
The Anatomy of Conodonts

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The anatomy of conodonts

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SUMMARY

Specimens from the Carboniferous Granton shrimp bed of Edinburgh, Scotland, provide the most complete record of conodont anatomy. Ten specimens are now known, six of which are previously undescribed, and form the basis of a new description and restoration of the conodont animal. The feeding apparatus is present in eight of the specimens; all but two of these can be assigned to *Clydagnathus* on the basis of the elements. A different genus and species is represented by the other two. The soft tissue morphology of all the specimens is similar.

The Granton animals are elongate, 21–55 mm in preserved length with a short head, a trunk with V-shaped myomeres, and a ray-supported caudal fin. The head is characterized by two lobate structures, which are interpreted as hollow sclerotic cartilages indicating the position of large eyes. One specimen preserves traces of possible otic (auditory) capsules and branchial structures. Ventral and immediately posterior to the eyes lies the feeding apparatus, with the ramiform elements at the anterior end. There is no evidence of tissue surrounding this apparatus, indicating incomplete preservation of ventral soft parts, at least at the anterior end of the specimens.

The trunk of most specimens displays the notochord as a pair of axial lines which represent its margins. In one specimen the area between the two lines is mineralized and displays a transverse fibrous structure. The notochord tapers anteriorly and posteriorly; it extends as far forwards as the ramiform elements of the feeding apparatus but does not reach the anterior tip of the head. Two specimens show a possible trace of the dorsal nerve cord. V-shaped myomeres are particularly well-preserved along the trunk of some of the new specimens; their preservation as distinct chevrons is attributed to a little *post-mortem* shrinkage. Possible traces of original muscle fibres are preserved in the myomeres of one specimen.

The tail is present on two specimens, with fin rays representing a caudal fin that may be symmetrical or may be slightly more extensive on the ventral margin.

The evidence of the soft-part anatomy, together with features of element histology, show that the conodonts are vertebrates. Hypotheses that conodonts have affinities with nemerteans, molluscs, chaetognaths, or cephalochordates are refuted. Nor do the conodonts represent a separate phylum. Within the Vertebrata, the conodonts are considered to lie crownwards of the myxinooids, forming a primitive sister group of the Heterostraci + Myopterygii.

1. INTRODUCTION

Conodonts are primarily known from the scattered elements of their feeding apparatuses, which have an excellent fossil record from the Upper Cambrian to the uppermost Triassic. Conodont elements are normally microscopic (0.25–2 mm) in size and are composed of calcium phosphate (carbonate fluorapatite). Complete feeding apparatuses comprising 15 or more elements may be preserved undisturbed on sedimentary bedding planes in favourable circumstances, where there has been no current activity, scavenging, or bioturbation. Fossilized evidence of the soft parts of conodonts is, however, extremely rare.

An early report of possible soft tissues associated with conodont apparatuses is that of Du Bois (1943, p. 156), who recognized impressions he believed to represent parapodia or cirri of a worm-like creature. These occurred in a brown film on Carboniferous black shales from Illinois that also contained undisturbed apparatuses and faecal clusters of conodont elements. However, there is no clear relationship between these traces and any complete apparatus, and re-examination of the Du Bois collection and of additional material from the same locality has failed to reveal soft tissues associated with any conodont remains. A later report by Scott (1969) of Carboniferous conodont elements contained within asphaltic blebs and associated with a reticulate 'skin' pattern is patently based on faecal material, as the elements are chaotically arranged, commonly broken, and do not constitute complete apparatuses.

Specimens of *Typhloesus wellsi* (Melton & Scott), a bizarre soft-bodied metazoan from the Carboniferous Bear Gulch Limestone of Montana, commonly contain conodont elements within the alimentary canal, and were originally believed to be conodont animals (Melton & Scott 1973). This claim, however, received a mixed reception from conodont specialists, and *Typhloesus* was convincingly shown to be a conodontophage by Conway Morris (1985, 1990). More uncertainty surrounds the nature of *Odontogriphus omalus* Conway Morris, an annulated creature from the Middle Cambrian Burgess Shale of British Columbia. Conway Morris (1976) interpreted the single known specimen as a possible conodont animal, but the lack of preserved phosphate in the feeding apparatus of *Odontogriphus* and the stratigraphical horizon of the Burgess Shale (older than the oldest euconodonts) render any relationship equivocal (Briggs *et al.* 1983; Aldridge 1987; Conway Morris 1989).

The first undoubted record of conodont soft parts was of a single specimen of an animal containing a complete apparatus in its head region, from the

Carboniferous Granton shrimp bed of Edinburgh, Scotland (Briggs *et al.* 1983). Subsequent collecting from the same horizon produced three additional specimens, which provided more information on the soft tissues of conodonts, even though these specimens were less completely preserved than the first (Aldridge *et al.* 1986). Together, the four specimens from Granton indicated a chordate affinity for the conodonts. A single poorly-preserved specimen of a panderodontid conodont has also been recorded from the Silurian of Waukesha, Wisconsin (Mikulic *et al.* 1985*a,b*; Smith *et al.* 1987), and traces of soft tissues have been found in association with giant conodont apparatuses in the Upper Ordovician of South Africa (Aldridge & Theron 1993). The latter specimens display details of structures in the head, and one preserves a possible trunk trace, but the Granton specimens still provide the most complete evidence of conodont anatomy.

In this contribution we assess the state of our knowledge of conodont anatomy, based upon the Granton specimens. Six new specimens have been collected, some of them with particularly well-preserved features of the head and trunk, allowing corroboration, refinement and extension of earlier interpretations. The chordate affinities of the conodonts have also been confirmed by the histological investigations of Sansom *et al.* (1992), providing an independent justification for interpreting the soft tissues of conodonts through comparative anatomy with other primitive vertebrates.

2. MATERIAL

Specimen 1. (IGSE 13821, 13822), part and counterpart (figures 1–2), the first specimen recovered from Granton (Briggs *et al.* 1983), complete length 40.5 mm, head, apparatus, trunk, fin rays.

Specimen 2. (RSM GY 1986.17.1), part and counterpart, described by Aldridge *et al.* (1986), incomplete length 42 mm, apparatus, trunk.

Specimen 3. (HU Y221), part and counterpart, described by Aldridge *et al.* (1986), incomplete length 23 mm, tail, fin rays.

Specimen 4. (BM X1065), counterpart only, described by Aldridge *et al.* (1986), incomplete length 18 mm, apparatus, trunk.

Specimen 5. (RMS GY 1992.41.1), part (figures 3–6) and incomplete counterpart, length 38 mm (lacking only end of tail), head, apparatus, trunk.

Specimen 6. (RMS GY 1992.41.2), part (figures 8–9) and incomplete counterpart, incomplete length 38 mm, apparatus, trunk.

Specimen 7. (RMS GY 1992.41.3), part (figures 10–

12) and counterpart, incomplete length 55 mm, apparatus, trunk, largest and most heavily phosphatized specimen preserving traces of musculature.

Specimen 8. (RMS GY 1992.41.4), part only, incomplete length 21 mm, apparatus, trunk.

Specimen 9. (RMS GY 1992.41.5), part and counterpart, incomplete length 16 mm, section of trunk.

Specimen 10. (HU Y356a,b), part and counterpart, incomplete length 16 mm, apparatus, trunk.

Repositories: IGSE, British Geological Survey, Murchison House, Edinburgh; RMS, Royal Museum of Scotland, Edinburgh; HU, Hunterian Museum, Glasgow; BM, Natural History Museum, London.

3. TAPHONOMY

The Granton shrimp bed has a preserved fauna dominated by shrimps, mainly *Waterstonella*, *Crangopsis* and *Palaemysis* (Briggs & Clarkson 1983; Briggs *et al.* 1991). It represents a brackish water lagoon or interdistributary bay environment (Cater 1987; Briggs *et al.* 1991). The conodonts, and other fully marine taxa such as nautiloids, were presumably introduced by brief marine incursions. The genus *Clydagnathus*, to which the Granton specimens are provisionally assigned, is characteristic of early Carboniferous shallow-water nearshore facies (Austin 1976).

Lithologically, the Granton shrimp bed comprises laminations of organic-rich dark silt and organic-poor brown dolomite. There is no evidence for rapid, episodic burial and the sediment may have been stabilized by algal colonization. Bioturbation is confined to a microscopic scale, almost within laminations, and it is likely that the sediment was anoxic just below the surface. The fossils are preserved in fluorapatite (Briggs *et al.* 1983). The animals are thought to have been periodically the victims of mass mortalities, perhaps induced by algal blooms, which may have contributed to the conditions required to promote phosphatization (Briggs *et al.* 1991).

Phosphatization relies on a critical balance between decay which releases phosphate and promotes bacterial precipitation, and mineralization which preserves the soft tissue before much morphological detail is lost. Some decay of the conodonts has clearly taken place. The V-shaped myomeres have shrunk to become discrete structures, rather than a continuous muscle sheet. Only in rare cases (e.g. specimen 7, figures 10–12) are muscle traces preserved in relief, showing fibres (this relief preservation may be a function of size; specimen 7 is the largest). The notochord commonly appears hollow, its margins indicated by lines where collapse has led to thickening at the edges (such collapse occurs in the notochord of the lancelet *Branchiostoma* in decay experiments; Briggs & Kear 1993). Decay prior to mineralization has removed the gut, the tissues which supported the feeding apparatus, and the ventral epidermis. There is no evidence of gonads. Thus, the degradation of conodonts may have paralleled that shown in experimental decay of *Branchiostoma*, where much of the ventral epidermis and gut disappears early (Briggs &

Kear 1993). The preservation of intact feeding apparatuses, in their original configuration and associated with the rest of the organism, indicates that although some decay took place, the carcasses of the conodonts were undisturbed by bioturbation or water currents.

4. TAXONOMY

Naming of the Granton animals is not easy, as it relies on identification of the elements of the apparatus, all of which are partly or completely concealed by rock matrix. This difficulty is compounded by the fact that the taxonomy of cavusgnathid conodonts is itself in some confusion. The genus *Clydagnathus* is currently differentiated from *Cavusgnathus* by the possession of a nodose rather than a ridged ornament on the upper surface of the Pa element (Purnell 1992*b*). However, the nature of the apparatus of the type species of *Clydagnathus*, *C. cavusformis* Rhodes *et al.*, is currently unknown, so the degree of similarity or difference between the other elements of the two genera cannot be assessed. Briggs *et al.* (1983) made a tentative assignment of specimen 1 to *Clydagnathus?* cf. *cavusformis*, and in the present state of knowledge reference of this specimen and of others with a comparable apparatus to the genus *Clydagnathus* is appropriate. The specific designation is more open; Purnell (1992*b*) considered the apparatus in specimen 1 to be consistent with an assignment to *Clydagnathus windsorensis* (Globensky), while conceding that more than one species may be currently residing under that name.

Two specimens (2 and 7) have apparatuses that clearly differ from the remainder. Although the Pa element, only seen clearly in specimen 2 (Aldridge *et al.* 1986, fig. 3), is similarly cavusgnathoid, the ramiform elements are robust with peg-like denticles, in contrast to the slender, delicate, finely denticulate ramiform elements of specimens 1, 4, 5, 6, 8 and 10. This indicates that these two specimens represent a different taxon, although a name cannot currently be allocated.

