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A late-surviving Triassic protomonaxonid sponge from the Paris Biota, Idaho, USA

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Abstract. Protomonaxonid sponges are a major group of Cambrian and Ordovician fossils in exceptionally preserved (especially Burgess Shale-type) faunas, but are rare thereafter. Rare examples of apparent surviving lineages are known from the late Palaeozoic and Mesozoic, but by

this time more derived groups of sponges have generally displaced them in at least shallow-water (shelf depth) ecosystems. The early Spathian (Early Triassic) Paris Biota includes abundant material of a new leptomitid protomonaxonid, *Pseudoleptomitus advenus* nov. gen. et nov. sp., distinguished by having an unbundled longitudinal skeleton and very weak transverse component. This is the first post-Ordovician leptomitid known, and indicates long-term survival of the group in unknown environments. Its occurrence near storm wave base is similar to the preferred environment of earlier examples of the family, such either ecological rarity or taphonomic reasons for their absence from later Palaeozoic rocks.

Keywords: Porifera, Protomonaxonida, Lazarus taxa, Spathian, Paris Biota

1. Introduction

Protomonaxonid sponges are one of the dominant poriferan groups found in Cambrian Konservat-Lagerstätten, with numerous widespread genera being typical of the Burgess Shale-type faunas (Carrera and Rigby, 1999; Muir et al., 2015, 2017). Their affinities are debated, having traditionally been assigned to the demosponges (Finks and Rigby, 2004), but now reinterpreted as an early-branching group perhaps associated with the stem lineage of Porifera (Botting and Muir, 2018). The group as a whole may also be polyphyletic, even excluding the small-spiculed taxa that form the root of crown-group Demospongiae (Botting et al., 2013), in that the problematic *Heteractenigma* Botting and Zhang, 2012, suggests an independent origin of the Leptomitidae relative to other large-spiculed protomonaxonids.

The protomonaxonids survived in significant numbers in Ordovician offshore communities (Botting et al., 2015; Botting, 2016) and at least in some areas, were most prevalent in intermediate water depths around storm wave base (Muir and Botting, 2015). Later occurrences of protomonaxonids are scarce, although the Choiidae are also known from Silurian (Botting, 2007; Beresi et al., 2010), Devonian (Stürmer et al., 1980), and even Jurassic deposits (Keupp and

Schweigert, 2012). Most other families appear to have not survived past the Ordovician, and post-Ordovician protomonaxonids are limited to unique taxa that appear to be related to earlier forms (e.g., *Musaspongia* Jell and Cook, 2011). Surviving members of other Cambrian lineages of protomonaxonids are not known from after the Ordovician, although some undescribed Devonian sponges with some protomonaxonid features were illustrated by Kühl et al. (2012, figs. 11, 12).

The reason for the disappearance of protomonaxonids from the Palaeozoic fossil record may be genuine extinction (or population reduction), habitat shift towards less preservable environments, or closure of taphonomic windows in the environments that they occupied. The protomonaxonids are difficult to preserve articulated, and isolated spicules are effectively identical to hexactinellid root tufts spicules (except where original mineralogy can be determined for biomineralic taxa; see Botting and Muir, 2018). Their absence from the upper Palaeozoic fossil record may therefore be misleading. This paper illustrates the point by describing a leptomitid protomonaxonid from the early Spathian (Early Triassic) Paris Biota, deposited after the Permo-Triassic mass extinction.

2. Geological Background

The Paris Biota (Brayard et al., 2017) is a diverse assemblage of early Spathian (~250.6 Ma) fossils from shortly after the late Smithian extinction, during the Permo-Triassic transition. The assemblage has been recovered from the early Spathian Lower Shale Unit near Paris, Idaho, which is part of a sequence of alternating, thin-bedded shales and silty limestones (Brayard et al., 2017). The environmental interpretation is as an offshore, storm-influenced facies in a relatively shallow interior sea, indicated by sedimentary structures that include irregular lamination and hummocky cross-stratification, together with winnowed concentrations of sponge spicules (Brayard et al., 2017). The single species of articulated sponge is one of the most abundant taxa in the deposit, which also preserves a range of animal groups including cephalopods, echinoderms, crustaceans and fish remains (see other papers in this volume and Doguzhaeva et al., 2018).

