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The earliest reef-building anthaspidellid sponge *Rankenella zhangxianensis* n. sp. from the Zhangxia Formation (Cambrian Series 3), Shandong Province, China

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Abstract.—This study reports the earliest known reef-building anthaspidellid sponge, *Rankenella zhangxianensis* n. sp., from the Cambrian Series 3 (late Stage 5–early Guzhangian) deposit of the Zhangxia Formation, Shandong Province, China. *Rankenella zhangxianensis* mostly occurs within *Epiphyton-Rankenella-Cambroctoconus* reefs, with minor occurrence from inter-reef grainstone. The species has anthaspidellid-type regular ladderlike spicule networks consisting of dendroclones and trabs, and is characterized by trabs parallel/subparallel to the gastral surface that diverge and meet the dermal surface, which is typical of the genus. Compared to *R. mors* and *R. hamdii*, reported from the late Cambrian Series 2–late Cambrian Series 3 of Australia and the late Cambrian Series 3–early Furongian of Iran, respectively, *R. zhangxianensis* is characterized by a relatively thicker wall, high angle (~90°) between dermal surfaces and intersecting trabs, and minor occurrence of differentiated canals. On the other hand, *R. zhangxianensis* mainly shows obconical shape, which is far less diverse than the other two species showing conicocylindrical, digitate, explanate, or bowl shapes. These Cambrian Series 3 reefs from China are the ancestors of the Furongian anthaspidellid-microbial reefs and the Early Ordovician anthaspidellid-microbial reefs that flourished worldwide. They represent the resurgence of reef-building metazoans after the extinction of archaeocyaths at the end of Cambrian Series 2.

Introduction

Metazoan reef-builders began to occur in the late Proterozoic (Grotzinger et al., 2000) and flourished throughout the Phanerozoic (James and Wood, 2010). The Cambrian–Ordovician was a transitional period in terms of reef evolution between the Proterozoic and Phanerozoic, containing various metazoan-microbial reefs that fluctuated throughout the period. Archaeocyaths, now considered as a separate class under phylum Porifera (Rowland, 2001; Debrenne et al., 2012), mainly constructed reefs during the early Cambrian (Terreneuvian and Series 2). They required the assistance of microbes to construct reef (Rowland and Shapiro, 2002), although some archaeocyaths could form reef frameworks by themselves (Riding and Zhuravlev, 1995). After the major decline of archaeocyaths at the end of Cambrian Series 2, it has been generally suggested that microbialites thrived and formed reefs during the Cambrian Series 3–Furongian. This period was considered to be the longest Phanerozoic metazoan "reef gap" (Rowland and Shapiro, 2002; Kiessling, 2009).

Reef-building metazoans (mainly anthaspidellid sponges with some *Calathium*, corals, stromatoporoids, bryozoans, and pelmatozoans) generally resurged during the Early Ordovician (Cañas and Carrera, 1993; Rowland and Shapiro, 2002; Webby, 2002; Kwon et al., 2003; Adachi et al., 2009, 2011; Choh et al., 2013; Hong et al., 2014; Li et al., 2014). Similar to the archaeocyath-microbial reefs of the early Cambrian, the Early Ordovician reef-building metazoans also required microbes for reef building (Adachi et al., 2011), although recent studies suggest that some anthaspidellid sponges, *Calathium*, bryozoans, and pelmatozoans could have formed frameworks by themselves (Adachi et al., 2011; Li et al., 2014). The metazoan-microbial reefs were eventually replaced by metazoan-dominated reefs during the Middle–Late Ordovician (Webby, 2002).

Recent discoveries of reef-building metazoans shed light on the Cambrian Series 3–Furongian "metazoan reef gap" (Fig. 1) (Hamdi et al., 1995; Mrozek et al., 2003; Dattilo et al., 2004; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Hong et al., 2012; Kruse and Reitner, 2014; Lee et al., 2014a). Among them, anthaspidellid sponges, which appeared in the late Cambrian Series 2 (Kruse, 1983, 1996) and diversified greatly during the Early Ordovician (Carrera and Rigby, 2004), occupied a major portion among the Cambrian Series 3–Furongian metazoan reef-builders (Fig. 1). In this study, we present a new reef-building anthaspidellid sponge *Rankenella zhangxianensis* n. sp. from the middle Cambrian Series 3 (late Stage 5–early Guzhangian) deposits of the eastern North China Platform, which is the oldest example of a reef-building anthaspidellid sponge. The material was discovered by Woo (2009), but no detailed paleontological or sedimentological study

