Protomelission is an early dasyclad alga and not a Cambrian bryozoan

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The animal phyla and their concomitant body plans trace their origins to a singular burst of evolution in the Cambrian period, over 500 million years ago[1]. Phylum Bryozoa, the colonial "moss animals", have been the exception: convincing skeletons of this biomineralizing clade have been curiously absent from Cambrian strata, in part because potential bryozoan fossils are difficult to distinguish from the modular skeletons of other animal and algal groups[2,3]. At present, the strongest candidate[4] is the phosphatic microfossil *Protomelission*[5]. Here, we describe exceptionally preserved non-mineralized anatomy in *Protomelission*-like macrofossils from the Xiaoshiba Lagerstätte[6]. Taken alongside the detailed skeletal construction and the potential taphonomic origin of 'zooid apertures', we consider that *Protomelission* is better interpreted as the earliest dasycladalean green alga – emphasizing the ecological role of benthic photosynthesizers in early Cambrian communities. Under this interpretation, *Protomelission* cannot inform the origins of the bryozoan body plan; despite a growing number of promising candidates[7–9], there remain no unequivocal bryozoans of Cambrian age.

Introduction

The phyla – the principal subdivisions of the animal kingdom – had diverged by the start of the Cambrian “explosion”[10]. The origins of their distinctive body plans can be resolved only by reference to the fossil record, as surviving lineages are characterized by rapid early innovation[11] overprinted by half a billion years of subsequent evolution and extinction. The recognition of “extinct phyla” as offshoots of surviving animal lineages[12,13] has uncovered unexpected connections between disparate animal phyla[14,15], and revealed the otherwise unpredictable morphologies that characterize ancestors of modern animal groups[16,17] – cementing the role of the fossil record as a reliable eyewitness to the origins of animal diversity[18].

However, despite the near-simultaneous appearance of other “shelly” bilaterian phyla (Euarthropoda, Mollusca, Brachiopoda and Echinodermata) close to the start of Cambrian Stage 3[12,19,20], Phylum Bryozoa lacks convincing representatives in the Cambrian fossil record. Proposed Cambrian bryozoans are putative[8], disputed[2,9] or discredited[7,21]. Presently, the most compelling candidate is the Stage 3– 4 microfossil *Protomelission*[4,5], whose reinterpretation as a bryozoan[4] would complete the Cambrian roster of mineralizing body plans.

Protomelission gatehousei is a millimetre-scale organism comprising secondarily phosphatized cataphract modules, organized around a central cavity to form a holdfast and an erect axis. The axis is preserved as a bifacial structure, possibly reflecting the early compaction of an originally hollow club-shaped organism. Modules are arranged at 25° to the central cavity, and comprise thin-walled chambers with a small basal aperture on their internal surface; and a large, external distal aperture, whose margin is typically irregular due to breakage, leaving its original shape and size speculative[4,5] – if indeed an aperture was even present before abrasion. The shape, size, and distal opening of modules have been taken to indicate a position in the bryozoan total group[4], but these features are not necessarily sufficient to render this the only, or even the most likely, possible affinity. In fact, the thinness of the walls and the irregular folding of peripheral modules are difficult to square with a bryozoan interpretation[5,22].

Here we compare phosphatized *Protomelission* microfossils previously described from Wirrealpa (five specimens) and Xiaoyangba (one specimen)[4,5] with twelve probable *Protomelission* macrofossils from the Xiaoshiba biota (Cambrian Stage 3).

Results

Our new specimens comprise an originally clavate thallus (Fig. 1a, d, e) and a basal holdfast, which is in some cases attached to an animal shell (Fig. 1d, e, h). Compaction of the thallus is reflected by ridges and wrinkling of its surface (Fig. 1a). Its preservation across two separate surfaces within the matrix (Figs 1b, d, 2a, f, g) reveals the internal and external surfaces of the thallus in juxtaposition. One specimen displays budding or branching (Fig. 1b).

The thallus comprises quincuncially arranged, slightly rounded modules, each around 250 µm long, 200 µm wide (Figs 1–2) and 1 000 µm deep (Fig. 2e). Reflecting their close packing, modules are broadly hexagonal or rhombic in outline, and are slightly elongated parallel to the axis of the thallus. Each module is enclosed by a thin but robust layer associated with elevated concentrations of iron and phosphorous (Fig. 2d; Extended Data Fig. 1), which opens internally with a small (5–8 µm) proximal aperture (Figs 1c, 2i) and externally at a large distal aperture whose irregular outline and size reflects partial survival of the original surface layer (Figs 2a–d, 3b, d–e, h; Extended Data Fig. 1a).