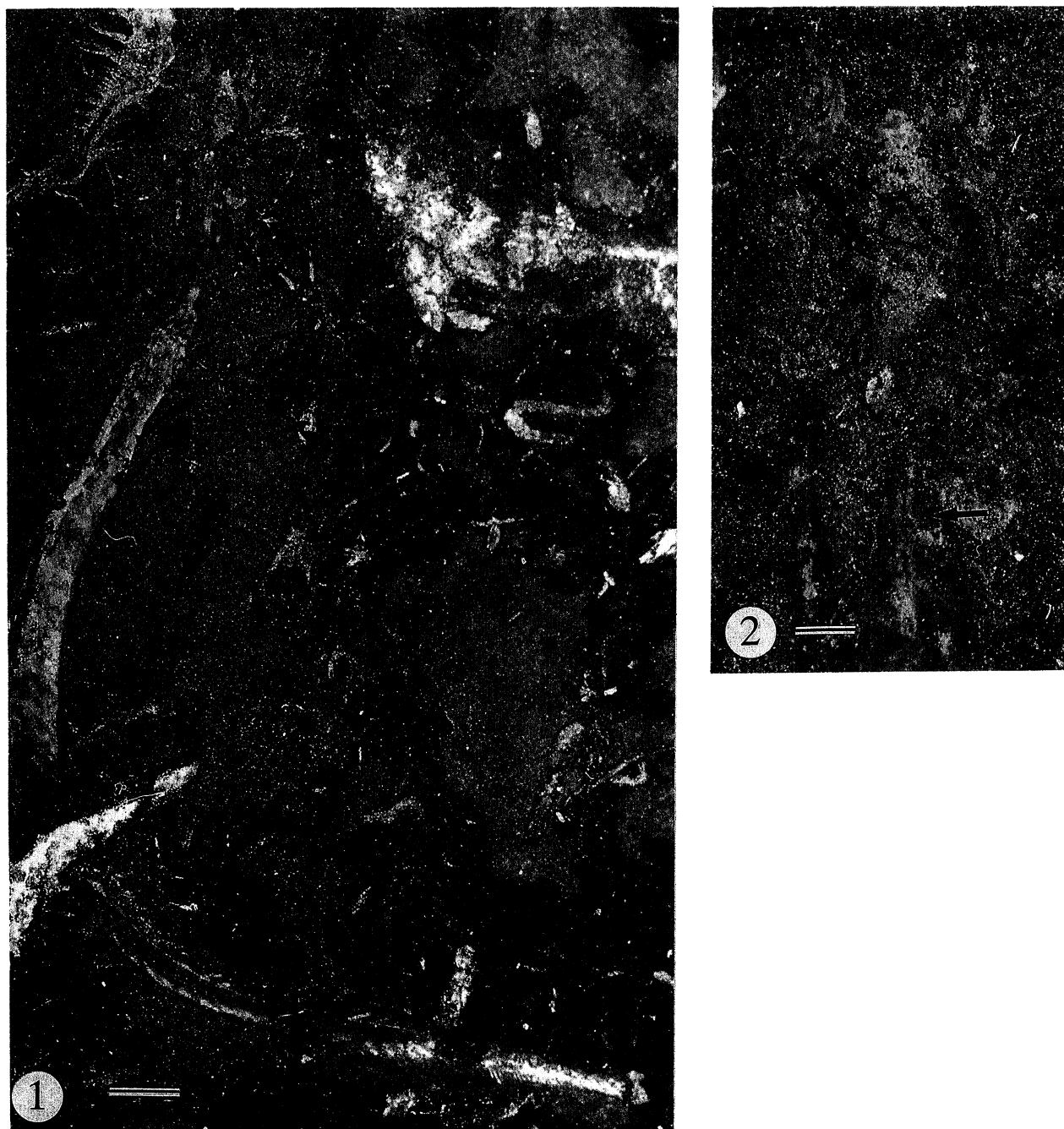
5. THE ANATOMY OF THE GRANTON CONODONTS

(a) General remarks

Even though at least two taxa are represented in the Granton animals, we are unable to detect any differences in the preserved soft-part anatomy of the ten known specimens, and they are treated together here.

The Granton conodonts are small, laterally compressed, eel-like animals, which were probably swimming predators. A short head region, which accommodated the feeding apparatus, was followed by a trunk made up of V-shaped somites, which terminated in a ray-supported caudal fin.

The complete length of the animal is not preserved in most specimens. The largest individual (specimen 7: figure 10) was probably only slightly longer than the 55 mm preserved. The smallest (specimen 8) was a little more than 21 mm and may represent a juvenile (the elements in the feeding apparatus are proportionately small). The only specimen which preserves



Figures 1 and 2. Specimen 1, counterpart (IGSE 13822). Figure 1. Complete specimen, scale bar 2 mm. Figure 2. Anterior portion, showing eye structures, feeding apparatus and possible axial trace of dorsal nerve cord (arrowed); scale bar 0.5 mm.

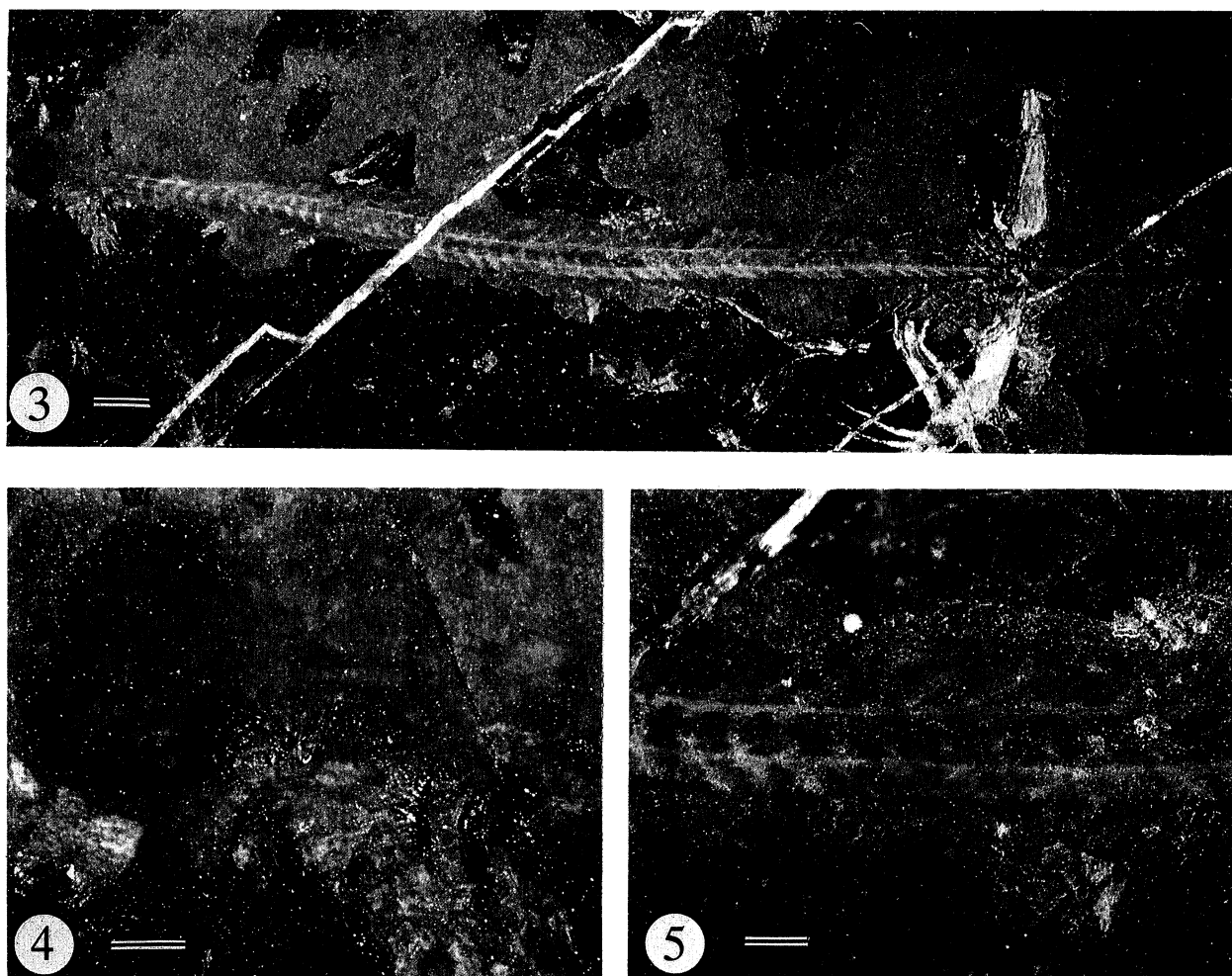
the complete length (specimen 1: figure 1) is 40.5 mm long and this is about the size of other near complete specimens (5 and 6: figures 3 and 8). All the specimens are 1 to 2 mm in preserved height.

(b) The head

The anterior margin of the head is only evident in two specimens (1 and 5: figures 1 and 3). At the anterior are two lobate structures. In specimen 1 they are sub-rhomboid in outline (figures 1 and 2; Briggs *et al.* 1983, fig. 3). Their configuration is roughly symmetrical about the axis of the trunk, and they are separated by a gap of about 0.5 mm. This, and the

axial position of the apparatus behind them, suggests that they are preserved with the sagittal plane normal to bedding. In specimen 5, on the other hand, the two structures are subcircular in outline (figure 4) and lie slightly anterior and dorsal of the feeding apparatus. The left lobe overlaps the right, indicating that the head is preserved in a near lateral attitude, but the lobes are offset due to a slightly oblique orientation to the bedding.

The lobes are darker in colour than the mineralized structures of the trunk. In specimen 5 the margins of the lobes are defined by a broad dark band and patches of dark material occur in a loosely concentric arrangement within them (figures 4 and 6). Closely



Figures 3–5. Specimen 5, part (RMS GY 1992.41.1). Figure 3. Complete specimen, anterior to left; scale bar 2 mm. Figure 4. Anterior portion, showing eye structures, feeding apparatus (partially concealed by rock matrix) and anterior part of trunk with notochord; scale bar 0.5 mm. Figure 5. Detail of trunk anterior of mid-length, scale bar 0.5 mm; small spots on ventral margin particularly apparent at anterior end of figure.

similar structures are associated with very large conodont feeding apparatuses from the Ordovician Soom Shale of South Africa (Aldridge & Theron 1993). The lobes on the Ordovician specimens are 2.1–3.1 mm in length, about twice the size of those on the Granton animals, whereas the ramiform elements in the Ordovician apparatuses are an order of magnitude larger; it is, therefore, unlikely that the lobes represent a hood that covered the feeding apparatus (Aldridge & Theron 1993). Other interpretations of

the well-preserved, paired structures considered by Aldridge & Theron (1993) included otic (auditory) capsules or a cavity enclosing the semicircular canals, but these were dismissed on the basis of size, shape and position. Comparison with other fossil agnathans, including the Silurian anaspid *Jamoytius* (see Ritchie 1968), suggests that the lobes in the Ordovician and Carboniferous specimens represent sclerotic cartilages which surrounded the eyes. In the Granton animal these cartilages appear to have been deep, inwardly tapering hollow rings indicating that the eyes were relatively large and faced laterally (specimen 1: figure 2; Briggs *et al.* 1983, fig. 3). The dark areas within the rings in specimen 5 may represent remnants of the eyes themselves.

Only specimen 1 preserves traces of additional soft-tissue morphology in the head region. Small, paired sub-circular dark patches posterior to the sclerotic rings (Briggs *et al.* 1983, figs 2C and 3A) were previously tentatively inferred to be the eyes (Aldridge & Briggs 1989), but are now considered more likely to represent otic capsules. Similar structures in the Carboniferous lamprey *Mayomyzon*, and the hagfish *Myxiniakela*, from the Mazon Creek fauna of Illinois

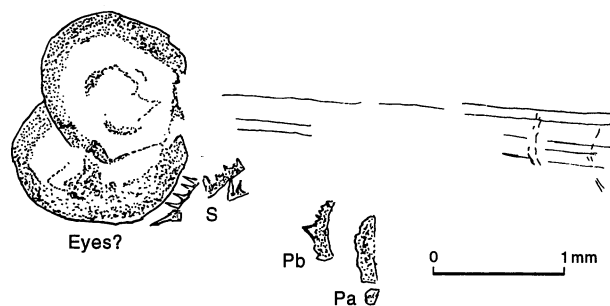


Figure 6. Interpretative drawing of the anterior portion of specimen 5 (RMS GY 1992. 41. 1); anterior to left.

have been interpreted in this way (Bardack & Zangerl 1971; Bardack 1991). Immediately posterior to the eyes (sclerotized cartilages) of specimen 1 are faint transverse traces (Briggs *et al.* 1983, figs 2C and 3A) that are comparable with features in *Jamoytius* interpreted as branchial structures by Ritchie (1968).

