Contributions to the Proterozoic and Cambrian
Evolution of Eukaryotes

Lin Dong

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Shuhai Xiao (Chair)
Patricia Dove
Michal Kowalewski
J. Fred Read
Stephen E. Scheckler

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Abstract

This thesis makes several contributions to improve our understanding of Proterozoic-Cambrian evolution of eukaryote life. Chapter 1 provides, for the first time, a quantitative characterization of the evolutionary trends of Proterozoic macroalgae. The analysis reveals that morphological disparity of Paleoproterozoic macroalgae was low but increased in the Mesoproterozoic and Ediacaran, with a plateau in between. There was also a significant increase in thallus surface/volume ratio and maximum canopy height of the Ediacaran macroalgal communities. The prolonged plateau between the Mesoproterozoic and Ediacaran may be related to either nutrient stress or the absence of animal grazing pressure. The Ediacaran increase in surface/volume ratio and morphological complexity may have been driven by decreasing pCO$_2$ levels and increasing animal grazing pressure.

Chapter 2 presents a systematic re-examination of the carbonaceous compression fossils *Protoarenicola baiguashanensis* Wang, 1982, *Pararenicola huaiyuanensis* Wang, 1982, and *Sinosabellidites huainanensis* Zheng, 1980, from the early Neoproterozoic Liulaobei and Jiuliqiao formations in northern Anhui, North China. These fossils were previously interpreted as worm-like metazoans. Our study reveals new morphological features that weaken the metazoan interpretation. Instead, the new data indicate that these fossils can be alternatively interpreted as erect epibenthic organisms, possibly coenocytic algae.

Chapter 3 examines two important eukaryote fossils: *Horodyskia* Yochelson and Fedonkin, 2000, and *Palaeopascichnus* Palij, 1976, from the upper Ediacaran chert of the Liuchapo Formation in central Guizhou, South China. These exceptionally preserved fossils offer us a unique opportunity to investigate their body constructions and affinities. The morphologies of *Horodyskia* and *Palaeopascichnus* support a phylogenetic relationship with agglutinated foraminifers, shedding new light on the divergence of bikont eukaryotes, the rise of rhizarians, and the ecological importance of heterotrophic eukaryotes in Proterozoic ecosystems.

Chapter 4 focuses on Cambrian microfossils that represent the primary producers—cyanobacteria and eukaryotic phytoplankton (acritarchs). Careful investigation of the basal Cambrian Yanjiahe Formation in the Yangtze Gorges area and the Yurtus Formation in the Aksu area revealed abundant acanthomorphic acritarchs, clustered coccoidal microfossils, filamentous cyanobacteria, and tubular microfossils. This study confirms previous stratigraphic correlation between the Yanjiahe and Yurtus formations and suggests that animals and phytoplankton radiated in tandem during the Cambrian explosion.
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INTRODUCTION AND OVERVIEW OF THE RESEARCH

Eukaryotic organisms have a long evolutionary history. The earliest eukaryotic body fossil, *Grypania*, is known from rocks that are 1.9 billion years old (Schneider et al., 2002). Biomarker evidence suggests that stem-group eukaryotes might have diverged since 2780 Ma (Brocks et al., 1999). Despite their early origin, the diversity of eukaryotes remained modest until the Ediacaran-Cambrian radiation of animals (Knoll, 1992; Butterfield et al., 1994; Yuan et al., 2002; Knoll, 2006). In addition to their relatively low diversity, Proterozoic eukaryotes tend to have long temporal ranges. The stratigraphic ranges of *Tawuia* and *Chuaria*, are more than a billion years, suggesting long stasis and constraint on their morphology. It has been proposed that extraordinary stasis among pre-Ediacaran eukaryotes is dictated by the overly simple ecological interactions in the absence of metazoans (Peterson and Butterfield, 2005; Butterfield, 2007). To test this hypothesis, it is essential to evaluate and re-evaluate the Proterozoic and early Cambrian eukaryote fossil record.

Proterozoic and early Cambrian eukaryotic fossils are preserved in three types of taphonomic windows, including carbonaceous compression, permineralization, and casting and molding. Carbonaceous compressions are organic films compressed on the bedding planes of shales and sometimes limestones (Butterfield, 1995). Permineralized fossils are three-dimensionally encased in early diagenetic minerals such as silica and phosphate (Grey and Williams, 1990; Zhang et al., 1998; Xiao and Knoll, 2000). The most famous Proterozoic cast/mold preservation is represented by the Ediacara biota in the late Ediacaran Period (Narbonne, 2005). This dissertation focuses on the systematic description, morphological reconstruction, and phylogenetic interpretation of certain Proterozoic eukaryotic fossils, including carbonaceous macrofossils from Proterozoic shales and argillaceous limestones and silicified microfossils from Ediacaran and early Cambrian cherts. The results of this research are presented in four chapters.

Chapter 1 presents a narrative overview and a quantitative analysis of Proterozoic macroalgal fossils, most of which are preserved as carbonaceous compressions. Macroalgae are macroscopic and mostly benthic algae. They play an important ecological role in highly productive coastal ecosystems. Dense turfs and giant underwater forests formed by macroalgae provide grazing, breeding, and encrusting substrates for animals. Despite the geobiological
importance of macroalgae, our knowledge about the evolution and ecology of Proterozoic macroalgae is limited. The goal of this chapter is to characterize the broad evolutionary trends of Proterozoic macroalgae and to explore their implications for Proterozoic ecosystems and biogeochemical cycles.

In order to quantify the morphological evolution of macroalgae in the Proterozoic, we carried out a literature-based morphospace analysis of Proterozoic macroalgal fossils. We collected our data from 17 published monographs and coded 19 morphological characters of 578 carbonaceous compression specimens that range from Paleoproterozoic to Neoproterozoic in age. We then performed a non-parametric multidimensional scaling (MDS) analysis of the pooled data, and the MDS scores were assigned to four geochronological bins (Paleoproterozoic, Mesoproterozoic, early Neoproterozoic, and Ediacaran). As a proxy for morphological disparity, MDS variance for each geochronological bin was calculated. Randomization analysis was performed to test whether variation in MDS variance was due to varying sample intensity in the four geochronological bins.

Our analysis shows that morphological disparity of Proterozoic macroalgae increased in two steps in the Mesoproterozoic and Ediacaran, with a plateau in between. This pattern is quite similar to the morphological variance of Proterozoic acritarchs, most of which are interpreted as phytoplankton (Huntley et al., 2006). The Ediacaran expansion of macroalgal morphospace was also accompanied by significant increase in thallus surface/volume ratio and maximum canopy height of benthic macroalgae.

We hypothesize that the Ediacaran increase in morphological complexity and surface/volume ratio may have been driven by decreasing pCO$_2$ levels after the Cryogenian glaciation. Alternatively, the Ediacaran expansion of macroalgal morphospace may have been stimulated by the emergence of animal grazing pressure (Peterson and Butterfield, 2005; Butterfield, 2007). The prolonged plateau between the Mesoproterozoic and Ediacaran, on the other hand, may be related to nutrient stress that characterizes the Mesoproterozoic and early Neoproterozoic oceans.

Among the Proterozoic carbonaceous compression fossils discussed in Chapter 1, three taxa—*Protoarenicola baiguashanensis* Wang, 1982, *Pararenicola huaiyuanensis* Wang, 1982, and *Sinosabellidites huainanensis* Zheng, 1980—are particularly intriguing because they were
interpreted as possible worm-like bilateral animals (Zheng, 1980; Wang et al., 1984; Sun et al., 1986; Chen, 1988). These three species occur in the mid-Neoproterozoic (700–900 Ma) Liulaobei and Jiuliqiao formations, in northern Anhui, North China. Given the possible age of 700–900 Ma, they have been regarded as direct paleontological evidence in support of a deep divergence of metazoans as inferred from molecular clock data (Wray et al., 1996). However, both the molecular-clock estimates and the interpretation of many pre-Ediacaran metazoan fossils have been questioned in recent years (Peterson and Butterfield, 2005). In light of these recent developments, we carried out a systematic re-evaluation of the taxonomy, morphology, paleoecology, and phylogenetic affinity of *Protoarenicola baiguashanensis*, *Pararenicola huaiyuanensis*, and *Sinosabellidites huainanensis*, on the basis of a large number of specimens collected from the Liulaobei and Jiuliqiao formations. The results are presented in Chapter 2.

Although the three genera are all characterized by annulated tubes, they can be differentiated by their terminal structures. *Protoarenicola* is characterized by a bulb-like holdfast at one end of the tube, indicating that it was probably an erect epibenthic organism. The tube of *Sinosabellidites* is rounded at both ends, indicating that it was probably a procumbent epibenthic organism. *Pararenicola* is relatively small compared with other two genera, and has an opening at one end and a rounded terminus at the other. Its paleoecology has not been unambiguously understood; it could have been epibenthic or even planktonic. Nonetheless, their morphology and inferred paleoecology does not allow a confident identification with animals, let alone an interpretation of bilaterian worms. Instead, their inferred paleoecology and some aspects of their morphology broadly ally them with the Mesoproterozoic *Tawuia*-like fossil *Radhakrishnania* Kumar, 2001, which is generally regarded as a benthic alga. Furthermore, it is possible that at least *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis* may represent reproductive or taphonomic fragments of the same organism. Regardless, the erect epibenthic life style of *Protoarenicola*, which can be up to 30 mm in height, suggests that ecological tiering of early Neoproterozoic marine communities reached as much as 30 mm in height. This is significantly higher than that of currently documented Mesoproterozoic tiering levels (<2 mm), although it is still much lower than the tiering height of Ediacaran communities (up to a meter).

It is also interesting to note that *Protoarenicola baiguashanensis* and many early erect epibenthic organisms had simple, discoidal holdfasts, rather than complex rhizoidal holdfasts [Kumar, 2001 #571; Du, 1985 #2; Qian, 2000 #573; Clapham, 2002 #143; Gehling, 2000 #488].
The first evidence for rhizoidal holdfasts does not occur until the Ediacaran Period (Xiao, 2002). It is possible that the transition from predominately discoidal holdfasts to overwhelmingly rhizoidal holdfasts was driven by an increasingly unstable substrate associated with the decline of microbial mats and/or the rise of bioturbation during the Ediacaran–Cambrian Period (Hagadorn and Bottjer, 1999; Seilacher, 1999; Bottjer et al., 2000).

Although animals, including bilaterian animals capable of bioturbating, first appeared in the Ediacaran Period, this geological period distinguishes itself from other periods by the enigmatic Ediacara fossils that occur in many late Ediacaran successions. Most Ediacara fossils are preserved as casts and molds in sandstones and siltstones, making it very difficult to understand their morphology, particularly their internal anatomy. However, it has been recognized recently that some classical Ediacara taxa can also be preserved in other taphonomic windows, for example as carbonaceous compressions (Xiao et al., 2002; Droser et al., 2005). In our investigation of late Ediacaran successions in South China, we identified for the first time silicified Ediacara fossils preserved in cherts. The results are presented in Chapter 3.

Chapter 3 describes two taxa, *Horodyskia minor* new species and *Palaeopascichnus jiumenensis* new species, from the late Ediacaran Liuchapo Formation in the central Guizhou province of South China. The genera *Horodyskia* and *Palaeopascichnus* have previously known as casts and molds from Mesoproterozoic and late Ediacaran successions, respectively (Gehling et al., 2000; Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002). Often, it is very difficult to recognize fossils preserved in different taphonomic windows (e.g., casting and molding vs. silicification) as representing the same taxon. However, in this case the identification of *Horodyskia* and *Palaeopascichnus* in the silicification window is facilitated by their distinctive morphologies (i.e., the “string-of-beads” morphology of *Horodyskia* and the “stack-of-dishes” morphology of *Palaeopascichnus*).

*Horodyskia* represents one of the oldest macroscopic fossils that can be traced back to the Mesoproterozoic (Grey and Williams, 1990; Fedonkin and Yochelson, 2002; Mathur and Srivastava, 2004). *Palaeopascichnus* is a common Ediacara member that has a worldwide distribution (Urbanek and Rozanov, 1983; Sokolov and Fedonkin, 1990; Gehling et al., 2000; Haines, 2000; Shen et al., In press). Both taxa have a similar bodyplan, which is characterized by uniserially arranged segments of comparable size and shape. Both have previously known as
preserved as casts and molds in siliciclastic sequences, but their affinity are still unknown. The silicified specimens of Horodyskia and Palaeopascichnus from the Liuchapo chert, although sharing the basic bodyplan with those preserved as casts and molds in siliciclastic rocks, reveal additional features such as an enveloping aureole and connecting filaments between the uniserially arranged segments. Such features are not preserved in any previously described casts and molds, and they provide new insight into the phylogenetic affinity of Horodyskia and Palaeopascichnus.

The fundamental bodyplan of Horodyskia and Palaeopascichnus encourages a morphological comparison with uniseriate agglutinated foraminifers. The uniserially arranged segments are analogous to foraminifer chambers. Connections between segments may represent passages between chambers that allow cytoplasm to move between chambers. And the carbonaceous-free, microcrystalline quartz aureole is interpreted as agglutinated test. Thus, Horodyskia and Palaeopascichnus are interpreted as fossil foraminifers, possibly stem-group foraminifers.

The interpretation of Horodyskia and Palaeopascichnus as stem-group foraminifers has further implications for the early evolution of eukaryotes. First, this interpretation implies that the earliest rhizarians and heterotrophic eukaryotes can be extended back to the Mesoproterozoic. Second, the divergence of bikonts from unikonts, as well as the divergence of rhizarians from other bikonts, must have occurred before 1.4 Ga, given the Mesoproterozoic occurrences of Horodyskia. This inference is consistent with other bikont eukaryotes in the Mesoproterozoic. Three of the four bikont clades (i.e., rhizarians, chromalveolates, excavates, and plants which are alternatively known as archaeplastids) are represented in the Mesoproterozoic fossil record. In addition to rhizarians, chromalveolates are represented by the xanthophyte alga Palaeovaucheria from the >1005 ± 4 Ma Lakhanda Group in southeastern Siberia (Woods et al., 1998), and plants by the red alga Bangiomorpha from the 1204 ± 22 Ma Hunting Formation in arctic Canada (Butterfield, 2000). In addition, there are also potential candidates for Mesoproterozoic and early Neoproterozoic unikont fossils. For example, Tappania (occurring in the 1430 Ma Roper Group in northern Australia, the >1000 Ma Ruyang Group in northern China, and the early Neoproterozoic Wynniatt Formation in northwestern Canada) and Cheilofilum (occurring in the Neoproterozoic Wynniatt Formation) have both been interpreted as possible fungi (Butterfield, 2005).
Finally, the occurrence of *Horodyskia* in Mesoproterozoic and Ediacaran rocks indicates an extremely long range (~900 million years) of this genus. Its striking morphological stasis is similar to other long-ranging Proterozoic genera such as *Chuaria* and *Tawuia*. The morphological stasis echoes the Mesoproterozoic–Neoproterozoic plateau revealed in the morphometric analysis of Proterozoic macroalgal fossils (Chapter 1) and acritarchs (Huntley et al., 2006), and it is in sharp contrast to the rapid taxonomic turnover in the Phanerozoic fossil record. The contrast between the tempos of Proterozoic and Phanerozoic evolution, with the Ediacaran Period representing a transitional interval, accentuates the ecological and macroevolutionary impacts of the Cambrian explosion (Butterfield, 2007).

The Cambrian explosion is the most fundamental evolutionary event in the history of life. Much has been learned about the evolutionary patterns of animals during the Cambrian explosion, but little is known about the primary producers during this evolutionary event. Chapter 4 describes the taxonomical diversity of eukaryotic phytoplankton (“acritarchs”), coccoidal and filamentous cyanobacteria, and other enigmatic microfossils from two early Cambrian successions that are also rich in skeletal animal fossils. The acritarch fossils were collected from the basal Cambrian Yanjiahe Formation in the Yangtze Gorges area (South China) and the Yurtus Formation in the Aksu area (NW China), both of which contains abundant small shelly fossils and *Micrhystridium*-like acritarchs.

The acritarch assemblages in the Yanjiahe and Yurtus formations include *Heliosphaeridium ampliatum* Wang, 1985, *Comasphaeridium densum* new species, and *Paracymatiosphaera uniformis* new species. Coccoidal and filamentous cyanobacterial microfossils include *Archaeophycus venustus* Wang et al., 1983, *Siphonophycus robustum, Cynomena majus* new species, and *Oscillatoriopsis sp*. In addition, a phylogenetically unresolved microfossil, *Megathrix longus* Yin, 1987, also occurs in the Yanjiahe and Yurtus formations. Our study supports the biostratigraphic correlation between the Yanjiahe and Yurtus formations and suggests that the appearance of complex process might be an ecological response to animal predation pressure.

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Chapter 1
On the Morphological and Ecological History of Proterozoic Macroalgae

1. INTRODUCTION

Multicellular or coenocytic, eukaryotic algae that are visible to the unaided eye (i.e. > 1 mm) are usually considered macroalgae. The cut-off between micro- and macroalgae is somewhat arbitrary, but may be of ecological significance because most macroalgae are, with notable exceptions, benthic. Macroalgae are ecologically and biogeochemically important in modern ecosystems. They form dense turfs or giant (~50 m in height) underwater forests in on the photic portions of continental shelves. The productivity rate (measured in gram biomass per unit area per unit time) of such benthic macroalgal communities is impressive,—more than ten times greater than that of the open ocean (Bunt, 1975). In addition, algal turfs and forests partition the benthic ecosystem into a myriad of ecological habits, many of which are the grazing, breeding, and encrusting substrates for animals.

Despite the potential geobiological importance of macroalgae, however, the evolution and ecology of macroalgae in the Proterozoic is rarely discussed in the literature. This is partly due to the poor fossil record of Proterozoic macroalgae. Before the rise of calcareous algae in the early Paleozoic (Johnson, 1961; Wray, 1977), the preservation of macroalgae usually occurred in exceptional taphonomic conditions. In fact, most well-preserved Proterozoic macroalgal assemblages, such as the Little Dal assemblage in northwest Canada (Hofmann and Aitken, 1979; Hofmann, 1985), the Liulaobei and Jiuliqiao assemblages of North China (Sun et al., 1986), and the Miaohe assemblage in South China (Xiao et al., 2002), can be considered as Konservat-Lagerstätten that allow the preservation of non-mineralizing organisms (Butterfield, 2003). The exceptional nature of Konservat-Lagerstätten dictates that the stratigraphic completeness of macroalgal fossils is relatively poor although the quality of preservation can be extraordinary.

Another challenge in the study of Proterozoic algae lies in the difficulty of phylogenetic and ecological interpretations. Biochemical and cytological data, which are used routinely in the classification and phylogenetic analysis of modern algae, are not available in algal fossils. Thallus morphology is of limited phylogenetic significance because of pervasive convergence.
among different algal clades. Only a handful of algal fossils have been phylogenetically resolved into modern clades on the basis of cellular structures (Butterfield et al., 1994; Xiao et al., 1998a; Butterfield, 2000, 2004; Xiao et al., 2004). For simple algal fossils, not only their phylogenetic affinities but also their paleoecology is difficult to constrain. As an example, Chuaria-like circular carbonaceous compressions—the most ubiquitous form in Proterozoic shales—have been variously interpreted as floating cyanobacteria colonies (Sun, 1987; Steiner, 1997), as planktonic acritarchs (Ford and Breed, 1973; Vidal and Ford, 1985; Butterfield et al., 1994), as propagules of benthic chlorophyte or xanthophyte algae (Kumar, 2001), as benthic organisms (Butterfield, 1997, 2001), or as distant relatives of metazoans or fungi (Teyssèdre, 2003).

Despite these challenges, however, we can still learn a great deal about the morphological and ecological history of Proterozoic macroalgae at the broadest scale. The pervasive morphological convergence among different algal clades (e.g., chlorophytes, rhodophytes, and phaeophytes) indicates strong physiological and mechanical—as well as developmental and phylogenetic—constraints on algal morphology (Niklas, 2004). Thus, although morphological convergence is a noise in phylogenetic analysis, it is a bonus in ecological analysis of benthic macroalgae; for example, the functional-form model widely used in ecological analysis of modern macroalgal communities emphasizes ecologically important morphological features (e.g., surface/volume ratio) regardless of phylogenetic affinities (Littler and Littler, 1980; Littler and Arnold, 1982; Padilla and Allen, 2000). To explore the morphological and ecological history of Proterozoic macroalgae, we take a simple approach to characterize the morphological complexity, surface/volume ratio, and maximum canopy height of Proterozoic macroalgae. Our data show that the history of macroalgal morphological disparity in the Proterozoic is broadly similar to that of acritarchs (Huntley et al., 2006), showing stepwise increase in the Mesoproterozoic and Ediacaran with a plateau in between. The Ediacaran expansion of macroalgal morphospace was also accompanied by significant increase in thallus surface/volume ratio and maximum canopy height of benthic macroalgal communities.

The causes of the Mesoproterozoic to early Neoproterozoic stasis and the Ediacaran rise in macroalgal morphological disparity are less clear. It is possible that the Mesoproterozoic to early Neoproterozoic plateau may be related to nutrient stress (Brasier and Lindsay, 1998; Anbar and Knoll, 2002) due to bottom-up ecological constraints. Alternatively, morphological evolution of Mesoproterozoic and early Neoproterozoic macroalgae may have been held back by absence
of animal grazing pressure, which has been proposed to be a major top-down ecological force that drove the diversification of Ediacaran acritarchs (Peterson and Butterfield, 2005) and perhaps macroalgae. We also discuss the possibility that the Ediacaran rise in surface/volume ratio and morphological disparity may have been driven by decreasing pCO$_2$ levels after the Cryogenian glaciation. Since thallus surface/volume ratios appear to be positively correlated with bioproduction rate, macroalgae were probably more productive in the Ediacaran than previously. If true, the increased bioproductivity may have some impacts on the global carbon cycle and oxygen evolution in the Ediacaran Period. These hypotheses and speculations necessarily need to be tested in the future with more geochemical, paleontological, and geochronological data.

We emphasize the exploratory character of this study and the preliminary nature of our conclusions, because the macroalgal affinity of some carbonaceous compression fossils included in this study may be debatable, and also because the geochronological resolution and stratigraphic completeness of our database are rather poor. Nonetheless, this exploratory exercise serves a starting point for more extensive studies of Proterozoic macroalgae in the future, and we hope that it will stimulate paleoecological and geobiological investigation of Proterozoic macroalgae.

2. A SYNOPSIS OF PROTEROZOIC MACROALGAL FOSSILS

Most Proterozoic macroalgae are preserved as carbonaceous compressions. Relatively few macroalgae are preserved in the permineralization windows (i.e., silicification and phosphatization), which are widely open for Proterozoic microorganisms (Schopf, 1968; Knoll, 1985); it is worth mentioning in passing that the contrast between the compression and permineralization windows may represent some major taphonomic biases or environmental heterogeneity. Recently, it has been recognized that some Ediacaran macroalgae may have been preserved as casts and molds, in a way similar to the preservation of classical Ediacara fossils (Droser et al., 2004), but the diversity of these macroalgal fossils awaits systematic documentation.

Hofmann (1994) compiled a comprehensive database of Proterozoic carbonaceous compressions and he classified them into thirteen formally defined families. Several new reports of Proterozoic carbonaceous fossils have been published since 1994 (Chen et al., 1994a; Chen et
al., 1994b; Steiner, 1994; Ding et al., 1996; Gnilovskaya et al., 2000; Xiao et al., 2002); however, most of these new fossils can be classified into one of the thirteen families. Because these families were defined on morphological basis, it is likely that some of these families may be polyphyletic. However, as long as we can ascertain that these families represent macroalgae, these morphologically defined families may be to some degree analogous to macroalgal functional-form groups (Littler and Littler, 1980), and they should have ecological if not phylogenetic significance. Four of the thirteen families were considered as likely (Saarinidae and Sabelliditidae) or possible (Sinosabelliditidae and Protoarenicolidae) metazoans, and their nomenclature followed the ICZN rules (Hofmann, 1994). These family names are preserved here for convenience, even though we believe that the sinosabelliditids and protoarenicolids are probably macroalgae. Below we briefly consider the algal affinity of these groups.

Chuariaceae: This group includes the circular compressions Chuaria (millimetric diameters; Fig. 1.1A) and Beltanelliformis (centimetric diameters). Both often have concentric wrinkles and sometimes simple splits (Butterfield et al., 1994; Steiner, 1997; Xiao et al., 2002), indicating that in life they were spherical vesicles. Three-dimensionally preserved casts and molds confirm their spherical morphology (Hofmann, 1985; Narbonne and Hofmann, 1987; Yuan et al., 2001). Thus, both genera can be reconstructed as spherical fluid-filled vesicles with a flexible organic wall. This morphological reconstruction is inconsistent with an affinity with cyanobacterial colonies such as Nostoc balls (Sun, 1987; Steiner, 1997), where filaments are held in a mucilaginous matrix (Graham and Wilcox, 2000). More likely, both Chuaria and Beltanelliformis are structurally similar to acritarchs with a coherent and resistant organic wall (Ford and Breed, 1973; Vidal and Ford, 1985; Butterfield et al., 1994). In fact, some Chuaria-like compressions have been interpreted as benthic organic vesicles (Butterfield et al., 1994; Butterfield, 1997, 2001), or as planktonic propagules of Tawuia-like thalli that are considered as benthic chlorophytes or xanthophytes (Kumar, 2001). Likewise, Beltanelliformis has been compared to spherical gametophytes of the benthic coenocytic green alga Derbesia (Xiao et al., 2002). Parachuaria simplicis, another Chuaria-like fossil, has a millimetric circular compression with a subtending filament (Yan et al., 1992; Tang et al., 1997), which may well represent a stipe-like structure that tethered the spherical vesicle to a benthic substrate, in a way similar to Longfengshania (Hofmann, 1985; Du and Tian, 1986). Thus, Chuaria and Beltanelliformis are best considered as benthic or having a benthic stage in their life cycle. It is
also probable that they may have been photosynthetic eukaryotes, given that their spherical vesicles have morphological analogues among modern coenocytic algae (e.g., *Derbesia* and *Valonia*), but not among animals or fungi. Thus we tentatively regard chuariaceans as macroalgae. It should be noted, however, that the major patterns of macroalgal morphological history would probably stay even if we had removed chuariaceans from our analysis, because chuariaceans are ubiquitous throughout the entire Proterozoic.

**Tawuiaceae:** *Tawuia*, the eponymous genus of this group, is reconstructed as a tubular structure with closed and round termini (Hofmann and Aitken, 1979; Hofmann, 1985). Like *Chuaria*, it can be preserved as two-dimensional compressions or three-dimensional molds (Hofmann and Aitken, 1979; Hofmann, 1985). Because all reported populations co-occur with *Chuaria*, *Tawuia* is generally considered ontogenetically or phylogenetically related to *Chuaria* (Duan, 1982; Hofmann, 1985). Recently, Kumar (2001) reported a population of carbonaceous compressions from the Suket Shale of the lower Vindhyan Supergroup in the Rampura-Chittorgarh area, central India. The Suket population, probably between 1600 and 1140 Ma (Kumar, 2001; Rasmussen *et al.*, 2002; Ray *et al.*, 2002; Ray *et al.*, 2003; Sarangi *et al.*, 2004), includes *Chuaria*- and *Tawuia*-like fossils. The termini of several Suket *Tawuia*-like specimens bear circular (*Chuaria*-like) or trapezoidal structures, which Kumar interpreted as compressed spherical cysts and holdfasts, respectively. Kumar gave different taxonomic names to the different parts of the same specimen; the trapezoidal holdfast was described as *Tilsoia* or *Suketea* depending on how it is preserved, the cylindrical stem as *Tawuia*, the spherical cyst as *Chuaria*, and the complete organism was named *Radhakrishnania*. While the identification of the Suket tubular fossils as *Tawuia dalensis* is debatable and the taxonomic practice of Kumar is undesirable, the Suket population does provide a general model by which *Chuaria* and *Tawuia* may be ontogenetically related. This model implies 1) *Tawuia* represents only the benthic stage of a biphasic alga and 2) *Chuaria* and *Tawuia* should have similar geographic, environmental, and stratigraphic distribution. However, these implications are difficult to test, because *Chuaria* is almost certainly a polyphyletic taxon and also because planktonic cysts (i.e., *Chuaria*) can be preserved beyond the geographic and environmental distribution of their benthic vegetative parents (i.e., *Tawuia*). Given that *Tawuia* populations from the type locality (Hofmann and Aitken, 1979; Hofmann, 1985) and elsewhere (Zhang *et al.*, 1991) also contain individuals, including some U-shaped individuals, with a terminal disk at one end, it is probable that *Tawuia*
and *Chuaria* may indeed be organ taxa of the same organism. Other *Tawuia*-like fossils, for example *Bipatinella* (Fig. 1.1B) from the early Neoproterozoic Liulaobei Formation and Shijia Formation in northern Anhui of North China (Zheng *et al.*, 1994) also appear to have terminal swellings. If *Tawuia* and *Chuaria* are indeed organ taxa of the same organism, the combination of characters (a planktonic stage and a benthic stage with holdfast) is most consistent with a macroalgal interpretation for *Tawuia*. Thus, in our compilation, we follow the traditional view that *Tawuia* represents a benthic, tubular macroalga.

Ellipsophysaceae: *Ellipsophysa* (Fig. 1.1D) and related genera from the Liulaobei, Jiuliqiao, Xiamaling, and Changlongshan formations in North China, are elliptical to oval compressions with a maximum/minimum axis ratio between 1.4 and 2 (Zheng, 1980; Du and Tian, 1986). It is uncertain whether these compression fossils should be classified in the *Chuariaceae* or in a separate family. Nonetheless, their elliptical/oval morphology is intermediate between *Chuaria* and *Tawuia*, and by analogy they may also be interpreted as macroalgae.

Longfengshaniaceae: *Longfengshania* (Fig. 1.1C) and *Paralongfengshania* can be reconstructed as algal thalli with an ellipsoidal, ovoidal, or panduroidal vesicle and a subtending stipe (Hofmann, 1985; Du and Tian, 1986). Some specimens preserve a simple discoidal holdfast (for example, Du and Tian, 1986, plate X, figs. 2, 8a, 9; plate XI, figs. 9–11), suggesting a benthic habit. *Longfengshania* was once interpreted as a bryophyte (Zhang, 1988), but this interpretation was disputed because it lacks any diagnostic bryophyte features (Liu and Du, 1991). The simple morphology and marine habitat of *Longfengshania* and *Paralongfengshania* is more consistent with a macroalgal interpretation. Indeed, several modern algae such as *Botrydium* (a xanthophyte), *Botryocladia* (a rhodophyte), and *Valonia* (a chlorophyte), all of which have a balloon-like vesicle tethered to a holdfast or a branch (Abbott, 1999; Graham and Wilcox, 2000), are good interpretive analogues for *Longfengshania* and *Paralongfengshania*.


Eoholyniaceae: Hofmann (1994) created this family to accommodate all branching forms. Some fine filaments, such as *Daltaenia* (Hofmann, 1985) and *Chambalia* (Kumar, 2001), appear to have branches and would be included in this family. However, the junctions of these branching
filaments tend to be T-shaped rather than Y-shaped; they could be cyanobacterial branches (e.g. *Fischerella*) and are thus excluded from our analysis. Instead, we focus on carbonaceous fossils with dichotomous, monopodial, or helical branches, because these are more likely eukaryotic algae. A number of carbonaceous compressions from the Ediacaran Doushantuo and Lantian formations, including *Anomalophyton*, *Doushantuophyton* (Fig. 1.2D), *Enteromorphites*, *Konglingiphyton*, *Longifuniculum*, and *Miaohephyton* (Chen and Xiao, 1992; Steiner, 1994; Ding et al., 1996; Yuan et al., 1999; Xiao et al., 2002; Yuan et al., 2002), are considered members of this group. Some fan-shaped thalli, such as *Anhuiophyton*, *Flabellophyton*, and *Huangshanophyton* from the Lantian Formation, may also contain rare dichotomously branching filaments (Yan et al., 1992; Chen et al., 1994a; Steiner, 1994; Yuan et al., 1999), but this is difficult to verify because of dense compaction of fine filaments. Nonetheless, the macroscopic thallus size, morphological complexity, and the presence of a holdfast structure (in *Flabellophyton* at least) independently suggest their macroalgal affinity and benthic habit. Thus, these Lantian forms are also considered members of this family.

