

Bryozoans from the early Cambrian Chengjiang Biota

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Abstract

Bryozoa are colonial, aquatic, generally sessile coelomate metazoans, with a retractable lophophore and U-shaped digestive tract. They are widely distributed and highly diverse in extant marine and freshwater environments. Current confident fossils of the earliest bryozoan only occur in the Early Ordovician, although molecular estimation date their origin in or prior to the early Cambrian, rendering the origin and early evolution of bryozoans are intensely debated. Here, we describe two cyclostomes, *Panpipora yunnanensis* gen. et. sp. nov. and *Corynotrypa* sp., having been recovered from the Cambrian Chengjiang Biota (~ 518 m.y.) in Southwest China. The bryozoans represent the earliest fossils of Bryozoa, predating the record of the phylum by more than 30 million years. Our finding reveals that the Bryozoa, as all other skeletonised metazoans, first evolved during the Cambrian Explosion, and it is congruent with estimation of molecular clock that the cyclostomes is the earliest biomineralised clade. *Corynotrypa* might be derived from unmineralized ctenostomes by stolonial mineralization and change of growth direction of polypides from vertical to creeping. The unmineralised frontal exterior wall might be a share character existed in all ancestral clades. Encrusting specimens that inhabited in muddy environments have been confirmed here, further suggesting that encrusting bryozoans underwent a profound ecological migration from soft- to hard-bottom facies from Cambrian to Ordovician.

Introduction

Bryozoans (also known as Ectoprocta) are colonial protostome metazoans¹ that are abundant and widely distributed in marine habitats and freshwater environments. They have occupied various communities and played an important role in carbonate deposition and reef construction in strata since the Early Ordovician. Despite a long research history of more than two centuries, the phylogenetic position of Bryozoa among metazoans^{2,3} and the evolutionary relationships within the phylum are both still uncertain⁴. Three classes have been established in the phylum Bryozoa, Phylactolaemata, Gymnolaemata and Stenolaemata. Molecular and anatomical data placed the Phylactolaemata as sister group of the Gymnolaemata + Stenolaemata^{3,5}. The Phylactolaemata has been regarded as the earliest branch of all bryozoans^{5,6}. Ctenostomes compose a unique order within the Paleozoic-aged Gymnolaemata and have been inferred ancestral to Stenolaemata^{7,8}. The stenolaemates have biomineralised skeletons. They exclusively inhabit marine environment. Corynotrypid cyclostomes are inferred to be earliest stenolaemates deriving from a ctenostome-like ancestor^{9,10}.

Compared with molecular and morphological data, investigations on the bryozoan fossils lagged far behind. Much of the speculations above were not supported by fossil evidences. Despite being repetitively argued that bryozoans must have already diversified long before the latest Cambrian based on morphological and molecular clock estimation^{11,12}, yet no unambiguous bryozoan fossils of Cambrian have been accepted^{13,14}. To date, the earliest unequivocal bryozoan fossils are trepostome *Prophyllodictya*, having been recorded in the Early Ordovician (Tremadocian, 485–477 Ma) from Central China^{14,15}. Remarkably, *Prophyllodictya* exhibits various exterior morphologies and complex interior

structures, suggesting that bryozoans most likely had been underwent a cryptic radiation of biomineralisation before the Early Ordovician^{15,16}. The latest Cambrian phosphatised *Pywackia* from southern Mexico has ever been described as bryozoans¹⁷, but was lately been inferred to be an octocoral^{4,15,18-20}. The earliest fossils of cyclostomes have been discovered in Dapingian (470–467 Ma) of Russian²¹. Cyclostomes and trepostomes are both characterised by mineralised skeleton that is resistant to degradation, whereas the cyclostomes firstly appeared later, and have never been abundant or diversified in the Palaeozoic⁶ like that of the trepostomes. Cornotrypids, as the inferred first mineralised clade that evolved from soft-bodied ctenostomes, could also only be dated back to the Middle Ordovician²². The explanation for the discrepancies between the molecular and the fossil data may be lack of knowledge available from early bryozoan fossils.

In this study, a new cyclostome bryozoan, as well as a specimen in open nomenclature, are reported from the Chengjiang Biota. They are served as the earliest bryozoan known fossils (Stage 3, early Cambrian, ~ 518 Ma), predating the record of this phylum by at least 30 Ma. The newly described bryozoans support the hypothesis that the Cyclostomata represents the earliest skeletonised lineage that may branch off from the non-biomineralized Ctenostomata^{10,16,23}, and is congruent with the speculation that the most earliest known stenolaemate is a corynotrypid species^{8,9}. The diverse mineralised bryozoans from the Chengjiang Biota, further support the well-established hypothesis that all metazoan phyla with mineralised skeleton have already evolved during or prior to the early Cambrian^{11,12}, just like the groups (*e.g.* Brachiopoda, Ectoprocta, Phoronida) that have ever been inferred to be closely related with bryozoans in phylogeny^{2,19}. The discovery of the soft-bodied frontal exterior wall of the earliest cyclostomes from Chengjiang Biota indicates that the calcified frontal exterior wall might not be an exclusive character of the order Cyclostomata, but a common and stem character that existed in all ancestral bryozoans. Encrusting bryozoans have never been expected in soft substrates^{22,24}. The Chengjiang bryozoans found in the laminated mudstone, might be the earliest and the only two encrusting examples for the Bryozoa. They inhabited in soft-bottom environment, indicating that the encrusting bryozoans likely had migrated or expanded from soft to hard substrate from Cambrian to Ordovician.

Systematics

The specimens described herein are deposited at the Yunnan Key Laboratory for Palaeobiology (YKLP), Yunnan University, Kunming, China. The morphology and classification of bryozoans follow those of Boardman et al.²⁵ and Ernst¹⁰.

