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Late Cambrian *Pywackia* is a cnidarian, not a bryozoan: Insights from skeletal microstructure

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Abstract.—The phylum Bryozoa had long been the only major phylum unknown from the Cambrian and by inference the Cambrian Explosion of biodiversity. When described in 2010 as a late Cambrian cryptostome bryozoan, *Pywackia baileyi* Landing in Landing et al., 2010 became the oldest known bryozoan (early Cambrian bryozoans have since been described). Controversy remains about the phylum-level identification of *Pywackia* Landing in Landing et al., 2010—one study proposed an interpretation of *Pywackia* as an octocoral. No previous studies of the skeletal microstructure of *Pywackia* have employed the analysis of petrographic thin sections and high-magnification scanning electron microscopy. These two methods, with the addition of data from previous studies, are employed in this analysis of skeletal microstructure, a feature often important for higher-level taxonomic identification. Although many candidate groups were considered, *Pywackia*'s distinctive pillar and laminae, porous skeleton like many Cnidaria, topology of the body walls, and growth of modules are consistent with a cnidarian affinity. *Pywackia* skeletons with primary microstructure were 100% phosphate mineral and were collected from a setting of pervasive phosphatic replacement, which leaves uncertainty as to the original skeletal composition. *Pywackia* is not assigned here to a cnidarian class and likely represents an early, rare, short-lived cnidarian evolutionary group.

Introduction

The monospecific genus *Pywackia* was described by Landing in Landing et al. (2010) as a late Cambrian bryozoan but is here recognized as a cnidarian without further taxonomic assignment. The search for a bona fide Cambrian bryozoan has a long history (150+ years) because it was the only major skeletonized phylum not known from the Cambrian and by inference was not represented in the 'Cambrian Explosion' (Taylor et al., 2013; Landing et al., 2018). Taylor et al. (2013) summarized a series of purported Cambrian bryozoan occurrences, each of which was later dismissed. Recent discoveries described as lower Cambrian bryozoans (Zhang et al., 2021; Pruss et al., 2022) are currently under review (e.g., Yang et al., 2023). Landing et al. (2010) proposed *Pywackia* as a late Cambrian Bryozoa, 8.3 Myr older than the undisputed Early Ordovician material from China (Xia et al., 2007; Ma et al., 2014, 2015, 2022). With their assertion of a bryozoan identification of *Pywackia* (Landing et al., 2010), all major skeletonized phyla would be represented by the Cambrian fauna. This assertion received considerable attention in the popular science media and led to rapid updating of the taxonomic range for the phylum in metadatabases, e.g., WoRMS (World Register of Marine Species, https://www.marinespecies.org/).

Taylor et al. (2013) disputed the bryozoan affinity of *Pywackia* and suggested instead that it was an octocoral, with morphologic similarities to some pennatulate corals. However, with a 400 Myr gap between *Pywackia* and the first occurrence of pennatulaceans, Taylor et al. (2013) did not assign *Pywackia* to the order Pennatulacea. Landing et al. (2015) defended the bryozoan assignment and dismissed the pennatulate coral interpretation. Recently, Zhang et al. (2021) described a convincing bryozoan specimen from the early Cambrian. This discovery removes some of the heat from the discussion as to whether *Pywackia* is the oldest bryozoan, but it does not resolve the important question of *Pywackia*'s phylum-level assignment.

The goal of this paper is, for the first time, to incorporate the study of thin sections and scanning electron microscopic (SEM) imaging of skeletal microstructure into the taxonomic assignment of the late Cambrian specimens of *Pywackia*. These procedures are routine in the study of stenolaemate bryozoans (Boardman, 1983) and evaluation of skeletal microstructure is important for comparison among broader groups (e.g., Majewske, 1974). By following these procedures, we were able to confirm a cnidarian identification.

Materials and methods

All material studied was collected by Ed Landing (New York State Museum, retired) from a type section of the Tiñu Formation, Yudachica Member, upper Cambrian, near Río Salinas

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village, Oaxaca State, Mexico (Sour-Tovar, 1990; Landing et al., 2007, figs. 1, 2). Acid dissolution methods for extracting the phosphatic material from the bulk limestone were summarized by Landing et al. (2007). From the New York State Museum (NYSM) in Albany, we borrowed three deep-well micropaleontology slides, each with ~50 *Pywackia* specimens of various sizes and degrees of preservation. The slides contain specimens from three stratigraphic intervals (old NYSM catalog numbers Tu-2.05 [studied by Taylor et al., 2013], Tu-4.3, and Tu-4.95). Six specimens were selected for SEM analysis (low vacuum, uncoated) and photographed with a Keyence 3D Digital Microscopy System: NYSM E5072 1 Tu, E5072 2 Tu, E5072 3 Tu, E5072 4 Tu, E5072 5 Tu, and E5072 6 Tu. Four specimens selected for thin sectioning were epoxy embedded, cut, and polished: NYSM E5072 7 Tu-4.95, E5074 8 Tu, E5074 9 Tu, and E5074 10 Tu. Additional unpicked acid-residue material, including *Pywackia* from the type locality, is reportedly available in the Stratigraphic Collections of the National Museum of Natural History, Washington, D.C. (personal communication, R.A. Robison, 2020) but was not examined during this study.

Morphological terminology has been updated here from Landing et al. (2010, 2015) to reflect a cnidarian assignment.

Repositories and institutional abbreviations.—Types and all other *Pywackia* specimens examined during this study are deposited in the New York State Museum, Albany (NYSM). Figured specimens of *Lituaria* cited by Taylor et al. (2013) are deposited in the Raffles Museum, Singapore.

Systematic paleontology

Phylum Cnidaria Hatschek, 1888
Class, Order, and Family indet.
Genus *Pywackia* Landing in Landing et al., 2010
Figures 1, 2, 3.1

Type species.—*Pywackia baileyi* Landing in Landing et al., 2010 from the upper Cambrian *Cordylodus andresi* Biozone, Tiñu Formation (lower Yudachica Member) near Río Salinas, Oaxaca State, Mexico (only known occurrence). Type specimen: NYSM 13515 (Landing et al., 2010, fig. 2K) from sample Tu-4.95.

Diagnosis.—Cylindrical to spindle-formed, stem-like, nonbifurcating colonies of linear to helically emplaced polygonal modules, constructed entirely of thin walls (no axial core, modular or skeletal). Mature primary modules have imperforate vertical walls that are longitudinally crenulated (growth bands) and locally thickened at colony exteriors, club-like in section. The skeletal microstructure of all walls is porous, with radiating pillars in layers that are bilaterally symmetrical with arcs peaking at the medial wall. Most walls also have enveloping, exterior, massive skeletal layers that can also be present as symmetrical growth checks in wall tips. Medial layers are not present in walls. Skeletal composition was either phosphatic or calcareous (calcite/aragonite), completely replaced by a phosphate mineral.

