The origin of tetraradial symmetry in cnidarians

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LETHAIA

Serially arranged sets of eight septa-like structures occur in the basal part of phosphatic tubes of *Sphenothallus* from the early Ordovician (early Floian) Fenxiang Formation in Hubei Province of China. They are similar in shape, location and number, to cusps in chitinous tubes of extant coronate scyphozoan polyps, which supports the widely accepted cnidarian affinity of this problematic fossil. However, unlike the recent Medusozoa, the tubes of *Sphenothallus* are flattened at later stages of development, showing biradial symmetry. Moreover, the septa (cusps) in *Sphenothallus* are obliquely arranged, which introduces a bilateral component to the tube symmetry. This makes *Sphenothallus* similar to the Early Cambrian *Paiutitubulites*, having similar septa but with even more apparent bilateral disposition. Biradial symmetry also characterizes the Early Cambrian tubular fossil *Hexaconularia*, showing a similarity to the conulariids. However, instead of being strictly tetraradial like conulariids, *Hexaconularia* shows hexaradial symmetry superimposed on the biradial one. A conulariid with a smooth test showing signs of the 'origami' plicated closure of the aperture found in the Fenxiang Formation supports the idea that tetraradial symmetry of conulariids resulted from geometrical constrains connected with this kind of closure. Its minute basal attachment surface makes it likely that the holdfasts characterizing *Sphenothallus* and advanced conulariids are secondary features. This concurs with the lack of any such holdfast in the earliest Cambrian *Torellella*, as well as in the possibly related *Olivooides* and *Quadrapyrgites*. Bilaterally arranged internal structures in polyps representing probably the oldest medusozoans support the suggestions based on developmental evidence that the ancestor of cnidarians also was a bilaterally symmetrical animal. This is one more example of fossil data that strictly fit the molecular phylogenetic evidence but not necessarily morphology-based zoological interpretations. □ *China, evolution, Medusozoa, Ordovician, polyps.*

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Phosphatic tubes are common fossils in Palaeozoic strata, the oldest ones coming from the base of the Cambrian. They are mostly of a rather simple morphology, as exemplified by *Byronia* and *Hyolithellus* (e.g. Rozanov *et al.* 1969; Skovsted & Peel 2011). Their similarity to tubes secreted by polyps of extant coronate scyphozoans has been noticed by Kozłowski (1967), which supported the proposal of a similar taxonomic placement for the conulariids (Werner 1966, 1967). The discovery by Bischoff (1989) of Silurian and Devonian phosphatic tubes with seriate internal septa-like structures, similar and probably homologous to cusps in coronate polyps, provided a strong support for the presence of these medusozoans in the Early Palaeozoic. Bischoff identified these tubes as *Byronia*, but the evidence presented below shows that they actually represent proximal parts of the ubiquitous putative

Palaeozoic cnidarian *Sphenothallus* (Van Iten *et al.* 1992). Unlike *Byronia*, the cross section of these tubes is flattened, which suggests affinity to the Early Cambrian tubes of *Paiutitubulites*, which bear similar internal structures (Tynan 1983).

Here we report on more complete *Sphenothallus* fossils from the Early Ordovician Fenxiang Formation of China, as well as the Silurian and Early Devonian of Podolia, Ukraine. These fossils all show that the septa-like structures were restricted in their distribution to proximal regions of the tubes and were serially arranged, which makes *Sphenothallus* closely similar to the present-day polyps of the coronate scyphozoans. The presence of such polyps in the Early Palaeozoic fossil record becomes truly meaningful as molecular evidence places the Coronatae scyphozoans at the base of the whole medusozoan clade (Kayal *et al.* 2013; although Van Iten *et al.*

2014 prefer Stauromedusae in the basal position). The main difference between the present-day medusozoans and their probable ancient relatives is that the tubes of the latter are biradially symmetrical and the disposition of their 'septa' is bilateral. Both these aspects of the ground plan can be traced to the Early Cambrian, which may be of significance in interpreting the early evolution of cnidarians.

Materials and methods

This study is based on material collected from the middle and upper parts of the Fenxiang (transcribed also as Fenhsiang) Formation at Tianjialing village (Xingshan county) and from quarries near Huanghua and Jiangjiafan villages near Yichang (about 80 km SE from Xingshan town), in Hubei Province (Baliński & Sun 2013, 2015). The investigated area is located at the centre of the South China Yangtze Platform. A continuous sequence of shelly limestone and graptolite shale was deposited in the area during the Early Ordovician. The occurrence of the conodont *Acodus triangularis* in Bed 13 at Tianjialing indicates that at least the upper part of the formation is of Early Floian (Arenig) age (Baliński *et al.* 2012). The Fenxiang Formation consists mainly of dark grey to grey skeletal and peloidal limestone intercalated with greenish grey shale. The fossil assemblage consists mostly of skeletal fossils typical of the Early Ordovician shale facies: brachiopods, bryozoans and trilobites. Carbonized rhabdosomes of dendroid and pelagic graptolites are also common (Maletz & Kozłowska 2013). Of special interest are phosphatized antipatharian coralla (Baliński *et al.* 2012), pyritized traces of activity of nematodes (Baliński *et al.* 2013), and pyritized soft tissues of brachiopods (Baliński & Sun 2013), hydroids (Baliński *et al.* 2014) and problematic clonal organisms of possible hemichordate affinities (Dzik *et al.* 2016). Compressed macroscopic specimens were collected in exposures, fragmentary pyritized and phosphatized specimens were recovered from the acid-resistant residue of limy intercalations.

Specimens of *Torellella* from the Siberian Early Cambrian localities Tiktirikteekh and Bydyangaia near the village Isyt' were recovered with acetic acid from samples collected in 1987 and 2006 (Dzik 1991, 1994; Mazurek 2014). Two specimens of *Sphenothallus* showing development of septa-like structures were found in limestone samples from the uppermost Silurian Dzvenyhorod Beds at Dnistrove and the Early Devonian Mytkiv Formation at Mychalkiv, Podolia, Ukraine, digested in acetic acid.

