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New palaeoscolecoidan worms from the Lower Cambrian: Sirius Passet, Latham Shale and Kinzers Shale

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Palaeoscolecoidan worms are an important component of many Lower Palaeozoic marine assemblages, with notable occurrences in a number of Burgess Shale-type Fossil-Lagerstätten. In addition to material from the lower Cambrian Kinzers Formation and Latham Shale, we also describe two new palaeoscolecoidan taxa from the lower Cambrian Sirius Passet Fossil-Lagerstätte of North Greenland: *Chalazoscolex pharkus* gen. et sp. nov. and *Xystoscolex boreogyrus* gen. et sp. nov. These palaeoscolecoidans appear to be the oldest known (Cambrian Series 2, Stage 3) soft-bodied examples, being somewhat older than the diverse assemblages from the Chengjiang Fossil-Lagerstätte of China. In the Sirius Passet taxa the body is composed of a spinose introvert (or proboscis), trunk with ornamentation that includes regions bearing cuticular ridges and sclerites, and a caudal zone with prominent circles of sclerites. The taxa are evidently quite closely related; generic differentiation is based on degree of trunk ornamentation, details of introvert structure and nature of the caudal region. The worms were probably infaunal or semi-epifaunal; gut contents suggest that at least *X. boreogyrus* may have preyed on the arthropod *Isoxys*. Comparison with other palaeoscolecoidans is relatively straightforward in terms of comparable examples in other Burgess Shale-type occurrences, but is much more tenuous with respect to the important record of isolated sclerites. These finds from Greenland provide further evidence that palaeoscolecoidans possessed a complex anterior introvert directly comparable to a number of priapulid-like taxa from other Burgess Shale-type assemblages. Although these palaeoscolecoidans have been allied with the nematomorphs, molecular data in conjunction with our observations suggest that this hypothesis is untenable. Palaeoscolecoidans and similar priapulid-like taxa are probably primitive cycloneuralians and as such may indicate the original bodyplan of this important group of ecdysozoans. In addition, we describe another sclerite-bearing fossil from the Sirius Passet Fossil-Lagerstätte that may be related to the cambroclaves.

Key words: Palaeoscolecida, *Chalazoscolex*, *Xystoscolex*, Cycloneuralia, Cambrian, Kinzers Formation, Latham Shale, Sirius Passet, Greenland, California, Pennsylvania.

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Introduction

Amongst the most characteristic component of Burgess Shale-type faunas are worms with a spiny introvert and a striking ornamentation of small sclerites. These typify an assemblage referred to as the palaeoscolecoidans. Whilst a spiny introvert is also typical of a variety of priapulid-like taxa, and to which the palaeoscolecoidans are evidently related, the diagnostic feature of the latter group is a segmental array of sclerites. Because in at least some palaeoscolecoidan taxa the sclerites had a primary phosphatic composition so the fossil record of this group is augmented by recovery of sclerites (solitary or semi-articulated) by acid-processing of calcareous sediments. Whilst this latter material significantly extends the known diversity of palaeoscolecoidans it renders phylogenetic analysis problematic for two reasons. First, whilst some material occurs in articulated series (e.g., Müller and Hinz-Schallreuter 1993), more often the sclerites are isolated and as form-taxa conceivably de-

rive in some instances from the one worm. In articulated material, however, with few exceptions (e.g., Conway Morris 1997; Ivantsov and Wrona 2004) microstructure of the sclerites is usually poorly preserved (e.g., Conway Morris and Robison 1986). A further difficulty is that this articulated material evidently mostly occurs as “bags of cuticle” and the extremities are not always preserved. In the palaeoscolecoidan-like *Louissella pedunculata* from the Burgess Shale (Conway Morris 1977) and an array of taxa from the Chengjiang Lagerstätte (e.g., Hou and Bergström 1994; Chen 2004; Hou et al. 2004; Hu 2005; Hu et al. 2008), the introvert is, however, seen to be directly comparable to those of the other priapulid-like taxa that typify Cambrian soft-bodied assemblages. Such is also the case for the two new taxa described here from the Sirius Passet fauna. As with many Burgess Shale-type taxa these fossils are potentially central to the documentation of various aspects of early metazoan evolution. In the case of the palaeoscolecoidans it is evident that they are both related to a diverse assemblage of

worms with spiny or armoured introverts, some of which (e.g., *Ottoia*) are evidently stem-group priapulids (see Wills 1998) as well as more generally the cycloneuralians that encompass not only the priapulids but other groups such as the loriciferans and nematomorphs. Whilst the detailed phylogeny of this group is yet to be elucidated it is likely that some palaeoscolecidan taxa are amongst the most primitive known ecdysozoans.

Institutional abbreviations.—MGUH, The Geological Museum of the University of Copenhagen (Museum Geologicum Universitatis Hauniensis), now incorporated into the Natural History Museum of Denmark; NMNH&S, North Museum of Natural History and Science, Franklin and Marshall College, Lancaster, Pennsylvania; UCR, University of California, Riverside.

The Sirius Passet Fossil-Lagerstätte

The Sirius Passet biota from the Buen Formation of Peary Land, North Greenland (geographical co-ordinates latitude 82°47.6'N, longitude 42°13.3'W, obtained from National Survey and Cadastre 1989 1: 100,000 orthophoto map 82 Ø3 NV; Conway Morris 1998; Conway Morris et al. 1987; Babcock and Peel 2007), is the oldest major Fossil-Lagerstätte known from the Cambrian of the Laurentian palaeocontinent. The occurrence of the trilobite *Buenellus higginsii* Blaker, 1988 indicates an age equivalent to the *Nevadella* Zone of North American usage (Palmer and Repina 1993) and Series 2, Stage 3 of the provisional stratigraphic scheme for the Cambrian (Zhu et al. 2006). Whilst this zone seemingly extends into the early Botomian (Hollingsworth 2005), the occurrence of the nevadid *Limniphacos perspicillum* Blaker and Peel, 1997 at much higher levels in the Buen Formation indicates that the Sirius Passet biota is of older, Atdabanian, age in terms of the Siberian Standard (Zhuravlev and Riding 2001). The Botomian age of the Chengjiang Fossil-Lagerstätte noted by Zhuravlev and Riding (2001) is re-stated following recent comparison of trilobite faunas between Australia and South China (Paterson and Brock 2007).

Whilst unable to rival the diversity and quality of preservation available from the enormous collections made during almost a century from the 10 Ma younger Burgess Shale Fossil-Lagerstätte (middle Cambrian; Cambrian Series 3, Stage 5), the inaccessible Sirius Passet locality has yielded about 40 taxa dominated by arthropods (e.g., Budd 1995, 1997, 1999; Budd and Peel 1998; Williams et al. 1996; Taylor 2002; Lagerbro et al. 2009; Peel and Stein 2009; Stein in press; Stein et al. in press). Other highlights include articulated halkieriids (Conway Morris and Peel 1995) and the oldest annelids (Conway Morris and Peel 2008). In terms of sedimentary environment the Sirius Passet locality is reminiscent of the Burgess Shale, that is with the fossiliferous mudstones accumulating immediately basinwards of the prominent outer scarp of a carbonate platform. In both cases

the mudstones were thus deposited in considerably deeper water than the shallow marine siliciclastic sediments which preserve the Chengjiang Fossil-Lagerstätte (Babcock and Zhang 2001), although this important assemblage is slightly younger than the Sirius Passet biota.

Material and methods

Two new taxa of palaeoscolecidan worms, *Chalazoscolex pharkus* gen. et sp. nov. and *Xystoscolex boreogyrus* gen. et sp. nov., are described here on the basis of compressions on bedding surfaces of thinly bedded dark shale (Figs. 1–5) and SEM illustrations of latex impressions (Fig. 6). Their formal nomenclature is provided at the end of the paper. Both show the style of preservation that characterizes this exceptional fossil deposit (e.g., Conway Morris et al. 1987; Conway Morris and Peel 1995), with the fossils preserved in shale that has been metamorphosed to the chloritoid grade. It is thus equivalent in terms of diagenetic and metamorphic history to the Burgess Shale (e.g., Conway Morris 1990: fig. 2B, C), but as with the latter deposit there is no penetrative cleavage (perhaps owing to the tectonic shielding by the adjacent dolomites of the Portfjeld Formation). Whilst this history has clearly influenced the preservation of the biota, there is no reason to think that any of the features we interpret as original anatomy are artefacts of post-depositional processes. Apart from the minor relief of cuticular structures and some gut infillings, the fossils occur as thin films. When this film extends beneath layers of sediment its subsequent removal may only partially reveal the remaining parts of the specimen. All fossils are effectively bedding-plane parallel and as with other elements of this fauna there is little evidence as to whether they are effectively in situ or are allochthonous. Nevertheless, the entombing deposits lack evidence of grading or other features suggestive of sediment transport. The characteristically coiled disposition of *Xystoscolex*, however, might indicate a mortal response to oxygen depletion.

Specimens were photographed in white light, with the surface coated with sublimate to enhance the generally low relief of the fossil surfaces. In addition, a selection of material had latex impressions taken, which after coating with a conducting gold film were examined in an SEM (Zeiss).

The palaeoscolecidan *Chalazoscolex* gen. nov.

