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Source: Acta Palaeontologica Polonica, 57(2) : 423-436

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2011.0028

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Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China

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Harvey, T.H.P., Ortega-Hernández, J., Lin, J.-P., Zhao, Y., and Butterfield, N.J. 2012. Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China. *Acta Palaeontologica Polonica* 57 (2): 423–436.

Diverse carbonaceous microfossils, including exceptionally preserved remains of non-biomineralizing metazoans, are reported from a basal middle Cambrian interval of the Kaili Formation (Guizhou Province, China). The application of a gentle acid maceration technique complements previous palynological studies by revealing a larger size-class of acritarchs, a richer assemblage of filamentous microfossils, and a variety of previously unrecovered forms. Metazoan fossils include *Wiwaxia* sclerites and elements derived from biomineralizing taxa, including chancelloriids, brachiopods and hyolithids, in common with previously studied assemblages from the early and middle Cambrian of Canada. In addition, the Kaili Formation has yielded pterobranch remains and an assemblage of cuticle fragments representing "soft-bodied" worms, including a priapulid-like scalidophoran. Our results demonstrate the wide distribution and palaeobiological importance of microscopic "Burgess Shale-type" fossils, and provide insights into the limitations and potential of this largely untapped preservational mode.

Key words: Kaili biota, Priapulida, acritarchs, palynology, taphonomy, Cambrian, Guizhou Province, China.

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Received 8 March 2011, accepted 4 June 2011, available online 8 June 2011.

Introduction

The record of macroscopic carbonaceous fossils is dominated by organisms with particularly recalcitrant organic compositions, such as woody plant tissues, sclerotized arthropod body parts, and pterobranch periderm. At the opposite end of the taphonomic spectrum are cellular tissues and more delicate types of extracellular cuticle, which are typically restricted to instances of exceptional preservation. Among carbonaceous Konservat-Lagerstätten, so-called "Burgess Shale-type" assemblages are notable for having originated in fully marine depositional settings, where organic preservation appears to be comparatively unlikely (Butterfield 1995).

Not all Burgess Shale-type fossils are large, however, and it is becoming clear that their microscopic counterparts offer an important complementary view of early Palaeozoic palaeobiology. "Exceptional" carbonaceous microfossil biotas in Cambrian marine deposits (hereafter, "Burgess Shale-type microfossils"; cf. Butterfield 1995; Butterfield and Nicholas 1996) have been recovered not only from the middle Cambrian Burgess Shale itself (Butterfield 1990a, b, 1996; Gostlin 2006), but also from elsewhere in Canada, notably the early to middle Cambrian Mount Cap Formation in the Northwest Territories (Butterfield 1994; Butterfield and Nicholas 1996; Harvey and Butterfield 2008), the early Cambrian Mahto Formation of Alberta (Butterfield 2008), and the early Cambrian Forteau Formation of Newfoundland (Harvey 2010). These assemblages of mostly disarticulated and fragmentary microfossils have substantially expanded the palaeogeographic and geological age range of various taxa, even in the absence of their corresponding macrofossils.

Although microscopic Burgess Shale-type assemblages are significantly more common than their macroscopic counterparts, the controls on their distribution remain poorly understood. Certainly the fossilization of such relatively labile features as carbonaceous films requires a particular combination of both early and late diagenetic circumstances (Butterfield et al. 2007; Page et al. 2008; Gaines et al. 2008), while acid extraction of the larger, more complex and more palaeobiologically informative specimens requires a particularly

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gentle maceration technique (e.g., Butterfield 1990b, 1994, 2008; Butterfield et al. 1994; Butterfield and Nicholas 1996; Harvey and Butterfield 2008; Harvey 2010).

In this study, we extend our work on carbonaceous Burgess Shale-type microfossils to China, focussing on the early to middle Cambrian Kaili Formation, Guizhou Province, China. The Kaili Formation is notable for preserving a Burgess Shale-type macrofossil assemblage including non-biomineralizing arthropods, worms, eldoniids, "algae" and *Wiwaxia*, in addition to diverse shelly fossils (e.g., Zhao et al. 1994a, b, 2005; Lin 2009). Exceptional macrofossil preservation in the Kaili is primarily via carbonaceous films with or without early authigenic mineralization, in common with assemblages from Chengjiang (early Cambrian, Yunnan Province, China) and the Burgess Shale itself (middle Cambrian, British Columbia, Canada) (see Zhu et al. 1999; Gaines et al. 2008). However, unlike the Burgess Shale, which has undergone greenschist-grade metamorphism (Powell 2003; Butterfield et al. 2007) and the Chengjiang, which has suffered intense weathering, the Kaili has experienced less severe alteration and preserves more of the original, carbonaceous fossil expression (Lin and Briggs 2010). The Kaili Formation therefore occupies an intermediate position in both time and taphonomic history, and offers a key opportunity for exploring the corresponding microfossil signal.

Previous palynological work on the Kaili Formation has yielded a modest diversity of small acritarchs, fragments of putative multicellular cyanobacteria and algae, and a spinose specimen tentatively identified as arthropodan (Yin and Yang 1999; Yang and Yin 2001; Yin et al. 2009, 2010). All of these carbonaceous microfossils are small and/or fragmentary; however, their predominately orange colour indicates limited thermal alteration (TAI ~2.5; CAI ~1.5; ca. 100°C; see Williams et al. 1998) and therefore a potential for recovering more informative results using our modified extraction procedures.

Institutional abbreviation.—NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing ,China.

Other abbreviation.—KMA, Kaili microfossil assemblage.

Geological setting

The Kaili Formation and closely equivalent units are exposed at eleven localities in the eastern part of Guizhou Province, South China, along a ~370 km outcrop belt (Zhao et al. 2005; Lin 2009). The succession includes carbonates and fine-grained siliciclastics and forms part of the Jiangnan Slope Belt at the southeastern margin of the South China (Yangtze) Platform (see Lin 2009). Stratigraphically, the Kaili Formation spans the boundary between the proposed Cambrian Series 2 and 3 (equivalent to the "Lower"/"Middle" Cambrian boundary of previous usage), which is positioned at the lowest occurrence of the candidate marker trilobite *Oryctocephalus indicus* (e.g., Zhao et al. 2008; Lin 2009). The middle part of the Kaili Formation has yielded assemblages of exceptionally preserved macrofossils at four localities within a small (ca. 4 km^2) area of Jianhe (formerly Taijiang) County (see Zhao et al. 1994a, 2005; Lin 2009). Sedimentation in this area was characterized by low energy conditions, probably taking place within the lower limits of the photic zone (Lin 2009).

Two of the Jianhe County localities were investigated in the present study, though the focus is on collections from the Miaobanpo Quarry (26°45' N, 108°25' E), the principal locality for exceptionally preserved Kaili macrofossils (see Zhao et al. 1999a, 2001, 2010). Locally the Kaili Formation measures at least 156 m thick and is dominated by mudstone that is often silty and/or calcareous; the Miaobanpo Quarry exposes a particularly fossiliferous interval ~10 m thick that begins around 2 m above the lowest occurrence of *Oryctocephalus indicus* (i.e., 30–40 m above the base of the local succession, = unit GTBM-9; see Zhao et al. 2001, 2010; Lin 2009). Thus the material we present here derives from an interval that has yielded exceptionally preserved macrofossils and is dated, in informal terms, to the early middle Cambrian. The Miaobanpo Quarry mudstone is moderately fissile and varies from dark-grey to olive green; the presence of penetrative olive-green rims points to extensive secondary weathering.

Material and methods

Nine mudstone samples from the Miaobanpo Quarry and six from the nearby Wuliu-Zengjiayan section (see Zhao et al. 2001; Lin 2009) were examined for microfossils in the present study; the Wuliu-Zengjiayan section yielded only rare fragmentary material so we do not consider it further. The Miaobanpo Quarry samples were collected from talus blocks, focussing on fine-grained lithologies with low carbonate content and minimal evidence of weathering. Six of the nine samples preserved various small (<5 mm) macrofossils, including trilobites, agnostids, brachiopods and *Wiwaxia* sclerites.

For microfossil extraction, 50–100 g of each sample was immersed in 40% hydrofluoric acid (HF) until disaggregated, with residues gently washed over a 63 μm sieve and recovered in water. Individual specimens were picked from suspension using a fine pipette and transferred to glass coverslips where the water was then removed. Coverslips with adhering microfossils were prepared for transmitted light microscopy by mounting onto glass slides with a heat-setting epoxy resin, or for SEM by mounting on stubs followed by gold-coating. Figured specimens have been deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China, numbered sequentially from NIGP153940 to NIGP154010; the figure legends provide details of sample number (prefix KAIL-), slide number, and England Finder co-ordinates.

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Description and discussion

Microfossil occurrence and preservation

We picked and mounted ca. 925 specimens of organic walled microfossils from the nine Miaobanpo samples. Although some samples were more productive than others, the relative proportions of taxa and overall aspect of assemblages were remarkably consistent. In the absence of any recognizable stratigraphic distinction we refer to them collectively as the "Kaili microfossil assemblage" (KMA). The samples contained more specimens than it was practical to pick, so efforts were concentrated on larger and distinctively shaped metazoan fossils which are therefore over-represented in our collections (at 18%) relative to filaments (58%) and acritarchs (6%; indeterminate specimens constitute the remaining 18%).

Although mostly fragmentary, the recovered microfossils exhibit low thermal maturity (yellow, orange, and brown in colour) and moderate to good morphological preservation (resolution to less than one micron in the best specimens).

