



REINTERPRETATION OF THE CAMBRIAN ‘BRYOZOAN’ *PYWACKIA* AS AN OCTOCORAL

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ABSTRACT—*Pywackia baileyi* Landing in Landing et al., 2010, from the upper Cambrian Yudachica Member of Oaxaca State, southern Mexico, consists of small, phosphatic, proximally tapering cylindrical rods covered by shallow polygonal calices. The bryozoan-like morphology of this fossil prompted its interpretation as the first bryozoan known from the Cambrian. However, restudy of some of the original material, employing scanning electron microscopy for the first time, questions the assignment of *Pywackia* to the Bryozoa. Striking similarities between *Pywackia* and the modern pennatulacean octocoral *Lituarina* lead to an alternative hypothesis interpreting *Pywackia* an early fossil octocoral. While *Pywackia* is probably not a true pennatulacean, a group with a definitive fossil record stretching back only to the Late Cretaceous, it can be envisaged as having had a similar skeletal structure and ecology to *Lituarina*, the rods representing mineralized axes of tiny colonies that lived with their proximal ends buried in the sediment and distal ends covered by feeding polyps. Landing et al. (2010) considered the phosphatic composition of *Pywackia* specimens to be the result of diagenetic replacement, but the evidence is equivocal. If *Pywackia* had a primary phosphatic skeleton, this would support the hypothesized existence of phosphatic biomineralization early in the evolutionary history of Cnidaria, as well as providing further evidence that *Pywackia* is not a bryozoan.

INTRODUCTION

MUCH HAS been written about the Cambrian explosion. Importantly, all animal phyla with biomineralized skeletons make their first appearance in the Cambrian, with the notable exception of the Bryozoa. Most species of modern bryozoans have calcareous skeletons, and this is well reflected by the rich fossil record of these colonial lophotrochozoans. Nevertheless, there are no unequivocal Cambrian bryozoans and the undisputed fossil history of the phylum does not begin until the Early Ordovician (Taylor and Ernst, 2004). Several claims of the existence of bryozoans of Cambrian age have been made in the past but none have stood up to close scrutiny. Notable among these are some unnamed putative bryozoans described by Cobbold (1931) and by Cobbold and Pocock (1934), from Comley and Rushton, respectively, in Shropshire, England, and two species of *Archeotrypa* Fritz, 1947, from the upper Cambrian of Alberta, Canada. The material from Shropshire has been examined by one of us (PDT) and appears to consist of pieces of pitted arthropod exoskeleton. The zig-zag ‘zoecial’ walls of *Archeotrypa prima* Fritz, 1947 in longitudinal section raise serious doubt about its identity as a bryozoan but, unfortunately, Kobluk’s (1984) revision of this species, as well as the poorly preserved *A. secunda* Fritz, 1947, proved inconclusive.

The latest fossil claimed to be a Cambrian bryozoan is *Pywackia baileyi* Landing, 2010, described from the late Cambrian of southern Mexico in Landing et al. (2010). The aim of the current paper is to re-evaluate the taxonomic affinity of *Pywackia*, based on a study of topotypic material. This is the first investigation to use scanning electron microscopy (SEM) on this fossil. The evidence for *Pywackia* being a bryozoan is questioned and an alternative interpretation is proposed that it is an octocoral with an originally phosphatic skeleton and a colonial morphology resembling that seen in the recent pennatulacean *Lituarina*.

MATERIAL AND METHODS

Through the courtesy of Ed Landing (New York State Museum) we were able to examine a cavity slide (NYSM Tu-2.05) containing more than 50 specimens of *Pywackia baileyi* Landing in Landing et al., 2010. Although these specimens were not designated as primary types and are not figured in the original paper, they are part of the “nearly 150 stem-like fragments” obtained from the three localities by Landing et al. (2010, p. 548) and are clearly conspicuous with the holotype (NYSM 13515; Landing et al. 2010, fig. 2K). Individual specimens from this slide are referred to below by the cell number.

Studied specimens come from the Yudachica Member of the Tinu Formation, near Rio Salinas village, Oaxaca State, southern Mexico. Landing et al. (2007) dated the Yudachica Member as uppermost upper Cambrian (upper ‘Olenidian Series’). Samples yielding *Pywackia* were obtained from the basal part of the Yudachica Member, which falls within the *Corylodus andresi* conodont zone of Baltica, correlating with the Laurentian *Eoconodontus notchpeakensis* conodont subzone (Landing et al., 2007, fig. 4). The Yudachica Member is a thin (up to 16 m), condensed deposit comprising interbedded limestones and silty shales, interpreted as a temperate zone carbonate deposited in the photic zone. Episodic high-energy, wave-dominated deposition was apparently punctuated by intervals during which the bottom sediments, and possibly the bottom waters too, were poorly oxygenated. During these times, phosphatization of gastropods, hyoliths, brachiopods, ostracods and trilobites apparently occurred beneath the oxygen minimum layer, with some of the phosphatized fossils later being exhumed and eroded on the sea floor (Landing et al., 2007, p. 913). All of the material of *Pywackia* was recovered as insoluble, phosphatic residues after breakdown of Yudachica Member limestones using formic acid.

