MACROSCOPIC CARBONACEOUS COMPRESSIONS IN A TERMINAL PROTEROZOIC SHALE: A SYSTEMATIC REASSESSMENT OF THE MIAOHE BIOTA, SOUTH CHINA

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ABSTRACT—Carbonaceous compression fossils in shales of the uppermost Doushantuo Formation (ca. 555–590 Ma) at Miaohe in the Yangtze Gorges area provide a rare Burgess-Shale-type taphonomic window on terminal Proterozoic biology. More than 100 macrofossil species have been described from Miaohe shales, but in an examination of published and new materials, we recognize only about twenty distinct taxa, including *Aggregatosphaera miaoheensis* new gen. and sp. Most of these fossils can be interpreted unambiguously as colonial prokaryotes or multicellular algae. Phylogenetically derived coenocytic green algae appear to be present, as do regularly bifurcating thalli comparable to red and brown algae. At least five species have been interpreted as metazoans by previous workers. Of these, *Protoconites minor* and *Calyptrina striata* most closely resemble animal remains; either or both could be the organic sheaths of cnidarian scyphopolyps, although an algal origin cannot be ruled out for *P. minor*. Despite exceptional preservation, the Miaohe assemblage contains no macroscopic fossils that can be interpreted with confidence as bilaterian animals. In combination with other late Neoproterozoic and Early Cambrian body fossils and trace fossils, the Doushantuo assemblage supports the view that body-plan diversification within bilaterian phyla was largely a Cambrian event.

INTRODUCTION

OUR UNDERSTANDING OF body-plan diversification during the Cambrian Period rests disproportionately on a small number of assemblages exceptionally preserved as carbonaceous compressions. The Burgess Shale holds pride of place as the first and most extensively studied of these deposits, but older assemblages such as those at Chengjiang and Sirius Passet indicate that already in the late Early Cambrian, the oceans hosted morphologically complex animals belonging to both stem and crown groups of bilaterian phyla (Conway Morris, 1998a). Trace fossil distributions suggest that at least some of these forms are unlikely to have originated before the beginning of the Cambrian Period. Nonetheless, a Burgess-Shale-type taphonomic window on terminal Proterozoic biology would considerably sharpen our undertsanding of early body-plan evolution.

Burgess Shale-type preservation is defined as "non-mineralizing organisms preserved as carbonaceous compressions (organic preservation) in fully marine sediments" (Butterfield, 1995). Although clay mineral replication may play a taphonomic role (Towe, 1996; Orr et al., 1998), the prior entombment of organic matter is key in Burgess Shale-type preservation (Butterfield, 1990, 1995, 1996).

Shales in the uppermost part of the terminal Proterozoic Doushantuo Formation, exposed at Miaohe, Hubei Province, and roughly age-equivalent beds of the Lantian Formation at Lantian, Anhui Province (Fig. 1), contain unusually well-preserved carbonaceous compressions. Preserved organisms lived in a (partially restricted) marine environment and show no evidence of biomineralization. Previous study has demonstrated that at least some Miaohe fossils are preserved as coherent organic films that can survive HF maceration (Xiao et al., 1998a). Indeed, the carbonaceous nature of the Miaohe assemblage is apparent in almost all macroscopic fossils. As such, the Miaohe biota can be considered as a terminal Proterozoic example of Burgess-Shale-type preservation as defined by Butterfield (1995).

Fossils from Miaohe and Lantian have been described in a number of papers (Zhu and Chen, 1984; Bi et al., 1988; Chen and Xiao, 1991, 1992; Ding et al., 1992, 1996; Chen et al., 1994a, 1994b, 1995; Steiner, 1994; Yuan et al., 1995, 1999; Tang et al., 1997; Xiao et al., 1998a), making it clear that compression fossils are abundant and diverse. Just how diverse, however, remains an open question. Sixty-six generic names and more than 110 specific epithets have been applied by various authors to carbonaceous macrofossils from Miaohe alone. In addition, Ding et al. (1996) listed more than 180 species of organic-walled microfossils from the same locality, including more than two dozen new species without designated type specimens.

This paper represents an attempt to clarify the systematic paleontology of Miaohe macrofossils, as well as an effort to understand their implications for our understanding of the early evolution of multicellular organisms. In light of a collaborative re-examination of macrofossils described by Chen and Xiao (1991, 1992), Chen et al. (1994b), Steiner (1994), Yuan et al. (1995); a careful restudy of the Ding et al. (1992, 1996) collection by one of us (XY); and examination of newly collected materials, we recognize only about twenty distinct taxa in the Miaohe biota. Derived lineages of green and, probably, red and brown algae are present in the assemblage, and simple sponge- and cnidarian-grade animals may be, as well. Miaohe fossils, however, display no trace of complex bilaterian body plans found in taphonomically similar Cambrian assemblages.

STRATIGRAPHY AND TAPHONOMIC SETTING

The South China craton originated by collision between the Yangtze Platform and the Cathaysia Block during the broadly Grenville-age Sibao orogeny (Li et al., 1995). Sedimentary infilling of a ca. 750 Ma rift basin is recorded by the lowermost unit of the Sinian System, the Liantuo Formation (Chen et al., 1997). Younger Sinian units accumulated in a passive margin setting. In its type area in the Yangtze Gorges, the younger portion of the Sinian System consists of, in ascending order, the Nantuo tillite, Doushantuo Formation, and Dengying dolomite (Fig. 1). Stratigraphic correlations between the Yangtze Gorges area and more southern regions (e.g., in southern Hunan and Guangxi provinces) have been controversial. For example, it is debatable whether the Banxi Group in the northeast-southwest Sibao orogenic belt is completely pre-Sinian (Chen et al., 1997) or can be correlated with Liantuo sandstones in the Yangtze Gorges area (Liu, 1991). Similarly, it is uncertain how to correlate the Nantuo tillite in the Yangtze Gorges area with the two distinct tillites to the south (Liu,
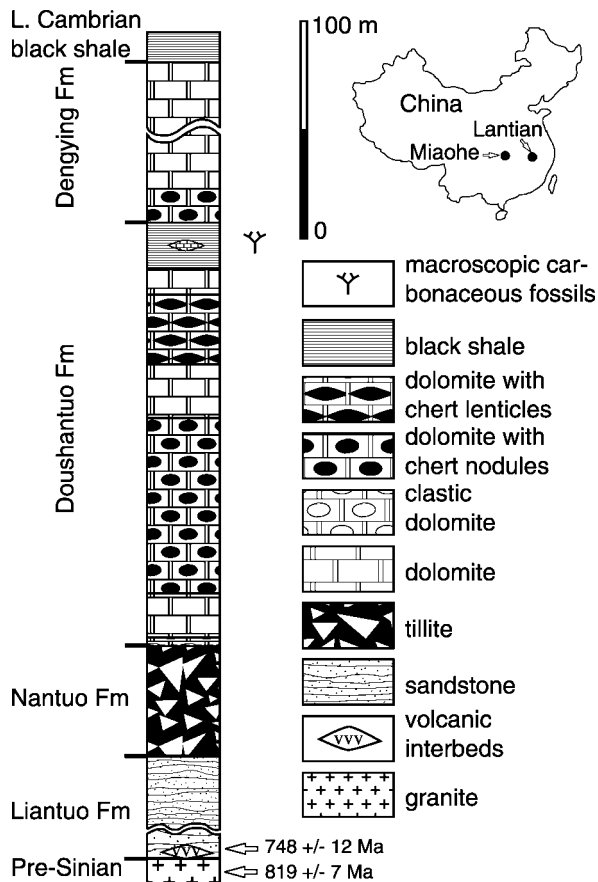
FIGURE *1*—Upper Neoproterozoic (Sinian) stratigraphic section at Miaohe in the Yangtze Gorges area. Carbonaceous fossils described in this paper are collected from uppermost Doushantuo black shales at Miaohe.

Bengtson, 1989). Therefore, the fossiliferous shales of the Doushantuo Formation are subtended by a late Neoproterozoic tillite and overlain by Ediacaran-fossil-containing rocks. Acanthomorphic acritarchs found lower in the Doushantuo Formation (Yin, 1987; Zhang et al., 1998) are characteristic of a diverse and taxonomically distinctive assemblage that commonly postdates the Marinoan glaciation but predates diverse Ediacaran assemblages in Australia (Zang and Walter, 1992), Scandinavia (Vidal, 1990), eastern Siberia (Moczydłowska et al., 1993), and the Lesser Himalaya (Tiwari and Knoll, 1994). On the basis of chemo- and biostratigraphic correlations with better-dated Neoproterozoic successions elsewhere in the world, Knoll and Xiao (1999) suggested that the depositional age of the Doushantuo Formation is between 555 and 590 Ma.

A BROADER PICTURE OF PROTEROZOIC CARBONACEOUS MACROFOSSILS

Hofmann (1992, 1994) reviewed Proterozoic occurrences of macroscopic carbonaceous remains and classified them into 13 family-level morphological categories. Palaeoproterozoic carbonaceous fossils are of low diversity, but include forms such as *Grypania spiralis* (Han and Runnegar, 1992), which has also been reported from Mesoproterozoic deposits (Walter et al., 1990; Kumar, 1995); putative vendotaenids; and chuarids (Hofmann and Chen, 1981; Zhu and Chen, 1995; Yan and Liu, 1997). Mesoproterozoic carbonaceous fossils are known from more occurrences, but display only slightly greater diversity than their Palaeoproterozoic counterparts (Hofmann, 1992). In contrast, Neoproterozoic carbonaceous fossils occur in much greater abundance and morphological diversity (Hofmann, 1994). Early Neoproterozoic megafossils include *Chuaria*, *Tawuia*, *Longfengshania*, *Sinosabellidites*, *Pararenicola*, *Protorenicola*, and other compressions whose phylogenetic interpretations remain controversial. Macroscopic compressions in later Neoproterozoic and Early-Middle Cambrian rocks are still more diverse and include unambiguously branching forms (Walcott, 1919; Conway Morris and Robison, 1988; Mao et al., 1994; Chen et al., 1996; Steiner and Fatka, 1996). In broad outline, this macrofossil record is consistent with micropaleontological evidence suggesting that major algal clades had begun to diverge by the beginning of the Neoproterozoic Era (Knoll, 1992a; Woods et al., 1998; Xiao et al., 1998a, 1998b; Porter and Knoll, 2000; Butterfield, 2000).

A number of authors have commented on the over-representation of Burgess-Shale-type preservation in Lower and Middle Cambrian rocks relative to younger strata (Aronson, 1992; Allison and Briggs, 1993; Butterfield, 1995). On a broader time scale, however, it appears that Burgess-Shale-type preservation became increasingly abundant through the Proterozoic and culminated in the Early-Middle Cambrian before declining sharply. The apparent increase (in both diversity and abundance; see Hofmann, 1992, 1994) of carbonaceous macrofossils through the Proterozoic Eon is likely a result of combined biological and environmental evolution. In the Paleo- and Mesoproterozoic eras, microbial mats and sea-floor precipitates dominate proximal portions of (mostly rimmed) platforms (Grotzinger, 1989; Grotzinger and Kasting, 1993; Knoll and Sergeev, 1995; Kah and Knoll, 1996); carbonaceous fossils (planktonic, at least in part) are best represented in shales deposited in more off-shore settings (Knoll et al., 1991; Butterfield and Chandler, 1992). With the diversification of benthic seaweeds (as evidenced by the Miaohe and Lantian biotas) and the decreasing importance of both stromatolites (Awramik, 1992) and sea-floor precipitates (Grotzinger and Kasting, 1993; Kah and Knoll, 1996; Grotzinger and Knoll, 1999), ramp-like platforms became more important in the late Neoproterozoic

1991; Evans et al., 2000). In contrast, the post-glacial Doushantuo and Dengying Formations developed across the Yangtze Platform and regional correlations based on bio- and chemostratigraphy are widely accepted.

In the Yangtze Gorges area, the Doushantuo Formation comprises a ca. 200-m-thick succession of cherty carbonates and variably phosphatic black shales deposited during the development of two stratigraphic sequences (Fig. 1; see detailed discussions in Zhao et al., 1985, 1988; Steiner, 1994; Ding et al., 1996; Wang et al., 1998; Xiao et al., 1998a; Zhang et al., 1998). Carbonaceous and siliceous shales in the uppermost unit of the formation at Miaohe and elsewhere developed during marine transgression across a low-relief platform (Wang et al., 1998). The shales are organic rich (TOC up to 5.3 percent) and extremely fine-laminated (mm-scale). They are interpreted as having been deposited in a quiet, subtidal environment, likely within a restricted basin (Xiao et al., 1998a; Wang et al., 1998). In its entirety, the upper shale member is more than 20 m thick, but well-preserved macrofossils are restricted to a 2-m interval near the base of the shale member. Fossils were sealed off from obliterating microorganisms by burial beneath thin layers of clay. The upper Doushantuo shale unit is conformably overlain by dolomitic grainstones of the lower Dengying Formation.

The Dengying Formation contains a rare Ediacara-type fossil (*Paracharnia*; Sun, 1986) and vendotaenids (Steiner, 1994) in its middle member, *Cloudina*-like shelly fossils (*Sinotubulites baimatuoensis*) in its upper part (Chen et al., 1981), and basal Cambrian small shelly fossils at its top (Qian et al., 1979; Qian and

TABLE 1—List of taxa in the Miaohe carbonaceous biota and their possible interpretations.

Taxon name	Interpretation
Aggregatosphaera miaoheensis n. gen and sp.	Eukaryotic alga
Anomalophyton zhangzhongyingi	Eukaryotic alga
Baculiphyca taeniata	Eukaryotic alga
Beltanelliformis brunsae	Green alga or colonial cyanobacterium (Steiner, 1997)
Calyptrina striata	Scyphozoan or pogonophoran tube
Cucullus fraudulentus	Sponge or siphonous green alga?
Doushantuophyton lineare	Eukaryotic alga
Doushantuophyton quyuani	Eukaryotic alga
Enteromorphites siniansis	Eukaryotic alga
Glomulus filamentum	Filamentous cyanobacterium
Jiuqunaoella simplicis	Siphonous green alga?
Konglingiphyton erecta	Eukaryotic alga
Liulingjitaenia alloplecta	Siphonous green alga?
Longifuniculum dissolutum	Filamentous cyanobacterium or eukaryotic alga?
Miaohephyton bifurcatum	Eukaryotic alga (possibly brown?)
Protoconites minor	Scyphozoan tube or eukaryotic alga?
Sinocylindra yunnanensis	Filamentous cyanobacterium or eukaryotic alga?
Sinospongia chenjunyuani	Sponge, cnidarian or siphonous green alga
Sinospongia typica	Sponge, cnidarian or siphonous green alga
Siphonophycus solidum	Filamentous cyanobacterium
Unnamed forms (Fig. 10.4–10.21)	Eukaryotic algae
Putative trace fossil (Fig. 10.22–10.24)	Pseudofossil (questionable trace fossil?)
Putative bilaterian metazoan (Fig. 11)	Bilaterian (highly speculative)
Other species (not described in this paper, but possibly exist in the Miaohe biota)	
Doushantuophyton rigidulum (Ding et al., pl. 14, fig. 11)	Eukaryotic alga
Rugosilina farciminiforma (Ding et al., pl. 31, figs. 8–10)	Siphonous green alga
Unnamed forms (Steiner, 1994, pl. 12, figs. 12–14)	Cyanobacterium

(Knoll and Sergeev, 1995). Thus, both the abundance of macroscopic organisms and the geological opportunities for their preservation as compressions expanded in the later Neoproterozoic and Early-Middle Cambrian. The decline of Burgess-Shale-type preservation thereafter has been explained in the context of increasing bioturbation (Allison and Briggs, 1993) and changing clay-organic interaction (Butterfield, 1995). These two hypotheses are not necessarily mutually exclusive. Increasing bioturbation may have also caused a habitat shift of marine seaweeds: initially moderate (Ediacaran) and eventually intensive (early Paleozoic) bioturbation may have rendered the soft level-bottom an unstable substrate for benthic seaweeds, relegating them to more rocky substrates where most seaweeds live in the present day. The Miaohe biota, therefore, represents a terminal Neoproterozoic taphonomic window that is comparable in preservational style and quality to the Cambrian Burgess Shale, facilitating a taphonomically-controlled comparison of the two assemblages.

THE DIVERSITY AND PALEOBIOLOGICAL IMPLICATIONS OF MIAOHE FOSSILS

As detailed in the systematic paleontology section, the macroscopic compression biota at Miaohe comprises some twenty distinct taxa, most of them multicellular algae (Table 1). Miaohe compressions preserve morphological characters such as holdfasts, dichotomous branching, apical meristematic growth, and reproductive structures that occur uniquely in multicellular eukaryotic algae. Doushantuo carbonaceous and phosphatized algal fossils (Zhang, 1989; Zhang and Yuan, 1992; Xiao et al., 1998b; Yuan and Hofmann, 1998; Zhang et al., 1998), along with other Proterozoic algal fossils such as *Proterocladus* (Butterfield et al., 1994), *Bangiomorpha* (Butterfield, 2000), and *Palaeovaucheria* (Hermann, 1990), indicate that red, green, and heterokont algae began to diverge no later than the late Mesoproterozoic and achieved a fair measure of morphological-reproductive complexity and taxonomic diversity by the end of the Proterozoic Eon.

Particularly abundant in the terminal Proterozoic are fossils that likely represent coenocytic green algae belonging to derived branches of the ulvophyte clade. *Valonia*-like compressions (*Gesinella hunanensis*) occur in the late Neoproterozoic Liuchapo Formation in Hunan (Steiner, 1994). Some of the most distinctive fossils at Miaohe—centimeter-scale compressions of spheres assigned to *Beltanelliformis brunsae*—are here interpreted in terms of the attached, spherical gametophyte produced by the caulerpalean green alga *Derbesia* (described as the distinct genus *Halicystis* in older literature; Fritsch, 1965a, 1965b; Eckhardt et al., 1986). Reasons for this interpretation are detailed in the systematic paleontology section. The principal implication of this interpretation is that some of the small spheroidal casts and molds found in canonical Ediacaran fossil assemblages may be algae rather than cnidarian-grade animals.

A few Miaohe taxa, including *Calyptrina*, *Cucullus*, *Jiuqunaoella*, *Sinospongia*, and *Protoconites*, have been interpreted as possible metazoans by various authors. *Jiuqunaoella simplicis*, *Sinospongia typica*, and *Calyptrina striata* have been interpreted either as annelid worms or vermiform animals (Chen and Xiao, 1991; Chen et al., 1994b; Li *in* Ding et al., 1996), mostly based on transverse structures interpreted as metameric segmentation and on poorly preserved structures interpreted as cephalization. Such interpretations are unconvincing. Structures interpreted as head and setae (Li *in* Ding et al., 1996) are likely preservational artefacts. Transverse structures in *Jiuqunaoella simplicis* are very faint and irregular, more likely to be folds on tubular structures than body segments (Steiner, 1994). Transverse marks in *Sinospongia typica* are more regular but, again, appear to be folds or wrinkles. *Sinospongia chenjunyuani* and *Cucullus fraudulentus* have been interpreted as fossil sponges (Chen and Xiao, 1992; Chen et al., 1994b; Li *in* Ding et al., 1996). We cannot exclude the possibility of a sponge interpretation for *S. chenjunyuani* or *C. fraudulentus*, but no convincing sponge spicules have been found in association with these fossils, and alternative algal interpretations are possible.

Calyptrina striata is characterized by regularly and widely spaced transverse organic bands and has been interpreted as a possible worm or pogonophoran tube (Sokolov, 1967, 1997; Chen

et al., 1994b). Specimens in our collections support the interpretation of this fossil as a cylindrical tube that grew at the apical end, episodically thickening to form flange-like structures. Such a growth pattern does call to mind worm tubes (as well as the Ediacaran skeletal fossil *Cloudina*), and it is not a pattern easily reconciled with algal morphogenesis. Nonetheless, *C. striata* does not necessarily record a bilaterian body plan. It could easily be an organic sheath of the type formed by strobilating cnidarian scyphopolyps (Werner, 1966). Like *Beltanelliformis*, *Calyptrina* occurs in the lowermost part the Ediacaran Redkino succession on the Russian Platform (Fedonkin, 1990, and personal commun., 1999).

Protoconites minor is another conical tube that could be of cnidarian origin. Certainly, its broad morphological similarity to the probably cnidarian Cambrian fossil *Cambrohytium* (Conway Morris and Robison, 1988) is consistent with such a suggestion; however, *Protoconites* specimens lack key features that give confidence to the interpretation of *Cambrohytium*.

Some irregular "string-of-beads"-like structures have been interpreted as metazoan trace fossils (Li and Ding *in* Ding et al., 1996). As discussed more fully in the systematic paleontology section, such structures may be pseudofossils. Finally, a single specimen of a ribbon-like carbonaceous compression (here described as "putative bilaterian metazoan") bears a dark organic trace that superficially resembles the digestive tract of a bilaterian. However, we are unable to exclude the alternative proposition that this dark organic trace is a taphonomic rather than biologic feature.

