





ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/talc20

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To cite this article: Yunong Cui & Guangxu Wang (2021) Revision of late Katian (Late Ordovician) heliolitine corals from Northern Kuruktag in northeastern Tarim Basin of China, Alcheringa: An Australasian Journal of Palaeontology, 45:2, 178-194, DOI: 10.1080/03115518.2021.1934898

To link to this article: https://doi.org/10.1080/03115518.2021.1934898

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Published online: 05 Jul 2021.



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Yunong Cui and Guangxu Wang

ABSTRACT

The Katian (Late Ordovician) saw the origin and early evolution of heliolitine tabulate corals; however, the group has not been well depicted owing to the lack of an adequately documented fossil record from this interval. In this paper, we systematically revise heliolitines from the upper Katian Hadabulaktag Formation of northern Kuruktag in northeastern Tarim, Xinjiang, China. We examine previously identified type material and describe new specimens from the type horizon. Our investigation shows that the Tarim heliolitine assemblage includes protoheliolitids *Khangailites sinkiangensis, Wormsipora sinkiangensis*, and *Wormsipora orientalis*, the plasmoporellids *Plasmoporella subtilis* and *Plasmoporella maxima*, and a proporid *Propora squameosa*. These taxa compositionally compare with coeval faunas from the Kazakstan terranes, and more distantly with South China and Australia.

ARTICLE HISTORY

Received 5 January 2021 Revised 23 April 2021 Accepted 23 May 2021

Tarim; biogeography

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THE KATIAN (Late Ordovician) represents the late stage of the Great Ordovician Biodiversification Event, and witnessed the emergence and early evolution of heliolitine tabulate corals (Webby & Kruse 1984, Webby *et al.* 2004, Mõtus & Zaika 2012). However, heliolitines from this interval are not well understood because only a few well-documented records are known from Australia (Dixon & Jell 2012, Zhen *et al.* 2017), North America (Webby *et al.* 2004, Elias *et al.* 2013), South China (Lin & Chow 1977), Baltica (Mõtus & Hints 2007), and Siberia (Bondarenko & Ulitina 2009).

This study deals with the systematics of late Katian heliolitines recorded from the Tarim Basin, which are best-represented by fossils from the Hadabulaktag Formation of northern Kuruktag in eastern Xinjiang. This assemblage was previously documented in Chinese by Yu (1960) and Kong & Song (1990), with a total of five genera and 12 species recognized. However, the taxa are only briefly described and poorly illustrated, thus a revision of this material is necessary.

In this paper, we reassess the late Katian heliolitines from the Tarim Basin based on the type specimens published by Yu (1960), as well as new material from the same strata. We also discuss their Palaeogeographical implications.

Institutional abbreviation

NIGP: Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Anatomical abbreviations

LS: longitudinal section; TS: transverse section; TaD: tabularium diameter; WT: wall thickness; Ta5: number of tabulae/5 mm; Di5: number of coenenchymal dissepiments/5 mm.

Geological setting

Fossiliferous rocks of Late Ordovician age are well exposed in the Kuruktag region of the northeastern Tarim Basin in Xinjiang, northwestern China (Norin 1937, Zhong & Hao 1990, Zhao *et al.* 2000, Jia et al. 2004, Zhang & Munnecke 2016) (Fig. 1). In northern Kuruktag, they primarily consist of carbonates that yield abundant shelly fossils, but are dominated by siliciclastics toward the south (Zhong & Hao 1990, Zhou *et al.* 1990).

In northern Kuruktag, the Upper Ordovician succession includes the Sailikdaban (in part), Uligezitag and Hadabulaktag formations (Zhong & Hao 1990, Zhang & Munnecke 2016). The heliolitine fossils were collected from the Hadabulaktag Formation (Fig. 2). This unit consists of dark-gray calcareous mudstones and argillaceous limestones that produce corals, brachiopods, cephalopods, trilobites, conodonts, and bryozoans. The conodonts correlate with the Aphelognathus pyramidalis Biozone (Zhong & Hao 1990), which is comparable with the Dicellograptus complanatus graptolite Biozone of late Katian age (Chen et al. 2012, Zhang & Munnecke 2016). This is consistent with conodonts from the underlying Uligezitag Formation, which cor-Yaoxianognathus relate with the kuruktagensis,

KEY WORDS heliolitine corals; late Katian: Late Ordovician:

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Figure 1. Maps showing the locality (red triangle) of the material studied in this paper.



Figure 2. Stratigraphical occurrence of heliolitine corals examined in this study. See the text for discussion.

Yaoxianognathus 'dolboricus', and *Y. xinjiangensis* biozones of middle Katian age (Zhong & Hao 1990).

