Available online at www.sciencedirect.com
ScienceDirect
Palaeogeography, Palaeoclimatology, Palaeoecology 258 (2008) 138–161
PALAEO
www.elsevier.com/locate/palaeo

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

Lin Dong [a], Shuhai Xiao [a,*], Bing Shen [a], Xunlai Yuan [b], Xianqin Yan [b], Yongbo Peng [c]

[a] *Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA*
[b] *Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing 210008, China*
[c] *Department of Geology and Geophysics, Louisiana State University, Baton Rouge, LA 70803, USA*

Accepted 3 May 2007

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, *P. baiguashanensis* bears a bulbous terminal structure at one end of its tube. *P. huaiyuanensis* is characterized by a constricted opening at one end and a closed termination at the other. The two ends of *S. huainanensis* tubes are both closed and round. The bulbous terminal structure in *P. 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 *Radhakrishnania* Kumar, 2001, and the frondose Ediacara fossil *Charniodiscus* Ford, 1958. Furthermore, it is possible that at least *P. baiguashanensis* and *P. huaiyuanensis* may represent reproductive or taphonomic fragments of the same organism. This reinterpretation weakens the previous interpretation that *P. baiguashanensis* and *P. 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. The predominance of discoidal holdfasts, as opposed to rhizoidal holdfasts, in pre-Ediacaran epibenthic organisms was probably related to more stable substrates in the presence of microbial mats and in the absence of bioturbating animals.

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

* Corresponding author.
E-mail address: xiao@vt.edu (S. Xiao).

0031-0182/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2007.05.019

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. 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., 2007). This pattern in North China is 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 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

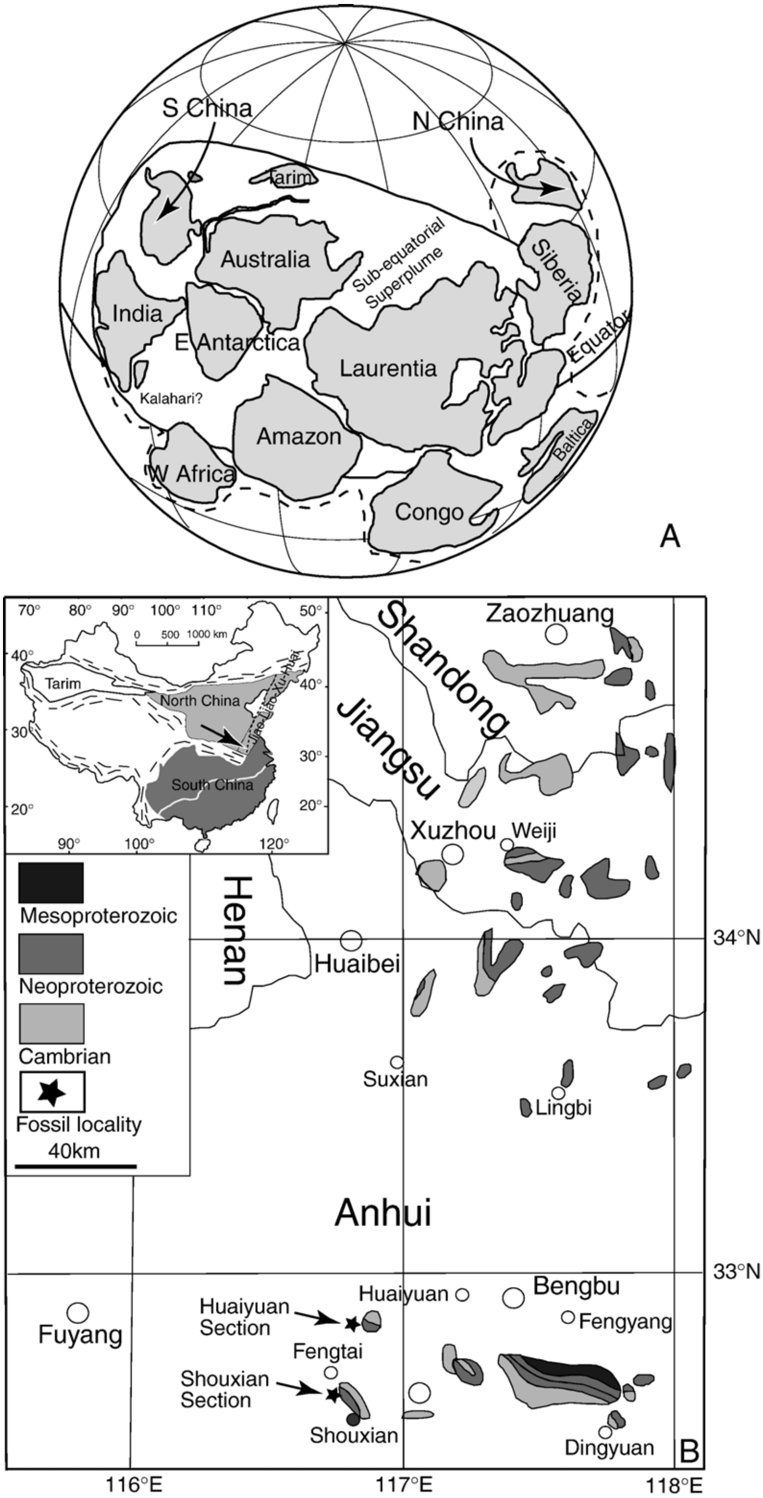

Fig. 1. (A) One version of paleogeographic reconstruction (modified from Li et al., 2004), showing the location of the North China and South China blocks in the early Neoproterozoic. (B) Geological map showing Neoproterozoic outcrops in the Huainan area of northern Anhui Province. Stars indicate fossil 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.

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 Jiao-Liao-Xu-Huai stratigraphic realm (Jiao: Shandong; Liao: Liaoning; Xu: Xuzhou; Huai: Huai 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., 2007).

The exposure of early Neoproterozoic outcrops in the Huai River Drainage of northern Anhui is sporadic (Fig. 1B). For historical reasons, lithostratigraphic nomenclatures in the northern and southern parts of this region are different (Table 1, Fig. 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 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). 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 m 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 leiosphere 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 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

Table 1
A sample of different opinions in the stratigraphic subdivision and correlation of Neoproterozoic successions in the Huainan and Huaibei regions

	(Yang et al., 1980)		(Wang et al., 1984)		(Zheng et al., 1994)		
	Huainan Region	Huaibei Region	Huainan Region	Huaibei Region	Huainan Region	Huaibei & Subei Region	
	Houjiashan Fm.		Houjiashan Fm.		Houjiashan Fm.		
Suxian Group	Hiatus	Gouhou Fm.	Wugangji Fm.	Gouhou Fm.	Yutaishan Fm.	Langan Gp.: Gouhou Fm.	Hiatus
Suxian Group	Hiatus	Jinshanzhai Fm.	Fengtai Fm.	Jinshanzhai Fm.	Wanxi Fm.	Langan Gp.: Jinshan-zhai Fm.	Hiatus
Xuhuai Group	Hiatus	Wangshan Fm.	Hiatus	Wangshan Fm.	Fengtai Fm.	Hiatus	Hiatus
Xuhuai Group	Hiatus	Shijia Fm.	Hiatus	Shijia Fm.	Hiatus	Hiatus	Hiatus
Xuhuai Group	Hiatus	Weiji Fm.	Hiatus	Weiji Fm.	Hiatus	Hiatus	Xuhuai Group: Weiji Fm.
Xuhuai Group	Hiatus	Zhangqu Fm.	Hiatus	Zhangqu Fm.	Hiatus / Huainan Group: Nainaimiao Fm.	Hiatus	Xuhuai Group: Zhangqu Fm.
Xuhuai Group	Sidingshan Fm.	Jiudingshan Fm	Sidingshan Fm.	Jiudingshan Fm	Huainan Group: Sidingshan Fm.	Hiatus	Xuhuai Group: Jiudingshan Fm.
Xuhuai Group	Sidingshan Fm.	Niyuan Fm.	Sidingshan Fm.	Niyuan Fm.	Huainan Group: Sidingshan Fm.	Suxian Group: Wangshan Fm.	Xuhuai Group: Niyuan Fm.
Xuhuai Group	Sidingshan Fm.	Zhaowei Fm.	Jiuliqiao Fm.	Zhaowei Fm.	Huainan Group: Sidingshan Fm.	Suxian Group: Wangshan Fm.	Xuhuai Group: Zhaowei Fm.
Huainan Group	Jiuliuqiao Fm.	Jiayuan Fm.	Jiuliqiao Fm.	Jiayuan Fm.	Huainan Group: Jiuliuqiao Fm.	Suxian Group: Wangshan Fm.	Xuhuai Group: Jiayuan Fm.
Huainan Group	Shouxian Fm.	Jushan Fm.	Shouxian Fm.	Jushan Fm.	Huainan Group: Shouxian Fm.	Suxian Group: Wangshan Fm.	Xuhuai Group: Jiayuan Fm.
Huainan Group	Liulaobei Fm.	Xinxing Fm.	Liulaobei Fm.	Xinxing Fm.	Huainan Group: Liulaobei Fm	Suxian Group: Shijia Fm. / Hiatus?	Hiatus?
Huainan Group	Bagongshan Fm.	Lanling Fm.	Bagongshan Fm.	Lanling Fm.	Bagongshan Fm.	Suxian Group: Hiatus?	Hiatus?
Huainan Group	Caodian Fm.		Caodian Fm.		Bagongshan Fm.	Suxian Group: Hiatus?	Hiatus?
	Fengyang Group		Fengyang Group				Hiatus?

Gray shading indicates stratigraphic hiatus, and black shading indicates the Liulaobei and Jiuliqiao formations from which the fossils described in this paper were collected.

