An early Cambrian polyp reveals an anemone-like ancestor for medusozoan cnidarians

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ABSTRACT

Cnidarians are a disparate phylum of animals and their diploblastic body plan represents a key step in animal evolution. Cnidarians are split into two main Classes; anthozoans (sea anemones, corals) are benthic polyps, while medusozoans (hydroids, jellyfishes) generally have alternating life cycle stages of polyps and medusae. A sessile polyp is present in both groups and is widely regarded as the ancestral form of their last common ancestor. However, the nature and anatomy of the ancestral polyp, particularly of medusozoans, is controversial, owing to the divergent body plans of the extant lineages and the scarcity of medusozoan soft tissues in the fossil record. Here, we redescribe *Conicula striata* Luo et Hu from the early Cambrian Chengjiang biota, south China, which has previously been interpreted as a polyp, lophophorate or deuterostome. Through re-examination of the holotype and 51 exceptionally preserved specimens, we show that *C. striata* possessed features of both anthozoans and medusozoan polyps. A conical, annulated organic skeleton (periderm) fully encasing a polyp is found in fossil and living medusozoans, while a tubular pharynx extending from the mouth into a gut partitioned by ~28 mesenteries, resembling the actinopharynx of anthozoans. Our phylogenetic analyses recover *C. striata* as a stem-group medusozoan, implying that the wealth of medusozoan diversity derived, ultimately, from an anemone-like ancestor.

Keywords: Cnidaria, medusozoan polyp, evolution, early Cambrian, Chengjiang biota

INTRODUCTION

Cnidarians are united by the presence of tentacles with stinging cells (cnidocytes) used in prey capture, a blind gastric cavity that is often partitioned by mesenteries/septa and a sessile polypoid phase in at least part of their lifecycle in most groups (Hyman 1940). The phylum mainly includes two monophyletic subgroups: Anthozoa and Medusozoa (Schuchert 1993; Marques & Collins 2004). Anthozoans are primarily benthic, polypoid animals encompassing widely known groups such as sea anemones and corals (Brusca *et al.* 2016), whereas medusozoans usually have a biphasic lifestyle, with sessile polyps giving rise to swimming medusae (jellyfishes) via asexual reproduction (Collins 2002). Interpretations of cnidarian interrelationships support a scenario in which the common ancestor of the crown group was a sessile polyp, and the swimming medusa represents a synapomorphy of Medusozoa (Marques & Collins 2004; Collins *et al.* 2006; Kayal *et al.* 2018; McFadden *et al.* 2021). However, the anatomy of the polyp in living anthozoans and medusozoans differs in several respects (Daly *et al.* 2007; Technau & Steele 2011; Khalturin *et al.* 2019), meaning it is not clear if the ancestral polyp was plesiomorphically medusozoan- or anthozoan-like.

Anthozoan polyps possess a tubular pharynx (actinopharynx) that extends from the mouth to a gastric cavity that is partitioned by well-developed mesenteries (Daly *et al.* 2007). The pharynx contains either one or two ciliated siphonoglyphs that impart a bilateral/biradial symmetry (Malakhov 2016). In contrast, medusozoan polyps are generally small and possess an exoskeleton (periderm) that is derived from the ectoderm, most of which are made of chitin (Mendoza-Becerril *et al.* 2016). This organic skeleton can encase the entire body of the polyp, such as coronate scyphozoans (*e.g.*, Fig. S5 in Song *et al.* 2021a), or be reduced to just the basal portion of the polyp as in, for example, cubozoans (Mendoza-Becerril *et al.* 2016). In medusozoan polyps, the mouth is usually extended away from the columnar body on a protuberance referred to as the scyphopharynx or hypostome. Unlike the situation in anthozoans, the gastric cavity is not always partitioned by septa, with the polyps of Hydrozoa (Bouillon & Boero 2000) and Cubozoa (Chapman 1978) lacking them.

Molecular clock estimates suggest that the cnidarian crown group radiated in the Ediacaran or the Cryogenian (Park *et al.* 2012; dos Reis *et al.* 2015), but cnidarian fossils before the Cambrian are rare and/or controversial (Liu *et al.* 2014; Van Iten *et al.* 2014b; Van Iten *et al.* 2016; Dunn *et al.* 2022; Leme *et al.* 2022). Cambrian deposits, however, yield a wealth of cnidarian fossils with exceptionally preserved soft tissue structures (Conway Morris 1993; Hou *et al.* 2005; Cartwright *et al.* 2007; Han *et al.* 2016; Ou *et al.* 2022) and even records information on embryonic development (Dong *et al.* 2016). Such fossils are crucial to understand the origin and early evolution of cnidarian clades (*e.g.*, Song *et al.* 2021b). Here, we redescribe *Conicula striata* Luo et Hu (Luo *et al.* 1999) from the Cambrian (Epoch 2, Age 3) Chengjiang biota of Yunnan Province, south China. *C. striata* has previously been interpreted as a lophophorate (spiralian) (Luo *et al.* 1999), an actiniarian (anthozoan cnidarian) (Hu 2005) or a phlogitid (putative deuterostome) (Caron *et al.* 2010). However, with only one specimen reported, *C. striata* has remained as one of the most poorly understood early Cambrian fossils. In this study, we redescribe the detailed morphology of *C. striata* based on the holotype and 51 exquisitely preserved specimens, revealing mosaic morphological characteristics as seen in both extant anthozoans and medusozoans. These features place *C. striata* into a phylogenetic position that subtends other potential medusozoan fossils and the crown group of Medusozoa (as recovered by our phylogenetic analysis), suggesting that early medusozoan polyps were anemone-like forms encased in an extensive periderm.

