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# AN INTERMEDIATE TYPE OF MEDUSA FROM THE EARLY CAMBRIAN KUANCHUANPU FORMATION, SOUTH CHINA

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**Abstract:** The tetradial or pentaradial fossil embryos and related hatched individuals from the early Cambrian Kuanchuanpu Formation are of great interest for understanding the early evolution of medusozoans. The phylogenetic and evolutionary significance of their external and internal characters (e.g. manubrium, tentacles, septa and claustra) is still controversial. Here we describe a new pentamerous medusozoan, *Hanagyroia orientalis* gen. et sp. nov., characterized by five well-developed periradial oral lips around a remarkably large manubrium, a conspicuous equatorial groove, and five short interradial pairs of extensible tentacles at the bell margin. Internally, five broad and stout interradial septa join horizontally to form the claustra. *Hanagyroia orientalis* lacks the frenula, apertural lappet and velarium seen in coeval microfossils and extant cubozoans. Although *H. orientalis* resembles extant coronate scyphozoans in its round medusalike bell margin and equatorial groove, cladistic analysis suggests close affinity with cubozoans. *Hanagyroia* may represent an intermediate morphological type between scyphozoans and cubozoans. The well-developed oral lips and paired short strong tentacles of *Hanagyroia* suggest direct development.

**Key words:** Cnidarian, cubozoan, oral lip, Kuanchuanpu Formation, early Cambrian.

EXTANT medusozoans comprise approximately 3700 species (Daly et al. 2007) grouped into four major classes (Staurozoa, Hydrozoa, Scyphozoa and Cubozoa) that can be distinguished by the morphology and arrangement of various external and internal features (e.g. gonads, interradial canals, apertural lappets, tentacles) and their lifecycle. The body plan of most medusae is characterized by a tetradial symmetry, with rare exceptions (pentaradial symmetry described by: Burkenroad 1931; Lin et al. 2013). This symmetry is expressed by the extension of oral lips or arms, which are traditionally used as landmarks to define the meridian planes of medusozoans (Fig. 1; Haeckel 1879; Conant 1898; Mayer 1910; Hyman 1940; Meglitsch 1967; Lesh-Laurie & Suchy 1991). The earliest unambiguous macroscopic crown-group jellyfish are known from the early Cambrian Chengjiang biota (c. 520 Ma; Han et al. 2016a) and the middle Cambrian of Utah (Cartwright et al. 2007). Although preserved

as compression fossils, the Chengjiang medusozoans display a clear tetradial symmetry exemplified by their 16 pairs of marginal tentacles, 16 rhopalia and 16 marginal lappets (see Han et al. 2016a). Comparable radial and symmetrical structures also occur in the middle Cambrian medusae from Utah (e.g. tentacles, coronal muscles; see Cartwright et al. 2007). Divergence of developmental forms of putative medusozoans has been also discovered in a new Burgess Shale-type Lagerstätten, the Qingjiang biota (c. 518 Ma) from South China (Fu et al. 2019). Phosphatized tube-shaped polyps such as *Sphenothallus* Hall, 1847 from the Lower Ordovician Fenxiang Formation, Hubei Province, South China (c. 477 Ma; Dzik et al. 2017) have a biradial symmetry expressed by the tetradial pattern of their eight septa and two longitudinal thickenings running from the holdfast to the aperture. The biradial and tetradial symmetry of *Sphenothallus* resembles that of extant anthozoans and medusozoans. However, the affinity of *Sphenothallus* is still unknown. Phosphatized microfossils from the Kuanchuanpu Formation (c. 535 Ma) often display exceptionally well-preserved three-dimensional external and internal features (Briggs et al. 1993; Xiao et al. 1998) that can be imaged and reconstructed using microtomographic methods (Dong et al. 2013; Han et al. 2013; Steiner et al. 2014). Some tetradial or pentaradial embryos and juveniles have been interpreted as medusozoans (Dong et al. 2013, 2016; Han et al. 2013, 2016b; Liu et al. 2014, 2017; Steiner et al. 2014; Wang et al. 2017; Shao et al. in press). Coeval microscopic fossil medusozoans with biradial, hexaradial or even octaradial symmetry have been also reported (Xian et al. 2018). These assumed fossil medusozoans share numerous morphological features with extant medusae (e.g. double-wall system, manubrium, interradial septa, claustra, gonad-lamellae) and have either a pentaradial or, more rarely, a tetradial symmetry. As in the extant medusozoans, their body is subdivided by meridian planes in interradial or perradial positions. However, the existence of important diagnostic features such as the manubrium with oral lips is still uncertain. Here we describe a new, pre-hatched pentamerous medusozoan fossil, *Hanagyroia orientalis* which had a ring of five pairs of subumbrellar tentacles anchored near the outermost margin of the bell-shaped body. Its equatorial groove is reminiscent of the coronal groove of coronate scyphozoans (Mayer 1910; Hyman 1940; Russell 1970). More importantly, *H. orientalis* has a conspicuous manubrium and a large mouth fringed with well-developed oral lips in perradial position. In addition, *Hanagyroia* provides clues concerning the orientation and lifecycle of early Cambrian medusozoans.

## **MATERIAL AND METHOD**

The four specimens described here were collected from the lower Cambrian Kuanchuanpu Formation at the Shizhonggou section, Ningqiang County, Shaanxi Province, China (Qian 1977). Fossils were recovered by digesting the limestone in 10% acetic acid. Specimens were observed under a scanning electron microscope (SEM) (Fig. 2) at Northwest University, China, and analysed using x-ray microtomography (XTM) at Tohoku University, Japan. Thousands of images of virtual sections

(Fig. 3; Wang et al. 2020, appendix 2) through the specimen ELISN107-470 were acquired at a resolution of 1004 9 1004 pixels (XTM). XTM data were processed using V.G. Studio 2.2 Max, to enhance contrast between key internal anatomical features using artificial colours and to generate detailed three-dimensional reconstructions of the microscopic fossil (Figs 3, 4). Cladistic analysis was carried out using PAUP\* v. 4.0 b10 (Swofford 2003) and TNT 1.1 (Goloboff et al. 2008). The unweighted analysis of the data matrix (Wang et al. 2020, appendices 3–4, 6–7) contain 23 groups and 104 unordered characters taken from Marques & Collins (2004), Dong et al. (2013), Van Iten et al. (2006), Han et al. (2013, 2016a) and Wang et al. (2017). All specimens are deposited at the Early Life Institute, Northwest University, China (ELI). This material and microtomography data are available on request from JH and also in Wang et al. (2020).

