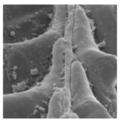
An Early Ordovician clonal organism from China with a zig-zagged suture on branches

JERZY DZIK, ANDRZEJ BALIŃSKI & YUANLIN SUN



An enigmatic clonal organism from the earliest Floian (Arenig) Fenxiang Formation at Tianjialing in Hubei Province, China and here named *Crinisdendrum sinicum* gen. et sp. nov., shows a puzzling combination of anatomical characters. Lateral colony branches that originate from tubular stolons are built of C-shaped serial oblique units resembling fuselli and merging along a zig-zagged suture, a set of features generally believed to be unique to pterobranch hemichordates. At least most branches taper near their tips and are closed in a manner resembling the termination of thecae previously reported in the extant pterobranch *Rhabdopleura normani*. The main drawback of the pterobranch model is that previous observations of terminating thecae in *R. normani* have neither been confirmed by more recent zoological studies nor explained in functional and developmental terms. Pyritized *Crinisdendrum* specimens preserved in shale were scanned using X-ray microtomography, enabling restoration of early stages of colony development (astogeny). Pyritic internal moulds of probable thecae, showing their interiors in negative relief, and phosphatized walls of thecae overgrown by black corals were recovered chemically from samples of calcareous intercalations in the Fenxiang Formation. Both sets of specimens exhibit a thread-like cylindrical structure resembling a stolon inside the theca and located below the zig-zagged suture. A similar organization of branches also characterizes the feathery colonies of *Webbyites* from the Early Ordovician Klabava Formation of Bohemia, although these colonies are known in less detail. A new family, Crinisdendridae is proposed to encompass these two genera. Further testing of the hypothesis of a pterobranch affinity for these 470-million-year-old organisms will require a better understanding of the anatomy and growth of extant clonal hemichordates. • Key words: China, Ordovician, problematica, Rhabdopleuridae, Pterobranchia, Hemichordata.

DZIK, J., BALIŃSKI, A. & SUN, Y. 2016. An Early Ordovician clonal organism from China with a zig-zagged suture on branches. *Bulletin of Geosciences 91(2)*, 319–329 (5 figures, supplementary data). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received September 15, 2015; accepted in revised form May 12, 2016; published online June 27, 2016; issued June 30, 2016.

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Since mid-Cambrian times marine bottom environments characterized by low sedimentation rates and strong currents have hosted diverse communities of passive suspension feeders, mostly modular clonal invertebrates, attached to hard bottoms or objects. In present-day seas of relatively high primary productivity but low temporal stability such communities are dominated by colonies of erect hydroids and bryozoans (*e.g.*, Voronkov *et al*. 2010, Ronowicz *et al*. 2013). Autotrophic unicellular algae contribute significantly to the diet of the generally omnivorous hydroids (Gili *et al*. 2008) and could have been a source of energy to early suspension feeders. In environments with relatively low energy input but long-term temporal stability hydroids and bryozoans are replaced by gorgonian octocorals or antipatharians (black corals), which have lower metabolic rates but much longer life spans (*e.g.*, Wagner *et al*. 2012). These two ecological guilds are exemplifications of extremes in life-history strategies: opportunistic ephemeral hydrozoans maximize clonal expansion by uninterrupted modular iteration as long as conditions are favourable to growth and until environmental instability triggers sexual reproduction. In contrast, corals growing slowly in persistent habitats may eventually modify their environment (Coma *et al*. 1998). Hydroids may co-occur with antipatharians, and cases of symbiosis between these two groups have been reported (Bo 2011). Somewhat surprisingly, a community of passive suspension feeders dominated by black corals and hydroids has recently been recognized in 470-million-year-old Ordovician strata (Baliński *et al*. 2012, 2013, 2014).