MATERIALS AND METHODS

51 specimens were collected in fieldwork from 2014 to 2019 in Haikou area, Kunming, eastern Yunnan province, south China. Nearly all specimens were preserved in the well-weathered yellowish mudstones and generally in high fidelity (see Table S1). All specimens were examined and prepared under a Leica M205C stereomicroscope. A fine needle was used to remove the matrix and expose the fossils when necessary. The specimen size was measured on images with ImageJ 1.51j8. All specimens are housed in the Yunnan Key Laboratory for Palaeobiology (YKLP), Yunnan University, China. The holotype (He-f-6-5-112, 113) is deposited in the Yunnan Institute of Geological Survey, Kunming, China.

12 out of 51 specimens, plus the holotype, were figured. Photographs were taken either by a Canon EOS 5DS R digital camera mounted with Canon MP-E 100mm or 65mm (1-5X) macro lens, using high/low angle cross-polarized light, or by a Leica DFC 5000 camera mounted on Leica M205C microscope (to obtain morphological details). Interpretative drawings were produced based on the combined evidence of camera lucida drawings done under Nikon SMZ1000 stereomicroscope and digital photographs. Fluorescence images were obtained using a Leica DFC7000 T digital camera linked to a Leica M205 FA fluorescence microscope. All figures were processed in Adobe Photoshop CC 2019 to adjust the levels, brightness and contrast. The reconstruction of the body plan was drafted in Adobe Illustrator CC 2019. SEM images were collected with a FEI Quanta 650 FEG in low-vacuum mode using an accelerating voltage of 15kV. Images of elemental mapping were acquired with an EDAX Pegasus mounted on SEM using accelerating voltages of 15kV.

Phylogenetic analyses were performed in MrBayes 3.2.7 (Ronquist *et al.* 2012) under the mkv + gamma model (Lewis 2001). 20,000,000 generations were requested, with analyses stopping automatically once the average deviation of split frequencies was <0.01. Ancestral character states for selected nodes were reconstructed in separate analyses using monophyly constraints also performed in MrBayes 3.2.7. Posterior probabilities for ancestral character states are plotted as pie charts at the front of nodes.

RESULTS

Morphology

General shape. Specimens of *Conicula striata* are usually preserved in lateral view and are conical (Fig. 1A-D). Specimens preserved in oblique-lateral view may exhibit a circular cross section (Fig. 1E-G). The body is 10-38 mm long with maximum width ranging between 4-17 mm (see Table S1), and width/length ratio among complete specimens is 0.38-0.45. Some specimens preserve evidence of both a rigid, external skeleton (periderm) (Fig. 2), circumoral tentacles (Fig. 3) and a columnar body with internal anatomical features (Fig. 4).

Exoskeleton. The external skeleton appears to have been originally inflexible and robust, and fully encloses the aboral portion of the body (“Pd”, Fig. 2A-B, G-I). The skeleton forms a conical structure in the proximal portion, which during growth expanded and then narrowed to form a distal globular chamber (Fig. 2D), resulting in a shape resembling a classic, well-loaded ice cream cone. The skeleton is ornamented and shows parallel annulations (“Al”, Fig. 2G-I), with slight relief under low angle light (Fig. 2I), most visible in the aboral section. The space between adjacent annulations is around 0.2-0.4 mm. The appearance of the exoskeleton is consistent with the periderm of medusozoan cnidarians. Dark, spine-like structures project into the interior of the skeleton. They are arranged in one whorl and surround internal features, particularly the region housing the digestive tract, and are interpreted here as peridermal teeth (“Pt”, Fig. 2B-C, E-F).

Tentacles. At least six tentacles are exhibited clearly at the distal part of the body (“Te”, Figs 1A-B, 3), either approximately straight (Fig. 3A-E) or curved (Fig. 3F) and vary in aspect ratio, suggesting that they were capable of protruding and retracting when alive. The tentacles are smooth, with no identifiable branches or pinnules (Fig. 3C-F). When present, the tentacles are buckled and intertwined as a dark organic-rich mass within the globular chamber, making it difficult to trace each tentacle (Fig. 1C-D). It is challenging to surmise the total number of tentacles due to twisting and/or superposition of multiple tentacles as well as incomplete exposure and varying degrees of decay and so we provide a minimum estimate.

