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Cambrian Stem-group Cnidarians with a New Species from the Cambrian Series 3 of the Taebaeksan Basin, Korea

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Abstract: Five species, *Lipopora lissa* Jell and Jell, 1976, *Lipopora daseia* Jell and Jell, 1976, *Tretocylichne perplexa* Engelbretsen, 1993 from Australia, *Cambroctoconus orientalis* Park, Woo, Lee, Lee, Lee, Han and Chough, 2011 from China, and *Cambroctoconus kyrgyzstanicus* Peel, 2014 from Kyrgyzstan, belonging to the Cambrian stem-group cnidarians have been documented in the fossil record. *Cambroctoconus coreaensis* sp. nov., interpreted here as a stem-group cnidarian, from the Seokgaejae section in the Daegi Formation, Taebaek Group (Cambrian Series 3), Taebaeksan Basin, central-eastern Korean Peninsula, has a slender cup-shaped skeleton. A cladistic analysis produced 21 most parsimonious trees, which invariably placed the six stem-group cnidarians below the crown-group, but their relationships within the stem-group are unresolved. Nine out of the 21 trees suggest a monophyletic relationship for the Cambrian stem-group cnidarians, whereas in six other trees a monophyly of *Cambroctoconus* and *Tretocylichne* appeared as the sister-group to the crown-group cnidarians with *Lipopora* at the most basal branch. This result may reflect the fact that crown-group cnidarians evolved in the Precambrian, and suggests that the diversity of stem-group cnidarians was a result of an independent radiation in the Cambrian.

Key words: Phylogeny, Cnidaria, Cambrian, Drumian, Taebaeksan Basin, Korea

1 Introduction

Although the concept and unraveling of fossil stem-groups have contributed to understanding of the morphological origins of extant animals (e.g. Budd and Jensen, 2000; Shu et al., 2004; Shu et al., 2006; Caron et al., 2006; Conway Morris and Caron, 2007; Liu et al., 2011), stem-group cnidarians have rarely been documented. The "tabulate fossil" *Sinocyclocyclicus guizhouensis* Xue, Tang and Yu, 1992 from the Ediacaran Doushantuo Formation of China was interpreted to have "tabula-like structures", which were considered equivalent to the tabulae of tabulate corals, and hence the taxon was regarded as a possible stem-group cnidarian (Xiao et al., 2000). However, the "tabula-like structures" in this taxon are too regularly and closely spaced to be compared to the tabulae of tabulate corals. The size of *S. guizhouensis* with a diameter of less than 200 μm is also apparently too small to shelter cnidarian polyps. In addition, the branching of *S. guizhouensis* is incomparable to the vertical fission of a corallite in a cerioid colony such as that of the Ordovician favositoid tabulate *Saffordophyllum newcombae* (see Xiao et al., 2000, fig. 3g). The possible cnidarian affinity of the early Cambrian *Olivooides* has also been doubted, and recently a cycloneuralian affinity was suggested (Steiner et al. 2014).

Park et al. (2011) reported a Cambrian stem-group cnidarian, *Cambroctoconus orientalis* from the Drumian Stage (Cambrian Series 3) of Shandong Province, North China, which is a colonial animal with octagonal cup-shaped skeletons and paired septa. The morphology of this stem-group cnidarian suggests that octoradial symmetry

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and colonial occurrence appeared earlier than other cnidarian features during the course of cnidarian evolution. More recently, Geyer et al. (2014) reported *Cambroctoconus kyrgyzstanicus* Peel, 2014 from Cambrian Stage 5 of Kyrgyzstan, which has a rather short and trochoidal octagonal cup-shaped skeleton. In addition, the octagonal cup-shaped morphology of stem-group cnidarians has led to the recognition of three other Cambrian stem-group cnidarian species from Australia: *Lipopora lissa* Jell and Jell, 1976 (Cambrian Stage 4), *Lipopora daseia* Jell and Jell, 1976 (Cambrian Stage 4), and *Tretocylichne perplexa* Engelbretsen, 1993 (Cambrian Stage 5).

This study reviews the characteristics of all known Cambrian stem-group cnidarians, and documents a new species of *Cambroctoconus* from the Daegi Formation (Drumian Stage, Cambrian Series 3), of the Taebaek Group, Taebaeksan Basin, located in eastern part of Korean peninsula. The new species is characterized by the most slender cup-shaped skeleton of all known cnidarians. In addition, a cladistics analysis was conducted to elucidate the phylogenetic relationships of Cambrian stem-group cnidarians to the crown-group cnidarians.

2 The New Korean Species from the Taebaeksan Basin

2.1 Geology, locality and material

The Cambro-Ordovician rocks in Korea, known as the Joseon Supergroup, are exposed in the Taebaeksan Basin, which is situated in the central-eastern part of the Korean Peninsula. Paleogeographically during the Paleozoic, the Taebaeksan Basin was part of the North China Platform (Chough et al., 2000). The Joseon Supergroup is divided into the Taebaek, Yeongwol, Pyeongchang, Yongtan, and Mungyeong groups, each with a unique lithologic succession and geographic distribution (Choi, 1988). The Taebaek Group consists of carbonates with subordinate siliciclastic rocks, representing deposition in a shallow marine continental shelf environment (Choi et al., 2004; Kwon et al., 2006; Lee, 2014). The Taebaek Group is subdivided into the Jangsan/Myeonsan, Mybong, Daegi, Sesong, Hwajeol, Dongjeom, Dumugol, Makgol, Jigunsan, and Duwibong formations, in ascending order, with the Cambrian–Ordovician boundary lying within the lowermost part of the Dongjeom Formation (Choi et al., 2004).

Fossils of *Cambroctoconus coreaensis* sp. nov. documented herein were collected from the Daegi Formation at Seokgaejae section (129° 08' 45.05" E, 37° 04' 27.9" N), which is located about 20 km southeast of Taebaek City (Fig. 1). The ca. 1100-m-thick Taebaek Group is well exposed along a forest road, and was described in detail by Choi et al. (2004). The Daegi Formation generally comprises a bright, massive to thin-bedded limestone, with some oolitic and dolomitic limestones. It is ca. 180 m in thickness in the Seokgaejae section, and characterized by oncoid/ooid grainstone, massive grainstone, wackestone, limestone-shale couplets, nodule-bearing shale, parallel-laminated mudstone, and greenish-gray homogeneous mudstone (Choi et al., 2004). The formation has been interpreted to represent shallow-marine settings such as lagoon and ooid shoal with microbial mounds (Choi et al., 2004; Kwon et al., 2006; Hong et al., 2012).