3. Systematic Palaeontology

Order? “PROTOMONAXONIDA”

Originally applied to a heterogenous group of Cambrian sponges (Finks and Rigby, 2004), this is an informal, early-branching group of monaxon-bearing sponges that are not demosponges; for usage in this sense, see Group 1 protomonaxonids of Botting et al. (2013). Formal organisation of the taxonomy is awaiting a clearer understanding of the relationships of various problematic groups of early sponges.

Family Leptomitidae De Laubenfels, 1955

Included genera: *Leptomitus* Walcott, 1886; *Leptomitella* Rigby, 1986; *Paraleptomitella* Chen, Hou and Lu, 1989; probably also *Wareiella* Rigby and Harris, 1979.

Genus *Pseudoleptomitus* nov. gen.

Derivation of the name: After the close similarity to *Leptomitus* Walcott, 1920, despite some taxonomically significant differences. Gender *m*.

Type species: *Pseudoleptomitus advenus* nov. sp.

Occurrence: Paris Canyon, Lower Shale member, Thaynes Group, west of Paris, Bear Lake County, Idaho, USA.

Diagnosis: Tall, narrow leptomitids in which slightly inclined, sub-longitudinal spicules are not bundled, and form a near-homogeneous thatch with locally overlapping and slightly oblique

skeleton; transverse spicules sparse and weakly bundled or isolated.

Remarks: The genus is very similar to *Leptomitus* and *Leptomitella*, but differs from both in the absence of longitudinal spicule bundling. Of the two, it is closer to *Leptomitella*, as the bundles of *Leptomitus* are separated rather than set into a continuous thatched fabric. The lack of bundling in the new genus may have evolved in combination with strength advantaged conferred by a slightly thicker skeletal wall with locally overlapping sub-longitudinal domains. *Paraleptomitella* is a more complex sponge with arcuate longitudinal spicules and bundled transverse spicules, whereas *Wareiella* is too poorly known to discuss; even its familial affinity was left open by Rigby and Harris (1979), and it was placed into the Leptomitidae by Finks and Rigby (2004). Additional descriptive details were added by Finks and Rigby (2004), but no further illustrations were provided, and it is not possible to discern spicules in the published images. Based on that description, it appears to be differentiated from the other genera by the presences of long root tuft spicules and distinct marginalia (referred to as oscular prosthelia by Finks and Rigby, 2004). These are also sufficient to separate *Wareiella* from *Pseudoleptomitus* nov. gen., despite the uncertainty of its other characteristics.

Pseudoleptomitus advenus nov. sp.

Derivation of the name: Derived from the Latin *advena*, meaning a stranger or foreigner; an unexpected guest. Reflects the surprising occurrence of a member of the family in rocks of this age.

Diagnosis: As for genus.

Type material: Holotype UBGD 30504 (Fig. 1A–D); six paratypes. PC-15-062 (Fig. 2A), PC-15-65 (Fig. 2C–F), PC-15-223 (Fig. 2B); UBGD 30505, UBGD 30506, UBGD 30507?

Other material: Numerous additional specimens are also represented in the collections, but in most cases yield few fine details that are taxonomically informative.

Type locality and horizon: Paris Canyon, west of the city of Paris, Bear Lake County, Idaho, United States of America; Early Triassic, early Spathian (after Brayard et al., 2017).

Description: Preservation is complex, with spicules in many cases dissolved, and soft tissues replaced by thin film of calcium phosphate, which shows wrinkling resulting from compression. Iron oxides replace spicules in parts of a few specimens, and elsewhere they are sometimes preserved as impressions in the surface. Where visible, spicula broadly align some of the dominant wrinkle fabrics, showing that compressional deformation of the body wall was constrained by the skeleton before dissolution.

Tall, conical to subcylindrical sponges with near-constant gradual widening over entire length, and more than ten times as tall as wide. Outline often slightly undulating due to torsion of the skeleton, which appears too consistent to be taphonomic. Body wall very thin, effectively a single layer composed of sub-longitudinal monaxons and minor transverse elements. Longest specimens exceed 150 mm, with maximum width up to 10 mm.