The length of the head region, measured to the position of the posteriormost (Pa) elements in the apparatus, is 7% (specimen 1: figure 1) to 7.5% (specimen 5: figure 3) of the total length of the animal. In dorsal view, the head (as defined by the eyes) is 40% wider than the anterior half of the trunk.

(c) *The feeding apparatus*

The feeding apparatus of most of the Granton conodonts is of the ozarkodinid type (figures 7 and 9). It consists of 11 comb-like ramiform elements which make up an anterior basket thought to function in prey capture; posterior to these are two successive pairs of pectiniform (Pb and Pa) elements which were used in processing the food (Dzik 1976, 1991; Jeppsson 1979; Briggs *et al.* 1983; Aldridge *et al.* 1987; Purnell & von Bitter 1992). The first ramiform elements just overlap the posterior margin of the putative eye capsules (specimens 1 and 5: figures 2 and 4), indicating that the eyes lay immediately antero-dorsal of the apparatus. The feeding apparatus is evident on all but two of the ten Granton specimens (3 and 9). That of specimen 1 was described by Briggs *et al.* (1983), those of specimens 2 and 4 by Aldridge *et al.* (1986); details of the apparatuses of specimens 5–8 and 10 are given in Appendix 1.

The ozarkodinid apparatus may be preserved in a variety of configurations depending on its orientation to bedding (Aldridge *et al.* 1987). The apparatuses of all the Granton specimens, however, are flattened

laterally (most corresponding to the standard orientation of Aldridge *et al.* (1987)). In specimen 7 the anterior ramiform elements are aligned more nearly parallel to the posterior pairs of pectiniform elements than in the other specimens. This may be the result of a slight lateral and antero-posterior tilting of the head relative to the plane of bedding (Aldridge *et al.* 1987).

Although the apparatus of specimen 1 is preserved in the standard lateral configuration, the symmetry of the eyes and other soft tissues in the head suggest dorso-ventral flattening (figure 2; Briggs *et al.* 1983, fig. 3). This apparent paradox may be a consequence of some degradation of the tissues supporting the apparatus, allowing it to rotate relative to the remainder of the head. In specimens 1 (figures 1 and 2) and 4 (Aldridge *et al.* 1986, fig. 5) the feeding apparatus lies close to the line of the trunk axis, reflecting a dorso-ventral orientation of the anterior of the animal. In the most specimens, however, the elements, although retaining their configuration within the feeding apparatus, are consistently offset to one side of the trunk axis and extend beyond the preserved traces of soft tissue (specimens 2, 5, 6, 8 and 10: figures 3, 4 and 8). Clearly the tissue surrounding the apparatus must have been more susceptible to decay, or at least less prone to phosphatization, than other structures.

(d) *The trunk*

The main features of the trunk preserved are the notochord, myomeres and caudal fin rays. There is no evidence of gill slits, viscera, or gonads.

(i) *Notochord*

Most of the specimens preserve at least some evidence of a pair of axial lines (figures 3, 5 and 8). These have been the subject of a number of previous interpretations, most notably as the gut or notochord (Briggs *et al.* 1983; Aldridge *et al.* 1986). New evidence indicates that they do indeed represent the notochord (as suggested by Conway Morris 1989).

The paired lines which are normally preserved (figure 5) represent the margins of the notochord. In specimen 7 (figure 10), however, which is more heavily phosphatized than the others, the area between the lines is mineralized (figures 10–12) and preserved in relief (it is similarly preserved in the tail of specimen 1 (Briggs *et al.* 1983, fig. 4), but details are obscured by heavy mineralization). The phosphate has a fibrous appearance, the fibres oriented normal to the axis of the trunk (figure 12), and in places they differ in colour from the mineral preserving other features of the specimen. While this mineral texture could simply be diagenetic in origin, it may reflect the fibrous nature of the notochord sheath. A similar pattern of transverse lineations is preserved in the notochord of the Carboniferous chordate *Gilpichthys greenei* from Mazon Creek (Bardack & Richardson 1977). An alternative possibility, that the texture reflects transversely oriented discoidal muscle cells within the notochord sheath, is less likely. Although such cells occur in *Branchiostoma* they are much more

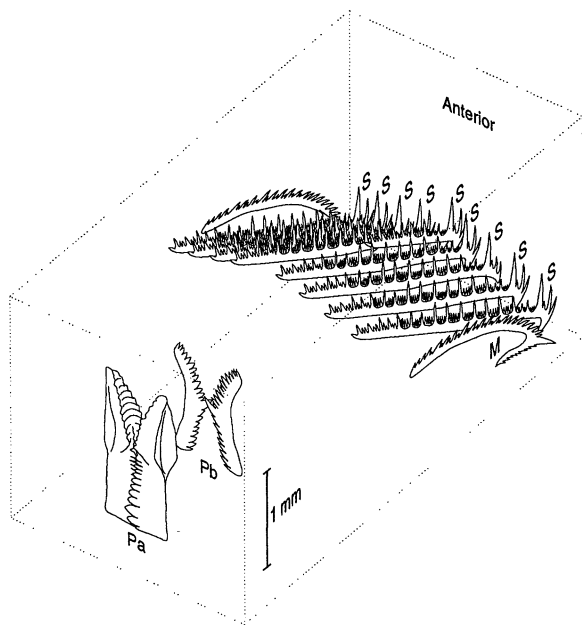
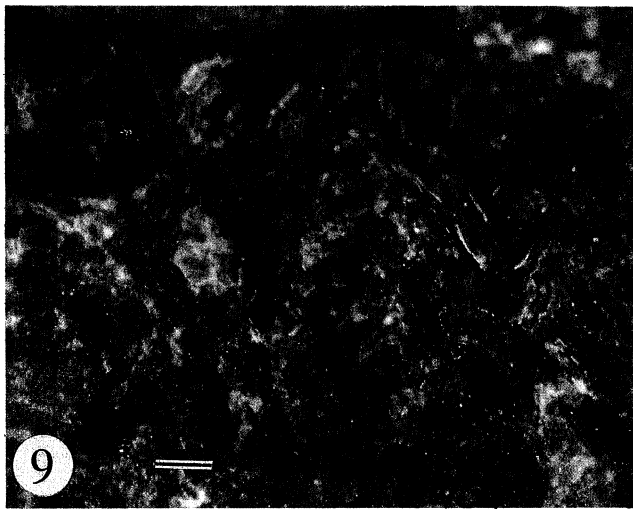
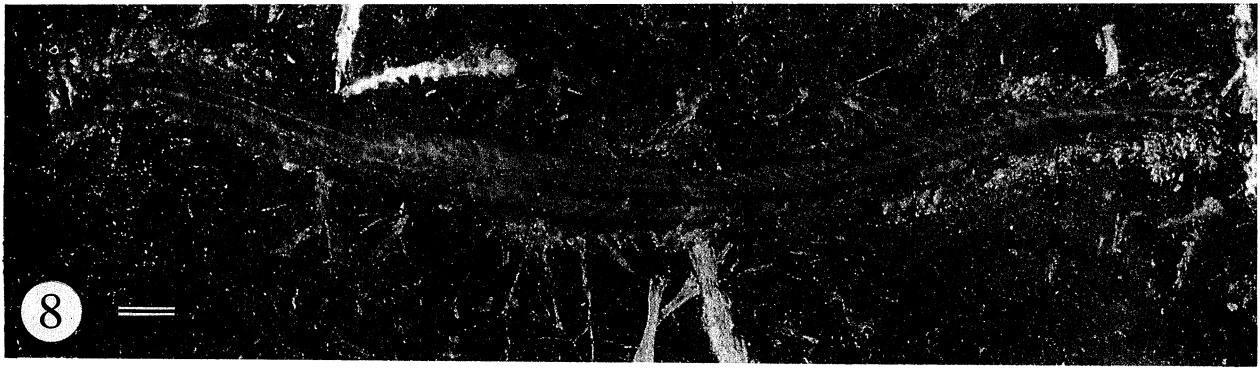


Figure 7. Architectural diagram of a complete ozarkodinid conodont apparatus; S and M elements in the anterior ramiform set are shown more widely spaced than in life. After Aldridge *et al.* (1987) and Purnell (1993).



Figures 8–9. Specimen 6, part (RMS GY 1992.41.2). Figure 8. Complete specimen, anterior to right; scale bar 2 mm. Figure 9. The feeding apparatus, partially concealed by rock matrix; scale bar 0.25 mm.

susceptible to decay than the notochordal sheath (which is one of the most decay-resistant structures; Briggs & Kear 1993). These muscle cells may be a primitive feature of *Branchiostoma* or an adaptation for burrowing in sediment (Q. Bone, personal communication); they are unknown in higher chordates.

The notochord occupies about 40% of the preserved height of the trunk (figures 3, 5 and 8); this compares with 12.5–20% in extant agnathans. It is parallel sided through most of its length, but tapers at both ends (specimens 5, 6 and others: figures 3 and 8). It extends posteriorly to the tip of the tail (Briggs *et al.* 1983, figs 4 and 5; Aldridge *et al.* 1986, fig. 4). Anteriorly it is preserved reaching as far as the ramiform elements of the feeding apparatus (specimens 5 and 6: figures 4 and 8), but not to the anterior extremity of the head. The position of the notochord varies along the length of the specimens. In specimen 5, for example, it lies closer to the dorsal margin of the head than to the ventrally situated elements of the feeding apparatus (figures 3 and 4). It runs more or less along the median axis in the tail, but it appears anomalously ventral in position along the mid-length of the trunk (figures 3 and 8). This ventral 'displacement' may be the result of movement of the notochord following degradation of the tissues which support it (this occurs in *Branchiostoma*, for example; Briggs & Kear 1993). Alternatively the ventral margin may have extended beyond the preserved outline (see comment under § 5d

(iii) below). In specimen 7, for example, the trunk is hardly preserved on the ventral side of the notochord (figure 10). The margins of the notochord vary in their degree of definition along the length of the trunk (e.g. specimen 6: figure 8) but there is no consistent pattern and this appears to be simply a function of preservation.

(ii) Nerve cord

In two specimens (4, and the counterpart of 1) the anterior part of one of the axial lines delimiting the notochord appears thickened and divided medially by a darker trace (figure 2). This feature was figured in specimen 4 by Aldridge *et al.* (1986, figs 5 and 8) who suggested that it might represent, *inter alia*, the dorsal nerve cord, a possibility also raised by Conway Morris (1989). The dorso-ventral as opposed to lateral flattening of the anterior end of both the specimens which preserve this feature supports a nerve cord interpretation, as this would explain its preservation directly on top of the notochord. On the other hand, the line with the dark median trace appears to be continuous with just one of the two delimiting the notochord further posteriorly (Aldridge *et al.* fig. 5), which might indicate that this feature is not axial, but displaced to one side. Twisting of the anterior portion of the trunk could produce the preserved configuration, but in the absence of independent evidence of such torsion, the identification of the nerve cord remains equivocal.