Specimens are generally incomplete, but this is a result of rock breakage rather than decay. The longest known specimens are each about 90 mm in length (Fig. 1A₁, B₁). The smallest specimens are incomplete, but on the assumption that the body had a similar width to length ratio to the adults they would have been approximately 50 mm long. Specimens are usually more or less straight with at most a gentle curvature (Figs. 1B₁, 2A₁, B₁, D₁, F₁, 4B₂), but on occasion they are either strongly re-

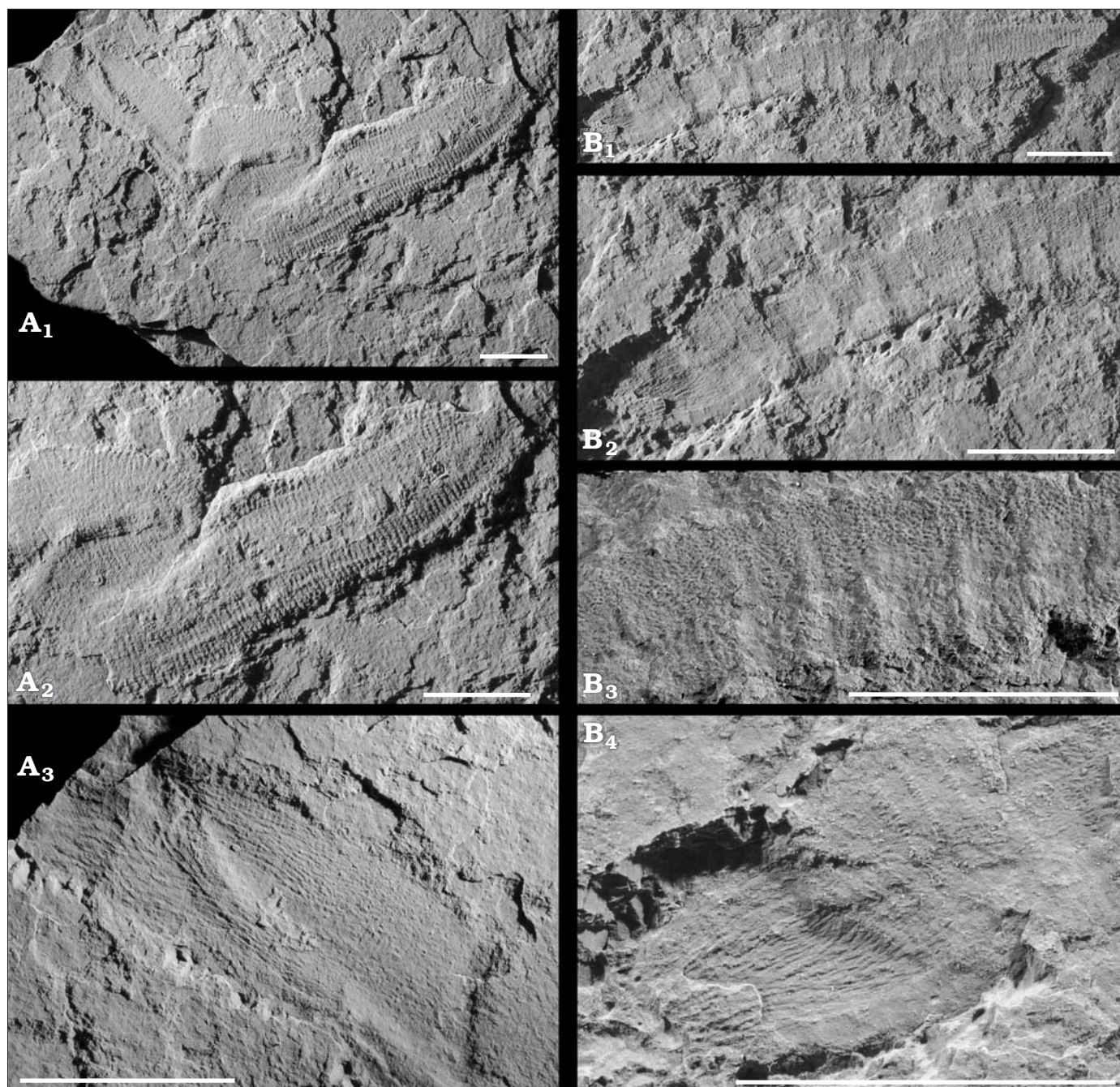
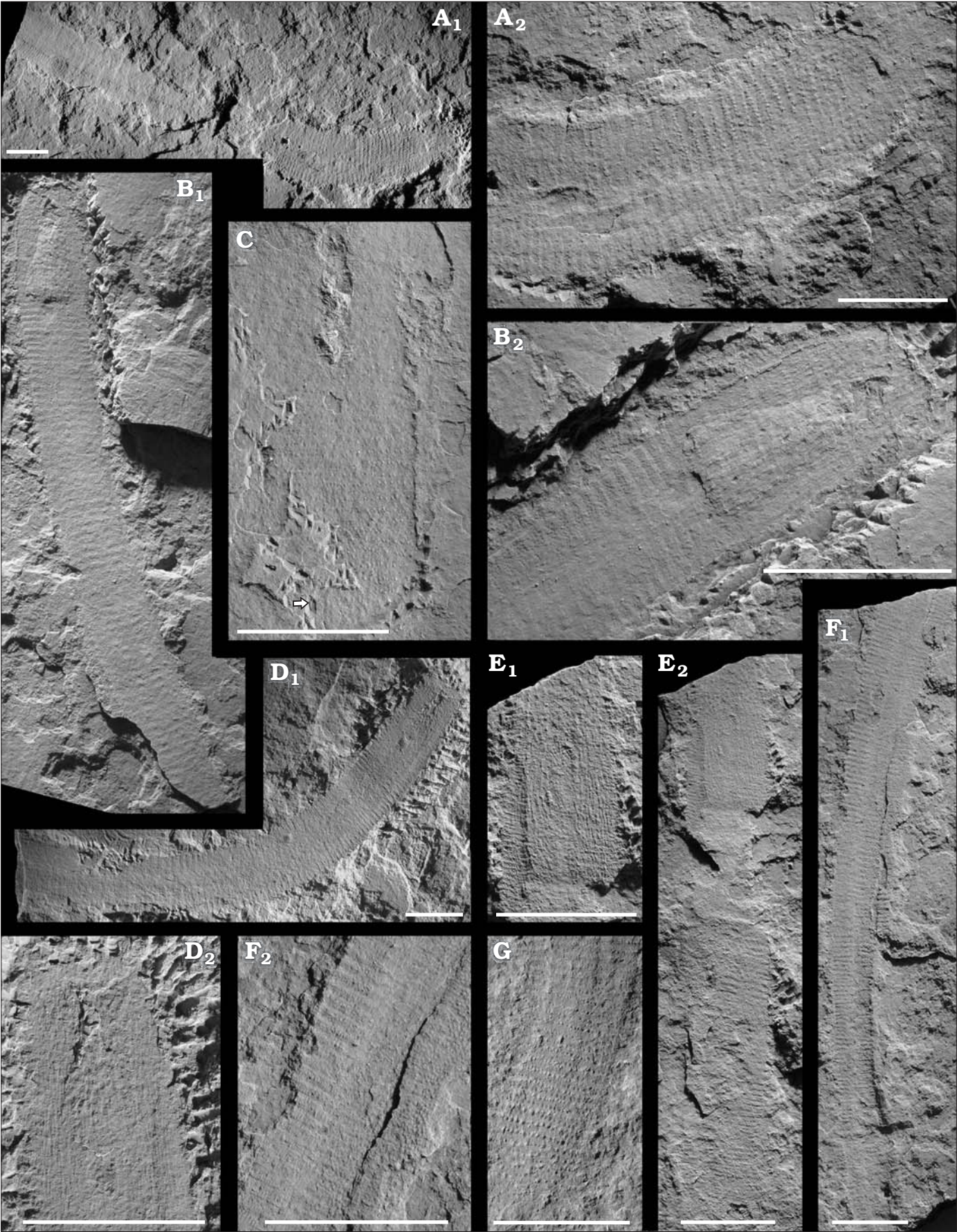


Fig. 1. Palaeoscolecidan *Chalazoscolex pharkus* gen. et sp. nov., lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. **A.** MGUH 29133, entire specimen (A_1) and enlargements of trunk (A_2) and introvert (A_3); see also Fig. 6B. **B.** MGUH 29134, entire specimen (B_1) and enlargements of anterior (B_2), trunk (B_3), and introvert (B_4). Scale bars 10 mm. All specimens coated with sublimate.

curved or sharply folded (Fig. 1A₂). This style of preservation suggests that the cuticle was relatively robust, and that the degree of contractibility was relatively restricted.

The body can be divided into three sections, of which the mid-portion of the trunk occupies the greatest proportion and separates an anterior introvert (Figs. 1A₃, B₄, 2B₂, D₂, E₁, 4B₁) (alternatively named the proboscis) from a distinct caudal region (Fig. 2A₂, C, G). The most obvious feature of the introvert is a dense array of scalids which on the exterior are posteriorly directed (Fig. 2B₂, E₁). In the majority of cases their ar-

rangement is not very regular, but on occasion a transverse pattern is evident (Fig. 2B₂). The scalids are simple, tapering to a fine point from an expanded base (Figs. 4B₁, 6G), and are about 500 μ m in length. Although sometimes appearing asymmetrical this is most likely preservational. In some specimens the posterior part of the introvert bears a series of narrow, anastomosing grooves and ridges (Figs. 1A₃, B₄, 2D₂, 2E₁), each with an approximate width of 100 μ m (Fig. 6B). The fact they tend to be most prominent where the introvert narrows anteriorly (Fig. 1B₄) suggests that these ridges could have



served to accommodate constriction. The ability of the introvert to engage in retraction is uncertain. However, a configuration where the scalids appear to be restricted to the anterior-most region (e.g., Fig. 2D₂) suggests that some degree of withdrawal was possible. In some specimens the introvert contains a massive structure with positive relief (Fig. 2B₂, D₂). This presumably represents the pharyngeal area, but in only one or two specimens is there a faint quincunxial pattern (Fig. 2E₁) that presumably reflects the teeth that lined the pharynx.

