

Articulated sponges from the Lower Cambrian Hetang Formation in southern Anhui, South China: their age and implications for the early evolution of sponges

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Abstract

A well-preserved benthic, epifaunal assemblage of articulated sponges is described from the stone coal beds of the Lower Cambrian Hetang Formation at Lantian, southern Anhui Province, South China. These sponges are Meishucunian–Qiongzhusian (=Diandongian–early Qiongzhusian) in age. In Siberian terminology, they are probably Tommotian–Atdabanian, approximately 535–520 Ma. The Hetang sponge fauna is taxonomically diverse and morphologically complex. Eleven species of both demosponges and hexactinellids, including three new taxa (*Choia? striata* sp. nov., *Protospongia gracilis* sp. nov., and *Lantianospongia palifera* gen. et sp. nov.), are described. Two undetermined forms are also illustrated. The Hetang and other Neoproterozoic–Cambrian sponge fossils, at their face value, indicate that hexactinellids evolved no later than the Nemakit–Daldynian–Tommotian and perhaps in the late Neoproterozoic, and the demosponges and calcareans evolved no later than the Atdabanian. The divergence of sponge classes therefore appears to be part of the Cambrian Radiation event. In comparison with the eumetazoans which probably diverged at ca. 600 Ma, however, the sponges (particularly the demosponges and calcareans) appear to have a missing fossil record in the late Neoproterozoic and earliest Cambrian. The minimum implied gaps (MIGs) of the calcareans and demosponges are substantial (tens of Myrs to perhaps more than 100 Myrs), particularly if the calcareans constitute a sister group of the eumetazoans—a topology supported by currently available molecular evidence.

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Keywords: Early Cambrian; Hetang Formation; South China; Sponges; Phylogeny

1. Introduction

The evolution of early animals at the Neoproterozoic–Cambrian transition (ca. 600–520 Ma) is a key

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event in the history of life. Much of the current discussion has been centered on bilaterian animals (Budd and Jensen, 2000). Bilaterians are duly important because of their great diversity, but non-bilaterian animals (cnidarians and sponges) and protists are also part of the Cambrian radiation puzzle (Lipps, 2001; Moczyłowska, 2001). For example, phytoplankton was a crucial component of the Neoproterozoic–Cambrian food chain (Butterfield, 2001), and non-bilaterians were important players in ecological tiering in Neoproterozoic–Cambrian epifaunal communities (Yuan et al., 2002; Clapham and Narbonne, 2002).

The focus of this paper is the sponges. Traditionally, sponges have been treated as a monophyletic group with three classes (Hexactinellida, Demospongia, and Calcarea), each of which is taken to be monophyletic (Reitner and Mehl, 1996). Molecular phylogenetic analyses in the recent years, however, appear to support sponge paraphyly with calcareans being a sister group to the eumetazoans, although the monophyly of the three individual classes has not been challenged. Whether the molecular data support a demosponge+hexactinellid grouping to form a monophyletic Silicea is a matter of current controversy (Borchiellini et al., 2001; Medina et al., 2001).

Few have questioned and evaluated the quality of the sponge fossil record, despite considerable debate on a possible deep, but missing, bilaterian history in the Precambrian (Wray et al., 1996; Conway Morris, 1997; Budd and Jensen, 2000). The incongruence between sponge phylogeny and stratigraphy can be used to evaluate the quality of the sponge fossil record and to estimate the minimum implied gaps (MIGs)—minimum fossil gaps or range extension required for the congruence between stratigraphic and phylogenetic data (cf. Benton and

Storrs, 1996; Benton et al., 2000). Given the antiquity of eumetazoans, all sponge phylogenies (particularly those based on molecular data) require long MIGs in the early record of calcareans and demosponges, both of which first appeared certainly in the Atdabanian (and possibly in the Tommotian for demosponges described in this paper). This simple analysis of stratigraphy against phylogeny highlights the incompleteness of early sponge fossils.

2. Geologic background and stratigraphic correlation

The sponge fossils were collected from the Early Cambrian Hetang Formation at Lantian (29°55'N, 118°05'E; Fig. 1), southern Anhui Province in South China. Because the age of these fossils is critical to our stratigraphic–phylogenetic analysis, we present in this section detailed discussion on the correlation between the Hetang Formation in southern Anhui and better known Early Cambrian sections in eastern Yunnan (regional type sections), Siberia, and Newfoundland (Neoproterozoic–Cambrian GSSP).

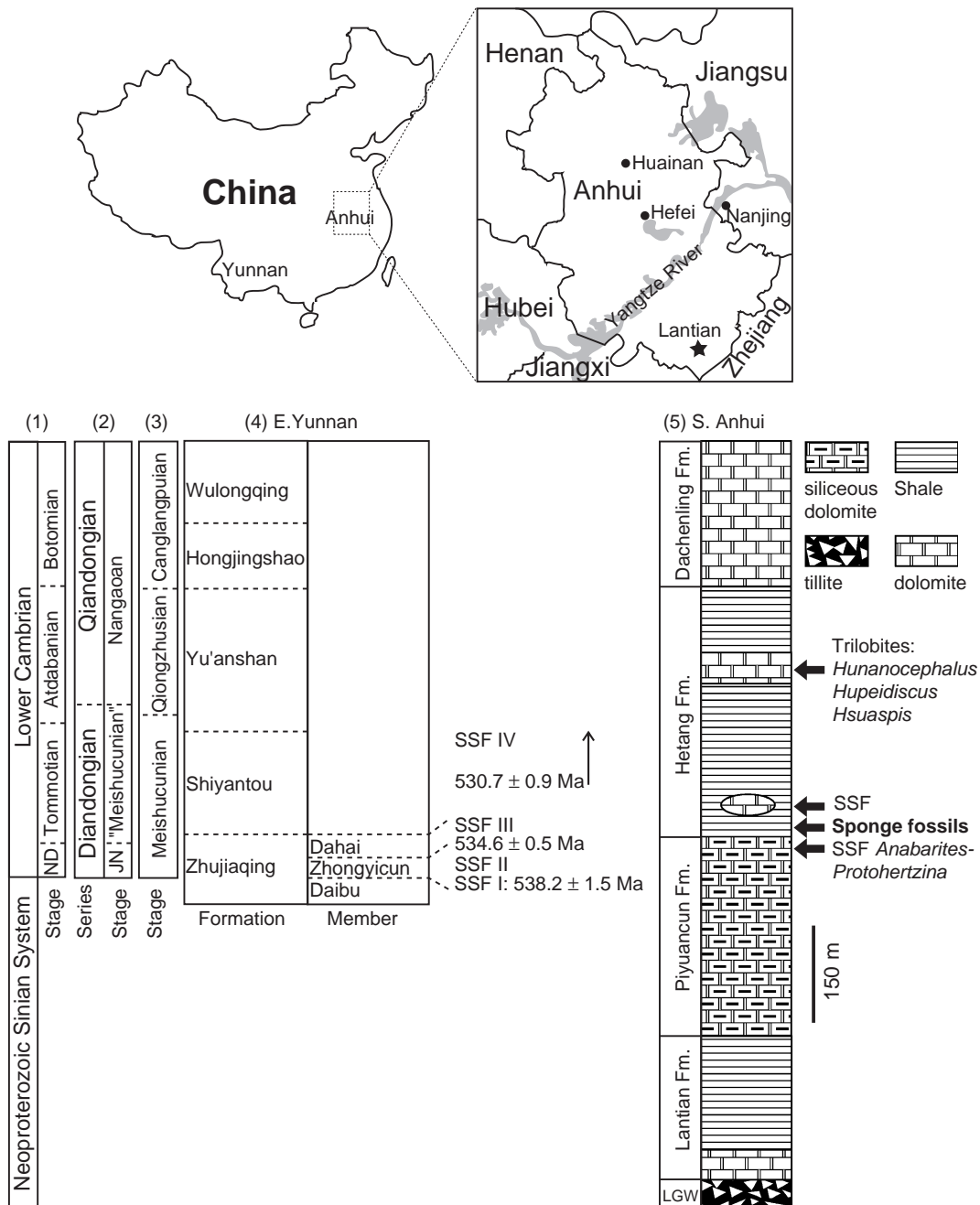
2.1. Eastern Yunnan

In South China, the Early Cambrian successions typically begin with a few to a few tens of meters of phosphatic dolostones that contain basal Cambrian small shelly fossils (SSFs). The phosphatic dolostones are succeeded by black shales that are widespread in South China (Erdtmann and Steiner, 2001; Steiner et al., 2001a). The Shiyantou and Hetang Formations, in eastern Yunnan and southern Anhui, respectively (see below), are examples of such black shales. On weathered landscape, the black shales contrast sharply

Fig. 1. Neoproterozoic–Lower Cambrian lithostratigraphy at Lantian (star on map), southern Anhui, and proposed correlations with eastern Yunnan and Siberian stages. Column (1): Lower Cambrian stages of Siberia. Column (2): Recently proposed Cambrian series and stages of south China (Peng and Babcock, 2001). Column (3): Traditional Lower Cambrian stages of south China. Column (4): Lower Cambrian lithostratigraphic units and SSF assemblages (I–IV) in eastern Yunnan. SSF I (*Anabarites trisulcatus*–*Protohertzina anabarica* assemblage), SSF II (*Siphonuchites triangularis*–*Paragloborilus subglobosus* assemblage), SSF III (*Heraultipegma yunnanensis*–*Watsonella crosbyi* assemblage), SSF IV (*Sinosachites flabelliformis*–*Tannuolina zhangwentangi* assemblage). An ash bed from the SSF I assemblage is dated from 538.2 ± 1.5 Ma (Jenkins et al., 2002). Dated ash beds from Siberia (534.6 ± 0.5 Ma; Bowring et al., 1993) and Avalonia (530.7 ± 0.9 Ma; Isachsen et al., 1994) are correlated to eastern Yunnan using the *Watsonella crosbyi* assemblage as a time indicator. Column (5): Stratocolumn at Lantian. Sponge fossils reported in this paper are from lower Hetang Formation, probably Meishucunian–Qiongzhusian in age. ND—Nemakit-Daldynian, JN—Jinningian, LGW—Leigongwu diamictite.

with thick-bedded dolostones of the terminal Neoproterozoic Dengying Formation and its equivalents (for example, the Liuchapo Formation in central Hunan and the Piyuancun Formation in southern Anhui).

The most intensively studied Neoproterozoic–Cambrian successions in South China are probably those in Yunnan Province. The Meishucun section in eastern Yunnan was once a strong contender for the Neoproterozoic–Cambrian boundary global stratotype



(Luo et al., 1982; Luo et al., 1984). The Meishucun and many other sections in eastern Yunnan are still used as yardsticks for Early Cambrian correlation in South China (Luo et al., 1994). The litho-, bio-, chemo-, and chronostratigraphy of Early Cambrian successions in eastern Yunnan has been published by others (Jiang et al., 1988; Brasier et al., 1990; Zhou et al., 1997; Shen and Schidlowski, 2000; Zhu et al., 2001) and is summarized below.

In eastern Yunnan, Neoproterozoic–Early Cambrian successions are divided into the Zhujiaping, Shiyantou, and Yu’anshan formations (Zhu et al., 2001; Fig. 1). The Heilinpu Formation (Luo et al., 1994; Babcock et al., 2001) is equivalent to the Shiyantou and Yu’anshan formations combined. The recently proposed Zhujiaping Formation (Zhu et al., 2001) avoids the confusion between lithostratigraphic and chronostratigraphic terms—the old lithostratigraphic term was the Meishucun Formation but Meishucun is also the namesake of the Lower Cambrian Meishucunian Stage in South China. The Zhujiaping Formation consists of, in ascending order, the Daibu (cherty dolostone, 0–56 m thick), Zhongyicun (phosphorite, 1–90 m thick), and Dahai (dolostone, 1–70 m thick) members. The Neoproterozoic–Cambrian boundary is placed at the base of the SSF *Anabarites trisulcatus*–*Protohertzina anabarica* assemblage, coincident with the base of the Zhongyicun Member of the Zhujiaping Formation (Zhu et al., 2001). Earlier reports of SSFs from the underlying Xiaowaitoushan Member of the Meishucun Formation near Meishucun (Luo et al., 1982) have not been confirmed by subsequent studies (Qian and Bengtson, 1989; Qian et al., 1996). Zhu et al. (2001) therefore considered the Xiaowaitoushan Member as part of the Baiyanshao Member of the Dengying Formation, because it is lithologically inseparable from the underlying Baiyanshao Member. The Daibu Member of the Zhujiaping Formation overlies the Baiyanshao Member and crops out in areas some 200 km northeast of Meishucun; in the Meishucun area, the Daibu Member is missing and corresponds to an unconformity between the Baiyanshao and Zhongyicun members. So far, no SSFs have been reported from the Daibu Member (Li et al., 2001) and the *A. trisulcatus*–*P. anabarica* assemblage in the lower Zhongyicun Member represents the earliest Cambrian SSF assemblage in South China. The second SSF

assemblage, the *Siphogonuchites triangularis*–*Paragloborilus subglobosus* assemblage, occurs in the upper Zhongyicun Member; most SSFs in this assemblage also extend upward into the Dahai Member (Qian and Bengtson, 1989; Qian et al., 2001). The Dahai Member contains a third and newly named SSF assemblage, the *Heraultipegma yunnanensis* assemblage (Qian et al., 1996; Qian et al., 2001); *H. yunnanensis* is probably a junior synonym of *Watsonella crosbyi* (Landing, 1989).