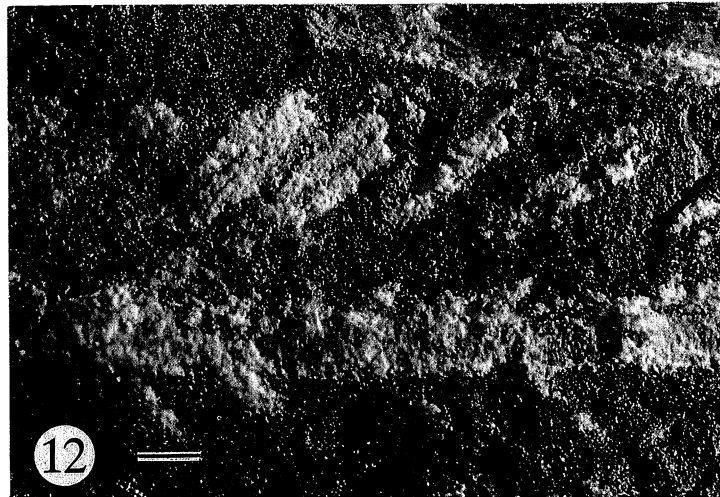
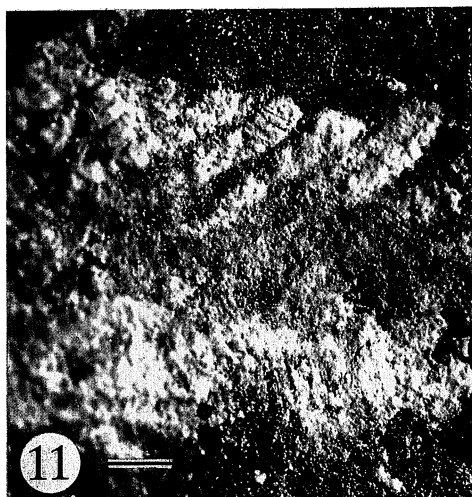
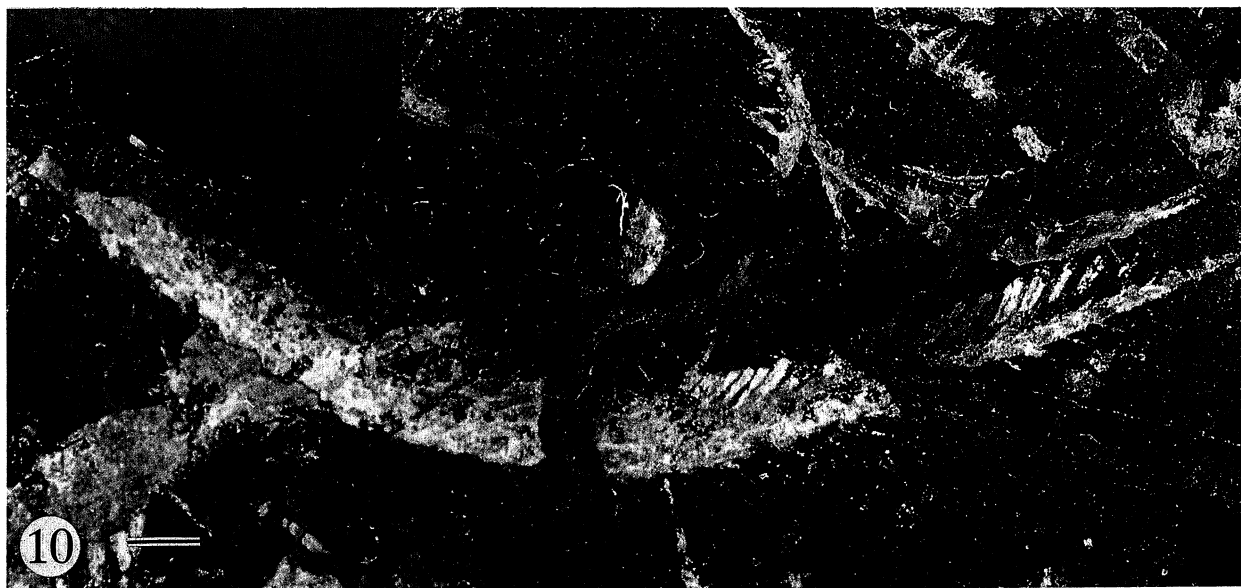
(iii) *Myotomal segments*

The identification of V-shaped myomeres in the Granton specimens has been one of the most compelling pieces of evidence for chordate affinity. A number of the new specimens (5 and 6: figures 3, 5 and 8) provide the clearest indication yet of the morphology of the muscle blocks. Their preservation as distinct and separated chevrons can be attributed to *post-mortem* shrinkage of the muscle fibres prior to phosphatization. Experimental work has shown that such shrinkage occurs early in the decay of the cephalochordate *Branchiostoma* (Briggs & Kear 1993).

The myomeres, apex directed anteriorly, are clearly evident along the length of the trunk in specimens 5 and 6 (figures 3 and 8); in both specimens they have an average spacing of 1.8 mm. The apices of the Vs form a sharper acute angle in the posterior and middle parts of the trunk of specimen 5, and become more rounded anteriorly (figures 3–5). This contrast is not evident on other specimens, however, and may reflect differences in preservation along the body. The posi-

tion of the Vs relative to the notochord varies along the trunk (figures 3 and 8), perhaps reflecting relative movement following some degradation (cf. Briggs & Kear 1993). The evidence from all the specimens is consistent with an arrangement of laterally paired V-shaped myomeres, their apices directed anteriorly and their limbs converging posteriorly to meet dorsally and ventrally along the midline (Aldridge *et al.* 1986, Conway Morris 1989).

On the dorsal side of specimen 7 the myomeres are heavily phosphatized and show very little shrinkage (figures 10–12). They reveal an internal structure, with possible traces of the original muscle fibres oriented sub-parallel to the trunk axis (figure 11). On the ventral side, on the other hand, the muscles are represented only by a few thin oblique traces (figures 10 and 12). Similarly, in the midsection of the trunk of specimen 6 (figure 8) very faint extensions of the myomeres suggest that the prominently preserved portions do not indicate the true ventral margin of the trunk.



Figures 10–12. Specimen 7, part (RMS GY 1992.41.3). Figure 10. Majority of preserved trunk, anterior to left; scale bar 2 mm. Figure 11. Detail of trunk posterior of mid-length, showing heavily phosphatized myomeres with oblique fibrous structure (arrowed); scale bar 0.5 mm. Figure 12. Detail of posterior portion of preserved trunk, showing heavily phosphatized notochord with transverse fibrous structure; scale bar 0.5 mm.

A series of small evenly-spaced spots of phosphate, slightly elongated normal to the trunk axis, are evident close to the ventral margin of specimen 5, some 14–26 mm from the anterior end (figure 5). There are no similar structures on the opposite margin. The nature of these structures, which may be a preservational artefact, is unknown.

(iv) *The tail*

The distribution of fin rays in specimen 3 (Aldridge *et al.* 1986, fig. 4), which preserves a prominent trace of the notochord extending into the tail, shows a caudal fin more extensively developed along one side of the tail than the other. In the absence of a preserved apparatus in this specimen there is no independent indication of whether the longer fin is dorsal or ventral. Fin rays are also clearly evident on one margin of the tail of specimen 1 (figure 1; Briggs *et al.* 1983, figs 4, 5), and a narrow strip of heavily phosphatized material on the opposing margin shows indistinct oblique traces which may represent concealed fin rays on that side. The latter margin also has an indentation 3 mm from the end, which may be an original feature or may have been produced by folding of the edge during flattening. The precise structure of the caudal fin remains equivocal; it may have been symmetrical, or it may have extended slightly further on the dorsal or ventral margin. If the true symmetry of the tail is revealed by specimen 1, then tracing of the margin with the longer fin to the anterior end of the animal shows that it lies to the same side of the trunk as the apparatus, which is ventral. However, as the soft tissues of the head indicate dorso-ventral compaction of the anterior part of the fossil, it would only take a little twisting of the specimen along the trunk for a dorsal fin to be compacted on the same side of the fossil as the apparatus.

(e) *Restoration*

A new restoration (figure 13) of the Granton

conodont animal is based on the evidence from all 10 available specimens. The relative dimensions are averaged. The animal is portrayed swimming in anguilliform mode, the most probable mode of locomotion of an animal of this shape. The feeding apparatus is restored surrounded by soft tissue, although evidence for the nature and extent of this tissue is lacking. Branchial openings are omitted in the absence of evidence for their form and position. The myomeres are outlined along the trunk, as is the likely position of the notochord, although this would presumably have been concealed in life by the body musculature. This restoration differs from a previous version (Aldridge & Briggs 1989) principally in the interpretation of the anterior lobes as large eyes. A restoration recently published by Dzik (1992, fig. 9.15) does not identify the eyes, but suggests a possible position of the anus anterior to the fins. Dzik reconstructs the anterior ramiform elements of the feeding apparatus in a different orientation from that shown by the Granton animals.

6. THE DEBATE ON CONODONT AFFINITIES

In the description of the first conodont animal specimen, Briggs *et al.* (1983) assessed the phylogenetic position of the conodonts with reference to two groups, chordates and chaetognaths. Features of the single specimen were open to different interpretations, and a conclusive assignment was impossible. Pending the discovery of additional specimens, Briggs *et al.* (1983) chose to follow Clark (1981) in placing the conodonts in a separate phylum Conodonta, a decision supported by Gould (1983). Subsequent specimens confirmed the chordate-like characters of the first specimen and led Aldridge *et al.* (1986) to dismiss the possibility of a chaetognath affinity and to propose that conodonts were most closely related to myxinoid craniates. The evidence of element histology (Sansom *et al.* 1992), and of the soft-tissue anatomy presented here, confirm

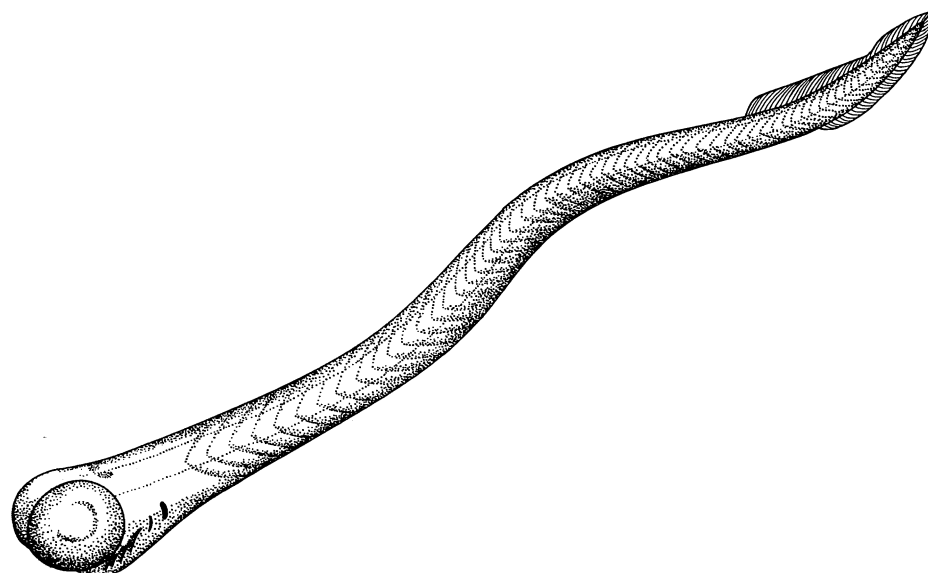


Figure 13. Restoration of the living conodont, approximately $\times 3.3$. Branchial openings are omitted in the absence of evidence to guide accurate restoration.

that assignment. Other hypotheses that have been forwarded in recent years can now be refuted.

(a) *Conodonts as a separate phylum*

Sweet (1988) argued strongly that the conodonts represent a separate phylum, a stance which has subsequently been rebutted (Aldridge & Briggs 1990; Smith 1990; Sansom *et al.* 1992). Sweet placed heavy reliance on the absence of a variety of morphological features in the Granton and Waukesha specimens, regarding a chordate affinity as tenable only if 'positive evidence or strong indirect indication' was found of three characters: (i) notochord; (ii) dorsal nerve cord; and (iii) gill slits. The axial lines in the Granton specimens can now be confidently interpreted as a notochord, a possibility considered by Aldridge *et al.* (1986) and favoured by Conway Morris (1989). The median strand at the anterior end of the axial lines of the fourth Granton specimen was suggested by Conway Morris (1989) to be possible evidence of the dorsal nerve cord, and this remains the most probable interpretation. The absence of evidence for other characters with a low preservation potential, such as gill slits, clearly cannot be afforded the same weighting as diagnostic characters which are present. The assertion by Sweet (1988) that trunk structures in other groups such as nemerteans and aplacophoran molluscs could also produce the V-shaped structures identified as somites by Aldridge *et al.* (1986) cannot be sustained (Briggs *et al.* 1987; Aldridge & Briggs 1990).