The main trunk region occupies much of the remainder of the body (Figs. 1A₂, B₂, 2B₁, D₁, F₁). It shows an obvious segmentation that can overlap with the longitudinal ridges extending from the proboscis (Figs. 1A₃, 2D₂, E₁). The segments have a width of 0.5 mm, so a typical specimen would have possessed approximately 140 segments. The ornamentation of the trunk was subdivided into at least two longitudinal zones (Figs. 1A₂, B₃, 2B₂, F₂, 4B₁). In one of the zones the segments bear individual sclerites, with two to three occupying the width of each segment. Although poorly preserved (Fig. 6F₁) their individual diameter ranges between ca. 100–200 µm. Apart from having a circular shape, no details of any microstructure are preserved. These sclerite-bearing segments evidently formed a single zone, and in some material (e.g., Fig. 2F₂) the orientation of the trunk with respect to the bedding plane means that the upper series of sclerites appear in positive relief while the lower are seen in negative relief. The other main zone on the trunk bears characteristic short longitudinal ridges (ca. 80 µm wide). These are somewhat irregular (Fig. 6C) and overall impart a wrinkled appearance to the segments (Fig. 2F₂). It appears also that the region that connects the sclerite- and ridge-bearing parts of each segment was more or less smooth and at most displayed only a subdued ornamentation (Fig. 2B₂).

The caudal region bears obvious transverse rows of sclerites (Fig. 2A₂, C, G), but these appear to have encircled the entire body. This region of the body is distinctive both on account of the regular arrangement of the sclerite rows, which total about 15, and the relatively large size of the individual sclerites (diameter ca. 200–300 µm). As with the more anterior sclerites, no microstructural details are evident (Fig. 6D). In one specimen (Fig. 2C) the trunk appears to extend beyond the segmented region as a short, smooth extension (ca. 6 mm long), possibly equivalent to the bursa seen in other Burgess Shale-type stem-group priapulids, notably *Ottoia prolifica* (Conway Morris 1977: pl. 8: 5–7, pl. 9: 1, pl. 13: 6).

Apart from the pharynx located at the anterior end, the only other evidence for internal anatomy is parts of the intestine. These are usually delimited by unidentifiable infill (Figs. 2A₂, C, 4B₂, G). The intestine can be fairly broad (ca. 2 mm, Fig. 4B₂, G), and the anus is assumed to have been terminal.

The palaeoscolecidan *Xystoscolex* gen. nov.

This palaeoscolecidan is less common than *Chalazoscolex*, with relatively few well-preserved specimens. They are often in a coiled configuration (Fig. 3A, B₁, D₂, E), although in some specimens (Fig. 3C₂) the anterior section is more or less straight. Other configurations are more unusual. They include an example of a sinuous disposition (Fig. 4C₂), whilst another specimen is strongly recurved (Fig. 5A). As noted below the coiled disposition may reflect a response to anoxia, but the other arrangements could reflect the results of transport (although in general there is little such evidence) or more advanced decay. In any event these various orientations make precise estimates of length somewhat difficult, but a typical length for this taxon is in the order of 120 mm (with a width of 10 mm).

The body is divided into three regions: anterior introvert (or proboscis), trunk and caudal region, of which the trunk accounts for most of the length. The proboscis bears two types of structure. Most obvious is a dense array of scalids. They do not have a regular arrangement (Figs. 3C₁, 4A, D, E₂, 5A, 6E) and can extend for up to ca. 12 mm along the body. The individual scalids are effectively spinose, with a wide base that tapers to a fine point (Figs. 3C₁, 5B, 6E). In addition, there are hints of a faint longitudinal texture on the cuticle between the scalids (Fig. 6A). Located to the anterior of the scalids is a series of relatively stout spines, the orientation of which is quite variable (Figs. 3C₁, 4A, 5). In some specimens the proboscis has a smooth oral cone that projects forward, and in one specimen (Fig. 4E) the entire pharyngeal region is everted in the same manner as a number of Burgess Shale-type priapulids (e.g., Conway Morris 1977: pl. 1: 4, pl. 2: 3, pl. 5: 5, pl. 6: 3, pl. 10: 5, pl. 11: 2; Huang 2005: fig. 33). Across much of its surface there is a rather faint quincunxial pattern, whilst at the anterior there are irregular striations (Fig. 4E₂). The quincunxial pattern most likely reflects the pharyngeal teeth, whilst the striations are perhaps equivalent to structures interpreted as anterior retractor muscles in *Ottoia prolifica* (Conway Morris 1977: pl. 6: 3, text-fig. 50).

The trunk is more or less smooth in the anterior region, but more posteriorly shows a subdued segmentation (Figs. 3B₂, D₂, 4C₂). The segments are narrow (ca. 400 µm) and bear a faint ornamentation that includes zones with circular sclerites and short ridges (Fig. 3B₂, D₁). It is likely, but cannot be proved with the material to hand, that the zones had a similar disposition to those of *Chalazoscolex*. The caudal region (Figs. 3D₁, 4C₁, 5A) forms a distinct region on account

← Fig. 2. Palaeoscolecidan *Chalazoscolex pharkus* gen. et sp. nov., lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. A. MGUH 29135, entire specimen (A₁), and enlargement of posterior trunk (A₂). B. MGUH 29136, entire specimen (B₁) and enlargement of introvert with presumed pharyngeal region in positive relief (B₂); see also Fig. 6C. C. MGUH 29137, detail of posterior trunk and gut (upper) with possible bursa arrowed; see also Fig. 4G. D. MGUH 29138, entire specimen (D₁), and detail of introvert (D₂). E. MGUH 29139, detail of anterior (E₁), and entire specimen (E₂). F. MGUH 29140, entire specimen (F₁) and detail of trunk (F₂). G. MGUH 29141, detail of posterior trunk; see also Fig. 6D. Scale bars 10 mm. All specimens coated with sublimate.