DOI 10.3140/bull.geosci.1575

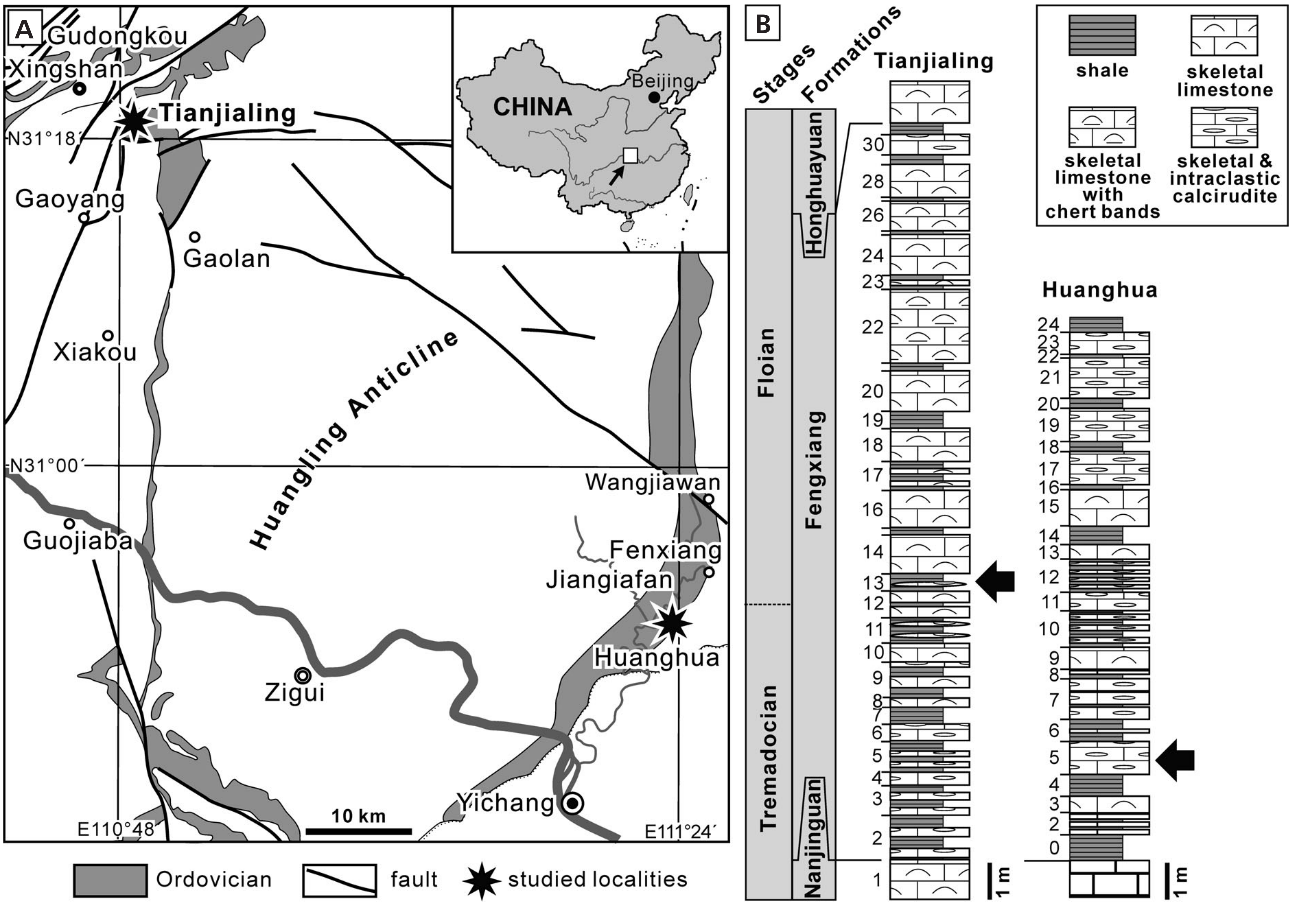

Figure 1. Geographic and geological setting of the source sites of the study material (modified from Baliński & Sun 2015). • A – map showing the study localities in the Three Gorges area, Hubei Province. • B – rock columns for the Tianjialing and Huanghua sections of the Fenxiang Formation; arrows indicate the stratigraphic positions of the *Crinisdendrum* specimens described herein.

A fundamentally different picture emerges if the fossil record of the earliest communities of erect suspension feeders of the Cambrian is considered. It appears that ecological niches occupied in later epochs by hydrozoans, bryozoans and octocorals with delicate ramose colonies were occupied in Cambrian times by pterobranch hemichordates and extinct organisms with obscure zoological affinities (*e.g.*, Bengtson & Urbanek 1986, Durman & Sennikov 1993, Rickards *et al.* 2001, Maletz *et al.* 2005, LoDuca *et al.* 2015). Therefore, the Early Ordovician appears to be of crucial importance in understanding how the composition of early communities of passive suspension feeders on hard substrates or bottoms approached their present day status.

Unfortunately, fossil evidence of Ordovician benthic clonal organisms other than dendroid graptolites is highly incomplete and controversial (Kraft *et al.* 2001; Cope 2005; Baliński *et al.* 2012, 2014). The major obstacle is taphonomic in nature: most early clonal organisms were equipped with an organic skeleton that had little chance of being fossilized in well-aerated reefal environments. To be preserved, their skeletal remains had to be transported to deeper waters surrounding the reef to be buried under a cover of clay sediment. Such was probably the taphonomic history of the fossil assemblage recovered from the Fenxiang Formation at Tianjialing in Hubei Province, China (Baliński & Sun 2015), where the most ancient bryozoans reefs were developed on elevations (Adachi *et al.* 2012). In the present paper we describe an enigmatic colonial organism from the Tianjialing assemblage that does not fit into the current scheme of biological classification. We discuss possible alternative interpretations of its phylogenetic affinities and the problems raised by each hypothesis.

Material and methods

The present study is based on specimens collected from the middle part of the Fenxiang (also transcribed as Fenhsiang) Formation at Tianjialing village in Hubei Province (Fig. 1). In addition, fragmentary pyritized and