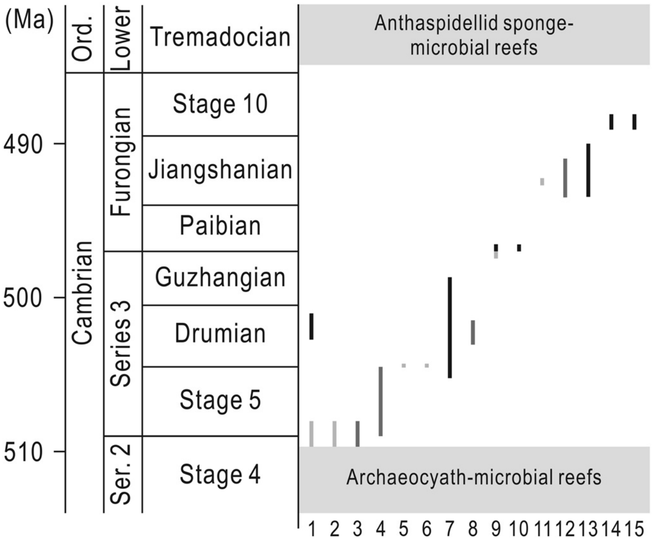

Figure 1. Occurrence of reef-building sponges and non-reef-building anthaspidellid sponges during the Cambrian Series 3–Furongian. Light gray lines: non-reef-building anthaspidellid sponges; dark gray lines: metazoan-microbial reefs not constructed by anthaspidellid sponges; black lines: reefs constructed by anthaspidellid sponges. (**1**) *Rankenella mors*, Tindall Limestone (Daly Basin) and Thorntonia Limestone (southern Georgina Basin), and *Angulocellularia-Taninia-R. mors* reef, Ranken Limestone (Undilla Sub-Basin, Georgina Basin), Australia (Kruse, 1983, 1996; Kruse and Reitner, 2014). (**2**) Unidentified anthaspidellid sponge, La Laza Formation (San Juan), Argentina (Beresi and Rigby, 1994). (**3**) *Kordephyton-Jawnya gurumal-Wagima galbanyin* reef, Tindall Limestone, Daly Basin, Australia (Kruse, 1996; Kruse and Reitner, 2014). (**4**) *Orlinocyathus-Epiphyton* reef, Dedebulak Formation, Kyrgyzstan (Vologdin, 1962). (**5**) *Fieldospongia*, Burgess Shale Formation, British Columbia, Canada (Rigby, 1986). (**6**) *Capsospongia*, Burgess Shale Formation, British Columbia, Canada (Rigby, 1986). (**7**) *Epiphyton-Rankenella zhangxianensis-Cambroctoconus orientalis* reef, Zhangxia Formation, Shandong Province, China (Woo, 2009; Park et al., 2011; this study). (**8**) Siliceous sponge-*Epiphyton* reef, Daegi Formation, Taebaeksan Basin, Korea (Hong et al., 2012). (**9**) *Rankenella hamdii* and *R. hamdii-Girvanella* reef, Mila Formation, Iran (Hamdi et al., 1995; Kruse and Zhuravlev, 2008). (**10**) *Gallatinospongia conica*-dendrolite reef, Bonanza King Formation, Nevada and California, USA (Shapiro and Rigby, 2004). (**11**) *Gallatinospongia conica*, Gallatin Formation, Wyoming, USA (Okulitch and Bell, 1955). (**12**) Siliceous sponge-microbial reef, Chaomidian Formation, Shandong Province, China (Lee et al., 2014a). (**13**) *Wilbernicyathus donegani-Girvanella-Tarthinia* reef, Wilberns Formation, Texas, USA (Johns et al., 2007). (**14**) *Wilbernicyathus donegani-Girvanella-Tarthinia* reef, Dotsero Formation, Colorado, USA (Johns et al., 2007). (**15**) Anthaspidellid sponge-microbial reef, Desert Valley Formation, Nevada, USA (Mrozek et al., 2003; Dattilo et al., 2004).

has been performed yet. This study contributes to an understanding of the recovery of reef-building metazoans after the end-Cambrian Series 2 extinction and diversification of early anthaspidellid sponges within reefs.

Geological setting

The North China Platform, an extensive epeiric platform, formed on a stable craton of Sino-Korean Block (Meng et al., 1997). The block was located near or at the margin of Gondwana during the early Paleozoic (McKenzie et al., 2011). Deposition on the North China Platform initiated during the Cambrian Series 2 and lasted until the Middle Ordovician (Meng et al., 1997; Kwon et al., 2006). Shandong Province, China, was located in the