## SYSTEMATIC PALAEOLOGY

Phylum CNIDARIA Verrill, 1865  
Subphylum MEDUSOZOA Peterson, 1979  
Class, Order UNCERTAIN  
Family OLIVOOIDAE Steiner et al., 2014  
**Genus HANAGYROIA nov.**

Derivation of name. From Hana, flower in Japanese; gyro, literally ‘turn’ in Greek.

Diagnosis. Bell-shaped body divided into a wide oral unit and a low cone-shaped aboral unit separated by a deep equatorial groove. Deep and narrow subumbrellar cavity. Central, flaring, large manubrium topped with a pentagonal-shaped mouth bearing five perradial slit-like oral lips. Circular subumbrellar rim with a circle of five interradial pairs of short tentacular buds. No frenula and velarium near the bell margin. No apertural lappets around the bell margin. Aboral end with five short, round-cornered perradial ridges; oral end of each perradial ridge with a triangular cornice. Internally, five broad and stout interradial septa horizontally connected to form the claustra. Exumbrellar and subumbrellar walls fused together near the oral margin.

Remarks. The most striking differences between this new genus and other previously described medusozoans from the Kuanchuanpu Formation are the absence of the frenula, apertural lappet and velarium. The new genus has a conspicuous manubrium with well-developed perradia oral lips and a narrow subumbrellar cavity which is surrounded by five paired stout tentacles.

### **Hanagyroia orientalis sp. nov.**

Figures 2A–C, 3–5

Derivation of name. Orientalis refers to China, an oriental country.

Diagnosis. As for genus.

Holotype. ELISN107-470; deposited at the Early Life Institute, Department of Geology, Northwest University, China.

Paratypes. ELISN66-15, ELISN96-77 and ELISN121-154.

Occurrence. Lower Cambrian Kuanchuanpu Formation (equivalent to the Fortunian Stage of the Terreneuvian Series), Shizhonggou section, Ningqiang, Shaanxi, China.

Description

As demonstrated by the holotype specimen ELISN107-470, *H. orientalis* forms a hat-shaped bell associated with a small vestigial egg envelope. The bell is c. 450  $\mu\text{m}$  wide and 300  $\mu\text{m}$  high (Fig. 2A, B). The low conical apical (aboral) region forms a five-fold pyramid that is delimited from the rest of the oral unit by a deep circumferential equatorial groove at the sub-middle height of the bell (Fig. 2B, C). Micro-CT data reveal more detailed anatomical structures that are arranged in a consistent pentaradial pattern (Figs 2–5; Wang et al. 2020, appendices 2, 5). Tentacles. The bell margin bears a circle of five pairs of short capitate projections of uniform size, c. 50  $\mu\text{m}$  in length and height and with an elliptical cross-section (Figs 2A, 6A–B). The projections in each pair are close to each other and located on the interradial. The surface of the projections bears fine circular wrinkles (cw) (Figs 2D, 6A–B), interpreted here as possible transverse muscular fibres. It is likely that these projections represent tentacle buds. Small lumens occur in each pair of tentacular buds, and are named here tentacular bud lumens (tbl; Figs 3G, 4B).

Manubrium. The central area of the bell is occupied by a rather large, flaring structure, approximately three-fifths of the diameter and height of the bell. It is interpreted here as a manubrium (mb). Its distal opening, the mouth (mo), is rounded in oral view and pentagonal in cross-section (Figs 2A, 4A–D; Wang et al. 2020, appendices 2, 5). The mouth bears five well-developed centripetal strips interpreted here as oral lips (ol) which converge towards the mouth opening (Figs 2A, 3H, 4A, D; Wang et al. 2020, appendix 5). These strips are reminiscent of the oral lips which occur around the manubrium of extant medusae (Fig. 1). The surface of each strip bears 3–5 fine stripes (Fig. 2A). The interradial of the holotype (ELISN107-470) are defined by paired tentacles as in extant medusozoans. The oral lips of ELISN107-470 are located on the perradial, approximately 72° offset from their position in extant pentaradial medusae (Fig. 1). The manubrium is separated from the peripheral bell margin by a deep but narrow subumbrellar cavity (Figs 2A, 4A–B, D). Aboral ridges and furrows. The aboral unit exhibits five evenly spaced and broadly arched perradial ridges (pr) which are intercalated with five triangular concave interradial depressions that are interpreted here as interradial furrows (if; Figs 2C, 4C, F, 6D; Wang et al. 2020, appendix 5). The oral end of each ridge ends as a prominent triangular cornice (co) above the equatorial groove (Figs 2B–C, 4C, 6C). The perradial ridges and interradial furrows form a corrugated external structure and converge towards the aboral apex (Figs 4C, F, 6C–D; Wang et al. 2020, appendix 5).

Interradial septa and claustra. The aboral end of *H. orientalis* is pentagonal in transverse section (Fig. 3B; Wang et al. 2020, appendix 2B). In section it shows a central chamber and five uniform septal structures arising from the endodermic side of each interradial depression of the exumbrella. This chamber and its associated septal structures are interpreted here as the central gastric cavity and the interradial septa, respectively (Fig. 3B–E). The septa are triangular in cross-section near the gastric floor (Figs 3B–E, 4D–E) and direct inwardly and orally. Each interradial septum seems to have an expanded proximal end with an inner hollow cavity. These cavities are named here interradial septal funnels (isf; Figs 4E, 5).

At the level of the equatorial groove, the distal ends of the septa reach the central part of gastric cavity (csc; Figs 4E, 5) and subdivide it into five perradial pockets (pp; Fig. 3B–E). More orally below this level, five vertical, axial walls (almost in perradial position) bridge the neighbouring interradial septa (Figs 3C–E, 5). This connecting structure is interpreted as the claustra (cl) which partitions the whole gastric cavity into five perradial pockets in addition to the central gastric cavity. Several tiny funnels can be seen on the claustra, connecting the central stomach cavity to the perradial pockets. They are interpreted as gastric ostia (go; Figs 3B, 5).

Umbrellar fusion. The transverse outline of the exumbrella varies according to its position along the oral-aboral axis. Apically it appears as a five-pointed star (eu; Figs 3B, 4F; Wang et al. 2020, appendix 2B); below the equatorial groove, the outline transforms into a round-cornered pentagon because of the thickening the interradial septa (Fig. 3C, D; Wang et al. 2020, appendix 2C–D); orally the pentagon becomes a circular structure representing the bell rim (Figs 3E–H, 4A; Wang et al. 2020, appendix 2E–H). The body wall at the equatorial groove is thinner than anywhere else. The subumbrella (su) which is thinner than the exumbrella (eu), can be traced aborally deep into the equatorial groove (eg). Immediately below the equatorial groove (at approximately one-third of the bell height) a narrow circular cleft separates the subumbrella from the exumbrellar wall (Figs 3F, 4D; Wang et al. 2020, appendix 2F). More orally, the two umbrellar walls fuse together, making the interradial septa (is) disappear almost completely and reducing the size of the subumbrellar cavity (Figs 3E–G, 4E, 6A–B; Wang et al. 2020, appendix 2E–G).