Cyanobacterial filaments

The KMA is dominated by filamentous structures, which occur abundantly in each sample (n = 535; Fig. 1A–I). The specimens are larger and more informative than previously reported examples (cf. Yin and Yang 1999; Yin et al. 2009), with individual fragments measuring up to 2 mm long and exhibiting a range of morphologies. Some specimens are reasonably assigned to extant groups. Strap-like forms containing tracts of dark carbonaceous inclusions, for example, are likely to represent cyanobacterial colonies in which cellular

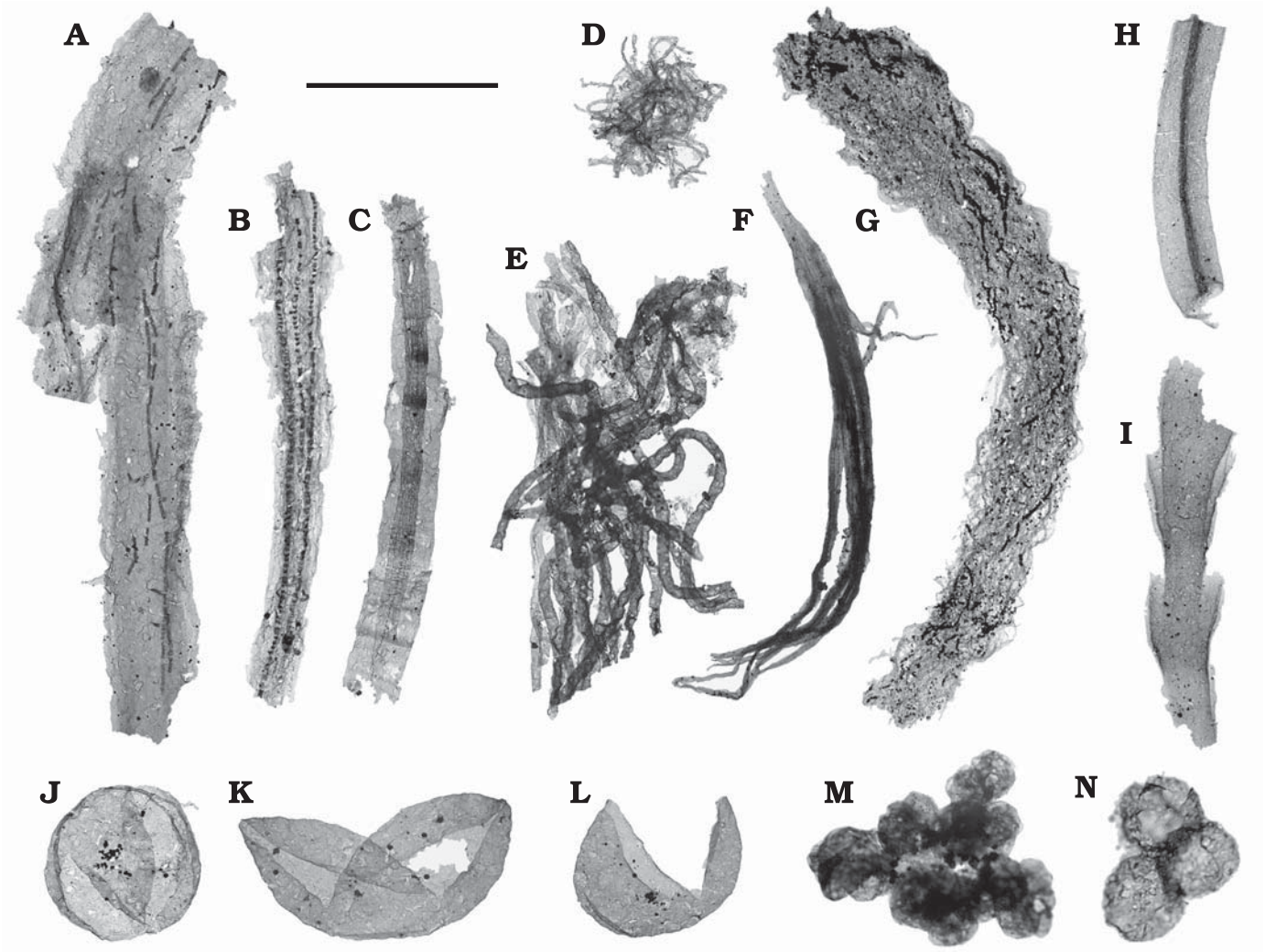


Fig. 1. Filaments and acritarchs (NIGP 153940–153953) from the middle Cambrian Kaili Formation, Guizhou, China. **A**–**G**. Cyanobacterial filaments. **A**–**C**. *Eomicrocoleus* Horodyski and Donaldson, 1980/*Siphonophycus* Schopf, 1968 emended Knoll, Swett, and Mark, 1991 with multiple cellular trichomes enclosed within a common sheath (in C, a double sheath). **D**,**E**,**G**. *Siphonophycus* spp. exhibiting a variety of growth forms. **F**. *Polytrichoides* Hermann, 1974 emend. Knoll, Swett, and Mark, 1991. **A**. KAIL-04-03-L44. **B**. KAIL-05-02-V31. **C**. KAIL-05-05-D13. **D**. KAIL-GTBM-9-35M-01-T45. **E**. KAIL-GTBM-9-37M-01-J23. **F**. KAIL-A-01-K26. **G**. KAIL-GTBM-9-2-b-M37. **H**, **I**. Filaments of uncertain affinity. **H**. KAIL-GTBM-9-35M-01-E44. **I**. KAIL-09-01-H12. **J**–**N**. Acritarchs, including forms with medial splitting (**K**, **L**) and possible vegetative colony growth (**M**). **J**. KAIL-A-01-O25. **K**. KAIL-04-05-T17. **L**. KAIL-04-05-G17. **M**. KAIL-GTBM-2-9-c-D21. **N**. KAIL-GTBM-9-2-d-S14. Scale bars A–F, J–L 200 μm; G–I 400 μm; M, N 100 μm.

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trichomes were enclosed within an extracellular sheath (Fig. 1A–C; cf. Butterfield et al. 1994: fig. 25). A cyanobacterial affinity is also likely for a broad range (3–110 μm diameter) of smooth-walled filaments characterized by various higher-level "behaviours", including the formation of tangled mats (Fig. 1D, E), false-branching bundles (Fig. 1F), and densely packed oriented colonies (Fig. 1G). The discontinuous preservation of inclusions reflects the differing degrees of decay and separation of the cells, in contrast to the more recalcitrant sheaths (e.g., Bartley 1996). Given the significant range of taphonomic artefacts associated with simple filamentous microfossils, and the potential for ecophenotypic variation, we limit our (form-)taxonomic designations to *Eomicrocoleus* Horodyski and Donaldson, 1980 where multiple cellular trichomes occur within a common sheath (Fig. 1A–C), *Polytrichoides* Hermann, 1974 emended Knoll, Swett, and Mark, 1991 for bundled filaments (Fig. 1F) and *Siphonophycus* Schopf, 1968 emended Knoll, Swett, and Mark, 1991 where the cellular structure is absent or indistinct (Fig. 1D–G; cf. Butterfield et al. 1994); some specimens clearly grade between two or more form taxa (Fig. 1A, C).

Other filaments in the KMA exhibit additional features that leave their wider affinities unclear. A specimen with a prominent medial stripe (Fig. 1H) may simply record a taphonomic variant in the expression of cyanobacterial trichomes, while a specimen with a repetitive flaring pattern (Fig. 1I) may indicate a funnel-shaped mode of cyanobacterial growth (cf. *Circumvaginalis* Sergeev, 1993 emended Sergeev, Knoll, and Grotzinger 1995). Alternatively, these particular fossils may have contrasting origins, possibly among the Metazoa.

Nevertheless, the overall prominence of confirmed or probable cyanobacteria among the Kaili microfossils is consistent with a depositional environment within the photic zone (Lin 2009) and with the identification of cyanobacteria-like growth forms among Kaili "macroalgae", notably *Marpolia* Walcott, 1919 (Mao et al. 1994; Yang et al. 2001). *Marpolia* from the Cambrian of Laurentia, including the Spence Shale of Utah (Conway Morris and Robison 1988) and the Burgess Shale of British Columbia (e.g., Mankiewicz 1992), and also from the Paseky Shale of the Czech Republic (Steiner and Fatka 1996) sometimes preserves a cellular structure of trichomes within sheaths and/or transverse banding, providing support for a cyanobacterial affinity and specific links to the fine-scale characters revealed in the Kaili microfossils.

Acritarchs

Previous studies have sampled small Kaili acritarchs using traditional palynological techniques, and have recovered a variety of sphaeromorphic and acanthomorphic forms (Yin and Yang 1999; Yang and Yin 2001; Yin et al. 2009, 2010). Only relatively large acritarchs have been sampled in the present study (n = 56), nominally those larger than the 63 μm sieve mesh, though smaller specimens are occasionally found in clusters or adhering to other fossils. We make no attempt to apply form-taxonomic concepts, which are of questionable value in this instance given the few characters available for analysis and the potential for artificially grouping structures as disparate as phytoplankton cysts and metazoan egg cases (e.g., Yin et al. 2007).

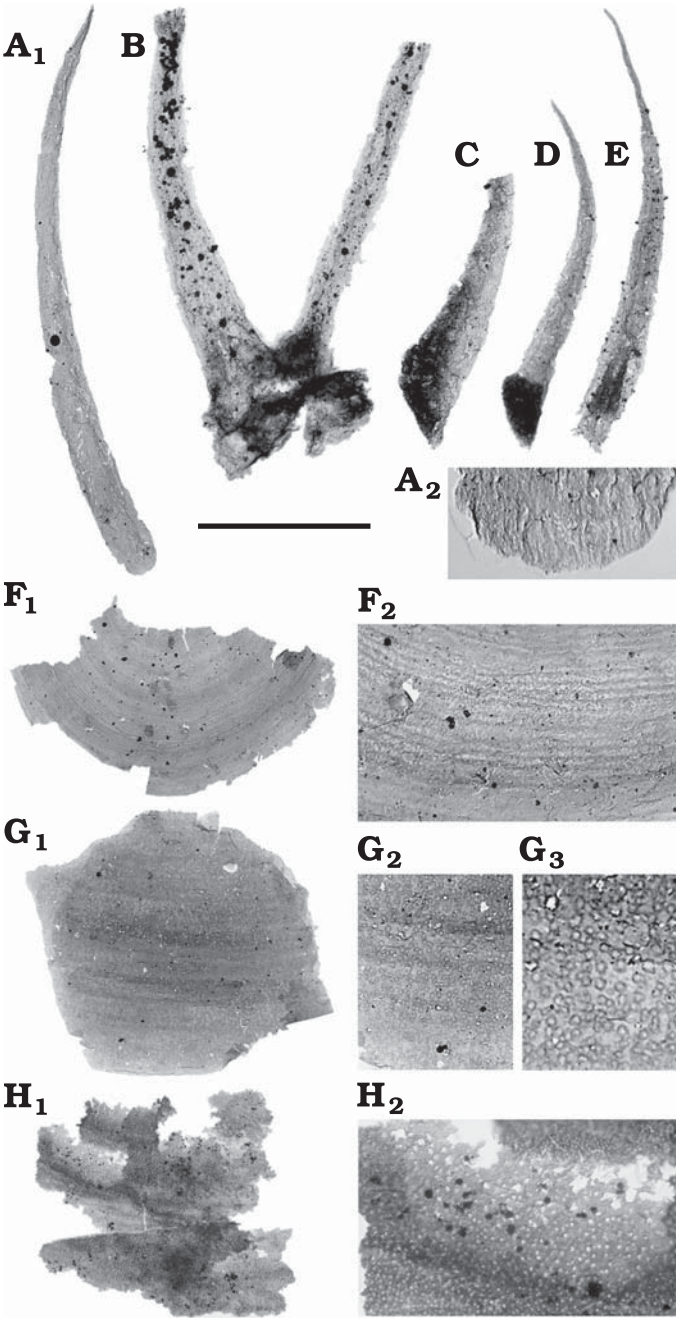


Fig. 2. Biomineralizing taxa preserved as small carbonaceous fossils (NIGP 153954–153961) from the middle Cambrian Kaili Formation, Guizhou, China. **A**. Hyolithid helen (A_1), with detail of rounded proximal end (A_2), KAIL-BP-01-J38. **B**. Multi-rayed chancelloriid sclerite, KAIL-A-01-P39. **C**-**E**. Single-rayed or disarticulated chancelloriid sclerites. **C**. KAIL-GTBM-9-2-b-E39. **D**. KAIL-05-05-O17 (image reversed). **E**. KAIL-09-01-U19. **F**–**H**. Brachiopod fragments (F_1, G_1, H_1), with details of microstructure (F_2, G_2, G_3, H_2). **F**. KAIL-07-01-U38. **G**. KAIL-05-05-E17. **H**. KAIL-GTBM-9-2-d-K41. Scale bars: A_1, B–E 200 μm; A_2 40 μm; F_1 400 μm; F_2 125 μm; G_1 250 μm; G_2 125 μm; G_3 60 μm; H_1 500 μm; H_2 150 μm.

