

# The biota of Upper Silurian submarine channel deposits, Welsh Borderland

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# The biota of Upper Silurian submarine channel deposits, Welsh Borderland

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## Abstract

The Upper Silurian submarine channel deposits at Leintwardine in the Welsh Borderland provide a unique palaeoenvironmental setting in the fossil record, that of an indigenous biota within shelf-edge channel heads. Along with typical Silurian fossils such as brachiopods and trilobites, the deposits contain an exceptionally preserved fauna including predominantly fully articulated echinoderms and disarticulated to articulated arthropods. The biota is interpreted to comprise indigenous and exotic elements, with variable transportation, both within and between species. The echinoderms are stelleroid-dominated although less abundant crinoids, echinoids and ophiocistioids also occur. The echinoderms occur within discrete horizons, so-called starfish beds, whereas other fossils occur sporadically through the remainder of the channel fill. Oxygen levels within the Church Hill Channel do not appear to have been restricted, and periodically high sedimentation rates, likely to be storm-triggered, are interpreted to be central to the preservation of much of the unusual biota.

The stelleroids are diverse, comprising 15 species; asteroids and ophiuroids are represented. One new ophiuroid species is erected, *Loriolaster calceatus* sp. nov. and the subspecies *Urasterella ruthveni* var. *leintwardinensis* Spencer is not maintained. A previously undescribed specimen, likely to be a juvenile, is described as *Coccaster?* sp. Specimens previously described in the literature as *Bdellacoma vermiformis* Salter and *Palasterina antiqua* (Hisinger) are reassigned to *Klasmura?* sp. and *Palasterina* sp., respectively.

The eurypterids comprise mainly carcosomatids, with a lesser number of pterygotids. The pronounced serration with a deep notch on the distal podomere of prosomal appendage VI is identified as being diagnostic of *Carcinosoma punctatum* Salter. Newly collected and previously described material is assigned to *Carcinosoma* sp. and *Carcinosoma?* sp. Previously undescribed material is assigned to *Erettopterus?* sp. A distal portion of a free ramus is reassigned to *Pterygotus?* sp.



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## INTRODUCTION TO THE LEINTWARDINE SUBMARINE CHANNELS

An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in several channel deposits in the Welsh Borderland area of the UK, around the small Herefordshire village of Leintwardine, approximately 10 kilometres to the west of Ludlow (Text-fig. 1.1). The unusual biota is preserved exclusively within the siltstone channel fill (Whitaker 1962).

The channel deposits are of scientific importance for several reasons. Firstly they provide a rare example of exceptional preservation of Silurian organisms, and they contain the type localities for many of the taxa recovered from them. Secondly, the set of shelf-edge submarine channels provide a unique palaeoenvironmental setting within the stratigraphic record of the British Isles.

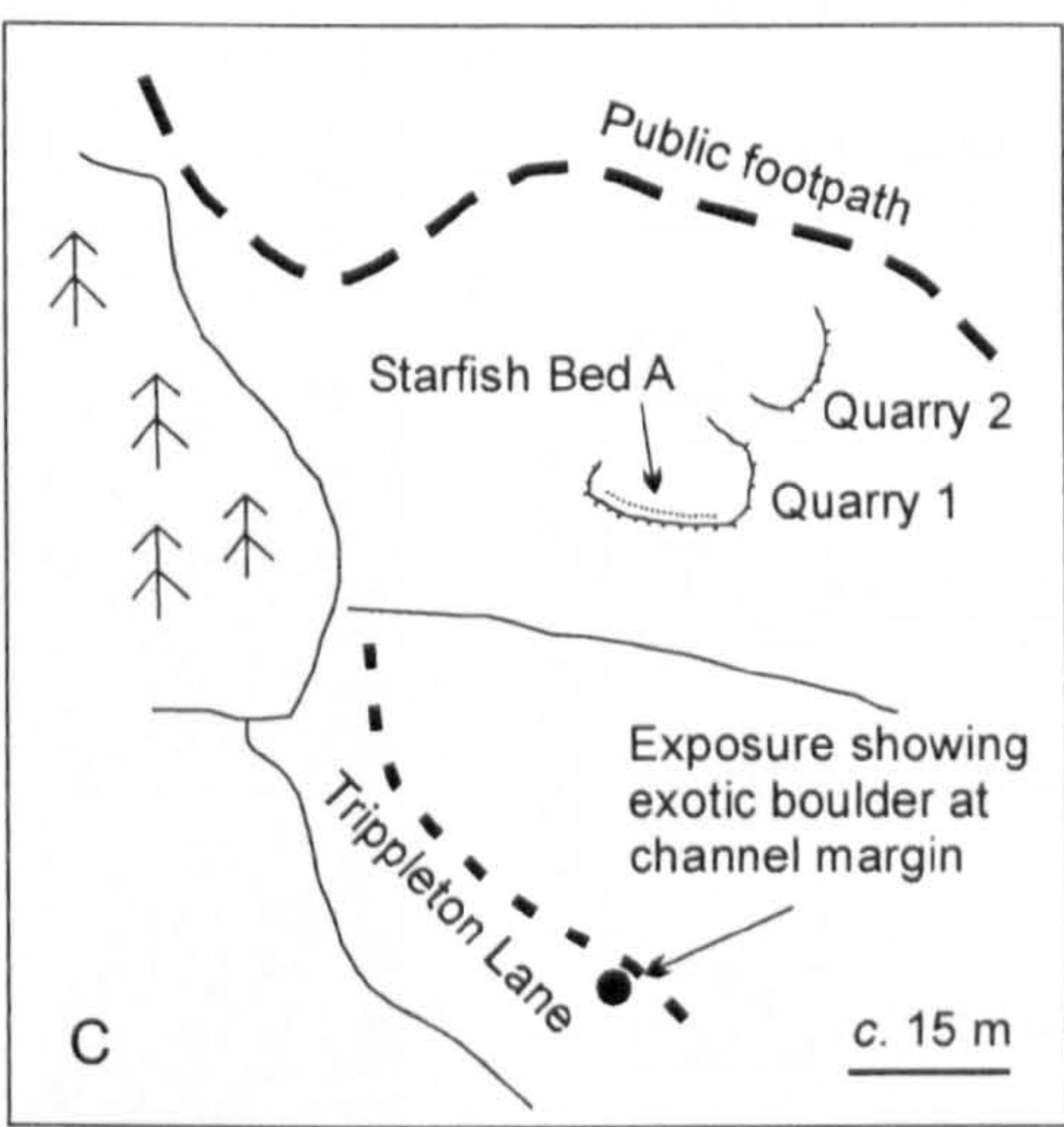
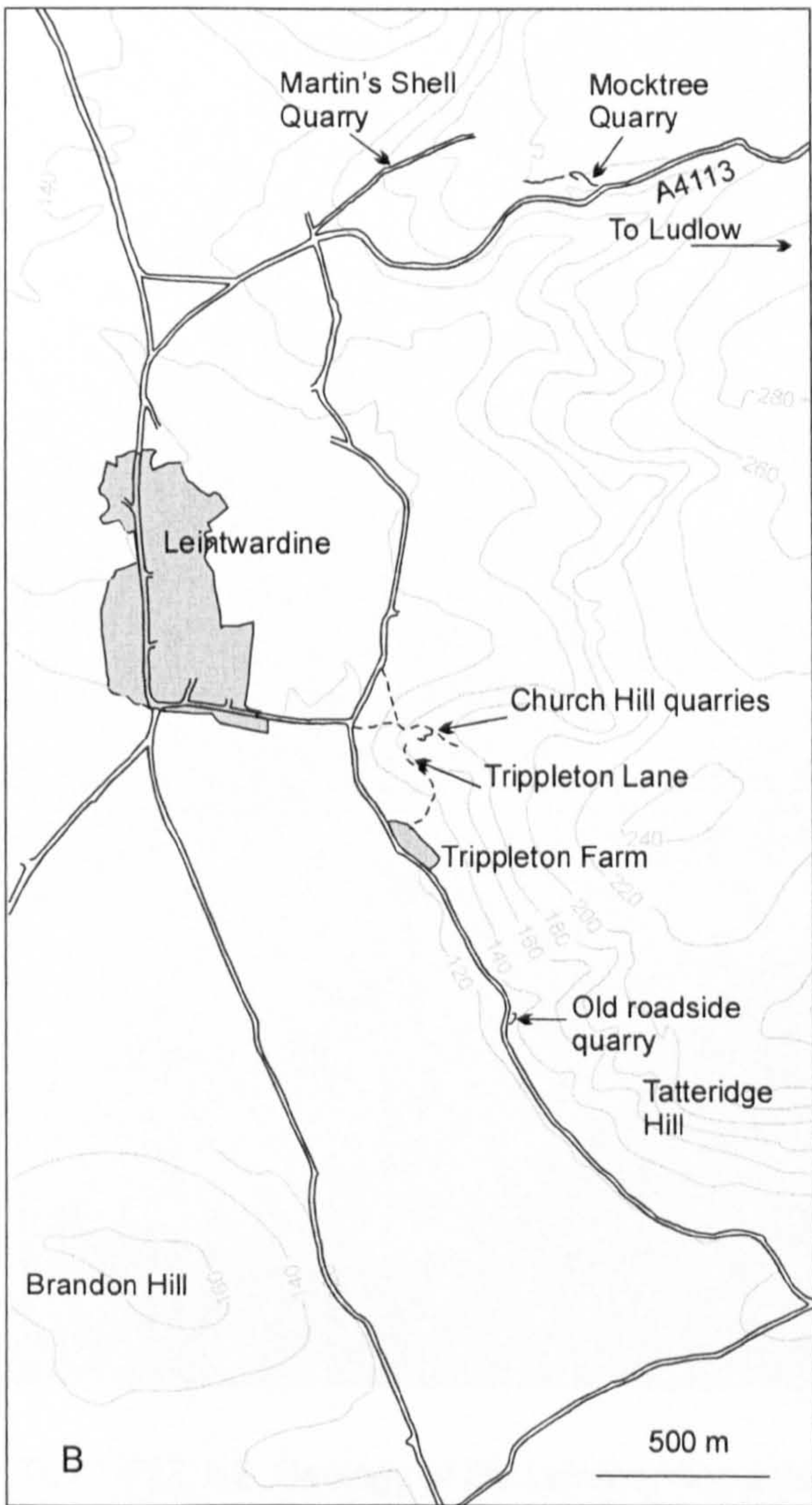
## GEOLOGICAL SETTING

### *Geographical location of channel deposits*

The channel deposits are situated in the central Welsh Borderland area, in the vicinity of the village of Leintwardine, approximately 10 km to the west of Ludlow (Text-fig. 1.1). Whitaker (1962) mapped six channels in total, approximately parallel to one another, trending in an ENE to WSW direction (Text-figs 1.2, 1.3A). The Tatteridge and Church Hill channels lie to the south of Leintwardine, whilst the Mocktree, Todding, Bagdon and Marlow channels are to the north. No unusual fauna has been documented from the latter two channels (e.g. Whitaker 1962). The present study concentrates on the four other fossiliferous channels, with particular emphasis on the Church Hill Channel, the site that has yielded by far the most fossils.

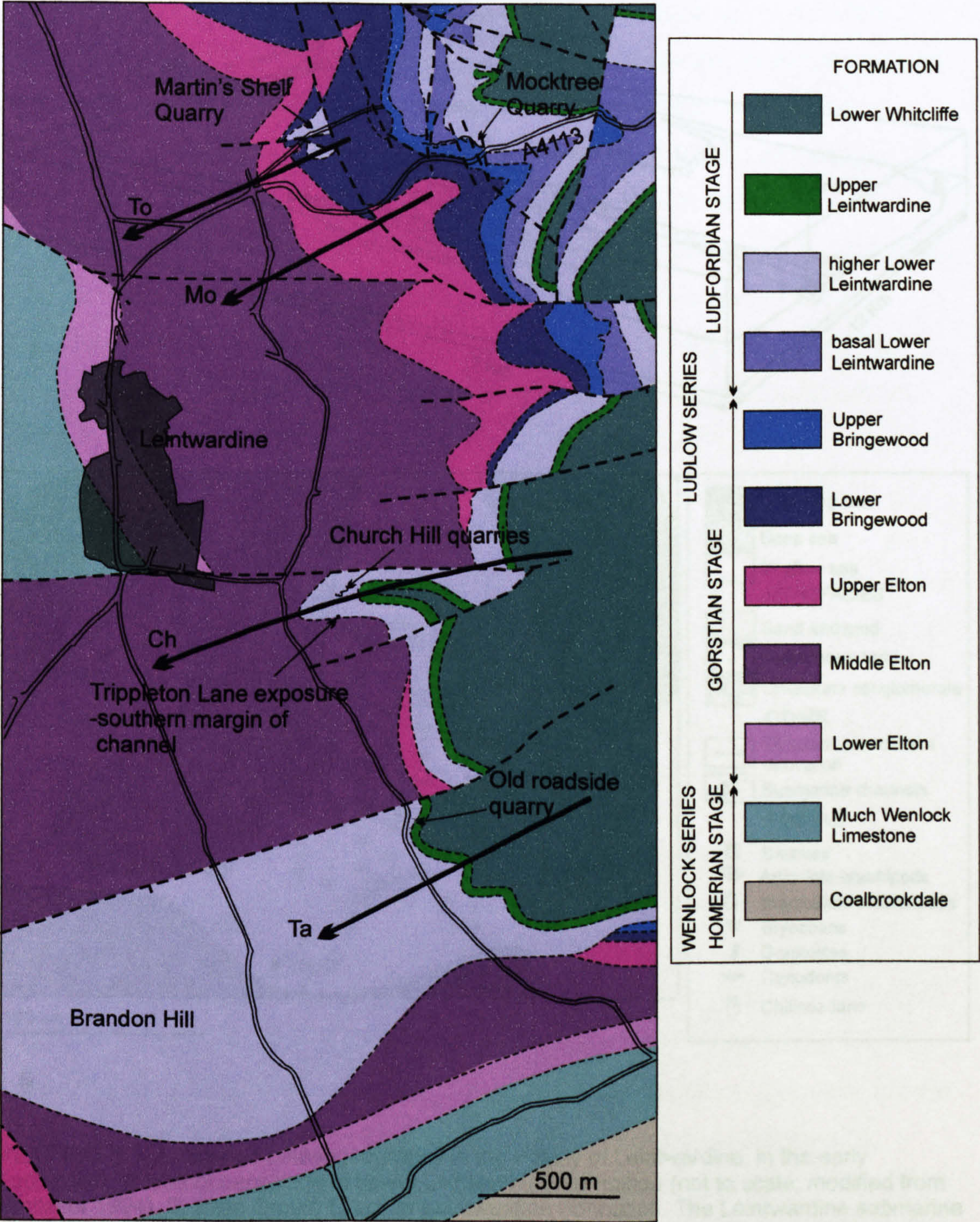
The Leintwardine area is situated at the extreme western end of the northern limb of the asymmetrical Ludlow Anticline, the fold axis of which trends ENE. The more steeply dipping northern limb dips by about 20 degrees whilst the southern limb has a dip of approximately 10 degrees. More specifically the area lies along the axis of the complementary Downton Syncline, the fold axis of which approximately follows the Teme Valley near Downton (Geological Survey Special 1: 25, 000 Sheet: Leintwardine-Ludlow).





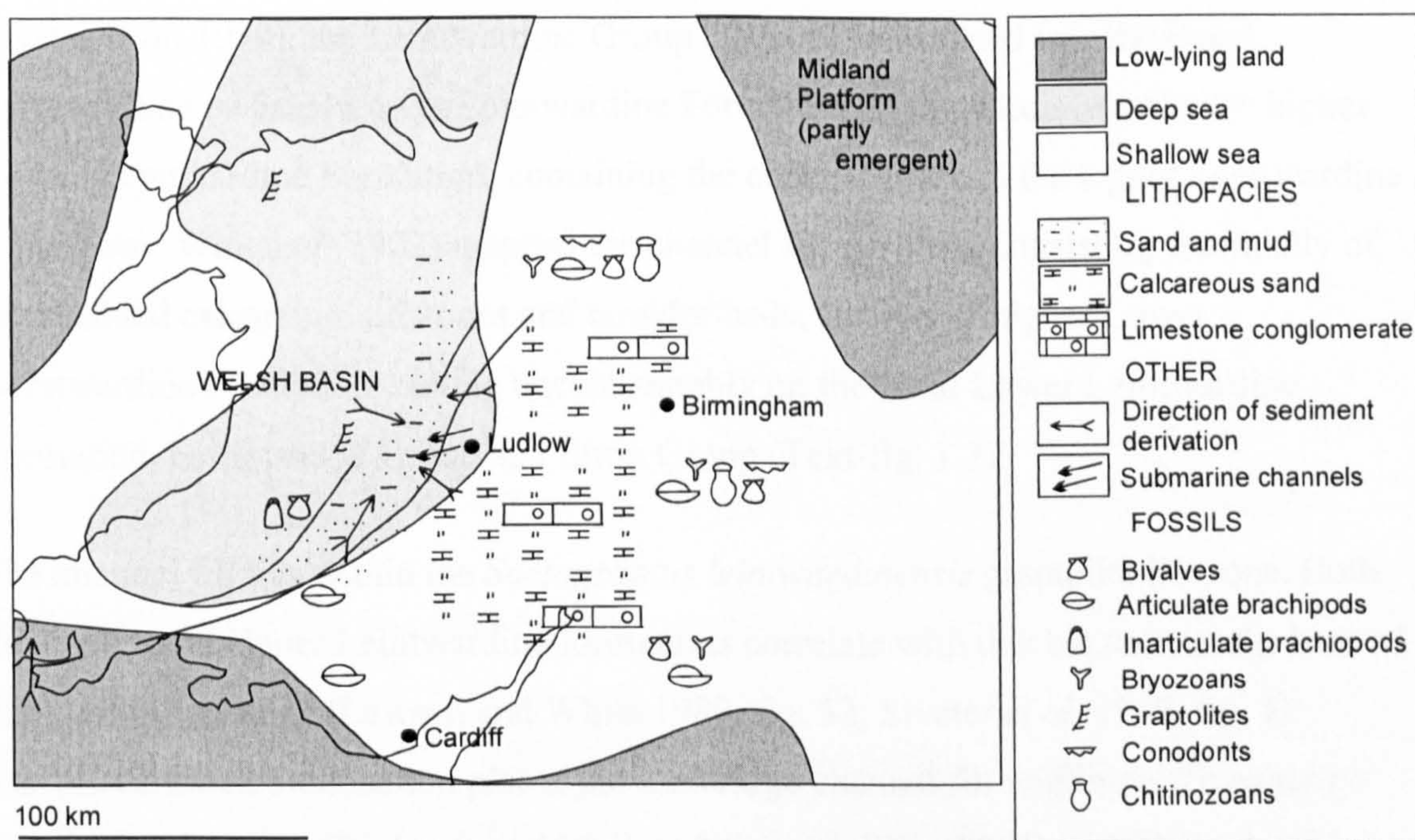
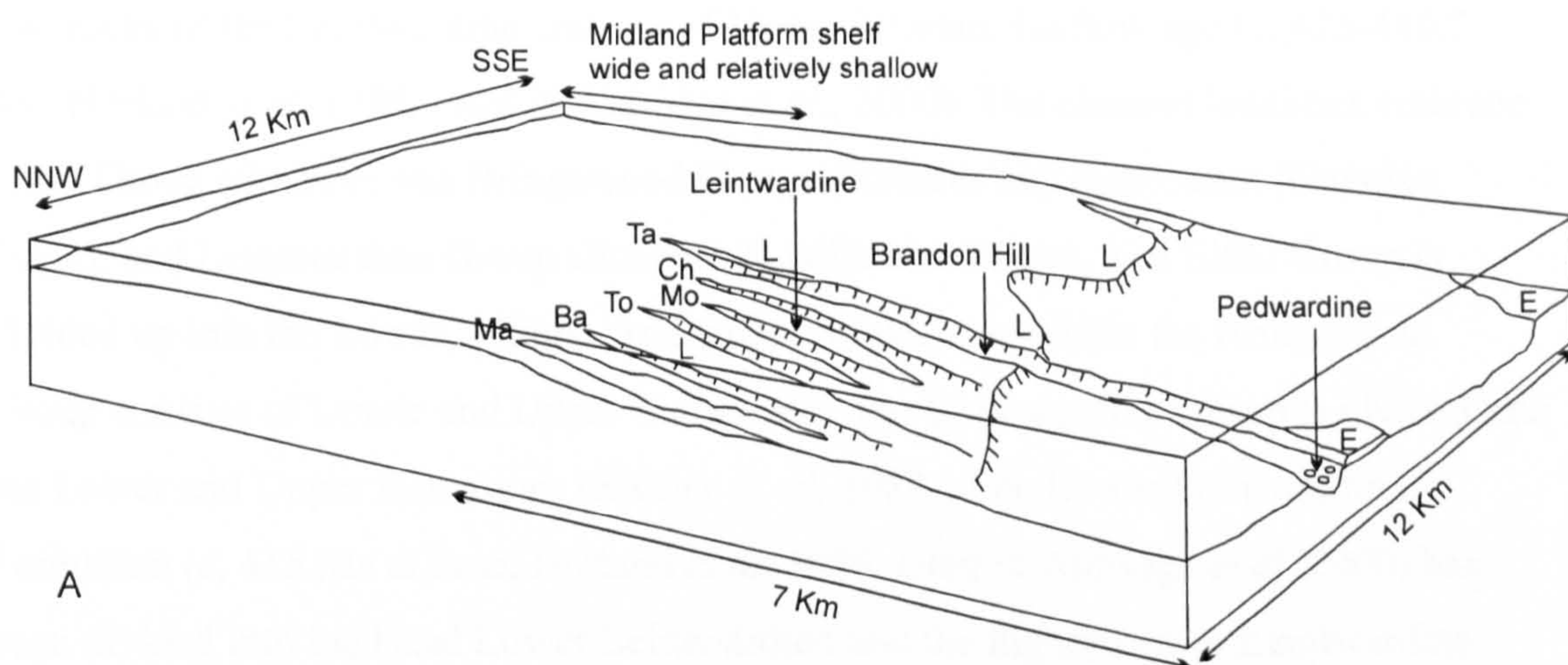
TEXT-FIG 1.1. A, Location of the study area around Leintwardine, approximately 10 km to the west of Ludlow, Shropshire. B, field localities around Leintwardine that show exposures of submarine channel deposits (from north to south): Martin's Shell Quarry (Todding Channel); Mocktree Quarry (Mocktree Channel); Church Hill quarries and Trippleton Lane (Church Hill Channel); old roadside quarry and Brandon Hill (Tatteridge Channel). C, field localities at Church Hill that show the re-exposed composite quarries and lateral extent of Starfish Bed A.





TEXT-FIG. 1.2. Geology of the Leintwardine area, showing the inferred position of the four fossiliferous submarine channels, trending ENE to WSW, and the associated field localities (modified from Whitaker 1962, and Holland *et al.* 1973): Todding Channel (To); Mocktree Channel (Mo); Church Hill Channel (Ch) and Tatteridge Channel (Ta).





TEXT-FIG. 1.3. A, Inferred palaeogeography in the vicinity of Leintwardine, in the early Ludfordian, at time of deposition of Lower Leintwardine Formation (not to scale; modified from Whitaker 1994). E, Elton Group; L, Lower Leintwardine Formation. The Leintwardine submarine channels are: Marlow (Ma), Bagdon (Ba), Todding (To), Mocktree (Mo), Church Hill (Ch) and Tatteridge (Ta). B, palaeogeographical reconstruction of Welsh Basin and Midland Platform area during the early Ludfordian, showing location of Leintwardine submarine channels (modified after Bassett *et al.* 1992).



*Stratigraphical background*

The rocks of the Leintwardine area are of Upper Silurian, Ludlow age (c. 425-410.7 Ma; Harland *et al.* 1989, cited in Aldridge *et al.*, 2000). The channel localities embrace Elton Group siltstones and Bringewood Group siltstones and limestones (Gorstian Stage), and Leintwardine Group siltstones (Ludfordian Stage). The Elton Group is divided up into the Lower, Middle, and Upper formations; whilst the Bringewood Group consists of Lower and Upper formations. The Leintwardine Group is divided into the Lower and Upper formations (Siveter *et al.* 1989). The Lower Leintwardine Formation (c. 415 Ma at base; Harland *et al.* 1989, cited in Aldridge *et al.* 2000) has been divided into the basal Lower Leintwardine and the higher Lower Leintwardine (consisting of the channel fill in the area) Beds by Whitaker (1962). More recently (see Siveter *et al.* 1989), the Leintwardine Group has been formalised into the Basal Leintwardine (= basal Lower Leintwardine Formation), Lower Leintwardine (= higher Lower Leintwardine Formation; containing the channel fill) and the Upper Leintwardine formations. Whitaker (1962) mapped the channel fill deposits, consisting essentially of interbedded calcareous siltstones and boulder-beds, as belts of higher Lower Leintwardine Formation, resting unconformably on the basal Lower Leintwardine Formation, Bringewood Group and Elton Group (Text-fig. 1.2).

The channel fill lies within the *Saetograptus leintwardinensis* graptolite Biozone. Both the Lower and Upper Leintwardine formations correlate with this biozone, at the base of the Ludfordian stage (Lawson and White 1989, fig. 52; Siveter *et al.* 1989, fig. 5). Current acritarch biozonation places the Tatteridge channel fill within the *Triangulina sanpetrenis* Biozone (Richards and Mullins 2003). Mullins (2001) and Richards and Mullins (2003) defined the *T. sanpetrensis* Biozone as extending from the middle of the Lower Leintwardine Formation to the base of the Whitcliffe Group. Analysis of acritarchs (*Salopidium aldridgei* Richards and Mullins, 2003 and the index taxon *Triangulina sanpetrenis*) by Richards and Mullins (2003) suggests that the channel fill of the Tatteridge Channel can be correlated with the Upper Leintwardine Formation of the type Ludlow area. Stratigraphical distribution of acritarchs that occur through the Tatteridge Channel fill (Richards and Mullins 2003, text-fig. 16) does not appear to indicate a relative duration for the rate of channel filling. Current chitinozoan biozonation (Sutherland 1994) has not been applied to the channel fill, although based

on published biozone ranges, biozones 9, 10 or 11 may be represented through the fill (just below base of basal Lower Leintwardine Formation to just below base of Lower Whitcliffe Formation).

### *Palaeogeographical setting*

In early Ludfordian times (c. 421 Ma; Bassett *et al.* 1992), the Ludlow-Leintwardine area occupied a shelf edge/break position of the Midland Platform (Holland and Lawson 1963), with the depositional Welsh Basin to the west (Text-fig. 1.3B). The channels themselves trend westwards off the shelf break area, down-slope towards the Welsh Basin. Shelf to basin relief is inferred to have been less than on a fully developed continental margin, being more comparable with that on the present-day Californian continental borderland basins (N. H. Woodcock pers. comm. in Whitaker 1994). The major facies types identified within the shelf edge to shelf slope area surrounding Leintwardine, at the time of Lower Leintwardine Formation deposition and the submarine channelling, are the 'calcareous siltstones facies' to the east of Leintwardine, extending over the shelfal area, and the 'laminated siltstones facies' at Leintwardine, continuing westwards down the shelf slope (Cherns 1988, text-fig. 13). At the time of deposition of the basal Upper Leintwardine Formation, the laminated siltstones give way to the 'calcareous siltstone facies' in the Leintwardine area (Cherns 1988).

The Welsh Borderland area lay on the microcontinent of Avalonia (Cocks *et al.* 1997; Woodcock 2000; Fortey and Cocks 2003). The microcontinent occupied a latitude of 25° S during the Silurian (Bassett *et al.* 1992). Sedimentation during the Ludlow Series was limited to mainly storm-redeposited sediment, although turbidite supply to the Welsh Basin continued (Tyler and Woodcock 1987).

### *Relative sea level*

The Ludlow Series shows a generalised marine regression (following an initial sea level rise), which can be observed throughout the British Isles (Johnson *et al.* 1991). This initial rise is exhibited in the Ludlow area with limestones of the Much Wenlock Limestone Formation overlain by siltstones of the Lower Elton Group (Siveter *et al.* 1989). Further basinward, in the Leintwardine area these limestones are overlain by graptolitic mudstone. The dominant regression of the Ludlow Series results in a shift



towards more calcareous lithologies in the area; the mudstones and siltstones of the Elton Group are replaced by calcareous siltstones and limestones of the Bringewood Group (Siveter *et al.* 1989). Clastic input increases through the Ludfordian, with the Upper Bringewood Formation limestones being succeeded by Leintwardine Group calcareous siltstones.

## OBJECTIVES

The objectives of this research are to:

- Document the channel biota, describing its vertical and lateral distribution and diversity throughout the channels, especially through the Church Hill Channel;
- Assess the setting and taphonomy of the biota, and determine whether the fauna was indigenous to the channels;
- Determine aspects of the autecology and community structure of the biota;
- Test the validity of the ‘channel model’ as the possible palaeoenvironmental setting for the biota;
- Address any evolutionary significance of the biota, with particular emphasis on the stelleroids, the most abundant and well preserved of the unusual channel faunas.

## HISTORICAL BACKGROUND

The geology of the Leintwardine area was first described by Murchison (1839) and the channel deposits themselves have been described in many subsequent papers through the latter part of the 19<sup>th</sup> Century and into the early 20<sup>th</sup> Century. The deposits at Church Hill, Mocktree and Todding were initially described by Lightbody (1863), Marston (1865) and Symonds (in Woodward 1866-78). A major account of the Church Hill deposits was given in Hawkins and Hampton (1927) and in 1936 the first description of the supposed channelling (in reference to Church Hill) was given by Alexander (1936) in her paper on the Aymestry Limestone (= Upper Bringewood Formation). The Leintwardine area was first mapped in detail by Whitaker (1962), whereby the six parallel channels were interpreted as Ludlovian submarine canyon heads. Whitaker (1962) noted that the channels showed many sedimentary features in common with their modern counterparts (e.g. La Jolla Canyon, California; Shepard 1949). Whitaker (1994)



further refined the submarine canyon head model in a study on slope sedimentation and mass movement in the adjacent Wigmore Rolls area. Recent overviews of the channel deposits at Church Hill and Mocktree can be found in Siveter *et al.* (1989) and Siveter (2000), whilst a review of the Leintwardine submarine canyons is featured in Pickering *et al.* (1989). The palaeoenvironmental setting and taphonomy of the channel biota are briefly discussed in Hawkins and Hampton (1927), Whitaker (1962), Jones (1969) and Goldring and Stephenson (1972).

The channel biota itself has been described in numerous papers and monographs. Lightbody (1863), Marston (1865) and Whitaker (1962) give general accounts, encompassing the overall fauna. The chelicerate taxa are described in Salter (1859a), Woodward (1865, 1866-1878, 1868b, 1872b), Kjellesvig-Waering (1961), Selden (1986) and Anderson (1996). The phyllocarid crustaceans are described in Jones and Woodward (1888-1899). Salter (1857), Spencer (1914-1940) and Goldring and Stephenson (1972) described the stelleroids; whilst Ramsbottom (1958) described the crinoids. Wyville Thompson (1861), Gregory (1897a), Hawkins and Hampton (1927) and Blake (1968) described the echinoid biota. The ophiocistioids feature in Sollas (1899), Ubaghs (1966) and Haude and Langenstrassen (1976a-b). The palaeoscolecoid worm *Protoscolex latus* Bather, 1920, recovered from both Church Hill and Todding channels, has been described by Bather (1920). Slater (1907) described some of the conulariids from Church Hill whilst Owen (1962) described bryozoan taxa from the sites. Fossil fish from the deposits are mentioned and described in Salter (1859c), Roberts (1861), Lankester (1868), Woodward (1891), White (1958), Denison (1964) and Dineley and Metcalf (1999).

## MATERIAL

Much of the data is based on extensive fossil collections held at various repositories: the Natural History Museum, London (BMNH); British Geological Survey, Keyworth (BGS GSM); Leicester University Geology Department (LEIUG); Oxford University Museum (OUM); Sedgwick Museum, Cambridge (CAMSM); Ludlow Museum (SHRCM); Royal Museum of Scotland, Edinburgh (NMS), Manchester University Museum (MM), Museum of Victoria, Australia (NMVP). Many of these collections date back to the mid 19<sup>th</sup> Century, and include type specimens of various taxa; many specimens have been figured and described in papers and monographs from the mid 19<sup>th</sup>

century on. A major limitation with the museum material is that provenance details are sometimes lacking. Many specimens are simply referred to as originating from Leintwardine, with no indication of the locality or channel involved. Where channel provenance is known, the vast majority of specimens originate from the Church Hill Channel; specimens of all the rare faunal groups have been documented from this site. A further limitation of the pre-existing collections is that in most cases their exact horizon within the channel fill is not known; in the case of the echinoderm material, it is not possible (based on these collections alone) to ascertain which ‘starfish bed’ specimens originated from (two starfish beds at Church Hill have been described in the literature; Hawkins and Hampton 1927).

This pre-existing material is supplemented by newly collected specimens, recovered during field study of the channels during autumn 2002 and winter 2003. Most study was concentrated upon the Church Hill site (Text-fig. 1.1C), due to its fossiliferous importance. Millimetre scale logging was carried out at this location through a 2.6 m vertical section of the channel fill, enabling exact horizon provenance to be discerned for the recovered material. Of the two starfish beds described in the literature (Hawkins and Hampton 1927), one was successfully located (termed ‘Starfish Bed A’ herein), and was traced along the full lateral extent of the Church Hill channel fill exposure (c. 15 m; Text-fig. 1.1C). Based on measurements given by Hawkins and Hampton (1927) and the taxa retrieved, this horizon may represent the lower of the two starfish beds that they described. The Marlow and Bagdon channels have not been examined in the field. These channels were omitted due to the lack of documented fossil content, and poor exposure.

## CHANNEL LOCATION AND ARCHITECTURE

Whitaker (1962) mapped the six approximately parallel channels, trending ENE to WSW, around the village of Leintwardine and the heads at least are inferred to have occupied a shelf edge/break setting within Ludfordian times (Text-fig. 1.3A). Calcareous siltstones around the channel fill represent shelfal-shelf edge facies.

With regard to channel morphology, Whitaker (1962) documented that the axial gradients were high (average 10 degrees) and that the sidewalls were sometimes steeply inclined. He recorded a maximum length and width of 4 km and 0.8 km respectively;



maximum incision westwards, away from source was recorded as approximately 200 m. In terms of tracing the channels along axis, only the Tatteridge Channel has been successfully traced west of Leintwardine, into the Wigmore Rolls area (Whitaker 1994).

### *Todding Channel*

A site showing part of the (presumably southern?) margin of the channel has been inferred to occur at a quarry exposure at SO47 4103 7537 (Whitaker 1962). Here the Lower Bringewood Formation is described as being discordantly overlain by the Lower Leintwardine Formation (channel fill?) containing derived Upper Bringewood Formation limestone cobbles and boulders. Whitaker (1962) described one boulder as actually resting on the channel floor. This site could not be re-examined due to its poor exposure and inaccessibility. The main site of the Todding Channel examined in the field is Martin's Shell Quarry (SO47 4109 7543; Text-fig. 1.1), an approximately 12 m long exposure showing interbedded calcareous siltstone and boulder-bed horizons.

### *Mocktree Channel*

A complete section through the channel occurs in the rock face at Mocktree Quarry (SO47 4165 7540; Text-fig. 1.1). Whitaker (1962) inferred that this site represents a true canyon head setting. The channel appears gently curved and is 27 m in width at this location; Whitaker (1962) documented its axial trend as 051 degrees. The channel is seen to incise down into the underlying basal Lower Leintwardine Formation siltstones, leaving about 0.7 m of this formation at the channel axis. Whitaker (1962) described the channel fill as containing successively overlapping catenary bedding. A down faulted block of fossiliferous siltstones (channel fill) occurs at the extreme eastern end of this quarry face.

A further outcrop is seen at a small roadside exposure, 50 m to the south of the entrance to Mocktree Quarry (SO47 4163 7531). An unconformable contact between underlying Upper Bringewood limestone and higher Lower Leintwardine Formation channel fill occurs and is inferred to be part of the western margin of the channel. Whitaker (1962) described the channel fill as having an original high dip of 23° SE, which declines dramatically eastwards from the margin to the centre of the channel. Whitaker added

that this exposure shows a steep 'canyon wall' margin in comparison to the gently dipping margin of the channel in the main exposure.

It should be noted that after recent excavation (David Gladwell; 2002), the siltstone underlying the wooded northern bank approximately 25 m south of the quarry face (SO47 4165 7538) does not appear to be higher Lower Leintwardine Formation (as mapped by Whitaker 1962 p. 331). This exposure lies just north of the roadside higher Lower Leintwardine Formation-Upper Bringewood Formation exposure and appears to be blockier than the true channel fill siltstone; a lack of the characteristic channel fauna was also noted.

### *Church Hill Channel*

Church Hill was first recognised as the site of a channel by Alexander (1936). An unconformable contact between higher Lower Leintwardine Formation siltstones (channel fill) and Middle Elton Formation mudstones, inferred to represent part of the southern margin of the channel can be seen at Trippleton Lane (SO47 4115 7372); this contact was described and figured by Whitaker (1962; fig. 4). Alexander (1936, p. 110) described these higher Lower Leintwardine Formation siltstones lying unconformably on the Elton Formation siltstones, although did not identify a contact. She added that boulders of Aymestry Limestone (Bringewood Formation limestone) occur within the channel fill siltstones of the quarry.

Whitaker (1962) stated that the northern contact of the channel has been effectively faulted out by an east-west trending fault, yet added that outcrops of the channel fill and the Middle Elton Formation occur in close proximity. An estimation of 176 m of incision into the underlying strata over a horizontal distance of 1066 m was postulated (Whitaker 1962), giving a channel axial gradient of 10 degrees. The two re-excavated quarries examined in the field occur at SO47 4115 7375 (termed 'Quarry 1' herein) and SO47 4119 7380 (termed 'Quarry 2'), inferred to represent an area towards the axis of the channel (Text-figs 1.1B-C, 1.2). The larger of the two (Quarry 1) is the site of the rare channel fauna.



*Tatteridge Channel*

Whitaker (1962) described this as representing the most extensively exposed of the channels in its exposure. The Tatteridge Channel continues into the north-east of the Wigmore Rolls area, south-west of the Leintwardine area, with its higher Lower Leintwardine Formation fill forming Brandon Hill (Text-figs 1.1B, 1.3A). It is suggested that here down cutting possibly occurs into the Middle Elton Group (Whitaker 1994). Whitaker (1994) added that the channel probably continued in a WSW trend, further down cutting into underlying strata; he also stated that anomalously positioned limestone boulders found at Wordell's farm near Pedwardine may have been transported down the channel (H. Boynton pers. comm. in Whitaker 1994; Text-fig. 1.3A).

## METHODOLOGY AND TECHNIQUES

*Material preparation*

Where appropriate, slabs containing fossils have been mechanically prepared, using an air pen or engraving drill. From time to time, counterparts have been lost during this process, although this was felt to be a justifiable procedure.

*Photography*

All macrophotography carried out by the author has been done so at Leicester using either Leitz aristophot (method of Siveter 1990) or Nikon equipment. A single light source from the top left hand side (NW) of the specimen was used in all instances; this was sometimes supplemented by a fluorescent ring light. Prior to photography, a light coating of ammonium chloride sublimate was applied to the specimen. Where noted, some photography of the echinoderm material was carried out by Dr. Peter Jell of the Queensland Museum, Brisbane. Due to the mouldic preservational nature of the echinoderm material, photography of these specimens is predominantly of silicone casts, not the original fossil.

Scanning electron microphotography (SEM) was undertaken on certain stelleroid specimens where morphological features were too fine for conventional photographic

techniques. All images were taken using backscattered emissions (BSE) under partial vacuum of uncoated silicone rubber casts.

### *Silicone Rubber Casting*

Standard silicone rubber casting techniques have been employed which essentially follow that of Siveter (1982). Casting was carried out at Leicester and the BMNH, London. Specimens which were deemed fragile were coated in a consolidant prior to casting, otherwise a 'separator' was applied.

#### 1. Silicone rubber and catalyst:

- Ambersil RTV 913 and CAT BLUE 5 (Ambersil Ltd);
- ELM 4503 (Beacon Hill Silicones Ltd) and Catalyst T35 (Wacker Silicones);
- Tiranti RTV 11 and DBT catalyst (Alec Tiranti Ltd).

#### 2. Consolidant:

- Polyvinyl butyral (PVB) and methanol;
- 5 % solution of 'Paraloid' in acetone.

#### 3. Separator:

- solution of 50 % teepol/ 50 % water.

### *Geochemical analysis*

Fourteen samples were selected for X-ray Fluorescence (XRF) analysis through the 2.6 m vertical section of channel fill siltstone at Church Hill, Quarry 1, in order to help determine whether the channel was oxygen-restricted. Trace metal abundances (e.g. Molybdenum), determined using XRF, were selected as palaeo-redox indicators (e.g. see Powell *et al.* 2003). Samples were selected to give a relatively even distribution through the section; four samples were taken through Starfish Bed A. Three non-*in situ* samples were also taken from this locality. Two of these contain extensive surface bioturbation (CH202 and CH260); the third contains a specimen of a palaeoscolecid 'worm' (CH214).

Prior to geochemical analysis, rock samples were sawn and polished to remove any weathered surfaces. Samples were then reduced to chips with a maximum grainsize of



2-3 mm in a flypress. Specimens were subsequently ground to a fine powder in a planetary mill, using agate-lined sample pots to minimise contamination. Samples were milled on 15-minute cycles at 275 rpm.

Pressed Powder Pellets were produced in order to allow trace element analysis. Standard techniques were employed; approximately 10 g of powder was mixed with Moviol 88 binding solution. Fusion Beads were produced to determine major element concentrations. Weight loss of volatiles was first determined. All but two samples (CH44 and CH45) showed a relatively low loss of ignitions (LOI) of 5%. Ignited samples were subsequently used for the Fusion Bead production. 3 g plus the determined weight loss of dried flux (lithium metaborate) was accurately weighed into a Pt/ Au crucible. 0.6 g of the ignited sample was added to the flux and mixed together. The crucible and contents were then placed over a Spartan gas burner in order to fuse. The contents were then poured onto a casting dish and the resulting bead was allowed to cool.

## THESIS STRUCTURE

Chapter 2 will discuss the sedimentology, taphonomy and ecology of the channel deposits and the associated fauna. Lithological description in hand specimen and thin section is undertaken. An overview of the channel biota is undertaken, commenting on general preservation and faunal diversity and abundance through the channels. As no modern taphonomic and palaeoecological research has been carried out on the sites prior to this study, the palaeoecology and biostratigraphy of the biota and the setting forms a fundamental component to the overall study. Chapters 3 and 4 will deal with the taxonomy of the stelleroids and eurypterids, respectively. The decision of selecting faunal groups for taxonomical treatment was based on the state of recent studies on the various groups. Certain groups such as the xiphosurans, phyllocarids and the palaeoscolecoid worms offered less scope for taxonomic studies even though they represent some of the more spectacular and rare taxa. Chapter 5 will provide overall discussion and conclusion.

Chapter 2 has been targeted for publication in the journal *Palaaios*, whilst chapters 3 and 4 have been targeted for *Palaeontology*. Journal decision has been based on subject suitability and maximum page allowance.

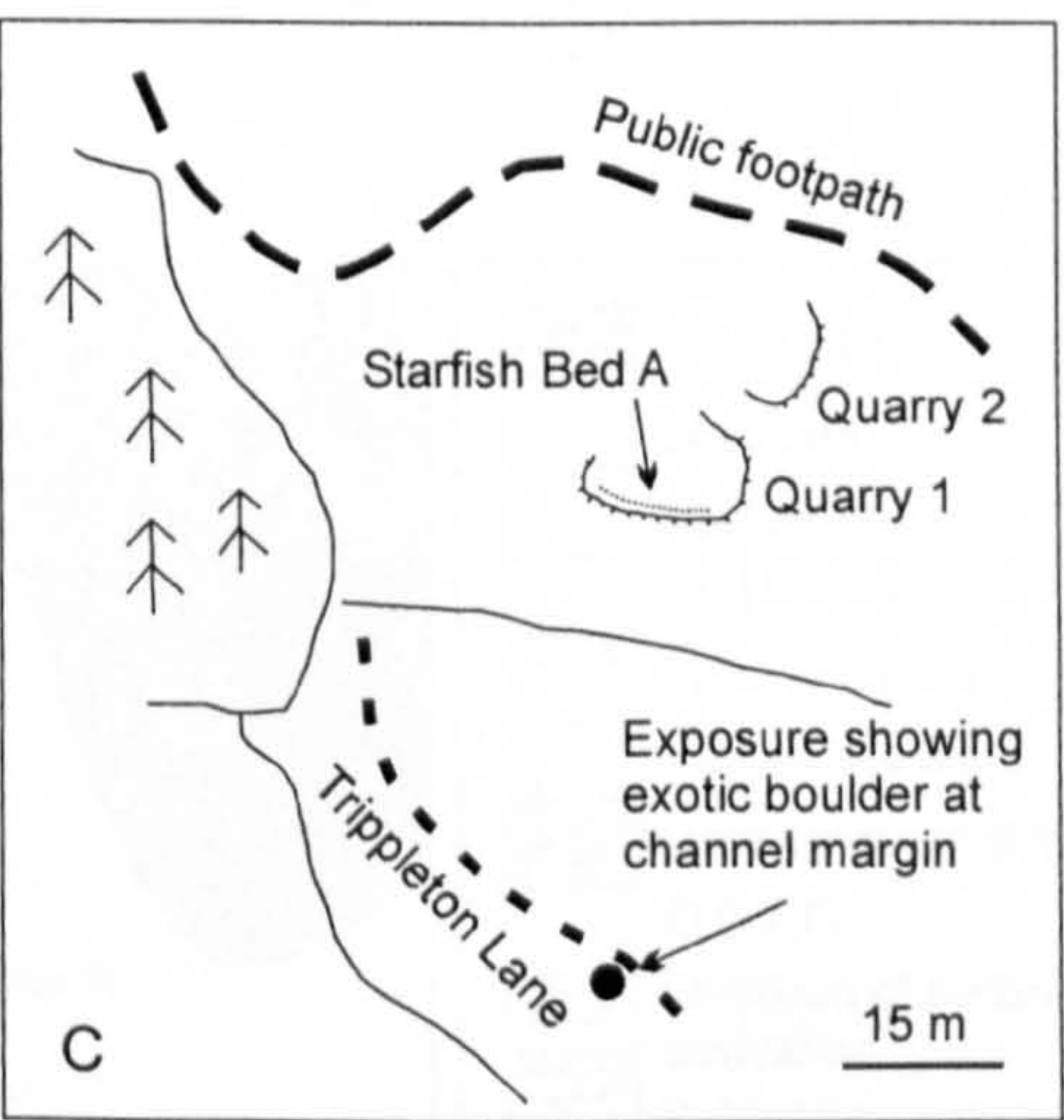
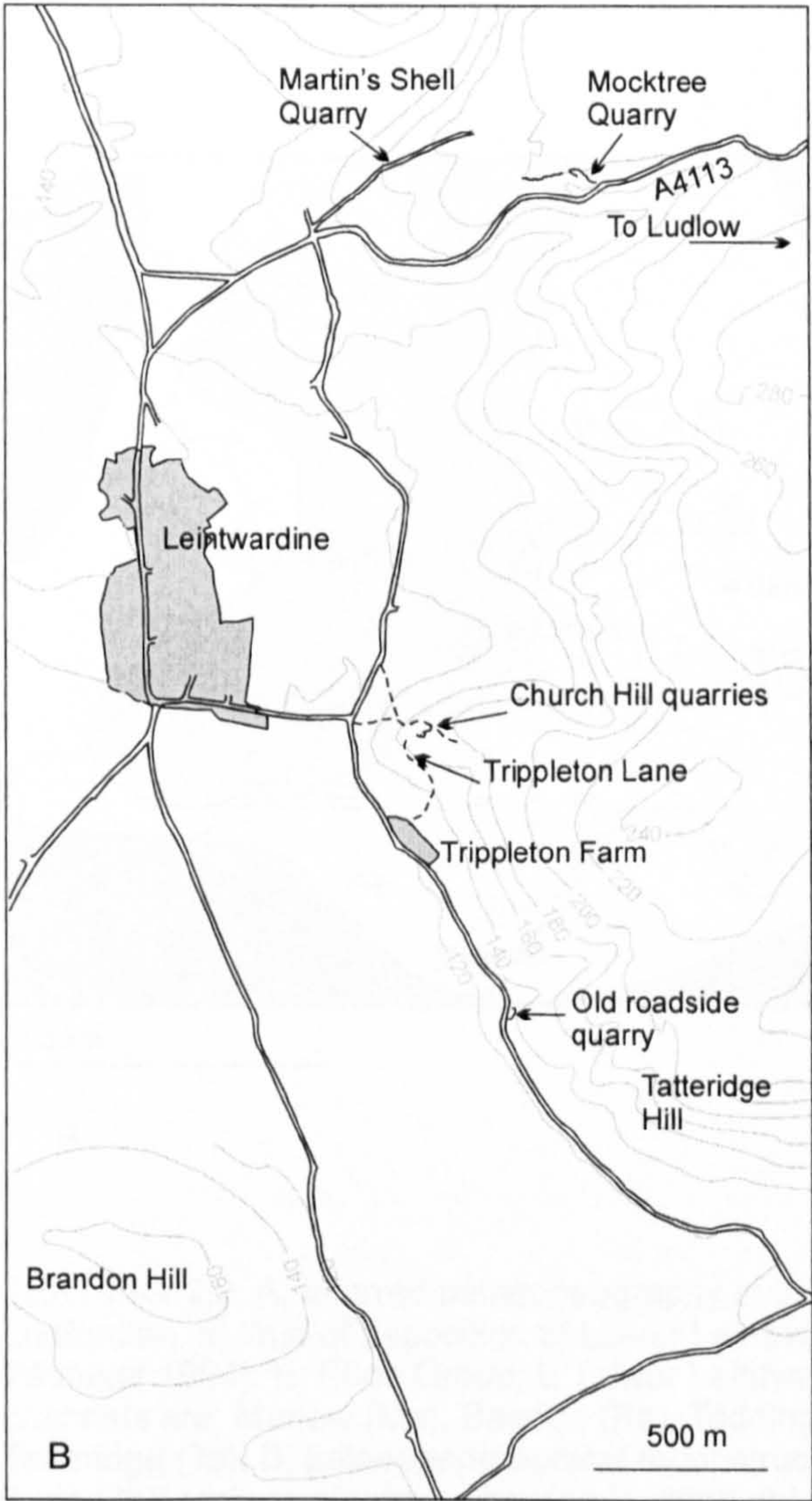
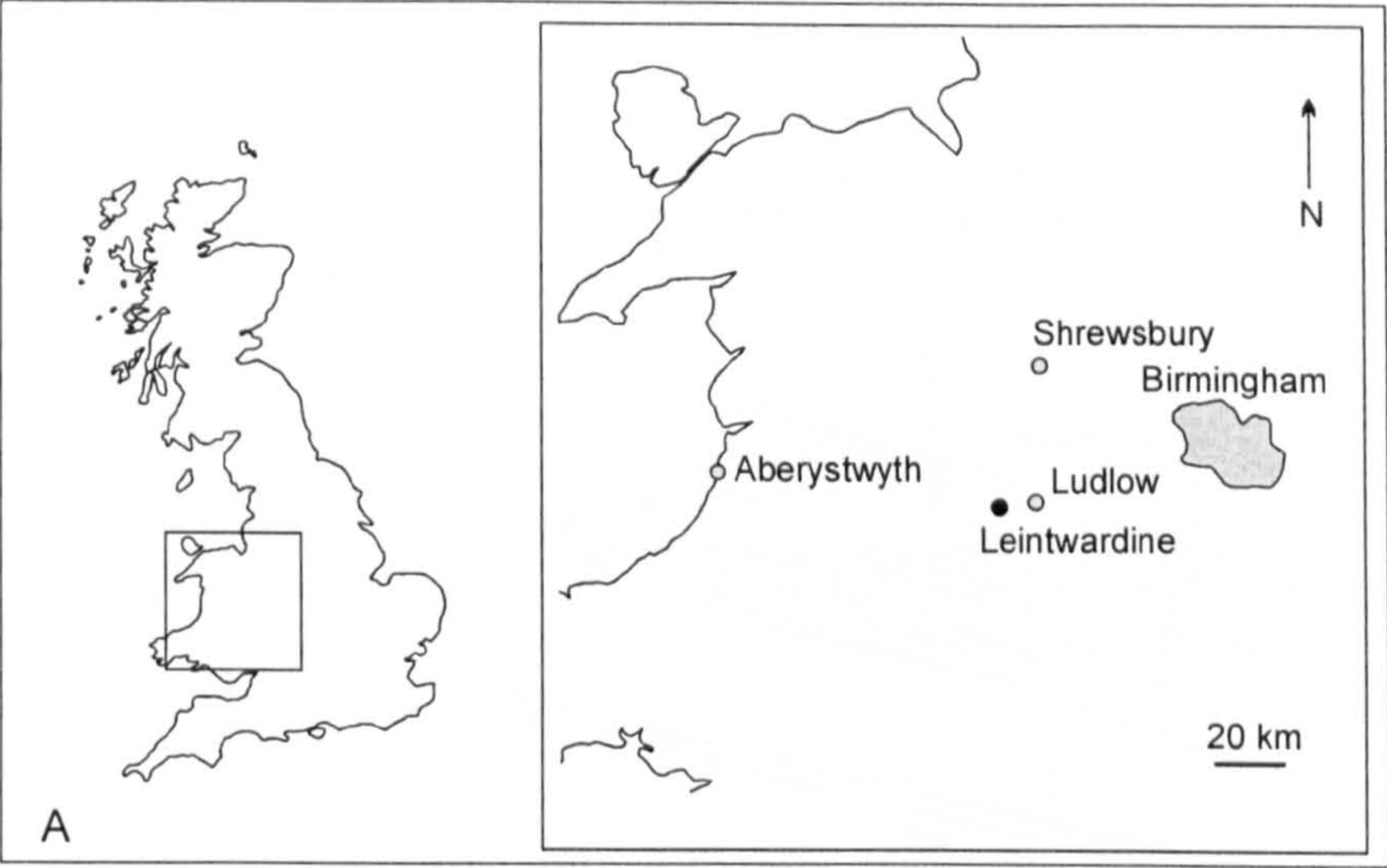


## TAPHONOMY AND PALAEOECOLOGY OF AN UPPER SILURIAN (LUDLOW SERIES) BIOTA FROM SUBMARINE CHANNELS, WELSH BORDERLAND

**ABSTRACT.** The Upper Silurian submarine channel deposits at Leintwardine in the Welsh Borderland provide a unique palaeoenvironmental setting in the fossil record, that of an indigenous biota within shelf-edge channel heads. Along with typical Silurian fossils such as brachiopods, graptolites and trilobites, the deposits contain an exceptionally preserved fauna including predominantly fully articulated echinoderms and disarticulated to articulated arthropods. The biota is interpreted to comprise indigenous and exotic elements, with variable transportation, both within and between species. The echinoderms are stelleroid-dominated although less abundant crinoids, echinoids and ophiocistioids also occur. The echinoderms occur within discrete horizons, so-called starfish beds, whereas other fossils occur sporadically through the remainder of the channel fill. Various biostratigraphic and palaeoecological criteria are used to assess whether the biota was indigenous to the channel heads. The stelleroids show variable way up orientations, entombment within the channel fill at slightly different horizons and current alignment; these factors along with an absence of apparent echinoderm bioturbation, suggest that stelleroid specimens have predominantly not been preserved *in situ*. When pooled, the stelleroid fauna shows a high diversity, in contrast to documented monospecific or low diversity autochthonous starfish beds in the literature, although the exact provenance of many of the Leintwardine species is not known. Stelleroid diversity through the Church Hill Starfish Bed is low, which suggests minimal transportation for many of these specimens. Some stelleroid taxa occur in monospecific assemblages; these are interpreted to have undergone minimal transportation; some solitary specimens may have undergone greater transportation. The echinoderms are predominantly parautochthonous to allochthonous and were indigenous to the channel head area including the immediately surrounding shelf. The semi-articulated to disarticulated arthropods have undergone transportation, and probably mostly represent exuviae. Brachiopods often occur in shelly lags, representing transportation. The relatively unbioturbated nature of the enclosing sediment suggests that deep burrowing organisms were restricted within the channel setting, which may imply that relatively high background sedimentation occurred over parts of the channel floor. Oxygen levels within the Church Hill Channel are not likely to have been restricted and periodically high sedimentation rates are interpreted to be central to the preservation of much of the exceptionally preserved biota.

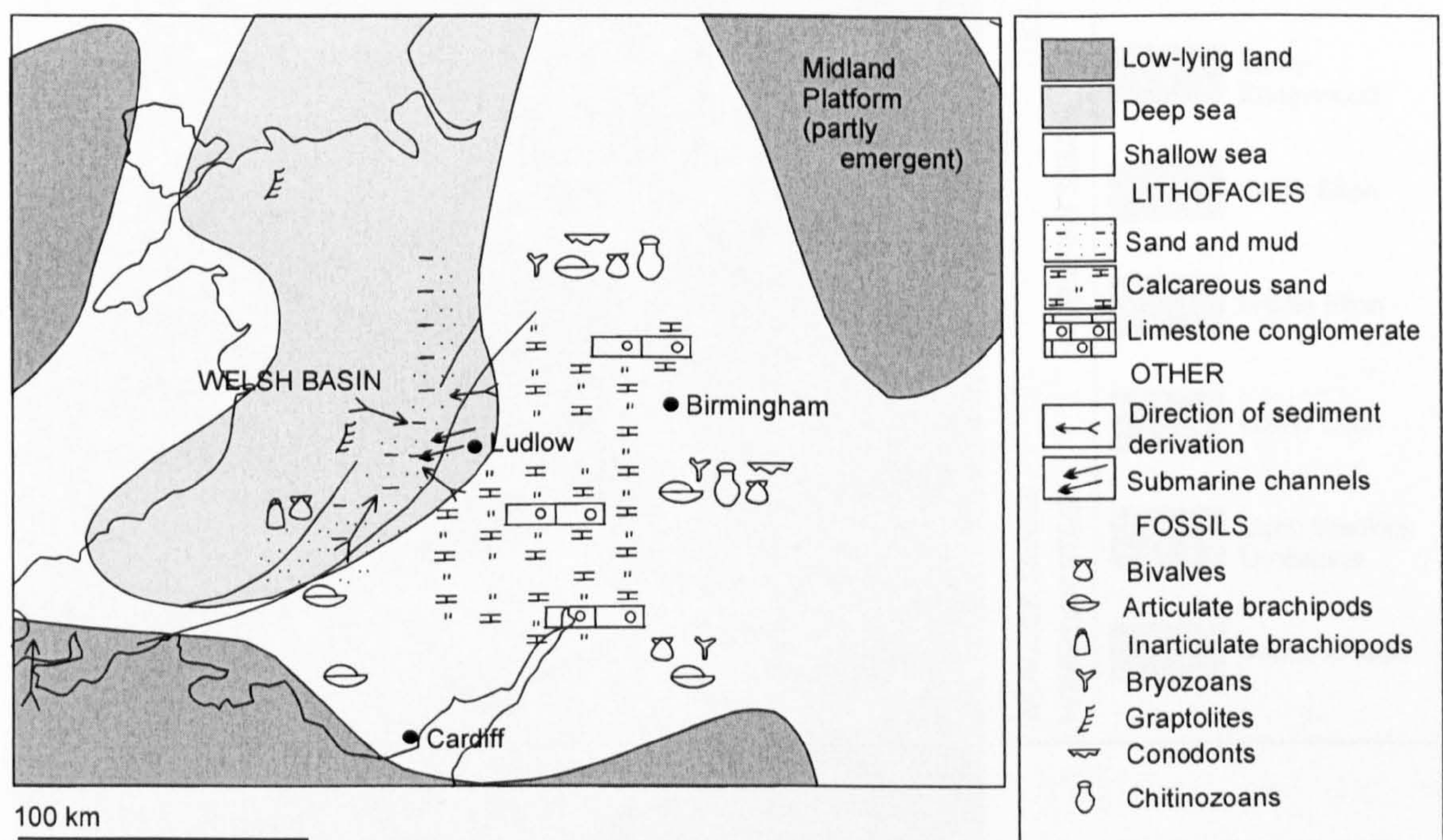
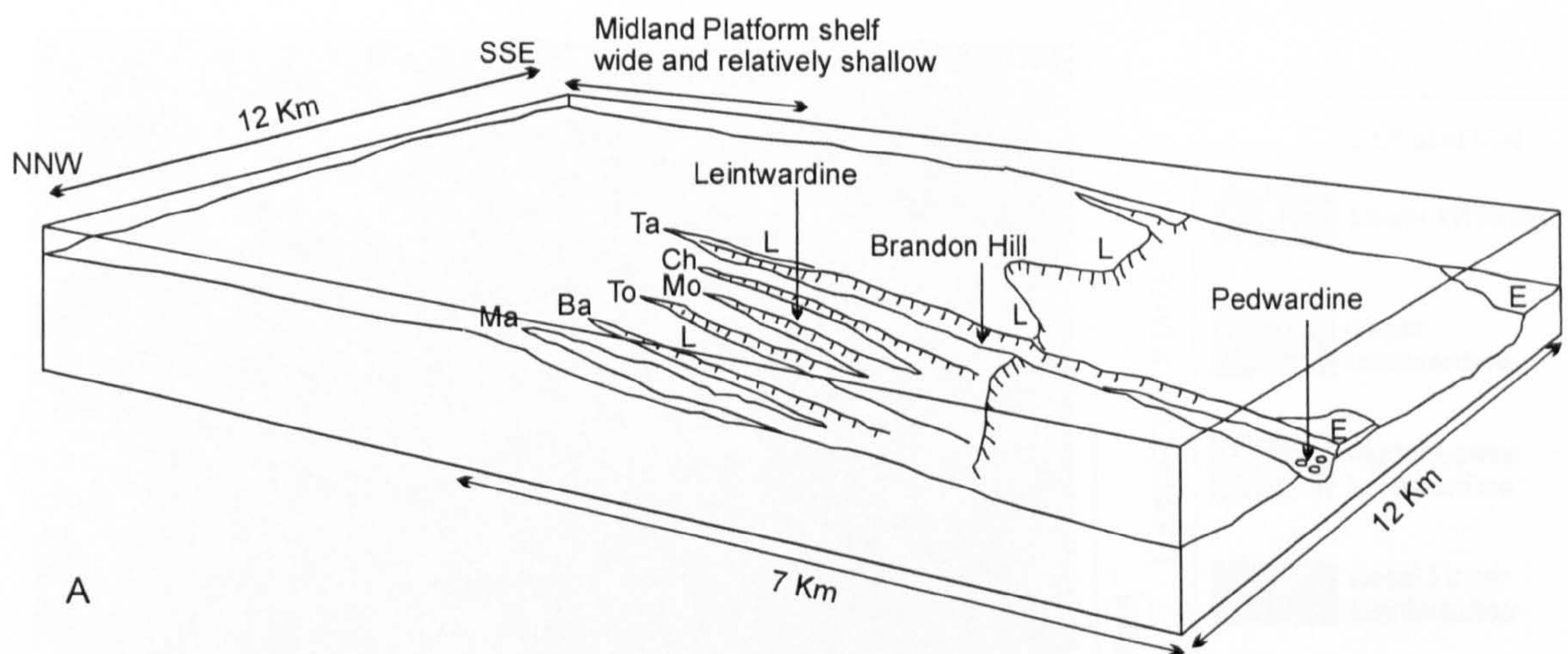
A DIVERSE, exceptionally preserved biota is preserved in four shelf-edge submarine channels in the Ludlow strata of the Leintwardine area of Herefordshire (Text-figs 2.1-3; Siveter 1989, 2000). Six channels have been mapped in the area, although only four of these have yielded fossils; from north to south these are: the Todding, Mocktree, Church Hill and Tatteridge channels (Text-figs 2.2A, 2.3; Whitaker 1962). The channels have been interpreted to represent shelf-break submarine canyon heads (Text-fig. 2.2) and the fill is mapped as the higher Lower Leintwardine Formation, of Ludfordian age (Text-fig. 2.3; Whitaker 1962, 1974; Siveter 1989, 2000). Along with





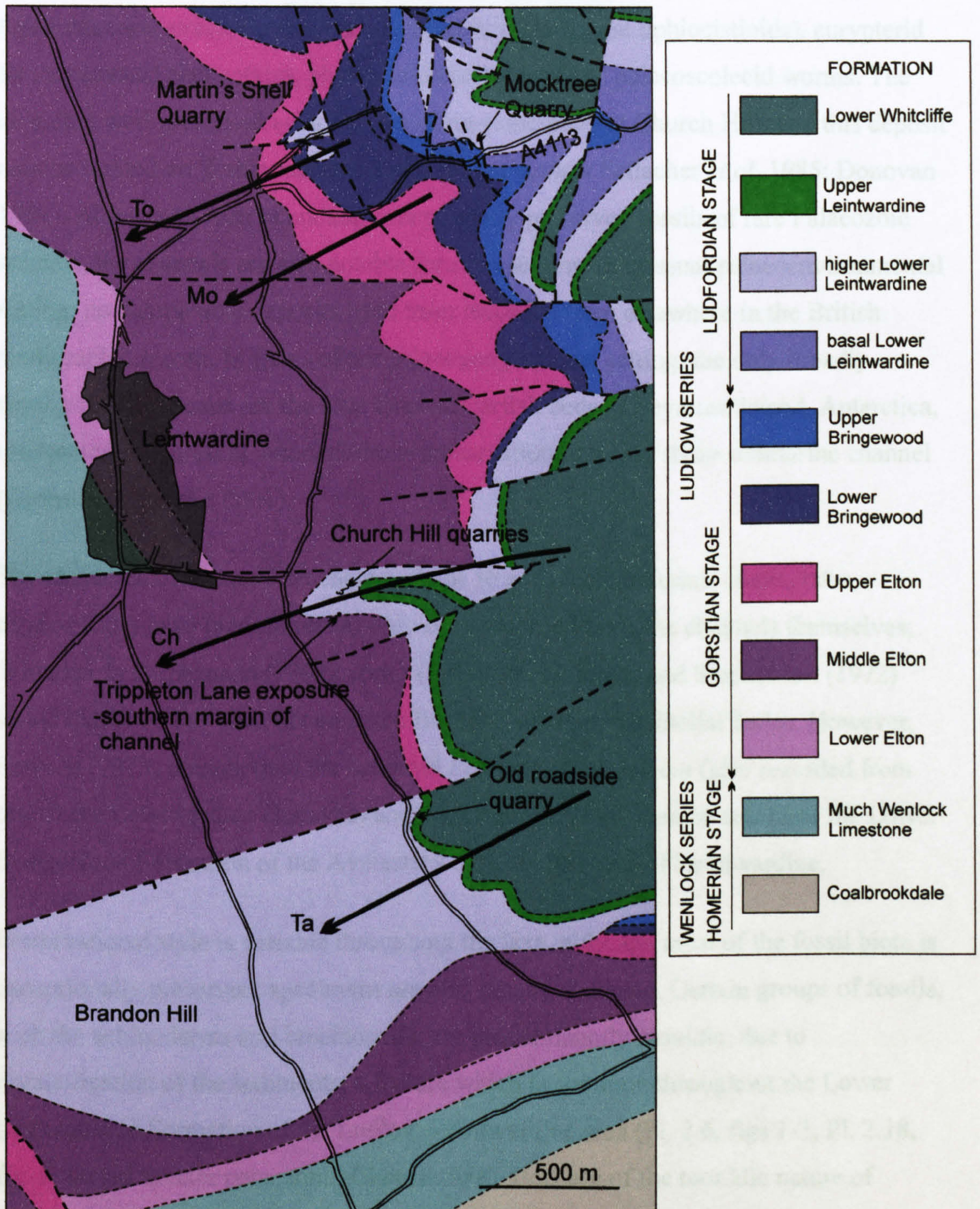
TEXT-FIG. 2.1. A, Location of the study area around Leintwardine, approximately 10 km to the west of Ludlow, Shropshire. B, field localities around Leintwardine that show exposures of submarine channel deposits (from north to south): Martin's Shell Quarry (Todding Channel); Mocktree Quarry (Mocktree Channel); Church Hill quarries and Trippleton Lane (Church Hill Channel); old roadside quarry and Brandon Hill (Tatteridge Channel). C, field localities at Church Hill that show the re-exposed composite quarries and lateral extent of Starfish Bed A.





TEXT-FIG. 2.2. A, Inferred palaeogeography in the vicinity of Leintwardine, in the early Ludfordian, at time of deposition of Lower Leintwardine Formation (not to scale; modified from Whitaker 1994). E, Elton Group; L, Lower Leintwardine Formation. The Leintwardine submarine channels are: Marlow (Ma), Bagdon (Ba), Todding (To), Mocktree (Mo), Church Hill (Ch) and Tatteridge (Ta). B, palaeogeographical reconstruction of Welsh Basin and Midland Platform area during the early Ludfordian, showing location of Leintwardine submarine channels (modified after Bassett *et al.* 1992).





TEXT-FIG. 2.3. Geology of the Leintwardine area, showing the inferred position of the four fossiliferous submarine channels, trending ENE to WSW, and the associated field localities (modified from Whitaker 1962, and Holland *et al.* 1973): Todding Channel (To); Mocktree Channel (Mo); Church Hill Channel (Ch) and Tatteridge Channel (Ta).



typical Silurian fossils such as brachiopods, graptolites and trilobites, there are also more unusual taxa within the channel fill such as abundant and diverse echinoderms (ophiuroid and asteroid stelleroids, echinoids, crinoids and ophiocistoids), eurypterid and xiphosurid chelicerates, phyllocarid crustaceans and palaeoscolecoid worms. The abundant well-preserved echinoderms occur principally at Church Hill, and this deposit may be termed an 'Echinodermen-Lagerstätten' (*sensu* Seilacher *et al.* 1985; Donovan 1991). Along with their abundant, exceptionally preserved fossils of rare Palaeozoic animals, the channels are also notable for representing an unusual palaeoenvironmental setting; no comparable deposits have been recorded from elsewhere in the British stratigraphic record. In terms of the palaeogeographical setting, the only broadly similar fossil deposits are the Late Eocene starfish beds of Seymour Island, Antarctica, interpreted to represent autochthonous preservation in a near shore submarine channel (Aronson and Blake 2001).

The characteristic taxa of the channel fauna (e.g. the echinoderms, chelicerates, phyllocarids) have predominantly only been recorded from the channels themselves; Whitaker *in* Stephenson (1963), Jones (1969) and Goldring and Stephenson (1972) stated that none has been documented from the surrounding shelfal facies. However, Lawson (1973) documented the echinoid *Echinocystites pomum* (also recorded from one of the Leintwardine channels) and the stelleroid ?*Urosoma hirudo* from the Lower Bringewood Formation of the Aymestrey area, to the south of Leintwardine.

Preservational style is variable throughout the taxa, although most of the fossil biota is exceptionally preserved; specimens are also mostly flattened. Certain groups of fossils, such the echinoderms and brachiopods, are predominantly mouldic, due to decalcification of the sediments, a feature which is common throughout the Lower Leintwardine Formation of the Ludlow-Leintwardine area (Pl. 2.6, figs 1-3; Pl. 2.18, fig. 5; David Siveter pers. com.; Cherns 1988). Because of the mouldic nature of preservation, the production of silicone casts has been undertaken where applicable to determine the original external morphology of the organism. Some echinoderms are preserved as recrystallised calcite, although in these instances, morphological detail is obscured (e.g. Pl. 2.3, figs 1-2). The majority of the biota shows only hard-part preservation; soft-body fossilisation is encountered in the form of possible gut trace preservation in the rare palaeoscolecoid worm fossils (Pl. 2.19, figs 1-2).



The aims of this paper are to ascertain whether the Leintwardine channel biota was indigenous to the unique palaeoenvironmental setting, to determine whether it is an autochthonous, parautochthonous or allochthonous assemblage (*sensu* Kidwell *et al.* 1986), and to identify the processes responsible for its preservation. The faunal diversity, abundance and palaeoecology throughout the channels are assessed in detail for the first time. Previous studies on the fauna of the channels were by Whitaker (1962) and Jones (1969). Jones' (1969) study was the most comprehensive, incorporating aspects of palaeoecology, although he omitted many of the unusual faunal groups such as the echinoderms and chelicerates, due to the lack of access to sufficient material. Detailed analysis of the sedimentology has also been carried out.

### PREVIOUS MODELS FOR THE ENVIRONMENTAL SETTING OF THE LEINTWARDINE FAUNA

Most previous studies on the channels have not concentrated on the taphonomic history of the fauna. Hawkins and Hampton (1927) interpreted the deposits to represent lagoonal facies and concluded that the fauna was indigenous to the setting; they added that rapid burial was responsible for the preservation of the echinoderms. Whitaker (1962) reinterpreted the deposits as channel facies, specifically submarine canyon heads, and felt that the rare fauna was indigenous to the setting, referring to the absence of stelleroids, echinoids, worms, phyllocarids and xiphosurans outside the channels (Stephenson 1963). Whitaker (*in* Stephenson 1963) stated that the channel fauna was likely to have been buried *in situ*, as suggested by the degree of articulation, the finely laminated, unbioturbated nature of the enclosing sediment and the relatively high sedimentation rates within the channels. He added that the earlier fauna of the channels was likely to be strictly confined to the setting, whilst relatively later faunas (e.g. representing the highest starfish beds at Church Hill, just below the base of the Upper Leintwardine Formation) may have been less confined, as the channels became progressively infilled (Stephenson 1963). Jones (1969) concluded that two distinct indigenous faunas were present within the channels: a nektobenthic fauna (e.g. phyllocarids and eurypterids) and a benthic fauna (e.g. the vagile echinoderms), which probably included lingulid brachiopods and worms. The only work to concentrate on the biostratinomy of the channel biota was by Goldring and Stephenson (1972) who studied the echinoderm-bearing starfish beds of the Church Hill and Todding channels.

They concluded that there was no conclusive evidence to prove that autochthonous thanatocoenoses has been preserved and stated (p. 621), “the echinoderms and other unusual fauna were introduced or incorporated and buried within fine-grained turbidite flows in the channels”.

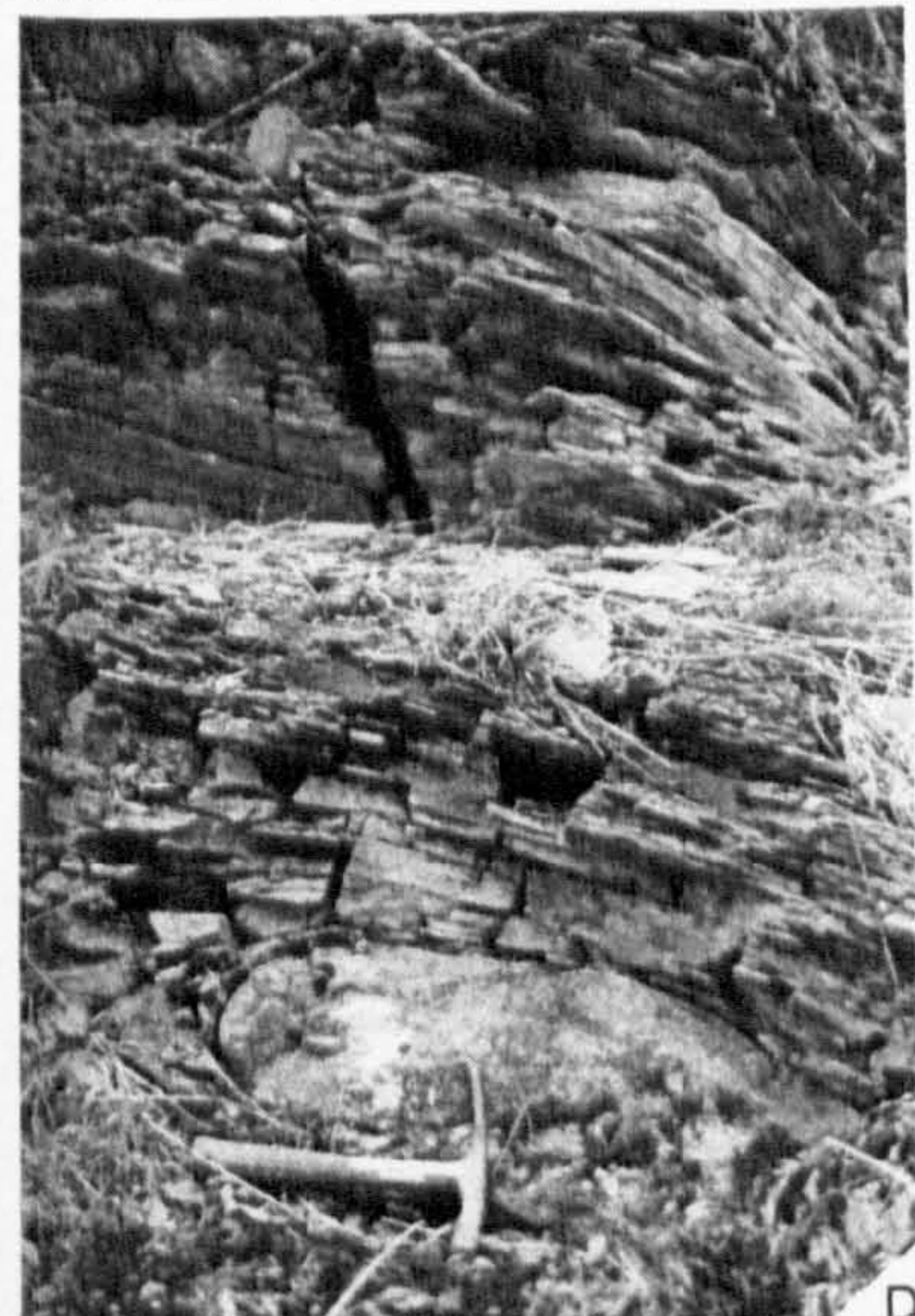
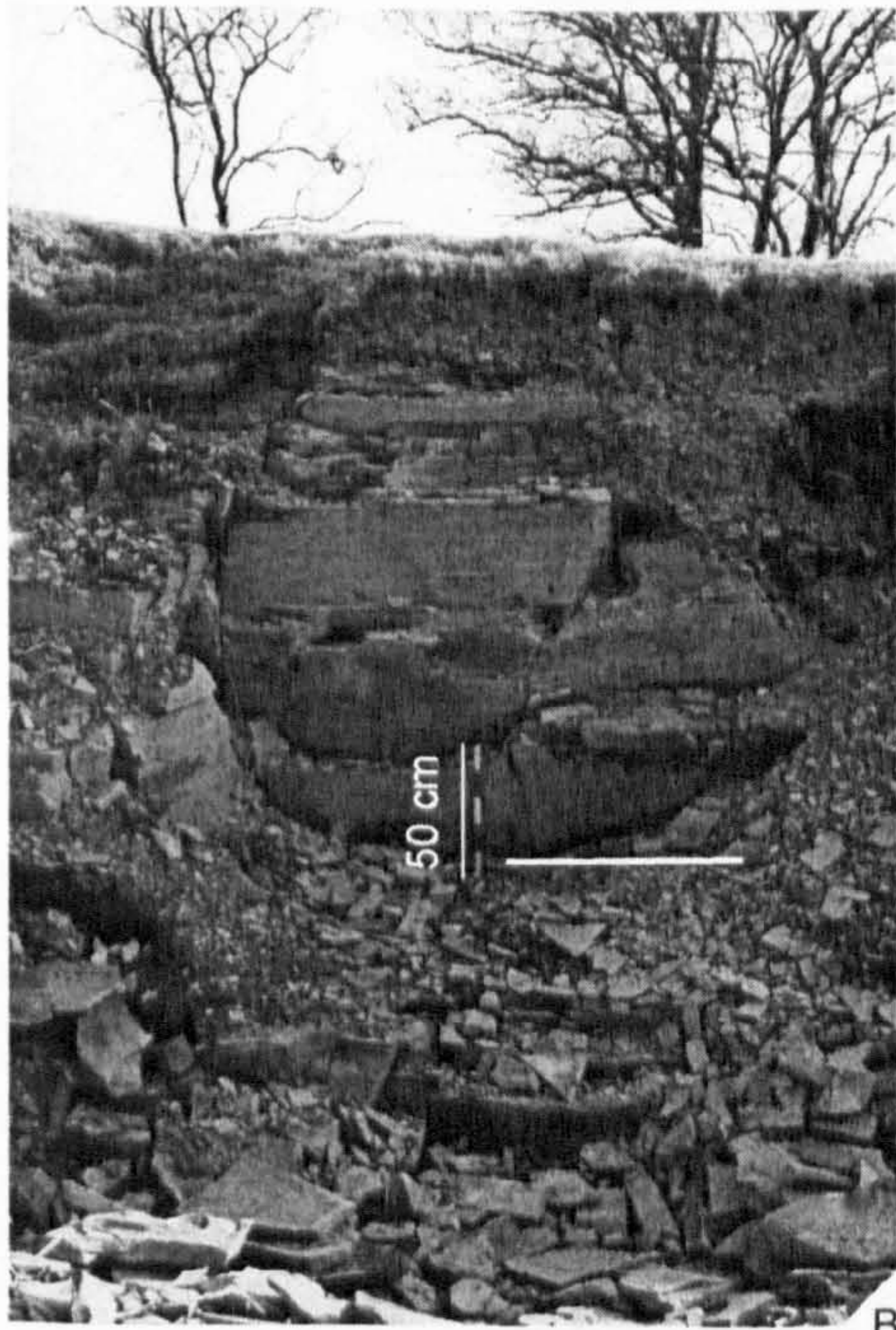
## MATERIAL AND METHODOLOGY

Pre-existing collections (see below) were re-examined along with newly collected *in situ* material. The four fossiliferous channels were restudied, with emphasis placed upon the Church Hill Channel because of its abundance of documented fossils.

Church Hill essentially consisted of a composite set of overgrown quarries, of which only those reported by Hawkins and Hampton (1927) could be relocated (Text-figs 2.1C, 2.4). Relocation was based on published location descriptions (Hawkins and Hampton 1927), positioning on the 1: 25 000 Ordnance Survey of the area, and surface topography (the positions of the quarries were indicated by pronounced amphitheatre-like surface depressions). Based on documentation from Hawkins and Hampton (1927), most study was concentrated on the more fossiliferous, larger southern quarry (here termed ‘Quarry 1’; SO47 4115 7375; Text-figs 2.1C, 2.4A-B), interpreted to lie towards the axis of the channel. Following re-excavation, lithological variation and exact horizon provenance for the *in situ* biota was determined at this quarry using millimetre-scale logging through a 2.6 m vertical section of channel fill (Text-fig. 2.5). A smaller, northern quarry (‘Quarry 2’, SO47 4119 7380; Text-figs 2.1C, 2.4 C) was also re-excavated, although this proved to be mostly unfossiliferous; several horizons of dense graptolite assemblages were found here, but no unusual faunas were recovered. An exposure along Trippleton Lane (SO47 4115 7372; Text-figs 2.1C, 2.4D) is inferred to represent part of the southern margin of the channel (Whitaker 1962).

Martin’s Shell Quarry (SO47 4109 7543), representing the Todding Channel and Mocktree Quarry (SO47 4165 7540), representing the Mocktree Channel (Whitaker 1962) were also restudied (Text-figs 2.6-7). Study of *in situ* strata of the main channel exposure at Mocktree Quarry was not possible due to its inaccessibility. Study was limited to fallen scree from the main channel exposure, and to a down-faulted block of channel fill to the east of the exposure, although this section proved to be relatively



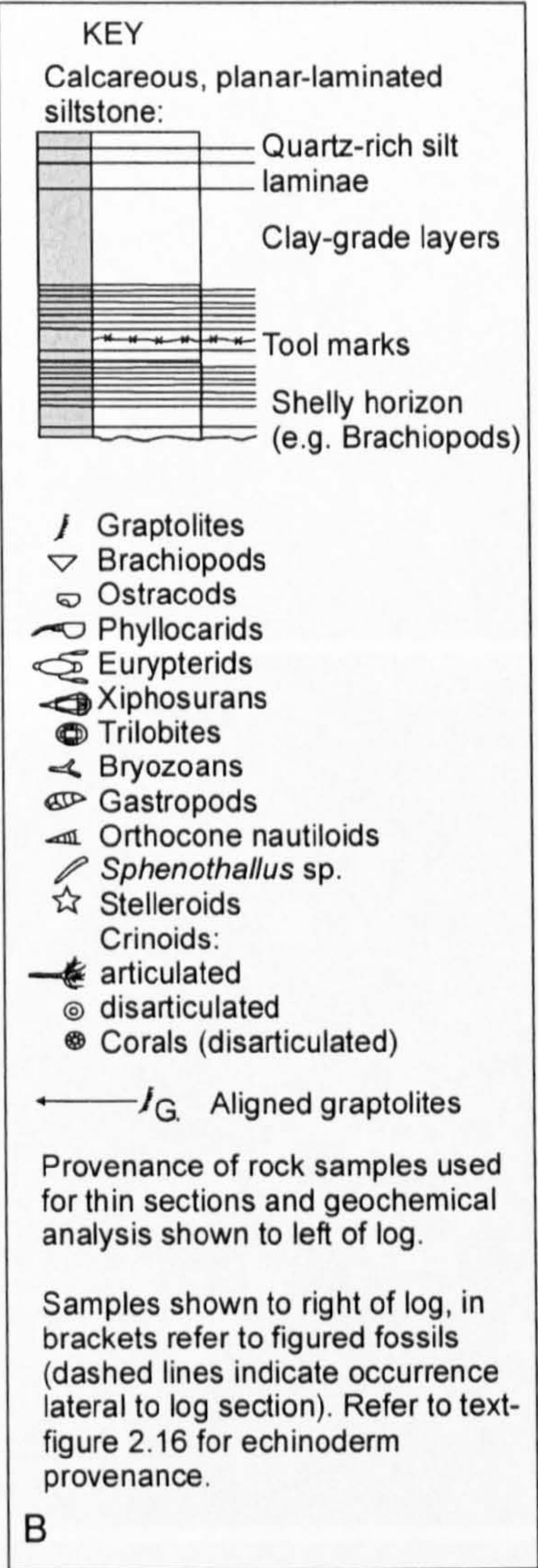


TEXT-FIG. 2.4. Church Hill quarries, Leintwardine. A-B, Quarry 1 (SO47 4115 7375), the site of the majority of the exceptionally preserved channel biota. A, View of re-exposed southern wall of quarry (c. 15 m in lateral extent), showing position of logged section and Starfish Bed A (view 194°S). B, detail of quarry face (view 172°S) showing logged section; base of Starfish Bed A also indicated. C, Quarry 2 (SO47 4119 7380), view 180°S. D, view of exotic boulder of limestone within channel fill, near channel flank; Trippleton Lane (SO47 4115 7372); (photos A and D: David Siveter).

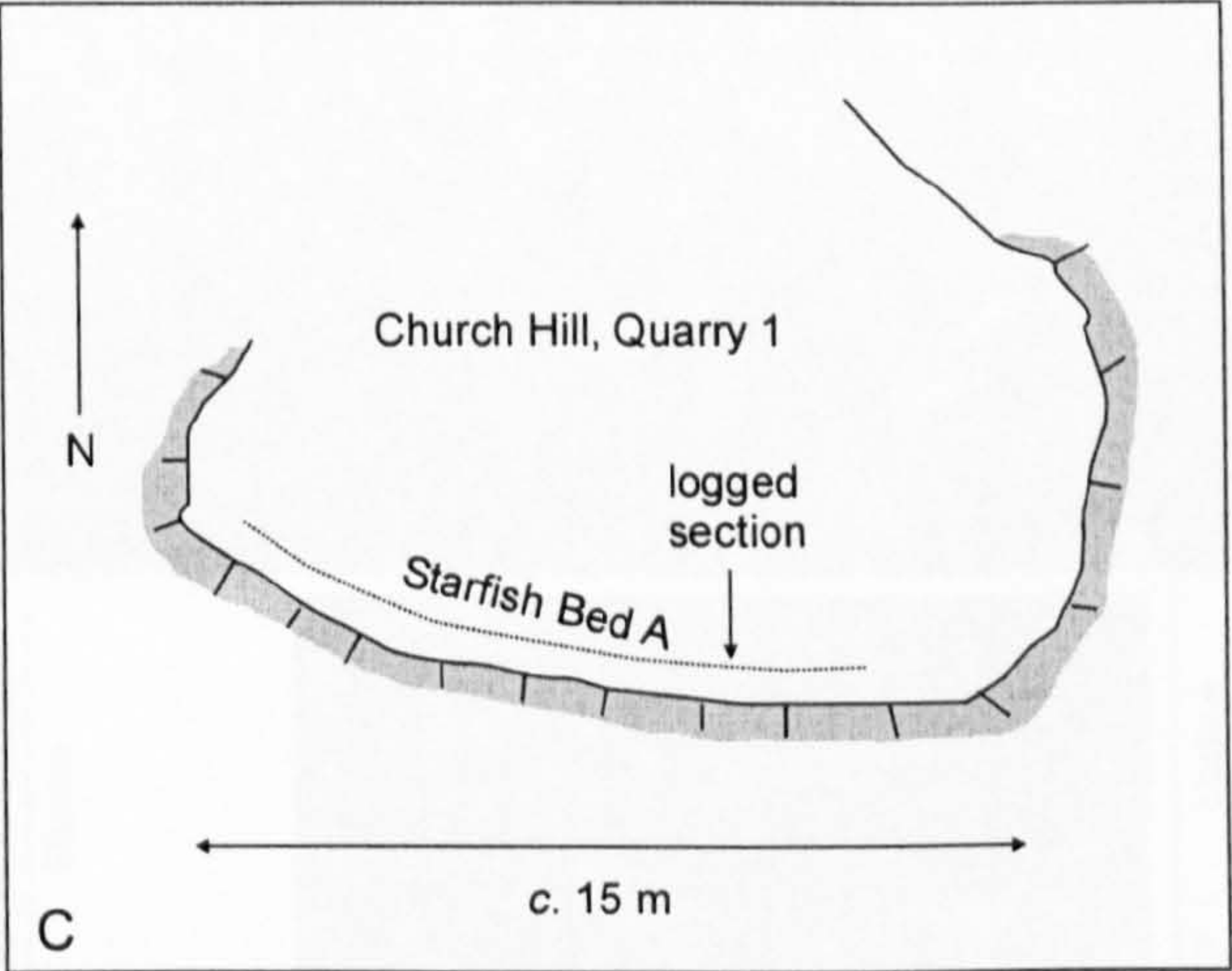




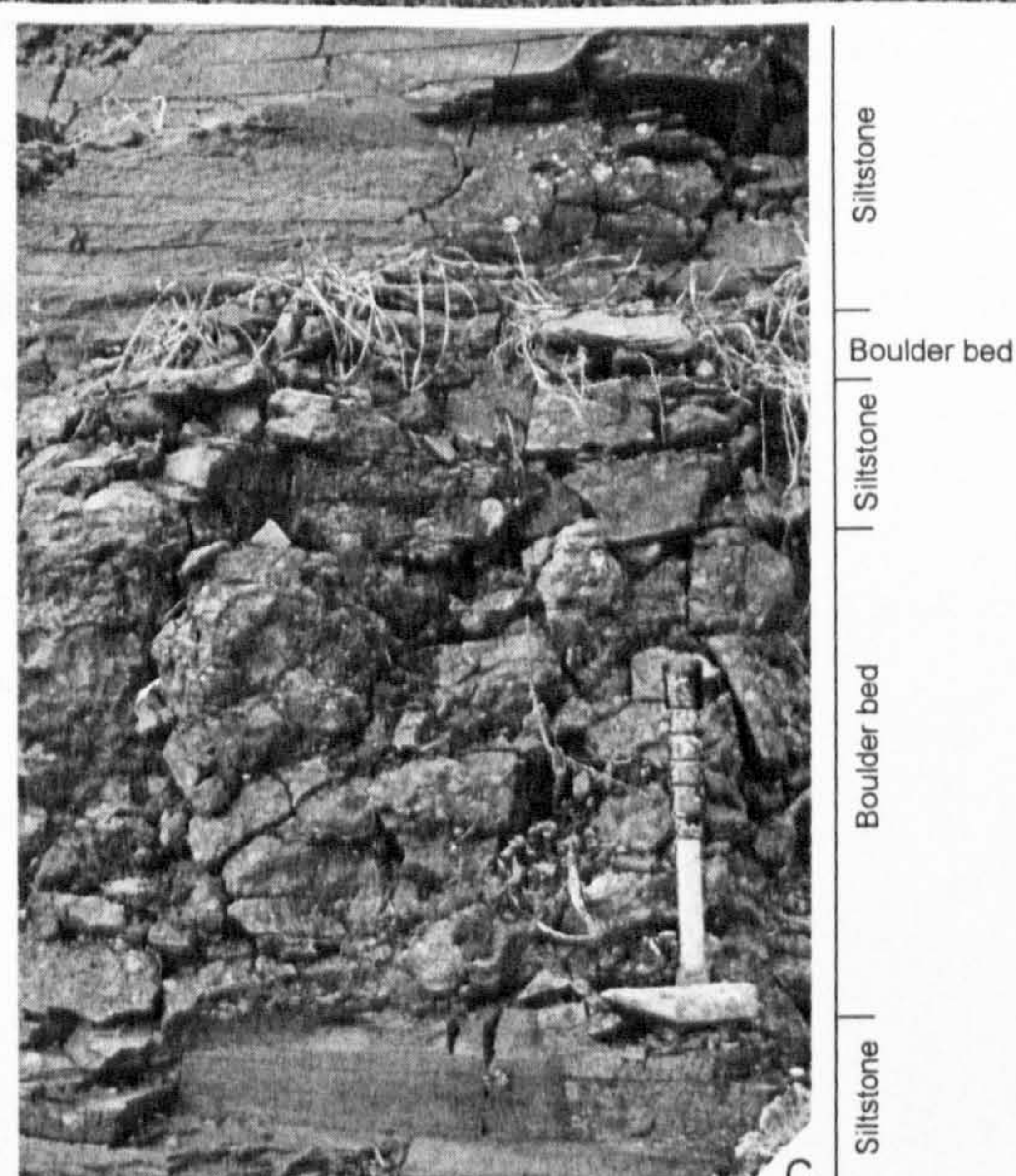
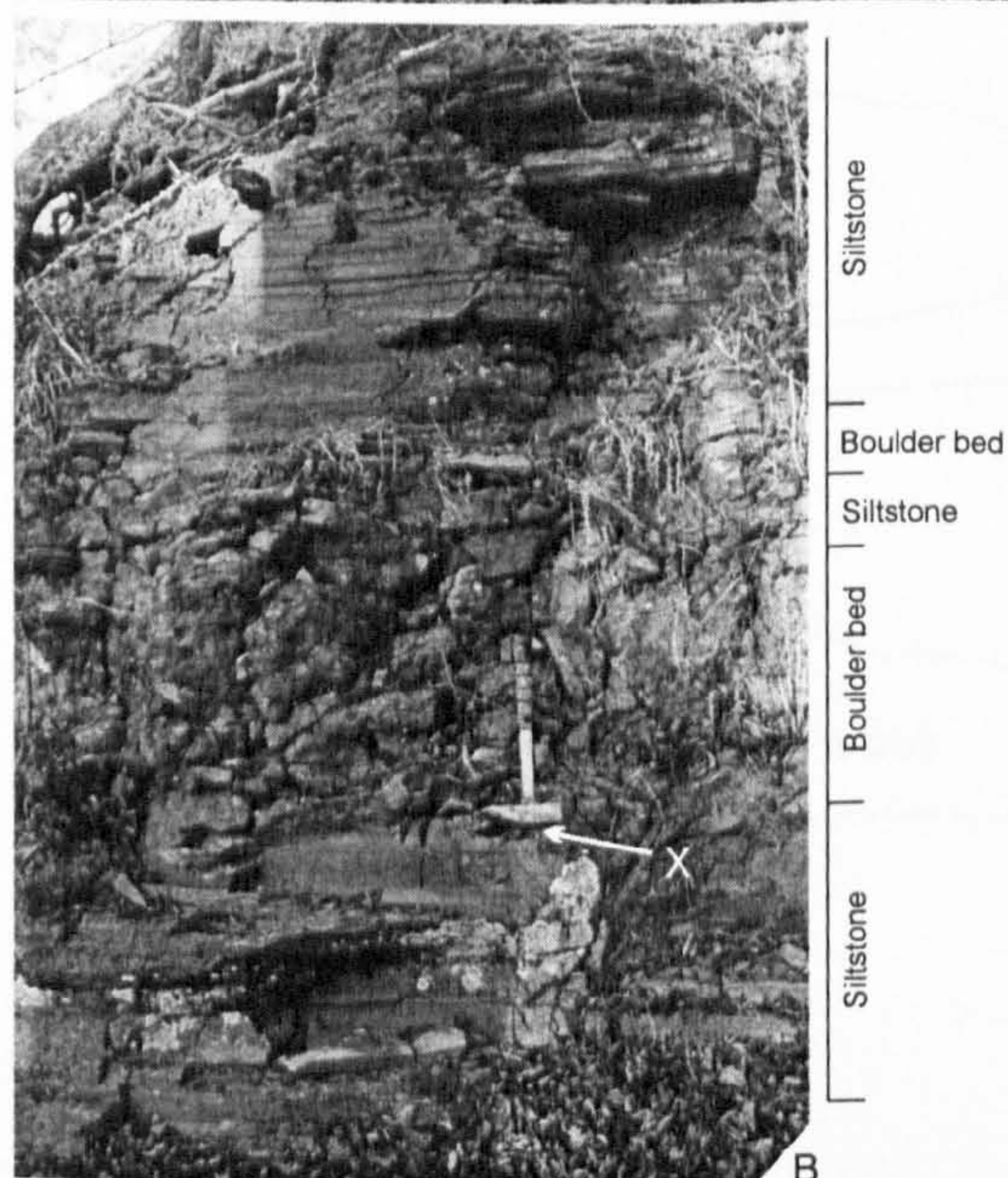
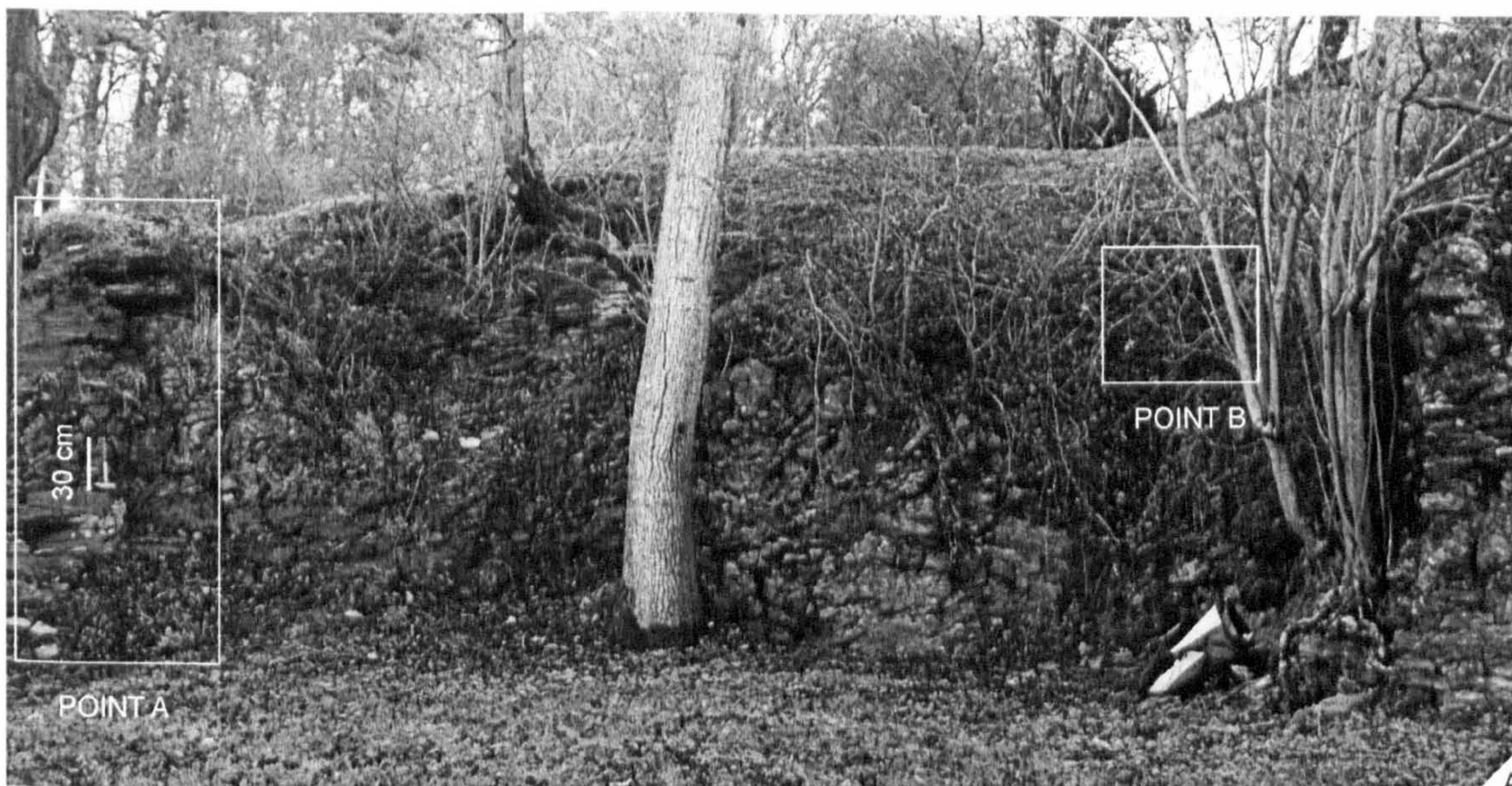




TEXT-FIG. 2.5. B, key to log through c. 2.6 m of channel fill at Church Hill, Quarry 1 (SO47 4115 7375). C, location of logged section and lateral extent of Starfish Bed A within quarry.





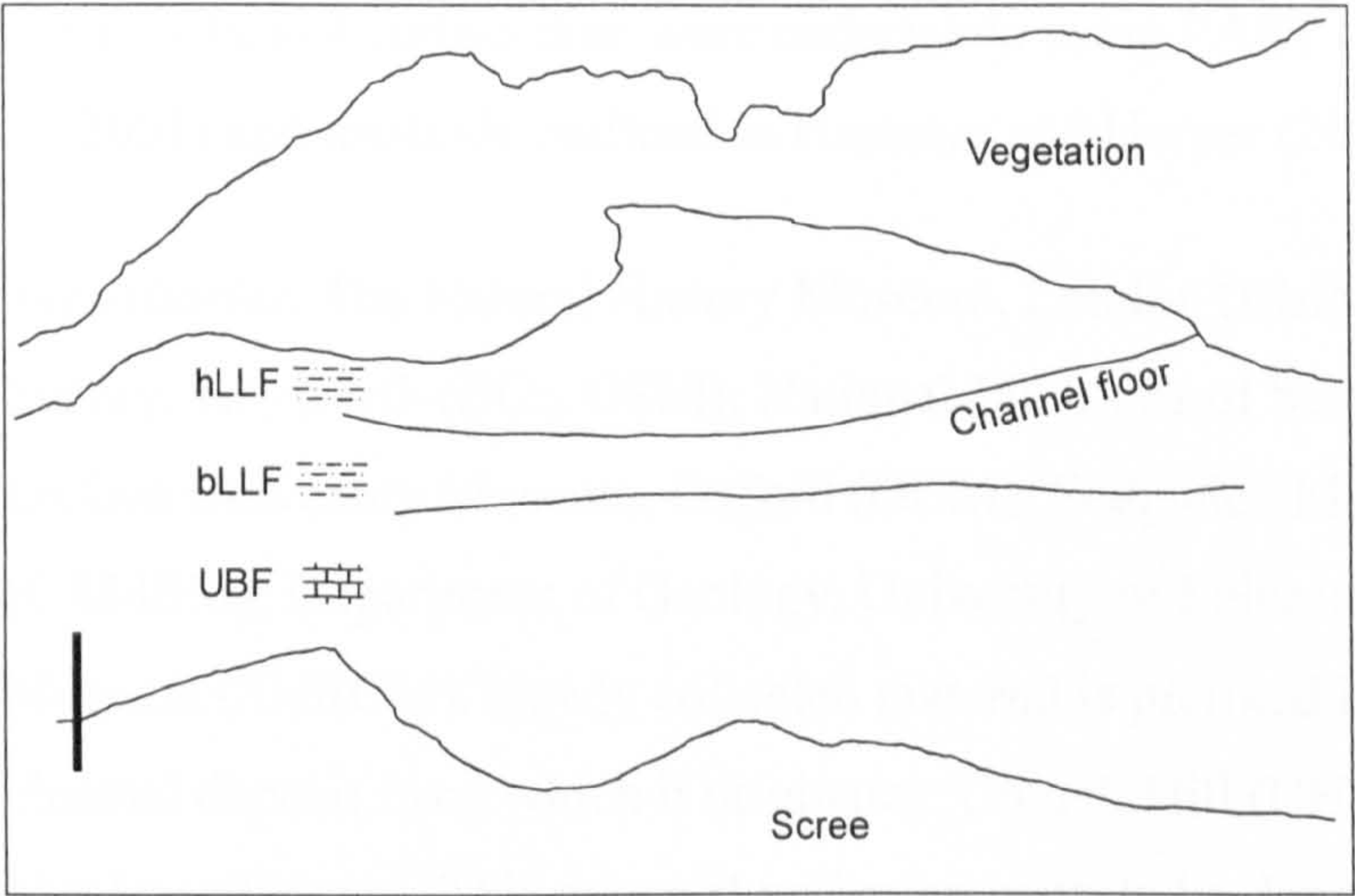


TEXT-FIG. 2.6. Martin's Shell Quarry, Leintwardine (SO47 4109 7543). A, view (015°N) of quarry face, with areas of interest 'Point A' and 'Point B' indicated. B, view of succession at northern end of quarry 'Point A', showing alternating siltstone and boulder beds; position of fossiliferous horizon containing abundant *Sphenothallus* sp. indicated as 'X'. C, detail of 'Point A', showing position of fossiliferous horizon. D, detail of succession at 'Point B', showing alternating siltstone and boulder beds and position of stelleroid (undet. sp.) recovered (indicated as 'Y'). Length of hammer represents 30 cm.





TEXT-FIG. 2.7. Mocktree Quarry (SO47 4165 7540), Leintwardine. View (016°NNE) of main quarry face, showing higher Lower Leintwardine Formation (hLLF) channel fill siltstone and base of channel incising into underlying basal Lower Leintwardine Formation (bLLF) siltstone. Width of channel c. 27 m. Upper Bringewood Formation (UBF) limestone underlies the Lower Leintwardine Formation. Scale bars represents 1.8 m. Photograph: David Siveter.





unfossiliferous. The small roadside quarry (SO47 4141 7298) representing the Tatteridge Channel (Whitaker 1962; Text-fig. 2.1B) was not restudied because of its inaccessibility; the site is completely overgrown with vegetation. Field surveying of Brandon Hill (SO47 4040 7225), representing the south-westerly extension of the Tatteridge Channel (Text-figs 2.1B, 2.2A, 2.3; Whitaker 1962, 1994), revealed a general lack of *in situ* rock exposure. The Brandon Hill field localities (SO47 4072 7230 and 4028 7265), documented to have yielded an abundant phyllocarid fauna collected in the early 1980's and deposited in Ludlow Museum, were not relocated.

Statistical analyses of size frequency distributions and way up orientations of stelleroid samples from Leintwardine were undertaken using PAST (version 1.40; see Hammer *et al.* 2001) and methods outlined in Hammer and Harper (2006).

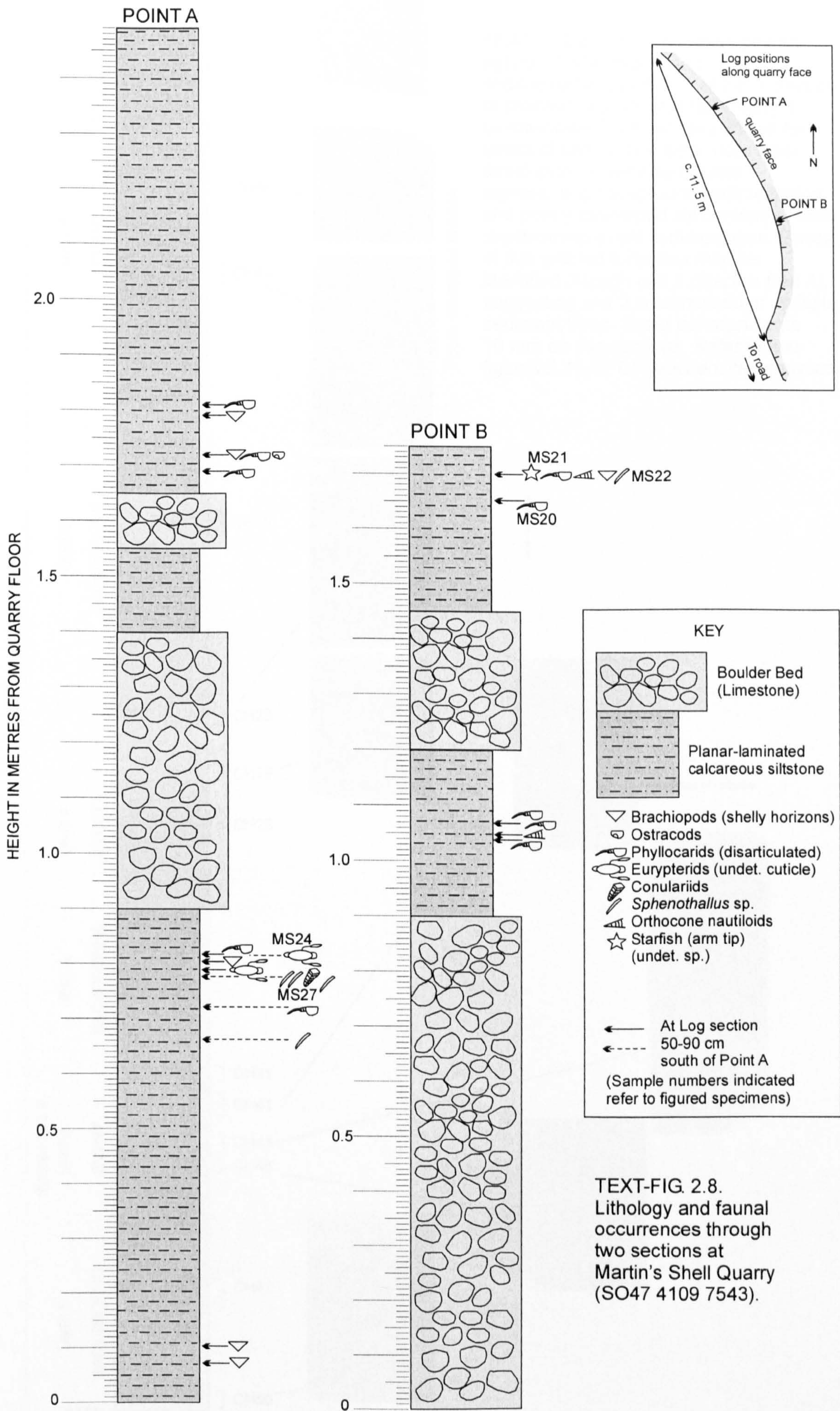
*Repositories.* The Natural History Museum, London (BMNH); British Geological Survey, Keyworth (BGS GSM); National Museums of Scotland, Edinburgh (NMS); Oxford University Museum, Oxford (OUM); Sedgwick Museum, Cambridge (CAMSM); Department of Geology, University of Leicester (LEIUG); Ludlow Museum (SHRCM). Newly collected material is prefixed by an identifier, denoting the channel deposit from which it originates: Church Hill (CH), Martin's Shell (MS) or Mocktree (Mock). This material will subsequently be deposited in the OUM, BGS and LEIUG collections.

## CHANNEL FILL SEDIMENTOLOGY

The channel fill, predominantly higher Lower Leintwardine Formation, comprises interbedded laminated siltstones and boulder-beds (Text-figs 2.3-9; Whitaker 1962). The boulder-beds are only seen at the Martin's Shell Quarry exposure of the Todding Channel, although derived isolated boulders occur at other channel exposures (e.g. the Trippleton Lane exposure of the Church Hill Channel margin; Text-figs 2.4D, 2.6, 2.8).

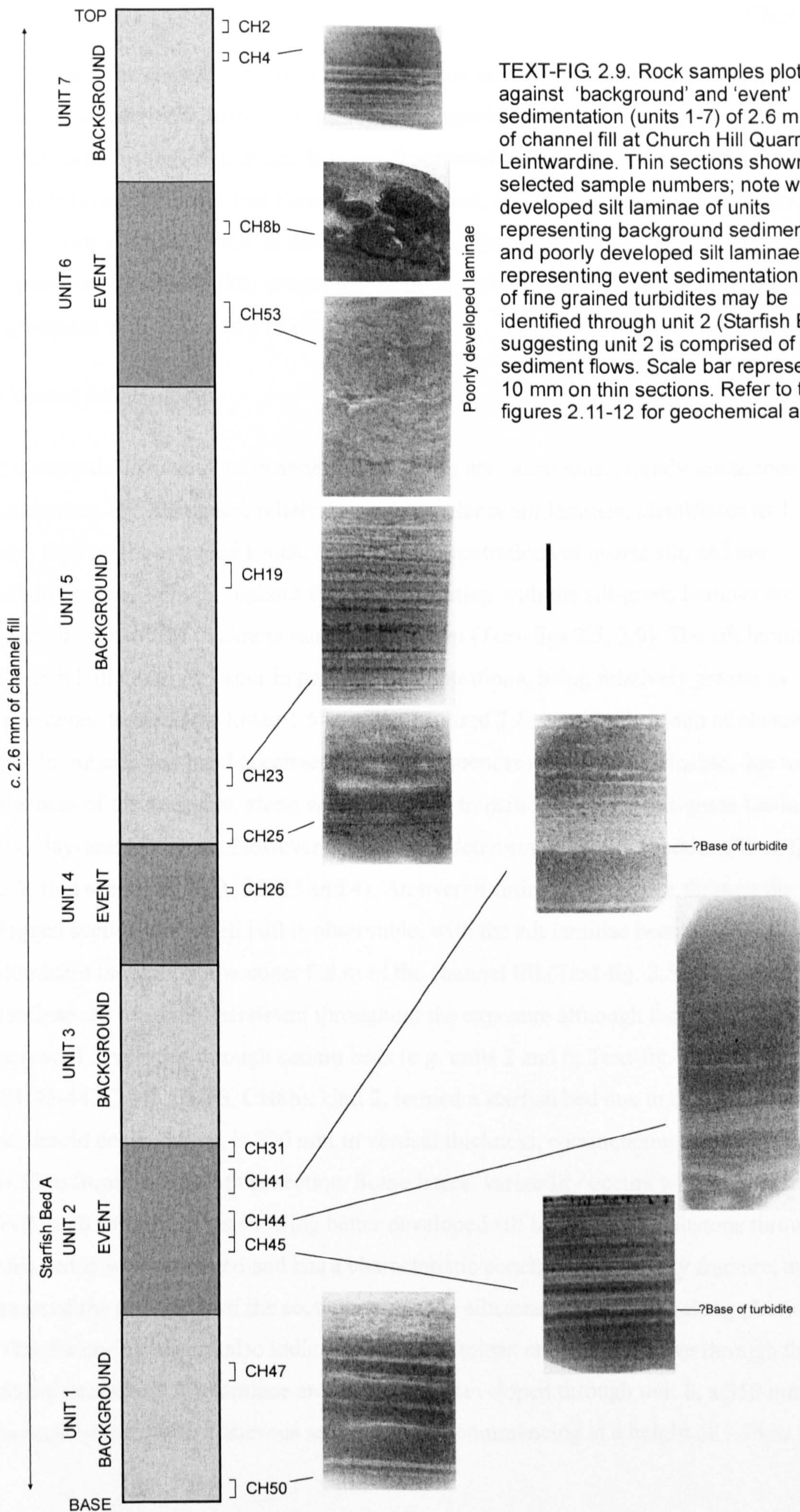
Both the higher and underlying basal Lower Leintwardine formations consist of laminated siltstone (Whitaker 1962; pers. obs.). Whitaker (1962) distinguished the formations on the carbonate content and laminae abundance, noting that the higher Lower Leintwardine Formation channel fill siltstones are less calcareous and more laminated than the surrounding Leintwardine Group shelfal siltstones. This would be





TEXT-FIG. 2.8.  
Lithology and faunal  
occurrences through  
two sections at  
Martin's Shell Quarry  
(SO47 4109 7543).





TEXT-FIG. 2.9. Rock samples plotted against 'background' and 'event' sedimentation (units 1-7) of 2.6 m section of channel fill at Church Hill Quarry 1, Leintwardine. Thin sections shown for selected sample numbers; note well-developed silt laminae of units representing background sedimentation and poorly developed silt laminae of units representing event sedimentation. Bases of fine grained turbidites may be identified through unit 2 (Starfish Bed A), suggesting unit 2 is comprised of multiple sediment flows. Scale bar represents 10 mm on thin sections. Refer to text-figures 2.11-12 for geochemical analyses.



expected if the channels received relatively more sedimentation than the surrounding facies. Cherns (1988, text-fig. 13) assigned the shelf-break area incorporating the Leintwardine submarine channels to her 'laminated siltstone facies' at the time of middle Lower Leintwardine Formation deposition, and to her 'more thickly flaggy, calcareous siltstone facies' at the time of basal Upper Leintwardine Formation deposition. Cherns' (1988) assignment of these facies in the channels is in broad agreement with Whitaker's (1962).

### *Channel fill lithology*

*Laminated siltstones.* The channel fill siltstones are calcareous, slightly micaceous and laminated. The numerous, relatively uniform, planar silt laminae, identifiable as 1-2 mm thick, light-coloured bands, consist of concentrations of quartz silt, and are relatively persistent throughout the fill. Alternating with the silt-grade laminae are clay grade layers, with a thickness range of 2-30 mm (Text-figs 2.5, 2.9). The silt laminae at Church Hill Quarry 1 occur in periodic concentrations, being relatively greater in abundance towards the lower 1.5 m of the exposed 2.6 m vertical section of channel fill. In outcrop and hand specimen, grading sequences are not determinable, due to the fineness of the grain size, along with the abrupt transition from the silt-grade laminae to the clay-grade laminae. However, fining up is determinable in thin section (Text-fig. 2.9; thin sections 44, 41, 25, 23 and 4). An overall fining up sequence through the logged section at Church Hill is observable, with the silt laminae becoming less dominant throughout the upper 0.8 m of the channel fill (Text-fig. 2.5). The silt laminae are relatively persistent throughout the exposure although they appear to be less well developed through certain beds (e.g. units 2 and 6; Text-fig. 2.9; thin sections CH45-44, CH41, CH53, CH8b). Unit 2, termed a starfish bed due to the abundance of stelleroid echinoderms, is 300 mm in vertical thickness, commencing at a height of 0.33 m from the base of the section. Some lateral variability occurs within the starfish bed, with some samples showing better developed silt laminae. The siltstone through this bed is well cemented and has a characteristic conchoidal or blocky fracture, unlike most of the remainder of the section, where the siltstone splits evenly along planes. This fracturing pattern also indicates that the laminae are less pervasive through this fossiliferous bed. Silt laminae are very poorly developed through unit 6, a 350 mm vertical section with numerous scour surfaces, commencing at a height of 1.95 m from



the base of the section (Text-fig. 2.9; thin sections 53, 8b). The siltstone throughout the fill is largely unbioturbated, as noted by Cherns (1988), preserving the planar lamination.

*Boulder-beds.* Laterally discontinuous boulder-beds (*sensu* Whitaker 1962) are identifiable through the fill at Martin's Shell Quarry (Text-figs 2.6, 2.8). The boulders are in the size range of 50-100 mm, and comprise a sparite-cemented, fossiliferous limestone (a biosparite) derived from the Upper Bringewood Formation. Fossils recorded include the large brachiopod *Kirkidium knightii* (indicative of the stratigraphical provenance), rhynchonellid brachiopods, and orthocone cephalopods. The beds are highly variable in thickness, ranging from approximately 0.1-0.9 m. As noted by Whitaker (1962), the calcareous siltstone can be seen to drape over the top of the boulders. The imbricate nature of the boulders (as recorded by Whitaker 1962) could not be ascertained due to the vegetation cover and the weathered surface of the exposure.

Whitaker (1962) described boulder-beds of derived Upper Bringewood Formation limestone occurring not far above the base of the Church Hill Channel at SO47 4106 7374, an exposure that is presently inaccessible. These cobbles and boulders were described as dominantly having their shortest axes vertical although some were imbricate, as at Martin's Shell Quarry (Whitaker 1962).

### *Sedimentary structures*

Several sedimentary structures have been identified within the channel fill at Church Hill and Martin's Shell quarries (Whitaker 1962; pers. obs.), indicative of a channel setting:

*Tool Marks.* Tool marks were recorded at several horizons throughout the channel fill at Church Hill, occurring in relative abundance through unit 6 in the log section (14 scour surfaces were recorded through this unit; Text-fig. 2.5; Pl. 2.1, fig. 1). A clear palaeocurrent direction is observable, with the structures trending parallel to the channel axis (c. NE-SW). Skip-casts and prod-casts parallel to the channel axis were recorded by Whitaker (1962).



*Derived Boulders.* These occur within the Todding and Church Hill channels, either within laterally discontinuous boulder-beds or as isolated boulders (Text-figs 2.4D, 2.6, 2.8). The boulders are composed of fossiliferous limestone of the Bringewood Limestone Formation and range in size from several centimetres (those within the boulder-beds) to 40-50 cm (isolated boulders). An excellent example of an isolated large derived boulder is seen at the Trippleton Lane exposure of the Church Hill Channel (SO47 4115 7372; Siveter 2000; Text-fig. 2.4D). The boulder occurs near the flank of the channel.

*Other structures.* Whitaker (1962) also identified slump-structures (down-flank and down-channel), ripple-marks perpendicular to the channel axis, and grooves (filled with broken fossils), parallel to the channel axis (e.g. LEIUG 19469, from the Todding Channel; Pl. 2.1, fig. 2). He concluded that these structures all supported his proposed canyon-head model for the Leintwardine channels.

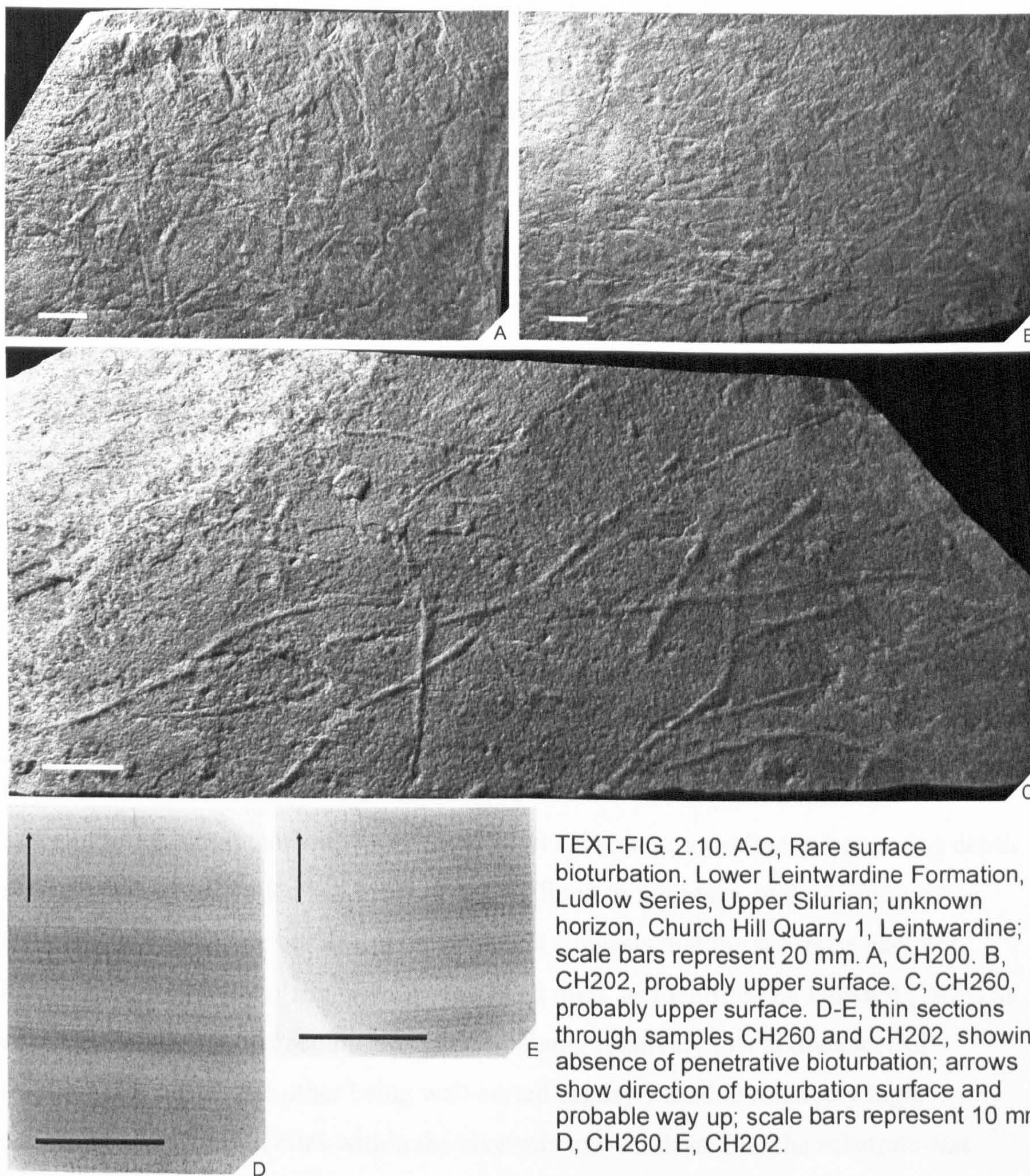
### *Current-aligned fossils*

Current-aligned fossils are relatively abundant within the laminated siltstone at Church Hill Quarry 1, again showing a NE-SW palaeocurrent direction. Orientated fossils include graptolites, orthoconic nautiloids and rhynchonellid brachiopods orientated with axes of symmetry parallel to current direction (Pl. 2.1, figs 3-4; Pl. 2.18, fig. 4; Appendix 9). Whitaker (1962) recorded brachiopod orientations in an umbone up-channel position. These fossils generally show a strong unimodal orientation indicating unidirectional currents. Stelleroid specimens often show a current alignment; arms or arm tips may show a pronounced direction of orientation (see below).

### *Extent of Bioturbation*

As with the sediments of the mid-high Lower Leintwardine Formation laminated siltstone facies of the shelf edge (see Cherns 1988), the channel fill siltstone is largely unbioturbated, indicating an absence or low abundance of infauna. Rare surface traces occur (Text-fig. 2.10), although convincing examples of penetrative bioturbation are lacking. During the Silurian the maximum burrowing depths in offshore facies were not greater than approximately 100-150 mm, and the amount of sediment disturbance by bioturbation was likely to be relatively minor at this time (Brett 1991). However, this





TEXT-FIG 2.10. A-C, Rare surface bioturbation. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; unknown horizon, Church Hill Quarry 1, Leintwardine; scale bars represent 20 mm. A, CH200. B, CH202, probably upper surface. C, CH260, probably upper surface. D-E, thin sections through samples CH260 and CH202, showing absence of penetrative bioturbation; arrows show direction of bioturbation surface and probable way up; scale bars represent 10 mm. D, CH260. E, CH202.



apparent absence of deep-burrowing organisms from the ecological community of the channels may indicate that some form of environmental stress was present within the channel head floor setting. Causes of the reduced bioturbation in the shelf edge sediments are unclear, although a transgression and deepening or possibly restricted circulation may have been responsible (Cherns 1988). Environmental factors within marine benthic settings that can influence the degree of burrowing include bathymetry, substrate type, oxygen availability, hydrodynamic energy, rate and style of deposition, and supply and type of organic matter (e.g. Howard 1975; Rhoads 1975; Byers 1982; Ekdale 1985; Bromley 1996, p. 275; Taylor *et al.* 2003). Another factor to take into account is that any penetrative bioturbation originally present in the channels may have been subsequently removed by erosion, although this in itself would be unlikely to account for a complete apparent absence of these structures. Water depth is perhaps unlikely to have been a significant inhibiting factor as the area was probably relatively shallow (see below).

*Substrate type.* Wignall (1993) stated that exceptionally soft substrates produce impoverished faunal assemblages that can be mistaken for oxygen-controlled assemblages, adding that with increasingly soft substrates, a decline in burrowing depth is noted as open, irrigated burrows become difficult to maintain. In the Leintwardine channels, the silt-grade content of the sediment suggests that the substrate may not have been a completely 'soupy water-saturated mud' as identified by Howard (1975) as one of two end-member sediment types containing relatively low abundances of infaunal organisms (the other being well-sorted sands). Possible relatively high, periodic sedimentation rates within the channels may indicate that the substrate was fairly soft; Wignall (1993) stated that firm substrates are commonly associated with very low sedimentation rates.

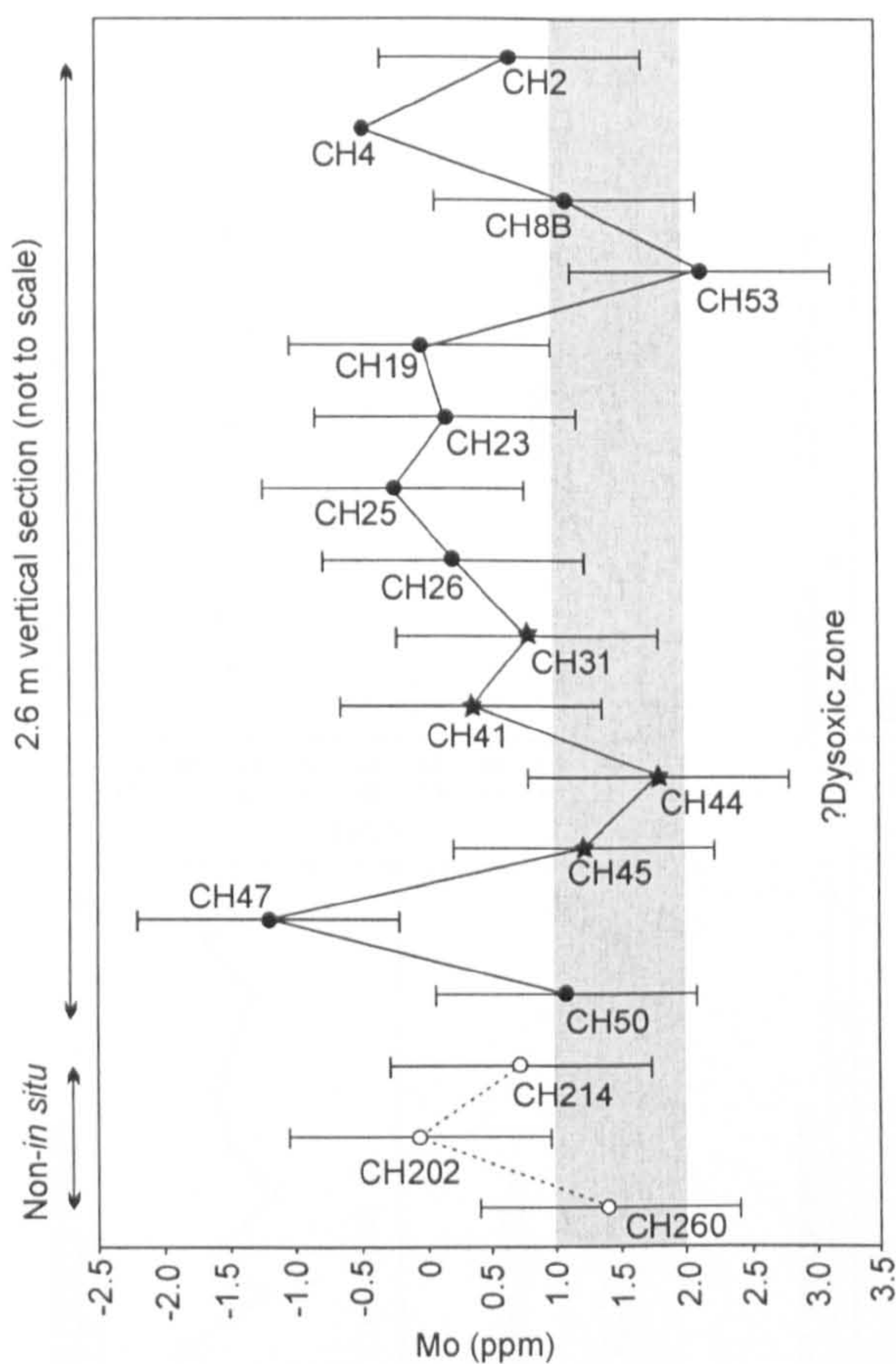
*Oxygen availability.* A low abundance of bioturbation may suggest sediment anoxia below the sediment water interface and possible low oxygen levels in the bottom water, as postulated by Tyler and Woodcock (1987) for the hemipelagites of the contemporaneous Bailey Hill Formation of the outer shelf area of the Welsh Basin. Based on ichnological evidence alone, complete anoxia is not likely to have been present at the sediment water interface, within the Church Hill Channel at least, as rare surface bioturbation is present (Text-fig. 2.10). Unfortunately these specimens are not



*in situ* so it cannot be determined which horizons these originate from. However, if oxygen-restricted conditions were present it may have been periodically aerobic, as sediment gravity flows may have introduced pulses of oxygenated water into the setting (as postulated by Byers 1977 for anoxic environments); this could allow opportunistic benthic faunas to temporarily inhabit such settings. This periodic fluctuation in oxygen levels may have been a scenario within the Leintwardine channel settings, although if this were the case, then one may expect to encounter periodic occurrences of associated penetrative bioturbation. Pyrite is not abundant within the sediments, which could suggest that conditions were not anoxic. However, this may not be conclusive as pyrite formation may be prohibited in conditions which are subjected to high sedimentation rates even if the setting is oxygen-stressed, as the accumulation of organic remains is diluted thus keeping its concentration below a critical value (Speyer and Brett 1988). This could theoretically account for the low abundance or lack of pyrite within the channel setting. Geochemical analysis reveals the channel sediments within the Church Hill Channel to contain concentrations of trace metals typically used as palaeo-redox indicators (e.g. molybdenum, nickel, uranium, vanadium, and zinc; Powell *et al.* 2003) that are comparable to those of average shale compositions (Text-figs 2.11-12; Appendix 1; Taylor and McLennan 1985). These concentrations are low and are sometimes below the lower limits of detection (Appendix 1). This suggests that bottom-water conditions in the Church Hill Channel were not dysoxic or anoxic and that oxygen levels below the sediment-water interface were unlikely to have been significantly depleted.

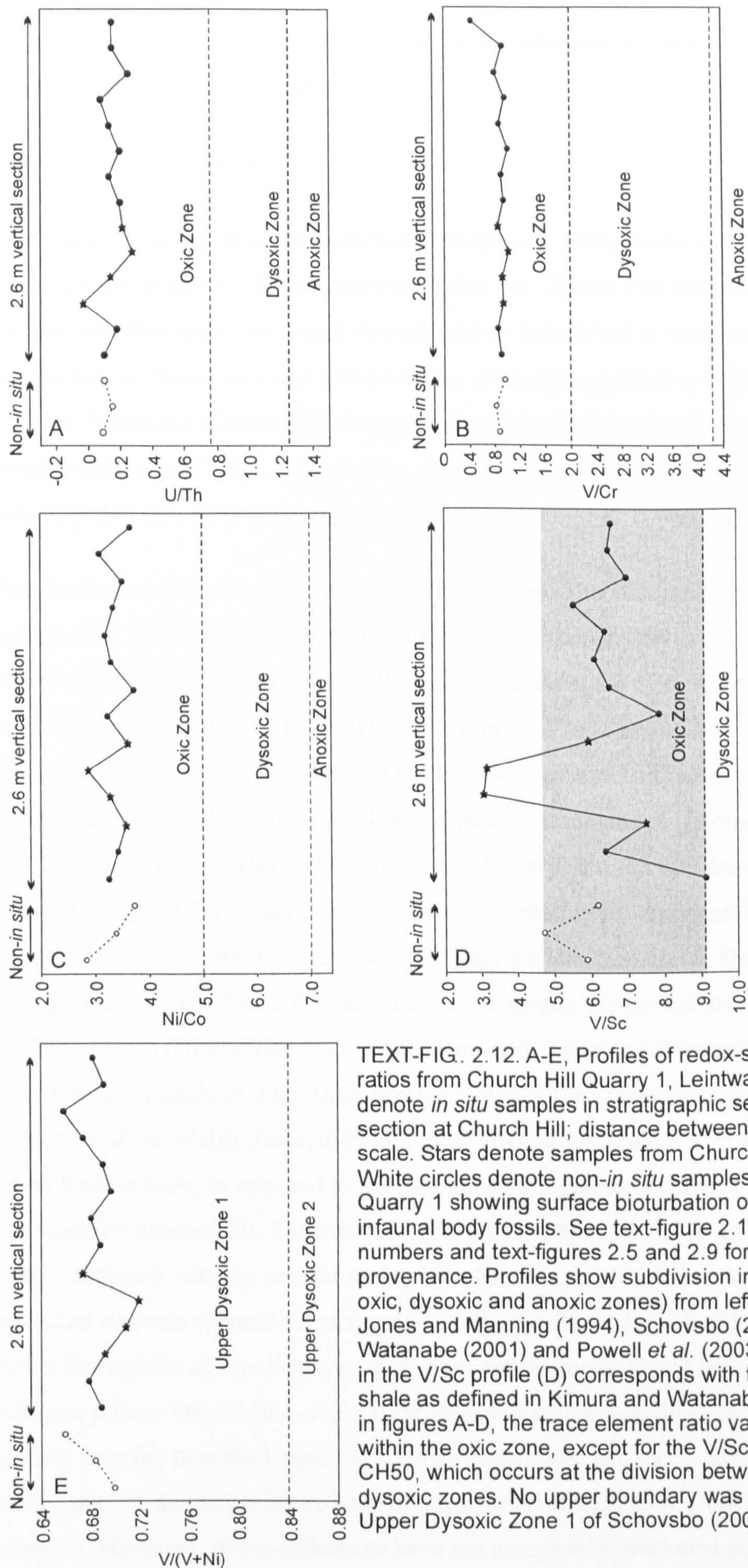
*Hydrodynamic energy and sedimentation rate.* Modern normal marine sediments are dominated by biological activity except in areas where continual current activity or rapid sedimentation occurs (Byers 1982). It may, therefore, be inferred that the Leintwardine channel setting was subjected to considerable hydrodynamic energy or sedimentation rates. The predominance of planar lamination indicates that the rate of deposition exceeded that of bioturbation; event deposition (as outlined by Bromley 1996, p. 283, see below) may be inferred. The postulated periodic high rate of sedimentation within the setting may in itself have been sufficient to suppress burrowing infaunal activity, which is absent from all beds, not just units interpreted to represent event deposits (e.g. Starfish Bed A). This is comparable in essence to the





TEXT-FIG. 2.11. Profile of Molybdenum composition (ppm) in channel fill siltstone from Church Hill Quarry 1, Leintwardine. Samples CH260, CH202, and CH214 (shown by white circles) are not *in situ*, but are included as they show surface bioturbation or are associated with benthic body fossils. Samples CH50 to CH2 (shown by black circles) are *in situ* from a stratigraphic sequence of 2.6 m; distance between samples is not to scale. Stars denote samples taken from Church Hill Starfish Bed A. Error bars = 1 ppm (limit of determination of Mo). See text-figures 2.5 and 2.9 for stratigraphical provenance of samples. The shaded area corresponds with the range of average shale as defined by Taylor and McLennan 1985). Note that Mo values generally do not occur above the average shale composition of 2 ppm, and are therefore likely to be indicative of oxic redox conditions. Samples correspond to those shown in text-figure 2.12.







example given by Byers (1982) to account for a continuous sequence of stratified units in which no bioturbation is present.

### *Patterns of sedimentation*

Two modes of sediment accumulation are recognised: *background* and *event/episodic* (*sensu* Brett and Baird 1986) deposition. Within the Church Hill channel, planar silt laminae are often more developed through phases interpreted to represent background sedimentation. Phases of event sedimentation generally exhibit less well-developed laminae. Within the Church Hill channel fill, seven units have been identified through a vertical thickness of 2.6 m, representing alternating phases of background and event sedimentation (see below; Text-figs 2.5, 2.9).

*Well-laminated siltstone (background sedimentation).* The alternating laminae superficially have the appearance of hemipelagites although they are not analogous with true hemipelagites as described throughout much of the Silurian in the deeper water settings of the Welsh Basin (Dimberline *et al.* 1990). Each silt and mud lamina couplet within the deeper water facies has been suggested to represent a periodical, approximately annual variation in silt and organic sedimentation (Dimberline *et al.* 1990; Woodcock and Tyler 1993). The hemipelagite described by Dimberline *et al.* (1990) throughout the Welsh Basin comprises alternating silt and organic carbon-rich laminae on a submillimetre scale. Hemipelagites are less common in shallower water settings of the Welsh Basin; they reach the basin slopes but are not found over the platformal areas (Dimberline *et al.* 1990). However, Tyler and Woodcock (1987) described an example of outer shelf hemipelagites of the contemporaneous Bailey Hill Formation of the Welsh Basin, although these alternating laminae are on a submillimetre scale, as opposed to the millimetre to centimetre scale of the Leintwardine channel fill. The inferred shelf-break setting for the Leintwardine channel heads, combined with the coarser scale of the laminae precludes interpretation of the laminated siltstone channel fill as true hemipelagites. The relatively thicker laminae shown through the channels may be due to the palaeogeographical location nearer to a sediment source. Dimberline *et al.* (1990) stated that hemipelagites are rarely preserved in strata younger than the Upper Gorstian stage (*nilssoni* Biozone), adding that this decline may be due to the breakdown of basin-water stratification from increased storm influence. However, storm-influences have not completely precluded post-Gorstian



hemipelagite deposition as evidenced in the Bailey Hill Formation (Tyler and Woodcock 1987). The laminated channel fill is interpreted to represent remobilised sediment, which had accumulated possibly on the outer shelf. Determining the precise nature and cause of the resedimentation is problematic; it could represent fine-grained turbidites and therefore be interpreted as distal storm deposit facies (N. Woodcock, pers. com. 2003). In this scenario, storm-mobilised sediments are inferred to have been deposited distally, below the storm wave-base. This facies may represent sedimentation resulting from relatively small-scale storm activity.

*Poorly-laminated siltstone (event deposits).* The siltstone occurring through units 2 (Starfish Bed A) and 6 (containing abundant scour surfaces) has planar silt laminae that are sometimes poorly developed (Text-figs 2.5, 2.9). Fining upwards grading of the laminae is also relatively poorly developed. Sedimentological and faunal evidence (see below) suggests that these horizons are likely to represent event sedimentation in the form of remobilised sediments possibly resulting from major storm activity. These horizons may therefore be interpreted to represent distal storm deposits. Starfish Bed A contains abundant articulated echinoderms; the lack of disarticulation strongly suggests rapid sediment burial. This horizon can be regarded as an obrution deposit (*sensu* Seilacher *et al.* 1985). A buried horizon (*sensu* Brett 1990) is indicated by the presence of a particularly shelly lag (e.g. CH175; Pl. 2.18, fig. 6) at the base of the starfish bed. The overlying burial layers of an obrution deposit are typically structureless although planar lamination may also occur (Brett 1990); the siltstone through Starfish Bed A does contain planar lamination.

### *Interpretation of channel fill sedimentation*

The boulder-beds occurring within the Todding Channel are interpreted to represent mass flows (e.g. rock slides or debris flows). Mass flows have been well documented from modern and ancient submarine canyons and channels (Shanmugam 2003). For example, Stanley *et al.* (1978) and May *et al.* (1983) documented debris flows from the Eocene-Oligocene Annot Sandstone canyon fill and the Eocene Torrey Canyon respectively. The alternating silt-mud laminae may be fine-grained turbidites or tidal rhythmites:

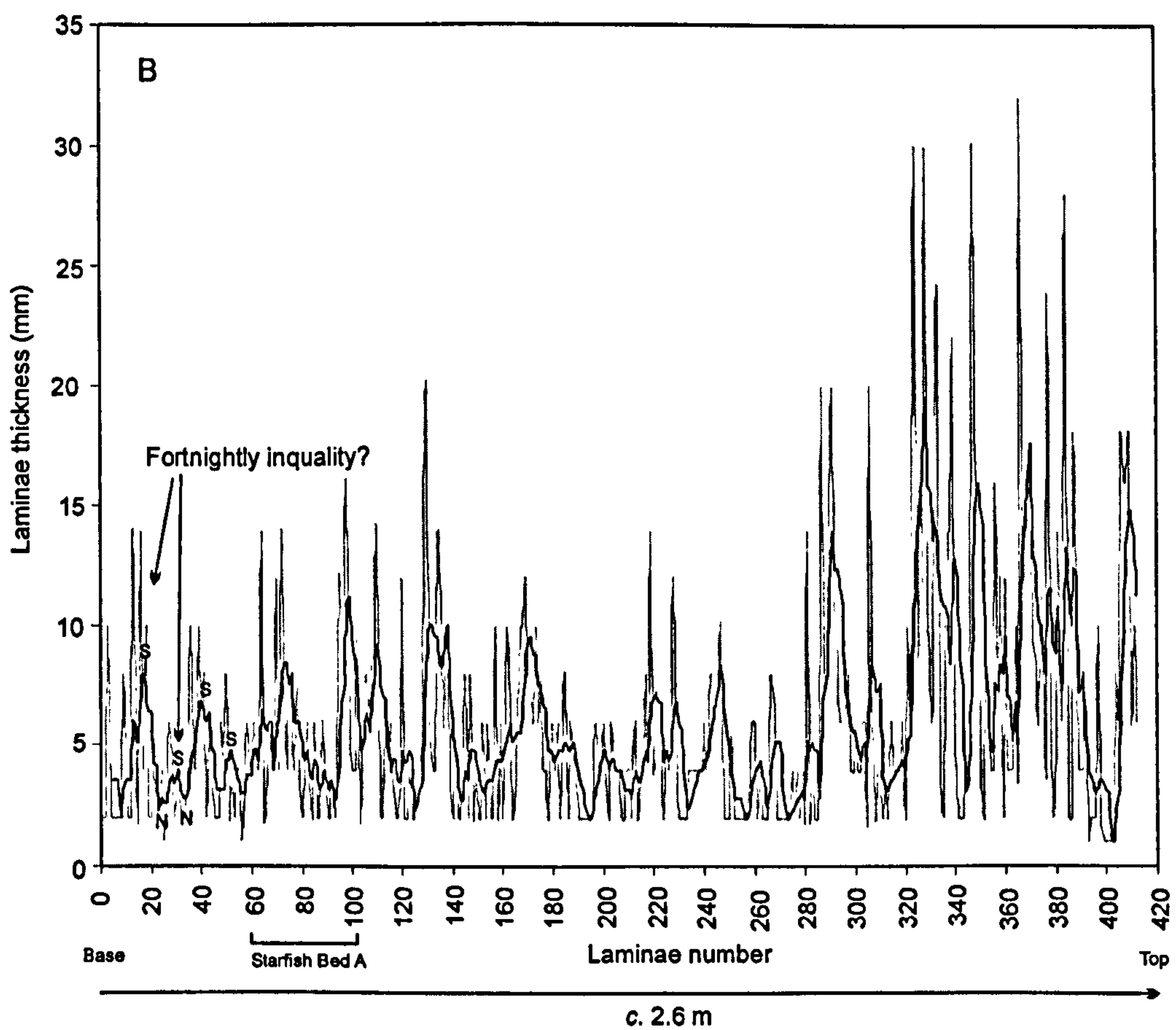
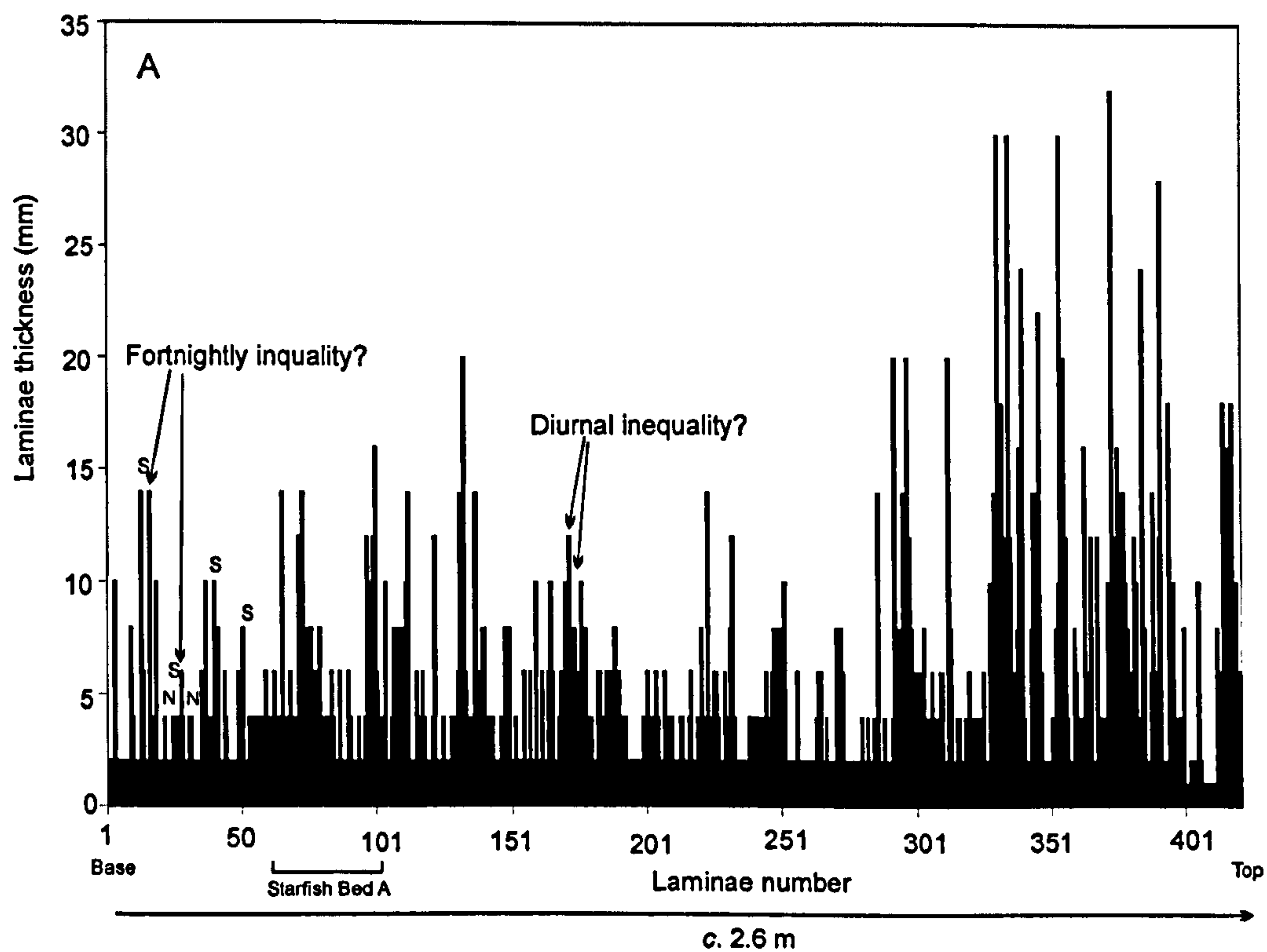


*Fine-grained turbidites?* The laminated siltstone may be interpreted to represent fine-grained distal turbidites (e.g. see Stow and Shanmugam 1980; Stow 1985), containing the D and E divisions of Bouma (1962) (Text-fig. 2.9). The basal C division (basal silt lamina), as identified in a typical fine-grained turbidite unit by Stow and Shanmugam (1980) and Stow (1985) is not present. The bases of several turbidites, here represented by division D, may be identified through Starfish Bed A (Text-fig. 2.9; thin sections 45, 41).

*Tidal rhythmites?* Analyses of the mud laminae thicknesses through the 2.6 m vertical section of channel fill from Church Hill Quarry 1 reveals apparent periodicities showing first and second order cyclicities (Text-fig. 2.13; Appendix 2). First order periodicity shows an alternating thickening and thinning of adjacent mud laminae. Second order periodicity shows a progressive thickening and thinning of groups of laminae. The cyclicities are similar in appearance to those documented as tidal rhythmites in proximal shelf environments, which show diurnal/semi-diurnal inequalities and neap-spring cycles (see Archer 1998; Kvale *et al.* 1999; Stupples 2002). Silt-grade quartz laminae thicknesses have not been analysed due to their relatively consistent thickness of 1-2 mm; no noticeable thickness variation was recorded. Mud laminae thicknesses were subjected to graphical analyses (as in Archer 1998; Kvale *et al.* 1999; Stupples 2001).

Graphically, a saw-tooth pattern is evident, with alternating thick and thin mud layers, suggestive of a semi-diurnal inequality from each pair of subordinate and dominant tidal deposits in a 24-hour period (Text-fig. 2.13A; Kvale *et al.* 1999; Stupples 2002). This may be identified as a first-order cyclicity, following Stupples (2002). A second-order cyclicity of pulses of alternating thickening and thinning laminae, possibly representing fortnightly inequality from neap and spring tides is also evident (Text-fig. 2.13A-B). These pulses can be observed visually through the 2.6 m stratigraphic section at Church Hill (particularly within the lower 1.7 m), as well as from measurements of laminae thicknesses in the form of a sinusoidal curve. The mud laminae do not exhibit perfectly preserved semi-diurnal and fortnightly inequality, as shown in published sequences of sand layers (e.g. Kvale *et al.* 1999; Stupples 2002) and are slightly erratic (as in the erratic cyclicity of mud layers in Stupples 2002, fig. 10). This may be due to a distal, relatively deep-water palaeoenvironmental setting, the





TEXT-FIG. 2.13. Analyses of mud layer thickness through 2.6 m vertical section of channel fill, Church Hill Quarry 1, Leintwardine. A, variability in mud layer thickness, showing sawtooth pattern of alternating thick and thin layers, suggesting a possible diurnal inequality; a possible fortnightly inequality is suggested by alternating greater and smaller peaks representing spring tides (S); neap tides (N) alternate with these. B, five-point moving average plot of mud layer thickness; note the sinusoidal pattern possibly indicative of a fortnightly inequality.



gradual settling of the suspended sediment, along with reworking and possible interference by occasional slumping and storm sedimentation.

Tidal rhythmites are not commonly documented in the literature from relatively deep-water settings, although examples have been recorded (Shanmugam 2003; Berger *et al.* 2004). Archer (1998) stated that tidal rhythmites can only occur in settings dominated by tidal sedimentation. The shelf-break position of the channels may imply relatively deep-water subtidal conditions, that could theoretically pose a problem in inferring that a tidal signature is evident within the channel fill. Smith *et al.* (1990) described subtidal deeper-water tidal rhythmites formed through a 'tidal drawdown' model; whereby high sediment concentrations from an intertidal setting are brought into the deeper water environment via small-scale density-driven underflows. Archer (1998) stated that this model could potentially explain the occurrence of tidal rhythmites from deeper water settings, such as that described by Williams (1991). Tidally controlled up- and down-axis currents in modern submarine canyons are documented in the literature (e.g. Shepard 1976; Shepard *et al.* 1979; Xu *et al.* 2002; Shanmugam 2003); if similar currents operated within the Leintwardine channels then they could have theoretically contributed to the patterns in mud laminae thicknesses observable within the channel fill. According to Greb and Archer (1998) and Choi and Park (2000), certain conditions are required for the preservation of tidal rhythmites that include adequate sediment supply, protected location, and accommodation space. These conditions are likely to have been met within the Leintwardine setting; the channels could have provided accommodation space (Archer 1998) along with periodically being a protected location.

Event sedimentation is likely to have been a complicating factor on any possible tidal signature (Park *et al.* 1995); storm depositional processes must be eliminated or overwhelmed by tidal deposition for sediments to retain a tidal signature (Archer 1998). Major storm events are inferred to have occurred over several stages of the channel infilling (e.g. Starfish Bed A), that are likely to have interfered with any tidal signature. Through Starfish Bed A, the uniform thickening and thinning laminae appear to persist undisturbed, which is curious as this unit is interpreted to represent an event deposit. The reoccurring sequence of shelly horizons through unit 4, may indicate a renewed phase of storm activity, although again the laminae thickness cyclicity appears



to be unaffected. The persistent sequence of scour surfaces through unit 6 also indicate storm activity. Mud layers at this height are relatively thicker and silt-grade laminae are somewhat diminished. Lamina thickness cyclicity is relatively more erratic, suggestive of increased disturbance, caused perhaps by sediment gravity flow.

If the channel fill at Church Hill is inferred to have a tidal signature, then it may be postulated that the entire infilling period was carried out over a relatively short duration (i.e. several years) and not over a period of several million years, as previously estimated by Whitaker (1974) and Pickering *et al.* (1989, p. 154). Even if a tidal signature is illusory and the sedimentation perhaps represents an annual-seasonal control (i.e. with increased sediment input in the winter periods) then the infill duration is still relatively rapid, perhaps over several tens of years.

#### *Comparison with sedimentation in modern submarine canyon settings*

Sedimentation patterns in modern submarine canyon head systems may prove useful analogues for the Leintwardine channels. Both coarse and fine-grained bedload materials and suspended sediments may be trapped within modern canyon settings (May *et al.* 1983). Sedimentation patterns within canyons heads along the California coast show heterogenous mixtures of fine-grained sand and silt along with much organic debris (May *et al.* 1983). Finer-grained channel fill occurs in canyon heads along the east coast of the United States (Shepard and Dill 1966); the lack of coarse-grained sediments has been attributed to the more distal position of these canyon heads (May *et al.* 1983). During periods of storm and high tidal surges, shelly sand and silt may be reworked and carried into the canyon setting, such as in the Wilmington Canyon (May *et al.* 1983). Dominant sediment transport processes identified in canyon heads detached from a nearshore source (as at Leintwardine) are (May *et al.* 1983): (1) shelf edge scour and spillover of sand and silt; (2) reworking and transport of fine sediment by channelised currents; and (3) slumping down canyon walls.

Suspended sediment may also be trapped within these settings, with canyons acting as traps and conduits for these sediments (May *et al.* 1983). Canyons may contain relatively dense nepheloid layers (e.g. Hydrographer, Hudson, Wilmington, and Willapa canyons; Baker 1976; Drake *et al.* 1976). Analysis of particulate



concentrations within the Willipa Submarine Canyon showed that they were up to three times that of the adjacent shelf and slope (Baker 1976).

Channelised currents may occur within canyon settings (Shepard *et al.* 1979), with up-canyon and down-canyon flow rarely ceasing. Flow velocity analysis shows these currents to not exceed 30cm/sec (Shepard *et al.* 1979). Strong down-canyon surges may also occur (velocities generally not exceeding 100cm/sec), attributed to periods of high river discharge, storm surges or exceptionally high tides (Shepard *et al.* 1979).

## DIVERSITY AND ABUNDANCE OF CHANNEL FAUNA

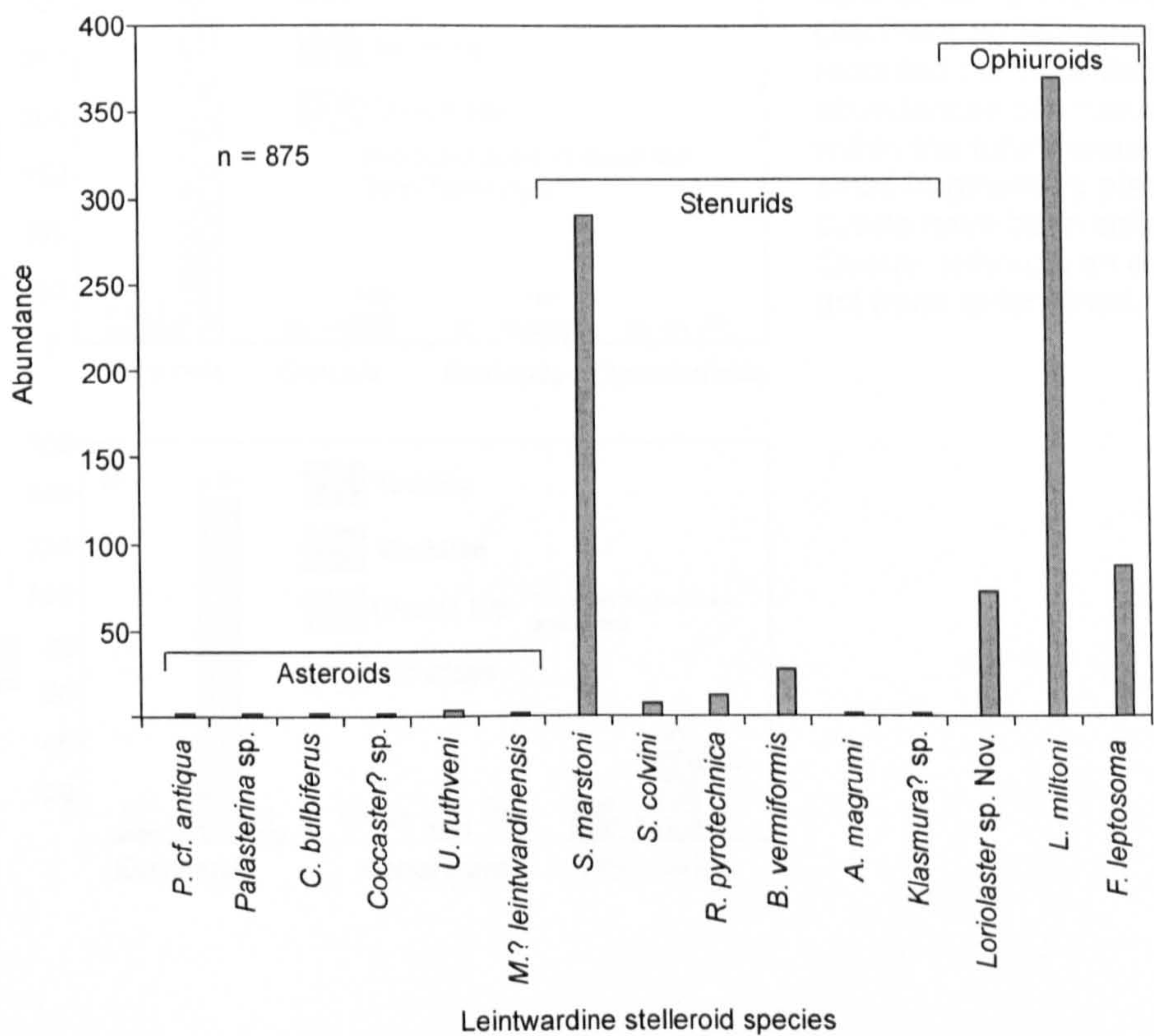
Research on existing museum collections and newly collected, predominantly *in situ* material, has enabled faunal abundances and diversities of the channels to be assessed. Species diversity within the channels is moderate to high; approximately 70 invertebrate species have been recorded (appendices 3-4). The exceptionally preserved unusual invertebrates such as the echinoderms, chelicerates and phyllocarids are relatively abundant.

### *Phylum Echinodermata*

The echinoderms are the most diverse and abundant of the unusual Silurian invertebrate groups, comprising 15 stelleroid taxa (c. 875 specimens, comprising 529 ophiuroids, 338 'stenurids' and eight asteroids), five crinoid taxa (89 specimens), two echinoid taxa (67 specimens) and one ophiocistiid taxon (19 specimens). Fossils are generally complete and articulated. Part and counterpart of specimens have been recovered where possible; in the case of the stelleroids, these show external moulds of the dorsal and ventral morphology. Specimens from museum collections often only consist of one part.

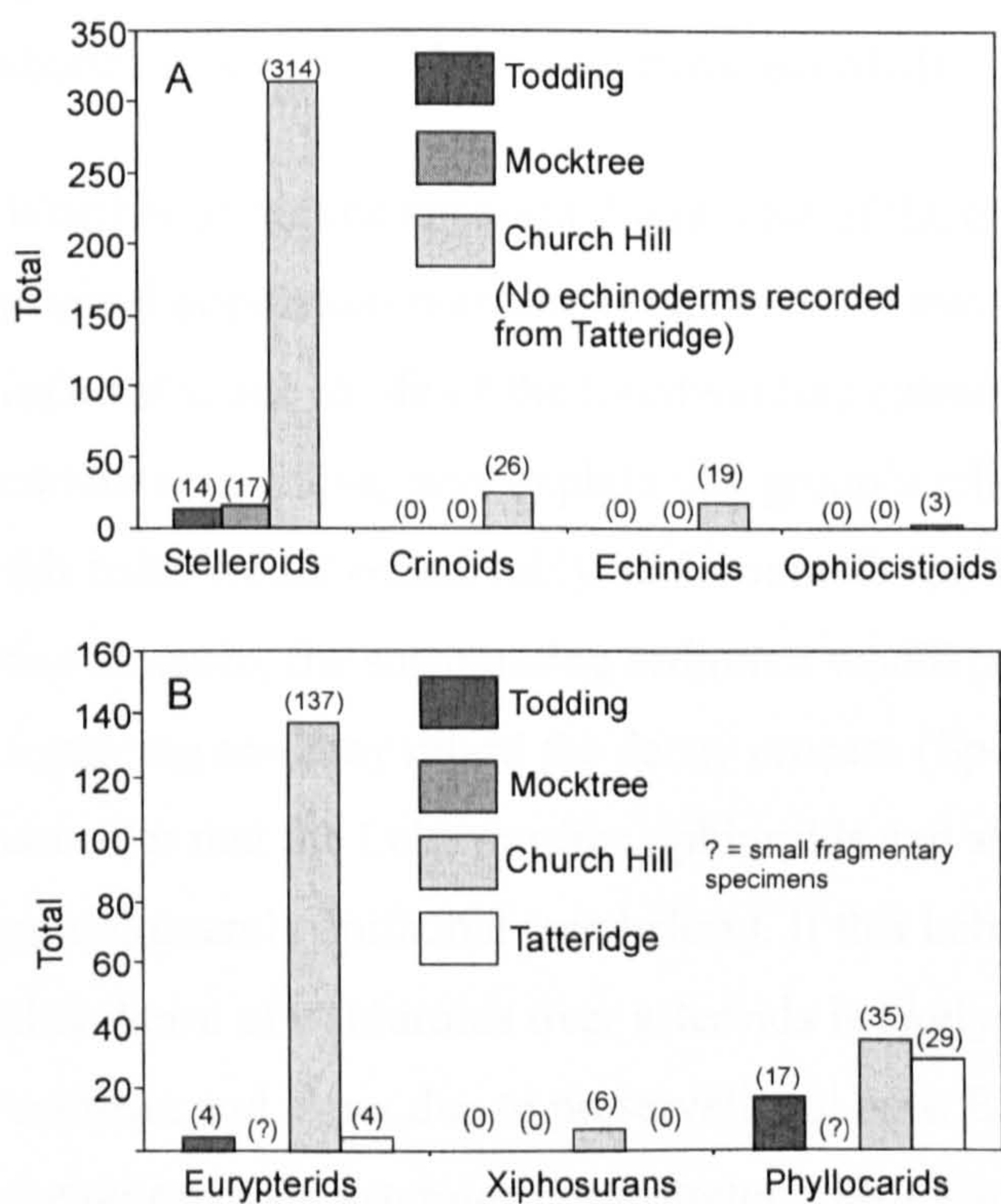
*Stelleroids.* The stelleroids are relatively diverse and abundant (Text-figs 2.14-15; Pls 2.2-10) and comprise three ophiuroid species (*Furcaster leptosoma*, *Lapworthura miltoni*, and *Loriolaster calceatus*), six stenurid taxa (*Antiquaster magrumi*, *Bdellacoma vermiformis*, *Klasmura?* sp., *Rhopalocoma pyrotechnica*, *Sturtzaster colvini*, *Sturtzaster marstoni*) and six asteroid species (*Coccaster bulbiferus*, *Coccaster?* sp., *Mesopalaeaster?* *leintwardensis*, *Palasterina* cf. *antiqua*, *Palasterina*





TEXT-FIG. 2.14. Total stelleroid abundance from Leintwardine. Note the dominance of the ophiuroid species, the abundant *Sturtzaster marstoni* stenurids, and the rare asteroids.





TEXT-FIG. 2.15. A, abundances of echinoderm groups within the fossiliferous channels; no specimens have been recorded from the Tatteridge Channel. B, abundances of unusual arthropod groups within the fossiliferous channels; some small fragmentary pieces of eurypterid cuticle have been collected from Mocktree Quarry, although an exact abundance has not been determined.



sp. and *Urasterella ruthveni*). Ophiuroids dominate, with *L. miltoni* being the most abundant species (c. 370 specimens recorded).

Whether or not the apparent dominance of the ophiuroids over asteroids is indicative of original population numbers is equivocal. Jones (1969) argued that the possible infaunal mode of life of the Leintwardine ophiuroids, based on comparisons with certain extant taxa, may explain this group's relative abundance within the channels, as this habit would conceivably be favourable for fossilisation (see Branstrator 1980). In this scenario, the surrounding sediment would protect the stelleroid skeleton from scattering and may retard the decay process (Spencer and Wright 1966). However, I consider that the Leintwardine ophiuroids and stenurids are likely to have been predominantly epifaunal (see below). If this habit is accepted, then the apparent abundance of ophiuroids over asteroids is likely to represent original population numbers and is not due to preservational bias. Extant ophiuroids are more often gregarious than asteroids (Branstrator 1980) leading to a higher likelihood of multiple ophiuroids occurring in a particular locality; this scenario may be a more plausible explanation for the high abundances of certain stelleroid taxa within the channels.

*Non-stelleroid echinoderms.* The crinoids show a relatively low taxonomic diversity, tentatively comprising five species, and are also low in abundance (Text-fig. 2.15; Pls 2.11-12). All major crinoid groups are represented: the Camarata, Flexibilia, Diparida and Cladida. They are not as abundant as the stelleroids, a feature typical of starfish beds (Brower 1975). Few specimens of each crinoid species have been recorded from existing collections and newly collected material is relatively limited comprising a few specimens of *Clematocrinus quinquepennis*, *Eutaxocrinus maccoyanus*, and *Mastigocrinus bravoniensis* from Church Hill Quarry 1. The most abundant species is *C. quinquepennis*, followed by *E. maccoyanus*. The remaining species (*Gissocrinus ludensis*, *M. bravoniensis*, *Cicerocrinus elegans*, *Dendrocrinus* sp.) are rare. Two species of echinoid, *Echinocystites pomum* and *Palaeodiscus ferox* occur but are relatively rare (Text-fig. 2.15; Pl. 2.13, figs 1-5). Approximately 30 specimens of the former and 40 specimens of the latter have been documented; only 22 echinoid specimens can be provenanced to a particular channel. Ophiocistoids are a very rare component of the fauna (Text-fig. 2.15A; Pl. 2.13, figs 6-9). 17 specimens, from existing museum collections, of *Sollasina woodwardi* have been documented; three



individuals have a Church Hill provenance whilst the remainder cannot be assigned to a specific channel. Only crinoids were recovered during restudy of the channels; echinoid and ophiocistoid specimens studied are from existing collections.

### *Phylum Arthropoda*

The arthropods comprise a relatively diverse and abundant component of the channel fauna (Text-fig. 2.15B). They predominantly consist of semi-articulated or disarticulated specimens of eurypterid and xiphosuran chelicerates, trilobites, ostracods and phyllocarids. The eurypterids are the most abundant of the unusual arthropod groups (193 specimens), followed by the phyllocarids (119 specimens), and xiphosurans (19 specimens). The arthropods, particularly the eurypterids, generally exhibit cuticular preservation.

*Moult-derivation and absolute faunal abundance.* The abundance of semi-articulated or disarticulated material may suggest that many of the specimens are moults; exuviae would be more susceptible to disarticulation than carcasses. Carcasses, however, may have been more susceptible to scavenging (Braddy *et al.* 2002). Ecdysis must be taken into account when dealing with faunal abundance as the presence of multiple moult stages may give a distorted picture of absolute individual numbers; however, according to Speyer and Brett (1988), the absolute number of living individuals (in this case trilobites) and the relative number indicated by moult and carcass remains is not significantly different. Speyer (1991) stated that the remains of an older aged arthropod population are more likely to be represented by carcasses than the younger proportion of the population, as they moult less frequently. He also noted that the differentiation of trilobite carcasses from exuviae is tenuous, adding that articulated to semi-articulated trilobite exuviae may be recognised by diagnostic orientations of the sclerites. Disarticulated components cannot be reliably differentiated (Speyer 1991), and disarticulated arthropod material from the channels could either represent moults or carcasses; splitting of sclerites along sutures, which would signify a moult derivation, have not been discerned.

It is equally problematic in determining whether the eurypterid material represents exuviae or carcasses. Kjellesvig-Waering (1958) stated that the presence of gut structures can distinguish a carcass, although Braddy *et al.* (1995) stated that these



structures cannot be used as the sole criterion as many arthropods shed parts of the gut during ecdysis. Braddy *et al.* (2002) stated that the presence of internal organs (e.g. the endosternite or muscle tissues) can be used to recognise carcasses. Braddy (2001) considered that most occurrences of eurypterids in the fossil record are likely to be exuviae as a single individual moults several times during ontogeny; Clarke and Ruedemann (1912) stated that exuviae are also less susceptible to scavenging than carcasses on the substrate. Both these factors suggest that specimens will show a bias towards being moult-derived. No determinable soft-tissue preservation is recorded on the Leintwardine material; there is therefore no conclusive evidence that any specimens represent carcasses. However, two complicating palaeoecological factors may be taken in account. Caster and Kjellesvig-Waering (1964) stated that eurypterids probably moulted in quiet, current-free environments, given their inferred defenceless state immediately following ecdysis, whilst Braddy (2001) suggested a 'mass-moult-mate' hypothesis in which individuals migrated en masse to near shore areas to moult and mate. If these palaeoecological theories are accepted, then, given the inferred periodically turbulent conditions in the shelf-break channel heads, it may be that some of the Leintwardine eurypterid fossils are outside the normal moulting environment and represent carcasses.

*Eurypterids.* Eurypterid fossils form a relatively abundant component of the arthropod fauna, although many specimens consist of small, undetermined fragments of cuticle. The group comprises at least four species (Text-fig. 2.15B; Pl. 2.14); however, identification of many fossils is problematic due to their semi-articulated preservation. There are two species of pterygotid: *Erettopterus marstoni* and *Pterygotus arcuatus*, although both are rare (three specimens of the former and one of the latter are known). One species of carcosomatid, *Carcinosoma punctatum* is documented; only five specimens can be assigned to the species with certainty, although *Carcinosoma* sp. specimens (e.g. semi-articulated prosomal appendages, fragmented cuticle) are relatively abundant. One eurypterid specimen, very tentatively classified as the slimoniid *Salteropterus longilabium*, has been documented although this is only based on two disarticulated fossils (Kjellesvig-Waering 1961). A prosoma of an undetermined species, not a pterygotid or carcosomatid is also known (Pl. 2.14, fig. 5).



*Xiphosurans.* Synziphosurine xiphosurans are a rare component of the arthropod fauna, comprising 19 specimens and four species: *Limuloides limuloides*, *Bunodes salweyi*, *Pseudoniscus* sp. and *Cyamocephalus loganensis* (Text-fig. 2.15B; Pl. 2.15). Older literature refers to a further species of *Limuloides* occurring (*Limuloides speratus*) although this has recently been considered a junior synonym of *L. limuloides* (Anderson 1998). *L. limuloides* is the most common species, although only five specimens, from museum collections, can be assigned to the Church Hill Channel with any certainty; provenance details of two remarkably complete type specimens of *L. limuloides* are scant, simply referring to a Leintwardine origin. One complete but poorly preserved specimen of *Pseudoniscus* sp., referred to in Eldredge (1974), originates from the Church Hill Channel. One specimen of *C. loganensis* has been tentatively recorded as originating from this locality (Anderson 1998), although again, provenance details are scant. Anderson (1998) argued that the associated collections at Oxford University Museum are of the same lithology as that which originates from Church Hill, and therefore considered it plausible to assume that *C. loganensis* also derives from this locality. A further specimen of *C. loganensis* (the paratype, BMNH I. 25, unlocated) also originates from Leintwardine.

*Phyllocarids.* The phyllocarids comprise one species, *Ceratiocaris* cf. *papilio* (Pl. 2.16). The phyllocarids form a relatively abundant component of the arthropod fauna, and may have been a faunal element of all four fossiliferous channels (Text-fig. 2.15B).

*Other groups.* The trilobites are locally relatively common throughout the channel fill (Pl. 2.17 figs 1, 3-5). Eight species are recorded from the channels, with *Alcymene lawsoni* being the most abundant. Other species recorded are *Calymene neointermedia*, *Platycalymene* sp., *Encrinurus ?stubblefieldi* (e.g. CH183), *Dalmanites myops*, *Dalmanites weaveri*, *Proetus stokesi*, *Proetus latifrons*, and *Warburgella ludlowensis*. Ostracods are relatively abundant, consisting of podocopes, beyrichiaceans (Pl. 2.11, fig. 7; Pl. 2.17, fig. 2), and less commonly, myodocopes such as ‘*Entomis*’ of the older literature (David Siveter, pers. comm. 2004).

### *Phylum Brachiopoda*

Brachiopods form a relatively diverse and abundant group of the total fauna, with 15 species recorded from the channel fill. The most abundant taxa are *Atrypa reticularis*,



*Dayia navicula*, *Leptaena depressa*, *Lingula lata*, *Microsphaeridiorhynchus nucula* and *Sphaerirhynchia wilsoni* (Pl. 2.18). *Orbiculoidea* sp. may also occur, in association with rhynchonellids and *D. navicula* (Pl. 2.18, figs 4-5). Other taxa recorded (e.g. Jones 1969) from the channels are *Chonetes grayi*, *Craniops implicate*, *Isorthis orbicularis*, *Leptostrophia filosa*, *Orbiculoidea rugata*, *Protochonetes ludloviensis*, *Schizocrania striata*, *Shagamella ludloviensis* and *Shaleria ornatella*.

### *Other fauna*

Rare palaeoscolecid worms (five specimens) are recorded in the form of compression fossils of the cuticle of the possible priapulid *Protoscolex latus* from the Church Hill and Todding channels (Pl. 2.19, figs 1-5). A single new, nearly complete specimen was collected from Church Hill Quarry 1 (Pl. 2.19, figs 3-4), although this is not *in situ*. Phosphatised *Sphenothallus longissimus* specimens are locally relatively abundant within the Todding Channel (Pl. 2.19, figs 6-7). *S. longissimus* is rare at Church Hill Quarry 1; one specimen (CH267) has been collected from a loose block. *S. longissimus* is found in association with *P. latus* at Martin's Shell Quarry (e.g. LEIUG 117524; Pl. 2.19, fig. 5).

Other invertebrate groups recorded are rare bryozoans (e.g. *Leptotrypella leintwardinensis*; Pl. 2.17, fig. 6), conulariids (e.g. *Conularia aspersa*, *Conularia subtilis*; Pl. 2.19, figs 8-9), bivalves (e.g. *Cardiola interrupta*, *Fuschella amygdalina*), gastropods (e.g. *Poleumita globosa*), *Tentaculites* sp. (Pl. 2.17, fig. 2), *Spirobis* sp., orthocones and scolecodonts of *Arabellites* sp. and the problematic *Spongarium edwardsii* (Slater 1907; Owen 1962; Whitaker 1962; Jones 1969; Pl. 2.19, fig. 10). *Conularia* sp. has been recorded from the Church Hill, Todding and Mocktree channels; one specimen each from Todding and Mocktree channels were newly collected (MS27, MOCK11; Pl. 2.19, fig. 9), whilst five new specimens have been recovered from the Church Hill channel (CH83, CH264-66). Specimens of *Tentaculites* sp. have been recorded from Church Hill, occurring in fine shelly horizons (e.g. CH170; Pl. 2.17, fig. 2). Graptolites within the channels are monospecific; *Saetograptus leintwardinensis* occurs abundantly, particularly in certain horizons at Church Hill Quarry 1, forming dense assemblages on bedding planes (e.g. CH200-204; Pl. 2.17, figs 7-8). Many of these graptolite-rich horizons do not contain any other fauna and these may represent planktonic blooms. A few disarticulated specimens of



the heterostracan fish *Archaeogonaspis ludensis* have been documented from the Church Hill Channel (e.g. BGS GSM49106; Pl. 2.17, fig. 9; Dineley and Metcalf 1999).

### *Distribution of echinoderms and unusual arthropods between channels*

Of the four channels, the Church Hill Channel is by far the most fossiliferous, yielding the majority of the echinoderms and unusual arthropods (Text-fig. 2.15). Where provenance details are lacking (many museum specimens are simply referred to as originating from Leintwardine), faunal and lithological comparison indicates it is likely that many of these specimens also came from this channel. The next most fossil prolific channel is the Tatteridge Channel, followed by the Mocktree and Todding channels. Two further Leintwardine channels, Marlow and Bagdon, have failed to yield any exceptionally preserved fauna (Whitaker 1962 and pers. obs. based on museum collections).

The echinoderms mostly originate from the Church Hill Channel; stelleroids (ophiuroids and asteroids), crinoids, echinoids and ophiocistioids have all been recorded from this channel (Text-fig. 2.15A). All but one of the documented Leintwardine stelleroid taxa have been recorded from the Church Hill Channel; most of these species are restricted to this channel (eight species, 314 specimens; Text-fig. 2.15; appendices 3-4). A few specimens (17 specimens, comprising *F. leptosoma* and *B. vermiformis*) have also been recorded from the Mocktree Channel (pers. obs.). BGS GSM54892-4, containing three individuals of *B. vermiformis* is recorded as originating from Mocktree. A newly collected assemblage (containing approximately eight poorly preserved individuals of *F. leptosoma*) is also recorded. Most of the remainder of the stelleroids (14 specimens representing two taxa, *B. vermiformis* and *L. miltoni*, based on museum collections and a newly collected specimen) originate from the Todding Channel. Crinoids, echinoids and ophiocistioids have not been recorded from the Todding and Mocktree channels; no echinoderms have been recorded from the Tatteridge Channel (Text-fig. 2.15A; appendices 3-4).

Where channel provenance is known, the eurypterid arthropods predominantly derive from the Church Hill Channel (137 specimens) although a small number have also been recorded from the other fossiliferous channels (Text-fig. 2.15B; appendices 3-4). Four specimens (including a gnathobase and undetermined portion of a prosomal appendage;



SHRCM unregistered, SHRCM G10451) are documented from the Brandon Hill area of the Tatteridge Channel. Four specimens, comprising undetermined cuticle, have been recorded from the Todding Channel; a small amount of fragmentary cuticle has also been recorded from the Mocktree Channel. The rare xiphosuran material has only been recorded from the Church Hill Channel (Text-fig. 2.15B; appendices 3-4).

Phyllocarids have been recorded from all four fossiliferous channels, again being most abundant at Church Hill (35 specimens; Text-fig. 2.15B; appendices 3-4). A relatively large amount also originates from the Brandon Hill area of the Tatteridge Channel (29 specimens). A few specimens have been recorded from the Todding Channel (17 specimens), although three small nearly intact individuals are documented from this channel (Pl. 2.16, figs 1, 3). A small amount of fragmentary material is also recorded from the Mocktree Channel.

### *Provenance of biota within the channels*

Much of the unusual fauna, in particular the echinoderms and bryozoans, is restricted to discrete horizons through the channel fill; the remainder of the fill is relatively barren (Text-fig. 2.5; Marston 1865; Hawkins and Hampton 1927; pers. obs). Re-examination of the Church Hill Channel has revealed that the stelleroids and crinoids occur exclusively within these horizons, although some of the unusual arthropods such as eurypterids and phyllocarids also occur sporadically at other levels (Text-fig. 2.5). The unusual fauna recovered through the channel fill generally occurs entombed within the siltstone body, often at slightly different stratigraphic levels. Shelly brachiopod-rich horizons occur sporadically through the fill (Text-fig. 2.5; Pl. 2.18, figs 1, 5-6). Graptolite-rich horizons, often depleted of other organisms, also occur sporadically through the fill (Pl. 2.17, figs 7-8).

*Todding Channel biota.* Several starfish horizons have been described at Martin's Shell Quarry, originally by Lightbody (1863) and Symonds *in* Woodward (1871), and later by Hawkins and Hampton (1927) and Goldring and Stevenson (1972). Lightbody (1863, p. 370) described the stelleroids as occurring in a bed "three feet thick...that lies conformably on a bed full of *Pentamerus knightii*, at least nine feet thick, and is covered by another *Pentamerus knightii*-bed eighteen inches thick". This description is also given in Symonds *in* Woodward (1871, text-fig. 28; incorrectly described as from Church Hill) in the form of a diagrammatic section. Hawkins and Hampton (1927)



described a starfish bed as occurring in the upper part of the quarry, although they do not mention its exact position. They documented *L. miltoni* specimens from this bed and added that the palaeoscolecoid worm *P. latus* has also been recorded from this quarry. Goldring and Stevenson (1972) collected *B. vermiformis* from two levels within an upper siltstone unit. From their diagrammatic section (1972, text-fig. 3), it is indicated that the upper level occurred at a depth of 220 mm and the lower at about 770 mm. The exact vertical and lateral position of these horizons in relation to the present exposure cannot be ascertained with any certainty, although in both cases they may have been tentatively located.

At Martin's Shell Quarry, a relatively thick unit of siltstone is observable at the base of the present exposure, being a maximum of 0.9 m in vertical thickness (Text-figs 2.6A-B, 2.8). This unit may well represent the lower "three feet thick" unit of Lightbody (1863) and Symonds *in* Woodward (1871); the lower portion of this unit and the underlying boulder bed are likely to have been obscured by backfill, forming the present quarry floor. No stelleroids were recovered from this lower siltstone unit, although small fragments of eurypterid cuticle were noted at a depth of 90 mm from the top of the unit (Pl. 2.14, fig. 2), along with a concentrated horizon, 120-170 mm in depth, of well-preserved phosphatised *Sphenothallus* fossils (Text-figs 2.6B-C, 2.8; Pl. 2.19, fig. 7). Numerous small elongate fossils, several millimetres in length, representing possible bioturbation, were recorded from the same approximate horizon. Conulariids also occur at the same approximate horizon as the *Sphenothallus* specimens (Text-fig. 2.8; Pl. 2.19, figs 7, 9). Overlying this lower siltstone unit is a 0.5 m thick conglomeratic boulder bed (Text-figs 2.6C, 2.8); this equates with the overlying "18 inch thick *Pentamerus* bed" of Lightbody (1863) and Woodward (1871).

A small, fragmentary piece of starfish arm (undet. sp.; MS21) was recovered from the uppermost siltstone unit of the exposure, approximately 5 m from the southerly point of the quarry and 250 mm up from the base of the unit (Text-fig. 2.8). This position approximately equates to the lower starfish level of Goldring and Stevenson (1972). A few phyllocarid fragments (*C. cf. papilio*) and phosphatised *Sphenothallus* specimens were also found in approximately the same lateral and vertical position (e.g. Pl. 2.16, fig. 6; Pl. 2.19, fig. 6). This may well represent one of the upper starfish horizons of Hawkins and Hampton (1927) and Goldring and Stevenson (1972). At Martin's Shell



Quarry, fragmented phyllocarid material (carapaces and telsons) is relatively common throughout the channel fill.

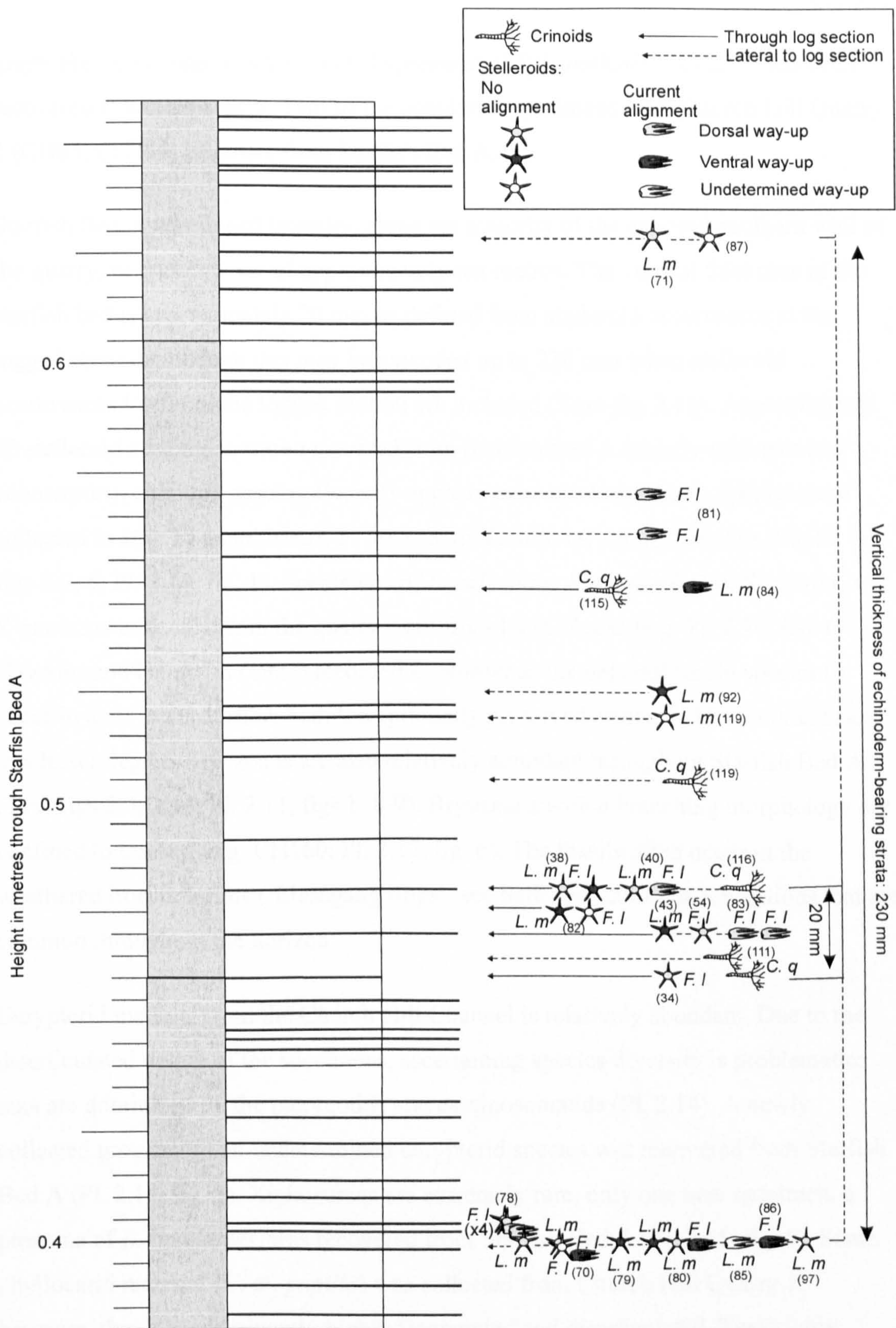
*Mocktree Channel biota.* Marston (1865) described a diverse fauna from Mocktree Quarry, consisting of stelleroids (*B. vermiformis*, *F. leptosoma*), phyllocarids, eurypterids, xiphosurans and *S. edwardsii* specimens. Whitaker (1962) described the site as containing the diverse, characteristic fauna of the other channels, and added that a starfish bed is also present, although he did not specify an exact horizon.

Material recovered from the scree includes fragments of eurypterid and phyllocarid cuticle, stelleroid specimens (*B. vermiformis*, ?*F. leptosoma*; Pl. 2.9, fig. 1) and *S. edwardsii* (Pl. 2.19, fig. 11). Several loose slabs containing shelly brachiopod and trilobite-rich layers have also been recovered.

*Church Hill Channel biota.* Marston (1865) described a diverse range of unusual taxa from Church Hill, mentioning stelleroids, echinoids, xiphosurans, eurypterids and phyllocarids. Hawkins and Hampton (1927) also described the rare faunal elements (stelleroids, echinoids and crinoids); this was the last time before the recent re-excavation that any of the quarries were studied. They described two quarries; the other quarries were noted to be completely overgrown (Hawkins and Hampton 1927). The more southerly of these was described (Hawkins and Hampton 1927, p. 578) as the famous “Starfish Quarry” of Marston; the other was stated to have yielded none of the rare fauna. Allender *et al.* (1960) described ophiuroids (*L. miltoni* and *F. leptosoma*) and crinoids (taxa unspecified) from the locality although these samples were not collected *in situ*; they were collected from scree over the overgrown sites and were described as originating from the highest of the starfish beds. Whitaker’s (1962) study of the Church Hill Channel did not incorporate direct study of these quarries.

At Church Hill Quarry 1, two starfish beds described by Hawkins and Hampton (1927, p. 579) were stated to occur at depths of “5 feet, 3 inches” and “10 feet, 6 inches”, respectively. What may represent the lower of the two, here termed Starfish Bed A, was relocated for this current investigation in 2002, yielding many exceptionally preserved *in situ* fossils (Text-figs 2.1C, 2.4A-B, 2.5, 2.16). Along with stelleroids and crinoids, the bed also includes arthropods (eurypterids, xiphosurans, phyllocarids, ostracods and trilobites), bryozoans, conulariids, *Sphenothallus*, brachiopods and





TEXT-FIG. 2.16. Distribution of *in situ* echinoderms (stelleroids and crinoids) through Starfish Bed A at Quarry 1 of Church Hill. Four general concentrations of stelleroids occur: i) at the base of bed; ii) at a height of 0.46 m; iii) at a height of 0.52 m; iv) at the top of bed. Numbers in brackets refer to specimen numbers. Stelleroid species are dominated by *Furcaster leptosoma* (*F. l*) and *Lapworthura miltoni* (*L. m*). *Bdellacoma vermiformis* (CH262) has also been collected from the starfish bed although the precise height is unknown. Specimens indicated by a dashed line, occur lateral to the logged section. Stelleroids were noted through a vertical thickness of 20 mm in the logged section. The base of the bed, defined by a shelly brachiopod horizon is not shown, although occurs c. 70 mm below the lowermost stelleroid occurrence (at a height of 0.33 m; see text-fig. 2.5).



graptolites. Only one newly collected specimen of *Sphenothallus* (CH267) has been recovered from this quarry. Two of the conulariid specimens from Church Hill Quarry 1 (CH83, CH264) originate from Starfish Bed A.

Starfish Bed A was traced laterally, along the majority of the exposed southern wall of the quarry, over a distance of approximately ten metres. The vertical thickness of the starfish bed is approximately 20 mm as defined from stelleroid occurrences at the logged section, although this may be extended up to 230 mm when stelleroid occurrences lateral to the logged section are included (Text-fig. 2.16). Approximately 50 stelleroid specimens were recovered from Starfish Bed A (mostly with part and counterpart), although species diversity appears to be moderate (three species were collected *in situ*: *B. vermiformis*, *F. leptosoma*, *L. miltoni*; e.g. Pl. 2.6, figs 2-3; Pl. 2.9, figs 2-3, 5; Pl. 2.10, fig. 1). Specimens of *L. calceatus*, *R. pyrotechnica*, *S. colvini*, and *S. marstoni* collected from the quarry were from loose blocks (e.g. Pl. 2.10, figs 6-7). Hawkins and Hampton (1927) recorded *L. miltoni* as the only ophiuroid species to occur in their lower starfish bed. Exceptionally preserved crinoids (15 specimens) and to a lesser degree, bryozoans are also relatively abundant throughout Starfish Bed A (Text-figs 2.5, 2.16; Pl. 2.11, figs 1, 8-9). Bryozoans with a branching morphology are confined to the bed (e.g. CH160; Pl. 2.17, fig. 6). The fossils often occur in the weathered iron-rich rims ('Liesegang rings', see Seilacher 2001) of concretions that are common throughout the horizon.

Eurypterid material from the Church Hill Channel is relatively abundant. Due to the disarticulated nature of the specimens, ascertaining species diversity is problematic; taxa are dominated by the pterygotids and carcosomatids (Pl. 2.14). A newly collected prosoma of an undetermined eurypterid species was recovered from Starfish Bed A (Pl. 2.14, fig. 5). Xiphosurans are extremely rare, only one new specimen, a prosoma of *L. limuloides*, was recovered from Starfish Bed A (Pl. 2.15, fig. 6). Some phyllocarid material (*C. cf. papilio*) was collected from Church Hill Quarry 1; however, this is predominantly highly fragmented and disarticulated. Two highly articulated specimens were recovered: one large specimen, missing the carapace and c. 300 mm in length, and a small complete specimen, 30 mm in length (Pl. 2.16, figs 2, 7). The former was collected from Starfish Bed A.



The upper starfish bed of Hawkins and Hampton (1927) was not re-located, possibly due to the limited lateral exposure at this depth (much of the exposure at this depth consists of backfill). According to Hawkins and Hampton this horizon is more species diverse than the lower one, yielding echinoids and crinoids along with a species of ophiuroid (*Furcaster* sp.). *F. leptosoma* is present in Starfish Bed A; this may have been missed by Hawkins and Hampton. Alternatively, Starfish Bed A may in fact represent their upper horizon, although this does not seem likely. Indeed, there may not be two separate starfish horizons, but only one, displaced by faulting.

The exposed southern margin of the channel at Trippleton Lane is predominantly unfossiliferous, although a small number of *Ceratiocaris* carapaces have been recovered from this location (e.g. LEIUG 56758; CH131). No unusual fauna was recorded from Church Hill Quarry 2; however, this site does contain abundant *S. leintwardinensis* graptolites.

*Tatteridge Channel biota.* The phyllocarids and the eurypterids are the only unusual fauna to have been recorded from the Tatteridge Channel (e.g. Pl. 2.16, fig. 5). However, these are relatively rare. Whitaker (1962) described the channel as being almost devoid of fossils except for *S. leintwardinensis*. No additional fossils were found in the channel in this study.

## BIOSTRATINOMY

Where possible, various biostratinomic and palaeoecological criteria have been assessed in order to determine the transportational history of the fauna. Because of the abundance and intact nature of the echinoderms, along with their benthic habit and dependence upon the substrate, emphasis has been placed on this group, particularly the stelleroids.

### *Phylum Echinodermata*

The Leintwardine echinoderms are often fully articulated and intact; minor disarticulation may occur in certain specimens (e.g. Pls 2.2, 2.11-13). Crinoids are generally not completely intact, although pinnulate taxa do retain the delicate pinnules along the brachia (e.g. *C. quinquepennis*; Pl. 2.11, figs 1-3, 7). The stelleroids are



predominantly fully intact; however, minor disarticulation may occur (e.g. disarticulated arm tips; Pl. 2.2, fig. 3). Delicate spine and pedicellariae articulation of the stelleroids and echinoids is often retained (Pl. 2.2, figs 5-10; Pl. 2.13, fig. 4).

The major controlling factors on disarticulation rate are the degree of decay and scavenging of the connective tissues (Allison 1990). The rate and degree of variation in decay, and therefore disarticulation, may be increased if transport is included and other physio-chemical conditions such as the amount of oxygen, nutrient supply to microbes, water temperature, type of enclosing sediment and microbial community composition, will also have a control on decay (Allison 1990; Kidwell and Baumillar 1990; Donovan 1991). Lower water temperatures may be more effective in retarding organic decomposition than anoxia (Kidwell and Baumillar 1990; LeClair 1993). Experimental taphonomy studies have revealed that the variability in disarticulation rates of extant echinoderm taxa occur both inter- and intraspecifically, although under aerobic conditions complete disarticulation usually takes place within one to two weeks after death (Schäfer 1972; Allison 1990; Kidwell and Baumillar 1990; Donovan 1991; LeClair 1993; Brett *et al.* 1997).

The type and amount of connective tissue joining the plates have a controlling effect on echinoderm disarticulation rate (Lewis 1980). Ligaments are denser and more resistant to decay and scavenging than muscles; therefore, muscular articulations (e.g. echinoid spines, ophiuroid arms and the arms of crinoid taxa from the Early Devonian to present) disarticulate relatively rapidly (Lewis 1980; Ausich and Baumillar 1993). Extant echinoderms possess an epidermis covering the entire endoskeleton (spines and ossicles; Chia and Koss 1994), and this is therefore inferred also for fossil taxa. Providing that decay of the epidermis has not occurred, the endoskeleton should not become abraded and fragmented. A lack of abrasion on the Leintwardine echinoderms indicates that skeletons have not remained unburied on the sediment surface for an extended period of time, which would have allowed the epidermis to decay.