The paratype specimens (ELISN66-15, ELISN121-154 and ELISN96-77) have pentamerous symmetry and a body size similar to that of the holotype. The external anatomy of specimen ELISN66-15 is well preserved but lacks internal information. Specimen ELISN96-77 shows a well-developed manubrium with lobed edges, surrounded by five paired stout tentacles that are smaller than those of the holotype, c. 20–40  $\mu\text{m}$  in length and height. A relatively thick periderm adheres to a thinner smooth layer interpreted as the egg membrane (Fig. 2F; Wang et al. 2020, appendix 1). Specimen ELISN121-154 shows the well-preserved paired tentacles and tentacular bud lumens, but lacks the oral part (Fig. 2E)

## TAPHONOMY BIAS

These phosphatized embryos are preserved in three dimensions and show exquisite details of their internal tissues (e.g. interradial septa and claustra) although some, or part, of them may have suffered from decay prior to their phosphatic mineralization. X-ray tomography clearly reveals that both external and internal structures are arranged with pentaradial symmetry. In view of this, it is evident that we are not dealing with artefacts (e.g. bridges created by mineral growth) but with true fossilized biological features. Symmetry and morphological consistency are widely accepted criteria to differentiate biological features from taphonomic artefacts in cnidarian fossils, including those from small shelly fossil (SSF) assemblages (e.g. Dong et al. 2013; Han et al. 2013; Steiner et al. 2014). Experimental taphonomy on a variety of soft-bodied animals including echinoderm embryos (Raff et al. 2008, 2014) indicates that the mineralization of soft tissues occurs extremely rapidly (within days) after death (e.g. Briggs et al. 1993; Xiao et al. 1998). Moreover, these laboratory experiments (Raff et al. 2008) show that bacterial biofilms colonize the embryos rapidly to form pseudomorphs which replace and model extremely fine details of cellular organization. These biofilms also play a crucial role in the mineralization of tissues, a necessary precondition for eventual fossilization. We think that the remarkably wellpreserved features observed in our cnidarian embryos result from comparable post-mortem processes which, as seen in taphonomic experiments, do not generate major taphonomic artefacts (see Raff et al. 2008). Under these conditions, there seems to be a higher probability that the lack of certain morphological features noted in *Hanagyroia* (e.g. frenula, apertural lappets and velaria) is natural rather than artefactual (e.g. resulting from selective preservation).

Another argument that goes against taphonomy bias is that these diagnostic features also occur in *Sinaster* (Wang et al. 2017) another medusozoan from the Kuanchuanpu biota. However, we are fully aware of two things that may lead to misleading or inaccurate interpretations. First, some of our specimens (or parts of them) may be affected by decay, resulting in a potential loss of morphological information (autolysis in Raff et al. 2008). Second, phosphatization may have persisted long after the early steps of post-mortem mineralization (Briggs et al. 1993), thus affecting the shape and thickness of original tissues. However, numerous internal structures (claustra, tentacles, perradial pouches, frenula and velarium) observed in Kuanchuanpu medusozoans have direct analogues in extant cnidarians thus contradicting the hypothesis of artefacts due to mineralization (Han et al. 2013; Wang et al. 2017). It should be also noted that most internal structures seen in our embryos are well expressed externally (e.g. the apertural lappets connected with the perradial frenula can be seen along the subumbrellar margin of *Sinaster*: see Wang et al. 2017). This configuration is again hardly consistent with an artefactual origin.

## AFFINITIES OF HANAGYROIA

Hanagyroia can be confidently interpreted as a cnidarian based on its radial symmetry, two body layers and one single body opening. Although extant medusozoans are overwhelmingly tetradial, both tetradial and pentaradial cnidarians co-existed in the early Cambrian Kuanchuanpu biota (Dong et al. 2013, 2016; Han et al. 2013, 2016b, c; Liu et al. 2014, 2017; Wang et al. 2017). Pentaradial symmetry cannot be treated as a strong argument to exclude Hanagyroia and other Kuanchuanpu microfossils from Cnidaria.

However, the assignment of Hanagyroia to any class of extant medusozoans is more difficult to establish. Several hypotheses need to be tested.

**Staurozoa option.** Hanagyroia *orientalis* evidently differs from extant stauromedusans (Hyman 1940; Miranda et al. 2016) in several characters such as the fusion of the subumbrella and exumbrella, the presence of a coronal (equatorial) groove and a large manubrium, and the lack of secondary tentacle clusters. However, *H. orientalis* has a claustra comparable with that of living staurozoans (Miranda et al. 2017). This feature has the function to partition the gastric cavity (central stomach cavity and the perradial pockets; Berrill 1963). This would suggest that the claustra may have evolved independently within distinct orders of medusozoans in possible relation with digestion efficiency.

**Hydrozoa option.** In extant hydrozoans (e.g. *Clytia hemisphaerica*; Houliston et al. 2010) the radial canals are usually reduced or weakly developed. In contrast, the interradial septa of *H. orientalis* are well-developed and have a triangular shape. Moreover, important diagnostic features of hydrozoans such as the broad velum surrounding the bell margin and the different location of gonads in different orders (Thiel 1966), are absent in *H. orientalis*. The hydrozoan hypothesis can be rejected on the basis of these major differences.