Kobayashi (1935, 1966) established the *Megagraulos*, *Solenoparia*, and *Olenoides* trilobite zones, in ascending order, within the formation without providing detailed biostratigraphic data. Kang and Choi (2007) revised the biostratigraphy of the formation, establishing the *Crepicephalina*, *Amphoton*, and *Cyclolorenzella* zones, in ascending order, which are better correlated with the biostratigraphy of North China. Later, the *Cyclolorenzella* Zone was replaced by the *Jiulongshania* Zone (Park et al., 2013). Hong et al. (2012) documented siliceous sponge-*Epiphyton* buildups from ca. 50 m above the base of the formation, and these beds rarely included “octagonal, cone-shaped organisms”. No trilobite biostratigraphic data has been found from this interval (see Kang and Choi, 2007), which is situated between the underlying *Crepicephalina*-occurring interval and the overlying *Amphoton*-occurring interval. Nevertheless, by definition, this interval is considered to be within the *Crepicephalina* Zone.

Specimens of “octagonal cone-shaped organisms” were recovered from the siliceous sponge-*Epiphyton* buildups documented by Hong et al. (2012). Blocks of a buildup were etched out with hydrochloric acid, and the rarely occurring octagonal cone-shaped specimens are now identifiable as the new species of *Cambroctoconus*. Thirty-one specimens of *Cambroctoconus coreaensis* sp. nov. were obtained from the acid-leached residue. Most of the specimens are coarsely silicified and poorly preserved. Due to the rare occurrence of the specimens, only two thin section images have been made for this study. The interiors of some silicified specimens were analyzed through X-ray microcomputed tomography scanning, using a SkyScan 1172 system at the Dental Research Institute of Seoul National University. The skeletons were scanned under the same conditions as in previous analyses (Park et al., 2011). The 3-D reconstructions (Fig. 3) were made with a resolution of 12.97 μm per voxel using the SkyScan software CTVox32. Other specimens were coated with magnesium oxide and photographed.

The specimens of *C. coreaensis* sp. nov. are housed in the Korea Polar Research Institute, Incheon City of Korea

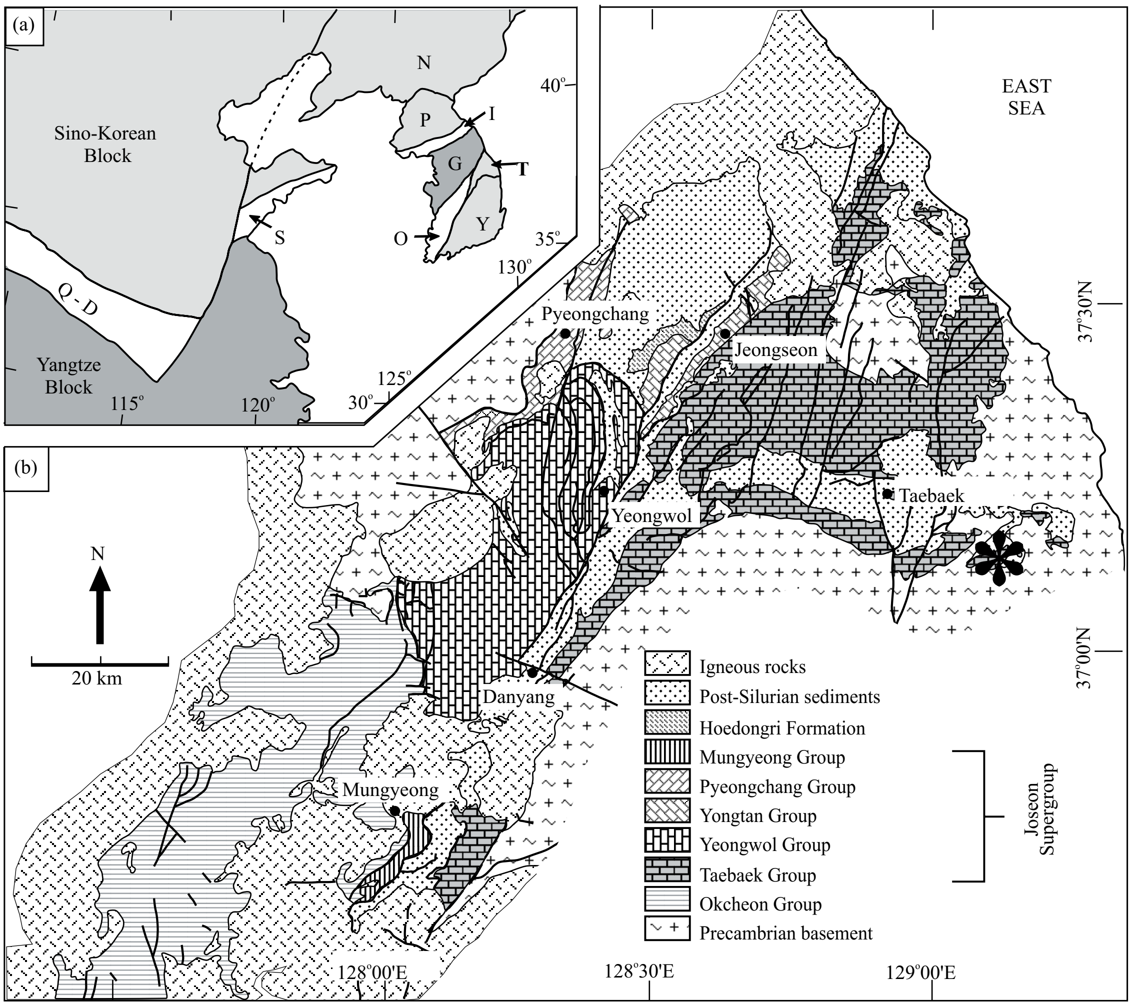

Fig. 1. Locality maps: (a), tectonic map of Korean peninsula and surrounding area showing the location of the Taebaeksan Basin; (b), geological map of the Taebaeksan Basin showing the distribution of the lower Paleozoic Joseon Supergroup in the Taebaeksan Basin. The asterisk indicates the location of the Seokgaejae section from which the material for this study was collected.

Q-D, Qinling-Dabie belt; S, Sulu Belt; N, Nangnim Massif; P, Pyeongnam Basin; I, Imjingang Belt; G, Gyeonggi Massif; O, Okcheon Belt; T, Taebaeksan Basin; Y, Yeongnam Massif.

with registered numbers prefixed with KOPRIF.

2.2 Systematic paleontology

Stem-group Cnidaria

Genus *Cambroctoconus* Park, Woo, Lee, Lee, Lee, Han, Chough and Choi, 2011.

Type species: *Cambroctoconus orientalis* Park, Woo, Lee, Lee, Lee, Han, Chough and Choi, 2011.