The Shiyantou Formation (formerly Shiyantou Member of the Qiongzhusi Formation; Chen et al., 1996) consists of black siltstones and shales with phosphatic nodules. Few fossils occur in the lower part of this formation, but the upper Shiyantou contains fossils belonging to the fourth SSF assemblage, the *Sinosachites flabelliformis*–*Tannuolina zhangwentangi* assemblage. This assemblage extends upward into the basal phosphorite bed (<50 cm thick) of the Yu’anshan Formation (formerly Yu’anshan Member of the Qiongzhusi Formation; Chen et al., 1996). This phosphorite bed is succeeded by black siltstones, black shales, and gray shales and siltstones that contain the earliest Chinese trilobites including, in ascending order, the *Parabadiella* and *Wutingaspis*–*Eoredlichia* zones (Steiner et al., 2001b), as well as the astounding Chengjiang Biota (Chen et al., 1996; Hou et al., 1999).

Traditionally, the Meishucunian Stage represents the first, pre-trilobite Cambrian chronostratigraphic unit in South China. The first occurrence of *Parabadiella* defines the base of the trilobite-bearing Qiongzhusian Stage. Recently, a new chronostratigraphic scale has been proposed for the Cambrian System in South China (Peng, 1999; Peng and Babcock, 2001). In this new scheme, the Cambrian is divided into four series, in ascending order, the Diandongian, Qiangdongian, Wulingian, and Hunanian. The first appearance of *Treptichnus pedum* marks the base of the Diandongian and the Precambrian–Cambrian boundary as defined by the stratotype at Fortune Head, Newfoundland (but see Gehling et al., 2001). The Diandongian is further divided into two stages, the lower Jinningian and the upper “Meishucunian”, with the first appearance of *Paragloborilus subglobosus* marking the base of the “Meishucunian”. The first appearance of trilobites defines the base of the Qiangdongian Series. This series

includes two stages, the Nangaoan and the Duyunian. It should be noted that Peng's definition of the "Meishucunian" differs from the traditional Meishucunian (Qian, 1977), hence the use of quotation marks. The Meishucunian Stage in the conventional sense includes the four SSF assemblages discussed above, roughly equivalent to the Jinningian plus the "Meishucunian" sensu Peng (1999). Both schemes are presented in Fig. 1.

2.2. Southern Anhui and correlation with eastern Yunnan

In southern Anhui and neighboring western Zhejiang and northern Jiangxi provinces, the Neoproterozoic Piyuncun Formation (siliceous dolostones) is overlain by the Cambrian Hetang Formation. Regionally, the Hetang Formation can be divided into four lithostratigraphic units—in ascending order, a phosphorite unit typically <1 m thick, a "stone coal" (flammable, organic-rich mudrock and shale) unit <50 m thick, a siliceous–carbonaceous shale unit <30 m thick, and a carbonaceous shale unit (with carbonate nodules) <100 m thick (Xue and Yu, 1979). Articulated sponges and millimeter-size orthothecid hyoliths were collected from the second lithostratigraphic unit, about 30 m above the base of the Hetang Formation, in a stone coal quarry near the village of Lantian (29°55'N, 118°05'E), Xiuning County, southern Anhui Province.

Correlation between the Lower Cambrian successions in southern Anhui and those in eastern Yunnan depends on SSFs, acritarchs, and trilobites from the Hetang Formation in the neighboring western Zhejiang province. This is justified because the Hetang Formation can be traced with confidence from southern Anhui to western Zhejiang (Xue and Yu, 1979). Key elements of the *Anabarites trisulcatus*–*Prothertzina anabarica* assemblage, including *A. trisulcatus* and *P. anabarica*, as well as other SSFs such as *Kaiyangites jianshanensis* and *Zhejiangorhabdion comptum*, have been recovered from basal phosphorite beds of the Hetang Formation in western Zhejiang (Zhao and Yue, 1987; Yue and He, 1989; He and Yu, 1992; Yue and Zhao, 1993), although these phosphorite beds sometimes are mapped as the uppermost Dengying Formation. These SSFs indicate that the sponge fossils from the stone coal unit cannot be older

than the *A. trisulcatus*–*P. anabarica* assemblage of the Meishucunian Stage. *Kaiyangites* has been reported from phosphorite beds of the lowermost Yangjiaping Formation in northwestern Hunan (Ding and Qian, 1988) and the lowermost Niutitang and uppermost Liuchapo formations in central Guizhou (Qian and Yin, 1984). These phosphorite beds are considered Meishucunian in age (Qian, 1999), but the exact range of *Kaiyangites* is unknown.

Carbonate nodules from the stone coal unit in western Zhejiang yield a unique SSF assemblage. Some elements in this assemblage have been identified as species of *Siphogonuchites* and *Lopochites* (He and Yu, 1992). If these SSFs are correctly identified, they suggest equivalency to the second SSF assemblage, the *Siphogonuchites triangularis*–*Paragloborilus subglobosus* assemblage. Qian (1999), however, questioned the identification of *Siphogonuchites* and *Lopochites* from the stone coal beds in western Zhejiang. Other SSFs such as *Jiangshanodus triangularis*, *Kijacus kijanicus*, *Hagionella cultrate*, and *Allonia tripodophora*, as well as bivalved arthropods (bradoriids), also occur in carbonate nodules of the stone coal beds (Yue and He, 1989; Yue and Zhao, 1993; Qian, 1999). The biostratigraphic significance of these small shelly fossils is not clear. Bradoriids, however, usually occur in Qiongzhusian or younger deposits in Yunnan, indicating that the stone coal beds may be Qiongzhusian.

Further upsection in the carbonaceous shale unit, trilobites such as *Hunanocephalus*, *Hupeiidiscus*, and *Hsuaspis* have been discovered in carbonate nodules (Li et al., 1990; He and Yu, 1992), suggesting a Qiongzhusian or early Canglangpuan age because these trilobites occur in Qiongzhusian to early Canglangpuan deposits in eastern Yunnan and eastern Guizhou (Zhou and Yuan, 1980; Steiner et al., 2001b). Taken together, SSFs and trilobites restrict the sponge-bearing stone coal beds to be no older than the Meishucunian and no younger than the Qiongzhusian Stage, equivalent to the Diandongian–early Qiandongian in Peng's chronostratigraphic system (Peng and Babcock, 2001). This is consistent with the fact that no trilobites have been recovered from the stone coal beds at Lantian.

Further stratigraphic constraints based on acritarchs and sponges can also be considered. First, abundant occurrence of *Micrhystridium*-like acri-

tarchs seems to coincide with the SSF *Anabarites trisulcatus*–*Protohertzina anabarica* assemblage on the Yangtze platform (Yin, 1995). Abundant occurrence of *Micrhystridium*-like acritarchs in the stone coal beds of the Hetang Formation therefore indicates a Meishucunian age (Xue and Yu, 1979; Yin, 1995). Second, an unusual type of pentact sponge spicule is found in the Hetang sponge *Sanshapentella dapingi*; similar although smaller pentacts co-occur with SSFs of the *A. trisulcatus*–*P. anabarica* assemblage in Hunan (Ding and Qian, 1988; Qian and Bengtson, 1989). Furthermore, pre-trilobite stone coal beds are distributed widely across the Yangtze platform in South China. Indeed, the Shiyantou Formation in eastern Yunnan, consisting of organic-rich siltstones, may be broadly correlated with the Hetang stone coal beds. If correct, the sponge-bearing Hetang stone coal beds may be older than the Qiongzhusian Chengjiang Biota that occurs in the trilobite-bearing Yu'an-shan Formation. However, these stratigraphic constraints are weak, as purely lithostratigraphic correlations may be misleading, and sponge spicules as biostratigraphic tools have not been independently tested. Furthermore, the identification of *Micrhystridium*-like acritarchs is problematic in many publications (see Moczydłowska, 1991, 1998, for discussion). Indeed, *Micrhystridium*-like acritarchs may have a longer range, from the Nemakit-Daldynian to the Atdabanian (Sergeev, 1989; Moczydłowska, 1991), than suggested by Yin (1995). In addition, a Meishucunian age is contradictory to the occurrence of bradoriids in the stone coal beds. Therefore, the stone coal beds can only be confidently constrained to be Meishucunian–Qiongzhusian in age.

2.3. Correlation with Siberia

More challenging is the correlation between Early Cambrian successions in South China and Siberia (Brasier et al., 1990; Landing, 1994; Zhuravlev, 1996; Qian et al., 2001; Jenkins et al., 2002). The difficulty lies in the strong provincialism of SSFs and facies dependence of archaeocyathans. Siberian SSF assemblages are markedly different from those in South China, making interregional correlation on the basis of SSFs a difficult exercise (Qian and Bengtson, 1989). For example, archae-

ocyathans first appeared in the pre-trilobite Tommotian in Siberia (Khomentovsky and Karlova, 1993), whereas their first appearance in the Qiongzhusian in South China postdates that of trilobites (Yuan et al., 2001). As a consequence, diverging opinions exist regarding the correlation between the Tommotian and the Meishucunian stages. Some think that the Tommotian is equivalent to the upper part of the Meishucunian (Brasier et al., 1990; Landing, 1994; Qian et al., 2001; Zhu et al., 2001). Others think that the Tommotian is largely missing in South China (Zhuravlev, 1996; Zhuravlev and Wood, 1996). Despite these uncertainties, opinion seems to converge on correlating the Meishucunian *Anabarites trisulcatus*–*Protohertzina anabarica* assemblage with either the entire Nemakit-Daldynian (Khomentovsky and Karlova, 1993; Landing, 1994; Geyer and Shergold, 2000) or only the *A. trisulcatus* Zone of the Nemakit-Daldynian Stage in Siberia (Brasier et al., 1990; Qian et al., 2001). Regardless, the sponge-bearing stone coal beds of the Hetang Formation overlie the *A. trisulcatus*–*P. anabarica* assemblage and thus can be no older than the Nemakit-Daldynian and probably no older than the Tommotian. The upper age limit for the stone coal beds depends on correlation between the trilobite-bearing Qiongzhusian and Atdabanian stages (Palmer, 1998). The exact correlation of trilobite zones between South China and Siberia is problematic, but most agree that the first appearance of the oldest Chinese trilobite *Parabadiella* in the Qiongzhusian Yu'an-shan Formation in eastern Yunnan (Zhang, 1987; Steiner et al., 2001b) cannot be much younger than Atdabanian (Palmer, 1998). Therefore, the age of the stone coal beds of the Hetang Formation is probably Tommotian or Atdabanian.

Carbon isotope chemostratigraphy is broadly consistent with these correlations. A prominent positive $\delta^{13}\text{C}$ excursion has been reported from the Dahai Member of the Zhujiqing Formation and its equivalents at multiple sections in South China (Brasier et al., 1990; Zhou et al., 1997). The Dahai positive is probably equivalent to the I (upper Nemakit-Daldynian) or the I' (lower Tommotian) positive excursion in Siberia (Brasier et al., 1994b; Knoll et al., 1995; Kouchinsky et al., 2001). Unfortunately, chemostratigraphic data from the Qiongzhusian and Canglang-

puan successions are not sufficient to allow a reliable correlation between South China and Siberia. Future chemostratigraphic research on the Lantian section may provide useful $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$ data for more precise correlation.

2.4. Correlation with Newfoundland

Still more challenging is the correlation between Lower Cambrian beds in South China and the chosen Neoproterozoic–Cambrian boundary GSSP at Fortune Head, southeastern Newfoundland (Landing, 1994). The first occurrence of *Treptichnus pedum* in the primarily siliciclastic Fortune Head section defines the Neoproterozoic–Cambrian boundary, although it has been recently discovered that the range of *T. pedum* extends a few meters below the designated boundary (Gehling et al., 2001). The base of the Nemakit–Daldynian and the Meishucunian is usually taken to approximate the Neoproterozoic–Cambrian boundary in carbonate successions (Narbonne et al., 1987; Brasier et al., 1994a; Landing, 1994; Rowland et al., 1998). This seems consistent with rare occurrences of *T. pedum* within the Meishucunian *Anabarites trisulcatus*–*Prothertzina anabarica* assemblage in eastern Yunnan (Zhu et al., 2001). Given the unknown (and presumably long) range of *T. pedum*, *A. trisulcatus*, and *P. anabarica* (Nowlan et al., 1985; Qian and Bengtson, 1989; Gehling et al., 2001), precise interfacies correlation cannot be achieved on the basis of scattered occurrences of these index fossils. Unfortunately, the siliciclastic nature of the Fortune Head stratotype does not allow an independent chemostratigraphic test of hypothesized interfacies correlations (Rozanov et al., 1997).