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The most abundant large acritarchs in the KMA (present in every sample) are simple thin-walled sphaeromorphs more than 100 μm in diameter, some of which preserve evidence for pre-burial splitting (Fig. 1J–L). Rarer forms include clusters of more irregularly outlined spheroids, apparently inter-connected and possibly representing proliferating vegetative colonies (Fig. 1M), and smaller (< 50 μm diameter) and thicker-walled forms which are sometimes associated in clusters of indeterminate biological or sedimentological origin (Fig. 1N). In common with assemblages from the Burgess Shale and Mount Cap formations (Butterfield 1990a; 1994; Butterfield and Nicholas 1996; Gostlin 2006), large acanthomorphic forms are conspicuously absent.

Biomineralizing taxa preserved as small carbonaceous fossils

Although the bulk of the "Burgess Shale-type" record appears to be dominated by non-biomineralizing organisms, it is clear that the carbonaceous components of "conventional" shelly fossils can also be preserved and recovered alongside other organic-walled microfossils (e.g., Butterfield and Nicholas 1996). The KMA includes the carbonaceous shell components or coverings of several biomineralizing taxa, including hyolithids, chancelloriids, and brachiopods (Fig. 2), exposing familiar Cambrian fossils in a new light.

Hyolithids.—Hyolithids are problematic Palaeozoic fossils known primarily from their meso- to macroscopic shelly fossils. They are abundantly represented on Kaili bedding surfaces (Zhao et al. 2005), but fully articulated specimens retaining the characteristic helens—paired lateral "appendages" of uncertain homology and function—have yet to be reported. We have identified a single hyolithid helen in the KMA (Fig. 2A), which exhibits the characteristically curved and tapering form seen in articulated macrofossils (e.g., Martí Mus and Bergström 2007; Butterfield and Nicholas 1996) as well as similar organic-walled specimens from the Little Bear assemblage of the Mount Cap Formation (Butterfield and Nicholas 1996). Like the Little Bear material, the Kaili helen displays a rounded, "erosive" base that truncates a subtle longitudinal microstructure without evidence for accretionary increments (Fig. $2A_2$). In contrast, helens preserved as three-dimensional calcitic fossils exhibit internal growth increments and a characteristic logarithmic curvature, implying an accretionary mode of growth (see Martí Mus and Bergström 2007). These observations can be reconciled, however, if the carbonaceous microfossils are interpreted as an external, periodically renewed "periostracum" surrounding an accretionary, biomineralizing element. An alternative derivation from an internal, organic-rich core, which has been identified in helens preserved as shelly fossils (see Martí Mus and Bergström 2007), is inconsistent with the expression of external helen sculpture in the Mount Cap specimens (Butterfield and Nicholas 1996: fig. 4.1, 4.6).

Chancelloriids.—Chancelloriids occur in the KMA as a singular specimen of a multi-rayed sclerite (Fig. 2B), and possibly also as disarticulated rays and/or one-rayed sclerites (n = 6; Fig. 2C–E). The latter are distinguished from other filamentous or spine-shaped microfossils by the presence of a conspicuous dark region at the wider end. Chancelloriids have been reported previously from the Kaili biota, where they occur as articulated scleritomes (e.g., Zhao et al. 2005: pl. I: 3,4). However, the carbonaceous microfossils resolve new histological detail. The dark regions in the Kaili specimens are presumably equivalent to the dark granular layer, or "pith", that has been distinguished in carbonaceous sclerites from the Little Bear assemblage (Butterfield and Nicholas 1996: fig. 5). In the latter specimens, the pith is clearly enclosed by the outer wall and often extends along the length of the each sclerite ray, although it is expressed most conspicuously in the proximal part. The poorer definition and more variable extent of the dark material in the Kaili specimens suggests an interpretation of the pith as a comparatively soft internal tissue that was more prone to decay than the outer sclerite wall, a histology that is implicit—but not directly observable—in the structure of mineralized specimens (e.g., Porter 2008).

Brachiopods.—The KMA contains innumerable fragmentary sheets with concentrically banded, accretionary fabrics that are likely to be derived from the periostracum and/or internal shell layers of organo-phosphatic brachiopods (Fig. 2F–H). The specimens are often composed of overlapping but apparently separate layers, at least in part, and exhibit one of three discrete microstructures, either fine-scale concentric laminae (Fig. 2F), "enclosed" pores or granules of ~3 μm diameter (Fig. 2G), or perforations that vary in diameter from ~2–5 μm (Fig. 2H). Occasional cracks and angular outlines imply the brittle deformation of once rigid, biomineralized structures, although residual biomineral is generally lacking, presumably having been dissolved during diagenesis or rendered fragile and unrecoverable during acid preparation.

Brachiopods are represented among the Kaili macrofossils by twelve genera, nine of which belong to groups with organo-phosphatic shells (see Huang et al. 1994; Zhao et al. 2005). The shell structure in comparable extant linguliforms such as *Discina* and *Lingula* contains both an external periostracum and internal organic layers, which can include chitinous and/or collagenous components (e.g., Williams et al. 1992, 1994). Comparable shell components in fossil taxa represent the most likely origin of the Kaili microfossils, and likewise the acid-isolated material reported from the Little Bear assemblage (see Butterfield and Nicholas 1996: figs. 3.3, 3.4). As such, the granular and perforate microstructures potentially record structural details of the periostracal layer (such as vesicles) and/or the organization of mineralized components (possibly calcareous granules) or setigerous tubes. Alternatively, the fossils could represent entirely non-mineralized, "soft-shelled" brachiopods such as those reported from the early Cambrian Mural Formation (Balthasar and Butterfield 2009) and the middle Cambrian Burgess

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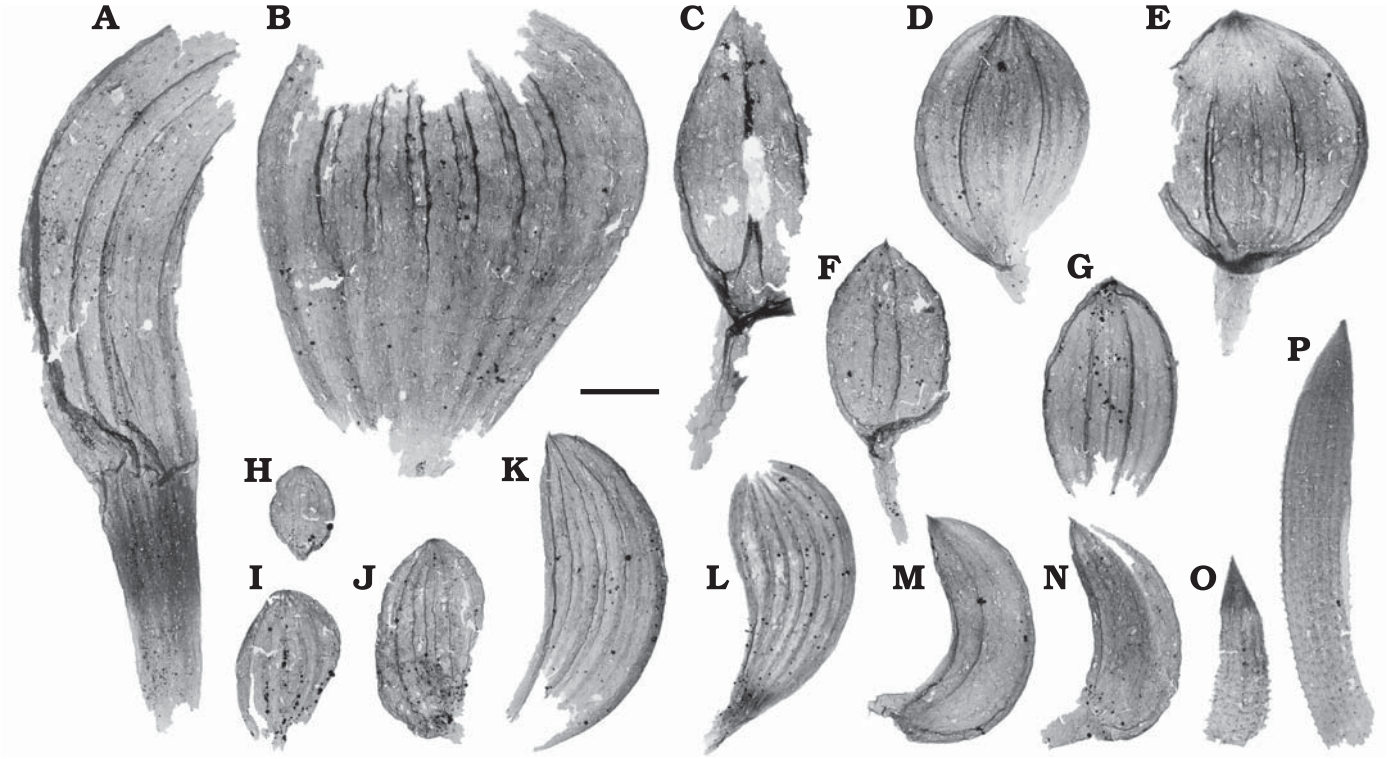


Fig. 3. Sclerites of the problematic lophotrochozoan *Wiwaxia* (NIGP 153962–153977) from the middle Cambrian Kaili Formation, Guizhou, China. **A**. KAIL-05-01-N28. **B**. KAIL-GTBM-9-2-a-M38. **C**. KAIL-05-01-S43. **D**. KAIL-GTBM-9-35M-02-F25. **E**. KAIL-05-01-T15. **F**. KAIL-A-01-R33. **G**. KAIL-05-03-L36. **H**. KAIL-GTBM-9-2-b-D40. **I**. KAIL-GTBM-9-2-d-P33. **J**. KAIL-GTBM-9-2-d-N34. **K**. KAIL-GTBM-9-35M-02-J34. **L**. KAIL-GTBM-9-37M-01-S46 (image reversed). **M**. KAIL-07-01-L24. **N**. KAIL-A-01-P37. **O**. KAIL-05-05-T6. **P**. KAIL-GTBM-9-37M-01-M22. Scale bars: A 200 μm, B–P 100 μm.