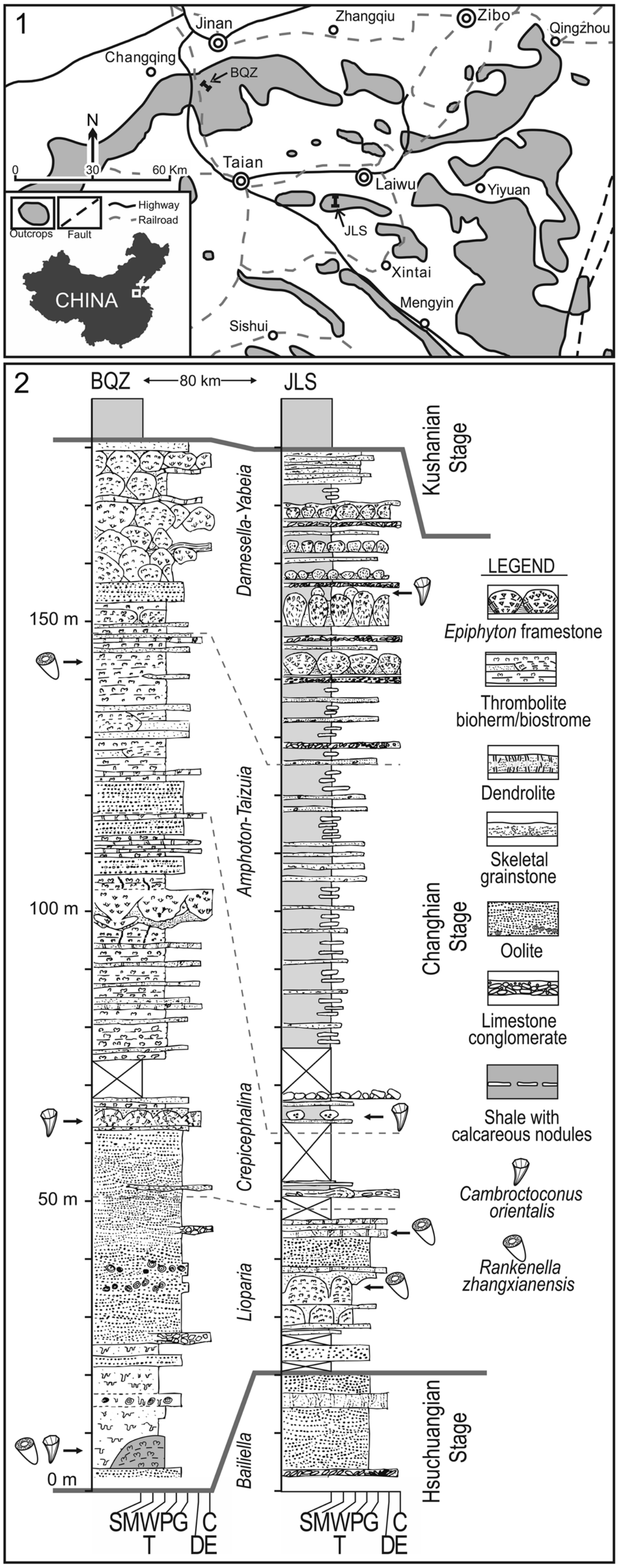

Figure 2. Geological setting and stratigraphy. (**1**) Location map of the outcrops. BQZ: Beiquanzi section (36°28'47"N, 116°55'28"E), JLS: Jiulongshan section (36°04'48"N, 117°44'51"E). (**2**) Detailed sedimentological log of the Zhangxia Formation in Beiquanzi (BQZ) and Jiulongshan (JLS) sections. Samples in this study are from the shaded interval in the basal part of BQZ section. S = Shale, M = Lime mudstone, W = Wackestone, P = Packstone, G = Grainstone, C = Conglomerate, T = Thrombolite, D = Dendrolite, E = *Epiphyton* framestone.

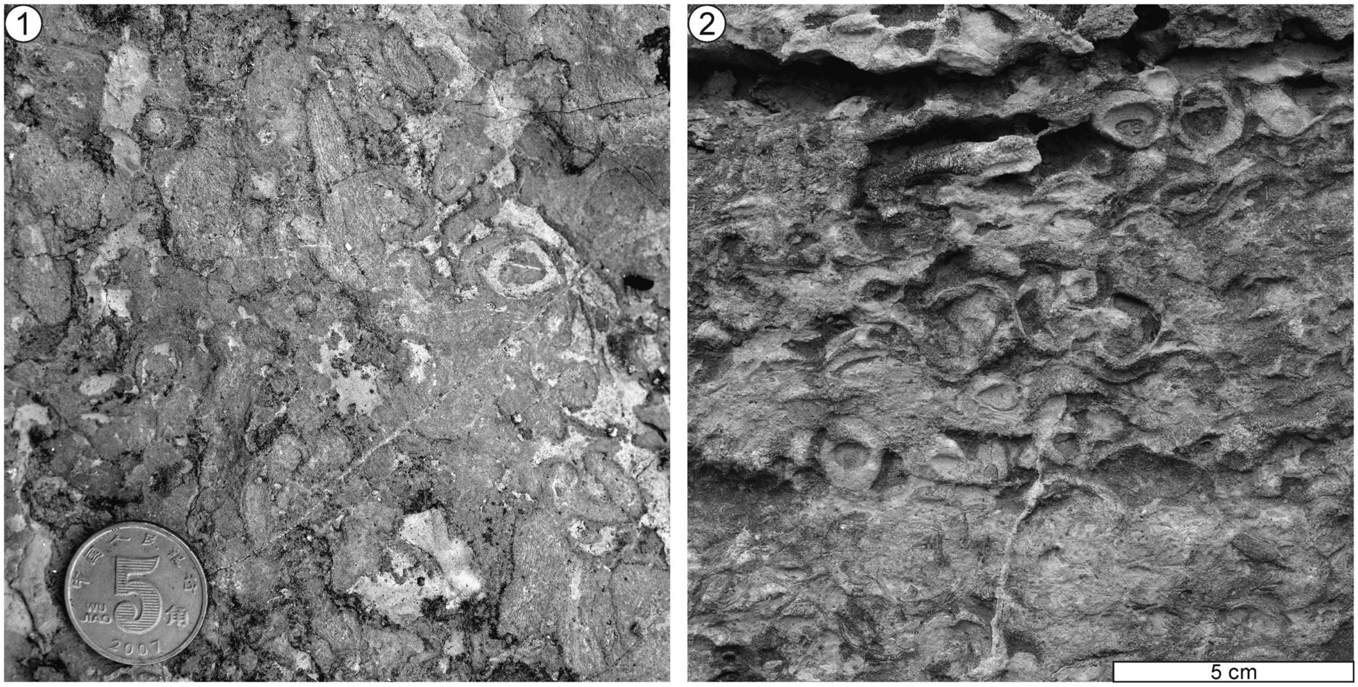

Figure 3. Outcrop photographs of *Rankenella zhangxianensis* in Zhangxia Formation, Beiquanzi section. For location, see Figure 2. (**1**) Bedding-plane view of *Epiphyton-R. zhangxianensis-Cambroctoconus orientalis* reef. Coin for scale is 20 mm in diameter. (**2**) Bedding-parallel view of *R. zhangxianensis* within the inter-reef grainstone.

central part of the platform (Fig. 2). Six lithologic units were identified from the Cambrian succession of Shandong Province: Liguan, Zhushadong, Mantou, Zhangxia, Gushan, and Chaomidian formations in ascending order (Chough et al., 2010). The siliciclastic-dominant Liguan Formation (37 m thick) was deposited in the eastern part of Shandong Province, unconformably overlying the Precambrian basement of granitic gneiss and sedimentary rocks. The Liguan Formation laterally and vertically changes into the carbonate-dominant Zhushadong Formation (up to 50 m thick), representing peritidal environments (Lee and Chough, 2011) with a few small microbial reefs containing various calcified microbes (Lee et al., 2014b). Overlying the Zhushadong Formation, the siliciclastic-dominant Mantou Formation (ca. 200 m thick) was deposited in supratidal to subtidal environments dominated by tidal processes (Lee and Chough, 2011).