Diagnosis: Stem-group cnidarian with calcareous conical cup-shaped skeletons; individual cup eight-sided, with holdfast, perforated wall, and octagonal opening in dorsal view; septa varying from absent to occurring as paired longitudinal lamellar structure projecting inwards from each corner of the cup.

Remarks: The diagnosis of *Cambroctoconus* given by Park et al. (2011) was on the basis of the numerous well-preserved specimens and a colony of the type species, *C. orientalis*. Since it is practically difficult to acquire such well-preserved material for stem-group cnidarians and more species have now been assigned to this group, the generic diagnosis is emended herein to better accommodate all the known species (*C. orientalis, C. kyrgyzstanicus,* and *C. coreaensis* sp. nov.). We consider that the most important characteristic of this genus is the conical cup-shaped skeleton. Other basal cnidarians differ such as *Lipopora* with sub-cylindrical skeletons, and the skeleton of *Tretocylichne* has an open aperture at the base, and thus these two taxa are not conical cup-shaped.

Cambroctoconus coreaensis sp. nov. (Figs. 2–3)

Holotype: KOPRIF5001 (Fig. 2a–b).

Etymology: Referring to the Latin name of Korea.

Diagnosis: Small slender cup-shaped skeleton of 11-16 mm in height and 3–6 mm in maximum width at the rim, octagonal in transverse view with perforated wall and a

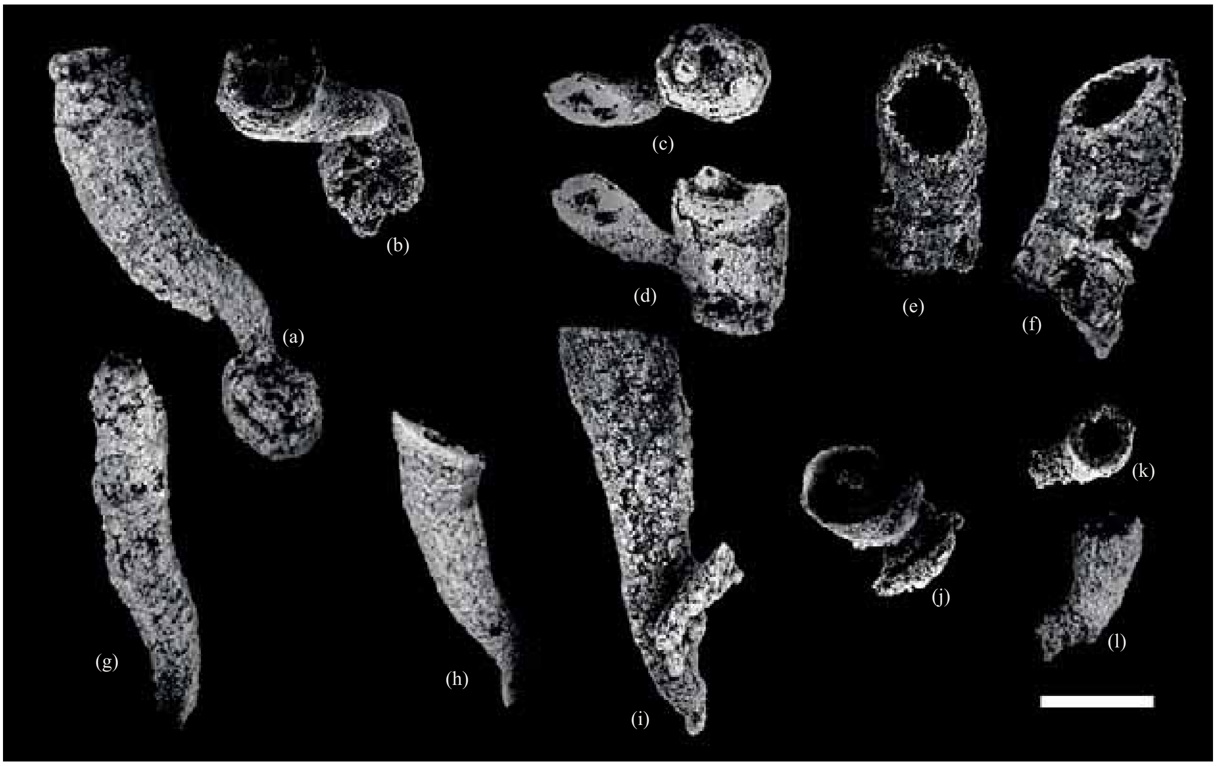

Fig. 2. *Cambroctoconus coreaensis* sp. nov. from the Cambrian Drumian Stage at Seokgaejae section, Daegi Formation, Taebaek Group, Taebaeksan Basin, Korea.

(a–b), holotype, KOPRIF5001, lateral and dorsal views; (c–d), paratype, KOPRIF5002, dorsal and lateral views; (e–f), paratype, KOPRIF5003, dorso-lateral and lateral views; (g), paratype, KOPRIF5004; (h), paratype, KOPRIF5005; (i–j), paratype, KOPRIF5006, lateral and dorsal views; (k–l), paratype, KOPRIF5007, dorsal and lateral views. Scale bar is 5 mm.

holdfast at the base; septa apparently lacking.

Description: Skeletal cups are usually 11–16 mm in height, 3–6 mm in maximum width at the rim and 1.2–1.7 mm in minimum width near the base (Fig. 2). The base of the cup forms a holdfast (Fig. 2a–b, h). The eight-sided shape of the cup is less prominent in acid-leached specimens, but the octagonal transverse view is evident from the thin section images (Fig. 3a, b). Budding from the outer surface of the parental cup is observed (Fig. 2a–d). Although it has been coarsely silicified, the wall is likely to be perforated, given the rugged surface of the cup.

Remarks: The coarsely silicified poor preservation hampers more detailed description. The new species has the most slender cup-shaped skeleton of all known stem-group cnidarians. The inside is often filled with silica (Fig. 2b–c, j, and Fig. 6a–b). In comparison, in *C. orientalis*, the conical protuberance and the basal cavity are frequently filled with silica (e.g. Park et al., 2011, fig. 2f, g). In contrast, the silica-infilling in C. *coreaensis* is of irregular shape, and does not reflect the presence of any internal structure (Fig. 2b–c, j, and Fig. 6a–b).