The heliolitines described by Yu (1960) were obtained from a section of 260 m thick thin-bedded marlstones in the Uligezitag region, which form part of the Hadabulaktag Formation (Xinjiang Stratigraphic Group 1981, Zhong & Hao 1990). The samples include 13 hand specimens and 26 thin-sections. Only the three specimens assigned to *Plasmoporella intermedia* Yu, 1960 are insufficiently well preserved for taxonomic reassessment. We also recovered seven hand specimens and have made 14 thin-sections of new specimens from this same horizon.

Faunal composition and biogeographical implications

We have revised the late Katian heliolitine corals previously identified by Yu (1960) and Kong & Song (1990) to include the protoheliolitids *Khangailites sinkiangensis* (Yu, 1960), *Wormsipora sinkiangensis* Yu, 1960 and *Wormsipora orienta-lis* (Yu, 1960), the plasmoporellids *Plasmoporella subtilis* Yu, 1960 and *Plasmoporella maxima* (Yu, 1960), and a proporid *Propora squameosa* (Yu, 1960) (Table 1).

Heliolitines of a similar age have been previously documented from the Ordovician Gondwanan regions of Kazakhstan, South China, and Australia (Fig. 3). Among these, the Tarim Basin assemblage shows closest affinity with those from Kazakstan. A similar heliolitine-dominated coral fauna is also known from the Katian Dulankara Formation of the Chu-Ili Terrane in southern Kazakhstan (Bondarenko 1958, 1992), and it incorporates *Plasmoporella* Kiaer, 1899 as the main component with some species bearing bifurcated septa like *P. maxima* and *P. subtilis* from the Hadabulaktag Formation. In the Junggar area of northwestern Xinjiang, which is also part of the Kazakhstan terranes, late Katian corals characteristically include *Plasmoporella* with bifurcated septa, with *P. maxima* common in both assemblages (Lin & Wang 1985, 1986, Deng 1999). In South China, diverse tabulate corals of late Katian age are well documented from the Sanqushan Formation of the Jiangshan-Yushan-Changshan area in southeastern China (Lin & Chow 1977). The heliolitines comprise *Plasmoporella*, *Heliolites* Dana, 1846 and *Wormsipora* Sokolov, 1955; however, *Khangailites* Bondarenko & Minzhin, 1980 is absent, and examples of *Plasmoporella* lack bifurcated septa.

Australian late Katian heliolitine corals are represented by the IIIb fauna of Queensland and New South Wales, which is typified by *Heliolites*, *Navoites* Leleshus & Ospanova, 1979, and *Plasmoporella* (Dixon & Jell 2012, Zhen *et al.* 2017, Wang *et al.* 2020), with the latter taxon lacking bifurcated septa and thus differing from the Tarim Basin Hadabulaktag Formation occurrences.

Systematic palaeontology

Morphological terminology follows Hill (1981) and Dixon & Jell (2012). Biometrics follow Young & Elias (1995).

Class ANTHOZOA Ehrenberg, 1834 Subclass TABULATA Milne-Edwards & Haime, 1850

 Table
 1. Revision of heliolitine corals from the Hadabulaktag Formation (upper Katian) of northern Kuruktag, northeastern Tarim Basin.

Original identifications	This paper		
Yu (1960)			
Heliolites sinkiangensis	Khangailites sinkiangensis		
Proheliolites squmeosus	Propora squmeosa		
Pr. orientalis	Wormsipora orientalis		
Pr. convexus	W. orientalis		
Plasmoporella subtilis	Plasmoporella subtilis		
Pl. convexotabulata var. maxima	PI. maxima		
Pl. intermedia	Pl. subtilis		
Wormsipora sinkiangensis	Wormsipora sinkiangensis		
Kong & Song (1990)			
Plasmoporella camptolithusoides	Plasmoporella subtilis		
Pl. convexotabulata maxima	PI. maxima		
Pl. granulosa	PI. maxima		
Neowormsipora xinjiangensis	Wormsipora sinkiangensis		

Order HELIOLITIDA Frech, 1897 Family PROHELIOLITIDAE Kiaer, 1899

Khangailites Bondarenko & Minzhin, 1980

Type species. Khangailites heteromorphosus Bondarenko & Minzhin, 1980.

Remarks. Several forms show close similarity to *Khangailites* in exhibiting poorly developed coenenchyme, including *Linhuangites* Bondarenko, 1992, *Kiaerolites* Bondarenko, 1977, *Protoheliolites* Bondarenko, 1977, *Mcleodea* Flower & Duncan, 1975, and *Wormsipora* Sokolov, 1955. Both *Linhuangites* and *Kiaerolites* can be separated from *Khangailites* by their better developed septal plates. *Linhuangites* further differs in the existence of an 'aulo' formed by the fusion of their twisted axial septal ends. *Protoheliolites* has downwardly or subhorizontally directed septal spines, which are absent in *Khangailites*. *Mcleodea* is distinguished from *Khangailites* by possessing an entirely dissepimental coenenchyme. *Wormsipora* also differs from *Khangailites* in its apparently better developed septal spines and more incomplete tubular walls.

