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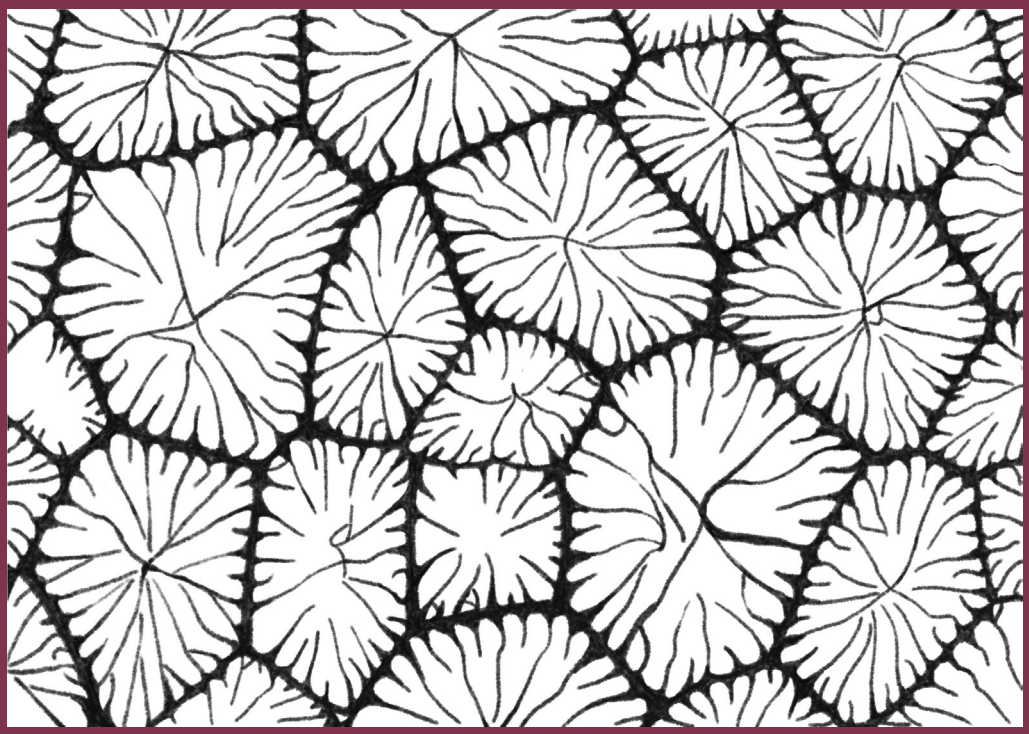
Systematics and evolution of cyathophylloidid and stauriid rugose corals (Late Ordovician–mid-Silurian)



Guang-Xu Wang

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Cover picture: Transverse section of *Stauria qijiangensis* He, 1978 (p. 91), a typical stauriid rugose coral displaying the characteristic KAC septal parricidal increase, commonly found in the Shihniulan Formation (upper Aeronian, Silurian) of the Upper Yangtze Platform, South China. Line drawing by Meng-Fei He.

Systematics and evolution of cyathophylloidid and stauriid rugose corals (Late Ordovician–mid-Silurian)

by

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Rugose corals attributed here to the families Cyathophylloididae and Stauriidae are common and internationally widespread in the Upper Ordovician–Wenlock strata. They were formerly considered as closely related constituents of the Stauriidae. Here, based on the described, mostly type material mainly housed at palaeontological institutions of China and Estonia, as well as a few new specimens, a great many taxa of the two families are systematically revised, and a comparative study of all known records is performed. The study highlights the evolutionary and taxonomic significance of modes of corallite increase. The Cyathophylloididae, consisting of *Palaeophyllum*, *Cyathophylloides*, *Favistina*, *Crenulites* and *Palaeolithostrotion*, is defined here as a group of non-dissepimented Stauriida exhibiting exclusively lateral increase. In contrast, the Stauriidae consists of Stauriida characterised by a septal parricidal increase (new term), in which new separating walls are formed from pre-existing septa of the parent. This is in contrast to aseptal parricidal increase (new term), in which pre-existing septa are not involved in the formation of neowalls. Within the Stauriidae, three subfamilies (i.e. the Stauriinae, Paraceriasterinae n. subfam., and Heininae n. subfam.) are recognised based on their essentially different septal increase modes. These are termed here KLAC, KAC, and KA, in which neowalls develop from respectively the two counter-lateral (KL), two alar (A) and cardinal (C) septa, the counter (K), two alar and cardinal septa, and the counter and two alar septa. Two new genera, *Heina* and *Yuina*, are proposed and included in the Heininae n. subfam. An updated summary of the stratigraphic distribution of both families is also given, offering insights into their origin and evolution. Cyathophylloidids might have originated from a *Favistina*-like ancestor during the late Sandbian and diversified rapidly during the Katian. However, only *Palaeophyllum*, *Cyathophylloides* and *Palaeolithostrotion* survived the Late Ordovician Mass Extinction around the Katian–Hirnantian boundary. Few representatives of the former two persisted into the early Llandovery, while those of *Palaeolithostrotion* continued into the Wenlock. Stauriids might have emerged by the earliest Silurian from ancestral forms whose septa tended to meet at the axis. This was followed by a flourishing of all three subfamilies through much of the Llandovery, which was subsequently succeeded by the extinction of Paraceriasterinae n. subfam. and Heininae n. subfam., along with a substantial decline in Stauriinae during the early Telychian. The surviving stauriinids extended into the late Sheinwoodian (early Wenlock) but did not endure beyond that interval. ☐ Keywords: *Rugose corals*, *Cyathophylloididae*, *Stauriidae*, *taxonomy*, *evolution, Late Ordovician, Silurian*.

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Introduction

Rugose corals that are attributed in this study to the families Cyathophylloididae and Stauriidae are common and globally widespread in Upper Ordovician–Wenlock strata. Previously they were generally placed within a single family, the Stauriidae Milne-Edwards & Haime, 1850 *sensu lato* (e.g. Hill 1981; Lin *et al.* 1995; Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013). Since the recognition of its first representative, *Stauria favosa* (Linnaeus, 1758), a considerable number of taxa have been added to this group (or its synonyms). Previous summaries on the knowledge of these corals were presented by Bassler (1950), Ivanovskiy (1969) and Tang *et al.* (2008a, b), among others. However, many aspects of classification and

evolution of this group of corals remain to be clarified, one of the major reasons being that quite a few taxa remain inadequately known by modern standards, and this hinders a reliable analysis of their origin and overall evolutionary history.

In this study, much of the published material of cyathophylloidids and stauriids housed in palaeontological institutions of China and Estonia, together with a few new specimens, is examined, allowing a critical revision of the related taxa and a refined taxonomy of the two families. Based on the new fossil data, this work aims to summarise the temporal and spatial distribution of these families, and hence to discuss their origin and evolution.

Concepts of early, middle and late Katian used in this work approximately correspond to the *Diplacanthograptus caudatus* and *D. spiniferus* biozones (Ka1), the *Geniculograptus pygmaeus* and *Dicellograptus elegans–Orthograptus quadrimucronatus* biozones (Ka2 and Ka3), and the *Dicellograptus complanatus, D. complexus* and *Paraorthograptus pacificus* biozones (Ka4), respectively. Definitions of Ka1–4 follow Bergström et al. (2009).

Materials and methods

Materials

The fossil material used in the present work is that of published cyathophylloidid and stauriid coral taxa housed in the collections of paleontological institutions in China and Estonia, supplemented by a few new specimens.

Methods

Morphological terminology adopted in this study largely follows Hill (1981), and, where possible, biometric methods of Young & Elias (1995) are employed. The notable exception is the terms concerning parricidal increase in rugose corals, discussed below.

Hill (1981) summarised two fundamentally different rugosan increase patterns, tabularial (axial) and marginarial (lateral), based on the fate of the parent during offsetting, which are equivalent to parricidal and non-parricidal increase modes of Scrutton (1998), respectively. Within the parricidal increase, Hill (1981) further distinguished staurioid and entelophylloid types, which were referred to as axial and peripheral increase, respectively, by Scrutton (1998) and many others (Hill 1935; Oliver 1968; Fedorowski & Jull 1976). According to their definition, new dividing walls develop across the axis of the parent tabularium in the former type, whereas neowalls occur in the outer part of the tabularium and extend into the dissepimentarium in the latter.

However, I argue that the essential difference between parricidal increase in *Stauria* and *Entelophyllum*-like forms lies in how, rather than where, new dividing walls are formed, and that the previous terminology cannot reflect such a distinction and instead is a cause of confusion. For instance, new offsets that develop in the axis but without involvement of pre-existing septa occur in different rugose coral groups (e.g. *Pycnostylus*, Hill 1981; *Melasmaphyllum*, Wright 1966), which were also referred to axial increase in the past. For this reason, it is useful to distinguish two substantially different parricidal increase types, termed here septal and aseptal, depending on whether neowalls are formed from pre-existing septa (Fig. 1). Furthermore, three septal parricidal increase modes (i.e. KLAC, KAC, and KA) are recognised in the Stauriidae, in which new separating walls develop from the two counter-lateral (KL), two alar (A) and cardinal (C) septa, the counter (K), two alar and cardinal septa, and the counter and two alar septa, respectively (Fig. 1). Of these, KLAC increase has been commonly referred to in the literature as a type of pentapartite increase, with KAC as quadripartite and KA as tripartite. This recognition forms the basis for the new subfamily classification of the Stauriidae proposed in this study, discussed below.

Repository. – The repositories for the type specimens considered in this work are indicated by prefixes for specimen numbers as follows: AM = Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; BM = British Museum (Natural History), London; CUGB = China University of Geosciences, Beijing; GIT = Geology of Tallinn University of Technology, Tallinn; GMC = Geological Museum of China, Beijing; GSC = Geological Survey of Canada, Ottawa; HU = Museum für Naturkunde der Humboldt-Universität zu Berlin (now Natural History Museum, Berlin), Berlin; MGU = Moscow State University, Moscow; MPUC = Museum of Paleontology of the University of California, Berkeley; NIGP = Nanjing Institute of Geology and Palaeontology, Nanjing; NMBM = New Mexico Bureau of Mines and Mineral Resources, Socorro; NMRFC = National Mineral Rock and Fossil Specimen Resource

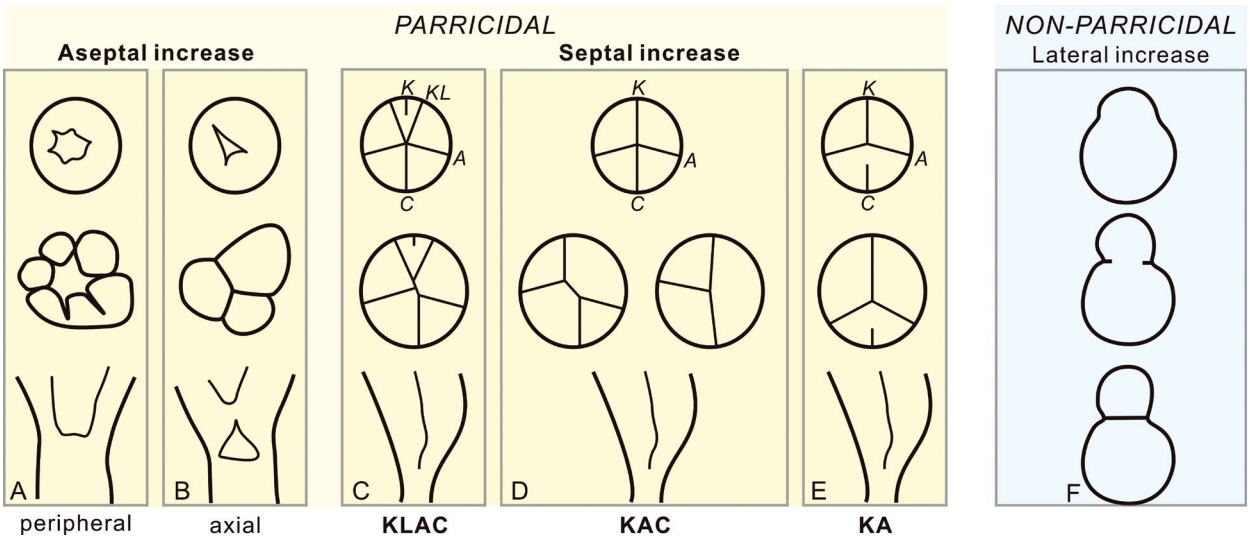


Fig. 1. Proposed classification of parricidal increase patterns (**A–E**) in rugose corals, along with a generalized non-parricidal lateral increase mode (**F**) for comparison. Newly introduced terms are indicated in bold. **A, B,** aseptal parricidal increase in which new separating walls are not based on pre-existing septa of the parent, modified after Scrutton (1998). **A,** peripheral aseptal parricidal increase in which offsets arise from the peripheral part of the tabularium, and do not meet in axis; based on *Entelophyllum articulatum* Wahlenberg, 1821. **B,** axial aseptal parricidal increase in which offsets meet in axis; based on *Thamnophyllum germanicum* Scrutton, 1968. **C–E,** septal parricidal increase in which new separating walls are formed from pre-existing septa of the parent. **C,** KLAC septal parricidal increase in which new separating walls are based on the two counter-lateral (KL), two alar (A), and cardinal (C) septa; based on *Parastauria shiqianensis* (Ge & Yu, 1974) (this study). **D,** KAC septal parricidal increase in which new separating walls are based on the counter, two (or rarely one) alar, and cardinal septa; based on *Stauria favosa* (Linnaeus, 1758) (Ezaki & Yasuhara 2004). **E,** KA septal parricidal increase in which new separating walls are based on the counter and two alar septa: based on *Paraceriaster major* (Fan in He, 1978) (this study). **F**, generalized non-parricidal lateral increase mode, adapted from Fedorowski & Jull (1976).

Center, Beijing; PMO = Paleontologisk Museum of Oslo, Oslo; SMC = Sedgwick Museum of Cambridge University, Cambridge; SNIIGGIMS = Geological Museum of the Siberian Research Institute of Geology, Geophysics, and Mineral Resources, Novosibirsk; SUP = Department of Geology, University of Sydney, Sydney; TUG = Geological Collections of the Natural History Museum, University of Tartu; UA = University of Aberdeen, Aberdeen; UNE = Department of Geology of the University of New England, Armidale; UpG = Museum of the Department of Geology and Subsoil Protection under the Council of Ministers of Tajikistan, Dushanbe; USNM = United States National Museum, Washington; VNIGRI = All-Russian Oil Research Prospecting Institute, Saint Petersburg; XACGS = Xi'an Center of Geological Survey, China Geological Survey, Xi'an; YPM = Yale Peabody Museum, New Haven.

Nomenclatural acts. – This published work and the nomenclatural acts it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:FEFCE21C-9ED5-4139-8DCD-49595B644BB3

Systematic palaeontology

With the exception of a few forms lacking proper illustration and/or description, all previously described cyathophylloidid and stauriid taxa are considered in this section. The primary exceptions include *Columnaria* cf. *kassariensis* Dybowski, 1873a of Kiær (1932) from the Kalstad Limestone (lower Katian) of Norway; *Columnaria* (?) *fascicularis* Radugin, 1936a from the upper Amzas Formation (Upper Ordovician) of the Gorny Altai; *Palaeophyllum stokesi* (Milne-Edwards & Haime, 1851) of Nelson (1963) from the Churchill River Group (middle Katian) of northern Hudson Bay Lowland; *Cyathophylloides* sp. of Olier *et al*. (1975a, b) from the Katian of Alaska; *Palaeophyllum* sp. of Bolton (1981) from the Amadjuak Formation (lower Katian) of southern Baffin Island; *Palaeophyllum siluriense* Cai, 1981 from the Jifuke Formation ("middle Silurian") of the Nilka area, northwestern Xinjiang; several "*Favistella*" species of Pak (1983) from the Sangso Formation (middle Katian?) of the southern Pyeongnam Basin; *Cyathophylloides* spp. A, B of Pandolfi (1985) from the middle Katian

portion of the Ely Springs Dolomite, Eastern Great Basin; and *Cyathophylloides* cf. C. *burksae* Flower, 1961 of Harris *et al.* (2019) from the Kope Formation (lower Katian) of northern Kentucky.

Among the taxa considered, species whose type material has been personally reassessed herein are redescribed and revised, with the examined specimens listed under "Referred Material" for each species. Species within each genus are presented in the order of their original publication, with the type species given priority and discussed first. It is worth noting that many species discussed are based on single specimens, which limits our understanding of their intraspecific variability. As a result, a more comprehensive investigation of larger collections may ultimately reveal that some of these species are synonymous.

The following anatomical abbreviations are adopted in this section: TS = transverse section; LS = longitudinal section; ACD (6+) = average diameter of corallites with 6 or more sides; Ta2, Ta5, Ta10 = number of tabulae per 2, 5, and 10 mm, respectively; WT = wall thickness.

Class Anthozoa Ehrenberg, 1834

Subclass Rugosa Milne-Edwards & Haime, 1850

Order Stauriida Verrill, 1865

Family Cyathophylloididae Dybowski, 1873a

1873a Cyathophylloididae Dybowski, p. 331 (*nom. correct.* Ivanovskiy 1967, p. 71, *pro* Cyathophylloidae Dybowski).
1873a Cyathophylloidinae Dybowski, p. 331 [*nom. correct.* Ivanovskiy 1973, p. 79, *pro* Cyathophylloinae Dybowski].
?1893 Favistellidae Chapman, p. 43.
1893 Favistellinae Chapman, p. 43 [*nom. transl.* He *et al.* 1989, p. 90, *ex* Favistellidae Chapman].

Diagnosis. – Stauriida with phaceloid to cerioid coralla, and exclusively lateral increase. Tabulae generally complete, flat to arched. Dissepiments are absent.

Definition. – Although a few workers formerly assigned cyathophylloidids and stauriids to separate families (e.g. Lavrusevich 1965, 1971, 1975, 1991; He & Li 1974, 1983; He 1980), they are now generally placed within a single family, the Stauriidae Milne-Edwards & Haime, 1850 (Ivanovskiy 1965, 1969; Hill 1981; He *et al.* 1989; Lin *et al.* 1995; Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013). In addition, many prefer to follow Ivanovskiy (1965) in regarding the two groups as two subfamilies of the Stauriidae (e.g. He *et al.* 1989; Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013).

In this study, since the evolutionary and taxonomic significance of increase modes in rugose corals is emphasised, cyathophylloidids and stauriids are both given full family status. The Cyathophylloididae is defined here as consisting of colonial (both fasciculate and cerioid) Stauriida with exclusively lateral increase, with typical members including *Palaeophyllum* Billings, 1858a, and *Favistina* Flower, 1961. It is distinguished from the Stauriidae Milne-Edwards & Haime, 1850 by lacking the septal parricidal increase of the latter. It should be mentioned that the original incorrect spelling of the family was in error, which was subsequently corrected by Ivanovskiy (1967, p. 71), rather than Ivanovskiy (1972, p. 75) as claimed by some workers (e.g. Hill 1981; McLean & Copper 2013).

Generic composition. – Genera that were formerly assigned to the Cyathophylloididae include *Palaeophyllum* Billings, 1858a, *Cyathophylloides* Dybowski, 1873a, *Synamplexoides* Stearn, 1956, *Parabrachyelasma* Tcherepnina, 1960, *Favistina* Flower, 1961, *Crenulites* Flower, 1961, *Modesta* Tcherepnina, 1962, *Proterophyllum* Sokolov in Ivanovskiy, 1969, *Palaeolithostrotion* Lavrusevich, 1975, *Leptelasma* Sytova, 1979b, and *Cereoelasma* Ivanovskiy, 1988 (Ivanovskiy 1969, 1975, 1988, 1992; Hill 1981; Sytova & Ulitina 1983; Lin *et al.* 1995; McLean & Copper 2013; He & Tang 2013). However, uncertainty remains as to the generic composition of the family.

Among these forms, *Palaeophyllum*, *Cyathophylloides*, *Favistina*, *Crenulites*, and *Palaeolithostrotion* are recognised in this study as valid members of the Cyathophylloididae. They are interpreted as phylogenetically related, forming a monophyletic group, as detailed in the Cyathophylloidid Origin and Evolution section, below. Additionally, some inadequately known Palaeophyllum-like forms, considered below, appear to differ primarily in possessing amplexoid septa, potentially representing a distinct cyathophylloidid genus. However, they are temporarily excluded from the Cyathophylloididae due to their uncertain affinities with some unrelated amplexoid forms. These include those exhibiting an aseptal parricidal increase mode, which suggests a close affinity with *Entelophyllum* Wedekind, 1927, as well as those typified by rather thin septa commonly coated by lamellar tissues, suggesting a close relationship with the family Amplexoididae Wang in Wang *et al.*, 2018.

The genera excluded here from the family are discussed as follows.

Synamplexoides Stearn, 1956, with the type species S. *varioseptatus* Stearn, 1956 from the middle Silurian Chemahawin Member of the Cedar Lake Formation of Ottawa, eastern Canada, was regarded by Hill (1981, p. F138) as a questionable synonym of *Palaeophyllum*. However, it differs in possessing amplexoid septa and a septal microstructure predominantly of lamellar

type (e.g. He & Tang 2013). These characteristics suggest a closer affinity with the family Amplexoididae Wang in Wang *et al.*, 2018.

Parabrachyelasma Tcherepnina, 1960 has the type species *P. lebediense* Tcherepnina, 1962 from the lower Tekhtan' Horizon of possible early Ashgill (middle Katian) age in the River Lebed area of the Gorny Altai (Ivanovskiy 1969, p. 112; McLean & Copper 2013, p. 55). Many authors (Ivanovskiy 1965, 1969; Webby 1972; McLean 1977) treated it as a synonym of *Palaeophyllum* Billings, 1858a, whereas others (e.g., Hill 1981; McLean & Copper 2013) preferred to include it within the Streptelasmatidae Nicholson in Nicholson & Lydekker, 1889. The reason for the latter placement is the development of "some joined septal lobes and lamellae in the axial area" (McLean & Copper 2013, p. 55). Although the type species was said by Tcherepnina (1960) to display lateral increase, a probably congeneric form described by Sytova & Ulitina (1983) as *Palaeophyllum virgultum* (Tcherepnina, 1960), from the Sairin Subhorizon (probably upper Katian; Ulitina *et al.* 2009) of the Khangai Horizon in Gobi Altai, shows a "quadripartite increase mode" (Sytova & Ulitina 1983, p. 101) possibly suggestive of an aseptal parricidal increase type. If verified, this feature supports a reassignment to *Entelophyllum*-like rugosans.

Modesta Tcherepnina, 1962, with the type species *M. prima* Tcherepnina, 1962 from the Upper Ordovician of the Gorny Altai, was assigned by Tcherepnina (1962) to the Streptelasmatidae Nicholson in Nicholson & Lydekker, 1889. Some authors (e.g. Ivanovskiy 1969; McLean 1977) later considered it as synonymous with *Palaeophyllum* Billings, 1858a and hence reassigned it to the Stauriidae. The latter treatment has now been generally retained, but this genus is regarded as separable from *Palaeophyllum* by having a thick peripheral stereozone and weakly developed tabulae (Hill 1981; Ulitina in Sytova & Ulitina, 1983; Lin *et al.* 1995; McLean & Copper 2013). However, septa of *M. prima* are of two orders, "laterally contiguous in wide peripheral stereozone", and each consists of "a single longitudinal series of contiguous trabeculae directed upward and inward", as described by Tcherepnina (1962, p. 141) and Hill (1981, pp. F135, F136). Such a septal feature is also shown in an enlarged transverse section of the other assigned species of the genus, *M. gobiensis* Ulitina in Sytova & Ulitina, 1983, from middle Katian rocks of the Gobi Altai, southern Mongolia (Sytova & Ulitina 1983, pl. 14, fig. 7). This, combined with the weak tabular development, indicates a close affinity with monacanthine rugose corals, to which *Modesta* is best referred.

Proterophyllum Sokolov in Ivanovskiy, 1969 has its type species, *Favistella simplex* Sokolov, 1955, from the "Middle Ordovician" of the Moyero River, Siberian Platform. It has been variably placed in the Stauriidae (Sokolov in Ivanovskiy 1969; Hill 1981; Lin *et al.* 1995; McLean & Copper 2013), or the Tryplasmatidae Etheridge, 1907 (Sytova 1979a; Hill 1981). In view of its spinose septal nature, *Proterophyllum* is considered here as a possible synonym of *Foerstephyllum* Bassler, 1941, a form now regarded as a tabulate coral (Hill 1981; Scrutton 1997).

Leptelasma Sytova, 1979b has *Tabularia oblonga* Zheltonogova, 1961 from the Chagyrka Horizon (Wenlock; Sennikov *et al.* 2015) of Altai as its type species, although Sytova & Ulitina (1983) inappropriately proposed *Dokophyllum sociale* Soshkina, 1937 to replace it as the type. *Tabularia oblonga* develops amplexoid septa, which was stated in the original description and shown in the illustrations (Zheltonogova 1961, p. 80, pl. S-18, 4a, b), but is otherwise like typical *Palaeophyllum*. This led Sytova & Ulitina (1983) to place *Leptelasma* in the Cyathophylloididae. However, weakly colonial coralla and thin, amplexoid septa justify the probable reassignment of *Leptelasma* to the Amplexoididae Wang in Wang *et al.*, 2018.

Cereoelasma Ivanovskiy, 1988 was also described by Ivanovskiy (1992) as a new form but spelt differently as *Cerioelasma*. The type species is *C. sibiricus* Ivanovskiy, 1988, occurring in the "lower Yaralinsky Formation" (now Yaralin Formation, Wenlock; Tesakov *et al.* 2003) on the Siberian Platform. It was originally attributed to the Cyathophylloididae, but the existence of one row of dissepiments justifies its exclusion from that family.

Subfamily classification. – For the present, given the close relationships among the assigned genera of the Cyathophylloididae, there is no good reason to make a subfamily classification. Note that Ivanovskiy (1975) split the family into the eponymous subfamily and the Agetolitinae Kim, 1962. This view is rejected here due to the strong tabulate affinity of the agetolitid corals (see also a thorough review in Wang & Cui 2025).

Excluded species. – Quite a few aporous colonial Ordovician and/or Silurian coral species were previously assigned to the Cyathophylloididae, and in early coral studies many were described under *Columnaria* Goldfuss, 1826, a genus long accepted as a senior synonym of *Favistella* Dana, 1846 (= *Favistina* Flower, 1961).

Species of Ordovician age that should be excluded from the family are as follows.

Lithostrotion stokesi Milne-Edwards & Haime, 1851, originally said to occur in the "Carboniferous" of the Lake Winnipeg area, Manitoba, Canada, was later assumed to be a *Palaeophyllum* species derived from the Upper Ordovician or possibly lower Silurian of the area (Bassler 1915, p. 261; Hill 1959, p. 10; Sinclair 1961, p. 13; McLean & Copper 2013, p. 58). A further possibility proposed by Flower (1961, pp. 88, 89) is that this species may belong to *Eridophyllum* Milne-Edwards & Haime, 1850 from the Silurian Interlake Group west of Lake Winnipeg, based on the existence of frequent processes connecting the corallites shown in its original illustration. In fact, the holotype of this taxon was studied in thin section by Easton & Oliver (1973). These authors concluded that it probably comes from a glacial drift of Early Devonian age, and belongs to *Acinophyllum* McLaren, 1959, a typical Devonian form referable to the family Eridophyllidae de Fromentel, 1861 (Hill 1981).

Favistella franklini Salter, 1852, from the "Richmondian" of Cape Riley, Wellington Channel, Qikiqtaaluk Region, Nunavut, Canada, was suggested by Flower (1961) to be a probable representative of *Saffordophyllum* Bassler, 1950.

Columnaria goldfussi Billings, 1858a is now known to occur in the Île aux Couleuvres Formation (probably lower Richmondian, middle Katian; Desbiens & Lespérence 1989, pp. 1194, 1195) of Couleuvres Island (formerly Snake Island), Lake St. John, Quebec. It was reassigned to *Nyctopora* Nicholson, 1879 by Bassler (1950), or to *Saffordophyllum* Bassler, 1950 by Flower (1961), with the latter of which I concur.

Columnaria erratica Billings, 1858a, from the Cobourg Formation equivalent (lower Edenian, lower Katian) of Lake St. John, Quebec, was regarded by Lambe (1901) as synonymous with *Palaeophyllum rugosum* Billings, 1858a from the same level and locality, a position echoed by subsequent authors (e.g. Bassler 1950; McLean & Copper 2013). However, a lectotype of this species was chosen and critically assessed by Sinclair (1961), who transferred it to *Eofletcheria* Bassler, 1950.

Columnaria parva Billings, 1859 and *C. incerta* Billings, 1859, both from the Chazy Group (Middle Ordovician) of the Mingan Islands, east of Quebec, Canada, were later chosen as the type species of *Billingsaria* Okulitch, 1936, and *Eofletcheria* Bassler, 1950, respectively (Hill 1981).

Columnaria carterensis Safford, 1869, from the Blackriveran strata (Sandbian) of Carters Creek, central Tennessee, USA, subsequently proved to be an example of *Lichenaria* Winchell & Schuchert, 1895 (Bassler 1950).

Cyathophylloides irregularis Dybowski, 1873a, originally described but not figured from the Silurian of "Karlso, Gotland", remains poorly understood. However, it is clearly not true *Cyathophylloides* because of its solitary form. Some workers regarded it as a possible species of *Cystiphyllum* (e.g. Lindström 1883, p. 8; Lang & Smith 1935a, p. 543), which is tentatively followed here.

Palaeophyllum divaricans Nicholson, 1875d was based on material from the Richmondian (middle–upper Katian) of the Cincinnati area, Ohio, with the lectotype designated by Elias (1982). It is now reassigned to *Streptelasma* Hall, 1847 (Elias 1982, 1983) or *Parastreptelasma* Li & Gong, 1996 (McLean & Copper 2013).

Streptelasma (*Palaeophyllum*) *aggregatum* Nicholson & Etheridge, 1878 has its type occurrence from the Craighead Limestone of Caradoc age, near Girvan (Nicholson & Etheridge 1878; Orita & Ezaki 2001). Wang (1948) also identified it from the Balclatchie Group of same age at Balclatchie. This species was assigned to *Palaeophyllum* by various workers (Wang 1948; Ivanovskiy 1969; Orita & Ezaki 2001), and tentatively by McLean & Copper (2013). Nicholson & Etheridge (1878, p. 72) noted "the summit of an old corallite dividing into no less than seven new ones" in this species, suggestive of an aseptal parricidal increase, which warrants its exclusion from both cyathophylloidids and stauriids.

Columnaria? *halli* Nicholson, 1879, from the "Trentonian" (upper Sandbian–lower Katian) of Canada, was subsequently designated as the type species of *Foerstephyllum* Bassler, 1941.

Columnaria parvituba Troedsson, 1928, from the Gonioceras Bay Formation (Sandbian; Rasmussen 2013) of Gonioceras Bay, North Greenland, was reassigned by Flower (1961) to *Billingsaria* Okulitch, 1936.

Columnaria crenulata Bassler, 1932, from the upper Hermitage Formation (lower Katian; Bergström *et al.* 2010a) of Tennessee, USA, was later reassigned to *Nyctopora* Nicholson, 1879 (Bassler 1950) or *Saffordophyllum* Bassler, 1950 (Flower 1961).

Columnaria simplissima Okulitch, 1936, probably from the Wardell Formation (Sandbian) east of Lexington, Kentucky, USA (Bassler 1950, p. 271), is now considered as a member of *Foerstephyllum* Bassler, 1941 (Bassler 1950; Flower 1961).

Columnaria magnifica Okulitch, 1938, from the "Blackriveran" (Sandbian) at Pauquette's Rapids, Ottawa River, Ontario, Canada, was regarded by some (Bassler 1950; Flower 1961) as a further species of *Foerstephyllum* Bassler, 1941.

Favistella simplex Sokolov, 1955, the type species of *Proterophyllum* Sokolov in Ivanovskiy, 1969, is derived

from the "Middle Ordovician" of the Moyero River, Siberian Platform. For the reason for its exclusion from cyathophylloidids, see remarks on that genus above.

Favistella major Yoh, 1959 comes from the lower "Pogoda Formation" (lower Katian) of the Huangping area, southeastern Guizhou Province. According to Yoh (1959, p. 400), it has large corallites (4–9 mm in diameter), short septa with "serrated inner margins" shown in longitudinal section, and sparse tabulae (6–8 in 10 mm). Yoh (1959) noted that it shows close resemblance with *Favistella simplex* Sokolov, 1955, which differs only in having smaller corallite size (up to 3 mm in diameter). Like the latter, considered above, this Chinese species is removed here to *Foerstephyllum* Bassler, 1941.

The three species, *Favistella ampla* Tcherepnina, 1960 and *F. densa* Tcherepnina, 1960 from the "Upper Ordovician" of the Amzas River basin, Shoria Mountain, and *F. ainkiensis* Tcherepnina, 1960 from the "Upper Ordovician" of the Anika River basin, Gorny Altai, all were synonymised by Ivanovskiy (1969) with *Proterophyllum simplex* (Sokolov, 1955), a species regarded here as belonging to *Foerstephyllum* Bassler, 1941.

Favistella grandis Tcherepnina, 1960 comes from the "Upper Ordovician" of the Lebed River basin, Gorny Altai. I follow Ivanovskiy (1969) in reassigning this species to *Proterophyllum* (= *Foerstephyllum* Bassler, 1941; this work).

Parabrachyelasma lebediensis Tcherepnina, 1960, the type species of *Parabrachyelasma* Tcherepnina, 1960, comes from the upper Gur'yanovka Formation of probably middle Katian age (Sennikov *et al.* 2019) in the River Lebed area of the Gorny Altai. Its exclusion from cyathophylloidids is discussed above in the remarks on *Parabrachyelasma*.

Parabrachyelasma virgulta Tcherepnina, 1960 occurs in strata now assigned to the Chebor Formation (Ivanovskiy 1969, p. 112), possibly of Hirnantian age (Sennikov *et al.* 2019), in the Samysh River area of the Gorny Altai. Its removal from cyathophylloidids has the same reason as *P. lebediensis* Tcherepnina, 1960, noted above.

Favistella (*Palaeophyllum*) *minimum* Yu, 1960 was documented from the "Upper Ordovician" (now Xiazhen Formation, uppermost Katian), Shiyang, JCY area, east China. Re-examination of the holotype indicates that its septa are of monacanthine type, supporting a transfer to monacanthine rugose corals.

Palaeophyllum gracile Flower, 1961, occurs in the lower Second Value Formation (middle Edenian, middle Katian; Sweet 1979, fig. 4; Elias 1985, p. 7) near the crest of the Scenic Drive, El Paso, Texas. Although corallites seem to grow mainly by lateral increase, one example of axial parricidal increase was noted by Flower (1961, pl. 47, fig. 5), where one corallite divided into three. This, combined with the absence of axial connection at septal ends, indicates an aseptal parricidal increase mode defined above, thereby supporting the exclusion of this species from both cyathophylloidids and stauriids.

Modesta prima Tcherepnina, 1962, the type species of the genus, occurs in the Upper Ordovician of the Gorny Altai. This form is removed here, possibly to monacanthine rugosans (see remarks on *Modesta* above).

Palaeophyllum proliferum Webby, 1972 is known from the strata of Fauna II age (early Katian) in central NSW (Webby 1972; McLean & Webby 1976). It has axial parricidal increase, and McLean & Copper (2013, p. 58) suggested a transfer to *Eostauria* He & Li, 1974. It is preferred to exclude it from both cyathophylloidids and stauriids owing to its probable aseptal parricidal increase mode.

Palaeophyllum pasense Stearn, 1956 of Caramanica (1973), from the upper Bighorn Formation (upper Katian) of the Bighorn Mountains, northern Wyoming, has amplexoid septa, and is better removed from cyathophylloidids.

Palaeophyllum jugatum McLean & Webby, 1976, from the Gunningbland Formation (upper Eastonian, middle Katian; Percival *et al.* 2023) of the Gunningbland area, NSW, was originally regarded by Webby (1969, p. 642) as a possible synonym of what is now known as *Palaeophyllum proliferum* Webby, 1972. It was subsequently thought to be distinct (Webby, 1972, p. 153) and formally erected as a new species by McLean & Webby (1976). Owing to its axial parricidal increase, it was reassigned to *Eostauria* He & Li, 1974 by many authors (He & Chen 2004, p. 185; Tang *et al.* 2008a, p. 309, 2008b, p. 413; McLean & Copper 2013, p. 58). Like *Palaeophyllum proliferum* Webby, 1972, discussed above, it is excluded here from both cyathophylloidids and stauriids.

Palaeophyllum thomi (Hall in Emory, 1857) of Latypov (1978) originates from the uppermost part (upper Katian?) of the Baraninsky Formation in the Sette–Daban area, northeastern Russia. Given its probable amplexoid septal nature, it is tentatively excluded from the Cyathophylloididae.

Palaeophyllum irregulare Lin & Chow, 1980, also introduced as a new species by Lin & Chow in Deng *et al.* (1983), is known from the lower Yenwashan Formation (Sandbian; Wang *et al.* 2015) of Daqiaotou, JCY area, east China. The holotype of this species was re-examined revealing a monacanthine septal nature, which hence supports a reassignment to monacanthine rugosans.

Modesta gobiensis Ulitina in Sytova & Ulitina, 1983, from the Sairin Subhorizon (probably upper Katian; Ulitina *et al*. 2009) of the Gobi Altai, southern Mongolia, is the only other assigned species of the genus. Compared with *M. prima* Tcherepnina, 1962, discussed above, it has similar septal and tabular development, differing only in having significantly larger corallites, and rare tabulae, and is also excluded here from cyathophylloidids for the same reason.

Palaeophyllum crassum Webby, 1972 and *Palaeophyllum patulum*? (McLean & Webby, 1976) of Sytova & Ulitina (1983) both occur in the Sairin Subhorizon (probably upper Katian; Ulitina *et al*. 2009) of the Khangai Horizon, Gobi Altai. The former has aseptal peripheral parricidal increase, with "up to 6 new corallites produced at the same time" Sytova & Ulitina (1983, p. 97), and it is therefore clearly not the species referred to and is therefore best excluded from both cyathophylloidids and stauriids. *Palaeophyllum patulum*? of Sytova & Ulitina (1983) is strongly similar to their *P. crassum*, although its increase mode remains to be clarified; the two forms are probably of the same group.

Palaeophyllum lebediense (Tcherepnina, 1960) and *Palaeophyllum virgultum* (Tcherepnina, 1960) of Sytova & Ulitina (1983), both from the Sairin Subhorizon (probably upper Katian; Ulitina *et al*. 2009) of the Khangai Horizon, Gobi Altai, are now excluded from cyathophylloidids (see remarks above on *Parabrachyelasma* Tcherepnina, 1960).

Palaeophyllum thomi (Hall in Emory, 1857) *sensu* Ulitina in Sytova & Ulitina (1983) comes from the Khangai Horizon (probably upper Katian; Ulitina *et al*. 2009), central Mongolia. This form has aseptal peripheral parricidal increase, indicated by the statement of "up to 7 new corallites produced at a time" and original illustrations (Sytova & Ulitina 1983, p. 98, pl. 14, figs 4, 5). This warrants its exclusion from both cyathophylloidids and stauriids.

Palaeophyllum gracile Flower, 1961 of Gierlowski & Langenheim (1985) is derived from the Horseshoe Mountain Member (middle Katian) of the Bighorn Formation in the Sawmill Flats area, northern Wyoming. Due to the presence of amplexoid septa, it is removed here from cyathophylloidids.

Palaeophyllum n. sp. *sensu* Melzak (2004) comes from the Laframboise Member (upper Hirnantian) of the Ellis Bay Formation, Anticosti Island, eastern Canada. This is a "dendroid *Palaeophyllum* with large corallites; a few septal lobes in axial region of larger corallites; increase generally octopartite, parricidal ('entelophylloid') as well as lateral; tabulae incomplete with complementary plates, or complete" (Melzak 2004, p. 284). The distinctive increase mode suggests a closer affinity with *Entelophyllum* Wedekind, 1927.

The excluded species of Silurian age are discussed below.

Columnaria gothlandica Milne-Edwards & Haime, 1851, from the "Stage f" (Lindström 1888, p. 21) now referrable to the lower Slite Group of late Sheinwoodian age (Calner *et al*. 2004) of Gotland, Sweden, was subsequently removed to *Favistella* (= *Favistina*) (Hill 1942a, p. 5) or to *Cyathophylloides* (Bassler 1950, p. 247). It was only illustrated in external view by Milne-Edwards & Haime (1851, pl. 16, fig. 2, 2a) and Bassler (1950, pl. 19, fig. 2), and a thin-section restudy is necessary to clarify its identity. Considering the significant stratigraphic gap between it and the youngest reliable records of both *Favistina* and *Cyathophylloides*, it is preferred here to be excluded from cyathophylloidids.

Palaeophyllum (*Cyathophylloides*?) *williamsi* Chadwick in Williams, 1919 occurs in the Manitoulin Formation (lower Rhuddanian), Manitoulin Island. This species was figured photographically by McLean (1977) and further revised by Fay (1983), suggesting the development of an intermittent, single row of dissepiments and strongly concave tabulae in its mature stages. McLean & Copper (2013, p. 78) therefore reassigned it to a ptychophyllid coral, *Strephophyllum* Lavrusevich, 1971.

Palaeophyllum umbellicrescens Chadwick in Williams, 1919 comes from the Manitoulin Formation (lower Rhuddanian), Manitoulin Island, with one syntype first figured by Bolton (1966). McLean & Copper (2013) recently reassessed its type material and chose a lectotype. Their revision implies that this species has a peripheral parricidal increase mode, and it is therefore excluded here from cyathophylloidids.

Palaeophyllum tubuliferum Reiman, 1958 *sensu* Ivanovskiy (1965), refigured by Ivanovskiy (1969) as *Palaeophyllum fasciculum* (Kutorga, 1837), from the "Llandovery" of Morkova River, Siberian Platform, has amplexoid septa, supporting its transfer to amplexoid corals.

"*Columnaria*" *gothlandica* Milne-Edwards & Haime, 1851 of Ivanovskiy (1969), with generic name incorrectly spelt *Colttmnaria*, shows prominent development of dissepiments. This led Ivanovskiy (1992) to transfer the material to his new genus *Cereoelasma*, a genus excluded here from cyathophylloidids, as discussed above.

Cyathophylloides fergusoni Merriam, 1973 comes from the "Coral Zone A" (upper Llandovery; Johnson & Oliver 1977) in the Roberts Mountains Formation at Ikes Canyon, Toquima Range, central Nevada. Pedder & Murphy (1997) suggested a probably Lochkovian

(Early Devonian) age for this coral horizon. This form is typified by cerioid coralla, major septa meeting axially, thick corallite walls, very short minor septa, and widely spaced tabulae. Given its considerable stratigraphic gap from the reliably documented records of cerioid cyathophylloidids, none of which extend beyond the Llandovery, it is tentatively excluded from the Cyathophylloididae in this study.

Palaeophyllum oakdalense McLean, 1975 comes from the "topmost Ordovician or basal Silurian" of the Mumbil area, central–western NSW, a horizon now assigned to the Bell River Member of the Dripstone Formation, of probable Homerian (Wenlock) age (McLean & Copper 2013). This species was proposed for the form earlier described by Strusz (1961) as *Palaeophyllum rugosum* Billings, 1858a, and the distinction of this form from the true *P. rugosum* was noted by Webby (1972) and McLean (1975). Given the peripheral parricidal increase and slightly amplexoid septa, it is removed here from cyathophylloidids.

Palaeophyllum halysitoides (Wilson, 1926) of Scrutton (1975) was collected from about 1750 m above the base of the Centrum Formation in southern Kronprins Christian Land, northeastern Greenland. Scrutton (1975) assigned it to the Late Ordovician; however, this designation is contradicted by the co-occurrence of the typical coral *Favosites*. This Greenland coral remains poorly understood, and the presence of somewhat amplexoid septa (Scrutton 1975, pl. 3, fig. 2) raises the possibility of its exclusion from the Cyathophylloididae.

?*Palaeophyllum* sp. of Scrutton (1975) is known from approximately 1150 m above the base of the Centrum Formation in the same area as his *P. halysitoides* discussed above. While Scrutton (1975) suggested a Late Ordovician age for this horizon, the associated *Favosites* indicates a Silurian age. In this Greenland form, "a single series of small, usually elongate dissepiments may be sporadically developed at the corallite margin" (Scrutton 1975, p. 20), suggesting its probable exclusion from cyathophylloidids.

Cyathophylloides silurica Guo, 1976, also introduced by Guo (1978) as a new form, occurs in the Xibiehe Formation (Ludlow; Li *et al.* 1985, Rong *et al.* 2013) of the Bateaobao (or Bater Obo) area, south–central Inner Mongolia. It has large corallites (7–8, rarely over 10 mm in diameter), thick peripheral stereozone consisting of laterally continuous distal septal ends, and carinate septa, and should be excluded from cyathophylloidids.

Cyathophylloides sp. f of Merriam & McKee (1976) is recorded from the lowermost, coral-brachiopod zone of possible Lochkovian (Early Devonian) age (Pedder & Murphy 1997) (formerly dated as "late Llandovery age"; Johnson & Oliver, 1977) in the Roberts Mountains Formation at Bootstrap Hill, Tuscarora Mountains, northern Nevada. This form shows weakly developed minor septa and widely spaced tabulae like *Cyathophylloides fergusoni*, discussed above, and the two species may be synonymous. However, a revision of this species is required to confirm their synonymy, since it was only figured without description and remains poorly known.

Palaeophyllum schuchertense McLean, 1977, from the Cape Schuchert Formation, Kap Schuchert, western Greenland, shows "calical, probably parricidal increase" (McLean 1977, p. 35), corresponding to the aseptal peripheral parricidal increase defined in this paper. It was regarded as an example of *Eostauria* He & Li, 1974 because of the superficially similar increase mode. However, it is best removed from both cyathophylloidids and stauriids, since such an increase type is very different from the two groups, as noted above.

Palaeophyllum bijishanense He, 1978 was described from the "lower Silurian" (probably equivalent to the Shihniulan Formation of late Aeronian age) of Biji Mountain, Yuexi area, southwestern Sichuan. McLean & Copper (2013, p. 58) commented that it may not belong to *Palaeophyllum* due to the possible amplexoid septa. In this study, the holotype of this species is re-examined, revealing the development of amplexoid septa, and a removal from cyathophylloidids is supported.

Palaeophyllum hubeiense of Kong & Huang (1978) from the Shihniulan Formation (upper Aeronian) of the Sinan area, northeastern Guizhou is included here within *Palaeophyllum major* He, 1985 from the same horizon and area, which is excluded (see below under the latter species).

Palaeophyllum xiashibeiense Guo, 1980, from the Xiashibei Formation ("upper Silurian", not "lower Silurian" stated by McLean & Copper 2013, p. 57) at Xiashibei, Naiman Banner, eastern Inner Mongolia, was briefly described and poorly illustrated, with septal microstructure unknown. According to the author, this form has fasciculate growth form characteristic of *Palaeophyllum*. However, it also shows large corallites (about 10 mm in diameter), short major septa (up to only 1/3 of corallite radius), and flat, widely spaced tabulae (Ta5 = 2). Since these characteristics are rare in *Palaeophyllum* and there exists a considerable stratigraphic gap from the youngest confirmed occurrences of the genus in the lower Llandovery, this species seems most likely unrelated to cyathophylloidids.

Palaeophyllum sp. *sensu* Bolton, 1981 is known from the Rhuddanian Becscie and possibly Merrimack formations of Anticosti Island, eastern Canada (McLean & Copper 2013, pp. 59, 60), with additional

material from the former horizon described by Melzak (2004). Part of Bolton's (1981) material was transferred by McLean & Copper (2013) to their new species *Palaeophyllum conjunctum*, discussed below. The presence of amplexoid septa in these specimens warrants its exclusion from cyathophylloidids, as also discussed above.