Phylum Bryozoa

Family Corynotrypidae

Genus *Corynotrypa*

Type species. *Hippothoa delicatula* James, 1878, Middle Ordovician of North America and Estonia (original designation); Upper Ordovician of North America(revised).

Revised diagnosis. Colony is encrusting and uniserial, in straight line or branching by lateral ramification and/or bifurcation. Astogenetic changes exhibit in early parts of colonies (primary zone), lateral branches occur in secondary zones. Zooids are monomorphic in each colony. They are elliptical, filiform, or clavate, narrow in the proximal portion, partly inflated in the middle, and dome-like distally, with a small sub-circular aperture distally positioned or centrally located. The frontal exterior walls could be calcified or not. The aperture may be ornamented with variable peristomes and is sometimes occluded by a terminal diaphragm.

Distribution. Cambrian Stage 3 to the Upper Permian; global.

Remark. The generic diagnosis of *Corynotrypa* was revised by Taylor and Wilson²². According to the Chengjiang specimen, three characters have been amended here: 1) Colony could form a straight-line without bifurcation or ramification, with new zooids only budding distally and in parallel to the parent zooids; 2) Aperture is centrally located, not only limited to a distally position; 3) The frontal exterior walls could be mineralised in calcified skeleton, or in soft-bodied perhaps without any biomineralisation.

***Corynotrypa* sp.**

Figures 1a-c

Material. Single specimen YKLP 15242a, b. from Stage 3 (*Eoredlichia–Wutingaspis* Zone) of the Cambrian Yu'an-shan Formation (Ercaicun outcrop), Haikou, Kunming, China. YKLP15242b is the counterpart of YKLP 15242a.

Description. Encrusting uniserial, straight-line colony with simple fusiform zooids (Fig. 1a, b). The colony is 37.5 mm in length. The proximal portion of the zooid is canal-like, at least 21 mm in length. Zooid outline could not estimate exactly on account of the overlapped tentacles soft tissues nearby. The basal wall might be mineralised (Fig. 1c), 1.3 mm in length, and 1.1 mm in width. Aperture is centrally located and 0.52 mm in diameter (Fig. 1c). The width of the canal-like partitions varies from 0.24 to 0.48 mm. No ancestrula are observed. New zooids only bud from the distal end of the parent zooid, making all zooids are (almost) parallel to each other. No bifurcation or ramification is observed. Between 18 and 26 tentacles are radially distributed from the centre outward to the zooid margin. The tentacles are 0.6-0.7 mm in length, and ~ 0.01mm in width. Lateral bands of cilia that extend along both sides of each tentacle are poorly preserved (Fig. 1c₁), whereas the points from which the cilia rise can be determined by the thickening of the tentacles (Fig. 1c₁).

Remarks. The incomplete preservation of the specimen do not allow exact species-level identification, especially due to the absence of the early growth stages and the length of the canal-like structure between two adjacent zooids. Notably, the Chengjiang *Corynotrypa* displays morphological similarities to

the stolon of *Ropalonaria* (Ctenostomata) which may be partially calcified and thus preserved in the rock record when they are (partly) embedded via excavating the surface of a calcified host²⁶. Nevertheless, the Chengjiang *Corynotrypa* has been discovered in a muddy shale, not on the surface of calcified host. Moreover, a relatively long narrow canal-like structure between two adjacent zooids, a central aperture and unmineralised frontal exterior walls, are all exclusive characters of the Chengjiang *Corynotrypa*.

Family Sagenellidae

Genus *Panpipora* Wei n. gen.

Material. Single specimen YKLP 15241a, b from Stage 3 (*Eoredlichia*–*Wutingaspis* Zone) of the Cambrian Yu'an-shan Formation, Dongshancun (outcrop), Kunming, China.

Type species. *Panpipora yunnanensis* Wei n. gen. and sp., early Cambrian, China.

Diagnosis. Encrusting, oligoserial, single-layered colony with simple, tube-like autozoecia. One or two zooids buds at the front end of the parent zooid. Chambers of contiguous zooids are long and tubular, share a common wall with the zooids nearby, and vary slightly in width along the growth axis. Apertures are rounded and accompanied by a few heterozooids. Nanozooids are inverted and funnel-shaped, occupied the centra of zooidal apertures. The boundary between two adjacent walls can be observed on the zooidal bifurcating points. Septa are present.

Occurrence. Presently known from the type locality.

Discussion and comparison. The characteristics of the Order Cyclostomata have been exhaustively summarized^{25,27}. The bryozoan *Panpipora* n. gen. noted here is assigned to the Cyclostomata in the light of its encrusting colonies, long and tube-like autozooids, rounded zoecial apertures, and low heterozooid densities. The presence of nanozooids accompanied by zoecial apertures nearby is a distinct character of cyclostomates²⁶. The encrusting and oligoserial zoariums of *Panpipora* are similar to that of *Sagenella* Hall 1851. Nevertheless, the tubes of *Sagenella* are marked by strong transverse wrinkles²⁶, without any heterozooids or nanozooids, both of which have performed multiple functions, including protection, reproduction, locomotion, respiration and structural support²⁷.

Etymology. English “panpipe”, for an instrument composed of a series of pipes that is morphologically similar to the fossils described here.

Panpipora yunnanensis n. sp.

Figures 1 d-g

Material. The same as for the genus.

Holotype. YKLP15241a from the Lower Yu'an-shan Formation in the Dongshancun outcrop, with YKLP15241b as its counterpart.

Diagnosis and discussion. As *P. yunnanensis* is a type species, the diagnosis and discussion of *P. yunnanensis* n. sp. is the same as for the genus.