Sinosabelliditidae and Protoarenicolidae: These two groups are characterized by ribbon-shaped compressions with transverse annulations (Fig. 1.2A–C). They occur in early Neoproterozoic rocks in North China (Sun et al., 1986), and similar forms have been reported from late Riphean rocks in southern Timan (Gnilovskaya et al., 2000). Some specimens are three-dimensionally preserved with a circular transverse cross section (Zheng, 1980; Wang, 1982; Wang and Zhang, 1984; Xing et al., 1985; Sun et al., 1986; Chen, 1988; Qian et al., 2000), suggesting that they were originally cylindrical tubes. Representative genera are *Sinosabellidites*, *Pararenicola*, *Protoarenicola*, *Parmia*, and many other synonyms (Wang and Zhang, 1984; Xing et al., 1985; Gnilovskaya et al., 2000). *Pararenicola* and *Protoarenicola* appear to bear a proboscis-like structure or a terminal opening in their presumed anterior end. The proboscis-like structure and transverse annulations led some to interpret *Pararenicola* and *Protoarenicola* as possible worm-like animals (Sun et al., 1986; Chen, 1988). *Sinosabellidites* has similar transverse annulations but no terminal opening or proboscis-like structure, and it was considered less likely to be an animal (Sun et al., 1986). It is interesting to note that a number of protoarenicolid specimens (for example, Wang and Zhang, 1984, plate 7, figure 2; Xing et al., 1985, plate 39, figure 1; Qian et al., 2000) appear to have holdfast-like structures. In fact, several transversely annulated or corrugated tubular fossils from the Doushantuo Formation, including *Cucullus* and
Sinospengia (Xiao et al., 2002), can be considered members of the Protoarenicolidae (Hofmann, 1994) and they also have holdfast-like structures. Our own observations of protoarenicolids suggest that some of them have a discoidal holdfast structure (Fig. 1.2A–C). Thus, it is possible that the proboscis-like structures present in a small number of specimens of protoarenicolids (Sun et al., 1986) may be poorly preserved holdfasts or artifacts due to physical tearing of the discoidal holdfast. If confirmed, these observations and interpretations would indicate that protoarenicolids are similar to tawuiaceans described from the Suket Shale in the Vindhyan Supergroup (Kumar, 2001) in having a holdfast structure. The only major difference is the presence or absence of transverse annulations, which is not a diagnostic animal feature (Sun et al., 1986; Chen, 1988). Thus, the animal interpretation of sinosabelliditids and protoarenicolids is poorly supported. A more likely interpretation is that they were siphonous macroalgae analogous to modern dasycladaleans (Berger and Kaever, 1992).

Moraniaceae, Beltinaceae, Vendotaeniaceae, Saarinidae, and Sabelliditidae: These groups are not included in the current study because their macroalgal affinity is problematic. Moraniaceans, beltinaceans, and vendotaeniaceans may represent bacterial colonies (Walcott, 1919; Vidal, 1989; Hofmann, 1994), although vendotaeniaceans have been interpreted as brown or red algae (Gnilovskaya, 1990; Gnilovskaya, 2003). In addition, beltinaceans and vendotaeniaceans are often fragmented and folded, making it difficult to reconstruct their morphology and paleoecology. Saarinids and sabelliditids have been interpreted as pogonophoran tubes (Sokolov, 1967; Hofmann, 1994); certainly, ultrastructures of Sabellidites cambriensis tubes, which consist of interwoven filaments with a diameter of 0.2–0.3 µm (Urbanek and Mierzejewska, 1977; Ivantsov, 1990; Moczydłowska, 2003), have no analogues among modern macroalgae.

Other Macroalgae: Baculiphyca (Fig. 1.2E) from the Doushantuo and Lantian formations in South China was questionably placed in the Protoarenicolidae (Hofmann, 1994). Baculiphyca was undoubtedly a benthic macroalga with clavate or blade-like thallus and rhizoidal holdfast but no transverse annulations (Xiao et al., 2002). Thus Baculiphyca does not belong to the same family (or functional-form group) as protoarenicolids that are characterized by cylindrical thallus, transverse annulations, and possible discoidal holdfast. Another taxon that was not classified in any of the formally defined families is Orbisiana from Vendian rocks in Russia (Sokolov, 1976). Orbisiana consists of serial or biserial rings or spheres 0.2–0.9 mm in diameter, and it is probably
an algal fossil (Jensen, 2003). Similar fossils (Fig. 1.1E), preserved as carbonaceous compressions and described as *Catenasphaerophyton* (Yan et al., 1992) or *Seirisphaera* (Chen et al., 1994a), have been known from the Ediacaran Lantian Formation in South China.

Permineralized Macroalgae: In addition to carbonaceous compressions, some permineralized algal fossils can also reach macroscopic size (Fig. 1.2F). Phosphatized and silicified algae in the Doushantuo Formation (Xiao, 2004; Xiao et al., 2004), for example, can be millimetric in size. However, the overall diversity and abundance of permineralized macroalgae is much lower than carbonaceous ones.

### 3. MORPHOLOGICAL HISTORY OF PROTEROZOIC MACROALGAE

#### 3.1 Narrative Description

Although many carbonaceous compressions have functional morphologies generally consistent with algal interpretation, their exact phylogenetic affinities are poorly resolved because of pervasive morphological convergence among algae. Possible exceptions include *Miaohephyton bifurcatum* and *Beltanelliformis brunsae* from the Doushantuo Formation; these have been compared, respectively, with fucalean brown algae and the coenocytic green alga *Derbesia* (Xiao et al., 1998a; Xiao et al., 2002). In addition, several microscopic compressions recovered from Proterozoic shales using palynological method are phylogenetically resolved. For example, *Proterocladus major* from the ~750 Ma Svanbergfjellet Formation in Spitsbergen has been interpreted as a clodophoran green alga (Butterfield et al., 1994). *Palaeovaucheria clavata* from the ~1000 Ma Lakhanda Group in southeastern Siberia and *Jacutianema solubila* from the Svanbergfjellet Formation are both interpreted as xanthophyte algae (Hermann, 1990; Butterfield, 2004). Finally, the silicified microfossil *Bangiomorpha pubescens* from the ~1200 Ma Hunting Formation in Arctic Canada has been interpreted as a bangiophyte red alga (Butterfield, 2000), and several phosphatized algae from the Ediacaran Doushantuo Formation have been interpreted as florideophyte red algae (Xiao et al., 2004). These fossils indicate that major algal clades diverged no later than the early Neoproterozoic (Knoll, 1992; Porter, 2004).

However, clade divergence needs not be temporally coupled with morphological, ecological, and taxonomic diversification. Therefore, it is useful to independently characterize important morphological innovations in macroalgal history. We begin by tabulating the temporal
distribution of some important macroalgal morphologies (Table 1.1), followed by a brief summary of macroalgal morphologies in the Proterozoic.

Paleoproterozoic and Mesoproterozoic macroalgae are mostly spherical, ellipsoidal, tomaculate, or cylindrical forms. Carbonaceous compressions similar to *Chuaria*, *Ellisophysa*, and *Tawuia* are known from the 1800-1700 Ma Changzhougou and Chuanlinggou formations in North China (Hofmann and Chen, 1981; Lu and Li, 1991; Zhu et al., 2000; Wan et al., 2003), although those from the Changzhougou Formation have recently been characterized as pseudofossils (Lamb et al., 2005). *Grypania* and *Grypania*-like fossils have been reported from the ~1900 Ma Negaunee Iron-Formation of Michigan (Han and Runnegar, 1992; Schneider et al., 2002), the Mesoproterozoic Rohtas Formation of central India (Kumar, 1995; Rasmussen et al., 2002; Ray et al., 2002), and the ~1400 Ma Gaoyuzhuang Formation in North China and the Greyson Shale in Montana (Walter et al., 1990); the Indian *Grypania* specimens are distinct in bearing transverse annulations. Abundant carbonaceous compressions occur in the ~1700 Ma Tuanshanzi Formation in the Jixian area (Hofmann and Chen, 1981; Yan, 1995; Zhu and Chen, 1995; Yan and Liu, 1997). Some of the Tuanshanzi fossils have been interpreted as macroalgae with holdfast-stipe-blade differentiation, but their variable morphologies appear to suggest that some of them may be fragmented algal mats. However, *Tawuia*-like fossils from the Mesoproterozoic Suket Shale in central India do appear to have simple discoidal holdfasts (Kumar, 2001).

Early Neoproterozoic macroalgal assemblages continued to be dominated by simple forms such as *Chuaria*, *Ellisophysa*, and *Tawuia*. But several morphological innovations did occur in the early Neoproterozoic. These include algal thalli with well-differentiated stipe and holdfast structures (in *Longfengshania* and *Paralongfengshania*), as well as cylindrical thalli with well-defined transverse annulations and holdfast structures (in *Sinosabellidites* and Pararenicolids).

Important morphological innovations evolved in the Ediacaran Period. The Doushantuo Formation (635-550 Ma) and equivalent rocks in South China contain diverse macroalgal assemblages (Steiner, 1994; Yuan et al., 1999; Xiao et al., 2002). Doushantuo macroalgae are featured with monopodial and spiral branching (e.g., *Doushantuophyton quyuani* and *Anomalophyton zhangzhongyingi*), true dichotomous branching and apical meristematic growth (e.g., *Doushantuophyton lineare*, *Miaohephyton bifurcatum*, *Konglingiphyton erecta*, and
Enteromorphites siniansis), rhizoidal holdfasts and flattened blade-like thalli (e.g., Baculiphyca taeniata), conical thalli (e.g., Protoconites minor), and fan-shaped thalli (e.g., Longifuniculum dissolutum, Anhuiphyton lineatum, Flabellophyton strigata, Flabellophyton lantianensis, and Huangshanophyton fluticulosum). These Doushantuo macroalgae were first reported (Zhu and Chen, 1984) from uppermost Doushantuo black shale that is less than 10 m below an ash bed dating from 551±1 Ma (Condon et al., 2005). Subsequently, similar fossils have also been found in Doushantuo black shales in southern Anhui (Bi et al., 1988; Yan et al., 1992; Chen et al., 1994a; Yuan et al., 1999) and north-eastern Guizhou (Zhao et al., 2004). More recently, at least one member of the Miaobe biota—Enteromorphites siniansis—has also been found in the lower Doushantuo Formation in the Yangtze Gorges area (Tang et al., 2006). The lower Doushantuo Formation is estimated to be between 635 Ma and 580 Ma (Condon et al., 2005). If this estimate is correct, morphological diversification of macroalgae began after the 635 Ma Marinoan glaciation (Hoffmann et al., 2004; Condon et al., 2005) but before the 580 Ma Gaskiers glaciation (Bowring et al., 2003) and perhaps before the diversification of animals (Xiao et al., 1998b; Condon et al., 2005; Narbonne, 2005).

Despite morphological innovations in the Ediacaran, several functional forms of modern macroalgae (Littler and Littler, 1980) have not been observed in any Ediacaran assemblages. These functional forms include very thin sheet-like (leafy), calcareous, and crustose thalli, which are common in modern macroalgal flora (such as Porphyra, Ulva, and coralline red algae). The lack of leafy thalli in the fossil record may be taphonomic, but the absence of calcareous and crustose thalli in the Precambrian is probably real (Steneck, 1983). Thus, the morphological diversity of Ediacaran macroalgae, although much greater than before, may still be comparatively lower than modern macroalgae.

3.2 Quantitative Analysis: Morphospace, Body Size, and Surface/Volume Ratio

3.2.1 Methods

To quantify the morphological evolution of macroalgae in the Proterozoic, we carried out a morphospace analysis of Proterozoic macroscopic carbonaceous compressions (> 1 mm in maximum dimension, with a few exceptions) that can be reasonably interpreted as macroalgal fossils (see above). Permineralized macroalgae were not included in our quantitative analysis.
because of the few examples of permineralized macroalgae and because of possible preservational biases between the compression and permineralization windows. After a preliminary analysis, we also excluded in our further analysis carbonaceous compressions from the Paleoproterozoic Tuanshanzi Formation reported by Zhu and colleagues (Yan, 1995; Zhu and Chen, 1995; Yan and Liu, 1997) because at least some of these may be fragmentary microbial mats (see above) and also because their morphologies are unstable.

We collected presence/absence data of 19 morphological characters or character states of 578 carbonaceous compression specimens from 17 published monographs (Table 1.2 and Table 1.3). This literature survey was by no means exhaustive, but it included representatives of most macroalgal forms. In our analysis, all characters or character states were treated as binary presence/absence variables. We performed a non-metric multidimensional scaling (MDS) analysis of the pooled data [for a detail description of the MDS method, see (Huntley et al., 2006)]. The MDS analysis allowed us to ordinate all specimens in a two-dimensional space (dimension 1 and dimension 2). The MDS scored specimens were then assigned to four geochronological bins (Paleoproterozoic 1800-1600 Ma; Mesoproterozoic 1600-1000 Ma; early Neoproterozoic 1000-750 Ma; Ediacaran 635-550 Ma) according to their probable age. MDS variances for dimension 1 and dimension 2 were then calculated for each geochronological bin. The sum of dimension 1 and dimension 2 variances is taken as a proxy for morphological disparity in each bin. The sum MDS variances are shown in Figs. 1.3–1.4. To test whether the geochronological pattern of MDS variance was due to varying sample intensity in the geochronological bins, we performed a randomization analysis (Huntley et al., 2006). The MDS score pairs associated with each specimen were shuffled randomly into one of the four geochronological bins, but the sample intensity of the geochronological bins was preserved. The MDS variance for each geochronological bin was recalculated. The process was repeated 1000 times, in order to obtain the mean and 95% confidence interval of the MDS variances after randomization (Figs. 1.3–1.4). If the observed MDS variances lie beyond the 95% confidence interval, they are unlikely to be explained by differing sampling intensity alone.

To evaluate the impact of the Tuanshanzi compressions (Yan, 1995; Zhu and Chen, 1995; Yan and Liu, 1997), we repeated our analysis with the Tuanshanzi fossils included and the results did not change significantly (compare Fig. 1.3 and Fig. 1.4). As the geochronological pattern of MDS variance show no significant difference whether the Tuanshanzi compressions are included
or excluded (Figs. 1.3–1.4), the Tuanshanzi fossils are excluded in all subsequent analyses (Figs. 1.5–1.8) because they are possibly fragmented microbial mats.

Scatter plots for each geochronological bin are shown in a two-dimensional space (Fig. 1.5A–D). Correlation coefficients were calculated between the morphological variables and MDS dimension 1 and dimension 2 scores for all species occurrences. R-values from correlation analysis were used to produce a loading chart relating the MDS morphospace to the original morphological characters (Fig. 1.5E).

As a proxy of body size, we also estimated the maximum dimension (e.g., long axis of an elliptical compression; maximum length of a ribbon-like compression; maximum height of a branching thallus; maximum dimension of a *Longfengshania* thallus including its vesicle and holdfast) of all carbonaceous compression fossils in our database. In addition, we estimated the surface/volume ratio for each specimen in our database, based on three-dimensional reconstructions of the compression fossils (see above). For example, *Chuaria circularis* was modelled as a spherical thallus with a diameter equivalent to its circular compression; *Tawuia dalensis* as a cylindrical thallus with semi-spherical ends; *Longfengshania stipitata* as a spherical to ovoidal vesicle with differentiated stipe and holdfast; and *Doushantuophyton lineare* as terete dichotomous branches with differentiated holdfast. The surface/volume ratio of *Longfengshania* and *Paralongfengshania* was estimated based on the vesicle, because it is likely that only the vesicle was photosynthetic; however, the ratio would not change significantly even if we consider the stipe and holdfast. Similarly, the holdfast of many Doushantu macroalgae, such as *Baculiphyca taeniata* and *Enteromorphites siniansis*, was not considered in the estimate of surface/volume ratio.

### 3.2.2 Results

The MDS analysis (Figs. 1.3–1.5) shows that macroalgal morphospace increased episodically in the Mesoproterozoic Era and in the Ediacaran Period, confirming the narrative description. This pattern cannot be a sampling artifact because (1) MDS scores show no correlation with bin characters (data density or geochronological duration); and (2) three of the four geochronological bins have morphological disparity outside the 95% confidence interval estimated from randomization analysis (Fig. 1.3). In addition, a discriminant analysis shows that MDS variances of all pairwise comparisons among the four geochronological bins are
significantly different (p<0.05), except the early Neoproterozoic vs. Paleoproterozoic comparison (p=0.10).

The median of the maximum dimension shows no significant change in the Proterozoic (Fig. 1.6). However, the range of maximum dimension expanded throughout the Proterozoic. The surface/volume ratio (Fig. 1.7) appears to have changed little until the Ediacaran, when both the maximum and median surface/volume ratio increased significantly (Wilcoxon test, p<0.05).

4. DISCUSSION

4.1 Comparison with Acritarch Morphological History

At the broadest scale, the MDS result appears to be similar to that of Proterozoic acritarchs (Huntley et al., 2006). Morphological disparity of Proterozoic acritarchs increased episodically in the early Mesoproterozoic and in the early Ediacaran, with a long-lasting plateau in between. The acritarch data also show morphospace contraction associated with Cryogenian (750–635 Ma) glaciations and late Ediacaran (575–542 Ma) radiation of Ediacara organisms. These details cannot be tested in the macroalgal data because of the poor geochronological resolution and the absence of macroalgal data in the Cryogenian and latest Ediacaran Period (550-542 Ma).

Given that most acritarchs were probably planktonic photoautotrophs, the first-order match between acritarch and macroalga morphological history is intriguing. The parallel between the morphological histories of Proterozoic acritarchs and macroalgae suggests an external (i.e., environmental or ecological) forcing on the morphological evolution of Proterozoic primary producers—both benthic and planktonic. Huntley et al. (2006) hypothesize that the Mesoproterozoic to early Neoproterozoic plateau of acritarch morphospace may be related to nutrient stress and a sluggish carbon cycle in approximately the same geological interval (Brasier and Lindsay, 1998; Anbar and Knoll, 2002). The macroalgal data appear to be consistent with this hypothesis, and would further imply that this environmental forcing affected both the pelagic and benthic realms. To further test this interpretation, more geochronological, chemostratigraphic (Halverson, 2006), paleoenvironmental, and paleontological data are needed to refine the temporal relationship between nutrient stress and algal evolution.
Alternatively, this Mesoproterozoic—early Neoproterozoic stasis may be interpreted in ecological terms. It has been recently proposed that the radiation of late Ediacaran large acanthomorphic acritarchs, some of which are interpreted as benthos (Butterfield, 2001), was an ecological response to macrophagous grazing by early eumetazoans which, according to molecular phylogeny and molecular clock data, diverged as benthic animals between 634 and 604 Ma (Peterson and Butterfield, 2005). Using the same argument, was the morphological evolution of macroalgae held back by the absence of animal grazing in the Mesoproterozoic—early Neoproterozoic, and was subsequently accelerated by a major top-down ecological forcing in the Ediacaran when herbivorous metazoans began to evolve? One potential problem with this hypothesis is that the macroalgal morphologies that evolved in the Ediacaran (e.g., dichotomous and monopodial branching, apical meristem, rhizoidal holdfast) do not appear to be effective morphological adaptations to defend against herbivory.

4.2 Surface/Volume Ratio

The surface/volume ratio is an important physiological factor controlling the metabolic rate of modern macroalgae. Mass-specific growth rate, measured as carbon fixed per unit of body mass per unit of time, tends to be greater in macroalgal functional-form groups with higher surface/volume ratio (Littler and Littler, 1980; Littler and Arnold, 1982). This relationship remains true whether the measurements are carried out for phylogenetically related or distant macroalgae (Hanisak et al., 1988; Steneck and Dethier, 1994; Garcia et al., 1996; Stewart and Carpenter, 2003). Clearly, the effect of surface/volume ratio on macroalgal growth rate overrides phylogenetic relatedness and is perversively convergent. Indeed, comprehensive data compilation shows that log(maximum growth rate) and log(surface/volume ratio) scale linearly over a wide range of surface/volume ratios spanning from unicellular algae, macroalgae, to rooted angiosperms (Fig. 1.8) (Nielsen and Sand-Jensen, 1990; Nielsen et al., 1996).

The surface/volume ratios of Proterozoic macroalgae are plotted toward the lower end of modern macroalgae (Fig. 1.8), but did show a significant increase in the Ediacaran (Fig. 1.7). This pattern appears to be consistent with the complete absence of some of the extremely fast-growing functional-form groups, such as leafy macroalgae [e.g., Ulva or Porphyra; (Littler and Arnold, 1982)] in the Proterozoic.
What might have caused the Ediacaran increase in surface/volume ratio? Certainly, the greater surface/volume ratios of Ediacaran macroalgae was introduced by morphological innovations of certain functional-form groups (e.g., delicately branching forms such as *Doushantuophyton*, *Anomalophyton*, and *Glomulus*), which did not appear until the Ediacaran. The question is whether the Ediacaran increase in surface/volume ratio was made possible by a major evolutionary breakthrough that overcame the intrinsic developmental barriers to greater surface/volume ratios, or it was also forced by external selective pressure.

At a fundamental level, the morphogenesis of macroalgae with greater surface/volume ratio (e.g., delicately branching forms and thin leafy forms) requires parenchymatous growth and controlled cell division. The restriction of cell division to a marginal zone of meristematic cells or an apical meristem consisting of one or a few cells appears to be a key innovation in the elaboration of thallus morphology (Graham et al., 2000; Niklas, 2000). Parenchymatous and meristematic growth has been independently achieved in all three macroalgal groups—the chlorophytes, rhodophytes, and phaeophytes, suggesting that it can be achieved with relative ease. The convergent evolution of complex thalli, together with the independent diversification of Ediacaran acritarchs, points to the possible role of external forcing as part of the equation.

Algal growth requires light, nutrient, and CO$_2$. Modern photosynthesis typically conserves <37% of the energy absorbed as photosynthetically active radiation (Falkowski and Raven, 1996), indicating that macroalgae probably have lived in light saturation even in the Paleoproterozoic when solar luminosity was about 80% of modern level (Kasting et al., 1988). Nutrient availability seems to be an unlikely driver either. Although it has been shown that nutrient uptake by micro- and macroalgae depends on surface/volume ratio (Hein et al., 1995), there is no evidence for greater nutrient availability in Mesoproterozoic oceans than in Ediacaran ones. On the contrary, pelagic oceans of the Mesoproterozoic are thought to have been nutrient-limited because of the low concentration of biologically important elements such as Fe, Mo, and P (Brasier and Lindsay, 1998; Anbar and Knoll, 2002). It is possible that the coastal oceans were decoupled, in terms of nutrient availability, from the pelagic oceans in the Mesoproterozoic—a scenario that would weaken the hypothesis to invoke nutrient stress as a factor holding back macroalgal morphological disparity in the Mesoproterozoic.

Surface-ocean CO$_2$, on the other hand, was probably more readily available in the Mesoproterozoic Era than in the Ediacaran Period, given what we know about Proterozoic
atmospheric pCO$_2$ levels (Kaufman and Xiao, 2003). Is it possible that a drop in pCO$_2$ level in the Cryogenian or Ediacaran Period may have forced macroalgae toward greater surface/volume ratio within their developmental possibilities to compensate for the lower pCO$_2$ level? There is some evidence of CO$_2$ limitation in modern macroalgae that do not use carbon concentrating mechanisms to store HCO$_3^-$ as carbon source (Raven, 2003). These algae have to depend on diffusion of CO$_2$ uptake, and their carboxylation rate is saturated at 25–35 µM [CO$_2$], while [CO$_2$] in the surface ocean is only ~10 µM (Hein and Sand-Jensen, 1997). Thus, algal growth in the absence of carbon concentrating mechanisms can be limited by [CO$_2$] under conditions of light and nutrient saturation. Indeed, controlled experiments show that growth rate of some macroalgae increases moderately with elevated [CO$_2$] or pCO$_2$ levels up to 5× present atmospheric level (Gao et al., 1993; Hein and Sand-Jensen, 1997; Kübler et al., 1999). Thus, it appears that both carbon concentrating mechanisms and greater surface/volume ratios could have been physiological and morphological responses to decreasing pCO$_2$ levels in the Ediacaran (Graham and Wilcox, 2000).

To the extent that macroalgal morphological diversification in the Ediacaran may have been driven by top-down ecological forcing by animal grazers (see 4.1), it is also possible that the Ediacaran increase in surface/volume ratio may have been caused by the same ecological process, because macroalgal surface/volume ratio may be coupled with morphological disparity. However, delicate macroalgal thalli with greater surface/volume ratio and faster growth rate (e.g., Ulva) tend to be poorly defended against metazoan grazing (Littler and Littler, 1980; Steneck and Dethier, 1994), and thus would not be the predicted outcome of herbivory forcing.

Whatever the cause, greater surface/volume ratios of Ediacaran macroalgae may have had significant consequence on the global carbon cycle. Eukaryotic phytoplankton and macroalgae are important autotrophs in coastal environments where most organic carbon burial occurs in modern oceans. Thus, macroalgal bioprodutivity could have considerable impact on the carbon cycle. A uniformitarian interpretation of the Proterozoic surface/volume data suggests that, on average, Ediacaran macroalgae were more than an order of magnitude more productive than those that came before (Fig. 1.8). Did more productive Ediacaran macroalgae (and perhaps microalgae as well?) contribute to a larger dissolved organic carbon reservoir (Rothman et al., 2003), more volatile carbon cycle, and perhaps the eventual rise of oxygen level in the Ediacaran? Here again, our ability to answer these questions is limited by the poor temporal resolution of the Proterozoic geological and paleontological record.
4.3 Maximum Canopy Height

Vertically oriented benthic organisms evolved in the Mesoproterozoic or earlier. If the presence of holdfasts in some of the Tuanshanzi compression fossils is confirmed, macroalgal canopy height was already millimeters to centimeters in the Paleoproterozoic (Yan, 1995; Zhu and Chen, 1995; Yan and Liu, 1997). *Bangiomorpha pubescens* from the Mesoproterozoic Hunting Formation has holdfast structures and was up to 2 mm in height (Butterfield, 2000). *Tawuia*-like fossils from the Mesoproterozoic Suket Shale also appear to bear holdfast structures (Kumar, 2001) and they could reach up to 14 mm in height (note that scales in Fig. 8 and Fig. 11 of Kumar, 2001 were incorrect). *Longfengshania stipitata* from early Neoproterozoic rocks (Hofmann, 1985; Du and Tian, 1986) has a well-preserved holdfast and was centimetric in height. Early Neoproterozoic *Pararenicola huaiyuanensis* and *Protoarenicola baiguashanensis* were interpreted as possible animal fossils (Sun *et al.*, 1986); however, new material (Fig. 1.2A–C) indicates that these carbonaceous compressions may represent holdfast-bearing, benthic macroalgae with a centimetric canopy height (Qian *et al.*, 2000).

The Ediacaran Period experienced a significant expansion of macroalgal canopy height. Some of the holdfast-bearing forms from the Doushantuo Formation, such as *Baculiphyca taeniata*, were decimetric in height (Xiao *et al.*, 2002). Maximum dimension of Proterozoic carbonaceous compressions, regardless whether they are benthic or planktonic, also shows a sharp increase in the Ediacaran Period (Fig. 1.6). Given that many specimens in our database are benthic macroalgae (with or without preserved holdfasts), the maximum dimension data can be taken as suggestive evidence that maximum canopy height was greater in the Ediacaran Period than before. The simultaneous increase in both maximum dimension and surface/volume ratio of Ediacaran macroalgae indicates greater morphological complexity, consistent with our morphometric analysis that shows a significant Ediacaran increase in MDS variance (Figs. 1.3–1.5).

4.4 Ecological Interactions with Animals

Ecological interactions among living organisms form a complex network (Fig. 1.9). The nature of ecological interactions includes competition, predation, symbiosis, parasitism, herbivory, and many others. Very little is known about ecological interactions in the Proterozoic
ecosystem (Fig. 1.9). Among the few examples of ecological interactions in the Proterozoic are predation on *Cloudina* animals (Bengtson and Yue, 1992; Hua *et al.*, 2003) and lichen-like algal-fungal symbiosis (Yuan *et al.*, 2005), both are preserved in Ediacaran rocks.

Is there paleontological evidence for Proterozoic macroalga-animal interactions? Herbivory is an important form of macroalga-animal interaction, but so far we have identified no direct evidence for herbivory in Proterozoic carbonaceous compression fossils. Proterozoic macroalgal fossils, at least those >550 Ma in age, typically do not have wounds, particularly healed wounds. There might be a taphonomic issue here; after all, healed wounds are not usually preserved in the meagre fossil record of Phanerozoic macroalgae either. The complete absence of crustose calcareous algae in the Proterozoic, however, is a real signal. In fact, some phosphatized algae from the Doushantuo Formation are probably phylogenetically related to modern calcareous coralline algae but lacked biocalcification (Xiao *et al.*, 2004). Insofar as biocalcification is an effective protection against herbivory and calcareous coralline algae depend on herbivore denudation to prevent epiphyte colonization (Steneck, 1983), the lack of calcareous algae in the Proterozoic is circumstantial evidence for the absence of herbivory, at least Phanerozoic-style herbivory. Incidentally, this inference is also consistent with conclusions derived from phylogenetic arguments that herbivores appeared relatively late among animal groups (Vermeij and Lindberg, 2000). In addition, the dominance of simple discoidal and delicate rhizoidal holdfasts in Proterozoic benthic macroalgae, as well as the concurrent absence of robust holdfasts (e.g., in modern seaweeds such as *Laminaria* and *Caulerpa*), indicates that animal bioturbation in normal marine soft substrates was relatively weak and that the microbially dominated substrates were firmer and less soupy prior to ~550 Ma (Seilacher, 1999; Bottjer *et al.*, 2000; Droser *et al.*, 2002).

The indirect evidence for the insignificance of herbivory and bioturbations can be interpreted in three different ways: animals did not evolve until 550 Ma; they were microscopic (millimetric or smaller) prior to 550 Ma, hence leaving unrecognizable traces; or they were macroscopic but not effective herbivores or burrowers. Regardless, the limited evidence seems to suggest that macroalga-animal interactions were comparatively weak or unrecognizable in the fossil record. This is particularly true for Phanerozoic-style herbivory, but it remains to be seen whether other forms of macroalga-animal interactions, for example parasitism, commensalism,
and herbivory on microalgae, played a significant role in the ecological evolution in the Ediacaran.

5. CONCLUSIONS

This chapter critically reviews the macroalgal affinity of Proterozoic carbonaceous compression fossils, particularly the sinosabelliditids and protoarenicolids, presents results of quantitative analysis of morphologies of presumed macroalgae of Proterozoic age, and discusses their paleoecological implications. The analysis reveals that the morphological history of Proterozoic macroalgae is similar to that of Proterozoic acritarchs. At the broadest scale, macroalgal morphological disparity in the Paleoproterozoic was low but increased in the Mesoproterozoic Era and in the Ediacaran Period, with a prolonged plateau in between. It is hypothesized that the morphological plateau in the Mesoproterozoic and early Neoproterozoic may be related to nutrient stress or/and the lack of ecological forcing by animals.