Occurrence: This species found at the Seokgaejae section occurs rarely in the siliceous sponge-*Epiphyton*

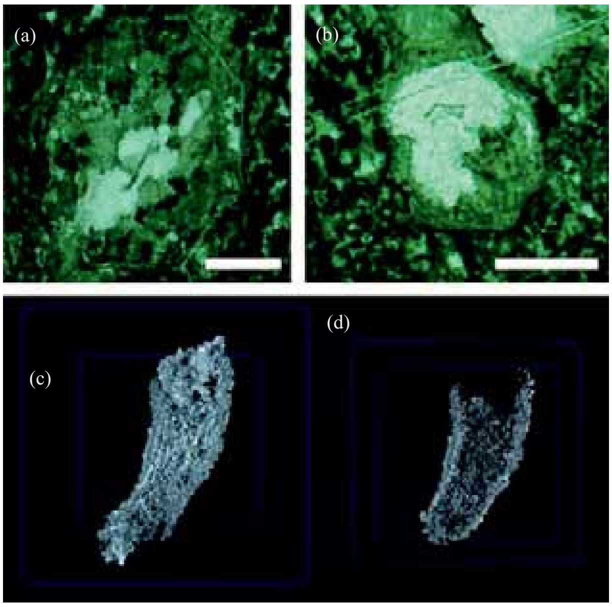

Fig. 3. *Cambroctoconus coreaensis* sp. nov. from the Cambrian (Drumian Stage) Daegi Formation, Taebaek Group, Seokgaejae section, Taebaeksan Basin, Korea.

(a–b), thin section images; paratype, (a), KOPRIF5008a; (b), KOPRIF5008b; (c), 3-D reconstructions of KOPRIF5007; (d), 3-D reconstructions of KOPRIF5007 showing a longitudinal-cut view. Scale bars are 2 mm.

buildups of the *Crepicephalina* Zone (Drumian Stage, Cambrian Series 3) of the Daegi Formation, Taebaek Group, Taebaeksan Basin, Korea.

3 Further Comparison and Review of Cambrian Stem-group Cnidarians

3.1 *Lipopora lissa* Jell and Jell, 1976 and *Lipopora daseia* Jell and Jell, 1976

The genus *Lipopora* was first reported from Cambrian Stage 4, in the Coonigan Formation of western New South Wales, Australia, with two species, *L. lissa* and *L. daseia* assigned to it (Jell and Jell, 1976). There is significant intraspecific variation in the cup-shaped skeleton; an eight-sided cup morphology is evident in some specimens (Jell and Jell, 1976, figs. 11f, 12b, 12g; Fig. 4b, f–g) whereas it is not recognizable in others. The size of the skeleton is smaller than *Cambroctoconus*; more specifically the maximum width of *Lipopora* ranges from 1–3 mm at the rim of the cup, while that of *C. orientalis* is 8–11 mm, *C. kyrgyzstanicus* 5–8 mm, and *C. coreaensis* sp. nov. 3–6 mm. The lateral view of *Lipopora* is less conical or almost subcylindrical, while that of *C. orientalis* is almost conical. However, the presence of the eight-sided cup-shape and septa suggests a close phylogenetic relationship with *C. orientalis*, indicating that *Lipopora* is a stem-group cnidarian genus. Despite the coarse silicification and lack of thin section images, the wall of *Lipopora* is likely to be perforated (Fig. 4d).

The cup-shaped skeleton of *Lipopora lissa* has a maximum width of 2–3 mm at the rim of the cup. Compared to *L. daseia*, this species has a smooth surface with sixteen short septa evenly spaced (Fig. 4b). Budding is observed from the outside of the parental cup (Jell and Jell, 1976, fig. 11b). Dichotomous branching is also shown in this species (Fig. 4c). The most notable feature of this species is ‘rejuvenescence’, with new cups growing on top of the parental cups (Fig. 4a).

Lipopora daseia has a diameter of 1 to 3 mm and is distinguished by the presence of transverse “growth rings” on the outer surface. Intraspecific variation of this species is more severe than that of *L. lissa*; one specimen shows a clearly eight-sided cup (Jell and Jell, 1976, fig. 12g; Fig. 4f), which is extremely similar to *C. orientalis*, but this feature is hardly recognizable in other specimens (Jell and Jell, 1976, fig. 12b; Fig. 4g). Eight broad septa are present in some, if not all, specimens (Fig. 4g). None of the known specimens show any indication of budding.

3.2 *Tretocylichne perplexa* Engelbretsen, 1993

This species was recovered from the Cambrian Stage 5, Murrawong Creek Formation, northeastern New South Wales, Australia (Engelbretsen, 1993). All the specimens (Fig. 5) are preserved by epidote-coating. The skeleton is eight-sided and has very short paired septa at each corner. The size is significantly smaller than *Cambroctoconus orientalis* and *C. coreaensis*; height of 1–2.5 mm; maximum width of 0.6–2.5 mm near the rim and minimum width of 0.5–1 mm near the base. The overall shape is almost as conical as that of *C. orientalis*. The epidote-coated preservation hinders a detailed observation of the cup wall, but the rugged surface and small pits on the surface might reflect a perforation of the wall (Fig. 5c–d). Budding from the outside of the cup is evident (Fig. 5e). The most notable feature of this stem-group cnidarian is the open aperture at the base, so that the skeleton can be

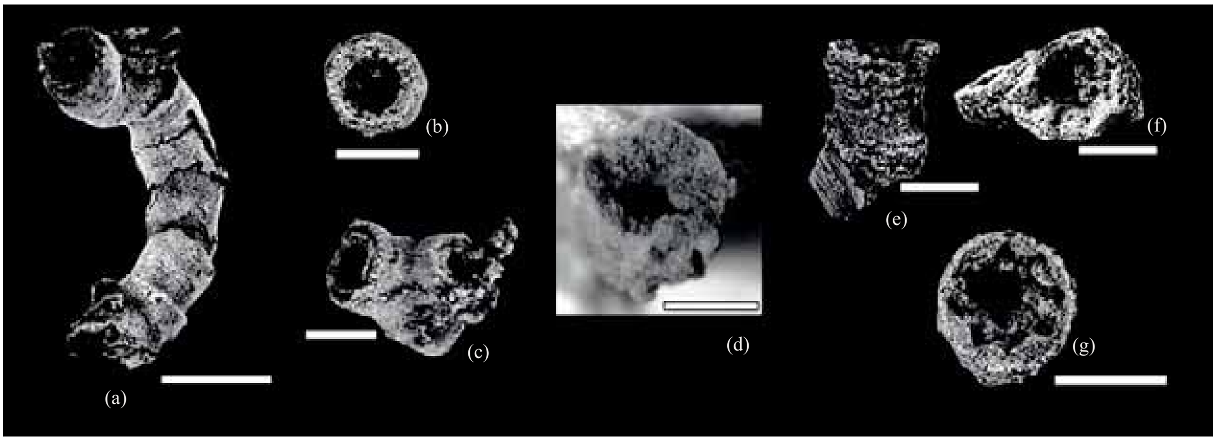

Fig. 4. *Lipopora* Jell and Jell, 1976 from the Cambrian Stage 4, Coonigan Formation of western New South Wales, Australia.