(b) *Conodonts as nemerteans*

Sweet (1988) drew comparisons between the soft parts of nemertean worms (phylum Nemertea or Rhynchocoela) and the Granton specimens. The serially repeated V-shaped structures along the axis of the trunk were likened to the numerous paired lateral diverticula which branch from the straight, axially located intestine of nemerteans. However, the diverticula of nemerteans are straight and it is difficult to envisage a collapse or compaction orientation which could produce the prominent V-shaped structures in the Granton specimens (Aldridge & Briggs 1990; Smith 1990). A living aberrant nemertean, *Annulone-merites*, has annulations on the surface that correspond to segmented divisions of internal organs (Berg 1985), but these take the form of circular constrictions and could not be preserved as chevrons. Sweet (1988) also suggested that the paired lines running the full length of the trunk of the Granton specimens might represent the nemertean rhynchocoel, but the latter is a relatively short cavity to accommodate the proboscis and does not run the full length of the body (Aldridge & Briggs 1990). A nemertean affinity for conodonts can be confidently discounted.

(c) *Conodonts as molluscs*

Tillier & Cuif (1986) and Tillier & Janvier (1986) argued for a relationship between conodonts and

aplacophoran molluscs. The apparent similarities were dismissed as superficial by Briggs *et al.* (1987; see also Conway Morris 1989), and Janvier (1988) subsequently acknowledged that the tail structure of the Granton specimens is strikingly chordate- and even craniate-like.

Beall (1991) undertook a combined cladistic and phenetic analysis of the phylogenetic affinities of *Tullimonstrum*, an enigmatic metazoan from the Upper Carboniferous Mazon Creek fauna of Illinois, U.S.A. The animal has an anterior proboscis with a jaw at the tip bearing 14 teeth or 'stylets', a bulbous but dorso-ventrally flattened trunk, and a pair of flexible, laterally compressed posterior fins. Beall concluded that the available evidence 'overwhelmingly indicated' that *Tullimonstrum* had affinity with either the Conodonts or the Mollusca. The most frequently encountered cladogram placed *Tullimonstrum* as a sister group of Conodonts + Mollusca, thereby apparently corroborating the Tillier & Cuif (1986) hypothesis. However, as Beall himself noted, this apparent relationship of conodonts and molluscs is to a degree an artefact of the limited range of taxa considered in his cladistic analysis. The limited availability of conodont data for the character states selected and the doubtful homology of some of these characters were also contributory factors. For example, homology between the 'stylets' of *Tullimonstrum* and the phosphatic elements of conodont apparatuses, or between the 'anterior bifurcate lobes' in both organisms, is far from established. The possible chordate or mollusc affinities of *Tullimonstrum* remain equivocal and this animal contributes little to the question of conodont affinities.

(d) *Conodonts as chaetognaths*

Following the description of the first Granton specimen, Bengtson (1983) compared the collapsed, non-operational position of the apparatus to that of chaetognaths, a suggestion first mooted by Rietschel (1973). This followed the documentation of a close histological similarity between extant chaetognath grasping spines and protoconodont elements by Szaniawski (1982); both display a trilaminar structure and are very similar morphologically. In addition, protoconodont elements occur in fused clusters which closely resemble chaetognath half-apparatuses in the retracted position. There is little doubt of the chaetognath affinities of protoconodonts, but a question remains over the relationship of protoconodonts to para- and euconodonts. Bengtson (1976) proposed an evolutionary sequence leading from proto- through para- to euconodonts, involving increasing retraction of the elements into pockets of the epithelium during growth. The histological work of Sansom *et al.* (1992), however, showed that this scenario is, at best, an oversimplification and that the question of paraconodont-euconodont relationships needs re-evaluation. Although some recent work has expressed or implied a preference for models of chaetognath affinity (Szaniawski 1987; Müller & Hinz 1991), the soft part evidence and the element histology fail to demonstrate

any synapomorphies between euconodonts and chaetognaths.

(e) *Conodonts as cephalochordates*

Nowlan & Carlisle (1987) listed a number of criteria in support of a cephalochordate affinity for conodonts.

1. The lack of paraxial or dermal elements. This argument is based, however, on the *a priori* assumption that an exoskeleton composed of dermal denticles represents the primitive vertebrate condition.

2. The 'V-shaped folding' of the muscle somites with the angle of the V pointing forwards. This was regarded as compatible with cephalochordate, but not craniate, affinity. Although the myomeric structure in conodonts is less complex than that in extant petromyzontids, a similar pattern does occur in various fossil 'Agnatha'. Anaspids, such as *Jamoytius*, display the anteriorly terminated conical myomeres which presumably represent the primitive condition, as does the early Caradoc *Sacabambaspis*, a possible anaspid which is one of the earliest vertebrates with a mineralized exoskeleton (Gagnier *et al.* 1986; Gagnier 1989; Blicek *et al.* 1991; Elliott *et al.* 1991).

3. The level of encephalization demonstrated by the anterior feeding apparatus, which is no higher than the oral hood of *Branchiostoma*; eyespots do not imply craniate affinities as some protochordates possess them. Our new interpretation of the lobate structures on the Granton specimens as sclerotized cartilages supporting large eyes, however, provides a marked contrast with the simple light sensory apparatus of cephalochordates. It also suggests a more substantial degree of encephalization than is represented by the oral hood of *Branchiostoma*.

4. Fin rays that do not correspond to the muscular somites and appear to lack any trace of basal articulation or musculature. Although these comments are pertinent to a comparison with higher fish, myxinooids and petromyzontids also possess unsupported fin folds.

In cephalochordates, the notochord extends to the rostral tip of the head, whereas in craniates it terminates posterior to the cranium at the basicranial fenestra (Gans & Northcutt 1983). None of the Granton specimens shows the notochord extending beyond the feeding apparatus. This provides additional evidence against a cephalochordate affinity.

Nicoll (1987) investigated the question of affinity purely in relation to apparatus function, and in particular to that of the Pa elements. Although the apparatus architecture arrived at by Nicoll (1987) and Nicoll & Rexroad (1987) is similar to that determined by Aldridge *et al.* (1987), their functional interpretation was radically different. A permanent soft tissue covering over the elements was invoked and a ciliated, microphagous filtering function suggested. The ramiform basket and platform array were likened to the unmineralized buccal cirri and wheel organ of cephalochordates. A filter-support function for the conodont elements cannot be unequivocally refuted on the basis of the Granton animals, but element morphology and arrangement suggest that the feeding

apparatus operated as an integrated set of grasping, shearing and grinding teeth (Jeppsson 1979; Aldridge *et al.* 1986; Weddige 1990; Purnell & von Bitter 1993). This functional interpretation is supported by ontogenetic changes in relative size and complexity of conodont elements within intact apparatuses (Purnell 1992a).

7. CONODONTS AS VERTEBRATES

There is a lack of consensus regarding the taxonomic scope of the Vertebrata. A frequently employed definition (e.g. Forey 1984; Schaeffer 1987) is that of Janvier (1981) who placed all fossil and extant Chordata with a cranium within the Craniata and chose to restrict the Vertebrata to those craniates possessing vertebral elements. This excludes the Myxinoidea and, possibly, the Heterostraci, although vertebral elements have been tentatively identified in some crownward heterostracans (Janvier & Blicek 1979). However, common usage continues to include all craniates *sensu* Janvier (1981) within the Vertebrata (e.g. Blicek & Janvier 1991; Blicek *et al.* 1991; Elliott *et al.* 1991), in accord with the definition employed by developmental biologists, which is based upon the possession of hard tissues or neural crest embryonic tissue (e.g. Hall 1987; Hall & Hörstadius 1988; Maisey 1988; Smith & Hall 1990). Neural crest is an ectodermally derived tissue which, in its capacity to generate a large number of unique vertebrate characters including hard tissues of the dermal exoskeleton and craniofacial region, may be regarded as the *sine qua non* of vertebrate organization (Northcutt & Gans 1983; Hall & Hörstadius 1988; Gans 1989; Smith & Hall 1990). On this basis the Craniata and Vertebrata are synonymous, and include the myxinooids, which possess neural crest tissues (Conel 1942; Janvier 1981; Hall & Hörstadius 1988). This is the sense in which we regard the Vertebrata here.

Histological and soft tissue characteristics indicate that conodonts are vertebrates. Aldridge *et al.* (1986) concluded that they are most closely related to myxinooids, sharing a laterally compressed body, myomeres, a tail fin and a bilaterally operating feeding apparatus. Conodonts differ from myxinooids in having phosphatic, rather than keratinous, oral elements.

A vertebrate affinity for conodonts has been proposed by several authors on the basis of the Granton specimens. They have been related to primitive craniates (Smith & Hall 1990; Hall 1992), the first crown group vertebrates (Jefferies 1986), agnathans (Dzik 1986) and, more specifically, myxinooids (Janvier 1983). Other authors cast doubt on hypotheses of vertebrate affinity, although some (Maisey 1986; Blicek 1988; Blicek & Janvier 1991) offered no supporting evidence. Gans (1989), however, contended that no uniquely derived character associates conodonts and vertebrates. More recently, the apparent histological differences between conodonts and Ordovician heterostracans, in particular the presence of 'lamellar, acellular' tissue in conodont element crowns and absence of the honeycombed or reticulated structure of the cancellous layer of astraspids and

heterostracans, were used to refute a close relationship (Elliott *et al.* 1991; Blicek 1992). While accepting conodonts as primitive craniates, Smith & Hall (1990) stressed the possibility that conodont hard tissues were independently derived from those in post-Llanvirn vertebrates. They pointed to the absence of evidence for the derivation of conodont elements from the dermal skeleton and concluded that the elements simulated teeth but were not tooth homologues.

Early work on the histology of conodont elements (Pander 1856; Gross 1954) indicated that the skeletal tissues were essentially vertebrate-like, but most subsequent investigators have concluded that the hard tissues of the elements are unique to conodonts (see Müller (1981) and Lindström & Ziegler (1981) for reviews). Recent histological work, however, demonstrated the presence of cellular bone, enamel homologues and probable calcified cartilage in coniform and ramiform-pectiniform elements (Sansom *et al.* 1992). Cellular bone is present in the central areas or cores of cusps and denticles, previously described as 'white matter'. Lamellar tissue homologous with enamel, with crystallites normal to the growth lines, occurs in the crown of *Cordylodus* and *Ozarkodina*. Enamel-like tissue in the crowns of panderodontid taxa differs from true enamel in having crystallites arranged asymptotically, rather than normal, to the incremental lines (Sansom *et al.* 1992). This tissue was also considered homologous with enamel by Sansom *et al.* (1992). The basal bodies of *Cordylodus*, *Panderodus* (Barnes *et al.* 1973; Sansom *et al.* 1992) and possibly *Coleodus* (Barskov *et al.* 1982) contain spherulitic structures which are strikingly similar to globular calcified cartilage in the Ordovician ?heterostracan *Eriptychius* and in cephalaspids, antiarchs and elasmobrachs.

The recognition of enamel in proconodontid and ozarkodinid conodonts confirms the homology between crown tissue and enamel postulated by Dzik (1986). Dzik (1986) did not mention white matter or its possible vertebrate homologues, but proposed homology between the basal body of conodont elements and dentine. His interpretation of basally-opening, axial canals and tubuli in the basal body of *Semiacontiodus* elements as dentine tubuli was dismissed by Smith & Hall (1990) and Blicek (1992), and no evidence of similar structures was found by Sansom *et al.* (1992). Dzik (1986) offered no detailed interpretation of the lamellar or spherulitic structures commonly found in basal bodies and interpreted by Sansom *et al.* (1992) as calcified cartilage.

Krejsa *et al.* (1990a,b) homologized conodont elements with the keratinous lingual teeth of myxinoids. They noted that the size ranges of conodont elements and juvenile myxinoid teeth overlap, and proposed histological similarities between white matter and the moribund nuclei and cancellous spaces (organelle remnants of pokal cells) in the myxinoid denticles. Sansom *et al.* (1992), however, revealed much closer similarities between white matter and the lacunae and interconnecting canaliculi of cellular bone, and there is no evidence that euconodont elements represent a form of biomineralized keratin.