Khangailites sinkiangensis (Yu, 1960) (Eigs AA = 5A = 6A = E)

- (Figs 4A-F, 5A-E, 6A-F)
- Heliolites sinkiangensis Yu, p. 85, pl. 9, figs 1-3, pl. 10, figs 3, 4.
- 1963 *Heliolites sinkiangensis* Yu; Yu *et al.*, pp. 293, 294, pl.
 92, fig. 1a, b.
- 1979 Heliolites cf. sinkiangensis Yu; Deng & Li, p. 10, pl. 6, fig. 5.
- 1980 *Khangailites sinkiangensis* Yu; Bondarenko & Minzhin, p. 41, pl. 4, figs 1–3.



Figure 3. Katian (Late Ordovician) palaeogeographical map, modified from Torsvik & Cocks (2013). Blue asterisks indicate the blocks mentioned in the text.



Figure 4. Khangailites sinkiangensis. A–D, holotype. A, B, NIGP10423, TSs; C, D, NIGP10424, LSs. E, F, paratype. E, NIGP10431, TS; F, NIGP10432, LS. The arrows in A, D, E, and F indicate incomplete tubular walls. Scale bars represent 2 mm unless otherwise indicated.

- 1981 *Khangailites sinkiangensis* Yu; Bondarenko & Minzhin, p. 106, pl. 18, figs 1–3, text-fig. 29.
- 2004 Khangailites cf. sinkiangensis (Yu, 1960), White & Yang, p. 55, pl. 16, fig. 5a, b.

Diagnosis. Khangailites with tabularium diameters 0.84-1.17 mm; septa variably developed, which can be absent, short, or composed of septal spines; tabulae complete; coenenchyme poorly developed, with corallite centers 1.50-1.92 mm apart.

Referred material. Holotype, NIGP10423 (TS) and NIGP10424 (LS); paratype, NIGP10431 (TS) and NIGP10432 (LS); four topotypes, NIGP174356, NIGP174357, NIGP174358, NIGP174359.

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype is of low domical form, 113.8 mm wide and 60 mm high; the paratype has a high domical form with a width of 82 mm and height of 57 mm. Corallites rounded to subrounded, tabularium diameter varies from 0.84 to 1.17 mm (average = 1.06 mm). Walls smooth or slightly wavy, 0.04-0.10 mm thick (average = 0.07 mm). Septa variably developed, which can be absent, short, or composed of septal spines. Tabulae complete, horizontal or slightly concave, Ta5 10-12. Corallites in contact or separated by 1 to 5 rows of coenenchymal tubules with corallite centers 1.50-1.92 mm apart (average = 1.68 mm). Coenenchyme consisting of prismatic tubules ranging from 0.28 to 0.46 mm in diameter with each corallite surrounded by 12 to 14 tubules. Diaphragms complete, generally horizontal, 18-20 per 5 mm (Table 2).

Remarks. Khangailites sinkiangensis was originally assigned to *Heliolites* by Yu (1960), presumably based on the tubular



Figure 5. Khangailites sinkiangensis. A–C, NIGP174356, topotype. A, TS; B, C, LSs. D, E, NIGP174357, topotype. D, TS; E, LS. The arrows in a and B indicate incomplete tubular walls. All scale bars represent 2 mm.

coenenchyme, although this is weakly developed. We follow Bondarenko (1992) in referral to *Khangailites* because of the incomplete tubular walls. *Khangailites sinkiangensis* is distinct from the type species, *K. heteromorphosus* Bondarenko & Minzhin, 1980, in its better developed and complete tubular walls, and more widely spaced corallites.

Deng & Li (1979) recorded *Heliolites* cf. *sinkiangensis* from the Upper Ordovician of Qilian, Qinghai in

northwestern China. Their material is virtually identical to the holotype of *K. sinkiangensis*, except in its more widely spaced corallites; we therefore treat the specimens as conspecific. The *K. sinkiangensis* fossils identified from central Mongolia by Bondarenko & Minzhin (1980, 1981) only differ in their more incomplete tubular walls. *Khangailites* cf. *sinkiangensis* from Upper Ordovician of Shalloch Mill in Girvan, Scotland only differs in having larger corallites



Figure 6. Khangailites sinkiangensis. A–D, NIGP174358, topotype. A, B, TSs; C, D, LSs. E, F, NIGP174359, topotype. E, TS; F, LS. All scale bars represent 2 mm unless otherwise indicated.

(1.15–1.30 mm in diameter) and more strongly concave tabulae (White & Yang 2004).

Protoheliolites tenuis Sokolov, 1949 described by Kong & Song (1990) from the middle Katian Uligezitag Formation lacks the distinctively downwardly directed septal spines of *Protoheliolites*, but has poorly developed coenenchyme typical of *Khangailites* and is therefore attributed to this genus. It is distinguished from *K. sinkiangensis* by possessing larger corallites (0.8–1.6 mm in diameter).