All specimens described and illustrated are housed at the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw, Poland) under the collection number ZPAL Sz 2.

Morphology of Sphenothallus tubes

Sphenothallus is a common fossil in the Fenxiang Formation, but most specimens in the collection are fragmented. Only two intact tubes with preserved attachment discs have been found. One of them is a juvenile 26.5 mm long, the other probably mature, 108.0 mm long (Fig. 1). In both specimens, the proximal part of the tube was overgrown by an unnamed black coral. Such overgrowths of this unnamed species and *Sinopathes reptans* Baliński *et al.* 2012 have been identified also in several isolated fragmentary specimens of various ontogenetic age (Fig. 2). In the juvenile complete specimen of *Sphenothallus*, the black coral covered about half of the tube length, in the mature one only about one-third. Probably the antipatharian coralla grew slower than the *Sphenothallus* tube enlarged its length. The first 7 mm of the large tube is not compacted, showing the original circular cross section. This concurs with the suggestion that the cylindrical shape of isolated specimens represents the juvenile stage of tube growth. The tubes become flatter later in ontogeny, and in the largest specimen, a thickening of the narrower tube sides and a sharp crests on its surface is distinguishable beginning from about 2 cm of the tube length.

Growth increments are preserved only on some portions of the tube. They are best visible in two areas near the aperture, where the surficial layer of phosphatic cuticle is well preserved (Fig. 1B). The distribution of increments is regular and rhythmic. In the middle part of the tube, its surface was originally covered with the black coral, which is exfoliated and the distribution of increments is recognizable as shallow transverse depressions. This makes measuring distances between each increment pair less reliable. To reduce uncertainty, distances between each third increment are shown on the plot (Fig. 1C). The spacing of increments increases in the ontogeny, as shown by their distribution in the middle part of the tube, but they are much denser in the last 1.5 cm to the aperture, which may be an expression of maturity and growth termination. The estimated complete number of increments was about 150. Because they are very regular in distribution, it seems reasonable to consider that they were added daily. If the number of days in the Ordovician year was similar to that of today (Zhao *et al.* 2007; but note that available data are not conclusive both in
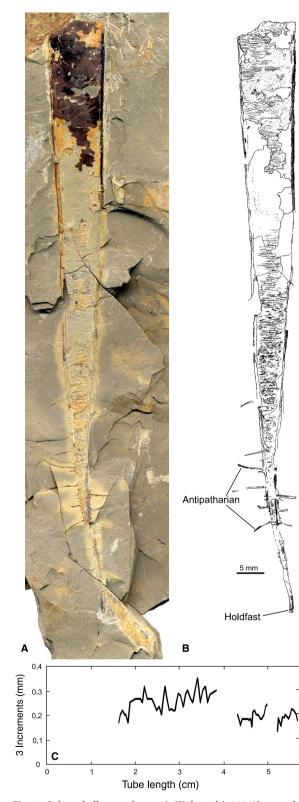
Fig. 1. Sphenothallus ruedemanni (Kobayashi 1934)? complete mature specimen ZPAL Sz. 2/1 from the Early Floian (Arenig) Bed 20 of the Fenxiang Formation at Huanghua quarry, Hubei Province, China. A, specimen on the shale. B, camera lucida drawing with traced rhythmic increments. C, the change in distance between each third increment during growth of the tube. [Colour figure can be viewed at wileyonlinelibrary.com]
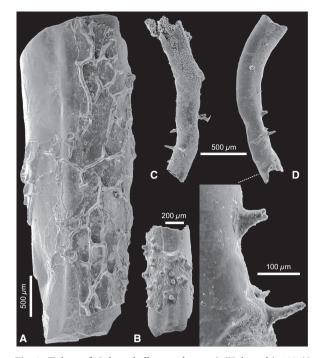

Fig. 2. Tubes of *Sphenothallus ruedemanni* (Kobayashi 1934)? overgrown with black corals from the Early Floian (Arenig) Fenxiang Formation. A, B, fragments of mature tubes ZPAL Sz. 2/2 and 3 with basal parts of coralla of *Sinopathes reptans* Baliński *et al.* 2012; Tianjialing section, Bed 13 (A) and Bed 4 (B). C, D, juvenile portions of the tubes ZPAL Sz. 2/ 4 and 5 with erect coralla of an unnamed antipatharian; Bed 19 at quarry near Huanghua village.

respect to solar year and synodic month, e.g. Rosenberg 1982), the tube reached its final size in less than half of it.

Attachment discs (holdfasts) of *Sphenothallus* are usually referred to as *Phosphannulus* (Müller *et al.* 1974). They are rarely encountered attached to tubes (Fig. 3A, G, H and P; Welch 1976; Werle *et al.* 1984; Bischoff 1989; Van Iten *et al.* 1992). In the Fenxiang Formation material, they are extremely variable in their size and shape, the largest one being of a diameter four times larger than the smallest one (Fig. 4). Such a great size difference may suggest species rank difference or evolutionary change, but this is contradicted by the vertical distribution of the within-sample variability. It does not exhibit any directional trend along either section sampled (Fig. 5). Like other species of the genus (Van Iten *et al.* 1992), the wall thickening proceeded centripetally, from the perimeter to the tube centre. The *Sphenothallus* holdfast apparently developed as a cuticular cover of a basal expansion of the polyp. The cuticle and phosphatic lamellae were secreted on its surface gradually, constricting the tube tip lumen, but at the flat base the skeleton remained thin (Van Iten *et al.* 1992, fig. 8). The rhythmic (presumed daily) increments are discernible beginning from about 0.1 mm

Fig. 3. Juvenile portions of tubes and pieces of mature tubes of *Sphenothallus ruedemanni* (Kobayashi 1934)? from the Early Floian (Arenig) Fenxiang Formation collected from Beds 23 (A, B, D–F, I), 12 (C, L), 18 (G, H), 13 (K, P, Q) and 7 (N) at the quarry near Huanghua village and Beds 4 (J) and 13 (M, O, R) at the Tianjialing section. Specimens ZPAL Sz. 2/6–23, respectively.

above the widened part of the tube (Fig. 3G). A possible explanation of the size variability is that the settling larva or polyp was of relatively large size and lacked cuticle. This perhaps allowed the larva to accommodate to the substrate by attaining various shapes prior to the secretion of the first layer of cuticle. Subsequent growth of the tube was incremental at the tube aperture.