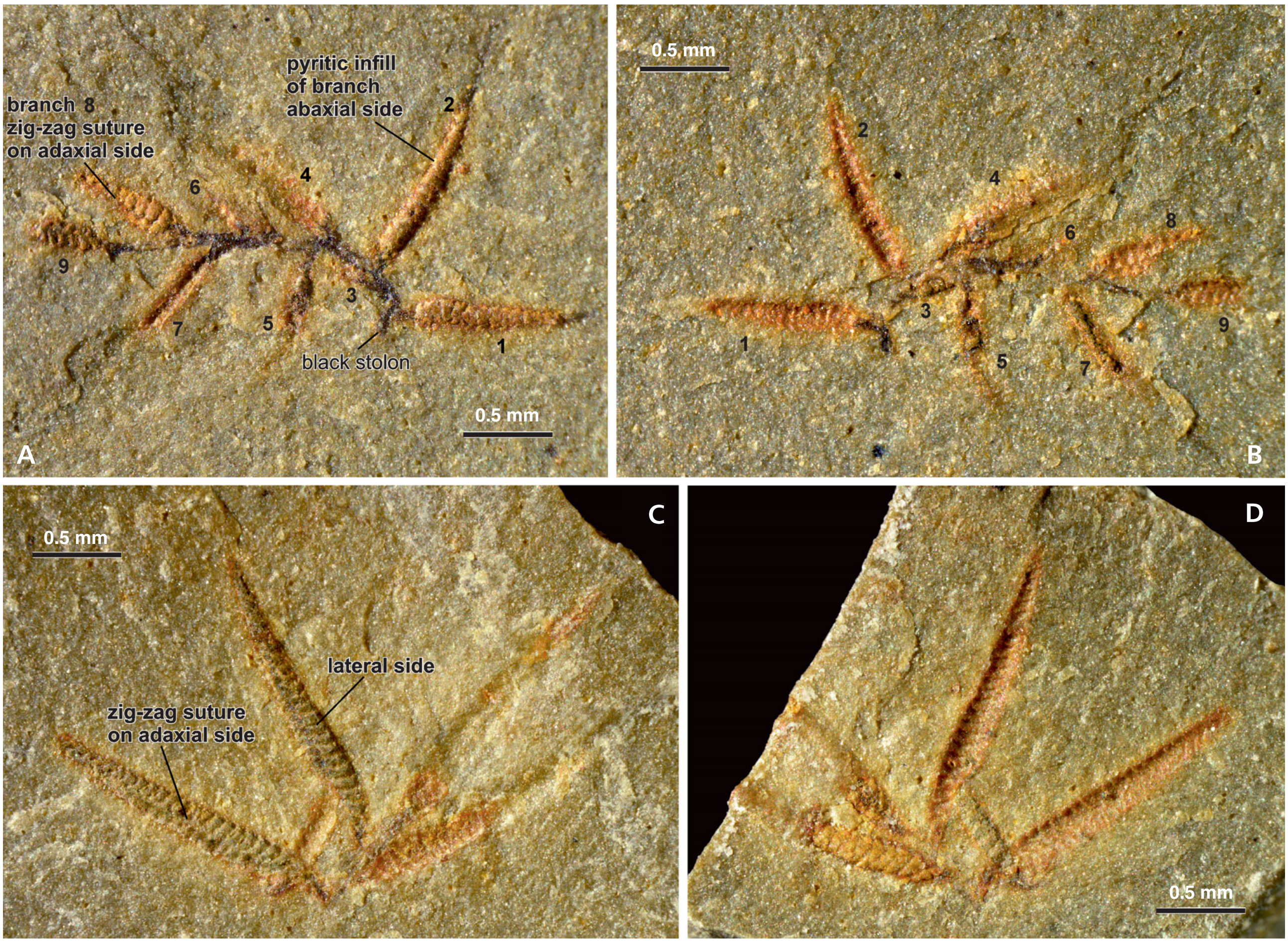

Figure 2. Early astogenetic stages of *Crinisdendrum sinicum* gen. and sp. nov. colonies from the earliest Floian (Arenig) Fenxiang Formation at Tianjialing (Hubei Province, China). • A, B – part and counterpart ZPAL Hz 4/5 with well preserved carbonized black stolons and pyrite-filled lateral branches seen from either adaxial and abaxial side, the latter showing zig-zag sutures. • C, D – part and counterpart ZPAL Hz 4/6 with pyrite-filled lateral branches seen from abaxial and lateral sides (see also Supplementary data movie).

phosphatised colony branches were found in the acid-resistant residue from a sample collected in a quarry near Huanghua village, about 80 km SE of Tianjialing. The study area is located at the centre of the South China Yangtze Platform. During the early Ordovician a continuous sediment sequence of shelly limestone and graptolite shale was deposited in the area (Zhan & Jin 2007). These strata are exposed at the periphery of the Huangling Anticline in the Three Gorges area of Hubei Province.

Geological setting

The Fenxiang Formation is about 40 m thick on the eastern limb of the anticline and about 20 m thick in the western regions. It consists mainly of dark grey to grey skeletal and peloidal limestone interstratified with greenish grey shale. The age of the Fenxiang Formation originally was interpreted as late Tremadocian (*e.g.*, Wu *et al.* 2010). However, the occurrence of the conodont *Acodus triangularis* in Bed 13 at Tianjialing indicates that at least the upper part of the formation is early Floian (Arenig) in age (Zhen *et al.* 2009, Baliński *et al.* 2012). The lithological and palaeontological characteristics of the formation suggest frequent changes of the sedimentary regime from low-energy, deep-water basin to energetic, shallow-water carbonate platform. Even though the shelly beds apparently were deposited in open-marine, rather deep-water settings, several elements of the fauna indicate an allochtonous, shallow-water origin. It seems that this fauna was transported basin-wards by currents or occasional heavy storms from settings adjacent to reefal build-ups. Reefs constructed mainly of bryozoans, lithistid sponges, stromatoporoids, pelmatozoan echinoderms and calcimicrobes have been described from the Fenxiang Formation at the Chenjiahe section in the Yichang area (Adachi *et al.* 2012, 2013).

Taphonomy

The dominant components of the fossil assemblage in bed 13 of the Fenxiang Formation at Tianjialing are originally organic (probably mostly chitinous), phosphatised skeletons of colonial black corals, represented by several species (Baliński *et al*. 2012) most of which have not yet been described. The sediment apparently was rich in organic matter, as suggested by abundant trace fossils of minute infaunal nematodes (Baliński *et al*. 2013), larger horizontal burrows, pyritized organic peduncles of lingulate brachiopods (Baliński & Sun 2013, 2015) as well as zooids of probable colonial hydrozoans (Baliński *et al*. 2014). Planktonic and benthic graptolites are common (Maletz & Kozłowska 2013), with their originally collagenous (Towe & Urbanek 1972, Armstrong *et al*. 1984) periderm preserved as coalified matter (transformed into aliphatic polymers: Briggs *et al*. 1995, Gupta *et al*. 2006) and frequently pyrite-filled thecae. This mode of preservation contrasts with that of probable hydroids, the originally organic skeleton of which has been pyritized (Baliński *et al*. 2014). Such preservation also characterizes the colonial organisms, which are the subject of the present study, although the stolonal parts of the colonies may show weak coalification.

Mature stages of colony development preserved in shale are represented by three specimens. In all of these specimens the original pyrite infilling of lateral branches and the axis has been oxidized through weathering, which is also the case with other similarly preserved colonial organisms (Baliński *et al*. 2014). The most complete specimen is ZPAL Hz 4/2; two other colonies are represented only by a part. In ZPAL Hz 4/12, both the part and counterpart have been collected, with the lateral branches displaced, which is also the case with specimen ZPAL Hz 4/9. Specimens ZPAL Hz 4/10 and 11 are fragmentary. Colony ZPAL Hz 4/15 shows bifurcation of its narrow stem with short lateral branches. Two juvenile colonies, specimens ZPAL Hz 4/5 and 6, consist of both a part and counterpart. One of them (ZPAL Hz 4/5) was scanned using X-ray microtomography (Supplementary data movie).

The new species also was found in residues from calcareous intercalations from bed 5 at Huanghua that were dissolved in dilute acetic acid. The specimens in question may represent pyritic internal moulds of lateral branches, showing their interiors in negative relief, or of lateral branches overgrown by secondarily phosphatized black corals. The specimens can be identified as such owing to their plait-like appearance emerging from under a thin cover of black coral skeletal tissue. In some cases the organic skeleton of the new organism underwent phosphatization, presumably stimulated by mineralization occurring on black coral tissue. No separate, phosphatized lateral branches were found in residues, suggesting that the composition the black coral organic skeletal tissue was different from that of the new organism.