Wormsipora Sokolov, 1955

?1977 Neowormsipora Lin & Chow, p. 172.

Type species. Heliolites hirsutus Lindström, 1899.

Remarks. Wormsipora is characterized by well-developed septal spines and incomplete tubular walls (a new feature identified herein). Wormsipora may be synonymous with *Neowormsipora* Lin & Chow, 1977 from the upper Katian Sanqushan Formation of southeastern China, but which differs in its better developed incomplete tubular walls and hence more dissepiments in the coenenchyme. *Propora* Milne-Edwards & Haime, 1849 and *Acdalopora* Bondarenko, 1958, both have similarly well-developed septal spines, but can be distinguished from *Wormsipora* by their dissepimental coenenchyme. *Propora* further differs by possessing more widely spaced corallites, and *Acdalopora* by having septal plates.

Wormsipora has been variously assigned to Taeniolitidae (Hill 1981, White & Yang 2004) or Proporidae (Lin *et al.*

Table 2.	Biometric	data on	protoheliolitids	described	in this	paper
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	TaD	WT	Ta5	Di5
Khangailites sinkingensis (Yu, 1960)				
Minimum	0.84	0.04	10	18
Maximum	1.17	0.1	12	20
Range of colony means	0.88-1.15	0.05-0.08	10.4–11.5	19–19.5
Mean	1.02	0.07	10.95	19.25
No. of measurements	49	40	27	21
No. of specimens studied	6	6	6	6
Wormsipora sinkingensis (Yu, 1960)				
Minimum	1.51	0.05	14	18
Maximum	1.72	0.09	16	20
Range of colony means	1.55-1.64	0.06-0.08	14–15	18.5–18.8
Mean	1.60	0.07	14.5	18.65
No. of measurements	28	24	11	8
No. of specimens studied	2	2	2	2
Wormsipora orientalis (Yu, 1960)				
Minimum	1.24	0.11	10	18
Maximum	1.56	0.22	18	22
Range of colony means	1.38-1.53	0.14-0.21	11–16.7	19–22
Mean	1.46	0.18	13.85	20.5
No. of measurements	31	27	10	9
No. of specimens studied	3	3	3	3

1988, Bondarenko 1992). However, considering that the genus has weakly developed coenenchyme, we attribute it to Proheliolitidae.

Wormsipora sinkiangensis Yu, 1960

(Fig. 7A-F)

- 1960 Wormsipora sinkiangensis Yu, p. 86, pl. 12, figs 1, 2.
- 1963 Wormsipora sinkiangensis Yu; Yu et al., p. 297, pl. 94, fig. 3a, b.
- 1979 Wormsipora cf. sinkiangensis Yu; Deng & Li, p. 11, pl. 6, fig. 6.
- ?1990 Neowormsipora xinjinagensis Kong & Song, p. 160, pl. 30, fig. 1.

Diagnosis. Wormsipora with tabularium diameters 1.51-1.72 mm; septa consisting of strongly upwardly directed spines extending almost to the axis; corallite centers 1.50-1.92 mm apart.

Referred material. Holotype, NIGP10443 (TS) and NIGP10444 (LS); topotype, NIGP174360.

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype is hemispherical. Corallites rounded or slightly stellated, with tabularium diameters varying from 1.51 to 1.72 mm (average = 1.62 mm). Walls 0.05-0.09 mm thick (average = 0.07 mm), moderately to strongly plicated, and sometimes extending into coenenchyme. Septa 12 in number, long, almost extending to the axis; consisting of continuous narrow plates with spines developed along their inner edges. Septal spines strongly inclined upwardly and shown as dark dots in TS (Fig. 7A,D). Tabulae complete, rarely incomplete, moderately to strongly convex, Ta5 14–16. Corallite centers 1.50-1.92 mm apart

(average = 1.68 mm). Coenenchyme consisting of tubules with incomplete walls. Dissepiments 0.24-0.68 mm wide (average = 0.42 mm), mostly 18-20 per 5 mm (Table 2).

Remarks. Wormsipora sinkiangensis is differentiated from all congeneric species by possessing an almost entirely dissepimental coenenchyme and dense tabulae. Wormsipora sinkiangensis was attributed to Acdalopora by Bondarenko (1992); however, we retain this form within Wormsipora owing to the presence of tubules. Material described by Deng & Li (1979) as Wormsipora cf. sinkiangensis from the Upper Ordovician of Qilian, Qinghai in northwestern China is consistent with W. sinkiangensis. Neowormsipora xinjinagensis Kong & Song, 1990 is also probably synonymous with W. sinkiangensis and has been recorded from the same locality and horizon. Neowormsipora xinjinagensis differs only in having a larger corallite size (1.8–2.0 mm in diameter) and more widely spaced tabulae.