Favistina magna Sytova in Sytova & Ulitina, 1983, from the upper Alash Horizon (upper Rhuddanian–lower Aeronian; Sennikov *et al*. 2015) on the left bank of the Alash River, western Tuva, has very large corallites (9.0–12.5 mm in diameter) and amplexoid septa, the latter not mentioned in the description but shown in figures. These features suggest a potential attribution to *Crenulites*. However, due to the substantial range gap since the reliably documented occurrences of the genus, primarily within the middle Katian, this species is provisionally excluded from *Crenulites*. Its generic placement remains uncertain and requires further confirmation.

Palaeophyllum tubuliferum Reiman, 1958 *sensu* Sytova & Ulitina (1983), from the Kyzylchiraa Horizon (upper Aeronian; Sennikov *et al*. 2015), western Tuva, lacks well-differentiated tabulae typical of the true *P. tubuliferum* but appears to show the sporadic development of dissepiments. Thus, it is tentatively removed from cyathophylloidids.

Palaeophyllum fenggangense He, 1985 comes from the Shihniulan Formation (upper Aeronian) of the Fenggang area, northern Guizhou. Re-examination of the type material demonstrates the presence of peripheral parricidal increase and amplexoid septa, and this species is therefore excluded from cyathophylloidids.

Palaeophyllum major He, 1985 is derived from the Shihniulan Formation (upper Aeronian) of the Sinan area, northeastern Guizhou. The type material of this form is reassessed, which shows the development of peripheral parricidal increase and amplexoid septa, as in the holotype of *Palaeophyllum fenggangense* He, 1985 discussed above. This species is therefore also removed from cyathophylloidids.

Cyathophylloides carinatus Cao & Ouyang 1987, from the Yanglugou Formation (Pridoli) of the Zoige (Ruoergai) area, northwestern Sichuan, is not a true cyathophylloidid owing to the presence of thick peripheral stereozone and carinate septa.

Cyathophylloides xinjiangensis Cai, 1989 was stated to occur in the lower Kuoersaikeer Formation ("upper Silurian") of the Balikun area, northeastern Xinjiang. It is characterised by large corallites (up to 26 mm in diameter), thick peripheral stereozone consisting of laterally continuous distal septal ends, and the development of carinate septa, and should be thus excluded from cyathophylloidids.

Palaeophyllum fasciculum (Kutorga, 1837) of Ivanovskiy (1992) from the Silurian of Siberian Platform is removed due to the presence of dissepiments.

Palaeophyllum sp. A and *Palaeophyllum* sp. B, both described by Chen *et al*. (2005) from the Sifengya Formation (lower Telychian) of the Daguan area, northeastern Yunnan, southwestern China, are further forms that should be excluded from cyathophylloidids based on a recent re-examination of their described material. The former shows concave series of tabulae and somewhat amplexoid septa, and the latter has well-developed amplexoid septa; these features are uncommon in fasciculate cyathophylloidids.

Palaeophyllum conjunctum McLean & Copper, 2013 is known from the basal Merrimack and possibly uppermost Becscie formations (upper Llandovery) of Anticosti Island, eastern Canada. It develops a peripheral parricidal increase mode and is therefore excluded from cyathophylloidids.

Transferred species. – The following Ordovician species formerly assigned elsewhere are transferred here to cyathophylloidids, with present revisions indicated in square brackets. For more details, see remarks under these species below.

Cyathophyllum fasciculum Kutorga, 1837 from the Vohilaid Member (Porkuni, Hirnantian) of the Ärina Formation, northern Estonia [= *Palaeophyllum fasciculum* (Kutorga, 1837)].

Columnaria thomi Hall in Emory, 1857 from the Aleman Formation (early Maysvillian–early Richmondian, middle Katian) of the Montoya Group, El Paso, Texas, USA [= *Palaeophyllum thomi* (Hall in Emory, 1857)].

Columnaria vacua Foerste, 1909 from the Liberty Formation (lower Richmondian, middle Katian) of Kentucky, USA [= *Crenulites vacuus* (Foerste, 1909)]

Diphyphyllum? *halysitoides* Wilson, 1926 from the Beaverfoot Formation (likely from its middle Katian portion) of Macdonald Platform, northeastern British Columbia, western Canada [= *Palaeophyllum halysitoides* (Wilson, 1926)].

Palaeofavosites grandis Yu, 1960 from the "Upper Ordovician" (now lower–middle Katian Beiguoshan Formation) of Guyuan, southern Ningxia, northwestern China [= *Crenulites grandis* (Yu, 1960)].

Agetolites minor Lin, 1963 from the "Upper Ordovician" (now Liangchakou Formation of probably middle Katian age) of Manchuan, Xizhaochuan (formerly Zhaochuan), Shanyang, southeastern Shaanxi, northwestern China [= *Crenulites minor* (Lin, 1963)].

Palaeofavosites grandis var. *infidus* Deng & Li, 1979 from Koumenzi Formation (lower–middle Katian) of

the Qilian area, northeastern Qinghai, northwestern China [= *Crenulites grandis* (Yu, 1960)].

Agetolites rariperforatus Deng & Li, 1979, from the Koumenzi Formation (lower–middle Katian) of the Qilian area, northeastern Qinghai, northwestern China [= *Crenulites intermediatus* (Yu, 1960)].

The following Silurian species is transferred here to cyathophylloidids.

Syringopora? *multicaulis* Hall, 1852 from the Gasport Formation (Homerian), Lockport, New York [= *Palaeolithostrotion multicaule* (Hall, 1852)].

Genus *Palaeophyllum* Billings, 1858a

1858a *Palaeophyllum* Billings, p. 168.
1858b *Palaeophyllum* Billings, p. 422.

Type species. – *Palaeophyllum rugosum* Billings, 1858a, Cobourg Formation equivalent (lower Edenian, lower Katian), Little Discharge, Lake St. John, Quebec, by original designation.

Diagnosis. – Corallum phaceloid, dendroid, catenoid or subcerioid, with exclusively lateral increase. Major septa slender, short to long, even extending near the corallite centre generally with a free axial zone. Minor septa short. Peripheral ends of septa may be dilated to form narrow stereozone. Tabulae are generally complete, flat to variably arched, with a central platform that may have axial depression. Dissepiments absent. Modified after McLean & Copper (2013, p. 55).

Remarks. – In early coral studies, *Palaeophyllum* was considered as a close relative of *Streptelasma* Hall, 1847 and thus included in the family Streptelasmatidae Nicholson in Nicholson & Lydekker, 1889 (e.g. Lang *et al*. 1940; Hill 1951, 1956), although some authors (Lambe 1899, 1901; Duncan 1956; Yu 1960) had recognised its close relationship with cerioid cyathophylloidids (like *Favistina* Flower, 1961 and its synonyms) at that time. The latter view was not widely adopted particularly until Hill (1959, 1961), who revised the concept of *Palaeophyllum* based on a redescription of the type material of its type species, *P. rugosum* and suggested that it differs from other cyathophylloidid genera chiefly in its fasciculate growth form (e.g. Hill 1981; McLean & Copper 2013). In this work, *Palaeophyllum* is further confined to forms with exclusively lateral increase.

Several other fasciculate Ordovician and/or Silurian genera show resemblance to *Palaeophyllum*. *Palaeolithostrotion* Lavrusevich, 1975, revised below, is primarily distinguished by its generally bilaterally arranged major septa with axial ends of some fused, as well as typically strongly arched tabulae. *Synamplexoides* Stearn, 1956, which Hill (1981, p. F138) considered a questionable synonym of *Palaeophyllum*, differs in having amplexoid septa and predominantly lamellar septal microstructure (e.g. He & Tang 2013). *Parabrachyelasma* Tcherepnina, 1960 is distinguished by developing joined septal lobes and lamellae in the axis and possibly aseptal parricidal increase, and *Modesta* Tcherepnina, 1960 by having a thick peripheral stereozone, weakly developed tabulae, and septa of probably monacanthine nature. See above for a detailed discussion of these genera.

As discussed above, a great many species previously assigned to *Palaeophyllum* should be excluded. The Ordovician forms include *Lithostrotion stokesi* Milne-Edwards & Haime, 1851, *Palaeophyllum divaricans* Nicholson, 1875d, *Streptelasma* (*Palaeophyllum*) *aggregatum* Nicholson & Etheridge, 1878, *Parabrachyelasma lebediensis* Tcherepnina, 1960, *P. virgulta* Tcherepnina, 1960, *Favistella* (*Palaeophyllum*) *minimum* Yu, 1960, *Palaeophyllum gracile* Flower, 1961, *Modesta prima* Tcherepnina, 1962, *Palaeophyllum proliferum* Webby, 1972, *P. crassum* Webby, 1972, *P. jugatum* McLean & Webby, 1976, *P. irregulare* Lin & Chow, 1980, and *Modesta gobiensis* Ulitina in Sytova & Ulitina, 1983. Also excluded are *Palaeophyllum lebediense* (Tcherepnina, 1960), *P. thomi* (Hall in Emory, 1857), *P. virgultum* (Tcherepnina, 1960), and *P. patulum*? (McLean & Webby, 1976) of Sytova & Ulitina (1983), and *P.* n. sp. of Melzak (2004). Excluded species of Silurian age are *Palaeophyllum* (*Cyathophylloides*?) *williamsi* Chadwick in Williams, 1919, *P. umbellicrescens* Chadwick in Williams, 1919, *P. oakdalense* McLean, 1975, *P. schuchertense* McLean, 1977, *P. bijishanense* He, 1978, *P. xiashibeiense* Guo, 1980, *P. fenggangense* He, 1985, *P. major* He, 1985, and *P. conjunctum* McLean & Copper, 2013, as well as *Palaeophyllum tubuliferum* Reiman, 1958 of Ivanovskiy (1965) and Sytova & Ulitina (1983), *P. halysitoides* (Wilson, 1926) and ?*P.* sp. of Scrutton (1975), *P. hubeiense* of Kong & Huang (1978), *P.* sp. of Bolton (1981), *P. fasciculum* (Kutorga, 1837) of Ivanovskiy (1992), and *P.* sp. A and *P.* sp. B of Chen *et al*. (2005).

Palaeophyllum rugosum Billings, 1858a

1858a *Palaeophyllum rugosum* Billings, p. 168.
1858b *Palaeophyllum rugosum* Billings, p. 422.
1899 *Columnaria rugosa* (Billings); Lambe, pp. 217–219.
1901 *Columnaria rugosa* (Billings); Lambe, pp. 101, 102, pl. 6, fig. 3, 3a, b.
1925 *Columnaria alveolata discreta* Foerste; Hume, p. 18.
1925 *Columnaria* (*Palaeophyllum*) *stokesi* (Milne-Edwards & Haime); Hume, p. 18.
1950 *Palaeophyllum rugosum* (Billings); Bassler, pl. 18, figs 15, 16 [refig. Lambe 1901, pl. 6, fig. 3a, b].
1959 *Palaeophyllum rugosum* Billings; Hill, pl. 1, fig. 6a, b.

non 1960 *Palaeophyllum rugosum* Billings; Pestana, p. 868, pl. 109, fig. 5.
1961 *Palaeophyllum rugosum* Billings; Hill, pp. 1, 2, pl. 1, figs 1–6 [3, 4, refig. Hill 1959, pl. 1, fig. 6a, b].
1961 *Palaeophyllum humei* Sinclair, pp. 11, 12, pl. 3, figs 1–6.
non 1961 *Palaeophyllum rugosum* Billings; Strusz, p. 341, pl. 42, figs 7, 8, 15, text-fig. 3.
1963 *Palaeophyllum stokesi* (Milne-Edwards & Haime); Nelson, p. 31, pl. 6, fig. 6.
1965 *Palaeophyllum rugosum* Billings; Ivanovskiy, text-fig. 46a–c [refig. Lambe 1901, pl. 6, fig. 3, 3a, b].
1969 *Palaeophyllum thomi* (Hall); Ivanovskiy *pars*, pp. 81–84, text-figs 16c, d [refig. Hill 1961, pl. 1, 3, 4] *only*.
non 1975 *Palaeophyllum* sp. cf. *P. rugosum* Billings; Hall, pp. 78, 79, pl. 1, figs a–e.
1981 *Palaeophyllum rugosum* Billings; Hill, fig. 74, 1a–d [refig. Hill 1961, pl. 1, figs 4, 2, 5, 3].
non 1985 *Palaeophyllum humei* Sinclair; Gierlowski & Langenheim, pp. 7, 8, pl. 1, figs 5, 6, pl. 2, figs 1–5, pl. 3, figs 1–3.
?1985 *Palaeophyllum humei* Sinclair; Pandolfi, pp. 35, 36, pl. 14, 1, 2, pl. 24, figs 1, 2.
1995 *Palaeophyllum rugosum* Billings; Lin *et al*., pl. 2, fig. 7a, b [refig. Hill 1961, pl. 1, figs 3, 4].

Remarks. – The type locality of *Palaeophyllum rugosum* is Little Discharge of Lake St. John, Quebec. However, there was some confusion as to its type horizon. It was said to occur in "Trenton" (Billings 1858a, b), "Black River or lowermost Trenton" (Hill 1961), or presumably the "Simard limestone of Black River age" (Flower 1961). McLean & Copper (2013) recently commented that the coral-bearing horizon is an equivalent of the Cobourg Formation of early Edenian (early Katian) age, and, according to Dr. Ross McLean (2024, pers. comm.), their stratigraphic data are derived from Sanford (1993, p. 751, fig. 11.7).

Billings (1858a, b) originally provided only a brief description but no illustrations of his *Palaeophyllum rugosum*, without any types designated. Lambe (1899, p. 218) selected and described a lectotype (GSC 1379) before presenting line drawings of its thin sections in 1901. This type specimen was later illustrated by Hill (1959, 1961, 1981), and a revision of *P. rugosum* was thereby given. Her revision shows that *P. rugosum* is characterised by lateral increase, fasciculate to slightly cerioid coralla, large corallites (commonly 5–6, rarely up to 9 mm in diameter), 20 major septa, reach or almost reach the corallite centre without axial structures, and complete tabulae generally with an axial depression.

Palaeophyllum humei Sinclair, 1961, considered here as a synonym of *P. rugosum*, is based on the type material (holotype, GSC 13627; paratypes, GSC 13628 to 13632) from "the Liskeard Formation", "2 miles west of New Liskeard", Lake Timiskaming outlier, Ontario, a level now belonging to the Farr Formation (lower Edenian, lower Katian) of the Liskeard Group (McLean & Copper 2013). Sinclair (1961) also includes *Columnaria alveolata discreta* and possibly *Columnaria* (*Palaeophyllum*) *stokesi sensu* Hume (1925) in this species. As defined by Sinclair (1961), *Palaeophyllum humei* has loosely cerioid or cateniform coralla, corallites 4.0–6.0 mm in diameter, long major septa extending to the corallite centre, short but prominent minor septa, and subhorizontal tabulae commonly with axial depression. This author suggested that "it is more halysitoid than *P. rugosum* and has longer secondary septa and more angular corallites" (Sinclair 1961, p. 12). However, these differences are best treated as natural variation, and the two species are therefore regarded here as synonymous.

Palaeophyllum humei Sinclair, 1961 of Pandolfi (1985) comes from the Lost Canyon Member (middle Katian) of the Ely Springs Dolomite, northern Egan Range, Nevada. It shows similar, partly cerioid or cateniform growth habit and septal development, but appears to differ in having smaller corallites (4–5 mm) and generally arched tabulae. "Major septa may be fused at their tips in groups of two or three" (Pandolfi 1985, p. 36), which cannot be confirmed from his illustrations. This form is tentatively included within *P. rugosum*.

The single specimen described by Pestana (1960) as *Palaeophyllum rugosum* comes from the Johnson Spring Formation (Trentonian, upper Sandbian–lower Katian) in Independence Quadrangle, California. The figure of the transverse section indicates the presence of a marked cardinal fossula, a feature never seen in cyathophylloidid corals, and this supports its exclusion from *Palaeophyllum*. Oliver in Ross (1966, pp. 23, 24) also remarked that it would not "justify comparison with Billings' species".

Palaeophyllum rugosum sensu Strusz (1961), revised by McLean (1975) as *P. oakdalense*, comes from the strata now assigned to the Bell River Member of the Dripstone Formation of probable Homerian (Wenlock, Silurian) age (McLean & Copper 2013). This form is now removed from cyathophylloidids, as discussed above.

Palaeophyllum sp. cf. *P. rugosum* Billings of Hall (1975) was described from the 'Uralba Beds' (middle Katian), southeast of Manilla, northeastern NSW, which was transferred by Wang *et al*. (2021) to *Palaeophyllum bothroides* Hall, 1975 (see discussion below under the latter species).

It should be noted that *Columnaria erratica* Billings, 1858a, from the same general area and stratigraphic level as *Palaeophyllum rugosum*, was regarded by Lambe (1899, 1901) as synonymous with *P. rugosum*, a position followed by McLean & Copper (2013). However, a lectotype of this species was chosen and studied by Sinclair (1961), who concluded with a probable transfer to *Eofletcheria* Bassler, 1950.

The material documented by Gierlowski & Langenheim (1985) as *Palaeophyllum humei*, from the upper part (Horseshoe Mountain Member, middle Katian–? basal upper Katian) of the Bighorn Dolomite

in the Sawmill Flats area, northern Wyoming, is transferred here to *Palaeolithostrotion vaurealense* (Twenhofel, 1928), discussed below.

Palaeophyllum fasciculum (Kutorga, 1837)

(Figs 2, 3)

1837	*Cyathophyllum fasciculum* Kutorga, p. 41, pl. 8, fig. 6, pl. 9, fig. 4.
1861	*Diplophyllum fasciculum* (Kutorga); Schmidt, p. 231.
1873a	*Cyathophyllum fasciculum* Kutorga; Dybowski, p. 380.
1873b	*Cyathophyllum fasciculum* Kutorga; Dybowski, p. 124.
1958	*Palaeophyllum tubuliferum* Reiman, pp. 43, 44, pl. 2, figs 1–3, text-fig. 1.
non 1965	*Palaeophyllum tubuliferum* Reiman; Ivanovskiy, pp. 113, 114, pl. 28, fig. 1a, b.
non 1969	*Palaeophyllum fasciculum* (Kutorga); Ivanovskiy, pp. 85, 87–89, pl. 8, fig. 2a, b [refig. Ivanovskiy 1965, pl. 28, fig. 1a, b], pl. 9, figs 1a, b, 2a, b, text-figs 19–22.
non 1974	*Palaeophyllum fasciculum* (Kutorga); Ivanovskiy & Kulkov, pp. 32, 33, pl. 8, fig. 1a, b, pl. 9, fig. 1a, b.
non 1983	*Palaeophyllum tubuliferum* Reiman; Sytova & Ulitina, p. 100, pl. 15, fig. 1a, b.
?1986	*Palaeophyllum fasciculum* (Kutorga); Sultanbekova, p. 88, pl. 22, fig. 2a–c, pl. 23, figs 1, 2a, b.
non 1992	*Palaeophyllum fasciculum* (Kutorga); Ivanovskiy, pp. 122, 123, pl. 21, fig. 2a, b.

Referred material. – TUG 1788-15, topotype, Ärina Formation (Porkuni Stage, Hirnantian), Kaomäe Quarry, central Estonia, figured here (Fig. 2A–D). GIT 397-1905, labelled "*Palaeophyllum fasciculus* (Kutorga, 1837)", collected by Silvi Mägi in 1964, figured here (Fig. 2E–G), lower (but not the lowermost) Varbola Formation (lower Rhuddanian; Meidla *et al.* 2023a), Härgla Quarry, northern Estonia. GIT 124-2 (formerly Co 1273), holotype of *Palaeophyllum tubuliferum* Reiman, 1958, original of Reiman (1958, pl. 2, figs 1–3), refigured here (Fig. 3), Hilliste Formation (upper Rhuddanian–? lower Aeronian), Rohuküla Quarry, western Estonia.

Remarks. – Without a designated type, *Palaeophyllum fasciculum* is derived from the rocks now referable to the Vohilaid Member (Hirnantian) of the Ärina Formation (Hints *et al.* 2000; Meidla *et al.* 2023b) at Kaomäe Quarry, northern Estonia. Kutorga (1837) originally provided a brief description with line drawings of external views, and no thin-section study has since been performed. According to Dybowski's (1873a, p. 380) description, the diagnostic features of this species include lateral increase, medium-sized corallites (3–5 mm in diameter), and well-differentiated "bell-shaped" tabulae. These features are also evident in the topotype (TUG 1788-15) figured here both externally and internally (Fig. 2A–D).

Palaeophyllum tubuliferum Reiman, 1958 was initially documented from the slightly younger, lower (but not the lowermost) Juuru Stage (lower Rhuddanian; Meidla *et al.* 2023a) of Estonia. Given the inadequate quality of original illustrations, its holotype, along with a clearly conspecific specimen labelled "*Palaeophyllum fasciculum* (Kutorga, 1837)" from the same horizon at Rohuküla Quarry, is refigured here. As noted by Reiman (1958), this species has corallite size and septal number similar to *P. fasciculum*, differing only in exhibiting distinctive tabular differentiation into axial and peripheral zones. However, as demonstrated above, such a tabular feature also occurs in *P. fasciculum*, and there is therefore no reason for a specific separation from the latter, a view also held by Sultanbekova (1986) and Ivanovskiy (1969, 1992).

Apart from its occurrences in Estonia, this species was also listed from Etage 5a and 5b (Katian) of the Asker area, southern Norway (Kiær 1902; Kaljo *et al.* 1963). However, this record has not been formally described thus far.

Palaeophyllum fasciculum of Sultanbekova (1986), from the Chokpar Formation of latest Katian age (Apollonov *et al.* 1980; Popov *et al.* 2023) in the Anthar river valley, appears to have larger corallites (6–7 mm in diameter) and thicker peripheral zone; its identity remains uncertain.

Palaeophyllum tubuliferum of Ivanovskiy (1965) comes from the "Llandovery" of Morkova River, Siberian Platform, and of Sytova & Ulitina (1983) from the "upper Llandovery" of western Tuva, both of which should be excluded. The reason is that the former develops amplexoid septa, indicating a transfer to amplexoid corals, and the latter lacks well-differentiated tabulae characteristic of *P. fasciculum*.

The material figured by Ivanovskiy (1969) as *Palaeophyllum fasciculum* contains three specimens attributable to different species, and all are again not true *P. fasciculum*. The one from the "lower Llandovery" of the Moyero River, Siberian Platform (Ivanovskiy 1969, pl. 8, fig. 2a, b), possesses amplexoid septa. The other two specimens (Ivanovskiy 1969, pl. 9, figs 1a, b, 2a, b) are holotypes of *Parabrachyelasma virgulta* Tcherepnina, 1960, and *Modesta prima* Tcherepnina, 1962, two unrelated species from the Upper Ordovician of the Gorny Altai.

Palaeophyllum fasciculum (Kutorga, 1837) of Ivanovskiy (1974), from the "Chinetinsky Horizon" (Llandovery; Sennikov *et al.* 2015) of the Gorny Altai, is revised here as *Palaeophyllum*? sp., considered below.

Palaeophyllum tubuliferum Reiman, 1958 *sensu* Sytova & Ulitina (1983), from the Kyzylchiraa Horizon (upper Aeronian), western Tuva, is removed from cyathophylloidids, as discussed above.

The specimen documented by Ivanovskiy (1992) as this species from the Silurian of Siberian Platform is

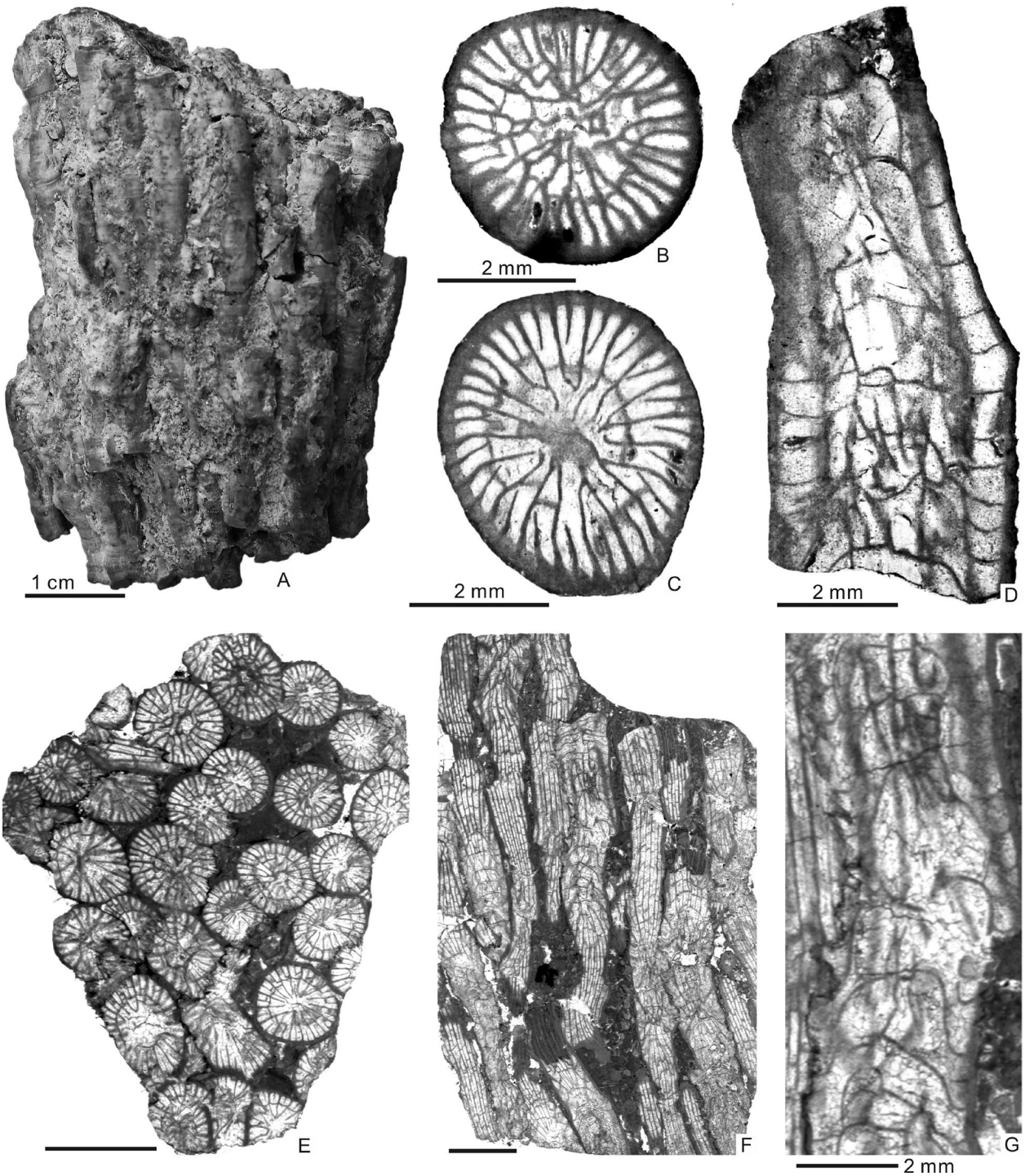


Fig. 2. Palaeophyllum fasciculum (Kutorga, 1837). **A–D,** TUG 1788-15, topotype, Ärina Formation (Porkuni Stage, Hirnantian), Kaomäe Quarry, central Estonia. **A,** side view; **B, C,** TSs; **D,** LS. **E–G,** GIT 397-1905, labelled "*Palaeophyllum fasciculus* (Kutorga, 1837)", collected by Silvi Mägi in 1964, lower Varbola Formation (Rhuddanian), Härgla Quarry, central Estonia. **E,** TS; **F, G,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated. All photos by Gennadi Baranov.

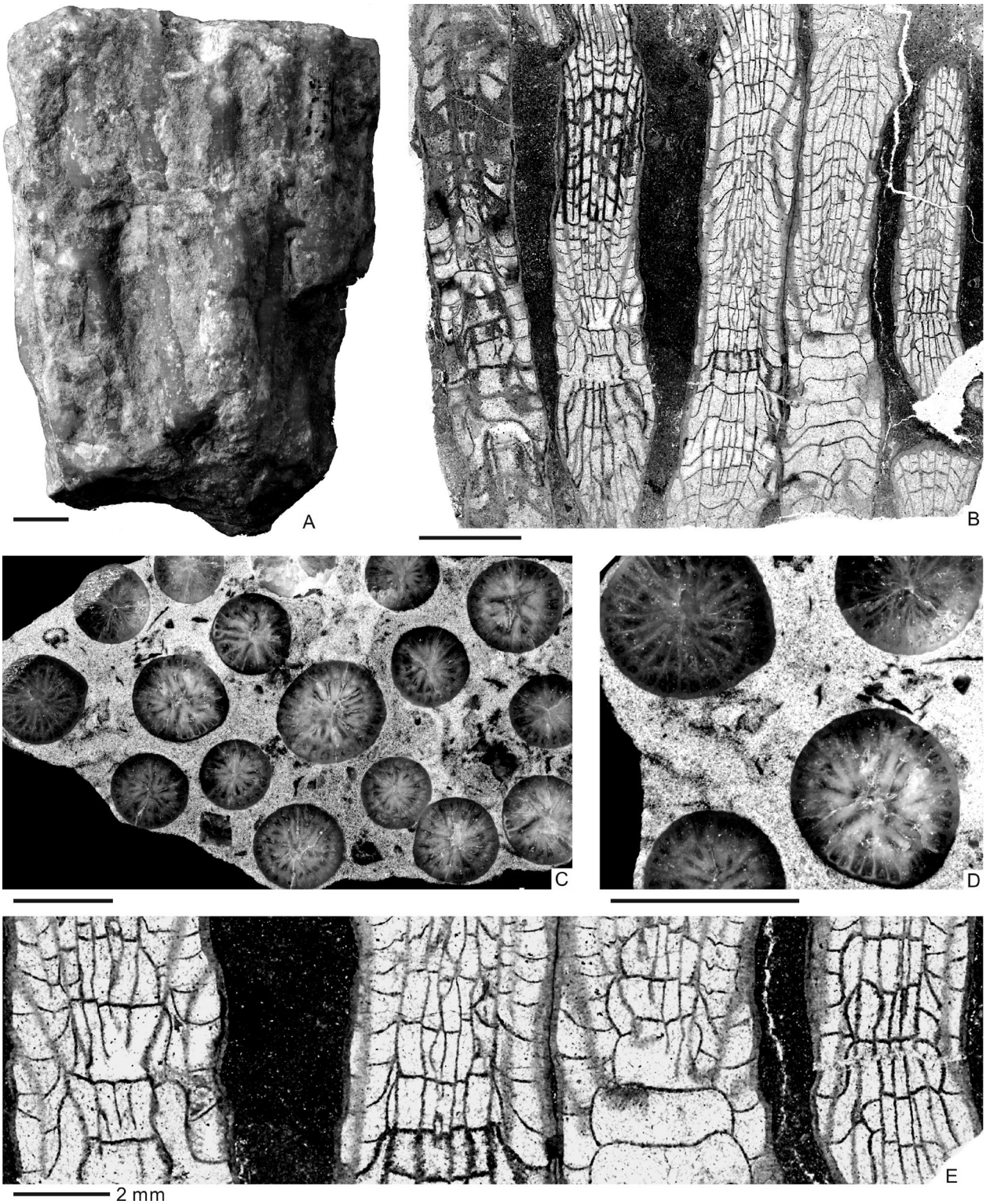


Fig. 3. Palaeophyllum fasciculum (Kutorga, 1837). GIT 124-2 (formerly Co 1273), holotype of *Palaeophyllum tubuliferum* Reiman, 1958, Hilliste Formation (upper Rhuddanian–? lower Aeronian), Rohuküla Quarry, western Estonia. **A,** side view; **B, E,** LS and an enlarged portion; **C, D,** TS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated. All photos by Gennadi Baranov.

also excluded, due to the presence of dissepiments, as shown in the figure of its longitudinal section.

Palaeophyllum thomi (Hall in Emory, 1857)

1857 *Columnaria thomi* Hall in Emory, pl. 20, fig. 1a–d.
1904 *Cyathophylloides thomi* (Hall); Walcott, pl. 29, figs 1a–d [refig. Hall in Emory 1857, pl. 20, fig. 1a–d], 2a, b.
1915 *Columnaria* (*Palaeophyllum*) *thomi* (Hall); Bassler, p. 261.
1950 *Palaeophyllum thomi* (Hall); Bassler, pl. 18, fig. 12–14, pl. 19, fig. 12.
1959 *Palaeophyllum thomi* (Hall); Hill, pp. 4–6, pl. 1, figs 1a–e, 2a–d.
non 1959 *Palaeophyllum thomi*? (Hall); Hill, pp. 6, 7, pl. 1, fig. 3.
1961 *Palaeophyllum thomi* (Hall); Flower, pp. 91, 92, pl. 47, fig. 9, pl. 51, 1–8, pl. 52, 1–7.
1969 *Palaeophyllum thomi* (Hall); Ivanovskiy *pars*, pp. 81–84, pl. 7, figs 2a, b, 3, pl. 8, 1a, b, text-figs 16a, b [refig. Hill 1959, pl. 1, 1a, d], *non* text-figs 16c, d, 17a, b.
non 1969 *Palaeophyllum thomi* var. *cateniforme* Flower; Ivanovskiy, pp. 84, 85, text-fig. 18a, b.
non 1975 *Palaeophyllum* sp. cf. *P. thomi* (Hall); Hall, p. 80, pl. 1, figs k–n.
non 1978 *Palaeophyllum thomi* (Hall); Latypov, p. 84, pl. 26, fig. 3a, b.
1979a *Palaeophyllum thomi* (Hall); Sytova, pp. 175, pl. 33, fig. 3a, b.
non 1983 *Palaeophyllum thomi* (Hall); Ulitina in Sytova & Ulitina, pp. 98, 99, pl. 13, fig. 2a, b, pl. 14, figs 4, 5.
non 1984 *Palaeophyllum thomi simplex* Deng, p. 319, pl. 3, fig. 1a, b.

Remarks. – The occurrence of *Palaeophyllum thomi* was not originally provided by Hall in Emory (1857), but Walcott (1904, p. 29) remarked that "the U. S. Geological Survey has collected this species in abundance about El Paso, Texas, associated with *Halysites*, *Hebertella insculpta*, *Rhynchotrema capax*, etc., indicating the Richmond formation". More precise stratigraphic data were subsequently given by Flower (1961, p. 92), who stated that *P. thomi* was from "the vicinity of El Paso, and none whatsoever as to its origin in the narrow coral zone within the Aleman", a rock unit now dated as early Maysvillian–early Richmondian (middle Katian) (Sweet 1979, fig. 4; Elias 1985, p. 7).

According to Walcott's (1904) statement, the material on which *Palaeophyllum thomi* was proposed is a single specimen (holotype, USNM 9851; Hill 1959, p.2; Flower 1961, p. 92) figured only externally by Hall in Emory (1857) without description. Thin-section study of this specimen was later presented by Bassler (1950) and Hill (1959), which was followed by Flower (1961), who described and figured five additional hypotypes from the Montoya Group of the general region. These studies show that *P. thomi* is typified by having lateral increase, corallites 4–5, and rarely 6 mm in diameter, major septa 20–22, rarely up to 24 in number and extending to or almost to the corallite centre, weakly developed minor septa, and arched tabulae commonly with an axial depression, and Ta5 = 7.

Specimens documented by Ivanovskiy (1969) and Sytova (1979a) from the Burian Horizon (upper Katian) of the Podkamennaya Tunguska River Basin exhibit mature corallites measuring 5–6 mm in diameter, occasionally reaching 7 mm. They possess relatively short major septa that do not extend to the corallite centre, weakly developed minor septa, and widely spaced tabulae (Ta5 = 8–10), which are arched with a distinct concave centre. Their morphological characteristics closely resemble those of *Palaeophyllum thomi*, particularly in septal and tabular development, with the primary distinction being their slightly larger corallite size. Given these similarities, their inclusion within *P. thomi* appears well justified.

The material figured by Hill (1959) as *Palaeophyllum thomi*? is from the slightly older Second Value Formation of the Mud Springs Mountains, which was subsequently removed by Flower (1961) to his new species *P. margaretae* (see remarks under that species below).

Palaeophyllum sp. cf. *P. thomi sensu* Hall (1975) comes from the 'Uralba Beds' (middle Katian), southeast of Manilla, northeastern NSW, a form recently regarded by Wang *et al*. (2021) as synonymous with *P. bothroides* Hall, 1975, considered below.

The materials documented as this species by Latypov (1978) from the uppermost part (upper Katian?) of the Baraninsky Formation in the Sette–Daban area of northeastern Russia and by Sytova & Ulitina (1983) from the Khangai Horizon (probably upper Katian) in the Gobi Altai are both excluded from the Cyathophylloididae (see remarks on the family above).

Palaeophyllum thomi simplex Deng, 1984, from the Beiguoshan Formation (lower–middle Katian) of Beiguoshan, Longxian area, western Shaanxi Province, is now revised as *Palaeophyllum*? *simplex* Deng, 1984, discussed below.

Palaeophyllum halysitoides (Wilson, 1926)

1926 *Diphyphyllum*? *halysitoides* Wilson, p. 18, pl. 2, figs 8, 9.
1928 *Columnaria halysitoides* Troedsson, p. 113, pl. 28, figs 1–5.
?1950 *Columnaria halysitoides* Troedsson; Ivanov & Myagkova, pp. 10, 13, pl. 2, fig. 1.
?1955 *Columnaria halysitoides* Troedsson; Ivanov & Myagkova, p. 35, pl. 18, fig. 2a, b [2b, refig. Ivanov & Myagkova 1950, pl. 2, fig. 1).
?1963 *Palaeophyllum halysitoides* (Wilson); Nelson, pp. 31, 32, pl. 5, fig. 4.
non 1975 *Palaeophyllum halysitoides* (Wilson); Scrutton, pp. 19, 20, pl. 3, figs 1, 2.

Remarks. – *Palaeophyllum halysitoides* is based on the poorly preserved material from the Beaverfoot Formation (possibly within its middle Katian part) in Beaverfoot Range, southeastern British Columbia, without designating a type. It was originally described briefly and illustrated externally and has never been studied in thin section. However, based on her observations, this species has a phaceloid to cateniform growth form with lateral increase and corallites ranging from 3 to 5 mm in diameter, though its tabulae are not preserved. Regarding septal structure, she noted that they are "about forty in number, primary and secondary, the former very fine, reaching nearly to the centre" and that "one corallite which is preserved almost to the centre shows a tendency for the gathered ends of the septa to make a very slight twist" (Wilson 1926, p. 18). Kirk (1927, pp. 287, 288) noted that this species "may be referable to *Palaeophyllum*", a similar position held by Nelson (1963), McLean & Copper (2013) and the present author.

Columnaria halysitoides Troedsson, 1928, from the Cape Calhoun Formation of late Edenian–early Maysvillian (middle Katian) age, western North Greenland, has remarkably similar diagnosis. Consequently, this species was synonymised by Nelson (1963) with *Palaeophyllum halysitoides* (Wilson, 1926), with which I concur, although it was treated by Bolton (1979, p.6) as a distinct species.

Additional possible examples of this species include *Columnaria halysitoides* Troedsson, 1928 *sensu* Ivanov & Myagkova (1950, 1955) from the "Upper Ordovician", which was subsequently suggested by Shurygina (1973) to be of "middle Caradoc" age, and *Palaeophyllum halysitoides* (Wilson, 1926) *sensu* Nelson (1963) from the Bad Cache Group (lower Katian), northern Hudson Bay Lowland. Both are inadequately known, and revisions are required.

The specimen documented by Scrutton (1975) as *Palaeophyllum halysitoides* (Wilson, 1926) from the upper part (Silurian?) of the Centrum Formation of northeast Greenland is excluded from cyathophylloids (see above).

Palaeophyllum? *pasense* Stearn, 1956

1956 *Palaeophyllum pasense* Stearn, pp. 89, 90, pl. 16, fig. 7.
non 1973 *Palaeophyllum pasense* Stearn; Caramanica, pp. 322–327, pl. 16, figs 4, 5.

Remarks. – This species comes from the lower Stonewall Formation (upper Katian; Elias *et al.* 2013a) of southern Manitoba. Its specific features include cateniform growth habit, medium-sized corallites (3.0–4.5 mm in diameter), 15 major septa that extend toward the corallite centre without converging and weakly developed minor septa (Stearn 1956). Caramanica (1973, p. 325) stated that septa of the holotype (GSC 10403) may be amplexoid, which cannot be confirmed from its original figures. Thus, an open nomenclature is used for this uncertainty.

Palaeophyllum pasense Stearn, 1956 of Caramanica (1973), from the upper Bighorn Formation (middle Katian–? basal upper Katian) of the Bighorn Mountains, northern Wyoming, is removed from *Palaeophyllum* due to well-developed amplexoid septa (see above).

Palaeophyllum? *parvum* Stearn, 1956

1956 *Palaeophyllum pasense parvum* Stearn, p. 90, pl. 7, fig. 5.

Remarks. – *Palaeophyllum*? *parvum* (holotype, GSC 10482; paratype, GSC 10494) occurs in the same horizon and general locality as *P*?. *pasense*, considered above. This form resembles the latter in halysitoid growth habit and weak development of minor septa but is separable by having much smaller corallites (1.7–2.0 mm in diameter) and fewer major septa (10 in number); it is therefore treated as a distinct species. It may belong to *Palaeophyllum*, but uncertainties regarding its septal nature and mode of increase justify the use of an open nomenclature.

Palaeophyllum mazourkense Pestana, 1960

1960 *Palaeophyllum mazourkensis* Pestana, pp. 867, 868, pl. 110, figs 1, 2.

Remarks. – The type material (holotype, MPUC 37701) comes from the Johnson Spring Formation (Trentonian, upper Sandbian–lower Katian) in Independence Quadrangle, California, and is the most abundant coral in that formation (Pestana 1960). The specific features include variable corallite size (3.8–8.6 mm in diameter), major septa long, but not extending to the corallite centre, subhorizontal, sparsely spaced tabulae (1.0–1.7 mm apart), and the absence of minor septa. Its mode of increase was not specified in the original description; however, the accompanying illustrations show a lateral increase.

Palaeophyllum mazourkensis resembles *P. rugosum* Billings, 1858a from the contemporary Simard limestone of the Lac St-Jean outlier, Quebec in general aspects but was said by Pestana (1960) to differ in having sparser tabulae and lacking minor septa. *P. rugosum* is further separable by having partly cerioid

coralla and longer major septa that extend almost to the corallite centre.

Palaeophyllum argus Sinclair, 1961

1879 *Diphyphyllum stokesi* Milne-Edwards & Haime; Whiteaves, pp. 152, 153, pl. 17, fig. 5, 5a, b.
1961 *Palaeophyllum argus* Sinclair, pp. 12, 13, pl. 4, figs 1–4, pl. 7, fig. 4.
1969 *Palaeophyllum fasciculum* (Kutorga); Ivanovskiy *pars*, pp. 85, 87, 88, text-fig. 20 [refig. Sinclair 1961, pl. 7, fig. 4, pl. 4, fig. 2] *only*.

Remarks. – The type material of *Palaeophyllum argus* (holotype, GSC 6878; paratype, GSC 6877) collected from the Red River Formation at Lower Fort Garry of southern Manitoba is actually from the Selkirk Member (Caramanica 1973, p. 321) of Maysvillian (middle Katian) age (Jin & Zhan 2001), rather than the stratigraphically lower, Dog Head Member (Edenian, lower Katian; Jin & Zhan 2001, as originally stated by Sinclair (1961, p. 12). The designated paratype is the specimen figured by Whiteaves (1879) as *Diphyphyllum stokesi*.

This species is characterised by having spiniform processes, a partly cerioid growth habit, corallites 5–7 mm in diameter, thick corallite walls, relatively long major septa, and complete, wall-spaced tabulae (Ta5 = 6). Although its mode of increase is not explicitly detailed in the original description or shown in the illustrations, it is probably lateral, as indicated by the statement that corallites are "attaining full size and growing from the parent" (Sinclair 1961, p. 12).

Palaeophyllum margaretae Flower, 1961

1959 *Palaeophyllum thomi*? (Hall); Hill, pp. 6, 7, pl. 1, fig. 3.
1959 *Palaeophyllum*? sp., Hill, pp. 9, 10.
1961 *Palaeophyllum margaretae* Flower, p. 90, pl. 47, figs 10, 11, pl. 48, figs 1–8.
1969 *Palaeophyllum fasciculum* (Kutorga); Ivanovskiy *pars*, pp. 85, 87, 88, text-fig. 21 [refig. Flower 1961, pl. 47, figs 10, 11] *only*.

Remarks. – *Palaeophyllum margaretae* (holotype, NMBM 688) is common in the Second Value Formation (middle Edenian to earliest Maysvillian age, middle Katian; Sweet 1979, fig. 4; Elias 1985, p. 7) in New Mexico. As outlined by Flower (1961, p. 90), this species is typified by medium-sized corallites (4.0–4.5, rarely 5.0 mm, in diameter), 20–24 major septa extending close to the corallite axis, well-developed minor septa (up to 1/3 the length of major septa), and complete to incomplete tabulae that are differentiated into axial and peripheral zones. Although a lateral increase was not explicitly mentioned in his description, it is evident in the figures of the holotype (Flower 1961, pl. 48, figs 1, 2).

Flower (1961) included the material described by Hill (1959) as *Palaeophyllum thomi*? and *P.*? sp. in his *P. margaretae*, from the outlier near Morenci, Arizona, and the Mud Springs Mountains, respectively, which is followed herein.

Palaeophyllum cateniforme Flower, 1961

1959 *Palaeophyllum* sp., Hill, pp. 7–9, pl. 1, figs 4, 5.
1961 *Palaeophyllum cateniforme* Flower, p. 91, pl. 49, figs 1–6, pl. 50, figs 1–5.
1969 *Palaeophyllum thomi* var. *cateniforme* Flower; Ivanovskiy, pp. 84, 85, text-fig. 18a, b [refig. Flower 1961, pl. 50, figs 3, 5].
1976 *Palaeophyllum cateniforme* Flower; Bolton in Workum *et al*., p. 168, pl. 1, figs 7, 8.
non 2007 *Palaeophyllum cateniforme* Flower; Erina, p. 36, pl. 37, fig. 3a–c.

Remarks. – *Palaeophyllum cateniforme* is based on the holotype (NMBM 688) from the Second Value Formation (middle Edenian to lowest Maysvillian, middle Katian; Sweet 1979, fig. 4; Elias 1985, p. 7) at the southern end of the Frankin Mountains, El Paso. This species is characterised by cateniform growth, large corallites (commonly 6 mm in diameter), long major septa that do not extend to the corallite axis, very short minor septa (up to 1/6 the length of major septa), and strongly sinuate, axially depressed, closely spaced tabulae (Ta10 = 12–15). A lateral increase is clearly illustrated in the figures of its holotype (Flower 1961, pl. 49, figs 1, 2, 4, 5).

The material described by Hill (1959) as *Palaeophyllum* sp., from the coeval strata in east–central Arizona, was placed by Flower (1961) in *P. cateniforme*, with which I concur. Further material included in *P. cateniforme* comes from the strata of similar age on Akpatok Island (Bolton in Workum *et al*. 1976).

The coral described by Erina (2007) as *Palaeophyllum cateniforme* Flower, 1961, from the uppermost Archalyk Member (uppermost Katian; Ghobadi Pour *et al.* 2023) of the Shahriomon Formation in Zeravshan–Hissar, is revised as *Palaeolithostrotion*? sp. B, discussed below.