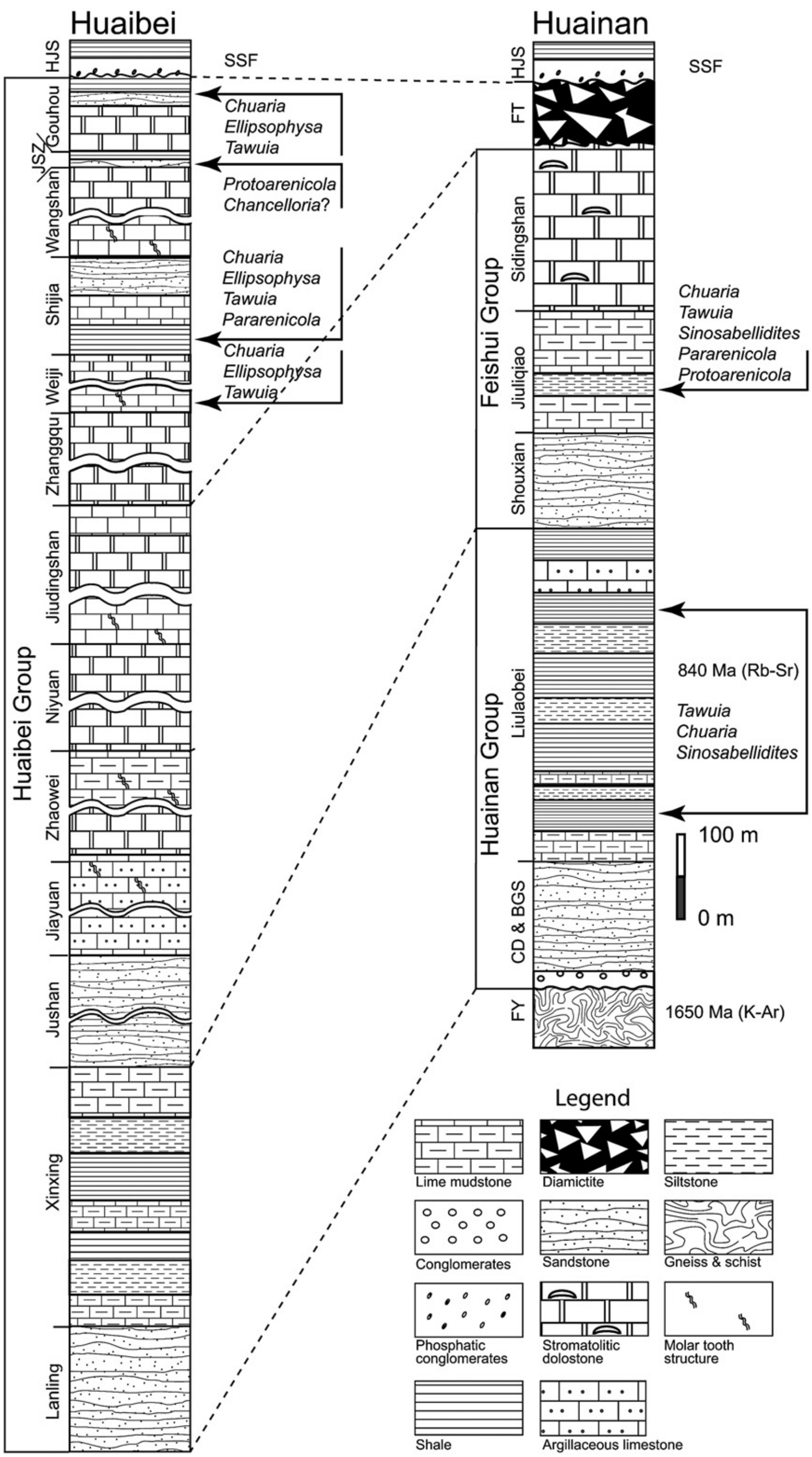

Fig. 2. Stratigraphic columns of Neoproterozoic successions in the Huaibei (left) and Huainan (right) regions, and the currently accepted correlation between these two regions. HJS: Houjiashan Formation; JSZ: Jinshanzhai Formation; FT: Fengtai Formation; CD & BGS: Caodian and Bagongshan formations; FY: Fengyang Group (Mesoproterozoic); SSF: small shelly fossils.

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 diamicitite (Cryogenian or Ediacaran in age) or the early Cambrian Houjiashan Formation.

As mentioned above, the correlation between the Neoroterozoic successions in the Huaibei and Huainan areas is uncertain. The currently accepted correlation (Fig. 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). 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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,

Table 2
List of published taxa of annulated ribbon-shaped carbonaceous compressions from the Jiao-Liao-Xu-Huai area

Species	Source	Notes
Anhuiella sinensis Yan and Xing, 1984	in (Wang et al., 1984a), plate 6, Fig. 4.	Incomplete; invalid name (no diagnosis or holotype designation).
Anhuiella sinensis Yan and Xing, 1985	in (Xing et al., 1985), p. 189, plate 39, Fig. 5.	Incomplete specimen.
Anhuiella xiwafangensis Liu and Huang, 1991	in (Hong et al., 1991), p. 161–162, plate 4, Figs. 5–7, 11; plate 6, Figs. 1, 2.	Invalid name (no holotype designation); one specimen [(Hong et al., 1991), plate 4, Fig. 5] has been synonymized with *Protoarenicola baiguashanensis* in this paper; the others are incomplete specimens.
Calyptrina striata Sokolov, 1965	(Wang et al., 1984a), plate 7, Fig. 2; (Xing et al., 1985), p. 189, plate 39, Fig. 1.	Incomplete specimen.
Chulania anfracta Yan, 1984	in (Wang et al., 1984a), plate 7, Fig. 4.	Invalid name (no diagnosis or holotype designation); incomplete specimens; lack of diagnostic characters; synonymized with cf. *Paleolina* sp. by (Xing et al., 1985).
Huaiyuanella baiguashanensis Yan and Xing, 1984	in (Wang et al., 1984a), plate 6, Fig. 2.	Invalid name (no diagnosis or holotype designation); homonym of *Huaiyuanella baiguashanensis* 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.
Huaiyuanella baiguashanensis Xing, Yan, and Yin, 1984	in (Xing, 1984), p. 151–152, plate 1, Figs. 1–4; (Xing et al., 1985), p. 189–190, plate 40, Figs. 1–3.	Synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella cylindrica Wang, 1982	(Wang, 1982), p. 12, plate 1, Figs. 5, 9.	Synonymized with *Sinosabellidites huainanensis* by (Sun et al., 1986) and in this paper
Huaiyuanella jiuliqiaoensis Xing and Yan, 1984	in (Wang et al., 1984a), plate 6, Fig. 1.	Invalid name (no diagnosis or holotype designation). Objective synonym of *Huaiyuanella marginata* Yan and Xing *in* (Xing et al., 1985); synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella aff. *jiuliqiaoensis* Yan and Xing, 1984	in (Wang et al., 1984a), plate 7, Fig. 3.	Objective synonym of *Huaiyuanella* aff. *marginata* Yan and Xing *in* (Xing et al., 1985); synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella marginata Yan and Xing, 1985	in (Xing et al., 1985), p. 190–191, plate 39, Fig. 6.	Synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella aff. *marginata* Yan and Xing, 1985	in (Xing et al., 1985), p. 191, plate 39, Fig. 7.	Synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella minuta Xing, 1984	(Xing, 1984), p. 152, plate 1, Figs. 5–9; (Xing et al., 1985), p. 190, plate 40, Figs. 4–7.	Synonymized with *Pararenicola huaiyuanensis* in this paper.
Huaiyuanella minuta Xing, 1984	(Hong et al., 1991), p. 163, plate 4, Figs. 8, 9.	Lack of diagnostic features.
Huaiyuanella striata Xing, Yan, and Yin, 1984	in (Xing, 1984), p. 152, plate 1, Figs. 10, 11; (Xing et al., 1985), p. 190, plate 39, Figs. 8–9.	Lack of diagnostic features.
Huaiyuanella sp.	(Hong et al., 1991), p. 162–163, plate 4, Fig. 10.	Incomplete specimen.
cf. *Huaiyuanella* sp.	(Xing et al., 1985), plate 40, Fig. 8.	Incomplete specimen.
Paleolina evenkiana Sokolov, 1965	(Xing et al., 1985), p. 188–189, plate 39, Figs. 3, 4.	Synonymized with *Protoarenicola baiguashanensis* in this paper.
Paleolina cf. *evenkiana* Sokolov, 1965	(Lin and Xing, 1984), p. 56, plate 1, Fig. 5; (Xing et al., 1985), plate 38, Fig. 8.	Incomplete specimen.
Paleolina liaonanensis Xing and Lin, 1984	in (Lin and Xing, 1984), p. 56, plate 1, Fig. 7; plate 2, Fig. 1; (Xing et al., 1985), plate 38, Figs. 5–6.	Synonymized with *Protoarenicola baiguashanensis* in this paper.
Paleolina liaonanensis Xing and Lin, 1984	(Xing et al., 1985), plate 38, Fig. 7.	Incomplete specimen.
Paleolina cf. *liaonanensis* Xing and Lin, 1984	(Lin and Xing, 1984), plate 2, Fig. 9.	Incomplete specimen.