The study material is housed in the Institute of Paleobiology, Polish Academy of Sciences (abbreviated ZPAL).

Astogeny and adult colony structure

Juvenile colony ZPAL Hz 4/5 (Figs 2A, B and 5A, B,) shows clearly that its initial parts were strong organic tubules of a nature different from that of the plait-like portion of the lateral branches. These slender branching structures, referred to here as stolons in the general botanical and zoological meaning, are about 0.07 mm wide (probably a little less prior to compaction). The lateral branches are preserved as pyritic (secondarily oxidized) infillings of presumably originally organic tubes. They emerge from the lateral outshoots of the black stolon. The base of the pyritic infilling is more or less rounded, suggesting the former presence of a hemispherical wall (septum) there. The branches are composed of C-shaped segments measuring about 0.07 mm in width and extending transversely over the abaxial side of the branch (as shown by mature colonies) but merging alternately in a plait-like manner adaxially. The pyritic infillings of all complete branches are more or less cylindrical proximally but at some distance from the base they slowly decrease in diameter becoming very slender near their tips. X-ray tomography (see Supplementary data movie) shows that the narrowing is primary rather than the result of the branches submerging into the rock matrix. The point of initiation of growth of the entire stolonal system probably is not preserved in specimen ZPAL Hz 4/5. This feature was either broken or emerged from a structure of low fossilization potential.

The specimen ZPAL Hz 4/15 (Fig. 5C) shows the transition from the branching early astogenetic stage to mature stages having a compound cylindrical axis represented by the specimens on slab ZPAL Hz 4/2. The axis is composed of tubules measuring about 0.06 mm in diameter and presumably constituting a continuation of the black stolons observed in the early stages of astogeny, although their walls are pyritized rather than carbonaceous. The diameter of the axis changes at a distance of 39 mm along the preserved part of the most complete colony (colony 1) on slab ZPAL Hz 4/2 (Fig. 3A, B), decreasing from about 0.9 mm at the proximal end to 0.5 mm near the distal end. This means that most of the tubes in the axis did not divide. The tubes are cylindrical and lack any recognizable additional structures. The tubes are also slightly separated from each other, suggesting that there was an organic matrix between them holding the whole structure together. In certain places, the axial tubes bend outwardly and change into

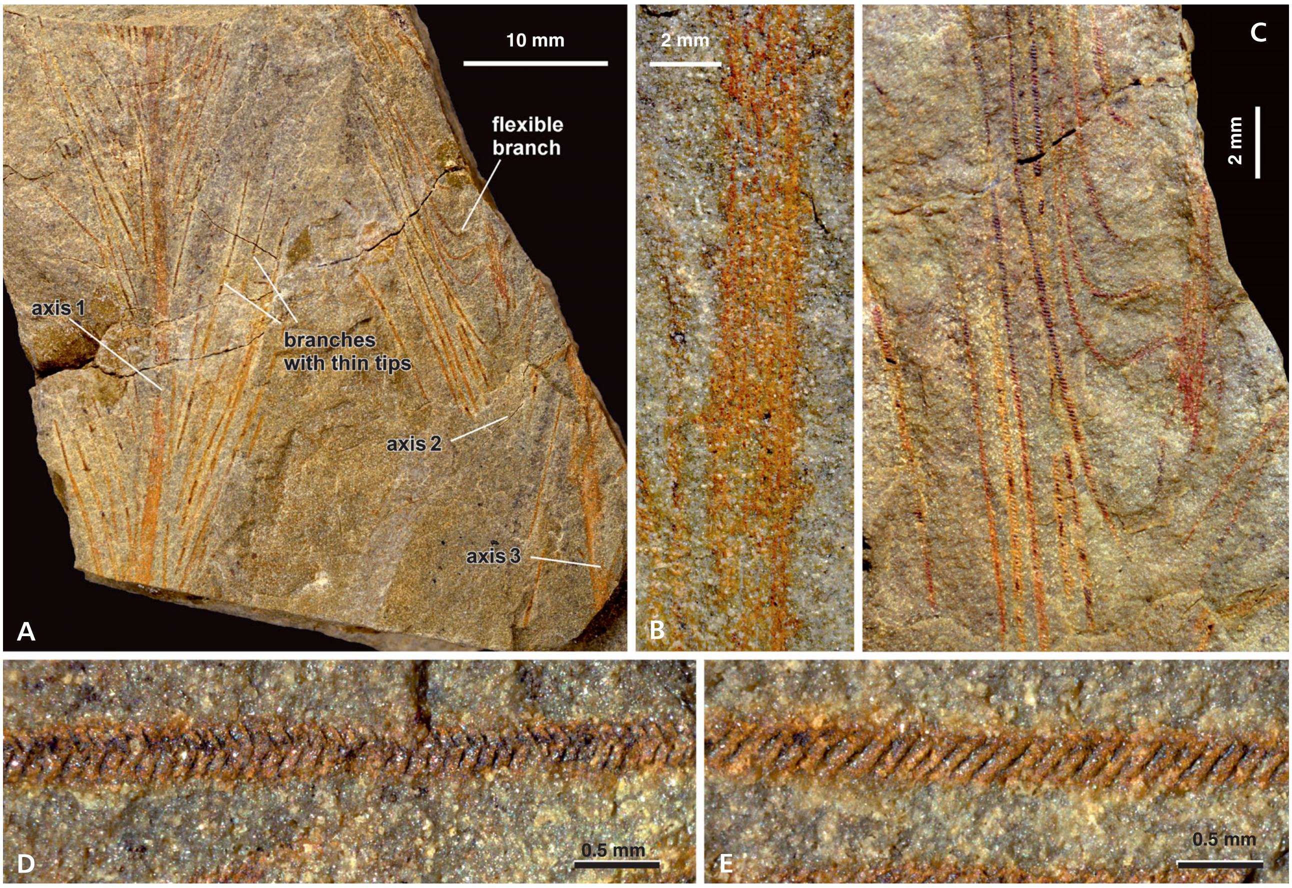

Figure 3. Slab ZPAL Hz 4/2 with three mature colonies of *Crinisdendrum sinicum* gen. and sp. nov. from the earliest Floian (Arenig) Fenxiang Formation at Tianjialing (Hubei Province, China); colony 1 is the holotype. • A – general view. • B – axis of the holotype colony (colony 1) with a pyritized (oxidized during weathering) bunch of tubes presumably corresponding to the black stolons in juvenile colonies. • C – colony 2 with branches gently bent during deposition, proving their flexibility. • D – dorso-ventrally compressed pyritized branch with plait-like structure on the abaxial side. • E – laterally compressed branch.