As with the phosphatized Wirrealpa specimens (Fig. 3c, g, j), the nature of the external aperture varies between modules and between specimens, in a manner consistent with abrasion of a delicate external membrane: in many Xiaoshiba (Fig. 3b, i) and Wirrealpa

(Fig. 3c, j) specimens, the majority of the external membrane is absent. Even where the external membrane is at its most complete, the irregular shape, size and position of the sub-elliptical apertures (Fig. 3e, f) do not correspond with the consistent regularity expected of a bryozoan colony, and a taphonomic origin is difficult to dismiss.

On the basis of the close correspondence in construction, size, and arrangement of the modules with those of the Wirrealpa microfossils (Fig. 3a–c, e–j; Extended Data Table 1), we tentatively assign our material to *Protomelission*? sp. – though we stress that any comparison must account for the complementary preservational pathways of the two deposits. The Wirrealpa material was entombed in lime-rich sediment (since removed by acid maceration) and secondarily replaced, soon after death, by phosphate – protecting the material from further compaction[4,23]. Phosphatized deposits tend to contain early developmental stages or fragments of larger organisms[23], reflecting a taphonomic bias towards small (< 5 mm) specimens. In contrast, Xiaoshiba-style preservation entails rapid burial of relatively complete organisms, followed by substantial post-burial compaction. Fossils are exposed by splitting mudstones along planes of weakness, which typically correspond to internal or external fossil surfaces[24].

These preservational differences account for certain differences between the material. Firstly, the Wirrealpa material presents an external view of (sometimes abraded) specimens, whereas the planes of fracture within Xiaoshiba material variously coincide with internal and external surfaces of modules, or divide modules internally. Secondly, the size difference between the deposits (108–160 × 32–43 mm in Xiaoshiba, 1.8–2.2 × 1.0–1.5 mm in Wirrealpa) likely reflects the preservation of larger or more complete specimens in Xiaoshiba – just as palaeoscolecid worms are represented by sub-millimetric fragments of cuticle in Wirrealpa[5] and complete centimetre-scale specimens in Xiaoshiba[25]. The small size of Wirrealpa fragments precludes the recognition of macroscopic features, such as budding.

Most significantly, the best-preserved of our compression fossils additionally preserve non-skeletal tissue, which is never evident in Wirrealpa. Unornamented sub-conical flanges, around 500 µm in length, emerge orthogonally from each module (Figs 1b, f; 2a–e). These structures were originally labile, denoted by depletion in iron and phosphorous (Fig. 2d, Extended Data Fig. 1). They are best displayed at the lateral margins of specimens, where they are preserved parallel to the plane of bedding; because they are oriented perpendicular to the plane of splitting in the medial thallus, their full outline is not visible, though the chemical signature of their bases is evident across the thallus (Extended Data Fig. 1b, c). (Analogous preservation is seen in the centripetal sclerites of certain priapulan worms, which can be difficult to distinguish from somatic tissue except at the edges of fossils – e.g. fig. 8 in ref. 14.)

Discussion

Protomelission? flanges lack tentacles or other complex structures, which would be expected if they corresponded to the soft bodies of a colonial metazoan. Regular polygonal modules also characterize the inner surface of certain archaeocyath-like sponges[26], but the largely enclosed nature of *Protomelission* modules and the presence of external flanges are difficult to reconcile with an archaeocyath construction. Rather, *Protomelission*? sp. is more convincingly interpreted as the oldest[21] dasyclad green alga (Extended Data Table 1); a stem-group position is implied by molecular clock estimates (with c. 95% posterior probability) of a post-Cambrian crown-group radiation[27].

We interpret the phosphatized Wirrealpa specimens as representing replacements of skeletal material. Zhang et al.[4] interpret a wrinkled microstructure as indicating an originally non-mineralized composition, but in view of the absence of other non-mineralized elements in the Wirrealpa assemblage[5], we are reluctant to rule out the possibility that the phosphate replaces original calcium carbonate, with the idiosyncratic microstructure reflecting the deposition of carbonate within the algal cell wall or an encompassing mucilage layer, as in extant dasycladaleans[28].