### *Stelleroids*

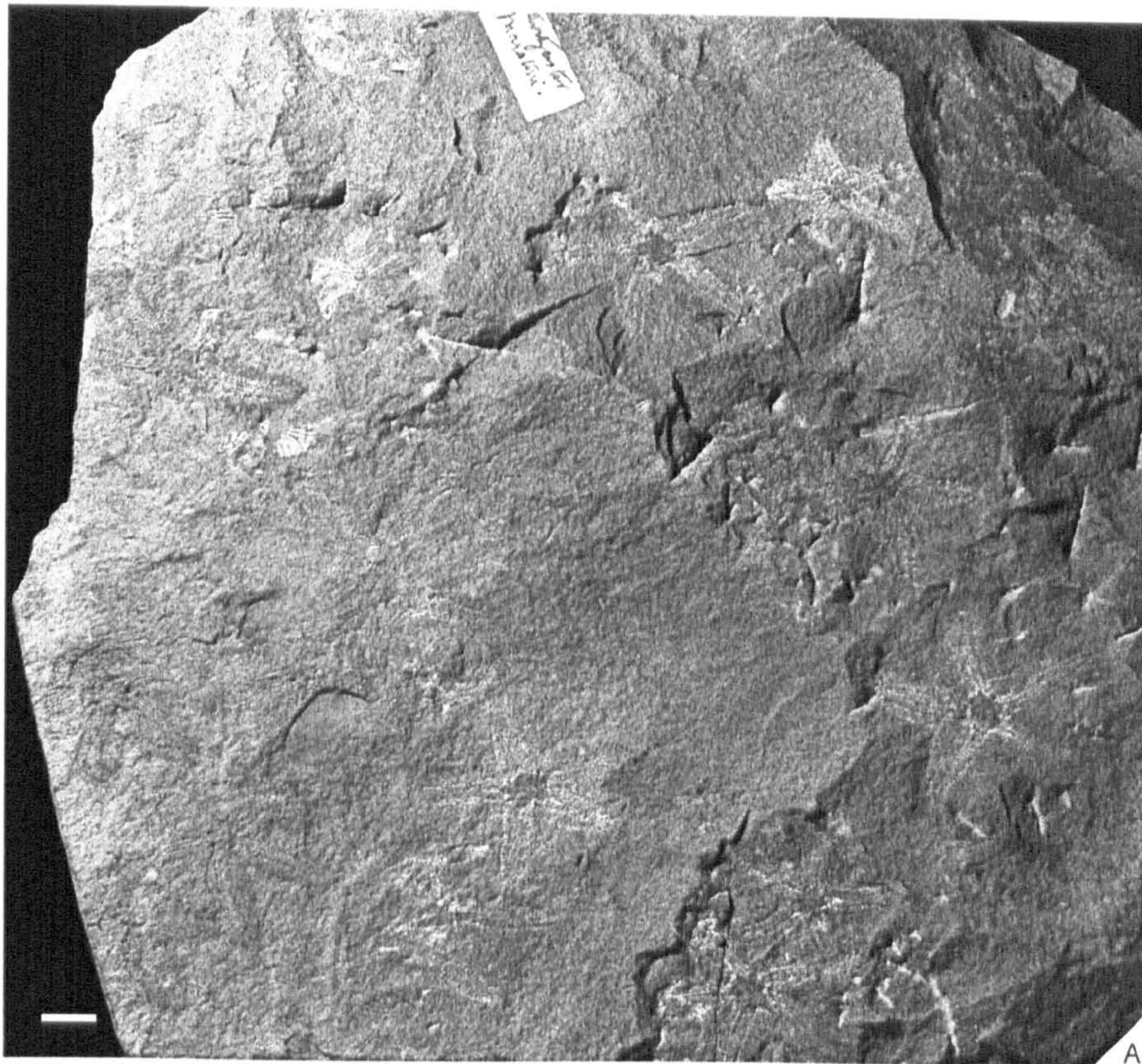
*Population density.* Approximately 875 stelleroid specimens are recorded from the Leintwardine channels, and these probably predominantly originate from the Church Hill Channel (Text-fig. 2.15). The most common species are *L. miltoni* and *S. marstoni*,



with significant numbers of *F. leptosoma* and *L. calceatus* also occurring (Text-fig. 2.14). The majority of *in situ* specimens (*B. vermiformis*, *F. leptosoma*, *L. miltoni*) recovered from Church Hill Quarry 1 occur as solitary individuals, although some slabs with multiple specimens (up to a maximum of five specimens in heterospecific associations) may occur (Pl. 2.7, figs 1, 3-5). A number of slabs from museum collections show assemblages of monospecific taxa, generally on a single bedding plane (e.g. *L. calceatus*, *S. marstoni*; Pls 2.3-4). *L. miltoni*, although the most abundant taxon, occurs either individually or with just a few other individuals (up to five individuals; Pl. 2.2, fig. 1; Pl. 2.5). Slabs with assemblages of *S. marstoni* are more common (e.g. Text-fig. 2.17; Pl. 2.4). OUM C.17040, the largest of the slabs recorded from Leintwardine, has 28 individuals, whilst NMS G1882651627 has 24 specimens. Three slabs with *L. calceatus* assemblages have been recorded (BMNH 38527: 12 individuals; BMNH E 20250: 30 individuals; BGS GSM25351: 26 individuals; Text-fig. 2.18; Pl. 2.3). The latter two exhibit the highest density of ophiuroid assemblages from Leintwardine, with individuals relatively crowded together.

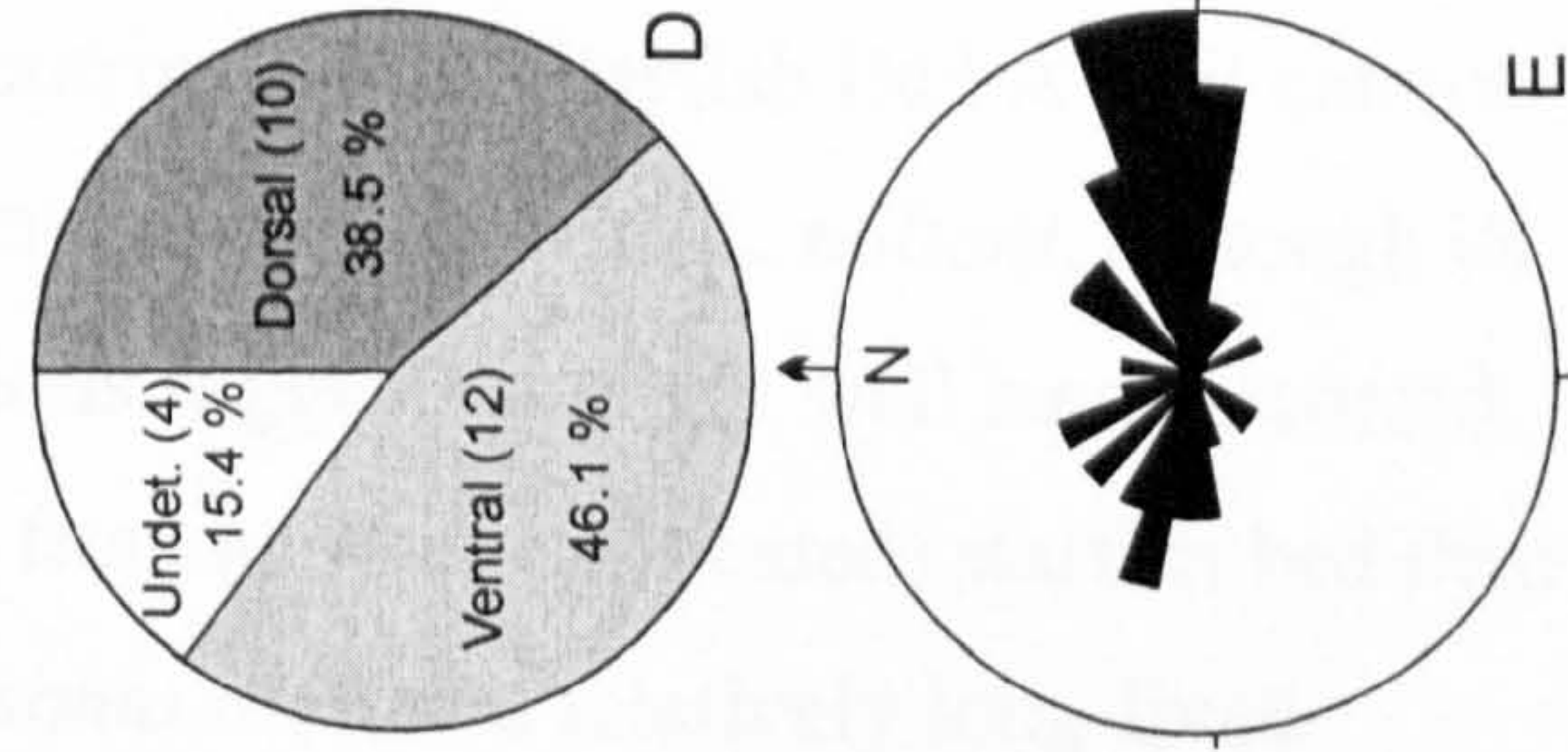
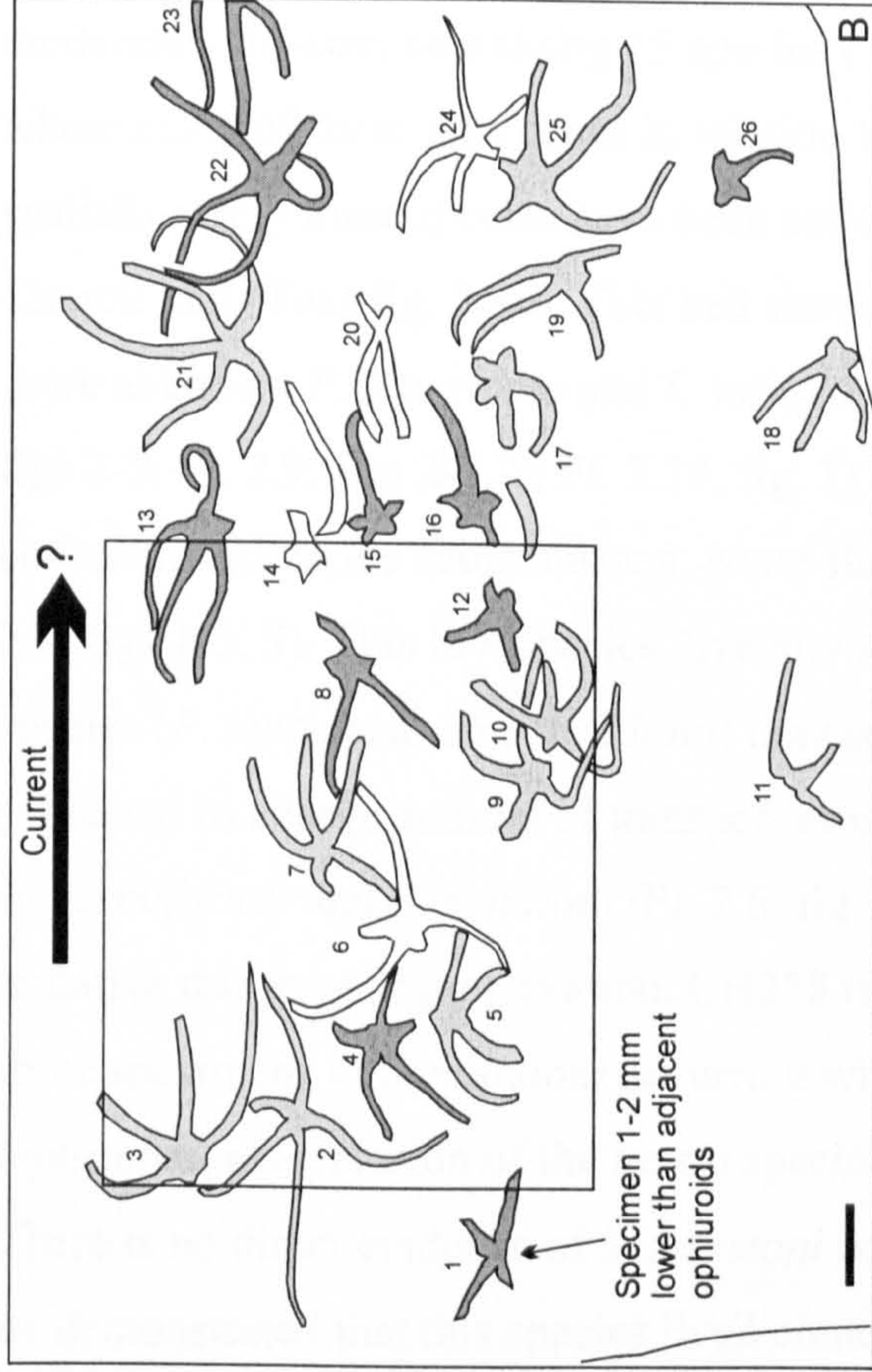
Extant ophiuroids occur either in dense populations or adopt a cryptic habit (Aronson 1989). Modern populations can exhibit high densities with individuals reaching thousands per square metre (Aronson 1989; Aronson and Blake 2001). Populations of *Ophiothrix oerstedii* from a saltwater lake in the Bahamas show a mean density of 432.2/m<sup>2</sup>; this community may have been similar in its ecology, due to a lack of predators, to that of certain Palaeozoic populations (Aronson and Harms 1985). Population densities of the extant British species *Ophiothrix fragilis* can range from 340/m<sup>2</sup> to more than 2000/m<sup>2</sup> (Vevers 1952; Warner and Woodley 1975), whilst *Ophiocomina nigra* shows variable densities ranging from 3/m<sup>2</sup> to 100/m<sup>2</sup> (Wilson *et al.* 1977). Autochthonous fossil brittlestar beds often exhibit high densities, generally in hundreds per square metre (Aronson and Sues 1988). Kesling and Le Vasseur (1971) gave population density estimates of 4500/m<sup>2</sup> for the autochthonous Mississippian *Strataster ohioensis* brittlestar bed of Ohio, whilst Radwański (2002) gave density estimates of 2000/m<sup>2</sup> for the transported Triassic *Asiduriella ludeni* brittlestar bed of Poland. In contrast to many extant populations and fossil autochthonous assemblages, individuals within the Leintwardine assemblages are generally relatively sparsely distributed. The number of slabs recovered showing assemblages are too few to confidently postulate original population densities for *S. marstoni* and *L. calceatus*.





TEXT-FIG. 2.17. *Sturtzaster marstoni* assemblage (NMS G1882651627). Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. A, entire slab with 24 individuals showing a variable way up orientation. B, interpretive drawing of assemblage, showing variable way up orientation of specimens: 13 specimens show ventral-up orientation (light grey); eight show dorsal-up orientation (dark grey); three specimens are undetermined in their orientation (white). Scale bars represent 10 mm.





TEXT-FIG 2.18. *Loricaster calceatus* assemblage BGS GSM25351. Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. A, entire slab, showing c. 26 specimens. B, interpretive drawing of entire assemblage; 12 specimens showing ventral-up orientation (light grey), ten showing dorsal-up orientation (dark grey), four specimens undetermined orientation (white); specimens 2-3 show possible traces of an enlarged body disc; a few specimens (e.g. specimen 1) occur at different vertical levels of 1-2 mm. C, detail of assemblage; area indicated in B. D, graphical representation of relative way up variability in assemblage; numbers in brackets refer to number of specimens. E, orientation of ophiuroid arms in assemblage, showing pronounced alignment, ( $n = 43$ ; segment interval =  $10^\circ$ ); arbitrary 'north' ( $000^\circ$ ) value assigned for slab. Scale bars represent 10 mm.



*Species diversity.* The total stelleroid fauna from the Leintwardine channel deposits is moderately diverse, containing 15 species (Text-fig. 2.14). However, it is not known where many of these taxa occur in relation to one another, both temporally and spatially. Only three species have been collected *in situ*, within Starfish Bed A at Church Hill (Text-fig. 2.16). This bed shows a low species diversity, comprising the more abundant *F. leptosoma* and *L. miltoni* and the rare *B. vermiformis* (e.g. Pl. 2.6, figs 2-3; Pl. 2.9, figs 2-3, 5; Pl. 2.10, fig. 1). Along with field evidence showing their co-occurrence in the same horizon, some slabs show co-occurrence of these taxa (Pl. 2.6, figs 1-3, 5). This low species diversity and the relative abundance of just two species (*F. leptosoma* and *L. miltoni*) may suggest that these specimens have not been subjected to a large amount of transportation. OUM C.17117 shows a co-occurrence of *B. vermiformis* and *S. marstoni* (Pl. 2.6, fig. 6); however, species assignation is tentative due to poor preservation. CH258 (undetermined horizon, not *in situ*) shows three specimens of *S. marstoni* occurring with another ophiuroid species, possibly *F. leptosoma*; preservation of the fourth specimen is poor so identification is tentative. There is no direct evidence of *S. marstoni* occurring within Starfish Bed A so it cannot be demonstrated that this species lived contemporaneously with *L. miltoni*, although its relatively high abundance in museum collections suggests it might well have occurred in the same horizon. If *S. marstoni* originates from another (unlocated) starfish bed then it is possible that *B. vermiformis* and *F. leptosoma* formed a relatively long-lived component of the stelleroid benthos in the area, occurring within both species associations. BMNH E 1479 contains *S. colvini* and *L. miltoni*, indicating that these species lived together (Pl. 2.6, fig. 4).

*A. magrumi*, *Klasmura?* sp., *L. calceatus* and *R. pyrotechnica* have not been found in association with other species. The comparative rarity of *A. magrumi*, *Klasmura?* sp. and *R. pyrotechnica* suggests that they did not live in dense populations; some of these species may have adopted a cryptic habit. It may be that these are rarer because they were transported from a greater distance than the more abundant taxa, but this is countered by their equally high articulation (e.g. *A. magrumi* and *B. vermiformis* retain spine and pedicellariae ornamentation; Pl. 2.2, figs 5-6).

The generally isolated nature of specimens recovered from Starfish Bed A in this study contrasts with specimens in pre-existing collections, which commonly show



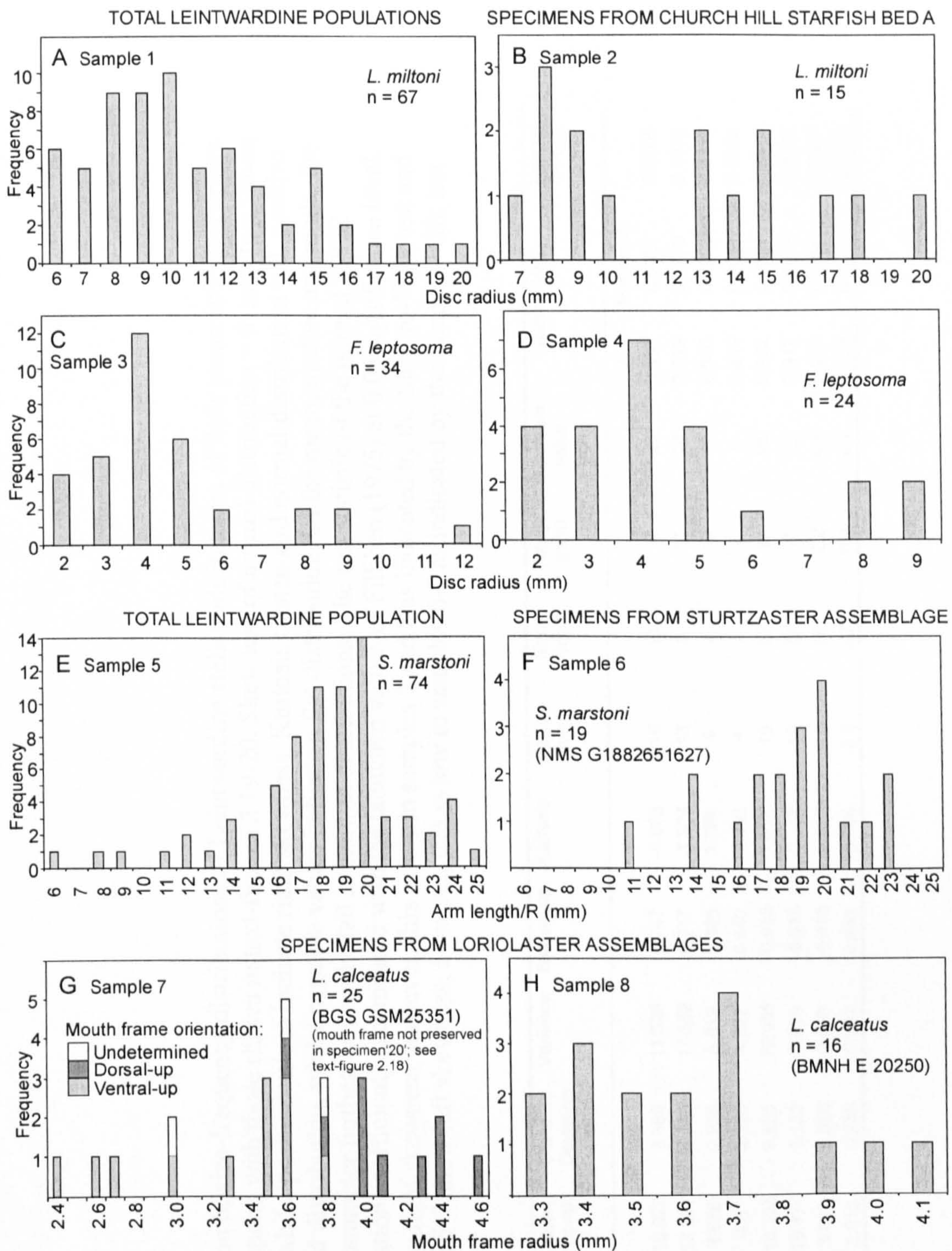
monospecific assemblages. This may purely be an artefact of collecting, although it may indicate that the material represents at least two different starfish beds.

Extant and fossil dense ophiuroid populations tend to show a low species diversity (e.g. Aronson 1989). Extant dense ophiuroid populations are often essentially monospecific, although small numbers of other species may also occur within the area of the brittlestar bed. For example, *O. nigra* may occur as a small component of heterospecific populations with *O. fragilis* (Warner 1971; Wilson *et al.* 1977). Several monospecific dense ophiuroid assemblages have been described in the fossil record; examples include the autochthonous Mississippian *S. ohioensis* assemblage (Kesling and Le Vasseur 1971) and the autochthonous late Eocene *Ophiura hendleri* assemblages (Aronson *et al.* 1997; Blake and Aronson 1998).

The Leintwardine deposits are species diverse, in comparison to documented extant and fossil autochthonous assemblages (e.g. Kesling and Le Vasseur 1971; Aronson *et al.* 1997). The number of species at Leintwardine is comparable with those documented in some allochthonous stelleroid deposits (e.g. 19 species from the Upper Ordovician Lady Burn starfish beds, Girvan, Scotland; Spencer 1914-1940; Donovan *et al.* 2002). This is evidence that, taken as a whole, the stelleroids are not likely to represent autochthonous thanatocoenoses. The diversity of the Leintwardine taxa may imply that multiple discrete populations inhabited the channel head area, possibly adopting specific ecological niches. Based on relative abundance and preservation within assemblages, taxa postulated to have occurred within dense populations are *L. miltoni*, *L. calceatus*, and *S. marstoni*.

*Size-frequency analyses.* Standard parametric descriptors have been used (e.g. following Sokal and Rohlf 1995; Hammer and Harper 2006) to describe the size-frequency distributions of eight samples, representing the more abundant stelleroid species from Leintwardine, *F. leptosoma*, *L. miltoni*, and *S. marstoni* (Text-fig. 2.19; Table 2.1; Appendix 5). Following Hammer and Harper (2006), the Shapiro-Wilk test and normal probability plot were used to test for normality (significance level of 0.05 used;  $H_0$  of Shapiro-Wilk test and normal probability plot correlation coefficient: the sample has been taken from a population with normal distribution; Table 2.1; Text-fig. 2.20).





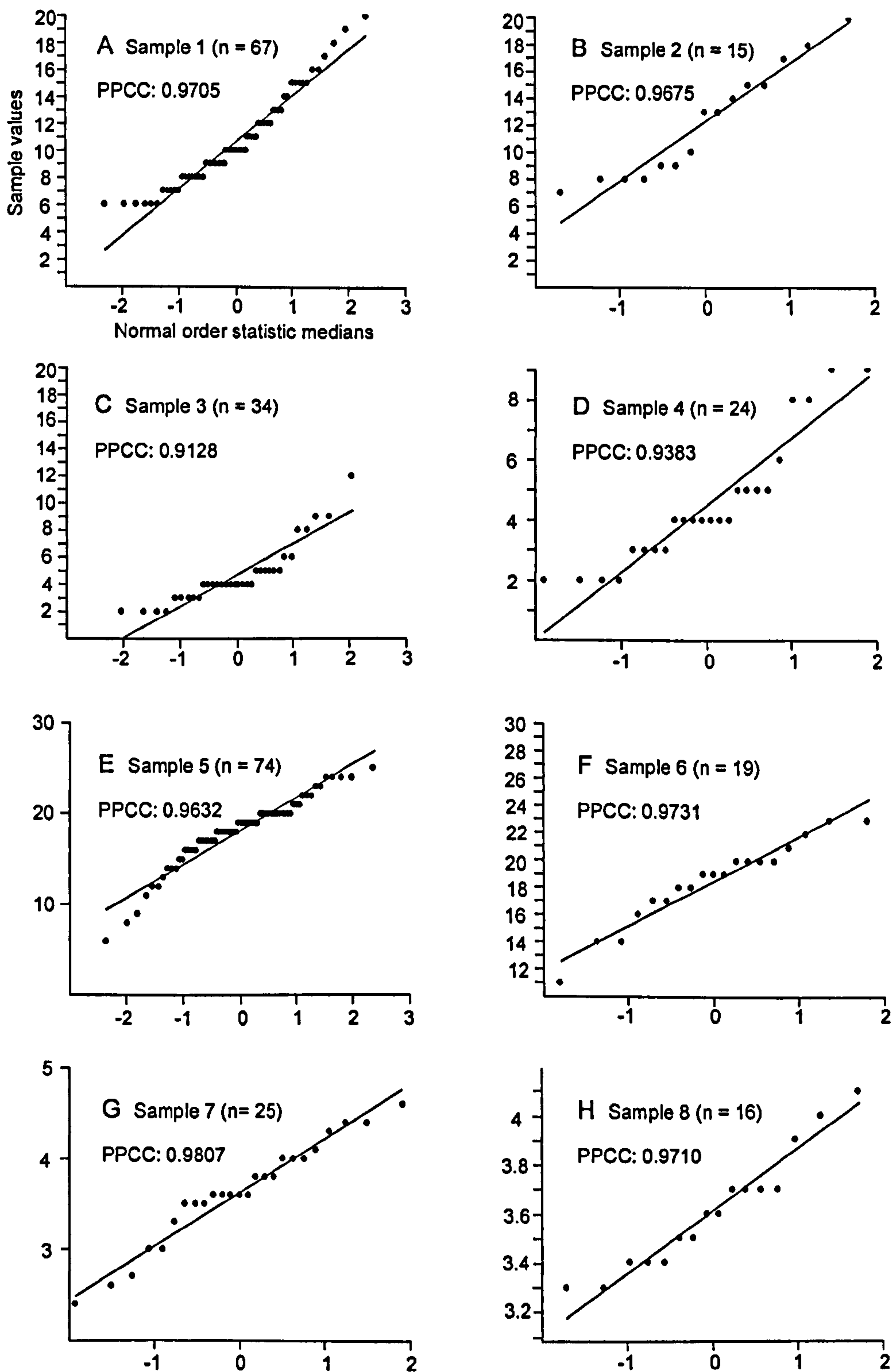
TEXT-FIG. 2.19. Size-frequency analyses of stelleroid specimens from Leintwardine. A, distribution of total population of *L. miltoni*; provenance of specimens in relation to one another is not known; neotype and three specimens from Church Hill Starfish Bed A are included within sample. B, distribution of *L. miltoni* specimens from Church Hill Starfish Bed A. C, distribution of *F. Leptosoma* from Leintwardine. D, distribution of *F. leptosoma* specimens from Church Hill Starfish Bed A. E, distribution of total population of *S. marstoni*; provenance of specimens in relation to one another is not known. F, distribution of *S. marstoni* specimens from assemblage NMS G1882651627. G, distribution of *L. calceatus* specimens from assemblage BGS GSM25351; specimens in dorsal view have a relatively larger mouth frame radius. H, distribution of *L. calceatus* specimens from assemblage BMNH E 20250; Church Hill.



TABLE 2.1. Comparison of size-frequency distributions of Leintwardine stelleroids in terms of their parametric descriptors. Sample numbers correspond with those shown in text-figures 2.19-20. Skewness of normal distribution = 0; negative values indicate left skewness whilst positive values indicate right skewness. Kurtosis of standard normal distribution = 0; positive values indicate a peaked distribution, whilst negative values indicate a flat distribution. Of the mean, median and mode, the mean is generally the parameter furthest out on the tail in skewed distributions. The test statistic of the normal PPCC (probability plot correlation coefficient) is compared with the tabulated values of Filliben (1975) at 0.05 significance level. Samples 1-4 and 8 show right skewness; however, this is low in samples 2 and 8 as indicated by the Shapiro-Wilk test and normal PPCC. Samples 5-7 show left skewness; however, this is low in samples 6-7 as indicated by the Shapiro-Wilk test and normal PPCC.

Sample	n	Mean (mm)	Standard Deviation (mm)	Variance	Skewness	Kurtosis	Median (mm)	Mode (mm)	Range (mm)	Maximum value (mm)	Shapiro-Wilk	Normal PPCC
1	67	10.627	3.366	11.328	0.747	-0.063	10	10	14	20	0.937	0.9705
2	15	12.267	4.166	17.352	0.317	-1.384	13	8	13	20	0.919	0.9675
3	34	4.676	2.239	5.013	1.385	1.766	4	4	10	12	0.840	0.9128
4	24	4.5	2.126	4.522	0.845	-0.346	4	4	7	9	0.869	0.9383
5	74	18.135	3.605	12.995	-0.918	1.452	19	20	19	25	0.932	0.9632
6	19	18.474	3.133	9.819	-0.613	-0.257	19	20	12	23	0.947	0.9731
7	25	3.628	0.566	0.320	-0.410	-0.517	3.6	3.6	2.2	4.6	0.958	0.9807
8	16	3.613	0.239	0.057	0.493	-0.866	3.6	3.7	0.8	4.1	0.933	0.9710





**TEXT-FIG. 2.20.** Normal probability plots for stelleroid samples 1-8, showing departures from normality; refer to text-figure 2.19 for size frequency distributions. The data are relatively well described by a straight line, indicating an affinity to normal distributions. A-D, H, show hollowing upwards (U-shaped) indicating right-skewed data. F-G, show hollowing downwards indicating left-skewed data. Normal probability plot correlation coefficients (PPCC) shown for each sample (also refer to table 2.1). At significance level of 0.05, test statistics of samples 1, 3-5 are less than tabulated values of Filliben (1975);  $H_0$  (normal distribution) is therefore rejected for these samples.



The samples show variable size-frequency distributions with differing amounts of skewness (Text-figs 2.19-2.20; Table 2.1). The distributions of samples 1 and 3, representing the total populations of *L. miltoni* and *F. leptosoma* are right- or positively skewed (Table 2.1; Text-figs 2.19-20A,C). Samples 2 and 4, representing *L. miltoni* and *F. leptosoma* specimens recovered directly from Church Hill Starfish Bed A also show right skewness although they are less defined due to the limited sample numbers available for analysis (Table 2.1; Text-figs 2.19-20B,D). Sample 2 shows a low skewness, which is supported by the Shapiro-Wilk test ( $p = 0.1876$ ; Table 2.1); the  $H_0$  (normal distribution) therefore cannot be rejected at the chosen significance level. This result is in agreement with the normal probability plot (PPCC) correlation coefficient for this sample. The null hypothesis of the Shapiro-Wilk test and normal PPCC is rejected for samples 1, 3 and 4 (Table 2.1).

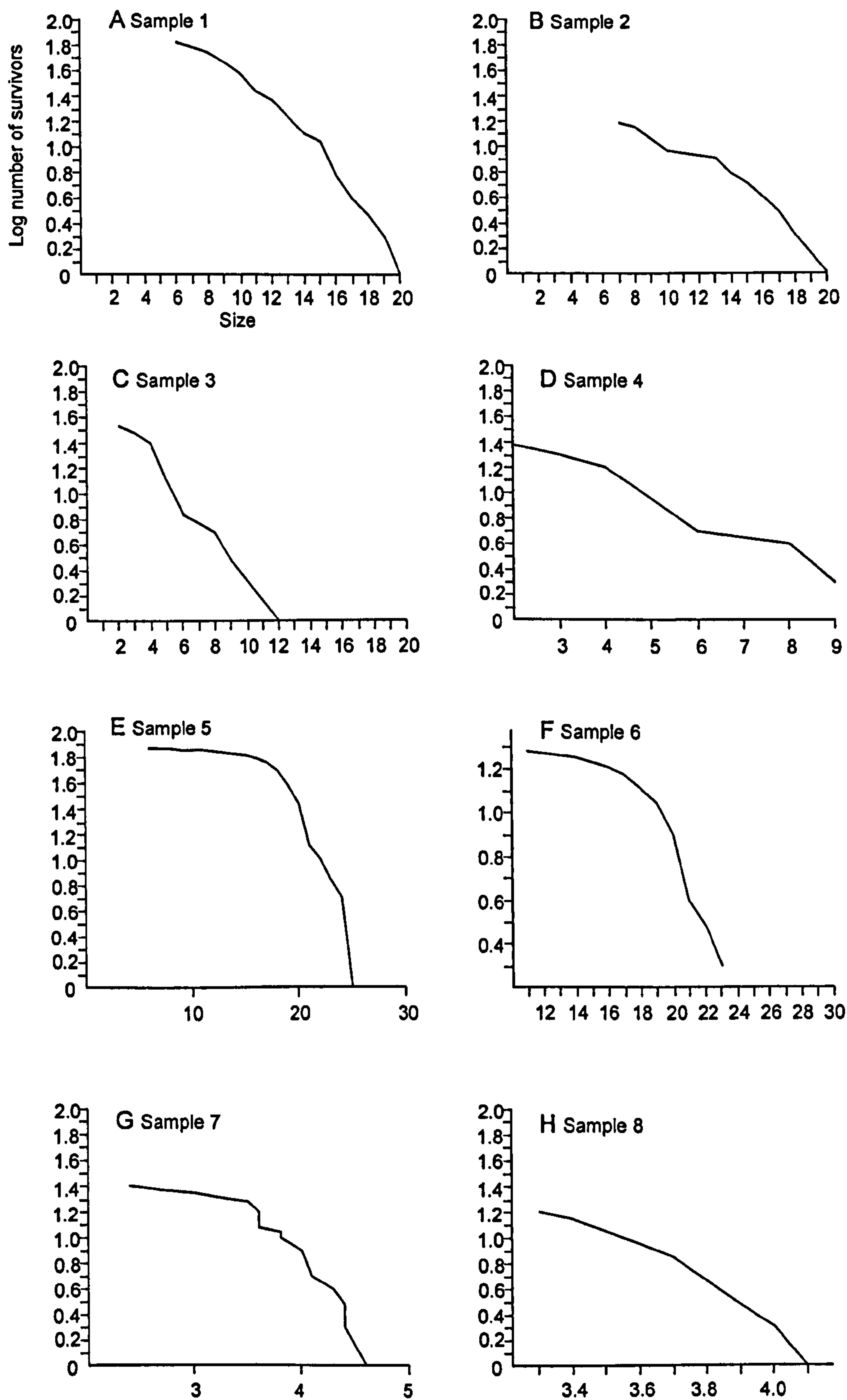
Samples 5 and 6, representing the distributions for the total population and assemblage NMS G188265127 of *S. marstoni*, respectively, show left or negative skewness; very few small specimens have been documented (Table 2.1; Text-figs 2.19-20E-F). The skewness of sample 5 is low. This is supported by the Shapiro-Wilk test and the normal PPCC (Table 2.1); the  $H_0$  (normal distribution) therefore cannot be rejected.

Samples 7 and 8, representing specimens of *L. calceatus* from two assemblages originating from Church Hill show low left and right skewness, respectively (Table 2.1; Text-figs 2.19-20G-H). The  $H_0$  (normal distribution) for the Shapiro-Wilk test and normal PPCC cannot be rejected at the chosen significance level (Table 2.1).

Survivorship curves for samples 1 to 8 were plotted in order to elucidate mortality patterns (Text-fig. 2.21; Appendix 6). As the stelleroids are interpreted to represent census populations (*sensu* Hallam 1972), the 'time-specific' method of construction was employed (following Raup and Stanley 1978, pp. 82-85). The survivorship curves are convex to linear (Type III to Type I, respectively of Deevey 1947), representing an increasing or constant mortality with age, respectively (e.g. Hallam 1972; Brenchley and Harper 1998). Samples 5 to 7 show a pronounced increasing mortality rate (Text-fig. 2.21E-F).

Determining whether or not the size-frequency distributions are indicative of transportation is problematic. Boucot (1953), Fagerstrom (1964), Cummins *et al.*





TEXT-FIG. 2.21. Survivorship curves of stelleroids from Leintwardine; sample numbers correspond to those of text-figures 2.19-20 and table 2.1.



(1986) and Brenchley and Harper (1998, p. 220) argued that normal distributions may be interpreted as being indicative of transportation, whereby the smaller, more juvenile components of the population have been winnowed out by transportation.

Alternatively, size-frequency distributions have been used to interpret population dynamics (e.g. Craig and Hallam 1963; Hallam 1967, 1972; Bitner 2001; Fürsich *et al.* 2001). Craig and Hallam (1963) and Hallam (1967) argued that size-frequency distributions of fossil assemblages are more likely to be reflective of growth and mortality rates rather than size-sorting. Craig and Hallam (1963, text-fig. 8) argued that distributions showing either normal or slightly right skewed forms can be generated for example, by a combination of changing growth rate and constant mortality or constant growth and increasing mortality rate. Constant rates of growth and mortality were inferred to result in strongly right skewed distributions, whilst left skewed distributions could be generated by changing growth and increasing mortality rates (Craig and Hallam 1963, text-fig. 8). Size selective predation may also have an effect on size frequency distribution (Noble and Logan 1981; Cummins *et al.* 1986; Brenchley and Harper 1998, p. 220).

As the Leintwardine stelleroid samples represent census assemblages, it is likely that the size-frequency distributions are relatively reflective of the original population dynamics (e.g. see Levington and Bambach 1970; Kidwell and Bosence 1991). The associated constant to increasing mortality rates (Text-fig. 2.21) support this interpretation. The right skewed distributions of *L. miltoni* and *F. leptosoma* (Text-fig. 2.19A-D) show close to constant mortality rates (Text-fig. 2.21A-D), which following Craig and Hallam (1963) would be expected with these types of distributions. However, these distributions may in part at least, be a direct result of the sedimentation event(s) responsible for preserving the stelleroids, whereby the smaller specimens are likely to have been less able to escape from the sediment burial layer and more susceptible to death. It is unlikely that these distributions reflect purely natural mortality within the populations, as the stelleroid carcasses would be highly susceptible to disarticulation and would not remain exposed on the substrate for any significant length of time (see below).

The left skewed distributions of *S. marstoni* (Text-fig. 2.19E-F) could be representative of the samples original population dynamics, being a result of changing growth rate



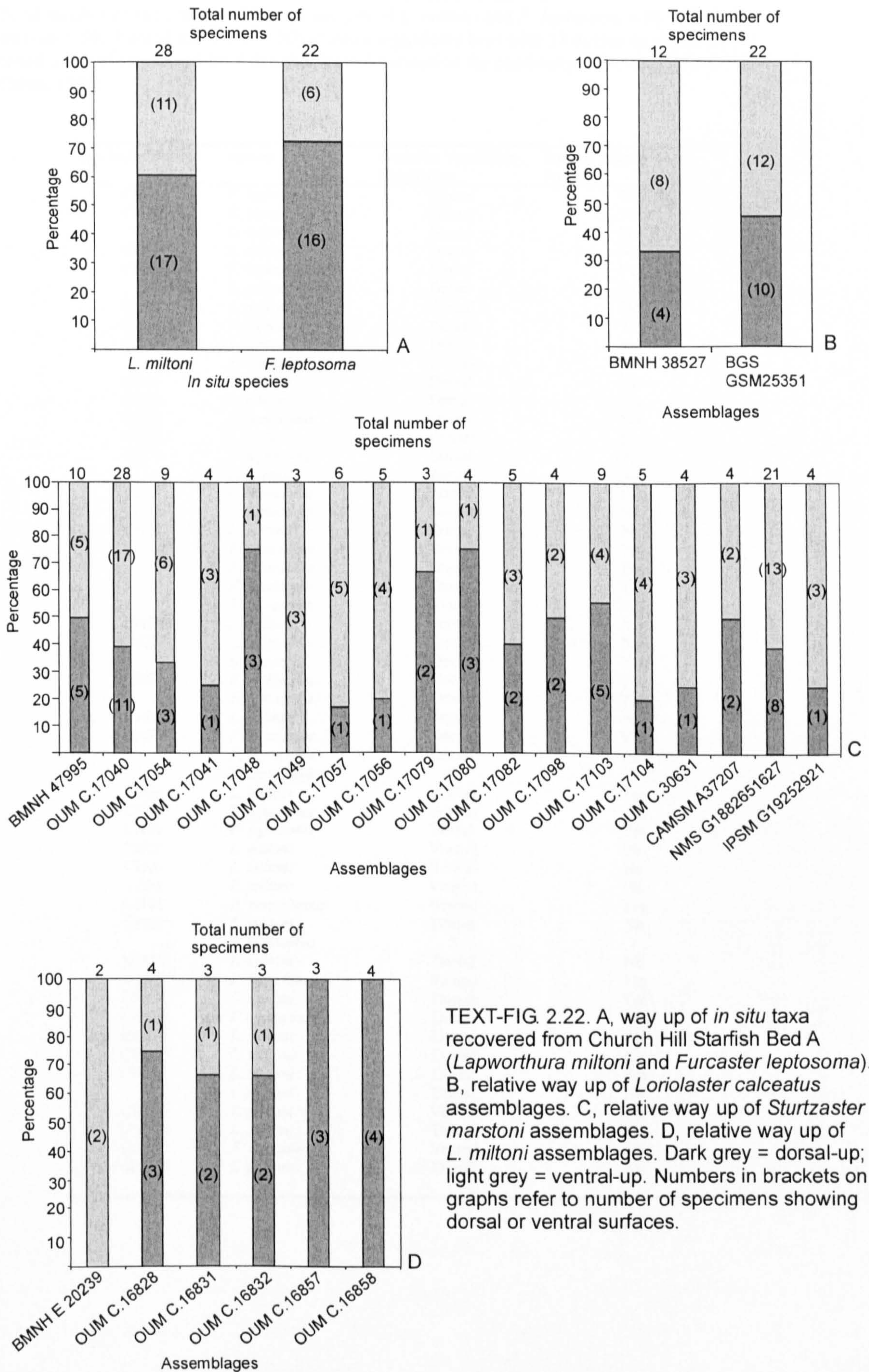
and constantly increasing mortality rate (Text-fig. 2.21E-F; following Craig and Hallam 1963). In this interpretation, the samples are likely to have undergone minimal transportation. Alternatively, these distributions may reflect size-sorting by taphonomic processes, whereby the smaller specimens have been subjected to relatively greater transportation and winnowing. The low left skewed distribution of *L. calceatus*, sample 7, could be a result of a constantly increasing mortality rate (as shown in Text-fig. 2.21G); an alternative possibility is that size sorting has occurred. Sample 8, showing a low right skewness, may be representative of a combination of growth and constant to increasing mortality rate.

In conclusion, the interpretation of the size-frequency distributions is difficult, owing to a range of possible causal factors. A further potential problem is that relatively small sample sizes are present in some cases, which could produce artificial skewing (Jones 1988). However, this is unavoidable owing to the relative rarity of the material sampled. Transportation is not proven by any of the distributions, although based on the associated mortality rates, it is interpreted to be minimal.

*Ichnofossil preservation.* There is a lack of bioturbation associated with the echinoderms; no vertical escape structures or locomotary/ resting traces on the substrate, such as those described by Seilacher (1953), Lewarne (1964), Reineck *et al.* (1968), Sutcliffe (1997), Mángano *et al.* (1999) and Bell (2004), have been recorded. This would be consistent with transportation of the animals as carcasses. Three slabs with undetermined surface bioturbation have been collected from Church Hill Quarry 1 (Text-fig. 2.10); however these are from loose blocks and they do not show any features diagnostic of stelleroid trackways.

*Way up orientation of individuals.* Analysis of the way up of *in situ* specimens of *L. miltoni* and *F. leptosoma* from Starfish Bed A reveals variability, with a bias towards dorsal-up positioning (Text-fig. 2.22A; Table 2.2): 39 % of *L. miltoni* specimens (n = 28) are positioned in a ventral-up orientation; 61 % show a dorsal-up orientation. 27 % of *F. leptosoma* specimens (n = 22) are ventral-up; 73 % are dorsal-up. In order to determine whether this bias is significant, null hypothesis  $H_0$ : the observed and expected frequencies agree (10 ventral, 10 dorsal) is tested using  $\chi^2$  (e.g. following Fowler and Cohen 1990). If these *in situ* specimens are pooled (n = 50), with 33 specimens dorsal-up, then the bias is deemed significant ( $P < 0.05$ ;  $p(H_0) = 0.024$ ;  $\chi^2 =$





TEXT-FIG. 2.22. A, way up of *in situ* taxa recovered from Church Hill Starfish Bed A (*Lapworthura miltoni* and *Furcaster leptosoma*). B, relative way up of *Loriolaster calceatus* assemblages. C, relative way up of *Sturtzaster marstoni* assemblages. D, relative way up of *L. miltoni* assemblages. Dark grey = dorsal-up; light grey = ventral-up. Numbers in brackets on graphs refer to number of specimens showing dorsal or ventral surfaces.



TABLE 2.2. *In situ* stelleroid taxa from Starfish Bed A, Church Hill.  
 Total number of specimens = 53; total number of *L. miltoni* and *F. leptosoma* with determined way-up = 50. Pooled sample (n = 50) shows a significant bias with 33 dorsal-up specimens, tested using  $\chi^2$  (corrected for 1 df using Yates' correction for continuity, following Fowler and Cohen 1990).

Specimen Number	Species	Dorsal or Ventral Up Orientation	Current Alignment Present?
CH34	<i>F. leptosoma</i>	?Dorsal	No
CH38	<i>F. leptosoma</i>	Ventral	No
	<i>L. miltoni</i>	Dorsal	No
CH39	<i>L. miltoni</i>	Dorsal	No
CH40	<i>F. leptosoma</i>	Dorsal	Yes
	<i>L. miltoni</i>	Dorsal	No
CH43	<i>L. miltoni</i>	Ventral	No
CH54	<i>F. leptosoma</i>	Dorsal	Yes
CH70	<i>L. miltoni</i>	Dorsal	No
	<i>F. leptosoma</i>	Ventral	Yes
CH71	<i>L. miltoni</i>	Dorsal	No
CH72	<i>L. miltoni</i>	Dorsal	No
CH73	<i>F. leptosoma</i>	Dorsal	No
CH74	<i>L. miltoni</i>	Ventral	No
CH75	<i>F. leptosoma</i>	Dorsal	Yes
	<i>L. miltoni</i>	Ventral	No
CH76	<i>F. leptosoma</i>	Ventral	Yes
CH77	<i>F. leptosoma</i>	Dorsal	No
CH78	<i>L. miltoni</i>	Dorsal	No
	<i>F. leptosoma</i>	Dorsal	Yes
	<i>F. leptosoma</i>	Dorsal	Yes
	<i>F. leptosoma</i>	Dorsal	Yes
	<i>F. leptosoma</i>	?Dorsal	Yes
CH79	<i>L. miltoni</i>	Ventral	No
CH80	<i>L. miltoni</i>	Ventral	No
	<i>L. miltoni</i>	Dorsal	No
CH81	<i>F. leptosoma</i>	Dorsal	Yes
	<i>F. leptosoma</i>	Dorsal	Yes
CH82	<i>L. miltoni</i>	Ventral	No
CH83	<i>F. leptosoma</i>	Dorsal	Yes
	<i>F. leptosoma</i>	Dorsal	No
	<i>F. leptosoma</i>	?	?
CH84	<i>L. miltoni</i>	Ventral	Yes
CH86	<i>F. leptosoma</i>	Ventral	Yes
CH88	<i>F. leptosoma</i>	Dorsal	Yes
CH89	<i>L. miltoni</i>	Ventral	No
CH90	<i>L. miltoni</i>	Ventral	No
CH92	<i>L. miltoni</i>	Ventral	No
CH94	<i>B. vermiformis</i>	Ventral	Yes
CH95	<i>L. miltoni</i>	Dorsal	No
	<i>F. leptosoma</i>	?	?
CH97	<i>L. miltoni</i>	Dorsal	No
CH98	<i>F. leptosoma</i>	Ventral	Yes
CH100	<i>L. miltoni</i>	Dorsal	Yes
CH102	<i>F. leptosoma</i>	Dorsal	No
CH250	<i>L. miltoni</i>	Dorsal	Yes
CH251	<i>L. miltoni</i>	Dorsal	No
CH252	<i>L. miltoni</i>	Dorsal	Yes
	<i>L. miltoni</i>	Dorsal	No
CH253	<i>L. miltoni</i>	Ventral	No
CH254	<i>L. miltoni</i>	Dorsal	No
CH257	<i>F. leptosoma</i>	Ventral	No
CH263	<i>L. miltoni</i>	Dorsal	No



5.14; Table 2.2). This may indicate that some specimens have been preserved in life position, whilst others may have been subjected to transportation, and either settled in a dorsal-up orientation or overturned themselves, if still alive, into their life position. The dorsal surface of the body-disc and arms is likely to have been relatively convex, with the ventral surface relatively flattened; it is therefore conceivable that a dorsal-upward position would show a greater stability than ventral-upward positioning. However, Radwański (2002) inferred that for assemblages of the Triassic ophiuroid *Aspiduriella ludeni*, specimens may have preferentially settled in a ventral-up orientation with the heavier disc-bearing portion pointing downwards.

The way up of specimens from pre-existing collections cannot be ascertained, as the way up of the slabs cannot be determined. Goldring and Stephenson (1972) described certain specimens in museum collections in terms of way up, stating that this could be attained by using graded lamination within some slabs; I have not been able to determine any sedimentary way-up indicators (e.g. grading or cross lamination) in hand specimen and have thus relied on relative way-up amongst museum slabs showing assemblages (Text-fig. 2.22B-D; Appendix 7). Goldring and Stephenson (1972) described an assemblage of *L. calceatus* (BMNH E 20250, described therein as *F. leptosoma*) as showing different way up orientations of specimens in relation to one another (showing dorsal or ventral surface, although they did not comment on actual numbers in each orientation), and a specimen of *L. miltoni* (BMNH E 20235) as showing ventral surface upwards. Analysis of assemblages of *S. marstoni*, *L. calceatus* and *L. miltoni* reveals a variability in relative way up orientation in each case (Text-figs 2.17-18, 2.22B-D; Pls 2.3-5). It cannot be determined whether these represent original dorsal or ventral-up positions. Most large assemblages show an approximately even distribution in relative way up (Text-fig 2.22B-C; Pls 2.3-4). The two largest assemblages of *S. marstoni* (OUM C.17040, 28 specimens; NMS G1882651627, 21 specimens) show an approximately 60% bias to a particular way up (Text-figs 2.17, 2.22C). The largest *L. calceatus* assemblage where relative way up can be determined (BGS GSM25351, 22 specimens) shows 55% in one way up (Text-figs 2.18, 2.22B). Relative way up in the smaller *L. calceatus* assemblage (BMNH 38527, 12 specimens) shows a more pronounced bias with 73% in one way up. Relative way up through the smaller *S. marstoni* assemblages (with three to nine specimens) shows a variability in the amount of bias. *L. miltoni* assemblages, which are all relatively small, with a



maximum of four specimens in an assemblage, tend to show a bias towards one particular way up (Text-fig. 2.22D; Pl. 2.5).

If the dominant orientations are assigned to be dorsal-up, then it may be that these assemblages are essentially autochthonous, with flipping over of a few specimens. Hamman and Schmincke (1986) commented on the occurrence of stelleroid individuals in ventral-up positioning in autochthonous thanatocoenoses described in the literature (e.g. Rosenkranz 1971; Meyer 1984), and suggested that this may be due to dying and injured individuals turning on their backs during the death struggle. They added that this has been observed in extant specimens, citing Schäfer's (1972) description of the asteroid *Solaster papposus* as an example.

Alternatively, the specimens in the assemblages may have been transported, and deposited haphazardly, with many settling in a particular hydrodynamically stable orientation. If this particular settling orientation was mouth-up, then live specimens may have been able to overturn themselves to their life position (as suggested for assemblages of *Aspiduriella ludeni* by Radwański 2002). Thus, ventral-up specimens could indicate that individuals were transported dead, whilst some dorsal-up specimens could indicate live transportation (Radwański 2002). If the way up biases are taken to represent a dominant ventral-up positioning then this could suggest that the majority of specimens were transported dead.

*Degree of disarticulation, fragmentation and abrasion.* The rare Leintwardine asteroid specimens (*C. bulbiferus*, *M.? leintwardensis*, *P. cf. antiqua*, and *U. ruthveni*) are highly articulated (Pl. 2.7; figs 1-3). The ophiuroids and stenurids are predominantly fully articulated (e.g. Pl. 2.2, figs 1, 4; Pls 2.7-8), although disarticulated arm portions may occur in abundant, relatively long-armed ophiuroid taxa such as *L. miltoni* (Pl. 2.2, fig. 3). Spine articulation is preserved (e.g. in *F. leptosoma*, *L. miltoni*, *R. pyrotechnica* and *S. colvini*; Pl. 2.2, figs 7-10); *A. magrumi* and *B. vermiformis* retain pedicellariae (Pl. 2.2, figs 5-6). Enlarged, possibly membranous body discs are preserved in some specimens of *L. calceatus* (e.g. Pl. 2.2, fig. 2). Some specimens show slight disturbance of their ossicles (e.g. *P. cf. antiqua*, *M.? leintwardensis*; Pl. 2.7, figs 1, 3).

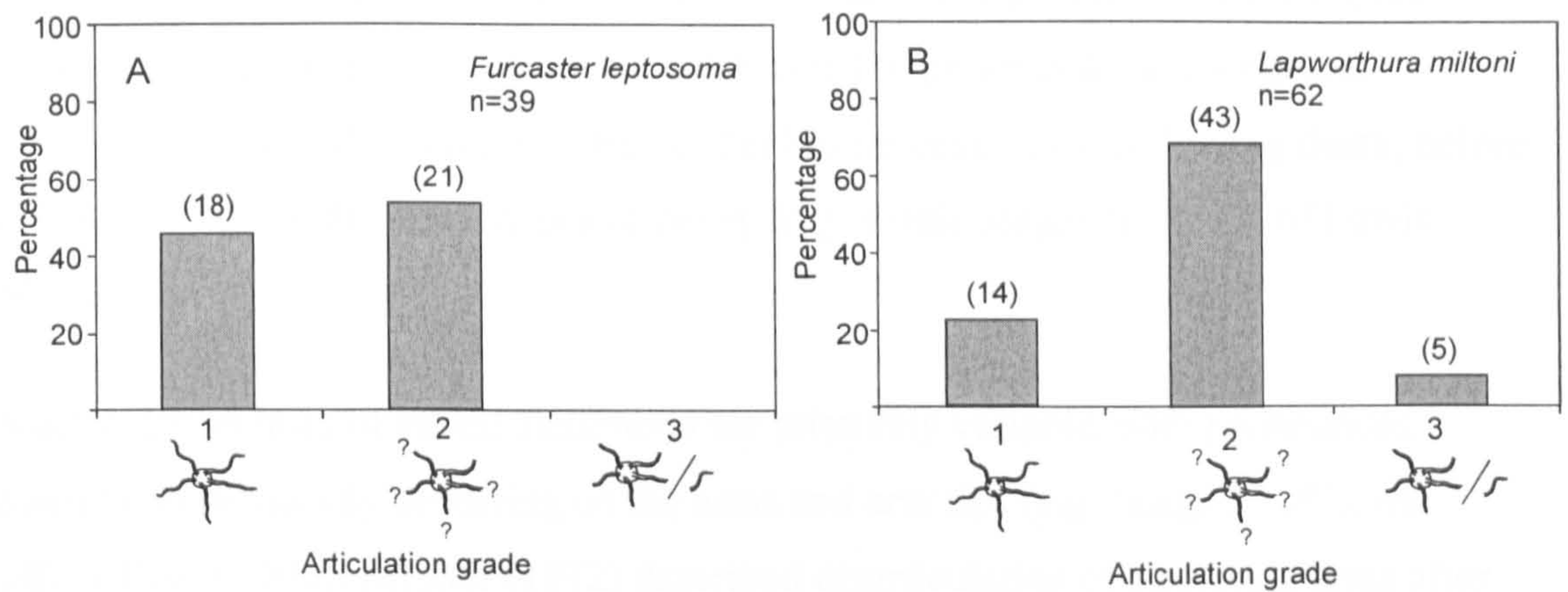
Fragmentation is sometimes evident in the spines of the Leintwardine stelleroids, with only the proximal portions of the structures being preserved with the test (Pl. 2.2, fig. 6). Abrasion is not evident.



A semi-quantitative scale (e.g. Mayor *et al.* 1989; Kidwell and Baumillar 1990; Taylor and Brett 1996; Baumillar 2003) has been used to assess the degree of disarticulation in the more abundant Leintwardine ophiuroids (*F. leptosoma*, *L. miltoni*; Text-fig. 2.23; Appendix 8). All newly collected specimens and a proportion of specimens from museum collections have been used. Stelleroids showing robust thickened arms (e.g. *S. marstoni*) has not been selected as they consistently show full articulation. Specimens preserved in their entirety, retaining the arm tips, are designated as ‘articulation grade 1’ (e.g. Pl. 2.8, figs 2, 4). It is not possible to determine if the full arm lengths are intact in many fossils as they are either preserved on the edge of slabs or the arm tips are preserved on slightly different stratigraphic levels (c. 1-2 mm) to the disc and proximal arms. Specimens which show this ambiguous preservation are designated as ‘articulation grade 2’ (e.g. Pl. 2.6, figs 1-2). In many specimens assigned to this state it is highly probable that full articulation is retained. Specimens which either have missing arm tips or consist of portions of the stelleroid arm, entirely disarticulated from the remainder of the body are assigned to ‘articulation grade 3’ (Pl. 2.2, fig. 3). Articulation grades 1 and 2 are analogous to ‘taphonomic grade A’ of Brandt (1989; later modified for echinoderms by Brett *et al.* 1997). Articulation grade 3 equates to ‘taphonomic grade B’ of these authors.

Articulation of the endoskeletons does not preclude transportation as experimental studies on the biostratinomy of extant taxa of other echinoderm groups (e.g. echinoids and crinoids; Kidwell and Baumillar 1990; Baumillar 2003) have shown that living or recently deceased echinoderms can be subjected to considerable transportation with minor disarticulation, providing that the process occurs before the decay of connective tissues has progressed (e.g. into ‘stage 3’ of Lewis 1987). Large accumulations of dead or dying stelleroids, washed up onto present day shorelines after storm activity have been observed (e.g. see Lawrence 1996); a lack of disarticulation in these transported stelleroids is apparent (e.g. at The Wash, UK; R. Clements, pers. comm. 2003). However, published observations do not comment on the extent of articulation of washed up ophiuroids subjected to mass mortality, such as *O. fragilis* and *Ophiura texturata* (e.g. Crisp 1964; Moyse and Nelson-Smith 1964; Perkins and Williams 1964). The low density of echinoderm stereom (Lewis 1980; Brett *et al.* 1997) would assist in carcasses being relatively easily transported. However, the high degree of articulation preserved in the Leintwardine stelleroids, particularly of delicate skeletal





TEXT-FIG. 2.23. Semi-quantitative analyses of ophiuroid articulation from Leintwardine. Specimens that are fully intact are designated as 'articulation grade 1'. Specimens where the degree of articulation is unclear are designated as 'articulation grade 2'. Specimens that comprise disarticulated arm tips are designated as 'articulation grade 3'. Numbers in brackets refer to number of specimens. A, *Lapworthura miltoni*. B, *Furcaster leptosoma*.



elements with decay-susceptible muscular articulations (e.g. spines and arms), may suggest that the carcasses have not been subjected to prolonged transportation; movement is inferred to have occurred either before death, or if following death, before the onset or during the early stages of decay (e.g. within stages '1' or '2' of Lewis 1987).

Disarticulation rates of extant stelleroids are relatively variable, with pronounced disarticulation initially occurring on the arms and arm tips (e.g. 'stage 2' of Lewis 1987; Allison 1990). Schäfer (1972) described disarticulation of ophiuroid arms after 15 hours whilst Lewis (1986) documented complete ophiuroid disarticulation as occurring over a period of several weeks. Schäfer (1972) described complete disarticulation of the asteroid *Asterias rubens* after 17 days whilst LeClair (1993) documented a decay threshold being reached between 6 and 9 days after death of the asteroid *Solaster stimpsoni*. Allison (1990) documented partial to complete disarticulation for three extant asteroid species after 48 days; the ophiuroid *Ophiura sarsi* showed disarticulation of arm tips after 48 days. However, these observations were based on 'closed-system' experiments and the relatively longer decay and disarticulation rates may be attributed to a lack of agitation, and a possible accumulation of toxic metabolites that reduced the rate of decay (Allison 1990). These generally rapid rates of decay and disarticulation are evidence that the Leintwardine stelleroids were buried relatively soon after death.

The high level of articulation, and predominance of undamaged spines and pedicellariae may suggest that many specimens including those assigned to articulation grades 1 and possibly 2, were subjected to minor transportation. Whereas the degree of articulation of the asteroids and stenurids, which have relatively robust, thickened arms is not necessarily indicative of zero transport, the articulated Leintwardine ophiuroids exhibiting slender, flexible arms (e.g. *F. leptosoma*, *L. calceatus*) may suggest minor transport, as in common with extant ophiuroids their arms are likely to have been relatively susceptible to disarticulation (Ausich 2001, p. 180). Specimens assigned to articulation grade 3, showing some disarticulation, are interpreted to have been subjected to increased transport and/or transported after decay was underway.

The intact, articulated and unabraded nature of most Leintwardine specimens is evidence that mortality, transportation and burial predominantly occurred over a

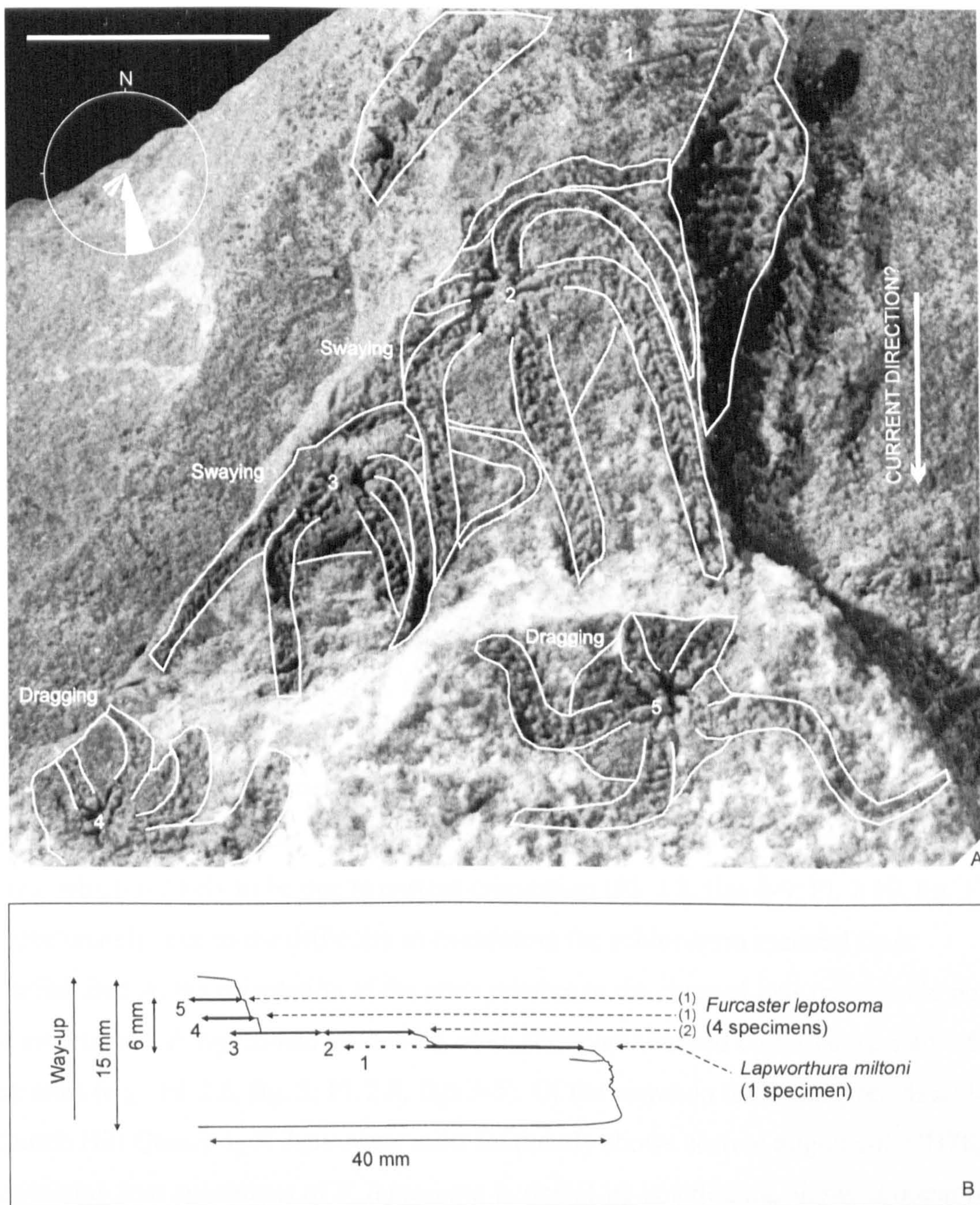


relatively short time span. Specimens showing minor disturbance of their ossicles, presumably indicative of current orientation, suggest that partial decay of their connective tissue occurred before burial. Provided that specimens were transported alive, or the period between death and transport was relatively short, then individuals may have been subjected to considerable transportation, possibly within a sediment-laden current, with minimal damage (as noted in experimental studies on extant crinoids by Baumiller 2003). Along with indicating rapid burial, the lack of abrasion may also be indicative of an offshore, relatively low energy muddy setting (Brett and Baird 1986).

*Arm position.* In order to analysis arm position in the Leintwardine stelleroids, the arms of specimens showing alignment in certain assemblages have been plotted on rose plots (Text-figs 2.18, 2.24; Appendix 9). Determination of the azimuthal orientation is often problematic, as the arms do not necessarily point in a down-current direction (see below). An alternative potential method of quantifying arm orientation in stelleroids, which would be of value for isolated specimens, would be to compare the interrarial angle of orientated and non-orientated specimens. However, this has not proved useful, as the arm alignment predominantly occurs distally from the interrarial area. Arm alignment of the Leintwardine stelleroids is relatively common and is in most cases interpreted as current alignment. Many of these specimens show arm positions similar in appearance to current aligned non-Leintwardine stelleroids described by Seilacher (1960), Müller (1979) and Hammann and Schminke (1986). Both swaying ('schwoien') and dragging ('schleifen') arm positions, interpreted by Seilacher (1960) to be current indicators, can be identified in the Leintwardine specimens (e.g. Text-fig. 2.24; Pl. 2.7, fig. 5; Pl. 2.9, fig. 2). Determining the relative current direction from the arm orientation is often problematic, as the arms may not necessarily point in a down current direction; in swaying the arms point down current, whilst in dragging they may point up current (Seilacher 1960; Müller 1979; Hammann and Schminke 1986). Diagnostic drag marks in the substrate (e.g. see Seilacher 1960, text-fig. 2) are not associated with the Leintwardine specimens.

Current alignment is generally not pronounced in the Leintwardine stelleroids exhibiting relatively short arms and a pentagonal skeleton; however, some specimens of *Sturtzaster* show pronounced arm alignment (e.g. Pl. 2.7, figs 5-6). One individual





TEXT-FIG. 2.24. Assemblage CH78, showing one *Lapworthura miltoni* specimen and four *Furcaster leptosoma* specimens occurring sporadically through a vertical thickness of 6 mm; refer also to plate 2.9, figure 2. All specimens show a dorsal-up orientation. Lower Leintwardine Formation, Ludlow Series; Starfish Bed A, Church Hill Quarry 1, Leintwardine, Herefordshire. A, specimens outlined showing inferred current orientation of *F. leptosoma* specimens; orientation of arms of specimens 2 and 3 shown on rose plot ( $n = 9$ ; segment interval =  $10^{\circ}$ ; arbitrary 'north' value assigned); scale bar represents 10 mm. B, schematic cross section through slab showing stratigraphical position of stelleroids.



on slab OUM C.30631 shows drawn out arms presumably in the current direction; the other appears to have been dragged along the substrate in the current direction, causing bending of the arms (Pl. 2.7, fig. 5). This co-occurrence of swaying and dragging may explain the appearance of the arms of both specimens being orientated in opposing directions. Other short-armed specimens may just show minor alignment in the form of bent arm tips (e.g. Pl. 2.7, figs 3-4, 7-8).

Alignment is relatively more pronounced in taxa with long, non-disc supported arms (e.g. *B. vermiformis*, *F. leptosoma*, *Klasmura?* sp., *L. miltoni*, *U. ruthveni*; Table 2.1; Pl. 2.8). A specimen of *Klasmura?* sp. shows current alignment; the arms are not outstretched but rather show bending in the current direction (Pl. 2.8, fig. 7). This specimen is interpreted to have undergone dragging. In *B. vermiformis*, a taxon exhibiting relatively long and flexible arms, a pronounced arm alignment is often apparent (Pl. 2.8, figs 8-9, Pl. 2.10, fig. 1). Goldring and Stephenson (1972) stated that a specimen of *B. vermiformis* collected by them (not located herein) from the Todding Channel, shows arm alignment parallel to the channel axis. Several specimens of *B. vermiformis* collected from Church Hill Quarry 1 clearly show an alignment of the arms, which is likely to be due to current orientation (Pl. 2.8, figs 8-9; Pl. 2.10, fig. 1). Unfortunately, due to the difficulty in excavating the echinoderm material from Starfish Bed A, the orientation of the arms relative to the channel axis trend could not be ascertained. *F. leptosoma* specimens often show pronounced current alignment of the arms (e.g. Pl. 2.6, fig. 3; Pl. 2.8, figs 3-5). Of the common taxa recovered *in situ* at Church Hill Quarry 1, *F. leptosoma* most frequently shows current alignment. CH78, containing four specimens of *F. leptosoma* in dorsal-up positioning, shows pronounced arm orientation in specimens 2 and 3 (Text-fig. 2.24; Pl. 2.9, fig. 2). One arm of specimen 2 overlies part of specimen 3; this is interpreted as evidence of swaying. Specimen 5 is interpreted to have predominantly undergone dragging, although some of the arm tips may show swaying. Arm alignment is pronounced in this species, which is presumably due to the slender, flexible arm arrangement. *L. miltoni* specimens may show alignment of the arms; however some of this may be interpreted as locomotory arm positioning (see below). Arm alignment due to current orientation is reasonably convincing in specimens on slabs OUM C.16828 and C.16832 (Pl. 2.5, figs 1-2). The relative robustness of the broad arms of *L. miltoni* could account for the lack of



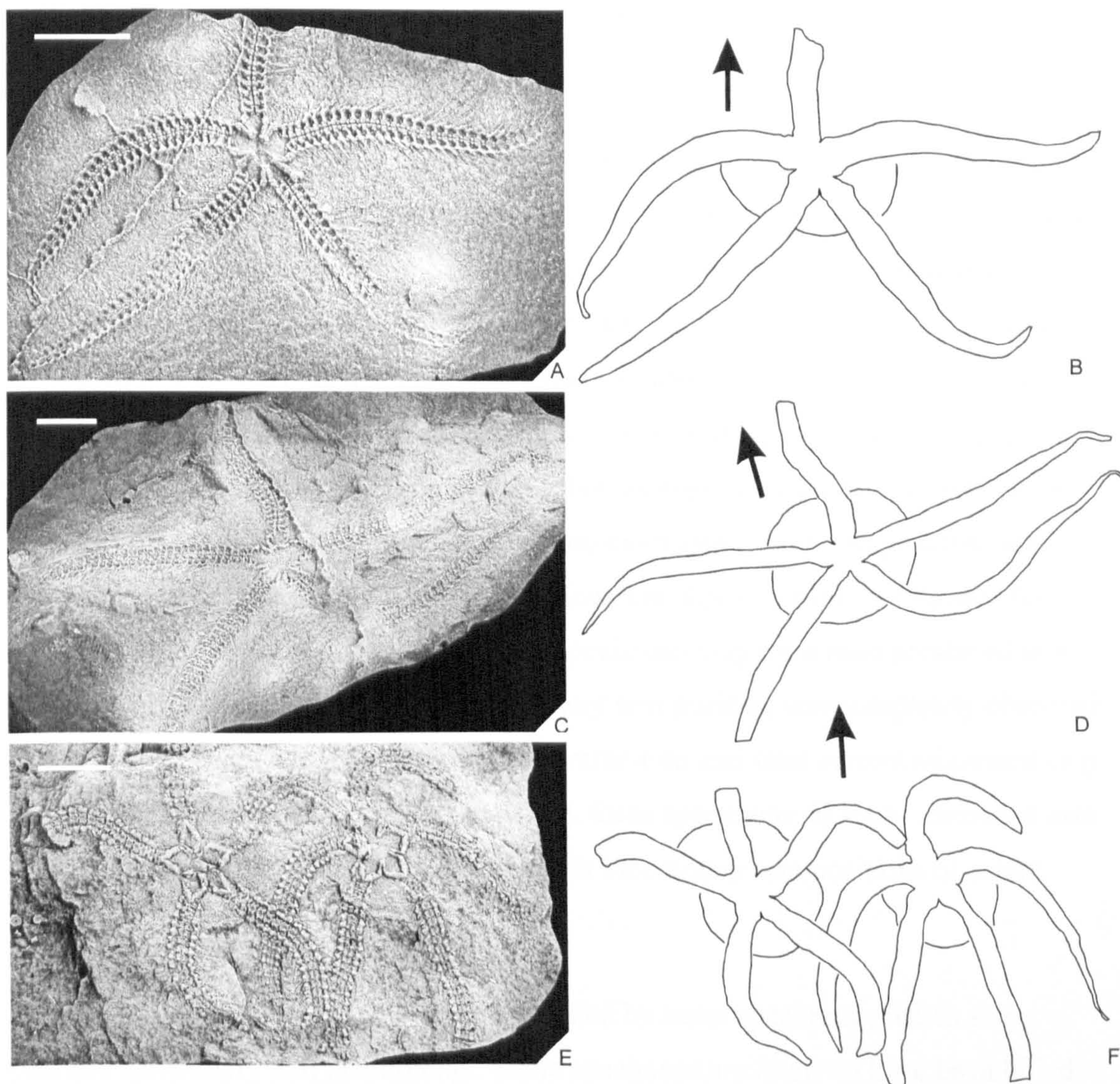
particularly pronounced arm alignment. A specimen of *U. ruthveni* appears to show arm alignment probably due to current orientation (Pl. 2.7, fig. 2).

Specimens of *L. calceatus* show arm alignment (Text-fig. 2.18; Pl. 2.3) although this is not as pronounced as in *F. leptosoma*. Specimens in assemblage BGS GSM25351 show a dominant current orientation, which is tentatively interpreted to be towards the right of the slab (Text-fig. 2.18). Swaying and dragging is exhibited throughout the assemblage although determining which specimens show either type of orientation is problematic. Assemblage BMNH E20250 appears to show two current directions; there is a dominant trend with a secondary trend perpendicular to it (Pl. 2.3, figs 1-2). The majority of specimens are aligned from top to bottom on figures 1-2. A possible explanation for the less obvious arm alignment on some *L. calceatus* specimens is that the arms were less flexible, and thus less susceptible to orientation, due to structural support from the enlarged body disc. One individual on slab BMNH 38527 shows sweeping round of the arm tips, which would presumably have been unsupported by the body disc (specimen at bottom right of assemblage; Pl. 2.3, fig. 3; 2.8, fig. 6).

Possible signs of duress in the Leintwardine taxa (e.g. tightly coiled arms; Schäfer 1972, p. 99) are not observed, which indicates that most specimens have not been preserved in natural death positions, or were not alive after transportation. However, original trauma posture may have been lost through metabolic relaxation during a gradual deterioration in environmental conditions, such as the water column becoming more sediment-laden (Downey, pers. comm. in Welch 1984), or through post mortem compaction (Blake, pers. comm. in Welch 1984).

Four *L. miltoni* specimens analysed show a remarkably consistent arm position; all show four arms in a symmetrically paired arrangement with a fifth unpaired arm (Text-fig. 2.25; Pl. 2.5, fig. 3). Spencer (1925) argued that this distinctive arrangement represents a locomotory life position, citing NMS G1882651518 as an example (Spencer 1925, text-fig. 175c). His interpretation was based on observations of locomotion in living ophiuroids carried out by von Uexküll (1905 and 1909, cited in Spencer 1925). Schäfer (1972, p. 93, text-fig. 56) described extant asteroids that escape horizontally from slow sediment burial by a characteristic drag-induced locomotion; the specimen moves with one or two arms leading or with all the arms trailing behind





TEXT-FIG. 2.25. Possible locomotory life position of certain *Lapworthura miltoni* specimens. Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. A-B, NMS G1882651518, ventral view. A, specimen. B, interpretive drawing showing life position and inferred direction of movement (arrowed). C-D, BGS GSM105645, ventral view. C, specimen. D, interpretive drawing showing life position and inferred direction of movement (arrowed). E-F, OUM C.16858, two specimens in ventral view. E, specimens. F, interpretive drawing showing life position and inferred direction of movement (arrowed); arms show current orientation. Scale bars represent 10 mm.



it; this arrangement shows a strong similarity to that shown by the two specimens on slab OUM C.16858 (Text-fig. 2.25E).

It is difficult to confirm that the arm arrangements of the aforementioned *L. miltoni* specimens represent at least remnants of a life positioning. I cannot test this conclusion, as I have been unable to determine unequivocally the way up of these specimens. Hunsrück ophiuroids described by Seilacher (1960, text-fig. 3a) illustrating a similar arm position were attributed to current orientation, whilst Schäfer (1972, p. 93) and Ausich (2001) stated that this arm positioning can be mistaken for current orientation. Goldring and Stephenson (1972) concluded that, as many specimens of *L. miltoni* are orientated in a mouth-up position and therefore overturned, their arm positions are more likely to be due to current alignment. However, this is not direct evidence for interpretation of this arm positioning; these specimens may have been preserved in a dorsal-up orientation. If the original locomotary arm position was completely obscured by subsequent death struggle, arm muscle contractions and later current alignment (e.g. Schäfer 1972), then this does not explain why these specimens all show consistent arm arrangements, showing strong similarities with locomotary arm positions of extant ophiuroids.

Transportation of living individuals is suggested by some specimens, which show possible locomotary arm positioning. Some specimens are likely to have been killed during transport, as indicated by current alignment of their arms. Based on observations by Schäfer (1971, pp. 96, 99), current alignment is likely to have occurred immediately preceding or subsequent to death.

*Vertical thickness and sedimentation rate of burial layer.* Only a small vertical thickness of sediment influx is sufficient to smother extant ophiuroids; Schäfer (1972, p. 98-99) stated that 50 mm of sediment is sufficient to immobilize and kill a living ophiuroid. *O. fragilis*, of a similar size to the Leintwardine ophiuroids, has a high intolerance to smothering; it is unlikely to be able to escape through 50 mm of sediment (Jackson 1999). Extant asteroids may need an increased thickness of sediment to be smothered; for example *Asterias rubens*, a relatively large form, typically 100 to 300 mm in diameter, and showing a low intolerance to smothering (Budd 2001), can be buried by 60 cm of sediment (Schäfer 1972, p. 92). However, asteroids documented from the channels are significantly smaller than *A. rubens* (the largest taxon *U.*



*ruthveni*, has a maximum arm length of 50 mm), so would require less sediment to be smothered. It is therefore probable that a relatively thin vertical thickness of sediment was responsible for burying the Leintwardine stelleroids. The sedimentation rate was probably relatively rapid, as extant ophiuroids can successfully burrow upwards through sediment if influxes are slow (Schäfer 1972, p. 99). Rapid storm-driven sedimentation results in the formation of starfish bed deposits (Donovan 1991).

*Provenance of specimens within siltstone.* Many of the Leintwardine stelleroids occur entombed within the body of the siltstone, at several different horizons, often only several millimetres apart (Text-figs 2.16, 2.24, Pl. 2.9). Stelleroids recovered from Starfish Bed A at Church Hill predominantly occur in isolation of one another; where multiple specimens occur, individuals are separated from one another by a vertical thickness of several millimetres up to a few centimetres. Slab CH70 contains two specimens of *F. leptosoma* and one specimen of *L. miltoni*, separated by a vertical thickness of 1-3 mm (Pl. 2.6, fig. 2). Slab CH78 has five specimens (one *L. miltoni*, four *F. leptosoma*), which occur intermittently through a vertical thickness of six millimetres (Text-fig. 2.24; Pl. 2.9, fig. 2). CH81 contains two specimens of *F. leptosoma*, separated by a vertical thickness of 15 mm (Pl. 2.9, fig. 5).

Five identifiable stelleroid horizons occur through Starfish Bed A (Text-fig. 2.16). Analysis of stelleroid occurrences (*F. leptosoma* and *L. miltoni*) through the 300 mm vertical thickness of the bed does not reveal discrete taxon-specific horizons. The greatest abundance of specimens occur towards the base of the bed with approximately equal numbers of both species, through a vertical thickness of 10 mm (15 specimens). A second horizon occurs approximately 50 mm above, over a vertical thickness of 20 mm (11 specimens). Again, this association contains a relatively even distribution of both species. Specimen numbers through the remainder of the bed are somewhat lower.

Specimens occurring in monospecific assemblages, essentially along a single plane are still often separated from one another by a small vertical thickness of a few millimetres; this is particularly evident with *S. marstoni* assemblages (Goldring and Stephenson 1972; pers. obs.; e.g. Text-fig. 2.17; Pl. 2.4, figs 3-4). *L. calceatus* assemblages show less vertical separation between specimens (Text-figure 2.18; Pl. 2.3), although a few individuals occur at a 1-2 mm vertical thickness from other specimens (e.g. specimen 1 on assemblage BGS GSM25351; Text-fig. 2.18).



The stelleroids may occur at slightly oblique angles to the bedding; this is more evident with long-armed ophiuroid taxa occurring as isolated specimens (e.g. *F. leptosoma*; specimens 4 and 5 on CH78; Text-fig. 2.24; Pl. 2.9, fig. 2) than those in monospecific assemblages, which essentially lie parallel to the bedding plane.

The occurrence of many stelleroids entombed within the burial layer, sometimes at an oblique angle to the bedding, is evidence that most specimens were probably transported and smothered within the moving sediment mass. Some of these individuals may have been in the process of attempting to escape from the sediment. Specimens occurring in assemblages approximately along a single plane are interpreted to essentially represent buried horizons. Some specimens of *F. leptosoma* and *L. miltoni*, for example those occurring in concentrations in the lowest horizon of Starfish Bed A, may not have undergone prolonged transportation.

*Association with other biota.* The Leintwardine stelleroids often occur in otherwise relatively barren siltstone, although they may also be found in association with shelly brachiopod-rich horizons, sometimes dominated by the rhynchonellids *M. nucula* and *S. wilsoni* (e.g. Pl. 2.10, figs 1, 6-7). CH262, showing two current-aligned specimens of *B. vermiformis*, also has current-aligned *M. nucula* valves. Slab CH258, also contains fragments of 'stick' bryozoans and *S. leintwardinensis*. Along with graptolites, other pelagic organisms such as orthocone cephalopods may rarely be found in association with the stelleroids (Pl. 2.10, fig. 3). CH170 contains *F. leptosoma* in association with a disarticulated crinoid brachia in a fine shelly horizon (Pl. 2.10, fig. 2). Stelleroid specimens also occur in association with crinoids (e.g. Pl. 2.10, figs 4-5); along with the stelleroids, the crinoids recovered from Church Hill were entirely restricted to Starfish Bed A (Text-figs 2.5, 2.16). Stelleroids occurring in association with shelly lags provide evidence for transportation.

*Comparison with other stelleroid occurrences.* In common with other major stelleroid-bearing occurrences, the Leintwardine stelleroids are highly articulated. Autochthonous stelleroid thanatocoenoses ranging from the Upper Ordovician to the Late Eocene have been described by Kesling (1969a), Kesling and Le Vasseur (1971), Rosenkranz (1971), Haude and Thomas (1983), Meyer (1984), Mikuláš *et al.* (1995), and Aronson and Blake (1997). In contrast to most of these deposits, the Leintwardine starfish beds are not monospecific and they do not exhibit high population densities (e.g. compare



with the dense *Strataster ohioensis* assemblage of the Early Mississippian, Lower Carboniferous, Ohio; Kesling and Le Vasseur 1971).

Some allochthonous deposits show an increased species diversity, for example the Upper Ordovician Lady Burn Starfish Beds of Girvan, Scotland (Goldring and Stephenson 1972; Donovan *et al.* 2002) and the Upper Jurassic Solnhofen Limestones of Bavaria, west Germany (Seilacher *et al.* 1985). However, monospecific allochthonous starfish beds are documented (e.g. the Jurassic La Voulte-sur-Rhône Lagerstätte of Southern France; Dietl and Mundlos 1972; Hammann and Schminke 1986; Etter 2002). A low diversity stelleroid fauna, predominantly comprising one ophiuroid species, from the Middle Silurian Rochester Shale of western New York and southern Ontario, USA, shows minimal transportation (Taylor and Brett 1996). The Lower Devonian Hunsrück Slate of Bundenbach, southwest Germany, contain an abundant diverse stelleroid component, which are interpreted to have undergone variable transportation; some specimens are autochthonous whilst others are parautochthonous or allochthonous (Bartels *et al.* 2002a). The Lower Jurassic Starfish Bed of Dorset, interpreted to show variable transportation, has low species diversity with two taxa (Goldring and Stephenson 1972).

Several examples of small isolated monospecific assemblages, comparable in numbers of individuals to some from the Leintwardine channels, are documented; these have been interpreted to have undergone transportation (e.g. from the Middle Ordovician of Spain, the Hunsrück Slate and the Middle Triassic of Poland; Hammann and Schminke 1986; Bartels *et al.* 2002a; Radwański 2002). Some of these assemblages may contain greater numbers of individuals: an allochthonous assemblage of *Encrinaster uederdorfensis* from the Lower Devonian of west Germany, contains 35 specimens (Strauch and Pockrandt 1985).

As with these allochthonous or parautochthonous assemblages, the stelleroids of the Leintwardine channels are commonly preserved in variable way up orientations and some specimens are current aligned. Along with the moderate to high species diversity and relatively low population densities, these characters suggest that they have more in common with transported rather than autochthonous thanatocoenoses. The Leintwardine stelleroids show taphonomic similarities to those of the Hunsrück Slate,

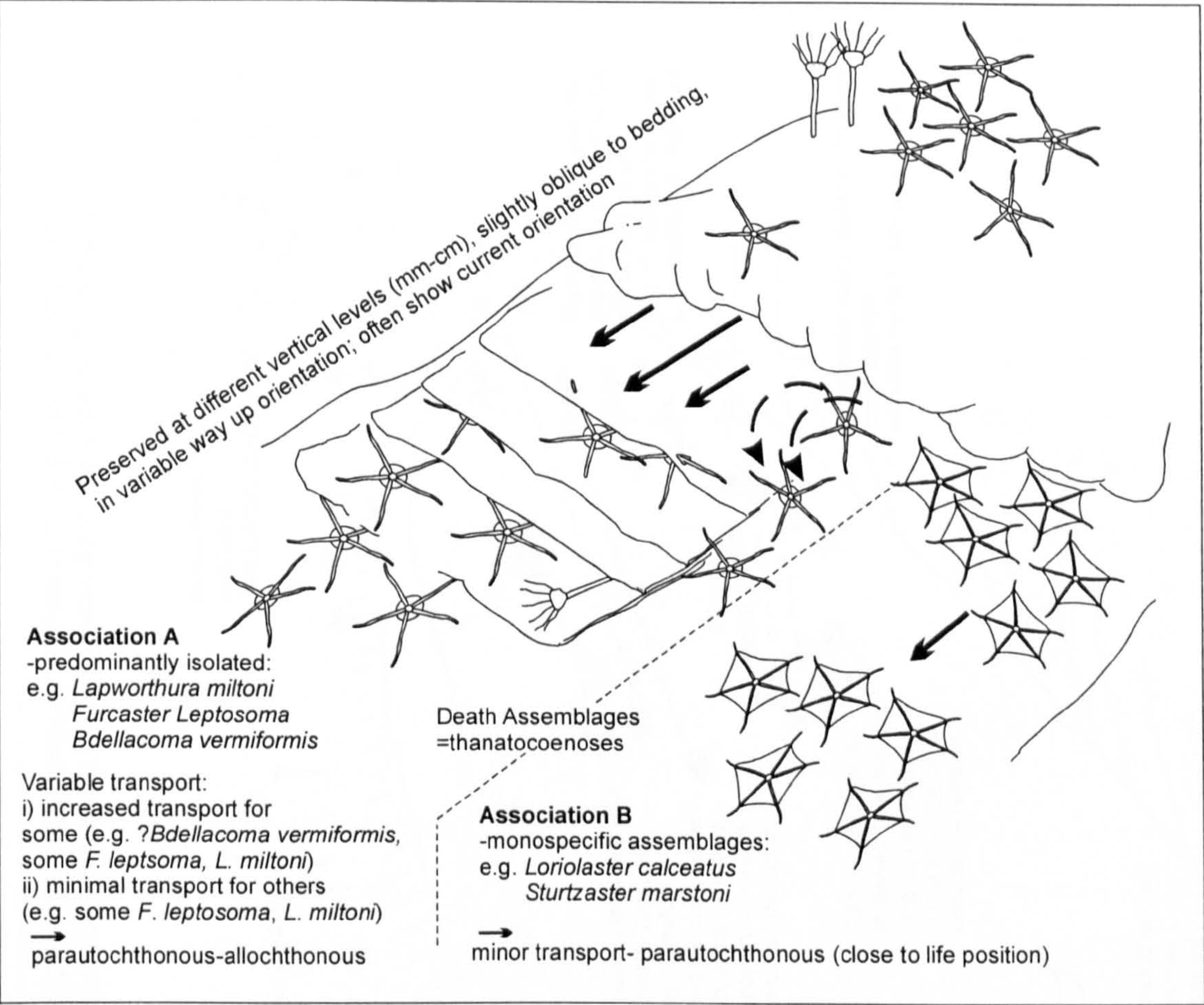


and in common with these deposits are interpreted to have undergone variable transportation.

*Discussion.* The stelleroid taxa of the Leintwardine channels were probably subjected to variable degrees of transportation (Text-fig. 2.26), as indicated by their high species diversity, low population density, size distribution, mode of occurrence within the siltstone, slight obliqueness to the angle of bedding, variable way up, current alignment, lack of associated bioturbation and association with transported shelly faunas. Autochthonous thanatocoenoses are predominantly not preserved.

The stelleroids are interpreted to have been essentially indigenous either to the channel heads themselves or the channel flanks and surrounding shelf (Text-fig. 2.27). The high level of articulation (particularly of the relatively delicate ophiuroid taxa), preservation of monospecific assemblages along a single horizon, low species diversity within Starfish Bed A and a virtually complete lack of recovered stelleroids in the well-studied surrounding shelfal areas (David Siveter, pers. comm. 2002; C. Holland, pers. comm. 2004) is evidence for minor transport for many of the specimens. It could be argued that populations of these stelleroids were widespread on the outer shelf but have simply not been preserved in these areas due to the lack of rapid burial and lack of protection from reworking and predation. However, it is a notable observation that no occurrences of these taxa have been documented in the shelfal areas. It was the view of Goldring and Stephenson (1972) that the echinoderms were introduced into the channels, however this does not account for the monospecific assemblages of stelleroids. Whitaker (1962) and Jones (1969) concluded that the stelleroids formed an indigenous element to the channels, although these authors did not take biostratinomy into account. On present evidence, the best interpretation is that the some of the stelleroids were parautochthonous, close to their original life position (e.g. taxa occurring in assemblages), whilst others were parautochthonous to allochthonous, subjected to greater transportation and brought in from the channel flanks, or perhaps the surrounding shelf. During the sedimentation event, specimens were transported and rapidly buried (Text-figs 2.26-27). Death of individuals would have occurred from initial overwhelming and smothering by the sediment layer.

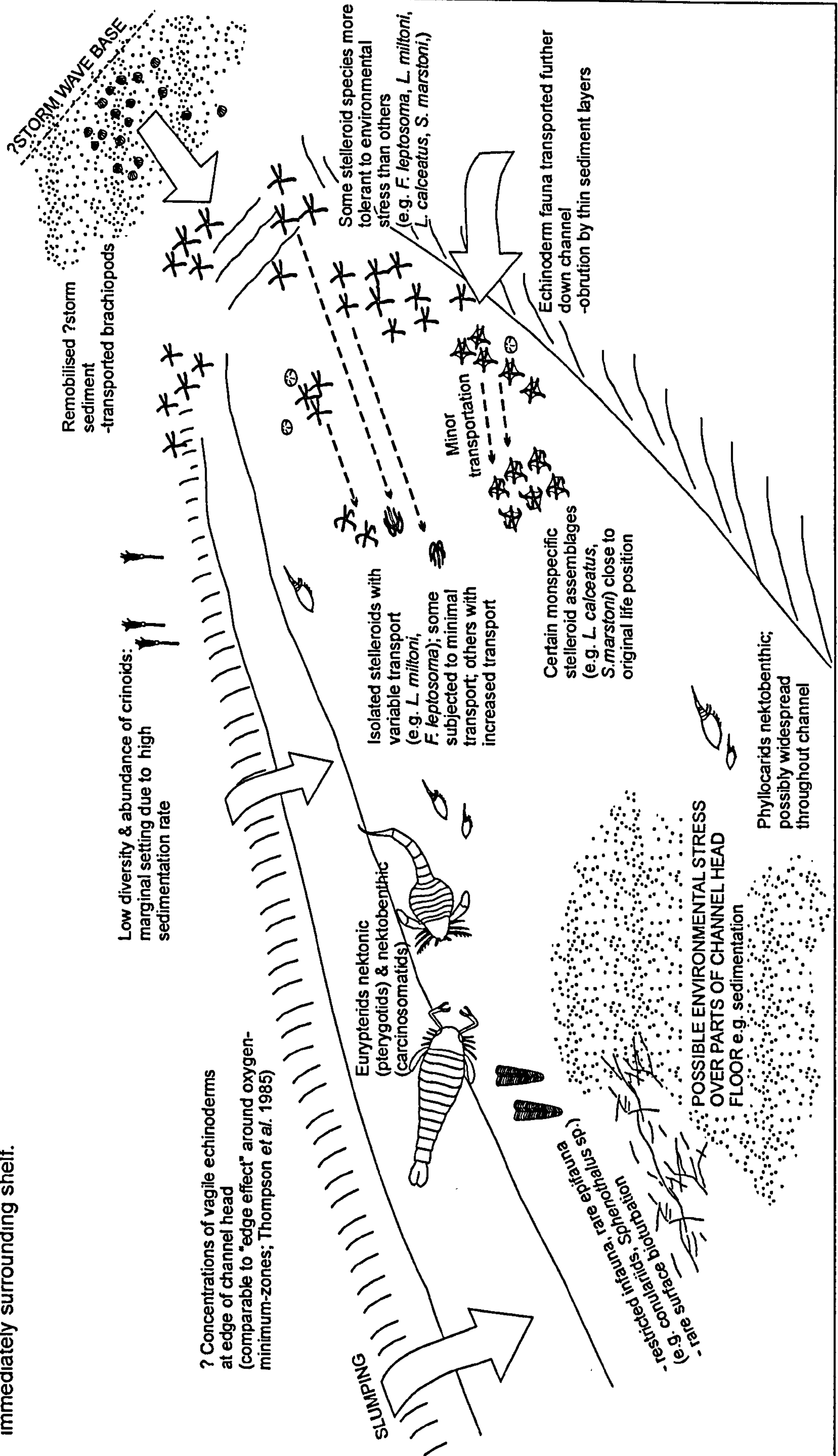




TEXT-FIG. 2.26. Inferred biostratinomy of Leintwardine echinoderms.



TEXT-FIG 2.27. Palaeoenvironmental reconstruction for channel head setting at shelf-break area of Leintwardine (e.g. Church Hill Channel). The indigenous echinoderm fauna is likely to have been relatively short-lived, occupying parts of the channel floor, the channel flanks and the immediately surrounding shelf.





*Non-stelleroid echinoderms*

*Crinoids.* The Leintwardine crinoids are articulated and often nearly fully intact; delicate pinnules are retained along the lengths of the brachia on pinnulate taxa (e.g. *C. quinquepennis*; Pl. 2.11, figs 1-3, 7), although some specimens show disarticulation of brachia from the calyx (e.g. certain *C. quinquepennis* specimens; Pl. 2.10, fig. 2). This preservation of delicate skeletal components is evidence that transport was minimal; subsequent burial is likely to have been rapid (e.g. disarticulation of brachia and cirri in extant comulatids occurs within three days; Meyer 1971; Lidell 1975; Lewis 1986; Ausich *et al.* 1999). Specimens are inferred to have possessed brachia with ligamentary articulations in life (muscular articulations are postulated to have evolved in the Early Devonian; Ausich and Baumiller 1993) and as such do not show preferential disarticulation of these components of the skeleton. The preservational potential of calyxes in different groups of crinoids may be variable, with a decreasing resistance to disarticulation exhibited progressively through the monobathrid camarates, disparids, cladids and flexibles (Meyer *et al.* 1989, Ausich *et al.* 1999). However, according to Ausich *et al.* (1999), this is not a factor when rapid burial is involved. The presence of intact species, representative of all these groups including the least disarticulation-resistant flexibles (i.e. *E. maccoyanus*; Pl. 2.12, figs 2-3, 5-6), indicates that rapid burial has occurred. The dominance of monobathrid camarates (i.e. *C. quinquepennis*) is therefore, not interpreted to be a taphonomic artefact. The crinoids were not exposed to prolonged transportation and reworking on the seafloor.

Slabs showing more than two specimens along a single horizon do not occur; specimens are often solitary, suggesting that they have been subjected to transportation. Slab BGS GSM89897 contains two heterospecific specimens (*C. quinquepennis* and *G. ludensis*) on the same horizon (Pl. 2.11, fig. 3). Slab CH111 has two conspecific specimens (*C. quinquepennis*) separated by a vertical thickness of four millimetres; both specimens appear to show a similar orientation, interpreted to be due to current alignment (Pl. 2.11, fig. 8).

Burial is likely to have been rapid; Schumacher (1986) stated that complete crinoid specimens can be preserved through storm-generated current sedimentation. Determining the exact degree of transportation is not possible, and it is therefore difficult to assess whether or not the crinoids were indigenous to the Church Hill



Channel. Although generally articulated, specimens do show minor disarticulation, although this may be partially due to compaction after burial. Specimens do not preserve the entire length of the column and no apparent terminal attachment/holdfast structures (as described in Brett 1981, 1984) are preserved (Pl. 2.10, fig. 4; Pl. 2.11, figs 3-4, 6; Pl. 2.12, figs 11-2). This indicates that individuals were probably subjected to some transportation, as postulated for crinoids of the Lady Burn Starfish Bed, Girvan by Ausich *et al.* (1999; Text-fig. 2.26). If a relatively small degree of transportation (e.g. several tens of metres) is assumed then some specimens may have lived along the channel flanks and surrounding shelf, whilst others may have occupied the channel head itself (Text-fig. 2.27). The relative rarity of specimens, in comparison to the stelleroids, may suggest that the crinoid fauna has been subjected to increased transportation. However, their high articulation suggests this is unlikely. This inequality in total numbers of specimens of the two classes is interpreted to reflect original life assemblage abundances with the crinoids forming relatively less dense populations in the channel head area.

*Echinoids.* Echinoid tests are intact and retain their delicate spines and pedicellariae on specimens of both species documented from Leintwardine (Blake 1968; pers. obs.; Pl. 2.13, figs 1-5). Some spines show minor fragmentation on their distal portions, although this is variable through specimens (e.g. *E. pomum*, Pl. 2.13, fig. 4). Studies on extant echinoids have revealed that they quickly lose their spines and pedicellariae after death (Kidwell and Baumillar 1990; Brett *et al.* 1997), thereby implying that specimens retaining these skeletal elements must have been buried rapidly (Schäfer 1972). Schäfer (1972) added that no spine coatings are noted on tests where carcasses have been subjected to transport. Experiments carried out on extant echinoids by Kidwell and Baumillar (1990) show that individuals can be subjected to considerable degrees of transportation without breakage of the test occurring, provided that decay of the connective collagen is not well underway. However, most Palaeozoic forms have tests composed of imbricate plates embedded in a thick layer of connective tissue (Smith 1984, Brett *et al.* 1997), resulting in considerably less durability during reworking. The plates merely comprise a relatively thin sheet of laminar stereom; no deeply penetrating sutural collagen fibres or further stereom layers are present, as in the more rigid tests of post-Palaeozoic taxa (Smith 1984). Complete echinoid tests with imbricate plating are unlikely to be preserved unless they have been buried alive (Smith 1984). As the



Leintwardine taxa retain intact tests, transportation is likely to have been minimal, and subsequent burial rapid.

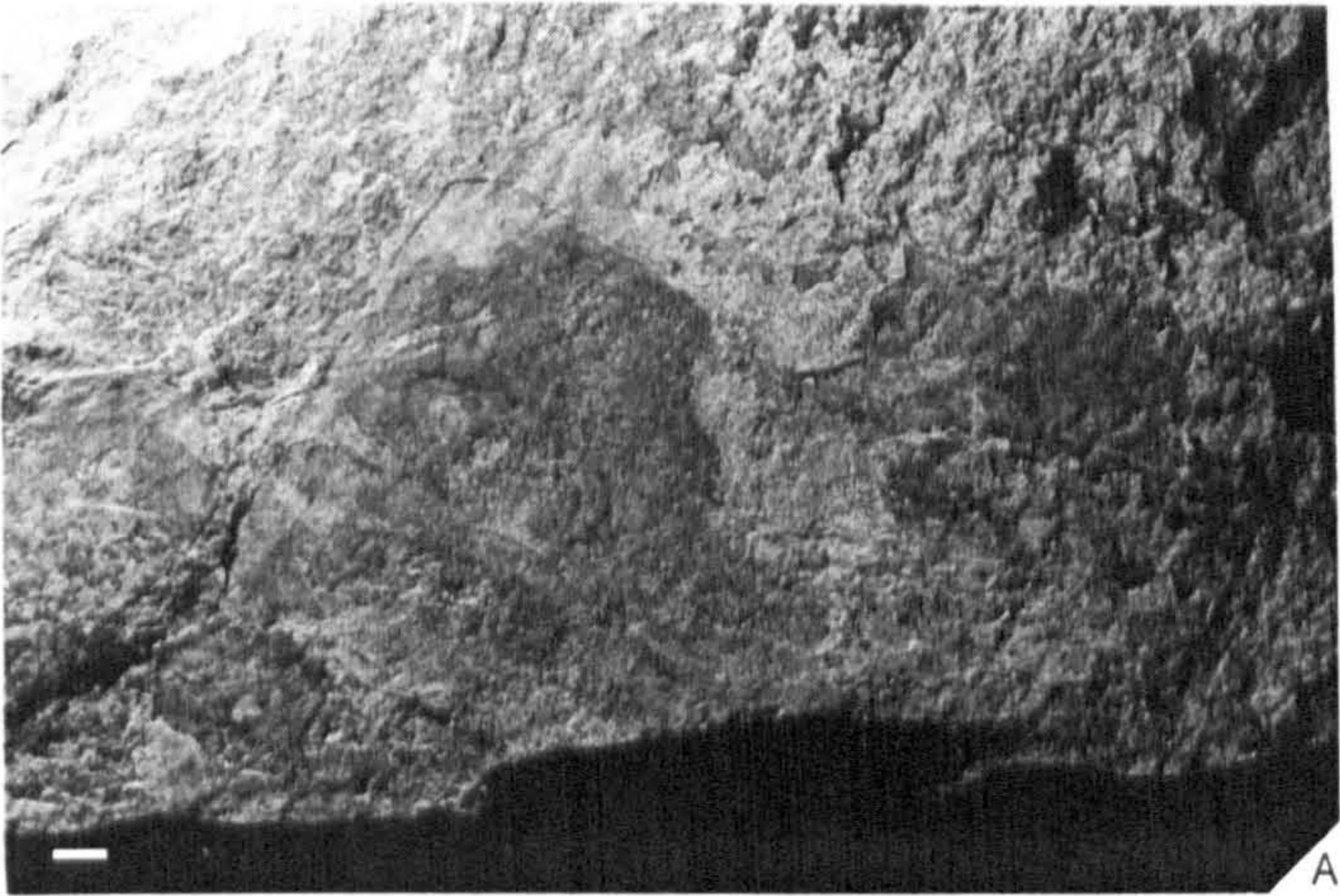
Direct assessment of the way-up orientation of specimens is not possible, as no *in situ* fossils have been recovered. Stephenson and Goldring (1972) stated that specimens of the two species recovered from Leintwardine (*E. pomum* and *P. ferox*) are orientated in a mouth-down life position, where they have been able to ascertain the original way up of the slab; I have been unable to find way-up indicators on the slabs (no apparent grading is determinable) so cannot verify this observation. Goldring and Stephenson (1972) also noted that the tests are slightly distorted so that the apical disc does not lie directly above the peristome, and alignment of spines may be present, both characters being due to rolling of individuals. These effects would be expected during a sediment influx.

*Ophiocistioids.* The ophiocistioids are generally intact, the tests retaining the peristome and buccal armature, and the enlarged articulated podia (Pl. 2.13, figs 6-9). The presence of these structures indicates minimal transportation and rapid burial. Slab BMNH E 27030 contains two specimens, one occurring 1-2 mm above the other; both specimens show their dorsal surface (Pl. 2.13, fig. 6). Original way up cannot be determined so it is uncertain whether these specimens are in their original dorsal-up positioning.

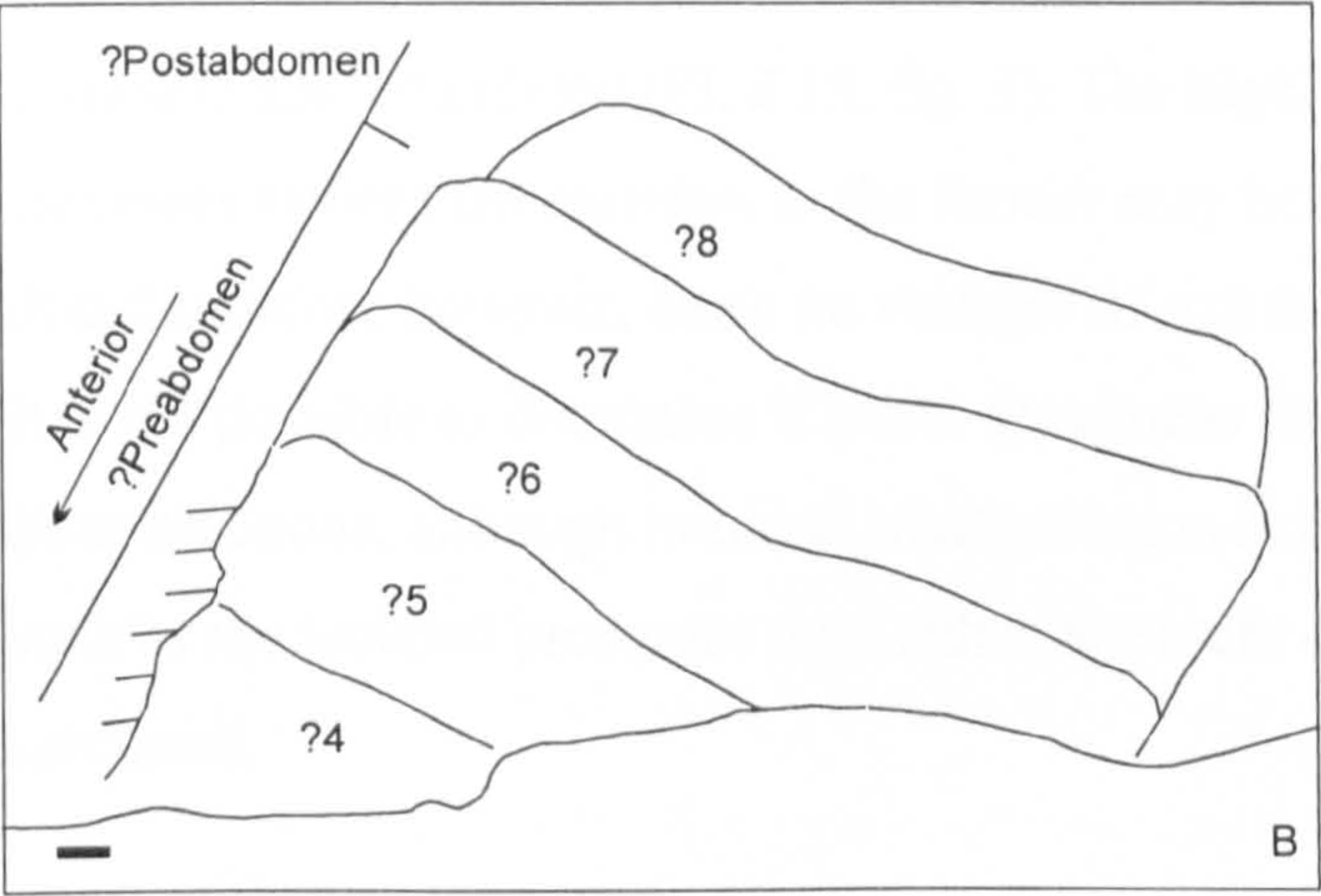
### *Phylum Arthropoda*

*Eurypterids.* The eurypterids are semi-articulated and are commonly represented by components of the prosomal appendages (e.g. the gnathobase, locomotary appendages or chelicerae) and abdominal segments, or fragments of undetermined cuticle showing the characteristic pustulose ornament (Pl. 2.14). A portion of eurypterid prosoma has also been recovered from Church Hill Starfish Bed A (Pl. 2.14, fig. 5). Intact metastomas are also preserved (Pl. 2.14, fig. 11). No complete eurypterid specimens have been documented but near-complete prosomal appendages and articulated tergites occur (e.g. Text-fig. 2.28; Pl. 2.14, figs 1, 8-10). Eurypterid fragments often occur in association with other fossils, particularly brachiopods (Pl. 2.14, fig. 3); these are interpreted to have been transported. Specimen CH106 contains a small fragment of eurypterid cuticle in association with the *C. quinquepennis* (Pl. 2.11, fig. 1). The





TEXT-FIG. 2.28. Semi-articulated opisthosoma of *Carcinsoma?* sp. (CH147); five articulated tergites are preserved. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. A, detail of specimen. B, interpretive drawing. Scale bars represent 10 mm.





eurypterid specimens are probably mostly transported and represent exuviae; no conclusive evidence for carcass preservation is preserved.

*Xiphosurans.* The synziphosurine specimens are sometimes remarkably complete, but also consist of disarticulated components such as prosomal head shields or the opisthosoma and telson (Pl. 2.15). A few specimens of *L. limuloides* are almost intact (Pl. 2.15, figs 1, 4). The only *in situ* specimen recovered from Starfish Bed A at Church Hill, a prosoma of *L. limuloides*, retains its posterior margin protuberances (Pl. 2.15, fig. 6). One specimen of *C. loganensis* from Leintwardine is relatively complete and articulated; the telson is broken away on the edge of the slab (Pl. 2.15, fig. 5). The only specimen of *Pseudoniscus* sp. documented from Leintwardine is also relatively complete and articulated (Pl. 2.15, fig. 3). The highly articulated specimens may be carcasses rather than exuviae, as the former may have been less susceptible to disarticulation; however, since no vestiges of soft tissue are preserved this is equivocal. It is not possible to determine if intact specimens such as BGS GSM32393 are autochthonous, although minimal transportation is likely. Disarticulated components such as the isolated prosomas may either represent exuviae, or possibly allochthonous carcasses.

*Phyllocarids.* Specimens are often disarticulated, predominantly consisting of bivalved carapaces, abdominal segments or portions of the telson (Pl. 2.16, figs 5-6). However, semi- to fully articulated specimens occur from both Church Hill and Martin's Shell quarries (Pl. 2.16, figs 1-4, 7). Newly collected material from Martin's Shell Quarry is generally of a relatively fragmented nature, often consisting of portions of the telson and caudal spines (e.g. Pl. 2.16, fig. 6). Two near-complete, articulated specimens have been recovered from Church Hill: a large specimen 200-300 mm in length, consisting of the telson and abdomen, and a smaller specimen, 25 mm in length, consisting of the carapace, abdomen and telson (CH62, CH128 respectively; Pl. 2.16, figs 2, 7). The variability in articulation suggests that the degree of transportation varied, although this may reflect whether specimens are carcasses or moults. Intact, articulated specimens are interpreted to have undergone minimal transport and are likely to have been indigenous to the setting.

*Other groups.* Ostracod specimens are well preserved, and have been reported as retaining their delicate spinose ornament (Jones 1969). The beyrichiaceans and



podocopes are locally relatively abundant, occurring in concentrations with other shelly fossils (Pl. 2.17, fig. 2). The trilobites are commonly represented by disarticulated cephalons, thoracic segments or pygidia (Pl. 2.17, figs 1, 3-5). A few articulated trilobite specimens have been documented from pre-existing museum collections (e.g. BMNH In. 48467, BGS GSM36747). Specimens that occur within the brachiopod-dominated shelly coquina horizons are parautochthonous or allochthonous.

### *Phylum Brachiopoda*

Specimens of *L. lata* occur as disarticulated flat-lying valves, parallel to bedding (Pl. 2.18, fig. 9). Specimens are not preserved in life position as they are not articulated and do not occur perpendicular to bedding, unlike some of those described in Cherns (1979). Emig (1986) stated that fossilisation of flat-lying, disarticulated valves may be due to coarse-grained sedimentation or storm process. Studies on extant taxa have revealed that the thin, fragile, chitinophosphatic valves are readily susceptible to complete fragmentation within two to three weeks after death; rapid sediment events, occurring over a duration of up to a few days are therefore generally responsible for entire shell preservation of fossil taxa (Emig 1983, 1986, 1990). Hawkins and Hampton (1927) described occurrences of articulated *Lingula* sp. specimens from the Leintwardine channel fill, stating that they were preserved in their life position, but I have not seen specimens in life orientation. Jones (1969) described all occurrences of *Lingula* as being disarticulated, with many valves showing a pronounced parallel current alignment; anterior ends were stated as being oriented up current.

Many brachiopod specimens occur in concentrated shelly coquina horizons through the Leintwardine channel fill. Several shelly horizons composed almost entirely of the rhynchonellids *M. nucula* and *S. wilsoni*, occur at Church Hill Quarry 1, towards the base of Starfish Bed A. Articulated and disarticulated specimens occur in these coquinas (e.g. CH175-176, CH179, CH262; Pl. 2.18, figs 1-3, 5-6). CH176, taken from the extreme western end of Church Hill Quarry 1 shows three dense shelly horizons occurring through a vertical thickness of 10 mm; the lower and upper horizons are dominantly composed of rhynchonellids (Pl. 2.18, fig. 5). Other brachiopod taxa (e.g. *Orbiculoidea* sp.; Pl. 2.18, fig. 5) sometimes occur within these horizons. A current orientation of rhynchonellid specimens is not apparent in these densely packed horizons. These shelly lags clearly provide evidence for transportation. Rhynchonellids



and other taxa occurring in less dense horizons may show a current alignment, with the axes of symmetry orientated parallel to the current direction (e.g. Pl. 2.1, fig. 4; Pl. 2.18, fig. 4); these are also interpreted to have undergone transport.

Brachiopods can be subjected to transportation without disarticulation (e.g. Kidwell and Bosence 1991, p. 157; Brenchley and Harper 1998). Alexander (1990), Brenchley and Harper (1998, p. 87) and Cherns (1988) stated that the retentive (cyrtomatodont hinge) articulation of rhynchonellids may mean that the valves are less susceptible to disarticulation; the teeth or sockets of taxa with this style of hinge must be broken before the valves will disarticulate (Sheehan 1978). Jones (1969) stated that the presence of articulated specimens of *S. wilsoni* with disarticulated specimens of *D. navicula* in the Lower Leintwardine Formation beds of the shelf suggests that the former taxon may be relatively resistant to disarticulation through transportation. *D. navicula* specimens may occur as infills in scoured grooves, which Whitaker (1962) inferred to be due to current action (e.g. LEIUG 19469, from the Todding Channel; Pl. 2.1, fig. 3). Both articulated and disarticulated *D. navicula* specimens occur on these slabs.

These transported specimens may originate from the mid to outer shelf, specifically derived from either the earlier '*Dayia navicula-Isorthis orbicularis-Shagamella minor*' or the later '*Shaleria ornatella*', or perhaps even the inner shelf '*Sphaerirhynchia wilsoni-Isorthis orbicularis-Microsphaeridiorhynchus nucula*' Lower Leintwardine Formation faunal associations of Cherns (1988, 1999). *M. nucula* was not a noticeable component of the mid to outer shelf *Dayia navicula-Isorthis orbicularis-Shagamella minor* Association (Cherns 1988, 1999), although specimens may still have originated from this setting, as the succeeding *Shaleria ornatella* Association of the high Lower Leintwardine to Upper Leintwardine Formation was composed of minor acmes of the species (Cherns 1988, 1999). However, the *Shaleria ornatella* Association may have been reduced or even absent from the offshore shelf region (Cherns 1988, p. 496). *S. wilsoni* was a common species of the *Dayia navicula-Isorthis orbicularis-Shagamella minor* Association (Cherns 1988, 1999), so individuals may originate from the mid to outer shelf. *M. nucula* and *S. wilsoni* were particularly abundant in the *Sphaerirhynchia wilsoni-Isorthis orbicularis-Microsphaeridiorhynchus nucula* Association of the inner shelf (Cherns 1988, 1999); specimens may therefore also



originate from this part of the shelf, implying considerable transportation. The environment inhabited by this faunal association was affected by numerous storm events (Cherns 1999), which may have been responsible for transporting shells to the outer shelf.

*D. navicula* and *Shagamella minor* were an abundant component in both the *Sphaerirhynchia wilsoni*-*Isorthis orbicularis*-*Microsphaeridiorhynchus nucula* and *Dayia navicula*-*Isorthis orbicularis*-*Shagamella minor* associations, being particularly dense in the mid shelf area of the latter (Cherns 1988, 1999). This suggests that specimens of these taxa were predominantly transported from the mid to outer shelf. *L. lata* had a distribution centred in the outer shelf to trough area, within the *Dayia navicula*-*Isorthis orbicularis*-*Shagamella minor* and ‘*Lingula lata*-*Saetograptus leintwardinensis*’ associations (Cherns 1988, 1999); the shelf-break position of the channel heads suggests that specimens could be derived from either of these faunal associations. Less abundant brachiopod taxa within the Leintwardine channel heads such as *Protochonetes ludloviensis* were locally abundant within the *Sphaerirhynchia wilsoni*-*Isorthis orbicularis*-*Microsphaeridiorhynchus nucula* Association (Cherns 1988, 1999), which may suggest transportation from the inner shelf.

### *Other fossils*

The Leintwardine bryozoans are well preserved and are generally intact (e.g. Pl. 2.17, fig. 6); preservation of the delicate branching skeletons (‘erect, rigid, delicate branching’ morphology of Smith 1995) indicates that transportation is likely to have been minimal and that specimens were probably indigenous to the channel flanks and surrounding shelf.

The conulariids are mostly intact (Pl. 2.19, figs 8-9); minor fragmentation may occur in some specimens although this could be due to compaction during burial. *Sphenothallus* specimens are predominantly incomplete and do not appear to preserve the holdfasts (e.g. Pl. 2.19, figs 6-7). One specimen on slab MS27 is nearly complete; the proximal end and possible holdfast structure are intact, although the specimen does not appear to be attached to a substrate, suggesting that it is not preserved in its life position (Pl. 2.19, fig. 7).



The palaeoscolecsids retain the characteristic papillate ornamentation of the (secondarily) phosphatised, plated cuticle; this is clearly visible in several specimens from the Church Hill and Todding channels (Pl. 2.19, figs 1-5). Two (or rarely one) transverse rows of papillae per annulus occur, with the number of papillae per row variable. The preservation of fine scale morphological detail on the palaeoscolecsids, indicates that they were subjected to minimal transportation and may well have been autochthonous to the channels. Possible soft body preservation, in the form of gut trace retention, indicates that individuals were subjected to rapid burial.

Rare specimens of the heterostracan fish *A. ludensis* occur in the form of disarticulated dorsal and ventral head shields (e.g. BGS GSM49106; Pl. 2.17, fig. 9). The lack of other apparent skeletal components, along with the extreme rarity of specimens indicates that the heterostracan fish components are likely to have been transported into the channel area. Pelagic organisms such as orthocone nautiloids and *S. leintwardinensis* often show some degree of current alignment (Pl. 2.1, fig. 3; Pl. 2.17, fig. 7); specimens may also be incomplete. These fossils are interpreted to represent allochthonous thanatocoenoses.

## AUTECOLOGY AND SYNECOLOGY

### *Phylum Echinodermata*

*Stelleroids*. Determining the ecology of Palaeozoic stelleroids is problematic, due to the variation in morphology between fossil taxa and because extant forms differ considerably in their construction from Palaeozoic representatives (e.g. extant ophiuroids have a highly flexible arm of fused vertebrae). Extant stelleroids commonly employ more than one feeding strategy (e.g. Jangoux 1982; Warner 1982); this adds to the complexity in inferring habits for fossil taxa.

Spencer (1951) and Gale (1987) considered that Ordovician and Silurian asteroid taxa were largely passive, relying on microphagous deposit-feeding. Evidence cited by Gale (1987) for this was the absence of suckered tube feet, the inability to feed extra-orally, and the lack of arm musculature (resulting in limited arm flexibility). Gale concluded that that these taxa lived on soft substrates, probably ingesting the sediment into the peristome using the proximal tube feet; small benthos may have been ingested whole,



in predation or scavenging. However, Blake and Guensburg (1988) argued that asteroid taxa from the middle Ordovician onwards showed broadly similar modes of life to modern forms. These authors felt that several lines of evidence supported this interpretation, for example: Palaeozoic asteroids had varied morphologies suggesting a range of habits; certain taxa were relatively large in relation to many associated benthos, implying predation; the presence or absence of suckered tube feet was not necessarily indicative of habit; ossicle articulation was sufficiently sturdy to infer arm flexibility. I concur with Blake and Guensburg (1988), in that Palaeozoic asteroids probably showed variable feeding habits. However, determining these habits is problematic; modern asteroids are often generalists (Lawrence 1987; Blake 2000), adopting a wide range of feeding habits, from suspension feeding to active predation (Jangoux 1982; Lawrence 1987; Blake and Guensburg 1988). They are generally solitary and epifaunal, although some taxa may adopt a slightly infaunal habit (Blake and Guensburg 1988). By using modern taxa as analogues it is inferred that the Leintwardine asteroids were solitary and possibly epifaunal; the rarity of specimens also suggest a solitary habit.

The podial basins of the Leintwardine asteroid *U. ruthveni* are relatively short longitudinally, and are predominantly concealed ventrally by the prominent adambulacrals (Pl. 2.20, fig. 1). Thus, despite an apparent lack of prominent muscle facets between the adambulacrals (Pl. 2.20, fig. 1), arm movement is likely to have been effected by small movements between the adambulacrals (as opposed to tube foot locomotion typical of asteroids; Dean 1999b, p. 147). The paxillate ossicles over the dorsal surface imply that *U. ruthveni* was semi-infaunal or infaunal (Pl. 2.20, fig. 1); Spencer (1951) considered that paxillae could help keep the dorsal surface free of sediment. However, paxillae alone do not imply an entirely infaunal mode of life (Blake 1994; Dean 1999b, p. 148). Modern paxillate asteroid taxa such as *Astropecten* and *Luidia* feed epifaunally, whilst solasteroids are entirely epifaunal (Blake 1994). As concluded for the paxillate taxon *Platanaster ordovicus* by Blake (1994), the paxillae may have protected the dorsal surface of *U. ruthveni* from sediment stirred by water motion caused by animal movement.

Determining feeding strategies for *U. ruthveni* is problematic. As noted by Dean (1999b, pp 154-155), a relative lack of arm musculature, and relatively well-developed



tube feet, in comparison to ophiuroids, suggests a microphagous feeding strategy. Suspension feeding is unlikely; the paxillae may have limited dorsally directed movement of the arms, and the ambulacrals appear to have lacked dorsal longitudinal musculature needed for arm elevation (Dean 1999b, pp 154-155). However, Dean (1999b) tentatively inferred that the terminal parts of the arms could be elevated for suspension feeding; she added that ciliary feeding was possible. The possible concealment of the tube feet by the adambulacrals suggests that deposit feeding is unlikely (Dean 1999b, p. 157). *Urasterella* is relatively large in relation to associated benthos, thus implying a predatory feeding strategy (Blake and Guensburg 1988). The only two specimens of *U. ruthveni* documented from Leintwardine are not particularly large (e.g. Pl. 2.7, fig. 2); other specimens of the species known from the Upper Silurian of the Lake District attained a larger size (maximum arm length of 50 mm). None-the-less, *U. ruthveni* is one of the larger asteroid taxa from Leintwardine and may have adopted an intraoral macrophagous, predatory feeding strategy. However, the axillaries of the mouth frame are poorly developed (Dean 1999b, p. 157; pers. obs.; Pl. 2.20, fig. 3); this suggests that *Urasterella* would not have ingested large prey.

Some of the marginals of the Leintwardine asteroid *C. bulbiferus* have large depressions between them similar to those identified by Blake and Guensburg (1988, text-fig. 4H) for *Hudsonaster incomptus* (Pl. 2.20, figs 4-5). In spite of this potential flexibility, *C. bulbiferus* is likely to have used predominantly tube foot locomotion, as suggested by the substantial podial basins. Further comparison with *Hudsonaster* is useful; a deep ambulacral groove, relatively inflexible marginals, and large axillaries and oral plates, inferred by Dean (1999b, p. 155) to suggest deposit feeding and ingestion of microprey, are present within *C. bulbiferus* (Pl. 2.20, fig. 4).

In common with the non-Leintwardine taxon *Stenaster* (see Dean 1999a), the Leintwardine stenurids (*A. magrumi*, *B. vermiformis*, *Klasmura?* sp., *R. pyrotechnica*, *S. colvini*, and *S. marstoni*) and the asteroid *Palasterina* are interpreted to have possessed relatively immobile arms, suggested by a weakly muscular skeleton, alternating or opposed unfused ambulacrals, and large tube feet (Pl. 2.20, figs 6-9). Large podial basins provide evidence for enlarged tube feet; soft-tissue preservation in a Lower Silurian *Bdellacoma* species from Herefordshire (Sutton *et al.* 2005) provides direct evidence for this genus. The podial basins are extended transversely by



abradially positioned axial ossicles, the sublaterals or podial plates, in *Antiquaster*, *Bdellacoma*, *Klasmura* and *Rhopalocoma* (terminology of Spencer and Wright 1966 and Dean Shackleton 2005, respectively; Pl. 2.20, fig. 9). Modern asteroids may provide more suitable analogues than ophiuroids for the habits of Palaeozoic stelleroid taxa possessing large podial basins; fossilised asteroid-like tube feet have also been reported in the Hunsrück ophiuroid *Bundenbachia* (Blake and Glass 2003). These stelleroids are interpreted to have adopted a vagile, essentially epifaunal habit, with predominantly tube foot locomotion. As suggested for *Stenaster* (Dean 1999a), large tube feet may have aided in suspension-feeding; this strategy is employed in some extant ophiuroids (Warner 1982). It is probable that the Leintwardine stenurids similarly adopted a predominantly deposit-feeding habit, as suggested by the relatively immobile arms and large tube feet. The relatively poorly developed jaw musculature and buccal slits also suggest a deposit feeding habit (e.g. Dean 1999b, p. 159). Some extant asteroids have closely analogous structures to buccal slits, which aid in increasing the mouth diameter for sediment ingestion (Gale 1987).

Prominent rows of pedicellariae are present along the dorsal surface of the arms in *Antiquaster* and *Bdellacoma* (Pl. 2.2, figs 5-6; Pl. 2.20, fig. 7). If the pedicellariae are interpreted as being used for prey-capture, as shown by some extant asteroids (Chia and Koss 1994; Sutton *et al.* 2005), then it could be that *A. magrumi* and *B. vermiformis* had a solitary, epifaunal, perhaps cryptic habit. It is unlikely that *A. magrumi*, *B. vermiformis* and *Klasmura?* sp. adopted a true infaunal suspension-feeding habit as the arms appear to have been relatively immobile and not truly ophiuroid-like. The presence of large pedicellariae is evidence for an epifaunal life position. The species are relatively rare and no occurrences of multiple individuals are documented. This suggests that it is unlikely that these taxa adopted an infaunal habit within a relatively dense feeding aggregation (as is generally observed in extant taxa adopting this strategy). A solitary habit is therefore inferred.

*Palasterina*, *R. pyrotechnica* and *Sturtzaster*, with their short, squat arms poorly differentiated from the body disc (e.g. Pl. 2.7, figs 1, 4-8), are likely to have adopted an epifaunal life position (Spencer and Wright 1966). The pronounced club-like dorsal spines of *R. pyrotechnica*, inferred to have served a protective function, also suggest such a life position (Dean 1999b, p. 148; Pl. 2.2, fig. 7). The taxa exhibit relatively



short, stiff arms; *Sturtzaster* may have had swollen arms in life, with a high swollen dorsal surface of the disc conducive to epifaunal life (Spencer and Wright 1966). *S. marstoni* often occurs in assemblages, indicating that it probably lived in relatively dense monospecific populations, as in common with some extant ophiuroid taxa (e.g. see Aronson 1989). The numerous acicular spines of *Sturtzaster*, along with having a protective function, may also have aided in mucus-net suspension-feeding (Pl. 2.2, fig. 9; Dean 1999b, p. 159). If suspension-feeding was employed then it probably occurred level with the substrate, as elevation of the arms may have been unlikely (Dean 1999b, p. 159). Spencer and Wright (1966, p. 80) considered that the inferred communal habit of *S. marstoni* was indicative of suspension-feeding. Extant suspension-feeding ophiuroid taxa such as *O. fragilis* and *O. nigra* often occur in dense monospecific populations (e.g. Wilson *et al.* 1977; Warner 1982); mucus-net suspension-feeding is documented as the main feeding habit for the latter species (Warner 1982). However, the short, squat, relatively immobile arms indicate a primarily deposit-feeding trophic strategy for *Sturtzaster*. A similar deposit-feeding habit is proposed for *Palasterina* and *R. pyrotechnica*, although their relative rarity suggests they were probably solitary.

The encrinasterid ophiuroid *L. calceatus* is interpreted to have adopted an epifaunal life position, as suggested by its enlarged, possibly membranous body-disc (Pl. 2.2, fig. 2). Alternating ambulacrals suggest that the arms were relatively immobile (Pl. 2.21, fig. 1), thereby suggesting that the species may have employed deposit-feeding. The taxon is likely to have lived in relatively dense monospecific populations, and may have used neighbouring members of the community for arm support during suspension feeding, as is observed in some extant taxa (e.g. *O. fragilis*; Warner 1982) and suggested for some Palaeozoic taxa that occur in dense aggregations (e.g. the protasterids *Strataster ohioensis* and *Taeniaster bohemicus*; Kesling and Le Vasseur 1971; Mikulás *et al.* 1995).

The Leintwardine ophiuroids *F. leptosoma* and *L. miltoni* are interpreted to have been highly mobile; both taxa exhibit opposing, although possibly unfused ambulacrals and pronounced arm musculature, as indicated by relatively developed muscle pits (Pl. 2.21, figs 2, 6). They are likely to have adopted an epifaunal mode of life more analogous with some extant ophiuroids. The podial basins, although moderate to large (Pl. 2.1, figs 3, 7), suggest relatively less pronounced tube feet than in the stenurids;



locomotion is inferred to have been predominantly arm-supported. The relatively short arms, large body discs and long spines of these taxa, in relation to those of extant infaunal species such as *A. filiformis*, suggest epifaunal life positions (see Dean 1999b, p. 149). However, some taxa exhibiting this morphology may have been able to burrow vertically using their tube feet, such as in *A. filiformis* (Lawrence 1987; Dean 1999b, p. 149). Specimens of *F. leptosoma* generally occur in isolation, suggesting a solitary habit. *L. miltoni* sometimes occurs in small assemblages, with a maximum of five individuals on a slab, although it is often in isolation. The general abundance of *L. miltoni* suggests that it was widespread and may have lived in populations.

*F. leptosoma* and *L. miltoni* have distal whip-like terminations to their arms, whereby the adambulacrals have ventrally covered the ambulacrals, and proximal open ambulacral grooves with large podial basins (Pl. 2.21, figs 4-5, 8-9). Hammann and Schminke (1986) concluded that this morphology is evidence for a microphagous to macrophagous feeding strategy. The whip-like distal arm terminations may have aided arm-loop behaviour (Hammann and Schminke 1986); this predatory feeding strategy has been observed in both microphagous and carnivorous taxa (e.g. *O. nigra* and *Ophiura textura*, respectively; Warner 1982). The open ambulacral groove with relatively large tube feet, proximal to the distal terminations, could have allowed food particles to be retrieved from the substrate by the tube feet and transported along the arm to the mouth; this deposit feeding strategy is used in many extant taxa (e.g. *O. nigra*; Warner 1982). The relatively long arm spines of *Furcaster* and *Lapworthura* (Pl. 2.2, figs 8, 10), in contrast to short spines of extant macrophagous taxa (Lawrence 1987, p. 33) may suggest that microphagous deposit or suspension feeding strategies were also used (Dean 1999b, p. 160). The relatively long spines of *F. leptosoma* and *L. miltoni* do not necessarily preclude arm-looping, as detailed quantitative comparison of spine lengths amongst fossil and extant microphagous and macrophagous taxa has not been undertaken. The relatively large tube feet may be indicative of deposit or suspension feeding or perhaps prey-manipulation in both species (e.g. following Hammann and Schminke 1986; Glass and Blake 2004, respectively). The muscular mouth frame of these species, as suggested by Dean (1999a) for *Furcaster trepidans*, is further evidence for a selective carnivory feeding strategy. In common with modern taxa (e.g. Warner 1982), *F. leptosoma* and *L. miltoni* are interpreted to be generalists adopting a range of feeding strategies.



As the stelleroids are vagile, background sedimentation in the channel head area is unlikely to have posed a significant environmental stress. Modern stelleroid taxa such as *A. filiformis*, *A. rubens* and *O. fragilis* show a low intolerance to increases in suspended sediment in the water column in current agitated areas (e.g. Jackson 1999; Budd 2001; Hill and Wilson 2005). The relatively more abundant Leintwardine taxa such as *F. leptosoma*, *L. miltoni*, *L. calceatus* and *S. marstoni* may have been more tolerant than other species to physical environmental stress such as sedimentation and turbidity, and thus able to colonise greater areas of the channel head floor. The relatively large size and robust, highly mobile arm morphology of *L. miltoni* could account for the proposed low intolerance to sedimentation in this species.

*Crinoids.* The Leintwardine crinoids are small and show a relatively low taxonomic diversity (five species), in comparison to contemporaneous echinoderm-bearing deposits (e.g. the Ludlow Series Brownsport Formation, Tennessee, USA, which has approximately 40 species; Brower 1975). This suggests that the channel setting only provided a marginal habitat for the crinoids (Text-fig. 2.27), as postulated for the Silurian Pentland Hills crinoids of Scotland (Brower 1975). It may reflect an environmental stress, for example, in the form of quiet water conditions and periodic inundations of high sedimentation. The pinnulate *C. quinquepennis* is the most abundant species, and may have possessed the most well adapted rheophilic feeding strategy for this environment. The setting is interpreted to have been periodically turbulent, perhaps carrying in increased organic detritus; these conditions are likely to have been advantageous for crinoid suspension-feeding (Brett 1984).

As documented by Brett (1984) for non-Leintwardine specimens, associated physical environmental stress in the form of sediment fouling or burial, is likely to have been lessened by the possession of tightly closing crowns or protective cover plates and relatively long columns. Brett (1984) added that short-stemmed taxa are commonly found in biostromal or reefal carbonates whilst long-stemmed forms tend to occur in argillaceous facies. Column lengths of taxa representative of two of the genera recorded from Leintwardine (*Gissocrinus* and *Dendrocrinus*) are documented as attaining considerable heights (Watkins and Hurst 1977; Brett 1984). Brett (1984) stated that the genera *Gissocrinus* and *Dendrocrinus* attained maximum column lengths of 200 mm and 150-200 mm, respectively, whilst Watkins and Hurst (1977, pl.1, fig.



A) figured a specimen of *Gissocrinus goniodactylus* from the Silurian Wenlock Limestone of Dudley, UK, with a column length of approximately 210 mm. Specimens recovered from Leintwardine all possess incomplete columns so determination of their column lengths is not possible (Table 2.3). The holotype of *G. ludensis* (BMNH E 26573; Pl. 2.11, fig. 6) has a comparable calyx height (7 mm) to that of the aforementioned *G. goniodactylus* specimen (8 mm); it is therefore possible that both species had similar column lengths (Table 2.3). Some crinoid taxa have also been shown to have inhabited muddy, sediment-laden seas; Ager (1963, p. 132) documented autochthonous crinoid specimens within shales from the Mississippian of Indiana, USA. It is probable that the majority of the Leintwardine crinoid fauna would have occupied perches, relatively sheltered from the majority of the sedimentation (e.g. inhabiting the channel flanks and surrounding shelfal facies).

Holdfasts are not preserved in the Leintwardine specimens and documentation of whether these species possess such structures is lacking. Species of *Gissocrinus* recorded from the Wenlock Limestone of Dudley possess cirri along the distal 20 mm portion of their column, which were apparently adapted for flexible penetration into unconsolidated sediment (Watkins and Hurst 1977). Brett (1984) stated that *Gissocrinus* possessed a distal portion of the column with stout, branching cirri, which was adapted for penetration into loose sediment, forming a rhizoid. It is therefore inferred that the Leintwardine species, *G. ludensis* may also have possessed similar secondary holdfast structures and mode of life. Watkins and Hurst (1977) added that holdfasts shown in the Dudley crinoids were probably adapted to accommodate some sediment movement of the substrate. If attachment was into a soft substrate then the holdfast would presumably have been of a root-like morphology, whilst hard-substrate attachment is likely to have taken the form of a cemented disc or comparable structure (Fell 1966). *Eutaxocrinus* possessed a discoidal holdfast (Brett 1981); taxa with these holdfasts may not have been limited to hard substrates provided a firm object for attachment was available (Franzén 1977). Brett (1984) stated that a semi-permanent holdfast structure of flexible cirri in the distal portion of the column occurs in the hapalocrinids and *Dendrocrinus*, which was adapted for attachment into muds. Watkins and Hurst (1977) described the hapalocrinid, *Clematocrinus retiarius*, from the Wenlock of Dudley, stating that it showed no evidence of a holdfast and had a short column with cirrinodals; they felt that it may have been effectively free-living. This



TABLE 2.3. Column lengths of Leintwardine crinoids; columns are incomplete therefore full length is unknown.

Species	Specimen Number	Column length (incomplete) mm
<i>C. quinquepennis</i>	BGS GSM89897 (Paratype)	38
<i>C. quinquepennis</i>	BGS GSM89900	30
<i>C. quinquepennis</i>	CH119	36
<i>G. ludensis</i>	BMNH E 26573 (Holotype)	65
<i>E. maccoyannus</i>	CH118	11
<i>E. maccoyannus</i>	BMNH E 26578	11
<i>E. maccoyannus</i>	BMNH E 1314	15
" <i>Actinocrinites</i> " sp.	BMNH E 46753	37
" <i>Cyathocrinus</i> "	BGS GSM90006	32



taxon was stated to be the dominant species in a soft-bottom, low-diversity crinoid assemblage, and Watkins and Hurst (1977) suggested that it may have lived in discrete populations surrounded by areas of unoccupied seafloor. Specimens of *C. quinquepennis* from Leintwardine do not preserve cirri nor the distal sections of the columns. The columns are not evidently short and since they do not possess proximal cirri, the species possibly had a distal portion of the column with cirri. The Leintwardine taxa inferred to have possessed flexible secondary holdfast attachment (e.g. *C. quinquepennis*, *G. ludensis*) are likely to have been able to adapt to a range of substrate and energy conditions (Brett 1984).

Pinnulate camerate taxa are postulated to have fed by forming orientated filtration fans with the brachia and pinnules, in the manner of extant crinoids (Macurda and Meyer 1974); the pinnulate Leintwardine species, *C. quinquepennis* is therefore inferred to have adopted this feeding strategy. Taxa with widely branched brachia probably fed by capturing relatively larger detritus (Macurda 1976; Meyer and Lane 1976; Brett 1984; Ausich *et al.* 1999). Brett (1984) assigned various Silurian taxa to six different modes of feeding. Within his 'rheophilic filtration fan feeding' mode he placed pinnulate camarates and several ramulate to pinnulate inadunates. Brett added that some species of *Gissocrinus*, with isotomous branching and relatively open-meshed filtration fans may have possessed tube feet that partially filled gaps in the baffle. The heterotomous branching of the mastigocrinids (e.g. *M. bravoniensis*) may have led to close-meshed filtration fans (Brett 1984). The flexibles, with their sparsely spaced brachia, were largely placed within the 'raptorial feeding' mode (Brett 1984); *E. maccoyannus* is tentatively suggested to have adopted this feeding strategy.

*Other echinoderms.* The Leintwardine echinoids taxa are 'regular' and are therefore inferred to have been epifaunal, adopting a vagile, deposit-feeding habit (Durham *et al.* 1966); ventrally positioned feeding apparatuses are prominent. The ophiocistioids are inferred to have adopted an epifaunal, vagile, deposit-feeding habit much like that of the echinoids (Ubaghs 1966). The ventrally positioned feeding apparatus, enlarged podia and the absence of food grooves suggest this habit (Hyman 1955). Assessing from ecological criteria whether the echinoids and ophiocistioids were indigenous to the channels is problematic, as general background sedimentation would not necessarily have posed a problem for these vagile echinoderms.



*Phylum Arthropoda*

*Eurypterids.* The pterygotids (e.g. *E. marstoni* and *P. arcuatus*) were nektonic, as indicated by the development of swimming paddles on prosomal appendage VI, small, slender non-spiniferous walking limbs on appendages II-V, and a large, laterally expanded telson (Plotnick and Baumillar 1988). Selden (1984) stated that the small size of the walking limbs indicated that they may have been used in a buoyant, tripling gait as in extant lobsters. The enlarged size of the chelicerae of the group (Pl. 2.14, fig. 9), combined with overall large body size, active swimming habit and inferred anterior stereoscopic vision, suggest a carnivorous feeding style (Selden 1984). Selden (1984) stated that the pterygotid chelicerae were likely to be well adapted to capturing nektonic vertebrate prey. *C. punctatum* also possesses swimming paddles developed on appendage VI, although the walking limbs are relatively better developed than in the pterygotids (Pl. 2.14, figs 1, 8, 10). Reconstructions of *Carcinosoma scorpionis* (Størmer 1955, fig. 23) show the opisthosoma to be relatively less streamlined than in the pterygotids; *Carcinosoma* possesses a distinct abdomen and postabdomen (Tollerton 1989). The telson is also of a styliform morphology, which would presumably be less well adapted to a fully nektonic mode of life. These characters suggest that *Carcinosoma* was likely to have adopted a nektobenthic habit, being less of an active swimmer than the pterygotid taxa.

*Xiphosurans.* Habits employed by the various synziphosurines are reported to be variable. The morphology of taxa such as *Limuloides* is regarded as intermediate between ancestral largely non-burrowing forms and extant burrowers, indicating limited burrowing and employment of an eurypterid-like hunting lifestyle (Bergström 1975; Stürmer and Bergström 1981). The morphology of *Psuedoniscus* and *Cyamocephalus* with their highly vaulted prosoma and widely separated ophthalmic ridges (Pl. 2.15, figs 3, 5), implies that they adopted a burrowing habitat (Fisher 1981).

*Phyllocarids.* Recent leptostracans have a nektobenthic mode of life, feeding on organic rich detritus (Rolfe and Beckett 1984). The archaeostracans are assumed to have employed a similar nektobenthic habit and may also show adaptations for burrowing, such as striae along the carapace (Vannier *et al.* 1997). Striae have not been noted on the carapaces of the Leintwardine specimens. Most archaeostracans are believed to have preferred quiet bottom waters (Rolfe and Beckett 1984) and the



sheltered outer shelf area probably offered these conditions. Detritus-feeding mechanisms employed by *Ceratiocaris* may have been variable (Rolfe and Beckett 1984). Smaller forms may have used their slender thoracopod limbs to lift bottom sediment into suspension; feeding (and respiratory) currents may also have been drawn in and directed through a feeding basket formed by these limbs. Rolfe and Beckett (1984) added that larger forms were probably macrophagous, being able to tear particles from carrion. Detritus particles may also have been picked up directly by the mouthparts. A life habitat within or surrounding the channel head system is suggested, with some articulated specimens inferred to have been indigenous to the setting (Text-fig. 2.27).

*Other groups.* The relative abundance and state of preservation of the ostracods may indicate that some taxa were indigenous to the channels. The relatively abundant palaeocope beyrichiaceans recorded from the deposits (Jones 1969) are generally regarded as having a nektobenthic mode of life, and typically occupied relatively shallow shelf and slope settings (Siveter 1984; Siveter *et al.* 1991). It is suggested that they occupied the immediately surrounding shelf-break areas, with some perhaps being indigenous to the channel heads. Most, though not all myodocopes are regarded as being pelagic; taxa that may not be pelagic include '*Entomozoe*' *tuberosa* (Siveter *et al.* 1991). The less abundant myodocopes of the channels (e.g. '*Entomis*') may or may not be pelagic. Myodocopes typically occur in unusual shelf troughs and/or more offshore shelf-slope settings.

### *Phylum Brachiopoda*

*L. lata* is inferred to have adopted an infaunal, burrowing lifestyle (Cherns 1979; Bassett 1984). Watkins and Berry (1977) proposed that occurrences of *L. lata* in graptolitic basin sediments may indicate an epiplanktic attachment to *Sargassum*-like rafts. Sheehan (1977) stated that a deep-water shelly fauna could be explained by the theory that specimens were benthic, attaching themselves to firm substrates provided by sunken seaweed rafts on the sea floor. Cherns (1979) argued that *L. lata* was more likely to have been infaunal within the relatively deep-water basinal environments. Rare *in situ*, articulated specimens of *L. lata* occur in basinal areas of the Welsh Basin (Cherns 1979), supporting the theory that the species is an infaunal taxon, which may inhabit relatively deep-water settings.



The other taxa are likely to have assumed an essentially epifaunal lifestyle. Liberosessile ambitopic (secondarily free-lying, adapted for resting on soft-bottoms) taxa described from the channel fill are *A. reticularis*, *L. filosa*, *P. ludloviensis*, *S. ludloviensis*, *S. ornatella*, and probably *C. grayi* (Bassett 1984). *P. ludloviensis* may have obtained stabilisation from oblique hinge spines on the convex pedicle valve (Cherns 1988). *L. filosa* and *S. ornatella* are likely to have shown intolerance to sedimentation, due to the positioning of their apertures close to the sediment surface (Cherns 1977). As with other chonetaceans (Bassett 1984), *S. ludloviensis* was probably liberosessile and ambitopic; it was likely to have lived in quiet conditions, inhabiting soft substrates (Cherns 1977, 1988). In common with other spiriferids (Bassett 1984), *D. navicula* is likely to have been liberosessile; its small size and free-living habit were suggested by Cherns (1977) to be adaptations to quiet conditions. The species may have formed cosupportive populations, obtaining stability from partial sediment burial and close juxtaposition with neighbouring individuals (Cherns 1988). *L. depressa* was probably quasi-infaunal (Bassett 1984). *Orbiculoidea* sp. and *S. striata* probably adopted a fixosessile, encrusting lifestyle (Bassett 1984).

The rhynchonellid *M. nucula* is inferred to have been fixosessile and pedunculate, strongly attached to a hard substrate by a muscular functional pedicle (based on studies of beak morphology and pedicle-type by Richardson 1981, cited in Ratcliffe 1991). The pedunculate nature of the taxon indicates that it occupied hard substrates (Cherns 1988). Fürsich and Hurst (1981) stated that *S. wilsoni* was likely to have adopted a liberosessile ambitopic life strategy, with adults being semi-infaunal, whilst Cherns (1977) and Ratcliffe (1991) assumed a similar life strategy for *S. wilsoni* as for *M. nucula*, with the species being adapted for life in turbulent conditions. Fürsich and Hurst (1981) argued that the apparent lack of a pedicle throughout ontogeny in *S. wilsoni* indicates that the species inhabited calm environments with slow rates of sedimentation. *S. wilsoni* may have formed close packed, cosupportive populations that added some mutual support (Cherns 1988, 1999).

Some specimens of the taxa (e.g. some *L. lata*, *M. nucula*) are interpreted to have perhaps been indigenous to the channel head area. Adaptations to turbulent conditions, such as large pedicle openings (indicating a stout pedicle for attachment) and thick shells with heavy ribbing (Fürsich and Hurst 1974), are exhibited by *M. nucula*



(Ratcliffe 1991). Liberosessile taxa may not have been well adapted to turbulent settings unless the shell was heavy enough to act as stabilisation (Fürsich and Hurst 1974). Increased sediment may not have posed a risk of sediment fouling for the rhynchonellids, as they possess strong zig-zag plicae (Rudwick 1964, cited in Fürsich and Hurst 1974) which could have acted as filters. However, the majority of brachiopod specimens are interpreted to have been transported from the shelf.

### *Other fauna*

Extant bryozoans have a sessile suspension-feeding habit and require a clean, firm substrate for settling, avoiding surfaces covered in fine sediment (Brood 1984). In areas subjected to high sedimentation, individuals tend to favour sheltered habitats behind rocks, corals and stromatoporids (Brood 1984). For these reasons, the availability of suitable substrates is a limiting factor in bryozoan distribution (Brood 1984). It is likely that Palaeozoic taxa were similarly constrained to suitable sheltered or relatively sediment-free substrates.

*Sphenothallus* and conulariids are likely to have been sessile, benthic organisms (Mason and Yochelson 1985, Bodenbender *et al.* 1989, Van Iken 1991), which may have been able to colonise soft, muddy substrates (Van Iken *et al.* 1996, Neal and Hannibal 2000). It is possible that these taxa were indigenous to the channels (Text-fig. 2.27).

The palaeoscolecsids may have had an infaunal, burrowing habit (Runnegar 1982; Conway Morris and Robison 1986; Conway Morris 1997); however, Gedik (1981, cited in Müller and Hinz-Schallreuter 1993) proposed a nektonic mode of life. Conway Morris and Robison (1986) stated that the absence of locomotor muscles and an inferred circular transverse section in the palaeoscolecid *Palaeoscolex* suggested an infaunal habit. The characteristic papillate ornamentation of the palaeoscolecsids (e.g. in *Palaeoscolex* and *Protoscolex*) bears a close resemblance to that of the Middle Cambrian infaunal priapulid *Louisella pedunculata* (Conway Morris 1977, 1997; Conway Morris and Robison 1986), further suggesting such a habit. It has been proposed that these transverse rows of plates may have aided in gripping sediment during burrowing (Conway Morris and Robison 1986; Conway Morris 1997). Müller and Hinz-Schallreuter (1993) suggested that, if a burrowing habit is accepted, then



different taxa may have adopted variable benthic habitats (coarser to finer sediments), inferred by the presence or absence of abrasion on the papillate ornament. SEM study shows fine scale morphological detail on the ornament of the palaeoscolecid worms recovered from the Leintwardine channels, with no noticeable abrasion, which may indicate that the worms inhabited a muddy environment. The palaeoscolecids are interpreted to have been indigenous to the channels.

### *Water depth inhabited by fauna*

The indigenous fauna of the channels would have occupied an essentially shelf-break position. Assessing absolute water depth for the shelf-break setting is problematic as no precise quantitative estimates exist for fossil assemblages (Brett *et al.* 1999). Average modern shelf margin depths are in the region of 200 m (Brett *et al.* 1993), and Shabica and Boucot (1976) inferred that mid-Palaeozoic shelf margins may also have been at equivalent depths. An absolute maximum water depth of 200 m can therefore be suggested for the Leintwardine channel heads, although the depth is likely to have been less, as the shelf area of the Midland Platform is generally accepted as being relatively shallow during the Ludlow Series, as suggested by the calcareous sediments of the area, and the marine regression at this time (Siveter *et al.* 1989; Johnson *et al.* 1991).

The three major brachiopod faunal associations of Cherns (1988, 1999), occupying the calcareous siltstone facies of the shelf area during times of Lower to Upper Leintwardine Formation deposition have all been assigned to BA3 (Cherns 1999). BA3 is equivalent to Ziegler's (1965) *Pentamerus* community of the Lower Silurian (Boucot 1975; Brett *et al.* 1993); an average depth of 30-40 m for this benthic assemblage has been postulated by Brett *et al.* (1993), with the outer limits perhaps reaching a depth of 66 m (Boucot 1975, p. 52). Boucot and Janis (1983) stated that the higher Lower Leintwardine Formation channel fill at Church Hill contained communities representing BA's 2 and 3. The shelf-break area may partially encompass a further brachiopod faunal association of Cherns (1988, 1999), occupying the laminated siltstone facies of the trough area (*Lingula lata-Saetograptus leintwardinensis* Association; Cherns 1988, 1999). This association has been assigned tentatively to BA4-5 (Cherns 1999). BA4 is equivalent to Zeigler's (1965) *Stricklandia* community of the Lower Silurian (Boucot 1975; Brett *et al.* 1993) and an average depth of 50-60 m has been suggested for this benthic assemblage by Brett *et al.* (1993).



Palaeozoic echinoderms typically inhabited relatively shallow depths (e.g. less than 100 m) whereas extant groups may occupy greater depths (e.g. Meyer and Macurda 1977; Aronson and Harms 1985; Aronson 1989; Oji 2001). This adaptation to inhabiting deeper marine environments has been attributed to predation pressure which arose in the late Mesozoic (e.g. Meyer and Macurda 1977; Aronson 1989). Obtaining a precise estimate of the likely depth ranges within the shallow shelf setting for the Palaeozoic echinoderm taxa is not possible, as, in common with extant forms, the groups are likely to be tolerant of a range of depths. Modern shallow water (less than 100 m) dense ophiuroid populations are found in a range of geographical locations including the northeastern Atlantic, the Mediterranean, the Antarctic and sub-Antarctic (Aronson 1989). Palaeozoic crinoids were common in shallow marine facies (e.g. as shallow as 5-10 m depth; Wilson 1975; Meyer and Macurda 1977), although they have been documented from greater depths. Sprinkle and Longman (1982) described crinoids from the Middle Ordovician which occupied depths ranging from 3-75 m, whilst Wilson (1975) described crinoids which may have lived at several hundred metres depth.

Kjellesvig-Waering (1961) assigned the Leintwardine eurypterid taxa to his 'Carcinosomatidae-Pterygotidae' Association (one of three eurypterid biofacies proposed representing varying degrees of salinity-tolerance), adding that it represented fully marine conditions. However, Størmer (1976) stated that that the association was more likely to suggest a marine to brackish water environment. Boucot (1975) noted that the carcosomatid and pterygotid taxa of the Welsh Borderland occurred within the ranges BA1 to BA3. Plotnick (1999) stated that the Leintwardine eurypterid 'Carcinoma-Pterygotina' association can be assigned to Boucot's (1975) benthic assemblage BA3, implying subtidal conditions within the photic zone; this assignment was based on the associated brachiopods. Manning (1993) modified Kjellesvig-Waering's model, concluding that a 'palaeoecological gradient' between taxa was evident, with inter-phase mixing between species occurring. Braddy (2001) rejected Kjellesvig-Waering's (1961) model as too simplistic, adding that many of the assemblages have mixed compositions. Braddy (2001) proposed that each genus was likely to have had a broad range of suitable habitats with juveniles occupying near shore and lagoonal environments (as part of his 'mass-moult-mate' hypothesis). An



apparent lack of juvenile specimens within the Leintwardine assemblages may support Braddy's (2001) model.

Anderson (1998) stated that most synziphosurines occur within marginal marine sediments, in association with eurypterids, although he added that examples of deeper water occurrences from the fossil record may occur (e.g. the Lower Devonian synziphosurine *Weinbergina* from the Hunsrück Slate of Germany). Rare examples of the extant *Limulus* occurring within deeper marine settings have also been recorded; Shuster (1982, cited in Anderson 1998) cited *Limulus* as being recorded at depths of 246 m on the continental shelf. These observations indicate that fossil taxa may occupy relatively deep water, distal settings; these ecological ranges, combined with the completely articulated nature of some of the Leintwardine material indicates that at least some of the specimens were likely to be indigenous to the channel settings or the immediately surrounding shelf.

In conclusion, the water depth inhabited by the fauna of the shelf break area was probably relatively shallow. Determining a precise depth is difficult; however, depths in the region of 50 m are likely. This inferred depth is likely to be representative of both BA's 3 and 4.

## MODERN SUBMARINE CANYON BIOTAS-A COMPARISON

Modern submarine canyons can harbour higher local densities and diversities of benthic and pelagic faunas than the surrounding continental shelf and slope or at least may harbour distinct canyon 'indicator' species (e.g. Griggs *et al.* 1969; Rowe 1971; Rowe *et al.* 1982; Greene *et al.* 1988; Vetter 1994; Cartes 1998; Vetter and Dayton 1998; Gilli *et al.* 2000). These canyon-specific species have been recorded in the Hatteras, Alvin and Hudson canyons, eastern USA (Rowe 1971; Haedrich *et al.* 1975, 1980), the Monterey, Scripps/ La Jolla canyons, central and southern California (Vetter 1998; Summers *et al.* 2000), and the Capbreton Canyon, Bay of Biscay, NE Atlantic (Marquiegui and Sorbe 1999). In some canyons, biomass may be the same or lower than in the surrounding areas (Rowe *et al.* 1982; Gage and Tyler 1992). In the Hudson Canyon, biomass is only higher in the canyon head area, where the system is 'inactive' and filling with organic-rich, fine-grained sediments (Rowe *et al.* 1982). Although



faunal abundances are higher in this part of the canyon, species diversity is not significantly different from the surrounding non-canyon area (Rowe *et al.* 1982).

Extant canyon faunas comparable with those of the Leintwardine channels are well documented; these settings can harbour increased abundances of echinoderms and arthropods relative to the surrounding environment, or canyon-specific representatives of these groups. The Hudson and Alvin canyons harbour stelleroid-dominated faunas with canyon-specific ophiuroids; the Hudson Canyon has two species (*Ophiura sarsi* and *Ophiura signata*) whilst the smaller Alvin Canyon has *Amphilimna olivacea* (Haedrich *et al.* 1975, 1980). The Hudson Canyon also has a canyon-distinct asteroid species, *Psilaster flora* (Haedrich *et al.* 1980). Rowe (1971) documented the asteroid *Astropecten americanus* as occurring within the upper Hatteras Canyon, although it is not clear if this is a canyon indicator species. A high mean abundance of ophiuroid species occurs within the deeper (>500 m depth) Monterey Canyon (Summers *et al.* 2000), whilst ophiuroids have been documented in the head of La Jolla Canyon (Warne *et al.* 1978). Echinoids have been documented within the Hueneme Canyon, California and the Santa Maria Canyon, California (Bouma 1965; Scott and Birdsall 1978).

A dense assemblage of canyon-specific leptostracan phyllocarids (*Nebalia hessleri* and *Nebalia* sp.) has been documented within the Scripps Canyon; along with two species of amphipod these taxa comprise 99% of the fauna of the canyon (Vetter 1998). Abundant leptostracan also occur in localised areas within the Monterey Canyon (Okey 1993). Other canyon-specific crustaceans (amphipods, tanaids, isopods) have been documented within the Capbreton Canyon, Bay of Biscay (Marquiegui and Sorbe 1999).

Increased biomass in submarine canyons has been attributed to upwelling and downwelling, higher sedimentation rates with organic and inorganic debris, and hydrodynamics conducive to unique faunal communities (Gilli *et al.* 2000). Vetter and Dean (1998) attributed increased infaunal biomass within the Scripps and La Jolla canyons to organic enrichment by macrophyte (kelp and surfgrass) detritus, adding that strong currents may have winnowed out the fine organic particulates. Several mechanisms are involved in supplying the enhanced food supply to canyon faunas: accelerated rates of nutrient-carrying currents would be of particular benefit to



suspension-feeding benthic faunas, whereas high sedimentation rates in ‘inactive’, infilling settings, may supply deposit-feeding faunas with increased food supply (Vetter and Dayton 1998). Accumulations of macrophyte detritus have been held responsible for the concentrations of crustaceans within the Scripps and Monterey canyons (Vetter 1998).

### RAPID BURIAL – OBRUTION

Obrution is likely to be a major process in the preservation of the channel fauna, particularly the echinoderms; Brett (1990, p. 239) stated that “obrution is involved in most, if not all examples of exceptionally preserved, articulated fossils”. The articulated nature of much of the fauna indicates rapid entombment (Brett 1990). Brett (1990) added that each obrution deposit consists of two components: the ‘buried horizon’ and the ‘burial layer’. Factors characteristic of the buried horizon are hardgrounds, concentrations of shelly or skeletal material, occurrence of sessile or semisessile organisms on the buried surface or fossils of infaunal organisms directly below the surface (Brett 1990). The rapidly deposited (hours to days), overlying burial layer is generally less fossiliferous or barren and is often of a structureless mudstone or siltstone lithology (Brett 1990). Burial layers may also show a fining up in grain size and planar and cross lamination, indicative of a waning current (Brett 1990). Several of the shelly lags within the Church Hill Channel fill probably represent a buried horizon, each overlain by a burial layer (e.g. the dense rhynchonellid horizon c. 70 mm below the base of Starfish Bed A; CH175; Pl. 2.18, fig. 6). Brett and Seilacher (1991) noted that obrution layers contain not just sessile faunas but also vagile faunas such as stelleroids and trilobites in concentrations higher than would normally be expected of carcasses on the seafloor. They added (1991) that typical obrution deposits therefore require a number of factors including: availability of adequate numbers of undecayed carcasses; rapid deposition of a sedimentary blanket thick enough to hold the articulated skeletons together, and to protect them against disarticulation from scavengers and bioturbators; permanent removal of the burial ground from the reach of subsequent event erosion and resedimentation. Relatively low energy environments, just below normal storm wave base may be the most conducive area for obrution deposit preservation (Brett 1990). This setting is postulated for the shelf edge Leintwardine channel deposits (Text-fig. 2.27).



## CONDITIONS OPERATING WITHIN CHANNEL HEADS

The Church Hill Channel is interpreted to have had relatively calmer conditions than the Todding Channel, with background sedimentation alternating with influxes of increased (event) sedimentation (see below). Occasional slumping may have brought in sediment and derived boulders from the channel flanks. Sedimentation patterns through the 2.6 m section of channel fill at Quarry 1 may suggest that a tidal signature is present, in which case infilling of the channel head would have been rapid. However, this is not conclusive. Opportunistic echinoderm benthos are common, although short-lived, indicating that conditions within the channel head and surrounding shelf were amenable, for a certain time at least, for colonisation. The apparent absence of echinoderms above Starfish Bed A suggest that conditions became unfavourable for colonisation; increased sedimentation may have accounted for this.

The Todding Channel is notable for having boulder-beds alternating with the siltstone channel fill. This suggests that the channel head was subjected to periodically relatively high-energy conditions; this may account for the relative rarity of echinoderms within the deposit. Stelleroids have also been only rarely collected from the Mocktree Channel, suggesting this area may also have been less amenable to benthos than the Church Hill Channel.

### *Sedimentation through the vertical succession of Church Hill Channel fill siltstone*

The 2.6 m succession of channel fill at Church Hill Quarry 1 can be broadly divided into background and event (e.g. major storm) sedimentation (Text-fig. 2.9). Three main phases of increased current activity may be recognised: Unit 2 (= Starfish Bed A; with silt laminae less well developed); Unit 4 (abundance of shelly fossils, particularly brachiopods); Unit 6 (abundance of scour surfaces; silt laminae poorly developed). Scour surfaces are predominantly constrained to unit 6; none were recorded at unit 2; one at unit 4, and 14 through unit 6. The brachiopods and disarticulated arthropod material was recorded through all three units, although the echinoderms were confined to unit 2 (Starfish Bed A).

Alternating with these fossiliferous sections are relatively barren (although often graptolite-rich horizons) vertical sections of channel fill, generally showing well-



developed silt laminae. These phases indicate a return to periodically calmer background sedimentation, which may be tidally controlled: Unit 1, Unit 3, and Unit 7.

*Unit 1.* Comprises the lower 0.33 m of the section and contains some brachiopods (dominantly *M. nucula*, *S. wilsoni*; also *A. reticularis*, *L. depressa*, and *L. lata*), ostracods and graptolites. Silt laminae are well developed and mud laminae thicknesses appear to show a rhythmic periodicity (Text-figs 2.5, 2.9; thin section CH50).

*Unit 2 (Starfish Bed A).* The base of the starfish bed is defined at a particularly dense shelly brachiopod layer occurring at a height of 0.33 m from the base of the section (consisting of numerous *M. nucula* specimens; e.g. CH175; Pl. 2.18, fig. 6). This shelly brachiopod layer is not traceable laterally to the logged section. The top of the unit is defined at the uppermost stelleroid occurrence, at a height of 0.63 m from the base of the section. The vertical thickness of the starfish bed is 300 mm (Text-figs 2.5, 2.9, 2.16). Stelleroids are noted through a vertical thickness of 230 mm; the first occurrences are documented approximately 70 mm above the base of the unit (Text-figs 2.5, 2.16). Within the logged section, stelleroid specimens were only noted through a vertical thickness of 40 mm (Text-figs 2.5, 2.16). Starfish Bed A may represent a storm event, with increased current activity within the setting. The bed is interpreted as a burial layer(s) of an obrutionary deposit; the shelly brachiopod layer at the base is interpreted as a buried horizon. The fauna is interpreted to be parautochthonous to allochthonous. Stelleroid individuals occur entombed within the siltstone, at different horizons, often only several millimetres apart (Text-fig. 2.16; Pl. 2.8, figs 2-5). No high numbers of multiple occurrences were noted on a single bedding plane and museum specimens of stelleroid taxa recorded from this horizon likewise do not exhibit dense bedding plane aggregations (e.g. *B. vermiformis*, *F. leptosoma*, *L. miltoni*). Stelleroid specimens occur relatively sporadically through the bed, not occurring along a single bedding plane. Near-complete crinoids also occur sporadically through the bed (e.g. *C. quinquepennis*). The echinoderms are relatively more abundant towards the base of the starfish bed (Text-fig. 2.16).

Numerous other fossils occur within Starfish Bed A; for example brachiopods, current aligned graptolites, predominantly disarticulated arthropod material (e.g. eurypterids, phyllocarids), and intact bryozoans. Several brachiopod-rich (e.g. *D. navicula*, *L. depressa*, *L. lata*, and *M. nucula*) shelly horizons occur throughout this bed, also



containing crinoid ossicles and occasional gastropods. Some graptolites were also noted. Silt laminae continue through Starfish Bed A although they are relatively poorly developed (Text-fig. 2.9; thin sections CH45-44, 41).

*Unit 3.* The overlying 310 mm of channel fill are relatively barren although some graptolites occur (Text-fig. 2.5). Silt laminae are relatively well developed. This unit represents background sedimentation (Text-fig. 2.9).

*Unit 4.* A second fossiliferous section, approximately 210 mm in vertical thickness, containing several brachiopod-rich shelly layers (Text-fig. 2.5). Some semi-articulated arthropod material (e.g. trilobites, eurypterids and phyllocarids) occurs. Along with the shelly horizons, a scour surface also occurs. This unit may represent a second phase of storm activity.

*Unit 5.* The overlying 795 mm is relatively barren (Text-fig. 2.5). Very occasional brachiopods, arthropods and crinoid ossicles occur, and the unit contains abundant graptolites. There are a few signs of current activity. At a height of approximately 1.65 m, a scour surface is recorded; just above this aligned graptolites were documented. Silt laminae are relatively well developed (Text-fig. 2.9; thin sections CH25, 23). This unit is interpreted to represent background sedimentation.

*Unit 6.* A third fossiliferous unit (c. 355 mm, representing a third pulse in current activity) overlies the barren section, bearing abundant brachiopods and arthropod material (Text-fig. 2.5). The section contains 14 scour surfaces, indicating an increase in erosive current activity. Graptolites continue up through the section, and tend to show current alignment. Based on depth observations of Hawkins and Hampton (1927), the unlocated upper starfish bed is inferred to occur within unit 6. Silt laminae are poorly developed through this unit (Text-fig. 2.9; thin sections CH53, 8b). This section is interpreted to represent a further storm event.

*Unit 7.* This relatively barren unit, containing abundant graptolites, and a few brachiopods (Text-fig. 2.5), is interpreted to represent a return to calmer background sedimentation. Silt laminae are relatively well developed (Text-fig. 2.9; thin section CH4).



## FAUNAL PROVENANCE - A SYNTHESIS

Sedimentological, biostratigraphic and palaeoecological criteria have been used to determine whether the fauna was indigenous, representing autochthonous or parautochthonous thanatocoenoses or exotic, representing allochthonous thanatocoenoses, to the channel setting. The channel biota is interpreted to consist of both indigenous and exotic components, with variable degrees of transportation both inter- and intraspecifically (Text-figs 2.26-27). The indigenous channel fauna is inferred to have been composed of nektonic (chelicerates, phyllocarids, possibly myodocope ostracods) and benthic (e.g. conulariids, echinoderms, palaeoscolecid worms, *Sphenothallus*) elements (Text-fig. 2.27). Pelagic organisms that occur periodically in abundance through the channel fill (e.g. *S. leintwardinensis*, orthocone nautiloids) represent allochthonous thanatocoenoses.

The lack of penetrative bioturbation in the channel fill suggests that some form of environmental stress was present at the floor of the channel heads, and that skeletal disturbance of buried carcasses by bioturbators and scavengers is likely to have been minimal. The lack of bioturbation, if taken alone, could be used to infer that the echinoderms and some of the other transported fauna (e.g. brachiopods, arthropods) were carried into an oxygen-depleted zone of the channel setting. This would theoretically have increased their preservation potential, by discouraging bioturbation, scavengers, and depending on the degree of dysoxia, the rate of soft-tissue decay may have been retarded. However, dysoxia is not proven in the channel heads, based on geochemical analyses of the Church Hill Channel fill. Instead, relatively high sedimentation rates and slumping are likely over much of the channel head floor, and are interpreted to have acted as a faunal inhibitor. A restricted infauna is interpreted for this part of the channel head. A rare epifaunal component existed within parts of the channel head floor. Sedimentation rate is proposed to be central to the preservation of the fauna, with Starfish Bed A at Church Hill essentially representing an obrution deposit.

The echinoderms are interpreted to be dominantly indigenous to the setting based on palaeoecological and biostratigraphic factors, combined with comparisons with modern submarine canyon biotas. The stelleroids are interpreted to have been mostly indigenous to the channel head and immediately surrounding shelf area, based on the



high degree of articulation, preservation of monospecific assemblages along a single horizon, low species diversity within Starfish Bed A and a lack of recovered stelleroids in the outer shelfal areas. The degree of transportation is inferred to have been variable, intra- and interspecifically; a few specimens may be autochthonous, whilst the majority are interpreted as parautochthonous to allochthonous. The echinoderms are constrained to discrete starfish beds, which suggests they formed a short-lived faunal component of the setting.

The vagile echinoids, stelleroids and ophiocistioids, interpreted to be essentially epifaunal, are unlikely to have been affected by background sedimentation in the channel head area. The stelleroids form the dominant echinoderm component; the crinoids are rare by comparison. This is inferred to be a direct reflection of the original community structure, with many of the stelleroid taxa living in relatively dense populations. The setting is likely to only have provided a marginal habitat for the comparatively rare crinoids (Text-fig. 2.27), as suggested by their low specific diversity and abundance, and small, fragile nature. The crinoids are interpreted to have possessed cover plates and relatively long columns allowing them to inhabit a periodically turbid marginal setting. None-the-less, they are likely to have occupied specific niches within the setting, such as the channel flanks, that were out of reach or sheltered from most of the sedimentation. Rarer solitary echinoderm groups such as the echinoids and ophiocistioids would have formed a minor component of the channel benthos. The echinoderms were possibly concentrated around the edges of the channel heads, away from the bulk of sedimentation occurring at the channel head floor (Text-fig. 2.27). This is comparable to the “edge effect” around oxygen minimum zones documented by Thompson *et al.* (1985). Some stelleroid taxa such as *L. calceatus* and *S. marstoni* may have inhabited parts of the channel floors (Text-fig. 2.27); as with some extant stelleroid taxa (e.g. see Jackson 1999; Budd 2001), these species may have been more tolerant to turbidity and suspended sediment.

The echinoderm biota is dominantly transported, indicated by variable way up orientation, current alignment, positioning at slightly oblique angles to bedding, entombment within the sediment mass (whereby specimens occur at slightly different levels through the siltstone) and a lack of horizontal locomotary traces or vertical escape structures. The echinoderms are interpreted to have been buried alive and



transported either alive or immediately subsequent to death. Reworking is generally not likely to have occurred, as specimens remain predominantly articulated and unabraded. Sessile taxa (i.e. the crinoids) are not preserved *in situ*; distal portions of the columns, including potential holdfasts are not preserved.

The monospecific stelleroid assemblages (i.e. *L. calceatus*, *S. marstoni*) are likely to have undergone relatively less transportation than taxa occurring as solitary individuals (e.g. *B. vermiformis*, *F. leptosoma*, *L. miltoni*, *R. pyrotechnica*), and are interpreted to represent parautochthonous assemblages with minimal transportation. If they were subjected to increased transportation (and were indeed allochthonous), then there may be difficulty in explaining how such relatively dense monospecific assemblages have been preserved. It is unlikely that they represent strictly autochthonous assemblages as individuals show a variable way up orientation and may occur at slightly different levels (separated by 1-2 mm) within the siltstone. Stelleroid taxa generally occurring in isolation and entombed within the siltstone body are often inferred to have undergone greater transportation than the monospecific assemblages, being incorporated into the moving sediment mass. However, some of these taxa may have undergone minimal transport (e.g. certain *F. leptosoma* and *L. miltoni* specimens, such as those towards the base of Starfish Bed A).

The other major faunal group represented, the arthropods, also shows variability in transportation. The eurypterid material in particular, may largely represent exuviae; it is unlikely that nektobenthic taxa (e.g. the carinosomatids) would have been overwhelmed by an obrution deposit, owing to their large size (*C. punctatum* specimens may have attained a length of 2.5 m; Kjellesvig-Waering 1961). The semi-articulated preservation suggests specimens may be largely transported into the setting. The eurypterids and phyllocarids occur sporadically through the entire channel fill, which is interpreted to be a result of their nektobenthic or nektonic habit. They were therefore not confined to the palaeoenvironmental setting, and are interpreted to have formed a long-lived faunal component of the channel heads (Text-fig. 2.27). Some of the phyllocarids, which are completely to semi-articulated are likely to represent carcasses rather than exuviae, and some of these may have been indigenous to the channels. The comparative rarity of the synziphosurines suggests that these formed a limited component of the arthropod fauna within the channels; intact specimens may



represent carcasses, and suggest minimal transport. Trilobites are dominantly disarticulated which suggests that fossils are likely to represent exuviae. Many specimens occur in association with shelly lag horizons, providing strong evidence for transportation.

Of the other fauna, the brachiopods are likely to be largely transported from the shelf area (Text-fig. 2.27); some specimens may have been transported over considerable distances. Specimens show variable degrees of valve articulation; the rhynchonellids are often articulated, although this does not preclude transportation. The rhynchonellids often occur in shelly lags, which indicate transport; these dense shelly layers may represent buried horizons. Some specimens (e.g. *L. lata*) may have been indigenous to the setting. *Sphenothallus*, the palaeoscolecoid worms and the conulariids probably represented a limited indigenous benthic component of the channel heads (Text-fig. 2.27). Other relatively rare faunal elements such as the bryozoans, if indigenous to the setting, are interpreted to have occupied specific niches, sheltered from most of the sedimentation.

This relatively high abundance and diversity of the channel fauna could reflect a concentration of organic and inorganic debris from the water column into the channel system, as has been observed in modern canyon settings (Rowe *et al.* 1982; McHugh *et al.* 1992; Vetter 1995; Gili *et al.* 2000). Extant submarine canyons are prone to up-channel currents and associated nutrient enrichment (e.g. May *et al.* 1983; Gili *et al.* 2000); however, there is no direct evidence to suggest that these conditions were occurring within the Leintwardine channels. Modern canyons often yield a higher local abundance and diversity of benthic and pelagic fauna than in other continental shelf and slope habitats or at least may harbour canyon-distinct species (Greene *et al.* 1988; Cartes 1998; Gili *et al.* 2000); therefore these settings are interpreted to provide modern analogues for the Leintwardine channels and their biota.



## EXPLANATION OF PLATE 2.1

Sedimentary structures and orientated fossils (non stelleroids) indicating current activity; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm.

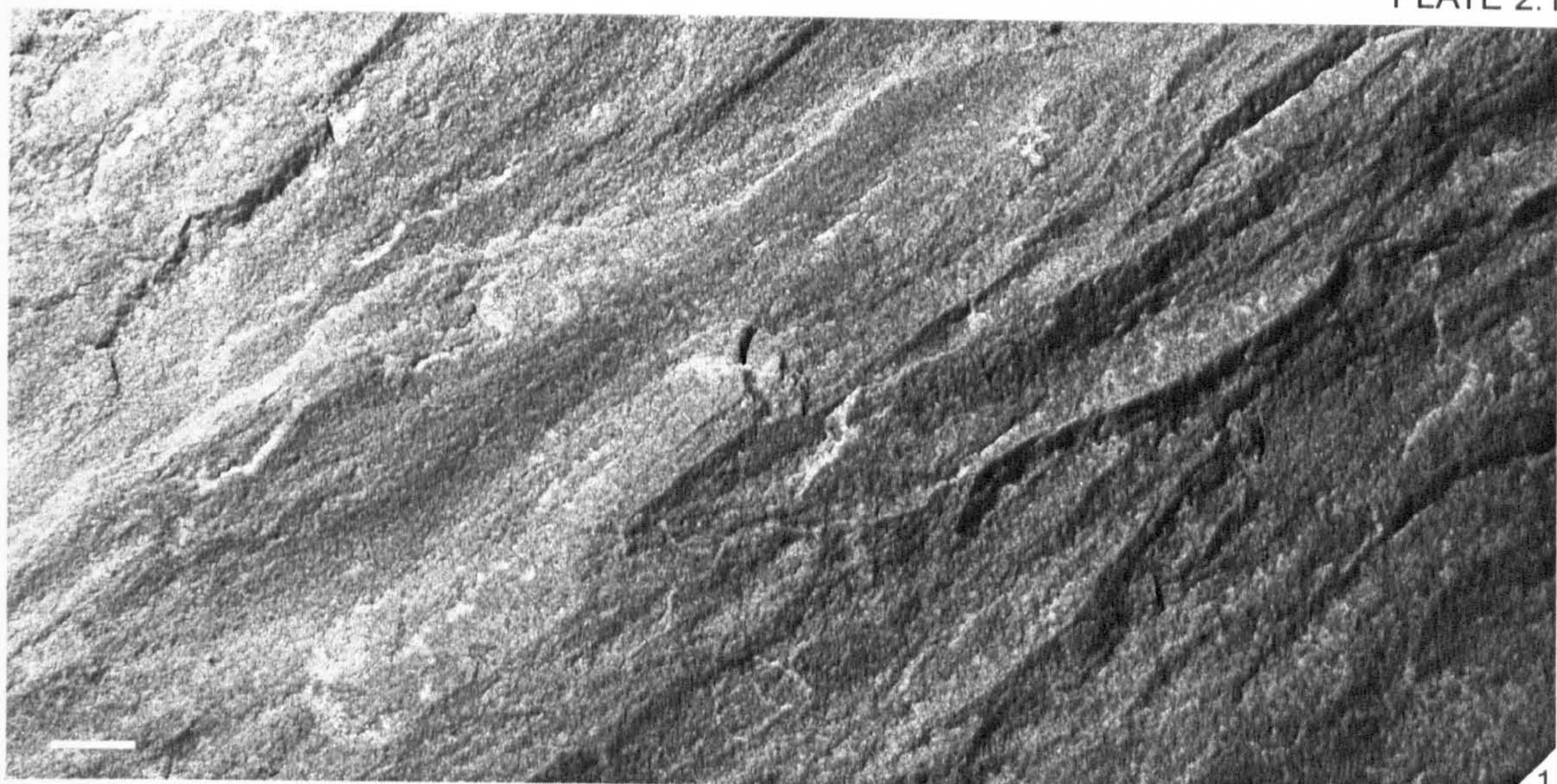
Fig. 1. Scour surface; CH8, upper surface; unit 6, Church Hill Quarry 1.

Fig. 2. Groove filled with broken fossils including *Dayia navicula*; LEIUG 19469; Todding.

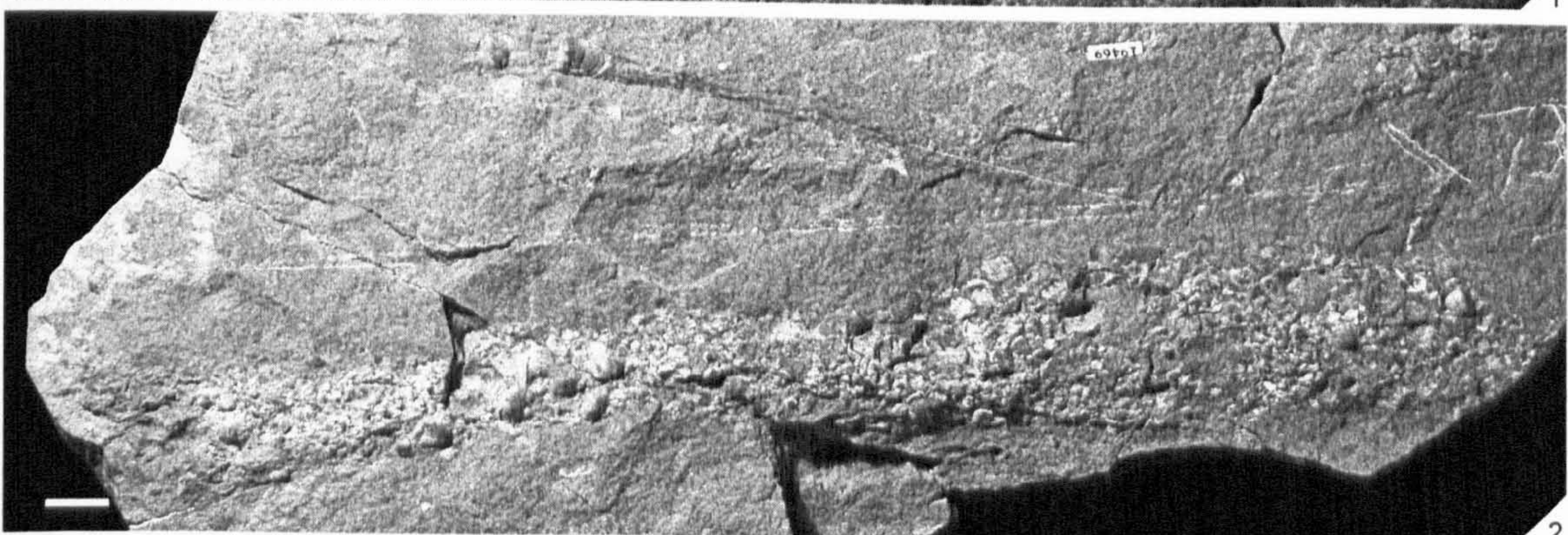
Fig. 3. Aligned orthocone nautiloids; CH178; loose block, Church Hill Quarry 1.

Fig. 4. Aligned rhynchonellid brachiopods; LEIUG 19463, 12 specimens with majority showing umbone alignment towards the left of figure (arrowed); arbitrary 'north' value assigned for slab (segment interval of rose diagram = 10°); Church Hill.





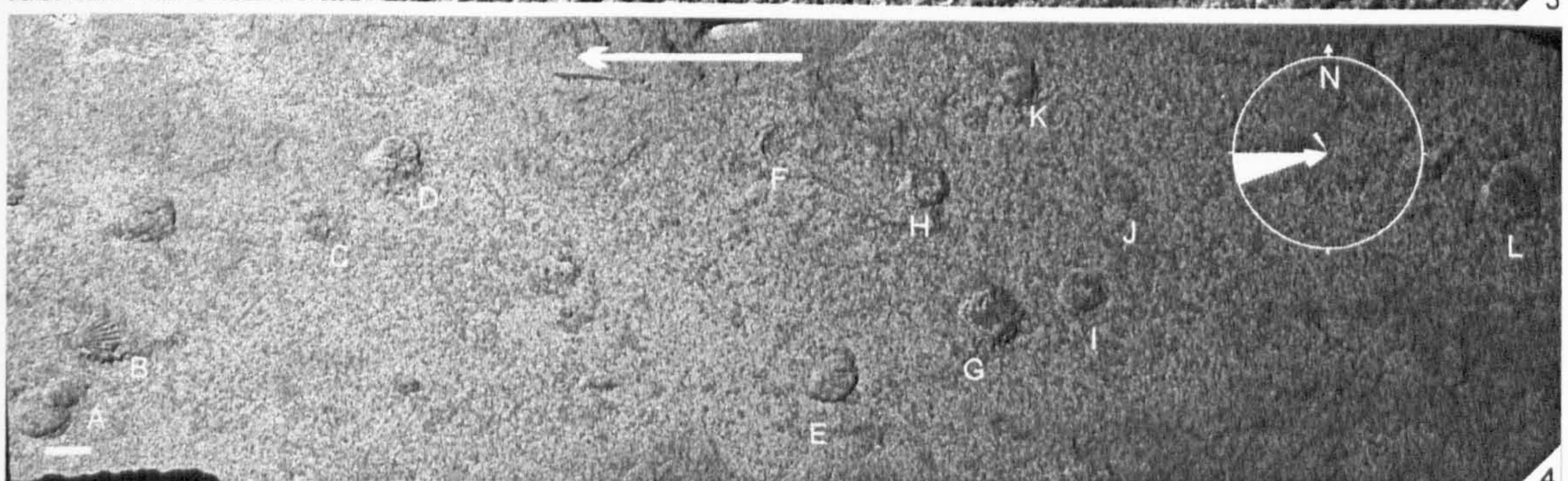
1



2



3



4



## EXPLANATION OF PLATE 2.2

Stelleroid articulation; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. All figures are of silicone casts except 2 and 10.

Figs 1, 3, 10. *Lapworthura miltoni*. 1, BMNH E 20232, nearly complete specimen missing arm tips; Church Hill; scale bar represents 10 mm. 3, BMNH E 52982, disarticulated arm tip; Martin's Shell Quarry; scale bar represents 10 mm. 10, BMNH E 20235a, articulated marginal arm spines; Church Hill; scale bar represents 2 mm.

Fig. 2. *Loriolaster calceatus*; BGS GSM25351, detail of vestigial enlarged body disc of specimen 2 in assemblage (extent of disc arrowed; also refer to Text-fig. 2.18); scale bar represents 10 mm.

Figs 4, 6. *Bdellacoma vermiformis*. 4, NMS G1882651523, neotype, nearly complete specimen retaining long strap-like arms; scale bar represents 10 mm. 6, BMNH 40297, detail of articulated pedicellariae on dorsal surface of arm; Church Hill; scale bar represents 2 mm.

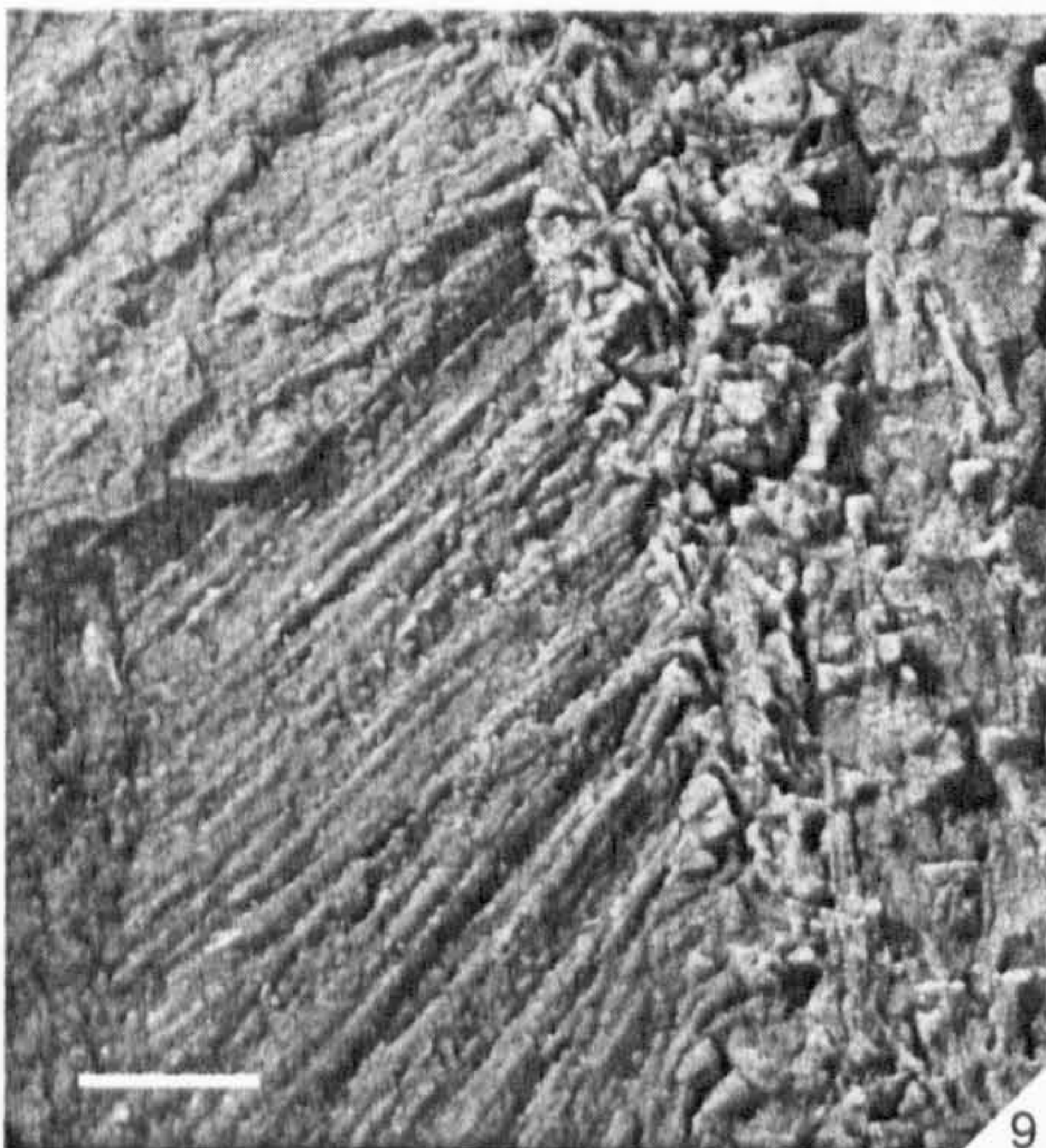
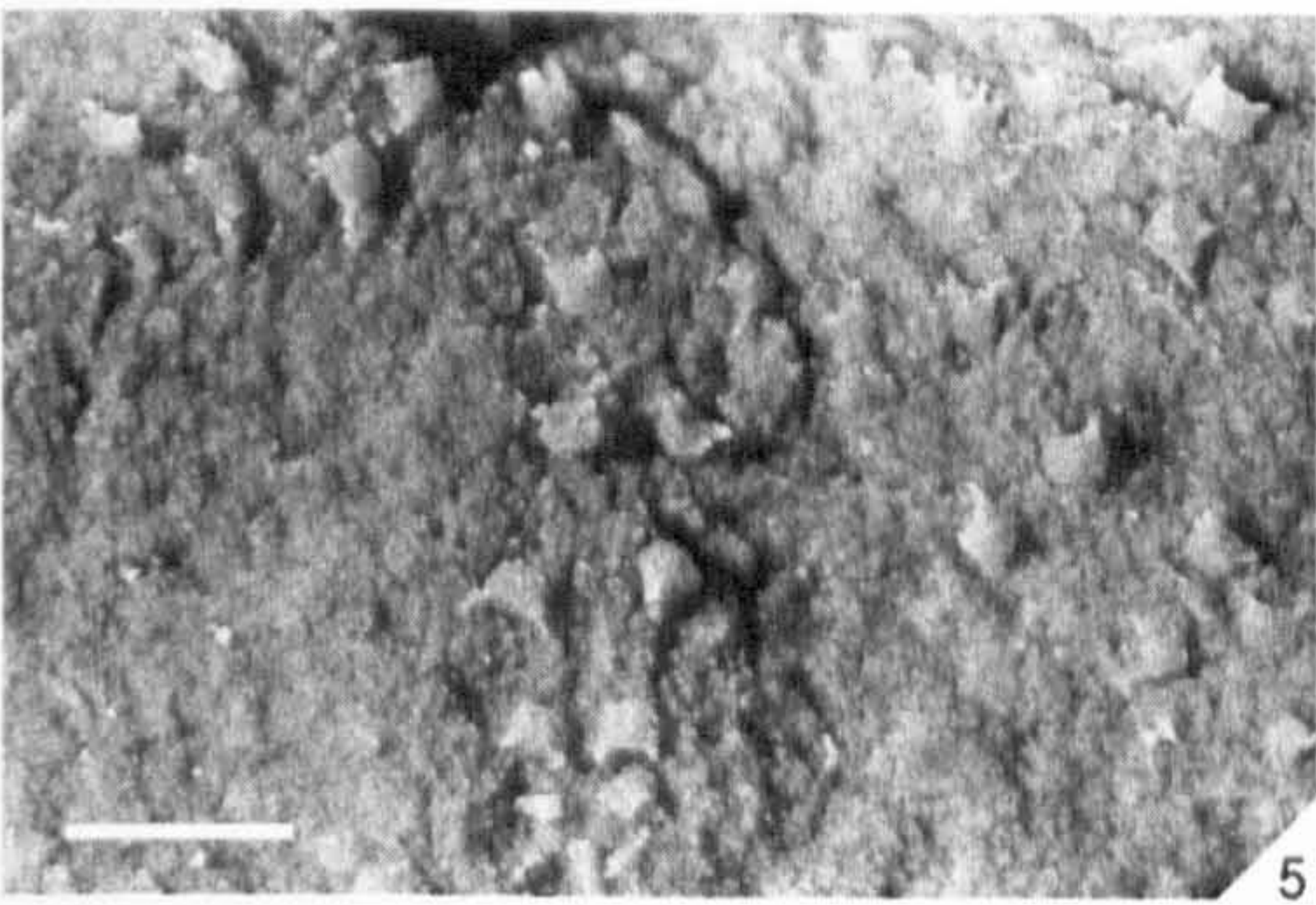
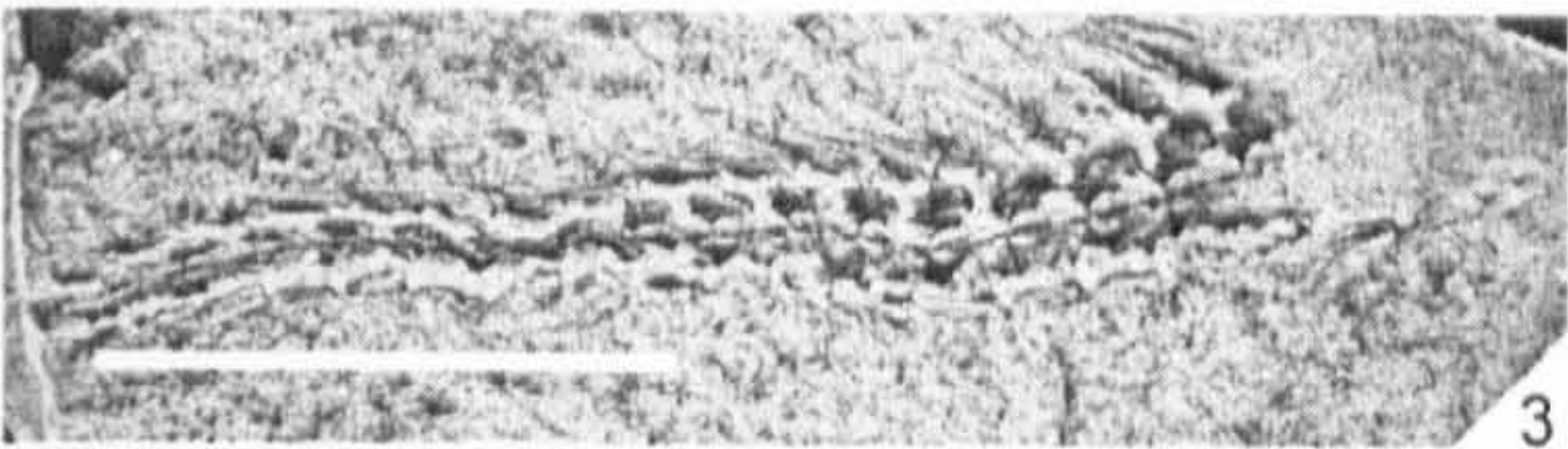
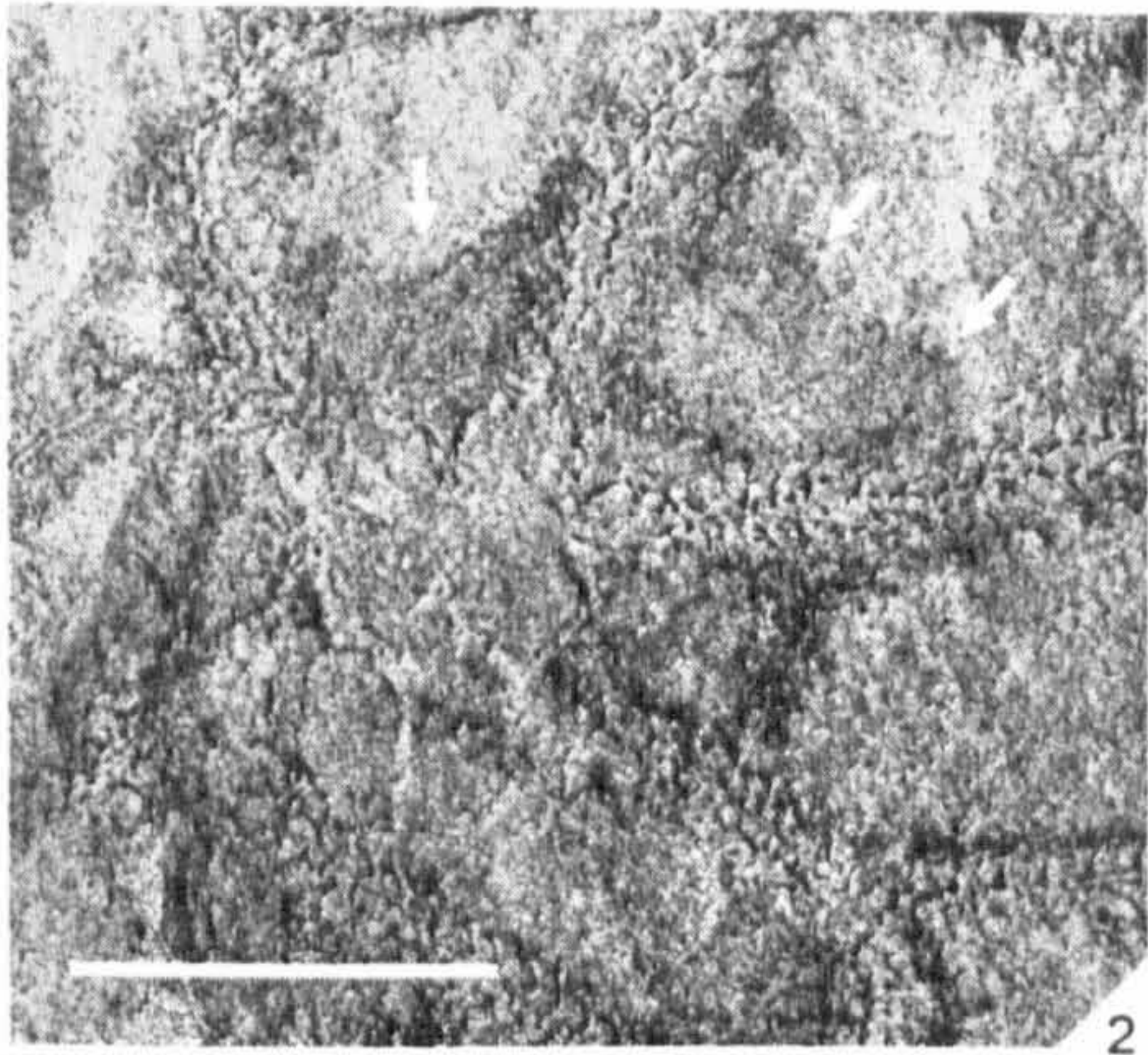
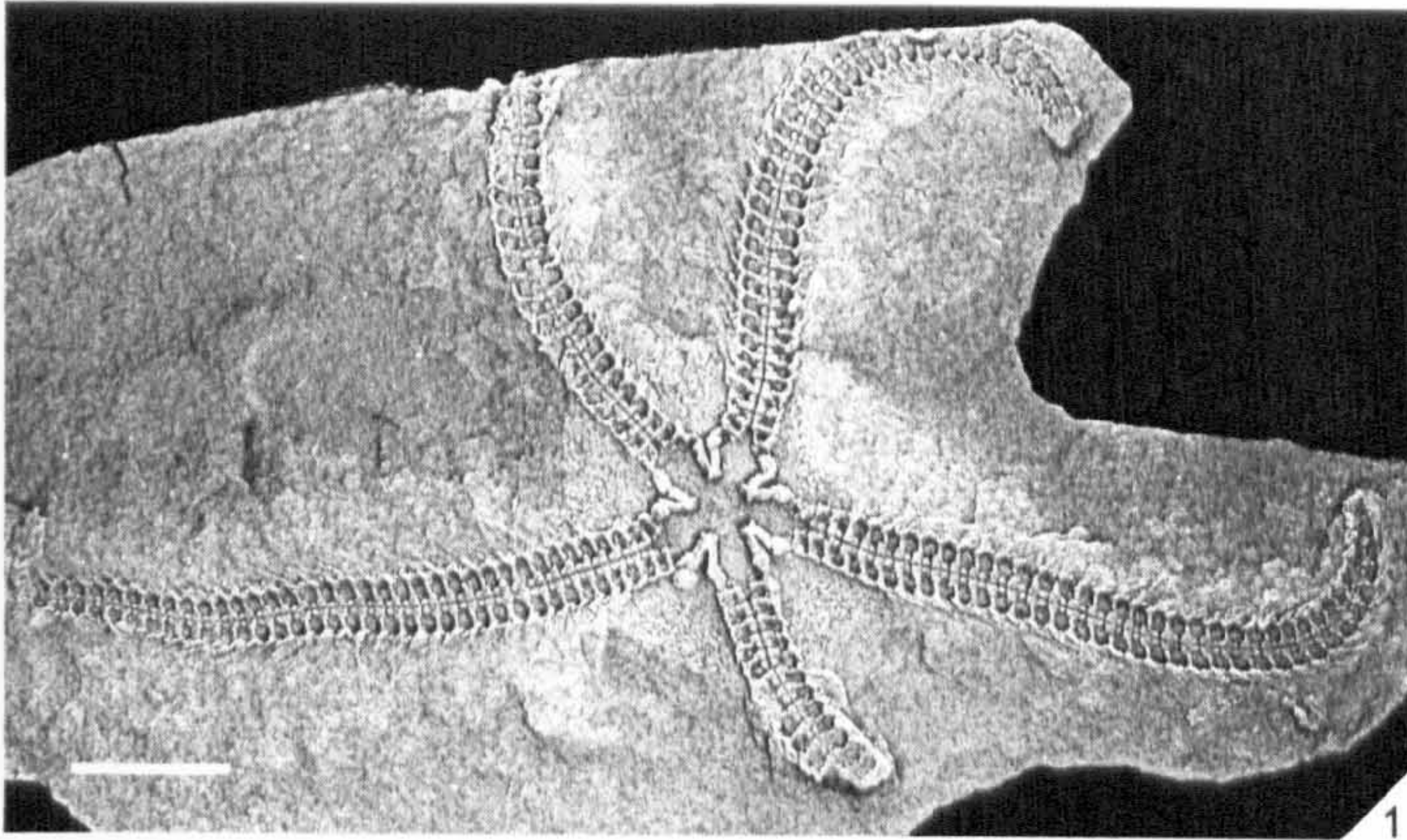
Fig. 5. *Antiquaster magrumi*; BMNH 40296a, detail of articulated pedicellariae arranged in columns along dorsal arm surface; Church Hill; scale bar represents 1 mm.