The tube curvature, cross section and expansion vary within the sample. In some specimens (Fig. 3A), the tube remained very narrow for a significant distance; in others, it widened almost immediately after starting the incremental growth. Tube flattening developed at various growth stages, its wider sides gradually losing convexity. In larger tubes, the narrower sides become acute, with a

longitudinal crest developing there on the tube surface, and subsequently, the wall thickened from inside (Fig. 3R).

At the tube width 0.3–0.5 mm, short longitudinal thickenings developed within at least some tubes from the Fenxiang Formation. They eventually formed prominent septa (cusps) projecting towards the tube midline and restricting most of its lumen (Fig. 6C). As can be seen through semitransparent tubes (Fig. 7), they are arranged in rows oblique to the tube axis. Usually, each oblique row consists of mirror image series of three prominent cusps on each flat side of the tube and a smaller cusp at each of the narrower sides (Fig. 6C, F). Altogether, eight cusps form a set arranged in a biradial pattern. The Fenxiang *Sphenothallus* tube wall is of laminar
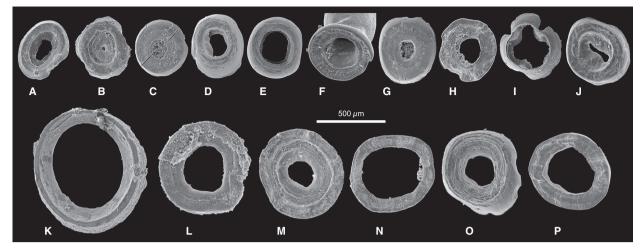
Fig. 4. Isolated attachment discs ('*Phosphannulus*') of *Sphenothallus ruedemanni* (Kobayashi 1934)? from the Early Floian (Arenig) Beds 10, 13, 18, 20 and 23 at quarry near Huanghua village (A–C, F–J, L–P), and Bed 4 of the Fenxiang Formation at Tianjialing village (D, E, K). Specimens ZPAL Sz. 2/24–28, 13, 29–38, respectively.

structure, as in other species of the genus (e.g. Vinn & Kirsimäe 2015). Particular laminae show a fibrous microstructure and fibres in successive layers differ in orientation, which results in a ply texture (Fig. 6A).

The Fenxiang material shows that the *Sphenothallus* tubes are very variable morphologically but generally changed their cross section from almost round as juveniles to flat at late ontogenetic stages. Internal septa occur only in specimens representing basal (proximal) parts of mature tubes, with circular or slightly compressed, but rounded, cross section. This means that earlier reports of such septate phosphatic tubes probably refer to species of *Sphenothallus* or its relatives.

Early Palaeozoic septa-bearing phosphatic tubes

Phosphatic tubes of round or flattened cross section and rows of internal septa-like protuberances (apophyses) from New South Wales, ranging in age from Early Silurian to Early Devonian, were grouped by Bischoff (1989) in his genus *Praestephanoscyphus*. The number of apophyses varies in the Australian material, but usually three rows of prominent protuberances were represented on each side of a flattened tube. Deviations from strict radial symmetry are known also in extant scyphozoan polyps (Berking & Herrmann 2007). More data are required to determine whether *Praestephanoscyphus* and *Sphenothallus* are synonyms, but this seems likely.

The oldest known phosphatic tubes with longitudinal septa are those of *Paiutitubulites variabilis*

Tynan 1983 from the Early Cambrian (Atdabanian; *Nevadella* Zone) Montenegro Member of the Campito Formation and the overlying lower member of the Poleta Formation in California (Tynan 1983). The *Paiutitubulites* tubes are circular to elliptical in cross section, fragments described rarely exceeding 1 mm in length. The number of septa varies, and a maximum of seven may be present. Commonly, three septa formed during early ontogeny and two additional pairs intercalated may be present or added during later growth stages. The septa would be arranged in a tetraradial pattern if it were not for the lack of septum on the side opposing the medial primary septum. This makes symmetry of the tube bilateral. The edge of particular septa in the *Paiutitubulites* tube is usually wavy in profile and may be discontinuous, which makes its septa similar to those of the Fenxiang *Sphenothallus* and Bischoff's (1989) *Praestephanoscyphus*. Tynan (1983) proposed the new order Paiutiida for *Paiutitubulites,* which may also encompass *Sphenothallus* and *Praestephanoscyphus* (as Paiutitubulitida emend.).

It may be surprising that septation has not been noticed previously in *Sphenothallus*, which is a rather common fossil. Either not all species of the genus developed such structures or the mode of preservation precluded identification of the internal structure of the proximal (basal) part of the tube. Such flat tubes, with thickening of their margins, continue to occur up to the upper Carboniferous (e.g. Schmidt & Teichmüller 1958; Brood 1987; Lerner & Lucas 2011) and perhaps even to the Permian. *Sphenothallus ruedemanni* (Kobayashi 1934) from the Tremadocian of Korea (Choi 1990) is of similar geological age to the Fenxiang species and comes from
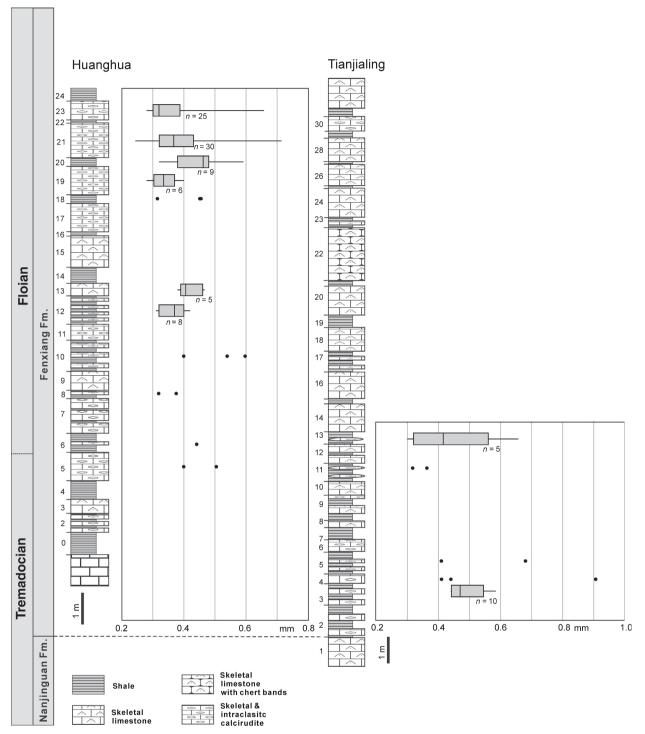
Fig. 5. Stratigraphical size distribution of isolated attachment discs ('*Phosphannulus*') of *Sphenothallus ruedemanni* (Kobayashi 1934)? in the Early Floian (Arenig) sections of the Fenxiang Formation at Tianjialing village and the quarry near Huanghua village.