Primary spicules are long, fine monaxons, probably oxeas, but limitations of preservation prevent clear indication of spicule terminations in most cases; no distinctive or rounded terminations observed. Maximum observed thickness of spicules around 0.1 mm. Spicules are inclined to the longitudinal axis, twisting helically at around 10–30° to vertical, but varying with local torsion of the body wall. Longitudinal spicules not bundled, with sub-parallel fabric composed of locally aligned monaxons; in some areas the orientation shifts through 5–10° and spicule domains conflict and slightly overlap each other (Fig. 1A, B, 2A). In a few specimens (Fig. 1F, 2B), fine transverse spicules are locally apparent, generally sparse and either isolated or in very small

bundles (one to three overlapping spicules), separated by 0.2–0.3 mm. Orientation of transverse spicules is variable, with some spicules apparently sinuous (Fig. 2B), but this may be partly taphonomic or exaggerated by preservation of wrinkles in the phosphatised soft tissue. In small specimens, transverse spicules are normally up to 2.5 mm long, and less than 0.05 mm wide.

Apical region (Fig. 1C) varies between slightly flared to slightly narrowed in compressed specimens. Longitudinal spicules in holotype are increasingly distinct in apical 2 mm, but this may be taphonomic as no consistent distinction is seen in other specimens. Where visible, longitudinal spicules with sharp terminations project from the apex by a short distance (up to 0.2 mm). The upper part of the sponge is helically twisted in several specimens (Fig. 1D, E), but as this is in opposing directions in different specimens, this twisted structure is likely to be variable, and may to some extent be ecophenotypic or taphonomic. The skeleton was therefore prone to such deformation, but not in a strictly constrained manner.

Lower region evenly tapered to a narrow base, the extreme end of which is not normally preserved. In rare cases this is associated with a brachiopod shell that may have formed the basis for a fixed (basiphytose) attachment (see Brayard et al. 2017, fig. S11).

4. Discussion

The preservation of the sponges in the Paris Biota is unusual, which makes recognition of their poriferan nature difficult in many specimens. It is only from the large amount of material that it was initially possible to determine the affinities of the fossil, with preservation of key characters occurring in different specimens. Due to the dissolution of spicules in most specimens, reconstruction of the skeleton is challenging and no specimen shows all the diagnostic features. If a single typical specimen were found in isolation, expecting to recognise it even as a sponge would be optimistic. The abundant material, however, has allowed the full reconstruction provided here (Fig. 4), including sufficient details to confirm an affinity with the

Leptomitidae. The discovery of a Triassic leptomitid is remarkable for the lack of records of the family after the Cambrian Burgess Shale-type faunas, where they are widespread (Rigby and Hou, 1995; Rigby and Collins, 2004). The group did not go extinct in the Cambrian, however, as unnamed leptomitids are known from the Early Ordovician Fezouata Biota of Morocco (Botting, 2016) and there is also undescribed material from the Middle Ordovician of the Llanfawr Mudstones Formation of Wales (mentioned by Muir and Botting, 2015). No later leptomitids have yet been described. The leptomitid skeleton is fragile, but composed of very long monaxial spicules that themselves have a high preservation potential. These spicules are not distinctive among protomonaxonids, however, and recognition of the family from disarticulated remains is not possible; isolated long monaxons can also be confused with hexactinellid root tuft spicules such as those of *Hyalostelia* (Young and Young, 1876), or body spicules of *Pyritonema* (Botting, 2005). Turbulent environments are therefore unlikely to have preserved recognisable fossils. Inhabitation of such environments is, however, equally unlikely; the delicate unfused skeleton and thin wall of protomonaxonids were adapted to relatively quiet-water conditions around storm wave base, as seen in the Cambrian and Ordovician facies distribution (Muir and Botting, 2015). The Paris Biota assemblage is from similar, relatively shallow water, with sedimentary indications that it was also near storm wave base (the absolute depth of storm waves in a shallow inland sea is, however, likely to have been much less than in the Welsh Basin). It is therefore not possible to explain the lack of later Palaeozoic fossils as being due to inhabiting turbulent environments, since there is no indication from known ecology or from functional morphology that they were able to inhabit such settings. Occurrence in sheltered inshore water is also problematic, as no leptomitids or similar sponges have yet been recorded from the numerous Late Ordovician and Silurian algal Lagerstätten (LoDuca and Brett, 1997; Tinn et al., 2009; Young et al., 2013); this suggests that if they did colonise lagoons or sheltered epeiric seas, it was not until at least the Devonian Period. In offshore shelf environments, spiculate sponges have much higher preservation potential so long as there is episodic rapid sedimentation (Botting and Muir,

