

## *Malongitubus*: a possible pterobranch hemichordate from the early Cambrian of South China

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**Abstract.**—*Malongitubus kuangshanensis* Hu, 2005 from the early Cambrian Chengjiang Lagerstätte of China is redescribed as a pterobranch and provides the best evidence to demonstrate that hemichordates were present as early as Cambrian Stage 3. Interpretation of this taxon as a hemichordate is based on the morphology of the branched colony and the presence of resistant inner threads consistent with the remains of an internal stolon system. The presence of fusellar rings in the colonial tubes cannot be unambiguously proven for *Malongitubus*, probably due to early decay and later diagenetic replacement of the thin organic material of the tubarium, although weak annulations are still discernible in parts of the tubes. The description of *M. kuangshanensis* is revised according to new observations of previously reported specimens and recently collected additional new material. *Malongitubus* appears similar in most features to *Dalyia racemata* Walcott, 1919 from the Cambrian Stage 5 Burgess Shale, but can be distinguished by the existence of disc-like thickenings at the bases of tubarium branching points in the latter species. Both species occur in rare mass-occurrence layers with preserved fragmentary individuals of different decay stages, with stolon remains preserved as the most durable structures. Benthic pterobranchs may have occurred in some early Cambrian shallow marine communities in dense accumulations and provided firm substrates and shelter for other benthic metazoans as secondary tierers.

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### Introduction

The Pterobranchia are a group of colonial or pseudocolonial hemichordates with a long evolutionary history ranging from the Cambrian to the present day. Extant pterobranchs are benthic and classified into two major orders: the Cephalodiscida and the Rhabdopleurida. A close relationship between rhabdopleurid pterobranchs and graptolites was suggested by some previous studies (Urbanek, 1986, 1994; Urbanek and Dilly, 2000; Mierzejewski and Kulicki, 2003) and confirmed by a cladistic investigation (Mitchell et al., 2013), which indicated that the extinct Graptolithina should be included in the Pterobranchia. On the basis of scanning electron microscope back-scatter electron (SEM-BSE) analyses (Maletz et al., 2005), some fossils previously presumed to represent Cambrian algae have been reinterpreted as pterobranchs (Maletz et al., 2005; Maletz, 2014; LoDuca et al., 2015a, 2015b; Maletz and Steiner, 2015), greatly improving our knowledge of the early fossil record of the Pterobranchia. However, the age of the oldest pterobranchs and even of the Hemichordata is still not settled. The earliest potential candidate for hemichordate fossils so far known is acid-isolated organic fragments of *Sokoloviina costata*

Kirjanov, 1968 representing tubaria with zigzag-shaped fusellar collars from the basal Cambrian Rovno Formation of Ukraine (Sokolov, 1997, pl. 8.4). Other remains have been reported from Cambrian Stage 5 (Series 3), including the potential colonial pterobranch *Yuknessia simplex* Walcott, 1919 (LoDuca et al., 2015a) and the tubicolous enteropneust hemichordates *Spartobranchus tenuis* Caron, Conway Morris, and Cameron, 2013 and *Oesia disjuncta* Walcott, 1911 (Caron et al., 2013; Nanglu et al., 2016) from the Burgess Shale, and undescribed fragments from the Kaili Formation in Southwest China (Harvey et al., 2012). Frond-like fossil remains with a pair of tentacles from the Chengjiang Lagerstätte were described as *Galeaplumosus abilus* Hou et al., 2011 and interpreted as a possible hemichordate zooid (Hou et al., 2011). The assignment of the sole known specimen to the hemichordates, however, was questioned by recent studies (LoDuca et al., 2015a; Maletz and Steiner, 2015; Ou et al., 2017). Another potential rhabdopleurid pterobranch from the Niutitang Formation of China (Cambrian Stage 2; Zhao et al., 1999) requires further study, and its pterobranch affinity remains uncertain (Maletz, 2014; LoDuca et al., 2015a; Maletz and Steiner, 2015). The earliest widely accepted occurrences of pterobranchs are from the basal part of

Stage 5 of the Cambrian Period (Maletz, 2014; LoDuca et al., 2015a; Maletz and Steiner, 2015). In this study, we reinterpret *Malongitubus kuangshanensis* Hu, 2005 from the early Cambrian Chengjiang Konservat-Lagerstätte (Series 2, Stage 3) as a possible pterobranch, judging mostly from the identification of a resistant internal stolon system.