Shale (Holmer and Caron 2006). Either way, the carbonaceous microfossils resolve anatomical details that are not discernable in macroscopic specimens.

Recalcitrant remains of non-biomineralizing metazoans

Carbonaceous preservation is relatively common when the structures involved are inherently recalcitrant, as shown by the abundance of fossilized lignin, sporopollenin and graptolite periderm in the fossil record. This sort of fossil expression is certainly not "exceptional", but it nevertheless requires certain taphonomic circumstances to be expressed, and provides an important complement to other taphonomic modes. The KMA includes the remains of at least two metazoan taxa represented by this kind of robust material: sclerites of the problematic lophotrochozoan *Wiwaxia* (Fig. 3), and fragmentary remains of pterobranch periderm (Fig. 4).

***Wiwaxia* sclerites**.—The KMA *Wiwaxia* occur as isolated sclerites (n = 38) which are identifiable by their distinctive outlines and a characteristic longitudinal microfabric that is also present in acid-extracted specimens from the Burgess Shale (Butterfield 1990b) and subsurface Mount Cap biotas (Butterfield 1994). Although fully articulated *Wiwaxia* are limited almost entirely to the Burgess Shale— with rare specimens documented from the Kaili (Zhao et al. 2005)—the conspicuously wide distribution of acid-isolated sclerites (NJB and THPH unpublished data) attests to their substantially sclerotized constitution.

Wiwaxia sclerites in the KMA range from a little over 100 μm to more than 1.8 mm in length. They occur in all nine of the sample assemblages and include a broad representation of sclerite types (see Conway Morris 1985), including comparatively rare elongate "spines" (n = 2; Fig. 3O, P) and asymmetrical "dorsal" or "ventro-lateral" forms (n = 5; Fig. 3K–N) in addition to more symmetrical "lateral" forms (n = 12; e.g., Fig. 3D–G); 19 fragmentary specimens are of indeterminate overall shape.

Wiwaxia has previously been recorded from several Kaili Formation localities, including the Miaobanpo Quarry, as compression fossils on bedding surfaces (Zhao et al. 1994b; 2005). Articulated scleritomes occur only rarely (n = 2) and have yet to be described in detail (see Zhao et al. 2005: 756, pl. 2: 2), though isolated sclerites are relatively common (Zhao et al. 1994b). The bedding-surface sclerites exhibit an equivalent variation in outline to the acid-extracted specimens, but are larger in size, with lengths ranging from 2.2 mm (only slightly larger than the largest "microfossils") to 8 mm, extending the overall length variation across almost two orders of magnitude (data in Zhao et al. 1994b). The macroscopic Kaili sclerites have been referred to a distinct species,

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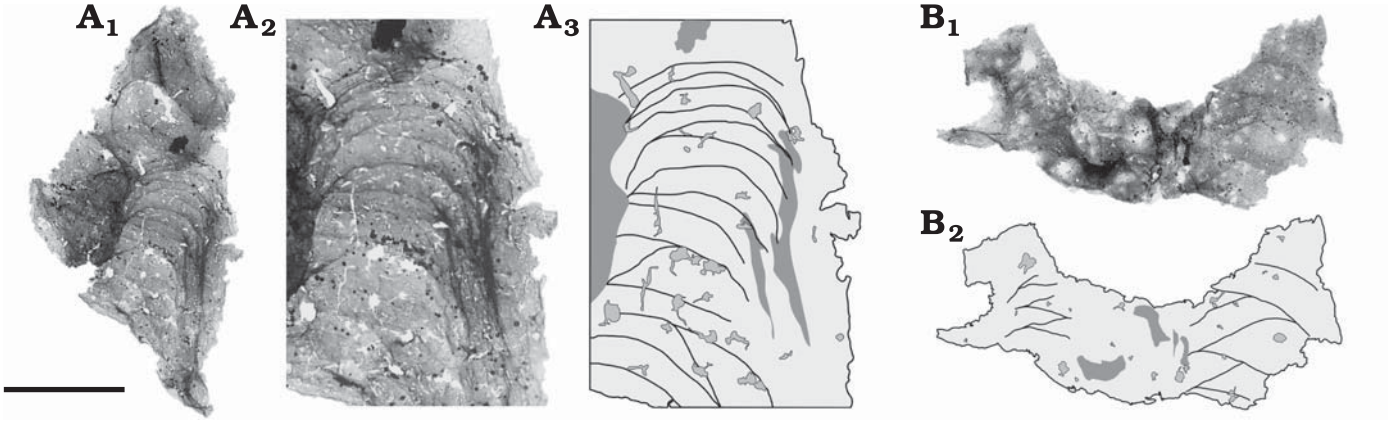


Fig. 4. Pterobranch periderm (NIGP 153978–153979) from the middle Cambrian Kaili Formation, Guizhou, China. **A**. KAIL-BP-01-N23. **B**. KAIL-A-01-R36. A_2 is a photographic detail of A_1; A_3 and B_2 are camera lucida drawings highlighting the fusellar microstructure, including characteristic oblique sutures developed locally in a "zig-zag" arrangement. Scale bars: A_1 200 μm; A_2, A_3 100 μm; B_1, B_2 400 μm.

Wiwaxia taijiangensis, which has been distinguished from the North American *W. corrugata* based on details of sclerite structure, including ribbing pattern (Zhao et al. 1994b). It is worth noting, however, that the ribbing patterns of acid-extracted Kaili specimens are much the same as their counterparts from the Burgess Shale and Mount Cap biotas (Butterfield 1990b; 1994). That said, the finer-scale features resolvable in the acid-extracted specimens have the potential to refine *Wiwaxia* taxonomy. For example, the Kaili, Mount Cap and Burgess Shale samples all include sclerites with a distinctive tuberculate ornamentation (e.g., Fig. 3O, P), a possible species-level distinction (Butterfield 1994).

Pterobranchs.—At least three fragmentary KMA specimens are characterized by a distinctively banded microstructure with a locally developed fabric comparable to the oblique and truncated (sometimes zig-zag) fusellar sutures of pterobranch periderm (Fig. 4; cf. Kozłowski 1947; Maletz et al. 2005). Although features diagnostic of specific subgroups—e.g., graptolites, rhabdopleurids or cephalodiscids—have not been preserved, we propose that they are most likely to represent rhabdopleurids, which have previously been reported from the middle Cambrian of Sweden and Siberia (Bengtson and Urbanek 1986; Durman and Sennikov 1993). In any case, they represent the first documented occurrence of pterobranchs in the Kaili Formation, and are among the oldest known examples of the group on record. In contrast to the relatively common and well-preserved occurrence of *Wiwaxia* sclerites, the Kaili pterobranch material is rather poorly preserved, suggesting significant reworking and transport before final burial.

Worm cuticles

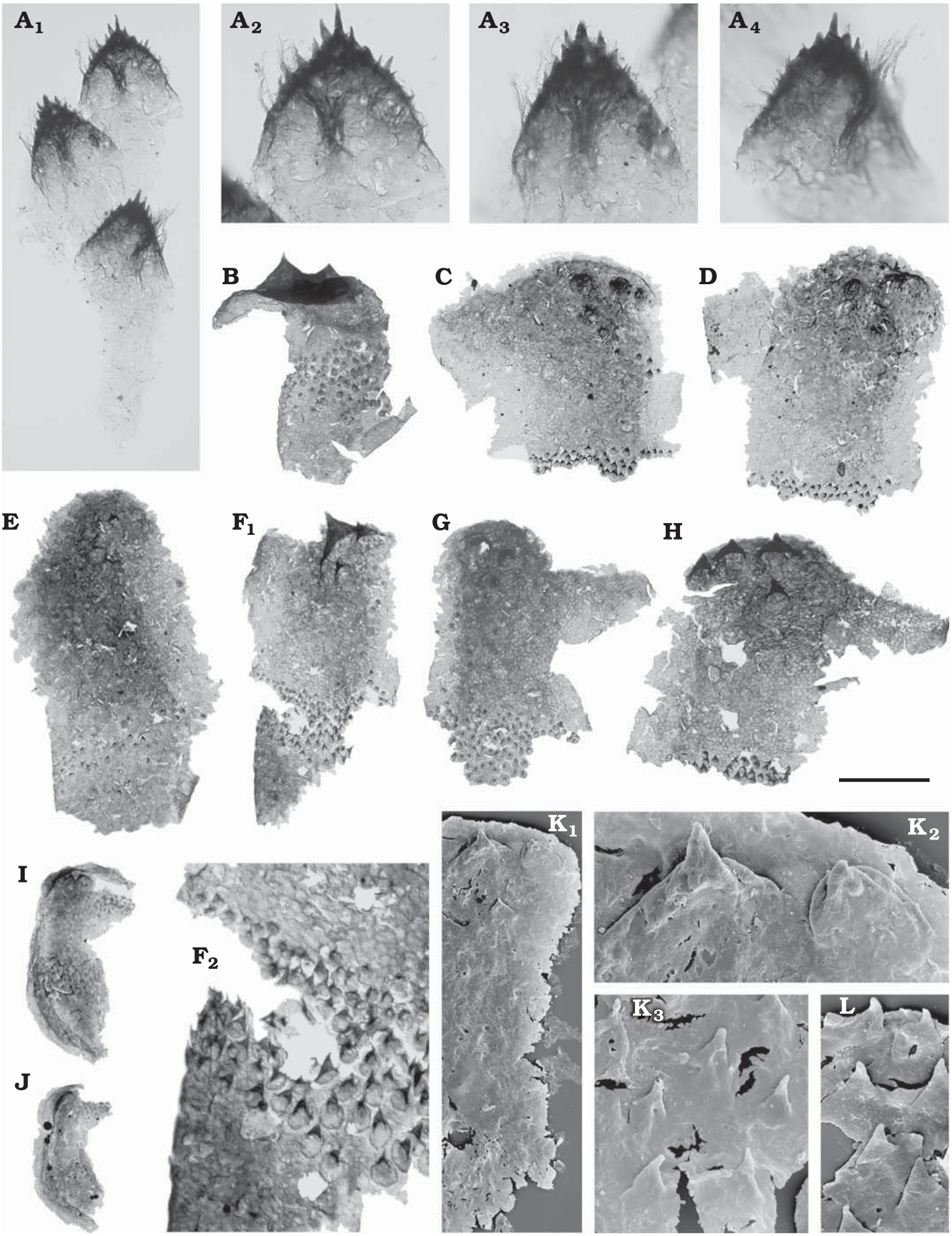
The KMA contains various fragments of ornamented cuticle that are likely to be derived from "soft-bodied" worms (Fig. 5). Cuticularized worms are a familiar component of Cambrian Burgess Shale-type macrofossil assemblages, and the Kaili macrobiota includes priapulid-like forms assigned to *Ottoia*, *Selkirkia*, *Palaeoscolex*, *Maotianshania*, *Cricocosmia*, and *Sicyophorus*/*Protopriapulites* (Zhao et al. 1999b, 2005). A detailed comparison of the two data sets is frustrated by the fragmentary (but finely detailed) nature of the microfossils, and the absence of documented fine structure in corresponding macrofossils. By the same token, however, the microfossils offer a novel window onto Cambrian worm anatomy, with some forms providing an important complement to "conventional" macrofossil data.