the same palaeobiogeographical province. Although there is hardly any character in its shape that could be used for taxonomic identification, it is likely that it represents the same species. The type species of the genus, *Sphenothallus angustifolius* Hall, 1847 comes from the Early Late Ordovician 'Utica shale' of

Canajoharie region, New York, and has been widely identified in coeval strata of North America (Bodenbender *et al.* 1989; Bolton 1994) and northern Europe (Vinn & Kirsimäe 2015). The tubes of *S. angustifolius* frequently occur gregarious in clusters, attached to firm objects lying on soft bottoms (or floating in the sea
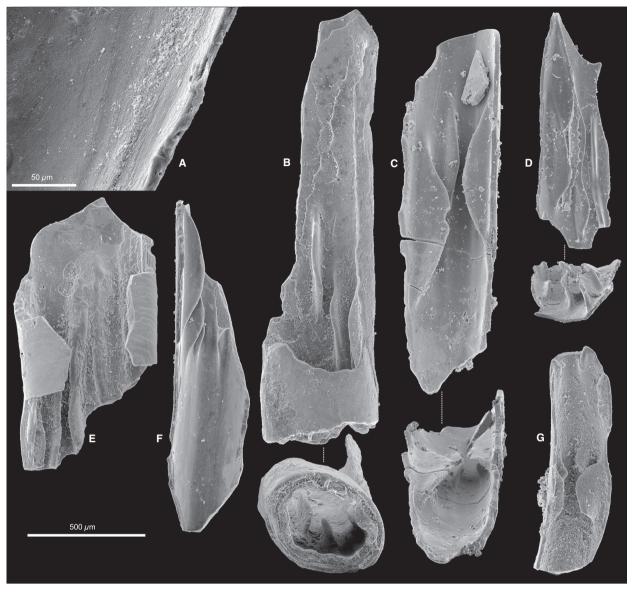
Fig. 6. Tubes of *Sphenothallus ruedemanni* (Kobayashi 1934)? from the Early Floian (Arenig) Beds 18 and 23 of the Fenxiang Formation at quarry near Huanghua village. A, internal surface of mature tube fragment ZPAL Sz. 2/39 showing a fibrillar plywood structure. B–G, juvenile portions of tubes with internal septa (cusps); specimens ZPAL Sz. 2/40–45, respectively.

water). Probably some *Sphenothallus* species propagated by clonal budding (Van Iten *et al.* 1992). Their phosphatic composition seems to be original, but they show some mineralogical difference in respect to the conulariids (Vinn & Kirsimäe 2015). The thickening of the narrow sides of otherwise thin-walled flat phosphatic tubes is used to define the genus, but at the moment, no species diagnostic aspects of morphology are available. In the case of specimens flattened in shale, it is not possible to determine the original cross section in enough detail to distinguish the Ordovician *Sphenothallus* from Cambrian tubes of similar morphology (Fatka & Kraft 2013). Longitudinal thickenings in some mid-Cambrian forms have been interpreted as developed inside the tube (Fatka *et al.*

2012), which would make them similar to both the Fenxiang *Sphenothallus* and to *Pajutitubulites*. Possibly, the morphological aspect that may allow the taxonomic separation of *Sphenothallus*-like fossils from before the Late Cambrian is their attachment structure.

Cambrian roots of Sphenothallus

Isolated holdfasts of the *Phosphannulus*-type are not known from strata older than Late Cambrian. The oldest *Sphenothallus*-like tubes with fully developed circular basal discs come from the Late Cambrian Maardu Formation of Estonia, classified in *Torellella* by Vinn (2006). The Late Early Cambrian three
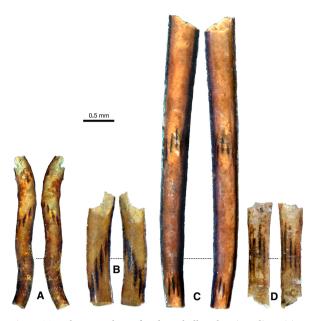
Fig. 7. Translucent tubes of *Sphenothallus* showing disposition of internal septa (cusps). A, B, specimens of *Sphenothallus ruedemanni* (Kobayashi 1934)? from the Early Floian (Arenig) Bed 21 of the Fenxiang Formation at the quarry near Huanghua village; ZPAL Sz. 2/46–47. C, specimen from the Early Devonian Mytkiv Formation at Mychalkiv, Podolia, Ukraine; ZPAL. Sz. 2/48. D, specimen from the uppermost Silurian Dzvenyhorod Beds at Dnistrove, Podolia, Ukraine; ZPAL Sz. 2/49. [Colour figure can be viewed at wileyonlinelibrary.com]

dimensionally preserved phosphatic tubes from the Shaanxi Province, China, classified in *Sphenothallus* by Li *et al.* (2004) do not show any flat *Phosphannulus*-like base with negative imprints of the substrate that would indicate cementation. Their tips are only swollen. The wall in distal part of the tube is of uniform thickness, thus of morphology similar to the earliest Cambrian *Torellella*. Thus, these fossils are transitional between *Torellella* and typical Ordovician *Sphenothallus*.