### Geological setting, materials, and methods

All material is from a single bedding plane in a small quarry on the northwest slope of a hillside near Kuangshan village, ~10 km southwest of the county town Malong, 100 km east of Kunming in Yunnan Province, China (25°20'15"N, 103°30'20"E). Stratigraphically, this interval belongs to the upper part of the *Eoredlichia*–*Wutingaspis* Zone within the Yu'an-shan Formation and is equivalent to the strata containing the renowned Chengjiang Biota in Chengjiang County and the Haikou district of Kunming (Luo et al., 1994; Zhang et al., 2001). Associated fossils from the same interval include arthropods (trilobites, bradoriids, and other arthropods), sponges, cnidarians, anomalocaridids, lobopodians, priapulids, hyolithids, brachiopods, cancelloriids, vetulicolians, and algae (a detailed list of fossils is available in the appendices of Hu, 2005 and Zhao et al., 2012), representing a local assemblage of the Chengjiang biota. The lithology of the section and the occurrence of the pterobranch-bearing layer were illustrated previously (Hu, 2005, text-fig. 9; Wang et al., 2012, fig. 1B). The preservation of the probable pterobranchs and other associated fossils was interpreted to be the result of rapid burial by a distal storm event (Hu, 2005; Zhao et al., 2012).

The specimens of *Malongitubus kuangshanensis* are compressed, often fragmentary, and commonly partly superimposed on one another on the bedding surface. In most cases, the tubes are whitish or pale in color due to intense weathering, with occasional dark remains of original organic material. The materials were prepared using a sharp blade under a binocular microscope. Overall images of the specimens were obtained with a Canon Mark II Camera with an EF 100 mm f/2.8L IS USM close-up lens under direct light. Enlargements of details at the millimeter scale were photographed with a Zeiss Smartzoom 5 microscope system under fiber-optic lights. BSE pictures were obtained using a HITACHI SU3500 in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China, with an accelerating voltage of 20–30 kV. SEM microphotographs were obtained and energy-dispersive spectroscopic analysis was conducted at the State Key Laboratory of Continental Dynamics, Northwest University, Xi'an, China, with a ZEISS-SUPRA 40VP.

*Repositories and institutional abbreviations.*—Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China (NIGP); Early Life Institute of Northwestern University (ELI). A specimen of *Dalyia racemata* from the Burgess Shale was also examined in this study (specimen number USNM 194121, Smithsonian Institution, Washington DC, USA). The nomenclature applied in this study follows that of recent works on pterobranchs (Maletz et al., 2005; LoDuca and Kramer, 2014; Maletz, 2014; LoDuca et al., 2015a; Maletz and Steiner, 2015).

### Systematic paleontology

- ? Phylum Hemichordata Bateson, 1885
- ? Class Pterobranchia Lankester, 1877
- ? Subclass Graptolithina Bronn, 1849, emend. Mitchell et al., 2013
- Genus *Malongitubus* Hu, 2005

*Type species.*—*Malongitubus kuangshanensis* Hu, 2005.

*Diagnosis (emended).*—Colonial organism with long, slender, and branching thecal tubes. Thecal tubes parallel-sided, each with an internal continuous thread. There are usually four, or less commonly five, terminal thecal tubes, which are free and in similar widths and lengths. Fine annulations present on the surface of thecal tubes. Terminal thecal tubes narrow distally, commonly with thickened apertures.