The Ediacaran increase in macroalgal morphological disparity during 635-550 Ma is coupled with concurrent increase in thallus surface/volume ratio and maximum canopy height of benthic macroalgal communities. A uniformitarian interpretation of this pattern suggests that Ediacaran macroalgal communities, in comparison with earlier ones, were dominated by taller and more complex benthic algae that grew faster. It is hypothesized that the elaboration of macroalgal morphology and increase in surface/volume ratio may have been driven by lower pCO2 levels and/or by herbivory forcing in the Ediacaran Period. Regardless, benthic macroalgal communities probably have been some of the highly productive areas since the Ediacaran, and they may be an important piece in the puzzle of Ediacaran carbon cycle, carbon isotope excursions, and oxygen evolution. As a final remark, we would like to reiterate the preliminary nature of these conclusions, which should be tested in the future with an expanded database, better resolved geochronology, and further improved phylogenetic interpretations.

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Kumar, S., 2001, Mesoproterozoic megafossil *Chuaria–Tawuia* association may represent parts of a multicellular plant, Vindhyan Supergroup, Central India, *Precambrian Res.* **106**: 187-211.


Table 1.1. Temporal distribution of important macroalgal features (+: presence; ?: possible presence).

<table>
<thead>
<tr>
<th></th>
<th>Paleoproterozoic (2500-1600 Ma)</th>
<th>Mesoproterozoic (1600-1000 Ma)</th>
<th>early Neoproterozoic (1000-750 Ma)</th>
<th>Ediacaran (635-542 Ma)</th>
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<tbody>
<tr>
<td><strong>Thallus Morphologies</strong></td>
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<tr>
<td>Spherical</td>
<td>+</td>
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<td>Ellipsoidal</td>
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<td>Tomaculate</td>
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<td>Cylindrical</td>
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<td>Conical</td>
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<td>Fan-shaped</td>
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<td><strong>Thallus Differentiation</strong></td>
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<td>Holdfast present</td>
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<td>Discoidal holdfast</td>
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<td>Rhizoidal holdfast</td>
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<td>Stipe</td>
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<td>Blade</td>
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<td><strong>Other Features</strong></td>
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<tr>
<td>Transverse annulation</td>
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<td>Dichotomous Branching</td>
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<td>+</td>
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<td>Monopodial branching</td>
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<td>Apical meristem</td>
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<td>Thallus differentiation</td>
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<tr>
<td>2. Ellipsoidal</td>
<td>10. Discoidal holdfast</td>
<td>15. Dichotomous Branching</td>
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<td>6. Conical</td>
<td></td>
<td>19. Colonial appearance (e.g., in some <em>Beltanelliformis</em> populations)</td>
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<tr>
<td>7. Fan-shaped</td>
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<tr>
<td>8. Filamentous</td>
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Table 1.3. List of geochronological bins and source data.

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<tr>
<th>Geochronological Bin</th>
<th>Source Data</th>
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<tbody>
<tr>
<td><strong>Paleoproterozoic (1800–1700 Ma): 29 specimens, 4 described species</strong></td>
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</tr>
<tr>
<td>Changzhougou Fm., 1800–1625 Ma</td>
<td>(Zhu et al., 2000)</td>
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<tr>
<td>Tuanshanzi Fm., 1800–1625 Ma</td>
<td>(Du and Tian, 1986)</td>
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<tr>
<td>Tuanshanzi Fm., 1800–1625 Ma</td>
<td>(Zhu and Chen, 1995), 10 specimens not included in further analysis</td>
</tr>
<tr>
<td><strong>Mesoproterozoic (1600–1000 Ma): 46 specimens, 7 described species</strong></td>
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<tr>
<td>Hongshuizhuang &amp; Gaoyuzhuang Fm., ~1400 Ma</td>
<td>(Du and Tian, 1986; Walter et al., 1990)</td>
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<td>Rohtas Fm., 1600–1000 Ma</td>
<td>(Kumar, 1995)</td>
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<tr>
<td>Suket Shale, 1600–1000 Ma</td>
<td>(Kumar, 2001)</td>
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<tr>
<td><strong>Early Neoproterozoic (1000–750 Ma): 422 specimens, 76 described species</strong></td>
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<td>Liulaobei, Jiuliqiao, Jinshanzhai, Shijia, Weiji, &amp; Gouhou Fm., ~850 Ma</td>
<td>(Duan, 1982; Wang and Zhang, 1984; Steiner, 1997)</td>
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<tr>
<td>Wyniatt Fm., 1077–723 Ma</td>
<td>(Hofmann and Rainbird, 1994)</td>
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<tr>
<td>Xiamaling, Changlongshan, &amp; Nanfen Fm., ~850 Ma</td>
<td>(Duan, 1982; Du and Tian, 1986)</td>
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<td>Halkal Formation, ~850 Ma</td>
<td>(Maithy and Babu, 1996)</td>
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<tr>
<td>Shihuiding Formation, ~850 Ma</td>
<td>(Zhang et al., 1991; Zhang et al., 1995)</td>
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<tr>
<td>Little Dal Formation</td>
<td>(Hofmann, 1985)</td>
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<tr>
<td>Late Riphean Pav’yuga Formation (?)</td>
<td>(Gnilovskaya et al., 2000)</td>
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<tr>
<td><strong>Ediacaran (635–550 Ma): 91 specimens, 27 described species</strong></td>
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<tr>
<td>Doushantuo Formation, 635–550 Ma</td>
<td>(Steiner, 1997; Xiao et al., 2002)</td>
</tr>
<tr>
<td>Lantian Formation, 635–550 Ma</td>
<td>(Yuan et al., 1999)</td>
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Figure 1.1. (A) *Chuaria circularis* from the early Neoproterozoic Huaibei Group, North China. (B) *Bipatinella cervicalis* (a *Tawuia*-like fossil) from the early Neoproterozoic Huaibei Group, North China. (C) *Longfengshania stipitata* from the early Neoproterozoic Little Dal Group, northwestern Canada. Photo courtesy of Hans Hofmann. (D) *Ellipsophysa axicula* from the early Neoproterozoic Jiuliqiao Formation, North China. (E) *Seirisphaera zhangii* from the Ediacaran Lantian Formation, South China. Photo courtesy of Chen Meng’e. Scale bar represents 1 mm if not otherwise indicated.
Figure 1.2. (A–C) Specimens that can be identified as *Protoarenicola baiguashanensis* from the early Neoproterozoic Huaibei Group, North China. Transverse annulations not well preserved in (A). Note discoidal holdfast-like structures (arrows). Figure (C) courtesy of Xunlai Yuan. (D) *Doushantuophyton lineare* from the Ediacaran Doushantuo Formation, South China. (E) *Baculiphyca taeniata* from the Ediacaran Doushantuo Formation, South China. (F) Phosphatized algal thallus (possibly *Thallophyca ramosa*) from the Ediacaran Doushantuo Formation, South China. Scale bars represent 1 mm.
Figure 1.3. Results of MDS analysis and randomization test with the Tuanshanzi material excluded. Shaded bars represent MDS variances of the four geochronological bins. Filled squares, diamonds, and triangles represent the 97.5% percentile, mean, and 2.5% percentile of the randomization test. Thus, the filled square and triangle bracket the empirically determined 95% confidence interval for each bin. Note that three of the four bins have MDS variances outside the 95% confidence intervals.
Figure 1.4. Results of MDS analysis (A) and randomization test (B) with the Tuanshanzi material included. See Fig. 3 for explanation.
Figure 1.5. (A–D) Scatter plots showing realized morphospace in each geochronological bin (convex hulls in dashed line) in comparison with occupied morphospace when all Proterozoic data are pooled (convex hulls in solid line). The seemingly small occupied morphospace in Mesoproterozoic as compared with early Neoproterozoic may be related to its smaller sample size. (E) Loading diagram showing characters with significant loadings.
Figure 1.6. Maximum dimension (in mm) of Proterozoic carbonaceous compressions in linear (left) and \( \log_{10} \) scales (right). Box-and-whisker plots show median, lower and upper quartiles, and maximum and minimum values of each geochronological bin.
Figure 1.7. Surface/Volume ratio (in mm^2/mm^3) of Proterozoic carbonaceous compressions in linear (left) and log_{10} scales (right). Box-and-whisker plots show median, lower and upper quartiles, and maximum and minimum values of each geochronological bin.
Figure 1.8. Top: the relationship between surface/volume ratio and maximum growth rate (left vertical scale) of modern photosynthetic eukaryotes [modified from (Nielsen and Sand-Jensen, 1990)]. Mean surface/volume ratios for the four Proterozoic bins are plotted along the regression line, to show the Ediacaran increase in surface/volume ratio. Bottom: surface/volume ratio distribution (right vertical scale) of all Proterozoic macroalgae in our database.
Figure 1.9. Organismal interactions in modern ecosystems (left) compared with what we know about ecological interactions in the Proterozoic (Bengtson and Yue, 1992; Seilacher, 1999; Yuan et al., 2005). Animal-algal interactions are indirectly inferred based on arguments presented by Peterson and Butterfield (2005), not on direct fossil evidence. Modified from (Taylor et al., 2004).
Chapter 2

Restudy of the worm-like carbonaceous compression fossils *Protoarenicola*, *Pararenicola*, and *Sinosabellidites* from early Neoproterozoic successions in North China

Abstract

The carbonaceous compression fossils *Protoarenicola baiguashanensis* Wang, 1982, *Pararenicola huaiyuanensis* Wang, 1982, and *Sinosabellidites huainanensis* Zheng, 1980, from the early Neoproterozoic Liulaobei and Jiuliqiao formations in northern Anhui, North China, were previously interpreted as worm-like metazoans, largely on the basis of transverse annulations and purported proboscis structures. If correct, these would be some of the earliest known bilaterian animals and would provide a key paleontological calibration to molecular clock analyses. In this study, we examine a large population of these carbonaceous fossils, clarify their taxonomy, and provide new insights into their morphological, paleoecological, and phylogenetic interpretations.

Although all three species are characterized by annulated tubes, *Protoarenicola baiguashanensis* bears a bulbous terminal structure at one end of its tube. *Pararenicola huaiyuanensis* is characterized by a constricted opening at one end and a closed termination at the other. The two ends of *Sinosabellidites huainanensis* tubes are both closed and round. The bulbous terminal structure in *Protoarenicola baiguashanensis* was previously interpreted as an animal proboscis, but new observations suggest that it was more likely a holdfast structure analogous to discoidal holdfast structures of the Mesoproterozoic *Tawuia*-like fossil *Radhakrishnaniana* Kumar, 2001, and the frondose Ediacara fossil *Charniodiscus* Ford, 1958. Furthermore, it is possible that at least *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis* may represent reproductive or taphonomic fragments of the same organism. This reinterpretation weakens the previous interpretation that *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis* were worm-like bilaterian animals. Instead, they can be alternatively interpreted as erect epibenthic organisms, possibly coenocytic algae reaching a tiering height of 30 mm.
Keywords: Protoarenicola, Pararenicola, Sinosabellidites, Neoproterozoic, North China, bilaterian animal, coenocytic algae

1. INTRODUCTION

The fossil record of pre-Ediacaran metazoans has been controversial. Among the purported pre-Ediacaran metazoan fossils are early Neoproterozoic carbonaceous fossils discovered several decades ago from the Liulaobei and Jiuliqiao formations in northern Anhui of North China (Zheng, 1980; Wang, 1982; Xing, 1984; Sun et al., 1986; Chen, 1988). These fossils have been classified in the families Protoarenicolidae and Sinosabelliditidae (Hofmann, 1994), and have been interpreted as possible worm-like bilaterian animals (Zheng, 1980; Wang, 1982; Xing, 1984; Sun et al., 1986; Chen, 1988). Because of their possible age of 700–800 Ma, they have also been cited as paleontological evidence in support of a deep protostome-deuterostome divergence in the Mesoproterozoic or early Neoproterozoic as estimated by some molecular clock studies (e.g., Wray et al., 1996). Thus, a critical evaluation of their possible animal affinity becomes crucial as to whether there is solid paleontological support for such deep molecular clock estimates. A restudy of the worm-like fossils from the Liulaobei and Jiuliqiao formations is particularly warranted, because preliminary analysis of similar fossils from the probably equivalent Jinshanzhai Formation, also in northern Anhui, questions the bilaterian interpretation of the Liulaobei and Jiuliqiao material (Qian et al., 2000).

Worm-like fossils from the Liulaobei and Jiuliqiao formations are preserved as carbonaceous compressions. They are considered as early Neoproterozoic examples of Burgess Shale-type preservation (Butterfield, 1995). Despite their exceptional preservation, the study of these fossils is met by two significant challenges. First, because these fossils are compressed in two dimensions, their three dimensional morphology and paleoecology are usually difficult to reconstruct. This challenge is not unique to this particular study. Paleontologists working on Burgess Shale-type fossils face exactly the same challenge. As has been demonstrated in the study of Burgess Shale fossils (e.g., Whittington, 1985), careful examination can offer incredible insight into the three-dimensional morphology and paleoecology of these fossils. A greater challenge, however, is the relatively simple morphologies of these fossils. Like many pre-Ediacaran carbonaceous compression fossils (Xiao and Dong, 2006), the Liulaobei and
Jiuliqiao assemblages are dominated by simple ribbon-shaped, tomaculate, elliptical, or circular compressions that are broadly similar to *Tawuia dalensis* Hofmann *in* (Hofmann and Aitken, 1979) and *Chuaria circularis* Walcott, 1899. The simple ribbon-shaped to circular morphologies can be achieved convergently by a number of developmental pathways, making phylogenetic interpretation difficult.

Fortunately, on the basis of a large population of newly collected specimens, we were able to identify rare specimens that are preserved three-dimensionally in carbonates of the Jiuliqiao Formation. Additionally, a number of specimens from the Jiuliqiao Formation have very well preserved terminal structures. The purpose of this paper is to report these new observations, which together with the recently reported material from the Jinshanzhai Formation (Qian et al., 2000) will significantly aid the morphological, paleoecological, and phylogenetic interpretation of these early Neoproterozoic carbonaceous compression fossils.

2. GEOLOGICAL SETTINGS AND STRATIGRAPHY

The paleogeographic location of the North China Block during the Neoproterozoic has not been well constrained. There have been some paleomagnetic data reported from the Liulaobei and Jiuliqiao formations in northern Anhui; however, these are considered as possible Mesozoic overprint (Zhang et al., 2006). One version of paleogeographic reconstruction places the North China Block in mid- to low-latitude areas during the early to middle Neoproterozoic (Fig. 2.1A; Li et al., 2004).

Early Neoproterozoic successions are well known and studied in the North China Block (Tianjin Institute of Geology and Mineral Resources, 1980). For example, the Qingbaikou System in the Jixian area near Beijing has been regarded as a yardstick in early Neoproterozoic stratigraphy in North China, and has been studied intensively. Equivalent early Neoproterozoic strata in southern Liaoning Province, northern Anhui Province, and northern Jiangsu Province have also been investigated thoroughly. However, late Neoproterozoic (i.e., Cryogenian and Ediacaran) outcrops are few and poorly documented in the North China Block (Shen et al., in press). This pattern in North China is in sharp contrast to South China, where early Neoproterozoic successions are poorly developed but Cryogenian-Ediacaran strata are widespread and well documented (Liu, 1991). This contrast is not surprising because the two
blocks were separated in the Neoproterozoic and Paleozoic, until they collided in late Paleozoic
to early Mesozoic (Wang, 1985).

Early Neoproterozoic successions in the southeastern margin of the North China Block
(i.e., in the Xuzhou area of northern Jiangsu Province and Huai River Drainage of northern Anhui
Province) are similar to those in the northeastern margin (i.e., eastern Shandong Province and
southeastern Liaoning Province). These lithostratigraphic successions are also similar to those in
North Korea, of which only preliminary information has been published (Yin, 1990). The
lithostratigraphic similarities indicate that early Neoproterozoic successions in these areas were
probably deposited in a contiguous basin but were later separated by the sinistral Tanlu Fault
(Zhang, 1997; Chung, 1999; Qiao et al., 2001). These areas, forming an elongate strip >1000 km
long and ranging from northern Anhui to southern Liaoning, are collectively known as the
River). Early Neoproterozoic successions in the Jiao-Liao-Xu-Huai realm typically begin with
coarse quartz sandstone, succeeded by mudstone/shale, and finally by carbonate (Xing, 1989;
Xing et al., 1996). This tripartite sequence is unconformably overlain by a diamictite deposit,
possibly of Cryogenian or Ediacaran age (Shen et al., in press).

The exposure of early Neoproterozoic outcrops in the Huai River Drainage of northern
Anhui is sporadic (Fig. 2.1B). For historical reasons, lithostratigraphic nomenclatures in the
northern and southern parts of this region are different (Table 2.1, Fig. 2.2) and the correlation
between them has been in a state of flux. Following Cao et al., (1989), the early Neoproterozoic
sequence in the northern part, or the Huaibei (northern Huai) region, is named the Huaibei Group.
The Huaibei Group consists of, in ascending order, the dominantly siliciclastic Lanling, Xinxing,
and Jushan formations, followed by carbonate units (Jiayuan, Zhaowei, Niyuan, Jiudingshan,
Zhangqu, and Weiji formations), shale/sandstone/carbonate of the Shijia Formation, molar tooth
carbonate of the Wangshan Formation, shale/sandstone/carbonate of the Jinshanzhai Formation, and
dolostone/shale/sandstone with halite molds of the Gouhou Formation. This succession is
overlain, probably unconformably, by the early Cambrian Houjiashan Formation that contains
small shelly fossils and trilobites. Previous investigators (Wang et al., 1984a) also reported small
shelly fossils such as *Chancelloria* Walcott, 1920 and *Cupitheca* Duan in Xing et al., 1984 from
the Jinshanzhai Formation, but this has not been confirmed by our own investigation. Molar tooth
structures, similar to those found in carbonates of the Mesoproterozoic Belt Supergroup
Horodyski, 1976; Frank and Lyons, 1998) and the Neoproterozoic Little Dal Group (Hofmann, 1985; James et al., 1998), occur in the Huaibei Group, including the Jiayuan, Zhaowei, Jiudingshan, Weiji, and particularly the Wangshan Formation (Jia et al., 2003; Meng and Ge, 2004); it is worth noting that molar tooth structures are also common in early Neoproterozoic successions in southern Liaoning Province (Fairchild et al., 1997). The carbonaceous fossils Chuaria, Ellipsophysa Zheng, 1980, and Tawuia have been reported from the Weiji, Shijia, and Gouhou formations (Wang et al., 1984a; Zheng et al., 1994). More relevant to the theme of this paper is the occurrence of the worm-like carbonaceous compression fossils Pararenicola huaiyuanensis from the lowermost shale of the Shijia Formation (Wang et al., 1984a; Xing et al., 1985) and Protoarenicola baiguashanensis from shaly interbeds of the Jinshanzhai Formation (Wang et al., 1984a; Xing et al., 1985; Qian et al., 2000).

The focus of this paper, however, is Neoproterozoic successions in the southern Huai River Drainage, or the Huainan (southern Huai) area. The early Neoproterozoic succession in the Huainan area, following Sun et al. (1986), is divided into two groups—in ascending order, the Huainan and Feishui groups that are interpreted to represent two fining-upward cycles (Fig. 2.2). Siliciclastic lithologies dominate the Huainan Group, which consists of the Caodian, Bagongshan, and Liulaobai formations. The Caodian Formation unconformably overlies the metamorphosed Mesoproterozoic Fengyang Group (Yao and Zhang, 1985). It is variable in thickness (0–21 m) and consists of polymictic conglomerate with clasts derived from quartzite, phyllite, schist, and marble. The overlying Bagongshan Formation also varies in thickness (40–86 m) and consists mainly of light grey quartz sandstone. The conformably overlying Liulaobei Formation is about 700–800 meters thick and can be divided into two members. The lower member consists of purplish red to yellowish green, thin- to medium-bedded calcareous mudstone intercalated with purplish red calcareous shale. The upper member is composed of yellowish green shale with thin-bedded, fine-grained quartz sandstone, and argillaceous limestone. The Liulaobei Formation yields abundant leispherid acritarchs (Yan, 1982; Yin, 1983; Wang et al., 1984a; Yin, 1985; Zang and Walter, 1992; Yin, 1994; Yin, 1999) and macroscopic carbonaceous compression fossils such as Chuaria, Tawuia, Ellipsophysa, and Sinosabellidites Zheng, 1980 (Wang et al., 1984a; Xing et al., 1985; Sun et al., 1986).

The Feishui Group represents another fining-upward cycle. It begins with light grey, thick-bedded, calcareous quartz and feldspathic sandstone of the Shouxian Formation (34–92 m
thick). Well-developed parallel and cross laminations in the Shouxian sandstone suggest in a nearshore to shallow marine environment (Xing et al., 1996). The conformably overlying Jiuliqiao Formation (26–45 m thick) consists mainly of thin-bedded argillaceous limestone, stromatolitic limestone, with calcareous siltstone intercalations. Macroscopic carbonaceous compression fossils, including *Chuaria*, *Ellipsophysa*, *Sinosabellidites*, as well as the annulated worm-like fossils *Pararenicola* Wang, 1982, and *Protoarenicola* Wang, 1982, are abundant in this formation (Zheng, 1980; Wang, 1982; Wang et al., 1984b; Xing et al., 1985; Chen and Zheng, 1986; Sun et al., 1986; Chen, 1988; Fu, 1989; Hofmann, 1992; Hofmann, 1994) The Jiuliqiao Formation also contains a moderately diverse leospherid acritarch assemblage that is broadly similar to the underlying Liulaobei assemblage (Hong et al., 2004). The Jiuliqiao Formation is conformably overlain by the ~250-m-thick Shidingshan Formation, which can be subdivided into three lithostratigraphic members. The lower member consists of grey medium- to thick-bedded dolomicrite, whereas the middle and upper members are composed of dolostones with chert nodules. Abundant columnar stromatolites occur in the Shidingshan Formation, which represents the uppermost Feishui Group and is unconformably overlain by the Fengtai diamicite (Cryogenian or Ediacaran in age) or the early Cambrian Houjiashan Formation.

As mentioned above, the correlation between the Neoproterozoic successions in the Huaibei and Huainan areas is uncertain. The currently accepted correlation (Fig. 2.2) is based solely on lithostratigraphy. There are reasons to be cautious about this correlation, because the lithostratigraphic succession in the Huaibei region is based on concatenated sections at isolated outcrops (Wang et al., 1984a; Zheng et al., 1994). In addition, the occurrence of *Pararenicola* and *Protoarenicola* in the Jiuliqiao Formation (Huainan) and Shijia and Jinshanzhai formations (Huaibei) is inconsistent with the currently accepted correlation (Fig. 2.2). Zheng et al. (1994) proposed, on the basis of the common occurrence of *Chuaria* and *Tawuia* fossils, that the Shijia Formation and the lower Wangshan Formation in Huaibei may be correlated with the Liulaobei Formation in Huainan. The biostratigraphic significance of *Chuaria*, *Tawuia*, *Protoarenicola*, and *Pararenicola* remains to be tested, and in this paper we cautiously follow the traditional correlation (Wang et al., 1984a).

The age of the Neoproterozoic successions in the Huainan area is poorly constrained. Previous investigators have proposed that the Huaibei, Huainan, and Feishui groups are entirely or partly late Neoproterozoic in age and have correlated some of these units with the Sinian
System in South China (Wang et al., 1984a; Sun et al., 1986; Xing, 1989; Zang and Walter, 1992; Xing et al., 1996); the Sinian System, before it was redefined to include only the Ediacaran strata of the Doushantuo and Dengying formations (China Commission on Stratigraphy, 2001), was equivalent to the Cryogenian and Ediacaran systems. The basis for the late Neoproterozoic age assignment and Sinian correlation was the interpretation of *Protoarenicola* as an animal fossil and the assumption that bilaterian animals only occur in the Ediacaran. This biostratigraphic basis is weak because, as we argue in this paper, the bilaterian interpretation of *Protoarenicola* is problematic.

On the other hand, several investigators have proposed that the Huaibei, Huainan, and Feishui groups are early Neoproterozoic in age, predating the Cryogenian glaciations (Cao et al., 1989; Fu, 1989; Steiner, 1994; Xue et al., 2001). This conclusion was based on stromatolite biostratigraphy and the occurrence of *Chuaria*, *Ellipsophysa*, and *Tawuia* in the Huaibei, Huainan, and Feishui groups. Limited chemostratigraphic data are also consistent with an early Neoproterozoic age. The Huainan and Feishui groups are characterized by moderately positive $d^{13}C$ values (0–4‰ PDB) and $^{87}Sr/^{86}Sr$ values between 0.706178 and 0.708711 (Zang and Walter, 1992; Yang et al., 2001). Similarly, the Huaibei Group is characterized by $d^{13}C$ values of 0–4‰ with a few outliers and by $^{87}Sr/^{86}Sr$ values between 0.705252 and 0.708711 (Zang and Walter, 1992; Yang et al., 2001).

No reliable geochronometric data have been published for the Huaibei, Huainan, and Feishui groups. A number of Rb-Sr and K-Ar ages were reported in the 1980’s, but these ages are not reliable because of their large uncertainty and the unpredictable behavior of the Rb-Sr and K-Ar geochronological systems. For example, a Rb-Sr isochron age of 840 ± 72 Ma from the Liulaobei Formation (Wang et al., 1984a), a K-Ar age of 738.6 Ma from the Shouxian Formation, a K-Ar glauconite age of 749.8 Ma from the Shouxian Formation (Wang et al., 1984a), and a K-Ar age of 738.5 Ma from the Jiuliqiao Formation have been cited in many publications (Sun et al., 1986; Chen, 1988; Fu, 1989; Zheng et al., 1994), although the isotopic measurements have never been formally published. In the Huaibei region, most published radiometric ages are also between 650 Ma and 850 Ma (Yang et al., 1980, Zheng et al., 1994). More recently, Yang and colleagues attempted Sm-Nd dating of diagenetic cherts from the Sidingshan Formation in the Huainan region, which gave an isochron age of 801±46 Ma (Yang et al., 2004a). Furthermore, Liu and colleagues reported SHRIMP zircon U-Pb ages between 976±24 Ma and 1038±26 Ma.
from dolerites that intrude the Zhaowei and Niyuan formations of the Huaibei Group in the Huaibei region (Liu et al., 2005). Broadly similar zircon SHRIMP zircon U-Pb ages (904±15 Ma and 1125±38 Ma) have been reported from dolerites that cut the correlative Neoproterozoic rocks in northern Jiao-Liao-Xu-Huai (i.e., southern Liaoning Province), although these ages have been interpreted as representing inherited zircons in magmas emplaced in the Triassic (Yang et al., 2004b). Given these admittedly weak age constraints and the lack of any characteristic Ediacaran acritarchs, we tentatively interpret the Huaibei, Huainan, and Feishui groups as early Neoproterozoic (probably pre-Cryogenian) deposits.

Fossils described in this paper were collected mostly from the Jiuliqiao Formation at the Shouxian and Huaiyuan sections in the Huainan region, with a small number of specimens from the Liulaobei Formation at the Shouxian section (Fig. 2.1). These fossils mostly occur in calcareous mudstone interbedded between carbonates of the Jiuliqiao Formation, and in grey shale of the Liulaobei Formation. The fossiliferous beds were probably deposited in subtidal environments. The fossils were examined under a dissecting microscope. Selected rock chips with exposed fossils were embedded in epoxy and thin-sectioned in controlled orientations.

3. SYSTEMATIC PALEONTOLOGY

A number of species of macroscopic carbonaceous compression fossils have been described from early Neoproterozoic successions in the Jiao-Liao-Xu-Huai stratigraphic realm. In this paper, we focus on annulated ribbon-shaped fossils (*Protoarenicola*, *Pararenicola*, and *Sinosabellidites*) that were interpreted as bilaterian animals, based on material collected from the Liulaobei and Jiuliqiao formations in the Huainan region. We will also discuss similar annulated, ribbon-shaped fossils from early Neoproterozoic successions in the Huaibei region (i.e. the Jinshanzhai Formation; Wang et al., 1984a; Xing et al., 1985; Qian et al., 2000) and in the southern Liaoning area (e.g., the Changlingzi, Nanguanling, and Getun formations; Hong et al., 1991). Other carbonaceous compression fossils, such as *Chuaria*, *Ellipsophysa*, and *Tawuia*, also occur in the Liulaobei and Jiuliqiao formations, but their systematics is not treated here.

The synonym lists provided in the systematic description are limited to carbonaceous compression fossils from the Jiao-Liao-Xu-Huai realm. A number of annulated ribbon-shaped fossils, many of which are incompletely preserved, have been described under a variety of
taxonomic names. Some of these can be considered junior synonyms of *Protoarenicola*, *Pararenicola*, or *Sinosabellidites*, while others do not have sufficient diagnostic features, because of incomplete preservation, to allow synonymization or to justify separate taxonomic names (Table 2.2).

All illustrated specimens are reposited at the Virginia Polytechnic Institute and State University Geosciences Museum (VPIMG).

Genus *PROTOARENICOLA* Wang, 1982, emended

*Type species.*—*Protoarenicola baiguashanensis* Wang, 1982

*Emended diagnosis.*—Slender cylindrical tubular organisms typically preserved as compressed ribbons. Ribbons straight or slightly curved, millimetric to submillimetric in width, millimetric to centimetric in length, and ornamented with transverse annulations (~15 annuli per mm length; Fig. 2.3). A distinct bulbous structure (preserved as elliptical or circular terminal disc) is present at one end that is arbitrarily designated as the proximal end. Terminal disc not annulated and typically darker than the ribbon. Ribbon may taper slightly toward the terminal disc.

*Discussion.*—Wang (1982) first established this genus based on two specimens, one of which was illustrated as the holotype (Wang, 1982, plate 2, figure 3). This specimen has transverse annulations and an ovate body at one end. Wang (1982) described the terminal ovate body as a proboscis and interpreted *Protoarenicola* as an annelid worm. The amended diagnosis of Sun et al. (1986) identifies two features that distinguish *Protoarenicola* from *Pararenicola*: (1) its ovate terminal disc that he also interpreted as a proboscis; and (2) its slender tube with a width/length ratio less than 1/20. Whereas the width/length ratio of *Protoarenicola* is indeed smaller than *Pararenicola*, the 1/20 cutoff is arbitrary and impractical because many specimens are incompletely preserved. For example, measurements of our specimens and published illustrations show that many terminal disc-bearing specimens have a width/length ratio greater than 1/20 (Fig. 2.4), partly because the ribbons are incompletely preserved. Chen (1988) noted that the terminal proboscis-like structure is morphologically irregular and interpreted this irregularity as representing different degrees of proboscis eversion. While some of Chen’s (1988) specimens have terminal discs, others do have irregular terminal structures (e.g., Chen, 1988, pl. 3, fig. 14). However, the irregular terminal structures appear to be torn discs and are thus likely
preservational artifacts. The amended diagnosis proposed here removes preservational artifacts (i.e., irregular terminal structures) and the arbitrary width/length ratio cutoff from the identification criteria of this genus.

*Protoarenicola* can be differentiated from other annulated ribbon-shaped compressions by its characteristic terminal disc. *Pararenicola* and *Sinobellidites*, which co-occur with *Protoarenicola*, are similarly annulated, but they do not have a terminal disc; instead, *Pararenicola* has one closed end and the other with a constricted opening, while both ends of *Sinobellidites* are round and closed. In addition, *Pararenicola* ribbons are typically shorter. Possibly, *Pararenicola* ribbons are propagation forms that abscised from *Protoarenicola*, a possibility that will be discussed below under the morphological and ecological reconstruction of *Pararenicola huaiyuanensis*. If correct, then *Pararenicola* and *Protoarenicola* would be considered as synonyms, and the former would have page priority (Wang, 1982). At present, we do not have sufficient evidence to verify the possible ontogenetic or taphonomic relationship between *Pararenicola* and *Protoarenicola*, and these two genera are kept separate for practical reasons.