The absence of definitively bilaterian body plans at Miaohe is striking, standing in strong contrast to its younger taphonomic counterparts. Evidence for a Cambrian radiation of bilaterian body plans comes from trace, skeletal, and soft-bodied fossils. Interpretation of metazoan traces, and particularly bilaterian traces, is sometimes difficult and can be controversial (Brasier and McIlroy, 1998; Collins et al., 2000; Seilacher et al., 1998). Nonetheless, metazoan traces in the late Neoproterozoic are simple and relatively sparse, whereas their Cambrian counterparts are deeper penetrating, highly complex, and abundant. At a minimum, this suggests a behavioral and morphological breakthrough in the Early Cambrian (Crimes, 1994; Fedonkin, 1994). Bilaterian skeletal fossils are rare in upper Neoproterozoic rocks, but diversify markedly in the Early Cambrian. Insofar as skeletons are integral parts of some bilaterian body plans, this corroborates trace fossil occurrences in suggesting Cambrian body-plan diversification (Bengtson, 1994).

But what about bilaterians that neither burrow nor make mineralized skeletons? Almost all extant bilaterian body plans are represented in Early and Middle Cambrian soft-bodied Lagerstätten (Chen et al., 1996; Conway Morris, 1998a). It might be argued that their absence in terminal Proterozoic rocks reflects taphonomic circumstance as much as evolution; however, the very existence of the Maiohe biota requires a more nuanced articulation of *taphonomic bias for bilaterian absence*. The preservational quality of Miaohe algal fossils indicates a potential for the preservation of fine morphological details that is comparable to, if not better than, that of the Burgess Shale or Chengjiang. Metazoan cuticle commonly survives a degree of organic diagenesis that destroys algal tissues. Thus, selective destruction of bilaterian reamins can be entertained only within certain limits. It is possible that simple, flatworm-like bilaterians existed but left no mark on accumulating sediments. It is much less likely that cuticular remains such as arthropod exoskeletons were preferentially removed. The argument that an anoxic Miaohe seafloor precluded bilaterian colonization is contradicted by the observation that many Miaohe algae (which had aerobic metabolism) were preserved in place. And, there are no physical or paleobiological indicators of high

salinity or other environmental features that might have excluded animals.

At present, the South China assemblages are unique. Nonetheless, the sharp contrast in bilaterian megafossil diversity between the Miaohe and the Burgess Shale/Chengjiang biotas is fully consistent with the hypothesis that the Cambrian Explosion records bilaterian body-plan diversification as well as a behavioral breakthrough and skeletalization event.

The absence of macroscopic bilaterian fossils in the Miaohe biota is not inconsistent with molecular clock estimates of early protostome-deuterostome divergence (which are, themselves, highly divergent; Wray et al., 1996; Nikoh et al., 1997; Ayala et al., 1998; Bromham et al., 1998; Gu, 1998; Wang et al., 1999). As pointed out by a number of authors (Fortey et al., 1996; Knoll and Carroll, 1999; Valentine et al., 1999), the evolution of bilaterian body plans must postdate the cladogenetic separation of lineages leading to these animal phyla. It remains unclear how long the "lag-time" may have been (compare, for example, Bromham et al., 1998 and Conway Morris, 1998b) and whether the planktotrophic larvae of modern metazoans provide an appropriate model for the earliest bilaterians (Davidson et al., 1995; Peterson et al., 2000; Runnegar, 2000). Regardless, molecular clock estimates and developmental hypotheses like that of Davidson and colleagues spur paleontological research because they encourage us to focus on microscopic rather than macroscopic search images for the earliest bilaterians and preservational environments (e.g., phosphorites and phosphatic limestones) where such micrometazoans might be recovered (Zhang and Pratt, 1994; Bengtson and Yue, 1997; Xiao et al., 1998b; Yue and Bengtson, 1999).

COMMENTS ON THE SYSTEMATICS OF THE MIAOHE CARBONACEOUS MACROFOSSILS

In Proterozoic carbonaceous fossils, ultrastructural and biochemical characters are unavailable, and anatomical and reproductive structures are uncommon. Therefore, the classification of such remains is usually based solely on gross morphology. A simple form taxon, such as *Chuaria circularis*, may embrace a polyphyletic array of organisms that includes cyanobacteria as well as protists. More complex thalloid compressions may display morphologies that are localized within a given phylum but convergent among phyla. Nonetheless, morphology is what the record preserves, and discrete patterns of size, shape, and branching enable us to assess the taxonomic diversity and, in favorable cases, systematic affinities of Miaohe taxa.

Three issues, however, need to be addressed in dealing with the systematics of the carbonaceous Miaohe fossils. First, to a greater degree than most permineralized or skeletal remains, compression morphologies may be considerably modified by taphonomic processes. Soft-tissues can be compressed, overlapped, wrinkled, folded, twisted, bent, or torn during burial and compaction. Such preservational alteration adds to the difficulty of establishing a systematic framework for Miaohe fossils. As discussed below, many synonymous taxa are based on preservational artefacts.

Second, since most Miaohe carbonaceous remains are multicellular algae (Table 1), the tremendous developmental plasticity and intraspecific variation of some modern seaweeds (Fritsch, 1965a, 1965b) must be taken into account. For example, fortuitous branches or hairs are common in modern seaweeds; these features are easily observed, but they do not provide sound characters for taxonomic diagnosis. The approach followed in this paper is to restrict taxonomic circumscriptions to sets of characters observed repeatedly in populations.

A final issue is technical. Since few if any of the Miaohe macrofossils can be unambiguously identified as metazoans, we apply

ICBN rules in dealing with the systematics. ICBN rules were not strictly observed in some previous publications. For example, Chen and Xiao (1991) did not specify the repository of type specimens, violating ICBN article 37.5. In consequence, all new taxa erected by Chen and Xiao (1991), including *Doushantuophyton lineare* Chen, *Miaohephyton bifurcatum* Chen, *Jiuqunaoella simplicis* Chen, *Niuganmafeia obesa* Chen, and *Diaoyapolites longiconoidalis* Chen, are considered invalid (Steiner, 1994). Steiner (1994) validated *D. lineare* and *M. bifurcatum* by designating new type specimens. We follow Steiner's (1994) systematic practice in this paper.

SYSTEMATIC PALEONTOLOGY

All specimens described by Chen and Xiao (1991), as well as by Chen and Xiao (1992) and Chen et al. (1994), are permanently reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica. Specimens described by Ding et al. (1996) are identified by the prefix SM- and are reposited in the Xi'an Institute of Geology in Xi'an. The type specimen of *Enteromorphites sinensis* is currently reposited in the Beijing Institute of Geology, Academia Sinica. Specimens illustrated in this paper are reposited in three institutions. Specimens with the prefix MH- are reposited in the Harvard University Herbaria Paleobotanical Collection under the collection number HUHPC 62707 (except the holotype of *Aggregatosphaera miaoheensis*, which has its own HUHPC number). Specimens with the prefixes HBM- and HM- are reposited in the Nanjing Institute of Geology and Palaeontology, while specimens with the prefix MMi are reposited in the Institute of Applied Geosciences at the Technical University of Berlin.

Genus AGGREGATOSPHAERA new genus

Type species.—*Aggregatosphaera miaoheensis* new genus and species, by monotypy.

Diagnosis.—Colonial organisms consisting of loosely packed, spherical cell-like vesicles. Colonies contain one to several spherical vesicles, preserved three-dimensionally. Vesicles generally 50–80 μm in diameter; colony size 150 to 200 μm. No evidence for a common envelope enclosing the colony.

Etymology.—From the Latin *aggregatus* and *sphaera*, with reference to the loosely packed aggregates of spherical bodies characteristic of this genus.

Discussion.—Its unique preservation and morphology differentiate *Aggregatosphaera* from other published genera (see below for more detailed discussion).

AGGREGATOSPHAERA MIAOHEENSIS new genus and species
Figure 2.9–2.14

Diagnosis.—As per genus.
Description.—Found on surface partings of laminated black shales, colonies contain one to six (rarely more) spherical cell-like vesicles preserved as three-dimensional external molds. Spherical vesicles 50–80 μm in diameter, loosely packed and generally in point contact. Colonies 150–200 μm in diameter. Coalified organic matter may be present in concave external molds.

Etymology.—After the village of Miaohe, in the Yangtze Gorges area, where Doushantuo carbonaceous compressions are exceptionally preserved.

Type.—The specimen illustrated in Figure 2.12 is designated as the holotype, reposited in the Harvard University Herbaria Paleobotanical Collection (HUHPC 62994; MH0030-31).

Material.—Seven specimens (MH0058-2, MH0168-1, MH0030-42, MH0030-31, MH0030-50, MH0030-54, MH0052-33), six of which are illustrated.

Occurrence.—Upper Doushantuo black shales at the village of Miaohe, about 70 km west of Yichang.

Discussion.—Four larger (ca. 500–2000 μm in diameter), compressed specimens (one of them is illustrated in Fig. 2.8) contain several dozen to as many as one hundred spherical units 20–40 μm in diameter within a single colony. These specimens share the same colonial organization as *Aggregatosphaera miaoheensis*, but are much larger and contain more but smaller spherical units. We are unsure of their relationship to *Aggregatosphaera miaoheensis*; at present, they are treated under an open nomenclature (genus and species undetermined).

Several Proterozoic taxa bear broad similarity to this new taxon, although different preservational modes complicate comparisons. *Chuaria* consists of large compressed spheroids, but does not occur in colonial aggregations and is not known to preserve a comparable degree of three-dimensionality. Phosphatized *Parapandorina* from Doushantuo phosphorites at Weng'an, interpreted first by Xue et al. (1995) as volvocacean green algae and later by Xiao et al. (1998b; Xiao and Knoll, 2000) as animal embryos, do contain multiple internal bodies; however, these are invariably enclosed within an envelope. In addition, the size of *Parapandorina* "colonies" remains statistically constant with repeated doubling of internal vesicle number. This does not appear to be the case in *Aggregatosphaera miaoheensis*. Finally, in early developmental stages, the internal bodies of *Parapandorina* are typically tightly compacted polyhedra rather than loosely aggregated spheroids.

The specimen illustrated in Figure 2.8 also bears at least superficial similarity to the phosphatized globular microfossil, *Megaclonophycus*, from Doushantuo phosphorites (Xue et al., 1995; Xiao and Knoll, 2000); however, this and other similar specimens in Doushantuo shales lack a common outer envelope. Silicified and phosphatized microfossils of *Paratetraphycus giganteus* (Zhang, 1985; Zhang et al., 1998) broadly resemble *A. miaoheensis*, but have smaller cell-like units (typically less than 20 μm in maximum diameter) that are tightly packed into planar tetrads.

Aggregated cell-like units also occur in a number of silicified coccoidal prokaryotes, such as *Tetraphycus*, *Sphaerophycus*, *Myxococcoides*, *Phanerosphaerops*, *Gloeodiniopsis*, and *Gleonobotrydion* (Schopf, 1968; Schopf and Blacic, 1971; Oehler, 1978; Knoll and Golubic, 1979; Horodyski and Donaldson, 1980; Hofmann and Jackson, 1991). However, cells in these genera are all much smaller than the spherical vesicles of *Aggregatosphaera miaoheensis*. Cell aggregates of organic-walled compressions (such as *Synsphaeridium*, *Symplassosphaeridium*, *Coneosphaera*; Hermann, 1990; Hofmann and Jackson, 1994) can be distinguished from *A. miaoheensis* by their smaller cell-like vesicles and typically tightly packed colonies. Organic vesicles of *Leiosphaeridia* (Jankauskas et al., 1989; Butterfield et al., 1994) can be as big as or even bigger than the spherical vesicles of *A. miaoheensis*; however, *Leiosphaeridia* is invariably flattened by compression and rarely forms consistent colonies. Organic compressions of *Sysphaera* (Ding et al., 1996) and *Beltanelliformis* (=*Beltanelloides*, Chen et al., 1993) from Doushantuo black shales in Miaohe may be reconstructed as colonies of organic-walled spherical bodies; however, individual spheroids (1–2 mm in *Sysphaera* and 5–15 mm in *Beltanelliformis*) are much larger than those of *A. miaoheensis*. In addition, there exist concentric folds in compressions of *Sysphaera* and *Beltanelliformis*.

The biological interpretation of *A. miaoheensis* is unclear. Its unusual preservation as a three-dimensional external mold suggests that it does not represent cyanobacterial envelopes or acritarch walls of standard strength and thickness. Reproductive bodies with greater mechanical strength, such as the cysts produced by dasycladalean green algae (Berger and Kaever, 1992), provide appropriate analogs—and perhaps homologs—for interpretation.
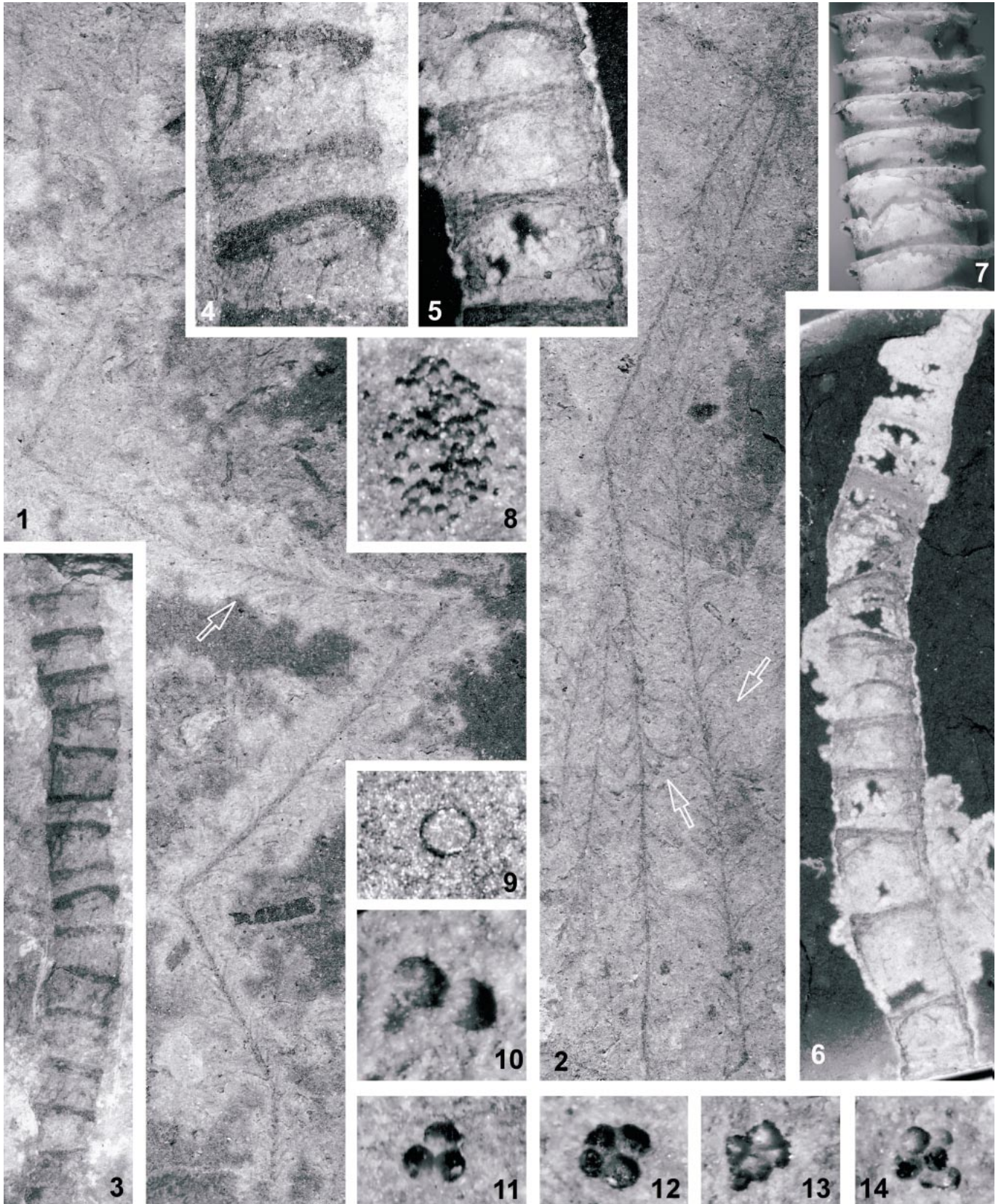
FIGURE 2—*1–2, Anomalophyton zhangzhongyingi.* Notice side branchlets (arrows). All five specimens (one illustrated in *1,* four in *2*) preserved on one slab were designated as holotypes, HBM-498, ×8; *3–6, Calyptrina striata. 3,* HBM-466, ×3; *4,* a magnified view of the middle part of *3,* ×8; *5,* a magnified view of the middle part of *6,* showing details of organic bands, HBM-522, ×4; *6,* HBM-522, ×2; *7,* a modern pogonophoran tube (courtesy of Harvard University Museum of Comparative Zoology), ×4; *8,* unnamed fossil with organizational similarity to *Aggregatosphaera*

Genus ANOMALOPHYTON Chen, Xiao, and Yuan, 1994, emend.

Axalga HU *in* DING ET AL., 1996.

Type species.—*Anomalophyton zhangzhongyingi* Chen, Xiao, and Yuan, 1994.

Emended diagnosis.—Thallus consists of a central axis and spirally arranged side branchlets. Side branchlets typically filamentous, rarely branching.

Discussion.—New observation of the type specimens reveals rare branchings in side branchlets. The emended diagnosis accommodates this rare character. No distinction was made between *Axalga* and *Anomalophyton* when Hu (*in* Ding et al., 1996) established the former genus; in our opinion, the two genera are synonymous, sharing a common axial organization with short, filamentous side branchlets, arranged helically.

ANOMALOPHYTON ZHANGZHONGYINGI Chen, Xiao, and Yuan, 1994, emend.
Figure 2.1, 2.2

Anomalophyton zhangzhongyingi CHEN, XIAO, AND YUAN, 1994, p. 392–393, pl. 1, figs. 1, 2; DING ET AL., 1996, p. 94, pl. 19, fig. 8.
Axalga brachyclada HU *in* DING ET AL., 1996, p. 89, pl. 19, fig. 6.
Axalga adaequata HU *in* DING ET AL., 1996, p. 89–90, pl. 19, fig. 5.

Emended diagnosis.—As per genus.
Description.—Main axis 20–40 mm long and 0.1–0.5 mm wide, cylindrical or slightly tapering toward apex. Side branchlets densely and helically arranged, less than 3 mm long and typically 0.01–0.05 mm wide. Side branchlets diverge from main axis at an angle of 20–50 degrees, with two to five side branchlets per mm length along main axis. No specimens with holdfast have been discovered.

Types.—Five specimens on two slabs (part and counterpart, HBM-498, Fig. 2.1, 2.2) were designated by Chen et al. (1994) as holotypes and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica. (The type of a non-vascular plant species may consist of more than one individual, as permitted under ICBN article 8.1).

Other materials examined.—SM$_I$-7-A-003, SM$_I$-7-A-131, SM$_I$-7-9-229.

Occurrence.—Upper Doushantuo black shales at the village of Miaohe, about 70 km west of Yichang.

Discussion.—Side branchlets of *Anomalophyton zhangzhongyingi* are similar in size to *Doushantuophyton* branches. However, side branchlets of *A. zhangzhongyingi* rarely dichotomize, indicating that *Doushantuophyton* cannot be fragmented parts of *A. zhangzhongyingi*. Two poorly preserved specimens identified as *Axalga brachyclada* and *A. adaequata* (Hu *in* Ding et al., 1996) are better ascribed to *A. zhangzhongyingi*; they differ from Chen et al.'s (1994) collection only in their slightly thicker (ca. 0.5 mm) and upward-tapering main axis and a few vague striae (likely to be diagenetic in origin) on the main axis.

The presence of spirally arranged side branchlets may indicate that peripheral primordia were important in the morphogenesis of *A. zhangzhongyingi*. Alternatively, the branchlets may represent inflated hairs, or paraphyses, as found on some phaeophyte sporophytes or rhodophyte tetrasporophytes. *Chorda filum* and *Dasya baillouviana* provide modern architectural analogs among the brown and red algae, respectively (Bold and Wynne, 1985).

Genus BACULIPHYCA Yuan, Li, and Chen, 1995, emend.

Diaoyapolites CHEN *in* CHEN AND XIAO, 1991, *nom. nud.*
Eoscytosiphon DING *in* DING ET AL., 1992, *nom. nud.*
Miaohenella DING *in* DING ET AL., 1992, *nom. nud.*

Type species.—*Baculiphyca taeniata* Yuan, Li, and Chen, 1995.

Emended diagnosis.—Unbranching clavate algal thallus up to 10 cm long, attached to its substrate by a basal rhizoidal or globose holdfast. Lower part of clavate structure is terete, upper part compressed to a lamina; upper termination squared or rounded.