(continued on next page)

Table 2 (*continued*)

Species	Source	Notes
Paleolina sp.	(Lin and Xing, 1984), p. 56–57, plate 2, Fig. 6; (Xing et al., 1985), plate 38, Fig. 9.	Incomplete specimen.
cf. *Paleolina* sp.	(Lin and Xing, 1984), plate 1, Fig. 4; plate 2, Fig. 5; (Xing et al., 1985), plate 39, Fig. 2; plate 40, Fig. 10.	One specimen [(Xing et al., 1985), plate 40, Fig. 10] has been synonymized with *Protoarenicola baiguashanensis* in this paper; The others are incomplete specimen.
?*Paleolina* sp.	(Lin and Xing, 1984), p. 57, plate 2, Fig. 4; (Xing et al., 1985), plate 38, Fig. 10.	Incomplete specimens.
Paleolina tortuosa Wang, 1982	(Wang, 1982), p. 11–12, plate 2, Figs. 1, 5; (Wang et al., 1984a), plate 7, Fig. 1.	Incomplete specimens.
Paleorhynchus anhuiensis Wang, 1982	(Wang, 1982), p.13, plate 1, Fig. 3; (Wang et al., 1984a), plate 6, Fig. 7; (Sun et al., 1986), p. 390–392, plate 4, Fig. 5.	Incomplete specimens; synonymized with *Pararenicola huaiyuanensis* by (Sun et al., 1986)
Pararenicola fuzhouensis Liu and Yang, 1991	in (Hong et al., 1991), p. 160, plate 5, Figs. 1-5.	Incomplete specimens; invalid name (no holotype designation).
Pararenicola huaiyuanensis Wang, 1982	(Wang, 1982), p. 11, plate 1, Fig. 1; (Wang et al., 1984a), plate 6, Fig. 3; (Sun et al., 1986), p. 390–392, plate 4, Fig. 4.	These specimens are identified as *Pararenicola huaiyuanensis* in this paper.
Pararenicola huaiyuanensis Wang, 1982	(Wang, 1982), p. 11, plate 1, Figs. 1, 2, 4, 6, 7; (Wang et al., 1984a), plate 6, Fig. 9, plate 7, Figs. 5, 7; (Sun et al., 1986), p. 390-392, plate 4, Figs. 5–6; plate 7, Figs. 1–12; (Chen, 1988), p. 201–202, plate 1, Figs. 1–4.	These specimens are either incompletely preserved or have no diagnostic feature to allow taxonomic designation.
Protoarenicola baiguashanensis Wang , 1982	(Wang, 1982), p. 22, plate 2, Fig. 3; (Wang et al., 1984a), plate 6, Fig. 5; (Sun et al., 1986), p. 394–396, plate 4, Fig. 7; (Chen, 1988), p. 202–204, plate 1, Figs. 5, 6; plate 3, Figs. 9–11.	These specimens are identified as *Protoarenicola baiguashanensis* in this paper; specimens shown in Chen (1998, plate 1, Figs. 5, 6) are possible detached holdfast structures.
Protoarenicola baiguashanensis Wang , 1982	(Chen, 1988), p. 202–204, plate 2, Figs. 7, 8; plate 3, Figs. 12–15; plate 4, Figs. 16–19; plate 5, Figs. 20–24; (Hong et al., 1991), p. 160, plate 6, Figs. 3–6.	These specimens are incompletely preserved and do not have the characteristic terminal discoidal structure. Their taxonomic designation is unclear.
Protoarenicola xiaogaojiatunensis Liu and Huang, 1991	in (Hong et al., 1991), p. 160–161, plate 5, Fig. 6; plate 7, Figs. 1–4.	Incomplete specimens; no terminal discoidal structure.
Pseudoarenicola varians Liu and Huang, 1991	(Hong et al., 1991), p. 161, plate 7, Figs. 5–12.	Some specimens [(Hong et al., 1991) plate 7, Figs. 6–8] have been synonymized with *Protoarenicola baiguashanensis* in this paper; the others are incomplete specimens.
Ruedemannella minuta Wang, 1982	(Wang, 1982), p. 12–13, plate 1, Fig. 8; plate 2, Fig. 4; (Wang et al., 1984), plate 6, Figs. 6, 8.	Synonymized with *Pararenicola huaiyuanensis* by (Sun et al., 1986); lack of diagnostic features to allow taxonomic identification.
Sabellidiitidae	(Lin and Xing, 1984), plate 1, Figs. 8, 9.	Incomplete specimens.
?*Sabellidiitidae*	(Lin and Xing, 1984), plate 1, Fig. 2.	Incomplete specimen
?*Sabellidites* sp.	Zheng, 1980, plate 2, Fig. 30.	Synonymized with *Protoarenicola baiguashanensis* in this paper.
cf. *Sabellidites* sp.	(Xing et al., 1985), plate 39, Fig. 10.	Incomplete specimen.
?*Sabellidites.*	(Lin and Xing, 1984), plate 2, Fig.7.	Incomplete specimen.
cf. *Sabellidites.*	(Lin and Xing, 1984), plate 2, Fig. 8; (Xing et al., 1985), plate 39, Fig. 10.	Incomplete specimens.
Sabellidites cambriensis Yanishevsky, 1926	(Xing et al., 1985), p. 188, plate 40, Fig. 9; (Hong et al., 1991), plate 4, Fig. 12.	Incomplete specimens.
Sabellidites aff. *cambriensis* Yanishevsky, 1926	(Lin and Xing, 1984), plate 1, Fig. 1; (Xing et al., 1985), plate 38, Figs. 1, 2.	Incomplete specimens.
Sabellidites sp.	(Wang, 1982), p. 14, plate 2, Fig. 2.	Incomplete specimen.
Sabellidites sp. 1	(Lin and Xing, 1984), p. 55, plate 1, Fig. 4; (Xing et al., 1985), plate 38, Fig. 3.	Incomplete specimen.

Table 2 (*continued*)

Species	Source	Notes
Sabellidites sp. 2	(Lin and Xing, 1984), p. 55, plate 2, Fig. 3; (Xing et al., 1985), plate 38, Fig. 4.	Incomplete specimen.
Sinosabellidites huainanensis Zheng, 1980	(Zheng, 1980), p. 63, plate 2, Figs. 18, 19, 20a, 20b; (Sun et al., 1986), p. 385–391, plate 4, Figs. 1, 2.	These specimens are identified as *Sinosabellidites huainanensis* in this paper. The purported axial cord (Zheng, 1980) does not exist.
Unnamed fossils	(Qian et al., 2000), plate 1, Figs. 1–5.	Synonymized with *Protoarenicola baiguashanensis* in this paper.

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. 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).

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

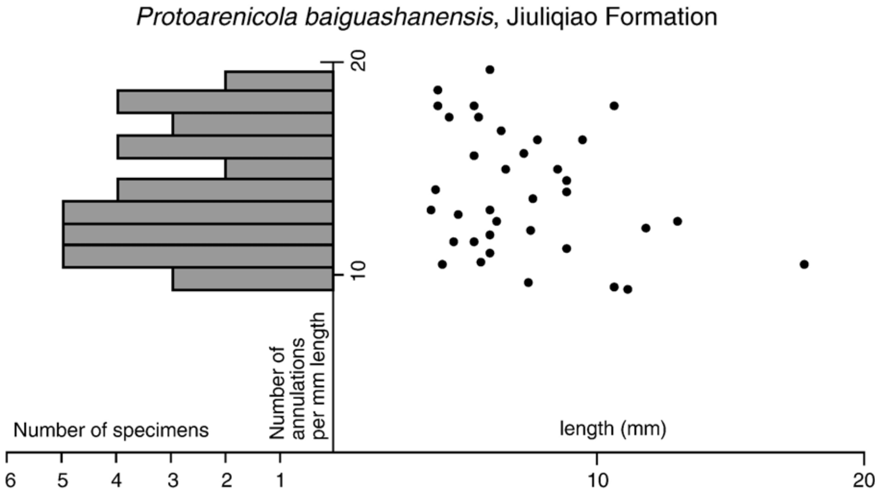

Fig. 3. Measurements of *Protoarenicola baiguashanensis* specimens from the Jiuliqiao Formation. The left plot shows the frequency distribution of annulation density. The right plot shows the relationship between fossil length and annulation density.

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. 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, Fig. 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. 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, plate 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.

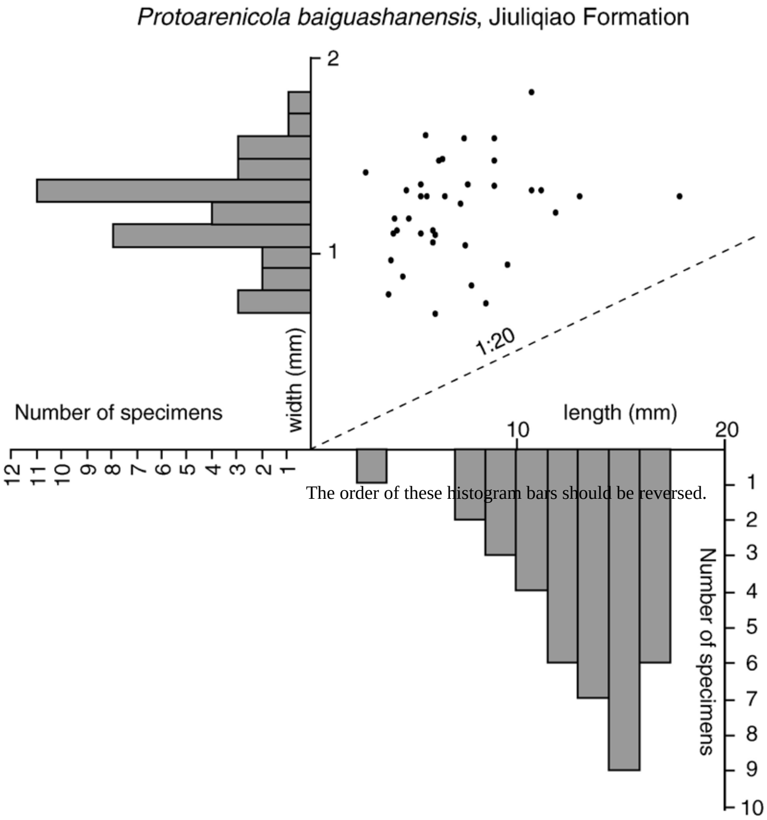

Fig. 4. Cross-plot and frequency distribution of length and width measurements of *Protoarenicola baiguashanensis* specimens from the Jiuliqiao Formation. The 1:20 line represents the cutoff width:length ratio between *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis*, proposed by Sun et al. (1986).