Complete colonies display three developmental zones. The distal end is rounded, with modules budding in a linear to helical arrangement, with immature modules that are oval to polygonal, with slightly convex to straight to weakly concave sides. The colony propagates through budding at the distal margin but does not grow indefinitely. In the middle primary region, modules grow radially from the axis and are typically six-sided with a flared, broadly elliptical to circular opening. Vertical lateral walls are smooth and imperforate but often display growth bands (crenulations on module walls with varying degrees of development). Short median ridges present in the base of some modules are a by-product of budding new modules from a basal wall. Irregularly placed partitions of short, vertical skeletal walls are present in some primary modules but are not regularly placed as deterministic partitions (e.g., not septa or diaphragms). Early growth stages (immature) modules are present at budding zones of secondary budding, but no polymorphs were observed.

Proximal colony end is attenuated, spike-like, flat to triangular in cross section, with very immature, elongated modules present, too shallow to house polyps. In a number of specimens, protomodules (elongate with incipient lateral walls, e.g., Landing et al., 2015, figs. 1.4, 2.2, 4) extend proximally, well beyond the lowermost, first complete module. This suggests proximal growth during later development in larger colonies. Neither colony axis nor walls are thickened in the proximal zone. Holdfasts are absent; pointed proximal end might have stuck into soft sediment.

Diagnosis emended from Landing et al. (2010, 2015).

Remarks.—Landing et al. (2010, 2015) recognized 14-hedron budding as an important characteristic of *Pywackia*. We did not find this a practical feature for specimen description.

Diagenetic alteration is common on the interior of walls, resulting in pervasive bands of silica, iron minerals, or recrystallized phosphate mineral. Altered interior walls can be misinterpreted as medial walls, but they are clearly variable in placement and not systematically medial.

A cnidarian affinity for *Pywackia*

Colony, module shape, and budding.—A line of support for *Pywackia* as a cnidarian is the overall radial (spindle, rod) shape of the colony (Williams, 2011, fig. 1 for colony shape in Pennatulacea). Colonies are composed entirely of thin walls, with no region of skeletal thickening or presence of axial modules or bundles (Fig. 2.1). The structure is reminiscent of radial, unfolded, thin geometric paper, such as that found in holiday table decorations (Supplemental Fig. 2.4).

Modules grow in two directions. They are budded at the rounded distal end, extending the colony through elongation (Fig. 2.2). No *Pywackia* specimens are exceptionally long (maximum 40 mm; Taylor et al., 2013), so their size is not entirely indeterminant. In contrast, mature specimens bud frontally, away from the colony axis (Fig. 1.6B). This implies that the soft parts (polyps) have a determinant size (~0.30 mm) and life cycle. Basal thickening then thinning of walls indicates mature *Pywackia* colonies that exhibit secondary (frontal)
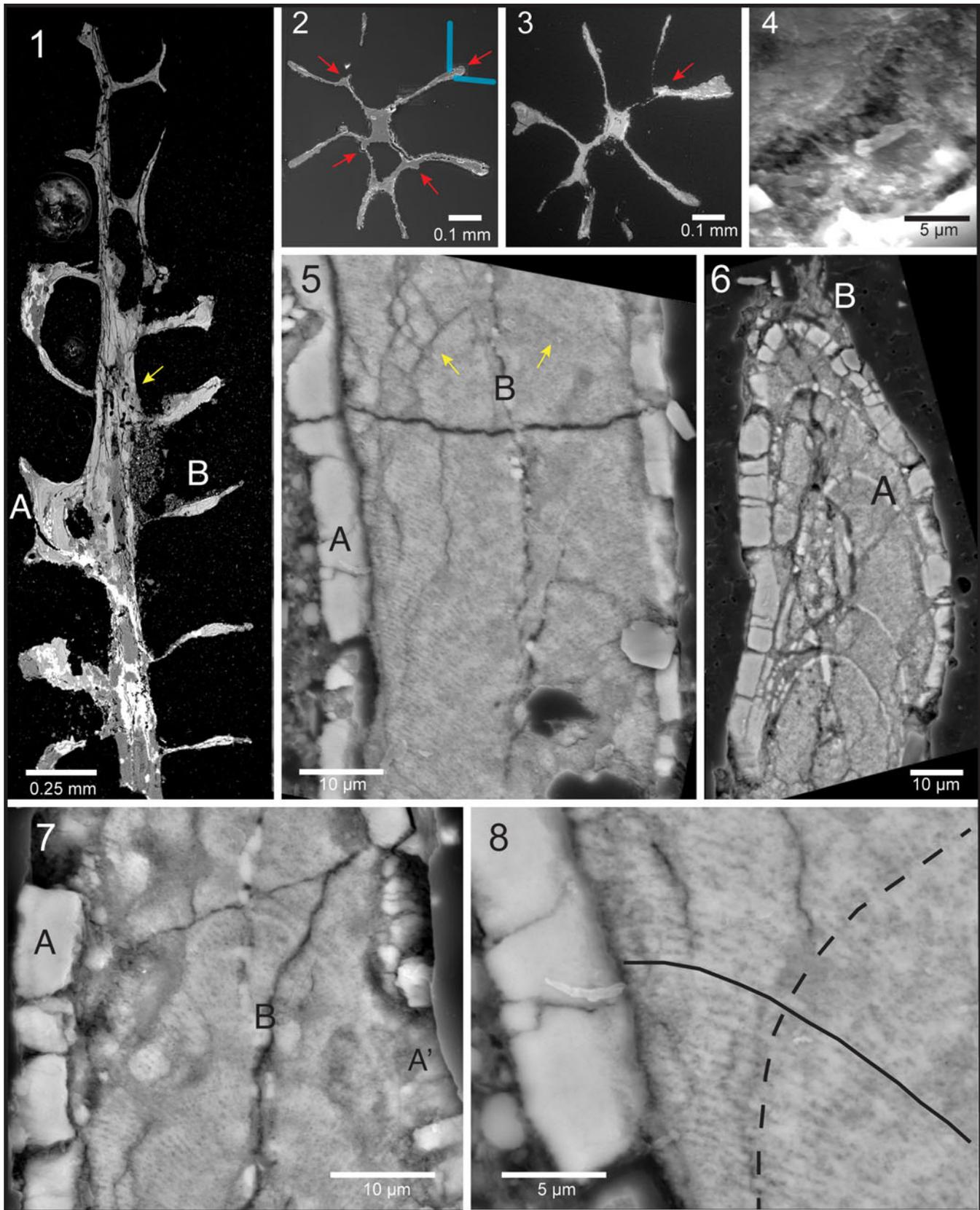
Figure 1. Interior views of *Pywackia*. All walls are thin; broader-appearing walls are oriented longitudinally through wall section: (**1–3**) NYSM E5074 8 Tu-205: (**1**) longitudinal section of a diagenetically altered colony; longitudinal section through thin, vertical wall (A) and thickened walls (B) appearing as clubs in section, with secondary module growth extending beyond the club; arrow marks endolithic, curved, cylindrical microborings: (**2, 3**) transverse sections, arrows point to 'keels,' which are a function of module walls budding prior to terminus of previous wall; blue lines are hypothetically projected growth of vertical walls of the next module to be budded. (**4–8**) NYSM E5072 7 Tu-4.95: (**4**) detail of wall structure (growth to lower right) showing prominent porous regions of skeleton typical of cnidarians, with laminated pilers of phosphate mineral and exterior wall of massive phosphate mineral; (**5**) longitudinal section of module wall with exterior massive walls of phosphate (A) and porous, interior skeleton of pillared phosphate mineral, arcuate and bilaterally symmetrical about the middle (B); in places (arrows), unmineralized arcuate layers outline the position of a previous growing tip; cracks in skeletal walls are typically filled with silica or iron oxide in more highly altered specimens, forming the pseudomedial walls observed by Landing et al. (2010, fig. 2h) and Taylor et al. (2013, fig. 2.10, 2.11); (**6**) in other regions, growth checks at the position of previous growth tips are mineralized (A), similar to the exterior wall; alternating intervals of exterior and interior wall microstructure, growth checks, and reinitiation of growth are evident in the distal part of some module walls (B); many walls have intact growth tips, which would preclude the theory that these walls are entirely internal and that there was widespread loss of outer walls (Landing et al., 2015); (**7**) longitudinal view of a different wall shows features described in (**6**); the massive exterior wall is not developed everywhere (see A vs. A') and interior cracks do not always form down the middle of the wall (B); (**8**) massive exterior wall (left), with well-developed interior skeleton; the porous layers of phosphatic pillars grow toward the exterior wall (solid line, up and away from wall center). Growth lines of the lamina and massive skeleton in places (dashed line and examples in **6, 7**) form arcs, which are low on the margins and peak in the center of the wall.