Well-developed attachment discs were probably missing also in the species from the mid-Cambrian Kaili Formation of Guizhou, China (Zhu *et al.* 2000; Peng *et al.* 2005). Attachment discs remain unknown in the Tommotian or Atdabanian *Torellella* (e.g. Álvaro *et al.* 2002). The tube tip has a smooth margin (Fig. 8A; Bengtson *et al.* 1990), and it seems that the attachment disc of the tube, if present, was not mineralized. The type species of the genus, *Torellella laevigata* (Linnarsson 1871) comes from the Early Cambrian *Mickwitzia* Sandstone (*Eophyton* sandstone) at Lugnås, Sweden (Linnarsson 1871; Hagenfeldt & Söderberg 1994). The earliest Cambrian fossils from Siberia classified in the genus by Rozanov *et al.* (1969) show great population variability (Fig. 9) and may represent a single species probably conspecific with the Swedish form (Kouchinsky *et al.* 2015). A specimen from the Atdabanian Parara Limestone of South Australia that fits such morphology was attributed to *Byronia* by Bengtson *et al.* (1990).

The wall of the Early Cambrian *T. laevigata* is of 'ply' structure, being composed of fibrous lamellae with changing orientation of fibres (Fig. 8B; Kouchinsky *et al.* 2015). It does not seem different in this respect from *Sphenothallus* (Fig. 6A). The tubes of *Torellella* and *Sphenothallus* show biradial symmetry in their cross section. It is superimposed on the octoradial pattern expressed in the number of septa (epiphyses, cusps) in the Fenxiang species. Their oblique disposition introduces bilateral symmetry, which is also discernible in the septation of *Paiutitubulites*. Such a complex body plan makes these Palaeozoic organisms different from the typical Medusozoa, showing a rather strict tetraradial disposition of organs. In the Early Palaeozoic, such symmetry characterized only the conulariids (Fig. 10).
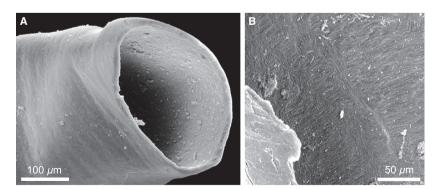

Fig. 8. *Torellella laevigata* (Linnarsson 1871) from the earliest Cambrian (Tommotian) *Dokidocyathus lenaicus* Zone at Tiktirikteekh (A) and Bydyangaia (B) on the Lena River near Yakutsk, Siberia. A, basal end of tube ZPAL Sz. 2/57. B, internal surface of tube ZPAL Sz. 2/64 showing a ply fibrous structure.
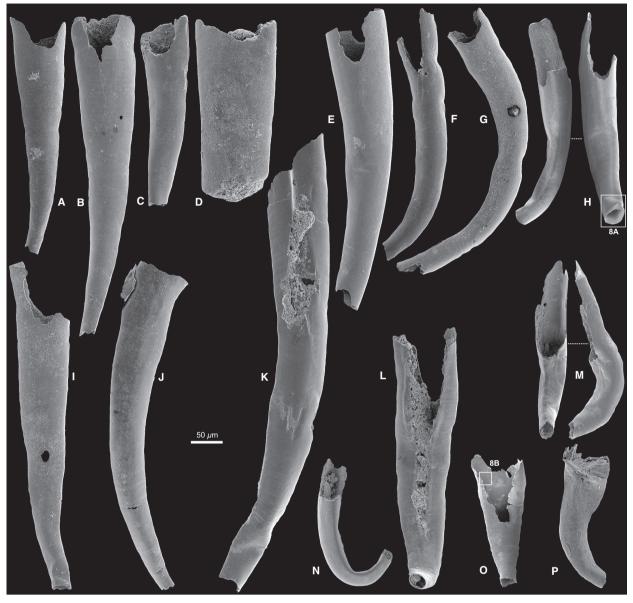
Fig. 9. *Torellella laevigata* (Linnarsson 1871) from the earliest Cambrian (Tommotian) *Dokidocyathus lenaicus* Zone at Tiktirikteekh (A–H) and Bydyangaia (I–P) on the Lena River near Yakutsk, Siberia; specimens ZPAL Sz. 2/50–65, respectively.

Conulariids

Based on their symmetry and general appearance, the conulariids were proposed as sedentary scyphozoans similar to the Stauromedusae by Kiderlen (1937) but later Werner (1966, 1967) compared them with polyps of the Coronatae, the tubes of which do not show such a clear symmetry in their external morphology. The new data on the most ancient of putative coronate polyps indicating biradial or even bilateral symmetry are puzzling in this context. The question of homology between the tetraradiality of conulariids and extant coronates emerges.

Only one specimen of a conulariid has been encountered in the Fenxiang Formation. It is unusual and informative enough to be commented on in the context of the associated *Sphenothallus*. The test is 16.5 mm long, which means that the individual is not a juvenile, but its wall is extremely thin and lacks any surface ornamentation except for the corner grooves and weak midlines (Fig. 10A–C). The attachment surface on the proximal end represents an oblique flat area of about 0.3 mm width. The specimen is compressed, which prevents observation of details of the attachment, but clearly there was no any attachment disc. There are also no signs of angularity of the narrow holdfast, but some distance above it the test corners are delimited by a
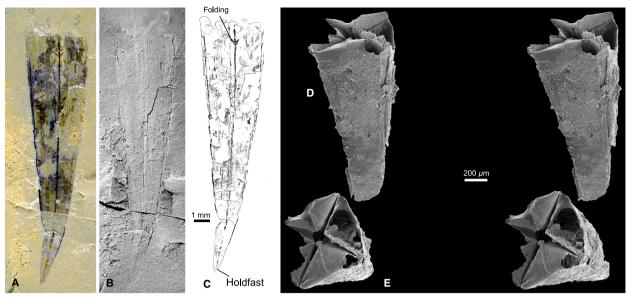
Fig. 10. Conulariids with 'origami' plicated closure and smooth test. A–D, specimen ZPAL Sz. 2/66 from the Early Floian (Arenig) Bed C 20 of the Fenxiang Formation at Jiangiafan quarry on the shale (A), whitened with ammonia chloride (B) and its camera lucida drawing (C). D, E, juvenile conulariid with closed aperture from the Late Silurian Kok Formation at Cellon, Carnic Alps, Austria; SEM stereopairs (illustrated also in Dzik 1994, fig. 26E; specimen destroyed during manipulation). [Colour figure can be viewed at wileyonlinelibrary.com]