Digestive tract. The tentacle base surrounds a disc with a central dark, tongue-shaped structure, likely representing the mouth opening (“Mo”, Fig. 2C). An elongate, narrow tubular structure (about 6.5 mm and 7.7 mm long in YKLP 13484a and 13485a, respectively) connects the opening to the lower part of the body (“Ph”, Figs 3A-B, 4A-C), in which an oval-shaped structure with a dark outline expands to near the body margin (“Gc”, Figs 3A-B, 4A-C, E, G). The tapering band and oval-shaped structure are distinct from other regions by their preservation in a red-brown or dark colour when viewed with cross-polarized light or fluorescence microscopy, respectively (Fig. 4B-C), and their higher amounts of carbon and iron in elemental maps (Fig. 4I-J). The tubular structure and oval-shaped structure are interpreted as a pharynx and a gastric cavity, respectively, based on their shape, size and position within the body (Figs 4D, 5).

The gastric cavity was partitioned by structures preserved as dark, longitudinal lines (“Me”, Figs 1B-C, 4E). In YKLP 13212a, these dark lines are nearly parallel to each other and extend from the base of the oval-shaped structure to the distal region of the columnar body (Fig. 4E, G-J). The spacing between two adjacent lines in the central region is ~0.39 mm, suggesting a total of 28 lines or so (calculated by dividing this interval by the body circumference≈11.3 mm). However, dark lines are sometimes inconspicuous, with some superposition from either side of the body, making their precise number difficult to determine across specimens. These dark lines are carbonaceous in preservation (Fig. 4J) and are interpreted as mesenteries/gastric septa according to their appearance and position (Figs 4K, 5).

A further dark patch, with a circular, crescentic, or triangular outline, attaches at the base of the gastric cavity (“Bgc”, Figs 3A, 4A-C, E, G). It contains a high abundance of carbon as revealed by elemental maps (Fig. 4J). This structure is regarded as the extension of the gastric cavity. In a few specimens such as YKLP 13212a, a slightly curved, narrower ribbon-like structure (~0.34 mm wide), sometimes with modest relief under low angle light, protrudes from the bottom of the dark patch to the proximal end of the exoskeleton ("Rs", Fig. 4E-F). It is herein tentatively interpreted as the remains of the much-narrowed columnar body.

Phylogenetic position

The phylogenetic position of *Conicula striata* was inferred using a dataset of 99 taxa (40 living cnidarians and 9 fossil cnidarians) and 304 morphological characters. The selected characters have been employed in previous studies of either fossil or living cnidarian taxa (Marques & Collins 2004; Van Iten *et al.* 2014a; Duan *et al.* 2017; Zhao *et al.* 2019; Dunn *et al.* 2022). The placement of *C. striata* in the trees is stable in our phylogenetic results. Analysis of this dataset without any topological constraints recovers *C. striata* in the medusozoan stem group and other tubular fossils that are regarded as cnidarians (*e.g.*, conulariids, olivooids and others) in a clade that is in a polytomy with extant medusozoan taxa (Figs 6A, S1A). When removing these tubular fossils, *C. striata* is still recovered in the medusozoan stem group while extant medusozoan taxa are monophyletic (Fig. S1B). This analysis also recovers the paraphyly of Scyphozoa, a result that used to found in molecular phylogenies (Dawson 2004) and in many recent morphological phylogenies (Duan *et al.* 2017; Zhao *et al.* 2019). Constraining the in-group relationships of cnidarians based on recent molecular phylogenies (Zapata *et al.* 2015; Kayal *et al.* 2018; McFadden *et al.* 2021) still recovers *C. striata* in the stem group of Medusozoa (Fig. S2A).

DISCUSSION

A mixed anthozoan-medusozoan body plan

The exoskeleton of *Conicula striata* preserves regularly arranged annulations in the proximal portion in many specimens (Figs 1A, 2G-I). While compaction could have enhanced their relief, they are unlikely to be artefactual due to the regular arrangement and the common occurrence across many specimens. Such annulations resemble the growth lines caused by the marginal accretion of an exoskeleton, which are widely present in extant cnidarians (*e.g.*, medusozoan periderm) and spiralians (such as molluscs, brachiopods and tubular polychaetes). Given that the polypoid body and internal structures of

C. striata are incompatible with known bilaterian comparators, we limit comparisons of the skeleton to those of cnidarians. Anthozoans also produce skeletons, which are found in living antipatharians, ceriantharians, scleractinians and octocorallians, and extinct rugose and tabulate corals, but they are thought to have evolved multiple times independently and the anthozoan ancestor was likely not skeletonized (Kayal *et al.* 2018; McFadden *et al.* 2021). Among these, *C. striata* only superficially resembles the ceriantharians, which produce tubes made of mucus and ptychocysts (Stampar *et al.* 2015). The accretionary exoskeleton of *C. striata* is directly comparable to the periderm of medusozoans and we infer that these features are homologous.