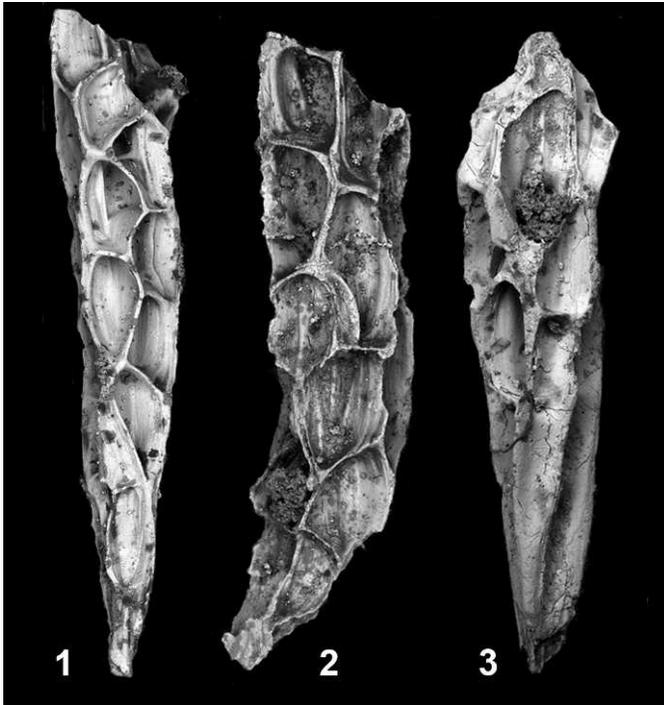


FIGURE 1—Back-scattered scanning electron micrographs of the putative bryozoan *Pywackia baileyi* from the upper Cambrian Yudachica Member of Oaxaca State, Mexico, NYSM Tu-2.05. 1, well preserved rod tapering towards the proximal end, cell 36, $\times 31$; 2, unusual curved rod, cell 29, $\times 47$; 3, rod with longitudinal walls slightly torted, cell 7, $\times 34$.

Comparative material was studied from the fossil bryozoan collections of the Natural History Museum, London (NHM), and the recent pennatulacean octocoral collections of the NHM and the Muséum national d'Histoire naturelle, Paris (MNHN). Additional material of an unnamed species of the pennatulacean *Lituarina* ('sea-pencil') was kindly collected on our behalf by S. K. Tan (Raffles Museum, Singapore; abbreviated RMS) from a sand flat in the intertidal zone near the Changi Ferry Terminal, Singapore.

The cavity slide containing specimens of *Pywackia* was initially studied using an optical microscope prior to detailed SEM examination. The availability of a low vacuum SEM (LEO 1455-VP) enabled the entire cavity slide to be placed in the large specimen chamber without the need for coating or detachment of the *Pywackia* specimens affixed to it. Imaging was undertaken using backscattered electrons. As no attempt was made to clean these delicate specimens, traces of sediment, pyrite and possibly glue, which have a different molecular weight than the skeleton of *Pywackia*, are visible in the micrographs as darker or lighter areas. Recent material of *Lituarina* was bleached to remove all organic material and expose the underlying skeleton before scanning.

MORPHOLOGY OF *PYWACKIA*

Specimens of *Pywackia* comprise spindle-shaped, invariably straight rods that do not bifurcate (Fig. 1.1). One rod is an exception in showing slight bending at the proximal end (Fig. 1.2). All examples are fragmented to varying degrees, being broken at the tapering proximal end, the broader distal end, or both ends. The original description of *P. baileyi* lacked any explicit data on size, apart from that which could be calculated from the magnifications of the figures. The longest (incomplete) rod in the cavity slide studied measured 3 mm. In a subsample

of 25 SEM-imaged specimens, rod width averaged 0.59 mm (SD 0.137 mm, CV 24.4), with a range of 0.32–0.80 mm.

Presumed proximal ends of rods could be observed to taper at varying rates. In some instances tapering is rapid and the proximal end is moderately rounded, but in others tapering is slower and the proximal end appears more pointed (Fig. 1.1, 1.3). Landing et al. (2010, fig. 2J) illustrated what they interpreted to be an "apical tip", the rod in question seemingly having a rounded distal end. However, in most specimens the distal end is incomplete, often with clear evidence having been fractured.

Rod surfaces are covered by an array of polygonal, calyx-like modular units (Figs. 1.1, 1.2, 2.3) defined by walls perpendicular to the rod axis. These units were interpreted by Landing et al. (2010) as autozoecia but are here referred to as modules to avoid the connotation that *Pywackia* is necessarily a bryozoan. The modules generally form 4 to 6 series around the circumference of the rod and tend to be arranged in alternating series. However, there are irregularities in the patterning of the modules reflecting their variability in shape and size. While most of the modules are 6-sided and have six neighbors, some are 3-, 4-, 5-, or 7-sided, with a corresponding number of neighboring modules. Modules are invariably longer than wide, ranging from 0.27–0.59 mm in length and 0.15–0.38 mm in width. Exceptionally, however, modules at the tapering proximal end of the rods may be at least 1.25 mm long and very narrow. Slight torsion of the longitudinal walls bounding these apical modules is occasionally evident (Fig. 1.3). Individual modules extend almost to the centers of the rods and can be at least 0.33 mm in depth (Fig. 2.1).