Palaeophyllum? *crassum* Webby, 1972

1972 *Palaeophyllum crassum* Webby, pp. 153, 154, pl. 9, figs 1–3.
non 1983 *Palaeophyllum crassum* Webby; Sytova & Ulitina, pp. 96, 97, pl. 13, fig. 3a, b.
non 2003 *Palaeophyllum crassum* Webby; Ulitina, pl. 5, fig. 4, pl. 6, fig. 5 [refig. Sytova & Ulitina 1983, pl. 13, fig. 3a, b].

Remarks. – *Palaeophyllum*? *crassum* is solely based on the poorly preserved holotype (SUP 43237) from the upper Cargo Creek Limestone (middle Katian) southeast of a tributary of Canomodine Creek, central NSW.

Its key features include variable corallite size (6–12 mm in diameter), long major septa extending almost to the corallite centre and forming an "aulos-like structure", well-developed minor septa, and closely spaced tabulae (Ta5 = 7–11) that tend to develop well-differentiated axial and peripheral zones (Webby 1972, pp. 153, 154). However, the mode of increase of this species remains unestablished due to the limited material. Thus, its attribution to *Palaeophyllum* is still uncertain.

Palaeophyllum crassum Webby, 1972 *sensu* Sytova & Ulitina (1983), refigured by Ulitina (2003), from the Khangai Horizon (probably upper Katian; Ulitina *et al*. 2009) of the Gobi Altai, is excluded from cyathophylloidids in view of its parricidal increase pattern, as discussed above.

***Palaeophyllum*? *hubeiense* Ge & Yu, 1974**

(Fig. 4)

1974 *Palaeophyllum hubeiense* Ge & Yu, p. 166, pl. 73, figs 21, 22.
1977 *Palaeophyllum hubeiense* Ge & Yu; Jia & Wu, p. 17, pl. 5, fig. 2a, b [refig. Ge & Yu 1974, pl. 73, figs 21, 22].
?1977 *Palaeophyllum* cf. *hubeiense* Ge & Yu; McLean, p. 37, pl. 10, figs 3, 5, 7, 8, pl. 11, 5–7.
non 1978 *Palaeophyllum hubeiense* Ge & Yu; Kong & Huang, p. 59, pl. 18, fig. 2a, b.
1984 *Palaeophyllum hubeiense* Ge & Yu; Liu, p. 91, pl. 37, fig. 5a, b [refig. Ge & Yu 1974, pl. 73, figs 21, 22].
1987 *Palaeophyllum paradoxum* Jia in Jia & Lin, p. 202, pl. 3, fig. 7a, b, pl. 4, fig. 2a, b.
2019 *Palaeophyllum hubeiense* Ge & Yu; Zhu & Ma, p. 16, pl. 11, fig. 5a, b [refig. Ge & Yu 1974, pl. 73, figs 21, 22].

Referred material. – NIGP 22096 (TS) and NIGP 22097 (LS), holotype, original of Ge & Yu

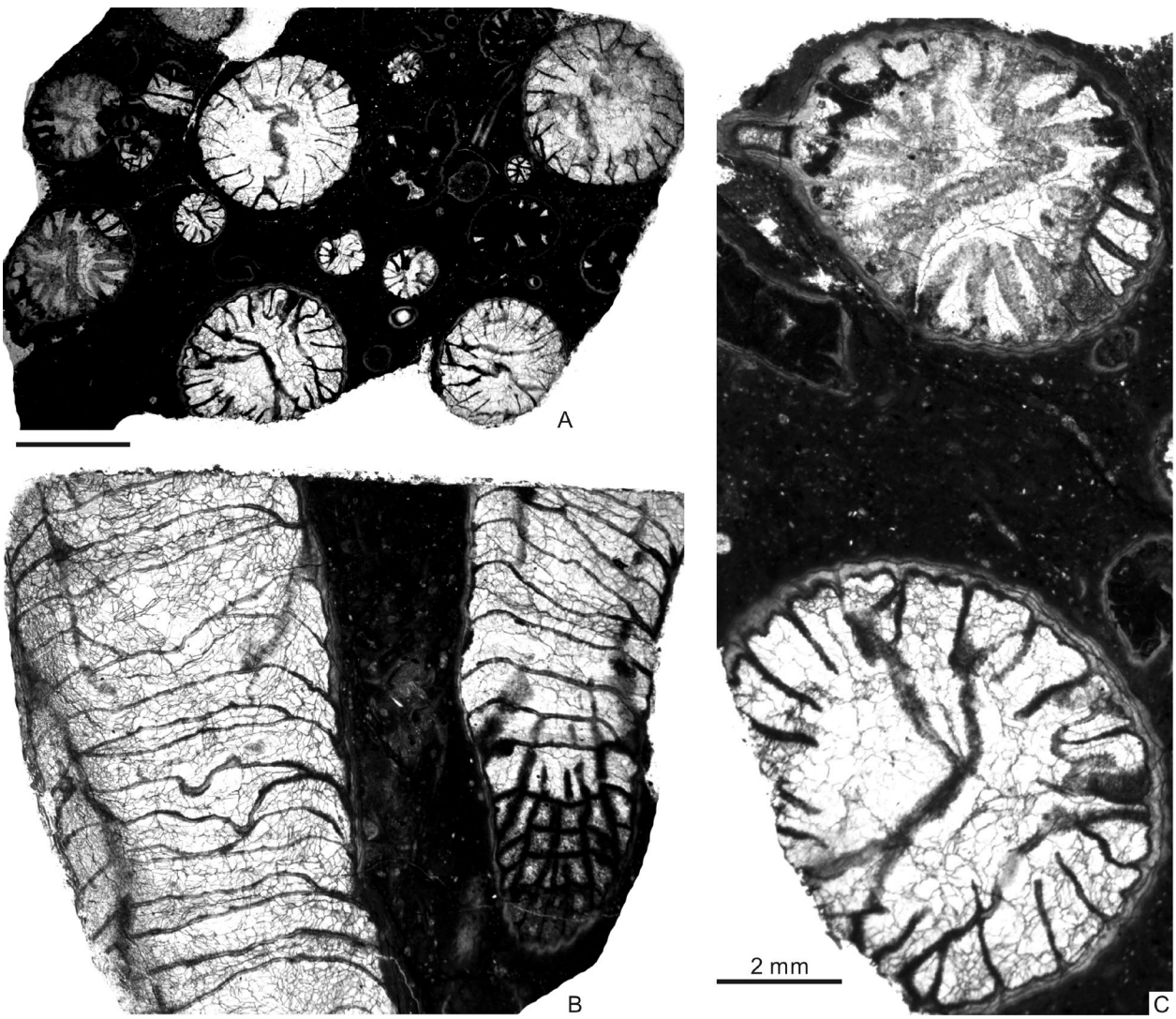


Fig. 4. Palaeophyllum? *hubeiense* Ge & Yu, 1974. NIGP 22096 (TS) and NIGP 22097 (LS), holotype, Lojoping Formation (upper Aeronian), Dazhongba, Yichang, southwestern Hubei Province. **A, C,** TS and an enlarged portion. **B,** LS. Scale bars are 5 mm unless otherwise indicated.

(1974, pl. 73, figs 21, 22), refigured here (Fig. 4), Lojoping Formation (upper Aeronian), Dazhongba, Yichang area, southwestern Hubei Province.

Diagnosis. – *Palaeophyllum* with large mature corallites (6.1–7.8 mm in diameter) and short major septa. Tube-like connecting structures are present.

Description. – Modified from Ge & Yu (1974, p. 166). Coralla fasciculate, with original growth form and size unknown. Increase mode not well established, appearing to be lateral. Spacing of corallites ranging from 3.5 to 10 mm, with tube-like connecting structures present. Corallite cylindrical, variably in size, with mature diameters of 6.1–7.8 mm. Septa of two orders. Peripheral stereozone narrow. Septa exhibiting bilateral arrangement in early stages, which becomes less apparent in later stages. Major septa slightly amplexoid? (Fig. 4A, B), about 20 in number, thin, slightly curved, short, accounting for 1/3 of the corallite radius. Minor septa weakly developed, slightly beyond corallite walls. Tabulae complete, slightly arched, with a broad, subhorizontal to slightly concave central platform, well-spaced (Ta5 = 6).

Remarks. – The revised description and diagnosis of *Palaeophyllum*? *hubeiense* given above are based on a reassessment of the holotype and only known specimen of this species. However, the possible amplexoid nature of the septa, combined with a narrow peripheral stereozone and thin septa, renders its attribution to *Palaeophyllum* tentative.

Palaeophyllum paradoxum Jia in Jia & Lin, 1987, from the same horizon of the nearby Wangjiawan, Yichang area, southwestern Hubei, shows strong similarities to *Palaeophyllum*? *hubeiense*. It was said by the author to differ from the latter only in developing tube-like connecting structures, a feature also developed in *P.*? *hubeiense*, as noted above, and the two species are clearly synonymous, as also suggested by McLean & Copper (2013, p. 58).

Palaeophyllum cf. *hubeiense sensu* McLean (1977), from the Cape Schuchert Formation of similar Aeronian age of Kap Schuchert, western Greenland, is still inadequately understood. It was claimed to differ from the species itself in having "generally slightly longer and more numerous septa and somewhat more widely spaced tabulae" (McLean 1977, p. 37). Additional difference may be the lack of the distinctive tube-like connecting of the latter. It is tentatively included within *Palaeophyllum*? *hubeiense*, although the true identity remains to be clarified.

Regarded here as unrelated to *Palaeophyllum*? *hubeiense* is a form described by Kong & Huang (1978) as this species from the Shihniulan Formation (upper Aeronian) of the Sinan area, northeastern Guizhou. It possesses a peripheral parricidal increase mode and amplexoid septa, as suggested in the original description and figures. He (1985) noted the distinctive increase mode of this form and reassigned it to his *Palaeophyllum major* from the same horizon and area, a species excluded here from cyathophylloids (see remarks on the family above).

Palaeophyllum? sp.

1974 *Palaeophyllum fasciculum* (Kutorga); Ivanovskiy & Kulkov, pp. 32, 33, pl. 8, fig. 1a, b, pl. 9, fig. 1a, b.

Remarks. – This species is recorded from the Yarovsky Beds (upper Llandovery; Ivanovskiy & Kulkov 1974; Sennikov *et al.* 2015) of the "Chinetinsky Horizon" in the Gorny Altai, though it remains inadequately known due to poor illustrations. Based on its original description, it exhibits lateral increase, large corallites (up to 10 mm in diameter), relatively short major septa (typically extending two-thirds of the corallite radius), and complete, frequently flat, well-spaced tabulae (commonly 0.5 mm apart). These characteristics suggest a marked distinction from *Palaeophyllum fasciculum* (Kutorga, 1837), which has much smaller corallites (3–5 mm in diameter) and incomplete, well-differentiated tabulae. Given its unusually large corallite size for typical *Palaeophyllum* and the limited available data, its attribution to *Palaeophyllum* in this study remains provisional.

Palaeophyllum bothroides Hall, 1975

1975 *Palaeophyllum bothroides* Hall, p. 79, pl. 1, figs f–j.
1975 *Palaeophyllum* sp. cf. *P. rugosum* Billings; Hall, pp. 78, 79, pl. 1, figs a–e.
1975 *Palaeophyllum* sp. cf. *P. thomi* (Hall); Hall, p. 80, pl. 1, figs k–n.
1975 *Palaeophyllum trelawneyense* Hall, pp. 80, 81, pl. 1, figs o–q.
?1976 *Palaeophyllum arrectum* McLean & Webby, p. 237, pl. 27, figs 8, 9, pl. 28, figs 1, 2, text-fig. 3C.
2021 *Palaeophyllum bothroides* Hall; Wang *et al.*, pp. 60–64, figs 6a–g, 7a–j, 8a–e.

Remarks. – A total of six specimens (including the holotype UNE-F11575 and one paratype UNE-F11573) were used by Hall (1975) to erect *Palaeophyllum bothroides*, all from the 'Uralba Beds', southeast of Manilla, northeastern NSW. Hall (1975) also described *P.* sp. cf. *P. rugosum* Billings and *P.* sp. cf. *P. thomi* (Hall), and erected a further species, *P. trelawneyense*, from the coeval 'Trelawney Beds' of southeast of Tamworth. Based on nine new topotypes from the 'Trelawney Beds' of the area, Wang *et al.* (2021) recently included all these forms within *P. bothroides* in view of their

trivial differences. Their revision suggests that *P. bothroides* is characterised by lateral increase, a wide peripheral stereozone and weakly developed minor septa. It differs from *Palaeophyllum rugosum* Billings, 1858a, the type species of the genus, and *P. thomi*, as the latter two show well-developed minor septa (Hill 1959, 1961). *P. rugosum* further differs in being partly cerioid, and having a narrower peripheral stereozone, and *P. thomi* (Hall in Emory, 1857) in better development of incomplete tabulae.

Palaeophyllum arrectum McLean & Webby, 1976 (holotype, SUP 75158), documented from the upper part of the Canomodine Limestone (middle Katian) of Canomodine, central NSW, has poorly developed minor septa as in *P. bothroides*, but differs mainly in having a consistently narrower peripheral stereozone. I therefore follow Wang *et al.* (2021) in considering it a probable synonym of *P. bothroides*.

***Palaeophyllum*? *patulum* McLean & Webby, 1976**

1976 *Palaeophyllum*? *patulum* McLean & Webby, p. 238, pl. 28, figs 3–7.
non 1983 *Palaeophyllum patulum*? McLean & Webby; Sytova & Ulitina, pp. 101, 102, pl. 14, fig. 6a, b.

Remarks. – *Palaeophyllum*? *patulum* (holotype, SUP 75194; paratypes, SUP 29731, SUP 75182–75190), occurring in the Ballingoole Formation (middle Katian) of the Bowan Park Group at Malachi's Hill, the Bowan Park area, central NSW, has solitary–dendroid coralla, very large corallites (10–14 mm in diameter), 52–64 septa in mature corallites with the major not extending to the axis, and incomplete to complete tabulae (McLean & Webby 1976, p. 238). Its original tentative assignment to *Palaeophyllum* was because of lacking "typical fasciculate growth habit of the genus" (McLean & Webby 1977, p. 238), a position followed here.

Palaeophyllum patulum? (McLean & Webby, 1976) *sensu* Sytova & Ulitina (1983), from the Sairin Subhorizon (probably upper Katian; Ulitina *et al.* 2009) of the Khangai Horizon, Gobi Altai, is now tentatively excluded from cyathophylloidids (see discussion above).

***Palaeophyllum*? *laxum* McLean & Webby, 1976**

1976 *Palaeophyllum*? *laxum* McLean & Webby, p. 238, pl. 28, figs 8–10, pl. 29, figs 1–3.

Remarks. – *Palaeophyllum*? *laxum* (holotype, SUP 75163; paratypes, SUP 43264, SUP 75164–75175, SUP 75177–75180) is derived from the upper Canomodine Limestone (middle Katian) in the Cargo–Canomodine area, central NSW. Like *Palaeophyllum*? *patulum* McLean & Webby, 1976, considered above, it shows a solitary–fasciculate growth habit, differing in having "more dilated septa in the peripheral stereozone, longer minor septa, and the tabulae more steeply inclined peripherally with more prominent downflexing in the axial region" (McLean & Webby 1976, p. 238). Following McLean & Webby (1976), it is tentatively placed within *Palaeophyllum*, for a reason similar to that of *Palaeophyllum*? *patulum* McLean & Webby, 1976.

***Palaeophyllum*? *jingheense* Cai, 1981**

1981 *Palaeophyllum jingheense* Cai, p. 25, pl. 15, fig. 8a–c.

Remarks. – *Palaeophyllum*? *jingheense* is based on the holotype (XR-014) and only known specimen from the Hudukedaban Formation (probably upper Katian) on northern slopes of the Borohoro Mountains, Jinghe area, western Xinjiang. However, it has probably been lost (Weihua Liao & Baoyu Wang pers. comm.). This species was only briefly documented with low-quality illustrations, requiring a revision based on new material. The major diagnostic features include large corallites (8–9 mm in diameter), long major septa extending to the corallite centre, short, well-developed minor septa, and closely spaced tabulae (5 in 3 mm) (Cai 1981). Its inclusion within *Palaeophyllum* remains uncertain due to the lack of information on its mode of increase. It was said to differ from *Palaeophyllum*? *distans* Cai, 1981 from the same horizon and locality, considered below, in having longer major septa, better developed minor septa, and much denser tabulae.

***Palaeophyllum*? *distans* Cai, 1981**

1981 *Palaeophyllum distans* Cai, p. 25, pl. 15, fig. 7a, b.

Remarks. – *Palaeophyllum*? *distans* occurs in the same unit and locality as *P.*? *jingheense* Cai, 1981, discussed above. It has large corallites (about 9 mm in diameter), short major septa not extending to the corallite centre, poorly developed minor septa that are confined to peripheral stereozone, and widely spaced tabulae (2.2–2.5 mm apart) (Cai 1981). Like *P.*? *jingheense*, it was illustrated solely by the holotype (XR-013), which is now likely lost (Baoyu Wang & Weihua Liao pers. comm.) and needs revision. The lack of information on its mode of increase casts doubts on its generic attribution. Its comparison with the associated *P.*? *jingheense* is given above.

***Palaeophyllum*? *guyuanense* Lin in Cao & Lin, 1982**

1982 *Palaeophyllum guyuanense* Lin in Cao & Lin, p. 33, pl. 9, fig. 9a, b.

Remarks. – *Palaeophyllum*? *guyuanense* is based solely on the holotype originally numbered 75-85-10 from the Beiguoshan Formation (lower–middle Katian) at Yindonggou, Guyuan, southern Ningxia, northwestern China. This specimen is now stored at Geological Museum of China, Beijing (Baoyu Lin pers. comm.); however, I was unable to locate it for the present study. According to the original description, *P.*? *guyuanense* is typified by medium-sized corallites (5.0–6.5 mm in diameter), short major septa (accounting for about 60% of corallite radius), poorly developed minor septa, and densely spaced tabulae (Ta5 = 10–13), and a combination of these characters appears to distinguish it from other known species of the genus. Given that its mode of increase remains unknown, its assignment to *Palaeophyllum* requires further confirmation.

***Palaeophyllum*? *simplex* Deng, 1984**

(Fig. 5)

1984 *Palaeophyllum thomi simplex* Deng, p. 319, pl. 3, fig. 1a, b.

Referred material. – NIGP 63624 (TS) and NIGP 63625 (LS), holotype, original of Deng (1984, pl. 3, fig. 1a, b), refigured here (Fig. 5), Beiguoshan Formation (lower–middle Katian) of Beiguoshan, Longxian area, western Shaanxi Province.

Diagnosis. – A possible species of *Palaeophyllum* with corallites 5.13 mm in diameter and thick peripheral stereozone. Major septa extending near the corallite centre. Minor septa short, confined to peripheral stereozone. Tabulae moderately arched, with a prominent, deep axial depression, closely spaced (Ta5 = 14–15).

Description. – Modified from Deng (1984, p. 319). The single specimen is fasciculate, with original growth form, size, and increase mode unknown. Corallites cylindrical, 5.13 mm in diameter. Marginarium a distinct peripheral stereozone, composed of peripheral septal ends and thick lamellar sclerenchyma, 0.58–0.69 mm thick, accounting for 23–27% of corallite radius. Septa of two orders, thick, tapering axially. Major septa 21 in number, extending to the corallite centre, with axial ends of some joined but not forming a solid axial structure. Minor septa short, normally confined to the peripheral stereozone. Tabulae complete, rarely incomplete, moderately arched, with prominent, deep axial depression, and downturned margins, moderately spaced (Ta5 = 14–15).

Remarks. – The form resembles *Palaeophyllum thomi* (Hall in Emory, 1857), as previously noted by Deng (1984), particularly in corallite size and tabular development. However, it differs in having a thicker marginal stereozone, longer septa extending to the axis, better development of minor septa, and denser tabulae. Due to the unknown mode of increase in this species, it is identified here as *Palaeophyllum*? *simplex*.

***Palaeophyllum qinghaiense* Lin, 1985a**

(Figs 6, 7)

1985a *Palaeophyllum qinghaiense* Lin, p. 285, pl. 2, figs 1a, b, 2a, b.

Referred material. – GMC-77-17P10H22-31, holotype, original of Lin (1985a, pl. 2, fig. 1a, b), refigured here (Fig. 6); paratype, GMC-77-17P10H22-37,

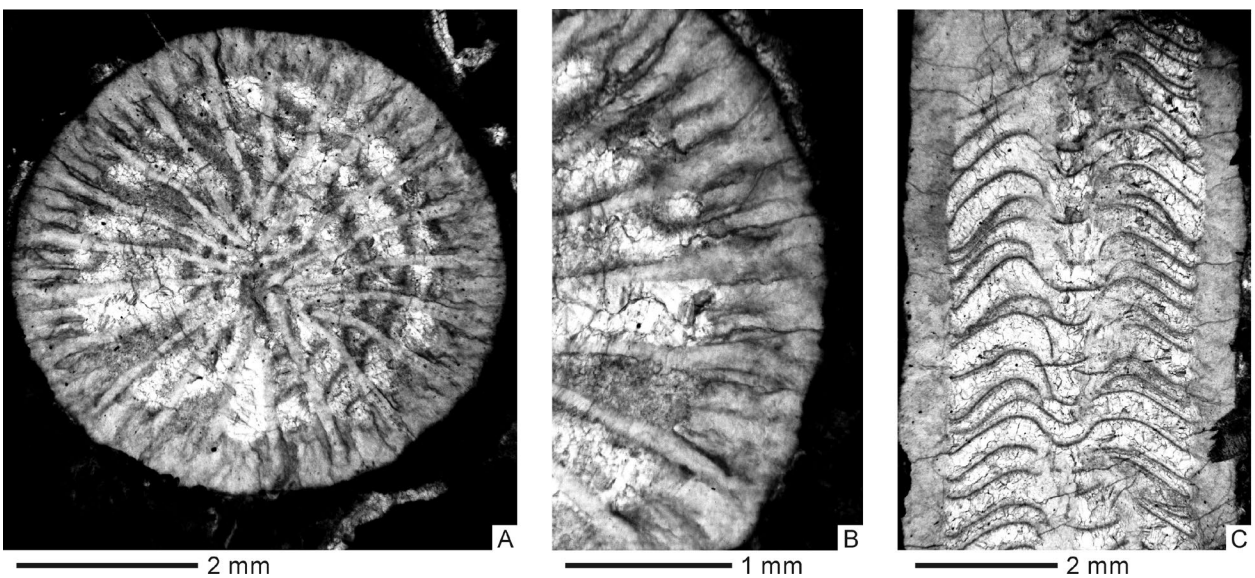


Fig. 5. Palaeophyllum? *simplex* Deng, 1984. NIGP 63624 (TS) and NIGP 63625 (LS), holotype, Beiguoshan Formation (lower–middle Katian), Beiguoshan, Longxian area, western Shaanxi Province. **A, B,** TS and an enlarged portion. **C,** LS.

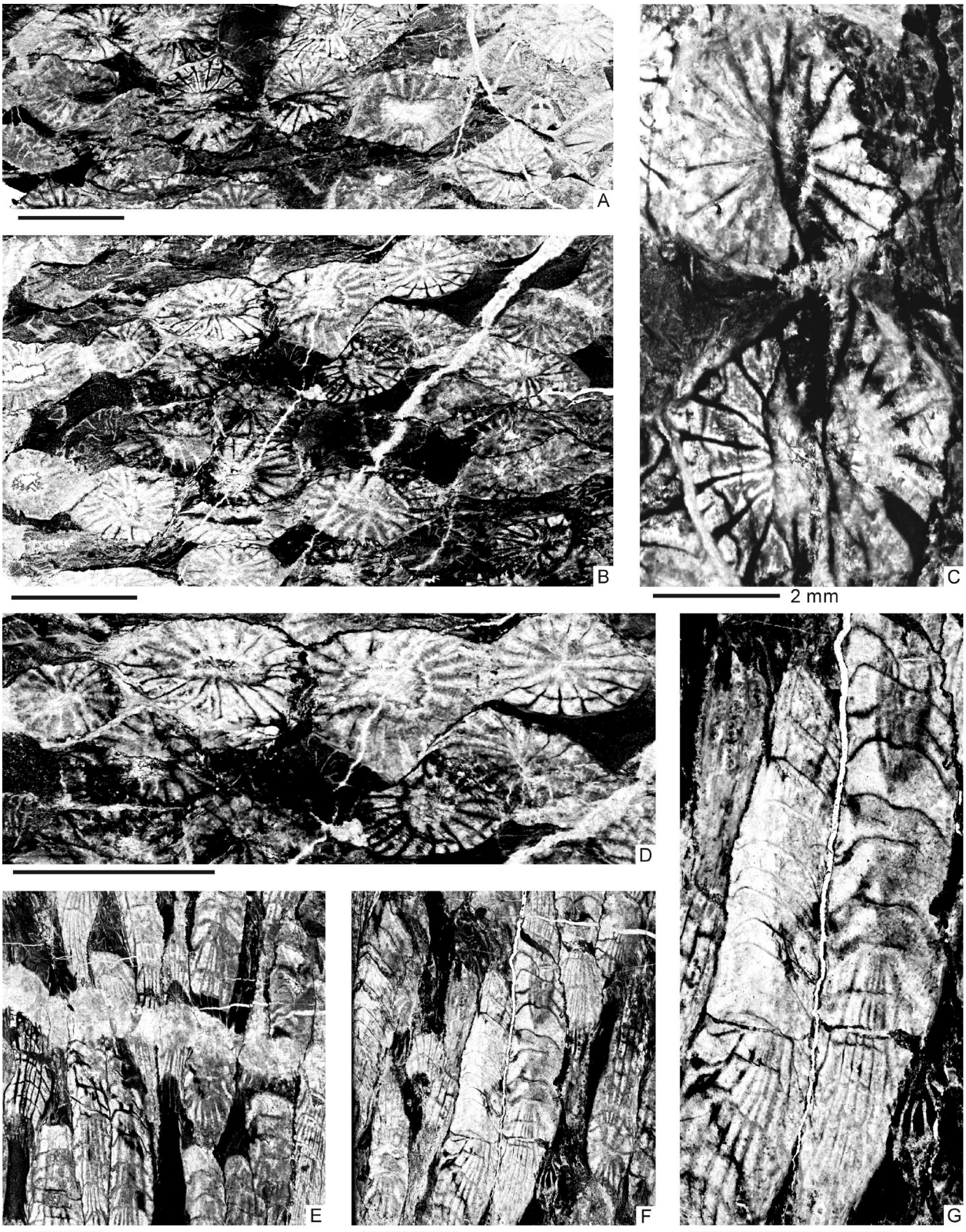


Fig. 6. Palaeophyllum qinghaiense Lin, 1985a. GMC-77-17P10H22-31, holotype, Saishiteng Group ("Upper Ordovician"), Haihegou, Saishiteng, Dachaidan, northern Qinghai Province, northwestern China. **A–D**, TSs (**A, B**) and enlarged portions, respectively (**C, D**); **E–G**, LSs (**E, F**) and an enlarged portion (**G**) of **F**. Scale bars are 5 mm unless otherwise indicated.

original of Lin (1985a, pl. 2, fig. 2a, b), refigured here (Fig. 7). Both come from the Saishiteng Group ("Upper Ordovician"), Haihegou, Saishiteng, Dachaidan, northern Qinghai Province, northwestern China.

Diagnosis. – *Palaeophyllum* with a somewhat cateniform growth, medium-sized corallites (3.69–5.75 mm in diameter), 16–18 major septa, weak minor septa, and complete, arched, widely spaced tabulae (Ta5 = 3–7).

Description. – Modified from Lin (1985a, p. 285). Coralla fasciculate, with original growth form and size unknown. Increase lateral, showing a somewhat cateniform growth habit. Corallites cylindrical, subcylindrical to polygonal, with adult diameters ranging from 3.69 to 5.75 mm. Walls thin, 0.10–0.15 mm in thickness. Septa of two orders. Major septa tapering axially, 16–18 in number, accounting for 5/6 of corallite radius. Minor septa almost absent to weakly developed, up to some 20% of corallite radius. Tabulae complete, slightly to moderately arched, with broad, subhorizontal or slightly concave central platform and downturned margins, widely spaced (Ta5 = 3–7).

Remarks. – A combination of a somewhat cateniform growth habit, relatively short major septa, and widely spaced tabulae is sufficient to distinguish the present species from other named *Palaeophyllum* species.

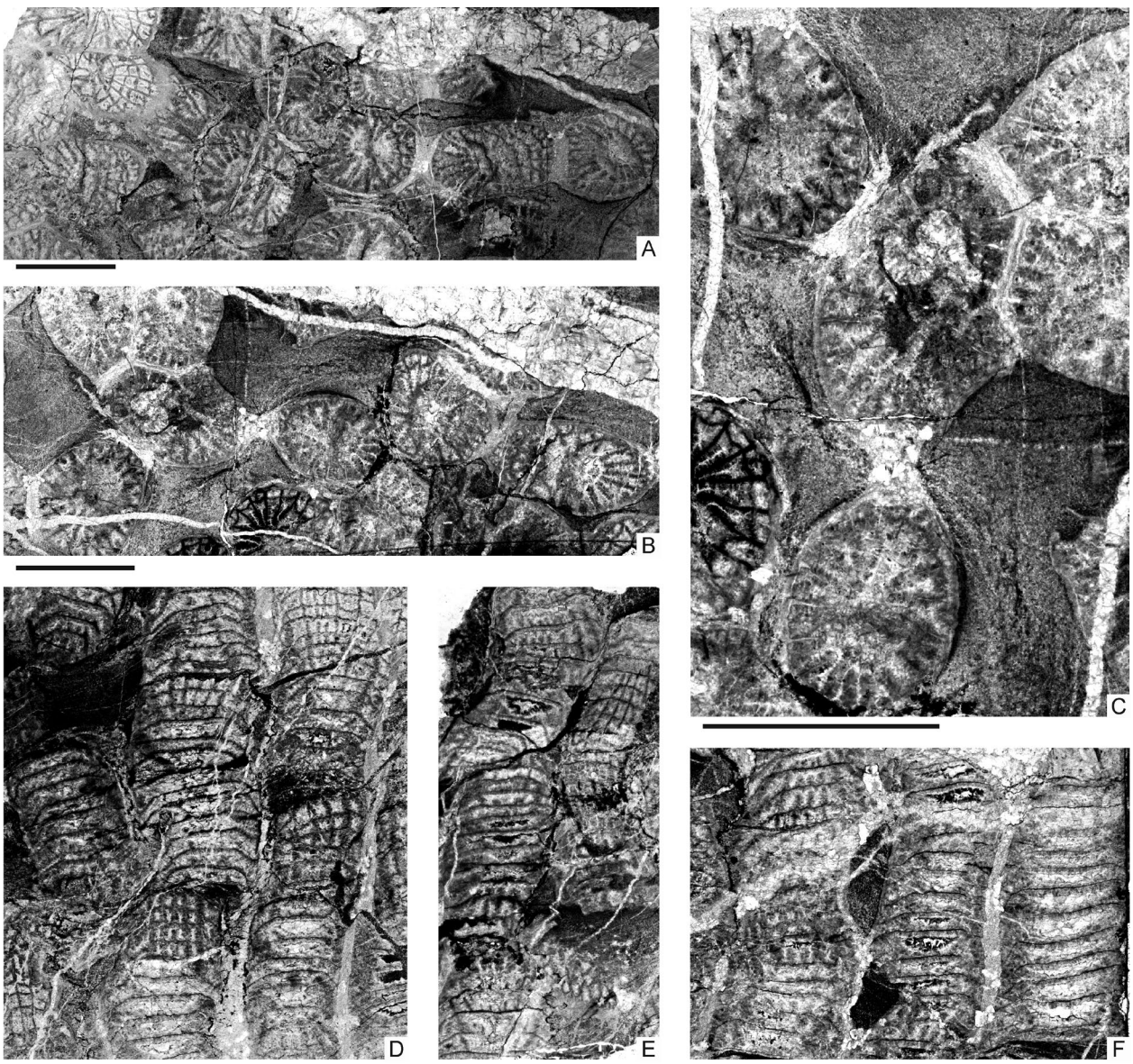


Fig. 7. Palaeophyllum qinghaiense Lin, 1985a. GMC-77-17P10H22-37, paratype, Saishiteng Group ("Upper Ordovician"), Haihegou, Saishiteng, Dachaidan, northern Qinghai Province, northwestern China. **A–C,** TSs (**A, B**) and an enlarged portion (**C**) of **B**; **D–F**, LSs. Scale bars are 5 mm.

Genus *Cyathophylloides* Dybowski, 1873a

1873a *Cyathophylloides* Dybowski, p. 379.
1873b *Cyathophylloides* Dybowski, p. 123.

Type species. – *Cyathophylloides kassariensis* Dybowski, 1873a, "Kassar Island, Dagden Island (near Keinis) (Z. 5)" (Dybowski 1873a, p. 379), West Estonian islands, subsequent designation by Sherzer (1891, p. 278), not by Lang & Smith (1935a, p. 543).

Diagnosis. – Cerioid; increase lateral, nonparricidal, corallites with long major septa running together in groups axially, and with long minor septa; septa thin, peripheral stereozone narrow; tabulae domed, in some interseptal loculi with strongly upturned margins? (= biform tabularium), and complete or incomplete. Modified after Hill (1981, p. F135).

Remarks. – Some authors (e.g. Browne 1965, p. 1186; Flower & Duncan 1975, p. 176) noted that in certain cerioid, non-amplexoid cyathophylloidid species, major septa exhibit variable lengths, with some extending to the corallite centre. Based on these observations, they proposed that *Favistina* and *Cyathophylloides* are intergradational and thus synonymous. However, as demonstrated elsewhere in this study, forms characterised by the consistent connection of major septal axial ends appeared later than typical *Favistina* with free axial zones, and persisted beyond them, extending well into the Silurian. These findings highlight the evolutionary and, consequently, taxonomic significance of this septal characteristic, which, along with prominently arched tabulae, serves to differentiate *Cyathophylloides* from *Favistina*.

Cyathophylloides spans from the middle Katian to the Rhuddanian, with assigned species detailed below. Previous reports of this genus that are now excluded, discussed above in the remarks on the family Cyathophylloididae, include *Cyathophylloides irregularis* Dybowski, 1873a from the Silurian of "Karlsö, Gotland", *Palaeophyllum* (*Cyathophylloides*?) *williamsi* Chadwick in Williams, 1919 from the Manitoulin Formation (lower Rhuddanian) of Manitoulin Island, *Cyathophylloides fergusoni* Merriam, 1973 and *C.* sp. f *sensu* Merriam & McKee (1976) from the Lochkovian of Nevada, *C. silurica* Guo, 1976 from the Xibiehe Formation (Ludlow) of south–central Inner Mongolia, *C. carinatus* Cao & Ouyang 1987 from the Yanglugou Formation (Pridoli) of the Zoige (Ruoergai) area, northwestern Sichuan, and *C. xinjiangensis* Cai, 1989 from the lower Kuoersaikeer Formation ("upper Silurian") of the Balikun area, northeastern Xinjiang.

Some poorly known forms may belong to *Cyathophylloides*, but their classification requires confirmation. They include *Cyathophylloides* spp. A, B of Pandolfi (1985) from the Lost Canyon Member (middle Katian) of the Ely Springs Dolomite, Utah, *Cyathophylloides* cf. *C. burksae* of Harris *et al*. (2019) from Kope Formation (lower Katian) of Kentucky, and *Cyathophylloides* sp. of Oliver *et al*. (1975a) from the Katian strata of western Seward Peninsula, Alaska.

Cyathophylloides kassariensis Dybowski, 1873a

(Figs 8–10)

1845 *Columnaria sulcata* Goldfuss; Lonsdale, pp. 601, 602, pl. A, fig. 1, 1a–c.
1851 *Stauria astreiformis* Milne-Edwards & Haime *pars*, p. 316.
1860 *Stauria astreiformis* Milne-Edwards & Haime; Eichwald, p. 519.
1861 *Columnaria sulcata* Goldfuss; Eichwald, p. 105.
1861 *Stauria astreiformis* Milne-Edwards & Haime; Schmidt, p. 230.
1873a *Cyathophylloides kassariensis* Dybowski, p. 379.
1873b *Cyathophylloides kassariensis* Dybowski, p. 123.
1897 *Cyathophylloides kassariensis* Dybowski; Weissermel, p. 870, text-fig. 1a, b.
1950 *Cyathophylloides kassariensis* Dybowski; Bassler, pl. 17, figs 10, 11 [refig. Weissermel 1897, text-fig. 1a, b].
1965 *Cyathophylloides kassariensis* Dybowski; Ivanovskiy, pl. 26, fig. 4a, b, text-fig. 45a, b [refig. Weissermel 1897, text-fig. 1a, b].
1969 *Cyathophylloides kassariensis* Dybowski; Ivanovskiy, pp. 74, 75, pl. 5, figs 1a, b [refig. Ivanovskiy 1965, pl. 26, fig. 4a, b], 2a, b, text-fig. 12a, b [refig. Weissermel 1897, text-fig. 1a, b].
1973 *Cyathophylloides kassariensis* Dybowski; Fedorowski & Gorianov, pp. 26, 27, pl. 6, fig. 1a, b.
1981 *Cyathophylloides kassariensis* Dybowski; Hill, fig. 69, 2a, b.
1995 *Cyathophylloides kassariensis* Dybowski; Lin *et al*., fig. 130a, b [refig. Hill 1981, fig. 69, 2a, b].

Referred material. – TUG 1368-31 (formerly Co 1335), holotype, figured here (Fig. 8), probably from the Hilliste Formation (upper Rhuddanian–? lower Aeronian), Orjaku, Kassari, West Estonian islands (Ursula Toom pers. comm.). GIT 397-2178 and GIT 397-2179, two topotypes, the former figured here (Figs 9, 10), Sarve harbour, Hiiumaa Island; GIT 398-879 and GIT 397-1035, two topotypes, Eiglaküla Quarry; all four topotypes from the Hilliste Formation (upper Rhuddanian–? lower Aeronian), western Estonia.

Remarks. – Designation of a holotype for *Cyathophylloides kassariensis* was not made by Dybowski (1873a, b). However, his collection contains only one syntype (TUG 1368-31, formerly Co 1335), which probably comes from the Hilliste Formation (upper Rhuddanian–? lower Aeronian) at Orjaku of Kassari, West Estonian islands (Ursula Toom pers. comm.). Accordingly, this specimen

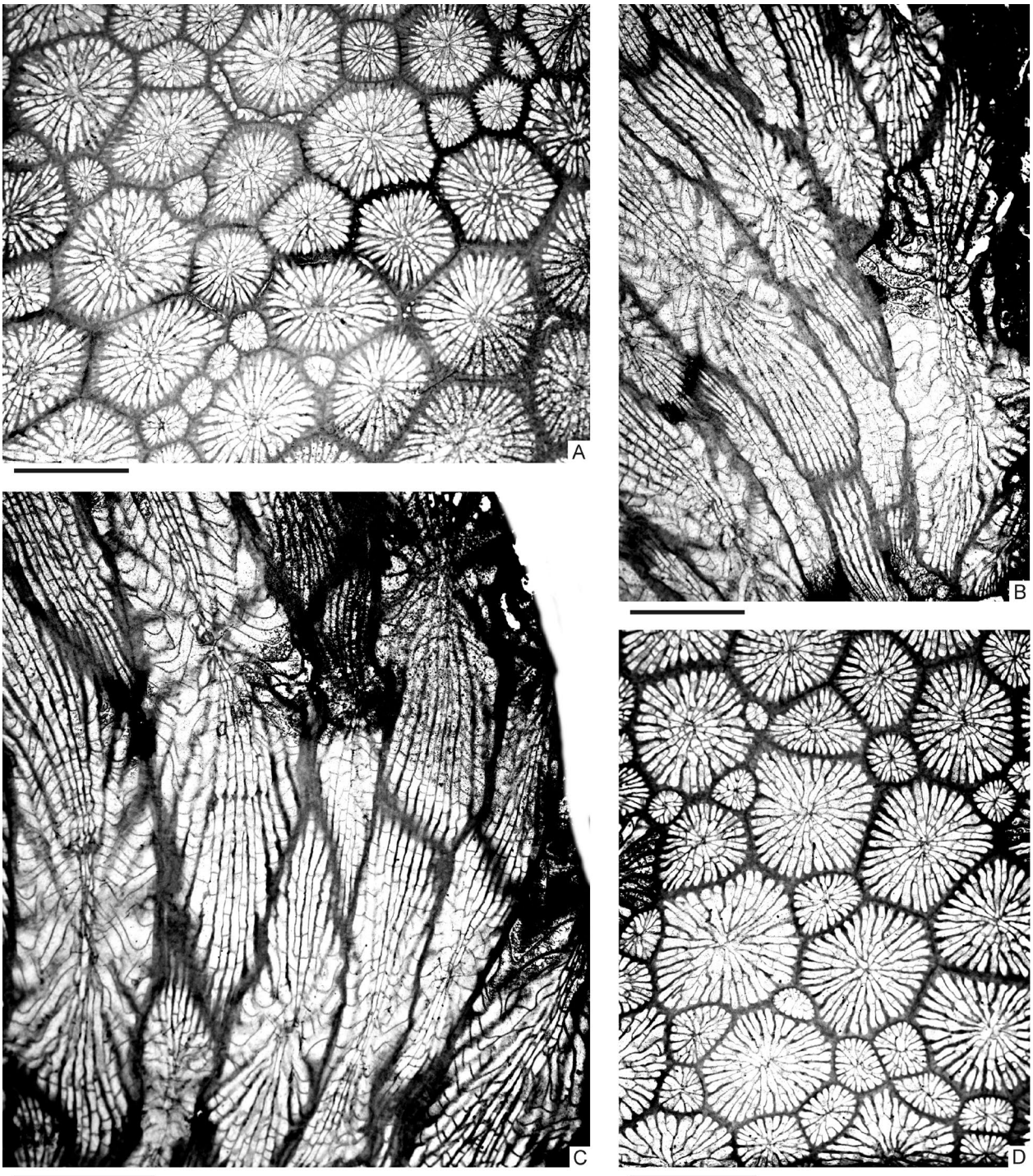


Fig. 8. Cyathophylloides kassariensis Dybowski, 1873a. TUG 1368-31 (formerly Co 1335), holotype, probably from the Hilliste Formation (upper Rhuddanian–? lower Aeronian), Orjaku, Kassari, West Estonian islands (Ursula Toom pers. comm.). **A, D,** TSs; **B, C,** LSs. Scale bars are 5 mm.

automatically qualifies as the holotype of the species under the International Commission on Zoological Nomenclature (ICZN). The specimen illustrated by Weissermel (1897), from the Raikküllian Horizon (lower Silurian) of northern Estonia, was claimed by Ivanovskiy (1969, p. 74, 112) to be the monotype and hence the holotype. However, the specimen was reportedly "located in Munich" (Weissermel 1897, p. 870), making it impossible to be the type for this species.

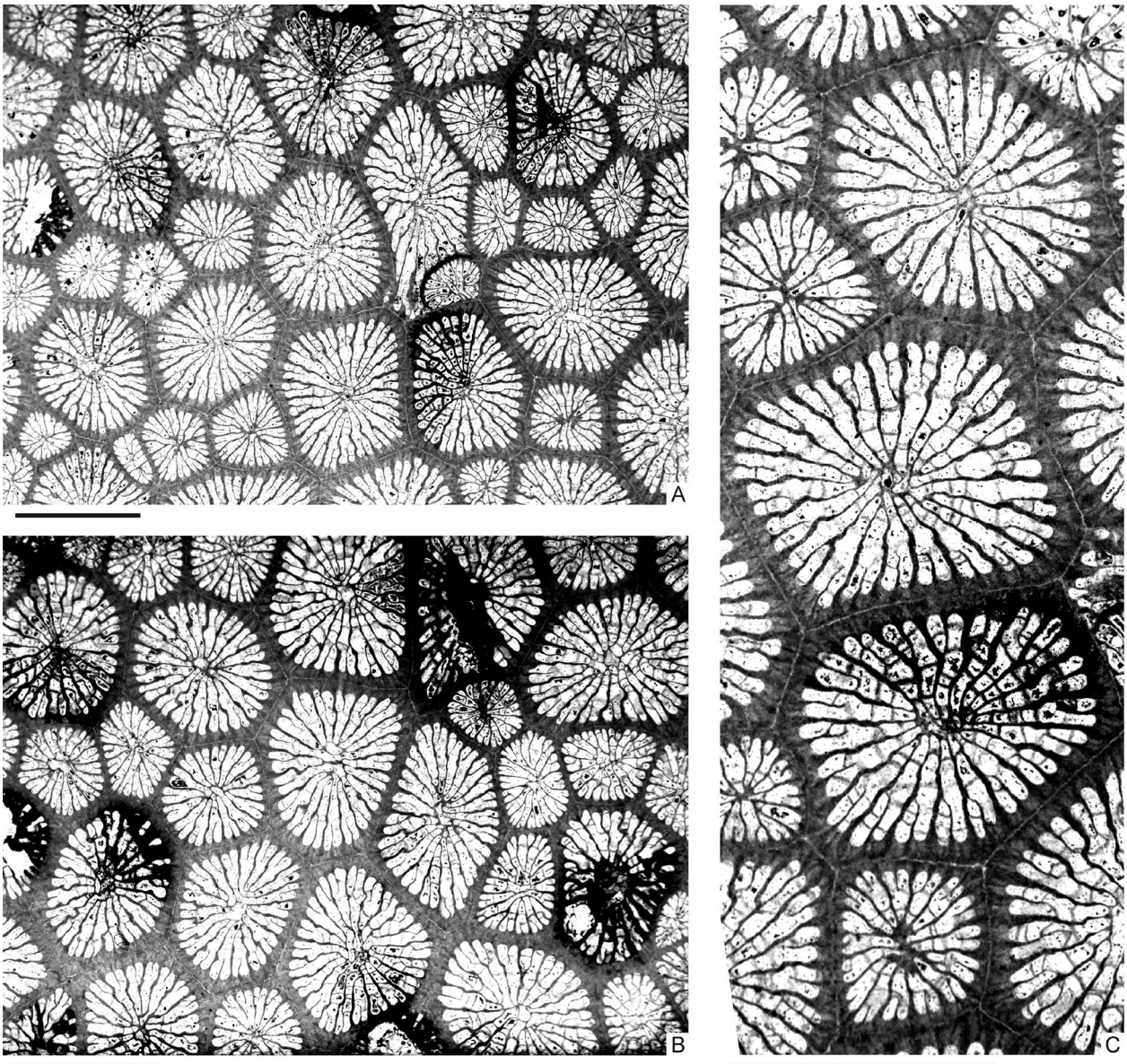


Fig. 9. Cyathophylloides kassariensis Dybowski, 1873a. GIT 397-2178, topotype, Hilliste Formation (upper Rhuddanian–? lower Aeronian), Sarve harbour, Hiiumaa Island, western Estonia. **A–C,** TSs (**A, B**) and an enlarged portion (**C**) of A. Scale bars are 5 mm.

In this study, the holotype is illustrated in thin section for the first time (Fig. 8). Additionally, thin sections of several topotypes collected from the Hilliste Formation (upper Rhuddanian–? lower Aeronian) of the same area are prepared and examined, with one well-preserved specimen (GIT 397-2178) illustrated here (Figs 9, 10).