*Remarks.*—*Malongitubus* closely resembles *Dalyia* Walcott, 1919 from the Burgess Shale (Cambrian Series 3, Stage 5) in overall colony shape and in having nearly parallel-sided thecal tubes and inner threads of relatively constant dimensions, herein interpreted as a stolon system. The close similarity between the two taxa led to the suggestion of possible synonymy (Maletz and Steiner, 2015). However, *Malongitubus* differs in having a greatly variable branching distance, from millimeters to centimeters. In addition, the presence of round structures at the branching points of *Dalyia* (Maletz and Steiner, 2015) allows differentiation of the two taxa. On the basis of this difference, *Malongitubus* is retained as a separate taxon. Holdfast structures and initial (larval) development of both taxa are unknown. The development of fuselli cannot be proven, but is likely. No zooid remains have been preserved. Comparing to *Yuknessia* from the Cambrian of British Columbia and Utah, the thecal tubes of *Malongitubus* are completely free and parallel-sided or slightly expanding, whereas those of *Yuknessia* conspicuously widen distally. In addition, the presence of repent and erect thecae in *Yuknessia* also distinguish it from *Malongitubus*. The absence of more differentiated thecal types, such as autothecae, bithecae, and stolothecae, in *M. kuangshanensis* indicates that it differs from dendroid graptolites, which have been reported from the traditional “middle Cambrian” and younger strata (Rickards et al., 1990; Johnston et al., 2009; LoDuca and Kramer, 2014).