Fig. 7. *Rhopalocoma pyrotechnica*; BMNH 5013a, detail of articulated large club-like dorsal spines; Church Hill; scale bar represents 1 mm.

Fig. 8. *Furcaster leptosoma*; BMNH E 13135, detail of articulated, acicular, marginal arm spines; scale bar represents 1 mm.

Fig. 9. *Sturtzaster colvini*; BMNH E 20648, articulated marginal arm spines; Church Hill; scale bar represents 1 mm.





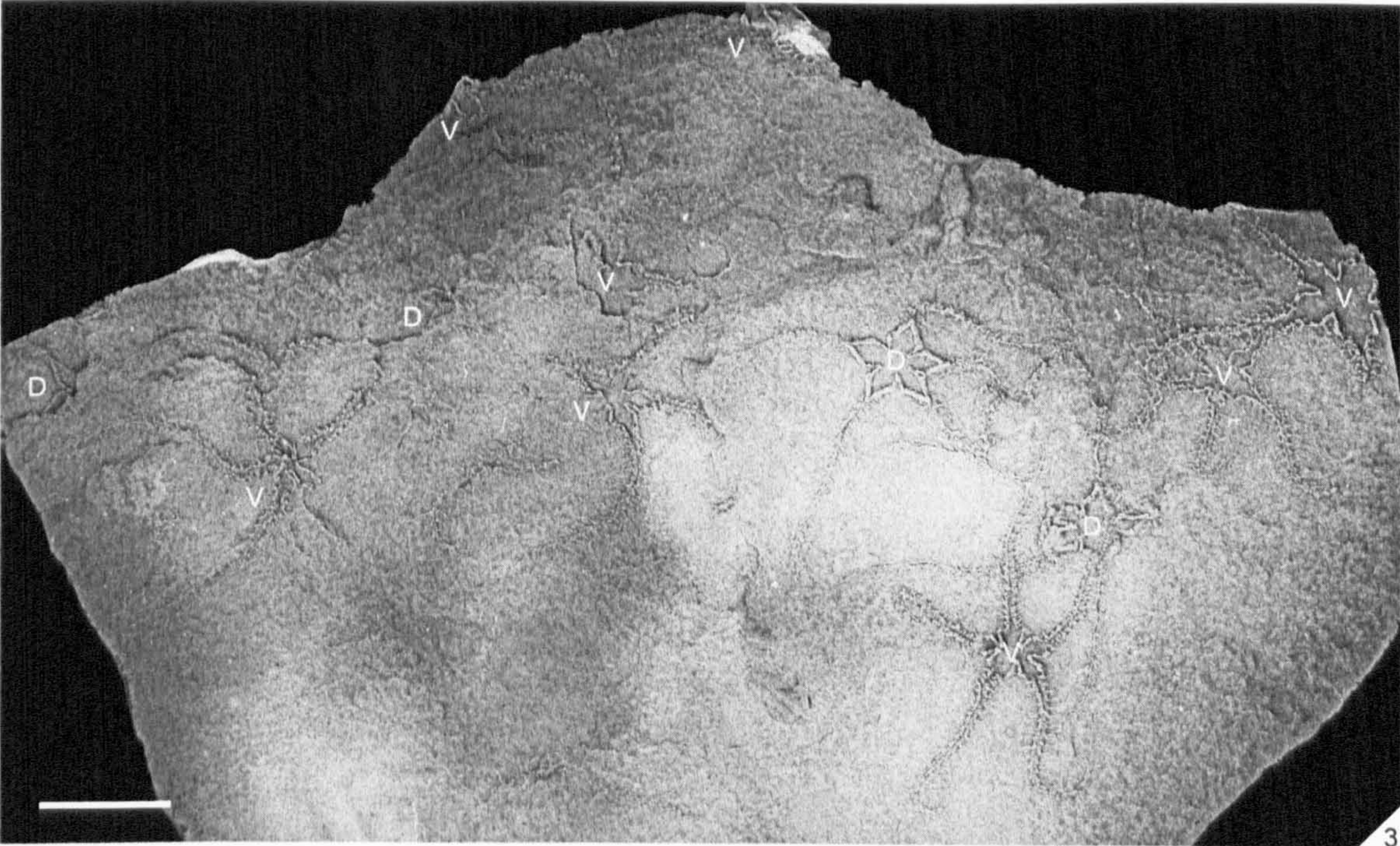


## EXPLANATION OF PLATE 2.3

Stelleroid assemblages; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm.

Figs 1-3. *Loriolaster calceatus*. 1, BMNH E 20250c, about 25 specimens with some showing current alignment; Church Hill. 2, BMNH E 20250a-b, counterpart to BMNH E 20250c. 3, BMNH 38527, 12 specimens showing variable relative way up orientation: four dorsal-up (lettered D), eight ventral-up (lettered V); some showing current alignment; silicone cast. Photograph shown in figure 3: Peter Jell.





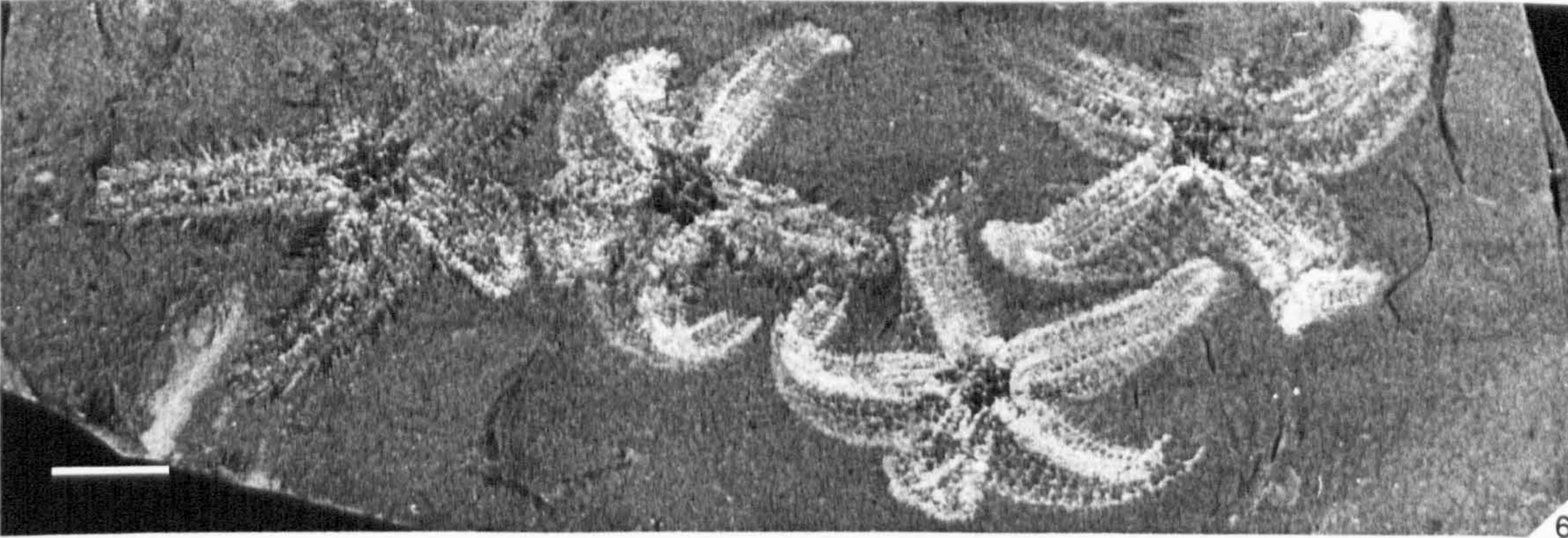
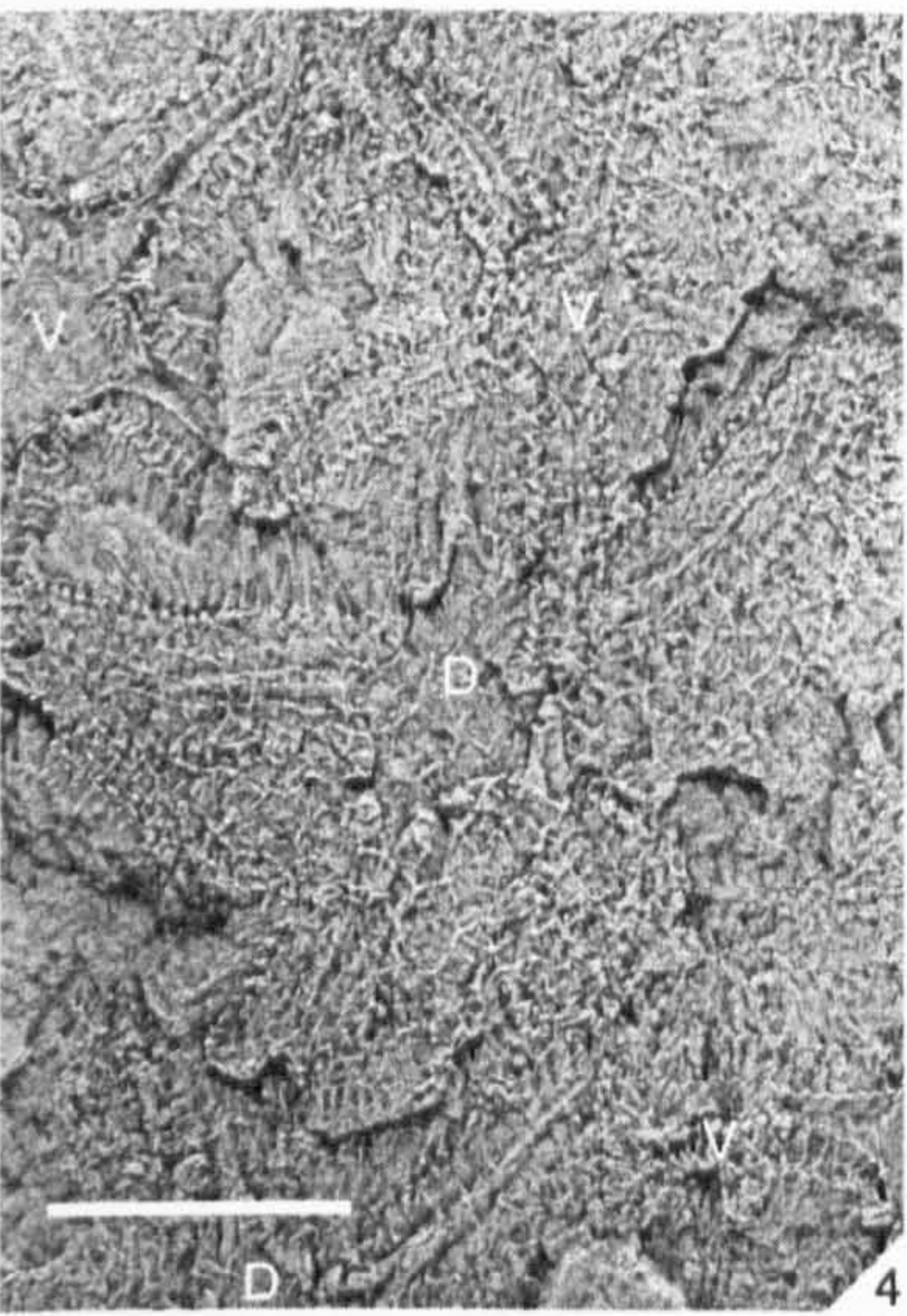
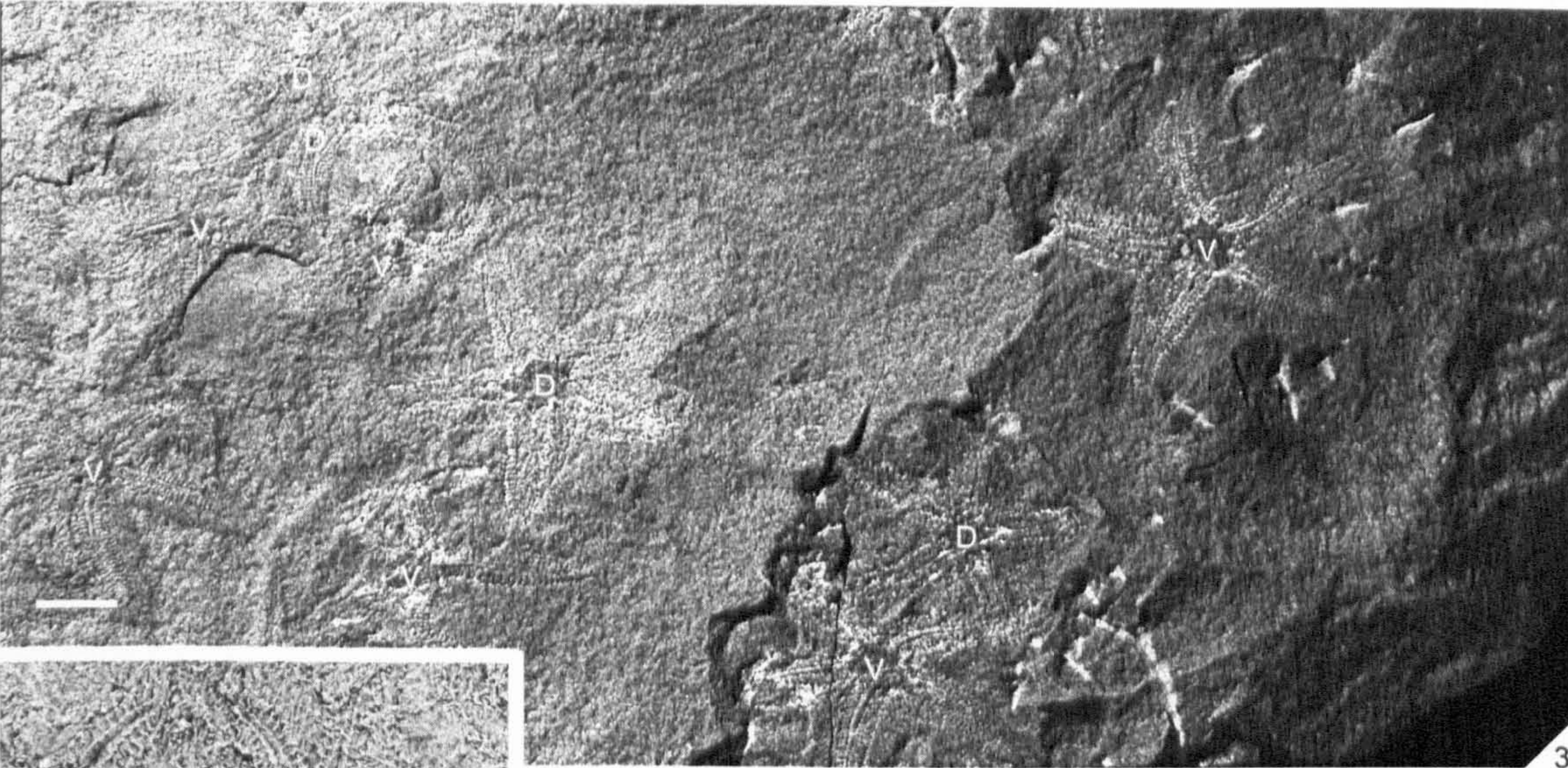
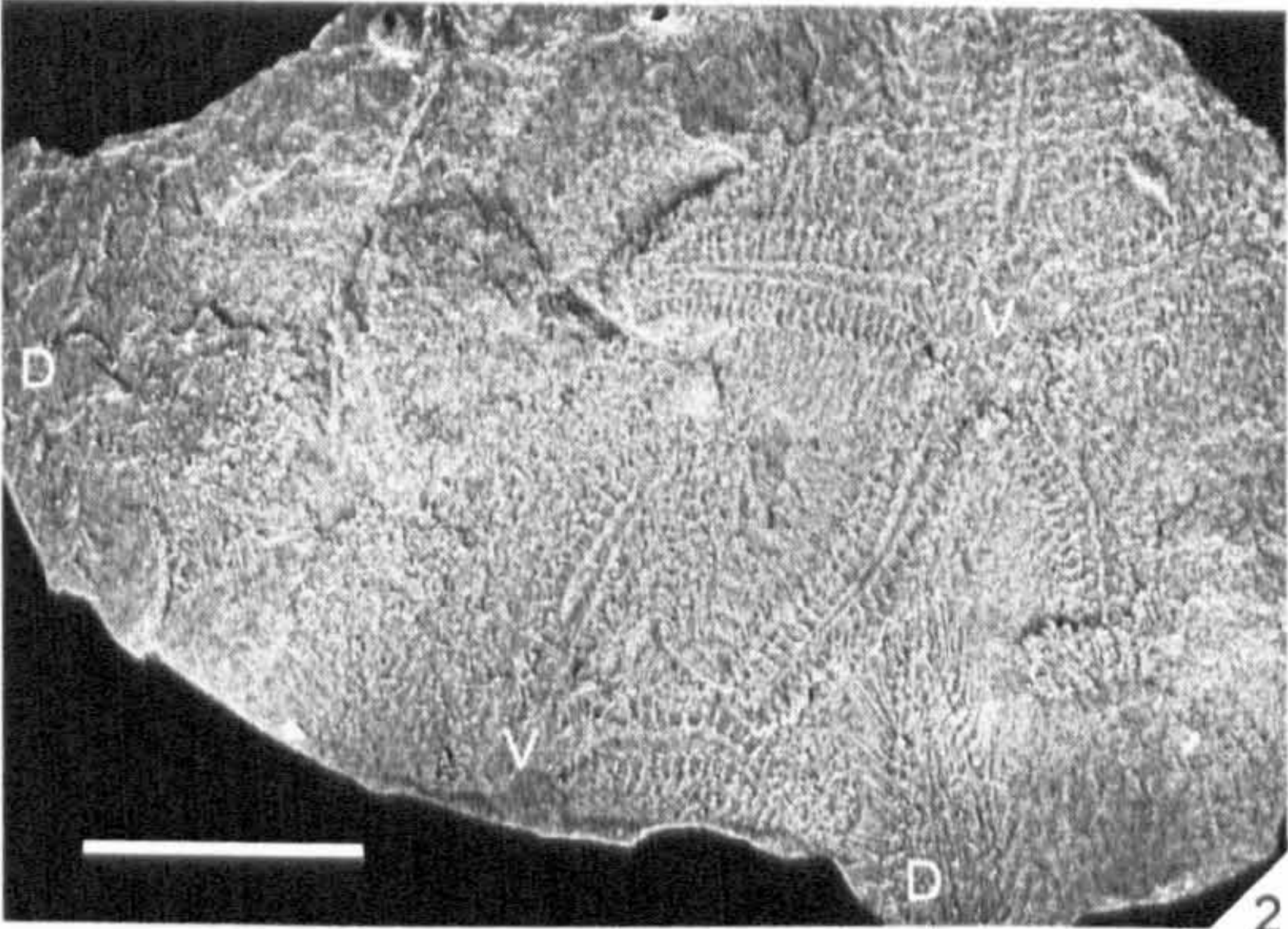
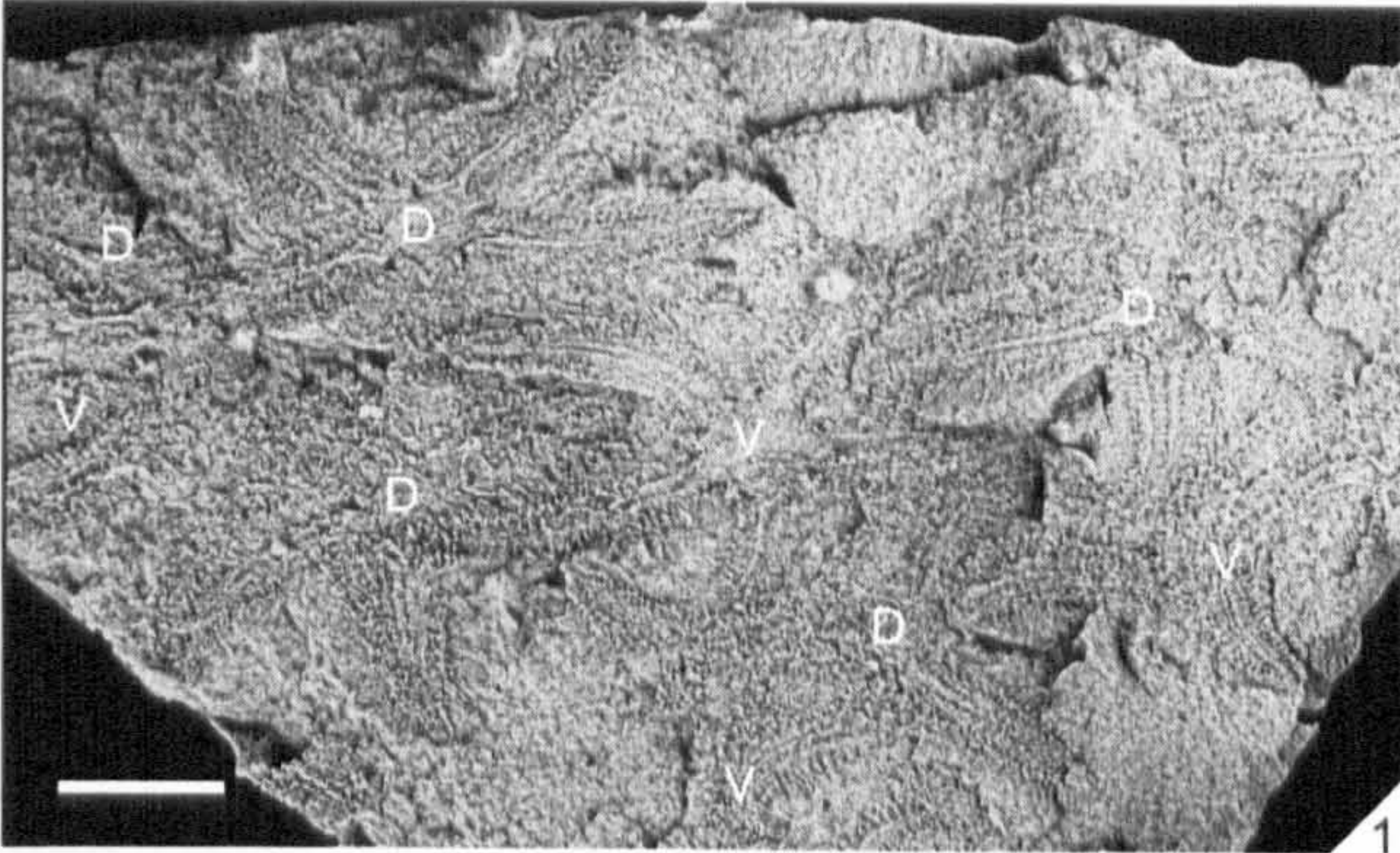


## EXPLANATION OF PLATE 2.4

Stelleroid assemblages; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm.

Figs 1-6. *Sturtzaster marstoni*. 1, BMNH 47995, nine specimens showing variable relative way up orientation: five dorsal-up (lettered D), four ventral-up (lettered V); Church Hill; silicone cast. 2, CAMSM A37207, four specimens showing variable relative way up orientation: two dorsal-up (D), two ventral-up (V); silicone cast. 3, NMS G1882651627, detail of ten specimens showing variable relative way up: four dorsal-up (D), six ventral-up (V); specimens towards top left of figure are not complete; refer also to text-figure 2.17. 4, OUM C.17103, five specimens showing variable relative way up orientation: two dorsal-up (D), three ventral-up (V); silicone cast. 5, IPSM G19252921, detail showing five specimens (lettered A to E); possibly from Church Hill. 6, OUM C.54, four specimens showing some alignment. Photographs shown in figures 1-2, 4: Peter Jell. Photograph shown in figure 6: Derek Siveter.





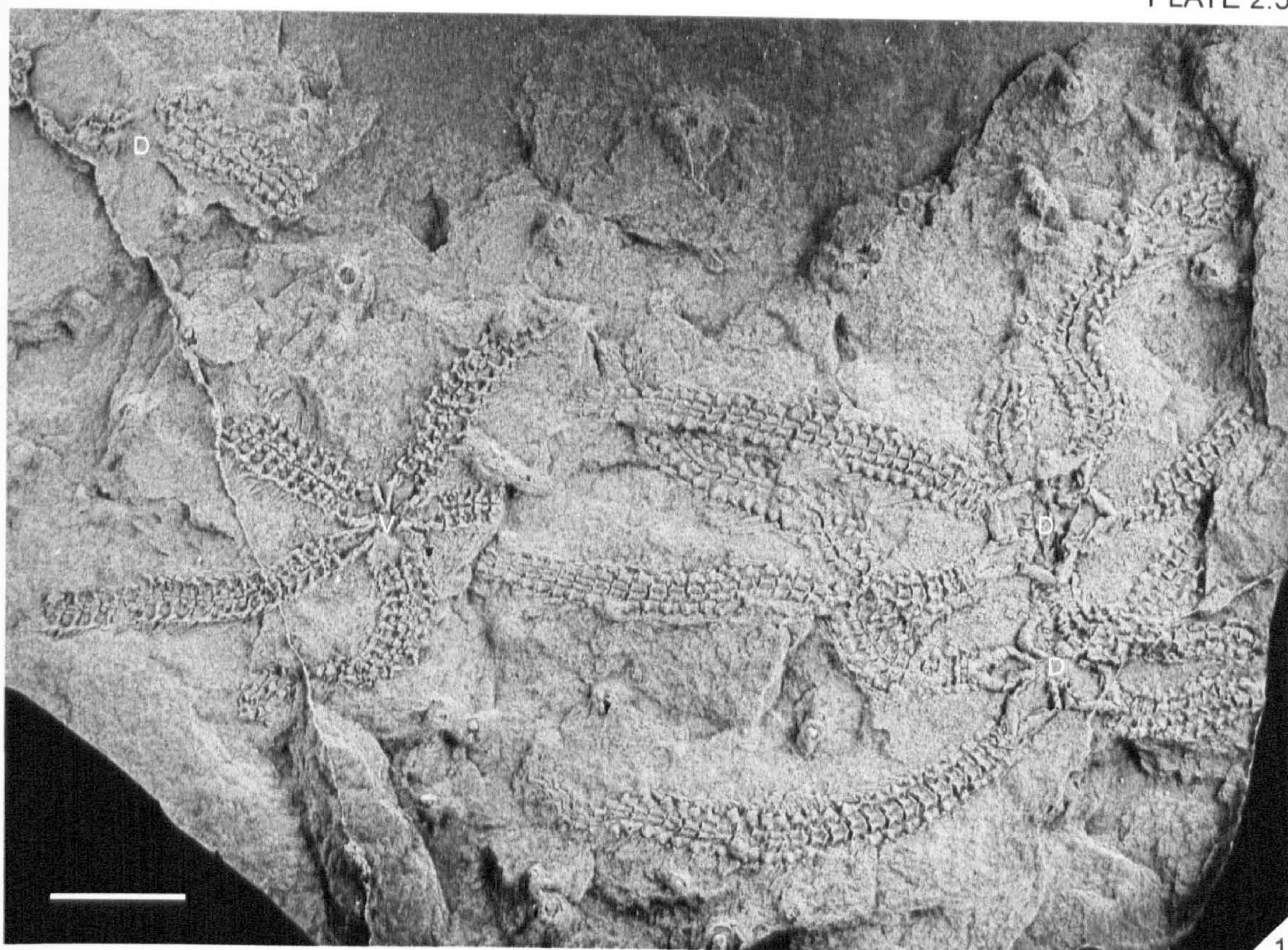


## EXPLANATION OF PLATE 2.5

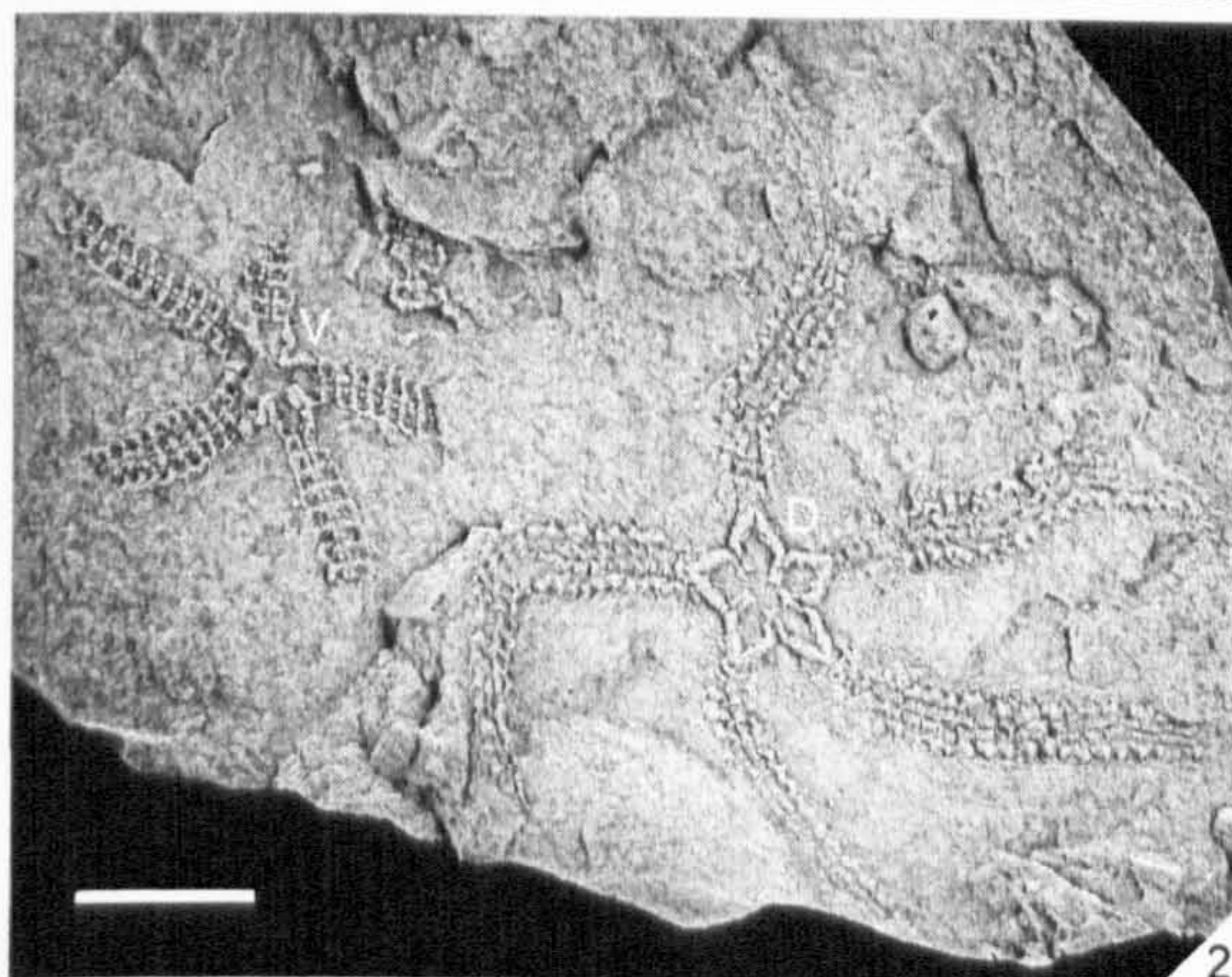
Stelleroid assemblages; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. All figures are of silicone casts except 4.

Figs 1-5. *Lapworthura miltoni*. 1, OUM C.16828, four specimens showing variable relative way up: three dorsal-up (lettered D), one ventral-up (lettered V). 2, OUM C.16832, two specimens showing opposite relative way up orientation: dorsal-up (D) and ventral-up (V). 3, OUM C.16858, three specimens showing the same relative way up orientation: dorsal-up. 4, BMNH 38619, two specimens showing opposite relative way up orientation; Church Hill. 5, BMNH E 20239, two specimens showing the same relative way up orientation: ventral-up; Church Hill. Photographs shown in figures 1-3, 5: Peter Jell.

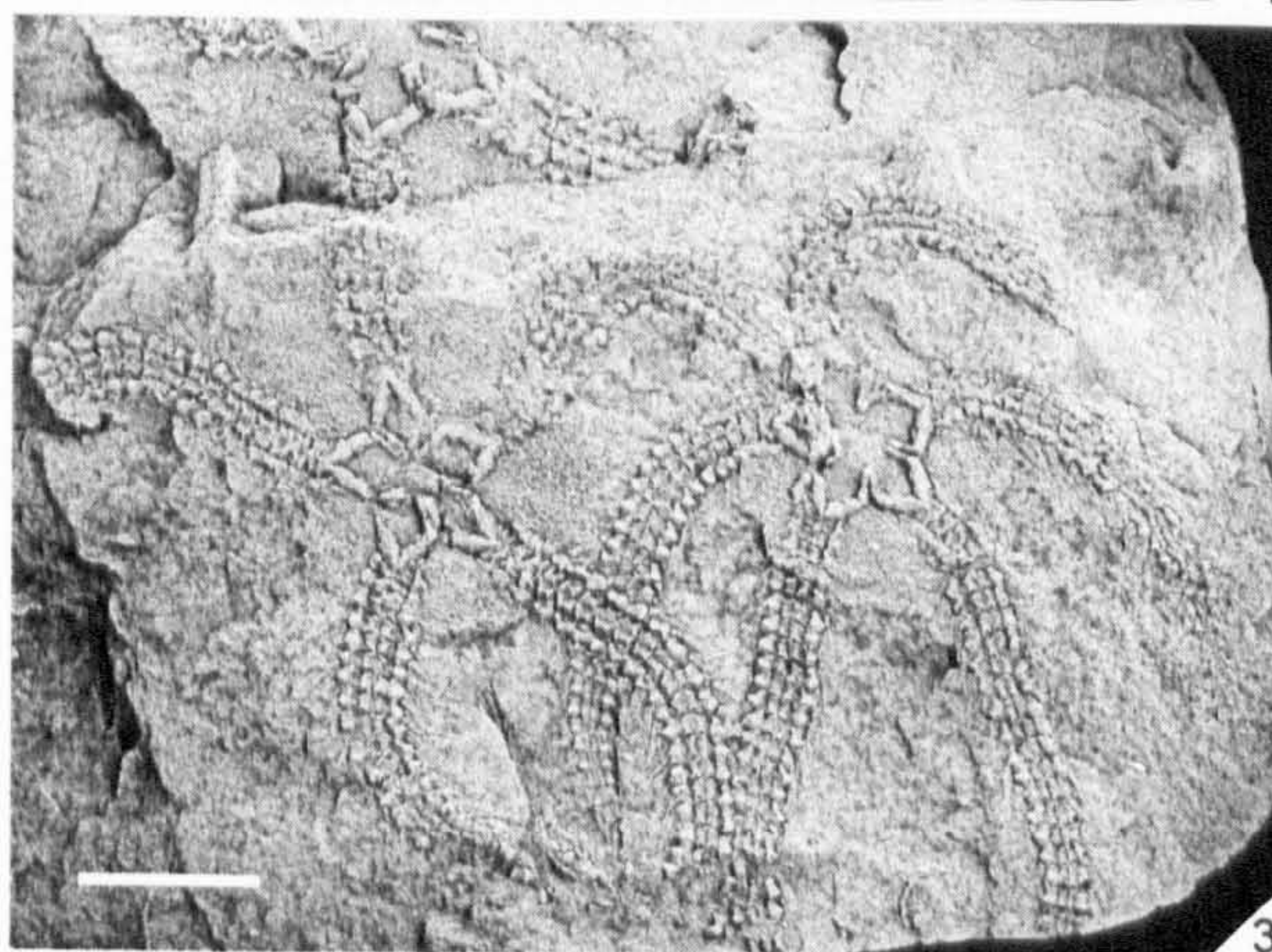




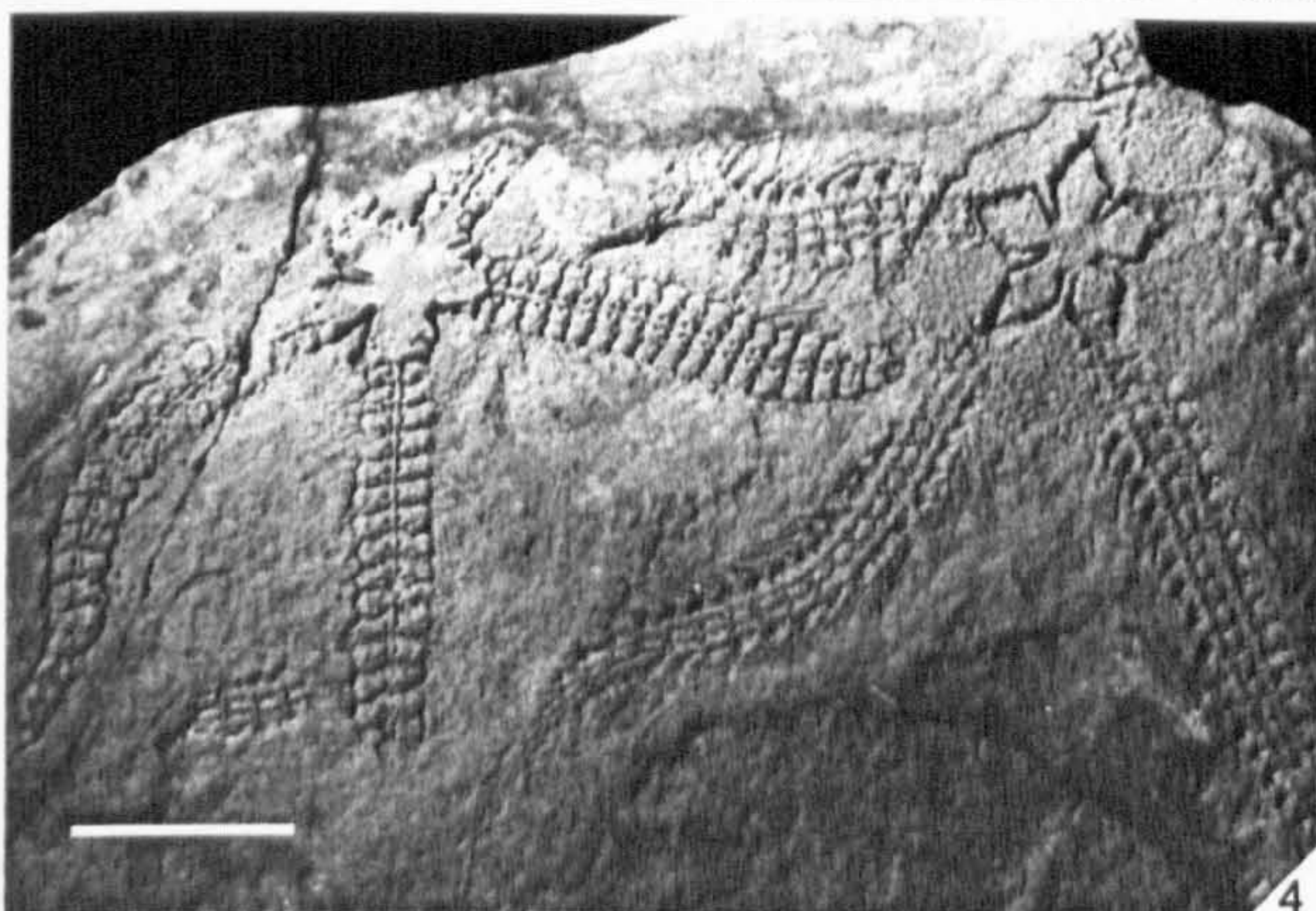
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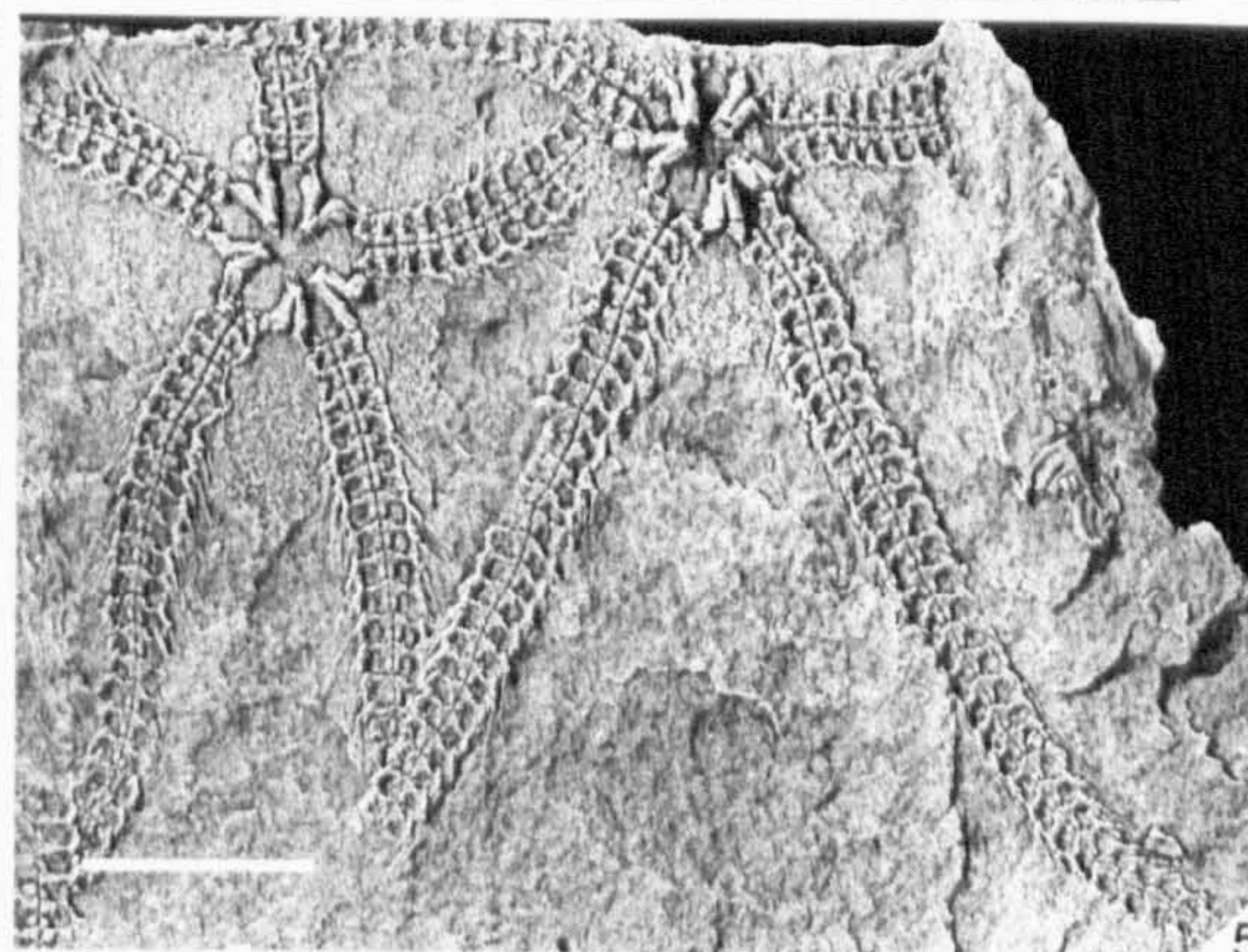
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5



## EXPLANATION OF PLATE 2.6

Heterospecific stelleroid assemblages; Lower Leintwardine Formation; Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. Refer to text-figure 2.16 for stratigraphical provenance of CH40 and CH70.

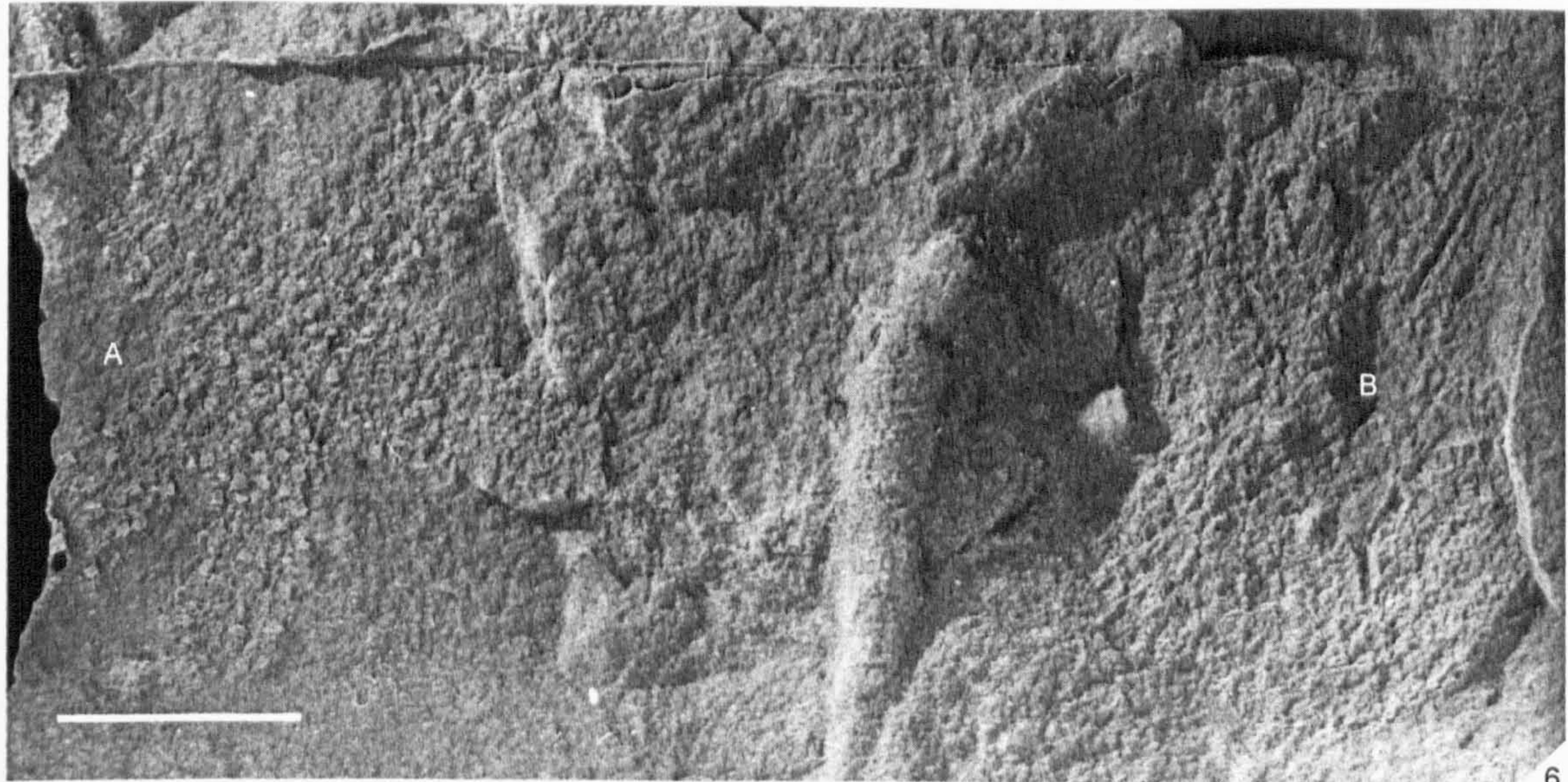
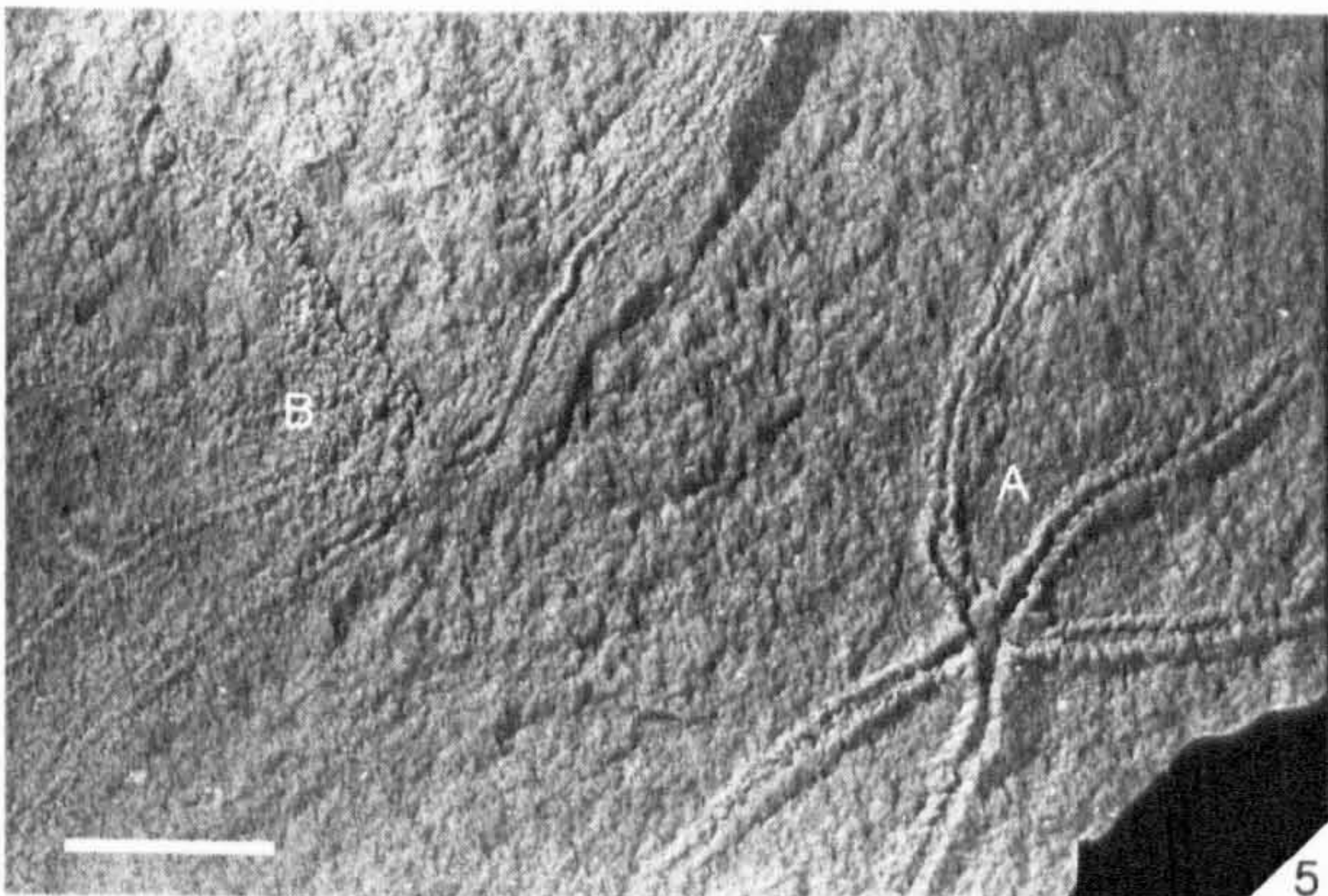
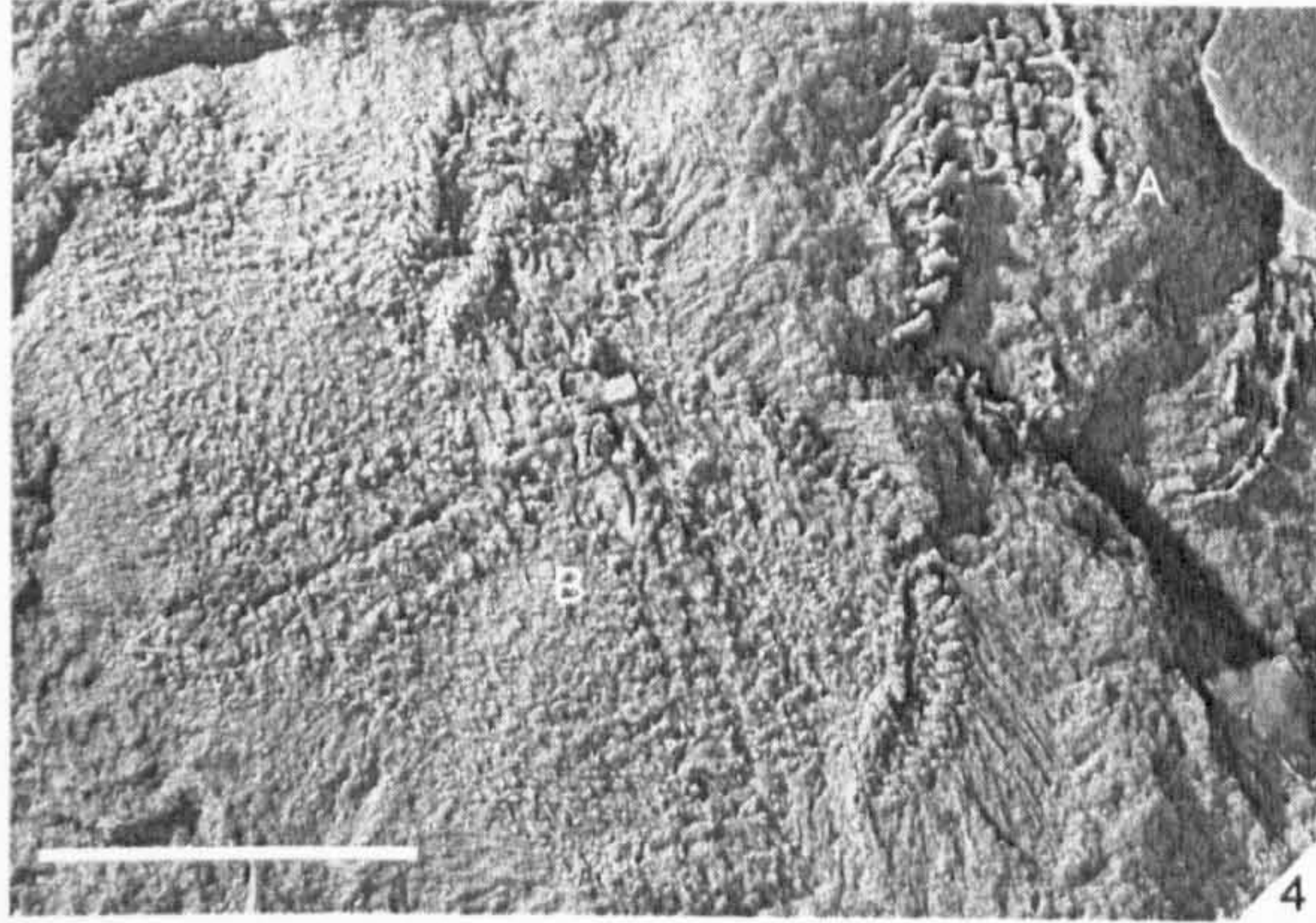
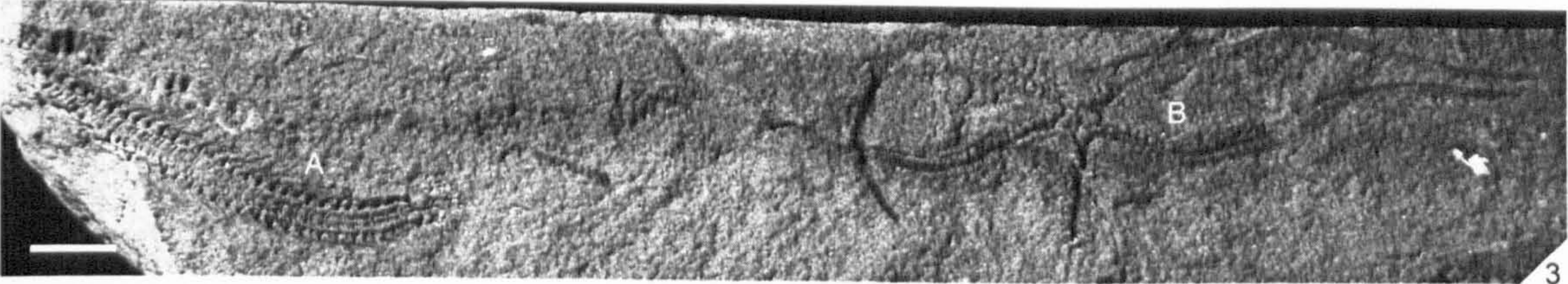
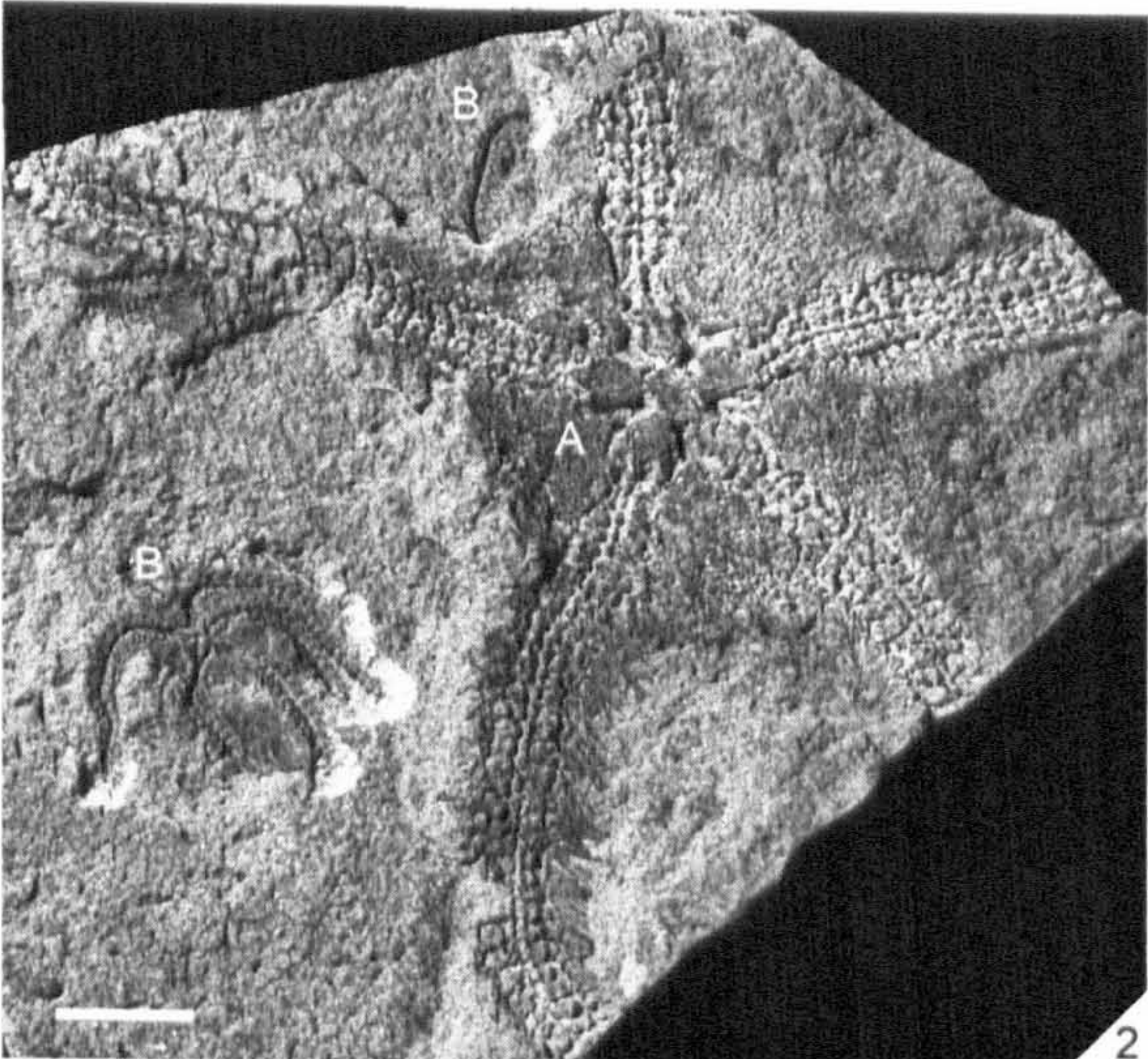
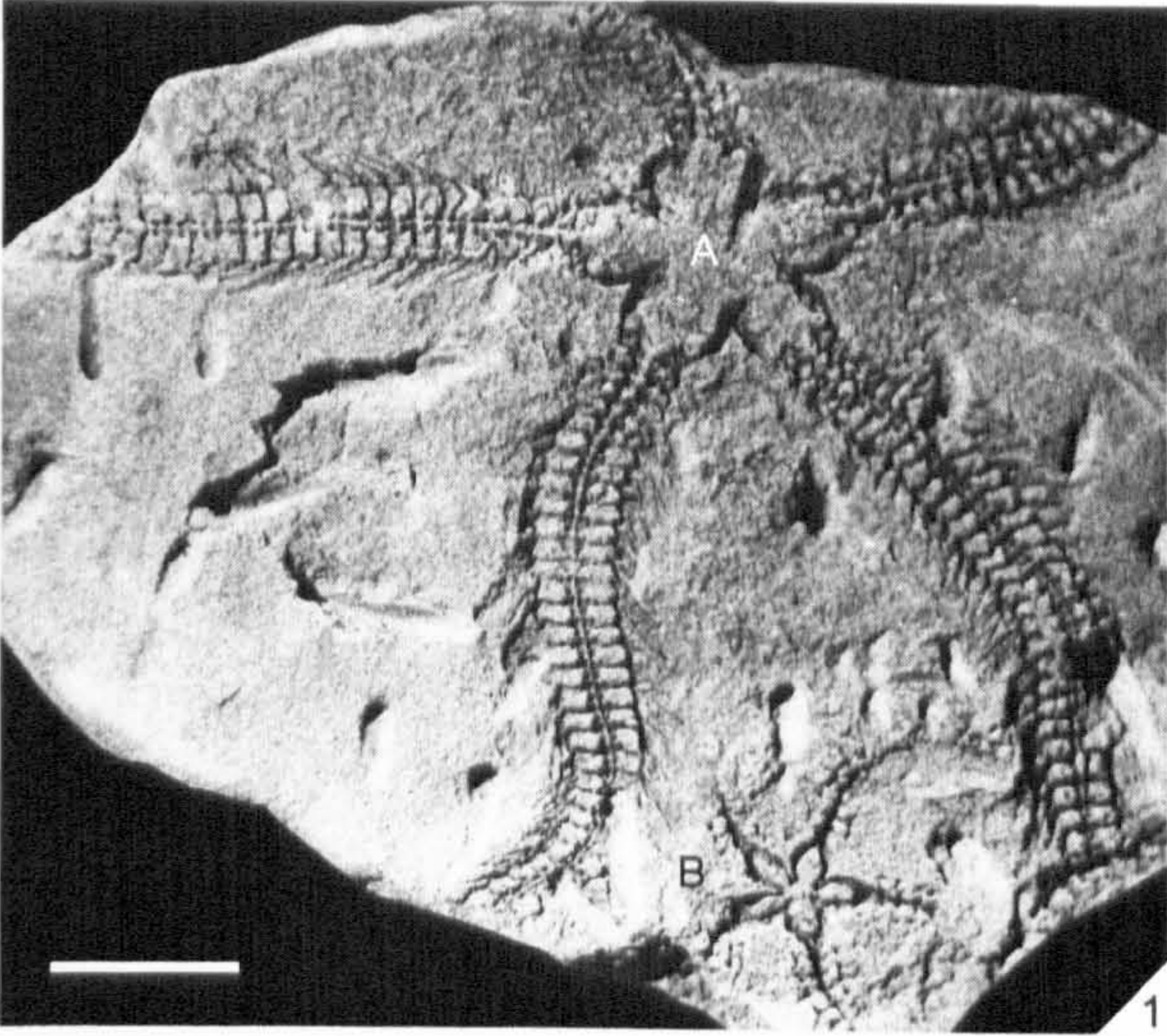
Figs 1-3. *Lapworthura miltoni* and *Furcaster leptosoma* assemblages. 1, BMNH E 13131, one specimen of each species. 2, CH70, one specimen of *L. miltoni* (lettered A) and two of *F. leptosoma* (lettered B); only one arm of one specimen of *F. leptosoma* visible towards top of figure; *L. miltoni* shows dorsal-up orientation, the completely exposed *F. leptosoma* specimen shows ventral-up orientation; Starfish Bed A, Church Hill Quarry 1. 3, CH40, arm of *L. miltoni* (A) and complete *F. leptosoma* (B), showing dorsal-up orientation; *F. leptosoma* shows current alignment; Starfish Bed A, Church Hill Quarry 1.

Fig. 4. *Lapworthura miltoni* (lettered A) and *Sturtzaster colvini* (lettered B); BMNH E 1479, only arm portions of *L. miltoni* preserved towards top right of figure; Church Hill; silicone cast.

Fig. 5. *Furcaster leptosoma* (lettered A) and *Bdellacoma vermiformis* (lettered B); BMNH E 20243, showing the same relative way up orientation: ventral-up; Church Hill; silicone cast.

Fig. 6. *Bdellacoma vermiformis* (lettered A) and *Sturtzaster marstoni* (lettered B); OUM C.17117, showing variable relative way up orientation; pedicellariae along dorsal surface of *B. vermiformis* clearly visible; silicone cast.







## EXPLANATION OF PLATE 2.7

Stelleroids showing current orientation; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; 1-2, 6-8 from Church Hill. All figures are of silicone casts.

Fig. 1. *Palasterina* cf. *antiqua*; BMNH 40299a, slight displacement of dorsal ossicles; scale bar represents 2 mm.

Fig. 2. *Urasterella ruthveni*; MM L11020, orientation of arms; scale bar represents 10 mm.

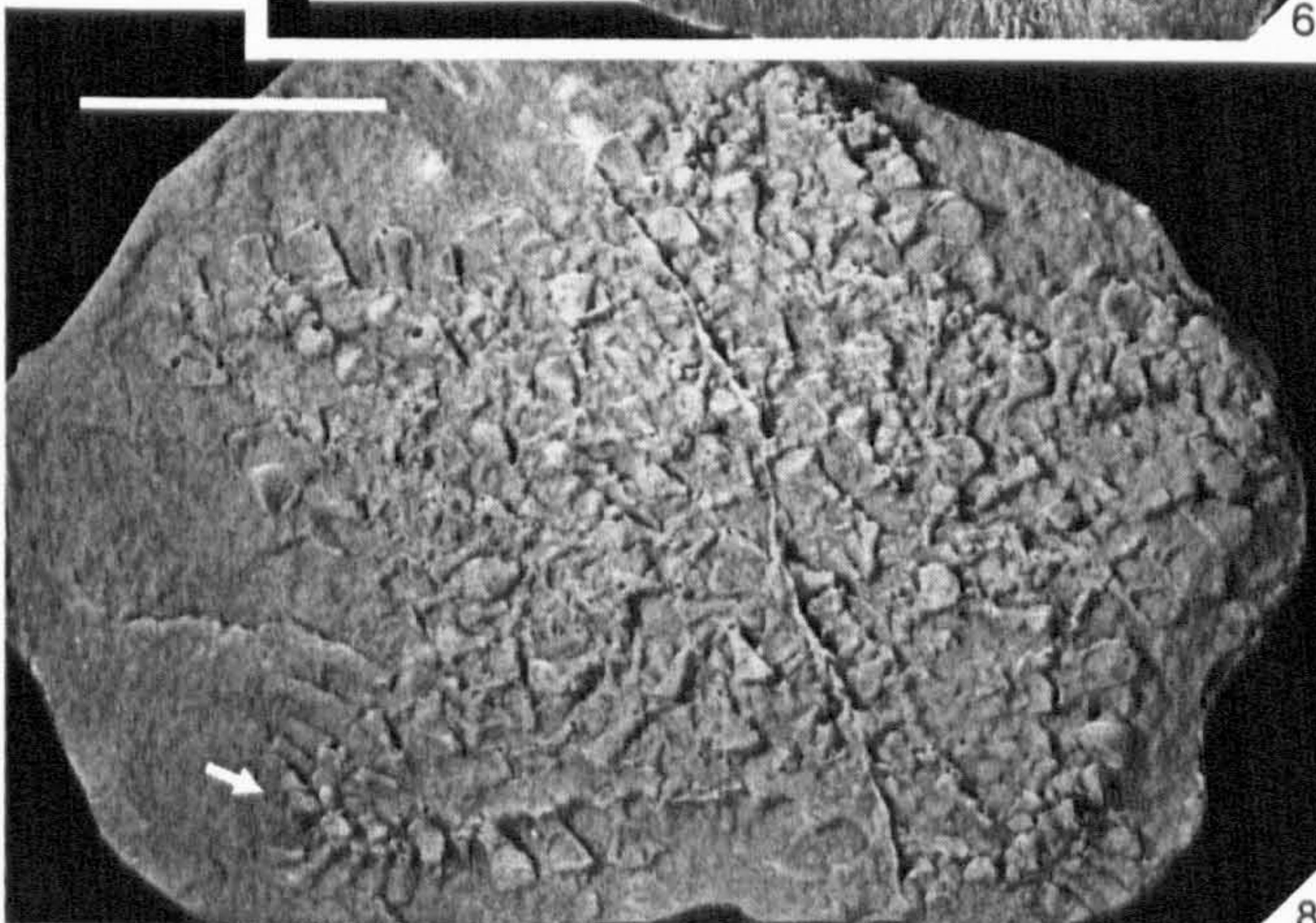
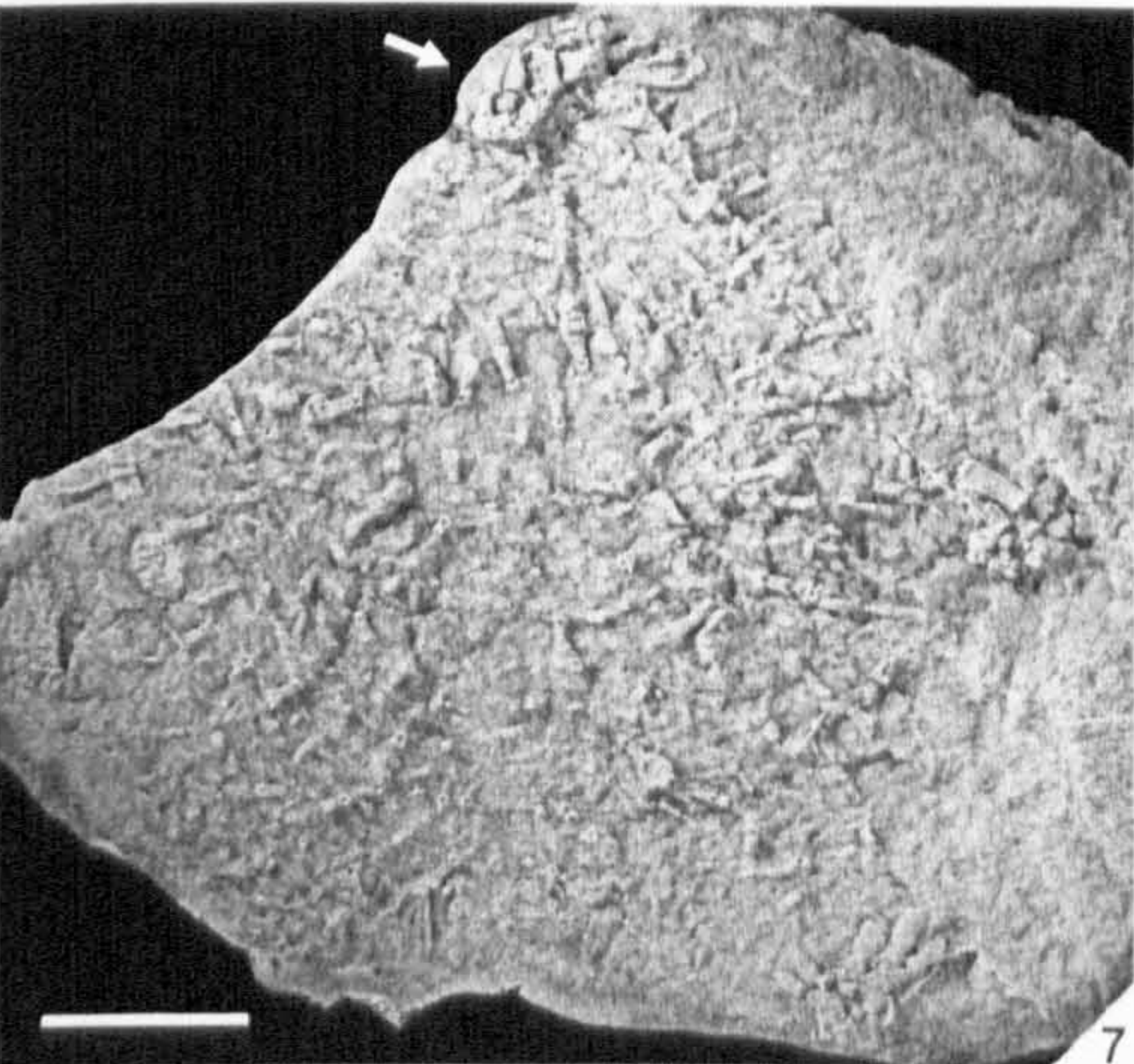
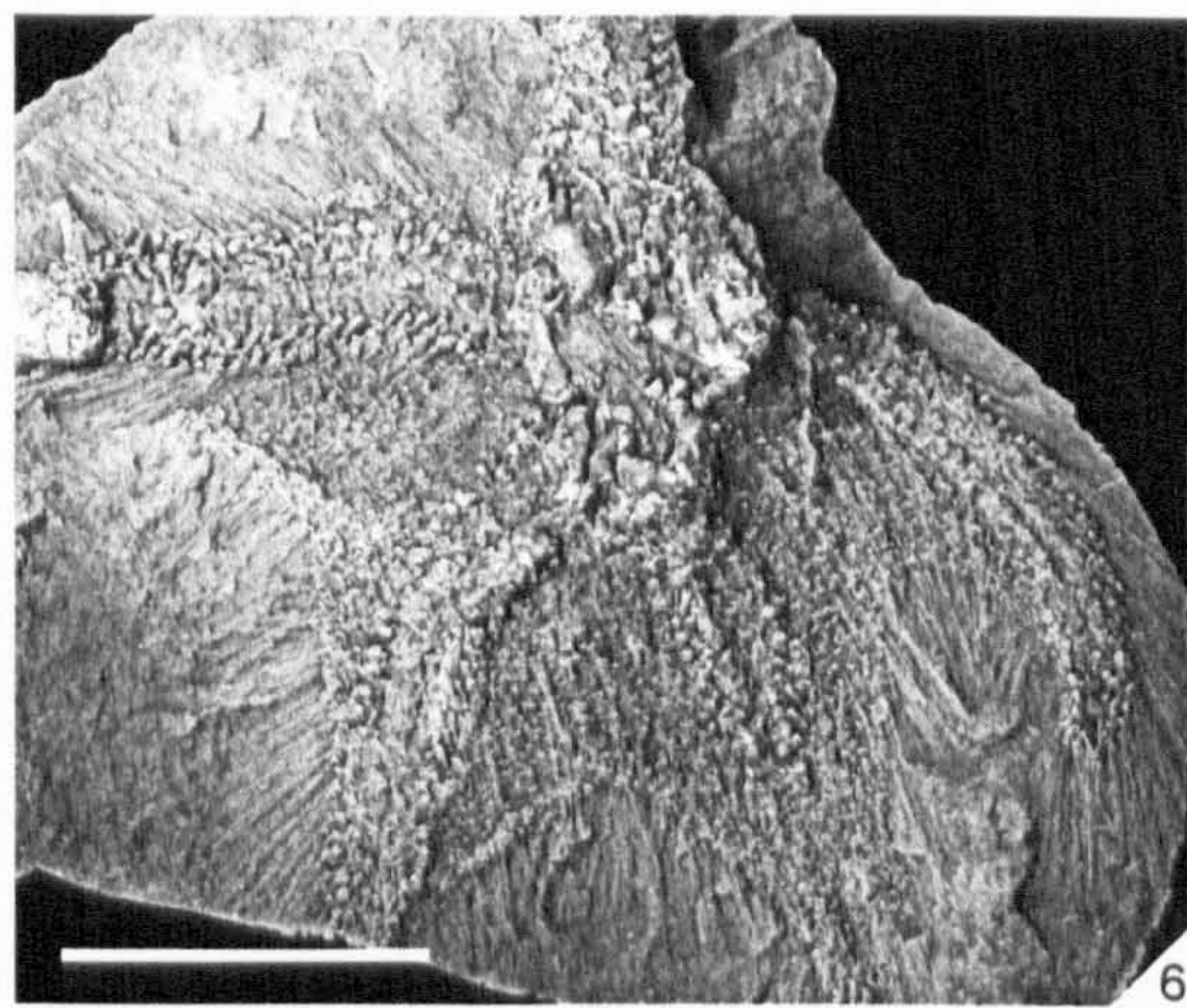
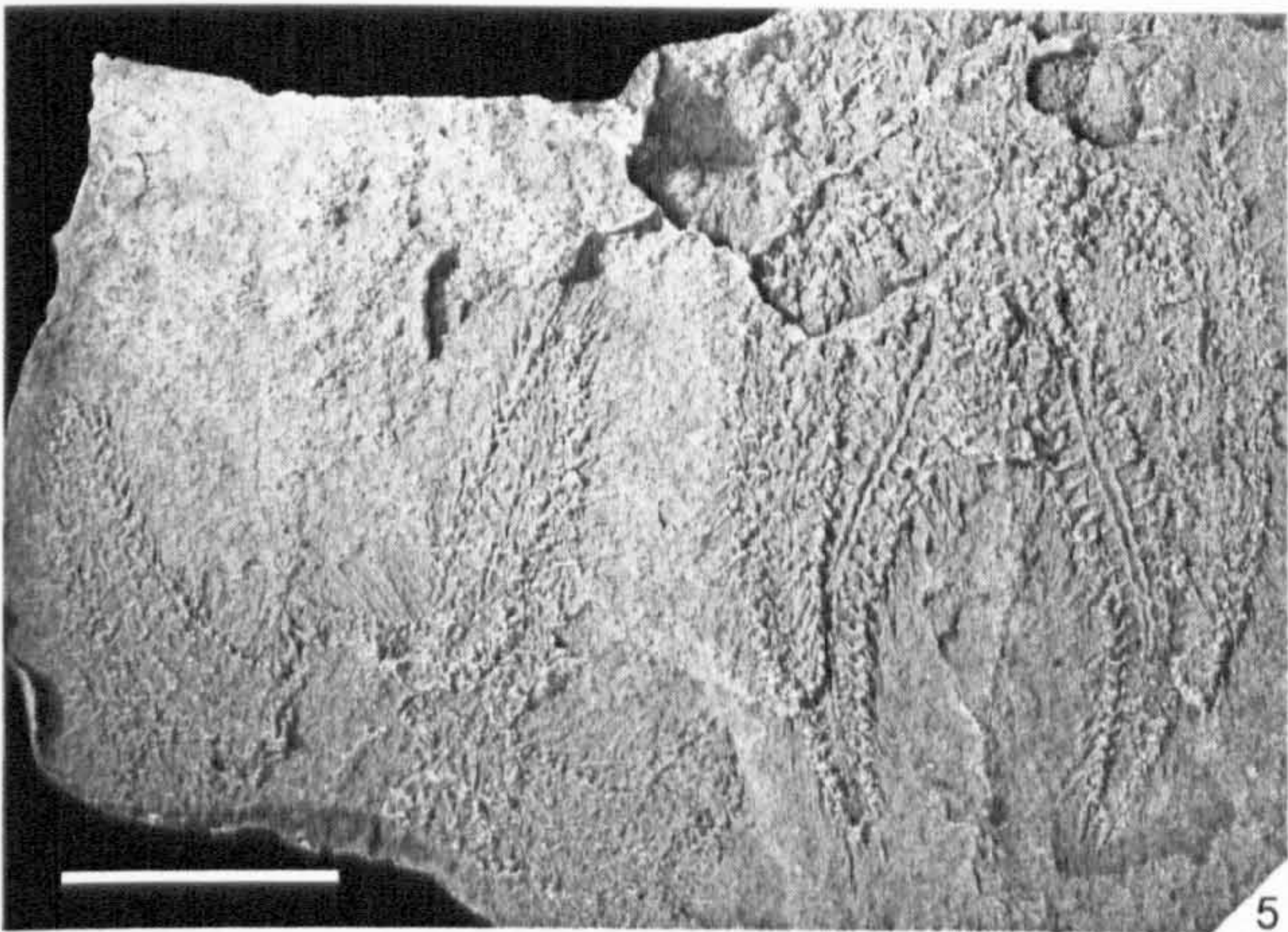
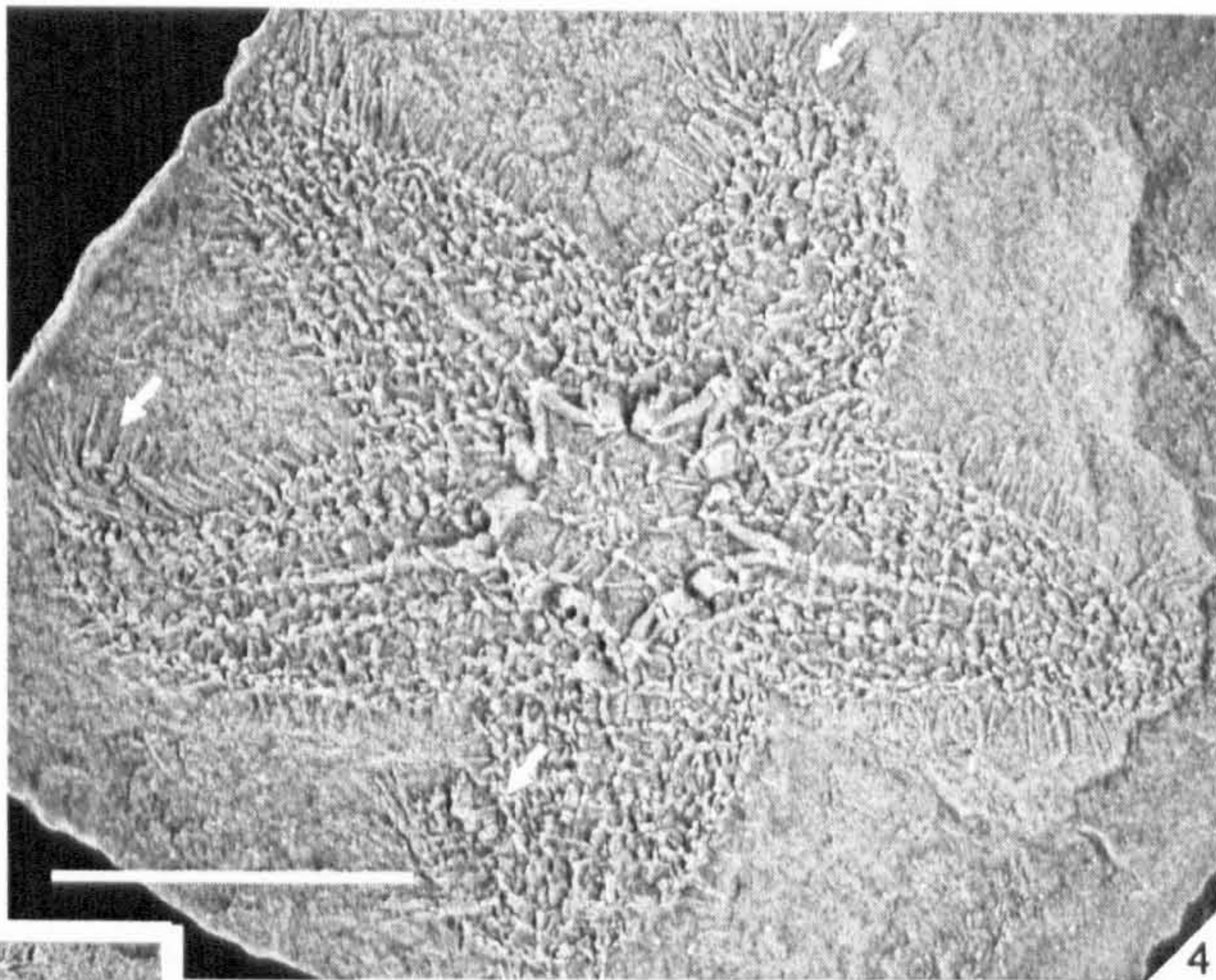
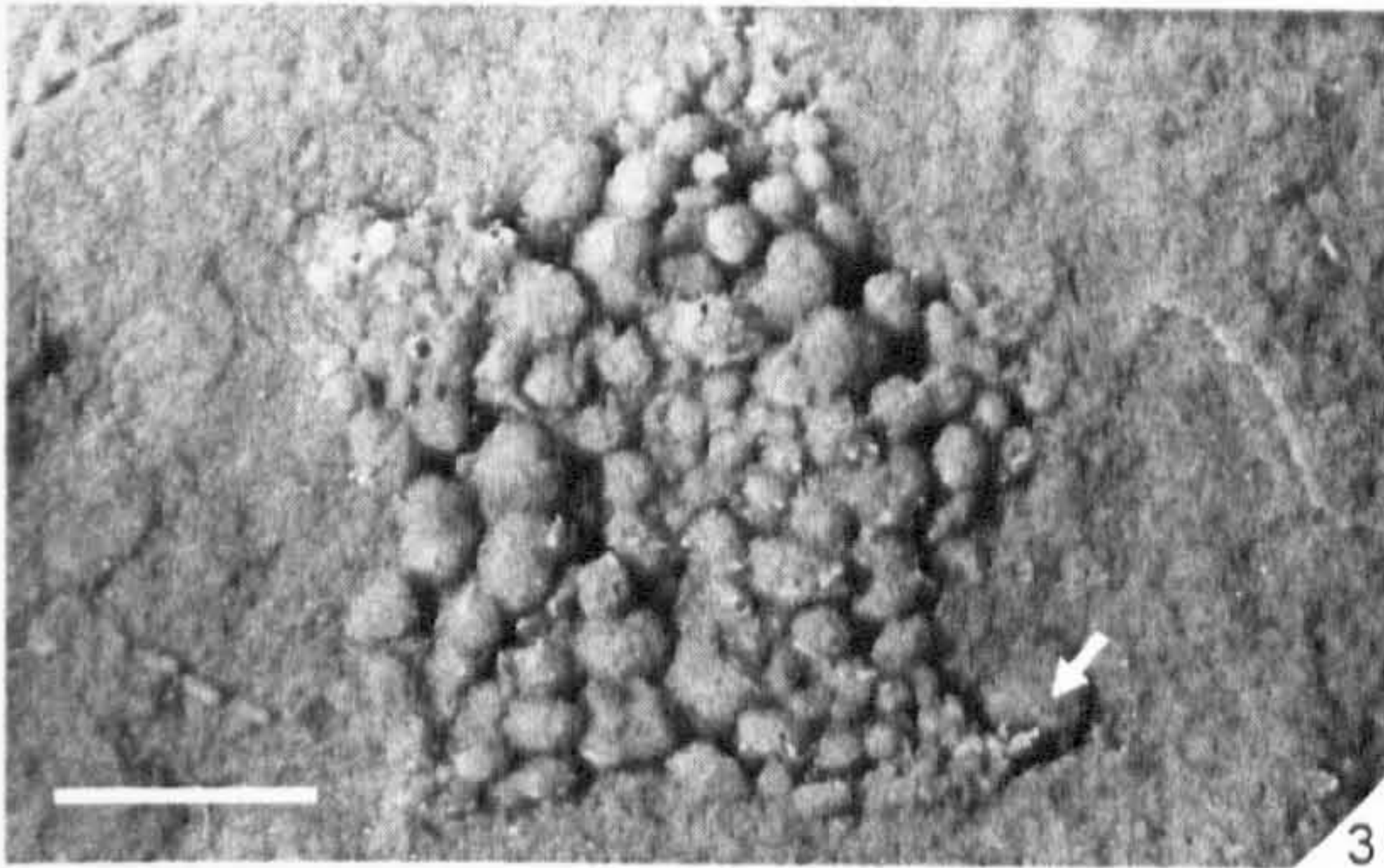
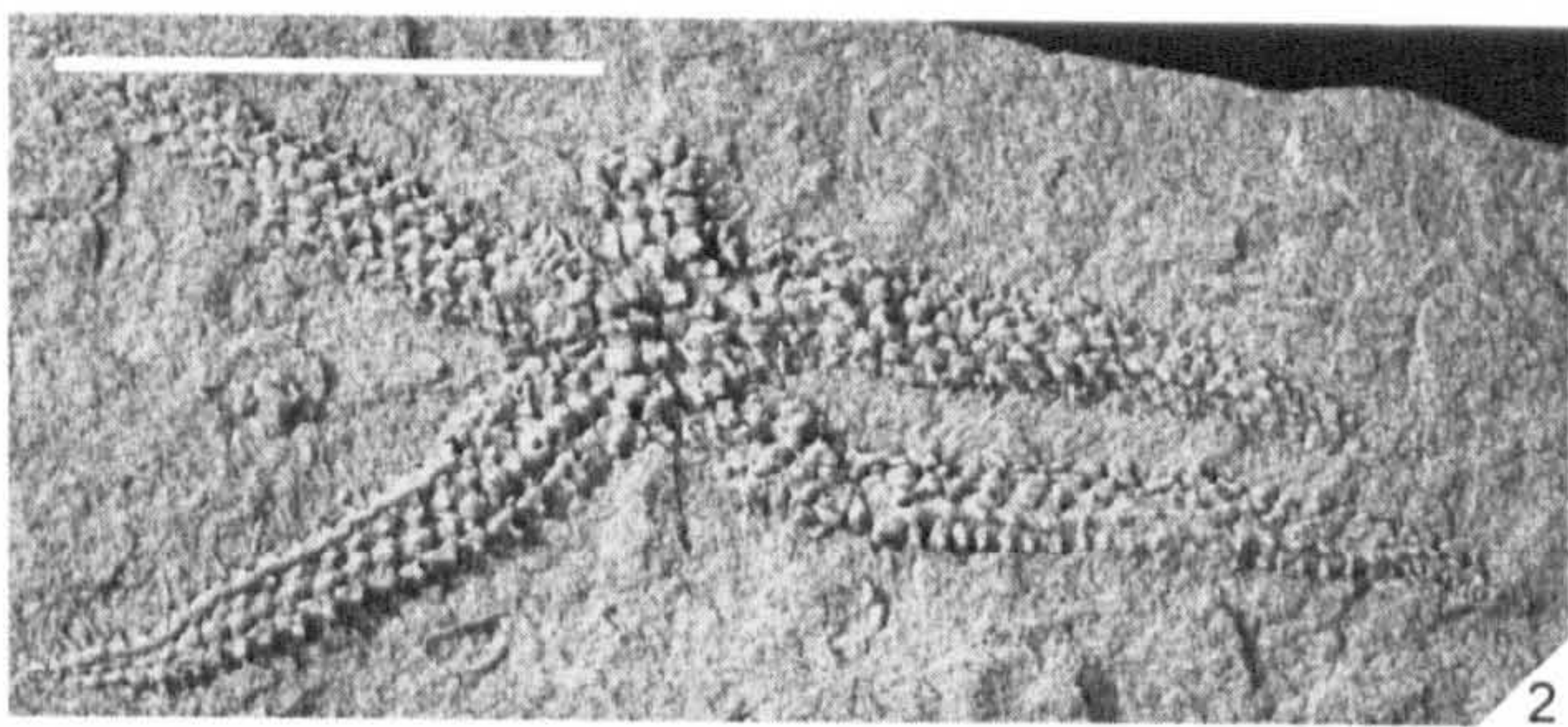
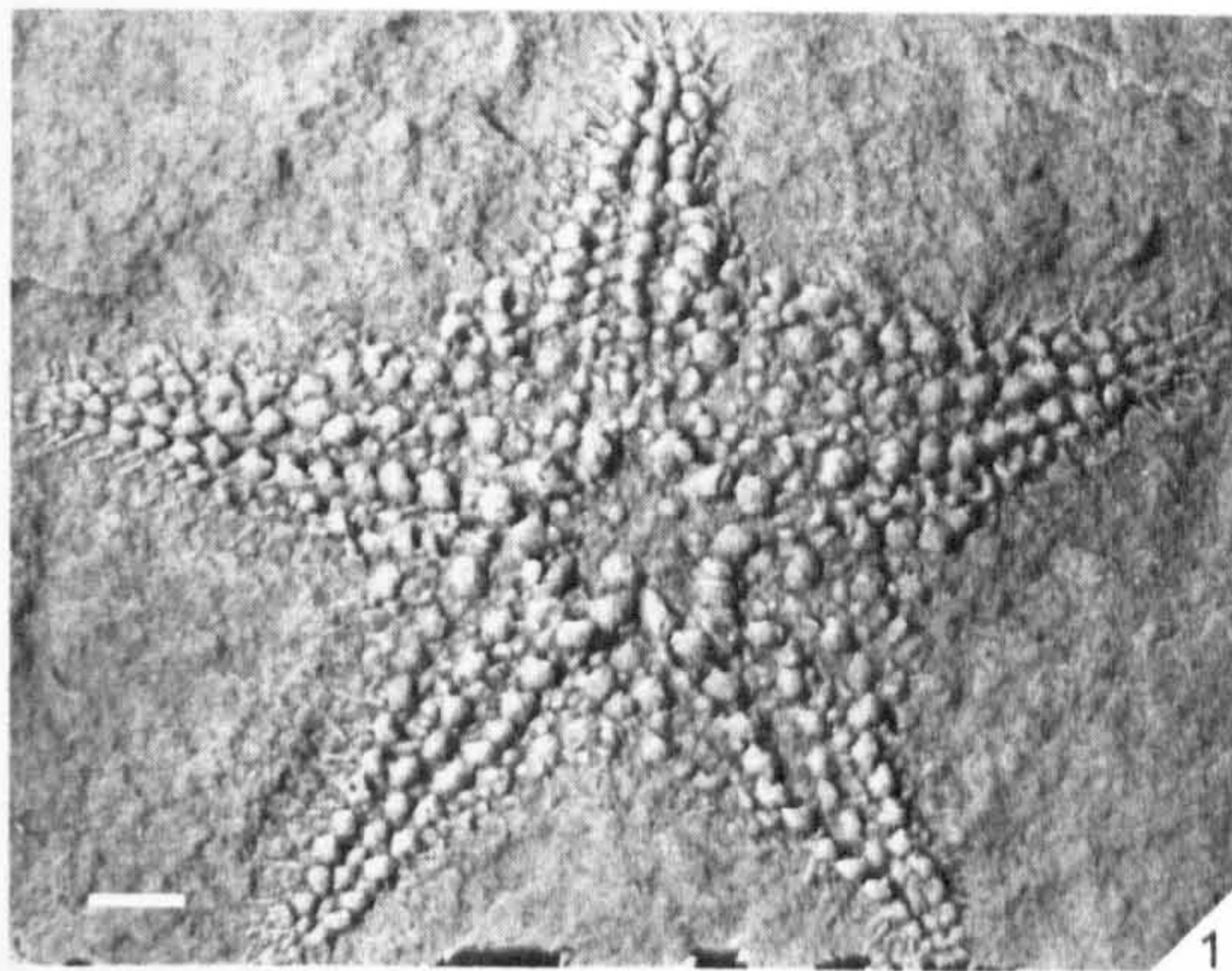
Fig. 3. *Mesopalaeaster?* *leintwardensis*; BMNH E 13153, orientation of arm tip (arrowed); scale bar represents 2 mm.

Figs 4-5. *Sturtzaster marstoni*. 4, BGS GSM6517, orientation of arm tips (arrowed); scale bar represents 10 mm. 5, OUM C.30631b, pronounced arm orientation; scale bar represents 10 mm.

Fig. 6. *Sturtzaster colvini*; BMNH E 20648, pronounced arm orientation; scale bar represents 10 mm.

Figs 7-8. *Rhopalocoma pyrotechnica*. 7, BMNH 46601, orientation of arm tip (arrowed); scale bar represents 10 mm. 8, BMNH E 5013a, slight orientation of arm tips (arrowed); scale bar represents 10 mm.







## EXPLANATION OF PLATE 2.8

Stelleroids showing pronounced current orientation of arms; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. All figures are of silicone casts except 8-9.

Figs 1-2. *Lapworthura miltoni*. 1, BMNH 57425; Church Hill. 2, NMS G18826515111.

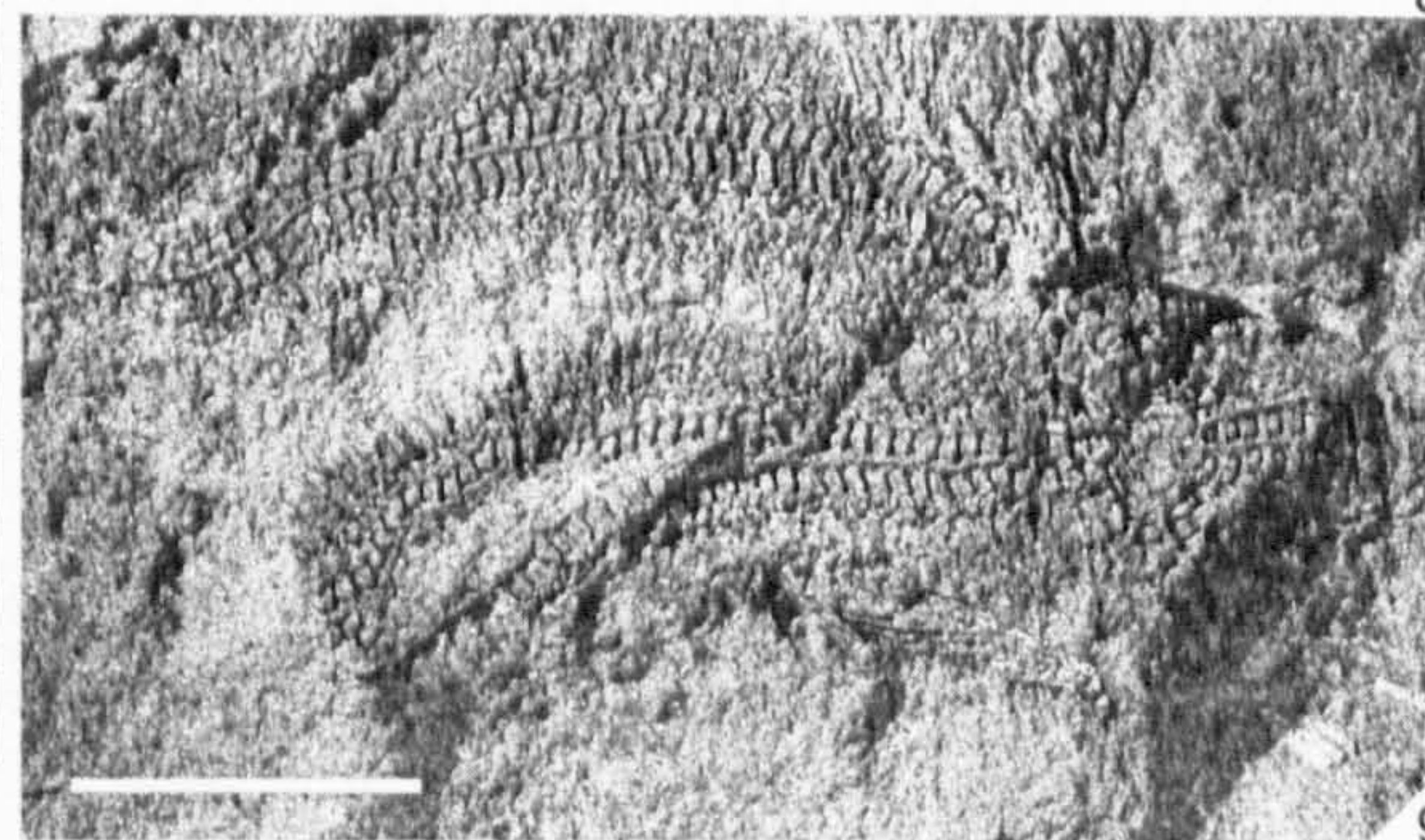
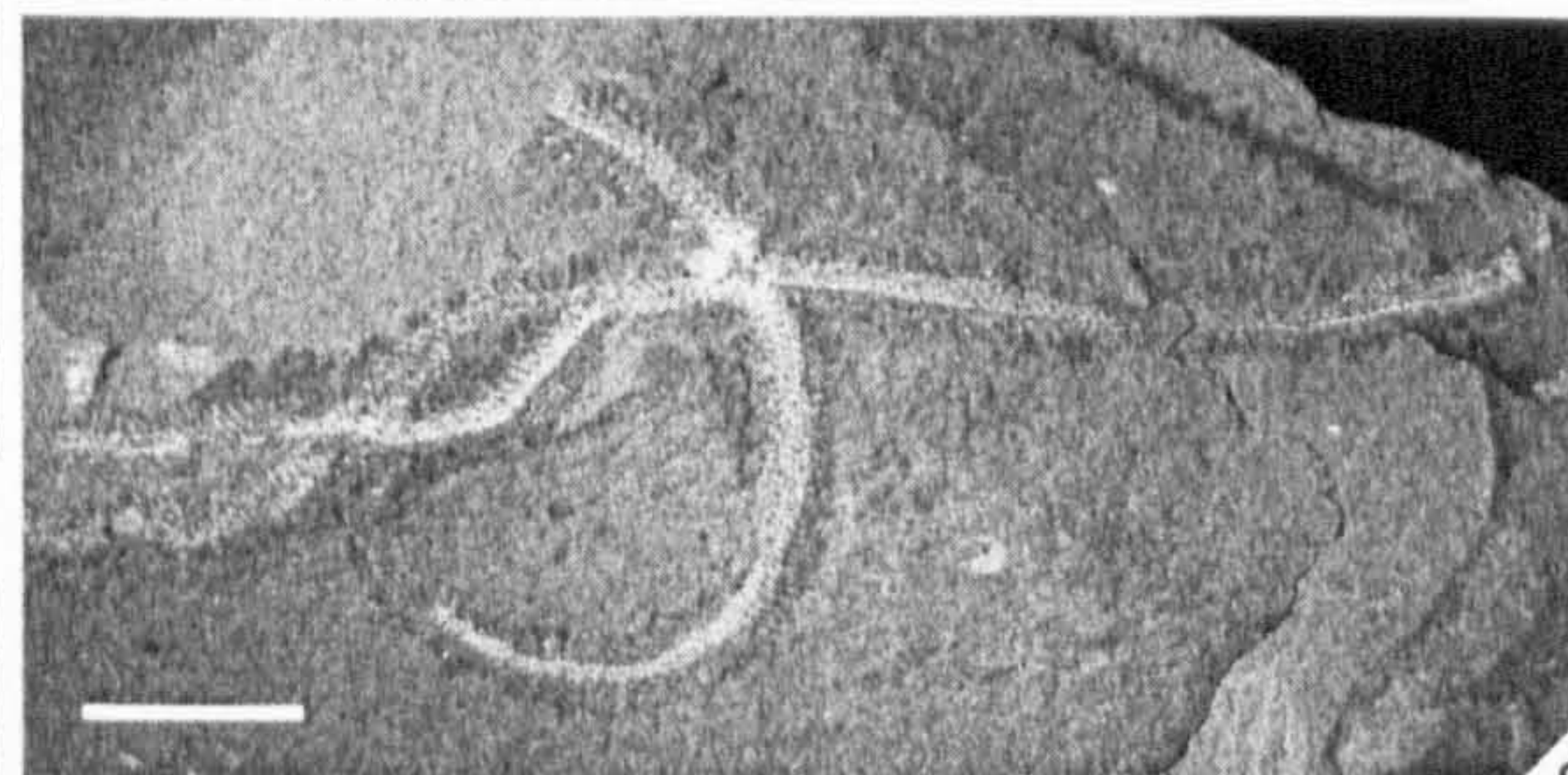
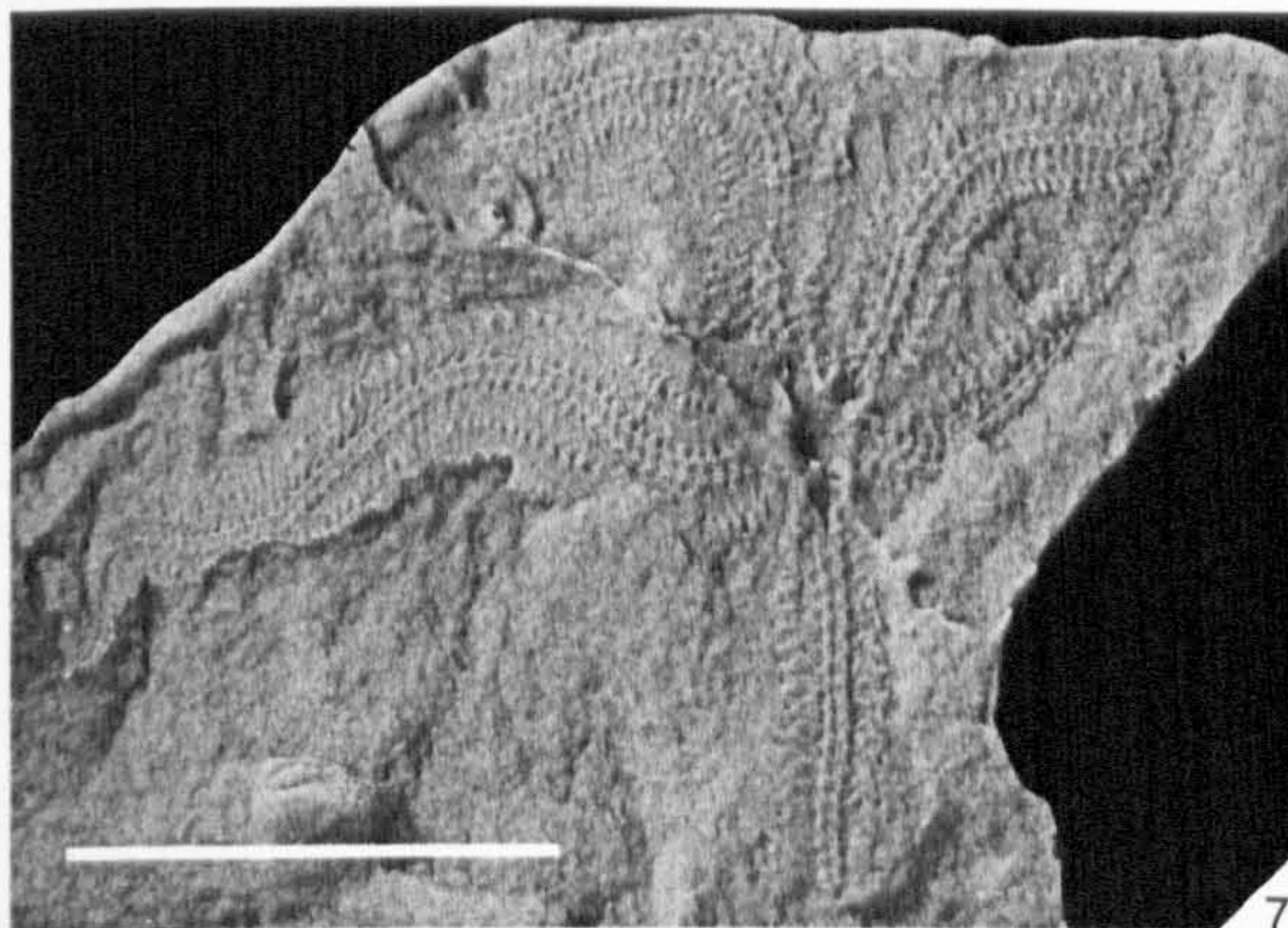
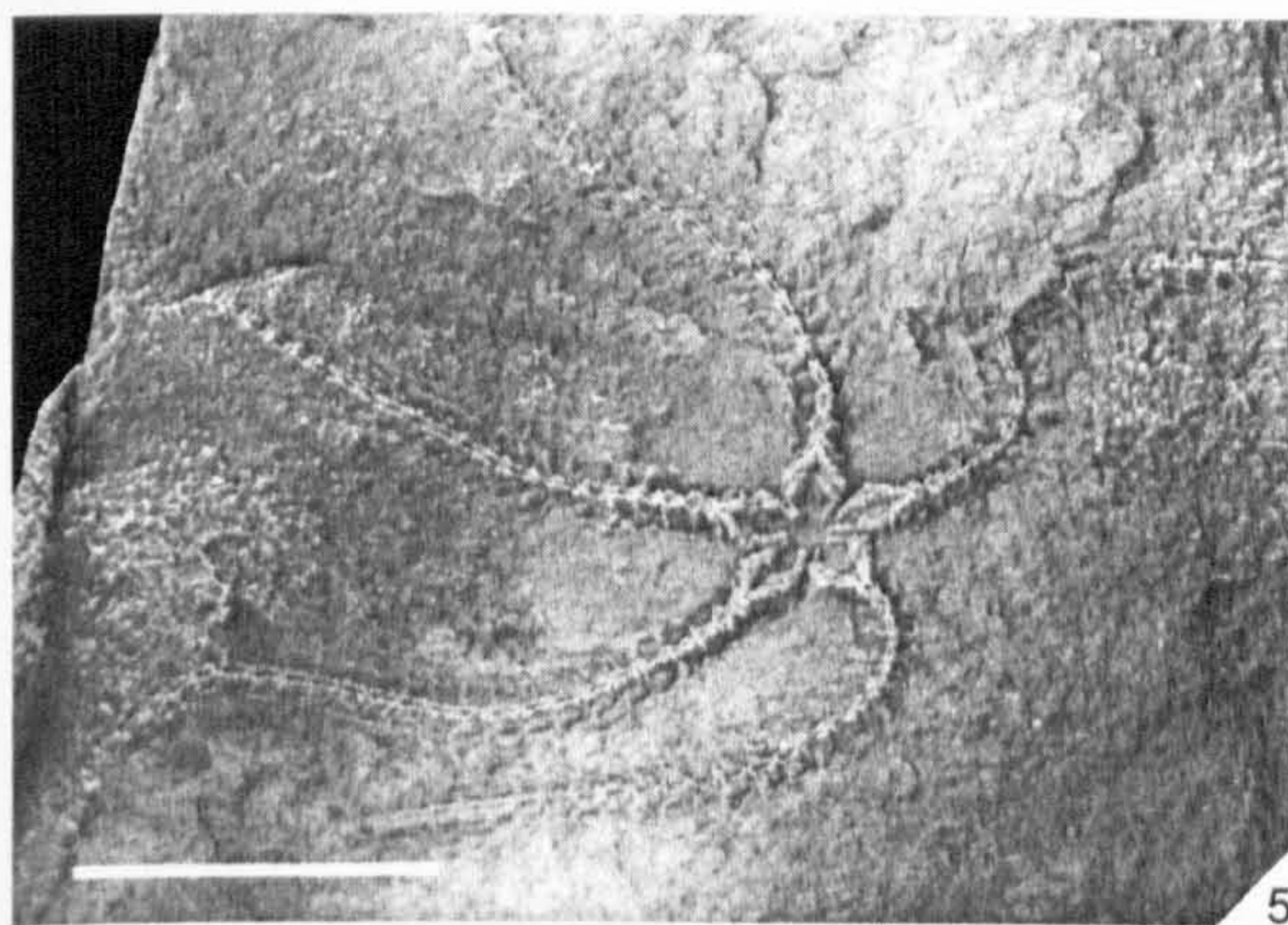
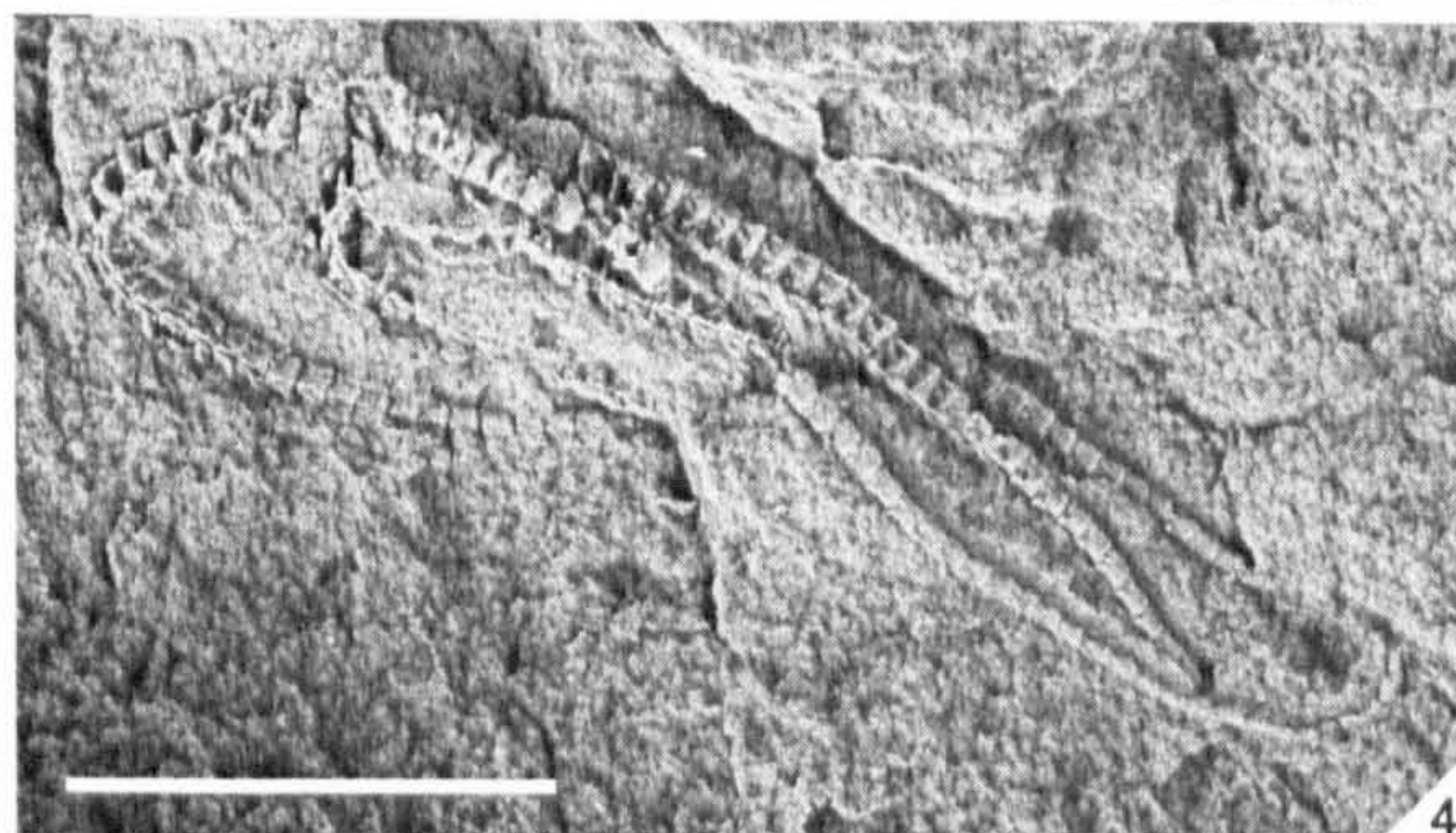
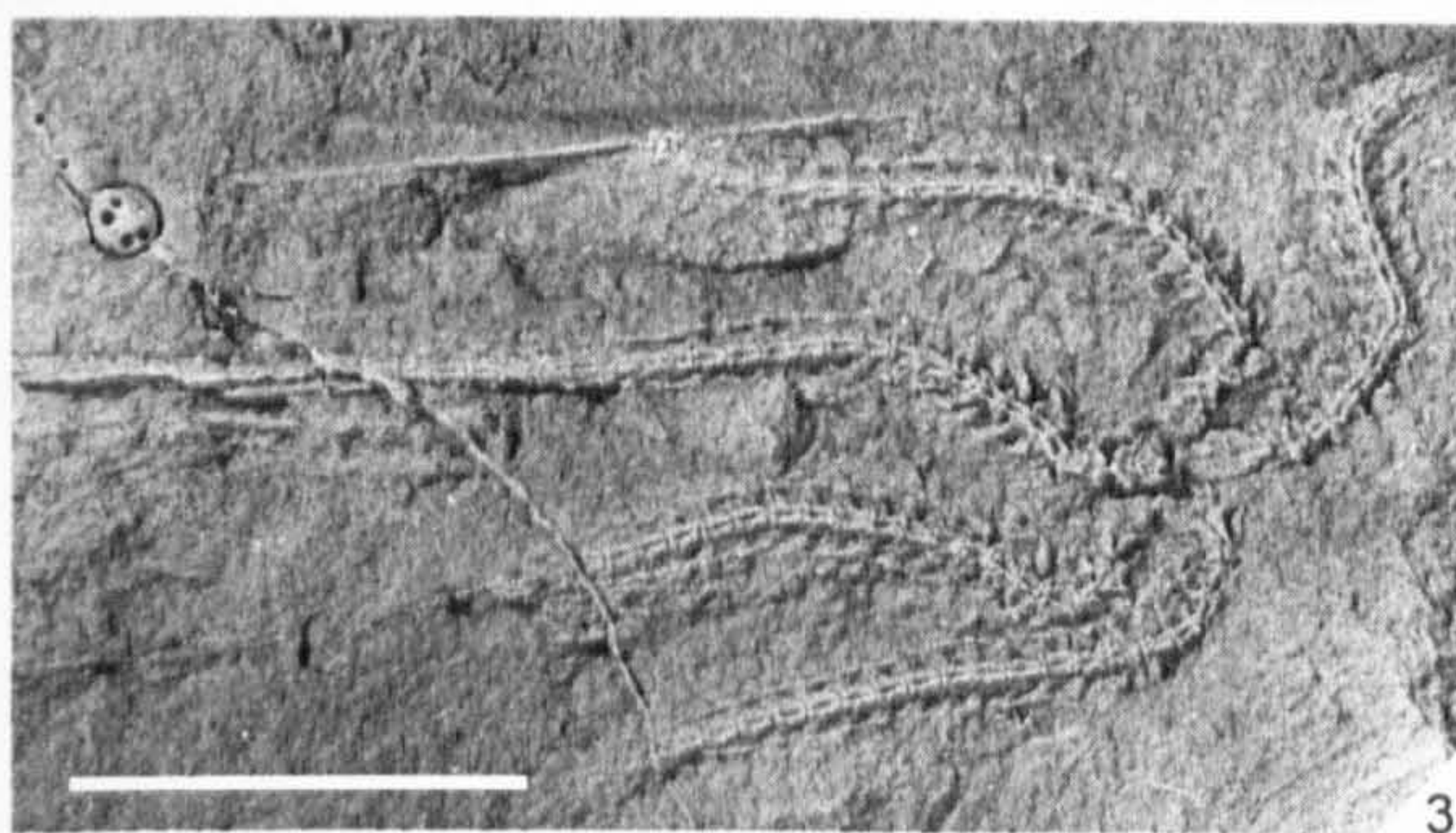
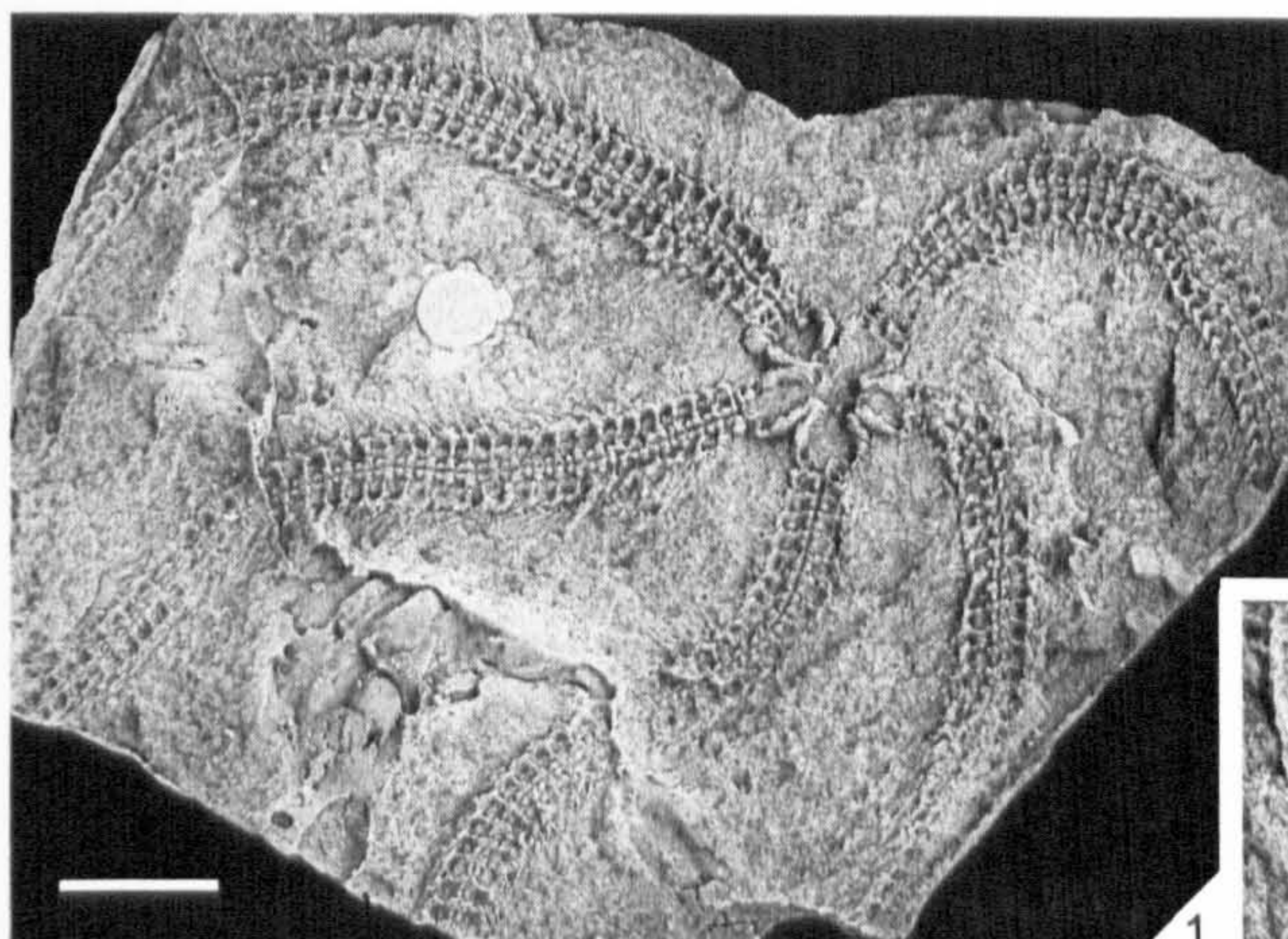
Figs 3-4, 5. *Furcaster leptosoma*. 3, OUM C.514. 4, BMNH E 20258; Church Hill. 5, OUM C.17291.

Fig. 6. *Loriolaster calceatus*; BMNH 38527, detail of specimen in assemblage; curving round of arm tips (arrowed) may demarcate original extent of the enlarged body disc.

Fig. 7. *Klasmura?* sp.; BMNH 40300; Church Hill.

Figs 8-9. *Bdellacoma vermiformis*. 8, CH211a, loose block, Church Hill Quarry 1. 9, CH94, Starfish Bed A, Church Hill Quarry 1.







## EXPLANATION OF PLATE 2.9

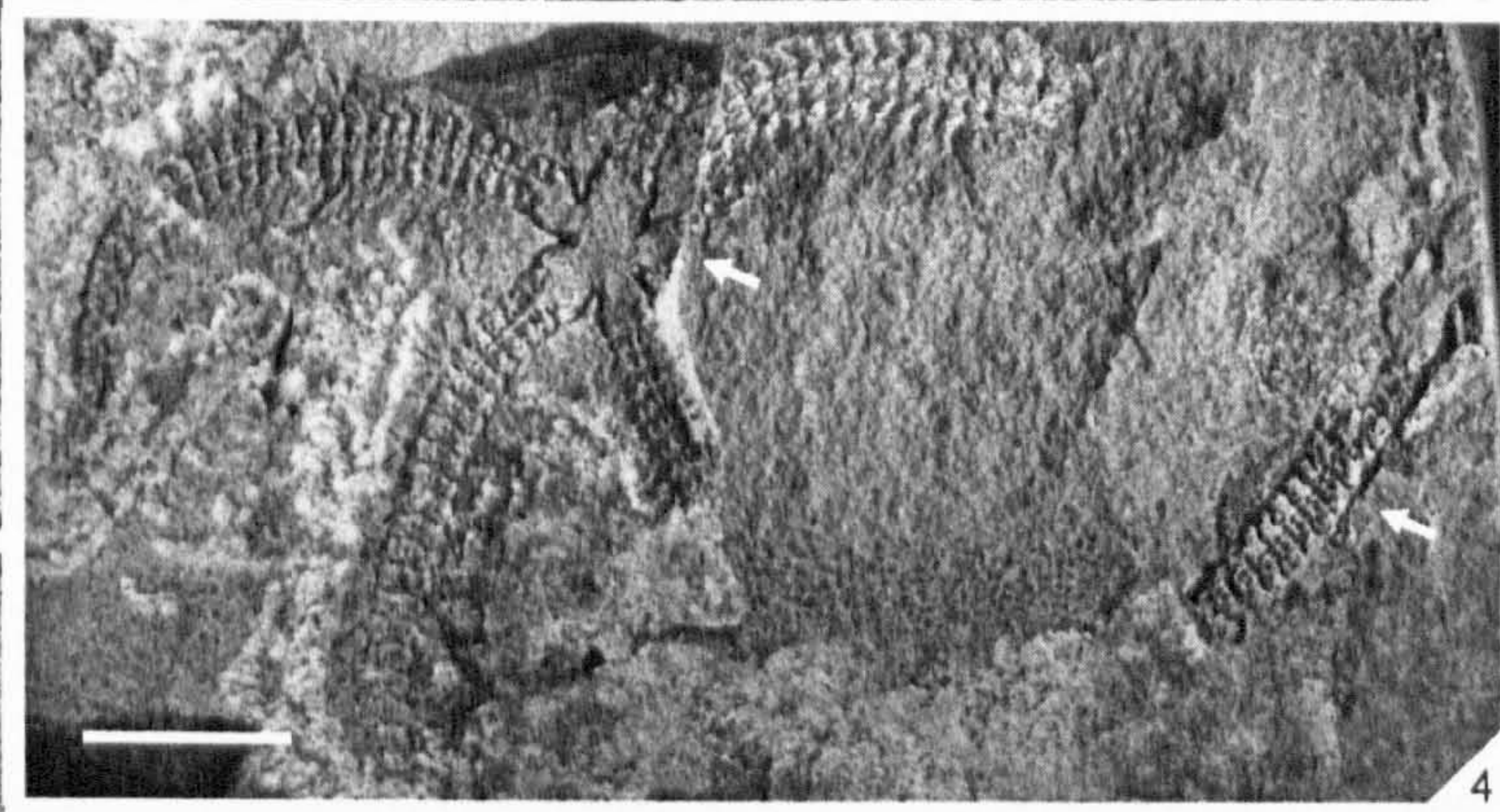
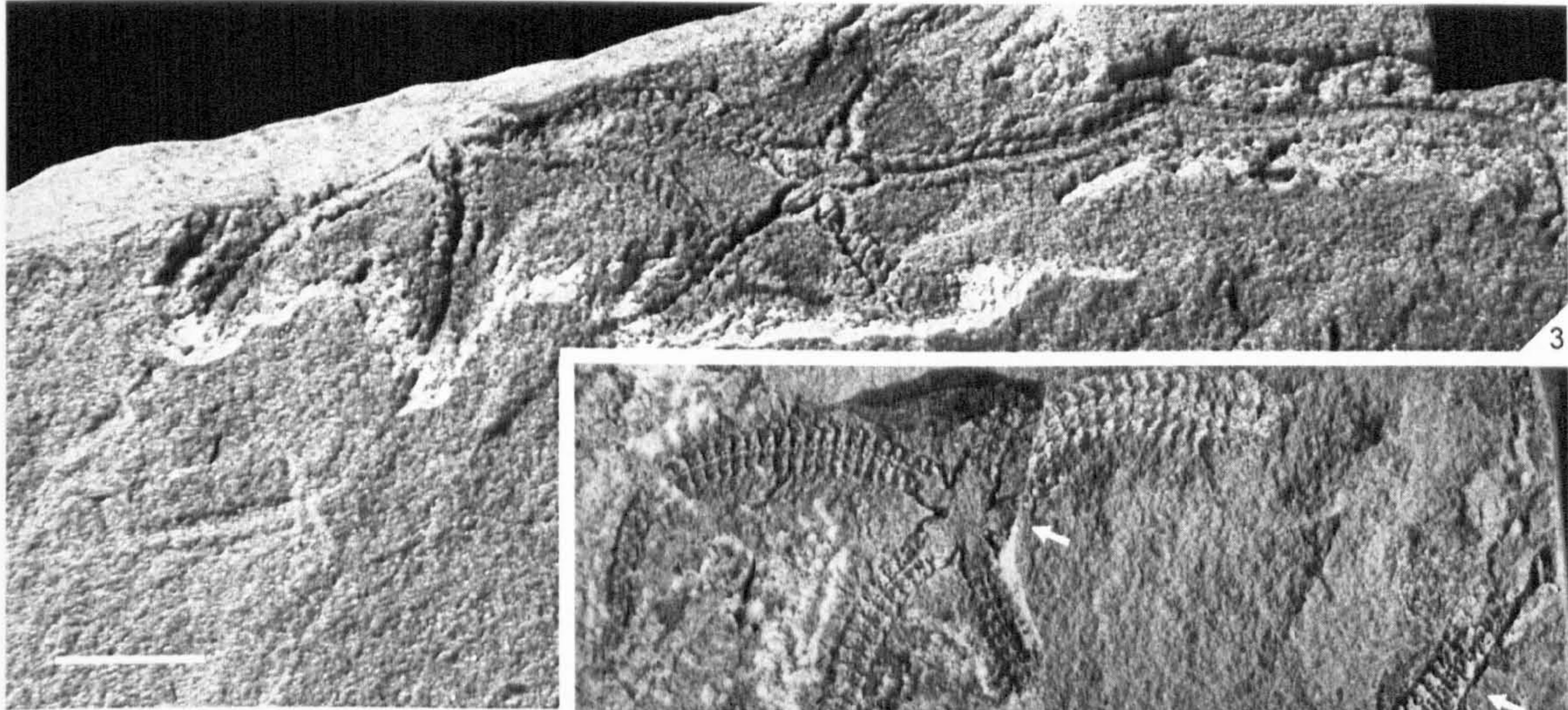
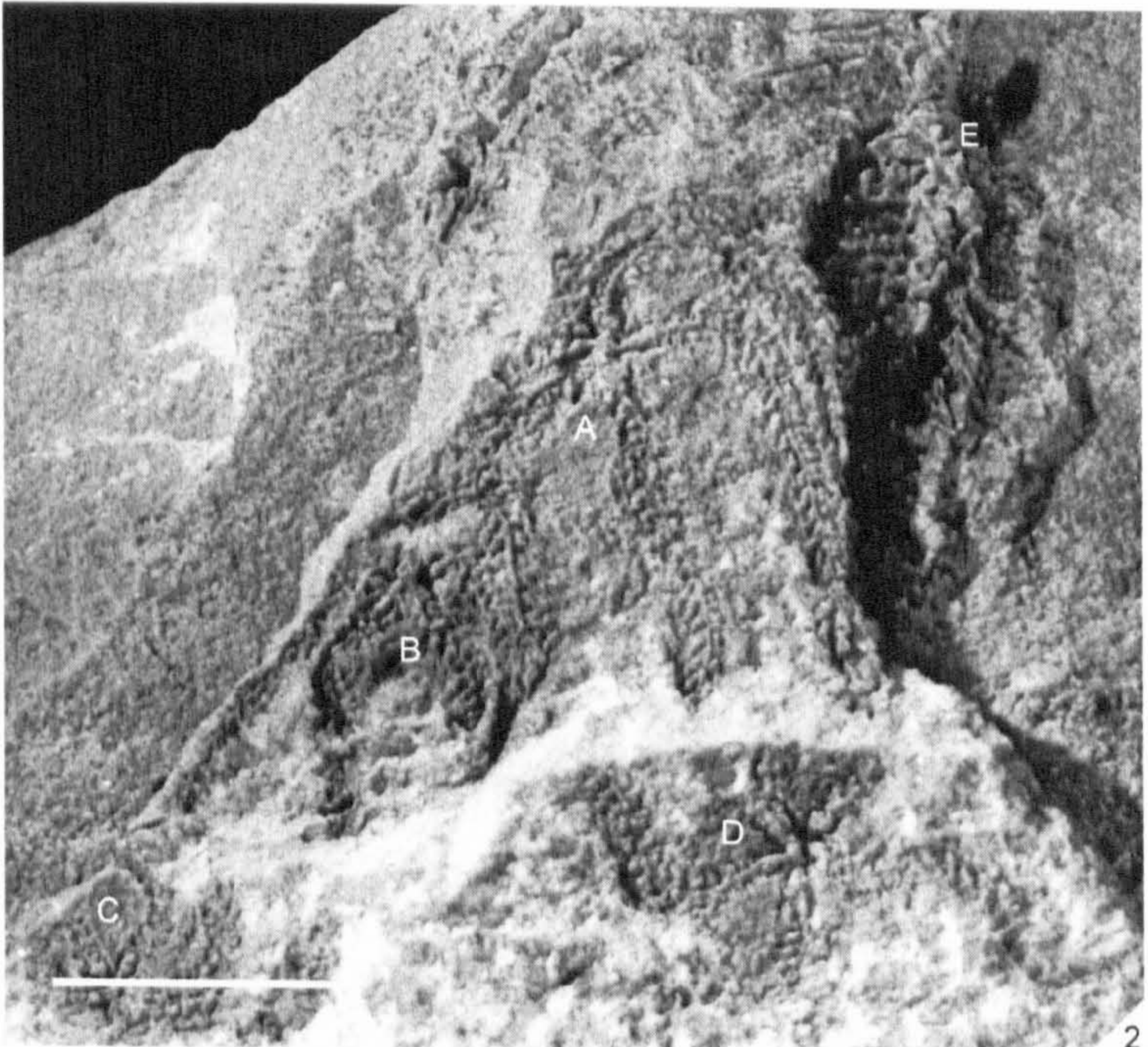
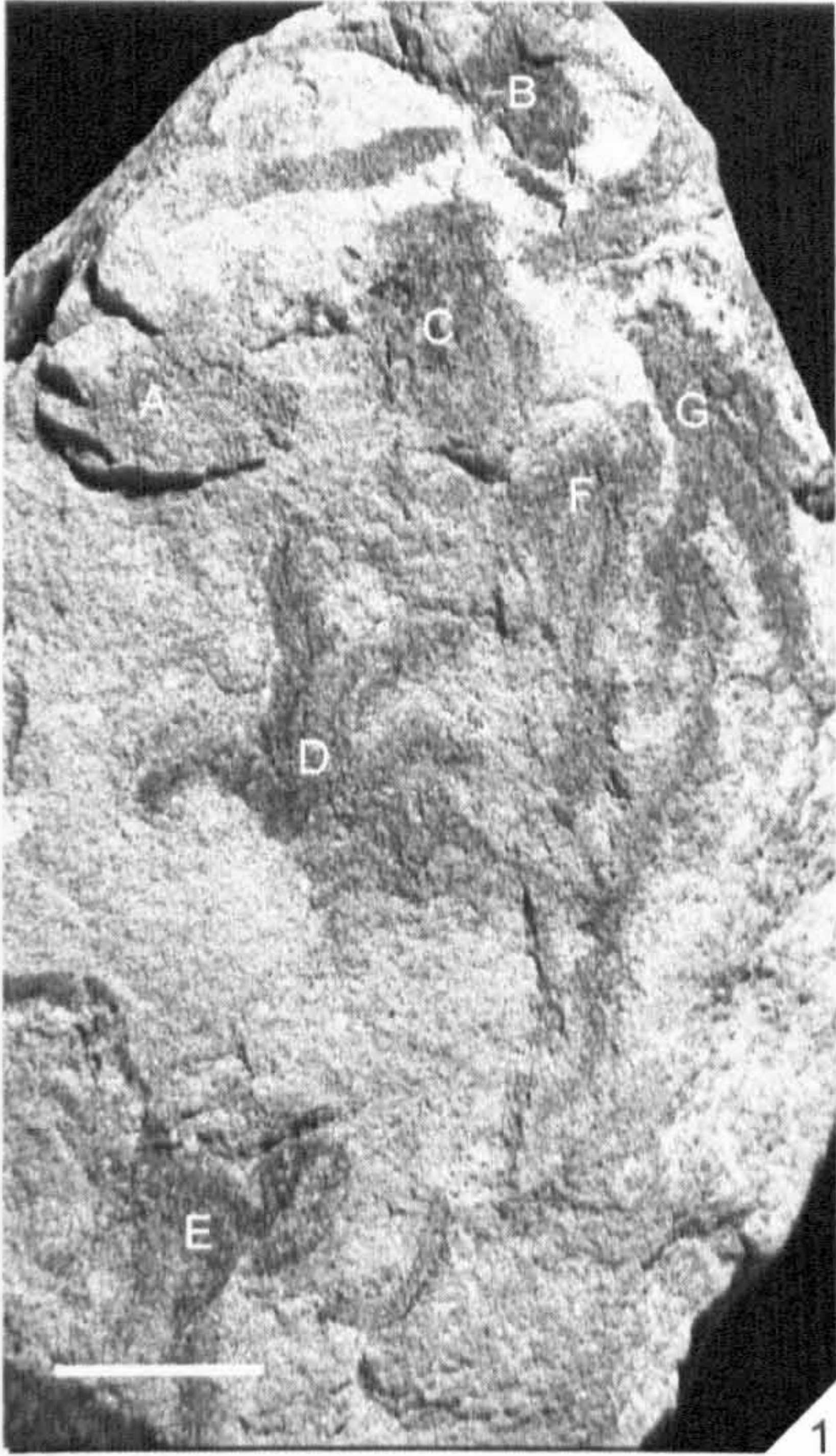
Stelleroid provenance within channel fill siltstone; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. Refer to text-figure 2.16 for stratigraphical provenance of CH78, CH81 and CH83.

Figs 1, 3, 5. *Furcaster leptosoma*. 1, MOCK1, seven specimens at slightly different stratigraphic levels (lettered A to G); Mocktree Quarry. 3, CH83, two specimens from the same horizon; Starfish Bed A, Church Hill Quarry 1. 5, CH81, two specimens separated by vertical thickness of 15 mm; Starfish Bed A, Church Hill Quarry 1.

Fig. 2. *Furcaster leptosoma* (lettered A to D) and *Lapworthura miltoni* (lettered E); CH78, four specimens of *F. leptosoma* occurring through 6 mm of siltstone; all specimens show a dorsal-up orientation (also see Text-fig. 2.23); Starfish Bed A, Church Hill Quarry 1.

Fig. 4. *Lapworthura miltoni*; CH91, two specimens (arrowed) separated by about 4 mm vertical thickness; loose block, Church Hill Quarry 1.







## EXPLANATION OF PLATE 2.10

Stelleroids and other biota; Lower Leintwardine Formation, Ludlow Series;  
Leintwardine, Herefordshire.

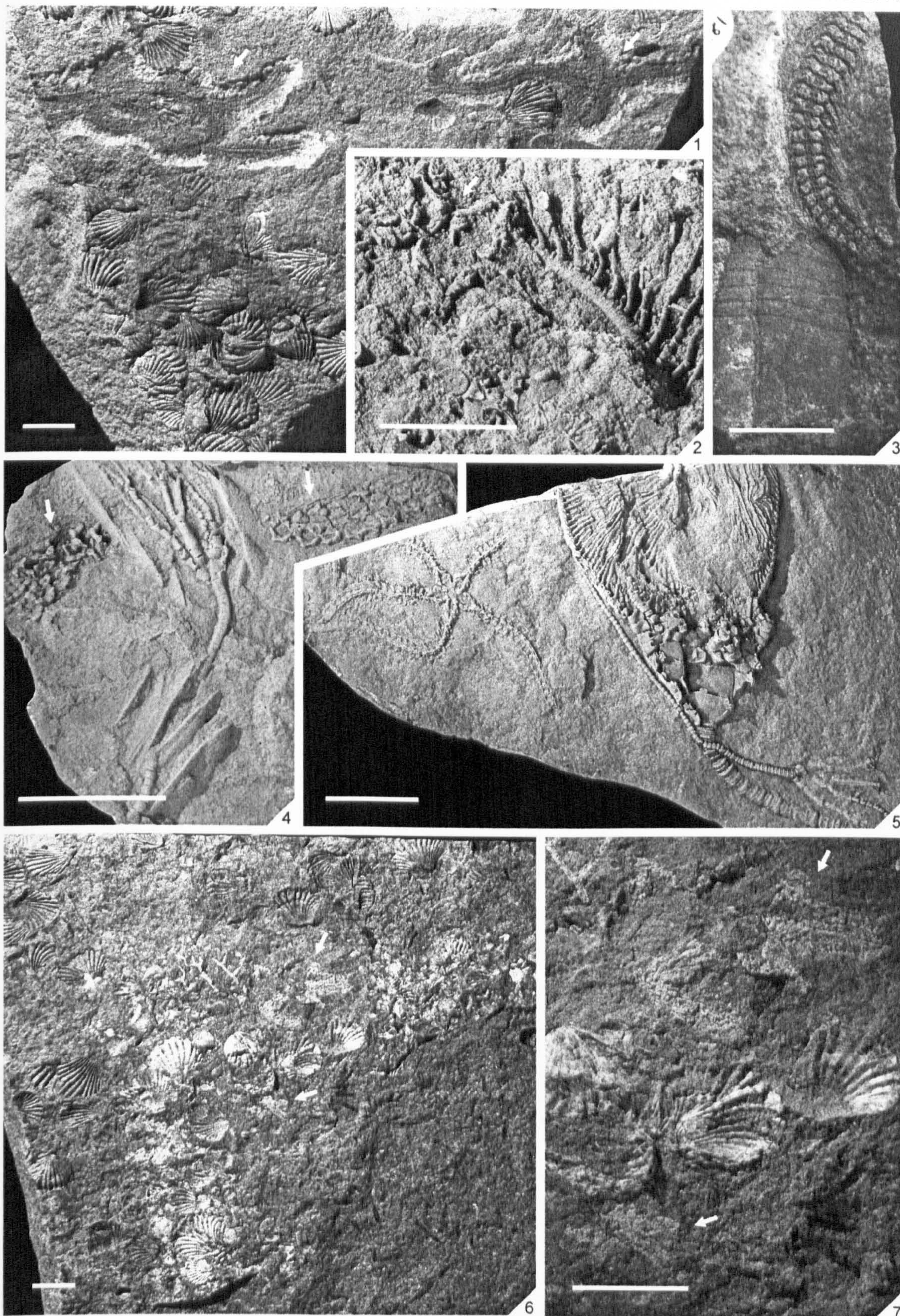
Fig. 1. *Bdellacoma vermiformis*; CH262, two specimens (arrowed) showing arm alignment in association with rhynchonellid brachiopods; Starfish Bed A, Church Hill Quarry 1; scale bar represents 10 mm.

Figs 2, 5. *Furcaster leptosoma*. 2, CH170, poorly preserved specimen (arrowed) in fine shelly horizon; crinoid brachia seen to right of ophiuroid mouth frame; Starfish Bed A, Church Hill Quarry 1; silicone cast; scale bar represents 5 mm. 5, BGS GSM89904, complete specimen with *Clematocrinus quinquepennis*; Church Hill; silicone cast; scale bar represents 10 mm.

Figs 3-4. *Lapworthura miltoni*. 3, BMNH E 52981, arm portion and orthocone cephalopod; Martin's Shell Quarry; scale bar represents 10 mm. 4, BGS GSM89994, arm portion (arrowed) and *Mastigocrinus bravoniensis*; silicone cast; scale bar represents 10 mm.

Figs 6-7. *Sturtzaster marstoni*; CH258; loose block, Church Hill Quarry 1; scale bars represent 10 mm. 6, two specimens (arrowed) in shelly horizon with rhynchonellid brachiopods and bryozoans; graptolites occur on a slightly different stratigraphic level. 7, detail of stelleroids (arrowed), with smaller specimen towards bottom of figure.







## EXPLANATION OF PLATE 2.11

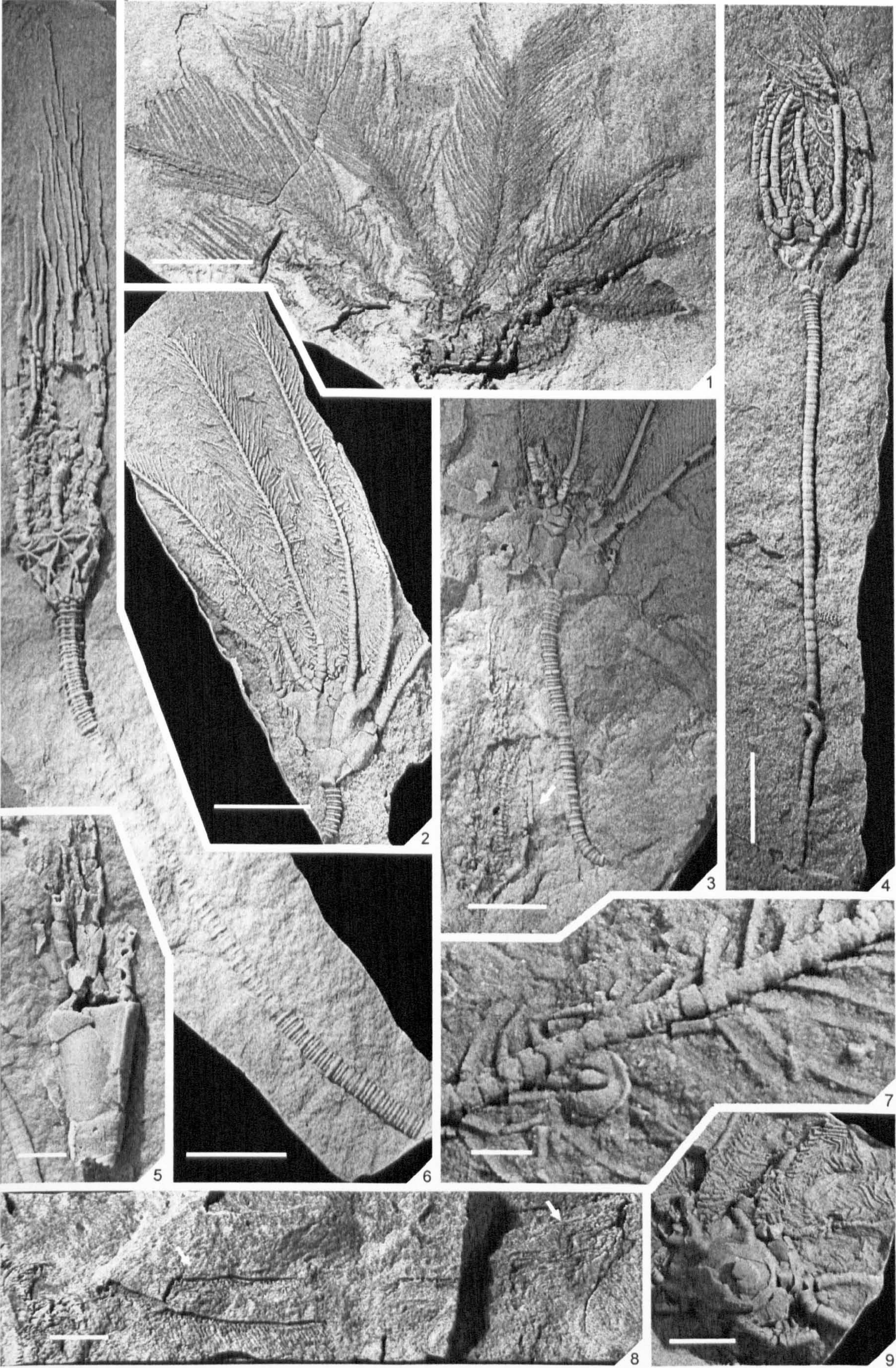
Crinoids; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. Refer to text-figure 2.16 for stratigraphical provenance of CH111 and CH115. All figures are of silicone casts except 1 and 8.

Figs 1-3, 7-9. *Clematocrinus quinquepennis*. 1, CH106, specimen lacking column; Starfish Bed A, Church Hill Quarry 1; scale bar represents 10 mm. 2, BMNH E 26576a, well preserved specimen; Church Hill; scale bar represents 10 mm. 3, BGS GSM89897, specimen retains most of column, associated with *Gissocrinus ludensis* (arrowed); scale bar represents 10 mm. 7, BMNH E 26576a, detail of brachia and articulated pinnules; Church Hill; scale bar represents 1 mm. 8, CH111, two specimens (arrowed) occurring at slightly different stratigraphic levels; Starfish Bed A, Church Hill Quarry 1; scale bar represents 10 mm. 9, CH115, specimen missing column with some disarticulation of pinnules; Starfish Bed A, Church Hill Quarry 1; scale bar represents 5 mm.

Fig. 4. Undet. specimen; BGS GSM90006, nearly complete missing distal most portion of column; scale bar represents 5 mm.

Fig. 5. *Cicerocrinus elegans*; BMNH EE 958, incomplete specimen; Church Hill; scale bar represents 2 mm.







## EXPLANATION OF PLATE 2.12

Crinoids; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire.  
All figures are of silicone casts except 2.

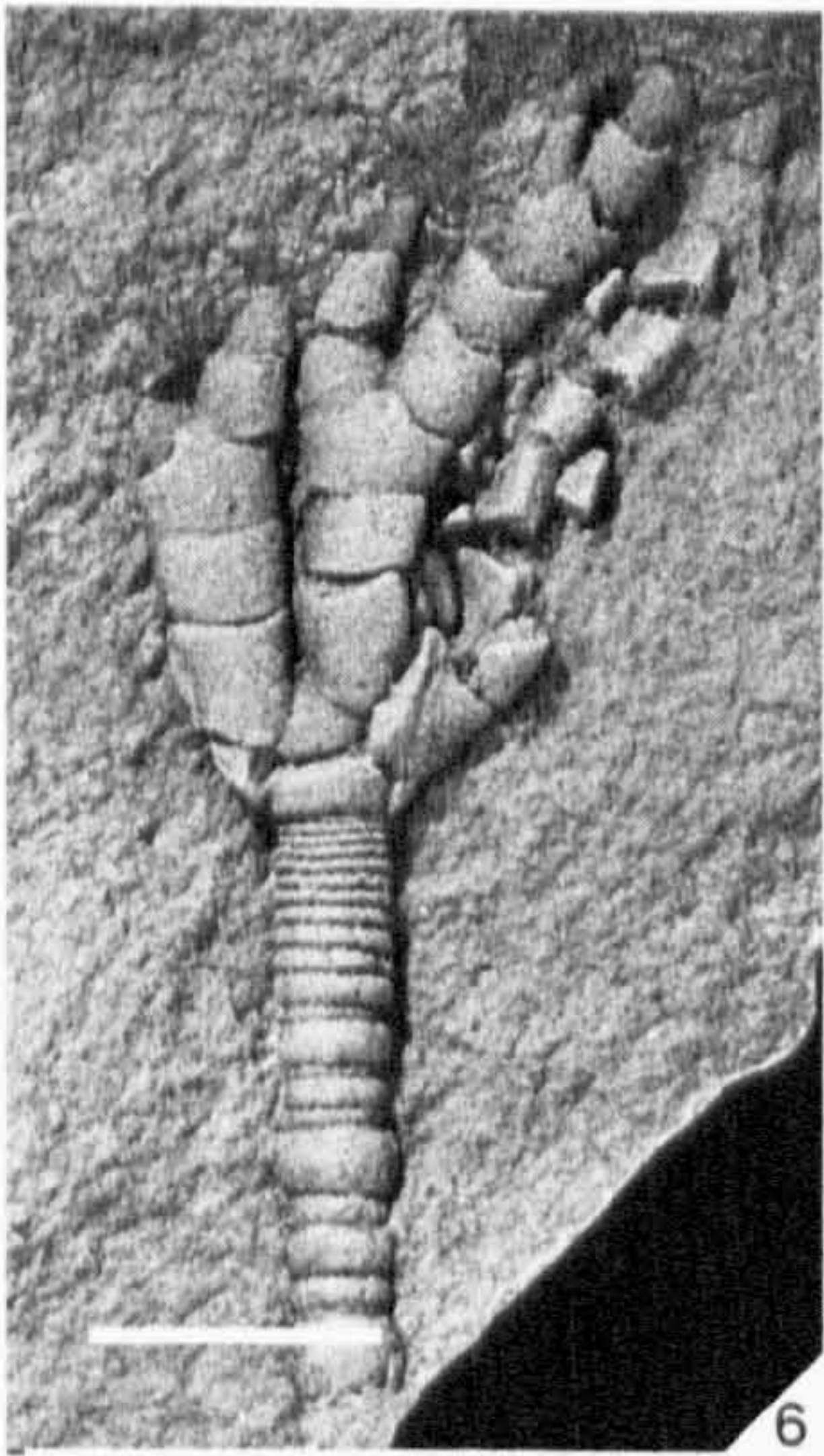
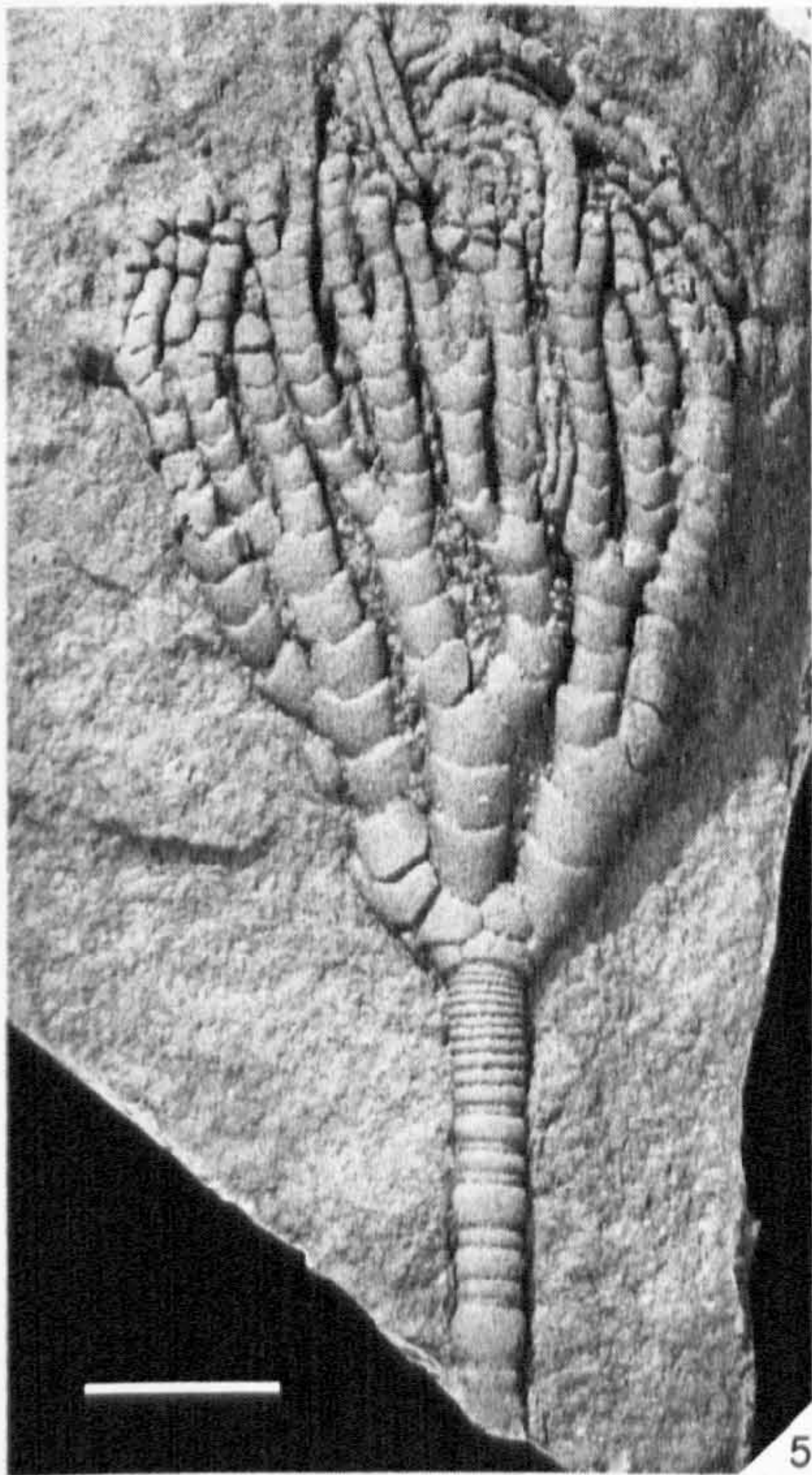
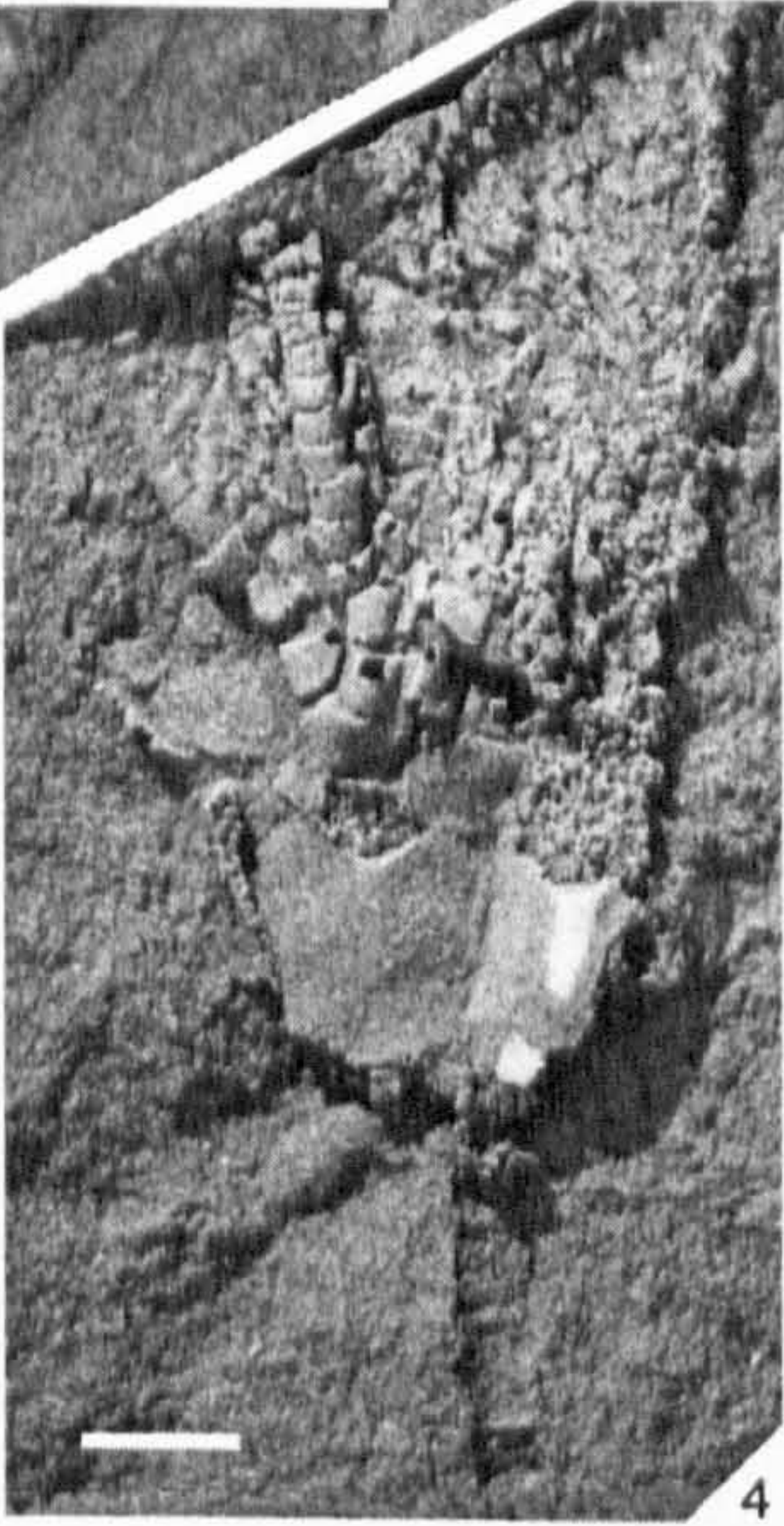
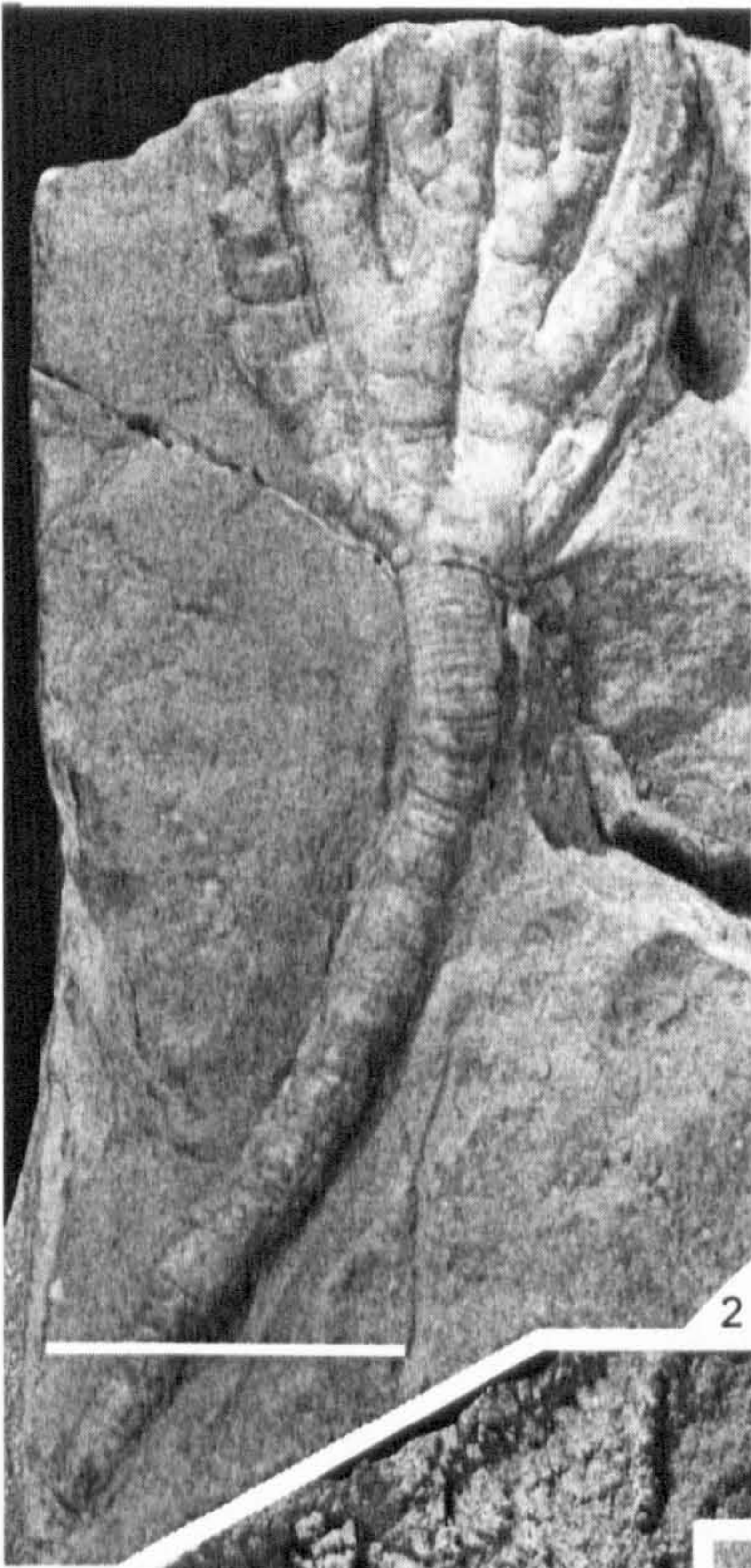
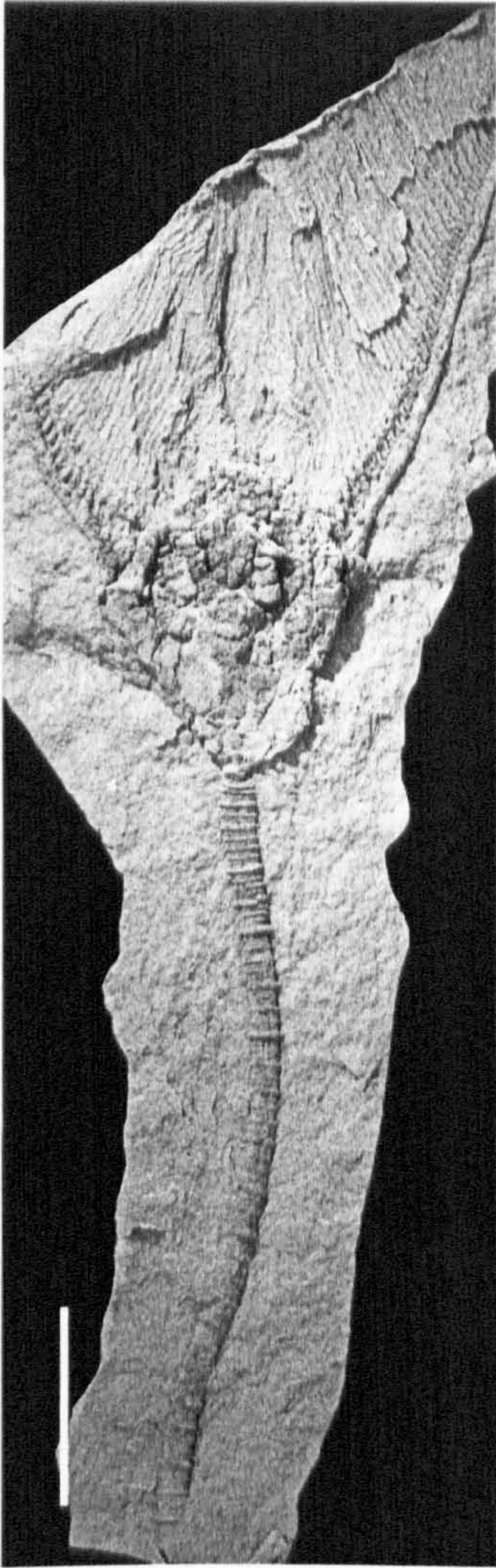
Fig. 1. Undet. specimen; BMNH 46753, nearly complete missing distal part of column;  
scale bar represents 10 mm.

Figs 2-3, 5-6. *Eutaxocrinus maccoyanus*. 2, BGS GSM89989, specimen missing distal  
column and brachia; scale bar represents 10 mm. 3, BMNH E 26578, nearly complete,  
missing distal column; Church Hill; scale bar represents 10 mm. 5-6, CH118a-b, part  
and counterpart, nearly complete, distal column not preserved; Starfish Bed A, Church  
Hill Quarry 1; scale bar represents 5 mm.

Fig. 4. Undet. specimen; CH113a, poorly preserved with some disarticulation; Starfish  
Bed A, Church Hill Quarry 1; scale bar represents 2 mm.

Figs 7-8. *Mastigocrinus bravoniensis*; CH120a-b, part and counterpart, nearly complete,  
distal column not preserved; loose block, Church Hill Quarry 1; scale bar represents 2  
mm.







## EXPLANATION OF PLATE 2.13

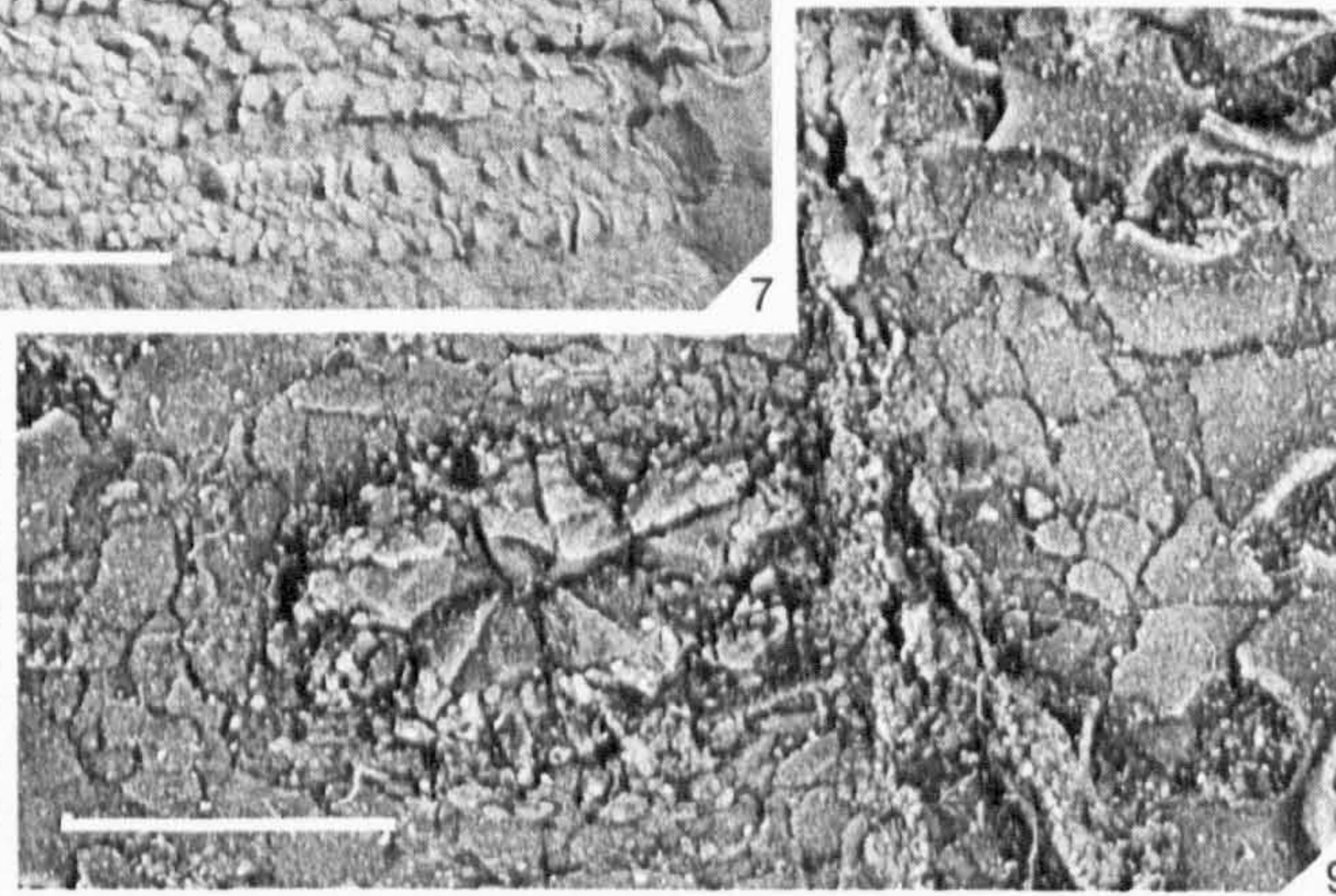
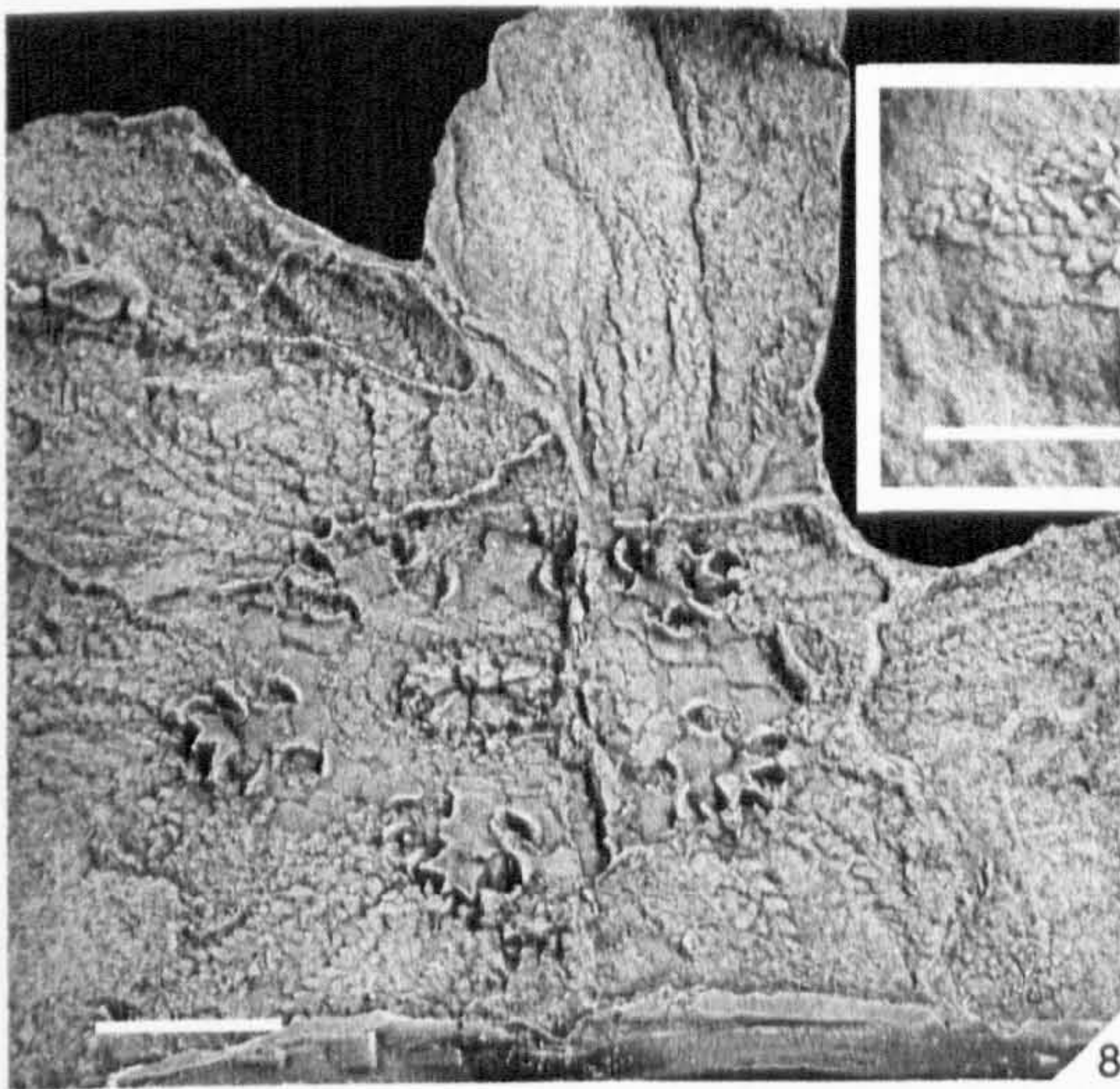
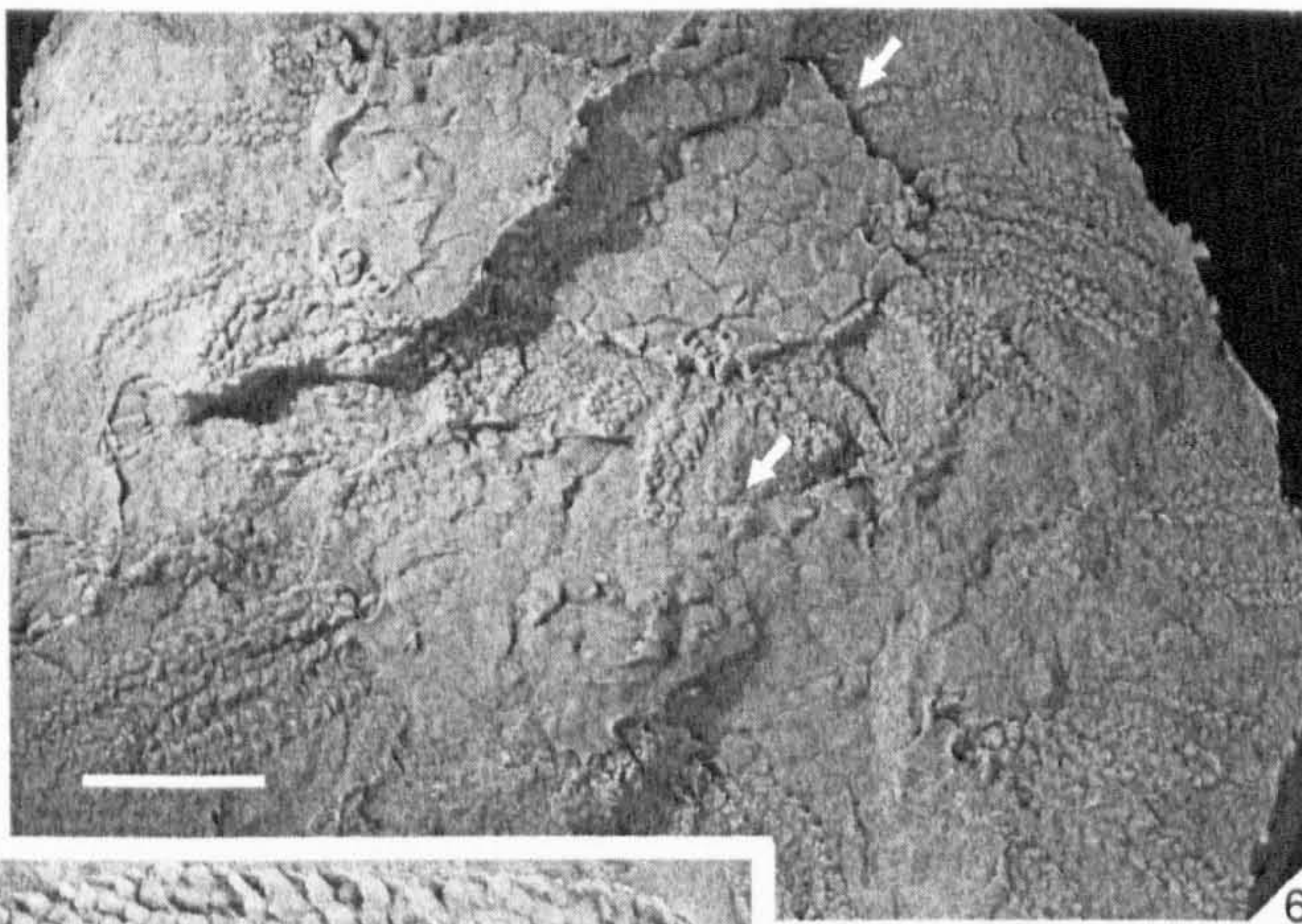
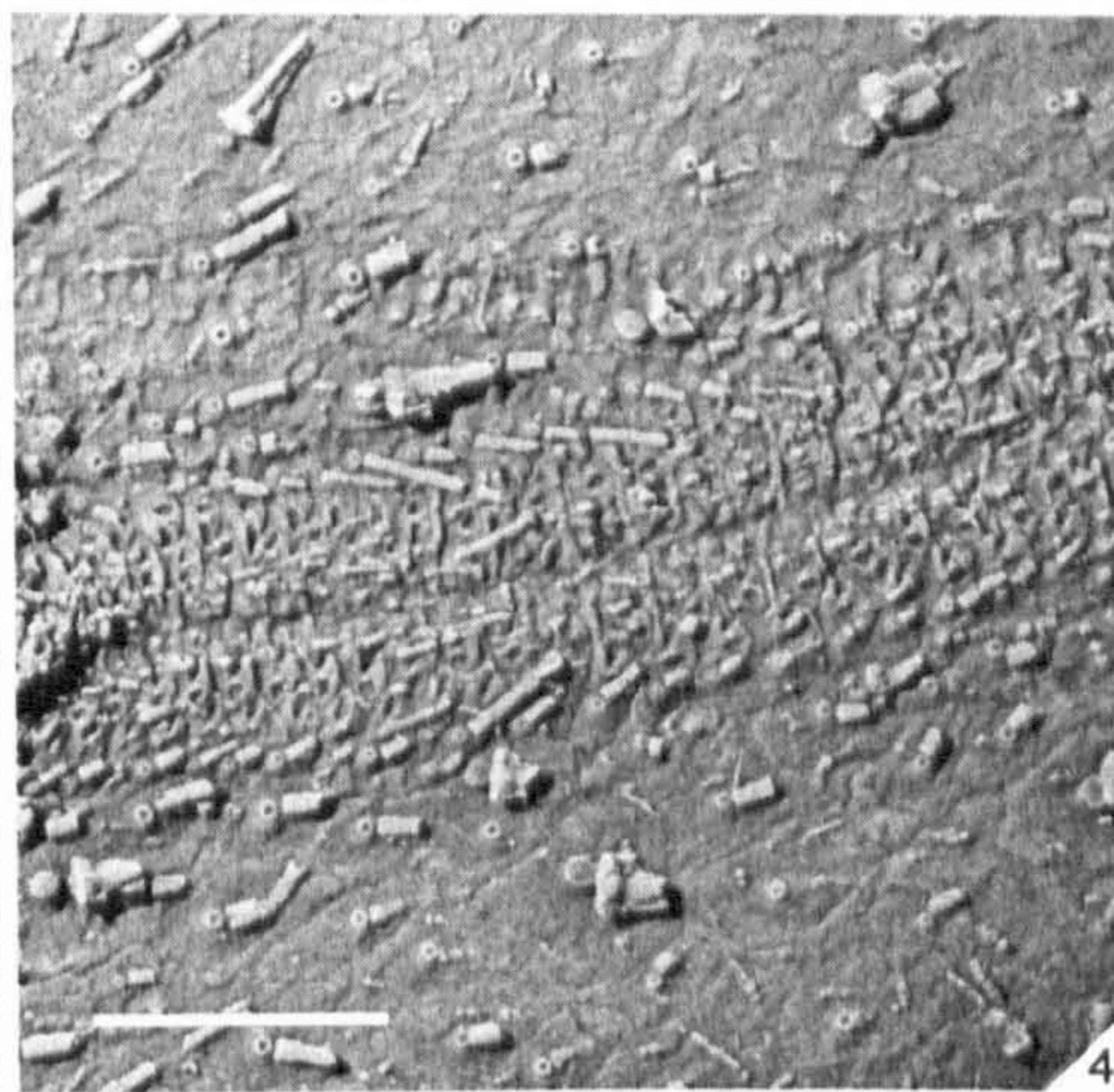
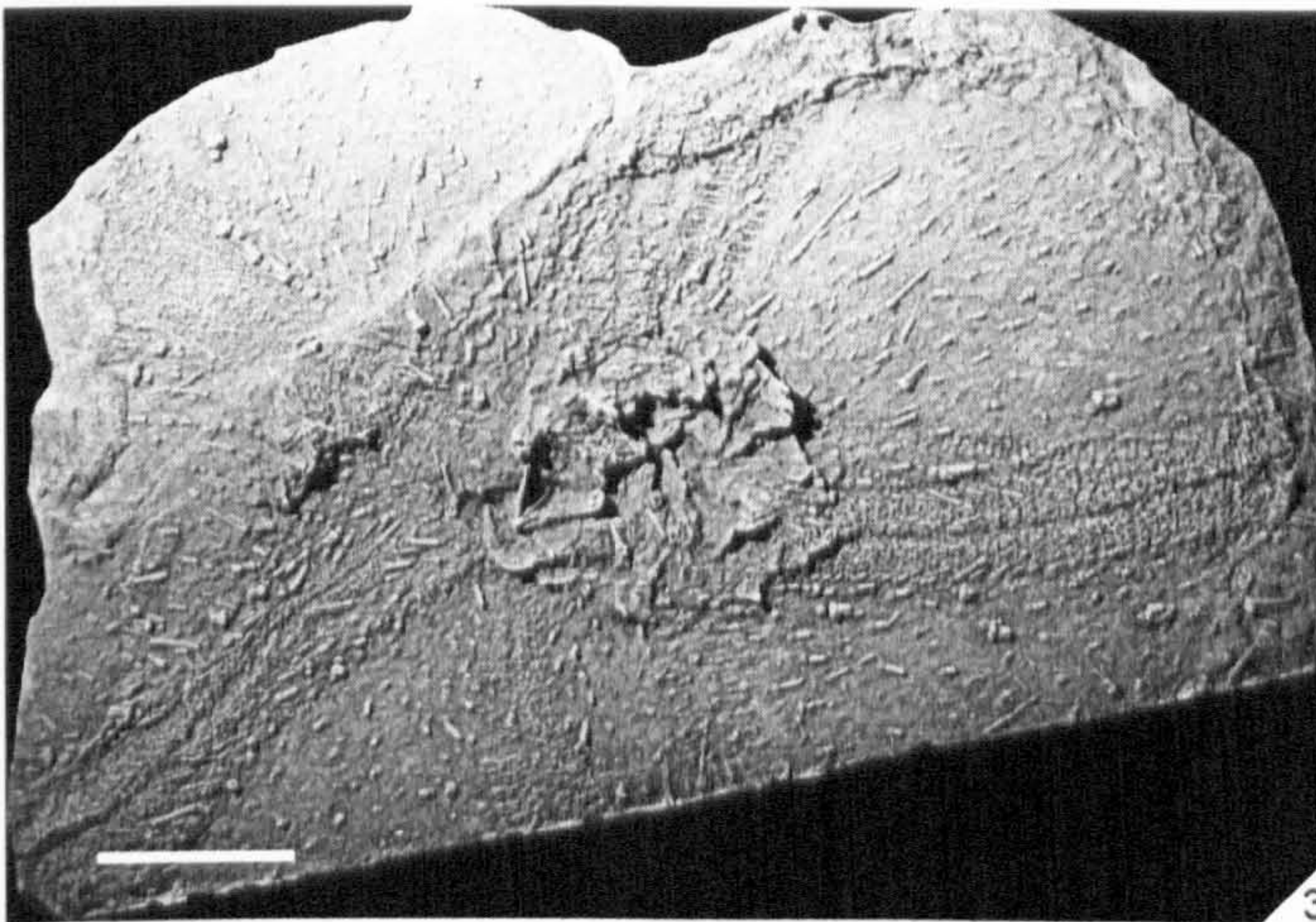
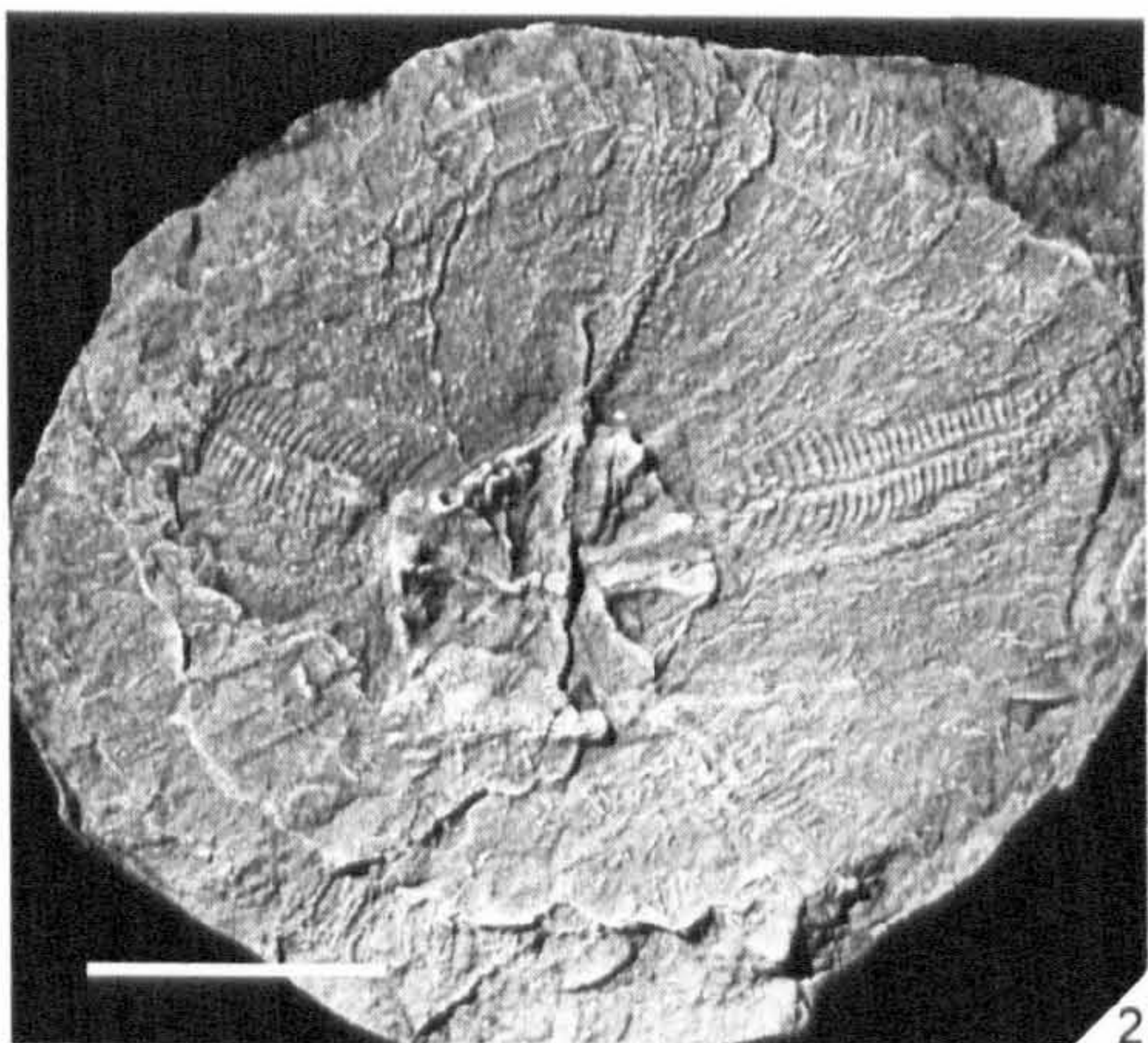
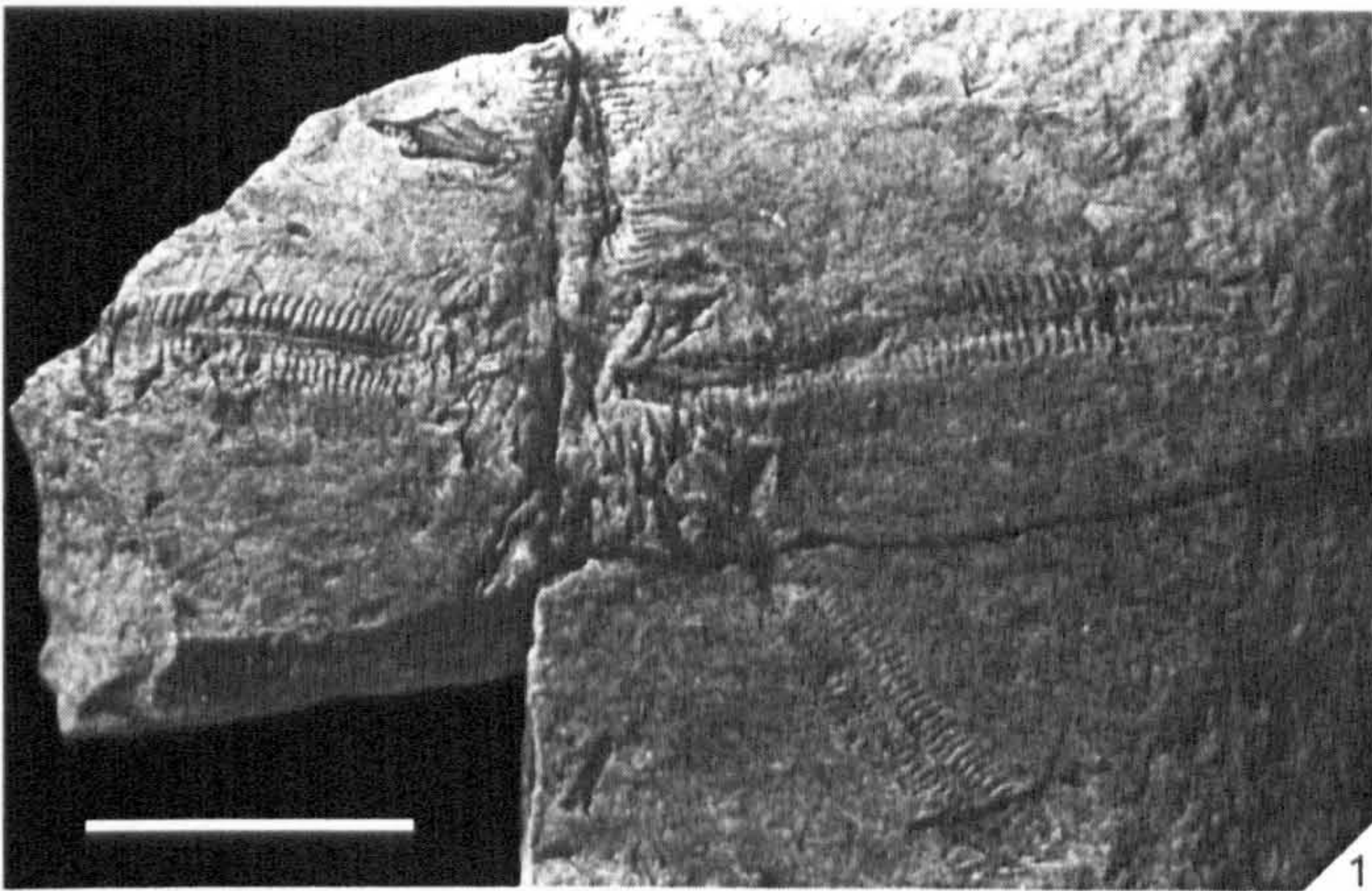
Echinoids (Figs 1-5) and ophiocistioids (Figs 6-9); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. All figures are of silicone casts except 1 and 5.

Figs 1-2, 5. *Palaeodiscus ferox*. 1, BMNH E 10655, nearly complete; scale bar represents 10 mm. 2, BMNH E 34362, complete; Church Hill; scale bar represents 10 mm. 5, BGS GSM47577, nearly complete; scale bar represents 10 mm.

Figs 3-4. *Echinocystites pomum*; BMNH E 34352; Church Hill. 3, well preserved and nearly complete; scale bar represents 10 mm. 4, detail of proximal ambulacrum showing articulated spines and pedicellariae; scale bar represents 5 mm.

Figs 6-9. *Sollasina woodwardi*. 6-7, BMNH E 27030; Church Hill; scale bar represents 10 mm. 6, two articulated specimens (arrowed) on a slightly different stratigraphic level. 7, detail of articulated podia. 8-9, OUM C.44. 8, entire articulated specimen; scale bar represents 10 mm. 9, detail of buccal apparatus; scale bar represents 5 mm.







## EXPLANATION OF PLATE 2.14

Eurypterids; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm except on Fig. 6, where it represents 5 mm. Refer to text-figure 2.5 for stratigraphical provenance of CH144.

Figs 1, 10-11. *Carcinosoma* sp. 1, BMNH In. 48405, prosomal appendage III, IV or V; Church Hill. 10, CH146a, prosomal appendage III, IV or V; loose block, Church Hill Quarry 1. 11, BMNH 59222, metastoma.

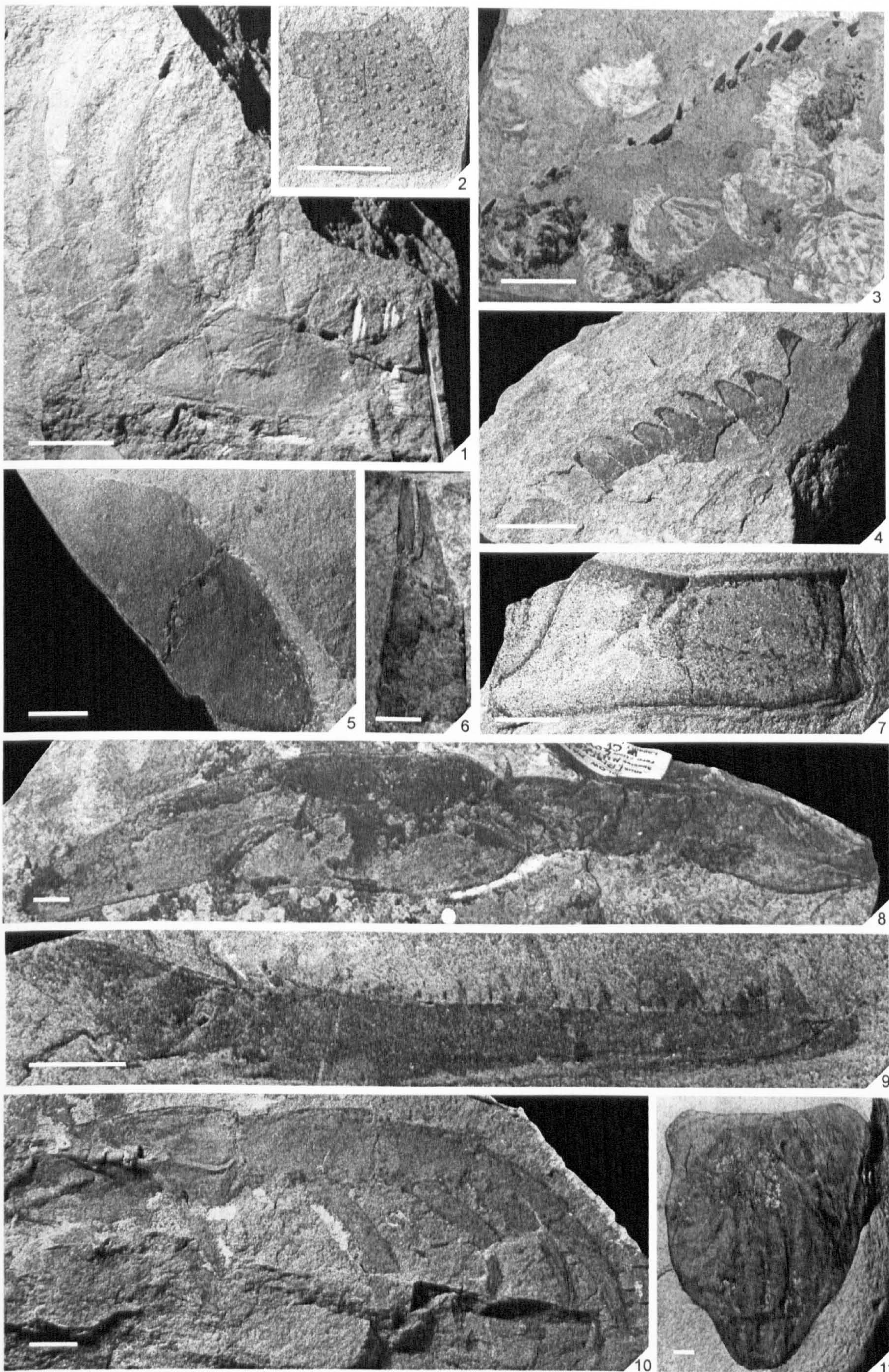
Figs 2-5, 7. Undet. specimens. 2, MS24, cuticle; Martin's Shell Quarry. 3, SHRCM G10445, gnathobase with rhynchonellid brachiopods; Church Hill. 4, BMNH 41892, incomplete gnathobase; Church Hill. 5, CH144, incomplete prosoma; Starfish Bed A, Church Hill Quarry 1. 7, SHRCM G10451b, part of prosomal appendage; Brandon Quarry.