plait-like lateral branches measuring about 0.12 mm in diameter, or roughly two times wider than the axial tubes. The lateral branches are straight and depart from the axis at a low angle of 10–20°.

The lateral branches were flexible. This is shown by the smaller colony (colony 2) on slab ZPAL Hz 4/2 (Fig. 3C), in which the lateral branches were deformed during deposition. Their plait-like appearance emerges immediately after the tubes diverge from the axis, with the width of the lateral branches being about 0.1 mm. Unlike juvenile specimens, the mature branches are very long, although their tips are usually not preserved (probably because they were broken before deposition). In fully preserved branches, showing such termination, their length is about 30 mm. It is unclear whether all of the branches exhibit this morphology.

Together, the narrowing of the colony axis and the uniform distribution of branches along the axis preclude secondary thickening of the axis from the outside through addition of secondary tissue. Presumably, new stolon buds developed in the central part of the axis near its base, and the new branches emerged apically after the growing stolons reached the apex of the axis.

The critical problem here is whether the pyrite impregnating the lateral branches corresponds to a solid interior or is merely an infilling. The latter hypothesis is weakly supported by the difference between the dark crust restricted to the exterior of some outgrowths and the light-coloured and soft interior, but this may be a matter of sequential deposition of iron sulphide within the tube. More convincing evidence may be preserved in phosphatized specimens overgrown by black corals. In such specimens, there is no difference in internal structure between the phosphatized external tissue layer belonging to the black coral and the phosphatized tube of the organism under study. Apparently, phosphatization homogenized to some degree the original tissue structure. In one specimen (Fig. 4C–G), a narrow empty space separates the tube from the overgrowing black coral. An alternative interpretation then is that all of the layers belong to the black coral, and the interior of the fossil is a replica in negative of the external surface of the lateral branch. However, this interpretation is inconsistent with the morphology of the pyritic infilling of the branches, which shows the acute margins of annular serial structures, which rather precisely correspond to furrows in the phosphatised specimens (Fig. 4A, B). Even more convincing is the apparent correspondence between the furrow along the plait-like adaxial surface in the pyritic specimen and the thread-like medial structure in the phosphatized specimen. According to this interpretation, the wall of phosphatized specimen ZPAL Hz 4/13 was gently annulated on the external surface (Fig. 4F) and bore prominent internal ridges of distal orientation (Fig. 4D, E). The surface between the annular ridges is smooth and gently concave (Fig. 4G). Indistinct growth increments visible on broken transverse surfaces of the annuli suggest that secretion progressed from the outside towards the tube lumen (Fig. 4D). As a result the inner ridges became more acute. Near the adaxial (upper) midline the ridges changed into distally oriented processes with paraboloid ends. This means that the ribs were serial structures having a C-like shape and being separate at least adaxially. The acute ends of the ribs meet alternately, forming the zig-zagged suture (Figs 2A, C and 3D) on pyritic infillings of the tubes. This suggests that secretion of the tips of the C-shaped units did not proceed simultaneously on both sides of the tube midline, but rather that something produced them separately.

The thread-like structure, which measures 0.006 to 0.007 mm thick, extends along the midline of the tube below and between the tips of the C-shaped annular units. The thread-like structure is separate from the tube wall, although as a result of indiscriminate phosphatization both structures are firmly connected to each other, and in places their phosphatic matter is in continuity (Fig. 4F). There is no space for soft tissue between them, which means that the tubular structure developed later, after secretion of the annular thickenings was completed.

Taken together, data from specimens preserved as compressions in shale, from pyritic internal moulds, and from phosphatized walls of the lateral branches, allow us to propose a partial reconstruction of the whole skeleton. The development of the colony (if one is dealing with an animal; thallus if this was an alga) started from a stolon covered with a dense, organic-rich wall. During the early stages of development the stolon furcated in a rather regular, presumably helicoidal ("spiral") way (Fig. 5B). Each of the lateral branches of the stolon formed an annulated tube with a hemispherical base in pyritized specimens. The interior of the stolon was built of C-shaped units arranged more or less obliquely to the axis. The abaxial (lower) sides of the C-shaped units were more or less transverse and continuous, whereas on the adaxial (upper) side the distally curved tips of the C-shaped units merged alternately to form a zig-zagged suture. Initially the thin continuous wall of the tube was secreted, presumably by soft tissue covering the animal body. Then the C-shaped units were added from the inside in a way suggestive of a force drawing the C-shaped units towards their free tips. The tips alternate, and thus the whole unit was not secreted instantaneously but one of its tips was added with some delay, after the other had been already in place. Below the suture, on the inner side of the tube, there is a thin thread-like structure of the same diameter as the black stolons and tubes in the erect colony axes. It seems likely that the thread-like structure initiates from the stolon. Because the thread-like structure was apparently added after secretion of the C-shaped units was completed, it is unlikely that it continues into a whip-like structure at the tip of the lateral branch. After more (in large specimens) or less (in early astogenetic stages) prolonged growth without change in diameter, the tube gradually narrowed and extended into a whip.

Affinities

Probably the best-known Early Palaeozoic fossil with a feather-like appearance is the Silurian to Late Devonian *Plumalina* (Muscente & Allmon 2013). Museum specimens from the Late Devonian Mount Marion Formation of New York State examined by us exhibit lateral branches with smooth margins and rounded tips. This fact rules out the hypothesis of a hydrozoan affinity proposed by Muscente & Allmon (2013) and makes *Plumalina* rather a *Caulerpa*-like alga. Whatever its affinities, *Plumalina* is not similar to the Tianjialing organism.