longitudinal line, slightly darker than the remaining area. The test is distorted about 3.7 mm above its base, possibly by pre-depositional injury. Midlines are recognizable from about 2 mm above this region, becoming increasingly darker towards the test's aperture, which means that the wall interior is strongly thickened there and forms a carina projecting into the test lumen. Probably the most informative aspect of the sub-apertural portion of the test is a V-shaped depression at its corner. This is exactly the location where the test of conulariids folds while forming the 'origami' closure. Such plicated aperture folding is well exemplified by the juvenile conulariid from the Kok Formation of the Carnic Alps (Fig. 10D, E). The Fenxiang conulariid is probably the oldest one showing signs of the plicated aperture folding. This supports the suggestion that the tetragonal box-like shape of the conulariid test originated as a result of such folding, which predates formation of a rigid, ribbed wall (Dzik 1993).

The mode in which the conulariid aperture closed also provides evidence of their 'coelenterate' nature. Such aperture folding implies a significant reduction of the body volume, which required outflow of the internal fluids. This is easily achievable in case of the cnidarian's coelenteron, but would not be possible if the body cavities (protocoel or coelom) were closed (Dzik 1993). The weakly sclerotized conulariid aperture was folded inward presumably by action of four sets of muscles, to form a box-like structure (Kowalski 1935; Dzik 1994; Sendino *et al.* 2011). The best

fit in this kind of closure is offered by tetraradial symmetry. Rarely, the test of conulariids may express triradial (Van Iten 1991) or pentaradial (Kwiatkowski 1953) symmetry, but these are likely developmental anomalies (Sendino *et al.* 2012). Van Iten *et al.* (2008) proposed that the presence of plicated closure is teratological, connected with regeneration of musculature after formation of a diaphragm (schott).

Van Iten *et al.* (2013, Fig. 3A, B) described a conulariid test devoid any transverse ribs or other ornamentation from the Early Floian Tonggao Formation near the town of Sandu, Guizhou Province of China. It may be conspecific with the Fenxiang specimen. The lack of surface ornamentation in these Early Ordovician conulariids may be meaningful. They differ in this respect from their mid-Ordovician successors, and a rather irregularly ornamented surface without transverse ridges characterizes also the oldest known Late Cambrian conulariids (Hughes *et al.* 2000; unless the fragmentary specimen from the latest Ediacaran Tamengo Formation illustrated by Van Iten *et al.* (2014) is a conulariid). In more advanced conulariids, having the test ornamented with rows of protuberances, a small expanded holdfast may occur (Kozłowski 1968). Enlarged protuberances may develop anchoring rootlets at early ontogenetic stages of some species (Kozłowski 1968). Probably independent of these aspects of conulariid skeletal anatomy are minute pores perforating the test (Fig. 10E; Van Iten
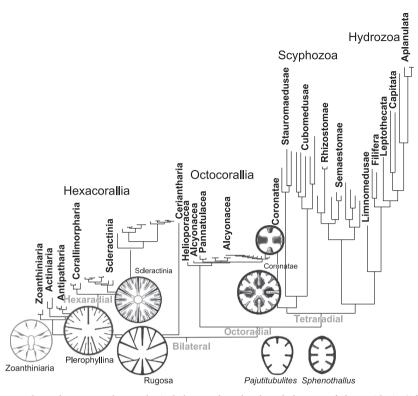
Fig. 11. Proposed correspondence between palaeontological data and molecular phylogeny of the Cnidaria (after Kayal *et al.* 2013). Transverse sections of the skeleton (black) and soft tissue (grey) of basal cnidarians are inserted. Ceriantharia and Medusozoa differ in the rate of mitochondrial DNA mutation from the other cnidarians (Stampar *et al.* 2014), which prevents calibration of this diagram with stratigraphical evidence. *Olivooides*, *Quadrapyrgites*, *Hexaconularia* and conulariids are probably basal to the crown-group cnidarians.

et al. 2005). There is little doubt, however, that the skeleton of conulariids was thickened by addition of phosphatic laminae from inside (Van Iten 1992; Ford *et al.* 2016). The protuberances and pores were eventually filled with the skeletal tissue.

Conulariids did not survive the end of Triassic (Lucas 2012). They differ significantly from both fossil and extant coronate polyps. The enigmatic pyritized structures proposed to represent their soft organs (Steul 1984) are of questionable connection with conulariids and may rather represent artefacts (Hughes *et al.* 2000; Van Iten *et al.* 2006). Another internal object preserved as calcite (Van Iten 1991) is difficult to interpret in terms of the medusozoan anatomy but may have been connected with strobilation (Jerre 1994, p. 105), unless this is a bryozoan zoarium.

The seriated midline invaginations present in the Late Cambrian conulariids (Hughes *et al.* 2000) resemble discontinuous septa of *Sphenothallus*. This similarity is strengthened by stadial or even rhythmic growth of the septum shown by isolated specimens of *Eoconularia loculata* from the Ludlovian Hemse Beds of the island of Gotland (Jerre 1994). The septa in the middle of the flat wall are prominent and they bifurcate. The split portion of the septum in some

specimens is composed of V-shaped units, resembling serially invaginated midlines of Hughes *et al.* (2000) in the Late Cambrian *Baccaconularia*. The pattern of termination of septa suggests that they developed in the basal, thick-walled part of a mature test, as in the Fenxiang *Sphenothallus*. The same applies to the Early Silurian (Llandoverian) *Circoconularia* (Bischoff 1978). All this supports the relationship of conulariids with *Sphenothallus* but suggests also that they represent a blind extinct lineage of coronate scyphozoans.