Womsipora orientalis (Yu, 1960) shares long septal spines and poorly developed coenenchyme with W. sinkiangensis. However, it differs in having a much smaller corallite size (1.24-1.56 mm in diameter), thicker corallite walls, and sparser septal spines. Lin & Chow (1977) described Womsipora shiyangensis Lin & Chow, 1977 and Womsipora maxima Lin & Chow, 1977 from the upper Katian Sanqushan Formation in Zhejiang, southeastern China. These species both share a poorly developed coenenchyme with W. sinkiangensis, but W. shiyangensis differs in having much shorter septa and much denser tabulae, while W. maxima has much larger corallites (1.8-1.9 mm in diameter) and shorter septa (Lin & Chow 1977).

Wormsipora orientalis (Yu, 1960)

(Figs 8A-F, 9A-D)

- 1960 Proheliolites orientalis Yu, p. 90, pl. 11, figs 1-4, 7.
- 1960 Proheliolites convexus Yu, p. 91, pl. 11. figs 5, 6.
- 1963 Proheliolites orientalis Yu; Yu et al., p. 94, fig. 5a, b.
- 1963 Proheliolites convexus Yu; Yu et al., p. 304, fig. 6a, b.



Figure 7. Wormsipora sinkiangensis. A-C, holotype. A, NIGP10443, TS; B, C, NIGP10444, LSs. D-F NIGP174360, topotype. D, TS; E, F, LSs. All scale bars represent 2 mm.

Diagnosis. Wormsipora with TDs 1.24–1.56 mm; septal spines numerous, moderately upwardly curved; corallites in contact or narrowly separated, with their centers 1.33–2.42 mm apart.

Referred material. Holotype, NIGP10437 (TS) and NIGP10438 (LS); paratype, NIGP10439 (TS) and NIGP10440 (LS); NIGP10441 (TS) and NIGP10442 (LS),



Figure 8. Womsipora orientalis. A–D, holotype. A, B, NIGP10437, TSs; C, D, NIGP10438, LSs. E, F paratype. E, NIGP10439, TS; F, NIGP10440, LS. All scale bars represent 2 mm.

originally designated as the holotype of *Proheliolites convexus* Yu, 1960.

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype is of high domical form, measuring 24 mm wide and 23 mm high; the specimen, NIGP 10441 (TS) and NIGP10442 (LS), has a low domical form, with a width of 17.5 mm and a height of 11 mm. Corallites rounded and subrounded, tabularium diameters varying from 1.24 to 1.56 mm (average = 1.40 mm). Walls 0.11-0.22 mm thick (average = 0.17 mm), slightly wavy. Septa 12, each consisting of a series of discrete spines. Septal spines numerous, moderately upwardly curved, shown as

dark dots in TS (Fig. 8E). Tabulae complete, horizontal, or slightly convex or concave, Ta5 10–18. Corallites in contact or separated by narrow coenenchyme, with their centers 1.33-2.42 mm apart (average =1.88 mm). Coenenchyme consisting of strongly arched dissepiments. Dissepiments 0.16-0.41 mm wide (average = 0.29 mm), 18-22/5 mm (Table 2).

Remarks. Original placement of Wormsipora orientalis within Protoheliolites by Yu (1960) was based on its weakly developed coenenchyme. However, the well-developed septal spines and incomplete tubular walls are consistent with Wormsipora. Wormsipora convexus Yu, 1960 is likely a junior synonym W. orientalis based on its comparable corallite size and septal development, but has more strongly convex tabulae.



Figure 9. Womsipora orientalis. A–D, holotype of Proheliolites convexus. A, B, NIGP10441, TSs; C, D, NIGP10442, LSs. All scale bars represent 2 mm.

Neowormsipora jiangxiensis from the upper Katian Sanqushan Formation (Lin & Chow 1977) is also similar to W. orientalis, but differs in its larger corallite size (1.7–1.8 mm in diameter) and better developed septal spines.

Family PROPORIDAE Sokolov, 1949

Propora Mile-Edwards & Haime, 1849

Type species. Porites tubulata Lonsdale, 1839.

Propora squameosa (Yu, 1960) (Fig. 10A–D)

- 1960 *Proheliolites squameosa* Yu, pp. 90, 91, pl. 10, figs 1, 2.
- 1963 *Proheliolites squameosa* Yu; Yu *et al.*, pp. 303, 304, pl. 94, fig. 7a, b.
- 1985 Propora densa Lin & Wang, p. 353, pl. 3, fig. 3a, b.

Diagnosis. Propora with tabularium diameters 1.38–1.73 mm, and with short septal spines; corallite centers 1.22–1.55 mm apart, separated by narrow dissepimental coenenchyme.

Referred material. Holotype, NIGP10429 (TS) and NIGP10430 (LS).