2.5. Numerical age

It can be concluded from the preceding discussion that the stone coal beds of the Hetang Formation were likely deposited during the Meishucunian–Qiongzhusian, or, in Siberian terminology, the Tommotian–Atdabanian stages. An ash bed from the (presumably Nemakit–Daldynian) *Anabarites trisulcatus*–*Prothertzina anabarica* assemblage of the lower Zhongyicun Member in eastern Yunnan gives an age of 538.2 ± 1.5 Ma (σ ; Jenkins et al., 2002). This age

can be regarded as a maximum age for the stone coal beds in southern Anhui.

The numerical age of the Tommotian Stage critically depends on the definition of the Nemakit–Daldynian–Tommotian boundary and inter-regional correlation (Rowland et al., 1998; Khomentovsky and Karlova, 2002). An ash bed (530.7 ± 0.9 Ma) in the lower Placentian Series in New Brunswick was interpreted as upper Nemakit–Daldynian (Isachsen et al., 1994). In northern Siberia, an ash bed (534.6 ± 0.5 Ma) in the Tyuser Formation was interpreted as lowest Tommotian (Bowring et al., 1993). These interpretations are contradictory and both ashes have later been reinterpreted as middle Tommotian (Vidal et al., 1995; Jenkins et al., 2002). It appears that the New Brunswick ash (530.7 ± 0.9 Ma) postdates and the Siberia ash (534.6 ± 0.5 Ma) predates the *Watsonella crosbyi* zone (Bowring et al., 1993; Jenkins et al., 2002). Because the stone coal beds of the Hetang Formation can be probably correlated with the black shales of the lower Shiyantuo Formation, which overlies the *Watsonella crosbyi* (= *Heraultipegma yunnanensis*) assemblage in the Dahai Member of the Zhujiqing Formation, the radiometric date of 534.6 ± 0.5 from Siberia can be taken as a maximum age of the stone coal beds. A Re–Os date of 542 ± 11 Ma from Lower Cambrian black shales in Hunan and Guizhou provinces in South China (Li et al., 2002), which are correlative to the stone coal beds in southern Anhui, is marginally consistent with our estimate.

The minimum age of the stone coal beds is constrained by the Atdabanian–Botomian boundary, approximately 520 Ma (Bowring and Erwin, 1998; Landing et al., 1998; Jenkins et al., 2002). The stone coal beds are therefore broadly constrained to be between 535 and 520 Ma, making the sponge fossils reported in this paper among the earliest known articulated sponges (see also Steiner et al., 1993).

3. Description of sponge fossils

All specimens described in this paper are from the stone coal bed of the Hetang Formation at Lantian ($29^{\circ}55'N$, $118^{\circ}05'E$), southern Anhui Province. Most articulated sponges are preserved as compressed body fossils. Siliceous spicules are typically replaced by

diagenetic pyrite. On the weathered outcrop, the pyrite is typically oxidized to form rusty limonite.

The illustrated sponge fossils are reposit at Nanjing Institute of Geology and Palaeontology under the catalog numbers NIGPAS-134519 to 134543.

Class Demospongea Sollas, 1875

Order Monaxoniida Sollas, 1883

Family Choiidae DeLaubenfels, 1955

Genus *Choia* Walcott, 1920

Type species.—*Choia carteri* Walcott, 1920, from the Middle Cambrian Burgess Shale in British Columbia.

Remarks.—The genus *Choia* is characterized as a disc-shaped sponge consisting of two types of radiating monaxonal spicules: fine monaxons thatched in a central disc and larger coronal monaxons that extend beyond the central disc. Species of *Choia* are differentiated by the radius of the central disc and the length of the coronal spicules (Rigby, 1986).

Choia utahensis Walcott, 1920

(Fig. 2)

Choia utahensis Walcott, 1920, p. 25, pl. 75, fig. 1; Rigby, 1978, p. 1331, pl. 2, fig. 2; Rigby, 1983, p. 252, fig. 5A,C.

Choia-like demosponge, Yuan et al., 2002, p. 364, fig. 3D.

Description.—Hemispherical demosponge that consists of a well-defined central disc and two types of monaxonal spicules, both radiating from the center of the central disc. The central semicircular disc is about 20 mm in radius and thatched with fine monaxons; they are typically 0.01 mm in diameter but their full length is difficult to determine because of they are densely matted in the central disc. Large coronal oxeas are 0.3–2 mm in maximum width and can extend 20–30 mm beyond the margin of the central disc.

Discussion.—Coronal spicules of *Choia utahensis* from the Middle Cambrian Marjum Limestone and Wheeler Shale in Utah are typically less than 0.5 mm in maximum diameter (Walcott, 1920; Rigby, 1978, 1983). The Hetang specimens have larger coronal oxeas but are otherwise similar to the North American specimens. The semicircular central disc of the Hetang specimens is perhaps a result of preservation; similarly preserved semicircular *Choia* is also known from Middle Cambrian in Utah (Rigby, 1983).

Rigby (1986) reconstructed *Choia carteri* as a conical sponge with its apex pointing upward. This is in contrast to Walcott's (1920) original interpretation in which *Choia* was envisioned as a conical sponge with the apex pointing downward. The Rigby reconstruction is hydrodynamically more stable, but such a sponge is less likely to have been preserved as a semicircular body fossil upon compression. The



Fig. 2. *Choia utahensis* Walcott, 1920. Fine spicules in the central disc are not discernible at this magnification. NIGPAS-134519. Specimen is about 100 mm in height.

semicircular specimen from the Hetang Formation is more consistent with Walcott's reconstruction.

Choia xiaolantianensis from the Lower Cambrian Chengjiang Biota is minimally described (Hou et al., 1999). Published photographs suggest that it is conspecific with either *Ch. utahensis* or the smaller *Ch. carteri* (Rigby, 1986).

Material.—Four specimens.

Choia? striata sp. nov.
(Fig. 3A–D)

Diagnosis.—A possible species of *Choia* with a poorly defined central disc and abundant, densely packed coronal oxeas. Coronal oxeas large (up to 2.5 mm in maximum width and 50–100 mm in length), speckled with subcircular patches of organic matter. Fine monaxons about 0.07–0.1 mm in diameter are distributed in the central disc area. Coronal oxeas and some fine monaxons bear longitudinal striae.

Description.—An incomplete, fan-shaped specimen about 110×240 mm in size. The poorly defined central disc is roughly 30–40 mm in radius. Numerous fine monaxons (0.07–0.1 mm in diameter and about 1–10 mm in length) occur in the central disc, but the central disc is not thatched. Coronal oxeas, 1.0–2.5 mm in maximum width and 50–100 mm in length, taper to pointed ends at both termini. Coronal oxeas are flattened in their middle part where the width is the greatest, and become cylindrical toward tapering termini. Subcircular patches (about 0.1 mm in diameter) of amber-colored organic matter are found on most coronal oxeas, but not in rock matrix. Striae occur in both types of spicules with a consistent spacing of 0.03–0.04 mm, but some spicules have no striae probably because of poor preservation.

Discussion.—This new species can be differentiated from all other *Choia* species (Walcott, 1920; Rigby, 1978, 1983, 1986) by its poorly defined central disc, large and striated coronal spicules, and organic speckles on the coronal spicules. These features depart from the original diagnosis of *Choia*; thus this species is placed in the genus *Choia* with uncertainty. Indeed, even the sponge affinity of this species can be questioned, but more specimens are needed for further study.

Etymology.—*Striatus*, Latin, referring to the striae on the large blade-like coronal oxeas.

Holotype.—NIGPAS-134520, Fig. 3A–D.

Material.—A single specimen.

Class Hexactinellida Schmidt, 1870

Subclass Amphidiscophora Schulze, 1887

Order Reticulosa Reid, 1958

Superfamily Protospongioidea Finks, 1960

Family Protospongiidae Hinde, 1887

Genus *Diagoniella* Rauff, 1894

Type species.—*Diagoniella coronata* (Dawson and Hinde, 1889) from Cambro-Silurian strata in Little Métis, Quebec.

Remarks.—The genus *Diagoniella* is characterized by its diagonally oriented stauracts. Stauracts in the genus *Protospongia* are more or less parallel to the principal axis of the sponge body. The goblet-shaped *Gabelia* consists mostly of regularly oriented hexacts rather than stauracts (Rigby and Murphy, 1983).

Diagoniella cyathiformis (Dawson and Hinde, 1889)

(Fig. 3E–F)

Diagoniella cyathiformis (Dawson and Hinde, 1889), p. 23; Rigby, 1978, p. 1336, pl. 1, fig. 2–3, pl. 2, fig. 1; Rigby, 1983, p. 255, fig. 6F–H.

Description.—Subconical to oval, thin-walled, protosponge with diagonally oriented stauracts. Sponge has a somewhat rounded base and wide osculum. Sponge body 25–90 mm in height and 15–45 mm in maximum width. Stauracts are regularly spaced 1.5–3 mm apart to form rhombic quadrules. Each quadrule appears to be formed by two (rather than four) first-order stauracts. First-order stauracts have ray diameters of 0.03–0.05 mm and ray lengths about 2.5 mm. Second-order stauracts occur in quadrules. No marginalia or prostalia are preserved. The Hetang specimens are closely similar to *Diagoniella cyathiformis* from the Middle Cambrian Wheeler Shale and Marjum Limestone (Rigby, 1978, 1983).

Material.—Three specimens.

Genus *Protospongia* Salter, 1864

Type species.—*Protospongia fenestrata* Salter, 1864, from the Cambrian of Wales, Great Britain.

Remarks.—*Protospongia* is a common sponge genus in the Cambrian. It can be distinguished from

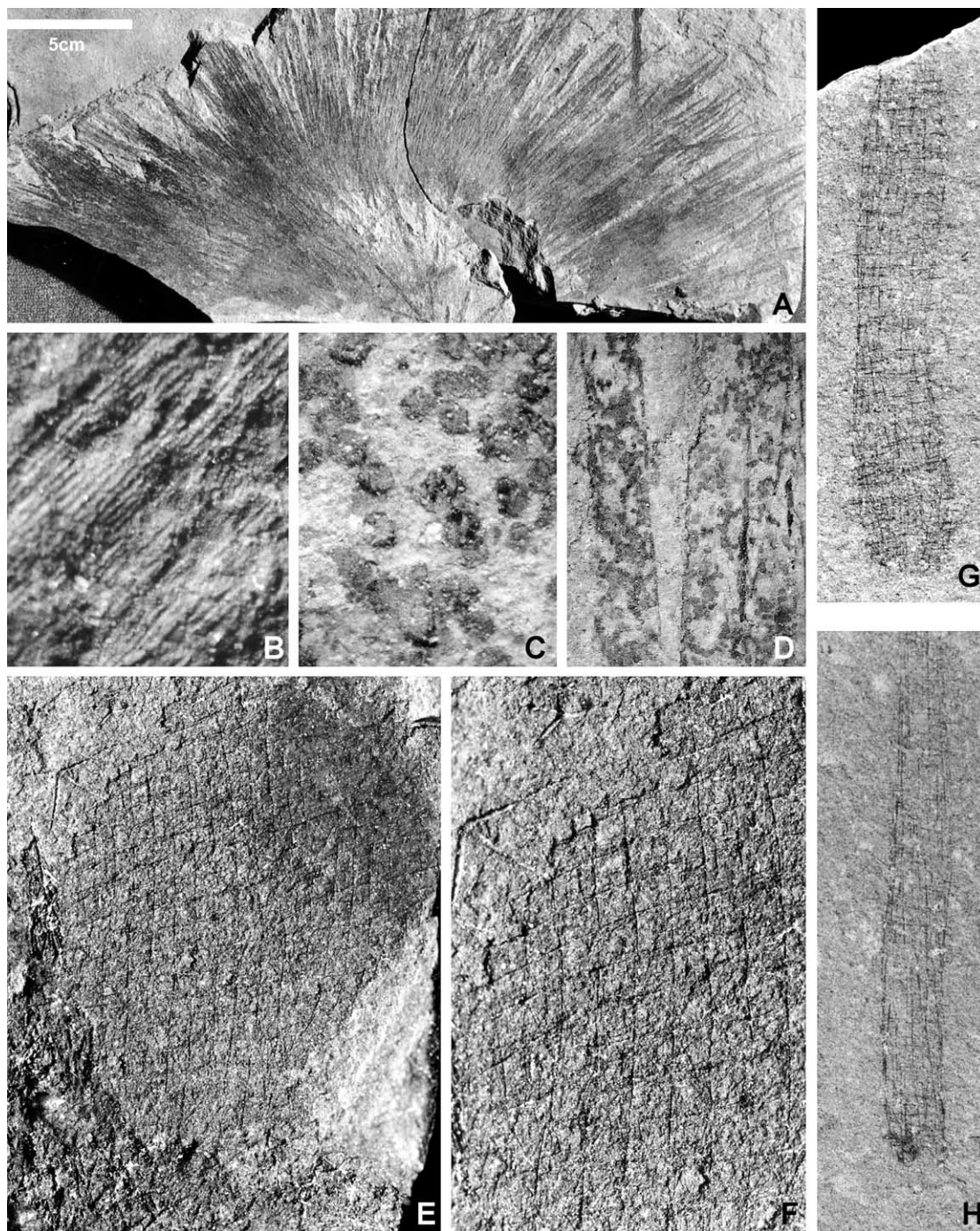


Fig. 3. (A)–(D) *Choia? striata* sp. nov. (B)–(D) are magnified views of coronal spicules to show striae (B), organic speckles (C), and general morphology of coronal spicules (D). NIGPAS-134520, holotype. (E)–(F) *Diagoniella cyathiformis* (Dawson and Hinde, 1889). (F) is close-up of the upper left part of (E). NIGPAS-134521. (G)–(H) *Protospongia gracilis* sp. nov. G, NIGPAS-134522, holotype. (H) NIGPAS-134523. Both specimens are incompletely preserved. Scale bar in (A) is 50 mm for (A); 0.5 mm for (B)–(C); 2.5 mm for (D); 10 mm for (E); 6 mm for (F); 8 mm for (G) and (H).

other genera (for example *Diagoniella*, *Gabelia*, *Phormosella*, *Cyathophycus*, *Plectoderma*) in this family by its thin-walled skeleton consisting of regularly arranged stauracts parallel to the principal body axis (Rigby, 1978, 1986; Rigby and Murphy, 1983).