Discussion.—*Diaoyapolites*, *Eoscytosiphon*, and *Miaohenella* are invalid taxa and are synonymous with *Baculiphyca* (see below). Yuan et al. (1995) restricted *Baculiphyca* to those clavate forms with rhizoidal holdfasts and thus differentiated it from *Diaoyapolites*, which has a globose holdfast according to Chen and Xiao (1991). However, rhizoids can be seen in the globose holdfast of *Diaoyapolites* (Chen and Xiao, 1991, pl. 4, fig. 3) and the lack of rhizoids in some of Chen and Xiao's (1991) materials is probably preservational. Therefore, the diagnosis of *Baculiphyca* is here broadened to include forms with both rhizoidal (e.g., Fig. 3.2) and globose (e.g., Fig. 3.6) holdfasts.

BACULIPHYCA TAENIATA Yuan, Li, and Chen, 1995, emend.
Figure 3

Baculiphyca taeniata YUAN, LI, AND CHEN, 1995, p. 97, pl. 2, figs. 2, 3, 5, 6.
Diaoyapolites longiconoidalis CHEN *in* CHEN AND XIAO, 1991, (*nom. nud.*), p. 320–321, pl. 3, fig. 6; pl. 4, figs. 1–6; CHEN AND XIAO, 1992, p. 519–520, text-fig. 3, pl. 3, figs. 1–5; CHEN, XIAO, AND YUAN, 1994, p. 394, pl. 2, figs. 1, 2; YUAN, LI, AND CHEN, 1995, p. 97–98, pl. 2, fig. 7.
Eoscytosiphon pristinus DING *in* DING ET AL., 1992, (*nom. nud.*), p. 109–110, pl. 19, figs. 1, 2; pl. 20, fig. 5.
Miaohenella typicura DING *in* DING ET AL., 1992, (*nom. nud.*), p. 110, pl. 19, fig. 3; pl. 20, fig. 1; DING ET AL., 1996, p. 86, pl. 26, figs. 1, 5, 6, 11, 12; pl. 27, figs. 8, 10, 11; pl. 28, figs. 1–4, 7–8.
Miaohenella eleganta DING *in* DING ET AL., 1992, (*nom. nud.*), p. 110–111, pl. 19, fig. 4; DING ET AL., 1996, p. 87, pl. 26, figs. 2, 10; pl. 28, fig. 6.
?*Gesinella gracilis* STEINER, 1994, p. 121–122, pl. 17, fig. 5; pl. 20, figs. 1–6; text-figs. 73, 74.
Miaohenella conica DING *in* DING ET AL., 1996, p. 87, pl. 26, fig. 3; pl. 27, figs. 1–4, 7.
*Miaohenella rhomba* DING *in* DING ET AL., 1996, p. 86, pl. 26, figs. 4, 9; pl. 27, fig. 6.
Miaohenella nana. DING *in* DING ET AL., 1996, p. 87, pl. 26, figs. 2, 10.

Emended diagnosis.—As per genus.
Description.—Elongate and unbranching clavate thallus up to 100 mm long and 4 mm wide. Holdfast typically bears fine (ca. 0.1–0.3 mm in diameter) filamentous rhizoids at its base. Lower part of blade typically 0.5–1.5 mm thick and three-dimensionally preserved; in some specimens, an ill-defined, terete stipe appears to be present (Fig. 3.1, 3.6–3.8). The stipe expands apically (angle of expansion less than 10 degrees) into an upper portion that is more blade-like, possibly reflecting lower mechanical strength during compression. Apical terminations rounded (Fig. 3.5) or squared (Fig. 3.1, 3.4, 3.6, 3.7). Squared termini may represent breakage—either biological or physical. Bent and folded thalli (Fig. 3.3, 3.5) indicate an originally flexible upper structure. Casts

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miaoheensis, MH0030-5, ×67. *9–14, Aggregatosphaera miaoheensis,* n. gen. and sp. *9,* MH0058-2 (one vesicle), ×67; *10,* MH0168-1 (two vesicles), ×67; *11,* MH0030-42 (three vesicles), ×67; *12,* MH0030-31 (four vesicles, holotype, HUHPC-62994), ×67; *13,* MH0030-50 ×67; *14,* MH0030-54, ×67.
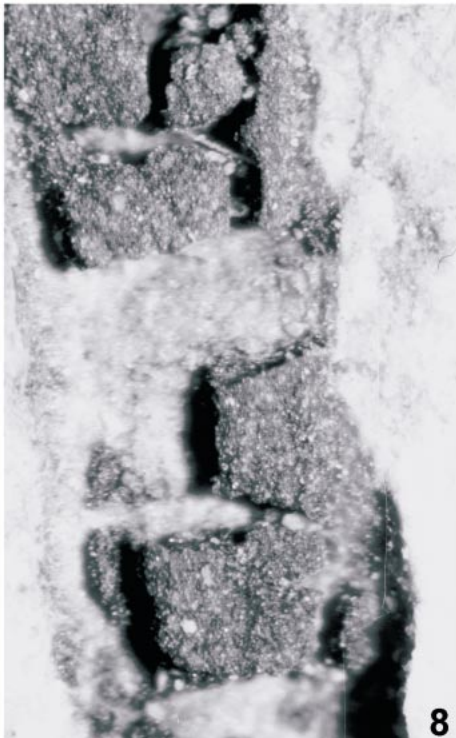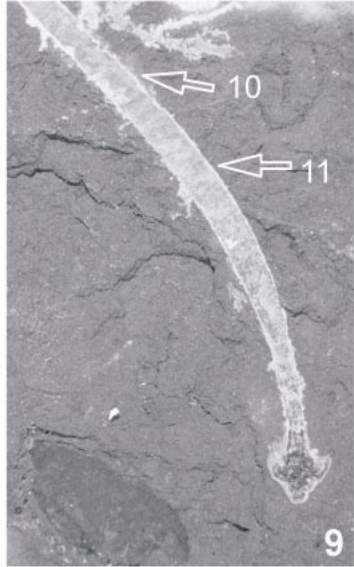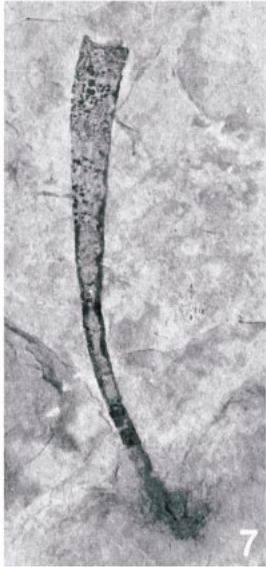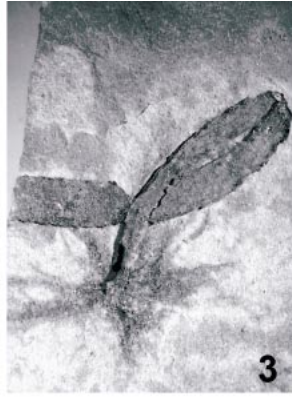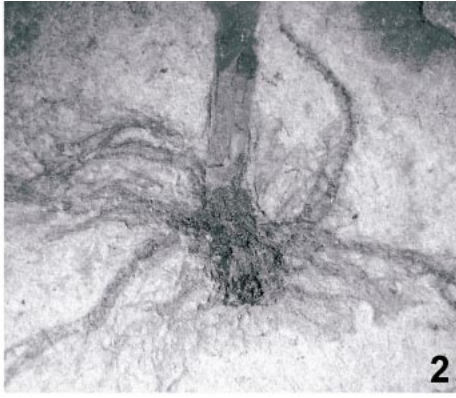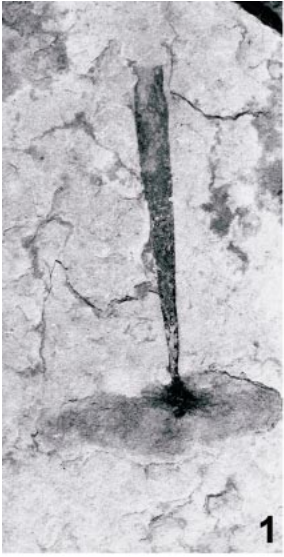
of stipes and lower blades contain organic matter (Fig. 3.8, commonly fractured during diagenesis) and in some cases pyrite (or iron hydroxides due to oxidation). Rosette (Fig. 3.10) and spherical microstructures (20–40 μm in diameter; Fig. 3.11) are found associated with iron hydroxides; such structures are probably due to secondary weathering.

Types.—Holotypes (HM9106 and HM9107; Fig. 3.2, 3.3) and paratypes (HM9108 and HM9109) were designated by Yuan et al. (1995) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0053-3, MH0186-1, MH0236 to MH0249, MH0255, MH0265, MH0295, MMi 018, MMi 020A, MMi 021B, MMi 033A, MMi 034A, MMi 036A, HBM-53, HBM-83, HBM-108, HBM-506, HBM-534, HBM3-27, HM9115. The Ding et al. (1992, 1996) collection has been examined by XY.

Occurrence.—Upper Doushantuo black shales at the village of Miaohe, about 70 km west of Yichang.

Discussion.—Despite its distinct morphology in the Miaohe biota, *Baculiphyca taeniata* has been a source of nomenclatural confusion. Chen and Xiao (1991) first established the genus *Diaoyapolites* and its monotypic species *D. longiconoidalis* for the morphotype described here. Unfortunately, Chen and Xiao (1991) did not specify the repository of the type specimens of *D. longiconoidalis*. Steiner (1994) considered this a violation of ICBN Article 37.5 and treated this morphotype as a new species placed with some uncertainty within the genus *Gesinella* as *?G. gracilis*. On the basis of a similar population from Miaohe, Ding et al. (1992) erected the genus *Miaohenella* with two constituent species (*M. eleganta* and type species *M. typicura*). No type specimens, however, were designated for *M. typicura* or *M. eleganta*; therefore, *Miaohenella*, *M. typicura*, and *M. eleganta* are invalid taxa. *Eoscytosiphon pristinus* (Ding et al., 1992), which is in our opinion part of the same population as *Baculiphyca taeniata*, is also invalid because no holotype was designated. *Baculiphyca taeniata* was considered to differ from *D. longiconoidalis* on the basis of its rhizoidal (or hairy) rather than globose holdfast (Yuan et al., 1995); however, the difference in holdfasts is probably preservational. Therefore, the correct generic name for the fossils described here is either *Gesinella* Steiner et al., 1992 or *Baculiphyca* Yuan et al., 1995. The Miaohe population described here is distinct from the diagnosis of *Gesinella* based on Liuchapo materials in Hunan (Steiner et al., 1992; Steiner, 1994); *Gesinella* shows evidence of episodic growth and bears lateral branches and papillate structures on its blade. [One specimen of *Baculiphyca taeniata* described by Chen et al. (1994b) may show episodic growth; this remains to be confirmed.] For these reasons, we choose to place the Miaohe populations in the genus *Baculiphyca*, within its type species *B. taeniata* whose diagnosis is emended here. Whatever name one may choose, the fossils described here under *Baculiphyca taeniata* represent an abundant, distinct component in the Miaohe biota.

Distinctions among the four described species of *Miaohenella* (*M. typicura*, *M. eleganta*, *M. conica*, *M. rhomba*) are based on diagenetic features (such as rosette structures and dehydration fractures filled with microquartz) or taphonomic variation in holdfast morphology (for example, spheroidal, rhomboidal, or conical holdfasts); we therefore consider these taxa to be conspecific.

Miaohenella nana is slightly shorter (6.5–14 mm in height) than typical *Baculiphyca taeniata*, but may represent broken specimens or juvenile individuals.

Some blades with no holdfast structures (e.g., Fig. 10.4, 10.6; *Miaohenella* sp. of Ding et al., 1992; aff. *Gesinella gracilis* of Steiner, 1994) are probably incomplete specimens of *Baculiphyca taeniata*. Others, however, appear to be completely preserved (e.g., Fig. 10.7); such specimens are here placed in open nomenclature.

The presence of a rhizoidal holdfast in association with bent and folded blades suggests that *B. taeniata* is a fossil alga. Further support for this interpretation comes from the three-dimensional preservation of the ill-defined, but mechanically reinforced stipe section. This construction is similar to that of some modern siphonous green algae, including the Siphonocladales and Dasycladales. Several species in these orders have weakly calcified lower thalli.

Genus BELTANELLIFORMIS Menner *in* Keller, Menner, Stepanov, and Chumakov, 1974

Type species.—*Beltanelliformis brunsae* Menner *in* Keller, Menner, Stepanov, and Chumakov, 1974.

Discussion.—This population provides another example of a simple and distinctive form with a complex taxonomic history. As originally used, *Beltanelliformis* refers to rounded, cup-like casts preserved three-dimensionally on the soles of sandy beds. In contrast, *Beltanelloides* has been employed for essentially two-dimensional compressions preserved on bedding planes in shale (Gnilovskaya et al., 1988; Fedonkin, 1990). *Beltanelliformis* has commonly been interpreted as a polypoid cnidarian, an interpretation embedded in the language of Menner's original diagnosis (English translation in Fedonkin, 1990). *Beltanelloides*, in turn, has been viewed as a spherical alga (Gnilovskaya et al., 1988). Despite preservational differences, however, *Beltanelliformis* and *Beltanelloides* share a common spherical morphology. This, and the observation that the genus *Beltanelloides* is an invalidly published genus, has led several commentators to propose that both forms be included within *Beltanelliformis* (Gureev, 1985; Narbonne and Hofmann, 1987; Steiner, 1994), a practice continued here.

BELTANELLIFORMIS BRUNSAE Menner *in* Keller, Menner, Stepanov, and Chumakov, 1974
Figure 4.1–4.3

Beltanelliformis brunsae MENNER, 1974, emend. STEINER, 1994, p. 94–95, pl. 12, figs. 1, 2; text-fig. 56. (and synonyms therein)
Beltanelloides podolicus ISTCHENKO, *in* CHEN, XIAO, AND YUAN, 1993, p. 313–314, pl. 1, figs. 1–4; YUAN, LI, AND CHEN, 1995, p. 97, pl. 1, fig. 1.
Sanxiamedusa pentamera DING, *in* DING ET AL., 1996, p. 103–104, pl. 38, figs. 1–3.
Maopingimedusa circularis DING, *in* DING ET AL., 1996, p. 104–105, pl. 38, fig. 5.
Palaeomedusa circvittata DING, *in* DING ET AL., 1996, p. 105–106, pl. 38, fig. 6; pl. 39, fig. 3.
Palaeomedusa polycarpa DING, *in* DING ET AL., 1996, p. 106, pl. 39, figs. 1, 2.

Description.—Circular carbonaceous fossils formed by the

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FIGURE 3—*Baculyphyca taeniata. 1,* squared upper termination, MH0241-1, ×1.4; *2–4,* rhizoidal holdfast and folded blade (in *3*); *2,* HM9106 (holotype), ×4; *3,* HM9107 (holotype), ×4; *4,* MH0242, ×4; *5–6,* bent blade; *5,* MH0265, ×4; *6,* MH0053-3, ×4; *7,* MH0238, ×3; *8* is a magnified view of the lower part in *7,* showing three-dimensional preservation of organic remains in lower blade, ×50; *9–11,* MH0240, *10* and *11* are magnified views of *9* (arrowed areas). Notice rosette (*10*) and microspheroidal (*11*) structures, both of which are probably diagenetic. *9,* ×1.4; *10,* ×14; *11,* ×50.
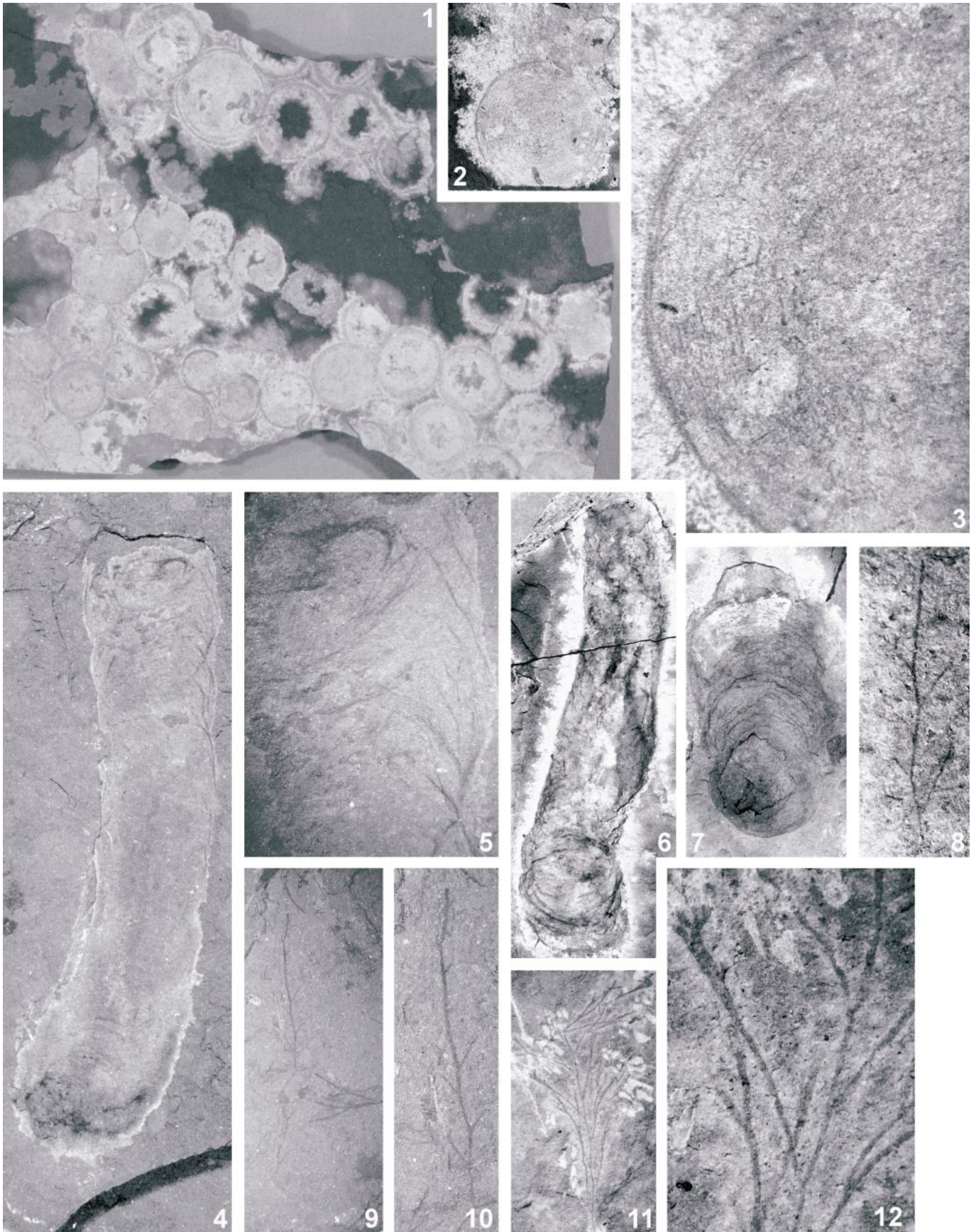
compression of thin-walled, originally spherical bodies; compressions with well-preserved concentric folds. Diameter 8–40 mm; marginal folds can be dense, ca. 4–6 per mm of radius (Fig. 4.3). Organic films are typically well preserved, although a few specimens are essentially shallow impressions.

Other material examined.—MH0030, MH0130-1, MH0195, MH0199-1, MH0201, MMi 063A, MMi 065B, HBM-469, HM9101, SM_I-7-4-8a, SM_I-7-4-12, SM_I-7-5a, SM_I-7-9a, SM_I-7-B-223a, SM_I-7-B-220a.

Occurrence.—The Redkino Series of the Russian Platform; the upper Windermere Supergroup of the Wernecke Mountains, Canada; Upper Doushantuo black shales at Miaohe.

Discussion.—Populations illustrated in Sokolov (1972), Gureev (1985), Narbonne and Hofmann (1987), Fedonkin (1990), and this paper display a facies-related continuum in degree of compression, from slightly compressed casts and molds in sandstone to completely flattened forms in shale. If, as appears likely, all are taphonomic variants of a single biological entity, the range of preservational forms places important constraints on what that entity could have been. The commonly gregarious but non-overlapping distribution of fossils on bedding planes indicates that the original organisms were benthic, presumably tethered to their substrates by a small holdfast. Doushantuo compressions may have originated as undifferentiated spheres. Casts and molds in populations from the Wernecke Mountains, northwestern Canada (Narbonne and Hofmann, 1987) confirm a spherical morphology for classical *Beltanelliformis brunsae* preserved in sandstone. Doushantuo compressions make it clear that these organisms had thin, flexible walls; whereas sandstone casts require that the original organisms had sufficient mechanical strength to retain their three-dimensional shape when inundated by sand.

One living organism that satisfies all morphological and preservational observations is the gametophytic thallus of the caulerpalean green alga *Derbesia*. Originally described as the distinct genus *Halicystis*, the *Derbesia* gametophyte is benthic, is attached by a minute holdfast, and has the right shape and size (Fritsch, 1965a, 1965b; Eckhardt et al., 1986). What's more, it is organized as a coenocytic film of cytoplasm within a elastic and strong wall and surrounding one or more large, fluid-filled vacuoles (Wheeler and Page, 1974). That is, the *Derbesia* gametophyte is like a water balloon, providing an explanation for the preservation of both shale compressions and sandstone casts. Some herbarium sheets of *Derbesia* gametophytes are strikingly similar to the Doushantuo fossils, folds and all.