budding (Supplemental Fig. 1.1). However, secondary budding occurs only after considerable extension of the primary module with narrow growth bands (Fig. 2.6). The advantage is unclear for secondary frontal budding versus simple extension of the modules through incremental growth.

Modules are generally six-sided with six adjacent neighbors but typically bud in series of four to six, although three to seven sides with corresponding neighbors are not uncommon (Taylor et al., 2013). Modules are longer than wide, 0.27–0.59 mm × 0.15–0.38 mm, and at least 0.33 mm in depth (Taylor et al., 2013). At the proximal end of the branch, modules taper and are long (> 1.25 mm; Fig. 2.3; Taylor et al., 2013). Module walls vary between 10 and 20 µm in total thickness, with the outer, massive layer to 5 µm thick (Fig. 1.7, 1.8; Taylor et al., 2013, fig. 2.10, 2.11).

New modules are formed by budding from previous walls, often just prior to termination of the previous wall, as expected in the modular patterns of corals (Rosen, 1986, p. 127, fig. 2). In *Pywackia*, this results in a 'Y-shape' with a small ridge (keel) of the previous wall (Fig. 1.2, hypothetical, new, blue walls centered on keel). Modules open 'up,' away from the axis, generally with the largest area at the terminus (Figs. 1.1, 2.1, 2.2). Exteriors of walls have regularly spaced crenulations that parallel the opening (Fig. 2.1, 2.5, 2.6). Their origin deserves further evaluation, but they could represent incremental growth bands.

Pywackia skeletal composition.—The original skeletal composition of *Pywackia* remains unclear and has been proposed to be: (1) originally calcitic, diagenetically altered to a phosphate mineral; (2) as original skeletal phosphatic mineral; or (3) either (1) or (2) plus diagenetic silicate and iron oxide minerals (Landing et al., 2010, 2015; Taylor et al., 2013). Based on extensive Energy Dispersive Spectroscopy (EDS), well-preserved regions within colonies display detailed, primary skeletal microstructure (see section below, Fig. 1.7B, 1.8), which are now 100% phosphate mineral. However, most specimens are preserved as a combination of a phosphate mineral, especially the more-resistant, massive exterior walls, often with a core of diagenetically altered interior walls (Fig. 2.7).

Results from EDS performed at multiple target sites on two specimens (NYSM 5702, E5074) are summarized in Table 1, for data in three groups: (1) interior porous layers, (2) massive blocky layers at sites that did not appear to be altered (i.e.,

clear microstructure), and (3) diagenetically altered zones (primary microstructure obscured). The 'unaltered microstructure' is nearly 100% phosphatic mineral (Table 1), whereas the altered regions are silicate or iron oxides (Table 1).

Additional support for a skeleton originally of a phosphate mineral is that no residual calcium (carbonate) was detected in any of the EDS analyses (Fig. 1.6–1.8). Thus, if skeletons are secondary phosphate mineral, the replacement process was truly 100% complete at the microskeletal level. Therefore, although not definitive, we retain the hypothesis that the skeleton of *Pywackia* was originally and entirely a phosphatic mineral. However, support for complete calcite to phosphatic diagenetic replacement is that the Tiñu Formation hosts abundant and diverse fauna of phosphatized specimens (Landing et al., 2007).

The uncertain original skeletal composition of *Pywackia* does not affect its assignment to the phylum Cnidaria. Replacement of a carbonate mineral (calcite, aragonite, or a mixture) conforms with the calcareous skeletons for the majority of cnidarian coral groups, including *Pywackia* candidates of tabulates and octocorals (Sorauf, 1996). Alternatively, a primary phosphatic skeleton raises the need for comparisons with conulariids and other cnidarian groups with incipient phosphatic skeletonization (Vinn, 2022).

Other potential processes of preservation for Tiñu *Pywackia* were investigated but dismissed due to topological and microstructural constraints. These included replacement of organic tissue, steinkerns of either original void spaces or moldic skeletons, or early diagenetic overgrowth (mineralized crust) of either skeleton or tissue.