(a–d), *Lipopora lissa* Jell and Jell, 1976. (a–b), holotype, ANU29521, lateral and dorsal views, showing sixteen short septa in the dorsal view; (c), ANU29522, dorso-lateral view, showing dichotomous branching; (d), ANU29552, ventral view, showing a perforated wall; (e–g), *Lipopora daseia* Jell and Jell, 1976. (e), holotype, ANU29553, lateral view; (f), ANU29557, dorsal view; g, ANU29555, dorsal view, showing eight short septa. Scale bars are 5 mm for a and 2 mm for b–g. Specimens are housed in the paleontological collections of Australian National University, Australia. All images except for (d) are re-illustrated from Jell and Jell (1976).

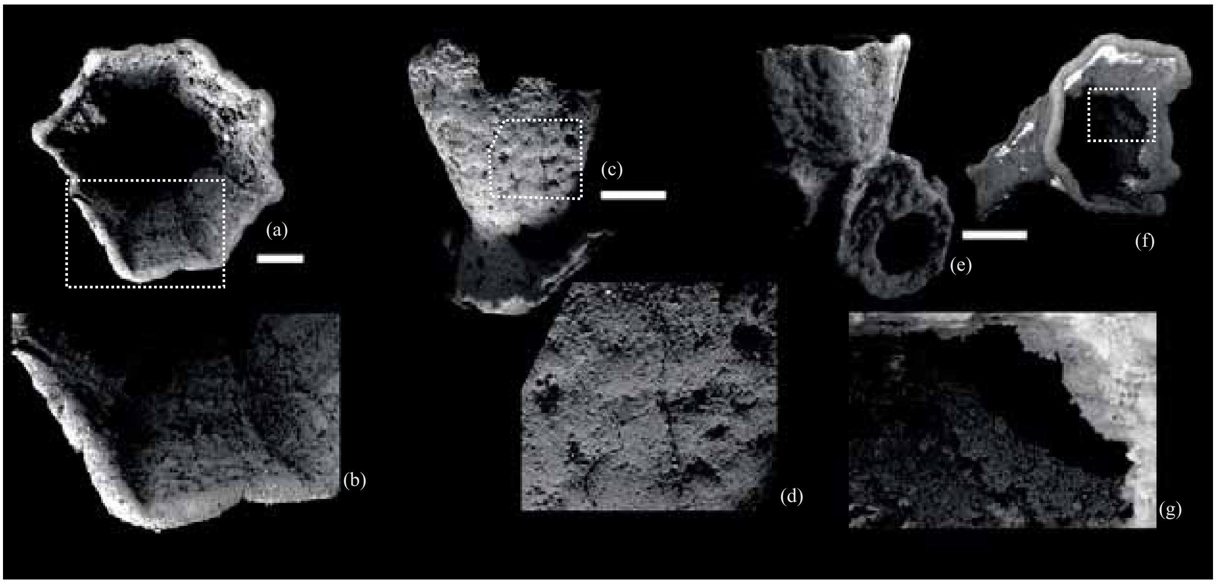

Fig. 5. *Tretocylichne perplexa* Engelbretsen, 1993 from the Cambrian Stage 5, Murrawong Creek Formation, northeastern New South Wales, Australia.

(a–b), MU52714. (a), dorsal view, showing eight-sided morphology and eight pairs of short septa; (b), magnified view of the dotted rectangle in a; (c–d), MU52791. (c), lateral view, showing pits and a rugged outer surface; (d), magnified view of the dotted rectangle in (c); (e–g), holotype, MU52711. (e), lateral view, showing a budding from the outside; (f), dorsal view; (g), magnified view of the dotted rectangle in f. Scale bars are 0.5 mm. Specimens are housed in the paleontological collections of Macquarie University, Australia.

described as conical cylinder-shaped, not cup-shaped. Nevertheless, the presence of the eight-sided shape of the skeleton, eight pairs of septa, and holdfast around the aperture at the base demonstrates a close phylogenetic relationship with *Cambroctoconus*. The offset newly budded from the outside of the parental cup is represented by a hole with crater-shaped surrounding (Fig. 5e). A folded band-like structure is also formed on the inside of the parental cup (Fig. 5f–g). This is significant in regard to the tissue integration of the skeletal wall.

Park et al. (2011) suggested that the skeletal wall of *C. orientalis* must have been highly integrated with soft tissue, given the fact that the offsets budded from both inner and outer surfaces of the cup. In *T. perplexa*, the parental cup initially must have had a complete cylinder-shaped skeleton without a hole, and then when the new offset budded, a hole with the crater-shape surrounding it appeared to form the base of the new offset. The appearance of a hole in the skeletal wall implies that the skeletal wall of *T. perplexa* must have been highly integrated with soft tissue.

3.3 *Cambroctoconus orientalis* Park, Woo, Lee, Lee, Lee, Han, Chough and Choi, 2011

Park et al. (2011) described this species based on numerous silicified specimens and thin sections collected from the Drumian Zhangxia (Changhia) Formation in Shandong Province, North China; they gave a detailed morphological analysis based on this material. The skeletal cup is usually 11–13 mm in height, 8–11 mm in maximum width at the rim and 1.5–3 mm in minimum width near the base, being the largest of all known stem-group cnidarians. Budding from the outside, the inside, and the rim of the parental cup is observed (see Park et al., 2011). In *Lipopora daseia*, transverse “growth rings” are present on the outer surface of the cup, but in *C. orientalis*, similar transverse lines are expressed in the inner surface of the cup (Fig. 6b-c). There can be four different internal structures in the cup base: 1) cups without any significant structure (Fig. 6a–c); 2) cups with a basal cavity defined by a subhorizontal element (Fig. 6d–g); 3) cups with a large conical protuberance (Fig. 6h–l) and; 4) cups with tubular structures (Fig. 6m–n). The function and homology of these structures are currently unknown. An almost complete colony was discovered on a bedding plane at the Xintai Section in Shandong, where the laterally growing individual cups are oriented roughly into two directions, forming a branching pattern within the colony (Park et al., 2011, fig. S4). Park et al. (2011) mentioned that *C. orientalis* possessed cnidarian features such as the longitudinal septa and octoradial symmetry, and also noted non-cnidarian features such as the perforated wall and basal cavity. They ran a cladistic analysis that resulted in *C. orientalis* being located below the crown-group cnidarians, i.e., at a stem-group cnidarian position.