Protoarenicola can be differentiated from other annulated ribbon-shaped compressions by its characteristic terminal disc. *Pararenicola* and *Sinosabellidites*, 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 *Sinosabellidites* 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 *P. 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 *Sinosabellidites* 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 *Sinosabellidites*. The Doushantuo specimens are incomplete and it is uncertain if they had a terminal structure. *Sinospongia 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

Figs. 5.1–5.9, 6

?Sabellidites sp., Zheng, 1980, plate 2, Fig. 30.

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

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

Paleolina evenkiana Sokolov 1965; Xing et al., 1985, p. 188–189, plate 39, Figs. 3, 4.

cf. *Paleolina* sp. Xing et al., 1985, plate 40, Fig. 10.

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

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

Unnamed fossils, Qian et al., 2000, p. 520, plate 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. 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. 3). Terminal disc elliptical to circular in shape and slightly wider than the

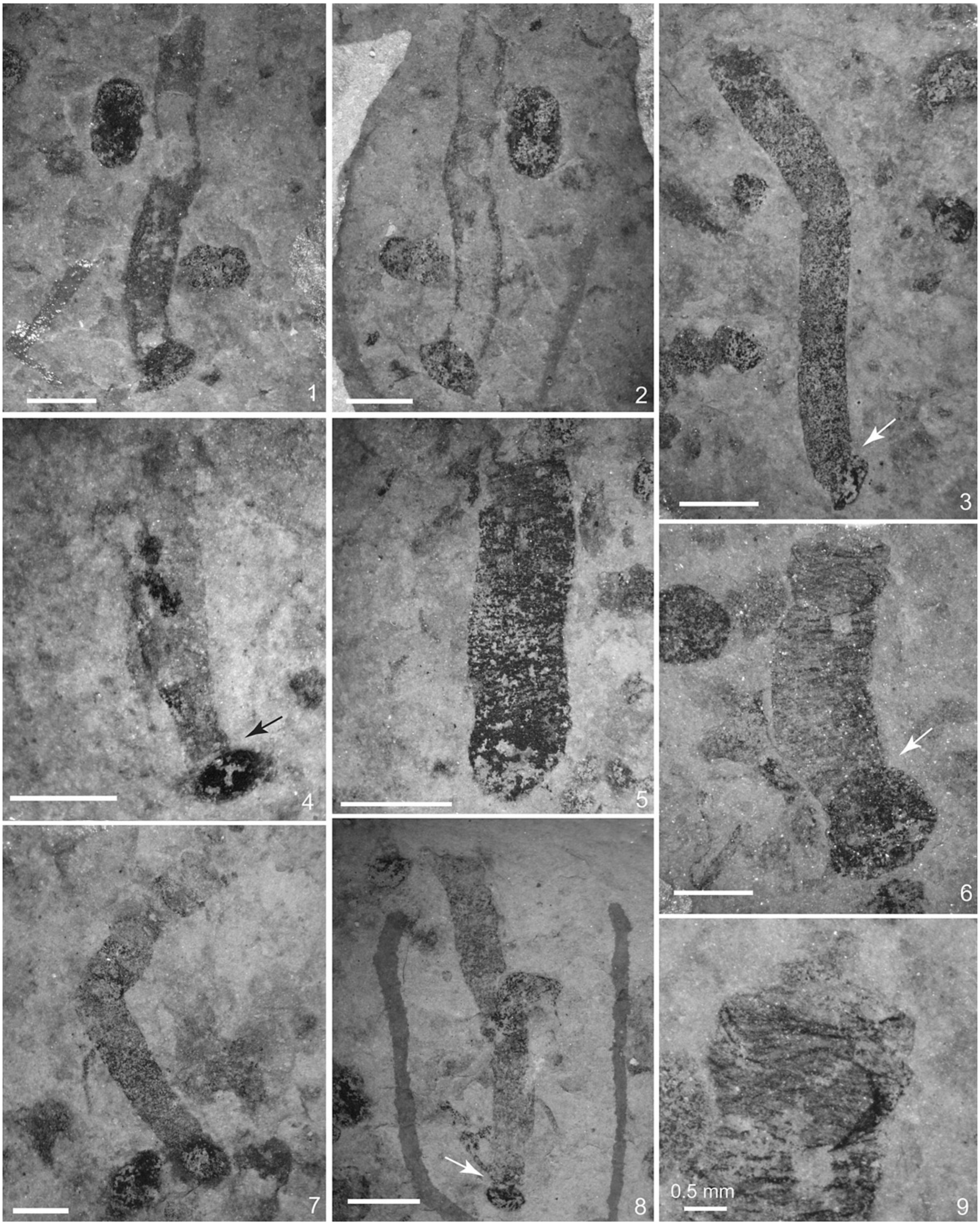

Fig. 5. *Protoarenicola baiguashanensis* Wang, 1982, from the Jiuliqiao Formation (1−9). 1–2, part and counterpart. JLQS-7 (VPIGM-4578); 3, JLQS-32 (VPIGM-4579); 4, JLQS-10(VPIGM-4580), note that holdfast is preserved darker than the ribbon; 5, JLQS-4 (VPIGM-4581); 6, 9, JLQS-4 (VPIGM-4582), 9 is magnified 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., 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.

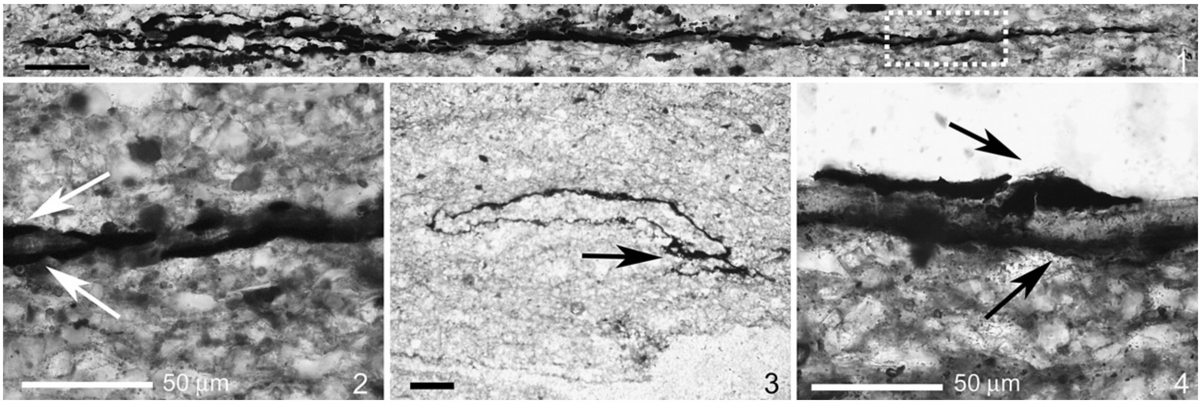

Fig. 6. Thin section photomicrographs of *Protoarenicola baiguashanensis* specimens from the Jiuliqiao Formation fortuitously cut in-situ (1–3) or embedded in epoxy (4). Thin sections were cut perpendicular to bedding plane. 1–2, JLQS-4 (VPIGM-4585). Note compressed ribbon superimposed on compressed terminal discoidal structure on the left end of 1. 2 is magnified view of rectangled area in 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.

ribbon. Constriction often occurs between terminal disc and ribbon (Fig. 5.3, 5.4, 5.6, 5.8). Constriction can be subtle (e.g., Fig. 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. 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. 6.1–6.3) 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. 6.1, 6.3). Tube apparently separated from terminal disc by a carbonaceous septum (arrow in Fig. 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 *P. baiguashanensis* is the presence of a terminal disc at one end of an annulated ribbon. *P. liaonanensis* Xing and Lin (*in* Lin and Xing, 1984, plate 2, Figs. 1a, 1b, 7a), *Anhuiella xiwafangensis* Liu and Huang (*in* Hong et al., 1991, p. 161–162, plate 7, Figs. 6, 7), and *P. evenkiana* Sokolov, 1965 (*in* Xing et al., 1984, p. 188, plate 39, Figs. 3, 4) fit this diagnosis and are regarded as synonyms of *P. baiguashanensis*. In addition, unnamed specimens reported from the Jinshanzhai Formation in the Huaibei region (Qian et al., 2000, p. 517–518, plate 1, Figs. 1–5), specimens described as cf. *Paleolina* sp. (Xing et al., 1985, plate 40, Fig. 10) and as ?*Sabellidites* sp. from the Jiuliqiao Formation (Zheng, 1980, plate 2, Fig. 30) all have the characteristic features of *P. baiguashanensis*.

Particularly worth mentioning are two *P. baiguashanensis* specimens illustrated in Chen (1988, plate 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. 7).