Multiple specimens described from the same general horizon and locality are clearly examples of *Cyathophylloides kassariensis*. These include materials described by Lonsdale (1845) from the "Lower Silurian" at "Habsal, near Reval", by Weissermel (1897) from the Raikküllian Horizon ("Lower Silurian"), by Ivanovskiy (1965, 1969) from the "Llandovery of Haapsalu", and by Hill (1981) from the "L. Sil, Est. Tamsalu". Additionally, a fossil described by Eichwald (1860, 1861) and redescribed by Fedorowski & Gorianov (1973) from strata near Pühalepa on Hiiumaa Island, which belongs to the Juuru Stage (Fedorowski & Gorianov 1973, p. 27), of latest Hirnantian–earliest Silurian age (Meidla *et al*. 2023a). Based on descriptions and illustrations of these published types, the key specific features of *Cyathophylloides kassariensis* are well defined, as outlined in the diagnosis of the genus above.

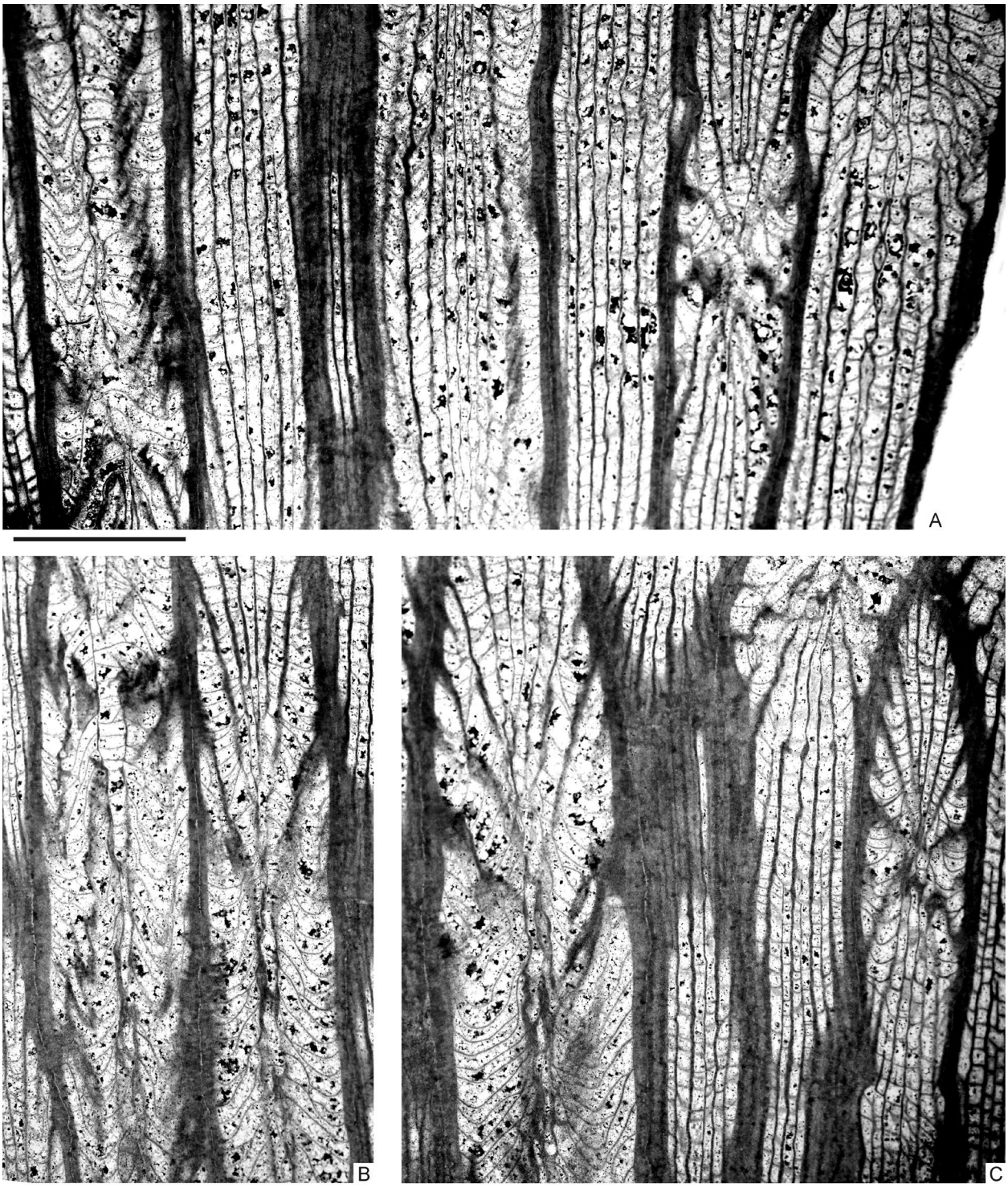


Fig. 10. Cyathophylloides kassariensis Dybowski, 1873a. GIT 397-2178, topotype, Hilliste Formation (upper Rhuddanian–? lower Aeronian), Sarve harbour, Hiiumaa Island, western Estonia. **A–C,** LSs. Scale bars are 5 mm.

Cyathophylloides calicinaeformis (Tcherepnina, 1960)

1960 *Favistella calicinaeformis* Tcherepnina, pp. 392, 393, pl. O-12, fig. 1a, b.

Remarks. – *Cyathophylloides calicinaeformis* (holotype, SNIIGGIMS K135-a), from the generalised Upper Ordovician of the Samysh River area, Gorny Altai, was originally described by Tcherepnina (1960) as having corallites 2.5–4.0 mm in diameter, 13–15 major septa mostly reaching the corallite centre, short minor septa, and slightly arched, moderately spaced tabulae (8–10 in 5 mm). In view of the presence of the connection of septa in the corallite axis, I agree with Ivanovskiy (1969) in reassigning it to *Cyathophylloides*.

Favistina calicinaeformis was considered by Ivanovskiy (1969) as a synonym of *Columnaria septosa* Sokolov, 1950. However, the latter species has typical amplexoid septa and lacks a prominent axial structure, and is now transferred to *Crenulites*, considered below.

Cyathophylloides burksae Flower, 1961

1961 *Cyathophylloides burksae* Flower, pp. 83, 84, pl. 43, figs 1–10, pl. 44, figs 1–5.
non 1965 *Cyathophylloides* cf. *burksae* Flower; Browne, pp. 1188, 1189, pl. 147, fig. 5, pl. 148, figs 1a, b, 4a, b, pl. 149, fig. 4, pl. 150, figs 1a–c, 2.
non 1986 *Favistina* cf. *burksae* (Flower); Deng, pp. 650, 651, pl. 1, fig. 1a–d.

Remarks. – The type material of *Cyathophylloides burksae* (holotype, NMBM 680; paratypes, NMBM 671–684) occurs in the Aleman Formation (middle Katian) of the Montoya Group. It is characterised by having corallites ranging from 3.5 to 5.5 mm in diameter, 10–12 major septa that are irregularly joined in the corallite axis, variably long minor septa (up to half the length of major septa), and generally arched, widely spaced tabulae (Ta5 = 5–9) (Flower 1961, p. 83). A further diagnostic feature may be the occasional development of free rounded corallites, as shown in the paratype NMBM 681 (Flower 1961, pl. 43, fig. 5).

The material described by Browne (1965) as *Cyathophylloides* cf. *burksae* Flower, 1961 from the roughly coeval, basal parts of the Waynesville and Whitewater formations of Kentucky is now tentatively included within *Favistina crenulata* Flower, 1961, discussed below.

The specimen documented by Deng (1986) as *Favistina* cf. *burksae* (Flower, 1961), from the Xiazhen Formation (uppermost Katian) in the JCY area, east China, is re-examined, resulting in a revision as *Cyathophylloides* sp. B, discussed below.

Cyathophylloides aktshaulicus Smelovskaya, 1963

1963 *Cyathophylloides aktshaulicus* Smelovskaya, p. 179, pl. 27, figs 5, 6.
1969 *Cyathophylloides aktshaulicus* Smelovskaya; Ivanovskiy, pp. 77, 78, text-fig. 14.

Remarks. – *Cyathophylloides aktshaulicus* (holotype, MGU-47/2-1) is known from the basal Akchaul Formation (middle Katian) of the Tarbagatai area. It has corallite diameters of 5–7 mm, strongly thickened peripheral septal ends that form a thick peripheral stereozone, 15–16 major septa extending to the corallite axis and forming an axial structure, short minor septa that do not extend beyond corallite walls, and convex tabulae (Smelovskaya 1963). It was believed by the author to differ from all other known species of *Cyathophylloides* by its strongly thickened peripheral septal ends.

Cyathophylloides kiaeri Spjeldnæs, 1963

non 1932 *Columnaria* cf. *kassariensis* Dybowski; Kiær, p. 112, pl. 15, fig. 2.
1963 *Cyathophylloides kiaeri* Spjeldnæs, pp. 2–4, figs 1, 2.

Remarks. – The holotype of *Cyathophylloides kiaeri* (PMO 69929) comes from the basal part of the Tretaspis Limestone (now Grimsøya Formation of late Katian age; Nielsen *et al*. 2023), northeastern Kalvøya, Bærum, Oslo-Asker, Norway. This species has corallites about 3 mm in diameter, 13–16 major septa, well-developed minor septa (up to 50% the length of major septa), and complete, flat or slightly arched tabulae, differing from other *Cyathophylloides* species in having "short secondary septa and straight tabulae" (Spjeldnæs 1963, p. 2).

Columnaria cf. *kassariensis* Dybowski, 1873a *sensu* Kiær (1932), from the older, Kalstad Limestone (lower Katian; Bergström 1997) of the Trondheim region, Norway, was described and figured only in transverse section. It was compared with *C. kiaeri* by Spjeldnæs (1963), who concluded that the two are possibly conspecific. This needs confirmation since "the tabulae are not known in the Trondheim material" (Spjeldnæs 1963, p. 3). However, Kiær's form has much larger corallites (5 or sometimes up to 6–8 mm in diameter), which appears to be sufficient to distinguish it from *C. kiaeri*.

Cyathophylloides sp. A

1965 *Favistella dybovskii* Soshkina; Ivanovskiy, p. 112, pl. 27, fig. 3a, b.
1969 *Cyathophylloides septosum* (Sokolov); Ivanovskiy *pars*, pp. 75–77, pl. 5, figs 3a, b [refig. Ivanovskiy 1965, pl. 27, fig. 3a, b], *non* 4a, b, text-fig. 13a, b.

Remarks. – *Favistella dybovskii* Soshkina in Ivanova *et al.*, 1955 of Ivanovskiy (1965), refigured by Ivanovskiy (1969) as *Cyathophylloides septosum* (Sokolov, 1950), comes from the Dolborian Horizon (middle Katian) of the Podkamennaya Tunguska River Basin. Its major septa are non-amplexoid and generally connected in the corallite axis, warranting a transfer to *Cyathophylloides*. The open nomenclature is used due to the limited knowledge of this form.

Cyathophylloides junctus Hall, 1975

1975 *Cyathophylloides juncta* Hall, p. 82, text-fig. 6, pl. 2, figs c, d.
2021 *Cyathophylloides juncta* Hall; Wang *et al.*, pp. 56, 60, fig. 5a–g.

Remarks. – *Cyathophylloides junctus* (holotype, UNE-F11701) comes from the 'Trelawney Beds' (upper Eastonian, middle Katian) in the Devonian Drik-Drik Formation of New England Region. It is typified by having small to medium-sized corallites [ACDs (6+) = 2.30–4.10 mm], thick corallite walls (WT = 0.16–0.40 mm), moderately to strongly dilated septa, well-developed minor septa (up to half length of major septa), and arched, closely spaced tabulae (Ta5 = 13–21) (Wang *et al.* 2021, p. 60).

Cyathophylloides semeniuki Webby, 1988, the only other Australian species of the genus, comes from the younger, top part (uppermost Katian) of the Malachis Hill Formation of central NSW. Compared with *C. junctus*, it shows more consistently developed minor septa and much sparser tabulae (Ta5 = 9–10), as noted by Webby (1988, p. 151). It further differs in developing thinner septa (Webby 1988, p. 151; Wang *et al.* 2021, p. 60), and smaller corallites (1.43–3.35 mm in diameter).

Cyathophylloides taoqupoensis Lin in Cao & Lin, 1982

1982 *Cyathophylloides taoqupoensis* Lin in Cao & Lin, p. 33, pl. 9, fig. 1a, b.

Remarks. – The holotype and only known specimen of *Cyathophylloides taoqupoensis* (originally numbered 75-50-6) comes from the Taoqupo Formation (lower–middle Katian) at Taoqupo of Yaozhou, Shaanxi Province, northwestern China. It is likely housed at the Geological Museum of China, Beijing (Baoyu Lin & Weihua Liao pers. comm.); however, it was not found during the present study.

This species was originally described briefly with poor illustrations, necessitating a thorough revision. Based on the initial description, its major septa are long, with some fused at the corallite centre, suggesting an attribution to *Cyathophylloides*. Key specific features include large corallites (2.5–7.5 mm in diameter), major septa 15–16 in number, well-developed minor septa of varying lengths (typically 1/5–1/4 of the major septa), and complete, widely spaced tabulae (Ta5 = 5). A combination of these characteristics distinguishes it from other documented *Cyathophylloides* species.

A similar species is *C. shuinychangensis* Lin in Li & Lin, 1982, revised below, from the Shihuichang Formation of similar age in northern Nachitai, central–western Qinghai. Both share comparable corallite sizes and widely spaced tabulae, but *C. shuinychangensis* differs in having fewer major septa (typically 10–13 in number) and shorter minor septa (generally less than 1/5 of the corallite radius).

Cyathophylloides shuinychangensis Lin in Li & Lin, 1982

(Figs 11, 12)

1982 *Cyathophylloides shuinychangensis* Lin in Li & Lin, p. 39, pl. 3, figs 4a, b, 5a, b.
1982 *Cyathophylloides* sp., Lin in Li & Lin, pl. 3, fig. 6.

Referred material. – GMC-75f-2-25, holotype, original of Li & Lin (1982, pl. 3, fig. 5a, b), refigured here (Fig. 11A–D); GMC-Nf-2-5, topotype, original of Li & Lin (1982, pl. 3, fig. 4a, b), refigured here (Fig. 11E, F); GMC-75f-2-23, a further topotype, described by these authors as the same species, figured here for the first time (Fig. 12A, B); GMC-Nf-2-4, described by Lin in Li & Lin (1982) as *Cyathophylloides* sp., original of Li & Lin (1982, pl. 3, fig. 6), refigured here (Fig. 12C–E). All from the Shihuichang Formation (probably middle Katian) near Shihuichang, northern Nachitai, central–western Qinghai.

Diagnosis. – *Cyathophylloides* with large corallites [ACDs (6+) = 5.07–7.12 mm], 10–13 curved major septa, short minor septa (generally less than 1/5 of corallite radius), and complete, widely spaced tabulae (Ta5 = 5–7).

Description. – Modified from Lin in Li & Lin (1982, p. 39). External form and size of coralla unknown. Corallites polygonal, 4–7 sided, large [ACDs (6+) = 5.07–7.12 mm]. Corallite walls straight to slightly wavy, variably thick, about 0.12–0.26 mm in thickness, separated by prominent dark lines. Septa of two orders. Major septa 10–13 in number, long, curved, extending to the corallite centre, with twisted axial ends of some fused and forming an axial structure. Minor septa well developed, short, generally less than 1/5 of the corallite radius. Tabulae complete, slightly to moderately arched, moderately spaced (Ta5 = 5–7).

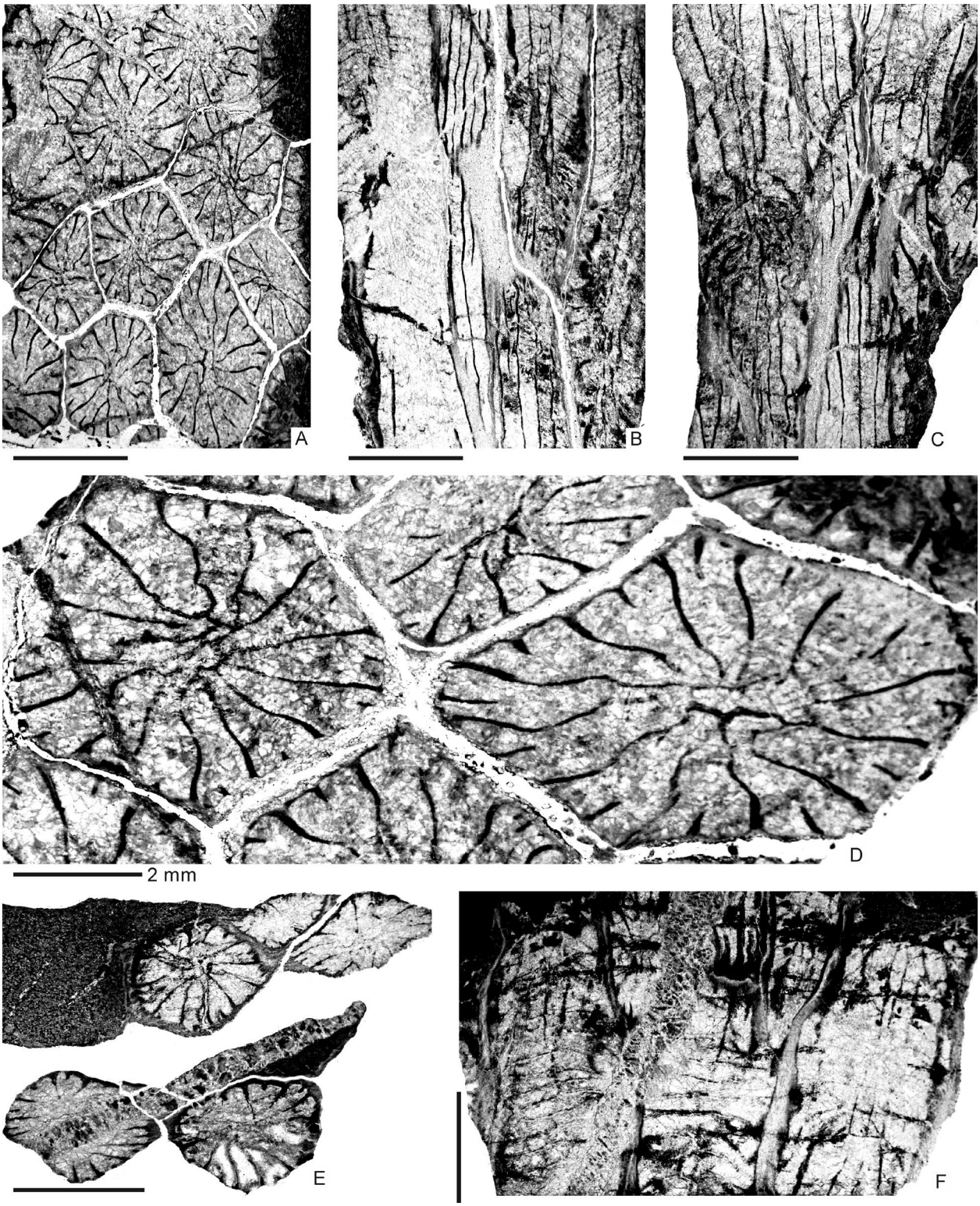


Fig. 11. Cyathophylloides shuinychangensis Lin in Li & Lin, 1982. **A–D**, GMC-75f-2-25, holotype. **A, D,** TS and an enlarged portion; **B, C,** LSs. **E, F,** GMC-Nf-2-5, topotype. **E,** TS; **F,** LS. Both specimens from the Shihuichang Formation (probably middle Katian) near Shihuichang, northern Nachitai, central–western Qinghai Province. Scale bars are 5 mm unless otherwise indicated.

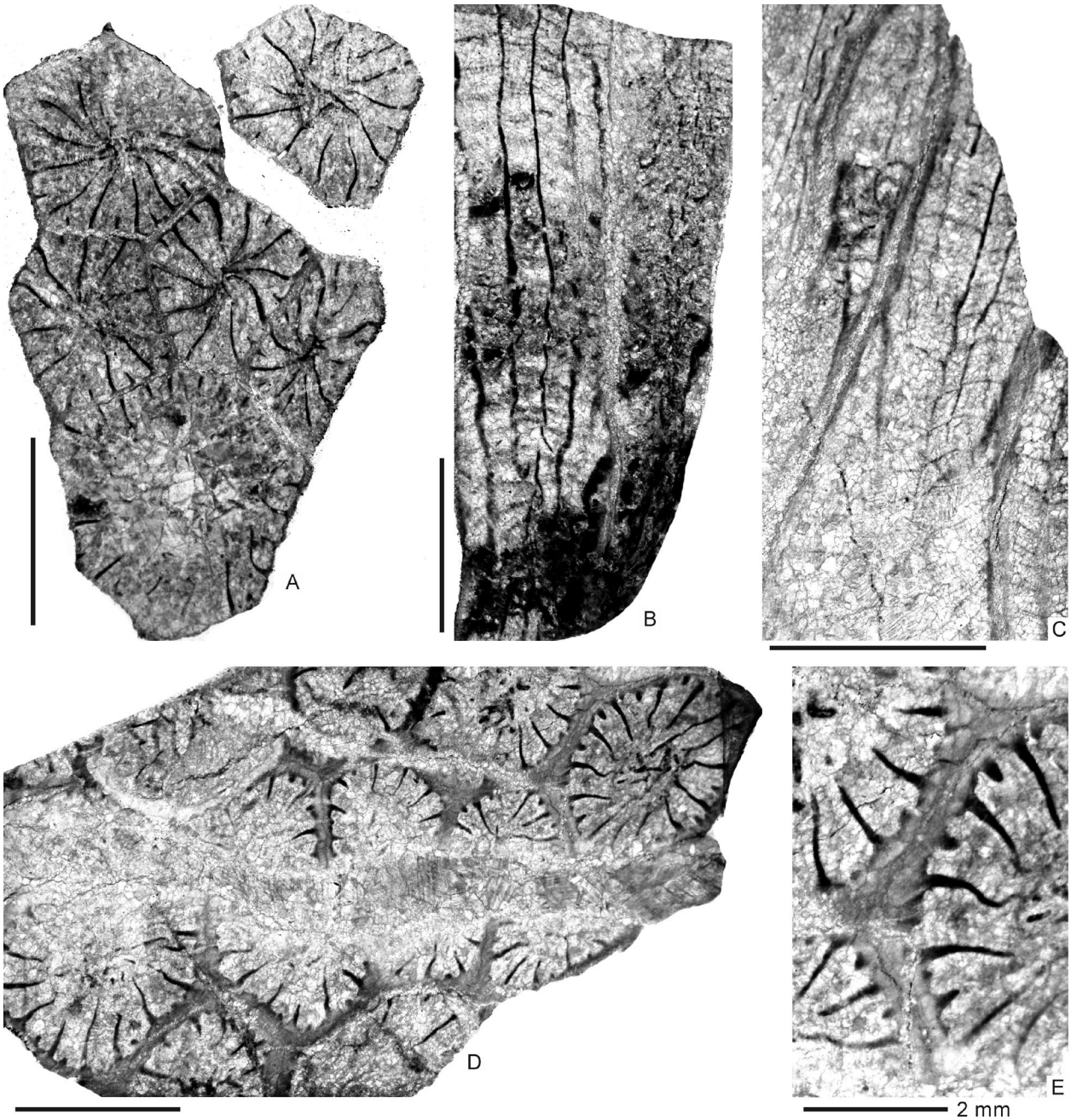


Fig. 12. Cyathophylloides shuinychangensis Lin in Li & Lin, 1982. **A, B,** GMC-75f-2-23, described but not figured by Lin in Li & Lin (1982) as this species. **A,** TS; **B,** LS. **C–E,** GMC-Nf-2-4, described by Lin in Li & Lin (1982) as *Cyathophylloides* sp. **C,** LS; **D, E,** TS and an enlarged portion. Both specimens from the Shihuichang Formation (probably middle Katian) near Shihuichang, northern Nachitai, central–western Qinghai Province. Scale bars are 5 mm unless otherwise indicated.

Remarks. – The revised concept of *Cyathophylloides shuinychangensis* presented above is based on a reassessment of the holotype (GMC-75f-2-25) and two topotypes (GMC-Nf-2-5, GMC-75f-2-23) from the Shihuichang Formation (probably middle Katian) near Shihuichang, northern Nachitai, central–western Qinghai.

Cyathophylloides sp. figured by Lin in Li & Lin (1982) from the same horizon and locality as the type material of *C. shuinychangensis* is re-illustrated here (Fig. 12C–E). This form is included here within *C. shuinychangensis*, since it has comparable corallites (with one measured 5.70 mm in diameter), and similar septal and tabulae development, thus falling well within variation of *C. shuinychangensis* revised above. A comparison with the closely similar species *C. taoqupoensis* Lin in Cao & Lin, 1982, from the roughly coeval Taoqupo Formation of Shaanxi Province, is provided above in the discussion of that species.

Cyathophylloides strigosus (Deng, 1984)

(Fig. 13)

1984 *Favistina strigosa* Deng, p. 318, pl. 4, fig. 3a, b.

Referred material. – NIGP 63636 (TS) and NIGP 63637 (LS), holotype, original of Deng (1984, pl. 4, fig. 3a, b), refigured here (Fig. 13), Taoqupo Formation (early–middle Katian), Tiewadian–Xilingou, Jingyang area, central Shaanxi Province.

Diagnosis. – *Cyathophylloides* with small corallites (ACDs (6+) = 2.61–2.69 mm), few major septa (generally 10 in number), and arched, widely spaced tabulae (Ta5 = 5–7).

Description. – Modified from Deng (1984, p. 318). External form and size of the single specimen unknown. Corallites polygonal, 4–6 sided, rather small [ACDs (6+) = 2.61–2.69 mm]. Corallite walls straight to slightly wavy, thin, about 0.1 mm in thickness, separated by dark lines. Septa of two orders. Major septa 9–10 in number, long, extending to the corallite centre, with twisted axial ends of some connected. Minor septa weakly to well developed, variably long, some up to 1/2 of corallite radius. Tabulae complete, slightly to moderately arched, widely spaced (Ta5 = 5–7).

Remarks. – The revised description and diagnosis of *Cyathophylloides strigosus* given above are based on a reassessment of the holotype and only known specimen of this species. A combination of the small corallite size and widely spaced tabulae distinguishes it from all other species of *Cyathophylloides*.

Cyathophylloides sp. B

(Fig. 14)

1986 *Favistina* cf. *burksae* (Flower); Deng, pp. 650, 651, pl. 1, fig. 1a–d.

Referred material. – NIGP 94556, 94558 (TSs) and NIGP 94557, 94559 (LSs), original of Deng (1986, pl. 1, fig. 1a–d), refigured here (Fig. 14), Xiazhen Formation (uppermost Katian), Zhuzhai, JCY area, east China.

Remarks. – The specimen documented by Deng (1986) as *Favistina* cf. *burksae* (Flower, 1961), from the Xiazhen Formation (uppermost Katian) in the JCY area, east China, is re-examined here. It features medium-sized corallites [ACDs (6+) = 3.14–4.67 mm], thin to moderately thick corallite walls (0.12–0.25 mm in thickness), and 12–14 major septa, most of which extend to or nearly reach the corallite centre, where some display twisted axial connections. The minor septa are well developed, reaching up to 1/4–1/3 of the corallite radius, while the tabulae are generally complete, subhorizontal to slightly arched, and closely spaced (Ta5 = 8–10).

This Xiazhen specimen differs from the holotype of *Cyathophylloides burksae*, which exhibits occasional fasciculate portions, slightly larger corallites (3.5–5.5 mm in diameter), fewer major septa (12), longer minor septa (extending up to half the length of the major septa), and commonly arched, variably spaced tabulae (Ta5 = 5–9). Given these differences, along with the palaeogeographical separation between South China and Laurentia, the Xiazhen form is considered a distinct species. However, due to the limited understanding of its intraspecific variation, it is identified here as *Cyathophylloides* sp. B.

Cyathophylloides semeniuki Webby, 1988

1988 *Cyathophylloides semeniuki* Webby, pp. 149, 151, fig. 8.7–8.9.

Remarks. – *Cyathophylloides semeniuki*, occurring in the top (uppermost Katian) of the Malachis Hill Formation of central NSW, is typified by having diameters of 1.43–3.35 mm, thin to slightly thick corallite walls (up to 0.3 mm in thickness), 10–14 major septa, and generally arched, widely spaced tabulae (Ta5 = 9–10). Its comparison with the other congeneric Australian species, *C. junctus* Hall, 1975 from the older, 'Trelawney Beds' (upper Eastonian, middle Katian) in the Devonian Drik-Drik Formation of New England Region is discussed above under the latter species.

Cyathophylloides tachengensis (Cai, 1988)

1988 *Favistella tachengensis* Cai, p. 55, pl. 1, figs 1a–c, 2a, b, 6.
1988 *Favistella xinjiangensis* Cai, p. 55, pl. 2, figs 1a–c, 2a, b.

Remarks. – The type material of *Cyathophylloides tachengensis* (holotype, XT-001; paratypes, XT-002, XT-003) comes from the Bulunggor Formation (possibly upper Katian) on the southern slopes of Tarbagatai Mountains, Tacheng Prefecture, northwestern Xinjiang. It was said by Cai (1988) to have corallites mostly 4–5 mm in diameter, 14–16 major septa with some extending to the axis and connected, short minor septa, and slightly wavy, closely spaced tabulae (13–15 in 5 mm). The connection of axial ends of some septa justifies its transfer to *Cyathophylloides*.

Favistella xinjiangensis Cai, 1988, with type material (holotype, XT-008; paratype, XT-007) occurring in the same horizon and locality as *Cyathophylloides tachengensis*, is almost identical, and thus synonymised here with the latter. It differs in having septa that are dilated distally and taper toward the corallite axis, which is regarded here as intraspecific variation.

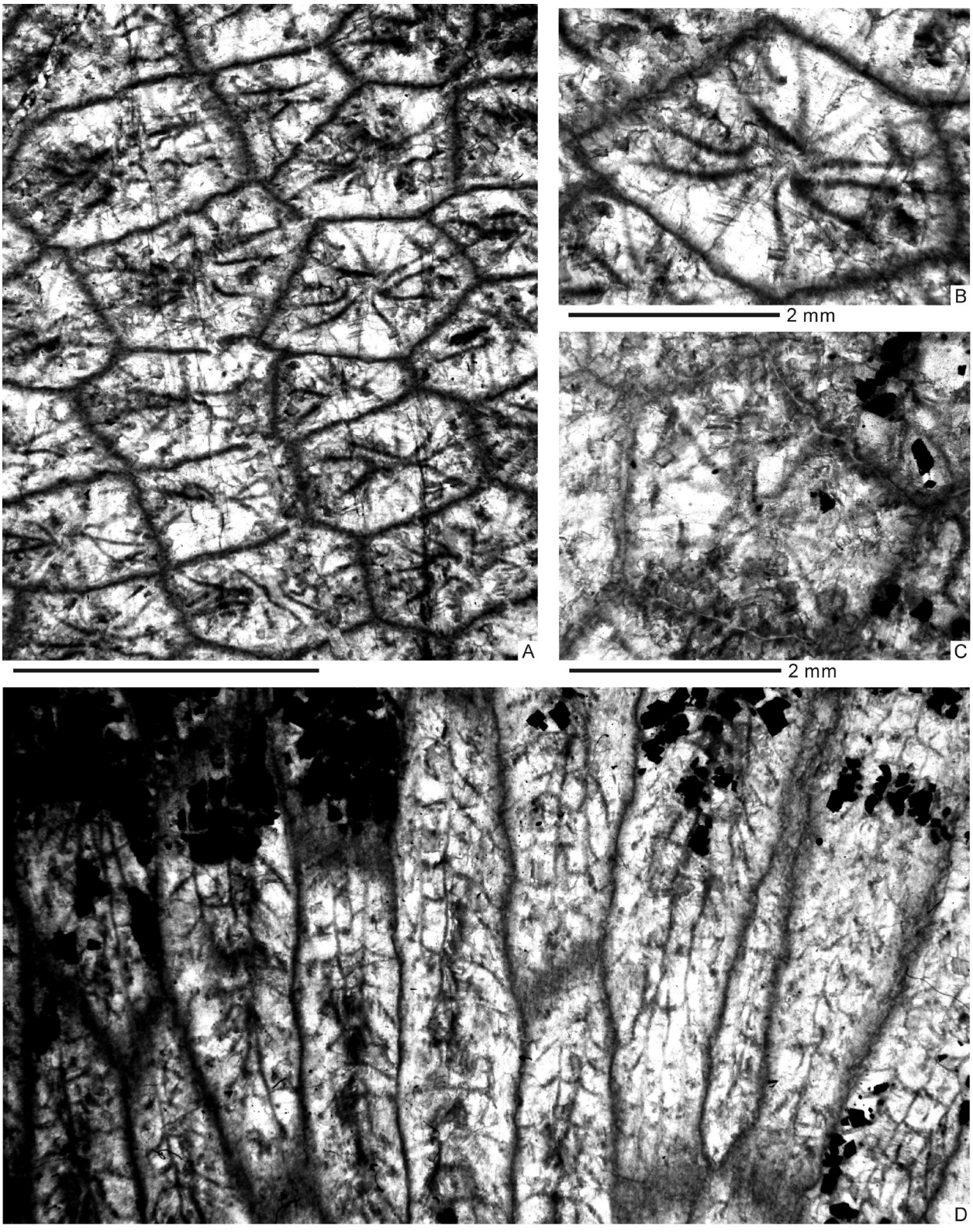


Fig. 13. Cyathophylloides strigosus (Deng, 1984). NIGP 63636 (TS) and NIGP 63637 (LS), holotype, Taoqupo Formation (middle Katian), Tiewadian–Xilingou, Jingyang area, central Shaanxi Province. **A–C,** TS and two enlarged portions. **D,** LS. Scale bars are 5 mm unless otherwise indicated.

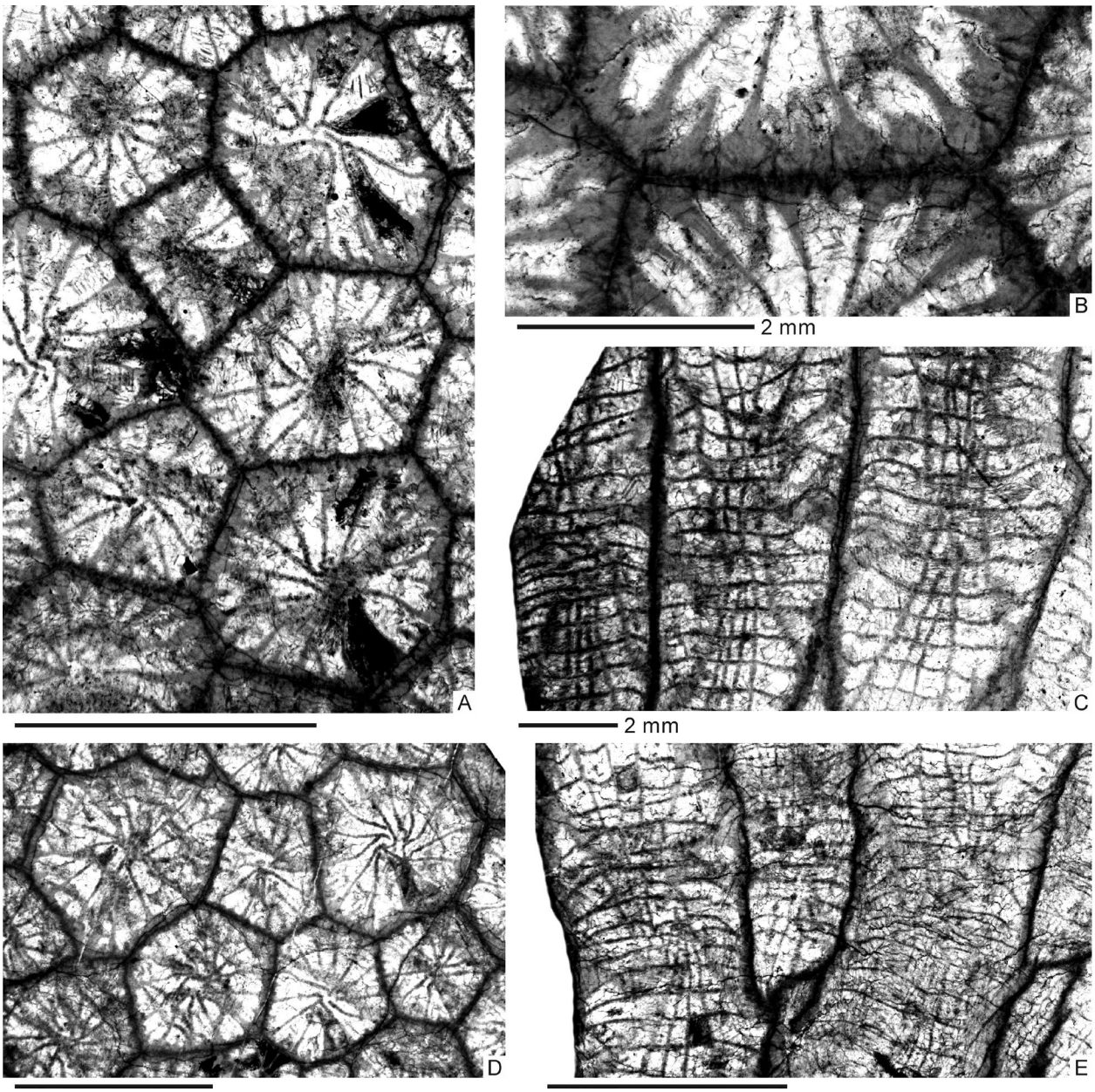


Fig. 14. Cyathophylloides sp. B. NIGP 94556 and NIGP 94558 (TSs), and NIGP 94557 and NIGP 94559 (LSs), all from one corallum, described by Deng (1986) as *Favistina* cf. *burksae* (Flower, 1961), Xiazhen Formation (uppermost Katian), Zhuzhai, JCY area, east China. **A, B, D,** TSs (**A, D**) and an enlarged portion (**B**) of **A**; **C, E,** LSs. Scale bars are 5 mm unless otherwise indicated.

Genus *Favistina* Flower, 1961

?1846 *Favistella* Dana, p. 538.
non 1847 *Favistella* Hall, p. 275.
1961 *Favistina* Flower, p. 77.
1982 *Favistella* (*Favistella*) Dana; Lin in Cao & Lin, p. 30.

Type species. – *Favistella undulata* Bassler, 1950, "Blackriveran" (possibly Sandbian), Wisconsin, USA, by original designation.

Diagnosis. – Cerioid to partly fasciculate corals, with walls of axial plates and sclerenchyme, the sclerenchyme extended as 10 or more primary septa of considerable length, but not completely joining at the centres of the corallites; minor septa may develop between major septa; tabulae generally horizontal, but irregular, some with edges narrowly downturned, some with slight median depressions, and some faintly arched upward. Modified After Flower (1961, p. 77).

Remarks. – Before the 1930s, corals presently attributed to *Favistina* Flower 1961 (formerly *Favistella* Dana, 1846) were generally considered synonymous with *Columnaria* Goldfuss, 1826. This treatment stemmed from Milne-Edwards & Haime's (1851) interpretation of *Columnaria* based on *C. alveolata* Goldfuss, 1826, a possible Ordovician form from North America designated by them as the type species. The general similarities between *C. alveolata* and the type species of *Favistella* led them to conclude that the two genera are synonymous, a view followed by most later authors. However, as noted by Lang & Smith (1935b, p. 426), *Columnaria sulcata* Goldfuss, 1826 was chosen earlier by McCoy (1849, p. 121) as the type species of this genus, which comes from the upper Givetian (or lower Frasnian) of the "Bensberg" area, Bergische Gladbach, Germany (Hill 1981, p. F263; McLean 2010, pp. 50, 51). The holotype of *C. sulcata* has been well illustrated in thin section by Lang & Smith (1935b, text-figs 1, 2; pl. 12, figs 1, 2), Birenheide (1969, pl. 2, fig. 5a, b), Coen-Aubert (1990, pl. 6, figs 35–37), and more recently by McLean (2010, pl. 25, figs 1–4). It proves to have 1–2 rows of dissepiments, which readily distinguishes *Columnaria* from the Late Ordovician non-dissepimented *Favistina* (Hill 1939, 1956, 1981), and *Columnaria* is now generally placed in a separate family, the Columnariidae Nicholson, 1879 (e.g. Hill 1981; McLean 2010).

Flower (1961) introduced a new genus *Favistina* to replace the problematic *Favistella* Dana, 1846, a situation adopted by almost all later workers (Hill 1981; McLean & Copper 2013) and herein. The complicated nomenclatural history of *Favistella* and the reason for such a replacement were discussed in detail by Flower (1961), thus needing no repetition here.

Favistina undulata (Bassler, 1950)

1901 *Columnaria alveolata* Goldfuss; Lambe, pp. 98, 99, pl. 6, fig. 1, 1a.
?1932 *Columnaria alveolata* Goldfuss; Bassler, pl. 22, fig. 9.
1941 *Favistella* sp., Roy, pp. 69, 70, fig. 35a, b.
1950 *Favistella undulata* Bassler, p. 273, pl. 16, fig. 1, pl. 17, figs 12–14.
1956 *Favistella undulata* Bassler; Duncan, pl. 24, fig. 5a, b [refig. Bassler 1950, pl. 17, figs 13, 14].
1965 *Favistella alveolata* (Goldfuss); Ivanovskiy, text-fig. 44a, b [refig. Lambe 1901, pl. 6, fig. 1, 1a].
1969 *Favistella alveolata* (Goldfuss); Ivanovskiy *pars*, pp. 66, 69–71, pl. 3, figs 1a, b [refig. Lambe 1901, pl. 6, fig. 1, 1a] *only*.
1981 *Favistella undulata* Bassler; Hill, fig. 72, 1a–c, e [refig. Bassler 1950, pl. 16, fig. 1, pl. 17, figs 12–14].
1995 *Favistina undulata* (Bassler); Lin *et al.*, fig. 131 a–c [refig. Bassler 1950, pl. 17, figs 12–14].

Remarks. – The type material of *Favistella undulata* (holotype, USNM 46294) comes from the "Platteville limestone" (now Platteville Formation, upper Sandbian; Bergström *et al.* 2010a) of Wisconsin, USA. It has corallites 5 mm in diameter, 12–14 major septa not meeting in the corallite axis, weakly developed minor septa, and complete, generally flat, widely spaced tabulae (Bassler 1950, p. 273; Flower 1961, p. 79).

Favistella sp. of Roy (1941) occurs in the "Richmond" (now Amadjuak Formation; Bolton 2000) of lower Katian age. It exhibits septal and tabular development comparable to the holotype of *Favistina undulata*, differing only in having slightly larger corallites (3–6 mm in diameter). This supports an inclusion of this form within *Favistina undulata*.

The specimen described by Lambe (1901) as *Columnaria alveolata* Goldfuss, 1826, and later refigured by Ivanovskiy (1965, 1969), comes from the "Black River limestone" (Sandbian) of Ontario. The original line drawings depict typical septal and tabular features characteristic of *Favistina undulata*, supporting its classification within this species.

Columnaria alveolata Goldfuss, 1826 of Bassler (1932), from the Catheys Formation (lower Katian) of Tennessee, was illustrated only externally. The figure depicts a corallite size and septal length comparable to *Favistina undulata*, a species abundantly present in rocks of this age in the region. This form may therefore belong to *F. undulata* but requires confirmation.

Favistina interventa (Foerste, 1914)

1914 *Columnaria alveolata interventa* Foerste, pp. 122, 123, pl. 4, fig. 1A–J.
1950 *Favistella alveolata interventa* (Foerste); Bassler, p. 272, pl. 19, fig. 8.

Remarks. – The specimens documented by Foerste (1914) as this species come from the Benson Member of the "Lexington limestone" (now Lexington Formation, lower Katian; Bergström *et al.* 2010a) of central Kentucky, without a designated type. They were originally illustrated externally only. Flower (1961, p. 79) suggested that Foerste's original illustrated material may include three species, one being probably attributable to *Crenulites*, and the others to *Saffordophyllum* and *Cyathophylloides*. A critical revision of this taxon is apparently necessary.

Favistina minima (Foerste, 1914)

1914 *Columnaria alveolata minima* Foerste, p. 123.
1950 *Favistella alveolata minima* (Foerste); Bassler, p. 272.

Remarks. – Foerste's material is derived from the "Millersburg member of the Cynthiana formation"

(now Point Pleasant Formation, lower Katian; Brett *et al*. 2020, fig. 4), at a locality "between New Forest station and the overhead bridge two miles south of Millersburg", and no type was designated. This species was originally briefly described without illustrations. It was said by Foerste (1914, p. 123) to have small corallites with an average diameter of "nearer 3 mm", however, with other features undescribed.

Favistina discreta (Foerste, 1914)

1914 *Columnaria alveolata discreta* Foerste, pp. 123, 124.
1938 *Columnaria discreta* (Foerste); Okulitch, pp. 106, 107, pl. 1, figs 1, 2.
1950 *Favistella alveolata discreta* (Foerste); Bassler, p. 272.
1961 *Favistina discreta* (Foerste); Flower, p. 82.

Remarks. – The specimens documented by Foerste (1914) as *Favistina discreta* occur in the "the upper part of the Black river limestone" ("Blackriveran", Sandbian) of Ottawa, and Cloche Island in Ontario, Canada, and no type was designated. His material was only briefly described and has not been illustrated so far. The specimens described by Okulitch (1938) as this species from the "Black River at Paquette's Rapids" were only figured externally.

According to Foerste's (1914, p. 124) original description, this form has large corallites "often reaching a diameter of 7 mm", and tends to be "discrete, with rounded corallites". A thin-section study is clearly required, as suggested by Flower (1961).

Favistina neminghensis (Etheridge, 1918)

1918 *Columnaria neminghensis* Etheridge, pp. 50, 51, pl. 8, pl. 9, figs 1, 2.
1942b *Favistella neminghensis* (Etheridge); Hill, p. 158, pl. 2, fig. 4a, b.
1975 *Cyathophylloides sinuata* Hall, pp. 81, 82, pl. 2, figs a, b.
1988 *Favistina neminghensis* (Etheridge); Webby, pp. 146, 149, fig. 8.1, 8.2, fig. 8.3–8.5 [refig. Etheridge 1918, pl. 9, figs 1, 2; Hill, 1942b, pl. 2, fig. 4a].
2021 *Favistina neminghensis* (Etheridge); Wang *et al.*, pp. 55, 56, fig. 2a–c.

Remarks. – *Favistina neminghensis* was said by Etheridge (1918) to occur in the "Devonian" of Por 181, Ph Nemingha, Co Parry, Tamworth District (southern slopes of East Gap Hill, east of Nemingha and approximately 10 km east of Tamworth; Webby 1988, p. 146). These strata now prove to be allochthonous limestones of late Eastonian (middle Katian) age deposited in the Devonian Drik-Drik Formation (Percival *et al.* 2023).

The holotype is composed of four thin sections, with two (AM 4339 and AM 4338) documented by Etheridge (1918) and the others (AM 903A and AM 903B) by Hill (1942b); three of them were refigured by Webby (1988). The specimen itself, however, is "now presumed lost" (Webby 1988, p. 146). In addition, a few topotypes were described by Webby (1988) and Wang *et al.* (2021). Based on Webby's (1988) description of the holotype, *Favistina neminghensis* is typified by having small corallites (1.47–3.40 mm in diameter), 11–13 major septa almost reaching the corallite centre, generally short minor septa, and widely spaced tabulae (Ta5 = 7–10).

Cyathophylloides sinuata Hall*, 1975,* from the same general horizon and locality, is almost identical to, and hence conspecific with *Favistina neminghensis*, as suggested by previous authors (Webby 1988; Wang *et al.* 2021).

Favistina stellaris (Wilson, 1926)

1926 *Columnaria alveolata* var. *stellaris* Wilson, p. 16, pl. 3, figs 1, 2.
1950 *Favistella alveolata stellaris* (Wilson); Bassler, p. 273.
1963 *Favistella alveolata* var. *stellaris* (Wilson); Nelson, pp. 44, 45, pl. 5, fig. 2.