Pywackia skeletal microstructure.—The skeletal microstructure of *Pywackia* (Fig. 1.4–1.8) provides the strongest support for a cnidarian assignment. Like many cnidarian groups, e.g., corals and conulariids (Leggat et al., 2019, p. 2727, fig. 3I, J; Van Iten et al., 2022, fig. 4a–d), *Pywackia* has a porous primary skeleton (Fig. 1.8). This is not the same as the void cells of Taylor et al. (2013, fig. 2.10, 2.11), which are a product of diagenesis (see Fig. 1.8 [primary pores] vs. Fig. 2.7 [diagenetic voids]). The pores result from a radiating growth of small pillars connected by lateral layers (Fig. 1.4, 1.7, 1.8). When preserved, this structure forms the interior of all walls in *Pywackia* (Fig. 1.5–1.8). The exterior layer of most body walls has a massive layer of resistant phosphate mineral of
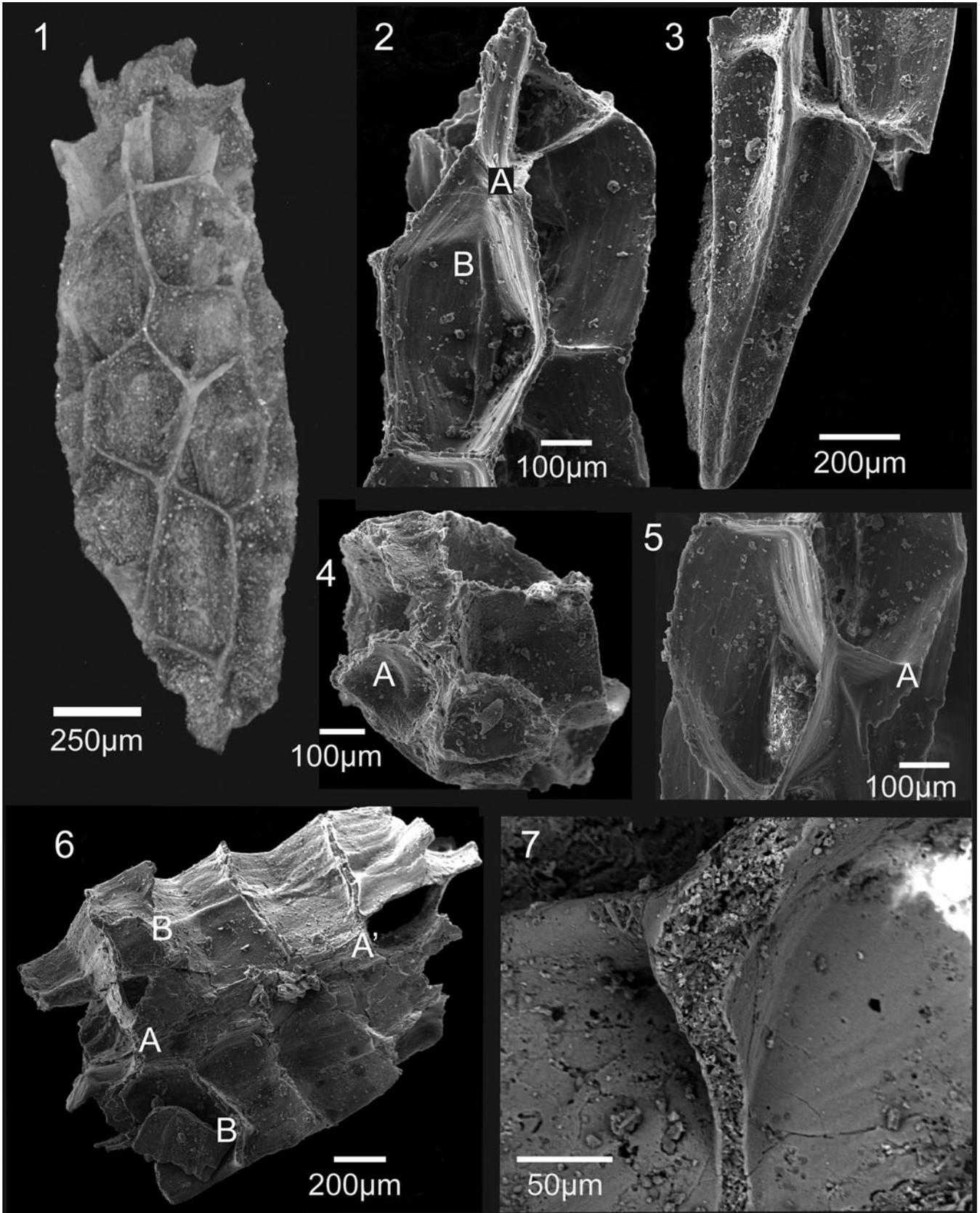
Figure 2. Exterior views of *Pywackia*. (**1**) NYSM E5074 9 Tu-205, colony fragment, truncated proximally and distally; radial modules, polygonal and thin walled. (**2–5**) NYSM E5072: (**2**) growing, budding, distal tip, showing thin, crenulated module wall (A) and basal ridge ('keel') resulting from budding of the opposite wall (B); (**3**) proximal colony tip, tapered with elongated, incipient modules; (**4**) distal growing tip, end-on, with immature, basal ridge ('keel') resulting from budding of the opposite wall (A); (**5**) detail of primary modules and crenulated walls, with an immature module secondarily budding (A). (**6, 7**) NYSM E5072 7 Tu-4.95: (**6**) fragment of a large colony, naturally split longitudinally; thin module walls forming the axis of the colony (A–A'); growth checks and secondary growth of modules can be seen in the form of thickened walls (upper B) and change of growth direction (lower B); (**7**) wall with diagenetic replacement of the interior but retaining massive original external layers.

Table 1. Summary of Energy Dispersive Spectrum (EDS) analysis from three microskeleton types, from multiple *Pywackia* colonies/sections. All values expressed as %.

Element	Porous internal, original skeleton 13 EDS sites	Massive external and internal bands, original skeleton 21 EDS sites	Mixed interior/exterior diagenetic skeleton 15 EDS sites
Al	0.0	0.0	0.6
Ca	36.9	36.5	22.2
Fe	0.4	0.7	5.7
O	42.7	41.8	48.5
P	15.8	15.3	8.8
Si	0.0	3.0	5.6
Cl	0.0	0.1	0.4
C	2.8	1.4	7.4
F	1.3	1.1	0.2
Total	100.0	100.0	99.3
	'pure phosphate'	'pure phosphate' + undetected diagenetic silica	phosphate + iron oxide + silicate minerals + minor, other

variable thickness (Fig. 1.5–1.8). It is unclear whether this massive wall is primary or secondary, because it thins in places, represented by pillars and porous structure (Fig. 1.7A). Massive skeletal wall is also present internally (Fig. 1.6B), where it wraps around the end of an earlier growing tip. In some specimens, this growth alternates with interior pillar and porous skeleton, representing a number of growth checks (Fig. 1.6).