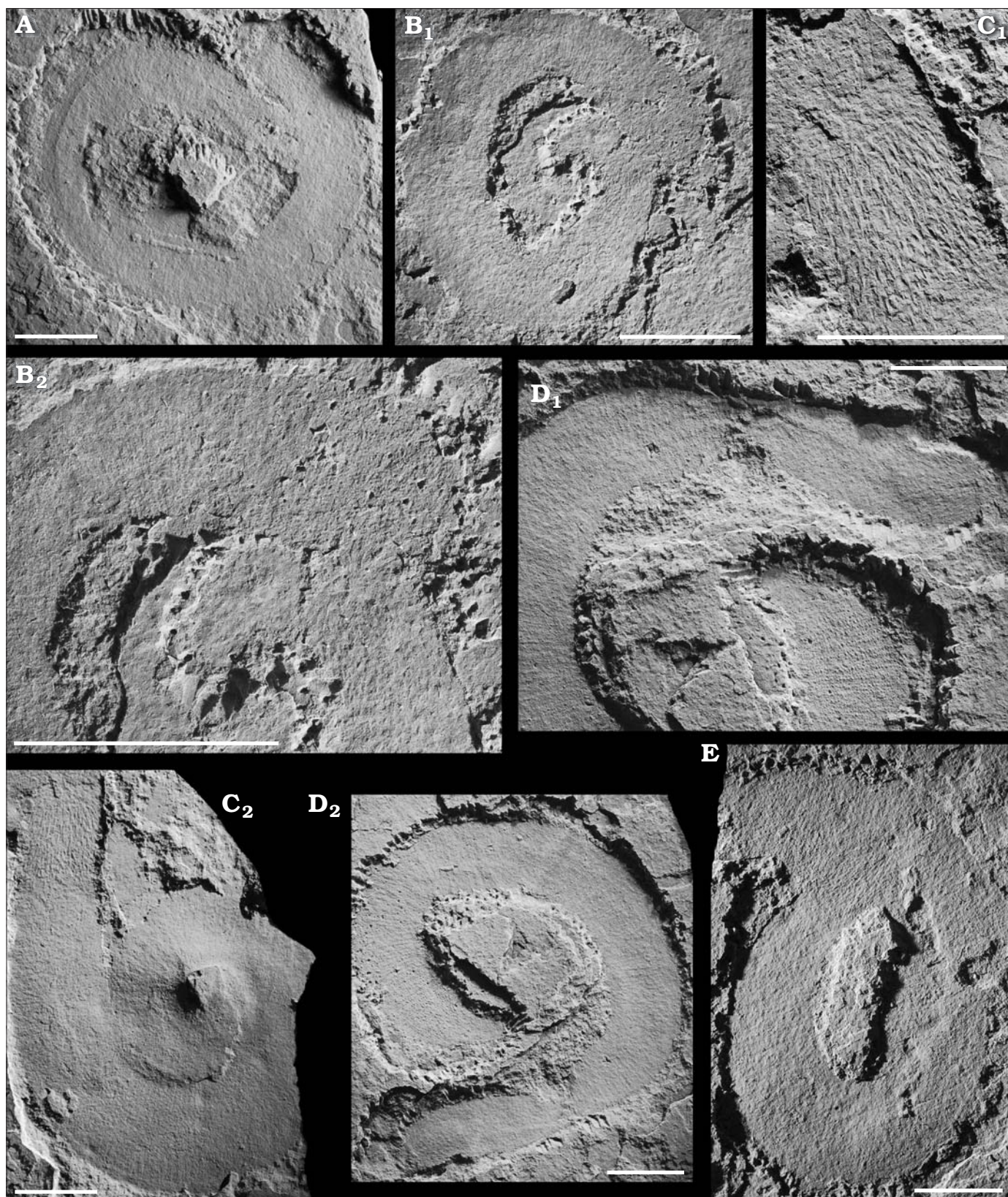


Fig. 3. Palaeoscolecid *Xystoscolex boreogyrus* gen. et sp. nov., lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. **A.** MGUH 29142, entire specimen with introvert at top right; note also gut trace. **B.** MGUH 29143, entire specimen (B₁) and enlargement of posterior (upper) and introvert with anterior spines (B₂). **C.** MGUH 29144, detail of introvert (C₁) and entire specimen (C₂); see also Fig. 6E. **D.** MGUH 29145, detail of introvert (upper) and posterior termination (lower right) (D₁) and entire specimen (D₂). **E.** MGUH 29146, entire specimen. Scale bars 10 mm. All specimens coated with sublimite.

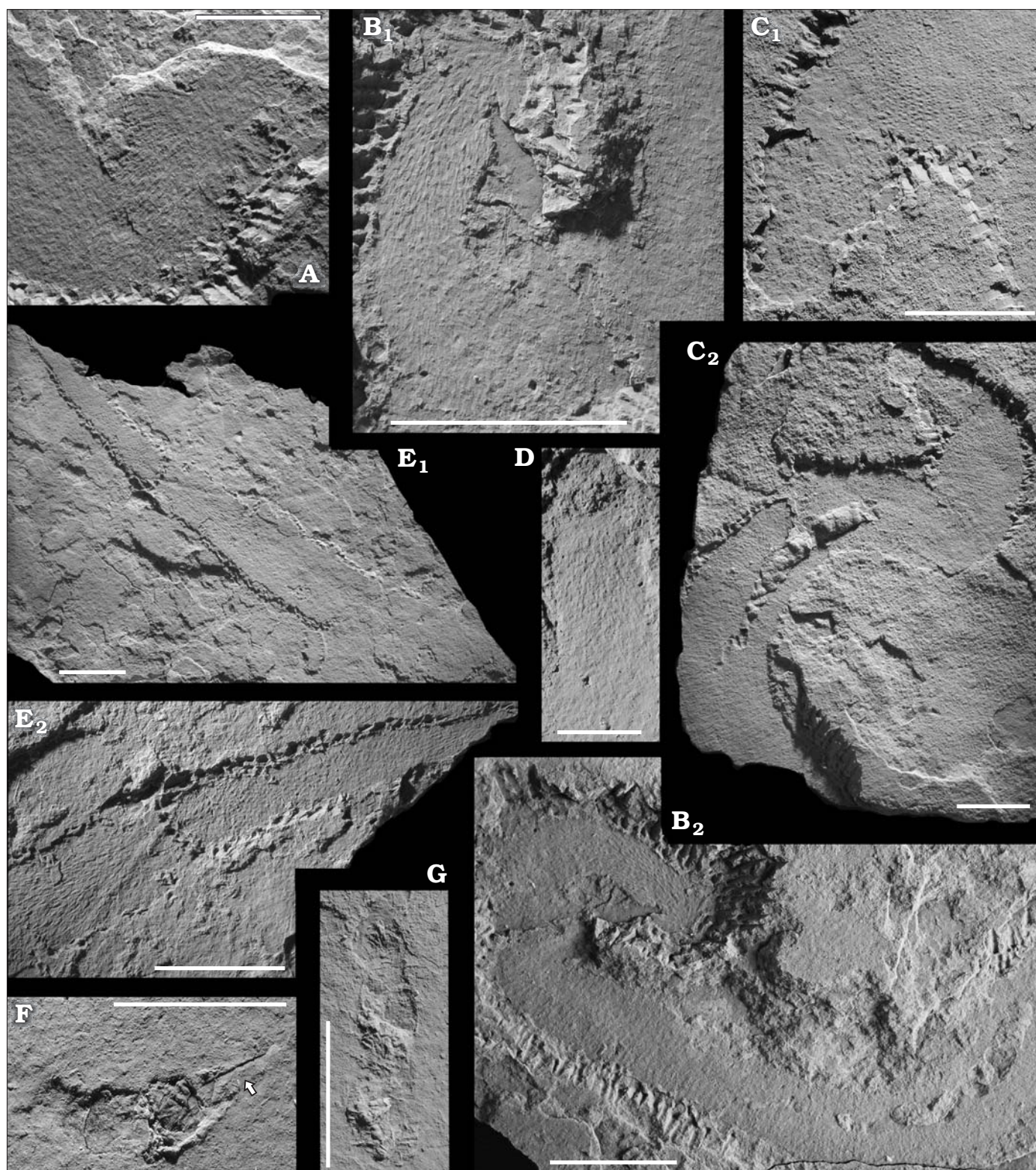


Fig. 4. Palaeoscolecidans *Xystoscolex boreogyrus* gen. et sp. nov. (A, C–F) and *Chalazoscolex pharkus* gen. et sp. nov. (B, G), lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Fossil-Passet Lagerstätte, Peary Land, North Greenland. A. MGUH 29147, anterior with introvert. B. MGUH 29148, enlargement of introvert and anterior trunk (B₁) and entire specimen with gut trace (B₂); see also Fig. 6F. C. MGUH 29149, enlargement of posterior end (C₁) and entire specimen with gut trace (C₂). D. MGUH 29142, enlargement of introvert, see also Fig. 3A. E. MGUH 29150, entire specimen (E₁) and enlargement of introvert with everted pharyngeal region (E₂); see also Fig. 6A. F. MGUH 29151, gut trace containing arthropod *Isoxys volucris* Williams, Siveter, and Peel, 1996 with characteristic spinose extension arrowed. G. MGUH 29137, gut trace; see also Fig. 2C. Scale bars 5 mm in D, G; otherwise 10 mm. All specimens coated with sublimate.

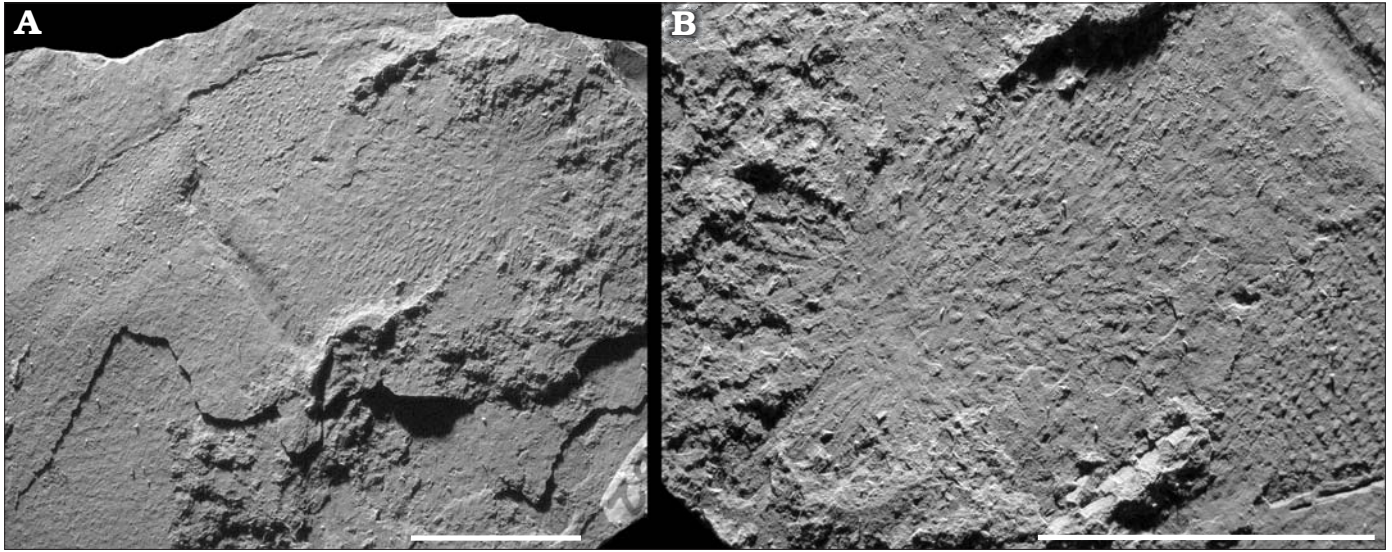


Fig. 5. Palaeoscolecid *Xystoscolex boreogyrus* gen. et sp. nov., lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. MGUH 29152. **A.** Anterior and posterior (upper left) ends of folded specimen. **B.** Detail of introvert with anterior scalids and in lower right sclerites of posterior (lower left). Scale bars 10 mm. Specimen coated with sublimate.

of a prominent series of closely spaced segments (ca. 45), each of which carries relatively large sclerites (ca. 100–200 μm diameter). They evidently have a more or less circular shape, but no microstructure is visible (Fig. 5B).