Remarks. – The type material of this species, with specimen numbers and repository details not originally specified, occurs in the Beaverfoot Formation (possibly within its middle Katian part) of the Beaverfoot Range, southeastern British Columbia. It has not been studied in thin section so far. According to Wilson (1926), this species has small corallites (averaging about 2–3 mm in diameter), 10–12 major septa reaching the corallite centre, weakly developed minor septa, and widely spaced tabulae (about 1 mm apart).

The specimen documented by Nelson (1963) as *Favistella alveolata* var. *stellaris* (Wilson, 1926) occurs in the Churchill River Group (middle Katian; Desrochers *et al*. 2023), Nelson River, northern Hudson Bay Lowland. It appears to be identical to the type material of *Favistina stellaris* based on his documentation.

Favistina minor (Bassler, 1932)

1932 *Columnaria alveolata* var. *minor* Bassler, pl. 11, figs 1, 2.
1950 *Favistella alveolata minor* (Bassler); Bassler, p. 273, pl. 16, fig. 4 [refig. Bassler 1932, pl. 11, fig. 2], pl. 18, figs 6, 7.

Remarks. – The holotype of *Favistina minor* (USNM 80503), from the basal Hermitage shales (now basal Hermitage Formation, upper Sandbian; Bergström *et al*. 2010a) of Tennessee, USA, was only figured externally, but a clearly conspecific specimen, from the underlying upper Carters limestone (upper Sandbian; Bergström *et al*. 2010a), was later illustrated internally by Bassler (1950). According to

Bassler's (1932, 1950) documentation, this species is typified by having rather small corallites (2.5 mm in diameter), 12 major septa extending well toward the corallite centre, short minor septa, and complete, flat, widely spaced tabulae. It may be a valid species, as noted by Flower (1961).

Favistina cerioides (Hill, 1942a)

1942a *Favistella cerioides* Hill, p. 5, pl. 2, fig. 2a, b.
1988 *Favistina cerioides* (Hill); Webby, p. 145, figs 6.7, 6.8.

Remarks. – *Favistina cerioides* was initially established based on the holotype (AM-F5487) probably from the middle part of the "Chudleigh Limestone" (now Chudleigh Subgroup of the Gordon Group, upper Sandbian–middle Katian; Percival *et al.* 2023) at Liena, Mersey River, Tasmania. An additional specimen was figured by Webby (1988) from the same horizon in the Mole–Creek–Railton area of northern Tasmania.

According to Hill (1942a, p. 5), the diagnosis of *Favistina cerioides* includes "corallites about 5 mm in diameter, about 18 major septa, short minor septa, and slightly domed or horizontal, close tabulae", which is about 10 in 5 mm. Webby (1988, p. 145) remarked that this species has "relatively longer minor septa, up to half the length of major septa", a feature also shown in the figure of its transverse section.

Favistina magister (Bassler, 1950)

1950 *Favistella magister* Bassler, 1950, p. 273, pl. 16, figs 5, 6, pl. 18, figs 19, 20, pl. 19, fig. 11.
1961 *Favistina magister* (Bassler); Flower, p. 81, pl. 41, figs 1, 2, 4.
1965 *Cyathophylloides magister* (Bassler); Browne, p. 1190, pl. 151, fig. 2a, b.

Remarks. – The type material of *Favistina magister* (holotype, USNM 73325) comes from the "Arnheim shales" (now Arnheim Formation, middle Katian; Bergström *et al.* 2010a) of Tennessee, USA. This species is typified by having large corallites (up to 10 mm in diameter), 12 major septa that extend close to the corallite centre but with free axial ends, long minor septa (more than 1/2 of the length of major septa), and complete, horizontal, irregular, widely spaced tabulae (Ta5 = 4–7) (Bassler 1950, p. 273; Flower 1961, p. 81).

As well as the type occurrence, *Favistina magister* was documented by Flower (1961) from the "Saluda beds" of Madison, Indiana, and by Browne (1965) from the corresponding stratigraphic level of Bullitt, Kentucky. This coral horizon belongs to the basal part of the Whitewater Formation (Browne 1965) of middle–possibly earliest late Katian age (Brett *et al.* 2020; Daniel Goldman & Patrick McLaughlin pers. comm.).

Favistina crenulata Flower, 1961

?1950 *Favistella alveolata* (Goldfuss); Bassler, pp. 271, 272, pl. 16, fig. 3.
?1961 *Favistina stellata* (Hall); Flower *pars*, pp. 79–81, pl. 38, figs 1–8, 10, 11, pl. 39, figs 1–3, 9, 10, pl. 40, figs 7–9, *non* pl. 38, figs 12, 13, pl. 39, figs 4–8.
1961 *Favistina crenulata* Flower, pp. 81, 82, pl. 41, figs 3, 5–9.
?1965 *Cyathophylloides* cf. *burksae* (Flower); Browne, pp. 1188, 1189, pl. 147, fig. 5, pl. 148, figs 1a, b, 4a, b, pl. 149, fig. 4, pl. 150, figs 1a–c, 2.
1965 *Cyathophylloides crenulata* (Flower); Browne, p. 1190, pl. 151, fig. 1a, b.

Remarks. – The holotype of *Favistina crenulata* (NMBM 736) is derived from a stratigraphic interval now recognised as the basal part of the Whitewater Formation (Browne 1965) of the middle–? earliest late Katian age (Brett *et al.* 2020; Daniel Goldman & Patrick McLaughlin pers. comm.). A further conspecific specimen was described by Browne (1965) from the coeval horizon of Bullitt, Kentucky. The typical features include corallites commonly 5–6, rarely 7 mm in diameter, strongly crenulate corallite walls, relatively long major septa, some of which meet in groups of two or three, and complete, well-spaced tabulae (Ta5 = 4–7). The absence of consistent septal fusion at the corallite centre and of prominently arched tabulae supports its original generic assignment to *Favistina*.

Materials previously assigned to *Favistina stellata* (Hall, 1847) *sensu* Flower (1961), from the Cutter Formation of New Mexico and the basal Liberty Formation of Kentucky, lack amplexoid septa and do not belong to Hall's species, which is reassigned to *Crenulites* (see discussion below under that species). Another form similar to Flower's materials is the poorly known specimen illustrated externally by Bassler (1950) as *Favistella alveolata* (Goldfuss, 1826) from the Liberty Formation of Clarksville, Ohio. All these exhibit comparable major septal lengths that do not extend to the corallite centre and weak development of minor septa. In these aspects, they closely resemble the holotype of *Favistina crenulata*, differing primarily in their slightly smaller corallites (typically 5 mm in diameter). Given the minor nature of this distinction, they are tentatively included within *Favistina crenulata*, though further study is required to clarify their relationship.

The material described by Browne (1965) as *Cyathophylloides* cf. *burksae* Flower, 1961 was reported from the basal parts of the Waynesville and Whitewater formations in the same region, although all figured specimens originate from the latter horizon. Browne (1965, p. 1189) noted that her specimens exhibit similarities to *Cyathophylloides burksae* Flower, 1961, discussed above, from the Aleman Formation (middle Katian) of the Montoya Group,

differing chiefly in that "some corallites in which major septa fail to reach the centre thus show intergradation with corallites in which septa join axially in groups". However, the absence of axially fused septa supports their attribution to *Favistina*. Within *Favistina*, Browne's (1965) material closely resembles the holotype of *Favistina crenulata* from the same horizon, particularly in its septal and tabular development. The key distinctions between them lie in the former possessing smaller corallites (3.5–5 mm in diameter) and slightly longer major septa that extend near the corallite centre. Because these differences appear to be relatively minor, her material is temporarily placed within *Favistina crenulata*.

Favistina paleophylloides Flower, 1961

1961 *Favistina paleophylloides* Flower, p. 82, pl. 42, figs 1–8.

Remarks. – The type material of *Favistina paleophylloides* (holotype, NMBM 735; paratype, NMBM 794) is from the "Lowville beds" (Black River Group, upper Sandbian; Desrocher *et al*. 2023) of Fourth Chute, near Eganville, Ontario. It exhibits a cerioid growth pattern in early stages, with corallites measuring 5–6 mm in diameter, before transitioning to a partially fasciculate form in later development, where corallite diameters decrease to 4–5 mm. Additional distinguishing features include 14–15 major septa in mature corallites, short but well-developed minor septa, and commonly complete, irregularly spaced tabulae.

Favistina sp. A

1969 *Favistella alveolata* (Goldfuss); Ivanovskiy *pars*, pp. 66, 69–71, pl. 3, figs 3a, b *only*.

Remarks. – This species is represented by the specimen illustrated by Ivanovskiy (1969) as *Favistella alveolata* (Goldfuss, 1826) from the Dolborian Horizon (middle Katian; Kanygin *et al.* 2019) of the Siberian Platform. Based on the illustration, the major septa of this cerioid form are non-amplexoid and do not extend to the corallite centre, thereby forming a free axial zone, features that support its attribution to *Favistina*. It is distinguished from other known congeneric species by its relatively large corallites (approximately 5 mm in diameter) and its complete, irregularly shaped (concave, flat, or convex), widely spaced tabulae (Ta5 = 2–4). In light of the current gaps in knowledge regarding its variation, an open nomenclatural approach is warranted.

Favistina honoratensis Bolton, 1979

1979 *Favistina honoratensis* Bolton, p. 2, pl. 1.1, figs 1, 2, 5, 8, 9, pl. 1.2, figs 1, 2.

Remarks. – *Favistina honoratensis* (holotype, GSC 61611; paratypes, GSC 61612–61619) was described from the Honorat Group of the Mount Saint Joseph area, southern Gaspé Peninsula, Quebec (Bolton 1979, 1980). This coral is almost certainly from the upper, Garin Formation of the group, which, according to Riva & Malo (1988), contains graptolites of the *Climacograptus spiniferus* to *Paraclimatograptus manitoulinensis* biozones indicative of a middle Katian age. The specific features include small corallite size (2.5–3.0 mm in diameter), 12 major septa extending nearly to the corallite centre where their axial ends are rarely fused in pairs, short but distinct minor septa, and complete, slightly convex, well-spaced tabulae (Ta5 = 8–10). As noted by Bolton (1979), it closely resembles North American species *Favistina minima* (Foerste) and *F. minor* (Bassler, 1932), considered above, in corallite size. However, *F. minima* is still poorly known so that a proper comparison is impossible, whereas *F. minor* is separable by having shorter septa and sparser tabulae.

Favistina mediana Deng, 1984

(Fig. 15)

1984 *Favistina mediana* Deng, p. 316, pl. 2, fig. 1a, b.

Referred material. – NIGP 63618 (TS) and NIGP 63619 (LS), holotype, original of Deng (1984, pl. 2, fig. 1a, b), refigured here (Fig. 15), Longmendong Formation (lower Katian) of Heiyingsigou, Longxian area, western Shaanxi Province.

Diagnosis. – *Favistina* with small corallites [ACDs (6+) = 3.05–3.76 mm], short major septa (commonly accounting for 40–70% of corallite radius), weakly developed minor septa, and moderately spaced tabulae (Ta5 = 6–7).

Description. – Modified from Deng (1984, p. 316). The single specimen is of unknown external form and size. Corallites polygonal, 4–7, commonly 5–6 sided, small [ACDs (6+) = 3.05–3.76 mm]. Corallite walls straight to slightly wavy, moderately thick, ranging from 0.11 to 0.18 mm in thickness, separated by prominent dark lines. Septa of two orders. Major septa 10–11 in number, commonly accounting for 40–70% of corallite radius, or rarely almost reaching the corallite centre. Minor septa weakly developed, extending slightly beyond corallite walls. Tabulae complete, or rarely incomplete, flat, slightly wavy or slightly arched, moderately spaced (Ta5 = 6–7).

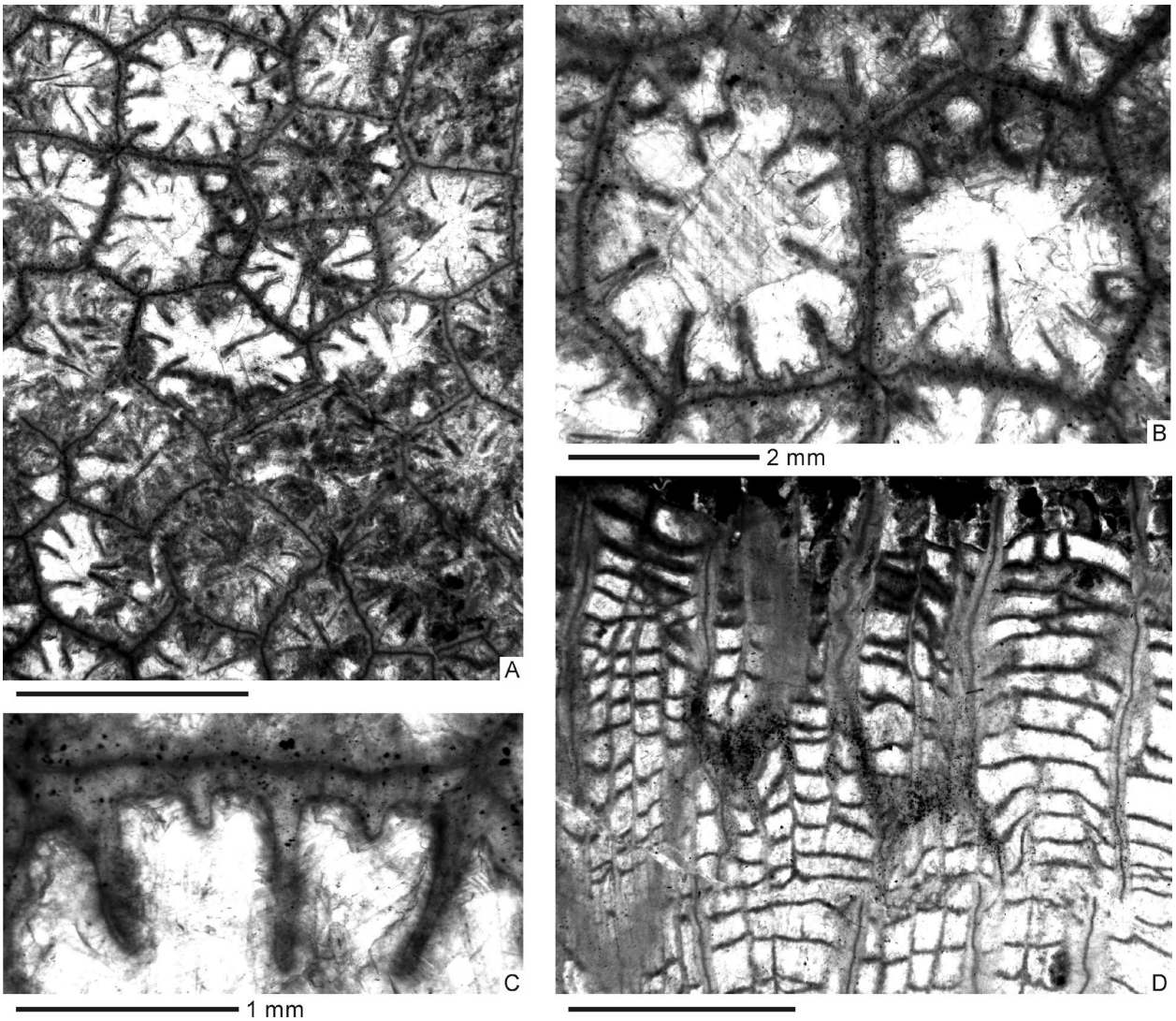


Fig. 15. Favistina mediana Deng, 1984. NIGP 63618 (TS) and NIGP 63619 (LS), holotype, Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

Remarks. – The revised description and diagnosis of *Favistina mediana* given above are based on a reassessment of the holotype, the only known specimen attributed to this species. The relatively small corallites and rather short major septa are sufficient to distinguish it from other *Favistina* species.

***Favistina pachytheca* Deng, 1984**

(Fig. 16)

1984 *Favistina pachytheca* Deng, pp. 316, 317, pl. 2, fig. 3a, b.
?1991 *Favistina* sp., Lin & Wang in Wang, p. 164, pl. 1, fig. 2a, b.

Referred material. – NIGP 63622 (TS) and NIGP 63623 (LS), holotype, original of Deng (1984, pl. 2, fig. 3a, b), refigured here (Fig. 16), Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province.

Diagnosis. – *Favistina* with medium-sized corallites [ACDs (6+) = 4.25–5.32 mm], thick, wavy corallite walls (WT = 0.17–0.25 mm), long major septa extending commonly to the corallite centre, relatively long minor septa (up to 30% of corallite radius), and moderately spaced tabulae (Ta5 = 5–6).

Description. – Modified from Deng (1984, pp. 316, 317). External form and size of the single specimen unknown. Corallites polygonal, 4–7, commonly 5–6 sided, medium-sized [ACDs (6+) = 4.25–5.32 mm]. Corallite walls slightly to moderately wavy, thick (WT = 0.17–0.25 mm), separated by prominent dark lines. Septa of two orders, tapering axially. Major septa 14–16 in number, long, some extending almost to or slightly beyond the corallite centre with slightly twisted axial ends, without forming an axial structure. Minor septa short but prominent, commonly up to 30% of corallite radius. Tabulae complete or rarely

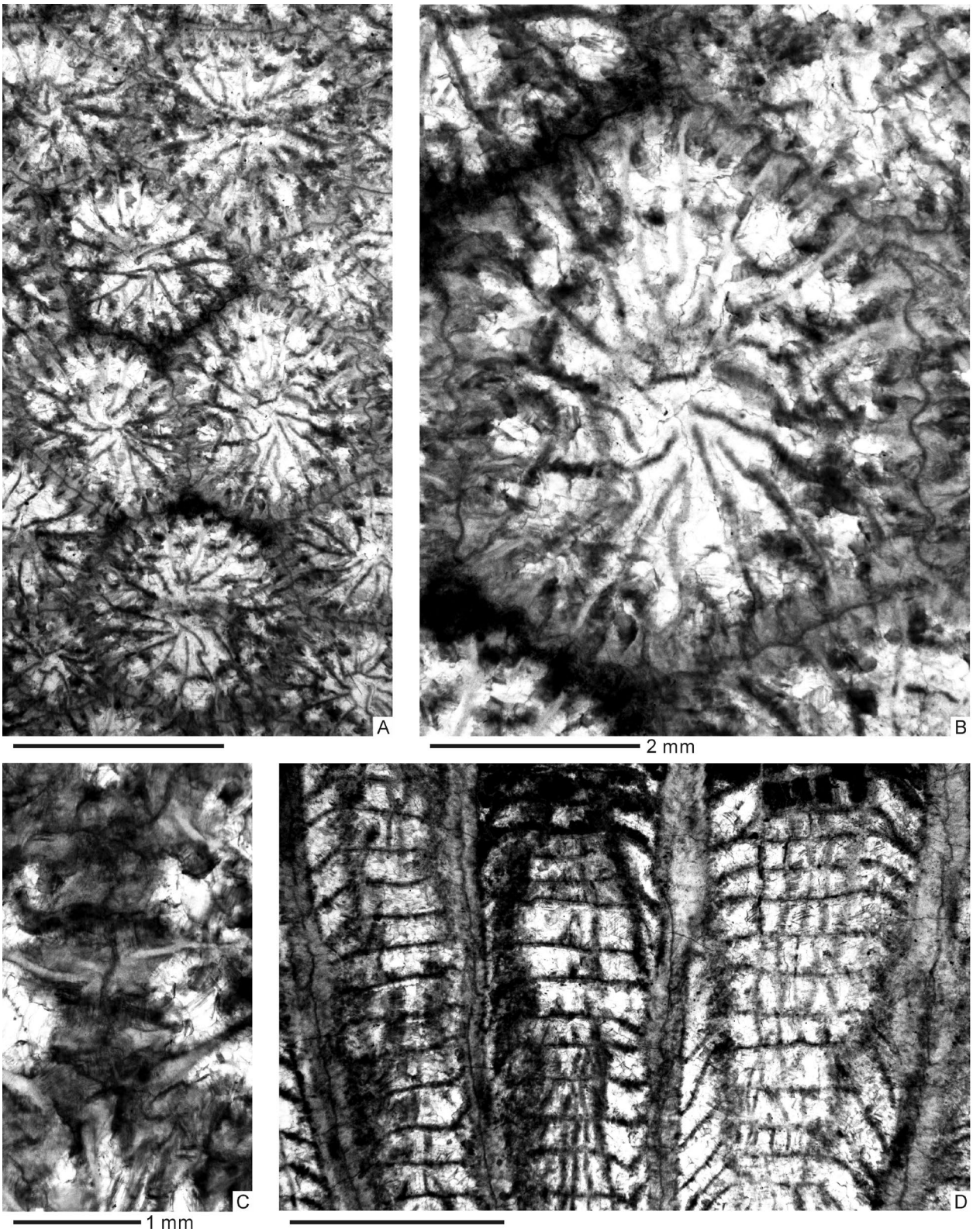


Fig. 16. Favistina pachytheca Deng, 1984. NIGP 63622 (TS) and NIGP 63623 (LS), holotype, Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

incomplete, generally slightly arched with a broad, flat central platform, moderately spaced (Ta5 = 5–6).

Remarks. – The revised concept of *Favistina pachytheca* presented above is based on a restudy of the holotype and only known specimen of this species. The features serving to distinguish it from other *Favistina* species include thick, wavy corallite walls, long major septa, and widely spaced tabulae.

The specimen figured by Lin & Wang in Wang (1991) as *Favistina* sp. comes from the middle Shiyanhe Formation (middle Katian) of Shiyanhe, Xichuan, southwestern Henan Province. It has comparable corallite size (2.5–6.0 mm in diameter), thick corallite walls and septa, and relatively long minor septa, differing in having slightly less major septa (11–12), and closer tabulae (Ta5 = 8–10), and may be synonymous with *Favistina pachytheca*.

Favistina longxianensis Deng, 1984, considered below, from the same horizon and locality as *F. pachytheca*, shows closest similarities to the latter. The major differences lie in the presence of slightly alveolitoid corallites, and slightly smaller corallite size [ACDs (6+) = 3.63–4.53 mm] of the former, and the two forms are possibly synonymous.

***Favistina longxianensis* Deng, 1984**

(Fig. 17)

1984 *Favistina longxianensis* Deng, pp. 317, 318, pl. 3, fig. 2a, b.

Referred material. – NIGP 63626 (TS) and NIGP 63627 (LS), holotype, original of Deng (1984, pl. 3, fig. 2a, b), refigured here (Fig. 17), Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province.

Diagnosis. – *Favistina* with slightly alveolitoid, small to medium-sized corallites [ACDs (6+) = 3.63–4.53 mm], thick corallite walls (WT = 0.18–0.21 mm), long major septa, well-developed minor septa (up to 30–50% of the majors), and evenly spaced tabulae (Ta5 = 6–8).

Description. – Modified from Deng (1984, pp. 317, 318). The single specimen is of unknown external form and size. Corallites polygonal to slightly alveolitoid,

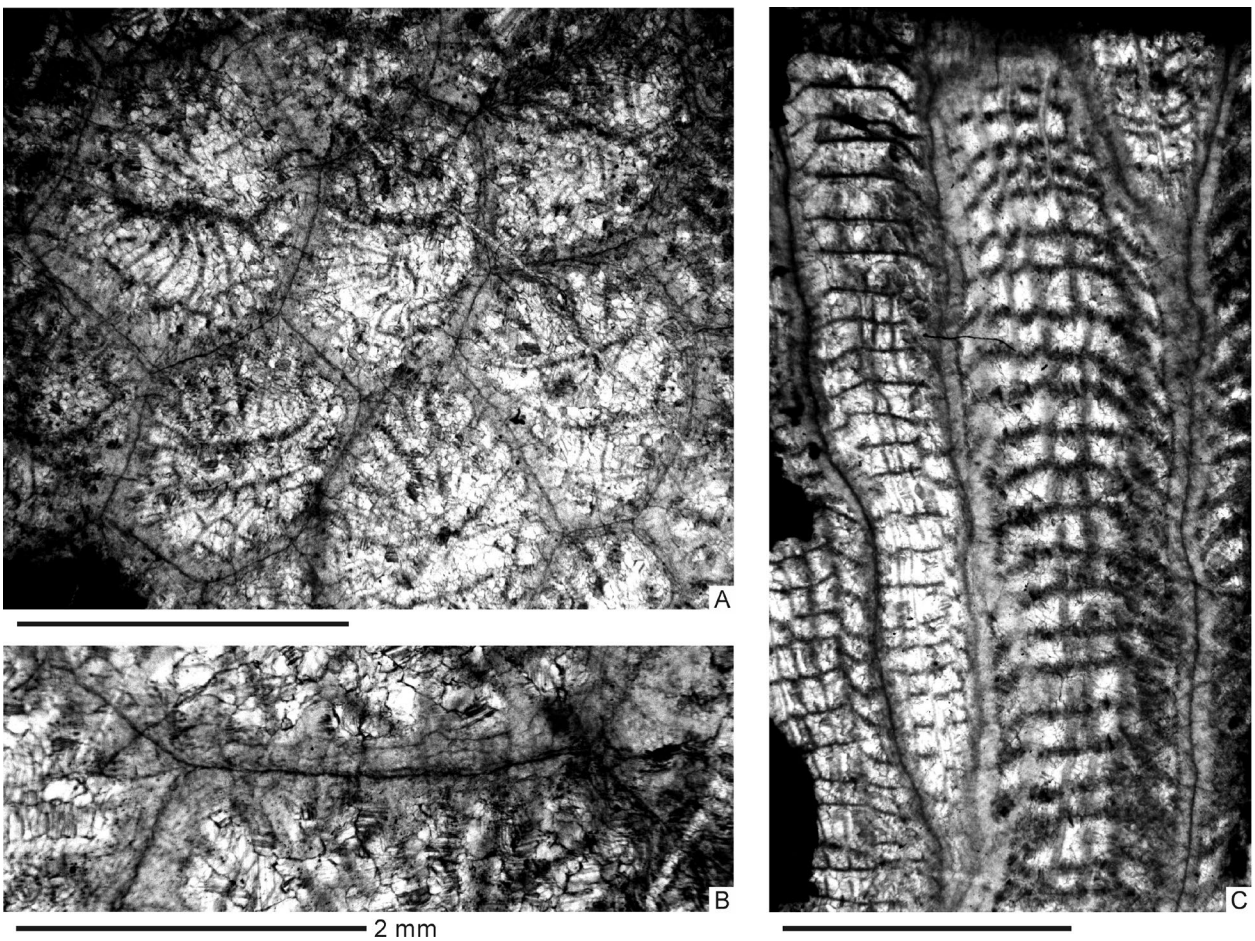


Fig. 17. Favistina longxianensis Deng, 1984. NIGP 63626 (TS) and NIGP 63627 (LS), holotype, Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

commonly 5–6 sided, small to medium-sized [ACDs (6+) = 3.63–4.53 mm]. Corallite walls straight to slightly curved, moderately thick, ranging from 0.18 to 0.21 mm in thickness, separated by prominent dark lines. Septa of two orders. Major septa about 12–13 in number, long, extending almost to the corallite centre. Minor septa well developed, alternating in length with the major, commonly up to 30–50% of the majors. Tabulae complete, flat, slightly wavy or slightly arched, commonly with a broad, subhorizontal axial platform, evenly spaced (Ta5 = 6–8).

Remarks. – The revised description and diagnosis of *Favistina longxianensis* given above are based on a restudy of its holotype, which is the only known specimen attributed to this species. Its comparison with the most similar form, *Favistina pachytheca* Deng, 1984, from the same horizon, is presented above under the latter species.

***Favistina arcuta* Deng, 1984**

(Fig. 18)

1984 *Favistina arcuta* Deng, p. 318, pl. 4, fig. 2a, b.

Referred material. – NIGP 63634 (TS) and NIGP 63635 (LS), original of Deng (1984, pl. 4, fig. 2a, b), refigured here (Fig. 18), Taoqupo Formation (lower–middle Katian), Tiewadian–Xilingou, Jingyang area, central Shaanxi Province.

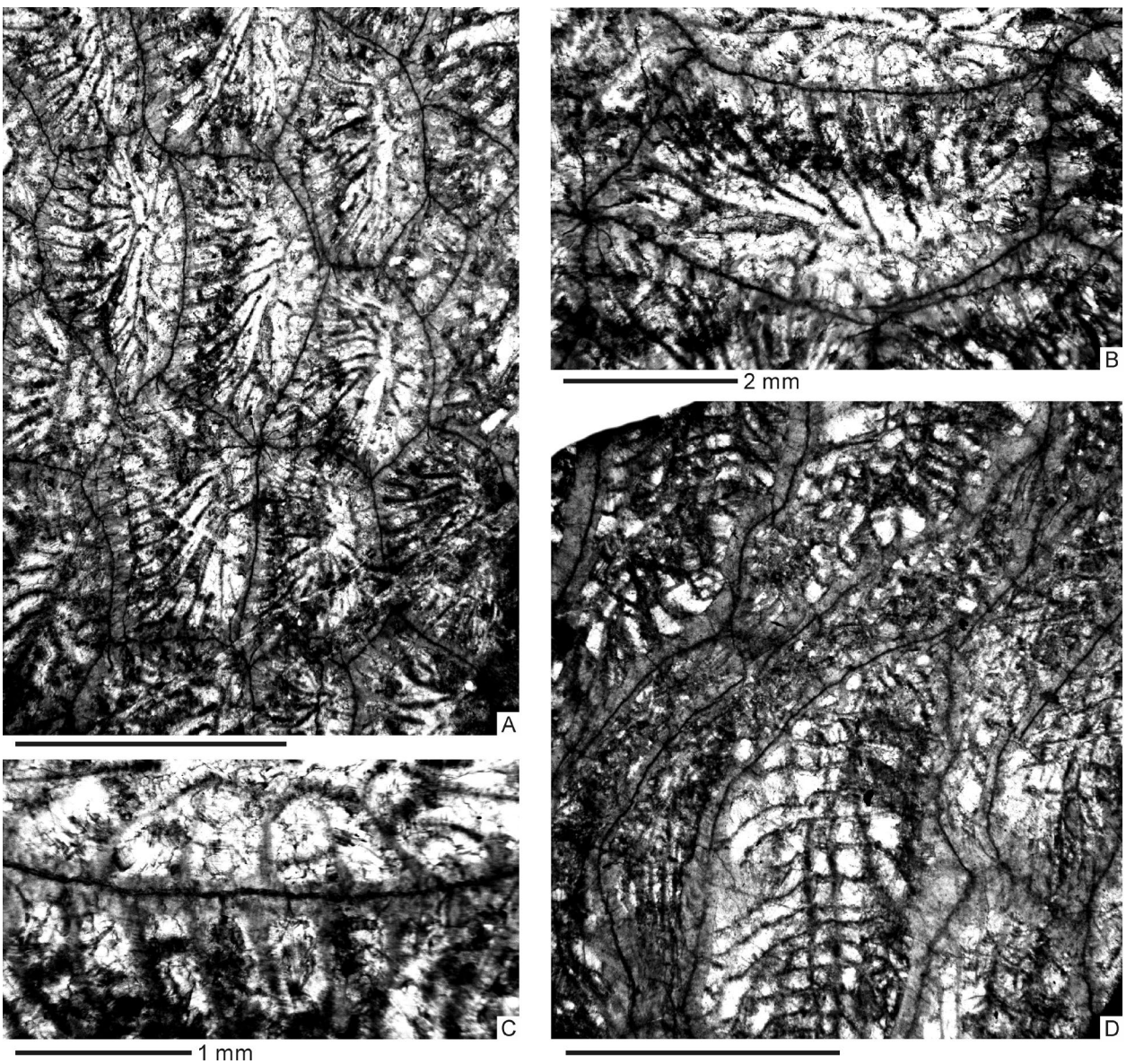


Fig. 18. Favistina arcuta Deng, 1984. NIGP 63634 (TS) and NIGP 63635 (LS), holotype, Taoqupo Formation (lower–middle Katian) at a locality between Tiewadian and Xilingou, Jingyang area, central Shaanxi Province. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

Diagnosis. – *Favistina* with alveolitoid corallites that are small to medium-sized [ACDs (6+) = 3.21–4.33 mm], moderately thick corallite walls (WT = 0.24–0.25 mm), long major septa, well-developed minor septa (length up to 1/2 of the majors), and closely spaced tabulae (Ta5 = 10–11).

Description. – Modified from Deng (1984, p. 318). External form and size of the single specimen unknown. Corallites irregularly polygonal, commonly 5–7 sided, alveolitoid, small to medium-sized [ACDs (6+) = 3.21–4.33 mm]. Corallite walls slightly arc-shaped, moderately thick, 0.24–0.25 mm in thickness, separated by prominent dark lines. Septa of two orders. Major septa about 14–15 in number, long, slightly curved, extending to or almost to the corallite centre but without forming an axial structure. Minor septa well developed, alternating in length with the major, generally about 1/2 of the majors. Tabulae complete, slightly arched, closely spaced (Ta5 = 10–11).

Remarks. – The revised description and diagnosis of *Favistina arcuta* given above are based on the holotype, which is the only known specimen attributed to this species. The distinctive alveolitoid corallites characterise this species.

***Favistina* sp. B**

(Fig. 19)

1987 *Favistina* aff. *shifosiensis* (Cao); Deng, p. 621, pl. 3, fig. 2a, b, pl. 4, fig. 2.
?1991 *Favistina* aff. *shifosiensis* (Cao); Lin & Wang in Wang, p. 164, pl. 1, fig. 1a, b.
2020 *Favistina* aff. *shifosiensis* (Cao); Liang, p. 496, pl. 5-9-1, figs 5, 6 [refig. Deng 1987, pl. 3, fig. 2a, b].

Referred material. – NIGP 99383 (TS) and NIGP 99384 (LS), original of Deng (1987, pl. 3, fig. 2a, b, pl. 4, fig. 2), refigured here (Fig. 19), probably middle Shiyanhe Formation (middle Katian) of Shiyanhe, Xichuan, southwestern Henan Province.

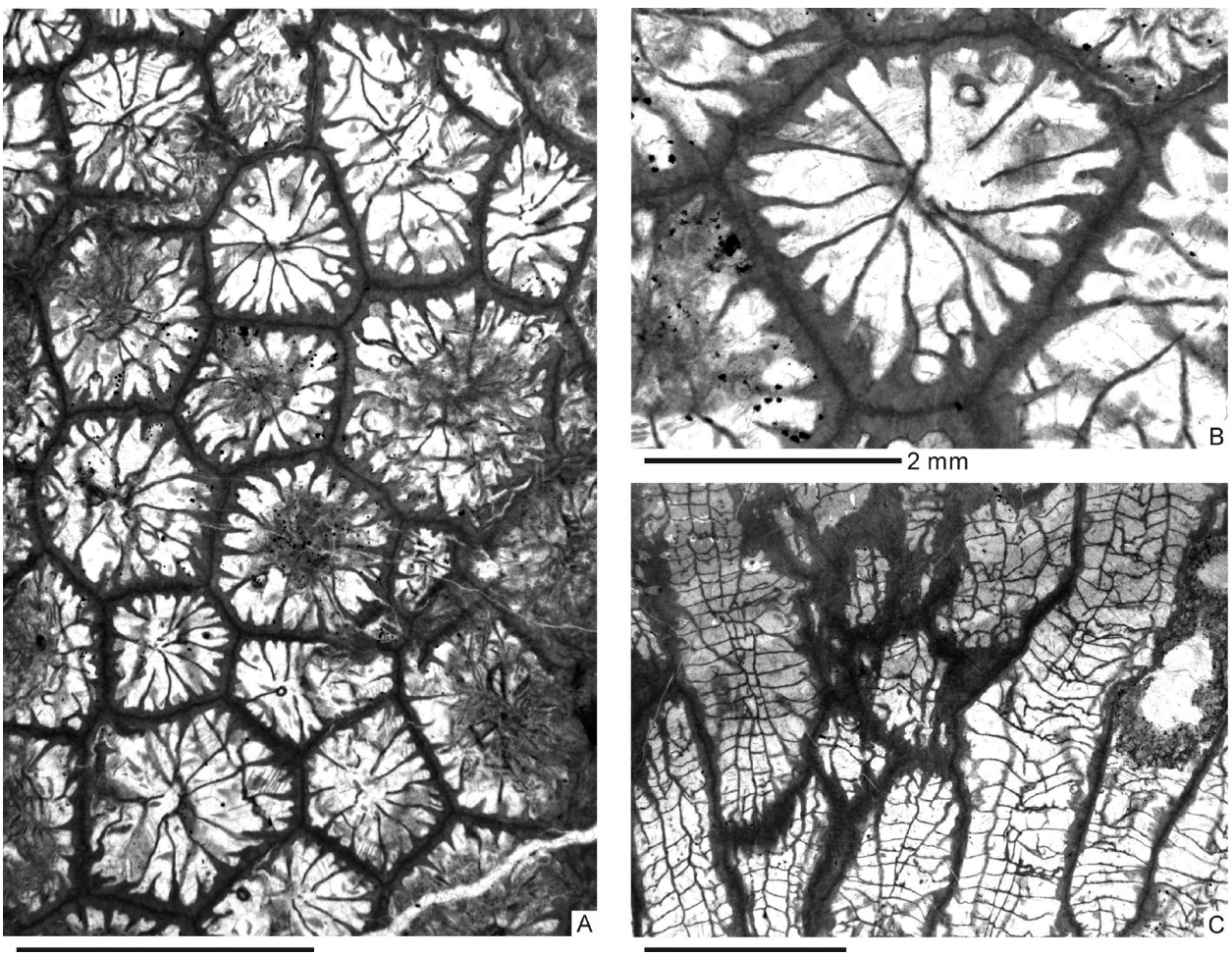


Fig. 19. Favistina sp. B. NIGP 99383 (TS) and NIGP 99384 (LS) from one corallum, described by Deng (1987) as *Favistina* cf. *shifosiensis* (Cao, 1982), probably middle Shiyanhe Formation (middle Katian), Shiyanhe, Xichuan, southwestern Henan Province. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

Description. – Modified from Deng (1987, p. 621). External form and size of the single specimen unknown. Corallites polygonal, 4–7 sided, small [ACDs (6+) = 3.14–4.02 mm]. Corallite walls slightly wavy, moderately thick, 0.11–0.19 mm in thickness, separated by prominent dark lines. Septa of two orders. Major septa of mature corallites 11–12 in number, long, extending to, or almost to the corallite centre but without forming an axial structure. Minor septa well developed, alternating in length with the major, short, generally less than 1/4 of corallite radius. Tabulae complete to incomplete, concave or rarely slightly arched, closely spaced (Ta5 = 9–13).

Remarks. – The present revision of this species is based on the specimen described by Deng (1987) as *Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982). It is not true *Favistella* (*Favistella*) *shifosiensis* Cao in Cao & Lin, 1982 from the Liangchakou Formation (probably middle Katian) of the Shanyang area, southeastern Shaanxi, which is revised in this work as *Crenulites minor* (Lin, 1963), discussed below. Key specific features of Deng's (1987) form include small corallites (ACDs (6+) = 3.14–4.02 mm), and commonly incomplete, concave, densely spaced tabulae (Ta5 = 9–13), and these are sufficient to distinguish it from other known species of *Favistina*. However, the scarcity of material precludes the formal erection of a new taxon in this study.

The specimen figured by Lin & Wang in Wang (1991) as *Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982) comes from the same horizon and locality as *Favistina* sp. B. It was not described but stated to show "corallite size, septal number, wall thickness, and tabular spacing identical to Deng's material" (Lin & Wang in Wang 1991, p. 164), and is probably conspecific with the latter. These authors also commented that this fossil "appears to develop squamulae and rare corner pores, and is thus possibly attributable to *Agetolitoides* Lin, 1986". In my view, this seems very unlikely, since corner pores in agetolitids, when present, are very common (Wang & Cui 2025).

Favistina floweri Webby, 1988

1988 *Favistina floweri* Webby, pp. 142, 144, 145, figs 3.1–3.6.

Remarks. – The type material of *Favistina floweri* (holotype, SUP 95154; paratypes, SUP 43239, 43241, 95153) occurs in the Malongulli Formation (middle Katian) of the Cliefden Caves area, and the coeval, upper Cargo Creek Limestone of the Cargo–Canomodine area, central NSW, eastern Australia. The specific features include variably sized corallites (1.24–5.29 mm in diameter), 12–17 major septa that extend to, or close to the corallite axis where they may be fused in irregularly arranged groups, irregularly developed minor septa, and complete to incomplete, flat to slightly arched, variably spaced tabulae (Ta5 = 8–13).

Favistina plus Webby, 1988

1988 *Favistina plus* Webby, pp. 145, 146, figs 3.7, 3.8, 6.1, 6.2.
2022 *Favistina plus* Webby; Zhen *et al.*, p. 704, fig. 6a–g.

Remarks. – The type material of *Favistina plus* (holotype, SUP 43240) is known from the lower Malongulli Formation (middle Katian) of Cliefden Caves area, central NSW, eastern Australia. It has medium-sized corallites (3.79–5.59 mm in diameter), 16–21 major septa in mature corallites that extend to, or close to the corallite axis and sometimes loosely aggregate at the centres, and commonly complete, flat to slightly arched, moderately to closely spaced tabulae (Ta5 = 9–11). This species has recently been documented by Zhen *et al.* (2022) from carbonate rocks of a drill hole (WNDD0002) immediately west and northwest of Peak Hill, central NSW.

Favistina gleesonensis Webby, 1988 from the same horizon and general locality is a similar form, which was said by Webby (1988) to differ in having smaller corallites (2.52–4.65 mm in diameter) and thinner corallite walls. Since there is some overlap in their corallite size, and because the thickness of corallite walls may be due to intraspecific variation, the two species may eventually prove synonymous.

Favistina gleesonensis Webby, 1988

1988 *Favistina gleesonensis* Webby, p. 146, fig. 6.5–6.6.

Remarks. – The occurrence of *Favistina gleesonensis* (holotype, SUP 95150) is the same as that of *Favistina plus* Webby, 1988 considered above (i.e. the lower Malongulli Formation of middle Katian age in the Cliefden Caves area of central NSW, eastern Australia. Its comparison with the latter is presented above under the latter.

Favistina sp. A of Webby, 1988

1988 *Favistina* sp. A, Webby, p. 149, fig. 7.6–7.7.

Remarks. – All four specimens described by Webby (1988) as this species occur in the upper Canomodine Limestone (middle Katian) of the Cargo–Canomodine

area, central NSW, eastern Australia. It has corallite diameter of 1.85–3.35 mm, 11–13 major septa that are either free or fuse in loosely aggregated groups in the corallite centre, and complete, flat to slightly arched, well-spaced tabulae (Ta5 = 6–11, rarely 7–9) (Webby 1988). The reason for the use of an open nomenclature was not given by Webby (1988), a decision cautiously accepted here.

Closest similarities lie with *Favistina floweri* Webby, 1988, considered above, from the Malongulli Formation of the same age in central NSW. The latter differs in having larger corallites (1.24–5.29 mm in diameter) and slightly more major septa (12–17 in number).

Favistina sp. B of Webby, 1988

1988 *Favistina* sp. B, Webby, p. 149, fig. 7.8–7.9.

Remarks. – This form is represented solely by a single specimen from the upper Malongulli Formation (middle Katian) of Cliefden Caves area central NSW, eastern Australia. Its specific features include corallites up to 4.49 mm in diameter, 12–13 major septa, and thin, relatively long minor septa (1/3–1/2 of the adjacent majors). A revision based on more material is necessary.

Genus *Crenulites* Flower, 1961

1847 *Favistella* Hall, p. 275.
1961 *Crenulites* Flower, p. 84.
1982 *Favistella* (*Parafavistella*) Lin in Cao & Lin, p. 32.

Type species. – *Crenulites duncanae* Flower, 1961, upper Second Value Formation, upper Edenian to lowest Maysvillian age (middle Katian) (Sweet 1979, fig. 4; Elias 1985, p. 7), El Paso, western Texas, by original designation.

Diagnosis. – Like *Favistina*, but with variably amplexoid septa. A biform tabularium may be observed.

Remarks. – As outlined by Flower (1961, p. 84), *Crenulites* is "essentially an amplexoid edition of *Favistina*, with the added feature of tabulae downturned at the edges and scalloped, being turned down most strongly between the septa". This tabular character was later termed the biform tabularium (Weyer 1972, p. 439; Hill 1981, p. F25). However, in many *Crenulites* species, as illustrated below, this characteristic is often difficult to discern, likely due to its weak development or complete absence. Additionally, the presence of biform tabulae in several unrelated coral groups (Weyer 1972) further diminishes its taxonomic significance.

This genus was synonymised with *Favistina* Flower, 1961 by some (e.g., Ivanovskiy 1969; Sytova 1979). However, the delayed appearance of amplexoid septa in *Favistina*-like forms underscores the evolutionary and taxonomic importance of this septal feature. Consequently, *Crenulites* is regarded here as valid, a position advocated by many others (e.g., Hall 1975; Hill 1981; Webby, 1988; Lin *et al.* 1995; Webby *et al.* 2004; Wang *et al.* 2021).

Favistella Hall, 1847 has its type species *F. stellata* Hall, 1847 fixed by monotypy (Lang *et al.* 1940), which is reassigned here to *Crenulites*, considered below. As a result, this genus is synonymous with *Crenulites*. However, since Hall's *Favistella* is preoccupied by *Favistella* Dana, 1846 (Stumm 1948), a genus now widely regarded as indeterminate (Lang *et al.* 1940; Flower 1961; Hill 1981; this study), *Crenulites* is considered a valid name in this study.

Favistella (*Parafavistella*) Lin in Cao & Lin, 1982, with the type species *F.* (*P.*) *guyuanensis* Lin in Cao & Lin, 1982, from the Beiguoshan Formation (lower–middle Katian) at Yindonggou of the Guyuan area, southern Ningxia, northwestern China, has been overlooked since its establishment. The author commented that it is distinguished from *Favistina* by the weak development of minor septa, a feature regarded here as insignificant. Instead, the existence of amplexoid septa, which was not mentioned in Lin's original description but is clearly shown in the illustrations of the holotype of its type species, is of generic importance. The concept of *Favistella* (*Parafavistella*) is consequently consistent with that of *Crenulites*, justifying their synonymy.

Crenulites duncanae Flower, 1961

1961 *Crenulites duncanae* Flower, pp. 84, 85, pl. 16, fig. 1, pl. 19, figs 1–6, pl. 20, figs 1–5.
1973 *Crenulites duncanae* Flower; Caramanica, pp. 417–421, pl. 22, figs 2, 4, 5.
1981 *Crenulites duncanae* Flower; Hill, fig. 70, 1a, b [refig. Flower 1961, pl. 19, figs 3, 1].
1995 *Crenulites duncanae* Flower; Lin *et al.*, fig. 129a, b [refig. Flower 1961, pl. 19, figs 3, 1].

Remarks. – *Crenulites duncanae* is the type species of the genus, with its type material (holotype, NMBM 671; paratypes, NMBM 672, NMBM 673) from the upper Second Value Formation (middle Katian) of El Paso, western Texas. In addition to the type occurrence, this species was documented by Caramanica (1973, 1992) from the coeval, basal Bighorn Formation

of the Bighorn Mountains, northern Wyoming, and from the Selkirk Member (Maysvillian, middle Katian; Jin & Zhan 2001) of the Red River Formation in the Williston Basin, southern Manitoba.

Based on Flower's (1961) study, this species is characterised by having small to medium-sized corallites (commonly 3, rarely up to 4 mm in diameter), highly amplexoid septa, 8–12 major septa extending almost to the corallite centre, weak minor septa, and irregularly spaced tabulae (Ta5 = 8–14).