The dark, spine-like structures (Fig. 2B-C, E-F) are arranged radially and encircle the basal portion of the columnar body (Fig. 5). These structures conform in topological relationship to the tube and in morphology to peridermal teeth. These are internal projections of the tube which are observed in living and fossil medusozoans. The teeth in *C. striata* are simple, unpaired and form a single whorl, but other early Palaeozoic medusozoan tubes show variable arrangements. *Olivooides* exhibits paired lobate teeth (Dong *et al.* 2013), while *Eoconularia* (conulariid) exhibits Y-shaped teeth (Jerre 1994)which are continuous down the length of the tube, though conulariid tooth morphology more generally is diverse (Van Iten 1992; Van Iten *et al.* 1996). Other tubular fossils, like *Sphenothallus* can show irregular morphologies, discontinuously arranged through the tube (Dzik *et al.* 2017). We find the teeth of *C. striata* probably occupy most of the room in the proximal cone, restricting the size of the polyp body (Fig. 5) and find no evidence for these peridermal teeth extending into the apertural part of the organism. Extant coronate polyps possess well-developed whorls of complex peridermal teeth, which are protrusions of the inner layer of the periderm towards the central chamber, functioning to narrow and lift the polypoid body (Jarms 1991). These peridermal teeth are often repeated along the length of the tube wall (Jarms 1991), but in *C. striata* they probably occur in a single whorl towards the aboral end of the tube, inferred by the presence of a circle of dark spines (Fig. 2B-C, E-F).

The regular, longitudinal dark lines preserved in association with the columnar body wall and the gastric cavity (Fig. 4E, G-J) indicate the presence of mesenteries. Similar structures have been identified in Cambrian exceptionally preserved fossils before, preserved either as longitudinal ridges (~6-7 in lateral side) in *Archisaccophyllia* (Hou *et al.* 2005) or as finger-like projections (~18) in some juvenile *Xianguangia* (Zhao *et al.* 2019). Partitioning of the gastric cavity by mesenteries/septa is found in both living anthozoans and medusozoans (Fig. 4D, K) (Daly *et al.* 2007); anthozoans show at least 8 well-developed mesenteries but often exhibit well in excess of this number, while within the Medusozoa scyphozoan and staurozoan polyps consistently have 4 gastric septa, they are absent in polyps of Hydrozoa (Bouillon & Boero 2000) and Cubozoa (Chapman 1978). The number of mesenteries observed in *C. striata* (~28) is, therefore, more consistent with that of living and fossil anthozoans. The elongate tubular structure of *C. striata* that extends from the gastric cavity to the oral disc and mouth corresponds in size and topological position to the actinopharynx of anthozoans (Fig. 4A-D) (Daly *et al.* 2003; Daly *et al.* 2007) and is distinct from the scyphopharynx/hypostome of medusozoans which is an oral extension at the distal end of the body. The digestive system of *C. striata* therefore closely resembles the condition seen in extant anthozoans.

Alternative hypothesis

Conicula striata was previously tentatively regarded as a lophophorate (Luo *et al.* 1999) and this hypothesis was reformulated recently in a preprint, in which *C. striata* is interpreted as an intermediate taxon between brachiopods and phoronids (Zeng *et al.* 2022). On the basis of their interpreted U-shaped gut, the authors also criticized the cnidarian hypothesis that was also in a preprint released in December 2021 (Zhao *et al.* 2021). Lophophorates are bilaterian animals, typically with a U-shaped gut and a lophophore (Brusca *et al.* 2016). However, the presence of such features (U-shaped gut, lophophore and bilateral symmetry) in *C. striata* are not supported with careful scrutiny of all available evidence.

U-shaped gut. In both hypotheses, a black region lying in the upper part of the conical skeleton is interpreted as a digestive organ. The margin of this black patch is normally clear, although variation occurs in its size and morphology in different specimens. Zeng *et al.* (2022) further interpret a tubular extension as emerging from this patch laterally and as intestine with an anus opening near the conical skeleton wall (fig. 3i, m-n there). However, this tubular extension is different from the patch in colour and in many specimens it runs curvedly through the black patch to both sides of the conical skeleton and overlaps on, or beneath, the black patch (*e.g.*, fig. 3c, n there), indicating that it is a different structure. Indeed, this tubular extension is more likely the band-like circular structure that delimits the basal gastric cavity from the rest of the body under different modes of taphonomic deformation ('Bc', Fig. 3A-B). Note that this feature shown in the well-preserved specimen in Fig. 3 is approximately symmetrical in lateral view extending over both the right and left side of the specimen, unlike what would be expected for a U-shaped gut.

The position of the anus is also problematic (Zeng *et al.* 2022, fig. 3i, m-n there). If the position is correct, it would inevitably have to emerge from the side of the conical skeleton which is formed through marginal accretion, based on the presence of growth increments. This would result in a situation where the anus would continually have to emerge from the side by breaking down the sclerotized wall and resealing its former entrance during ontogeny. Such a repositioning of the anus would require continual remodelling of an accretionary skeleton during growth, a feature that, to our knowledge, is not observed in lophophorates or any other animal group, casting doubt on the identification of a putative anus in *C. striata.*