Landing et al. (2010) identified three types of individuals in *Pywackia*: normal 'autozoecia', small, nanozoecia-like polymorphs located at some autozoecial corners, and tube-like axial zooids. The small polymorphs could represent modules at the extreme end of the spectrum of small size rather than being discrete polymorphs. The presence of axial zooids is neither clearly demonstrated in the figures of Landing et al. (2010), nor have our SEM investigations revealed their existence: end views of a rod (Fig. 2.1) suggest that modules extend all the way to the center of the rod without space for an axial zooid.

The basic polygonal, cup-shaped morphology of the modular units in *Pywackia* is complicated by the presence of a variety of structures developed in some but not all modules. Landing et al. (2010, fig. 2K, L) figured "bilobed keels" forming low longitudinal ridges (i.e., oriented parallel to the rod axis) on the module basal walls. Such keels seem more often to comprise single structures without bilobation (Fig. 2.2). Longitudinally elliptical holes are visible adjacent to the keels in at least one rod, but it is unclear whether these are original or taphonomic in origin. Basal walls of modules are marked by numerous longitudinal lineations of low relief in a few rods (Fig. 2.6). Partial subdivision of some modules is brought about by the development of transverse to obliquely transverse walls of generally higher relief than the longitudinal keels (Fig. 2.4, 2.5). These walls resemble those bounding each module but are shallower and differ from most bounding walls (cf. Fig. 2.7) in not extending to the very outside of the rod. An unusual dipping, diaphragm-like wall has been observed in one module (Fig. 2.8).

Wall surfaces are smooth and relatively flat apart from a mild crenulation. There are no spines, tubercles or pores. The ends of walls are well rounded (Fig. 2.9). Broken walls show thickness to range from about 10 to 20 μm and may reveal a tripartite substructure with dense outer layers, up to 5 μm in thickness, sandwiching a less dense central layer containing voids (Fig. 2.10, 2.11).