Description. Encrusting, unilamellar and multiserial colonies, extending 6.6–15.6 mm in length, 3.7–5.5 mm in width, and 0.23–0.42 mm in thickness. Zooids are tube-like, 1.2–1.3 mm in length, and 0.75–1.0 mm in width (Fig. 1d, e). Apertures are circular, 0.17–0.20 mm (mean: 0.18 mm) in diameter and space at an interval of 1.18–1.67 mm (mean: 1.2 mm) apart along the zooidal growth direction (Figs. 2f, g). Heterozooids are developed nearby the aperture and have diameters of 0.06–0.09 mm. Each zoecial aperture is surrounded by 1–3 heterozooids. The nanozooids are tube-like and 0.025–0.038 mm in diameter. The centre of each aperture is occupied by 1–3 outside-projecting nanozooids, like an inverted funnel. Zoecial walls are slightly wavy along the growth direction, and is 0.04–0.05 mm in thickness, up to 0.1–0.13 mm in the bifurcating regions (figs. 2a, b).

Etymology. '*Yunnanensis*' is a combination of the province of Yunnan, in which the bryozoan was first discovered, and the Latin suffix '-ensis', indicating a place name.

Evolutionary Importance

Bryozoans are exclusively sessile colonial animals that mostly inhabit in marine environments and rarely occur in freshwater environments. They have plastic morphology in terms of zooids and colonies, whereas in a unitary species colony, the majority of zooids are in homomorphy (except polymorphism), like some type of modular units, and thus bryozoans are also known as polyzoan.

Cambrian explosion is characterised by the rapid appearance of the majority of phyla of modern animal life. Especially in the interval from Cambrian Stage 2 to Stage 3, biomineralisation bloomed in great abundance. Many metazoans evolved a variety of mineralised shells or carapaces in response to predation pressure²⁸. Despite putative bryozoans have been repeatedly noted in Cambrian^{17,23}, yet none of these fossils are convincing^{14,20}. Bryozoa is among the handful phyla and the unique skeletonised group that is still lacking representatives in the Cambrian Explosion^{6,20}. The discovery of the Chengjiang bryozoans indicates that the Bryozoa had shown up in the Stage 3, like coeval biomineralised brachiopods²⁹, soft-bodied phoronids^{30,31} and entoprocts³² that have been inferred to be closely related. All skeletonised metazoan phyla first appeared by no later than the early Cambrian.

Plenty of studies has been on intra-subgroup relationships and evolution of bryozoans based on colony and zooid morphology, life histories, ecological habits and etc.^{8,27,33}, with particular interests focused on the gene or genome based data^{1,2,5,34}. Some agreements on molecular phylogeny of bryozoans have been achieved. Phylactolaemata has been supposed to be the most basal extant class¹⁹, of which all members live exclusively in the freshwater, lack biomineralised skeletons, and consequently have no

indisputable fossil record⁴ except for the Permian chitinous statoblasts³⁵. Ctenostomes have been inferred to be the ancestor of all skeletonised bryozoans^{10,16,23}. They are also soft-bodied, without biomineralisation, and thus seldom fossilised except for some examples formed by borings^{36,37}, bioimmuration^{38,39} or lithoimmuration⁴⁰. All ctenostome remains are negative relief or natural mould, without any information about their internal structure and soft parts.

Largeststätten are characterised by the preservation of soft tissue of metazoans. They have been reported repeatedly throughout the geological history. Especially in Cambrian, many biotas yielding fossils with soft tissues have been described in various locations globally (e.g. Chengjiang and Guanshan biotas from South China, Burgess Shale-type Biota from Canada, Sirius Passet Biota from Greenland etc.). Most of the biotas above have attracted wide attention^{28,41,42}. In the celebrated Chengjiang Biota, despite extensive investigation has been on various species³¹, yet no remain of soft-bodied bryozoans has been reported until now. The missing of phylactolaemates or ctenostomes in all Cambrian biotas may be closely related with the lacking of degrade-resistant tissues⁵, such as cuticle which could be exquisitely preserved in Largeststätten.

Cyclostomata has been inferred to be the earliest skeletonised clade and the out-group to all other Palaeozoic stenolaemate orders according to the morphological and molecular evidence²⁴, whereas the earliest cyclostome species (*Gorjunovia*) have been noted in the Middle Ordovician²¹, later than the early Ordovician trempostome *Prophyllodictya*¹⁵. Based on the fossil stratigraphic extension, some authors argued that the cyclostomes derived from the Palaeozoic trempostomes^{16,43}. Obviously, the fact that the predicted bryozoans are difficult to find does not exclude their existence in undiscovered place. The unexpected unavailability of bryozoans from early strata can be cause by their extremely low diversity, abundance or limited geographic distribution in the early Cambrian^{6,44}, and thus leading them undiscovered hitherto. The discovery of the Chengjiang cyclostomes in the early Cambrian, is congruent with the molecular and morphological inferences that the Cyclostomata is the first mineralised stenolaemate. The ancestor of this animal phylum might have existed in or prior to the early Cambrian⁴, as with the hypothesis on sponges⁴⁵, perhaps in the forms of soft-bodied (e.g. phylactolaemates and ctenostomes), but not preserved as fossils.

Corynotrypa (cyclostomes) has been supposedly to be the most basal known genus among stenolaemates. It has been deduced to be derived from a ctenostome-like ancestor^{4,9} because *Corynotrypa* and ctenostomes share a highly similar simple skeletal construction and a runner-like encrusting colony without any polymorphism^{7,46}. Nevertheless, the earliest *Corynotrypa* fossils have been noted in the Middle Ordovician, later than that of *Prophyllodictya*. The bryozoan fossil from the early Cambrian Yu'anshan Formation support the hypothesis that *Corynotrypa* is the earliest representative of mineralised stenolaemate, and may be the best evidence to depict the morphological evolution between *Corynotrypa* and ctenostomes.