Extinct relatives

Colonial organisms with a feathery appearance are known also from the Ordovician of Bohemia (Kraft *et al.* 2001). In fact, except for the shape of the colony, all other aspects of the ground plan of the Bohemian and Chinese organisms are mutually similar. The axis of the Bohemian *Webbyites* colony is composed of a bunch of tubules; lateral branches consist of a series of obliquely arranged units. The preservation of the Bohemian material is relatively poor because of the coarse-grained rock matrix. The adaxial (upper) parts of the oblique units are compressed, resulting in a serrated appearance interpreted as thecal openings by Kraft *et al.* (2001). This is why they were interpreted as thecae. To explain counterintuitive orientation of the oblique units, with the upper ends of these features directed towards the colony axis, Kraft *et al.* (2001) hypothesized that the thecae changed their direction of growth being bent in their middle length. The evidence offered by the Tianjialing fossils

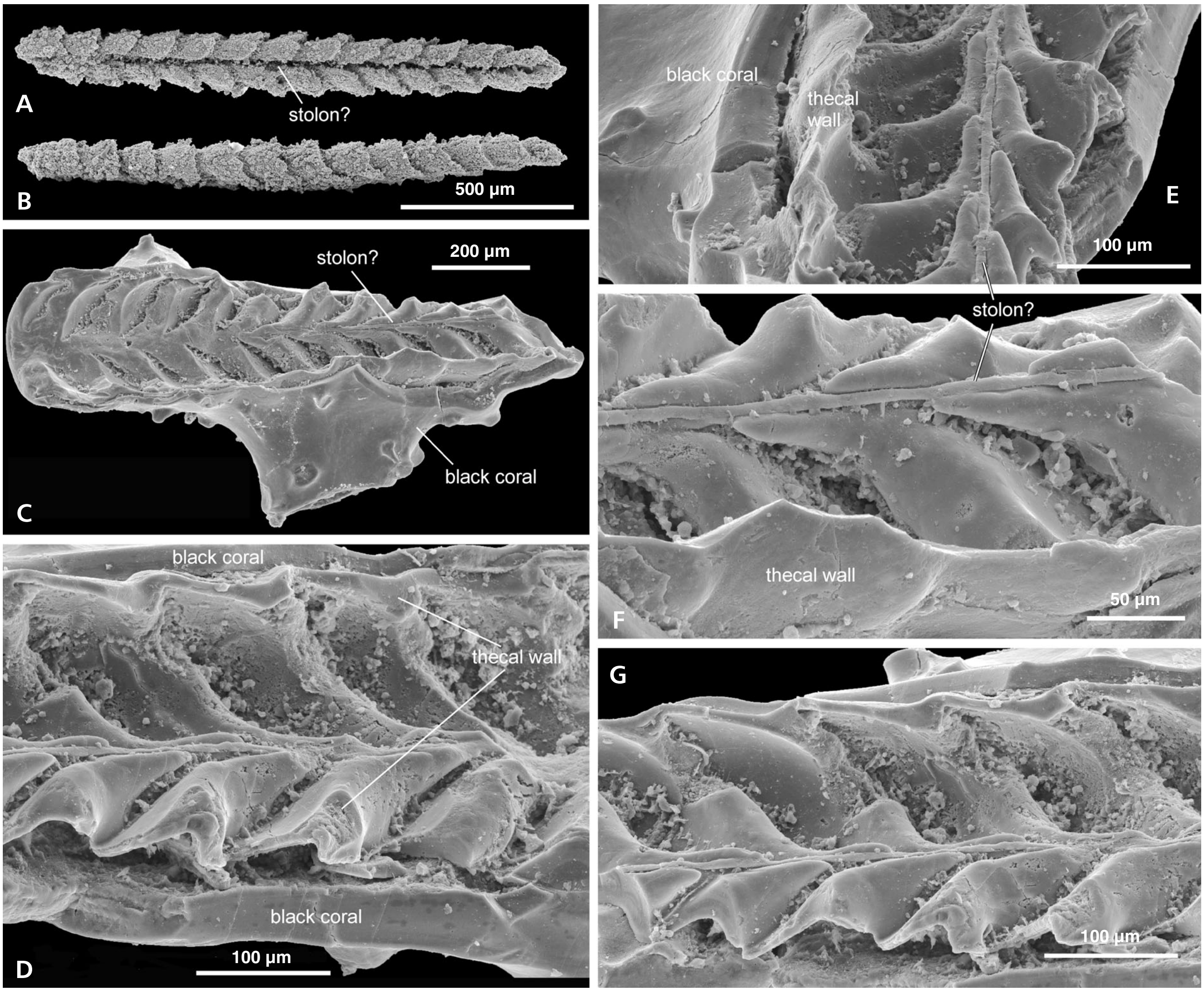

Figure 4. Fragments of lateral branches of *Crinisdendrum sinicum* gen. and sp. nov. from the earliest Floian (Arenig) Fenxiang Formation at Huanghua (A, B) and Tianjialing (C–G) (Hubei Province, China) showing their structure. • A, B – pyritic infilling of the branch ZPAL Hz 4/14 showing, in negative relief, the distribution of the internal oblique ribs and the position of the probable stolon. • C–G – phosphatised overgrowth of black coral specimen ZPAL Hz 4/13, showing the distinction between the coral and the branch walls and possible growth increments (D), details of the stolon (E, F), and the shape of the cavities between the putative fuselli (G).

shows that these are not series of thecae, but rather that the entire branch was a tubular structure with internal oblique constrictions. *Webbyites rokycanensis* from the Early Ordovician Klabava Formation is geologically younger than the Tianjialing organism. Having a regularly pinnate form, it may be more advanced in the evolution of the erect colony organization. They differ also in the angle of inclination of the oblique constriction within the lateral branches, which ranges from 10° to 26° in *Webbyites* and from 35° to 65° in the Chinese organism. Although the Bohemian material confirms our interpretation of the structure of the Chinese material, this fact does not help much in determining the zoological affinities of the Chinese specimens.