In terms of internal anatomy apart from the specimen with an everted pharyngeal region (Fig. 4E₂), the only feature is part of the intestinal tract, which varies in width. For the most part the infill is non-descript (Figs. 3A, 4C₂, F), but in one specimen there are the remains of the arthropod *Isoxys volucris*, identifiable on the basis of its characteristic spines (Fig. 4F; see Williams et al. 1996: fig. 6).

Modes of life

Palaeoscolecidans are usually reconstructed as infaunal, although at least some taxa may have engaged in epifaunal excursions (e.g., Huang 2005; Han et al. 2007a–c; Maas et al. 2007). Note that the claim by the latter authors (Maas et al. 2007: 301) that one of us (SCM) reconstructed *Selkirkia* as embedded posterior-end in the sediment is the exact reverse of what was stated: see Conway Morris 1977: 44; also Conway Morris and Whittington 1979: 127, and Conway Morris 1998: 74, colour plate 1). So far as *Chalazoscolex* and *Xystoscolex* are concerned an entirely infaunal or semi-epifaunal mode of life is conceivable, but their invariable bedding parallel orientation gives no clue as to the original modes of life. The characteristic coiling of *Xystoscolex* (Fig. 3A, B₁, D₂) is conceivably a response to environmental stress, possibly oxygen shortage, whilst the occasionally folding seen in *Chalazoscolex* (Fig. 1A₁) may be the result of transport.

One potential clue in support of a semi-epifaunal habit, however, might come from the trunk ornamentation, both in terms of the obvious circumferential distinction between regions of cuticle bearing sclerites as against being occupied

by ridges. One could, therefore, speculate that the sclerite-bearing areas would provide more effective traction against the substrate. On the other hand the striking caudal section, with its prominent rings of sclerite-bearing segments, points to an entirely infaunal habitat. In this scenario the worm would engage in the classic burrowing cycle with the proboscis achieving forward movement whilst the caudal region served as the penetration anchor. Finally, when considering the more subdued ornamentation seen in *Xystoscolex* (relative to *Chalazoscolex*) one might argue that this reflects habitation in a different type of substrate, possibly one that was fine-grained and/or more fluid. Finding *Isoxys* as a gut content (Fig. 4F) may reflect a benthic habit for these arthropods (see also Siveter et al. 1996: 115). Whilst the occurrence of hyoliths in the intestine of the Burgess Shale taxon *Ottoia* is well-known (Conway Morris 1977; see also Han et al. 2007b for a similar example from the Chengjiang Fossil-Lagerstätte) this appears to be the first evidence that arthropods may have formed part of the diet of some Cambrian priapulid-like forms, although Huang et al. (2004a: fig. 6) hypothesised such feeding in the Chengjiang *Corynetis*. Intriguingly, although *Corynetis* is not otherwise very similar to *Xystoscolex*, both taxa possess a prominent circlet of anterior spines (as does *Louisella*; see Conway Morris 1977: pl. 20: 6, 7, pl. 21: 3) and Huang et al. (2004a) speculated that the spines served to attract prey.

Comparisons

Chalazoscolex and *Xystoscolex* are similar with respect to the size and shape of the introvert scalids, the nature of the trunk ornamentation and possession of a distinct caudal region. They differ most obviously in the strength of the trunk ornamentation, details of the segmentation in the caudal region, and in *Xystoscolex* the possession of additional probos-

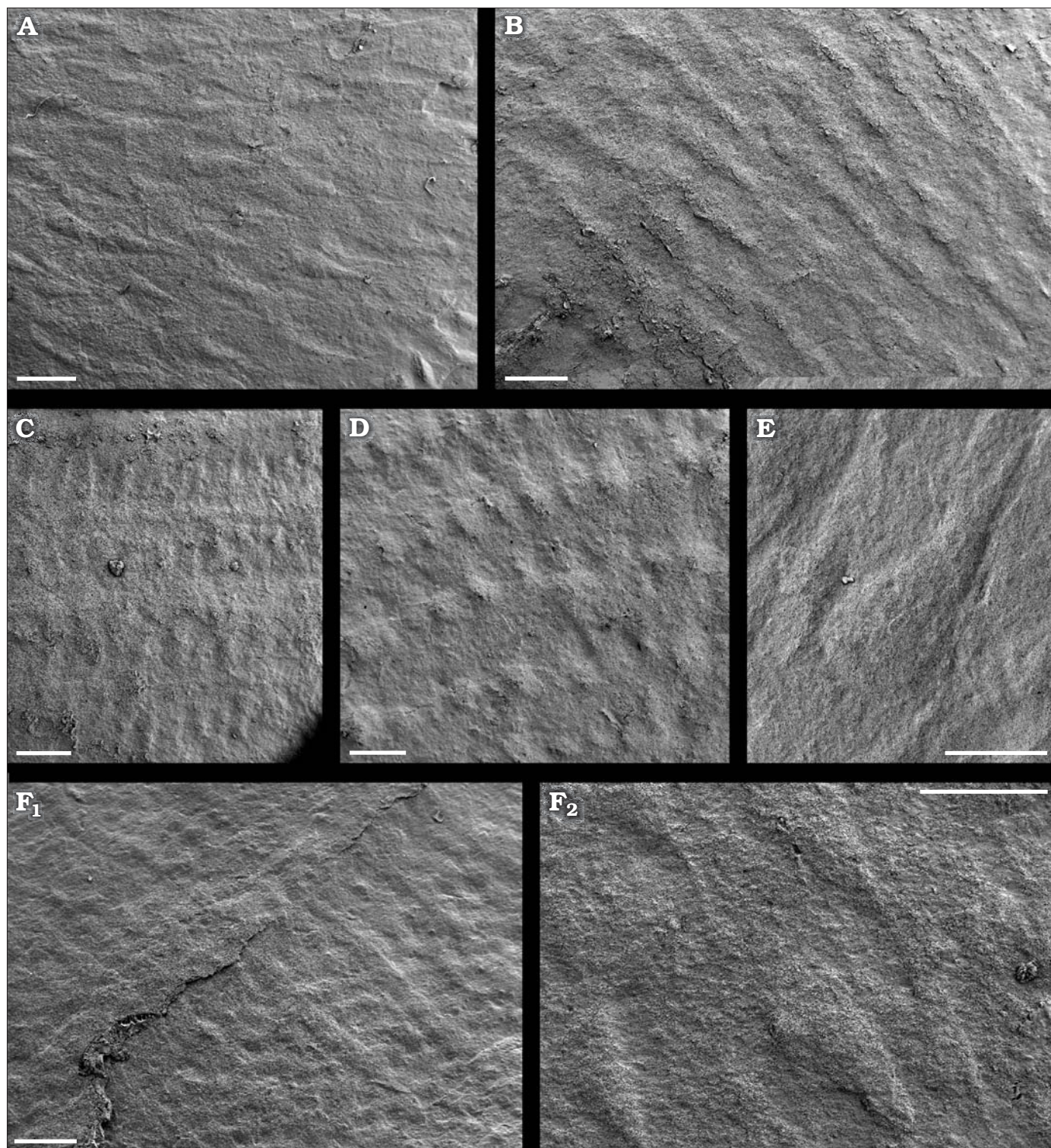


Fig. 6. Scanning electron micrographs of *Xystoscolex boreogyrus* gen. et sp. nov (A, E) and *Chalazoscolex pharkus* gen. et sp. nov (B–D, F), lower Cambrian (Series 2, Stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. **A.** MGUH 291560, scalids of the introvert, see also Fig. 4E. **B.** MGUH 29133, grooves and ridges on the introvert, see also Fig. 1A. **C.** MGUH 29136, segments of trunk showing longitudinal cuticular ridges, see also Fig. 2B. **D.** MGUH 29141, posterior trunk with larger sclerites, see also Fig. 2G. **E.** MGUH 29144, detail of scalid, distal point to upper right, see also Fig. 3C. **F.** MGUH 29148, segments with rows of sclerites and intervening unarmoured areas of cuticle (F₁) and scalids of introvert (F₂), see also Fig. 4B. Scale bars 400 μ m (A+F₁), otherwise 300 μ m. All specimens coated with gold film.

cis spines (Fig. 5). In addition, assuming that it is not a post-mortem feature, the longitudinal ridges seen in the proboscis

of some specimens of *Chalazoscolex* (Figs. 1A₃, B₄, 6B) find no counterpart in *Xystoscolex*, whilst the ability to extrude

most of the introvert in the latter taxon (Fig. 4E₂) may also be a defining feature (although it is only seen in one specimen, and was conceivably induced by severe stress). For these various reasons we argue that despite the similarities, the obvious differences merit a distinction at the level of genus.