Ctenostomes might evolve into *Corynotrypa* by stolon mineralization and change of growth direction of polypides from vertical to creeping. *Corynotrypa* was inferred to have evolved from ctenostomes through division of the body cavity into two parts⁴⁶. The outer part mineralised and became calcified zooidal wall, while the inner part remained its soft-bodied, perhaps play as membranous sac that could protrude tentacles by the muscles⁴⁷. The flatten and partially distorted stolon of the Chengjiang *Corynotrypa* is an evidence for its quality of being soft and easy to distort, likely in uncomplete biomineralisation. The fully exposure of tentacles may suggest that polypides were enclosed by a thin layer of soft tissue, rather than a calcified wall. In that case, the frontal exterior walls of the Chengjiang *Corynotrypa* might not be biomineralised, and thus could easily degrade in the process of fossilisation. From ctenostomes (*e.g. Ropalonaria*) to the Chengjiang *Corynotrypa*, the stolon might biomineralize and the fusiform internodes eventually acted as a basal wall of the zooid like that in *Corynotrypa*. The unmineralised frontal exterior wall, together with the slightly biomineralised basal wall, formed the zooids that were capable to completely accommodate the polypides. All ctenostomes have soft-bodied tubular zooids, in which the polypides can vertically extend, with centrally located openings in the stolon internodes, whereas in the Chengjiang *Corynotrypa*, the zooids are creeping in fusiform outline, with distal openings in the unmineralized frontal exterior wall of zooids. Compared with the upwards tubular zooids of ctenostomes, the recumbent zooids of the Chengjiang *Corynotrypa* would limit the vertical extension of the polypides and ultimately lead to a creeping growth.

Ctenostomes and the Chengjiang *Corynotrypa* rooted themselves on the internode or the basal wall respectively. Because of the their unmineralised zooids or soft-bodied frontal exterior wall, both ctenostome and the Chengjiang *Corynotrypa* could change the outline of polypides and flap around when they encountered water flow. This outline change and flapping ability could buffer the impact of the water flow, and could be interpreted as an adaptive strategy to the unsound connection between the Chengjiang *Corynotrypa* colony and the soft bottom. The frontal exterior wall of the Chengjiang *Corynotrypa* is inferred to be soft-bodied, whereas all *Corynotrypa* species have been noted with calcified frontal exterior walls since the Middle Ordovician. From early Cambrian to the Middle Ordovician, biomineralization perhaps happened in the frontal exterior wall of *Corynotrypa*. This biomineralisation might completely limit the vertical growth of the polypides and lead to their creeping growth. The biomineralisation of the whole zooidal walls of the Chengjiang *Corynotrypa* could be an adaptive strategy to the pressure of predation, just like that of the small shelly fossils in Stage 2, Cambrian most of which retreated themselves into shells to fend off predators. The biomineralised frontal exterior wall might not be an exclusive character of the order Cyclostomata, but a share character that existed in all bryozoan orders initially. The difference between Cyclostomata and other bryozoans is the former acquired biomineralized frontal exterior wall lately, but the other orders did not. Accompanied by the mineralization of the front exterior wall, *Corynotrypa* might had also undergone remarkable evolution by complexity of budding patterns. Hitherto, all known *Corynotrypa* colonies are characterised by branching via bifurcation and/or lateral ramification, with distal apertures. The Chengjiang *Corynotrypa* contain a daughter zooid distally, without any bifurcation or branching, thereby making the long axis of the parent and daughter zooids

(nearly) parallel. The bifurcation or branching might not be the ancestral characters, but a derived trait that evolved later.

Corynotrypa species have been inferred to be opportunistic²², and were more frequent in relatively unstable environments because they were harder to break or prey upon²⁷. Uniserial colonies are highly directional, which increases the opportunity for occupying favorable refugia on a heterogeneous terrain⁴⁸. Nevertheless, zooids in a chain without neighbors have limited abilities to protect themselves, and thus any zooid has a high risk of dying, while the probability that some zooids in the colony will find a refuge and survive is also high²⁷. The great distance (long stolon between adjacent zooids) of the Chengjiang *Corynotrypa* would have been beneficial for the rapid expansion and for minimizing the mortality risk of the colony. Compared with the uniserial *Corynotrypa*, multiserial colonies (e.g. *Panpipora yunnanensis*) are inferred to predominate in stable environments. *Panpipora yunnanensis* exhibits heavily calcified zooids and multitype zooids which could be closely collaborative with each other. For example, the *Panpipora* nanozooids might be functioned as the cleaner or/and protector for the polypides surrounding the zooidal apertures.

Cyclostome tentacles, as soft tissues, were generally difficult to be preserved in the fossil record. In modern aqueous environments, the polypides of cyclostomes have 8–17 tentacles, with a median of 10⁴⁴. The tentacle length of living, full-sized cyclostome polypides ranges from 145–1041 μm , with a median of 331 μm ²⁷. The Chengjiang *Corynotrypa* possesses a large number (18–26) and long tentacles (600–700 μm). The number of tentacles has been inferred to be correlated with the spacing between centres of adjacent autozooids⁴⁹. Obviously, the Chengjiang *Corynotrypa* has the longest stolon between two adjacent zooids. That is congruent with the large number of the Chengjiang *Corynotrypa* tentacles. The long and dense tentacles of *Corynotrypa* are inferred to an adaption to the muddy and relatively quiet environment therein. The strata yielding the Chengjiang Biota are mainly laminated mudstone. They deposited in a marine basin influenced by weak bioturbation and occasional storms³¹. The laminated mudstone of the Yu'an-shan Formation indicates that the habitat occupied by bryozoans were in low turbulence, being filled with clay particles. The muddy water would greatly reduce the penetration of sunlight, and thus was inhospitable to the survive of phytoplankton which were the main food of many organisms. Because of the shortage of phytoplankton near the sediment-water interface, the encrusting bryozoans would starve to death if they did not improve their filter feeding efficiency. Meanwhile, the laminated mudstone is inferred to deposit in a quiet environment, with slow-flowing water. The low velocity of water means less food particle was flowing through the bryozoan tentacles in the same time interval, making it less efficient to acquire food. Apparently, the long and dense tentacles of the Chengjiang *Corynotrypa* might give rise to a dense feeding capacity and a broad filter-feeding range, thus represent an adaptive strategy to the quiet and turbid environment.