Protospongia gracilis sp. nov.
(Fig. 3G–H)

Unnamed sponge, Yuan et al., 2002, p. 364, fig. 2F.

Diagnosis.—A thin-walled protosponge with slender tubular skeletal net. Skeletal net composed principally of stauracts, but with some hexacts. Stauracts with elongate vertical rays that are parallel to the long axis of the skeletal net. Quadrules are irregularly arranged. Spicular ranks are not apparent. Longitudinal rays of stauracts converge at oscular margin. Some horizontal rays protrude from sponge surface.

Description.—Sponges about 3–5 mm in diameter and 30–70 mm in height. Stauracts have ray diameters of approximately 0.03–0.05 mm and ray lengths of 2–3 mm (vertical rays) and 0.8 mm (horizontal rays). Quadrules vary in size, about 0.5–1 mm in maximum dimensions. Stauracts in the holotype (Fig. 3G) appear to be arranged such that the horizontal rays are somewhat bundled, but this may be a preservational artifact.

Discussion.—This new species differs from other Cambrian *Protospongia* species (Walcott, 1920; Rigby, 1986) in its slender tubular form, irregular quadrules, and vertically elongate stauracts. It is somewhat similar to the Silurian protosponge *Gabelia* (Rigby and Murphy, 1983; Rigby and Maher, 1995), but its slender form is distinct from the goblet-shaped sponge body of *Gabelia*. Furthermore, *Gabelia* is primarily composed of hexacts rather than stauracts.

Etymology.—*Gracilis*, Latin, referring to the slender tubular form of this new species.

Holotype.—NIGPAS-134522, Fig. 3G.

Material.—Three specimens.

Protospongia cf. *conica* Rigby and Harris, 1979 (Fig. 4A)

Protospongia conica Rigby and Harris, 1979, p. 974, pl. 1, fig. 1, pl. 2, fig. 1, 5, text-fig. 2, 3.

Description.—A single specimen with spindle-shaped skeletal net that is composed primarily of stauracts with some hexacts. Stauracts slightly elongate vertically. Rectangular quadrules occur between stauracts. Spicular ranks are not apparent. Longitudinal rays of stauracts converge at both ends of sponge body. Some stauract rays protrude from sponge surface.

The specimen is about 20 mm in height and 9 mm in width. Stauracts have ray diameters of approximately 0.03–0.05 mm and ray lengths of 1.2 mm (vertical rays) and 0.8 mm (horizontal rays). Quadrules vary in size, between 0.6 and 0.8 mm in maximum dimensions.

Discussion.—*Protospongia conica* was first described from the Silurian in northern British Columbia (Rigby and Harris, 1979). The specimen from the Hetang Formation resembles the Silurian specimens with its pointed base and somewhat irregularly arranged spicules. The Silurian specimens, however, are larger (up to 44 mm in height) and have ranked stauracts (0.04–0.1 mm in ray diameter and 0.4–1.0 mm in ray length). Their oscular end does not narrow as much as the Hetang specimen. Considering these differences and the Cambrian age of the Hetang specimen, it is possible that the Hetang specimen represents a new protosponge species. More specimens are needed to differentiate the Hetang and the Silurian populations. At present, we tentatively place the single specimen from the Hetang Formation in open nomenclature, *Protospongia* cf. *conica*.

Material.—A single specimen.

Genus *Gabelia* Rigby and Murphy, 1983

Type species.—*Gabelia pedunculus* Rigby and Murphy, 1983, from Devonian shales in the northern Roberts Mountains, Nevada.

Gabelia sp. indet.
(Fig. 4B–E)

Description.—A fragmented specimen with more or less regularly arranged hexacts. Putative stauracts may be present too. First-order hexacts have ray diameters of 0.16 mm and ray lengths of 3–5 mm. Smaller hexacts of several ranks divide, although unevenly, quadrules between larger spi-

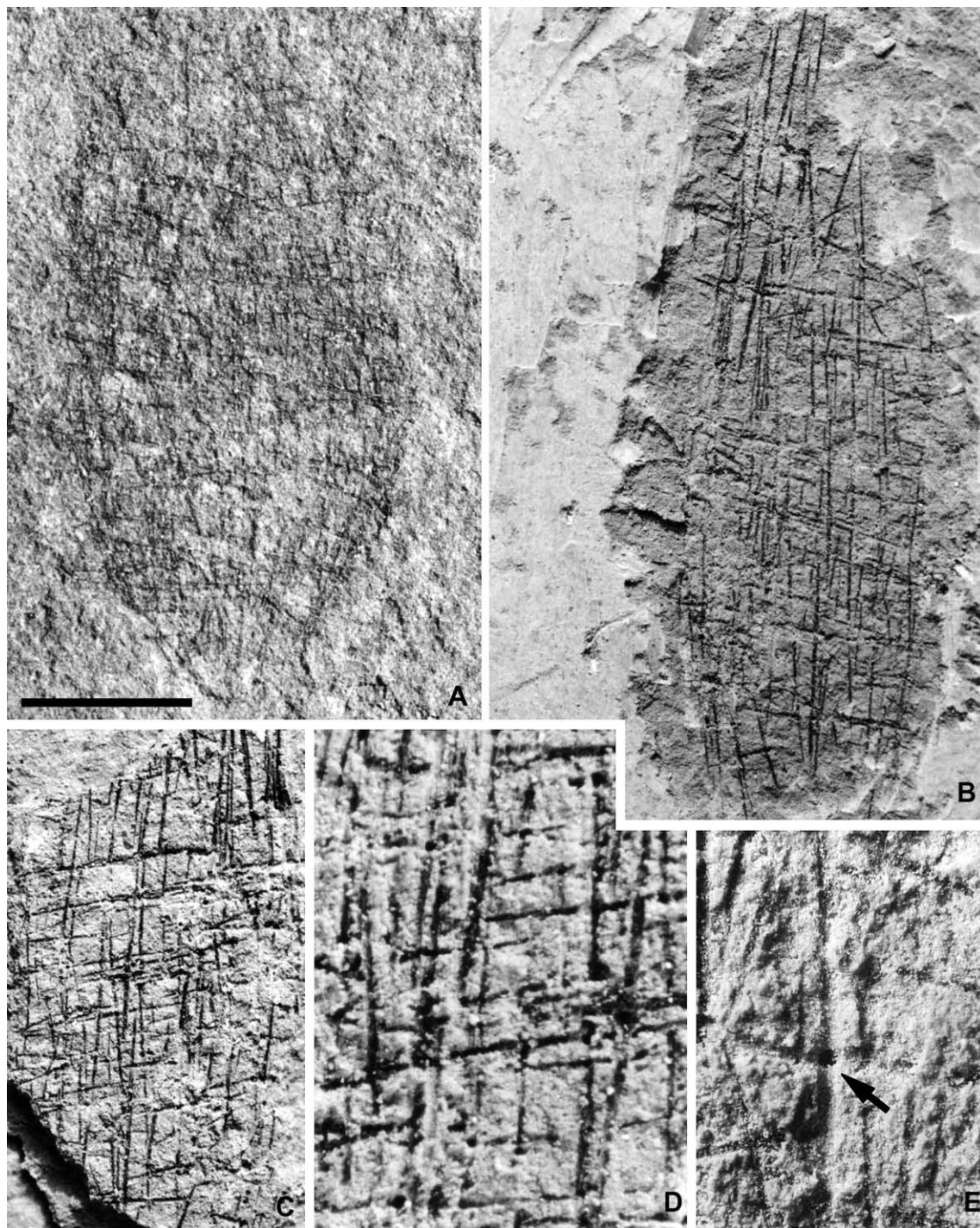


Fig. 4. (A) *Protospongia* cf. *conica* Rigby and Harris, 1979. NIGPAS-134524. (B)–(E) *Gabelia* sp. indet. (C) is counterpart of (B). (D) and (E) are close-ups of (B) and (C), respectively, to show molds of hexacts; two of the six rays are perpendicular to the bedding plane, making a hole (arrow) on the bedding plane. NIGPAS-134525. Scale bar in (A) is 5 mm for (A); 4 mm for (B); 5 mm for (C); 2 mm for (D); 1 mm for (E).

cules. Because of its incomplete preservation, identification at species level is impossible, but its skeleton composed primarily of hexacts places

this form in the genus *Gabelia* (Rigby and Murphy, 1983; Rigby et al., 1991; Rigby and Maher, 1995).

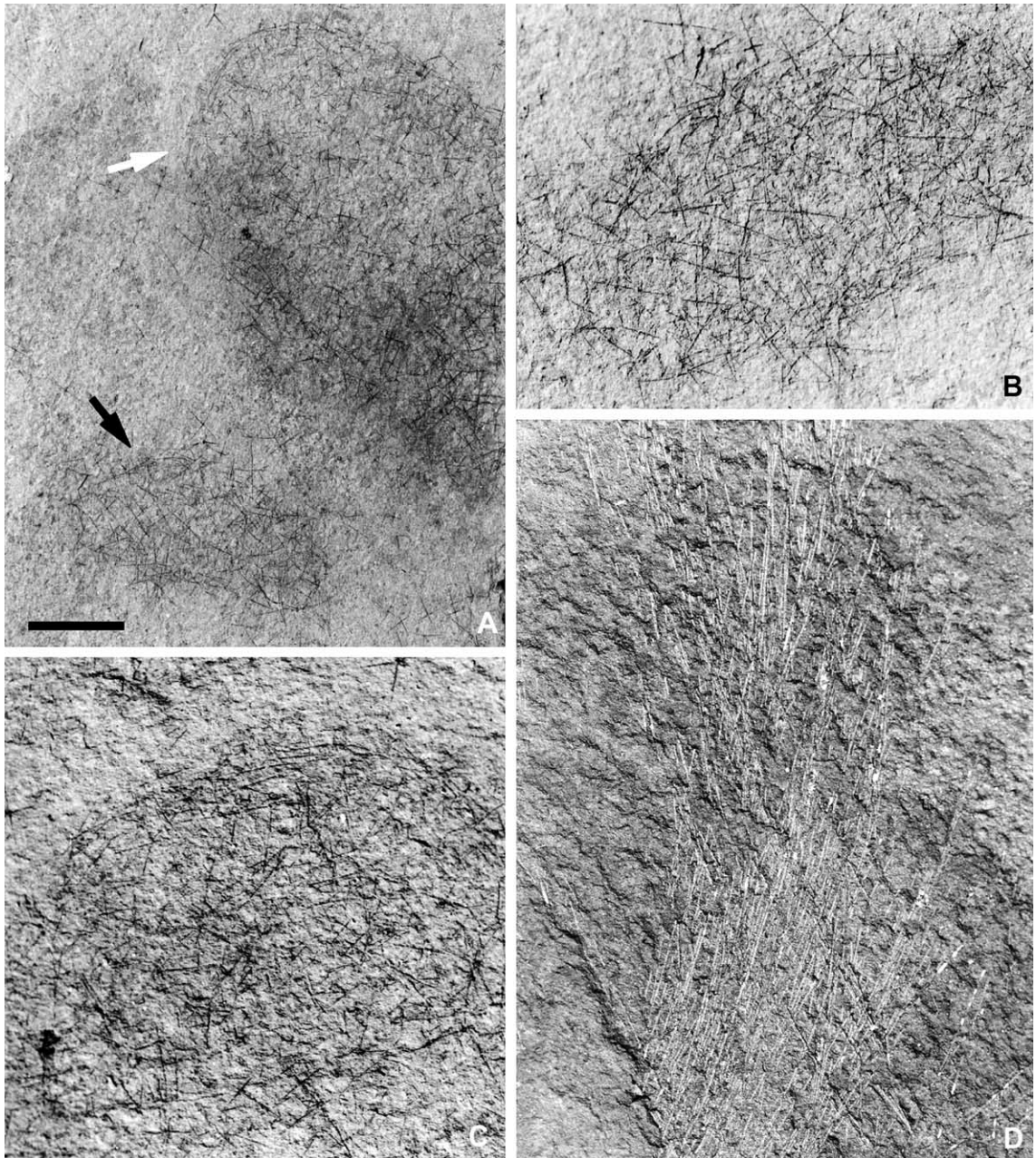


Fig. 5. (A)–(C) *Triticispongia diagonata* Mehl and Reitner in Steiner et al., 1993. (A) shows two specimens—one in the upper right, the other lower left. (B) is close-up view of the lower left specimen in (A) (black arrow). NIGPAS-134526. (C) is a close-up view of the upper right specimen in (A) (white arrow). NIGPAS-134527. (D) *Hyalosinica archaica* Mehl and Reitner in Steiner et al., 1993. NIGPAS-134544. Scale bar in (A) is 10 mm for (A); 4 mm for (B) and (C); 7 mm for (D).