Comparisons with other palaeoscolecoid taxa, as well as the related priapulans, are not straightforward for several reasons. First, only some of the material occurs in the form of soft-bodied specimens. These show considerable variation in the quality and style of preservation, ranging from more-or-less typical Burgess Shale-type compression material (e.g., Whit-tard 1953; Robison 1969; Conway Morris 1977; Glaessner 1979; Mikulic et al. 1985; Conway Morris and Robison 1986; Sun and Hou 1987; Hou and Sun 1988; Hou and Bergström 1994; Lin 1995; Huang et al. 2004a, b; Chen 2004; Hou et al. 2004; Hu 2005; Huang 2005; Han et al. 2007a, b; Hu et al. 2008) to effectively mouldic fossils (Kraft and Mergl 1989; Conway Morris 1997). Also abundant, however, are isolated sclerites that are recovered during acid digestion of calcareous sediments (e.g., Peel and Larsen 1984; van den Boogaard 1989a, b; Hinz et al. 1990; Wrona and Hamdi 2001). This distinction, however, is far from absolute. This is because phosphatised material can occur as semi-complete worms (Müller and Hinz-Schallreuter 1993), and other fragments of cuticle (e.g., Brock and Cooper 1993; Zhang and Pratt 1996; Lehnert and Kraft 2006), whilst the palaeoscolecoidans from the lower Cambrian of Siberia occur effectively as entire worms delineated by a dense array of phosphatic sclerites (Ivantsov and Wrona 2004). In soft-bodied material that displays arrays of in situ sclerites their quality of preservation varies from very good (e.g., Conway Morris 1997, Ivantsov and Wrona 2004) or moderate (e.g., Hu 2005; Han et al. 2007a; Huang 2005; Hu et al. 2008), to the more usual instances where little or no micro-structural detail is evident (e.g., Robison 1969; Glaessner 1979; Conway Morris and Robison 1986; Steiner et al. 2005: fig. 9A, B). Such, unfortunately, is the case with the Sirius Passet material (Fig. 6D, F₁). It will be evident, therefore, that this combination of preservational styles makes comparisons amongst the palaeoscolecoidans far from straightforward, both in terms of incomplete diagnoses (notably with entirely isolated sclerites) and the likelihood of undetected synonymies. What is evident, however, is that the diversity of palaeoscolecoidan forms is very considerable and includes a striking array of morphologies that encompass overall body form, patterns of ornamentation reflected in the wide variety of sclerites (and associated microstructures) and other cuticular specialisations (that include larger plate-like structures (Han et al. 2007a; see also Huang 2005) and prominent spines (Han et al. 2007b)).

To the first approximation palaeoscolecoidans are characterised by a relatively thick and segmented trunk that bears sclerites (that in turn are often ornamented with nodes or spines), and may occur in different sizes (especially plate-lets), together with an associated wealth of other cuticular modifications. The richness of these morphological details (e.g., Kraft and Mergl 1989; Müller and Hinz-Schallreuter 1993; Conway Morris 1997; Han et al. 2007a, c) is valuable

for taxonomic distinctions, but in the case of such taxa as *Chalazoscolex* and *Xystoscolex* where fine microstructure is not preserved the comparisons are less satisfactory and they must rely on more general arrangements. That said, it is evident that the distinctive trunk arrangement in the *Chalazoscolecidae* nov. fam. whereby each segment has two regions with sclerites (Fig. 6D, F) and ridges (Fig. 6C) respectively finds no obvious counterpart in any published material. Whilst it is the case that some of the other palaeoscolecoidans have areas of wrinkled cuticle (e.g., Müller and Hinz-Schallreuter 1993; Ivantsov and Wrona 2004), in no case are they that similar to the Sirius Passet material. Moreover, although the Ordovician palaeoscolecoidan *Gamascolex herodes* has clearly demarcated dorsal and ventral sections of the trunk in either case they are defined on the basis of the strength of tuberculation (Kraft and Mergl 1989). Finally, the Chengjiang worm *Tabelliscolex* bears lateral and dorsal sclerites, but these have a characteristic hexagonal ornamentation (Han et al. 2003, 2007a; Huang 2005). This taxon is likely to be a priapulid (or near-relative), but it has no notable similarity to the Greenland material.

Some comparisons can also be made with other soft-bodied palaeoscolecoidans, although once again these appear to be rather generalised and of limited phylogenetic utility. Whilst the proboscis and pharyngeal regions are not known in a number of palaeoscolecoidans (e.g., Conway Morris and Robison 1986; Ivantsov and Wrona 2004), the material from the Chengjiang Lagerstätte has yielded important information. Most notable in this respect is *Mafangoscolex sinensis* (see Hou and Bergström 1994: figs. 1A, 2A; Chen 2004: fig. 267A, B; Hou et al. 2004: 60; Hu 2005: 182–185; Huang 2005: figs. 36b, c), *Guanduscolex minor* (Hu et al. 2008: fig. 1, pl. 1: 3) and *Maotianshanella cylindrica* (e.g., Sun and Hou 1987: pl. 1: 1, 2, pl. 2: 6, 7; Chen 2004: fig. 262A, B; Hou et al. 2004: fig. 11.5a; Hu 2005), as well as a number of other taxa such as *Cricocosmia jinningensis* (see Han et al. 2007a: figs. 1D₁, 6A; see also Chen 2004: fig. 264A, B; Hou et al. 2004: fig. 11.1; Huang 2005: figs. 31, 35) and *Tylotites petiolaris* (Han et al. 2007b: fig. 1: 1, 2, 4, fig. 2: 1, 2, 5). Nevertheless, as is evident from both the Chinese and Sirius Passet taxa, this region is organised in the same manner as many other Cambrian priapulid-like taxa (e.g., Conway Morris 1977; Sun and Hou 1987; Chen 2004; Han et al. 2004; Hou and Bergström 1994; Hou et al. 2004). This, of course, supports the generally held notion that palaeoscolecoidans are closely related to these other priapulid-like forms.

In terms of other comparisons, the most useful might be with the Burgess Shale taxon *Louisella pedunculata* (Conway Morris 1977). The differences with the Sirius Passet taxa, notably in *Louisella* the presence of prominent rows of feathery appendages (presumed gills), require little emphasis. However, apart from sharing a palaeoscolecoidan pattern of segmental sclerites (Conway Morris 1977: pl. 22: 6, 7, pl. 23: 4), there is a similarity with respect to *Xystoscolex* in terms of the possession of the anteriorly-located elongate proboscis spines (Fig. 5). Finally it is worth mentioning that

while the details of scalid structure may be difficult to discern in Burgess Shale-type material, not only are the scalids of *Chalazoscolex* (Figs. 4B₁, 6G), and more particularly *Xystoscolex* (Figs. 3C₁, 5B, 6A, E), relatively well preserved but they appear to be similar to the Burgess Shale taxon *Ancalagon minor* (Conway Morris 1977: pl. 25: 2, 3).

So far as the wider phylogeny position of the palaeoscolecidans is concerned these questions can be conveniently divided into two topics: (i) their immediate relationships to priapulid-like forms, evidence for which is for all intents and purposes confined to the Cambrian, and (ii) their position within the super-clade Edysozoa (Fig. 7). With respect to the first point, that is the inter-relationships of the palaeoscolecidans and related taxa, matters are unfortunately not straightforward. Thus, as already noted the variety of preservational types, combined with the real possibility that some fragmentary material currently assigned to different taxa is actually synonymous, conspires against a coherent analysis. It is also far from clear just how distinct the palaeoscolecidans are as a group. This is now evident from the Sirius Passet taxa (and a considerable number of forms already described from the Chengjiang Lagerstätte), in as much as they are equipped with proboscis structures that if found detached would be readily assigned to the priapulid-like forms. Although no phylogenetic inference need be drawn, the Chengjiang *Maotianshan* (e.g., Sun and Hou 1987; Hou and Bergström 1994; Chen 2004; Hou et al. 2004) could serve as an intermediate because in addition to possessing a typical proboscis (e.g., Sun and Hou 1987; Chen 2004), the trunk bears numerous small sclerites (Hu 2005: pl. 1-16: 2-8; see also Huang 2005: 27a-c). These, however, have a rather uniform distribution (see also Sun and Hou 1987: pl. 1: 4, 5) rather than occurring in the organised bands characteristic of most other palaeoscolecidans. In addition, although otherwise not particularly similar, it is worth noting that other Cambrian priapulids, notably *Cricocosmia* (e.g., Chen 2004; Hou et al. 2004), possess a complex cuticular ornamentation (Han et al. 2007a).

The wider relationships of these priapulid-like forms have also proved to be controversial. Although the concept of the Edysozoa (Aguinaldo et al. 1997) has won very wide acceptance, the inter-relationships of the component phyla have

proved to be somewhat more refractory. There is, however, a general consensus that the Nematoda, comprising the nematodes and nematomorphs, is a monophyletic group (e.g., Bleidorn et al. 2002; Dunn et al. 2008), although the molecular data are not entirely robust (e.g., Bourlat et al. 2008). The Nematoda in turn is allied to the group usually referred to as the Scalidophora (Lemburg 1995). This encompasses the kinorhynchs and priapulids (e.g., Schmidt-Rhaesa et al. 1998) and together with the nematoids comprises the Cycloneuralia (the name being a reference to the arrangement of the pharyngeal brain). So far as the fossil record of the cycloneuralians is concerned, however, it is effectively composed of entirely priapulid-like forms. A key development in the phylogenetic discussion, therefore, was the proposal by Hou and Bergström (1994) that the palaeoscolecidans should be placed in the nematomorphs. In part this arose from the entirely justifiable suspicion that this group could not be placed in the Annelida, but the comparison between palaeoscolecidans and nematomorphs largely rested on the larval form of the latter group, together with the shared possession of a posterior spine-like structure (Hou and Bergström 1994). These authors stressed that the parasitic life-style of the nematomorphs hindered comparisons.