Fig. 6. *Carcinosoma?* sp.; BGS GSM89581, chelicera; Church Hill.

Fig. 8. *Carcinosoma punctatum*; BMNH In. 43804, nearly complete prosomal appendage VI; Church Hill.

Fig. 9. *Erettopterus marstoni*; BMNH In. 43790, free ramus of chelicera; Church Hill.







## EXPLANATION OF PLATE 2.15

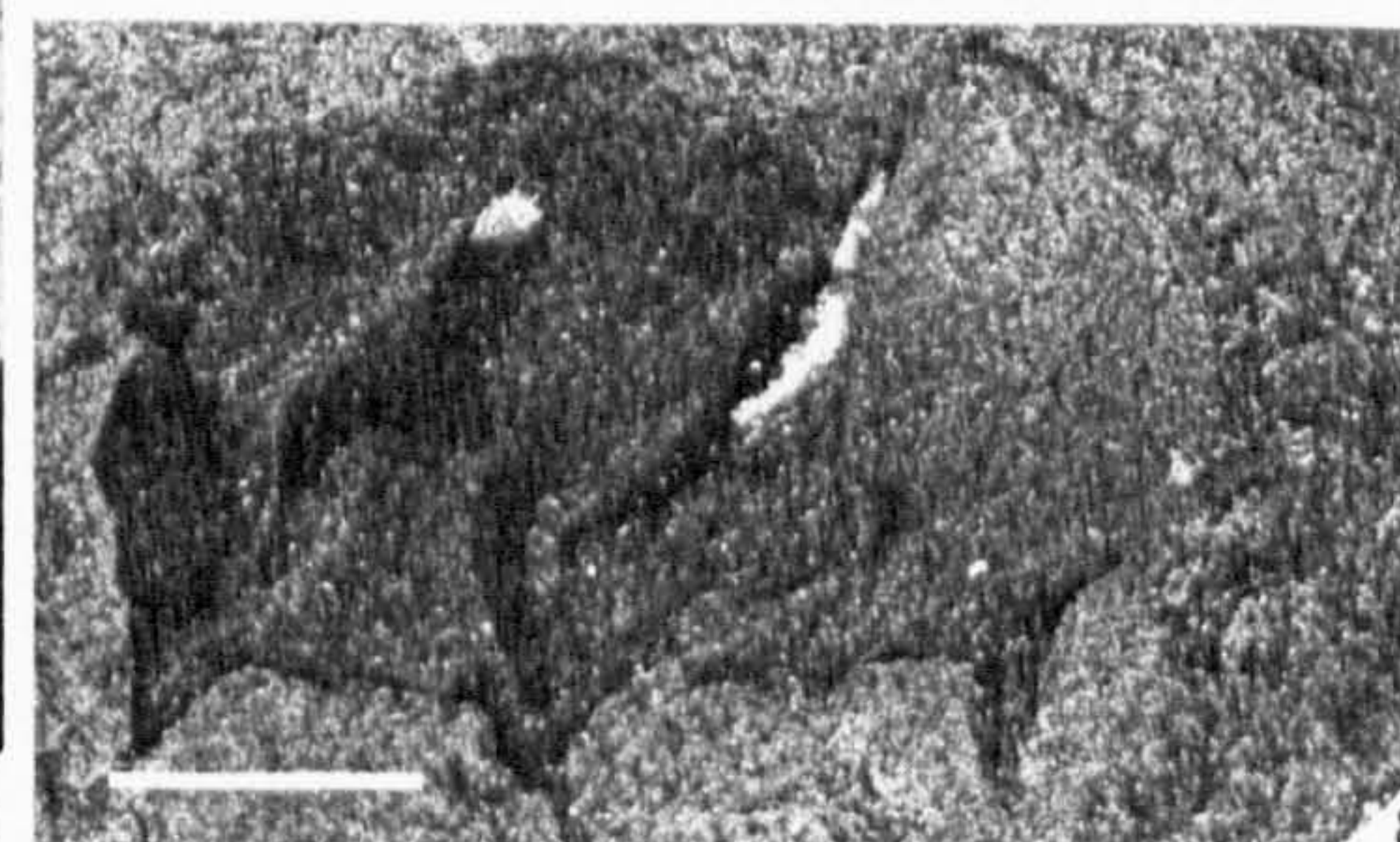
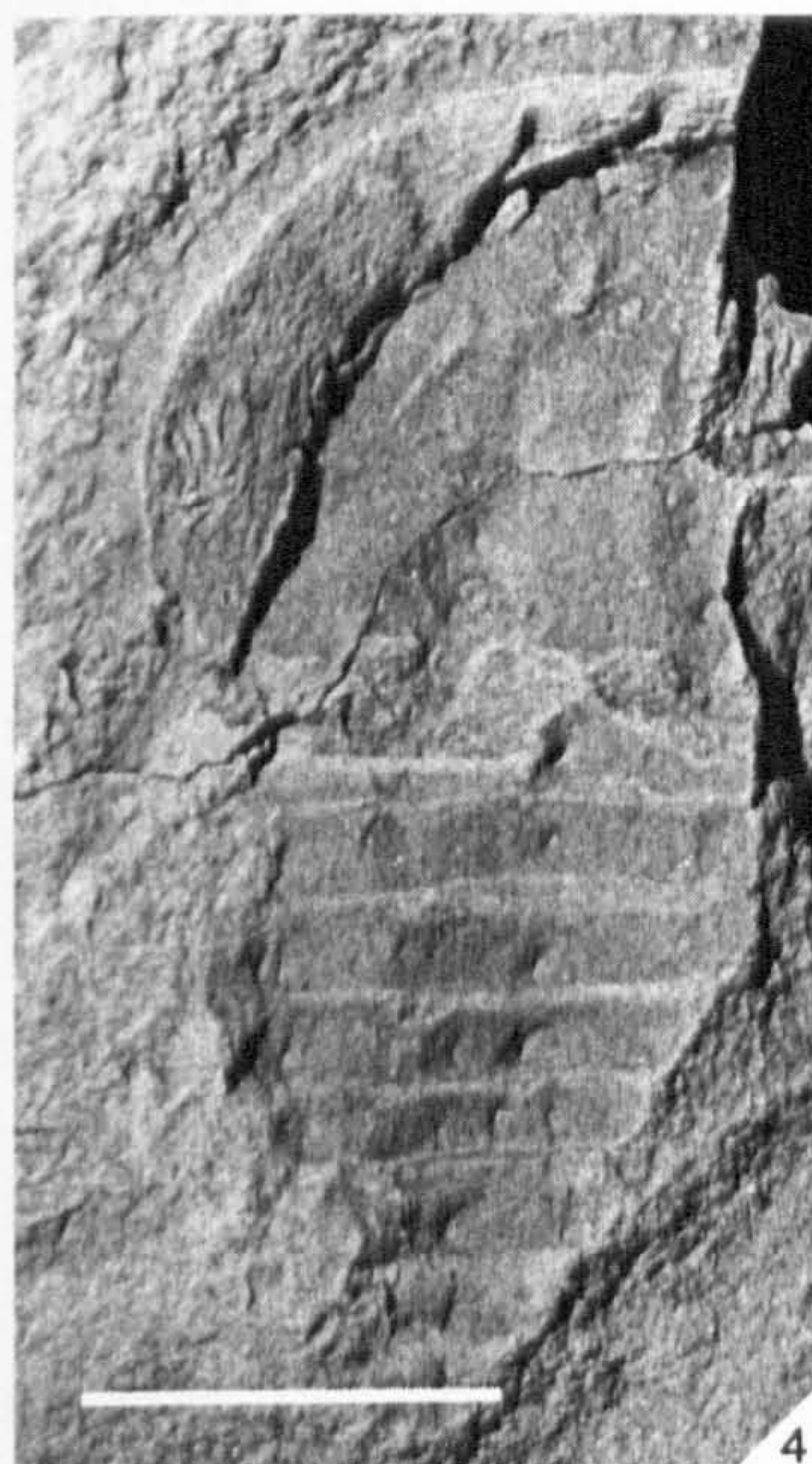
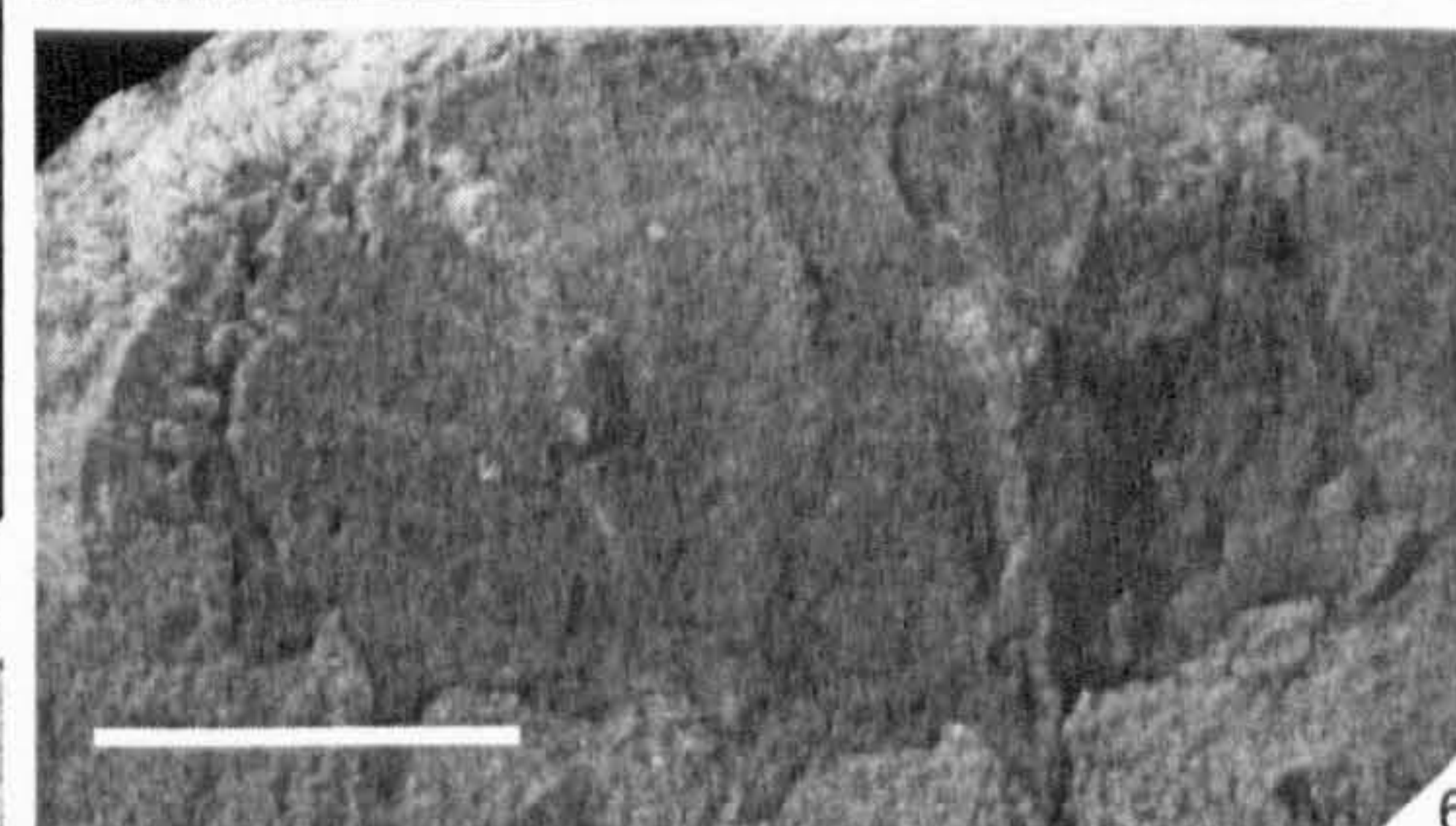
Xiphosurans; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm except on Fig. 3, where it represents 5 mm. Refer to text-figure 2.5 for stratigraphical provenance of CH145.

Figs 1-2, 4, 6-8. *Limuloides limuloides*. 1, BGS GSM32393, complete. 2, BMNH In. 48423, articulated opisthosoma and telson; Church Hill. 4, BGS GSM89612, articulated prosoma and opisthosoma; Church Hill. 6, CH145, prosoma; Starfish Bed A, Church Hill Quarry 1. 7, BGS GSM89607, prosoma. 8, BGS GSM89613, prosoma; Church Hill.

Fig. 3. *Pseudoniscus* sp.; BMNH In. 48428, complete; Church Hill.

Fig. 5. *Cyamocephalus loganensis*; OUM C.20151, missing telson; silicone cast.





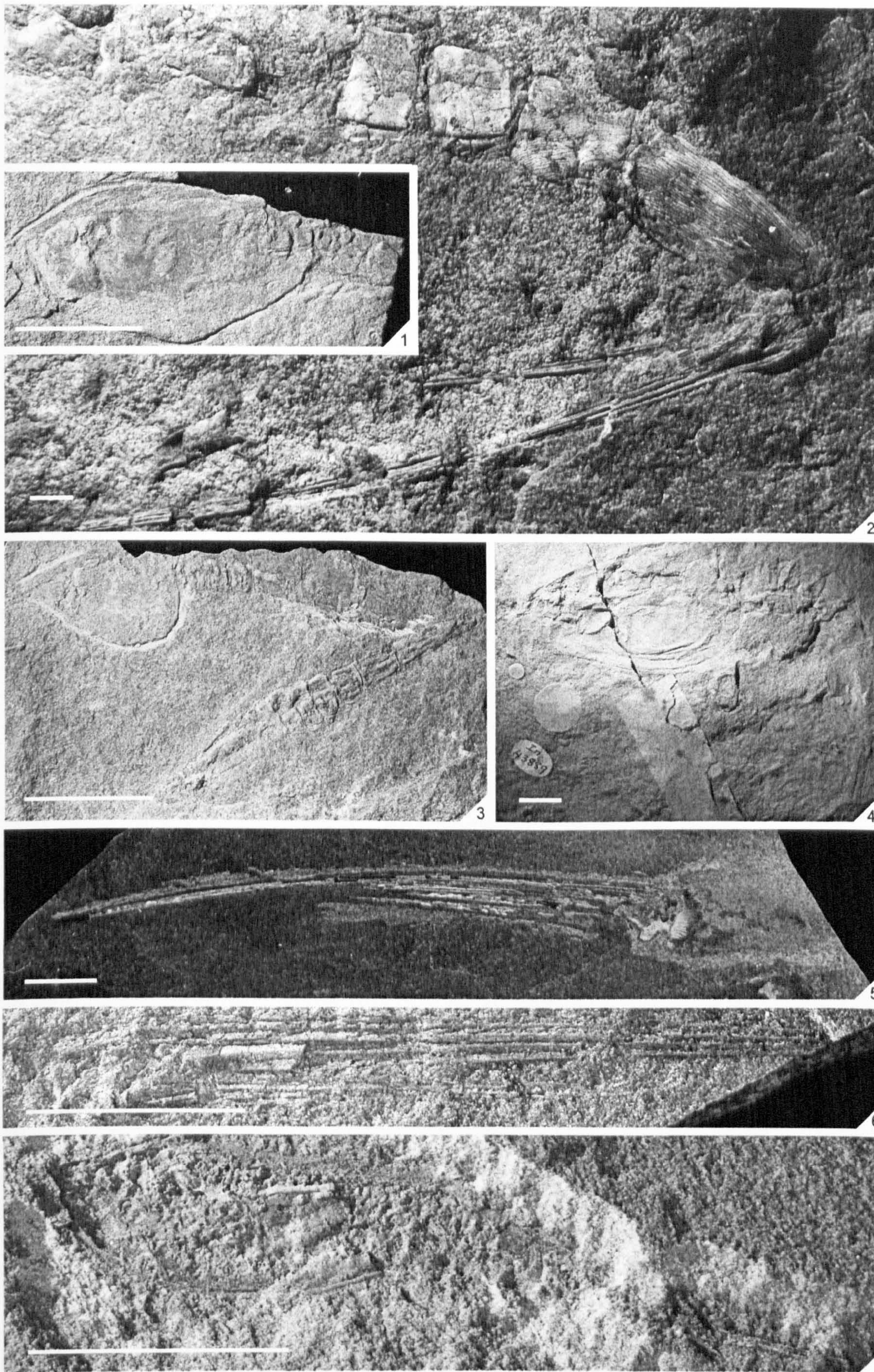


## EXPLANATION OF PLATE 2.16

Phyllocarids; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. Refer to text-figures 2.5 and 2.8 for stratigraphical provenance of CH62 and MS20, respectively.

Figs 1-7. *Ceratiocaris* cf. *papilio*. 1, BMNH In. 19139, articulated, telson not preserved; Martin's Shell Quarry. 2, CH62, large articulated specimen missing carapace; Starfish Bed A, Church Hill Quarry 1. 3, BMNH In. 19137, two articulated specimens; Martin's Shell Quarry. 4, BMNH In. 43889, nearly complete; Church Hill. 5, SHRCM G9523. 15, well preserved telson; Brandon Hill. 6, MS20a, telson; Martin's Shell Quarry. 7, CH128a, small complete specimen; loose block, Church Hill Quarry 1.







## EXPLANATION OF PLATE 2.17

Various fossils; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm except on Fig. 2, where it represents 1 mm.

Figs 1-3, fine shelly horizons; Starfish Bed A, Church Hill Quarry 1. 1, 3, CH187a-b (not part and counterpart), disarticulated trilobite cephalata and pygidia (selected specimens arrowed). 2, CH170, ostracod and tentaculid (both arrowed); silicone cast.

Fig. 4. *Alcymene lawsoni*; CH183b, cephalon; Church Hill Quarry 1.

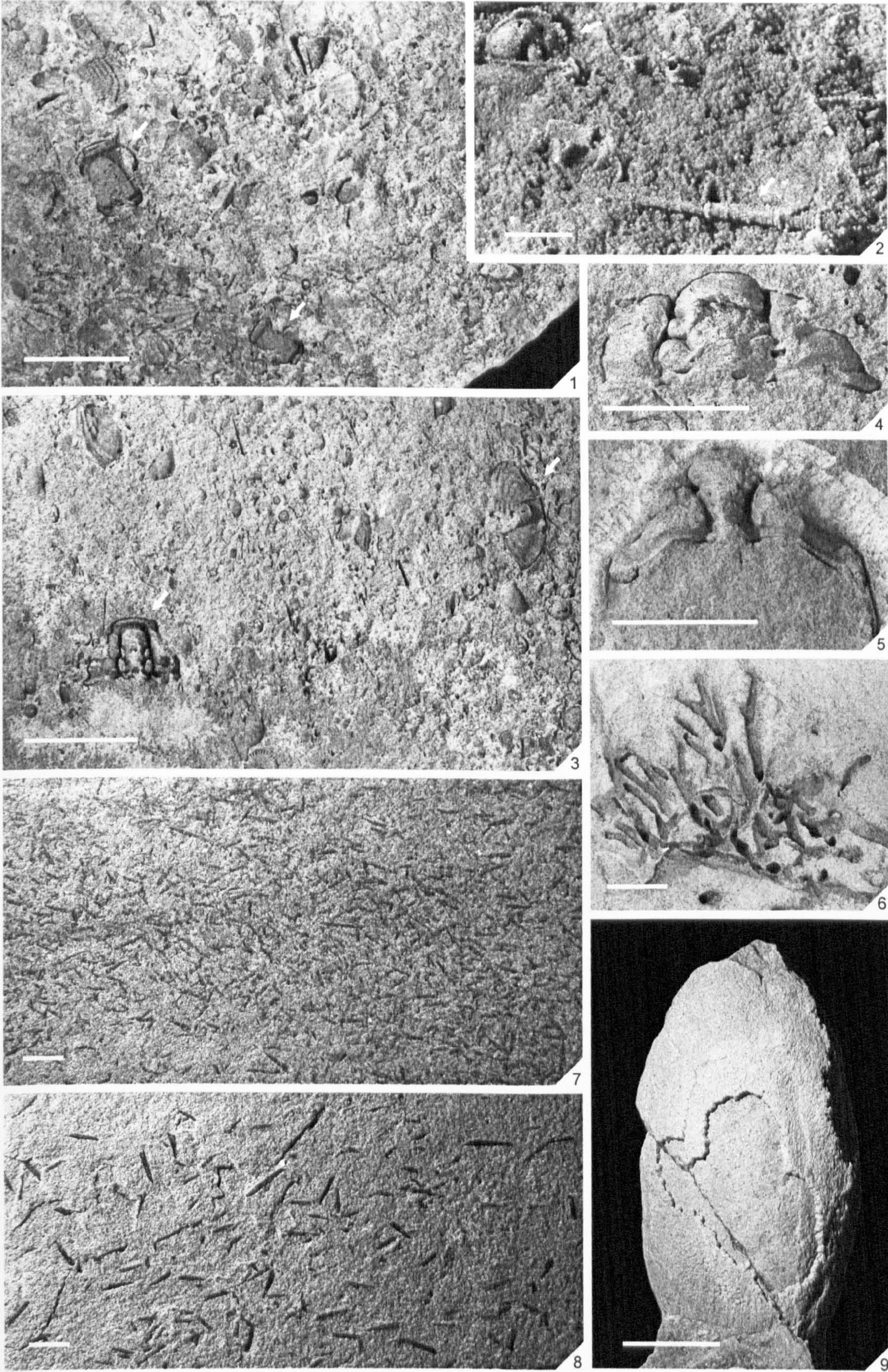
Fig. 5. *Encrinurus* sp.; CH183a, cephalon; Church Hill Quarry 1.

Fig. 6. Undet. bryozoan specimen; CH160, well preserved; Starfish Bed A, Church Hill Quarry 1.

Figs 7-8. *Saetograptus leintwardinensis*; loose blocks, Church Hill Quarry 1. 7, CH203c, dense assemblage, with some specimens showing current alignment. 8, CH201, detail of assemblage with well preserved specimens.

Fig. 9. *Archaeognaspis ludensis*; BGS GSM49106, complete dorsal shield; Church Hill.







## EXPLANATION OF PLATE 2.18

Brachiopods; Lower Leintwardine Formation, Ludlow Series; Church Hill Quarry 1, Leintwardine, Herefordshire. Refer to text-figure 2.5 for stratigraphical provenance of CH175d.

Figs 1, 5-6. Shelly brachiopod horizons; predominantly *Microsphaeridiorhynchus nucula*; scale bars represent 10 mm. 1, CH179a, well preserved rhynchonellids, several articulated. 5, CH176, three horizons including *Orbiculoidea* sp. (arrowed) towards top left of figure. 6, CH175d, well preserved rhynchonellids; base of Starfish Bed A.

Figs 2-3. *Microsphaeridiorhynchus nucula*; articulated specimens; scale bars represent 5 mm. 2, CH179a. 3, CH188c, Starfish Bed A.

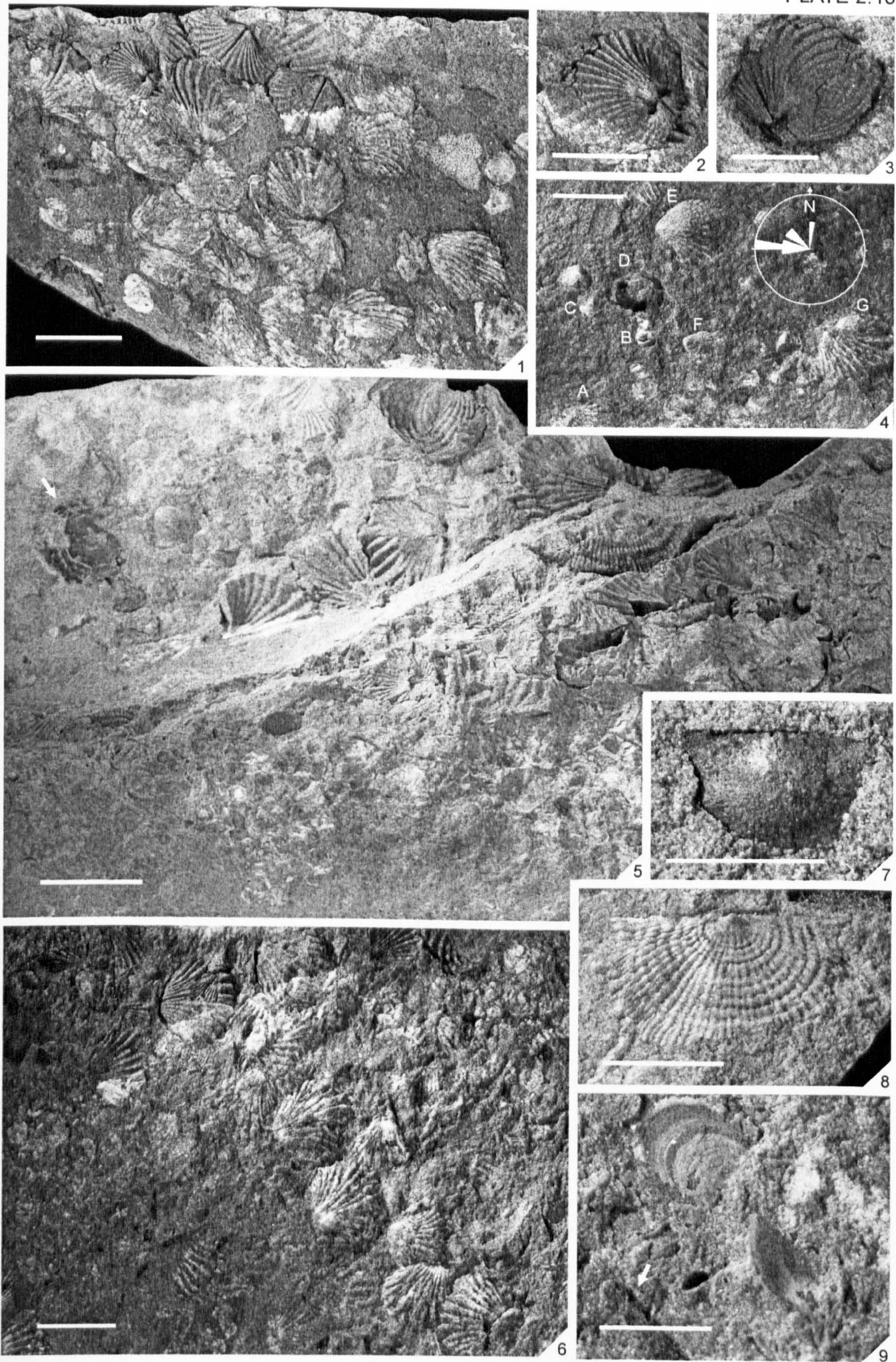
Fig. 4. *Microsphaeridiorhynchus nucula* (lettered A, E-G), *Dayia navicula* (lettered B-C), *Orbiculoidea* sp. (lettered D); CH189, 7 specimens with 6 showing umbone alignment to left of figure (*Orbiculoidea* sp. orientated by axis of symmetry); arbitrary 'north' value assigned for slab (segment interval of rose diagram = 10°); scale bar represents 10 mm.

Fig. 7. *Shagamella ludloviensis*; CH186b, scale bar represents 2 mm.

Fig. 8. *Leptaena depressa*; CH179a; scale bar represents 5 mm.

Fig. 9. *Lingula lata*; CH109, two disarticulated valves; note portion of *Saetograptus leintwardinensis* (arrowed) at bottom left of figure; Starfish Bed A; scale bar represents 2 mm.







## EXPLANATION OF PLATE 2.19

Various fossils; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. Refer to text-figure 2.8 for stratigraphical provenance of MS22 and MS27.

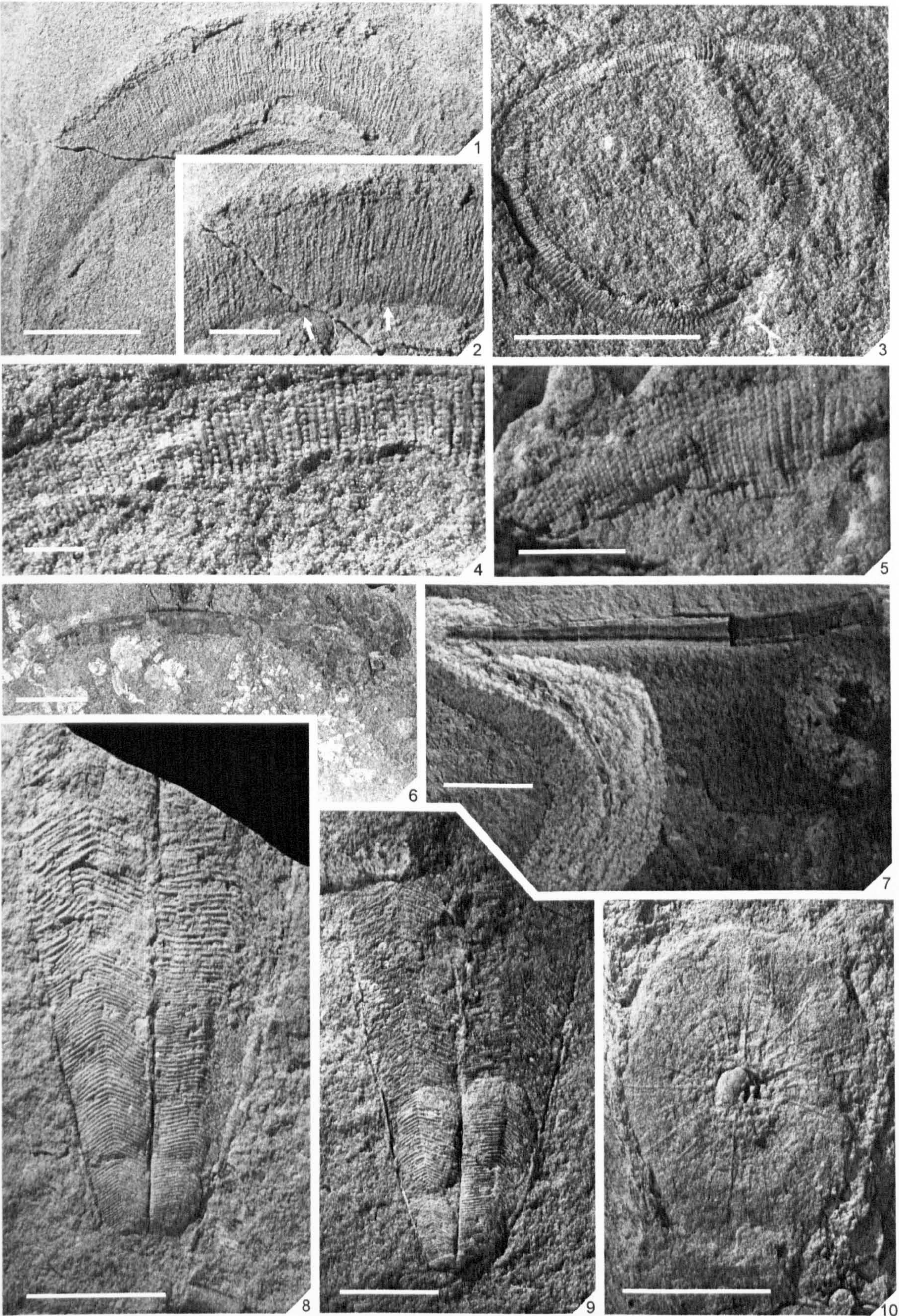
Figs 1-5. *Protoscolex latus*. 1-2, SHRCM G10474, Church Hill. 1, entire specimen; scale bar represents 5 mm. 2, detail of ornament, with possible darkened gut trace (arrowed) along bottom edge; scale bar represents 2 mm. 3-4, CH214a, loose block, Church Hill Quarry 1. 3, entire specimen which is relatively long and complete; scale bar represents 10 mm. 4, detail of papillae arranged into rows; scale bar represents 1 mm. 5, LEIUG 117524, entire incomplete specimen; slab also contains *Sphenothallus longissimus*; Martin's Shell Quarry; scale bar represents 2 mm.

Figs 6-7. *Sphenothallus longissimus*; Martin's Shell Quarry; scale bars represent 10 mm. 6, MS22, incomplete; associated with shelly brachiopod horizon. 7, MS27, nearly complete, well preserved.

Figs 8-9. *Conularia* sp.; Martin's Shell Quarry; scale bars represent 10 mm. 8, LEIUG 117525, nearly complete. 9, MS27, nearly complete.

Fig. 10. *Spongarium edwardsii*; LEIUG 25877, entire specimen; Mocktree Quarry; scale bar represents 10 mm.







## EXPLANATION OF PLATE 2.20

Stelleroid functional morphology; all figures are of silicone casts.

Figs 1-3. *Urasterella ruthveni*. 1, 3, CAMSM A5497, Bannisdale Slates; Lake District. 1, detail of wide ambulacrals (two arrowed), ventrally enclosed by adambulacrals; scale bar represents 1 mm. 3, poorly developed mouth frame ossicles (arrowed); scale bar represents 2 mm. 2, BMNH E 13952, detail of dorsal paxillae; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 1 mm.

Figs 4-5. *Cocaster bulbiferus*; BMNH E 13956, Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 4, large podial basins, deep ambulacral groove and large axillaries of proximal arm, ventral view; scale bar represents 1 mm. 5, detail of inferomarginals separated by depressions (arrowed); ventral view; scale bar represents 500  $\mu$ m.

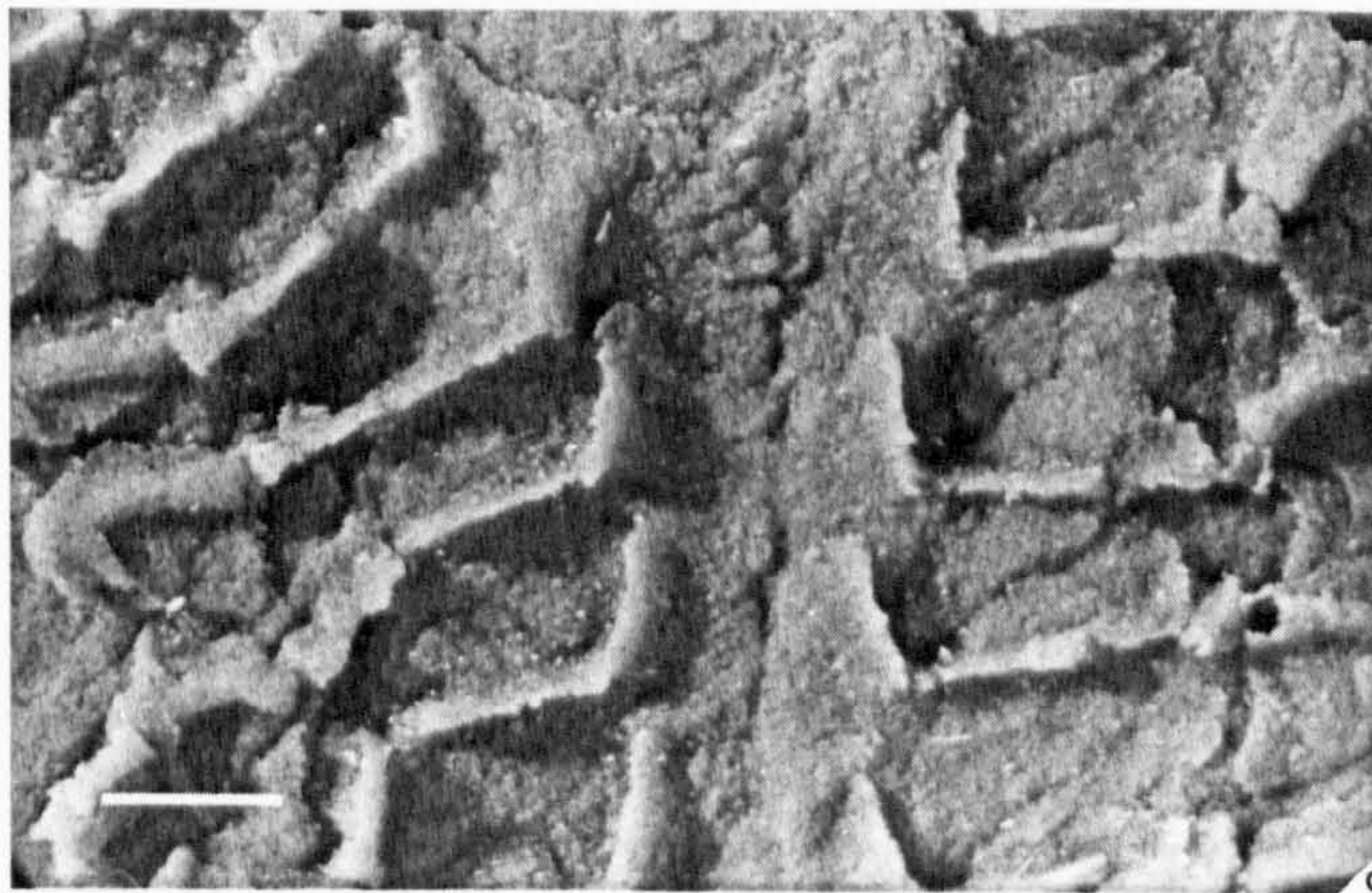
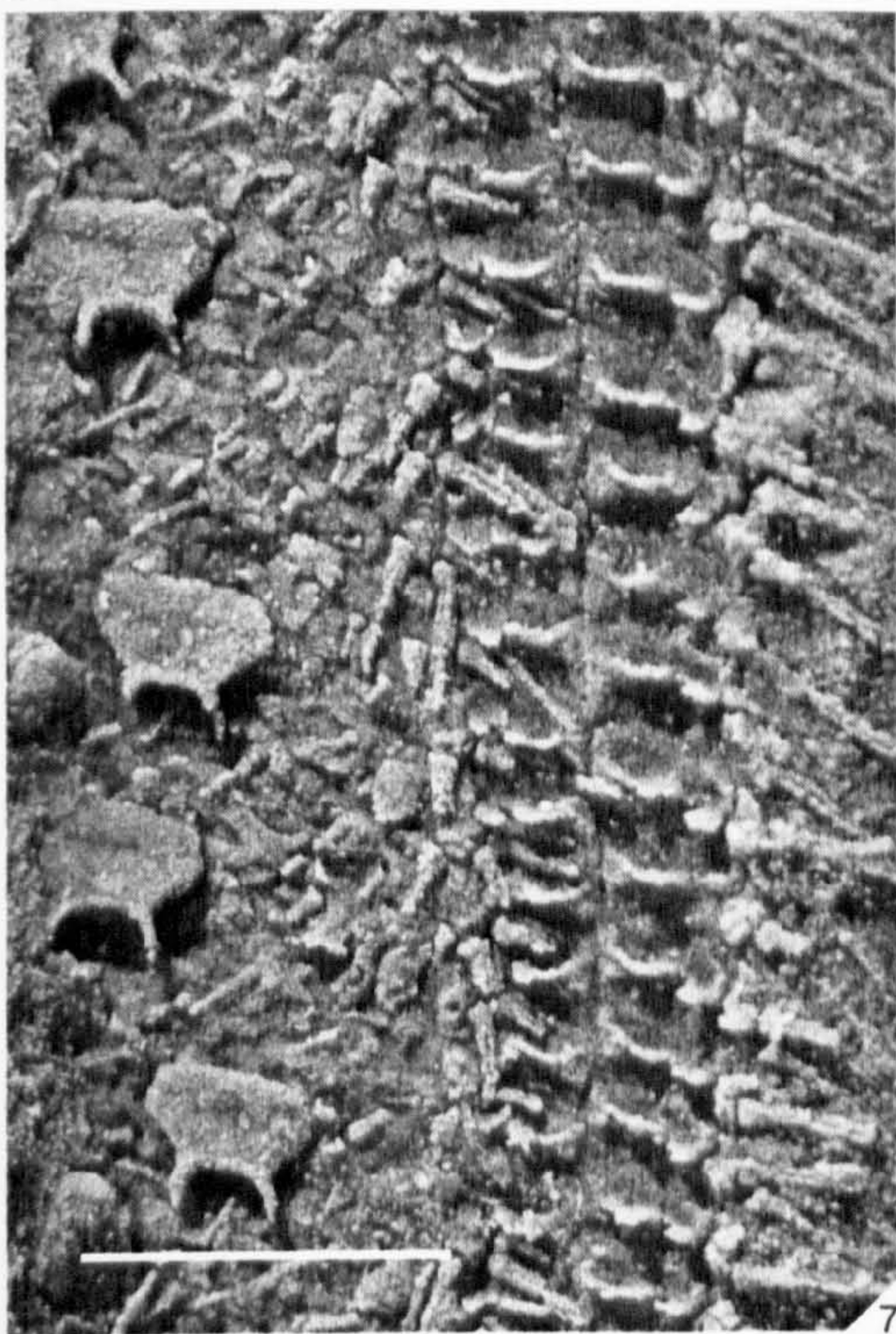
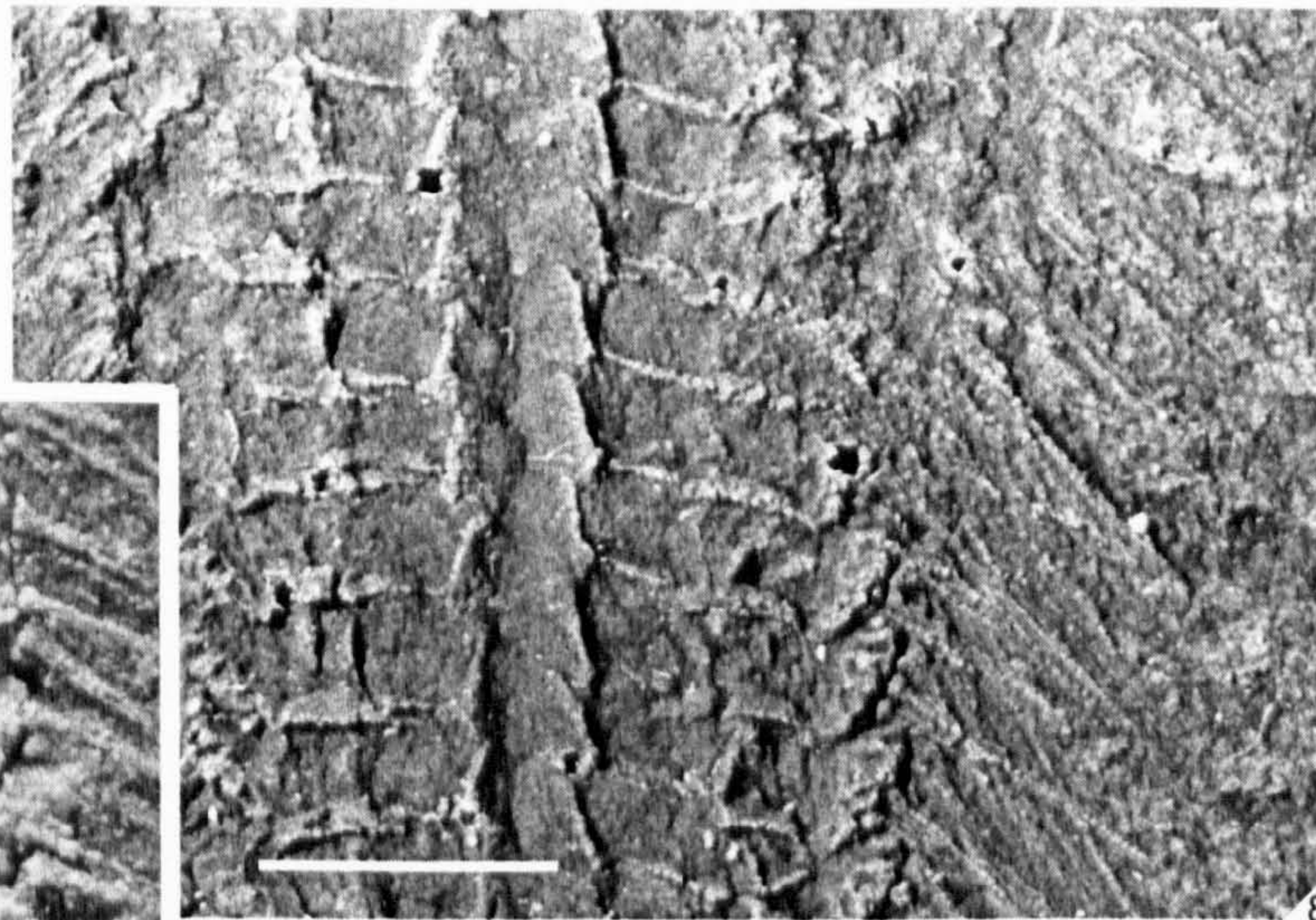
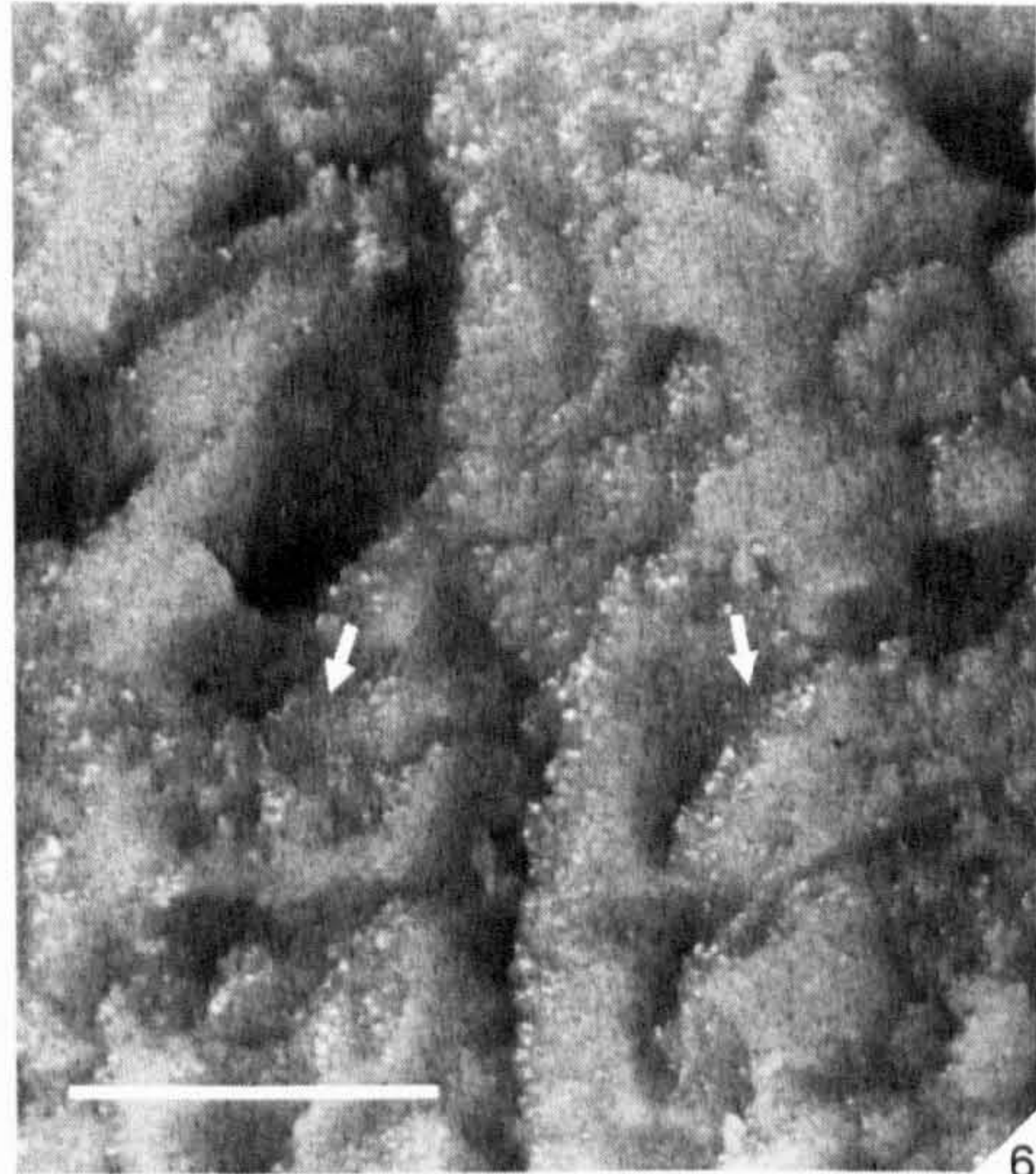
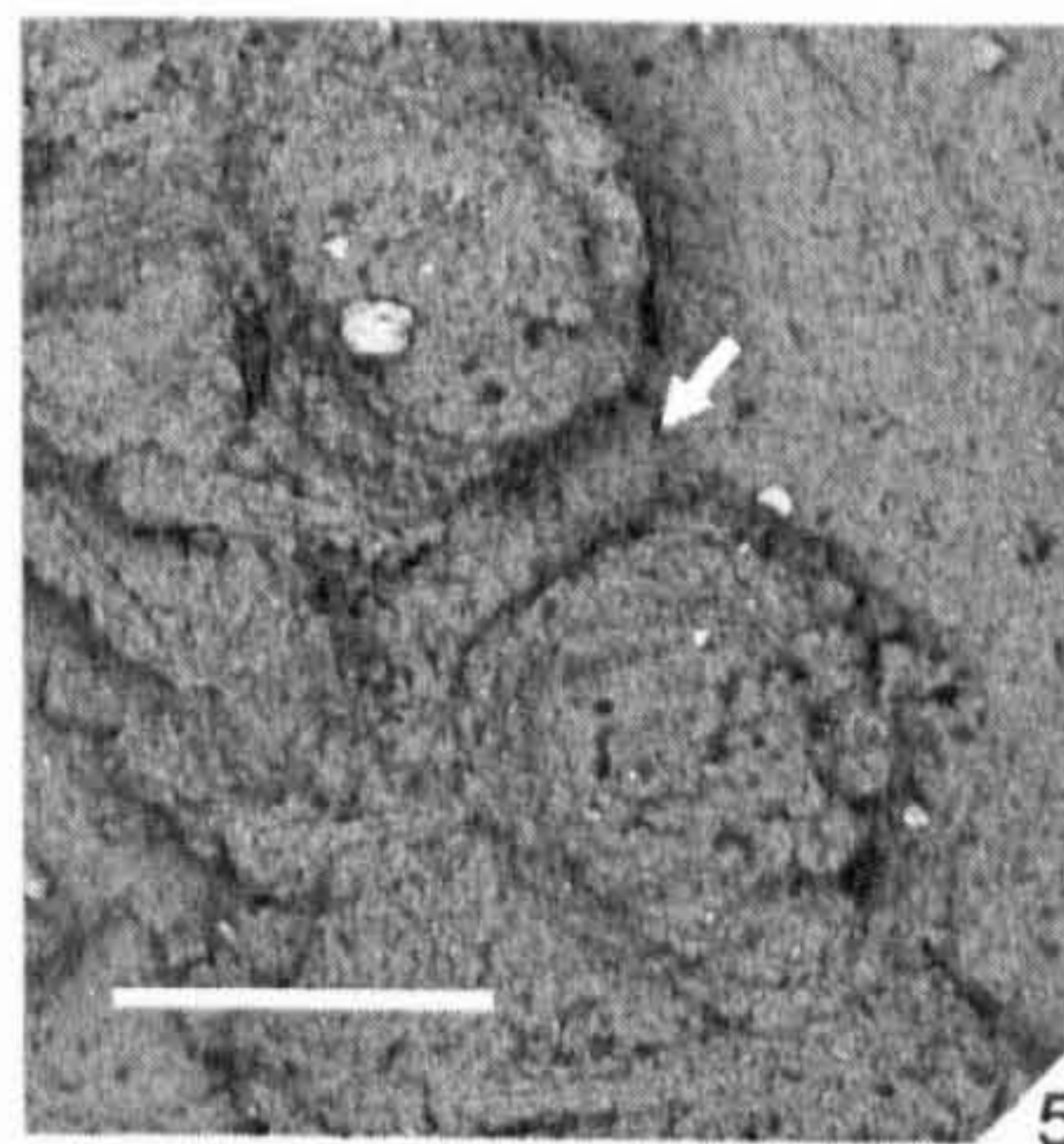
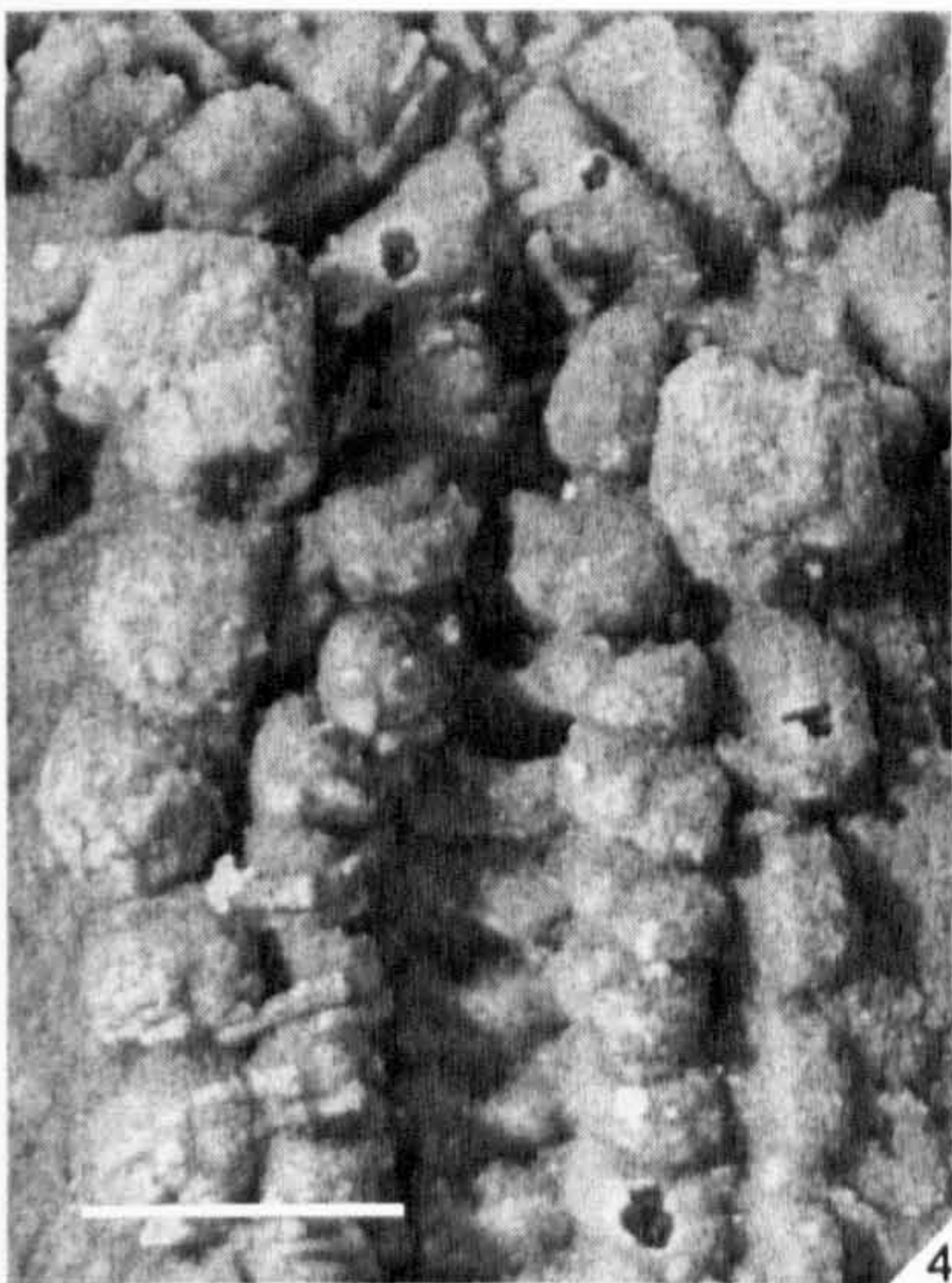
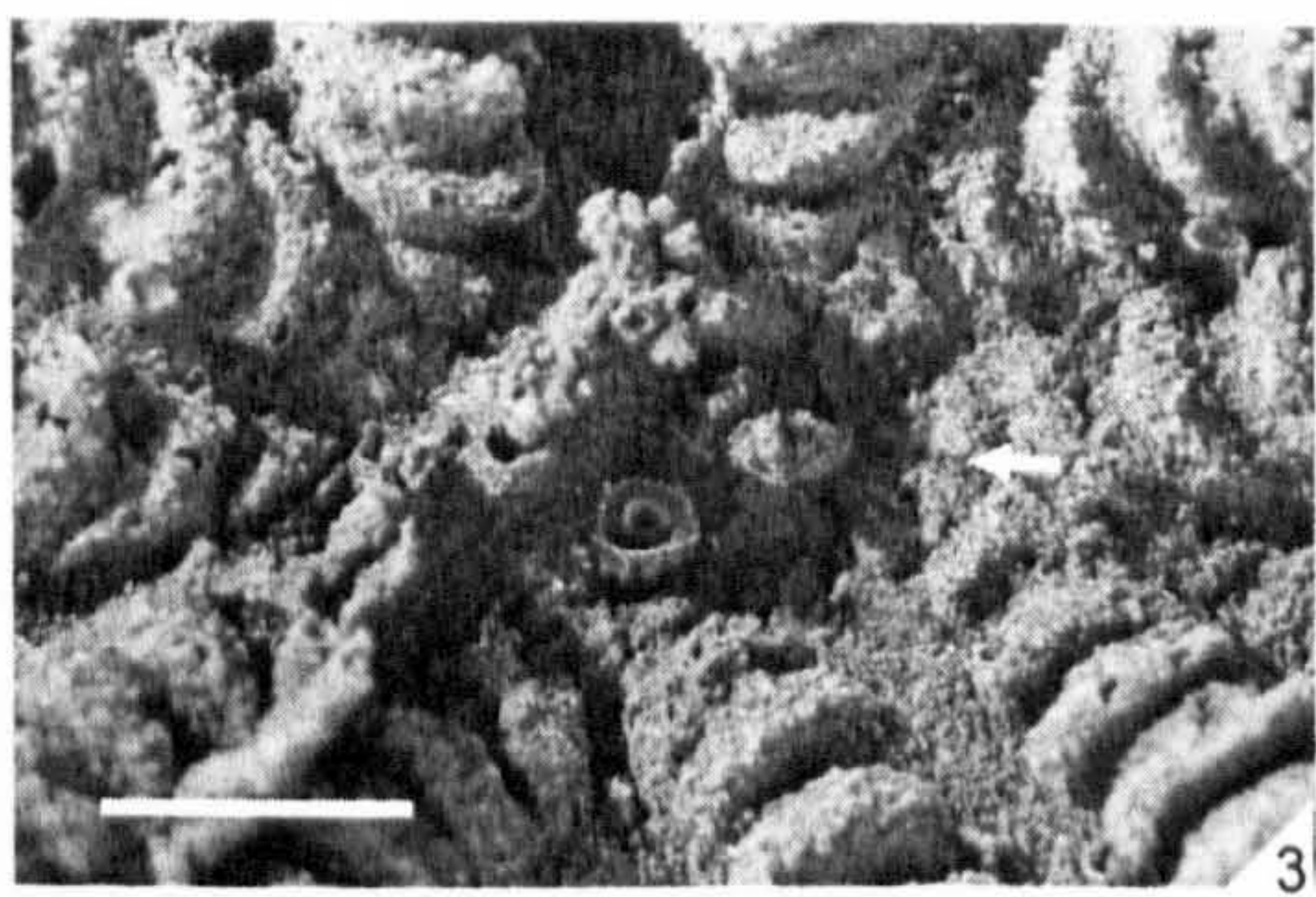
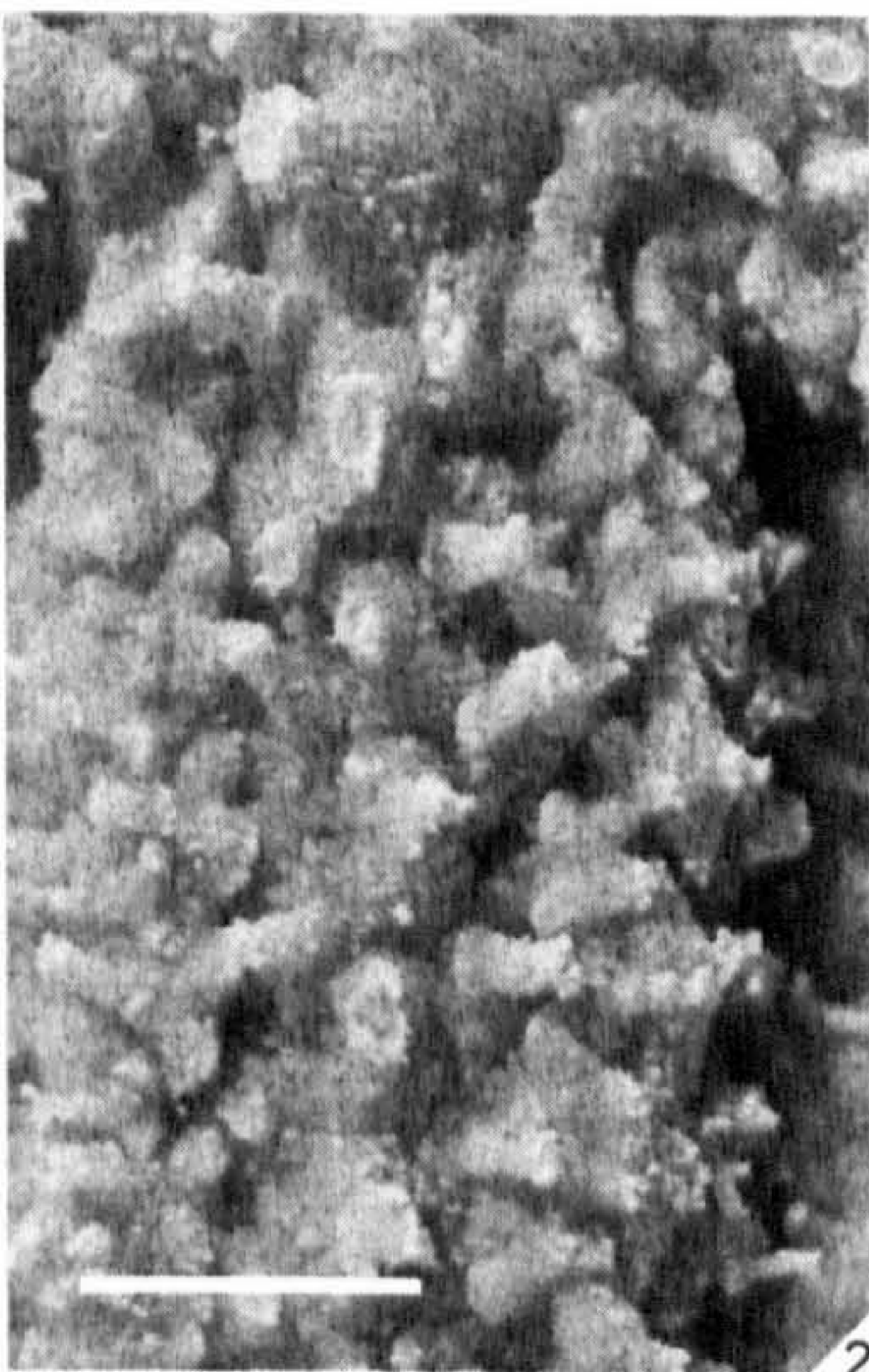
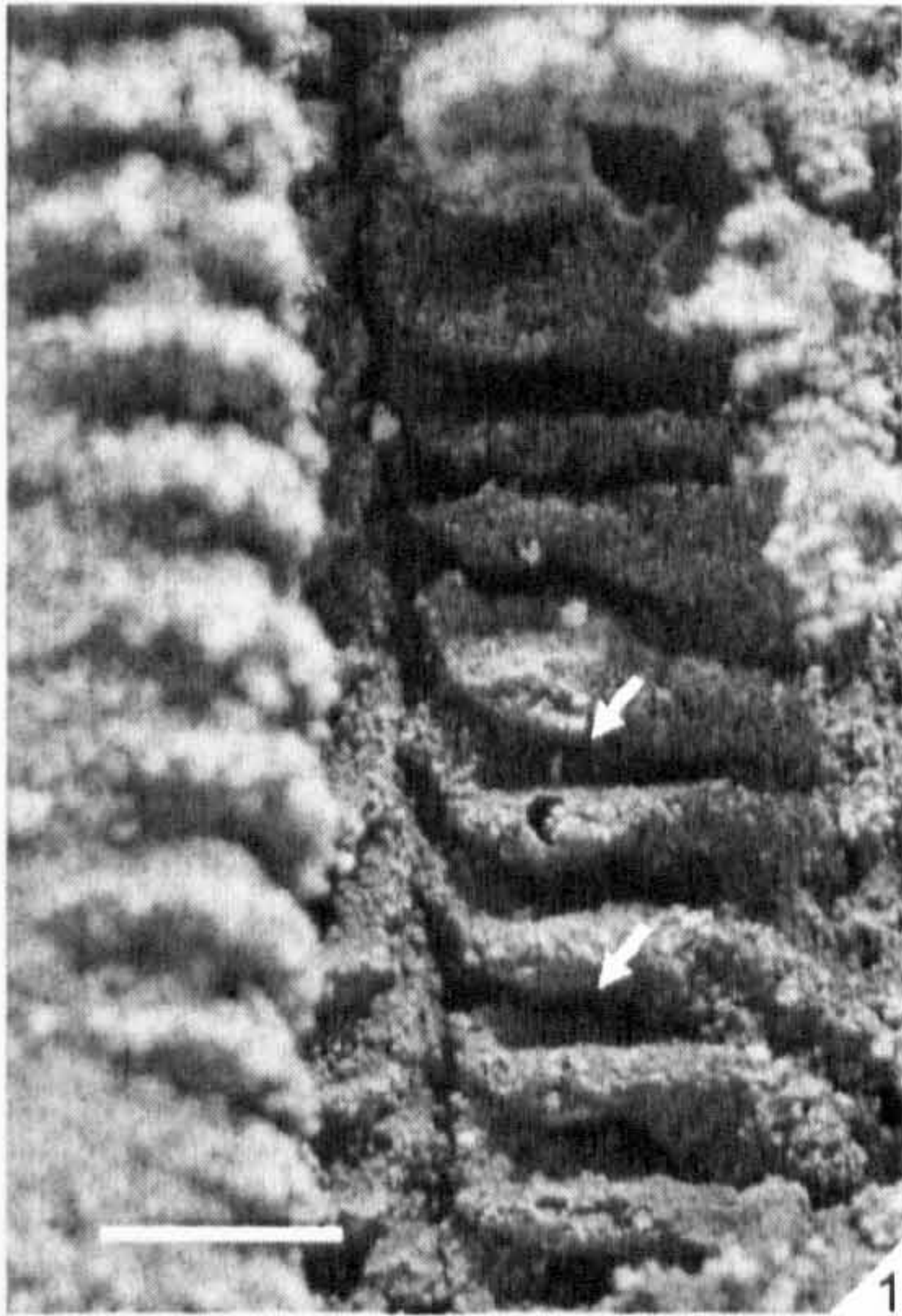
Fig. 6. *Palasterina* cf. *antiqua*; BMNH 40299b, detail of large podial basins (two arrowed) of proximal arm, ventral view; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 1 mm.

Fig. 7. *Bdellacoma vermiformis*; BMNH 40297, large podial basins and pedicellariae, ventral view; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 2 mm.

Fig. 8. *Sturtzaster marstoni*; BMNH E 13949, large podial basins, ventral view; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 2 mm.

Fig. 9. *Rhopalocoma pyrotechnica*; BMNH 40293, large wide podial basins of proximal arm, ventral view; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 1 mm.







## EXPLANATION OF PLATE 2.21

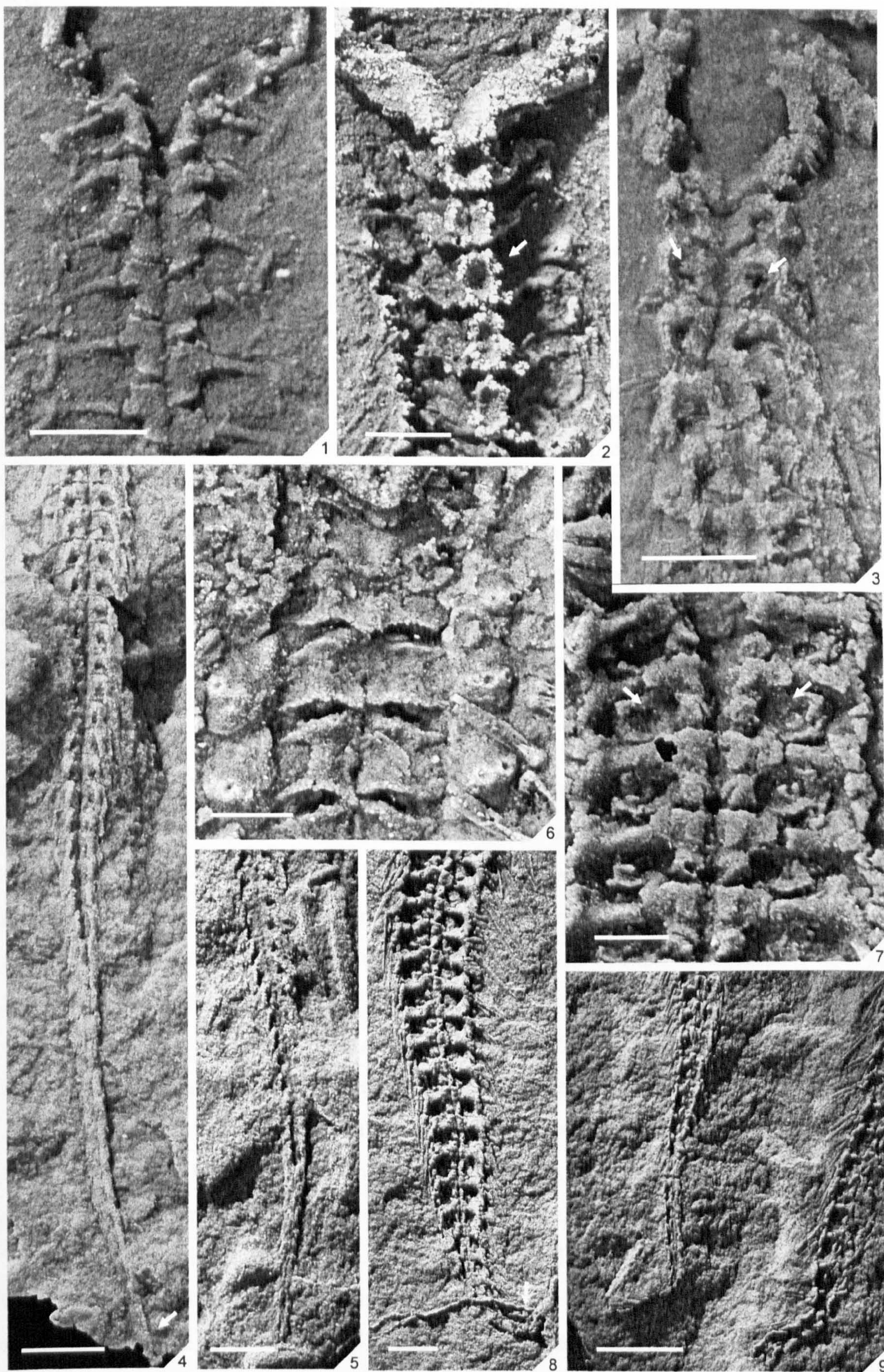
Stelleroid functional morphology; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. All figures are of silicone casts.

Fig. 1. *Loriolaster calceatus*; BMNH 47953, alternating ambulacrals of proximal arm, ventral view; scale bar represents 1 mm.

Figs 2-5. *Furcaster leptosoma*. 2, IPSM G9252917, opposing ambulacrals with well developed arm muscle pits (arrowed on one ambulacral), dorsal view; Church Hill; scale bar represents 1 mm. 3-4, BMNH E 13138. 3, moderate to large podial basins (two arrowed) of proximal arm, ventral view; scale bar represents 1 mm. 4, whip-like distal termination of arm (arrowed), ventral view; scale bar represents 2 mm. 5, OUM C.16838, whip-like distal termination of arm, ventral view; scale bar represents 2 mm.

Figs 6-9. *Lapworthura miltoni*. 6, BMNH E 20239, opposing ambulacrals with well-developed muscle pits, dorsal view; Church Hill; scale bar represents 1 mm. 7, BMNH E 20232, moderate to large podial basins (two arrowed) of proximal arm, ventral view; Church Hill; scale bar represents 1 mm. 8, NMS G1882651518, whip-like distal termination of arm (arrowed), ventral view; scale bar represents 2 mm. 9, BGS GSM105645, whip-like distal termination of arm, ventral view; scale bar represents 5 mm.





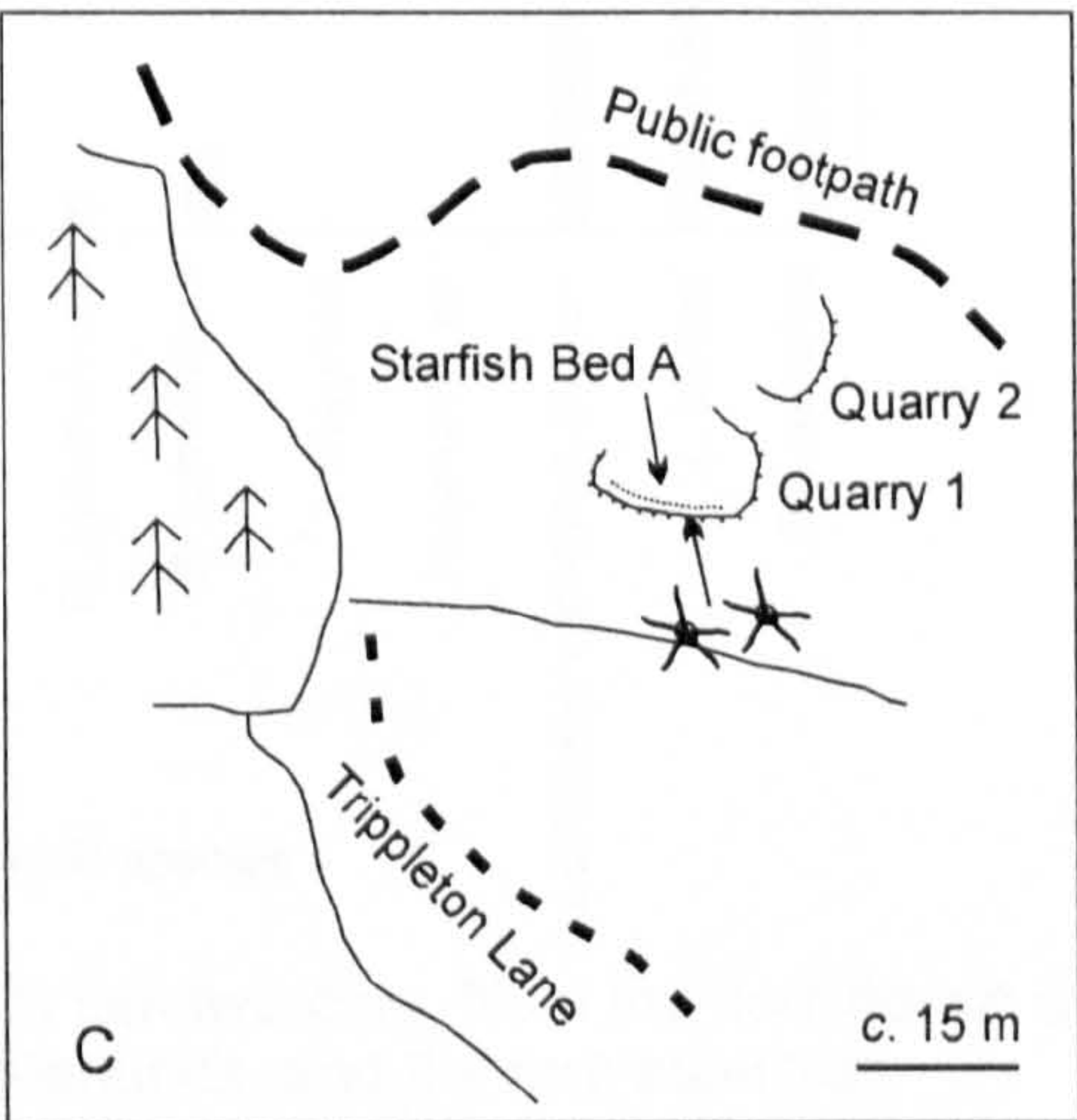
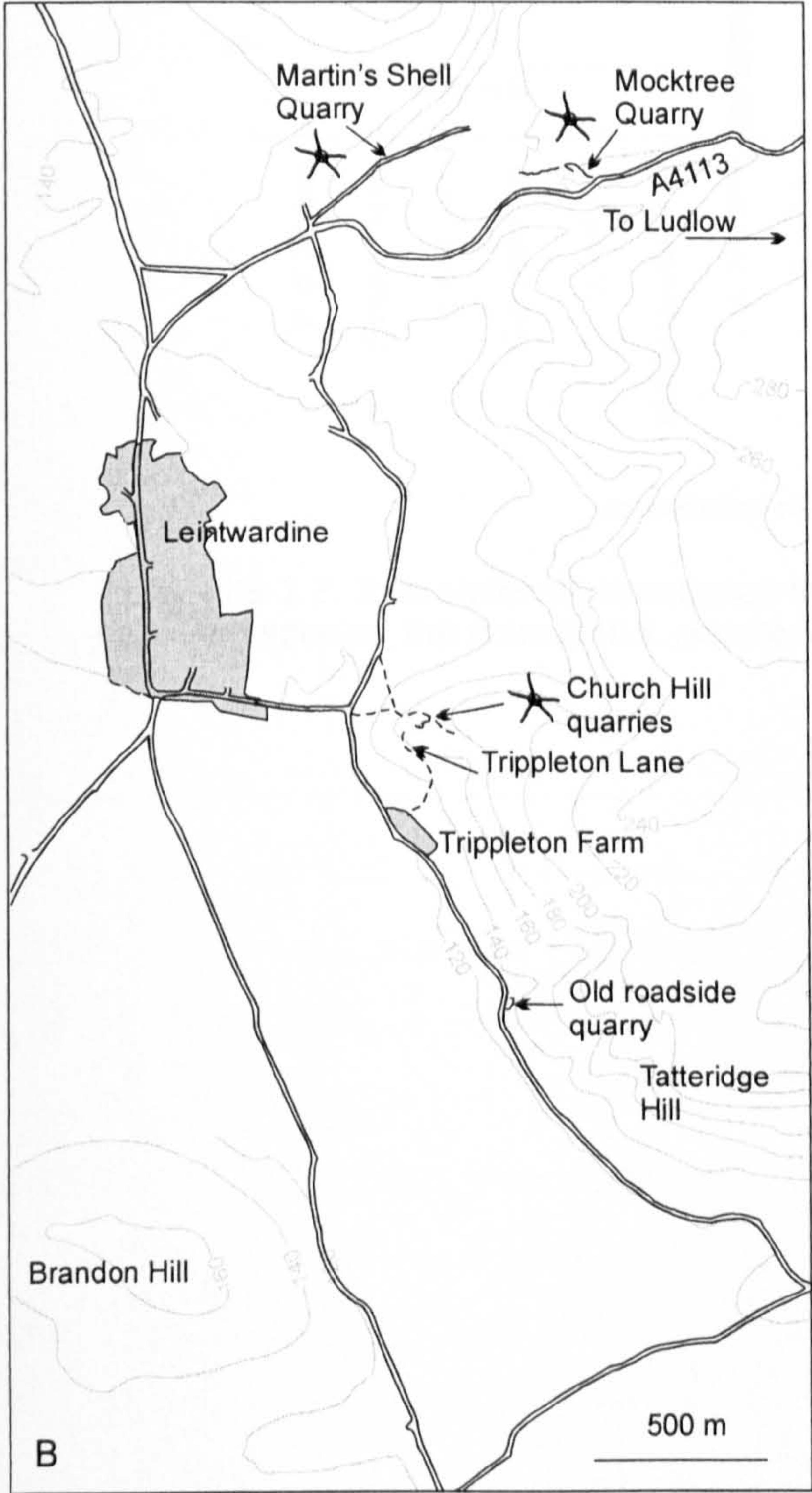


# STELLEROIDS FROM THE LUDLOW SERIES (UPPER SILURIAN) OF LEINTWARDINE, HEREFORDSHIRE

**ABSTRACT.** A diverse stelleroid fauna, comprising 15 species, is described from the Upper Silurian channel deposits at Leintwardine, Welsh Borderland, UK, the first time such a study has been undertaken since Spencer's treatment of British Palaeozoic starfish taxa in the early to mid 20<sup>th</sup> Century. The stelleroids are exceptionally preserved and generally fully articulated, preserving the finest skeletal elements such as spines and pedicellariae. Study has been based on newly collected material (comprising eight species) from the Church Hill Starfish Bed, along with extensive pre-existing museum collections. One new ophiuroid species is erected, *Loriolaster calceatus* sp. nov., and the asteroid subspecies *Urasterella ruthveni* var. *leintwardinensis* Spencer is not maintained. A previously undescribed asteroid specimen, likely to be a juvenile, is described as *Cocaster?* sp. Specimens described in the literature as *Bdellacoma vermiformis* Salter and *Palasterina antiqua* (Hisinger) are reassigned to *Klasmura?* sp. and *Palasterina* sp., respectively. Pedicellariae are identified in *Antiquaster magrumi* Kesling. Intermediate axial ossicles, the sublaterals, are not present in *Sturtzaster colvini* (Salter) and are equivocal in *Sturtzaster marstoni* (Salter).

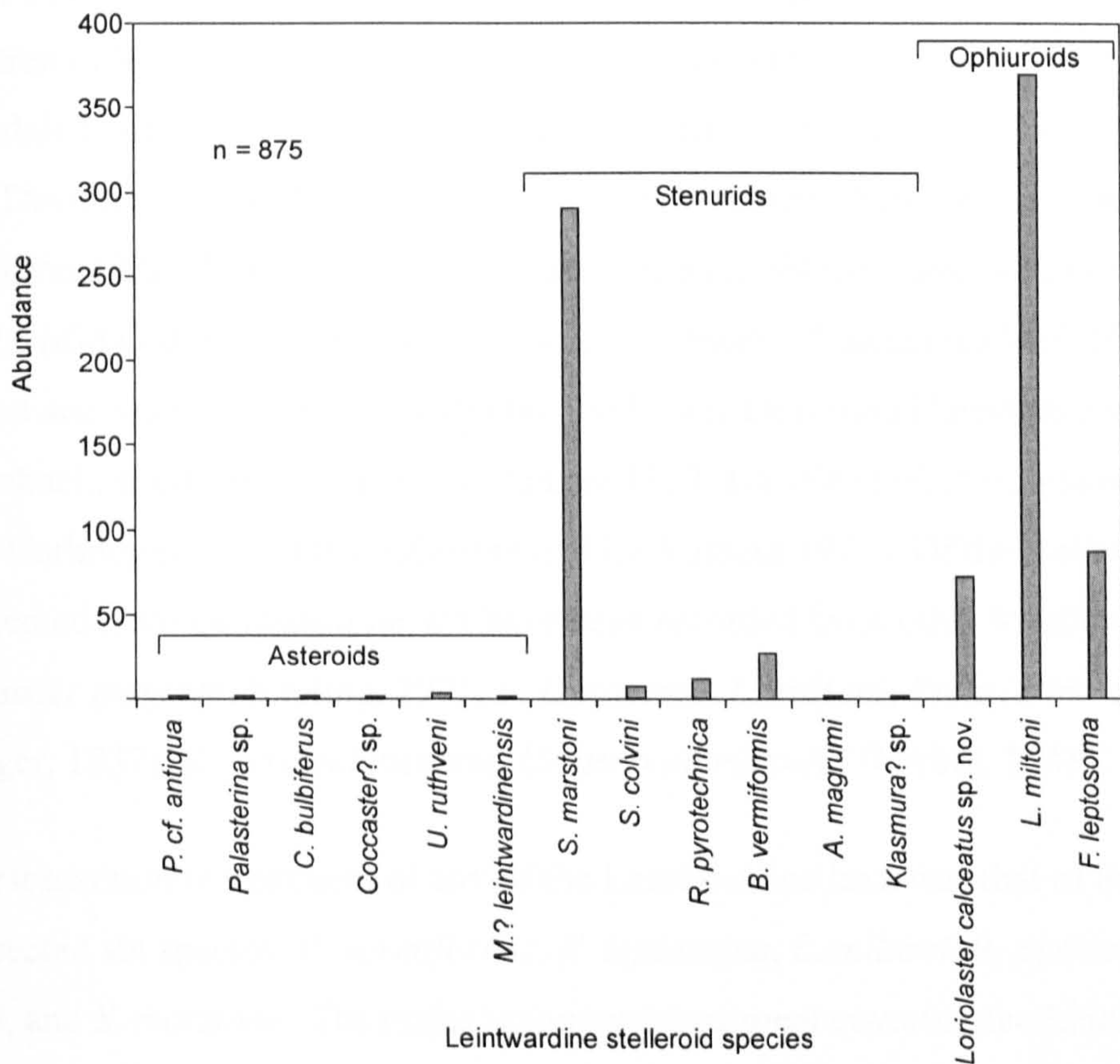
Diverse, exceptionally preserved stelleroids (asteroids and ophiuroids) are recorded from submarine channel deposits of Ludfordian (late Ludlow) age around the village of Leintwardine, approximately ten kilometres to the west of Ludlow (Text-fig. 3.1). They occur within discrete starfish beds. The stelleroids are the most abundant and diverse echinoderms recorded from the Leintwardine submarine channel localities; approximately 875 specimens comprising 15 species have been documented from these deposits (Text-fig. 3.2). The channel exposures are the type localities for nine of the stelleroid taxa: *Bdellacoma vermiformis* Salter, 1857, *Cocaster bulbiferus* Spencer, 1916, *Furcaster leptosoma* (Salter, 1857), *Lapworthura miltoni* (Salter, 1857), *Loriolaster calceatus* sp. nov., *Mesopalaeaster?* *leintwardensis* (Spencer, 1916), *Rhopalocoma pyrotechnica* Salter, 1857, *Sturtzaster colvini* (Salter, 1857) and *Sturtzaster marstoni* (Salter, 1857). Other British Palaeozoic sea-star occurrences are rare (Goldring and Stevenson 1972; Aronson and Sues 1988). Aside from the Leintwardine deposits the only major examples with diverse, well-preserved specimens are the Upper Ordovician Lady Burn starfish beds at Girvan, Scotland (Spencer 1914-1940; Owen 1965; Goldring and Stevenson 1972; Harper 1982, Donovan *et al.* 2002) and the Lower Silurian Gutterford Burn starfish beds of the Pentland Hills, Midlothian, Scotland (Spencer 1916, 1918, 1922, 1927, 1930; Owen 1965; Aldridge 2000; Gladwell in press). The Leintwardine starfish beds provide the most diverse occurrences of stelleroids from the Silurian of the UK; approximately nine species have been





TEXT-FIG. 3.1. A, Location of the study area around Leintwardine, approximately 10 km to the west of Ludlow, Shropshire. B, stelleroid localities around Leintwardine, showing submarine channel deposits (from north to south): Martin's Shell Quarry (Todding Channel); Mocktree Quarry (Mocktree Channel); Church Hill quarries (Church Hill Channel). C, localities at Church Hill, showing the re-exposed composite quarries and lateral extent of Starfish Bed A.





TEXT-FIG. 3.2. Total stelleroid abundance from Leintwardine. Note the dominance of the ophiuroid species, the abundant *S. marstoni* stenurids, and the rare asteroids.



documented from Gutterford Burn (Spencer 1916, 1918, 1922, 1927, 1930). A small number of stelleroids have also been documented from the Much Wenlock Limestone Formation of Wenlock age at Dudley, West Midlands (Spencer 1916, 1918, 1922), the Bannisdale Slates of Ludlow age in the Lake District (Spencer 1918, 1940) and the Upper Devonian Pilton Beds of north Devon (Whidborne 1896-1907; Goldring and Stephenson 1972). Major worldwide Palaeozoic assemblages have been documented from the Mid Ordovician and Mid Devonian of Ontario, Canada (Liddell 1975, cited in Aronson and Sues 1988; Kesling 1969a), the Lower Devonian Hunsrück Slate of Bundenbach, southwest Germany (Lehmann 1957; Bartels *et al.* 2002a-b) and the Lower Carboniferous of Ohio (Kesling and Le Vasseur 1971). Of the stelleroid taxa documented from Leintwardine, six have been recorded from other localities: *Antiquaster magrumi* Kesling, 1971, *F. leptosoma*, *L. miltoni*, *Palasterina* cf. *antiqua* (Hisinger, 1837), *R. pyrotechnica* and *Urasterella ruthveni* (Forbes, 1848).

The first taxonomic treatment of any of the Leintwardine taxa was that of Salter (1857) who erected six species: *B. vermiformis*, *F. leptosoma*, *L. miltoni*, *R. pyrotechnica*, *S. colvini*, and *S. marstoni*. The major taxonomic treatment covering the Leintwardine stelleroids was by Spencer (1914-40), who restudied all the taxa from the area and erected three asteroid taxa: *C. bulbiferus*, *M.? leintwardensis*, and *U. ruthveni* var. *leintwardinensis*. Spencer's descriptions were partly limited by a lack of high quality latex/silicone rubber casts of the predominantly mouldic specimens, and the photographic reproduction was also inadequate in some respects. Spencer and Wright (1966) revised the classification of the stelleroids, assigning *Bdellacoma*, *Rhopalocoma* and *Sturtzaster* to the ophiuroid order Stenurida. Recent work (Sutton *et al.* 2005) suggests *Bdellacoma* is likely to be an asteroid; further studies are needed to determine the affinity of the remaining stenurid taxa. Dean Shackleton (2005) redescribed four of the Leintwardine taxa, *L. miltoni*, *P. antiqua*, *R. pyrotechnica* and *S. marstoni*, although this work relied solely on pre-existing collections. She reassigned *Palasterina*, along with *Rhopalocoma* and *Sturtzaster* to the family Eopentaroidea Dean Shackleton, 2005, informally grouped within the 'protophiuroids'. The classification adopted herein for these genera retains that of Spencer and Wright (1966).

This study aims to redescribe the stelleroids from the Ludlow Series deposits of the Leintwardine area, and is the first study to encompass all such taxa since Spencer's



(1914-40) monograph of British Palaeozoic Asterozoa. Specimens from extensive existing collections are here supplemented by newly collected, well-preserved material (representing eight species: *B. vermiformis*, *F. leptosoma*, *L. miltoni*, *L. calceatus*, *R. pyrotechnica*, *S. marstoni* and *S. colvini*). Several of the newly collected specimens provide some of the best preserved material available of the species (e.g. CH215: *S. colvini*). One new species is erected. Reclassification of several specimens previously described as *B. vermiformis* and *F. leptosoma* has been undertaken and the subspecies *Urasterella ruthveni leintwardinensis* Spencer, 1918 is herein not maintained.

Based on existing higher-level classification (e.g. Spencer and Wright 1966), the greatest number of Leintwardine stelleroid specimens belong to the ophiuroid Order Oegophiurida Matsumoto, 1915 (three species assigned to *Furcaster*, *Lapworthura* and *Loriolaster*), with *L. miltoni* being particularly common (c. 370 specimens have been recorded). Most of the remainder belong to the Order Stenurida Spencer, 1951 (six species assigned to *Antiquaster*, *Bdellacoma*, *Klasmura*, *Rhopalocoma* and *Sturtzaster*). The existing higher-level classification of taxa united within the order Stenurida is unsatisfactory; these have traditionally been regarded as ophiuroids (Spencer and Wright 1966) although there is an indication that some of the taxa (e.g. *Bdellacoma* at least; see Sutton *et al.* 2005) are more correctly to be regarded as asteroids. The Leintwardine taxa traditionally classified in the literature (e.g. Spencer 1914-1940; Spencer and Wright 1966) as asteroids (*C. bulbiferus*, *M.? leintwardensis*, *P. antiqua*, and *U. ruthveni*) form an extremely rare and limited component of the biota; only eight specimens of these taxa have been documented. Many of the Leintwardine genera are monospecific.

Aside from the stelleroids, the channel deposits yield a diverse and abundant rare Silurian biota including articulated crinoids, echinoids and ophiocistioids along with eurypterid and xiphosuran chelicerates, phyllocarids, palaeoscolecoid worms, conulariids, and heterostracan fish. As with the stelleroids, this unusual fauna predominantly originates from the Church Hill Channel. Where exact channel provenance is known, the non-stelleroid echinoderms occur solely at this site; the other unusual fossils are also known from three of the other submarine channels in the Leintwardine area (Todding, Mocktree and Tatteridge channels).



## MATERIAL AND METHODOLOGY

All the Leintwardine specimens are from channel fill deposits of the higher Lower Leintwardine Formation (lower Ludfordian Stage). The stelleroids are found within calcareous laminated siltstone. Where precise provenance is known, the majority of the material originates from Church Hill Quarry 1, Church Hill (SO47 4115 7375; Text-fig. 3.1B-C), representing the Church Hill Channel, the most fossiliferous of the six submarine channels in the Leintwardine area. Other quarries representing two of the other channels also yield some stelleroid specimens. These are Martin's Shell Quarry (SO47 4109 7543) and Mocktree Quarry (SO47 4165 7540) representing the Todding Channel and Mocktree Channel, respectively (Text-fig. 3.1B). Exact horizons within the channel fill are not known for the material from museum collections. Where exact horizon provenance is known (e.g. Hawkins and Hampton 1927), all the stelleroids originate from discrete starfish beds. Newly collected *in situ* material (*L. miltoni*, *F. leptosoma* and *B. vermiformis*) originates from a single starfish bed (300 mm in vertical thickness, at an approximate depth of two metres) at the southerly of the two Church Hill quarries (Quarry 1; Text-fig. 3.1C). New specimens of *B. vermiformis*, *L. calceatus*, *R. pyrotechnica*, *S. marstoni*, and *S. colvini* have also been retrieved from loose blocks from this quarry.

Much of the Leintwardine material, particularly that housed in Oxford University Museum, is labelled as originating from Leintwardine and no exact provenance details are known. However it is extremely likely, based on preservational and lithological characteristics, that such material also originates from the channels, most likely that at Church Hill.

Specimens are predominantly mouldic and were cast mostly using silicone rubber (Ambersil RTV 913 and catalyst CAT BLUE 5, or Beacon Hill Silicones ELM 4503 and catalyst T35 from Wacker Silicones). A small number of specimens were cast using latex rubber. Casts were whitened using ammonium chloride prior to photography and camera lucida drawing. All macrophotography carried out by the author has been done so at Leicester using either Leitz aristophot (method of Siveter 1990) or Nikon equipment. A single light source from the top left hand side (NW) of the specimen was used in all instances; this was sometimes supplemented by a fluorescent ring light.



Scanning electron microphotography (SEM) was undertaken on certain stelleroid specimens where morphological features were too fine for conventional photographic techniques. All images were taken using backscattered emissions (BSE) under partial vacuum of uncoated silicone rubber casts.

*Repositories.* The Natural History Museum, London (BMNH); British Geological Survey, Keyworth (BGS); National Museums of Scotland, Edinburgh (NMS); Sedgwick Museum, Cambridge (CAMSM); Oxford University Museum, Oxford (OUM); The Manchester Museum, University of Manchester, (MM); Department of Geology, University of Leicester (LEIUG); Ipswich Museum (IPSMG); Museum of Victoria, Australia (NMVP); University of Michigan, Museum of Paleontology, USA (UMMP); Museum für Naturkunde, Berlin, Germany (MfN); Geological Museum, University of Copenhagen (MGUH). Newly collected material is prefixed by an identifier, denoting the channel deposit from which it originates: Church Hill (CH), Martin's Shell (MS) or Mocktree (Mock). This material will subsequently be deposited in the OUM, BGS and LEIUG collections.

## TERMINOLOGY AND CLASSIFICATION

Suprageneric classification follows that of Spencer and Wright (1966), Hotchkiss (1976) and Jell (1997). Terminology follows that of Spencer and Wright (1966) except for the following (terms adopted herein are italicised; also refer to Text-fig. 3.3 and Table 3.1):

*Ossicles:*

*Abactinals* (following Dean Shackleton 2005) = primarily dorsal plating; occur dorsal to InfMM

*Actinals* (following Dean Shackleton 2005) = ventral plating, between Adambb and InfMM

*Amb1* (following Smith and Jell 1990) = MAPP (Mouth Angle Plates)

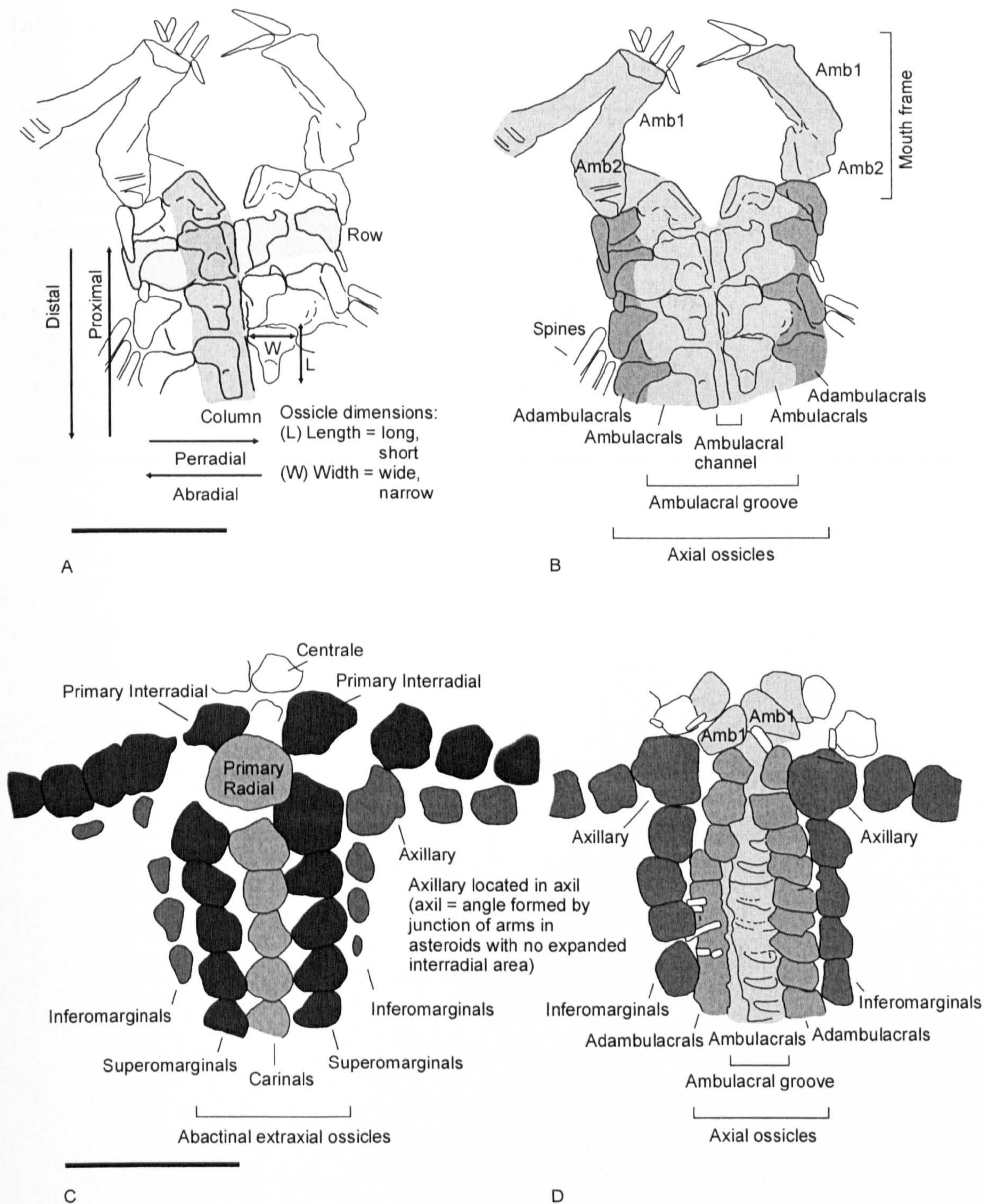
*Amb2* (following Smith and Jell 1990) = Amb1 (of Spencer and Wright 1966)

*Axillary* (following Kesling 1969b) = Odontophore

*Column* = series of ossicles, in radial direction

*Row* = series of ossicles in perradial-abradial direction across arm





TEXT-FIG. 3.3. Stelleroid terminology. A, orientations and dimensions used for stelleroids. B, main features of the ventral surface of the ophiuroid *Lapworthura miltoni* (Salter, 1857), based on specimen NMS G1882651515. C-D, main features of the dorsal and ventral surface, respectively, of the asteroid *Cocaster bulbiferus* Spencer, 1916, based on specimens NMS G65158a and BMNH E 13956. Specimens from the Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. Scale bars represent 2 mm.



TABLE 3.1. Abbreviations used in text-figures.

Amb(b)	Ambulacral(s)
SubL(L)	Sublateral(s)
Adamb(b)	Adambulacral(s)
InfM(M)	Inferomarginal(s)
SupM(M)	Superomarginal(s)
Ax	Axillary
C	Centrale
Ca	Carinal (Radial)
PR	Primary Radial
PI	Primary Interradial
M	Madreporite



*Axial skeleton* (following Mooi and David 1997) = Ambb, SubLL, Adambb

*Extraxial skeleton* (following Mooi and David 1997) = skeletal elements outside axial skeleton

#### *Orientation:*

*Dorsal* = Apical/ aboral surface of body and ossicles

*Ventral* = Oral surface of body and ossicles

*Abradial* = away from arm axis (following Branstrator 1980)

*Perradial* = towards or at arm axis (following Branstrator 1980)

*Proximal* = towards mouth

*Distal* = away from mouth

#### *Dimensions:*

*rad.* = radial direction or length of arm

*per.- ab.* = perradial - abradial direction across arm

dimensions referred to as:

*Long, short* = in radial direction

*Wide, narrow* = in direction across arm

#### *Measurements:*

*R (arm length)* = measured from centre of disc to arm tip

*r* = disc radius

## PRESERVATION

The material is predominantly preserved fully articulated, revealing fine hard-part morphology. Some material is semi-articulated; for example specimens may be missing the distal portions of the arms. Some specimens show minor displacement of their ossicles (e. g. BMNH 40299), which may be due to pre-burial current orientation. The material is predominantly preserved as external moulds, although some specimens retain recrystallised calcite; many of the moulds show reddish brown staining.



## SYSTEMATIC PALAEOLOGY

Specific synonymies are annotated using symbols listed in Matthews (1973).

Subphylum ASTEROZOA Zittel, 1895

Class STELLEROIDEA Lamarck, 1816

Subclass ASTEROIDEA de Blainville, 1830

Order VALVATIDA Perrier, 1884

Suborder PUSTULOSINA Spencer, 1951

Family HUDSONASTERIDAE Schuchert, 1914

Subfamily COCCASTERINAE Spencer and Wright, 1966

Type genus. *Cocaster* Spencer, 1916, by original designation.

Genus COCCASTER Spencer, 1916

1916 *Cocaster novum*.; Spencer, p. 75.

1950 *Cocaster* Spencer; Spencer, p. 406.

1966 *Cocaster* Spencer; Spencer and Wright, p. U51.

*Type species.* *Cocaster bulbiferus* Spencer, 1916, by original designation, from the Upper Silurian of Leintwardine.

*Diagnosis.* Stellate, small. Arms five, long, wide. Disc small. Adambb prominent, bordering deep ambulacral groove. InfMM large, prominent, bordering Adamb. Axillary large, wide (per.-ab.), differentiated from neighbouring InfMM. Primary radials large, swollen, dorsally convex. Centrale surrounded by primary circlet of five radially positioned plates not forming protrusible cap (emended after Spencer and Wright 1966).

*Remarks.* The genus is based on a single well-preserved specimen from Leintwardine. Spencer (1950, p. 406) noted that *Cocaster* could be diagnosed on its InfMM: "axillary well differentiated (from the neighbouring InfMM) but broader than long". Spencer and Wright (1966) erected Coccasterinae in which to place *Cocaster*, stating its characters as "like Hudsonasterinae but no protrusible cap on disc". The generic



diagnosis was based on the possession of swollen primary radial ossicles (Spencer and Wright 1966). The genus is monospecific.

*Cocaster bulbiferus* Spencer, 1916

Plate 3.1; Text-figure 3.4

- v\*. 1916 *Cocaster bulbiferus*, n. sp., Spencer, pp. 75-78, text-figs 33, 38-39, pl. 2, fig. 1, pl. 3, fig. 2.
- v. 1965 *Cocaster bulbiferus* Spencer; Owen, p. 568.
- v. 1966 *Cocaster bulbiferus* Spencer; Spencer and Wright, p. U51, text-fig. 48. 2a-b (cop. Spencer 1916).

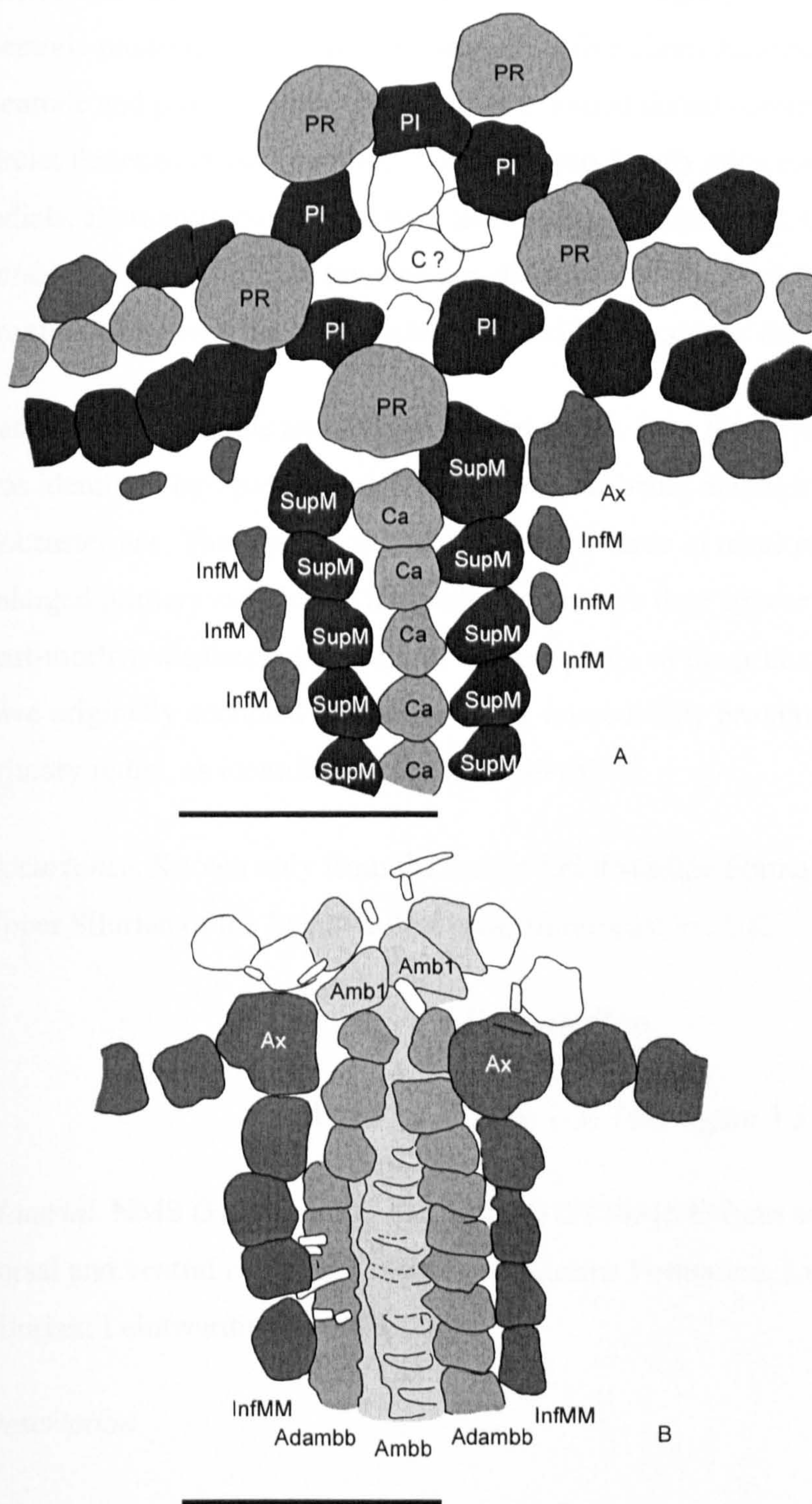
*Holotype*. BMNH E 13956, ventral external mould (part; Spencer 1916, text-fig. 39, pl. 3, fig. 2); NMS G188265158a dorsal external mould (counterpart; Spencer 1916, text-fig. 38, pl. 2, fig. 1). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Diagnosis*. As for the genus.

*Description*

*Overall form*. Stellate,  $R = 6.6$  mm,  $r = 2.4$  mm, small. Arms five, up to 2.4 mm proximal width. Disc small. Adambb prominent, covered by short detached spines, border deep ambulacral groove. Approximately three Adambb to every two InfMM. InfMM large, prominent, subquadrate, with convex perradial and abradial faces, appear subcylindrical (radially elongated) when not fully exposed, ornamented by fine tubercles (spine-bearing), abradially adjacent to Adambb. Axillary large, prominent, subpentagonal, with proximal face triangular and pointed (towards mouth frame), perradial faces slightly concave, distal face with small notch (shallow, narrow groove extends over ventral face from notch), Axillary interrarial at proximal end of InfMM columns, in median position between InfMM. Amb1 triangular, paired interradially just proximal of axillary. Dorsal surface of arms with prominent column of SupMM abradially positioned on either side of perradial median column of carinals. InfMM abradial of SupMM. Carinals, SupMM and InfMM terminate distally in single prominent rounded plate. Primary radials large, rounded, convex dorsally. Primary





TEXT-FIG. 3.4. Camera lucida drawings of *Coccaster bulbiferus* Spencer, 1916 (part & counterpart; NMS G65158a & BMNH E 13956; holotype). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, dorsal view of disc and proximal part of arms, showing primary circlet of enlarged primary radials and interradials (NMS G65158a). B, ventral view of proximal part of arm showing the deep ambulacral groove, Ambb, Adambb and InfMM (BMNH E 13956). Based on specimens shown in plate 3.1, figures 3-4. Scale bars represent 2 mm.



interradials large, pointed proximally, flattened to slightly convex dorsally and distally. Centrale prominent, rounded, surrounded by five plates forming primary circlet. Centrale and primary circlet do not form a domed dorsal corona. Plates of primary circlet flattened dorsally, radial in position, proximally adjacent to large primary radials, alternating proximally with large primary interradians. Carinals rounded, dorsally convex. SupMM rounded abradially to distally, slightly concave perradially to proximally, convex dorsally. InfMM and axillaries convex dorsally.

*Remarks.* The centrale and primary circlet do not form a protrusible cap; this character was identified by Spencer and Wright (1966) as being diagnostic of the Subfamily Coccasterinae. These plates are sunken ventralwards in relation to the surrounding enlarged primary radials and interradians, although they appear to have undergone some post-mortem displacement. Each of the five plates of the primary circlet are inferred to have originally occupied a radial position, immediately proximal to the corresponding primary radial, as identified by Spencer (1916).

*Occurrence.* Known only from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK.

*Coccaster? sp.*

Plate 3.2, figures 1-3; Text-figure 3.5

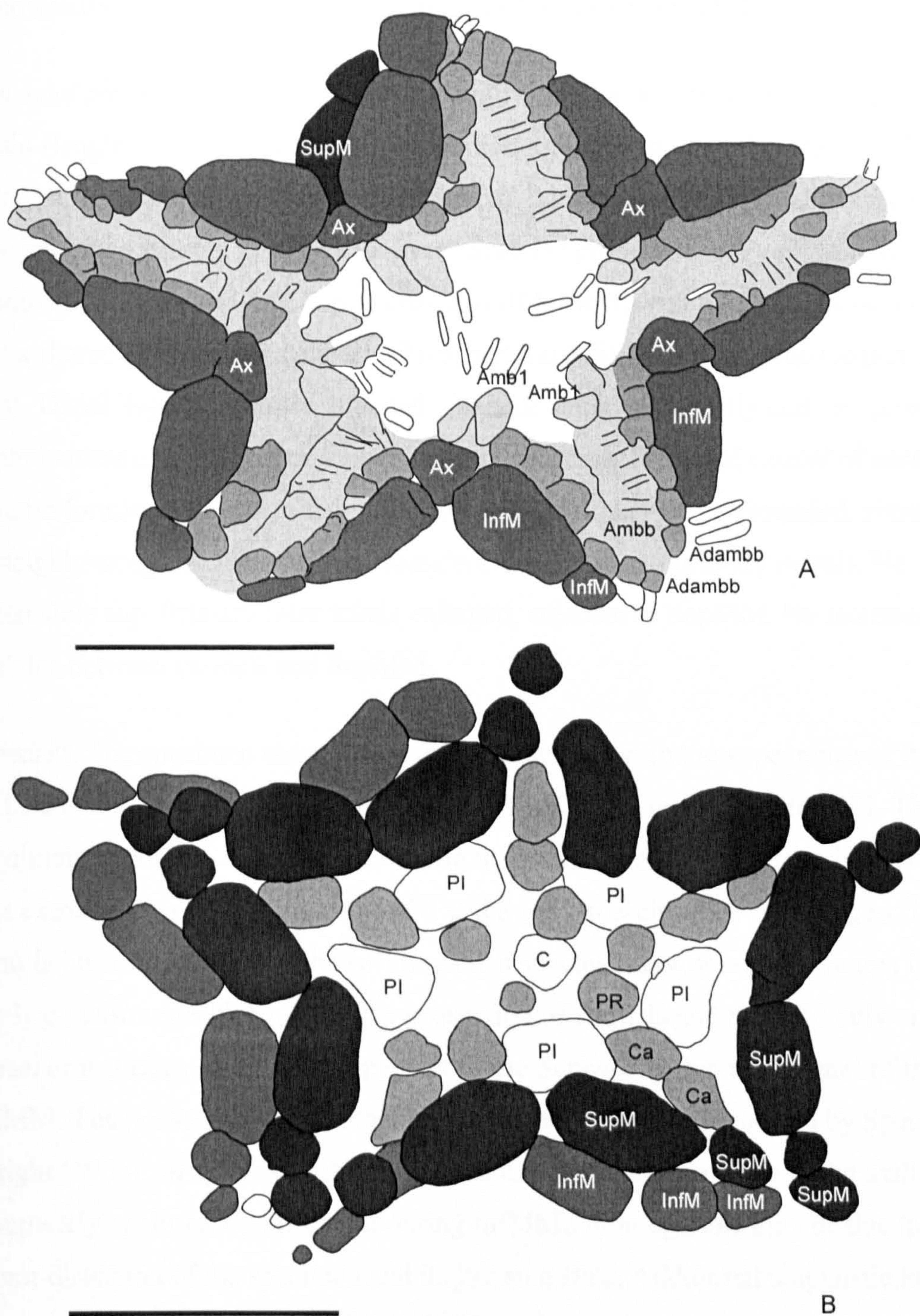
*Material.* NMS G1882651591 and NMS G1882651593 (part and counterpart), showing dorsal and ventral surfaces. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire.

*Description*

*Overall form.* Pentagonal,  $R = 3$  mm,  $r = 1.8$  mm, small. Arms 5, short, wide (proximal width 1.8 mm). Disc relatively large.

*Axial arm plating.* Columns of Ambb and Adambb clearly visible in ventral view. Ambulacral groove wide, exposing Ambb. Ambb opposing, with transverse median ridge that thickens abradially. Podial basins subrectangular, wide. Adambb subquadrate to subrectangular, long.





TEXT-FIG. 3.5. Camera lucida drawings of *Coccaster?* sp. (part and counterpart). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, ventral view showing large InfMM, bordering Adambb and deep ambulacral groove (NMS G1882651593). B, dorsal view showing carinals, enlarged SupMM and InfMM (NMS G1882651591). Based on specimens shown in plate 3.2, figures 1-3. Scale bars represent 2 mm.



*Mouth frame.* Composed of paired Ambb1 and Ambb2. Amb1 elongate, paired interradially. Amb2 similar to succeeding Ambb, paired perradially.

*Extraxial plating.* InfMM prominent, ventrally convex, proximal ossicle large and ovoid (length 1.2 mm), distal ossicles smaller, arranged in ventral marginal column adjacent to Ambb, in line with axillary in axil. Axillary subpentagonal, pointed distally, proximal face straight to slightly convex. SupMM prominent, convex, form dorsal marginal column overlying or just proximal of InfMM, with two ossicles per column and a shared distal terminal ossicle. Proximal SupMM large and ovoid (length 1.2 mm). Distal SupMM smaller, rounded. Carinals rounded, dorsally convex, arranged in central column, with three or four ossicles per column. Proximal carinal of each column forming a circlet of five primary radials. Primary radials rounded, similar size to neighbouring carinals. Centrale rounded, similar size to primary radials. No protrusible cap. Primary interradials enlarged, adjacent to SupMM. No intermediate ossicles between carinals and SupMM.

*Remarks.* The specimen shows some minor distortion with the appearance of the dorsal surface being sheared laterally, exposing portions of the underlying InfMM. This specimen is likely to be a juvenile, owing to its small size and few marginal ossicles. The extremely enlarged proximal InfM and SupM in each series also suggest that the form is juvenile. Assigning the specimen to a species is not possible although it is very likely a hudsonasterid, based on the possession of carinals and SupMM only on the dorsal arm surface, and the arrangement of the SupMM within the 'frame' of the InfMM. The possession of the other hudsonasterid character identified by Spencer and Wright (1966), an axillary with a free distal edge, is equivocal (one of the axillaries is completely enclosed by the neighbouring InfMM), although this may be due to the minor distortion of the specimen and its juvenile state. Additional diagnostic familial characters used by Dean Shackleton (2005) such as enlarged primary interradials, and primary radials and primary interradials forming a ring, are also identified, the latter character only tentatively. The lack of an apparent 'protrusible cap' or 'domed aboral corona' (terminology of Spencer and Wright 1966 and Dean Shackleton 2005, respectively) suggests the specimen can be assigned to the subfamily Coccasterinae. However, it is quite possible that this structure may not yet have developed in the juvenile specimen. If this absence of the domed dorsal corona is accepted as not merely



an ontogenetic feature, then the specimen could be tentatively assigned to *Cocaster*. The absence of enlarged primary radials, a diagnostic character of *Cocaster*, may be due to the specimen's juvenile stage.

### Incertae subfamiliae

Genus MESOPALAEASTER Schuchert, 1914

*Mesopalaeaster? leintwardensis* Spencer, 1916

Plate 3.2, figures 4-5; Text-figure 3.6

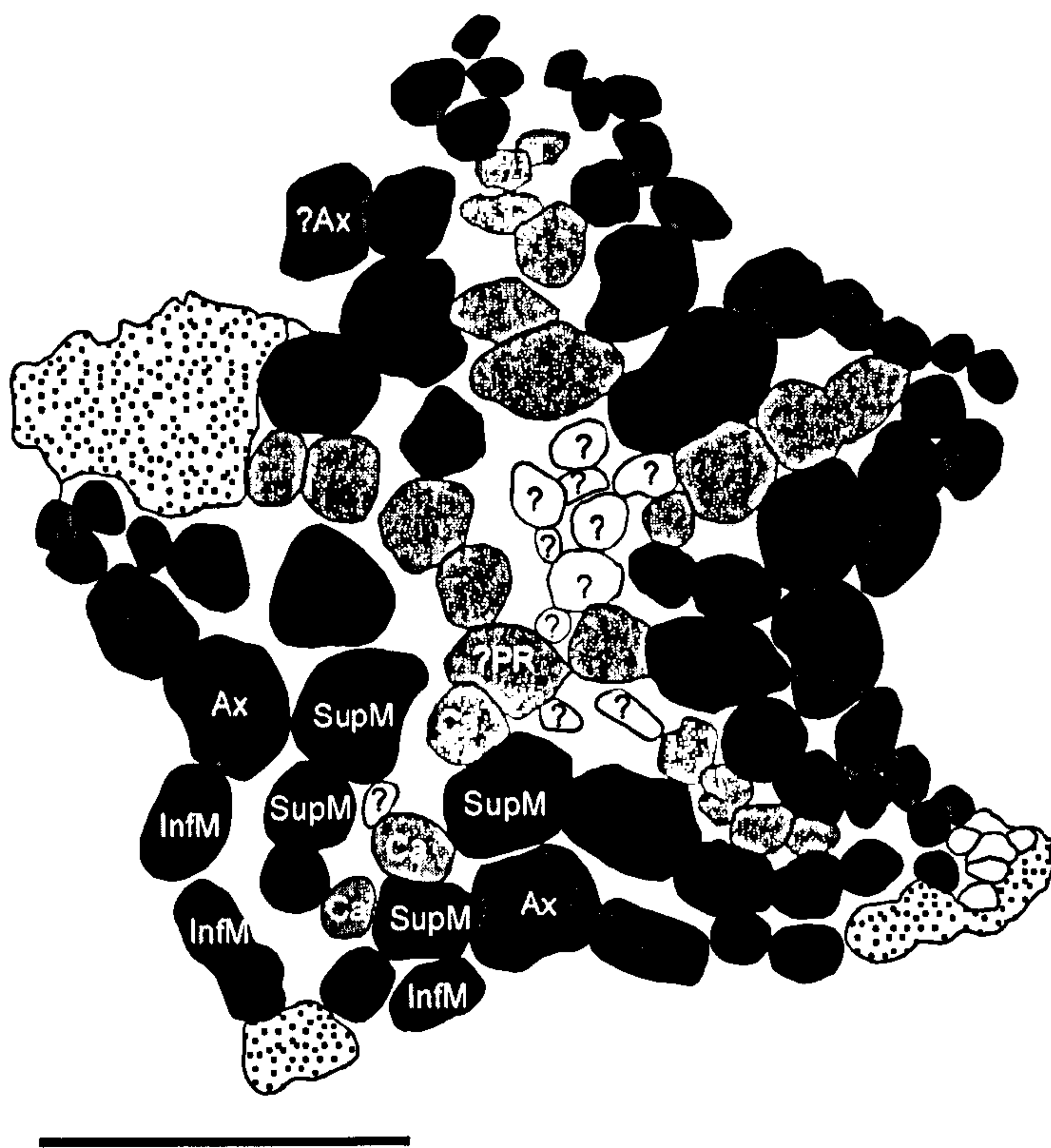
- v\*. 1916 *Mesopalaeaster (?) leintwardensis* n. sp., Spencer, pp. 89-90, text-fig. 49, pl. 2, fig. 5.
- v. 1965 *Yarravaster leintwardensis* (Spencer); Owen, p. 569.
- v. 1966 *Arisaigaster leintwardinensis* (Spencer); Spencer and Wright, p. U51, text-fig. 49. 3a (cop. Spencer 1916).
- 2003 *Mesopalaeaster ? leintwardinensis* Spencer; Botting, p. 704.

*Holotype*. BMNH E 13153, external mould of dorsal surface (Spencer 1916, p. 12, text-fig. 49, pl. 2, fig. 5). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

### Description

*Overall form*. Stellate, small. Arms five, short (arm length 3.3 mm), wide (proximal width 2.4 mm). Disc large (radius 2.1 mm), with central area sunken. Extraxial ossicles highly convex. Five columns of ossicles on dorsal surface of arm. Carinals subcircular to oval, decrease in size distally, not very prominent, form perradial column. SupMM subcircular to oval, proximal ossicle of column large and kidney shaped, decrease in size distally, form prominent column of relatively large ossicles either side of carinals (three to four per column; not including arm tips, which are poorly preserved). InfMM subrounded to oval, abradially positioned, form marginal column (three ossicles per column; not including arm tips). InfM columns of adjacent arms diverge from large interrarial plate (axillary); axillary lies median of proximal ossicle of each marginal





TEXT-FIG 3.6. Camera lucida drawing of dorsal surface of *Mesopalaeaster? leintwardensis* (Spencer, 1916) (BMNH E 13153; holotype). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. Entire specimen, showing carinals, SupMM, InfMM, and axillaries; stippled areas indicate obscured surface. Based on specimen shown in plate 3.2, figures 4-5. Scale bar represents 2 mm.



column. Axillary subquadrate to subrounded, with distal surface concave, appears to point inwards proximally.

*Remarks.* The ossicles are distorted, making their identification problematic, which has led to confusion in the literature over the specimen's generic affinity. The assignment of the columnal ossicles as SupMM and InfMM is based on terminology of Kesling (1969b). The outer column of marginals incorporates the axillary, and is not articulated with the carinals so these marginals are therefore termed InfMM. The inner prominent column of ossicles, bordering the carinals, are termed the SupMM, as they are in contact with the carinals. The ossicle interpretation given here differs from that of Spencer (1916) who interpreted the outer column of marginals as SupMM, identifying an enlarged proximal SupM in each series. Spencer's (1916) reconstruction (text-fig. 49) differs considerably from the interpretation adopted herein; no intermediate column of adradials has been identified between the carinals and SupMM. This column of 'adradials' is reinterpreted as SupMM.

Spencer (1916) tentatively assigned the specimen to *Mesopalaeaster*. However, comparison with reconstructions of the dorsal and ventral surfaces of the type species, *Palaeaster shafferi* Hall, 1868, (Spencer and Wright 1966, text-figs 49.2b-c) shows the arrangement of the axillary and InfMM to be fundamentally different. *Mesopalaeaster shafferi* has an axillary completely enclosed by the neighbouring InfMM whilst *M.? leintwardensis* has an axillary with a free distal edge.

Owen (1965) assigned the species, presumably from Spencer's text-figure reconstruction, to *Yarravaster* Spencer, 1950 but did not give any formal diagnosis. This assignment was probably due to the supposed presence of an intermediate column of adradials. The dorsal morphology of the type species of *Yarravaster* (*Caractacaster yarraensis* Withers and Keble, 1934) has an intermediate column of small ossicles (?adradials), separating the carinals from the SupMM, whilst in *M.? leintwardensis*, the carinals are in direct contact with the SupMM. The overall shape of the two specimens also differs, *M.? leintwardensis* exhibiting far shorter and wider arms, although this may be due to its possible juvenile stage.

Spencer and Wright (1966) assigned the specimen to *Arisaigaster* Spencer, ?1953, a genus which was differentiated from other members of the Subfamily



Mesopalaeasterinae solely by the possession of a large disc and short, broad arms (Spencer and Wright 1966). Direct comparison with the type species *Arisaigaster parviusculus* (Billings, 1860) is not possible due to corresponding surfaces not being known in both species. *M.? leintwardensis* is only known by its dorsal surface whereas *A. parviusculus* is only known by its ventral surface (see Spencer and Wright 1966, text-figures 49. 3a-b). The original type species description was based on details of the overall form and the ventral surface (Billings 1860, cited in Schuchert 1915).

Specimens of *A. parviusculus* showing ventral morphology are described by Schuchert (1915) and McLearn (1924). The arrangement of the InfMM in relation to the axillary (viewed dorsally) on *M.? leintwardensis* does not resemble that of the arrangement shown in the ventral morphology of *A. parviusculus*, suggesting that they are not of the same genus. *A. parviusculus* has an axillary completely enclosed by the neighbouring InfMM, whilst in *M.? leintwardensis*, the axillary has a free distal edge, lying median to the two columns of InfMM.

As only the dorsal surface is known, assignment at generic and suprageneric level is tentative. The specimen is assigned to the hudsonasterids with caution, based on: the possession of a single axillary with a free distal edge, SupMM lying within the frame of the InfMM, and the dorsal arm surface consisting of carinals and SupMM only. Ossicle morphology is difficult to determine proximal to the carinals and SupMM; the arrangement of the centrale to the surrounding ossicles cannot be determined. The specimen is not assigned to the Subfamily Silurasterinae Spencer and Wright, 1966, as there is a lack of intermediate ossicles between the carinals and SupMM (see Spencer and Wright 1966). Assignment to either of the subfamilies Hudsonasterinae or Coccasterinae cannot be determined, as the proximal ossicle morphology is obscured. Assignment of *M.? leintwardensis* unequivocally to a genus is not possible, due to the degree of distortion, lack of a ventral surface and the possible juvenile nature of the specimen.

**Occurrence.** Known only from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire.



## Order FORCIPULATIDA Perrier, 1884

## Suborder URACTININA Spencer and Wright, 1966

## Family URASTERELLIDAE Schuchert, 1914

*Type genus. Urasterella* M'Coy, 1851, by original designation.

## Genus URASTERELLA McCoy, 1851

- 1851 *Urasterella*; McCoy, p. 59 (not defined).
- 1886b *Urasterella* McCoy; Stürtz, p. 152.
- 1914 *Urasterella* McCoy; Schuchert, pp. 5, 7, 28, 36-37, 39, 44 (*pars*).
- 1915 *Urasterella* McCoy; Schuchert, pp. 41-42, 45, 47, 49, 50, 69, 164, 173-75, 194, 212 (*pars*).
- 1918 *Urasterella* McCoy (emend.); Spencer, p. 135-137.
- 1918 *Salteraster* Stürtz; Spencer, p. 149.
- 1950 *Urasterella* McCoy; Spencer, p. 406.
- 1950 *Phillipaster* gen. nov.; Spencer, p. 406.
- 1966 *Urasterella* M'Coy; Spencer and Wright, p. U71.
- 1966 *Phillipaster* Spencer, 1950; Spencer and Wright, p. U71.
- 1966 *Salteraster* Stürtz, 1893; Spencer and Wright, p. U71.
- 1998 *Urasterella* M'Coy; Bartels *et al.*, p. 204.
- 2005 *Urasterella* McCoy; Dean Shackleton, p. 99.

*Type species. Uraster ruthveni* Forbes, 1848, by original designation, from the Upper Silurian of the Lake District.

*Diagnosis.* Arms relatively long, narrow, parallel-sided to gradually tapering, distinct from disc. Disc small. Ambbb opposing, subrectangular, wide. Adambb subrectangular, wide, overlapping, bordering a deep ambulacral groove. Distinct columns of paxillose ossicles dorsally. Carinals form prominent perradial column. Three to four adradial columns and column of InfMM on either side of carinals (emended after Spencer and Wright 1966 and Dean Shackleton 2005).

*Remarks.* Spencer (1918) recognised three British species of *Urasterella*: *Urasterella thraivensis* Spencer, 1918 (Upper Ordovician, Girvan, Scotland), *Urasterella ruthveni*



(Forbes, 1848) and *Urasterella gutterfordensis* Spencer, 1918 (Llandovery Series, Lower Silurian, Pentland Hills, Scotland). Spencer (1918) differentiated the former two species on the position of transverse ridges on the Adambb. *U. thraivensis* was diagnosed by medianly positioned Adamb ridges, whilst *U. ruthveni* was diagnosed by distally positioned Adamb ridges (Spencer 1918). The third species was described as possessing Ambb and Adamb ridges as in *U. thraivensis* and an ossicle adjacent to the centrale as in *U. ruthveni* (Spencer, 1918). Spencer (1950) erected a new genus *Ulrichaster* to include species with two perradial rows of ossicles along the dorsal surface of the arms; he subsequently included *U. gutterfordensis* within this genus. Two further species have been described from the Lower Devonian Hunsrück Slate of Germany: *Urasterella asperula* Roemer, 1863, and *Urasterella verruculosa* Lehmann, 1957 (Lehmann 1957, Spencer and Wright 1966). Lehmann (1957, p. 132-133) described *U. verruculosa* as possessing five primary radials, indicating its generic status; however, he also described several features atypical of the genus. The Ambb were stated as being alternating, a feature uncharacteristic not just of the genus but also traditionally of the Asteroidea (Spencer and Wright 1966, p. U13, Dean 1999, p. 117). Lehmann (1957, p. 133) also mentioned “small, roundish plates, that carry tiny spines”, along the edges of the arms. Inspection of Lehmann’s text-figure 25 and plates 45 and 46, indicates that these plates may in fact be pedicellariae, such as those seen in species of *Antiquaster* Kesling, 1971 and *Bdellacoma* Salter, 1857 (see this chapter; Sutton *et al.* 2005). It may well be that *U. verruculosa* is in fact a synonym of a species of *Bdellacoma*, although direct analysis of the type specimens will need to be undertaken before one can be sure of its affinity. Dean Shackleton (2005) reassigned *Palaeaster asperrimus* Salter, 1857 to *Urasterella*, although she did not formally state its diagnostic characters.

### *Urasterella ruthveni* (Forbes, 1848)

Plates 3.3-4; Text-figure 3.7

- \* 1848 *Uraster Ruthveni*, Forbes, pp. 463-464.
- 1849 *Uraster ruthveni* Forbes; Forbes, p. 1, pl. 1, fig. 1.
- 1851 *Uraster ruthveni* Forbes; McCoy, p. 51.
- 1857 *Palaeaster Ruthveni* Forbes; Salter, p. 326.
- 1867 *Palaeaster Ruthveni* Forbes; Murchison, p. 225, text-fig. 57.3.



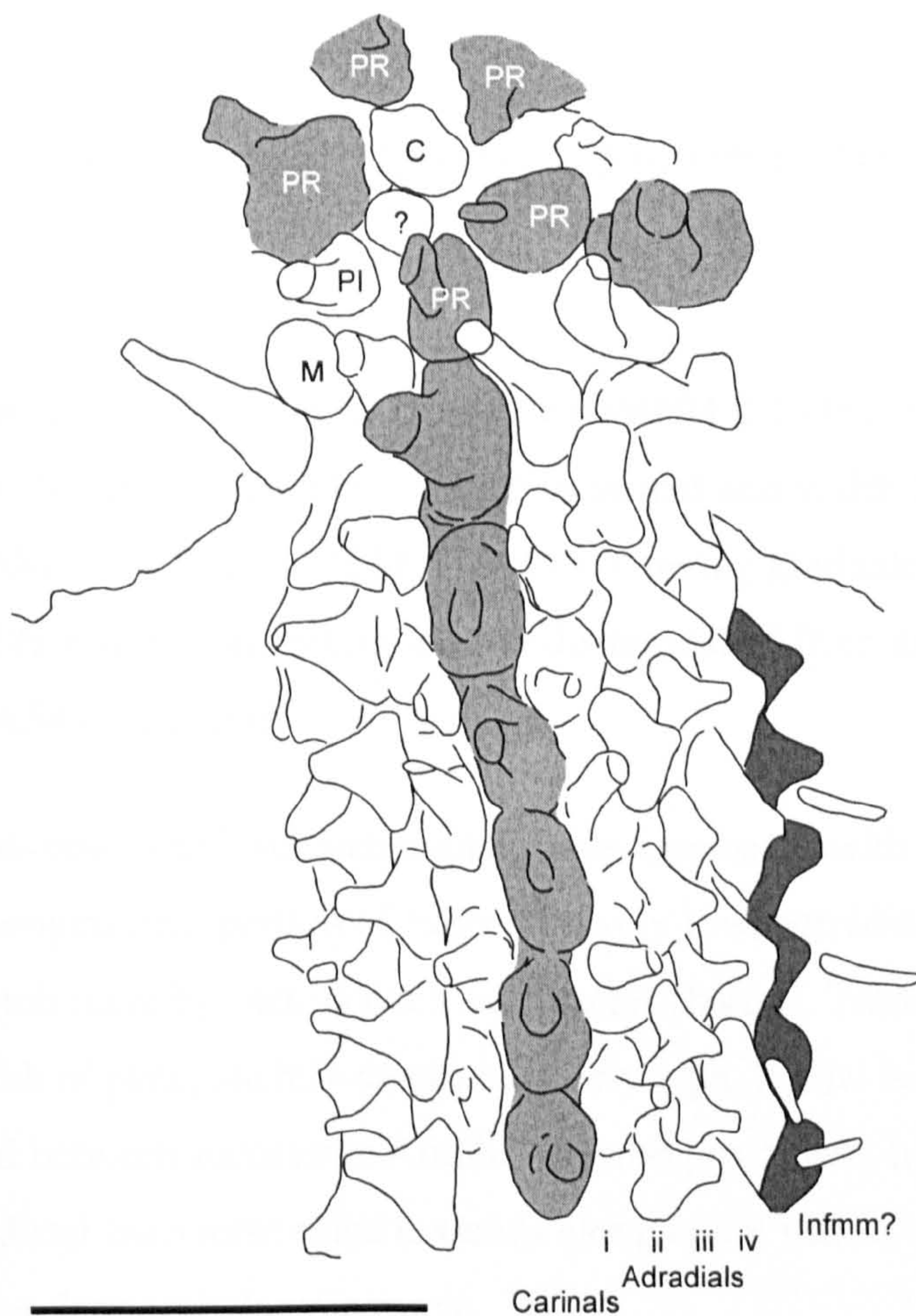
- 1862 *Palaeaster ruthveni* Forbes; Wright, p. 25.
- 1873 *Palaeaster Ruthveni*, Forbes; Salter, p. 163.
- 1884 *Palaeaster Ruthveni*; La Touche, pl. 17, fig. 547.
- 1914 *Urasterella ruthveni* (Forbes); Schuchert, pp. 44-45.
- 1915 *Urasterella ruthveni* (Forbes); Schuchert, pp. 174-175 (*pars*), 187.
- v. 1918 *Urasterella ruthveni* (Forbes); Spencer, pp. 140-142, text-figs 90-91, pl. 9, fig. 5, pl. 10, figs 4-6.
- v. 1918 *Urasterella ruthveni* var. *leintwardinensis* nova.; Spencer, pp. 142-144, 147 (*pars*), text-fig. 92, pl. 9, figs 3, 4.
- 1952 *Urasterella ruthveni leintwardinensis* Spencer; Wienberg Ramussen, p. 17.
- v. 1965 *Urasterella ruthveni* (Forbes); Owen, p. 565.
- v. 1965 *Urasterella ruthveni* var. *leintwardinensis* Spencer; Owen, p. 565.
- v. 1966 *Urasterella ruthveni* (Forbes); Spencer and Wright, p. U71, text-fig. 64. 6b (cop. Spencer 1918).
- v 1979 *Urasterella ruthveni leintwardinensis* Spencer; Franzén, pp. 220-221, text-fig. 68A.
- 2004 *Urasterella ruthveni* (Forbes); Kutscher, pp. 620-626, text-figs 1-2, pls 1-3.
- . 2005 *Urasterella ruthveni*; Dean Shackleton, p. 99.

*Holotype*. CAMSM A5497, incomplete arm tips, external mould of ventral surface ('a.920' in Spencer 1918, text-fig. 91, pl. 10, fig. 4). Bannisdale Slates, Ludlow Series, Upper Silurian; Lake District, UK.

*Additional material*. CAMSM A5501 (= 'a.516' not 'a.510' of Spencer 1918, pl. 10, fig. 5); A5502 (= 'B1' of Spencer 1918, pl. 10, fig. 6); A5498 (= 'a.921' of Spencer 1918). All external moulds of ventral surface and from the Bannisdale Slates, Ludlow Series; Underbarrow, Lake District, UK. MGUH 27642 (Franzén 1979, text-fig. 68A); Wenlock Series; Visby, Gotland.

BMNH E 13952 ('Ludlow Museum, no. IV' in Spencer 1918, text-fig. 92, pl. 9, figs 3, 4); MM L11020, NMS G188265158b, unlocated. All external moulds of the dorsal surface. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine; Herefordshire, UK. Spencer (1918) assigned BMNH E 13952 as the





TEXT-FIG. 3.7. Camera lucida drawing of dorsal surface of *Urasterella ruthveni* (Forbes, 1848) (BMNH E 13952). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. View of central disc and proximal part of arm, showing centrale, circlet of primary radials, madreporite and carinals, adradials (?four columns) and InfMM; SupMM absent. Based on specimen shown in plate 3.3, figures 1-3. Scale bar represents 2 mm.



holotype for *Urasterella ruthveni* var. *leintwardinensis*. The Leintwardine material (three specimens) was originally described as *U. ruthveni* var. *leintwardinensis* Spencer, 1918.

*Diagnosis.* Transverse Adamb ridges distally positioned (after Spencer 1918).

### *Description*

*Overall form.* Arms five, distinct from disc (BMNH E 13952: R = 15 mm, r = 2.1 mm), long, relatively narrow (BMNH E 13952: proximal arm width 2.4 mm), parallel-sided (e.g. CAMSM A5497-8, CAMSM A5501) to tapering gradually (e.g. BMNH E 13952, MM L11020), rounded in section, clearly distinguished from disc. Disc small (CAMSM A5497: 2.2 mm).

*Axial arm plating.* Ambb subrectangular, wide, opposing, with L- shaped ridge ventrally. Longitudinal portion of ridge relatively low, perradially separated from opposing Amb ridge by narrow deep ambulacral channel. Transverse section of ridge extends width of plate, slightly distal, relatively high. Podial basins subrectangular, deep, shared between successive Ambb. Adambb prominent, high, subrectangular, wide, with distal transverse ridge (extends along entire ventro-abradial surface of plate), border deep ambulacral groove.

*Mouth frame.* Only seen from ventral view. Amb1 small, subtriangular, paired interr radially. Amb2 obscured by overlying Adamb.

*Madreporite.* Small (BMNH E 13952: 0.51 mm diameter), oval, slightly convex, with radiating pattern of grooves on surface, dorsal, interr adial and proximally positioned, distally adjacent to enlarged interr adial ossicle.

*Extraxial plating.* Carinals prominent, subrectangular, long, paxillose with prominent process extending dorsally, arranged in perr adial column, dorsal. Proximal ossicle of each column forms one of five primary radials surrounding sunken centrale ossicle. Centrale rounded, dorsally convex, lacks process. Small secondary ossicle adjacent to centrale in BMNH E 13952, interr adial in position, rounded, dorsally convex, lacks process. Circlet of primary radials incorporates smaller sixth ossicle (enlarged primary interr adial ossicle). Primary interr adial forms most proximal ossicle of first adradial



column, proximally adjacent to madreporite. Aadrals strongly paxillose, form three to four columns of ossicles either side of carinals (third column of small aadrals only present proximally; absent distally), dorsal, show size differentiation perradially to abradially. Ossicles of first column relatively prominent; those of second column slightly less so. Aadrals of third column small. Aadrals of fourth column relatively large, subcylindrical, long. Ossicles of second, third and fourth aadrals columns have fallen sideways in BMNH E 13952, exposing their aadrals face. Aadrals appear triangular perradially, with process extending abradially. InfMM subcylindrical, long, paxillose with process extending abradially, form marginal column along arm, ventrally adjacent to aadrals. SupMM absent.

*Remarks.* Due to the deep ambulacral groove, the Ambb are often difficult to determine in their entirety; part of an arm section on the holotype is broken away however, fully exposing the Ambb (Pl. 3.4, fig. 2).

Spencer (1918) and Spencer and Wright (1966) identified three columns of aadrals and a marginal InfM column in BMNH E 13952. I consider that the column originally identified as InfMM is more likely to represent a fourth column of aadrals, as paxillose ossicles, inferred to be the InfMM, occur ventrally to these (Text-fig. 3.7; Pl. 3.3, figs 2-3). This further column of ossicles is not interpreted to represent the Adambb, in contrast to Spencer's (1918) interpretation, as their paxillose morphology is unlike that of the Adambb of the taxon (as shown in specimens revealing the ventral arm surface, e.g. CAMSM A5497; Pl. 3.4, fig. 6). No axillary ossicles (as identified by Spencer 1918, text-fig. 92) are identified in dorsal view (Pl. 3.3, figs 2-3); therefore, the determination of the InfMM in dorsal view remains tentative. However, InfMM are clearly seen on specimens showing ventral surfaces (e.g. CAMSM A5497, A5501; Pl. 3.4, fig. 6). Spencer (1918) stated that genera of the Urasterellidae only possessed InfMM, with SupMM not being represented, adding (p. 126) that strong development of the Adambb pushed the InfMM over to the dorsal surface. I concur that SupMM are absent within this form. Kutscher's (2004) schematic reconstruction of the dorsal arm plating of the species was based on Spencer's (1918) description; Kutscher recognised only two columns of aadrals, presumably distally on the arm. This interpretation cannot be compared with Kutscher's (2004) newly described specimen from a Silurian glacial erratic boulder as only the ventral arm plating is preserved.



Spencer (1918) erected *U. ruthveni* var. *leintwardinensis* based on three specimens from the Leintwardine area, and differentiated it from typical *U. ruthveni* on differences in relative overall size. The Leintwardine specimens were deemed a subspecies, *U. ruthveni leintwardinensis* by Wienberg Rasmussen (1952), Franzén (1979) and Kutscher (2004). No subspecies is maintained herein. Material originally described by Spencer (1918) as *U. ruthveni* var. *leintwardinensis* only shows dorsal morphology, whilst the Lake District material assigned to *U. ruthveni* shows only ventral morphology. No part and counterpart specimens are known from the original material. Examination of the syntypes of the urasterellid '*Salteraster*' *selwyni* (McCoy) (NMVP12207 & 12208, part and counterpart, showing the ventral and dorsal surfaces respectively; Withers and Keble 1934, pl. 11, figs 1-2) shows the ossicle arrangement to resemble the ventral *U. ruthveni* material and dorsal *U. ruthveni* var.

*leintwardinensis* material. Spencer (1950) regarded *Salteraster* to be a synonym of *Phillapaster*, based on the degree to which the dorsal surface was swollen. However, Dean Shackleton (2005) considered that this was an unreliable generic character and synonymised *Salteraster* and *Phillapaster* within *Urasterella*, with which I concur. By comparison with the complete '*Salteraster*' *selwyni* (= ?*Urasterella selwyni*) specimen, the two dorsal (Leintwardine) and four ventral (Lake District) specimens of *Urasterella* are regarded as the same species, *U. ruthveni*. This classification is in agreement with that of Kutscher (2004). Comparison of the newly assigned dorsal material of the type species of *Urasterella* with the dorsal morphology of *Salteraster* and *Phillipaster* confirms that these genera are likely to be synonymous.

A single specimen, showing its ventral surface, has been described in the literature from the Wenlock Series of Visby, Gotland (MGUH 27642; Spencer 1918; Franzén 1979; Kutscher 2004; Pl. 3.4, figs 4-5). The specimen has been restudied, as it is not possible from Franzén's (1979) text-figure to determine whether it belongs to the species. The specimen is retained within the species based on the possession of pronounced transverse Adamb ridges (Pl. 3.4, fig. 5). The species possibly shows an Upper Silurian palaeogeographical range from Avalonia to Baltica (c. 25° S to 19° S; Bassett *et al.* 1992; Smethurst *et al.* 1998).

**Occurrence.** From the Lower Leintwardine Formation, Ludlow Series of the Leintwardine area and the Bannisdale Slates of the Lake District, UK. Also from the



Wenlock Series, Middle Silurian of Visby, Gotland and from a Silurian glacial erratic boulder from Niederlehme, near Berlin, Germany.

Order PAXILLOSIDA Spencer, 1951

Suborder HEMIZONINA Spencer, 1951

Family PALASTERINIDAE Gregory, 1899

*Type genus. Palasterina* M'Coy, 1851, by original designation.

Genus PALASTERINA McCoy, 1851

- 1848 *Uraster*; Forbes, p. 463.
- 1851 *Palasterina*; McCoy, p. 59.
- 1857 *Palasterina* M'Coy; Salter, pp. 324, 327.
- 1890 *Palasterina* M'Coy; Stürtz, p. 246.
- 1893 *Palasterina* M'Coy; Stürtz, pp. 43, 60.
- 1914 *Palasterina*; Schuchert, pp. 5, 7, 29-30 (*pars*).
- 1915 *Palasterina* McCoy; Schuchert, pp. 150-153.
- 1922 *Palasterina* McCoy; Spencer, pp. 219-223.
- 1966 *Palasterina* M'Coy; Spencer and Wright, p. U45.
- 2005 *Palasterina* McCoy; Dean Shackleton, p. 71.

*Type species. Uraster primaevus* Forbes, 1848, by original designation, from the Upper Silurian of the Lake District, UK.

*Diagnosis.* Pentagonal. Arms five, long, wide, tapering rapidly to arm tip. Disc extensive, with large interradial area. Ambb subrectangular, wide, opposing proximally, alternating distally. Dorsally with prominent columns of carinals and SupMM along arms. Primary interradials enlarged. Minor ossicles between SupMM and InfMM (emended after Dean Shackleton 2005).

*Remarks.* The genus has been traditionally regarded as an asteroid (Spencer 1922; Spencer and Wright 1966). However, Dean Shackleton (2005) assigned *Palasterina*, along with *Rhopalocoma* and *Sturtzaster*, to the Order Eopentaroidea Dean Shackleton, 2005, a stem group 'protophiuroid'. *Palasterina* shares several Amb characters with *Rhopalocoma* and *Sturtzaster*, such as alternating plates with L-shaped ventral ridges.



Both *Palasterina* and *Rhopalocoma* have extensive actinal plating and InfMM bearing spines. However, other diagnostic characters of the eopentaroids, identified by Dean Shackleton (2005), such as stellate actinals and a madreporite in contact with InfMM are equivocal in *Palasterina* (pers. obs.). The actinals are blocky in *Palasterina primaeva* (Forbes, 1848) although are slightly stellate in *Palasterina* cf. *antiqua* (Pl. 3.6, fig. 1). The madreporite appears to be in contact with the InfMM in *P. primaeva* (e.g. CAMSM A5507), although in *P. cf. antiqua* I have identified intermediate actinals between it and the InfMM (Pl. 3.6, fig. 1). Suprageneric classification of *Palasterina* remains tentative; therefore I have retained the classification of Spencer and Wright (1966) awaiting further study.

Three species were recognised by Spencer (1922): *P. primaeva* (Upper Silurian, UK), *Palasterina antiqua* (Hisinger, 1837) (Upper Silurian, UK and Gotland), and *Palasterina follmanni* Stürtz, 1890 (Lower Devonian, Germany). Spencer (1922) differentiated the former two on relative numbers of ossicles in the interrarial area. The third species was described as being a larger form, with swollen arms, dorsally bearing many rows of similar ossicles (Spencer 1922). Withers and Keble (1934) erected three species from the Silurian of Victoria, Australia, namely: *Palasterina flemingtonensis*, *Palasterina stachi*, and *Palasterina umbonata*. Spencer (1950) considered that the first of these was more likely to be a species of *Baliactis* Spencer 1922 and the second a species of *Eoactis* Spencer, 1914. Lehmann (1957) named further species from the Lower Devonian of Germany: *Palasterina marginata*, *Palasterina maucheri*, *Palasterina taenibrachiata* and *Palasterina tilmanni*.

Spencer's (1922) differentiation of *P. primaeva* and *P. antiqua* was based on the number of ossicles in the interrarial area of the disc, *P. antiqua* exhibiting a relatively larger number. My examination of specimens of *P. primaeva* from the Upper Silurian Bannisdale Slates of the Lake District, UK (CAMSM A5506-8, A5512-14, A5517), confirms the difference in this character.



*Palasterina* cf. *antiqua* (Hisinger, 1837)

Plate 3.5; Plate 3.6, figures 1-2; Text-figure 3.8

- cf 1837 *Asterias antiqua*, Hisinger, p. 89, pl. 26, fig. 6.
- 1857 *Palasterina primaeva* Forbes; Salter, p. 327, pl. 9, fig. 2.
- 1862 *Palasterina primaeva* Forbes; Wright, p. 26, text-fig. 16.
- v. 1899 *Palasterina Bonneyi*, n. sp.; Gregory, pp. 349-350, text-figs 1-3, pl. 16, figs 2a-b.
- 1914 *Palasterina bonneyi* Gregory; Schuchert, p. 31.
- 1915 *Palasterina bonneyi* Gregory; Schuchert, p. 153.
- vp. 1922 *Palasterina antiqua* (Hisinger); Spencer, pp. 232-234 (*pars*), text-figs 168-169, pl. 16, figs 1-2.
- vp. 1965 *Palasterina antiqua* (Hisinger); Owen, p. 562 (*pars*).
- vp. 1966 *Palasterina antiqua* (Hisinger); Spencer and Wright, p. 45, text-fig. 43.2d (cop. Spencer 1922).
- v. 2005 *Palasterina antiqua* (Hisinger); Dean Shackleton, p. 71, pl. 5, figs 1-2.

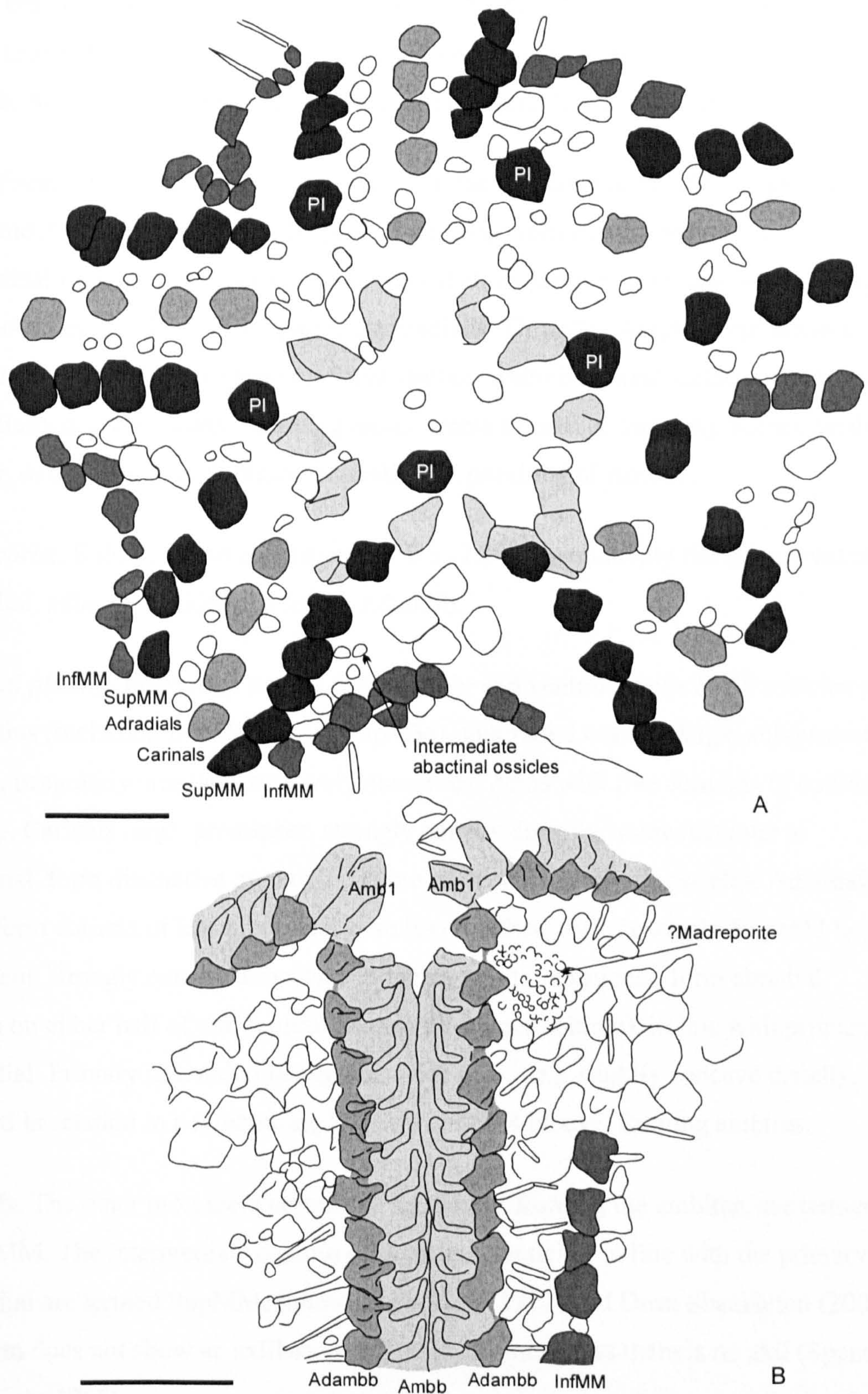
*Material.* BMNH 40299a-b, external moulds of dorsal and ventral surface (holotype of '*Palasterina bonneyi*', Gregory 1899) (Spencer 1922, text-figs 168-169, pl. 16, figs 1-2). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description*

*Overall form.* Pentagonal (BMNH 40299: R = 13 mm, r = 5 mm). Arms five, long, wide (proximal arm width of BMNH 40299: 5 mm), petaloid, tapering rapidly to arm tip. Disc moderate size, extends to Adamb14 perradially, with extensive interr radial area.

*Axial arm plating.* Axial plates only seen on ventral surface. Ambulacral groove wide, fully exposing Ambb. Ambb subquadrate, wide, with L-shaped ridge on each plate, opposing proximally, alternating distally near arm tips. Perradial longitudinal ridges of transversely neighbouring plates separated by wide perradial groove (the ambulacral channel). Podial basins shared, subquadrate, deep. Adambb convex abradially, with





TEXT-FIG. 3.8. Camera lucida drawings of *Palasterina cf. antiqua* (Hisinger, 1837). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, dorsal view of disc and proximal portions of arms; mouth frame can be seen pressing through (shown in light grey) (BMNH 40299a). B, ventral view of proximal part of arm and mouth frame, showing Ambb, Adambb, large interrarial area, InfMM, and possible madreporite (BMNH 40299b). Based on specimen shown in plate 3.5 and plate 3.6, figures 1-2. Scale bars represent 2 mm.



median transverse ridge adjoining transverse Amb ridge, form prominent abradial margin to ambulacral groove. Spines acicular, one to two on abradial face of each Adambb. Spine length approximately twice longitudinal length of Adambb.

*Mouth Frame.* Viewed on dorsal and ventral surfaces. Constructed of five pairs of Amb1 and Amb2 ventrally. Ambb1 prominent, long, convex ventrally, with longitudinal ridge and corresponding abradial shallow groove on ventral surface (ridge and groove run length of plate), paired interradially. Dorsally, Ambb1 form distinct petaloid structure of frame (preservational feature; whereby dorsal surface of specimen has partially degraded away, allowing mouth frame to emerge through). Spines small, acicular, detached in mouth region ventrally just proximal of Ambb1.

*Madreporite.* Subcircular to oval (diameter 0.9 -1.2 mm), relatively flat lying, ventral, interradiial, adjacent to third and fourth Adambb.

*Extraxial plating.* Interradiial area of disc dorsally and ventrally with 27-30 ossicles per interradius (including InfMM but not SupMM). Interradiial ossicles large, subquadrate, convex, irregularly arranged, relatively numerous. Arms with five columns of ossicles dorsally. Carinals large, prominent, strongly convex dorsally, subrectangular to hexagonal, form distinctive perradiial column of approximately 12 ossicles. Adradials small, form column of less prominent ossicles on either side of carinals. SupMM large, prominent, strongly convex dorsally, subrectangular to hexagonal, form abradial column on either half of arm (approximately 12-13 per column), in line with primary interradiial. Primary interradiial hexagonal, wide (per.-ab.), slightly concave distally, not enlarged in relation to neighbouring SupMM. InfMM blocky, forming ambitus.

*Remarks.* The outer prominent column of marginals, forming the ambitus, are termed the InfMM. The intermediate column of prominent ossicles, in line with the primary interradiial are termed SupMM, following Spencer (1922) and Dean Shackleton (2005). The form does not show an axillary in line with the InfMM as there is no axil (Spencer and Wright 1966).

BMNH 40299 was originally described as *P. primaeva* (Forbes, 1848) by Salter (1857). Gregory (1899) erected *P. bonneyi* for this specimen, figuring it and assigning it as the holotype. Spencer (1922) reassigned the specimen to the existing *P. antiqua* (Hisinger,



1837), although based on Spencer's specific character of the number of interradial ossicles, the form differs considerably from the holotype of *P. antiqua* (Mineralogical Museum, Copenhagen number 306; figured in Gregory 1899; Spencer 1922) from the Ludlow Series of Gotland. In order to attempt to ascertain if this character is in fact a result of ontogeny, the arm length and disc radius of BMNH 40299 and the types of *P. primaeva* and *P. antiqua* were compared. The lectotype of *P. primaeva* (CAMSM A5509) is of the same size as BMNH 40299 (both specimens:  $R=13$  mm,  $r = 5$  mm), and yet still shows considerably fewer interradial ossicles (*c.* 20 less per interradius), suggesting that this is not an ontogenetic feature. However, the holotype of *P. antiqua*, with its increased number of interradial ossicles (*c.* 50-60 per interradius) is larger than BMNH 40299, (*P. antiqua* holotype:  $R = 16$  mm,  $r = 10$  mm), which may suggest that the increased number of interradial ossicles in relation to BMNH 40299 is a result of ontogenetic variation. The disc radius of the holotype and the number of interradial ossicles are both approximately twice that of BMNH 40299. BMNH 40299 is tentatively retained with the species. If the specimen is retained within the taxon, then a palaeogeographical range from Baltica to Avalonia (*c.* 19° S to 25° S; Bassett *et al.* 1992; Smethurst *et al.* 1998) can be inferred for the species.

*Occurrence.* From the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK.

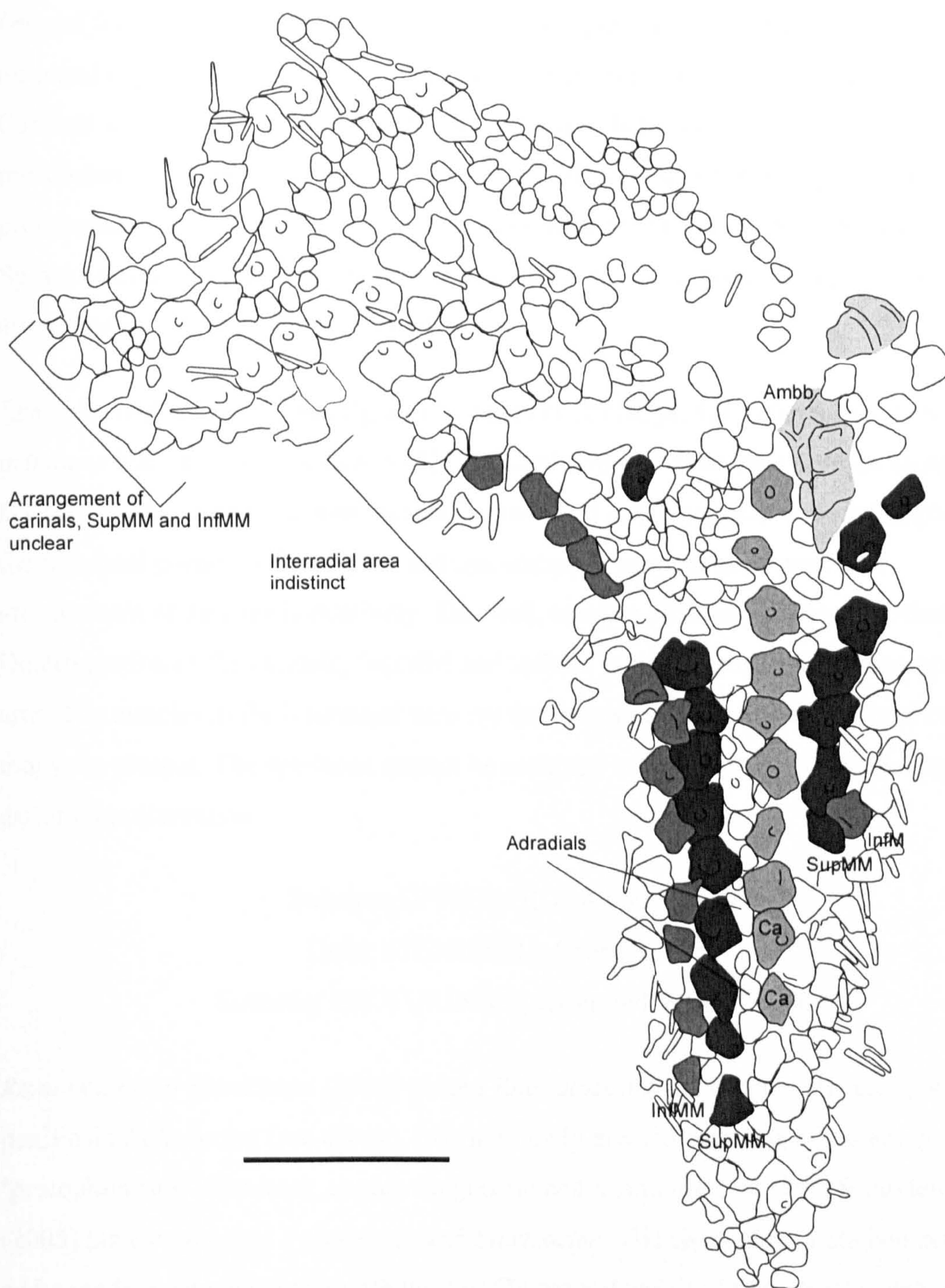
*Palasterina* sp.

Plate 3.6, figures 3-4; Text-figure 3.9

- v. 1916 *Palasterina primaeva* (Forbes, 1848); Spencer, pl. 4, figure 6.
- vp. 1922 *Palasterina antiqua* (Hisinger, 1837); Spencer, pp. 232-234 (*pars*), text-figure 158b.
- vp. 1965 *Palasterina antiqua* (Hisinger); Owen, p. 562 (*pars*).

*Material.* BMNH 40301, external mould of dorsal surface (Spencer 1922, text-figure 158b, pl. 4, figure 6). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.





TEXT-FIG. 3.9. Camera lucida drawing of *Palasterina* sp. (BMNH 40301). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. View of entire incomplete specimen in dorsal view, showing carinals, SupMM and InfMM. Dorsal surface of Ambb in proximal arm are visible. Based on specimen shown in plate 3.6, figures 3-4. Scale bar represents 5 mm.



*Description*

*Overall form.* Arms long ( $R = 26$  mm,  $r = 8$  mm), gradually tapering. Abactinals arranged in prominent columns along arms, comprising carinals, SupMM and InfMM. Carinals and SupMM relatively large, pentagonal to hexagonal, with dorsal protuberance (probably for spine attachment). InfMM smaller, possibly with dorsal protuberance. Adradials small, form less prominent column on either side of carinals. Spines acicular, small, not preserved articulated to ossicles, occur along margins of arms. Interradial area relatively small.

*Remarks.* BMNH 40301 was figured by Spencer (1916; pl. 4, fig. 6) as *Palasterina primaeva* but was later (Spencer 1922) included within *Palasterina antiqua* along with BMNH 40299. Only the dorsal surface is preserved and the specimen is incomplete; the proximal portions of two arms and one complete arm are preserved. The arrangement of ossicles is relatively disturbed, causing difficulty in identification. Determination of the carinals, SupMM and InfMM is not possible on the incomplete arm. The ossicles in the interradial area are unclear, so it cannot be determined how many are present. The specimen cannot be assigned to a species due to its incomplete, distorted preservation.

Subclass OPHIUROIDEA Gray, 1840

Order STENURIDA Spencer, 1951

Suborder PROTURINA Spencer and Wright, 1966

*Remarks.* Dean Shackleton (2005) placed *Rhopalocoma* and *Sturtzaster*, along with the paxilloid *Palasterina* (see above), into her newly erected eopentaroids, stem group ‘protophiuroids’. However, certain diagnostic characters used by Dean Shackleton (2005) are equivocal in *Palasterina* and *Sturtzaster*. The characters of stellate actinals and a madreporite in contact with the InfMM are not present in *Sturtzaster*; the genus does not have InfMM or discernible actinals. I have therefore retained the classification of Spencer and Wright (1966) awaiting further study.



## Family PRADESURIDAE Spencer, 1951

*Type genus. Pradesura* Spencer, 1951, by original designation.

## Genus STURTZASTER Etheridge, 1899

- 1857 *Palaeocoma* n. g.; Salter, pp. 324, 327 (name preoccupied).
- 1862 *Palaeocoma* Salter; Wright, pp. 29-30.
- 1886a *Palaeocoma* Salter; Stürtz, p. 96.
- 1886b *Palaeocoma* Salter; Stürtz, p.96.
- 1890 *Palaeocoma*; Stürtz, p. 246.
- 1893 *Palaeocoma* Salter; Stürtz, pp. 45, 62.
- 1899 *Sturtzaster*; Etheridge, p. 129.
- 1914 *Stürtzaster* Etheridge; Schuchert, pp. 5, 8, 29, 40.
- 1915 *Stürtzaster* Etheridge; Schuchert, pp. 252-253.
- 1940 *Sturtzaster* Etheridge; Spencer, pp. 513-517.
- 1957 *Erinaceaster* Lehmann; n. gen.
- 1966 *Stuertzaster* Etheridge; Spencer and Wright, p. U80.
- 1998 *Stuertzaster* Etheridge; Bartels *et al.*, p. 221.
- 2005 *Stuertzaster* Etheridge; Dean Shackleton, p. 74.

*Type species. Palaeocoma marstoni* Salter, 1857, by subsequent designation of Schuchert (1914), from Upper Silurian of Leintwardine, Herefordshire, UK.

*Diagnosis.* Pentagonal. Arms five, relatively short and broad. Disc large, circular. Ambb alternating, with T-shaped or L-shaped ridge and shallow podial basins ventrally. Amb1 ventrally subtriangular to radially elongated. Adambb ventrally with thickened marginal edge. Marginals absent. Disc with meshwork of radiate abactinals. Madreporite, when present ventral. Spines acicular, arranged in dense fringe along arm margins (emended after Spencer and Wright 1966 and Dean Shackleton 2005).

*Remarks.* Three species were erected by Salter (1857): *Sturtzaster marstoni*, *Sturtzaster colvini* and *Sturtzaster cygnipes*, all from Leintwardine, Herefordshire. Salter distinguished the former two on relative spine length, *S. colvini* possessing longer spines. *S. cygnipes* was distinguished primarily on its more slender and longer arms. I do not consider this character to be reliable in specific diagnosis. A specimen



showing three individuals labelled as *S. cygnipes* has been studied (BGS GSM37357); species assignment cannot be carried out due to the extremely poor preservation. Spencer (1940) recognized a fourth species, *Sturtzaster spinosissimus* (Roemer, 1863), distinguished from *S. marstoni* by relatively longer spines in the dorsal surface, but did not recognise *S. cygnipes*. Spencer (1940) described the specimen labelled as *S. cygnipes* in the BGS collections (GSM37357) and noted its poor preservation adding that it is probably *S. colvini*. Along with *S. spinosissimus*, Bartels *et al.* (1998) also recognised *Sturtzaster giganteus* and *Sturtzaster tenuispinosus* from the Hunsrück Slate of Germany.

*Sturtzaster*, along with the other taxa united within the suborder Proturina, is regarded in the literature to contain an intermediate column of axial plates between the Ambb and Adambb, the SubLL (Spencer 1940; Spencer and Wright 1966; Kesling 1982). SubLL have not been identified in *S. colvini* and are only identified tentatively in *S. marstoni*; no material has been examined which clearly and unequivocally exhibits their morphology. Within the other two Leintwardine taxa of the suborder, *Rhopalocoma* and *Bdellacoma*, the SubLL are more clearly exhibited and suggest the presence of such an intermediate plate in these genera.

The genus is spelt *Sturtzaster*, following Etheridge's (1899) original spelling, as in accordance with article 32 of the International Code of Zoological Nomenclature, there is no clear evidence of an inadvertent error. Etheridge's (1899) consistent spelling of the genus without an umlaut, named after Dr. B. Stürtz, suggests this spelling was deliberate; there is no clear evidence to suggest that an inadvertent error had taken place, and therefore no reason to alter the name to *Stuertzaster* as undertaken by Spencer and Wright (1966).

### *Sturtzaster marstoni* (Salter, 1857)

#### Plates 3.7-8; Text-figure 3.10

- \* 1857 *Palaeocoma Marstoni* n. sp., Salter, p. 328, pl. 9, figs 3a-c.
- . 1862 *Palaeocoma Marstoni* Salter; Wright, p. 30, text-fig. 17.
- . 1867 *Palaeocoma Marstoni* Salter; Murchison, p. 127, text-fig. 21.3.
- 1873 *Palaeocoma Marstoni*, Salter; Salter, p. 163.

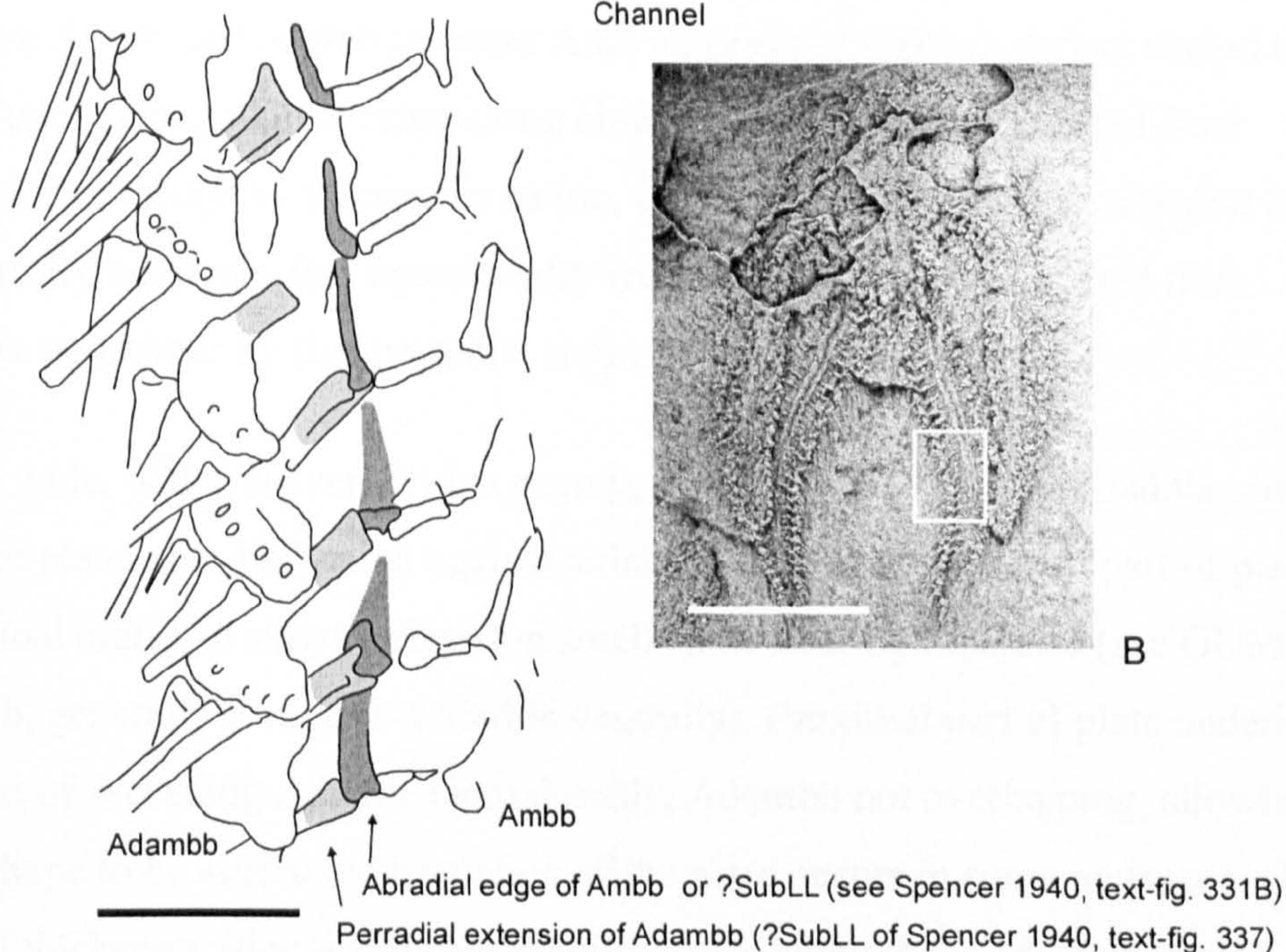
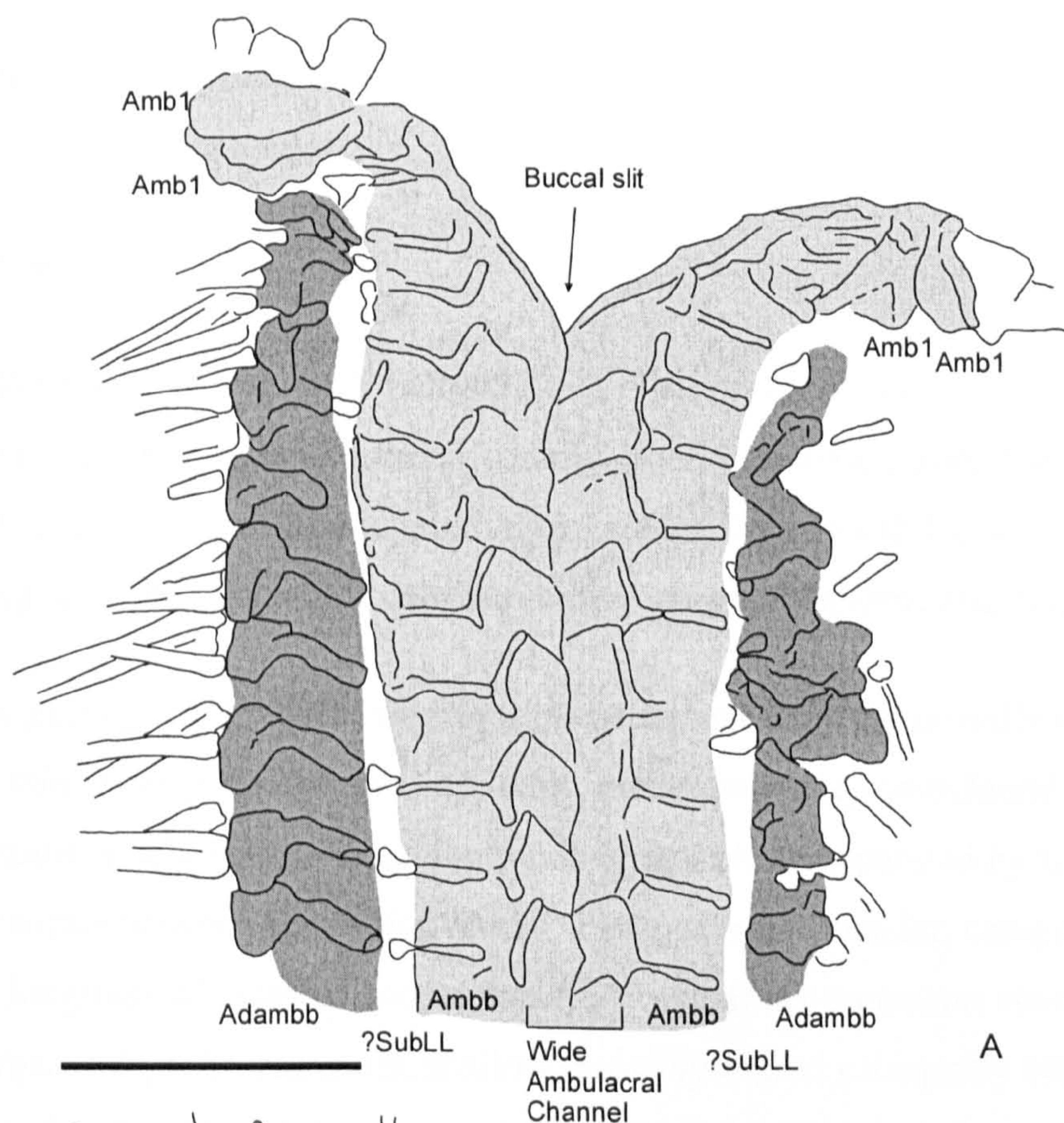


- . 1876 *Palaeocoma Marstoni*; Quenstedt, pl. 92, fig. 43.
- 1878 *Palaeocoma Marstoni* Salter; Salter, p. 117.
- . 1884 *Palaeocoma Marstoni*; La Touche, pl. 17, fig. 541 (cop. Murchison 1867).
- 1886a *Palaeocoma Marstoni* Salter; Stürtz, pp. 91-92.
- 1890 *Palaeocoma Marstoni* Salter; Stürtz, p. 207.
- 1914 *Stürtzaster marstoni* (Salter); Schuchert, pp. 29, 40.
- 1915 *Stürtzaster marstoni* (Salter); Schuchert, p. 253.
- v. 1940 *Sturtzaster marstoni* (Salter); Spencer, pp. 518-521, text-figs 334, 337-338, pl. 33, fig. 3, pl. 34, figs 1-2, pl. 35, fig. 3, pl. 37, fig. 6.
- 1951 *Sturtzaster marstoni* (Salter); Spencer, p. 95, text-fig. 5 (cop. Spencer 1940).
- v. 1965 *Sturtzaster marstoni* (Salter); Owen, p. 547.
- v. 1966 *Stuertzaster marstoni* (Salter); Spencer and Wright, p. U80, text-figs 68. 1a-e (cop. Spencer 1940).
- 1982 *Sturtzaster marstoni* (Salter); Blake, p. 169, text-fig. 1a (cop. Spencer 1940).
- v. 2005 *Stuertzaster marstoni* (Salter); Dean Shackleton, p. 75, pl. 5, figs 5-6.

*Neotype*. MM L4383, designated by Spencer (1940) p. 518, (Spencer 1940, text-fig. 337, pl. 34, fig. 2). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK; not located.

*Additional material*. Casts made of about 150 specimens (some accession numbers contain assemblages of specimens): BMNH E 1299, E 2593 (Spencer 1940, pl. 33, 'var. *nana*'); E 13144, E 13948 (Spencer 1940, pl. 37), E 13949, E 54157, 47995, BGS GSM6517 (Spencer 1940, pl. 35); CAMSM A37207, OUM C.517, C.17040-43, C.17046-51, C.17054, C.17056-57, C.17059-61, C.17064, C.17068, C.17070-71, C.17073-75, C.17077-86, C.17088-90, C.17093, C.17094, C.17097-98, C.17101, C.17103-04 (part & counterpart); C.17123, C.17128, C.17132-33, C.20219, C.30631a-b (part & counterpart of two specimens); C.30632-33, IPSMG R92529119, R9252921, NMVP 11412-6, NMVP 26176, NMVP 74317, CH210, CH258. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. Approximately 140 further specimens from Leintwardine are housed in the OUM, BMNH, BGS, NMS, CAMSM and LEIUG collections.





TEXT-FIG. 3.10. Camera lucida drawings of ventral surface of *Sturtzaster marstoni* (Salter, 1857). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, view of mouth frame and proximal part of arm (OUM C.30631a; specimen '1'); also refer to plate 3.7, figure 3; scale bar represents 2 mm. B, detail of ventral arm ossicles, showing inferred position of SubLL as identified by Spencer (1940) for the species (e.g. Spencer 1940, text-figs 331B, 337) (OUM C.30631b; specimen '2'); SubLL are not likely to be present and these 'plates' are likely to be the abradial extremities of the Ambb or the perradial portions of the Adambb; position of detail is shown on photograph; scale bar on drawing represents 1 mm, and that on photograph represents 10 mm.



*Diagnosis.* Spines along arm margins of moderate length. Ambulacral channel open, wide. Ambb ventrally with T-shaped ridge. Amb1 subquadrate dorsally, subtriangular ventrally. Madreporite absent.

### *Description*

*Overall form.* Pentagonal (BGS GSM6517:  $R = 16$ ,  $r = 8$ ). Arms five, relatively short and wide proximally, rapidly tapering distally, poorly separated from disc. Disc large, extensive, reaching considerable interrarial distance from mouth frame. Ambb slightly alternating, unfused. Acicular spines numerous, marginal on arms and disc.

*Axial arm plating.* Ambb wide, slightly alternating, overlapping, dorsally subquadrate, ventrally with T-shaped ridge and with wide, moderately deep ambulacral channel between transversely neighbouring longitudinal cross bars, separated by zigzag perrarial suture between alternating Ambb. T-shaped ridge slender, comprising a perrarial longitudinal crossbar and an abradially extending transverse stem. Podial basins large, wide, subrectangular, shallow, possibly shared subequally between successive Ambb (although transverse Amb sutures not visible), do not extend laterally onto Adambb. Longitudinal ridge along abradial edge of Amb separated from transverse Amb ridge by fracture or suture, demarcates lateral extent of podial basin. Amb dorsally relatively flat, occasionally with perrarial ridge, separated from transverse neighbour by fine perrarial suture (BGS GSM6517).

Adambb wide, with transverse ridge passing abradially into marginal saddle-shaped portion of plate, abradially abut against axial ossicles. Saddle-shaped part of plate with longitudinal marginal ridge; exhibiting small spine-bearing tubercles (see OUM C.30631b, generally four to five visible ventrally). Proximal part of plate underlain by distal part of preceding Adamb. Occasionally, Adambb not overlapping, allowing their overall shape to be ascertained; rotation of the plate occurs in some instances whereby the distal thickened ridge is directed longitudinally along the edge of the arm. Spines of moderate length (OUM C.30631a, specimen '1': 2.5 mm), greater than twice Adamb length, acicular, attached to distal face of Adambb, numerous along arm margin.

*Mouth frame.* Petaloid, composed of five pairs of Amb1, Amb2 and Amb3. Amb1 dorsally small and subquadrate, ventrally subtriangular, paired interradially. Amb2 and



Amb3 perradial, dorsally subquadrate, similar in size to succeeding Ambb of arm, bordered perradially by elongate ridge (thickened adradial extension of Amb1 and Amb2); ridge of either half of arm forms distinctive V-structure. Ambb1 and 2 strongly diverging, separated by wide buccal slit.

*Madreporite.* Not known.

*Extraxial skeleton.* Absence of actinals and marginals. Abactinals spicular, radiate (triradiate to quadradiate), with central tubercle for spine attachment, form dense meshwork covering dorsal surface of disc and arms.

*Remarks.* Spencer (1940) identified SubLL intermediately positioned between the Ambb and Adambb. The arrangement shown in Spencer's text-figure 337 (MM L4383, specimen not located) appears to be misleading; analysis of this morphology shows that the transverse ridge that appears to be identified as a SubL is in actual fact the perradial part of the Adamb, indicating that they are not separate plates (e.g. see BMNH E13948, OUM C.30631b; Text-fig. 3.10B). However, the plate arrangement shown in Spencer's text-figure 331B (undetermined specimen) is a relatively accurate representation of the plate arrangement seen in the studied specimens (compare with OUM C.30631a-b). None of the specimens analysed here clearly shows the plate arrangement intermediate of the Ambb and Adambb and there remains uncertainty over whether these SubLL are in fact the abradial edge of the Ambb. Dean Shackleton (2005) stated that SubLL ('podial plates' in her terminology) are absent in *Sturtzaster marstoni*. SubL plates are not present in the other British species of the genus, *Sturtzaster colvini* (Text-fig. 3.11).

The abactinals of the dorsal extraxial skeleton are occasionally preserved on the ventral surface, such as within the mouth frame, where the overlying dorsal surface has pressed through onto the ventral surface.

*Occurrence.* Known only from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK: Church Hill.



*Sturtzaster colvini* (Salter, 1857)

Plates 3.9-10; Text-figure 3.11

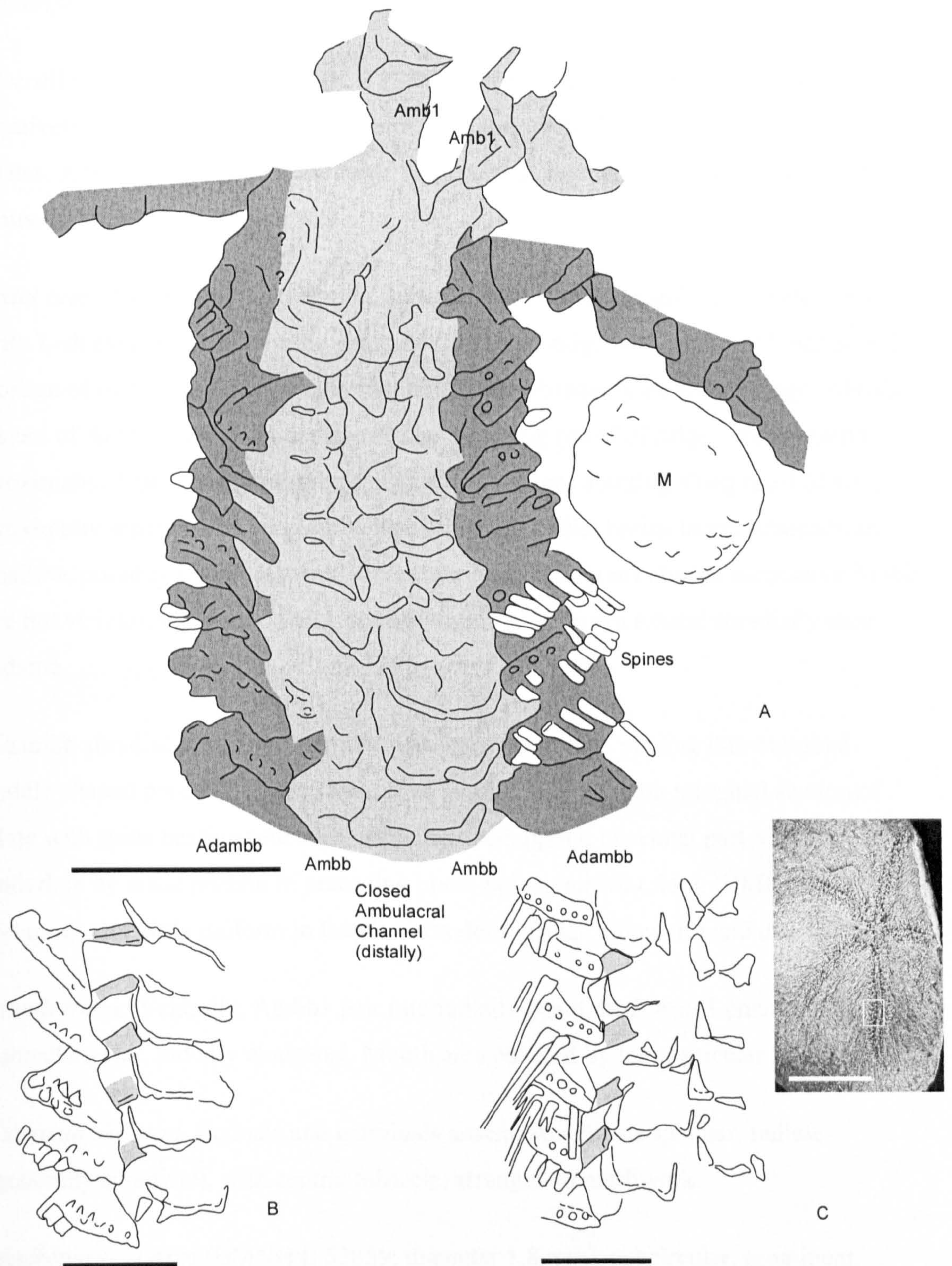
- \* 1857 *Palaeocoma Colvini* n. sp., Salter, pp. 328-329.
- 1862 *Palaeocoma Colvini*, Salter; Wright, p. 30.
- . 1867 *Palaeocoma Colvini*; Murchison, p. 127, text-fig. 21. 4.
- 1878 *Palaeocoma Colvini* Salter; Salter, p. 117.
- . 1884 *Palaeocoma Colvini*; La Touche, pl. 17, fig. 542 (cop. Murchison 1867).
- 1914 *Stürtzaster colvini* (Salter); Schuchert, pp. 29, 40.
- 1915 *Stürtzaster colvini* (Salter); Schuchert, p. 253.
- v. 1940 *Sturtzaster colvini* (Salter); Spencer, pp. 521-525, text-figs 335, 339, 349, pl. 35, figs 1-2, pl. 37, fig. 7.
- v. 1965 *Sturtzaster colvini* (Salter); Owen, p. 547.
- v. 1966 *Stuertzaster colvini* (Salter); Spencer and Wright, p. U80, text-figs 68. 1f-h (cop. Spencer 1940).

*Neotype.* BMNH E 52859, designated by Spencer (1940) p. 521, (Spencer 1940, text-fig. 339, pl. 35, fig. 1, pl. 37, fig. 7). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. Salter's (1857) holotype not identified. Spencer (1940) assigned both BMNH E 52859 and E 20648 as neotypes; Owen (1965) subsequently questioned this, designating the former specimen as the neotype.

*Additional material.* BMNH E 1479, E 13950, E 20648 (Spencer 1940, text-fig. 340b, pl. 35, fig. 2); OUM C.16843, C.16848, CH215. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Diagnosis.* Spines along arm and disc margin long, form dense fringe. Ambulacral channel closed along most of arm axis. Ambb ventrally with L-shaped ridge. Amb1 subrectangular, radially long. Madreporite present.





TEXT-FIG. 3.11. Camera lucida drawings of ventral surface of *Sturtzaster colvini* (Salter, 1857). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, view of proximal portion of arm and mouth frame, showing large madreporite and distal closed ambulacral channel; based on specimen shown in plate 3.9, figures 1-2; scale bar represents 2 mm (BMNH E 52859; neotype). B-C, detail of arm ossicles, showing inferred position of SubLL as identified by Spencer (1940) for the species (e.g. Spencer 1940, text-fig. 339); SubLL are not likely to be present and these 'plates' are likely to be adradial portions of the Adambb; scale bars on drawings represent 1 mm, that on photograph represents 10 mm. B, based on specimen shown in plate 3.9, figure 6 (CH215). C, position of ossicles shown in photograph (BMNH E 13950).



*Description*

*Overall form.* Pentagonal (BMNH E 13950:  $R = 17.2$  mm,  $r = 7.6$  mm). Arms five, relatively narrow (BMNH E 13950: proximal arm width 2.5 mm), with two columns of plates: Ambb and Adambb. Disc large. Spines long, acicular, marginal on disc and arms, forming dense fringe.

*Axial arm plating.* Ambb alternating, subquadrate to subrectangular and wide dorsally, with L-shaped and slender ridge ventrally. L-shaped ridge with perradial longitudinal portion of ridge passing abradially into transverse, abradially extending ridge. Abradial extent of Amb occasionally demarcated by sweeping round of ridge, which extends proximally. Transversely neighbouring perradial ridges abutting along most of arm, proximally separated by wide ambulacral channel. Podial basins large, subquadrate, shallow, possibly shared between successive Ambb (sutures between successive Ambb are not visible), bordered on all sides by Amb ridges, do not extend abradially onto Adamb.

Adambb abradial of Ambb, ventrally with transverse ridge passing into marginal saddle-shaped portion of plate. Thickened longitudinal ridge on marginal section of plate with spine bearing tubercles. Adambb overlapping; proximal part of plate underlain by distal portion of preceding plate. Spines acicular, long (BMNH E 20648: 3-4 mm), relatively uniform in length, form dense fringe along arm and disc margin.

*Mouth frame.* Ventrally, Ambb1 pair interradially positioned. Amb1 enlarged, subrectangular, radially elongated. Mouth area covered by long, acicular spines.

*Extraxial skeleton.* Actinals and marginals absent. Abactinals spicular, radiate (generally triradiate), with central tubercle, arranged in meshwork.

*Madreporite.* Large (BMNH E 52859: diameter 1.8 mm), subcircular, prominent, ventral, interradiial and proximally located.

*Remarks.* Ventrally, the arms are relatively narrower than in *S. marstoni*, and do not show such a pronounced distal tapering. Dorsally, the arm width and tapering are more in common with *S. marstoni* (e.g. BMNH E 20648). Spencer (1940) noted the difference in relative arm width between the species; he remarked that this might be a



post mortem feature and not a true representation of the specific characters. I concur with Spencer and this character is not retained as a diagnostic character.

Salter (1857) distinguished the two species on the basis of relative spine length, *S. colvini* possessing relatively longer spines. This is clearly exhibited by specimen BMNH E 20648 (Pl. 3.10, figs 4, 6). Spencer (1940) differentiated *S. colvini* on the possession of a closed ambulacral channel. This generally appears to be the case with this taxon, although as previously mentioned this may be variable; proximally, a wide ambulacral channel is present between the longitudinal ridges of transversely adjacent Ambb (e.g. BMNH E 13950, BMNH E 52859, CH215; Text-fig. 3.11A; Pl. 3.9, figs 2, 4). A large, pronounced madreporite is also characteristic of the species (e.g. BMNH E 52859, OUM C.16848, CH215); no madreporite has been observed in *S. marstoni*.

Detail of the mouth frame is difficult to discern, owing to poor preservation and the area being obscured by long acicular spines. Spencer (1940) noted that the mouth frame is generally of a relatively smaller diameter than that of *S. marstoni*; however, this is not conclusive, and may vary depending on the relative gape of the mouth and the degree to which it is exposed. The first Ambb are reasonably clear in ventral view, though, and appear to be more radially elongate than those of *S. marstoni* (BMNH E 52859, CH215; Pl. 3.9, figs 4-5).

Spencer's (1940) and Spencer and Wright's (1966) distinction of SubLL and Adambb does not appear to remain true in *S. colvini*; no SubLL have been identified by myself in the species. Spencer's (1940) description of the species mentioned SubLL, stating that the plates are only intermittently visible where the Adambb have swung outwards (dorsally and abradially). He also figured the SubLL in his text-figure 339, although the plates are in fact part of the Adambb (specimen BMNH E 52859; Text-fig. 3.10A); the transverse adradial ridge of the Adambb, directly abutting the Amb was incorrectly identified by Spencer as the SubL. Specimen BMNH E 52859 does not give particularly clear views of this ventral plating; however, specimens BMNH E 13950 and CH215 clearly show that SubLL are absent (Text-fig. 3.11B-C). Spencer and Wright (1966, text-fig. 68.1f) reproduced the figure of the neotype, again incorrectly identifying SubLL, labelling part of the Ambb as these plates.



Specimens OUM C.16843 and C.16848 are assigned to the species, the former only tentatively due to poor preservation. Both specimens show relatively narrow arms in comparison to *S. marstoni*. OUM C.16848 has a large pronounced madreporite (diameter 2.1 mm) and distally Ambb are not separated by an open ambulacral channel. A newly collected specimen, CH215, is the only example of the species with part and counterpart preserved; the ventral surface is particularly well preserved, showing the diagnostic characters (Pl. 3.9, figs 3-6; Pl. 3.10, figs 1-2, 5).

*Occurrence.* Known only from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire: Church Hill.

#### Family RHOPALOCOMIDAE Spencer and Wright, 1966

*Type genus.* *Rhopalocoma* Salter, 1857, by original designation.

#### Genus RHOPALOCOMA Salter, 1857

- 1857 *Palaeocoma* (*Rhopalocoma*) n. g.; Salter, pp. 324-325.
- 1863 *Palaeocoma* (*Rhopalocoma*) Salter; Wright, p. 31.
- 1886a *Rhopalocoma*; Stürtz, p. 96.
- 1893 *Rhopalocoma* Salter; Stürtz, pp. 46, 63.
- 1914 *Rhopalocoma* Salter; Schuchert, pp. 5, 8, 29, 37.
- 1915 *Rhopalocoma* Salter; Schuchert, pp. 252, 254.
- 1940 *Rhopalocoma* Salter; Spencer, pp. 534-539.
- 1966 *Rhopalocoma* Salter 1857; Spencer and Wright, p. U81.
- 2005 *Rhopalocoma* Salter; Dean Shackleton, p. 73.

*Type species.* *Palaeocoma* (*Rhopalocoma*) *pyrotechnica* Salter, 1857, by original designation, from the Ludlow Series, Upper Silurian of Leintwardine.

*Diagnosis.* Pentagonal. Arms five, wide, short and blunt. Disk large, nearly reaching arm tips. Ambb alternating, ventrally with L-shaped ridge. SubLL present, wide. Adambb ventrally with T-shaped ridge. InfMM cylindrical. Abactinals stellate. Spines large, distally widening, widely grooved. Adammb spines relatively slender. Abactinal and InfM spines may be club-shaped (emended after Spencer and Wright 1966 and Dean Shackleton 2005).



*Remarks.* Salter (1857) erected *Rhopalocoma* as a subgenus of *Palaeocoma* Salter, 1857. *Rhopalocoma* has since been assigned to generic status by Stürtz (1893). The generic diagnosis is based primarily on the possession of large club-shaped spines on the dorsal surface and margin. The genus is monospecific.