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

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

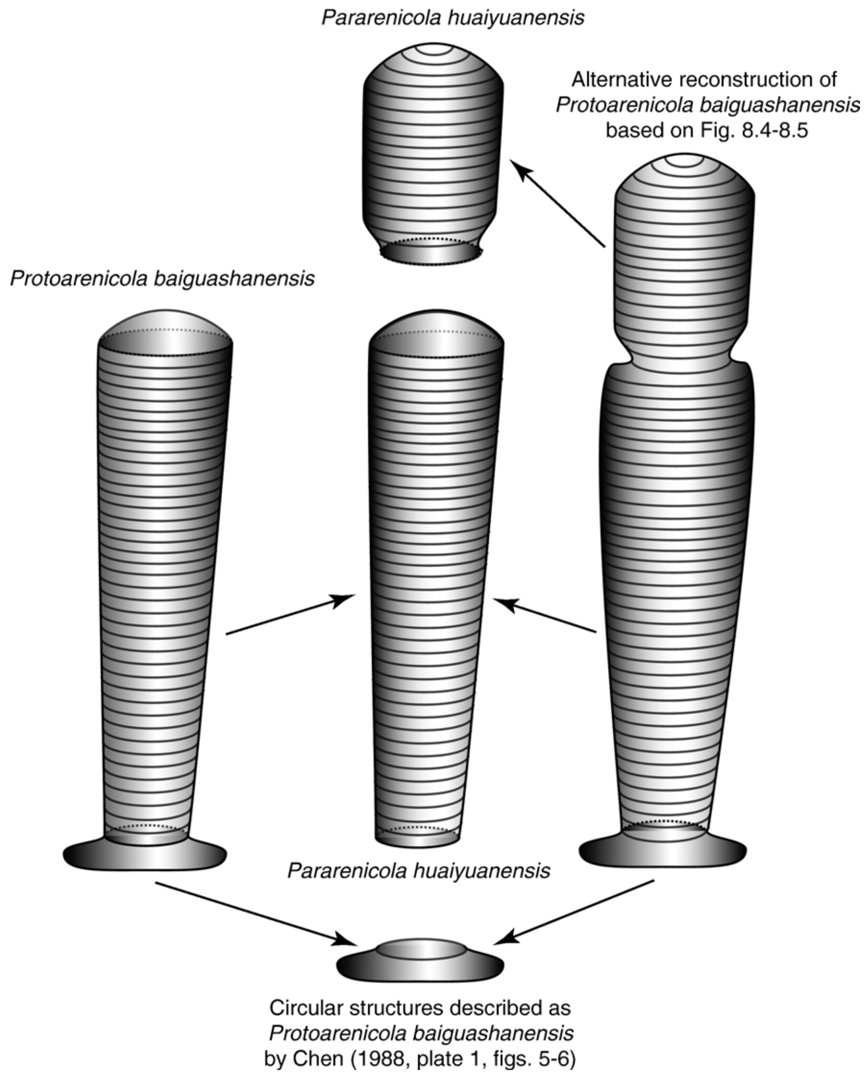

Fig. 7. Two alternative morphological reconstructions of *Protoarenicola baiguashanensis* and possible connections between *Protoarenicola baiguashanensis* and *Pararenicola huaiyuanensis* Wang, 1982.

Chen (1988) also identified as *P. baiguashanensis* many annulated ribbons that do not have a terminal discs or have a hardly recognizable terminal structure (Chen, 1988, plate 2, Figs. 7–8; plate 3, Figs. 11–15; pls. 4–5). Similarly, he considered *Paleolina tortuosa* (Wang, 1982, p. 13–14, plate 2, Fig. 1, 5; Wang et al., 1984a, plate 7, Fig. 1) and *Anhuiella sinensis* Yan and Xing *in* Xing et al., 1985 (plate 39, Fig. 5; see also Wang et al., 1984a, plate 6, Fig. 4) as junior synonyms of *P. baiguashanensis*. Additionally, he also listed under the synonym list of *P. baiguashanensis* some specimens identified as *P. 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 *P. baiguashanensis*.

Morphological and ecological interpretations. Thin section observations unequivocally demonstrate that the *P. baiguashanensis* organism consists of a cylindrical tube with an inflated bulbous structure at the proximal end (Fig. 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 *M. 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 *P. baiguashanensis* is an inflated discoidal structure, not an abscission septum, although it is separated from the cylindrical tube by a transverse septum (Fig. 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 *Radhakrishnania* from the Mesoproterozoic Suket Shale (Kumar, 2001). If correct, it implies that *P. 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 *Radhakrishnania* 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. *P. 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. 8.1–8.3
P. huaiyuanensis Wang, 1982, p. 11, plate 1, Fig. 1 (partim); Wang et al., 1984a, plate 6, Fig. 3 (partim); Sun et al., 1986, p. 390–394, plate 4, Fig. 4 (partim); Chen, 1988, p. 201–202, plate 1, Fig. 1 (partim).
Huaiyuanella baiguashanensis Xing, Yan, and Yin *in* Xing, 1984, p. 151–152, plate 1, Figs. 1–4; Xing et al., 1985, p. 189–190, plate 40, Figs. 1–3.
H. baiguashanensis Yan and Xing in Wang et al., 1984a, plate 6, Fig. 2 (nom. nud.).
Huaiyuanella minuta Xing, 1984, plate 1, Figs. 5–9; Xing et al., 1985, p. 190, plate 40, Figs. 4–7.
H. jiuliqaoensis Xing and Yan in Wang et al., 1984a, plate 6, Fig. 1 (nom. nud.).
H. aff. *jiuliqaoensis* Yan and Xing *in* Wang et al., 1984a, plate 7, Fig. 3 (nom. nud.).
Huaiyuanella marginata Yan and Xing *in* Xing et al., 1985, p. 190–191, plate 39, Fig. 6.
H. aff. *marginata* Yan and Xing *in* Xing et al., 1985, p. 191, plate 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 mm, and width from 1.0 to 2.0 mm (Fig. 9). Transverse annulations well developed, ~ 10 per mm length (Fig. 8.1–8.3). 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, plate 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; plate 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; plate 1, Fig. 1), which has a terminal opening, is here designated as a lectotype.
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 *P. 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; plate 1, Fig. 1) has a distorted terminal opening. Wang (1982) interpreted this terminal opening as an oral opening. Subsequently, Sun et al. (1986) characterized *P. huaiyuanensis* as an annulated

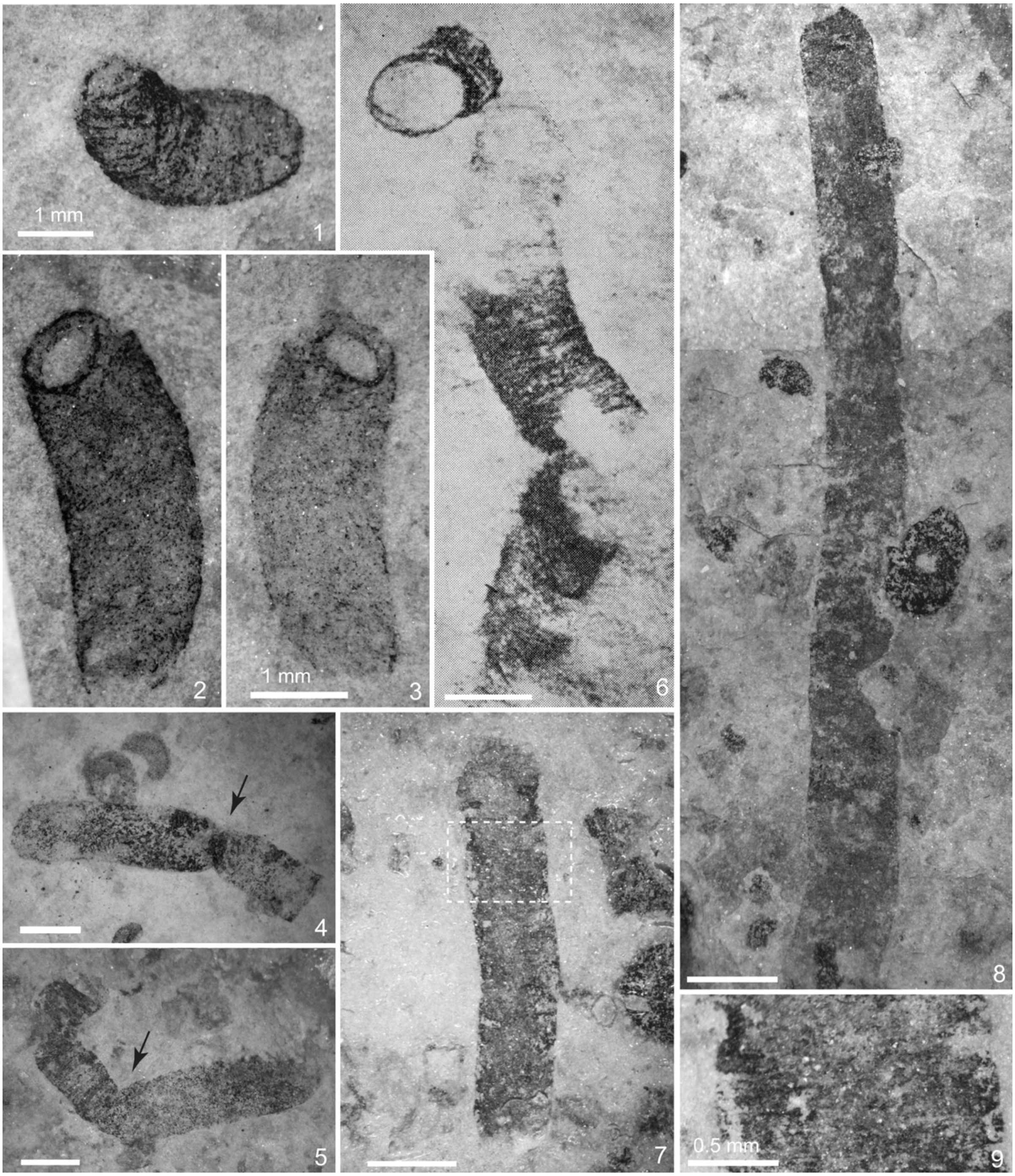

Fig. 8. *Pararenicola huaiyuanensis* Wang, 1982 (1–3), possible *Pararenicola huaiyuanensis* fragments with constrictions (arrows, 4–5), *Anhuiella sinensis* Yan and Xing in Xing et al., 1985 (6), and *Sinosabellidites huainanensis* Zheng, 1980 (7–9). 1, JLQS-23 (VPIGM-4587); 2–3, part and counterpart, JLQS-23 (VPIGM-4588); 4, JLQS-31 (VPIGM-4589); 5, JLQS-7 (VPIGM-4590); 6, reproduced from Wang et al., 1984a, plate 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.