It is possible that the massive phosphatic skeleton could be secondary to, and independent of, the interior porous, pillar skeleton (i.e., a diagenetic result of alteration of the portion of the porous interior). We reject this interpretation because of the internal growth checks but acknowledge that the massive layers are not constant in thickness and can even be absent in places.

Medial wall layers have been described as common in some specimens (Supplemental Fig. 2.3, 2.9, 2.10), but these laminar mineral bodies (silica and iron) commonly form in cracks of *Pywackia* walls (Fig. 1.5B). Although approximately medial in some specimens, these mineralized zones cut across specimens (Fig. 1.7B). Thus, although walls are bilaterally symmetrical in the lateral section, *Pywackia* has no biologically derived medial layers.

Microstructure comparison to other cnidarians.—The skeletons of conulariids are phosphatic, composed of carbonate apatite (Ford et al., 2016). Their composition is similar to that of *Pywackia*. If *Pywackia* also had a skeleton of a primary phosphate mineral, comparisons to the conulariid group are in order. The periderm of *Conularia* Miller in J. Sowerby, 1820 and *Paraconularia* Sinclair, 1940 (Ford et al., 2016) consists of extremely thin (1–3 μm) more or less distinct, alternating organic-rich and organic-poor microlamellae that are generally

parallel to the outer surface of periderm. Interestingly, the organic-rich microlamellae are cross-connected by thread-like pillars of organic material originally embedded in apatite (Ford et al., 2016), although this organic pillar architecture is quite opposite to what we see in *Pywackia* in which pillars have mineral composition (Fig. 3.5).

The microlamellae of conulariids can be pierced by microscopic circular pores ranging from ∼5–10 μm in diameter (Fig. 3.9), which can be quite numerous in some cases (Van Iten et al., 2005a, b). These pores, which extend through no more than two or three microlamellae, are of unknown origin. They might be primary microstructural features, or they might be microborings or microbioclaustrations, which could have been produced by parasitic or pathogenic microbes or fungi (Van Iten et al., 2005b). However, these pores are circular shafts in conulariid phosphatic laminae and are thus quite different in shape from the pores between pillars in *Pywackia*.

Another supposed cnidarian related to conulariids, *Sphenothallus* Hall, 1847, also has a phosphatic skeleton composed of apatite (Vinn and Kirsimäe, 2014; Vinn and Mironenko, 2021). The skeleton of *Sphenothallus* has a microlamellar structure (Fig. 3.4) but one that is different from *Pywackia* because its phosphatic lamellae are massive and devoid of any pores.

There is a restricted number of modern studies available on the microstructure of Paleozoic tabulate and rugose corals (Coronado et al., 2013, 2015, 2016; Coronado and Rodríguez, 2016). Resources such as Flügel (2004) provide rich information for fossil identification at the petrographic scale but limited guidance for the details of skeletal microstructure.

Three principal kinds of calcite crystals occur in syringoporids, i.e., lamellae, fibers, and granules (Rodríguez et al., 2014). Lamellae and microlamellae are flat crystals that resemble scales or shields (Rodríguez et al., 2014; Fig. 3.7), which can be compared with lateral layers that connect pillars in *Pywackia*. Fibers are also common in the microstructure of tabulate corals and somewhat resemble pillars in the structure of *Pywackia*. Tabulate fibers are elongate crystals with irregular morphology, but in some cases, they are barrel-shaped or tabular, depending on their situation in the skeleton (Coronado et al., 2015). The granules in tabulates are equidimensional crystals, with indentations to their edges, flake morphologies, and irregular distribution (see Coronado et al., 2015, fig. 6C). The granules could be analog to the massive phosphatic structure of *Pywackia*.

In rugose corals, the different bricks that compose the microstructure are lamellae, fibers, and granules (Coronado et al., 2016) (Fig. 3.8). Similar to tabulate corals, they can be compared with structural elements of *Pywackia* in the same way as the analogous structural elements of tabulates that were compared above.