The Zhangxia Formation is a carbonate-dominated succession (~180 m thick) that formed on top of the Mantou Formation. The formation consists of various carbonate facies including limestone-shale alternation, bioturbated lime mudstone, wackestone, packstone, oolitic/oncolitic/skeletal grainstone, and various microbial reefs including *Epiphyton* framestone, thrombolites, dendrolites, and stromatolites, deposited on a stable carbonate platform (Woo et al., 2008; Woo, 2009; Woo and Chough, 2010; Howell et al., 2011). It was formed during the Changhian Stage, including trilobite biozones of *Lioparia*, *Crepicephalina*, *Amphoton-Taizuia*, and *Damesella-Yabeia*, which corresponds to the late Stage 5 to the early Guzhangian of the Cambrian Series 3 (Geyer and Shergold, 2000; Chough et al., 2010; Peng et al., 2012). The reef-building sponges are generally found within the thrombolites throughout the Zhangxia Formation, but mainly in the basal part (Woo, 2009) (Fig. 2.2). Some sponges also occur in dendrolites (Fig. 2.2).

The study materials were collected from the basal part of the Zhangxia Formation (*Lioparia* Zone), indicating the late Cambrian Stage 5 (Geyer and Shergold, 2000; Chough et al., 2010) (Fig. 2B). In the Beiquanzi section, where samples were collected, sponges sporadically occur within thrombolites of more than 7 m in height and 30 m in width. Several buildups are stacked vertically and laterally, causing difficulty in differentiating their outlines. The buildups are surrounded by skeletal and oolitic packstone to grainstone with a relatively sharp boundary. Within the buildups, *Rankenella zhangxianensis* n. sp. was found together with the calcified microbe (cyanobacteria) *Epiphyton* Bornemann, 1886 and a stem-group cnidarian *Cambroctoconus orientalis* Park et al., 2011 (Fig. 3.1). *Rankenella zhangxianensis* also occasionally occurs within the inter-reef packstone to grainstone (Fig. 3.2).

Systematic paleontology

Class Demospongia Sollas, 1885
Order Orchocladina Rauff, 1895
Family Anthaspidellidae Miller, 1889
Genus *Rankenella* Kruse, 1983

Type species.—*Rankenella mors* Gatehouse, 1968. Late Cambrian Stage 4–early Guzhangian, Ranken Limestone, Tindall Limestone, and Thorntonia Limestone, Australia (cf. Kruse and Reitner, 2014).

Table 1. Summary of reported Cambrian anthaspidellid sponges

Genus	Occurrence	Age	Outer morphology	Canal	Skeletal net	Reference
Rankenella	Australia, Iran, China	Stage 4–Paibian	Conicocylindrical with deep, cylindrical spongocoels, digitate or explanate	Absent	Trabs parallel to gastral surface, and diverging upward toward dermal surface. Some spicular modification in dermal layer.	Kruse, 1983, 1996; Kruse and Zhuravlev, 2008; this study
Wilbernicyathus	Colorado and Texas, USA	Jiangshanian–Stage 10	Crudely discoidal to obconical to almost cylindrical, with moderately thick wall and spongocoel extending nearly to base	Transverse radial canals longitudinally stacked and nearly straight. Longitudinal canals often present, scattered in endosomal spiculature	One trab between radial canals; trabs cored by bundled oxeas; amphiarborescent dendroclones dominate and connect adjacent trabs transversely.	Johns et al., 2007
Gallatinospongia	California and Nevada, USA	Paibian	Obconical stalked sponge with broad open spongocoel and thin walls	Coarse transverse canals generally normal to gastral and dermal surfaces in outer half of wall; fine, closely spaced, sublongitudinal canals that curve gently and gastrally in inner part of wall	Rodlike trabs oriented longitudinally in gastral part of wall but curve upward and outward to become approximately normal to dermal surface; trabs cored by a few parallel monaxial spicules but largely formed of combined branched terminal rays of dendroclones whose principal shafts extend runglike between trabs in ladderlike structures.	Shapiro and Rigby, 2004
Capsospongia	Canadian Rockies	Drumian	Annulate, conicocylindrical, thin walled	Canals parallel upwardly divergent skeleton.	Irregular, vertical trabs formed by combined tips of horizontal dendroclones to produce septate-appearing wall	Rigby, 1986
Fieldospongia	Canadian Rockies	Drumian	Moderately thin walled, conical to cylindrical with deep spongocoel	Absent	Possible dendroclones that cross connect vertical strands; strands may be arranged in bladelike elements.	Rigby, 1986

Other species.—*Rankenella hamdii* Kruse and Zhuravlev, 2008. Late Cambrian Series 3 (Guzhangian)–early Furongian (Paibian), Mila Formation, northern Iran.

Diagnosis.—“Smooth-walled conicocylindrical, digitate or explanate sponges with deep, cylindrical spongocoels in the former. Skeletal spicule net of regular anthaspidellid type, trabs parallel to gastral surface, and diverging upward toward dermal surface. Differentiated canal systems absent. Some spicular modification in dermal layer” (Kruse, 1983, p. 51; 1996, p. 164).