Palaeozoic dasycladaleans such as the cyclocrinitids preserve tessellating modules corresponding to a robust, often calcified layer that surrounds lateral branches that emerge from a central cavity. Each such module exhibits a small basal aperture opening into the central cavity, and a larger distal opening from which a non-mineralized flange emerges[3,29], corresponding to the structures seen in our compression fossils (Figs 1–2). As with many fossil dasyclads[30], gametophores are not preserved in *Protomelission* – potentially signifying that the fossil material represents vegetative stages, or an endospore taxon.

A subset of phosphatic microfossils assigned to Cambroclavida[31] – a problematic early–mid Cambrian group restricted to open marine environments within the photic zone[32] – also comprise articulated arrays of hollow modules with taphonomically abraded distal openings (Fig. 3d, k, l; Extended Data Table 1). In certain taxa, these openings correspond to the base of a compositionally distinct conical flange[33,34]. The parallel morphology hints that at least some cambroclaves may represent more heavily skeletonized relatives of *Protomelission*-like dasycladaleans, potentially extending the record of these algae to span the stratigraphic gaps between *Protomelission* and other putative[35] Cambrian dasyclads[3,21].

Taken together, this indicates that benthic algae had a greater role in Cambrian communities than previously appreciated. Whereas eukaryotic macroalgae have been a significant component of benthic ecosystems since at least the Ediacaran[36], they account for a small proportion of the biomass and diversity in most Burgess Shale-type settings[37–42] (particularly after excluding 'algal' taxa now assigned to cyanobacteria or hemichordates[43,44]). Whereas photosynthetic microorganisms exploited changing ocean chemistry to secrete carbonates from the base of the Cambrian[45], *Protomelission* potentially indicates an onset of mineralization in macroalgae broadly coincident with the proliferation of animal body plans, and the concomitant ecosystem shifts, at the opening of Cambrian Age 3.

Whether or not our compression fossil material ultimately proves synonymous with secondarily phosphatized *P. gatehousei*[4,5], it demonstrates that the suite of features used to assign *Protomelission* to Bryozoa do not exclusively characterize that group (Extended Data Table 1): a bryozoan affinity can be considered tentative at best. A growing number of Cambrian fossils, including *Protomelission*, the Harkless bryomorph[8], *Pywackia*[9], the overlooked cambroclave *Deltaclavus*[31], and the disfavoured[2,21] *Cambroporella* and *Archaeotrypa*[7], display characteristics that might be reconciled with a bryozoan affinity – but on the basis of presently available material, no taxon can be interpreted with sufficient certainty to document a pre-Ordovician origin of Bryozoa. Taken alongside the early origin of poriferan-like[46] and cnidarian-like fossils[47,48] and the continued absence of multiple extant phyla across ever more modes of exceptional fossil preservation[49–51], the origin of bilaterian body plans need not necessarily be compressed into a unique period in the heat of the Cambrian ‘explosion’.

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Figure legends

Figure 1 | *Protomelission*-like dasyclad algae from Xiaoshiba. a–c, YKLP 12446, large thallus with bud, showing inner and outer surfaces (at bottom and top of panel, respectively); **b**, enlargement of area *B* in a, showing budding structure with lateral flanges (white arrows);

c, enlargement of area *C* in a; inner surface of thallus, showing regular arrangement of individual modules with regularly situated fine holes (arrows); **d**, YKLP 12447, showing clavate form and attachment to brachiopod shell; **e**, YKLP 12448, complete specimen attached to indeterminate shell fragment (orange arrow), showing lateral flanges (white arrows); **f**, YKLP 12449, showing inner surface of thallus, with lateral profile of marginal modules (white arrows), and flanges extending centripetally into matrix (orange arrows); **g**, YKLP 12447; enlargement of area *G* in d, showing inner surface of thallus with regularly situated fine holes (arrows); **h**, YKLP 12450, two specimens anchored by holdfasts (arrow) to a brachiopod shell.

Figure 2 | Preservation of *Protomelission*? sp. a–e, YKLP 12451: **a**, entire specimen, showing outer surface (on right), poorly preserved inner surface (on left), and lateral section (box *E*); **b**, enlargement of area *B* in a, showing lateral aspect of modules and flanges (arrowed); **c**, fluorescence photograph of area *B* in a, showing flanges; **d**, energy dispersive X-ray spectrograph showing iron abundance in area *B* in a: abundance elevated in module walls, and depressed relative to the matrix in flanges; **e**, enlargement of area *E* in a, showing lateral aspect of modules, and flanges (arrows); **f–g**, YKLP 12452, external surface (majority of f) juxtaposed with internal surface (g); in which fine holes occur at bases of each module (arrows); **h–i**, YKLP 12453, displaying internal surface of thallus.