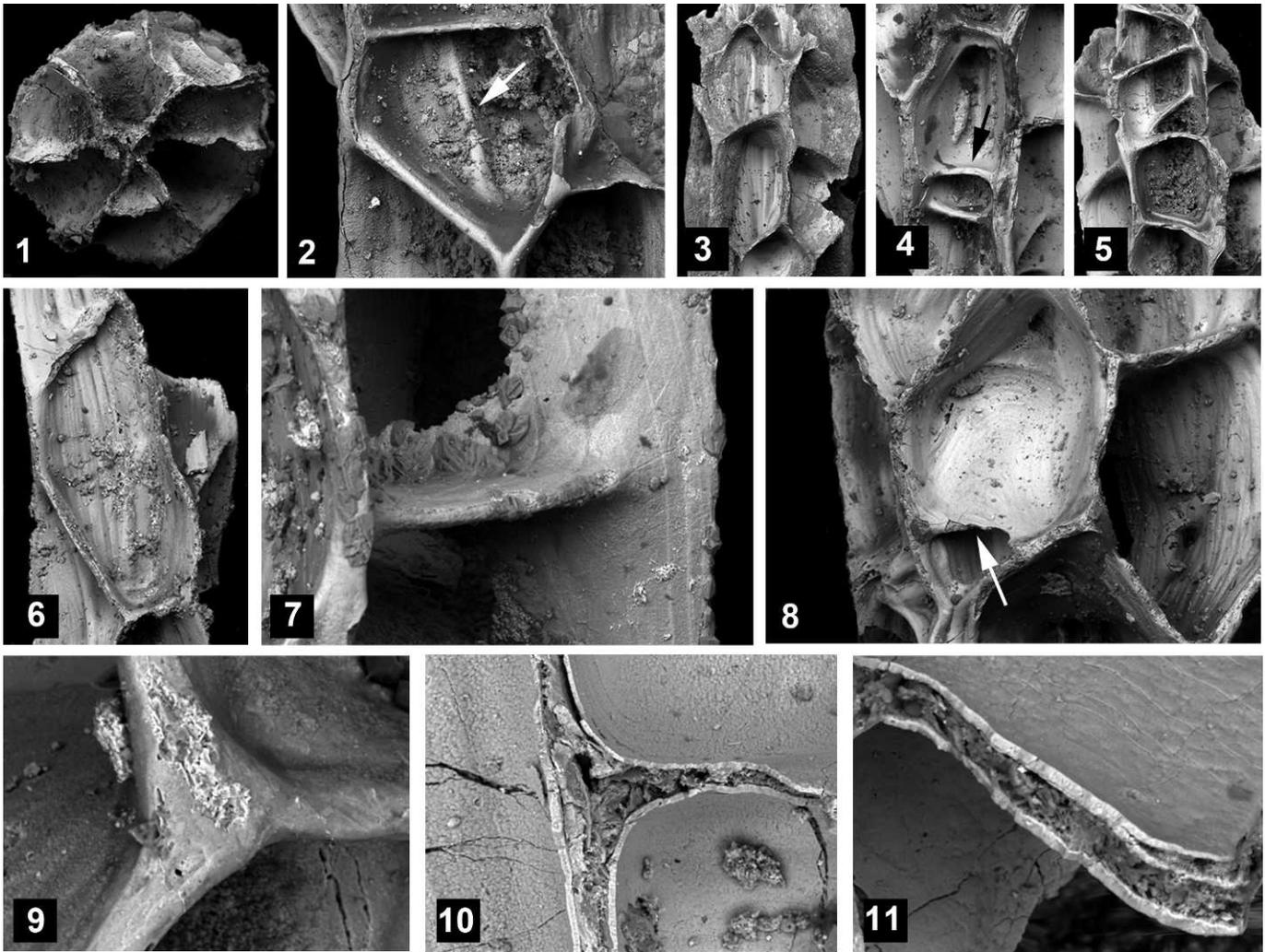


FIGURE 2—Back-scattered scanning electron micrographs of the putative bryozoan *Pywackia baileyi* from the upper Cambrian Yudachica Member of Oaxaca State, Mexico, showing details of the modules and skeletal walls, NYSM Tu-2.05. 1, distal end of a rod showing apparent lack of an axial, stolon, cell 13, $\times 54$; 2, five-sided module with a slightly oblique longitudinal keel at the base (arrow), cell 2, $\times 100$; 3, well preserved rod with longitudinal fabric at the base of the modules, cell 1, $\times 36$; 4, module partly subdivided by a transverse wall (arrow), cell 20, $\times 60$; 5, modules containing oblique transverse walls, cell 20, $\times 40$; 6, broken module with longitudinal striations on the basal wall, cell 3, $\times 82$; 7, transverse wall bounding a module but not extending fully to the outside of the rod, cell 44, $\times 210$; 8, unusual dipping, diaphragm-like wall slightly broken at the edge (arrow), cell 24, $\times 125$; 9, detail of smooth wall surface at triple junction between three modules, cell 36, $\times 650$; 10, 11, broken walls showing dense outer layers and median layer containing voids, cell 34; 10, $\times 370$; 11, $\times 600$.

BRYOZOAN VERSUS OCTOCORAL AFFINITIES

Inferring the phylum-level affinity of *Pywackia* demands comparison with appropriate organisms, preferably living, of certain identity to ascertain which provides the closest match. Ideally, one should seek synapomorphies (shared homologous features). This is notoriously difficult in organisms of simple skeletal morphology, particularly when this morphology is also plastic, as in *Pywackia*. Here we summarize the hypothesis of Landing et al. (2010) that *Pywackia* is a bryozoan, and present an alternative hypothesis interpreting it as an octocoral.

Bryozoan hypothesis.—Landing et al. (2010) believed *Pywackia* to be a Cambrian bryozoan. In particular, they compared it with cryptostomes, a group of stenolaemate bryozoans well known from post-Cambrian Paleozoic rocks. Implicitly, their comparison was with rhabdomesine (Fig. 3) rather than ptilodictyine cryptostomes as the former have narrow, equidimensional branches like *Pywackia*, whereas the latter have flattened, bifoliate branches, often robust, that do not resemble *Pywackia*. They pointed to the presence of axial zooids in *Pywackia* as evidence for a cryptostome affinity; axial zooids are present in

cryptostomes such as *Rhabdomeson* (see Wyse Jackson and Bancroft, 1995) but seem not to be developed in any other Paleozoic bryozoan groups. Other lines of evidence used by Landing et al. (2010) to support a bryozoan affinity were the presence of keels, indicating a bilaterally (e.g., metazoan) rather than radially (e.g., hydrozoan) symmetrical animal, and polymorphism, which they used to rule out a coral affinity. They further pointed out that the tapered proximal end, bilamellar wall construction, shallow autozoecia, diaphragms (Landing et al., 2010, fig. 2H) and hemiphragms (Landing et al., 2010, fig. 2G) of *Pywackia* are all features that can be found among cryptostome bryozoans. Although the size of the modules was not specified in the original paper, the submillimetric diameters (0.15–0.59 mm) are also consistent with a bryozoan affinity.

Nevertheless, important aspects of the morphology of *Pywackia* are inconsistent with the bryozoan model. The modules of *Pywackia* are shallow cups on the rod surface, whereas the zooids of cryptostomes and other mineralized Paleozoic bryozoans are tubular (e.g., Blake, 1983, fig. 268; Dzik, 1994, fig. 9e), narrow initially and expanding in diameter towards the aperture. This