Crenulites stellatus (Hall, 1847)

1847 *Favistella stellata* Hall, pp. 275, 276, pl. 75, fig. 1a–c.
1961 *Favistina stellata* (Hall); Flower *pars*, pp. 79–81, pl. 38, figs 12, 13, pl. 39, figs 4–8, *non* pl. 38, figs 1–8, 10, 11, pl. 39, figs 1–3, 9, 10, pl. 40, figs 7–9.
1965 *Cyathophylloides stellata* (Hall); Browne *pars*, pp. 1186, 1188, pl. 148, figs 2a, b, pl. 149, figs 1, 2.
?1965 *Cyathophylloides stellata* (Hall); Browne *pars*, pp. 1186, 1188, pl. 148, figs 3a, b, pl. 149, fig. 3.
1973 *Cyathophylloides hollandi* Caramanica, pp. 422–427, pl. 22, figs 6, 7, text-fig. 57.
1976 *Favistina stellata* (Hall); Fedorowski & Jull, pp. 55, 56, pl. 8, fig. 1a, b, pl. 10, fig. 2a–k, pl. 11, figs 1a–k, 2a–i, pl. 13, fig. 1a–l, pl. 15, fig. 2a, b, text-fig. 5.
1979 *Favistina stellata* (Hall); Bolton, pl. 1.1, figs 3, 4, 6, 7, pl. 1.2, figs 4, 5.
non 1979a *Favistina stellata* (Hall); Sytova, p. 172, pl. 36, fig. 2a, b.
1981 *Favistina stellata* (Hall); Hill, fig. 72, 1d, f–h [1d, refig. Browne 1965, pl. 149, fig. 2; 1f–h, Flower, 1961, pl. 39, figs 7, 8, 6].
1992 *Cyathophylloides hollandi* Caramanica, pp. 80–82, pl. 6, figs 6, 7, text-fig. 20.

Remarks. – The type occurrence of *Favistina stellata* has now been recognised as the basal Saluda Member of the Whitewater Formation (Browne 1965), likely corresponding to middle–? basal upper Katian (Gray & Burger 1986; Brett *et al*. 2020; Daniel Goldman & Patrick McLaughlin pers. comm.). Hall (1847) did not designate a holotype for this species, and Browne (1965) later selected a lectotype (AMNH 1168/A) from Hall's original specimens. Note that Flower (1961, pl. 39, figs 4–8) illustrated a syntype labeled "AMNH 1168/1", which was regarded by Hill (1981) and the present author as the same specimen as the lectotype. Several topotypes of *Favistina stellata* were studied by Fedorowski & Jull (1976).

According to Browne (1965) and Flower (1961), the lectotype of *Favistina stellata* has corallites generally 5 mm in diameter, 12–14 major septa that extend about halfway to, or almost to, the corallite centre with axial ends always free or rarely joined, short minor septa, and complete, slightly convex, well-spaced tabulae (5–7 in 5 mm). In addition, the partly amplexoid nature of this specimen, not mentioned by these authors, is clearly shown in its illustrations (Flower 1961, pl. 39, figs 6, 8; Browne 1965, pl. 149, fig. 2), as well as in those of figured topotypes listed in the synonymy list. Thus, this species is reassigned here to *Crenulites*.

Cyathophylloides hollandi Caramanica, 1992 was also introduced by Caramanica (1973, unpublished PhD thesis) as a new species. The holotype (UND 13727) and only specimen of this species was collected as "float on the Bighorn Formation about 4 meters (13ft) above the top of the Hunt Mountain Beds in the Bighorn Range, northern Wyoming" (Caramanica 1992, p. 81). This stratigraphic level corresponds to middle Katian–? basal upper Katian. The present transfer of this species to *Crenulites* is based on its slightly amplexoid septa. Its specific features include an alveolitid outline at the base and periphery of the corallum, corallites 1.7–5.8 mm in diameter, 10–16 major septa of somewhat amplexoid type, and complete, flat to moderately arched, well-spaced tabulae (0.83–1.37 mm apart). It appears to differ from *Crenulites stellatus* primarily in the partial presence of an alveolitid outline and is therefore considered here a synonym of the latter species.

Apart from the type occurrence, this species was documented from the roughly coeval Kagawong beds of the Georgian Bay Formation of Manitoulin Island (Bolton 1979), the Waynesville Formation in Kentucky (Browne 1965), and the Aleman and Cutter formations (middle Katian–? basal upper Katian) of New Mexico and western Texas (Flower 1961).

Favistina stellata (Hall, 1847) *sensu* Sytova (1979a), from the Dolborian Horizon (middle Katian) of the Podkamennaya Tunguska River Basin, is regarded here as a possible example of *Crenulites septosus* (Sokolov, 1950), discussed below.

Crenulites blainvilli (Billings, 1858a)

1858a *Columnaria blainvilli* Billings, pp. 166, 167.
1858b *Columnaria blainvilli* Billings, p. 421.
1915 *Columnaria alveolata* Goldfuss; Bassler *pars*, p. 259.
1924 *Columnaria alveolata blainvilli* (Billings); Foerste, pp. 67, 68, pl. 5, fig. 2.
1950 *Favistella alveolata* (Goldfuss); Bassler *pars*, pp. 19, 20.
1961 *Crenulites blainvilli* (Billings); Flower, p. 86.

Remarks. – *Crenulites blainvilli* occurs in the strata now assigned to the Île aux Couleuvres Formation (probably lower Richmondian, middle Katian; Desbiens & Lespérence 1989, pp. 1194, 1195) of Couleuvres Island (formerly Snake Island), Lake St. John, Quebec. The original description by Billings (1858a, b) was not accompanied with illustrations. Foerste (1924) presented for the first time an external

view of a specimen (GSC 8437) from Billings' type collection and provided brief descriptive remarks. A study of the type material in thin section is clearly required to clarify its true identity.

The current concept of *Crenulites blainvilli* is largely based on the accounts given by the above-mentioned authors, as follows. Billings (1858a, p.166; 1858b, p. 421) described it as "forming large sub-globose pyriform or hemispheric masses of polygonal corallites one line and a-half in diameter; about eighteen radiating septa which reach the centre; transverse diaphragms three or four to one line". Foerste (1924) remarked that this form possesses corallites about 3 mm in diameter, septa conspicuous, almost or quite reaching the centre, and 6–8 tabulae occurring in a length of 10 mm. It is important to note that Flower (1961, p. 86) recognised the amplexoid septal nature of this form by noting that Foerste's illustration exhibits "unmistakable crenulate edges to the tabulae and traces of the septa".

Early authors (e.g. Foerste 1924; Bassler 1915, 1950) included this form within *Columnaria alveolata* Goldfuss, 1826. This treatment was rejected by Flower (1961), who instead transferred it to *Crenulites* based on the development of amplexoid septa. He also concluded that *Crenulites blainvilli* differs from the associated *C. rigidus* (Billings, 1858a), considered below, with the latter having larger corallites (4.0–5.0 mm in diameter) and slightly sparser tabulae (6–10 in 10 mm).

Crenulites rigidus (Billings, 1858a)

1858a *Columnaria rigida* Billings, p. 167.
1858b *Columnaria rigida* Billings, p. 421.
1915 *Columnaria alveolata rigida* (Billings); Bassler, p. 259.
1924 *Columnaria alveolata rigida* (Billings); Foerste, pp. 67, 68, pl. 5, fig. 1.
1950 *Favistella alveolata rigida* Billings; Bassler, p. 273.
1961 *Crenulites rigidus* (Billings); Flower, pp. 85, 86, pl. 29, figs 1–10.
1973 *Crenulites rigidus* (Billings); Caramanica, pp. 412–416, pl. 21, figs 14, 15, pl. 22, fig. 1.

Remarks. – *Crenulites rigidus* comes from the same stratigraphic interval and locality as *Crenulites blainvilli* Billings (1858a), discussed above. Like the latter, *C. rigidus* was originally described without illustration by Billings (1858a, b). This was followed by Foerste (1924) who figured externally a specimen from Billings' type collection (GSC 8438?) and made an additional description. A subsequent assessment of two hypotypes from the same horizon by Flower (1961) has also improved the knowledge of this form.

Billings (1858a, p.167; 1858b, p. 421) described this form briefly as "forming large masses of polygonal corallites usually three lines in diameter, but with numerous smaller ones, and occasionally others of a larger size; radiating septa, about twenty, not reaching the centre; transverse diaphragms from two to four in one line". In describing a syntype, Foerste (1924, p. 68) mentioned that "corallites mostly larger, frequently attaining a diameter of 4 or 5 mm, septa from 7 to 8 in a length of 10 mm, as a rule short, but some reaching the centre". Based on two hypotypes, as well as Foerste's illustration, Flower (1961) confirmed the amplexoid nature of its septa.

Rather than being included in the synonymy of *Columnaria alveolata* Goldfuss, 1826 by some authors (e.g. Foerste 1924; Bassler 1915, 1950), *Crenulites rigidus* was placed by Flower (1961) in *Crenulites* because of its amplexoid septal nature. In Flower's (1961, pp. 85, 86) view, its specific features include large corallites (4.0–5.0 mm in diameter), consistently widely spaced tabulae (6–10 in 10 mm), and "septa continuous at the corallite margin", the latter of which indicates that it may represent a transitional form between *Favistina* and *Crenulites*. Its distinction from the associated *Crenulites blainvilli* (Billings, 1858a) is discussed above under the latter species.

In addition to the type occurrence, *Crenulites rigidus* was also described by Caramanica (1973, 1992) from within the basal 41 m of the lower massive portion of the Bighorn Formation (middle Katian), the Bighorn Mountains, northern Wyoming, and from the Selkirk Member (Maysvillian, middle Katian; Jin & Zhan 2001) of the Red River Formation, the Williston Basin, southern Manitoba.

Crenulites calicinus (Nicholson, 1875a)

1875a *Favistella* (*Columnaria*) *calicina* Nicholson, pp. 89, 90.
1875b *Columnaria* (*Favistella*) *calicina* (Nicholson); Nicholson, p. 279.
1875c *Favistella calicina* Nicholson; Nicholson, pp. 24, 25, text-fig. 9.
?1876 *Columnaria herzeri* Rominger, p. 90.
1879 *Columnaria calicina* Nicholson; Nicholson, pp. 197–199, fig. 128, pl. 10, fig. 2, 2a, text-fig. 28 [refig. Nicholson 1875c, text-fig. 9].
1901 *Columnaria calicina* Nicholson; Lambe, pp. 102, 103, pl. 6, fig. 4.
1924 *Columnaria calicina* Nicholson; Foerste, pp. 68, 69, pl. 4, fig. 3a, b.
1950 *Favistella alveolata calicina* (Nicholson), Bassler, p. 272, pl. 19, fig. 4.
1961 *Favistina calicina* (Nicholson); Flower, pp. 82, 83, pl. 40, figs 1–6.
1965 *Cyathophylloides wellsi* Browne, pp. 1189, 1190, pl. 147, figs 3a, b, 4a–c, pl. 152, fig. 6.

1976 *Favistina calicina* (Nicholson); Fedorowski & Jull, pp. 58, 60, pl. 8, fig. 2a, b, pl. 12, figs 1a–o, 2a–k, pl. 13, fig. 2a–n, text-fig. 6.
1976a *Favistina calicina* (Nicholson); Jull, pp. 457–459, pl. 1, figs 1–4.

Remarks. – A lectotype (UA 8589), along with duplicate sections numbered GSC 32061, was selected and described by Jull (1976a) for *Crenulites calicinus* from the upper Georgian Bay Formation (middle Katian) in the valley of the Credit River near Streetsville, west of Toronto, Canada. Based on his study of this specimen, as well as a few topotypes, this species is characterised by having partly fasciculate colonies, adult corallites 4–5, or rarely 6 mm in diameter, and slightly amplexoid septa extending to the corallite axis without forming an axial structure (Jull 1976a, p. 458). The development of amplexoid septa warrants its present transfer to *Crenulites*.

The material described by Fedorowski & Jull (1976) and Flower (1961) as *Favistina calicina* comes from the same horizon and area. Both were included by Jull (1976a) within this species, although Flower's (1961) material possesses less amplexoid septa, slightly larger corallites (up to 7.5–9.0 mm in diameter) and slightly more septa, as noted by Jull (1976a).

Cyathophylloides wellsi Brown (1965), from the coeval Liberty Formation in Kentucky, was considered by Jull (1976a) as a further synonym of *Crenulites calicinus*. This is because it differs from the latter only in having slightly larger corallites (5–6 mm in diameter). Also added tentatively by Jull (1976a) to *Crenulites calicinus* were specimens from the same horizon in Kentucky assigned to this species by Bassler (1915, 1950), although many remain to be properly described.

Columnaria herzeri Rominger, 1876, from the "Cincinnati group of Kentucky", was originally described without illustrations as having corallites "partially in close contiguity" and "partially free, circular, laterally joining into chain-like rows" (Rominger 1876, p. 90), with other features similar to the associated form referred to *Columnaria stellata*. It was considered synonymous with *Crenulites calicinus* by many workers (e.g. Lambe 1901; Foerste 1924; Bassler 1950; Jull 1976a). However, the corallite size of this form is much smaller (about 3 mm in diameter) than that of *C. calicinus*, and therefore there must be some reservation until the type of *Columnaria herzeri* Rominger, 1876 is examined in thin section.

Crenulites vacuus (Foerste, 1909)

non 1879 *Columnaria*? *halli* Nicholson, pp. 200, 201, figs 28, 29, pl. 10, fig. 3, 3a.
1892 *Columnaria*? *halli* Nicholson; James, p. 99.
1909 *Columnaria vacua* Foerste, p. 313, pl. 11, fig. 2.
non 1950 *Columnaria vaqua*? Foerste; Sokolov, p. 238, pl. 3, fig. 9.
1950 *Foerstephyllum vacuum* (Foerste); Bassler, pp. 269, 270, pl. 12, figs 1–3, pl. 19, figs 9, 10.
1965 *Foerstephyllum vacuum* (Foerste); Browne, pp. 1182, 1183, pl. 146, figs 3a, b, 5, pl. 152, fig. 2.
1965 *Foerstephyllum vacuum magnum* Browne, p. 1183, pl. 146, figs 1a, b, 2a, b, 4, pl. 152, fig. 1.
1976b *Foerstephyllum vacuum* (Foerste); Jull, pl. 2, figs 2a, b, 3a–i, 4, text-fig. 3a–f.

Remarks. – *Crenulites vacuus* was said by Foerste (1909, p. 313) to occur in "the great coral reef at the base of the Liberty bed in Jefferson, Bullitt, Nelson, and Marion counties, Kentucky". Subsequent investigations by Browne (1965) revealed the presence of two distinct coral-bearing stratigraphic intervals in the region: one at the base of the Liberty Formation and the other at the base of the Whitewater Formation. These two horizons are predominantly within the middle Katian, with the latter potentially extending into the earliest late Katian (Bergström *et al*. 2010a; Daniel Goldman & Patrick McLaughlin pers. comm.). Foerste's (1909) figured type, from the basal Whitewater Formation of Bardstown, Kentucky (Browne 1965, p. 1181), was unfortunately lost "in the Miami River Dayton flood of 1913" (Bassler 1950, p. 269). The present concept of this form is chiefly based on the neotype (USNM 147047) chosen by Browne (1965) from the same horizon, as well as several topotypes documented by Bassler (1950), Browne (1965) and Jull (1976b). The description of the type material by Browne (1965, pp. 1182, 1183) mentions that *C. vacuus* has corallites averaging 4 mm in diameter, corallite walls separated by strong dark lines, and irregularly spaced tabulae (0.5–2.5 mm apart), and also that "septal spines are so sparsely distributed that many sections do not show them" and "may be very long". This account provides useful information to characterise this species.

In the past, *Crenulites vacuus* was regarded as a species of *Foerstephyllum* by almost all authors (e.g. Flower 1961; Browne 1965; White & Yang 2004), which was presumably based on their mistaken belief that its septa are composed of spines. Sokolov (1955, p. 241) was the first to consider that this species probably "belongs to *Favistella*". Jull (1976b) proposed that this species may represent a separate genus. In this work, this species is reassigned to *Crenulites*, since

its septa are interpreted as belonging to the laminar, amplexoid type, which is evident in the published figures of the neotype, as well as additional topotypes. This explains why its septa are seldom shown in thin sections, and if observed, "may be very long" (Browne 1965, p. 1182), and is consistent with the observation of Jull (1976b, p. 389) that septa "are developed uncommonly on the upper surface of some tabulae". In fact, such an interpretation was already proposed by Simmons & Oliver (1967, p. F11), who remarked that septa of this species "may be locally amplexoid, extending nearly to the axis on the upper surfaces of the tabulae", although they still retained its placement within *Foerstephyllum*.

Foerstephyllum vacuum magnum Browne, 1965 is represented by the holotype (USNM 147044) and a paratype (USNM 147045) from the basal Liberty Formation, alongside an additional paratype (USNM 147046) from the basal Whitewater Formation, all within the same region associated with *Crenulites vacuus*. It was stated by Browne (1965) to differ from the latter mainly in having larger corallites (up to 4.5–5.0 mm in diameter) and more undulating corallite walls, as well as more widely spaced tabulae. However, these differences are better regarded as intraspecific variation, and the two taxa are therefore synonymous, as also suggested by Simmons & Oliver (1967, p. F11).

Foerstephyllum porosum Flower, 1961 and *F. minutum* Flower, 1961, both from the Richmondian at an elevation of 800 feet of Harp Burn, Akpatok Island, were assigned with *Crenulites vacuus* by Flower (1961) to the "*vacuum* group" of *Foerstephyllum*. However, these two species develop mural pores, discrete septal spines, and favositid wall structure, warranting their reassignment to *Palaeofavosites* Twenhofel, 1914, as also suggested by Scrutton (1979, 1984) and White & Yang (2004). An alternative suggestion by Jull (1976b) that these two Akpatok forms possibly belong to *Nyctopora* Nicholson, 1879 seems very unlikely due to the existence of mural pores and corallite walls typical of favositid corals.

The following forms are excluded from *Crenulites vacuus*. *Columnaria*? *halli* Nicholson, 1879 included specimens of *Crenulites vacuus* prior to the erection of the latter. It now proves to be a member of *Foerstephyllum*. *Columnaria vaqua* Foerste? *sensu* Sokolov (1950) comes from the Dolborian Horizon (middle Katian) of Podkamennaya Tunguska River Basin. Compared with the neotype of *Crenulites vacuus*, it has much larger corallites (commonly 8–9, or rarely 10 mm in diameter), and well-developed septa, and is therefore regarded here as distinct.

Crenulites ulrichi (Bassler, 1950)

1950 *Cyathophylloides ulrichi* Bassler, p. 274, pl. 16, fig. 2, pl. 18, figs 8, 9.

Remarks. – *Crenulites ulrichi* (holotype, USNM 24919) was described by Bassler (1950) as occurring in the Maquoketa Shale of Bristol Township, Fillmore Co., Minn., USA, and a refined stratigraphy indicates that the formation corresponds to the upper *Amplexograptus manitoulinensis* to lower *Dicellograptus complanatus* graptolitic biozones (Goldman & Bergström 1997). Although the exact horizon yielding this coral remains uncertain, it seems more likely to be from its lower, *A. manitoulinensis* zone (middle Katian) portion of that formation.

Flower (1961) transferred this Maquoketa species to his *Crenulites*, this being apparently based on the recognition of its amplexoid septal nature. According to Bassler's (1950, p. 274) description, key specific features of this species include small corallites (2 mm in diameter) and irregularly spaced tabulae, which are "about half their diameter apart" in "immature zone" and 7–8 in number "in a tube diameter".

Crenulites septosus (Sokolov, 1950)

?1950 *Columnaria alveolata* Goldfuss; Sokolov, pp. 236, 237.
1950 *Columnaria septosa* Sokolov, p. 237, pl. 2, figs 9, 10.
1950 *Columnaria septosa* var. *major* Sokolov, pp. 237, 238, pl. 3, fig. 10.
1955 *Favistina dybovskii* Soshkina in Ivanova *et al.*, p. 125, pl. 6, fig. 5, pl. 10, figs 1, 2.
non 1965 *Favistella dybovskii* Soshkina; Ivanovskiy, p. 112, pl. 27, fig. 3a, b.
1969 *Cyathophylloides septosum* (Sokolov); Ivanovskiy *pars*, pp. 75–77, pl. 5, figs 3a, b [refig. Ivanovskiy 1965, pl. 27, fig. 3a, b], *non* 4a, b, text-fig. 13a, b.
?1979a *Favistina stellata* (Hall); Sytova, p. 172, pl. 36, fig. 2a, b.
1979a *Cyathophylloides dybovskii* (Soshkina); Sytova, pp. 173, 174, pl. 36, fig. 4a, b.

Remarks. – *Crenulites septosus* comes from the Dolborian Horizon (middle Katian) of the Podkamennaya Tunguska River Basin. Initially inadequately illustrated by Sokolov (1950), the holotype from Sokolov's collection (VNIGRI 8122, Saint Petersburg) has probably been lost (Sytova 1979a, p. 161). The original description of this species mentions that "the tabular surface is covered with many short, hooked spines" (Sokolov 1950, p. 237). This indicates that its septa are of amplexoid type, thus supporting a reassignment to *Crenulites* Flower, 1961. Major specific features include large corallites (4.0–8.5, often 6.0 mm in diameter), thick major septa extending almost to the corallite centre, and dense tabulae (0.3–0.7 mm apart) (Sokolov 1950).

Two taxa that are now considered as synonymous with *Crenulites septosus* are *Columnaria septosa* var. *major* Sokolov, 1950, and *Favistella dybovskii* Soshkina in Ivanova *et al.*, 1955, both from the same stratigraphic level and general locality. The former differs chiefly in possessing slightly larger corallites (7.5–11.0 mm in diameter), and is regarded here as conspecific with the latter, as also suggested by Sytova (1979a). Similarly, *Favistella dybovskii* also exhibits comparable corallite size (4.0–8.5 mm in diameter) and septal features that are indistinguishable from *Crenulites septosus*.

The material described but not figured by Sokolov (1950) as *Columnaria alveolata* Goldfuss, 1826 was regarded by Sytova (1979a) as conspecific with *Crenulites septosus*. However, it was stated to have corallites ranging from 3.0–6.0 mm in diameter, much smaller than that of *Crenulites septosus*, and its inclusion in the latter species is questionable. It appears more likely to be conspecific with *Favistina stellata* (Hall, 1847) *sensu* Sytova (1979a) from the same horizon and locality.

Crenulites asper (Sokolov, 1955), discussed below, was suggested by Ivanovskiy (1965, 1969) and Sytova (1979a) to be conspecific with *C. dybovskii* (Soshkina in Ivanova *et al.*, 1955) (= *C. septosus*; this work). However, *C. septosus* has much larger corallites (up to 11.0 mm in diameter), and weaker amplexoid septa, a combination of which readily distinguishes it from *C. asper*.

Favistella dybovskii Soshkina in Ivanova *et al.*, 1955 *sensu* Ivanovskiy (1965), refigured by Ivanovskiy (1969) as *Cyathophylloides septosum* (Sokolov, 1950), from the Dolborian Horizon (middle Katian) of the Podkamennaya Tunguska River Basin, is revised as *Cyathophylloides* sp. A, considered above.

Crenulites sp. A

1950 *Columnaria alveolata* Goldfuss; Ivanov & Myagkova, p. 13, pl. 2, fig. 2.
1955 *Columnaria alveolata* Goldfuss; Ivanov & Myagkova, p. 36, pl. 18, fig. 1a, b [1a, refig. Ivanov & Myagkova 1950, pl. 2, fig. 2).
1973 *Favistella alveolata* (Goldfuss); Shurygina, pp. 146, 147, pl. 26, figs 4, 5.

Remarks. – This species occurs in the Sur'ya Horizon, now referable to the Upper Malaya Tavrota Subformation in the Middle Urals (Antoshkina 2003) of probable middle Katian age. Ivanov & Myagkova (1950) initially figured a specimen externally, and a transverse section of the same specimen was later figured by Ivanov & Myagkova (1955). Although not noted in their description, the published figures clearly exhibit a partly amplexoid type of septa, leading me to reassign this species to *Crenulites*. Its key diagnostic features include small to medium-sized corallites (3.0–5.0 mm in diameter), 20–30 septa, and complete, slightly arched, well-spaced tabulae (Ta5 = 8) (Ivanov & Myagkova 1955).

The specimen described by Shurygina (1973) as *Favistella alveolata* (Goldfuss, 1826) from the same horizon and locality is nearly identical to the material of Ivanov & Myagkova (1950, 1955). Accordingly, I concur with Shurygina (1973) in considering them conspecific. Considering the limited available knowledge, this form is provisionally recognised as a distinct species identified as *Crenulites* sp. A.

Crenulites breviseptatus (Sokolov, 1955)

?1950 *Columnaria vaqua*? Foerste; Sokolov, p. 238, pl. 8, fig. 9.
1955 *Favistella breviseptata* Sokolov, p. 464, pl. 68, figs 1, 2.
1965 *Favistella breviseptata* Sokolov; Ivanovskiy, pp. 111, 112, pl. 27, fig. 2a, b.
1969 *Proterophyllum simplex* (Sokolov); Ivanovskiy *pars*, pp. 63, 64, pl. 2, fig. 1a, b, *non* pl. 1, fig. 1a–d.
1979a *Favistina breviseptata* Sokolov; Sytova, pp. 171, 172, pl. 36, fig. 1a, b.

Remarks. – This species comes from the "Mangazeian Stage" (now Baksian Stage, upper Sandbian–lower Katian; Kanygin *et al.* 2019) of Chunya River, Podkamennaya Tunguska, Siberian Platform (Sokolov 1955; Ivanovskiy 1965, p. 111). Its type material, housed in Sokolov's collection (VNIGRI 8122, Saint Petersburg), was likely lost (Sytova 1979a, p. 161). Ivanovskiy (1965) and Sytova (1979a) illustrated topotypes of the species. The present reassignment to *Crenulites* is owing to its amplexoid septal nature, as shown in original illustrations of the holotype (Sokolov 1955, pl. 68, figs 1, 2). Other typical features include large corallites (5.0–6.0 mm in diameter), widely spaced tabulae (1.0–2.5 mm apart), and short major septa that do not extend more than 50% of corallite radius (Sokolov 1955).

The specimen described by Sokolov (1950) as *Columnaria vaqua*? Foerste, from the same horizon and general area, was transferred by Sytova (1979a, p. 161) to *Crenulites breviseptatus*, although she did not include it in her synonymy of the latter species. However, it was stated by Sokolov (1950) to have much larger corallites (commonly 8–9, or rarely 10 mm in diameter), and therefore may represent a separate species.

Favistella nanshanensis Yu, 1960 and *F. obliquiseptata* Yu, 1960, considered below, both from the Koumenzi Formation (lower–middle Katian) of the Qilian area, northwestern China, were synonymised

by Ivanovskiy (1965) with *Crenulites breviseptatus*. However, as noted below, I agree with the synonymy of the two Qilian species within *Crenulites nanshanensis*, but argue that *C. nanshanensis* is easily separated from *C. breviseptatus* in having larger corallites, longer major septa, and closely spaced tabulae.

Crenulites asper (Sokolov, 1955)

1955 *Cyathophylloides asper* Sokolov, p. 464, pl. 68, figs 3, 4.

Remarks. – *Crenulites asper* is based on the holotype and only known specimen from the "Upper Ordovician" of Podkamennaya Tunguska, Siberia. The specimen, originally part of Sokolov's collection (VNIGRI 8122, Saint Petersburg), was presumably lost (Sytova 1979a, p. 161). The figure of its longitudinal section (Sokolov 1955, pl. 68, fig. 4) clearly indicates the development of amplexoid septa, justifying its transfer to *Crenulites*. According to the author, key specific characteristics include small corallites (3.0–3.5 mm in diameter), and consistently widely spaced tabulae (usually 0.7–1.0 mm apart).

Ivanovskiy (1965, 1969) and Sytova (1979a) regarded *Crenulites asper* as conspecific with *C. dybovskii* (Soshkina in Ivanova *et al.*, 1955) (= *C. septosus*; this work) from the same level, discussed above. *Crenulites septosus* is regarded here as distinct, as discussed above.

Crenulites nanshanensis (Yu, 1960)

(Figs 20–29)

1960 *Favistella alveolata* (Goldfuss); Yu, p. 77, pl. 3, figs 1**,** 2.
1960 *Favistella nanshanensis* Yu, pp. 77, 78, pl. 3, figs 3**,** 4, pl. 4, fig. 5.
1960 *Favistella obliquiseptata* Yu, p. 78, pl. 3, figs 5**,** 6.
1960 *Favistella alveolata* (Goldfuss) var. *maxima* Yu, pp. 78**,** 79, pl. 4, figs 1**,** 2.
1963 *Favistella alveolata* (Goldfuss); Yu *et al.*, p. 149, pl. 41, fig. 1a, b [refig. Yu 1960, pl. 3, figs 1**,** 2].
1963 *Favistella alveolata* (Goldfuss) subsp. *maxima* Yu; Yu *et al.*, pp. 149, 150, pl. 41, fig. 2a, b [refig. Yu 1960, pl. 4, figs 1**,** 2].
1963 *Favistella nanshanensis* Yu; Yu *et al.*, p. 151, pl. 42, fig. 1a, b [refig. Yu 1960, pl. 3, figs 3**,** 4].
1963 *Favistella obliquiseptata* Yu; Yu *et al.*, pp. 151, 152, pl. 42, fig. 2a, b [refig. Yu 1960, pl. 3, figs 5**,** 6].
1979 *Favistella* aff. *nanshanensis* Yu; Li & Liao, p. 17, pl. 9, figs 1**,** 2.
1979 *Favistella* cf. *intermediata* Yu; Li & Liao, p. 17, pl. 8, fig. 3, pl. 9, fig. 5.
1979 *Favistella luotuoheensis* Deng & Li in Li & Liao, p. 17, pl. 9, figs 3, 4.
1982 *Favistella* (*Favistella*) *dybovskii* Soshkina in Ivanova *et al.*; Cao in Cao & Lin, p. 30, pl. 9, fig. 3a**,** b.
1982 *Favistella* (*Favistella*) *multiseptata* Cao in Cao & Lin, p. 31, pl. 10, fig. 10a**,** b.
?2013 *Favistella alveolata* (Goldfuss); Jiang *et al.*, p. 249, pl. 4, figs 5, 6.
2020 *Favistella obliquiseptata* Yu; Liang, p. 496, pl. 5-9-1, figs 7, 8 [refig. Yu 1960, pl. 3, figs 5**,** 6].

Referred material. – The material described by Yu (1960) from the Koumenzi Formation (lower–middle Katian) at Daliang of the Menyuan area, northeastern Qinghai Province, northwestern China: NIGP 10391 (TS) and NIGP 10392 (LS), holotype, original of Yu (1960, pl. 3, figs 3**,** 4), refigured here (Fig. 20A–C); NIGP 10399 (TS), original of Yu (1960, pl. 4, fig. 5), refigured here (Fig. 20D–F); NIGP 10389 (TS) and NIGP 10390 (LS), described by Yu (1960) as *Favistella alveolata* (Goldfuss, 1826), original of Yu (1960, pl. 3, figs**,** 1, 2), refigured here (Fig. 21); NIGP 10393 (TS) and NIGP 10394 (LS), holotype of *Favistella obliquiseptata* Yu, 1960, original of Yu (1960, pl. 3, figs 5**,** 6), refigured here (Fig. 22); NIGP 10395 (TS) and NIGP 10396 (LS), holotype of *Favistella alveolata* (Goldfuss) var. *maxima* Yu, 1960, original of Yu (1960, pl. 4, figs 1**,** 2), refigured here (Fig. 23). The material described by Li & Liao (1979) from the Koumenzi Formation (lower1middle Katian) of the Qilian area, northeastern Qinghai Province, northwestern China: NIGP 11423 (TS) and NIGP 11424 (LS), described as *Favistella* aff. *nanshanensis* Yu, 1960, original of Li & Liao (1979, pl. 9, figs 1**,** 2), refigured here (Fig. 24), south of Caishitu River; NIGP 41422 (TS) and NIGP 41427 (LS), described as *Favistella* cf. *intermediata* Yu, 1960, original of Li & Liao (1979, pl. 8, fig. 3, pl. 9, fig. 5), refigured here (Fig. 25), Kunkaitou River; NIGP 41425 (TS) and NIGP 41426 (LS), holotype of *Favistella luotuoheensis* Deng & Li in Li & Liao, 1979, original of Li & Liao (1979, pl. 9, figs 3**,** 4), refigured here (Fig. 26), Zhalongshui. Two specimens described by Cao in Cao & Lin (1982) from the Beiguoshan Formation (lower–middle Katian) at Dongzhuang, Liquan, Shaanxi Province: XACGS-R-040, described as *Favistella* (*Favistella*) *dybovskii* Soshkina in Ivanova *et al.*, 1955, original of Cao in Cao & Lin (1982, pl. 9, fig. 3a**,** b), refigured here (Fig. 27); XACGS-R-052, holotype of *Favistella* (*Favistella*) *multiseptata* Cao in Cao & Lin, 1982, original of Cao in Cao & Lin (1982, pl. 10, fig. 10a**,** b), refigured here (Fig. 28). NIGP 205569, a new specimen, figured here (Fig. 29), from the Taoqupo Formation (lower–middle Katian) at Tiewadian, the Jingyang area, central Shaanxi Province.

Diagnosis. – *Crenulites* with medium to large-sized corallites [ACDs (6+) = 3.15–7.44, commonly over 6.00 mm], short minor septa (generally represented by short stubs), and complete, commonly widely spaced tabulae (Ta5 = 2–8).

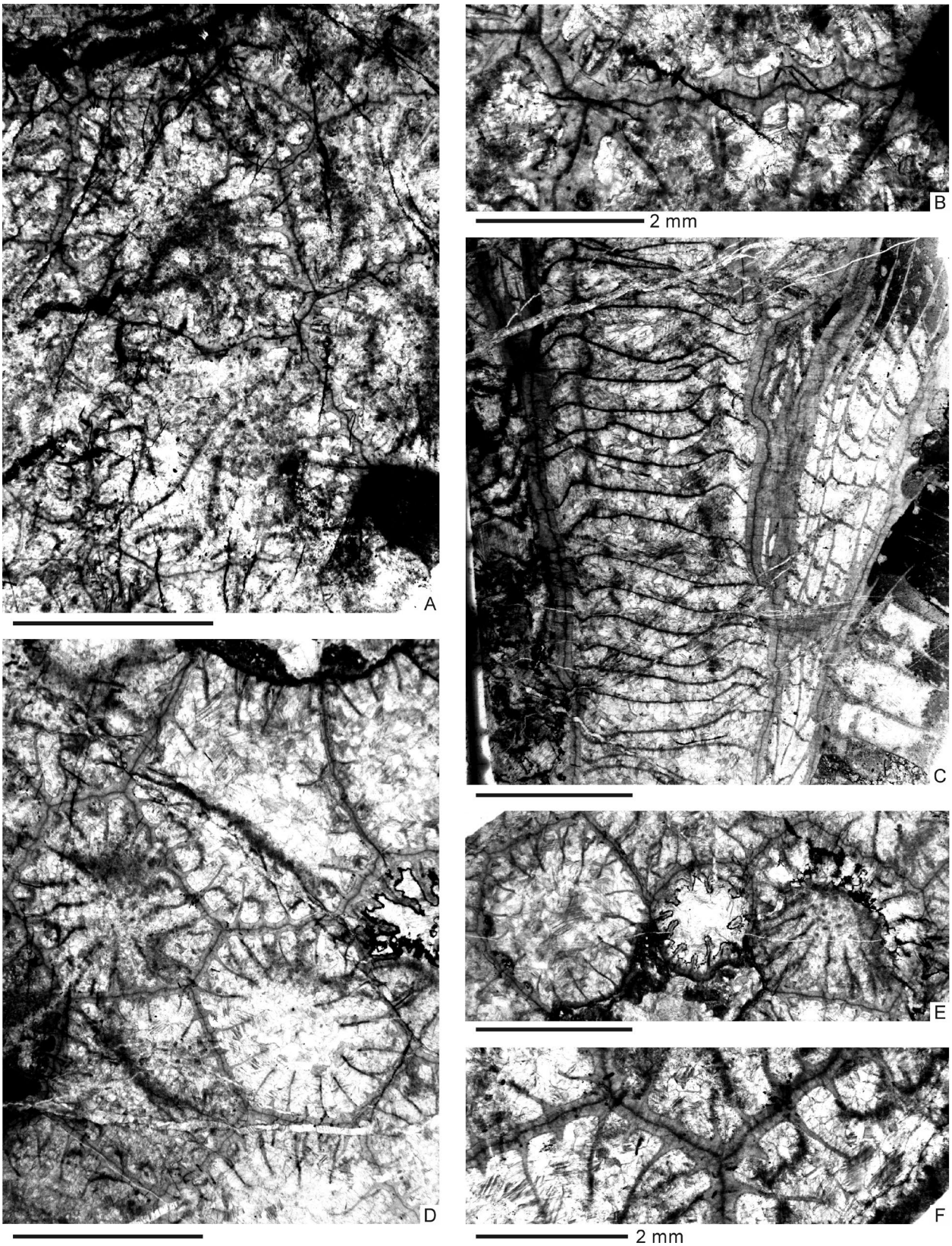


Fig. 20. Crenulites nanshanensis (Yu, 1960). **A–C,** NIGP 10391 (TS) and NIGP 10392 (LS), holotype. **A, B,** TS and an enlarged portion; **C,** LS. **D–F,** NIGP 10399 (TS), topotype. **D–F,** two TSs (**D, E**) and an enlarged portion (**F**). Both specimens from the Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. Scale bars are 5 mm unless otherwise indicated.

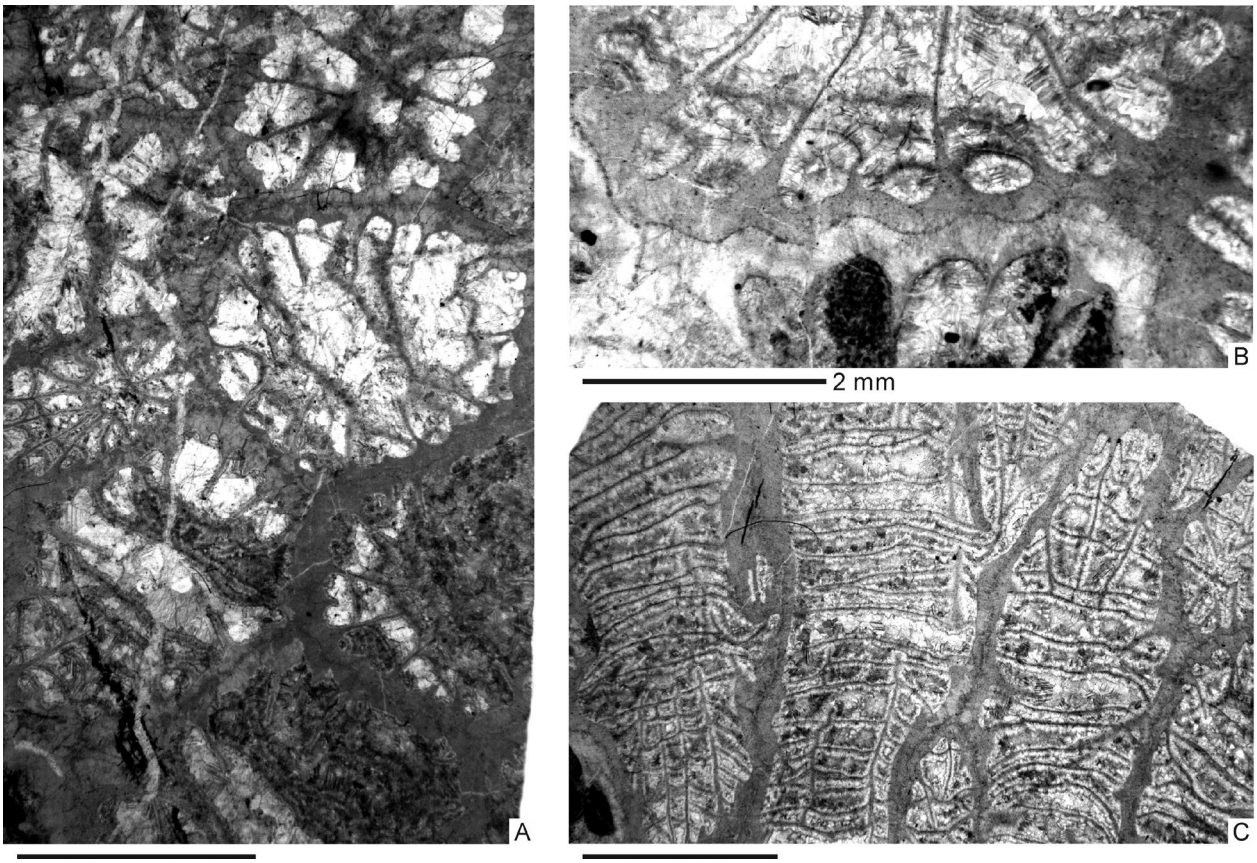


Fig. 21. Crenulites nanshanensis (Yu, 1960). NIGP 10389 (TS) and NIGP 10390 (LS) from one corallum, described by Yu (1960) as *Favistella alveolata* (Goldfuss, 1826), Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

Description. – Coralla massive, with one specimen [NIGP 10393 (TS) and NIGP 10394 (LS)] measured externally, of domical form, 45 mm wide and 40 mm high. Corallites polygonal, 4–7 sided, medium to large-sized [ACDs (6+) = 3.15–7.44, commonly over 6.00 mm]. Corallite walls straight, or slightly wavy, separated by thin dark lines, thin to moderately thick, 0.13–0.46 mm in thickness. Septa of two orders, partly amplexoid. Major septa 12–16 in number, long, thin, extending close to the corallite axis. Minor septa weakly developed, generally represented by short stubs, rarely up to 1/4–1/5 of corallite radius. Tabulae complete, flat to slightly arched, commonly with flat or slightly concave central platform and downturned edges, generally widely spaced (Ta5 = 2–8).

Remarks. – The presently revised concept of *Crenulites nanshanensis* is based on the holotypes of *Favistella nanshanensis* Yu, 1960, *F. obliquiseptata* Yu, 1960, *F. alveolata* (Goldfuss) var. *maxima* Yu, 1960, and *F. luotuoheensis* Deng & Li in Li & Liao, 1979, as well as the specimens described by Yu (1960) as *F. alveolata* (Goldfuss, 1826), and by Deng & Li in Li & Liao (1979) as *F.* aff. *nanshanensis* Yu, 1960 and *F.* cf. *intermediata* Yu, 1960, all from the Koumenzi Formation (lower–middle Katian) of the Menyuan or Qilian areas, northeastern Qinghai. These specimens are regarded here as synonymous, since they share large corallites [ACDs (6+) = 6.57–7.09, 5.27–7.04, 6.43–7.44, 4.41–6.23, 6.95–7.21, 3.15–6.18, and 4.60–6.35 mm, respectively], generally short major septa, and complete, commonly sparse tabulae (Ta5 = 4–6, 2–3, 3–4, 3–6, 5–8, 4–7, and 3–5, respectively).

Favistella (*Favistella*) *dybovskii* Soshkina in Ivanova *et al.*, 1955 *sensu* Cao in Cao & Lin, 1982, from the Beiguoshan Formation (lower–middle Katian) at Dongzhuang, Liquan area, Shaanxi Province, has medium to large-sized corallites [ACDs (6+) = 5.28–6.46 mm], well-developed minor septa (up to 1/4–1/3 of corallite radius), and complete, flat to moderately

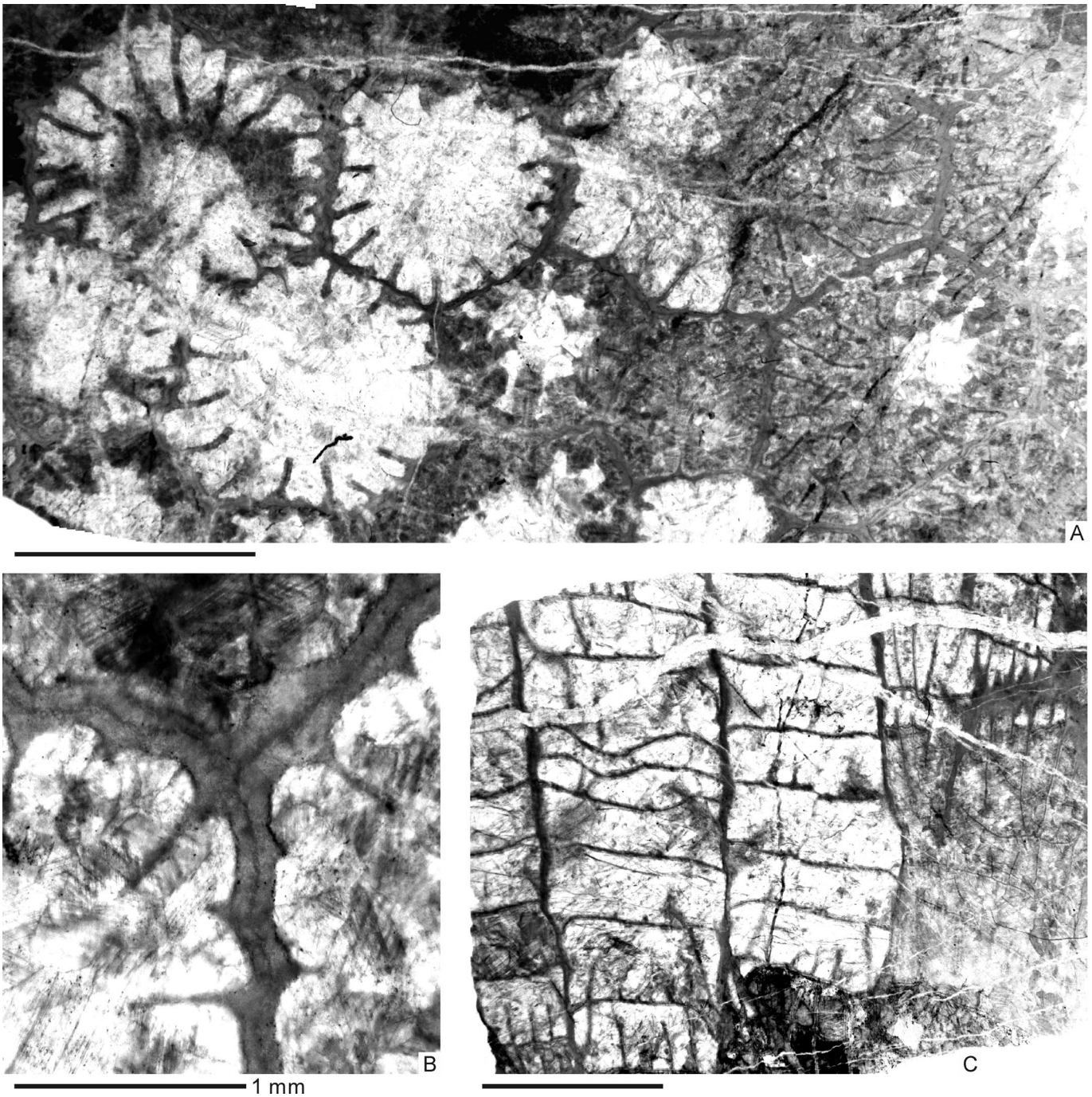


Fig. 22. Crenulites nanshanensis (Yu, 1960). NIGP 10393 (TS) and NIGP 10394 (LS), holotype of *Favistella obliquiseptata* Yu, 1960, Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

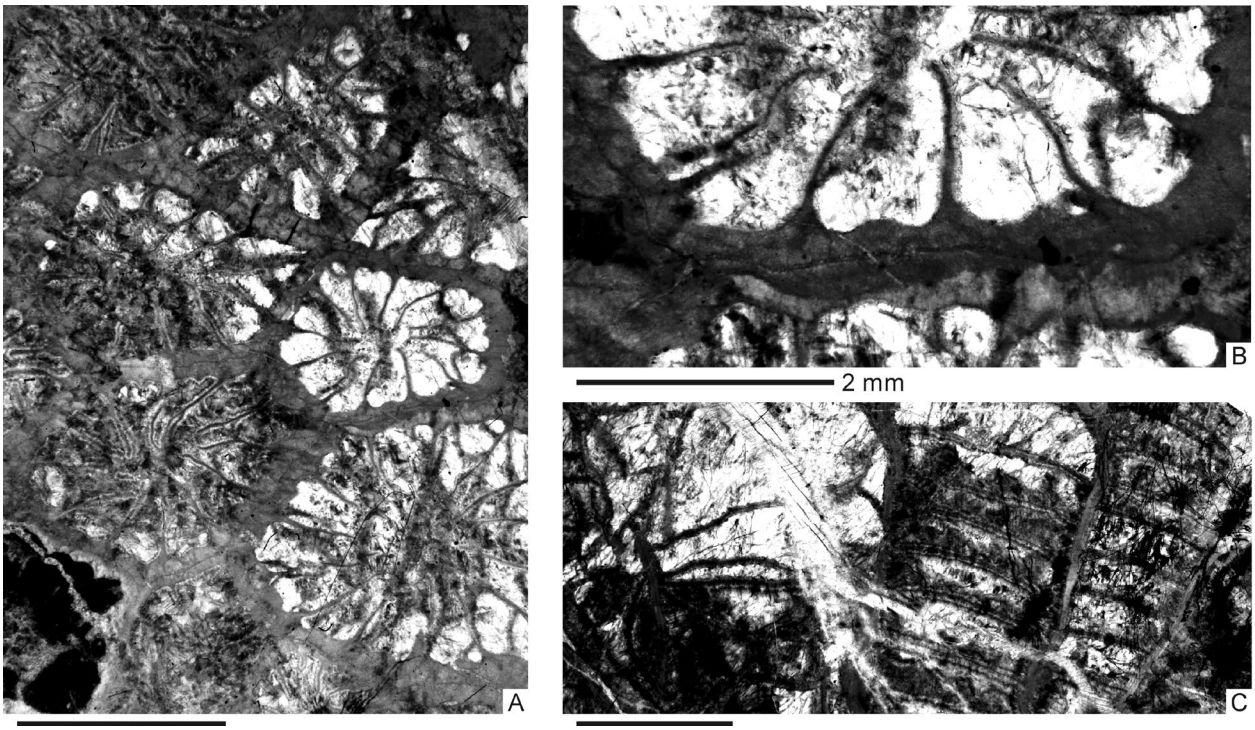


Fig. 23. Crenulites nanshanensis (Yu, 1960). NIGP 10395 (TS) and NIGP 10396 (LS), holotype of *Favistella alveolata* (Goldfuss) var. *maxima* Yu, 1960, Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

arched, widely spaced tabulae (Ta5 = 3–5). All agree well with the revised concept of *Crenulites nanshanensis*, and this form is thus synonymised with the latter.