Lophophore. The lophophore of living and fossil lophophorates is not known to show multiple arms in a radial arrangement, with only paired arms in a bilateral arrangement instead (Temereva 2019; Kuzmina *et al.* 2021), suggesting that these 'arms' are not likely to represent a lophophore. There is no clear evidence to show the presence of branches along the interpreted arm fringe, even when the 'arms' are stretched out of the body, as seen either in Zeng *et al.* (2022) (fig. 2a-b there) or this study (Fig. 3). These branches – visible in one specimen (fig. 2f-g there) – are probably a taphonomic artefact resulting from broken up organic material derived from the highly decayed body. Even if the branches are correctly identified, their dimension (~100-150 µm wide) (Zeng *et al.* 2022) is larger than the expected diameter of tentacles borne on paired arms of lophophorates, of which the size is only 10-60 µm (see measured data Fig. 7, Table S2). The constant range of lophophoral tentacle size may represent a functional constraint using cilia to gather and transport small suspended particles (Strathmann 1973; Riisgård & Larsen 2010). Instead, the presence of such branches on arms is a feature already known, but not described in Zeng *et al.* (2022), to define the tentacle pattern of octocoral cnidarians, suggesting that if these features are substantiated by further specimens they might support a cnidarian affinity over a lophophorate affinity in any case.

The interpreted morphology of arms in the lophophorate hypothesis is inconsistent with features preserved in specimens. For example, in Zeng *et al.* (2022) fig. 2c-d, the upper and the lower parts of 'arms' are preserved in two layers with a different colour, indicating that the lower part of 'arm' does not directly connect with the upper part. Indeed, in the elemental mapping of their fig. S5a-d (the same specimen), the lower part of the 'arms' appears to have negative elemental profile of carbon, implying that it has a different composition and is more rigid than the upper part. This difference is also apparent in their X-ray computed tomography (fig. S8b there), which displays regularly arranged, stiff 'arms', which contradicts their interpretation that the arms were able to contract inside the skeleton. Instead, the lower part of the 'arm' is more likely the rigid, regularly arranged mesenteries that we identify under the cnidarian hypothesis, which is further corroborated by the supposed digestive cavity posed in this study (Fig. 4A-C, E, G-J) and also visible in multiple individuals illustrated by Zeng *et al.* (2022).

Symmetry. Both hypotheses agree that the arms/tentacles of *C. striata* are arranged in radial pattern. This is unlike the condition in most lophophorates, where the tentacular apparatus has bilateral symmetry, for example the horseshoe shape that gives phoronids their common name of horseshoe worms (Temereva & Malakhov 2009). The lophophorate hypothesis would further require that the body of *C. striata* had bilateral symmetry, which is clearly not the case as shown by many specimens in which the body exhibits radial features. In all known specimens with oblique-lateral compaction (Fig.

1F-G) or in the X-ray computed tomography of laterally compacted specimen (Zeng *et al.* 2022, fig. S8b there), the body and attached structures are arranged in a radial pattern. With the evidence that the part of the 'U-shaped gut' is a different structure from the digestive remains (see above), indicating that *C. striata* showed radial rather than bilateral symmetry.

The vascular tissue in the lophophorate hypothesis. Zeng *et al.* (2022) also identify 'vascular tissue' with two different morphologies in *C. striata*. The dark spines are definitely arranged in a circle (figs 3f, S6e-h there), whereas the longitudinal dark lines originate from the region disparate from the spine circle and can extend above to the arm/tentacle region (figs 3g, S5e-h there). They should be interpreted as two separate structures due to different topological position, arrangement and morphology. These two structures correspond to peridermal teeth (Fig. 2E-F) and mesenteries (Fig. 4G-J) as identified in the present study. These features are all preserved in a manner that is consistent with a radial symmetry, reinforcing the lack of bilateral symmetry in *C. striata.*

Mode of life

Conicula striata is inferred here to have been a solitary organism with an annulated periderm fully encasing the polyp (Fig. 5), indicating a benthic and sessile lifestyle commonly seen in coronate and hydrozoan polyps. However, all specimens lack a holdfast at the aboral end and instead appear to taper naturally, with no evidence of attachment to other organisms or substrates, suggesting *C. striata* may have embedded the apex into the seafloor for anchoring, similar to some conulariids (Van Iten *et al.* 2013). Alternatively, *C. striata* may have been recumbent, but the conical skeleton does not curve to facilitate such a mode of life like that of horn corals (Scrutton 1998). An alternative, but less plausible, scenario is that *C. striata* was planktonic, with buoyancy provided by the inflated distal chamber, possibly having an intermediate lifestyle between the benthic polyps and pelagic medusae, although we do not consider this likely.

Evolutionary implications

Historically, many tubular fossils from the Ediacaran-Cambrian have been interpreted as cnidarian polyps (Table S3)(Van Iten *et al.* 2014b), such as the microfossils Olivooidae, Carinachitidae and Hexangulaconulariidae(Guo *et al.* 2020), as well as macrofossils *Corumbella* and conulariids(Van Iten *et al.* 2016; Leme *et al.* 2022). The features revealed in these tubular fossils, such as radial symmetry, transverse ribs/crests, peridermal teeth and a single opening, are the primary lines of evidence for a cnidarian interpretation, with particularly close comparisons made to the peridermal tubes of medusozoan polyps (Conway Morris & Chen 1992; Zhu *et al.* 2000; Van Iten *et al.* 2006; Dong *et al.* 2016). Soft tissues are extremely scarce among these fossil tubes, and their cnidarian affinities and interpretations are accordingly not without previous controversy (Steiner *et al.* 2014; Walde *et al.* 2019). They are recovered as a paraphyletic grade of total group medusozoans in our Bayesian analyses (Figs 6A, S1A, S2). *C. striata* not only shares similar exoskeletal features with those tubular fossils, but also provides unique new evidence for the soft tissues of early medusozoans, such as mesenteries, the digestive tract and tentacles, characters that are not available from the overwhelming majority of tubular fossil taxa, shedding light on character state changes that occurred early in medusozoan evolutionary history.