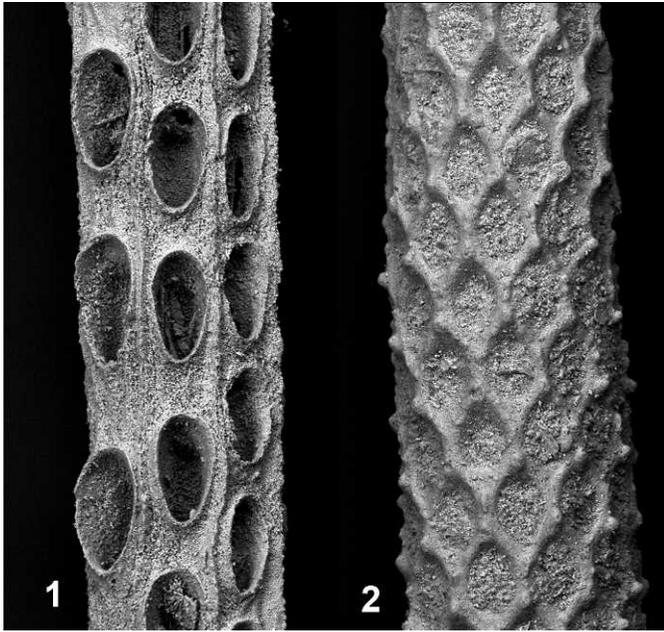


FIGURE 3—Back-scattered scanning electron micrographs of representative rhabdomesine cryptostome bryozoans for comparison with *Pywackia*. 1, arthrostylid *Nematopora lineata* (Billings, 1862), calcium fluoride-replaced branch showing aligned autozooids with elliptical apertures, NHM BZ 5983, Ordovician, Ashgill, Ojl Myr flint, Gotland, Sweden, $\times 42$; 2, rhabdomesid *Rhabdomeson profragile* Wyse Jackson and Bancroft, 1995, sediment-filled, hexagonal apertures of autozooids arranged quincuncially and separated by skeletal walls covered by short styles, NHM BZ 5982, Lower Carboniferous, Haimyres, East Kilbride, Scotland, $\times 42$.

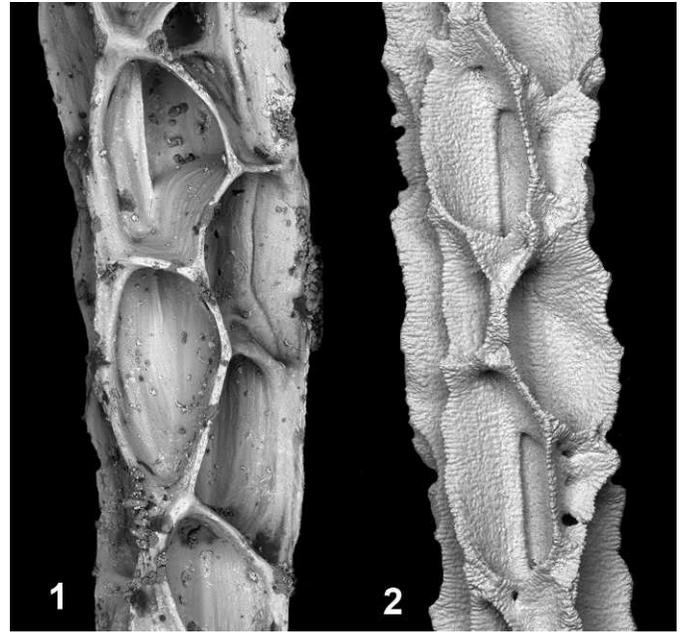


FIGURE 4—Back-scattered scanning electron micrographs illustrating the resemblance between the Cambrian *Pywackia baileyi* and the axis of the Recent pennatulacean octocoral *Lituaria* sp. 1, *Pywackia baileyi*, upper Cambrian, Yudachica Member, Oaxaca State, Mexico, NYSM Tu-2.05, cell 36, $\times 78$; 2, *Lituaria* sp., Recent, sand flat near Changi Ferry Terminal, Singapore, RMS ZRC.CNI.0935, $\times 13.3$.

morphology gives them a clear polarity, lacking in the modules of *Pywackia*. The irregularity and morphology of the various structures within the modules would also be unusual for a bryozoan. While complete transverse partitions (diaphragms), partial transverse partitions (hemiphragms) and less frequently blade-like structures (Hinds, 1973) do occur in a range of bryozoans, these have regular morphologies and distributions within species. The low profile keels and longitudinal lineations visible on the bases of some *Pywackia* modules have no obvious analogues among bryozoans.

Interpretation of the tapering proximal ends of the rods raises a further problem. Landing et al. (2010, p. 548) implied that a tapered end for substrate attachment was a feature of bryozoans, but this is not the case. Instead, cryptostome and other Paleozoic bryozoans most often have expanded colony bases cemented to hard or firm substrates. Exceptions can be found among some ptilodictyine and arthrostylid rhabdomesine cryptostomes (Blake, 1979) with jointed colonies, but these have ball and socket joints at the ends of the branches of which there is no evidence among known material of *Pywackia*. If the colonies were unjointed, as believed by Landing et al. (2010), the proximal ends of *Pywackia* rods should contain the first-formed zooids of these small colonies consisting of just one branch. In this case they should preserve a founding zooid (ancestrula) with the bulb-like proximal protoecium that is typical of stenolaemates. Although it is possible to explain the absence of a protoecium in *Pywackia* by loss through breakage, the elongate proximal modules do not resemble the ancestrula or other astogenetically immature zooids of known bryozoans.

Finally, the existence of zooidal polymorphism in *Pywackia* can be disputed. No distinct axial zoecia could be identified in any of the samples studied by SEM. The ‘small polymorphs’ of

Landing et al. (2010) seem to represent the smallest modules at the end of a continuous range of size variation—there is no clear evidence of bimodality in size or shape.

Octocoral hypothesis.—The notion that *Pywackia* is an octocoral cnidarian was raised through the chance discovery by one of us (BB) of a webpage <<http://www.wildsingapore.com/wildfacts/cnidaria/others/pennatulacea/pencil.htm>> showing a photograph of the skeleton of a Recent ‘sea pencil’ from Singapore bearing a striking resemblance to *Pywackia*. We were able to obtain dried specimens of this animal, collected on our behalf by S.K. Tan (RMS). Gary Williams (California Academy of Sciences), based on images sent to him, was able to identify the Singapore sea pencil as a species of the pennatulacean *Lituaria* sp. Unlike more familiar pennatulaceans with bilaterally symmetrical, foliose colonies (e.g., Williams, 2011, fig. 7B, C, E, H, I), *Lituaria* belongs to the family Veretillidae in which colonies are radially symmetrical and cylindrical (Williams, 1995; see Williams, 2011, fig. 7A). The genus is unusual among pennatulaceans in having axes covered by polygonal depressions, each presumably corresponding to the location of a polyp, contrasting with the smooth axes seen in other genera.