Possible pterobranch affinity

The most unusual aspect of the Tianjialing organism is the plait-like appearance of the adaxial side of its lateral branches, which results from alternate distribution of tips of serial units forming the wall. Each C-shaped unit is inclined to the branch axis, and the free tips follow the thin tubular structure located on the internal side of the adaxial wall. It is tempting to homologize the serial units with fuselli, as their way of merging on one side is similar in size and morphology to the zigzag suture in the creeping parts of the theca of the pterobranch *Rhabdopleura* (*e.g.*, Mierzejewski & Kulicki 2001, 2003), and the tubular structure inside the tube with the stolon (*e.g.*, Urbanek & Dilly 2000).

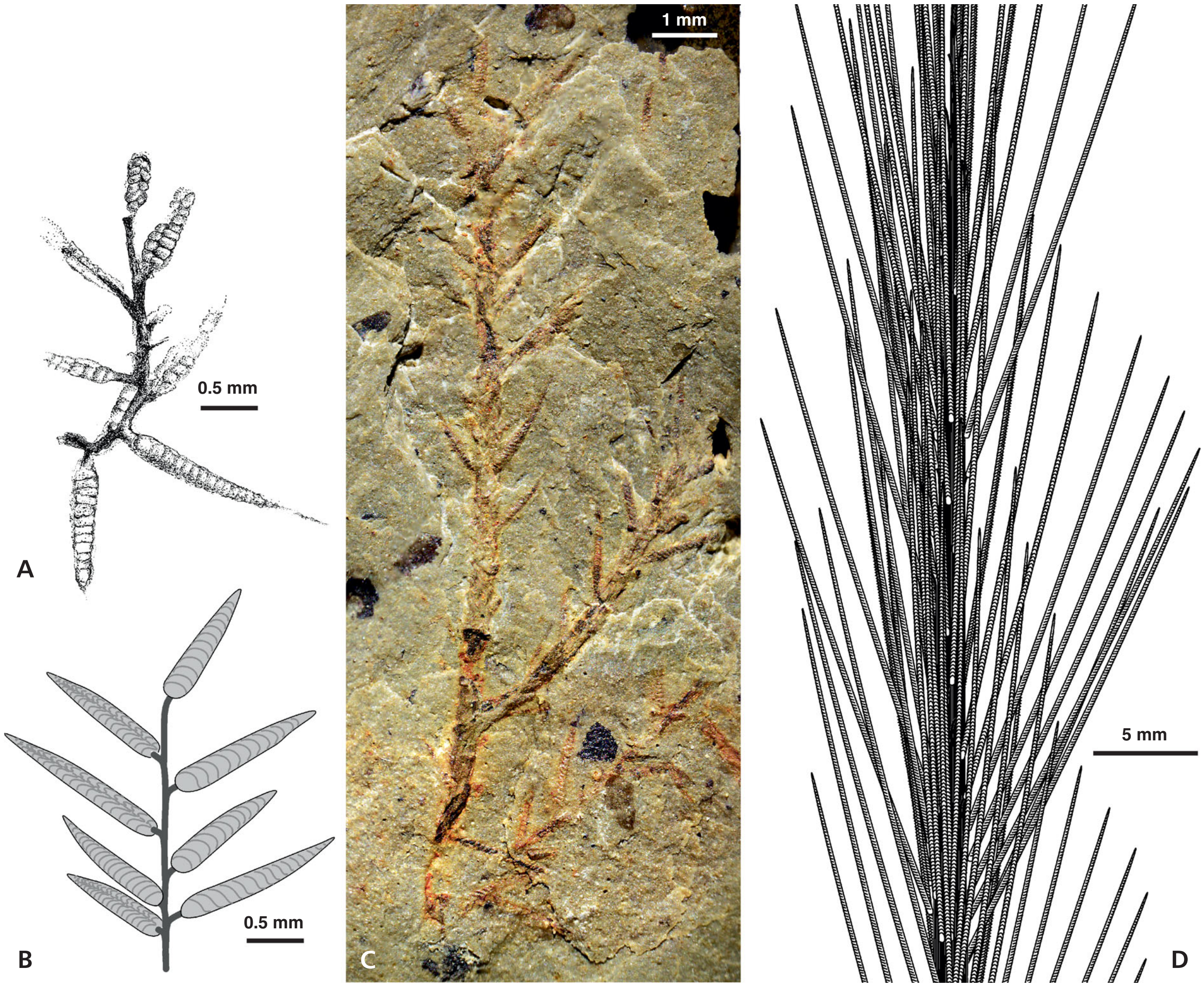

Figure 5. *Crinisdendrum sinicum* gen. and sp. nov. from the earliest Floian (Arenig) Fenxiang Formation in Hubei Province, China. • A – superimposed *camera lucida* drawings of the part and counterpart of specimen ZPAL Hz 4/5, a juvenile colony from Tianjialing. • B – diagrammatic provisional reconstruction of the juvenile colony. • C – branching colony ZPAL Hz 4/15 from Huanghua. • D – proposed restoration of a mature colony based on specimen ZPAL Hz 4/2 from Tianjialing.

The difference in preservation between the Tianjialing organism and associated graptolites may be due to the predominance in the graptolites of fusellar tissue, which forms a spongy meshwork instead of cortical, densely ordered fibrils (Mierzejewski & Kulicki 2001; but both kinds of tissues are present in the rhabdopleurids according to Mierzejewski & Kulicki 2003). Also, the hemispherical base of the tube and its emergence from the black stolon closely resemble the stolon system of extant *Rhabdopleura*. An inflation of the stolonal sheath forms a diaphragm inside the fusellar tube (Urbanek & Dilly 2000). The sheath obviously was secreted by the epithelium of the zooid body (Urbanek & Dilly 2000) and not mortared with collagen by the preoral disc.