*Malongitubus kuangshanensis* Hu, 2005

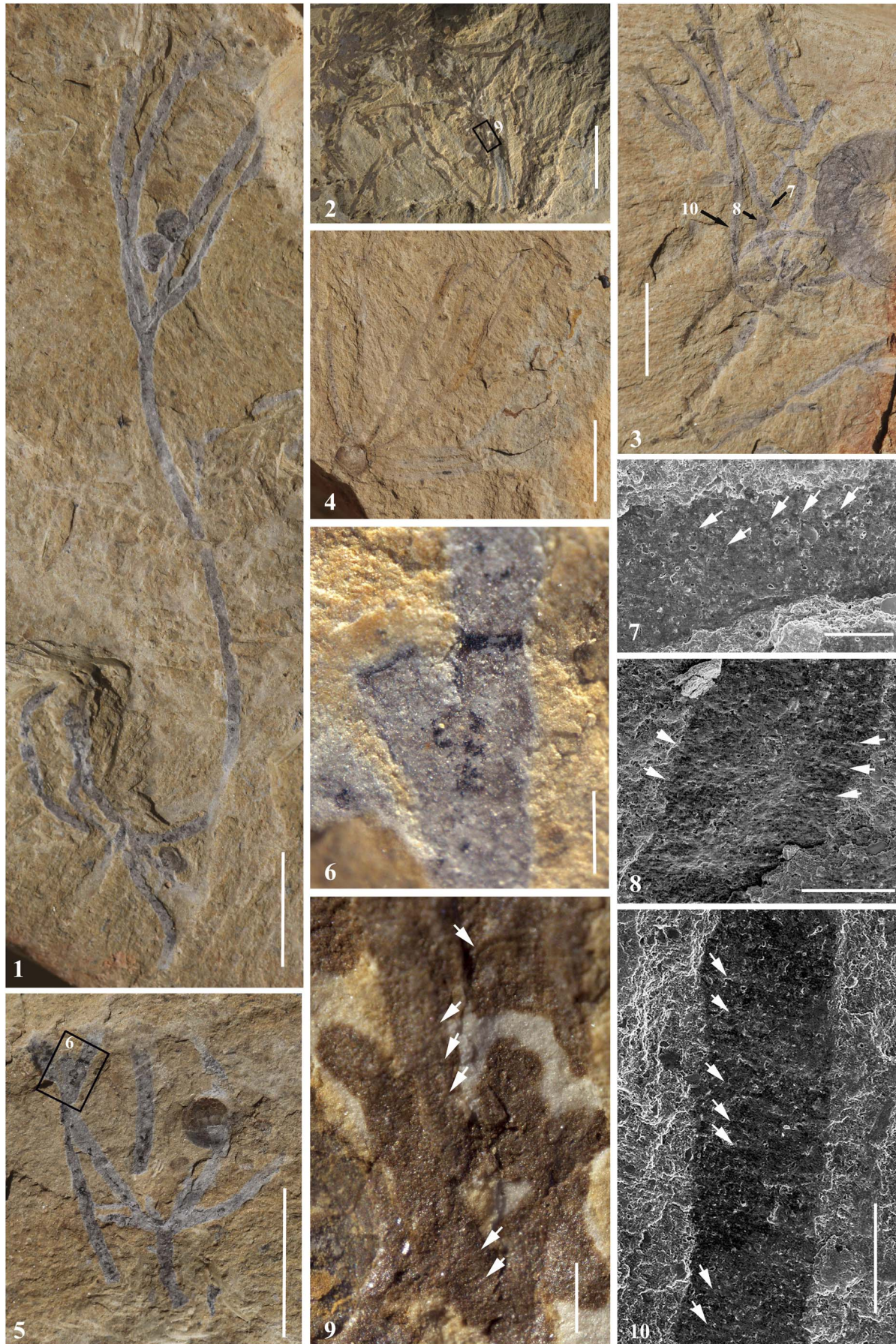
Figures 1, 2

- 2005 *Malongitubus kuangshanensis* Hu, p. 187, pl. 18, figs. 1–7.
- 2012 *Malongitubus kuangshanensis*; Wang et al., p. 62, fig. 2A–G.

*Holotype.*—NIGP-165028 (labeled as Kuangshan-01 in Hu, 2005), a large, nearly complete (base missing) multibranching tubarium with four terminal thecal tubes (Fig. 2.1).

*Occurrence.*—Kuangshan village, Malong County, Yunnan Province, China. Upper part of the *Eoredlichia*–*Wutingaspis* Zone, Yu'an-shan Formation, Cambrian Stage 3, Series 2, early Cambrian.







*Description.*—Maximum height of the tubarium is 6 cm. Tubarium branches are 0.4 to 0.5 mm wide. Distances between bifurcations vary from 1 mm to several centimeters. Remains of soft-bodied zooids are not evident. Thecal tubes mostly straight or curved, sometimes bent (Fig. 1.1). The angle of the thecal tubes to the stipe varies from 15 to 70 degrees. The width of the terminal thecal tubes varies from 250  $\mu\text{m}$  at the aperture to 400  $\mu\text{m}$  at the location just above the branching point. The number of terminal thecal tubes is usually four, or less commonly five (Hu, 2005, pl. 18, figs. 4, 5). The terminal thecal tubes are free with similar widths and lengths. The apertures of the thecal tubes appear to narrow slightly and are thickened (Fig. 1.6; Hu, 2005, pl. 18, fig. 5). Energy-dispersive spectroscopic analysis reveals that the dark remains on the tubes are organic carbon (Fig. 2.9–2.15).

A number of remains of tubaria show a darker internal thread of relatively constant width, herein interpreted as remains of an original stolon system (Figs. 1.5, 2.3, 2.6). As a result of weathering and early decay, the stolon system is preserved as fragments (Figs. 1.5, 2.4), with only a few cases in which the stolon is visible as a continuous thread for a distance of more than a few millimeters (Fig. 2.6). The stolon is divided where the tubarium branches. The width of the stolon is about 10  $\mu\text{m}$ . Transverse annulations of the tubaria are sometimes faintly preserved (Fig. 1.7–1.10) and may have resulted from previously existing fusellar structures. The heights of the annulations are about 20  $\mu\text{m}$ . However, no unequivocal fusellar structures are presently documented.

Due to fragmentary preservation of all available specimens, no basal parts of tubaria are observed; thus, the means of colony attachment to the substrate cannot be determined.

*Other material.*—About 20 specimens with incomplete parts of the tubarium and a large number of incomplete thecal tubes or branches.

*Remarks.*—When the taxon *Malongitubus kuangshanensis* was erected, the phylogenetic affinity of the species was kept open, and the similarity with *Dalyia racemata* from the Burgess Shale was discussed briefly. At that time, the latter was considered to be an alga, but is now recognized as a possible pterobranch hemichordate (Maletz and Steiner, 2015). The possible pterobranch affinity of *M. kuangshanensis* was also mentioned by Maletz and Steiner (2015) but not discussed in detail. The identification of a resistant stolon system indicates that it has a close affinity to the Pterobranchia and more generally that it is a colonial organism. A “stolon” has sometimes been reported from extant hydrozoan colonies, which are morphologically and functionally differentiated into hydrorhiza, hydrocaulus, and especially swollen hydrotheca (Brusca and Brusca, 2003; Ruppert et al., 2004). However, in colonial hydrozoans, the “stolon” represents a thin extension of the hydropolyp, which is