Priapulid scalids.—One of the most informative specimens in the KMA consists of three triangular scale-like structures, each measuring 50–60 μm in length, that are attached to a thin cuticular sheet (Fig. 5A). Each of the scales bears a marginal series of stout pointed teeth, a marginal or sub-marginal fringe of fine hair-like projections, and a bundle of long, coarser hair-like projections arising from a rod-like process positioned proximally and medially (Fig. $5A_2$–$5A_4$). Broadly comparable structures are characteristic of various living and fossil priapulids, which develop a wide range of cuticular projections (e.g., van der Land 1970; Conway Morris 1977). When positioned on the pharynx, such structures are known as teeth, whereas those on the trunk or introvert are termed scalids (van der Land 1970). Scalids and pharyngeal teeth are commonly ordered in a quincuncial pattern, consistent with the offset arrangement of the partly articulated Kaili fossil.

The fine features of the individual scales in this specimen are strikingly similar to the anterior trunk scalids of the extant meiofaunal priapulid *Meiopriapulus fijiensis*, including similar hair-like projections developed as a marginal fringe and a midline bundle (Fig. 6; see also Morse 1981; Storch et al. 1989: figs. 15–17). To our knowledge, equivalent structures have not been documented in any other taxon. Whether this shared character carries any phylogenetic weight is difficult to assess given its restricted taxonomic distribution, but the pronounced morphological similarity strongly suggests that the fossil derives from a meiofaunal form comparable in size to *M. fijiensis* (<3 mm long). The identification of meiofaunal priapulids in the early middle Cambrian is significant in that such forms have previously been resolved as exclu-

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sively "modern" (Wills 1998). Thus, the evidence from the KMA fundamentally revises the evolutionary history of this group, and reveals a major taphonomic bias against small, non-biomineralizing animals.

Spiny cuticles.—Distinctive spiny cuticle fragments that occur in seven of the nine samples (n = 23; Fig. 5B–L) seem also to be derived from small soft-bodied worms, although their precise affinities are unclear. The fragments are irregularly shaped except for a longitudinal edge preserved in four specimens (Fig. 5B, F, I, J) but share a distinctive ornamentation of hollow conical projections with well-defined circular bases ("spines") and a polygonal background microstructure. The spines are oriented in a common direction, defining an overall polarity of "proximal" to "distal", and are borne in "transverse" zones perpendicular to this axis. Different zones are distinguished by the distribution of spines of different sizes, or their absence. Viewed collectively, the fragments reveal a more or less consistent pattern of four zones. From proximal to distal these are: (i) an unornamented zone (preserved in eight specimens; e.g., Fig. 5B, F, I, J); (ii) a zone of densely packed and uniformly small spines (in 22 specimens); (iii) a largely unornamented zone with occasional scattered small spines (in 20 specimens); and (iv) a zone with comparatively large, widely spaced spines, with or without scattered small spines (in 17 specimens).

The consistency of this ornamentation is matched by a general uniformity in size. Typically, specimens measure less than 350 μm in maximum dimension and bear small spines of ~5–10 μm, larger spines of ~20–30 μm, and a distance between the two spiny zones of ~110–160 μm. Only three specimens differ substantially in size and/or ornamentation. Two exhibit the typical banding pattern but on a smaller scale, with small spines of ~3–5 μm, larger spines of ~10–20 μm, and unornamented-zone widths of ~50 and 60 μm (Fig. 5I, J), whereas one specimen is notably larger (500 μm) and bears a contrasting ornamentation of scattered small spines (Fig. 5E).

Individually, the spines resemble smaller versions of various conical microfossils with circular bases, including the mineralized, conodontiform *Formichella* (albeit without the defining accretionary growth pattern; see Bengtson 1983) and also the organic-walled "acritarch" *Ceratophyton* (see Zang et al. 2007), which potentially represents, at least in part, the disarticulated remains of Kaili-type cuticles. However, it is the articulated arrangement seen in the Kaili specimens that provides information on possible affinities. The banded zonation of oriented spines is broadly comparable to the arrangements of scalids and teeth in extant and fossil scalidophorans, especially priapulids (cf. van der Land 1970; Banta and Rice 1976; Conway Morris 1977), and especially the innermost regions of the pharynx where the teeth are numerous, simple in shape and closely spaced (e.g., Théel 1911: pl. 1). Moreover, the individual spines in the Kaili specimens are hollow like those of extant priapulids (vs. the solid projections of nematodes and nematomorphs; see Schmidt-Rhaesa 1998), and the background cuticle exhibits a polygonal pattern (e.g., Fig. 5F–H) that is characteristic of various living and extinct scalidophorans (see Harvey et al. 2010). However, the introvert scalids and pharyngeal teeth of priapulids are distributed, by definition, in strict geometrical arrangements (Adrianov and Malakhov 2001) and discrete bands (Conway Morris 1977) whereas the Kaili spines are scattered irregularly in part, so the resemblance appears to be superficial.

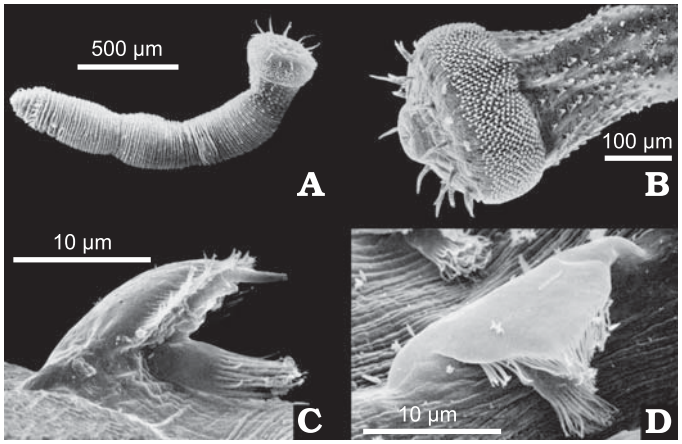


Fig. 6. A modern meiofaunal priapulid worm, *Meiopriapulus fijiensis* Morse, 1981 from Fiji. **A**. Overview. **B**. Detail of the anterior end, illustrating the terminal mouth, the regularly arranged introvert scalids, and the more irregularly arranged trunk scalids. **C**. Detail of a trunk scalid in lateral view. **D**. Detail of a trunk scalid in oblique view. Note the presence of marginal teeth, a marginal fringe of hairs, and a midline bundle of hairs, in common with the priapulid scalids from the Kaili microfossil assemblage (cf. Fig. 5A). Images are scanning electron micrographs, reproduced from Morse (1981) with permission of John Wiley and Sons Ltd. and the author.

Instead of the introvert and pharynx, it is possible that these fragments derive from the trunk region of a priapulid-like worm. Broadly comparable arrangements in extant species include the fields of trunk tubuli in *Halicryptus higginsi* (Shirley and Storch 1999), the trunk "scalids" of *Meiopriapulus fijiensis* (Fig. 6B), and the diverse ventral projections of male *Tubiluchus corallicola* (van der Land 1970: figs. 66, 67). Various Cambrian worms with (broadly) priapulid affinities also possess spiny trunks (see Conway Morris 1977; Huang et al. 2004a; Han et al. 2007), although those that are preserved in detail by virtue of early diagenetic

← Fig. 5. Worm cuticles (NIGP 153980–153991) from the middle Cambrian Kaili Formation, Guizhou, China. **A**. KAIL-04-06-O21; an array of three priapulid scalids (A_1); details (A_2–A_4). **B**–**L**. Spiny cuticles of uncertain affinity. **B**. KAIL-BP-01-H25. **C**. KAIL-07-01-M37. **D**. KAIL-07-01-F19. **E**. KAIL-GTBM-9-2-d-S26. **F**. KAIL-BP-01-J27 (F_1); detail (F_2). **G**. KAIL-GTBM-9-2-a-H38. **H**. KAIL-04-05-G21. **I**. KAIL-04-12-W38. **J**. KAIL-05-05-D8. **K**. KAIL-SEM-GTBM-9-2-1-3 (K_1); details (K_2, K_3). **L**. KAIL-SEM-04-1-6. Images are transmitted light micrographs except for K_1–K_3 and L, which are scanning electron micrographs. Scale bars: A_1 55 μm; A_2–A_4 30 μm; B–D, F_1, G–J 100 μm; E 135 μm; F_2 35 μm; K_1 70 μm; K_2 25 μm; K_3, L 12 μm.