C. striata shows a tubular pharynx, which is similar to the actinopharynx of anthozoans in topological location, inferred function and architecture. The presence of an anthozoan-like pharynx in the medusozoan stem group is also supported in our ancestral state reconstruction (Fig. 6A). It is recovered as a plesiomorphic trait of cnidarians (Fig. 6A), indicating that the tubular pharynx in the stem group of Medusozoa is homologous with the actinopharynx in anthozoans, but it was subsequently lost prior to the origin of crown group medusozoans. Whether other tubular fossil taxa have an anthozoan-like pharynx is not known and would depend on the discovery of soft tissues in these groups. Moreover, *C. striata* possesses ~28 mesenteries lining the gastric cavity, a feature commonly seen in extant hexacorallians, which is also recovered as being plesiomorphic for medusozoans and cnidarians in our analysis (Fig. 6A).

We infer that the organic exoskeleton (periderm) is likely a true medusozoan synapomorphy (Mendoza-Becerril *et al.* 2016), but is absent in the common ancestor of Anthozoa, and probably of Cnidaria (Fig. 6A). This inference is congruent with earlier cnidarian fossils from the Ediacaran-Cambrian (Table S3), in which potential medusozoan polyps share a well-developed, annulated exoskeleton. In contrast, all known Cambrian anthozoan fossils lack a comparable exoskeleton/periderm (Hou *et al.* 2005; Han *et al.* 2010; Ou *et al.* 2022), which is readily fossilized compared with other body parts and should be identifiable if present. Based on our ancestral state reconstruction, a polyp encased fully by a periderm is recovered as a plesiomorphic trait of the medusozoan total group (Fig. 6A).

We reconstruct the ancestral medusozoan as an anemone-like polyp, which possessed a tubular pharynx (actinopharynx) connecting the mouth and gastric cavity that is partitioned by ~28 mesenteries and unbranched tentacles, with the body encased fully by an annulated exoskeleton (periderm) (Fig. 5). If this scenario is extensively corroborated in the further studies on related fossil taxa, the body plan of *C. striata* might bridge the long-known morphological gap between living anthozoan and medusozoan polyps (Fig. 6B), suggesting that several features previously regarded as anthozoan apomorphies (*e.g.*, an actinopharyx) have a deeper origin and are shared by medusozoan stem groups. These conclusions are further supported by the recent description of *Auroralumina attenboroughii* (Dunn *et al.* 2022), an interpreted stem-group medusozoan fossil from the Ediacaran of Charnwood Forest, UK, which also shows chimeric medusozoan-anthozoan characters in large polyp size and simple and robust tentacles alongside a sulcate peridermal exoskeleton. Crucially, however, *A. attenboroughii* (Dunn *et al.* 2022) was preserved as an external impression meaning it is not possible to glean information about the internal anatomy of the organism, something our new specimens of *C. striata* are able to shed light on.

Given the anatomical simplicity in crown medusozoan polyps (Ruppert *et al.* 2004), we infer that several characters, including well-developed mesenteries and a tubular actinopharynx, experienced subsequent reduction and even total loss in some or all extant medusozoan lineages (Fig. 6B). Our analyses indicate that this is a component of a broader trend of polyp simplification in Medusozoa where the lifecycle is now dominated by the medusa stage.

CONCLUSIONS

Conicula striata (Cambrian Epoch 2, Age 3, Chengjiang biota) is re-described in this study based on the holotype and 51 recent specimens. New material reveals previous unknown soft tissues, including an annulated exoskeleton, peridermal teeth, a tubular pharynx and an expanded gastric cavity partitioned by mesenteries. *C. striata* possesses a radially symmetrical body with mixed features of anthozoan (digestive tract) and medusozoan polyps (periderm and teeth). *C. striata* is recovered as a stem-group medusozoan in the phylogenetic results, suggesting that medusozoan polyp likely originated from an anemone-like ancestor. *C. striata* thus represents the first known medusozoan polyp with soft tissues preserved in the early Cambrian. It provides us novel insights into the body plan evolution of cnidarian polyps during the Cambrian Explosion.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Verrill 1865

MEDUSOZOA Petersen 1979

Conicula striata Luo et Hu in Luo *et al.*, 1999

(Figures 1-4)

v.*1999 *Conicula striata* Luo *et al.*, p. 87, text-fig. 35, pl. 22, fig. 5a,b.

v.2002 *Conicula striata* Chen *et al.*, p. 8, 39, pl. 20, fig. 2.

2005 *Conicula striata* Hu, p. 73, 79-80.