*Rhopalocoma pyrotechnica* Salter, 1857

Plates 3.11-12; Text-figure 3.12

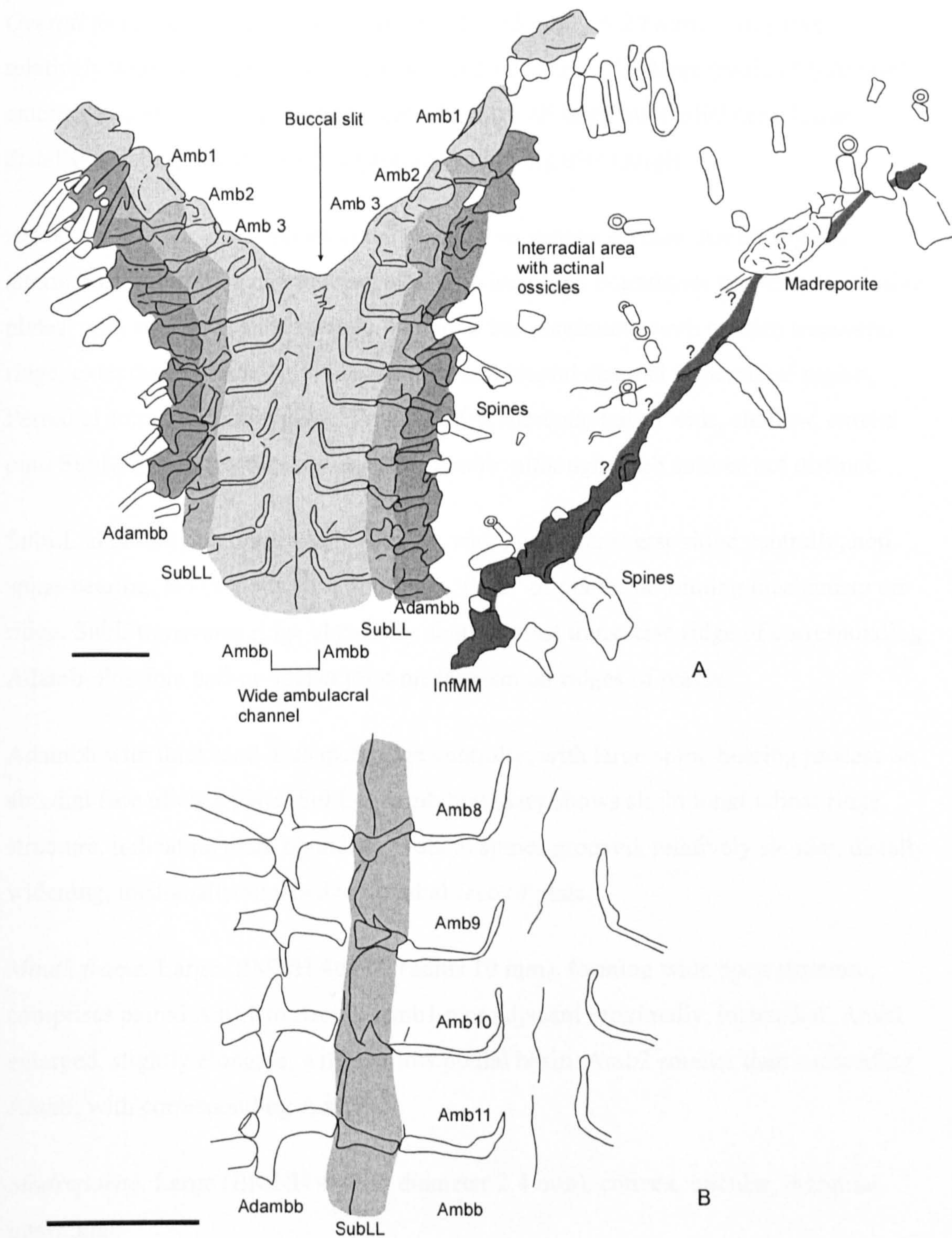
- \* 1857 *Palaeocoma (Rhopalocoma) pyrotechnica*, n. sp., Salter, pp. 329-330.
- 1862 *Palaeocoma (Rhopalocoma) pyrotechnica* Salter; Wright, p. 31.
- 1878 *Rhopalocoma pyrotechnica* Salter; Salter, p. 117.
- 1914 *Rhopalocoma pyrotechnica* Salter; Schuchert, p. 37.
- 1915 *Palaeocoma (Rhopalocoma) pyrotechnica* Salter; Schuchert, p. 254.
- v. 1940 *Rhopalocoma pyrotechnica* Salter; Spencer, pp. 539-540, text-figs 331-332, 335e, 336, pl. 36, figs 1-2.
- v. 1965 *Rhopalocoma pyrotechnica* Salter; Owen, p. 546.
- v. 1966 *Rhopalocoma pyrotechnica* Salter; Spencer and Wright, p. U81, text-figs 68. 2a-c (cop. Spencer 1940).
- v. 2005 *Rhopalocoma pyrotechnica* Salter; Dean Shackleton, pp. 73-74, pl. 5, figs 3-4, text-figs 8A, 12F.

*Neotype.* BMNH 40293, designated by Spencer (1940), (Spencer 1940, text-figs 332 and 347, pl. 36, fig. 2). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Additional material.* BMNH E 5013a-b (part and counterpart; Spencer 1940, p. 539, text-fig. 335, text-fig. 346, pl. 36, fig. 1); E 13951 (counterpart to MM L11003); 40294, 40304, 46601, MM L11003, L11004, BGS GSM28823 (Spencer 1940, text-fig. 347); OUM C.17115a-b (part and counterpart); C.17290, C.27921, CH143. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Diagnosis.* As for the genus.





TEXT-FIG. 3.12. Camera lucida drawings of ventral surface of *Rhopalocoma pyrotechnica* Salter, 1857 (BMNH 40293; neotype). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, view of proximal portion of arm and interradial area, showing Ambb, SubLL, Adambb, InfMM and madreporite; ventral extent of InfMM is unclear. B, detail of arm plating, showing column of SubLL ossicles intermediate to Ambb and Adambb. Based on specimen shown in plate 3.11. Scale bars represent 2 mm.



*Description*

*Overall form.* Pentagonal (BMNH 40293: R = 33 mm, r = 20 mm). Arms five, relatively wide, short and blunt. Arm length 20-35 mm. Disc large (radius 11-20 mm), extensive, nearly reaching arm tips perradially, with large interrarial area. Large distally widening spines on dorsal surface and along disc margin.

*Axial arm plating.* Axial skeleton only visible on ventral surface. Ambb slightly alternating, wide, subquadrate ventrally, with indistinct boundaries between successive plates, with slender L-shaped ridge. Perrarial bar continuous with median transverse ridge, extending abradially. Wide, shallow ambulacral channel in perrarial region. Perrarial suture weakly zig-zag. Podial basins subrectangular, wide, shallow, extend onto SubLL, shared between successive Ambb; although Amb sutures not distinct.

SubLL abradially abutting against Ambb, wide, with transverse ridge ventrally, non spine-bearing. No obvious plate suture on 'floor' of plates, or jointing mechanism on ridge. SubL transverse ridge abradially abuts against transverse ridge of corresponding Adamb. Possible ball-or-socket joint mechanism on ridges of plates.

Adambb with thickened T-shaped ridge ventrally, with large spine-bearing process on abradial face of each plate. SubL-Adamb boundary shows slight longitudinal ridge structure, indicating plate boundary. Adamb spines grooved, relatively slender, distally widening, medianally attached to abradial face of plate.

*Mouth frame.* Large (BMNH 40293: radius 10 mm), forming wide open structure, comprises paired Amb1 to Amb4. Amb1 pair adjacent proximally, interrarial. Amb1 enlarged, slightly elongate, with shallow podial basin. Amb2 smaller than succeeding Ambb; with corresponding Adamb.

*Madreporite.* Large (BMNH 40293: diameter 2.4 mm), convex, circular, marginal, interrarial.

*Extraxial skeleton.* Actinals not clearly exposed, may be subpolygonal, some with circular hollow process for spine attachment. Spines of actinals relatively slender, distally widening. InfMM subquadrate to subcylindrical, arranged in single row along margin of disc, extend along entire margin, proximally separated from Adambb by



actinals, distally in contact with Adambb, show size decrease and marked overlapping perradially, with large circular process for spine articulation, each with large distally widening club-shaped spine. Spines of InfMM may show a wide groove, with small tubercles over ventral face. Dorsal surface covered by extensive extraxial skeleton; Ambb, SubLL and Adambb not visible. Abactinals stellate, relatively pronounced, with central circular process for spine attachment, each with distally widening spine. Spines of abactinals may be either large and club-shaped or small and slender, sometimes show a pronounced groove.

*Remarks.* The Leintwardine specimens are well preserved, although some skeletal detail is not easily determined. Some specimens are partially calcified (e.g. BMNH E 13951 and MM L11003 thereby inhibiting casting of parts of the skeleton); others show disturbance of skeletal components.

*R. pyrotechnica* (as with *Bdellacoma vermiformis*, *Sturtzaster marstoni* and *Sturtzaster colvini*) was described by Spencer (1940) as possessing two outer columns of axial plates, the ‘inner laterals’ (=SubLL) and ‘outer laterals’ (=Adambb). Existence of a separate column of Ambb and SubLL is suggested by the consistent point of separation of the transverse (SubL) ridge from the Amb ridge through the length of the arm (Text-fig. 3.12; Pl. 3.11, figs 3, 5). No obvious plate suture or jointing mechanism on the ridges is evident. Even so, these two sections of the ridge are regarded as two separate plates. Dean Shackleton (2005) also identified these plates terming them ‘podial plates’.

Specimen BMNH E 5013 shows thickened, blocky, distally widening spines with minute tubercles over their ventral convex edges, along its ventral arm margins (Pl. 3.12, figs 2-3, 6); these structures are not seen in the neotype or any other specimens.

*Occurrence.* From the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area (Church Hill, Martin’s Shell), Herefordshire, UK. Spencer (1940) also described a specimen (e.g. Kendal Museum, numbers 13 and 14; part and counterpart) from the Upper Silurian of the Lake District, although did not sufficiently figure any of this material to allow corroboration of this identification. His text-figure 336 shows part of the dorsal surface of the specimen, although it cannot be determined



from this if the specimen is *R. pyrotechnica*; no spines are evident in this illustration. This specimen has not been located.

### Family BDELLACOMIDAE Spencer and Wright, 1966

*Type genus. Bdellacoma* Salter, 1857, by original designation.

### Genus BDELLACOMA Salter, 1857

- 1857 *Palaeocoma* (*Bdellacoma*) n. g.; Salter, p. 324.
- 1862 *Bdellacoma* Salter; Wright, p. 31.
- 1886 *Bdellacoma* Salter; Stürtz, p. 96.
- 1890 *Bdellacoma* Salter; Stürtz, p. 246.
- 1893 *Bdellacoma* Salter; Stürtz, pp. 46, 63.
- 1914 *Bdellacoma* Salter; Schuchert, pp. 5, 8, 13, 29.
- 1915 *Bdellacoma* Salter; Schuchert, pp. 252, 254.
- 1940 *Bdellacoma* Salter; Spencer, pp. 525-528.
- 1966 *Bdellacoma* Salter; Spencer and Wright, p. U81.

*Type species. Palaeocoma* (*Bdellacoma*) *vermiformis* Salter, 1857, by original designation, from the Upper Silurian of Leintwardine.

*Diagnosis.* Arms five, very long, relatively wide. Disc small. Ambb alternating. SubLL present. Pedicellariae bivalved, roundedly subtriangular to short and wide, with process on either distolateral corner of valve, dorsally positioned in columns. Spines prominent, distally-widening, on dorsal surface or along ambulacral groove.

*Remarks.* Salter's (1857) main diagnostic character was the possession of short, 'clavate tubercles' on the dorsal surface; these are taken to be the squat, thick spines of Spencer (1940). These structures are interpreted as pedicellariae (Sutton *et al.* 2005), and were first described by Jones (1887) who named them *Bursulella* and interpreted them as ostracods. Boczarowski (2001) described similar material from the Devonian of Poland, interpreting them as echinoid pedicellariae. Salter (1857) and Spencer (1940) described the possession of pedicellariae as a useful generic/specific character for *Bdellacoma* however this is true only when taking other characters (i.e. alternating Ambb and distally-widening spines) into account as well. Small ossicles arranged in



columns along the dorsal surface of the rare Leintwardine stelleroid *Antiquaster magrumi* are similar, albeit smaller, to the pedicellariae in *Bdellacoma* (e.g. BMNH 40296). These ossicles are interpreted to also be pedicellariae. Their occurrence in at least two genera indicates that the possession of these structures alone may not be a useful discriminator.

Salter (1857) described the ambulacral groove of *Bdellacoma vermiformis* as being relatively broad, when compared with the commonly associated Leintwardine stelleroid *Sturtzaster*. The apparent SubL abradial plates are only evident in *B. vermiformis*; in *Bdellacoma* sp. recrystallisation has obscured the plate morphology (see Sutton *et al.* 2005, fig. 2b, g).

Two species are recorded, the type species from the Ludlow Series of Leintwardine and *Bdellacoma* sp. from the Wenlock Series of Herefordshire (Sutton *et al.* 2005).

Differences in spine morphology distinguish the species. *Bdellacoma* sp. possesses long, distinct, distally-widening, oar-like spines along the margin of the ambulacral groove; no such structures are readily apparent in *B. vermiformis* in this position.

Distally-widening, although less oar-like spines occur, densely arranged over the dorsal surface of both species. Pedicellariae shape is not felt to be a useful specific character due to the high variability observed in single specimens of *B. vermiformis* (e.g. NMS G1882651521). Pedicellariae shape observed in *Bdellacoma* sp. are comparable to some of those observed in *B. vermiformis*.

*Urasterella verruculosa* Lehmann, 1957 described from the Hunsrück fauna (Lehmann 1957, pp. 131-134; pl. 45, figs 1-3; pl. 46, figs 1-4) may in fact be a species of *Bdellacoma*; both possess a similar gross morphology of long, narrow arms along with short, wide pedicellariae-like structures (pers. obs. of Lehmann's figures and plates). However, plate arrangements have not been compared, so the exact affinity of *U. verruculosa* remains questionable.



*Bdellacoma vermiformis* Salter, 1857

## Plate 3.13; Text-figure 3.13

- \* 1857 *Palaeocoma (Bdellacoma) vermiformis*, n. sp.; Salter, p 324.
- 1862 *Bdellacoma vermiformis* Salter; Wright, p. 31.
- 1873 *Bdellacoma vermiformis* Salter; Salter, p. 163.
- vp. 1940 *Bdellacoma vermiformis* Salter; Spencer, pp. 525-529 (*pars*), pls. 36-37.
- vp. 1965 *Bdellacoma vermiformis* Salter; Owen, p. 548 (*pars*).
- v. 1966 *Bdellacoma vermiformis* Salter; Spencer & Wright, pp. U80-81, figs 2a-b (cop. Spencer 1940).

In prep. *Bdellacoma vermiformis* Salter; Lewis, Donovan & Crabb.

*Neotype*. NMS G1882651523, a complete specimen, designated by Spencer (1940), (Spencer 1940, text-fig. 341a, pl. 36, fig. 3). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

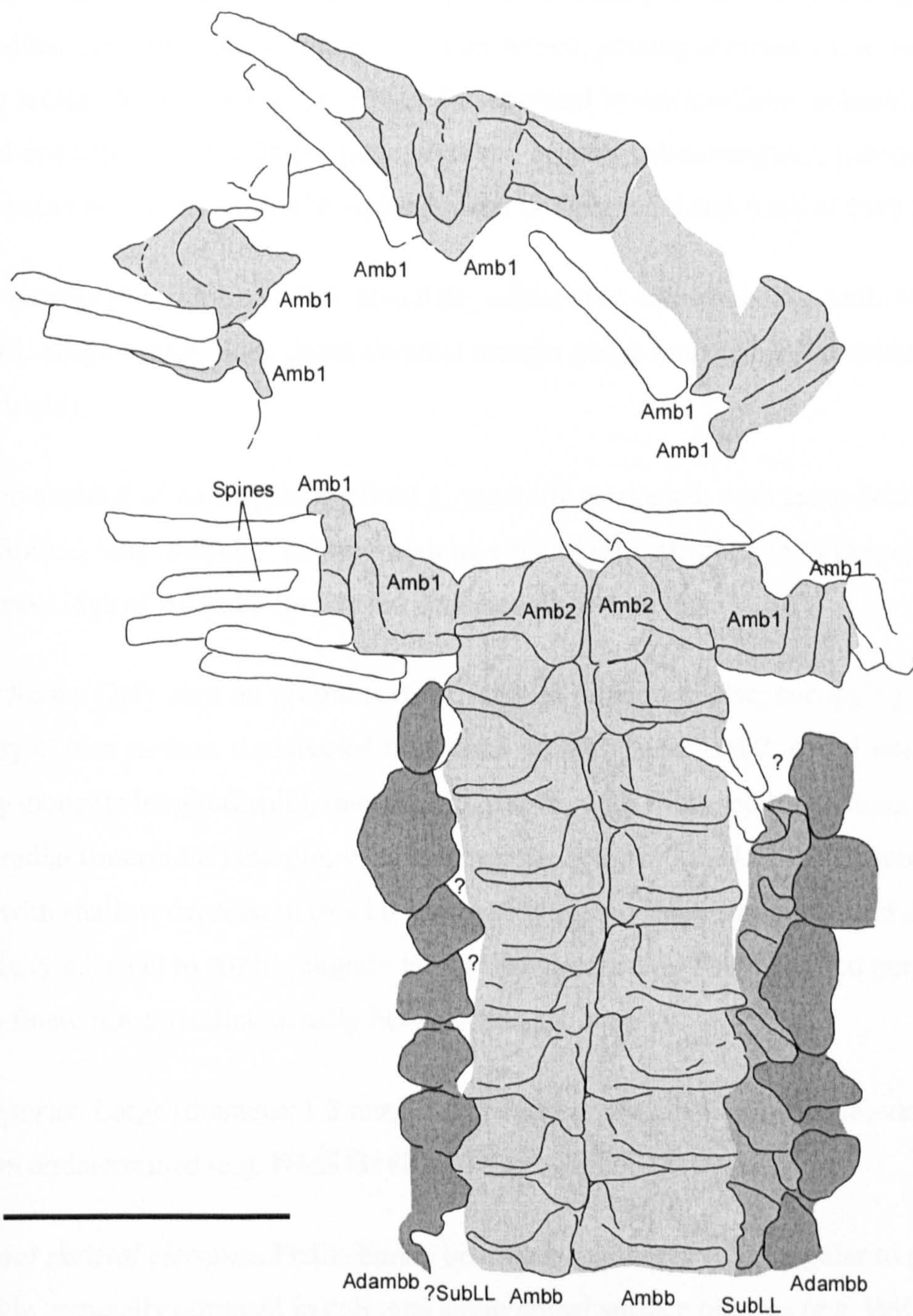
*Additional material*. 27 specimens: BMNH E 1254, E 1259, E 1480, E 13151, E 20243 (slab also contains *Furcaster leptosoma*), 38666, 40297 (Spencer 1940, text-fig. 335c, text-fig. 342b, pl. 37, fig. 8), 47952, OUM C.17106-10, C.17113, C.17117 (slab also contains *Sturtzaster marstoni*), C.17118-22, BGS GSM105646, NMS G1882651521, G1882651522, G1882651526, CH94, CH211, CH262. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

*Diagnosis*. Ambulacral groove without distally-widening, oar-like spines.

### *Description*

*Overall form*. Arms five, up to 45 mm long in neotype, relatively wide (due to transversely extensive Ambb and SubLL), highly distinct from disc. Disc small (NMS G1882651523: radius 1.8 mm). Three columns of axial plates: Ambb, SubLL and Adambb. Pedicellariae short, wide, highly distinctive with two small processes on distolateral corners. Spines on dorsal surface, widening distally.





TEXT-FIG. 3.13. Camera lucida drawing of ventral surface of *Bdellicoma vermiformis* Salter, 1857 (NMS G1882651523). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire. View of mouth frame and proximal part of arm, showing Ambb, SubLL and Adambb. Note absence of oar-like spines along ambulacral groove. SubLL are not clearly exposed along the left side of the arm. Based on specimen shown in plate 3.13, figure 1. Scale bar represents 2 mm.



*Arm plating.* Ambb alternating, ventrally subrectangular and wide (proximal Amb width 0.9 mm, arm width 2.7 mm in neotype), with broadly T- to L-shaped ridge, with longitudinal perradial ridge (crossbar of T) thickened; passing abradially into narrow distally located transverse ridge (neck of T), separated by narrow deep ambulacral channel and suture. Podial basins large, shallow, broadly subrectangular, subequally shared between successive Ambb with majority of basin on distal Amb of each pair.

SubLL narrow (0.5 x Amb width), abradially adjacent to corresponding Amb, with narrow L-shaped ridge along distal-abradial margin (ridge marks abradial extent of podial basin).

Adambb abradial of corresponding SubLL, medially thickened, with spine-bearing ridge. Spines, long, acicular, numerous along edge of arm, attached to thickened transverse ridge of Adambb (preserved detached from ossicles).

*Mouth frame.* Only seen on ventral surface, large in relation to disc; occupying majority of disc surface, constructed from pairs of Amb1 and Amb2. Amb1 enlarged, slightly elongate longitudinally, interradi ally paired, with L-shaped ridge along distal and abradial (interradial) margin, with long narrow spine attached to each interradial ridge, with shallow depression (podial basin) proximal to ridge structure. Amb2 perradially adjacent to Amb1, slightly larger than succeeding Ambb, paired perradially. Mouth frame not extending distally between second Ambb.

*Madreporite.* Large (diameter 1.5 mm), subcircular to slightly heart-shaped, ventral, position undetermined (e.g. NMS G1882651522, OUM C17109).

*Extraxial skeletal elements.* Pedicellariae bivalved, roundedly subtriangular to short and wide, generally arranged in columns along dorsal surface of arms (e.g. BMNH 38666), also on ventral surface lateral of ambulacral groove (NMS G1882651523), with serrated teeth structures along commissural margin of valves, apically bearing a long spine on each distolateral corner of valve, with paired spines diverging by an average of 54.8 degrees, with thickened ridge along distolateral margin of valves, with outer face of valves convex.



Spines long, of two types: acicular and distally widening. Acicular spines particularly numerous along lateral margins of arms. Distally-widening spines subcircular in cross-section proximally, gradually widen and ‘unwrap’ distally, broad at distal extremity, typically occur as dense covering over dorsal surface (BMNH E 1259, 38666, 47952), may occur ventrally around mouth frame (in neotype).

*Remarks.* The pedicellariae show considerable variability in outline, often within a single specimen; NMS G1882651521 shows a noticeable variability along the length of a single arm, with pedicellariae ranging from subtriangular to short and wide. Some pedicellariae appear slightly concave along their outer surface (e.g. see BMNH 40297), a feature that is likely to be due to compaction. In these cases the thickened distolateral margin of the valves is apparent.

Part and counterparts of *B. vermiformis* are restricted to CH94, a newly collected specimen. The specimen however shows considerable ossicle disturbance and fine plating detail of both surfaces is not readily apparent. Correlating certain specimens showing the dorsal and ventral surfaces is partially problematic. One of the main characters of the dorsal surface of *B. vermiformis*, the dense covering of distally-widening spines (described by Spencer 1940, as “fan-shaped”), are generally not evident on the ventral surface. All dorsal and ventral specimens show the pedicellariae-like structures. Some dorsal specimens (e.g. BMNH E 1259) show traces of the axial skeleton emerging through the extraxial skeleton, whereby the characteristic alternating Ambb are seen. The ventral morphology of the neotype shows some distally-widening spines around its mouth frame. BMNH 40297, which exhibits a clear view of the ventral surface, along with part of the dorsal surface compressed laterally, shows some likely examples of the diagnostic spines. Most spines on this example are broken away distally, although it can still be observed that some do in fact distally-widen. The characteristic dense covering is not evident on this example, the proximal portions of the spines form a relatively sparse covering.

Arm plating in the neotype and OUM C.17108 differs slightly from that seen in BMNH 40297. In the former two, the Ambb are overlapping one another slightly; presumably the position in life. Each Amb slightly dorsally overlaps its distal neighbour. This gives the appearance of the transverse portion of the ridges (neck of T) as being situated slightly distally on the plate (when in actual fact the distal portion of the plate is hidden



from view underneath the succeeding Ambb. The majority of the podial basin is also therefore seated on the distal of the two successive plates. BMNH 40297 shows plates in which the transverse ridge appears more median in position; the podial basins also appear more equally shared. This may be due to post-mortem relaxation of the connective soft tissue subsequent spreading apart of the Ambb.

*Occurrence.* From the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK: Church Hill & Martin's Shell quarries. Upper Silurian specimens are also documented from the Pentland Hills, Scotland and Lower Devonian specimens have been documented from the Bundenbach slates, Germany (Spencer, 1940). The non-Leintwardine material has not been re-examined (no accession details were provided by Spencer 1940), although due to the disparity in geographical and geological age provenance, the German material is doubtfully assigned to this species.

#### Suborder SCALARINA Hotchkiss, 1976

#### Family KLASMURIDAE Spencer, 1925

*Type genus.* *Klasmura* Ruedemann, 1916, by original designation.

#### Genus ANTIQUASTER Kesling, 1971

1971 *Antiquaster* n. gen.; Kesling, pp. 184, 187.

1976 *Antiquaster* Kesling; Hotchkiss, pp. 8-9.

*Type species.* *Antiquaster magrumi* Kesling, 1971, by original designation, from the Middle Devonian of Ohio.

*Diagnosis.* Arms five, long, parallel-sided. Disc small. Ambb opposing, narrow. SubLL present, wide. Adambb saddle-shaped, lacking enlarged spine-like processes. Buccal slit small. Ambb1 pronounced. Pedicellariae small, short, wide, with process on either distolateral corner, arranged in two columns on dorsal surface of arms Arm width : Mouth frame diameter ratio: 1.1-1.2 (emended after Kesling 1971 and Hotchkiss 1976).



*Remarks.* According to Hotchkiss (1976), *Antiquaster* Kesling, 1971 may only be distinguished from *Klasmura* Ruedemann, 1916, by its mouth frame. Measurements by Hotchkiss (1976) described the arm width : mouth frame diameter ratio of *Klasmura* as 0.6-0.8. In the type species of *Antiquaster*, *Antiquaster magrumi* Kesling, 1971, the ratio is 1.1-1.2, indicating a proportionally wider arm width, when compared to mouth frame diameter (Hotchkiss 1976). This character is possibly lacking in value as factors such as the relative gape of the mouth frame and how exposed it is from the rock matrix will affect its diameter. Until further material is recovered, generic assignment remains tentative.

Pedicellariae are described herein, within *A. magrumi*; whether or not they are present in *Klasmura* is uncertain. Hotchkiss (1976) did not describe such structures in *Klasmura*. However, Spencer (1927, p. 327) described “minute calcarerous granules” over parts of the dorsal surface of the disc and arms of a specimen of *Klasmura mirabilis* Ruedemann, 1916, figured by Ruedemann (1916, pl. 23, fig. 2). This specimen has not been studied and it is not possible from Ruedemann’s figure to determine whether these structures are pedicellariae.

*Antiquaster magrumi* Kesling, 1971

Plate 3.14, figs 1-5; Text-figure 3.14

v. 1940 *Bdellacoma vermiformis* Salter; Spencer, p. 529 (*pars*).

v\*. 1971 *Antiquaster magrumi* n. sp., Kesling, pp. 187-191, text-fig. 1, pls 1-4.

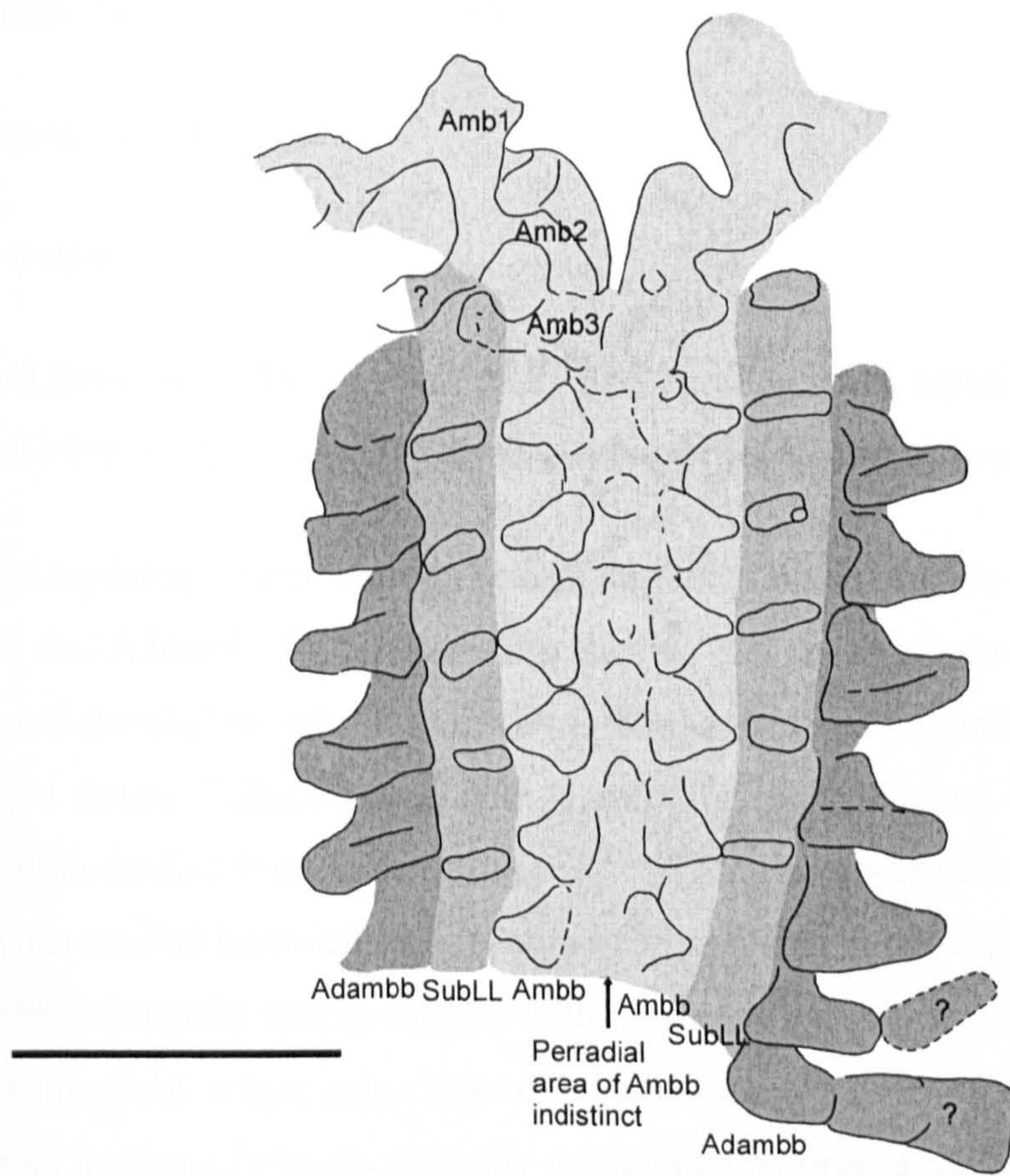
v. 1976 *Antiquaster magrumi* Kesling, 1971; Hotchkiss, pp. 8-9, ?pl. 8, fig. 4; pl. 9, fig. 1.

*Holotype.* UMMP 57863a, nearly complete specimen (Kesling 1971, pls 1-4). Silica Formation, Givetian Stage, Middle Devonian; Silica, Ohio, USA.

*Paratype.* UMMP 57863b, incomplete specimen. Silica Formation, Givetian Stage, Middle Devonian; Silica, Ohio, USA.

*Additional material.* BMNH 40296a-b (part and counterpart; Hotchkiss 1976, pl. 9, fig. 1). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.





TEXT-FIG. 3.14. Camera lucida drawing of ventral surface of *Antiquaster magrumi* Kesling, 1971 (BMNH 40296b). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. View of mouth frame and proximal part of arm, showing Ambb, SubLL and Adambb. Note poorly preserved spine-like processes on Adambb 9-10. Based on specimen shown in plate 3.14, figures 1, 3. Scale bar represents 1 mm.



NYSM 13227 (Hotchkiss 1976, pl. 8, fig. 4). Ludlowville Formation, Middle Devonian; Danby, New York, USA. Not located.

*Diagnosis.* As for the genus.

### *Description*

*Overall form.* Arms five, distinct from disk, parallel-sided, tapering distally. Disk small (BMNH 40296: disc radius 0.8 mm). Ambulacral groove shallow.

*Axial arm plating.* Only seen on ventral surface. Three columns of axial plates: Ambb, SubLL and Adambb. Ambb opposing, narrow, composed of perradial longitudinal ridge and abradial broadly T-shaped ridge, separated from opposing Amb by faint perradial suture. T-shaped ridge with longitudinal portion (cross bar of T) perradial and short, with median transverse ridge (neck of T) abradial and narrow. SubLL wide (per.-ab.), with median transverse ridge, abradially adjacent to corresponding Ambb. Adambb perradially saddle-shaped, with thickened transverse ridge distally adjacent to succeeding SubL ridge; only ridge of Adambb seen in this arrangement, arranged so that proximal portion of plate is ventrally overlapped by preceding Adambb, with abradially extending thick spine-like process. Adambb may be displaced distally (not overlapping), exposing the full saddle shape of the plate. Podial basins shallow, large, subrectangular, likely to be shared (although suture between successive Ambb not visible), demarcated perradially on three sides by T-ridges of radially adjacent Ambb, extend abradially onto SubLL, bounded proximally and distally by ridges of successive Adambb.

*Mouth frame.* Relatively large, pronounced (disc does not project beyond frame; no interbrachial area), composed of paired Ambb1 and Ambb2. Amb1 enlarged, long, with thickened L-shaped ridge along abradial and distal margins, with podial basin proximal of ridge, paired interradially. Amb2 smaller than succeeding Ambb, with no corresponding SubL and Adambb. Small buccal slit, projecting as notch between Amb2 pair.

*Madreporite.* Not known.



*Extraxial skeleton.* Pedicellariae-like structures dorsal, small (width 0.3 mm), subsemicircular to subquadrate, bivalved, bear a process on each distolateral corner of valve, arranged in two columns extending the length of the arm.

*Remarks.* Measurements of the mouth frame diameter of BMNH 40296b fall within the range of *Antiquaster* (1.2), as defined by Hotchkiss (1976); this character, although of possible limited value, is used to tentatively retain the species within *Antiquaster*.

Perradial detail of the Ambb is obscure in BMNH 40296; the longitudinal ridges perradial to the T-shaped ridges, described in the holotype by Kesling (1971; e.g. pl. 2) are not clearly observed. This is possibly a preservational artefact. A slight trace of two Adamb spine-like processes occurs on BMNH 40296b, on Adamb9-10 (Text-fig. 3.14; Pl. 3.14, fig. 3). Preservation of the structures is poor so their identification is tentative. No other Adamb processes are seen on the specimen, which may seem curious. However, these processes are only seen along certain parts of the arms on the holotype of the species, being particularly clear along an arm figured by Kesling (1971, pl. 4, figs 1-2).

Small bivalved pedicellariae-like structures, similar to, but smaller than those in *Bdellacoma* Salter, 1857 (e.g. see Sutton *et al.* 2005), are noted on the dorsal surface of BMNH 40296. Thus these structures are not specific to one genus and their presence cannot be used alone as a diagnostic character. Kesling (1971, p. 187) noted their occurrence in the holotype of *A. magrumi*, although he did not elaborate on their structure or hint at their possible affinity to pedicellariae. He described the dorsal surface of the arms as “studded distally by small rather closely spaced ossicles, proximally by larger ossicles becoming aligned in longitudinal rows”.

*Occurrence.* From the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK and the Middle Devonian of Ohio and New York, USA.



## Genus KLASMURA Ruedemann, 1916

*Klasmura?* sp.

Plate 3.14, figs 6-7

v. 1940 *Bdellacoma vermiformis* Salter; Spencer, p. 529 (*pars*).

*Material.* BMNH 40300. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description.* Arms five, long (arm length *c.* 18 mm; arm tips not complete however), with up to 60 Ambb, parallel-sided, tapering distally. Ambb opposing, narrow, with broadly T-shaped ventral ridge. Ambulacral channel wide, shallow. SubLL wide, with median transverse ridge. Adambb saddle-shaped. Ambulacral groove shallow. Disk small (disc radius 1.25 mm) Arm width : mouth frame diameter ratio: 0.7.

*Remarks.* Axial plating is not readily discernable from that of *Antiquaster*; none-the-less, the specimen is tentatively assigned to *Klasmura*, based on the arm width : mouth frame diameter ratio, which falls into the range as defined by Hotchkiss (1976). No vestiges of spine-like processes on the Adambb are seen; however, this is likely to be a preservational artefact. Specimens of *Antiquaster magrumi* Kesling, 1971 (UMMP 57863a, BMNH E 42096) do not show these processes on many of the Adambb.

Order OEGOPHIURIDA Matsumoto, 1915

Suborder LYSOPHIURINA Gregory, 1896

Family CHEIROPTERASTERIDAE Spencer, 1934

*Type genus.* *Cheiropteraster* Stürtz, 1890, by original designation.

Genus LORIOLASTER Stürtz, 1886

1886a *Loriolaster* n. g.; Stürtz, pp. 91, 94.1890 *Loriolaster* Stürtz; Stürtz, pp. 208, 246.1893 *Loriolaster* Stürtz; Stürtz, pp. 47, 63.1914 *Loriolaster* Stürtz; Schuchert, pp. 5, 8, 23.1915 *Loriolaster* Stürtz; Schuchert, p. 201.



- 1934 *Loriolaster* Stürtz.; Spencer, pp. 446-448.
- 1957 *Loriolaster* Stürtz; Lehmann, p. 38.
- 1966 *Loriolaster* Stürtz; Spencer and Wright, p. U86.
- 1997 *Loriolaster* Stürtz; Jell, pp. 306-307.
- 1998 *Loriolaster* Stürtz; Bartels *et al.*, pp. 215-216.

*Type species.* *Loriolaster mirabilis* Stürtz, 1886 by original designation, from the Lower Devonian of Germany.

*Diagnosis.* Arms five, long, slender, tapering to whip-like extremity. Disc extremely large extending to near arm tips, unplated. Ambb alternating, cylindrical dorsally, boot-shaped ventrally. Adambb wide (per.-ab.), short, transversely elongate, spoon-shaped or L-shaped. Podial basin with no 'flooring' plate in Adambb portion.

*Remarks.* Two species are recognised in the literature: *Loriolaster mirabilis* Stürtz, 1886 and *Loriolaster gracilis* Lehmann, 1957, from the Hunsrück Slate, Upper Pragian to Lower Emsian, Lower Devonian of Germany (Lehmann 1957). They are distinguished on their relative Ambb and arm width. Lehmann (1957) described the Ambb of *L. gracilis* as being relatively longer and narrower than those of *L. mirabilis*.

*Loriolaster calceatus* sp. nov.

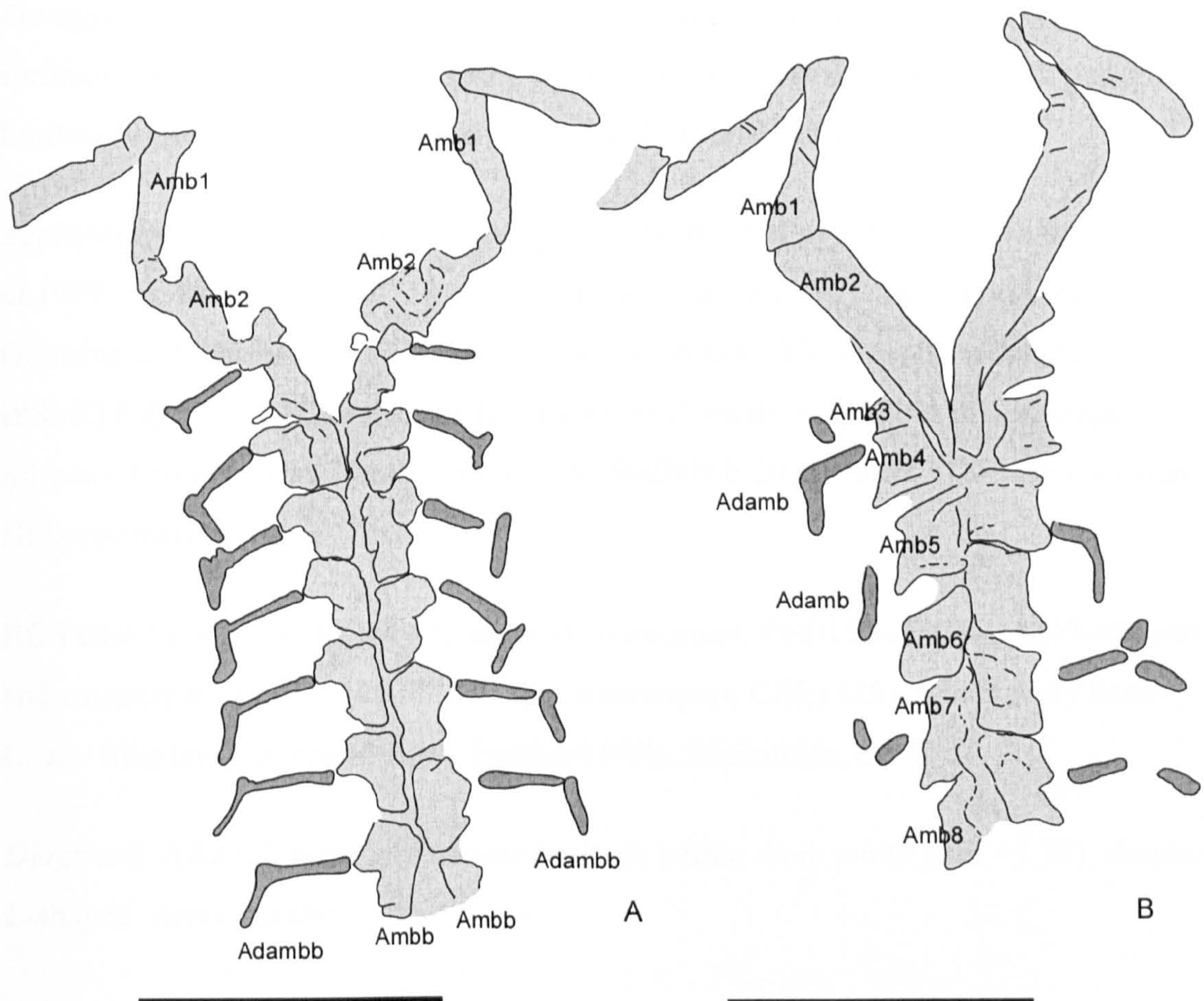
Plate 3.15; Plate 3.16, figures 1-3; Text-figure 3.15

- v. 1925 *Furcaster leptosoma* (Salter); Spencer, text-fig. 212c.
- v. 1965 *Furcaster leptosoma* (Salter); Owen, p. 556 (*pars*).
- v. 1972 *Furcaster leptosoma* (Salter); Goldring and Stephenson, p. 620, fig. 4c.
- v. 1999 cf. *Loriolaster gracilis*; Hotchkiss *et al.*, pp. 189, 193.

*Derivation of name.* Latin, *calceatus*, shod or booted, referring to the diagnostic L-shaped Adambb.

*Holotype.* BMNH 47953, nearly complete specimen showing ventral surface (cited in Hotchkiss *et al.* 1999, pp. 189, 193). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.





TEXT-FIG. 3.15. Camera lucida drawings of *Loriolaster calceatus* sp. nov. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, ventral view of mouth frame and proximal part of arm, showing diagnostic L-shaped Adambb (BMNH 47953; holotype). B, dorsal view of mouth frame and proximal part of arm (L-shaped Adambb are still visible) (BMNH 38527; paratype). Based on specimens shown in plate 3.15. Scale bars represent 2 mm.



*Paratypes.* BMNH 38527, assemblage of 11 specimens, three showing the dorsal surface (cited in Hotchkiss *et al.* 1999, pp. 189, 193). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

*Additional material.* 61 Leintwardine specimens: BMNH 47949 (cited in Hotchkiss *et al.* 1999, pp. 189, 193); E 20250 (30 individuals; Spencer 1925, text-fig. 212a, c; Goldring and Stephenson 1972, text-fig. 4c); BGS GSM25351 (c. 28 individuals); IPSMG R925292, CH213. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK (BMNH E 20250 and CH213 have a Church Hill provenance).

BGS GSE15243, GSE15244-45, part and counterpart; GSE15246, GSE15247-48, part and counterpart; GSE15249-50, part and counterpart; GSE15251. Llandovery Series, Lower Silurian; Gutterford Burn, Pentland Hills, Midlothian, Scotland.

*Diagnosis.* Adambb relatively narrow (Adamb width: Amb width ratio = 1.75), slender, L-shaped. Arms slender.

### *Description*

*Overall form.* Arms five, long (19-22 mm), tapering to whip-like extremities, 1.8-2.2 mm wide proximally. Disc large, extending to near arm tips (e.g. on some specimens in assemblages BMNH 38527 and BGS GSM25351).

*Axial arm plating.* Ambb alternating, unfused (wide groove sometimes developed along perradial suture in ventral view), dorsally subquadrate (proximal width 0.6-0.9 mm, length 0.6 mm) to longitudinally subrectangular and becoming more elongate distally, may show slight transverse ridge along proximal and distal edge of dorsal surface, with median portion slightly concave, boot-shaped ventrally with short transverse ridge extending abradially (toe of boot). Adambb wide (proximal width in BMNH 47953: 0.7 mm), c. 1.75 times Amb width, L-shaped, each abutting against abradial edge of corresponding Amb ridge; transverse portion elongate, generally slender, thickens slightly at perradial extremity; longitudinal portion marginal, directed distally. Spines not evident along arm edge. Podial basins subrectangular, wide and shallow, bordered perradially by Amb ridges. Abradially bordered by Adamb ridges.



No flooring plates to Adamb portion of basins (transverse Adamb ridges also viewed dorsally).

*Mouth frame.* Prominent petaloid structure dorsally. Five pairs of Amb1, Amb2 and Amb3. Amb1 long and narrow, pair joined interradially. Dorsally, small groove, approximately half way along length of plate, extends along dorso-perradial face (BMNH 38527). Amb2 enlarged, perradially paired, forming V-shaped structure dorsally, overlaps Amb3 and Amb4. Ventrally, relatively deep, subcircular podial basin of Amb2 perradially positioned towards distal end of plate. Amb3 same size as succeeding Ambb, with corresponding Adamb.

*Madreporite.* Not observed.

*Remarks.* Specimens BMNH E 20250, 38527, 47949, 47953 and BGS GSM25351 were labelled as *Furcaster leptosoma*. Hotchkiss (1999) assigned BMNH 38527, 47949, 47953 to cf. *Loriolaster gracilis*. Study of their morphology confirms they are not *F. leptosoma* (e.g. they possess alternating Ambb), and are likely to be a species of *Loriolaster*. Specimens in assemblage BMNH E 20250 (Spencer 1925, text-fig. 212c, Goldring and Stephenson, p. 620, fig. 4c) although originally described as *F. leptosoma*, are assigned to *L. calceatus* sp. nov. The alternating Ambb and transversely elongate Adambb (illustrated in an individual specimen in Spencer 1925, text-fig. 212c) are characteristics of *Loriolaster*. Specimens from Leintwardine predominantly show ventral morphology (e.g. slab BMNH 38527 has eight specimens showing a ventral surface and three showing a dorsal surface). *L. calceatus* specimens commonly occur as assemblages on a single bedding plane (BGS GSM25351, BMNH E 20250, 38527), in contrast to many of the other taxa from the deposits that occur in isolation.

Re-examination of the holotype (MB.E 784, showing the dorsal surface; figured as 'G. L. 183' in Lehmann 1957) and 'cotype' (MB. E 785, showing the ventral surface; figured as 'G. L. 10' in Lehmann 1957) of *L. gracilis* and one of Stürtz's (1886) figured specimens of *L. mirabilis* (MB. E 769; figured in Stutz 1886, pl. 6, fig. 2) has been undertaken as detailed published illustrations are not available (e.g. Stürtz 1886; Lehmann 1957). The Leintwardine form differs from both *L. mirabilis* and *L. gracilis* in the L-shaped Adambb, which are elongate and spoon-shaped in the former two species. This is regarded as a valid specific character as it is consistent through the



Leintwardine population (consisting of *c.* 70 specimens); where the Adambb are preserved all show the characteristic L-shaped morphology. No Adambb on either *L. mirabilis* or *L. gracilis* show this shape (pers. obs; Sturtz 1886; Lehmann 1957). The Leintwardine specimens also lack any apparent marginal spines. If this is regarded as a preservational artefact, then there is difficulty in explaining their complete absence through the entire population. Of the two established Hunsrück species, the Leintwardine form bears the most resemblance to *L. gracilis*, although the Adambb are relatively narrower in the former. The Adamb width is 1.75 times the Amb width in the Leintwardine form, whilst in *L. gracilis* the Adamb width is 2.3 times the Amb width. Temporal and spatial provenance differences combined with morphological differences suggest that the Leintwardine material is unlikely to belong to either of the Hunsrück *Loriolaster* species. The German *Loriolaster* material is from the Lower Pragian Stage, Lower Devonian, and is approximately 25 Ma younger than the Leintwardine specimens.

The diagnostic character of a large body disc is not preserved on most of the specimens, and where it does occur it is very indistinct. One specimen on slab CH213 and several specimens in assemblage BGS GSM25351 show possible vestiges of a large disc on the original fossil, in the form of slight darkening on the rock surface (Pl. 3.15, fig. 2). The body discs do not extend as far as the arm tips, as observed in the other *Loriolaster* species, although this may be a preservational artefact. In the majority of cases, no direct visible traces of the body disc are apparent. In a few instances (e.g. an individual in assemblage BMNH 38327) the disc is inferred due to the relatively straight appearance of the proximal portion of some of the arms (inferred to be disc-supported) and the more flexible, sharply curved appearance of the distal portions (unsupported). The lack of body disc preservation is presumably due to its extremely delicate membranous nature. The complete lack of a preserved body disc in most of the specimens may be inferred in itself to suggest that the disc was originally delicate.

Several specimens from the Llandovery Series of Gutterford Burn, Scotland, are tentatively assigned to the species (e.g. GSE15249-50, part and counterpart; Pl. 3.16, figs 1-3). The Ambb are slightly alternating, although this character is not as pronounced as in the Leintwardine material, and the diagnostic L-shaped Adambb and enlarged body disc are present. The L-shaped Adambb sometimes appear less slender



than in the Leintwardine specimens, although the robustness of these plates appears to be variable, within the same specimen (e.g. Pl. 3.16, figs 2-3). One specimen shows vestiges of an enlarged body disc (Pl. 3.16, fig. 1). Spencer (1925, p. 320) described another stelleroid specimen (NMS G189732496) from Gutterford Burn as showing a “strong general resemblance” to his text-figure 212c (BMNH E 20250, assigned herein to *L. calceatus*); this further suggests that *L. calceatus* occurs at both Leintwardine and Gutterford Burn. This discovery extends the range of the genus back to the Lower Silurian.

*Occurrence.* Known from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK: Church Hill. Tentatively also from the Llandovery Series, Lower Silurian of Gutterford Burn, Pentland Hills, Scotland.

Suborder ZUEGOPHIURINA Matsumoto, 1929

Family LAPWORTHURIDAE Gregory, 1897

*Type genus.* *Lapworthura* Gregory, 1897, by original designation.

Genus LAPWORTHURA Gregory, 1897

1897b *Lapworthura* nov. gen.; Gregory, p. 1037.

1925 *Lapworthura* Gregory; Spencer, pp. 301-302.

1966 *Lapworthura* Gregory; Spencer and Wright, p. U88.

1996 *Lapworthura* Gregory; Donovan *et al.*, p. 247.

2005 *Lapworthura* Gregory; Dean Shackleton, p. 87.

*Type species.* *Protaster miltoni* Salter, 1857, by Gregory (1897b), from the Upper Silurian of Leintwardine.

*Diagnosis.* Arms relatively wide, robust. Ambb opposing, boot-shaped ventrally with oblique groove along distal perradial region, subquadrate (proximal) to subrectangular (distally) dorsally with depressed perradial region and well developed abradial indentations giving an hour-glass appearance. Adambb prominent, sickle-shaped ventrally, subtriangular dorsally. Spines long, acicular, along arm margins. Disc large.



Madreporite large, crenulated (emended after Spencer and Wright 1966 and Dean Shackleton 2005)

*Remarks.* *Lapworthura* is monospecific.

*Lapworthura miltoni* (Salter, 1857)

Plate 3.16, figures 4-6; Plates 3.17-19; Text-figures 3.3, 3.16

- \* 1857 *Protaster Miltoni* n. sp., Salter, pp. 330, 331, pl. 9, figs 4a, ?b, ?c (= dorsal surface).
- 1861 *Protaster Miltoni* Salter; Salter, p. 484-486, pl. 18, figs 9-11.
- p 1862 *Protaster Miltoni* Salter; Wright, pp. 32-33 (*pars*), text-figs 18 a, ?b- ?c (cop. Salter 1857).
- 1867 *Protaster Miltoni* Salter; Murchison, p. 127, text-fig. 21.1-2.
- 1873 *Protaster Miltoni*, Salter; Salter, p. 164.
- 1876 *Protaster Miltoni*; Quenstedt, pl. 92, fig. 36.
- 1878 *Protaster Miltoni* Salter; Salter, p. 116.
- 1884 *Protaster Miltoni*; La Touche, pl. 17, fig. 538 (cop. Murchison 1867).
- 1886a *Protaster Miltoni* Salter; Stürtz, pp. 79, 94, ?pl. 8, fig. 6 (cop. Salter 1857).
- 1886b *Protaster Miltoni* Salter; Stürtz, p. 148.
- 1897b *Lapworthura miltoni* (Salter); Gregory, p. 1037, fig. 5.
- . 1912 *Lapworthura miltoni* (Salter); Sollas and Sollas, pp. 214-222, pl. 9, figs 1, 2.
- . 1914 *Lapworthura miltoni*; Spencer, pp. 25-26, 32-33, 35-36, pl. 1, fig. 9.
- . 1914 *Lapworthura sollasi* n. sp.; Spencer, pl. 1, fig. 10.
- 1914 *Lapworthura miltoni* (Salter); Schuchert, p. 22.
- 1915 *Lapworthura miltoni* (Salter); Schuchert, p. 251.
- 1915 *Lapworthura sollasi* Spencer; Schuchert, p. 251.
- v. 1925 *Lapworthura miltoni* (Salter); Spencer, pp. 302-309, text-figs 175, 188-191, 203-205, pl. 1, figs 9-10, pl. 19, figs 3-6, pl. 20, figs 2-3, pl. 21, figs 7-8.
- v. 1965 *Lapworthura miltoni* (Salter); Owen, p. 555.

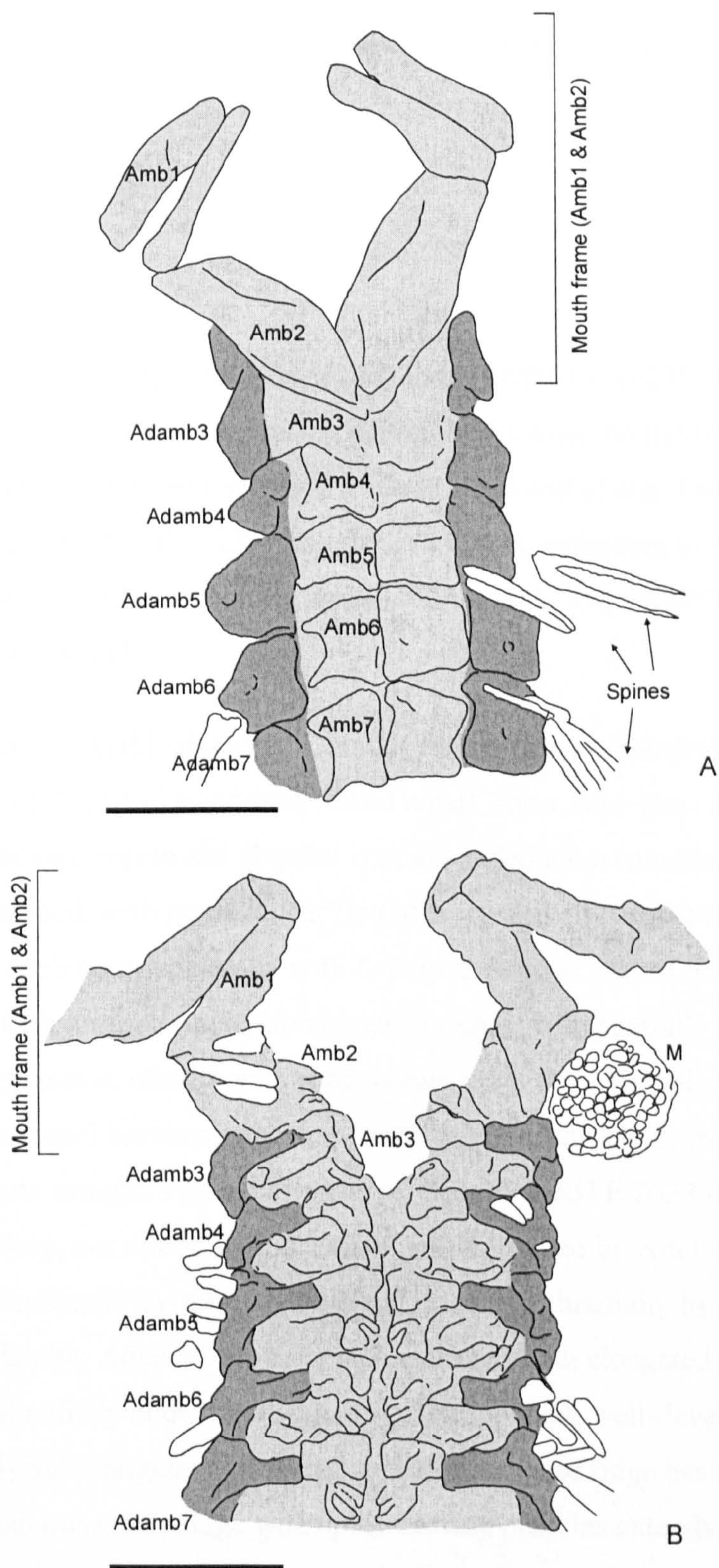


- v. 1966 *Lapworthura miltoni* (Salter); Spencer and Wright, p. U88, text-figs 77. 4a-d (cop. Spencer 1925).
- 1996 *Lapworthura miltoni* (Salter); Donovan *et al.*, p. 247.
- v. 2005 *Lapworthura miltoni* (Salter); Dean Shackleton, pp. 87-88, pl. 2, figs 10-12.

*Neotype*. BMNH E 20235a-b (part & counterpart), a complete calcified specimen, designated by Spencer (1925), (Spencer 1925, pl. 20, fig. 2). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Additional Material*. About 120 specimens cast: NMS G1882651511 (= '65. 151. K', Spencer 1925, pl. 19, fig. 5, text-fig. 204b); NMS G1882651515 (= '65. 151. E', Spencer 1925, pl. 19, fig. 3); NMS G1882651518 (= '65. 151. H', Spencer 1925, pl. 21, fig. 8, text-figs 175c, 204a); BMNH E 1297, E 13130, E 20231-2 (syntypes of '*Lapworthura sollasi*'; Spencer 1914, pl. 1, fig. 10); E 20239, E 20247, E 52973, E 52982 (Spencer 1925, text-fig. 204c); E 53885, 57425 (Gregory 1897b, fig. 5); 57709, CAMSM A37217-19, BGS GSM105645, OUM C.56, C.511a-b (part & counterpart); C.512-13, C.5116, C.16826-36, C.16839, C.16840-41 (part & counterpart); C.16842, C.16844-46, C.16849-50, C.16857-58, C.16862, C.16864, C.16867, C.16869, C.16871-72, C.16876-77, C.16879-80, C.16881a-b (part & counterpart); C.16882a-b (part & counterpart); C.16888, C.16894-95, C.16897, C.16902-03, C.16905, C.16908, C.16916, C.16923-24 (part & counterpart); C.16927-28, C.16944-47, C.16948-49, C.16950 (part & counterpart); C.16952-53 (part & counterpart); C.16956-57, C.16997, C.17010 (slab also contains *Furcaster leptosoma*); C.17292, C.20222, C.29276, NMVP11410-1, NMVP11404-5, NMVP26173, NMVP26174, NMVP26175, NMVP26180, NMVP74312-16, CH38 (slab also contains *F. leptosoma*); CH39, CH40 (slab also contains *F. leptosoma*); CH43, CH70 (slab also contains *F. leptosoma*); CH71, CH72, CH74, CH75 (slab also contains *F. leptosoma*); CH78 (slab also contains *F. leptosoma*); CH79, CH80 (slab also contains *F. leptosoma*); CH82, CH84, CH85, CH89-92, CH95-97, CH100, CH250-254, CH263. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill and Martin's Shell, Leintwardine, Herefordshire, UK. Approximately 260 further Leintwardine specimens housed in the OUM, BMNH, NMS, BGS GSM and CAMSM collections.





TEXT-FIG. 3.16. Camera lucida drawings of *Lapworthura miltoni* (Salter, 1857). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, dorsal view of mouth frame and proximal part of arm (BMNH E 20239). B, ventral view of mouth frame and proximal part of arm, showing enlarged, elongate Amb1 pair and smaller Amb2 pair (forming the mouth frame) and subsequent boot-shaped Ambbb and pronounced Adambbb (BMNH E 20232). Based on specimens shown in plate 3.18, figures 1-4 and plate 3.19, figures 1-3, 5. Scale bars represent 2 mm.



BMNH E 52442a-b (part & counterpart; a='G. C., D71', Spencer 1925, pl. 21, fig. 7); E 53891a-b (part & counterpart). Ashgill Series, Upper Ordovician; Lady Burn starfish beds, Girvan, Scotland.

*Diagnosis.* As for the genus.

### *Description*

*Overall form.* Arms five, distinct from disc, long (BMNH E 20235: arm length 70 mm), wide due to transverse expansion of Ambb and Adambb (BMNH E 20235: proximal arm width 4.5 mm), tapering towards distal end of arm. Disc circular, relatively large (BMNH E 20235: disc radius 17 mm), extending to Ambb7-8, ornamented with triradiate spicules. Spines on Adambb, long (BMNH E 20235: c. length 3-4 mm), acicular.

*Axial arm plating.* Ambb opposing. Dorsally Ambb convex, subquadrate and wide (proximal most) to rod-like and long (distal most), show hour-glass shape due to perradial depressed region and abradial concave indentation (muscle pits). Ventrally Ambb boot-shaped, with perradial bar (leg of boot) and distal transverse bar (abradial toe of boot). Amb boot proximally with L-shaped ridge at heel of boot, with curved ridge at toe, with rounded depression between ridges, with centrally positioned shallow transverse depression, distally with subquadrate ridge and obliquely transverse groove. Ambulacral channel between opposing Ambb ridges relatively deep and pronounced. Perradial suture straight. Podial basins large, wide (BMNH E 20235: width 1 mm), subcircular, deep, not shared by successive Ambb, floored by Ambb, bordered perradially-proximally by Amb boot-shaped ridge and abradially by ridges of proximal and distal Adambb. Adambb ventrally sickle-shaped with elongated nose extending perradially, abradially abut directly against corresponding well-developed socket of Amb, dorsally subtriangular and with a median transverse ridge bearing large acicular spines. Median transverse ridge with spine-bearing pustules extends along dorsal-abradial face of Adambb. Spines large, acicular, twice radial length of two Ambb, set at angle to arm axis, arranged in transverse row along Adambb, one row on each plate (spines preserved detached from dorsal-most tubercles). Marginals absent.



*Madreporite*. Rounded, with crenulated surface, relatively large (diameter up to 1.3 mm), prominent, ventrally and interradially positioned, occurs adjacent to Amb2 or Amb3.

*Mouth frame*. Composed of five pairs of Amb1-Amb3, prominent on ventral surface. Amb1 paired interradially, ventrally elongate, possibly bearing torus and row of spines (only detached rows of spines preserved, projecting into mouth region), dorsally rod-like and long. Amb2 large, perradial, dorsally overlaps proximal portion of Amb3 and pair form distinct bow-shaped structure, with prominent dorso-proximal to ventro-distal trending groove running along perradial face, with two small circular pores along groove. Proximal extension of groove on dorsal face of Amb1. Suture between Amb1 and Amb2 not always apparent.

*Remarks*. Salter (1857) noted the opposing arrangement of the Ambbb although his reconstructions of the arm plate morphology (pp. 330-331, pl. 9, figs 4b-c) are misleading. Salter's plate 9, figures 4b and c are described as the dorsal and ventral surfaces respectively although in fact figure 4b represents the ventral surface and 4c the dorsal. Salter (1857) interpreted the ventral surface to be covered by ventral shields (see Spencer 1925), which is shown on his reconstruction. This interpretation of the ventral morphology (fig. 4b) does not accurately illustrate the nature of the boot-shaped ridges of the Ambbb in this view. The dorsal reconstruction (fig. 4c) relatively accurately illustrates the plate morphology on this surface showing the subquadrate Ambbb and convex Abamb. Wright (1863) reproduced Salter's (1857) two illustrations, although correctly identified the dorsal and ventral arm surfaces. Gregory's (1897b) reconstruction of the ventral arm morphology (text-fig. 5, specimen BMNH 57425) appears to show several inaccuracies. The transverse adradially extending ridge of the Adamb appears to be part of the Amb in Gregory's reconstruction.

Salter (1857) assigned the species to *Protaster* Forbes, 1849, although he did not recognise that the Ambbb of the type species of this genus, *P. sedgwickii* Forbes, 1849 are alternating in contrast to the opposing Ambbb of *L. miltoni*. Gregory (1897b) subsequently erected *Lapworthura* to differentiate taxa possessing the opposing Ambbb.

The Leintwardine material is well preserved and shows extremely fine detail, and *L. miltoni* appears to be one of the better preserved taxa of the area, presumably partly due



to the robust nature of the Ambb. The arm lengths are not always observable due to a common lack of preservation of the arm tips. Regarding the likelihood or not of the Ambb being fused, Sollas and Sollas (1912) and Spencer (1925) stated that displacement of the ossicles has occurred in some specimens; this suggests that the Ambb were not fused. Dean Shackleton (2005) stated that the Ambb are not fused.

The slight variability in position of the madreporite (e.g. BMNH E 20239 and NMS G1882651515) may be due to it being embedded in relatively flexible disc plating and not sutured directly to an arm as in some related taxa (P. Jell, pers. com.). The large transverse groove mid-way along the ventral surface of the Amb perradial ridge is interpreted as the remnants of the water vessel canal (see Spencer 1925, p. 307-308). The smaller, shallower groove is interpreted as the remnants of the pseudohaemal canal and nerve to the podia (following Spencer 1925).

Of the various stelleroid taxa from the Leintwardine area, *L. miltoni* is the most abundant; 370 specimens have been recorded from the channels. *L. miltoni* typically occurs as solitary individuals, rather than as multiple specimens together. In rare cases several individuals may occur on a single slab (e.g. OUM C.16828 and C.16858, four specimens each; OUM C.16831-32, and C.16857, three specimens each). Specimens from Girvan are noticeably smaller than the Leintwardine material; for example BMNH 52442 has a disc radius of c. 6 mm (Pl. 3.16, figs 4-6). The Scottish material is also less abundant than the Herefordshire material; 16 specimens are housed in the BMNH collections, and seven of these were mentioned by Spencer (1925).

**Occurrence.** Known from the Ashgill Series, Upper Ordovician, of the Lady Burn starfish beds, Girvan, Scotland and the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK: Church Hill & Martin's Shell quarries. Specimens are particularly abundant at Church Hill.



## Family FURCASTERIDAE Stürtz, 1900

*Type genus. Furcaster* Stürtz, 1886, by original designation.

## Genus FURCASTER Stürtz, 1886

- 1886a *Furcaster* n. g.; Stürtz, p. 79.
- 1897b *Furcaster* Stürtz, 1886; Gregory, p. 1038.
- 1925 *Furcaster* Stürtz; Spencer, pp. 312-316.
- 1957 *Furcaster* Stürtz; Lehmann, pp. 63-65.
- 1966 *Furcaster* Stürtz; Spencer and Wright, p. U88.
- 1983 *Furcaster* Stürtz; Haude and Thomas, p. 127.
- 1996 *Furcaster* Stürtz; Donovan *et al.*, p. 248.
- 1999 *Furcaster* Stürtz; Dean, pp. 239-246.
- 2005 *Furcaster* Stürtz; Dean Shackleton, p. 84.

*Type species. Furcaster palaeozoicus* Stürtz, 1886 (Stürtz, 1886a, pl. 8, figs 4, 5), by original designation, from the Lower Devonian Bundenbach Slates of Germany.

*Diagnosis.* Arms five, long, slender, tapering distally into whip-like extremity, distinct from circular disc. Ambb opposing, boot-shaped ventrally, with perradial longitudinal ridge and median groove dorsally. Adambb dorsally forming distinct margin to arms. Spines along arm margin, acicular, parallel to arm axis. Mouth frame petaloid (emended after Spencer and Wright 1966).

*Remarks.* Three species of *Furcaster* have been documented from the Lower Devonian Hunsrück Slate of Germany: *Furcaster decheni* (Stürtz, 1886), *Furcaster palaeozoicus*, and *Furcaster zitteli* (Stürtz, 1886) (Stürtz, 1886a, 1990; Lehmann 1957; Bartels *et al.* 2002b). Spencer (1925) recognised only two species within the genus: *Furcaster leptosoma* (Salter, 1857) from Leintwardine, UK, and *Furcaster trepidans* Spencer, 1925 from the Ashgill Series, Upper Ordovician of Thraive Glenn, Girvan, Scotland. Spencer (1925) synonymised the three Hunsrück species within *F. leptosoma*, although based on morphological evidence and specimen provenance this is likely to be incorrect. Haude and Thomas (1983) described two further species of *Furcaster* from the Famennian Stage, Upper Devonian, of the Northern Rhenish area of Germany.



In *F. trepidans*, Spencer (1925) identified a transverse ridge along the dorsal surface of each Amb with a median groove (structure referred to as a 'wing', Spencer 1925, p. 317), giving the dorsal surface of the arm margin a rippled appearance. Dean Shackleton (2005) identified these ridges as possessing well-developed longitudinal muscle facets, diagnostic of the species. In *F. leptosoma* the transverse ridges (if present) are slight and the groove on the 'wings' is reduced to a thin eyelet on proximal Ambb, the structure being absent on distal Ambb. The Ambb of *F. leptosoma* predominantly show an indistinct, flattened dorsal surface, with occasionally a slight transverse ridge and groove structure. No specimens show the pronounced transverse ridge and groove structure characteristic of *F. trepidans*. These structures are interpreted as dorsal muscle pits (Donovan *et al.* 1996; Dean 1999; Dean Shackleton 2005), with *F. trepidans* possessing deeper pits than *F. leptosoma*.

*Furcaster leptosoma* (Salter, 1857)

Plates 3.20-22; Text-figure 3.17

- \* 1857 *Protaster leptosoma* n. sp., Salter, pp. 331-332, pl. 9, fig. 5.
- 1862 *Protaster leptosoma* Salter; Wright, p. 33.
- 1876 *Protaster leptosoma*; Quenstedt, pl. 95, fig. 12 (cop. Salter 1857).
- 1878 *Protaster leptosoma* Salter; Salter, p. 116.
- ? 1884 *Protaster leptosoma*; La Touche, pl. 17, fig. 540.
- 1886a *Furcaster palaeozoicus* n. sp., Stürtz, pp. 79-80, pl. 8, figs 4-5.
- ? 1886a *Protaster leptosoma* Salter; Stürtz, p. 79.
- 1890 *Furcaster palaeozoicus* Stürtz; Stürtz, pp. 214-215, pl. 31, figs 40, 40a.
- 1897b *Sturtzura leptosoma* (Salter); Gregory, p. 1035.
- 1897b *Furcaster palaeozoicus* Stürtz; Gregory, p. 1038.
- 1912 *Rhodostoma leptosoma* (Salter); Sollas and Sollas, pp. 223-226, text-fig. 4c, pl. 9, figs 3-4.
- 1914 *Furcaster palaeozoicus* Stürtz; Schuchert, p. 20.
- 1914 *Sturtzura leptosoma* (Salter); Schuchert, p. 41.
- 1915 *Sturtzura leptosoma* (Salter); Schuchert, pp. 236-237.
- 1915 *Furcaster palaeozoicus* Stürtz; Schuchert, pp. 259, 261.

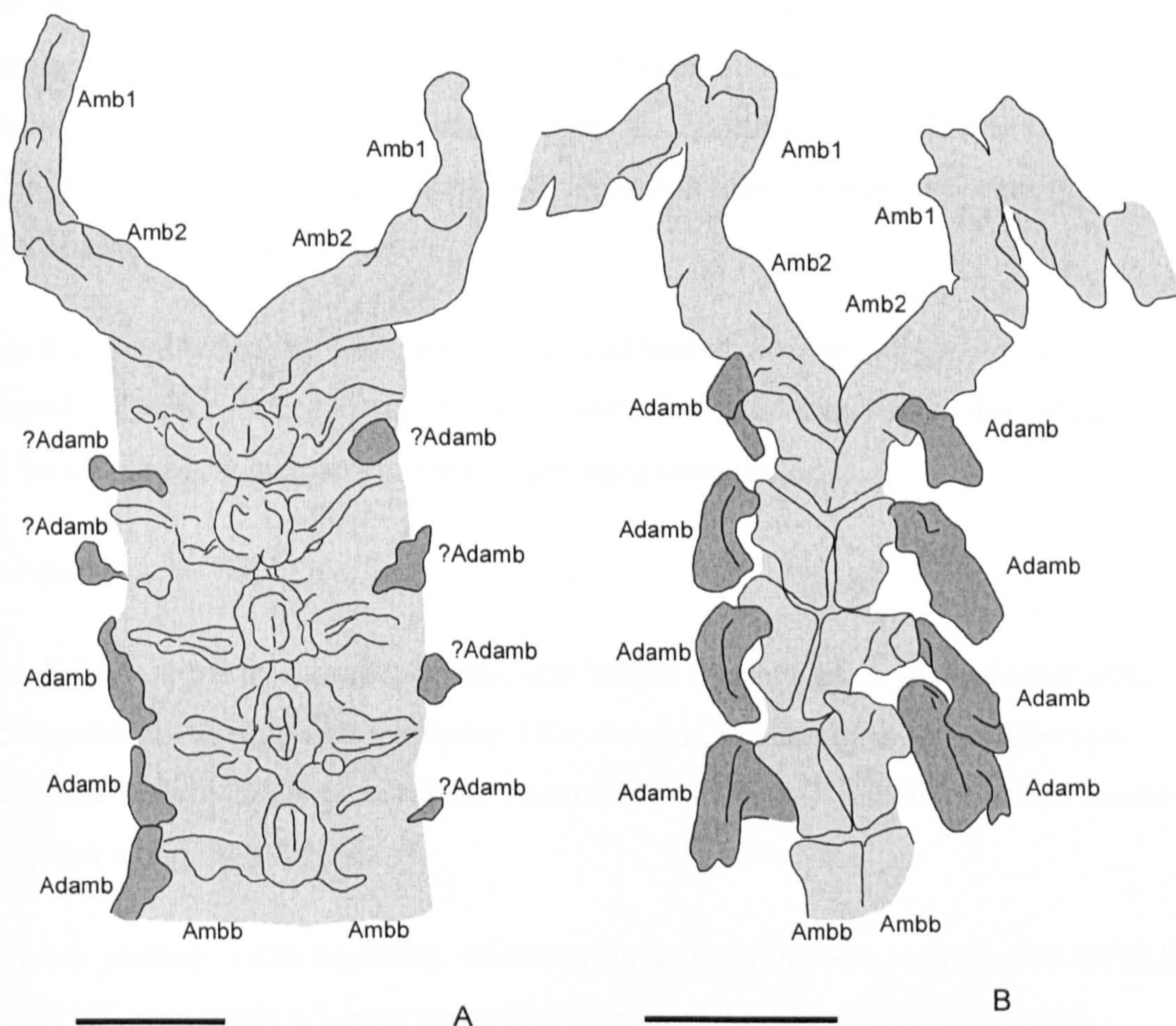


- vp. 1925 *Furcaster leptosoma* (Salter); Spencer, pp. 319-324 (*pars*), text-figs 207-208, 211-212 (*pars*), *non* 212c (= *L. calceatus* sp. nov.), pl. 18, fig. 4, pl. 22, figs 3-5, ?6-10.
- ? 1927 *Furcaster leptosoma* (Salter); Spencer, pp. 325-326.
- 1957 *Furcaster leptosoma* (Salter); Lehmann, p. 64.
- 1957 *Furcaster palaeozoicus* Stürtz; Lehmann, pp. 65-69, text-figs 17, 20a, pl. 18, figs 1-6.
- vp. 1965 *Furcaster leptosoma* (Salter); Owen, pp. 556-557 (*pars*).
- vp. 1966 *Furcaster leptosoma* (Salter); Spencer and Wright, pp. U88-89, text-figs 77. 2a-b (cop. Spencer 1925).
- 1983 *Furcaster leptosoma* (Salter); Haude and Thomas, p. 130.
- ? 1996 *Furcaster leptosoma* (Salter); Donovan *et al.*, p. 248.
- v. 2005 *Furcaster leptosoma* (Salter); Dean Shackleton, p. 85.

*Neotype*. IPSMG R9252912, nearly complete specimen showing dorsal surface, designated by Owen (1965), ('co-type' 'S9', Spencer 1925, p. 321, pl. 22, fig. 3). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

*Additional material*. About 65 Leintwardine specimens cast: IPSMG R9252917 ('co-type' 'S7', Spencer 1925, p. 320, text-fig. 211); BMNH E 13135, E 13138-39, E 20256, E 20258 ('Ludlow Museum no. ii', Spencer 1925, text-fig. 212e); E 20260 ('Ludlow Museum no. x', Spencer 1925; pl. 18, fig. 4); BGS GSM28819 (Spencer 1925, pl. 12, fig. 4); NMS G188265143, OUM C.514, C.16838, C.16893, C.16930-31 (part & counterpart); C.17012, C.17015a-b (part & counterpart); C.17016-23, C.17025-26, C.17032-36, C.17039, C.17125-27, C.17131, C.17291, C.170158, CH34, CH38 (slab also contains *Lapworthura miltoni*); CH40 (slab also contains *L. miltoni*); CH54, CH70 (slab also contains *L. miltoni*); CH73, CH75 (slab also contains *L. miltoni*); CH76, CH77 (part & counterpart); CH78 (slab also contains *L. miltoni*); CH80 (slab also contains *L. miltoni*); CH81, CH83, CH86, CH88, CH98, CH101-104, CH173, CH257, CH259, Mock1. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill and Mocktree, Leintwardine, Herefordshire. Specimens are particularly abundant at Church Hill. 22 further Leintwardine specimens are housed in the BMNH, BGS and NMS collections.





TEXT-FIG. 3.17. Camera lucida drawings of *Furcaster leptosoma* (Salter, 1857). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, dorsal view of mouth frame (Amb1 and Amb2) and proximal part of arm, showing diagnostic perradial oval ridge and groove of Ambb; positioning of some of the Adambb is tentative (IPSM G9252917). B, ventral view of mouth frame and proximal part of arm, showing boot-shaped Ambb (BMNH E 13138). Based on specimens shown in plate 3.20, figures 3-5 and plate 3.21, figures 1-3. Scale bars represent 1 mm.



Non-Leintwardine specimens: BMNH E 52826a-b. Ashgill Series, Upper Ordovician; Lady Burn, Threave Glen, Scotland. BGS GSE 12033. Llandovery Series, Lower Silurian; Gutterford Burn, Pentland Hills, Midlothian, Scotland. BMNH E 3364 (Stürtz 1890, pl. 31, fig. 40a); E 3365 (Stürtz 1890, pl. 31, fig. 40a); E 3366 (Stürtz 1890, pl. 31, fig. 40); E 3805 (Stürtz, pl. 31, fig. 40). Hunsrück Slate, Lower Devonian; Bundenbach, southwest Germany.

*Diagnosis.* Ambb dorsally with pronounced oval perradial ridge and groove, with flattened indistinct surface abradially, with median to distal transverse ridge (which may be separated by median groove) on proximal most plates.

### *Description*

*Overall form.* Arms five, long (neotype: arm length 22 mm), up to 44 Ambb per arm, tapering distally to whip-like extremity. Disc circular, extending to Amb7 (neotype: disc radius 5 mm). Finely tuberculated surface of disc. Row of radially directed needle-like spines along each Adamb.

*Axial arm plating.* Ambb opposing, relatively wide in comparison to arm width (IPSM G9252917: Amb width 2.2 mm; arm width 2.7 mm at Amb5) and subrectangular dorsally, relatively narrower in comparison to arm width and boot-shaped ventrally. Toe of boot-shaped ridge extends abradially. Distal leg of boot with fine transverse groove, extending to podial basin. Deep, narrow ambulacral channel between neighbouring ambulacral ridges. Podial basins relatively deep, subcircular (BMNH E 13138: proximal diameter 0.3 mm), not shared between successive Ambb. Ambb dorsally with perradial longitudinal ridge, separated from ridge of opposing Amb by a narrow, sometimes pronounced, median groove. Perradial ridges of each Amb pair converge at their proximal and distal extremities. Arrangement gives each row an appearance of having a dorsal oval median hollow. Ambb are poorly defined dorso-abradially. Proximal most Ambb abradially with slight median transverse ridge and groove (dorsal muscle pits). Adambb form pronounced margin to arm ventrally, form slight arm margin dorsally, subquadrate laterally with transverse spine bearing ridge along distal edge of abradial face (6 pits along each ridge; BMNH E 20258), abut directly against corresponding Ambb. Spines acicular, delicate, relatively long (spine length twice Amb length) proximally, shorter distally (1-1.5 x Amb length), at higher



angle to arm axis proximally, at lower angle (may be parallel) distally, six per transverse row on each Adamb, occur along length of arm.

*Madreporite*. Not evident.

*Mouth frame*. Formed by five pairs of Amb1 and Amb2, dorsally petaloid. Amb1 elongate, rod-like, paired interradially, often at angle to Amb2, sometimes separated from Amb2 by indistinct suture, with lack of apparent torri or spines proximal to plates, with slight transverse groove (nerve ring) located proximally ventral-wards. Amb2 paired perradially, large and pronounced, partially overlapping Amb3 in dorsal view, with broad groove (water vascular ring) running along perradial/ dorsal face (e.g. BMNH E 20260), with circular pore midway along groove.

*Remarks*. Salter (1857) erected the species and assigned it to *Protaster* Forbes, 1849, but failed to note the opposing arrangement of the Ambb in contrast to the alternating arrangement of those of the type species of *Protaster*, *P. sedgwicki* Forbes, 1849. Spencer (1925) correctly reassigned the species to *Furcaster* Stürtz, 1886.

The inner perradial face of the Adambb is unclear due to the swing of the plates towards the ventral surface of the arms. The wide swing of the Adambb partially encloses the ambulacral groove, obscuring the podial basins (e.g. BMNH E 13135), particularly distalwards on the arms. The Adambb are less prominent on the dorsal surface due to this ventral swing. Spines are often preserved detached from the arm, although occasionally they may be preserved attached (e.g. BMNH E 13135) to the transverse ridge on each Adamb. The detail of the abradial face of the Adambb is shown in BMNH E 20258, a specimen preserved laterally (Pl. 3.22, figs 2-3). The specimen does not preserve the mouth frame and body disc, although the characteristic perradial oval ridge and groove of the dorsal Amb surface is preserved along sections of the arms, confirming the specimen's specific identity.

No madreporite has been observed on any of the material, although Spencer (1925, p. 321) stated that an unspecified specimen from the Manchester Museum "shows a thin madreporite in the usual position". This specimen has not been relocated so the observation cannot be confirmed.



The perradial ridges that occur dorsally on the Ambb are inferred to have assisted in cross furrow musculatory-articulation; the associated median hollows may have acted as points of origin for the muscles (as postulated for *F. trepidans* by Dean 1999). Dean (1999) and Dean Shackleton (2005) also stated that *F. trepidans* has well developed dorso-lateral Amb muscle fields. These muscle fields are less pronounced in *F. leptosoma*. These characters are likely to have assisted in making the arms of *F. leptosoma* highly flexible.

Salter (1857) based his diagnosis on the overall small size of the individual along with the dorsal petaloid shape of the mouth frame and narrow Ambb in relation to the Adambb in ventral aspect. Salter (1857, p. 332) described the Ambb as being “scarcely half the width” of the Adambb. This is due to the swing ventrally of the Adambb, in which the Ambb are partially enclosed and is probably not suitable for a diagnostic character. Salter (1857, p. 331) described the exact shape of the dorsal mouth frame as “formed of three pairs of bones”, noting that in *Lapworthura miltoni* “only two are distinct”. This character is also regarded to be unsuitable due to the variable nature in mouth frame preservation. Spencer’s (1925) differentiation of the taxon from *F. trepidans*, based on the less pronounced character of the transverse ridge and groove (dorso-lateral muscle pits) on the dorsal Amb surface appears to be consistent and is therefore retained.

Some of Spencer’s (1925) observations regarding plating in the species may be questionable as they are based on a specimen in assemblage BMNH E 20250c which Spencer (1925, text-fig. 212c) originally described as *F. leptosoma* but is here reassigned to *L. calceatus*. Spencer’s figure shows the specimen to have a wide ambulacral groove, fully exposing the Ambb, a character that is atypical of the *F. leptosoma* specimens studied. The Adambb each possess a transverse, elongate ridge that extends over the ‘floor’ of the plate, abutting against the Amb. This character has not been noted on any of the other specimens. Examination of BMNH E 20250 reveals that no Adamb ‘floor’ is present and these plates are represented purely by an elongate transverse ridge. The Ambb are shown to be alternating (again atypical of *Furcaster*), Spencer (1925, p. 322) describing them as being “forced into an alternating position” thereby implying that they are unfused.



Spencer (1925) regarded the Lower Devonian Hunsrück *Eoluida decheni* Stürtz, 1886, *Furcaster palaeozoicus* Stürtz, 1886, and *Palastropecten zitteli* Stürtz, 1886 to be synonyms of *F. leptosoma*. Some of the Hunsrück specimens are considerably larger than the Leintwardine material; for example BMHN E 3360, described by Stürtz (1890) as *E. decheni* has a disc radius of 30-35 mm and an arm length of approximately 180 mm. However, this in itself cannot be considered a diagnostic character. Specimens BMNH E 3364-66 and E 3805, described and figured by Stürtz (1890, pl. 31, figs 40-40a) as *F. palaeozoicus* have been examined. These specimens possess a pronounced oval perradial ridge and groove on the dorsal surface of the Ambb. The transverse ridges and grooves are relatively more pronounced and rounded than in the Leintwardine material although this could be due to preservational differences of the Hunsrück fossils. Following Spencer (1925), *F. palaeozoicus* is tentatively synonymised with *F. leptosoma*.

Specimens BMNH E 3351-52, E 3354, E 3360, described and figured by Stürtz (1890, pl. 26, figs 10-13) as *E. decheni* and *P. zitteli* have also been examined although the morphology of the dorsal surface of the Ambb is difficult to determine due to preservation. BMNH E 3351 (*P. zitteli*) possesses pronounced dorso-lateral Amb muscle fields although the precise shape cannot be determined due to distortion of the specimen. It is not possible herein to determine the affinity of these specimens.

Spencer (1925) also described a stelleroid specimen (BMNH E 52826) from the Upper Ordovician of Thraive Glenn, Scotland, and several specimens from the Lower Silurian of Gutterford Burn, Scotland (e.g. NMS G189732333, 1897324931-1897324932, 189732496, 189732502, 189732505, 189732515; unavailable for study) as *F. leptosoma* and other species as synonyms of the taxon: *Squamaster echinatus* Ringueberg, 1886, from the Silurian Rochester Shale, USA (NYSM no. 7783, not located), *Sympterura minveri* Bather, 1905, from the Lower Devonian of Cornwall (BMNH E 5036), UK, and *Ophiurella ? gregaria* Whidborne, 1898, from the Lower Carboniferous of Devon, UK (BGS GSM25353, not located). The age and geographical provenance of the non-Leintwardine material may suggest it is unlikely that these are all the same species. Although relatively poorly preserved, specimen BMNH E 52826 shows the dorsal perradial ridge and groove diagnostic of the species (Pl. 3.22, fig. 6). The characteristic boot-shaped Ambb are also preserved ventrally (Pl.



3.22, fig. 7). This specimen is retained within the species. BMNH E 5036 is insufficiently preserved to determine its specific affinity. The specimens described by Spencer (1925) from Gutterford Burn have not been available for restudy although Spencer (1925, p. 320) described one individual (NMS G189732496) as “bearing a strong general resemblance” to the specimen illustrated in his text-figure 212c (BMNH E 20250, designated herein as *L. calceatus*). Since BMNH E 20250 is not *F. leptosoma*, doubt can be placed on the specific affinity of some of the Gutterford Burn specimens. However, specimen BGS GSE12033 shows the diagnostic perradial oval ridge and groove and is herein retained within the species (Pl. 3.22, fig. 8). *F. leptosoma* has a wide stratigraphical range, from the Upper Ordovician to possibly the Lower Devonian. According to Spencer (1925) it may even extend to the Lower Carboniferous. It also shows an extensive geographical range.

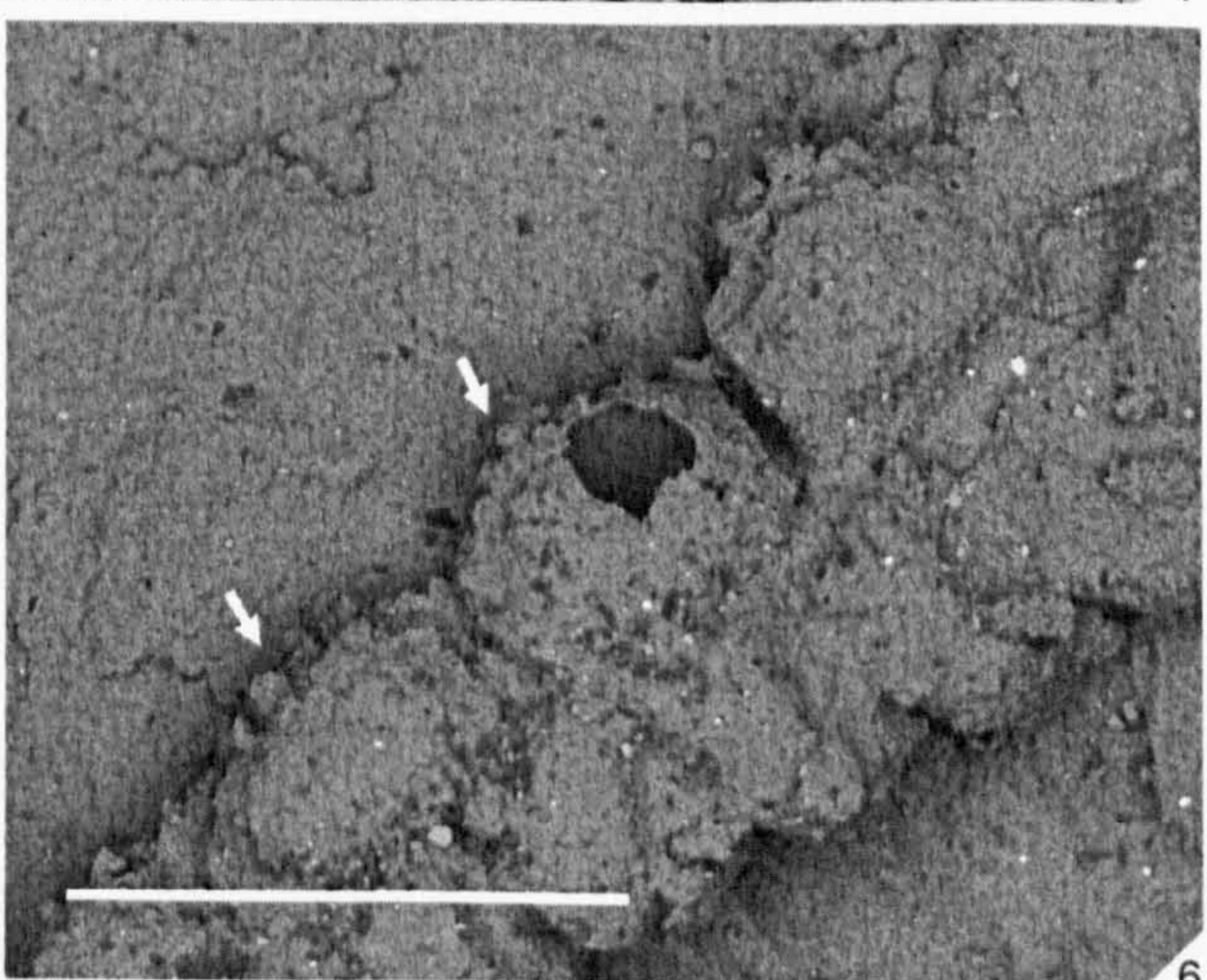
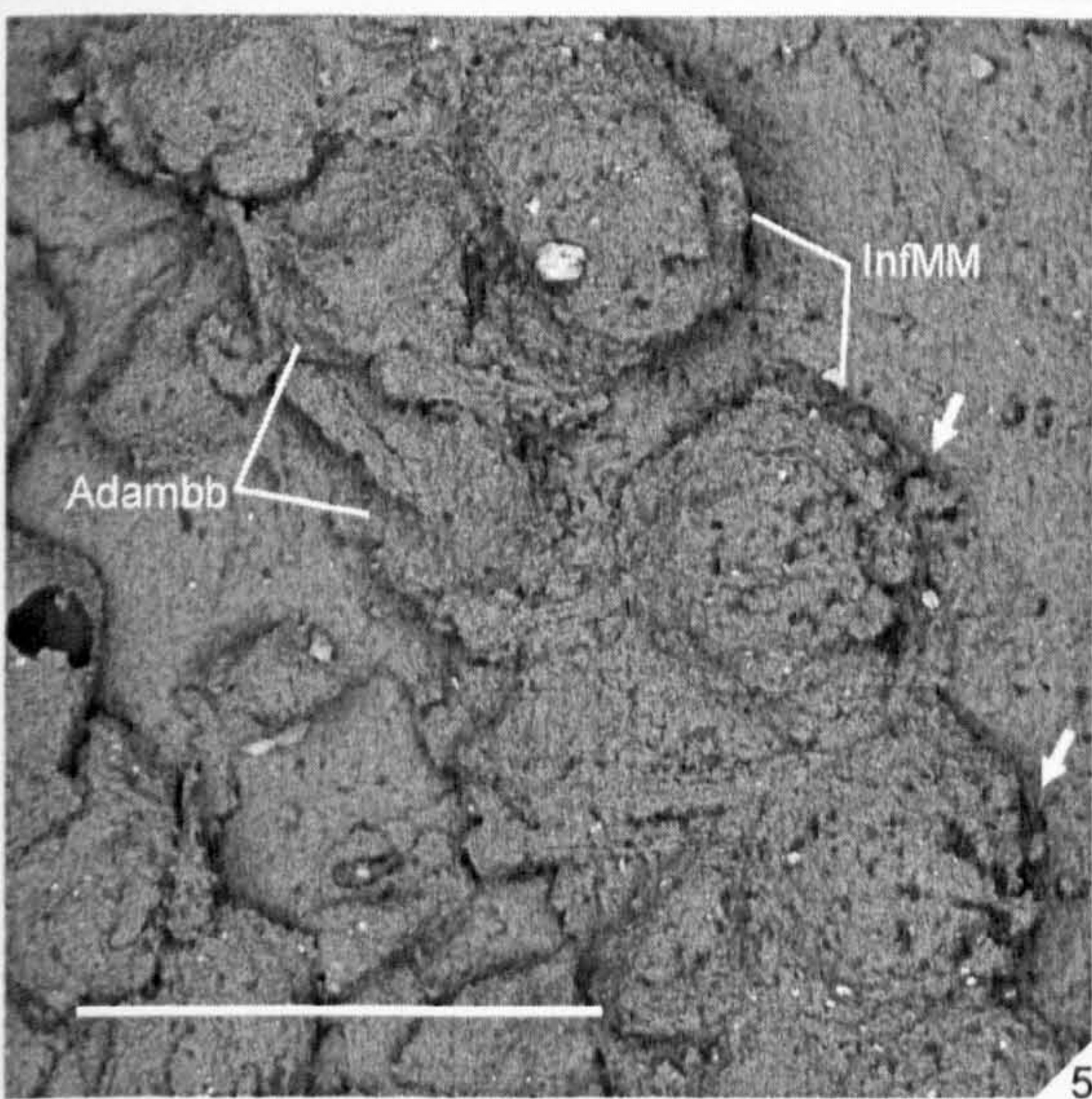
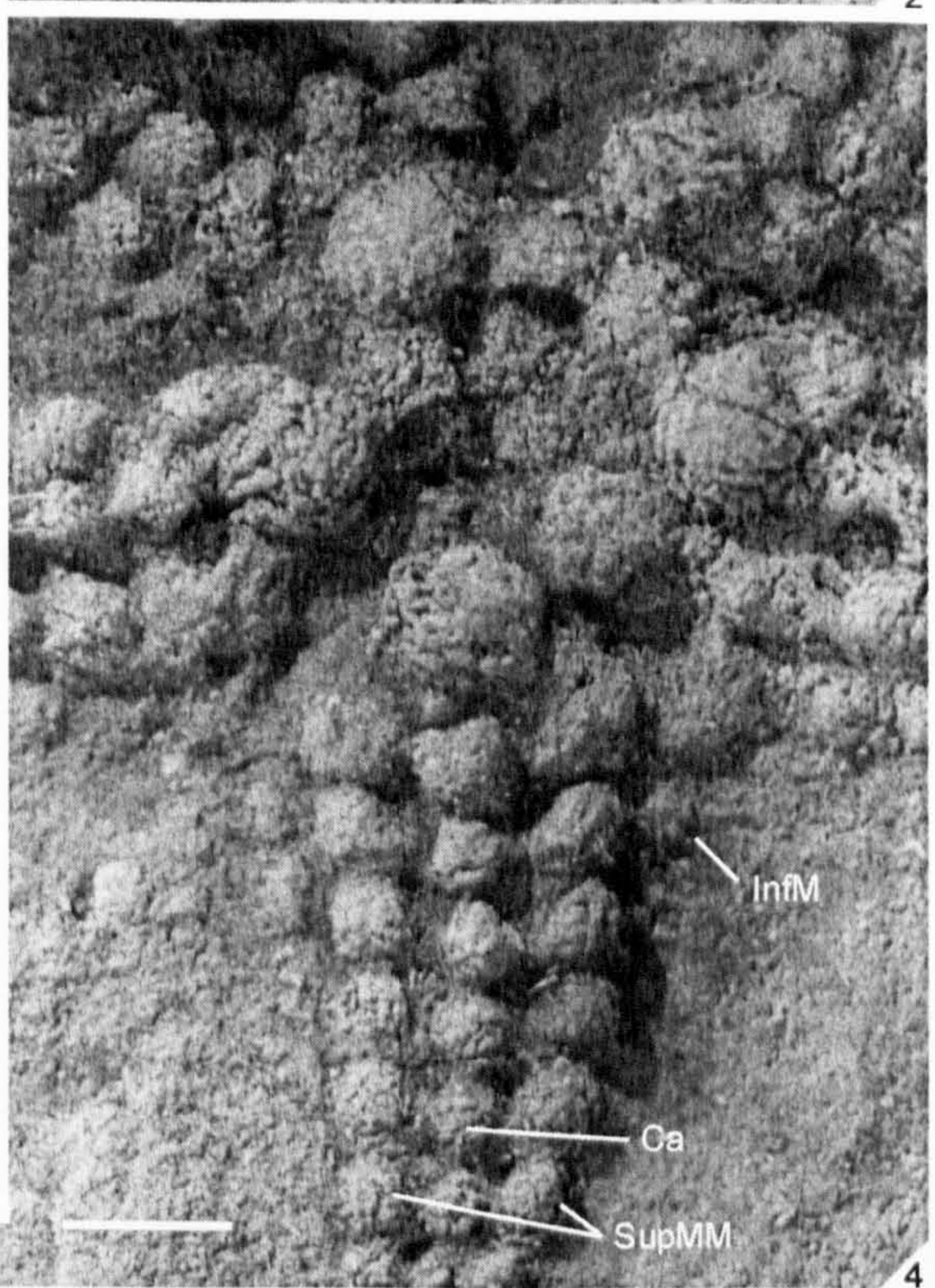
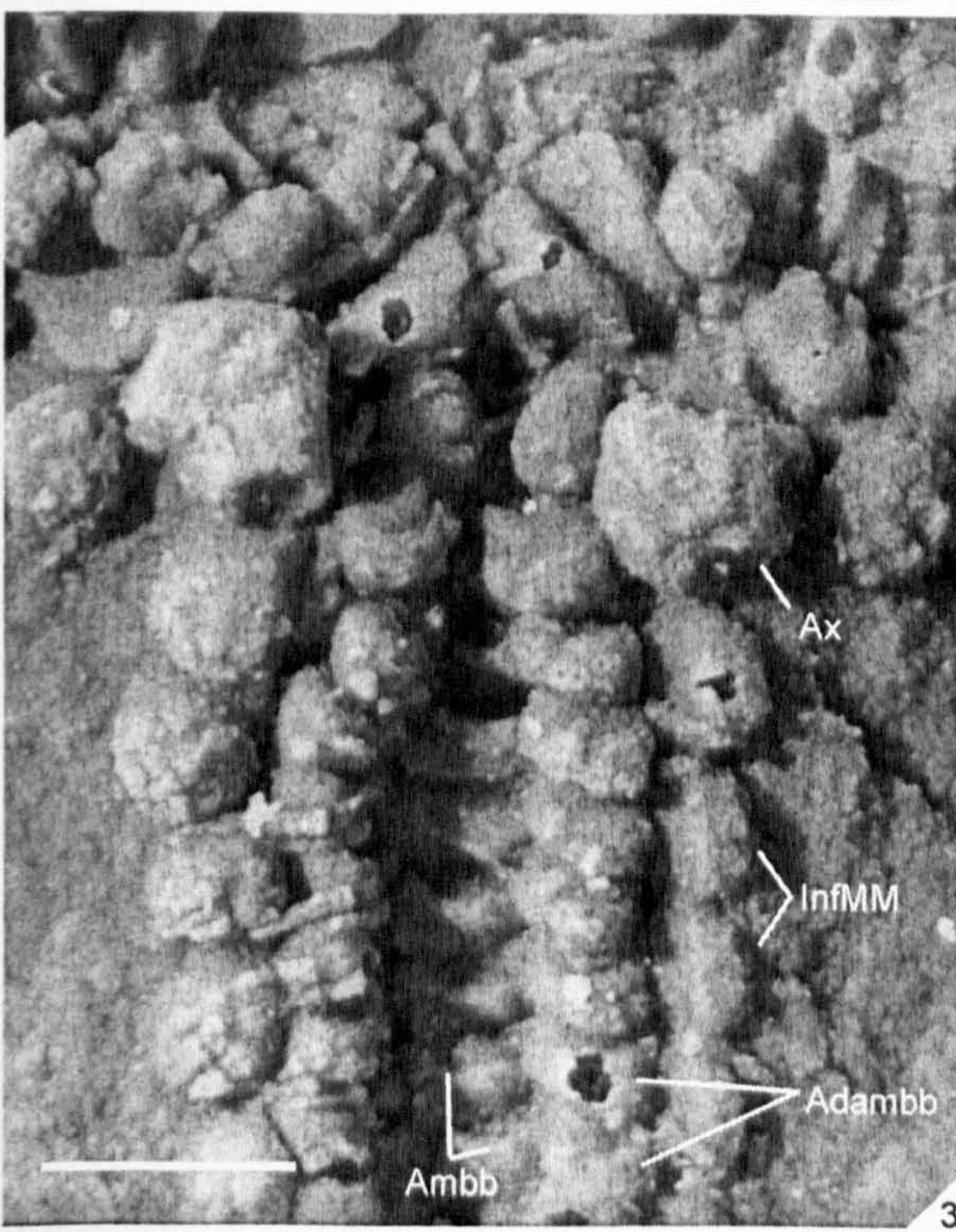
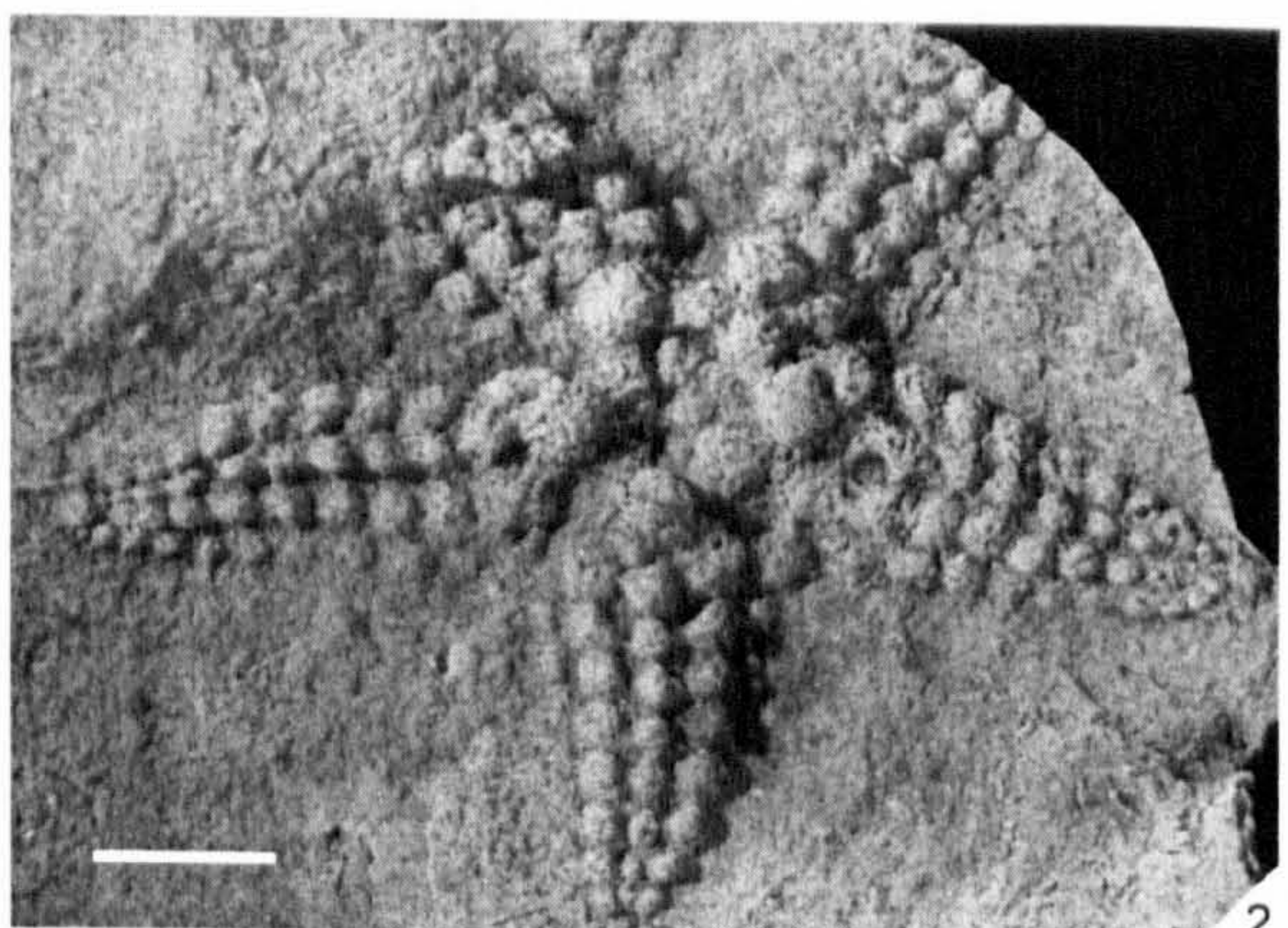
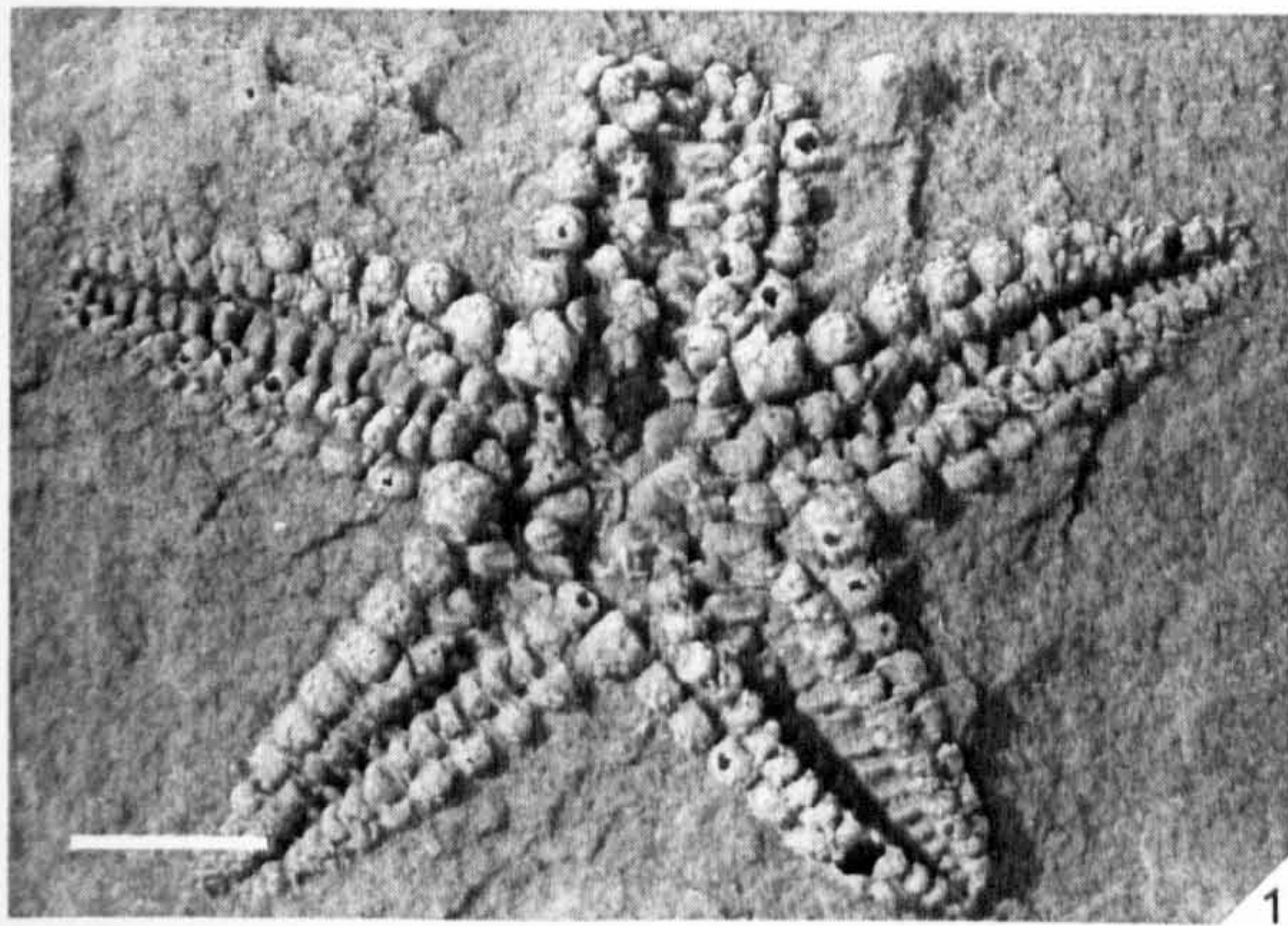
*Occurrence.* From the Ashgill Series, Upper Ordovician Lady Burn Starfish Beds of Girvan, Scotland; the Llandovery Series, Lower Silurian starfish beds of Gutterford Burn, Pentland Hills, Midlothian, Scotland; the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area, Herefordshire, UK: Church Hill, Martin’s Shell and Mocktree quarries; and possibly the Lower Devonian Hunsrück Slate of Bundenbach, southwest Germany. Specimens are described in the literature (e.g. Spencer 1925) from other localities, although it is not possible herein to determine their specific affinity: the Mid Silurian of western New York, USA; the Lower Devonian of north Cornwall, UK; and the Lower Carboniferous of Devon, UK.



## EXPLANATION OF PLATE 3.1

Figs 1-6. *Cocaster bulbiferus* Spencer, 1916; holotype, part and counterpart; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, 3, 5-6, BMNH E 13956. 1, entire specimen, ventral view; scale bar represents 2 mm. 3, detail of proximal arm, ventral view; scale bar represents 1 mm. 5-6, detail of Adambb and InfMM (surfaces of InfMM bearing fine tubercles arrowed), ventral view; scale bars represent 1 mm; SEM photomicrographs. 2, 4, NMS G188265158a. 2, entire specimen, dorsal view; scale bar represents 2 mm. 4, detail of proximal arm and central disc, dorsal view; scale bar represents 1 mm. All figures are of silicone casts.







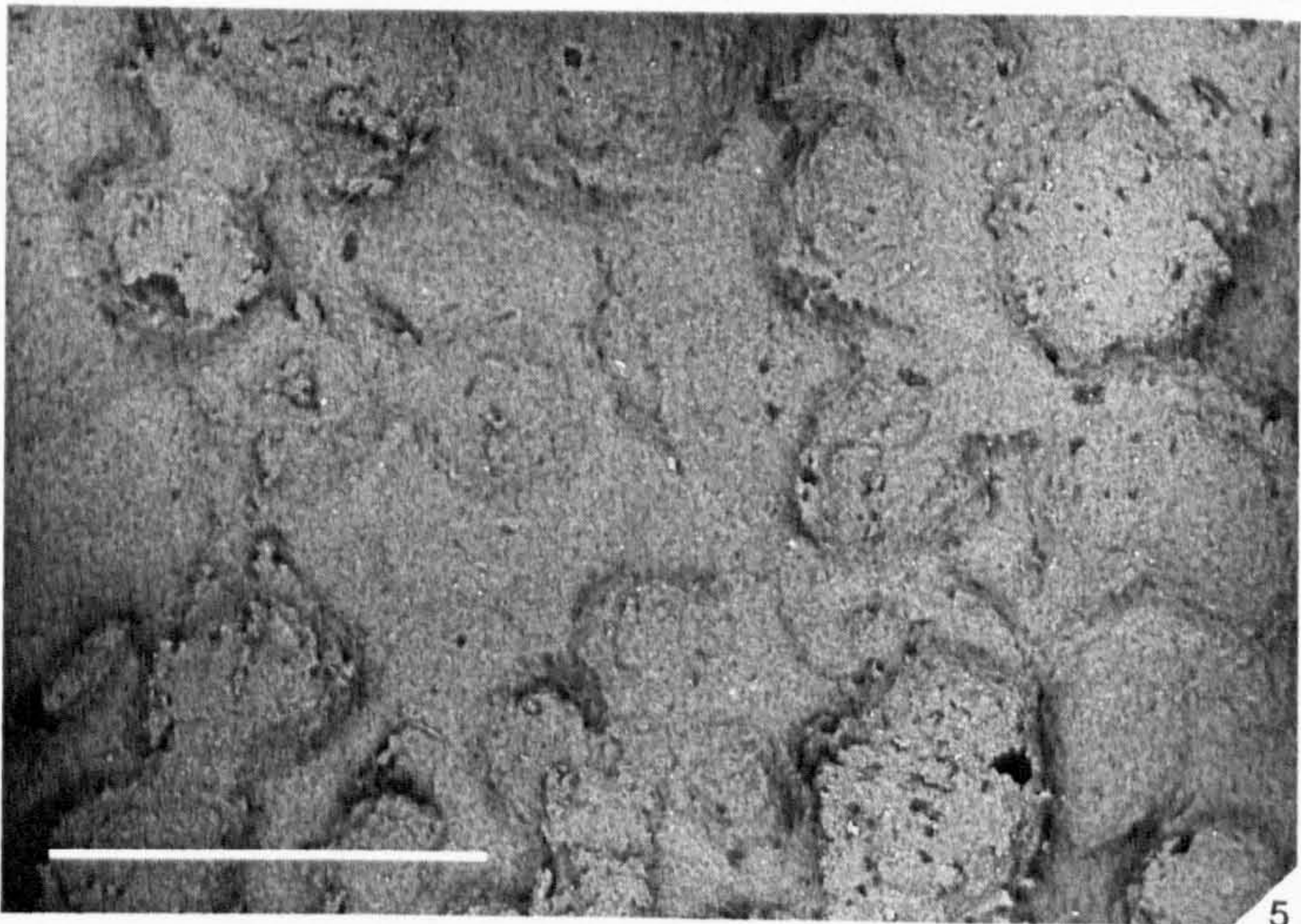
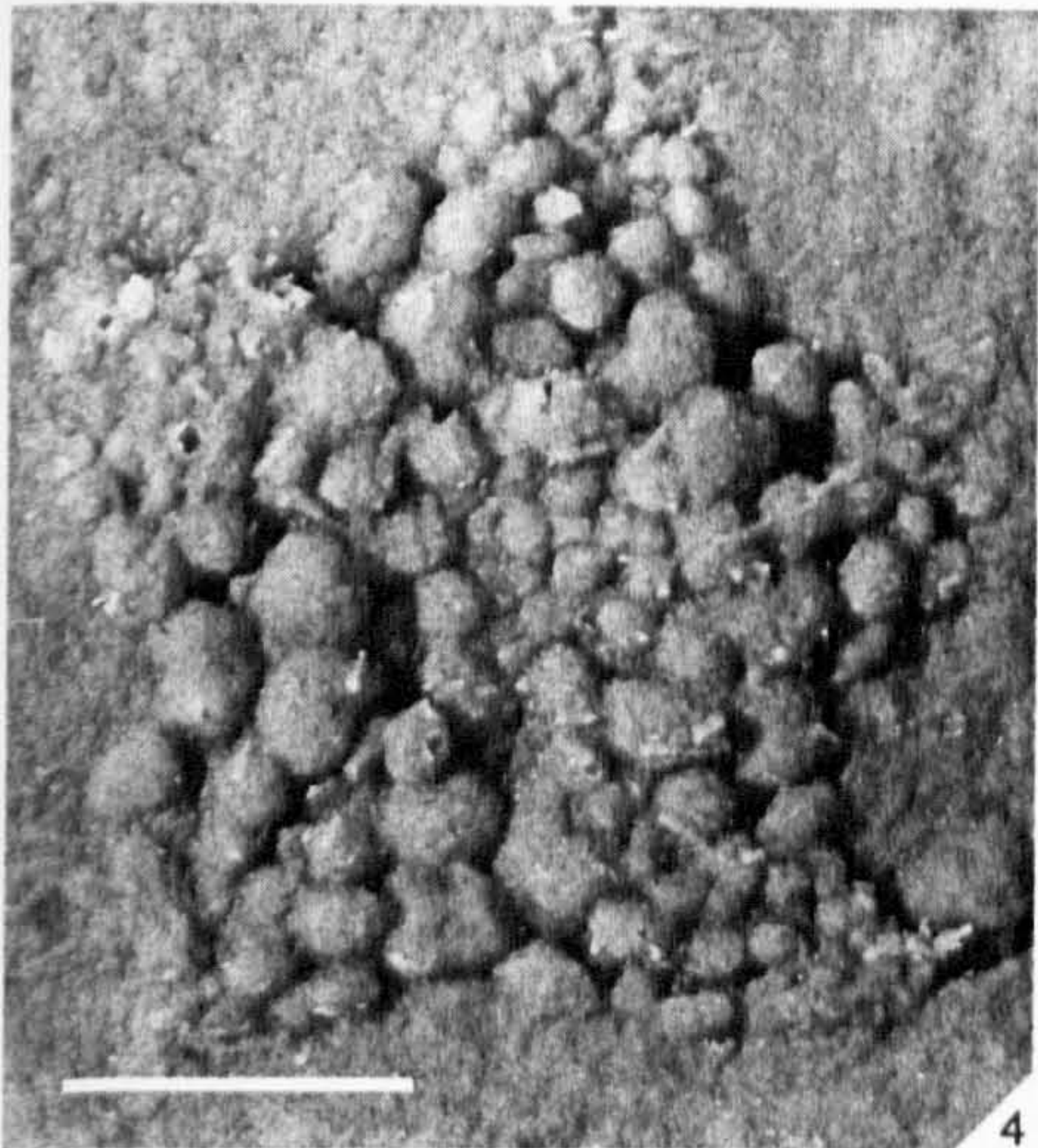
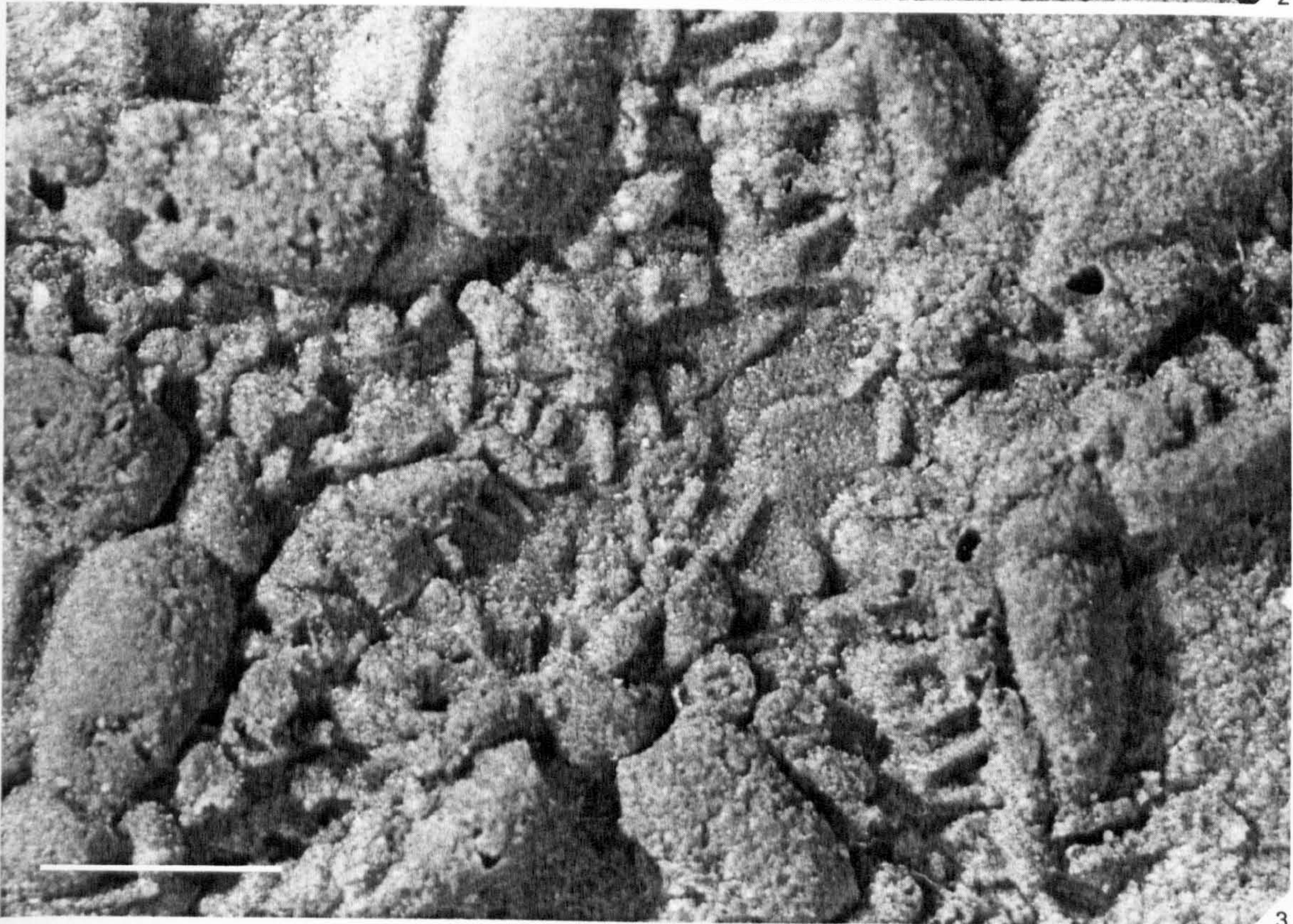
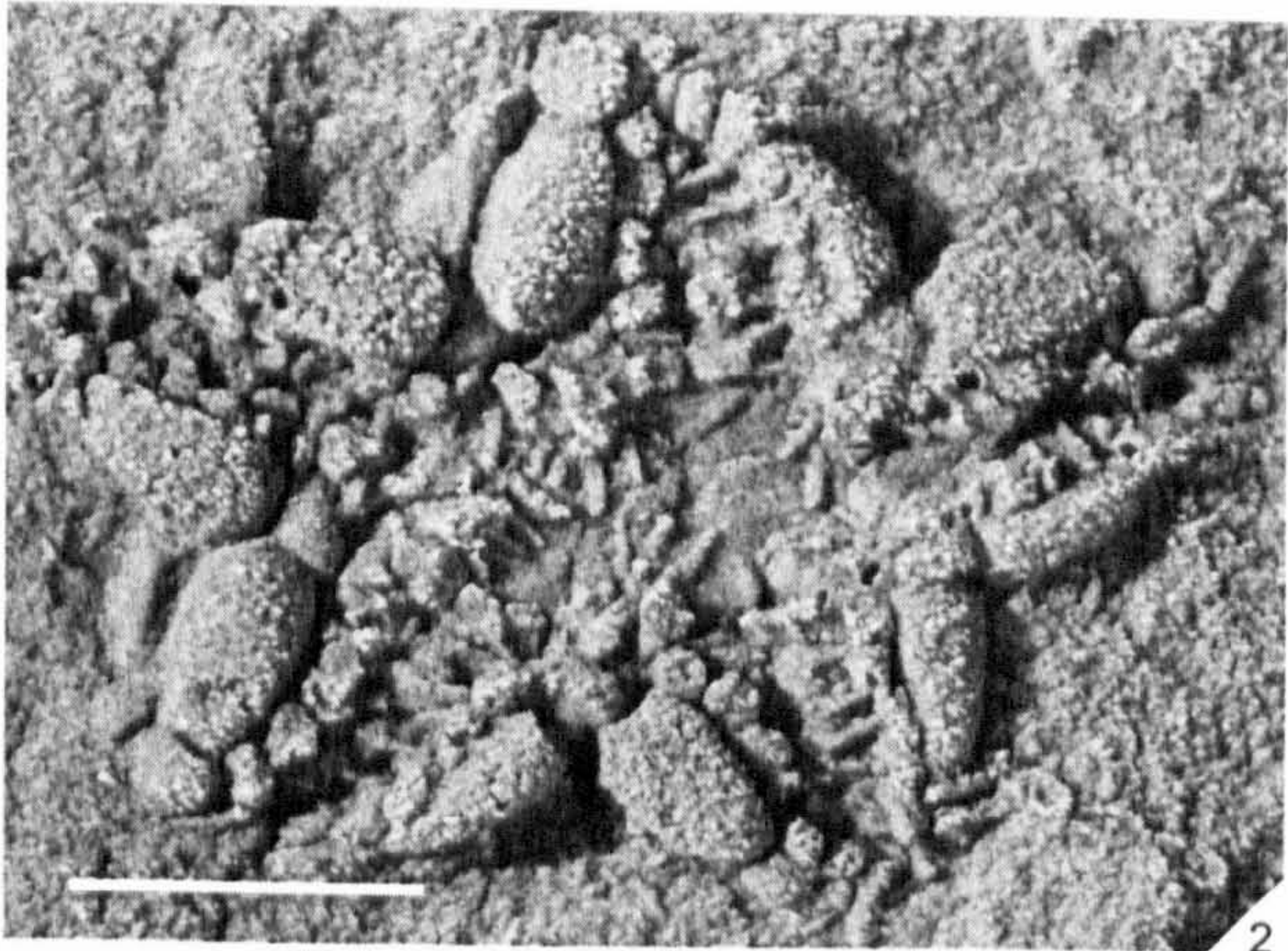
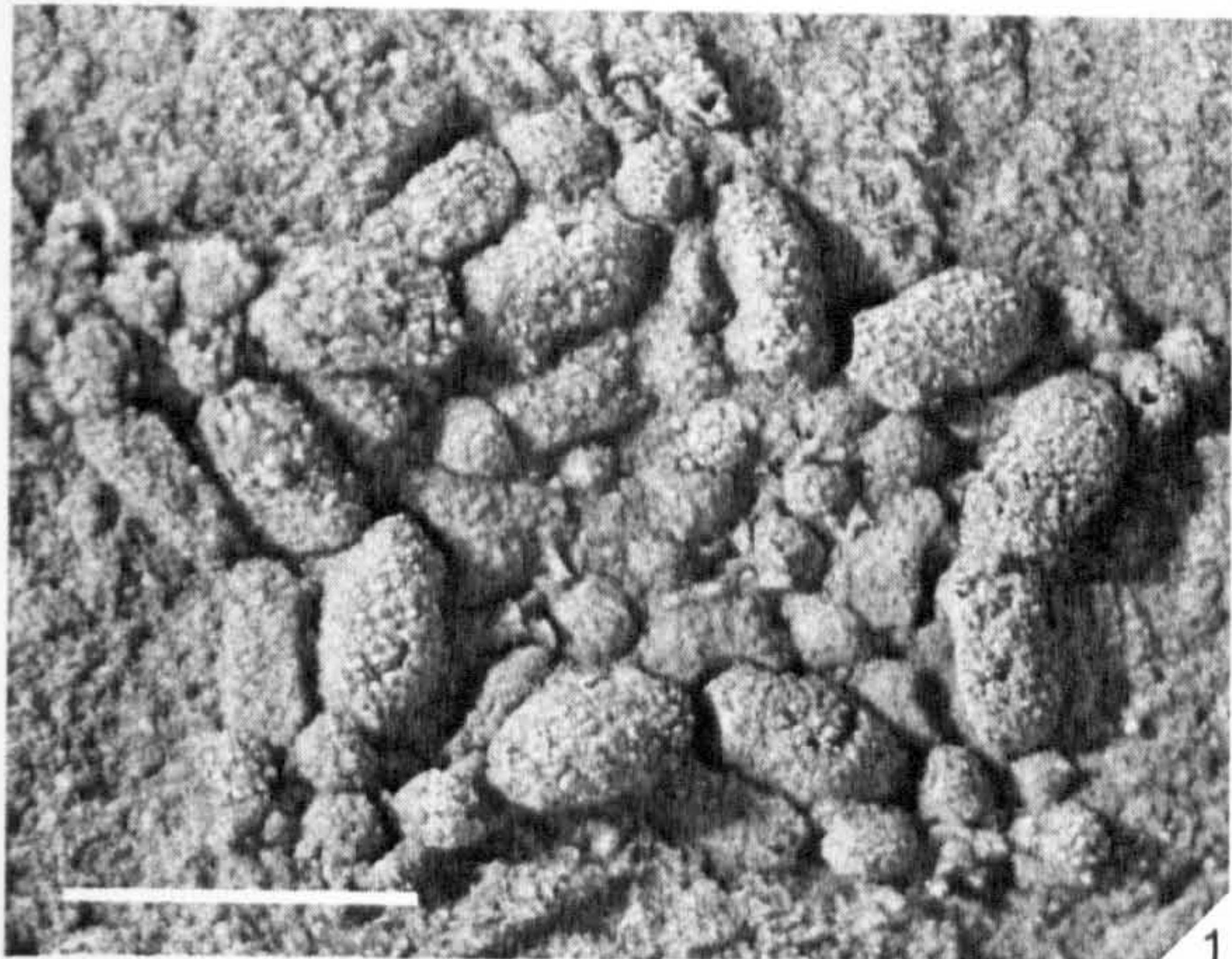
## EXPLANATION OF PLATE 3.2

Figs 1-3. *Cocaster?* sp.; part and counterpart. 1, NMS G1882651591. 1, entire specimen, dorsal view; scale bar represents 2 mm. 2-3, NMS G1882651593. 2, entire specimen, ventral view; scale bar represents 2 mm. 3, detail of mouth frame and proximal arms, ventral view; scale bar represents 1 mm.

Figs 4-5. *Mesopalaeaster? leintwardensis* Spencer, 1916. 4-5, BMNH E 13153, holotype. 4, entire specimen, dorsal view; scale bar represents 2 mm. 5, detail of central disc; scale bar represents 1 mm; SEM photomicrograph.

All specimens from the Lower Leintwardine Formation, Ludlow Series, Leintwardine, Herefordshire. All figures are of silicone casts.



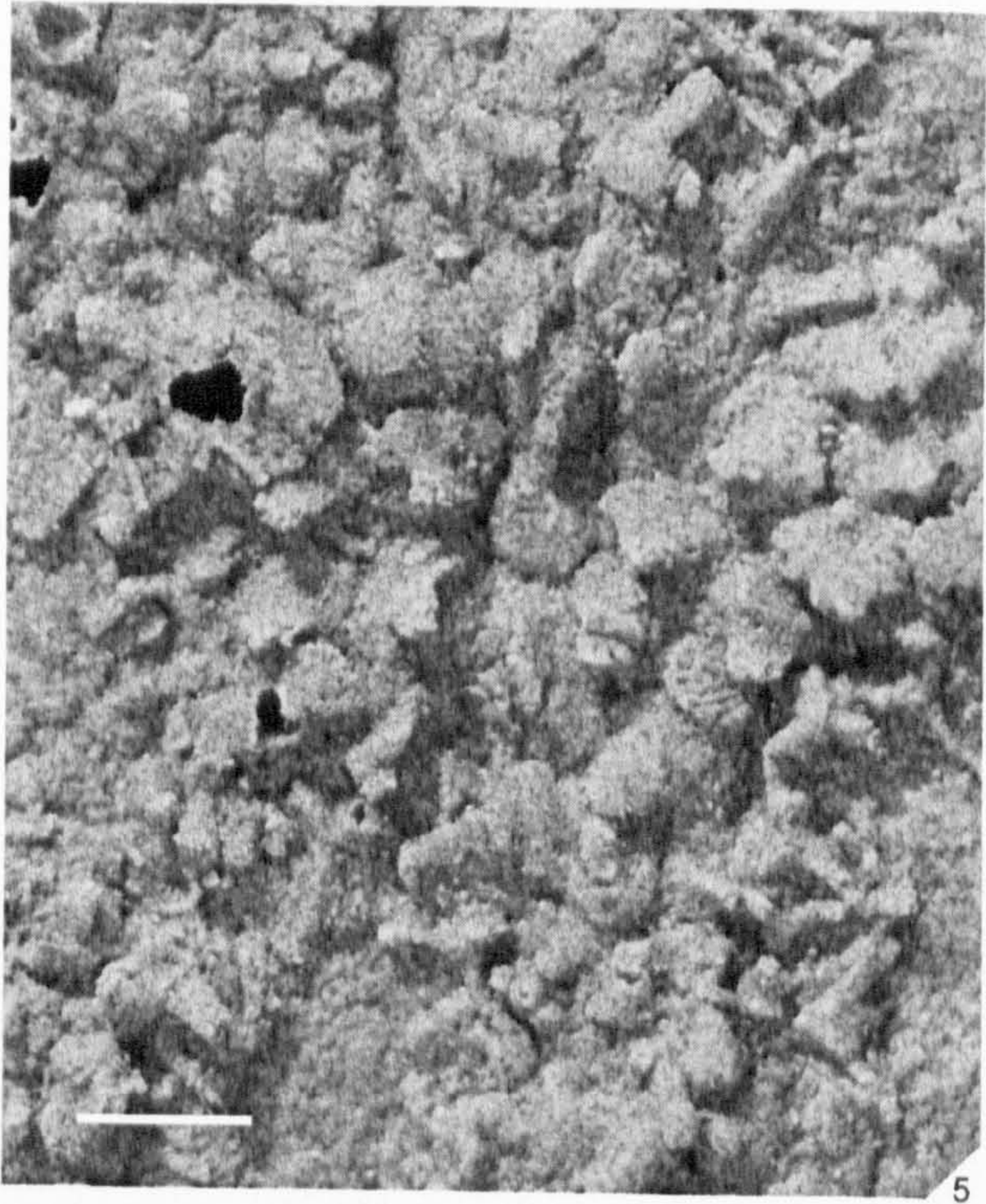
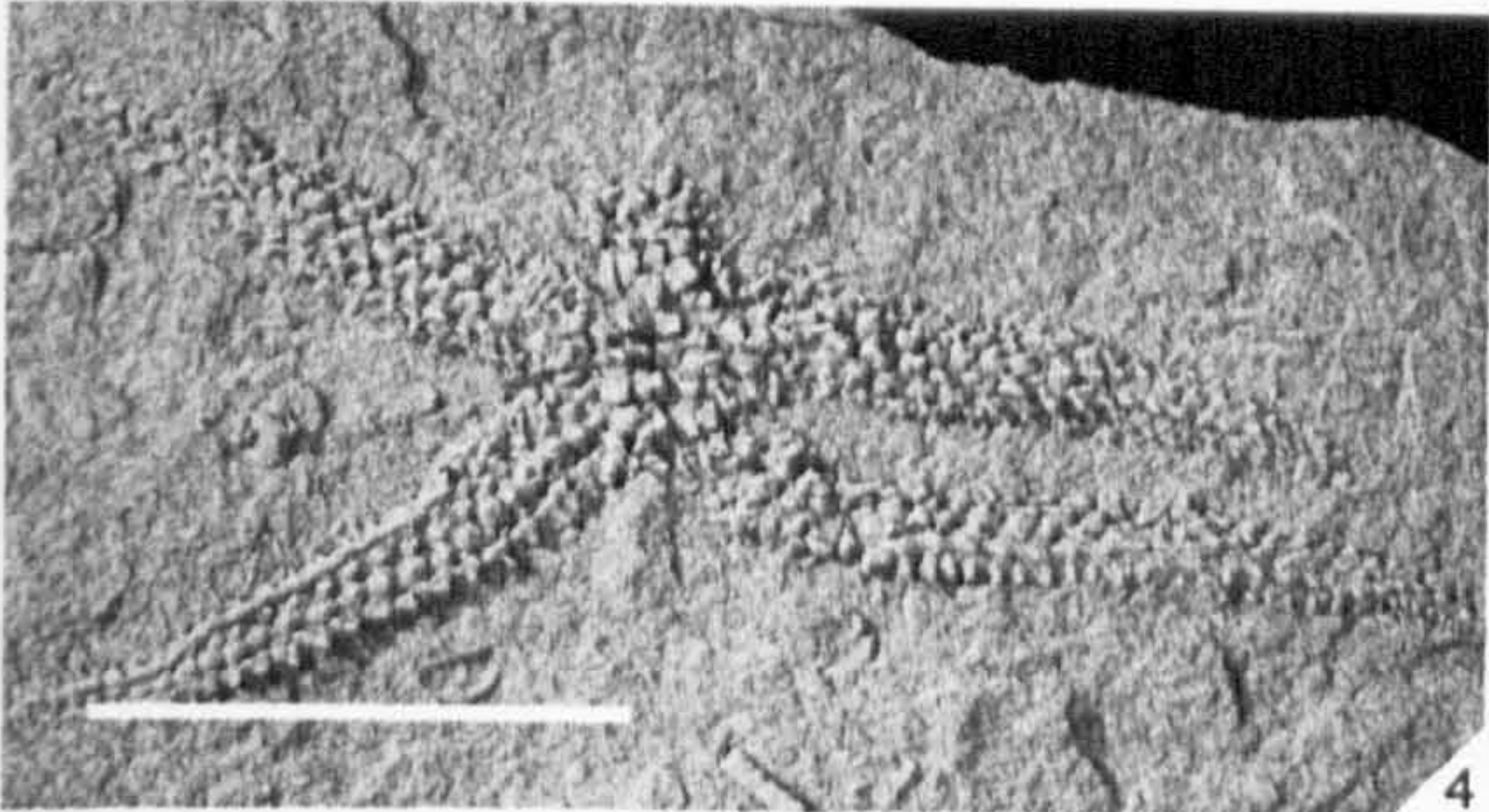
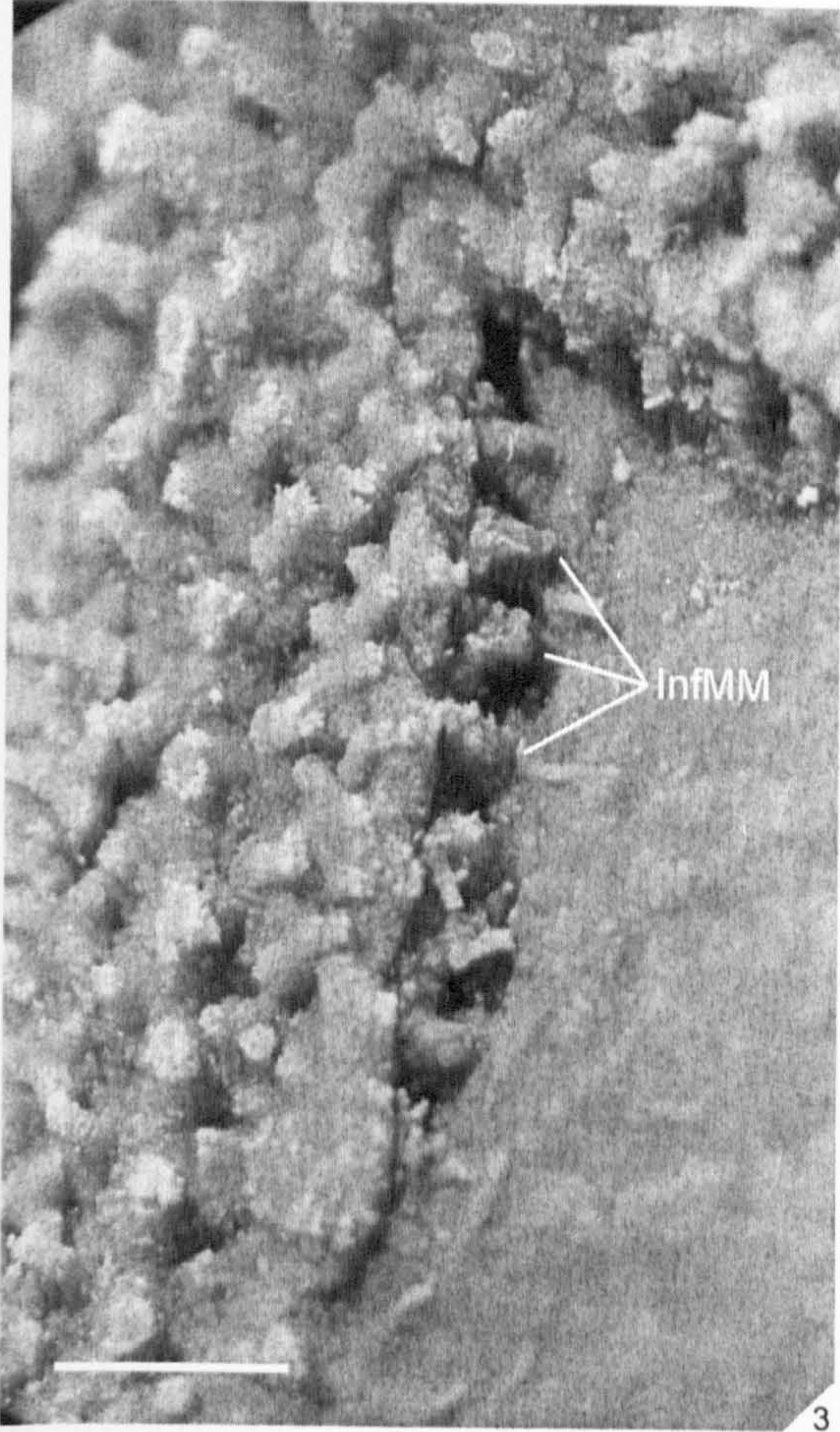
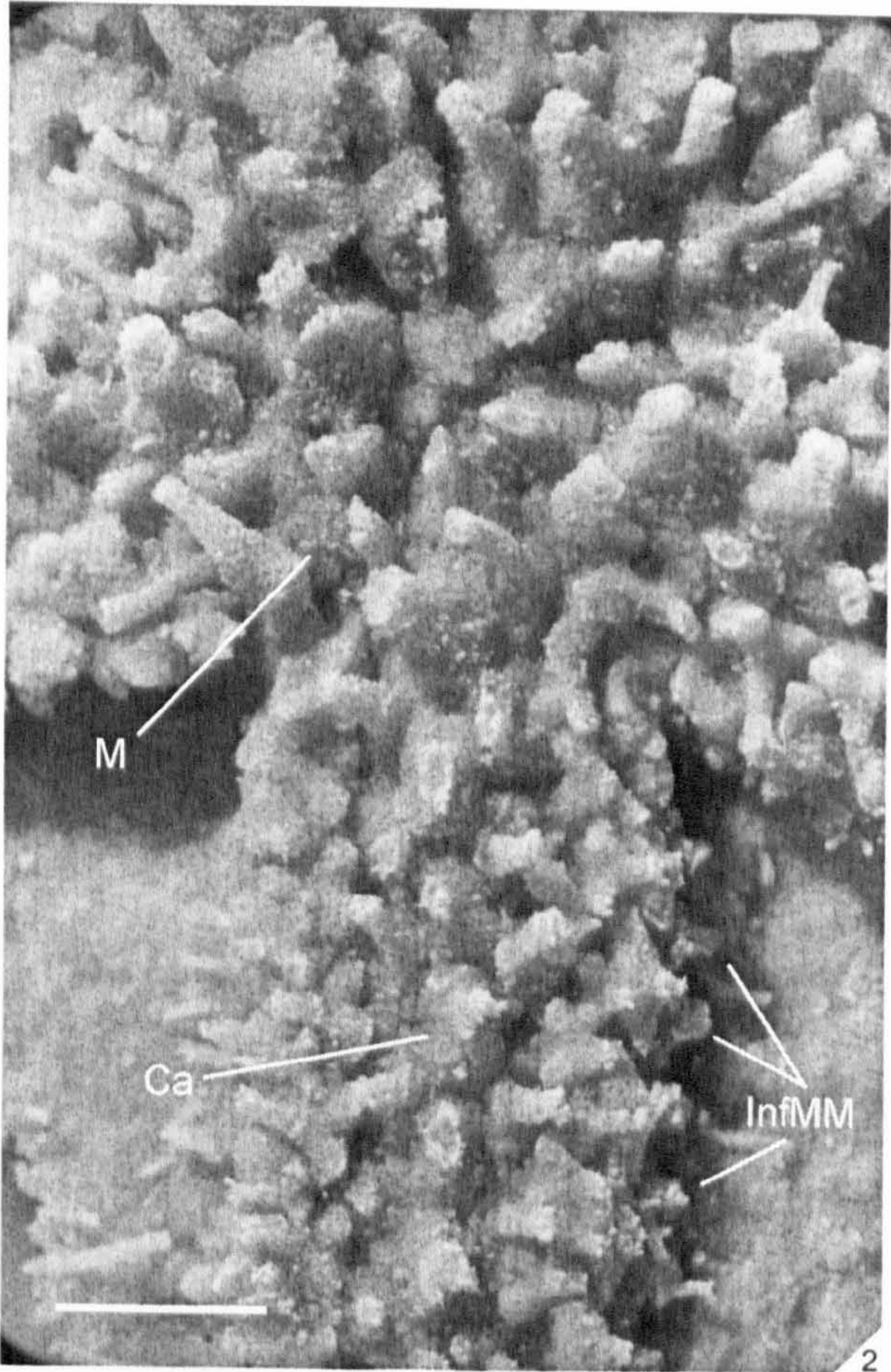
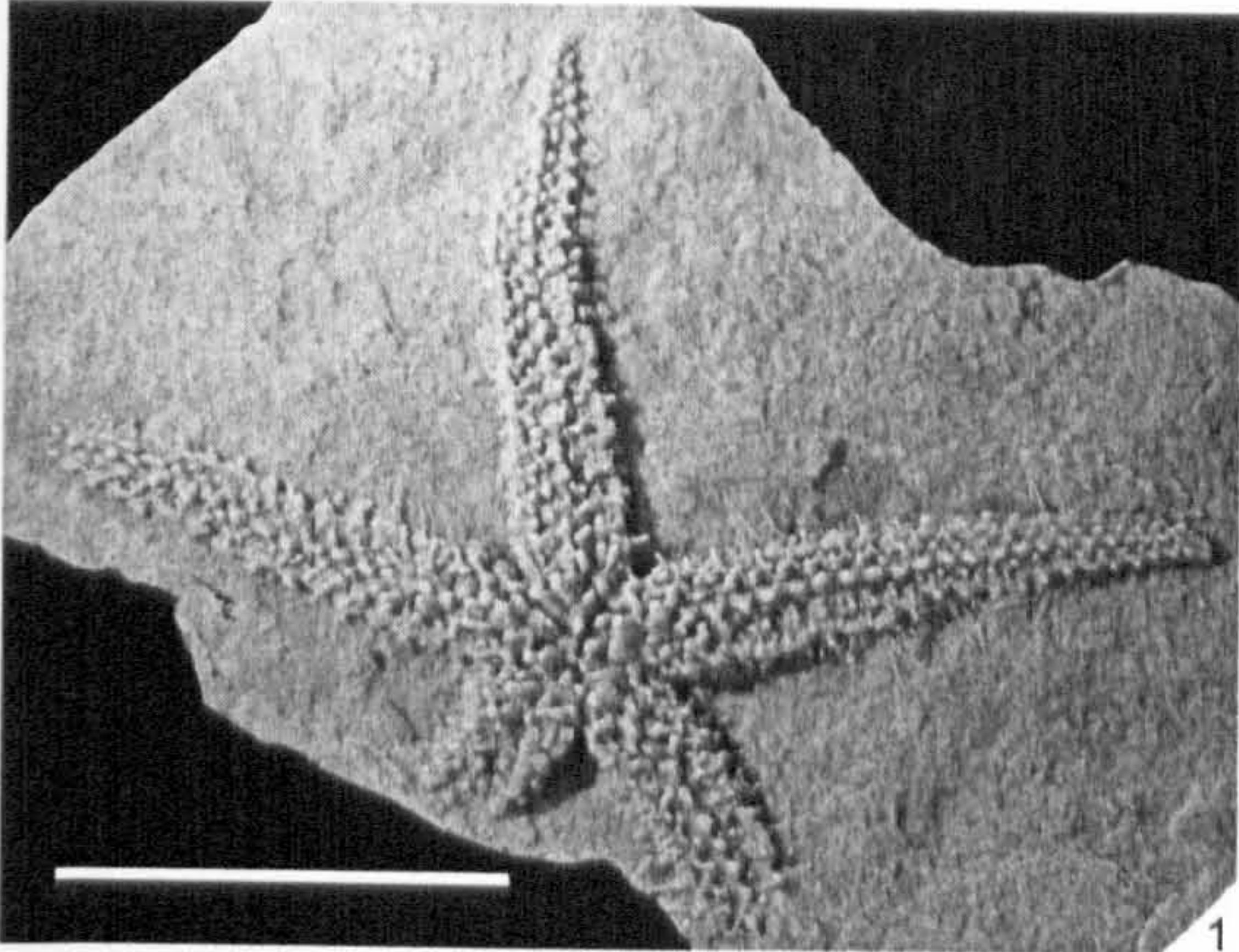




### EXPLANATION OF PLATE 3.3

Figs 1-5. *Urasterella ruthveni* (Forbes, 1848); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-3, BMNH E 13952. 1, entire specimen, dorsal view; scale bar represents 10 mm. 2, detail of central disc and proximal arm showing paxillose abactinals arranged into discrete columns, dorsal view; scale bar represents 1 mm. 3, detail of proximal arm showing paxillose abactinals and InfMM, dorsolateral view; scale bar represents 1 mm. 4-5, MM L11020. 4, entire specimen, dorsal view; scale bar represents 10 mm. 5, detail of central disc and proximal arms; scale bar represents 1 mm. All figures are of silicone casts.



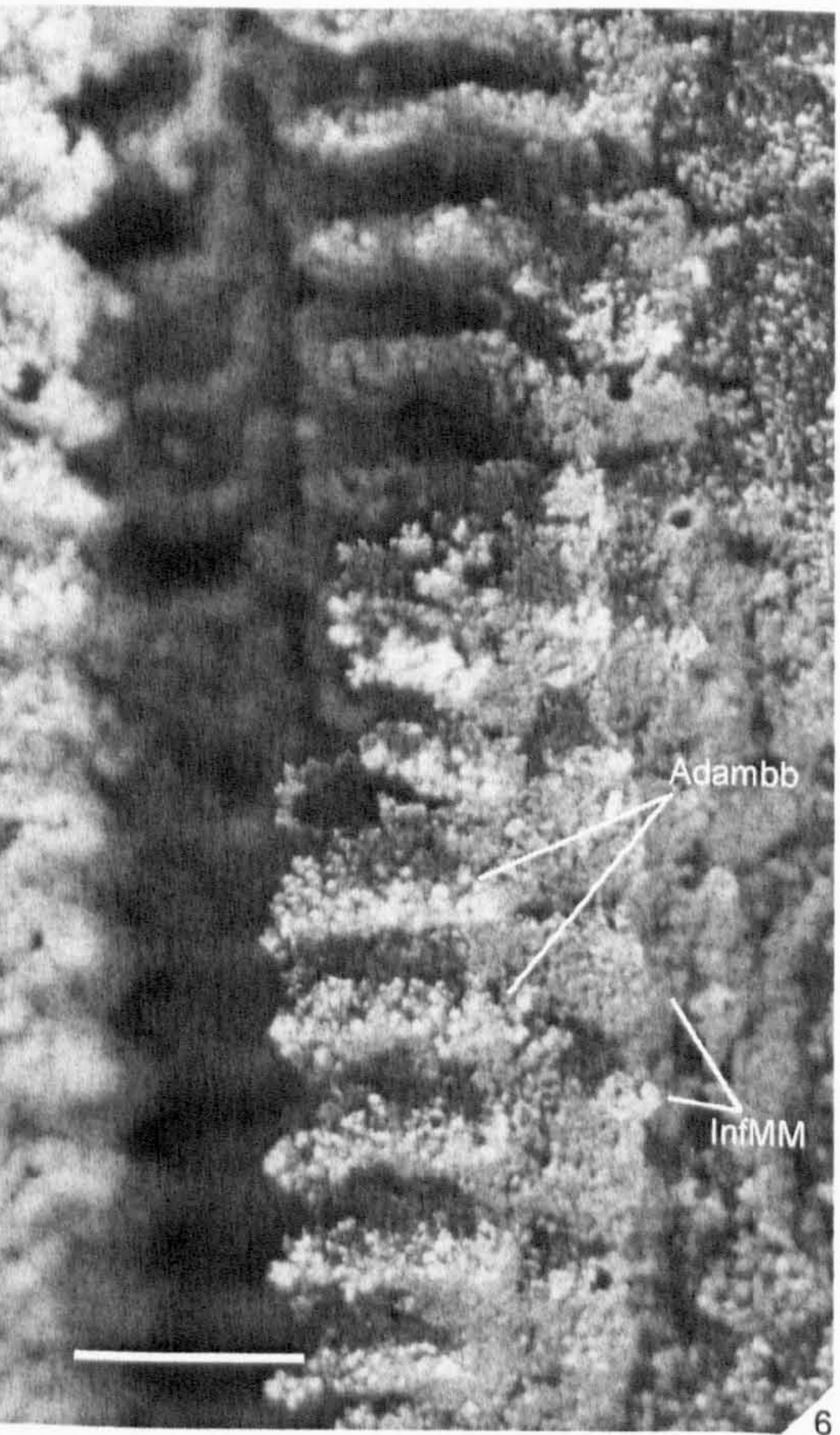
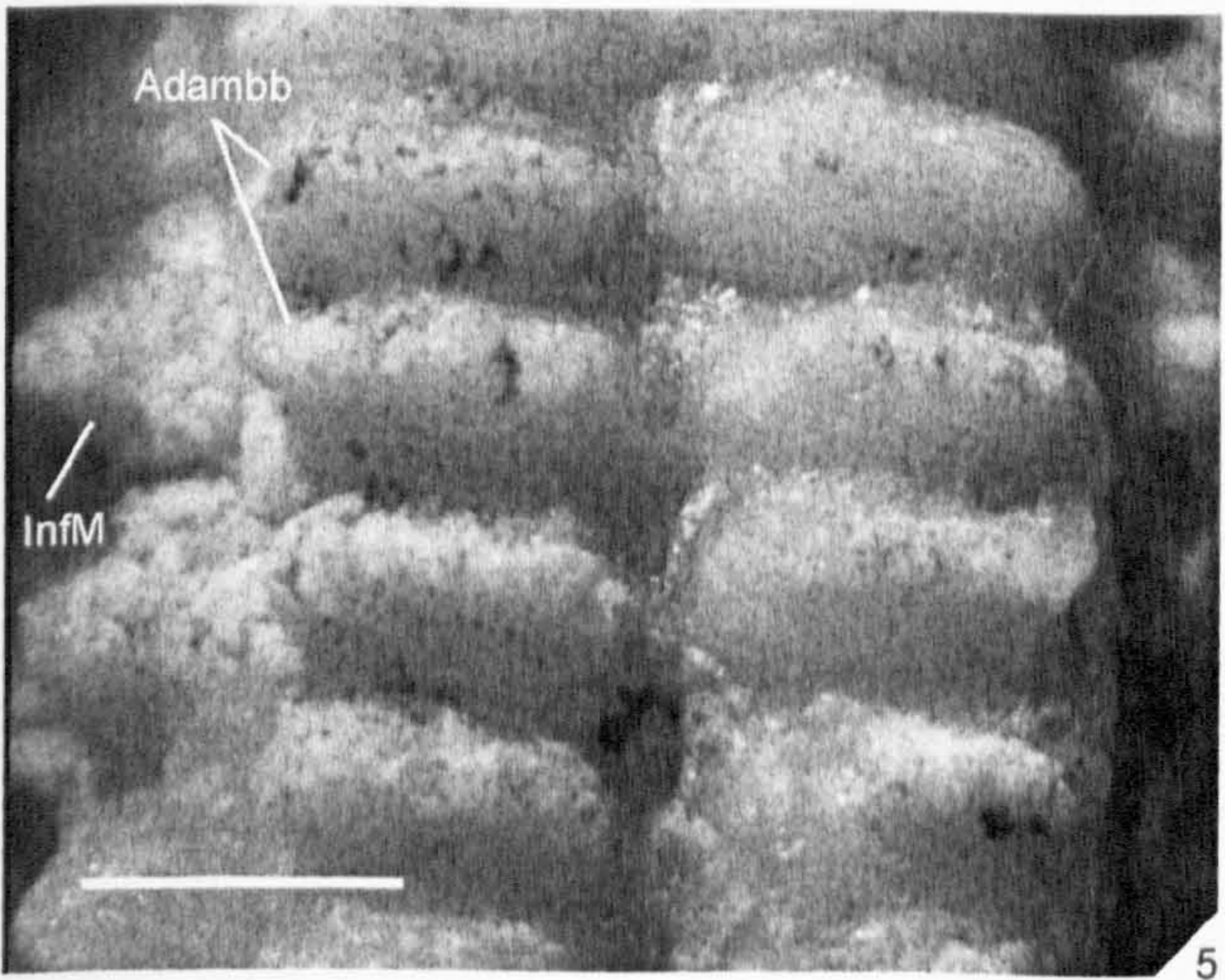
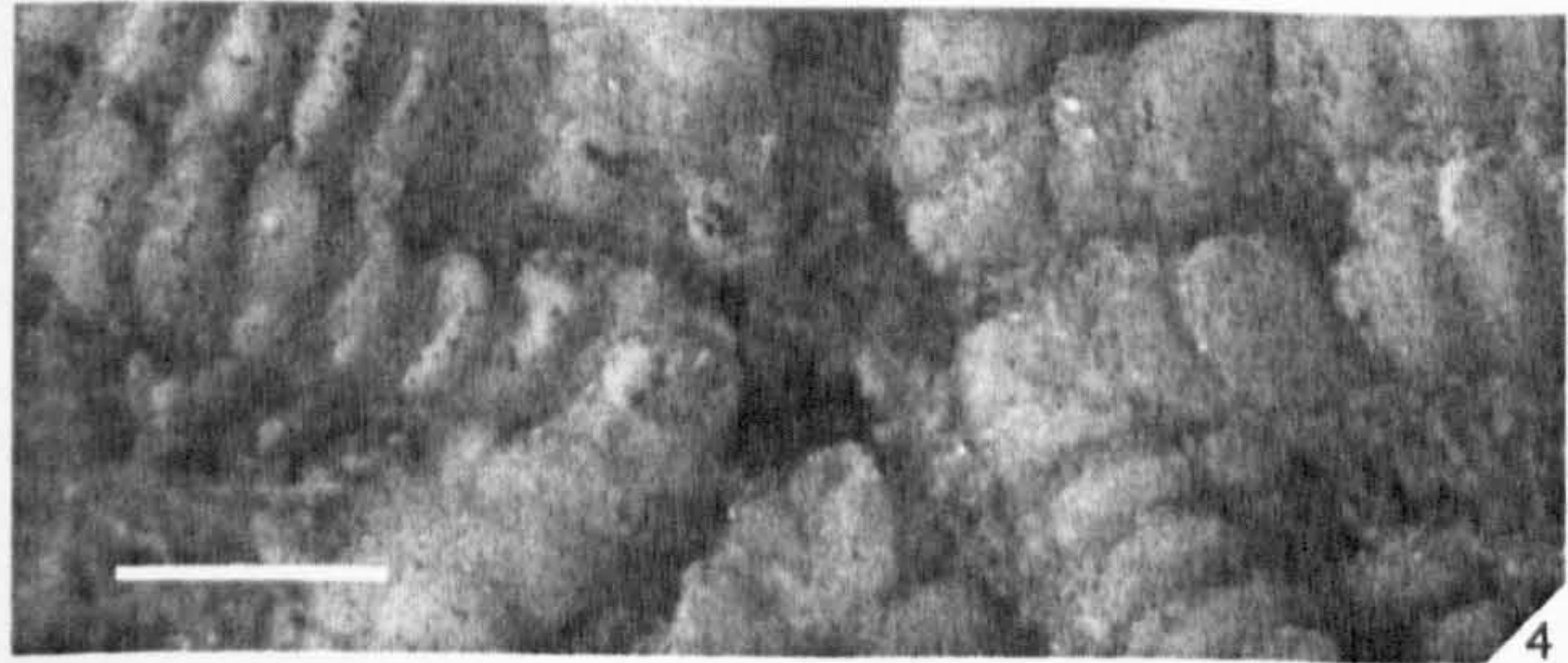
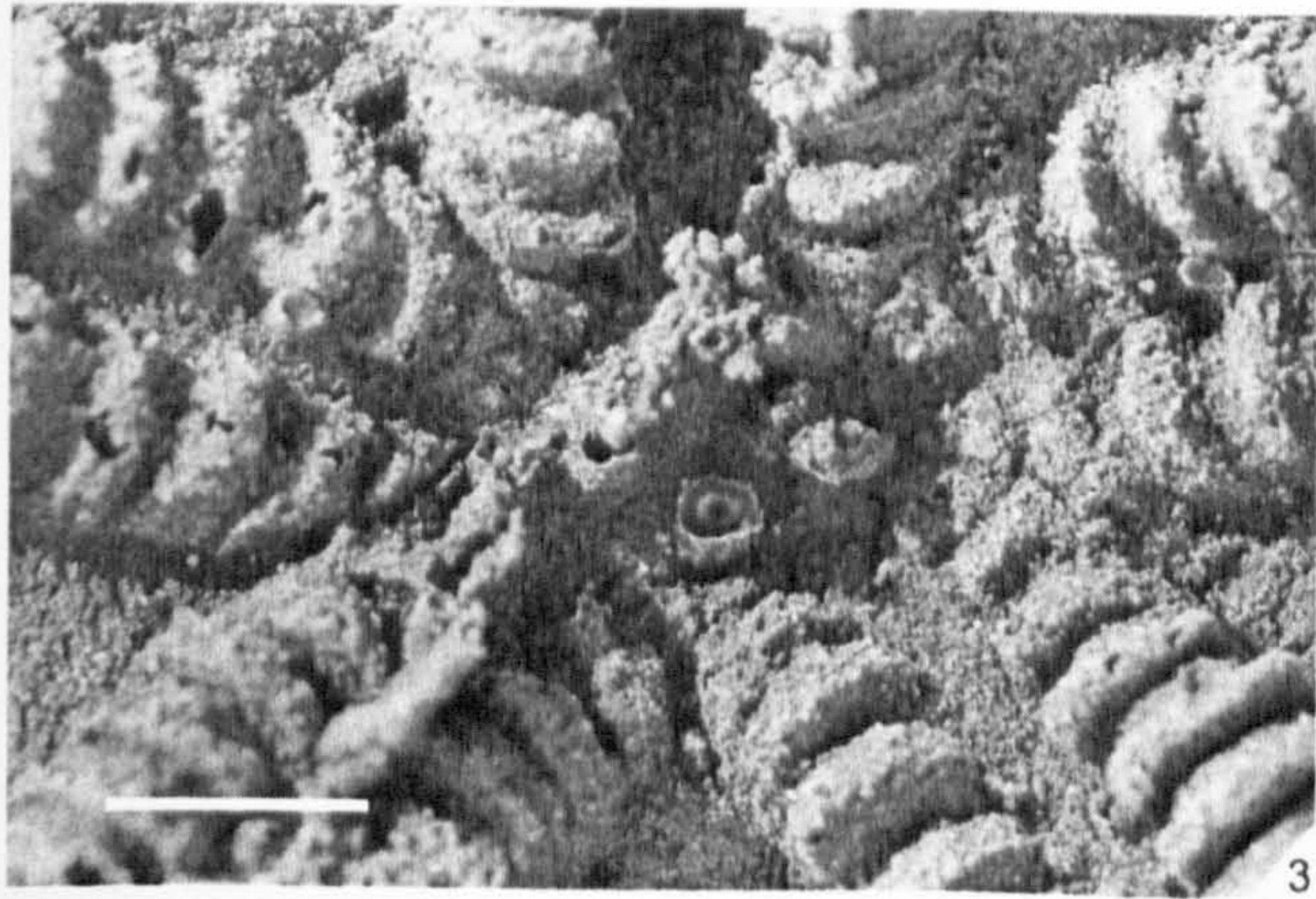
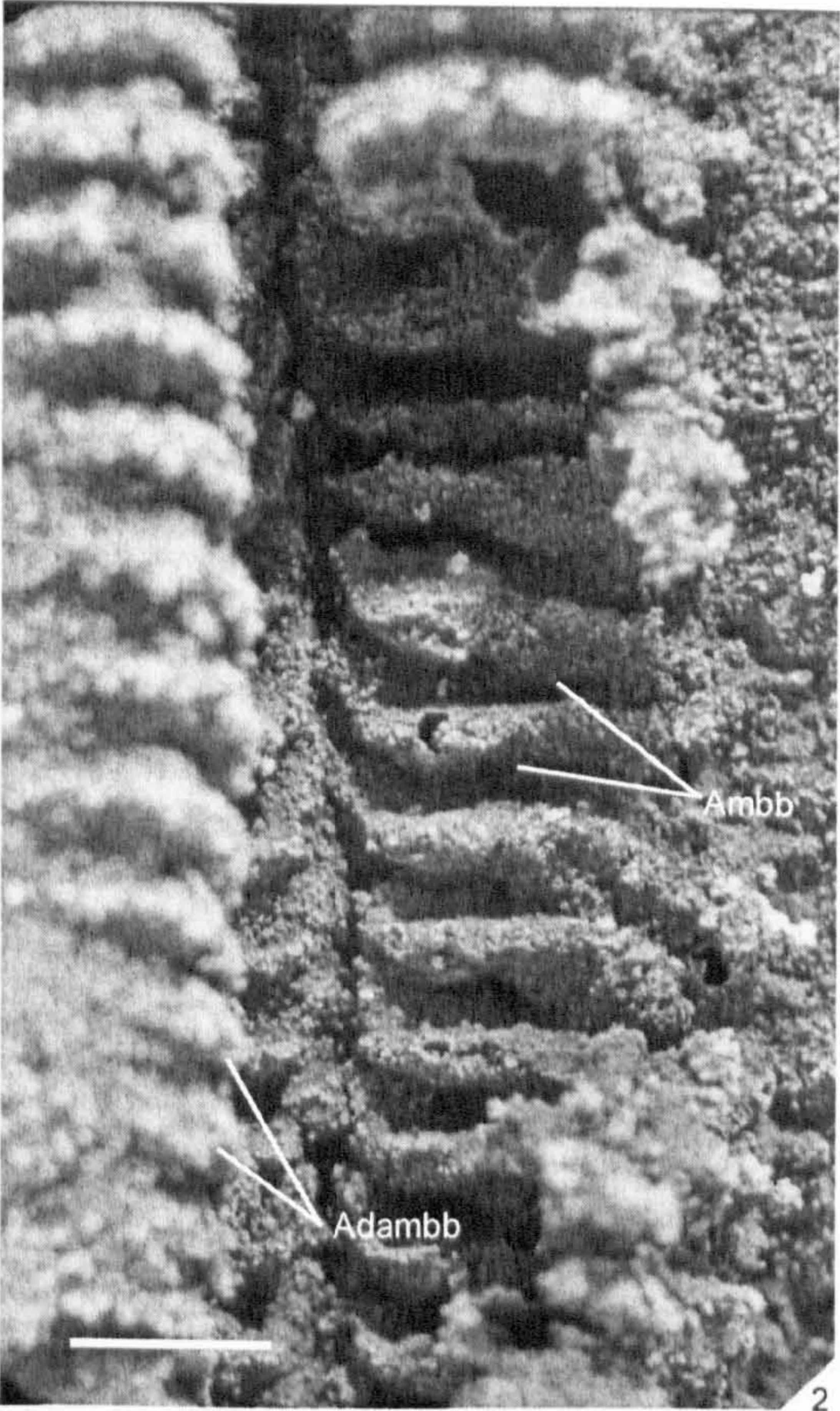
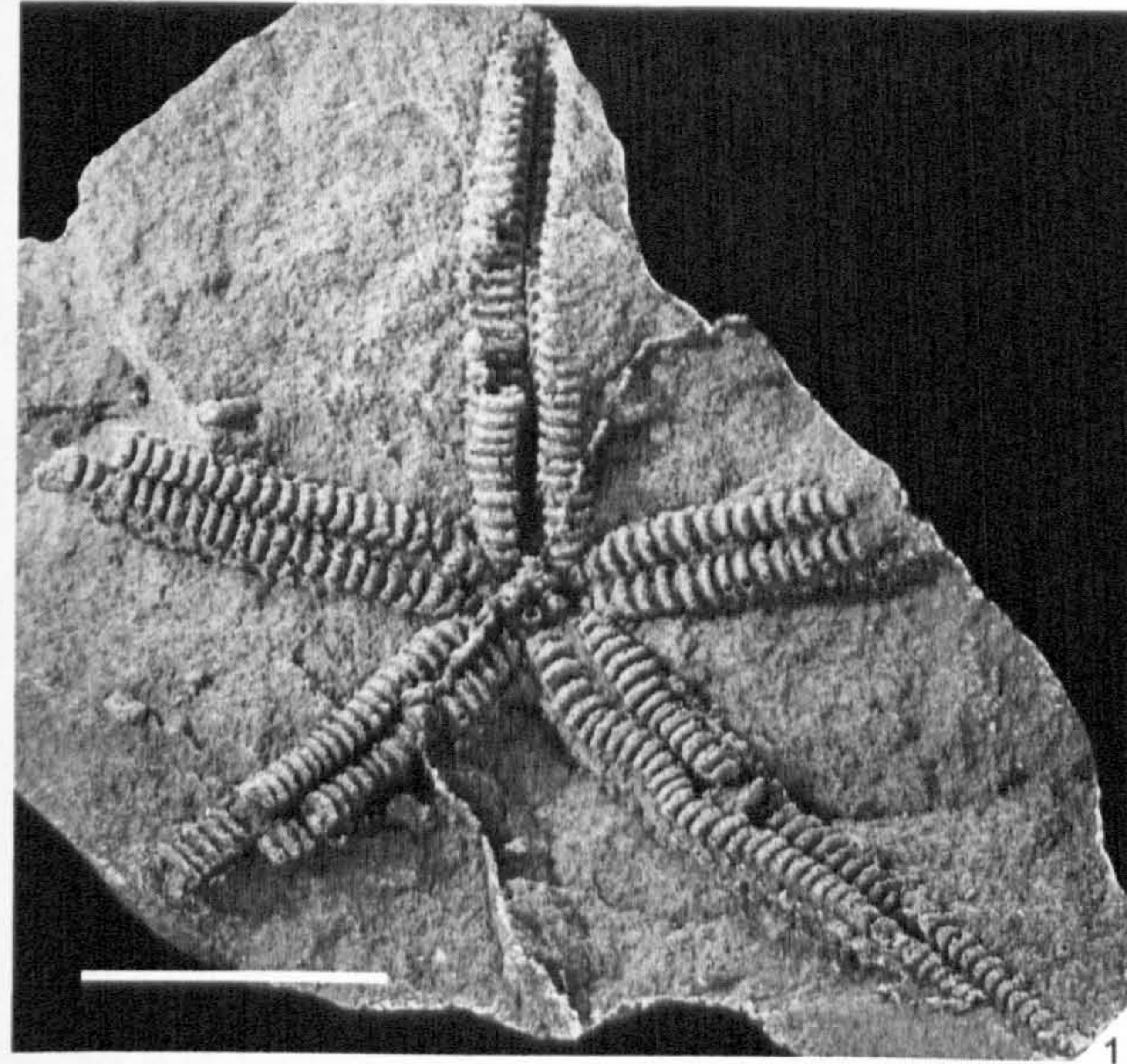




## EXPLANATION OF PLATE 3.4

Figs 1-6. *Urasterella ruthveni* (Forbes, 1848). 1-3, 6, CAMSM A5497, holotype; Bannisdale Slates, Ludlow Series; Underbarrow, Lake District, UK. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of mid arm showing Ambb; scale bar represents 1 mm. 3, detail of disc and proximal arms; scale bar represents 2 mm. 6, detail of mid arm showing Adambb with pronounced transverse ridges; scale bar represents 1 mm. 4-5, MGUH 27642; Wenlock Series, Visby, Gotland. 4, detail of mouth frame and proximal arms, ventral view; scale bar represents 2 mm. 5, detail of mid arm showing Adambb with pronounced transverse ridges; scale bar represents 1 mm. All figures are of silicone casts except 4-5.



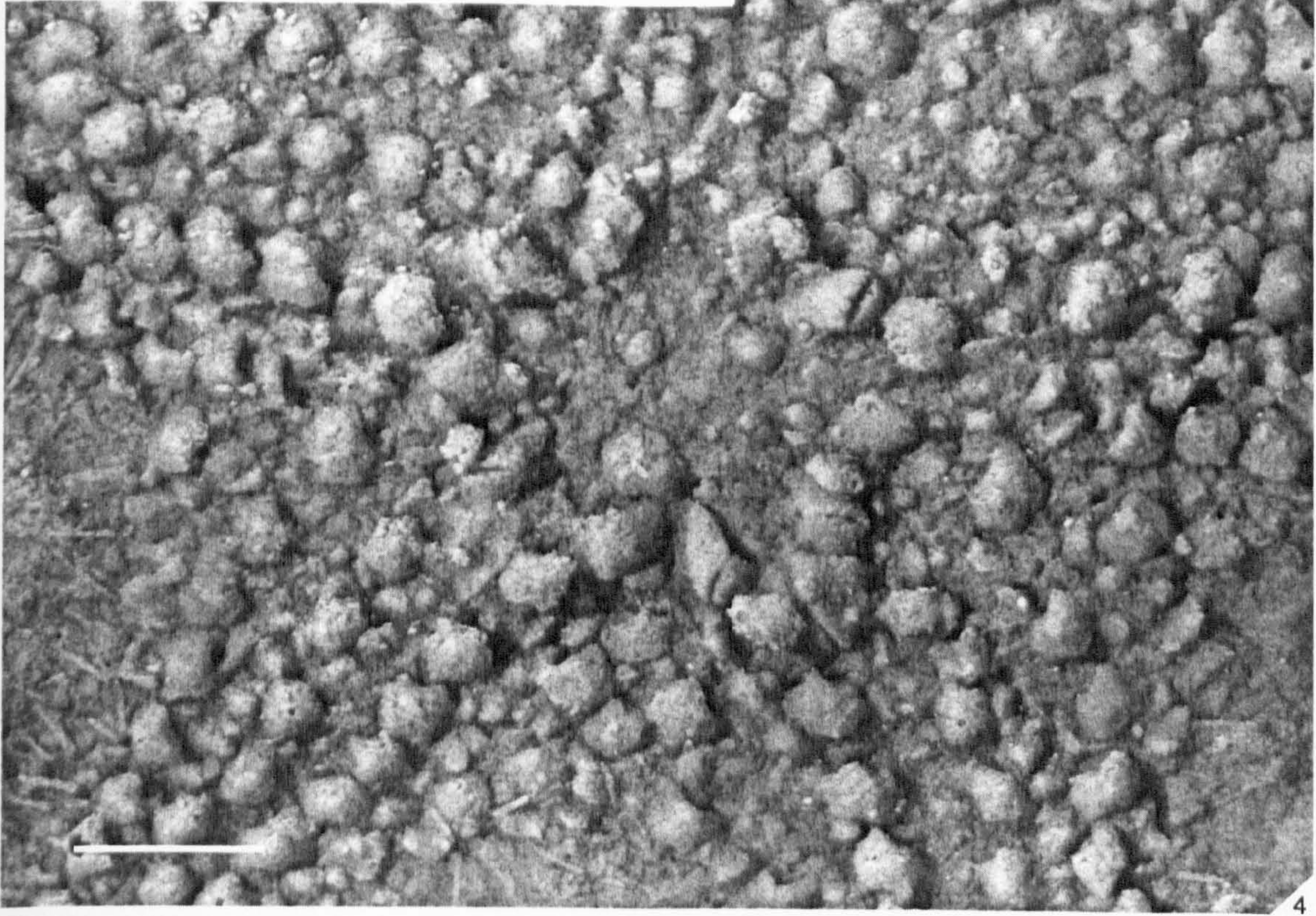
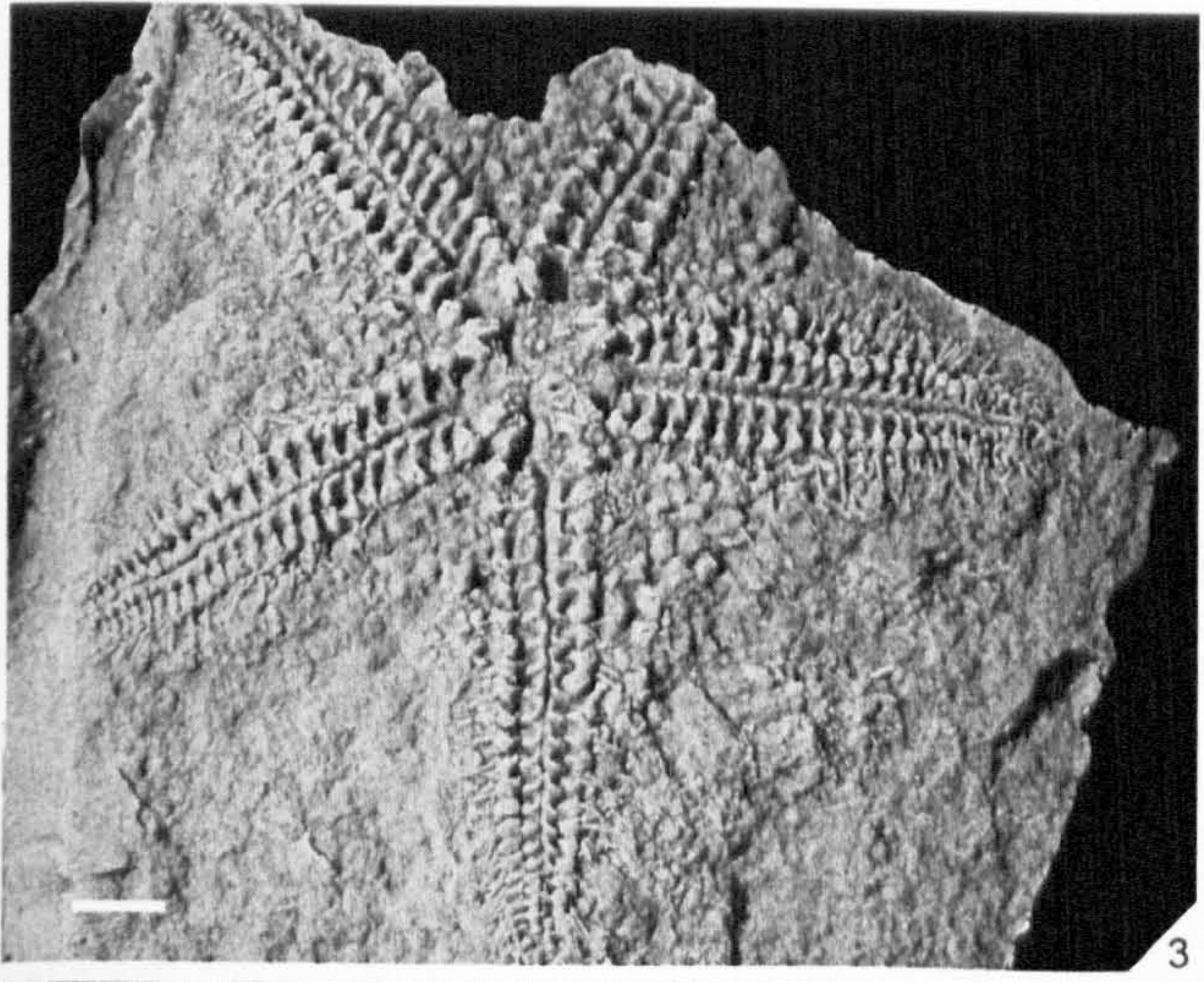
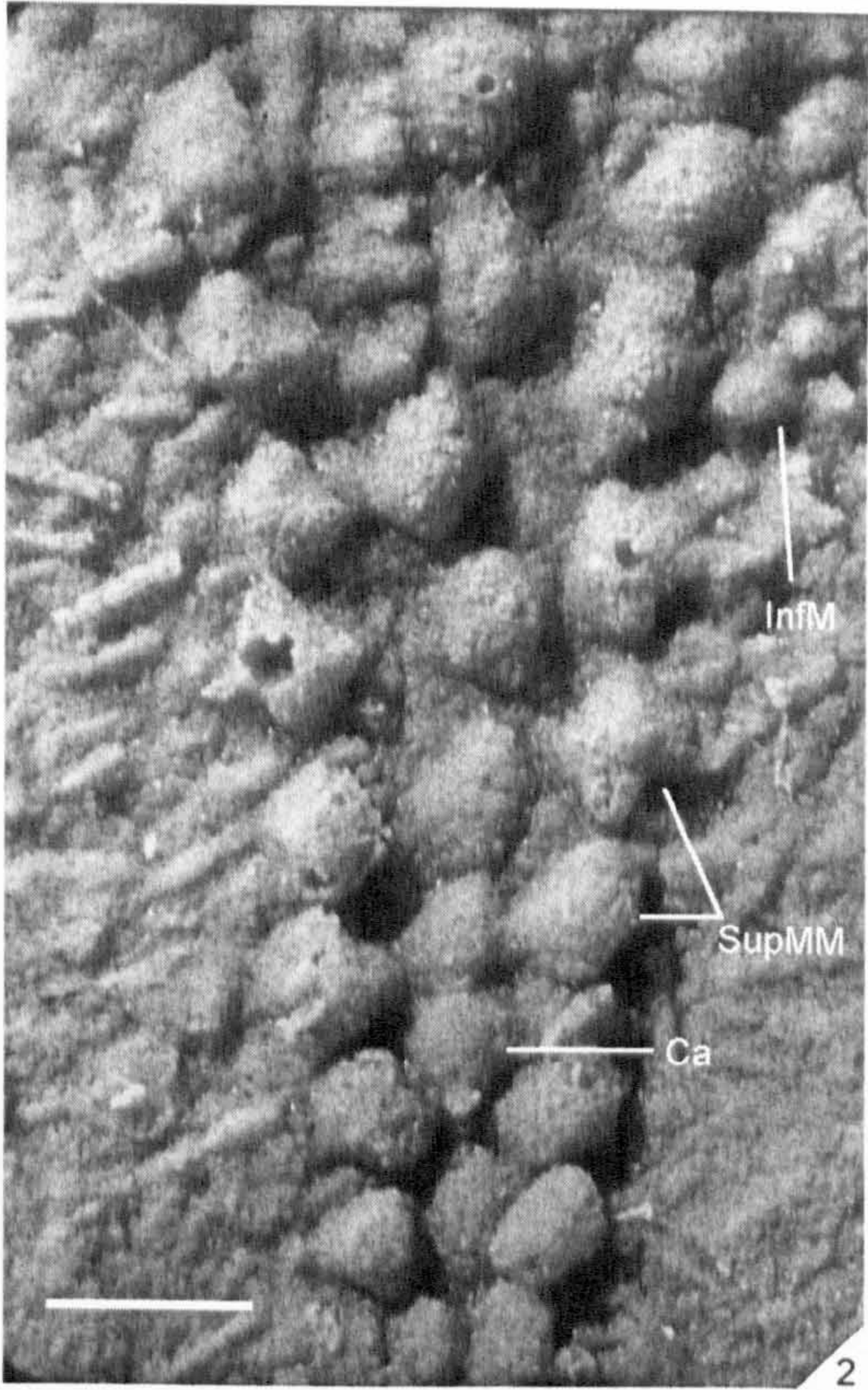
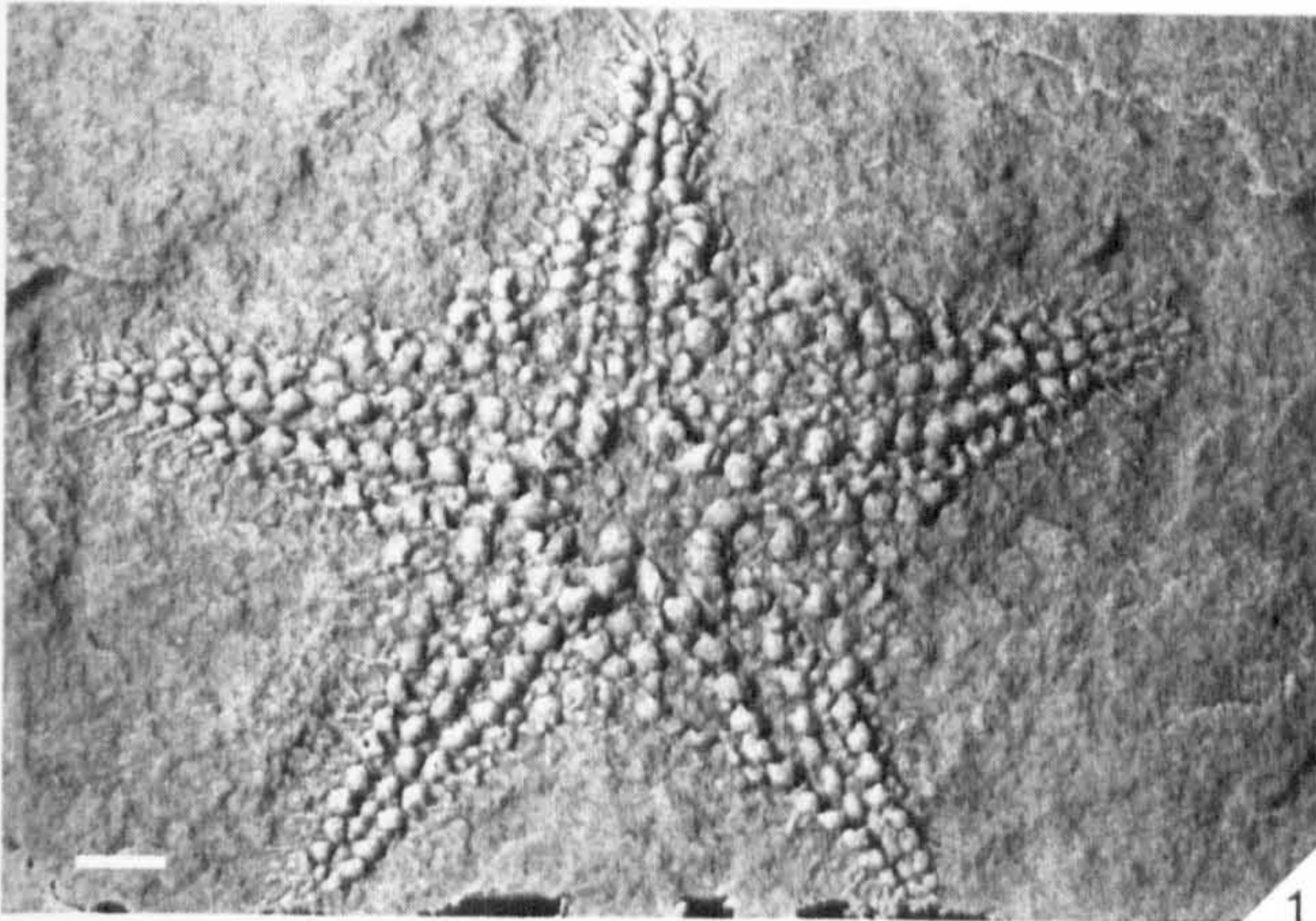




## EXPLANATION OF PLATE 3.5

Figs 1-4. *Palasterina* cf. *antiqua* (Hisinger, 1837); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-4, BMNH 40299a-b, part and counterpart. 1, 2, 4, BMNH 40299a. 2, entire specimen, dorsal view; scale bar represents 2 mm. 2, Detail of proximal arm showing carinals, SupMM and InfMM, dorsal view; scale bar represents 1 mm. 4, dorsal view of central disc and proximal arms showing carinals, SupMM, InfMM and abactinals; scale bar represents 2 mm. 3, BMNH 40299b, entire specimen, ventral view; scale bar represents 2 mm. All figures are of silicone casts.



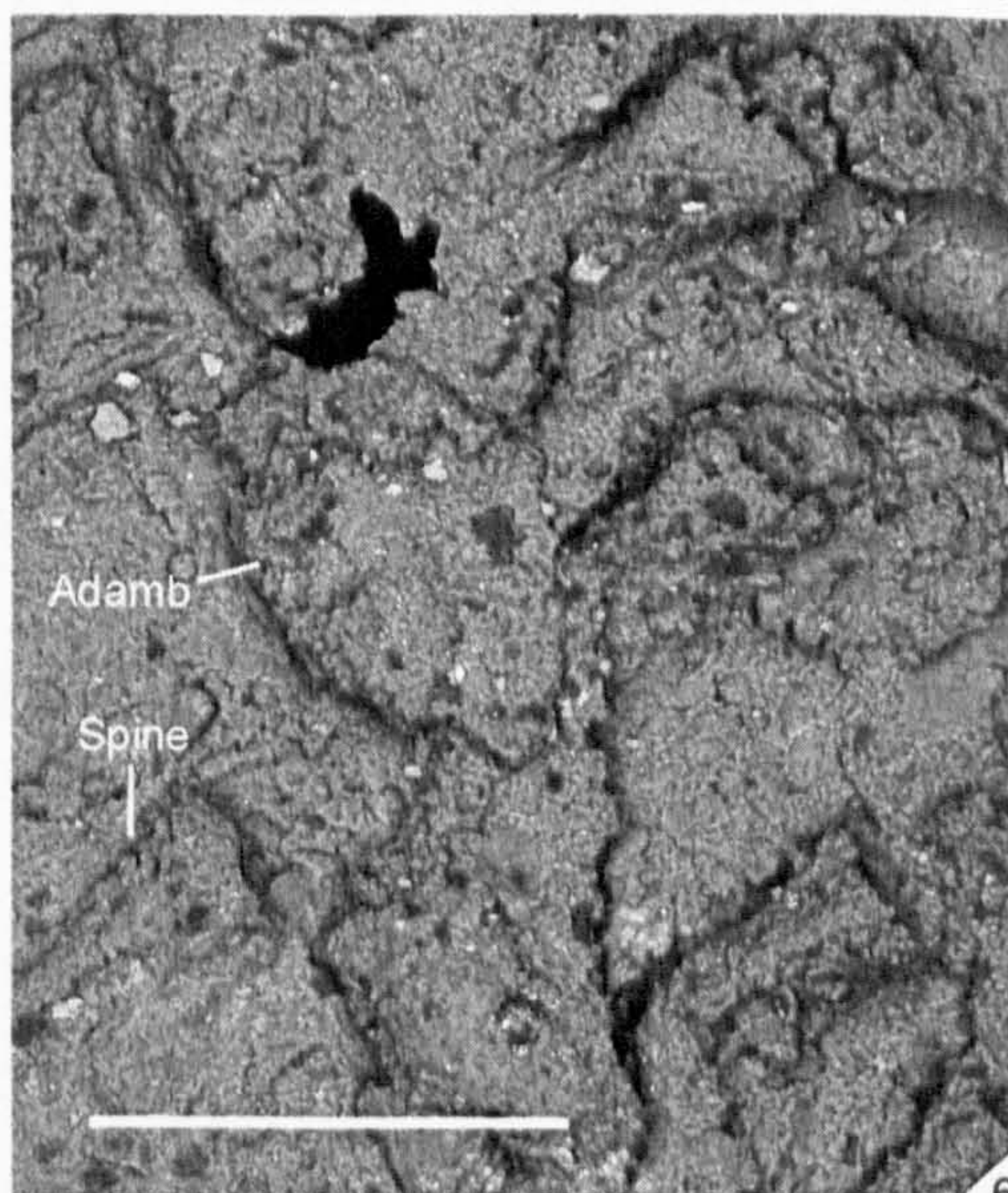
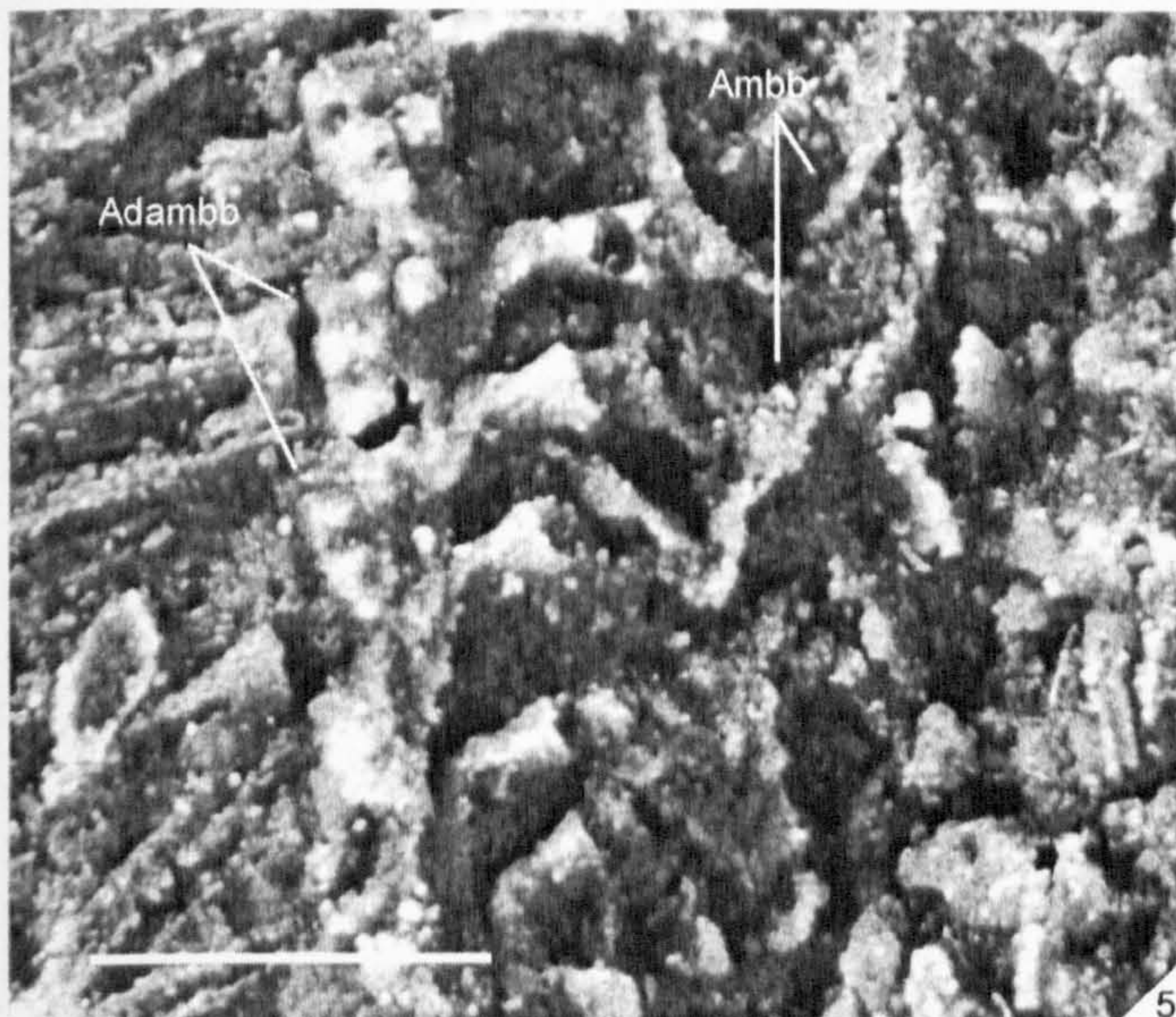
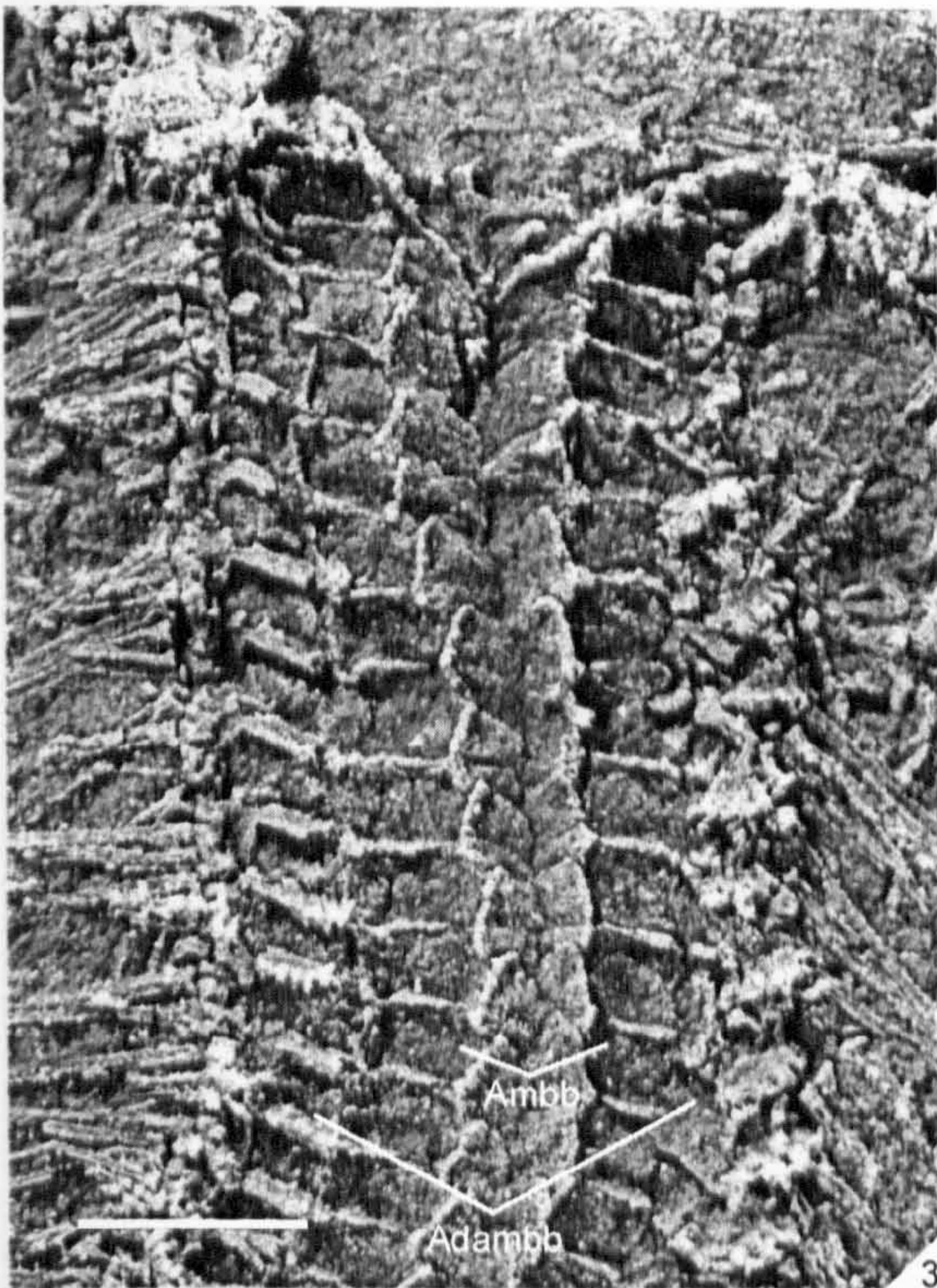
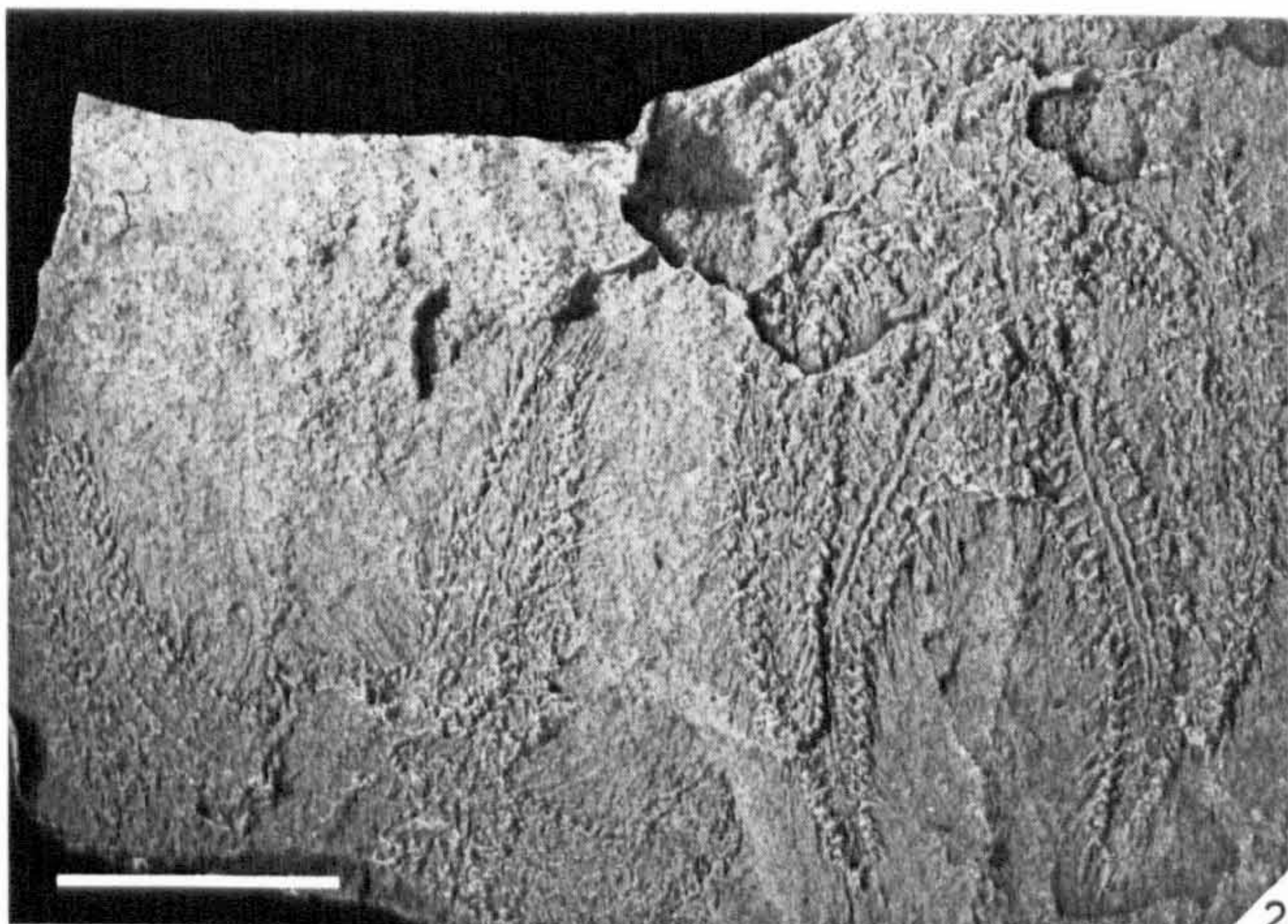
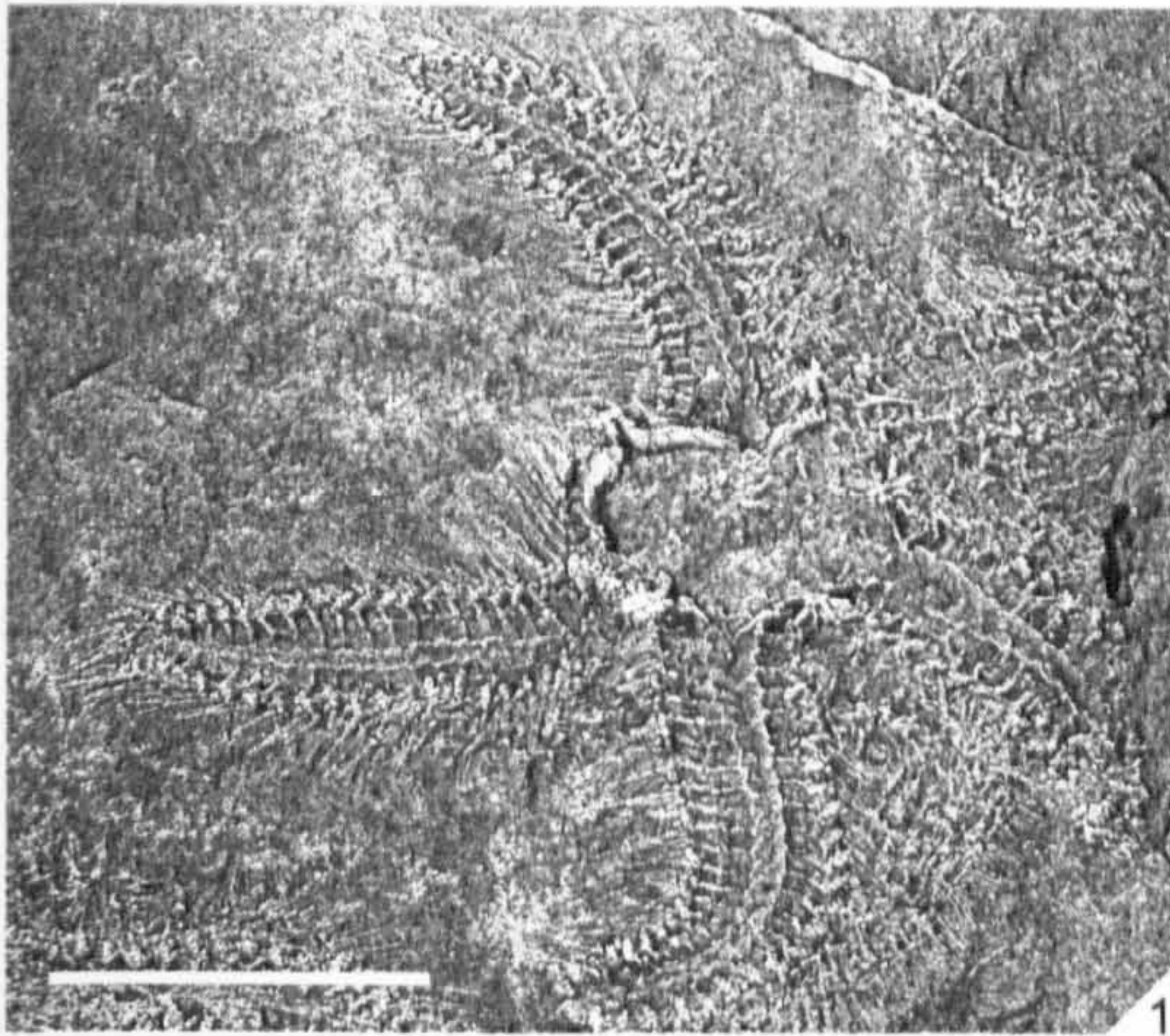




## EXPLANATION OF PLATE 3.7

Figs 1-6. *Sturtzaster marstoni* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, 3, OUM C.30631a. 1, entire specimen (specimen '1'), ventral view; scale bar represents 10 mm. 3, detail of proximal arm of specimen '1', ventral view; scale bar represents 1 mm. 2, 4, OUM C.30631b. 2, two entire specimens, one in dorsal view (specimen '1'), one in ventral view (specimen '2'); scale bar represents 10 mm. 4, detail of arm showing Ambb, Adambb and wide open ambulacral channel of specimen '2', ventral view; scale bar represents 1 mm. 5-6, BMNH E 13948. 5, detail of distal arm showing Adambb, ventral view; scale bar represents 1 mm. 6, detail of Adambb, ventral view; scale bar represents 500  $\mu\text{m}$ ; SEM photomicrograph. All figures are of silicone casts.