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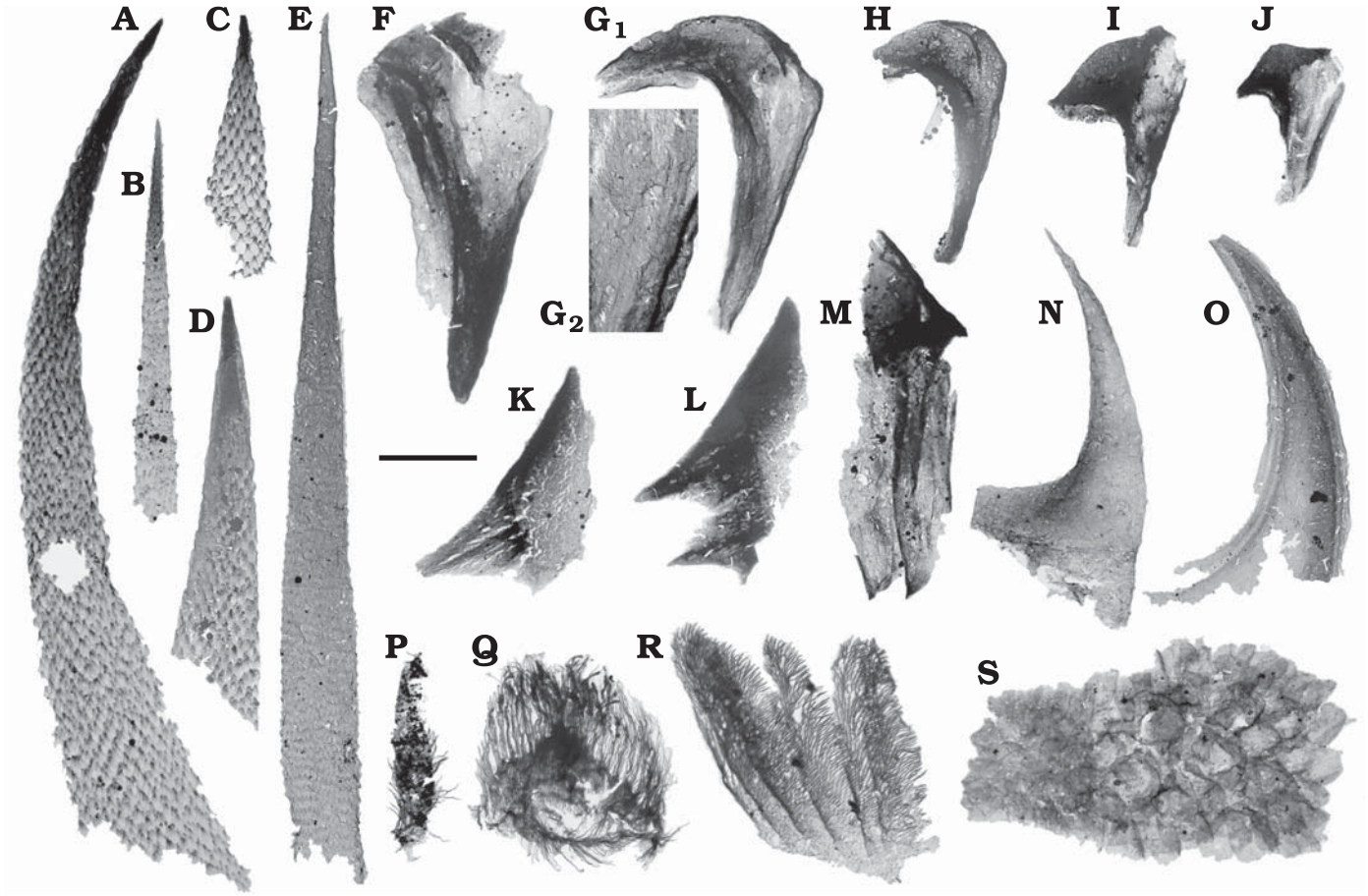


Fig. 7. Problematic metazoan microfossils (NIGP 153992–154010) from the middle Cambrian Kaili Formation, Guizhou, China. **A**–**F**. Ornamented spines cf. *Rushtonites*/*Mongolitubulus*. **A**. KAIL-04-05-M10. **B**. KAIL-GTBM-9-35M-02-G23. **C**. KAIL-BP-01-K41. **D**. KAIL-X-01-P42. **E**. KAIL-09-01-S31. **F**-**J**. Possible elements of a lophotrochozoan jaw apparatus. **F**. KAIL-05-01-U23. **G**. KAIL-04-2-T39 (G_1); detail (G_2). **H**. KAIL-GTBM-9-2-d-F6 (image reversed). **I**. KAIL-BP-01-N25 (image reversed). **J**. KAIL-GTBM-9-2-d-E9. **K**-**O**. Diverse spinose forms including possible elements of a radula-like apparatus (**M**, **N**). **K**. KAIL-04-07-Q33. **L**. KAIL-05-03-J25. **M**. KAIL-GTBM-9-35M-02-N41. **N**. KAIL-05-03-M17. **O**. KAIL-04-09-X27. **P**, **Q**. Possible arthropodan seta (P) and setal array (Q). **P**. KAIL-X-01-M28. **Q**. KAIL-GTBM-9-35M-01-W29. **R**, **S**. Complex forms of unknown affinity. **R**. KAIL-05-03-U21. **S**. KAIL-05-01-F35. Scale bars: A–P, S 100 μm; Q, R 50 μm; G_2 40 μm.

phosphatization—namely palaeoscolecids (e.g., Harvey et al. 2010), the fossil embryos *Markuelia* (e.g., Dong et al. 2010) and the larval forms *Shergoldana* and *Orstenoloricus* (Maas et al. 2007, 2009)—exhibit distinct cuticular ornamentations.

Alternatively, the spinose Kaili cuticles could be derived from sipunculan worms, which are closely related to annelids (Lophotrochozoa) despite their superficial similarity to priapulids, and possess robust extracellular cuticles ornamented with a variety of cuticular projections including irregular arrays of hollow, conical forms (e.g., Stephen and Edmonds 1972; Rice 1993: figs. 22–28; Saiz-Salinas 1995: figs. 1E, 2). Sipunculan worms have been reported from the early Cambrian Chengjiang biota (Huang et al. 2004b), but have yet to be identified among the Kaili macrofossils.

If the spiny Kaili cuticles come from priapulids, they offer a window onto their detailed anatomy that is not available from co-occurring macrofossils. If they come from sipunculans (or another group), they reveal a taxonomic bias in preservation potential between macroscopic and microscopic modes. More generally, they bridge a conspicuous gap in preservational scale and resolution between the macroscopic Burgess Shale/Chengjiang-type record of carbonaceous compressions and the microscopic Doushantuo/Orsten-type mode of phosphatization, potentially reconciling two largely disjunct views of early worm evolution.

Problematic metazoan microfossils

The KMA contains a variety of metazoan remains of uncertain affinity (Fig. 7). Elongate tapered spines ornamented with distally directed spines or scales (Fig. 7A–E) represent a rare but fairly consistent component of the assemblage (six specimens from six different samples). Closely comparable forms have been described from the Burgess Shale (Butterfield 1990b: fig. 5) and Mount Cap assemblages (Butterfield 1994; Butterfield and Nicholas 1996). Although first suggested to represent components of the *Wiwaxia* animal (Butterfield 1990b, 1994), they have more recently been

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compared to the "small shelly fossil" *Rushtonites*, on the basis of a distinctive surface ornamentation (Butterfield and Nicholas 1996). The similar and perhaps synonymous small shelly taxon *Mongolitubulus* (see Skovsted and Peel 2001) clearly represents, at least in part, the isolated spines of bradoriid arthropod carapaces (see Topper et al. 2007). Nevertheless, it is not certain that these carbonaceous fossils, which have not been found attached to carapaces, or even with flared proximal attachment regions, belong in the same biological category.

Novel problematica from the Kaili Formation include a suite of wedge- or hook-shaped forms with a partially fibrous composition (n = 7; Fig. 7F–J). Though the specimens are now flattened, originally complex three-dimensional morphologies are implied by the presence of ridges, thin-walled regions or, as in one specimen, a layered or stepped appearance (Fig. 7F). The microstructure of parallel longitudinal striae (Fig. $7G_2$) implies that in the living animal these structures were secreted by microvilli in the style of various lophotrochozoan "tough parts", such as annelid chaetae and molluscan radulae (see Butterfield 2008), and they conceivably represent the disarticulated elements of a lophotrochozoan jaw apparatus. Similar carbonaceous microfossils from the Mount Cap and Forteau formations (THPH and NJB unpublished data) point to the wide distribution of a probably robust and recalcitrant body part, but so far lend no new clues as to its precise biological affinities. Other Kaili spines exhibit a robust composition and approximately triangular shape but lack obvious signs of a fibrous construction (Fig. 7K–O). Nevertheless, two specimens (Fig. 7M, N) show similarities to particular specimens of the "fibrous" and "spinose" components, respectively, of a radula-like apparatus from the early Cambrian Mahto Formation (cf. Butterfield 2008: figs. 4.1, 6.12). None of the triangular/ hook-shaped KMA spines (with the exception of Fig. 7M) exhibits an obvious aperture, which suggests that any similarity in outline to conodontiform fossils or the sclerites of halkieriids and siphogonuchitids (e.g., Qian and Bengtson 1989) is likely to be superficial.

Arthropod cuticle is surprisingly rare in the KMA given the prominence of this group among the Kaili macrofossils (e.g., Zhao et al. 2005). Possible fragmentary remains include a seta-like form with secondary setules (Fig. 7P), and a fan of branching filaments (Fig. 7Q) that superficially resembles a crustacean "filter plate" as described from the Mount Cap Formation (Harvey and Butterfield 2008), although the diagnostic fine-scale pattern of setulation is lacking. Neither specimen resembles the previously figured fragment of a "possible metazoan (Arthropoda?)" (Yin et al. 2009: 111, fig. 3n) which is a thick-walled fragment with a serrated edge.

Finally, two specimens, each of distinctive and so far unique morphology—an articulated series of six lobes with finely branching filaments (Fig. 7R) and a structure composed in part from overlapping scales (Fig. 7S)—suggest that future processing may yield further interesting forms.

A new window onto the Kaili biota

Just as the non-biomineralizing Kaili macrofossils augment an otherwise typical Cambrian shelly biota (e.g., Zhao et al. 1994a, 1999a, 2005; Lin 2009), the Kaili microfossils provide a new dimension of palaeobiological detail. A comparison with previous palynological studies (Yin and Yang 1999; Yang and Yin 2001; Yin et al. 2009, 2010) suggests that a gentle preparation technique is required to tease out the full diversity of Kaili microfossils (though our use of a relatively coarse filter and hand picking introduces its own bias against small forms). Our preliminary results provide the first evidence in the Kaili Formation for pterobranchs, and hint at the presence of meiofaunal priapulids, radula-bearing molluscs and other "jawed" lophotrochozoans. Shelly Cambrian fossils are preserved as robust, acid-extractable films, providing the second documented record of this taphonomic phenomenon, and confirming its distinctive contribution to the histological reconstruction of extinct modes of biomineralization. There is obvious untapped potential in the targeted extraction of carbonaceous components from specific Kaili brachiopods, in particular.