Among the crown-group cnidarians, the morphology of the Staurozoa was especially noted; being phylogenetically situated between the Anthozoa and

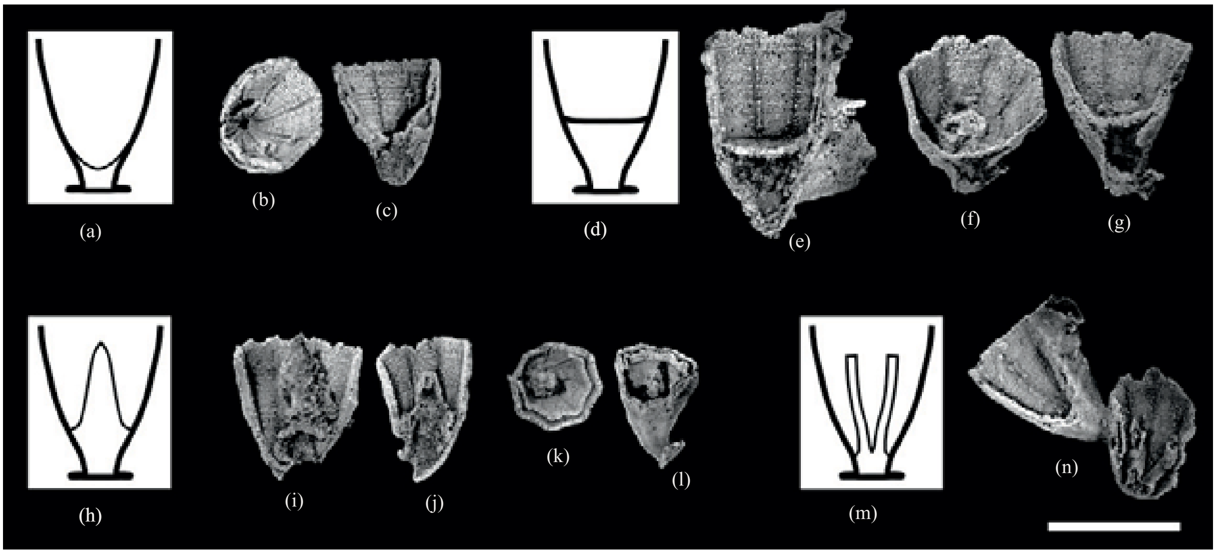

Fig. 6. *Cambroctoconus orientalis* Park, Woo, Lee, Lee, Lee, Han, Chough, and Choi, 2011, from the Cambrian Drumian Stage, Zhangxia Formation, Shandong Province, China.

(a), diagram of a cup without significant structure; (b–c), KOPRIF17013, dorsal and lateral views, showing no significant internal structure; (d), diagram of a cup with a basal cavity defined by a subhorizontal element; (e–g), cups with a basal cavity defined by a subhorizontal element; (e), KOPRIF17011, lateral view; (f–g), KOPRF15001, dorso-lateral and lateral views; (h), diagram of a cup with a large conical protuberance; (i–l), cups with a large conical protuberance; (i), KOPRIF15002, lateral view; (j), KOPRIF17014, lateral view; (k–l), KOPRIF17015, dorsal and lateral views; (m), diagram of a cup with tubular structures; (n), KOPRF17016, lateral view of a cup with tubular structures. Scale bar is 10 mm. specimens previously housed in the paleontological collections of Seoul National University have been transferred to the paleontological collections of the Korea Polar Research Institute, Incheon, Korea Rep. and given registered numbers prefixed with KOPRIF.

Medusozoa (Collins and Daly, 2005; Collins et al., 2006), the Staurozoa comprise conical cup-shaped forms, with eight tentacle-bearing arms around the mouth and a holdfast-like attachment disc at the base. An individual cup in *C. orientalis* resembles this pattern.

3.4 *Cambroctoconus kyrgyzstanicus* Peel *in* Geyer et al., 2014

This species was collected from the Cambrian Stage 5 of the Alay Range, western Kyrgyzstan (Geyer et al., 2014). The maximum length of the cup is 7 mm with the maximum width of 5–8 mm. The height of the cup is almost half of that of *C. orientalis*, and thus Geyer et al. (2014) described it as trochoidal. Compared to the slender conical shape of *C. coreaensis*, this species looks stubby. Budding from the outside of the parental cup was observed (Geyer et al., 2014, fig. 2e, i; Fig. 4a). Septa are absent or present as a single thin septum (Fig. 7a), which is markedly different from the eight-paired septa in *C. orientalis*.

Geyer et al. (2014) suggested that the porous skeleton with densely packed, meandering pores was a diagnostic feature of this species, although the pores can be obscured by recrystallization in the material and have not been detected in cross-sections.

4 Phylogenetic Analysis

The phylogenetic relationships were analyzed by using TNT version 1.1 (Globoff et al., 2008).

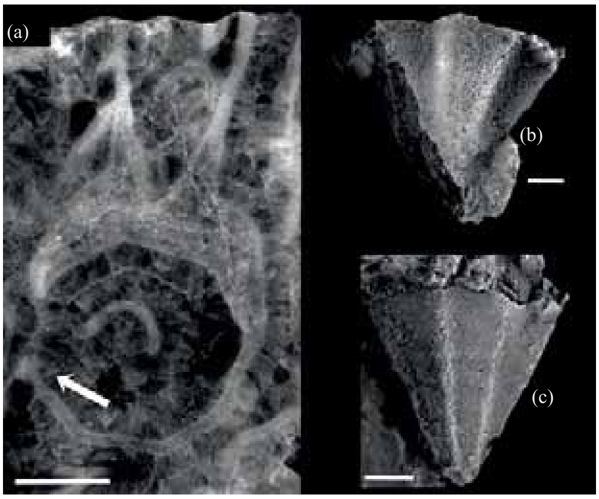

Fig. 7. *Cambroctoconus kyrgyzstanicus* Peel *in* Geyer et al., 2014 from Cambrian Stage 5 of the Alay Range, western Kyrgyzstan.

(a), FG596/XII/19a, transverse polished section, showing a septum (arrow); (b), holotype, FG596/XII/034a, lateral view; (c), FG596XII/022a, lateral view. Scale bars are 1 mm. Specimens are housed in the geological collections of the Technische Universität Bergakademie Freiberg, Germany (FG). All images are taken from Geyer et al. (2014).

4.1 Method

Thirty-seven characters were coded for fourteen taxa including an outgroup. Sponges (Porifera) were selected as the outgroup, and seven taxa of crown-group cnidarians were included as in the previous study by Park et al. (2011); nine new characters were added to the 28 characters used in that previous study. Sixteen characters (Characters 22–37) were employed from previous research (Marques and Collins, 2004). All characters were equally weighted and unordered. Lower metazoan phylogeny (Placozoa, Ctenophora, Porifera, Cnidaria, Bilateria) has not yet been settled. Although the Porifera was selected as the outgroup, this does not imply that they are phylogenetically closer to the Cnidaria than to other lower metazoan groups (Placozoa and Ctenophora).