Favistella (*Favistella*) *multiseptata* Cao in Cao & Lin, 1982, again from the Taoqupo Formation (lower–middle Katian) at Dongzhuang of the Liquan area, Shaanxi Province, shows great similarities to *Crenulites nanshanensis* in general aspects, and differs only in having slightly smaller corallites [ACDs (6+) = 4.05–5.22 mm]. It is therefore included within *C. nanshanensis*.

Favistella alveolata (Goldfuss, 1826) of Jiang *et al.* (2013) is from the Beiguoshan Formation (middle Katian) of Tiewadian, Chunhua, Shaanxi Province. This form was briefly described and poorly illustrated, and its identity remains uncertain.

***Crenulites intermediatus* (Yu, 1960)**

(Figs 30, 31)

1960 *Favistella intermediata* Yu, p. 79, pl. 4, figs 3, 4.
1963 *Favistella intermediata* Yu; Yu *et al.*, p. 150, pl. 41, fig. 3a, b [refig. Yu 1960, pl. 4, figs 3, 4].
1979 *Agetolites rariperforatus* Deng & Li, p. 6, pl. 1, figs 3, 4.
?2013 *Favistella intermediata* Yu; Jiang *et al.*, p. 249, pl. 4, figs 7, 8.

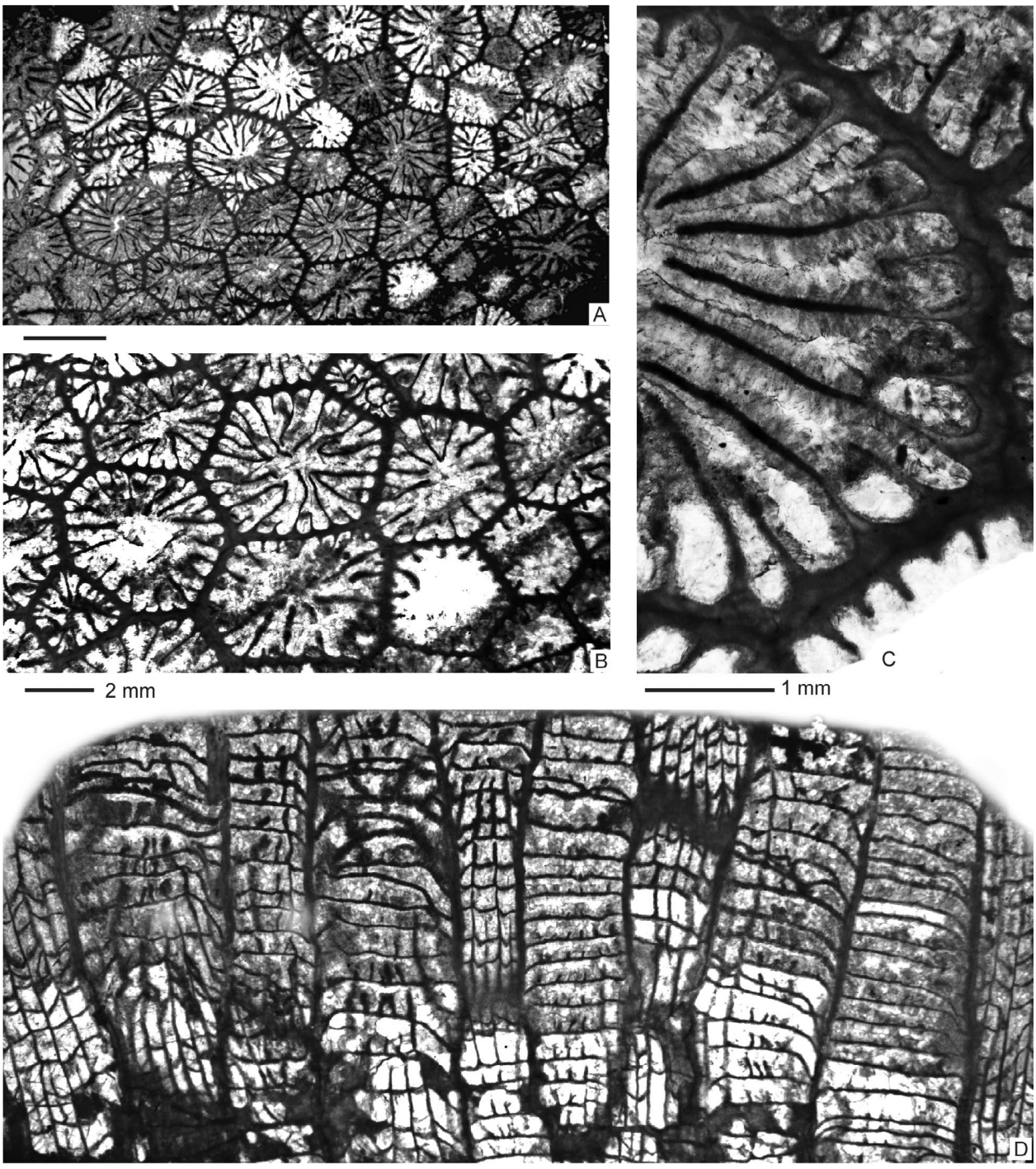


Fig. 24. Crenulites nanshanensis (Yu, 1960). NIGP 11423 (TS) and NIGP 11424 (LS) from one corallum, described by Li & Liao (1979) as *Favistella* aff. *nanshanensis* Yu, 1960, Koumenzi Formation (lower–middle Katian), south of Caishitu River, Qilian area, northeastern Qinghai Province, northwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

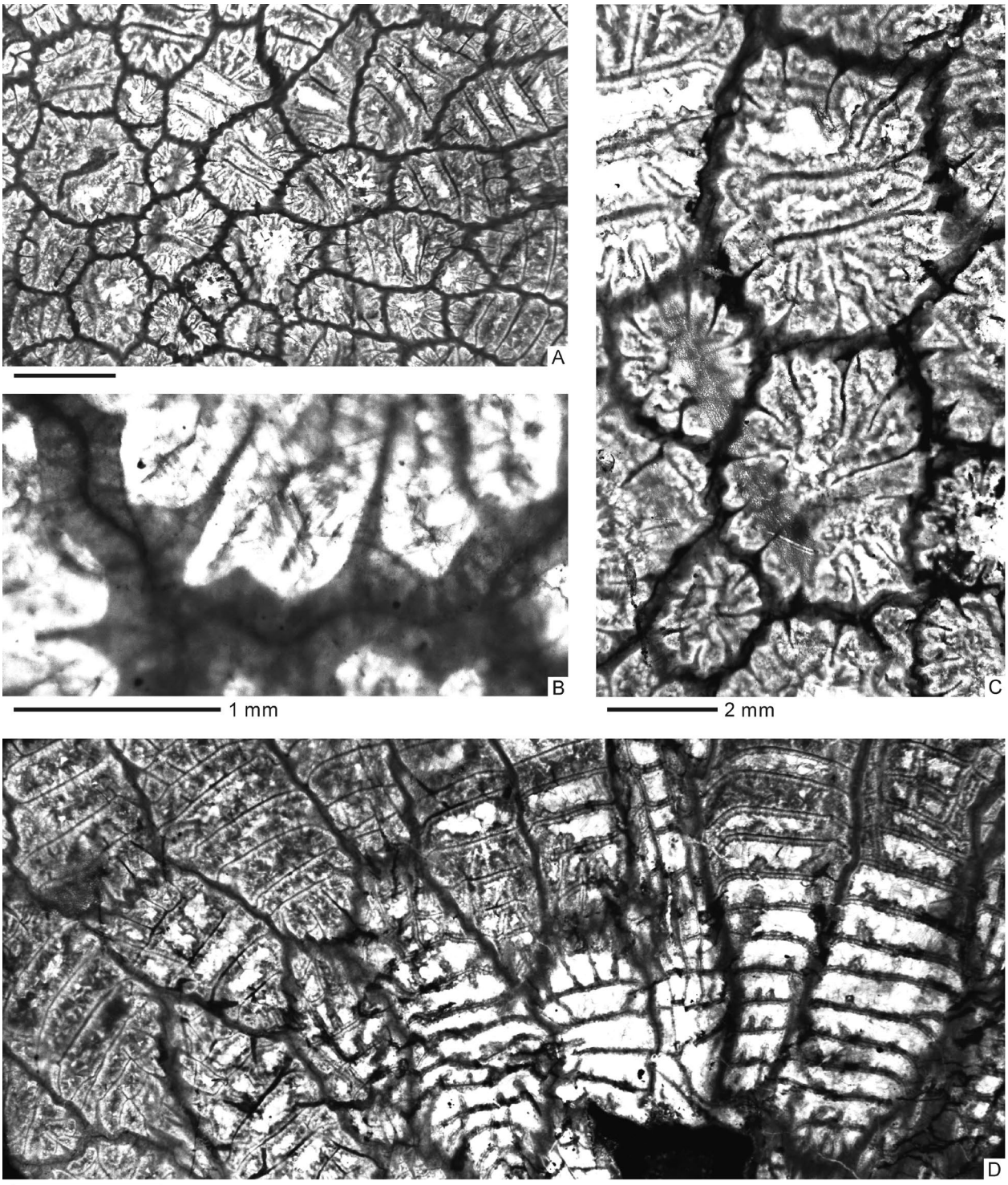


Fig. 25. Crenulites nanshanensis (Yu, 1960). NIGP41422 (TS) and NIGP41427 (LS) from one corallum, described by Li & Liao (1979) as *Favistella* cf. *intermediata* Yu, 1960, upper Koumenzi Formation (lower–middle Katian), Kunkaitou River, Qilian area, northeastern Qinghai Province, northwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

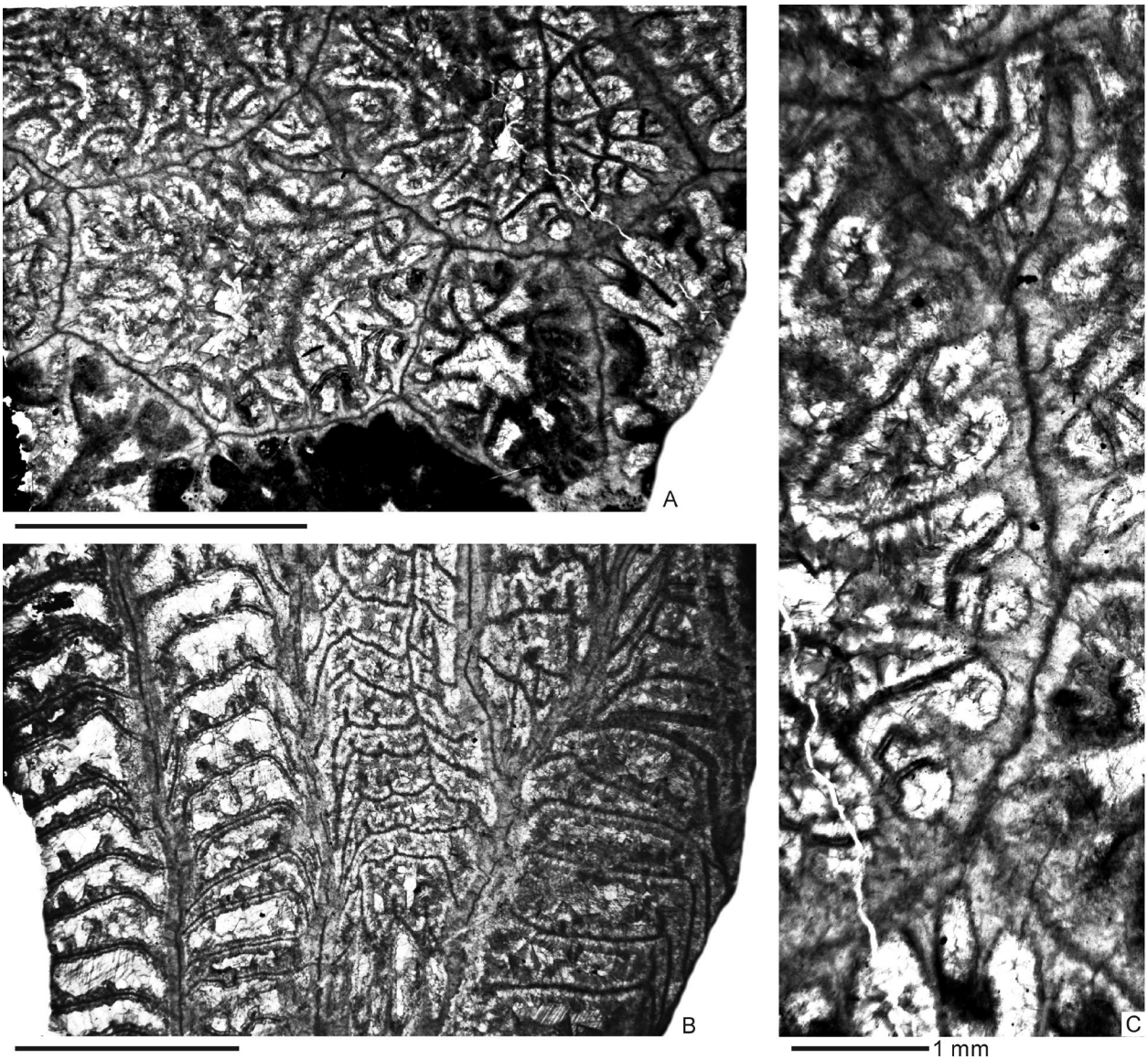


Fig. 26. Crenulites nanshanensis (Yu, 1960). NIGP 41425 (TS) and NIGP 41426 (LS), holotype of *Favistella luotuoheensis* Deng & Li in Li & Liao, 1979, upper Koumenzi Formation (lower–middle Katian), Zhalongshui, Qilian area, northeastern Qinghai Province, northwestern China. **A, C,** TS and an enlarged portion; **B,** LS. Scale bars are 5 mm unless otherwise indicated.

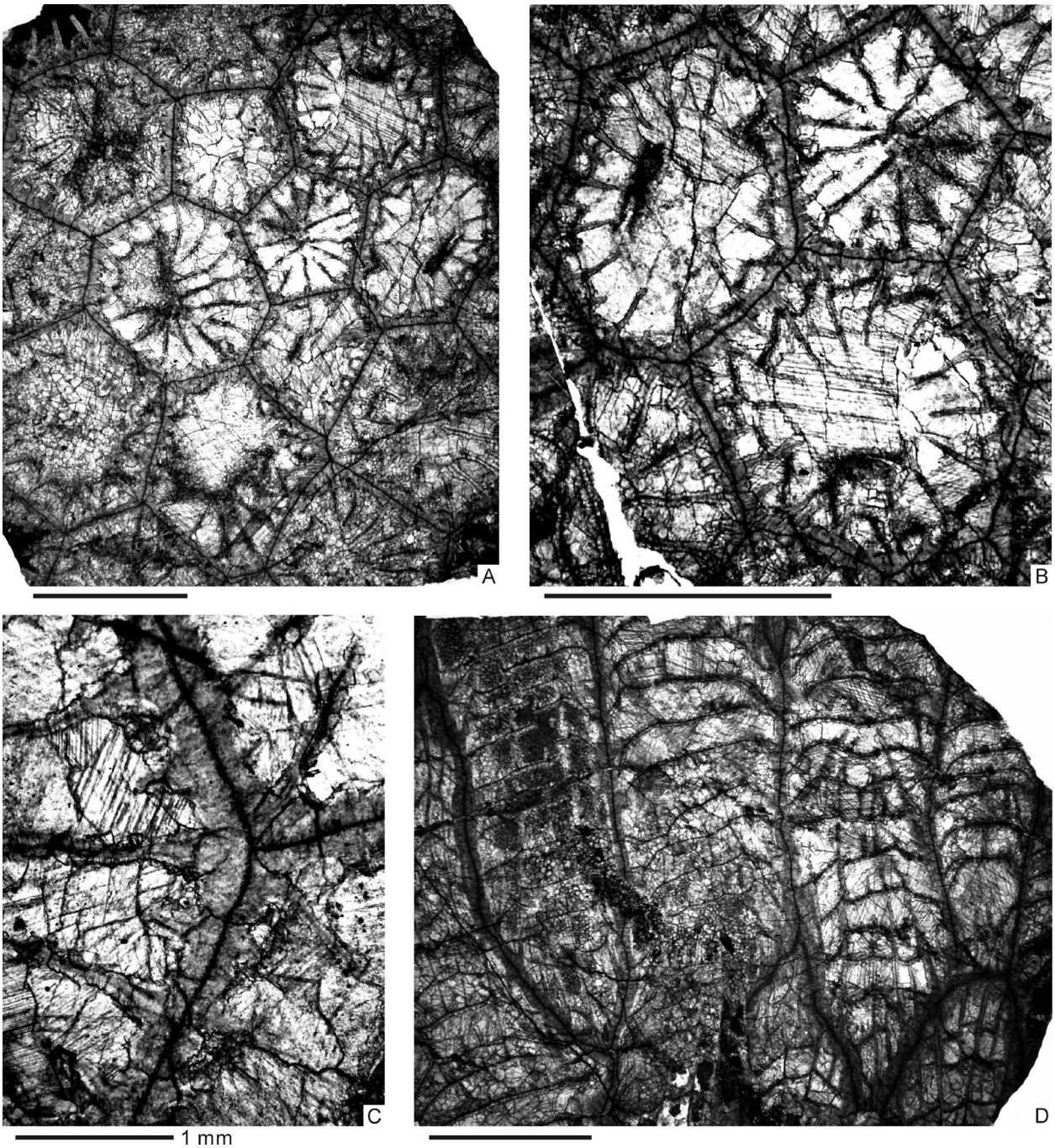


Fig. 27. Crenulites nanshanensis (Yu, 1960). XACGS-R-040, described by Cao in Cao & Lin (1982) as *Favistella* (*Favistella*) *dybovskii* Soshkina, 1955, Beiguoshan Formation (lower–middle Katian), Dongzhuang, Liquan, Shaanxi Province. **A–C,** TS and two enlarged portions. **D,** LS. Scale bars are 5 mm unless otherwise indicated.

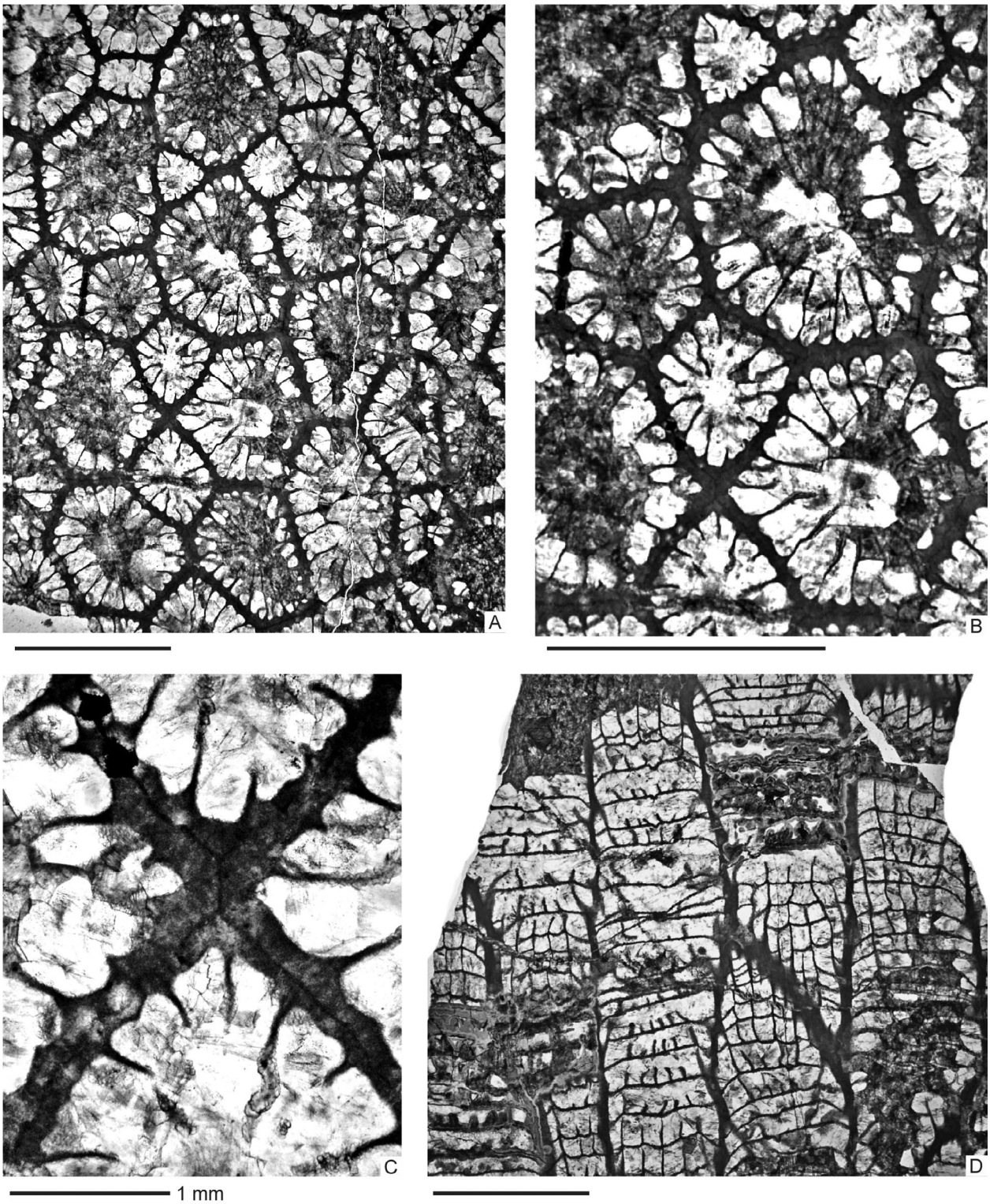


Fig. 28. Crenulites nanshanensis (Yu, 1960). XACGS-R-052, holotype of *Crenulites multiseptatus* (Cao in Cao & Lin, 1982), Beiguoshan Formation (lower–middle Katian), Dongzhuang, Liquan, Shaanxi Province. **A–C,** TS and two enlarged portions. **D**, LS. Scale bars are 5 mm unless otherwise indicated.

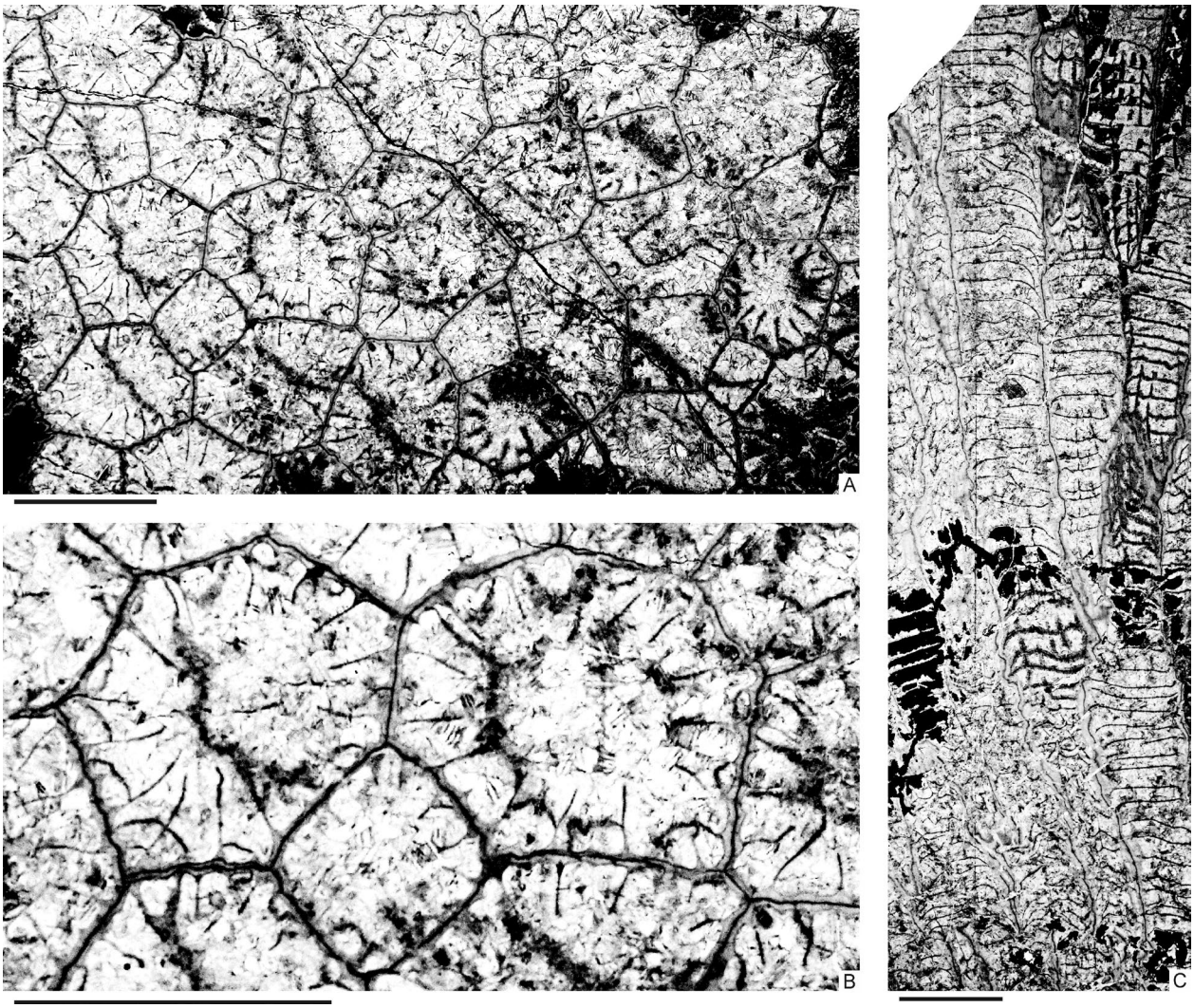


Fig. 29. Crenulites nanshanensis (Yu, 1960). NIGP 205569, new specimen, Taoqupo Formation (middle Katian), Tiewadian, Jingyang area, central Shaanxi Province. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm.

Referred material. – NIGP 10397 (TS) and NIGP 10398 (LS), holotype, original of Yu (1960, pl. 4, figs 3**,** 4), refigured here (Fig. 30), Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. NIGP41373 (TS) and NIGP41374 (LS), holotype of *Agetolites rariperforatus* Deng & Li, original of Deng & Li (1979, pl. 1, figs 3, 4), refigured here (Fig. 31), lower Koumenzi Formation (lower–middle Katian), Kunkaitou River, Qilian area, northeastern Qinghai Province, northwestern China.

Diagnosis. – *Crenulites* with medium to large-sized corallites [ACDs (6+) = 4.97–6.44 mm], 12–14 short major septa extending only to less than 1/2 of corallite radius, weak minor septa, and complete, widely spaced tabulae (Ta5 = 4–8).

Description. – Modified from Yu (1960, p. 79) and Deng & Li (1979, p. 6). Coralla massive, with external form and size unknown. Corallites polygonal, medium to large-sized corallites [ACDs (6+) = 4.97–6.44 mm]. Corallite walls straight, or slightly wavy, separated by thin prominent dark lines, moderately to strongly dilated, varying in thickness from 0.17 to 0.44 mm. Septa wedge-shaped, thick, tapering axially, partly amplexoid. Major septa 12–14 in number, short, commonly extending to less than 1/2 of corallite radius. Minor septa weakly developed, generally extending slightly beyond corallite walls. Tabulae

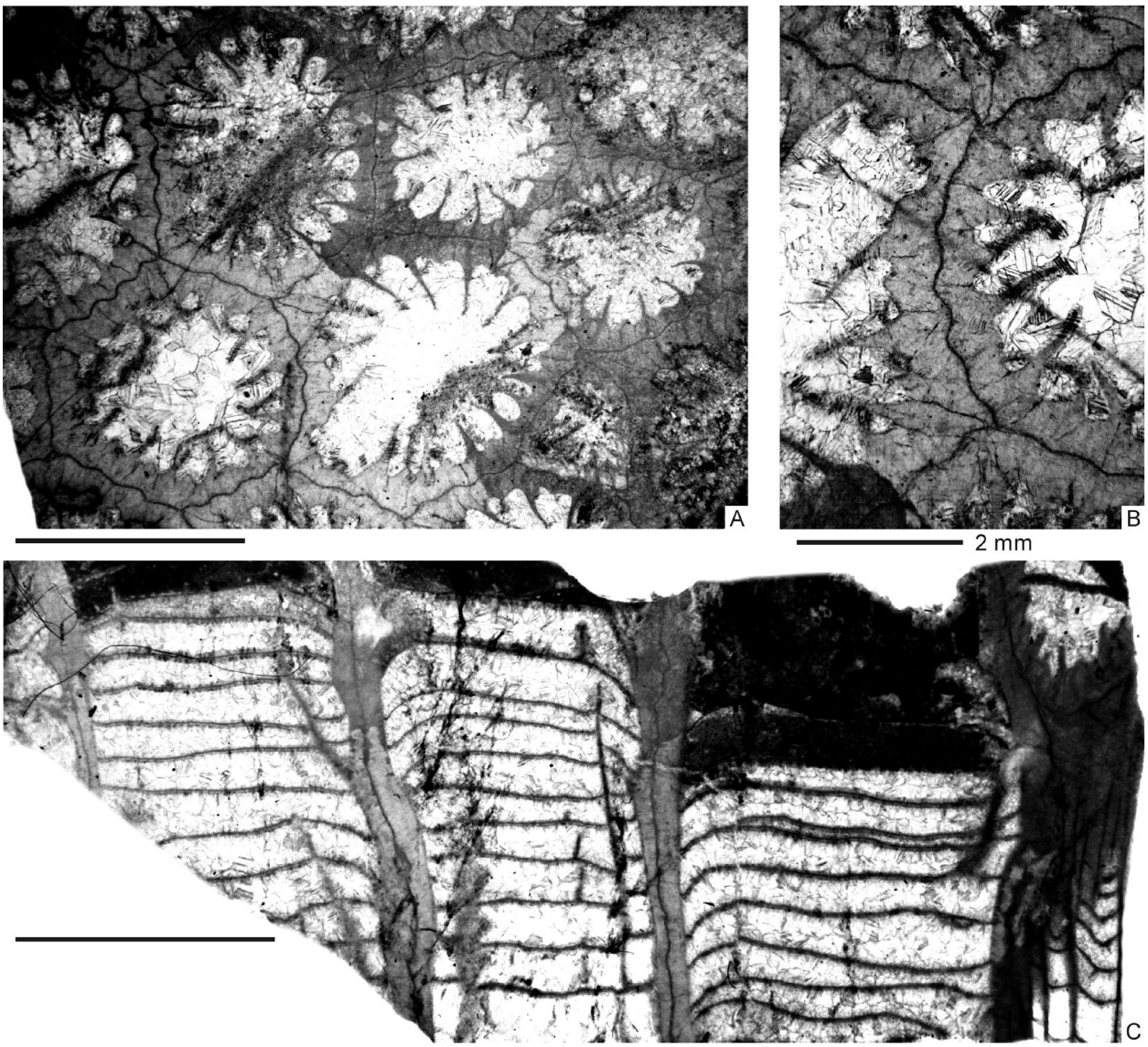


Fig. 30. Crenulites intermediatus (Yu, 1960). NIGP 10397 (TS) and NIGP 10398 (LS), holotype, Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

complete, flat, wavy, slightly arched or slightly concave, widely spaced (Ta5 = 4–8).

Remarks. – The presently revised concept of *Crenulites intermediatus* is based on the holotypes of *Favistella intermediata* Yu, 1960, and *Agetolites rariperforatus* Deng & Li, 1979, from the Koumenzi Formation (lower–middle Katian), of the Menyuan and Qilian areas of northeastern Qinghai Province, respectively. The two specimens are evidently synonymous, since they share large corallite size [ACDs (6+) = 4.97–6.44, and 5.06–5.82 mm, respectively], thick corallite walls (WT = 0.29–0.44, and 0.17–0.30 mm, respectively), short, amplexoid major septa, weak minor septa, and complete, widely spaced tabulae (Ta5 = 4–7, and 6–8, respectively).

Favistella intermediata Yu, 1960 of Jiang *et al.* (2013), from the Beiguoshan Formation (middle Katian) of Tiewadian, Chunhua, Shaanxi Province, lacks sufficient documentation, casting doubt on its synonymy with the true *Crenulites intermediatus*.

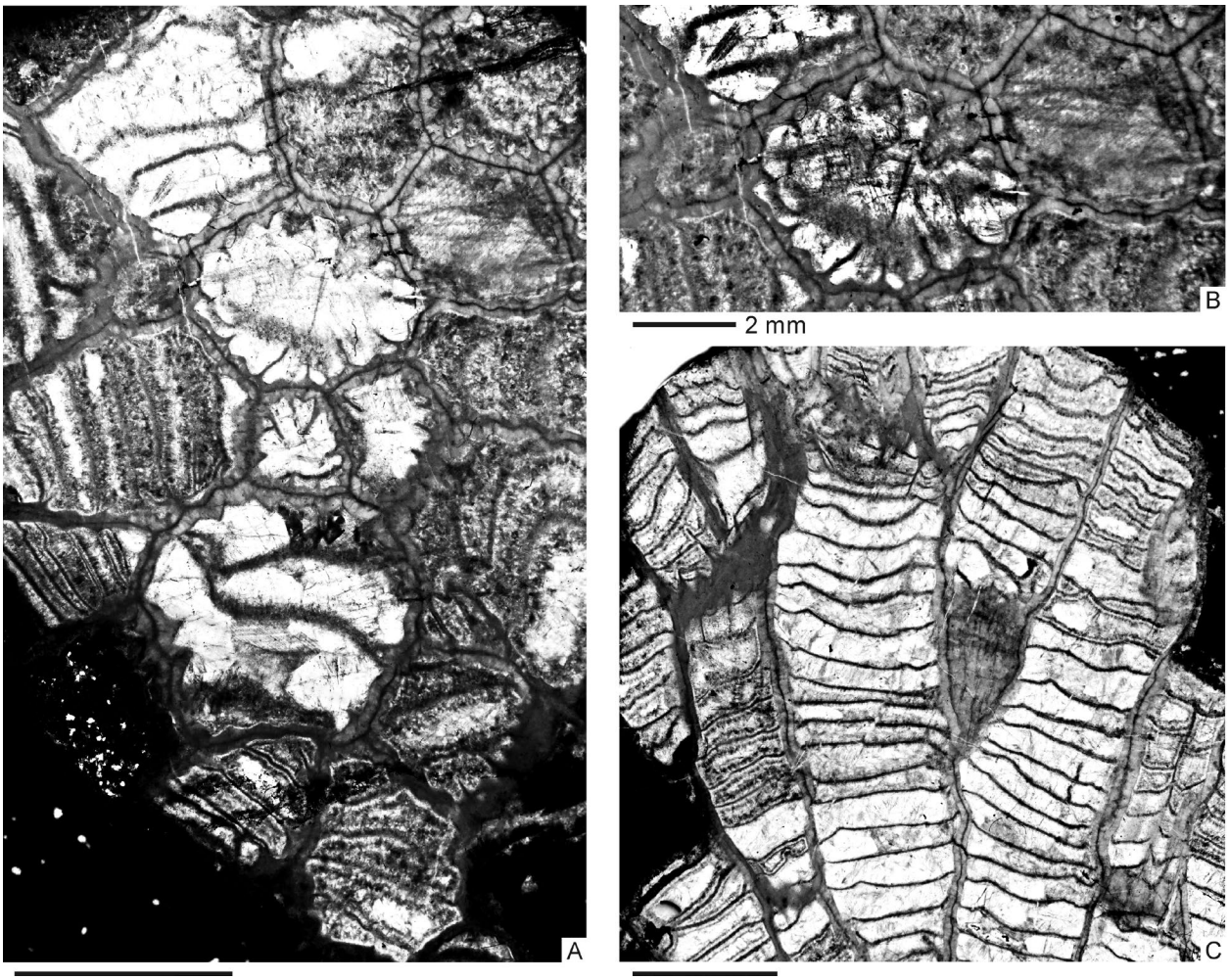


Fig. 31. Crenulites intermediatus (Yu, 1960). NIGP41373 (TS) and NIGP41374 (LS), holotype of *Agetolites rariperforatus* Deng & Li, 1979, lower Koumenzi Formation (lower–middle Katian), Kunkaitou River, Qilian area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

***Crenulites irregularis* (Yu, 1960)**

(Figs 32, 33)

1960 *Favistella irregularis* Yu, p. 79, pl. 5, figs 5–7.
1963 *Favistella irregularis* Yu; Yu *et al.*, p. 151, pl. 41, fig. 5a–c [refig. Yu 1960, pl. 5, figs 5–7].
1979 *Favistella qilianensis* Deng & Li in Li & Liao, p. 16, pl. 8, figs 1, 2.

Referred material. – NIGP 10405 (TS), NIGP 10406 (LS) and NIGP 10407 (polished surface, probably lost), holotype, original of Yu (1960, pl. 5, figs 5–7), refigured here (Fig. 32), Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. NIGP 41420 (TS) and NIGP 41421 (LS), holotype of *Favistella qilianensis* Deng & Li in Li & Liao, 1979, original of Deng & Li in Li & Liao (1979, pl. 8, figs 1**,** 2), refigured here (Fig. 33), upper Koumenzi Formation (lower–middle Katian) of Kunkaitou River, Qilian area, northeastern Qinghai Province, northwestern China.

Diagnosis. – *Crenulites* with medium to large-sized corallites [ACDs (6+) = 4.70–6.23 mm], thick corallite walls (WT = 0.15–0.35 mm), long major (extending close to the corallite axis) and minor (up to 1/3–1/2 of corallite radius) septa, and partly incomplete, irregularly and closely spaced tabulae (Ta5 = 5–12).

Description. – Modified from Yu (1960, p. 79), and Deng & Li in Li & Liao (1979, p. 16). Coralla massive. The holotype is of domical form, 69 mm wide and 58 mm high. Corallites polygonal, medium to large-sized [ACDs (6+) = 4.70–6.23 mm]. Corallite walls straight or slightly wavy, separated by thin prominent dark lines, moderately to strongly dilated (WT = 0.15–0.35 mm). Septa wedge-shaped, moderately thick, tapering axially, partly amplexoid. Major septa 14–16 in number, long, extending close to the corallite axis. Minor septa well developed, short to relatively long, up to 1/3–1/2 of corallite radius. Tabulae complete or incomplete, irregularly and closely spaced (Ta5 = 5–12).

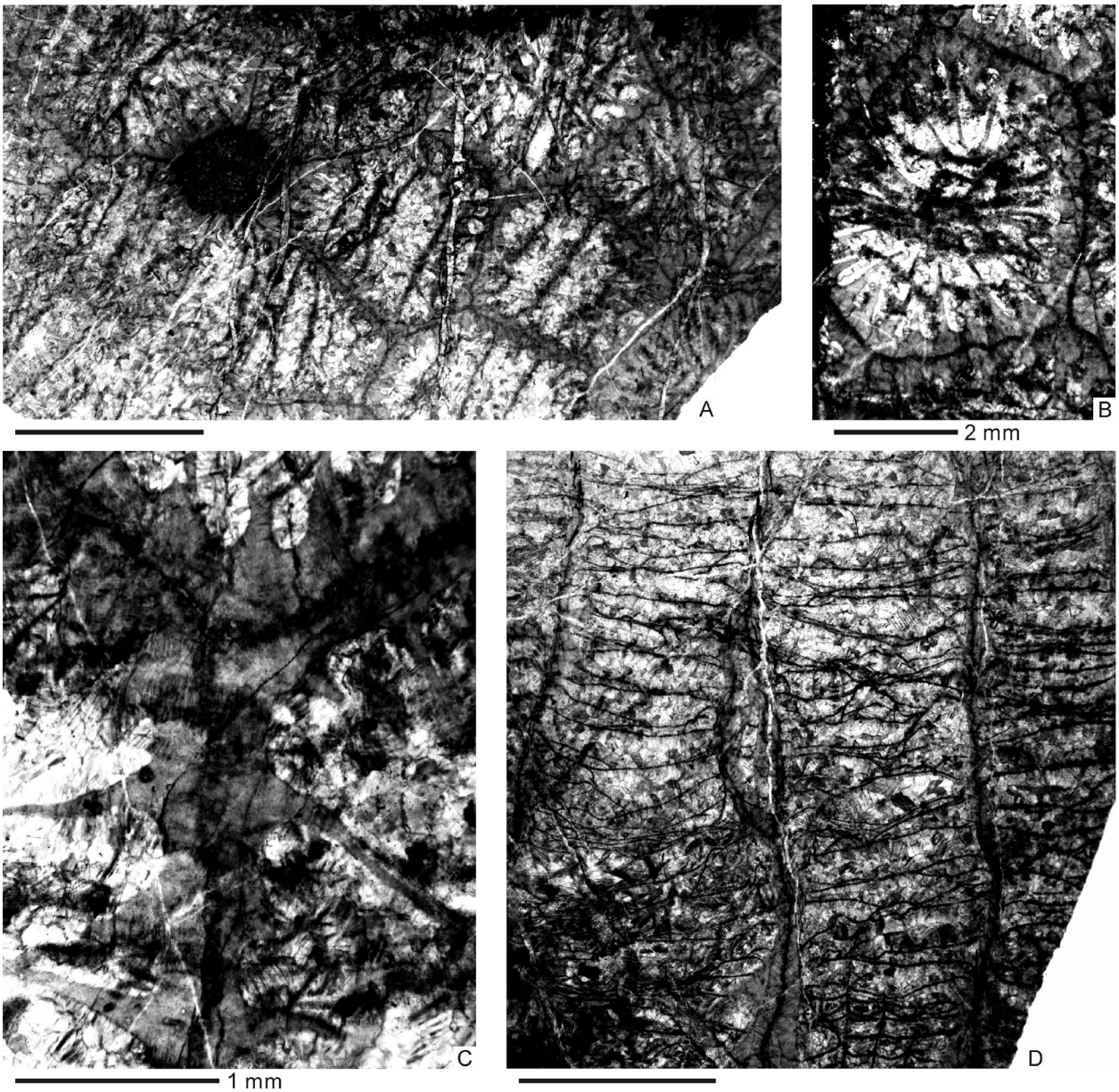


Fig. 32. Crenulites irregularis (Yu, 1960). NIGP 10405 (TS) and NIGP 10406 (LS), holotype, Koumenzi Formation (lower–middle Katian), Daliang, Menyuan area, northeastern Qinghai Province, northwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

Remarks. – The diagnosis and description of *Crenulites irregularis* given above are based on the holotypes of two synonymous species, *Favistella irregularis* Yu, 1960, and *Favistella qilianensis* Deng & Li in Li & Liao, 1979, from the Koumenzi Formation (lower–middle Katian) of the Menyuan and Qilian areas of northeastern Qinghai Province, respectively. Re-examination of the two specimens shows that they have similar corallite size [ACDs (6+) = 4.70–5.76, and 5.41–6.23 mm, respectively], corallite wall thickness (WT = 0.19–0.35, and 0.15–0.34 mm, respectively), septal number (14–15×2 and 14–16×2 respectively), and septal and tabular development (Ta5 = 7–12 and 5–10, respectively). Deng & Li in Li & Liao (1979, p. 16) commented that *Favistella qilianensis* differs from *F. irregularis* only in septal number, which is 16×2 and 14×2, respectively. However, this statement is inconsistent with the present observation, noted above.