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 *P. huaiyuanensis*, Sun et al. (1986) regarded

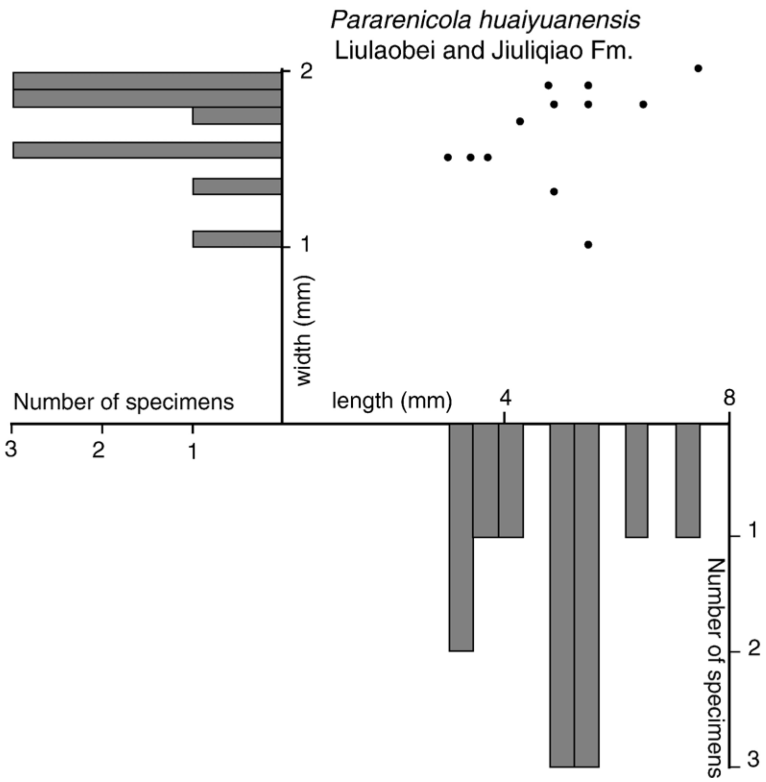

Fig. 9. Cross-plot and frequency distribution of length and width measurements of *Pararenicola huaiyuanensis* from the Jiuliqiao and Shijia formations. Measurements are based on our own material as well as those published in Wang et al. (1984a) and Xing et al. (1985).

Ruedemannella minuta Wang, 1982, *P. anhuiensis* Wang, 1982, and *P. tortuosa*, as synonyms of *P. huaiyuanensis*. Chen (1988), on the other hand, did not include the presence of a terminal opening in the diagnosis of *P. huaiyuanensis*. Instead, he characterized *P. huaiyuanensis* as a short tubular organism with a "narrowly rounded" anterior end and a "bluntly rounded" posterior end, and *P. baiguashanensis* as a proboscis-bearing worm. Thus, *R. minuta* was synonymized with *P. huaiyuanensis*, whereas *P. anhuiensis* and *P. tortuosa* were synonymized with *P. baiguashanensis* by Chen (1988).

To bring order to the taxonomic chaos, we designate the more complete specimen in the original publication (Wang, 1982, plate 1, Fig. 1) as a lectotype. 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 *P. huaiyuanensis*, because (1) none of the originally published specimens of *P. 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 (e.g., Wang et al., 1984a, plate 6, Fig. 7; Sun et al., 1986, Fig. 4.5; Chen, 1988, plate 3, Fig. 14) is a taphonomic artifact due to physical tearing or degradation.

Huaiyuanella jiuliqiaoensis Xing and Yan *in* Wang et al., 1984a and *H. 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, *H. baiguashanensis* Xing, Yan, and Yin *in* Xing, 1984 was validly published based on different specimens; thus *H. baiguashanensis* Yan and Xing is a homonym of *H. baiguashanensis* Xing, Yan, and Yin. Several other species of *Huaiyuanella* were published in 1984 and 1985. These include *H. 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 *H. 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 *P. huaiyuanensis*, despite the description and illustration of these species agreeing with the diagnosis of *P. huaiyuanensis*.

Thus these species of *Huaiyuanella* are treated as junior synonyms of *P. huaiyuanensis*, and accordingly *Huaiyuanella* as a junior synonym of *Pararenicola*.

Pararenicola fuzhouensis Liu and Yang (*in* Hong et al., 1991, p. 160, plate 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 *P. 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, plate 1, Figs. 2, 4, 6, 7; Sun et al., 1986, Figs. 4.5–4.6, 7; Chen, 1988, plate 1, Figs. 2–4) are excluded from *P. huaiyuanensis*. For similar reasons, we do not follow Sun et al.'s synonymization of *P. anhuiensis* and *P. tortuosa* with *P. huaiyuanensis*. The case of *R. minuta*, which was synonymized with *P. huaiyuanensis* by Sun et al. (1986) and Chen (1988), is less clear. Sun et al. (1986) proposed that *R. minuta* could probably be a juvenile or contracted form of *P. huaiyuanensis*. This is an attractive hypothesis, and it is supported by the similar outlines (short, slightly curved ribbons) of these two species (Wang, 1982, plate 1, Fig. 8, plate 2, Fig. 4; Wang et al., 1984a, plate 6, Figs. 6, 8; Sun et al., 1986, plate 7, Figs. 9, 10). However, the diagnostic terminal opening is not clearly identifiable in these specimens. Thus, we tentatively exclude *R. minuta* and similar fossils from the synonym list of *P. 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 *P. huaiyuanensis* (Fig. 8.1–8.3; Wang, 1982, plate 1, Fig. 1; Wang et al., 1984a, plate 6, Fig. 3; Xing et al., 1985, plate 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 *A. sinensis* (Wang et al., 1984a, plate 6, Fig.4; Xing et al., 1985, plate 39, Fig. 5; reproduced here in Fig. 8.6) has an elliptical opening with a diameter similar to that of the tube. There is no constriction at the terminal opening of *A. sinensis*, indicating that its terminal opening probably resulted from physical breakage along annulations.

Morphological and ecological interpretations. On the basis of available material, *P. 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 *P. huaiyuanensis* as described here indeed represents a complete organism. The lack of a well-defined holdfast structure indicates that *P. 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 *P. huaiyuanensis* might have been a planktonic organism, although we suspect that *P. huaiyuanensis* as described here may not represent the complete organism. It is entirely possible that the constricted terminal opening of *P. 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. 7). If so, then *P. huaiyuanensis* may represent biologically (perhaps ontogenetically given its generally smaller size) or physically fragmented specimens of *P. baiguashanensis*. This interpretation is intriguing because *P. baiguashanensis* tubes tend to constricted where they are in contact with the discoidal holdfast (Fig. 5.3, 5.4, 5.6, 5.8). If confirmed, *P. huaiyuanensis* and *P. baiguashanensis* should be regarded as synonyms, in which case *P. huaiyuanensis* would have page priority. Alternatively, *P. huaiyuanensis* as described here may represent segments of constricted tubular organisms that were fragmented along the constrictions (Fig. 7). Indeed, a few specimens do have constricted sausage-like morphologies (Fig. 8.4, 8.5), and the constricted segments are similar in size and shape to *P. huaiyuanensis* described in this paper. This alternative interpretation is analogous to biological abscission or physical fragmentation of constricted algal thalli of the Ediacaran fossil *M. bifurcatum* (Xiao et al., 1998).

Regardless, the potential link between *P. huaiyuanensis* and *P. baiguashanensis* further weakens the bilaterian interpretation and suggests that *P. 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 *P. huaiyuanensis* and *P. baiguashanensis* than bilaterian animals.

Genus *SINOSABELLIDITES* Zheng, 1980
Huainanella Wang, 1982.
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 *S. 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 *S. 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. 8.7–8.9

S. huainanensis Zheng, 1980, p. 63, Figs. 18, 19, 20a, 20b; Sun et al., 1986, p. 385–391, plate 4, Figs. 1, 2.

Huainanella cylindrica Wang, 1982, plate 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. *S. 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). *H. cylindrica*, as discussed above, should be regarded as a synonym of *S. huainanensis*.

Sun et al. (1986) remarked on the morphological similarity between *S. huainanensis* and *Tawuia dalensis*. Both species occur in the Liulaobei Formation in the Huainan region and have a tomaculate outline (Duan,

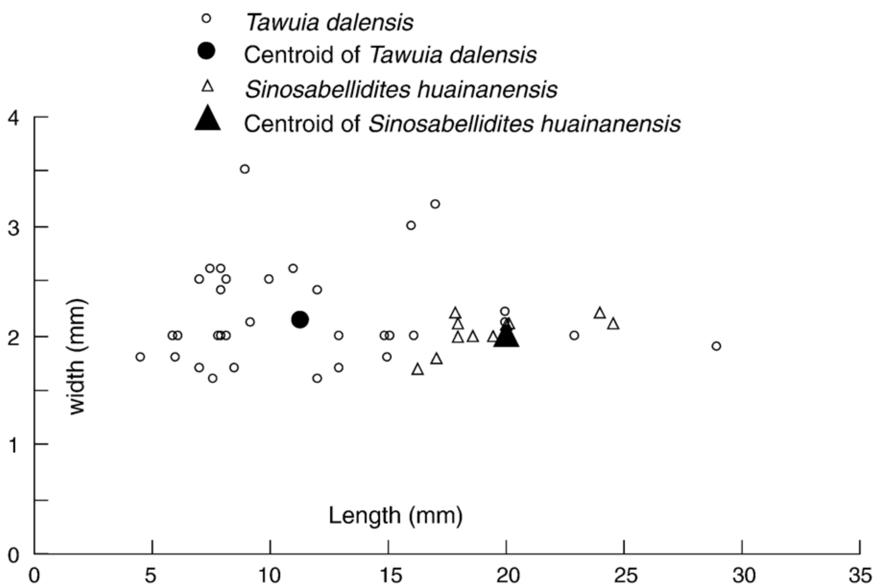

Fig. 10. Width and length measurements of completely preserved specimens of *Sinosabellidites huainanensis* and *Tawuia dalensis* Hofmann *in* Hofmann et al., 1979 from the Jiuliqiao and Liulaobei formations. Measurements are based on our own material as well as those published in Zheng (1980), Wang (1982), and Duan (1982).