**Scyphozoa option.** Typical scyphozoan features such as well-defined interradial septa, rounded medusa bell margin, the presence of both exumbrella and subumbrella, and oral lips occur in Hanagyroia (Hyman 1940). Extant

Scyphozoa include three orders: Semaestomeae, Rhizostomeae and Coronatae (Daly et al. 2007). *Hanagyroia orientalis* has no rhopalia, ring canals or developed folded oral arms, which characterize extant semaestomes (e.g. *Aurelia aurita*; Fig. 1B, F). Rhizostomes and semaestomes have the same overall morphology, except that rhizostomes bear distinctive marginal tentacles and a large manubrium with numerous tiny suckers (Mayer 1910). Unlike *H. orientalis*, extant rhizostomes lack interradial furrows and perradial ridges, and possess well-developed oral lips. For this reason, *H. orientalis* is unlikely to belong to Semaestomeae or Rhizostomeae. *Hanagyroia* is reminiscent of extant coronates in that its medusa bell is separated into two parts by a conspicuous equatorial (coronal) groove. However, *Hanagyroia* does not possess apertural lappets and pedalia which are two diagnostic characters of extant coronates (Marques & Collins 2004). Cubozoa option. Resemblances between *Hanagyroia* extant cubozoans should also be noted. The paired tentacles of *Hanagyroia*, which are located on interradia and directed inwards without second tentacular clusters, are exclusively found in extant cubozoans (e.g. *Tripedalia cystophora* with pedalia bearing only one tentacle; Werner et al. 1971; Coates et al. 2006). The claustra of *Hanagyroia* obviously plays an important role in partitioning the gastric cavity into the central gastric cavity and five peripheral perradial pockets, as seen in extant cubozoans. This partitioning may have increased the digestive capacities of the medusae. However, important diagnostic features of extant cubozoans (frenula, velarium, pedalia) seem to be missing in *Hanagyroia*.

## PHYLOGENY

We performed a preliminary cladistic analysis on the basis of 22 taxa and 104 characters by using PAUP\* 4.0 b10 and TNT 1.1 (Fig. 7B; Wang et al. 2020, appendices 3–4, 6–7) in order to clarify the phylogenetic placement of *H. orientalis* in the total-group medusozoans. The data matrix was obtained by combining new data with those from previous work (Marques & Collins 2004; Van Iten et al. 2006; Han et al. 2013, 2016c; Dong et al. 2016; Wang et al. 2017). The 104 characters have equal weight, with 9 of them constant, 28 variable characters parsimony-uninformative, and 67 characters parsimony-informative. One strict consensus tree was acquired using PAUP\* 4.0 b10, with tree length (TL) = 90.67, consistency index (CI) = 0.84, and rescaled consistency index (RC) = 0.76. We acquired another consensus tree based on four best trees by using TNT 1.1 (Wang et al. 2020, appendix 7). Our cladistic results (Fig. 7B) are consistent with the phylogenies obtained by previous authors (Marques & Collins 2004; Collins et al. 2006; Van Iten et al. 2006). *Hanagyroia orientalis* is resolved as a possible basal cubozoan. *Hanagyroia*, other coeval fossil medusozoans and extant cubozoans form a clade (Fig. 7B) with *Hanagyroia* more closely related to cubozoans than to hydrozoans. This cladistic analysis supports the placement of *Hanagyroia* in the stem group Cubozoa although its remarkable equatorial groove suggests affinities with coronate scyphozoans. However, there's still the undeniable fact that *Hanagyroia* may represent an intermediate form between scyphozoans and cubozoans based on its combined morphological characters. The cladistic analysis of Dong et al. (2016) (Fig. 7A),



based mostly on external morphological characters, indicated that *Olivoooides* and related fossils form a clade within the crown-group Scyphozoa and a sister group of Coronata. Our results are not consistent with this placement. Most *Olivoooides* and *Olivoooides*-like fossils from the Kuanchuanpu Formation have a well-preserved external ornament (periderm) which indeed superficially resembles that of extant coronates (e.g. *Stephanoscyphus*; Thiel 1966; Chapman & Werner 1972). We incorporated both external and internal morphological characters in our cladistic analysis, which lead to different phylogenetic relationships between *Olivoooides* and the rest of cnidarians. *Olivoooides* displays mixed features typical of those found in both polypoid and medusoid phases (Wang et al. 2017). Many characters seen in *Olivoooides*, including internal ones, appear to have counterparts in extant medusozoans.

## POLYP-SHAPED MEDUSAE

*Olivoooides* and its allied forms have a well-documented continuous development from early dividing embryos to post-hatching larvae (Bengtson & Yue, 1997; Dong et al. 2013; Han et al. 2013; Steiner et al. 2014) with no gap that would imply the existence of a polypoid form. Extant polyps of cnidarians are column-like structures with an external periderm and an internal gastrovascular cavity. These features are generally reduced in those medusozoans with an unidentifiable symmetrical bauplan (i.e. Scyphozoa + Cubozoa; Brusca & Brusca 2003). However, *Hanagyroia* and the co-occurring cnidarians of the Kuanchuanpu Formation show clear symmetrical patterns (Dong et al. 2013; Han et al. 2013; Liu et al. 2014; this work), unlike the polyps. Meanwhile, the well-developed endodermic structures and gastrovascular cavities found in *Hanagyroia* (such as the perradial pockets, the interradial septa, the oral lips, the claustra, the paired tentacles and the huge manubrium) are comparable with the living juvenile medusae. Taking into account all of the above, we incline to the view that *Hanagyroia* are medusae with a polypoid form in appearance or ‘polyp-shaped medusae’ at the pre-hatched stage.

## DEVELOPMENT

With its spherical shape and smooth periderm (paratypes ELISN96-77 and ELISN66-15), *H. orientalis* superficially resembles *Olivoooides* (Qian 1977). The developmental lifecycle of *Olivoooides*-like fossil medusozoans was first described by Bengtson & Yue (1997) and reconstructed in more detail by later authors (Han et al. 2013; Steiner et al. 2014) who suggested that *Olivoooides* and its related forms underwent direct development.

The specimens discussed herein provide some information on the developmental lifecycle of *H. orientalis*. The paratypes ELISN96-77 and ELISN66-15, and holotype (ELISN107-470) specimens may represent three distinct developmental stages (Fig. 8). ELISN96-77, with a complete periderm adhering to the egg membrane, seems to belong to a pre-hatching stage. ELISN107-470 with: (1) a comparatively large size; (2) a conspicuous lobed manubrium with an opened mouth opening; (3) well-developed oral lips located in perradii; and (4) paired short but strong tentacles located in interradii, may correspond to a hatching stage. With its incomplete periderm, ELISN107-470

may represent the last developmental stage or taphonomic bias. ELISN66-15 may represent an intermediate developmental stage. These three specimens are c. 450–500  $\mu\text{m}$  wide and 300–350  $\mu\text{m}$  high. This size range suggests a direct lecithotrophic development as in extant direct developers (Berrill 1949; Han et al. 2013). The large mouth opening of *H. orientalis* indicates that the animal could feed once hatched. Its well-developed oral lips, large manubrium and retractile tentacles suggest predatorial (carnivorous) feeding habits.

