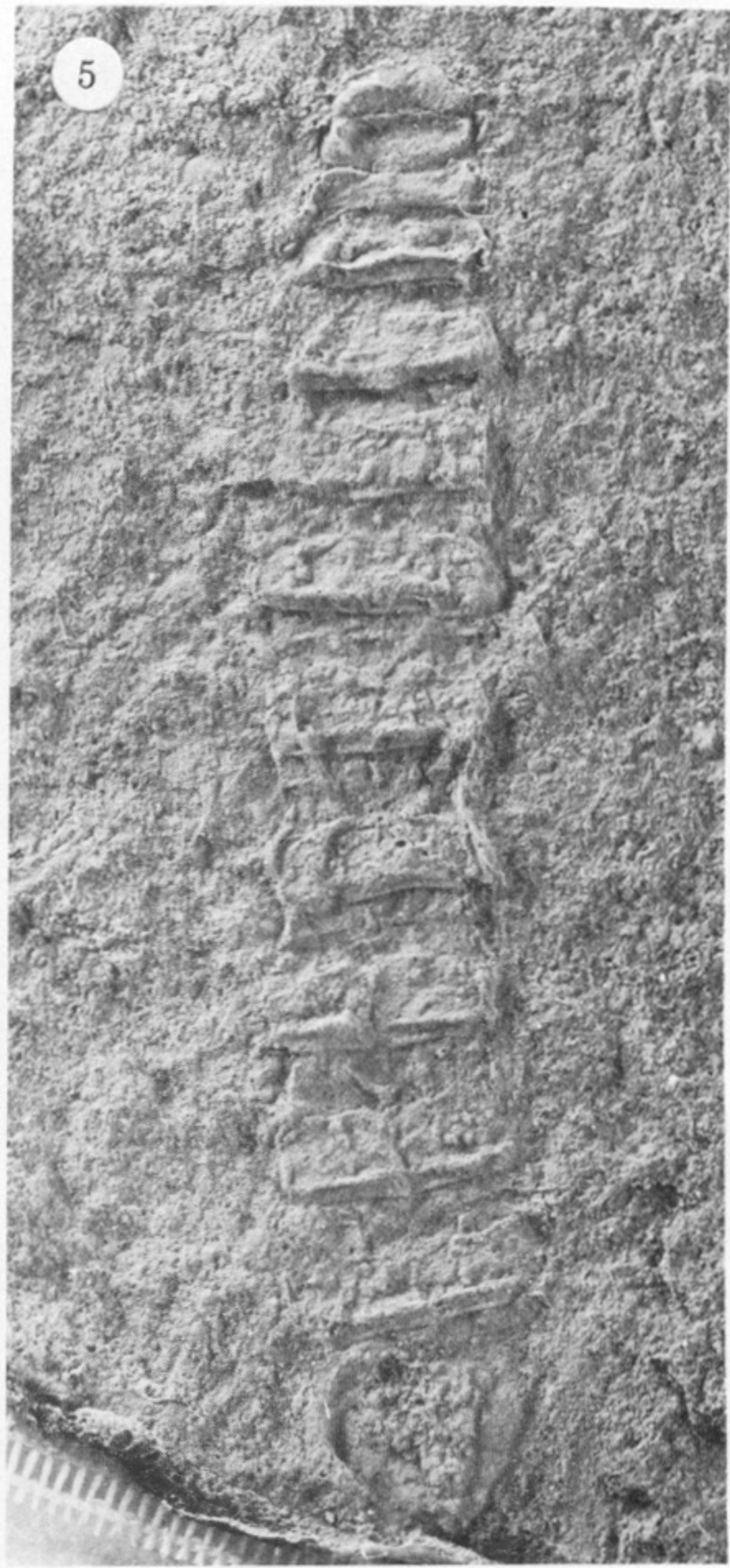
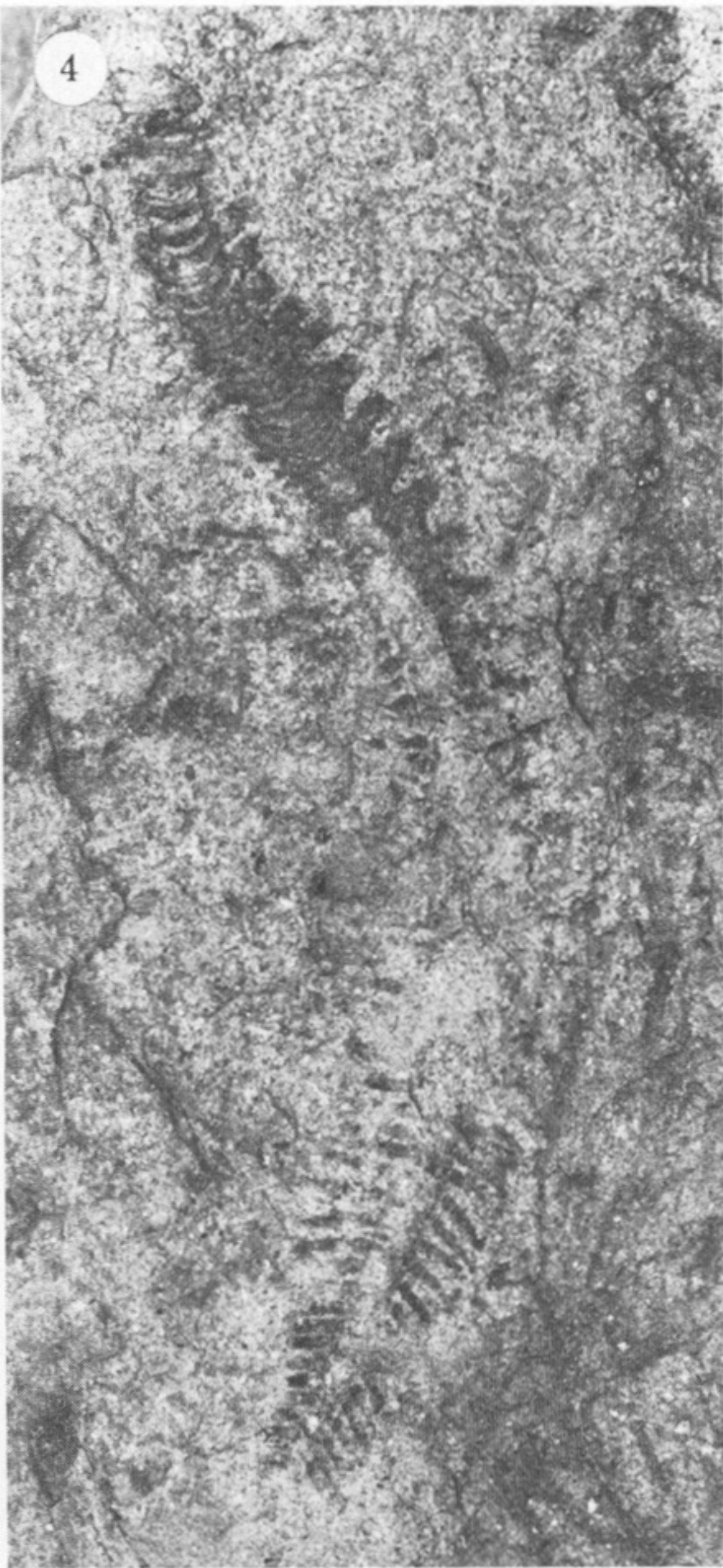
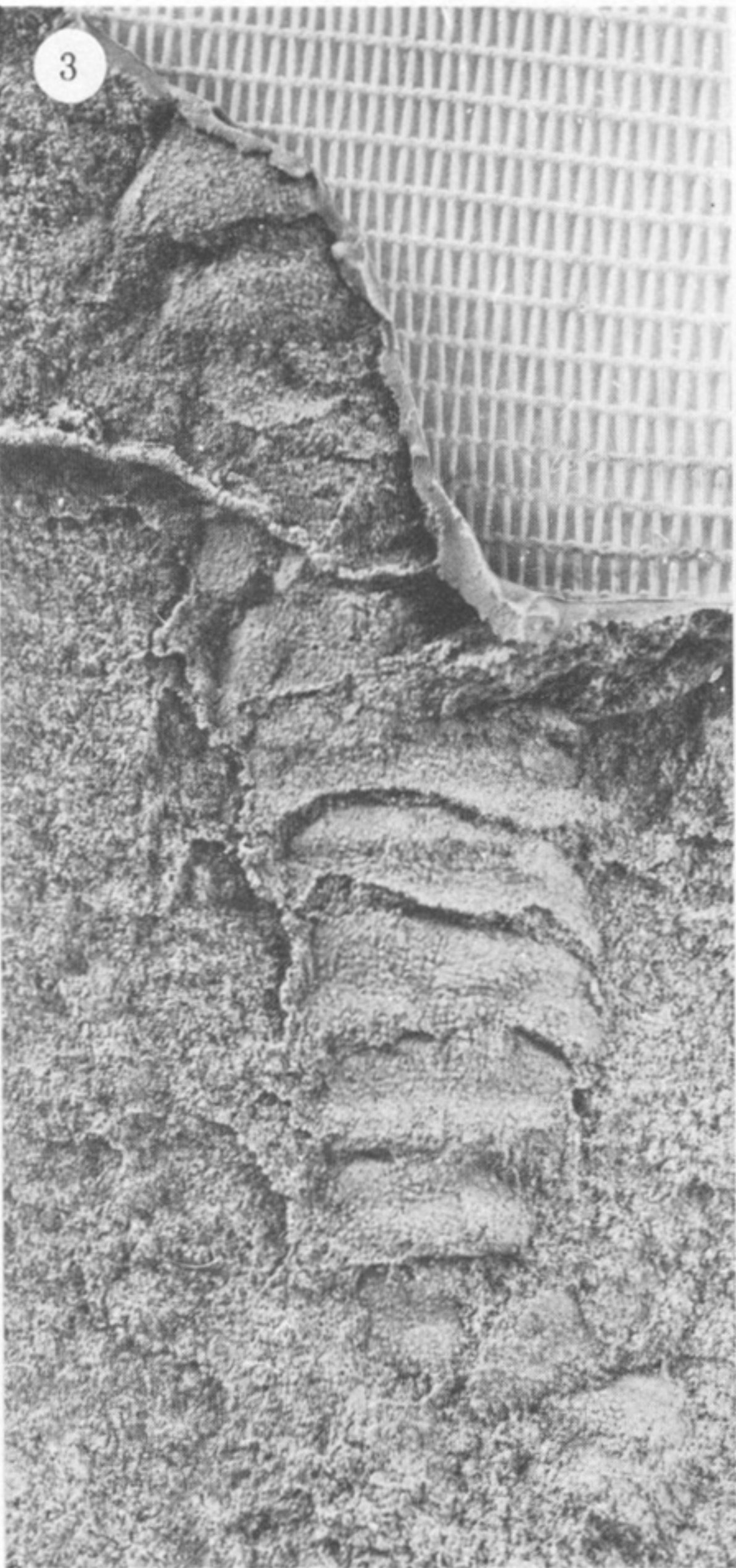
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FIGURES 3–8. For description see opposite.