Enigmatic anabaritids are usually referred to the Cnidaria. The phosphate replicated tubes of early Cambrian anabaritids
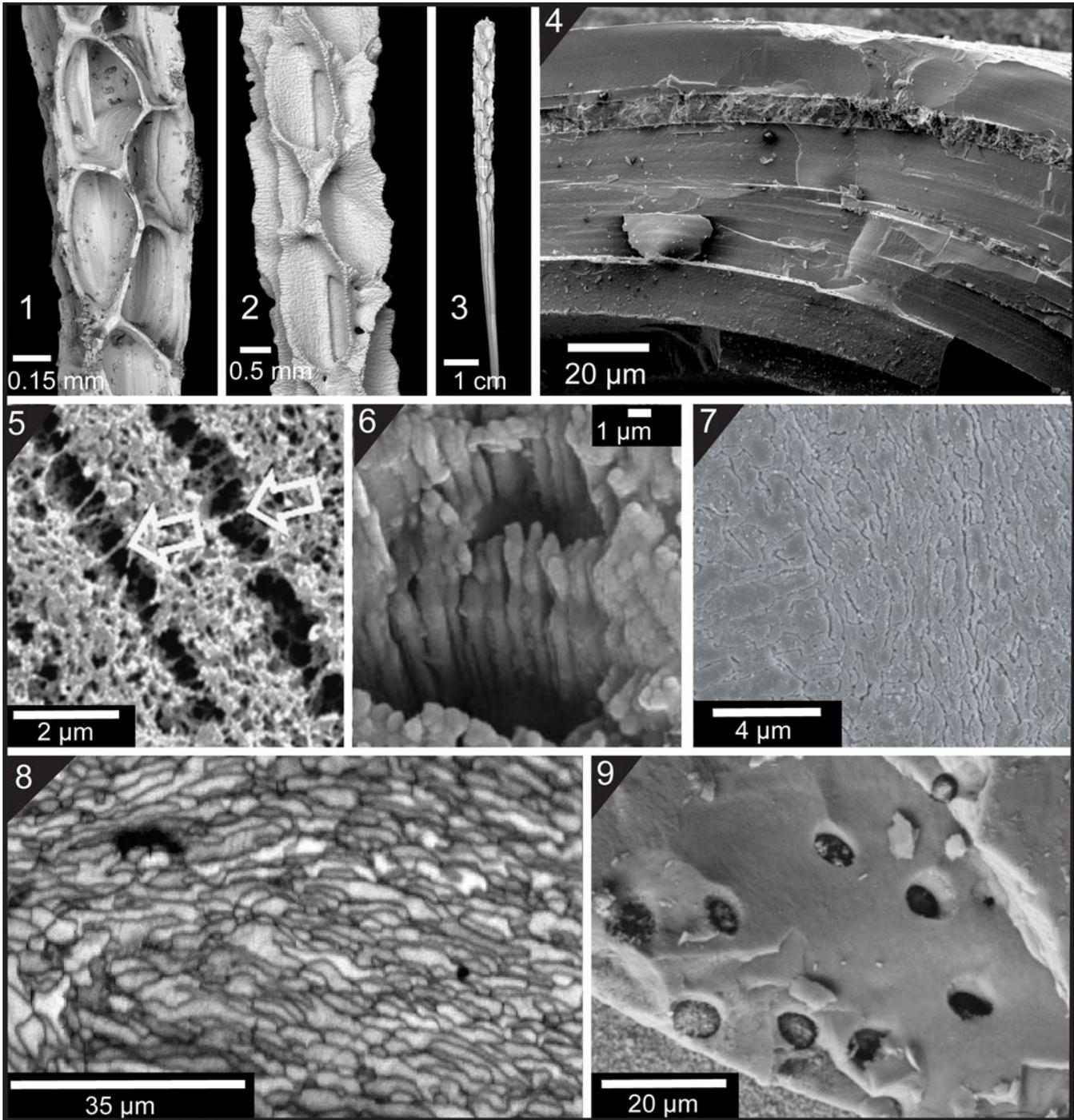
Figure 3. (**1**) Colony of *Pywackia* (after Taylor et al., 2013, fig. 4.1). (**2, 3**) Colony of the modern octocoral *Litularia* Valenciennes in Milne Edwards and Haime, 1850: (**2**) modules (after Taylor et al., 2013, fig. 4.2); (**3**) whole colony (after Taylor et al., 2013, fig. 5.1). (**4**) Microlamellar phosphatic (apatitic) wall of *Sphenothallus* Hall, 1847 (supposed cnidarian related to conulariids) in cross section, Upper Ordovician, Estonia. (**5**) Microlamellae in the conulariid skeleton, showing extremely slender strands of organic matrix (arrows) crossing the narrow gaps (organic-poor microlamellae) left by acid etching (after Ford et al., 2016, fig. 3.8). (**6**) Fibers in the anabaritid *Jacutiochrea tristicha* (Missarzhevsky in Rozanov et al., 1969), lower Cambrian, Siberia (after Kouchinsky and Bengtson, 2002, fig. 3E, used under Creative Commons Attribution License (CC BY), *Acta Palaeontologica Polonica*, Institute of Paleobiology, Polish Academy of Sciences). (**7**) SEM images showing the gradual transition from lamellae to fibers in the tabulate *Multithecopora hontoriense* Rodríguez and Ramírez, 1987 (after Rodríguez et al., 2014, fig. 4C, reproduced with permission of The Paleontological Association). (**8**) Gradual transition between the lamellae and the fibers in the rugose coral *Calceola sandalina* (Linnaeus, 1771), Devonian (after Coronado et al., 2016, fig. 6C, reproduced with permission of Elsevier). (**9**) Pores in *Holoconularia rossica* Van Iten, Mironenko, and Vinn, 2022, Carboniferous, central Russia (Van Iten et al., 2022, reproduced with permission of A. Mironenko). Figures 1.1–1.3 and 1.5 are reproduced with permission of The Paleontological Society.

have walls that consist of fibers (Kouchinsky and Bengtson, 2002), reflecting an original aragonitic fabric. In anabaritids, bundles of fibers are arranged in growth lamellae, and the latter form an angle of at least 45° with the inner tube wall. The architecture of growth lamellae in anabaritids (Kouchinsky and Bengtson, 2002) is different from that of *Pywackia,* but the fibers

(Fig. 3.6) can roughly be compared with pillars in the structure of *Pywackia*.

Assignment to a cnidarian subgroup.—Based on the overall morphology (module and colonies), we acknowledge similarities with certain tabulate corals (e.g., Landing et al., 2010, 2015). Landing et al. (2010) dismissed tabulate coral affinities for *Pywackia* based on the absence of intermodule pores.

Colony forms and module shapes of the single modern genus *Lituaria* Valenciennes in Milne Edwards and Haime, 1850 (very narrow pennatulacean octocoral known as a sea-pencil) are strikingly similar to those of *Pywackia* (Fig. 3.3; Taylor et al., 2013). The term 'sea-pen' is used widely for the pennatulacean group of octocorals, whereas use of the term 'sea-pencil' is restricted to the genus *Lituaria* (Fig. 3.3; Taylor et al., 2013, and avocational SCUBA divers in Singapore, e.g., http://www.wildsingapore.com/wildfacts/cnidaria/others/pennatulacea/pencil.htm). Direct comparison of *Pywackia* and *Lituaria* (Fig. 3.1, 3.2) reveals that their sizes are clearly different and there is a nearly 400 Myr time gap between *Pywackia* and the first appearance of pennatulaceans (Taylor et al., 2013). In addition, neither tabulate nor octocoral skeletal microstructure is similar to that of *Pywackia* (see Coronado et al., 2013).

Our data support assignment of *Pywackia* to the phylum Cnidaria. Although specimens share morphologies or compositional similarities with several cnidarian groups (tabulate corals, conulariids, and octocorals), we view *Pywackia* as a member of a rare, independent, and unnamed cnidarian group. *Pywackia*'s latest Cambrian age places it at the cusp of the Ordovician Biodiversity Event (Servais et al., 2009), which includes the first occurrences of some other cnidarian groups (Elias et al., 2021). A phylogeny for modern cnidarians was provided by Kayal et al. (2018). Although this phylogeny does not include extinct taxa, it provides a context for comparison. We believe that *Pywackia* is not so much in phylogenetic alignment with one of these traditional cnidarian groups, but rather a reminder of convergent evolution reinventing forms and features within the Bauplan of Cnidaria.

Reevaluation of *Pywackia* as an ostensible bryozoan

We independently and carefully evaluated the possibility that *Pywackia* is a bryozoan; however, we reject this hypothesis based on the information above and comparisons below. Landing et al. (2010) considered *Pywackia* to be a bryozoan rather than a tabulate coral based on four primary criteria: (1) presence of axial modules ('zooecia'), (2) presence of polymorphic nanozooids, (3) a bilobed keel in the base of the modules, and (4) bilaminar, originally calcareous, wall structure. Our reinterpretation of these features and identification as a cnidarian comes from use of SEM images of exterior, freshly fractured walls and petrographic thin sections, both standard petrographic techniques for studying Paleozoic stenolaemate bryozoans, and Energy Dispersive Spectroscopy. None of these was available to Landing et al. (2010, 2015), who relied on abraded specimens to reveal internal structures. However, these techniques were critical in our evaluation of *Pywackia*.