Cellular bone, enamel and globular calcified carti-

lage are all unique to vertebrates. Cellular bone of the oral cavity develops from ectomesenchymal cells, which in turn are derived from the neural crest (Smith & Hall 1990; Smith 1991), and enamel is produced by ameloblasts of the ectodermal epithelium through a sequence of epigenetic cascades involving epithelial-ectomesenchymal interactions (Lumsden 1987, 1988; Smith & Hall 1990). Although some workers regard the evidence from conodont element histology to be equivocal (Forey & Janvier 1993), the identification of neural-crest derived skeletal tissues complements the soft-body evidence, and together these provide a compelling case for vertebrate affinity.

8. PHYLOGENETIC POSITION OF CONODONTS WITHIN THE VERTEBRATES

Integration of the new soft part information with the histological data of Sansom *et al.* (1992) permits a re-appraisal of the phylogenetic relationships proposed by Aldridge *et al.* (1986). Although a variety of phylogenetic schemes for pre-gnathostome vertebrates have been produced in recent years, there is now a degree of consensus based around the cladogram of Janvier (1981), subsequently modified by Forey (1984), Janvier (1984), Maisey (1986, 1988) and Blicek (1992). We note, however, that several relationships remain controversial, and that there is some renewed support for the hypothesis of cyclostome monophyly (Stock & Whitt 1992). For the present, we find the modified Janvier (1981) scheme the most appropriate, and we can now assign the conodonts to their position on this cladogram (figure 14). Although a large number of biochemical, developmental and soft tissue characters have been incorporated in some of the published phylogenetic analyses, particularly that of Hardisty (1982), only those with a reasonably high preservation potential, either directly or indirectly, are discussed below.

The primitive condition of the Euchordata ((Cephalochordata + Vertebrata) = the somitic chordates of Schaeffer (1987); node A on figure 14) comprises a bilaterally flattened body, myomeres, a notochord, dorsal nerve cord, a post-anal tail and a median fin ridge (Schaeffer 1987; Gans 1989). The Vertebrata (node B on figure 14) are characterized by the possession of neural crest (Janvier 1981; Schaeffer 1987; Gans 1989), but other synapomorphies include the cranium (Gans & Northcutt 1983; Northcutt & Gans 1983), a cartilaginous endoskeleton (Reif 1982; Maisey 1986), a bilaterally operative feeding apparatus (unmineralized in myxinoids) (Janvier 1981), the lateral line system (Maisey 1986) and a branchial apparatus with a separate series of gills (Janvier & Blicek 1979; Maisey 1986). The vertebrates are also characterized by paired olfactory, optic and auditory capsules (Maisey 1986), sensory organs that develop from epidermal placodes, an embryological feature closely related to the neural crest (Gans & Northcutt 1983).

A number of these synapomorphies can be identified, with varying degrees of certainty, in the Granton conodonts, including a bilaterally operative feeding

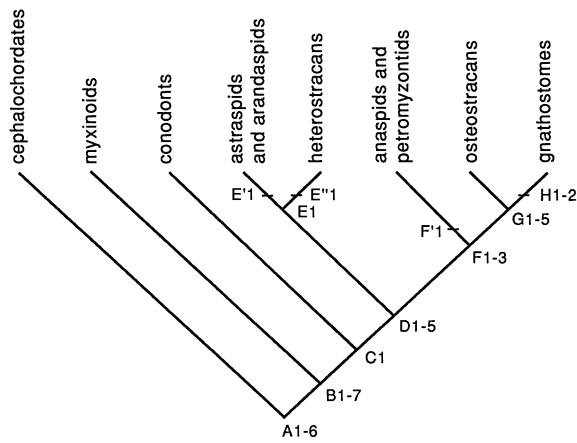


Figure 14. Hypothesis of the relationship of conodonts to other chordates, based on the evidence from preserved soft tissues and element histology. Characters at node A: 1, bilaterally symmetrical body; 2, myomeres; 3, notochord; 4, dorsal nerve cord; 5, post-anal tail; 6, median fin ridge. Characters at node B: 1, neural crest; 2, cranium; 3, cartilaginous endoskeleton; 4, bilaterally operative feeding apparatus; 5, lateral line system; 6, branchial apparatus with a separate series of gills; 7, paired olfactory, optic and auditory capsules. Character at node C: 1, first vertebrate hard tissues (cellular dermal bone, enamel homologues, calcified cartilage). Characters at node D: 1, dermal ossification; 2, dentine; 3, perfected lateral line system; 4, gill chambers lying opposite each other; 5, vertebral elements? Character at node E: 1, aspidin; E'1, multiple (eight?) external branchial openings; E''1, single paired external opening. Characters at node F (Myopterygii): 1, true dorsal, anal and caudal fins with a distinct body lobe and caudal fin web; 2, paired fins (secondarily absent in petromyzontids); 3, muscularized unpaired fins (secondarily absent in petromyzontids); F'1, gill slits arranged in a slanting line. Characters at node G: 1, perichondral bone; 2, cranial nerves IX and X issuing from the brain case; 3, heterocercal tail with change of scale orientation at the caudal peduncle; 4, pectoral fins concentrated at base; 5, sclerotic ossification. Characters of Gnathostomata: H1, jaws comprising bilateral upper palatoquadrate and lower mandible; H2, endochondral bone.

apparatus (Aldridge *et al.* 1987), and possibly a branchial apparatus and paired olfactory or otic capsules. The notochord of the Granton conodonts, like that of myxinoids and higher chordates, does not extend to the anterior tip of the animal (e.g. specimen 5). The presence of large eyes also suggests a higher degree of encephalization than that in cephalochordates.

Characters defining node C include the first vertebrate hard tissues. The presence of cellular dermal bone, enamel homologues and calcified cartilage in conodonts (Sansom *et al.* 1992) confirms that they lie crownward of myxinoids (Aldridge *et al.* 1986; Briggs 1992) as a sister group of higher vertebrates. Until recently, cellular bone was believed to be phylogenetically advanced and stratigraphically young, present only in osteostracans and gnathostomes (Janvier 1981, 1984; Forey 1984). The presence of cellular bone in an un-named Harding Sandstone (Caradoc) vertebrate (Smith 1991) could be interpreted in two ways: either the species concerned was an osteostracan that pre-

dated known Osteostraci by around 40 million years, or cellular bone is a more primitive vertebrate tissue than previously thought. The discovery of cellular bone in early Ordovician conodonts (Sansom *et al.* 1992) supports the latter alternative.

The possession of dermal ossification unites heterostracans *sensu lato* and myopterygians at node D. Individual hard tissue types have not generally been coded independently, but the absence of dentine in the conodonts examined histologically to date (Sansom *et al.* 1992) indicates that dentine may also characterize this node. Dentine has previously been regarded as one of the primitive, first-evolved hard tissues (Reif 1982; Northcutt & Gans 1983; Gans 1989), but it now appears that it was relatively advanced, appearing later than bone, enamel and calcified cartilage. The earliest vertebrate hard tissues now recognized developed in the oral cavity, and this may represent the primitive condition, in contrast to the frequently expressed view that they first appeared as dermal armour, with possible sensory precursors (Reif 1982; Northcutt & Gans 1983; Gans 1989). Other characters at node D include a perfected lateral line system (Janvier 1981; Maisey 1986), gill chambers lying opposite each other (Forey 1984) and the possible presence of vertebral elements (Janvier & Blicek 1979). None of these characters can be determined in the Granton specimens.

Ordovician astraspids and arandaspids have traditionally been placed within the heterostracans. However, the discovery of eight external branchial openings on each side of *Astraspis* as opposed to a single pair (Elliott 1987) has led to its exclusion from the Heterostraci, together with *Arandaspis* and *Sacabambaspis*, which also have a series of openings (Elliott *et al.* 1991). Blicek (1992) suggested that the astraspids and arandaspids are sister taxa of heterostracans *sensu stricto*, with which they are united by the autapomorphic possession of aspidin (a distinctive type of acellular bone). The position of *Eriptychius* remains uncertain in the absence of articulated material, although Blicek (1992) included the genus in the Heterostraci.

Node F (figure 14) is defined by the possession of true dorsal, anal and caudal fins with a distinct body lobe and caudal fin web (Forey 1984), together with paired fins and muscularized unpaired fins (Janvier 1981). Petromyzontids + anaspids differ from the crown group by having gill slits arranged in a slanting line (Janvier 1981; Forey 1984).

At node G, osteostracans and gnathostomes share the following characters: perichondral bone, cranial nerves IX and X issuing from the brain case, a heterocercal tail with change of scale orientation at the caudal peduncle, pectoral fins concentrated at the base, and sclerotic ossification (Janvier 1981; Forey 1984). Janvier (1981) and Forey (1984) also included cellular bone at this node but this must now be regarded as a more primitive character.

The evidence of conodont anatomy, including the histology of the elements, indicates that conodonts are primitive vertebrates. They lie crownward of myxinoids, forming a primitive sister group of the Heterostraci + Myopterygii. A number of outstanding issues

remain, which will only be resolved with new discoveries of element histology and soft tissue preservation. These include the relationships of proto-, para- and euconodonts, the mode of growth and function of elements and the variability of soft part morphology in different conodont taxa.

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APPENDIX. Details of feeding apparatuses of newly discovered specimens

Specimen 5

Apparatus preserved in standard orientation (*sensu* Aldridge *et al.* 1987), indicative of lateral compaction, with the sinistral side revealed (figure 4). The cusp of a ramiform element, probably an Sc, is preserved overlying the lower posterior margin of the right hand lobe. Traces of moulds of other Sc elements are discernible dorsal of this cusp. The distal posterior processes of three S elements bear posteriorly inclined

denticles, the largest at the posterior end. The Pb element is angulate with the posterior process almost perpendicular to the line of the trunk. Although the cusp and denticles are partly obscured, they are clearly broad. The Pa element is largely buried in the matrix. It is oriented perpendicular to the line of the trunk, with the platform dorsal. The denticulate surfaces of all elements face towards the eyes. The Pa element is not sufficiently exposed to allow the taxon to be identified, but the denticulation of the ramiform elements suggests that the apparatus is similar to that of specimen 1.

Specimen 6

Apparatus preserved in standard orientation (figure 9). At the anterior, preparation has revealed two ramiform elements from the dextral side of the apparatus. The outer element, probably an Sc, has a short anterior process and a long posterior process directed at an angle of 60° to the trunk. The posterior process bears discrete denticles inclined away from the cusp. At the distal end of the process the denticles become larger and more inclined. The cusp is prominent but largely buried in the matrix. A second S element, probably an Sc or an Sb, lies behind, oriented sub-parallel to the first. The two elements are compacted together so that the denticulate surface of the second is only clear at the distal end, where the denticles are large and strongly inclined. Part of a third ramiform element, probably also from the right hand side of the apparatus, is evident behind these two, separated from them by a short space in which indistinct traces of another element are evident. The Pb element is angulate, with the posterior process sub-parallel to the Selements. The anterior process lies at an angle of 80° to the line of the trunk. The Pa element bears a short free blade and is low distally rising rapidly proximally to a prominent cusp. The platform is about twice as long as the blade; the denticulate surface is obscured by matrix but the lateral edges of a row of nodes may be discerned. The long axis of this element is approximately perpendicular to the line of the trunk. The denticulate surfaces of all the elements point anteriorly. The Pa element is not sufficiently exposed to allow the taxon to be positively identified, but as far as can be determined all the elements compare well with those of specimen 1.

Specimen 7

Apparatus preserved in parallel orientation (Aldridge *et al.* 1987). Most of the apparatus is preserved on the counterpart, where it has been revealed by preparation; only indeterminate traces of elements are evident on the part. The elements are directed nearly normal to bedding so that most display only oblique basal views. Four dextral S elements are apparent, alongside a crowded set of P or sinistral S elements. Although it is clear that the ramiform elements are robust like those of specimen 2, it is not possible to identify the taxon represented.