Ancestry of coronate polyps

A tube-secreting sedentary polyp stage (traditionally referred to as '*Stephanoscyphus*') is known in more than twenty species of Coronatae (Morandini & Jarms 2005, 2010). These species differ mostly from each other in the outer structure of the periderm tube and also in the number and shape of internal cuticular septa (cusps) developing serially in the basal part of tube. The cusps are transversely expanding structures significantly reducing the lumen of the tube. They mechanically block the passage of digested particles larger than about 50 μm to

the basal region of the coelenteron (Baumann & Jarms 1997). Usually, four large and four smaller cusps are developed in a tetraradial arrangement (Chapman & Werner 1972) and an additional eight, minute, cusps may intercalate (Werner 1971), but only one pair of larger and a pair of smaller (Morandini & Jarms 2012), or just one cusp may be present (Werner 1974; Jarms *et al.* 2003). The cuticular tube is not the only unique aspect of the coronate polyps. They are unlike all other cnidarian polyps also in having a ring sinus surrounding the oral region, which contacts the coelenteron through four openings. The ring sinus does not contribute to digestion, and its function is probably hydraulic mechanical (Baumann & Jarms 1997). There are four small septa in the oral region supporting gastric filaments (Chapman & Werner 1972).

The presence of a cuticular skeleton is probably plesiomorphic for the medusozoans (Mendoza-Becerril *et al.* 2016) because a delicate cuticle, which may be a vestigial tube, surrounds the aboral end of the sedentary developmental stage of some Semaestomae and Rhizostomae (Arai 1997). Regarding the original number of septa (cusps), eight cusps in the basal portion of the tube in probable Early Palaeozoic coronates suggest that this is their most plesiomorphic skeletal trait. However, unlike the present-day Medusozoa, their fossil relatives do not strictly adhere to the tetraradial symmetry.

There are reasons to believe that the ancestral cnidarian body plan did not include tetraradial symmetry. The concept of ancestral radial status of the cnidarians was disproved long ago by the discovery that the mitochondrial DNA is secondarily linear in the radially organized medusozoans but preserved its circular form in corals, of much more complex anatomy and less apparent radiality (Warrior & Gall 1985; Bridge *et al.* 1992; Kayal *et al.* 2012). It is now clear that the tetraradial symmetry of the medusozoans (Scyphozoa and Hydrozoa) is a derived feature that developed late in the evolution of Cnidaria (Kayal *et al.* 2013). The evidence that 470 million years old probable predecessors of coronate polyps show aspects of biradial and bilateral symmetry concurs with the molecular phylogenetic interpretations. This requires a critical evaluation of the oldest fossils attributed to the Cnidaria (reviewed by Van Iten *et al.* 2006).

Symmetry of the earliest Cnidaria

Radial symmetry is the aspect of body plan that developed independently in many lineages of plants and animals. It cannot be used alone to determine phylogenetic position of a fossil. Some sponges may show radial symmetry, including a tetraradial one (Botting *et al.* 2014), but this is hardly an ancient aspect of the poriferan body plan, although the early evolution of sponges is poorly documented with fossils (Antcliffe *et al.* 2014). Because of assumed medusozoan aspect of the ancestral animals, for decades all circular imprints of pre-Cambrian animals were interpreted as medusae although these are mostly basal discs of sedentary organisms or globular microbial structures (e.g. MacGabhann 2007; Ivantsov *et al.* 2014). Incompleteness of the fossil record was blamed for the lack of congruence with zoological expectations until enough data have been assembled to make this unlikely (Dzik 1991).

The rarity of tetraradial body plan among the earliest animal fossils is somewhat surprising. One may find its closest approximation in the octoradial component of the symmetry of ctenophores, which were very diverse in the Cambrian and possibly had Ediacaran roots (Conway Morris & Collins 1996; Dzik 2002; Ou *et al.* 2015), but the body plan of ctenophores is biradial. Another peculiar combination of symmetries is exhibited by *Hexaconularia*, with its hexaradial symmetry superimposed over the biradial one (Van Iten *et al.* 2010). It differs in this respect from the probably related *Olivooides* that shows a regular pentaradial symmetry with ten apertural folds (Dong *et al.* 2016). In the closely similar *Quadrapyrgites*, the tube apex is tetraradial and the number of folds closing the tube aperture is 12 (Shao *et al.* 2015). The mode of aperture closure in these enigmatic organisms somewhat resembles that of the conulariids, but the number of apertural folds was larger. Although these fossils are likely to represent cnidarians with a cuticular skeleton, the lack of holdfast indicates that their life cycle was different from that of the crown-group Medusozoa. Perhaps the smooth surface of the larval part of the skeleton of *Quadrapyrgites* (Shao *et al.* 2015) fits into a series of transformations from a thin cuticular cover of the flagellate larva in *Olivooides* to a more rigid structure in *Hexaconularia*. The lack of any cuticular larval skeleton in *Torellella* and subsequent formation of the holdfast in the evolution towards *Sphenothallus* suggests that the larva had an attachment organ developed before it settled on the substrate.