2010 *Conicula striata* Caron *et al.*, p. 2.

Holotype. Part, He-f-6-5-112 (Figs 1A, 3E), counterpart, He-f-6-5-113. Both are deposited in the Yunnan Institute of Geological Survey, Kunming, China.

Other figured material. YKLP 13210a (Fig. 2B, E); 13212a (Fig. 4E-J); 13214b (Fig. 2I); 13215a (Fig. 2C, F); 13220 (Fig. 2A, D); 13288a (Figs 1B, 3F); 13484a (Fig. 3A-D); 13485a (Fig. 4A-C); 13488 (Fig. 2G-H); 13492a, b (Fig. 1E-G); 13494a (Fig. 1C); 13495a (Fig. 1D).

Amended diagnosis (amended from Luo *et al.* 1999, p. 87). Solitary polypoid metazoan encased in a conical, annulated exoskeleton (periderm). The polypoid body possesses unbranched, flexible circumoral tentacles that can protrude outwards from the distal end of the periderm, and a blind digestive tract consisting of an elongate, tubular pharynx and a mesentery-partitioned gastric cavity.

Occurrence. Conicula striata occurs in the Yu'anshan Member of the Chiungchussu Formation (Yunnan local lithostratigraphic unit), corresponding to the *Eoredlichia-Wutingaspis* trilobite biozone (Babcock & Zhang 2001), Cambrian Series 2, Stage 3.

Description. See the section of morphology.

Remarks. Conicula striata was erected in 1999 based on one incomplete specimen preserving a tentacular, annulated conical body (Luo *et al.* 1999). It has been variously interpreted as a lophophorate (Luo *et al.* 1999), a sea anemone (Hu 2005) or a cambroernids (presumed deuterostomes) (Caron *et al.* 2010). Our 51 new specimens corroborate the validity of this genus and species and further provide new insights into its morphology and phylogenetic position. Lophophorates (brachiopods, bryozoans and phoronids) possess a unique feeding apparatus, the lophophore, consisting of bilateral lophophoral arms with rows of slender tentacles, plus a U-shaped through gut (although this is reduced in derived articulate brachiopods). These anatomical features are contradicted by the circumoral, larger tentacles (Fig. 7) and a spacious and blind digestive tract (Fig. 4) identified in material of *C. striata* studied here. Note some authors have mentioned that *C. striata* may represent a phlogitid, a group that belongs to the cambroernids (*Herpetogaster*, *Phlogites* and eldoniids) (Caron *et al.* 2010). *Phlogites* is a benthic organism consisting of a stalk, a bell-shaped theca and at least one pair of branched tentacles, and lacks an annulated exoskeleton (Hou *et al.* 2006). Although tentacles are present in both groups, the tentacles in *C. striata*, based on current evidence (Fig. 3), had a radial arrangement and were unbranched or not bifurcated. The coiled digestive tract with a terminal opening of anus seen in *Phlogites* (Fig. 5 in Caron *et al.* 2010) is likewise absent in *C. striata*. Therefore, it is unlikely that *C. striata* has a close relationship with either lophophorates or cambroernids. The radial arrangement of a digestive tract and tentacles impart radial symmetry onto the body of *C. striata*, a feature that points to a diploblastic grade of organisation and is clearly distinct from the bilateral symmetry that is dominantly present in triploblastic taxa. *C. striata* lacks the characteristics of ctenes/comb rows or similar structures, ruling out ctenophore affinities, the other clade of diploblastic organisms. Cnidarians are therefore the extant clade with the largest number of characters that can be identified in *C. striata.* Our new observations of an annulated exoskeleton and the anemone-like polypoid body further support the hypothesis that *C. striata* is probably a cnidarian. *C. striata* is herein assigned to Medusozoa cnidarian, rather than Anthozoa, based on our phylogenetic results (Figs 6A, S1-2).

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Author contributions

Y.Z. and P.-Y.C. designed research; Y.Z., P.-Y.C., X.-G.H., Y.-J.L. and F.W. collected fossil material; Y.Z., L.A.P. and J.V. performed research, analysed data and prepared all figures; Y.Z., F.S.D. and L.A.P. collated the morphological data and conducted phylogenetic analyses; Y.Z. and L.A.P. wrote the initial manuscript with significant input from J.V., P.-Y.C., F.S.D. and other authors.

DATA ARCHIVING STATEMENT

Supporting data for this study are available in MorphoBank: http://morphobank.org/permalink/?P4276. [login with user name 4276; password Conicula] **[please note that the data for this paper are not yet published and this temporary link should not be shared without the express permission of the author]**

SUPPORTING INFORMATION

Appendix S1. Includes Figure S1-S2, Table S1-S3 and a list of characters

Figure S1. Results of phylogenetic analyses under the condition of unconstraint

Figure S2. Results of phylogenetic analyses under the condition of constraint

Table S1. Brief description of examined specimens of *C. striata*

Table S2. Collated width of lophophoral tentacle for living lophophorates and *C. striata*

Table S3. The main occurrence of potential cnidarian fossils in the Ediacaran and Cambrian period

Data S1. Phylogenetic matrix.