Although concentrating more on the question of the relative size of the earliest cycloneuralians, Budd (2001) noted the palaeoscolecidans are unlikely to be nematomorphs per se, but might be regarded as being either stem-group Nematoda or stem-group Cycloneuralia. Much the same position was adopted by Maas et al. (2007). In addition, some recent molecular data appear to support the latter view. Thus, Sørensen et al. (2008) linked the nematomorphs to the loriciferans, even though the general consensus had allied the latter group to the kinorhynchs and priapulids. In their scheme these scalidophorans would form the sister-group to the other cycloneuralians (plus arthropods, with onychophorans). Importantly Sørensen et al. (2008) also outlined a phylogenetic scenario whereby the most primitive ecdysozoans possess a life cycle that includes a loriciferan-like larva and a priapulid-like adult. We would suggest that the palaeoscolecidans and related forms are equivalent to this stage of ecdysozoan evolution (Fig. 7), so that the characteristic priapulid introvert (Conway Morris 1977) is in fact plesiomorphic to the cycloneuralians (see e.g., Maas et al. 2007), if not the ecdysozoans. This explains why so far as the Cambrian taxa are concerned it is routine to refer to them as priapulids, priapulimorphs, etc. (e.g., Huang et al. 2006; see also Han and Hu 2006). So far as the priapulids in the Cambrian are concerned, most likely they only occur as stem-group forms (see Wills 1998) represented by such taxa as *Ottoia prolifica* (Conway Morris 1977). Moreover, whilst the phylogeny of Sørensen et al. (2008) appears to drive a wedge between the scalidophorans and other priapulid-like cycloneuralians, it is necessary to stress that the morphological (and most likely genetic) differences in the earliest stages of this ecdysozoan radiation were most likely trivial, even though their end-products include the disparate phyla represented by the arthropods, nematoids, kinorhynchs, and priapulids.

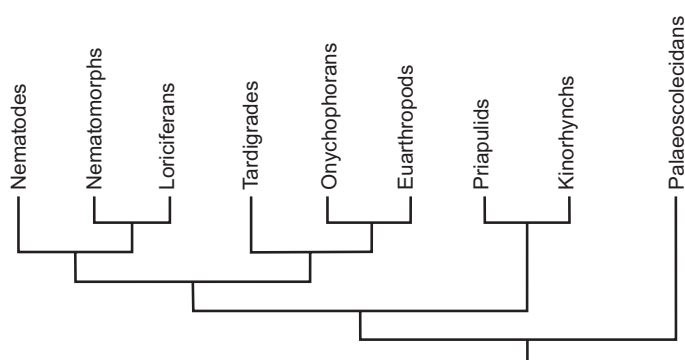


Fig. 7. Outline phylogeny of Edysozoa, principally based on Sørensen et al. (2008), to indicate possible basal position of the palaeoscolecidans and related taxa.

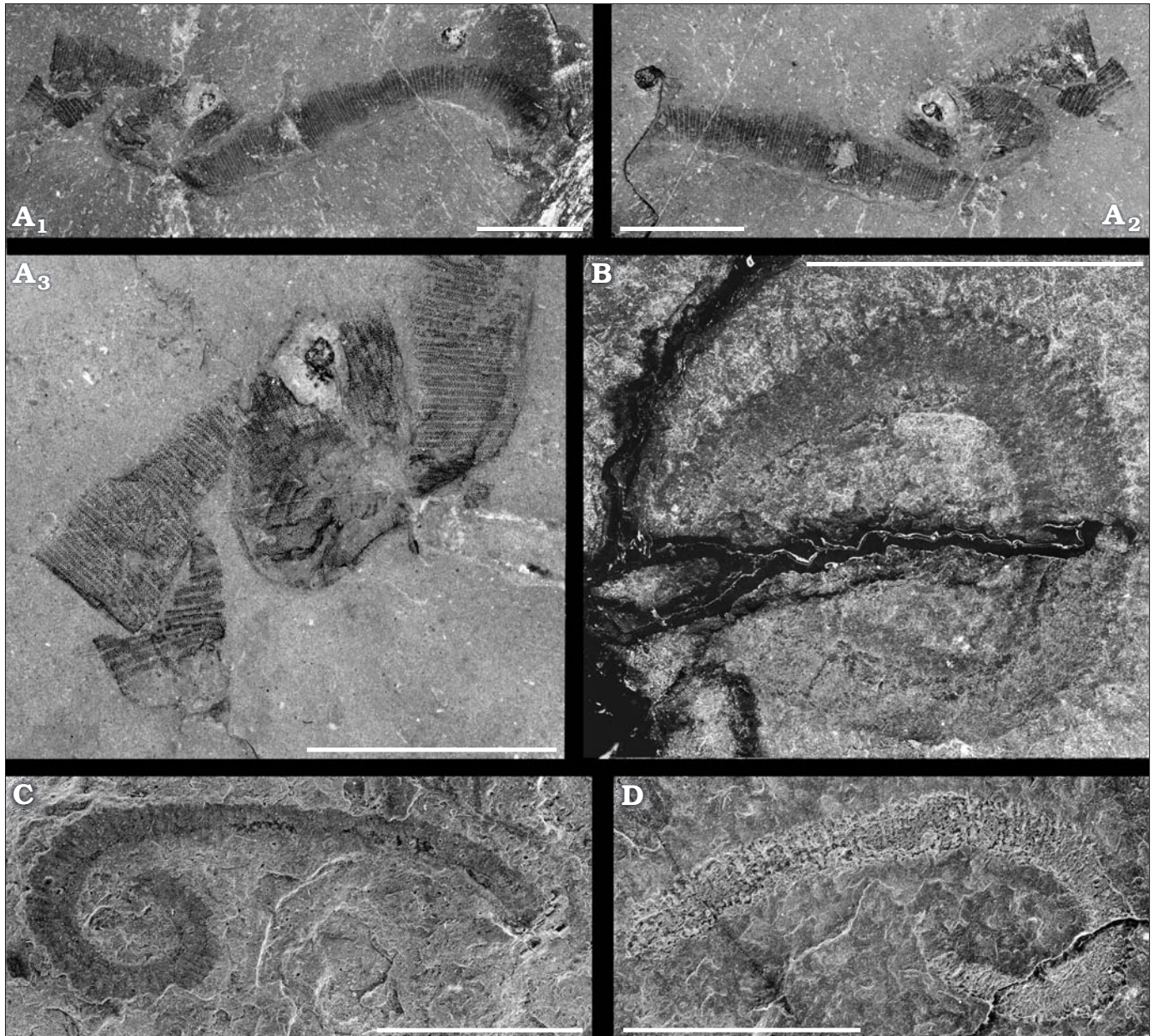


Fig. 8. Un-named early Cambrian palaeoscolecidans from the Latham Shale, Marble Mountains, California (A) and Kinzers Formation, south-eastern Pennsylvania (B–D). A. UCR 7003/1, counterpart (A₁), part (A₂), and detail of body (A₃). B. NMNH&S P-V-80. C. NMNH&S P-V-81. D. NMNH&S P-V-10. Scale bars 10 mm.

Two other palaeoscolecidans from the lower Cambrian of Laurentia

In addition to the celebrated Burgess Shale (and Sirius Passet) Fossil-Lagerstätte the Laurentian craton yields a significant number of more minor Lagerstätten, including the Latham Shale of the Marble and Providence Mountains (California) and the Kinzers Formation (Pennsylvania). The Latham Shale forms part of an important lower Cambrian sequence, succeeding the Zabriskie Quartzite and falling within the *Bornia–Olenellus* Zone (e.g., Mount 1976, 1980). It has attracted attention on account of a diverse assemblage of well-preserved

trilobites (notably *Bristolia* and *Olenellus*), but has also yielded soft-bodied material, which evidently occurs in the distal-most units and it was only here that Burgess Shale-type preservation could occur (Gaines and Droser 2002). The exceptionally preserved fossils include the stem-group arthropod *Anomalocaris* (Briggs and Mount 1982) and the alga *Margaretia* (Waggoner and Hagadorn 2004). In addition, a specimen referred to as “Annelid-new genus and species” was noted by Mount (1976: fig. 20, 1980: fig. 20). Although only illustrated as a drawing this is clearly a palaeoscolecidan. A field-trip to the locality, the classic “quarry” in the Providence Mountains (University of California, Riverside locality no. 7003: co-ordinates are given as SE1/4 of section 17, T. 11 N., R. 14. E, at the upper end of

Summit Wash, on the opposite side of the ridge (facing west from the abandoned Providence Mine), was undertaken in the hope of recovering more soft-bodied material. In the event the only specimen recovered, by Rachel Wood (Edinburgh University, UK), transpired to be the counterpart of the specimen (UCR 7003/1) collected by Mount in 1972 (Fig. 8A). Either side is well-preserved, and consists of an incomplete body, one end of which is broken into shorter units. Segmentation is clear, and defined by classic sclerite bearing zones separated by unarmoured regions (Fig. 8A₃). At the “broken” end of the specimen there are ca. 4–5 sclerites across each segment, whereas at the opposite end of the preserved body they number ca. 2–3. The edge of the body appears to be unarmoured, but it is not clear if this is original or preservational. The sclerites are well-defined, evidently circular with a diameter of ca. 40 µm. No microstructure is evident.