Specimen 8

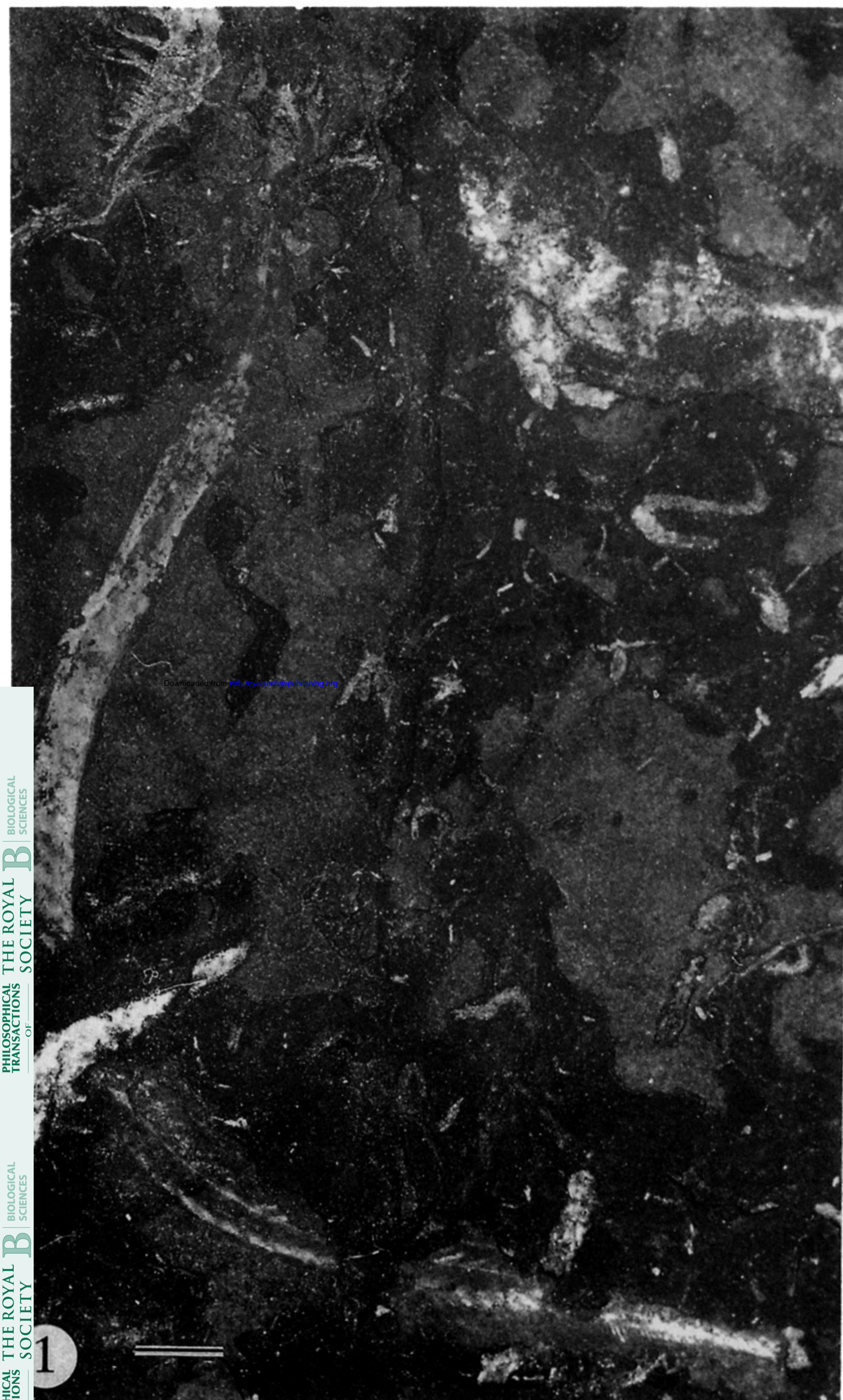
Apparatus preserved in standard orientation, some

2 mm anterior of the preserved trunk, and offset from the line of the trunk margin by 1 mm. Only a trace of the Pa element is apparent, but an angulate Pb is oriented perpendicular to the line of the trunk with its denticulate surface pointing forwards. To the anterior the distal portions of at least three S elements are evident inclined at an angle of 10–15° to the Pb element with the denticulate surfaces pointing forwards. All the elements are small and delicate suggesting that the animal is a juvenile. In the absence of a more fully revealed Pa element, no identification can be made.

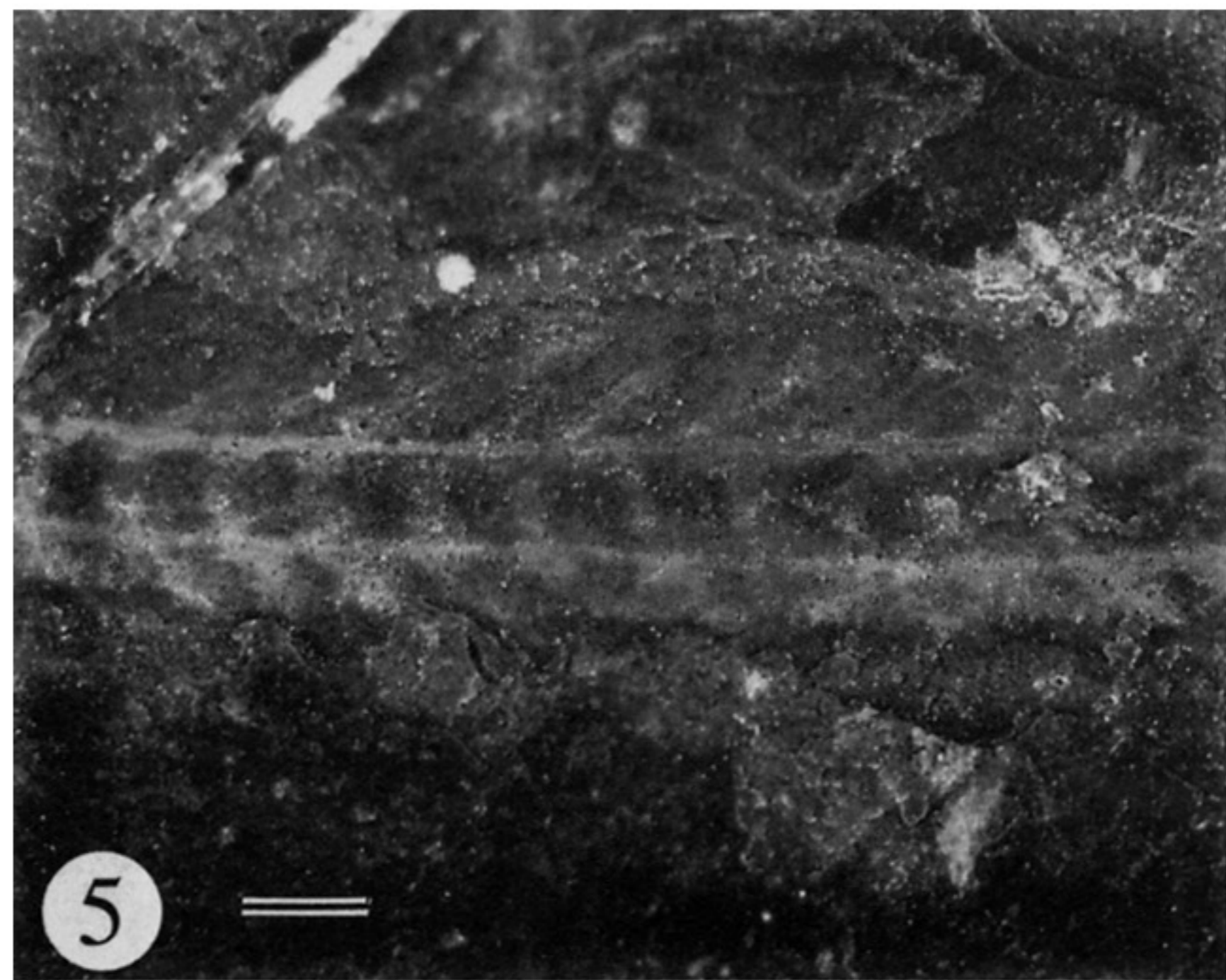
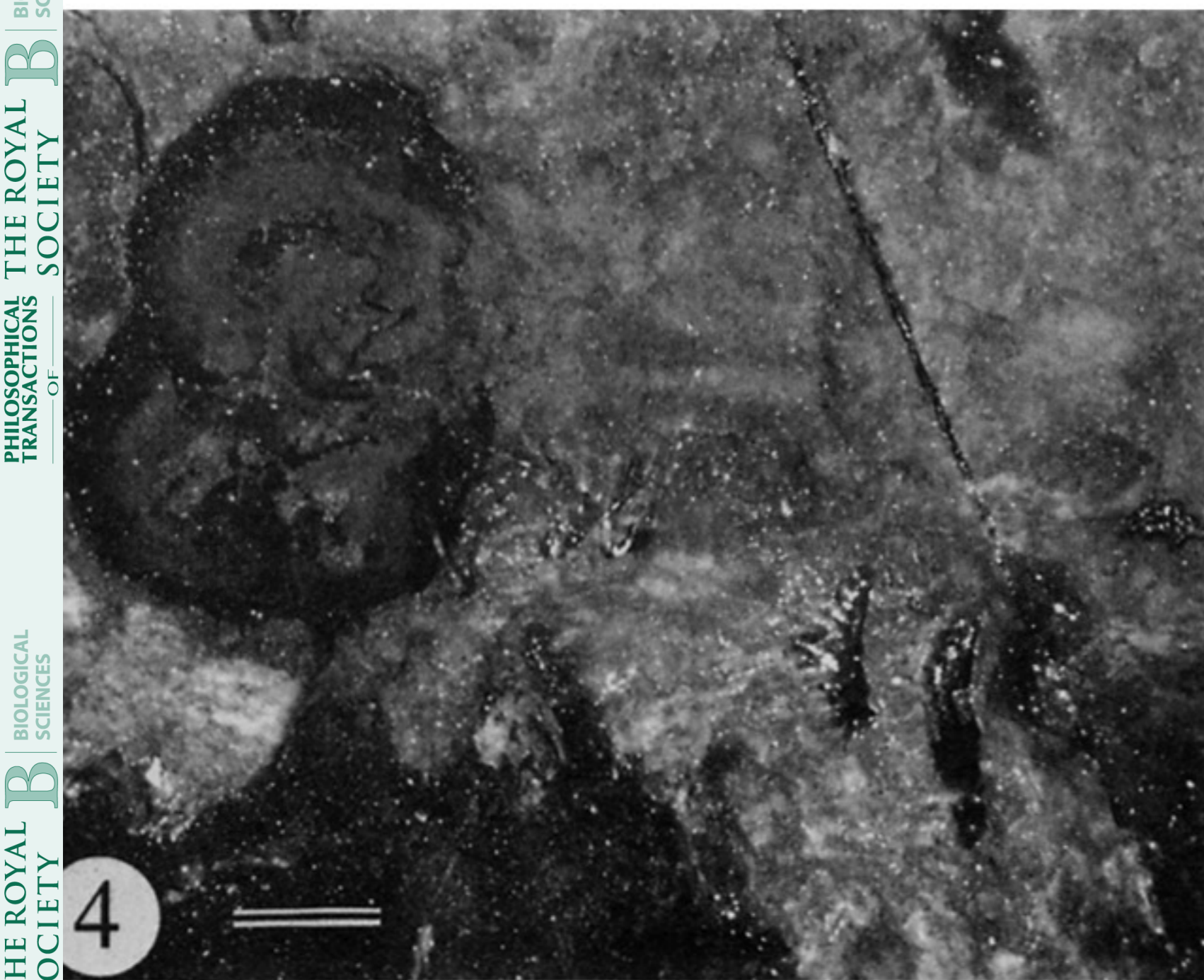
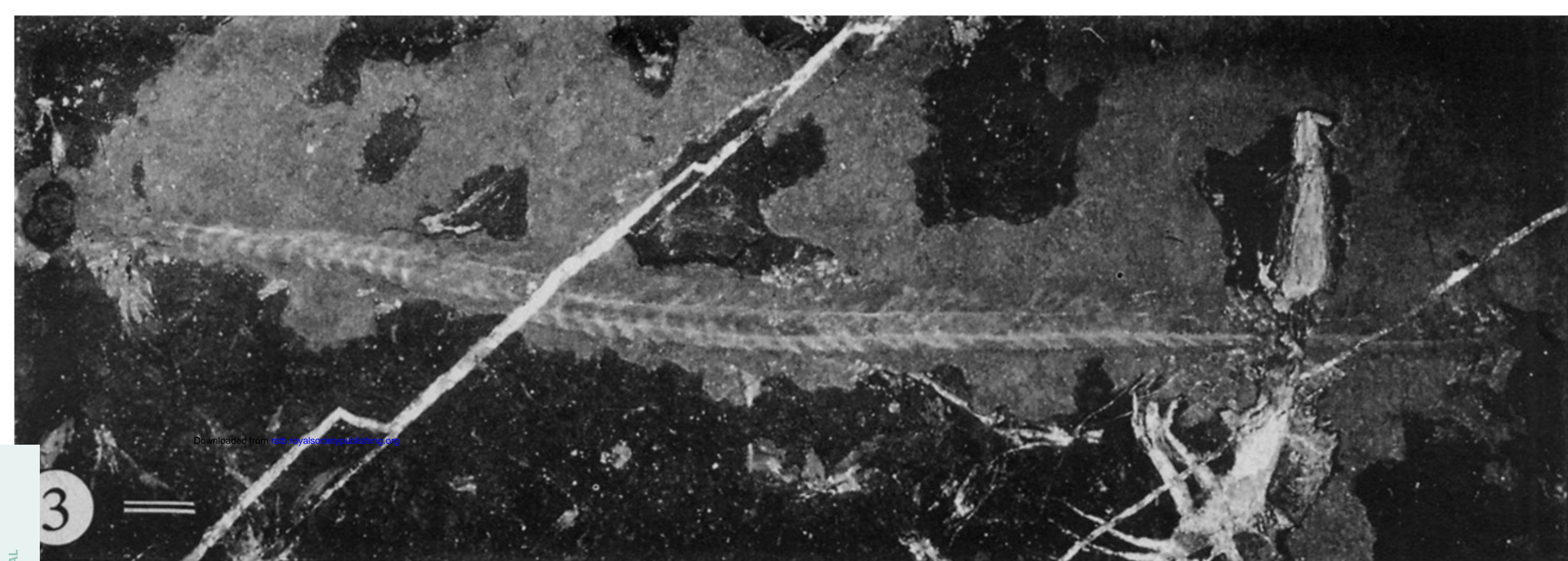
Specimen 10