Derbesia thus provides a strong candidate for the modern counterpart of *Beltanelliformis brunsae* and its many synonyms. More broadly, coenocytic algae provide better models for interpreting *B. brunsae* than do living cnidarians. If proposed synonymies are correct, it is likely that many of the simple, radially symmetric fossils found in Ediacaran biotas were algae, and not animals.

Both *Beltanelliformis brunsae* and *Chuaria circularis* are circular compressions with concentric folding, but *B. brunsae* is much larger and appears to have been benthic, unlike the type populations of *Chuaria circularis*. Ding (*in* Ding et al., 1996) further described *Sanxiamedusa* and *Maopingimedusa* from Doushantuo black shales at Miaohe and interpreted them as medusae based on claimed subumbrellar radial canals and tentacles. Such structures are barely visible and, in any event, appear to

have originated during diagenesis. A few closely appressed vesicles of *Sanxiamedusa pentamera* are hexagonal rather than circular in shape, but this reflects close packing and compression, not systematic variation. Therefore, *S. pentamera* and *Maopingimedusa circularis* are considered as junior synonyms of *Beltanelliformis brunsae*. Specimens assigned to *Palaeomedusa circvittata* and *P. polycarpa* from Doushantuo black shales at Miaohe (Ding et al., 1996) are also likely to be *B. brunsae*; proposed tentacular structures are superimposed on circular carbonaceous compressions (XY, personal examination).

Genus CALYPTRINA Sokolov, 1967

Type species.—*Calyptrina partita* Sokolov, 1965.

CALYPTRINA STRIATA Sokolov, 1967
Figure 2.3–2.6

Ziguivermites tentaculitiformis CHEN, XIAO, AND YUAN, 1994, *nom. nud.*, p. 397, pl. 3, figs. 9, 10; DING ET AL., 1996, p. 110, pl. 31, figs. 3, 4.
Ziguivermites. sp., DING ET AL., 1996, pl. 31, figs. 1, 6, 11.
Sinospongia tubulata. STEINER, 1994, p. 136–137, pl. 15, figs. 10–12, text-figs. 85, 85.

Description.—Carbonaceous remains 3–10 mm wide and up to 70 mm long (incomplete specimen). Flange- or lip-like transverse bands are about 1–2 mm in width and are separated by 2–6 mm intervening intervals.

Material examined.—MH0087, MH0088-2, MH0090, MH0092, MH0099, MMi 154, MMi 162, MMi 203B, HBM466, HBM522.

Occurrence.—The Redkino Series of the Russian Platform; Upper Doushantuo black shales at Miaohe.

Discussion.—Chen et al. (1994b) described a compressed tubular form with regularly spaced, transverse organic bands as *Ziguivermites tentaculitiformis* and interpreted it as a worm, but this species is invalid because no holotype was designated. In the same year, Steiner (1994) named a similar form *Sinospongia tubulata*. However, the Miaohe specimens are similar to, though slightly larger than, the holotype (3 mm wide) of *Calyptrina striata* from the Russian Platform (Sokolov, 1967, 1997). In his 1967 paper, Sokolov listed *C. striata* as occurring in drill core samples of the Lower Cambrian Baltic Series, but subsequent stratigraphic research indicates that the rocks come from the lowermost part of the terminal Proterozoic Redkino Series. In Russia, *Calyptrina* occurs in the same horizon as *Beltanelliformis* (=*Beltanelloides*) and beneath Redkino beds that contain diverse Ediacaran casts and molds.

Saarina, another tubular fossil from the Russian Platform, is characterized by articulated rings that extend beyond the tube to form collar-like flange structures, leading to its interpetation as a probable pogonophoran (Sokolov, 1967, 1997; see Fig. 2.7 for flange structures in modern pogonophorans). Transverse bands in *C. striata*, however, do not extend to form conspicuous flange structures; a pogonophoran interpretation for *C. striata* is therefore premature. An alternative interpretation is that *C. striata* preserves the episodically elongating organic sheath of a budding scyphozoan (e.g., *Stephanoscyphus*, Werner, 1966). The morphology of *Calyptrina* is less easily reconciled with known algal growth models.

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FIGURE 4—*1–3, Beltanelliformis brunsae. 1,* HM9101, ×1; *2,* MH0130-1, ×1.4; *3,* a magnified view of the left part of *2,* ×7; *4–7, Cucullus fraudulentus. 4,* HBM-354, ×1.4; *5,* a magnified view of upper right part of *4,* showing folded membranous wall, ×4; *6,* MH0129, ×0.9; *7,* MH0127, the lower part of this fossil penetrates several sediment laminae, ×1.4; *8–10, Doushantuophyton quyuani. 8,* MH0280-1, ×7; *9,* HBM-477 (holotype), ×4; *10,* a magnified view of the upper part of *9,* ×7; *11, 12, Doushantuophyton lineare. 11,* HBM-368, ×4; *12,* a magnified view of the middle left part of *11,* ×13.5.

Genus CUCULLUS Steiner, 1994
Doushantuospongia LI *in* DING ET AL., 1996.

Type species.—*Cucullus fraudulentus* Steiner, 1994.

Discussion.—Specimens described by Steiner (1994) as *Cucullus fraudulentus* bear only faint curvilinear folds. *Doushantuospongia* Li (*in* Ding et al., 1996) is similar in morphology, but has more pronounced folds. Given the range of variation seen in our Doushantuo population, we interpret these differences as preservational and therefore place *Doushantuospongia* in synonymy with *Cucullus*.

Cucullus also shares some features with *Sinospongia*: both have a membraneous, tubular or sac-like construction. *Sinospongia*, however, is generally smaller; has thicker walls; and bears pronounced, regularly transverse or reticulate folds.

CUCULLUS FRAUDULENTUS Steiner, 1994
Figure 4.4–4.7

Sinospongia hubeiensis CHEN ET AL., 1994b, p. 396, pl. 3, fig. 7; pl. 4, fig. 1. (*nom. nud.*).
Cucullus fraudulentus STEINER, 1994, p. 125–126, pl. 14, figs. 1–3, 7–9.
Cuculus fraudelentus [*sic*] DING ET AL., 1996, p. 119, pl. 35, figs. 5, 6.
Doushantuospongia cylindrica. LI *in* DING ET AL., 1996, p. 118, pl. 36, fig. 2.
Cuculus homotropus [*sic*] LI *in* DING ET AL., 1996, p. 119, pl. 36, figs. 3, 5; pl. 37, figs. 3, 6, 7.
Cuculus complexus [*sic*] LI *in* DING ET AL., 1996, p. 119, pl. 37, figs. 2, 8.

Description.—Elongate carbonaceous compressions, typically 10–30 mm wide and up to 150 mm long, bearing thin, curvilinear folds oriented sub-perpendicular to the main axis. In some specimens (Fig. 4.7), concentric elliptical marks appear at the lower end.

Types.—Holotype (MMi 130) was designated by Steiner (1994) and reposited in the Institute of Applied Geosciences at the Technical University of Berlin.

Other material examined.—MH0109-1, MH0111, MH0112, MH0113, MH0116, MH0120-1, MH0121, MH0122-1, MH0123, MH0124, MH0126, MH0127, MH0129, MH0136, MH0137, MMi 125B, MMi 130A, MMi 133, MMi 159B, MMi 161A, MMi 192A, HBM-354, HBM-471, HBM-573.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—*Cuculus homotropus* [*sic*], *C. complexus*, and *Doushantuospongia cylindrica* are subjective synonyms of *C. fraudulentus*. *Sinospongia hubeiensis* (Chen et al., 1994b) is also similar to *C. fraudulentus*; unfortunately, no type specimen was designated for *S. hubeiensis* (Chen et al., 1994b).

Cucullus fraudulentus was probably a benthic, tubular to sac-like organism with a rounded bottom and squared-off apex (Fig. 4.4). It is not clear whether it was hollow in life or open at the upper end, although both are possible. No conspicuous rhizoidal holdfast has been found, although the lower end of a few specimens (Fig. 4.7) is darkly colored and penetrates several sediment laminae. Possibly, *C. fraudulentus* achieved benthic stability by nestling into its substrate, a life style shared with some Ediacaran fossils (Steiner, 1994; Seilacher, 1999).

Some modern sponges and some living algae [for example, the siphonocladalean green algae *Bornetella*, *Boergesenia*, and *Valonia* (Tseng, 1983) or the red alga *Halosaccion* (Graham and Wilcox, 2000)] exhibit sacciform or tubular morphologies. No mineralized spicules or organic skeleton has been detected. Thus, at present, a poriferan interpretation can be neither ruled out nor unequivocally supported.

Genus DOUSHANTUOPHYTON Steiner, 1994
Doushantuophyton CHEN *in* CHEN AND XIAO, 1991, (*nom. nud.*).
Archaeocladiphyton CHEN, XIAO, AND YUAN, 1994.

Cilialga HU *in* DING ET AL., 1996.
Villosalga HU *in* DING ET AL., 1996.

Type species.—*Doushantuophyton lineare* Steiner, 1994, emend.

Other species.—*D. quyuani* (Chen, Xiao, Yuan, 1994) new combination, *D. rigidulum* Steiner, 1994.

Occurrence.—Upper Doushantuo black shales at Miaohe; the Lantian Formation at Lantian (Chen et al., 1994a; Steiner, 1994; Yuan et al., 1999).

Discussion.—Branching algal thalli are common in the Miaohe biota, comprising approximately a quarter of the observed species diversity. We recognize the following taxa: *Doushantuophyton lineare*, *D. quyuani*, *Enteromorphites siniansis*, *Miaohephyton bifurcatum*, and *Konglingiphyton erecta*. Additionally, *Anomalophyton zhangzhongyingi* has helically arranged side branchlets or hairs, and occasional dichotomies are found in *Longifuniculum dissolutum*. These taxa can be distinguished by differences in 1) overall thallus morphology (e.g., fan-shaped thallus in *Longifuniculum* and monopodial thallus in *Anomalophyton*); 2) branching pattern and frequency; 3) branch width; 4) change of branch width along the length of the thallus; and 5) diagnostic microstructures on thalli (e.g., compressed circular structures on some branches of *Miaohephyton*).

The hair-thin (typically between 0.04 and 0.2 mm wide), dichotomous or pseudomonopodial branches characteristic of *Doushantuophyton* easily differentiate it from other branching algal thalli of the Miaohe biota. This genus so far includes three species: *D. lineare* with a regular dichotomous thallus, *D. quyuani* (new combination) with a pseudomonopodial thallus that bears a zigzag or nearly straight main axis and dichotomous side branches, and *D. rigidulum* with infrequent dichotomies (typically near the base) and long, stiff branches.

Cilialga, *Villosalga*, and *Archaeocladiphyton* all have hair-like branches less than 0.1 mm wide. The two former genera have sparse dichotomies and stiff branches; thus, both are similar to *Doushantuophyton rigidulum*. *Archaeocladiphyton* has modified dichotomous or pseudomonopodial branches. All three genera fall within the diagnosis of *Doushantuophyton* (Steiner, 1994).

DOUSHANTUOPHYTON LINEARE Steiner, 1994, emend.
Figures 4.11, 4.12, 5.1–5.6

Doushantuophyton lineare STEINER, 1994, p. 112–113, pl. 18, figs. 1, 3, 7, 9, 10, 11, text-fig. 65.
Doushantuophyton lineare CHEN *in* CHEN AND XIAO, 1991, *nom. nud.*, p. 319, pl. 1, figs. 2, 3; pl. 3, figs. 1, 2; CHEN AND XIAO, 1992, p. 517, pl. 2, fig. 3; CHEN, XIAO, AND YUAN, 1994, p. 394, pl. 1, figs. 5, 6; pl. 2, fig. 8; pl. 3, fig. 3; YUAN, LI, AND CHEN, 1995, p. 98, pl. 2, fig. 1; DING ET AL., 1996, p. 77, pl. 15, figs. 1, 4, 6(?); pl. 19, figs. 2, 3, 4, 10.
Doushantuophyton sinuolatum HU *in* DING ET AL., 1996, p. 76–77, pl. 19, fig. 1.

Emended diagnosis.—A species of *Doushantuophyton* with regular dichotomies that are more or less uniformly distributed along branches. Internode and terminal segments are between 1 mm and 3 mm in length. Branches with constant width (Fig. 5.1–5.3) or slight expansion distally (Figs. 4.11–4.12, 5.4–5.5). In some specimens, constrictions occur at dichotomies (Figs. 4.12, 5.4–5.5). A few specimens are preserved three-dimensionally (Fig. 5.6).

Type.—Holotype (MMi 221A) was designated by Steiner (1994) and reposited in the Institute of Applied Geosciences at the Technical University of Berlin.

Other material examined.—MH0098-2, MH0143-2, MH0180-1, MH0204-3, MH0206-2, MH0210-1, MH0211-1, MH0213, MH0214, MH0215, MH0289-1, MMi 170B, MMi 171B, MMi
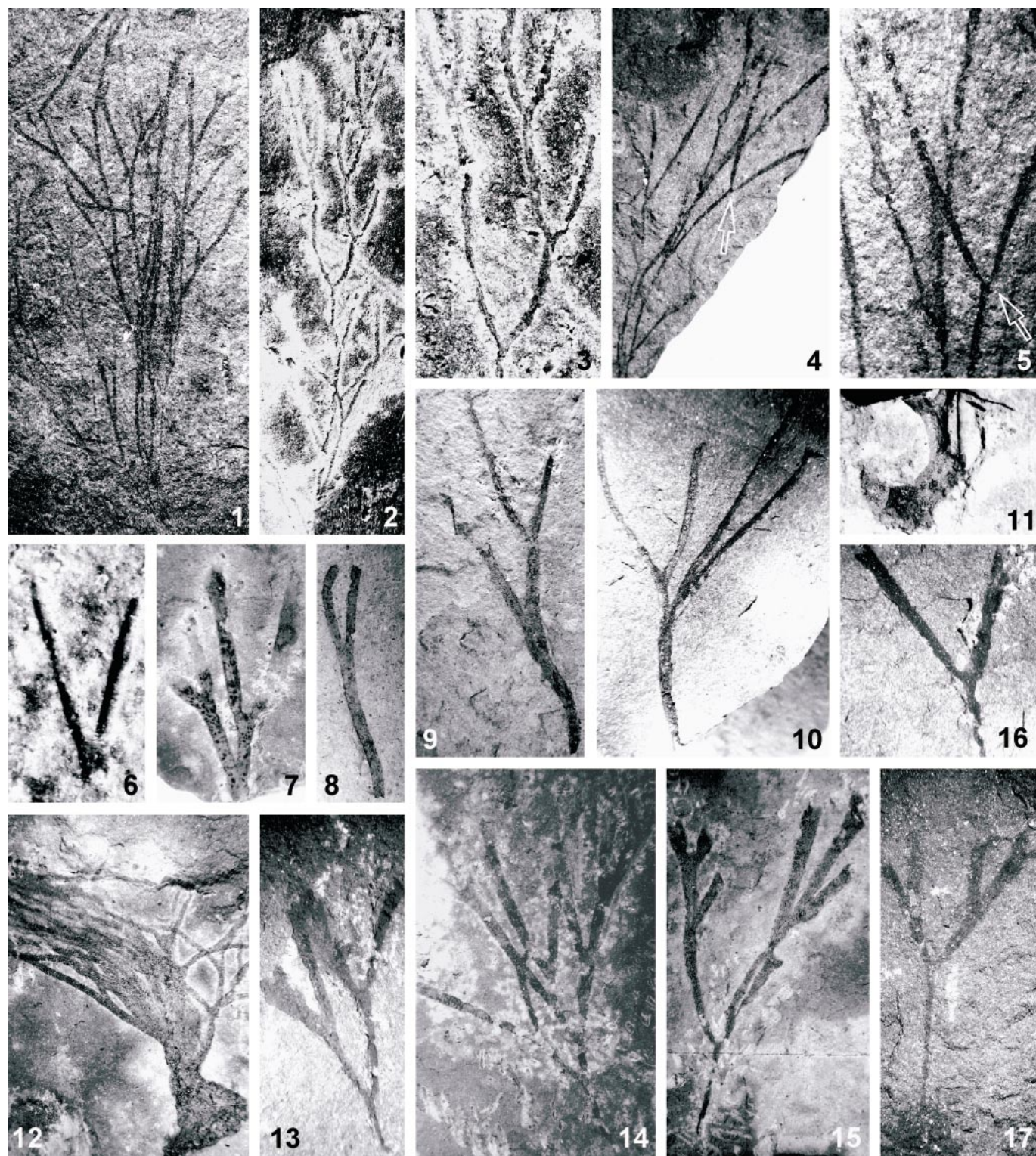
FIGURE 5—*1–6, Doushantuophyton lineare*. *1,* HBM-505, ×7.5; *2,* MH0180-1, ×9.5; *3,* a magnified view of the middle part of *2,* ×19; *4,* notice constriction at dichotomy (arrows in 4 and 5), MH0210-1, ×5; *5,* a magnified view of the middle right part of *4,* ×9.5; *6,* three-dimensional preservation, MH0289-1, ×38.5; *7–12, Enteromorphites siniansis*. *7,* MH0220, ×5; *8,* HBM-75, ×4; *9,* MH0223, ×4; *10,* MH0218, ×5; *11,* holdfast and lower thallus, showing three-dimensional preservation, MH0120-2, ×9.5; *12,* MH0221, ×4; *13–17, Konglingiphyton erecta*. *13,* MH0226, ×5; *14,* MMi 149, ×4; *15,* HM9123, ×4; *16,* MH0227, ×5; *17,* HBM-63 (holotype), ×4.

220B, HBM3-10, HBM3-12, HBM-368, HBM-505, HBM-491, HBM-514, HM9116.

Occurrence.—Upper Doushantuo black shales at Miaohe and the Lantian Formation at Lantian.

Discussion.—The diagnosis is emended to reflect new observations on constrictions at dichotomies; such constrictions may have biological significance, particularly at lower taxonomic levels.

This species differs from *Doushantuophyton rigidulum* in its more regular and frequent dichotomies and larger angle of branch divergence. *D. quyuani* can be distinguished from this species by its pseudomonopodial branching pattern. Middle Cambrian algal thalli identified as *Marpolia spissa* (Mao et al., 1994) have branch size comparable to *D. lineare* but less regular dichotomies. *Doushantuophyton sinuolatum* is similar to *D. lineare* in branch width and branching pattern and is therefore treated as a synonym of *D. lineare*.

Modern analogs of *Doushantuophyton lineare* can be found in a number of phyla. For example, the coenocytic green algae *Dichotomosiphon* and *Cladophora* both have thin, dichotomous branches, and *Dichotomosiphon* branches additionally have basal constrictions. That noted, at least broadly similar forms occur in ectocarpalean brown and florideophyte red algae.

DOUSHANTUOPHYTON QUYUANI (Chen, Xiao, and Yuan, 1994)
new combination
Figure 4.8–4.10

Doushantuophyton lineare STEINER, 1994 (*partim*), 1994, pl. 18, fig. 2.
Archaeocladiphyton quyuani CHEN, XIAO, AND YUAN, 1994, p. 393, pl. 2, fig. 3; DING ET AL., 1996, p. 93, pl. 18, fig. 3; pl. 19, fig. 7.
Archaeocladiphyton jinyugani CHEN, XIAO, AND YUAN, 1994, (*nom. nud.*), pl. 1, fig. 7; DING ET AL., 1996, p. 93, pl. 18, fig. 6.
Archaeocladiphyton dendriticum HU *in* DING ET AL., 1996, p. 93, pl. 17, fig. 2; pl. 18, figs. 4, 5.
Archaeocladiphyton sp., DING ET AL., 1996, pl. 17, fig. 4.

Diagnosis.—Thallus with pseudomonopodial branching pattern. Zigzag main axis clearly indicates side branches resulted from overtopping rather than peripheral primordia. Main axis can in some cases be nearly straight. Side branches rarely show dichotomous branching.

Basionym.—*Archaeocladiphyton quyuani* Chen, Xiao, and Yuan, 1994.

Type.—Holotype (HBM-477; Fig. 4.9, 4.10) was designated by Chen et al. (1994) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0280-1, MMi 181A, HBM-474.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—This species is accommodated by the diagnosis of *Doushantuophyton* (Steiner, 1994) but differs from the other two species of *Doushantuophyton* in its unique branching pattern. It is perhaps closely related to *D. lineare* (see Fig. 4.11, 4.12). One specimen identified as *D. lineare* by Steiner (1994, pl. 18, fig. 2) better fits in the diagnosis of *D. quyuani*. *Archaeocladiphyton jinyugani* appeared in Chen et al.'s (1994) figure captions, but no diagnosis was associated with it. Re-examination of the specimens regarded by Chen et al. (1994b) and Ding et al. (1996) as *A. jinyugani* suggests it is similar in every aspect to *D. quyuani*. Hu (*in* Ding et al., 1996) contended that *A. dendriticum* differs from *D. quyuani* in its straighter main axis and longer side branches. However, *A. dendriticum*, as well as *Archaeocladiphyton* sp. (Ding et al., 1996, pl. 17, fig. 4), are in fact comparable to the holotype of *D. quyuani*.