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype of hemispherical form, measuring 160 mm wide and 90 mm high. Corallites rounded or slightly stellated; tabularium diameters varying from 1.38 to 1.73 mm (average = 1.52 mm). Walls slightly crenulated, 0.15-0.27 mm thick (average = 0.20 mm). Each corallite having 12 low septal spines with lengths one-eighth the tabularium diameters. Tabulae complete, horizontal or slightly convex, Ta5 10–12. Corallites in contact or separated by narrow coenenchyme, with corallite centers 1.22-1.55 mm apart (average = 1.34 mm). Coenenchyme consisting of overlapping small domed dissepiments. Dissepiments 0.25-0.49 mm wide (average = 0.39 mm), mostly 15–18 per 5 mm (Table 3).

Remarks. Propora squameosa was referred to Protoheliolites by Yu (1960), and *Khangailites* by Bondarenko (1992); however, the presence of dissepimental coenenchyme justifies our generic designation as *Propora*.

Propora densa Lin & Wang, 1985, from the Katian Jiabosaer Formation of Jiabosaer in northern Xinjiang has comparable coenenchyme and corallite size (1.2–1.7 mm in diameter), but differs from *P. squameosa* in its less developed septa and coenenchyme; nonetheless, we consider these species synonymous.

Propora proheliolitoides Barskaya, 1965, from Upper Ordovician strata along the upper Kaindy-Odru River in Gornyy Altay, and Propora jiabosarensis Lin & Wang, 1981 from the Jiabosaer Formation show closest similarity to *P. squameosa*, particularly in their rare development of



Figure 10. Propora squameosa. A–D, holotype. A, B, NIGP10429, TSs; C, D, NIGP10430, LSs. The arrow in D indicate dissepimental coenenchyme. All scale bars represent 2 mm.

coenenchyme. *Propora proheliolitoides* is distinguished by smaller corallite size (1.1–1.3 mm in diameter) and the absence of septa; *P. jiabosarensis* differs in its much larger corallites (2.2–2.7 mm in diameter) and less developed septa. Family PLASMOPORELLIDAE Kiaer, 1903

Plasmoporella Kiaer, 1899

Type species. *Plasmoporella convexotabulata* forma *typica* Kiaer, 1899.

Plasmoporella subtilis Yu, 1960

(Figs 11A-G, 12A-H)

- 1960 Plasmoporella subtilis Yu, pp. 87, 88, pl. 12, figs 3, 4.
- 1960 *Plasmoporella intermedia* Yu, pp. 88, 89, pl. 12, fig. 5, pl. 14, figs 1-4, p. 15, fig. 6.
- 1963 *Plasmoporella subtilis* Yu; Yu *et al.*, pp. 300, 301, pl. 93, fig. 3a, b.
- 1963 Plasmoporella intermedia Yu; Yu et al., pp. 301, 302, pl. 94, fig. 1a, b.
- ?1986 Plasmoporella intermedia Yu; Lin & Wang, p. 54, pl.9, fig. 6a, b.
- 1990 Plasmoporella subtilis Yu; Kong & Song, p. 157, pl. 29, fig. 3a, b.

 Table
 3. Biometric
 data
 on
 plasmoporellids
 and
 a
 proporid
 described
 in
 this
 paper.

<u> </u>				
	TaD	WT	Ta5	Di5
Propora squmeosa (Yu, 1960)				
Minimum	1.38	0.15	10	15
Maximum	1.73	0.27	12	18
Mean	1.52	0.2	11	16.7
No. of measurements	12	11	5	4
No. of specimens studied	1	1	1	1
Plasmoporella subtilis (Yu, 1960)				
Minimum	2.59	-	10	16
Maximum	3.44	-	16	22
Range of colony means	2.86-3.11	-	11–15.7	17–20.3
Mean	2.99	-	13.35	18.65
No. of measurements	31	-	15	10
No. of specimens studied	5	-	5	5
Plasmoporella maxima (Yu, 1960)				
Minimum	2.21	-	10	18
Maximum	2.64	-	14	24
Range of colony means	2.42-2.59	-	11.3–13.3	19–21.5
Mean	2.51	-	12.3	20.25
No. of measurements	21	-	10	9
No. of specimens studied	3	-	3	3

?1990 Plasmoporella camptolithusoides Kong & Song, pp. 157, 158, pl. 28, fig. 3.



Figure 11. Plasmoporella subtilis. A–E, holotype. A–C, NIGP10445, TSs; D, E, NIGP10447, LSs. F, G, NIGP174361, topotype. F, TS; G, LS. The arrows in C and F indicate bifurcated septa. Scale bars represent 2 mm unless otherwise indicated.