Material.—A single specimen with part and counterpart.

Genus *Triticispongia* Mehl and Reitner in Steiner et al., 1993

Type species.—*Triticispongia diagonata* Mehl and Reitner in Steiner et al., 1993

Diagnosis.—This monospecific genus is diagnosed as “sponge body hardly exceeds 10 mm total size. Spicules are small triaxons, mainly stauracts with their paratangentialia in a diagonal arrangement” (Mehl and Reitner in Steiner et al., 1993).

Triticispongia diagonata Mehl and Reitner in Steiner et al., 1993
(Fig. 5A–C)

Triticispongia diagonata Mehl and Reitner in Steiner et al., 1993, p. 307, pl. 3, fig. 3; Rigby and Hou, 1995, p. 1011, fig. 4.1–4.2

Description.—Compressed sponge oval to subcircular. Two specimens measure 13×27 mm and 30×55 mm in size, respectively. Spiculation made mainly of stauracts that typically have a ray diameter about 0.03–0.05 mm and ray length about 3–5 mm. Second-order, shorter stauracts and hexacts (about 0.03–0.05 mm in ray diameter and 1–2 mm in ray length) are also present. Because of compression, quadrular spicule organization is not obvious.

Discussion.—Rigby and Hou (1995) observed marginalia and root tufts, as well as crude quadrules of at least three ranks, in *Triticispongia diagonata* from the Lower Cambrian Chengjiang Biota. These features are poorly preserved in the Hetang specimens and those from the coeval Niutitang Formation in northwestern Hunan (Steiner et al., 1993). Additionally, the Hetang specimens are larger than those from the Niutitang Formation in northwestern Hunan (Steiner et al., 1993) and the Chengjiang Biota in eastern Yunnan (Rigby and Hou, 1995), which are typically less than 10 mm in height.

Material.—Two specimens.

Superfamily Hintzespongioidea Finks, 1983

Family Hintzespongiidae Finks, 1983

Genus *Lantianospongia* gen. nov.

Type species.—*Lantianospongia palifera* gen. et sp. nov.

Diagnosis.—A genus of the Hintzespongiidae with ovoidal skeleton. Sponge walls thin and perforated by numerous, large, elliptical to circular parietal gaps. Skeletal net composed of irregularly oriented stauracts of several sizes. Basal part of sponge body reinforced by long, diagonally oriented, probably bundled monacts or diacts. Oscular margins with regularly spaced serrations and indentations. Long, bundled monact or diact supports each of the serrations; the bundled spicules fan out beneath the apex of serrations (Fig. 6E).

Discussion.—Several hexactinellids have parietal gaps in their skeletal nets. *Stephenospongia* Rigby, 1986, from the Middle Cambrian Burgess Shale, is more than 44 mm high and has elliptical parietal gaps 10–14 mm in maximum diameter. Its skeleton is made of hexactine-based spicules with uniform diameter (ca. 0.06 mm) but variable ray length (from less than 1 mm to more than 3 mm). Three other hexactinellid genera, *Ratcliffespongia* (Rigby, 1969), *Hintzespongia* (Rigby and Gutschick, 1976; Rigby, 1983), and *Valospongia* (Rigby, 1983), all from the Middle Cambrian Marjum Formation in western Utah, also bear parietal gaps in their skeletal nets. *Ratcliffespongia* (up to 70 mm high) has somewhat smaller parietal gaps (3–5 mm in maximum diameter) and loosely woven stauracts of several sizes (ray diameter between 0.02 and 0.06 mm, ray length between 0.5 and 3.5 mm). *Hintzespongia* (22–32 mm) has double-layered walls, with parietal gaps (0.5–0.7 mm in diameter) occurring on the inner wall, and stauracts of several sizes (ray diameter between 0.02 and 0.06 mm, ray length between 0.3 and 2 mm). Parietal gaps (or “mounds” in the terminology of Rigby, 1983) of two sizes (2 mm and 6–8 mm in diameter) occur in the endosomal net of *Valospongia* (193 mm high, 90 mm wide). *Valospongia* has several sizes of hexactine-based spicules, ranging from 0.3 mm to several centimeters in ray length and from 0.04 to 0.3 mm in ray diameter.

Lantianospongia shares some characters, such as the presence of parietal gaps and several sizes of stauracts, with the Middle Cambrian genera mentioned above, indicating close evolutionary relationships with them. It can be differentiated from those Middle Cambrian sponges, however, by its basal diagonal monacts/diacts and oscular supporting monacts/diacts as well as its serrated oscular margin.

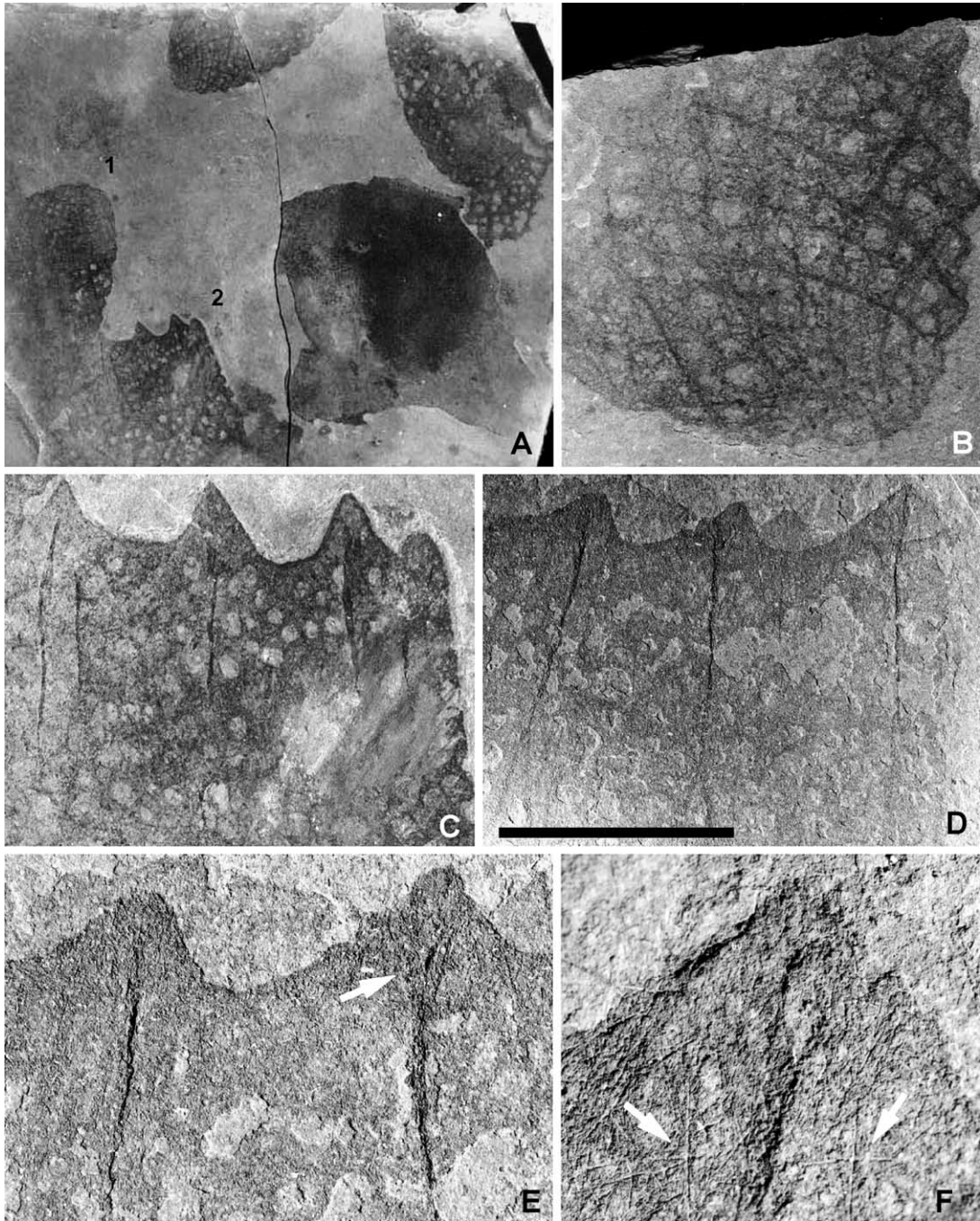


Fig. 6. *Lantianospongia palifera* gen. et sp. nov. (A) A slab with five incompletely preserved specimens. (B) Close-up view of the counterpart of specimen 1 in (A), showing diagonally arranged spicule bundles near the base of the sponge body. NIGPAS-134528. (C) Close-up view of specimen 2 in (A), showing serrated oscular margin, parietal gaps, and vertically oriented spicule bundles. Holotype, NIGPAS-134529. (D)–(F) Another specimen with serrated oscular margin and vertically oriented spicule bundles. NIGPAS-134530. (E) and (F) are closer views of serrated oscular margin. Bundled supporting spicules appear to fan out below the right serration in (E) (arrow). Notice stauracts in (F) (arrows). Scale bar in (D) is 300 mm for (A); 60 mm for (B); 80 mm for (C); 60 mm for (D); 30 mm for (E); 15 mm for (F).

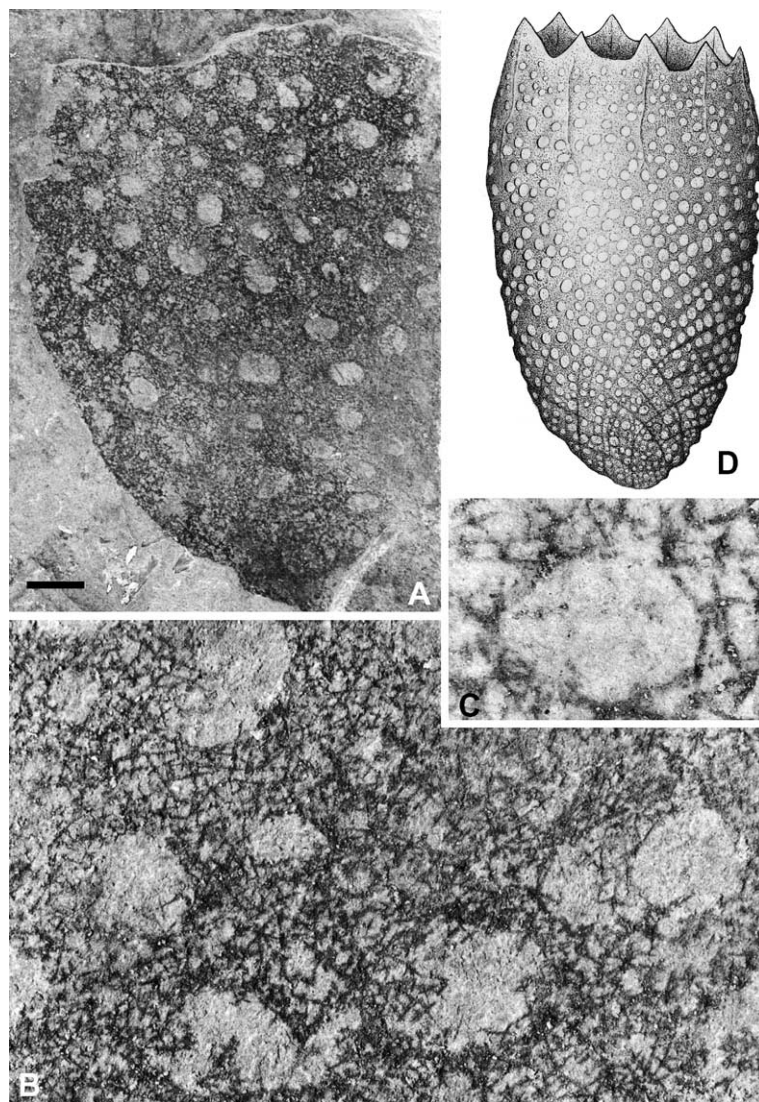


Fig. 7. *Lantianospongia palifera* gen. et sp. nov. (A)–(C) A specimen with parietal gaps of variable sizes. Neither serrated oscular margin nor bundled supporting monaxons are preserved, probably due to the fragmentary nature of this specimen. (B) and (C) are close-ups of (A), showing variable sizes of parietal gaps (B) and spicule arrangement around parietal gaps (C). NIGPAS-134531. (D) Conceptual reconstruction. Scale bar in (A) is 10 mm for (A); 2.5 mm for (B); 1.5 mm for (C).