Genus ENTEROMORPHITES Zhu and Chen, 1984, emend., nom. corr.

Yemaomianiphyton CHEN AND XIAO, 1992.
Lanlingxiphyton CHEN AND XIAO, 1992.
Zhongbaodaophyton CHEN, XIAO, AND YUAN, 1994.
Capilliphyca YUAN, LI, AND CHEN, 1995.
Gymnogongrusoides HU *in* DING ET AL., 1996.
Yichangella HU *in* DING ET AL., 1996.
Polycladalga HU *in* DING ET AL., 1996.
non *Enteromorphites tubulosus* HU *in* DING ET AL., 1996.

Type species.—*Enteromorphites siniansis* Zhu and Chen, 1984, emend.

Original diagnosis.—Benthic thallus on hard substrates. Thallus may or may not branch. Internode length (length between successive branching points) increases distally. No significant change in width of successive branches. (Translated from Zhu and Chen, 1984).

Emended diagnosis.—Cm-scale thallus consisting of originally cylindrical axes that branch dichotomously one to as many as six times; broadly discoidal holdfast occasionally preserved. Axes typically 0.3 to 0.8 mm wide, changing little or tapering slightly toward apices. Thallus surface smooth.

Orthography.—Zhu and Chen (1984) established this generic name with reference to the modern green algal genus *Enteromorpha*; however, the original name was spelled "*Enteromophites.*" This was clearly a typographic error, as one of the original authors applied the name *Enteromorphites* in subsequent publications (Chen and Xiao, 1991, 1992). According to ICBN Article 60, the correct spelling of this genus should be *Enteromorphites*.

Occurrence.—Upper Doushantuo black shales at Miaohe and the Lantian Formation at Lantian (Yuan et al., 1999).

Discussion.—As discussed above, branching thalli of the Miaohe biota are differentiated according to thallus morphology, branching pattern, branch width and morphology, and other diagnostic microstructural features. The diagnosis of *Enteromorphites* has accordingly been emended to circumscribe this genus better. *Enteromorphites* differs from *Doushantuophyton* in its wider branches.

A number of genera can be treated as junior synonyms of *Enteromorphites*. Among them, *Yemaomianiphyton* (Chen and Xiao, 1992) was established based on incomplete specimens that are similar to *Enteromorphites* in branching morphology. Described "linear structures" in *Yemaomianiphyton bifurcatum* (Chen and Xiao, 1992, pl. 2, fig. 1) are likely to be diagenetic in origin. The one specimen published as *Yemaomianiphyton bifurcatum* by Steiner (1994, pl. 17, fig. 4) likely fits within *Enteromorphites siniansis*. Specimens identified as *Zhongbaodaophyton*, *Gymnogongrusoides*, *Yichangella*, *Polycladalga*, and *Capilliphyca* all fit comfortably within the emended diagnosis of *Enteromorphites*. One specimen described as *Enteromorphites tubulosus* (Ding et al., pl. 15, fig. 7), however, does not seem to be a dichotomous thallus; it appears to consist of bundled filaments.

ENTEROMORPHITES SINIANSIS Zhu and Chen, 1984, emend.
Figure 5.7–5.12

Enteromophites siniansis ZHU AND CHEN, 1984, p. 559–560, pl. 1, figs. 1, 2; STEINER, 1994, p. 117–118, fig. 70; YUAN, LI, AND CHEN, 1995, p. 98, pl. 2, fig. 8.
Enteromorphites siniansis ZHU AND CHEN, 1984; CHEN AND XIAO, 1991, p. 318–319, pl. 1, figs. 1, 4; CHEN AND XIAO, 1992, p. 518, pl. 2, fig. 4.
Lanlingxiphyton formosa CHEN AND XIAO, 1992, p. 517, pl. 4, fig. 1.
Yemaomianiphyton bifurcatum CHEN AND XIAO, 1992, p. 517–518, pl. 2, figs. 1, 2; STEINER, 1994, p. 123–124, pl. 17, fig. 4, text-fig. 75.
Zhongbaodaophyton crassa CHEN, XIAO, AND YUAN, 1994, p. 395, pl. 2, figs. 4, 5.

Capilliphyca flexa YUAN, LI, AND CHEN, 1995, p. 97, pl. 3, fig. 3.
Palaeocodium yichangicum HU *in* DING ET AL., 1996, p. 72–73, pl. 18, fig. 2.
Enteromorphites flexuosus HU *in* DING ET AL., 1996, p. 73, pl. 16, fig. 7.
Enteromorphites compressus HU *in* DING ET AL., 1996, p. 73–74, pl. 14, fig. 5.
Enteromorphites epicharis HU *in* DING ET AL., 1996, p. 74, pl. 17, fig. 3.
Enteromorphites sp., DING ET AL., 1996, p. 74, pl. 13, fig. 5; 16, fig. 3.
Gymnogongrusoides regularis HU *in* DING ET AL., 1996, p. 76, pl. 14, fig. 8.
Gymnogongrusoides irregularis HU *in* DING ET AL., 1996, p. 76, pl. 14, fig. 6.
Yichangella erecta HU *in* DING ET AL., 1996, p. 81, pl. 14, fig. 1.
Zhongbaodaophyton palmatum HU *in* DING ET AL., 1996, p. 81, pl. 16, fig. 1.
Polycladalga ramispina HU *in* DING ET AL., 1996, p. 82, pl. 16, fig. 2.

Emended diagnosis.—As per genus.
Description.—Most specimens are incomplete, with only two or three successive dichotomies. But more complete specimens that bear preserved holdfasts can have as many as 6 successive dichotomies (Fig. 5.12). Branches may in some cases be aborted or overtopped, resulting in short branches and irregular dichotomies. The branch width of 13 measured specimens ranges from 0.3 mm to 0.8 mm, typically decreasing toward the apex. The style of preservation indicates somewhat flexible branches in *Enteromorphites siniansis* (compare with more rigid branches in *Doushantuophyton rigidulum* and *Konglingiphyton erecta*); one specimen is preserved three-dimensionally, confirming the originally cylindrical nature of the axes (Fig. 5.11).
Type.—When they first described this species, Zhu and Chen (1984) illustrated only one specimen. According to ICBN Articles 8.4 and 9.1, this specimen must be accepted as the holotype; it is currently reposited in the Beijing Institute of Geology, Academia Sinica.
Other material examined.—MH0120-2, MH0218, MH0220, MH0221, MH0222, MH0223, MH0230, MH0241-2, MMi 176, MMi 218A, HBM-64, HBM-75, HBM-85, HBM-476, HBM-570, HBM3-5, HBM3-17, HBM-129, HM9120, HM9122. The Ding et al. (1996) collection has been examined by XY.
Occurrence.—Upper Doushantuo black shales at Miaohe and the Lantian Formation at Lantian (Yuan et al., 1999).
Discussion.—*Enteromorphites siniansis* differs from species of *Doushantuophyton* in its broader branches. It differs from *Konglingiphyton erecta* in that the branches of the latter species typically constrict at the base of dichotomies and expand distally. *Miaohephyton bifurcatum* is typically preserved as fragmented thalli and therefore has fewer than three successive dichotomies; it also has thinner branches (<0.5 mm) that may bear compressed circular structures (Xiao et al., 1998a). *E. siniansis* is also different from most branching algal thalli from the Burgess Shale (Walcott, 1919), such as *Yuknessia*, *Waputikia*, *Dalyia*, and *Waphia*—all of which have larger thalli and more complex branching systems.
As discussed above, *Yemaomianiphyton*, *Zhongbaodaophyton*, *Capilliphyca*, *Gymnogongrusoides*, *Yichangella*, and *Polycladalga* can all be regarded as synonyms of *Enteromorphites*. Furthermore, *Z. crassa*, *Z. palmatum*, *G. regularis*, *G. irregularis*, *Y. erecta*, and *P. ramispina* all have dichotomous branches that are about 0.3–0.6 mm in width and that taper gradually distally; they fit quite well within the circumscription of *Enteromorphites siniansis*. The only specimen of *P. ramispina* bears a few small, irregular branches, but is otherwise similar to *E. siniansis*; it does not merit a separate taxon. Three species of *Enteromorphites* established by Hu (*in* Ding et al., 1996), *E. flexuosus*, *E. compressus*, and *E. epicharis*, as well as *E.* sp. (Ding et al., 1996), are each based on a single specimen that clearly belongs to the same

population of *E. siniansis*. *Lanlingxiphyton formosa* and *Palaeocodium yichangicum* both have relatively rigid branches, but their branching pattern and branch width are similar to *E. siniansis*. *Capilliphyca flexa* (Yuan et al., 1995) was diagnosed as an unbranched, spaghetti-like thallus; however, closer examination of the only specimen assigned to *C. flexa* reveals that it is in fact a dichotomous branching thallus and can be considered as a junior synonym of *E. siniansis*.
Cylindrical, dichotomously branched axes are found widely among green, brown, and red algae. In the absence of more diagnostic features, the phylogenetic affinities of *Enteromorphites siniansis* cannot be further constrained.

Genus GLOMULUS Steiner, 1994

Longenema DING, 1996.

Type species.—*Glomulus filamentum* Steiner, 1994.
Occurrence.—Upper Doushantuo black shales at Miaohe.
Discussion.—Ding (*in* Ding et al., 1996) did not compare her new genus *Longenema* with *Glomulus*, but the features of these two taxa are the same.

GLOMULUS FILAMENTUM Steiner, 1994
Figure 6.1–6.6

Glomulus filamentum STEINER, 1994, p. 103–105, pl. 5, figs. 3, 4, 6, 7; pl. 13, figs. 4–7; pl. 15, fig. 10.
Longenema bellum [*sic*] DING *in* DING ET AL., 1996, p. 70–71, pl. 21, figs. 1–6.
?*Cometiphylla pinnata* DING *in* DING ET AL., 1996, p. 71–72, pl. 22, figs. 1, 2, 4, 5.

Description.—Irregular colonies consisting of numerous unbranched filaments, aggregated into multiple sinuous to folded bundles; colony size usually less than 5×5 mm (typically 1–2 mm in maximum dimension); filaments typically 5–10 μm in diameter, forming bundles less than 0.5 mm wide. Possible sheaths have been observed enclosing filaments (Steiner, 1994).
Type.—Holotype (MMi 086; Fig. 6.4) was designated by Steiner (1994) and reposited in the Institute of Applied Geosciences at the Technical University of Berlin.
Other material examined.—MH0012, MH0017, MH0051-1, MH0052-25, MH0052-29, MH0177-1, MH0177-2, MH0180-2, MH0207-1, MH0208-1, MMi 033A, MMi 093, MMi 171B.
*Occurrence.*—Upper Doushantuo black shales at Miaohe.
Discussion.—As discussed under the genus *Glomulus*, the only species of *Longenema*, *L. bella*, is regarded as synonymous with *Glomulus filamentum*. Aggregated filaments of *G. filamentum* are in some ways similar to those of the cyanobacterial sheath bundles *Polytrichoides lineatus* found widely in Proterozoic shales and cherts (Hermann, 1990; Knoll, 1992b). *Longifuniculum dissolutum* is another colonial filamentous cyanobacterium in the Miaohe biota, differentiated from *G. filamentum* by its larger, fan-shaped colonies and larger (ca. 40 μm in diameter) filaments.
Given the thin filaments and possible sheaths, *Glomulus filamentum* is likely to be a cyanobacterial colony, but trichomes that might seal the issue have not been observed.

Genus JIUQUNAOELLA Chen *in* Chen and Xiao, 1991, *ex* Chen Meng'e, emended and validated

Type species.—*Jiuqunaoella simplicis* Chen *in* Chen and Xiao, 1991, *ex* Chen Meng'e, emended and validated.
Emended diagnosis.—Carbonaceous remains preserved as ribbon-like compressions. Ribbons can be more or less straight, sinuous, twisted, or convoluted. Width of ribbon (typically 0.5 to 3 mm) remains more or less constant along its length, although apparent width may vary because of twisting and folding. Most
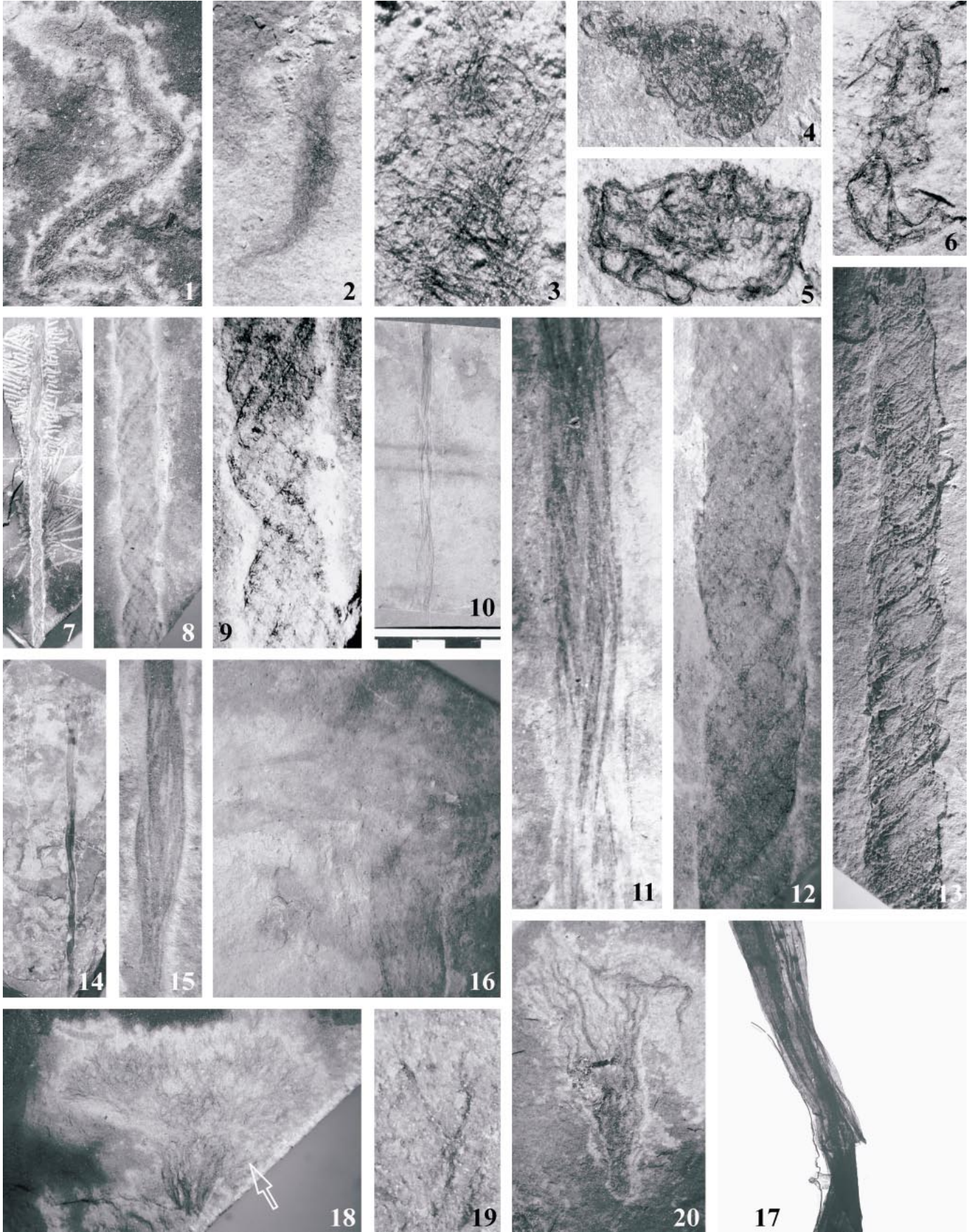
specimens with unornamented walls, although weakly developed, closely spaced transverse wrinkles may be present.

Orthography.—Chen (*in* Chen and Xiao, 1991) established *Jiuqunaoella* and its type species, *J. simplicis*. Unfortunately, no type repository was given (thus violating ICBN Article 37.5) for the type species; thus, *J. simplicis* Chen (*in* Chen and Xiao, 1991), as well as *Jiuqunaoella* Chen (*in* Chen and Xiao, 1991), are invalid and have no status. After consulting with Dr. Chen Meng'e, the original author, we know that the two type specimens of *J. simplicis* are reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica. By completion of the repository, *Jiuqunaoella* and *J. simplicis* are validated here and can be cited in the future as *Jiuqunaoella* Chen (*in* Xiao et al.), 2001 and *J. simplicis* Chen (*in* Xiao et al.), 2001, according to ICBN Article 46.6, Note 2, Ex. 23.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—The diagnosis is emended to accommodate convoluted ribbon-like compressions later published under *Jiuqunaoella simplicis* by Chen et al. (1994).

Rugosilina farciminiforma (Li *in* Ding et al., 1996) is also a ribbon-like compression in the Miaohe biota that is similar in size and gross morphology to *Jiuqunaoella simplicis*, but it differs from *J. simplicis* in its rare but well-preserved, straight septum-like structures and possible side branches. It remains possible that the type specimens of *J. simplicis* may be poorly preserved specimens assignable to *R. farciminiforma*; for the present, however, the two taxa are retained.

Jiuqunaoella simplicis Chen *in* Chen and Xiao, 1991, *ex*
Chen Meng'e, emended and validated
Figures 7.2–7.4, 8.1

Jiuqunaoella simplicis Chen *in* Chen and Xiao, 1991, *nom. nud.*, p. 320, pl. 5, fig. 6; pl. 6, figs. 1, 2; Chen, Xiao, and Yuan, 1994, p. 396–397, pl. 4, figs. 7–9; Ding et al., 1996, p. 112, pl. 32, fig. 5; pl. 33, figs. 1, 4, 10; pl. 34, fig. 11.
Vendotaenia sp., Yuan, Li, and Chen, 1995, p. 98, pl. 2, fig. 9.
Jiuqunaoella convoluta Li *in* Ding et al., 1996, p. 112, pl. 33, figs. 2, 3.
Jiuqunaoella minia Li *in* Ding et al., 1996, p. 112–113, pl. 32, fig. 6.
Jiuqunaoella sp., Ding et al., 1996, pl. 34, fig. 6.
non Jiuqunaoella simplicis Chen *in* Chen and Xiao, 1991, *nom. nud.* Chen and Xiao, 1992, p. 520, pl. 1, fig. 7; pl. 5, fig. 7. (? =*Sinospongia*).

Emended diagnosis.—As per genus.

Description.—Ribbon-like compressions; width between 0.5 and 3 mm, length up to a few cm. Ribbon may twist and fold. Some specimens bear vague, discontinuous, and closely spaced transverse wrinkles.

Type.—Chen and Xiao (1991) designated two specimens (HBM3-1a, b) as holotypes. Although it is permitted under ICBM Article 8.1 to designate multiple specimens as holotypes, it is strongly recommended to designate a single specimen as the holotype. Since *Jiuqunaoella simplicis* is validated here, a single specimen (HBM3-1a) is chosen as the holotype. It is reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0143-2, MH0150, MH151, MH0152, MH153, MH0167, MH0303-1, MMi 163B, HBM3-1b, HBM3-30, HBM-501, HBM-533, HBM-552, HM9127.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—*Jiuqunaoella simplicis* differs from *Sinospongia* in its generally smaller size (width generally less than 3 mm) and lack of conspicuous ornamentation (see below for description of *Sinospongia* species). However, the lower part of *Sinospongia typica* may lack conspicuous markings (e.g., Fig. 8.7) and, in fragmentary form, might resemble *J. simplicis*. That noted, the featureless lower part of *Sinospongia typica* is generally short and expands distally in width. Thus, most *J. simplicis* specimens, especially the convoluted ones (Chen et al., 1994b, pl. 4, fig. 9; Ding et al., 1996, pl. 33, fig. 2) are unlikely to be fragmented parts of *Sinospongia*.

Sinuous cord-like ribbons of *Sinocylindra yunnanensis* in the Miaohe biota are thinner (about 0.3 mm in width), smoother, and more uniform in width than *Jiuqunaoella simplicis* ribbons. *Vendotaenia* and *Tyrasotaenia* are both somewhat longer and thinner than *J. simplicis*. Well-preserved specimens of *V. antiqua* also display longitudinal striations and other microstructural features not observed in *J. simplicis* (Vidal, 1989; Gnilovskaya, 1990). *Jiuqunaoella convoluta* and *J. minia* (Li *in* Ding et al., 1996) represent convoluted and relatively thin (ca. 0.5 mm wide) ribbons that fit well within the emended diagnosis of *J. simplicis* (see Chen et al., 1994b). Two Doushantuo specimens identified as *Vendotaenia* sp. (Yuan et al., 1995) and *Jiuqunaoella* sp. (Ding et al., 1996) can also be classified as *J. simplicis*.