The external similarity between *Pywackia* and *Lituaria* is clear in Figure 4. Colonies of *Lituaria* comprise straight axes, lacking bifurcations and tapering at their proximal ends, very like rods of *Pywackia*. Dimensions, however, are considerably greater than *Pywackia*: the largest specimen of *Lituaria* is 250 mm long with a maximum diameter of 6 mm. The smallest specimen in the collection is about 40 mm long with a maximum width of 1.82 mm (Fig. 5.1). Proximal ends of the skeletal axes taper gradually almost to a point (Fig. 5.1), while the distal growing tip has an axial prominence (Fig. 5.2). The comparison with *Pywackia* is made more compelling by the covering of polygonal modular units very similar to those of the Cambrian fossil: ridge-like longitudinal walls define shallow, cup-like polygonal modules (Fig. 5.1–5.5) over the entire surface of the skeletal axes except

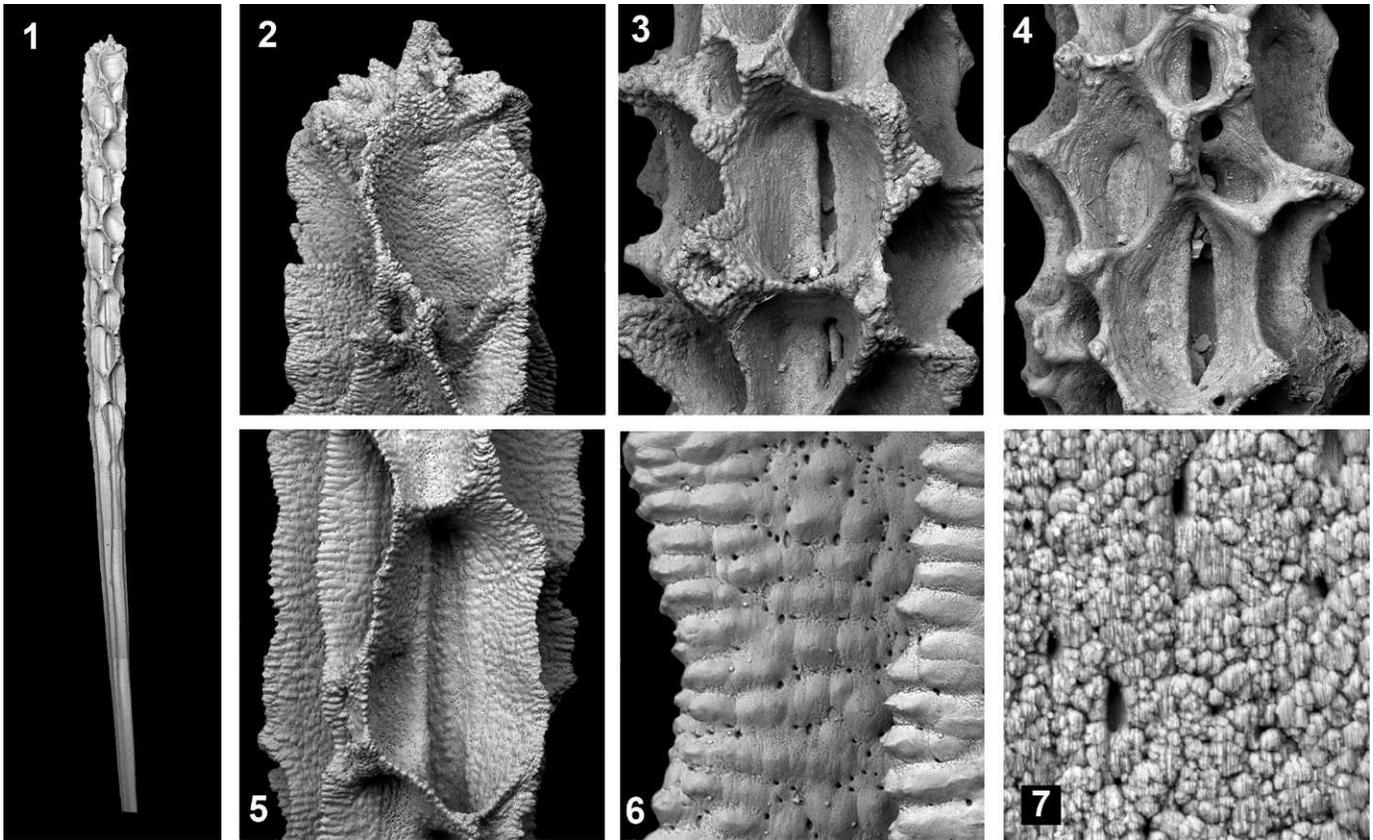


FIGURE 5—Back-scattered scanning electron micrographs of the axis of the pennatulacean octocoral *Lituaria* sp., Recent, sand flat near Changi Ferry Terminal, Singapore. 1, montage of small, almost complete specimen (proximal apex broken off), RMS ZRC.CNI.0935, $\times 3.4$; 2, distal tip, RMS ZRC.CNI.0935, $\times 17$; 3, 4, polygonal modules of variable size and with longitudinal fissures in some of the basal walls, RMS ZRC.CNI.0936 (dried, unbleached), both $\times 28$; 5, module with a longitudinal keel, RMS ZRC.CNI.0935, $\times 22$; 6, profile of the serrated edges of two walls, RMS ZRC.CNI.0935, $\times 110$; 7, microstructure of a skeletal wall surface with granular fabric and occasional pits/pores, RMS ZRC.CNI.0935, $\times 590$.