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Figure legends

Fig. 1. General morphology of *C. striata*

(A) The part of holotype, He-f-6-5-112. (B) YKLP 13288a. (C) YKLP 13494a. (D) YKLP 13495a. (E) YKLP 13492b. (F-G), YKLP 13492a, showing a circle-shaped cross section. *Abbreviations*: Al, annulation; Bgc, basal gastric cavity; Me, mesentery; Pd, periderm; Ph, pharynx; T1-T6, tentacles. Scale bars represent: 5 mm (A-D); 2 mm (E-F); 1 mm (G).

Fig. 2. Exoskeleton/periderm of *C. striata*

(A) YKLP 13220, complete specimen showing smooth periderm in the broken globular region. (B) YKLP 13210a, showing a polyp preserved soft tissues within the periderm. (C) YKLP 13215a, showing a tongue-shaped dark structure, possible a mouth of the polyp. (D) Magnification of the broken globular region in A. (E-F) Close-up of the extension of the gastric cavity, encircled by dark, spine-like peridermal teeth, in B and C, respectively. (G-H) YKLP 13488, complete specimen preserving parallel annulations in the apical portion of the skeleton. (I) YKLP 13214b, under low angle light, showing slight relief of annulations in the proximal portion. *Abbreviations*: Al, annulation; Bgc, basal gastric cavity; Gc, gastric cavity; Pd, periderm; Ph, pharynx; Pt, peridermal teeth; T1-T6, tentacles. Scale bars represent: 5 mm (A-C, G, I); 2 mm (D); 1 mm (E-F, H).

Fig. 3 Tentacles of *C. striata*

(A-B) YKLP 13484a, whole specimen and its interpretative drawing. (C-D) Close-up of tentacles (T1-T4), showing flexible, unbranched features, in direct light (C) and fluorescent light (D). (E-F) E, He-f-6-5-112, F, YKLP 13288a, close-up of the distal region, showing unbranched tentacles (T1-T6). *Abbreviations*: Bc, band-like circular structure; Bgc, basal gastric cavity; Gc, gastric cavity; Ph, pharynx; T1-T6, tentacles. Scale bars represent: 5 mm (A-B); 2 mm (E); 1 mm (C-D, F).

Fig. 4. Internal anatomy of *C. striata*

(A-C) YKLP 13485a, whole specimen (E) and the details of internal structures under direct light (B) and fluorescent light (C), showing a tubular pharynx and gastric cavity. (D) Extant sea anemone *Cactosoma abyssorum* (Sanamyan *et al.* 2016, Fig. 1B), longitudinal section of the distal half of the columnar body, showing circumoral tentacles, an actinopharynx and mesenteries. (E-J) YKLP 13212a, E, whole specimen; F, the profile of ribbon-like structure under low angle light; G-J, details of the gastric cavity partitioned by longitudinal, dark lines (mesenteries), imaged in direct light (G), backscatter SEM (I) and elemental map of carbon (J). (K) Living sea anemone *Cactosoma abyssorum* (Sanamyan *et al.* 2016, Fig. 1E), longitudinal section of the proximal part of the columnar body, showing a gastric cavity partitioned by more than eight mesenteries. Figure D, K were generously provided by Karen E. Sanamyan. *Abbreviations*: Bgc, basal gastric cavity, Gc, gastric cavity; Me, mesentery; Pd?, periderm; Ph, pharynx; Pt?, Peridermal teeth; Rs, ribbon-like structure; Te, tentacle. Scale bars represent: 5 mm (A); 2 mm (B-E, K); 1 mm (F, G-J).

Fig. 5. Technical reconstruction of *C. striata*

(A) Technical reconstruction showing the exterior gross morphology, interior anatomy and cross section of gastric cavity and basal gastric cavity. (B) Three-dimensional model of *C. striata.*

Fig. 6. Phylogenetic analysis

(A) Bayesian phylogenetic analysis (304 characters, 99 taxa, mkv + gamma model), *C. striata* is placed in the medusozoan stem group. The fossil taxa are indicated by dagger symbol. Pie charts illustrate ancestral states from Bayesian analysis. Numbers at the nodes are posterior probabilities, and the scale bar is the expected number of substitutions per site. (B) Simplified cladogram of cnidarians based on the topological result of A, showing that *C. striata* has mosaic characters of anthozoan (a high number of mesenteries and a tubular pharynx) and medusozoan (an annulated periderm and teeth) polyps. See also Figs S1 and S2 for full results and additional information.

Fig. 7 Lophophoral tentacle width

(A) The width range of lophophoral tentacle for living lophophorates, including brachiopods, bryozoans and phoronids, showing the width range of lophophoral tentacle is 10-60μm. Left, box chart of the average width of lophophoral tentacle for each given taxon, right, lognormal distribution of the frequency histogram for lophophoral tentacle width. The data is collated from a range of living lophophorates (see Table S2). (B) The width range of interpreted 'lophophoral tentacle' of *C. striata*, showing the interpreted tentacle width larger than any of living lophophorates. Orange circle in the dark line indicates the average value of each width range, and text to the left side of dark line refers to reference or specimen number.