Etymology.—The generic name refers to the locality (Lantian of southern Anhui Province, South China) where the type species *Lantianospongia palifera* was collected.

Lantianospongia palifera gen. et sp. nov.

(Figs. 6 and 7)

Unnamed sponge, Yuan et al., 2002, p. 364, fig. 3A–B.

Diagnosis.—Same as for genus.

Description.—Ovoidal skeletal net 100–300 mm high and 80–150 mm wide. Basal end rounded. Lower part consists of conspicuous, probably bundled monacts/diacts that are diagonally oriented. Oscular margin serrated. There are at least 4 serrations, separated by indentations, on oscular margin. Neighboring serration apices are about 50 mm apart. Serration apices stand about 15 mm above the base of indentations. Each

serration is subtended by a group of bundled monacts or diacts that extend downward about one-third of sponge height. Parietal gaps circular or elliptical, between 5 and 15 mm in maximum diameter (mean=8.4 mm, $N=20$) and spaced at 15–20 mm apart. They tend to be concentrated in the upper part of the sponge. Basal diagonal monacts/diacts and oscular supporting monacts/diacts can be 50–100 mm in length and are organized in bundles of 0.8–1.5 mm in diameter. Much smaller diacts, about 0.15 mm in diameter and 15 mm in length, occur sporadically on the skeletal net. Most stauracts in tracts have ray diameters of 0.04–0.08 mm and ray length of 0.5–1.5 mm. Larger stauracts (about 0.2–0.25 mm in ray diameter and 1.5–2 mm in ray length) sporadically occur in tracts. Most parietal gaps are void of spicules, but a few stauracts can occur in some parietal gaps although their density is much lower than in the tracts. This is probably because of the same sponge wall superimposed on itself as a result of compression.

Discussion.—Comparison with other parietal-gap-bearing hexactinellids has been given in discussion of the genus.

Etymology.—*Palus*, Latin, pole, referring to the supporting monacts/diacts beneath each serration on the oscular margin. *Fero*, Latin, carry.

Holotype.—NIGPAS-134529, Fig. 6C.

Material.—Eight specimens, five of which preserved on a single slab.

Class Hexactinellida Schmidt, 1870

Subclass, Order, Superfamily, and Family indet.

Genus *Sanshapentella* Mehl and Erdtmann, 1994

Type species.—*Sanshapentella dapingi* Mehl and Erdtmann, 1994

Remarks.—This monospecific genus is characterized by its dermal pentacts with their four paratangential rays bent toward the spongocoel. Stauracts and hexacts also occur in this genus. It is clearly a hexactinellid genus, but its systematic relationships with established hexactinellid orders and families (Finks, 1983) cannot be determined.

Isolated pentacts from the Lower Cambrian Yangjiaping Formation (probably coeval to the Hetang stone coal beds), identified as *Hunanospongia delicata* (Ding and Qian, 1988), are broadly similar to pentacts of *Sanshapentella dapingi*. Spicules in *H. delicata*,

however, are about an order of magnitude smaller than pentacts of *S. dapingi*. We agree with Mehl and Erdtmann (1994) that these two taxa should be separated, but *Hunanospongia* and *Sanshapentella* are probably closely related.

Sanshapentella dapingi Mehl and Erdtmann, 1994 (Fig. 8)

?*Hunanospongia* sp. Mehl and Reitner in Steiner et al., 1993, p. 4, fig. 2.

Sanshapentella dapingi Mehl and Erdtmann, 1994, p. 316, pl. 1, fig. 1–3; Yuan et al., 2002, p. 364, fig. 2A–D.

Description.—An incomplete specimen measures about 500 mm in height (Fig. 8A); a complete individual may have been over 1 m high. Skeletal net appears to consist of two layers of spicules. The dermal spicules are large pentacts (about 0.4 mm in ray diameter). Such pentacts have one short ray (about 1 mm in ray length) pointing outward and four longer paratangential rays (about 3–5 mm in ray length) sharply pointing toward the spongocoel. The short ray may be greatly reduced or absent. Sponge body has sharp protrusions where these large pentacts are present. The large pentacts are found mostly along the periphery and become rare toward the center of the compressed sponge body; this may have to do with the way the pentacts are compressed—laterally compressed pentacts are more easily recognized. Subjacent to the dermal pentacts are smaller (0.10–0.15 mm in ray diameter and 1–2 mm in ray length) stauracts and occasionally hexacts. A lateral bud is present in one specimen (Yuan et al., 2002, fig. 2D); dermal spiculation can be traced from the bud to the stem.

Discussion.—This species was established on the basis of fragmented specimens (Mehl and Erdtmann, 1994). Better-preserved specimens from the Hetang Formation indicate this is a very large, cylindrical sponge.

Material.—Eight specimens.

Genus *Hyalosinica* Mehl and Reitner in Steiner et al., 1993

Type species.—*Hyalosinica archaica* Mehl and Reitner in Steiner et al., 1993

Remarks.—The monospecific genus *Hyalosinica* was established on the basis of incomplete fragments

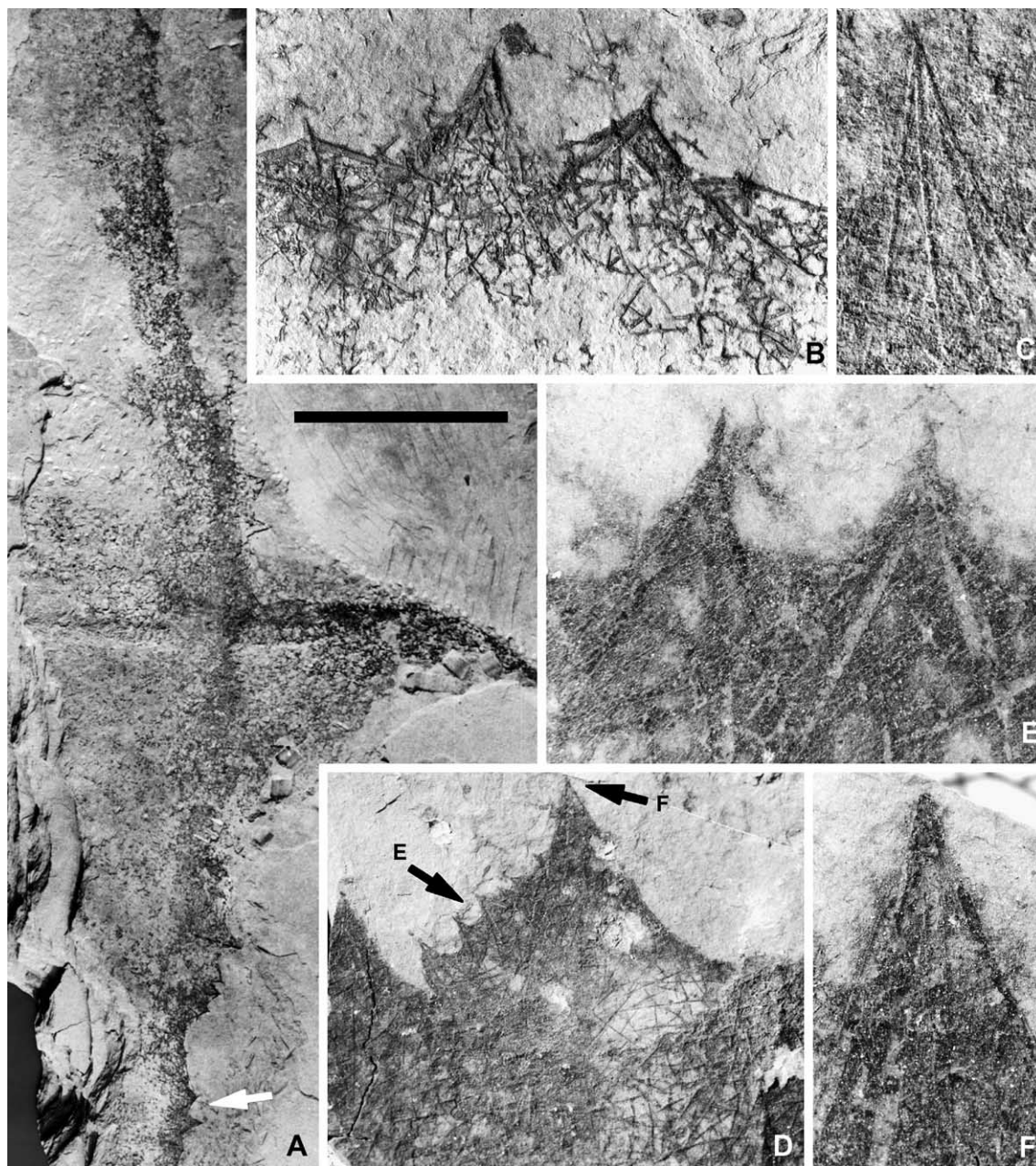


Fig. 8. *Sanshapentella dapingi* Mehl and Erdtmann, 1994. (A) Slab showing possibly two overlapping specimens. (B) Close-up of the counterpart of (A) (corresponding to arrowed area in A) showing details of pentact spicules. NIGPAS-134532. (C) An isolated pentact spicule. NIGPAS-134533. (D)–(F) A specimen showing marginally arranged pentacts. (E) and (F) are close-ups of (D) (arrows in D). NIGPAS-134534. Scale bar in (A) is 100 mm for (A); 10 mm for (B); 13 mm for (C); 24 mm for (D); 5 mm for (E) and (F).

interpreted as root tufts (Steiner et al., 1993). The root tufts are associated with triaxonal spicules and thus *Hyalosinica* was interpreted as a hexactinellid (Steiner

et al., 1993). Its systematic relationships with the established hexactinellid orders and families (Finks, 1983), however, are uncertain.

Hyalosinica archaica Mehl and Reitner in Steiner et al., 1993
(Fig. 5D)

Hyalosinica archaica Mehl and Reitner in Steiner et al., 1993, p. 305, pl. 4, fig. 1a–b.

Unnamed sponge, Yuan et al., 2002, p. 364, fig. 3G.

Discussion.—A single fragmented specimen is composed of twisted tufts of long (about 50 mm) monacts or diacts. Individual spicules are about 0.1–0.2 mm in maximum diameter. The Hetang specimen is similar to those described from the Niutitang black shales (equivalent to the Hetang stone coal beds) in northwestern Hunan Province (Steiner et al., 1993). *Hyalosinica archaica* is considered to be

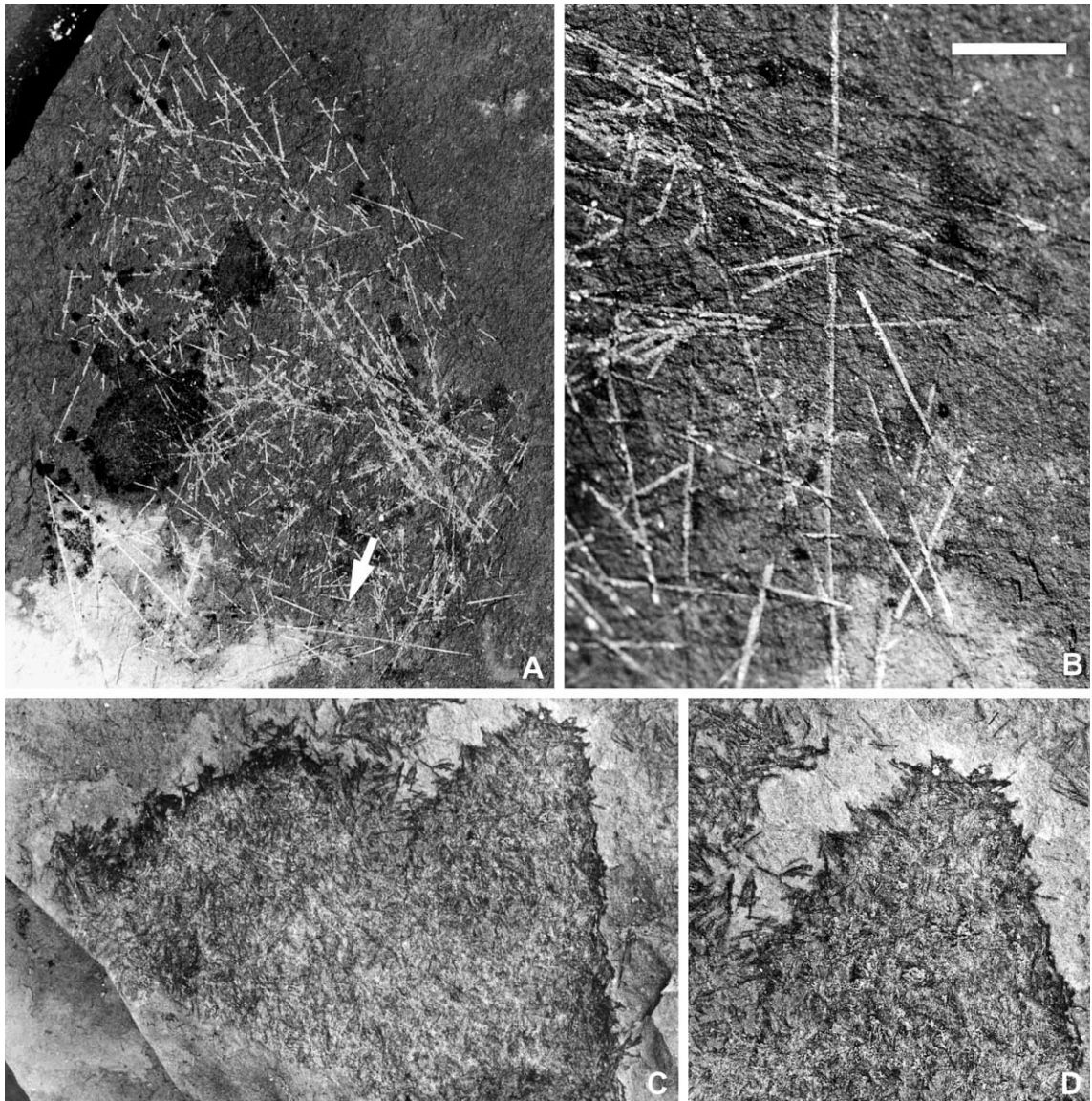


Fig. 9. (A)–(B) *Solactiniella plumata* Mehl and Reitner in Steiner et al., 1993. (B) is magnified view of (A) (arrow). NIGPAS-134535. (C)–(D) Undetermined form 1. (D) is magnified view of the upper left of (C). NIGPAS-134536. Scale bar in (B) is 20 mm for (A); 5.5 mm for (B); 10 mm for (C); 5 mm for (D).

a hexactinellid because some spicules appear to have four paratangential rays (Steiner et al., 1993). No paratangential rays have been observed in this specimen.