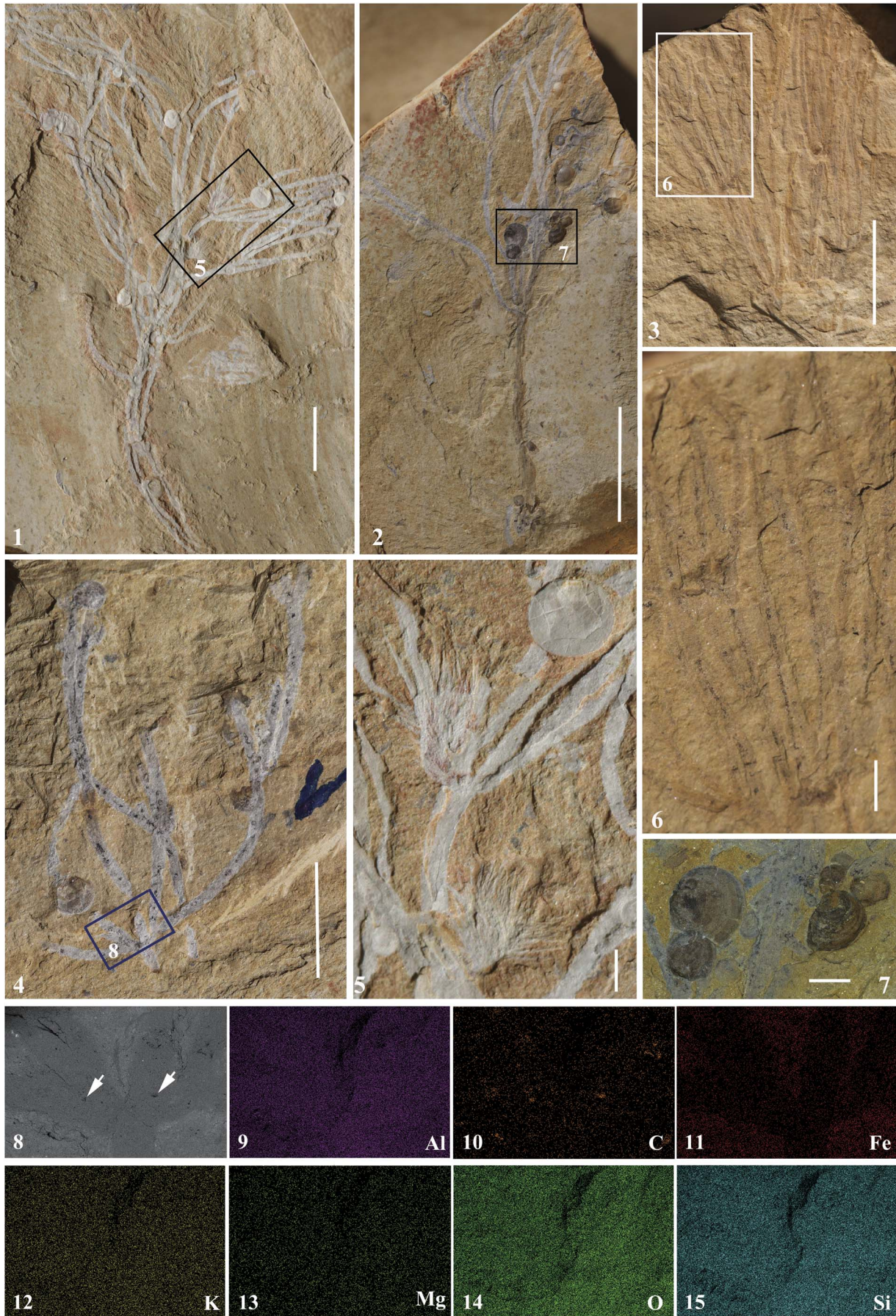
not sclerotized as in pterobranchs and is thus differentiated as coenosarc. While the chitinous perisarc and hydrothecae of colonial hydrozoans may have some fossilization potential, it is rather unlikely that the coenosarc would be preserved in the fossil record. By contrast, decay experiments on modern pterobranchs have demonstrated that the sclerotized stolon system is one of the most durable structures of pterobranch colonies and may prevail until most of the zooids and tubarium have decayed (Beli et al., 2017). In *Malongitubus*, and notably also in the closely related *Dalyia racemata* from the Cambrian Stage 5 Burgess Shale, the putative stolon system is the most resistant structure of the fossil remains. This is also shown by the fact that sometimes only stolons remain after decay or parts of stolons extend out of decayed tubaria (Fig. 3). *Dalyia* was originally interpreted as a red alga (Walcott, 1919), but was recently reinterpreted as a colonial graptolite by Maletz and Steiner (2015) from the identification of a possible stolon system. Therefore, *M. kuangshanensis* is also interpreted as a probable pterobranch due to the existence of a sclerotized stolon system. Its placement within the Cephalodiscida can be excluded, since the latter are noncolonial and lack a stolon system. Further assignment within the Graptolithina is not attempted herein.