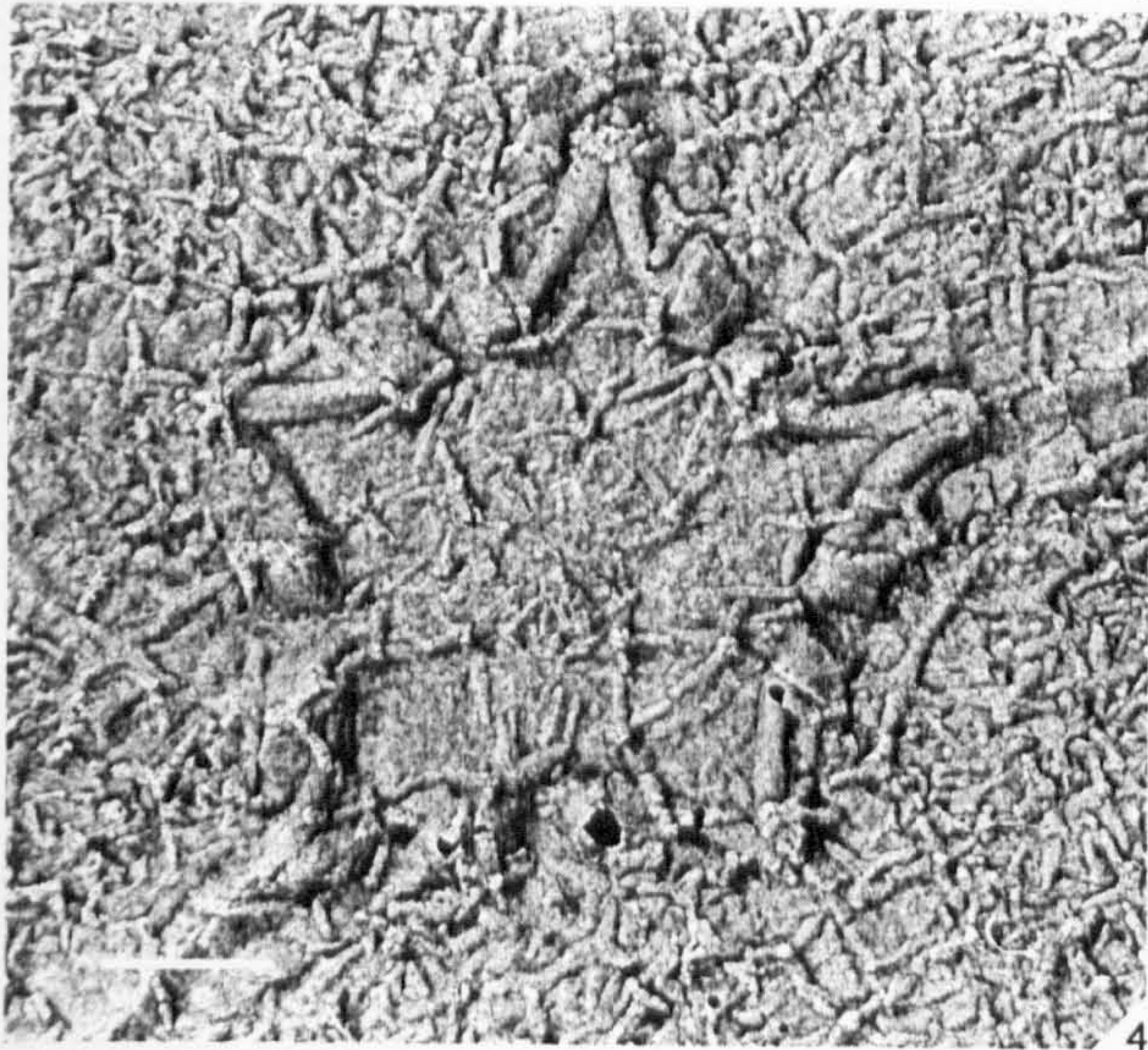
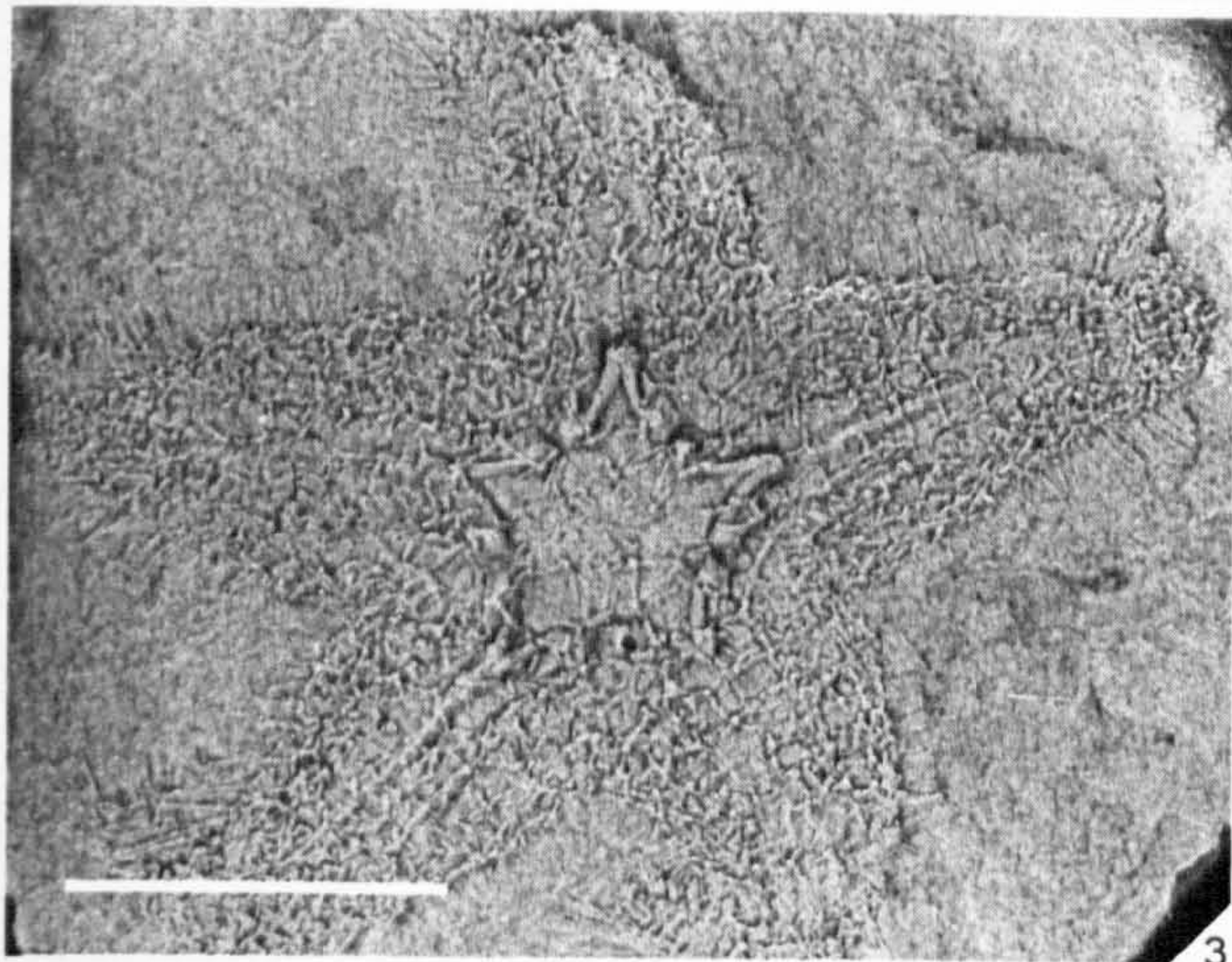
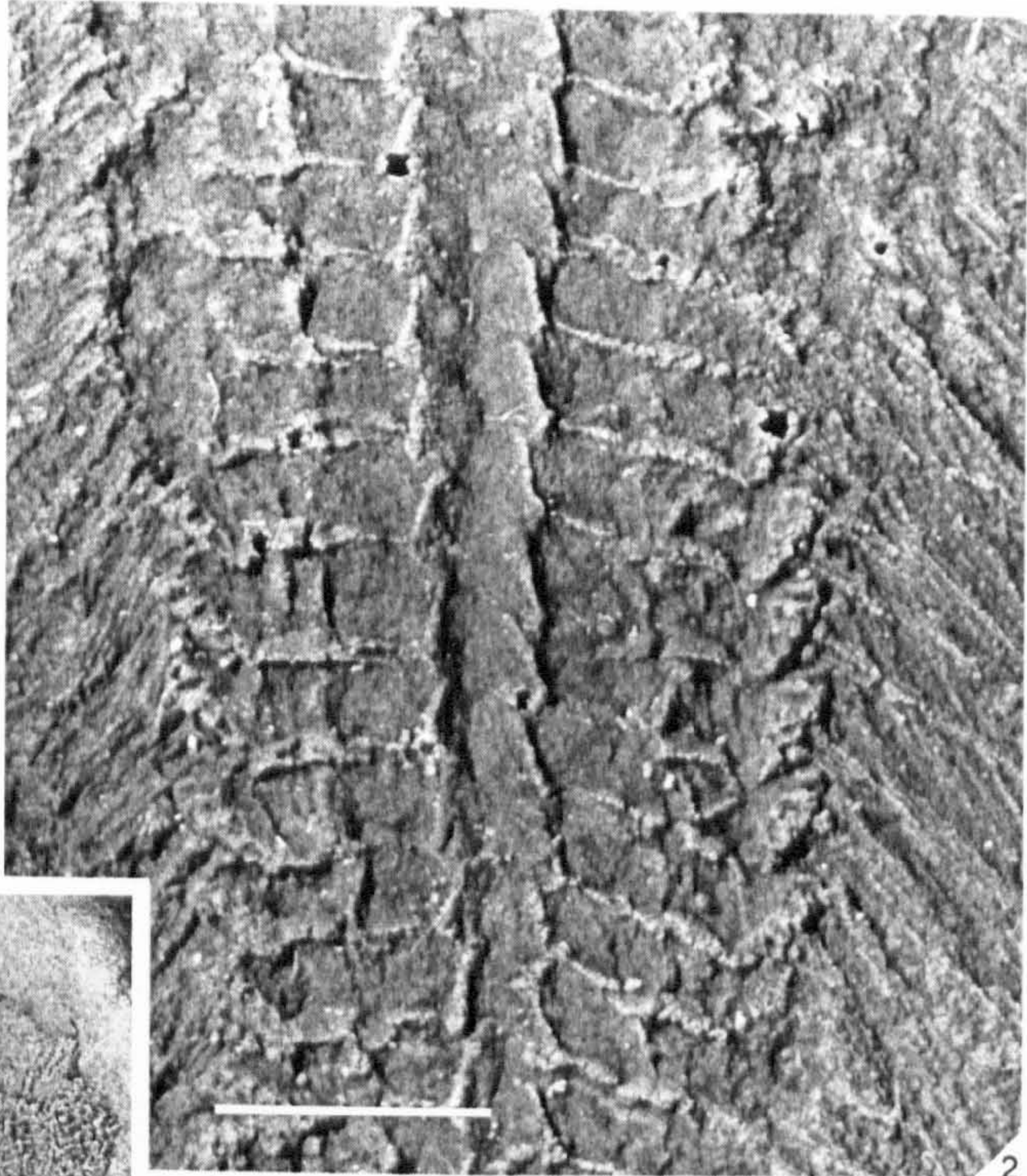
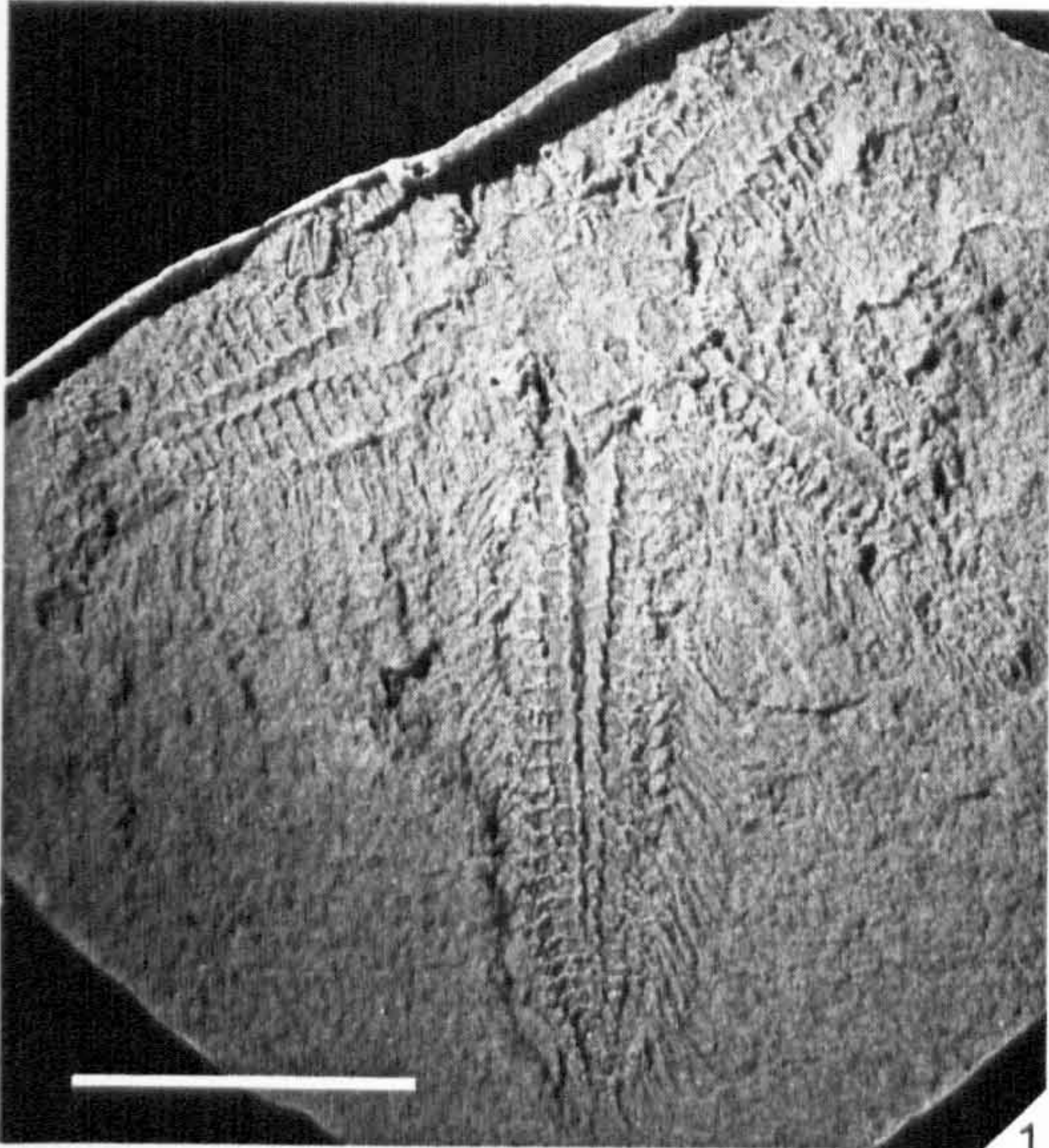




## EXPLANATION OF PLATE 3.8

Figs 1-5. *Sturtzaster marstoni* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-2, BMNH E 13949. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of arm showing Ambb, Adambb and wide open ambulacral channel; scale bar represents 2 mm. 3-5, BGS GSM6517. 3, entire specimen, dorsal view; scale bar represents 10 mm. 4, detail of mouth frame, dorsal view; scale bar represents 2 mm. 5, detail of proximal arm, dorsal view; scale bar represents 2 mm. All figures are of silicone casts.



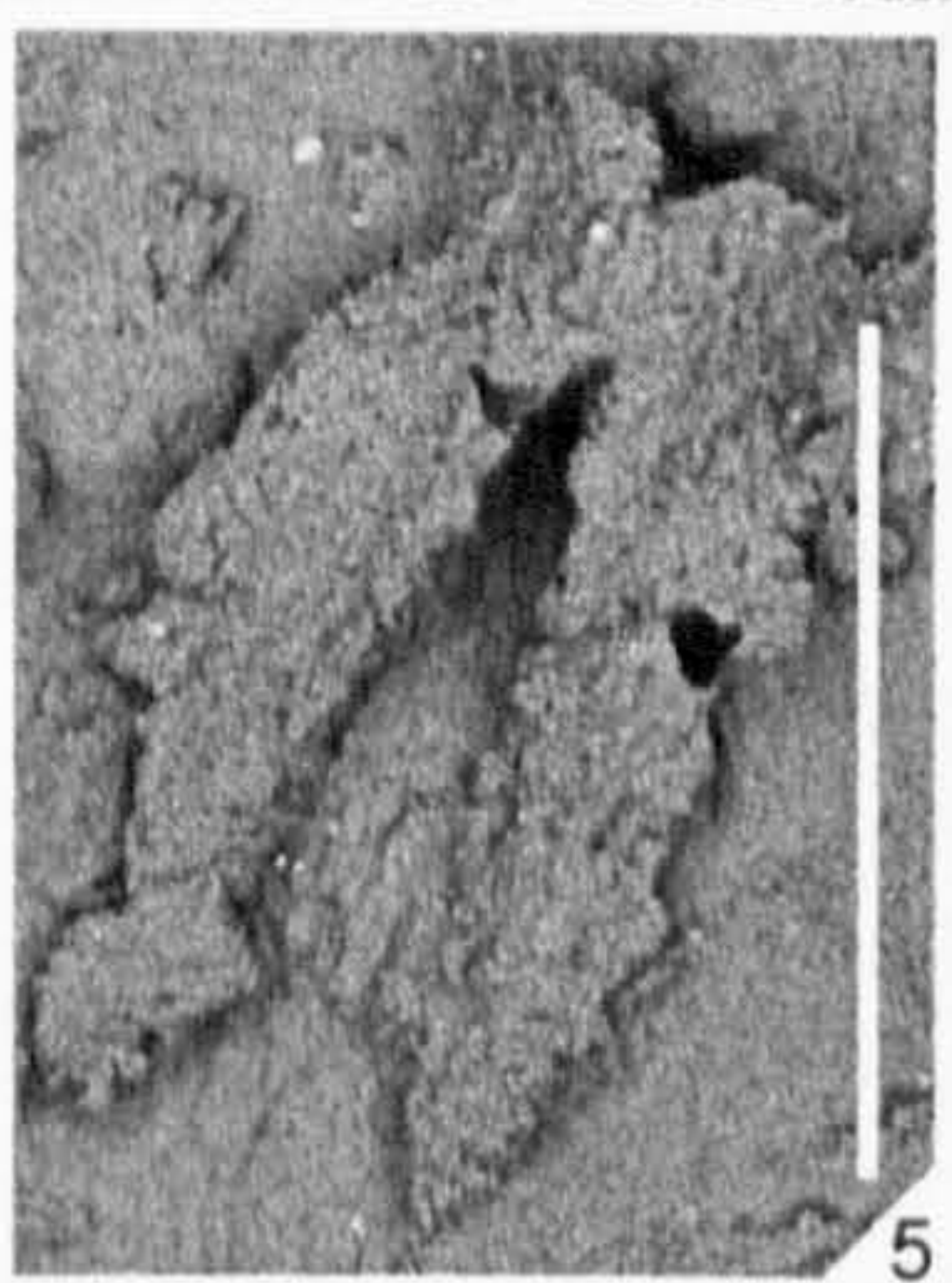
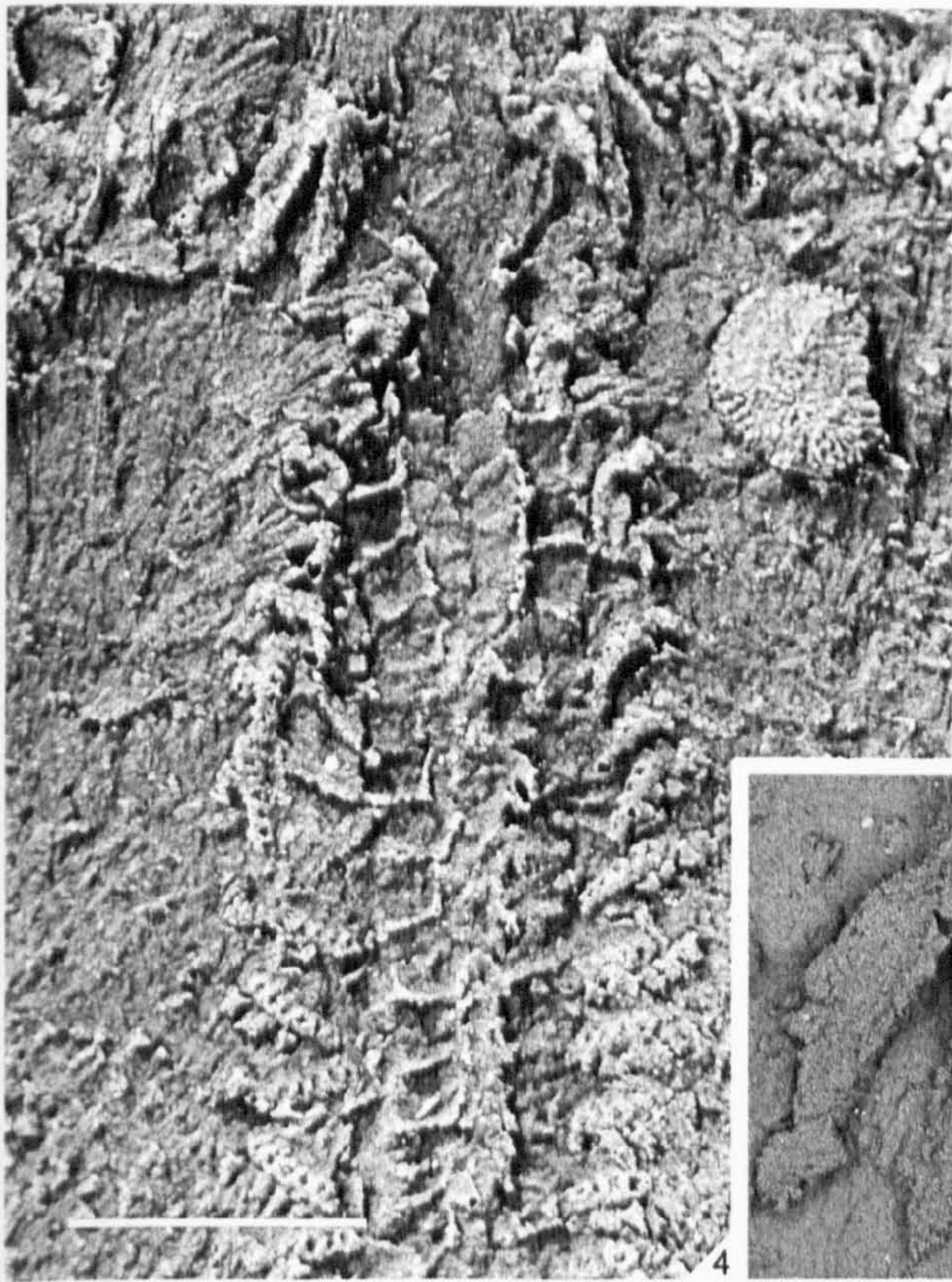
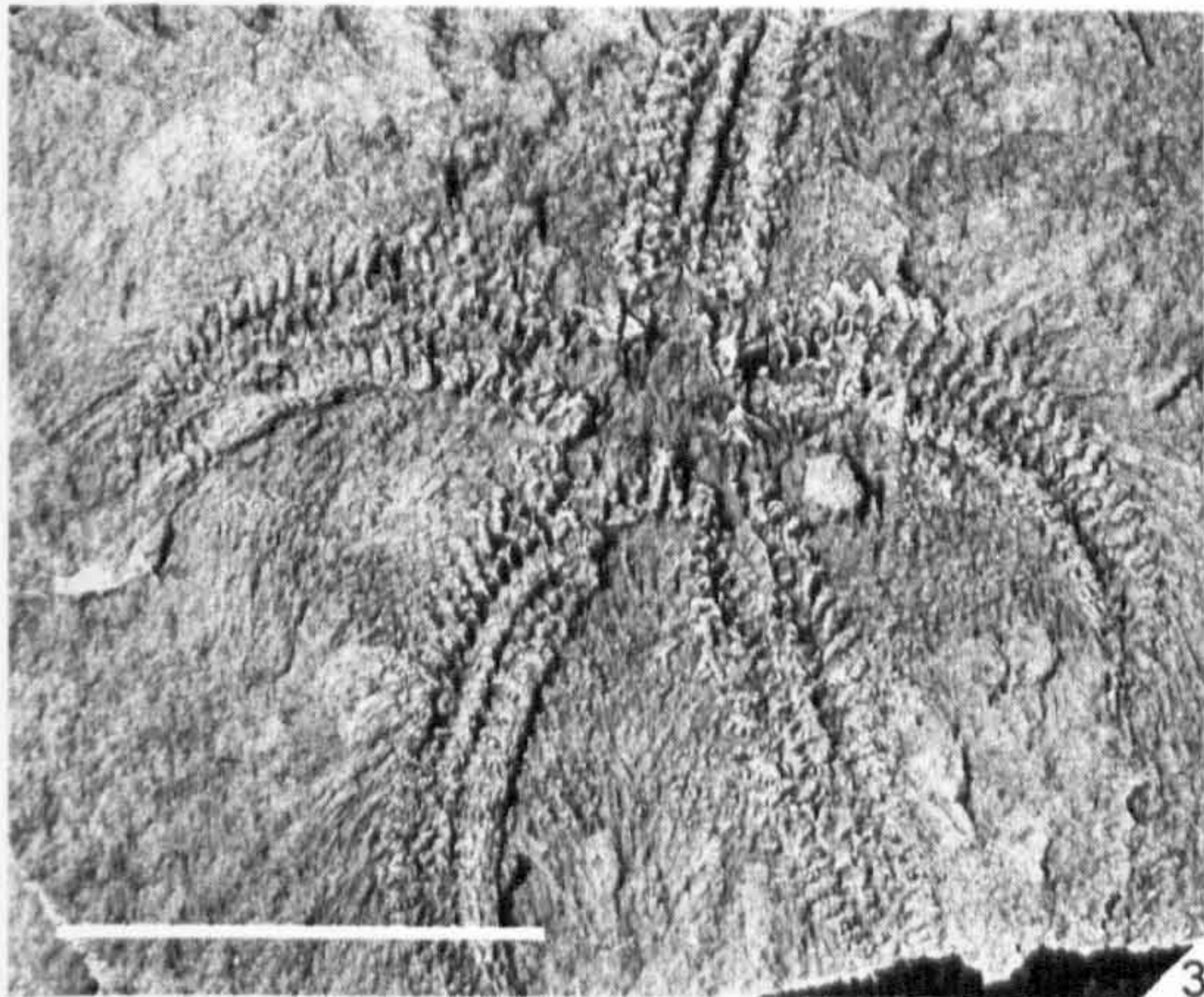
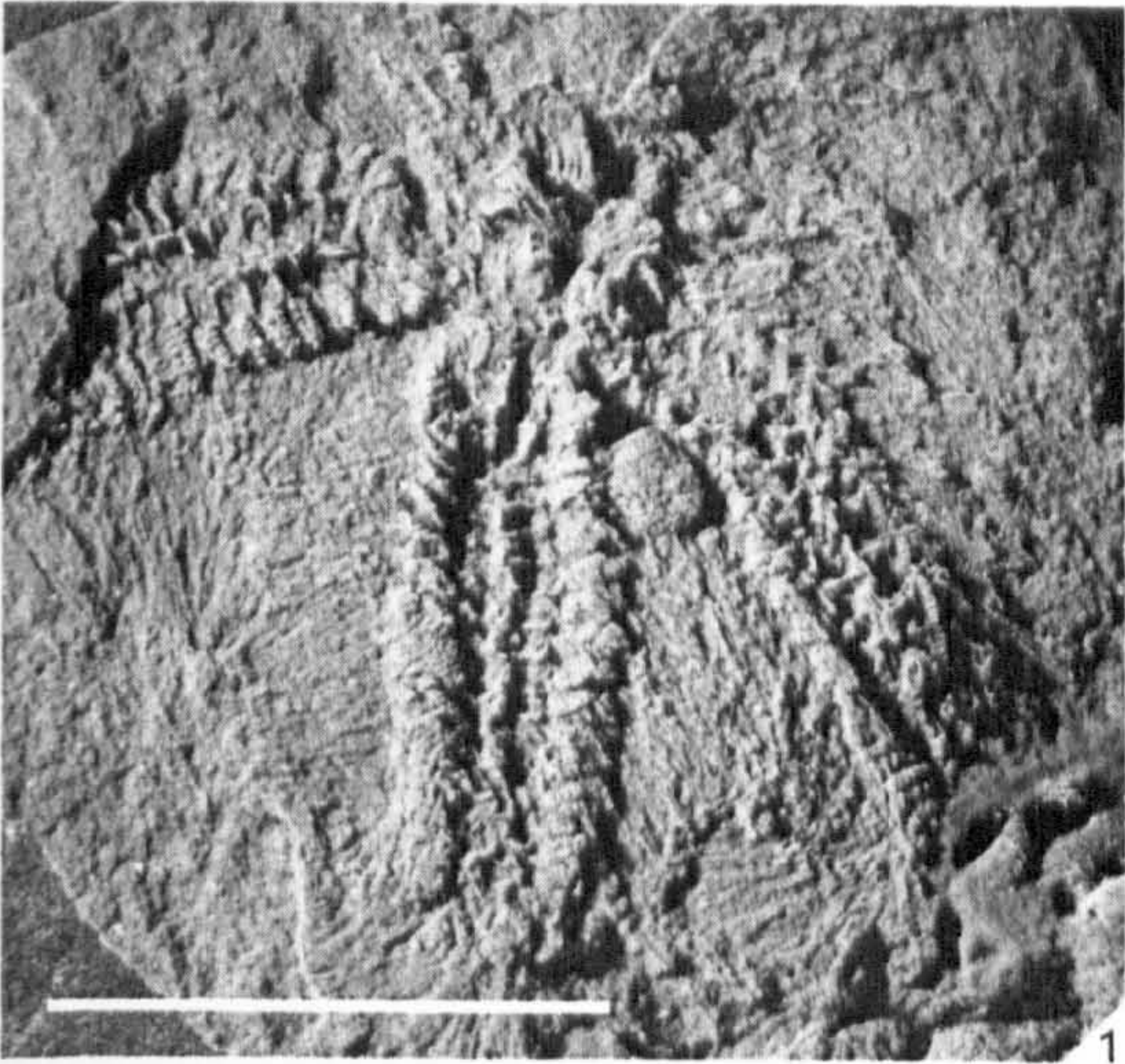




## EXPLANATION OF PLATE 3.9

Figs 1-6. *Sturtzaster colvini* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-2, BMNH E 52859, holotype. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of proximal arm showing distally closed ambulacral channel (point of closure arrowed) and large madreporite, ventral view; scale bar represents 2 mm. 3-6, CH215. 3, entire specimen, ventral view; scale bar represents 10 mm. 4, detail of proximal arm, ventral view; scale bar represents 2 mm. 5, detail of Amb1 pair, ventral view; scale bar represents 1 mm; SEM photomicrograph. 6, detail of arm margin showing Ambb and Adambb, ventral view; scale bar represents 1 mm. All figures are of silicone casts.



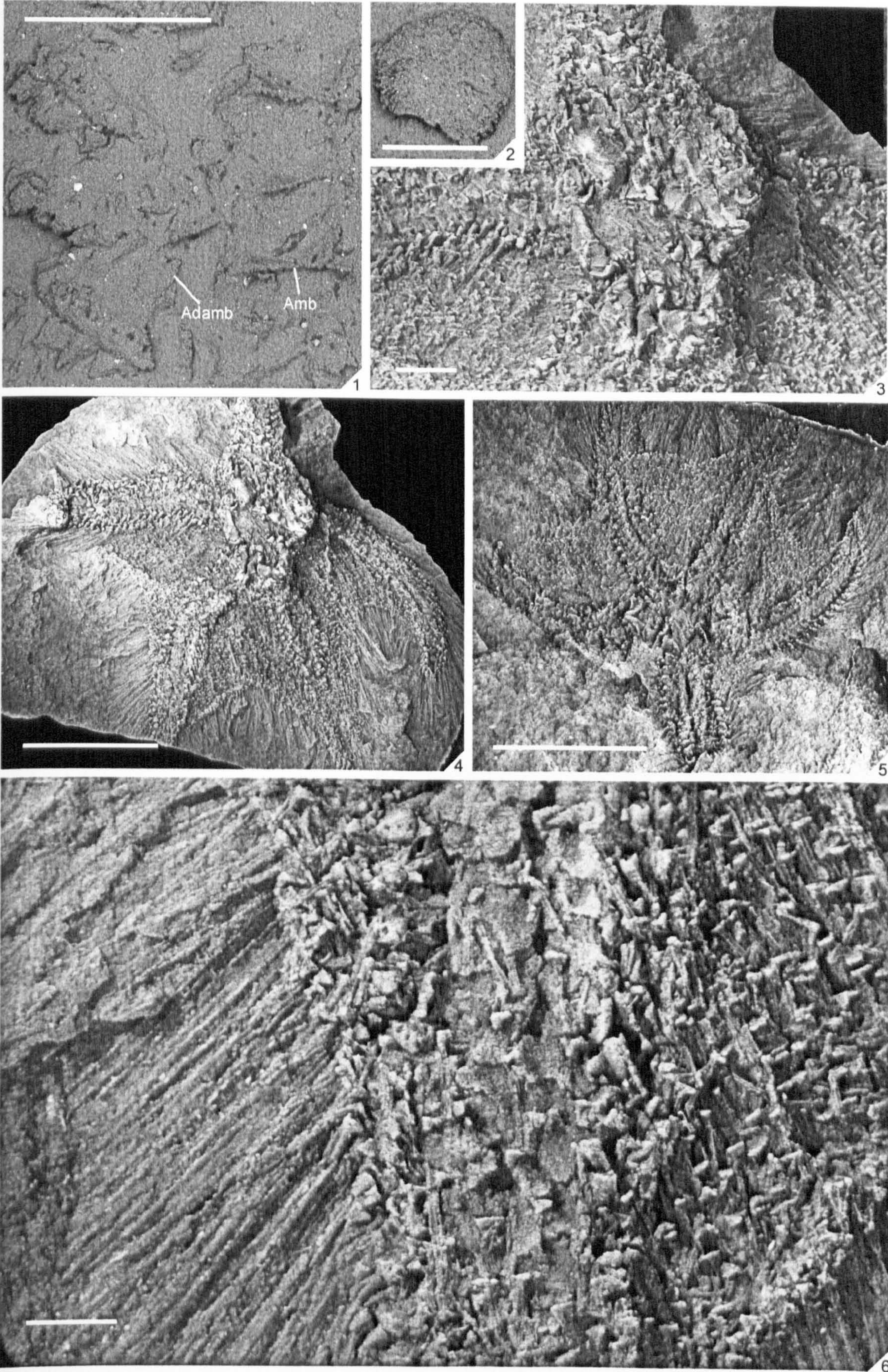




## EXPLANATION OF PLATE 3.10

Figs 1-6. *Sturtzaster colvini* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-2, CH215a. 1, detail of Adambb, ventral view; scale bar represents 1 mm; SEM photomicrograph. 2, detail of madreporite, ventral view; scale bar represents 1 mm; SEM photomicrograph. 3-4, 6, BMNH E 20648. 3, detail of disc and proximal arms, dorsal view; scale bar represents 2 mm. 4, entire specimen, dorsal view; scale bar represents 10 mm. 6, detail of distal arm showing dense fringe of long spines, dorsal view; scale bar represents 1 mm. 5, CH215, entire specimen, dorsal view; scale bar represents 10 mm. All figures are of silicone casts.



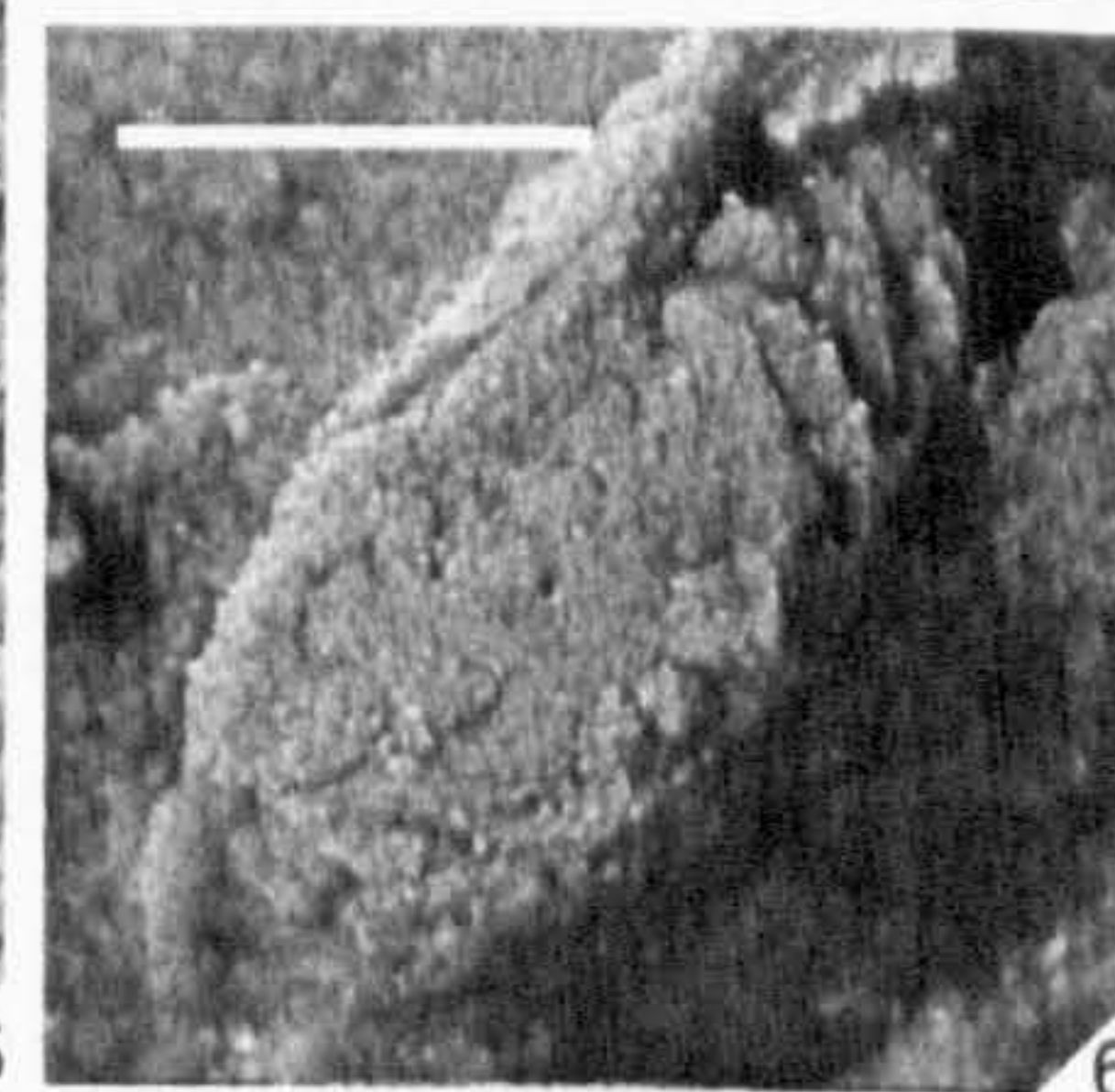
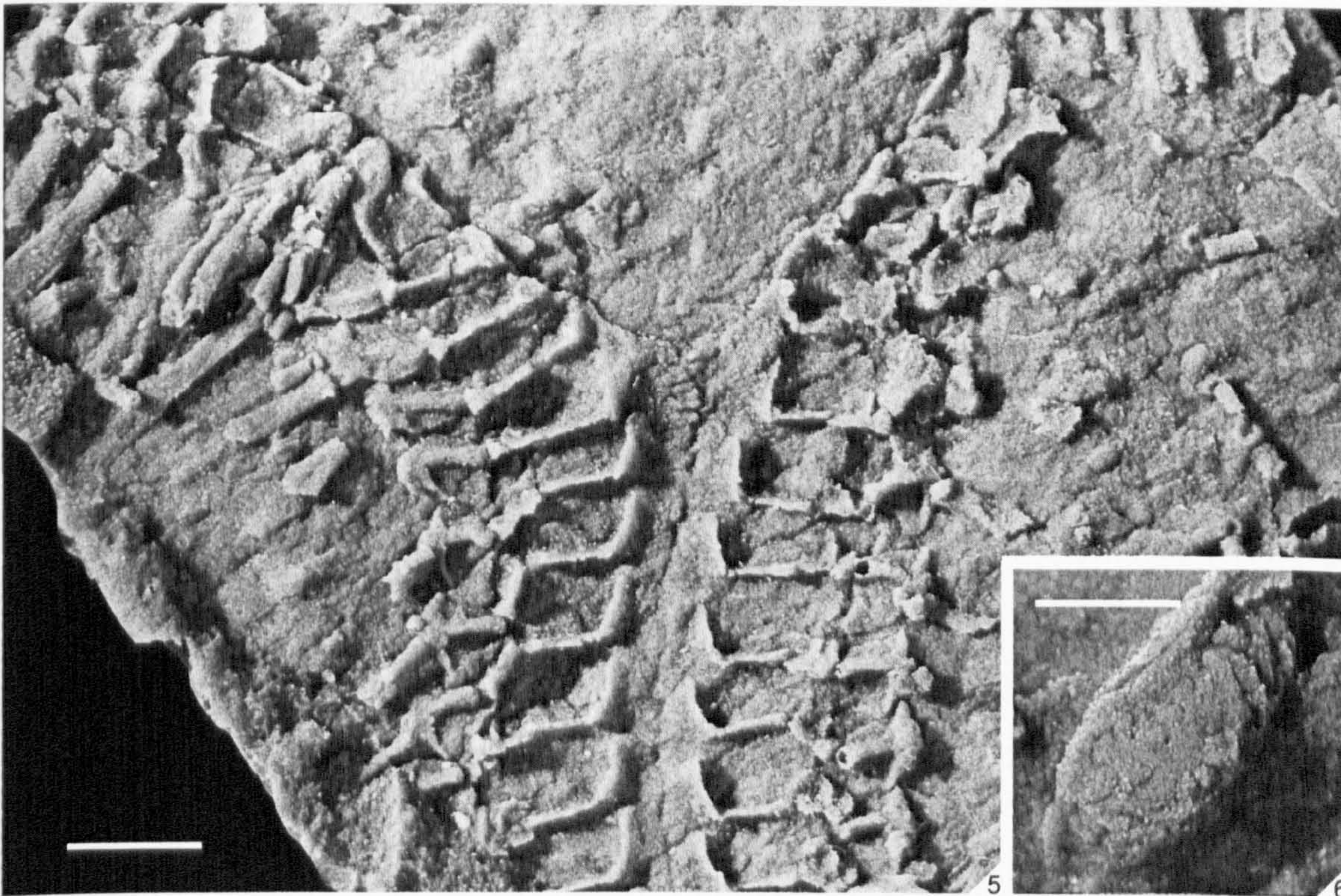
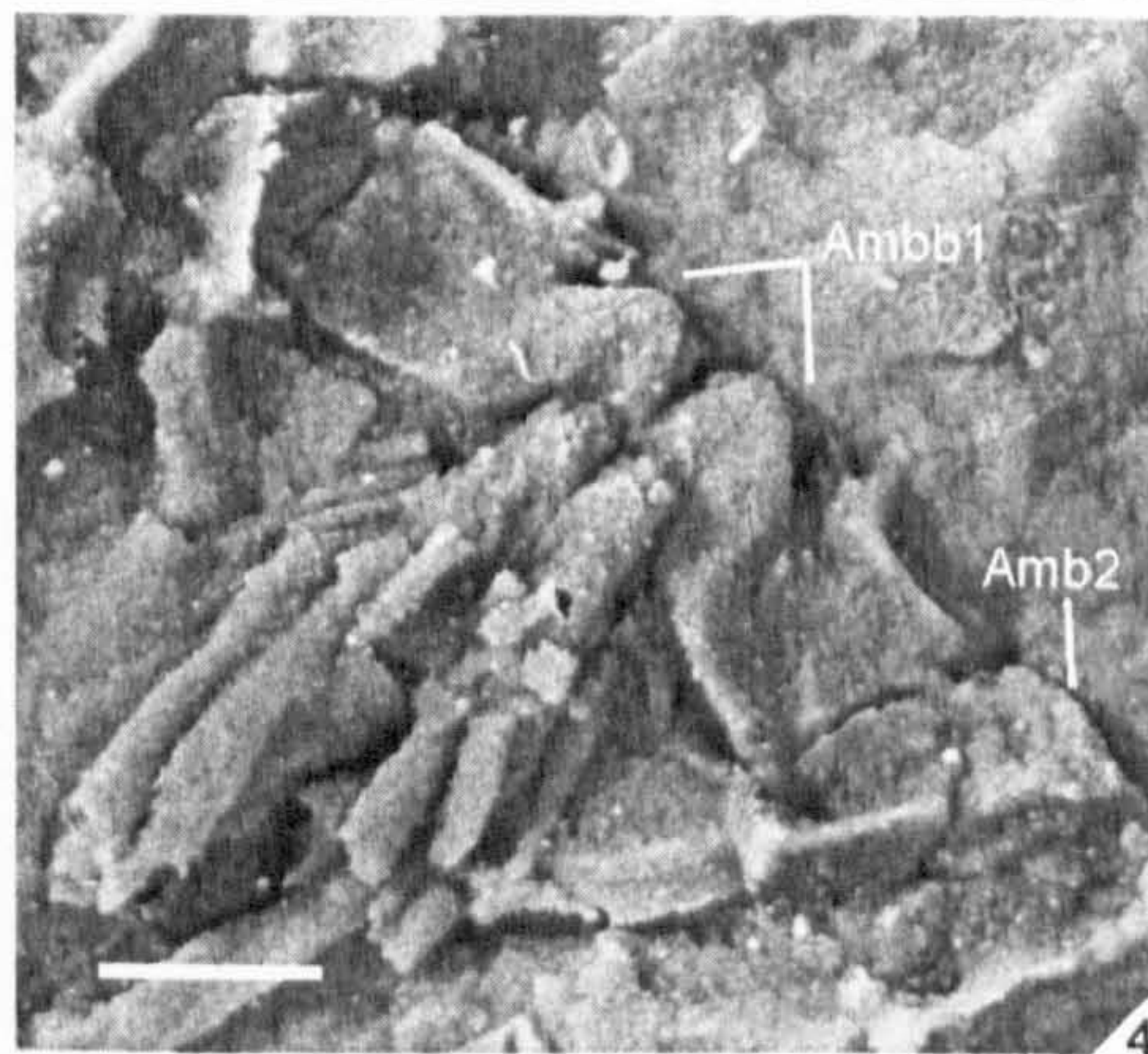
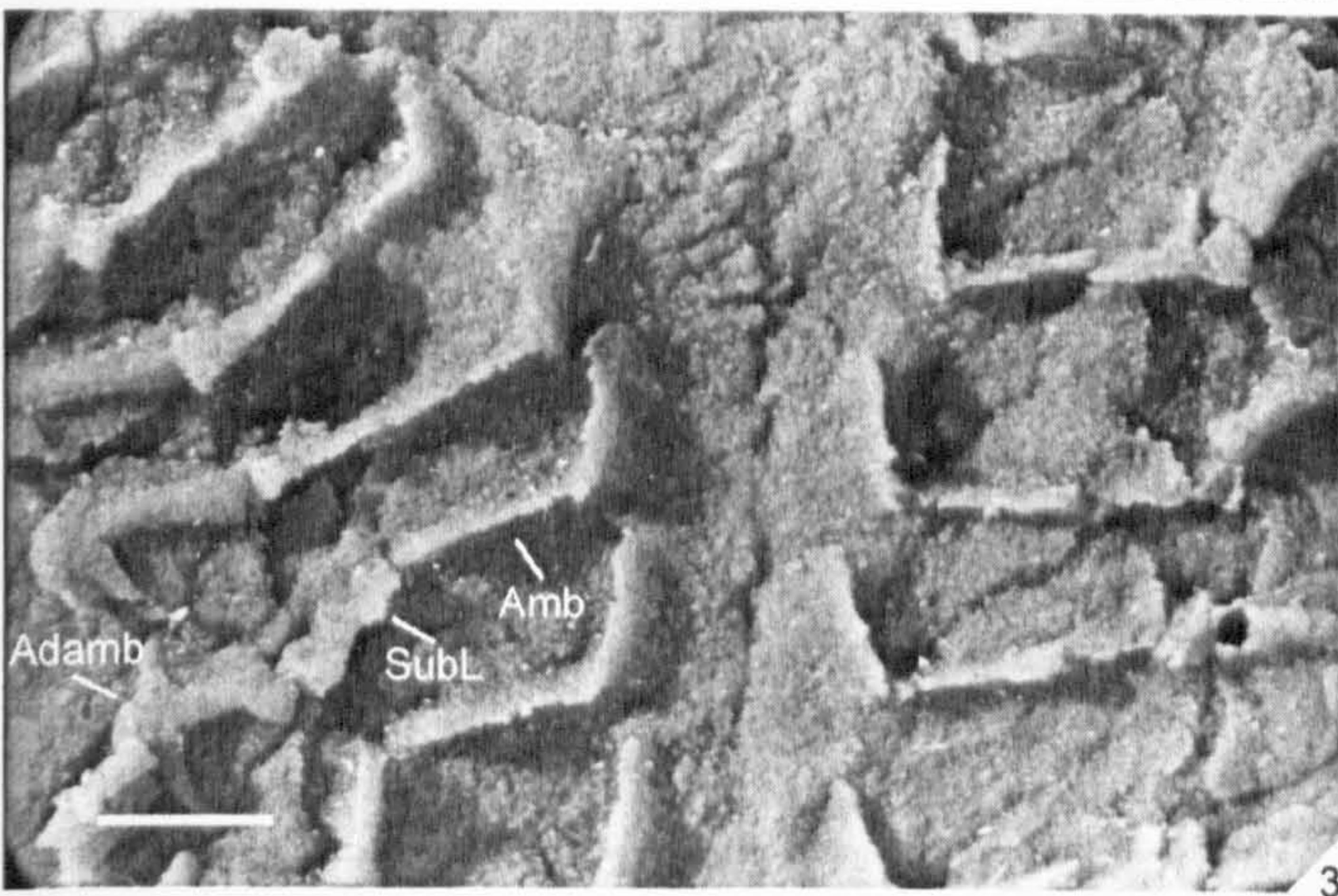
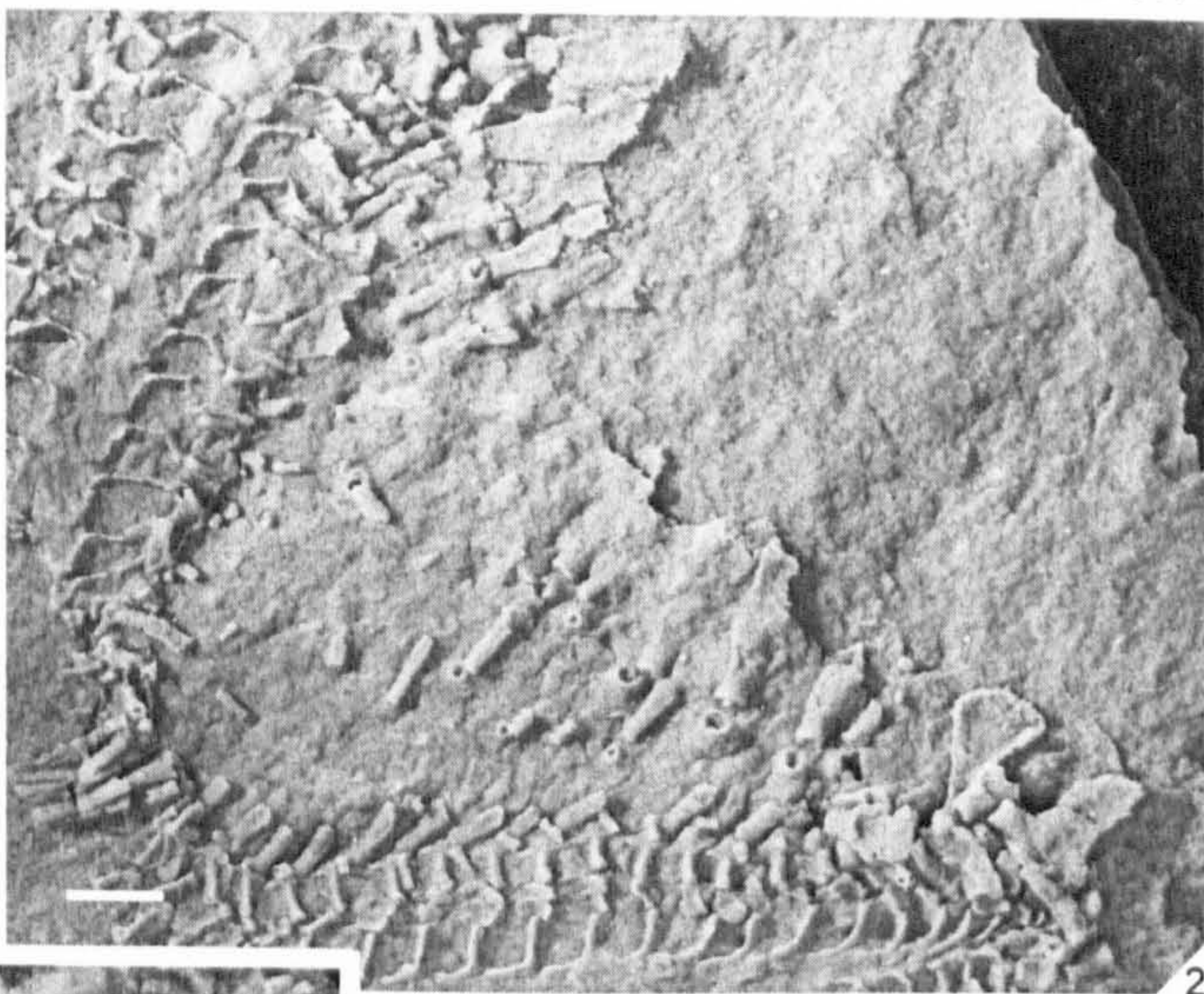
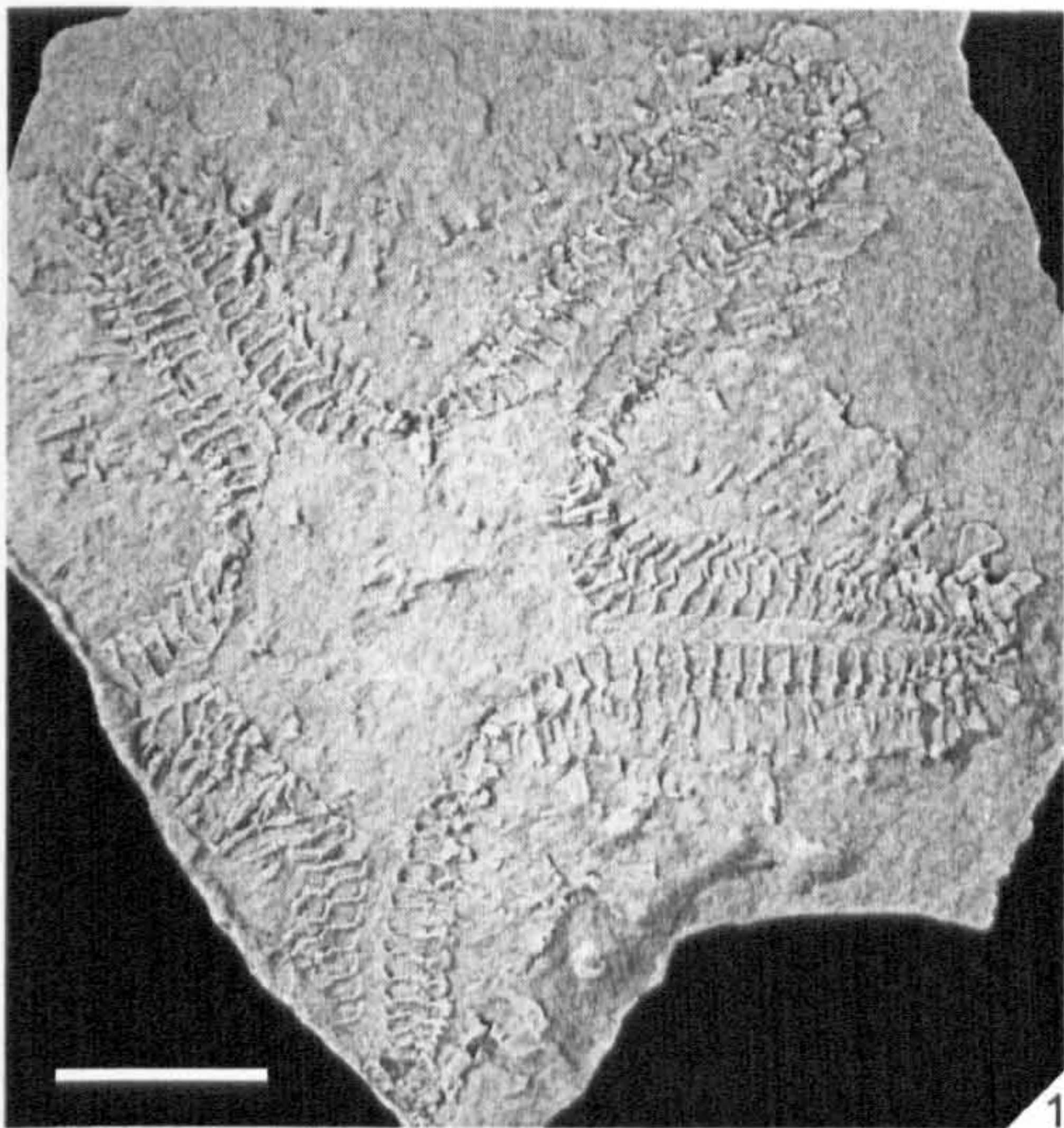




## EXPLANATION OF PLATE 3.11

Figs 1-6. *Rhopalocoma pyrotechnica* Salter, 1857; BMNH 40293, holotype; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of interrarial area, ventral view; scale bar represents 2 mm. 3, detail of proximal Ambb, ventral view; scale bar represents 1 mm. 4, detail of Amb1 pair, ventral view; scale bar represents 1 mm. 5, detail of proximal arm, ventral view; scale bar represents 2 mm. 6, detail of madreporite, ventral view; scale bar represents 1 mm; SEM photomicrograph. All figures are of silicone casts.



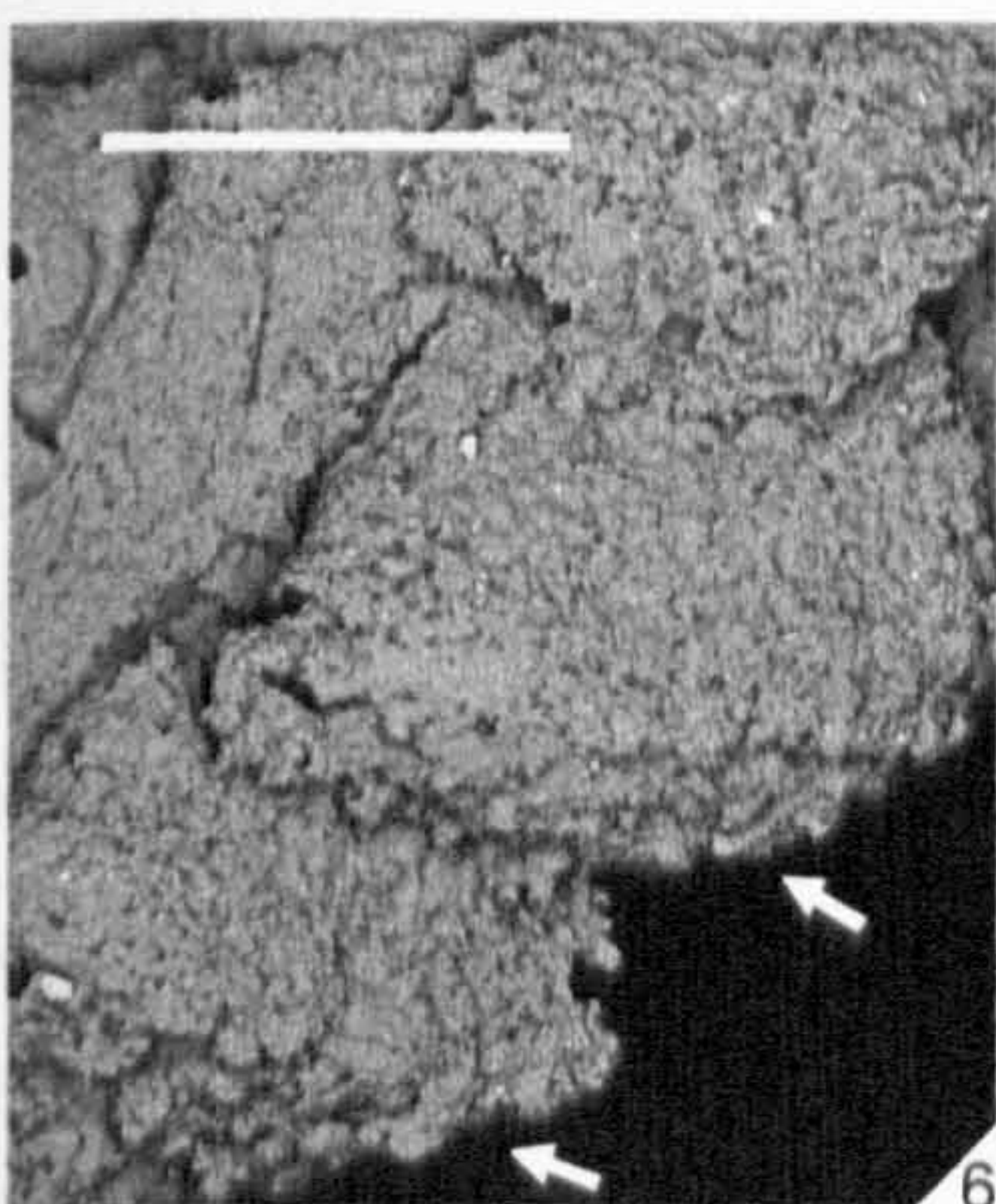
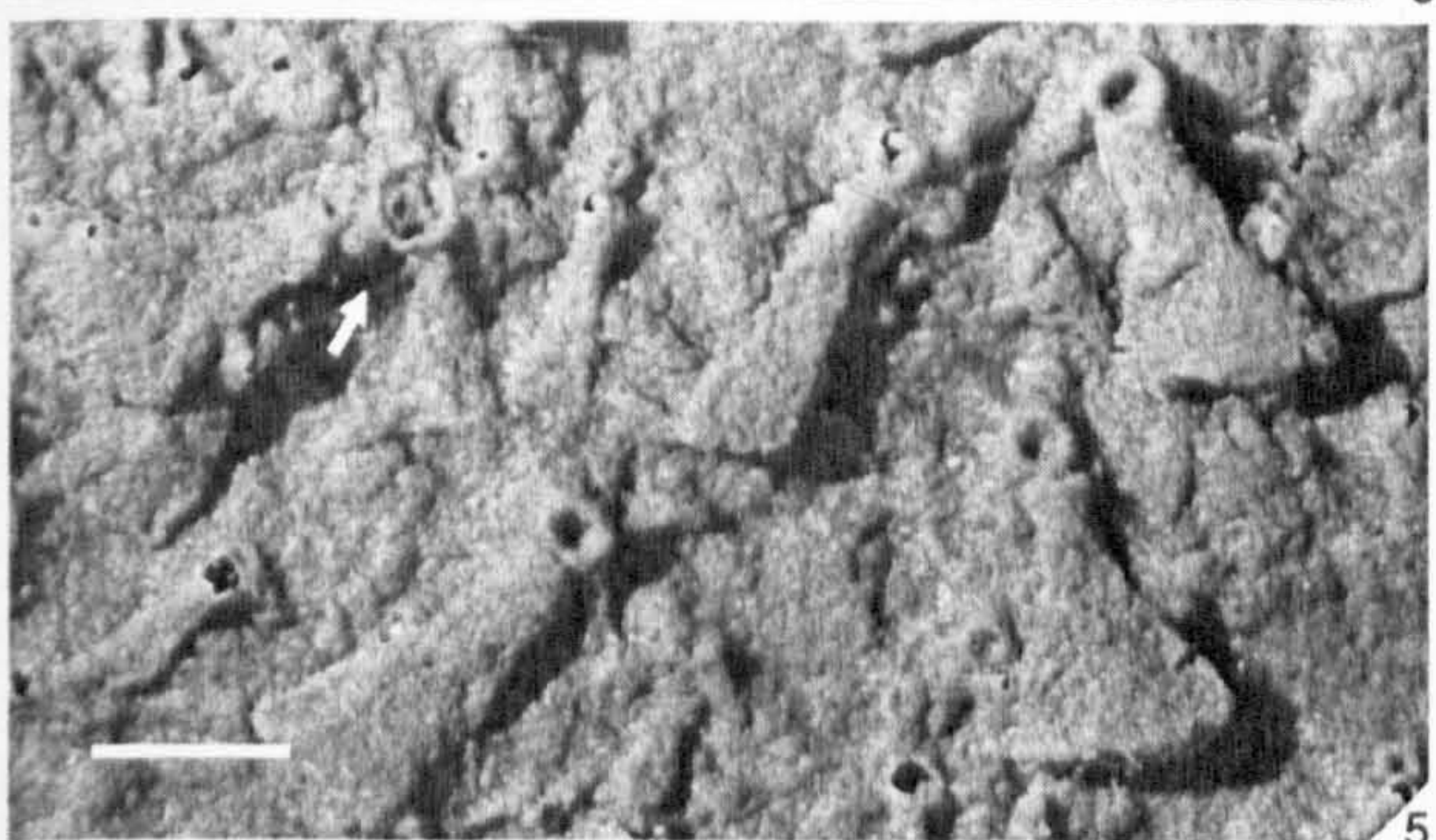
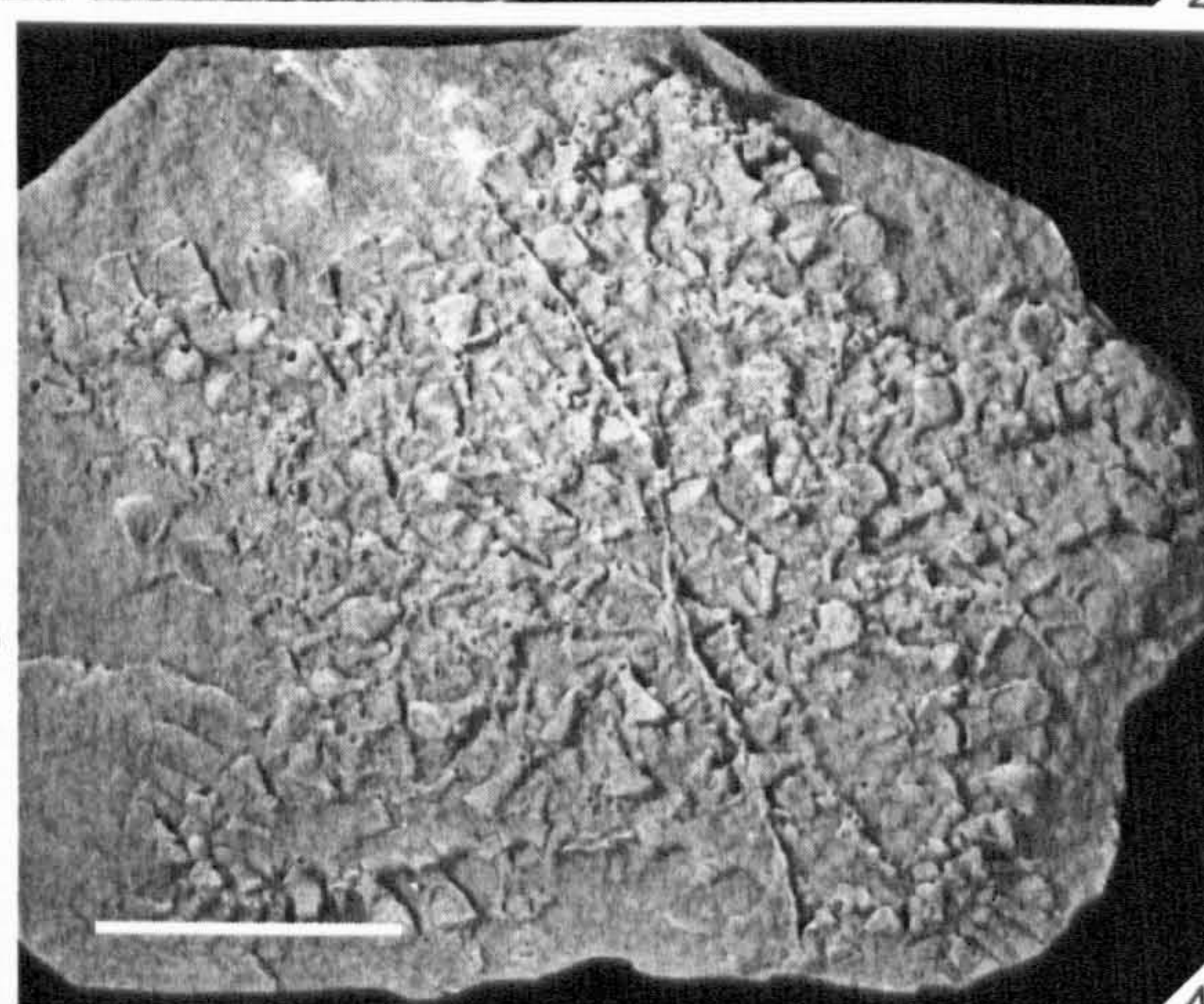
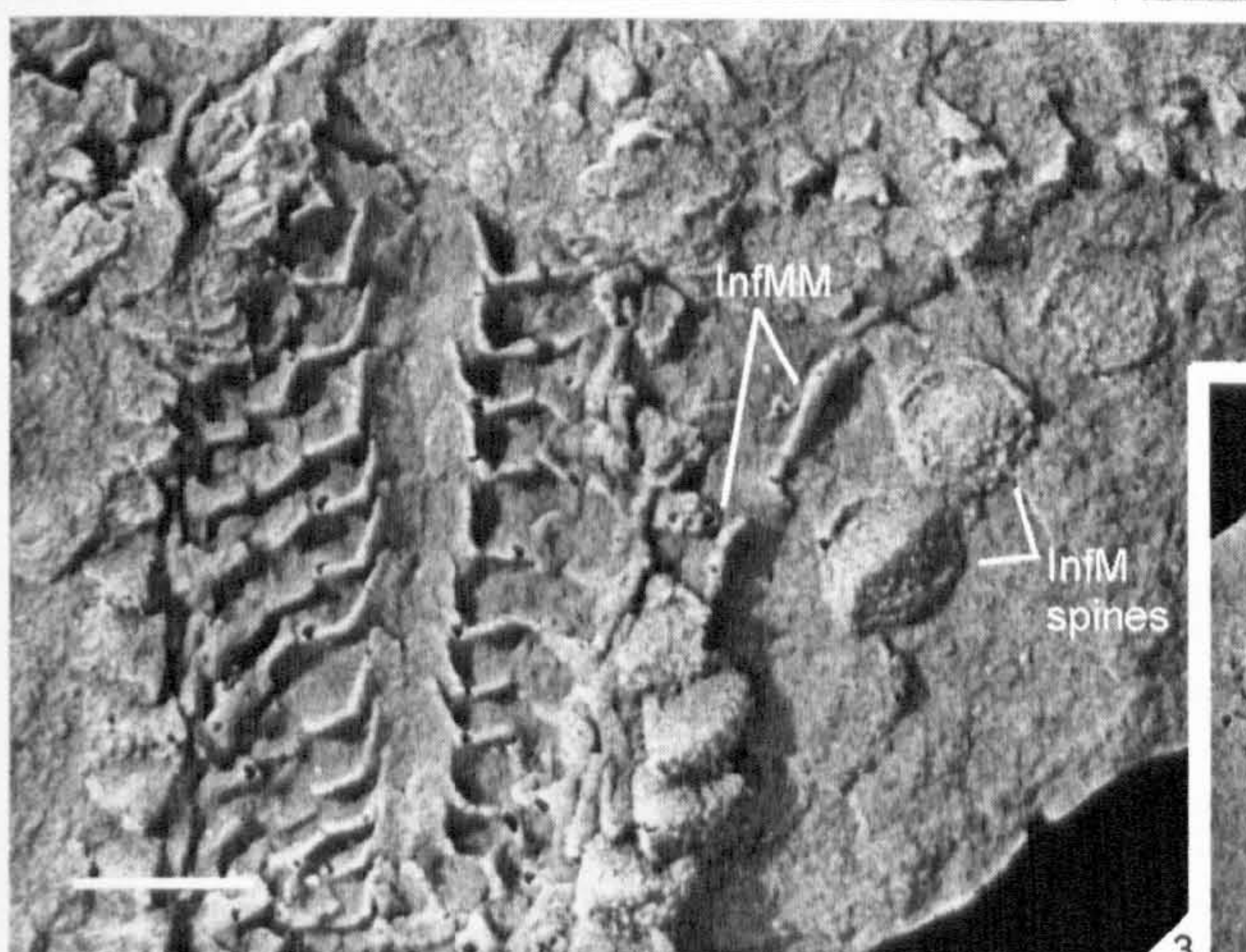
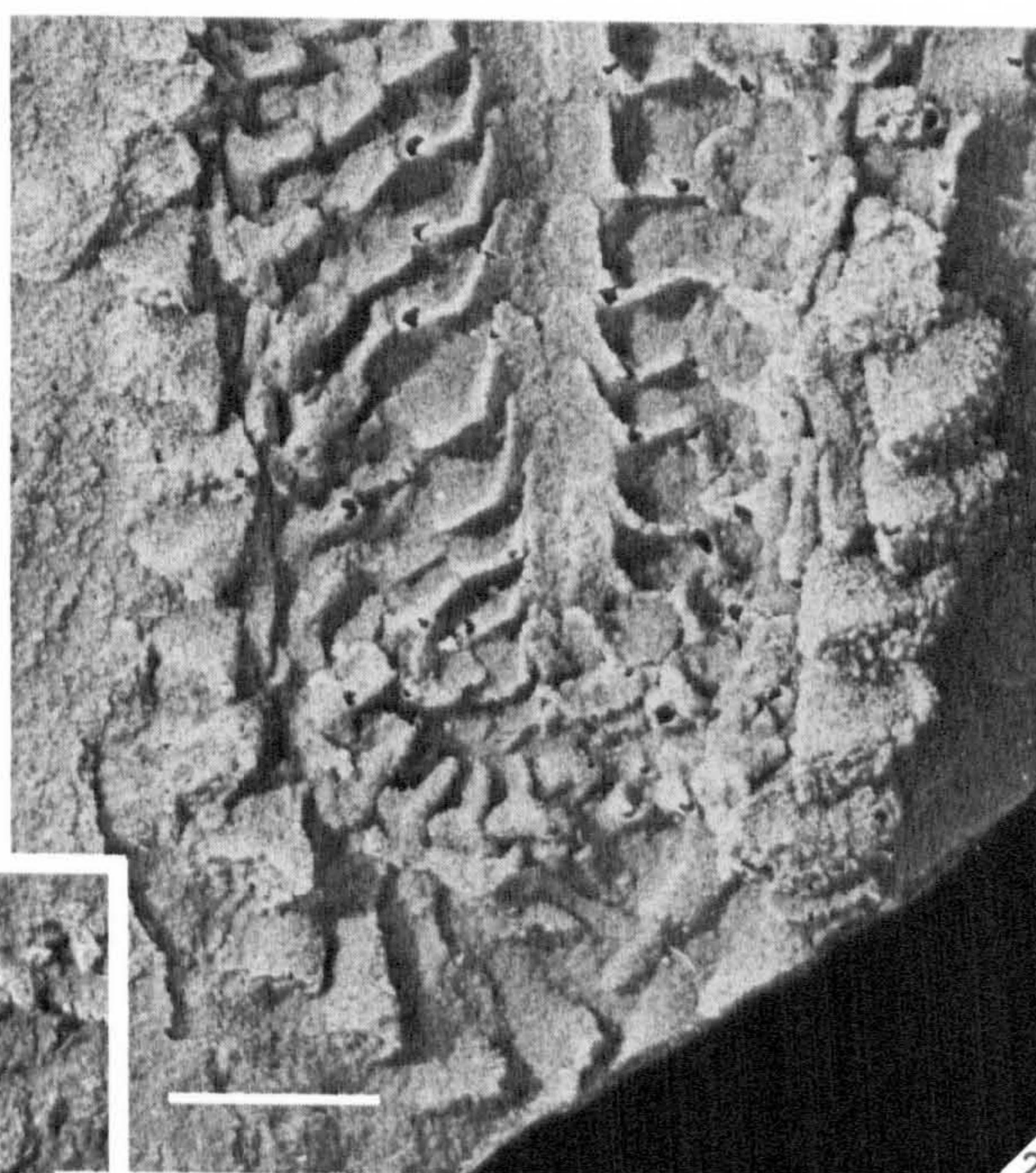
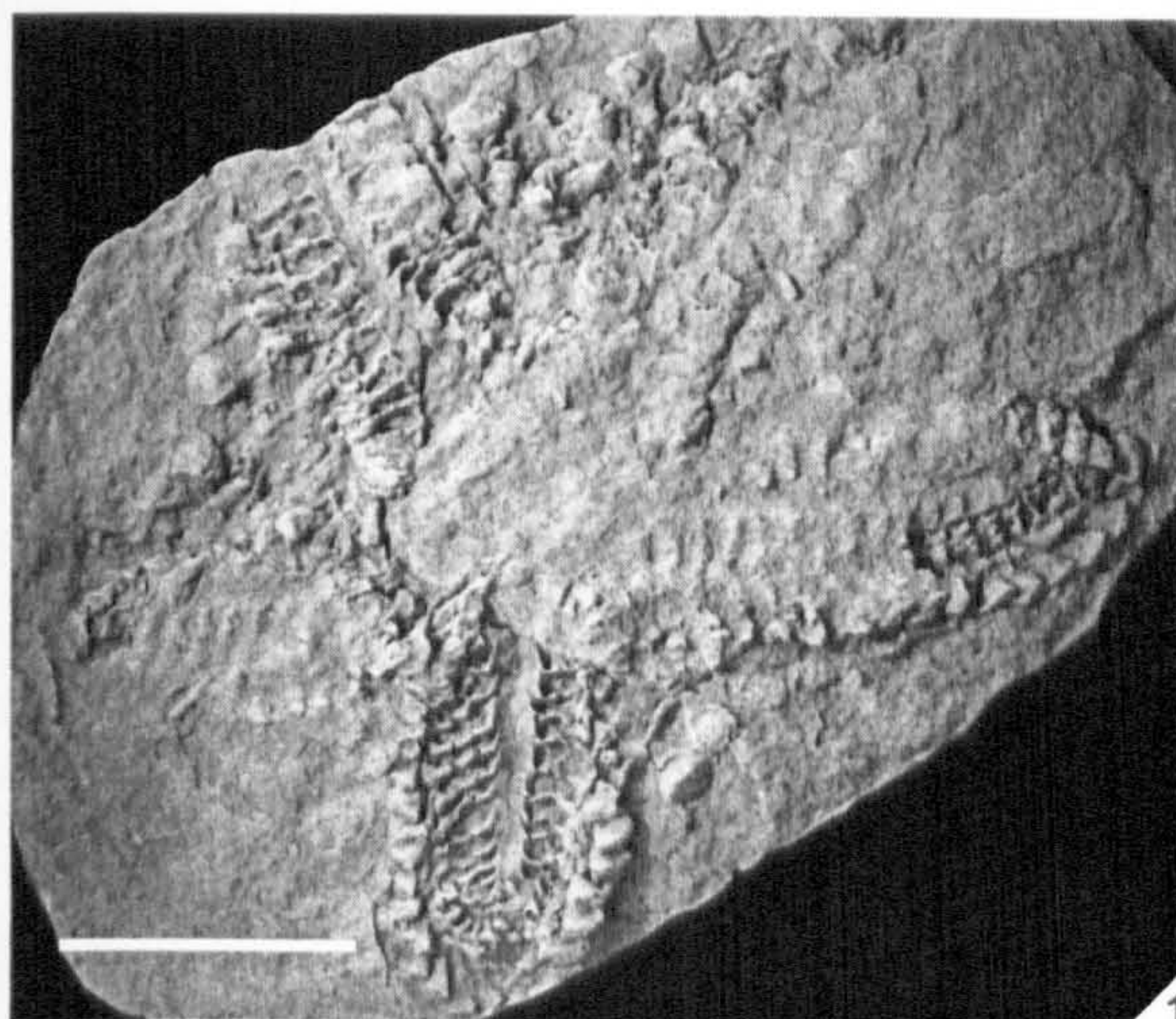




## EXPLANATION OF PLATE 3.12

Figs 1-7. *Rhopalocoma pyrotechnica* Salter, 1857; BMNH E 5013a-b, part and counterpart; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-3, 6, BMNH E 5013b. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of distal arm, ventral view; scale bar represents 2 mm. 3, detail of proximal arm and interrarial area, ventral view; scale bar represents 2 mm. 6, detail of arm spines (surface of spines bearing tubercles arrowed), ventral view; scale bar represents 1 mm; SEM photomicrograph. 4-5, 7, BMNH E 5013a. 4, entire specimen, dorsal view; scale bar represents 10 mm. 5, detail of abactinal spines (stellate abactinal with circular process for spine attachment arrowed), dorsal view; scale bar represents 1 mm. 7, detail of arm showing abactinal and InfM spines, dorsal view; scale bar represents 2 mm. All figures are of silicone casts.



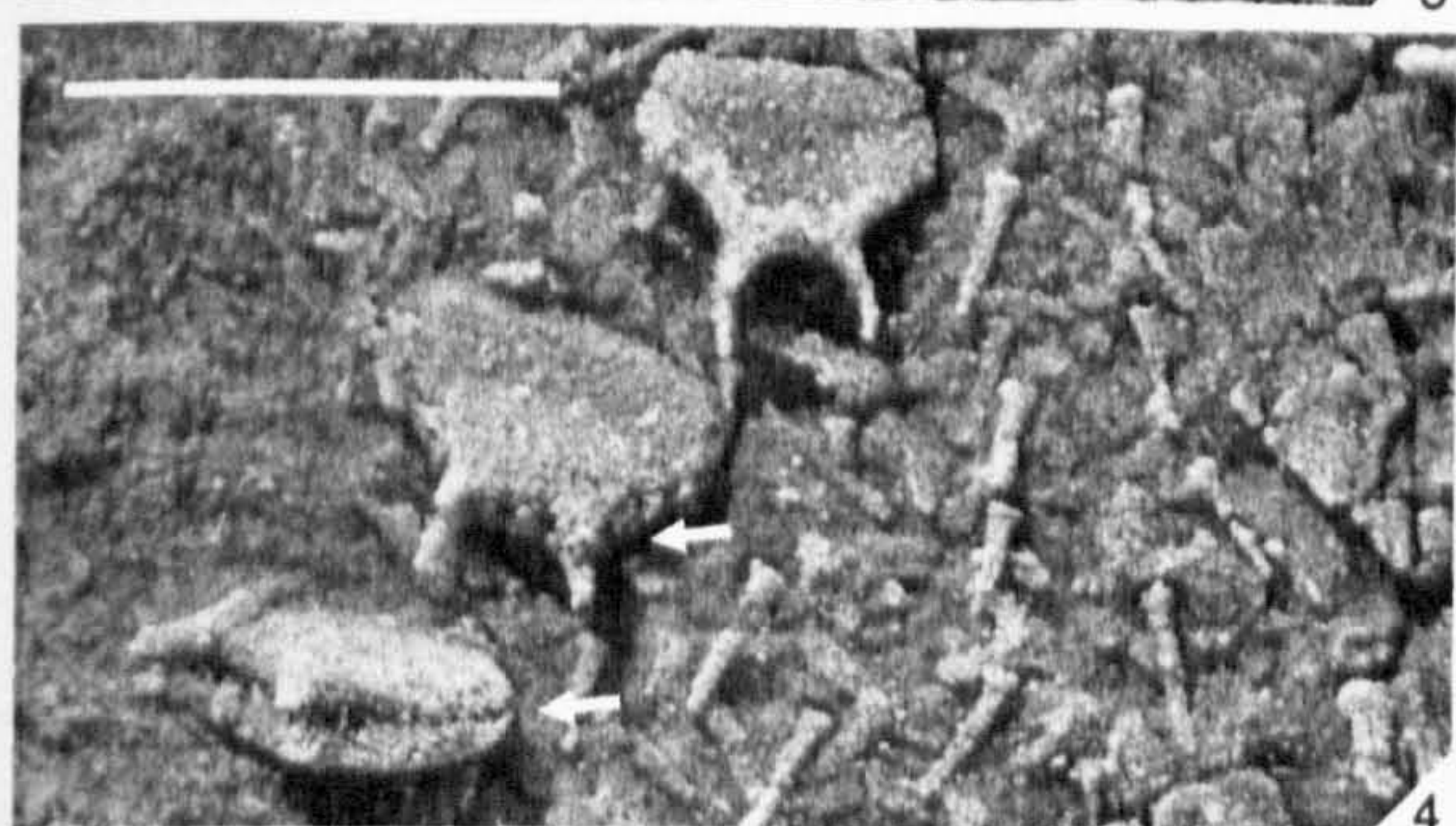
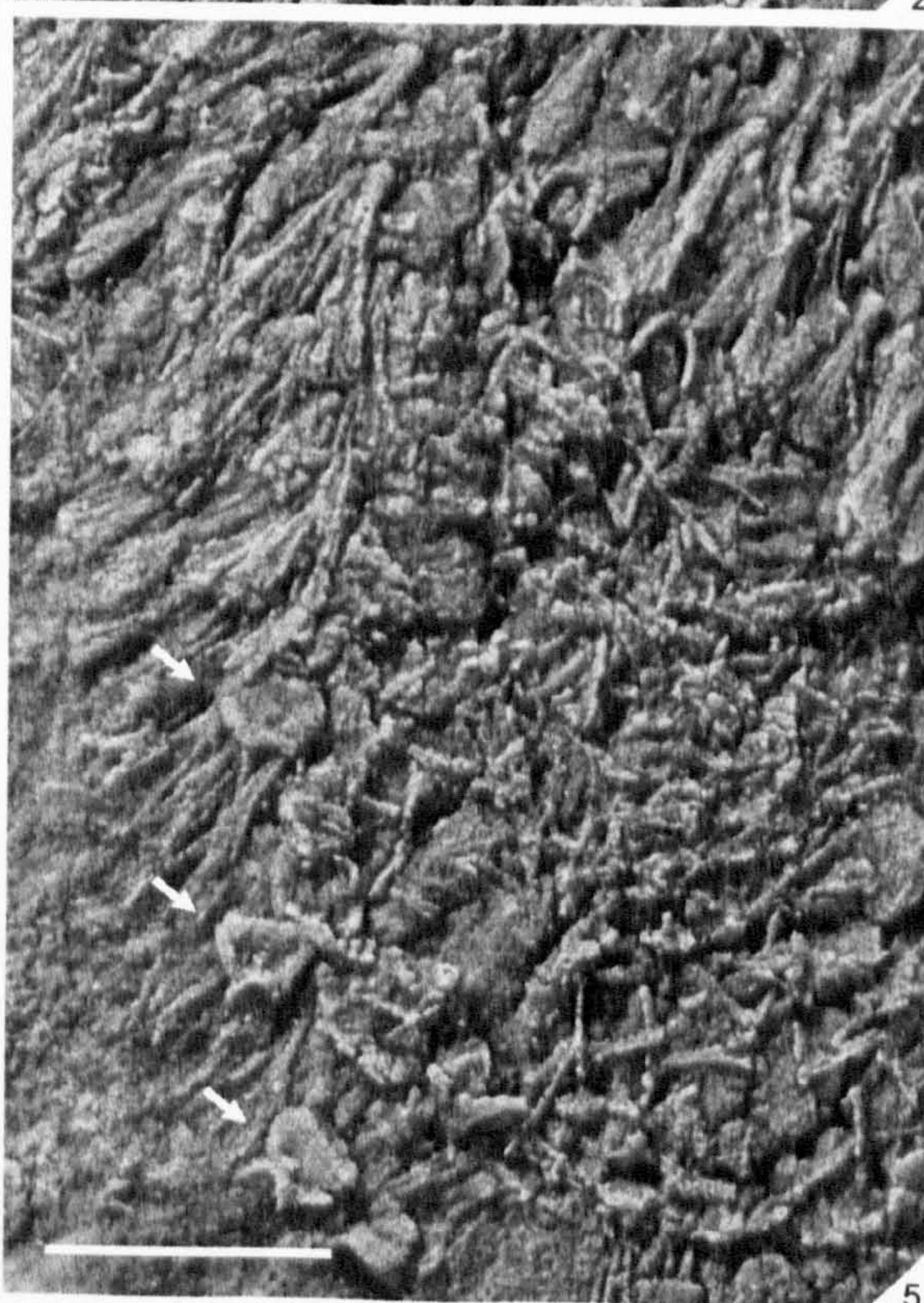
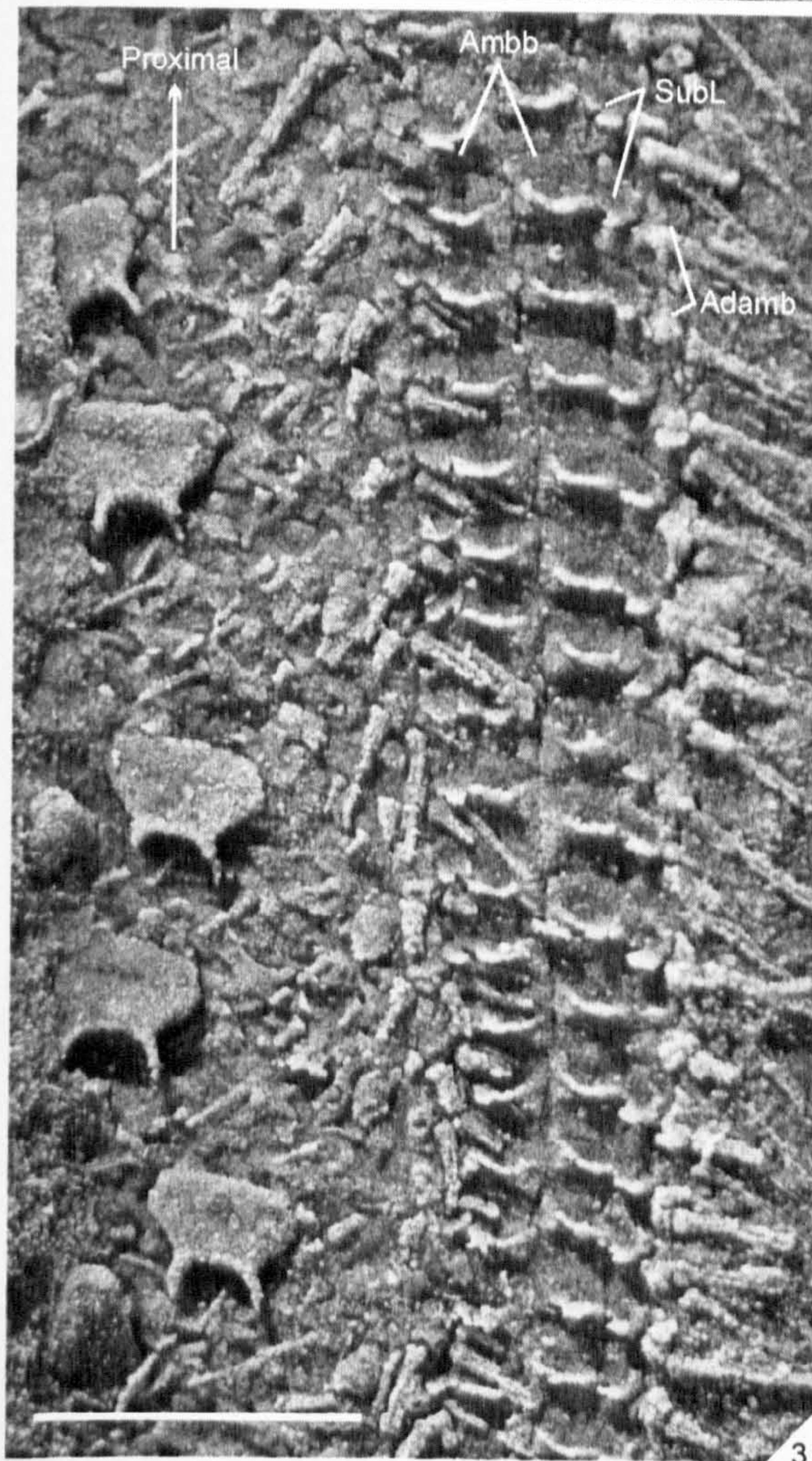
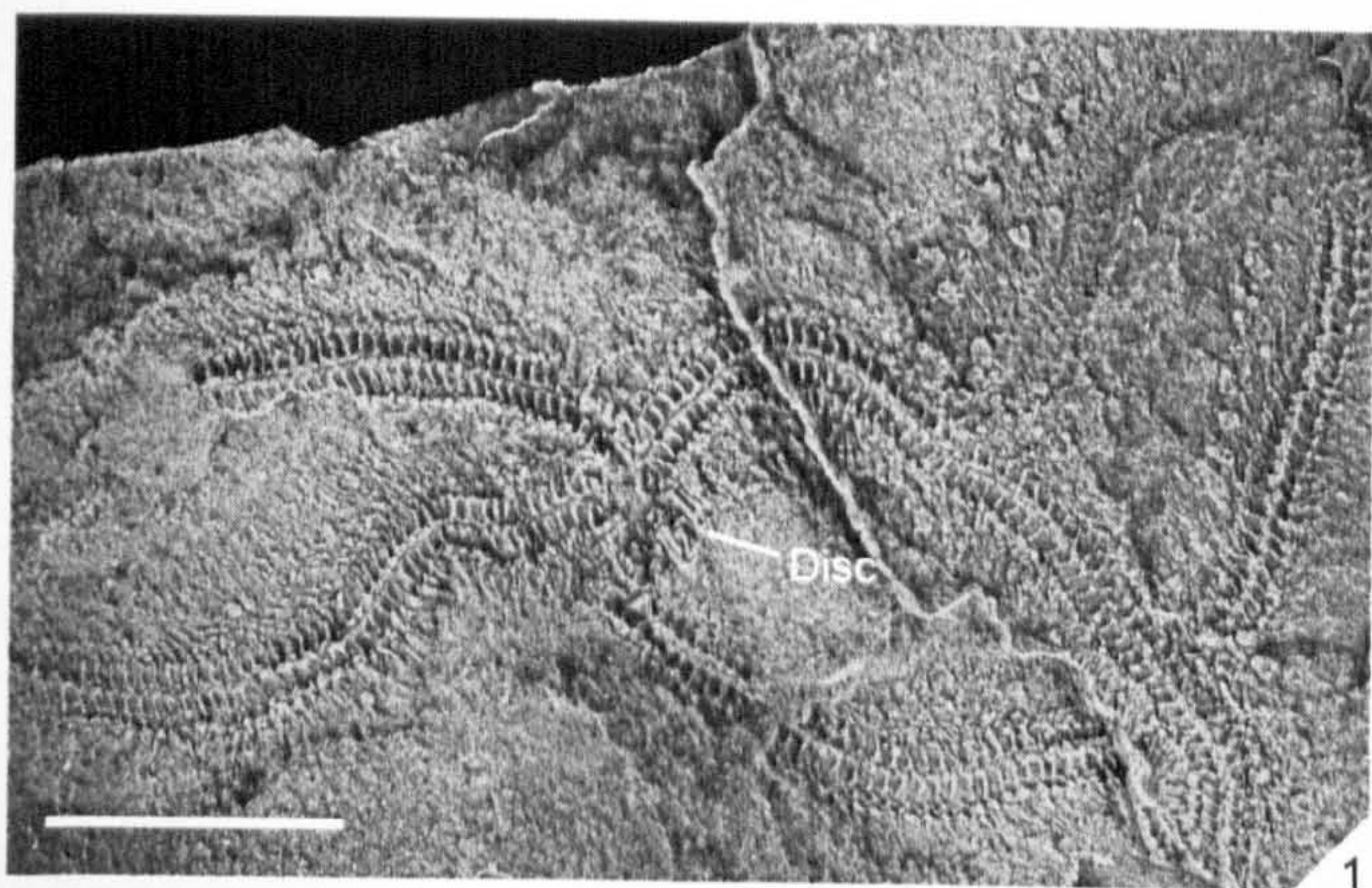




## EXPLANATION OF PLATE 3.13

Figs 1-5. *Bdellacoma vermiformis* Salter, 1857; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, NMS G1882651523, neotype, entire specimen, ventral view; scale bar represents 10 mm. 2, BMNH E 1259, detail of proximal arm showing distally-widening spines, dorsal view; scale bar represents 2 mm. 3-4, BMNH 40297. 3, detail of portion of arm showing adambulacral groove lacking oar-like spines, and pedicellariae laterally, ventral view; scale bar represents 2 mm. 4, detail of pedicellariae proximal to those shown in 3, showing bivalved morphology (commissural margin of two pedicellariae arrowed), ventral view; scale bar represents 2 mm. 5, BMNH 38666, detail of distal portion of arm showing distally-widening spines and pedicellariae (arrowed), dorsal view; scale bar represents 2 mm. All figures are of silicone casts.







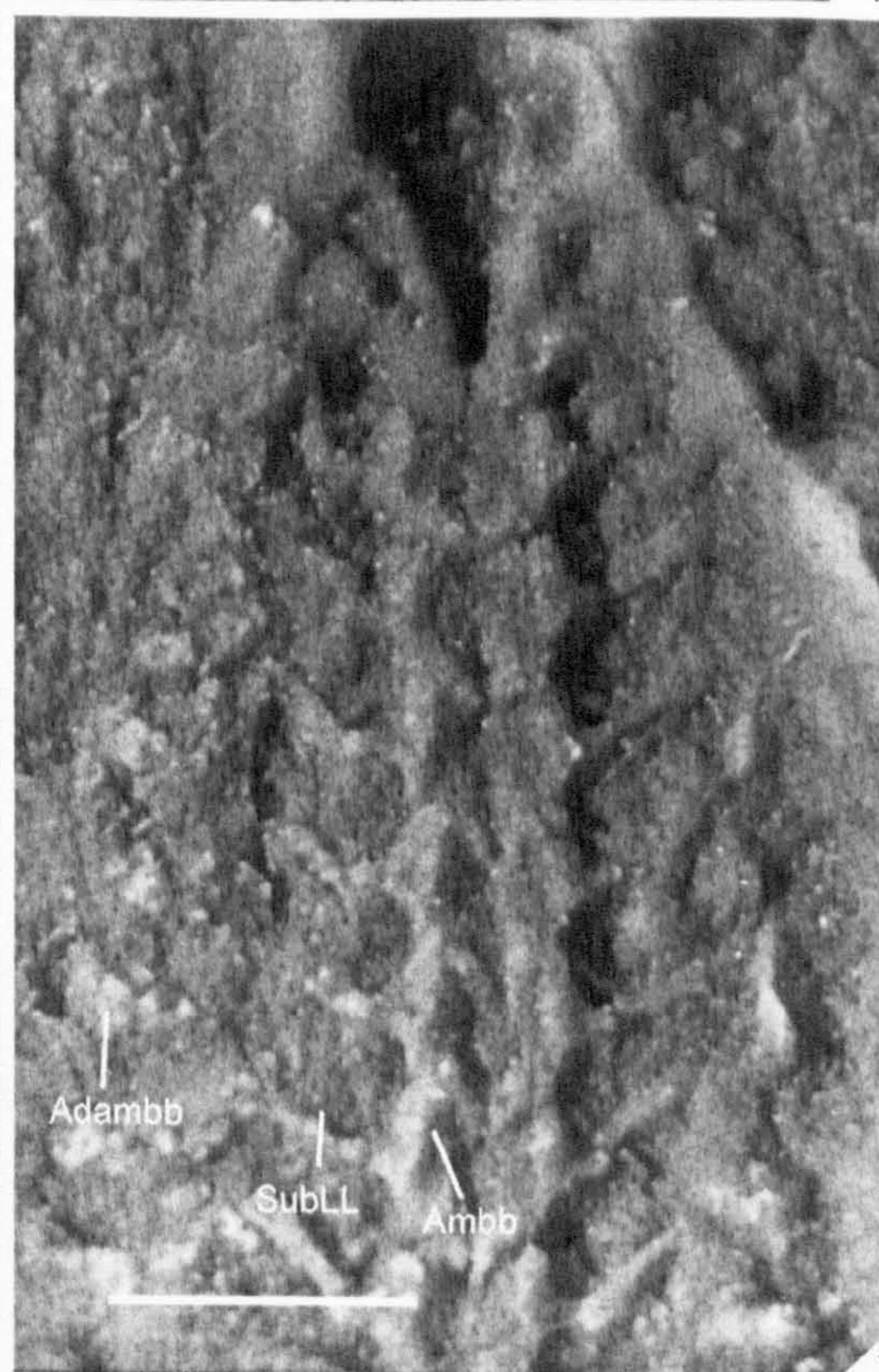
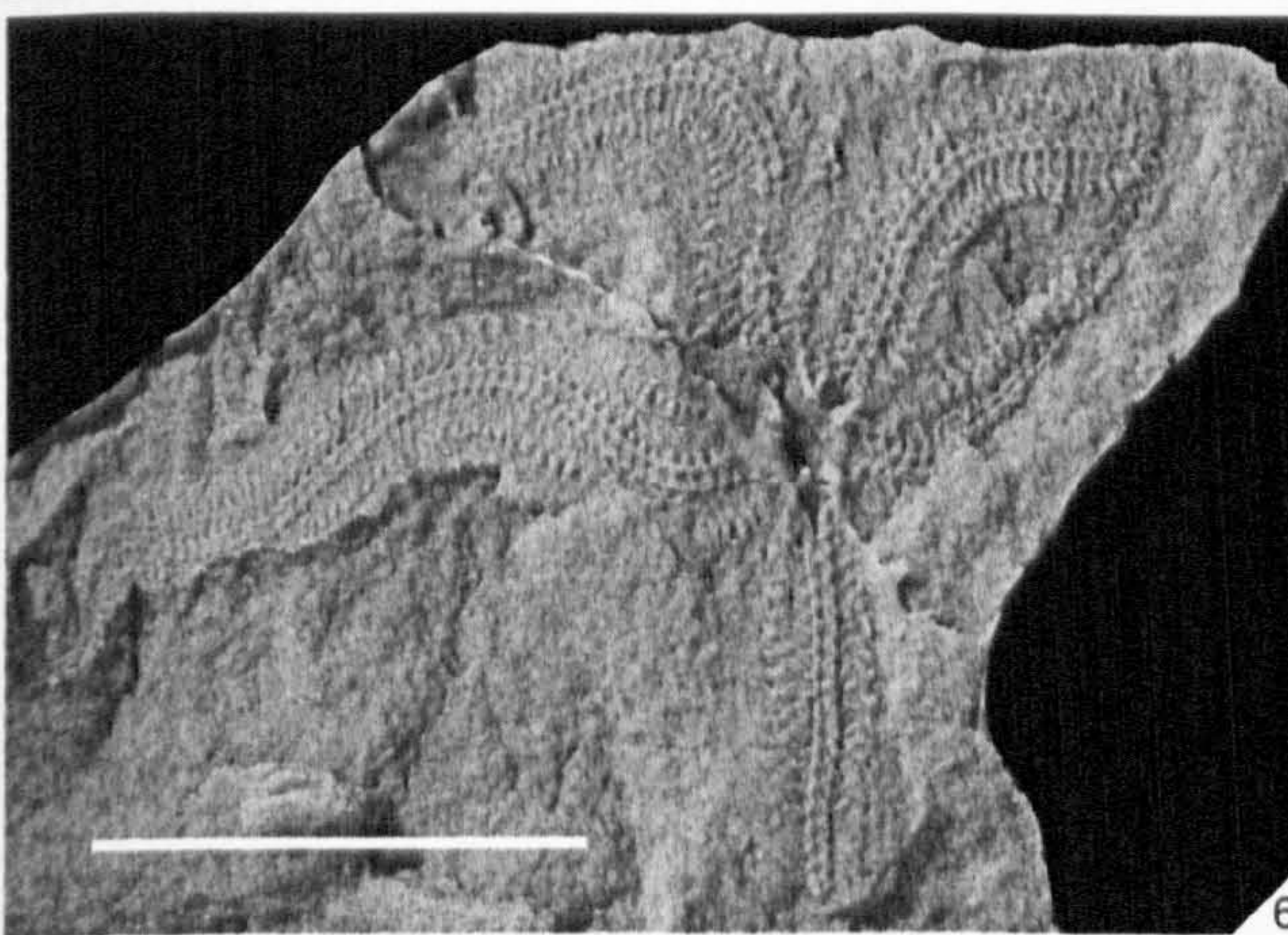
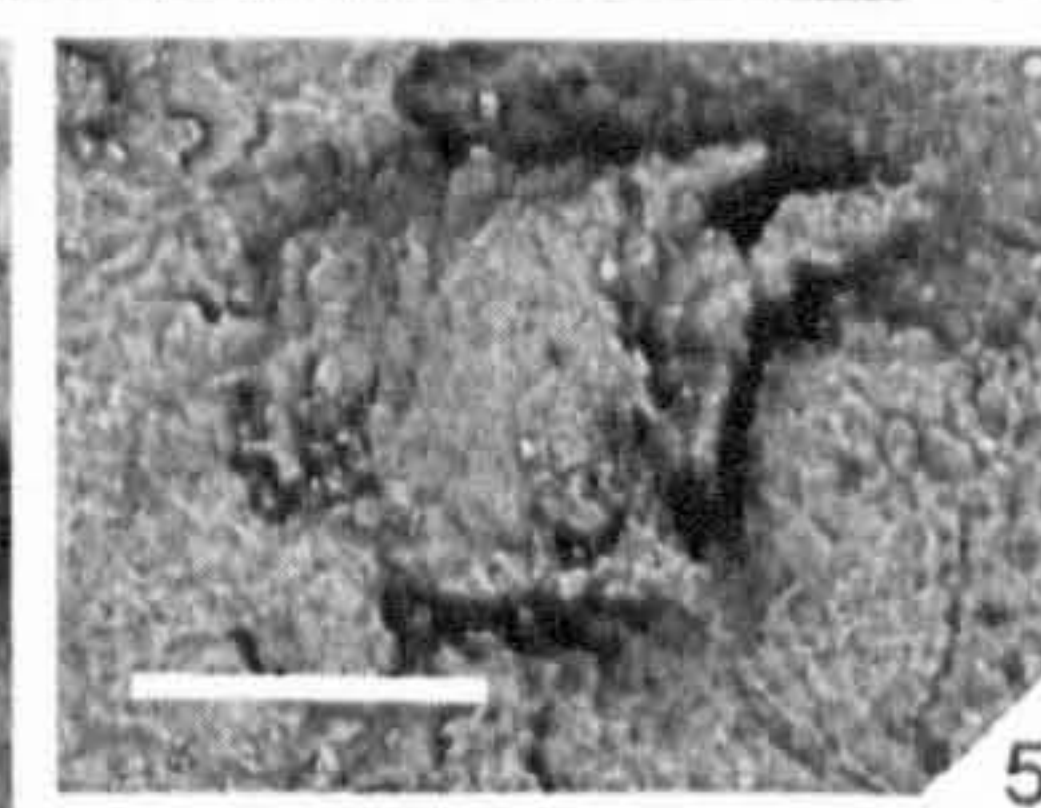
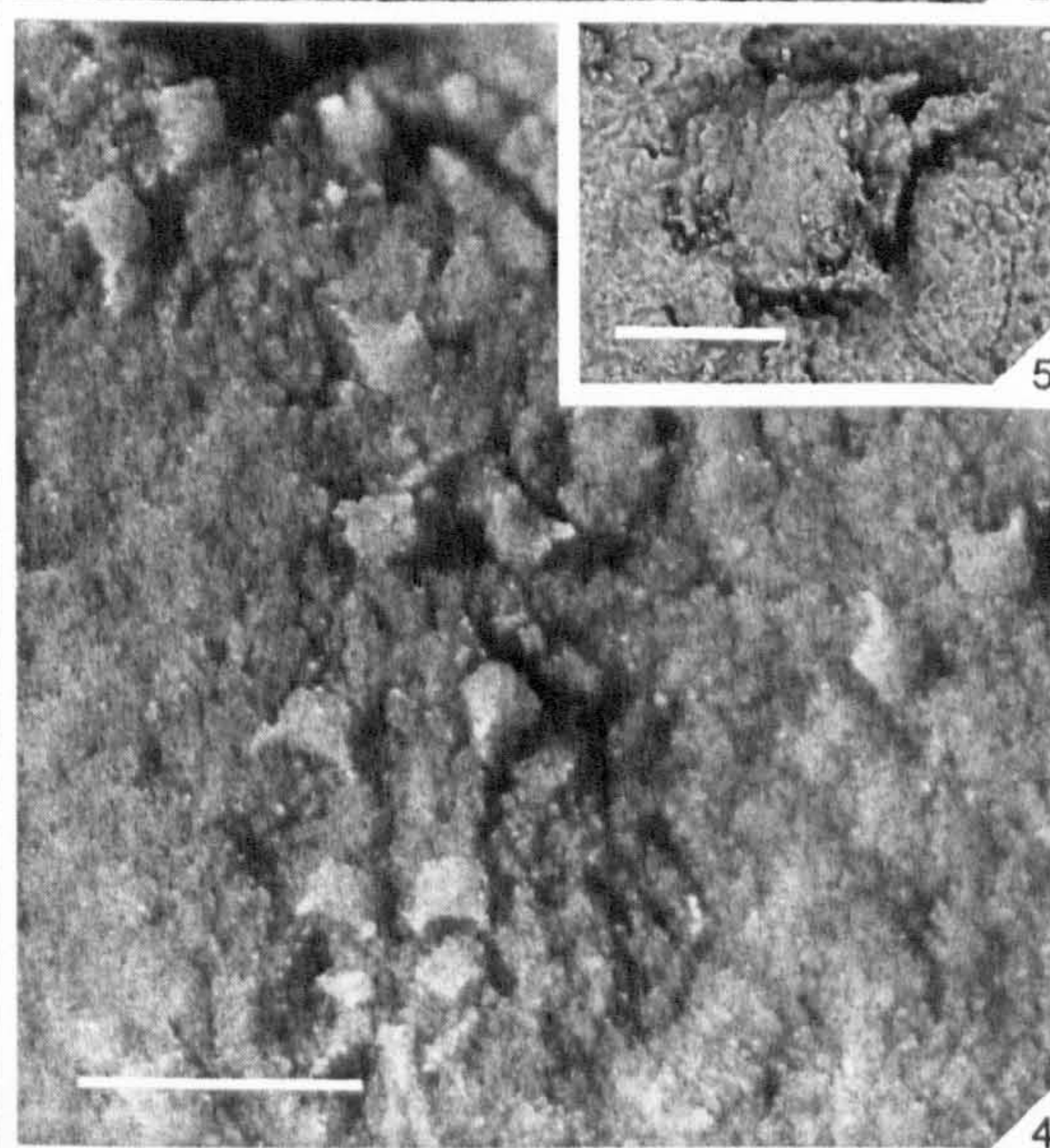
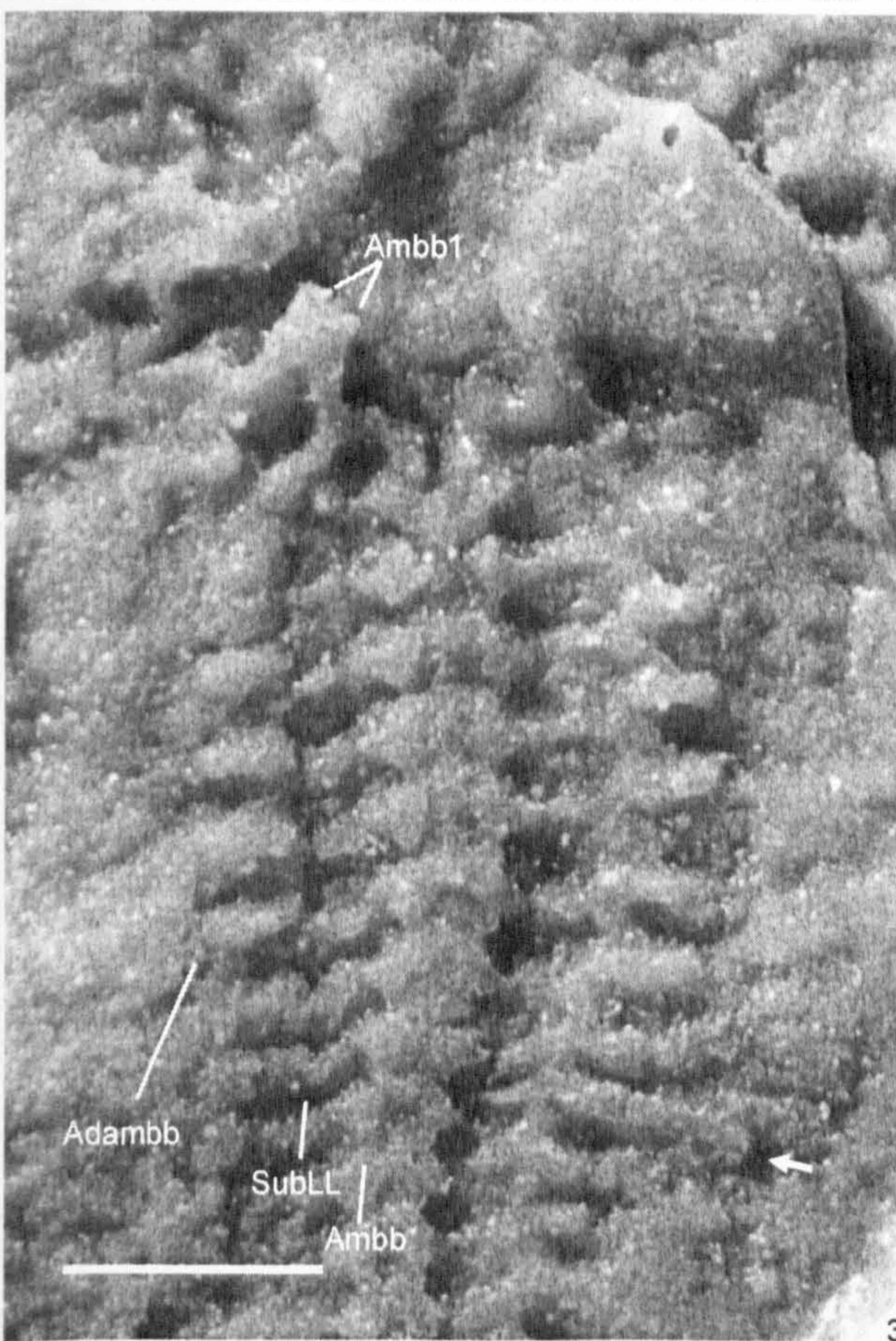
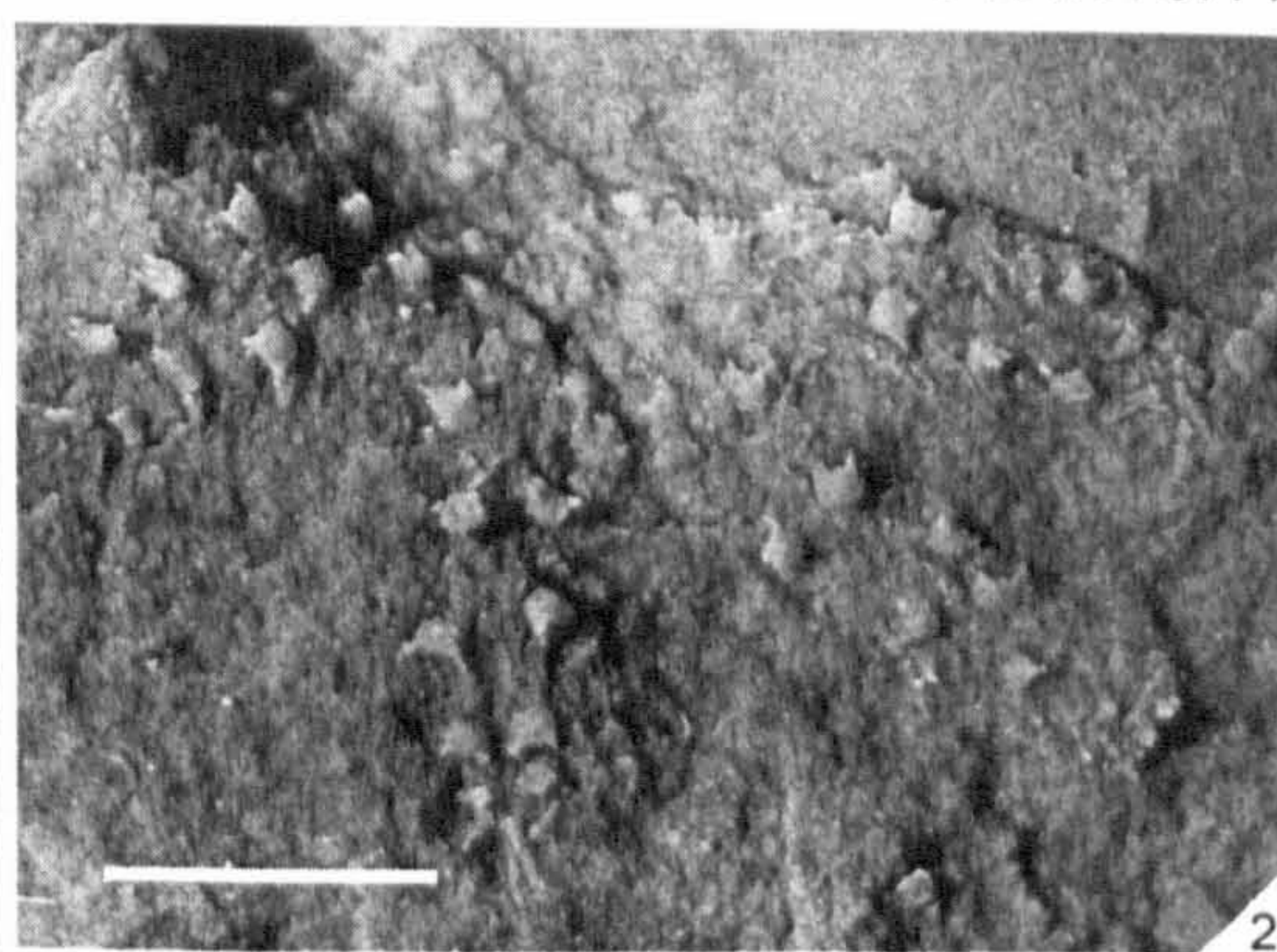
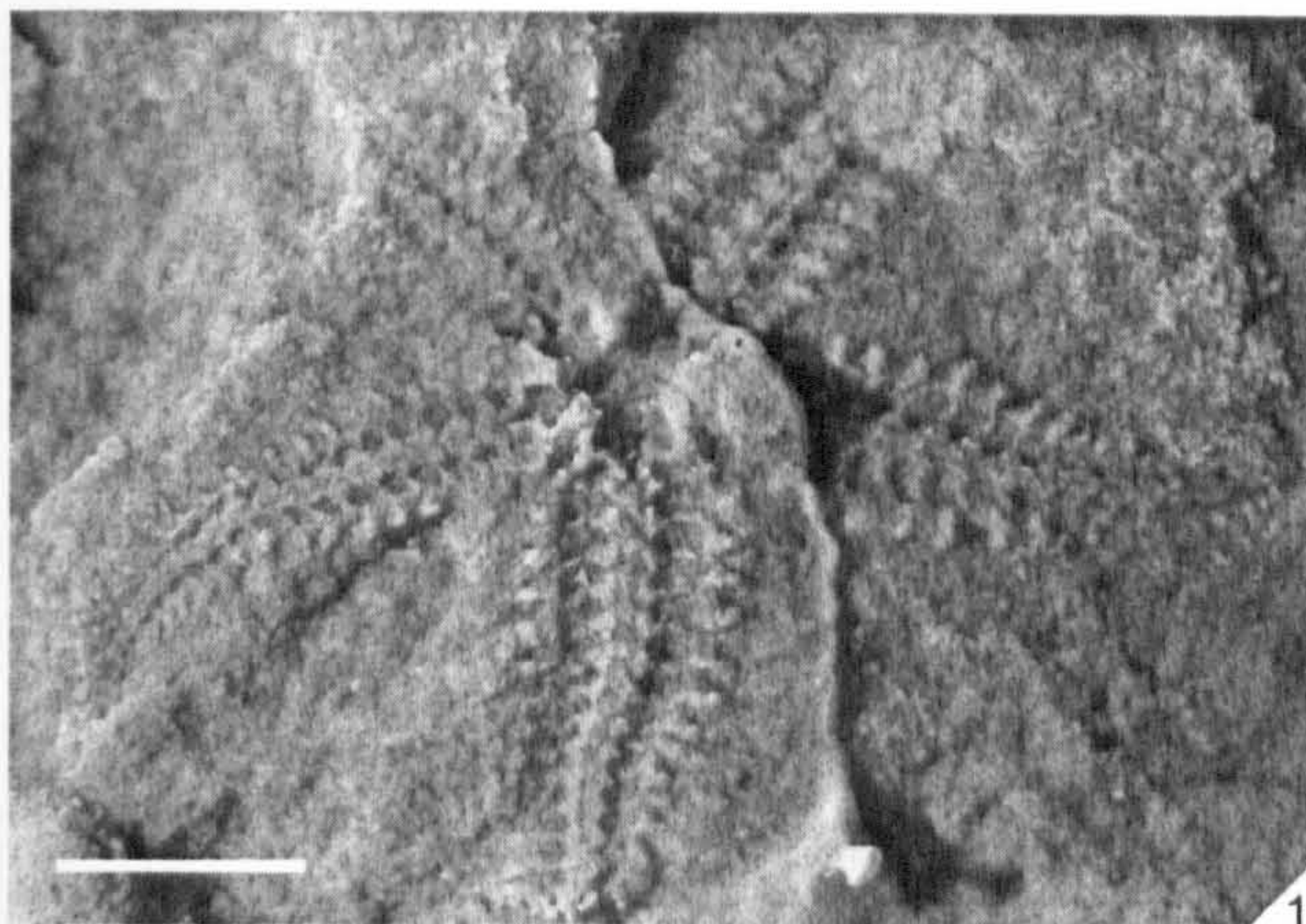
## EXPLANATION OF PLATE 3.14

Figs 1-5. *Antiquaster magrumi* Kesling, 1971; BMNH 40296a-b, part and counterpart; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, 3, BMNH 40296b. 1, entire specimen, ventral view; scale bar represents 2 mm. 3, detail of proximal arm and mouth frame (vestiges of Adamb process arrowed), ventral view; scale bar represents 1 mm. 2, 4-5, BMNH 40296a. 2, entire specimen, ventral view; scale bar represents 2 mm. 4, detail of pedicellariae, dorsal view; scale bar represents 1 mm. 5, detail of pedicellariae, dorsal view; scale bar represents 200  $\mu$ m; SEM photomicrograph.

6-7. *Klasmura?* sp.; BMNH 40300, Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 6, entire specimen, ventral view; scale bar represents 10 mm. 7, detail of proximal arm, ventral view; scale bar represents 1 mm.

All figures are of silicone casts.



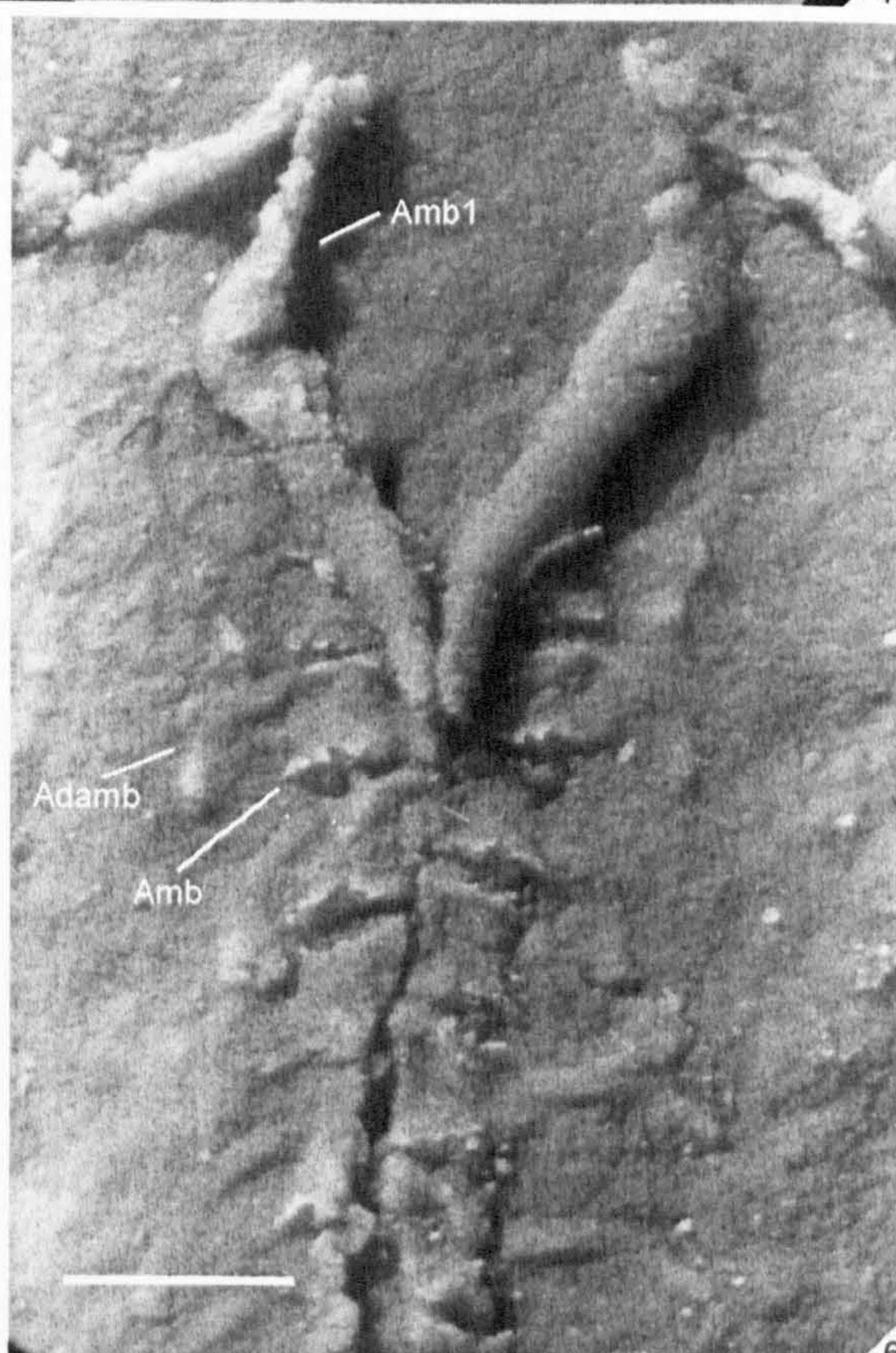
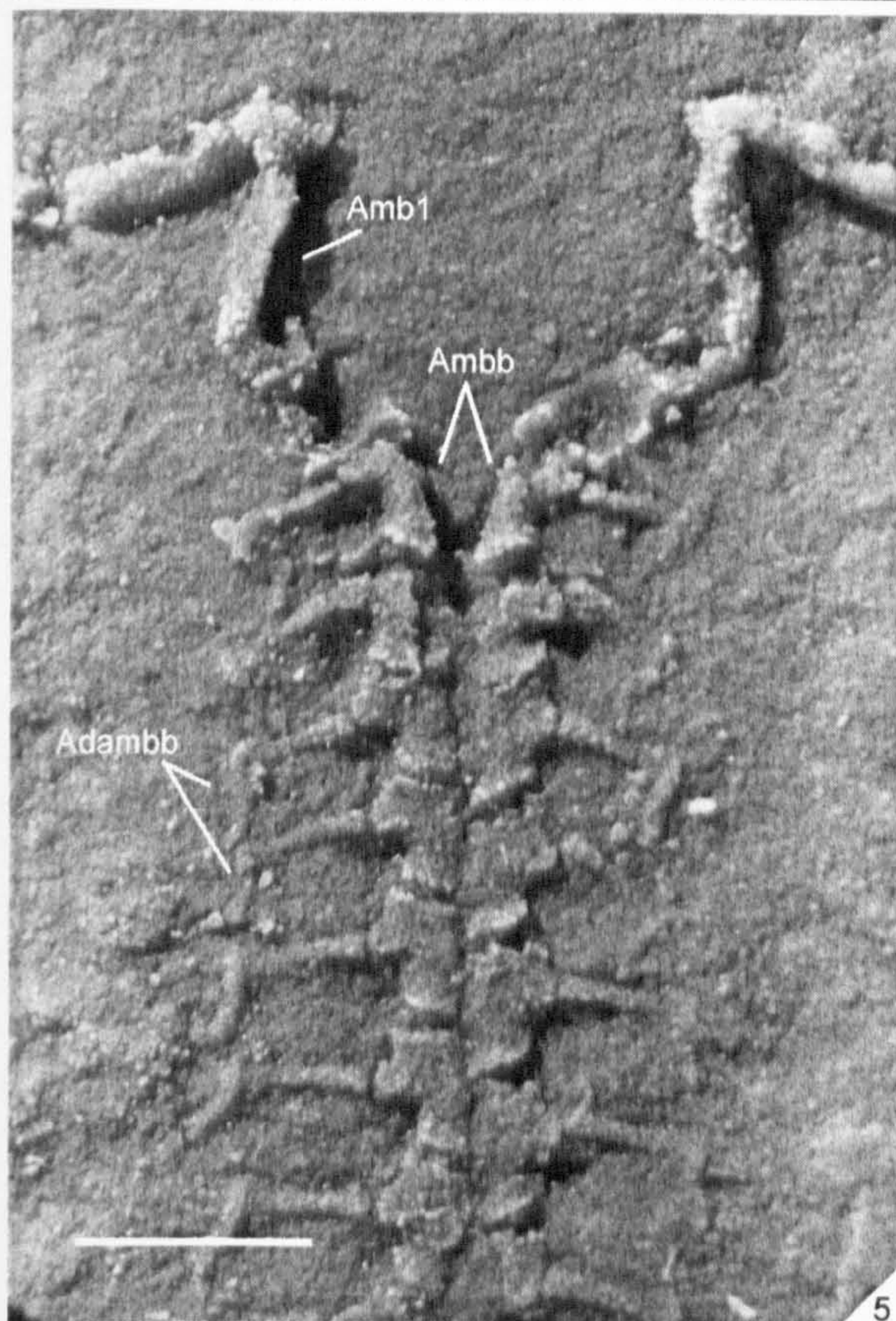
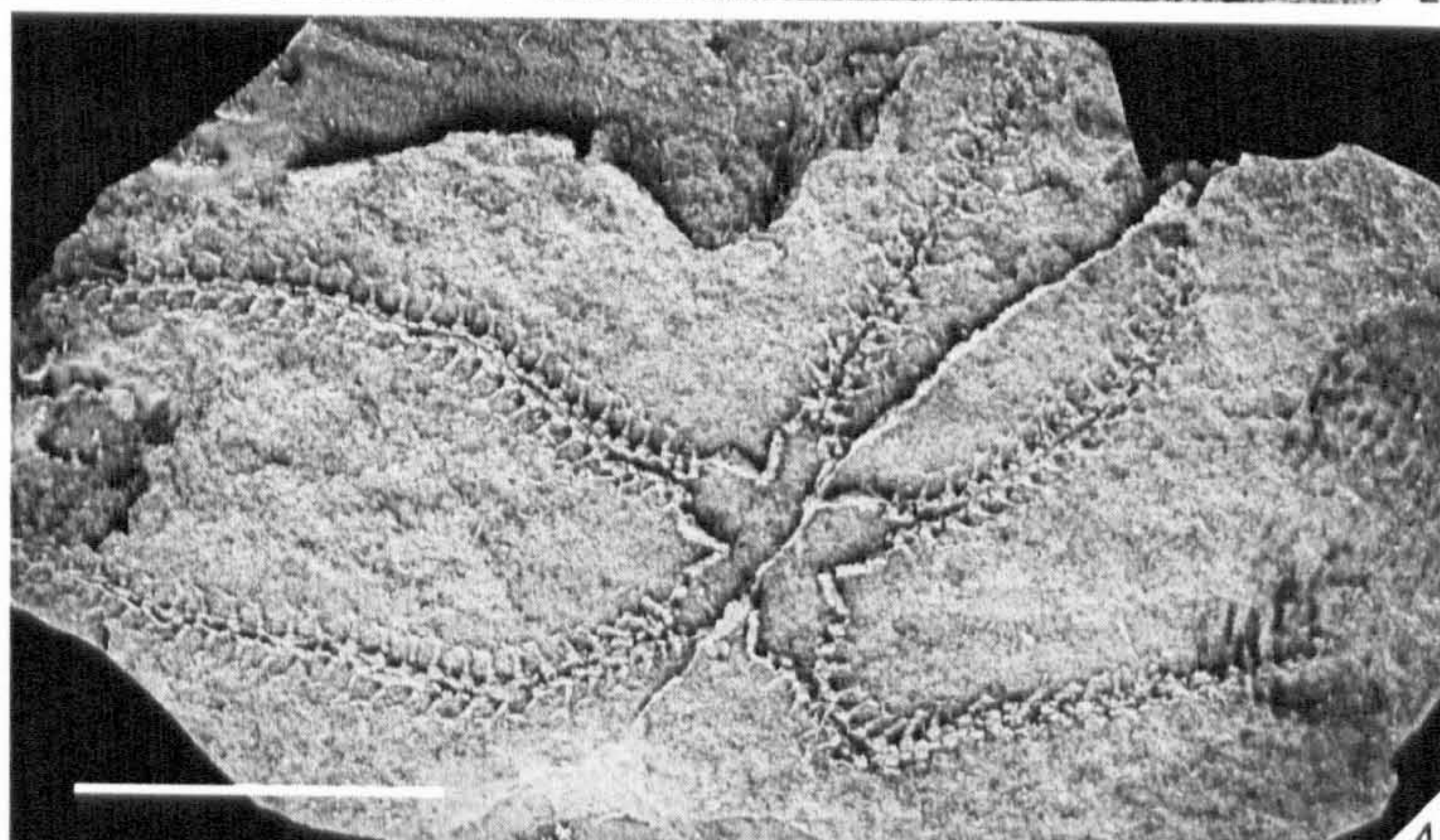
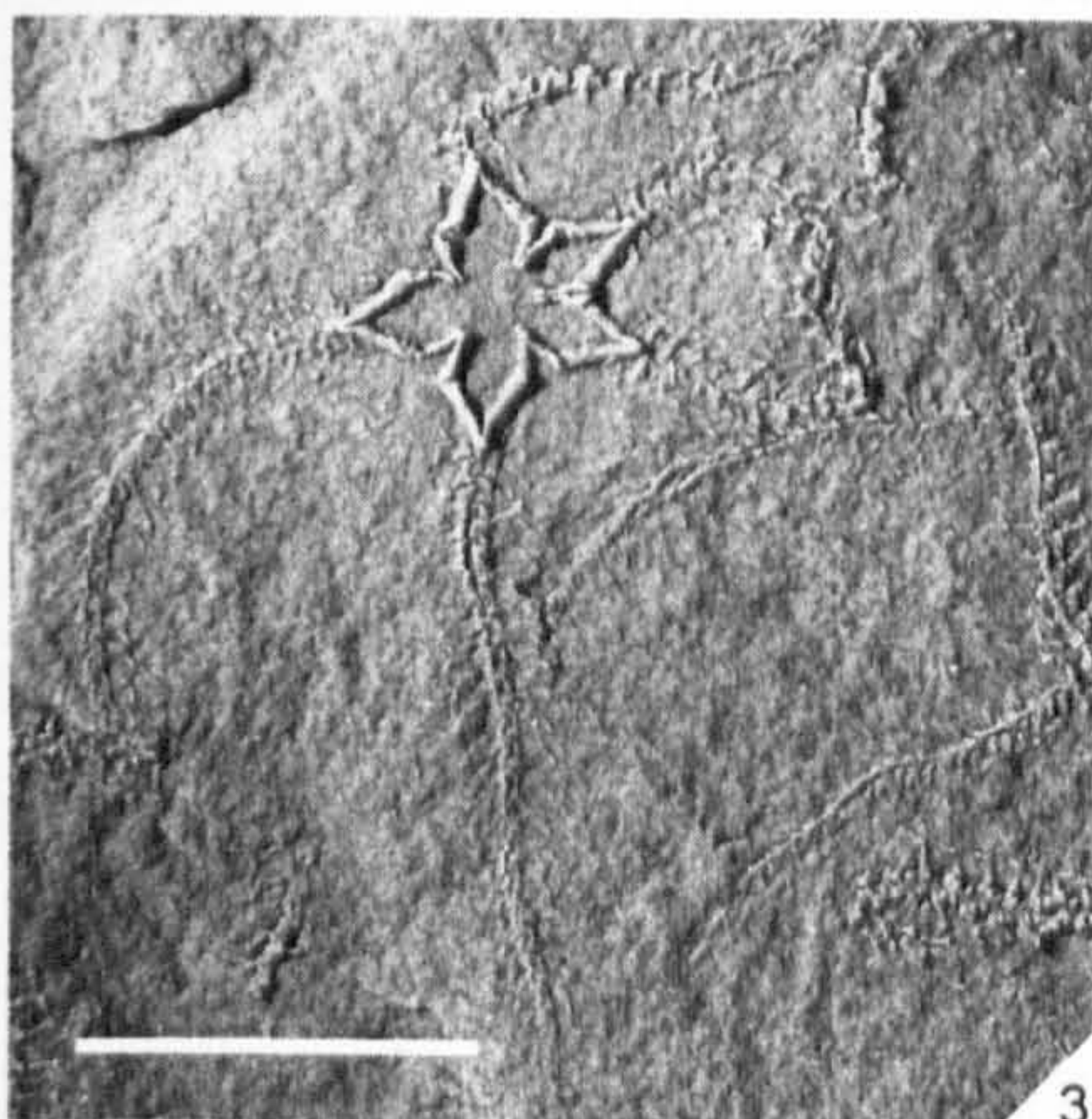
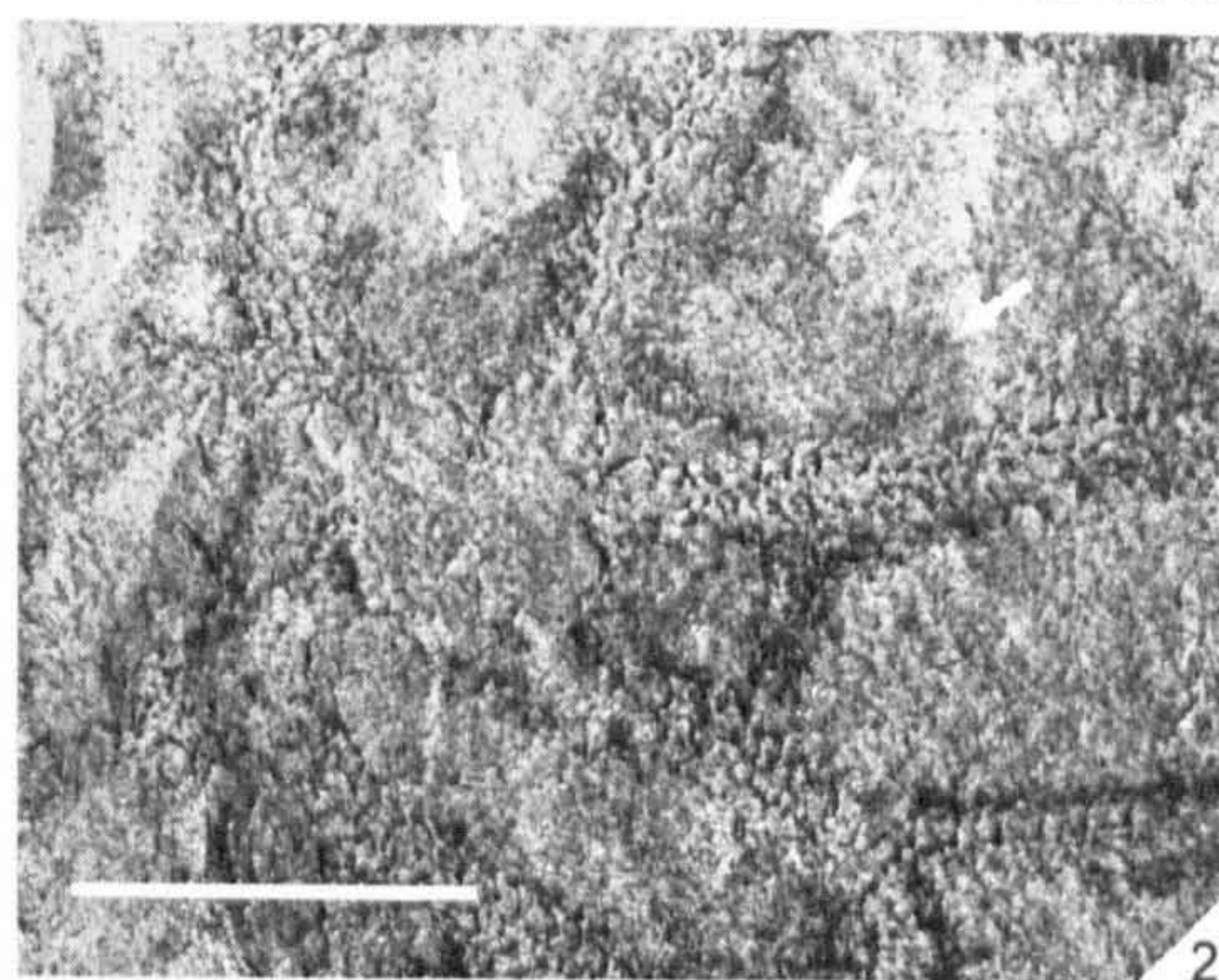
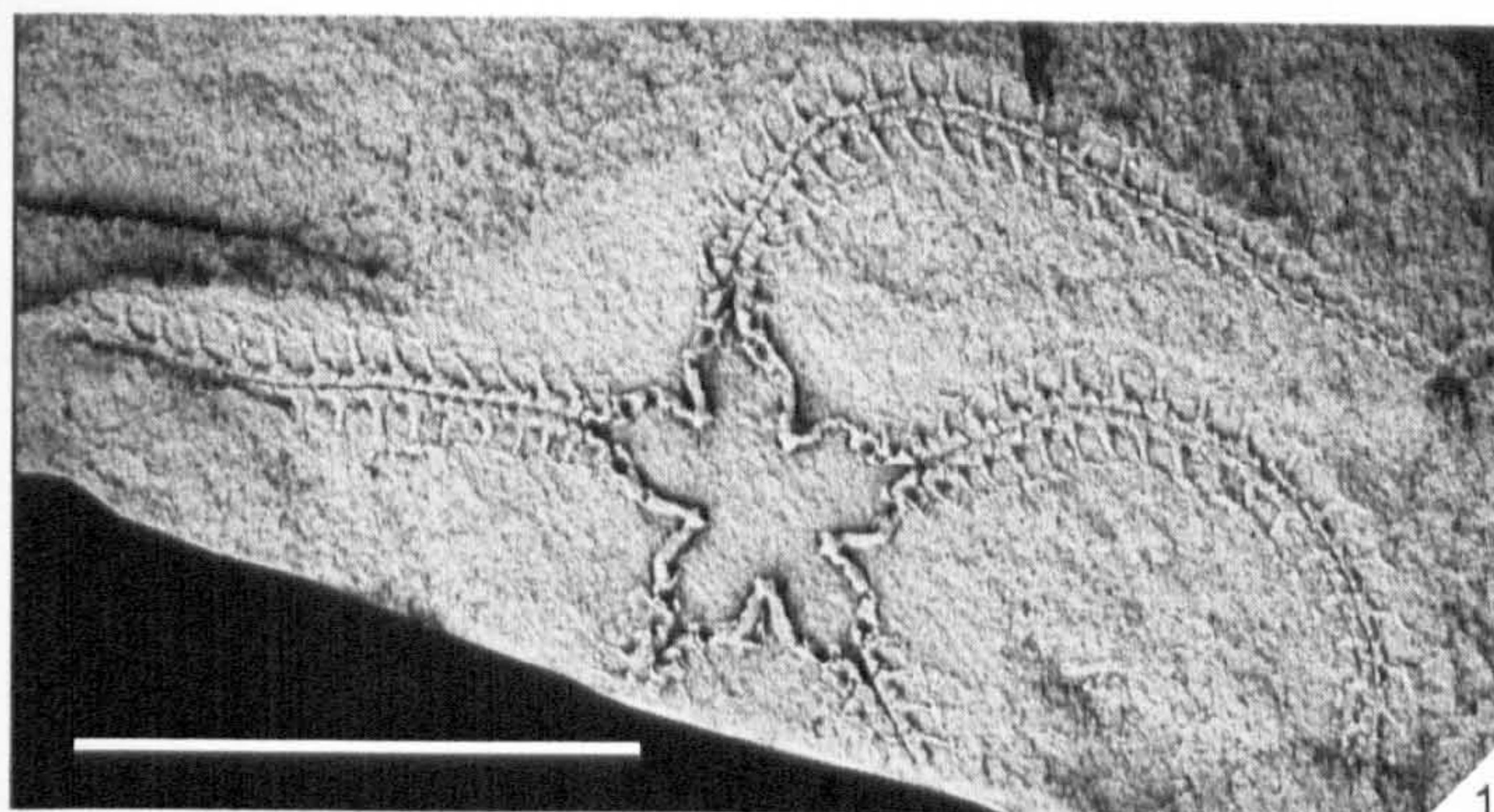




## EXPLANATION OF PLATE 3.15

Figs 1-6. *Loriolaster calceatus* sp. nov.; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, 5, BMNH 47953, holotype. 1, entire specimen, ventral view; scale bar represents 10 mm. 5, detail of proximal arm showing diagnostic L-shaped Adambb, ventral view; scale bar represents 1 mm. 2, BGS GSM25351, detail of possible vestiges of large membranous disc, ventral view (extent of disc arrowed); scale bar represents 10 mm. 3, 6, BMNH 38527, paratype. 3, entire specimen, dorsal view; scale bar represents 10 mm. 6, detail of proximal arm and part of mouth frame, dorsal arm; scale bar represents 1 mm. 4, BMNH 47949, entire specimen, ventral view; scale bar represents 10 mm. All figures are of silicone casts except 2.







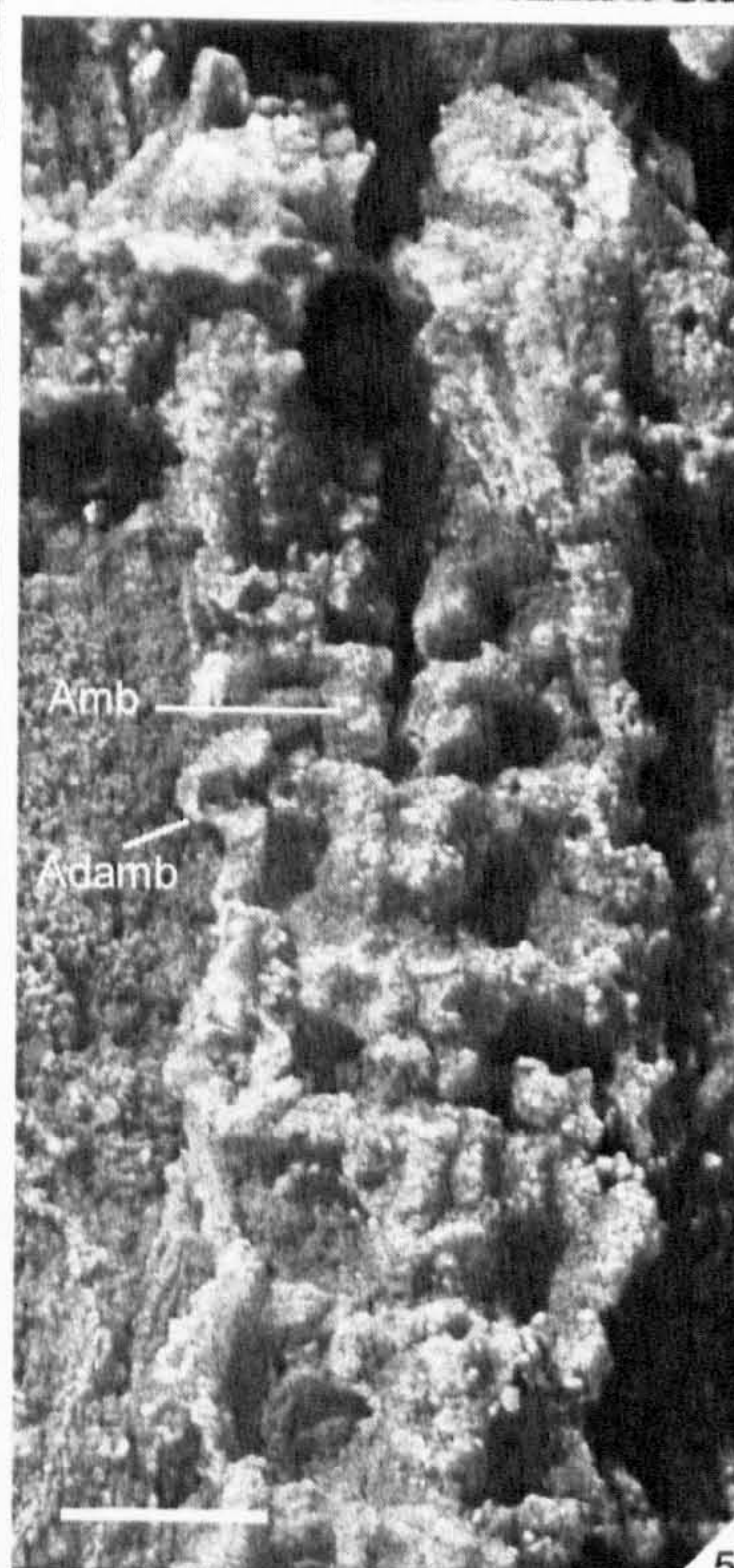
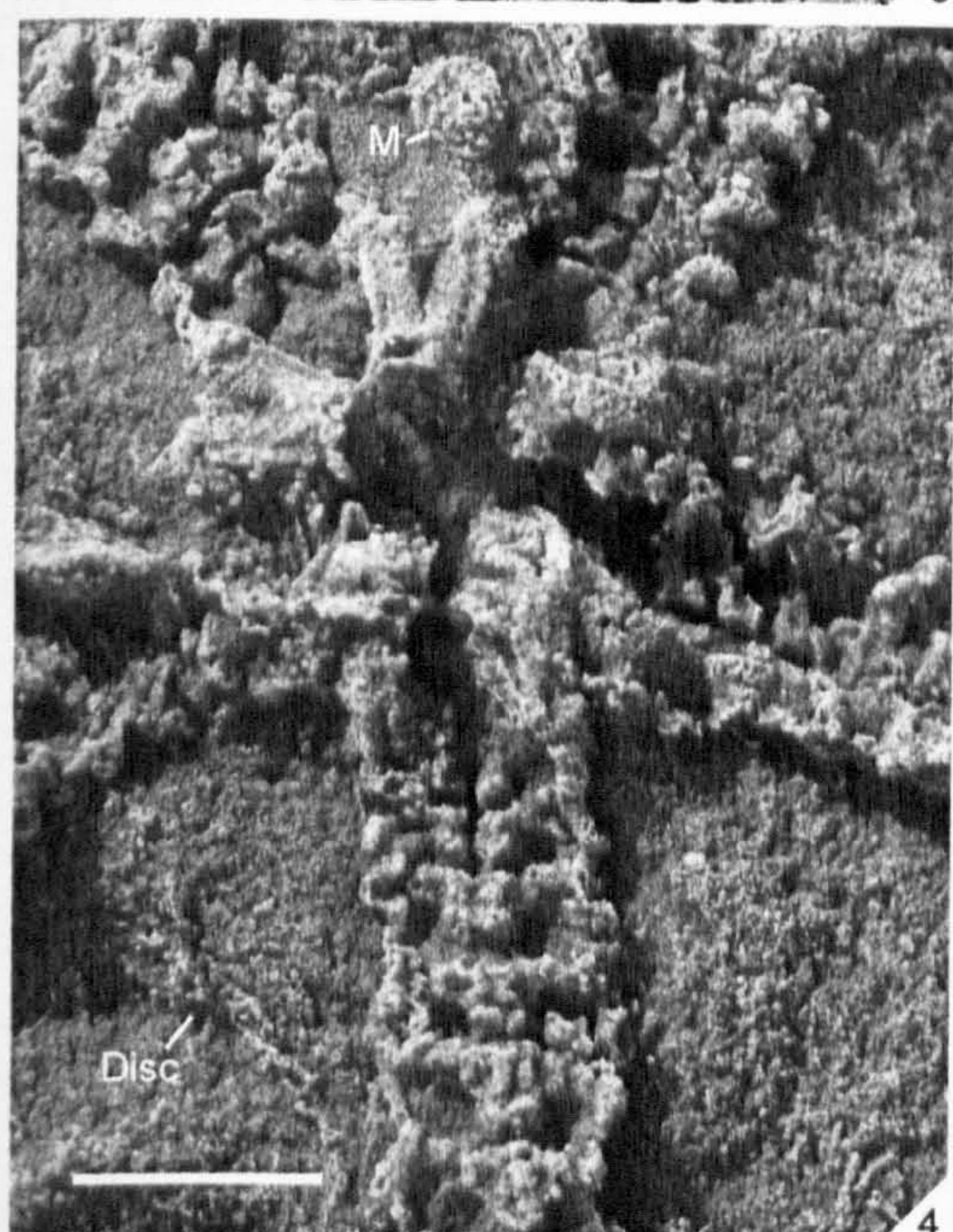
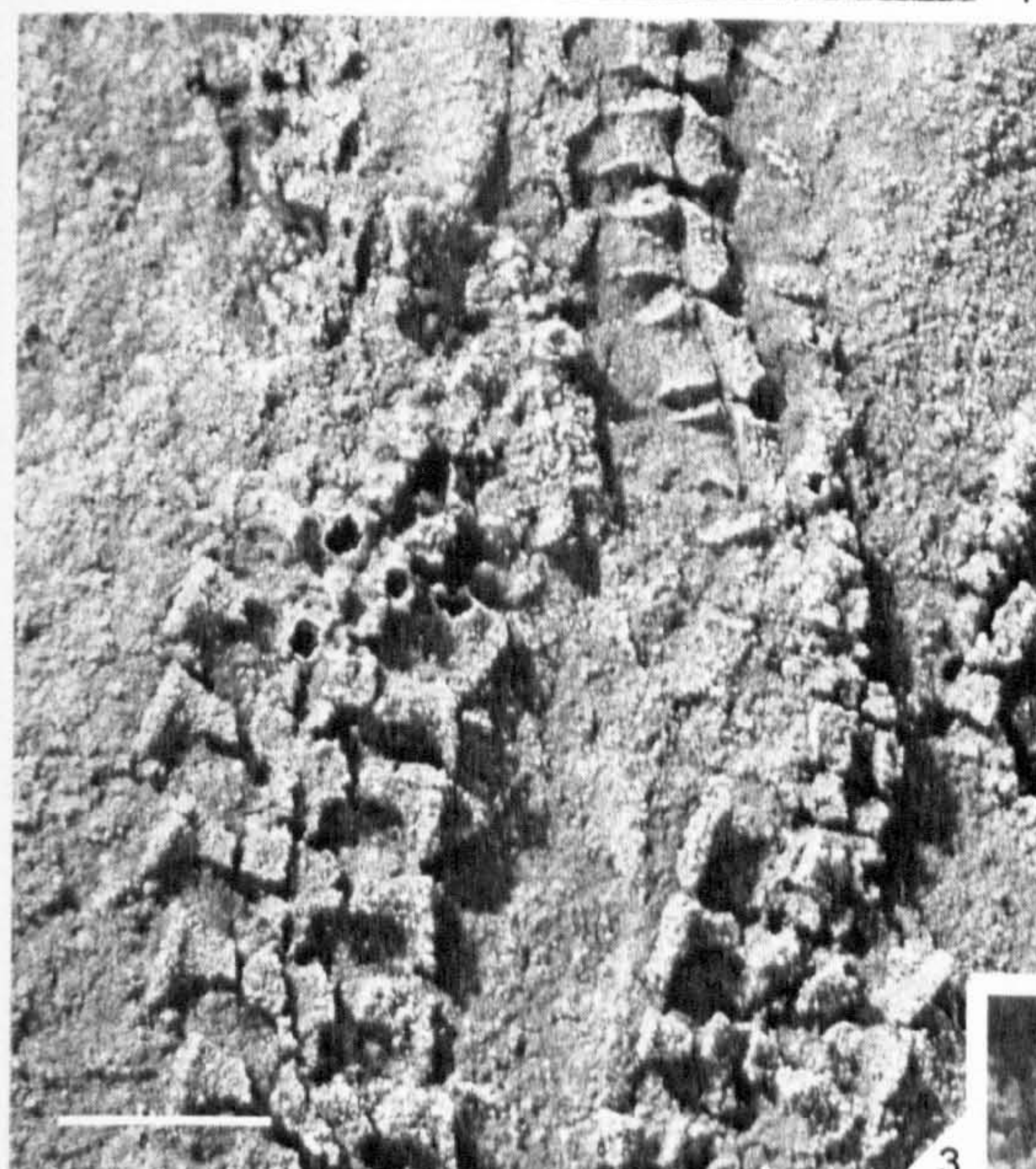
## EXPLANATION OF PLATE 3.16

Figs 1-3. *Loriolaster calceatus* sp. nov.; BGS GSE15249-50, part and counterpart; Llandovery Series; Gutterford Burn, Pentland Hills, Midlothian, Scotland. 1, 3, BGS GSE15249. 1, entire specimen showing possible vestiges of large membranous disc, lateral view (extent of disc arrowed); original fossil; scale bar represents 10 mm. 3, detail of arms showing ventral and dorsal surfaces; scale bar represents 1 mm. 2, BGS GSE15250, detail of proximal arm and mouth frame, ventral view; scale bar represents 1 mm.

Figs 4-6. *Lapworthura miltoni* (Salter, 1857); BMNH E 52442a-b, part and counterpart; Ashgill Series; Lady Burn, Girvan, Scotland. 4-5, BMNH E 52442a. 4, detail of proximal arms and mouth frame, ventral view; scale bar represents 2 mm. 5, detail of proximal arm, ventral view; scale bar represents 1 mm. 6, BMNH E 52442b, detail of proximal arm, dorsal view; scale bar represents 1 mm.

All figures are of silicone casts except 1.



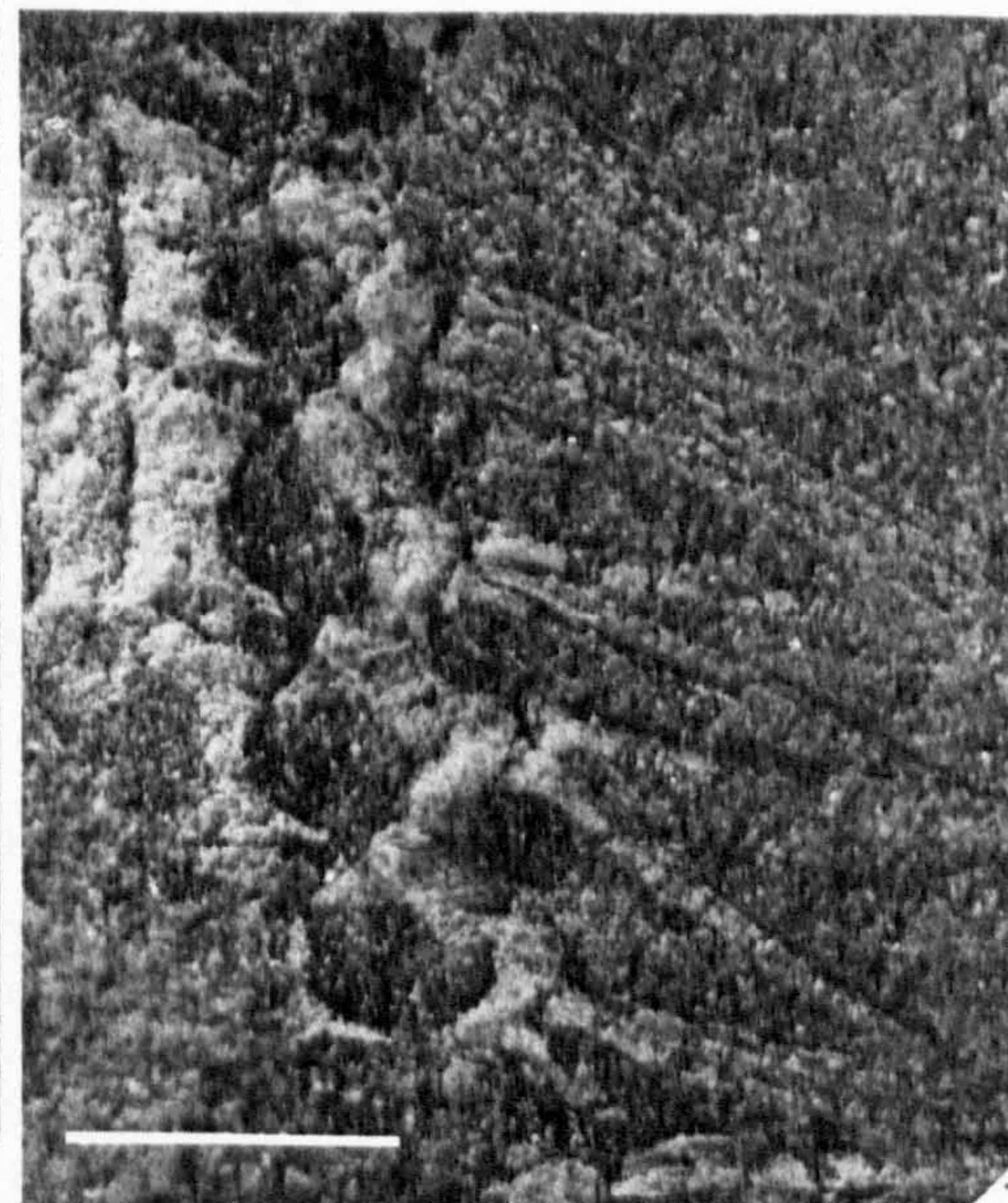
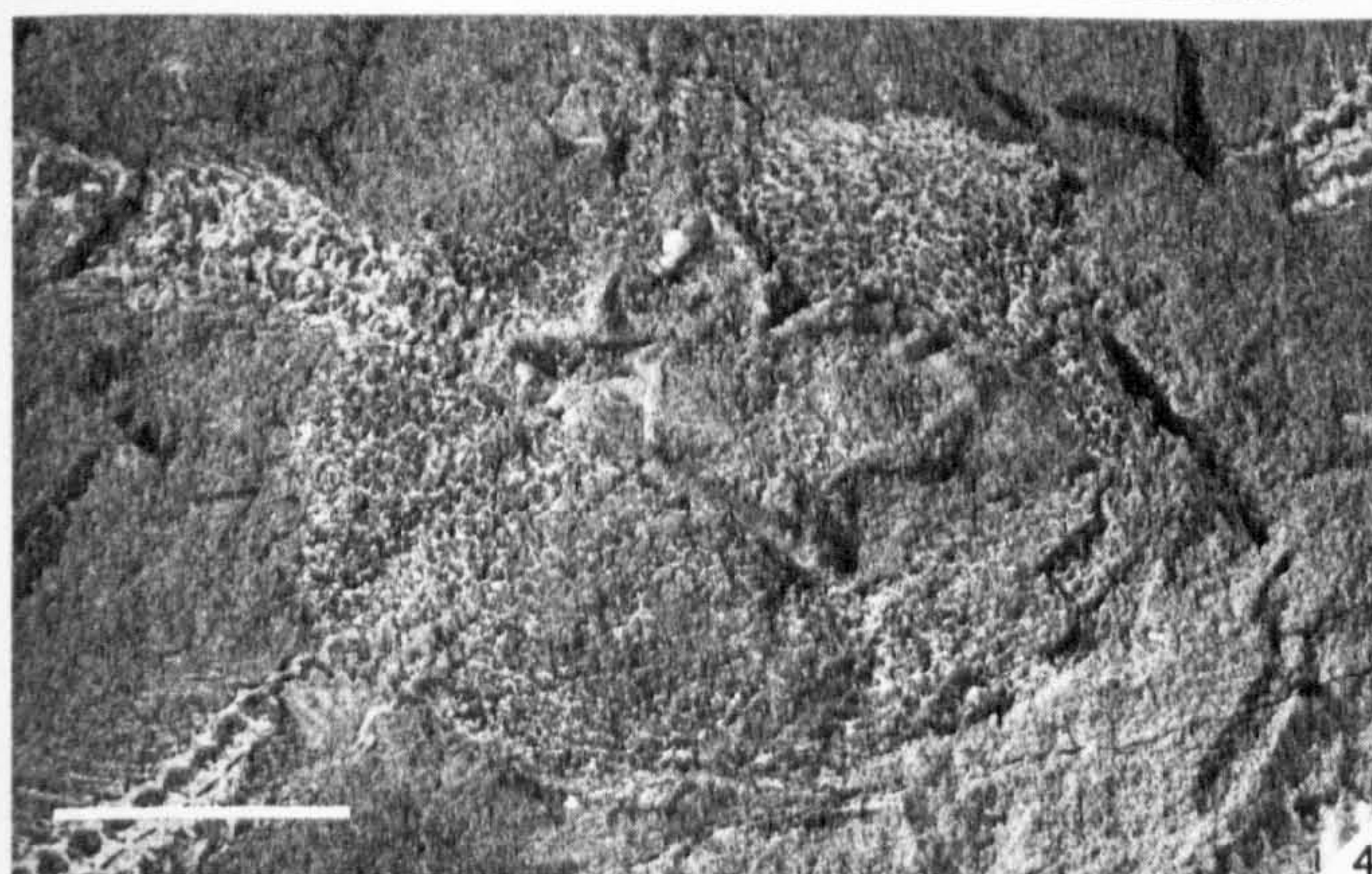
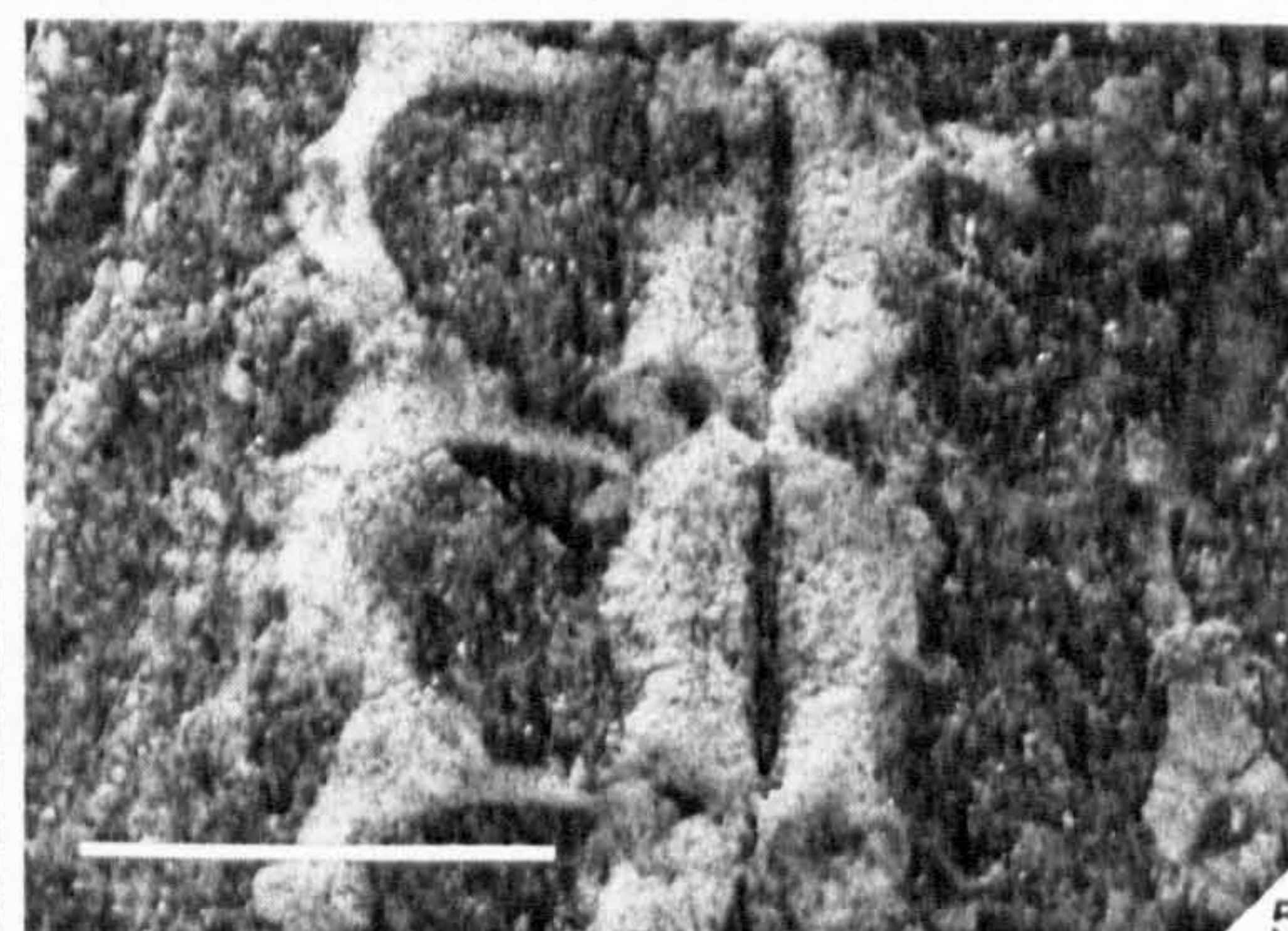
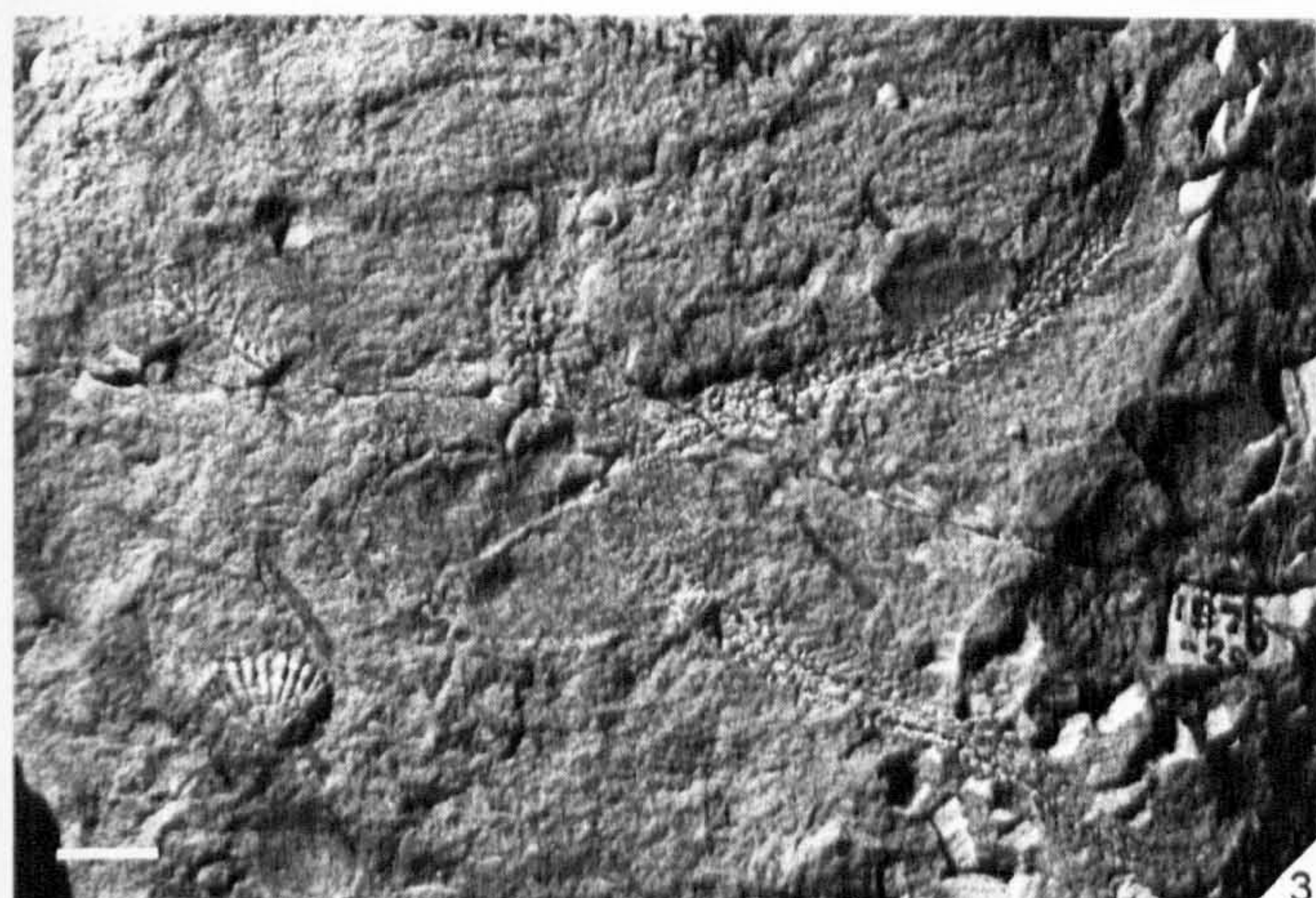
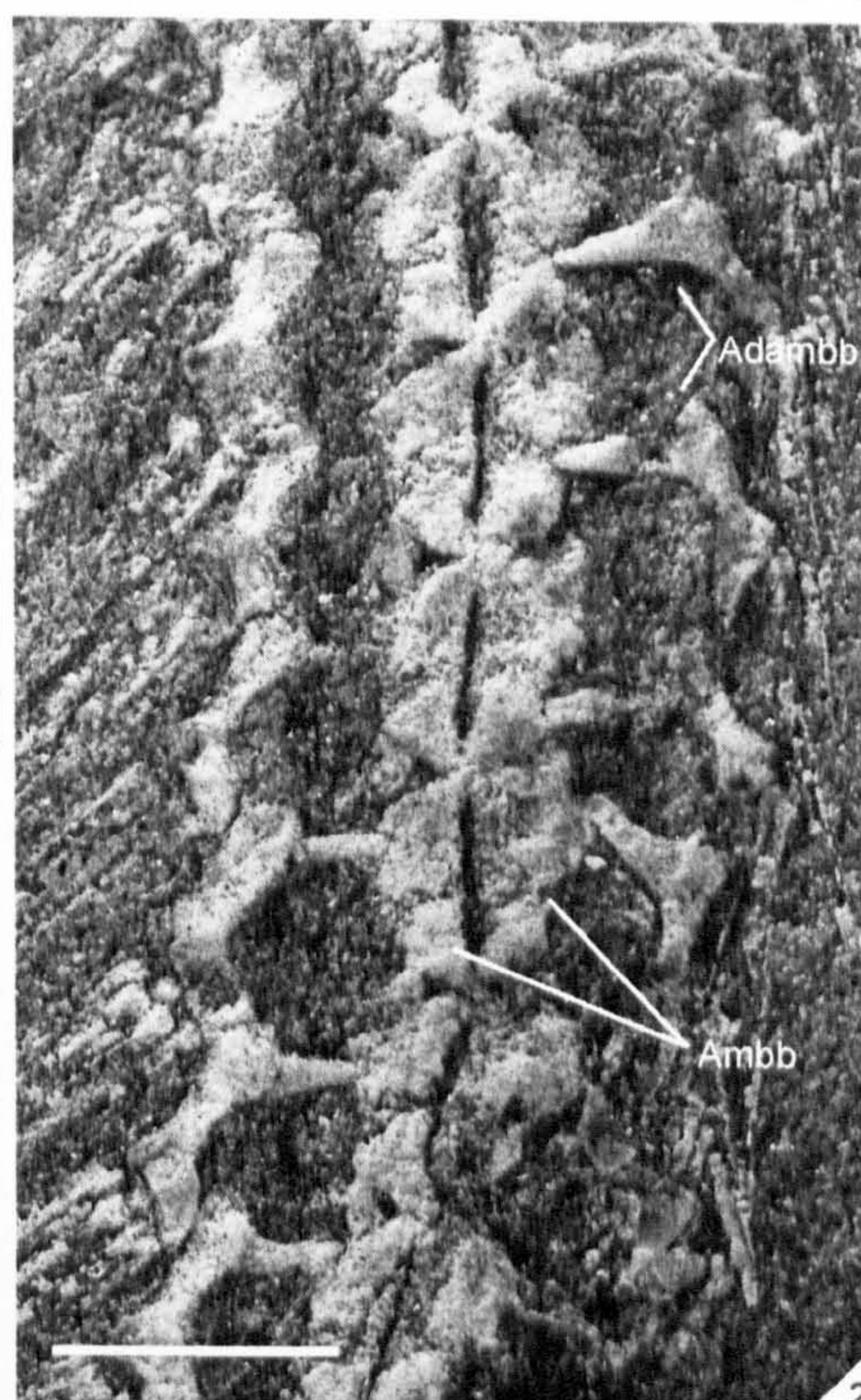




## EXPLANATION OF PLATE 3.17

Figs 1-7. *Lapworthura miltoni* (Salter, 1857); BMNH E 20235a-b, holotype, part and counterpart; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-2, 4-7, BMNH E 20235a. 1, entire specimen; scale bar represents 10 mm. 2, detail of arm showing Ambb and Adambb; scale bar represents 2 mm. 4, detail of disc; scale bar represents 10 mm. 5, detail of Ambb and Adambb; scale bar represents 2 mm. 6, detail of spicules over surface of disc; scale bar represents 1 mm. 7, detail of spines articulated to Adambb; scale bar represents 2 mm. 3, BMNH E 20235b, entire specimen; scale bar represents 10 mm.



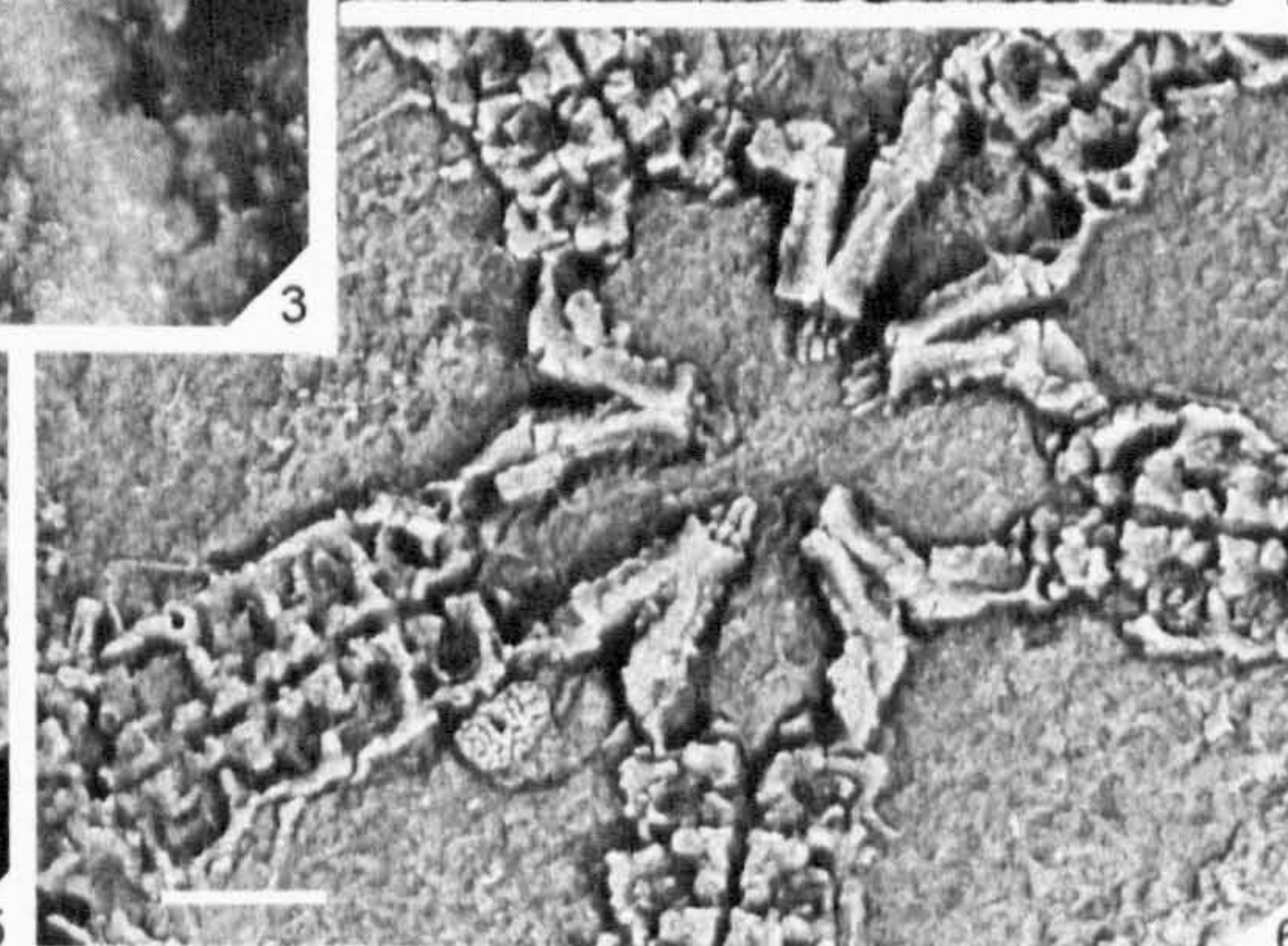
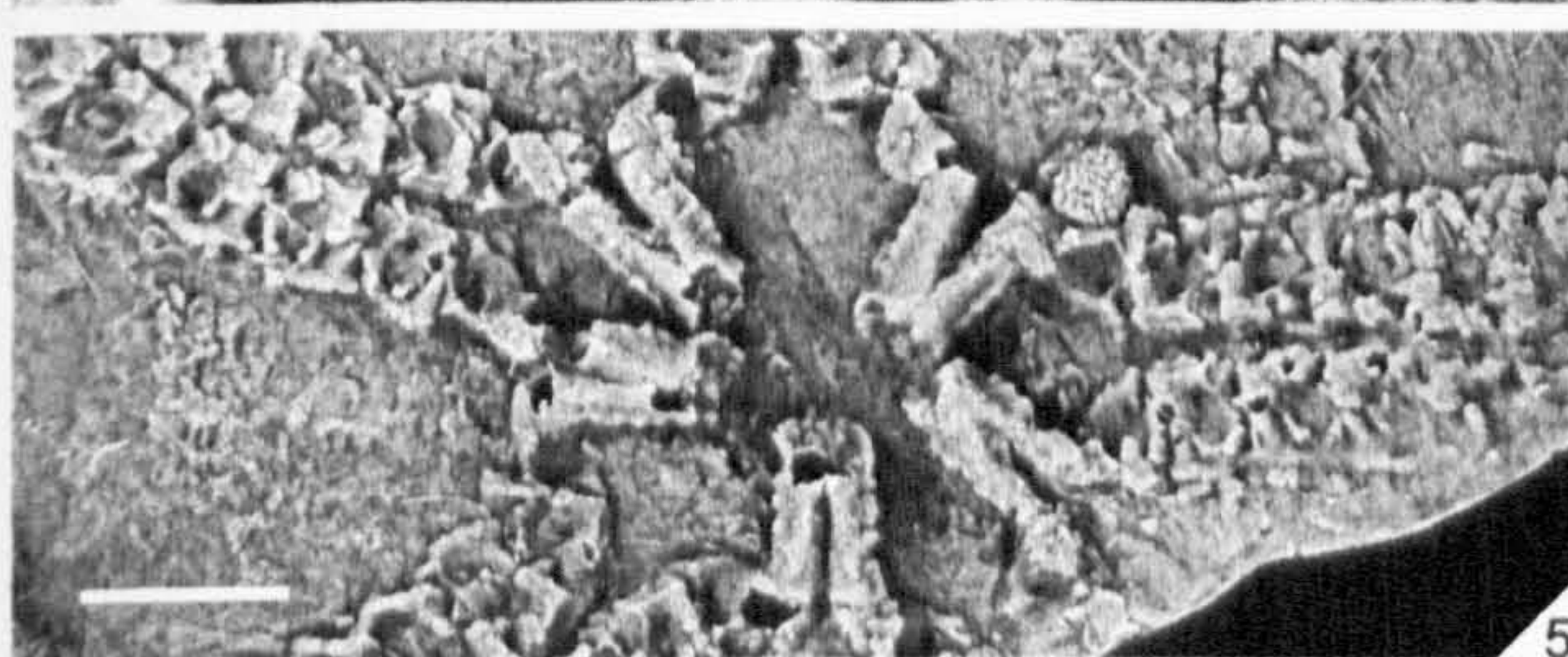
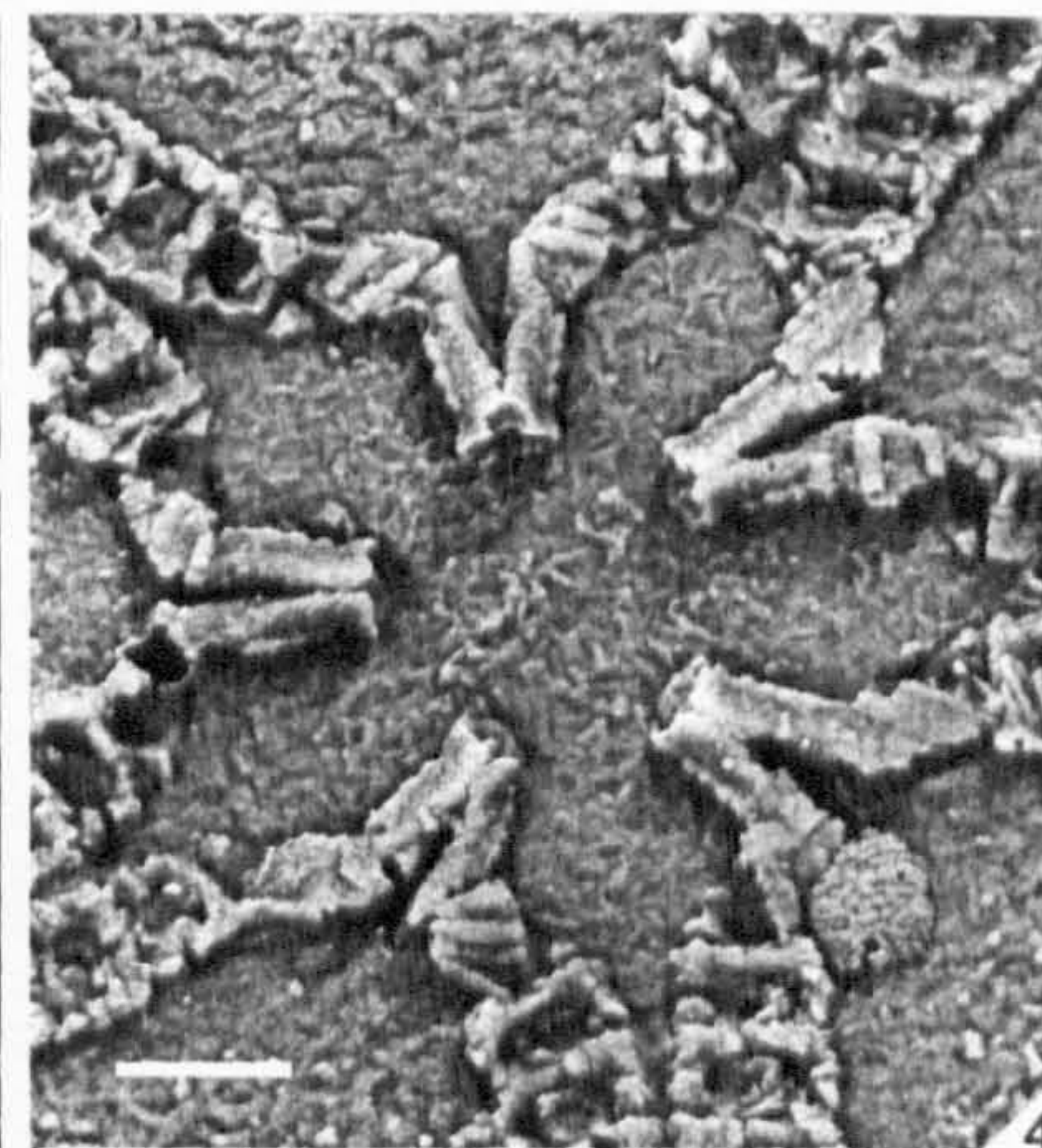
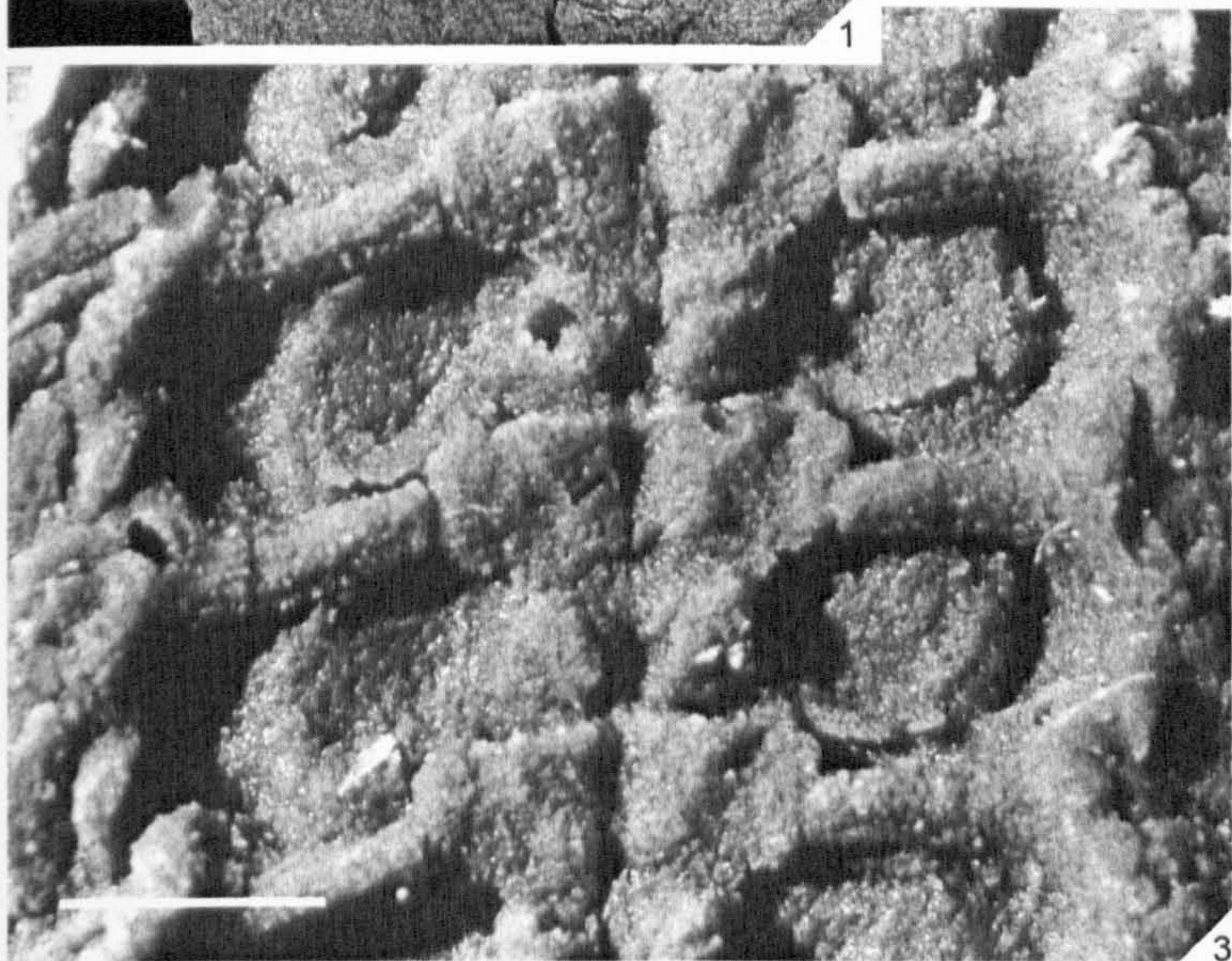
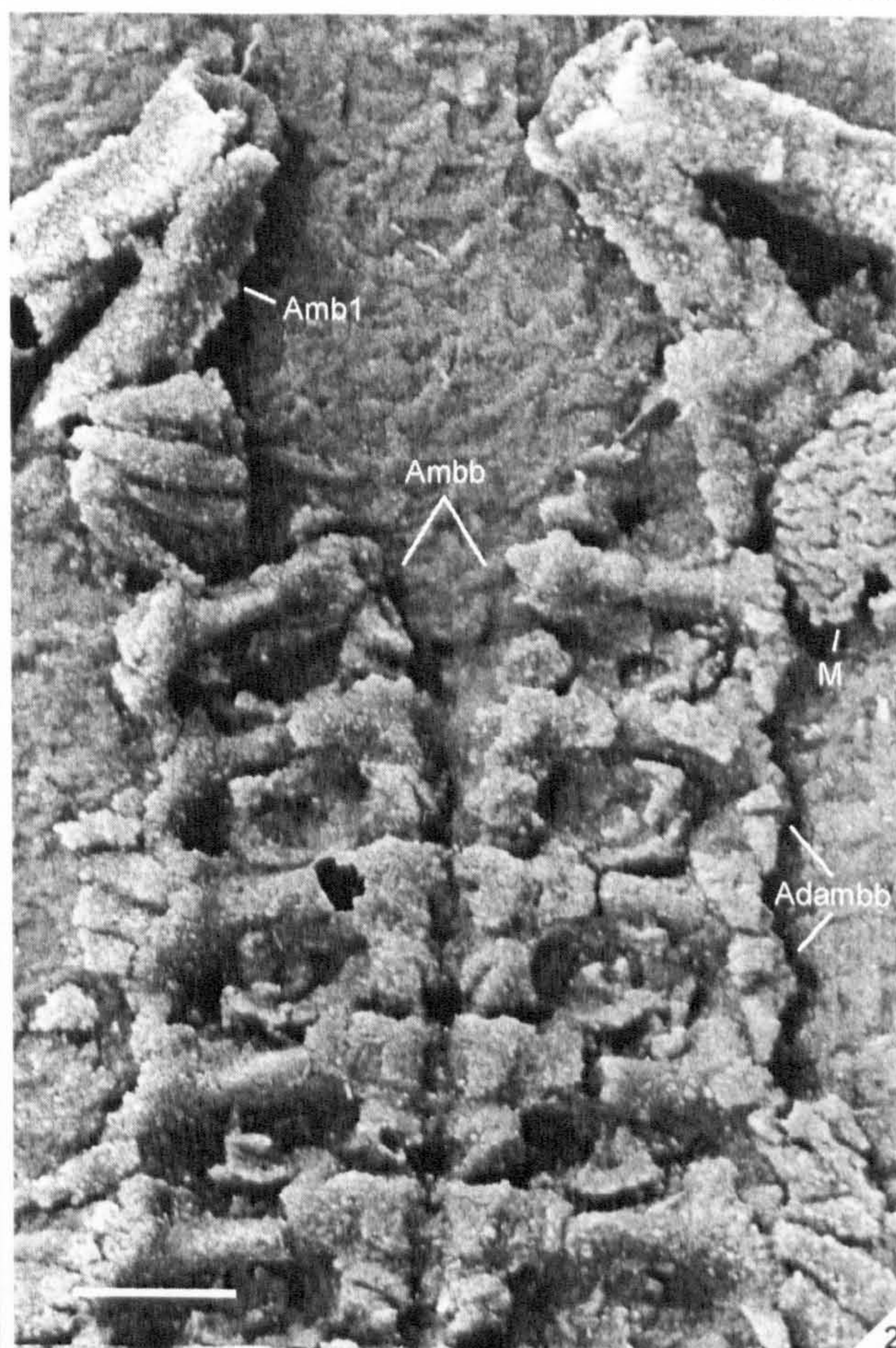
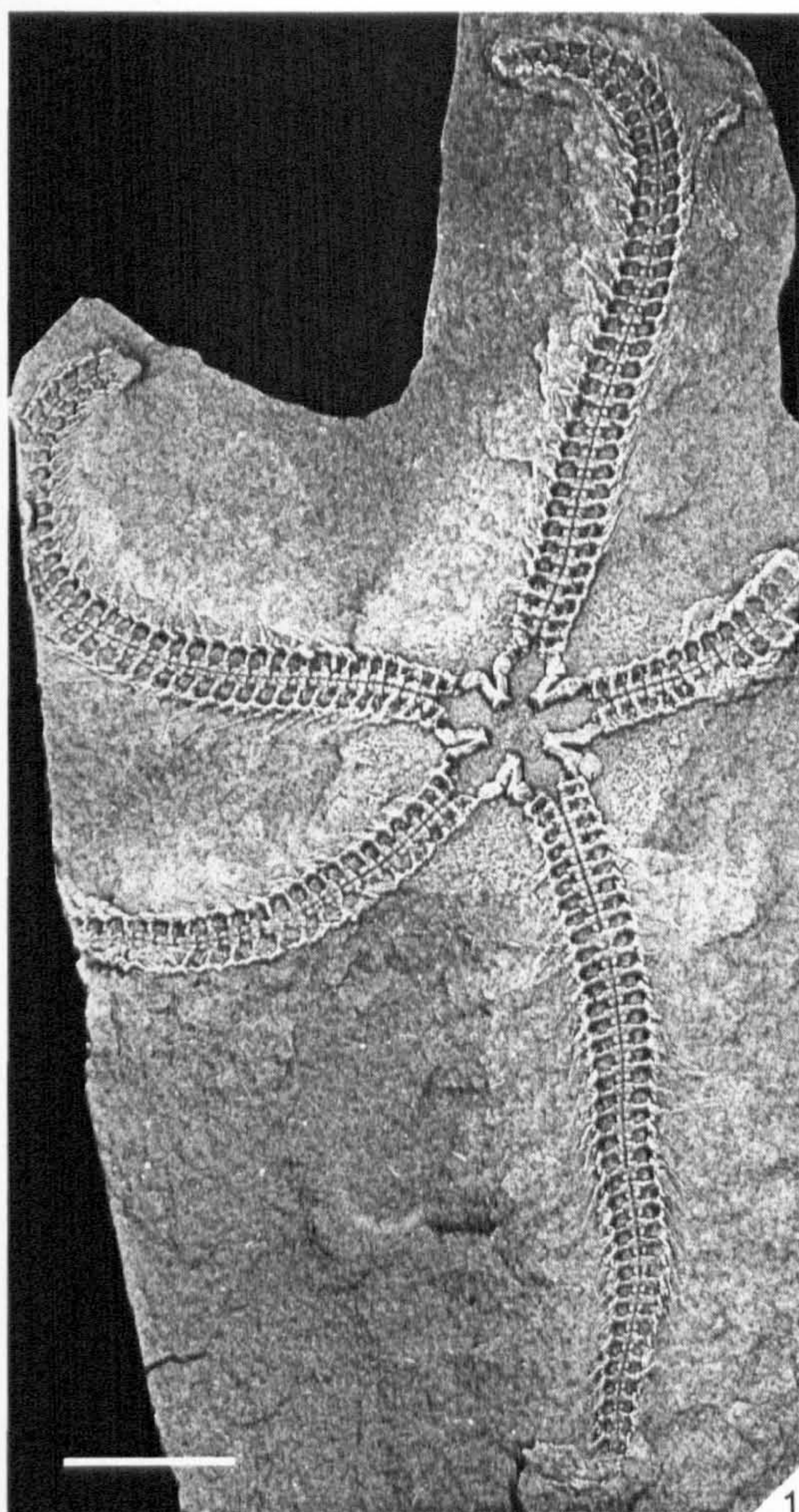




## EXPLANATION OF PLATE 3.18

Figs 1-6, *Lapworthura miltoni* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-4, BMNH E 20232. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of proximal arm, ventral view; scale bar represents 1 mm. 3, detail of Ambb and Adambb, ventral view; scale bar represents 1 mm. 4, detail of mouth frame, ventral view; scale bar represents 2 mm. 5, BMNH E 20239, specimen '1', detail of proximal arms and mouth frame, ventral view; scale bar represents 2 mm. 6, BMNH E 20239, specimen '2', detail of proximal arms and mouth frame, ventral view; scale bar represents 2 mm. All figures are of silicone casts.