*Parmia* Gnilovskaya, 1998 from upper Riphean deposits of southern Timan is another early Neoproterozoic annulated ribbon-shaped fossil and shows some striking similarities to *Protoarenicola*, *Pararenicola*, and *Sinobellidites* in size and annulation density (Gnilovskaya, 1998; Gnilovskaya et al., 2000). However, *Parmia* is said to have two closed ends and a longitudinal cord, and does not have a terminal disc. Similarly, *Saarina* Sokolov, 1965, *Sabellidites* Yanishevsky, 1926, *Parasabellidites* Sokolov, 1967, *Sokoloviina* Kirjanov, 1967 in Sokolov, 1967, and *Calyptrina* Sokolov, 1967 are all annulated ribbon-shaped fossils from early Cambrian rocks, but they do not have a terminal disc either. Additionally, they are interpreted as cuticular tubes of pogonophoran animals (Sokolov, 1965; Sokolov, 1967; Sun et al., 1986). Furthermore, the tube walls of *Sabellidites* consist of interwoven nanometer-sized filaments (Urbanek and Mierzejewska, 1977; Ivantsov, 1990; Moczydlowska, 2003), a feature that does not occur in any of the Huainan material.

Ribbon-shaped compressions identified as *Grypania spiralis* Walter et al., 1976 from the Mesoproterozoic Rohtas Formation of central India are also annulated (Kumar, 1995). However, their annulations are much sparser than *Protoarenicola*, their ribbons are characteristically coiled, and they do not have a terminal disc.
Two carbonaceous compression genera from the Neoproterozoic Doushantuo Formation also have transverse annulations (Xiao et al., 2002). *Calyptrina striata* Sokolov, 1967 has flange-like transverse bands that are much more widely spaced than the transverse annulations in *Protoarenicola*, *Pararenicola*, and *Sinosabelldites*. The Doushantuo specimens are incomplete and it is uncertain if they had a terminal structure. *Sinospingia typica* Li in (Ding et al., 1996) from the Doushantuo Formation does have a discoidal (or sometimes rhizoidal) terminal structure, but its conical tube is much larger in size (3–15 mm in maximum width and up to 150 mm in length).

*Radhakrishnania* Kumar, 2001, from the Suket Shale of the Mesoproterozoic Vindhyan Supergroup in central India, does have a terminal disc (Kumar, 2001). Kumar (2001) reconstructed *Radhakrishnania* as a benthic chlorophyte/xanthophyte alga with a discoidal to trapezoidal holdfast, a *Tawuia*-like blade, and a *Chuaria*-like distal cyst. While Kumar’s reconstruction of *Radhakrishnania* may provide some guide to our interpretation of *Protoarenicola*, these two genera are different in the presence/absence of transverse annulations.

**Protoarenicola baiguashanensis** Wang, 1982, emended

Figures 2.5.1–2.5.9, 6

*?Sabellidites* sp., Zheng, 1980, pl. 2, fig. 30.

*Protoarenicola baiguashanensis* Wang, 1982, p. 22, pl. 2, fig. 3; Wang et al., 1984a, pl. 6, fig. 5; Sun et al., 1986, p. 394–396, pl. 4, fig. 7; Chen, 1988, p. 202–204, pl. 1, figs. 5–6; pl. 3, figs. 9, 10, 11 (partim); Hong et al., 1991, p. 160, pl. 6, figs. 3–6.

*Paleolina liaonanensis* Xing and Lin in Lin and Xing, 1984, p. 56, pl. 2, figs. 1, 7; Xing et al., 1985, pl. 38, figs. 5, 6 (partim).

*Paleolina evenkiana* Sokolov 1965; Xing et al., 1985, p. 188–189, pl. 39, figs. 3, 4.

*cf. Paleolina* sp. Xing et al., 1985, pl. 40, fig. 10.

*Anhuiella xiwafangensis* Liu and Huang in Hong et al., 1991, p. 161–162, pl. 4, fig. 5 (partim).

*Pseudoarenicola varians* Liu and Huang in Hong et al., 1991, p. 161, pl. 7, figs. 6–8 (partim).

Unnamed fossils, Qian et al., 2000, p. 520, pl. 1, figs. 1–5.

**Emended diagnosis.**—Same as emended genus diagnosis by monotypy.
Description.—Fossils preserved as carbonaceous ribbons on bedding surface. Width ranges from 0.6 to 2.0 mm and length from 2 to 30 mm (Fig. 2.4; Sun et al., 1986). Specimens mostly straight or slightly curved, with a few longer (and more complete) ones displaying significant curvatures. Fossils delineated by clear and smooth boundaries, and usually have uniform width throughout length. Some specimens slightly taper toward proximal (terminal disc-bearing) end. About 15 transverse annulations per millimeter length (Fig. 2.3). Terminal disc elliptical to circular in shape and slightly wider than the ribbon. Constriction often occurs between terminal disc and ribbon (Fig. 2.5.3, 2.5.4, 2.5.6, 2.5.8). Constriction can be subtle (e.g., Fig. 2.5.5), presumably depending on how disc and ribbon were compressed. No annulations on terminal disc.

Ribbon made of two carbonaceous layers, although they can be incomplete or discontinuous as shown in thin sections (Fig. 2.6.4). Carbonaceous layers about 5 µm thick and separated by calcite microspars. Two unexposed specimens fortuitously cut in thin sections perpendicular to bedding plane (Fig. 2.6.1–2.6.3) have well preserved carbonaceous layers. With different degrees of compression, these two specimens consistently demonstrate that terminal disc consists of two carbonaceous layers and ribbon is compressed over terminal disc (Fig. 2.6.1, 2.6.3). Tube apparently separated from terminal disc by a carbonaceous septum (arrow in Fig. 2.6.3).

Material.—More than 50 specimens from the Jiuliqiao Formation at Shouxian and Huaiyuan sections in the Huainan area, northern Anhui.

Occurrence.—The Jiuliqiao Formation in the Huainan region (Wang, 1982; Wang et al., 1984a; Xing et al., 1985; Sun et al., 1986; Chen, 1988), the Jinshanzhai Formation in the Huaibei region (Xing et al., 1985; Qian et al., 2000), and the Changlingzi and Nanguanling Formations in southern Liaoning Province (Hong et al., 1991).

Discussion.—The key feature of Protoarenicola baiguashanensis is the presence of a terminal disc at one end of an annulated ribbon. Paleolina liaonanensis Xing and Lin (in Lin and Xing, 1984, pl. 2, figs. 1a, 1b, 7a), Anhuiella xiwafangensis Liu and Huang (in Hong et al., 1991, p. 161–162, pl. 7, figs. 6, 7), and Paleolina evenkiana Sokolov, 1965 (in Xing et al., 1984, p. 188, pl. 39, figs. 3, 4) fit this diagnosis and are regarded as synonyms of Protoarenicola baiguashanensis. In addition, unnamed specimens reported from the Jinshanzhai Formation in the Huaibei region (Qian et al., 2000, p. 517–518, pl. 1, figs. 1–5), specimens described as cf.
Paleolina sp. (Xing et al., 1985, pl. 40, fig. 10) as ?Sabellidites sp. from the Jiuliqiao Formation (Zheng, 1980, pl. 2, fig. 30) all have the characteristic features of Protoarenicola baiguashanensis.

Particularly worth mentioning are two Protoarenicola baiguashanensis specimens illustrated in Chen (1988, pl. 1, figs. 5–6). These are circular discs with a concentric opening in the center. Chen (1988) interpreted them as cross sections, but they could alternatively be terminal discs that were detached from the tubular structures (Fig. 2.7).

Sun et al. (1986) also synonymized Sabellidites sp. from the Jiuliqiao Formation (Wang, 1982, p. 14, pl. 2, fig. 2) with Protoarenicola baiguashanensis. Sabellidites sp. described by Wang (1982) does not have the characteristic terminal disc of Protoarenicola baiguashanensis, and Sun et al.’s synonymization is not followed here.

Chen (1988) regarded annulated ribbons with irregular terminal structures as Protoarenicola baiguashanensis. For example, he proposed that Paleorhynchus anhuiensis (Wang, 1982, p. 13, pl. 1, fig. 3; Wang et al., 1984a, pl. 6, fig. 7) is a junior synonym of Protoarenicola baiguashanensis. While it is possible that the irregular terminal structures represent taphonomic modification of terminal discs, the single specimen of Paleorhynchus anhuiensis is a fragment and it may or may not be a fragmented piece of Protoarenicola baiguashanensis.

Chen (1988) also identified as Protoarenicola baiguashanensis many annulated ribbons that do not have a terminal discs or have a hardly recognizable terminal structure (Chen, 1988, pl. 2, figs. 7–8; pl. 3, figs. 11–15; pls. 4–5). Similarly, he considered Paleolina tortuosa (Wang, 1982, p. 13–14, pl. 2, fig. 1, 5; Wang et al., 1984a, pl. 7, fig. 1) and Anhuiella sinensis Yan and Xing in Xing et al., 1985 (pl. 39, fig. 5; see also Wang et al., 1984a, pl. 6, fig. 4) as junior synonyms of Protoarenicola baiguashanensis. Additionally, he also listed under the synonym list of Protoarenicola baiguashanensis some specimens identified as Pararenicola huaiyuanensis by Sun et al. (1986, p. 390–394, fig. 7.1–7.2, 7.4–7.7). All these specimens are incompletely preserved, often fragmented along transverse annulations, and none of them have the characteristic terminal discs. Thus, we do not follow Chen’s (1988) suggestion to treat them as synonyms of Protoarenicola baiguashanensis.
Morphological and ecological interpretations.—Thin section observations unequivocally demonstrate that the *Protoarenicola baiguashanensis* organism consists of a cylindrical tube with an inflated bulbous structure at the proximal end (Fig. 2.7).

The terminal disc is superficially similar to the abscission disc of *Miaohephyton bifurcatum* Steiner, 1994 from the Ediacaran Doushantuo Formation of South China (Xiao et al., 1998). The abscission disc is a transverse septum that divides the cylindrical branches of *Miaohephyton bifurcatum* into shorter segments (Xiao et al., 1998). It appears to be more resistant to compression, and is typically preserved in darker color than the cylindrical branches. However, thin section observations clearly show that the terminal disc of *Protoarenicola baiguashanensis* is an inflated discoidal structure, not an abscission septum, although it is separated from the cylindrical tube by a transverse septum (Fig. 2.6.3).

The observation that the terminal disc is not annulated and is typically preserved as darker compression than the ribbon indicates that the terminal bulbous structure and the cylindrical tube were probably functionally distinct. Previous investigators interpreted the terminal bulbous structure as an evertible proboscis (Wang, 1982; Sun et al., 1986; Chen, 1988), but this interpretation is inconsistent with the lack of a mouth-like opening on the disc.

We consider an alternative hypothesis in which the terminal discoidal structure is interpreted as a holdfast, and the cylindrical tube as an erect part of the *Protoarenicola* organism (Qian et al., 2000). This interpretation is very similar to that of *Radhakrishmania* from the Mesoproterozoic Suket Shale (Kumar, 2001). If correct, it implies that *Protoarenicola baiguashanensis* was a benthic organism with a discoidal holdfast, perhaps buried just below the water-sediment interface, and an erect cylindrical tube. This ecological interpretation is more akin to modern coenocytic algae such as *Valonia* Agardh, 1823 and *Boergesenia* Feldmann, 1938, than to bilaterian animals. Of course, most benthic coenocytic algae in modern marine ecosystems have rhizoidal rather than discoidal holdfasts. This difference may be related to the little bioturbated and hence more stable substrate in the Neoproterozoic as compared to the Phanerozoic (Bottjer et al., 2000). In fact, in addition to *Radhakrishmania* mentioned above, discoidal holdfasts also exist in many Ediacara fossils (Clapham and Narbonne, 2002), including *Charniodiscus* Ford, 1958 and *Aspedilla* Billings, 1872 (Gehling et al., 2000).

Genus *PARARENICOLA* Wang, 1982, emended
Huaiyuanella Xing, Yan and Yin, 1985.

Type species.—Pararenicola huaiyuanensis Wang, 1982.

Emended diagnosis.—Annulated tubular organisms preserved as compressed ribbons, with millimetric width and length. About 10 annulations per mm length. Constricted, circular opening with thickened edge occurs at one end of tube. The other end rounded and complete.

PARARENICOLA HUAIYUANENSIS Wang, 1982, emended

Fig. 2.8.1–2.8.3

Pararenicola huaiyuanensis Wang, 1982, p. 11, pl. 1, fig. 1 (partim); Wang et al., 1984a, pl. 6, fig. 3 (partim); Sun et al., 1986, p. 390–394, pl. 4, fig. 4 (partim); Chen, 1988, p. 201–202, pl. 1, fig. 1 (partim).

Huaiyuanella baiguashanensis Xing, Yan, and Yin in Xing, 1984, p. 151–152, pl. 1, figs. 1–4; Xing et al., 1985, p. 189–190, pl. 40, figs. 1–3.

Huaiyuanella baiguashanensis Yan and Xing in Wang et al., 1984a, pl. 6, fig. 2 (nom. nud.).

Huaiyuanella minuta Xing, 1984, pl. 1, figs. 5–9; Xing et al., 1985, p. 190, pl. 40, figs. 4–7.

Huaiyuanella jiuliqaoensis Xing and Yan in Wang et al., 1984a, pl. 6, fig. 1 (nom. nud.);

Huaiyuanella aff. jiuliqaoensis Yan and Xing in Wang et al., 1984a, pl. 7, fig. 3 (nom. nud.).

Huaiyuanella marginata Yan and Xing in Xing et al., 1985, p. 190–191, pl. 39, fig. 6.

Huaiyuanella aff. marginata Yan and Xing in Xing et al., 1985, p. 191, pl. 39, fig. 7.

Emended diagnosis.—Same as emended genus diagnosis by monotypy.

Description.—Ribbons straight or slightly curved. Length ranges from 3.0 to 8.0 millimeters, and width from 1.0 to 2.0 millimeters (Fig. 2.9). Transverse annulations well developed, ~10 per mm length (Fig. 2.8.1–2.8.3). One end of ribbon characterized by slightly constricted, circular to elliptical, terminal opening with thickened edge. Terminal opening can be twisted sideways (e.g., Wang, 1982, pl. 1, fig. 1; probably a taphonomic artifact as transverse annulations are twisted accordingly).

Holotype.—Wang (1982) designated five specimens from the Jiuliqiao Formation at the Huaiyuan section as holotypes (Wang, 1982; pl. 1, figs. 1, 2, 4, 6, 7). These five specimens are incompletely preserved and may be morphologically different. To avoid potential taxonomic confusion, the relatively complete specimen (Wang, 1982; pl. 1, fig. 1), which has a terminal opening, is here designated as the only holotype.
Material.—Four specimens collected from the Jiuliqiao Formation at Shouxian section, southern Anhui.

Occurrence.—The Jiuliqiao Formation at the Shouxian and Huaiyuan sections in the Huainan area (Wang, 1982; Wang et al., 1984a; Xing et al., 1985) and the Shijia Formation in Suxian county of the Huaibei area, Anhui province (Wang et al., 1984a; Xing et al., 1985).

Discussion.—The diagnosis of *Pararenicola huaiyuanensis* (and the genus *Pararenicola*) has been chaotic, partly because five incompletely preserved and morphologically different specimens were designated as holotypes (Wang, 1982). Of these, the more completely preserved specimen (Wang, 1982; pl. 1, fig. 1) has a distorted terminal opening. Wang (1982) interpreted this terminal opening as an oral opening. Subsequently, Sun et al. (1986) characterized *Pararenicola huaiyuanensis* as an annulated cylindrical organism with a “circular aperture (mouth), showing a large, long, irregular, proboscis-like structure in front”, although a circular mouth and a proboscis have never been observed in the same specimen. Recognizing the large, irregular “proboscis” as part of the diagnostic features of *Pararenicola huaiyuanensis*, Sun et al. (1986) regarded *Ruedemannella minuta* Wang, 1982, *Paleorhynchus anhuiensis* Wang, 1982, and *Paleolina tortuosa*, as synonyms of *Pararenicola huaiyuanensis*. Chen (1988), on the other hand, did not include the presence of a terminal opening in the diagnosis of *Pararenicola huaiyuanensis*. Instead, he characterized *Pararenicola huaiyuanensis* as a short tubular organism with a “narrowly rounded” anterior end and a “bluntly rounded” posterior end, and *Protoarenicola baiguashanensis* as a proboscis-bearing worm. Thus, *Ruedemannella minuta* was synonymized with *Pararenicola huaiyuanensis*, whereas *Paleorhynchus anhuiensis* and *Paleolina tortuosa* were synonymized with *Protoarenicola baiguashanensis* by Chen (1988).

To bring order to the taxonomic chaos, we designate the more complete specimen in the original publication (Wang, 1982, pl. 1, fig. 1) as the sole holotype. This specimen has a distorted terminal opening but no proboscis. Accordingly, we emend the diagnosis so that this species is recognized by its short, slightly curved, and annulated tube with a constricted opening at one end and a round termination at the other. The presence of an irregular proboscis is not regarded as a feature of *Pararenicola huaiyuanensis*, because (1) none of the originally published specimens of *Pararenicola huaiyuanensis* have a recognizable proboscis, (2) terminal openings do not co-occur with proboscis, and (3) we cannot exclude the possibility that the irregular proboscis
Huaiyuanella jiuliqiaoensis Xing and Yan in Wang et al., 1984a and Huaiyuanella baiguashanensis Yan and Xing in Wang et al., 1984a were invalidly published because no holotype was designated and no diagnosis was provided. In the same year, Huaiyuanella baiguashanensis Xing, Yan, and Yin in Xing, 1984 was validly published based on different specimens; thus Huaiyuanella baiguashanensis Yan and Xing is a homonym of Huaiyuanella baiguashanensis Xing, Yan, and Yin. Several other species of Huaiyuanella were published in 1984 and 1985. These include Huaiyuanella minuta Xing, 1984, Huaiyuanella marginata Yan and Xing in Xing et al., 1985, and Huaiyuanella aff. marginata Yan and Xing in Xing et al., 1985. Xing et al. (1985) regarded the two invalidly published species—Huaiyuanella jiuliqiaoensis Xing and Yan and Huaiyuanella baiguashanensis Yan and Xing in Wang et al., 1984a—were synonyms of Huaiyuanella marginata. Taxonomic confusion aside, the authors of these species did not make comparison with Pararenicola huaiyuanensis, despite the description and illustration of these species agreeing with the diagnosis of Pararenicola huaiyuanensis. Thus these species of Huaiyuanella are treated as junior synonyms of Pararenicola huaiyuanensis, and accordingly Huaiyuanella as a junior synonym of Pararenicola.

Pararenicola fuzhouensis Liu and Yang (in Hong et al., 1991), p. 160, pl. 5, figs. 2, 5a, 5b) from the early Neoproterozoic Changlingzi Formation in southern Liaoning Province does not have the characteristic terminal opening, and thus does not belong to the genus Pararenicola as we have emended it.

A number of specimens identified as Pararenicola huaiyuanensis by Wang (1982), Sun et al. (1986), and Chen (1988) are either incomplete or do not have the diagnostic terminal opening. These specimens (Wang, 1982, pl. 1, figs. 2, 4, 6, 7; Sun et al., 1986, figs. 4.5–4.6, 7; Chen, 1988, pl. 1, figs. 2–4) are excluded from Pararenicola huaiyuanensis. For similar reasons, we do not follow Sun et al.’s synonymization of Paleorhynchus anhuiensis and Paleolina tortuosa with Pararenicola huaiyuanensis. The case of Ruedemannella minuta, which was synonymized with Pararenicola huaiyuanensis by Sun et al. (1986) and Chen (1988), is less clear. Sun et al. (1986) proposed that Ruedemannella minuta could probably be a juvenile or contracted form of Pararenicola huaiyuanensis. This is an attractive hypothesis, and it is supported by the similar outlines (short, slightly curved ribbons) of these two species (Wang, 1982, pl. 1, fig. 8, pl. 2, fig.
4; Wang et. al., 1984, pl.6, figs. 6, 8; Sun et al., 1986, pl. 7, figs. 9, 10). However, the diagnostic terminal opening is not clearly identifiable in these specimens. Thus, we tentatively exclude *Ruedemannella minuta* and similar fossils from the synonym list of *Pararenicola huaiyuanensis*, pending further examination of the original and addition material to determine whether the absence of terminal opening can be taphonomic or ontogenetic.

We would like to emphasize that the constricted terminal opening in *Pararenicola huaiyuanensis* (Fig. 2.8.1–2.8.3; Wang, 1982, pl. 1, fig. 1; Wang et al., 1984a, pl. 6, fig. 3; Xing et al., 1985, pl. 40, figs. 1–3) is a stable feature of biological significance. It can be differentiated from non-constricted terminal openings of *Anhuiella sinensis* Yan and Xing in Xing et al., 1985. The single specimen of *Anhuiella sinensis* (Wang et al., 1984a, pl. 6, fig.4; Xing et al., 1985, pl. 39, fig. 5) has an elliptical opening with a diameter similar to that of the tube. There is no constriction at the terminal opening of *Anhuiella sinensis*, indicating that its terminal opening probably resulted from physical breakage along annulations.

*Morphological and ecological interpretations.*—On the basis of available material, *Pararenicola huaiyuanensis* was probably a short ellipsoidal to cylindrical tube with a constricted terminal opening. However, it is difficult to envision how such an organism can function, if *Pararenicola huaiyuanensis* as described here indeed represents a complete organism. The lack of a well-defined holdfast structure indicates that *Pararenicola huaiyuanensis* could not have been an erect epibenthic organism. Neither could it have been a procumbent epibenthic organism, because sediments would presumably enter the tubular chamber through its distal opening. We cannot completely falsify the hypothesis that *Pararenicola huaiyuanensis* might have been a planktonic organism, although we suspect that *Pararenicola huaiyuanensis* as described here may not represent the complete organism. It is entirely possible that the constricted terminal opening of *Pararenicola huaiyuanensis* may have resulted from biological abscission during sexual/asexual reproduction or from physical fragmentation. It is conceivable that the constricted terminal opening represents the abscission scar after detachment from a discoidal holdfast (Fig. 2.7). If so, then *Pararenicola huaiyuanensis* may represent biologically (perhaps ontogenetically given its generally smaller size) or physically fragmented specimens of *Protoarenicola baiguashanensis*. This interpretation is intriguing because *Protoarenicola baiguashanensis* tubes tend to constricted where they are in contact with the discoidal holdfast (Fig. 2.5.3, 2.5.4, 2.5.6, 2.5.8). If confirmed, *Pararenicola huaiyuanensis* and *Protoarenicola baiguashanensis* should be
regarded as synonyms, in which case *Pararenicola huaiyuanensis* would have page priority. Alternatively, *Pararenicola huaiyuanensis* as described here may represent segments of constricted tubular organisms that were fragmented along the constrictions (Fig. 2.7). Indeed, a few specimens do have constricted sausage-like morphologies (Fig. 2.8.4, 2.8.5), and the constricted segments are similar in size and shape to *Pararenicola huaiyuanensis* described in this paper. This alternative interpretation is analogous to biological abscission or physical fragmentation of constricted algal thalli of the Ediacaran fossil *Miaohephyton bifurcatum* (Xiao et al., 1998).

Regardless, the potential link between *Pararenicola huaiyuanensis* and *Protoarenicola baiguashanensis* further weakens the bilaterian interpretation and suggests that *Pararenicola huaiyuanensis* may be an algal fossil as well. Many modern tubular algae (for example *Enteromorpha*) and coenocytic algae (for example *Valonia*) are elongate cylindrical thalli with constrictions, and they often can reproduce asexually through fragmentation (Bold and Wynne, 1985). They serve as a better interpretative analog for *Pararenicola huaiyuanensis* and *Protoarenicola baiguashanensis* than bilaterian animals.

**Genus Sinosabellidites Zheng, 1980**


*Type species.*—*Sinosabellidites huainanensis* Zheng, 1980

*Diagnosis.*—Tubular organisms preserved as compressed ribbons with parallel transverse annulations. Ribbons mostly straight, with millimetric width, centimetric length, and 8–10 annulations per mm length. Both ends of ribbons are rounded, without terminal opening or discoidal structures (Sun et al., 1986).

*Discussion.*—When Zheng (1980) established this genus, he noted that the two ends of *Sinosabellidites huainanensis* are different: one end is inflated while the other asymmetrically constricted. Zheng (1980) also noted the presence of an axial cord in the ribbon *Sinosabellidites huainanensis*. Neither of these features can be verified by examination of the published illustrations. Sun et al. (1986) made a similar conclusion and diagnosed the genus *Sinosabellidites* by its elongate ribbon-like compression with rounded ends and the lack of terminal structures. This diagnosis is followed here.
The genus *Huainanella* is similar to *Sinosabellidites*. In fact, the original author of *Huainanella* specifically acknowledged the possibility that these two genera might be synonymous (Wang, 1982), and the genus *Huainanella* was proposed because Wang (1982) did not agree with the pognophoran interpretation of *Sinosabellidites* (Zheng, 1980). The disagreement in phylogenetic affinity does not justify a new taxonomic name, and the two genera are here regarded as synonymous (see also Sun et al., 1986).

**SINOSABELLIDITES HUAINANENSIS** Zheng, 1980

Fig. 2.8.7–2.8.9

*Sinosabellidites huainanensis* Zheng, 1980, p. 63, figs. 18, 19, 20a, 20b; Sun et al., 1986, p. 385–391, pl. 4, figs. 1, 2.

*Huainanella cylindrica* Wang, 1982, p. 12, pl. 1, figs. 5, 9.

*Diagnosis.*—Same as genus diagnosis by monotypy.

*Description.*—Ribbons typically 16–24 mm in length and 0.8–2.2 mm in width. Most straight, showing no strong curvature or folding. Lateral margins of ribbons distinct, smooth, and typically parallel or sub-parallel with each other.

*Material.*—Four specimens from the Jiuliqiao and Liulaobei formations at the Shouxian section in the Huainan area, northern Anhui.

*Occurrence.*—The Jiuliqiao and Liulaobai formations in the Huainan area, northern Anhui.

*Discussion.*—*Sinosabellidites huainanensis* is characterized by its tomaculate body with rounded ends and transverse annulations. It is different from the genus *Sabellidites* that typically has a cuticle tube wall that consists of interwoven nanometer-sized filaments (Ivantsov, 1990; Moczydlowska, 2003). *Huainanella cylindrica*, as discussed above, should be regarded as a synonym of *Sinosabellidites huainanensis*.

Sun et al. (1986) remarked on the morphological similarity between *Sinosabellidites huainanensis* and *Tawuia dalensis*. Both species occur in the Liulaobei Formation in the Huainan region and have a tomaculate outline (Duan, 1982; Wang et al., 1984a; Sun et al., 1986), although *Tawuia dalensis* lacks any transverse annulations. Sun et al. (1986) showed that the width and length ranges of *Sinosabellidites huainanensis* overlap with those of *Tawuia dalensis* (=*Tawuia sinensis* Duan, 1982). We plotted the width and length measurements (Fig. 2.10) of completely
preserved specimens of *Sinosabellidites huainanensis* and *Tawuia dalensis* based on our own collection and those published in Zheng (1980), Wang (1982), and Duan (1982). Discriminant analysis of the compiled data suggests that the measurements of *Sinosabellidites huainanensis* and *Tawuia dalensis* are significantly different (*p* = 0.0017). Their centroids in the width-length plot (Fig. 2.10) are clearly separated from each other because of the difference in length (two tail t-test, *p*<<0.0001). The average width of *Sinosabellidites huainanensis* and *Tawuia dalensis*, however, is not significantly different from each other (two tail t-test, *p*=0.1892).

**Morphological and ecological interpretations.**—*Sinosabellidites huainanensis* is inferred as an originally cylindrical organism, with no terminal opening and holdfast. It was unlikely an erect epibenthic organism given the lack of a holdfast and its length up to 24 mm. Thus, we speculate that it was either a planktonic or, more likely, a procumbent epibenthic organism. It is also possible that *Sinosabellidites huainanensis* represents fragments detached from erect epibenthic organisms such as *Protoarenicola baiguashanensis*; this interpretation is analogous to the interpretation of *Tawuia* as fragment detached from *Radhakrishnania* (Kumar, 2001). However, *Protoarenicola baiguashanensis* does not occur in the Liulaobei Formation where *Sinosabellidites huainanensis* is common, although both species do co-occur in the Jiuliqiao Formation.

**4. DISCUSSIONS AND CONCLUSIONS**

Our systematic study recognizes three taxa of annulated, ribbon-shaped carbonaceous compression fossils from the early Neoproterozoic Liulaobei and Jiuliqiao formations in the Huainan area of northern Anhui Province. *Protoarenicola baiguashanensis* is characterized by a cylindrical tube (as evidenced by thin section observation of partly compressed specimens) with a terminal discoidal structure that is interpreted as a holdfast. This interpretation implies that *Protoarenicola baiguashanensis* was an erect epibenthic organism. *Pararenicola huaiyuanensis* is smaller than *Protoarenicola baiguashanensis*, and has a constricted terminal opening and a rounded end. It is uncertain whether *Pararenicola huaiyuanensis* as described in this paper represents a complete organism and, if so, how it functioned. The observations that some *Protoarenicola baiguashanensis* tubes are constricted where they are attached to the terminal discoidal structure and that a few ribbon-shaped specimens have intercalary constrictions suggest that *Pararenicola huaiyuanensis* may represent segments detached from *Protoarenicola*
baiguashanensis or similar organisms, either through biological abscission or physical fragmentation. Sinosabellidites huainanensis was a cylindrical organism with two rounded ends, but its paleoecology is not well understood.

The phylogenetic affinity of the three genera remains unresolved. However, because the previously described “proboscis” structures are likely taphonomic artifacts, the bilaterian interpretation (Sun et al., 1986; Chen, 1988) is weakened. The possibility that Protoarenicola baiguashanensis and Pararenicola huaiyuanensis may represent reproductive or physical fragments of an erect benthic organism with a discoidal holdfast (Fig. 2.7) further weakens the worm interpretation. A worm tube (e.g., pogonophoran) interpretation is also unlikely, given their lack of physical strength to support a worm inhabitant and (for Sinosabellidites huainanensis at least) closed ends. An alternative and more likely interpretation championed here is that all three genera represent erect benthic, possibly coenocytic, algae.

Insofar as Protoarenicola baiguashanensis can be interpreted as an erect benthic organism (possibly an alga), it is important to point out that a maximum canopy height of centimeters (up to 30 mm) was achieved by early Neoproterozoic benthic communities, possibly driven by competition for light among photosynthetic organisms. This height is less than some of the tallest tierers in the Ediacaran and Cambrian benthic communities (Ausich and Bottjer, 2001; Clapham and Narbonne, 2002; Yuan et al., 2002), but it is significantly greater than benthic algae in late Mesoproterozoic communities. For example, Bangiomorpha pubescens Butterfield, 2000, from the Mesoproterozoic Hunting Formation of Arctic Canada, is less than 2 mm in height (Butterfield, 2000), and Radhakrishnanian from the Mesoproterozoic Suket of central India reached up to 14 mm in height (Kumar, 2001). Thus, together with other early Neoproterozoic benthic tierers such as Longfengshania stipitata Du, 1982 from early Neoproterozoic rocks in North China and northwestern Canada (Hofmann, 1985), the early Neoproterozoic carbonaceous compression fossils from the Jiao-Liao-Xu-Huai region of North China provide direct paleontological evidence for elevated tiering structure in early Neoproterozoic benthic communities. The trend of increasing canopy height of benthic algae continued into the Ediacaran, when macrobenthic algae reached height of up to 150 mm above the water-sediment interface (Xiao and Dong, 2006).