Attempts at identifying fusellar structures by SEM-BSE were unsuccessful in the current study. This is probably due to the loss of most of the original organic material of the tube wall as a result of early decay and weathering, leaving only weak imprints of annulations, which are likely to be difficult to detect. The loss of organic material in the main part of the tubarium is also confirmed by the energy-dispersive spectroscopic analysis (Fig. 2.9–2.15). This interpretation also can be applied to *Dalyia racemata* from the Burgess Shale. As indicated by Maletz and Steiner (2015), all available specimens of *D. racemata* are diagenetically altered and pale in color, and no original organic material is present.

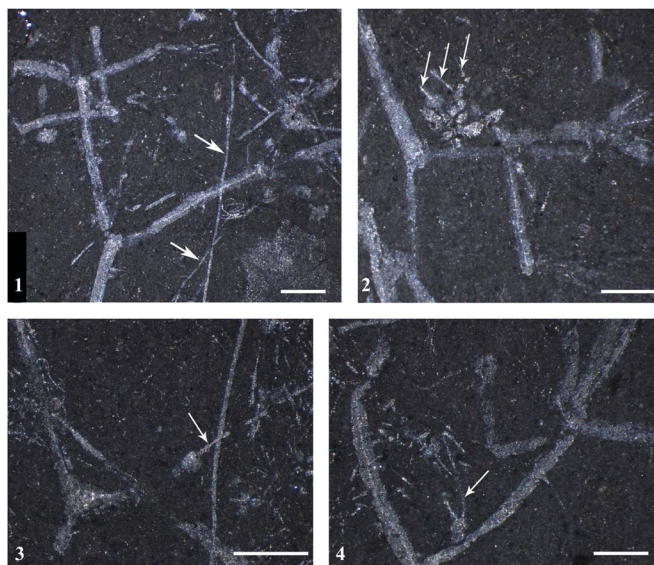
Taphonomic experiments on modern pterobranchs (Briggs et al., 1995; Beli et al., 2017) show different rates of decay between zooids, tubaria, and the stolon system. The zooids decay rapidly and become unrecognizable after a few days, whereas the tubes and the interior stolon system can last for several months. This decay process of modern pterobranchs can be applied to *M. kuangshanensis*, which shows well-preserved tube outlines and stolon system and the absence of any zooids. Preservation of zooids is extremely rare in the fossil record of pterobranchs. The most substantial record is the putative reports by Durman and Sennikov (1993) and Sennikov (2016) of soft tissue in a middle Cambrian (Drumian) rhabdopleurid from Siberia. Remarkably, a few specimens of arthropods (e.g., *Naraoia*) from the same bedding plane as *M. kuangshanensis* show well-preserved diverticula (Hu, 2005, pl. 13, fig. 7; Zhao et al., 2012, fig. 7N), indicating favorable conditions for soft-tissue preservation. It seems likely that individuals of *M. kuangshanensis* were exposed on the seafloor and subjected

**Figure 1.** *Malongitubus kuangshanensis* from the upper part of the Yu'an-shan Formation. (1) NIGP-165029: a colony with a bent lower portion and a branched upper portion. (2) NIGP-105030: dense tubaria overlapping each other. The framed area is enlarged in (9). (3) NIGP-105031: a branched colony with a priapulid worm, *Maotianshania cylindrica*, to the right. The areas indicated by the black arrows are enlarged in (7, 8, 10). (4) ELI-B CLP K007A: a radiating colony. Note the brachiopod to the bottom left. (5) ELI-B CLP K010, part: a colony with a branching tubarium and a stolon system. (6) Thecal apertures. Close-up of the area framed in (5). (7, 8) SEM photograph showing the weak imprints of annulations. White arrows indicate the annulations interpreted as traces of possible fusellar construction. (9) Close-up of the area framed in (2), showing annulations of the tubarium. Some of the annulations are indicated by white arrows. (10) SEM photograph showing the weak imprints of annulations. (1–5) Scale bars = 5mm; (6, 9, 10) scale bars = 0.5 mm; (7) scale bar = 200  $\mu\text{m}$ ; (8) scale bar = 300  $\mu\text{m}$ .