## CONCLUSION

*Hanagyroia orientalis* gen. et sp. nov. is different from coeval medusozoans from the Kuanchuanpu Formation and extant representatives of the group in important aspects of its internal and external morphology such as a large manubrium and paired tentacles. Although *Hanagyroia* resembles coronate scyphozoans (e.g. the equatorial groove), our cladistic analysis may suggest affinities within an intermediate form of medusozoan. We suggest that *H. orientalis* underwent direct development. This developmental mode may be applicable to other coeval medusozoans from the Kuanchuanpu Formation.

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## DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/C33D36FE-8E10-471D-8023-D26DF91ECDC8>. Data and appendices for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.np5hqbzpt>.

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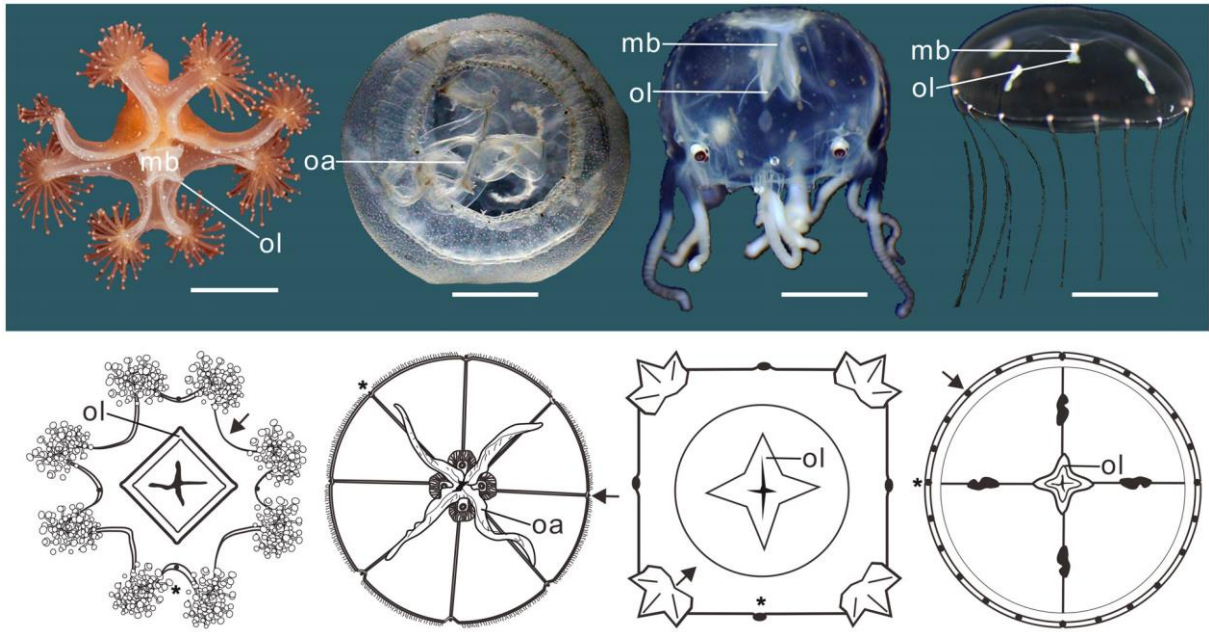
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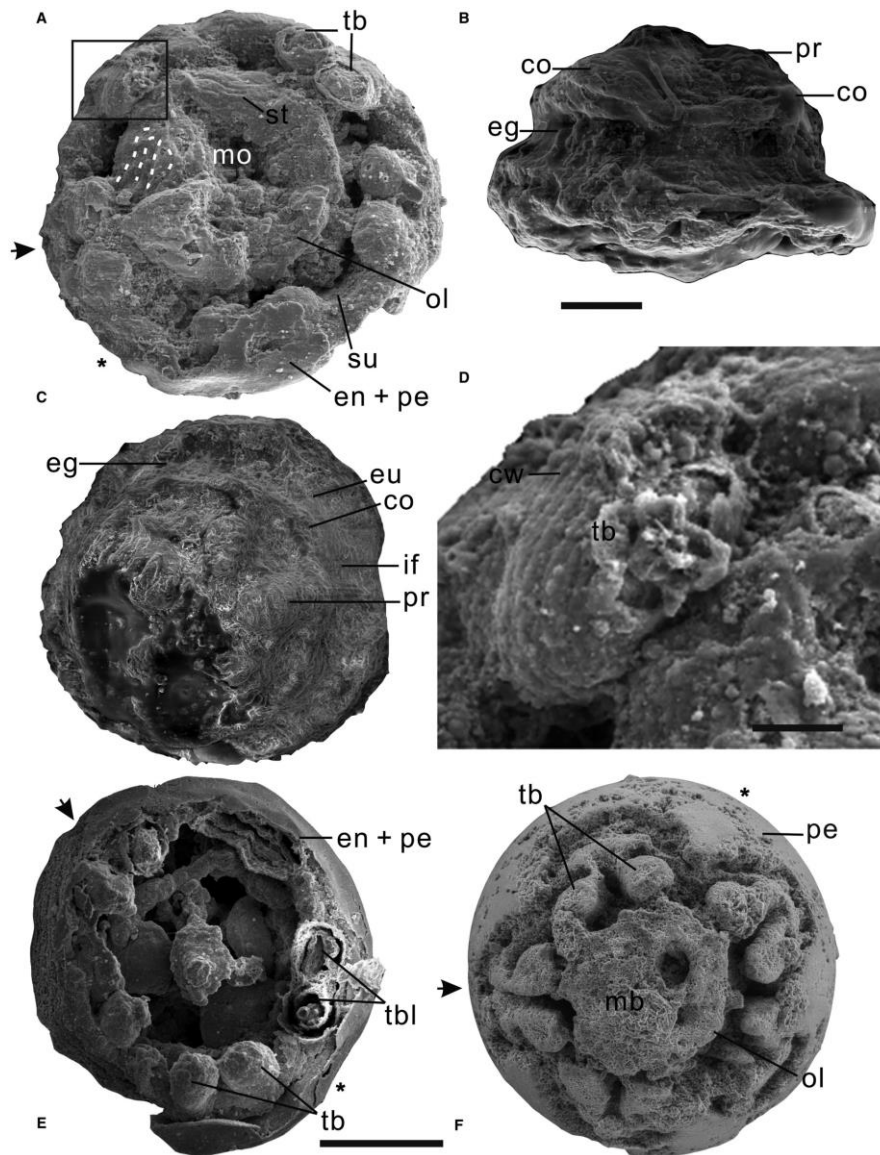
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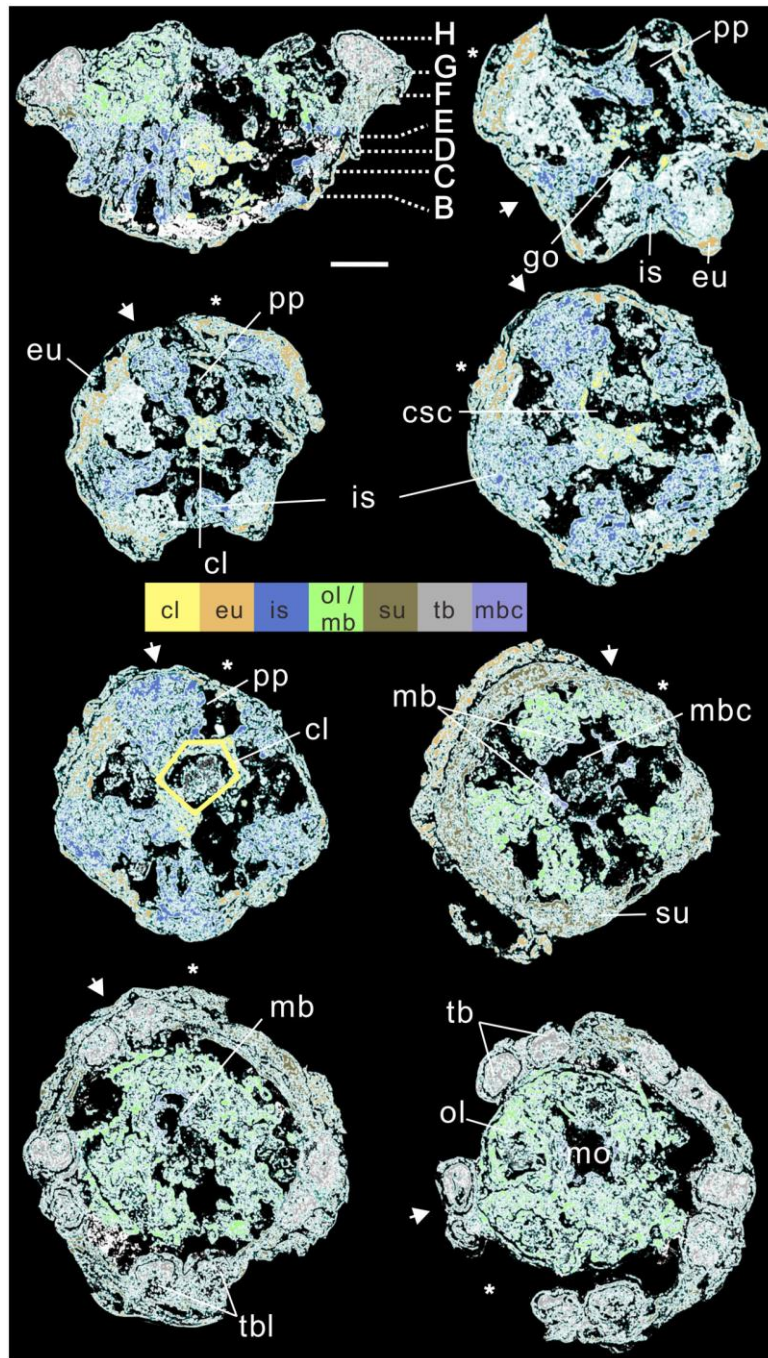
## FIGURES