Remarks.—*Rankenella* represents one of the oldest sponges of the family Anthaspidellidae, which occurs from the late Cambrian Series 2 to the early Furongian. There are two other anthaspidellid genera reported from Cambrian reefs, *Wilbernicyathus* Wilson, 1950, and *Gallatinospongia* Okulitch and Bell, 1955 (Table 1). Both *Wilbernicyathus* and *Gallatinospongia* have canal system, and can be easily differentiated from *Rankenella*. Two other non-reefal anthaspidellid sponges, *Capsospongia* Rigby, 1986, and *Fieldospongia* Rigby, 1986, both from the early–middle Cambrian Series 3 Burgess Shale, are also different from *Rankenella* (Table 1). *Capsospongia*, a thin-walled, obconical sponge with vertical trabs, has major canals parallel to the trabs. *Fieldospongia* lacks an organized canal system, but it has vertically arranged trabs.

Rankenella zhangxianensis new species
Figures 3–5

Diagnosis.—Trabs parallel/subparallel to gastral surface, diverging outward and almost perpendicularly meet dermal surface. Approximately 7–12 trabs occur between dermal and gastral surfaces. Between trabs, 3–7 ladderlike series of dendroclones occur. Spicular modification in dermal layer absent.

Description.—Mostly obconical in shape with deep cylindrical spongocoels (Fig. 4.1, 4.2). Digitate or planar forms absent. Length ranges up to 610 mm (Fig. 4.1). Transverse sections of obconical structure have diameter 3–21 mm, with spongocoels 1–14 mm in diameter, although most are 5–10 mm total diameter and 3–6 mm spongocoel diameter (Figs. 4.1–4.7, 5.1, 5.2, 6). Ratio of spongocoel diameter/total diameter is 17%–69%, and many are 39%–58% (Fig. 6). Wall generally thicker in larger specimens, with higher ratio of spongocoel diameter/total diameter. Several specimens have holdfasts, which have similar spicule arrangements as other parts of body (Figs. 4.2, 5.1–5.3).

Dermal and gastral surfaces generally smooth. Secondary thickening of skeletal net is absent, except for boundary between