Diagnosis. Species of *Plasmoporella* with tabularium diameters 2.59–3.44 mm; corallite centers 2.32–3.74 mm apart; septa slender, bifurcated but without laterally contiguous bases, projecting adaxially as much as one-sixth the tabularium diameter; coenenchyme consisting of small convex dissepiments.

Referred material. Holotype, NIGP10445 (TS) and NIGP10446 (LS); NIGP10456 (TS) and NIGP10457 (LS), NIGP10458 (TS) and NIGP10459 (LS), originally designated

as holotype and paratype of *Plasmoporella intermedia* Yu, 1960; two other topotypes, NIGP10447 (TS) and NIGP10465 (LS), NIGP174361.

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype is of an irregular form, measuring 65 mm wide and 120 mm high. The specimens, NIGP10456



Figure 12. Plasmoporella subtilis. A–D, holotype of Plasmoporella intermedia. A, B, NIGP10456, TSs; C, D, NIGP10457, LSs. E, F, paratype of Plasmoporella intermedia. E, NIGP10458, TS; F, NIGP10459, LS. G, H, topotype of Plasmoporella intermedia. G, NIGP10447, TS; H, NIGP10465, LS. The arrows in B, E and G indicate bifurcated septa. All scale bars represent 2 mm.

(TS) and NIGP10457 (LS), and NIGP10458 (TS) and NIGP10459 (LS) are hemispherical to spherical with a width of 50-105 mm and height of 55-58 mm. Corallites slightly stellated with tabularium diameters ranging from 2.59 to

3.44 mm (average = 3.02 mm). Corallite walls defined largely by downturned margins of coenenchymal dissepiments. Twelve slender septa with a maximum width of 0.34-0.53 mm; generally with bifurcated bases extending



Figure 13. Plasmoporella maxima. A–C, holotype. A, NIGP10461, TS; B, C, NIGP10462, LSs. D, E, paratype. D, NIGP10463, TS; E, NIGP10464, LS. All scale bars represent 2 mm.

into coenenchyme. Septa elongate radially, 0.44-0.68 mm long (average = 0.55 mm); some extending as much as onesixth the tabularium diameter. Tabulae complete or incomplete, subhorizontal, moderately to strongly convex; Ta5 10-16. Corallite centers 2.32-3.74 mm apart (average = 3.03 mm). Intercorallite spaces filled with coenenchyme of small convex dissepiments. Dissepiments adjacent to corallites smaller with widths 0.22-0.42 mm (average = 0.32 mm), medially large and wider (0.64-0.99 mm; average = 0.78 mm). The number of dissepiments in 5 mm 16-22 (Table 3).

Remarks. Plasmoporella subtilis is typified by the consistent development of bifurcated septa (not mentioned by Yu 1960), which might be diagnostic at genus level. Kong & Song (1990) described *P. subtilis* from the middle Katian Yuanbaoshan Formation of Yaerdang in the southern Kuruktag, but their material differs only in



Fig. 14. Plasmoporella maxima. A–C, NIGP174362, topotype. A, TS; B, C, LSs. All scale bars represent 2 mm.

possessing more closely spaced tabulae. Lin & Wang (1986) reported *Plasmoporella intermedia* from the Upper Ordovician Bulongor Formation of Hobuksar in north-western Xinjiang, but we tentatively assign it to *P. subtilis. Plasmoporella camptolithusoides* Kong & Song, 1990, also from the Hadabulaktag Formation differs in having slightly smaller corallite size (2.2-2.8 mm in diameter), but is also likely synonymous.

Plasmoporella maxima is distinguished from *P. subtilis* in having stouter and more weakly bifurcated septa, and smaller corallite size (2.21-2.64 mm in diameter).

Plasmoporella maxima (Yu, 1960)

(Figs 13A-E, 14A-C)

- 1960 Plasmoporella convexotabutate var. maxima Yu, p. 88, pl. 15, figs 1-3, 4, 5.
- 1963 Plasmoporella convexotabutate var. maxima Yu; Yu et al., p. 301, pl. 94, fig. 2a, b.
- 1977 Plasmoporella convexotabutate maxima Yu; Lin & Chow, p. 191, pl. 60, figs 1a, b, 2a, b.
- 1981 Plasmoporella convexotabutate maxima Yu; Lin & Wang, p. 70, 71, pl. 36, fig. 4a, b.
- 1982 Plasmoporella convexotabutate var. maxima Yu; Li & Lin, p. 90, pl. 28, fig. 2a, b.
- 1985 Plasmoporella convexotabutate maxima Yu; Lin, p. 121, pl. 2, fig. 2a, b.
- 1986 Plasmoporella convexotabutate maxima Yu; Lin & Wang, p. 53, pl. 9, fig. 4a, b.