Material.—A single specimen.

Phylum Porifera

Class, Order, and Family undet.

Genus *Solactiniella* Mehl and Reitner in Steiner et al., 1993

Type species.—*Solactiniella plumata* Mehl and Reitner in Steiner et al., 1993

Solactiniella plumata Mehl and Reitner in Steiner et al., 1993

(Fig. 9A–B)

Solactiniella plumata Mehl and Reitner in Steiner et al., 1993, p. 309, pl. 2, fig. 1.

Unnamed sponge, Yuan et al., 2002, p. 364, fig. 3E.

Description.—Compressed sponge body 40×60 mm in size, consists principally of diacts that are up to 40 mm in length and 0.1–0.2 mm in diameter. These diacts seem to be tangentially oriented along sponge margin, but a few also

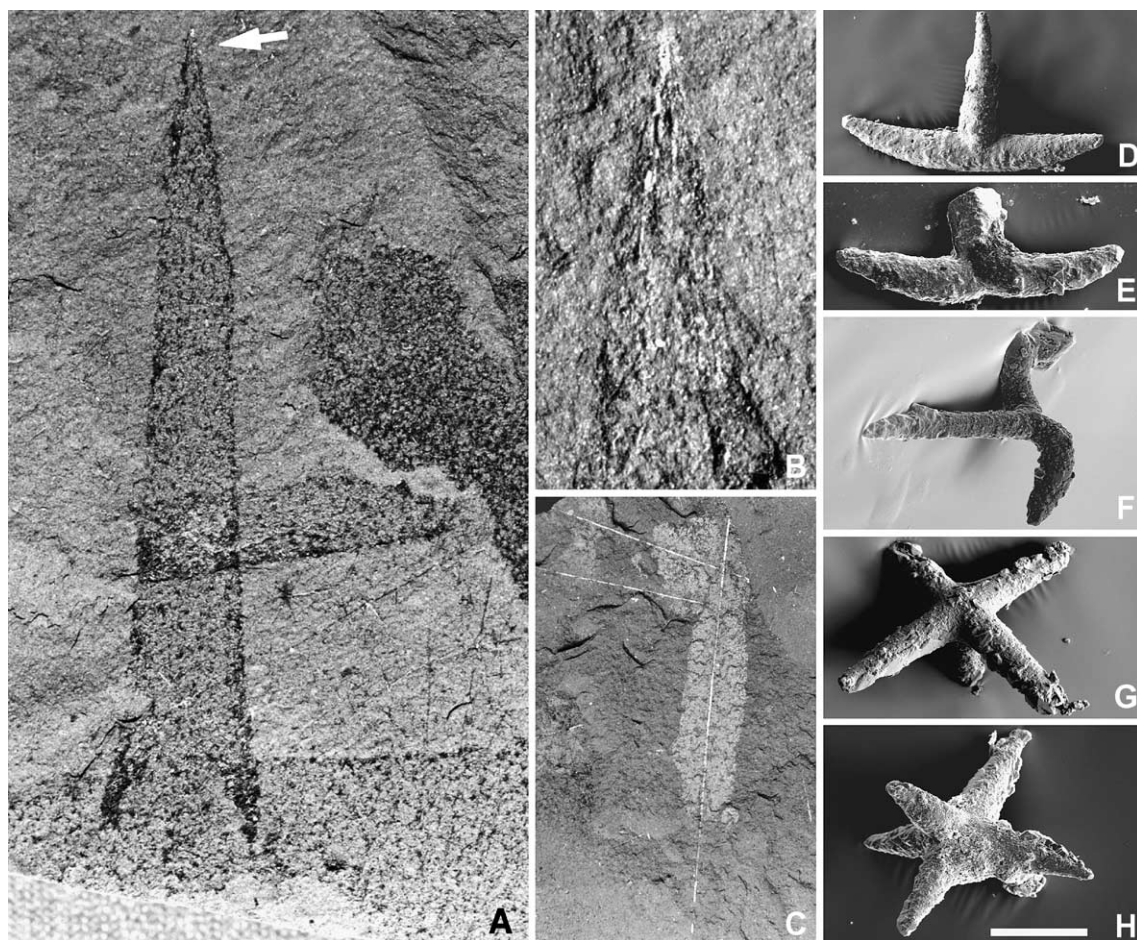


Fig. 10. (A)–(B) Undetermined form 2. (B) is magnified view of (A) (arrow), showing a single pentact spicule at the apex of the conical sponge. NIGPAS-134537. (C) Pyritized monaxonal spicules. NIGPAS-134538. (D)–(H) Triaxonal spicules including triacts (D–F), pentacts (G), and hexacts (H). (D) NIGPAS-134539. (E) NIGPAS-134540; (F) NIGPAS-134541; (G) NIGPAS-134542; (H) NIGPAS-134543. Scale bar in (H) is 10 mm for (A); 4 mm for (B); 2.5 mm for (C); 0.25 mm for (D); 0.1 mm for (E), (F), (H); 0.15 mm for (G).

protrude beyond the margin. Shorter (0.2–1 mm) and slightly thinner (0.05–0.1 mm in diameter) diacts are present preferentially in the center of compressed sponge body. Probable stauracts are rarely present, but these may be superimposed diacts—the poor preservation of the single available specimen does not allow an unambiguous determination of stauracts.

Discussion.—Because of the inability to identify unambiguous triaxonal spicules, we cannot be certain whether this sponge is a hexactinellid or demosponge. The Hetang specimen differs from those from the Niutitang population in its spicule orientation; the Niutitang specimens tend to have plumose arrangement of diacts (Steiner et al., 1993). At present, the Hetang specimen is tentatively described under *Solactiniella plumata*.

Material.—A single specimen.

Undetermined form 1
(Fig. 9C–D)

Unnamed sponge, Yuan et al., 2002, p. 364, fig. 3C.

Description.—Poorly preserved sponge consisting of short spicules, possibly oxeas. Shape of sponge body unknown because of the fragmentary nature of the only known specimen. The preserved fragment is about 50×70 mm in size. The specimen does not appear to be spicule mat, because it has clearly defined boundaries. Spicules about 3–4 mm in length and 0.1–0.5 mm in maximum diameter, and randomly oriented in the compressed specimen; they seem to be centrally dilated and distally tapering. It is difficult to determine whether the spicules are monaxons or modified triaxons with shortened paratantential rays.

Discussion.—Spicules of this Hetang sponge superficially resemble those of the Silurian hexactinellid *Divaricospongia dilata* (Rigby and Maher, 1995), but the latter is a cylindrical sponge with unambiguously hexact-based spicules. Because only one specimen is available, it is described here as an unnamed form.

Material.—A single specimen.

Undetermined form 2
(Fig. 10A–B)

Description.—A conical sponge body that appears to be a branch of a larger specimen. The branching, however, could be an artifact because of two specimens overlapping each other; if so, this conical sponge may have its apex attached to the substrate. The conical sponge body is about 15 mm in maximum width and gradually tapers toward a pointed apex along its 78 mm height. There appear to be spicule-like objects, about 0.5–1 mm in length and 0.1–0.2 mm in diameter, on the sponge body, but the nature of these spicules (possibly stauracts or hexacts) cannot be determined with confidence. There is one large pentact spicule, about 0.1 mm in ray diameter and 6 mm in ray length, present at the apex of this sponge (Fig. 10B). This pentact is similar to those in *Sanshapentella dapingi* and may indicate a close affinity with *S. dapingi*.

Material.—A single specimen.

Dispersed sponge spicules
(Fig. 10C–H)

Abundant dispersed siliceous and secondarily pyritized sponge spicules, including monacts, diacts, triacts, stauracts, pentacts, and hexacts, occur in the stone coal beds of the Hetang Formation. Some spicules can be as long as 15 cm (Fig. 10C). A thin (3–20 µm), organic or pyritic axial filament is present in the center of some spicules (Yuan et al., 2002, fig. 3K). Concentric layers of silica were deposited around the axial filaments (Yuan et al., 2002, fig. 3L), indicating incremental spicule growth similar to modern sponge spicules (Simpson, 1984).

4. Discussion

4.1. Sponge fossil record in the Neoproterozoic–Cambrian transition: are sponges part of the Cambrian radiation?

Animal phylogeny indicates that sponges (or stem-group sponges) must be among the earliest animals. Indeed, sponge biomarkers have been reported in lower Neoproterozoic rocks (McCaffrey et al., 1994), suggesting the presence of at least stem-group sponges. The fossil record of crown-group

sponges, however, occurs much later in the geologic history. Spicule-like objects have been reported from the late Neoproterozoic Doushantuo and Dengying formations in South China (Tang et al., 1978; Zhao et al., 1988; Steiner et al., 1993) and the uppermost Neoproterozoic rocks in Mongolia (Brasier et al., 1997); these are often interpreted as sponge spicules, but alternative interpretations (such as casts and molds of cyanobacterial filaments, volcanic shards, twined arsenopyrite crystals) have been proposed (Steiner et al., 1993; Zhou et al., 1998). Possible sponge body fossils occur in the late Neoproterozoic Doushantuo Formation (Li et al., 1998), but these have been questioned by Zhang et al. (1998) and Yin et al. (2001). The Ediacaran fossil *Palaeophragmodictya reticulata* has been interpreted as a hexactinellid by Gehling and Rigby (1996) but alternatively as a stem-group sponge by Mehl (1998). Therefore, Neoproterozoic sponge fossils are scanty and their phylogenetic interpretations are problematic. Currently, no unquestionable demosponges or calcareans are known from the Neoproterozoic.

Lower Cambrian sponge fossils are diverse and abundant. Dispersed hexactinellid spicules are common in Nemakit-Daldynian–Tommotian deposits (Ding and Qian, 1988; Rozanov and Zhuravlev, 1992; Qian, 1999). Archaeocythans, now accepted as a sponge group (Wood, 1999; Rowland, 2001), also appeared in the Tommotian. Demosponge spicules made their first appearance in the fossil record during the Lower Cambrian Atdabanian (Bengtson et al., 1990; Gruber and Reitner, 1991; Rozanov and Zhuravlev, 1992; Zhang and Pratt, 1994; Reitner and Mehl, 1995). Calcarean spicules, such as *Dodecaactinella cynodonota* and *Eiffelia araniformis* (Bengtson et al., 1990; Reitner and Mehl, 1995), also occur in Atdabanian deposits, although Steiner et al. (1993, p. 302) considered *D. cynodonota* demosponge spicules.