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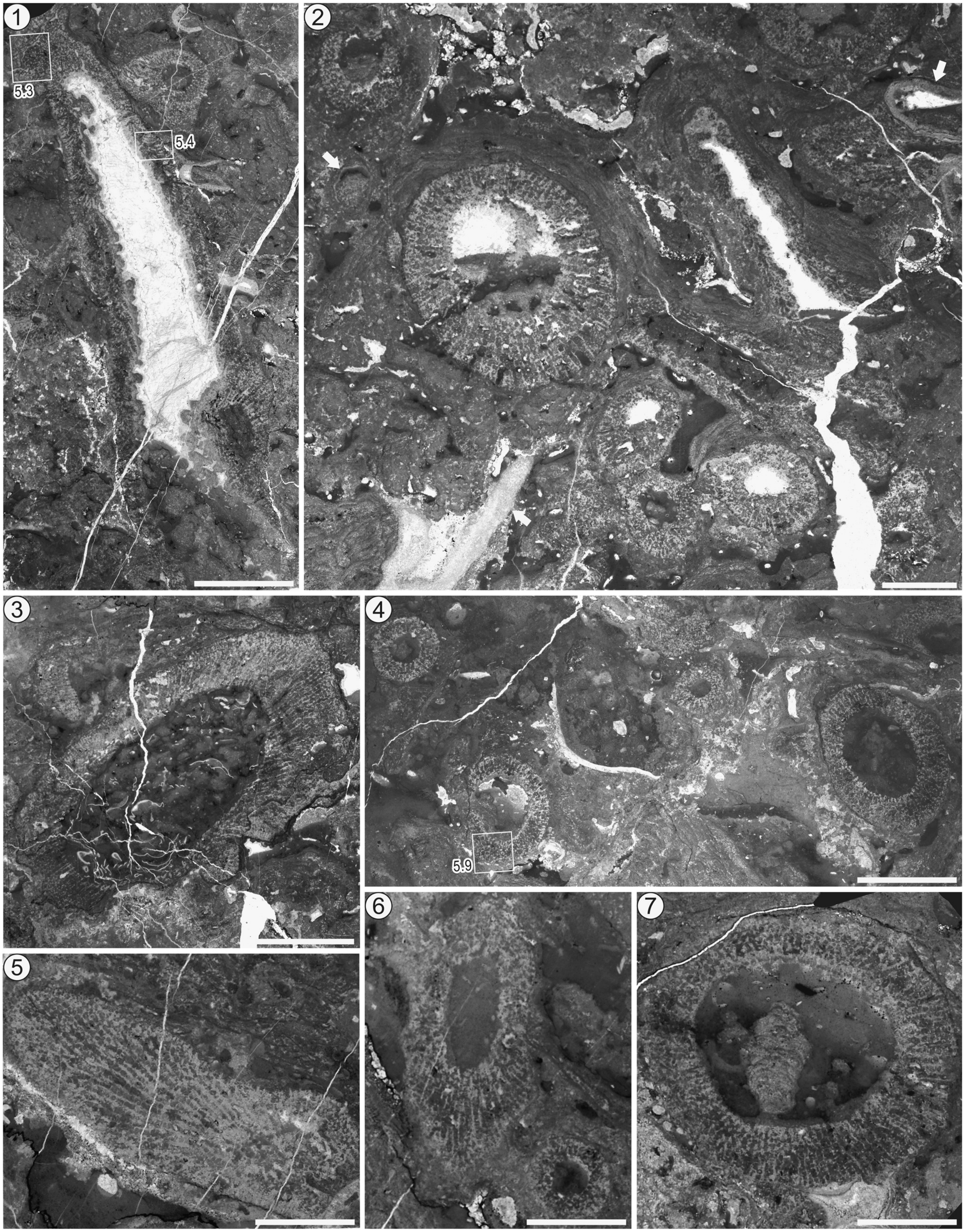
Figure 4. Photomicrographs of *Rankenella zhangxianensis* in Zhangxia Formation, Beiquanzi section. All photomicrographs are taken from bedding-parallel thin sections. For location, see Figure 2. (**1**) Holotype NIGPAS159373. Longitudinal section. (**2**) NIGPAS519388. Two individuals in longitudinal section and five individuals in transverse section. Two *Cambroctoconus orientalis* (longitudinal and transverse sections; white arrows), characterized by octagonal conical shape, occur with *R. zhangxianensis*. (**3**) NIGPAS519385. Oblique section of the largest identified individual. (**4**) NIGPAS519382. Transverse section of four individuals. (**5**) NIGPAS519389. Longitudinal section of the wall. (**6**) NIGPAS519390. Oblique and transverse sections. (**7**) NIGPAS519391. Transverse section. Note occurrence of microstromatolite within the spongocoel. Scale bars: (**1**, **3**, **4**: 10 mm; **2**, **5–7**: 5 mm).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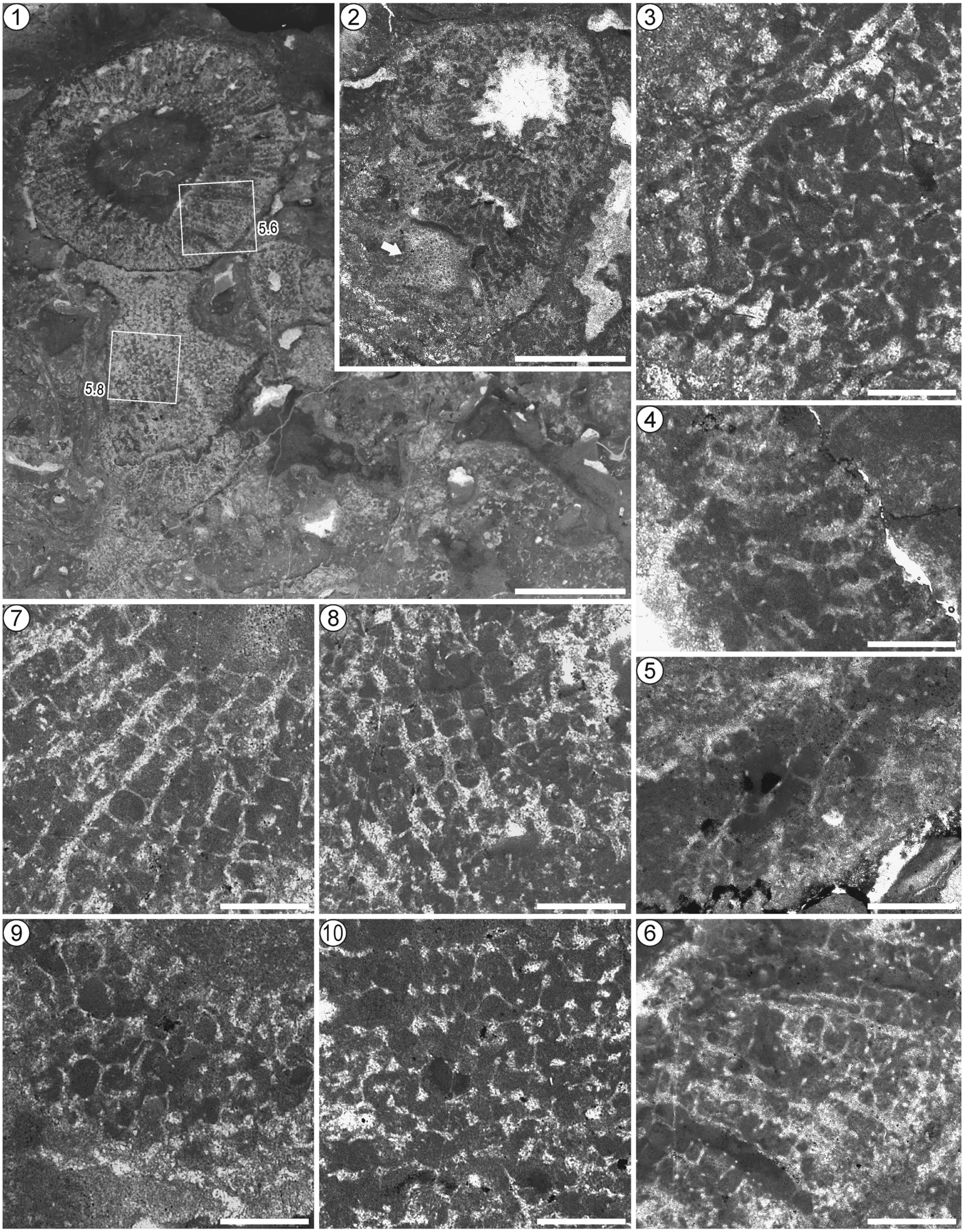
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holdfast and attached substrate (Fig. 5.3). In longitudinal sections, trabs parallel/subparallel to gastral surface, diverging outward and meet dermal surface perpendicularly or subangularly (Fig. 5.4, 5.5). Thicknesses of trabs ~0.1 mm (Fig. 5.6–5.8). Individual spicules not identified within trab. Trabs linked by 3–7 dendroclones, forming ladderlike series. Dendroclones measured from center of a trab to other center of a trab are ~0.02 mm wide and 0.3–0.35 mm long. A few Y-shaped dendroclones identified (Fig. 5.9, 5.10). Approximately 7–12 trabs occur between dermal and gastral surfaces (14–24 mm thick) (Figs. 4.1, 4.2, 5.4). Differentiated canal systems generally absent, although two specimens contain well-differentiated canals (Fig. 5.6).