Erect epibenthic organisms typically secure themselves on the substrate through a holdfast. Thus, the evolution of holdfast is a key innovation for erect epibenthic organisms,
particularly macroscopic ones. It is interesting to note that many early erect epibenthic organisms had simple, discoidal holdfasts, rather than complex rhizoidal holdfasts. Some examples include the Mesoproterozoic Tawuia-like fossil Radhakrishnania (Kumar, 2001), the early Neoproterozoic erect benthic organisms Longfengshania stipitata (Du and Tian, 1986) and Protoarenicola baiguashanensis (Qian et al., 2000), and the Ediacaran fossils Charniodiscus and Aspedilla (Clapham and Narbonne, 2002; Gehling et al., 2000). The first evidence for rhizoidal holdfasts does not occur until the Ediacaran Period, as shown by some macroalgal fossils (e.g., Baculiphyca taeniata Yuan, Li, and Chen, 1995) preserved in black shales of the Doushantuo Formation in South China (Xiao et al., 2002). It is possible that the decreasing effectiveness of simple discoidal holdfast and increasing importance of rhizoical holdfasts were driven by an increasingly unstable substrate for non-mobile benthic organisms. The transition from predominately discoidal holdfasts to overwhelmingly rhizoidal holdfasts may have caused by the decline of microbial mats and/or the rise of bioturbation during the Ediacaran–Cambrian Period (Hagadorn and Bottjer, 1999; Seilacher, 1999; Bottjer et al., 2000). This intriguing hypothesis can be tested by carefully examining black shales of the Doushantuo Formation for evidence of bioturbation (e.g., Schieber, 2003). If this hypothesis is confirmed in the future, then the presence of discoidal holdfasts and the lack of complex holdfasts in the Liulaobei and Jiuliqiao formations provide indirect evidence for the absence of bioturbating animals in the early Neoproterozoic. This inference, together with the reinterpretation of Protoarenicola baiguashanensis, Pararenicola huaiyuanensis, and Sinosabellidites huainanensis presented in this paper, weakens the paleontological evidence for early Neoproterozoic bilaterian animals.

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Table 2.1. A sample of different opinions in the stratigraphic subdivision and correlation of Neoproterozoic successions in the Huainan and Huaibei regions. Gray shading indicates stratigraphic hiatus, and black shading indicates the Liulaobei and Jiuliqiao formations from which the fossils described in this paper were collected.

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<th>Huainan Region</th>
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<td>Wangshan Fm.</td>
<td>Shijia Fm.</td>
<td>Gouhou Fm.</td>
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<td>Weiji Fm.</td>
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<td>Zhangqu Fm.</td>
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<td>Jiudingshan Fm.</td>
<td>Sidingshan Fm.</td>
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<td>Niyuan Fm.</td>
<td>Zhaowei Fm.</td>
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<td>Shouxi Fm.</td>
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<tr>
<td>Liulaobei Fm.</td>
<td>Xinxing Fm.</td>
<td>Liulaobei Fm.</td>
<td>Xinxing Fm.</td>
<td>Liulaobei Fm.</td>
</tr>
<tr>
<td>Bagongshan Fm.</td>
<td>Lanling Fm.</td>
<td>Bagongshan Fm.</td>
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<td>Caodian Fm.</td>
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<td>Caodian Fm.</td>
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<td>Bagongshan Fm.</td>
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<tr>
<td>Liulaobei Fm.</td>
<td>Xinxing Fm.</td>
<td>Liulaobei Fm.</td>
<td>Xinxing Fm.</td>
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<tr>
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<td>Lanling Fm.</td>
<td>Bagongshan Fm.</td>
<td>Lanling Fm.</td>
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<td>Caodian Fm.</td>
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<td>Caodian Fm.</td>
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<tr>
<td>Fengyang Group</td>
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</table>

Notes:
- Gray shading indicates stratigraphic hiatus.
- Black shading indicates the Liulaobei and Jiuliqiao formations.
Table 2.2. List of published taxa of annulated ribbon-shaped carbonaceous compressions from the Jiao-Liao-Xu-Huai area.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anhuiella sinensis Yan and Xing, 1984</td>
<td>in (Wang et al., 1984), pl. 6, fig. 4.</td>
<td>Incomplete; invalid name (no diagnosis or holotype designation).</td>
</tr>
<tr>
<td>Anhuiella sinensis Yan and Xing, 1985</td>
<td>in (Xing et al., 1985), p. 189, pl. 39, fig. 5.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Anhuiella xiwafangensis Liu and Huang, 1991</td>
<td>in (Hong et al., 1991), p. 161-162, pl. 4, figs. 5-7, 11; pl. 6, figs. 1. 2.</td>
<td>Invalid name (no holotype designation); one specimen ([Hong et al., 1991], pl. 4, fig. 5] has been synonymized with Protoarenicola baiguashanensis in this paper; the others are incomplete specimens.</td>
</tr>
<tr>
<td>Calyptrina striata Sokolov, 1965</td>
<td>(Wang et al., 1984), pl. 7, fig. 2; (Xing et al., 1985), p. 189, pl. 39, fig. 1.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Chulania anfracta Yan, 1984</td>
<td>in (Wang et al., 1984), pl. 7, fig. 4.</td>
<td>Invalid name (no diagnosis or holotype designation); incomplete specimen; lack of diagnostic characters; synonymized with cf. Paleoolina sp. by (Xing et al., 1985).</td>
</tr>
<tr>
<td>Huaiyuanella baiaguashanensis Yan and Xing, 1984</td>
<td>in (Wang et al., 1984), pl. 6, fig. 2.</td>
<td>Invalid name (no diagnosis or holotype designation); homonym of Huaiyuanella baiaguashanensis Xing, Yan, and Yin, in (Xing, 1984); objective synonym of Pararenicola marginata Yan and Xing in (Xing et al., 1985). Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella baiaguashanensis Xing, Yan, and Yin, 1984</td>
<td>in (Xing et al., 1985), p. 189-190, pl. 40, figs. 1-3.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella cylindrica Wang, 1982</td>
<td>(Wang, 1982), p. 12, pl. 1, figs. 5, 9.</td>
<td>Synonymized with Sinosabellidites huainanensis by (Sun et al., 1986) and in this paper</td>
</tr>
<tr>
<td>Huaiyuanella jiuliqiaoensis Xing and Yan, 1984</td>
<td>in (Wang et al., 1984), pl. 6, fig. 1.</td>
<td>Invalid name (no diagnosis or holotype designation). objective synonym of Huaiyuanella jiuliqiaoensis Yan and Xing in (Xing et al., 1985); synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella aff. jiuliqiaoensis Yan and Xing, 1984</td>
<td>in (Wang et al., 1984), pl. 7, fig. 3.</td>
<td>Objective synonym of Huaiyuanella aff. marginata Yan and Xing in (Xing et al., 1985); synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella marginata Yan and Xing, 1985</td>
<td>in (Xing et al., 1985), p. 190-191, pl. 39, fig. 6.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella aff. marginata Yan and Xing, 1985</td>
<td>in (Xing et al., 1985), p. 191, pl. 39, fig. 7.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella minuta Xing, 1984</td>
<td>(Xing, 1984), p. 151-152, pl. 1, figs. 1-4; (Xing et al., 1985), p. 189-190, pl. 40, figs. 1-3.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella minuta Xing, 1985</td>
<td>(Xing, 1984), p. 190, pl. 40, figs. 4-7.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella striata Xing, 1984</td>
<td>(Xing, 1984), p. 152, pl. 1, figs. 5-9; (Xing et al., 1985), p. 190, pl. 40, figs. 4-7.</td>
<td>Synonymized with Pararenicola huaiyuanensis in this paper.</td>
</tr>
<tr>
<td>Huaiyuanella sp. Xing and Lin, 1984</td>
<td>(Lin and Xing, 1984), p. 56, pl. 1, fig. 8, 9.</td>
<td>Lack of diagnostic features.</td>
</tr>
<tr>
<td>Huaiyuanella sp. Xing, 1984</td>
<td>(Hong et al., 1991), p. 163, pl. 4, figs. 8, 9.</td>
<td>Lack of diagnostic features.</td>
</tr>
<tr>
<td>cf. Huaiyuanella sp. Xing, 1984</td>
<td>(Hong et al., 1991), p. 162-163, pl. 4, fig. 10.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Paleolina evenkiana Sokolov, 1965</td>
<td>(Xing et al., 1985), p. 188-189, pl. 39, figs. 3, 4.</td>
<td>Synonymized with Protoarenicola baiguashanensis in this paper.</td>
</tr>
<tr>
<td>Paleolina cf. evenkiana Sokolov, 1965</td>
<td>(Lin and Xing, 1984), p. 56, pl. 1, fig. 5; (Xing et al., 1985), pl. 38, fig. 8.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Paleolina liaonanensis Xing and Lin, 1984</td>
<td>in (Lin and Xing, 1984), p. 56, pl. 1, fig. 7; pl. 2, fig. 1; (Xing et al., 1985),</td>
<td>Synonymized with Protoarenicola baiguashanensis in this paper.</td>
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<tr>
<td><em>Paleolina liaonanensis</em>&lt;br&gt;Xing and Lin, 1984</td>
<td>(Xing et al., 1985), pl. 38, fig. 7.</td>
<td>Incomplete specimen.</td>
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<tr>
<td><em>Paleolina cf. liaonanensis</em>&lt;br&gt;Xing and Lin, 1984</td>
<td>(Lin and Xing, 1984), pl. 2, fig. 9.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td><em>Paleolina sp.</em></td>
<td>(Lin and Xing, 1984), p. 56-57, pl. 2, fig. 6; (Xing et al., 1985), pl. 38, fig. 9.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>cf. <em>Paleolina sp.</em></td>
<td>(Lin and Xing, 1984), pl. 1, fig. 4; pl. 2, fig. 5; (Xing et al., 1985), pl. 39, fig. 2; pl. 40, fig. 10.</td>
<td>One specimen [(Xing et al., 1985), pl. 40, fig. 10] has been synonymized with <em>Protoarenicola baiguashanensis</em> in this paper; The others are incomplete specimen.</td>
</tr>
<tr>
<td>?<em>Paleolina sp.</em></td>
<td>(Lin and Xing, 1984), p. 57, pl. 2, fig. 4; (Xing et al., 1985), pl. 38, fig. 10.</td>
<td>Incomplete specimens.</td>
</tr>
<tr>
<td><em>Paleolina tortuosa</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p. 11-12, pl. 2, figs. 1, 5; (Wang et al., 1984), pl. 7, fig. 1.</td>
<td>Incomplete specimens.</td>
</tr>
<tr>
<td><em>Paleorhynchus anhuiensis</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p.13, pl. 1, fig. 3; (Wang et al., 1984), pl. 6, fig. 7; (Sun et al., 1986), p. 390-392, pl. 4, fig. 5.</td>
<td>Incomplete specimens; synonymized with <em>Pararenicola huaiyuanensis</em> by (Sun et al., 1986).</td>
</tr>
<tr>
<td><em>Pararenicola fuzhouensis</em>&lt;br&gt;Liu and Yang, 1991</td>
<td>in (Hong et al., 1991), p. 160, pl. 5, figs. 1-5.</td>
<td>Incomplete specimens; invalid name (no holotype designation).</td>
</tr>
<tr>
<td><em>Pararenicola huaiyuanensis</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p. 11, pl. 1, fig. 1; (Wang et al., 1984), pl. 6, fig. 3; (Sun et al., 1986), p. 390-392, pl. 4, fig. 4.</td>
<td>These specimens are identified as <em>Pararenicola huaiyuanensis</em> in this paper.</td>
</tr>
<tr>
<td><em>Pararenicola huaiyuanensis</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p. 11, pl. 1, figs. 1, 2, 4, 6, 7; (Wang et al., 1984), pl. 6, fig. 9, pl. 7, figs. 5, 7; (Sun et al., 1986), p. 390-392, pl. 4, figs. 5-6; pl. 7, figs. 1-12; (Chen, 1988), p. 201-202, pl. 1, figs. 1-4.</td>
<td>These specimens are either incompletely preserved or have no diagnostic feature to allow taxonomic designation.</td>
</tr>
<tr>
<td><em>Protoarenicola baiguashanensis</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p. 22, pl. 2, fig. 3; (Wang et al., 1984), pl. 6, fig. 5; (Sun et al., 1986), p. 394-396, pl. 4, fig. 7; (Chen, 1988), p. 202-204, pl. 1, figs. 5, 6; pl. 3, figs. 9-11.</td>
<td>These specimens are identified as <em>Protoarenicola baiguashanensis</em> in this paper; specimens shown in Chen (1998, pl. 1, figs. 5, 6) are possible detached holdfast structure.</td>
</tr>
<tr>
<td><em>Protoarenicola baiguashanensis</em>&lt;br&gt;Wang, 1982</td>
<td>(Chen, 1988), p. 202-204, pl. 2, figs. 7, 8; pl. 3, figs. 12-15; pl. 4, figs. 16-19; pl. 5, figs. 20-24; (Hong et al., 1991), p. 160, pl. 6, figs. 3-5.</td>
<td>These specimens are incompletely preserved and do not have the characteristic terminal discoidal structure. Their taxonomic designation is unclear.</td>
</tr>
<tr>
<td><em>Protoarenicola xiaogaojiatunensis</em>&lt;br&gt;Liu and Huang, 1991</td>
<td>in (Hong et al., 1991), p. 160-161, pl. 5, fig. 6; pl. 7, figs. 1-4.</td>
<td>Incomplete specimens; no terminal discoidal structure.</td>
</tr>
<tr>
<td><em>Pseudoarenicola varians</em>&lt;br&gt;Liu and Huang, 1991</td>
<td>(Hong et al., 1991), p. 161, pl. 7, figs. 5-12.</td>
<td>Some specimens [(Hong et al., 1991) pl. 7, figs. 6-8] have been synonymized with <em>Protoarenicola baiguashanensis</em> in this paper; the others are incomplete specimens.</td>
</tr>
<tr>
<td><em>Ruedemannella minuta</em>&lt;br&gt;Wang, 1982</td>
<td>(Wang, 1982), p. 12-13, pl. 1, fig. 8; pl. 2, fig. 4; (Wang et al., 1984), pl. 6, figs. 6, 8.</td>
<td>Synonymized with <em>Pararenicola huaiyuanensis</em> by (Sun et al., 1986); lack of diagnostic features to allow taxonomic identification.</td>
</tr>
<tr>
<td><em>Sabellidiitidae</em>&lt;br&gt;Lin and Xing, 1984</td>
<td>(Lin and Xing, 1984), pl. 1, figs. 8, 9.</td>
<td>Incomplete specimens.</td>
</tr>
<tr>
<td>?<em>Sabellidiitidae</em>&lt;br&gt;Lin and Xing, 1984</td>
<td>(Lin and Xing, 1984), pl. 1, fig. 2.</td>
<td>Incomplete specimen</td>
</tr>
<tr>
<td>?<em>Sabellidites sp.</em>&lt;br&gt;Zheng, 1980, pl. 2, fig. 30.</td>
<td>Synonymized with <em>Protoarenicola baiguashanensis</em> in this paper.</td>
<td></td>
</tr>
<tr>
<td>cf. <em>Sabellidites sp.</em>&lt;br&gt;Xing et al., 1985, pl. 39, fig. 10.</td>
<td>Incomplete specimen.</td>
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<td>?Sabellidites.</td>
<td>(Lin and Xing, 1984), pl. 2, fig.7.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>cf. Sabellidites.</td>
<td>(Lin and Xing, 1984), pl. 2, fig. 8; (Xing et al., 1985), pl. 39, fig. 10.</td>
<td>Incomplete specimens.</td>
</tr>
<tr>
<td>Sabellidites cambriensis Yanishevsky, 1926</td>
<td>(Xing et al., 1985), p. 188, pl. 40, fig. 9; (Hong et al., 1991), pl. 4, fig. 12.</td>
<td>Incomplete specimens.</td>
</tr>
<tr>
<td>Sabellidites aff. cambriensis Yanishevsky, 1926</td>
<td>(Lin and Xing, 1984), pl. 1, fig. 1; (Xing et al., 1985), pl. 38, figs. 1, 2.</td>
<td>Incomplete specimens.</td>
</tr>
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<td>Sabellidites sp.</td>
<td>(Wang, 1982), p. 14, pl. 2, fig. 2.</td>
<td>Incomplete specimen.</td>
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<tr>
<td>Sabellidites sp. 1</td>
<td>(Lin and Xing, 1984), p. 55, pl. 1, fig. 4; (Xing et al., 1985), pl. 38, fig. 3.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Sabellidites sp. 2</td>
<td>(Lin and Xing, 1984), p. 55, pl. 2, fig. 3; (Xing et al., 1985), pl. 38, fig. 4.</td>
<td>Incomplete specimen.</td>
</tr>
<tr>
<td>Sinosabellidites huainanensis Zheng, 1980</td>
<td>(Zheng, 1980), p. 63, pl. 2, figs. 18, 19, 20a, 20b; (Sun et al., 1986), p. 385-391, pl. 4, figs. 1, 2.</td>
<td>These specimens are identified as <em>Sinosabellidites huainanensis</em> in this paper. The purported axial cord (Zheng, 1980) does not exist.</td>
</tr>
<tr>
<td>Unnamed fossils</td>
<td>(Qian et al., 2000), pl. 1, figs. 1-5.</td>
<td>Synonymized with <em>Protoarenicola baiguashanensis</em> in this paper.</td>
</tr>
</tbody>
</table>
FIGURE 2.1—(A) One version of paleogeographic reconstruction (modified from Li et al., 2004), showing the location of the North China and South China blocks. (B) Geological map showing Neoproterozoic outcrops in the Huainan area of northern Anhui Province. Stars indicate fossil localities at the Huaiyuan and Shouxian sections. Arrow in inset map points to the Huainan area in the Jiao-Liao-Xu-Huai stratigraphic realm of North China. Dashed line in inset map represents the Tanlu fault.
**Figure 2.2**—Stratigraphic columns of Neoproterozoic successions in the Huaibei (left) and Huainan (right) regions, and the currently accepted correlation between these two regions. HJS: Houjiashan Formation; JSZ: Jinshanzhai Formation; FT: Fengtai Formation; CD & BGS: Caodian and Bagongshan formations; FY: Fengyang Group (Mesoproterozoic); SSF: small shelly fossils.
Fig. 2.2

Legend:
- Limestone
- Chertstone
- Slate
- Conglomerates
- Sandstone
- Phosphatic conglomerates
- Dolostone
- Argillaceous dolostone
- Molar tooth structure
- Stromatolite

Huaibei Group
- Huaiyan
- Jiaoyuan
- Juaihnan
- Zhaowei
- Nnyian
- Huaihou
- Huaihe

Huainan Group
- Liulinl
- Shexian
- Sisongshan
- Feishui Group
- Jiaxiang
- Zhangqu
- Weiji
- Shiji
- Wenguang
- Yuxinl
- Congou
- Houshou

SSF

840 Ma (Rb-Sr)
Tawulia
Chuaria
Sinosabelidites
Paroarenicola
Protoarenicola

1650 Ma (K-Ar)

0 m
100 m
Figure 2.3—Measurements of *Protoarenicola baiguashanensis* specimens from the Jiulijiiao Formation. The left plot shows the frequency distribution of annulation density. The right plot shows the relationship between fossil length and annulation density.
Figure 2.4—Cross-plot and frequency distribution of length and width measurements of *Protoarenicola baiguashanensis* specimens from the Jiulijiao Formation. The 1:20 line represents the cutoff width:length ratio between *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis*, proposed by Sun et al. (1986).
FIGURE 2.5—*Protoarenicola baiguashanensis* Wang, 1982, from the Jiuliqiao Formation (1–9). 1–2, part and counterpart. JLQS-7 (VPIGM-4578); 3, JLQS-32 (VPIGM-4579); 4, JLQS-10 (VPIGM-4580), note that holdfast is preserved darker than the ribbon; 5, JLQS-4 (VPIGM-4581); 6, 9, JLQS-4 (VPIGM-4582), 9 is magnified view of 6, showing transverse annulations and possible physical or biological fragmentation at distal end; 7, JLQS-7 (VPIGM-4583); 8, JLQS-4 (VPIGM-4584). Transverse annulations are not preserved in some specimens (e.g., 5.2). Arrows point to constrictions at the contact between ribbons and terminal discoidal structures. Scale bars represent 2 mm unless otherwise noted. Field collection number: JLQS-xxx denotes specimens collected from the Jiuliqiao Formation at the Shouxian section. VPIGM-xxx refers to catalog numbers at the Virginia Polytechnic Institute Geosciences Museum.
FIGURE 2.6—Thin section photomicrographs of *Protoarenicola baiguashanensis* specimens from the Jiuliqiao Formation fortuitously cut in-situ (1–3) or embedded in epoxy (4). Thin sections were cut perpendicular to bedding plane. 1–2, JLQS-4 (VPIGM-4585). Note compressed ribbon superimposed on compressed terminal discoidal structure on the left end of 1. 2 is magnified view of rectangled area in 6.1, showing two discontinuous carbonaceous layers (arrows) separated by a narrow gap. 3, JLQS-4 (VPIGM-4586). A less compressed specimen showing a transverse septum (arrow) separating the terminal discoidal structure (below arrow) and ribbon (above arrow). 4, JLQS-4 (VPIGM-4586). Embedded specimen showing two carbonaceous layers (arrows). Scale bars are 100 µm unless otherwise noted.
FIGURE 2.7—Two alternative morphological reconstructions of *Protoarenicola baiguashanensis* and possible connections between *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis* Wang, 1982.
FIGURE 2.8—Pararenicola huaiyuanensis Wang, 1982 (1–3), possible Pararenicola huaiyuanensis fragments with constrictions (arrows, 4–5), Anhuiella sinensis Yan and Xing in Xing et al., 1985 (6), and Sinosabellidites huainanensis Zheng, 1980 (7–9). 1, JLQS-23 (VPIGM-4587); 2–3, part and counterpart, JLQS-23 (VPIGM-4588); 4, JLQS-31 (VPIGM-4589); 5, JLQS-7 (VPIGM-4590); 6, reproduced from Wang et al, 1984, pl. 6, fig. 4. The opening is not constricted and may have resulted from physical breakage along transverse annulations. 7 and 9, JLQS-4 (VPIGM-4591). 9 is magnified view of rectangle area in 7. 8, JLQS-4 (VPIGM-4592). Scale bars are 2 mm unless otherwise noted.
Figure 2.9—Cross-plot and frequency distribution of length and width measurements of *Pararenicola huaiyuanensis* from the Jiuliqiao and Shijia formations. Measurements are based on our own material as well as those published in Zheng (1980) and Wang (1982).
FIGURE 2.10—Width and length measurements of completely preserved specimens of *Sinobellidites huainanensis* and *Tawuia dalensis* Hofmann in Hofmann et al., 1979 from the Jiuliqiao and Liulaobei formations. Measurements are based on our own material as well as those published in Zheng (1980), Wang (1982), and Duan (1982).
Chapter 3

String of beads and stack of dishes: Silicified *Horodyskia* and *Palaeopascichnus* from upper Ediacaran successions, and their implications for the early evolution of heterotrophic eukaryotes

ABSTRACT

*Horodyskia* Yochelson and Fedonkin, 2000, is one of the earliest macroscopic life forms whose fossil record goes back to the Mesoproterozoic, and *Palaeopascichnus* Palij, 1976, represents one of the key Ediacaran elements with a world-wide distribution. However, their body constructions and affinities have not been completely resolved, in part because previously described *Horodyskia* and *Palaeopascichnus* species are mostly preserved as casts and molds in siliciclastic rocks. Silicified *Horodyskia* and *Palaeopascichnus* from upper Ediacaran chert of the Liuchapo Formation in central Guizhou, South China, are here described as *Horodyskia minor* new species and *Palaeopascichnus jiumenensis* new species. The new material confirms that both genera share a bodyplan characterized by uniserially arranged, spheroidal or discoidal segments that are rich in organic carbon. The segments are connected by a carbonaceous cytoplasm-filled chambers that were cast with early diagenetic silica and clay minerals, the connection filament represents a small passage between chambers, and the aureole may represent the agglutinated test. If correct, this interpretation implies that the divergence of bikont eukaryotes and possibly rhizarians may have occurred in the Mesoproterozoic, because *Horodyskia* has a known fossil record that goes back to 1.4 Ga. The extremely long-ranging genus *Horodyskia* (~900 million years) echoes previous proposition of extended evolutionary stasis in the Precambrian and enriches our knowledge about the Precambrian fossil record of heterotrophic eukaryotes.

**Keywords:** Ediacaran, *Palaeopascichnus*, *Horodyskia*, foraminifer, eukaryote, Liuchapo Formation, South China

1. **INTRODUCTION**

*Horodyskia* and *Palaeopascichnus* are two enigmatic Proterozoic fossils sharing a body construction characterized by uniserially arranged units of similar shape (spheroidal in *Horodyskia* and discoidal/spheroidal in *Palaeopascichnus*) and size. *Horodyskia*, colloquially
known as “string of beads”, has been reported from the >1443 ± 7 Ma Appekunny Formation of the Belt Supergroup in Montana (Horodyski, 1982; Fedonkin et al., 1994; Evans et al., 2000; Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002) and the 1211–1070 Ma Manganese Group of the Bangemall Supergroup in Western Australia (Grey and Williams, 1990; Martin and Thorne, 2001; Martin, 2004), as well as in Ediacaran sequences of Lesser Himalaya and North China (Mathur and Srivastava, 2004; Shen et al., In press). *Palaeopascichnus*, characterized by uniserially arranged discoidal or saucer-shaped units (“stack of dishes”), is one of the most widely distributed Ediacara fossils and has been known from Russia, Australia, Newfoundland, and North China (Urbanek and Rozanov, 1983; Narbonne et al., 1987; Sokolov and Fedonkin, 1990; Jenkins, 1995; Gehling et al., 2000; Shen et al., In press).

Although both taxa are represented by a large number of specimens from multiple geographic regions, their body constructions and affinities are poorly understood. For example, *Horodyskia* was interpreted as a multicellular alga (Grey and Williams, 1990) or a tissue-grade multicellular eukaryotic organism with underground stolons that connect neighboring beads (Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002). Likewise, there is no consensus about the affinity of *Palaeopascichnus* either. It has been variably interpreted as a trace fossil (Urbanek and Rozanov, 1983), an alga (Haines, 2000), or a giant rhizopodan protist similar to modern xenophyophores (Seilacher et al., 2003). The divergent opinions about their phylogenetic affinities largely result from the poor resolution of their cast and mold preservation in relatively coarse-grained siliciclastic rocks. Here we report the occurrence of *Horodyskia* and *Palaeopascichnus* permineralized in fine-grained chert of the upper Ediacaran Liuchapo Formation in central Guizhou, South China. The new data shed additional light on the morphological reconstruction and phylogenetic interpretation of *Horodyskia* and *Palaeopascichnus*, and given the occurrence of *Horodyskia* in Mesoproterozoic rocks, have evolutionary and ecological implications for the evolutionary history of early heterotrophic eukaryotes.

2. GEOLOGICAL SETTINGS

The Liuchapo Formation in central Guizhou Province is underlain by the lower Ediacaran Doushantuo Formation and overlain by the lower Cambrian Jiumenchong Formation (Figs. 3.1, 3.2) (Bureau of Geology and Mineral Resources of Guizhou Province, 1987; Peng and Babcock,
The 20-m-thick Doushantuo Formation in this area predominantly consists of siltstone and mudstone with minor chert and phosphorite. The upper Doushantuo Formation in eastern Guizhou contains carbonaceous compression fossils that are taxonomically similar to those from the Miaohue Member of the uppermost Doushantuo Formation in the Yangtze Gorges area (Xiao et al., 2002; Zhao et al., 2004), confirming its Ediacaran age and correlation to the Yangtze Gorges area. The 40-m-thick Liuchapo Formation consists of dark gray and thin to medium-bedded chert, and it is traditionally regarded as a slope facies equivalent of the platform, carbonate-dominated Dengying Formation. The uppermost 0.25 m of the Liuchapo Formation, sometimes described as the Gezhongwu Member, contains abundant and diverse small shelly fossils indicating a Meishucunian (= Nemakit-Daldynian + Tommotian) age (Wang et al., 1984; Qian and Yin, 1984). The overlying 200-m-thick Jiumenchong Formation consists of carbonaceous black shale with hexactinellid sponges and eodiscinid trilobites (Bureau of Geology and Mineral Resources of Guizhou Province, 1987), and it is correlated with the lower Cambrian Niutitang Formation.

Fossils described in this paper were collected from the middle Liuchapo Formation at Jiumen village, Danzhai county, central Guizhou Province (Fig. 3.1). Fossils are restricted to a 3–m interval about 30 m below the Liuchapo–Jiumenchong boundary (Fig. 3.2). The fossiliferous horizon is regarded as upper Ediacaran in age because it underlies the Gezhongwu Member that contains Meishucunian small shelly fossils, it lacks any basal Cambrian small shelly fossils or Micrhystridium-like acritarchs, and it overlies the lower Ediacaran Doushantuo Formation. The Liuchapo Formation was deposited in a lower slope environment below wave base.

The fossils were studied in thin sections and in highly polished slabs using transmitted and reflected light microscopy. Selected specimens were serially ground in order to reconstruct their three-dimensional morphology. In order to characterize the compositional difference between the fossils and surrounding matrix, a few highly polished slabs were analyzed using an electron microprobe.

3. MORPHOLOGY

The middle Liuchapo assemblage includes abundant occurrences of only two forms (Figs. 3.3 and 3.4). One of them is identified as Horodyskia, which consists of uniseries of circular segments, or “string of beads” (Fig. 3.3) (Yochelson and Fedonkin, 2000; Fedonkin and
Yochelson, 2002; Martin, 2004; Mathur and Srivastava, 2004; Shen et al., In press). Most strings are preserved along bedding plane, although a few are vertically preserved (perpendicular to bedding plane; Fig. 3.3.15). Strings range from 0.5 to 8 mm in length, each consisting of 3–30 beads. The beads in the same string are quite uniform in size, but can vary between 0.1 and 0.7 mm among strings (measured in thin sections parallel to bedding plane; Fig. 3.5). They are relatively small compared to the type species of *Horodyskia, H. monoliformis* (Fig. 3.6). Spacing between beads is 0.02–1 mm and positively correlated with bead size. In some specimens, adjacent beads are connected by a thin filament of carbonaceous material (Fig. 3.3.5–3.3.6).

Serial thin sectioning shows that the beads are spheroidal, not barrel-shaped with a hemispherical top as described by Fedonkin and Yochelson (2002). In thin sections perpendicular to bedding plane, the beads are vertically compressed due to sediment compaction. The “strings of beads” are surrounded by a light-colored, carbonaceous-free, microcrystalline quartz aureole whose widest diameter is about 1–1.5 times and positively correlated with bead diameter (Fig. 3.3.3–3.3.4, 3.5).