A lack of completely preserved specimens hampers paleobiological interpretation of *J. simplicis*. On the basis of available materials, *J. simplicis* can tentatively be reconstructed as a sausage-like cylindrical tube, similar to some coenocytic green algae. The faint transverse markings found on some specimens have been cited as evidence for an affinity with annelids or other segmented metazoans (Chen and Xiao, 1991; Li *in* Ding et al., 1996); however, these features appear to be wrinkles introduced during compression.

Genus Konglingiphyton Chen and Xiao, 1992, emend.

Palaeoscinaia Hu *in* Ding et al., 1996.
Ramalga Hu *in* Ding et al., 1996.

Type species.—*Konglingiphyton erecta* Chen and Xiao, 1992, emend.

Emended diagnosis.—Dichotomously branching algal thallus, with two or more dichotomies typically present. Constrictions can be present at base of branches. Width of branch segments gradually increases distally; branches 0.1–0.2 mm wide at the narrowest point and up to 1 mm just below dichotomy.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—The diagnosis is emended to include the new observation of basal constrictions at dichotomies. This genus differs from other dichotomous thalli in the Miaohe biota in its distally expanding branches. Thalli of *Palaeoscinaia* and *Ramalga* (Ding et al., 1996) fit well within the definition of *Konglingiphyton*. Hu (*in* Ding et al., 1996) argued that *Palaeoscinaia* differs from *Konglingiphyton* in its more numerous dichotomies (up to six) and

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Figure 6—*1–6, Glomulus filamentum. 1,* MH0180-2, ×9; *2,* MH0051-1, ×9; *3,* a magnified view of the upper part of *2,* showing detail of filaments, ×35; *4,* MMi 086 (holotype), ×17.5; *5,* MH0177-2, ×17.5; *6,* MH0177-1, ×17.5; *7–16, Liulingjitaenia alloplecta. 7,* MH0102, ×0.9; *8,* a magnified view of the lower end of *7,* ×4.5; *9,* a magnified view of the lower end of *8,* ×9; *10,* MH0105-1, ×0.6; *11,* a magnified view of the upper half of *10,* ×4.5; *12,* MH0107B-6, ×9; *13,* MMi 207B, ×4.5; *14,* MH0104, ×0.6; *15,* a magnified view of the lower-middle part of *14,* ×4.5; *16,* a magnified view of the upper end of *14,* ×4.5; *17, Tyrasotaenia podolica* (from upper Vendian in the Russian Platform). Notice folded *Tyrasotaenia* walls. ×17.5; *18–20, Longifuniculum dissolutum. 18,* MH0189, ×4.5; *19,* a magnified view of the arrowed area in *18,* showing a branched filament, ×35; *20,* MH0206-1, ×4.5.
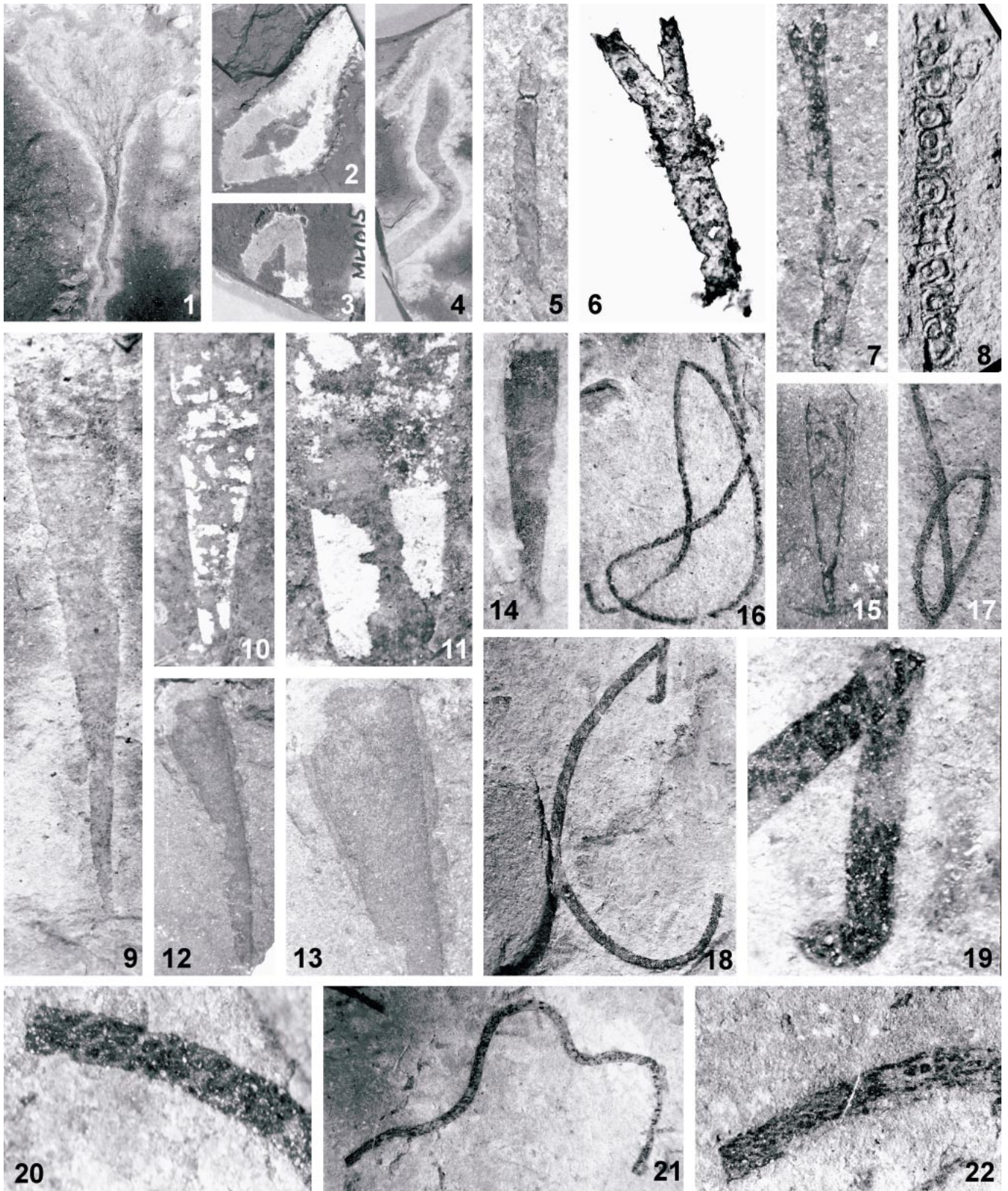
FIGURE 7—*1, Longifuniculum dissolutum*, MH0186-2, ×4.5; *2–4, Jiuqunaoella simplicis. 2,* MH0150, ×0.9; *3,* MH0151, ×0.9; *4,* MH0153, ×0.9; *5–8, Miaohephyton bifurcatum. 5,* MH0053-20, ×17.5; *6,* MH0042-m7-a, ×35; *7,* MMi 213A (holotype), ×35; *8,* MH0001, ×17.5; *9–11, 14–15, Protoconites minor. 9,* MH0304, ×9; *10,* this fossil is coated with white unidentified minerals, MH0306, ×4.5; *11,* a magnified view of the lower part of *10,* ×17.5; *14,* MH0104, ×4.5; *15,* MH0312, ×4.5; *12, 13,* a double-walled conical tube similar to *Protoconites minor. 12,* MH0307, ×4.5; *13,* a magnified view of the upper part of *12,* showing the double-walled construction, ×9; *16–22, Sinocylindra yunnanensis. 16,* MH0315,

the constrictions at dichotomy bases. However, variation in the dichotomy number is a result of post-mortem fragmentation. Basal constrictions at dichotomies are certainly present in specimens of *Konglingiphyton* (e.g., Chen et al., 1994b, pl. 2, figs. 6, 7). *Ramalga* (Hu *in* Ding et al., 1996) was established on the basis of a single specimen that bears irregular, dichotomous branches near its base but is otherwise very similar to the type specimen of *K. erecta*. One of us (XY), after careful examination of the only specimen of *Ramalga,* is convinced that the claimed irregular branches are actually a superimposed thallus of *Doushantuophyton lineare*. Therefore, we regard both *Palaeoscinaia* and *Ramalga* as junior synonyms of *Konglingiphyton*.

KONGLINGIPHYTON ERECTA Chen and Xiao, 1992, emend.
Figure 5.13–5.17

Konglingiphyton erecta CHEN AND XIAO, 1992, p. 516, pl. 1, fig. 5; CHEN, XIAO, AND YUAN, 1994, p. 394, pl. 2, figs. 6, 7; pl. 4, fig. 6; YUAN, LI, AND CHEN, 1995, p. 98, pl. 3, fig. 1; DING ET AL., 1996, p. 81, pl. 13, figs. 4, 6; pl. 15, fig. 2; pl. 18, fig. 8; STEINER, 1994, p. 115, pl. 18, figs. 6, 8, text-fig. 67.
Palaeocodium perelegans HU *in* DING ET AL., 1996, p. 72, pl. 16, fig. 9.
Palaeoscinaia ramulosa HU *in* DING ET AL., 1996, p. 75, pl. 14, figs. 2, 3, 10; pl. 16, fig. 8.
Palaeoscinaia constricta HU *in* DING ET AL., 1996, p. 75, pl. 14, fig. 4.
Ramalga sparsula HU *in* DING ET AL., 1996, p. 80, pl. 15, fig. 3.
Konglingiphyton regularum HU *in* DING ET AL., 1996, p. 80, pl. 14, fig. 12.
? *Tubulalga minuta* HU *in* DING ET AL., 1996, p. 92–93, pl. 14, fig. 9.
? *Furcatalga sinuosa* HU *in* DING ET AL., 1996, p. 93–94, pl. 16, figs. 5, 6.

Emended diagnosis.—As per genus.
Description.—Preserved thalli can be as long as 20 mm and bear as many as six successive dichotomies. Branches rarely bend and fold. Basal branches are typically 0.1–0.2 mm wide, but terminal branches can reach 1 mm in width. Branches may constrict at the base of dichotomies. Diverging angle varies between 10 and 40 degrees.
Type.—Holotype (HBM-63; Fig. 5.17) was designated by Chan and Xiao (1992) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.
Other material examined.—MH0119-4, MH0225, MH0226, MH0227, MH0228, MH0229, MH0231, MH0232, MH0314-3, MMi 149, MMi 178A, HBM-463, HBM-467, HBM-553, HM9123.
Occurrence.—Upper Doushantuo black shales at Miaohe.
Discussion.—*Palaeoscinaia constricta*, *P. ramulosa*, and *Ramalga sparsula* are essentially similar to *Konglingiphyton erecta* and are regarded as junior synonyms of *K. erecta*. *Konglingiphyton regularum* (Hu *in* Ding et al., 1996) is based on one specimen that differs from the type specimen of *K. erecta* only in its preservation of a holdfast. Clearly, this does not warrant a distinct morphospecies of *Konglingiphyton*. One specimen assigned to *Palaeocodium perelegans* (Hu *in* Ding et al., 1996), and, probably, poorly preserved specimens described as *Tubulalga minuta* and *Furcatalga sinuosa*, are all within the circumscription of *K. erecta*.

Dichotomous branching marked by basal constriction and distal expansion of branches is commonly observed among the florideophyte red algae, especially within the Nemaliales. For example, species of *Pseudogloiophloea*, *Scinaia*, and *Galaxaura* all

display gross morphological similarities with *K. erecta*. Thus, *Konglingiphyton* probably, although not definitively, belongs to the Rhodophyta.

Genus LIULINGJITAENIA Chen and Xiao, 1992, emend. Steiner, 1994

Eoulothrix DING, 1996.

Type species.—*Liulingjitaenia alloplecta* Chen and Xiao, 1992, emend. Steiner, 1994.
Occurrence.—Upper Doushantuo black shales at Miaohe.
Discussion.—In Chen and Xiao's (1992) original diagnosis, *Liulingjitaenia* was described as loose, rope-like bundles of filaments. Reexamination of a large population, however, shows clearly that *Liulingjitaenia* was a cylindrical tube, with plicated folds imparted by twisting and compression (Fig. 6.10–6.11, 6.13–6.15). Pleated folds on ribbons of *Vendotaenia* (see Gnilovskaya, 1990, pl. 33, fig. 6) and *Tyrasotaenia* (Fig. 6.17) provide a good model for these ''filamentous'' structures seen in *Liulingjitaenia*. Therefore, *Liulingjitaenia* is reconstructed as a membranous tubular organism. As discussed below, *Eoulothrix* is treated as a synonym of *Liulingjitaenia*.

LIULINGJITAENIA ALLOPLECTA Chen and Xiao, 1992, emend. Steiner, 1994
Figure 6.7–6.16

Liulingjitaenia alloplecta CHEN AND XIAO, 1992, p. 515, pl. 1, figs. 1–4; STEINER, 1994, p. 129–130, pl. 14, figs. 4–6.
Eoulothrix fibrillata DING *in* DING ET AL., 1996, p. 71, pl. 17, figs. 5–8.
Eoscytosiphon longitubulosum DING *in* DING ET AL., 1996, p. 88, pl. 22, figs. 3, 6.

Description.—Ribbon-like compressed tubes up to 200 mm long and 0.6–6.0 mm wide. Prominent plicate folds with a distinctive helical arrangement along tube axis.
Types.—Holotype (HBM-73) and paratype (HBM-89) were designated by Chen and Xiao (1992) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.
*Other material examined.*—MH0102, MH0103, MH0104, MH0105-1, MH0106, MH0107, MH0107B-3, 0107B-6, 0104, MMi 207A, MMi 207B, MMi 210A.
Occurrence.—Upper Doushantuo black shales at Miaohe.
Discussion.—Chen and Xiao (1992) illustrated two specimens of *Liulingjitaenia alloplecta*, one of which is loosely twisted and was designated as the holotype (Chen and Xiao, 1992, pl. 1, figs. 1, 2); the other, more tightly twisted specimen was designated as a paratype (Chen and Xiao, 1992, pl. 1, figs. 3, 4). Ding et al. (1996) argued that the two specimens illustrated by Chen and Xiao (1992) belong to two different taxa in the chlorophytic Ulotrichaceae and the phaeophytic Scytosiphonaceae, respectively. Ding et al. (1996) thus created two species, *Eoulothrix fibrillata* (for loosely twisted specimens) and *Eoscytosiphon longitubulosum* (for tightly twisted specimens). Ding et al.'s phylogenetic attributions are tenuous; their systematic determinations are unacceptable. First, *L. alloplecta*, with the holotype designated by Chen and Xiao (1992) as its nomenclatural type, should be preserved because it has priority over *Eoulothrix fibrillata*. Second, *Eoscytosiphon longitubulosum* does not at all conform to the diagnosis of *Eoscytosiphon* as typified by *E. pristinus* (Ding et al., 1992), regarded in this paper as a synonym of *Baculiphyca taeniata*. Ding et al. (1996) further suggested that loosely twisted

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×4.5; *17,* MMi 009, ×9; *18,* MH0025, ×9; *19,* a magnified view of the upper end of *18,* showing folded filament and rounded termination, ×35; *20,* a magnified view of the lower end of *18,* showing squared termination, ×35; *21,* MH0022, ×4.5; *22,* a magnified view of the left end of *21,* showing squared termination, ×17.5.
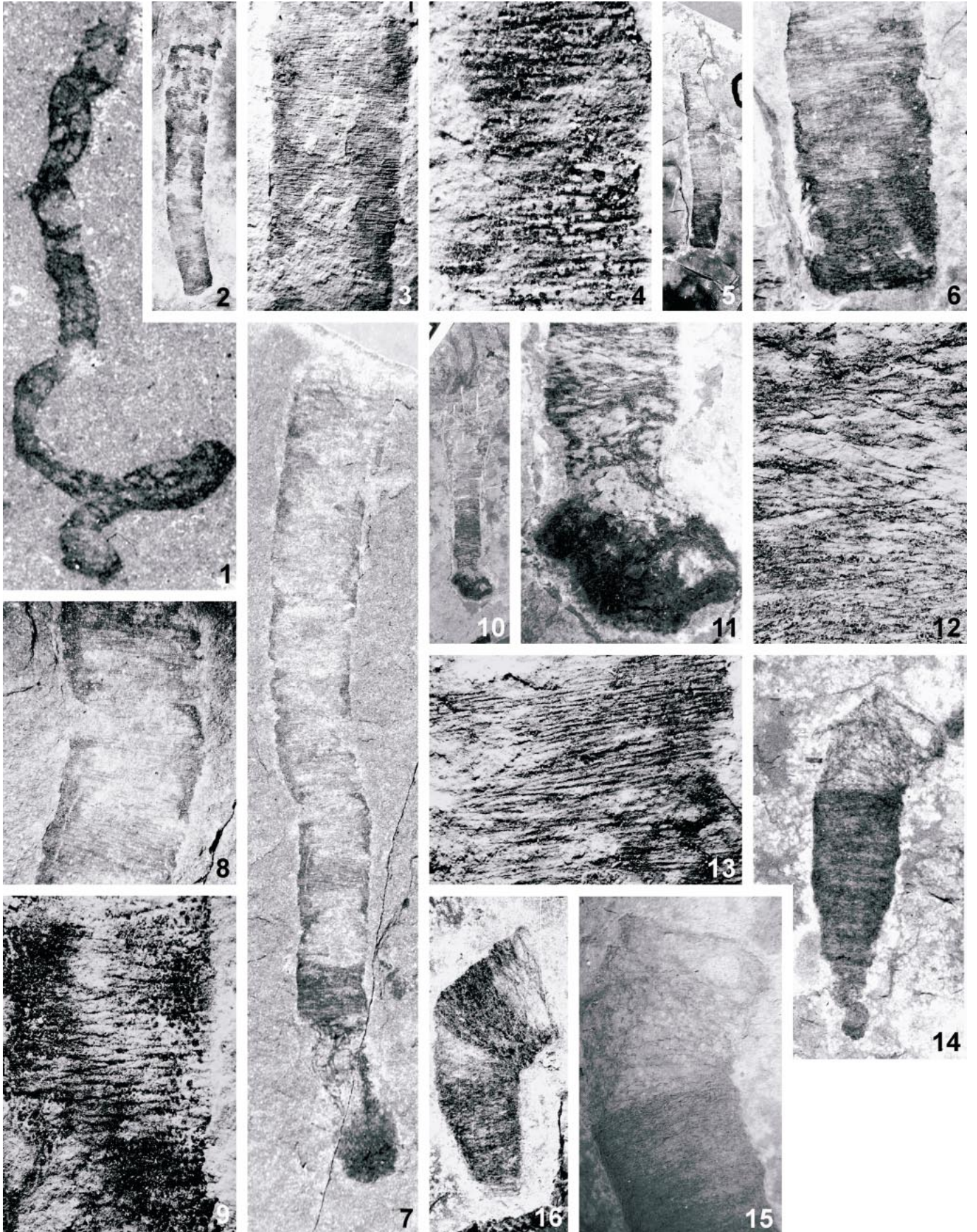
specimens consist of filaments, whereas tightly twisted ones have spiral thickenings on tubular walls. There is, however, a continuous spectrum from tightly to loosely twisted specimens in our collection. Furthermore, ''filamentous'' structures may actually be ruptured membranous walls. It is possible that there are spiral filamentous ribs on the tube surface to reinforce the structure; but firmer evidence is needed to support or reject this speculation. At present, we regard both *Eoulothrix fibrillata* and *Eoscytosiphon longitubulosum* as synonyms of *Liulingjitaenia alloplecta*.

No complete specimens of *Liulingjitaenia alloplecta* have been discovered, but its general morphology is clear: *L. alloplecta* was a long, thin tube with a strong but flexible bounding wall or membrane. Siphonaceous green algae provide possible morphological analogs. Tube-forming metazoans cannot be excluded, although evidence for animal affinities is scant.

Genus LONGIFUNICULUM Steiner, Erdtmann, and Chen, 1992

Guimenguania CHEN, XIAO, AND YUAN, 1994, *nom. nud.*
Sectoralga HU *in* DING ET AL., 1996.

Type species.—*Longifuniculum dissolutum* Steiner, Erdtmann, and Chen, 1992.
Occurrence.—Upper Doushantuo black shales at Miaohe and the Liuchapo Formation at Wenshanwan, Hunan Province, South China.
Discussion.—As will be discussed later, *Guimenguania* and *Sectoralga* are both considered as synonyms of *Longifuniculum*.