Random addition sequences followed by tree bisection-reconnection (TBR) branch swapping were employed. Inapplicable and unavailable character states were coded as "–", and "?", respectively. Polymorphic characters are coded as "[01]".

4.2 Results

The analysis yielded 21 most parsimonious trees of 42-tree length, with a consistency index of 0.833, and a retention index of 0.851. All parsimonious trees placed *Tretocylichne*, *Cambroctoconus*, and *Lipopora* at the stem-group cnidarian position below the crown-group cnidarians, although the relationships among the stem-group cnidarians are collapsed in the strict consensus tree (Fig. 8e). In nine out of the 21 trees the stem-group cnidarians form a monophyletic group (Fig. 8a), while in the remaining 12 trees the stem-group cnidarians are paraphyletic to the crown-group cnidarians (Fig. 8b–c). In six out of the 12 trees, *Cambroctoconus* and *Tretocylichne* form a monophyly, being the sister-group to the crown-group cnidarians (Fig. 8c–d) with *Lipopora* at the basal branch. In the other six trees, *C. coreaensis* or *C. kyrgyzstanicus* appears as the immediate sister-taxon of the crown-group cnidarians with the other two species of *Cambroctoconus* forming a monophyly with *Tretocylichne* at the outside (Fig. 8b). The unstable positions of the *Cambroctoconus* species in the last six trees might be ascribed to the lack of characteristics of slender cup-shaped *C. coreaensis* and trochoidal *C. kyrgyzstanicus* due to the rarity and poor preservation of the internal structure. *Lipopora* is situated at the most basal position no matter whether in the monophyly of the stem-group cnidarians or in the cases where the stem-group cnidarians are paraphyletic to the crown-group cnidarians (Fig. 8a–d). The basal position of *Lipopora*, if present, is formed by the skeletal shape (Character 1): i.e., *Lipopora* retains the sub-cylindrical skeletal shape, whereas *Cambroctoconus* and *Tretocylichne* have a conical skeletal shape. Although the crown-group Cnidaria has been grouped in the consensus tree (Fig. 8e), the ingroup relationship within the crown cnidarians is not robust except for the grouping of the Medusozoa. The Class Anthozoa (octocorals, scleractinians, and actinarians) receives very low bootstrap values (with 10000 replicates) (Fig. 8f), and is collapsed in the strict consensus tree (Fig. 8e). The monophyly of the Anthozoa has also recently been rejected based on recent molecular data using mitochondrial genomes (Kayal et al., 2013).

5 Discussion

This study deals with the six species of Cambrian stem-group cnidarians, including a new species *Cambroctoconus coreaensis*. Because the documentation of *Cambroctoconus orientalis* led to the recognition of a sequence of certain character evolution during the course of cnidarians (Park et al., 2011), the phylogenetic analysis using six species of stem-group cnidarians can be expected to further resolve the sequence of character evolution. However, the cladistic analysis including the six species of stem-group cnidarian conducted in this study does not seem to provide further elucidation of the sequence of character evolution because of the unresolved relationships within stem-group cnidarians (Fig. 8e). Our results rather indicate an independent radiation within the Cambrian stem-group cnidarians: i.e., nine out of the 21 most parsimonious trees suggest a radiation by which the stem-groups diverge into *Lipopora*, *Cambroctoconus*, and *Tretocylichne* (Fig. 8a), whereas the other six most parsimonious trees suggest a radiation of *Cambroctoconus* and *Tretocylichne* with *Lipopora* at the basal branch (Fig. 8c–d). This may reflect the fact that the crown-group cnidarians already evolved before the Cambrian, as suggested by the molecular evidence (Erwin et al., 2011; Park et al., 2012), and might indicate that the diversity of the Cambrian stem-group cnidarians is a result of independent radiation within the Cambrian. However, evolution of cnidarians in the Precambrian has not yet been proven by fossil evidence. A cnidarian affinity has been suggested for some Ediacaran fossils (Glaessner, 1984; Wood et al., 2002; Zhu et al., 2008), but this is dubious or the specimens later turned out to be interpreted as other animals rather than cnidarians (Antcliffe and Brasier, 2007, 2008; Tang et al., 2011). However, cnidarians are likely to have undergone a radiation before the Cambrian, and therefore cnidarian-related fossils are still to be expected in Precambrian strata.

6 Conclusions

A total of six Cambrian stem-group cnidarians have now been recognized, including *Lipopora lissa* Jell and Jell, 1976; *Lipopora daseia* Jell and Jell, 1976; *Tretocylichne perplexa* Engelbretsen, 1993; *Cambroctoconus orientalis* Park et al., 2011; *Cambroctoconus kyrgyzstanicus* Peel,