Taylor et al. (2013) and Taylor (2020) provided a detailed evaluation of why the morphological features of *Pywackia* do not justify an assignment to the phylum Bryozoa. We agree with their assessments, and further, our observations of *Pywackia*'s skeletal microstructure do not support a bryozoan identification. The observations of Taylor et al. (2013) and Taylor (2020), combined with ours, are given below.

Absence of axial zooecia.—Landing et al. (2010, 2015) compared the morphological features of *Pywackia* to those of rhabdomesine cryptostome, stenolaemate bryozoans, exclusive of other, related forms. They emphasized the presence of axial zooids in *Pywackia* as evidence for a cryptostome bryozoan affinity, a feature not well developed in other Paleozoic bryozoan groups. Taylor et al. (2013) could not identify 'axial zooecia' in any of their or Landing et al.'s (2010) SEM images of the colony exterior and fragmental sections. Based on cut, polished, transverse and longitudinal sections (Figs. 1.2, 1.3, 2.4, 2.6; Supplemental Figs. 1.1, 2.1, 2.6), no axial modules (zooecia) were seen in *Pywaxia*, but rather the 'central axis' of the colony is constructed of thin walls of essentially back-to-back modules. Thus, the longitudinal axis consists of a weakly defined zone of thin primary walls (Fig. 2.2, 2.4, 2.6; Supplemental Fig. 2.1, 2.6).

Absence of polymorphs (nanozooecia).—Landing et al. (2010, figs. 2e, f, 3c; 2015, fig. 1.2, 1.3) called on the presence of polymorphs (nanozooids) as support for bryozoan affinity. We agree with Taylor et al. (2013) that these structures likely represent immature modules, budded during the beginning of a second generation of growth (Fig. 1.9), rather than discrete polymorphs of a determinate size. This interpretation is supported by their presence in mature colonies, primarily in the zone of secondary growth (budding).

Body symmetry and basal 'bilobed keels.'—Another line of evidence used by Landing et al. (2010, fig. 2K, L; 2015, fig. 1.9, 1.10) to support a bryozoan affinity is the presence of 'bilobed keels'—small, proximodistal ridges on the base of some modules. They argued that these indicate bilateral rather than radially symmetrical soft parts of the animal polyp. Taylor et al. (2013) demonstrated that such longitudinal basal keels are not a mainstay of stenolaemate bryozoan morphology. Our examination of keels and module walls shows that the presence of keels is not ubiquitous in all modules or even colonies; in fact, the presence of bilobed keels is relatively rare in *Pywackia*. In transverse sections, we saw two laterally budding walls for the new module, arising from either side of the previous wall, but just before its end (tip). The combination of these form a broad 'Y' (Fig. 1.2, blue lines). Thus, a keel is a nonobligate extension of the previous wall into the newly budded module.

Wall microstructure and composition.—Most stenolaemate bryozoans have bilaminar walls, back-to-back lamellar crystals, which sometimes are centered on a medial granular wall (Hageman, 1991, figs. 1–4; Ma et al., 2014). Stenolaemate bryozoan skeletal microstructures are well documented (see Boardman, 1983; Hickey, 1987) and are therefore not illustrated here; for a review using contemporary imaging techniques, see Grenier et al. (2023).

The walls of *Pywackia* are porous, with annulated pillars and do not show lamellar crystals of stenolaemate bryozoans.

Landing et al. (2010, 2015) described *Pywackia* skeletal microstructure as 'granular or granular prismatic' based on high magnification of naturally polished *Pywackia* walls (Landing et al., 2015, fig. 1.7). They argued that some Paleozoic stenolaemates have granular or granular prismatic microstructure, which is true, but is not exclusive in any group, and when present, typically forms a small and predictable portion of the colony (e.g., core of fenestrates). Granular walls are present in early esthonioporine stenolaemate bryozoans (Ma et al., 2014), but even in these cases, questions remain about primary versus diagenetic origins of the granular skeleton (Ma et al., 2014). In the SEM view of microstructure (Fig. 1.5–1.8; Supplemental Fig. 1.10–1.12), *Pywackia* clearly displays porous, annulated pillars, with structured (layered, radiating) porous space, which is unknown in stenolaemate bryozoans.

We agree with Taylor et al. (2013) that the original skeletal composition is equivocal. The phosphatic state of the fossils does not affect cnidarian versus bryozoan versus other interpretations.

Within module partitions.—Landing et al. (2010, fig. 2G, H; 2015, figs. 1.6, 1.8, 2.1, 2.2) emphasized the presence of thin diaphragms (partitions across the module) and low hemiphragms (partial partitions of the module) as support for a bryozoan interpretation. We agree with the Taylor et al. (2013) argument that the placement of these structures in *Pywackia* is far more irregular than that seen in cryptostome (Paleozoic) bryozoan species.

Module shape and size.—Landing et al. (2010, 2015) described *Pywackia* modules in the terminology of bryozoans (e.g., autozooecia with apertures). Taylor et al. (2013), however, pointed out that the modules are cup-shaped, slightly flaring to the surface. Modules are not tubular or cylindrical as are the cryptostome bryozoans described by Landing et al. (2010). As a result, *Pywackia* does not have apertures in the sense of cryptostome bryozoans. Landing et al. (2015, fig. 2.2) claimed that *Pywackia* modules are not 'cup-like' but are in fact elongate. This was based on interpretation of what we consider to be module walls but was considered by them as diaphragms (e.g., module walls versus partitions).

Absence of frontal walls.—Landing et al. (2015, fig. 2.1) argued that weak frontal walls were originally present but were uniformly lost to abrasion. We did not find any evidence for frontal walls. Our observations suggest that of the ~150 *Pywackia* specimens studied, none had frontal walls removed/eroded and that no illustrated specimens to date represent eroded interiors. Although many specimens examined are eroded/abraded, we also observed many exterior surfaces with growing tips and edges that preserve the outermost wall (Fig. 1.2, 1.3, 1.6; Supplemental Fig. 1.1, 1.4, 1.6); they are not abraded and show no sign of a missing frontal wall. Although the size of the modules was not specified in the original paper (Landing et al., 2010), the submillimeter diameters (0.15–0.59 mm; Landing et al., 2015) are consistent with a bryozoan affinity (Taylor and Waeschenbach, 2015).