The Kinzers Formation has received considerable attention, yielding from the Emigsville Member (which is much the same age as the Latham Shale) a fairly diverse assemblage of soft-bodied and lightly skeletonised taxa (see Skinner 2005; see also Powell 2009). These include various worms (García-Bellido Capdevila and Conway Morris 1999), and arthropods (e.g., Briggs 1978, 1979). Amongst the priapulid-like forms are tubes of *Selkirkia* (Conway Morris 1977: pl. 30: 1–3) and a palaeoscolecidan (Conway Morris 1977: pl. 30: 5). In addition, Han et al. (2007b: 65) have suggested, on the basis of a comparison with *Tylotites*, that the worm *Atalotaenia adela* (García-Bellido Capdevila and Conway Morris 1999) might be a palaeoscolecidan, although the absence of any cuticular specialisation in the Kinzers specimen makes this suggestion speculative. Equally so is the comparison drawn by Huang et al. (2006) between the posterior of *Kinzeria crinata* (García-Bellido Capdevila and Conway Morris 1999) and certain Chengjiang priapulomorphs, not least because the anterior tentacular structures of the former taxon appear to find no counterpart in either the priapulomorphs or palaeoscolecidans (see also Han and Hu 2006: 252). With respect to undoubted palaeoscolecidans, the specimen illustrated by Conway Morris (1977; see also Resser and Howell 1938: pl. 1: 1) is deposited in the National Museum of Natural History, Washington, DC, but its counterpart (Fig. 8D) remains in the NMNH&S. The

mouldic preservation of this specimen is unusual, and the other material (Fig. 8B, C) is preserved in the typical style of Burgess Shale-type compressions. Specimens are typically recurved, and show a gut trace. The ornamentation is at best faintly apparent and offers little in the way of diagnostic details, although Skinner (2005: 185) noted “New specimens [that] consist of well-preserved cuticular fragments that exhibit rows of nodes typical of palaeoscolecidans ... remains are phosphatic in composition”. In no case is the anterior clearly preserved.

A possible cambroclavid

In addition to the undoubted palaeoscolecidan taxa from the Sirius Passet Fossil-Lagerstätte we also draw attention to a fragmentary specimen that may possibly be related to this group, and in addition conceivably a hitherto enigmatic group of small shelly fossils known as the cambroclavids (e.g., Conway Morris and Chen 1991).

At one end of the specimen (Fig. 9C) the body bears a series of closely spaced striations. The remainder of the surface is covered with a dense imbricated array of leaf-shaped sclerites, each apparently with a median ridge. These sclerites appear to arise in regular rows and their overlap imparts a well-defined diamond-shaped pattern; an arrangement that is clearest in the lower left of the specimen (Fig. 9A). On the assumption the sclerites are posteriorly imbricated, then the anteriorly located striations (Fig. 9B) are conceivably comparable to those observed on the proboscis of some specimens of *Chalazoscolex* (Fig. 1B₄). The latter, however, are considerably less regular and this comparison should be regarded as very tentative. In addition, the sclerites form an imbricated array that has no exact counterpart to any known palaeoscolecidan. Thus, although it is the case that *Rhomboscolex chaoticus* has a vaguely similar diamond-pattern on its cuticle (Müller and Hinz-Schallreuter 1993: text-fig. 9B) this is defined by the arrangement of the small intercalary platelets. They do, however, show some similarity to an otherwise enigmatic group of small shelly fossils from the lower Cambrian known as cambroclavids. Good arguments exist for these structures forming a coating of a metazoan (Bengtson et al. 1990: fig. 70; Conway Morris and Chen 1991: text-fig. 11). The observation of occasional assem-

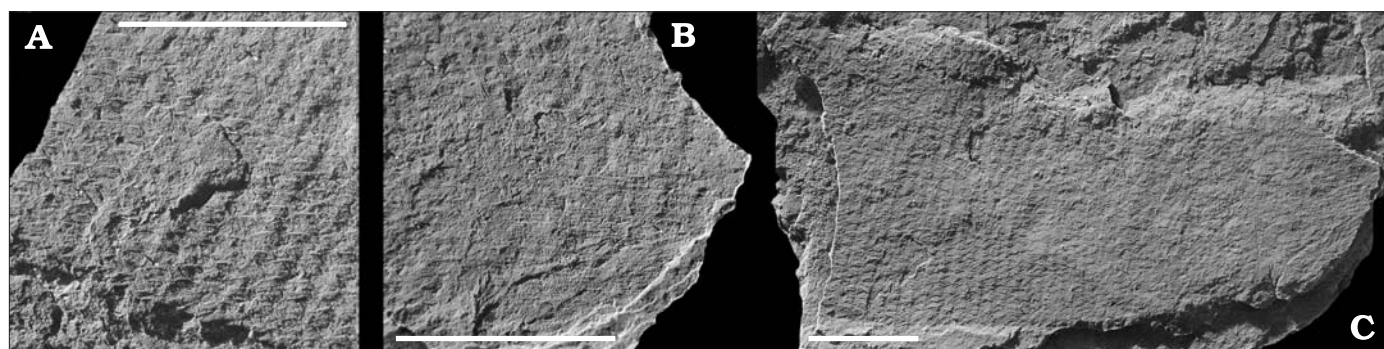


Fig. 9. Possible cambroclavid animal, lower Cambrian (Series 2, stage 3), lower Cambrian (Series 2, stage 3), Buen Formation, Sirius Passet Fossil-Lagerstätte, Peary Land, North Greenland. MGUH 3948, enlargement of sclerites (A), anterior striations (B), and entire specimen (C). Scale bars 5 mm. Specimen coated with sublimate.

blages of fused specimens in a back-to-back orientation (Conway Morris and Chen 1991: text-figs. 8c–e, 9d–h) may not be inconsistent with their forming the external armour of a worm-like animal because in some palaeoscolecidans a similar disposition has been identified, evidently as a result of the decay of the intervening soft-tissues (Ivantsov and Wrona 2004). Nevertheless, it is important to stress that these comparisons are very tentative and it is to be hoped more complete material is recovered from one or other of the Cambrian Lagerstätten.

Systematic palaeontology

“Phylum” Cycloneuralia

Class Palaeoscolecida Conway Morris and Robison, 1986

Family Chalazoscolecidae nov.

Diagnosis.—Palaeoscolecidans with a trunk ornamentation consisting of three distinct cuticular zones: with sclerites, with longitudinal folds, smooth.

Remarks.—Family comprised of two genera: *Chalazoscolex* gen. nov. and *Xystoscolex* gen. nov. As noted in the descriptions the two taxa have fundamentally similar styles of trunk ornamentation, but generic distinction is warranted on difference in strength of this ornamentation, as well as distinct introverts. In our opinion these differences do not, however, warrant a familial distinction.

Genus *Chalazoscolex* nov.

Etymology: An oblique reference to both the polar locality and also the tuberculate surface (Greek *chalaza*, hail and sleet, but also pimple and tubercle)

Type and only species: *Chalazoscolex pharkus* sp. nov.

Diagnosis.—As for the species.

Chalazoscolex pharkus sp. nov.

Figs. 1, 2, 4B, G, 6B–D, F.

Etymology: From the Greek for wrinkled (*pharkidos*), in reference to the trunk ornamentation.

Holotype: MGUH 29133 (Figs. 1A, 6B).

Type locality: Peary Land, central North Greenland, situated at the south-western end of the broad valley (Sirius Passet) that connects J.P. Koch Fjord and Brainard Sund; latitude 82°47.6'N, longitude 42°13.3'W, altitude 450 m above sea level.

Type horizon: Lower part of the Buen Formation (lower Cambrian, provisional Series 2, Stage 3), equivalent to the *Nevadella* Zone of North American usage.

Material.—The holotype and MGUH 29134–29141, 29148, 29151.

Diagnosis.—Palaeoscolecidan with introvert and trunk in two regions. Introvert with dense array of simple scalids. Anterior and median trunk with two types of ornamentation: ca. 140 segments with simple sclerites and longitudinal folds, separated by smoother zones. Posterior trunk with ca. 15 seg-

ments bearing more prominent sclerites. Gut includes anterior pharynx and straight intestine.

Stratigraphic and geographic range.—Buen Formation (Stage 3 of provisional Cambrian Series 2, equivalent to *Nevadella* Zone), Peary Land (North Greenland).

Genus *Xystoscolex* nov.

Etymology: From the Greek for smooth (*xystos*), in reference to the subdued ornamentation in comparison with *Chalazoscolex*.

Type and only species: *Xystoscolex boreogyrus* sp. nov.

Diagnosis.—As for the species.

Xystoscolex boreogyrus sp. nov.

Figs. 3, 4A, C–F, 5, 6A, E.

Etymology: From the Greek words *boreas* (northern) and *gyros* (ring), a reference to both the prominent tubercles encircling the posterior trunk and also the midnight sun encircling the Arctic skies.

Holotype: MGUH 29144 (Figs. 3C, 6E).

Type locality: Peary Land, central North Greenland, situated at the south-western end of the broad valley (Sirius Passet) that connects J.P. Koch Fjord and Brainard Sund; latitude 82°47.6'N, longitude 42°13.3'W, altitude 450 m above sea level.

Type horizon: Lower part of the Buen Formation (lower Cambrian, provisional Series 2, Stage 3), equivalent to the *Nevadella* Zone of North American usage.

Material.—The holotype and MGUH 29142–29147, 29149, 29150, 29152.

Diagnosis.—As for *Chalazoscolex*, but introvert with anterior spines. Trunk ornamentation substantially more subdued and posterior trunk with larger number of tuberculate segments encircling body.

Stratigraphic and geographic range.—Buen Formation (Stage 3 of provisional Cambrian Series 2, equivalent to *Nevadella* Zone), Peary Land (North Greenland).

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