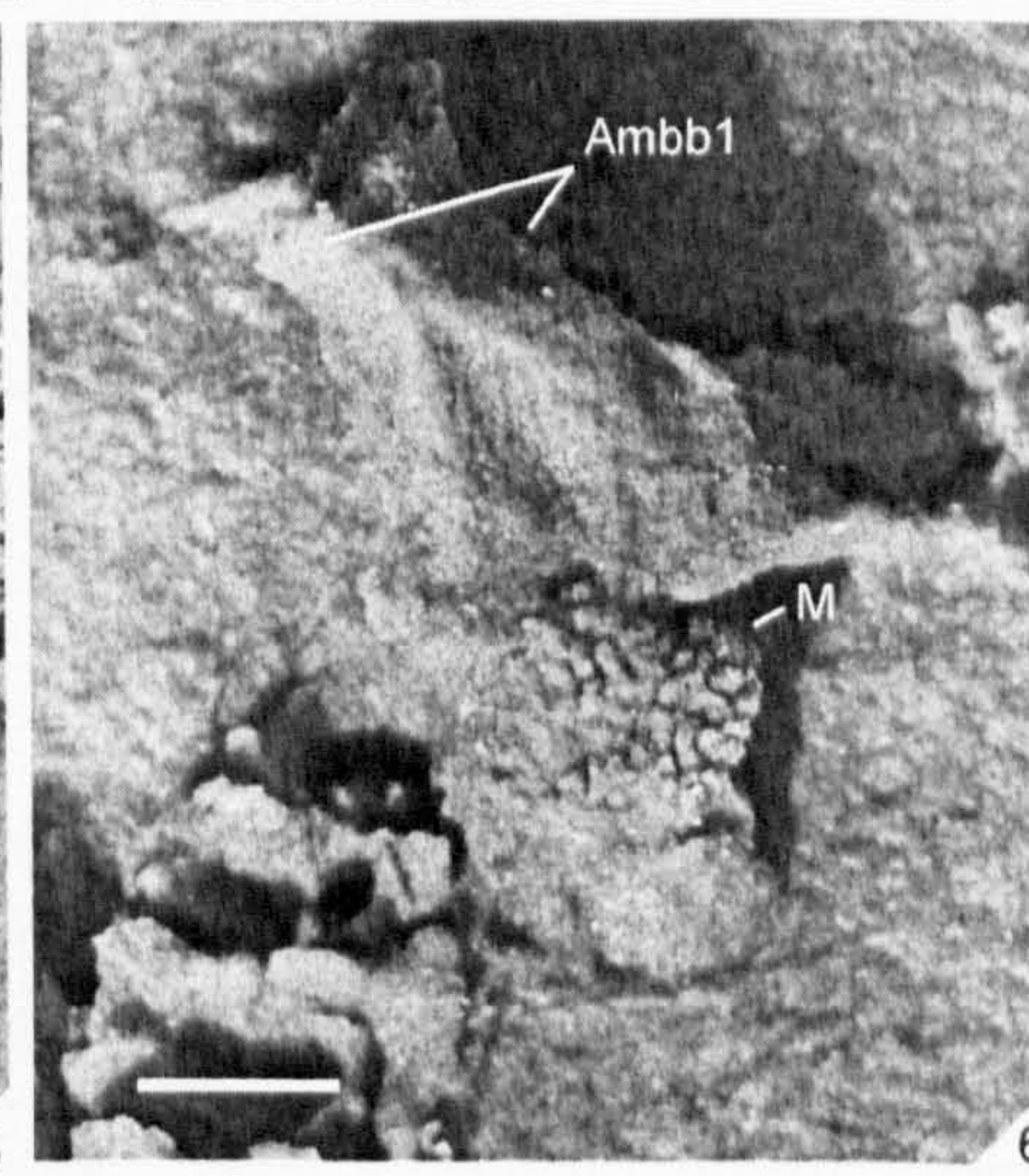
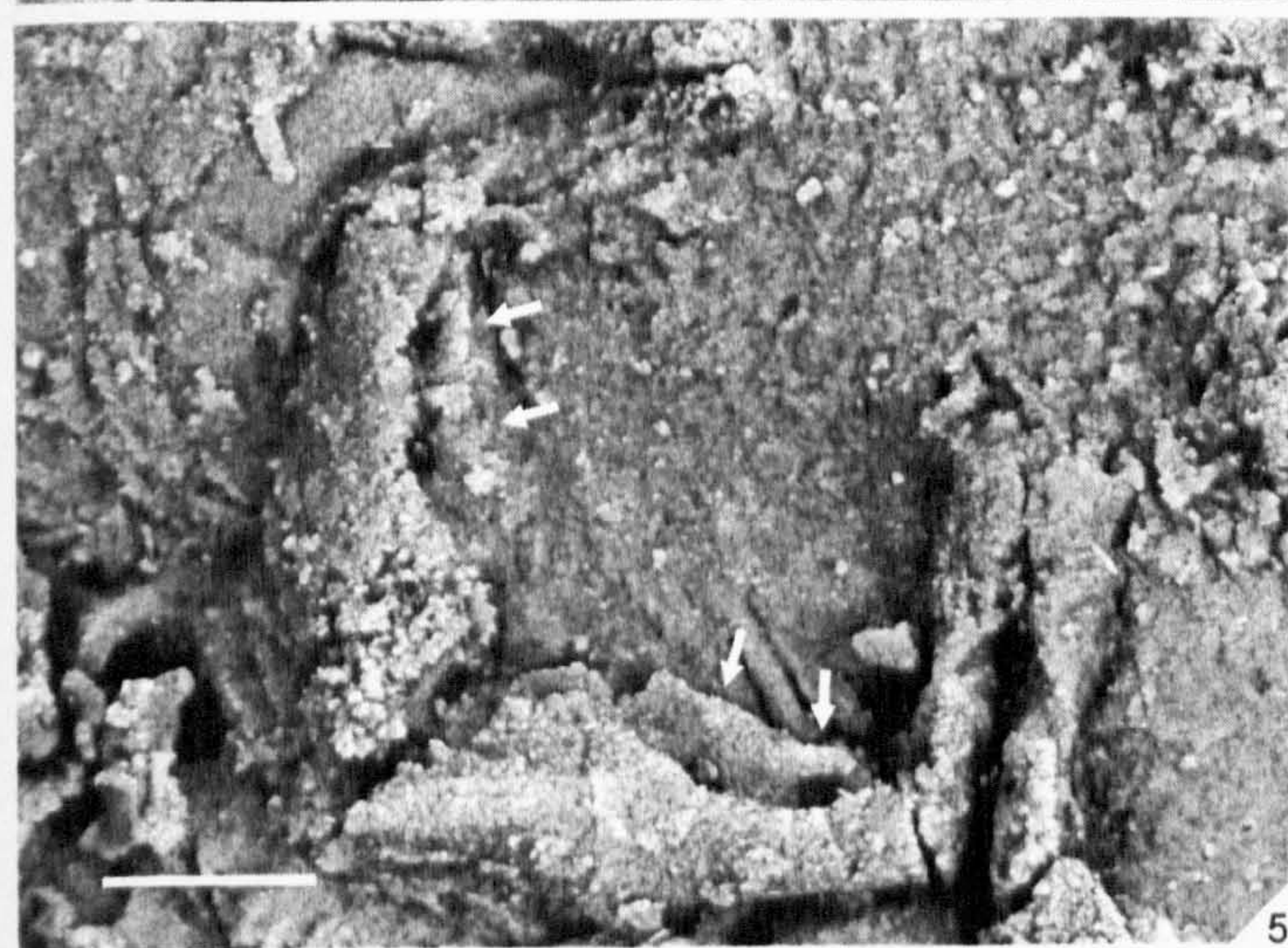
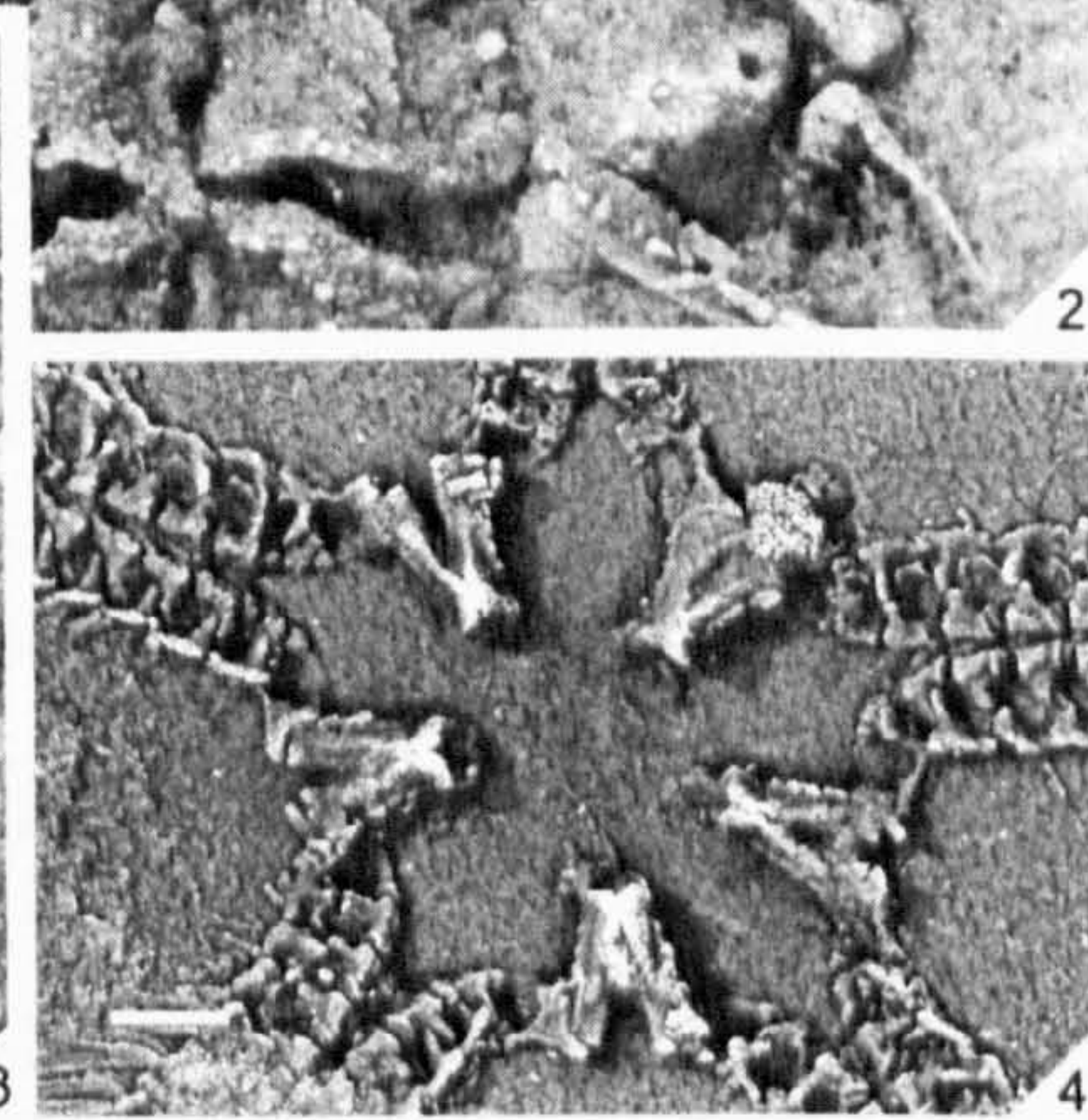
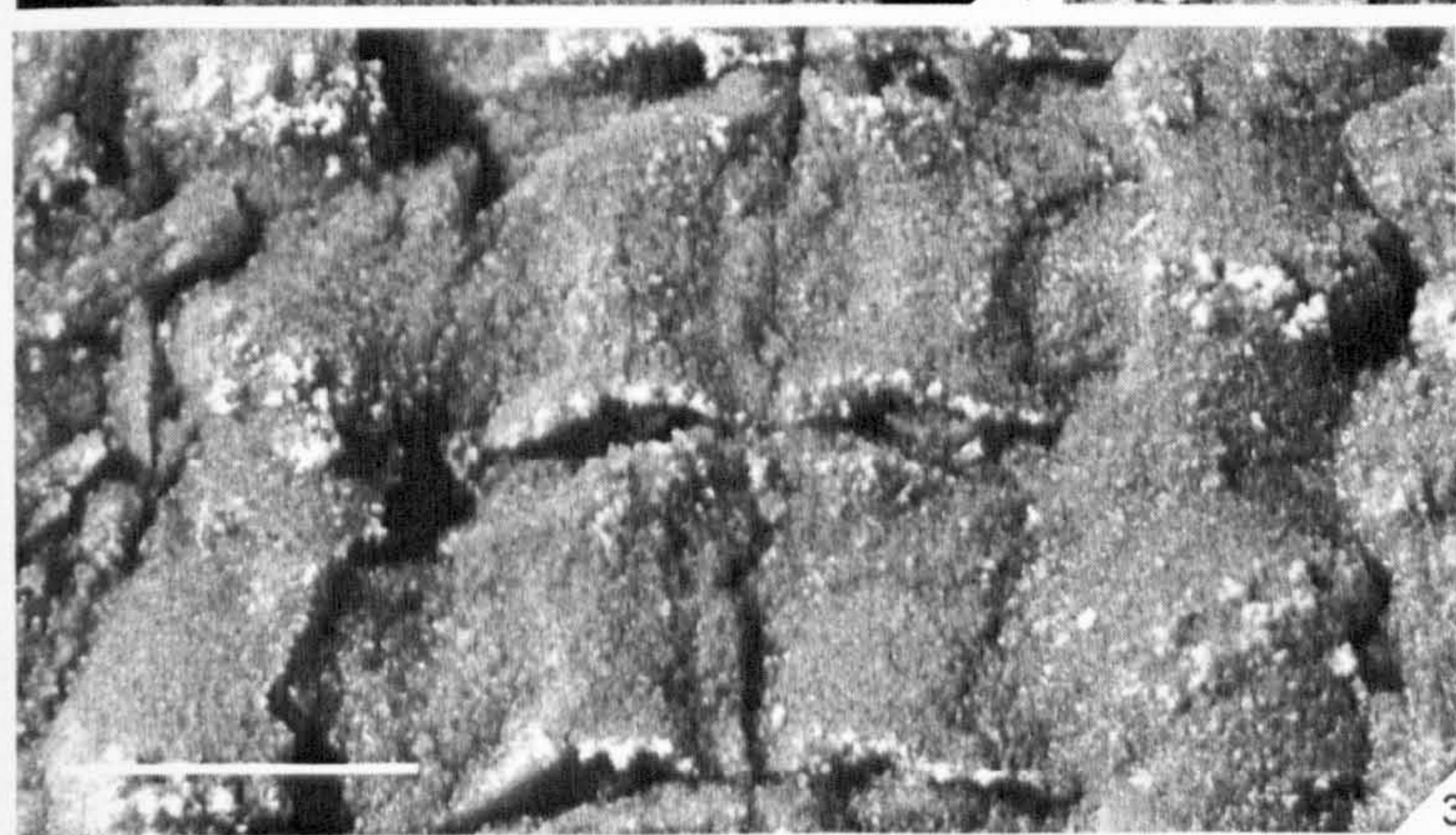
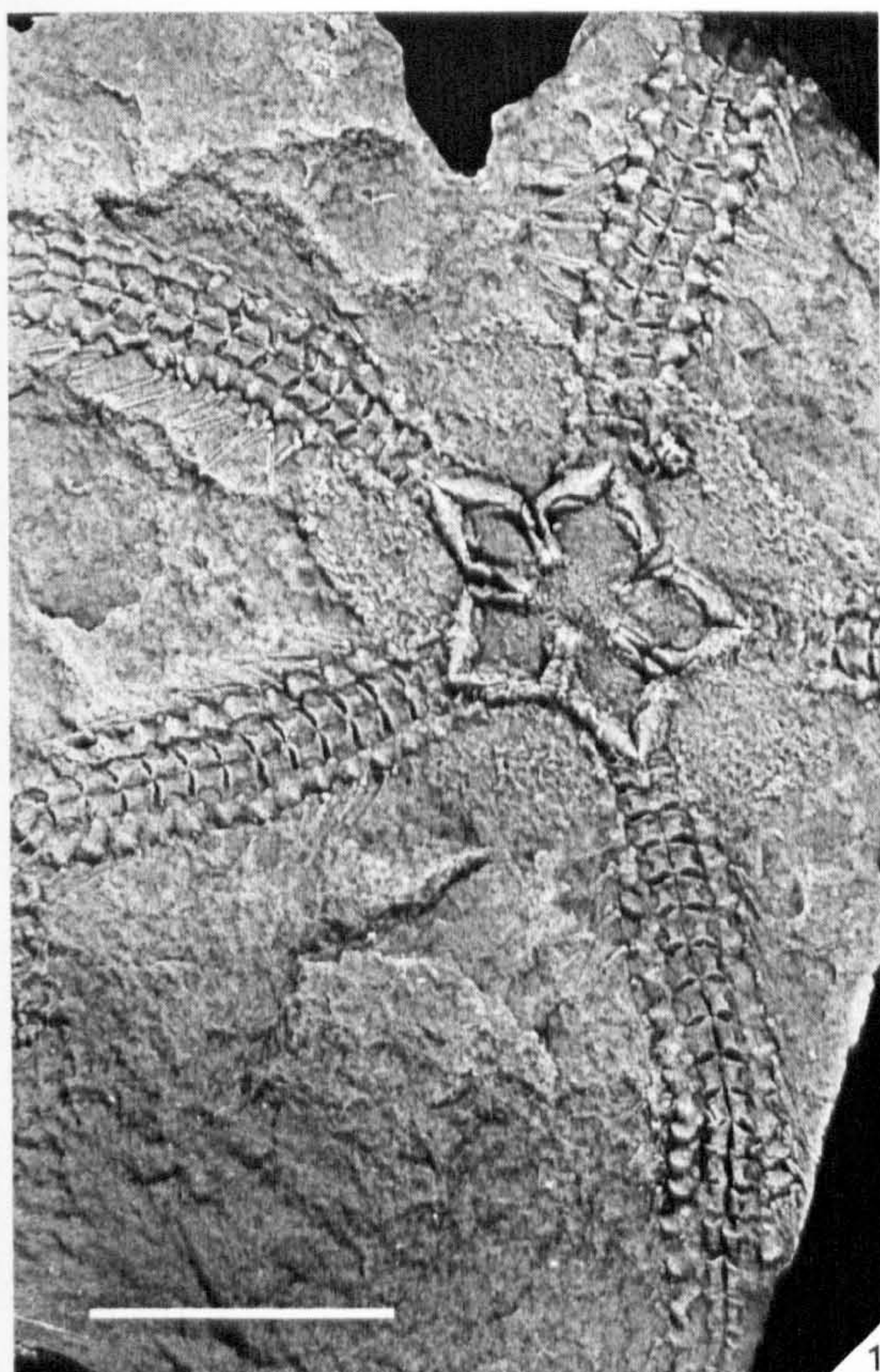




## EXPLANATION OF PLATE 3.19

Figs 1-6, *Lapworthura miltoni* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-3, 5, BMNH E 20239, specimen '3'. 1, entire specimen, dorsal view; scale bar represents 10 mm. 2, detail of proximal arm and part of mouth frame, dorsal view; scale bar represents 1 mm. 3, detail of Ambb and Adambb, dorsal view; scale bar represents 1 mm. 5, detail of Amb1 and Amb2 pair, showing perradial groove with circular pores (pores arrowed), dorsal view; scale bar represents 1 mm. 4,6, BMNH E 20231. 4, detail of mouth frame, ventral view; scale bar represents 2 mm. 6, detail of Amb1 pair and madreporite, ventral view; scale bar represents 1 mm. All figures are of silicone casts.



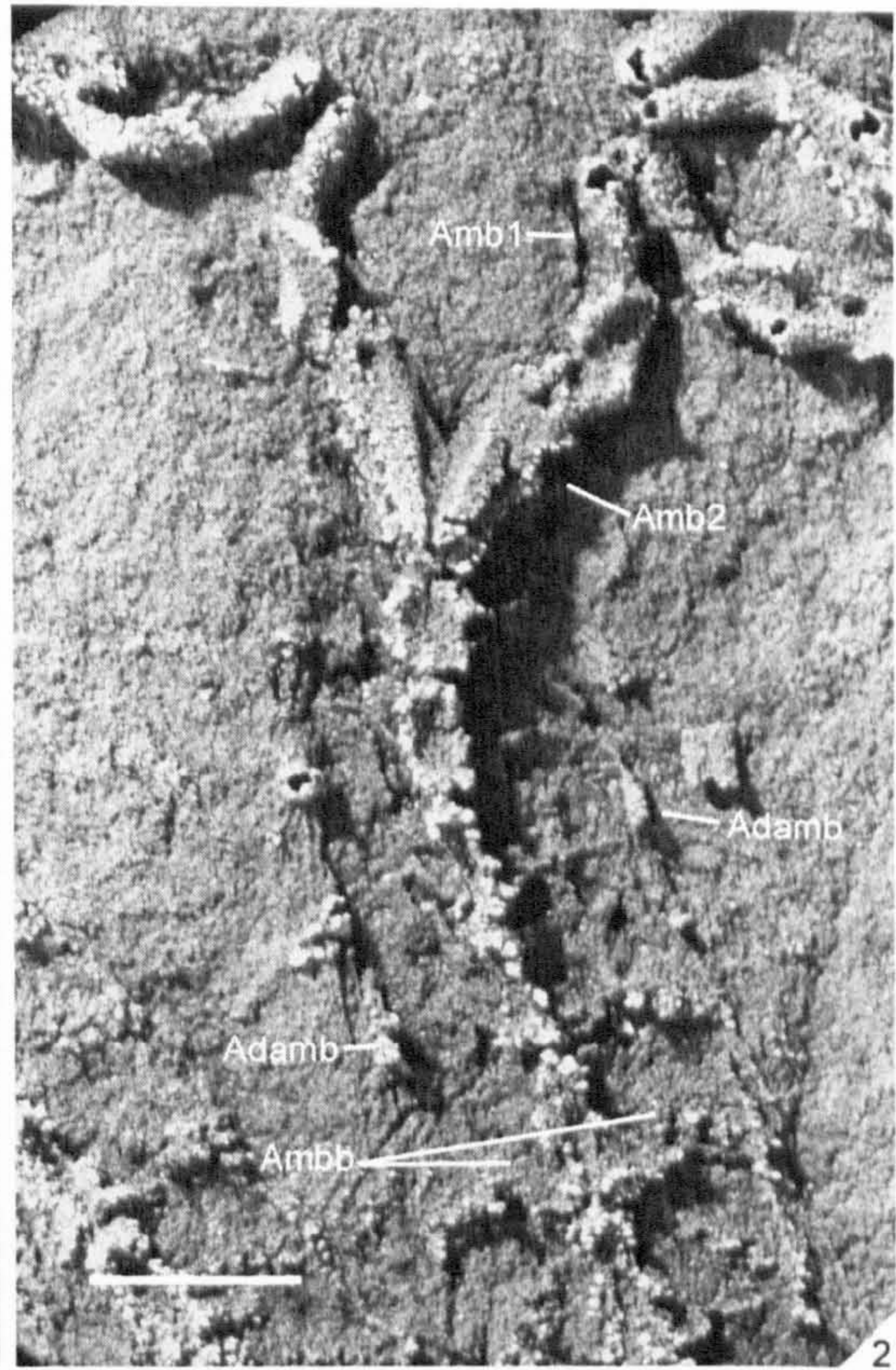
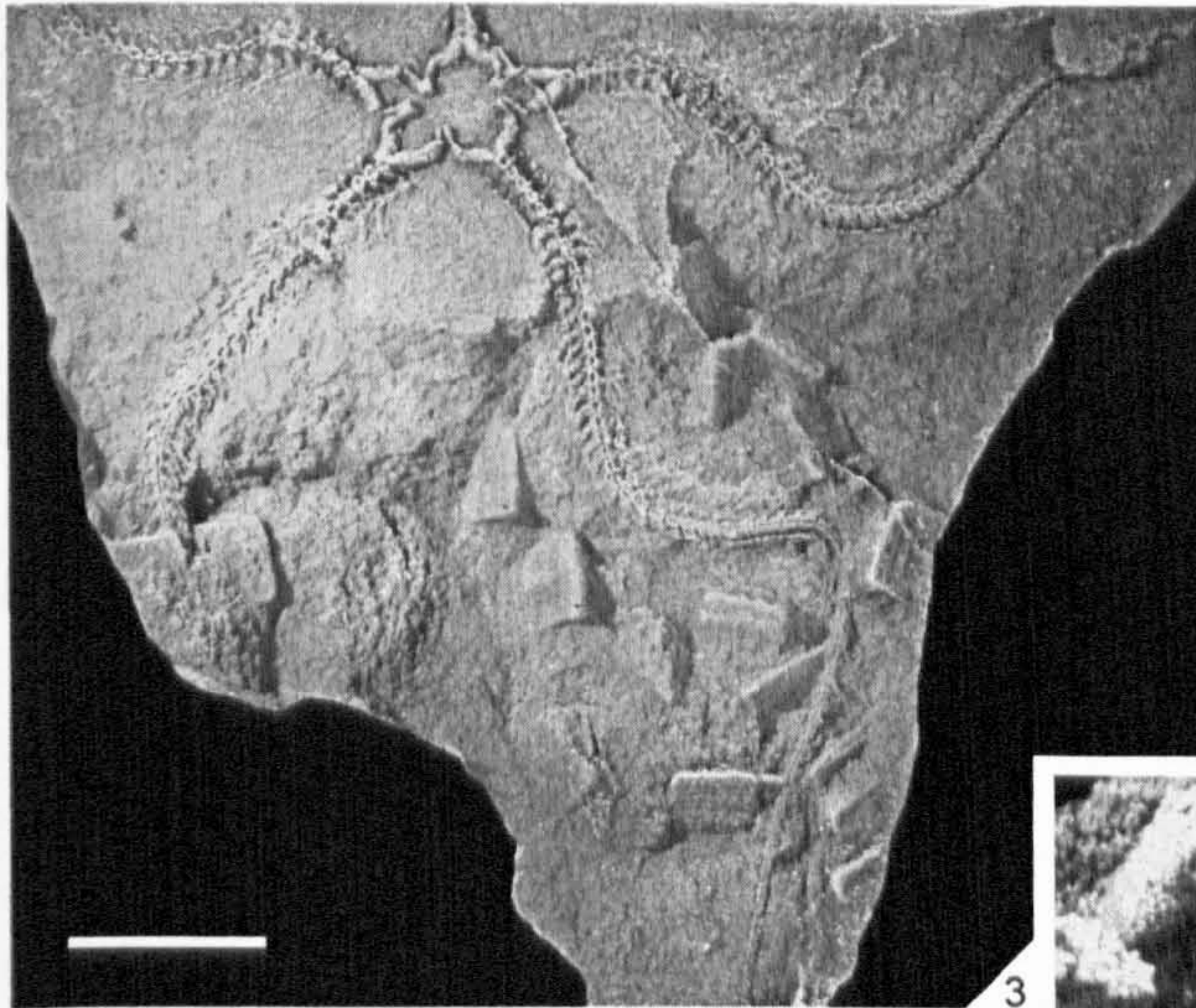
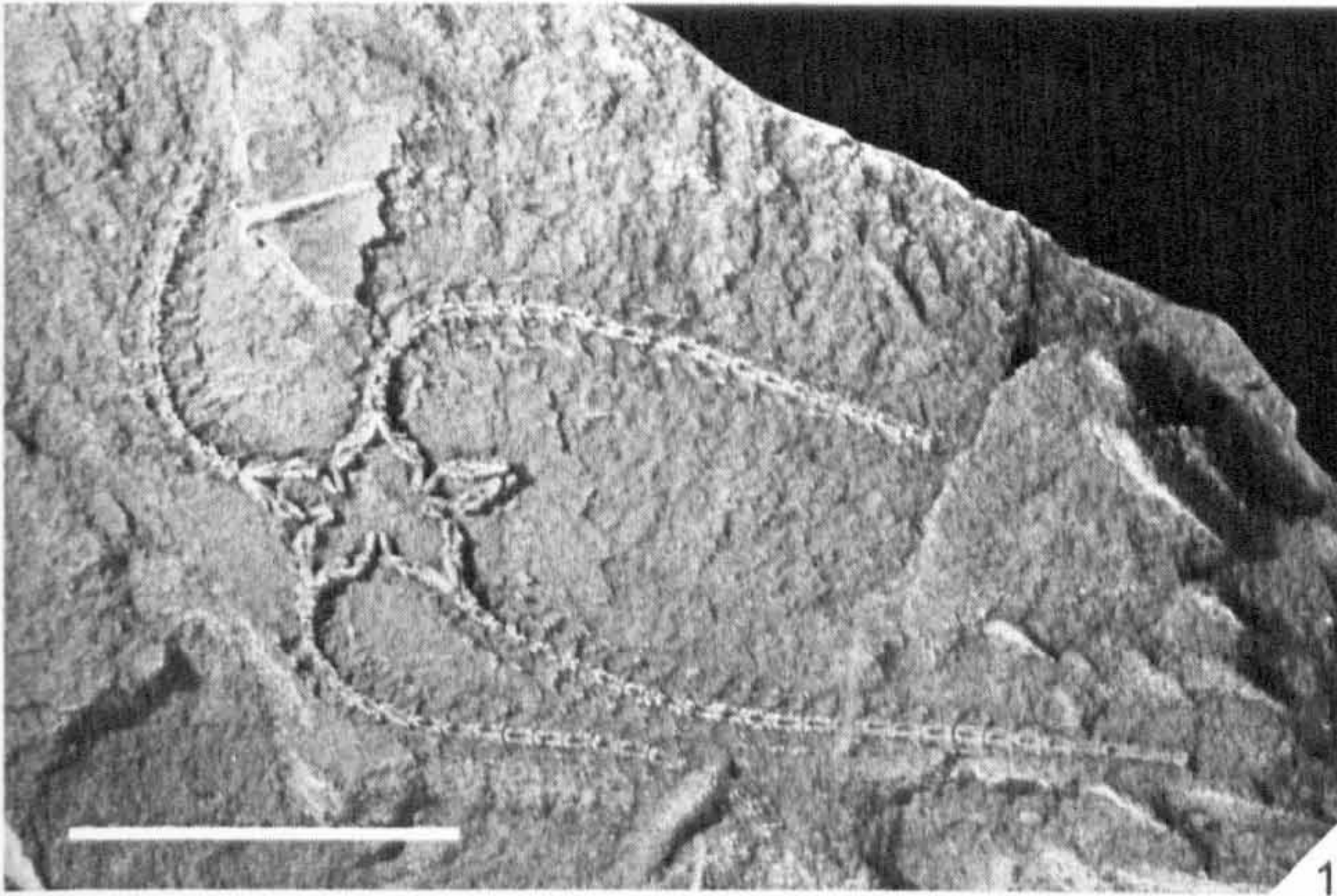




## EXPLANATION OF PLATE 3.20

Figs 1-5, *Furcaster leptosoma* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-2, IPSM G9252912, neotype. 1, entire specimen, dorsal view; scale bar represents 10 mm. 2, detail of part of mouth frame and proximal arm showing diagnostic perradial ridge and groove of Ambbb, dorsal view; scale bar represents 1 mm. 3-5, IPSM G9252917. 3, entire specimen, dorsal view; scale bar represents 10 mm. 4, detail of distal arm, dorsal view; scale bar represents 1 mm. 5, detail of part of mouth frame and proximal arm, dorsal view; scale bar represents 1 mm. All figures are of silicone casts.



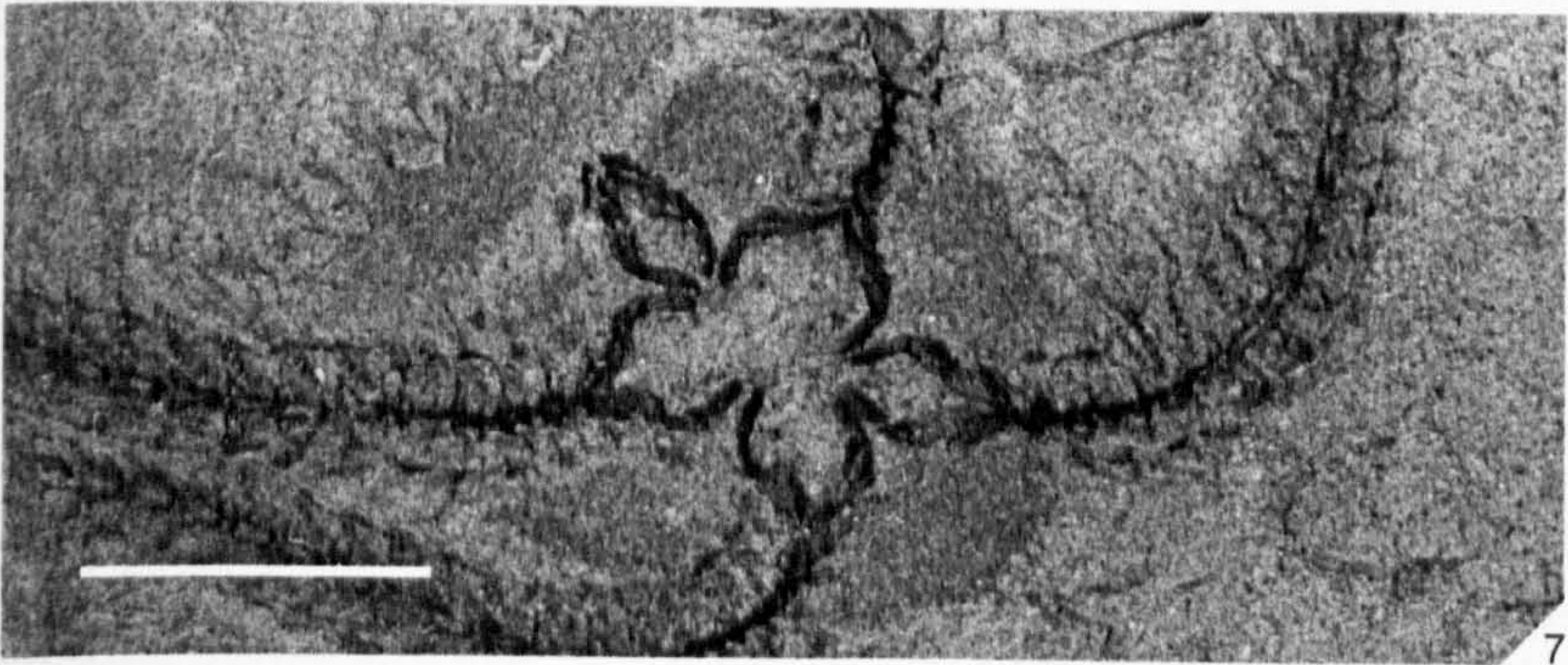
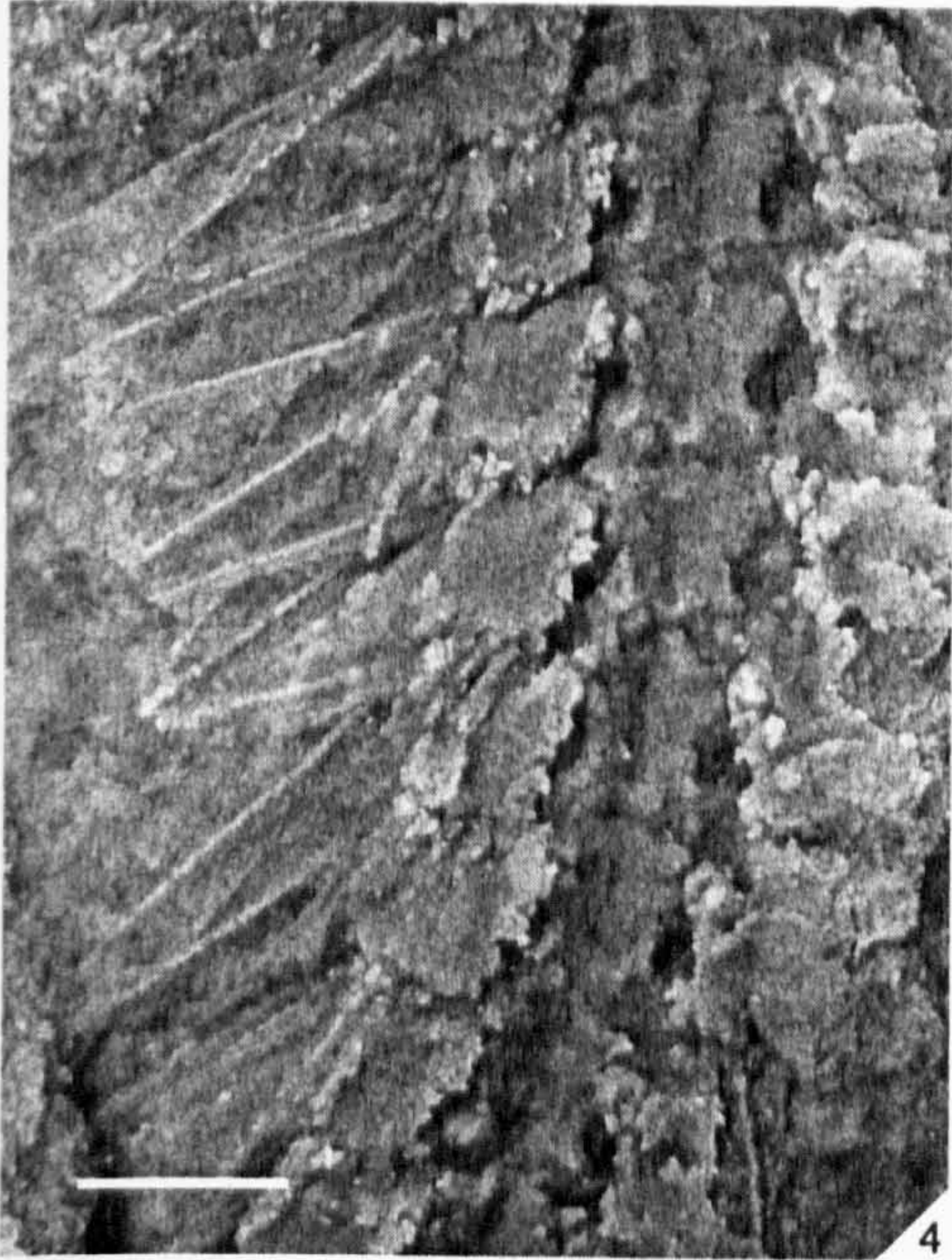
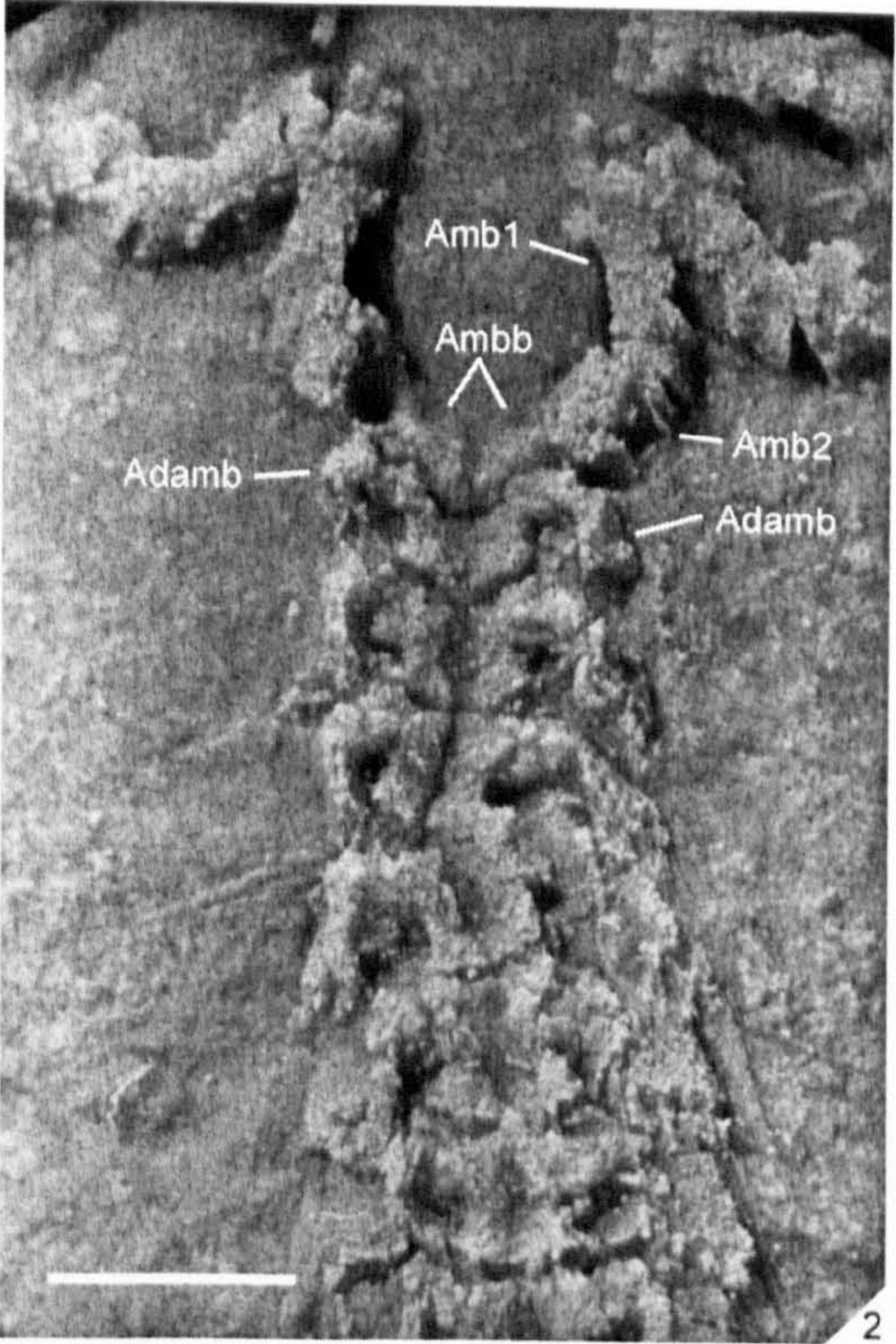
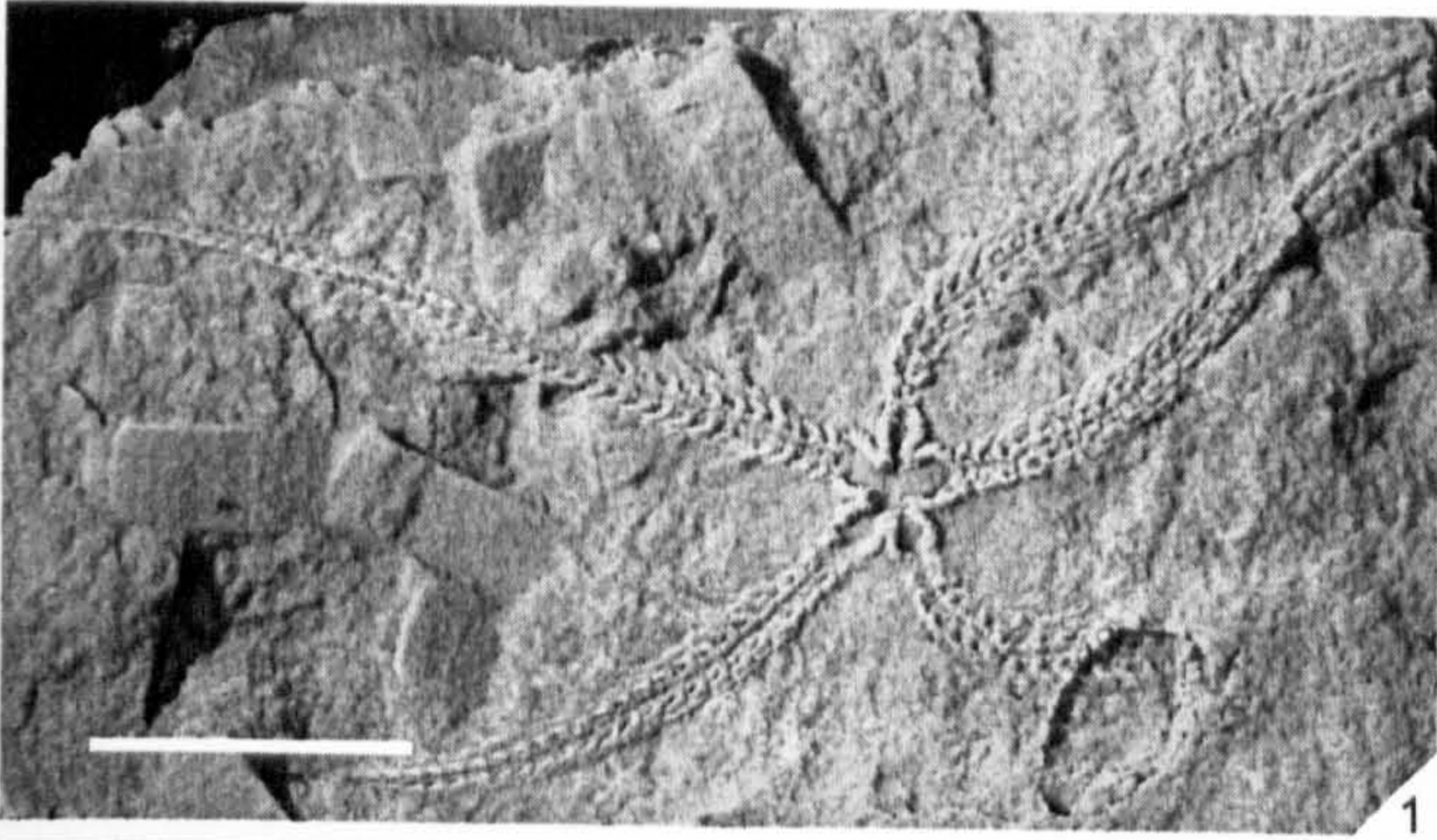




## EXPLANATION OF PLATE 3.21

Figs 1-7, *Furcaster leptosoma* (Salter, 1857); Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1-3, BMNH E 13138. 1, entire specimen, ventral view; scale bar represents 10 mm. 2, detail of part of mouth frame and proximal arm, ventral view; scale bar represents 1 mm. 3, detail of mouth frame, ventral view; scale bar represents 2 mm. 4-6, BMNH E 13135. 4, detail of proximal arm '1' showing long spines articulated to Adambb, ventral view; scale bar represents 1 mm. 5, detail of proximal arm '2', ventral view; scale bar represents 1 mm. 6, detail of distal arm '2' showing shorter spines articulated to Adambb, ventral view; scale bar represents 1 mm. 7, IPSM G9252912, neotype, detail of circular disc; scale bar represents 5 mm. All figures are of silicone casts except 7.



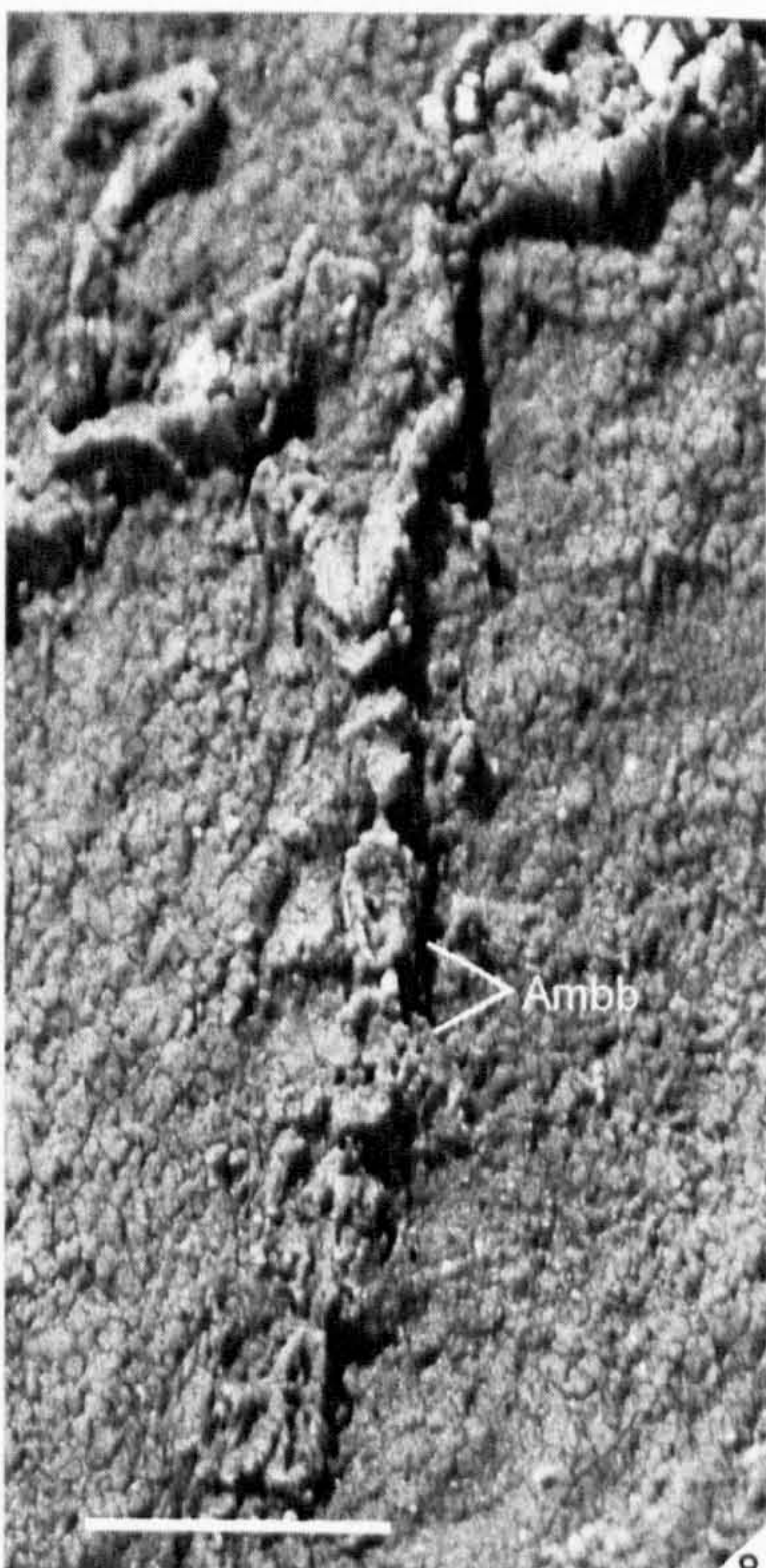
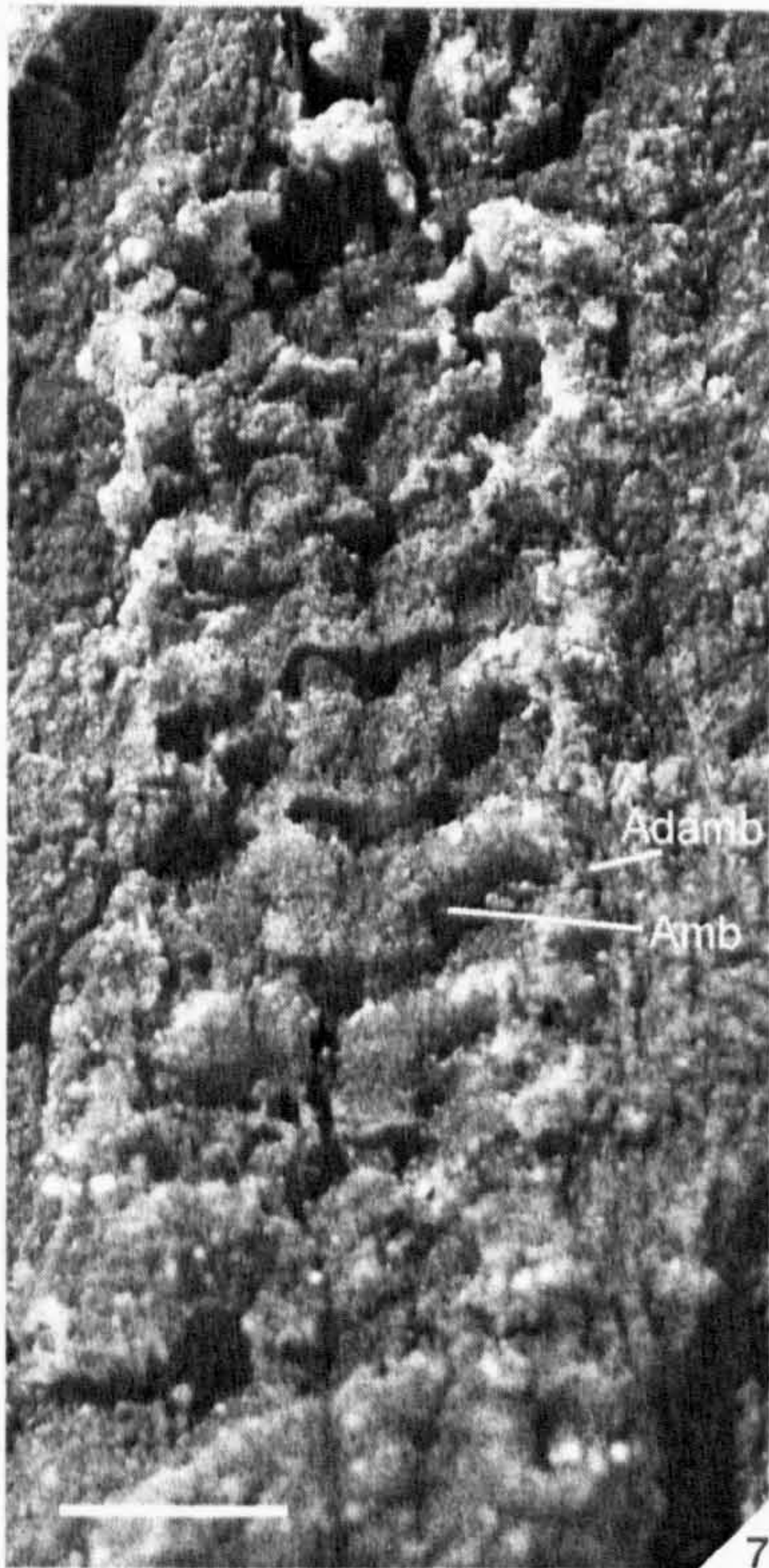
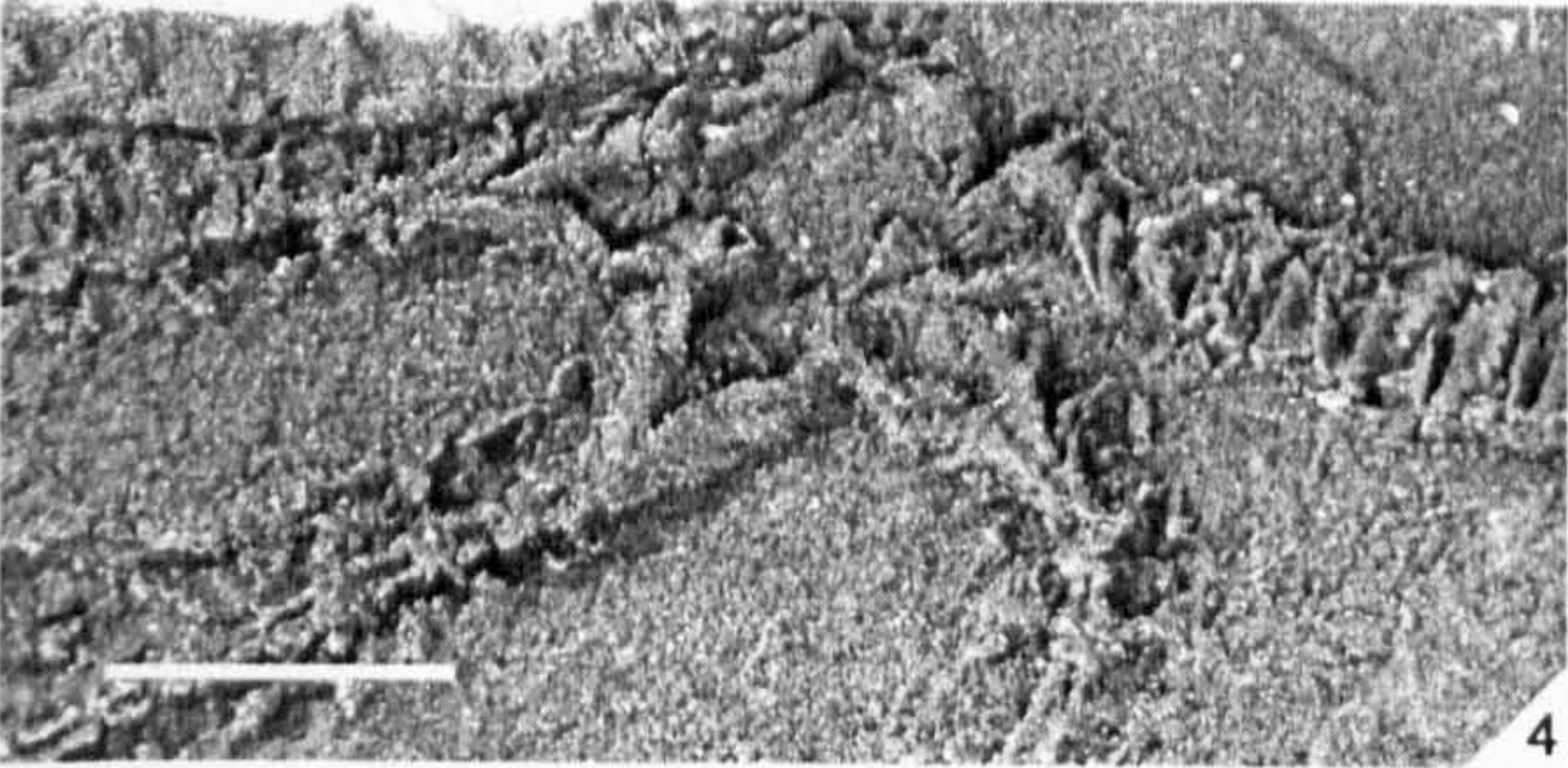
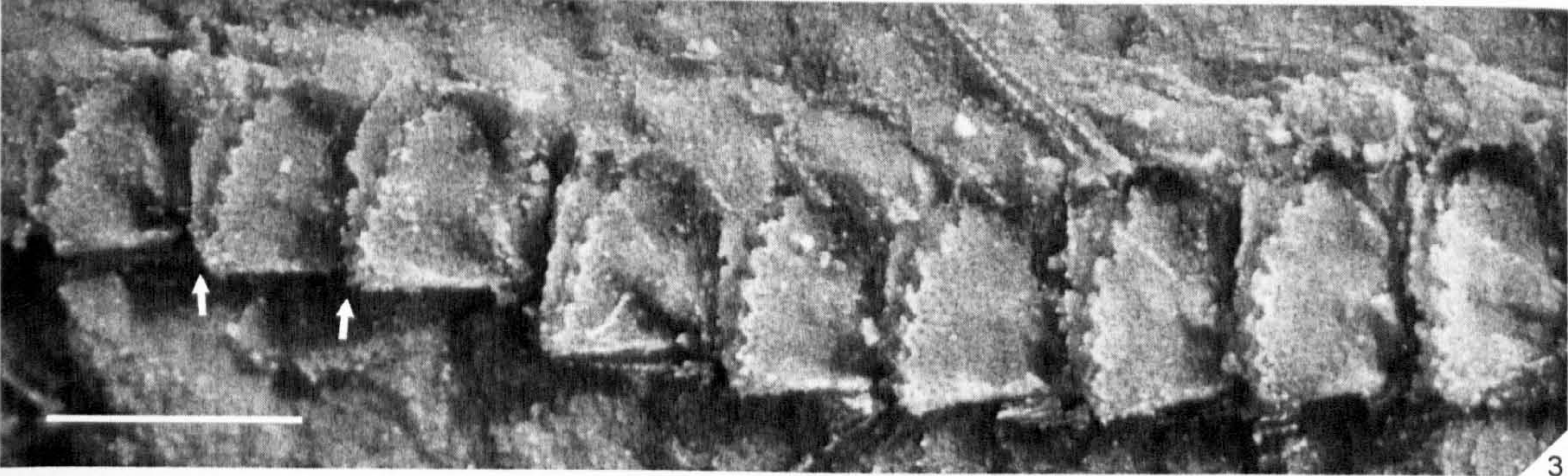
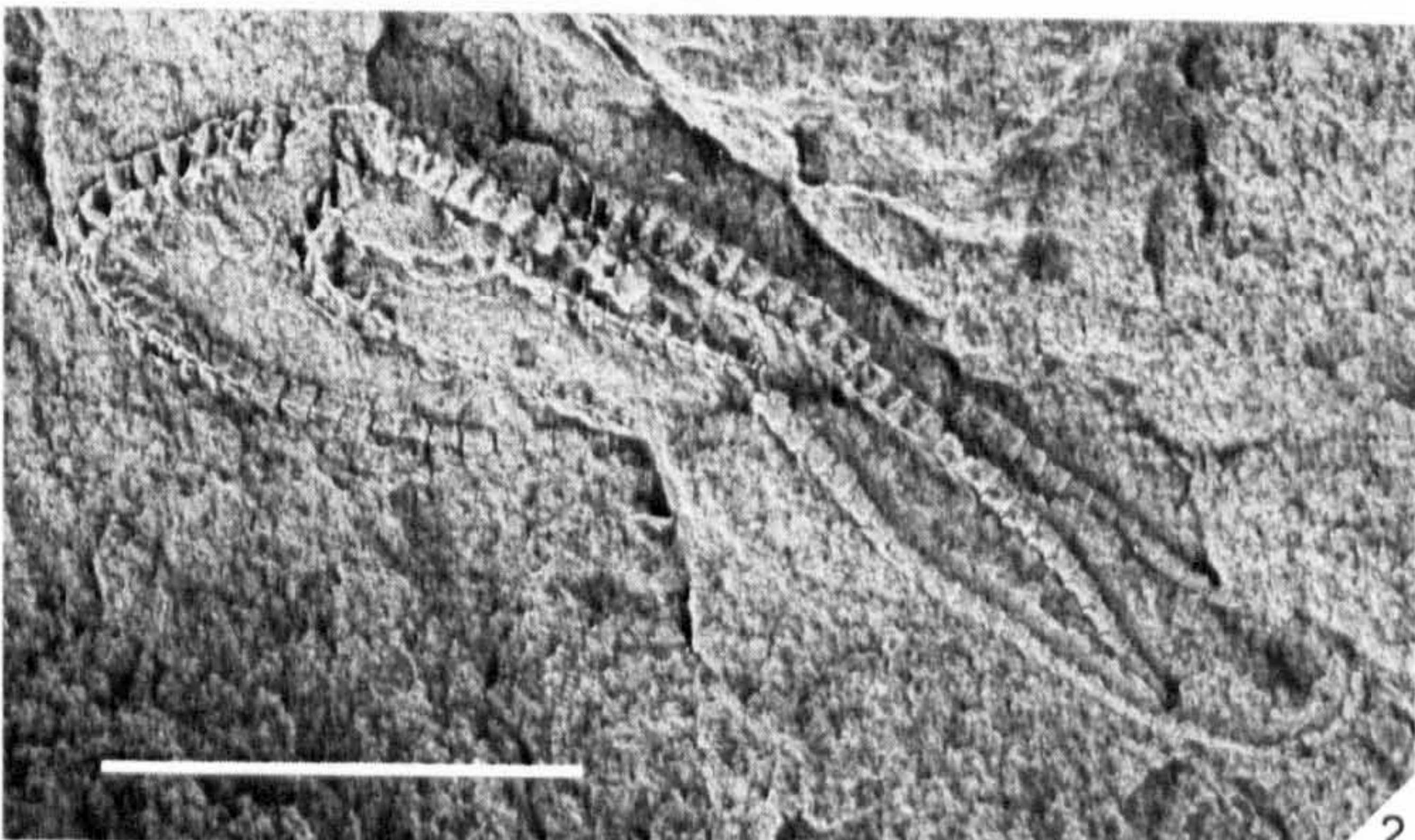
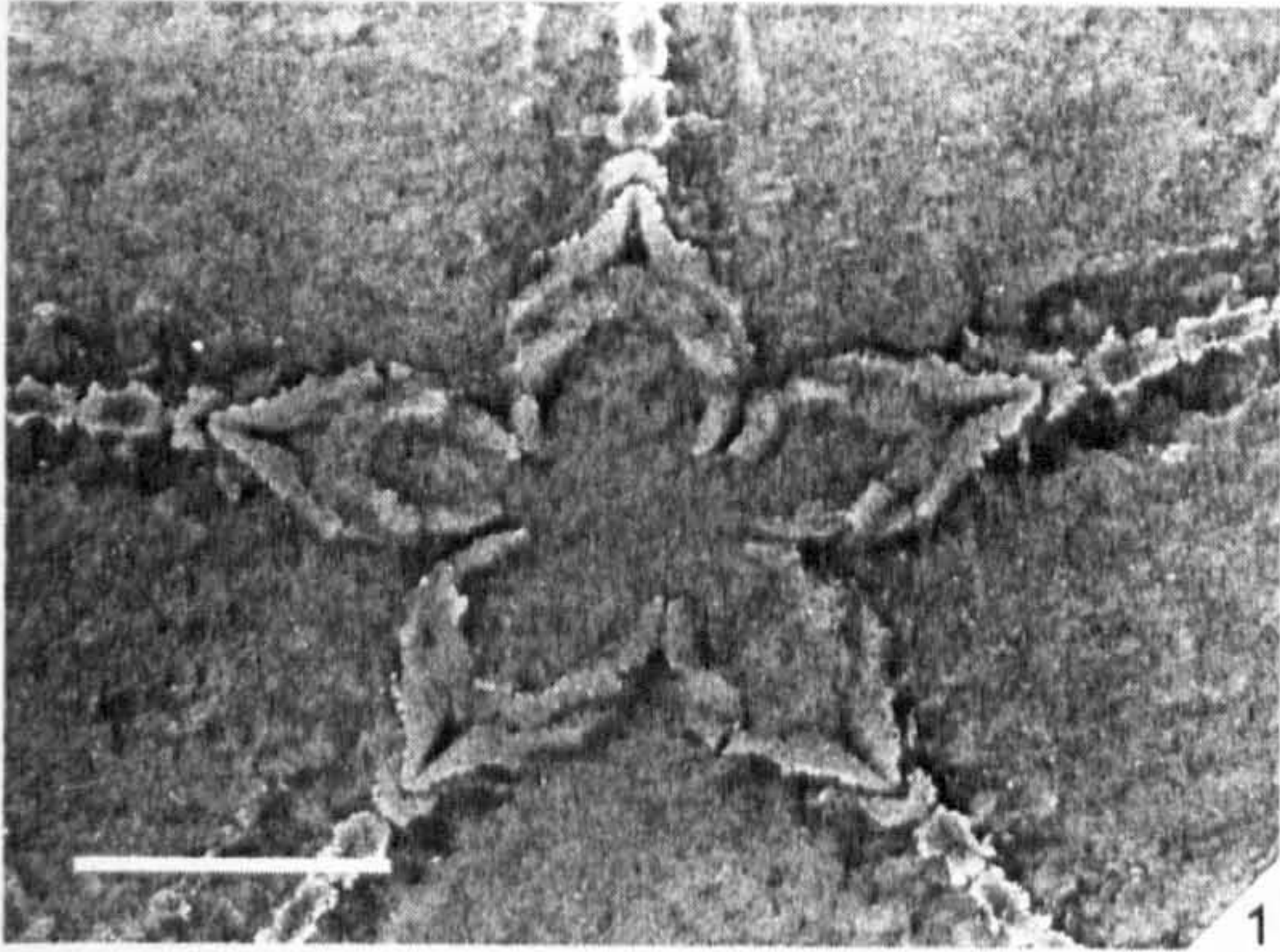




## EXPLANATION OF PLATE 3.22

Figs 1-8. *Furcaster leptosoma* (Salter, 1857). 1-5, Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 1, BMNH E 20260, detail of mouth frame, dorsal view; scale bar represents 2 mm. 2-3, BMNH 20258. 2, entire specimen, lateral view; scale bar represents 10 mm. 3, detail of Adambb showing ridges for spine attachment (arrowed on two Adambb), lateral view; scale bar represents 1 mm. 4-5, CH77a-b, part and counterpart; scale bars represent 2 mm. 4, CH77a, detail of mouth frame and proximal arms, dorsal view. 5, CH77b. 5, detail of mouth frame and proximal arms, ventral; view. 6-7, BMNH E 52826a-b, part and counterpart; Ashgill Series; Lady Burn, Girvan, Scotland. 6, BMNH E 52826a, detail of mouth frame and proximal arm, dorsal view; scale bar represents 2 mm. 7, BMNH E 52826b, detail of proximal arm showing boot-shaped Ambb, ventral view; scale bar represents 1 mm. 8, BGS GSE12033, Llandovery Series; Gutterford Burn, Pentland Hills, Midlothian, Scotland; detail of part of mouth frame and proximal arm showing diagnostic perradial ridge and groove of Ambb, dorsal view; scale bar represents 1 mm. All figures are of silicone casts.





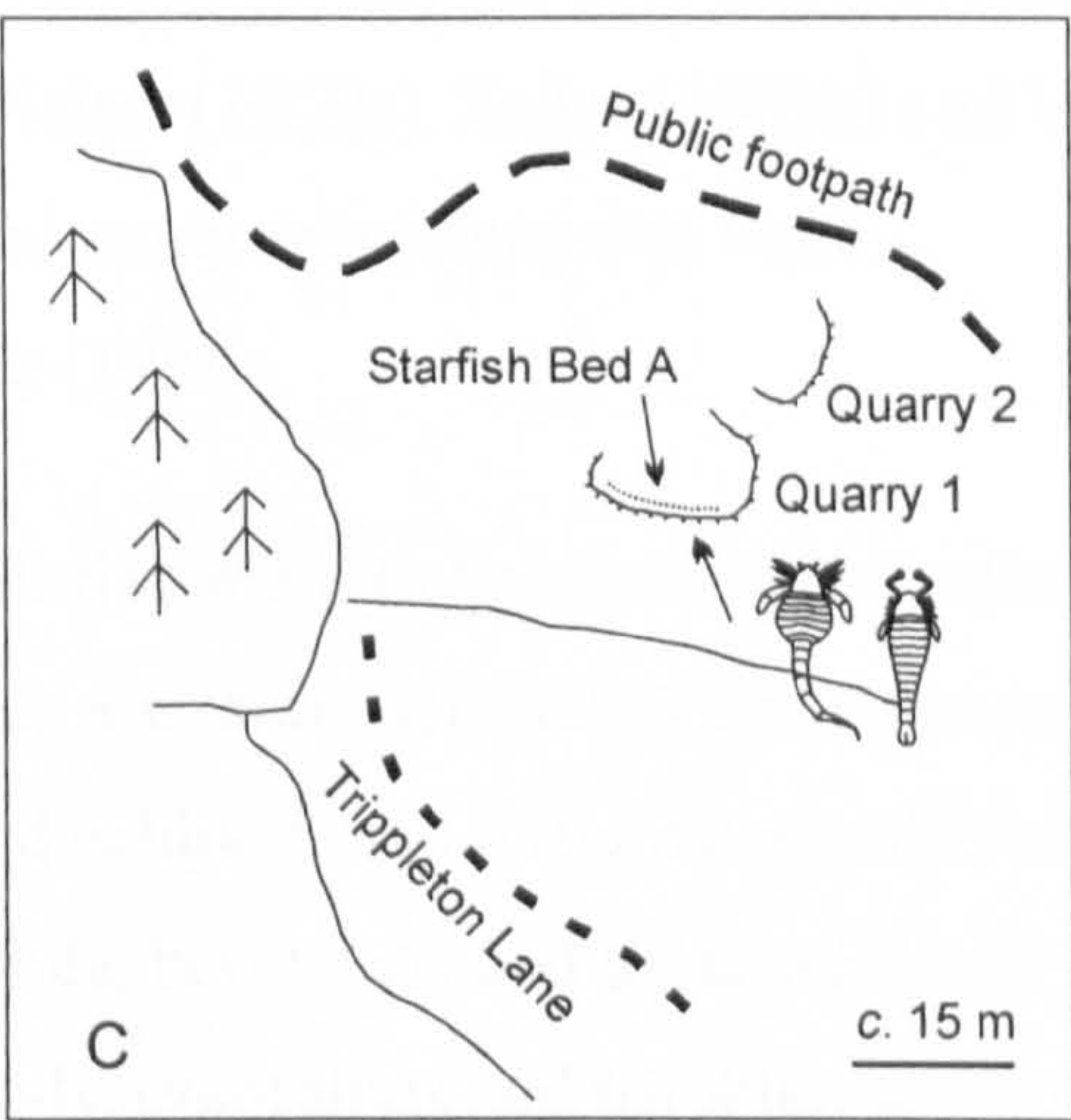
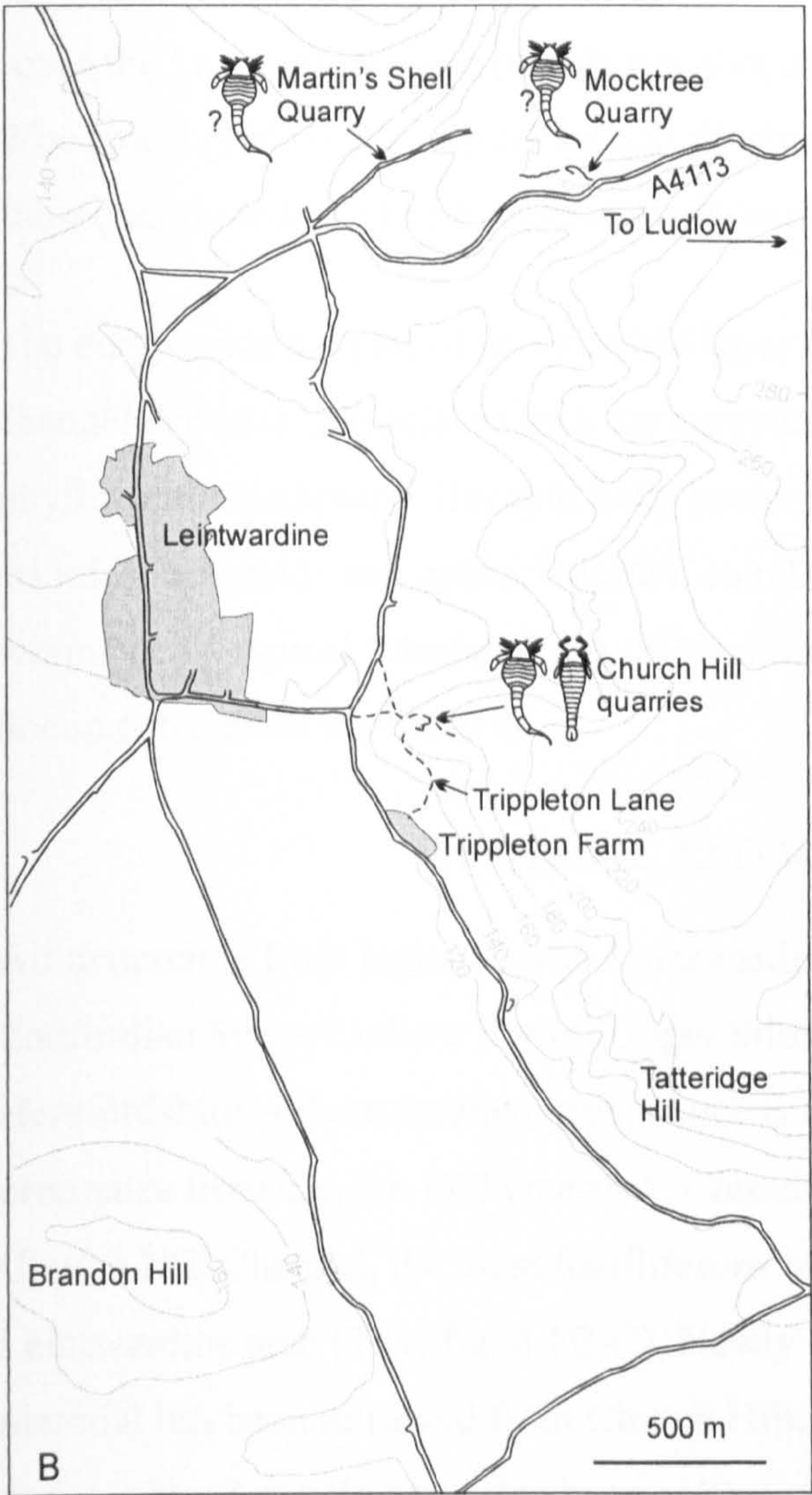


# EURYPTERIDS FROM THE LUDLOW SERIES (UPPER SILURIAN) OF LEINTWARDINE, HEREFORDSHIRE, UK

**ABSTRACT.** A diverse eurypterid fauna is described from the Upper Silurian channel deposits at Leintwardine, Welsh Borderland, UK. The fauna is composed mainly of carcosomatids, with a lesser number of pterygotids also present. The eurypterids are predominantly semi-articulated, often comprising portions of the opisthosoma or prosomal appendages; no fully articulated specimens are documented. Previously undescribed material of *Carcinosoma punctatum* Salter is described. The pronounced serration with a deep notch on the distal podomere of prosomal appendage VI is identified as being diagnostic of this species. Newly collected and previously described material is assigned to *Carcinosoma* sp. and *Carcinosoma*? sp. A previously undescribed specimen of a genital appendage (type A) is tentatively assigned to *Erettopterus*? sp. A full description of *Pterygotus arcuatus* Salter is presented for the first time. A distal portion of a free ramus is reassigned to *Pterygotus*? sp. The first documented semi-articulated carcosomatid opisthosoma and eurypterid prosoma from the Leintwardine deposits are described.

Eurypterid occurrences are relatively rare in the British Palaeozoic; however, they are most abundant through the Silurian. Aside from Leintwardine, Herefordshire, well preserved specimens have been documented from other Upper Silurian Welsh Borderland localities, in particular the Přídolí of Ludford Lane, Ludlow, Shropshire (Kjellesvig-Waering 1961; Manning 1993). The other major UK examples include the Llandovery (Lower Silurian) Eurypterid Bed of Gutterford Burn, Pentland Hills, Midlothian, Scotland (e.g. Lamont 1955; Aldridge 2000), and the Llandovery to Wenlock Lesmahagow and Hagshaw Hills inliers of the Midland Valley, Scotland (e.g. Salter 1859a; Woodward 1866-1878; Lamont 1955; Palmer *in* Aldridge 2000). A diverse eurypterid fauna is recorded from several Ludlow age submarine channel deposits around the Herefordshire village of Leintwardine (Text-fig. 4.1). They provide a rare example of these chelicerate fossils from the Silurian of the UK. The channel localities, particularly that of Church Hill, are the type areas for two pterygotid taxa described in the literature (e.g. Salter 1859a; Woodward 1871; Kjellesvig-Waering 1961): *Erettopterus marstoni* Kjellesvig-Waering, 1961, and *Pterygotus arcuatus* Salter, 1859. The Leintwardine taxa are predominantly unrecorded from other localities (e.g. see Kjellesvig-Waering 1961). There is confusion regarding the provenance of the type material of *Carcinosoma punctatum* (Salter, 1859), although the majority of specimens assigned to this species are from the channel localities (e.g. see Kjellesvig-Waering 1961).





TEXT-FIG. 4.1. A, Location of the study area around Leintwardine, approximately 10 km to the west of Ludlow, Shropshire. B, eurypterid localities around Leintwardine, showing submarine channel deposits (from north to south): Martin's Shell Quarry (Todding Channel); Mocktree Quarry (Mocktree Channel); Church Hill quarries (Church Hill Channel). C, localities at Church Hill, showing the re-exposed composite quarries; numerous semi-articulated and disarticulated eurypterid specimens collected from Quarry 1. Only small, fragmentary pieces of cuticle collected from Martin's Shell and Mocktree quarries.



This paper aims to redescribe the eurypterid material from the Leintwardine area, combining restudy of existing type specimens and other taxonomically important material with newly collected material from Church Hill. The material has not been studied since Kjellesvig-Waering's (1961) review of Welsh Borderland eurypterids. He provided a limited number of figures of the material and some of these are partially schematic. A formal diagnosis of *P. arcuatus* is presented here for the first time, and other specimens, assigned to *Carcinosoma* and *Erettopterus*, are newly described. The diagnoses and descriptions employed herein incorporate the standardised terminology of Tollerton (1989) in an attempt to minimise any subjectivity over morphology that has arisen in the literature. Prior to Kjellesvig-Waering (1961) the first major work to cover the Leintwardine eurypterids was that of Salter (1859a). Salter (1859a) and later Woodward (1866-1878) described and illustrated many specimens that were subsequently redescribed by Kjellesvig-Waering (1961).

The eurypterids are part of an unusual Upper Silurian biota to be recorded from the channel deposits. Associated with the eurypterids are rarer xiphosuran chelicerates and phyllocarid crustaceans. Exceptionally preserved echinoderms (articulated stelleroids, crinoids, echinoids and ophiocistioids), conulariids, bryozoans and palaeoscolecoid worms and a typical Silurian fauna of brachiopods, graptolites and trilobites are also documented from the deposits.

## MATERIAL AND METHODOLOGY

All material is from higher Lower Leintwardine Formation channel deposits, of basal Ludfordian Stage, Ludlow Series, Upper Silurian age, from Leintwardine, Herefordshire. Where detailed provenance is known, the majority of the material originates from Church Hill Quarry 1, Church Hill (SO47 4115 7375), representing the Church Hill Channel, the most fossiliferous of the six submarine channels in the Leintwardine area (Text-fig. 4.1B-C). Newly collected pterygotid and carcosomatid material has been retrieved from Church Hill. Small fragmentary pieces of undetermined cuticle have also been collected from Mocktree (SO47 4165 7540) and Martin's Shell (SO47 4109 7543) quarries, representing the Mocktree and Todding channels respectively.



*Repositories.* Some material illustrated here is from collections in the Natural History Museum, London (BMNH) and the British Geological Survey, Keyworth (BGS). Newly collected material is prefixed by an identifier, denoting the channel deposit from which it originates: Church Hill (CH) or Martin's Shell (MS). This material will be deposited in the BGS and Department of Geology, University of Leicester collections.

## TERMINOLOGY AND CLASSIFICATION

Terminology essentially follows that of Størmer (1955) and Tollerton (1989). The prosomal appendages are denoted by Roman numerals and individual podomeres are numbered proximally to distally. Podomere terminology follows that of Størmer (1974) and Selden (1981); this is in contrast to Kjellesvig-Waering's (1961) determination of podomere numbers, which did not incorporate the coxa. The scheme employed herein determines the coxa as podomere 1 and so on. Dimensions used for the swimming paddle of prosomal appendage VI follow that of Størmer (1973, text-fig. 1). The principal teeth of the pterygotid chelicerae are termed (from distal to proximal) D1-D6, following Waterston (1964), Chlupáč (1994) and Burrow *et al.* (2002). Suprageneric classification of the pterygotids follows that of Tollerton (1989). *Proximal* and *distal* are used for relative positioning of a particular structure (e.g. teeth positioned proximally on a ramus). *Anterior* and *posterior* are used for the direction in which a particular structure is orientated (e.g. teeth curved or inclined anteriorly).

## PRESERVATION

The material is preserved in planar laminated siltstone and predominantly consists of semi-articulated prosomal appendages, disarticulated opisthosomal tergites and fragmentary cuticle. No fully articulated specimens are documented. The material is likely to represent moulted exuviae, as there is no evidence to suggest that it represents carcasses (e.g. internal organs or muscle tissues; see Braddy *et al.* 2002). This may partially account for the generally disarticulated nature of the specimens as exuviae are easily dispersed by currents into their individual skeletal components (Braddy *et al.* 1995).



## SYSTEMATIC PALAEONTOLOGY

Generic synonymies only include entries that contribute useful nomenclatural or morphological information. Specific synonymies are annotated with symbols listed in Matthews (1973).

Suborder PTERYGOTINA Caster and Kjellesvig-Waering, 1964

Superfamily PTERYGOTOIDEA Clarke and Ruedemann, 1912

Family PTERYGOTIDAE Clarke and Ruedemann, 1912

*Remarks.* Kjellesvig-Waering (1961) recognised two genera within the family: *Pterygotus* Agassiz, 1844 and *Erettopterus* Salter, 1859, differentiated on morphology of the telson. Kjellesvig-Waering (1961) divided each of these genera into two subgenera, based on details of the chelicerae: *Pterygotus* (*Pterygotus*) Agassiz, 1844 and *Pterygotus* (*Acutiramus*) Ruedemann, 1935; and *Erettopterus* (*Erettopterus*) Salter, 1859 and *Erettopterus* (*Truncatiramus*) Kjellesvig-Waering, 1961. This classification modified that of Størmer (1955) which recognised just one genus, *Pterygotus*, which he subdivided into three subgenera: *P.* (*Pterygotus*), *P.* (*Acutiramus*), and *P.* (*Erettopterus*). Following Størmer (1974) the subgenera of Kjellesvig-Waering (1961) are elevated to generic status. Four genera are currently recognised: *Acutiramus*, *Erettopterus*, *Pterygotus*, and *Truncatiramus* (Tollerton 1989), and are here differentiated solely on the basis of cheliceral morphology, following Waterston (1964), Tollerton (1989) and Chlupáč (1994). Waterston (1964) amended pterygotid classification based on cheliceral morphology to include only the form of the free ramus; this is maintained herein.

Genus ERETTOPTERUS Salter, 1859

1856 *Himantopterus*, gen. nov.; Salter, pp. 27-28 (name preoccupied).

1859b *Erettopterus*; Salter, p. 230.

1955 *Pterygotus* (*Erettopterus*) Salter; Størmer, p. 31.

1961 *Erettopterus* (*Erettopterus*) Salter; Kjellesvig-Waering, pp. 812-813.

1964 *Erettopterus* (*Erettopterus*) Salter; Kjellesvig-Waering, pp. 331, 350.

1964 *Erettopterus* (*Erettopterus*) Salter; Waterston, p. 30.

1974 *Erettopterus* Salter; Størmer, p. 376.



1989 *Erettopterus* Salter; Tollerton, pp. 653, 655.

*Type species.* *Himantopterus bilobus* Salter, 1856, by subsequent designation (*vide* Størmer 1955), from the Ludlow Series of Lesmahagow, Lanarkshire, Scotland.

*Diagnosis.* Prosoma subquadrate. Chelicerae long, with narrow rami bearing posteriorly curved teeth without serrations, with angled distal extremities terminating in posteriorly inclined single tooth or double-tooth structure (on free ramus of certain taxa). Metastoma obovate, cordated anteriorly, deeply notched, narrow. Telson expanded, terminating in deep notch that divides it into a bilobed structure (emended after Waterston 1964 and Tollerton 1989).

*Remarks.* Kjellesvig-Waering (1961) erected three species from the Silurian of the Welsh Borderland: *Erettopterus brodiei*, *Erettopterus marstoni* and *Erettopterus spatulatus*. *E. brodiei* is distinguished by the large, hook-like terminal double-tooth structure of the free ramus (Kjellesvig-Waering 1961, text-fig. 2.24). *E. spatulatus* is distinguished by numerous small posteriorly inclined teeth along the ramus (Kjellesvig-Waering 1961, text-fig. 3.34). *Erettopterus bilobus* (Salter, 1859a), is distinguished by a free ramus with an enlarged terminal tooth D1, and five principal teeth that show a relatively constant size that are each separated by approximately four intermediate teeth (Kjellesvig-Waering 1964, text-fig. 12, pl. 53, figs 1-2; Waterston 1964, text-figs 3, 5f; pl. 1, fig. 3; pl. 3, figs 3-5). The variation of tooth structure of the rami is maintained as a species level character following Kjellesvig-Waering (1961, 1964), Waterston (1964), Tollerton (1989), Chlupáč (1994) and Burrow *et al.* (2002).

*Erettopterus marstoni* Kjellesvig-Waering, 1961

Plate 4.1, Plate 4.2, figures 1-2; Text-figure 4.2

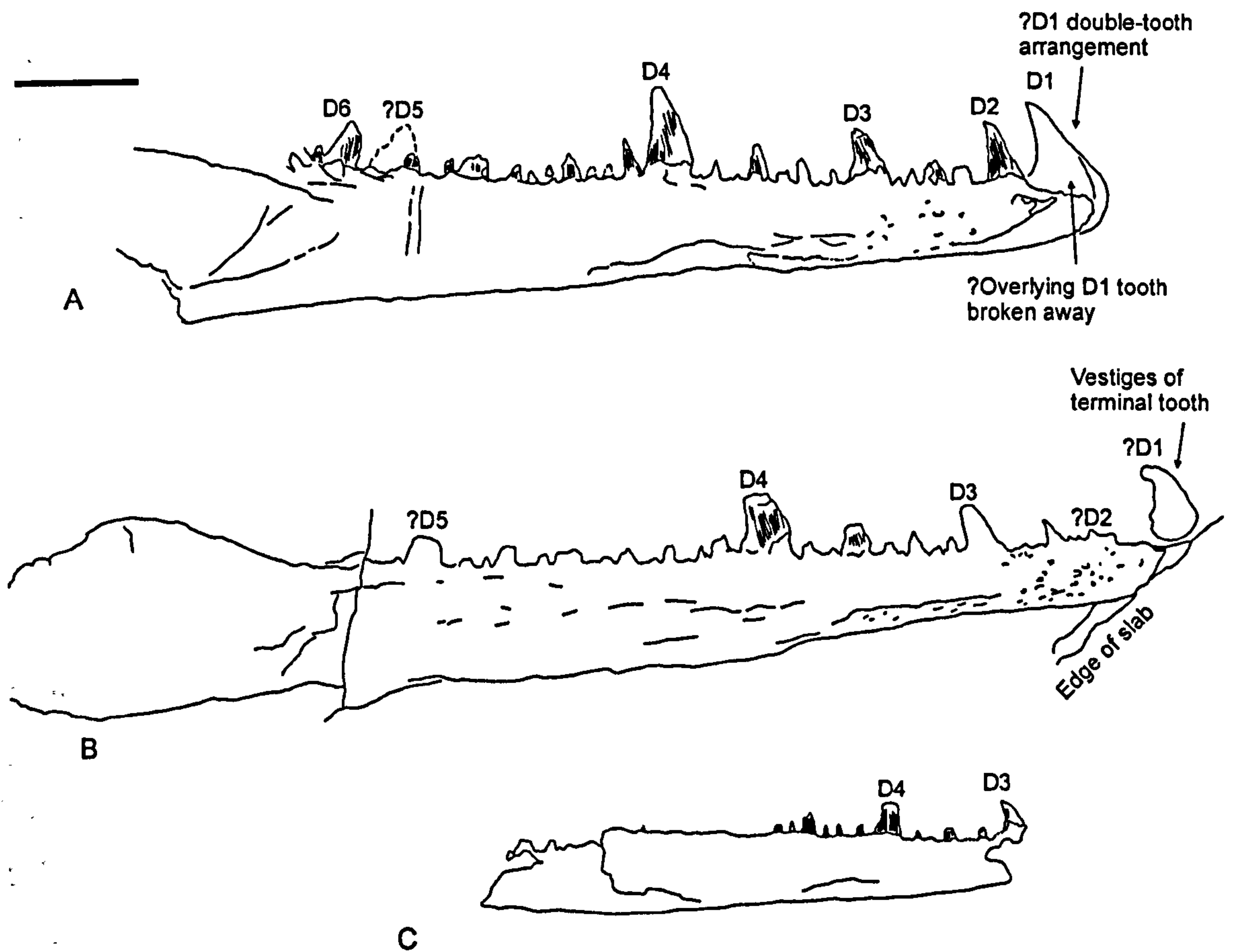
v. 1859a *Pterygotus punctatus*, Salter, pl. 11, figs 1-2, pl. 13, fig. 7.

vp.1961 *Erettopterus (Erettopterus) marstoni* n. sp., Kjellesvig-Waering, pp. 820-821 (*pars*), text-fig. 3.37-39.

1964 *Erettopterus (Erettopterus) marstoni* Kjellesvig-Waering; Kjellesvig-Waering, pp. 333, 339.

1986 *Erettopterus marstoni* Kjellesvig-Waering; Selden, p. 629.





TEXT-FIG. 4.2. Camera lucida drawings of the cheliceral rami of *Erettopterus marstoni* Kjellesvig-Waering, 1961. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, free ramus (BMNH In. 43790; holotype). B, fixed ramus (BMNH In. 43805; paratype). C, incomplete free ramus (BMNH 39394). Refer to plates 4.1-2. Scale bar represents 10 mm.



*Holotype.* BMNH In. 43790, free ramus of chelicera (Salter 1859a, pl. 11, fig. 2; Kjellesvig-Waering 1961, text-fig. 3.38). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Paratype.* BMNH In. 43805, fixed ramus of chelicera (Salter 1859a, pl. 11, fig. 1; Kjellesvig-Waering 1961, text-fig. 3.39). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Additional material.* BMNH 39394, incomplete free ramus (Salter 1859a, pl. 13, fig. 7; Kjellesvig-Waering 1961, text-fig. 3.37). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Diagnosis.* Cheliceral rami slender and tapering, angled distally. Teeth on rami curved posteriorly, relatively short and broad. Free ramus with three large principal teeth (D1-3) distally positioned, with large central tooth (D4), with large anteriorly inclined proximal teeth (D5-?D6). D1 broad, possibly laterally positioned and forming double-tooth structure on free ramus, immediately adjacent to slightly shorter D2 tooth. D4 tallest tooth along free ramus. Fixed ramus with corresponding arrangement of prominent teeth, with slight narrowing anterior of tooth D4 (emended after Kjellesvig-Waering 1961).

### *Description*

*Overall form.* Rami of chelicerae slender and tapering, angled distally, with relatively short teeth showing faint longitudinal striations. Teeth curved posteriorly, lacking serrations. Free and fixed rami with deep elongated pits distally positioned, distal of tooth D2.

*Free ramus.* Measurements of specimen BMNH 39394 in brackets. Length 90 mm, widening from 4 mm width at tooth D2 to 10 mm width at tooth D6. Tooth-bearing section of free ramus 55 mm long. Free ramus with posteriorly inclined teeth that are gently inclined ranging from 73-88 degrees along most of tooth-bearing section, with six large principal teeth (D1-6). Tooth arrangement distally to proximally: terminal principal tooth D1 (may form double-tooth structure), principal tooth D2, four smaller teeth, principal tooth D3, c. six small irregularly sized teeth (fourth tooth slightly



enlarged), enlarged central principal tooth D4, nine smaller teeth, ?principal tooth D5, principal tooth D6. Terminal tooth D1 large. Principal tooth D2 is 5 mm in height. Principal tooth D3 is 4.5 mm (2.4 mm) in height. Enlarged smaller intermediate tooth 3.3 mm (1 mm) in height (fourth tooth proximal of D3). Large central tooth D4 is 7.5 mm (2.6 mm, incomplete) in height. Principal teeth D5-D6 posteriorly curved, anteriorly inclined. Principal tooth ?D6 proximally positioned, 3.7 mm in height.

*Fixed ramus.* With posteriorly inclined teeth (ranging from 67-89 degrees); with corresponding principal teeth to free ramus (D1-5); with comparable arrangement of intermediate teeth; with slight narrowing anterior of large central tooth D4, widening from 5 mm width at tooth D2 to 10 mm width at D5. Tooth D3 is 3.9 mm in height.

#### *Remarks.*

The distal extremity of the free ramus BMNH In. 43790 (holotype) is poorly preserved, although vestiges of an enlarged terminal principal tooth D1 are preserved (Text-fig. 4.2A; Pl. 4.1, figs 1-2). Kjellesvig-Waering (1961) stated that the distal extremity of the ramus is broken away, apparently not recognising the poorly preserved D1 tooth (see his text-fig. 3.38); he added (p. 820) that this ramus "probably terminated in a double tooth", citing *E. brodiei* as a comparable example. Comparison with his text-figure 2.24 of *E. brodiei* (BGS GSM89411; holotype) shows the free ramus to possess an enlarged terminal tooth laterally positioned on either side of the ramus. It is unclear if this double-tooth arrangement is present in the free ramus of *E. marstoni*, or whether just one terminal D1 tooth is present. Tooth D1 is more faintly preserved than the proximal teeth, which may suggest that this tooth is set laterally below the ramus; the broken away portion of the ramus, referred to by Kjellesvig-Waering (1961) may represent the overlying missing D1 tooth (Pl. 4.1, fig. 2).

Specimen BMNH 39394, an incomplete ramus missing its distal portion, was identified as a free ramus of the species by Kjellesvig-Waering (1961). This is tentatively retained within the species due to its similar teeth arrangement with the holotype; a lack of any apparent narrowing of the ramus at tooth D4 (Text-fig. 4.2C; Pl. 4.2, figs 1-2), as seen in BMNH In. 43805, suggests that it is possibly the free ramus.



The distal extremity of the fixed ramus is poorly preserved; vestiges of a large terminal principal tooth D1 and tooth D2 are present (Text-fig. 4.2B; Pl. 4.1, figs 3-4). The tooth arrangement proximally is relatively consistent with that of the holotype of *E.*

*marstoni*, for example containing an enlarged D4 tooth, indicating this belongs to the same species. On the fixed ramus only the length of tooth D3 has been recorded, as the other principal teeth are not completely preserved.

Of the other documented eurypterid taxa of the Silurian of the UK, *E. marstoni* is most readily distinguished from *E. spatulatus*. It bears the most overall similarity to *E.*

*bilobus*; however, the anteriorly inclined enlarged D5-D6 teeth and the possible terminal double-tooth D1 are not present in *E. bilobus*. Only specimens showing the rami of the chelicerae may be assigned to *E. marstoni*; due to the highly disarticulated nature of the Leintwardine material, many specimens may only be assigned to the family Pterygotidae.

*Occurrence.* Known only from the type locality.

*Erettopterus?* sp. 1

Plate 4.2, figures 3-4

v. 1859a *Pterygotus arcuatus*, Salter, pl. 15, fig. 5.

v. 1871 *Pterygotus arcuatus*, Salter; Woodward, p. 90, text-fig. 23 (cop. Salter 1859a).

*Material.* BMNH 39396, complete metastoma (Salter 1859a, pl. 15, fig. 5; Woodward 1871, text-fig. 23); BGS GSM89601, complete metastoma. Specimens possibly part and counterpart, owing to identical size. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK: Church Hill.

*Description.* Metastoma obovate, narrowly rounded posteriorly, with narrowly rounded anterior shoulders, with sigmoidal sides, 56 mm in length, 31 mm in width.

*Remarks.* The taxonomic affinity of these metastomas are problematic. Both Salter (1859a) and Woodward (1871) figured specimen BMNH 39396 as *P. arcuatus*, whilst Kjellesvig-Waering (1961) doubtfully assigned it to *E. marstoni*. However, Kjellesvig-



Waering (1961) added that it is more likely to represent an undescribed genus. The specimens are unlikely to represent *Pterygotus*, since the metastoma shape in the type species of this genus, *Pterygotus anglicus* Agassiz, 1844 is relatively circular in outline (Salter 1859a, pl. 6, fig. 7; Størmer 1955, text-fig. 22.2e; Kjellesvig-Waering 1964, text-fig. 26; Tollerton 1989, text-fig. 5). The general obovate shape of the specimens conforms to Tollerton's (1989) designation of metastoma for the other documented pterygotid of Leintwardine, *Erettopterus*. However, there are some differences in shape, when compared with that of *E. bilobus* (Salter 1859a, pl. 6; Woodward 1868a, pl. 15, fig. 3). The metastoma of *E. bilobus* has relatively convex sides and a broadly rounded posterior, whereas those of BMNH 39396 and BGS GSM89601 have sinusoidal sides and a narrowly rounded posterior. The angle of anterior cordation is also less in *E. bilobus*. The specimens more closely resemble the metastoma of *Acutiramus* or *Truncatiramus* (e.g. Clarke and Ruedemann 1912, pl. 78, fig. 1; Størmer 1955, text-fig. 22.1e, 3d; Kjellesvig-Waering 1964, text-fig. 26). It may be that this specimen represents an undetermined species of one of these genera rather than *Erettopterus*, although this cannot be confirmed, as diagnostic chelicerae specimens of these genera have not been recovered from Leintwardine.

*Erettopterus?* sp. 2

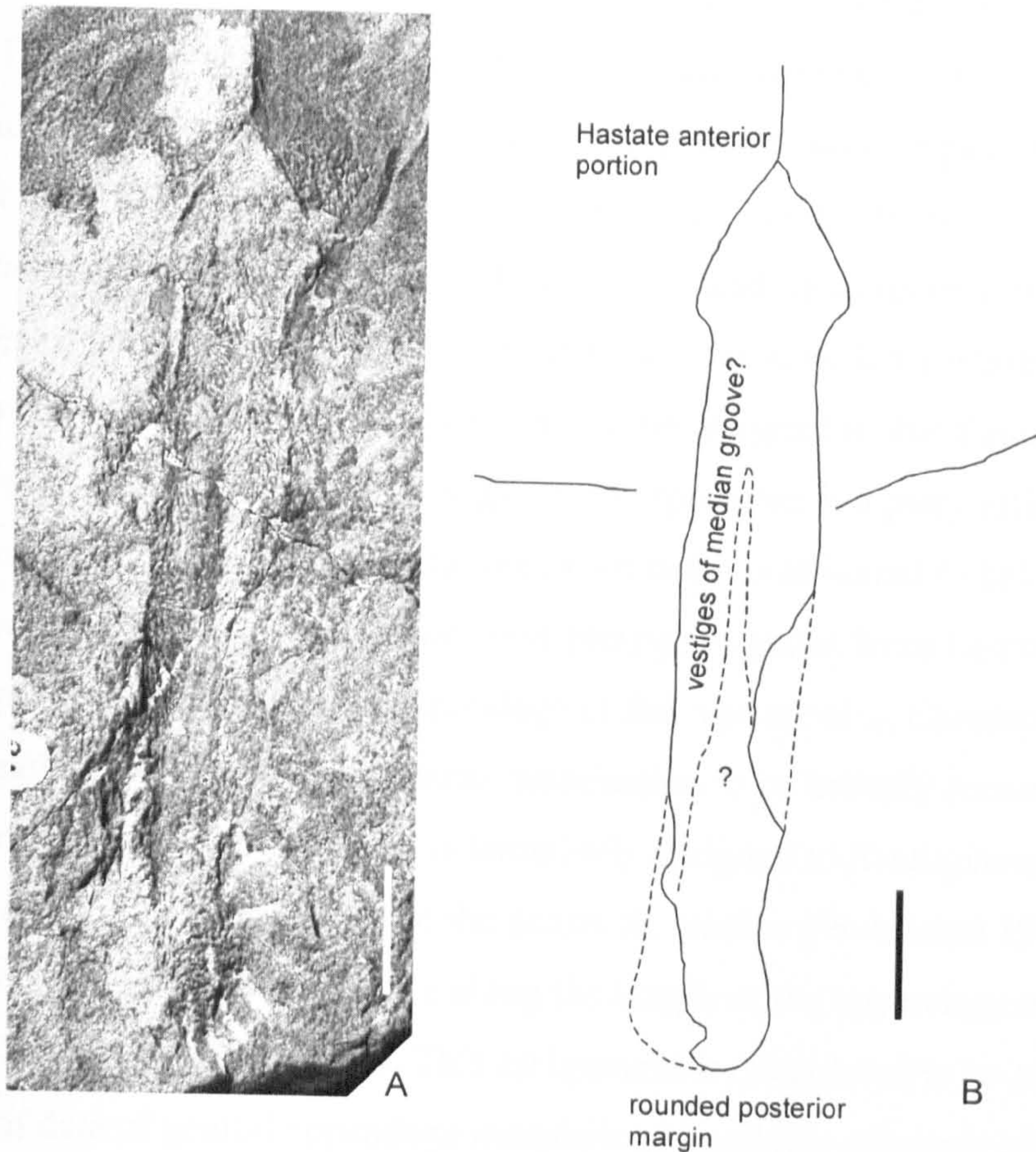
Plate 4.2, figure 5; Text-figure 4.3

v. 1871 *Pterygotus problematicus* Agassiz; Woodward, p. 88, text-fig. 20.

**Material.** BGS GSM89599, genital appendage type A (Woodward 1871, text-fig. 20). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

**Description.** Genital appendage type A long (73 mm anterior to posterior), narrow, with hastate anterior portion, 12 mm in width at widest point anteriorly; narrowest immediately posteriorwards to hastate portion (8 mm in width), increases slightly in width posteriorly to maximum distal width of c. 10 mm. Rounded posterior termination (spatulate to unilobed), unsegmented, with possible vestiges of a median groove, bordered by indistinct deltoid plates anteriorly.





TEXT-FIG. 4.3. Genital appendage (type A) of *Erettopterus?* sp. 2 (BGS GSM89599). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, detail of appendage. B, interpretive drawing of appendage. Note the rounded posterior margin of the appendage and the possible vestiges of a median groove. Also see plate 4.2, figure 5. Scale bars represent 10 mm.



*Remarks.* The appendage is inferred to be female, following the designation of Braddy and Dunlop (1997). Woodward (1871) illustrated the specimen, copied from an unpublished sketch by Salter, as *Pterygotus problematicus* Agassiz, 1839. This name, erected by Agassiz (1839) on undiagnostic fragmentary cuticle, is considered *nomen dubium*. Woodward's (1871) text-figure is misleading in its representation of the posterior termination of the appendage. Comparison with the genital appendages of pterygotids suggests that the specimen can be assigned to this family; the unilobed to spatulate posterior termination suggests the specimen is a pterygotid (e.g. see Waterston 1964, text-fig. 5). The specimen is not considered to belong to *Carcinosoma*, the only confirmed non-ptyerygotid genus from Leintwardine; comparison with the genital appendage of the type species, *Carcinosoma newlini* Claypole, 1890 shows the posterior termination to be broadly concave (Kjellesvig-Waering 1958). The specimen is tentatively assigned to *Erettopterus*, based on its similarity to the type species of the genus, *E. bilobus* (Waterston 1964); both specimens show traces of a median groove along the length of the appendage and this is taken as a possible diagnostic character. This assignment is considered to be tentative due to the lack of data of genital appendage morphology available on many eurypterid taxa, as the structure is not commonly preserved (Størmer 1973; Tollerton 1989). However, the morphology of the appendage does not resemble that of other eurypterid genera from the Silurian Welsh Borderland with known genital appendages (e.g. *Dolichopterus*, *Eurypterus*, *Hughmilleria*, *Mixopterus*; see Clark and Ruedemann 1912; Størmer 1955; Kjellesvig-Waering 1961).

#### Genus PTERYGOTUS Agassiz, 1844

1839 *Pterygotus*; Agassiz, pp. 605-606.

1844 *Pterygotus*, Agassiz, p. xix.

1859a *Pterygotus* Agassiz; Salter, p. 37.

1866 *Pterygotus* Agassiz; Woodward, p. 33.

1934 *Pterygotus* Agassiz; Størmer, pp. 93-95 (*pars*).

1955 *Pterygotus* (*Pterygotus*) Agassiz; Størmer, pp. 30-31.

1961 *Pterygotus* (*Pterygotus*) Agassiz; Kjellesvig-Waering, p. 812.

1964 *Pterygotus* (*Pterygotus*) Agassiz; Kjellesvig-Waering, pp. 331, 350.

1964 *Pterygotus* (*Pterygotus*) Agassiz; Waterston, p. 29.



- 1974 *Pterygotus* Agassiz; Størmer, p. 376.
- 1989 *Pterygotus* Agassiz; Tollerton, pp. 653, 655.
- 1994 *Pterygotus* Agassiz; Chlupáč, p. 151.

*Type species.* *Pterygotus anglicus* Agassiz, 1844, by monotypy, from the Devonian of Dundee, Scotland.

*Diagnosis.* Prosoma trapezoid. Cheliceral rami bearing posteriorly curved teeth lacking serrations. Free ramus rounded distally, terminating in a curved tooth that either extends anteriorly or is at right angles to the ramus. Metastoma circular or ovoid, cordate anteriorly, wide. Telson paddle-shaped, terminating in a spine (emended after Waterston 1964, Tollerton 1989 and Chlupáč 1994).

*Remarks.* Many species have been described in the literature, often diagnosed on the cheliceral morphology (e.g. Kjellesvig-Waering 1961, 1964; Chlupáč 1994). The type species, *P. anglicus*, is distinguished by relatively short, broad, numerous teeth along the cheliceral rami; the free ramus terminates in a large rounded tooth (Salter 1859a, pl. 6; Waterston 1964). Salter (1859a) erected *Pterygotus arcuatus* and *Pterygotus ludensis* from the Ludlow Series of the Welsh Borderland; however, his diagnoses were not clear and many of the disarticulated specimens assigned are not diagnostic of a particular species. Kjellesvig-Waering (1961) recognised *P. arcuatus* and *P. ludensis*, and erected a further three species: *Pterygotus denticulatus*, *Pterygotus grandidentatus* and *Pterygotus lightbodyi*, from the Silurian of the Welsh Borderland, differentiating them on cheliceral morphology. Kjellesvig-Waering (1961) did not include a description of the chelicerae of *P. arcuatus* and *P. ludensis*. Kjellesvig-Waering (1961, text-fig. 30) distinguished *P. denticulatus* from the other species of the Welsh Borderland, by the small, thick and posteriorly curved teeth of the rami. *P. grandidentatus* has a free ramus with a very long, relatively vertical and straight terminal tooth, and smaller teeth curved anteriorly and posteriorly (Kjellesvig-Waering 1961, text-fig. 29). *P. lightbodyi* has long, gently curved teeth along the rami; the terminal and central teeth are particularly long (Kjellesvig-Waering 1961, text-figs 23, 30, 32).



Other species from the Upper Silurian include *Pterygotus impactus* Kjellesvig-Waering, 1964 from the Ludlow Series of Estonia and *Pterygotus lanarkensis* Kjellesvig-Waering, 1964 from the Ludlow Series of Lesmahagow, Scotland. *P. impactus* is characterised by the free ramus terminating in a double tooth combination (Kjellesvig-Waering 1964, text-figs 20, 23). Kjellesvig-Waering (1964) listed several other species from North America; however, he did not provide descriptions of these taxa. Chlupáč (1994) described *Pterygotus barrandei* Semper, 1898 and *Pterygotus kopaninensis* Barrande, 1872 from the Upper Silurian of Bohemia. *P. barrandei* is distinguished by a free ramus with a long anteriorly curved to straight terminal tooth, and smaller proximal teeth (Chlupáč 1994).

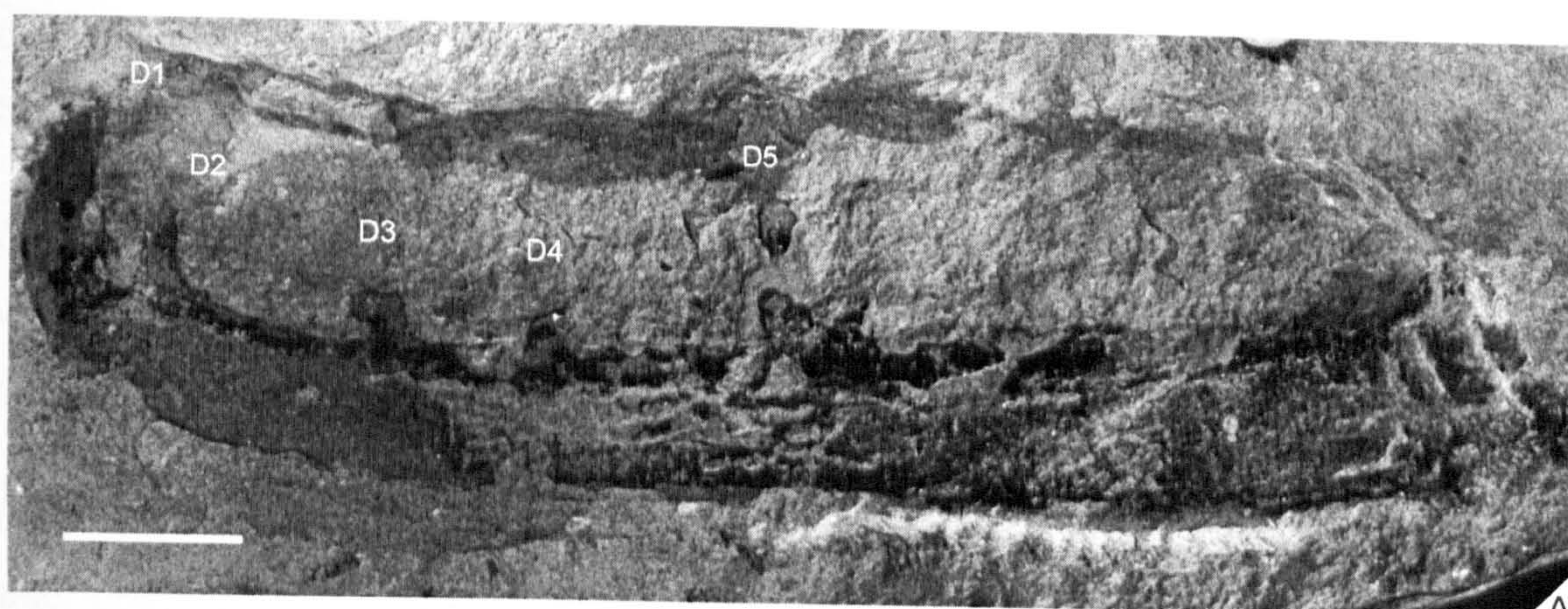
The majority of species show considerable variation in the form of the free ramus; this character is therefore retained as a diagnostic character following Waterston (1964).

*Pterygotus? arcuatus* Salter, 1859

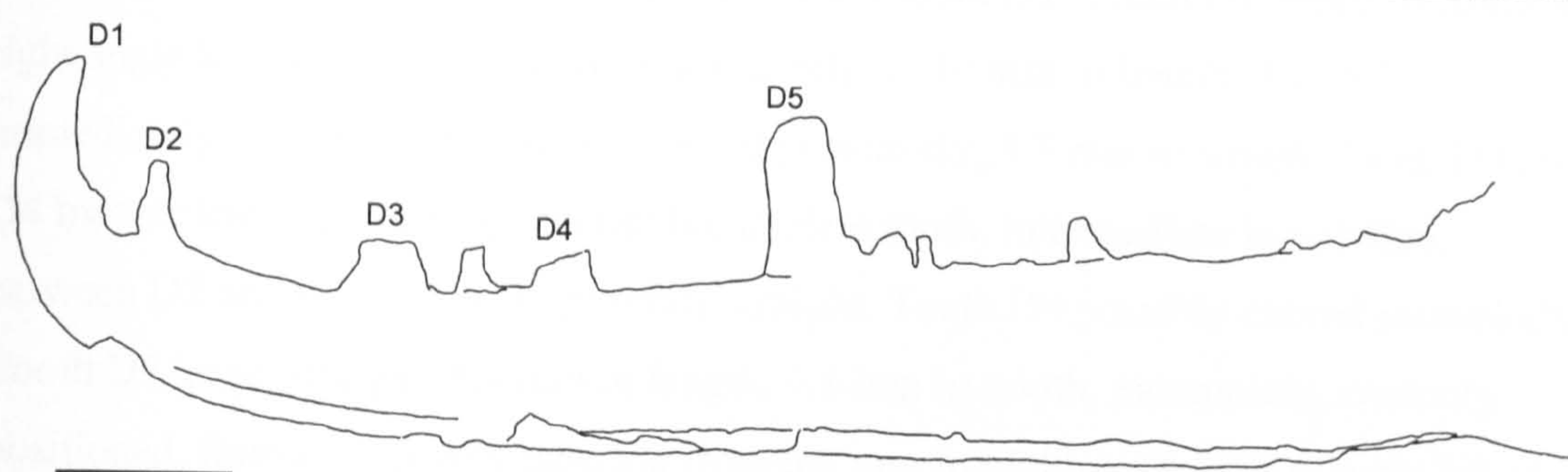
Text-figure 4.4

- vp. 1859a *Pterygotus arcuatus*, Salter, p. 95-97 (*pars*), pl. 13, fig. 8, *non* figs 12-13, 15-16, ? pl. 15, fig. 5.
- vp 1871 *Pterygotus arcuatus* Salter; Woodward, pp. 88-90 (*pars*), *non* text-figs 21-23.
- ? 1873 *Pterygotus arcuatus* Salter; Salter, p. 165.
- ?p 1888 *Pterygotus arcuatus* Salter; Etheridge, p. 66.
- p. 1924 *Pterygotus arcuatus* Salter; Diener, p. 10.
- ? 1934 *Pterygotus arcuatus* Salter; King, p. 563.
- ? 1934 *Pterygotus arcuatus*; Størmer, p. 95.
- vp. 1961 *Pterygotus (Pterygotus) arcuatus* Salter; Kjellesvig-Waering, p. 813, ?text-fig. 3.40.
- 1964 *Pterygotus (Pterygotus) arcuatus* Salter; Kjellesvig-Waering, pp. 332, 341.
- 1986 *Pterygotus arcuatus* Salter; Selden, p. 629.

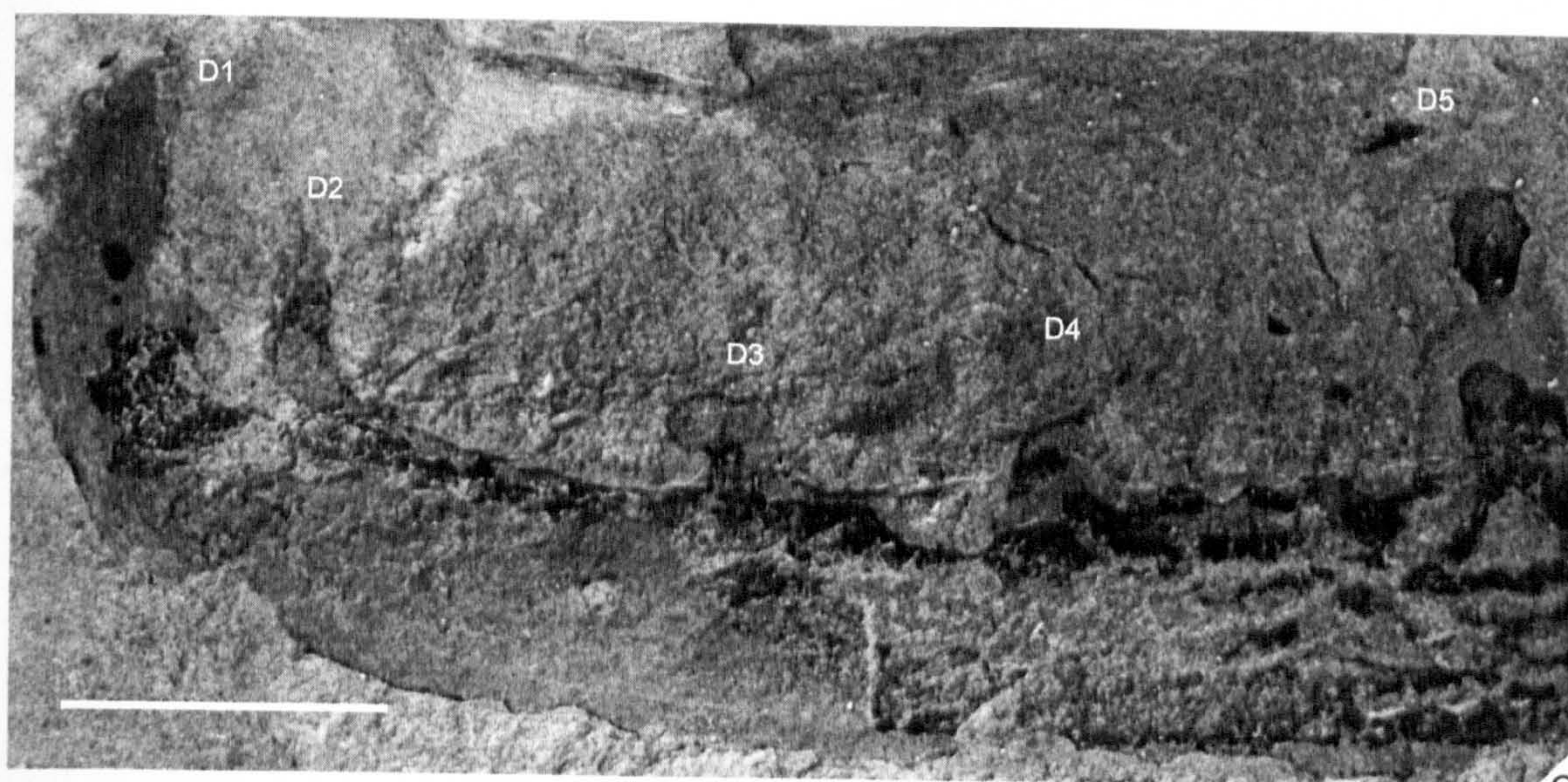




A



B



C

TEXT-FIG. 4.4. Chelical free ramus of *Pterygotus? arcuatus* Salter, 1859 (BMNH In. 43788; lectotype). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. A, complete free ramus, showing rounded distal end with enlarged straight terminal tooth D1. B, camera lucida drawing of complete free ramus. C, detail of distal portion showing curved termination and principal teeth D1-D5. Scale bars represent 10 mm.



*Lectotype.* BMNH 43788, free ramus of chelicera (Salter 1859a, pl. 13, fig. 8); designated by Kjellesvig-Waering (1961). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Diagnosis.* Cheliceral free ramus rounded distally, with long straight terminal tooth D1, with straight large central tooth D5. D1 c. twice length of adjacent D2, slightly taller than D5. Teeth few in number.

*Description.* Cheliceral free ramus with five prominent teeth (D1-D5), rounded anteriorly, terminating in large relatively straight tooth D1. Tooth D1 approximately at right angle to ramus, slightly curved posteriorly, c. 10 mm in length. Tooth D2 immediately adjacent to D1, small, curved posteriorly, 5.3 mm in length. Teeth D3 and D4 incomplete, separated by smaller incomplete tooth, intermediate in position between D2 and D5. Tooth D3 possibly straight. Tooth D4 possibly curved posteriorly. Tooth D5 large, straight, 8.4 mm in length, 4.8 mm in width, incomplete, centrally positioned. Ramus gradually tapering from 6.8 mm in width anteriorly at tooth D2 to 8.7 mm in width posteriorly at tooth D5.

*Remarks.* Only the lectotype can be assigned to the species with any certainty; no other specimens of chelicerae of *P. arcuatus* are known. Kjellesvig-Waering (1961) considered that certain specimens illustrated by Salter (1859a) and Woodward (1871) are unlikely to belong to the species. Kjellesvig-Waering (1961) assigned specimen BGS GSM89587, a gnathobase of the coxa, also to the species; however, herein it is considered that there is insufficient data to determine the specific affinity of this specimen.

Assignment of specimen BMNH 43788 to *Pterygotus* is tentative due to the lack of material, particularly as the distinction of the free ramus in this genus from that of *Jaekelopterus* Waterston, 1964 is not always clear. The terminal tooth in BMNH 43788 bears some similarity to that shown in the free ramus of *Jaekelopterus rhenaniae* (Jaekel, 1914), with both being of a curved appearance, at right angles to the ramus. Waterston (1964, p. 30) described *Jaekelopterus* as possessing chelicerae with “terminal teeth almost at right angles to the rami and principal teeth slightly inclined anteriorly”. However, the angle of the curved terminal tooth appears to be variable in *Pterygotus*, suggesting this might not be a reliable generic character. This character



appears to vary both intraspecifically within *P. anglicus* and interspecifically, for example between *P. barrandei*, *P. grandidentatus* and *P. lightbodyi* (e.g. Kjellesvig-Waering 1961, text-fig. 2; Waterston 1964, text-fig. 4; Chlupáč 1994, text-fig. 2a). The character of the principal teeth proximal to D1 is taken to be diagnostic. The specimen of *J. rhenaniae* figured by Waterston (1964, text-fig. 5c) does not appear to have posteriorly curved teeth, in contrast to those of *Pterygotus*. Teeth D2 and D4 of BMNH 43788 appear to be posteriorly inclined which suggest that the specimen can be retained within *Pterygotus*.

*Occurrence.* Known only from the type locality.

*Pterygotus?* sp.

Text-figure 4.5

v. 1859a *Pterygotus punctatus* Salter, pl. 11, fig. 3.

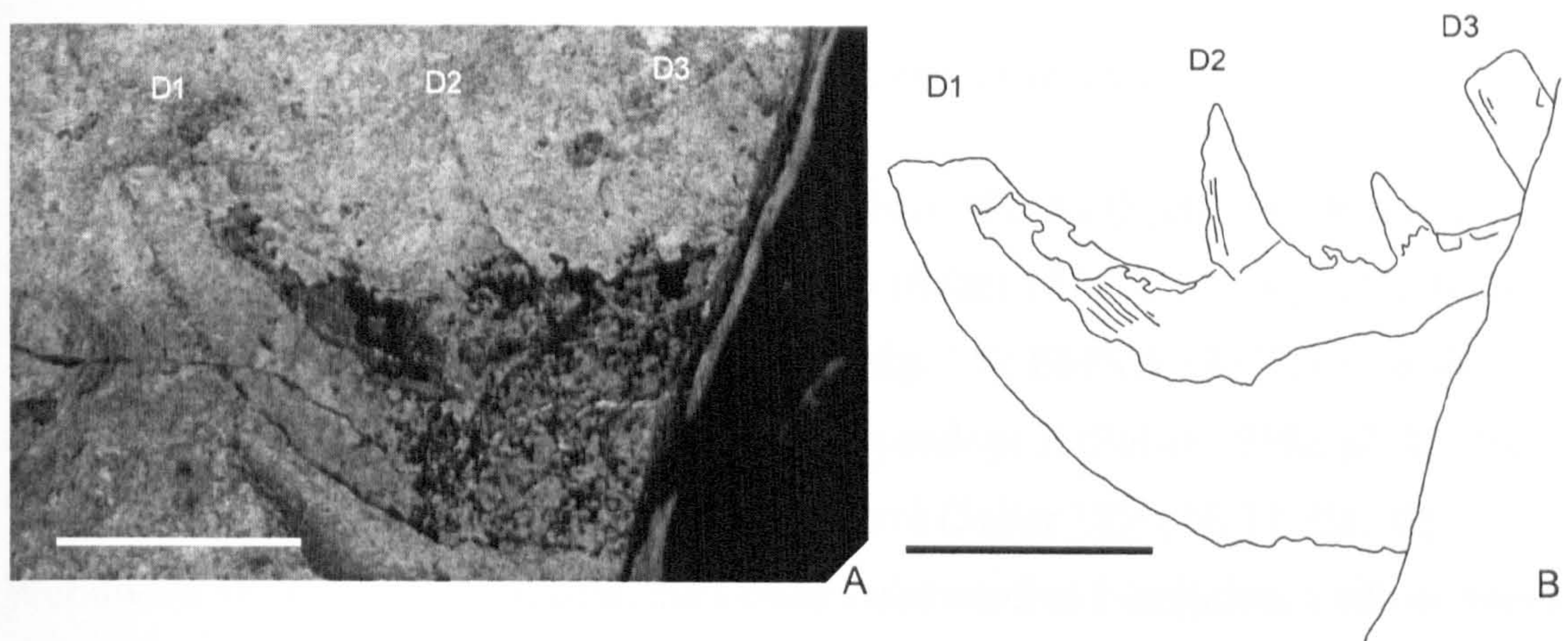
vp 1961 *Erettopterus marstoni* n. sp., Kjellesvig-Waering, p. 820 (*pars*).

*Material.* BGS GSM89573, incomplete free ramus, retaining distal teeth (Salter 1859a, pl. 11, fig. 3). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description.* Cheliceral free ramus rounded distally, with anteriorly extending terminal tooth D1. Tooth D1 incomplete. Tooth D2 curved posteriorly, 6.9mm in length. Small tooth proximal to D2 anteriorly inclined, slightly posteriorly curved. Tooth D3 incomplete, anteriorly inclined.

*Remarks.* Due to the extremely incomplete nature of the specimen, it is not possible to refer it to a species. Kjellesvig-Waering (1961) assigned the specimen to *E. marstoni*; however, the curved terminal tooth D1 suggests it can be assigned to either *Pterygotus* or *Jaekelopterus*. The terminal tooth is not at right angles to the ramus and extends anteriorly; following Waterston's (1964) diagnosis of *Jaekelopterus*, this suggests a *Pterygotus* affinity for the specimen. The posteriorly curved tooth D2 is also characteristic of *Pterygotus*. The two teeth proximal to D2 appear to be anteriorly inclined, which is uncharacteristic of the genus.





TEXT-FIG. 4.5. Incomplete cheliceral free ramus of *Pterygotus?* sp. (BGS GSM89573). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. A, entire specimen showing rounded distal end and enlarged, anteriorly directed terminal tooth D1. B, camera lucida drawing of specimen. Scale bars represent 10 mm.



The curved distal end and terminal tooth D1 indicate that the fragmented chelicera is part of a free ramus rather than a fixed ramus; the fixed ramus consistently terminates in an angled extremity in the pterygotids (e.g. see Waterston 1964).

Family PTERYGOTIDAE gen. *et* sp. indet.

*Material.* BGS GSM89567, GSM89587, gnathobase of coxa (Kjellesvig-Waering 1961, text-fig. 3. 40); BMNH 39388, gnathobase (Salter 1859, pl. 11, fig. 11); BMNH 39395, coxa of walking leg (Salter 1859, pl. 13, fig. 15); BMNH 39397, In. 43786, semi-articulated infracapitulum and prosomal appendage II (Salter 1959a, pl. 13, fig. 17; Selden 1986, text-figs 1A, 2A); In. 43787, coxa (Salter 1859, pl. 11, fig. 10; Woodward 1871, fig. 21). All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

*Remarks.* Kjellesvig-Waering (1961) assigned specimen BGS GSM89587 to *P. arcuatus*, although there is no conclusive evidence to support this specific designation, since the pterygotids are classified according to details of the chelicerae. BMNH In. 43786 was assigned by Selden (1986) to an undetermined pterygotid, representing the infracapitulum and prosomal appendage II (Pl. 4.2, fig. 6). It is not possible to fully determine the affinity of this specimen.

Family CARCINOSOMATIDAE Størmer, 1934

*Remarks.* Tollerton (1989) diagnosed the family on the spiniferous prosomal appendages II-V, and on morphology of prosomal appendage VI, which is developed into a swimming paddle with elongate, slightly expanded seventh and eighth podomeres. Tollerton also described the opisthosoma as showing a first order differentiation into a broad abdomen and narrow, cylindrical postabdomen. The family contains five genera (Tollerton 1989): *Carcinosoma* Calypole, 1890, *Eocarcinosoma* Caster and Kjellesvig-Waering, 1964, *Paracarcinosoma* Caster and Kjellesvig-Waering, 1964, *Rhinocarcinosoma* Novojilov, 1962 and possibly *Holmipterus* Kjellesvig-Waering, 1979. The morphology of the paddle of prosomal appendage VI is maintained as a generic character following Tollerton (1989).



Much of the material recorded from the Leintwardine sites consists of small, fragmentary undiagnostic pieces of cuticle, often exhibiting a particular ornament of small rounded tubercles/mucrones (e.g. Pl. 4.7, fig. 4). According to Størmer (1955), Kjellesvig-Waering (1961) and Caster and Kjellesvig-Waering (1964), characteristic ornamentation can be used to diagnose specimens to family level. The pterygotids were stated as possessing U- to V-shaped lunules (Størmer 1955, text-fig. 22. 3f; Kjellesvig-Waering 1961), whilst those of the carcinosomatids possess scattered minute tubercles or raised tongue-like scales (Størmer 1955, text-fig. 29. 3c; Caster and Kjellesvig-Waering 1964). Tollerton (1989) stated that although exceptions exist, surface markings are generally of no taxonomic use, adding that one species may show two or more types of ornamentation on a single morphological feature. Tollerton cited Selden's (1981) figure 1 as an example, which shows shape variations in lunules on the cuticle of *Baltoeurypterus tetragonophthalmus* (Fischer, 1839). However, these variations in ornament are essentially within one sculpture type, that of lunules; the variations described by Størmer (1955), Kjellesvig-Waering (1961) and Caster and Kjellesvig-Waering (1964) are between two distinct sculpture types (lunules and tubercles/mucrones). Three ornament types are tentatively recognised within the Leintwardine specimens: (i) rounded to slightly elongate tubercles (e.g. on an opisthosomal body segment of *Carcinosoma*, on slab BMNH 39389; Pl. 4.4, fig. 2); (ii) minute tongue-like tubercles (e.g. on CH144, a prosoma of undetermined affinity; Pl. 4.8, figs 3-5); (iii) U- to V-shaped lunules (e.g. on a metastoma and cuticle fragment, respectively of specimens of an unknown affinity; Pl. 4.8, figs 2, 6-7). It is apparent from these styles of ornament that a particular type may be broadly characteristic of perhaps a family. By comparison with the ornament type shown on specimen BMNH 39389, it can tentatively be proposed that many of the fragmentary pieces of cuticle bearing an ornament of small, rounded tubercles, belong to the carcinosomatids.

*Type genus.* *Carcinosoma* Claypole, 1890, by original designation.

#### Genus CARCINOSOMA Claypole, 1890

1890 *Carcinosoma* n. gen.; Claypole, p. 400.

1934 *Carcinosoma* Claypole; Størmer, p. 104.

1955 *Carcinosoma* Claypole; Størmer, p. 34.

1964 *Carcinosoma* Claypole; Caster and Kjellesvig-Waering, pp. 310-312.



1989 *Carcinosoma* Claypole; Tollerton, pp. 652-653 (*pars*).

2002 *Carcinosoma* Claypole; Braddy *et al.*, p. 902.

*Type species.* *Eurysoma newlini* Claypole, 1890, by original designation, from the Silurian of Indiana, USA.

*Diagnosis.* Prosoma subtriangular, with antelateral compound eyes. Chelicerae small, lacking teeth. Prosomal appendages II-V strongly developed, with pronounced spine pair on each podomere orientated anteriorly. Prosomal appendage VI long, developed into large paddle, reaching metastoma, with relatively long podomere 8 showing width: length ratio of 0.4. Metastoma shield-shaped. Postabdomen dorsoventrally flattened. Telson styliiform with post-telson (emended after Braddy *et al.* 2002).

*Remarks.* Kjellesvig-Waering (1961) recognised *Carcinosoma punctatum* (Salter, 1859) and erected *Carcinosoma harleyi* from the Ludlow Series of the Welsh Borderland. Kjellesvig-Waering (1961) differentiated *C. harleyi* from *C. punctatum* by its lack of serrations on the eighth podomere and lesser development of serrations on the ninth podomere of prosomal appendage VI. Caster and Kjellesvig-Waering (1964) recognised both of these species within their emended classification of *Carcinosoma*, although *C. harleyi* was only recognised tentatively. Caster and Kjellesvig-Waering (1964) recognised a further six Silurian species within the genus: *Carcinosoma libertyi* Copeland and Bolton, 1960, from Canada; *Carcinosoma* (?) *logani* (Williams, 1915) from Ontario; *Carcinosoma spiniferum* Kjellesvig-Waering and Heubusch, 1962 from New York; *Carcinosoma newlini* (Claypole, 1890) from Indiana; *Carcinosoma scorpioides* (Woodward, 1868b) from the Ludlow of Scotland and *Carcinosoma scoticum* (Laurie, 1898) from the Wenlock of Scotland. Of these further species, only *C. newlini* and *C. scorpioides* preserve prosomal appendage VI; however, the distal extremity of this appendage is not preserved in the latter (1872a, pls 29-30). The marginal serration along the distal podomeres of *C. newlini* is not as pronounced as in *C. punctatum* (see Kjellesvig-Waering 1958, text-fig. 5).

The width: length ratio (0.3) of the distal podomere 8, incorporating podomere 9 if present, is constant through all the Leintwardine *Carcinosoma* prosomal appendage VI specimens where complete (e.g. BGS GSM89561, BMNH 39389, BMNH In. 43804), although this in itself is not taken to be of specific diagnostic value as *C. newlini* also



shows the same ratio (see Kjellesvig-Waering 1958, text-fig. 5). However, complete distal podomeres of a specimen assigned to *Carcinosoma* sp. by Størmer (1974), from the Lower Devonian of Germany, shows a ratio of 0.4. The specimen shows a markedly shorter podomere 8 in contrast to the more elongate morphology typical of the genus. This sole specimen is the only documented *Carcinosoma* specimen from the Lower Devonian (Størmer 1974; Tollerton 1989). Comparison with the width: length ratio of the distal podomeres of prosomal appendage VI of the carcinomatid genus more typical of the Lower Devonian, *Paracarcinosoma* also shows a ratio of 0.4 (see Clarke and Ruedemann 1912, pl. 34). This genus typically shows a short prosomal appendage VI, in contrast to *Carcinosoma* (Caster and Kjellesvig-Waering 1964; Braddy *et al.* 2002). The specimen described as *Carcinosoma* sp. by Størmer (1974) may therefore represent a species of *Paracarcinosoma*. Comparison with other *Carcinosoma* material is not possible as swimming paddles with complete distal podomeres have not been documented from other species (e.g. see Woodward 1868b, 1872a; Copeland and Bolton 1960; Kjellesvig-Waering and Heubusch 1962). The constant dimension ratio of the distal podomeres of prosomal appendage VI through *Carcinosoma* suggests that this character may have diagnostic value at a generic level.

Only the Leintwardine material consisting of the complete or distal portions of prosomal appendage VI may be assigned to a species with any certainty. Data is insufficient to refer other specimens to a particular species. Specimens comprising near complete spiniferous walking appendages, of the '*Carcinosoma* type' (Tollerton 1989) are assigned to *Carcinosoma* sp.

#### *Carcinosoma punctatum* (Salter, 1859)

#### Plates 4.3-5; Text-figure 4.6

vp.1859a *Pterygotus punctatus* n. sp., Salter, pp. 99-105 (*pars*), pl. 10, figs 5-6, ?figs 1-4, 7-11; pl. 11, figs 14-15, ?figs 5-9, 12, *non* figs 1-2 (= *Erettopterus marstoni*), 3 (= *Pterygotus* sp.), 4 (= *Salteropterus? longilabium*), 13 (= *Carcinosoma* sp.); pl. 12, ?fig. 18, *non* fig. 19 (= *Carcinosoma harleyi*); pl. 13, ?figs 5-6, 9-11, 14, *non* fig. 7 (= *Erettopterus marstoni*).

? 1859 *Pterygotus punctatus*; Huxley, p. 21.



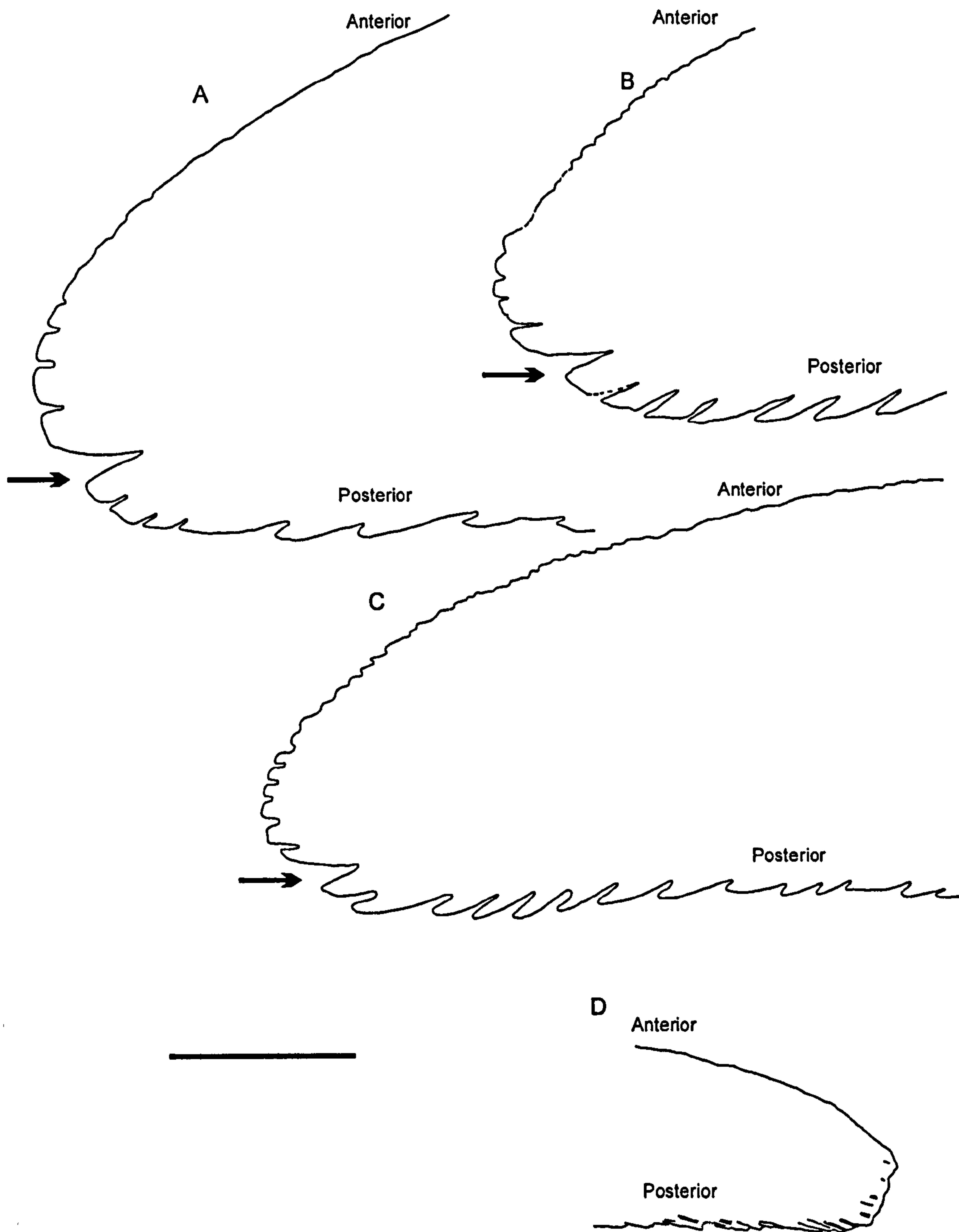
- ? 1859 *Pterygotus punctatus*; Bigsby, p. 322.
- ? 1864 *Pterygotus punctatus*; Powrie, p. 415.
- vp. 1872a *Eurypterus punctatus* Salter; Woodward, pp. 153-159 (*pars*), ?text-fig. 51;  
non text-figs 49-50 (fig. 50= *Carcinosoma* sp.), pl. 29, fig. 2.
- p 1888 *Eurypterus punctatus* Salter; Etheridge, p. 53.
- v 1912 *Eusarcus punctatus* Salter; Clarke and Ruedemann, p. 231, text-figure 52.
- ? 1934 *Eurypterus punctatus* Salter; King, p. 563.
- vp. 1961 *Carcinosoma punctatum* (Salter); Kjellesvig-Waering, pp. 828-830 (*pars*),  
text-fig 3.43, non text-figs 3.42, 3.44-45 (= *Carcinosoma*? sp.).
- 1964 *Carcinosoma punctatum* (Salter); Caster and Kjellesvig-Waering, p. 311.

*Lectotype*. BGS GSM89435, distal portion of prosomal appendage VI (Salter 1859a, pl. 11, fig. 14; Kjellesvig-Waering 1961, text-fig. 4); assigned by Kjellesvig-Waering (1961) as the lectotype. There is confusion regarding the provenance of the specimen; Salter (1859a) and Kjellesvig-Waering (1961) stated that the specimen is from the Middle Ludlow, Mocktree Shale of Leintwardine, Herefordshire, whilst the museum slip records the specimen as originating from the Ludlow Series (formation unknown) of the Whitcliffe, Ludlow, Shropshire. Kjellesvig-Waering (1961) stated that the species is confined to the Lower Leintwardine Formation at Leintwardine; if correct, the provenance details of the museum slip suggest that the species range could extend to the overlying Whitcliffe Formation. However, this is uncertain as the specimen may equally have originated from the Leintwardine Group of the Whitcliffe. Leintwardine Group or Whitcliffe Group, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire or Ludlow, Shropshire, UK.

*Additional material*. BMNH 39389, distal portion of prosomal appendage VI and opisthosomal tergite (separate specimens, Salter 1859a, pl. 10, fig. 5, pl. 11, fig. 14); BMNH In. 43804, nearly complete prosomal appendage VI (Salter 1859a, pl. 11, fig. 15; Woodward 1872a, pl. 29, fig. 2); BGS GSM89561, nearly complete prosomal appendage VI (Kjellesvig-Waering 1961, text-fig. 3. 43); BGS GSM89568, distal portion of prosomal appendage VI. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

HFDMG G87 (labelled as *Pterygotus ludensis*, in association with Upper Silurian eurypterid specimens); unknown provenance.





TEXT-FIG. 4.6. Camera lucida drawings of marginal serrations along distal podomeres of prosomal appendage VI of *Carcinosoma punctatum* (Salter, 1859); diagnostic deep serration 'A' marked by arrow. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, BGS GSM89435; lectotype. B, BGS GSM89568. C, BMNH 39389. D, BGS GSM89561, possible juvenile specimen; characteristic marginal serration is not pronounced. Refer to plates 4.3-5. Scale bar represents 10 mm.



The museum slip of BMNH 39389 records it as being figured by Salter (1859a) on plate 11, figure 14. However, this appears to be a mistake, as it is BGS GSM89435 that is figured.

*Diagnosis.* Prosomal appendage VI with pronounced marginal serrations along podomeres 8 (tarsus) and 9 (posttarsus), with particularly deep serration ('A' on Text-fig. 4.5) at distal extremity (emended after Kjellesvig-Waering 1961).

*Description.*

*Prosomal appendage VI.* Long (BMNH In. 43804: 235 mm), with wide podomere 7 (BMNH In. 43804: 35 mm width), with podomeres 7-?9 developed into large swimming paddle (BMNH In. 43804: 140 mm length). Podomeres 7 and 8 long. Podomere 8 narrower and slightly longer than podomere 7, with no surface ornament apparent. Distal podomeres (incorporating 8 and ?9) over twice as long as wide, with width: length ratio of 0.3, with pronounced marginal serrations. Marginal serrations show particularly deep serration at distal extremity of terminal podomere ('A' on Text-fig. 4.6), relatively more pronounced and pointed along posterior margin, blunted anteriorly of serration 'A', gradually lessen towards anterior margin.

*Postabdomen.* Relatively narrow (BMNH 39389: 55 mm width), ornamented by numerous rounded mucrones.

*Remarks.* Kjellesvig-Waering's (1961) diagnosis of the species, based on pronounced serrations on the distal portion of prosomal appendage VI is only valid for the lectotype, and specimens BMNH 39389, BMNH In. 43804, BGS GSM89561 and GSM89568. Kjellesvig-Waering (1961) did not cite BMNH In. 43804, a nearly complete prosomal appendage VI, retaining podomeres 1 to ?9, as an example of the species, although this is assigned to *C. punctatum* herein, due to the presence of a deep serration 'A' at the distal extremity of the terminal podomere, which is regarded to be of particular diagnostic value. This serration is also present in lectotype BGS GSM89435, and the majority of the remaining specimens (BGS GSM89568, BMNH 39389). Specimen BMNH In. 43804 does not show such pronounced marginal serrations as the lectotype, although this is likely be a preservational artefact. BGS GSM89561, an unusually small, possibly juvenile specimen, of a nearly complete



prosomal appendage VI, does not show the diagnostic serration 'A', although this may be due to the distalmost extremity of the appendage not being clearly preserved. However, pronounced marginal serrations are present along the proximal and distal margin, which suggests the specimen can be retained within *C. punctatum*.

Tollerton (1989) recognised the *Carcinosoma*-type prosomal appendage VI as possessing narrow podomeres 7 and 8, with podomere 8 being slightly narrower than podomere 7 and approximately twice as long as wide. These characters are all observed in the Leintwardine material. Podomere 9 (terminal/posttarsus) was described by Tollerton (1989) as being very prominent. Analysis of the lectotype of *C. punctatum* and specimens BGS GSM89568, BMNH 39389, BMNH In. 43804, reveals that podomere 9 does not appear to be present although this may be a preservational artefact.

A disarticulated skeletal component, figured in Salter (1859, pl. 10, fig. 5) and described as an opisthosomal body segment of *Pterygotus punctatus*, is tentatively retained within the species due to its occurrence on the same slab as a disarticulated prosomal appendage VI (BMNH 39389; Pl. 4.4, fig. 1). Its generic affinity is indicated by comparison with Kjellesvig-Waering's (1958) reconstruction of *C. newlini* and a nearly complete specimen of *C. scorioides* figured in Woodward (1868b, pl. 9, fig. 1, pl. 10, fig. 2; 1872a, pl. 29, fig. 1). The specimen is interpreted to represent a postabdominal tergite.

Due to the highly disarticulated nature of the material, it is questionable whether other specimens can be assigned to this species. Kjellesvig-Waering (1961) assigned a disarticulated chelicera (BGS GSM89581) and several specimens of the walking appendages (BGS GSM89565, GSM89583) to the species. Herein, these specimens are consigned, along with other specimens of disarticulated walking legs to *Carcinosoma* under open nomenclature. Although likely to belong to *Carcinosoma*, there is no conclusive evidence to assign these components to *C. punctatum*. The chelicerae are not known in *C. punctatum* and are also poorly known in the type species (Kjellesvig-Waering 1958). As for the disarticulated prosomal appendages II-V, again these have not directly been observed in *C. punctatum*. The species is likely to bear a close resemblance with *C. newlini*, based on the similarity of prosomal appendage VI (see Kjellesvig-Waering 1958), so therefore the walking legs are inferred to have been



equally spiniferous. Specimens BGS GSM89565 and GSM89583, inferred by Kjellesvig-Waering (1961) to represent prosomal appendage II of *C. punctatum*, due to the presence of a distinct wide, blunt spine on the podomere 2, appear to have no comparable examples in the genus (e.g. Woodward 1868a, 1872b; Kjellesvig-Waering 1958); they are therefore only tentatively retained within *Carcinosoma*.

*Occurrence.* From the Lower Leintwardine Formation, Ludlow Series, Upper Silurian of the Leintwardine area (Church Hill), Herefordshire, and possibly the Leintwardine or Whitcliffe Group, Ludlow Series of the Ludlow area, Shropshire, UK.

### *Carcinosoma* sp. 1

Plate 4.6, figures 1-3; Text-figure 4.7-8

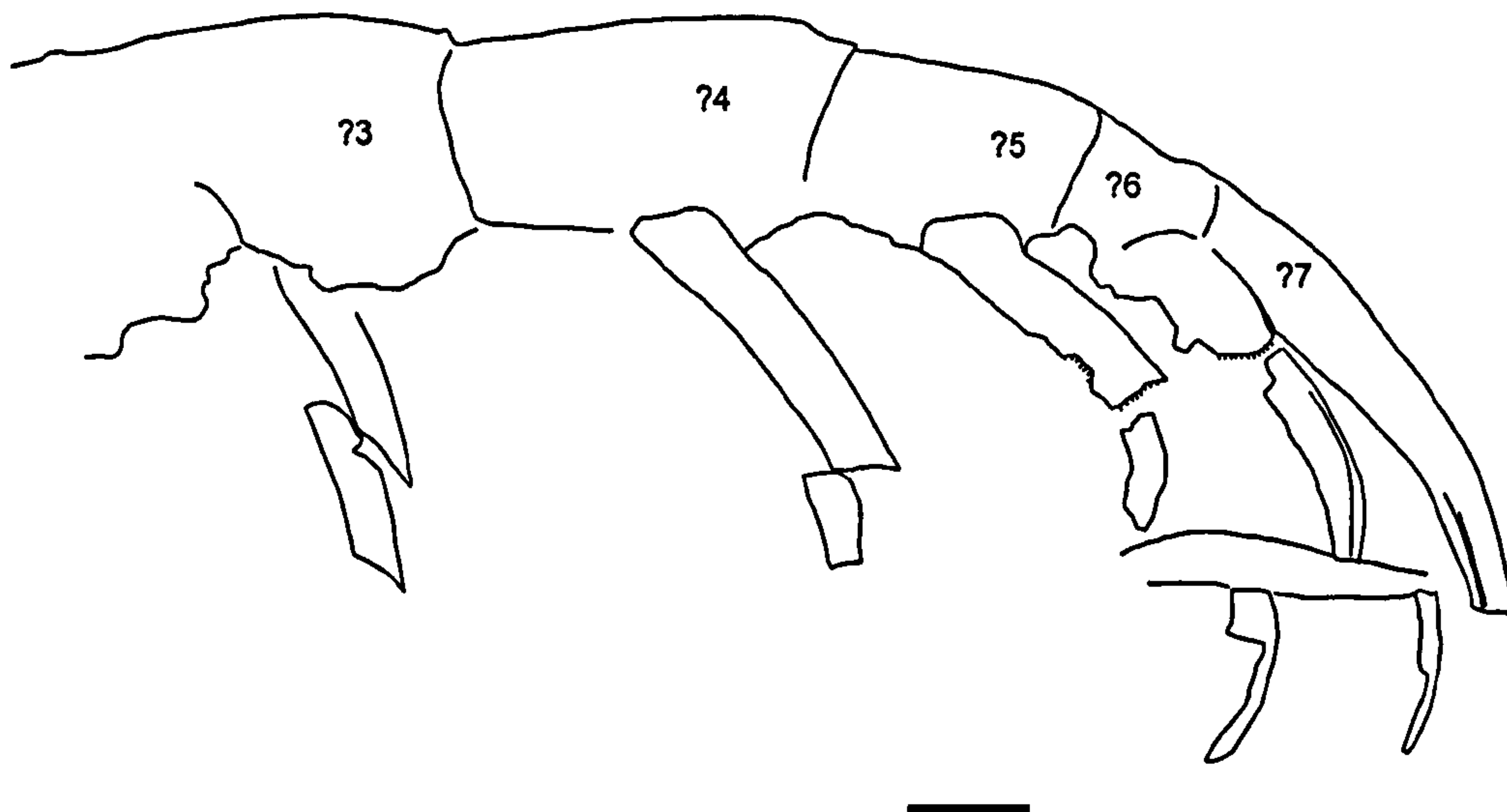
*Material.* CH146, nearly complete spiniferous prosomal appendage; BGS GSM89580, incomplete spiniferous walking appendage (Salter 1859a, pl. 11, fig. 8); GSM89590, incomplete spiniferous walking leg (Salter 1859a, pl. 11, fig. 7); BMNH In. 48405, near complete spiniferous walking leg; BMNH 39399, near complete spiniferous walking leg. All from the Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK (CH146 and BGS GSM89580 originate from Church Hill).

*Description.* Prosomal appendage (III, IV or V) spiniferous, with single pair of spines on each podomere. Spines long, slightly curved. Podomeres robust, subquadrate. Terminal podomere consists of a single spine.

*Remarks.* Comparison with other described species of *Carcinosoma*, confirms that specimens can be assigned to the genus. Tollerton (1989) described the *Carcinosoma*-type walking leg as showing a single, long spine on each podomere. CH146, a newly collected specimen, reveals that each podomere is likely to possess a pair of spines. Størmer (1974) stated that each podomere in *Carcinosoma* generally possesses a single pair of spines although sometimes two pairs may be present, as described in *C. newlini* by Kjellesvig-Waering (1958).

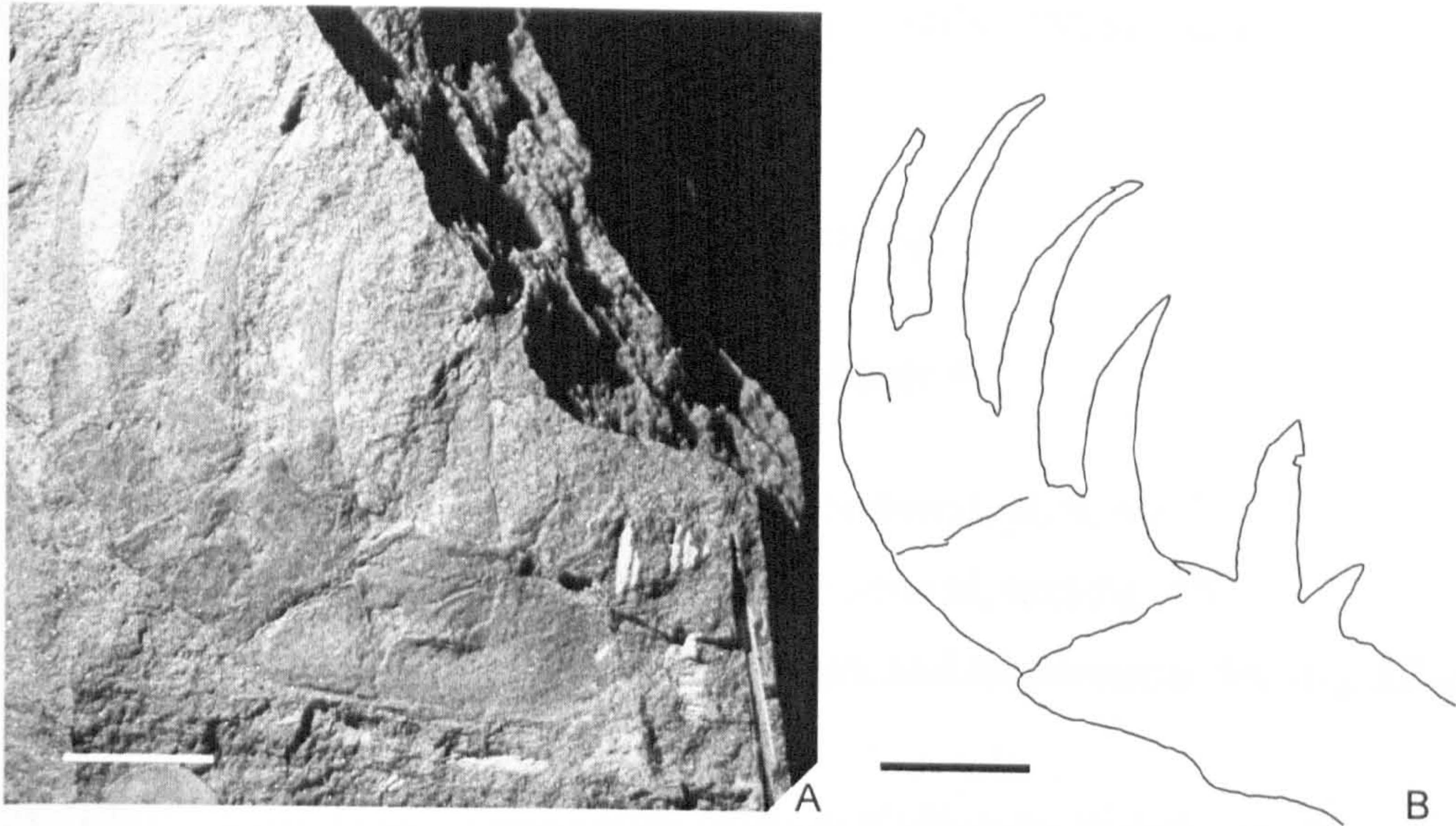
Specimen CH147 is incomplete and preserves the distal podomeres (c. podomere 4 onwards). It is not possible to ascertain precisely which prosomal appendage the





TEXT-FIG. 4.7. Interpretive drawing of spinose prosomal appendage of *Carcinosoma* sp. 1, showing tentative numbering of distal podomeres (CH146a). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. Refer to plate 4.6, figure 1. Scale bar represents 10 mm.





TEXT-FIG. 4.8. Prosomal appendage of *Carcinosoma* sp. 1 (BMNH In. 48405). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. A, detail of appendage. B, interpretive drawing of appendage, showing characteristic spinose morphology. Scale bars represent 10 mm.



specimen represents; based on comparison with relatively complete *Carcinosoma* specimens (e.g. Woodward 1872a; Kjellesvig-Waering 1958), the specimen represents appendage III, IV or V.

*Carcinosoma* sp. 2

Plate 4.6, figure 4

- v. 1868b *Eurypterus punctatus* Salter; Woodward, pl. 9, fig. 2.
- v. 1872a *Eurypterus punctatus* Salter; Woodward, text-fig. 50.
- v. 1912 *Eurypterus punctatus* Salter; Clark and Ruedemann, text-fig. 52 (cop. Woodward 1868a).
- v. 1961 *Carcinosoma punctatum* (Salter); Kjellesvig-Waering, p. 30.

*Material.* BMNH 59222, metastoma (Woodward 1868b, pl. 9, fig. 2; Woodward 1872a, text-fig. 50; Clark and Ruedemann 1912, text-fig. 52). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK.

*Description.* Metastoma shield-shaped, wide, broadly concave anteriorly, narrowly rounded posteriorly, with sigmoidal sides, length 125 mm, width 99 mm.

*Remarks.* The metastoma of *Carcinosoma* is relatively poorly known. Comparison with the metastoma of *C. newlini* cannot be undertaken as the plate is poorly preserved in this species (Kjellesvig-Waering 1958). However, specimen BMNH 59222 is retained within the genus, due to its similar shield-shaped outline to that of *C. scorpioides* (Woodward 1872a, pl. 30, fig. 9). This character shows interspecific variation; the metastoma of *C. scorpioides* has less sinusoidal sides and the posterior portion of the plate is also pointed. *C. libertyi* has a rounded, heart-shaped metastoma (Copeland and Bolton 1960, pl. 2, fig. 1; text-fig. 7), further suggesting that this character may be variable. Kjellesvig-Waering (1961) remarked that the length of the plate (130 mm), indicates that the length of this complete Leintwardine eurypterid would have been approximately two metres.



*Carcinosoma* sp. 3

## Plate 4.6, figure 5

**Material.** BMNH In. 43811, incomplete proximal portion of prosomal appendage VI (counterpart to BGS GSM89592, see Salter 1859a, pl. 11, fig. 13). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

**Description.** Prosomal appendage VI with large podomere 7 paddle. Podomere 7 c. 37 mm in width.

**Remarks.** The specimen, 80 mm in length, is incomplete, preserving podomeres 4 to 7; only the proximal most portion of podomere 7 is preserved. It is retained within the genus owing to its similarity in overall morphology and size with specimen BMNH In. 43804 (Pl. 4.5, figs 1-2). The width of podomere 7 in both specimens is very similar. It is possible that BMNH In. 43811 belongs to *C. punctatum*, although since the diagnostic distal end of the appendage is not preserved, species identification cannot be undertaken.

*Carcinosoma?* sp. 1

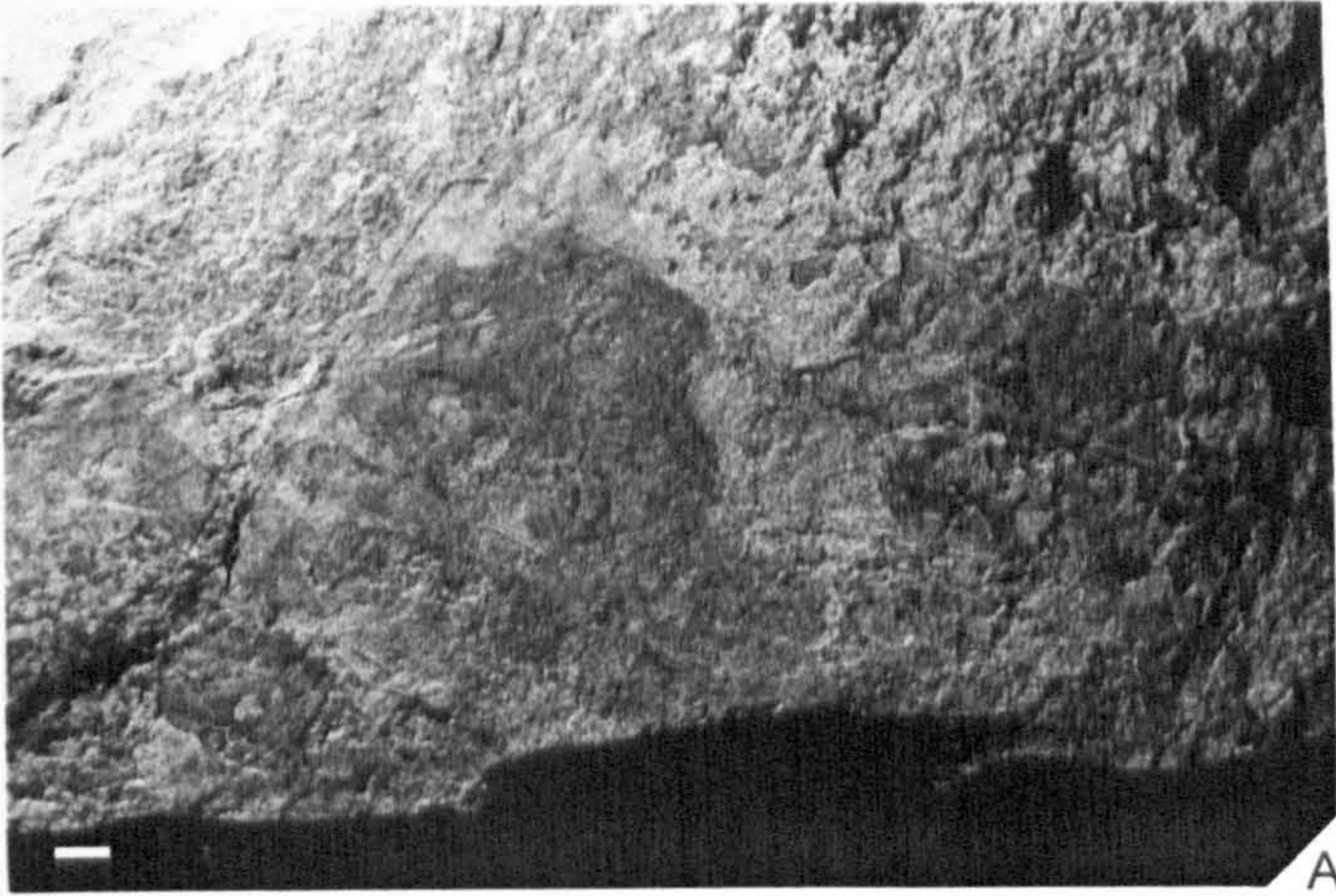
## Text-figure 4.9

**Material.** CH147, semi-articulated opisthosoma. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

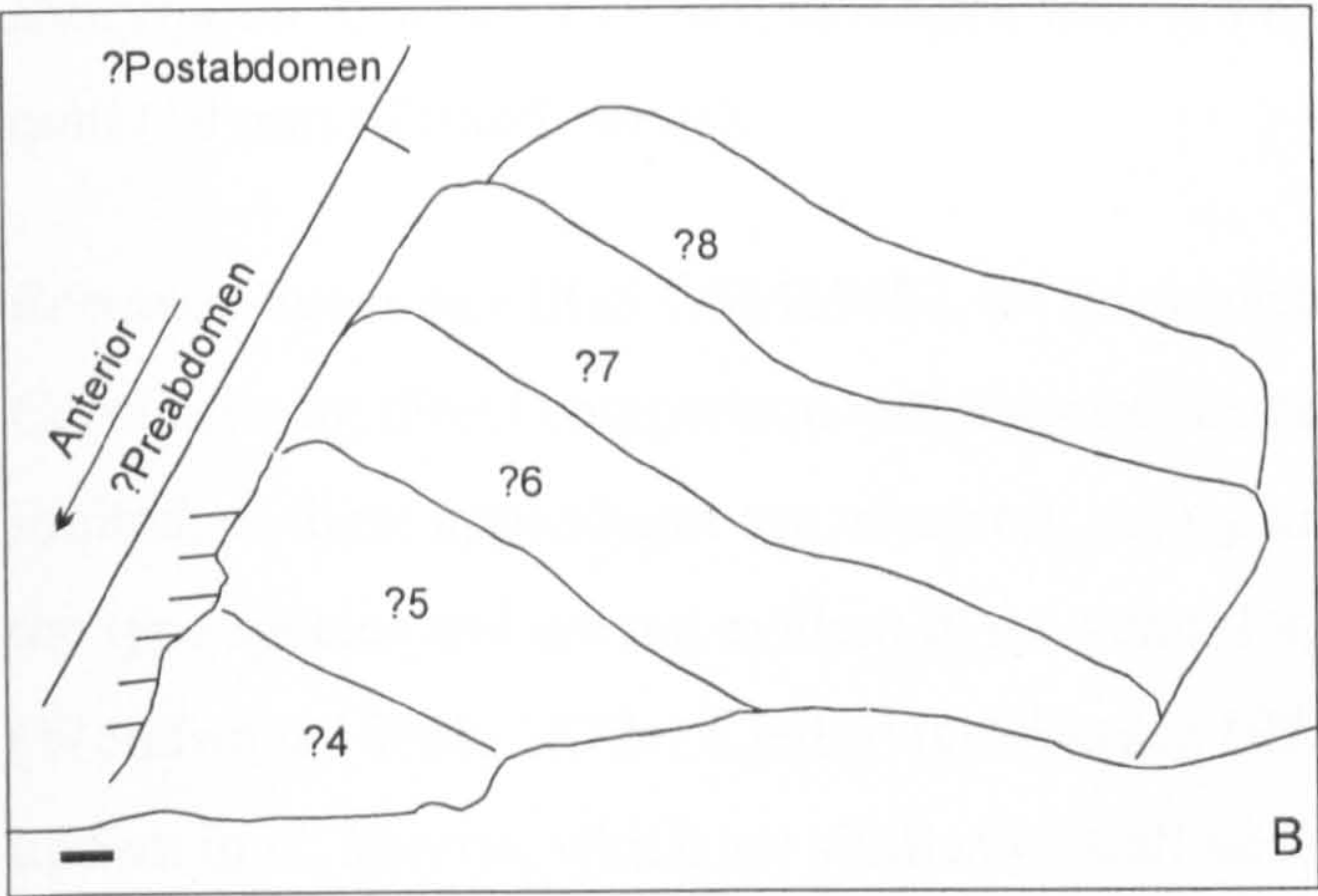
**Description.** Opisthosoma shows a first order differentiation into a preabdomen and postabdomen. Preabdomen width: 175 mm (measured at midsection of last preadominal tergite). Postabdomen width: 155 mm (measured at midsection of first postabdominal tergite).

**Remarks.** The specimen, the first documented semi-articulated opisthosoma from Leintwardine, is incomplete, comprising tergites 4-7 (preabdomen) and 8 (postabdomen). Vestiges of an ornament of small rounded tubercles, which may be characteristic of the genus, occur in a few places over the tergites.





TEXT-FIG. 4.9. Semi-articulated opisthosoma of *Carcinsoma?* sp. 1 (CH147); five articulated tergites are preserved. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. A, detail of specimen. B, interpretive drawing, showing possible first order differentiation of the abdomen, characteristic of the genus. Scale bars represent 10 mm.





*Carcinosoma?* sp. 2

## Plate 4.7, figure 1

v. 1961 *Carcinosoma punctatum* (Salter); Kjellesvig-Waering, p. 829, text-fig. 3.42.

**Material.** BGS GSM89581, incomplete chelicera (Kjellesvig-Waering 1961, text-fig. 3.42). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

**Description.** Chelicera 29 mm in length, with toothless slender distal extensions of rami (10 mm of fixed ramus).

**Remarks.** Specimen BGS GSM89581, an incomplete chelicera is tentatively referred to *Carcinosoma*; direct comparison with the chelicerae of other *Carcinosoma* species is limited, as these appendages are relatively poorly known. Chelicerae are not known in the type species and are not evident in the ventral morphology of *C. scorpioides* (Woodward 1868b, 1872a; Kjellesvig-Waering 1958). However, the chelicerae are known in *C. libertyi*, which are similarly small and pincer-like (Copeland and Bolton 1960, pl. 2, fig. 3; text-fig. 7). Though indicating the suborder Eurypterina, based on the small simple rami, lacking teeth (Caster and Kjellesvig 1964; Tollerton 1989), these features of BGS GSM89581 are not diagnostic of *Carcinosoma* alone. The chelicerae in the carcosomatid, *Paracarcinosoma scorpionis* (Grote and Pitt, 1875) have a similar broad, short morphology (Clarke and Ruedemann 1912, pl. 32). Braddy *et al.* (2002) described broad and short chelicerae from the Vietnamese Upper Silurian carcosomatid, *Rhinocarcinosoma dosonensis* Braddy, Selden and Truong, 2002, which are likely to be similar to those of *Carcinosoma*. The abundance of associated *Carcinosoma* specimens suggests that this specimen can tentatively be assigned to the genus.

The relatively large size of the chelicera, in comparison with those of *C. libertyi*, which are 2.5 mm in length (Copeland and Bolton 1960), suggests that the Leintwardine carcosomatids attained a considerable size.



*Carcinosoma?* sp. 3

Plate 4.7, figures 2-3, 5, 7; Text-figure 4.10

v. 1961 *Carcinosoma punctatum* (Salter); Kjellesvig-Waering, p. 829, text-fig. 3.44-45.

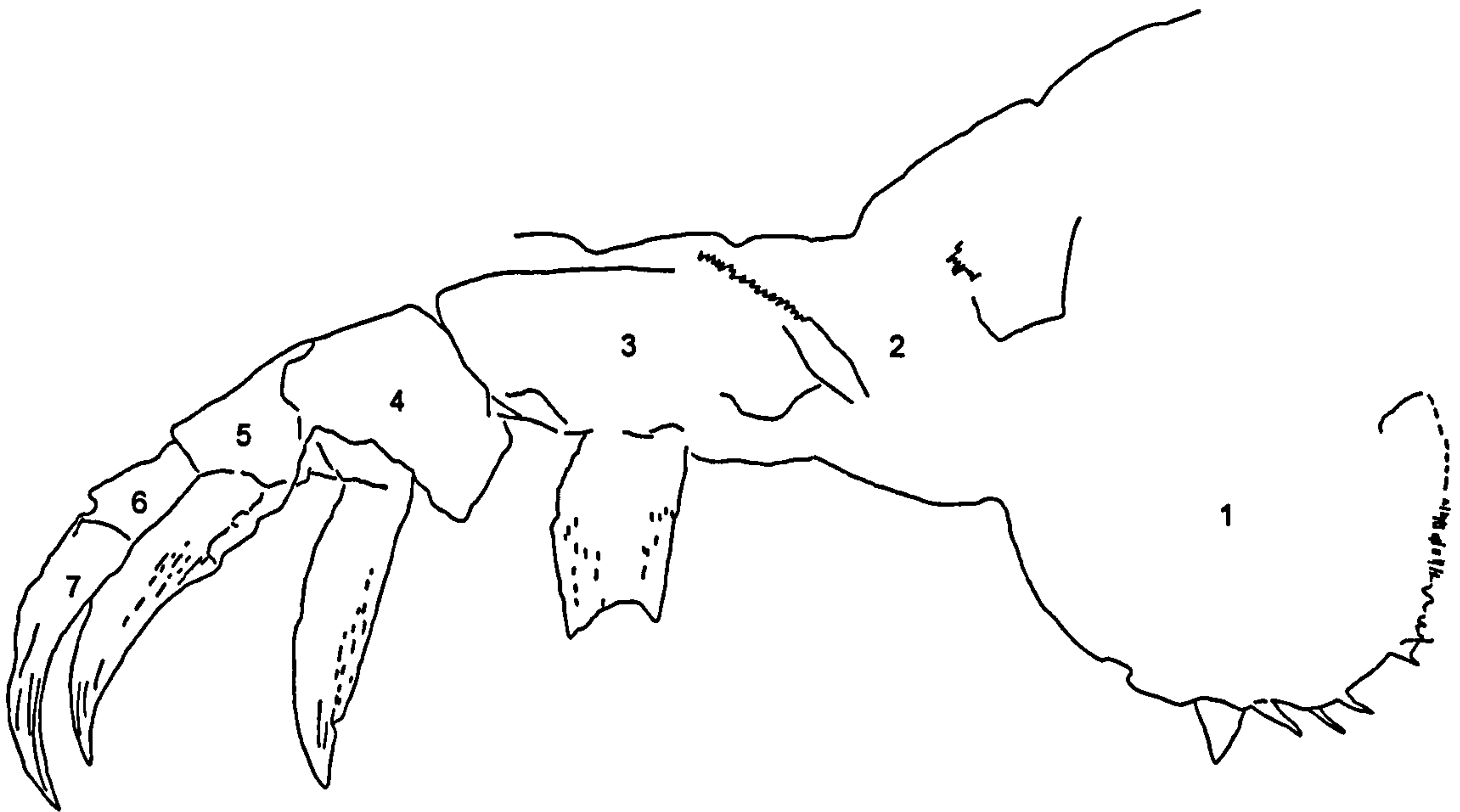
*Material.* BGS GSM89565, complete spiniferous prosomal appendage (Kjellesvig-Waering 1961, text-fig. 3.44); GSM89583, incomplete spiniferous prosomal appendage (Kjellesvig-Waering 1961, text-fig. 3.45). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Leintwardine, Herefordshire, UK. BGS GSM89565 originates from Church Hill.

*Description.* Prosomal appendage ?II with seven podomeres, 53-68 mm in length, spiniferous, with one (?or two) spines per podomere 2-7, with rounded podomere 1. Spines long, slightly curved on podomeres 4-7 (BGS GSM89565). Podomere 1 with distal large triangular tooth, with smaller proximal teeth directed posteriorly. Podomere 2 with minute teeth-like serrations along distal edge. Podomere 3 with relatively wide (5-7 mm maximum width) rounded spine (blunted distally on BGS GSM89583). Podomere 7 consists of a single spine.

*Remarks.* Kjellesvig-Waering (1961) interpreted these specimens as prosomal appendage II of *C. punctatum*, representing the first walking leg. Comparison with prosomal appendages of well-preserved eurypterid taxa shows appendage II to consistently comprise seven podomeres (e.g. *Baltoeurypterus tetragonophthalmus* (Fischer, 1839), *C. newlini*, *Lanarkopterus dolichoschelus* (Størmer, 1936), *Mixopterus kiaeri* Størmer, 1934; see Størmer, 1934; Kjellesvig-Waering 1958; Ritchie 1968; Selden 1981). These two specimens are therefore retained as prosomal appendage II, following Kjellesvig-Waering (1961).

Both specimens have a relatively wide, rounded spine on podomere 3. The spine on BGS GSM 89565 is incomplete, not preserving the distal portion so its shape cannot be unequivocally ascertained (Pl. 4.7, fig. 3). That of BGS GSM89583 is more completely preserved, revealing the spine to be relatively blunted distally (Pl. 4.7, fig. 7). Kjellesvig-Waering (1961, p. 829) described this spine as being “unusually stout” in





TEXT-FIG 4.10. Camera lucida drawing of spinose prosomal appendage II of *Carcinosoma?* sp. 3. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK. showing seven podomeres; possible modified spine is present on podomere 3 (BGS GSM89565). Refer also to plate 4.7, figures 2-3. Scale bar represents 10 mm.



both specimens. These spines may be sexually dimorphic, as observed in comparable modified spines in other taxa such as *B. tetragonophthalmus* and *M. kiaeri* (Størmer 1934; Selden 1981). Kjellesvig-Waering (1961) suggested that this distinct spine on podomere 3 may have had a clasping function, such as inferred for spine structures on appendage II or III in *B. tetragonophthalmus* and *M. kiaeri* (Størmer 1934; Selden 1981; Braddy and Dunlop 1997). Comparable short spine structures are seen on podomere 3 of appendage II in *M. kiaeri*, which were suggested to have been adapted for clasping during mating (Størmer 1934; Hanken and Størmer 1975). Modified spine structures have not been documented in *C. newlini* or any other species of *Carcinosoma* (e.g. Woodward 1872a; Kjellesvig-Waering 1958). However, appendage II of *C. newlini* is not illustrated in its entirety by Kjellesvig-Waering (1958, text-fig. 1) and the figures by Clarke and Ruedemann (1912, pls 37-38) do not show the appendage morphology in sufficient detail. Therefore it cannot be unequivocally ascertained if a comparable short, blunt spine is present on podomere 3. Woodward's (1872a, pls 29-30) figures of *C. scorpioides* do not clearly show the morphology of the appendage. Prosomal appendage II is known only by the coxa in *C. libertyi* (Copeland and Bolton 1960, pl. 2).

If the modified spines are interpreted to be sexually dimorphic, then they may not have been present in the dimorph of *C. newlini* described by Kjellesvig-Waering (1958). This specimen of *C. newlini* possesses a type A genital appendage which, following the classification of Braddy and Dunlop (1997) may be interpreted as female. If this specimen is indeed female and the short, blunt spine structures are interpreted as having a clasping adaptation during mating, then they may not have been present. Insufficient data is available to aid comparison with appendage II of other species of *Carcinosoma* (e.g. *C. harleyi*, *C. libertyi*, *C. scorpioides*, *C. spiniferum*; see Woodward 1872a; Copeland and Bolton 1960; Kjellesvig-Waering 1961; Copeland 1962; Kjellesvig-Waering and Heubusch 1962). As these structures may show variation due to sexual dimorphism, further comparative material is needed to unequivocally determine the affinity of the Leintwardine specimens; they are therefore tentatively retained within *Carcinosoma*.



*Carcinosoma?* sp. 4

## Plate 4.7, figure 6

*Material.* BMNH In. 48412, near complete spiniferous walking leg (counterpart to BMNH 4164). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description.* Prosomal appendage ?II, incomplete, spiniferous, with spine pair on each podomere. Spines wide, long, appear rounded distally.

*Remarks.* Of the documented taxa exhibiting spiniferous prosomal appendages, this specimen most closely resembles those of *Carcinosoma*, even though the spines appear wide and blunted (see Tollerton 1989, text-fig. 8) These spines may be sexually dimorphic modified structures of prosomal appendage II, and are similar in appearance to those of BGS GSM89583 (e.g. also see *B. tetragonophthalmus* and *M. kiaeri*; Størmer 1934; Selden 1981). Alternatively this apparent morphology may be a preservational artefact, due to the dorsal orientation in which the appendage is preserved. However, another slightly larger specimen, BMNH In. 48413, also shows a similar morphology; this may suggest that the wide, rounded spines are not a preservational artefact.

## Family SLIMONIIDAE Novojilov, 1962

*Type genus.* *Slimonia* Page, 1856, by original designation.

## Genus SALTEROPTERUS Kjellesvig-Waering, 1951

1951 *Salteropterus* n. gen.; Kjellesvig-Waering, pp. 14-15.

1955 *Salteropterus* Kjellesvig-Waering; Størmer, p. 30.

1961 *Salteropterus* Kjellesvig-Waering; Kjellesvig-Waering, p. 809.

1989 *Salteropterus* Kjellesvig-Waering; Tollerton, pp. 652-653.

*Type species.* *Eurypterus abbreviatus* Salter, 1859b, by original designation, from the "Downtonian Sandstone" (=Lower Přídolí Series) of Herefordshire.



*Diagnosis.* Telson triangular, broadly trigonal anteriorly, serrated along posterior edges, with posterior long, flat median stem. Metastoma petaloid D (emended after Kjellesvig-Waering 1951 and Tollerton 1989).

*Remarks.* Kjellesvig-Waering (1961) recognised *Salteropterus abbreviatus* (Salter, 1859b) and erected *Salteropterus (?) longilabium* from the Silurian of the Welsh Borderland.

*Salteropterus? longilabium* Kjellesvig-Waering, 1961

Plate 4.8, figures 1-2

v 1859 *Pterygotus punctatus* Salter n. sp.; Salter, pl. 11, fig. 4.

1872a *Slimonia (?) acuminata* Salter 1855; Woodward, pp. 154-155.

v 1961 *Salteropterus (?) longilabium* n. sp., Kjellesvig-Waering, pp. 809-810, pl. 96, fig. 2.

*Holotype.* BMNH 39386, a complete metastoma (Salter 1859a, pl. 11, fig. 4; Kjellesvig-Waering 1961, pl. 96, fig. 2). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description.* Metastoma long (102 mm length) narrow (maximum width: 36 mm), tapering posteriorly, rounded at anterior and posterior, notched anteriorly. Ornament of U to V-shaped lunules.

*Remarks.* The assignment of this material is extremely tentative. The metastomal morphology can be described as 'petaloid D', following the terminology of Tollerton (1989). Kjellesvig-Waering (1961) noted that the metastoma is similar to that of *Slimonia*, although lacks the deep anterior notch of that genus (see Tollerton 1989, text-fig. 5). He added that the only genus apparently similar to *Slimonia* in the Welsh Borderland is *Salteropterus*. There is no direct evidence to assign the metastoma to *Salteropterus*, as this plate is unknown in the type species, *S. abbreviatus* (Kjellesvig-Waering 1951). Kjellesvig-Waering (1961) noted the similarity in ornament style of a fragment of undetermined cuticle from Leintwardine (BGS GSM89579) with that of *S. abbreviatus* (see Kjellesvig-Waering 1951, text-figs 2D, H; Pl. 4.8, fig. 2). If at all, this



can be used to infer an affinity to *Salteropterus*; however, there is insufficient data to assign this specimen to a species.

### Incertae familiae

Undet. sp. 1

### Plate 4.8, figures 3-5

*Material.* CH144, incomplete prosoma. Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

*Description.* Prosoma semicircular, length (anterior-posterior) 35 mm, width 78 mm, with lateral angle of 120 degrees, with ornament of minute tongue-shaped tubercles. Eyes circular, 3.5 mm in diameter, antelaterally to centrilaterally positioned. Ocelli large, circular, 2 mm in diameter.

*Remarks.* The shape of the eyes does not conform to the classification outlined by Tollerton (1989), although they may possibly be crescentic; this ambiguity may be a preservational artefact. This is the first documented eurypterid prosoma from Leintwardine. Based on the length to width ratio and lateral angle, the prosoma is described as semicircular in shape, following Tollerton (1989). In appearance the prosoma is slightly trapezoid, showing some angularity at its antelateral margins. According to Tollerton's (1989) classification, the prosomal shape does not resemble that of *Pterygotus* (trapezoid), *Erettopterus* (subquadrate) or *Carcinosoma* (triangular). The position of the eyes in particular, dismisses the possibility of it belonging to any of the aforementioned taxa, as these possess marginal antelaterally positioned eyes (e.g. Clarke and Ruedemann 1912; Størmer 1955; Kjellesvig-Waering 1958, 1964). Comparison with Kjellesvig-Waering's (1961) other documented taxa of the Upper Silurian of the Welsh Borderland reveals the prosoma to most resemble that of *Eurypterus cephalaspis* (Salter in Burmeister, 1846) and *Parahughmilleria salteri* Kjellesvig-Waering, 1961, in terms of prosomal shape (semicircular-trapezoid) and eye position (antelateral-centrilateral). However, the eyes in these two taxa are reniform, unlike the circular, possibly crescentic form in CH144. Kjellesvig-Waering (1961) described the prosoma of *P. salteri* as being highly arched with a narrow marginal rim,



characters that are not evident in CH144. Any original arching of the prosoma may have been later removed by subsequent flattening during fossilisation. The possible form of the eyes in CH144 resemble the crescentic morphology documented in the Upper Silurian Welsh Borderland species *Stylonurus megalops* (Salter, 1859b). Kjellesvig-Waering (1951, 1961) also documented *Tarsopterella* (?) sp. from the Přídolí Series of the area; the prosoma which is only known in the type species *Tarsopterella scoticus* (Woodward, 1864) shows a crescentic eye morphology which may be similar to that of CH144 (see Woodward 1872a, pls 22-23). Further material is needed before the affinity of this specimen can be deduced. However, this does suggest that the Leintwardine deposits contain a relatively diverse assemblage of eurypterid taxa.

Undet sp. 2

Plate 4.8, figures 6-7

v. 1859a *Pterygotus arcuatus*? Salter, pl. 13, fig. 16.

**Material.** BGS GSM89603, incomplete metastoma (Salter 1859a, pl. 13, fig. 16; Woodward 1872a, text-fig. 25). Lower Leintwardine Formation, Ludlow Series, Upper Silurian; Church Hill, Leintwardine, Herefordshire, UK.

**Description.** Metastoma broadly rounded posteriorly, sides convex and converging posteriorly, 32 mm in width, with broad U-shaped lunules towards the anterior shoulders, with straight longitudinal lunules along sides.

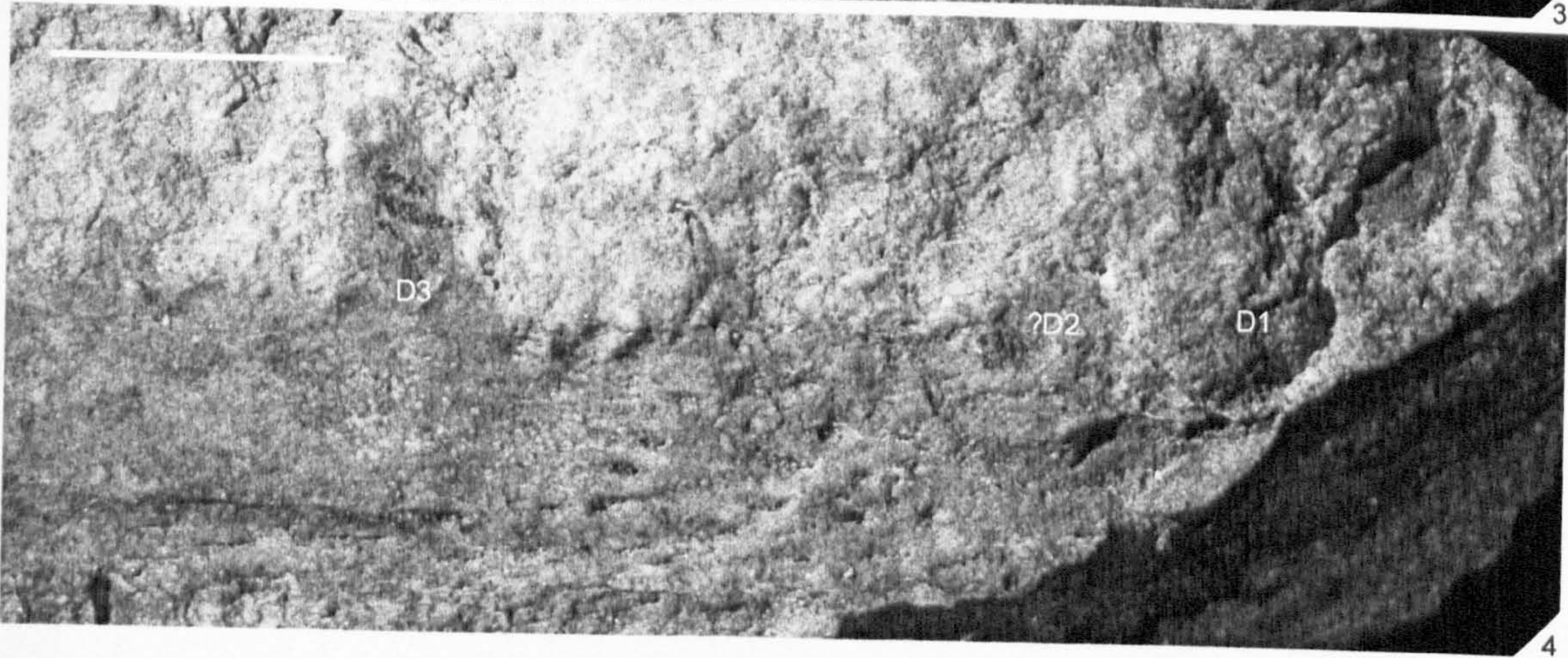
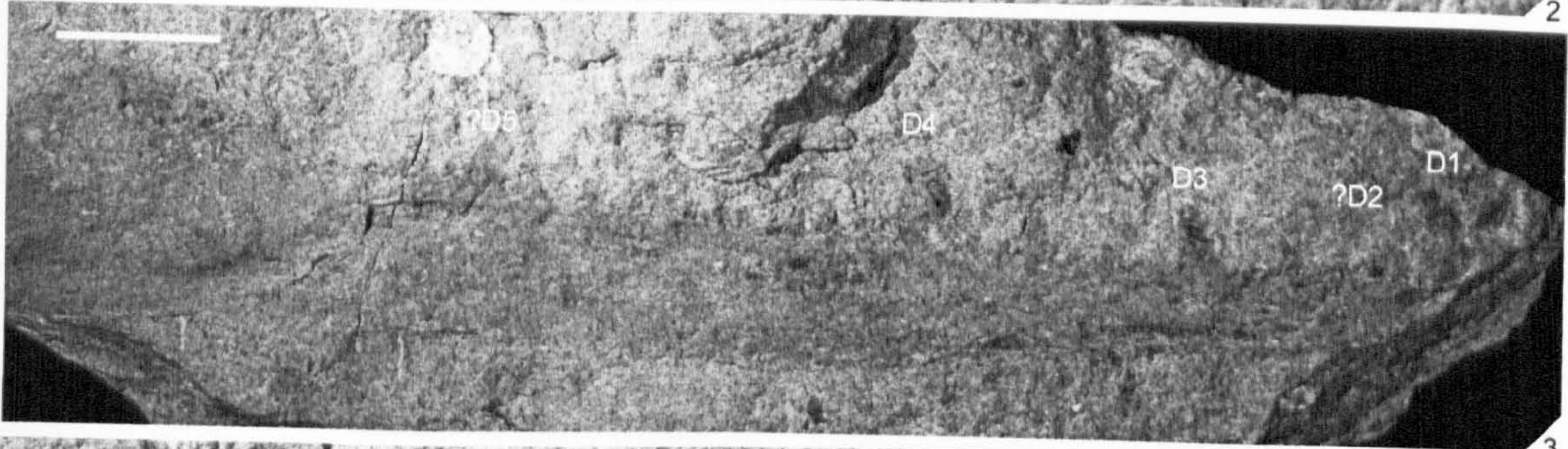
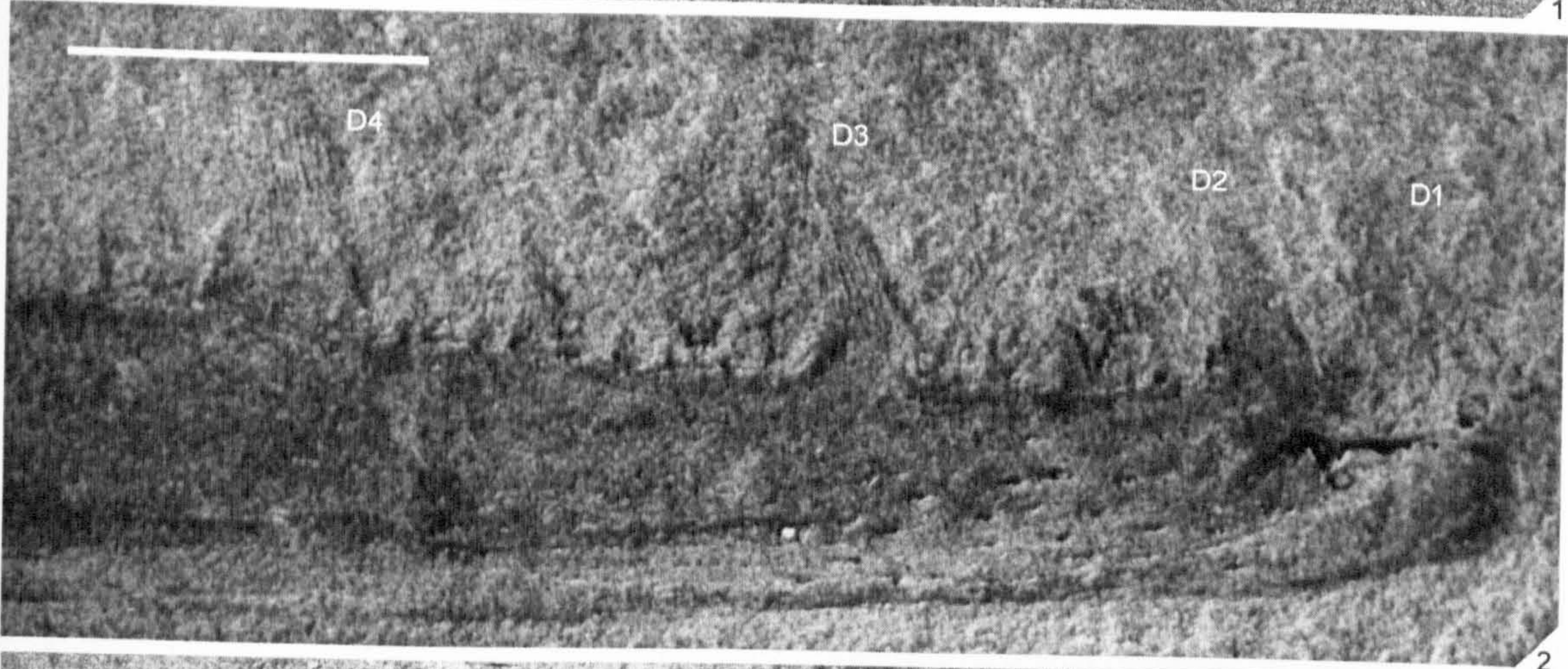
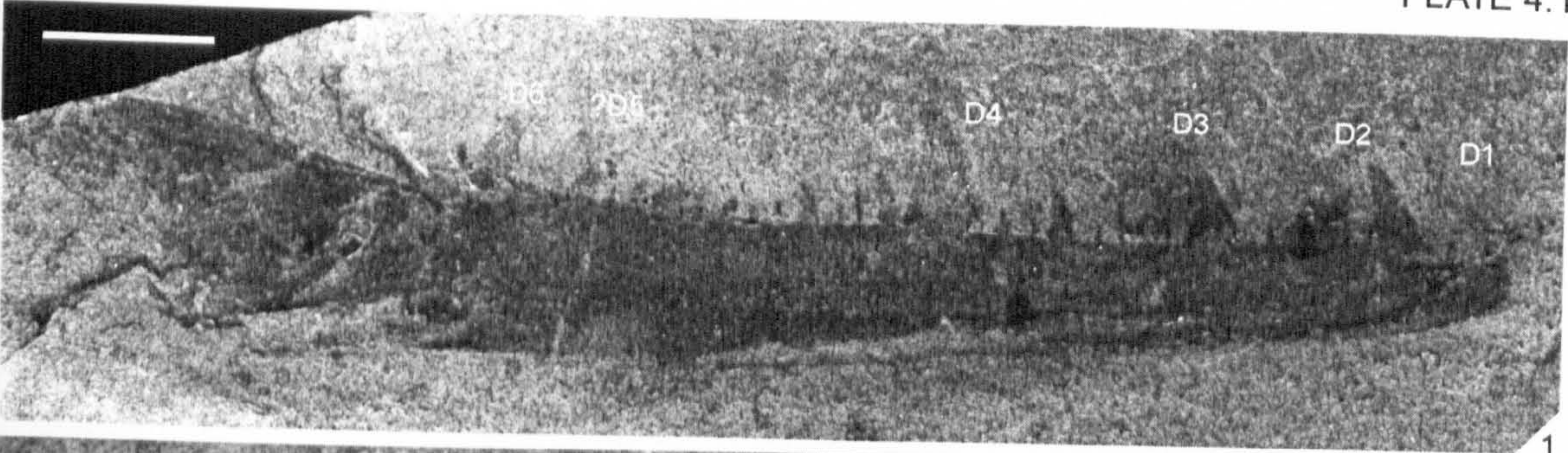
**Remarks.** As the metastoma is missing its anterior portion, it is not possible to fully ascertain its shape, and therefore suggest a generic affinity. However, it does not bear similarity to the known metastomas from Leintwardine, and is therefore likely to belong to taxon previously undescribed from the deposits. Full description awaits further specimens.