Articulated sponge fossils are not known from Nemakit-Daldynian deposits. The sponge body fossils described here, along with those from the Niutitang Formation in northwestern Hunan (Steiner et al., 1993; Mehl and Erdtmann, 1994; Table 1), are probably the earliest known sponge body fossils. They are broadly constrained to be Tommotian–Atdabanian in age. The Hetang and Niutitang assemblages contain both hexactinellids and demo-

Table 1

List of Hetang sponges described in this paper and their occurrences in the Niutitang Formation, Chengjiang Biota, and Middle Cambrian biotas (BMW, including the Burgess Shale, Marjum Limestone, and Wheeler Shale)

Taxa	Niutitang	Chengjiang	BMW
Demosponges			
<i>Choia utahensis</i>		Yes	
<i>Choia? striata</i> sp. nov.			
Hexactinellids			
<i>Diagoniella cyathiformis</i>			Yes
<i>Protospongia gracilis</i> sp. nov.			
<i>Protospongia</i> cf. <i>conica</i>			
<i>Gabelia</i> sp. indet.			
<i>Triticispongia diagonata</i>	Yes	Yes	
<i>Lantianospongia palifera</i>			
gen. et sp. nov.			
<i>Sanshapentella dapingi</i>	Yes		
<i>Hyalosinica archaica</i>	Yes		
Porifera incertae sedis			
<i>Solactiniella plumata</i>	Yes		
Undetermined form 1			
Undetermined form 2			

sponges, but articulated calcareans are lacking (Table 1). In the Atdabanian-age Chengjiang Biota, articulated hexactinellids and demosponges are diverse—at least 17 species have been described to date (Chen et al., 1989, 1990, 1996; Rigby and Hou, 1995; Hou et al., 1999). Interpretation of some Chengjiang sponge fossils (such as *Quadrolamiella*, Chen et al., 1990) as demosponges has been questioned (Reitner and Mehl, 1995; Mehl, 1998), but true demosponges such as *Choia*, *Choiella*, and *Allantospongia*, do occur in the Chengjiang Biota (Rigby and Hou, 1995; Chen et al., 1996; Hou et al., 1999). Articulated calcareans are absent from the Chengjiang Biota. The earliest known, articulated calcareans are probably the heteractinids (including *Eiffelia globosa* and *Canistrumella alternata*) from the Burgess Shale (Rigby, 1986).

The paleontological evidence collectively suggests that, although sponges may have diverged in the early Neoproterozoic, the hexactinellids did not evolve until near the Neoproterozoic–Cambrian transition, followed by archaeocythans in the Tommotian, and demosponges and calcareans no later than the Atdabanian. The paleontological data seem to suggest that much of the sponge diversification at the class-level occurred between the Nemakit-Dal-

dynian (or terminal Neoproterozoic if *Palaeophragmodictya reticulata* or Doushantuo spicules are accepted as hexactinellids) and the Atdabanian. Therefore, just like the bilaterians, sponges are part of the Cambrian Radiation, but only at the class level.

4.2. Stratigraphy meets phylogeny: are there significant gaps in the fossil record of early sponges?

The incompleteness of the early sponge fossil record has not attracted much attention among paleontologists. In the following paragraphs, we

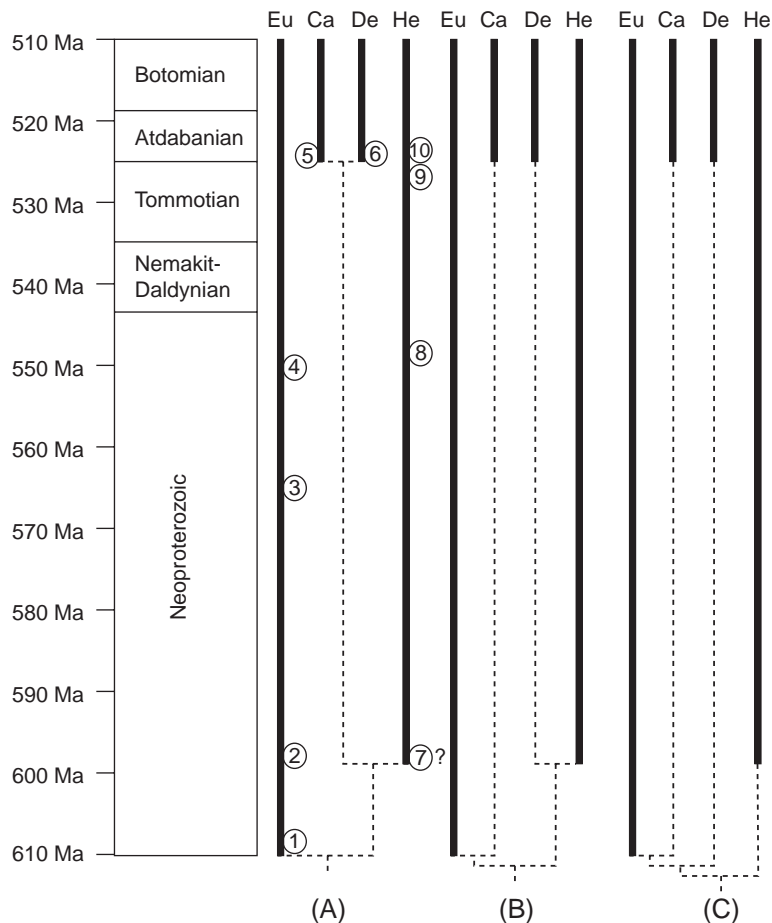


Fig. 11. Sponge phylogeny, fossil record, and minimal inferred gaps (MIGs). (A) Sponges are a monophyletic group and the demosponges and calcareans form the clade of Pinacophora (Reitner and Mehl, 1996). (B) Sponges are a paraphyletic group that represents an evolutionary grade, with calcareans being closely related to eumetazoans and hexactinellids and demosponges forming the clade of Silicea (Cavalier-Smith et al., 1996; Adams et al., 1999; Medina et al., 2001). (C) Hexactinellids, demosponges, and calcareans successively branch off from the metazoan tree (Kruse et al., 1998; Borchellini et al., 2001). Solid bars represent known fossil record, and dashed lines represent ghost lineages and gap extension. Early Cambrian time scale after Vidal et al., 1995, Bowring and Erwin (1998), Landing et al. (1998), and Jenkins et al. (2002). Paleontological and geochronological information: 1—Hofmann et al., 1990; 2—Xiao et al., 2000; Barfod et al., 2002; 3—Benus, 1988; 4—Fedonkin, 1994; Fedonkin and Waggoner, 1997; Martin et al., 2000; 5—Bengtson et al., 1990; Reitner and Mehl, 1995; 6—Chen et al., 1989; Bengtson et al., 1990; Gruber and Reitner, 1991; Rozanov and Zhuravlev, 1992; Zhang and Pratt, 1994; Reitner and Mehl, 1995; Rigby and Hou, 1995; Chen et al., 1996; Hou et al., 1999; this paper; 7—Tang et al., 1978; Zhao et al., 1988; but see Steiner et al., 1993; 8—Gehling and Rigby, 1996; 9—Ding and Qian, 1988; Rozanov and Zhuravlev, 1992; Qian, 1999; 10—Bengtson et al., 1990; Zhang and Pratt, 1994; Rigby and Hou, 1995, this paper. Demosponges and calcareans reported from the Doushantuo Formation by Li et al. (1998) are questioned by Zhang et al. (1998). Eu: eumetazoans; Ca: calcareans; De: demosponges; He: hexactinellids.

discuss the sponge fossil record in the context of sponge phylogeny and argue that, although sponges are part of the Cambrian Radiation, there are significant gaps in the fossil record of early sponges, particularly the calcareans and demosponges.

On the basis of morphological data, the Porifera has been traditionally treated both as a monophyletic clade and as the sister group of eumetazoans (e.g., [Reitner and Mehl, 1996](#)). Within the monophyletic Porifera, the three sponge classes (Hexactinellida, Demospongea, and Calcareia) are each monophyletic, and the cellular demosponges and calcareans form a monophyletic group, the Pinacophora, to the exclusion of the syncytial hexactinellids ([Reitner and Mehl, 1996](#); [Fig. 11A](#)). In recent years, there has been increasing molecular evidence suggesting that sponges are a paraphyletic group, with calcareans being more closely related to eumetazoans than to hexactinellids or demosponges ([Cavalier-Smith et al., 1996](#); [Collins, 1998](#); [Kruse et al., 1998](#); [Adams et al., 1999](#); [Borchiellini et al., 2001](#); [Medina et al., 2001](#)). The Porifera can be considered as an evolutionary grade rather than a phylogenetic clade. As such, some morphological features that are traditionally used to unite the three living sponge classes into a monophyletic phylum may be either plesiomorphic or convergent. A few molecular phylogenies further support a grouping of the two siliceous classes, demosponges and hexactinellids, to form the monophyletic Silicea ([Cavalier-Smith et al., 1996](#); [Adams et al., 1999](#); [Medina et al., 2001](#); [Fig. 11B](#)). The fact that hexactinellids and demosponges are the only major metazoan groups secreting a large amount of SiO_2 in biomineralization ([Bengtson and Conway Morris, 1992](#)) adds additional support to the Silicea hypothesis. A third alternative, in which the hexactinellids, demosponges, and calcareans successively branch off from the metazoan tree ([Fig. 11C](#)), cannot be rejected with confidence ([Kruse et al., 1998](#); [Borchiellini et al., 2001](#)).

Eumetazoans existed at least 550 Ma ([Fedonkin, 1994](#); [Fedonkin and Waggoner, 1997](#); [Martin et al., 2000](#)) and most likely earlier. Probable stem group cnidarians have been described from the ca. 600 Ma Doushantuo Formation and earlier deposits ([Hofmann et al., 1990](#); [Xiao et al., 2000](#); [Barfod et al., 2002](#)). Accepting each of the three sponge classes as a monophyletic clade ([Adams et al., 1999](#); [Borchiellini](#)

[et al., 2001](#)), it becomes apparent that significant gaps exist in the sponge fossil record, particularly the demosponges and calcareans. Allowing the uncertainties of sponge phylogeny and the earliest known eumetazoans, the minimum implied gaps (MIGs; [Benton and Storrs, 1996](#)) range from 50 to 180 Ma ([Fig. 12](#)). This implies that much of the early sponge history is missing from or remains to be discovered in the geological record. The sponge fossil record across the Neoproterozoic–Cambrian boundary should be carefully considered in future paleontological work, not only because early sponges are a key to understand early animal evolution ([Müller, 2001](#)) but also because sponges were important ecological players in epifaunal communities during the Neoproterozoic–Cambrian transition ([Yuan et al., 2002](#)).

The stratigraphic pattern of sponges, as currently observed, may be taken to favor the {eumetazoans+[hexactinellids+(demosponges+calcareans)]} topology ([Reitner and Mehl, 1996](#); [Fig. 11A](#)). This topology requires fewer sponge MIGs than the other two topologies, if eumetazoans diverged ca. 560 Ma or earlier. If eumetazoans diverged later, the phylogeny illustrated in [Fig. 11C](#) is favored by the stratigraphic data. Inclusion of stratigraphic data in phylogenetic

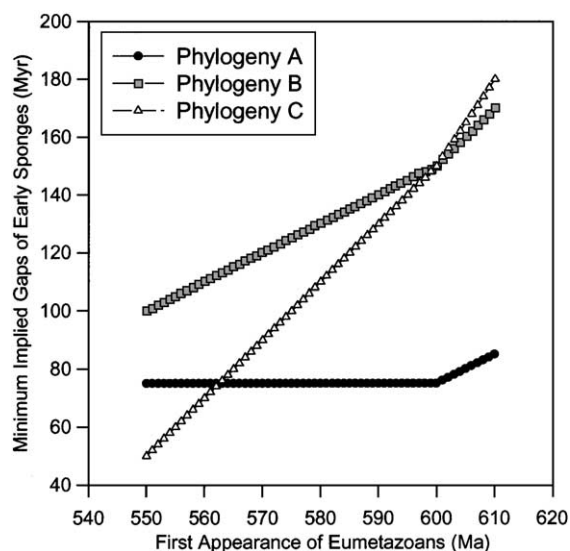


Fig. 12. Minimum implied gaps (MIGs, calculated according to [Benton and Storrs, 1996](#)) of the sponge fossil record assuming the three phylogenies illustrated in [Fig. 11](#) and the first appearance of eumetazoans between 550 and 600 Ma. MIGs of the early sponge fossil record ranges from 50 to 180 Ma.

reconstruction and optimization, however, is controversial (Smith, 2000). Until the completeness of the sponge fossil record is fully investigated and molecular, morphological, and paleontological data converge to a consensus, the current debate about Porifera, Pinacophora, and Silicea monophyly is likely to continue.

5. Conclusions

Both demosponges and hexactinellids, but no calcareans, occur in the Hetang assemblage. Eleven articulated sponge species (including three new taxa) and two undetermined forms are present in this assemblage. These sponge fossils are Meishucunian–Qiongzhusian in age. Paleontological evidence allows us to correlate Meishucunian–Qiongzhusian deposits in South China with Nemakit–Daldynian–Atdabanian deposits in Siberia. Radiometric dates from eastern Yunnan, Siberia, and Avalonia constrain the sponge fossils to be between ca. 535 and 520 Ma.

The Hetang and other sponge fossils suggest that hexactinellids evolved no later than the Nemakit–Daldynian–Tommotian and probably did so in the Neoproterozoic. Demosponges and calcareans evolved no later than the Atdabanian. The occurrence of eumetazoans at 550 Ma and probably 600 Ma implies substantial gaps in the fossil record of early sponges. The minimum implied gaps (MIGs) are particularly evident if the sponges are a paraphyletic group and the calcareans are a sister group of the eumetazoans, a topology that is supported by current molecular data.

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