Many of the Kaili microfossils add to an emerging "syndrome" of widespread, long-ranging forms with no discernable bioprovinciality, presumably reflecting some degree of evolutionary/biogeographic signal (see Conway Morris 1989) combined with the homogenizing influence of differential decay. Some elements of the KMA are distinctive, however, and point to future discoveries via localized occurrences. The spiny cuticles, for example, are of moderate abundance and represent either a new view onto a known Kaili worm or the first record of a new one. The conspicuous consistency of the size and ornamentation of the specimens suggests a shared taphonomic "behaviour" stemming from the preferential preservation of a particular body part and/or growth stage. Interestingly, a similar level of taphonomic specificity (but with different effects) has been implicated in the small-scale phosphatization of Cambrian worms (e.g., Dong et al. 2010). Clearly, all modes of preservation will be biased, but only by examining additional modes can we hope to identify the biases and control for them.

Implications for "Burgess Shale-type" preservation

The Kaili macrobiota qualifies as an example of "Burgess Shale-type" (BST) preservation (sensu Butterfield 1995) by virtue of its "exceptional" information content and its expression as carbonaceous compressions in a fully marine siliciclastic setting. The Kaili occurrence is temporally intermediate between older BST biotas, most notably the Chengjiang, and the Burgess Shale itself (e.g., Zhu et al. 2006). It has also been viewed as taphonomically intermediate, because it is less weathered than the Chengjiang and less metamorphosed than the Burgess Shale, and indeed the Kaili macrofossils preserve more of their original carbona-

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ceous expression (Lin and Briggs 2010). That said, the recovery of "Burgess Shale-type" microfossils in the KMA provides the opportunity for a complementary analysis of the fine-scale preservation, which reveals a more nuanced pattern of carbonaceous taphonomy.

Extractable microfossils from the Burgess Shale are comparatively uncommon, black in colour and mostly cracked or otherwise deformed (Butterfield 1990a, b; Gostlin 2006). This is consistent with the volatization/oxidation of organic matter during greenschist-grade metamorphism of the host rocks (see Butterfield et al. 2007). By contrast, the host rocks of the Chengjiang biota have been subject to intense weathering and have yet to yield any carbonaceous microfossils (NJB unpublished data). The Kaili, however, managed to avoid the extremes of both deep burial and prolonged exposure, thereby facilitating the preservation of abundant microfossils with limited metamorphic alteration.

Despite this fortuitous post-preservational history, it is worth noting the presence of a fine-scale fabric of surface "corrosion" that characterizes almost all of the Kaili microfossils (see Figs. $2A_2$, 5A, K, L, $7G_2$)—in contrast to the much finer-scale detail preserved in, for example, many of the Mount Cap arthropod fossils (Butterfield 1994; Harvey and Butterfield 2008). Given the low thermal maturity of the Kaili specimens, this texture was clearly acquired in early diagenesis—during the preservational process itself. As such, there is little likelihood of the Kaili preserving very fine cuticular features, even if they were originally present. Indeed, the KMA is dominated by fairly recalcitrant taxa and body parts, with only rare examples of more "labile" tissues, such as the unsclerotized background cuticle of the priapulid scalid array (Fig. 5A) and the putative arthropod setae with setules (Fig. 7P, Q). Like all fossil assemblages, the Kaili microbiota has been taphonomically filtered (not least, during our processing procedure), and it is important to appreciate that the individual filters are rarely the same. Even so, these data shed important new light on the taxonomic, environmental and biogeographic distribution of Cambrian life midway between the Chengjiang and Burgess Shale.

Acknowledgements

We thank Patricia Morse (Friday Harbour Laboratories, Washington, USA) for her permission to reprint figures of *Meiopriapulus*, and Uwe Balthasar (University of Glasgow, Glasgow, UK), Christian B. Skovsted (Swedish Museum of Natural History, Stockholm, Sweden) and Oldřich Fatka Fatka (Charles University, Prague, Czech Republic) for valuable reviews. We gratefully acknowledge the following sources of funding: a NERC studentship, a Palaeontological Association travel grant, and Selwyn and Sidney Sussex colleges, Cambridge (THPH); CONACYT (Consejo Nacional de Ciencia y Tecnología), the University of Cambridge Trusts and Darwin College, Cambridge (JO-H); the Project-Oriented Hundred Talents Programme of the Chinese Academy of Sciences (KZCX2-YW-BR-23) (J-PL); and NERC grant NE/H009914/1 (NJB).

References

Adrianov, A.V. and Malakhov, V.V. 2001. Symmetry of priapulids (Priapulida). 1. Symmetry of adults. *Journal of Morphology* 247: 99–110.

Balthasar, U. and Butterfield, N.J. 2009. Early Cambrian "soft-shelled" brachiopods as possible stem-group phoronids. *Acta Palaeontologica Polonica* 54: 307–314.

Banta, W.C. and Rice, M.E. 1976. A restudy of the Middle Cambrian Burgess Shale fossil worm, *Ottoia prolifica*. *In*: M.E. Rice and M. Todorovic (eds.), *Proceedings of the International Symposium on the Biology of the Sipuncula and the Echiura, Vol. 2*, 79–90. Naucno Delo, Belgrade.

Bartley, J.K. 1996. Actualistic taphonomy of cyanobacteria: implications for the Precambrian fossil record. *Palaios* 11: 571–586.

Bengtson, S. 1983. The early history of the Conodonta. *Fossils and Strata* 15: 5–19.

Bengtson, S. and Urbanek, A. 1986. *Rhabdotubus*, a Middle Cambrian rhabdopleurid hemichordate. *Lethaia* 19: 293–308.

Butterfield, N.J. 1990a. Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* 16: 272–286.

Butterfield, N.J. 1990b. A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* 16: 287–303.

Butterfield, N.J. 1994. Burgess Shale-type fossils from a Lower Cambrian shallow-shelf sequence in northwestern Canada. *Nature* 369: 477–479.

Butterfield, N.J. 1995. Secular distribution of Burgess-Shale-type preservation. *Lethaia* 28: 1–13.

Butterfield, N.J. 1996. Fossil preservation in the Burgess Shale: reply. *Lethaia* 29: 109–112.

Butterfield, N.J. 2008. An early Cambrian radula. *Journal of Paleontology* 82: 543–554.

Butterfield, N.J. and Nicholas, C.J. 1996. Burgess Shale-type preservation of both non-mineralizing and 'shelly' Cambrian organisms from the Mackenzie Mountains, northwestern Canada. *Journal of Paleontology* 70: 893–899.

Butterfield, N.J., Knoll, A.H., and Swett, K. 1994. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. *Fossils and Strata* 34: 1–84.

Butterfield, N.J., Balthasar, U. and Wilson, L.A. 2007. Fossil diagenesis in the Burgess Shale. *Palaeontology* 50: 537–543.

Conway Morris, S. 1977. Fossil priapulid worms. *Special Papers in Palaeontology* 20: 1–95.

Conway Morris, S. 1985. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Philosophical Transactions of the Royal Society of London B* 307: 507–582.

Conway Morris, S. 1989. The persistence of Burgess Shale-type faunas: implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh* 80: 271–283.

Conway Morris, S. and Robison, R.A. 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. *University of Kansas Paleontological Contributions* 112: 1–48.

Dong, X.-P., Bengtson, S., Gostling, N.J., Cunningham, J.A., Harvey, T.H.P., Kouchinsky, A., Val'kov, A.K., Repetski, J.E., Stampanoni, M., Marone, F., and Donoghue, P.C.J. 2010. The anatomy, taphonomy, taxonomy and systematic affinity of *Markuelia*: Early Cambrian to Early Ordovician scalidophorans. *Palaeontology* 53: 1291–1314.

Durman, P.N. and Sennikov, N.V. 1993. A new rhabdopleurid hemichordate from the Middle Cambrian of Siberia. *Palaeontology* 36: 283–296.

Gaines, R.R., Briggs, D.E.G., and Zhao, Y. 2008. Cambrian Burgess Shale-type deposits share a common mode of fossilization. *Geology* 36: 755–758.

Gostlin, K.E. 2006. *Sedimentology and Palynology of the Middle Cambrian Burgess Shale*. 245 pp. Unpublished Ph.D. thesis, Department of Geology, University of Toronto.

Han, J., Yang, Y., Zhifei, Z., Liu, J., and Shu, D. 2007. New observations on

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the palaeoscolecid work *Tylotites petiolaris* from the Cambrian Chengjiang Lagerstätte, south China. *Paleontological Research* 11: 59–69.

Harvey, T.H.P. 2010. Carbonaceous preservation of Cambrian hexactinellid sponge spicules. *Biology Letters* 6: 834–837.

Harvey, T.H.P. and Butterfield, N.J. 2008. Sophisticated particle-feeding in a large Early Cambrian crustacean. *Nature* 452: 868–871.

Harvey, T.H.P., Dong, X., and Donoghue, P.C.J. 2010. Are palaeoscolecids ancestral ecdysozoans? *Evolution and Development* 12: 177–200.

Holmer, L.E. and Caron, J.-B. 2006. A spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica* 87: 273–290.

Horodyski, R.J. and Donaldson, J.A. 1980. Microfossils from the Middle Proterozoic Dismal Lakes Group, Arctic Canada. *Precambrian Research* 11: 125–159.

Huang, Y.-Z., Wang, H.-Y., Zhao, Y.-L., and Dai, X.-C. 1994. Brachiopods from Early–Middle Cambrian Kaili Formation in Taijiang, Guizhou [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 33: 335–344.

Huang, D.-Y., Vannier, J., and Chen, J.-Y. 2004a. Anatomy and lifestyles of Early Cambrian priapulid worms exemplified by *Corynetis* and *Anningvermis* from the Maotianshan Shale (SW China). *Lethaia* 37: 21–33.

Huang, D.-Y., Chen, J.-Y., Vannier, J., and Saiz Salinas, J.I. 2004b. Early Cambrian sipunculan worms from southwest China. *Proceedings of the Royal Society of London B* 271: 1671–1676.

Knoll, A.H., Swett, K., and Mark, J. 1991. Paleobiology of a Neoproterozoic tidal flat/lagoonal complex: the Draken Conglomerate Formation, Spitzbergen. *Journal of Paleontology* 65: 531–570.

Kozłowski, R. 1947. Les affinités des graptolithes. *Biological Reviews* 22: 93–108.

Lin, J.-P. 2009. Review of the depositional environment of the Kaili Formation (Cambrian Series 2–3 boundary interval: China). *Memoirs of the Association of Australasian Palaeontologists* 37: 131–149.