**FIG. 1.** Photographs and diagrams in oral view showing the tetradial symmetry, oral lips and manubrium of typical extant medusae. A, E, Staurozoa exemplified by *Haliclystus*. B, F, Scyphozoa exemplified by *Aurelia aurita*. C, G, Cubozoa exemplified by *Tripedalia cystophora* Conant, 1898 (Charybdeida). D, H, Hydrozoa exemplified by *Clytia hemisphaerica*. Abbreviations: mb, manubrium; oa, oral arm; ol, oral lip; \* perradial; ? interradial. Scale bars represent: 5 mm (A, B); 2 mm (C); 5 mm (D). Images in A and D courtesy of K. Telnes and T. Momose, respectively.

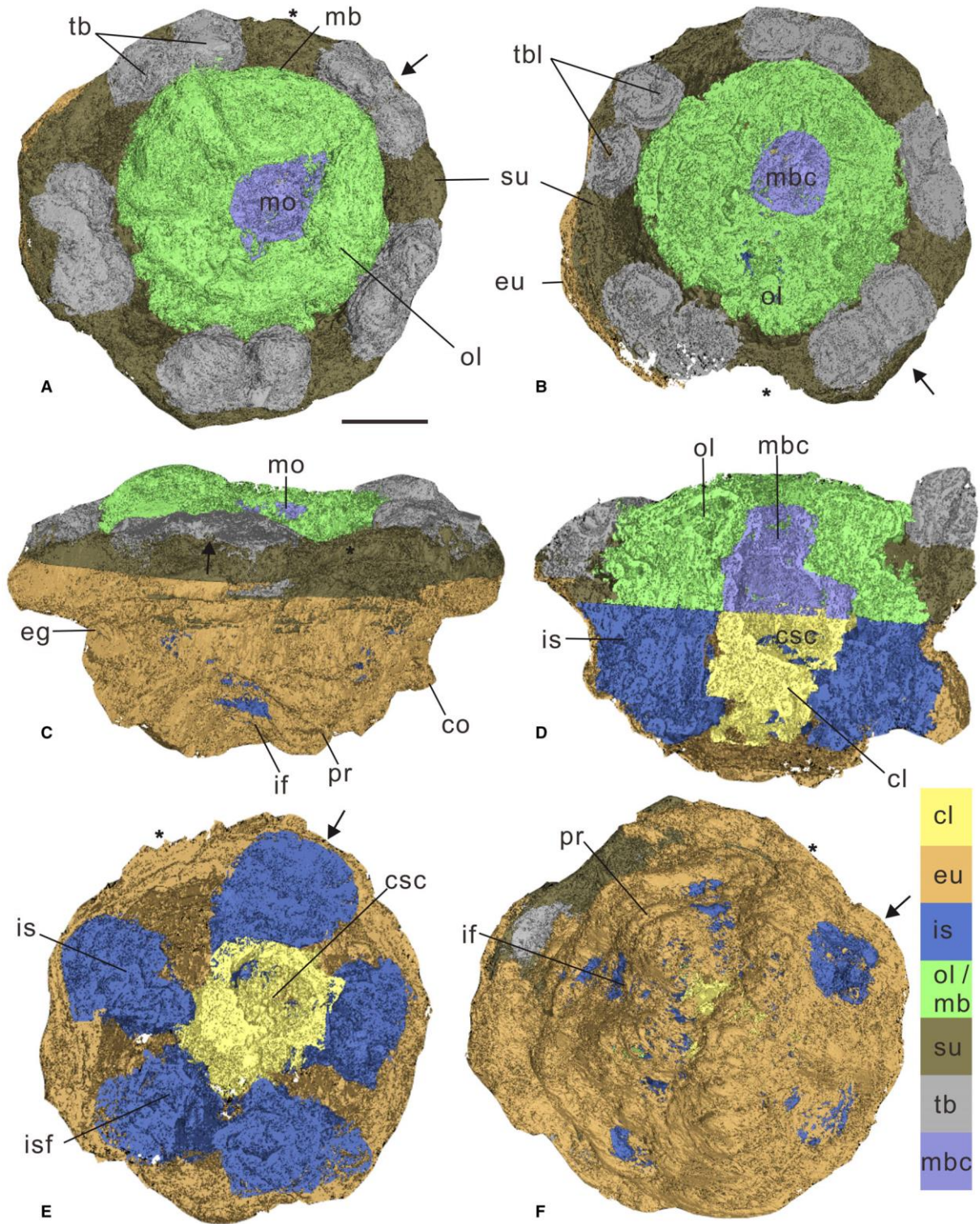


**FIG. 2.** *Hanagyroia orientalis* from the early Cambrian Kuanchuanpu Formation, South China. A–D, ELISN107-470, holotype: A, oral view showing paired tentacular buds (tb), and manubrium with perradial oral lips (ol); the dotted lines represent the stripes of the oral lips; B, lateral view showing equatorial groove and triangular cornice; C, aboral view showing perradial ridge; D, detailed view (see boxed area in A) showing circular wrinkles (cw) on tentacular buds. E, ELISN121-154, oral view showing tentacles and tentacular bud lumens (tbl). F, ELISN66-15, oral view showing perradial oral lips (ol). Abbreviations: co, cornice; cw, circular wrinkles; eg, equatorial groove; en, egg envelope; eu, exumbrella; mb, manubrium; mbc, manubrial cavity (esophagus); mo, mouth; ol, oral lip; pe, periderm; pr, perradial ridge; st, stripe; su, subumbrella; tb, tentacular bud; tbl, tentacular bud lumen; \* perradial; ? interradianal. Scale bars represent: 100 lm (A–C); 25 lm (D); 200 lm (E, F)

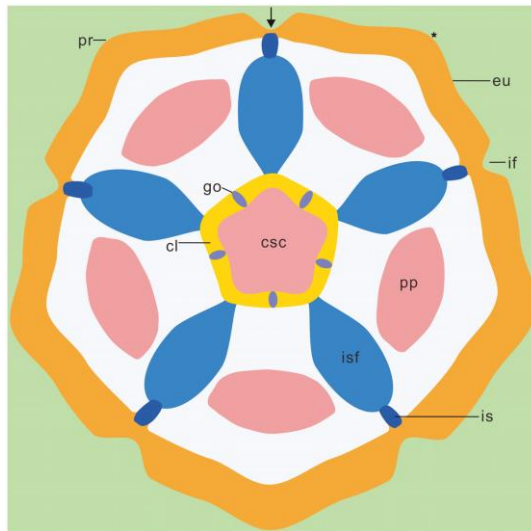


**FIG. 3.** *Hanagyroia orientalis* from the early Cambrian Kuanchuanpu Formation, South China; microtomographic sections through the holotype (ELISN107-470). A, lateral section through the manubrium of the holotype, indicating the position of transverse sections B–H. B–H, transverse sections perpendicular to the aboral-oral axis. Major external and internal structures are represented by colours generated by VG Studio 2.2 MAX (colourless sections available in Wang et al. 2020, appendix 2). Abbreviations: cl, claustra (yellow pentagon in E); csc, central stomach cavity; eu, exumbrella; go, gastric ostium; is, interradianal septum; mb, manubrium; mbc, manubrial cavity (esophagus); mo, mouth; ol, oral lip; pp, perradial pocket; su, subumbrella; tb, tentacular bud; tbl, tentacular bud lumen; \* perradial; ? interradianal. Scale bar represents 100  $\mu$ m.