Figure 3 │ Comparison of the Xiaoshiba *Protomelission*? sp. with Wirrealpa *P. gatehousei* and the Cambroclavid *Deltaclavus graneus*. a–b, Xiaoshiba *Protomelission*? YKLP 12446, 12451, showing cataphract module arrangement; **a**, outer membrane largely intact; **b**, taphonomically expanded apertures perforate the partially preserved membrane (arrows). **c**, Wirrealpa *P. gatehousei* SADME 10470, showing equivalent preservational pattern. **d**, *Deltaclavus* IAGS-BC-88-30181, showing cataphract module arrangement; taphonomically expanded apertures perforate the partially preserved membrane. **e–f** Xiaoshiba *Protomelission*? YKLP 12454: **e**, specimen with most complete preservation of external membrane; **f**, enlargement of area *F* in e shows irregularly located apertures (white arrows) in thin outer membrane of modules, with inconsistent size and shape, and similar damage lying across the boundaries of modules (orange arrows), presumably of taphonomic origin. **g**, Wirrealpa *P. gatehousei* SADME 10470-3; and **h**, Xiaoshiba *Protomelission*? YKLP 12452: both showing flat inner surface of modules with small basal aperture (arrows). In g, modules of the facing surface (white arrows) do not leave an impression on the inner surface of opposing modules, consistent with their separation, as in h (white arrows), by a central cavity in life, prior to compaction. **i**, Xiaoshiba *Protomelission*? YKLP 12451; enlargement of box 3I in Fig. 2a; and **j**, Wirrealpa *P. gatehousei* SADME 10470-2, both showing three-dimensional relief of outer surface, with apertures (asterisks) enclosed by partially preserved membrane (arrows). **k**, *Deltaclavus* IAGS-BC-88-30181, lateral view showing lateral profile of modules. **l**, *Deltaclavus* IAGS-BC-88-30178, showing three-dimensional relief of outer surface, with apertures (asterisks) enclosed by bounding ridge (arrows). Images of *Deltaclavus* courtesy S. Conway Morris; images of Wirrealpa *Protomelission* reproduced from ref. 4 under license (https://creativecommons.org/licenses/by/4.0/).

Methods

Twelve specimens from the Xiaoshiba biota were collected from outcrop of the Hongjingshao Formation, near Kunming, dated to the *Yunnanocephalus–Chengjiangaspis–Hongshiyanaspis* biozone, lower Canglangpuan Stage, Cambrian Series 2, Stage 3)[6,52]. Specimens were imaged under visible light under a LEICA M205-C stereomicroscope; and with fluorescence photography using a LEICA DFC 7000T monochrome digital camera attached to a LEICA

M205 FA fluorescence stereomicroscope under visible light. Backscatter electron microscopy and energy-dispersive X-ray spectroscopy were conducted using a FEI Quanta 650 scanning electron microscope under low vacuum and a 30 kV accelerating voltage.

Statistics and Reproducibility. Photographs and micrographs have been selected after examination of all available material in order to best represent the features under description.

Data availability. Specimens are accessioned at the Institute of Palaeontology, Yunnan University (YKLP12436–42).

Code availability. No custom software or code was used in this study.

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Competing interests. The authors declare no competing interests.

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Extended Data Figure 1 │ Elemental abundances in *Protomelission*? sp. Reflected light, backscatter electron, and energy-dispersive X-ray spectroscopy images of **a**, central thallus of YKLP 12451, corresponding to region 3I in Fig. 2a; **b–c**, flanges at thallus margin in **b**, YKLP 12451, corresponding to region B of Fig. 2a; **c**, YKLP 12446, corresponding to region of Fig. 1b.

Extended Data Table 1 | Anatomical comparison between *Protomelission* and possible relatives. Comparison of pertinent morphological features in *Protomelission gatehousei* from Wirrealpa and Xiaoyangba[4,5], *Protomelission*? sp. from Xiaoshiba (this study), the cambroclave *Deltaclavus*[31], and representatives of the dasycladalean algae and Bryozoa. Bold type emphasizes differences from the bryozoan body plan.