LONGIFUNICULUM DISSOLUTUM Steiner, Erdtmann, and Chen, 1992
Figures 6.18–6.20, 7.1

Longifuniculum dissolutum STEINER, ERDTMANN, AND CHEN, 1992, pl. 2, fig. 8, 8a; STEINER, 1994, p. 106–107, pl. 13, figs. 1–3, 8–10, text-fig. 61.
sp. undet., CHEN AND XIAO, 1992, pl. 4, fig. 2.
Guimenguania umbrellulatum CHEN, XIAO, AND YUAN, 1994, nom. nud., p. 394–395, pl. 3, figs. 1, 1a, 2, 2a.
Sectoralga typica HU *in* DING ET AL., 1996, p. 78–79, pl. 13, fig. 1.
Sectoralga supervoluta HU *in* DING ET AL., 1996, p. 79, pl. 12, fig. 1; pl. 13, fig. 8.
Sectoralga specialis HU *in* DING ET AL., 1996, p. 79, pl. 17, fig. 1.
Sectoralga umbellulata HU *in* DING ET AL., 1996, p. 79–80, pl. 12, figs. 3–7; pl. 13, figs. 3, 7.
Sectoralga grossa HU *in* DING ET AL., 1996, p. 80, pl. 13, fig. 2.
Sectoralga sp., DING ET AL., 1996, pl. 18, fig. 7.

Description.—Millimeter- to centimeter-scale, fan-shaped or dumbbell-shaped thallus consisting of a bundle of filaments that flare toward one or both ends. Filaments are typically tightly twisted and bundled, but may become separated in the middle part of the thallus. When the twisting is loosened and individual filaments become discernible, dichotomies can be clearly seen (Fig. 6.19). Filaments are less than 0.1 mm wide, typically 0.05 mm.
Types.—Holotype (Wen055; material from the Liuchapo Formation) was designated by Steiner et al. (1992) and reposited in the Institute of Applied Geosciences at the Technical University of Berlin.

Other material examined.—MH0165-1, MH0186-2, MH0187, MH0189, MH0206-1, MMi 016, MMi 017, HBM-65, HBM-534, HBM-542.
Occurrence.—Upper Doushantuo black shales at Miaohe and the Liuchapo Formation at Wenshanwan, Hunan Province, South China.
Discussion.—*Longifuniculum dissolutum* specimens from Miaohe closely resemble the type materials from the Liuchapo Formation (probably equivalent to the Dengying Formation) in Hunan Province (Steiner et al., 1992). The Liuchapo population has been interpreted as cyanobacterial colonies (Steiner et al., 1992). However, some Miaohe specimens contain rare but clear dichotomies (Fig. 6.19); whether such dichotomies are cyanobacterial false branching (Steiner et al., 1992) is unknown. Eukaryotic analogs include the ulvophyte green alga *Spongomorpha* (Graham and Wilcox, 2000).

The Miaohe specimens are broadly similar, at least in gross morphology, to the Middle Cambrian *Marpolia spissa*, a possible colonial cyanobacterium (Walcott, 1919; Satterthwait, 1976; Conway Morris and Robison, 1988). It is possible that continuing research will show *L. dissolutum* (and possibly *Glomulus filamentum* as well) to be a junior synonym of *M. spissa*.

Chen et al. (1994) published similar fossils from Miaohe under the genus *Guimenguania* and its single species *G. umbrellulatum*. No diagnosis, description, or type species were given for the genus *Guimenguania* (Chen et al., 1994b), although this may be rescued by assuming *G. umbrellulatum* as its type species (ICBN Article 37.2) and equating the diagnosis and description of the genus to those of its only constituent species (ICBN Article 42.1). Unfortunately, no holotype was specified for *G. umbrellulatum*. Therefore, both *Guimenguania* and *G. umbrellulatum* are invalid names.

Miaohe specimens described under the genus *Sectoralga* (Hu *in* Ding et al., 1996) are essentially the same as those described here under *Longifuniculum dissolutum*. If the Miaohe population is proved to be a taxon different from the Liuchapo population, then *Sectoralga* may be an appropriate genus name for the Miaohe population. The five species of *Sectoralga*, *S. grossa*, *S. supervoluta*, *S. specialis*, *S. typica*, and *S. umbellulata* (Hu *in* Ding et al., 1996), were established on the basis of dubious characters and insufficient specimens. Given the possibility that *L. dissolutum* may be a colonial cyanobacterium, some variation in colony form is to be expected. Therefore, we regard these variations as intraspecific and all five species of *Sectoralga*, as well as *Sectoralga* sp. (Ding et al., 1996, pl. 18, fig. 7), as synonyms of *L. dissolutum*.

Genus MIAOHEPHYTON Steiner, 1994, emend. Xiao, Knoll, and Yuan, 1998

Miaohephyton CHEN *in* CHEN AND XIAO, 1991, *nom. nud.*
Gracilogia DING *in* DING ET AL., 1992, *nom. nud.*

Type species.—*Miaohephyton bifurcatum* Steiner, 1994, emend. Xiao, Knoll, and Yuan, 1998
Occurrence.—Upper Doushantuo black shales at Miaohe.

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FIGURE 8—*1, Jiuqunaoella simplicis*, MMi 163B, ×3; *2–16, Sinospongia typica. 2,* MH0066, ×1.1; *3* and *4* are magnified views of *2,* showing details of transverse structures. *3,* ×4.5; *4,* ×17.5; *5,* MH0068-1, ×1.1; *6,* a magnified view of *5,* showing squared termination, ×4.5; *7,* note holdfast structure, MH0065, ×1.8; *8,* a magnified view of the middle part of *7,* showing transverse structures, ×4.5; *9,* note cross-cuttings of transverse structures in the middle, MH0251-2, ×17.5; *10,* note holdfast, MH0072, ×1.1; *11,* a magnified view of the holdfast structure in *10,* ×4.5; *12,* a magnified view of the upper part of *10,* showing cross-cuttings of transverse structures, ×9; *13,* details of transverse structures, MH0077, ×9; *14,* MMi 144A, ×1.8; *15,* a magnified view of the upper part of *14,* showing loosely arranged transverse structures at the upper end, ×3; *16,* a bending tubular fossil, MH0082-1, ×3.

MIAOHEPHYTON BIFURCATUM Steiner, 1994, emend. Xiao,
Knoll, and Yuan, 1998
Figure 7.5–7.8

Miaohephyton bifurcatum STEINER, 1994, emend. XIAO, KNOLL, AND YUAN, 1998, p. 1076, figs. 2–6 (except 6.1); and synonyms listed therein.

Type.—Holotype (MMi 213A; Fig. 7.7) was designated by Steiner (1994) and reposited in the Institute of Applied Geosciences at the Technical University of Berlin.

Other material examined.—MH0001, MH0002, MH0006, MH0010, MH0015, MH0028, MH0030-3, MH0030-17, MH0030-32, MH0031-1, MH0031-10, MH0031-14, MH0032-14, MH0033-7, MH0039-1, MH0052-27, MH0053-20, MH0042-m1, MH0042-m4, MH0042-m5, MH0042-m7-a, MH0042-m7-b, MH0042-m10, MH0042-m11-e, MH0042-m12-a, MH0042-m12-b, MH0042-m13, MH0042-m14-a, MH0042-m14-c, MH0053-20, MH0055-1, MH0058-3, MH0058-4, MH0063, MMi 081, MMi 082A, MMi 183, MMi 211B, HBM3-1a, HBM3-1b, HBM3-2, HBM3-3, HBM3-5, HBM3-6, HBM3-8, HBM3-9, HBM3-14a, HBM3-14b, HBM3-16a, HBM3-16b, HBM3-17.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—Xiao et al. (1998a) provided a detailed account of the morphology and development of *M. bifurcatum*. Apical and intercalary growth, dichotomous branching, fragmentation along pre-formed abscission surfaces, and wart-like conceptacles collectively distinguish this population and support its possible placement among the fucalean brown algae. Whatever their affinities, these small, ribbon-shaped fossils are the most abundant constituents of the Miaohe assemblage.

Genus PROTOCONITES Chen, Xiao, and Yuan, 1994, emend.

Type species.—*Protoconites minor* Chen, Xiao, and Yuan, 1994.

Emended diagnosis.—Small (typically less than 15 mm in height) conical compressions with one end pointed and the other apparently squared-off; no preserved holdfast structures. Angle of cone divergence 10–20 degrees. Smooth walls; no annulations or transverse markings.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—In their original diagnosis, Chen et al. (1994) noted annulations on *Protoconites*, but careful re-examination of both the type and new materials reveal no such features. Its small, featureless conical morphology and lack of holdfast structure distinguish *Protoconites* from other Miaohe fossils.

PROTOCONITES MINOR Chen, Xiao, and Yuan, 1994, emend.
Figure 7.9–7.11, 7.14–7.15

Protoconites minor CHEN, XIAO, AND YUAN, 1994, p. 397, pl. 4, figs. 10, 11; DING ET AL., 1996, pl. 33, fig. 9.

Emended diagnosis.—As per genus.

Description.—Smoothly conical tubes about 10 mm long, with a pointed apex that expands to a squared-off termination (possibly with an aperture). Tubes 0.2–0.4 mm in diameter at apex and up to 1.0–4.0 mm at aperture. Angle of divergence 10–20 degrees.

Types.—Holotype (HBM-496) and paratype (HBM-506) were designated by Chen et al. (1994) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0018, MH0104, MH0304, MH0305, MH0306, MH0307, MH0308, MH0309, MH0311, MH0312, MH0314-1.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—One unfortunately incomplete specimen (Fig. 7.12, 7.13; MH0307) shares the conical construction with other materials identified as *Protoconites minor*, but it preserves double

walls separated by 0.1–0.3 mm. This specimen is not formally classified as, but may be related to, *P. minor*.

Though much larger (30–50 mm long), the Middle Cambrian compression *Cambrorhytium major* (Conway Morris and Robison, 1988) and another species of *Cambrorhytium* from the Lower Cambrian Chengjiang biota (Chen and Zhou, 1997) share a broadly conical construction with *Protoconites minor*. *C. major* is further characterized by faint tentacle-like structures and transverse annulations. *C. major* has been interpreted as a possible scyphozoan cnidarian (Conway Morris and Robison, 1988), comparable to the sheaths that enclose budding polyps in coronate scyphozoans such as *Stephanoscyphus* (Werner, 1966). A comparable, and comparably tentative interpretation of *P. minor* is possible. Although broadly similar to some shelly fossils (hyoliths) in the Cambrian, *P. minor* lacks a mineralized skeleton. Another competing hypothesis, however, is that *P. minor* could be *Baculiphyca taeniata* at a juvenile stage. But, given its larger divergent angle and lack of any rhizoidal holdfast (a structure that typically appears early in benthic algal development), *P. minor* is more likely a distinct species from *B. taeniata*.

Genus SINOCYLINDRA Chen and Erdtmann, 1991

Type species.—*Sinocylindra yunnanensis* Chen and Erdtmann, 1991

Occurrence.—Upper Doushantuo black shales at Miaohe and the Qiongzhusi Formation at Chengjiang, Yunnan Province, South China.

SINOCYLINDRA YUNNANENSIS Chen and Erdtmann, 1991
Figure 7.16–7.22

Sinocylindra yunnanensis CHEN AND ERDTMANN, 1991, p. 73, pl. 2, fig. 5.

Description.—Smooth ribbons 0.2–0.35 mm wide and up to 40 mm long. Ribbons are flexible and can be folded (Fig. 7.18, 7.19). Terminations can be round (7.19) or square (Fig. 7.20, 7.22). No branching or holdfast structures are associated with these specimens.

Types.—Holotype (10854) was designated by Chen and Erdtmann (1991) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0022, MH0025, MH0031-4, MH0041-1, MH0042-1, MH0183-1, MH0183-2, MH0315, MMi 009.

Occurrence.—Upper Doushantuo black shales at Miaohe and the Qiongzhusi Formation at Chengjiang, Yunnan Province, South China.

Discussion.—These carbonaceous ribbons, in their living form, are likely to have been cylindrical. Their diameter is greater than all *Siphonophycus* species (<0.1 mm; Knoll et al., 1991; Butterfield et al., 1994) but smaller than *Jiuqunaoella simplicis*. *Sinocylindra yunnanensis* is similar in size to *Vendotaenia antiqua*, *Tyrasotaenia podolica*, and *Fusosquamula vlasovvi* in Vendian rocks of the East European Platform (Gnilovskaya et al., 1988), but it differs from the Vendian species in its long and smooth ribbon with regular width.

The simple morphology of these fossils precludes confident phylogenetic placement; comparably simple tubes can be found in all major clades of multicellular algae—for example, *Chaetomorpha* (green), *Nemalion* (red), and *Chorda* (brown). It appears unlikely, however, that such large and long filaments can be cyanobacteria. Hence *Sinocylindra yunnanensis* is kept separately from the genus *Siphonophycus* that is generally interpreted as cyanobacterial sheaths.

Genus SINOSPONGIA Chen *in* Chen and Xiao, 1992, emend.

Niuganmafeia CHEN *in* CHEN AND XIAO, 1991, *nom. nud.*
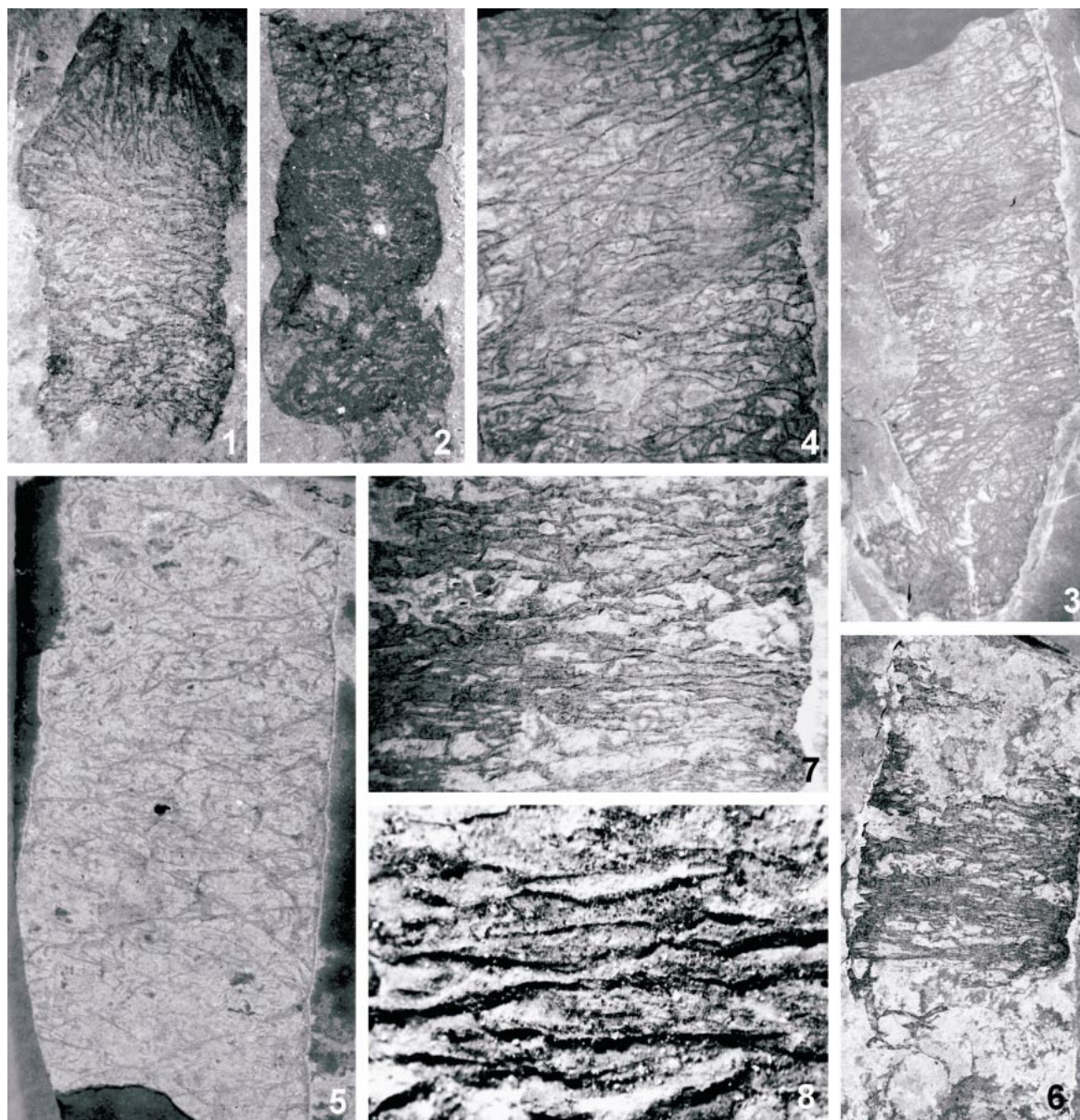*Xilinxiaella* Li *in* DING et al., 1996.

FIGURE 9—*Sinospongia chenjunyuani*. *1,* Notice vertical folding in the upper part, HBM-484, ×4; *2,* MMi 166A, ×4; *3,* HBM-126 (holotype), ×2; *4,* a magnified view of the upper right of *3,* showing reticulate structures, ×4; *5,* HBM-56 (paratype), ×2; *6,* MH0108, ×2; *7* and *8* are magnified views of the middle right of *6,* showing the nature of folding. *7,* ×4; *8,* ×20.

*Type species.*—*Sinospongia chenjunyuani* Chen (*in* Chen and Xiao), 1992, emend.

Emended diagnosis.—Carbonaceous compressions of benthic tubular organisms, bearing holdfasts and densely spaced, conspicuous transverse (*S. typica*) or reticulate structures (*S. chenjunyuani*). Compressions typically expand distally; maximum width generally greater than 3 mm and can be up to 3 cm. Lower part of the tube, where preserved, typically lacks distinct transverse features.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—Forms with dense transverse structures were first described by Chen and Xiao (1991) as *Niuganmafeia obesa* and interpreted as fossil worms. Unfortunately, no type repository was specified by Chen and Xiao (1991). *Niuganmafeia*, as well as its type species *N. obesa*, are therefore invalid (see Steiner, 1994). Forms with reticulate structures were described as *Sinospongia*

chenjunyuani (Chen and Xiao, 1992). Chen et al. (1994) also described a compressed tubular form with regularly spaced, transverse organic bands as *Ziguivermites tentaculitiformis*. Steiner (1994) broadened the diagnosis of *Sinospongia* to include forms that Chen and Xiao would call *Niuganmafeia obesa*, *Sinospongia chenjunyuani*, and *Ziguivermites tentaculitiformis*. He also synonymized *N. obesa* with *S. chenjunyuani* and established a new species *S. tubulata* that has a morphology similar to *Z. tentaculitiformis*. Later, Li (*in* Ding et al., 1996) described a number of species that are similar to *N. obesa*, including a new species of *Niuganmafeia*, *N. typica*.

As recognized by Steiner (1994), there are rare transitional forms between specimens bearing transverse (*Niuganmafeia obesa*) and reticulate (*Sinospongia chenjunyuani*) structures. Also, the lower parts of some *N. obesa* specimens bear no transverse structures (Fig. 8.7). However, *N. obesa* does represent a well-defined
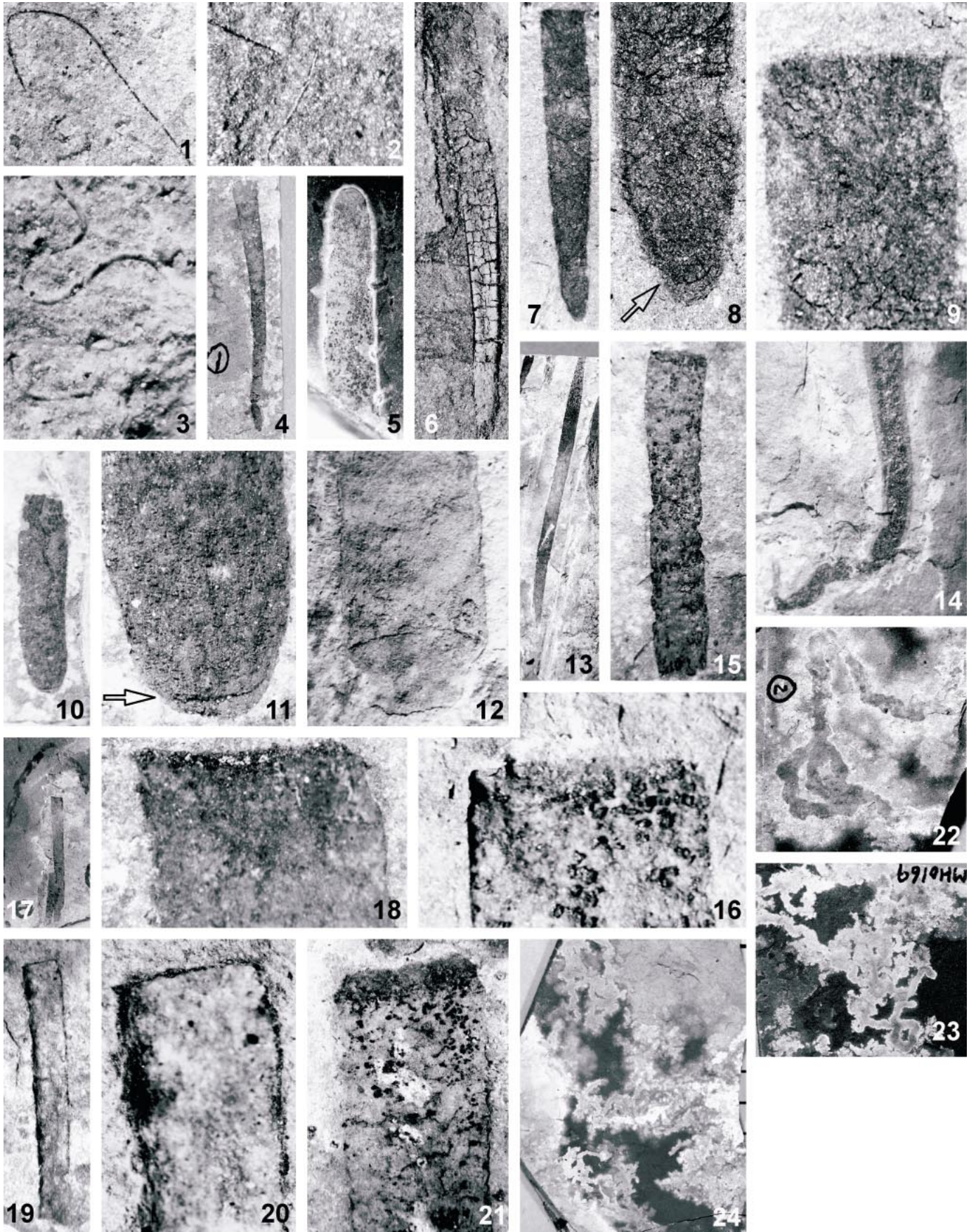
morphotype. Furthermore, *S. chenjunyuani* is based on incomplete type specimens and one cannot be sure whether these fragmented specimens of *S. chenjunyuani* are part of the *N. obesa* population in the Miaohe biota. Therefore, to preserve the probable underlying biology of transverse and reticulate structures, we prefer to keep these two morphotypes under separate names. Since *N. obesa* is an invalid name, we choose *N. typica* (Li *in* Ding et al., 1996) as a substitute for *N. obesa* but transfer *N. typica* to the genus *Sinospongia* because it is within the circumscription of *Sinospongia* as emended here.