No pre-Cambrian fossil is available that could provide evidence about polarity in development of various kinds of radial symmetry in the Early Cambrian tubular fossils. The early Ediacaran 'Lantian conulariid' proposed by Van Iten *et al.* (2014) to be the earliest representative of the Medusozoa has been shown by Wan *et al.* (2016) to be a morphotype within the alga *Lantianella*, closely similar to other

enigmatic algae in the assemblage. Probably the oldest example of clear tetraradial symmetry is that shown by the enigmatic tubular fossil *Corumbella* from the Ediacaran of the Americas. Its theca(?) was composed of four longitudinal rows of angularly bent sclerites, which gave it a tetragonal cross section (Forancelli Pacheco *et al.* 2015). Similar tubes tending to disintegrate into segments of a less regular appearance are common in coeval strata of Asia (e.g. Chen *et al.* 2008; Cai *et al.* 2011, 2013; Meyer *et al.* 2012), but clarification of their relationships requires additional data. A much more regular hexaradial symmetry than that of *Hexaconularia* characterizes *Vendoconularia* from the Vendian of Onega River in northern Russia (Ivantsov & Fedonkin 2002). However, its symmetry is misleading. Unlike true conulariids, the body is of a fusiform shape, with both ends tapering. It resembles rather the Australian *Protechiurus*, with indistinct transverse ornamentation and hexaradial symmetry (Dzik 2003). The internal serial structures emerging from below the external body wall make *Vendoconularia* similar to the pteridiniid *Ventagyrus* occurring in the same strata.

The strongest evidence in favour of an early origin of the conulariids is the fragmentary specimen from the latest Ediacaran of Brazil identified by Van Iten *et al.* (2014) as *Paraconularia*. Hopefully, more complete findings will clarify its identity and possible relationship to *Corumbella* or the Ediacarans *Vendoconularia* and perhaps *Ausia*.

It is tempting to consider the biradial symmetry of *Hexaconularia*, *Torellella* and *Sphenothallus* an expression of their distant relationship to the ctenophores. Molecular phylogenies tend to place the Ctenophora between cnidarians and sponges (Podar *et al.* 2001; Wallberg *et al.* 2004; Pisani *et al.* 2015). But again, such a simple picture is spoiled by molecular phylogenetic evidence inserting geometrically less regular body plans between the ctenophores and the medusozoans.

All the most basal cnidarian lineages in the molecular tree (Fig. 11) show more or less apparent aspects of bilateral symmetry (Shick 1991; Kayal *et al.* 2013; Rodríguez *et al.* 2014). These are the Ceriantharia and Zoanthiniaria, with a polarized origin of mesenteria and their clearly bilateral disposition (e.g. Ryland 1997; Sinniger *et al.* 2005). Both zoanthiniarian and ceriantharian polyps have two cycles of tentacles and a single siphonoglyph regarded as morphologically ventral. New septa (mesenteries) arise on either side of the ventral ones (Ryland 1997). Such was the pattern of emergence of septa in the Palaeozoic Rugosa, strongly suggesting that it is primitive for the corals. Bilateral symmetry

of the rugosan corals may have resulted from the mode of settlement of the pelagic larva on its ventral side, instead of the oral end, as it is in extant corals (Rozhnov 2014). A closely similar ground plan of the septal apparatus characterizes the Triassic pachythecaliine scleractinians that may represent a connecting link between the plerophyllid Rugosa of the Permian and modern scleractinians (Stolarski & Russo 2001). This would mean that the hexaradial symmetry of the scleractinian corals is a secondary feature, with their ancient groups expressing still bilaterality of the rugosan aspect. The idea of an originally bilateral ground plan of the Cnidaria finds support also in the bilateral expression of homeotic genes in extant sea anemones (Finnerty 2003). The alleged Early Cambrian sea-anemone *Eolympia*, with 18 putative tentacles and mesenteria, may actually be a fossil nemathelminthan (Liu *et al.* 2014).

Extant Octocorallia have a slit-like mouth opening with a single siphonoglyph, the aspect of bilateral symmetry apparently inherited after the ceriantharian-like ancestor. The octoradial symmetry of their tentacles is probably rooted in that of the Palaeozoic tabulates. However, instead of eight pinnate tentacles, the tabulate polyps bore 32 simple ones (Chatterton *et al.* 2008; Dixon 2010).

It appears thus that the strict radial symmetry of extant cnidarians is a phylogenetically late achievement, a result of selection pressure on developing a tentacular apparatus efficient in the sedentary life of these passive predators. The hexaradial symmetry of the Scleractinia, octoradial of the Octocorallia and tetraradial of the Medusozoa originated from the original status with variable number of tentacles and sub-divisions of the gastral cavity arranged in a more or less bilateral way. *Sphenothallus*, with its bilaterally arranged eight septa, represent an early stage of developing the body plan typical for the medusozoans.

Conclusions

The traditional textbook presentation of the evolution of multi-cellular animals places the emblematic *Hydra* near the base of the phylogenetic tree. Its radial symmetry and anatomical simplicity were for long time believed to represent the ancestral metazoan status. This concurs with the idea that ancestors of particular phyla were of anatomy similar to pelagic larvae (e.g. Nielsen 2013). Both concepts are unavoidable results of the method of inference on the course of evolution from morphological data on the present-day animals. It is assumed that simplicity is likely a primitive state and that those characters that are ancestral (plesiomorphic) show the most widespread distribution.

This makes conserved aspects of early ontogeny privileged in assembling the set of traits characterizing the hypothetical ancestor. However, such a picture fits neither molecular nor palaeontological evidence (e.g. Dunn *et al.* 2008, 2014).

Although it is unavoidable to accept a Gastrea-like anatomy of the earliest metazoan, it seems unlikely that recent phyla emerged directly from such a microscopic ancestor. There is growing evidence that diversification of phyla took place on a high level of anatomical complexity. Homology of arthropod and vertebrate segmental genes implies that their common ancestor was also segmented (Blair 2008). Macroscopic size and complex anatomy of virtually all adult metazoans known from the Ediacaran and Early Cambrian strata suggest that ancestors of phyla were of centimetre-size (Levinton 2001, p. 487). The presented above discovery of bilaterally arranged internal structures in polyps probably representing the oldest medusozoans supports the suggestions based on developmental evidence that also the ancestor of cnidarians was a bilaterally symmetrical animal (Finnerty 2003). This provides one more example of the fossil evidence that strictly fits the molecular phylogenetic evidence (Kayal *et al.* 2013) but not necessarily morphology-based zoological interpretations. The problem that remains to be solved is the meaning of biradial symmetry expressed in the body plan of these early cnidarians.

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