Lin, J.-P. and Briggs, D.E.G. 2010. Burgess Shale-type preservation: a comparison of naraoiids (Arthropoda) from three Cambrian localities. *Palaios* 25: 463–467.

Maas, A., Waloszek, D., Haug, J.T., and Müller, K.J. 2007. A possible larval roundworm from the Cambrian 'Orsten' and its bearing on the phylogeny of Cycloneuralia. *Memoirs of the Association of Australasian Palaeontologists* 34: 499–519.

Maas, A., Waloszek, D., Haug, J.T., and Müller, K.J. 2009. Loricate larvae (Scalidophora) from the Middle Cambrian of Australia. *Memoirs of the Association of Australasian Palaeontologists* 37: 281–302.

Maletz, J., Steiner, M., and Fatka, O. 2005. Middle Cambrian pterobranchs and the question: what is a graptolite? *Lethaia* 38: 73–85.

Mankiewicz, C. 1992. *Obruchevella* and other microfossils in the Burgess Shale: preservation and affinity. *Journal of Paleontology* 66: 717–729.

Mao, J.-R., Zhao, Y.-L., and Yu, P. 1994. Noncalcareous algae of Kaili Fauna in Taijiang, Guizhou [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 33: 345–349.

Martí Mus, M. and Bergström, J. 2007. Skeletal microstructure of helens, lateral spines of hyolithids. *Palaeontology* 50: 1231–1243.

Morse, M.P. 1981. *Meiopriapulus fijiensis* n. gen., n. sp.: an interstitial priapulid from coarse sand in Fiji. *Transactions of the American Microscopical Society* 100: 239–252.

Page, A., Gabbott, S.E., Wilby, P.R., and Zalasiewicz, J.A. 2008. Ubiquitous Burgess Shale-style "clay templates" in low-grade metamorphic mudrocks. *Geology* 36: 855–858.

Porter, S.M. 2008. Skeletal microstructure indicates chancelloriids and halkieriids are closely related. *Palaeontology* 51: 865–879.

Powell, W. 2003. Greenschist-facies metamorphism of the Burgess Shale and its implications for models of fossil formation and preservation. *Canadian Journal of Earth Sciences* 40: 13–25.

Qian, Y. and Bengtson, S. 1989. Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* 24: 1–156.

Rice, M.E. 1993. Sipuncula. *In*: F.W. Harrison and M.E. Rice (eds.), *Microscopic anatomy of invertebrates, Volume 12: Onychophora, Chilopoda, and Lesser Protostomata*, 237–325. Wiley-Liss, New York.

Saiz Salinas, J.I. 1995. Sipuncula of the southeastern Weddell Sea (Antarctica). *Polar Biology* 15: 307–317.

Schmidt-Rhaesa, A. 1998. Phylogenetic relationships of the Nematomorpha —a discussion of current hypotheses. *Zoologischer Anzeiger* 236: 203–216.

Sergeev, V.N., Knoll, A.H., and Grotzinger, J.P. 1995. Paleobiology of the Mesoproterozoic Billyakh Group, Anabar Uplift, Northern Siberia. Paleontological Society Memoir 39. *Journal of Paleontology* 69 (Supplement to No. 1): 1–37.

Shirley, T.C. and Storch, V. 1999. *Halicryptus higginsi* n.sp. (Priapulida): a giant new species from Barrow, Alaska. *Invertebrate Biology* 118: 404–413.

Skovsted, C.B. and Peel, J.S. 2001. The problematic fossil *Mongolitubulus* from the Lower Cambrian of Greenland. *Bulletin of the Geological Society of Denmark* 48: 135–147.

Stephen, A.C. and Edmonds, S.J. 1972. *The Phyla Sipuncula and Echiura*. 528 pp. Trustees of the British Museum (Natural History), London.

Steiner, M. and Fatka, O. 1996. Lower Cambrian tubular micro- to macrofossils from the Paseky Shale of the Barrandian area (Czech Republic). *Paläontologische Zeitschrift* 70: 275–299.

Storch, V., Higgins, R.P., and Morse, M.P. 1989. Ultrastructure of the body wall of *Meiopriapulus fijiensis* (Priapulida). *Transactions of the American Microscopical Society* 108: 319–331.

Théel, H. 1911. Priapulids and sipunculids dredged by the Swedish Antarctic Expedition 1901–1903 and the phenomenon of bipolarity. *Kungliga Svenska Vetenskaps Akademiens Handlingar* 47: 1–36.

Topper, T.P., Skovsted, C.B., Brock, G.A., and Paterson, J.R. 2007. New bradoriids from the lower Cambrian Mernmerna Formation, South Australia: systematics, biostratigraphy and biogeography. *Memoirs of the Association of Australasian Palaeontologists* 33: 67–100.

Van der Land, J. 1970. Systematics, zoogeography, and ecology of the Priapulida. *Zoologische Verhandelingen* 112: 1–118.

Walcott, C.D. 1919. Cambrian geology and paleontology IV, No. 5—Middle Cambrian algae. *Smithsonian Miscellaneous Collections* 67: 217–260.

Wills, M.A. 1998. Cambrian and Recent disparity: the picture from priapulids. *Paleobiology* 24: 177–199.

Williams, A., Makay, S., and Cusack, M. 1992. Structure of the organophosphatic shell of the brachiopod *Discina*. *Philosophical Transactions of the Royal Society of London B* 337: 83–104.

Williams, A., Cusack, M., and Mackay, S. 1994. Collagenous chitinophosphatic shell of the brachiopod *Lingula*. *Philosophical Transactions of the Royal Society of London B* 346: 223–266.

Williams, S.H., Burden, E.T., and Mukhopadhyay, P.K. 1998. Thermal maturity and burial history of Paleozoic rocks in western Newfoundland. *Canadian Journal of Earth Sciences* 35: 1307–1322.

Yang, R.-D. and Yin, L.-M. 2001. Acritarch assemblages from the Early–Middle Cambrian Kaili Formation of east Guizhou Province and biostratigraphic implications. *Acta Micropalaeontologica Sinica* 18: 55–69.

Yang, R.-D., Mao, J.-R., and Zhao, Y.-L. 2001. New macroalgal fossils from Middle Cambrian Kaili Biota in Guizhou Province, China. *Acta Botanica Sinica* 43: 742–749.

Yin, L.-M. and Yang, R.-D. 1999. Early–Middle Cambrian acritarchs in the Kaili Formation from Taijiang County, Guizhou, China. *Acta Palaeontologica Sinica* 38: 66–78.

Yin, L., Zhu, M., Knoll, A.H., Yuan, X., Zhang, J., and Hu, J. 2007. Doushantuo embryos preserved inside diapause egg cysts. *Nature* 446: 661–663.

Yin, L., Yang, R., Peng, J., and Kong, F. 2009. New data regarding acritarch biostratigraphy from the Early–Middle Cambrian Kaili Formation in Chuandong, Guizhou Province, China. *Progress in Natural Science* 19: 107–114.

Yin, L.-M., Zhao, Y.-L., Yang, R.-D., and Peng, J. 2010. Acritarchs from the Early–Middle Cambrian Kaili Formation in the Wuliu-Zengjiaya Section, east Guizhou Province, China. *Acta Palaeontologica Sinica* 49: 164–173.

http://dx.doi.org/10.4202/app.2011.0028

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Zang, W.-L., Moczydłowska, M., and Jago, J.B. 2007. Early Cambrian acritarch assemblage zones in South Australia and global correlation. *Memoirs of the Association of Australasian Palaeontologists* 33: 141–177.

Zhao, Y.-L., Yuan, J.-L., Huang, Y.-Z., Mao, J.-R., Qian, Y., Zhang, Z.-H., and Gong, X.-Y. 1994a. Middle Cambrian Kaili Fauna in Taijiang, Guizhou [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 33: 263–271.

Zhao, Y.-L., Qian, Y., and Li, X.-S. 1994b. *Wiwaxia* from Early–Middle Cambrian Kaili Formation in Taijing, Guizhou. *Acta Palaeontologica Sinica* 33: 359–366.

Zhao, Y.-L., Yuan, J.-L., Zhu, M.-Y., Yang, R.-D., Guo, Q.-J., Qian, Y., Huang, Y.-Z., and Pan, Y. 1999a. A progress report on research on the early Middle Cambrian Kaili Biota, Guizhou, PRC. *Acta Palaeontologica Sinica* 38 (Supplement): 1–14.

Zhao, Y.-L., Zhu, M.-Y., Guo, Q.-J., and Van Iten, H. 1999b. Worms from the Middle Cambrian Kaili Biota, Guizhou, PRC. *Acta Palaeontologica Sinica* 38 (Supplement): 79–87.

Zhao, Y., Yang, R., Yuan, J., Zhu, M., Guo, Q., Yang, X., and Tai, T. 2001. Cambrian stratigraphy at Balang, Guizhou Province, China: candidate section for a global unnamed series and stratotype section for the Taijiangian Stage. *Palaeoworld* 13: 189–208.

Zhao, Y., Zhu, M., Babcock, L.E., Yuan, J., Parsley, R.L., Peng, J., Yang, X., and Wang, Y. 2005. Kaili Biota: a taphonomic window on diversification of metazoans from the basal Middle Cambrian: Guizhou, China. *Acta Geologica Sinica* 79: 751–765.

Zhao, Y., Yuan, J., Peng, S., Babcock, L.E., Peng, J., Guo, Q., Lin, J., Tai, T., Yang, R., and Wang, Y. 2008. A new section of Kaili Formation (Cambrian) and a biostratigraphic study of the boundary interval across the undefined Cambrian Series 2 and Series 3 at Jianshan, Jianhe County, China with a discussion of global correlation based on the first appearance datum of *Oryctocephalus indicus* (Reed, 1910). *Progress in Natural Science* 18: 1549–1556.

Zhao, Y., Sumrall, C.D., Parsley, R.L., and Peng, J. 2010. *Kailidiscus*, a new plesiomorphic edrioasteroid from the basal Middle Cambrian Kaili Biota of Guizhou Province, China. *Journal of Paleontology* 84: 668–680.

Zhu, M.-Y., Erdtmann, B.-D., and Zhao, Y.-L. 1999. Taphonomy and palaeoecology of the early Middle Cambrian Kaili Lagerstätte in Guizhou, China. *Acta Palaeontologica Sinica* 38 (Supplement): 28–57.

Zhu, M.-Y., Babcock, L.E., and Peng, S.-C. 2006. Advances in Cambrian stratigraphy and paleontology: integrating correlation techniques, paleobiology, taphonomy and paleoenvironmental reconstruction. *Palaeoworld* 15: 217–222.

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