Forms with regularly spaced transverse bands (i.e., *Ziguivermites tentaculitiformis* of Chen et al., 1994b, or *Sinospongia tubulata* of Steiner, 1994) represent a distinct morphology from *Sinospongia chenjunyuani* and *S. typica*. The transverse bands are likely biological rather than preservational. Such transverse bands resemble similar structures in *Calyptrina striata*, a tubular fossil from Vendian rocks of the Russian Platform interpreted as possible pogonophoran tubes (Sokolov, 1967). In light of this, Miaohe tubular compressions with distinct transverse bands are here described under *Calyptrina striata*, and the diagnosis of *Sinospongia* is modified to reflect these taxonomic emendations.

Two specimens identified as *Xilinxiaella bella* and *X. minuta* (Li *in* Ding et al., 1996) also bear densely arranged transverse markings and conform to the diagnosis of *S. typica* (see below).

Within the Miaohe biota, *Baculiphyca, Cucullus, Liulingjitaenia,* and *Protoconites* can also be reconstructed as tubular constructions. But none of them displays regular transverse or reticulate structures. Furthermore, *Liulingjitaenia* is characterized by its unique helical folding along thin tubes, and the wall of *Cucullus* is apparently much thinner and more delicate than *Sinospongia*.

SINOSPONGIA CHENJUNYUANI Chen in Chen and Xiao, 1992, emend.
Figure 9.1–9.8

Sinospongia chenjunyuani CHEN *in* CHEN AND XIAO, 1992, p. 518–519, pl. 6, figs. 1–4; STEINER, 1994, p. 134–135, pl. 15, fig. 4; DING ET AL., 1996, p. 116, pl. 35, fig. 4; pl. 36, fig. 1. (*partim*).
Sinospongia chenjunyuani Chen and Xiao [*sic*], 1992. CHEN, XIAO, AND YUAN, 1994, p. 396, pl. 3, figs. 4–6; pl. 4, fig. 2.
Sinospongia dictyoforma Li *in* DING ET AL., 1996, p. 116–117, pl. 35, figs. 2, 3.

Emended diagnosis.—Carbonaceous remains of a tubular organism, typically 5–20 mm wide and 50–150 mm long. Irregular transverse structures are commonly preserved as ridges and grooves (Fig. 9.8). These transverse structures typically anastomose to form a reticulate network with rhombic windows.

Description.—Incomplete carbonaceous compressions about 5–20 mm wide and up to 100 mm long. Grooved transverse structures are typically less than 0.1 mm wide and a few millimeters long. Rhombic windows are about 1×2 mm in size. In an incomplete specimen (Fig. 9.1), most surface structures are transverse, but longitudinally oriented grooves may occur toward one end of preserved specimens.

Types.—Holotype (HBM-126; Fig. 9.3, 9.4) and paratype (HBM-56; Fig. 9.5) were designated by Chen (in Chen and Xiao,

1992) and reposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

Other material examined.—MH0108, MMi 166A, MMi 213A, HBM-463, HBM-474, HBM-484, HBM-502.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—Chen and Xiao (1992) argued that the living form of *Sinospongia chenjunyuani* was a spongocoel-like tubular structure and that the reticulate structures consist of sponge spicules. Our observations suggest that the irregular transverse and network structures reflect corrugation of the relatively tough organic wall of a tubular organism. Unmineralized structures of other taxa [e.g., *Aggregatosphaera miaoheensis* (Fig. 2.9–2.14); *Baculiphyca taeniata* (Fig. 3.6–3.8); *Doushantuophyton lineare* (Fig. 5.6); *Enteromorphites sinensis* (Fig. 5.11); *Siphonophycus solidum* (Fig. 10.3)] in the Miaohe biota can also be preserved in three-dimensional relief. The diagnosis of *S. chenjunyuani* is therefore emended to reflect new observations. The emendation and new observation, however, do not rule out a sponge interpretation of *S. chenjunyuani*; the earliest sponges may have had no mineralized spicules. Given the incomplete preservation of *S. chenjunyuani,* alternative interpretations, such as a cnidarian-grade organism or a siphonous green alga (especially of the order Dasycladales), should be entertained.

Network structures in *Sinospongia dictyoforma* (Li *in* Ding et al., 1996) were said to consist of bundles of fibrous filaments, but this is not at all clear from the published illustrations. After reexamination of Li's specimen by one of us (XY), we believe that *S. dictyoforma,* like *S. chenjunyuani,* has a reticulated surface that reflects diagenesis of a tough organic wall. *S. dictyoforma* is therefore treated as a synonym of *S. chenjunyuani.*

SINOSPONGIA TYPICA (Li *in* Ding et al., 1996) new combination and emend.
Figure 8.2–8.16

Niuganmafeia obesa CHEN *in* CHEN AND XIAO, 1991, *nom. nud.*, p. 320, pl. 3, fig. 3; pl. 5, figs. 1, 2; CHEN AND XIAO, 1992, p. 520, pl. 5, figs. 1–4; CHEN, XIAO, AND YUAN, 1994, p. 396, pl. 3, fig. 8; pl. 4, figs. 3–5; DING ET AL., 1996, p. 113, pl. 32, figs. 1, 2, 4; pl. 33, figs. 7, 8.
Sinospongia chenjunyuani Chen *in* CHEN AND XIAO, 1992. STEINER, 1994, p. 134–135, pl. 15, figs. 2–3, 7–9. (*partim*)
Niuganmafeia typica Li *in* DING ET AL., 1996, p. 113–114, pl. 32, fig. 8; pl. 33, fig. 6; pl. 34, figs. 1, 2, 5, 7.
Xilinxiaella bella Li *in* DING ET AL., 1996, p. 106–107, pl. 32, fig. 9.
Xilinxiaella minuta Li *in* DING ET AL., 1996, p. 107–108, pl. 32, fig. 3.
Niuganmafeia sp., DING ET AL., 1996, pl. 31, fig. 7.
Latizonivermes megista Li *in* DING ET AL., 1996, p. 110–111, pl. 34, fig. 10.
Rugospongia conica Li *in* DING ET AL., 1996, p. 117, pl. 35, fig. 1; pl. 36, figs. 4, 6; pl. 37, fig. 5.
Rugospongia miaoheensis Li *in* DING ET AL., 1996, p. 118, pl. 37, figs. 1, 4.

Emended diagnosis.—Tubular or conical carbonaceous remains with a discoidal holdfast. Maximum width 3–15 mm, length up to 150 mm. Transverse structures typically straight and parallel, with occasional cross-cuttings (Fig. 8.9, 8.12; note that some of

←

FIGURE 10—*1–3, Siphonophycus solidum. 1,* MH0030-15, ×20; *2,* MH0097-2, ×40; *3,* notice three-dimensional preservation, MH0079-3, ×40; *4–21,* unnamed ribbon-like carbonaceous compressions. *4,* MH0097-1, ×1; *5,* note rounded termination, MH0240-3, ×5; *6,* notice rounded upper termination, MH0075-1, ×6.7; *7,* notice rounded lower termination and squared upper termination, MH0254, ×5; *8,* details folds near the lower end (arrow) of *7,* ×20; *9,* a magnified view of the upper end of *7,* ×20; *10,* MH0275-2, ×5; *11,* a magnified view of the lower end of *10,* showing detail of folds (arrow), ×20; *12,* MH0281, possible folds(?), ×10; *13,* MH0266, ×1; *14,* MH0273, ×5; *15,* MH0258, ×5; *16* shows the squared upper termination in *15,* ×20; *17,* MH0282-2 (two specimens), ×1; *18* shows squared termination of the longer specimen to the right in *17,* ×20; *19,* MH0297-5, ×5; *20* shows the squared termination of *19,* ×20; *21,* showing squared termination and a dark cap at the terminus, MH0288, ×10; *22–24,* putative trace fossils. *22,* MH0068, ×1; *23,* MH0169, ×1; *24,* MMi 127, ×0.6.

these cross-cuttings may be due to superimposed foldings). Transverse structures densely and evenly distributed. The structure typically lacks conspicuous transverse structures in its lower part (Fig. 8.7, 8.11).

Description.—Most specimens have a maximum width between 3 and 15 mm, greater than *Rugosilina farciminiforma* but less than *Sinospongia chenjunyuani*. Length varies from about a centimeter in incomplete specimens to ca. 10 cm in relatively complete individuals. There are about 10 transverse marks per millimeter of length, with each trace being ca. 50 μm wide. Tightly arranged transverse structures can grade into somewhat loose and irregular structures (Fig. 8.14, 8.15). Fragmented specimens may bear square-ended termini (Fig. 8.2, 8.5, 8.6).

Basionym.—*Niuganmafeia typica* Li *in* Ding et al., 1996.

Types.—Holotype (SM1-7-A-12) and paratypes (SM1-7-2-10b and SM1-7-6-22a) were designated by Li (*in* Ding et al., 1996) and reposited in the Xi'an Institute of Geology.

Other material examined.—MH0065, MH0066, MH0067, MH0068-1, MH0069-6, MH0070, MH0071, MH0072, MH0074-1, MH0077, MH0079-1, MH0081, MH0082-1, MH0083, MH0093, MH0096, MH0251-1, MH0251-2, MMi 144A, MMi 167, MMi 169A, HBM3-19, HBM3-20, HBM-66, HBM-87, HBM-439, HBM-458, HBM-530, HBM-572.

Occurrence.—Upper Doushantuo black shales at Miaohe.

Discussion.—In its original diagnosis, *Sinospongia typica* was differentiated from *Niuganmafeia obesa* by its smaller size (less than 4 mm in maximum width) and was interpreted as a bilaterian metazoan (Li *in* Ding et al., 1996). It has been made clear in Chen's publications (Chen and Xiao, 1991, 1992; Chen et al., 1994b) that *N. obesa* varies from a couple of millimeters to a couple of centimeters in width. Therefore, *N. typica* represents the same population as *N. obesa* and is a proper substitute for the latter invalid name. Furthermore, there is no evidence for a bilaterian interpretation of *S. typica*; the transverse structures are not metameric segmentation but corrugation of a tough organic wall (see Fig. 8.4, 8.9, 8.12, 8.13). The diagnosis of *S. typica* is here emended to include specimens originally described as *N. obesa* by Chen and Xiao (1991).

Transverse structures in *Xilinxiaella bella* and *X. minuta* (Li *in* Ding et al., 1996) closely resemble those in *Sinospongia typica*; alleged digestive gut and anal cirri of these two *Xilinxiaella* species are taphonomic artefacts. Two specimens described as *Niuganmafeia* sp. (Ding et al., 1996, pl. 31, fig. 7) and *Latizonivermes megista* (Li *in* Ding et al., 1996, pl. 34, fig. 10) are fragments of *S. typica*. *Rugospongia conica* and *R. miaoheensis* (Li *in* Ding et al., 1996) are conical and cocoon-shaped carbonaceous compressions, but both share the closely spaced transverse structures with *S. typica*. We regard both species as synonyms of *S. typica*. *Changjiangivermia hamata, Palaeohirudo pristina, Pupillivermis robusta*, and *Ambomurica saligna* (Li *in* Ding et al., 1996) are based on insufficient, poorly preserved specimens; it is difficult to determine whether they represent distinct taxa or strongly degraded specimens of *S. typica* or *S. chenjunyuani*.

It is worth commenting on the distinction between *Sinospongia typica* and some other tubular fossils. Compressed tubes of *Platysolenites* and *Sabellidites* from Nemakit-Daldynian and Tommotian deposits on the Russian Platform display parallel transverse wrinkles that look superficially like the transverse structures of *Sinospongia typica*. These Cambrian forms are generally smaller and are preserved as agglutinated or chitinous tubes (Sokolov, 1967, 1997; Sun et al., 1986; McIlroy et al., 1994; Lipps and Rozanov, 1996). No holdfast structures have been found in the Cambrian tubes.

Sinosabellidites, *Pararenicola*, and *Protoarenicola* are carbonaceous ribbons described and interpreted as possible metazoans from the Neoproterozoic Liulaobei and Jiuliqiao formations in

northern Anhui, North China (Sun et al., 1986; Chen, 1988; but see Steiner, 1994, for an alternative interpretation). Annulations in *Sinosabellidites*, *Pararenicola*, and *Protoarenicola* are quite similar to the parallel transverse structures in *Sinospongia typica*, both in their straightness and density (Sun, 1986; Chen, 1988). Also, some materials from Neoproterozoic successions in northern Anhui bear holdfast structures (Qian et al., 2000). However, these Anhui ribbons are typically smaller (less than 2 mm in width and 8 mm in length) than *Sinospongia typica*.

Paleobiological interpretation of *Sinospongia typica* strongly depends on correct interpretation of the transverse structures. Although these structures reflect the corrugation of resistant walls, it is not clear whether the corrugation is biological or preservational. The compressions of *S. typica* can bend (Fig. 8.14, 8.16) but rarely fold (cf. Fig. 7.19), indicating that the living form may have been a flexible tube. At present, we cannot distinguish among three alternative systematic interpretations: a sponge, cnidarian, or siphonous green alga.

Genus SIPHONOPHYCUS Schopf, 1968, emend. Knoll, Swett, and Mark, 1991

Type species.—*Siphonophycus kestron* Schopf, 1968.

SIPHONOPHYCUS SOLIDUM (Golub, 1979), Butterfield, 1994
Figure 10.1–10.3

Description.—Unbranched filaments about 16 μm in diameter and up to 3 mm in length. One specimen is preserved as a hollow, three-dimensional tube (Fig. 10.3); it appears that the trichome or sheath was coated with minerals during early diagenesis.

Unnamed forms
Figure 10.4–10.21

Description and discussion.—The Miaohe biota contains numerous incompletely preserved ribbon-like compressions, probably produced by several different taxa. These include clavate ribbons with a rounded upper end and a somewhat pointed lower end (Fig. 10.4, 10.6), but devoid of any rhizoidal holdfast structures; such ribbons may be poorly preserved *Baculiphyca taeniata*. Some ribbons have a rounded and a squared end (Fig. 10.7–10.11), and there is evidence for folding or pleating of a tubular wall at the rounded end (Fig. 10.8, 10.11); these can be reconstructed as tubular fossils and interpreted as sponges or siphonous green algae. Some ribbons are lanceolate, pointed at both ends (Fig. 10.13). More common are incompletely preserved ribbons with a rounded (Fig. 10.5), pointed (Fig. 10.14), or squared end (Fig. 10.15–10.21). These characters probably reflect underlying biological structures and not physical breakage; in cases where the opposite end is clearly broken, it is irregularly ripped (see the lower ends in Fig. 10.15, 10.17, 10.19).

Putative trace fossil
Figure 10.22–10.24

Linbotulichnus Lɪ ᴀɴᴅ Dɪɴɢ *in* Dɪɴɢ ᴇᴛ ᴀʟ., 1996, p. 126, pl. 40, fig. 1.

Description and discussion.—Very irregular "meandering traces" on bedding planes. These "traces" are about 2–4 mm wide and can be several centimeters long. They tend to have a diffuse boundary. The "traces" can branch and cross-cut. The width of these "traces" is unstable; there are expansions and constrictions along a single meander (Fig. 10.22).

Li and Ding (*in* Ding et al., 1996) interpreted such structures as metazoan trace fossils. However, the diffuse boundary, unstable width, and irregular branching suggest that these structures may be pseudofossils. Similar caution must be applied to other trace fossils described by Li and Ding (*in* Ding et al., 1996). Therefore, we treat this group of structures under an open nomenclature.
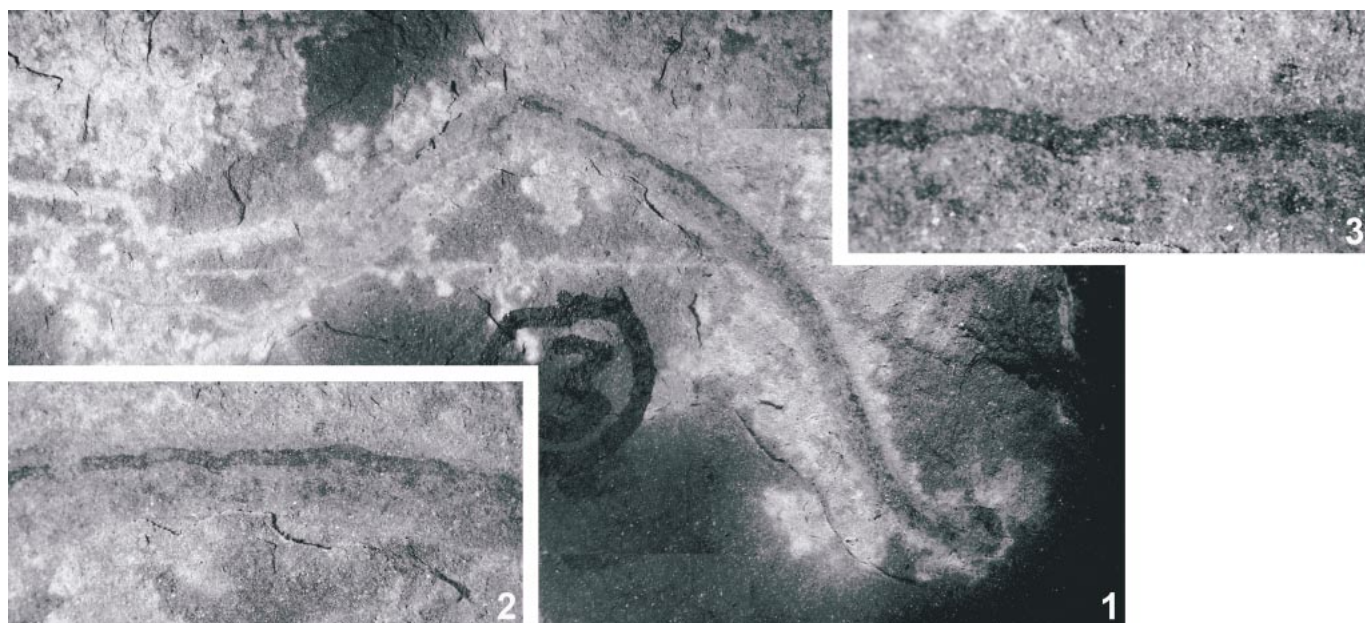
FIGURE *11*—Putative bilaterian metazoan, MH0143-3. *1,* notice the bulbous structure at the lower right. *2* and *3* are magnified views of the middle part of *1,* showing details of gut-like structure. *1,* ×4; *2,* ×8; *3,* ×16.

Putative bilaterian metazoan
Figure 11

Description and discussion.—A single specimen of ribbon-like compression, about 25 mm long and 1 mm wide. There is a dark organic trace, about 0.25 mm wide, running within the middle part of the ribbon. A bulbous structure is present at one end of the ribbon.

It is very hard to interpret this poorly preserved specimen. There is a slight possibility that the organic trace might be the digestive tract and the bulbous structure the head region of a bilaterian organism, but this is highly speculative and is presented here with serious doubt. The dark organic trace and bulbous structure could alternatively be diagenetic features.

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