The other form can be identified as *Palaeopascichnus* (Fig. 3.4), an enigmatic Ediacaran taxon with a world-wide distribution (Urbanek and Rozanov, 1983; Narbonne et al., 1987; Sokolov and Fedonkin, 1990; Jenkins, 1995; Gehling et al., 2000; Haines, 2000; Shen et al., In press). It is characterized by uniseriate arrangement (“series”) of saucer-shaped units (“segments”). The Liuchapo specimens consist of series that are typically 0.9–5 mm long and 0.3–1 mm wide. Series are often slightly curved, but some of the longer specimens can be sinuous. Typically they lie parallel to bedding plane, although some are oblique or perpendicular to bedding planes. The number of segments in a series varies from 3 to 25. The segments are rich in organic carbon and they are small compared to other described *Palaeopascichnus* species; they are 0.23–0.65 mm in width as measured in thin sections parallel to bedding plane (Figs. 3.7–3.8). Furthermore, unlike other described *Palaeopascichnus* species, which are characterized by homomorphic segments (crescent or circular or spheroidal), the Liuchapo population is characterized by the occurrence of both crescent and spheroidal segments in the same series (Figs. 3.4.1–3.4.2, 3.4.5–3.4.6). Crescent discs in the same series are of similar size and are arranged unidirectionally, with their concave side facing toward the same direction and forming a “stack of dishes”. A single segment, somewhat spheroidal in shape, is terminally positioned at the concave end of the “stack of dishes”. Spacing between segments is uniform within series and positively
correlated with segment size (Fig. 3.7). In well-preserved specimens neighboring segments are
connected by a thin filament of carbonaceous material (Fig. 3.4.1–3.4.4, 3.4.6, 3.4.7, 3.4.10–3.4.15). In thin sections cut perpendicular to bedding plane, the segments are somewhat
compressed in the vertical direction, probably due to sediment compaction. The “stack of dishes”
is usually surrounded by a light-colored, carbonaceous-free, microcrystalline quartz aureole,
whose thickness is positively correlated with segment size (Fig. 3.7).

4. TAPHONOMY

Most beads and dishes are organized in series, although some are disarticulated or
fragmented (Figs. 3.3 and 3.4). Regardless, the Liuchapo fossils are uniquely permineralized in
early diagenetic chert, and their preservational style is distinct from other occurrences of
Horodyskia and Palaeopascichnus, which are typically preserved as casts and molds (Gehling et
al., 2000; Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002)—sometimes highly
compressed (Haines, 2000; Shen et al., In press) —in siliciclastic rocks. Their segments and
connection filaments are defined by dark gray material enriched in organic matter and pyrite.
Elemental maps (Fig. 3.9) show that the segments have higher Al and Mg, but lower Si
concentrations than surrounding matrix, suggesting that the segments are also enriched in clay
minerals, which might have played an important role in the preservation of the segments
(Butterfield, 1995; Orr et al., 1998). The aureole, however, is free of carbonaceous material and
consists of microcrystalline (<10 µm) quartz. We interpret the aureole as an agglutinated test that
housed the “beads” and “dishes”, which were permineralized by early diagenetic microcrystalline
silica. Obviously, some degree of compaction must have occurred before permineralization.

5. COMPARISON WITH OTHER OCCURRENCES OF HORODYSKIA AND
   PALAEOPASCICHNUS

The Liuchapo specimens share the diagnostic bodyplan—uniserially arranged
segments—with other reported occurrences of Horodyskia and Palaeopascichnus, but they also
show some important differences, partly because of their unique preservation. The positive
correlation between bead size and spacing (Fedonkin and Yochelson, 2002), as well as the rare
preservation of connection filaments in siliciclastic facies (Martin, 2004), is confirmed in the
silicified specimens from the Liuchapo Formation. However, the bead size of the Liuchapo
population is significantly smaller than other described *Horodyska* species (Fig. 3.6). Thus, a new species is warranted.

*Palaeopascichnus* specimens from the Liuchapo Formation clearly show the presence of a connection filament (<10 µm in thickness) between segments, a feature that have not been described in previous reports of *Palaeopascichnus*, likely due to the poor taphonomic resolution associated with cast and mold preservation in siliciclastic rocks. In addition, the consistent occurrence of a spherical terminal segment at the concave end of multiple Liuchapo specimens is different from all other reported *Palaeopascichnus* species (Shen et al., In press), and this difference is unlikely taphonomic. Therefore, although the “stacks of dishes” from the Liuchapo Formation clearly belong to the genus *Palaeopascichnus*, it likely represents a new species.

6. PHYLOGENETIC AFFINITY

The phylogenetic affinity of *Horodyska* and *Palaeopascichnus* has been controversial. *Horodyska* was interpreted as inorganic sedimentary structures (Horodyski, 1982; Horodyski, 1983), dubiofossils (Fedonkin and Runnegar, 1992), or pseudofossils (Hofmann, 1992). Grey and Williams (1990) proposed its possible biological origin with affinity to the Phaeophyceae. Recently, *Horodyska* was reinterpreted as a tissue-grade colonial eukaryote, with its segments compared to cnidarian polyps (Fedonkin and Yochelson, 2002). Similarly, *Palaeopascichnus* was once regarded as a trace fossil (Urbanek and Rozanov, 1983), but this interpretation has been questioned by several authors (Jensen, 2003; Seilacher et al., 2003; Seilacher et al., 2005; Jensen et al., 2006; Shen et al., In press). Instead, *Palaeopascichnus* is recently reinterpreted as a giant rhizopodan protist similar to modern deep-sea xenophyophores (Seilacher et al., 2003), which are a group of agglutinated foraminifers (Tendal, 1972; Pawlowski et al., 2003b).

Our serial thin sectioning of silicified specimens from the Liuchapo Formation did not find evidence for a mouth-like opening that would be expected if *Horodyska* “beads” represented cnidarian polyps (Fedonkin and Yochelson, 2002). Nor it there evidence for multicellularity preserved in the silicified specimens. Furthermore, the polyp interpretation is inconsistent with the vertical orientation of some *Horodyska* (and *Palaeopascichnus*) series.

It is also worth comparing *Horodyska* (and *Palaeopascichnus*) with the recently discovered giant sulfide oxidizing bacterium *Thiomargarita namibiensis* Schulz et al., 1999. *Thiomargarita namibiensis* is described as “string of pearls” because of its chained cells that are
Thiomargarita namibiensis occurs abundantly in nutrient-rich sediments underlying the oxygen minimum zone. Its chained cells are held together by a mucous sheath. The cells are spherical, with a diameter of 100–300 µm in diameter, but can reach up to 750 µm in diameter. At first glance, these features make Thiomargarita namibiensis a favorable modern analog to Horodyskia. However, several lines of evidence argue against a close comparison between Horodyskia/Palaeopascichnus and Thiomargarita. First, Thiomargarita cells are closely spaced (with a space <1/10 of cell diameter) and are separated by the mucous sheath, whereas some Horodyskia beads are widely separated (with a spacing ¼ to 3 times bead diameter; Fig. 3.5) and are connected by a carbonaceous filament. Second, the light-colored, carbonaceous-free aureole around Horodyskia string of beads preserved in the Liuchapo Formation cannot be interpreted as mucous sheath because of the lack of organic matter. Third, Horodyskia beads from other Proterozoic successions (Fig. 3.6) significantly exceed the size of Thiomargarita cells. Finally, the fundamental similarity between the bodyplans of Horodyskia and Palaeopascichnus indicates that they represent a phylogenetically related group of organisms with uniserially arranged segments that can be bead- or dish-shaped. No Thiomargarita cells are known to be dish-shaped. There is also no evidence for elevated sulfur or phosphorous concentrations in Horodyskia and Palaeopascichnus, whereas Thiomargarita cells are able to accumulate sulfur and phosphate in their vacuoles (Schulz et al., 1999; Schulz and Schulz, 2005).

Instead, we found evidence suggesting that Horodyskia and Palaeopascichnus may be related to rhizarian eukaryotes, particularly uniseriate agglutinated foraminifers. Modern uniseriate agglutinated foraminifers, such as Cylindroclavulina Bradyi Cushman, 1911 (Fig. 3.10.2), look remarkably similar to Horodyskia and Palaeopascichnus from the Liuchapo Formation. Indeed, some modern uniserial foraminifers do have spherical or crescent chambers connected by a narrow passage (Fig. 3.10) (Loeblich and Tappan, 1988). Moreover, the spheroidal terminal segment in Palaeopascichnus is intriguingly similar to the proloculus of some uniseriate foraminifers (Fig. 3.10.2 and 3.10.3). It is thus tempting to consider the beads and dishes in Horodyskia and Palaeopascichnus as cytoplasm-filled chambers that were cast by early diagenetic silica. This interpretation is consistent with the preferential occurrence of organic matter and pyrite in the segments.
We further propose that the light-colored, carbonaceous-free, microcrystalline aureole may represent an agglutinated test that was recrystallized and silicified during early diagenesis. In fact, some *Horodyskia* specimens from the Belt Supergroup are surrounded by halos of iron oxide (Fedonkin and Yochelson, 2002), which may also be interpreted as agglutinated material. The lack of organic matter and the diffuse boundary of the aureole indicate that it was unlikely organic or calcareous. It follows that the connection filament would represent a narrow passage between chambers.

It is perhaps not surprising, given their Proterozoic age, that *Horodyskia* and *Palaeopascichnus* are difficult to assign to any living foraminifer subclades. Morphological features of *Horodyskia* and *Palaeopascichnus*, although suggestive of a foraminifer affinity, are not specific to any foraminifer subclade. Uniserially arranged chambers are a common feature among many modern foraminifer groups, including organic-walls allogromids (e.g. *Resigella moniliforme* Resig, 1982) (Gooday, 2002), agglutinated textularids (e.g. *Cylindroclavulina bradyi* Cushman, 1911), and calcareous foraminifers such as *Eonodosaria evlanensis* Lipina, 1950 (Loeblich and Tappan, 1988). Agglutinated tests also occur in a wide range of foraminifers, both unilocular and multilocular (Pawlowski and Holzmann, 2002; Pawlowski et al., 2003a); in fact, the early Palaeozoic foraminifer record is dominated by agglutinated tests (Sen Gupta, 1999; McIlroy et al., 2001). Elemental mapping of *Horodyskia* and *Palaeopascichnus* fossils from the Liuchapo Formation does not real elevated barium concentration (Fig. 3.9), as would be expected if they are xenophyophores, which are characterized by several unique features, including stercomata derived from fecal pellets, granellae, and barite precipitates in protoplasm (Tendal, 1972; Hopwood et al., 1997). Thus, synapomorphies allying *Horodyskia* and *Palaeopascichnus* with a specific foraminifer group is lacking, despite their general morphological similarities to the foraminifer bodyplan. *Horodyskia* and *Palaeopascichnus* are therefore most plausibly regarded as stem-group foraminifers.

7. DISCUSSIONS

Recent molecular phylogenetic analyses (Cavalier-Smith, 2002; Stechmann and Cavalier-Smith, 2002; Nikolaev et al., 2004; Embley and Martin, 2006; Burki and Pawlowski, 2006) have recognized six eukaryote clades: opisthokonts (animals and fungi), amoebozoans (lobose amoebae and slime molds), rhizarians (foraminifera, radiolarian, and cercozoans),
excavates (archaezoans, discicristates, and loukozoans), chromalveolates (chromists and alveolates), and plants or archaeplastids (rhodophytes, glaucophytes, and green plants). The exact phylogenetic relationships among the six clades are controversial, but there is some evidence suggesting that the deepest eukaryotic divergence occurred between the unikonts (opisthokonts and amoebozoans) and bikonts (the remaining four clades mentioned above) (Cavalier-Smith, 2002; Stechmann and Cavalier-Smith, 2002; Nikolaev et al., 2004; Embley and Martin, 2006).

Previously, the earliest fossil record of rhizarians was represented by the 742–770 Ma vase-shaped microfossil *Melicerion poikilon* Porter et al., 2003, which is interpreted as a filose testate amoeba, a member of cercozoan rhizarians (Porter et al., 2003). The earliest known foraminifer fossils are represented by the basal Cambrian agglutinated foraminifers *Platysolenites* and *Spirosolenites* (McIroy et al., 2001) and the Ediacara fossil *Palaeopascichnus* interpreted as a possible xenophyophore (Seilacher et al., 2003). If *Horodyskia* is a stem-group foraminifer, its occurrences in the Belt and Bangemall supergroups extend the rhizarian and foraminifer fossil record to the Mesoproterozoic. The interpretation also implies that the divergence of bikonts from unikonts, as well as the divergence of rhizarians from other bikonts, must have occurred before 1.4 Ga (Fig. 3.11). This inference is consistent with the occurrences of other bikont fossils in Mesoproterozoic rocks, including bangiophyte red algae from the 1204 ± 22 Ma Hunting Formation in arctic Canada (Butterfield, 2000), and xanthophyte algae (chromalveolates) from the >1005 ± 4 Ma Lakhanda Group in southeastern Siberia (Woods et al., 1998; Rainbird et al., 1998) and from the Neoproterozoic Svanbergfjellet Formation in Spitsbergen (Butterfield, 2004). There are also potential candidates for Mesoproterozoic and early Neoproterozoic unikont fossils. For example, *Tappania* (occurring in the 1430 Ma Roper Group in northern Australia, the >1000 Ma Ruyang Group in northern China, and the Neoproterozoic Wynniatt Formation in northwestern Canada) and *Cheilofilum* (occurring in the Neoproterozoic Wynniatt Formation) have both been interpreted as possible fungi (Butterfield, 2005b; Butterfield, 2005a). In addition, several genera of early Neoproterozoic vase-shaped microfossils have been interpreted as lobose testate amoebae, members of the unikont amoebozoan group (Porter and Knoll, 2000).

These possible fungal and testate amoeba fossils, together with the Mesoproterozoic *Horodyskia*, are among some of the earliest known heterotrophic eukaryotes. Given the taphonomic biases against the preservation of non-biomineralizing heterotrophic eukaryotes in Precambrian rocks (Porter, 2006), it is not surprising that their fossil record is sporadic and
stratigraphic gaps are large. In light of the spotty nature of Precambrian fossil record of heterotrophic eukaryotes, the occurrences of *Horodyskia* in the 1.4 Ga Appekuny Formation, 1211–1070 Ma Manganese Group, and the Ediacara Krol Group and Liuchapo Formation are comparable to other long-ranging Proterozoic taxa such as *Tappania* (Butterfield, 2007).

The Proterozoic featured a number of extremely long-ranging taxa, including *Tawuia*, *Chuaria*, *Valeria*, and *Tappania*. The taxonomic and morphological stasis over $10^7$–$10^8$ years is interpreted as macroevolutionary outcome resulting from the overly simple ecological interactions in the absence of metazoans (Butterfield, 2007). The addition of *Horodyskia* to the list of long-ranging Proterozoic taxa accentuates the hypobradytelic evolution of an ecosystem without animal predators and grazers (Schopf, 1994; Butterfield, 2007).

8. **CONCLUSIONS**

Silicified *Horodyskia* and *Palaeopascichnus* from the upper Ediacaran Liuchapo Formation allow us to better characterize their morphological constructions and to shed light on their phylogenetic affinities. Both genera are characterized by uniserially arranged spheroidal and discoidal segments that are connected by a thin organic filament. The silicified specimens also preserve evidence for an agglutinated test. The fundamental bodyplan of *Horodyskia* and *Palaeopascichnus* encourages a morphological comparison with agglutinated foraminifers, although their phylogenetic positions within the foraminifer clade (e.g., relation with xenophyophores) await further investigation. *Horodyskia* and *Palaeopascichnus* from the Liuchapo Formation significantly improve our knowledge about Proterozoic heterotrophic eukaryotes. The occurrence of *Horodyskia* in Mesoproterozoic rocks implies deep divergence of the bikonts and rhizarians, and extremely slow pace in Proterozoic morphological and taxonomic evolution in the absence of metazoans.
Genus HORODYSKIA Yochelson and Fedonkin, 2000

_Type species._ — *Horodyskia moniliformis* Yochelson and Fedonkin, 2000.

_Original diagnosis._ — Presumed colonial organisms of small, vertically oriented, short wide cones, hemispherical on upper surface, growing from horizontal tube (Yochelson and Fedonkin, 2000).

_Discussion._ — The earliest fossil record of “string of beads” was reported from the Belt Supergroup (Horodyski, 1982; Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002). Younger records include fossils from the Bangemall Supergroup, Western Australia (Grey and Williams, 1990; Martin, 2004), the Tal Formation, Lesser Himalaya (Mathur and Srivastava, 2004), and the Ediacaran Zhengmuguan Formation, North China (Shen et al., In press). *Horodyskia* was interpreted as seaweeds (Grey and Williams, 1990; Grey et al., 2000) or as tissue-grade eukaryotes (Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002). Fedonkin and Yochelson also noticed a positive correlation between bead size and spacing, and hypothesized that beads were connected by a stolon (Fedonkin and Yochelson, 2002). Indeed, one specimen from the Bangemall Supergroup of Northwestern Australia shows a groove between beads, which was interpreted as the impression of the hypothesized stolon (Martin, 2004).

Although their bead size is typically smaller (0.1–0.7 mm), the Liuchapo specimens share the “string of beads” morphology of the type species of *Horodyskia, H. moniliformis*. In addition, the Liuchapo specimens support previous observation of a positive correlation between bead size and spacing (Fig. 3.5). Several of the Liuchapo specimens (Figs. 3.3.5–3.3.6) also shows evidence for an organic filament that connects neighboring beads; this organic filament possibly represents the hypothesized stolon (Yochelson and Fedonkin, 2000; Fedonkin and Yochelson, 2002).

One feature that distinguishes the Liuchapo specimens from the type species, *H. moniliformis*, is the presence of a light-colored, organic-poor, microcrystalline quartz aureole around the string of beads. However, the type species has not been studied in thin sections, and
thus it is uncertain whether such an aureole is also preserved in the *Horodyskia* specimens from the Belt and Bangemall supergroups.

**HORODYSKIA MINOR** new species

(Figure 3.3)

*Diagnosis.*—Series ("string") consists of uniserially arranged spherical segments ("beads") that are separated by a gap ("spacing"). Specimens show positive correlation between bead size and spacing. Strings are commonly surrounded by an aureole made of light-colored, organic-poor, microcrystalline quartz. Beads are sub-millimetric in diameter.

*Description.*—Specimens are composed of uniserially arranged, sub-millimetric, spherical segments or beads, making a nearly straight to strongly curved series or string (Fig. 3.3). Strings are typically oriented parallel to bedding plane, with rare occurrences of vertically or obliquely oriented strings (Fig. 3.3.15). Several specimens show evidence for an organic filament that connects neighboring beads (Fig. 3.3.5, 3.3.6). Due to sediment compaction, beads are vertically compressed to become oblate rather than perfectly spherical structures; this is best seen in thin sections perpendicular to bedding plane (Fig. 3.3.15, 3.3.16). Beads are dark-colored in thin sections, and are presumably rich in carbonaceous material. They are separated by a gap that is comparable in size to bead diameter. Beads in the same series are of similar size. String is surrounded by an aureole that consists of light-colored, organic-poor, microcrystalline quartz. Bead size is positively correlated with bead spacing.

*Measurements.*—Strings are 0.5–5.5 mm in length (mean = 3.3 mm, s.d. = 1.3 mm, n = 16 specimens), with 3–30 beads per string. Beads are 0.1–0.7 mm in diameter (mean = 0.32 mm, s.d. = 0.15 mm, n = 20 measurements made on the largest bead in each of 20 specimens). Spacing between beads, measured as gaps between beads rather than distance between centers of neighboring beads, is 0.02–1 mm (mean = 0.29 mm, s.d. = 0.29 mm, n = 20 measurements made on 20 specimens). Bead diameter and spacing are positively correlated (correlation co-efficient $r = 0.35$; $r = 0.89$ if four outliers are excluded; Fig. 3.5).
Etymology.—Latin, *minor*, with reference to the small bead size compared to the type species, *Horodyskia monoliformis*.

Material.—More than 100 specimens collected from the Liuchapo Formation at Jiumen, Danzhai County, Guizhou Province, South China.

Types.—The specimen illustrated in Figure 3.3.1 (arrow) is designated as the holotype (slide number: JM-4; coordinates 143.8 × 15.8; museum catalog number: VPIGM-XXXX), reposited at Virginia Polytechnic Institute Geosciences Museum.

Occurrence.—The upper Ediacaran Liuchapo Formation at Jiumen in central Guizhou Province, South China.

Discussion.—The Liuchapo specimens differ from *Horodyskia monoliformis* from the Mesoproterozoic Belt and Bangemall supergroups in their size, aureole, and preservation. Their beads are 0.1–0.7 mm in diameter (Fig. 3.5), smaller than the Belt Supergroup specimens (0.5–4 mm in diameter; Fedonkin and Yochelson, 2002) and the Bangemall specimens (2–10 mm in diameter; Grey et al., 2000). The distinct aureole, which may represent agglutinated material, has not been reported from with the Belt or Bangemall specimens, although these specimens have not been studied in thin sections. Furthermore, such aureoles are less likely to be preserved as a recognizable feature in coarse-grained sediments of the Appekunny Formation and Manganese Group. The Liuchapo specimens are silicified and carbonaceous material is present in the beads, whereas those from the Appekunny Formation and Manganese Group are preserved as casts and molds, mostly as concave sole impressions (Grey et al., 2000). Finally, *Horodyskia monoliformis* from Appekunny Formation and Manganese Group are preserved on bedding surfaces. In the Liuchapo Formation, several specimens are preserved obliquely or vertically (Fig. 3.3.15), although most are preserved parallel to bedding plane.

*Horodyskia minor* from the Liuchapo Formation is also smaller than *Horodyskia monoliformis*? from the late Ediacaran Zhengmuguan Formation in North China, whose beads are 0.5–1.2 mm in diameter and are preserved as compressed casts (Shen et al., In press). Its beads are also smaller than *Horodyskia* beads from the late Ediacaran Kauriyala Formation (Krol D) in
the Lesser Himalaya, which are 1–2.5 mm in diameter (measured from illustrations published by Mathur and Srivastava, 2004) (Fig. 3.6).

Genus PALAEOPASCICHNUS Palij, 1976, emend. Shen et al., in press

_Type species._—*Palaeopascichnus delicatus* Palij, 1976.

_Discussion._—*Palaeopascichnus* is characterized by serially arranged segments that are subcircular, elliptical, curved, or crescent in shape (Shen et al., In press). It is one of the most important late Ediacaran genera with a world-wide distribution (Jensen et al., 2006; Shen et al., In press). It occurs in late Ediacaran successions in Baltica (Urbanek and Rozanov, 1983; Sokolov and Fedonkin, 1990), Newfoundland (Narbonne et al., 1987; Gehling et al., 2000), Australia (Glaessner, 1969; Jenkins, 1995; Haines, 2000), and North China (Yang and Zheng, 1985; Shen et al., In press). The Liuchapo specimens share the basic body construction with described *Palaeopascichnus* species, and they should be included in this genus.

PALAEOPASCICHNUS JIUMENENSIS new species

(Figure 3.4)

_Diagnosis._—Unbranched series consists of uniserially arranged segments, surrounded by an aureole of light-colored, organic-poor, microcrystalline quartz. Observed in thin sections, segments are mostly crescent in shape and are polarized, with the concave side pointing to the same direction. However, the terminal segment, located at the concave end of the series, is spheroidal rather than crescent in shape. Segments in the same series are more or less evenly spaced, but are connected with each other by a thin filament of carbonaceous material. Segment size and spacing are positively correlated.

_Description._—Most specimens are preserved parallel or nearly parallel to bedding plane. However, some of them are oblique or perpendicular to bedding plane (Fig. 3.4.8–3.4.9). A light-colored, carbonaceous-poor aureole of microcrystalline quartz material surrounds the series (Fig. 3.4.10, 3.4.11). Series length ranges from 0.9 mm to 5.0 mm, and width from 0.3 mm to 1.0 mm. Most series are sinuous or curved; straight strings are uncommon. They never branch, and
typically maintain a more or less constant width. Among observed specimens, there are 4–30 segments per series. Segments are typically dark colored, presumably because of the presence of carbonaceous material. Crescent segments in the same series have similar size and shape, and they are oriented in the same direction, with their concave side pointing to the terminal, spherical segment (Fig. 3.4.1–3.4.6). The spherical segment is slightly smaller than crescent segments, which have very sharp lateral edges. Segments are spaced evenly. In better preserved specimens, a carbonaceous filament that connects adjacent segments can be seen (Fig. 3.4.1–3.4.4, 3.4.6, 3.4.7, 3.4.10–3.4.15).

The three-dimensional morphology of the segments is best appreciated by combining thin sections cut perpendicular and parallel to bedding plane, as well as continuous grinding of specimens (Fig. 3.4.12–3.4.15). The crescent segments are curved discoids in three dimensions, uniserially arranged to form a “stack of dishes”. The spherical morphology of the terminal segment is confirmed by continuous grinding. However, due to sediment compactions the segments are typically vertically compressed, as can be seen in thin sections cut perpendicular to bedding plane (Fig. 3.4.8–3.4.9).

**Measurements.**—Crescent segments are 0.07–0.23 mm in thickness (mean = 0.12 mm, s.d. = 0.04 mm, n = 14), 0.23–0.65 mm in width (mean = 0.34 mm, s.d. = 0.13 mm, n = 14) wide, with a spacing of 0.03–0.35 mm (mean = 0.12 mm, s.d. = 0.09 mm, n = 14). The spherical terminal segment is slightly smaller than crescent ones, ranging from 0.14 mm to 0.55 mm in maximum diameter (mean = 0.27 mm, s.d. = 0.1 mm, n = 13). Segment width and spacing are positively correlated (correlation coefficient r = 0.95; Fig. 3.7).

**Etymology.**—Species epithet derived from the fossil locality, Jiumen village of central Guizhou Province in South China.

**Material.**—More than 80 specimens collected from the late Ediacaran Liuchapo Formation at Jiuman, Danzhai County, Guizhou Province, South China.
Types.—The specimen illustrated in Figure 3.4.10 is designated as the holotype (slide number: JM–3; coordinates 147.5 × 23.7; museum catalog number: VPIGM-XXXX), reposited at Virginia Polytechnic Institute Geosciences Museum.

Occurrence.—The upper Ediacaran Liuchapo Formation at Jiumen, central Guizhou Province, South China.

Discussion.—Previous authors described four formally named *Palaeopascichnus* species—*P. delicatus* Palij, 1976, *P. sinuosus* Fedonkin, 1985, *P. minimus* Shen et al., in press, and *P. meniscatus* Shen et al., in press—from Ediacaran successions in Russia, Newfoundland, and North China. In addition, unnamed *Palaeopascichnus*-like fossils have been reported from Ediacaran successions in Newfoundland (Narbonne and Hofmann, 1987) and South Australia (Haines, 2000). *Palaeopascichnus jiumenensis* from the Liuchapo Formation can be distinguished from other *Palaeopascichnus* species by its relatively small segment size (Fig. 3.8), the lack of branched series, the presence of both spheroidal and discoidal segments, connecting filament, and aureole. Admittedly, some of the morphological differences may be taphonomic; the Liuchapo specimens are preserved through silica premineralization, distinct from the cast and mold (sometimes strongly compressed) preservation of all other described *Palaeopascichnus* species.

The Segment size of previously described *Palaeopascichnus* species has been summarized in Shen et al. (In press) (Fig. 3.8). *Palaeopascichnus jiumenensis* is smaller than *P. delicatus, P. sinuosus, and P. meniscatus*, but is most similar to *P. minimus* in segment size; the latter species is characterized by segments 0.1–0.2 mm in thickness and 0.3–0.7 mm in width (Shen et al., in press). Thus, it is possible that *P. jiumenensis* and *P. minimus* are closely related or even synonymous.

Previously described *Palaeopascichnus* species have a wide range of segment shapes, including straight, curved, subcircular to elliptical, and crescent segments when viewed on bedding plane. To some degrees this variation reflects different orientations and compaction of originally discoidal segments (Shen et al., in press). *Palaeopascichnus jiumenensis* has curved discoidal (crescent in thin section) segments and a terminal spheroidal segment. It is possible that its discoidal segments, when compressed on bedding plane, would mimic those of *P. minimus*.
However, the presence of a terminal spheroidal segment in multiple specimens of *P. jiumenensis* from the Liuchapo Formation but in none of *P. minimus* from the Zhengmuguan Formation (Shen et al., in press) suggest that they represent two species, despite their similar segment size. Thus, we choose to keep them as separate species.

Other morphological features that are present in *Palaeopascichnus jiumenensis* but have not yet been demonstrated in any other *Palaeopascichnus* species include the connecting filament and aureole. The connecting filament in *P. jiumenensis* is represented by a thin string of carbonaceous material, which may not be preserved in casting and molding by coarse-grained sediments. The aureole consists of microcrystalline quartz but very little organic carbon, in sharp contrasts to the carbonaceous rich crescent segments. The aureole may be biologically significant because it may represent agglutinated material. The presence of similar aureole in other *Palaeopascichnus* species should be tested through thin section observations.

Previously described species of *Palaeopascichnus* are mostly preserved as casts and molds in sandstone and siltstone, some as positive hyporeliefs (Urbanek and Rozanov, 1983; Narbonne et al., 1987; Sokolov and Fedonkin, 1990), others as highly compressed clay veneers (Shen et al., In press). *Palaeopascichnus*-like fossils from the Ediacaran Wonoka Formation in South Australia are also highly compressed and appear to have carbonaceous material (Haines, 2000). *Palaeopascichnus jiumenensis* from the Liuchapo Formation represent a novel taphonomic pathway for *Palaeopascichnus* preservation and may provide complementary information about the taphonomy, morphology, and ecology of this genus. The discovery of *Palaeopascichnus* in Ediacaran cherts accentuates the recent observation that classical Ediacara fossils can be preserved in multiple taphonomic windows, including casting and molding in sandstone and siltstones (Gehling, 1999), carbonaceous compression in shales (Xiao et al., 2002), and now permineralization in cherts. Only when we combine the information from different taphonomic windows can we understand the complete morphological and ecological spectrum of Ediacara organisms.

Despite the distinct preservation of the *Palaeopascichnus jiumenensis* in the Liuchapo cherts, electron microprobe analysis suggests that the silicified specimens, like the compressed casts of *P. minimus* and *P. meniscatus* from the Ediacaran Zhengmuguan Formation in North China (Shen et al., in press), are characterized by elevated clay concentrations. Elemental maps show that, compared to surrounding matrix, the segments of *Palaeopascichnus jiumenensis* have
elevated Al and Mg concentrations but subdued Si concentration (Fig. 3.9). We interpret the elemental data as evidence for a moderate concentration of clay minerals in the segments. The taphonomic significance of the clay minerals is still uncertain, but given the recent interest in the role of clay minerals in exceptional preservation (Orr et al., 1998; Butterfield, 1995), it is important to note the preferential occurrence of clay minerals in Palaeopascichnus segments.