Other Cambrian Bryozoa candidates.—It is not a goal of this paper to evaluate other contenders for Cambrian bryozoan status, but recent publications demonstrate contemporary interest in the topic. Zhang et al. (2021) described evidence for apparently soft-bodied, early Cambrian Bryozoa from the Xiaoshiba Lagerstätte in China (Cambrian Age 3). This interpretation of these phosphatic specimens has been challenged by Yang et al. (2023) who suggested that the Xiaoshiba specimens are dasyclad algae and not bryozoans. Pruss et al. (2022) recently described mineralized bryomorph specimens from the Harkless Formation, Nevada (Cambrian Age 4), which they suggest are palaeostomate bryozoans. These specimens are phosphatic but are consistent with possible replacement of calcite (Pruss et al., 2022). Further study, combined with existing evidence could well confirm the promise of the Harkless bryomorph fossils as the earliest mineralized Bryozoa.

Other taxonomic affiliations considered but not selected for *Pywackia*

For this study, we considered the following features: overall colony shape and size, growth and orientation, shape and size of the modules, and skeletal composition and microstructure. Comparisons were made with the following taxa: graptolites, tunicates, foraminifera, tentaculitoids, phoronids, other lophophorates (brachiopods), red algae, green algae, chordates (conodontophores, otoliths), calcareous sponges, and other similar Problematica.

In lophophophorates (e.g., brachiopods), pores can occur in calcareous skeletons with either lamellar or prismatic microstructure (Pérez-Huerta et al., 2009). However, pores in brachiopods are shafts with circular cross sections in otherwise massive shell layers and thus are different from the pillar-based architecture of *Pywackia* skeletons. Pores also occur in microconchid tentaculitoids, which could be related to lophophorates and phoronids (Vinn and Taylor, 2007; Zatoń and Olempska, 2017). The microconchids have microlamellar skeletons, but their pores are similar to those found in brachiopods and are unlike the pillar architecture of microstructure in *Pywackia*. Moreover, modular skeletons do not occur in brachiopods or tentaculitoids.

Although visually similar with calcified partitions across tubules (West, 2011, figs. 1, 2, 10), the modules polyphyletic group of hypercalcified chaetetid-type Porifera are larger than the pillars and pores of *Pywackia* and the partitions (tabulae) do not align in growth bands in chaetetids (West, 2011, fig. 1). Absence of spicules (or pseudomorphs) in both fossil chaetitids (West, 2011) and *Pywackia* provides little insight to the affinities of the two groups. None of the microstructures of the calcareous skeleton of microlamellar, spherulitic, water-jet, or penicillate types, as outlined by Cuif and Gautret (1991), are seen in *Pywackia*. Modular skeletons do not occur in other calcareous sponges (e.g., stromatoporoids; Stock, 2001; Zapalski and Hubert, 2011, fig. 3).

Superficially, the inner cancellate skeleton is reminiscent of coralline red algae (Teichert et al., 2012, figs. 8–10), but *Pywackia*'s wall skeleton is distinct from the fibrous rods of the modern coralline red algae (Bianco-Stein et al., 2020, fig. 3). However, skeletal microstructure is not well documented

in Rhodophyta overall. The wall morphology of *Pywackia* is similar to the overall skeleton of some dasyclad green algae (e.g., Rashidi and Schlagintweit, 2019, fig. 3). However, the skeletal walls of *Pywackia* show no sign of the short, primary, rod-like (radiating or random) crystals of modern green algae (Barattolo, 2006, fig. 4).

The phosphatic composition and porous skeleton is consistent with those of primitive chordates and their ancestors, e.g., conodonts (Donoghue et al., 2000) and some ascidians (Lambert et al., 1990). Although laminar structure in conodonts (Donoghue et al., 2000, fig. 5B) is visually similar to layers in the *Pywackia* skeleton, the crystalline details differ. In addition, no modular/colonial forms are known in true chordates.

Conclusions

The late Cambrian phosphatic fossils identified as *Pywackia* from the Tiñu Formation, Yudachica Member near Río Salinas, Mexico, are cnidarians but are not assigned to a class or any other suprageneric taxonomic group. *Pywackia* likely represents a rare, minor clade in an otherwise unknown cnidarian group, possibly, but not directly related to conulariids, octocorals, and/or tabulates.

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Declaration of competing interests

The authors declare none.

Data availability statement

Data available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7915877.

Supplemental Figure 1. Mixed views of *Pywackia*. (**1**) Detail of module in Figure 2.6. (**2, 3**) NYSM E5072: (**2**) detail of wall in Figure 2.3, showing the regular spacing of crenulations (growth lines parallel module edge) (A-A') and growth lines resulting from either arcuate growth of walls, or diagenesis (B-B'); (**3**) proximal, tapered end of colony, with elongate immature module. (**4**) Foldable, paper, holiday decoration that is reminiscent of entirely thin-walled construction of *Pywackia* modules and colonies. (**5**) NYSM E5072, elongate endolithic borings in *Pywackia* exterior wall; vertical cylindrical opening connected to horizontal, cylindrical borings. (**6–8**) Energy Dispersive Spectra (EDS) (Table 1): (**6**) NYSM E5072 7 Tu-4.95, longitudinal section of module wall, with both massive (blocky) and porous layers, evidently 100% phosphate mineral; (**7**) longitudinal section of module wall terminus; massive (blocky) layer,

all phosphatic, and porous interior layer, a mix of phosphate and silicate mineral(s); (**8**) longitudinal section of module wall terminus, all replaced by silicate and iron oxide minerals. (**9, 10**) NYSM E5072 and E5074, respectively; endolithic borings in exterior wall show representative horizontal grooves and circular, vertical shafts. gen. = generation.

Supplemental Figure 2. Mixed views of *Pywackia*. (**1–7**) NYSM E5074 8 Tu-205, longitudinal section of colony; highly altered module walls thicken to growth check and then begin secondary, narrow wall growth: (**2**) highly altered section of wall, including 'medial' crack filled with epoxy; (**3**) longitudinal section of wall, exterior massive and interior porous evident with endolithic borings; (**4–7**) details of Supplemental Figure 1.1, module walls, with alteration and borings, interior porous interior layer, and massive exterior layers. (**8– 12**) NYSM E507: (**8**) detail of porous wall, showing pillars growing toward viewer; (**9**) module walls, with minimal alteration, porous layer, and massive exterior layers; (**10**) module walls, with cracks, and well-preserved porous interior layer and massive exterior layers; (**11**) oblique cut through thin wall, showing layering (growth bands) of interior layer, massive outer layer, with limited diagenetic alteration and endolithic borings; (**12**) module walls, with well-preserved porous interior layer and massive exterior layers.

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