## EXPLANATION OF PLATE 4.1

Figs 1-4. *Erettopterus marstoni* Kjellesvig-Waering, 1961; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 1-2, BMNH In. 43790, holotype, free ramus; scale bar represents 10 mm. 1, entire specimen. 2, detail of distal portion of ramus showing teeth D1-D4. 3-4, BMNH In. 43805, paratype, fixed ramus. 3, entire specimen with incomplete distal termination; scale bar represents 10 mm. 4, detail of distal portion showing teeth D1-D3; scale bar represents 5 mm.







## EXPLANATION OF PLATE 4.2

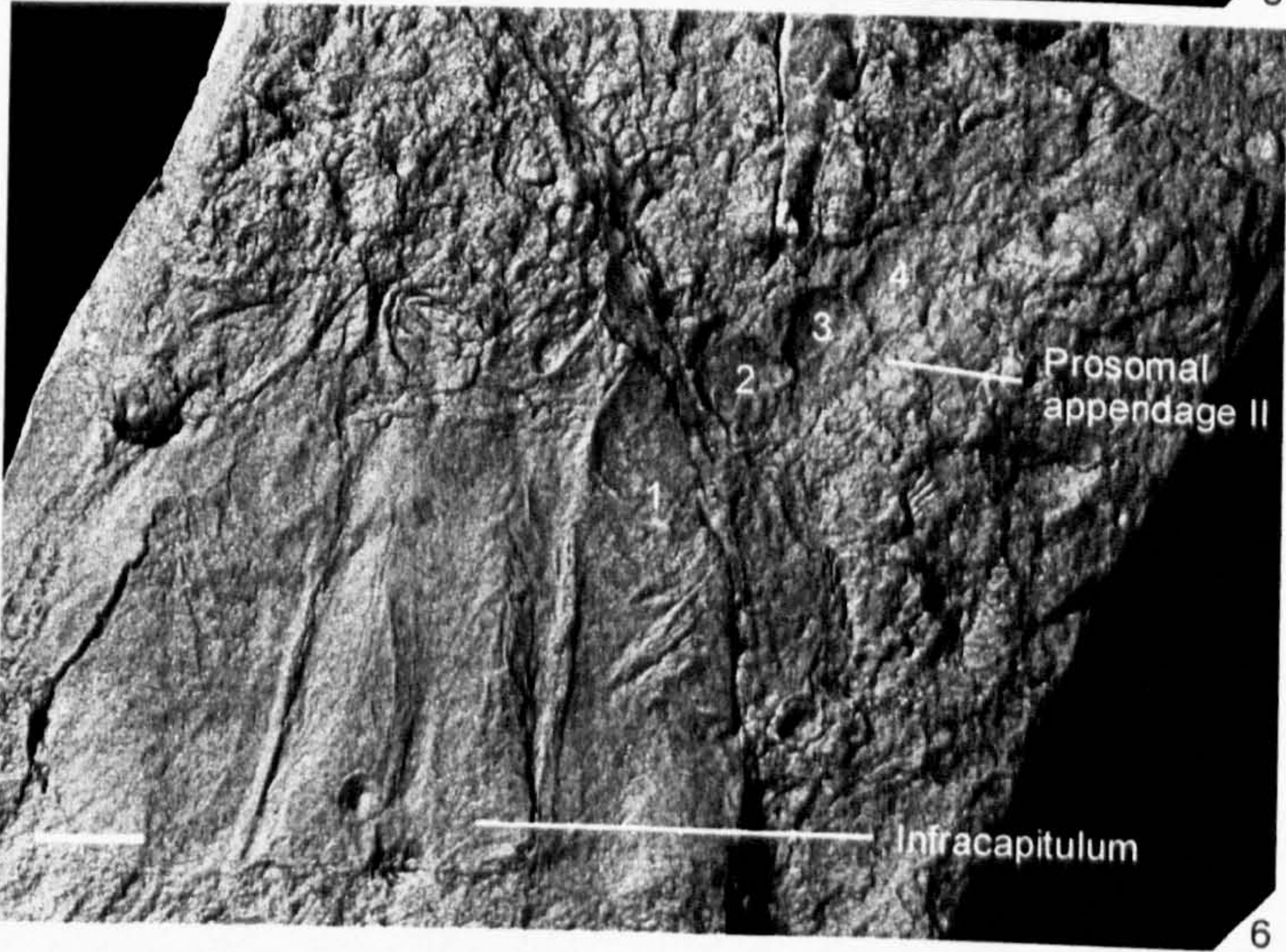
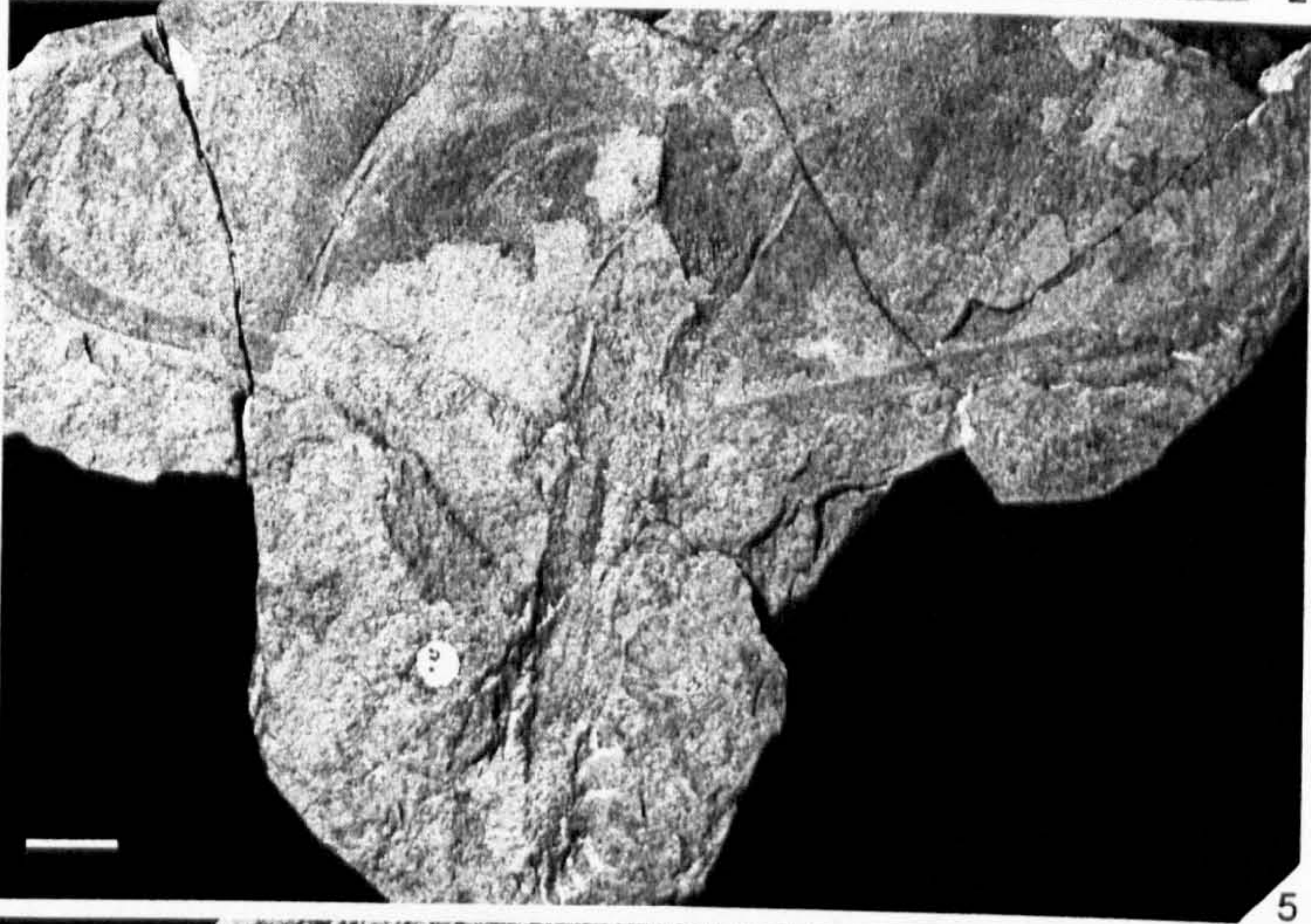
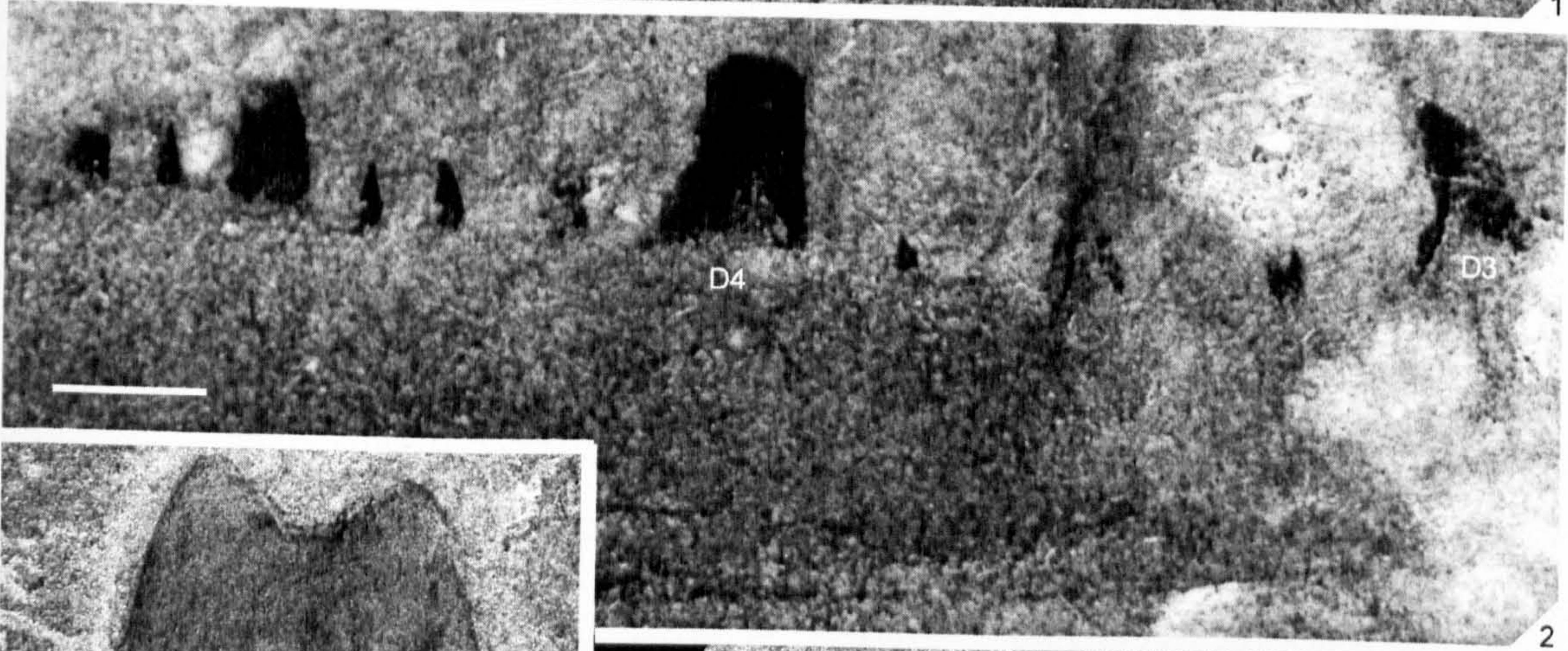
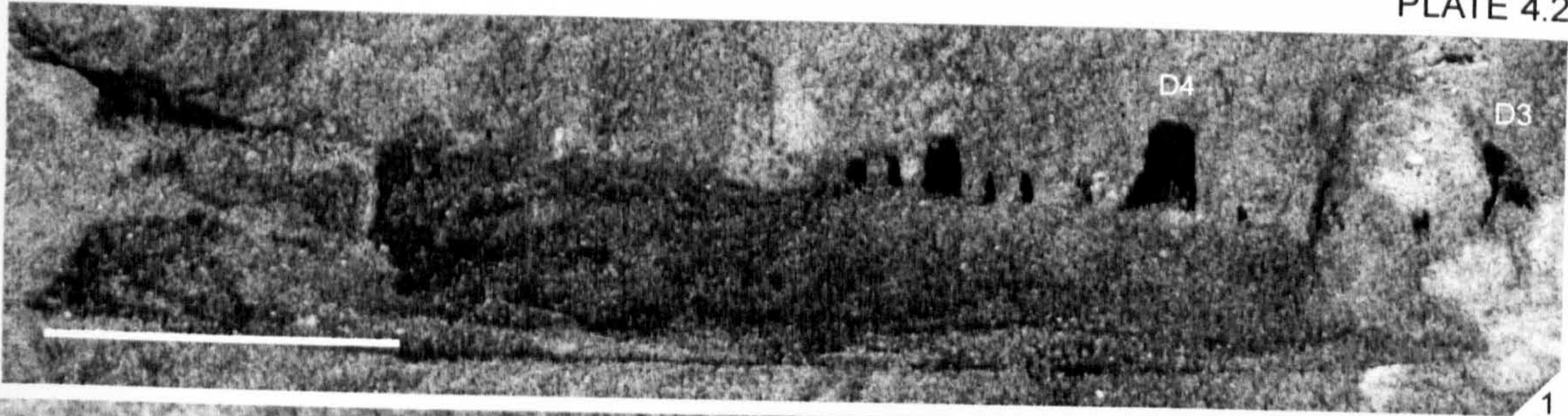
Figs 1-2. *Erettopterus marstoni* Kjellesvig-Waering, 1961; BMNH 39394, free ramus; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 1, entire specimen showing incomplete distal termination; scale bar represents 10 mm. 2, detail of tooth bearing portion showing terminal teeth D3-D4; scale bar represents 2 mm.

Figs 3-4. *Erettopterus?* sp. 1; metastomas; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bars represent 10 mm. 3, BMNH 39396, entire specimen showing obovate shape. 5, BGS GSM89601, possibly counterpart to 4.

Fig. 5. *Erettopterus?* sp. 2; BGS GSM89599, genital appendage type A; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bar represents 10 mm.

Fig. 6. Undet. pterygotid; BMNH In. 43786, infracapitulum and prosomal appendage II; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 10 mm.



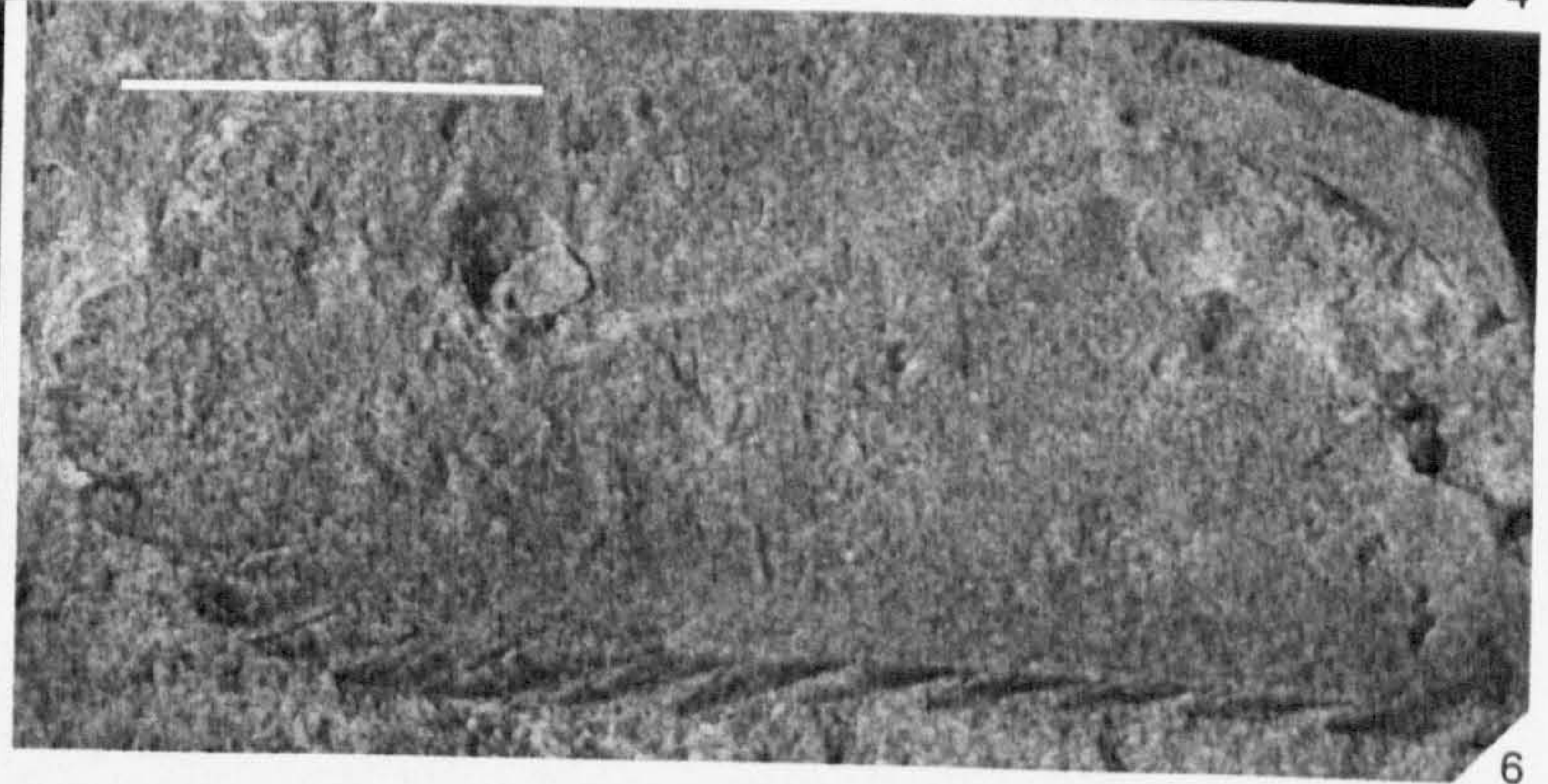
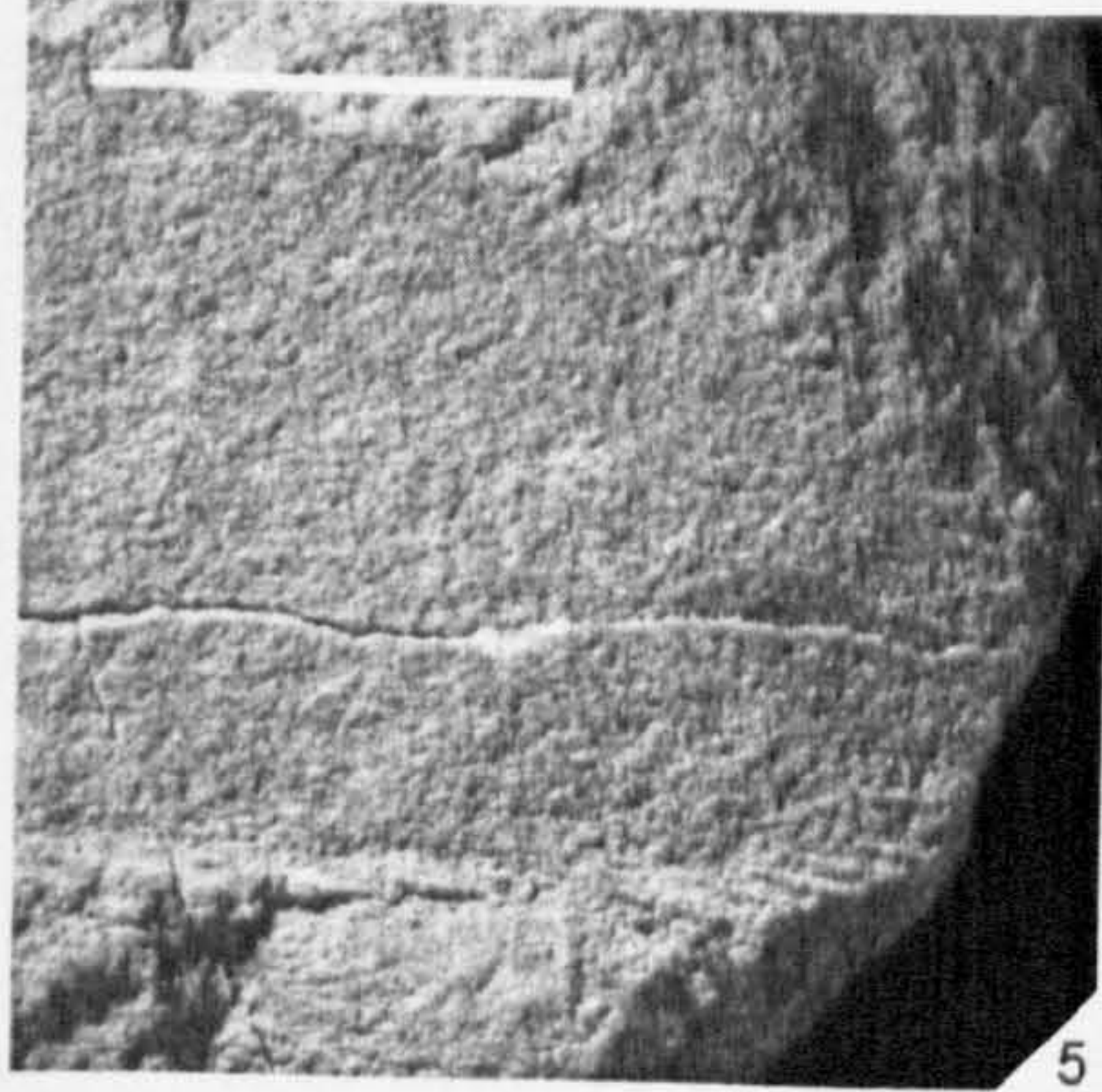
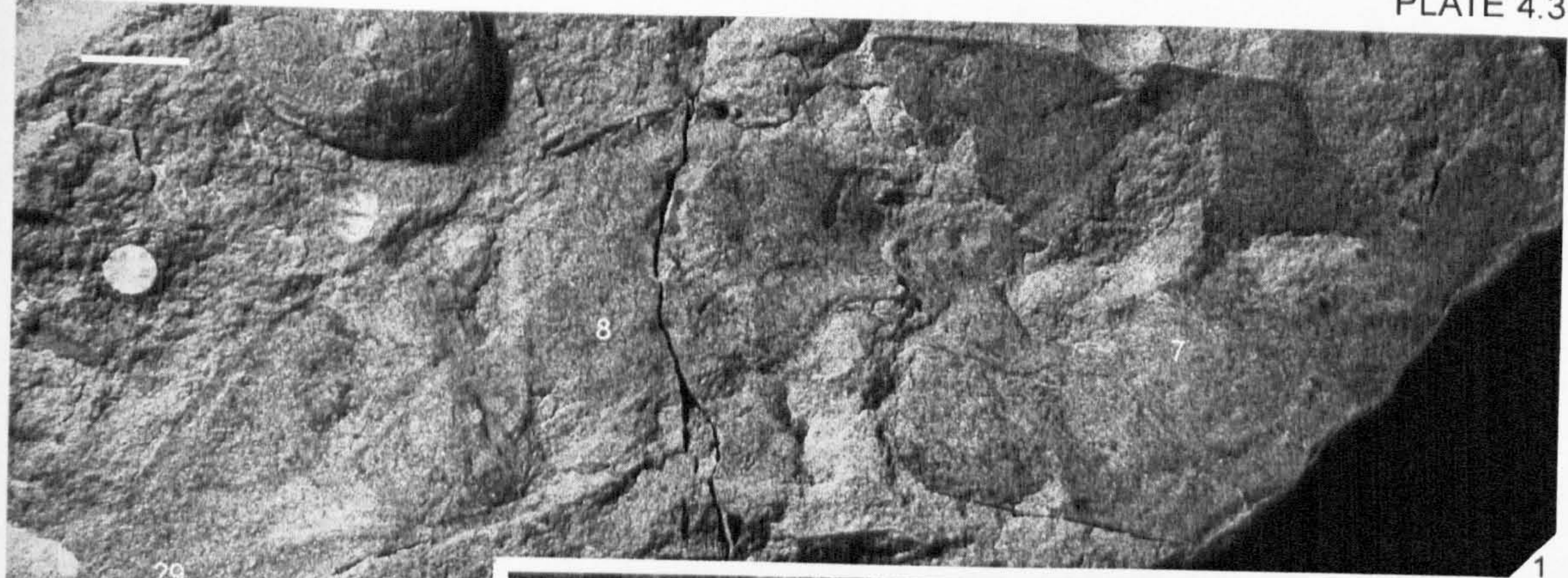




### EXPLANATION OF PLATE 4.3

Figs 1-6. *Carcinosoma punctatum* (Salter, 1859). 1-3, BGS GSM89435, ?lectotype, distal podomeres of prosomal appendage VI; Leintwardine Group or Whitcliffe Group; Leintwardine, Herefordshire or Ludlow, Shropshire. 1, entire specimen showing podomeres 7-?9; scale bar represents 10 mm. 2, detail of diagnostic deep serration; scale bar represents 5 mm. 3, detail of marginal serration; scale bar represents 10 mm. 4-5, BGS GSM89561, nearly complete prosomal appendage VI; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 4, entire specimen (podomeres proximal to podomere 6 are unclear); scale bar represents 10 mm. 5, detail of marginal serration on distal podomeres; scale bar represents 5 mm. 6, BGS GSM89568, distal podomere(s) of prosomal appendage VI; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 10 mm.



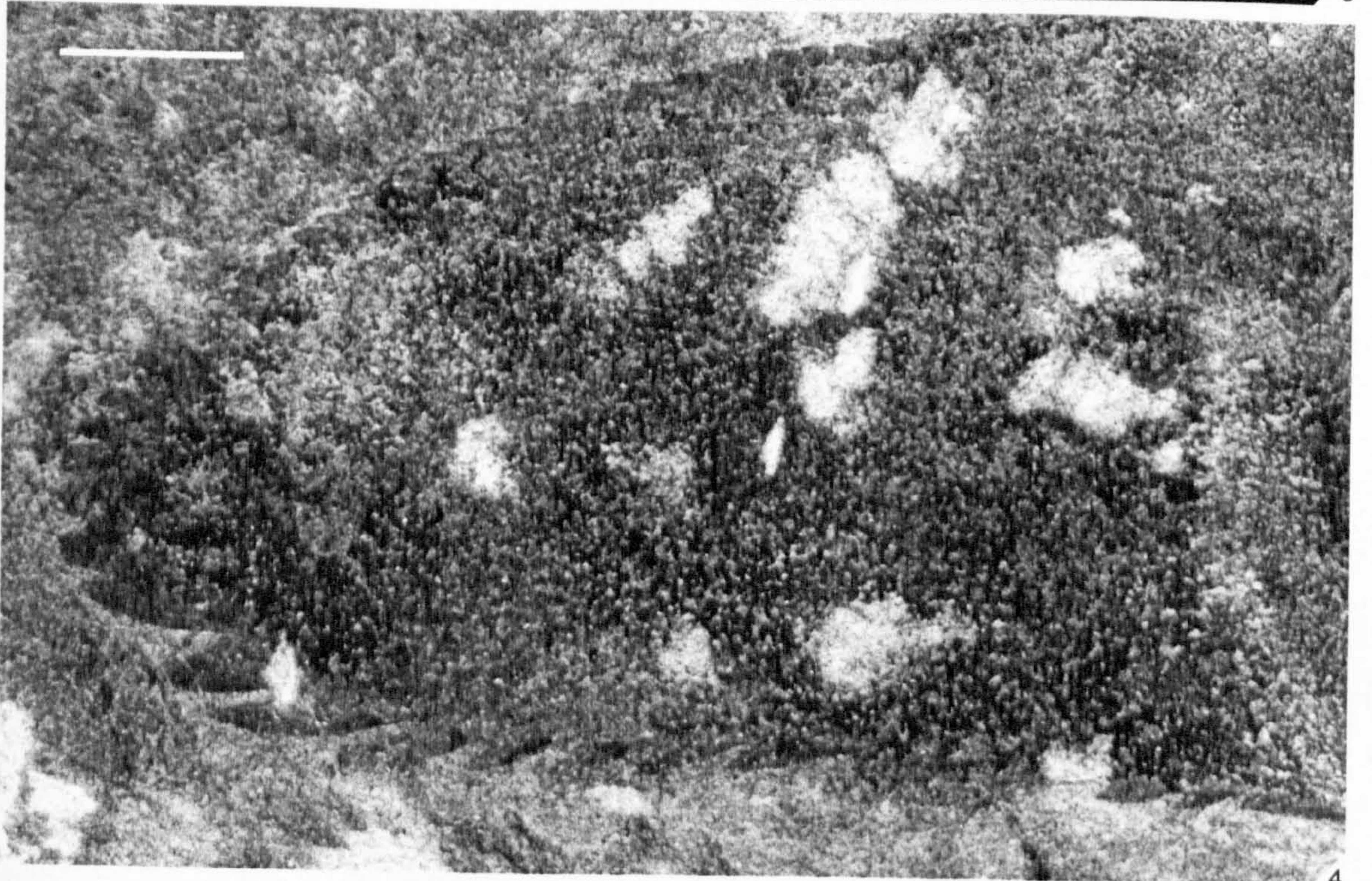
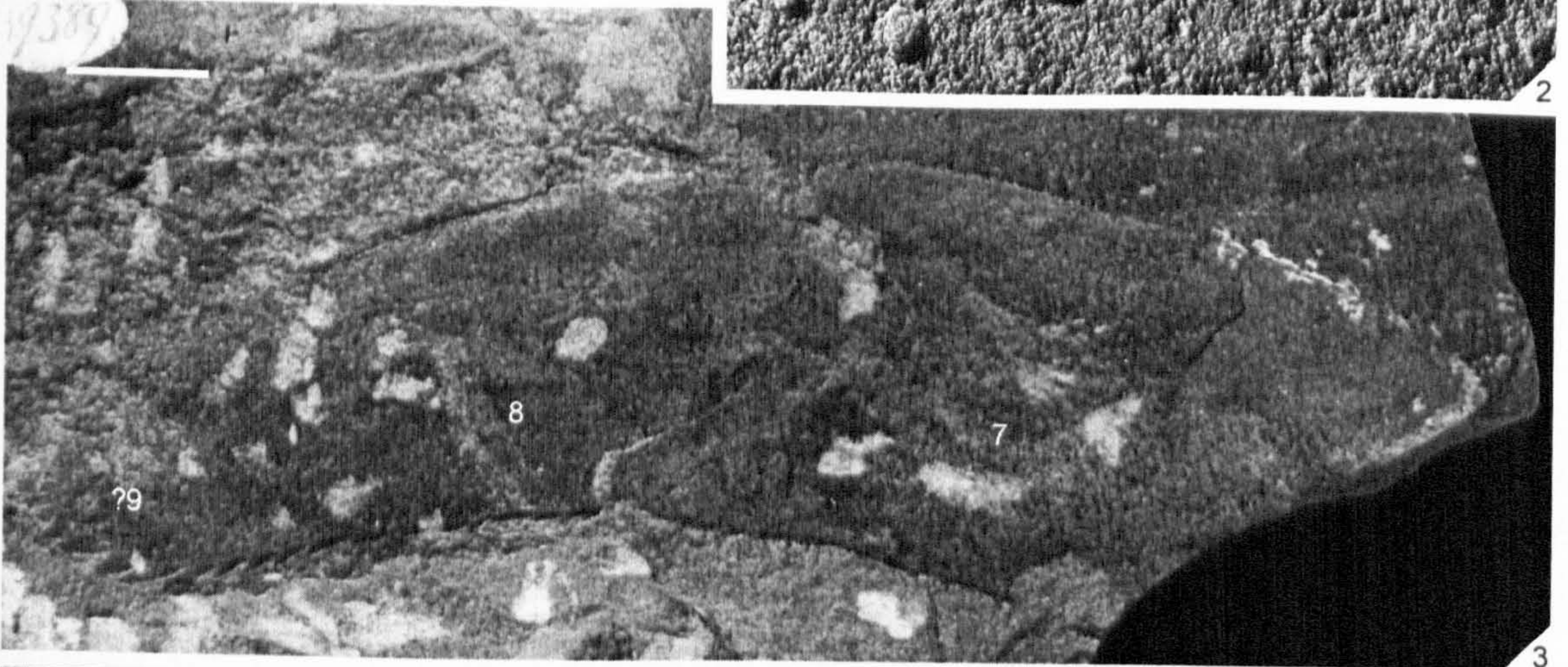
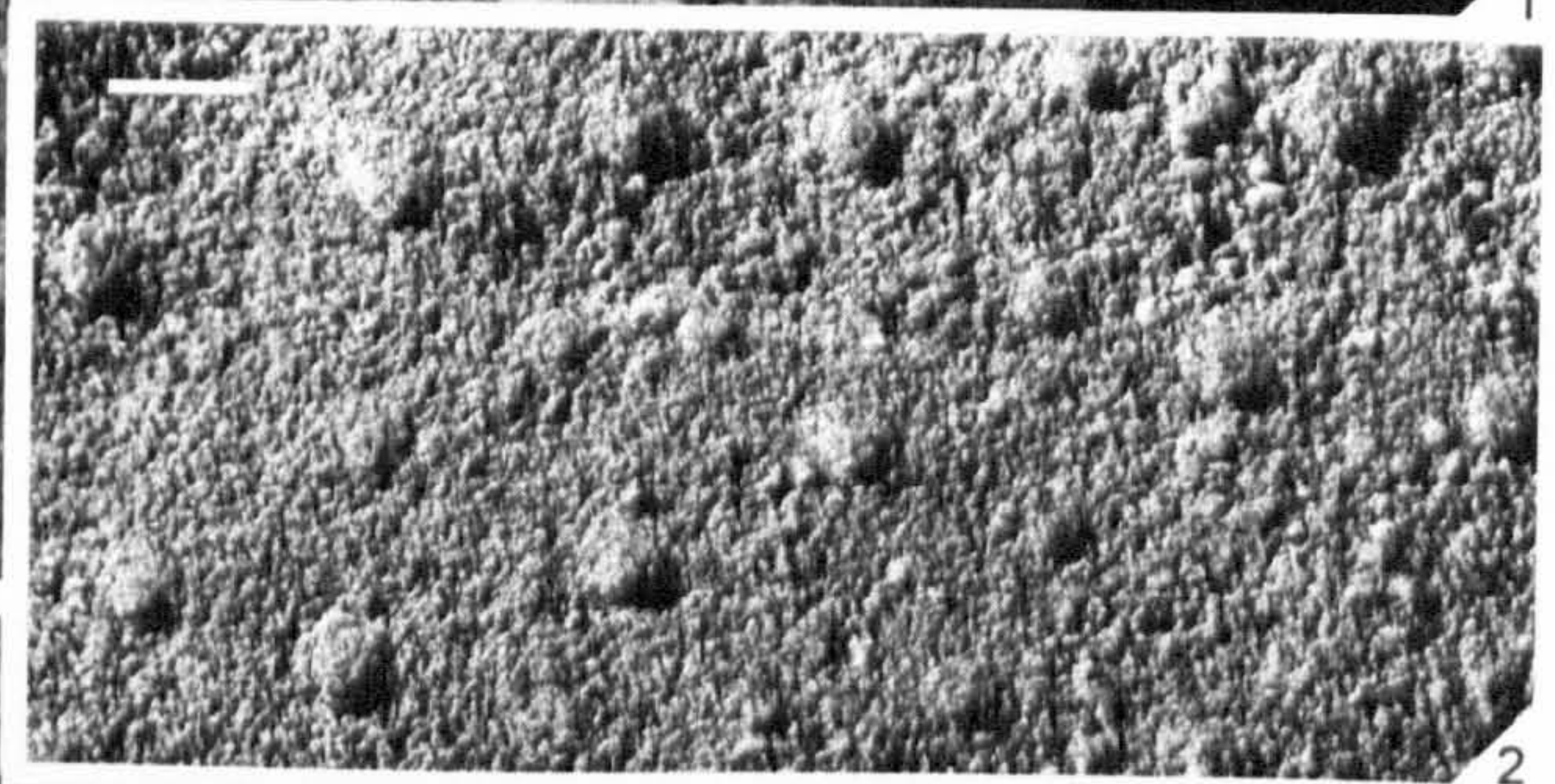
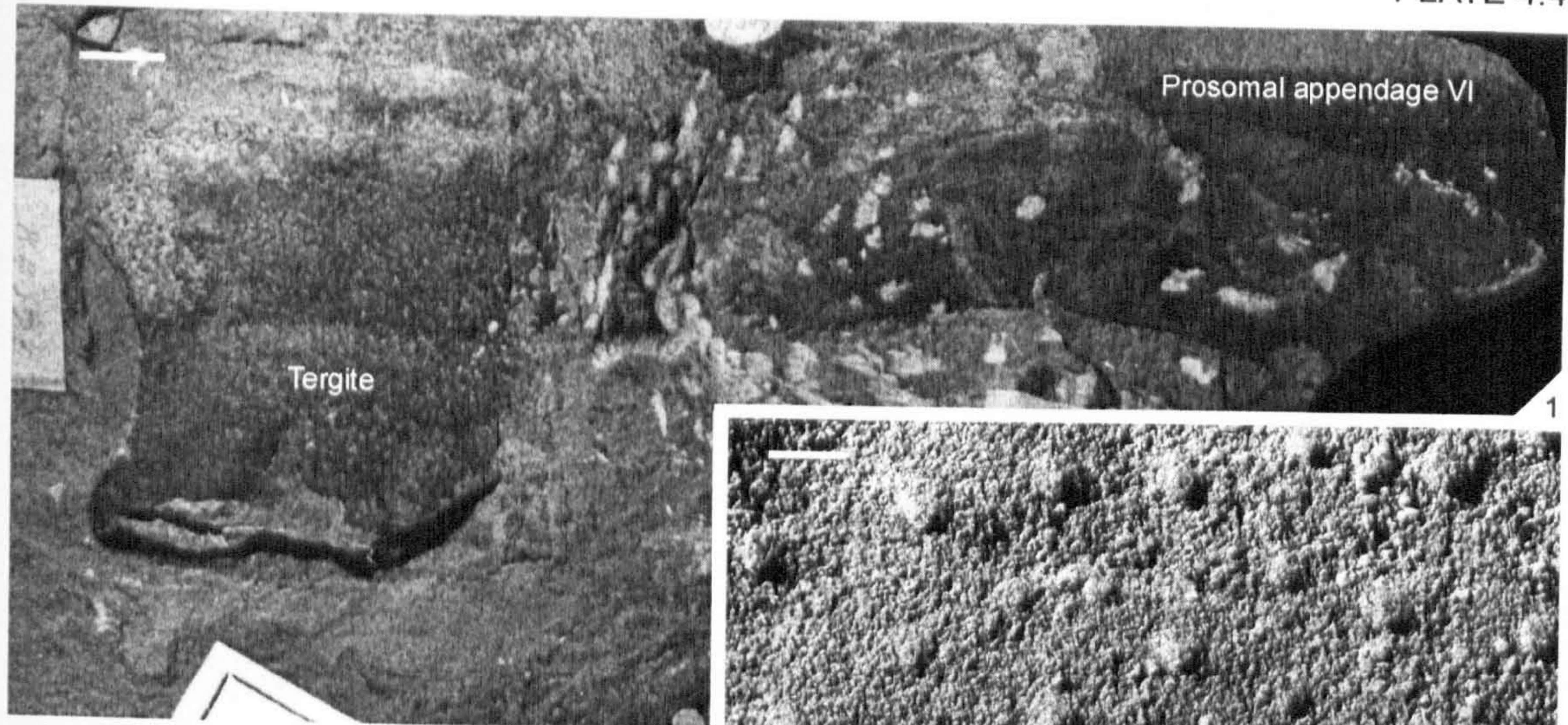




## EXPLANATION OF PLATE 4.4

Figs 1-4. *Carcinosoma punctatum* (Salter, 1859); BMNH 39389, distal podomeres of prosomal appendage VI; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 1, entire slab also containing tergite likely to belong to the species; scale bar represents 10 mm. 2, detail of ornament on associated tergite; scale bar represents 1 mm. 3, entire specimen showing podomeres 7-29; scale bar represents 10 mm. 4, detail of diagnostic deep serration; scale bar represents 5 mm.



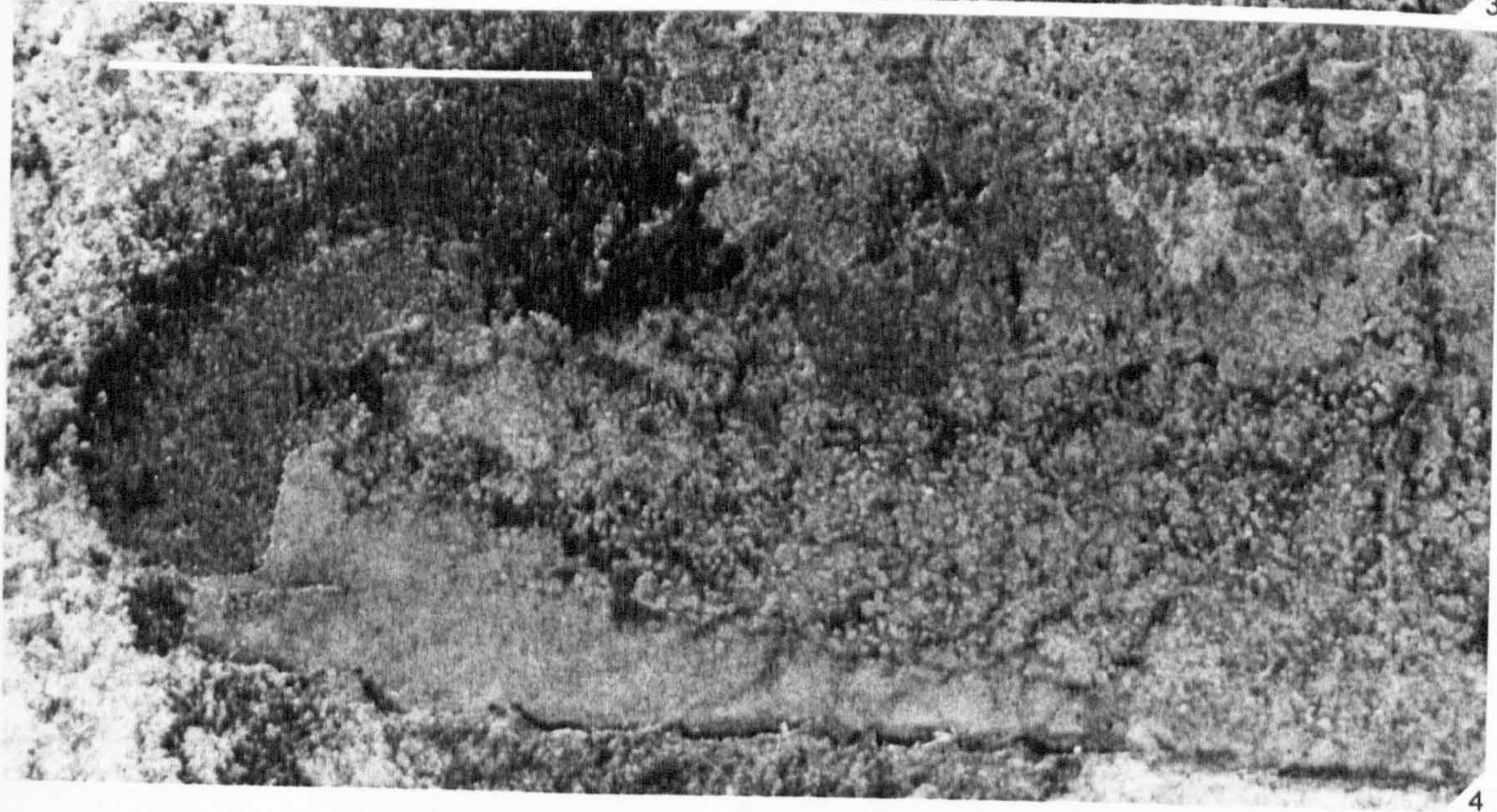
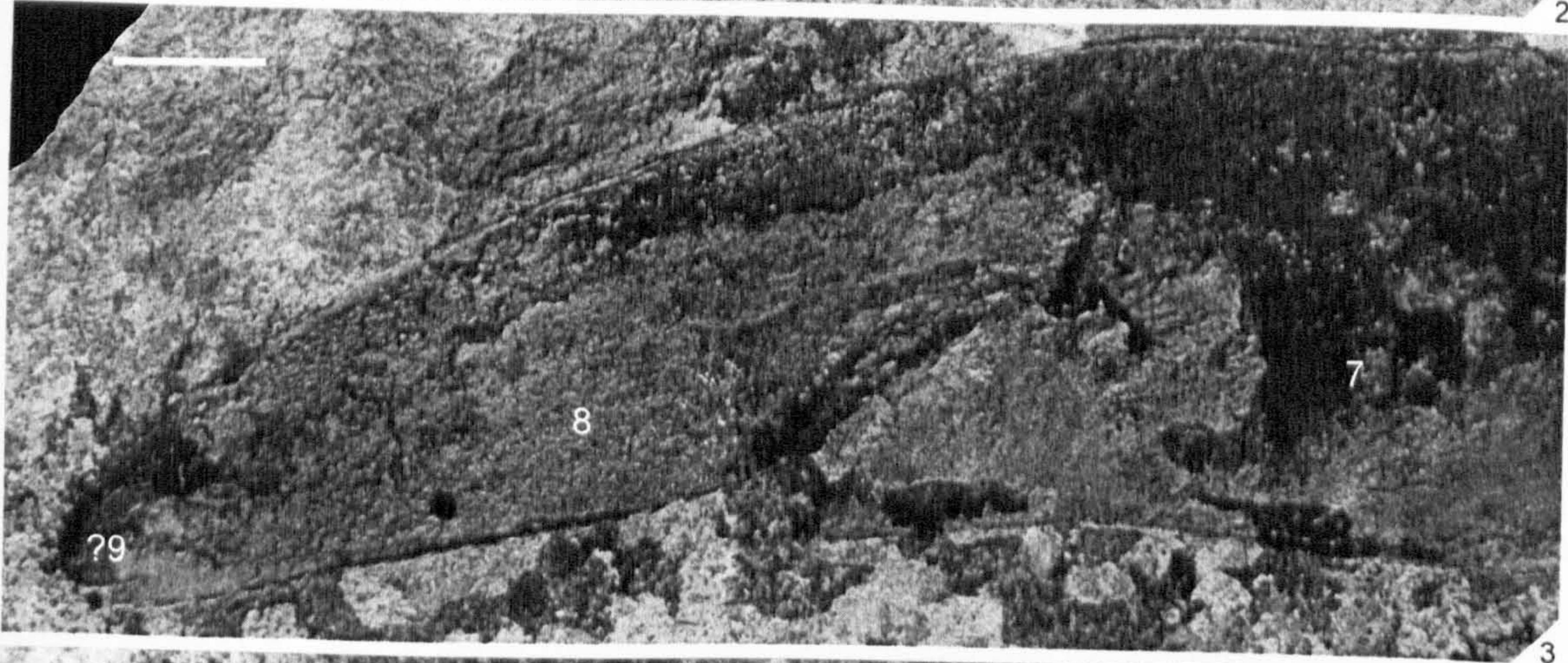
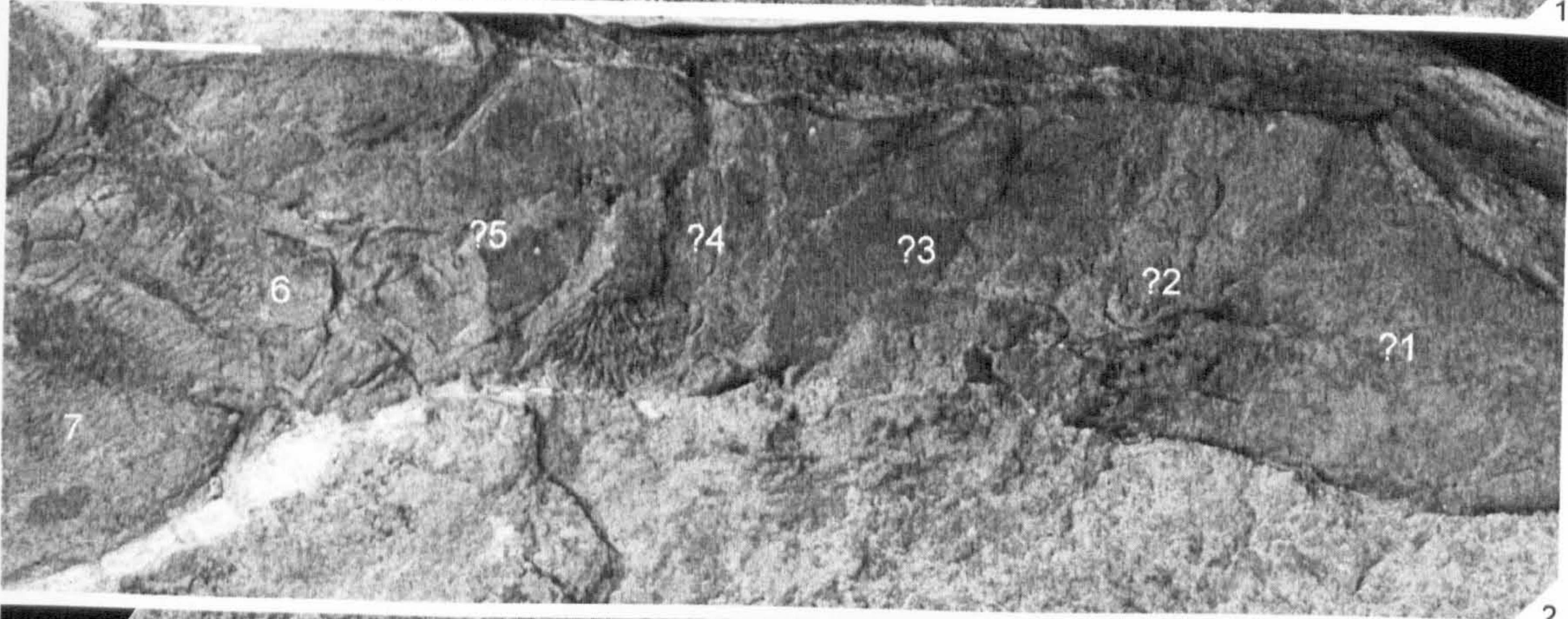
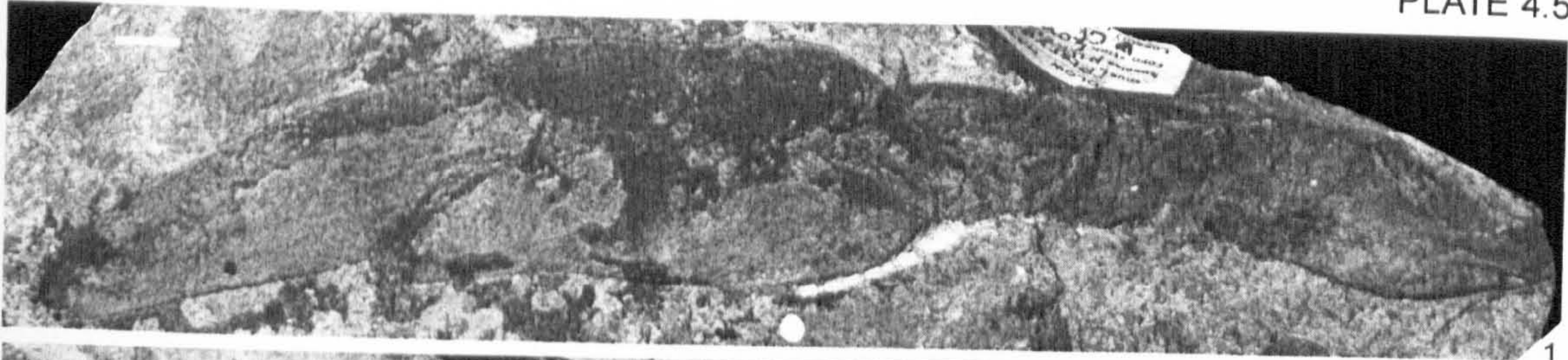




## EXPLANATION OF PLATE 4.5

Figs 1-4. *Carcinosoma punctatum* (Salter, 1859); BMNH In. 43804, nearly complete prosomal appendage VI; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bars represent 10 mm. 1, entire specimen. 2, detail of proximal portion of appendage showing podomeres ?1-7 (identification of podomeres 1-5 is tentative). 3, detail of distal podomeres 7-?9. 4, detail of marginal serration.







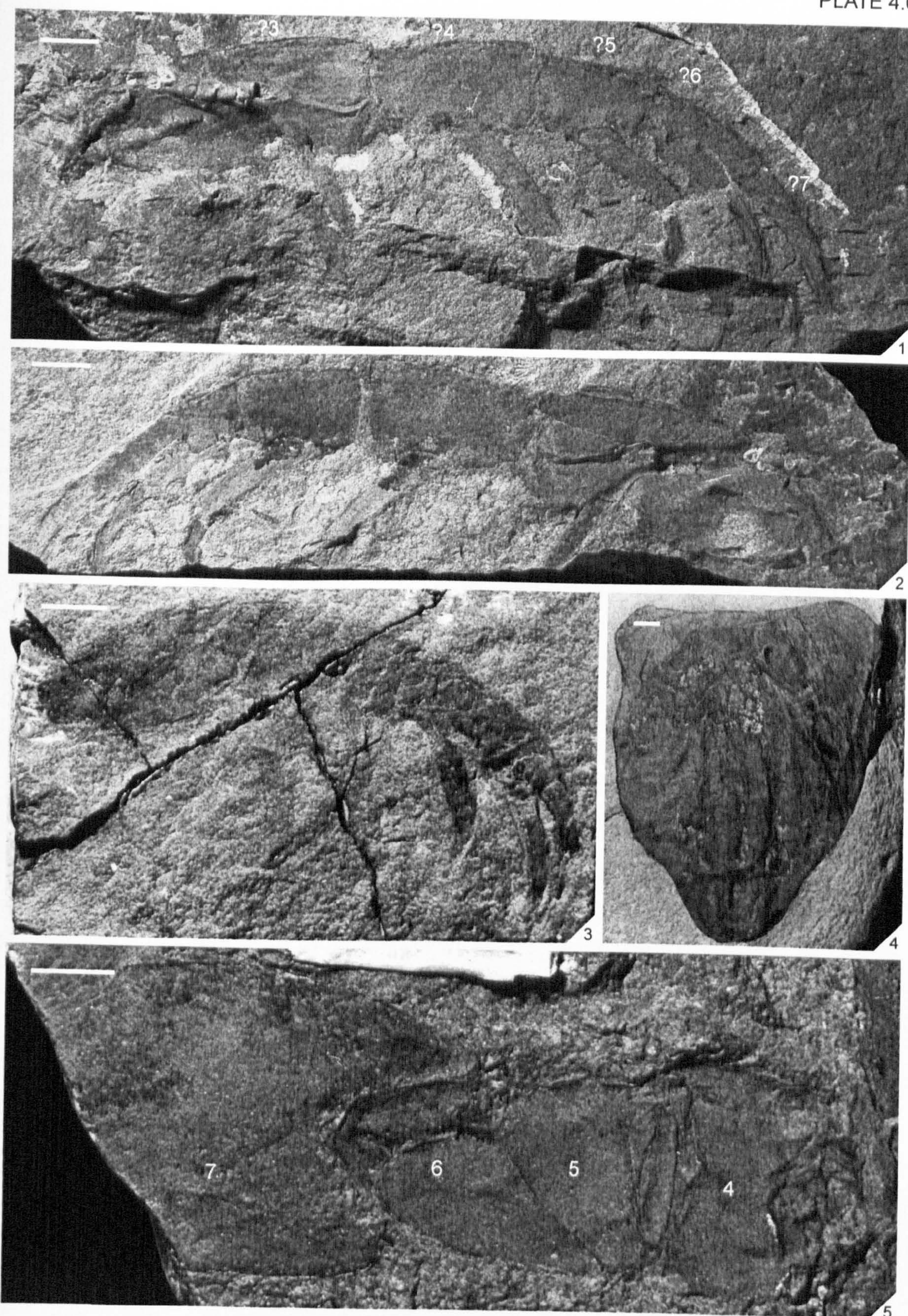
## EXPLANATION OF PLATE 4.6

Figs 1-3. *Carcinosoma* sp. 1; spiniferous prosomal appendage III, V or V; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bars represent 10 mm. 1-2, CH146a-b, part and counterpart; nearly complete appendage showing podomeres ?3-?7; Church Hill Quarry 1. 3, BMNH 39399, nearly complete appendage.

Fig. 4. *Carcinosoma* sp. 2; BMNH 59222, metastoma showing shield shape; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bar represents 10 mm.

Fig. 5. *Carcinosoma* sp. 3; BMNH In. 43811, proximal portion of prosomal appendage VI (podomere numbers indicated; podomere 7 incomplete); Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 10 mm.







## EXPLANATION OF PLATE 4.7

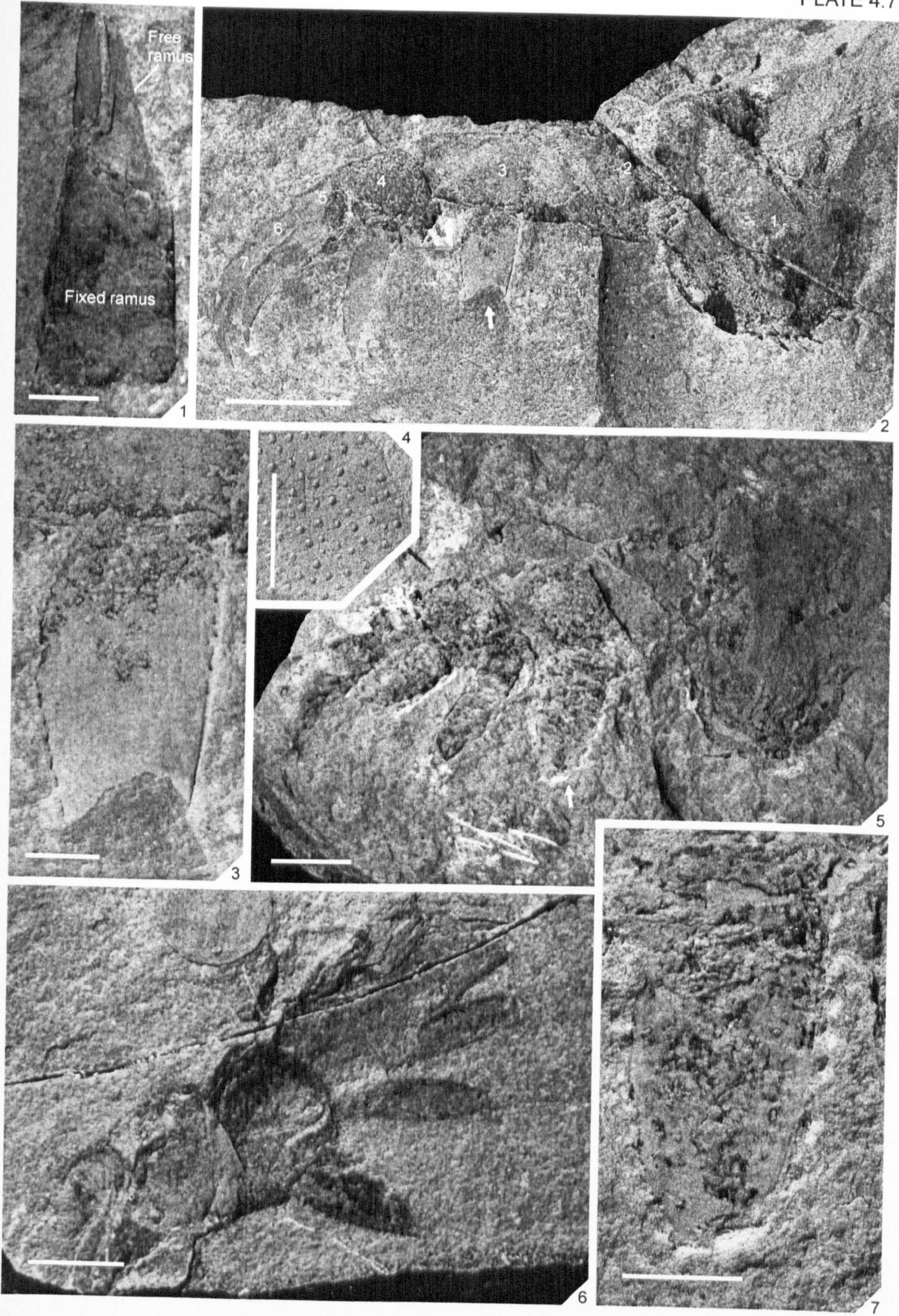
Fig. 1. *Carcinosoma?* sp. 2; BGS GSM89581, chelicera; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 5 mm.

Figs 2-3, 5, 7. *Carcinosoma?* sp. 3; prosomal appendage ? II; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire. 2-3, BGS GSM89565, well preserved, nearly complete; Church Hill. 2, entire specimen showing podomeres 1-7 (spine on podomere 3 arrowed); scale bar represents 10 mm. 3, detail of wide spine on podomere 3, incomplete; scale bar represents 2 mm. 5, 7, BGS GSM89583, nearly complete. 5, entire specimen (spine on podomere 3 arrowed); scale bar represents 10 mm. 7, detail of wide blunt spine on podomere 3, nearly complete; scale bar represents 2 mm.

Fig. 4. Undet. sp.; MS24, cuticle, possibly belonging to *Carcinosoma*; Lower Leintwardine Formation, Ludlow Series; Martin's Shell Quarry, Leintwardine, Herefordshire; scale bar represents 10 mm.

Fig. 6. *Carcinosoma?* sp. 4; BMNH In. 48412, prosomal appendage ?II, nearly complete; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 10 mm.







## EXPLANATION OF PLATE 4.8

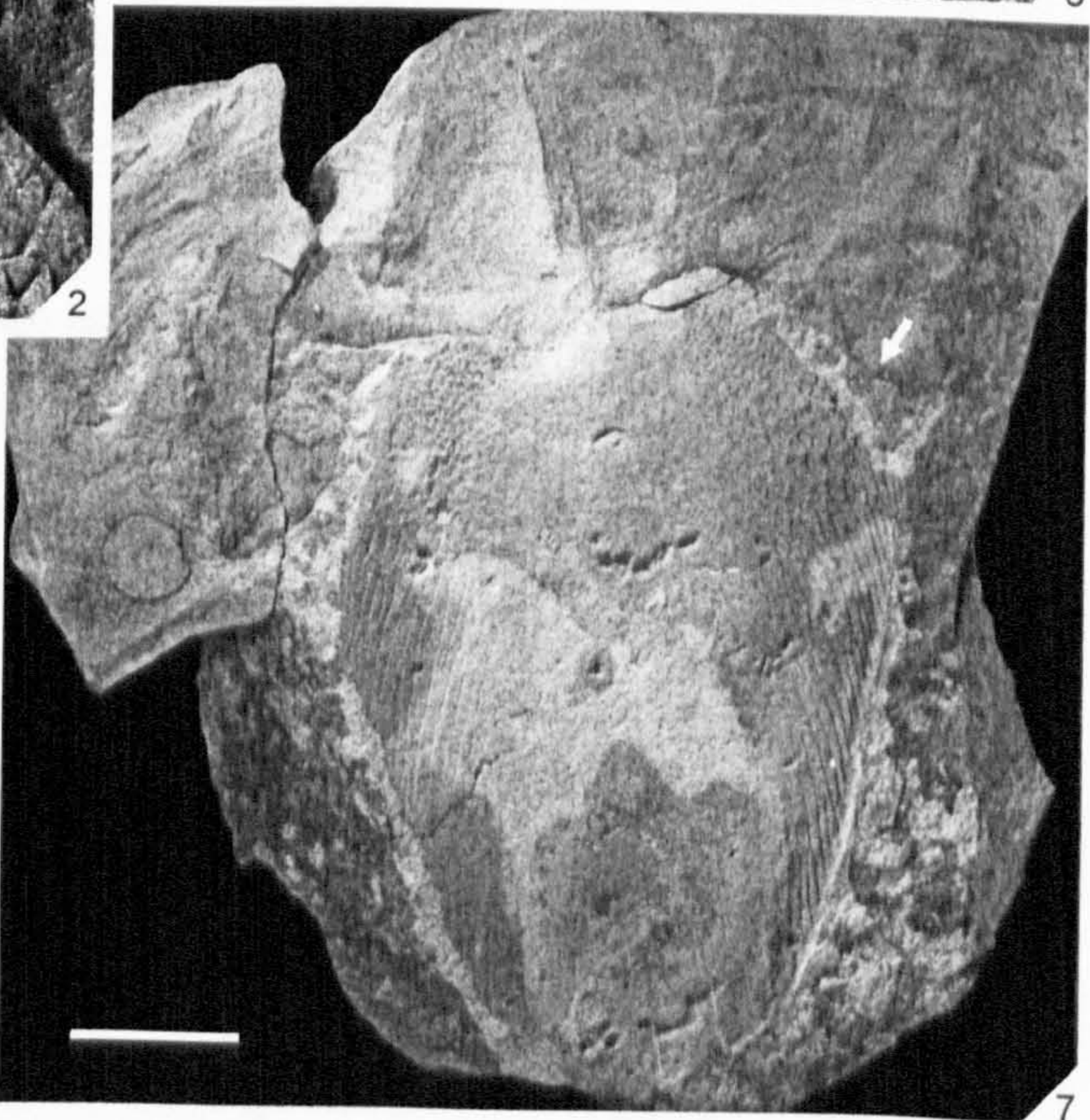
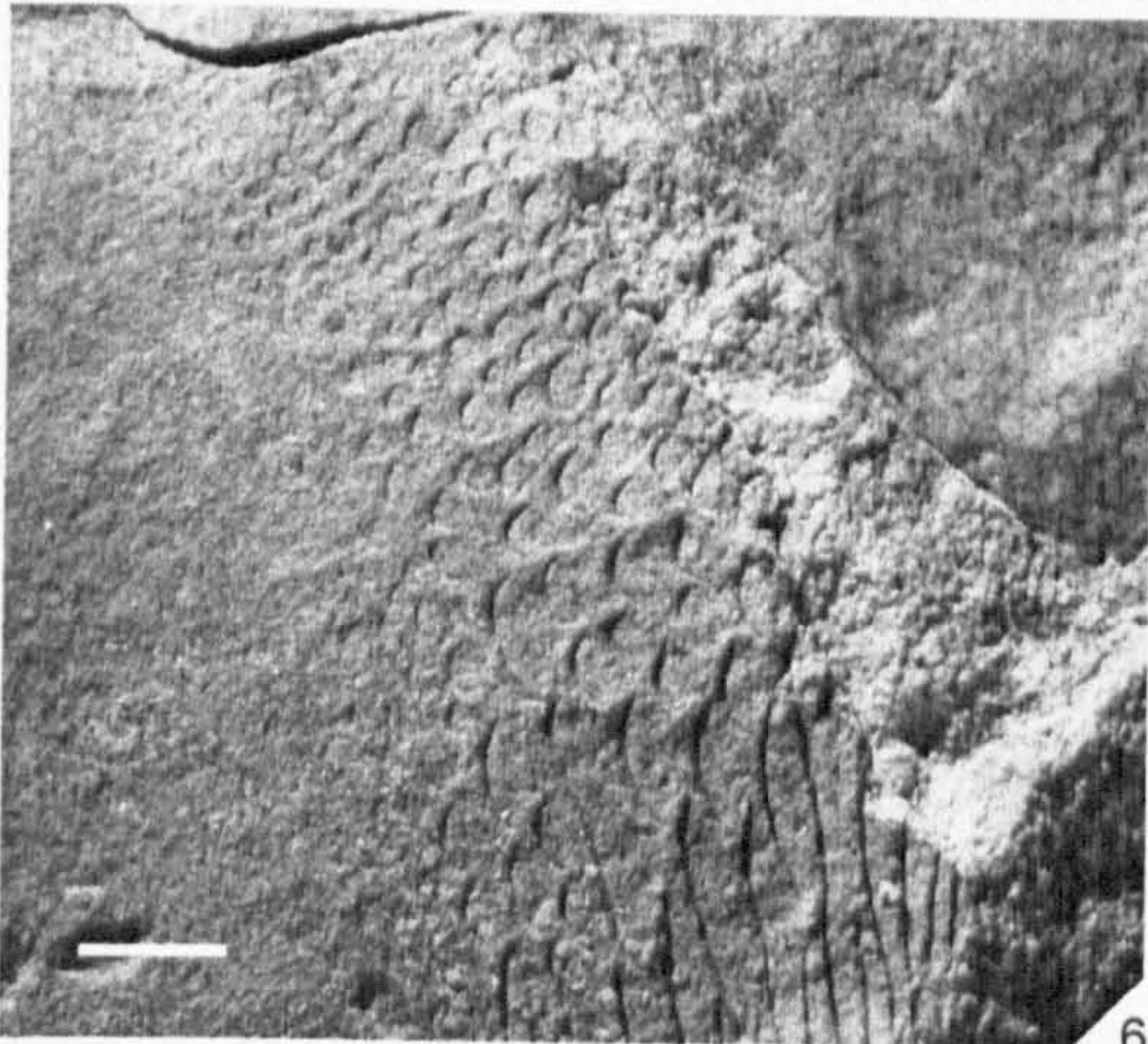
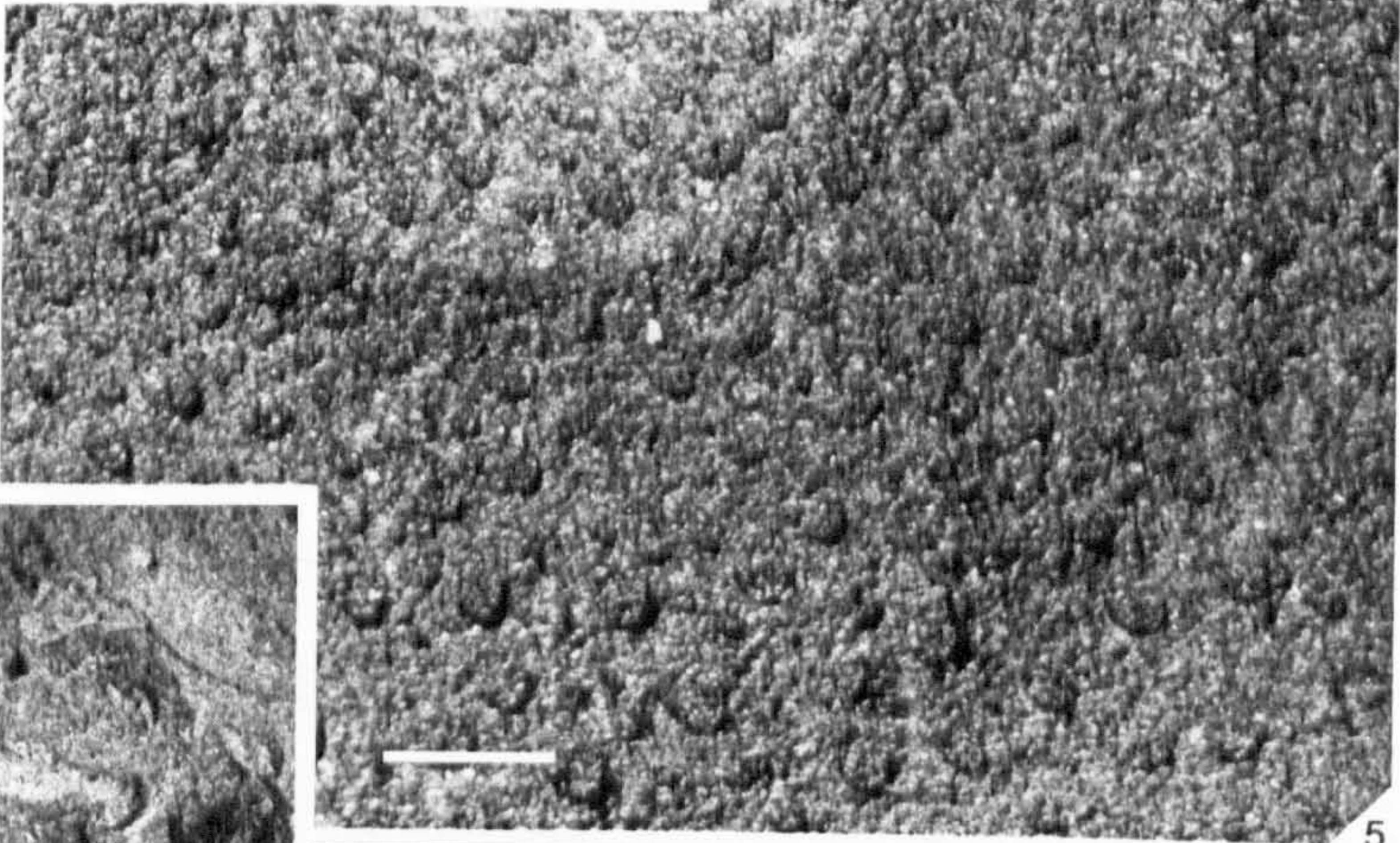
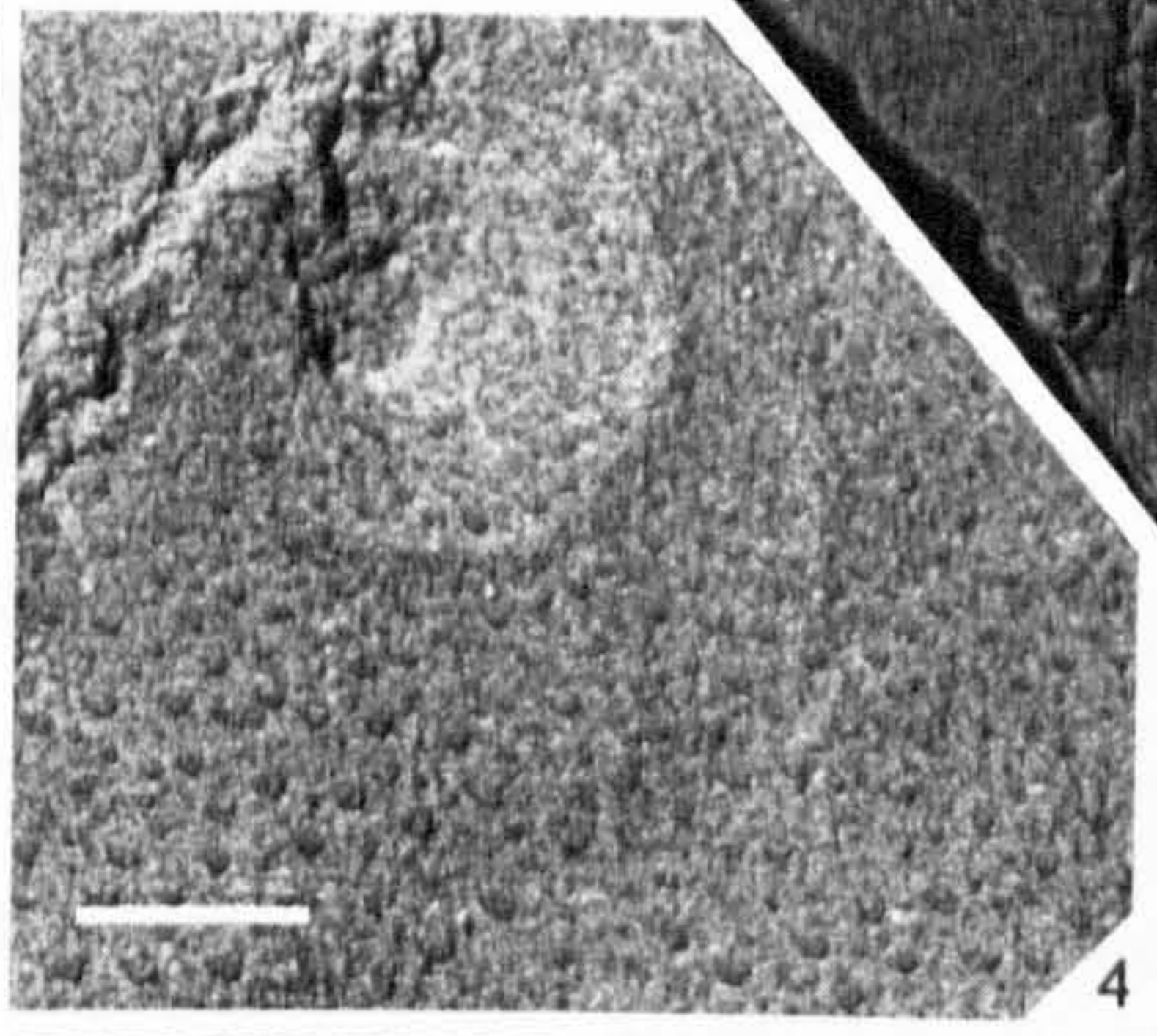
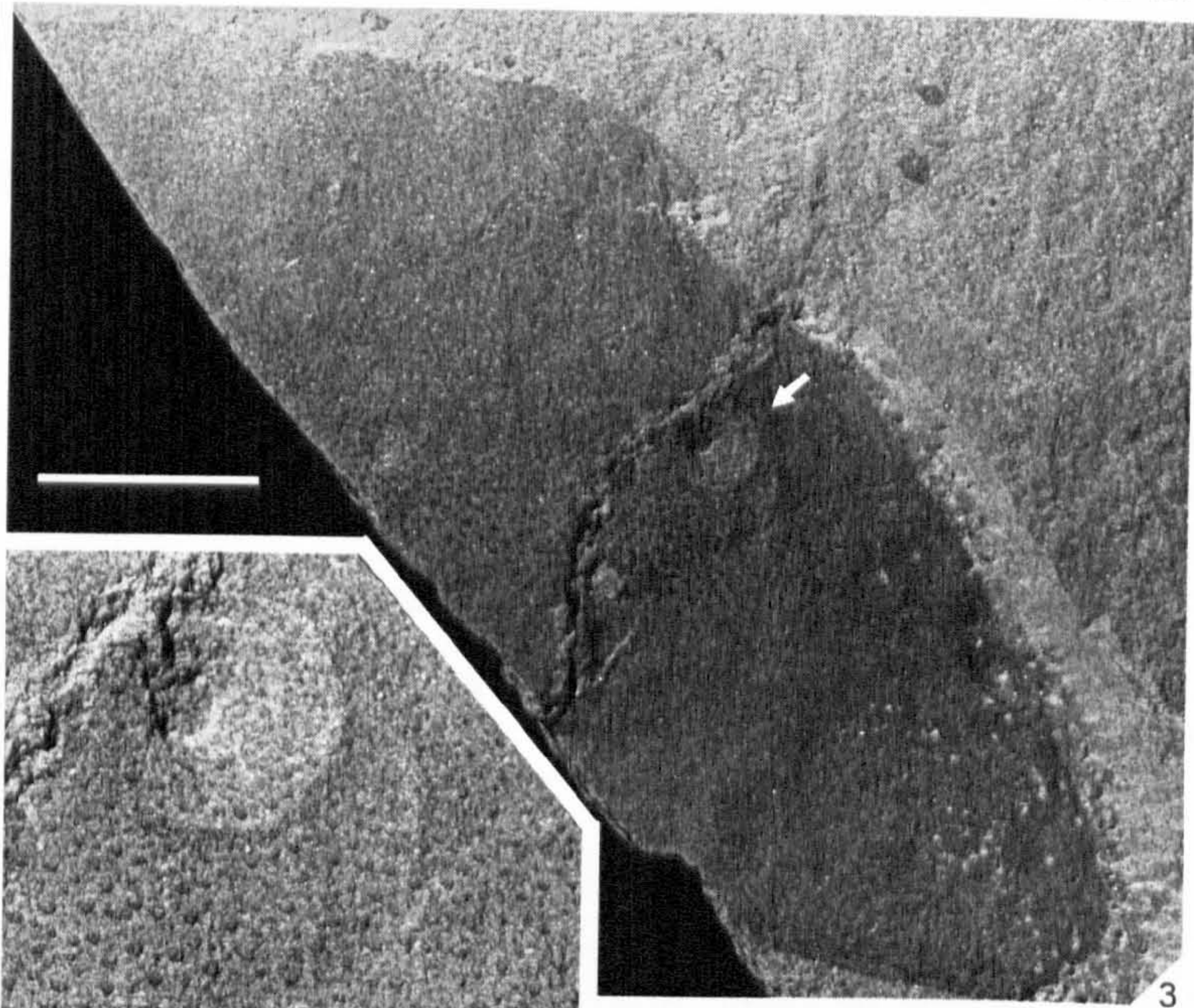
Fig. 1. *Salteropterus? longilabium* Kjellesvig-Waering, 1961; BMNH 39389, holotype, metastoma; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire; scale bar represents 10 mm.

Fig. 2. *Salteropterus? sp.*; BGS GSM89579, cuticle showing V-shaped lunules; Lower Leintwardine Formation, Ludlow Series; Leintwardine, Herefordshire; scale bar represents 2 mm.

Figs 3-5. Undet. sp. 1; CH144, prosoma; Lower Leintwardine Formation, Ludlow Series; Starfish Bed A, Church Hill Quarry 1, Leintwardine, Herefordshire. 3, entire specimen (eye arrowed); scale bar represents 10 mm. 4, detail of eye; scale bar represents 2 mm. 5, detail of ornament around eye; scale bar represents 1 mm.

Figs 6-7. Undet. sp. 2; BGS GSM89603, metastoma; Lower Leintwardine Formation, Ludlow Series; Church Hill, Leintwardine, Herefordshire. 6, detail of ornament; scale bar represents 2 mm. 7, entire specimen (area of ornament shown in detail arrowed); scale bar represents 10 mm.







## CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

## CONCLUSIONS

After study of the four fossiliferous submarine channels of Ludfordian (upper Ludlow) age at Leintwardine, Herefordshire, the following conclusions are made:

- The Leintwardine channels provide a unique palaeoenvironmental setting in the fossil record, that of an indigenous biota within submarine shelf-edge channel heads. The biota is interpreted to comprise indigenous and exotic elements, with variable transportation, both within and between species. Along with typical Silurian fossils, an exceptionally preserved element occurs which includes echinoderms, eurypterids, xiphosurans, phyllocarids and palaeoscolecoid worms. This fauna shows similarities to that of some modern submarine canyons; echinoderms can be locally abundant within these settings.
- Oxygen levels within the Church Hill Channel are not likely to have been restricted, and periodically high sedimentation rates (e.g. storm-triggered obrution deposits) are interpreted to be central to the preservation of much of the unusual biota. Background sedimentation within the channel heads may have been relatively high, possibly having a tidal influence; this is likely to have acted as a faunal inhibitor over parts of the channel head floor. A restricted infauna existed in the channel heads and the epifauna was rare over parts of the channel floor.
- The echinoderms are near to fully articulated and are interpreted to have undergone variable amounts of transportation, either alive or immediately following death, and rapid burial. Reworking is unlikely to have occurred. Autochthonous thanatocoenoses are predominantly not preserved. The echinoderms are interpreted to have been indigenous to the channel head area, and are likely to have been concentrated around the channel flanks and immediately surrounding shelf, sheltered from most of the sedimentation. The articulation of the stelleroids, their occurrence in monospecific assemblages and the low diversity Starfish Bed A, and their apparent absence in the surrounding shelf areas is evidence that they were dominantly indigenous to the setting. Some stelleroid species, such as those typically occurring in monospecific assemblages (e.g. *Sturtzaster marstoni*, *Loriolaster calceatus*) are interpreted to have



undergone minimal transportation and probably represent parautochthonous thanatocoenoses. Taxa such as these may have been more tolerant to environmental stress and thus able to colonise parts of the channel head floor. Starfish Bed A at Church Hill Quarry 1, Leintwardine, shows a low species diversity and dominantly comprises two stelleroid species (*Furcaster leptosoma* and *Lapworthura miltoni*); this suggests minor transport for many of these specimens. The crinoids show minor disarticulation; distal columns and holdfasts are not preserved indicating transportation. Their low diversity and abundance, and small size indicates that the channel heads only provided a marginal habitat for this group. The echinoderms are interpreted to have formed a short-lived opportunistic community within the setting as indicated by their confinement to discrete starfish beds.

- The arthropods show a variation in the degree of transportation; some specimens, such as certain xiphosurans and phyllocarids are nearly intact and probably underwent minimal transport. Semi-articulated to disarticulated specimens (e.g. eurypterids and trilobites) may indicate increased transport and probably mostly represent exuviae. The trilobites often occur in shelly lags, clearly the result of transportation. The eurypterids and phyllocarids occur sporadically through the channel fill; this is interpreted to be a result of their nektobenthic or nektonic habit and they were probably not confined to the channel setting.
- The brachiopods may either be articulated or disarticulated and are mostly transported, probably from the mid to outer shelf area. Rhynchonellids are particularly abundant and often occur in shelly lags. Other faunal elements such as the bryozoans, conulariids, *Sphenothallus* and palaeoscoleuids are interpreted to have undergone minimal transportation based on their mostly intact preservation and their ecology.
- The exceptionally preserved biota is mostly confined to the Church Hill Channel, and is stelleroid dominated. The ophiuroid *L. miltoni* is the most abundant species, followed by the stenurid *S. marstoni*. The asteroids form a rare component of the stelleroid fauna and this is interpreted to be a reflection of the original mode of life of the stelleroids, rather than preservational bias.
- The stelleroids are species diverse; 15 taxa are documented: six asteroids, comprising the valvatids, forcipulatids and paxillosids; six stenurids; and three



ophiuroids, comprising the oegophiurids. One new ophiuroid species is erected, *Loriolaster calceatus* sp. nov. This species is also tentatively recognised from the Gutterford Burn starfish beds of the Pentland Hills, Scotland, extending the range of the genus back to the Lower Silurian. The asteroid subspecies *Urasterella ruthveni* var. *leintwardinensis* Spencer is not maintained. A previously undescribed asteroid specimen, likely to be a juvenile, is described as *Cocaster?* sp. Specimens previously described as *Bdellacoma vermiformis* Salter and *Palasterina antiqua* (Hisinger) are reassigned to *Klasmura?* sp. and *Palasterina* sp., respectively. Bivalved pedicellariae are identified in *Antiquaster magrumi* Kesling; these are similar in appearance, although smaller, to those of *Bdellacoma*. Sublateral axial ossicles are not present in *Sturtzaster colvini* (Salter) and are equivocal in *Sturtzaster marstoni* (Salter); this contrasts with Spencer's (1940) view.

- The eurypterids are dominated by the carcinosomatids; a few pterygotids also occur. The pronounced serration with a deep notch on the distal podomere of prosomal appendage VI is identified as a primary diagnostic character of *Carcinosoma punctatum* Salter. Newly collected and previously described material is assigned or reassigned to *Carcinosoma* sp. and *Carcinosoma?* sp. These specimens do not comprise the diagnostic paddle of prosomal appendage VI; therefore there is insufficient data to refer these to species. A previously undescribed specimen of a genital appendage (type A) is assigned to *Erettopterus?* sp. A metastoma, previously described as *Pterygotus arcuatus* Salter, is reassigned to *Erettopterus?* sp. A distal portion of a free ramus, previously described as *Erettopterus marstoni* Kjellesvig-Waering, is reassigned to *Pterygotus?* sp.

## SUGGESTIONS FOR FUTURE WORK

The following areas are identified for future study:

- Further sedimentological study should be carried out through some of the other Leintwardine channels, particularly those of Todding and Mocktree. This would provide useful comparison with the Church Hill Channel. Logging through the currently inaccessible *in situ* exposure of the Mocktree Channel at Mocktree Quarry could also result in the location of any echinoderm-bearing horizons.



- The immediately surrounding non-channel facies area should be investigated for signs of a tidal signature, such as thickening and thinning laminae. This would prove useful in determining if the channel head sedimentation was significantly different from that of the surrounding shelfal areas.
- Geochemical sampling should be extended to the other channels to determine if oxygen levels were comparable to the Church Hill Channel. Other methods for determining possible oxygen levels within the channels should be investigated, for example pyrite framboid diameter in the sediments (see Wignall and Newton 1998).
- Comparable sedimentological and taphonomic studies could usefully be applied to other echinoderm-bearing deposits (e.g. Gutterford Burn starfish beds).
- The affinity of the stenurid stelleroid taxa from Leintwardine (*Antiquaster*, *Bdellacoma*, *Klasmura*, *Rhopalocoma* and *Sturtzaster*) remains equivocal; further systematic study is needed. Other non-Leintwardine stenurids would give useful information in comparative studies.



TABLE A1.1. XRF analyses for major elements in channel fill siltstone at Church Hill Quarry 1, Leintwardine.  
Samples CH2-50, taken through 2.6 m vertical section; samples CH214, CH202, CH260 are from loose blocks.  
Results quoted as component oxide weight percent, re-calculated to include LOI.

Sample	Bead	SiO2	TiO2	Al2O3	Fe2O3	MnO	MgO	CaO	Na2O	K2O	P2O5	LOI	Total
CH2	LF24179	64.99	0.90	13.45	5.39	0.055	2.44	3.12	1.81	2.823	0.168	4.88	100.02
CH4	LF24180	64.82	0.84	12.50	5.13	0.055	2.24	3.98	1.88	2.674	0.160	5.41	99.69
CH8B	LF24181	69.65	0.98	12.58	5.35	0.120	2.02	0.66	1.96	2.680	0.261	2.75	99.02
CH53	LF24192	64.26	0.90	13.41	5.45	0.042	2.33	3.37	1.80	2.961	0.258	5.21	99.99
CH19	LF24182	64.71	0.90	12.59	5.03	0.067	2.24	3.13	1.85	2.682	0.182	4.79	98.19
CH23	LF24183	66.67	0.88	12.58	4.98	0.070	2.09	3.15	1.87	2.615	0.226	4.64	99.75
CH25	LF24184	68.53	0.91	12.85	5.01	0.081	2.15	2.09	1.85	2.552	0.180	3.93	100.15
CH26	LF24185	65.68	1.00	15.04	5.91	0.053	2.58	0.60	1.75	3.409	0.170	3.47	99.65
CH31	LF24186	63.00	0.90	13.39	5.30	0.062	2.40	4.11	1.72	2.923	0.159	5.87	99.85
CH41	LF24187	40.86	0.44	7.85	3.44	0.242	1.62	22.61	1.45	1.567	0.124	19.47	99.66
CH44	LF24188	40.71	0.48	8.30	3.66	0.248	1.72	22.96	1.41	1.737	0.120	19.61	100.94
CH45	LF24189	65.19	0.90	13.73	5.30	0.053	2.34	3.04	1.80	2.951	0.161	4.99	100.46
CH47	LF24190	66.05	0.95	14.19	5.28	0.061	2.36	1.57	1.84	3.094	0.149	4.05	99.59
CH50	LF24191	67.88	0.99	13.95	5.51	0.077	2.33	0.99	1.83	2.944	0.195	3.41	100.08
CH214	LF24194	63.36	0.85	13.25	5.22	0.053	2.42	4.50	1.72	2.758	0.161	6.15	100.44
CH202	LF24193	64.03	0.87	11.51	4.69	0.078	2.04	6.02	1.83	2.175	0.170	6.77	100.18
CH260	LF24195	63.97	0.80	11.67	4.64	0.066	2.08	5.60	1.80	2.338	0.179	6.77	99.92



TABLE A1.2.1. XRF analyses for trace elements of channel fill siltstone at Church Hill Quarry 1, Leintwardine. Samples CH2-50, taken through 2.6 m vertical section; samples CH214, CH202, CH260 are from loose blocks. Results quoted in ppm.

Sample Pellet	As	Ba	Ce	Co	Cr	Cs	Cu	Ga	La	Mo	Nb	Nd	Ni	Pb	Rb
CH2 L43462	5.9	488.1	83.1	13.3	242.1	13.2	23.2	17.0	45.4	0.7	15.5	40.2	48.6	10.2	113.9
CH4 L43463	7.2	449.0	65.9	13.8	103.5	0.7	19.6	15.7	36.4	-0.5	13.6	30.8	42.5	5.5	101.1
CH8B L43464	5.7	512.6	100.9	14.9	126.7	5.9	21.0	16.1	53.3	1.1	17.6	52.5	52.1	16.5	104.3
CH53 L43475	9.3	480.6	85.5	15.0	108.5	14.7	22.5	17.0	46.3	2.1	15.4	45.0	49.9	12.0	113.4
CH19 L43465	5.7	456.0	93.8	14.2	116.2	7.1	20.4	17.2	48.9	0.0	16.9	47.2	45.2	7.1	104.4
CH23 L43466	5.5	455.3	82.4	13.1	98.1	9.3	17.5	15.8	39.9	0.2	16.5	45.9	43.2	15.1	102.1
CH25 L43467	2.6	467.5	76.0	12.4	109.8	6.5	19.0	16.0	44.2	-0.2	16.8	39.1	46.3	10.1	100.8
CH26 L43468	8.2	556.1	86.9	16.0	122.8	-0.2	28.0	20.1	46.2	0.2	17.3	43.5	51.6	12.1	131.2
CH31 L43469	4.8	455.2	79.7	14.2	125.3	2.3	20.8	18.3	38.3	0.8	16.5	36.7	51.2	12.7	114.6
CH41 L43470	3.2	235.4	64.8	9.9	70.6	7.0	15.9	10.9	34.3	0.4	11.5	32.5	28.3	9.9	66.7
CH44 L43471	2.7	240.6	58.2	9.0	77.2	7.6	17.0	11.4	32.5	1.8	8.7	28.9	29.3	8.7	71.5
CH45 L43472	4.7	471.3	78.9	13.3	114.8	-0.8	23.0	17.3	42.1	1.2	17.0	37.9	47.5	12.4	115.4
CH47 L43473	3.3	508.3	76.1	14.5	122.6	2.5	22.3	18.8	40.4	-1.2	17.2	36.7	49.7	5.9	119.9
CH50 L43474	7.2	522.6	81.9	14.9	120.2	4.2	21.0	18.5	40.5	1.1	18.8	41.5	48.3	6.1	118.4
CH214 L43477	5.1	449.2	75.0	14.2	107.4	-0.4	20.8	17.2	39.5	0.7	17.3	38.4	53.1	12.9	112.0
CH202 L43476	6.2	391.5	79.7	12.4	111.7	-1.2	17.8	14.4	42.6	-0.1	16.1	37.2	41.9	14.9	89.1
CH260 L43478	6.1	389.9	77.9	14.0	107.4	1.4	17.2	15.4	39.4	1.4	15.0	38.0	39.8	11.5	90.4



TABLE A1.2.2. XRF analyses for trace elements of channel fill siltstone at Church Hill Quarry 1, Leintwardine. Samples CH2-50, taken through 2.6 m vertical section; samples CH214, CH202, CH260 are from loose blocks. Results quoted in ppm.

Sample	Pellet	Sb	Sc	Se	Sn	Sr	Th	U	V	Y	Zn	Zr	Cl	F	S
CH2	L43462	-0.7	15.9	-0.7	-1.7	176.2	21.7	3.2	104.3	39.8	71.1	308.7	88	950	235
CH4	L43463	-3.3	14.7	-0.9	2.9	213.7	16.9	2.6	95.0	37.2	67.8	301.8	66	774	325
CH8B	L43464	-3.3	14.4	-0.7	-0.3	111.8	18.8	4.6	100.8	58.1	70.9	384.9	115	682	315
CH53	L43475	-3.1	18.7	0.7	2.8	175.7	18.2	1.5	103.3	48.3	71.1	297.3	52	703	345
CH19	L43465	0.5	15.8	-1.3	1.9	199.4	19.8	2.4	100.7	50.4	68.0	329.2	31	802	370
CH23	L43466	-0.6	16.3	0.8	2.1	192.3	16.4	2.8	99.3	48.8	62.7	326.9	41	897	275
CH25	L43467	2.1	15.2	0.9	3.1	146.1	13.8	1.8	98.7	47.8	58.6	326.5	39	631	379
CH26	L43468	0.9	14.5	0.5	1.9	102.5	18.1	3.5	113.8	39.1	80.5	290.6	24	560	397
CH31	L43469	-0.2	17.9	0.7	-1.7	213.4	17.5	3.8	106.1	37.6	74.3	274.5	32	735	293
CH41	L43470	2.4	22.9	-0.3	0.6	569.2	12.7	3.5	72.6	36.9	45.9	193.9	57	255	236
CH44	L43471	-2.5	23.3	1.2	-0.5	563.4	13.0	1.8	71.4	33.8	47.9	187.0	67	438	205
CH45	L43472	-0.8	14.2	-0.3	2.4	167.7	16.0	-0.5	106.7	35.3	69.2	278.9	24	677	362
CH47	L43473	3.2	16.4	-0.4	2.0	116.7	17.6	3.2	104.8	39.1	66.9	304.9	76	874	295
CH50	L43474	6.6	11.8	-0.3	1.0	111.5	17.8	1.7	107.3	44.2	62.9	344.8	40	862	220
CH214	L43477	3.4	16.8	-1.4	-1.5	196.1	18.4	1.8	103.1	35.5	72.0	264.4	44	815	322
CH202	L43476	-1.4	19.3	0.6	1.0	273.5	18.1	2.8	90.7	47.4	54.9	357.5	54	639	169
CH260	L43478	2.0	15.8	0.3	-0.5	269.2	14.1	1.3	92.7	38.8	60.0	311.7	81	576	254



**TABLE A1. 3. Lower limits of detection for XRF analysis of trace elements used as palaeo-redox indicators; analysis carried out on a Phillips PW1400 at the University of Leicester. Analytical precision is better than +/- 5 % at 100 times LLD value.**

Trace elements	Detection limit (ppm)
Co	3
Cr	2
Mo	1
Ni	2
Sc	2
Th	1
U	1
V	2



TABLE A2.1. Mud laminae thicknesses (mm) through 2.6 m logged section at Church Hill Quarry 1, Leintwardine (laminae 1-250).

Laminae #	Thickness	Laminae #	Thickness	Laminae #	Thickness	Laminae #	Thickness	Laminae #	Thickness
BASE									
1	2	51	2	101	4	151	2	201	4
2	2	52	4	102	10	152	6	202	2
3	10	53	2	103	2	153	2	203	6
4	2	54	4	104	4	154	6	204	4
5	2	55	4	105	8	155	2	205	4
6	2	56	1	106	8	156	2	206	4
7	2	57	4	107	6	157	10	207	2
8	2	58	6	108	8	158	2	208	2
9	8	59	4	109	10	159	6	209	4
10	4	60	4	110	14	160	2	210	4
11	2	61	6	111	2	161	6	211	2
12	2	62	4	112	2	162	10	212	4
13	14	63	4	113	6	163	6	213	6
14	6	64	14	114	4	164	2	214	2
15	2	65	2	115	6	165	4	215	4
16	14	66	4	116	4	166	6	216	4
17	4	67	6	117	2	167	10	217	8
18	10	68	4	118	2	168	10	218	4
19	2	69	4	119	4	169	12	219	14
20	2	70	12	120	12	170	8	220	4
21	4	71	4	121	2	171	8	221	6
22	2	72	14	122	2	172	6	222	6
23	2	73	8	123	4	173	10	223	4
24	4	74	4	124	2	174	6	224	2
25	1	75	8	125	2	175	8	225	6
26	4	76	6	126	4	176	4	226	4
27	6	77	4	127	4	177	4	227	8
28	4	78	8	128	6	178	2	228	12
29	2	79	4	129	14	179	6	229	4
30	4	80	2	130	20	180	6	230	2
31	4	81	4	131	6	181	4	231	2
32	2	82	6	132	4	182	6	232	2
33	2	83	4	133	4	183	2	233	2
34	2	84	2	134	14	184	6	234	4
35	6	85	6	135	14	185	8	235	4
36	10	86	2	136	6	186	2	236	4
37	4	87	2	137	8	187	6	237	4
38	4	88	6	138	8	188	4	238	4
39	10	89	4	139	4	189	4	239	4
40	6	90	2	140	2	190	2	240	6
41	8	91	2	141	4	191	2	241	4
42	2	92	4	142	2	192	2	242	6
43	6	93	2	143	2	193	2	243	8
44	4	94	4	144	4	194	2	244	8
45	2	95	12	145	8	195	2	245	8
46	2	96	10	146	2	196	4	246	8
47	2	97	12	147	8	197	6	247	10
48	6	98	16	148	2	198	4	248	2
49	4	99	6	149	4	199	4	249	2
50	8	100	4	150	2	200	6	250	2



TABLE A2.2. Mud laminae thicknesses (mm; laminae 251-412).

Laminae #	Thickness	Laminae #	Thickness	Laminae #	Thickness	Laminae #	Thickness
251	6	301	4	351	2	401	1
252	2	302	4	352	8	402	1
253	2	303	6	353	6	403	1
254	2	304	6	354	4	404	8
255	2	305	2	355	4	405	6
256	2	306	20	356	16	406	18
257	2	307	8	357	6	407	16
258	4	308	2	358	12	408	16
259	6	309	4	359	2	409	18
260	6	310	4	360	12	410	6
261	2	311	2	361	4	411	10
262	4	312	4	362	4	412	6
263	2	313	2	363	4	TOP	
264	2	314	6	364	10		
265	2	315	4	365	4		
266	8	316	4	366	32		
267	8	317	4	367	12		
268	6	318	4	368	16		
269	2	319	6	369	14		
270	2	320	2	370	14		
271	2	321	10	371	10		
272	2	322	6	372	8		
273	2	323	14	373	6		
274	2	324	30	374	12		
275	4	325	8	375	10		
276	2	326	18	376	4		
277	4	327	12	377	24		
278	2	328	30	378	8		
279	4	329	12	379	2		
280	2	330	6	380	6		
281	14	331	8	381	14		
282	2	332	16	382	6		
283	4	333	24	383	12		
284	2	334	4	384	28		
285	2	335	2	385	2		
286	4	336	8	386	2		
287	20	337	14	387	18		
288	8	338	14	388	10		
289	8	339	22	389	4		
290	14	340	6	390	4		
291	20	341	2	391	4		
292	12	342	2	392	8		
293	8	343	2	393	1		
294	6	344	4	394	2		
295	6	345	8	395	2		
296	6	346	10	396	2		
297	8	347	30	397	10		
298	4	348	20	398	2		
299	4	349	12	399	1		
300	6	350	4	400	1		



TABLE A3.1.1. Stelleroids; Leintwardine. Locality notes: Church Hill Quarry 1 (CHQ1); Starfish Bed A, Church Hill Quarry 1 (SBA); Martin's Shell Quarry (MS); Mocktree Quarry (Mocktree).

Specimen	Taxon	Description	Channel	Locality
BMNH				
?	<i>S. marstoni</i>	2 specimens	Ch	
?	<i>Sturtzaster</i>	well preserved	Ch	
38525	<i>S. marstoni</i>	c. 8 specimens	Ch	
38526	<i>L. miltoni</i>		Leint.	
38527	<i>L. calceatus</i>	9 specimens	Leint.	
38619	<i>L. miltoni</i>	2 specimens	Ch	
38666	<i>B. vermiformis</i>	2 specimens, well preserved	Ch	
40291	<i>L. miltoni</i>	nearly complete	Ch	
40293	<i>R. pyrotechnica</i>	Neotype	Ch	
40294	<i>R. pyrotechnica</i>		Ch	
40295	<i>L. miltoni</i>	small specimen	Leint.	
40296a-b	<i>A. magrumi</i>	small, well preserved	Ch	
40297	<i>B. vermiformis</i>	incomplete	Ch	
40298	<i>L. miltoni</i>	small specimen	Ch	
40299a-b	<i>P. cf. antiqua</i>	complete	Ch	
40300	<i>Klasmura?</i> sp.	well preserved	Ch	
40301	<i>Palasterina</i>	incomplete	Ch	
40303	<i>Sturtzaster</i>	2 small specimens	Ch	
40304	<i>R. pyrotechnica</i>		Ch	
40305	<i>F. leptosoma</i>	poorly preserved	Leint.	
40308	<i>S. marstoni</i>	3 specimens	Ch	
46601	<i>R. pyrotechnica</i>		Ch	
46753	undet.	poorly preserved	Leint.	
46753	<i>F. leptosoma</i>	small, poorly preserved	Leint.	
46753	<i>L. miltoni</i>	small, poorly preserved	Leint.	
46753	<i>L. miltoni</i>	poorly preserved	Leint.	
46753	<i>B. vermiformis</i>		Leint.	
46753	<i>Sturtzaster</i>		Ch	
47949	<i>L. calceatus</i>	well preserved	Leint.	
47951	<i>L. miltoni</i>	poorly preserved	Leint.	
47952	<i>B. vermiformis</i>		Ch	
47953	<i>L. calceatus</i>	well preserved	Leint.	
47954	<i>L. miltoni</i>	small, well preserved	Leint.	
47995	<i>S. marstoni</i>	10 specimens	Ch	
57021	<i>S. marstoni</i>		Ch	
57023	<i>L. miltoni</i>	well preserved	Leint.	
57425	<i>L. miltoni</i>	well preserved	Ch	
E 77	<i>L. miltoni</i>		Leint.	
E 653	<i>L. miltoni</i>	nearly complete	Ch	
E 653	<i>L. miltoni</i>	well preserved	Leint.	
E 1244	<i>L. miltoni</i>	arm fragment	Ch	
E 1244	<i>L. miltoni</i>	poorly preserved	Ch	
E 1254	<i>B. vermiformis</i>		Ch	
E 1252	undet.		Ch	
E 1259	<i>B. vermiformis</i>		Ch	
E 1297	<i>L. miltoni</i>	nearly complete	Leint.	
E 1297	<i>L. miltoni</i>	poorly preserved	Leint.	
E 1297	<i>L. miltoni</i>	nearly complete	Leint.	
E 1297	<i>L. miltoni</i>	small, poorly preserved	Leint.	



TABLE A3.1.2. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
BMNH				
E 1297	L. miltoni	arm fragment	Leint.	
E 1297	L. miltoni	poorly preserved	Leint.	
E 1297	L. miltoni	small, well preserved	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni			
E 1297	L. miltoni		Ch	
E 1297	L. miltoni		Ch	
E 1297	L. miltoni	well preserved	Leint.	
E 1297	L. miltoni	4 specimens	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni	nearly complete	Leint.	
E 1297	L. miltoni	well preserved	Leint.	
E 1297	L. miltoni	2 specimens; poorly preserved	Leint.	
E 1297	L. miltoni	incomplete	Leint.	
E 1297	L. miltoni	3 specimens	Leint.	
E 1297	L. miltoni	poorly preserved	Ch	
E 1298	F. leptosoma	poorly preserved	Leint.	
E 1298	F. leptosoma		Ch	
E 1298	F. leptosoma	poorly preserved	Leint.	
E 1298	F. leptosoma	incomplete	Ch	
E 1299	S. marstoni		Ch	
E 1299	S. marstoni		Ch	
E 1299	S. marstoni		Ch	
E 1299	Sturtzaster	3 specimens	Ch	
E 1299	Sturtzaster		Ch	
E 1299	Sturtzaster	poorly preserved	Ch	
E 1299	Sturtzaster	poorly preserved	Ch	
E 1299	Sturtzaster	2 specimens	Ch	
E 1299	Sturtzaster		Ch	
E 1308	S. marstoni		Leint.	
E 1311	L. miltoni	poorly preserved	Leint.	
E 1311	L. miltoni	2 specimens; poorly preserved	Leint.	
E 1311	L. miltoni	arm fragment	Leint.	
E 1311	L. miltoni		Leint.	
E 1311	L. miltoni	incomplete	Leint.	
E 1311	L. miltoni	incomplete	Leint.	
E 1311	L. miltoni	incomplete	Leint.	
E 1311	L. miltoni	arm fragment	Leint.	
E 1311	L. miltoni	incomplete	Leint.	
E 1311	L. miltoni		Leint.	
E 1311	L. miltoni	poorly preserved	Leint.	
E 1312	undet.	poorly preserved	Leint.	
E 1312	F. leptosoma	incomplete	Leint.	
E 1312	Sturtzaster		Leint.	
E 1313	undet.	incomplete	Leint.	
E 1313	Sturtzaster		Ch	
E 1313	S. marstoni		Ch	
E 1313	S. marstoni		Ch	
E 1313	S. marstoni		Ch	
E 1313	S. marstoni		Ch	



TABLE A3.1.3. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
E 1476	L. miltoni		Ch	
E 1476	L. miltoni		Ch	
E 1478	Sturtzaster	2 specimens	Ch	
E 1479	S. colvini, L. miltoni		Ch	
E 1480	B. vermiformis		Ch	
E 1483	F. leptosoma	complete	Leint.	
E 2590	S. marstoni	2 specimens; 1 incomplete	Ch	
E 2591	S. marstoni		Ch	
E 2592	B. vermiformis		Ch	
E 2593	S. marstoni	well preserved	Ch	
E 2612	Sturtzaster	2 specimens	Ch	
E 5013a-b	R. pyrotechnica	well preserved	Ch	
E 5014	S. marstoni		Ch	
E 5015	B. vermiformis		Ch	
E 5016a-b	undet.		Ch	
E 13125	S. marstoni		Ch	
E 13127	L. miltoni	3 specimens; 2 complete	Ch	
E 13128	L. miltoni	nearly complete	Leint.	
E 13129	L. miltoni			
E 13130	L. miltoni	nearly complete	Leint.	
E 13131	L. miltoni	also F. leptosoma	Leint.	
E 13132	L. miltoni	poorly preserved	Leint.	
E 13133	L. miltoni	poorly preserved	Leint.	
E 13134	L. miltoni	poorly preserved	Leint.	
E 13135	F. leptosoma	nearly complete	Leint.	
E 13136	F. leptosoma	nearly complete	Leint.	
E 13137	F. leptosoma	nearly complete	Leint.	
E 13138	F. leptosoma	nearly complete	Leint.	
E 13139	F. leptosoma	nearly complete	Leint.	
E 13140	F. leptosoma	nearly complete	Leint.	
E 13141	F. leptosoma	nearly complete	Leint.	
E 13142	F. leptosoma	nearly complete	Leint.	
E 13143	S. marstoni	6 specimens	Leint.	
E 13144	S. marstoni	nearly complete; well preserved	Leint.	
E 13145	S. marstoni	2 specimens	Leint.	
E 13146	S. marstoni	3 specimens, poor preservation	Leint.	
E 13147	S. marstoni	incomplete	Leint.	
E 13148	S. colvini		Leint.	
E 13149	B. vermiformis		Leint.	
E 13150	B. vermiformis		Leint.	
E 13151	B. vermiformis		Leint.	
E 13152	B. vermiformis		Leint.	
E 13153	M.? Leintwardensis	Holotype	Leint.	
E 13934	S. marstoni		Ch	
E 13948	S. marstoni	well preserved	Ch	
E 13949	S. marstoni	nearly complete	Ch	
E 13950	S. colvini	well preserved	Ch	
E 13951	R. pyrotechnica	poorly preserved	Ch	
E 13952	U. ruthveni	well preserved	Ch	
E 13953	undet.	c. 6 specimens	Ch	
E 13956	C. bulbiferus	Holotype	Ch	
E 13958	B. vermiformis	well preserved	Ch	
E 20231	L. miltoni	Syntype	Ch	
E 20232	L. miltoni	Syntype	Ch	



TABLE A3.1.4. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
E 20235a-b	L. miltoni	Neotype	Ch	
E 20239	L. miltoni	5 specimens, 3 well preserved	Ch	
E 20242	B. vermiformis	2 specimens; poorly preserved	Ch	
E 20243	B. vermiformis, F. leptosoma		Ch	
E 20245	B. vermiformis	well preserved	Ch	
E 20247	L. miltoni	well preserved	Ch	
E 20250a-c	L. calceatus	c. 30 specimens	Ch	
E 20256	F. leptosoma	nearly complete	Ch	
E 20258	F. leptosoma		Ch	
E 20260	F. leptosoma	nearly complete	Ch	
E 20648	S. colvini	well preserved	Ch	
E 52859	S. colvini	Neotype	Ch	
E 52970a-b	B. vermiformis		To	MS
E 52971a-b	B. vermiformis		To	MS
E 52972a-b	B. vermiformis	well preserved	To	MS
E 52973a-b	L. miltoni		To	MS
E 52974a-b	L. miltoni		To	MS
E 52975a-b	L. miltoni	incomplete	To	MS
E 52976	L. miltoni	incomplete	To	MS
E 52977	L. miltoni	incomplete	To	MS
E 52978	L. miltoni	incomplete	To	MS
E 52979	L. miltoni	nearly complete	To	MS
E 52980	L. miltoni	poorly preserved	To	MS
E 52981	L. miltoni	arm fragment	To	MS
E 52982	L. miltoni	arm fragment	To	MS
E 53686	F. leptosoma	nearly complete	Leint	
E 53878	L. miltoni		Leint	
E 53879	L. miltoni	well preserved	Ch	
E 53880	L. miltoni	2 specimens; poorly preserved	Ch	
E 53881	L. miltoni	poorly preserved	Ch	
E 53882	L. miltoni	incomplete	Ch	
E 53883	L. miltoni	incomplete	Ch	
E 53884	L. miltoni	nearly complete	Ch	
E 53885	L. miltoni	well preserved	Ch	
E 53886	L. miltoni	5 specimens	Ch	
E 53887	L. miltoni	poorly preserved	Ch	
E 53888	L. miltoni	2 specimens; 1 complete	Ch	
E 53889	L. miltoni	poorly preserved	Ch	
E 53890	L. miltoni	nearly complete	Leint	
E 53997	L. miltoni		Ch	
E 54157	S. marstoni	poorly preserved	Ch	
E 54021a-b	L. miltoni		Ch	
E 54023	B. vermiformis		Leint	
E 57709	L. miltoni	nearly complete	Leint	
BGS				
?	L. miltoni	nearly complete	Leint.	
?	L. miltoni	2 specimens	Leint.	
?	L. miltoni	nearly complete	Leint.	
?	L. miltoni	poorly preserved	Leint.	
?	L. miltoni		Leint.	
?	L. miltoni	2 small specimens	Leint.	
?	L. miltoni	small, incomplete	Leint.	
?	L. miltoni	poorly preserved	Ch	



TABLE A3.1.5. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>BGS</b>				
?	<i>L. miltoni</i>	nearly complete	Leint.	
?	<i>L. miltoni</i>	nearly complete	Leint.	
?	undet.		Mo	
?	<i>F. leptosoma</i>	nearly complete	Leint.	
?	<i>F. leptosoma</i>	2 small specimens	Leint.	
?	<i>F. leptosoma</i>	2 specimens		
?	<i>S. marstoni</i>	2 specimens	Leint.	
?	<i>S. marstoni</i>	2 specimens	Leint.	
?	<i>S. marstoni</i>	5 specimens; incomplete	Leint.	
?	<i>S. marstoni</i>		Leint.	
?	<i>S. marstoni</i>	2 specimens	Leint.	
?	<i>S. marstoni</i>	poorly preserved	Leint.	
?	<i>S. marstoni</i>	2 incomplete specimens	Leint.	
?	<i>S. marstoni</i>	2 incomplete specimens	Leint.	
?	<i>S. marstoni</i>	2 specimens; poorly preserved	Leint.	
?	<i>S. marstoni</i>	poorly preserved	Leint.	
?	<i>Bdellacoma</i>	poorly preserved	Leint.	
?	? <i>Bdellacoma</i>	poorly preserved	Mo	
?	<i>B. vermiformis</i>	complete, well preserved	Leint.	
GSM6517	<i>S. marstoni</i>	well preserved	Leint.	
GSM25351	<i>L. calceatus</i>	c. 26 specimens	Leint.	
GSM25354	<i>L. miltoni</i>	2 specimens; 1 nearly complete	Leint.	
GSM28819	<i>F. leptosoma</i>	well preserved	Leint.	
GSM28820-21	<i>F. leptosoma</i>	2 specimens	Ch	
GSM28823	<i>R. pyrotechnica</i>	well preserved	Leint.	
GSM28825	<i>L. miltoni</i>	poorly preserved	Leint.	
GSM37348	<i>R. pyrotechnica</i>	poorly preserved	Leint.	
GSM37357	<i>Sturtzaster</i>	2 specimens; poorly preserved	Leint.	
GSM54521	<i>S. marstoni</i>	poorly preserved	Leint.	
GSM54522	<i>L. miltoni</i>	arm fragment	Leint.	
GSM54746-7	<i>Sturtzaster</i>	2 specimens	Leint.	
GSM54748	<i>B. vermiformis</i>	poorly preserved	Leint.	
GSM54892-4	<i>B. vermiformis</i>	3 specimens; poorly preserved	Mo	
GSM57241	<i>L. miltoni</i>	incomplete	Ch	
GSM105645	<i>L. miltoni</i>	2 specimens, nearly complete	Leint.	
GSM105651	<i>L. miltoni</i>	2 specimens; 1 nearly complete	Leint.	
GSM105660	<i>L. miltoni</i>	3 specimens	Ch	
<b>NMS</b>				
G188265143	<i>F. leptosoma</i>	well preserved	Leint.	
G1882651511	<i>L. miltoni</i>	well preserved	Leint.	
G1882651512	<i>L. miltoni</i>	well preserved	Leint.	
G1882651513	<i>L. miltoni</i>	well preserved	Leint.	
G1882651514	<i>L. miltoni</i>	well preserved	Leint.	
G1882651515	<i>L. miltoni</i>	well preserved	Leint.	
G1882651516	<i>L. miltoni</i>	well preserved	Leint.	
G1882651517	<i>L. miltoni</i>	well preserved	Leint.	
G1882651518	<i>L. miltoni</i>	well preserved	Leint.	
G1882651519	<i>L. miltoni</i>	incomplete	Leint.	
G18826515110	<i>L. miltoni</i>	nearly complete	Leint.	
G18826515111	<i>L. miltoni</i>	well preserved	Leint.	
G18826515112	<i>L. miltoni</i>	well preserved	Leint.	
G18826515113	<i>L. miltoni</i>	incomplete	Leint.	



TABLE A3.1.6. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>NMS</b>				
G18826515114,16	<i>L. miltoni</i>	2 specimens; nearly complete	Leint.	
G18826515115	<i>L. miltoni</i>	2 specimens	Leint.	
G18826515117	<i>L. miltoni</i>	incomplete	Leint.	
G18826515118	<i>L. miltoni</i>	nearly complete	Leint.	
G18826515119	<i>L. miltoni</i>		Leint.	
G18826515120	<i>L. miltoni</i>		Leint.	
G18826515121	<i>L. miltoni</i>	3 specimens; well preserved	Leint.	
G18826515122	<i>L. miltoni</i>	nearly complete	Leint.	
G1882651521	<i>B. vermiformis</i>	well preserved	Leint.	
G1882651522	<i>B. vermiformis</i>	well preserved	Leint.	
G1882651523	<i>B. vermiformis</i>	Neotype	Leint.	
G1882651524	<i>B. vermiformis</i>	nearly complete	Leint.	
G1882651525	? <i>Bdellacoma</i>	poorly preserved	Leint.	
G1882651526	<i>B. vermiformis</i>	nearly complete	Leint.	
G188265157	<i>F. leptosoma</i>	2 specimens	Leint.	
G1882651591, 3	? <i>Cocaster</i>	well preserved	Leint.	
G1882651592	undet.		Leint.	
G1882651621	<i>S. marstoni</i>	well preserved	Leint.	
G1882651622	<i>S. marstoni</i>	well preserved	Leint.	
G1882651623	<i>S. marstoni</i>	well preserved	Leint.	
G1882651624	<i>S. marstoni</i>	well preserved	Leint.	
G1882651625	<i>S. marstoni</i>		Leint.	
G1882651626	<i>S. marstoni</i>	4 specimens	Leint.	
G1882651627	<i>S. marstoni</i>	23 specimens	Leint.	
G1882651628	<i>S. marstoni</i>	2 specimens	Leint.	
<b>CAMSM</b>				
X7561	<i>B. vermiformis</i>	poorly preserved	Ch	
A37202	<i>B. vermiformis</i>		Leint.	
A37203	<i>B. vermiformis</i>		Leint.	
A37204-10	<i>S. marstoni</i>	c. 12 specimens	Leint.	
A37211-6	<i>S. marstoni</i>	c. 13 specimens	Leint.	
A37217-8	<i>L. miltoni</i>	2 specimens; well preserved	Ch	
A37219	<i>L. miltoni</i>	well preserved	Leint.	
A37220-4	<i>L. miltoni</i>	fragmentary; 72 specimens	Leint.	
A109716	<i>S. marstoni</i>		Ch	
<b>OUM</b>				
C.54	<i>S. marstoni</i>	4 specimens; well preserved	Leint.	
C.510a-b	<i>L. miltoni</i>	well preserved; nearly complete	Leint.	
C.511a-b	<i>L. miltoni</i>	well preserved; incomplete	Leint.	
C.514	<i>F. leptosoma</i>	well preserved	Leint.	
C.517	<i>S. marstoni</i>	well preserved; complete	Ch	
C.16826	<i>L. miltoni</i>		Leint.	
C.16827	<i>L. miltoni</i>		Leint.	
C.16828	<i>L. miltoni</i>	4 specimens; well preserved	Leint.	
C.16829	<i>L. miltoni</i>	large specimen; incomplete	Leint.	
C.16830	<i>L. miltoni</i>		Leint.	
C.16831	<i>L. miltoni</i>	3 specimens; well preserved	Leint.	
C.16832	<i>L. miltoni</i>	3 specimens; well preserved	Leint.	
C.16833	<i>L. miltoni</i>		Leint.	
C.16834	<i>L. miltoni</i>		Leint.	
C.16835	<i>L. miltoni</i>		Leint.	



TABLE A3.1.7. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.16836	L. miltoni		Leint.	
C.16837	L. miltoni		Leint.	
C.16838	F. leptosoma	well preserved; incomplete	Leint.	
C.16839	L. miltoni		Leint.	
C.16840	L. miltoni		Leint.	
C.16841	L. miltoni		Leint.	
C.16842	L. miltoni		Leint.	
C.16843	?S. colvini	nearly complete	Leint.	
C.16844	L. miltoni		Leint.	
C.16845	L. miltoni		Leint.	
C.16846	L. miltoni		Leint.	
C.16847	L. miltoni		Leint.	
C.16848	S. colvini	incomplete	Leint.	
C.16849	L. miltoni		Leint.	
C.16850	L. miltoni		Leint.	
C.16851	L. miltoni		Leint.	
C.16852	L. miltoni		Leint.	
C.16853	L. miltoni		Leint.	
C.16854	L. miltoni		Leint.	
C.16855	L. miltoni		Leint.	
C.16856	L. miltoni		Leint.	
C.16857	L. miltoni	3 specimens	Leint.	
C.16858	L. miltoni	4 specimens; 2 nearly complete	Leint.	
C.16859	L. miltoni		Leint.	
C.16860	L. miltoni		Leint.	
C.16861	L. miltoni		Leint.	
C.16862	L. miltoni		Leint.	
C.16863	L. miltoni		Leint.	
C.16864	L. miltoni		Leint.	
C.16865	L. miltoni		Leint.	
C.16866	L. miltoni		Leint.	
C.16867	L. miltoni		Leint.	
C.16868	L. miltoni		Leint.	
C.16869	L. miltoni		Leint.	
C.16870	L. miltoni		Leint.	
C.16871	L. miltoni		Leint.	
C.16872	L. miltoni		Leint.	
C.16873	L. miltoni		Leint.	
C.16874	L. miltoni		Leint.	
C.16875	L. miltoni		Leint.	
C.16876	L. miltoni		Leint.	
C.16877	L. miltoni		Leint.	
C.16878	L. miltoni		Leint.	
C.16879	L. miltoni		Leint.	
C.16880	L. miltoni		Leint.	
C.16881	L. miltoni		Leint.	
C.16882a-b	L. miltoni		Leint.	
C.16883	L. miltoni		Leint.	
C.16884	L. miltoni		Leint.	
C.16885	L. miltoni		Leint.	
C.16886	L. miltoni		Leint.	
C.16887	L. miltoni		Leint.	
C.16888	L. miltoni		Leint.	



TABLE A3.1.8. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.16889	L. miltoni		Leint.	
C.16890	L. miltoni		Leint.	
C.16891	L. miltoni		Leint.	
C.16892	L. miltoni		Leint.	
C.16893	L. miltoni		Leint.	
C.16894	L. miltoni		Leint.	
C.16895	L. miltoni		Leint.	
C.16896	L. miltoni		Leint.	
C.16897	L. miltoni		Leint.	
C.16898	L. miltoni		Leint.	
C.16899	L. miltoni		Leint.	
C.16900	L. miltoni		Leint.	
C.16901	L. miltoni		Leint.	
C.16902	L. miltoni		Leint.	
C.16903	L. miltoni		Leint.	
C.16904	L. miltoni		Leint.	
C.16905	L. miltoni		Leint.	
C.16906	L. miltoni		Leint.	
C.16907	L. miltoni		Leint.	
C.16908	L. miltoni		Leint.	
C.16909	L. miltoni		Leint.	
C.16910	L. miltoni		Leint.	
C.16911	L. miltoni		Leint.	
C.16912	L. miltoni		Leint.	
C.16913	L. miltoni		Leint.	
C.16914	L. miltoni		Leint.	
C.16915	L. miltoni		Leint.	
C.16916	L. miltoni		Leint.	
C.16917	L. miltoni		Leint.	
C.16918	L. miltoni		Leint.	
C.16919	L. miltoni		Leint.	
C.16920	L. miltoni		Leint.	
C.16921	L. miltoni		Leint.	
C.16922	L. miltoni		Leint.	
C.16923	L. miltoni		Leint.	
C.16924	L. miltoni		Leint.	
C.16925	L. miltoni		Leint.	
C.16926	L. miltoni		Leint.	
C.16927	L. miltoni		Leint.	
C.16928	L. miltoni		Leint.	
C.16929	L. miltoni		Leint.	
C.16930	L. miltoni		Leint.	
C.16931	L. miltoni		Leint.	
C.16932	L. miltoni		Leint.	
C.16933	L. miltoni		Leint.	
C.16934	L. miltoni		Leint.	
C.16935	L. miltoni		Leint.	
C.16936	L. miltoni		Leint.	
C.16937	L. miltoni		Leint.	
C.16938	L. miltoni		Leint.	
C.16939	L. miltoni		Leint.	
C.16940	L. miltoni		Leint.	
C.16941	L. miltoni		Leint.	



TABLE A3.1.9. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.16942	L. miltoni		Leint.	
C.16943	L. miltoni		Leint.	
C.16944	L. miltoni		Leint.	
C.16945	L. miltoni		Leint.	
C.16946	L. miltoni		Leint.	
C.16947	L. miltoni		Leint.	
C.16948	L. miltoni		Leint.	
C.16949	L. miltoni		Leint.	
C.16950	L. miltoni		Leint.	
C.16951	L. miltoni		Leint.	
C.16952	L. miltoni		Leint.	
C.16953	L. miltoni		Leint.	
C.16954	L. miltoni		Leint.	
C.16955	L. miltoni		Leint.	
C.16956	L. miltoni		Leint.	
C.16957	L. miltoni		Leint.	
C.16958	L. miltoni		Leint.	
C.16959	L. miltoni		Leint.	
C.16960	L. miltoni		Leint.	
C.16961	L. miltoni		Leint.	
C.16962	L. miltoni		Leint.	
C.16963	L. miltoni		Leint.	
C.16964	L. miltoni		Leint.	
C.16965	L. miltoni		Leint.	
C.16966	L. miltoni		Leint.	
C.16967	L. miltoni		Leint.	
C.16968	L. miltoni		Leint.	
C.16969	L. miltoni		Leint.	
C.16970	L. miltoni		Leint.	
C.16971	L. miltoni		Leint.	
C.16972	L. miltoni		Leint.	
C.16973	L. miltoni		Leint.	
C.16974	L. miltoni		Leint.	
C.16975	L. miltoni		Leint.	
C.16976	L. miltoni		Leint.	
C.16977	L. miltoni		Leint.	
C.16978	L. miltoni		Leint.	
C.16979	L. miltoni		Leint.	
C.16980	L. miltoni		Leint.	
C.16981	L. miltoni		Leint.	
C.16982	L. miltoni		Leint.	
C.16983	L. miltoni		Leint.	
C.16984	L. miltoni		Leint.	
C.16985	L. miltoni		Leint.	
C.16986	L. miltoni		Leint.	
C.16987	L. miltoni		Leint.	
C.16988	L. miltoni		Leint.	
C.16989	L. miltoni		Leint.	
C.16990	L. miltoni		Leint.	
C.16991	L. miltoni		Leint.	
C.16992	L. miltoni		Leint.	
C.16993	L. miltoni		Leint.	
C.16994	L. miltoni		Leint.	
C.16995	L. miltoni		Leint.	



TABLE A3.1.10. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.16996	L. miltoni		Leint.	
C.16997	L. miltoni		Leint.	
C.16998	L. miltoni		Leint.	
C.16999	L. miltoni		Leint.	
C.17000	L. miltoni		Leint.	
C.17001	L. miltoni		Leint.	
C.17002	L. miltoni		Leint.	
C.17003	L. miltoni		Leint.	
C.17004	L. miltoni		Leint.	
C.17005	L. miltoni		Leint.	
C.17006	L. miltoni		Leint.	
C.17007	L. miltoni		Leint.	
C.17008	L. miltoni		Leint.	
C.17009	F. leptosoma		Leint.	
C.17010	F. leptosoma		Leint.	
C.17011	F. leptosoma, L. miltoni	well preserved	Leint.	
C.17012	F. leptosoma		Leint.	
C.17013	F. leptosoma		Leint.	
C.17014	F. leptosoma		Leint.	
C.17014	F. leptosoma		Leint.	
C.17015	F. leptosoma		Leint.	
C.17016	F. leptosoma		Leint.	
C.17017	F. leptosoma		Leint.	
C.17018	F. leptosoma		Leint.	
C.17019	F. leptosoma		Leint.	
C.17020	F. leptosoma		Leint.	
C.17021	F. leptosoma		Leint.	
C.17022	F. leptosoma		Leint.	
C.17023	F. leptosoma		Leint.	
C.17024	F. leptosoma		Leint.	
C.17025	F. leptosoma		Leint.	
C.17026	F. leptosoma		Leint.	
C.17027	F. leptosoma		Leint.	
C.17028	F. leptosoma		Leint.	
C.17029	F. leptosoma		Leint.	
C.17030	F. leptosoma		Leint.	
C.17031	F. leptosoma		Leint.	
C.17032	F. leptosoma		Leint.	
C.17033	F. leptosoma		Leint.	
C.17034	F. leptosoma		Leint.	
C.17035	F. leptosoma		Leint.	
C.17036	F. leptosoma		Leint.	
C.17037	F. leptosoma		Leint.	
C.17038	F. leptosoma		Leint.	
C.17039	F. leptosoma		Leint.	
C.17040	S. marstoni	27 specimens; well preserved	Leint.	
C.17041	S. marstoni	4 specimens; 2 complete	Leint.	
C.17042	S. marstoni	well preserved; nearly complete	Leint.	
C.17043	S. marstoni		Leint.	
C.17044	S. marstoni	well preserved; nearly complete	Leint.	
C.17045	S. marstoni		Leint.	
C.17046-7	S. marstoni	well preserved; nearly complete	Leint.	
C.17048	S. marstoni	4 specimens; 1 nearly complete	Leint.	
C.17049	S. marstoni	4 specimens	Leint.	



TABLE A3.1.11. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.17050	S. marstoni		Leint.	
C.17051	S. marstoni		Leint.	
C.17054	S. marstoni	8 specimens; 3 complete	Leint.	
C.17055	S. marstoni	6 specimens	Leint.	
C.17056	S. marstoni	6 specimens; 1 nearly complete	Leint.	
C.17057	S. marstoni	6 specimens; 2 nearly complete	Leint.	
C.17059	S. marstoni		Leint.	
C.17060	S. marstoni		Leint.	
C.17061	S. marstoni		Leint.	
C.17064	S. marstoni		Leint.	
C.17065	S. marstoni		Leint.	
C.17066	S. marstoni		Leint.	
C.17067	S. marstoni		Leint.	
C.17068	S. marstoni		Leint.	
C.17069	S. marstoni	7 specimens	Leint.	
C.17070	S. marstoni	3 specimens	Leint.	
C.17073	S. marstoni		Leint.	
C.17074	S. marstoni		Leint.	
C.17075	S. marstoni	5 specimens	Leint.	
C.17076	S. marstoni		Leint.	
C.17077	S. marstoni		Leint.	
C.17078	S. marstoni		Leint.	
C.17079	S. marstoni	3 specimens; 1 complete	Leint.	
C.17080	S. marstoni	5 specimens	Leint.	
C.17081	S. marstoni		Leint.	
C.17082	S. marstoni	6 specimens; 2 nearly complete	Leint.	
C.17083	S. marstoni		Leint.	
C.17084	S. marstoni		Leint.	
C.17085	S. marstoni		Leint.	
C.17086	S. marstoni		Leint.	
C.17087	S. marstoni		Leint.	
C.17088	S. marstoni	2 specimens	Leint.	
C.17089	S. marstoni		Leint.	
C.17090	S. marstoni		Leint.	
C.17093	S. marstoni		Leint.	
C.17094	S. marstoni		Leint.	
C.17095-6	S. marstoni		Leint.	
C.17097	S. marstoni		Leint.	
C.17098	S. marstoni	4 specimens; 2 complete	Leint.	
C.17099-C17100	S. marstoni, ?B. vermiformis		Leint.	
C.17101	S. marstoni		Leint.	
C.17102	S. marstoni	3 specimens	Leint.	
C.17103-4	S. marstoni	9 specimens	Leint.	
C.17105	B. vermiformis		Leint.	
C.17106	B. vermiformis	nearly complete	Leint.	
C.17107	B. vermiformis		Leint.	
C.17108	B. vermiformis	well preserved; Incomplete	Leint.	
C.17109	B. vermiformis	well preserved; Incomplete	Leint.	
C.17110	B. vermiformis	Incomplete	Leint.	
C.17111	B. vermiformis		Leint.	
C.17112	B. vermiformis	poorly preserved	Leint.	
C.17113	B. vermiformis	poorly preserved	Leint.	
C.17114	undet.		Leint.	
C.17115a-b	?Rhopalocoma		Leint.	



TABLE A3.1.12. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
OUM				
C.17116	undet.		Leint.	
C.17117	B. vermiformis, ?S. marstoni	poorly preserved	Leint.	
C.17118	undet.		Leint.	
C.17119	?Bdellacoma		Leint.	
C.17120	?Bdellacoma		Leint.	
C.17121	undet.		Leint.	
C.17122	?Bdellacoma		Leint.	
C.17123	undet.		Leint.	
C.17124	undet.		Leint.	
C.17125	undet.		Leint.	
C.17126	?Furcaster		Leint.	
C.17127	undet.		Leint.	
C.17128	S. marstoni		Leint.	
C.17129	?Sturtzaster		Leint.	
C.17130	undet.		Leint.	
C.17131	undet.		Leint.	
C.17132	S. marstoni		Leint.	
C.17133	?Sturtzaster		Leint.	
C.17290	R. pyrotechnica	poorly preserved; nearly complete	Leint.	
C.17291	F. leptosoma	well preserved; complete	Leint.	
C.20213	undet.		Leint.	
C.20214	undet.		Leint.	
C.20215	undet.		Leint.	
C.20216	undet.		Leint.	
C.20217	?Rhopalocoma		Leint.	
C.20218	undet.		Leint.	
C.20219	?S. marstoni		Leint.	
C.20220	undet.		Leint.	
C.20221	undet.		Leint.	
C.20222	L. miltoni	nearly complete	Leint.	
C.20223	undet.		Leint.	
C.27921	R. pyrotechnica	well preserved; incomplete	Leint.	
C.30631a-b	S. marstoni	4 specimens; 2 complete	Leint.	
C.30632	S. marstoni	arm portion	Leint.	
C.30633	S. marstoni		Leint.	
IPSM				
G19252911a	B. vermiformis	poorly preserved	?Ch	
G19252912	F. leptosoma	Neotype	?Ch	
G19252917	F. leptosoma	well preserved	?Ch	
G19252919	S. marstoni	incomplete	Leint.	
G19252921	S. marstoni	6 specimens	?Ch	
MM				
L11003	R. pyrotechnica	(cp to BMNH E 13951)	Ch	
L11004	R. pyrotechnica	incomplete	Ch	
L11020	U. ruthveni	well preserved; complete	Ch	



TABLE A3.1.13. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>NMVP</b>				
P11404-5	<i>L. miltoni</i>	2 specimens; well preserved	Ch	
P11406-9	<i>R. pyrotechnica</i>	well preserved	Ch	
P11410-1	<i>L. miltoni</i>		Ch	
P11412-6	<i>S. marstoni</i>	7 specimens; well preserved	Ch	
P11417-20	<i>B. vermiformis</i>	4 specimens; well preserved	Ch	
P11421-2	<i>R. pyrotechnica</i>	2 specimens	Ch	
P26173	<i>L. miltoni</i>		Leint.	
P26174	<i>L. miltoni</i>		Leint.	
P26175	<i>L. miltoni</i>		Ch	
P27176	<i>S. marstoni</i>		?Ch	
P26177	<i>S. colvini</i>		Ch	
P26178	? <i>Sturtzaster</i>	small specimen	Ch	
P26179	? <i>Sturtzaster</i>	small specimen	Ch	
P26180	<i>L. miltoni</i>		Leint.	
P26181	undet.	very small specimen	?Ch	
P74312	<i>L. miltoni</i>		Leint.	
P74313	<i>L. miltoni</i>		Leint.	
P74314	<i>L. miltoni</i>		Leint.	
P74315	<i>L. miltoni</i>		Leint.	
P74316	<i>L. miltoni</i>		Leint.	
P74317	<i>S. marstoni</i>		Leint.	
<b>SHRCM</b>				
G3816	<i>S. marstoni</i>	well preserved	Ch	
G3819	<i>F. leptosoma</i>	nearly complete	Ch	
G7550	<i>S. marstoni</i>	3-4 specimens	Ch	
G7551	<i>L. miltoni</i>		Ch	
G7552	<i>S. marstoni</i> ; <i>L. miltoni</i>	Fragmentary; poorly preserved	Ch	
G7553	<i>F. leptosoma</i>	poorly preserved	Ch	
G7554	<i>B. vermiformis</i>	poorly preserved	Leint.	
G7555	<i>B. vermiformis</i>		Leint.	
G7557	undet.	poorly preserved	Ch	
G7557A	<i>B. vermiformis</i>		Leint.	
G7558	undet.	poorly preserved	Ch	
G7559	undet.	poorly preserved		
G7560	undet.	poorly preserved	Ch	
G7561	undet.	poorly preserved	Ch	
G7562	<i>L. miltoni</i>	incomplete	Ch	
G7563	<i>L. miltoni</i>	incomplete	Ch	
G7564	<i>L. miltoni</i>	arm fragment	Ch	
G7704	<i>Sturtzaster</i>		Ch	
<b>HFDMG</b>				
G1317	? <i>Bdellacoma</i>		Ch	
G1320	<i>F. leptosoma</i>		Ch	
G1321-2	<i>L. miltoni</i>		Leint.	
G1323	<i>F. leptosoma</i>		Ch	
G1324	<i>L. miltoni</i>		Ch	
G1325	<i>L. miltoni</i>		Ch	
G1326	<i>L. miltoni</i>		Leint.	
G1327	<i>L. miltoni</i>		Leint.	
G1328	<i>L. miltoni</i>		Ch	
G1329	<i>Sturtzaster</i>		Leint.	



TABLE A3.1. 14. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>HFDMG</b>				
G1330	<i>S. marstoni</i>		Ch	
G1331	<i>S. marstoni</i>		Leint.	
G1332	<i>S. marstoni</i>		Ch	
G1333	<i>F. leptosoma</i>		Mo	
G1766	<i>S. marstoni</i>		Ch	
G1767	<i>L. miltoni</i>		Ch	
G1768	<i>S. marstoni</i>		Ch	
<b>LEIUG</b>				
117531	<i>F. leptosoma</i> , <i>L. miltoni</i> , ? <i>Sturtzaster</i>		Ch	
117532	<i>Lapworthura</i>	arm fragment	Ch	
117533	<i>Lapworthura</i>	arm fragment	Ch	
117534	<i>Furcaster</i>	arm fragment	Ch	
117535	<i>Furcaster</i>	arm fragment		
<b>Newly Collected</b>				
	(Church Hill specimens from Quarry 1)			
MOCK1	? <i>Furcaster</i>	10 specimens; poorly preserved	Mo	Mocktree
MOCK2	? <i>Furcaster</i>	poorly preserved	Mo	Mocktree
MOCK3	undet.	very poorly preserved	Mo	Mocktree
MOCK5a-b	? <i>Furcaster</i>	poorly preserved	Mo	Mocktree
CH34	<i>F. leptosoma</i>		Ch	SBA
CH38a-b	<i>F. leptosoma</i> , <i>L. miltoni</i>	incomplete	Ch	SBA
CH39a-b	<i>L. miltoni</i>	poorly preserved; incomplete	Ch	SBA
CH40a-b	<i>F. leptosoma</i> , <i>L. miltoni</i>		Ch	SBA
CH43a-b	<i>L. miltoni</i>	incomplete	Ch	SBA
CH54	<i>F. leptosoma</i>	well preserved; nearly complete	Ch	SBA
CH70a-b	<i>F. leptosoma</i> x2, <i>L. miltoni</i>	nearly complete	Ch	SBA
CH71a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH72a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH73a-b	<i>F. leptosoma</i>	incomplete	Ch	SBA
CH74a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH75a-c	<i>F. leptosoma</i> , <i>L. miltoni</i>	incomplete	Ch	SBA
CH76a-b	<i>F. leptosoma</i>		Ch	SBA
CH77a-b	<i>F. leptosoma</i>	well preserved; nearly complete	Ch	SBA
CH78a-b	<i>F. leptosoma</i> x5, <i>L. miltoni</i>	well preserved	Ch	SBA
CH79a-b	<i>L. miltoni</i>	arm portion	Ch	SBA
CH80a-b	<i>F. leptosoma</i> x2, <i>L. miltoni</i>		Ch	SBA
CH81	<i>F. leptosoma</i>	2 specimens	Ch	SBA
CH82a-b	<i>L. miltoni</i>	incomplete	Ch	SBA
CH83a-b	<i>F. leptosoma</i>	3 specimens; 2 nearly complete	Ch	SBA
CH84a-b	<i>L. miltoni</i>		Ch	SBA
CH85a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH86a-b	<i>F. leptosoma</i>	well preserved	Ch	SBA
CH87a-b	? <i>Furcaster</i>	incomplete	Ch	SBA
CH88a-b	<i>F. leptosoma</i>	well preserved	Ch	SBA
CH89a-b	<i>L. miltoni</i>	poorly preserved; incomplete	Ch	SBA
CH90a-b	<i>L. miltoni</i>	arm portion	Ch	SBA
CH91a-b	<i>L. miltoni</i>	2 specimens; incomplete	Ch	CHQ1
CH92a-b	<i>L. miltoni</i>	incomplete	Ch	SBA
CH93a-b	<i>L. miltoni</i>	arm portion	Ch	SBA
CH94a-b	<i>B. vermiformis</i>	well preserved; nearly complete	Ch	SBA
CH95a-b	<i>L. miltoni</i> , <i>F. leptosoma</i>	incomplete	Ch	SBA
CH96a-b	<i>L. miltoni</i>	arm portion	Ch	SBA
CH97a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA



TABLE A3.1.15. Stelleroids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
Newly Collected	(Church Hill specimens from quarry 1)			
CH98a-b	<i>F. leptosoma</i>	well preserved	Ch	SBA
CH99a-b	undet.	poorly preserved; incomplete	Ch	SBA
CH100a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH101a-b	<i>F. leptosoma</i>	incomplete	Ch	SBA
CH102	<i>F. leptosoma</i>	well preserved; incomplete	Ch	SBA
CH103a-b	<i>F. leptosoma</i>	nearly complete	Ch	
CH139a-b	?Furcaster	poorly preserved; incomplete	Ch	SBA
CH143a-b	<i>R. pyrotechnica</i>	incomplete	Ch	
CH210	<i>S. marstoni</i>		Ch	
CH211a-b	<i>B. vermiformis</i>	nearly complete	Ch	
CH213a-b	<i>Loriolaster</i>	2 specimens; well preserved	Ch	
CH215a-b	<i>S. colvini</i>	well preserved; nearly complete	Ch	
CH250a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH251a-b	<i>L. miltoni</i>	well preserved; incomplete	Ch	SBA
CH252a-b	<i>L. miltoni</i>	2 specimens; well preserved	Ch	SBA
CH253a-b	<i>L. miltoni</i>	incomplete	Ch	SBA
CH254a-b	<i>L. miltoni</i>	2 arm portions	Ch	SBA
CH255	?Furcaster	poorly preserved	Ch	SBA
CH256a-b	?Furcaster	small; incomplete	Ch	SBA
CH257a-b	<i>F. leptosoma</i>	small specimen	Ch	SBA
CH258a-b	<i>S. marstoni</i> x2, ?Furcaster, undet. specimen		Ch	
CH259a-b	<i>F. leptosoma</i>	poorly preserved; incomplete	Ch	SBA
CH262a-b	<i>B. vermiformis</i>	2 specimens; well preserved	Ch	SBA
CH263a-b	<i>L. miltoni</i>	incomplete	Ch	SBA
CH268	<i>L. mitloni</i>	incomplete	Ch	SBA
MS21	undet. sp.	poorly preserved arm portion	MS	



TABLE A3.2.1. Crinoids; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA); Church Hill Quarry 1 (CHQ1).

Specimen	Taxon	Description	Channel	Locality
<b>BMNH</b>				
40290	<i>G. ludensis</i>	poorly preserved	Leint.	
40292	undet. sp.	poorly preserved	Leint.	
40309	<i>Gissocrinus?</i> sp.	poorly preserved	Leint.	
40311	<i>C. quinquepennis</i>	nearly complete	Leint.	
46753	undet. sp.	nearly complete	Leint.	
EE 958	<i>C. elegans</i>		Ch	
E 1258	undet. sp.	brachia, incomplete	Ch	
E 1301	undet. sp.	incomplete	Leint.	
E 1314	<i>E. maccoyanus</i>	nearly complete	Leint.	
E 5668	<i>C. quinquepennis</i>	incomplete	Leint.	
E 7014	undet. sp.	poorly preserved	Ch	
E 7344	undet. sp.	incomplete	Ch	
E 7345	undet. sp.	stem	Ch	
E 7347	undet. sp.	incomplete	Ch	
E 14898	<i>C. quinquepennis</i>	2 specimens	Leint.	
E 14899	<i>C. quinquepennis</i>	nearly complete	Leint.	
E 14900	<i>C. quinquepennis</i>	Paratype	Leint.	
E 14901	<i>G. ludensis</i>	nearly complete	Leint.	
E 14902	<i>G. ludensis</i>	poorly preserved	Leint.	
E 14903	undet. sp.	poorly preserved	Leint.	
E 14904	<i>C. quinquepennis</i>	calyx, brachia	Leint.	
E 26573	<i>G. ludensis</i>	Holotype	Ch	
E 26574	<i>Dendrocrinus?</i> sp.	complete	Ch	
E 26575	<i>C. quinquepennis</i>		Leint.	
E 26576a-c	<i>C. quinquepennis</i>	Holotype	Ch	
E 26577	<i>G. ludensis</i>	Paratype	Ch	
E 26578	<i>E. maccoyanus</i>	nearly complete	Ch	
E 68719	undet. sp.	nearly complete	Leint.	
E 68720	undet. sp.	nearly complete	Leint.	
<b>BGS</b>				
GSM89897	<i>C. quinquepennis</i>	nearly complete	Leint.	
GSM89898-89900	<i>C. quinquepennis</i>	nearly complete	Leint.	
GSM89901-4	<i>C. quinquepennis</i>	nearly complete	Ch	
GSM89987	undet. sp.	poorly preserved	Ch	
GSM89989	<i>E. maccoyanus</i>	nearly complete	Leint.	
GSM89990	undet. sp.	nearly complete	Leint.	
GSM89991	<i>C. quinquepennis</i>		Leint.	
GSM89992	undet. sp.	poorly preserved	Leint.	
GSM89993	<i>M. bravoniensis</i>		Leint.	
GSM89994	<i>M. bravoniensis</i>	Holotype	Leint.	
GSM90006-7	undet. sp.		Leint.	



TABLE A3.2.2. Crinoids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>OUM</b>				
C.17154	undet. sp.		Leint.	
C.17155	undet. sp.		Leint.	
C.17156	undet. sp.		Leint.	
C.17157a-b	undet. sp.		Leint.	
C.17158	undet. sp.		Leint.	
C.17159	undet. sp.		Leint.	
C.17161a-b	undet. sp.		Leint.	
C.17162a-b	undet. sp.		Leint.	
C.17163	undet. sp.		Leint.	
C.17164	undet. sp.		Leint.	
C.17165	undet. sp.		Leint.	
C.17167a-b	undet. sp.	nearly complete	Leint.	
C.17168	undet. sp.		Leint.	
C.17169	undet. sp.		Leint.	
C.17170	undet. sp.		Leint.	
C.17171	undet. sp.		Leint.	
C.17172	undet. sp.		Leint.	
C.17173	undet. sp.		Leint.	
C.17174	undet. sp.		Leint.	
C.17175	undet. sp.		Leint.	
C.17176	undet. sp.		Leint.	
C.17177	undet. sp.		Leint.	
C.17178	undet. sp.		Leint.	
C.17179	undet. sp.		Leint.	
C.17180	undet. sp.		Leint.	
C.17181	undet. sp.	Fragmentary	Leint.	
C.17182	undet. sp.		Leint.	
C.17183	undet. sp.		Leint.	
C.17184a-b	undet. sp.		Leint.	
C.17185a-b	undet. sp.		Leint.	
C.17186a-b	undet. sp.		Leint.	
C.20938	undet. sp.		Leint.	
<b>Newly Collected</b>				
	(all specimens from Church Hill Quarry 1)			
CH101	C. quinquepennis	incomplete	Ch	SBA
CH105	Clematocrinus? sp.	part of brachia	Ch	SBA
CH106a-b	C. quinquepennis	well preserved; missing column	Ch	SBA
CH107a-b	Clematocrinus? sp.	incomplete	Ch	SBA
CH108a-b	Clematocrinus? sp.	part of brachia	Ch	SBA
CH109a-b	Clematocrinus? sp.	part of brachia	Ch	SBA
CH111a-c	C. quinquepennis	2 specimens; incomplete	Ch	SBA
CH112a-b	Clematocrinus? sp.	part of brachia	Ch	SBA
CH113a-b	undet. sp.	poorly preserved	Ch	SBA
CH114	Clematocrinus? sp.	part of brachia	Ch	SBA
CH115	C. quinquepennis	nearly complete; missing column	Ch	SBA
CH116a-b	Clematocrinus? sp.	part of brachia	Ch	SBA
CH118a-b	E. maccoyanus	well preserved; nearly complete	Ch	SBA
CH119a-b	C. quinquepennis	nearly complete	Ch	SBA
CH120a-b	M. bravoniensis	well preserved; nearly complete	Ch	CHQ1



TABLE A3.3.1. Echinoids; Leintwardine. Locality notes: “upper starfish bed of Hawkins & Hampton (1927), Church Hill Quarry”, based on museum slip (\*).

Specimen	Taxon	Description	Channel	Locality
BMNH				
9558	<i>P. ferox</i>		Leint.	
40155	<i>P. ferox</i>		Leint.	
40156	<i>E. pomum</i>	incomplete	Ch	
40157	<i>E. pomum</i>	nearly complete	Leint.	
40158	<i>E. pomum</i>	nearly complete	Ch	
40306	<i>P. ferox</i>		Ch	
40307	<i>P. ferox</i>	nearly complete	Leint.	
47956	<i>E. pomum</i>	nearly complete	Leint.	
47957	<i>P. ferox</i>		Leint.	
57022	<i>P. ferox</i>	complete	Leint.	
E 1252	<i>P. ferox</i>	nearly complete	Ch	
E 1256	<i>E. pomum</i>	nearly complete		
E 1300	<i>E. pomum</i>		Leint.	
E 1482	<i>P. ferox</i>	complete	Ch	
E 7714	? <i>E. pomum</i>	nearly complete	Ch	
E 9558	<i>P. ferox</i>	nearly complete	Ch	
E 9559	<i>P. ferox</i>	incomplete	Ch	
E 10655	<i>P. ferox</i>	nearly complete	Leint.	
E 10656	<i>E. pomum</i>		Leint.	
E 34352	<i>E. pomum</i>	Lectotype	Ch	
E 34360	<i>P. ferox</i>	nearly complete	Ch	
E 34361	<i>P. ferox</i>		Ch	
E 34362	<i>P. ferox</i>	complete	Ch	
E 75595	<i>E. pomum</i>	nearly complete	Ch	*
E 75596a-b	<i>E. pomum</i>	nearly complete	Ch	*
E 75597a-b	<i>P. ferox</i>	complete	Ch	*
E 75598a-b	<i>P. ferox</i>	complete	Ch	*
E 76648	<i>P. ferox</i>	complete	Leint.	
E 76649	<i>P. ferox</i>		Leint.	
BGS				
?	<i>E. pomum</i>	3 specimens	Leint.	
GSM7385	<i>E. pomum</i>	nearly complete	Leint.	
GSM47576	<i>E. pomum</i>	poorly preserved	Leint.	
GSM47577	<i>P. ferox</i>	nearly complete	Leint.	
GSM49772	<i>P. ferox</i>	poorly preserved	Leint.	
GSM49773-4	<i>P. ferox</i>	incomplete	Leint.	
GSM87361	<i>P. ferox</i>	complete	Ch	
OUM				
C.50	<i>E. pomum</i>	nearly complete	Leint.	
C.51	<i>E. pomum</i>		Leint.	
C.58	<i>P. ferox</i>		Leint.	
C.59	<i>P. ferox</i>		Leint.	
C.60	<i>P. ferox</i>		Leint.	
C.61	<i>P. ferox</i>	nearly complete	Leint.	



TABLE A3.3.2. Echinoids; Leintwardine

Specimen	Taxon	Description	Channel	Locality
OUM				
C.17135	P. ferox		Leint.	
C.17136	E. pomum		Leint.	
C.17137	E. pomum		Leint.	
C.17138	P. ferox		Leint.	
C.17139	E. pomum		Leint.	
C.17140	E. pomum		Leint.	
C.17141	E. pomum		Leint.	
C.17142	E. pomum		Leint.	
C.17143	E. pomum		Leint.	
C.17144	P. ferox		Leint.	
C.17145	P. ferox		Leint.	
C.17146	P. ferox		Leint.	
C.17147	P. ferox		Leint.	
C.17148	P. ferox		Leint.	
C.17149	P. ferox		Leint.	
C.17150	P. ferox		Leint.	
C.17151	P. ferox		Leint.	
C.17152	P. ferox		Leint.	
C.17153	P. ferox		Leint.	
CAMSM				
A60379	E. pomum		Leint.	
A60380	E. pomum		Leint.	
A60381	E. pomum		Ch	
SHRCM				
?	E. pomum	poorly preserved	Ch	



TABLE A3.4.1. Ophiocistioids; Leintwardine. Locality notes: no precise locality information.

Specimen	Taxon	Description	Channel	Locality
BMNH				
57780	S. woodwardi	Paratype	Ch	
E 27030a-b	S. woodwardi	2 specimens, nearly complete	Ch	
OUM				
C.43	S. woodwardi	Holotype	Leint.	
C.44	S. woodwardi	Lectotype	Leint.	
C.45	S. woodwardi	Paratype	Leint.	
C.46	S. woodwardi	Paratype	Leint.	
C.47	S. woodwardi	Paratype	Leint.	
C.409	S. woodwardi	Paratype	Leint.	
C.410	S. woodwardi	Paratype	Leint.	
C.411	S. woodwardi	Paratype	Leint.	
C.412	S. woodwardi		Leint.	
C.413	S. woodwardi		Leint.	
NMS				
G1882651541	S. woodwardi	nearly complete	Leint.	
G1882651542	S. woodwardi	incomplete	Leint.	
G1882651543	S. woodwardi	incomplete	Leint.	
G1882651544	S. woodwardi	incomplete	Leint.	
Banks Collection				
1681-2	S. woodwardi	2 complete specimens	Leint.	



TABLE A3.5.1. Eurypterids; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA); Church Hill Quarry 1 (CHQ1); Martin's Shell Quarry (MS); Mocktree Quarry (Mocktree); Brandon Quarry, SO47 4072 7230 (Brandon\*); Brandon Hill (Brandon\*\*).

Specimen	Taxon	Description	Channel	Locality
BMNH				
?	undet.	tergite	Ch	
?	undet.	?coxa	Ch	
2015	undet.	cuticle	Leint.	
4033	undet.	cuticle	Ch	
39384	undet.	part of telson?	Ch	
39385	undet.		Ch	
39386	S. (?) longilabium	Holotype	Ch	
39387	Carcinosoma sp.	prosomal appendage III, IV or V	Ch	
39388	undet.	gnathobase	Ch	
39389	C. punctatum	prosomal appendage VI, tergite	Ch	
39391	undet.	?part of metastoma	Leint.	
39394	E. marstoni	free ramus; incomplete	Ch	
39395	undet.	gnathobase	Ch	
39396	Erettopterus? sp.	(metastoma (cp to GSM89601?))	Leint.	
39397	undet.	tergite	Ch	
39398	undet. pterygotid	part of ramus	Ch	
39399	Carcinosoma sp.	prosomal appendage III, IV or V	Leint.	
39406	undet.	cuticle	Ch	
41892	undet.	gnathobase	Ch	
43788	P. arcuatus	Lectotype; free ramus	Ch	
43789	Carcinosoma sp.	prosomal appendage III, IV or V	Ch	
48420	undet.		Ch	
59222	Carcinosoma sp.	metastoma	Leint.	
60038	undet.		Leint.	
I. 1177	undet.	cuticle	Ch	
I. 1177	undet.	coxa & gnathobase	Ch	
I. 1177	Carcinosoma? sp.	part of prosomal appendage	Ch	
I. 4152	undet.		Leint.	
In. 4151	undet.		Leint.	
In. 43786	undet. pterygotid	infracapitulum & p. appendage II	Ch	
In. 43787	undet.	gnathobase	Ch	
In. 43790	E. marstoni	Holotype; free ramus	Ch	
In. 43793	undet.	cuticle	Ch	
In. 43804	C. punctatum	prosomal appendage VI	Ch	
In. 43805	E. marstoni	Paratype; fixed ramus	Ch	
In. 43811	Carcinosoma sp.	proximal prosomal appendage VI	Ch	
In. 43888	undet.	cuticle	Ch	
In. 43890	undet.	?tergites	Ch	
In. 48405	Carcinosoma sp.	prosomal appendage III, IV or V	Ch	
In. 48406	undet.		Ch	
In. 48407	undet.		Ch	
In. 48408	undet.	cuticle	Ch	
In. 48409	undet.	coxa & gnathobase	Ch	
In. 48410	undet.	cuticle	Ch	
In. 48411	undet.	cuticle	Ch	
In. 48412	Carcinosoma? sp.	(cp to 4164); prosomal appendage	Ch	
In. 48413	Carcinosoma? sp.	prosomal appendage II?	Ch	
In. 48414	undet.	coxa & gnathobase	Ch	
In. 48415	undet.	cuticle	Ch	
In. 61781	undet.	?prosomal appendage I?	Leint.	



TABLE A3.5.2. Eurypterids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
BGS				
GSM89551	undet.		Ch	
GSM89552	Carcinosoma sp.	prosomal appendage	Ch	
GSM89553	undet.		Ch	
GSM89555	undet.	tergite	Ch	
GSM89556	undet.		Ch	
GSM89557	undet.	tergite	Ch	
GSM89558	undet.	tergite	Ch	
GSM89559	undet.	cuticle	Ch	
GSM89560	undet.	?metastoma	Ch	
GSM89561	C. punctatum	prosomal appendage VI	Ch	
GSM89562	undet.	tergite	Ch	
GSM89563	undet.		Ch	
GSM89564	undet.	tergite	Ch	
GSM89565	Carcinosoma? sp.	prosomal appendage II?	Ch	
GSM89566	undet.	tergite	Ch	
GSM89567	undet.	gnathobase	Ch	
GSM89568	C. punctatum	distal prosomal appendage VI	Ch	
GSM 89569	undet.	coxa & gnathobase	Ch	
GSM89572	undet.		Leint.	
GSM89573	Pterygotus? sp.	free ramus	Ch	
GSM89574	undet.	tergite	Leint.	
GSM89575	undet.	tergite	Leint.	
GSM89576	undet.	tergite	Leint.	
GSM89577	undet.		Leint.	
GSM89578	undet.		Leint.	
GSM89579	S. (?) longilabium	cuticle	Leint.	
GSM89580	Carcinosoma sp.	prosomal appendage III, IV or V	Ch	
GSM89581	Carcinosoma? sp.	chelicera	Ch	
GSM 89582	undet.		Leint.	
GSM89583	Carcinosoma? sp.	prosomal appendage II?	Leint.	
GSM89584	undet.	(cp to GSM89575)	Leint.	
GSM89585	Carcinosoma sp.	prosomal appendage	Leint.	
GSM89586	undet.	?telson	Leint.	
GSM89587	undet.	gnathobase	Leint.	
GSM89589	Carcinosoma sp.	prosomal appendage III, IV or V	Leint.	
GSM89590	Carcinosoma sp.	prosomal appendage III, IV or V	Leint.	
GSM89591	Carcinosoma? sp.	prosomal appendage	Leint.	
GSM89592	Carcinosoma sp.	(cp to BMNH In 43811)	Ch	
GSM89593	undet.		Leint.	
GSM89594	undet.		Ch	
GSM89595	undet.		Leint.	
GSM89596-7	undet.	coxa & gnathobase	Leint.	
GSM89599	Erettopterus? sp.	genital appendage	Leint.	
GSM89600	undet.	tergite	Ch	
GSM89601	Erettopterus? sp.	(?cp to BMNH 39396)	Ch	
GSM89602	undet.	tergite	Leint.	
GSM89603	undet.	metastoma	Ch	
GSM89604	undet.	cuticle	Leint.	
CAMSM				
A37379	undet.		Leint.	
A37997	undet.	tergite	Leint.	



TABLE A3.5.3. Eurypterids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>OUM</b>				
C.139	undet.		Leint.	
C.140	undet.	gnathobase	Leint.	
C.141	undet.		Leint.	
C.20173	undet.		Leint.	
C.20197	undet.		Leint.	
C.20200	undet.		Leint.	
C.20201	undet.		Leint.	
C.20204	undet.		Leint.	
C.20206	undet.		Leint.	
C.20207	undet.		Leint.	
C.20208	undet.		Leint.	
C.20209	undet.		Leint.	
C.20210	undet.		Leint.	
C.20211a-b	undet.		Leint.	
C.20212a-b	undet.		Leint.	
C.29250a-b	undet.		Leint.	
<b>SHRCM</b>				
?	undet.	?cuticle	Ch	
?	undet.	cuticle	Ch	
?	undet.	cuticle	Ta	Brandon*
?	undet.	? part of prosoma	Ch	
?	undet.	?part of prosomal appendage	Ch	
?	undet.	?part of prosomal appendage	Ch	
?	undet.	?part of prosoma	Ch	
?	undet.	gnathobase	Ta	Brandon**
G6381	undet.	?cuticle	Ch	
G6396	undet.	cuticle	To	
G6403	undet.	tergite	Ch	
G6411	undet.	?coxa; poorly preserved	Ch	
G10445	undet.	gnathobase; well preserved	Ch	
G10451a-b	undet.	?part of prosomal appendage	Ta	Brandon*
<b>HFDMG</b>				
G87	C. punctatum	distal prosomal appendage VI	?	
<b>Newly collected</b>				
(Church Hill specimens from Quarry 1)				
MOCK10	undet.	cuticle	Mo	Mocktree
MS24	undet.	cuticle	To	MS
CH30a-b	undet.	cuticle	Ch	CHQ1
CH32a-b	undet.	?tergite	Ch	SBA
CH41	undet.	?distal prosomal appendage VI	Ch	SBA
CH61a-b	undet.	?tergite	Ch	SBA
CH135a-b	undet.	?tergite	Ch	SBA
CH136	Carcinosoma? sp.	proximal prosomal appendage VI	Ch	SBA
CH137a-b	undet.	cuticle	Ch	SBA
CH140a-b	undet.	cuticle	Ch	SBA
CH141a-b	undet.	cuticle	Ch	SBA
CH142a-b	undet.	tergite	Ch	SBA
CH144	undet.	prosoma	Ch	SBA
CH146a-b	Carcinosoma sp.	prosomal appendage III, IV or V	Ch	CHQ1
CH147	Carcinosoma? sp.	opisthosoma	Ch	CHQ1



TABLE A3.6.1. Xiphosurans; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA).

Specimen	Taxon	Description	Channel	Locality
<b>BMNH</b>				
I. 125	<i>C. loganensis</i>		Leint.	
In. 39408	<i>Limuloides</i>	prosoma	Leint.	
In. 48422	<i>L. limuloides</i>	opisthosoma,telson	Ch	
In. 48423	<i>L. limuloides</i>	opisthosoma,telson	Ch	
In. 48428	<i>Pseudoniscus</i>	complete specimen	Ch	
In. 60018	<i>L. limuloides</i>	complete specimen	Leint.	
In. 61511	<i>Limuloides</i>	Prosoma	Leint.	
<b>BGS</b>				
GSM32393	<i>L. limuloides</i>	complete specimen	Leint.	
GSM36756	? <i>Limuloides</i>	prosoma,opisthosoma	Leint.	
GSM82609-10	<i>Limuloides</i>	prosoma	Leint.	
GSM89607	<i>L. limuloides</i>	prosoma	Leint.	
GSM89611	<i>Limuloides</i>	prosoma	Leint.	
GSM89612	<i>L. limuloides</i>	nearly complete	Ch	
GSM89613	<i>L. limuloides</i>	prosoma	Ch	
GSM89616	<i>Limuloides</i>	prosoma	Leint.	
<b>OUM</b>				
C.721-722	<i>L. limuloides</i>	prosoma	Leint.	
C.17188	<i>Limuloides</i>	prosoma	Leint.	
C.20151	<i>C. loganensis</i>	nearly complete	Leint.	
<b>Newly collected</b>				
CH145	<i>L. limuloides</i>	prosoma	Ch	SBA



TABLE A3.7.1. Phyllocarids; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA); Church Hill Quarry 1 (CHQ1); Trippleton Lane, Church Hill (Trippleton); Martin's Shell Quarry (MS); Mocktree Quarry (Mocktree); Brandon Camp SO47 4028 7265 (Brandon\*); Brandon Hill SO47 4072 7230 (Brandon\*\*); Brandon Hill SO47 4027 7261 (Brandon Hill\*\*\*); Brandon localities based on museum slips.

Specimen	Taxon	Description	Channel	Locality
<b>BMNH</b>				
?	<i>C. cf. papilio</i>	carapace	Leint.	
1167	<i>C. cf. papilio</i>	carapace	Ch	
1169	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
1170	<i>C. cf. papilio</i>	carapace & abdomen	Leint.	
1179	undet.		Ch	
3397	undet.		Leint.	
4146	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
4147	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
4148	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
4156	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
5670	<i>C. cf. papilio</i>	abdomen; disarticulated	Ch	
19137-9	<i>C. cf. papilio</i>	3 specimens; nearly complete	To	MS
35583	<i>C. cf. papilio</i>	telson; nearly complete	To	
37709	<i>C. cf. papilio</i>	distal abdomen & telson	Leint.	
39400	<i>C. cf. papilio</i>	carapace & abdomen	Ch	
39401	<i>C. cf. papilio</i>	carapace; poorly preserved	Ch	
39404	<i>C. cf. papilio</i>	telson	Leint.	
39405	<i>C. cf. papilio</i>	part of telson	Leint.	
39817	<i>C. cf. papilio</i>	carapace	Ch	
43888	<i>C. cf. papilio</i>	part of carapace	Ch	
43889	<i>C. cf. papilio</i>	nearly complete	Ch	
43890	<i>C. cf. papilio</i>	incomplete	Ch	
43891	<i>C. cf. papilio</i>	nearly complete	Ch	
43892	<i>C. cf. papilio</i>	abdomen & telson	Ch	
43894a-b	<i>C. cf. papilio</i>	2 specimens; incomplete	Ch	
43896	<i>C. cf. papilio</i>	telson	Ch	
43898	<i>C. cf. papilio</i>	distal abdomen & telson	Ch	
48386	<i>C. cf. papilio</i>	telson; incomplete	?Ch	
48399	<i>C. cf. papilio</i>	telson	?Ch	
48400	<i>C. cf. papilio</i>	telson	?Ch	
48401	undet.	cuticle fragment	Ch	
60155	<i>C. cf. papilio</i>	telson	Ch	Trippleton
In. 37725	<i>C. cf. papilio</i>	carapace & abdomen	Leint.	
In. 43893	<i>C. cf. papilio</i>	abdomen & telson	Ch	
In. 43895	<i>C. cf. papilio</i>	part of abdomen	Ch	
<b>BGS</b>				
?	<i>C. cf. papilio</i>	carapace, abdomen; incomplete	Leint.	
?	<i>C. cf. papilio</i>	2 specimens; telsons	Leint.	
?	<i>C. cf. papilio</i>	carapace : abdomen	Leint.	
GSM1573	<i>C. cf. papilio</i>	small specimen	?Leint.	
GSM7451	<i>C. cf. papilio</i>	2 specimens; carapaces	Trippleton	
GSM7454	<i>C. cf. papilio</i>	carapace; well preserved	Ch	
GSM7456	<i>C. cf. papilio</i>	well preserved; nearly complete	Leint.	
GSM7470	<i>C. cf. papilio</i>	carapace	Leint.	
GSM7471	<i>C. cf. papilio</i>	3 specimens; telsons	Leint.	
GSM7473-4	<i>C. cf. papilio</i>	4 specimens inc. telsons	Leint.	
GSM7475	<i>C. cf. papilio</i>	abdomen & telson	Leint.	
GSM7476	<i>C. cf. papilio</i>	2 specimens; telsons	Leint.	
GSM7480	<i>C. cf. papilio</i>	carapace & abdomen	Leint.	



TABLE A3.7.2. Phyllocarids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
<b>OUM</b>				
C.146	C. cf. papilio	abdomen & telson	Leint.	
C.150	?phyllocarid	telson	Leint.	
<b>SHRCM</b>				
?	C. cf. papilio	abdomen & telson	Ta	Brandon*
?	C. cf. papilio	telson	Ch	
?	C. cf. papilio	telson	Leint.	
?	C. cf. papilio	carapace	Ta	Brandon**
?	C. cf. papilio	telson	Ta	Brandon**
?	C. cf. papilio	?telson	Ta	Brandon**
?	C. cf. papilio	telson	Ta	Brandon**
?	C. cf. papilio	telson & carapace; poorly preserved	Leint.	
?	C. cf. papilio		Ta	Brandon*
?	C. cf. papilio	abdomen & telson	Ta	Brandon*
?	C. cf. papilio	abdomen & telson; poorly preserved	Ta	Brandon*
?	C. cf. papilio	?part of abdomen	Ta	Brandon*
?	C. cf. papilio	?telson	Ta	Brandon*
?	C. cf. papilio	part of telson	Ta	Brandon*
?	C. cf. papilio	disarticulated abdomen	Ta	Brandon*
?	C. cf. papilio	carapace	Ch	
?	C. cf. papilio	?telson	Ch	
?	C. cf. papilio	telson	Ch	
?	C. cf. papilio	carapace	Leint.	
G3805-3805a	C. cf. papilio	disarticulated telson & abdomen	Ch	
G6420	C. cf. papilio	abdomen	Ch	
G9523.2	C. cf. papilio	carapace	Ta	Brandon***
G9523.4	C. cf. papilio	2 telsons	Ta	Brandon***
G9523.5	C. cf. papilio	telson; well preserved	Ta	Brandon***
G9523.6	C. cf. papilio	?part of abdomen	Ta	Brandon***
G9523.7	C. cf. papilio	?part of carapace	Ta	Brandon***
G9523.8	C. cf. papilio	?part of carapace	Ta	Brandon***
G9523.9	C. cf. papilio	?part of carapace	Ta	Brandon***
G9523.10	C. cf. papilio	?part of carapace	Ta	Brandon***
G9523.11	C. cf. papilio	?telson	Ta	Brandon***
G9523.15	C. cf. papilio	telson; well preserved	Ta	Brandon***
G9523.16	C. cf. papilio	abdomen & telson	Ta	Brandon***
G9523.17	C. cf. papilio	carapace; well preserved; incomplete	Ta	Brandon***
G9523.18	C. cf. papilio		Ta	Brandon***
G9523.19	C. cf. papilio		Ta	Brandon***
G9523.20	C. cf. papilio		Ta	Brandon***
<b>LEIUG</b>				
117526	C. cf. papilio	carapace	To	MS
56758	C. cf. papilio	carapace	Ch	Trippleton



TABLE A3.7.3. Phyllocarids; Leintwardine.

Specimen	Taxon	Description	Channel	Locality
Newly collected	(Church Hill specimens from Quarry 1)			
MOCK9	C. cf. papilio	?part of telson	Mo	Mocktree
MS2	?phyllocarid	articulated carapace	To	MS
MS8	C. cf. papilio	?part of abdominal segments	To	MS
MS9a-b	C. cf. papilio	part of telson	To	MS
MS10	C. cf. papilio	part of telson	To	MS
MS13	C. cf. papilio	?part of abdominal segments	To	MS
MS14a-b	C. cf. papilio	?part of telson	To	MS
MS29a-b	C. cf. papilio	distal abdomen; proximal telson	To	MS
MS20	C. cf. papilio	telson; well preserved	To	MS
CH18	C. cf. papilio	?abdomen & prox telson	Ch	CHQ1
CH27	C. cf. papilio	part of telson	Ch	CHQ1
CH62a-b	C. cf. papilio	carapace & telson; well preserved	Ch	SBA
CH125a-b	C. cf. papilio	?part of telson	Ch	CHQ1
CH126	C. cf. papilio	part of telson	Ch	CHQ1
CH127a-b	C. cf. papilio	telson	Ch	SBA
CH128a-b	C. cf. papilio	nearly complete; small specimen	Ch	CHQ1
CH131	C. cf. papilio	carapace; well preserved; incomplete	Ch	Trippleton
CH132a-b	C. cf. papilio	telson	Ch	?SBA



TABLE A3.8.1. Selected other fossils; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA); Church Hill Quarry 1 (CHQ1); Martin's Shell Quarry (MS); Mocktree Quarry (Mocktree).

Specimen	Taxon	Description	Channel	Locality
<b>Palaeoscoleuids</b>				
SHRCM G10474	Protoscolex latus	well preserved	Ch	
LEIUG 117524	P. latus	incomplete; also <i>S. longissimus</i>	To	MS
CH214	P. latus	well preserved; nearly complete	Ch	CHQ1
<b>Conulariids</b>				
LEIUG 117525	Conularia sp.	well preserved; nearly complete	To	MS
MS27	Conularia sp.	well preserved; complete	To	MS
MOCK11	Conularia sp.	poorly preserved	Mo	Mocktree
CH264	Conularia sp.	incomplete	Ch	SBA
CH265	Conularia sp.	2 specimens; poorly preserved	Ch	CHQ1
CH266	Conularia sp.	nearly complete	Ch	CHQ1
<b>Bryozoans</b>				
CH37	undet. sp.	poorly preserved	Ch	SBA
CH160	undet. sp.	well preserved	Ch	SBA
CH161	undet. sp.	poorly preserved	Ch	SBA
CH162	undet. sp.	poorly preserved	Ch	SBA
CH163	undet. sp.	poorly preserved	Ch	SBA
CH164	undet. sp.	poorly preserved	Ch	CHQ1
<b>Problematica</b>				
LEIUG 18639	Spongarium edwardsii		Mo	Mocktree
LEIUG 25877	S. edwardsii	nearly complete?	Mo	Mocktree
LEIUG 117527	S. edwardsii	well preserved	Mo	Mocktree
LEIUG 15040	Sphenothallus longissimus		To	MS
LEIUG 15041	S. longissimus		To	MS
MS22	S. longissimus	incomplete	To	MS
MS25	S. longissimus	incomplete	To	MS
MS27	S. longissimus	well preserved; nearly complete	To	MS
MS30	S. longissimus	incomplete	To	MS
MS31	S. longissimus	incomplete	To	MS
MS32	S. longissimus	incomplete	To	MS
MS33	S. longissimus	incomplete; 2 specimens	To	MS
MS34	S. longissimus	incomplete	To	MS
MS41	S. longissimus	incomplete	To	MS
CH267	S. longissimus	incomplete	Ch	CHQ1



TABLE A3.8.2. Selected other fossils; Leintwardine. Locality notes: Starfish Bed A, Church Hill Quarry 1 (SBA); Church Hill Quarry 1 (CHQ1); Martin's Shell Quarry (MS); Mocktree Quarry (Mocktree).

Shelly horizons				
CH33	fine shelly horizon		Ch	SBA
CH170	fine shelly horizon inc. disarticulated ophiuroid		Ch	SBA
CH172	fine shelly horizon		Ch	CHQ1
CH175	rhynchonellids, other brachiopod sp., graptolites		Ch	SBA
CH176	rhynchonellids, other brachiopod sp., graptolites		Ch	CHQ1
CH179	rhynchonellids		Ch	CHQ1
CH180	rhynchonellids		Ch	CHQ1
CH182	inc. large incomplete cephalopod		Ch	CHQ1
CH184	inc. disarticulated trilobites, brachiopods		Ch	CHQ1
CH185			Ch	CHQ1
CH186	inc. disarticulated trilobites, brachiopods		Ch	CHQ1
CH187	inc. disarticulated trilobites, brachiopods		Ch	CHQ1
CH188	rhynchonellids, eurypterid cuticle		Ch	SBA
CH189	aligned brachiopods		Ch	CHQ1
CH258	inc. <i>S. marstoni</i> , brachiopods, bryozoans, graptolites		Ch	CHQ1
Graptolite assemblages				
CH46	<i>S. leintwardinensis</i>	aligned	Ch	CHQ1
CH124	<i>S. leintwardinensis</i>	aligned	Ch	CHQ1
CH201	<i>S. leintwardinensis</i>	well preserved	Ch	CHQ1
CH203	<i>S. leintwardinensis</i>	well preserved	Ch	CHQ1
CH204	<i>S. leintwardinensis</i>		Ch	CHQ1
Other				
CH183a-b	<i>Encrinurus</i> , <i>Alcymene</i>	disarticulated cephalo	Ch	CHQ1



Leintwardine taxa	Provenance	Abundance of unusual echinoderms & arthropods through channels			
		To	Mo	Ch	Ta
Echinoderms					
Crinoids					
<i>Eutaxocrinus maccoyanus</i>	Ch			2	
<i>Gissocrinus ludensis</i>	Ch			2	
<i>Clematocrinus quinquepennis</i>	Ch			7	
<i>Mastigocrinus bravoniensis</i>	Ch			1	
<i>Cicerocrinus elegans</i>	Ch			1	
<i>Clematocrinus?</i> sp.	Ch			8	
undet. sp.	Ch			5	
<i>Dendrocrinus</i> sp.	Ch			1	
Echinoids					
<i>Echinocystites pomum</i>	Ch			8	
<i>Palaeodiscus ferox</i>	Ch			11	
Ophiocistioids					
<i>Sollasina woodwardi</i>	Ch			3	
Stelleroids					
<i>Antiquaster magrumi</i>	Ch			1	
<i>Bdellacoma vermiformis</i>	Ch; To; Mo	4	4	20	
<i>Coccaster bulbiferus</i>	Ch			1	
<i>Coccaster?</i> sp.	?			?	
<i>Furcaster leptosoma</i>	Ch; Mo		13	52	
<i>Klasmura?</i> sp.	Ch			1	
<i>Lapworthura miltoni</i>	Ch; To	10		99	
<i>Loriolaster calceatus</i>	Ch			32	
<i>Mesopalaeaster?</i> leintwardensis	?			?	
<i>Palasterina</i> cf. <i>antiqua</i>	Ch			1	
<i>Palasterina</i> sp.	Ch			1	
<i>Rhopalocoma pyrotechnica</i>	Ch			11	
<i>Sturtzaster colvini</i>	Ch			5	
<i>Sturtzaster marstoni</i>	Ch			88	
<i>Urasterella ruthveni</i>	Ch			2	
Arthropods					
Eurypterids					
<i>Carcinosoma punctatum</i>	Ch			4	
<i>Carcinosoma</i> sp.	Ch			2	
<i>Carcinosoma?</i> sp.	Ch			4	
<i>Erettopterus marstoni</i>	Ch			3	
<i>Erettopterus?</i> sp.	Ch			1	



<i>Pterygotus arcuatus</i>	Ch			1	
<i>Pterygotus?</i> sp.	Ch			1	
<i>Salteropterus?</i> <i>longilabium</i>	Ch			1	
Undet. sp.	Ch	4	?	120	4
<b>Xiphosurids</b>					
<i>Limuloides limuloides</i>	Ch			5	
<i>Bunodes salweyi</i>	?				
<i>Pseudoniscus</i> sp.	Ch			1	
<i>Cyamocephalus loganensis</i>	?				
<b>Phyllocarids</b>					
<i>Ceratiocaris</i> cf. <i>papilio</i>	To; Mo; Ch; Ta	17	?	35	29
<b>Trilobites</b>					
<i>Alcymene lawsoni</i>	Mo				
<i>Dalmanites myops</i>	Mo				
<i>Dalmanites weaveri</i>	Mo				
<i>Encrinurus</i> sp.					
<i>Platycalymene</i> sp.	Ch				
<i>Proetus stokesi</i>	Ch				
<b>Corals</b>					
<i>Favosites gothlandicus</i>	Ta				
<b>Brachiopods</b>					
<i>Atrypa reticularis</i>	Mo				
<i>Chonetes grayi</i>					
<i>Craniops implicata</i>					
<i>Dayia navicula</i>	Ch; Mo; To				
<i>Isorthis orbicularis</i>					
<i>Leptaena depressa</i>	Ch; Mo				
<i>Leptostrophia filosa</i>					
<i>Lingula lata</i>	Ch				
<i>Microsphaeridiorhynchus nucula</i>	Ch; To				
<i>Orbiculoidea rugata</i>					
<i>Orbiculoidea</i> sp.					
<i>Protochonetes ludloviensis</i>					
<i>Schizocrania striata</i>					
<i>Shagamella ludloviensis</i>	Ch				
<i>Shaleria onatella</i>					
<i>Sphaerirhynchia wilsoni</i>	Ch				
<b>Molluscs</b>					
<b>Bivalves</b>					
<i>Cardiola interrupta</i>	Mo				
<i>Fuschella amygdalina</i>	Ch				
<b>Cephalopods</b>					
<i>Gomphoceras ellipticum</i>	Mo				
<i>Orthoceras filsum</i>	Mo				
<i>Trochoceras giganteum</i>	Mo				
<i>Trochoceras</i> sp.	Mo				



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**Gastropods**

*Poleumita globosa*

**Graptolites**

*Saetograptus leintwardinensis* Ch; To

**?Annelids**

*Protoscolex latus* To; Ch

**Conulariids**

*Conularia subtilis* To; Ch

*Conularia aspersa*

**Problematica**

*Spongarium edwardsii* Mo

*Sphenothallus longissimus* To; Ch

**Bryozoans**

*Leptotrypella leintwardinensis* Ch

**Heterostracan Fish**

*Archaeogonaspis ludensis* Ch

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TABLE A5.1. Disc radii of *Lapworthura miltoni* specimens from Leintwardine. Specimens with 'CH' prefix originate from Starfish Bed A.

Specimen	Disc radii (mm)	Specimen	Disc radii (mm)
BMNH E 1297	16	GSM 105645	12
BMNH E13130	14	CAMSM A37217	9
BMNH E 20231	10	CAMSM A37218	7
BMNH E 20232	10	CAMSM A37219	9
BMNH E 20235	16	NMS G.1882.65.151.5	7
BMNH E 20239	9	NMS G.1882.65.151.8	6
	10	NMS G.1882.65.151.11	15
	8	CH70	17
BMNH 57425	15	CH71	9
BMNH 57709	8	CH72	8
BMNH 52973	12	CH74	13
BMNH 53885	11	CH82	13
OUM C56	12	CH84	9
OUM C511	10	CH89	15
OUM C513	11	CH92	15
OUM C5116	10	CH97	14
OUM C16828	11	CH100	18
OUM C16829	19	CH250	10
OUM C16832	6	CH251	7
OUM C16833	8	CH252	8
OUM C16835	10	CH253	20
OUM C16836	12	CH263	8
OUM C16857	10		
	6		
OUM C16858	9		
	10		
OUM C16880	11		
OUM C16881a	8		
OUM C16908	9		
OUM C16923	7		
OUM C16831	7		
	11		
OUM C16834	9		
OUM C16842	6		
OUM C16845	15		
OUM C16849	13		
OUM C16850	9		
OUM C16872	10		
OUM C16902	6		
OUM C16924	8		
OUM C16927	8		
OUM C16946	12		
OUM C16948	12		
OUM C16947	13		
OUM C29276	6		



TABLE A5.2. Disc radii of *Furcaster leptosoma* specimens from Leintwardine. Specimens With 'CH' prefix originate from Church Hill Starfish Bed A.

Specimen	Disc radii (mm)
BMNH E 13135	4
BMNH E 13138	5
BMNH E 13139	4
BMNH E 20260	4
OUM C16838	5
OUM C17291	4
BGS GSM28819	6
IPSM G9252912	4
IPSM G9252917	12
NMS G188265143	3
CH34	2
CH40	8
CH54	5
CH70	4
CH73	5
CH75	3
CH76	3
CH77	4
CH78	4
	5
	3
	4
CH80	4
CH81	6
CH83	2
	9
	9
CH86	2
CH88	5
CH98	4
CH101	3
CH102	8
CH257	4
CH259	2



TABLE A5.3. Arm lengths of *Sturtzaster marstoni* from Leintwardine.

Specimen	Arm length (mm)	Specimen	Arm length (mm)
BMNH 47995	20	OUM C17040	1 ?
	24		2 ?
	19		3 ?
	17		4 19
BMNH E2593	8		5 ?
BMNH E54157	9		6 16
BMNH E13949	22		7 20
BMNH E13948	12		8 ?
CAMSM A37207	18		9 18
BMNH E1299	18		10 ?
BGS GSM6517	17	OUM C17079	11 19
OUM C30631	17		12 17
	20		13 13
	25		14 19
IPSM G92529121	24		15 ?
	18		16 16
	16		17 ?
OUM C17103	17		18 ?
	20		19 ?
	20		20 17
OUM C17079	21	OUM C17104	21 20
	18		22 ?
	19		23 ?
OUM C17104	18		24 ?
	22		25 ?
	20		26 ?
OUM C17098	15		27 ?
	18	NMS G1882651627	1 21
	24		2 18
OUM C17082	24		3 20
OUM C17048	18		4 17
OUM C17056	20		5 17
	19		6 22
	18		7 ?
OUM C17057	15		8 ?
	16		9 18
	20		10 14
OUM C17054	19		11 19
	20		12 20
	21		13 23
	19		14 ?
			15 20
			16 19
			17 16
			18 19
			19 11
			20 ?
		CH210 CH258	21 23
			22 20
			23 14
			24 ?
			12
			14
			6



TABLE A5.4. Mouth frame radii of *Loriolaster calceatus* from Leintwardine.

Specimen		Mouth frame radii (mm)
BGS GSM25351	1	4.4
	2	3.8
	3	3.5
	4	4
	5	3.6
	6	3.6
	7	3
	8	3.6
	9	3.6
	10	2.7
	11	2.6
	12	4.3
	13	4.4
	14	3.8
	15	3.8
	16	4.6
	17	3.5
	18	3.6
	19	2.4
	20	?
	21	3.5
	22	4
	23	4.1
	24	3
	25	3.3
	26	4
BMNH E 20250	1	4
	2	3.55
	3	3.75
	4	3.4
	5	3.45
	6	3.75
	7	3.75
	8	4.15
	9	3.3
	10	3.6
	11	3.3
	12	3.45
	13	3.55
	14	3.9
	15	3.6
	16	3.75



TABLES A6.1-8. Life tables (time-specific method) for stelleroid samples 1-8, used for survivorship analysis.  $x$ = size class;  $d_x$ =number dying in size class ( $n_x-n_{x+1}$ );  $n_x$ =population size;  $l_x$ =proportion surviving: log of  $n_x$  ( $n_x/n_0$ );  $q_x$ =mortality rate ( $d_x/n_x$ ).

TABLE A6.1.

Sample 1: <i>L. miltoni</i> (total)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
6	6	67	1	0.090
7	5	61	0.910	0.082
8	9	56	0.836	0.161
9	9	47	0.701	0.191
10	10	38	0.567	0.263
11	5	28	0.418	0.179
12	6	23	0.343	0.261
13	4	17	0.254	0.235
14	2	13	0.194	0.154
15	5	11	0.164	0.455
16	2	6	0.090	0.333
17	1	4	0.060	0.25
18	1	3	0.045	0.333
19	1	2	0.030	0.5
20	1	1	0.015	1

TABLE A6.2.

Sample 2: <i>L. miltoni</i> (Starfish Bed A)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
7	1	15	1	0.067
8	3	14	0.933	0.214
9	2	11	0.733	0.182
10	1	9	0.6	0.111
11	0	8	0.533	0
12	0	8	0.533	0
13	2	8	0.533	0.25
14	1	6	0.4	0.167
15	2	5	0.333	0.4
16	0	3	0.2	0
17	1	3	0.2	0.333
18	1	2	0.133	0.5
19	0	1	0.066	0
20	1	1	0.066	1



TABLE A6.3.

Sample 3: <i>F. leptosoma</i> (total)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
2	4	34	1	0.118
3	5	30	0.882	0.167
4	12	25	0.735	0.480
5	6	13	0.382	0.462
6	2	7	0.206	0.286
7	0	5	0.147	0
8	2	5	0.147	0.4
9	2	3	0.088	0.667
10	0	1	0.029	0
11	0	1	0.029	0
12	1	1	0.029	1

TABLE A6.4.

Sample 4: <i>F. leptosoma</i> (Starfish Bed A)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
2	4	24	1	0.167
3	4	20	0.833	0.2
4	7	16	0.666	0.438
5	4	9	0.375	0.444
6	1	5	0.208	0.2
7	0	4	0.166	0
8	2	4	0.166	0.5
9	2	2	0.083	1



TABLE A6.5.

Sample 5: <i>S. marstoni</i> (total)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
6	1	74	1	0.014
7	0	73	0.986	0
8	1	73	0.986	0.014
9	1	72	0.973	0.014
10	0	71	0.959	0.000
11	1	71	0.959	0.014
12	2	70	0.946	0.029
13	1	68	0.919	0.015
14	3	67	0.905	0.045
15	2	64	0.865	0.031
16	5	62	0.838	0.081
17	8	57	0.770	0.14
18	11	49	0.662	0.224
19	11	38	0.514	0.289
20	14	27	0.365	0.519
21	3	13	0.176	0.231
22	3	10	0.135	0.3
23	2	7	0.095	0.286
24	4	5	0.068	0.8
25	1	1	0.014	1

TABLE A6.6.

Sample 6: <i>S. marstoni</i> (NMS G1882651627)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
11	1	19	1	0.053
12	0	18	0.947	0
13	0	18	0.947	0
14	2	18	0.947	0.111
15	0	16	0.842	0
16	1	16	0.842	0.063
17	2	15	0.789	0.133
18	2	13	0.684	0.154
19	3	11	0.579	0.273
20	4	8	0.421	0.5
21	1	4	0.211	0.25
22	1	3	0.158	0.333
23	2	2	0.105	1



TABLE A6.7.

Sample 7: <i>L. calceatus</i> (BGS GSM25351)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
2.4	1	25	1	0.04
2.5	0	24	0.96	0
2.6	1	24	0.96	0.042
2.7	1	23	0.92	0.043
2.8	0	22	0.88	0
2.9	0	22	0.88	0
3	2	22	0.88	0.091
3.1	0	20	0.8	0
3.2	0	20	0.8	0
3.3	1	20	0.8	0.05
3.4	0	19	0.76	0
3.5	3	19	0.76	0.158
3.6	5	16	0.64	0.313
3.7	0	11	0.44	0
3.8	3	11	0.44	0.273
3.9	0	8	0.32	0
4	3	8	0.32	0.375
4.1	1	5	0.2	0.2
4.2	0	4	0.16	0
4.3	1	4	0.16	0.25
4.4	2	3	0.12	0.667
4.5	0	1	0.04	0
4.6	1	1	0.04	1

TABLE A6.8.

Sample 8: <i>L. calceatus</i> (BMNH E 20250)				
(x)	(d <sub>x</sub> )	(n <sub>x</sub> )	(l <sub>x</sub> )	(q <sub>x</sub> )
3.3	2	16	1	0.125
3.4	3	14	0.875	0.214
3.5	2	11	0.687	0.182
3.6	2	9	0.562	0.222
3.7	4	7	0.437	0.571
3.8	0	3	0.187	0
3.9	1	3	0.187	0.333
4	1	2	0.125	0.5
4.1	1	1	0.063	1



TABLE A7. Relative way up orientation of stelleroid assemblages from Leintwardine.

Specimens	Dorsal	Ventral	Undet.	TOTAL
<i>Loriolaster calceatus</i>				
BMNH 38527	4	8		12
BGS GSM25351	10	12	4	26
<i>Sturtzaster marstoni</i>				
BMNH 47995	5	5		10
OUM C17040	11	17		28
OUM C17054	3	6		9
OUM C17041	1	3		4
OUM C17048	3	1		4
OUM C17049	0	3		3
OUM C17057	1	5		6
OUM C17056	1	4		5
OUM C17079	2	1		3
OUM C17080	3	1		4
OUM C17082	2	3		5
OUM C17098	2	2		4
OUM C17103	5	4		9
OUM C17104	1	4		5
OUM C30631	1	3		4
CAMSM A37207	2	2		4
NMS G1882651627	8	13	3	21
IPSM G19252921	1	3		4
<i>Lapworthura miltoni</i>				
BMNH E 20239	0	2		2
OUM C16828	3	1		4
OUM C16831	2	1		3
OUM C16832	2	1		3
OUM C16857	3	0		3
OUM C16858	4	0		4



TABLE A8.1. Articulation grades for *Lapworthura miltoni* specimens from Leintwardine.  
n= 62.

Specimen	Articulation grade	Specimen	Articulation grade
OUM C511	2	CH38	3
OUM C16828	2	CH40	3
	2	CH43	2
	2	CH71	3
	2	CH72	2
OUM C16831	2	CH74	2
	2	CH75	2
	2	CH78	2
OUM C16832	2	CH82	3
	2	CH84	1
	2	CH85	2
OUM C16857	2	CH89	2
	2	CH90	2
	2	CH91	2
OUM C16858	1		2
	2	CH92	2
	2	CH97	2
	2	CH100	1
BGS GSM105645	1	CH250	1
NMS G1882651515	2	CH251	2
NMS G1882651518	1	CH252	1
NMS G18826515111	1		1
CAM SM37217	1	CH253	2
CAM SM37218	2	CH254	2
CAM SM37219	2	CH263	2
BMNH E1297	1		
BMNH E13130	2		
BMNH E20231	2		
BMNH E20232	1		
BMNH E20235	1		
BMNH E20239	2		
	2		
BMNH E20247	2		
BMNH E52973	2		
BMNH E52982	3		
BMNH E53885	2		
BMNH 57425	1		



TABLE A8.2. Articulation grade for *Furcaster leptosoma* specimens from Leintwardine.  
n=39.

Specimen	Articulation grade
OUM C514	2
OUM C16838	2
OUM C17010	1
OUM C172921	1
BGS GSM28819	2
NMS G188265143	2
IPSM G9252917	1
IPSM G9252912	2
BMNH E13135	1
BMNH E13138	2
BMNH E13139	2
BMNH E20258	1
BMNH E20260	2
CH34	2
CH38	2
CH40	1
CH54	1
CH73	1
CH75	2
CH76	1
CH77	1
CH78	1
	2
	2
	2
CH80	2
CH81	1
	1
CH83	1
	2
	2
CH86	1
CH88	1
CH98	1
CH101	2
CH102	2
CH103	1
CH257	2
CH259	2



TABLE A9. Orientation data for selected fossil assemblages from Leintwardine. Data measured clockwise from arbitrary 'north' value. LEIUG 19463 and CH189 refer to aligned umbones of brachiopod assemblages. CH178 and BGS GSM25351 refer to aligned arms of stelleroid assemblages.

Specimens		Azimuth	Specimens		Azimuth
		(degrees)			(degrees)
LEIUG 19463	A	328	BGS GSM25351		68
	B	258			155
	C	269			272
	D	266			316
	E	267			87
	F	253			87
	G	270			92
	H	256			223
	I	261			71
	J	234			78
	K	258			90
	L	341			102
CH189	A	300			46
	B	269			78
	C	2			89
	D	274			97
	E	275			285
	F	288			290
	G	311			272
CH78	specimen 2: arm '1'	176			63
	arm '2'	165			83
	arm '3'	166			70
	arm '4'	176			289
	specimen 3: arm '1'	219			291
	arm '2'	176			331
	arm '3'	164			334
	arm '4'	184			112
	arm '5'	235			78
					0
					45
					60
					217
					312
					34
					35
					346
					284
					254
					266
					264
					85
					90
					123



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