REFERENCES


Figure 3.1. Geographic map showing the location of Jiumen Village, Danzhai County, central Guizhou Province. Inset shows the fossil locality (star) in the South China (SC) Block. NC, North China Block. TA: Tarim Block.
Figure 3.2. Stratigraphic column of the late Ediacaran and early Cambrian successions in Jiumen village, Danzhai County, South China, with fossil horizon indicated (arrow).
Figure 3.3. *Horodyskia minor* new species from the Liuchapo Formation. (2) and (6–15) are reflected light photomicrographs, among them, (2) and (6–11) are of serially ground specimens that have been destroyed. All other specimens were photographed in thin sections using transmitted light microscopy, and their thin section number and coordinates are given. Thin section prefix JM- denotes specimens collected from the Liuchapo Formation in the Jiumen Village. VPIGM-xxx refers to catalog numbers at the Virginia Polytechnic Institute Geosciences Museum. (1–14) are sections cut more or less parallel to bedding plane, whereas (15–16) are perpendicular to bedding plane. (1) JM-4 (143.8 × 15.8), arrowed specimen is holotype VPIGM-xxx; (3–4), JM-4 (158.0 × 3.5). Note aureole of light-colored, organic-poor, microcrystalline quartz. (4) was photographed using cross polarized light. (5) JM-A (115.3 × 21.0). Note connection filament between beads. (6) note connection filament. (7–11) the same specimen exposed during serial grinding. Note aureole. (12–14) JM-F-1. (13) shows broken edge along a crack that cut through beads. (14) close-up of (13), showing the three-dimensionality of the beads. (15) JM-G; (16) JM-4-1. Note vertically compressed beads in (15–16). Scale bars in (1–6) and (12–14) represent 1 mm, (7–11) and (16) 2 mm, and (14) and (15) 0.5 mm.
Figure 3.4. *Palaeopascichnus jiumenensis* new species from the Liuchapo Formation. (1–6), (8–9), and (12–15) are reflected light photomicrographs, among them, (1–6) and (12–15) are of serially ground specimens that have been destroyed. All other specimens were photographed in thin sections using transmitted light microscopy, and their thin section number and coordinates are given. (8–9) are sections cut more or less perpendicular to bedding plane, whereas others are parallel to bedding plane. (4–5) the same specimen exposed during serial grinding. Note spheroidal terminal segment (arrows) and connection filament (4, 6). (7), JM-4 (137.3 × 16.0), note connection filament. (8), JM-G-2; (9), JM-4-2, note vertical compression. (10–11), JM-3 (147.5 × 23.7), (11) is photographed using cross polarized light. Note the aureole. (12–15) serial grinding of the same specimen. Isolated circles may represent disarticulated *Horodyskia* beads. Scale bars represent 1 mm.
Figure 3.5. Bead size, bead spacing, and aureole width of *Horodyskia minor* from the Liuchapo Formation. Measurements were made in 20 specimens, with the maximum bead size, spacing, and aureole width taken from each specimen. Four outliers are indicated by empty diamonds.
Figure 3.6. Bead size of *Horodyskia* specimens from Liuchapo, North China (Shen et al., in press), Lesser Himalaya (Mathur and Srivastava, 2004), Montana (Fedokin and Yochelson, 2002), and Western Australia (Grey and Williams, 1990).
Figure 3.7. Measurements of *Palaeopascichnus jiumenensis* from the Liuchapo Formation. Measurements were made in 14 specimens, with the maximum segment thickness, width, and spacing taken from each specimen.
Figure 3.8. Segment size range of *Palaeopascichnus* species. Data for *P. delicatus*, *P. sinuosus*, *P. minimus*, *P. meniscatus*, and *P. sp.* (Glaessner, 1969; Haines, 2000) from Shen et al. (in press).
Figure 3.9. Elemental maps of a *Palaeopascichnus jiumenensis* specimen, showing the distribution of Aluminum, Silicon, Magnesium, and Barium. Scale bar is 0.5 mm.
Figure 3.10. Modern foraminifers. (1) *Resigella moniliforme*; (2) *Cylindroclavulina bradyi*; (3) *Eonodosaria evlanensis* ((Loeblich and Tappan, 1988). Scale bars represent 0.2 mm, 1.8 mm, and 0.1 mm for (1), (2), and (3), respectively.
Figure 3.11. An update of the eukaryotic fossils record mapped on the eukaryote phylogenetic tree (Porter, 2004) Eukaryote groups marked in red are heterotrophic. Those marked in green have photosynthetic members. The interpretation of *Horodyskia* as a stem-group foraminifer indicates that rhizarians must have diverged 1.4 Ga.
Chapter 4
Microfossils from the Basal Cambrian Yanjiahe Formation in the Yangtze Gorges area (South China) and Yurtus Formation in the Aksu area (Tarim Block, northwestern China)

Abstract:

The base of the Cambrian System marks the beginning of an important episode in the history of life. But most paleontological work on the basal Cambrian has been focused on skeletal animal fossils, and our knowledge about the primary producers—cyanobacteria and eukaryotic phytoplankton (acritarchs)—is limited. To partially fill this knowledge gap, we investigated basal Cambrian phosphorites and cherts of the Yanjiahe Formation in the Yangtze Gorges area (South China) and the Yurtus Formation in the Aksu area (NW China). Our study confirms the previous reports of the Asteridium-Comasphaeridium-Heliosphaeridium (ACH) acritarch assemblage in these two formations. The acritarch assemblage is dominated by Heliosphaeridium ampliatum (Wang, 1985) Yao et al., 2005, with rare occurrences of Comasphaeridium densum new species [=Comasphaeridium annulare (Wang, 1985) Yao et al., 2005] and Paracymatiosphaera? uniformis new species. In addition, the clustered coccoidal microfossil Archaeophycus venustus Wang et al., 1983, the tabulate tubular microfossil Megathrix longus Yin, 1987, and several filamentous microfossils including Siphonophycus robustus (Schopf, 1968), Cyanonema majus new species, and Oscillatoriopsis sp. are present in these basal Cambrian rocks. The occurrences of these microfossils support the stratigraphic correlation between the Yanjiahe and Yurtus formations, and together with the stratigraphic occurrence of skeletal animal fossils suggest that animals and phytoplankton radiated in tandem during the Cambrian explosion.

Key words: Early Cambrian, Tarim, South China, Acritarch, Cyanobacteria

1. INTRODUCTION

The history of life is punctuated by a number of evolutionary radiations and mass extinctions. Of these evolutionary events, the Cambrian explosion is perhaps the most significant; essentially all animal phyla evolved in the first 25 million years of the Cambrian, and apparently no new animal phyla evolved in the subsequent 520 million years after the Cambrian explosion.
(Marshall, 2006). Although much has learned about animal radiation patterns during the Cambrian explosion, our knowledge about the diversity of primary producers—cyanobacteria, macroalgae, and phytoplankton—is limited. This is in part because the Cambrian primary producers were dominated by non-biomineralizing photosynthesizers that have generally low preservability compared to contemporaneous skeletal animals. The preservation of cyanobacteria and macroalgae, for example, requires unusual taphonomic conditions (Butterfield, 2003). Phytoplankton—particularly those with a thick-walled resting stage, however, can be readily preserved as organic-walled microfossils (or acritarchs) in fine-grained siliciclastic rocks, cherts, and phosphorites. Such acritarch fossils provide a paleontological basis for us to understand the evolution of the primary producers during the Cambrian explosion. To gain insights into the evolution of primary producers, Vidal and Moczydlowska-Vidal (Vidal and Moczydlowska-Vidal, 1997) compiled the taxonomic diversity of Proterozoic and Cambrian acritarchs. Although their compilation of early Cambrian acritarchs was based on a limited number of assemblages from Baltica, Laurentia, and Avalonia, it reveals a pronounced early Cambrian diversification of acritarchs that parallels the Cambrian radiation of skeletal animals. To further enrich our knowledge about early Cambrian evolution of primary producers and to facilitate biostratigraphic correlations between early Cambrian faunal and floral assemblages, it is important to document the taxonomical diversity of primary producers in early Cambrian successions rich in skeletal animal fossils. In this context, we investigated the basal Cambrian Yanjiahe Formation in the Yangtze Gorges area and the Yurtus Formation in the Aksu area. Previous investigations have shown that both successions contain abundant and diverse small shelly fossils (Chen, 1984; Gao et al., 1985; Qian and Xiao, 1984) (Xiao and Duan, 1992; Yue and Gao, 1992; Yue and Gao, 1994); (Conway Morris and Chapman, 1996; Conway Morris and Chapman, 1997; Conway Morris et al., 1997), as well as a moderate diversity of Micrhystridium-like acritarchs (Yin, 1987a); (Ding et al., 1992); (Yin et al., 2003a); (Yao et al., 2005).

The Yanjiahe and Yurtus formations both consist of black chert, phosphorite, and dolostone. Previous paleontological studies (Yao et al., 2005) suggest that these two formations can be broadly correlated with each other on the basis of common occurrence of several microfossil taxa, including Heliosphaeridium Moczydlowska, 1991, Comasphaeridium Staplin, Jansonius and Pocock, 1965, and Megathrix Yin, 1987. In addition, both formations contain
similar small shelly fossils characteristic of the Meishucunian Stage (Chen, 1984; Gao et al., 1985; Qian and Xiao, 1984; Xiao and Duan, 1992; Yue and Gao, 1992; Yue and Gao, 1994; Conway Morris and Chapman, 1996; Conway Morris and Chapman, 1997; Conway Morris et al., 1997). The Meishucunian Stage in South China is correlated with, on the basis of small shelly fossil biostratigraphy, with the Nemakit-Daldynian and Tommotian stages in Siberia (Qian et al., 2001). Thus, the Yanjiahe and Yurtus formations record evolutionary history during the pre-trilobite Cambrian or the unnamed Cambrian series 1 (Babcock et al., 2005), and have the potential to illuminate the earliest episodes of the Cambrian explosion. The goal of this research is to systematically describe microfossils recovered from the black cherts of the Yanjiahe and Yurtus formations. Our study complements previous paleontological investigation on these units, which largely focused on small shelly fossils extracted from the carbonate facies in the two formations. Together, these paleontological data can be used to facilitate biostratigraphic correlation of early Cambrian strata and to test evolutionary hypotheses about possible ecological interactions between primary producers and animals during the Cambrian radiation (Butterfield, 1997; Butterfield, 2001; Moczydlowska, 2001; Moczydlowska, 2002).

2. STRATIGRAPHIC SETTINGS AND LOCALITIES

2.1. The Yurtus Formation in the Aksu area

The Aksu area is located in the northern margin of the Tarim Block (Fig. 4.1). Thick Neoproterozoic–Cambrian carbonate successions outcrop in this area. The lower Cambrian Yurtus Formation is about 12–35 m in thickness (Fig. 4.2.a). It unconformably overlies dolostone of the Ediacaran Qigeblaq Formation and conformably underlies trilobite-bearing dolostone of the lower Cambrian Xiaoerblaq Formation (Gao et al., 1985). Dolostones in both the Qigeblaq and Xiaoerblaq formations are characterized by abundant fenestrae, indicating intertidal to supratidal depositional environments. The Yurtus Formation consists of two lithostratigraphic units, the lower chert-phosphorite unit (< 5 m in thickness) and the upper silty and phosphatic dolostone unit (Fig. 4.2a). Detailed sedimentary facies analysis of the Yurtus Formation is not available, but the abundance of phosphatic peloids and intraclasts in the Yurtus Formation indicates a relatively shallow, possibly shallow subtidal, depositional environment.
Previous study (Yao et al., 2005) shows that the lower unit of the Yurtus Formation contains abundant *Micrystridium*-like acritarchs, including *Heliosphaeridium ampliatum* and *Comasphaeridium densum* new species (=*Comasphaeridium annulare*), as well as the small shelly fossil *Kaiyangites novilis* and the enigmatic tubular microfossil *Megathrix longus*. Yao et al. (2005) also reported *Asteridium tornatum*, *Heliosphaeridium ampliatum*, *Heliosphaeridium cf. lubomlense*, *Kaiyangites novilis*, and *Megathrix longus* from the basal Cambrian Xishanblaq Formation in the northeastern margin of the Tarim Block, which they correlated with the lower Yurtus Formation. Thus Yao et al. (2005) established the basal Cambrian *Asteridium–Heliosphaeridium–Comasphaeridium* acritarch assemblage on the basis of the lower Yurtus and Xishanblaq material.

Small shelly fossils have been described from a number of horizons in the upper unit of the Yurtus Formation, which consists of phosphatic dolostone and is amenable to acid digestion technique for fossil extraction (Gao et al., 1985; Qian and Xiao, 1984; Xiao and Duan, 1992; Yue and Gao, 1992; Yue and Gao, 1994); (Duan and Xiao, 1992); (Conway Morris and Chapman, 1996; Conway Morris and Chapman, 1997; Conway Morris et al., 1997). The small shelly fossils include *Anabarites*, *Protohertzina*, *Jiangshanodus*, *Cambroclavus*, *Wushichites*, *Zhijinites*, *Halkieria*, *Chancelloria*, *Archicladium*, *Archiasterella*, *Tannuolina*, *Lapworthella*, and many other genera. Rare occurrences of trilobite genal spines have also been reported from the upper Yurtus Formation (Qian, 1999), although these have not been illustrated in any formal publications. Together, these fossils indicate that the upper Yurtus Formation may be correlated with the upper Meishucunian to lower Qiongzhusian stages in eastern Yunnan of South China, or upper Tommotian to lower Attdabanian in eastern Siberia (Yue and Gao, 1992); (Conway Morris and Chapman, 1996).

The Yurtus microfossils described in this paper were collected from the lower chert-phosphorite unit at the Yurtus VI section located at 40°49.079’N, 79°25.380’E, elevation 1927 m. This section was described in detail by Gao et al. (1985), Conway Morris and Chapman (1996), and Yao et al. (2005).

### 2.2. The Yanjiahe Formation in the Yangtze Gorges area

The Yangtze Gorge area is located in the northern Yangtze Block (Fig. 4.1), where thick successions of Neoproterozoic-Paleozoic rocks are incised by the Yangtze River. Ediacaran and
Cambrian rocks are exposed around the Huangling anticline (Fig. 4.2b). Previous work on the Ediacaran-Cambrian transition has been focused mostly on the eastern flank of the Huangling anticline, where a depositional hiatus exists between the sub-trilobite Cambrian Tianzhushan Member and uppermost Ediacaran Baimatuo Member of the Dengying Formation (Xing et al., 1984). In the southern flank of the Huangling anticline, however, the sub-trilobite Cambrian strata are represented by the ~40-m-thick Yanjiahe Formation (Chen, 1984), which is equivalent to but much thicker than the <4-m-thick Tianzhushan Member in the eastern flank (Qian et al., 1979; Xing et al., 1984). Here, the Yanjiahe Formation overlies light grey, thick-bedded dolostone of the Ediacaran Baimatuo Member of the Dengying Formation, and the contact is said to be conformable (Chen, 1984). It is overlain by trilobite-bearing black shales of the Shuijingtuo Formation (Chen, 1984); (Ding et al., 1992). The Yanjiahe Formation is divided into three lithostratigraphic members. The lower member is about 12 m thick, and is composed of siliceous dolostone intercalated with carbonaceous shale. The middle member, about 4.5 m thick, is composed of chert interbedded with dolomite and carbonaceous shales. The upper unit, about 23 m thick, is characterized by carbonaceous limestone and carbonaceous shale.

Sedimentary structures indicative an intertidal and supratidal depositional environment, including tepees and fenestrae, occurs in the Baimatuo Member. The Yanjiahe Formation likely represents early transgressive stage during the Early Cambrian sea level rise. In petrographic thin sections, Yanjiahe cherts preserve original packstone fabrics. No evidence of subaerial exposure is found in the Yanjiahe Formation. Thus, we infer that it was deposited in a subtidal environment.

Two previous studies recovered microfossils from the lower member of the Yanjiahe Formation in the southern flank of the Huangling anticline. One chert horizon at the base of the Yanjiahe Formation at Jijiapo (for locality see Fig. 4.2b) yields abundant acritarchs described as Micrhystridium regulare, a taxon that was latter synonymized with Heliosphaeridium ampliatum (Yao et al., 2005). A similar but more diverse microfossil assemblage has been described from one horizon at the base of the Yanjiahe Formation (=Tianzhushan Member) at the Yemaomian section, about 20 km to the northwest of Jijiapo (Yin et al., 2003b). The Yemaomian assemblage includes the acritarchs Micrhystridium ampliatum and several species of Paracymatiosphaera, the tubular microfossil Megathrix longa, and the small shelly fossil Kaiyangites multispinatus (Yin et al., 2003b).
The middle and upper members of the Yanjiahe Formation at Jijiapo yield abundant small shelly fossils characteristic of the Meishucunian Stage, including *Anabarites trisulcatus*, *Protohertzina anabarica*, *Archaeospira* sp., and several species of *Circotheca* (Chen, 1984). The small shelly fossil assemblage in the middle Yanjiahe Formation (bed 4 and 5 in Chen, 1984) was correlated with the Meishucunian small shelly fossil assemblage I (the *Anabarites trisulcatus-Protohertzina anabarica* assemblage) in eastern Yunnan, and that in the upper Yanjiahe Formation (bed 6 and 7 of Chen, 1984) with the Meishucunian small shelly fossil assemblage II (the *Siphogonuchites triangularis-Paragloborilus subglobosus* assemblage). If correct, then the microfossils, including the *Micrhystridium*-like acritarchs, described from the lower Yanjiahe Formation (Ding et al., 1992; Yin et al., 2003a) can be no younger than Meishucunian SSF assemblage I. However, because the exact temporal range of Meishuncunian small shelly fossils has not completely documented, the age of the *Micrhystridium*-like acritarchs in the lower Yanjiahe Formation cannot be constrained finer than the Meishucunian Stage. This conservative age interpretation is also consistent with the presence in the basal Yanjiahe Formation of the small shelly fossil *Kaiyangites* (Yin et al., 2003a), which occurs above the Meishucunian SSF II in Guizhou (Qian and Yin, 1984).

The Yanjiahe microfossils described in this paper were collected from the lower Yanjiahe Formation at the Jiuqunao section located at 30°45.24’N, 111°1.95’E.

3. SYSTEMATIC PALEONTOLOGY

Since the phylogenetic and high-level taxonomic position of these microfossils are uncertain, in systematic description we break down the Yurtus and Yanjiahe microfossils into four morphological groups: acanthomorphic acritarchs, clustered coccoidal microfossils, filamentous microfossils, and tubular microfossils with both complete and incomplete cross-walls. All fossils described in this paper are reposited at the Virginia Polytechnic Institute Geosciences Museum (VPIGM).

3.1. Acanthomorphic acritarchs

Genus *Comasphaeridium* Staplin, Jansonius and Pocock, 1965
Type species. *Comasphaeridium cometes* (Valensi, 1948) Staplin, Jansonius and Pocock, 1965, Middle Jurassic, France.

*Comasphaeridium densum* new species

Figure 4.3.1 (bottom specimen), 4.3.2

*Comasphaeridium annulare* (Wang, 1985) Yao et al., 2005, p. 692, pl. 1, figs 5–7, but not the synonyms therein.

*Type specimen.*—The specimen illustrated in Fig. 4.3.1 is designated as the holotype, reposited at Virginia Polytechnic Institute Geosciences Museum (VPIGM-xxxx; thin section number YTS-54-1; coordinates 129.5 × 11.5).

*Derivation of name.*—Latin, *densum*, with reference to the densely distributed processes.

*Diagnosis.*—Spherical vesicle with densely and evenly distributed and radially arranged processes. Vesicle about 10 µm in diameter. Processes solid, simple, slender, somewhat stiff, and of uniform length. Processes are terminally truncated. No outer envelope is present.

*Description.*—Vesicles are 8.6–14.0 µm in diameter (mean = 11.6 µm, s.d. = 1.54 µm, n = 16) and are circular to ovate in outline with evenly and densely distributed processes. Processes are 1.8–3.0 µm in length (mean = 2.38 µm, s.d. = 0.41 µm, n = 16 measurements made on 16 specimens) and about 0.25 µm in thickness. There are about 70-90 processes in a circumference (mean = 81, s.d. = 5.96, n = 9). Vesicle diameter are not correlated with process length (r = 0.278, p = 0.3 for H₀: r = 0).

*Remarks.*—Wang (1985) described the species *Paracymatiosphaera annularis* as a *Micrhystridium*-like acritarch with solid processes and two envelopes, the outer of which surrounds the processes. Wang (1985) also noted that some specimens lack an outer envelope, probably because of poor preservation. Yao et al. (2005) transferred *Paracymatiosphaera annularis* Wang, 1985, to *Comasphaeridium annulare* (Wang, 1985) Yao et al., 2005, arguing that the outer envelope described in Wang (1985) is not clear in the poor illustrations or could be an optical artifact resulting from the uniformity of process length. Yao et al.’s specimens from the Yurtus Formation do not have any evidence of an outer envelope, and their solid and dense processes clearly identify them with the genus *Comasphaeridium*. The question is whether they represent a new species or an existing species. These specimens are very similar to
Paracymatiosphaera annularis in vesicle size, process length, and process density, except the possible existence of an outer envelope in Paracymatiosphaera annularis. If Paracymatiosphaera annularis does not have an outer envelope, then it is appropriate to transfer this species to the genus Comasphaeridium and it can be a taxonomic home for Yao et al.’s specimens. However, as we make more observations on basal Cambrian Micrhystridium-like acritarchs from the Yanjiahe and Yurtus formations, we feel that there are indeed some specimens that have a bona fide outer envelope. Thus, we choose to keep the species Paracymatiosphaera annularis for those acritarchs with two envelopes, and establish the new species Comasphaeridium densum for very similar acritarchs without an outer envelope.

Comasphaeridium densum can be differentiated from other Comasphaeridium species in its relatively short and rigid processes that are densely distributed on the vesicle. See Yao et al. (2005) for a detailed discussion on the difference between this species and other Comasphaeridium species.

Material.—Five specimens from the Yanjiahe Formation [JQN-chert-1 (135.8 × 11.8), JQN-chert-2 (125.9 × 10.7), (132.9 × 15.4), (133.7 × 12.7), (123.0 × 14.0)] and 11 specimens from the Yurtus Formation [YTS-54-1 (129.5 × 11.5), YTS-54-3 (135.5 × 15.7), (109.0 × 16.0), (125.4 × 18.3), (110.0 × 17.0), (109.0 × 16.8), YTS-54-4 (111.0 × 14), (118.8 × 12.5), (123.0 × 17.0), YTS-54-5 (119.5 × 8.5), YTS-54-6 (110.8 × 20.8)].

Distribution.—The early Cambrian Yanjiahe Formation in the Yangtze Gorges area and the Yurtus Formation in the Tarim Block (Yao et al., 2005).

Genus Heliosphaeridium Moczydlowska, 1991


Heliosphaeridium ampliatum (Wang, 1985) Yao et al., 2005

Figure 4.3.1 (top specimen), 4.3.3–4.3.4

Heliosphaeridium ampliatum (Wang, 1985) Yao et al., 2005, p. 693, pl. 1, figs 8–9, and synonyms therein.
Description.—Single-walled spherical vesicle with 6–16 processes that are hollow, straight, stiff, and taper toward a sharply pointed distal end. Processes are sparsely but evenly distributed on vesicle and communicate with vesicle interior.

Measurements.—Yao et al. (2005) provided measurements of *Heliosphaeridium ampliatum* from the Yurtus Formation. For comparison, measurements of the Yanjiahe population are presented below and in Fig. 4.4. Vesicle diameter is 6.5–11 µm (mean = 8.8 µm, s.d. = 1.37 µm, n = 23 measurements made on 23 specimens), indistinguishable from the Yurtus population. Process length is 9–17 µm (mean = 12.6 µm, s.d. = 2.17 µm, n = 23 measurements made on 23 specimens), similar to the Yurtus specimens. Vesicle size and process length are not correlated (correlation coefficient r = 0.04, n = 23, p = 0.85 for $H_0$: r = 0). Number of processes observed in a circumference is 4–16. Base of processes is 0.8–1.1 µm in diameter.

Remarks.—The genus *Heliosphaeridium* was established on the basis of material extracted from shales and mudstones (Moczydlowska, 1991). Permineralized acritarchs preserved in chert, such as those from the Yanjiahe and Yurtus formations (Ding et al., 1992; Yao et al., 2005), cannot be extracted and species identification is only based on thin section observations. Nonetheless, *Heliosphaeridium ampliatum* can be differentiated from other species in this genus by its relatively sparse and stiff processes (Yao et al., 2005). With several exceptions (for example, *Heliosphaeridium coniferum*), most *Heliosphaeridium* species preserved in shales and mudstones tend to have flexible processes. In contrast, permineralized *Heliosphaeridium* tend to have stiff processes, although the processes of *Heliosphaeridium* cf. *lubomlense* show some degree of flexibility (Yao et al., 2005). The difference in process flexibility seems to reflect underlying biological features, although it is also possible that early diagenetic permineralization may have assisted in the preservation of rigid processes in their original shape. Regardless, the morphological features of this species—hollow processes that open to vesicle cavity but are closed at the distal end—definitely fit the diagnosis of *Heliosphaeridium*.

Material.—About 300 specimens from the Yanjiahe Formation and 100 specimens from the Yurtus Formation.

Distribution.—The early Cambrian Yanjiahe Formation in Hubei (Ding et al., 1992; Yin et al., 2003a), Yurtus Formation in Xinjiang (Yao et al., 2005), Zhongyicun Member of the Zhujiaping Formation in Yunnan (Wang et al., 1983); (Yin, 1990), Yangjiaping Formation in
Hunan (Wang, 1985), Taozichong Formation in Guizhou Province (Wang, 1985); (Braun and Chen, 2003)), and Kuanchuanpu Formation in Shaanxi (Yin, 1987b).

Genus Paracymatiosphaera Wang, 1985

Type species.—Paracymatiosphaera regularis Wang, 1985.

Original Diagnosis.—“Spheroidal cell-like units with distinct radially arranged dense spine structures surrounded by another envelope, in appearance like some Cymatiosphaera fossils or Paracrassosphaera fossils. In many cases the outer envelope is disrupted and sometimes the cell-like wall is indistinct. The units are solitary, with slightly granular surface texture. The spine-like structures are setaceous, equal in diameter along a spine but there are some spines of greater diameter” (Wang, 1985, p. 41).

Remarks.—The genus Paracymatiosphaera was diagnosed as having two envelopes and apparently solid processes in between (Wang, 1985). However, examination of the poor illustrations in Wang (1985) does not confirm the presence of an outer envelope in the type species, Paracymatiosphaera regularis, although it is probable that the three other species, Paracymatiosphaera irregularis, P. annularis, and Paracymatiosphaera hunanensis may have an outer envelope. Wang (1985) pointed out that the absence of an outer envelope is because of taphonomic degradation, but Yao et al. (2005) argued that an apparent outer envelope may result from the concentration of organic matter and/or pyrite at the distal termini of processes. Yao et al. (2005) thus created a new combination Comasphaeridium annulare (Wang, 1985) based on Paracymatiosphaera annularis Wang, 1985, and synonymized all described species of Paracymatiosphaera with Comasphaeridium annulare. The specimens described by Yao et al. (2005) as Comasphaeridium annulare (= Comasphaeridium densum new species described in this paper) were collected from the Yurtus Formation at the Yurtus VI section (Fig. 4.1), and they do not show any sign of an outer envelope. The new material described here under Paracymatiosphaera? uniformis new species are from the same section, but they appear to have an outer envelope. Clearly, it is important to examine the original material published by Wang (1985) and to verify the presence of an outer envelope in species of Paracymatiosphaera. Unfortunately, the current authors do not have access to the material described in Wang (1985). Thus, the genus Paracymatiosphaera is tentatively preserved here as a taxonomic home for
specimens with double envelopes, pending future examination of the type material and emendation of its diagnosis.

Paracymatiosphaera? uniformis new species

Figure 4.3.5–4.3.16

Paracymatiosphaera annularis Wang, 1985; Yin et al., 2003, p. 81, pl. 2, fig 3.

Type specimen.—The specimen illustrated in Fig. 4.3.5 is designated as the holotype, reposited at Virginia Polytechnic Institute Geosciences Museum (VPIGM-xxxx; thin section number YTS-58-1; coordinates 143.0 × 29.8). Derivation of name.—Latin, uniformis, with reference to the uniform length of the processes.

Diagnosis.—Spheroidal vesicle about 10 µm in diameter, surrounded by evenly distributed, solid processes. Processes are extremely uniform in length (~1 µm long) and thickness (~0.4 µm in diameter). There are approximately 30–50 processes per circumference. There appears to be a spherical outer envelope that surrounds the processes.

Description.—Specimens are three-dimensionally preserved, although many are deflated or deformed. Process length represents about 10–15% of vesicle diameter. Processes are short, straight, and stiff (even in specimens whose vesicle and outer envelope are deformed). They are oriented perpendicular to and are confined between the vesicle wall and the outer envelope.

Measurements.—Specimens are typically deflated and deformed to some degrees. Maximum vesicle diameter 5.2–14.94 µm (mean = 8.67 µm, s.d. = 2.0 µm, n = 45), minimum vesicle diameter 2.9–14.76 µm (mean = 6.42 µm, s.d. = 2.3 µm, n = 45 measurements made on 45 specimens), process length 0.7–1.6 µm (mean = 1.1 µm, s.d. = 0.17 µm, n = 45 measurements made on 45 specimens), processes thickness 0.3–0.4 µm (mean = 0.4 µm, s.d. = 0.04 µm, n = 24 measurements made on 24 specimens), process spacing 0.9–1.3 µm (mean = 1.0 µm, s.d. = 0.08 µm, n = 24 measurements made on 24 specimens), and process density 30–50 per circumference. Process length is positively correlated with maximum vesicle diameter (correlation coefficient r = 0.71; n = 45; p<<0.01 for H0: r = 0; Fig. 4.5).

Remarks.—As discussed above, the existence of an outer envelope in the genus Paracymatiosphaera (particularly its type species) needs to be further verified. Thus, at the
present this species is questionably placed in the genus *Paracymatiosphaera* pending further research.

The key features that distinguish *Paracymatiosphaera? uniformis* from other species are its apparent outer envelope and evenly distributed, short, and rigid processes that are of uniform length and thickness. The most similar taxon is probably *Paracymatiosphaera annularis* if the latter indeed has double envelopes as described by Wang (1985); however, *Paracymatiosphaera annularis* has relatively longer (~3 \( \mu \)m in length, or 20% of vesicle diameter) and apparently denser than *Paracymatiosphaera? uniformis*. These feature also set *Paracymatiosphaera? uniformis* apart from species of *Comasphaeridium*, which typically have longer and denser processes (Moczydlowska, 1991; Moczydlowska, 1998; Yao et al., 2005). An additional feature that differentiates *Paracymatiosphaera? uniformis* from *Comasphaeridium*, including *C. densum* new species described above, is the lack of an outer envelope in the latter taxon.

Three other Proterozoic and Paleozoic acritarch genera also have two or more envelopes. These are *Cymatiosphaera* Wentzel, 1933, *Cymatiosphaeroides* Knoll, 1984, and *Distosphaera* Zhang et al., 1998, all of which are much larger than *Paracymatiosphaera? uniformis*. The vesicle (or inner envelope) of *Cymatiosphaera* is divided into many polygonal fields by membranes perpendicular to vesicle surface (Deflandre, 1954). Although the membrane junctions can be thickened, they are not processes. In contrast, the outer envelope of *Paracymatiosphaera? uniformis* is supported by short and stiff processes, as is evident from focusing planes that cut the processes transversely (Fig. 4.3.10). The only species of *Cymatiosphaeroides* described in the literature is *C. kullingii* Knoll, 1984 from the Proterozoic successions in Nordaustlandet and Spitsbergen (Knoll, 1984); (Knoll et al., 1991); (Butterfield et al., 1994). *Cymatiosphaeroides kullingii* is characterized by a multilaminate (up to 12) outer envelope and unevenly distributed, solid processes. Furthermore, the vesicle diameter of *Cymatiosphaeroides kullingii* (30–350 \( \mu \)m according to Butterfield et al., 1994) is much greater than that of *Paracymatiosphaera? uniformis*. *Distosphaera speciosa* Zhang et al., 1998 from the Ediacaran Doushantuo Formation in South China was originally identified as *Cymatiosphaeroides kullingii* (Yuan et al., 1993), although it has hollow conical processes on the outer envelope, as well as solid slender process between the inner and outer envelopes. Again, *Distosphaera speciosa* (outer envelope 75–125 \( \mu \)m and the inner envelope 32–55 \( \mu \)m in diameter) is much larger than *Paracymatiosphaera? uniformis*. 

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Specimens described as *Paracymatiosphaera annularis* Wang, 1985, from cherts of lowermost Cambrian Tianzhushan Member in Zigui County, Hubei Province, South China (Yin et al., 2003a), is similar to *Paracymatiosphaera? uniformis* in vesicle/process ratio, regular arrangement of uniform spines, as well as the apparent existence of an outer envelope. Thus we tentatively assign it under the species *Paracymatiosphaera? uniformis*.