Etymology.—From Zhangxia Formation, referring to the occurrence of the species.

Type material and repository.—All figured specimens are deposited in Nanjing Institute of Geology and Palaeontology (NIGPAS159373–159392). Holotype: NIGPAS159373, Paratypes: NIGPAS159374–159392. All samples are thin sections perpendicular to the bedding except for NIGPAS159387, which is a thin section parallel to the bedding. Late Cambrian Stage 5–early Guzhangian, Zhangxia Formation, Shandong Province, China.

Occurrence.—Two outcrops (Beiquanzi and Jiulongshan sections) of the Zhangxia Formation in Shandong Province, China (Fig. 2). Most specimens occur within bioherms, some within surrounding packstone to grainstone.

Remarks.—*Rankenella zhangxianensis* shows structures generally similar to the other two species of *Rankenella*: the type species, *R. mors* found in wackestone (late Cambrian Stage 4–early Cambrian Stage 5) and an *Angulocellularia*-*Taninia*-*Rankenella* reef (late Drumian) of Australia (Kruse, 1983, 1996; Kruse and Reitner, 2014), and *R. hamdii* reported from wackestone (late Cambrian Series 3) and a *Rankenella*-*Girvanella* reef (early Furongian) of Iran (Hamdi et al., 1995; Kruse and Zhuravlev, 2008). *Rankenella mors* is characterized by diverse shapes including conicocylindrical, digitate or explanate structures, and a relatively thin wall (3 to 5 trabs between dermal and gastral surfaces). On the other hand, *R. hamdii* has a thicker wall (4 to 10 trabs between dermal and gastral surfaces) and similar overall morphology with that of *R. mors*, plus notable occurrence of bowl shape. The number of dendroclones that connect two nearby trabs are 3–4 in *R. mors* and 3–10 in *R. hamdii*.

Compared to these two other species, *R. zhangxianensis* is characterized by less diverse shape (mostly obconical/cylindrical) and a thicker wall (7–12 trabs between dermal and gastral surfaces). Spongocoel diameter of *R. zhangxianensis* generally overlaps with that of *R. mors* (~13 mm) and *R. hamdii* (~11 mm in digitate shape; ~31 mm in bowl shape), although some specimens exceed these range (~21 mm in obconical shape). The number of dendroclones connecting each trab of *R. zhangxianensis* overlaps with the other species (3–7), although the number is generally larger than in *R. mors* and smaller than in *R. hamdii*. Secondary thickening of the spicule net adjacent to the dermal surface, which notably occurs in the other two species, is generally absent in *R. zhangxianensis*. On the other hand, angles between dermal surfaces and trabs intersecting the surfaces are also different; the angles are up to 90° in *R. zhangxianensis* (Fig. 5.4, 5.5), which is notably larger than ~60° in the other species. All these features collectively indicate that *R. zhangxianensis* is a new species that can be separated from *R. mors* and *R. hamdii*.

Minor occurrence of canals within *R. zhangxianensis* is noteworthy, because both Australian and Iranian species lack differentiated canals. The occurrence of canals within *R. zhangxianensis* suggests that the species may not belong to *Rankenella* because the genus has been characterized by absence of differentiated canal systems (Kruse, 1983, 1996). *Rankenella zhangxianensis* may be similar to young individuals of *Gallatinospongia*, which only develop distinct canals during the final stage of growth (R.S. Shapiro, personal communication, 2014). However, the absence of canals in the largest specimen of *R. zhangxianensis* (Fig. 4.3) and rare occurrence of canals within the species indicate that differentiated canal systems are most likely features that seldom developed in the species. Therefore, *R. zhangxianensis* is closer to *Rankenella* than to other genera, although the species may represent a transitional form between *Rankenella* and other Furongian genera with canals (*Gallatinospongia* and *Wilbernicyathus*). It is necessary to have more examples of Cambrian anthaspidellids in order to determine their evolutionary history.

Rankenella zhangxianensis and its implication to other early Paleozoic sponge-microbial reefs

Preliminary sedimentological results suggest that *Rankenella zhangxianensis* is the oldest known anthaspidellid sponge that constructed reefs. Although many specimens only show a transverse section, some specimens with a longitudinal section suggest that *R. zhangxianensis* encrusted on microbialite, *Cambroctoconus orientalis*, or other individuals of *R. zhangxianensis* (Figs. 4.1, 4.2, 5.1, 5.2). Both *R. zhangxianensis* and *C. orientalis* are commonly covered by microstromatolites, and interstitial spaces between these organisms are occupied by micrite (Figs. 4.2, 5.1). *Epiphyton* comprises a significant volume of the reef, mainly growing upward. These data collectively suggest that *Epiphyton*, *R. zhangxianensis*, and

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Figure 5. Photomicrographs of *Rankenella zhangxianensis* in Zhangxia Formation, Beiquanzi section. All photomicrographs are taken from bedding-parallel thin sections except for (**7**) and (**10**). For location, see Figure 2. (**1**) NIGPAS519384. Transverse and longitudinal sections. Note that one individual is attached to the other. (**2**) NIGPAS519390. *R. zhangxianensis* encrusting on *Cambroctoconus orientalis* (arrow). (**3**) Holotype NIGPAS159373. Transverse section of the holdfast. For location, see Figure 4.1. (**4**) Holotype NIGPAS159373. Transverse section. Trabs subparallel to gastral surface (lower left), diverge outward and almost perpendicularly meet dermal surface (upper right). For location, see Figure 4.1. (**5**) NIGPAS159392. Trabs parallel to gastral surface (upper left) and subvertically meet dermal surface (lower right). (**6–8**) Tangential views showing longitudinal trabs and dendroclones, forming ladderlike spicule networks. (**6**) NIGPAS159384. Note occurrence of canal-like structures. For location, see Figure 5.1. (**7**) NIGPAS159387. (**8**) NIGPAS159384. For location, see Figure 5.1. (**9, 10**) Transverse sections showing dendroclones between trabs with some Y-shaped dendroclones. (**9**) NIGPAS159382. For location, see Figure 4.4. (**10**) NIGPAS159387. Scale bars: (**1**) 5 mm, (**2**) 3 mm, (**3–10**) 1 mm.