1982; Wang et al., 1984a; Sun et al., 1986), although *T. dalensis* lacks any transverse annulations. Sun et al. (1986) showed that the width and length ranges of *S. huainanensis* overlap with those of *T. dalensis* (=*T. sinensis* Duan, 1982). We plotted the width and length measurements (Fig. 10) of completely preserved specimens of *S. huainanensis* and *T. 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 *S. huainanensis* and *T. dalensis* are significantly different ($p=0.0017$). Their centroids in the width-length plot (Fig. 10) are clearly separated from each other because of the difference in length (two tail t-test, $p \ll 0.0001$). The average width of *S. huainanensis* and *T. dalensis*, however, is not significantly different from each other (two tail t-test, $p=0.1892$).

Morphological and ecological interpretations. S. 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 *S. huainanensis* represents fragments detached from erect epibenthic organisms such as *P. baiguashanensis*; this interpretation is analogous to the interpretation of *Tawuia* as fragment detached from *Radhakrishnania* (Kumar, 2001). However, *P. baiguashanensis* does not occur in the Liulaobei Formation where *S. huainanensis* is common, although both species do co-occur in the Jiuliqiao Formation.

4. Discussion 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. *P. 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 *P. baiguashanensis* was an erect epibenthic organism. *P. huaiyuanensis* is smaller than *P. baiguashanensis*, and has a constricted terminal opening and a rounded end. It is uncertain whether *P. huaiyuanensis* as described in this paper represents a complete organism and, if so, how it functioned. The observations that some *P. 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 *P. huaiyuanensis* may represent segments detached from *P. baiguashanensis* or similar organisms, either through biological abscission or physical fragmentation. *S. 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 *P. baiguashanensis* and *P. huaiyuanensis* may represent reproductive or physical fragments of an erect benthic organism with a discoidal holdfast (Fig. 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 *S. 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 *P. 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 *Radhakrishnania* 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 *L. stipitata* (Du and Tian, 1986) and *P. 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 *P. baiguashanensis*, *P. huaiyuanensis*, and *S. huainanensis* presented in this paper, weakens the paleontological evidence for early Neoproterozoic bilaterian animals.

Acknowledgements

We thank Wang Jinlong and Zhou Chuanming at Nanjing Institute of Geology and Paleontology for field assistance. Constructive comments by Bob Gaines and Nick Butterfield have greatly improved this manuscript. Financial support for this research was provided by the American Chemical Society Petroleum Research Fund, National Science Foundation Sedimentary Geology and Paleobiology Program, National Natural Science Foundation of China, Chinese Ministry of Science and Technology, and National Aeronautics and Space Administration (NASA) Exobiology Program.

References

Agardh, C.A., 1823. Species algarum, 1 (part 2). Lund, Berling. 169–531 pp.

Ausich, W.I., Bottjer, D.J., 2001. Sessile invertebrates. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology II. Blackwell, Oxford, pp. 384–386.

Billings, E., 1872. Fossils in Huronian rocks. Can. Nat. Q. J. Sci. 6, 478.

Bold, H.C., Wynne, M.J., 1985. Introduction to the Algae. Prentice-Hall, Englewood Cliffs, New Jersey. 720 pp.

Bottjer, D.J., Hagadorn, J.W., Dornbos, S.Q., 2000. The Cambrian substrate revolution. GSA Today 10 (9), 1–7.

Butterfield, N.J., 1995. Secular distribution of Burgess Shale-type preservation. Lethaia 28, 1–13.

Butterfield, N.J., 2000. *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. Paleobiology 26, 386–404.

Cao, R., Zhao, W., Xiao, G., 1989. Late Precambrian stromatolites from north Anhui Province. Mem. Nanjing Inst. Geol. Palaeontol., Acad. Sin. 21, 1–54.

Chen, J., 1988. Precambrian metazoans of the Huai River drainage area (Anhui, E. China): their taphonomic and ecological evidence. Senkenbergiana Lethaea 69 (3–4), 189–215.

Chen, M., Zheng, W., 1986. On the pre-Ediacaran Huainan Biota. Sci. Geol. Sin. 3, 221–233.

China Commission on Stratigraphy, 2001. Stratigraphic Guide of China and Its Explanatory Notes (revised edition). Geological Publishing House, Beijing. 42 pp.

Chung, S., 1999. Trace and isotope characteristics of Cenozoic basalts around the Tanlu Fault with implications for the eastern plate boundary between North and South China. J. Geol. 107, 301–312.

Clapham, M.E., Narbonne, G.M., 2002. Ediacaran epifaunal tiering. Geology 30, 627–630.

Ding, L., Li, Y., Hu, X., Xiao, Y., Su, C., Huang, J., 1996. Sinian Miaohe Biota. Geological Publishing House, Beijing. 221 pp.

Du, R., 1982. The discovery of the fossils such as *Chuaria* in the Qingbaikou System in northwestern Hebei and their significance. Geol. Rev. 28 (1), 1–7.

Du, R., Tian, L., 1986. The Macroalgal Fossils of the Qingbaikou Period in the Yanshan Range. Hebei Science and Technology Press, Shijiazhuang. 114 pp.

Duan, C., 1982. Late Precambrian algal megafossils *Chuaria* and *Tawuia* in some areas of eastern China. Alcheringa 6, 57–68.

Fairchild, I.J., Einsele, G., Song, T., 1997. Possible seismic origin of molar tooth structures in Neoproterozoic carbonate ramp deposits, North China. Sedimentology 44, 611–636.

Feldmann, J., 1938. Sur un nouveau genre de Siphonocladacées. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences [Paris], vol. 206, pp. 1503–1504.

Ford, T.D., 1958. Precambrian fossils from Charnwood Forest. Proc. Yorks. Geol. Soc. 31, 211–217.

Frank, T.D., Lyons, T.W., 1998. "Molar-tooth"structures: a geochemical perspective on a Proterozoic enigma. Geology 26, 683–686.

Fu, J., 1989. Assemblage of Huainan biota and its characteristics. Acta Palaeontol. Sin. 28, 642–652.

Gehling, J.G., Narbonne, G.M., Anderson, M.M., 2000. The first named Ediacaran body fossil, *Aspidella terranovica*. Palaeontology 43, 427–456.

Gnilovskaya, M.B., 1998. The ancient annelidomorphs from the upper riphean of Timan. Dokl. Akad. Nauk 359, 369–372.