for the proximal extremities. The modules of *Lituaria* are elongate and typically measure about 1.3–2.3 mm long by 0.7–2.0 mm wide (cf. 0.27–0.59 by 0.15–0.38 mm in *Pywackia*). However, module shape and size shows considerable variation, and some of the modules are as little as 0.2 mm in diameter (Fig. 5.3). Longitudinal walls of the most proximally situated modules extend as low ridges towards the pointed proximal ends of the axes, very like those of *Pywackia* (Landing et al., 2010, fig. 2A, B). Elongate gaps can be observed on the basal walls of some zooids (Fig. 5.3, 5.4), recalling some *Pywackia* specimens, and longitudinal keels may also be present (Fig. 5.5).

Similarities between *Lituaria* and *Pywackia* are countered by a few notable differences, in addition to the size contrast between the modules. The walls of the modules are often prolonged at corners into broad, flattened spine-like structures (Fig. 5.4), a feature not seen in *Pywackia*. In addition, pustules occur over much of the outer parts of wall surfaces (Fig. 5.5). Related to these pustules are serrations developed at the edges of the walls in small specimens (Fig. 5.6). At high magnifications, the ultrastructure of the wall surface is distinctly granular, contrasting with the smooth walls of *Pywackia*, and small pits are present (Fig. 5.7).

DISCUSSION

Described as the first Cambrian bryozoan by Landing et al. (2010), *Pywackia baileyi* is sufficiently different from indisputable bryozoans to question its identification as a bryozoan. Notably, absence of branching and an encrusting base, the non-

tubular morphology of the modular units, the irregularity and morphology of partitioning walls within these modules, and the tapered proximal ends of the rods, are largely or totally inconsistent with a bryozoan affinity. The discovery of a modern pennatulacean octocoral showing striking morphological similarities to *Pywackia* allows an alternative hypothesis to be proposed: that *Pywackia* represents an octocoral. To evaluate the viability of this hypothesis it is necessary to consider aspects of the phylogeny, fossil record and biomineralization of octocorals.

Octocorallia is a subclass of anthozoan cnidarians that today includes sea pens (Order Pennatulacea), sea whips and fans (Order Gorgonacea), soft corals (Order Alcyonacea), some of which (e.g., *Tubipora*) have calcareous skeletons, and the biomineralized blue corals (Order Helioporacea). All octocorals are colonial and each polyp has eight tentacles, with a corresponding number of mesenteries. Biomineralization may be lacking or may take the form of calcareous spicules and/or calcified colony axes, depending on the species concerned.

While Octocorallia as a whole is believed to be monophyletic, the inter-relationships between different orders of octocorals have not been satisfactorily resolved, notwithstanding the molecular phylogeny of McFadden et al. (2006). Uncertainties in part reflect the fact that too few taxa of this very diverse and disparate group have been sequenced. With respect to the relationships between octocorals and other major groups of cnidarians, there are two alternative hypotheses: either Octocorallia are the sister-group of Hexacorallia and these two

subclasses together form the Anthozoa (Collins, 2009), or Octocorallia are the sister-group of Medusozoa (Park et al., 2012). Regardless of their relationships to other groups, octocorals are generally considered to be an ancient group of cnidarians: the calibrated molecular phylogeny of Park et al. (2012) estimated the divergence between octocorals and their sister-group to have occurred in the Neoproterozoic, about 700 Ma.

The fossil record of octocorals is patchy and poorly known, not least because many taxa are unmineralized. An early idea that *Charnia* and other frond-like fossils (rangeomorphs) are pennatulacean octocorals has lost credibility following detailed morphological comparisons between these Ediacaran fossils and modern pennatulaceans (Williams, 1997; Antcliffe and Brasier, 2007). Convincing octocoral spicules have been described from the Silurian (Bengtson, 1981). Some older fossils have been interpreted as axes of octocorals, notably *Echmatocrinus*, from the middle Cambrian (Burgess Shale) of British Columbia (Ausich and Babcock, 1998, 2000) and *Petilavenula* Cope, 2005, from the Lower Ordovician (Arenig) of Wales. Therefore, interpretation of *Pywackia* as an octocoral is consistent with the known fossil record of octocorals, which extends back with certainty to the Silurian and quite possibly to the Cambrian, as well as molecular estimates of the time of origin of Octocorallia. Moreover, it has been repeatedly suggested that Veretillidae, with their radially symmetrical colonies, are basal pennatulaceans (cf. Williams, 2011, p. 8).