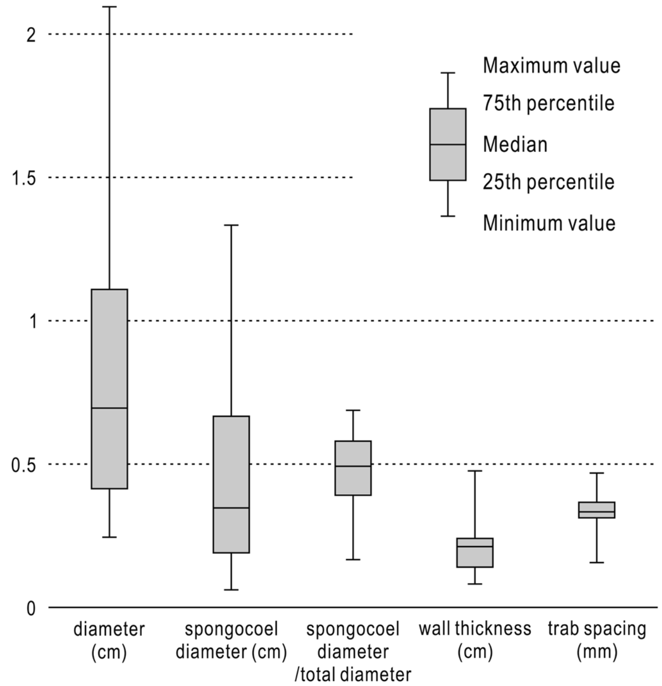

Figure 6. Box plots of measured values of some studied specimens (n = 53). For raw data, see Supplementary Table 1.

C. orientalis were framework builders, in which *R. zhangxianensis* and *C. orientalis* were encrusted and stabilized by microstromatolites. The *Epiphyton-Rankenella-Cambroctoconus* reefs most likely grew within a shallow subtidal environment, where ooid shoals formed (Woo, 2009). Some reef-building organisms would have been reworked and deposited within reef-flank sediments (Fig. 3.2).

The other examples of Cambrian reef-building anthaspidellid sponges include *R. mors* (late Drumian, Australia) (Kruse and Reitner, 2014), *R. hamdii* (early Paibian, Iran) (Hamdi et al., 1995; Kruse and Zhuravlev, 2008), *Gallatinospongia conica* Okulitch and Bell, 1955 (early Paibian, Nevada and California, USA) (Shapiro and Rigby, 2004), *Wilbernicyathus donegani* Wilson, 1950 (Jiangshanian–Stage 10, Texas and Colorado, USA) (Johns et al., 2007), and an unidentified anthaspidellid sponge (Jiangshanian–Stage 10, Nevada, USA) (Mrozek et al., 2003; Dattilo et al., 2004) (Fig. 1). Among these examples, reefs containing *R. mors* may be comparable to those of this study in terms of their age. Although the age of the Australian reef is only poorly constrained (late Drumian; Kruse and Reitner, 2014), the relatively large difference in time suggests that *R. zhangxianensis* (late Stage 5–early Guzhangian) is the oldest reef-building anthaspidellid sponge ever reported.

There are also some reports of reef-building non-anthaspidellid sponges during the Cambrian Series 3–Furongian. The heteractinide sponge *Jawonya gurumal* Kruse, 1987, and *Wagima galbanyin* Kruse, 1987 (late Cambrian Stage 4–early Cambrian Stage 5) occur within *Kordephyton*-dominant reefs as dwellers (Kruse, 1996; Kruse and Reitner, 2014). *Orlinocyathus* Krasnopeeva in Vologdin, 1962, which is classified in family Streptosolenidae (Finks et al., 2004) and thought to be a junior synonym of *Gallatinospongia* (Finks et al., 2004) or *Rankenella* (Kruse and Zhuravlev, 2008), formed reefs with *Epiphyton* in the early middle Cambrian succession of Kyrgyzstan, but it has not been studied in detail (cf. Teslenko et al., 1983). Two other reefs consisting of siliceous sponges of unknown affinity and microbes have been reported, from the Cambrian Series 3 (Drumian) of the Daegi Formation, Taebaeksan Basin, Korea (Hong et al., 2012), and the Furongian (Jiangshanian) of the Chaomidian Formation, Shandong Province, China (Lee et al., 2014a). Both siliceous sponges are unidentifiable from outcrops and only identifiable under the microscope, causing problems for identification. The characteristics of spicules and spicule networks of these sponges, however, suggest that both examples most likely belong to class Demospongia (Rigby, 1983; Hooper and Van Soest, 2002; Pisera, 2002). On the other hand, some of the sponges in the Daegi Formation (an eastward extension of the Zhangxia Formation) showing rectangular pattern spicules (Hong et al., 2012) may belong to the family Anthaspidellidae.

The occurrence of metazoan-microbial reefs in the Cambrian Series 3 together with other occurrences in the Furongian indicates that the metazoan reef gap after the decline of archaeocyaths could have been shorter than previously suggested (e.g., Hong et al., 2012; Kruse and Reitner, 2014; Lee et al., 2014a). Further studies on the Cambrian Series 3–Furongian reefs may improve our understanding of the geological events during these periods.

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Accessibility of supplemental data

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