2018), and a complete Palaeozoic history of protomonaxonids in their traditional environment cannot easily be reconciled with the lack of any fossil record. Deeper-water facies, however, on oceanic crust or on the continental slope, are rarely preserved due to tectonic subduction and recycling, and these regions are today home to diverse and abundant sponge faunas (e.g., Wolff, 1961; Foell and Pawson, 1986; Downey and Janussen, 2015). It is also now recognised that sponges were unusually successful after at least the end-Triassic (Ritterbush et al., 2015), Late Devonian (Vishnevskaya et al., 2002) and end-Ordovician (Botting et al., 2017) mass extinctions, and sponge-microbial buildups also proliferated after the Permo-Triassic crises (Brayard et al., 2011; Marengo et al., 2012; Vennin et al., 2015; Friesenbichler et al., 2018). The end-Ordovician extinction is of particular interest as the elevated abundance and diversity of sponges, including many lineages previously unknown from rocks this old, suggests colonisation of post-extinction shelf facies by deeper-water faunas (Li et al., 2015; Botting et al., 2017). Reduced competition, low oxygenation, and abundant suspended organic material appear to have produced ideal conditions during the latest Ordovician for sponges to have spread rapidly inshore, and take over the benthic ecology across very wide areas of at least South China (Botting et al., 2018), and some elements of these conditions appear to have been common during other ecological crisis intervals as well.

In the context of the Paris Biota leptomitids, there are two plausible interpretations for the unexpected reappearance of such a distinctive fossil group. One is that the lineage survived in nearshore but sheltered environments with low population sizes or restricted distributions, or that their preferred habitat in these areas led to near-complete destruction of their skeletons. The other is that the group recolonised shallower water from deep-water refugia during the ecological crisis interval, in the same manner seen following the end-Ordovician extinction. In the latter case, we should expect to see at least a brief interval during the crisis in which sponge remains (including large protomonaxonid spicules) are common in offshore shelf sediments. The general occurrence of leptomitids and other protomonaxonids in relatively highly oxygenated conditions with frequent water agitation (Muir and Botting, 2015) may also indicate that they were intolerant of low oxygen

conditions. In that case, survival in relatively turbulent environments of poor preservation potential, or as minor groups, may be a more likely hypothesis. The implications of the abundance of the new sponge for the ecology of the Paris Biota as a whole are not entirely clear. It does represent a major guild of erect suspension feeders that are otherwise rare or absent, in combination with predators, detritivores, and low-level suspension-feeders (Brayard et al., 2017; other papers in this volume), and this demonstrates a remarkably complex ecological structure. There is a striking comparison with the end-Ordovician Anji Biota, in which sponges entirely dominated the benthic fauna (Botting et al., 2017), but in that case the environment was much deeper-water and oxygenation much lower. Rare examples of other groups in Anji imply that a shallower-water community was still functioning with multiple trophic groups and complex interactions. The Paris Biota may represent the inshore, diverse communities that survived or reradiated in less severely affected environments. The low diversity of sponges in the Paris Biota is likely to indicate that only a few inshore sponges adapted to the crisis interval, but many more lineages may have survived in the more oxygen-stressed offshore environments where other animal groups with greater metabolic demands were unable to proliferate.

5. Conclusions

The abundant leptomitid sponges are one of the strangest aspects of the Paris Biota assemblage. Although clearly separated from previously described members of the family, the differences are relatively subtle and there is clear continuity with the Cambrian taxa. Without further information on mid and late Palaeozoic members of the group, it is difficult to assess the likely habitats in which the family survived undetected for over 200 million years.

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Figures

Fig. 1. Simplified stratigraphic log showing main Early Triassic units in the Paris Canyon area (modified after Brayard et al., 2017; Brayard et al., 2017, 2019).

Abbreviations: LL: Lower Limestone; LS: Lower Shale; ML: Middle Limestone; MS: Middle Shale; UCS: Upper Calcareous Siltstone; Meek: Meekoceras beds; Anasib: Anasibirites beds; Tirol: Tirolites beds; Colum: Columbites beds.