Could *Pywackia* be a pennatulacean octocoral like its morphological modern analogue *Lituarina*? Having eliminated rangeomorphs from the fossil record of pennatulaceans, the oldest indisputable pennatulaceans date from the Late Cretaceous. Reich and Kutscher (2011) reviewed the fossil record of pennatulaceans and described some of the oldest known examples: calcitic axes of two species of '*Graphularia*' from the Maastrichtian of Germany. The substantial gap (>400 my) in the fossil record from the upper Cambrian *Pywackia* to the Upper Cretaceous '*Graphularia*', seems difficult to explain, let alone the even larger gap (~500 my) from *Pywackia* to *Lituarina*. It is unlikely that *Pywackia/Lituarina*-like fossils would have been completely overlooked, although *Lituarina* with its peculiar axis is poorly known even in the Recent and it is just possible that fossils have not been identified as such. Alternatively, it is conceivable that a clade bookmarked by these two genera lost biomineralization of the colony axis during its evolution before subsequently regaining it. This idea is hard to test but loss of biomineralization is feasible in view of the occurrence of Recent pennatulaceans without axial biomineralization, such as species of *Cavernularia*, a veretillid closely related to *Lituarina* (Williams, 1995).

Even if *Pywackia* is not a pennatulacean, the similarity between it and *Lituarina* provides a compelling octocoral alternative to the hypothesized bryozoan affinity of this Cambrian fossil. The straight, proximally tapered and unbranched axes of *Lituarina* covered by shallow calyx-like modules strongly resemble scaled-up *Pywackia* rods. At the very least, *Lituarina* demonstrates the capacity of octocorals to produce colonial skeletons that could easily be mistaken for bryozoans. Although there is a significant contrast in the size of *Pywackia* and *Lituarina*, the approximately four-fold module size difference (length 0.3–0.6 mm in *Pywackia* vs. 1.3–2.3 mm in *Lituarina*) is actually exceeded by the interspecific variation in autozoid diameters of <1 mm (in *Veretillum tenue*) to 7 mm (in *Umbellula durissima*) among the modern pennatulacean species described by Hickson (1916). It must be noted, however, that the calyx-like modules of *Lituarina* need not necessarily

correspond exactly to the zooids. Modern pennatulaceans examined by one of us (BB) at the MNHN, showed considerable variability in axis length even within a species.

Many living gorgonian octocorals were shown by Bayer and Macintyre (2001) to contain appreciable amounts of amorphous carbonate hydroxylapatite within their axes. McIntyre et al. (2000) suggested that this may indicate phosphatic biomineralization early in the evolutionary history of cnidarians. Indeed, the putative Ordovician (Volkhovian) octocoral *Nonnegorgonides* has a phosphatic axis (Lindström, 1978), while some early Cambrian spicules described by Bengtson (in Bengtson et al., 1990) as *Microcoryne* that resemble octocoral spicules are preserved in phosphate, although this may represent replacement of an originally calcareous biomineral. Could the skeleton of *Pywackia* be composed of original rather than diagenetic phosphate? As with some recently described hexacorals from the Lower Ordovician of China which are also preserved as phosphate (Balinski et al., 2012), it is difficult to determine whether the *Pywackia* skeleton was originally phosphatic. While not conclusive, the non-homogeneous, tripartite structure of *Pywackia* walls, with dense outer layers sandwiching a central layer containing voids (Fig. 2.10, 2.11), supports the interpretation that the skeleton comprises biogenic phosphate. An originally phosphatic skeleton would be further evidence against the bryozoan affinity of *Pywackia*, notwithstanding the occurrence of thin phosphatic linings in some Paleozoic bryozoans that may be of bryozoan origin (e.g., Conti and Serpagli, 1988).

In conclusion, *Pywackia* is here reinterpreted as the biomineralized axis of an octocoral with a very similar organization to that of the modern pennatulacean *Lituarina*. The living colony of *Pywackia* is envisaged as a small colonial animal with a mineralized axis covered by polyps, each polyp sitting over one of the polygonal calices. The colony is inferred to have lived with its proximal end buried in sediment, and the distal, polyp-bearing part oriented vertically in the water column, much like comparable modern pennatulaceans (e.g., Imahara and Ogawa, 2006).

Following the elimination of *Pywackia* from the Bryozoa, the search for unequivocal bryozoans of Cambrian age must continue. Of relevance in this respect are findings from both classical morphological and molecular phylogenetic studies of modern bryozoans suggesting that bryozoans are primitively unmineralized. The most basal clade of bryozoans in most analyses (e.g., Waeschenbach et al., 2012) is the freshwater class Phylactolaemata, which are completely uncalcified, and models of marine bryozoan evolution suggest that the first biomineralized stenolaemates of Ordovician age evolved from uncalcified ctenostome-grade marine ancestors (e.g., see Taylor et al., 2010). Unfortunately, no soft-bodied bryozoans have yet been identified in the classic Cambrian Lagerstätten such as the Burgess Shale or Chengjiang biota. The absence of soft-bodied bryozoans from younger Lagerstätten within the established range of the phylum (e.g., Hunsrück Shale and Solnhofen Limestone) does not provide any grounds for optimism that Cambrian Lagerstätten will furnish soft-bodied bryozoans. Preservation of soft-bodied Cambrian bryozoans by bioimmuration (see Taylor, 1990) is possible but unlikely because of the paucity of skeletonized encrusters capable of producing bioimmurations.

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