Panpipora, as the earliest genus of Sagenellidae noted in the early Cambrian Chengjiang Biota, might not represent most basal clade in this family because of its polymorphism of zooids. The heterozooids and nanozooids could play the roles as cleaner and protection, indicating a close collaboration among

different polypides²⁷. *Sagenella* is characterized by encrusting, oligoserial, and single-layered colony that is ornamented by wrinkle structure. It has tubular zooids without any heterozooids. In comparison with the Chengjiang *Panpipora*, *Sagenella* seems to retain a simpler morphology though *Sagenella* could only be dated back to the Ordovician (Floian). The zooidal structure of *Panpipora* suggests that it had likely experienced a complex evolution process. The ancestral sagenellid group, likely possesses a similar or simple zooidal structure like that of the *Sagenella*, and may have been preserved in the strata in or prior to the early Cambrian, just not yet discovered.

Encrusting bryozoans have been considered to limit to patches of hard substrates or single shell fragments or grains of sand⁵⁰ since the Middle Ordovician. Single-layered, multiseriate encrusting cyclostome bryozoans are almost ubiquitous on Mesozoic hard substrates⁵¹. Clearly, the Chengjiang bryozoans did not inhabit in hard grounds, but rather muddy, soft bottom. From early Cambrian to Ordovician, a significant ecological expansion or migration of the encrusting bryozoans is deciphered herein from the soft muddy habitats to the hard carbonate or shelly grounds. The absence of *Corynotrypa* in strata of this time interval could be a result of exceedingly low abundance and/or species diversity, and poor preservation which may limit their recognition and lead to them being overlooked. As one of the earliest opportunistic encrusters, they were able to quickly occupy newly available habitats (e.g. hard carbonate), yet could not defend their territories against the invasion (e.g. *Amplexopora*)²². Because of this, *Corynotrypa* could only be patchily distributed at extremely low abundances and diversities in geological time.

Cyclostomata is an enigmatic clade that never flourished during the Palaeozoic⁴⁴. The oldest cyclostome fossil is *Gorjunovia* from the Dapingian (~470 Ma) of Russia²¹, much later than the first appearance of the Tremadocian trepostomes (~488 Ma) from South China⁵². Compared with the Dapingian cyclostomes, the Chengjiang fossils (~518 Ma)⁵³ predate the first appearance of the phylum Bryozoa by >30 Ma, and also predate the Order Cyclostomata by >48 Ma and make this group can be traced back to the early Cambrian.

The Chengjiang *Corynotrypa* is the earliest bryozoan fossil to date, whereas it is unlikely represent the ancestor of this phylum. Soft-bodied phylactolaemates and ctenostomes are inferred to be ancestral clades of bryozoans. They both have potential to be preserved as fossils. For examples, ctenostomes still could be preserved as fossils via lithological and organic overgrowth or as boring trace fossils in the Mesozoic^{23,37,39,40,54}. Phylactolaemates could be found as organic statoblasts in the Permian³⁵. Therefore, it is possible to find ctenostome fossils within the hard parts of other fossil organisms (e.g. brachiopods, hyoliths, trilobites, etc.) in the carbonate or other facies (e.g. small shelly fossils in phosphate), in which the ctenostome fossils could previously misinterpreted as trace fossils or sedimentary structure. Meanwhile, small carbonaceous fossils have been discovered in many Lagerstätten globally. The earliest phylactolaemate were probably marine organisms²⁴. There is a possibility to trace the phylactolaemate fossils through investigation on the small carbonaceous fossils in Lagerstätten globally. Moreover, stenolaemates (except cyclostomes) went extinction successively

during the Permian and Triassic, while cyclostomes seemed undisturbed by the crisis in generic diversity¹⁰. The cyclostomes survival across the Permian-Triassic boundary, as well as the rapid recovery in the Mesozoic¹⁰, suggest that these organisms are highly adaptable and can endure drastically environmental changes. Hence, cyclostome specimens may also exist in some unexpected and under-sampled habitats in and/or prior to the early Cambrian.

Geological Setting

Bryozoan specimens were collected from the lower part of the Yu'anshan Formation in the Dongshancun and Ercaicun outcrops on the south-western margin of the Yangtze Platform, Kunming, China (Fig. 3a). The geographic location and stratigraphic sequence of the Ercaicun outcrop have been investigated⁵⁵. Many palaeobiological, stratigraphic, geochronological and isotope geochemical studies have been conducted on the early Cambrian deposits that have yielded the Chengjiang Biota in Kunming and nearby areas (Luo et al., 1984; Zhu et al., 2001)^{56,57}.

The bryozoan specimen sampled from the Ercaicun outcrop seems to be earlier than that from the Dongshancun outcrop. The strata (Yu'anshan Formation) yielding the Chengjiang Biota are limited in the *Eoredlichia–Wutingaspis* Zone, Stage 3, Cambrian. In the Ercaicun outcrop, the bryozoan specimen was collected at the lower part of the Yu'anshan Formation, ~0.8 m above the top of the black siltstone, while in the Dongshancun outcrop, it was sampled at the middle part, ~24 m above the top of the black siltstone. The black siltstone in the Yu'anshan Formation has been considered to deposit in typical anoxic facies⁵⁷. It is widespread, with similar lithology, stratigraphic structure and comfortably contact with the overlying strata (Fig. 3b) in Yunnan Province. The black siltstone could be an event stratigraphic unit, as a significant index of regionally stratigraphic division and correlation. Actually, the black siltstone is correlated with *Parabadiella* Zone which could be stratigraphically correlated throughout the Yunnan Province. The top surface of the black siltstone could be the boundary between *Parabadiella* and *Eoredlichia–Wutingaspis* zones, is referred as isochron herein. In that case, *Cornotrypa* collected from the Ercaicun outcrop from the Yu'anshan Formation could be the earlier than that of the bryozoan from the Dongshancun outcrop.