**Material.**—About 80 specimens from the Yurtus Formation in the Aksu area in the Tarim Block.

**Distribution.**—The Yurtus Formation in the Aksu area in Xingjiang Province, northwest China.

### 3.2. Clustered coccoidal microfossils

Genus *Archaeophycus* Wang, Zhang, and Guo, 1983

*Paratetraphycus* Zhang, 1985, p. 166.

*Paratetraphycode* Cao, 1985, p. 189.

*Type species.*—*Archaeophycus venustus* Wang, Zhang, and Guo, 1983, from the basal Cambrian Zhujiaqing Formation (formerly Meishucun Formation) in Jinning, eastern Yunnan, South China.

**Diagnosis.**—The original diagnosis by Wang et al. (1983) is essentially accurate. This genus is characterized by monads, dyads, tetrads, octads, and often non-2^n cell clusters. Cells are sub-spherical or ellipsoidal in shape and 10–30 μm in diameter. No sheaths are present surrounding individual cells or clusters. Cells tend to be polyhedral when clustered, because they are tightly appressed against each other.

**Remarks.**—Clustered coccoidal microfossils from the Bitter Spring Formation and other Proterozoic successions have been described under numerous taxa, but typically they are not as tightly clustered as *Archaeophycus*, their cells tend to be smaller (<15 μm, and often < 5 μm, in diameter), and the cells or the clusters are surrounded by sheaths. *Sphaerophycus* Schopf, 1968, is diagnosed as sheathed spherical to ellipsoidal cells commonly solitary or loosely associated in clusters or uniseriate aggregates (Schopf, 1968). Individual cells of *Myxococoides* Schopf, 1968, are not distinctly sheathed, but they are embedded in a well-developed amorphous,
non-lamellated organic matrix. Cell clusters of *Caryosphaeroides* Schopf, 1968, and *Glenobotrydion* Schopf, 1968, are embedded in amorphous organic matrix or distinct sheaths, and their cells are characterized by subcellular structures of dubious biological significance (Knoll and Barghoorn, 1975; Knoll and Golubic, 1979). *Gloeodiniopsis* Schopf, 1968, and synonymous taxa (*Bigeminococcus* Schopf and Blacic, 1971; *Eozygion* Schopf and Blacic, 1971, and *Eotetrahedrion* Schopf and Blacic, 1971) are characterized by multilamellate sheaths (Knoll and Golubic, 1979; Schopf, 1968; Schopf and Blacic, 1971). Finally, *Tetraphycus* Oehler, 1978, from the Mesoproterozoic McArthur Group in northern Australia, is characterized by rather small cells (0.5–5 µm) embedded in an amorphous organic matrix (Oehler, 1978). Thus these Proterozoic taxa can be distinguished from *Archaeophycus* by their cell size, multilamellate sheaths or amorphous organic matrix, and relatively loose aggregation.

*Paratetraphycoides* Cao, 1985, and *Paratetraphycoides* Cao, 1985, both described from cherts and phosphorites of the Ediacaran Doushantuo Formation in South China (Cao, 1985; Zhang et al., 1998; Zhang, 1985), are indistinguishable from *Archaeophycus* in cell size, tight clustering, and lack of encompassing sheath or organic matrix. These two genera are regarded as junior synonyms of *Archaeophycus*. We also agree with Zhang (1985) that *Tetraphycus conjunctum* Lo, 1980, from the Ediacaran Yudoma Group, should be referred to the genus *Archaeophycus* (= *Paratetraphycus*).(Lo, 1980)

*Archaeophycus venustus* Wang, Zhang, and Guo, 1983

Figure 4.6.1–4.6.6


*Paratetraphycoides multa* Cao, 1985, p. 189, pl. 1, figs. 1, 2.

*Tetraphycoides multa* Cao, 1985, p. 189, pl. 1, figs. 1, 2.

Diagnosis.—Same as genus.

Description.—Individual cells can be solitary or form dyad, triad, tetrad, or octad clusters. Clusters often occur in aggregates. Cell boundary is delineated by dark cell walls (Fig. 4.6.1, 4.6.6).

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**Measurement.**—Cell diameter 9–15 µm (mean = 11.6 µm; s.d. = 1.4 µm; n = 52 measurements made on 20 clusters). Cell clusters 13–30 µm in size (mean = 19.5 µm; s.d. = 4.56 µm; n = 27). Cell walls about 0.5–1.0 µm in thickness.

**Remarks.**—*Bigeminococcus grandis* from the lower Zhujiaqing Formation (formerly Meishucun Formation) in Jinning of eastern Yunnan (Wang et al., 1983, fig. 13.1–13.4) is similar to *Archaeophycus venustus*. Although some *Bigeminococcus grandis* clusters described by Wang et al. (1983) appear to have surrounded by sheaths, others in the same colony are devoid of a sheath. It is not clear whether the apparent sheath is simply a thicker cell wall. *Bigeminococcus grandis* is otherwise indistinguishable from and is tentatively regarded as synonym of *Archaeophycus venustus*. As discussed under the genus remarks, *Paratetraphycus giganteus* and *Tetraphycoides multa* should also be regarded as junior synonyms of *Archaeophycus venustus*.

**Material.**—One specimen from the Yanjiahe Formation in the Yangtze Gorges area (thin section number JQN-chert-1; coordinates 142.8 × 15.7) and about 20 specimens from the Yurtus Formation in the Aksu area.

**Distribution.**—Ediacaran and Meishucunian successions in South China and northwestern China, including the Ediacaran Doushantuo Formation in the Yangtze Gorges and Weng’an areas (Cao, 1985; Zhang et al., 1998; Zhang, 1985) and the early Cambrian Zhujiaqing (formerly Meishucun) Formation in eastern Yunnan (Wang et al., 1983), Yanjiahe Formation in the Yangtze Gorges area (this paper), and Yurtus Formation in the Aksu area (this paper).

### 3.3. Filamentous microfossils

**Genus Cyanonema Schopf, 1968, emend. Butterfield et al., 1994**

**Type species.**—*Cyanonema attenuatum* Schopf, 1968, emend. Butterfield et al., 1994. The type species was originally described as *Cyanonema attenuata*. It should be spelt as *Cyanonema attenuatum* according to ICBN rules.

**Diagnosis.**—See Butterfield et al. (1994).

**Remarks.**—Butterfield et al. (1994) classified unbranched, unsheathed, uniserate cellular trichomes into two genera according to their cell length/diameter ratio. *Oscillatoriopsis* Schopf, 1968 has a length/diameter ratio less than one, and *Cyanonema* greater than one. In both genera,
cells within the same trichome tend to have similar length and diameter, although the trichomes may taper distally (Schopf, 1968).

_Cyanonema majus_ new species

**Figure 4.6.7–4.6.9**

**Type specimen.**—The arrowed specimen illustrated in Fig. 4.6.8 is designated as the holotype, repositoned at Virginia Polytechnic Institute Geosciences Museum (VPIMG-xxxx; thin section number YTS-54-8; coordinates 121.0 × 19.0).

**Derivation of name.**—Latin, _majus_, larger, with reference to the cells of the new species which are larger than other _Cyanonema_ species.

**Diagnosis.**—A species of _Cyanonema_ with cells that are 8–20 µ m in diameter and 20–40 µ m in length. Filaments typically are aggregated in parallel clusters.

**Description.**—Based on measurements made on 30 filaments, cells are 8.8–16.0 µ m in diameter (mean = 11.6 µ m, s.d. = 1.54 µ m, n = 30) and 20.0–38.7 µ m in length (mean = 31.9 µ m, s.d. = 4.6 µ m, n = 30). Cell length and diameter are relatively uniform in the same trichome, except where degradational shrinkage occurs (arrow in Fig. 4.6.9). Slight constriction occurs at cell boundaries. No sheath is present.

**Remarks.**—The current species is assigned to the genus _Cyanonema_ because its cell length (~32 µ m) is greater than cell diameter (~12 µ m). At least five species of _Cyanonema_ have been published previously, but their cells are smaller that the new species described here (Fig. 4.7). For comparison, the type species _Cyanonema attenuatum_ from the Bitter Spring Formation is characterized by terminally tapering filaments with medial cell measuring 1.3–2.4 µ m in diameter and 1.9–4.8 µ m in length, with a mean diameter of 1.7 µ m and a mean length of 3.3 µ m, averaged over 55 cells measured in 4 trichomes (Schopf, 1968). Medial cells of _Cyanonema inflatum_ Oehler, 1977, from the Mesoproterozoic McArthur Group in northern Australia, are 2.1–3.6 µ m in diameter and 2.1–5.4 µ m in length, with a mean diameter of 2.9 µ m and a mean length of 3.6 µ m, averaged over 40 measurements in 5 trichomoes (Oehler, 1977). _Cyanonema minor_ Oehler, 1977, also from the McArthur Group, has cells that are 1.1–1.5 µ m in diameter (mean = 1.4 µ m, n = 38 measurements in 4 trichomes) and 1.4–2.9 µ m in length (mean = 2.0 µ m). _Cyanonema ligamen_ Zhang, 1981, from the Mesoproterozoic Gaoyuzhuang Formation in North China, is also characterized by small cells, with a cell diameter of 1.2–2.2 (mean = 1.8 µ m, n =12)
and a cell length of 2.5–4.5 µm (mean = 3.2 µm) (Zhang, 1981). The single specimen of *Cyanonema* sp. from the Neoproterozoic Svanbergfjellet Formation of Spitsbergen is slightly larger, with cells 7 µm wide and 12 µm long (Butterfield et al., 1994). Finally, *Cyanonema disjuncta* Ogurtsova and Sergeev, 1987, has been transferred to *Oscillatoriopsis* because of its short cells whose length is smaller than diameter (Butterfield et al., 1994)).

**Material.**—About 40 specimens from the Yurtus Formation in the Aksu area of the Tarim Block. Slide numbers and coordinates are YTS54-1 (111.5 × 17.5), YTS54-2 (118.0 × 18.5), (111.5 × 17.5), YTS54-5 (118.9 × 21.3), YTS 54-8 (121.0 × 19.0; multiple specimens), YTS54-14 (121.0 × 9.0).

**Distribution.**—The basal Cambrian Yurtus Formation in the Tarim Block.


**Type species.**—*Oscillatoriopsis obtusa* Schopf, 1968, emend. Butterfield et al., 1994

**Synonyms.**—See Butterfield et al. (1994).

**Diagnosis.**—See Butterfield et al. (1994).

**Remarks.**—This genus is distinguished from *Cyanonema* by its smaller cell length to diameter ratios (<1), and from *Megathrix* Yin, 1987, by its flat and entirely complete cross-walls (see below for description of *Megathrix*).

*Oscillatoriopsis longa* Timofeev and Hermann, 1979, emend. Butterfield et al., 1994

**Figure 4.6.10–4.6.11**

**Synonyms.**—See Butterfield et al. (1994) and Zhang et al. (1998).

**Description.**—Unbranched, unsheathed, uniserate cellular trichome. Based on measurements made on 30 filaments, cells are 8.6–18.5 µm in length (mean = 13.7 µm, s.d. = 2.73 µm, n = 30) and 19–35 µm (mean = 27.4 µm, s.d. = 5.43 µm, n = 30) in diameter. Cells are uniform in length and diameter within the same trichome. No constrictions at cell boundaries.

**Remarks.**—Butterfield et al. (1994) recognized four species of *Oscillatoriopsis* according to their diameter, i.e., *O. vermiformis* (Schopf, 1968) Butterfield in Butterfield et al., 1994, 1–3 µm; *O. obtusa* Schopf, 1968, 3–8 µm; *O. amadeus* (Schopf and Blacic, 1971) Butterfield in Butterfield et al., 1994, 8–14 µm; and *O. longa* Timofeev and Hermann, 1979, 14–25 µm. Our
specimens are regarded as *O. longa*, although one of the three specimens is wider than 25 µm—the size limit recognized by Butterfield et al. (1994).

**Material.**—Three specimens from the Yurtus Formation in the Tarim Block. Slide number and coordinates are YTS-54-1 (111.0 × 21.6), (126.0 × 10.2), and (123.7 × 15.2).

**Distribution.**—This morphospecies is widely distributed in Proterozoic and Paleozoic successions. See Butterfield et al. (1994) and Zhang et al. (1998) for a list of described synonyms.


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

*Synonyms.*—See Knoll et al. (1991) and Butterfield et al. (1994).

*Remarks.*—The morphogenus *Siphonophycus* includes all unbranched, smooth-walled, nonseptate filamentous microfossils with little or no tapering toward filament termini (Knoll et al., 1991). Butterfield et al. (1994) suggested that species-level classification of *Siphonophycus* should be based on filament diameter, i.e., *S. thulenema* Butterfield in Butterfield et al., 1994, <1 µm; *S. septatum* (Schopf, 1968) Knoll et al., 1991, 1–2 µm; *S. robustum* (Schopf, 1968) Knoll et al., 1991, 2–4 µm; *S. typicum* (Hermann, 1974) Butterfield in Butterfield et al., 1994, 4–8 µm; *S. kestron* Schopf, 1968, 8–16 µm; *S. solidum* (Golub, 1979) Butterfield in Butterfield et al., 1994, 16–32 µm, and *S. punctatum* Maithy, 1975, 32–64 µm. Our material best fits the definition of *O. robustum*.

*Siphonophycus robustum* (Schopf, 1968) Knoll et al., 1991

Figure 4.6.12

*Synonyms.*—See Butterfield et al. (1994).

*Description.*—Tubular filaments with a diameter of 3.1–4.5 µm (mean = 3.7 µm, s.d. = 0.44 µm, n = 11 filaments). Filaments are open at both ends.

*Material.*—Two specimens from the Yurtus Formation in the Tarim Block. Slide number YTS58-1, coordinates 139.2 × 28.9 and 131.7 × 23.9.

*Distribution.*—This morphospecies is widely distributed in Proterozoic and Paleozoic successions.
3.4. Tubular microfossils with both complete and incomplete cross-walls

Genus Megathrix Yin, 1987, emend. Yao et al., 2005

*Type species.*—*Magathrix longus* Yin, 1987, emend., Yao et al., 2005, from the basal Cambrian Yanjiahe Formation (described as uppermost Dengying Formation in Yin, 1987) in the Yangtze Gorge area.

*Diagnosis.*—Tubular microfossils typically less than 100 µm wide and several hundred µm long. Tubes characterized by closely spaced transverse cross-walls that are either complete or incomplete (with a central perforation). Complete cross-walls are corrugated or flat. They are often intercalated with incomplete ones, although sometimes incomplete cross-walls are absent. Incomplete specimens are flat or less strongly corrugated than complete cross-walls, and they can reach various depths toward the center of the tube. Tubes rarely branch.

*Remarks.*—The diagnosis presented here emphasizes the intercalation of complete and incomplete cross-walls, a feature that was not explicitly described in Yao et al. (2005).

*Megathrix longus* Yin, 1987, emend. Yao et al., 2005

*Figure 4.8*

*Megathrix longus* Yin, 1987, p. 476, pl. 16, figs. 1–7; pl. 17, figs. 2–5, 7, 8, 10.

*Megathrix longus* Yin, 1987; Yao et al., 2005, p. 697–700, pl. 2, figs. 3–8, and synonyms therein.

*Emended diagnosis.*—Same as genus.

*Description.*—As most specimens are incompletely preserved and curved, it is difficult to reconstruct their three-dimensional morphology on the basis of thin section observation. Some specimens show apparent terminal tapering in thin sections (Fig. 4.8.1, 4.8.2, 4.8.4–4.8.6); either the tubes do indeed taper terminally or the apparent tapering in thin section is an artifact resulting from oblique cutting of curved tubes (Yao et al., 2005). On the other hand, several specimens show a square termination in thin sections (Yao et al., 2005, their plate 2, fig. 6). If the square termination represents true biological termination rather than physical or taphonomic breakage, then the tube has at least one truncated (and non-tapering) termination.
In some specimens, complete and incomplete cross-walls are regularly intercalated. This is best seen in longitudinal sections (Fig. 4.8.3, 4.8.11–4.8.13, and 4.8.15–4.8.16) where short spine-like incomplete cross-walls are interspersed between often more strongly corrugated complete cross-walls. The intercalation can also be observed in transverse sections (Fig. 4.8.8–4.8.10), where by adjusting the focusing level a succession of complete and incomplete cross-walls are brought into focus. In another transverse section (Fig. 4.8.14), a corrugated complete cross-wall and a flat incomplete cross-wall can both be seen at the same focusing level, indicating the complete cross-wall is strongly corrugated. In many other specimens (Fig. 4.8.1 and 4.8.5), however, complete cross-walls are not intercalated with incomplete ones, or else the incomplete cross-walls are extremely short.

A branching specimen from the Yurtus Formation was described in Yao et al. (2005, their pl. 2, fig. 6). Unfortunately, the thin section was damaged after photographing, and verification of the branching pattern by re-examining that specimen is difficult. None of our Yanjiahe specimens show evidence of branching.

The measurements of the Yanjiahe specimens are presented here for comparison with the Yurtus specimens (Yao et al., 2005). Tube length of the Yanjiahe population is 19.5–1100 µm (mean = 251.2 µm, s.d. = 210.0 µm, n = 20 incomplete specimens), tube diameter 34–80 µm (mean = 64.5 µm, s.d. = 12.49 µm, n = 20), spacing of complete cross-walls is 4–18 µm (mean = 12.2 µm, s.d. = 371 µm, n = 20 measurements made on 20 specimens), and spacing of all cross-walls is 3–9 µm (mean = 6.2 µm, s.d. = 1.72 µm, n = 15 measurements made on 15 specimens). Incomplete cross-walls extend 1/8–2/3 toward the center of tubes. There is no significant correlation between tube diameter and cross-wall spacing (r = 0.33, p = 0.15 for H0: r = 0) (Fig. 4.9).

Remarks.—*Megathrix longus* differs from filamentous cyanobacteria such as *Oscillatoriopsis* in its relatively large diameter, corrugated cross-walls, the intercalation of complete and incomplete cross-walls, and rare branches. Liu et al. (in press) described five species of tabulate tubular microfossils from the Ediacaran Doushantuo Formation at Weng’ an, Guizhou Province, South China. The diameter of the Doushantuo species (mostly 100–250 µm in diameter) is much greater than *Megathrix longus*, and they all have flat rather than corrugated cross-walls. Of the five Doushantuo species, *Ramitubus increscens* Liu et al., in press and *Ramitubus decrescens* Liu et al., in press are both characterized by regularly dichotomous
branching and rare incomplete cross-walls, \textit{Quadratitubus orbignoniatus} Xue et al., 1992 by tetragonal tubes, and \textit{Crassitubus costatus} Liu et al., in press by curved cylindrical tube with a longitudinal ridge (Liu et al., 2007). \textit{Sinocyclocyclicus guizhouensis} Xue et al., 1992 is most similar to \textit{Megathrix longus} except its greater diameter and flat cross-walls (Xiao et al., 2000; Xue et al., 1992). Additionally, \textit{Sinocyclocyclicus guizhouensis} has at least one tapering termination as shown in extracted specimens (Liu et al., 2007), and the comparison between these two species is difficult without extracted specimens of \textit{Megathrix longus}.

The phylogenetic affinity of \textit{Megathrix longus} is uncertain, but it is unlikely to be cyanobacteria (Yao et al., 2005) because of the presence of corrugated cross-walls and intercalation of complete and incomplete cross-walls.

\textit{Material}.—About 20 specimens from the Yanjiahe Formation and about 40 specimens from the Yurtus and Xishanblaq formations (Yao et al., 2005).

\textit{Distribution}.—The Yanjiahe Formation in the Yangtze Gorge area and the Yurtus and Xishanblaq formations in the Tarim Block (Yin, 1987a); (Yin et al., 1992); (Yin et al., 2003a); (Yao et al., 2005).

4. DISCUSSION

The Meishucunian Stage in South China follows the departure of the Ediacara biota (Amthor et al., 2003) and precedes the arrival of trilobite-dominated Cambrian fauna (Sepkoski, 1992). It is conventionally correlated with the Nemakit-Daldynian and Tommotian stages in Siberia (Qian, 1999). Therefore, a full characterization of the Meishucunian biota is critical to our understanding of the Tommotian biota \textit{sensu} Sepkoski (1992). Previous study of Meishucunian paleobiology has been focused on small shelly fossils. Yao et al. (2005) gave a thorough discussion on the biostratigraphic significance of Meishucunian \textit{Micrhystridium}-like acritarchs and established the \textit{Asteridium–Comasphaeridium–Heliosphaeridium} (ACH) acritarch assemblage on the basis of acritarchs from the lower Yurtus Formation. They suggested that the \textit{Asteridium–Comasphaeridium–Heliosphaeridium} (ACH) acritarch assemblage is minimally correlated with the Meishucunian small shelly fossil assemblages I and II (Qian, 1999) and maximally with the entire Meishucunian Stage. They further correlated the \textit{Asteridium–Comasphaeridium–Heliosphaeridium} (ACH) acritarch assemblage in the lower Yurtus Formation with the \textit{Asteridium tornatum–Comasphaeridium velvetum} acritarch zone in
the East Europe Platform (Moczydlowska, 1991; Moczydlowska, 1998; Yao et al., 2005). The current study provides a test of Yao et al.’s correlation scheme through a comparative study of basal Cambrian acritarchs from the Yurtus Formation in the Tarim Block and the Yanjiahe Formation in the Yangtze Gorges area. The taxonomic similarity between the lower Yanjiahe Formation and lower Yurtus Formation (Fig. 4.2) clearly support their biostratigraphic correlation. Further taxonomic documentation of other basal Cambrian acritarchs, particularly in the Tal Formation of the Lesser Himalaya (Tiwari, 1999) and the Chulaktau Formation of Kazakhstan (Sergeev and Ogurtsova, 1989), will provide additional test of the biostratigraphic significance of the *Asteridium–Comasphaeridium–Heliosphaeridium* (ACH) acritarch assemblage.

In addition to acanthomorphic acritarchs, the tubular microfossil *Megathrix longus* may also have biostratigraphic significance. It has so far been reported from the lower Yurtus and lower Yanjiahe formations, and it appears to be restricted to the Meishucunian Stage. Furthermore, the clustered coccoidal microfossil *Archaeophycus venustus* and the spiral filamentous fossil *Obruchevella* are common in basal Cambrian cherts and phosphorites in South China and the Lesser Himalaya (Song, 1984); (Tiwari, 1999), although they also occur in the Ediacaran Doushantuo Formation (Zhang et al., 1998).

It has been proposed that the diversification of acanthomorphic acritarchs, in both the Ediacaran and the early Cambrian, is an ecological response to increasing predation pressure through top-down ecological interactions (Butterfield, 1997; Butterfield, 2001; Peterson and Butterfield, 2005). This is an intriguing hypothesis, and it makes predictions about the stratigraphic appearance, functional biology, morphological complexity, and taxonomic diversity of acanthomorphic acritarchs relative to that of animals. However, the biostratigraphic resolution of basal Cambrian acritarchs and animals is insufficient for a biostratigraphic test of the top-down ecological coupling hypothesis, although there has been some biostratigraphic data indicating that acritarch diversification events appears to precede animal diversification events (Moczydlowska, 2001; Moczydlowska, 2002).

It is reasonable to suggest that one of the functions of complex processes is to defend against animal predators. Thus, another possible test of the top-down ecological coupling hypothesis is to examine the morphological complexity of acritarch processes. Acritarchs in the *Asteridium–Comasphaeridium–Heliosphaeridium* (ACH) assemblage are characterized by solid
or cylindrical, unbranching processes, much more complex than the *Leiosphaeridia*-dominated late Ediacaran acritarch assemblage (Huntley et al., 2006). Acritarch with branching processes (e.g., *Skiagia*), however, do not appear until the trilobite-bearing Atdabanian Stage (Moczydlowska and Zang, 2006). Still more complex acanthomorphic acritarchs with stable excystment structures occur in Ordovician and Silurian rocks (Martin, 1993; Yin, 1995). It would be profitable to carry out a quantitative study of the morphological complexity and taxonomic diversity of Paleozoic acritarchs (Huntley et al., 2006) and compare the patterns with animal morphological and taxonomic history. From a qualitative examination of published data, it appears that acritarchs experienced morphological and taxonomic diversification in the Meishucunian, Atdabanian, and early Ordovician, matching the diversification of the Tommotian, Cambrian, and Paleozoic evolutionary faunas (Sepkoski, 1981; Sepkoski, 1992). If confirmed, animals and phytoplankton may have radiated in tandem during the Paleozoic, at least at the broadest time scale.

5. CONCLUSIONS

Eight species, including three new species, are described from two basal Cambrian successions, including the lower Yurtus Formation in the Tarim Block and the lower Yanjiahe Formation in the Yangtze Gorges area. These two assemblages share a number of taxa characteristic of the *Asteridium-Comasphaeridium-Heliosphaeridium* acritarch assemblage, confirming their stratigraphic equivalency and the biostratigraphic significance of the *Asteridium-Comasphaeridium-Heliosphaeridium* acritarch assemblage. The acritarch assemblage is dominated by *Heliosphaeridium ampliatum*, with rare occurrences of *Comasphaeridium densum* new species and *Paracymatiosphaera? uniformis* new species. The genus *Asteridium* does not occur in the two formations, and previous study show that its occurrence may be stratigraphically lower than *Comasphaeridium* and *Heliosphaeridium* (Yao et al., 2005). The enigmatic tubular microfossil *Megathrix longus* may also be biostratigraphically useful. Other taxa, including *Archaeophycus venustus*, *Siphonophycus robustum*, *Cyanonema majus* new species, and *Oscillatoriopsis* sp. are less useful in biostratigraphic correlation.
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Figure 4.1. Geological maps showing the location of the Tarim and South China blocks (top), and Cambrian outcrops in the Yurtus area (middle) and the Yangtze Gorges area (bottom). The Yurtus VI and Jiuqunao sections are marked.

(cited from Yao et al., 2005)
Figure 4.2. Stratigraphic columns of the Yurtus and Yanjiahe formations. Sample numbers and fossil occurrences are indicated to the right of stratigraphic columns.
Figure 4.3. Thin section photomicrographs of *Comasphaeridium densum* new species (1, bottom specimen; 2), *Heliosphaeridium ampliatum* (1, top specimen; 3–4), and *Paracymatiosphaera? uniformis* new species (5–16). For Figs. 3, 6, and 8, slide number and coordinates of each photographed specimen are given. Thin section prefix YTS- denotes specimens from the Yurtus Formation at the Aksu VI section, JQN- denotes specimens from the Yanjiahe Formation at the Jiuqunao section, and YKG- denotes specimens from the Xishanblaq Formation at the Yukkanengol section in the Quruqtagh area (Yao et al., 2005). 1, YTS-54-1 (129.5 × 11.5), bottom specimen is holotype of *Comasphaeridium densum* new species, VPIGM-xxx; 2, JQN-chert-2 (125.9 × 10.7); 3, JQN-chert-2 (139.5 × 15.0); 4, JQN-chert-1 (131.9 × 11.9); 5, YTS-58-1 (143.0 × 29.8), holotype of *Paracymatiosphaera? uniformis* new species, VPIGM-xxx; 6, YTS-57-10-1 (120.8 × 17.9); 7, YTS-57-10-1 (116.4 × 19.5); 8, YTS-58 (138.8 × 27.4); 9–11, YTS-58-1 (130.5 × 33.4), photomicrographs of the same specimen at different focus levels, showing deformed vesicle wall and even distribution of solid processes; 12–16, YTS-58 (128.5 × 32.8), photomicrographs of the same specimen at different focus levels, showing deformed vesicle wall. Scale bars represent 10 µ m for 1–5, and 5 µ m for 6–16.
Figure 4.4. Cross-plot and frequency distribution of vesicle diameter and process length of *Heliosphaeridium ampliatum* from the Yanjiahe Formation (full circle) and Yurtus Formation (empty circle; data from Yao et al., 2005).
Figure 4.5. Cross-plot and frequency distribution of outer wall diameter and process length of *Paracymatiosphaera? uniformis* new species from the Yurtus Formation.
Figure 4.6. Thin section photomicrographs of *Archaeophycus venustus* (1-6), *Cyanonema majus* new species (7–9), *Oscillatoriopsis longa* (10-11), and *Siphonophycus robustum* (12). 1, YTS-57-10-1 (128.0 × 11.9); 2, YTS-58 (123.4 × 14.2); 3, JQN-chert-1 (142.8 × 15.7); 4, YTS-58-1 (143.7 × 30.7); 5, YTS-58-1 (147.3 × 21.0); 6, YTS-58 (139.9 × 15.1); 7–8, YTS-54-8 (121.0 × 19.0), arrowed specimen is holotype. 8 is close-up of 7; 9, YTS-54-5 (119.0 × 21.3) arrow points to degradational shrinkage; 10, YTS-54-1 (111.0 × 21.6); 11, YTS-54-1 (126.0 × 10.2); 12, YTS-58 (123.7 × 15.2). Scale bars represent 10 µm for 1–5, 20 µm for 6, 8–9, 12, and 50 µm for 7, 10–11.
Figure 4.7. Cross-plot of cell diameter and length of *Cyanonema majus* new species from the Yurtus Formation. Size range of *C. attenuatum*, *C. inflatum*, *C. minor*, *C. ligamen*, and *C. sp.* (Butterfield et al., 1994) are also indicated for comparison (data from Butterfield et al., 1994).
Figure 4.8. Thin section photomicrographs of *Megathrix longus* from the Yurtus and Jiuqunao formations. 1, reproduced from Yin et al., 1987, pl. 16, fig. 3; 2, JQN-chert-3 (120.1 × 18.8), note the tapering end; 3, JQN-chert-1 (150.3 × 7.6), note the short incomplete cross-wall; 4, JQN-chert-1 (133.7 × 11.9), note tapering ends; 5, YTS-57 (140.7 × 15.5); 6, JQN-chert-3 (134.2 × 5.7), note variation in tube width (arrow); 7-13, YKG-67-5 (134.6 × 7.4), four curved tubes cut longitudinally and transversely in the same section. 8-10 are magnified views of transverse sections at different focus levels. Note incomplete cross-walls (arrows in 8 and 10) and complete walls (9); 11-13 are magnified views of longitudinal sections at different focus levels. 11 and 13 are tangential sections and 12 is a section passing the center of the tube. Central perforations of incomplete cross-walls (arrows) are only visible in 12; 14, JQN-chert-1 (141.7 × 20.2), transverse section showing both complete (obliquely cut, black arrow) and incomplete (white arrow) cross-walls; 15-16, YKG-67-5 (110.5 × 5.0), longitudinal sections at different focus levels. Incomplete cross-walls (arrows) are best seen in centrally cut section (15), not in tangential section (16). Scale bars represent 100 µm for 1, 4, and 6, 50 µm for 2–3, 5, 7, 14–16, and 20 µm for 8–13.
Figure 4.9. Cross-plot and frequency distribution of tube diameter and cross-wall spacing of *Megathrix longus* from the Yanjiahe Formation (full circle) and Yurtus Formation (empty circle; data from Yao et al., 2005).
VITA

Lin Dong was born in Qingzhou City, China on February 11, 1980. She graduated with a Bachelor of Science degree in Geology from Nanjing University, China, in 2001. After that, she continued her study at Nanjing University and obtained her Master of Science degree in Paleontology and Stratigraphy in 2003. From August 2003 to March 2007, she studied in the Department of Geosciences, Virginia Tech toward her Ph.D degree of geosciences. Lin will be joining BP AMERICA INC. as a geoscientist in Houston, TX, in the summer of 2007.