A fundamental difficulty with this line of inference emerges immediately, namely the narrowing and terminal closure of the tubes and the presence of a whip at their tip. Although closely similar thecae (Endröhren) of *Rhabdopleura normani* were illustrated by Schepotieff (1907, p. 215, pl. 17, fig. 2, pl. 22, figs 10–13) as being pointed, sealed tubes, this interpretation has not been confirmed by later investigators. Mitchell *et al.* (2013) noticed that such sealing is inconsistent with the way *Rhabdopleura* zooids build their thecae. Specifically, the theca of *Rhabdopleura* cannot be constructed through the mortaring activities of the cephalic disc before the body of the zooid is fully developed. An alternative hypothesis is that the Endröhren held dormant buds similar to the resting cysts of *R. compacta* (Dilly 1975) and graptolites (Urbanek 1983, Mierzejewski 2000). Whatever the actual nature of Endröhren in *R. normani*, there is little doubt that they were present in the Schepotieff (1907) colonies. Zooids preserved as retracted within such thecae with acute tips occurred also in the rhabdopleurids from the Cambrian of Siberia (Sennikov 2015). Still, it remains to be explained how such closure of thecae developed, though this problem should not preclude homology of sealed thecae of *R. normani* with the lateral branches of the Tianjialing organism and *Webbyites*. Admittedly, this hypothesis introduces considerable uncertainty into their purported pterobranch affinities, and thus an alternative hypothesis should be offered.

Possible hydroid affinity

Even if the oblique constrictions in the lateral branches have nothing to do with zooids, an alternative to the pterobranch hypothesis may be looked for among the hydroids. The fusiform lateral branches resemble the "corbulae" of aglaopheniid hydrozoans (*e.g.*, Moura *et al.* 2012). These are series of structures housing the gonozooids, which are sexual zooids that are not released as medusae. Gonozooids exhibit a rather complex morphology, and open separately to free eggs or spermatozooids. In the aglaopheniids, the gonothecae are arranged in two series, with the chitinous protective cover of particular gonozooids emerging alternately from the stolon and merging in a zig-zag pattern in some species (*e.g.*, Svoboda & Cornelius 1991, fig. 1g). Still, in this case the similarity to the lateral branches of the Tianjialing organism, which consist of a series of C-shaped units (rather than two alternate series) inclined to the branch axis, is rather superficial. Thus the hypothesis of a hydrozoan affinity must be rejected.

Possible autotrophy

The hypothesis of an algal affinity for the Tianjialing fossils implies that the tubules in the axis were a kind of vascular tissue, the walls of the cells composing it having been composed of a polysaccharide. This hypothesis does not seem to be consistent with the diameter of the tubes, which are significantly wider than regular algal cells. The shape of the lateral branches suggests that all of the specimens collected thus far represent the reproductive stage of an organism of unknown vegetative anatomy. We are unable to offer any well-supported hypotheses of homology or analogy between these structures and algal organs. Moreover, the ground plan of the Tianjialing organism seems to be too regular for an alga.

The single remaining possibility is that the Tianjialing organism was chemoautotrophic and that the lateral branches housed individuals hosting symbiotic bacteria. This hypothesis explains their impregnation with iron sulphide and the final closure of the tubes. This interpretation may be consistent with the hypothesis of a rhabdopleurid affinity, but it requires that after mortaring of the tube with preoral disc was completed, the tubes' apices were constricted and closed.

Conclusions and taxonomic nomenclature

We conclude that the phylogenetic affinities of the Tianjialing organism are uncertain. Be that as it may, the pterobranch model appears to be the most likely hypothesis, though at this point the pterobranch model does not enable us to explain the tapering and termination of the lateral branches (Fig. 5). Resolution of this problem requires greater knowledge of the biology of *Rhabdopleura normani*. Despite uncertainty regarding the phylogenetic position of *Webbyites* and the Tianjialing organism, these two organisms differ enough from each other in organization of colonies to merit separate generic names, but they are sufficiently similar to each other to form a monophyletic unit of family rank.

Incertae sedis
Family Crinisdendridae fam. nov.

Diagnosis. – Erect clonal colonies with a bunch of stolons forming the colony axis and long laterally extending thecae(?) with internal constrictions in the form of C-shaped units (fuselli?) the free ends of which meet in a zigzag suture along the adaxial side of the theca.

Genera included. – *Webbyites* Kraft, Kraft & Prokop, 2001; *Crinisdendrum* gen. nov.

Genus *Crinisdendrum* gen. nov.

Type species. – *Crinisdendrum sinicum* gen. et sp. nov.

Etymology. – From the Latin *crinis* – plait, and the latinized Greek *dendron* – tree.

Included species. – Only the type species.

Diagnosis. – Mature colony with lateral branches (thecae?) distributed along the axis.

***Crinisdendrum sinicum* sp. nov.**
Figure 2–5

Holotype. – Colony 1 on slab ZPAL Hz 4/2 (Fig. 3A).

Type locality and horizon. – Earliest Floian (Arenig) Fenxiang Formation at Tianjialing in Hubei Province, China.

Etymology. – From the Latin *sinicum* – Chinese.

Diagnosis. – As for the genus.

Occurrence. – Tianjialing and Huanghua, Hubei Province, China.

Acknowledgements

This research was supported by the National Science Centre of Poland (grant DEC-2012/07/B/NZ8/02701). X-ray microtomography was conducted by Katarzyna Janiszewska in the NanoFun laboratory of the Institute of Paleobiology of the Polish Academy of Sciences, and was co-financed by the European Regional Development Fund within the Innovation Economy Operational Programme POIG.02.02.00-00-025/09. SEM photomicrography also was conducted at the Institute. We thank Cyprian Kulicki (Institute of Paleobiology, Warsaw), Lucy Muir (Llandrindod Wells), and Jörg Maletz (Freie Universität Berlin) for their critical comments on an earlier version of the manuscript. Reviews by Olev Vinn (University of Tartu, Estonia) and Heyo Van Iten (Hanover College, Indiana) are gratefully appreciated. Heyo Van Iten generously improved English language of the text.

Supplementary data

Movie based on X-ray microtomography of the counterpart of specimen ZPAL Hz 4/5 (see Fig. 2D); http://www.geology.cz/bulletin/contents/art1575.

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