PARIS CANYON AREA

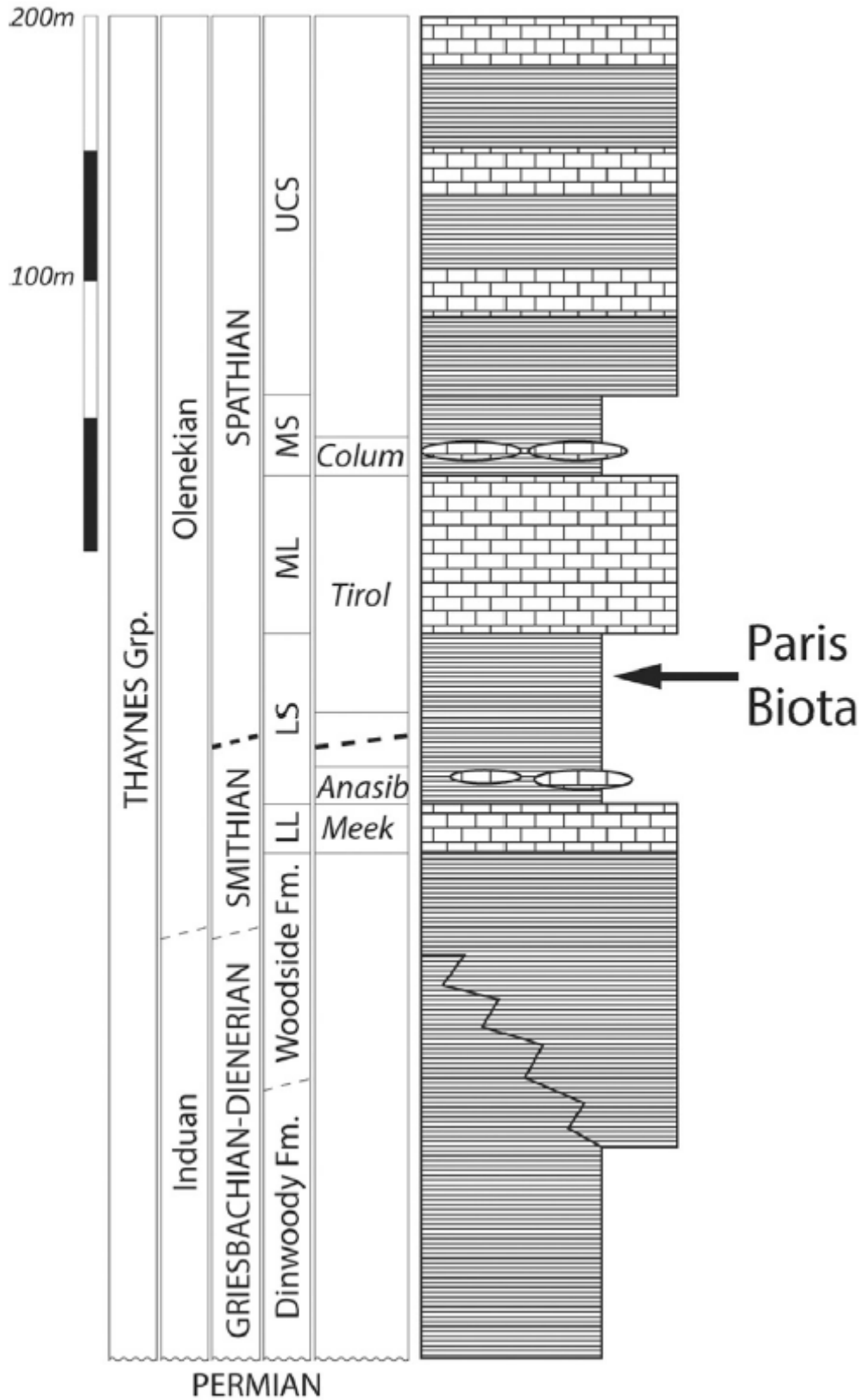


Fig. 2. *Pseudoleptomitius advenus* Botting nov. gen., nov. sp. A–D. Holotype UBGB 30504. A: apical region under low-angle light; B: the same with high-angle light and wetted; C: extreme apex under low-angle light, showing marginal projecting spicules; D: overall view of holotype. E–G. Paratype UBGB 30505. E: overall view of apical part of specimen; F: detail of twisted skeleton near apex; G: magnification of boxed region in F, showing interwoven longitudinal and irregularly transverse spicules. Scale bars: 2 mm (A, B, F), 1 mm (C, E), 5 mm (D).