Methodology

Bryozoans were sampled from the muddy and silty shale of the Lower Yu'anshan Formation. The specimens were prepared with steel needles under a stereo-microscope, and were photographed by a camera (Nikon D3) and a stereo-microscope (Leica M205C, Leica Camera AG, Germany). The morphological details and chemical composition of the fossils were investigated using a FEI Quanta 650 (FEI Co., USA) scanning electron microscope (SEM) equipped with an energy dispersive X-ray spectrometer (EDX) in YKLP.

Preservation

Bryozoan specimens were collected from yellow-green (originally grey) laminated mudstone. Sporadic fragmentary linear algae and brachiopod shells were also discovered in the horizon and the layers above or below. The holotype (YKLP15241a) of *Panpipora* is dark yellow, while the counterpart (YKLP15241b) is dark grey. It is preserved well, only lacking the ancestrula and a small portion nearby. The zooid wall, apertures, nanozooids, heterozooids, and septa of YKLP15241 are exquisitely preserved, indicating that the specimen has likely been preserved in situ. The missing ancestrula and separately nearby portion might have been scattered by water currents. The other specimen, *Corynotrypa* (YKLP15242), is reddish brown, and can be readily distinguished from the yellow host rocks. *Corynotrypa* is almost compressed, revealing the interior construction (e.g. tentacles and aperture) of the zooids. Only one zooid and adjoint partial stolon is observed. The incomplete preservation of the *Corynotrypa* colony may also attributed to taphonomic degradation via the water current.

The elemental composition of *Panpipora* (YKLP15241b) was analysed via SEM–EDX. The results showed that this fossil is mainly composing of Fe, O, Al, Si, Mg, S and minor amounts of C and K (Fig. 2e). Iron is concentrated in the apertural regions, while C, O, Na, S, and K are evenly distributed throughout the fossil. Aluminum, Si and Mg covers the fossil except for the apertural area. Scanning electron microscopy reveals the existence of framboid pyrite overlapping the fossil. In comparison with Fe, the S content is less, suggesting that the pyrite was oxidised into iron oxides. The periostracum, which may serve as an organic resource that facilitates local anoxia during degeneration and decomposition, may account for the concentration of Fe in and around the aperture region of the fossil body. Though it is a key skeletal element, the Mg in the fossil is likely derived from the host rocks, given its even distribution and extremely low content within the fossil and sediments (Fig. 2e).

Panpipora may originally have a calcareous zooid skeleton, but the calcareous walls were decomposed during diagenesis and could not be detected. Most bryozoan zooids contain an outer cuticle, calcareous skeleton and an inner epithelial that lines the body cavity. The calcareous skeleton, as the thickest layer, is most likely to be preserved as fossils. Aside from esthoniporines, with their high-Mg calcitic skeletons⁵⁸ and specimens without mineralised skeletons, bryozoan fossils are typically preserved as low-Mg calcitic skeletons⁵⁹. Indeed, except for C, most of the original components of the Chengjiang fossils have not been preserved due to diagenesis. Whether biomineralised or not, these fossils would have commonly been decomposed and preserved as pyrites (or Fe-oxides), Fe-rich aluminosilicates or apatite during diagenesis⁶⁰. The elemental compositions believed to originally be present in the mineralised skeletons (e.g. shells of hyoliths, spicules of cancelloriids or sponges, etc.) could not be recovered from the vast majority of fossils in the Chengjiang Biota. For examples, cancelloriid specimens have preserved sclerites (originally calcitic) that possess internal diagenetic crystals, with Fe-oxide internal cores enveloped by Fe-rich aluminosilicates⁶¹. There are abundant and diversified siliceous sponges in the Chengjiang Biota, whereas silica has never been found in the spicules of this group, but mainly carbon film for the unweather species, or clay and iron oxide for the weathered sponge fossils detected by SEM are Fe-oxide⁶².

Panpipora might have ever possessed highly calcified zooid wall that was later filled with pyrites, and thus it could be in three-dimensional preservation with low compression ratio. The average width and height of *Panpipora* zooids (YKLP15241a) were 0.9 mm and 0.3 mm respectively, and they exhibited an extremely low compression ratio (~ 0.66), perhaps representing one of the most exquisitely preserved Chengjiang fossils recovered to date. The three-dimensional preservation of the Chengjiang bryozoan indicates that the zooid walls might be in calcification, and thus could withstand the pressure from the sediments above without breakage or severe deformation. Indeed, most fossils in Chengjiang Biota are highly compressed, except for the muddy-filled intestinal tract or the specimens with mineralised skeletons (e.g. sponge, hyoliths, etc.). We ascribe the low compression ratio of the *Panpipora* to its mineralised skeleton, not the muddy filled intestinal tract. The average compression ratio for the Chengjiang fossil as a whole may be 0.1-0.2^{28,31}, but the compression of the mineralized bones in the fossil is clearly less than its overall compression. The spicules of *Halichondrites* can be seen in three-dimensions, with rounded cross sections without any obvious deformation⁶³. A similar degree of preservation can also be observed in the spicules of cancelloriids²⁸. The spicules of sponges and cancelloriids are often completely pyritised which in turn retains the dimension and relief of these skeletal structures. Despite cancelloriid spicules are originally hollow, yet their cavities are commonly fulfilled with pyrites and sediments, both of which would make the cancelloriid spicules more resistant to burial pressures and results in low compression ratios. Alternatively, the internal cavities of *Panpipora* zooids could also have been filled with pyrite and sediments. In the areas in and around apertures, framboid pyrites can be observed (Fig. 2d, e). The internal cavities of bryozoan zooids may be infilled by pyrites and sediments, making them preserved in three-dimension like the spicules of sponges (or cancelloriids) from the Chengjiang Biota.