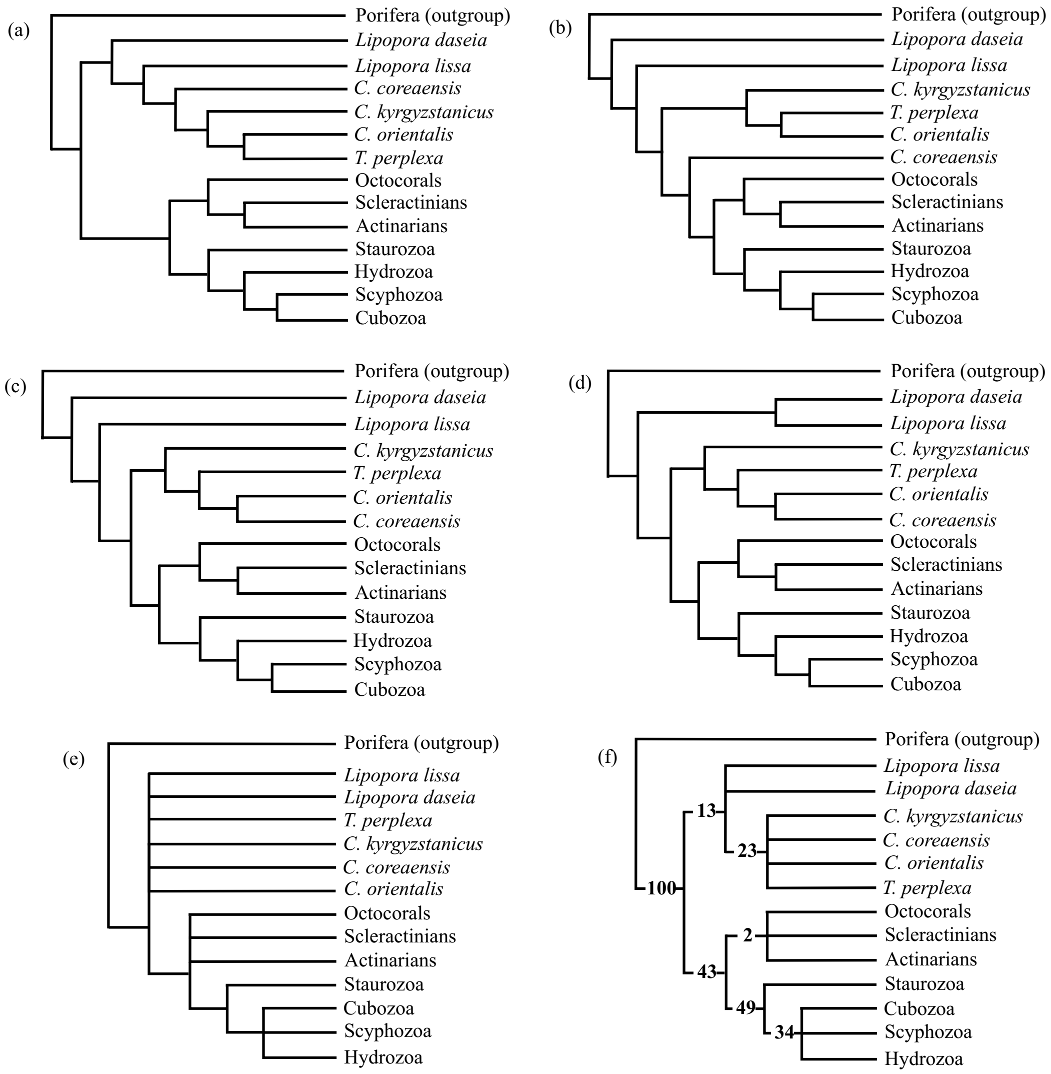

Fig. 8. Trees and bootstrap values from the cladistic analysis in this study of basal cnidarians.
(a–d), four out of 21 most parsimonious trees; (e), strict consensus tree; (f), bootstrap values with 10000 replicates. See text for explanation.

2014 *in* Geyer et al., 2014; and *Cambroctoconus coreaensis* sp. nov. The new species, *C. coreaensis*, described here, is characterized by the most slender cup-shaped skeleton of all known stem-group cnidarians.

A cladistic analysis including all six Cambrian stem-group cnidarians and crown-group cnidarians produced 21 most parsimonious trees, all of which invariably place the six Cambrian stem-group cnidarians below the crown-group cnidarians. However, the relationships within stem-group cnidarians are unresolved. Nine out of 21 trees produced a monophyly for Cambrian stem-group cnidarians, whereas in the other six trees, a monophyly of *Cambroctoconus* and *Tretocylichne* appeared as the sister-group to the crown-group cnidarians, with *Lipopora* at the most basal branch. This result may reflect the fact that the crown-group cnidarians had already evolved before the Cambrian as suggested by the molecular evidence, and thus the diversity seen in Cambrian stem-group cnidarians probably arose independently in the Cambrian.

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Appendices

Characters for cladistic analysis

1. Skeleton shape: (0) cylindrical or sub-cylindrical; (1) conical.
2. Attachment disc: (0) absent; (1) present.
3. Growth rings on the surface: (0) absent; (1) present.
4. Dichotomous branching: (0) absent; (1) present.
5. Opening of the skeleton base: (0) open; (1) closed.
6. Budding from inner surface of skeleton: (0) absent; (1) present.
7. Budding from rim of skeleton: (0) absent; (1) present.
8. Budding from outer surface of skeleton: (0) absent; (1) present.
9. Mineralized skeleton: (0) absent; (1) present.
10. Perforation of skeleton: (0) not perforated; (1) perforated.
11. Colonial life mode: (0) solitary; (1) colonial.
12. Shared colonial tissue (coenenchyme): (0) absent; (1) present.
13. Presence of septa: (0) absent; (1) present.
14. Paired septa: (0) absent; (1) present.
15. Number of mesenteries (or septa): (0) 4; (1) 6 or multiple of 6; (2) 8 or multiple of 8.
16. Axial symmetry: (0) absent; (1) present.
17. Bi-radial symmetry: (0) absent; (1) present.
18. Octagonal rim at oral end: (0) absent; (1) present.
19. Gastro-vascular cavity (archenteron): (0) absent; (1) present.
20. Mesoglea: (0) absent; (1) present.
21. Cnidae: (0) absent; (1) present.
22. Mitochondrial DNA: (0) circular; (1) linear.
23. Cellular mesoglea: (0) non-cellular; (1) cellular.
24. Euryteles: (0) absent; (1) present.
25. Life habit: (0) benthic adults; (1) planktonic adults.
26. Type of apical medusa formation: (0) strobilation; (1) metamorphosis without transverse fission.
27. Location of gonads: (0) gastrodermis; (1) epidermis.
28. Planular ciliation: (0) absent; (1) present.
29. Ephyrae: (0) absent; (1) present.
30. Medusoid phase: (0) absent; (1) present.
31. Rhopalia/rhopalioids: (0) absent; (1) present.
32. Nerve ring: (0) absent; (1) one; (2) two.
33. Gastric filament: (0) absent; (1) present.
34. Stratocyst: (0) absent; (1) present.
35. Manubrium: (0) absent; (1) present.
36. Nervous system organization: (0) GFNN absent; (1) GFNN present.
37. Ocelli: (0) absent; (1) present.

Character matrix

Characters	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–37
Porifera	0(01)0-(01)	---(01)(01)	(01)00--	(01)0000	00--0	-----	-----	--
T. perplexa	11000	00?11	?0112	101?0	??-?0	-??00	-----	--
L. lissa	01011	00111	?0102	10(01)?0	??-?0	-??00	-----	--
L. daseia	011?1	00?11	?0102	10(01)?0	??-?0	-??00	-----	--
C. kyrgizstanicus	11001	00111	?010-	101?0	??-?0	-??00	-----	--
C. coreaensis	11001	00111	?01??	101?0	??-?0	-??00	-----	--
C. orientalis	11001	11111	10112	101?0	??-?0	-??00	-----	--
Octocorals	-1-0-	--100	11102	11111	10100	-0100	-----	--
Scleractinians	-1-0-	--110	11101	11011	10100	-0100	-----	--
Actinarians	-1-0-	--100	0-101	11011	10100	-0100	-----	--
Staurozoa	-1-0-	--000	0-100	10111	11010	10000	10111	0(01)
Cubozoa	-1-0-	--000	0-100	10011	11011	10101	11111	11
Scyphozoa	-1-0-	--000	0-100	10011	11111	00111	10111	11
Hydrozoa	-1-0-	--100	(01)-00-	10011	11011	-1101	020(01)1	10