Fig. 3. Skeletal details of *Pseudoleptomitus advenus* Botting nov. gen., nov. sp. A. Paratype PC-15-062, with wrinkled preservation showing moderately well-preserved, coarse longitudinal spicules. B. Paratype PC-15-223, with short, curved transverse spicules (examples arrowed). C–E. Paratype PC-15-065, with locally well-preserved spicules. C: overall view; D: magnification of area with clear longitudinal spicules; E: magnification of boxed area in D, with fine longitudinal monaxons preserved partly as iron oxides. Scale bars: 2 mm (A, D); 5 mm (B, C).

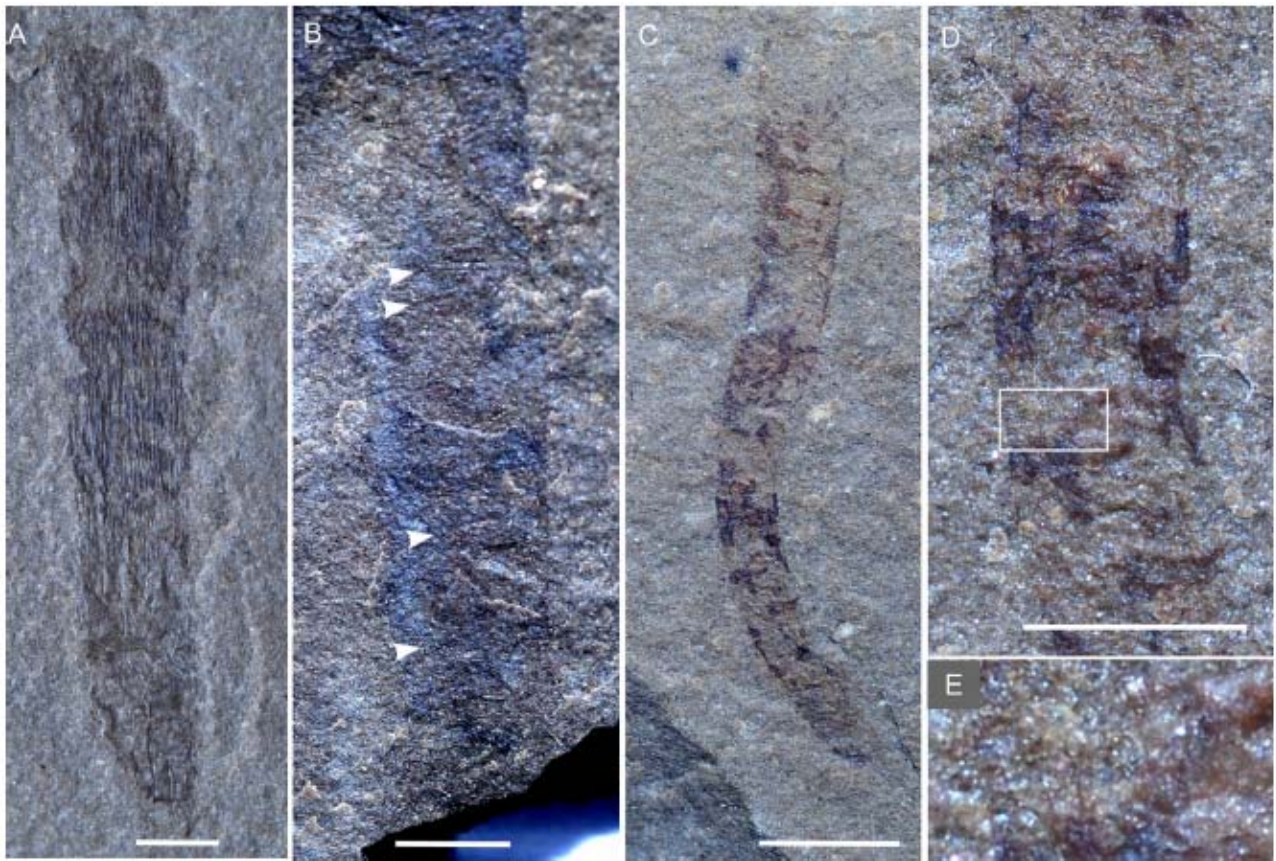


Fig. 4. Reconstruction of *Pseudoleptomitus advenus* Botting nov. gen., nov. sp., including details of outer longitudinal skeleton and irregularly transverse inner wall.