The different compression between *Panpipora* and *Corynotrypa* may be closely related to the degree of the zooid wall mineralisation. Zooid wall of the latter may not undergo an utterly mineralisation, like the wrinkled remains of *Chuandianella* carapaces which could be heavily compressed as a result of compaction³¹. The partially twisty stolon-like structure (Fig. 2a) also supported that the *Corynotrypa* body might be soft and thus could be deformed and heavily compressed in the process of preservation.

The complete exposure of tentacles and the flattened zooid of the Chengjiang *Corynotrypa* both suggest that the internal soft apparatus have not been encapsulated by the mineralized external wall but encompassed by some soft-tissue that were not likely preserved as fossils. The external walls of *Corynotrypa* might be entirely soft-bodied without any fossilized component. The radial tentacles were preserved in oral view, indicating they were protruding out their tentacles when they were submerged by sediments, instead of being housed within a zooid. The covering area of the full extended tentacles are always larger than that of the cross section of the beneath mineralized zooid. The fusiform region could not represent the outline of the mineralized zooid, but the area occupied by the tentacles and soft tissues nearby. Some fractures and deformations of the tentacles are concentrated on the outer edge of the inner and convex area (Fig. 1c) where the terminal tentacles have been interrupted, offset to the right. Correspondingly, the Chengjiang *Corynotrypa* polypide might have a displacement to the left in the process of preservation. In that case, the aperture of the Chengjiang *Corynotrypa* likely located in the

place near the right extremity initially. The inner and convex area is inferred to be the basal wall of the Chengjiang *Corynotrypa* zooid.