Displays a poorly preserved apparatus slightly offset from the axis of the trunk. A minimum of three elements are partially exposed, one the distal portion of an Sc which is directed at an angle of 80° of the trunk with the denticulate surface pointing anteriorly. Only small, unidentifiable traces of the other elements are evident.

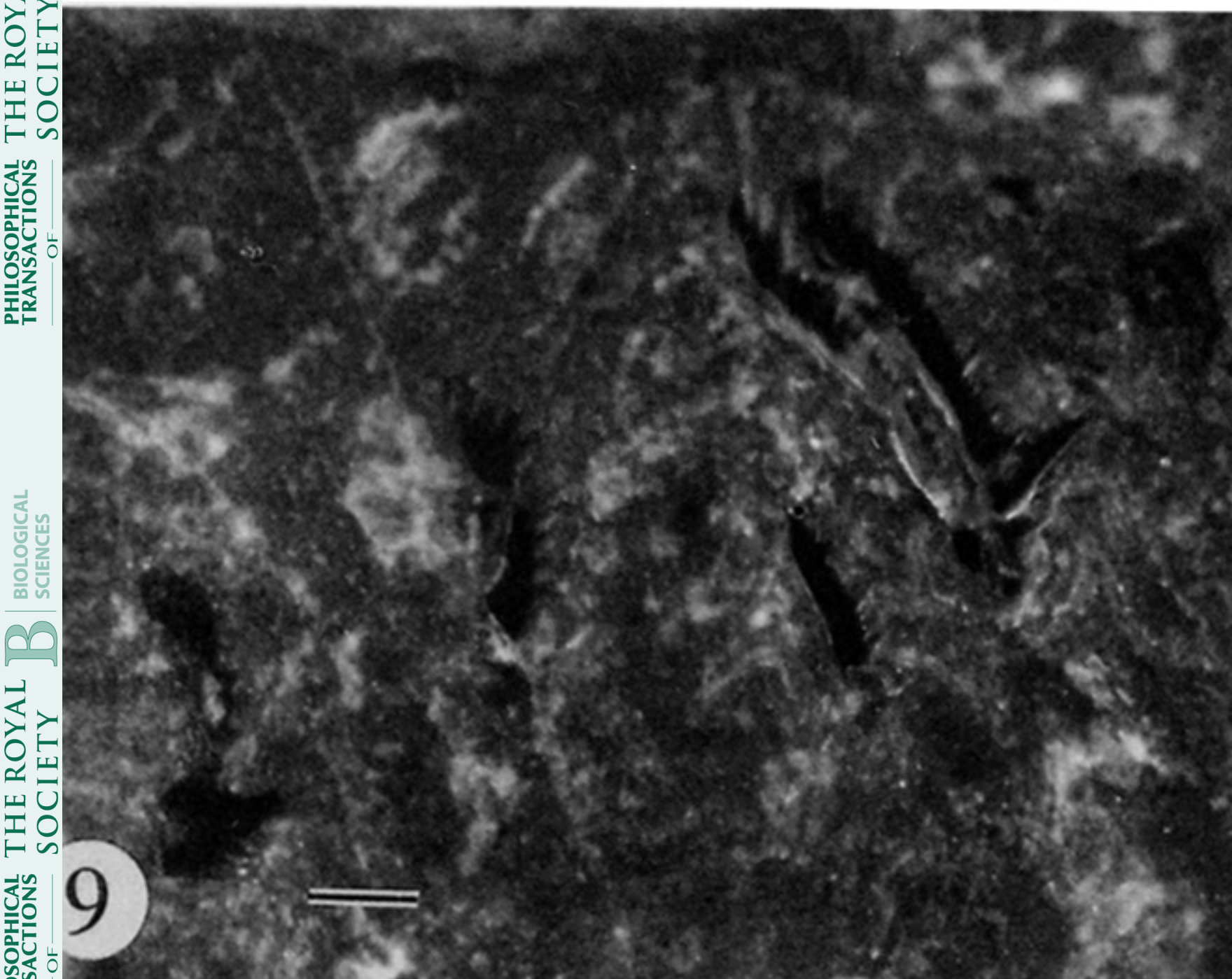
Downloaded from rslib.royalsocietypublishing.org



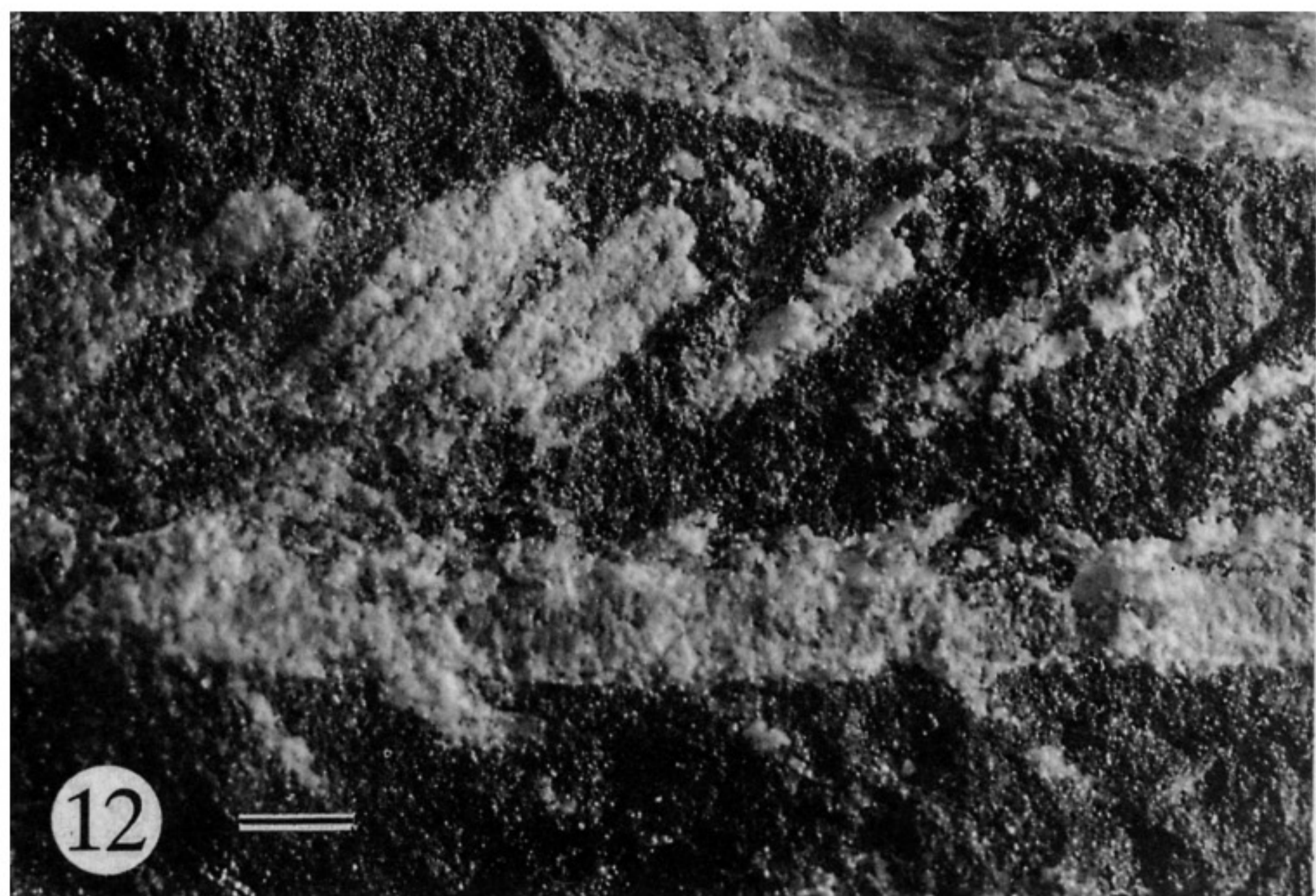
Figures 1 and 2. Specimen 1, counterpart (IGSE 13822). Figure 1. Complete specimen, scale bar 2 mm. Figure 2. Anterior portion, showing eye structures, feeding apparatus and possible axial trace of dorsal nerve cord (arrowed); scale bar 0.5 mm.



Figures 3–5. Specimen 5, part (RMS GY 1992.41.1). Figure 3. Complete specimen, anterior to left; scale bar 2 mm. Figure 4. Anterior portion, showing eye structures, feeding apparatus (partially concealed by rock matrix) and anterior part of trunk with notochord; scale bar 0.5 mm. Figure 5. Detail of trunk anterior of mid-length, scale bar 0.5 mm; small spots on ventral margin particularly apparent at anterior end of figure.



Figures 8–9. Specimen 6, part (RMS GY 1992.41.2). Figure 8. Complete specimen, anterior to right; scale bar 2 mm. Figure 9. The feeding apparatus, partially concealed by rock matrix; scale bar 0.25 mm.



Figures 10–12. Specimen 7, part (RMS GY 1992.41.3). Figure 10. Majority of preserved trunk, anterior to left; scale bar 2 mm. Figure 11. Detail of trunk posterior of mid-length, showing heavily phosphatized myomeres with oblique fibrous structure (arrowed); scale bar 0.5 mm. Figure 12. Detail of posterior portion of preserved trunk, showing heavily phosphatized notochord with transverse fibrous structure; scale bar 0.5 mm.