Gnilovskaya, M.B., Veis, A.F., Bekker, A.Y., Olovyanishnikov, V.G., Raaben, M.E., 2000. Pre-Ediacarian fauna from Timan (Annelidomorphs of the late Riphean). Stratigr. Geol. Correl. 8, 327–352.
Hagadorn, J.W., Bottjer, D.J., 1999. Restriction of a Late Neoproterozoic biotope: suspect-microbial structures and trace fossils at the Vendian–Cambrian transition. Palaios 14, 73–85.
Hofmann, H.J., 1985. The mid-Proterozoic Little Dal macrobiota, Mackenzie Mountains, north-west Canada. Palaeontology 28, 331–354.
Hofmann, H.J., 1992. Proterozoic and selected Cambrian megascopic carbonaceous films. In: Schopf, J.W., Klein, C. (Eds.), The Proterozoic Biosphere, A Multidisciplinary Study. Cambridge University Press, Cambridge, pp. 957–998.
Hofmann, H.J., 1994. Proterozoic carbonaceous compressions ("metaphytes" and "worms"). In: Bengtson, S. (Ed.), Early Life on Earth. Columbia University Press, New York, pp. 342–357.
Hofmann, H.J., Aitken, J.D., 1979. Precambrian biota from the Little Dal Group, Mackenzie Mountains, northwestern Canada. Can. J. Earth Sci. 16, 150–166.
Hong, T., Jia, Z., Yin, L., Zheng, W., 2004. Acritarchs from the Neoproterozoic Jiuliqiao Formation, Huainan region, and their biostratigraphic significance. Acta Palaeontol. Sin. 43, 377–387.
Hong, Z., Huang, Z., Liu, X., 1991. Upper Precambrian geology in southern Liaodong Peninsula. The Geological Publishing House, Beijing. 189 pp.
Horodyski, R.J., 1976. Stromatolites of the upper Siyeh limestone (middle Proterozoic), Belt Supergroup, Glacier National Park, Montana. Precambrian Res. 3, 517–536.
Ivantsov, A.Y., 1990. New data on the ultrastructure of sabelliditids (Pogonophora?). Paleontologicheskii Zhurnal 24 (4), 125–128.
James, N.P., Narbonne, G.M., Sherman, A.G., 1998. Molar-tooth carbonates: shallow subtidal facies of the mid-to late Proterozoic. J. Sediment. Res. 68, 716–722.
Jia, Z., Hong, T., Zheng, W., Li, S., 2003. The characters and environments of the seismites of the Neoproterozoic Wangshan Formation in north Anhui. J. Stratigr. 27, 146–149.
Kumar, S., 1995. Megafossils from the Mesoproterozoic Rohtas Formation (the Vindhyan Supergroup), Katni area, central India. Precambrian Res. 72, 171–184.
Kumar, S., 2001. Mesoproterozoic megafossil *Chuaria–Tawuia* association may represent parts of a multicellular plant, Vindhyan Supergroup, Central India. Precambrian Res. 106, 187–211.
Li, Z.X., Evans, D.A.D., Zhang, S., 2004. A 90° spin on Rodinia: possible causal links between the Neoproterozoic supercontinent, superplume, true polar wander and low-latitude glaciation. Earth Planet. Sci. Lett. 220, 409–421.
Lin, W., Xing, Y., 1984. Research on the Sinian metazoan fossils of Liaonan Group from southern Liaodong Peninsula. Bull. Shenyang Inst. Geol. Miner. Resour., Chin. Acad. Geol. Sci. 10, 51–63.
Liu, H., 1991. The Sinian System in China. Science Press, Beijing. 388 pp.
Liu, Y., Gao, L., Liu, X., Song, B., Wang, Z., 2005. Zircon U–Pb age determination of early Neoproterozoic mafic magmatic event in the Xu-Huai region. Chin. Sci. Bull. 22, 2514–2521.
Meng, X., Ge, M., 2004. The sedimentary features of Proterozoic microspar (molar-tooth) carbonates in China and their significance. Episodes 25, 185–195.
Moczydlowska, M., 2003. Earliest Cambrian putative bacterial nanofossils. Mem. Assoc. Australas. Palaeontol. 29, 1–11.
Qian, M., Yuan, X., Wang, Y., Yang, Y., 2000. New material of metaphytes from the Neoproterozoic Jinshanzhai Formation in Huaibei, North Anhui, China. Acta Palaeontol. Sin. 39, 516–520.
Qiao, X., Gao, L., Peng, Y., 2001. Neoproterozoic in Paleo-Tanlu fault zone. Geological Publishing House, Beijing.
Schieber, J., 2003. Simple gifts and buried treasures—implications of finding bioturbation and erosion surfaces in black shales. Sediment. Rec. 1 (2), 4–8.
Seilacher, A., 1999. Biomat-related lifestyles in the Precambrian. Palaios 14, 86–93.
Shen, B., Xiao, S., Dong, L., Zhou, C., Liu, J., 2007. Problematic macrofossils from Ediacaran successions in the North China and Chaidam blocks: Implications for their evolutionary roots and biostratigraphic significance. J. Paleontol. 81, 1396-1411.
Sokolov, B.S., 1965. The most ancient Early Cambrian deposits and sabelliditids (in Russian). In: Sokolov, B.S. (Ed.), All-Union Syposium on Paleontology of Precambrian and Early Cambrian. Akad Nauk SSSR, Novosibirsk, pp. 78–91.
Sokolov, B.S., 1967. Drevneyshiye pognofory [the oldest Pogonophora]. Dokl. Akad. Nauk SSSR 177 (1), 201–204 (English translation, page 252–255).
Steiner, M., 1994. Die neoproterozoischen Megaalgen Südchinas. Berl. Geowiss. Abh. 15, 1–146.
Sun, W., Wang, G., Zhou, B., 1986. Macroscopic worm-like body fossils from the Upper Precambrian (900–700 Ma), Huainan district, Anhui, China and their stratigraphic and evolutionary significance. Precambrian Res. 31, 377–403.
Tianjin Institute of Geology and Mineral Resources, 1980. Research in Precambrian Geology, Sinian Suberathem in China. Tianjin Science and Technology Press, Tianjin. 407 pp.
Urbanek, A., Mierzejewska, G., 1977. The fine structure of zooidal tubes in Sabelliditida and Pogonophora with reference to their affinity. Acta Palaeontol. Pol. 22, 223–240.
Walcott, C.D., 1899. Pre-Cambrian fossiliferous formations. Bull. Geol. Soc. Am. 10, 199–244 (plates 22–28).
Walcott, C.D., 1920. Middle Cambrian spongiae. Smithson. Misc. Coll. 67, 261–364.
Walter, M.R., Oehler, J.H., Oehler, D.Z., 1976. Megascopic algae 1300 million years old from the Belt Supergroup, Montana: a reinterpretation of Walcott's *Helminthoidichnites*. J. Paleontol. 50, 872–881.
Wang, G., 1982. Late Precambrian Annelida and Pogonophora from the Huainan of Anhui Province. Bull. Tianjin Inst. Geol. Miner. Resour., Chin. Acad. Geol. Sci. 6, 9–22.
Wang, G., Zhang, S., Li, S., Yan, Y., Dou, S., Fang, D., 1984a. Research on the Upper Precambrian of Northern Jiangsu and Anhui Provinces. Anhui Press of Science and Technology, Hefei, Anhui. 209 pp.
Wang, G., Zhou, B., Xiao, L., 1984b. Late Precambrian macrofossils from Huainan, Anhui and their significance. J. Stratigr. 84, 271–278.
Wang, H., 1985. Atlas of the Palaeogeography of China. Cartographic Publishing House, Beijing. 85 pp.
Whittington, H.B., 1985. The Burgess Shale. Yale University Press, New Haven. 151 pp.
Wray, G.A., Levinton, J.S., Shapiro, L.H., 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. Science 274, 568–573.
Xiao, S., Dong, L., 2006. On the morphological and ecological history of Proterozoic macroalgae. Neoproterozoic Geobiology. Springer, Dordrecht, the Netherlands, pp. 59–90.
Xiao, S., Knoll, A.H., Yuan, X., 1998. Morphological reconstruction of *Miaohephyton bifurcatum*, a possible brown alga from the Doushantuo Formation (Neoproterozoic), South China, and its implications for stramenopile evolution. J. Paleontol. 72, 1072–1086.

Xiao, S., Yuan, X., Steiner, M., Knoll, A.H., 2002. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: a systematic reassessment of the Miaohe biota, South China. J. Paleontol. 76, 345–374.

Xing, Y., 1984. Description of a new worm family Huaiyuanellidae Xing from the upper Sinian of north Anhui, China. Bull. Geol. Inst., Chin. Acad. Geol. Sci. 9, 151–154.

Xing, Y., 1989. The Upper Precambrian of China, Volume 3 of "The Stratigraphy of China". Geological Publishing House, Beijing. 314 pp.

Xing, Y., Dong, Q., Luo, H., He, T., Wang, Y., 1984. The Sinian–Cambrian boundary of China. Bull. Inst. Geol., Chin. Acad. Geol. Sci. 10, 1–262.

Xing, Y., Duan, C., Liang, Y., Cao, R., 1985. Late Precambrian Palaeontology of China. Geological Publishing House, Beijing. 1–243 pp.

Xing, Y., Gao, Z., Wang, Z., Gao, L., Yin, C., 1996. Chinese Stratigraphy Catalog: Neoproterozoic. Geological Publishing House, Beijing. 6–17 pp.

Xue, Y., Cao, R., Tang, T., Yin, L., Yu, C., Yang, J., 2001. The Sinian stratigraphic sequence of the Yangtze region and correlation to the late Precambrian strata of North China. J. Stratigr. 25, 207–234.

Yan, Y., 1982. Micropalaeoflora from the Liulaobei Formation of Sinian Subera in Fengyang region, Anhui Province. Bull. Nanjing Inst. Geol. Miner. Resour., Chin. Acad. Geol. Sci. 3 (3), 75–94.

Yang, J., Zheng, W., Wang, Z., Tao, X., 2001. Age determining of the upper Precambrian System of northern Jiangsu-Anhui by using Sr and C isotopes. J. Stratigr. 25, 44–47.

Yang, J., Zheng, W., Tao, X., Wang, Z., 2004a. The Sm–Nd age of cherts from Sidingshan Formation of the Huainan Group of Anhui Province. Geol. Rev. 50, 413–417.

Yang, J.H., Wu, F.Y., Zhang, Y.B., Zhang, Q., Wilde, S., 2004b. Identification of Mesoproterozoic zircons in a Triassic dolerite from the Liaodong Peninsula, northeast China. Chin. Sci. Bull. 49, 1958–1962.

Yang, Q., Zhang, Y., Zheng, W., Xu, X., 1980. Subdivision and correlation of Sinian Suberathem in northern Jiangsu and Anhui. In: Tianjin Institute of Geology and Mineral Resources (Ed.), Research in Precambrian Geology, Sinian Suberathem in China. Tianjin Science and Technology Press, Tianjin, pp. 231–265.

Yanishevsky, M.E., 1926. Ob ostatkakh trubchatykh chervej iz kembrijskoj Sinej Gliny [On remains of tube-dwelling worms from the Cambrian Blue Clay]. Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 4, 99–111.

Yao, Z., Zhang, S., 1985. Precambrian volume. Monographs Series Anhui Stratigraphy. Anhui Press of Science and Technology, Hefei. 1–174 pp.

Yin, C., 1985. Micropaleoflora from the late Precambrian in Huainan region of Anhui Province and its stratigraphic significance. Prof. Pap. Stratigr. Palaeontol., Chin. Acad. Geol. Sci. 12, 97–119.

Yin, L., 1983. Late Precambrian microfossils from Diaoyutai and Liulaobei Formation, in Liaoning and Anhui Provinces, respectively, of China. Bull. Nanjing Inst. Geol. Palaeontol., Acad. Sin. 6, 9–25.

Yin, L., 1990. New data on late Proterozoic microfossils in northern Korea Peninsula. J. Stratigr. 29, 460–466.

Yin, L., 1994. Microbiota from the Neoproterozoic Liulaobei Formation in the Huainan region, northern Anhui, China. Precambrian Res. 65, 95–114.

Yin, L., 1999. Neoproterozoic microphytoplanktonic fossils in China and their biostratigraphical implication. Acta Palaeontol. Sin. 38, 133–146.

Yuan, X., Li, J., Chen, M., 1995. Development and their fossil records of metaphytes from late Precambrian. Acta Palaeontol. Sin. 34, 90–102.

Yuan, X., Xiao, S., Parsley, R.L., Zhou, C., Chen, Z., Hu, J., 2002. Towering sponges in an Early Cambrian Lagerstätte: disparity between non-bilaterian and bilaterian epifaunal tiers during the Neoproterozoic–Cambrian transition. Geology 30, 363–366.

Zang, W., Walter, M.R., 1992. Late Proterozoic and Early Cambrian microfossils and biostratigraphy, northern Anhui and Jiangsu, central eastern China. Precambrian Res. 57, 243–323.

Zhang, K., 1997. North and South China collision along the eastern and southern North China margins. Tectonophysics 270, 145–156.

Zhang, S., Li, Z.-X., Wu, H., 2006. New Precambrian palaeomagnetic constraints on the position of the North China Block in Rodinia. Precambrian Res. 144, 213–238.

Zheng, W., 1980. A new occurrence of fossil group *Chuaria* from the Sinian System in north Anhui and its geological meaning. Bull. Tianjin Inst. Geol. Miner. Resour., Chin. Acad. Geol. Sci. 1, 49–69.

Zheng, W., Mu, Y., Zheng, X., Wang, J., Xin, L., 1994. Discovery of carbonaceous megafossils from Upper Precambrian Shijia Formation, north Anhui and its biostratigraphic significance. Acta Palaeontol. Sin. 33, 455–471.