- 1986 Plasmoporella pseudoproporoides Lin & Wang, p. 52, pl. 8, fig. 3a, b.
- ?1990 Plasmoporella convexotabutate maxima Yu; Kong & Song, p. 156, pl. 28, fig. 1a, b.
- 1990 Plasmoporella granulosa (Bondarenko); Kong & Song, p. 157, pl. 27, fig. 4.
- ?1999 Plasmoporella cf. convexotabutate maxima Yu; Deng, p. 232, pl. 36, fig. 2, pl. 37, fig. 2.

Diagnosis. Species of *Plasmoporella* with tabularium diameters 2.21–2.64 mm; septa commonly wedge-shaped with slightly bifurcated bases, extending as much as one-seventh the tabularium diameter; corallite centers 2.52–3.38 mm apart; coenenchyme consisting of well-developed dissepiments.

Referred material. Holotype, NIGP10461 (TS) and NIGP10462 (LS); paratype, NIGP10463 (TS) and NIGP10464 (LS); topotype, NIGP174362.

Type locality, unit and age. Northern Kuruktag (Tarim Basin), Xinjiang, China. Hadabulaktag Formation, upper Katian, Upper Ordovician.

Description. The holotype is of low domical form, measuring 130 mm wide and 100 mm high. Corallites slightly stellated, tabularium diameters 2.21-2.64 mm (average = 2.43 mm). Corallite walls defined largely by downturned margins of coenenchymal disseptiments. Septa consisting of

thick trabeculae, commonly wedge-shaped, with or without slightly bifurcated bases, 0.28-0.44 mm long (average = 0.35 mm), extending one-seventh the tabularium diameters. Tabulae complete, mainly subhorizontal or slightly convex, Ta5 10-14. Corallite centers 2.52-3.38 mm apart (average = 2.82 mm). Spaces between corallites occupied by coenenchymal dissepiments, with those immediately surrounding each corallite strongly convex. Dissepiments 0.22-0.46 mm wide (average = 0.35 mm), 18-24 per 5 mm (Table 3).

Remarks. Yu (1960) originally described *Plasmoporella maxima* as a variety of *Plasmoporella convexotabulata* Kiaer, 1899, but it differs in having larger corallite size and shorter septa, which we consider sufficient to define a separate species.

Plasmoporella convexotabutate maxima from the upper Katian Sanqushan Formation in Jiangxi (Lin & Chow 1977), middle Katian Beiguoshan Formation of Longxian in Shanxi (Li & Lin 1982), Katian Bulongor Formation of Hobuksar in northwestern Xinjiang (Lin & Wang 1981, 1986), Upper Ordovician strata at Ejin Banner in Inner Mongolia (Lin 1985), and the Hadabulaktag Formation (Kong & Song 1990) are all synonymous with *P. maxima*, with the Hadabulaktag Formation specimens having smaller corallites (2.0-2.4 mm in diameter). Deng (1999) also recorded *Plasmoporella* cf. *convexotabutate maxima* from the Bulongor Formation, which has much smaller corallite size (2.0-2.2 mm in diameter).

Plasmoporella granulosa Bondarenko, 1958 described by Kong & Song (1990) may also be attributable to *P. maxima* based on its comparable corallite size and septal development, but has longer septa. Likewise, *Plasmoporella pseudoproporoides* Lin & Wang, 1986 from the Bulongor Formation differs only in possessing slightly smaller corallites (1.8-2.6 mm) and sparser tabulae (Ta5 = 8-10).

Plasmoporella shiyanshanensis Lin & Chow, 1977 from the Sanqushan Formation shows comparable septal development to P. maxima, but differs in its much smaller corallites (1.3-1.5 mm in diameter) and better developed coenenchyme. Plasmoporella diffita Lin & Wang, 1985 from the Upper Ordovician Gabosar Formation of Gabosar in northern East Junggar, Xinjiang is also distinguished by smaller corallites (1.5-2.0 mm), better developed coenenchyme, and more concave tabulae. Plasmoporella giakuertensis Lin & Wang, 1985, again from the Gabosar Formation, otherwise differs in its larger corallites (3-3.5 mm in diameter). Finally, Plasmoporella bifida Bondarenko, 1958 and Plasmoporella grandis Bondarenko, 1958 from the Upper Ordovician Dulankara horizon of the Chu-Ili Terrane in southern Kazakhstan can be distinguished from P. maxima by their longer septa and much larger corallites (2.75-3 mm and 3-4.5 mm in diameter); P. bifida also possesses cystose tabulae.

Acknowledgements

We are grateful to Zhanqiu Deng for provision of specimens, and to Changmin Yu for helpful discussions. We also thank Mikolaj Zapalski, Kun Liang, Benjamin Kear, Timothy Topper, and two anonymous referees for their comments and editing of our manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The National Natural Science Foundation of China [42072007], the Youth Innovation Promotion Association of CAS [2020311], the Strategic Priority Research Program of Chinese Academy of Sciences [XDB26000000], and the State Key Laboratory of Palaeobiology and Stratigraphy financed our study.

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