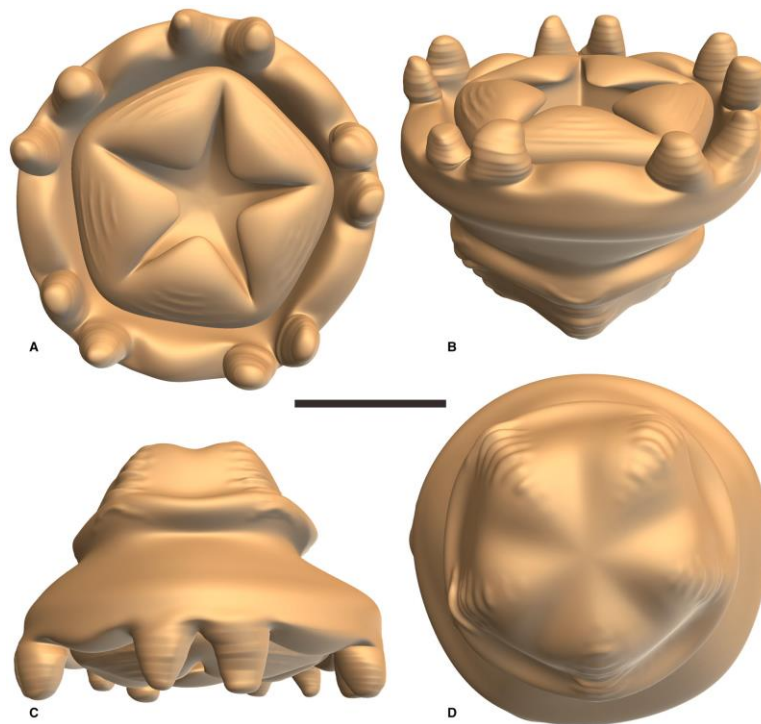




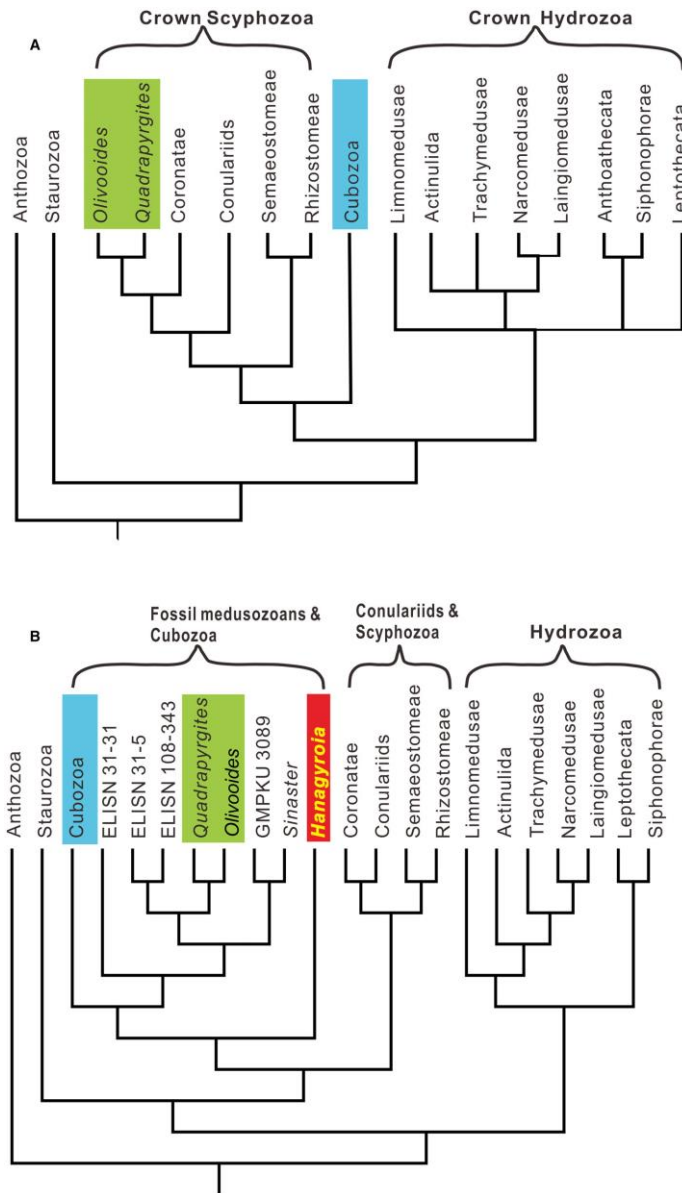
**FIG. 4.** *Hanagyroia orientalis* from the early Cambrian Kuanchuanpu Formation, Shaanxi Province, China; holotype (ELISN107-470), three-dimensional model generated by VG Studio 2.2 MAX. A–B, E, oral; C–D, lateral; F, aboral view. Colours indicate distinct anatomical structures. Abbreviations: cl, claustra; co, cornice; csc, central stomach cavity; eg, equatorial groove; eu, exumbrella; if, interradial furrow; is, interradial septum; isf, interradial septal funnel; mb, manubrium; mbc, manubrial cavity (esophagus); mo, mouth; ol, oral lip; pr, perradial ridge; su, subumbrella; tb, tentacular bud; tbl, tentacular bud lumen; \* perradial; ? interradial. Scale bar represents 100  $\mu$ m.



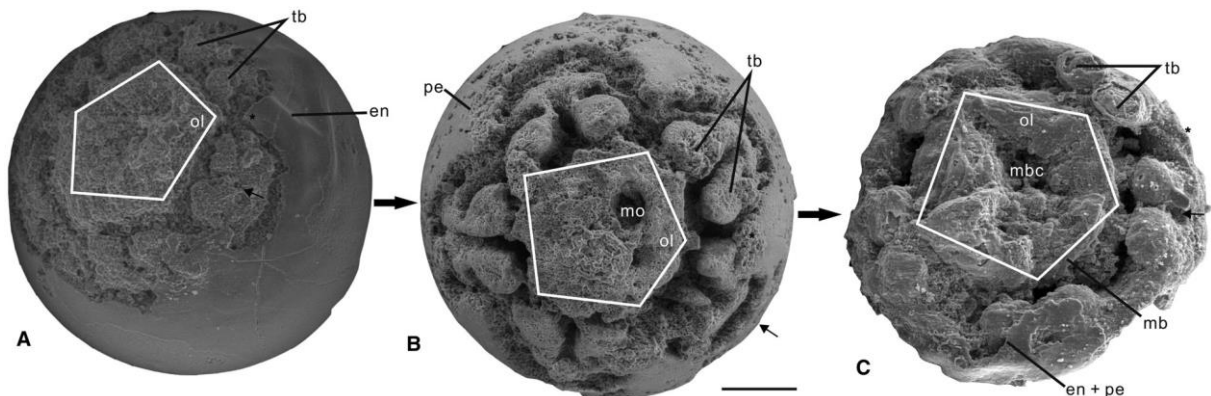
**FIG. 5.** Simplified transverse section through the middle part of the *Hanagyroia orientalis* from the early Cambrian Kuanchuanpu Formation, Shaanxi Province, China. Abbreviations: cl, claustra; csc, central stomach cavity; eu, exumbrella; go, gastric ostium; if, interradial furrow; is, interradial septum; isf, interradial septal funnel; pp, perradial pocket; pr, perradial ridge; \* perradial; ? interradial depression.



**FIG. 6.** Reconstructions of *Hanagyroia orientalis* from the early Cambrian Kuanchuanpu Formation, Shaanxi Province, China. A, oral; B–C, lateral; D, aboral view. Artistic 3D reconstruction by Xi Liu, Northwest University, Xi'an, China. Scale bar represents 150  $\mu$ m. Colour online.



**FIG. 7.** Cladistic analysis. A, cladogram proposed by Dong et al. (2016). B, strict consensus tree of cnidarians obtained here, based on both external and internal morphological characters and using PAUP\* 4.0 b10; the taxonomic status of ELISN31-5, ELISN108-343 and GMPKU3089 is uncertain (see Han et al. (2013, 2016b), Dong et al. (2013)); Sinaster was described by Wang et al. (2017); Quadrapyrgites is another form from the Kuanchuanpu Formation.



**FIG. 8.** Developmental stages of *Hanagyroia orientalis*. A, ELISN96-77 shown with a complete egg envelope + periderm may represent the pre-hatching stage. B, ELISN66-15 preserved with an almost complete periderm may represent an intermediate developmental stage. C, the holotype specimen ELISN107-470 may represent the hatched stage. Abbreviations: en, egg envelope; en + pe, envelope + periderm; mb, manubrium; mbc, manubrial cavity; mo, mouth; ol, oral lip; pe, periderm; tb, tentacular bud, \* perradial; ? interradian. Three irregular white pentagons show the pentamerous symmetry. Scale bar represents 200  $\mu$ m.