**Figure 3.** *Dalylia racemata* from the Cambrian Stage 5 Burgess Shale, No. USNM 194121, Smithsonian Institution. (1) Repeated dichotomous branching of tubarium with distinct threads within the partly decayed tubarium, interpreted as a sclerotized stolon system; thinner filaments besides the branched tubarium represent separated stolons from decayed colonies (arrows). (2) Branched tubarium with internal stolons; separated, decayed branching shows that tube material was decayed and only thickened round basal part of tube and fragments of stolons are left (arrows). (3) Partly decayed tubarium with retained left tube with inner stolon and decayed right tube with exposed stolon (arrow). (4) Branched tubarium with stolon in the left tube; remains of stolons of decayed colonies (arrow). Scale bars = 1.0 mm.

to microbial decay before final burial; consequently, the zooids disappeared due to protracted decay.

### Paleoecology

Tiny brachiopods are observed on some of the specimens (Fig. 2.1, 2.2, 2.4, 2.5, 2.7). The brachiopods range from 0.8 to 2.2 mm in diameter. The shells of the brachiopods are complete and articulated, with the two valves fitted together. These tiny brachiopods are called *Kuangshanotreta malungensis* Zhang, Holmer, and Hu in Wang et al., 2012 and are assigned to the acrotretoids (Wang et al., 2012). All individuals of *K. malungensis* are directly in contact with the tubes and are oriented with the posterior margin toward the tubes (Fig. 2.5, 2.7). Judging from the overall colony arrangement and the attachment of brachiopods, it seems likely that *M. kuangshanensis* was a benthic, erect pterobranch that was attached to a firm substrate while alive. The attached small brachiopods are interpreted as secondary tierers, which are benthic suspension feeders that use primary tierers to reach higher water levels above the seafloor to obtain a feeding advantage. This interpretation is also supported by the fact that these brachiopods are very rare in the surrounding matrix. Some other brachiopod species have also been interpreted

as secondary tierers (Zhang et al., 2010), but they were only able to occupy lower levels (less than 5 cm above the seafloor; Wang et al., 2012), whereas those on *M. kuangshanensis* could reach slightly higher elevations. In addition to the miniature brachiopods, five juvenile individuals of the sponge *Choia* sp. are attached to the tubarium of the holotype of *M. kuangshanensis* (Fig. 2.1, 2.5). The sponges are 4–5 mm tall (Fig. 2.5), implying probable secondary tiering. Benthic pterobranchs may have occurred in some early Cambrian shallow marine communities in dense accumulations and provided firm substrates and shelter for other benthic metazoans as secondary tierers. Pterobranchs played an important role in early Cambrian marine benthic communities. The interpretation of *M. kuangshanensis* as a pterobranch also indicates that a brachiopod–pterobranch association had likely developed by the Cambrian Series 2, representing an early form of metazoan commensalism.

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**Figure 2.** *Malongitubus kuangshanensis* and attached brachiopods and sponges as secondary tierers. (1) Holotype, NIGP-165028, showing the associated brachiopods and sponges. (2) NIGP-165032, showing the attachment of numerous brachiopods onto the tubes. (3) NIGP-165033. Densely arranged tubes. Close-up of the area framed in (6). (4) ELI-B CLP K010B, counterpart: a colony with both adult and juvenile brachiopods. (5) Close-up of the area framed in (1), showing two sponges and one brachiopod on the tubes. (6) Close-up of the area framed in (3), showing the dark, continuous stolon. (7) Close-up of the two juvenile brachiopods indicated by the framed area in (2). (8) BSE image of the area marked by the frame in (4). White arrows point to the organic remains. (9–15) Energy-dispersive spectroscopic analysis of the tubarium in (8). (1–3) Scale bars = 10 mm; (4) scale bar = 5 mm; (5, 6) scale bars = 1 mm; (7) scale bar = 0.5 mm.

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