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Figures

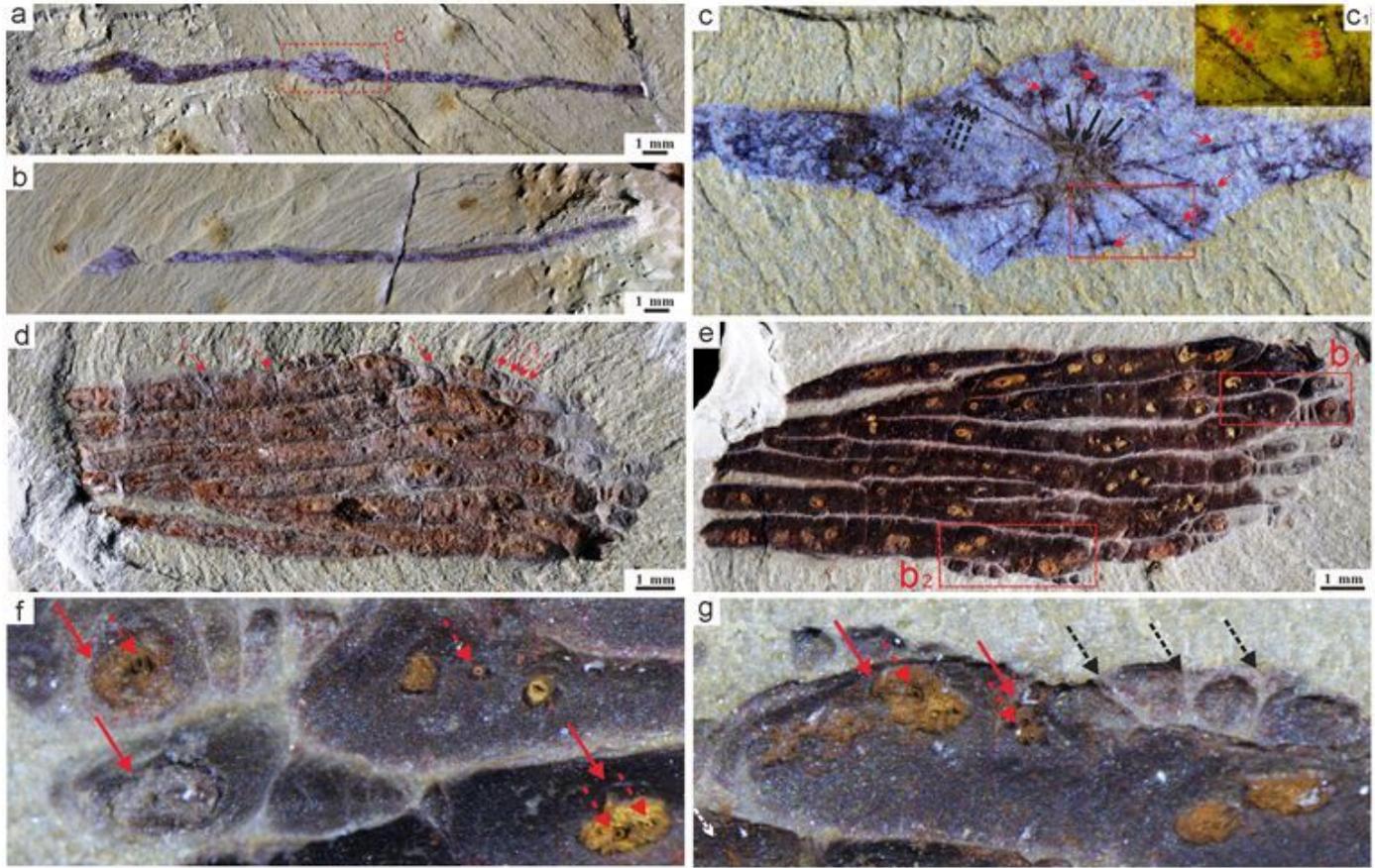


Figure 1

Early Cambrian bryozoan from the Yu'an-shan Formation in Kunming, South China. (a) *Corynotrypa* sp., YKLP 15242a, Ercaicun, Haikou, Kunming. (b) YKLP 15242b, counterpart of 15242a. (c) Close-up view of red rectangle in (a) showing aperture (black arrows), tentacles (black dotted arrows) and margin of the basal wall (red dotted arrows). (c1) Close-up view of red rectangle in (c) showing tentacles with lateral cilia (right red arrows) or cilia rudimentary (left red arrows) under a fluorescence microscope. (d) *Panpipora yunnanensis* gen. et sp. nov.. Holotype, YKLP 15241a, showing septa (right dotted arrows) Dongshancun, Anning, Kunming. (e) Counterpart of specimen A, YKLP 15241b. (f) Close-up view of red rectangle in (e) showing apertures (long red arrows) and nanozooids (short dotted arrows). (g) Close-up view of red rectangle in (e) showing septa (black arrows), apertures (red arrows) and nanozooids (short dotted arrows).



Figure 2

Preservation and morphological details of *Panpipora yunnanensis* gen. et sp. nov.. (a) Partly photograph of *Panpipora yunnanensis*. (b, c) Close-up view of red rectangle in (a) in the secondary electron (b) and the back-scattered electron detector (c), showing apertures, heterozoids, nanozoids and bifurcating wall. (d) Close-up view of red rectangle in (c), showing aperture with framboid pyrites. (e) Elemental mapping by EDX of Fig. A, illustrating the superposition of Fe in and nearby the bryozoan aperture and heterozoids.

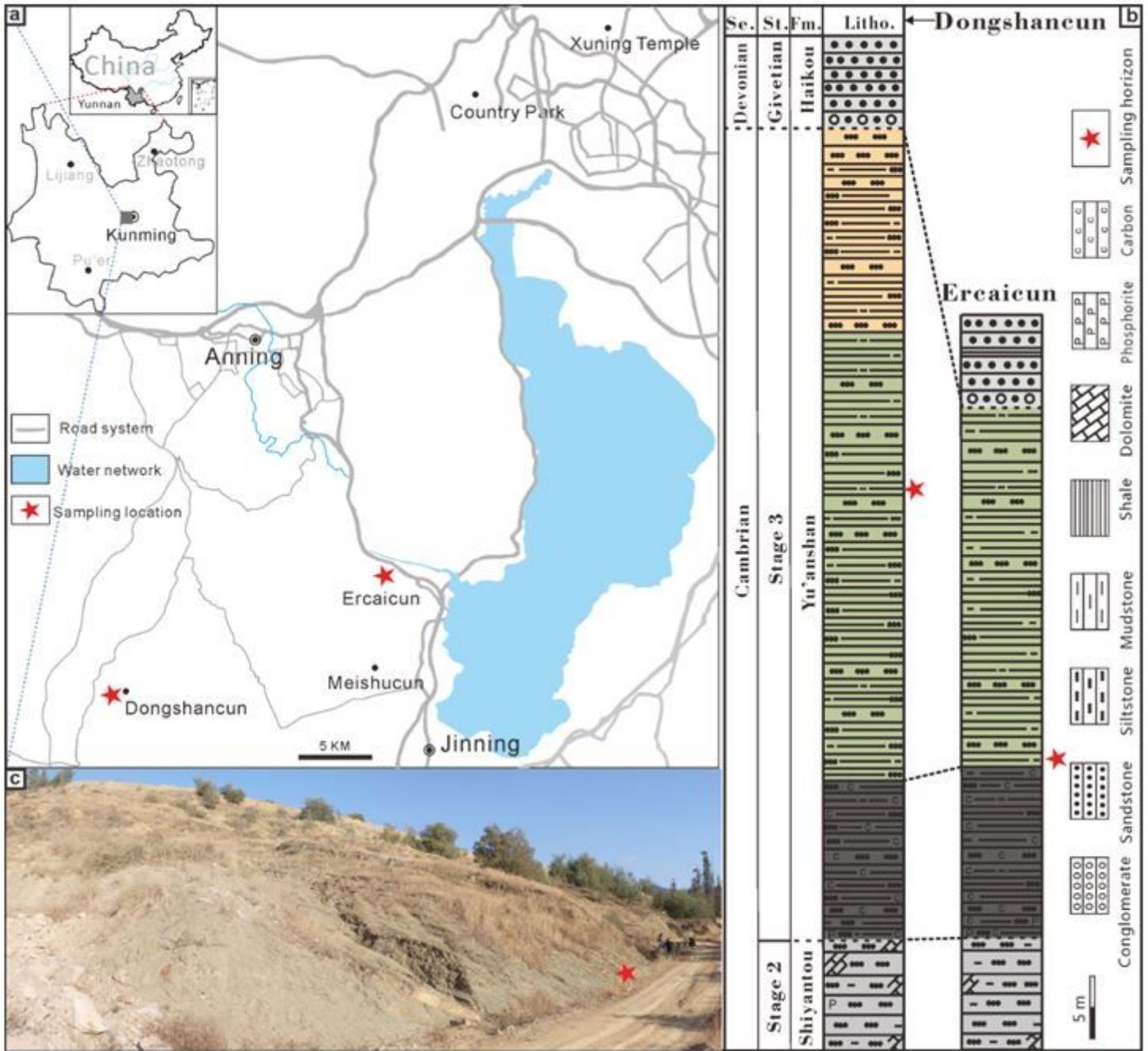


Figure 3

Sampling locations and stratigraphic columns of the early Cambrian in eastern Yunnan. (a) Geographic map showing locations of Dongshancun and Ercaicun outcrops. (b) Stratigraphic columns showing details of rock sequences in Donshancun and Ercaicun outcrops. (c) Photograph showing the Dongshancun outcrop in the field and the sampling horizon. The lithological column of the Ercaicun outcrop is modified after Luo et al.55, their fig. 3.