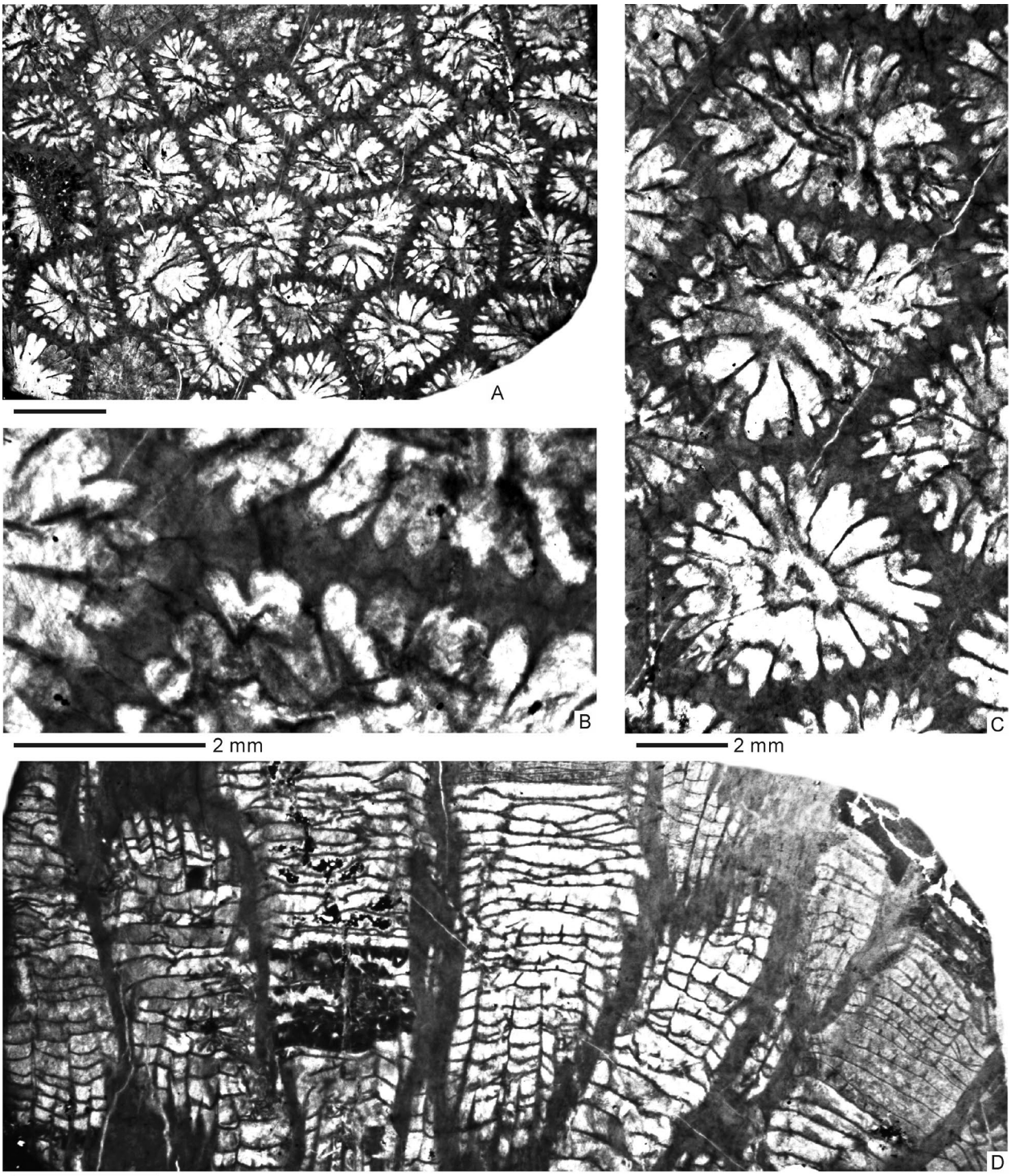


Fig. 33. Crenulites irregularis (Yu, 1960). NIGP 41420 (TS) and NIGP 41421 (LS), holotype of *Favistella qilianensis* Deng & Li in Li & Liao, 1979, upper Koumenzi Formation (lower–middle Katian), Kunkaitou River, Qilian area, northeastern Qinghai Province, northwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

***Crenulites grandis* (Yu, 1960)**

(Figs 34–37, ?Fig. 38)

1960 *Palaeofavosites grandis* Yu, p. 81, pl. 8, figs 1, 2.
1963 *Palaeofavosites grandis* Yu; Yu *et al*., p. 219, pl. 69, fig. 2a, b [refig. Yu 1960, pl. 8, figs 1, 2].
1979 *Palaeofavosites grandis* var. *infidus* Deng & Li, p. 7, pl. 2, fig. 7.
1979 *Saffordophyllum heiquanheensis* Deng & Li, p. 9, pl. 3, figs 3, 4.
1979 *Saffordophyllum inconstus* Deng & Li, p. 9, pl. 3, figs 1, 2.
?1984 *Palaeofavosites* cf. *grandis* Yu; Deng & Zhang, p. 18, pl. 1, fig. 4a, b.
2020 *Saffordophyllum inconstus* Deng & Li; Liang, p. 498, pl. 5-9-2, figs 1, 2 [refig. Deng & Li 1979, pl. 3, figs 1, 2].
2020 *Saffordophyllum heiquanheensis* Deng & Li; Liang, p. 498, pl. 5-9-2, figs 3, 4 [refig. Deng & Li, pl. 3, figs 3, 4].
?2020 *Palaeofavosites grandis* Yu; Liang, p. 510, pl. 5-9-2, figs 3, 4 [refig. Deng & Zhang 1984, pl. 1, fig. 4a, b].
2020 *Palaeofavosites borealis* Tchernychev; Liang, p. 510, pl. 5-9-2, figs 5, 6 [refig. Yu 1960, pl. 8, figs 1, 2].

Referred material. – NIGP10420 (TS) and NIGP10421 (LS), holotype, original of Yu (1960, pl. 8, figs 1, 2), refigured here (Fig. 34), "Upper Ordovician" (now Beiguoshan Formation of lower–middle Katian age), Shiqizi, Guyuan, southern Ningxia, northwestern China. NIGP41383, holotype of *Palaeofavosites grandis* var. *infidus* Deng & Li, 1979, original of Deng &

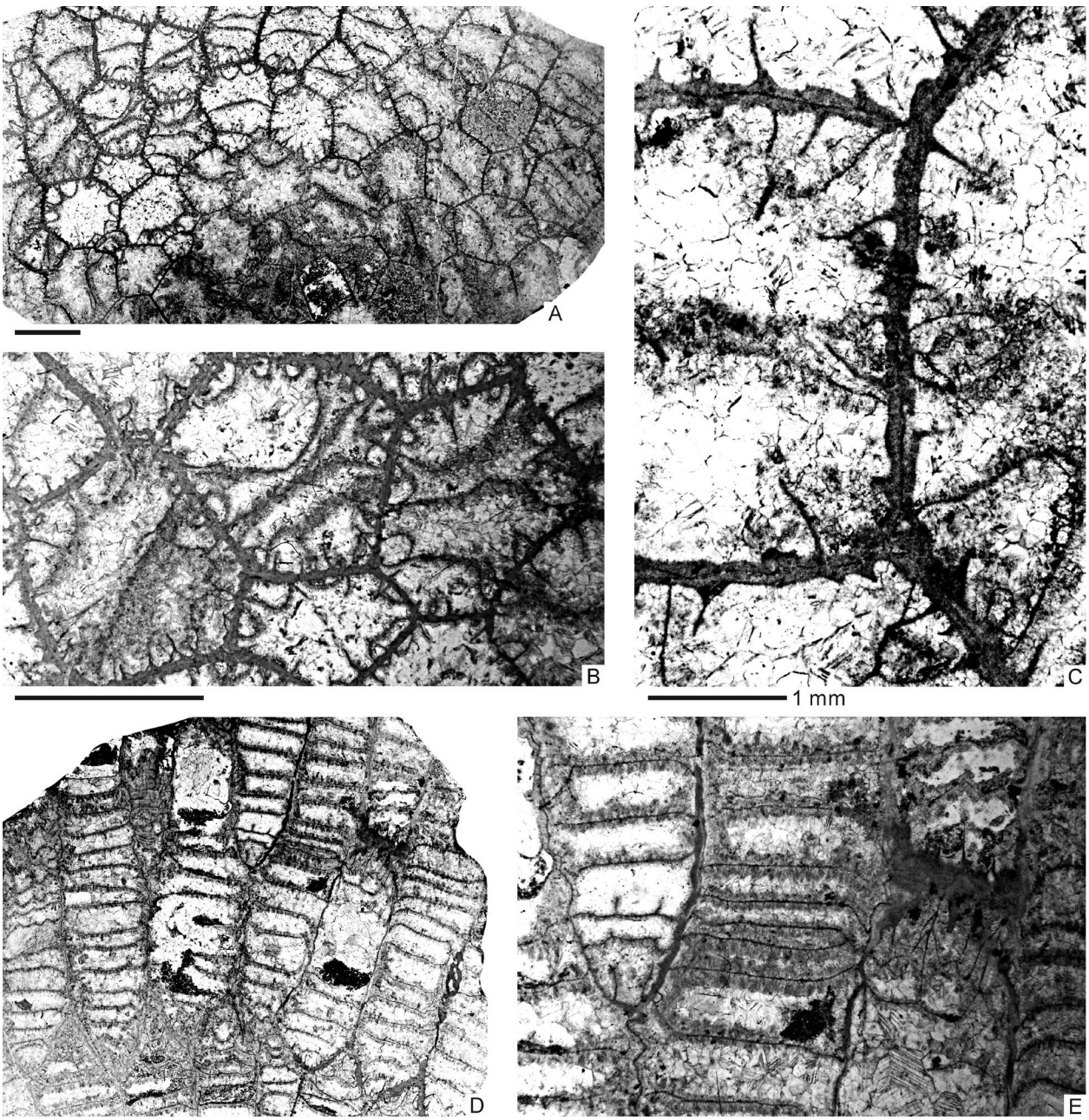


Fig. 34. Crenulites grandis (Yu, 1960). NIGP10420 (TS) and NIGP10421 (LS), holotype, Beiguoshan Formation (lower–middle Katian), Shiqizi, Guyuan, southern Ningxia. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Li (1979, pl. 2, fig. 7), refigured here (Fig. 35), lower Koumenzi Formation (lower–middle Katian), Caishitu River, Qilian area, northeastern Qinghai Province, northwestern China. NIGP41386 (TS) and NIGP41387 (LS), holotype of *Saffordophyllum heiquanheensis* Deng & Li, 1979, original of Deng & Li (1979, pl. 3, figs 3, 4), refigured here (Fig. 36), upper Koumenzi Formation (lower–middle Katian), Heiquanhe, Qilian area, northeastern Qinghai Province, northwestern China. NIGP41384 (TS) and NIGP41385 (LS), holotype of *Saffordophyllum inconstus* Deng & Li, 1979, original of Deng & Li (1979, pl. 3, figs 1, 2), refigured here (Fig. 37), lower Koumenzi Formation (lower–middle Katian), Caishitu River, Qilian area, northeastern Qinghai Province, northwestern China. NIGP59999 (TS) and NIGP60000 (LS), described by Deng & Zhang (1984) as *Palaeofavosites* cf. *grandis* Yu, 1960, original of Deng & Zhang (1984, pl. 1, fig. 4a, b), refigured here (Fig. 38), upper Wuluochipu Formation (probably lower–middle Katian), Zhongza, Batang, westernmost Sichuan Province.

Diagnosis. – *Crenulites* with very large corallites [ACDs (6+) = 4.53–8.00 mm], short major septa, weakly developed minor septa, and complete, widely spaced tabulae (Ta5 = 2–5).

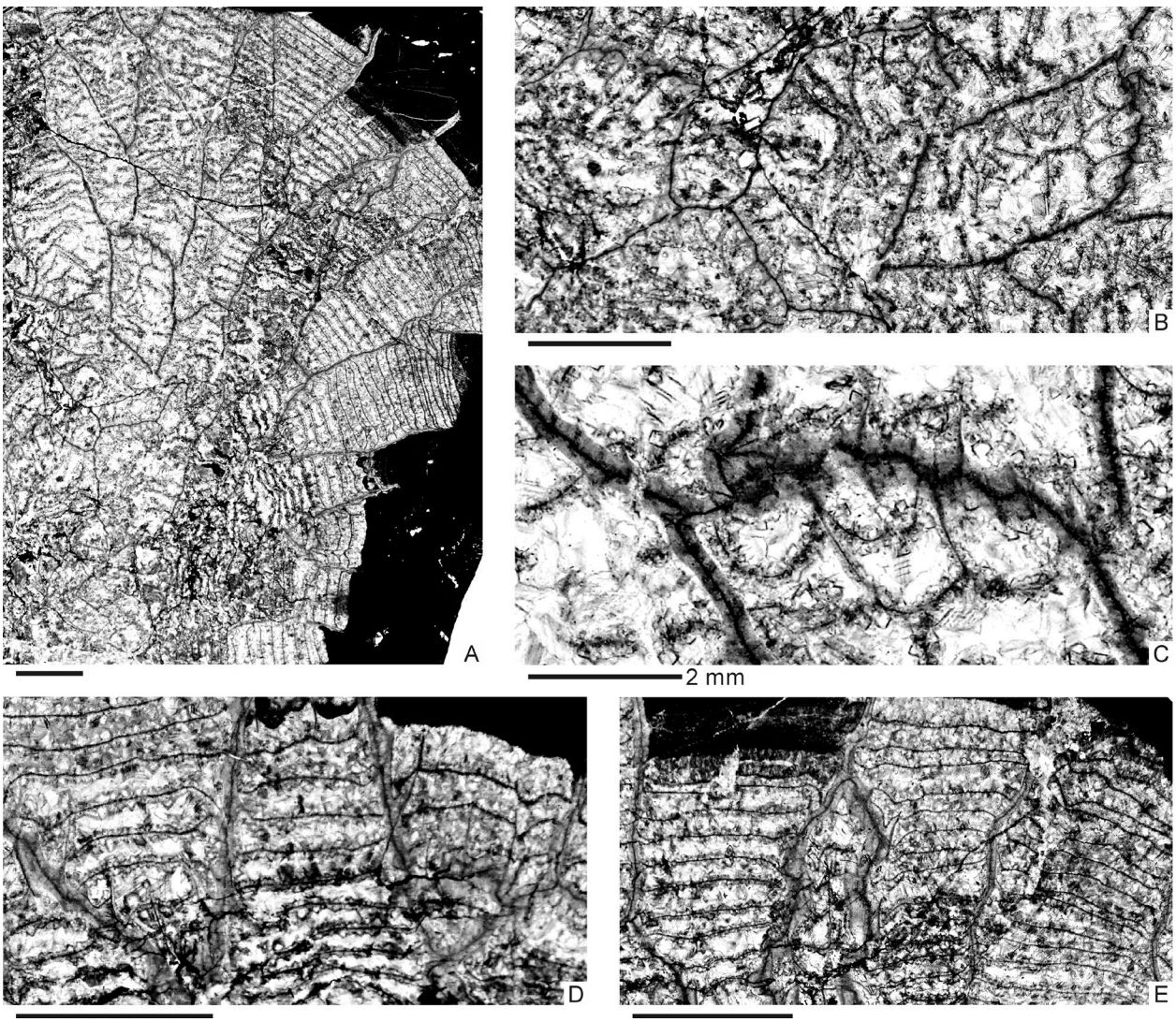


Fig. 35. Crenulites grandis (Yu, 1960). NIGP41383, holotype of *Palaeofavosites grandis* var. *infidus* Deng & Li, 1979, lower Koumenzi Formation (lower–middle Katian), Caishitu River, Qilian area, northeastern Qinghai Province, northwestern China. **A–E,** oblique–longitudinal section and four enlarged portions. Scale bars are 5 mm unless otherwise indicated.

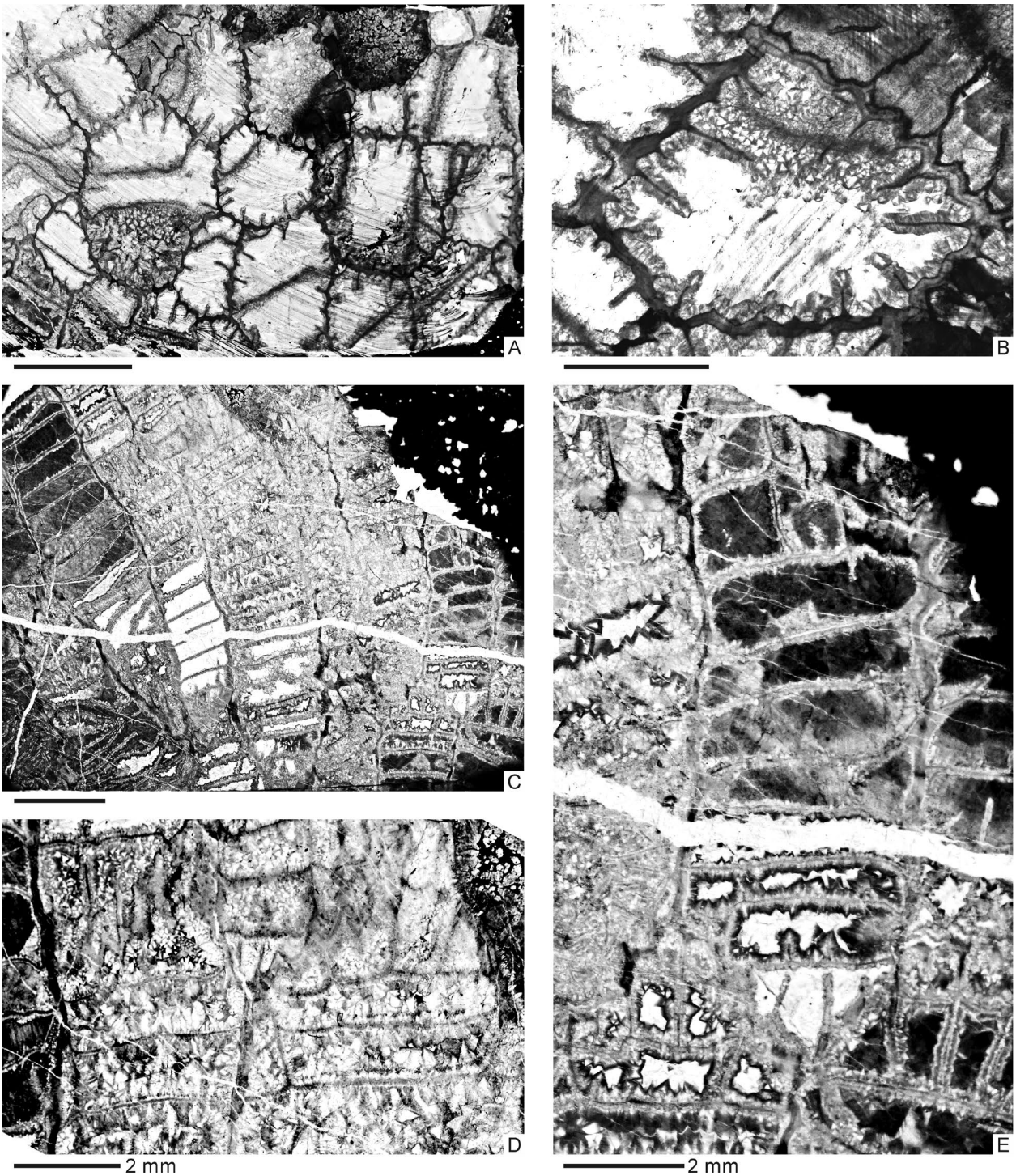


Fig. 36. Crenulites grandis (Yu, 1960). NIGP41386 (TS) and NIGP41387 (LS), holotype of *Saffordophyllum heiquanheense* Deng & Li, 1979, upper Koumenzi Formation (lower–middle Katian), Heiquanhe, Qilian area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C–E,** LS and two enlarged portions. Scale bars are 5 mm unless otherwise indicated.

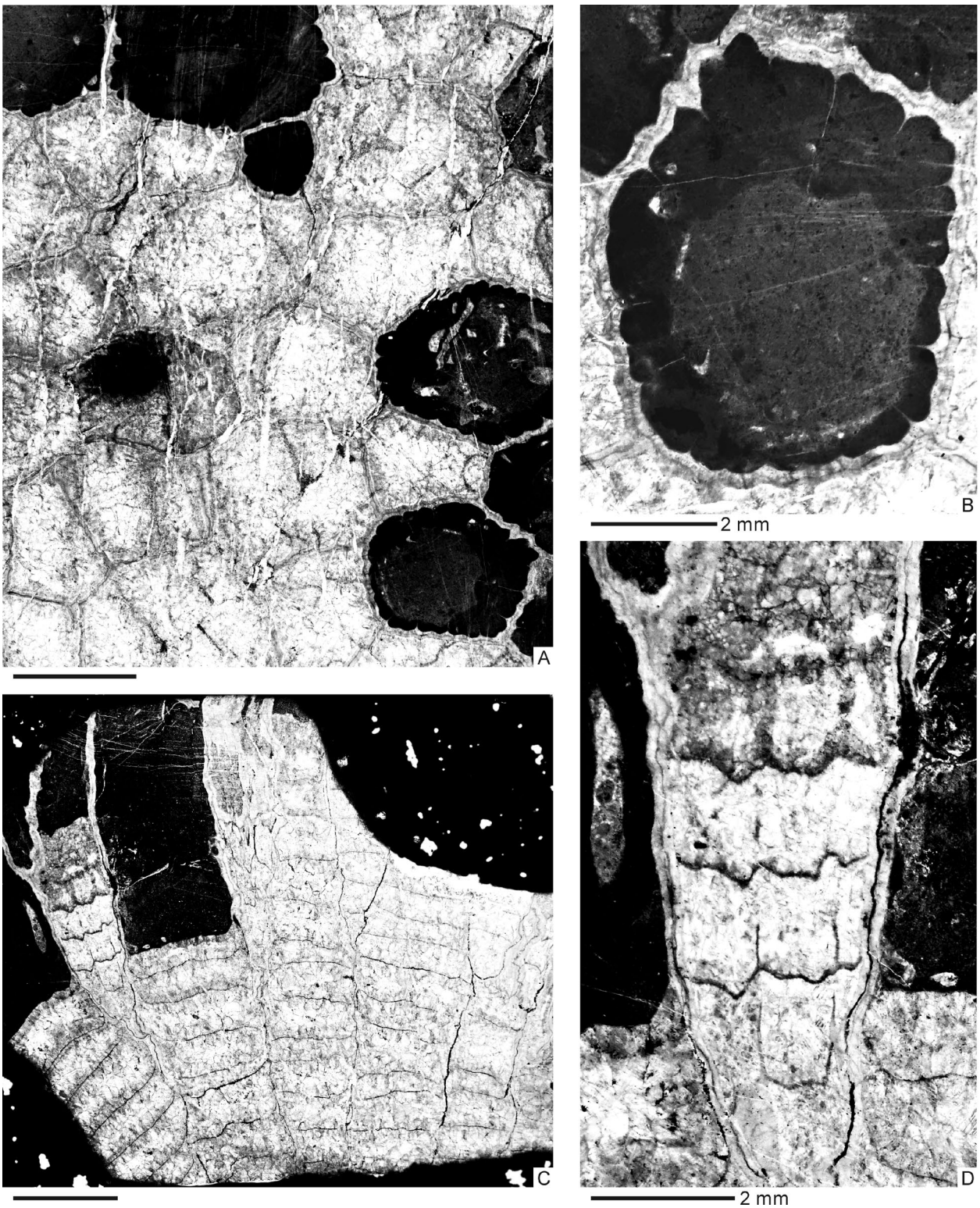


Fig. 37. *Crenulites grandis* (Yu, 1960). NIGP41384 (TS) and NIGP41385 (LS), holotype of *Saffordophyllum inconstus* Deng & Li, 1979, lower Koumenzi Formation (lower–middle Katian), Caishitu River, Qilian area, northeastern Qinghai Province, northwestern China. **A, B,** TS and an enlarged portion; **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

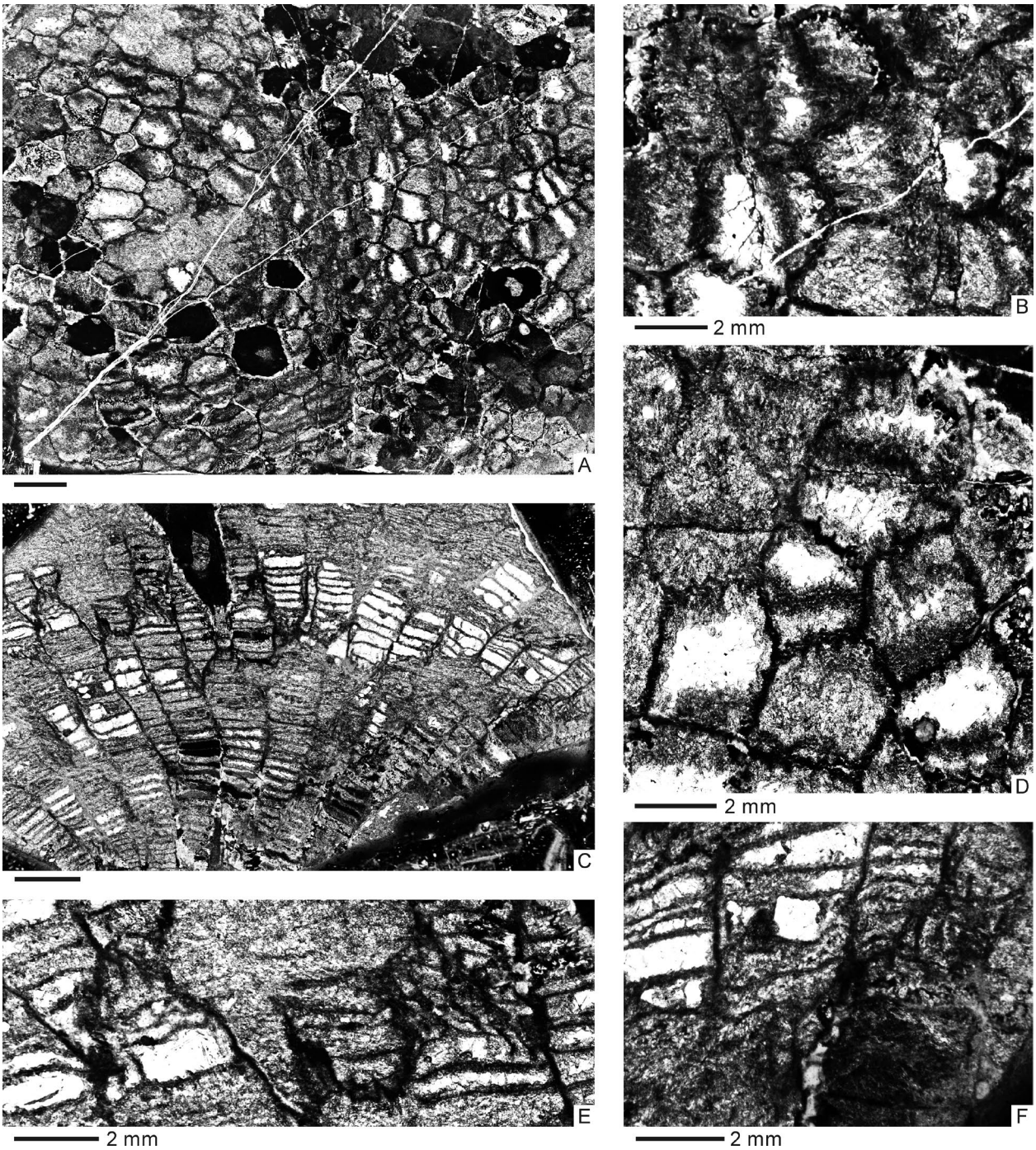


Fig. 38. Crenulites grandis? (Yu, 1960). NIGP59999 (TS) and NIGP60000 (LS) from one corallum, described by Deng & Zhang (1984) as *Palaeofavosites* cf. *grandis* Yu, 1960, upper Wuluochipu Formation (probably lower–middle Katian), Zhongza, Batang, westernmost Sichuan Province. **A, B, D,** TS and two enlarged portions; **C, E, F,** LS and two enlarged portions. Scale bars are 5 mm unless otherwise indicated.

Description. – The external form and size of coralla are unknown. Corallites polygonal, 4–8, mostly 6–8 sided, large [ACDs (6+) = 4.53–8.00 mm]. Corallite walls straight to slightly wavy, thin, with a thickness ranging from 0.10 to 0.19 mm, separated by thin dark lines. Septa of two orders, rather thin, of amplexoid nature. Septal number is difficult to be determined due to the wide tabular spacing. Major septa relatively short, up to about 1/2 of corallite radius. Minor septa weakly developed, short, mostly extending slightly beyond corallite walls. Tabulae complete, flat to wavy, or rarely slightly arched, widely spaced (Ta5 = 2–5).

Remarks. – The present revision of *Crenulites grandis* is based on the holotypes of *Palaeofavosites grandis* Yu, 1960, *Saffordophyllum heiquanheensis* Deng & Li, 1979 and *S. inconstus* Deng & Li, 1979, which are considered here as synonymous. This is because the three specimens share similar corallite size [ACDs (6+) = 5.42–6.76, 4.53–7.12, and 4.73–8.00 mm, respectively], short, thin, amplexoid septa, wall thickness (WT = 0.10–0.19, 0.11–0.13, and 0.10–0.15 mm, respectively), and complete, flat, widely spaced tabulae (Ta5 = 2–5, 3–5, and 2–3, respectively).

Crenulites grandis was originally assigned by Yu (1960) to *Palaeofavosites* since he believed that its holotype has spinose septa and mural pores. However, the present study demonstrates that septa of this specimen are laminar, as also noted by Lin (1974, 1986) who therefore transferred it to agetolitid tabulate corals, and that no reliable mural pores are confirmed. This, together with the consideration of an amplexoid septal nature, justifies its reassignment to *Crenulites*. Similarly, the transfer of both *Saffordophyllum heiquanheensis* Deng & Li, 1979 and *S. inconstus* Deng & Li, 1979 to *Crenulites* is due to the presence of amplexoid septa and thin dark lines separating corallite walls.

Palaeofavosites grandis var. *infidus* Deng & Li, 1979, from the Koumenzi Formation (lower–middle Katian) of the Qilian area, northeastern Qinghai, northwestern China, is based solely on one longitudinal section of the holotype. Deng & Li (1979, p. 7) said that septa of this form are sometimes developed as "long spines", and "corner pores are not obvious, which are rare and small". However, re-examination of the type material shows that septa are in fact amplexoid, and mural pores are lacking, supporting a transfer to *Crenulites*. Its present inclusion within *C. grandis* is because it has similar corallite size (up to 7.77 mm in diameter), wall thickness (0.13–0.15 mm), and septal development, differing only in having variably spaced tabulae (Ta5 = 5–11).

The specimen described by Deng & Zhang (1984) as *Palaeofavosites* cf. *grandis* Yu, 1960, refigured by Liang (2020) as *Palaeofavosites grandis* Yu, 1960, comes from the upper Wuluochipu Formation (probably lower–middle Katian), Zhongza, Batang, westernmost Sichuan Province. This form is reassessed here and tentatively placed within *Crenulites grandis*. The reason is that it has comparable corallite size [ACDs (6+) = 4.17–6.31 mm], amplexoid septa, wall thickness (0.11–0.13 mm), tabular development (Ta5 = 4–7), and similarly lacks mural pores, differing only in having weaker septa.

***Crenulites magnus* Flower, 1961**

1961 *Crenulites magnus* Flower, p. 85, pl. 33, figs 1–5, pl. 45, fig. 13.

Remarks. – *Crenulites magnus* (holotype, NMBM 787; paratypes, NMBM 788–790) comes from the Second Value Formation (middle Edenian to earliest Maysvillian age, middle Katian; Sweet 1979, fig. 4; Elias 1985, p. 7) of the Montoya Group at El Paso, Texas. It has large corallites (mostly 5 mm in diameter), prominent minor septa, and subparallel tabulae, which readily distinguish it from the type species, *C. duncanae* Flower, 1961.

Closest similarity lies with *Crenulites akpatokensis* Flower, 1961, discussed below, from the horizon of possible Red River age (middle Katian) on Akpatok Island, Canada. The latter shows similar corallite size (4–6 mm in diameter) and short major septa but differs in having tabulae that are "commonly normal to the walls of the corallites and are conspicuously more widely spaced" (Flower 1961, p. 85). The differences prompted Flower (1961) to treat *C. akpatokensis* as a subspecies of *C. magnus*. The two species may eventually prove to be synonymous.

***Crenulites akpatokensis* Flower, 1961**

1961 *Crenulites akpatokensis* Flower, pp. 86, 87, pl. 30, figs 1–9.

Remarks. – *Crenulites akpatokensis* is based on five syntypes (SMC-A50674, A50675, A50678–A50680, and USNM 92079) from the Ordovician of Akpatok Island, Canada, all lacking accurate horizon data. Among them, two were said to be from "sea level", and the statement of Flower (1961, p. 87) that "faunas from sea level to a 300-foot elevation suggest Red River age" may be indicative of a middle Katian age. This form has corallites with "widths of 4–6 mm", major septa that are 12–14 in number and amplexoid, short minor septa, and tabulae that are normal to the corallite axis and widely spaced (3–6 in 5 mm) (Flower 1961, pp. 86, 87).

Crenulites akpatokensis closely resembles *C. magnus* Flower, 1961, considered above, from the Second Value Formation (middle Katian) of the Montoya

Group at El Paso, Texas. The two forms may be synonymous, as discussed under the latter species above.

***Crenulites minor* (Lin, 1963)**

(Figs 39–42)

1963 *Agetolites minor* Lin, p. 120, pl. 1, figs 2a, b, 3a, b.
non 1966 *Agetolites minor* Lin; Kim, pp. 13, 14, pl. 5, fig. 2a–c.
non 1978 *Agetolites minor* Lin; Khayznikova, p. 35, pl. 6, fig. 1a, b.
non 1978 *Agetolites minor* Lin; Kim & Apekin, pp. 59, 60, pl. 4, fig. 3a, b.
1982 *Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, p. 31, pl. 10, fig. 5a**,** b.
1982 *Favistella* (*Favistella*) *shifosiensis* Cao in Cao & Lin, p. 31, pl. 9, fig. 2a**,** b.
non 1987 *Favistina* aff. *shifosiensis* (Cao); Deng, p. 621, pl. 3, fig. 2a, b, pl. 4, fig. 2.
non 1991 *Favistina* aff. *shifosiensis* (Cao); Lin & Wang in Wang, p. 164, pl. 1, fig. 1a, b.
non 1991 *Favistina* sp., Lin & Wang in Wang, p. 164, pl. 1, fig. 2a, b.
non 2020 *Favistina* aff. *shifosiensis* (Cao); Liang, p. 496, pl. 5-9-1, figs 5, 6 [refig. Deng 1987, pl. 3, fig. 2a, b].

Referred material. – GMC-IV04896 (formerly XI-8), holotype, original of Lin (1963, pl. 1, fig. 3a, b), refigured here (Fig. 39), Liangchakou Formation (probably middle Katian), Manchuan, Xizhaochuan (formerly Zhaochuan), Shanyang, southeastern Shaanxi, northwestern China. GMC-IV04895 (formerly XI-6659), described by Lin (1963) as *Agetolites*

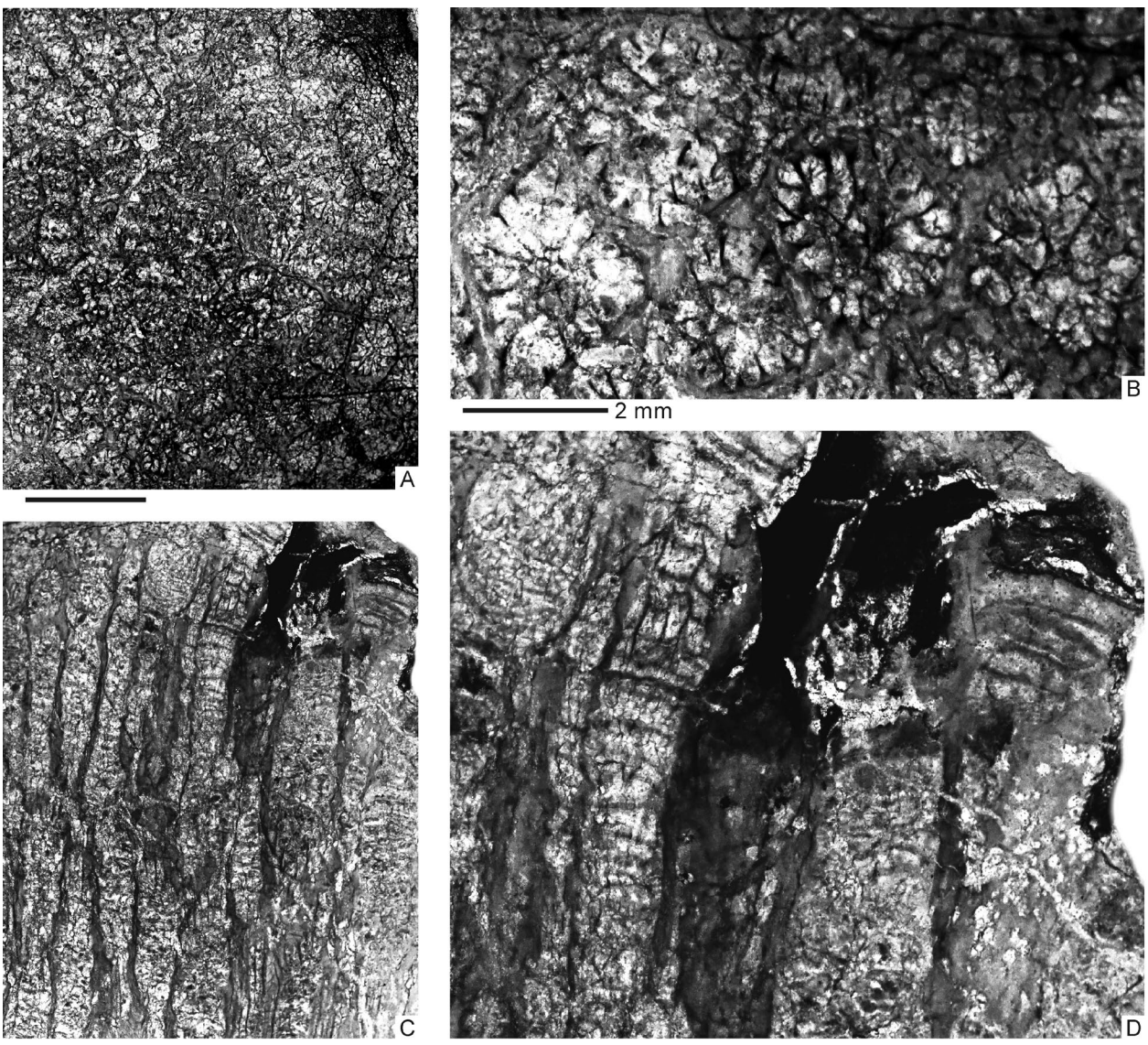


Fig. 39. Crenulites minor (Lin, 1963). GMC-IV04896 (originally XI-8), holotype, Liangchakou Formation (probably middle Katian), Xizhaochuan (formerly Zhaochuan), Shanyang, southeastern Shaanxi, northwestern China. **A, B,** TS and an enlarged portion; **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

minor Lin, 1963, original of Lin (1963, pl. 1, fig. 2a, b), refigured here (Fig. 40), same horizon and locality as the holotype. XACGS-R-048, holotype of *Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, 1982, original of Cao in Cao & Lin (1982, pl. 10, fig. 5a**,** b), refigured here (Fig. 41), Liangchakou Formation (probably middle Katian), Shifosi, Shanyang, southeastern Shaanxi Province. XACGS-R-039, holotype of *Favistella* (*Favistella*) *shifosiensis* Cao in Cao & Lin, 1982, original of Cao in Cao & Lin (1982, pl. 9, fig. 2a**,** b), refigured here (Fig. 42), Liangchakou Formation (probably middle Katian), Shifosi, Shanyang, southeastern Shaanxi Province.

Diagnosis. – *Crenulites* with small corallites [ACDs (6+) = 2.32–3.32 mm], and partly amplexoid septa.

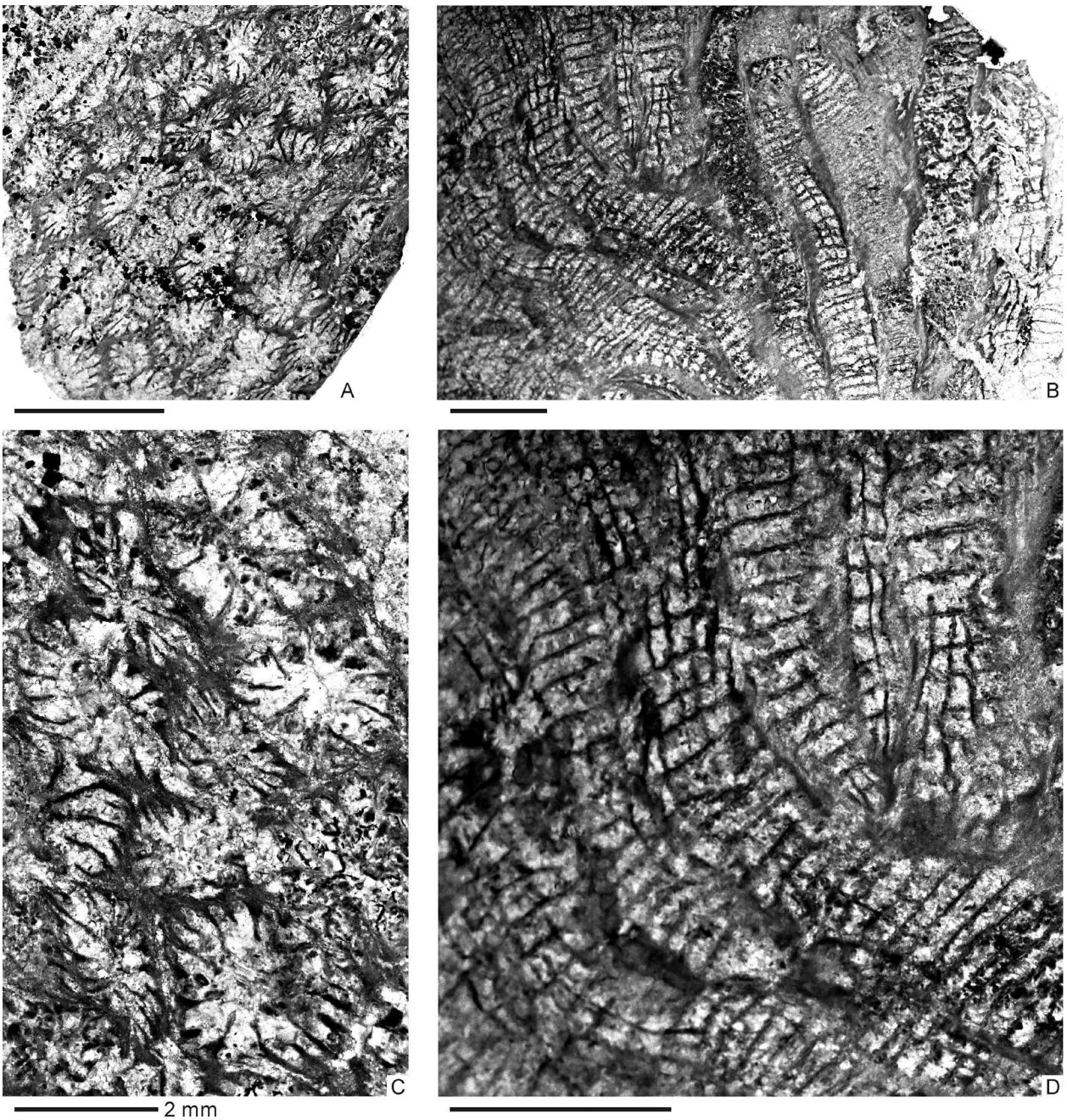


Fig. 40. Crenulites minor (Lin, 1963). GMC-IV04895 (originally XI-6659), described by Lin (1963) as *Agetolites minor* Lin, 1963, Liangchakou Formation (probably middle Katian), Xizhaochuan (formerly Zhaochuan), Shanyang, southeastern Shaanxi, northwestern China. **A, C,** TS and an enlarged portion; **B, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Major septa extending to the corallite axis. Minor septa variably developed. Tabulae complete, widely spaced (Ta5 = 5–11).

Description. – Modified from Lin (1963, p. 120) and Cao in Cao & Lin (1982, p. 31). The external form and size of coralla are unknown. Corallites polygonal, 4–7, mostly 5–6 sided, small [ACDs (6+) = 2.32–3.32 mm]. Corallite walls straight to slightly wavy, generally thick, with a thickness ranging from 0.07 to 0.16 mm, separated by thin dark lines. Septa of two orders, partly amplexoid. Major septa 9–10 in number, long, extending up to the corallite axis. Minor septa variable in length, short, extending slightly beyond

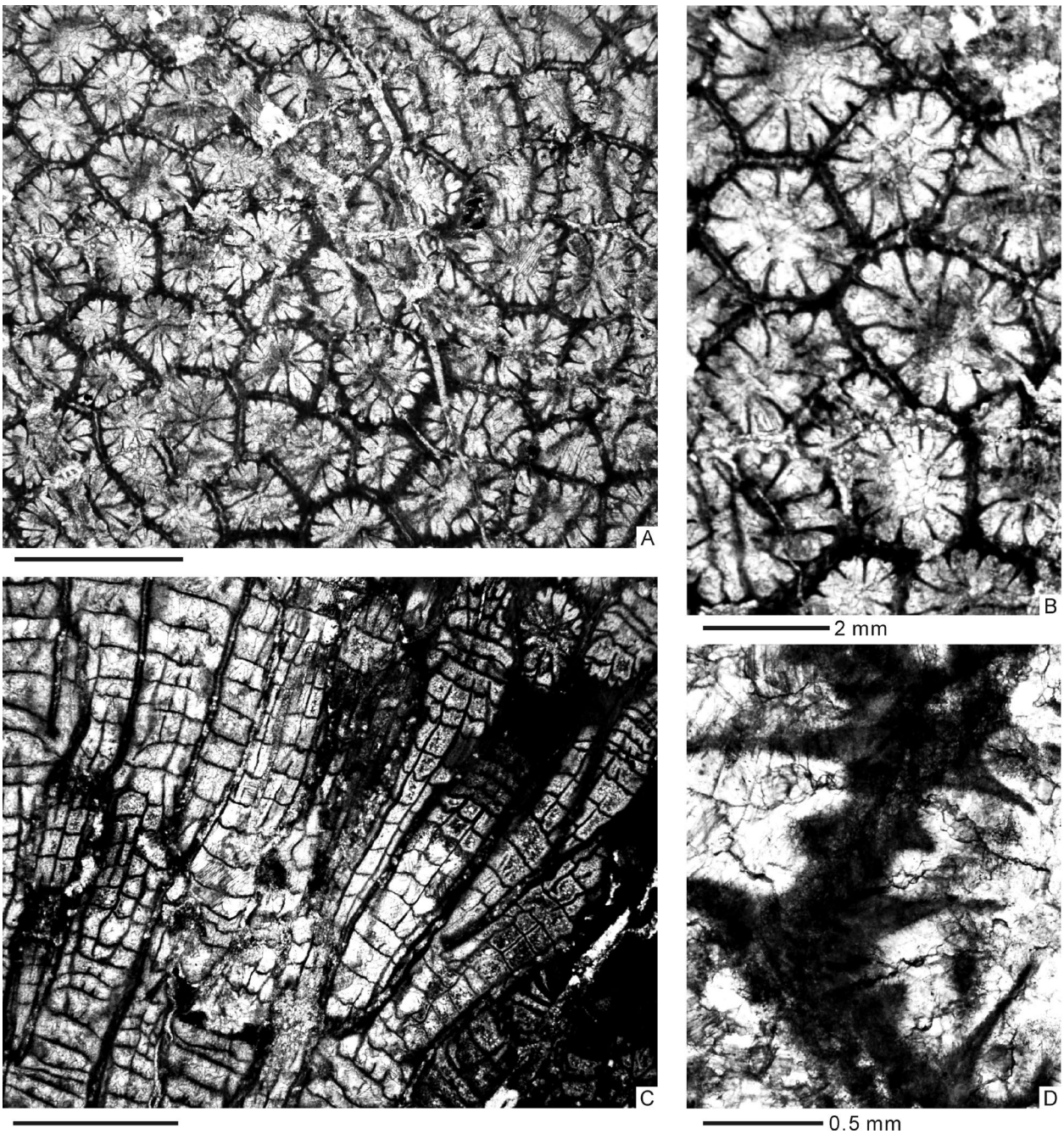


Fig. 41. Crenulites minor (Lin, 1963). XACGS-R-048, holotype of *Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, 1982, Liangchakou Formation (probably middle Katian), Shifosi, Shanyang, southeastern Shaanxi Province. **A, B, D,** TS and two enlarged portions. **C,** LS. Scale bars are 5 mm unless otherwise indicated.

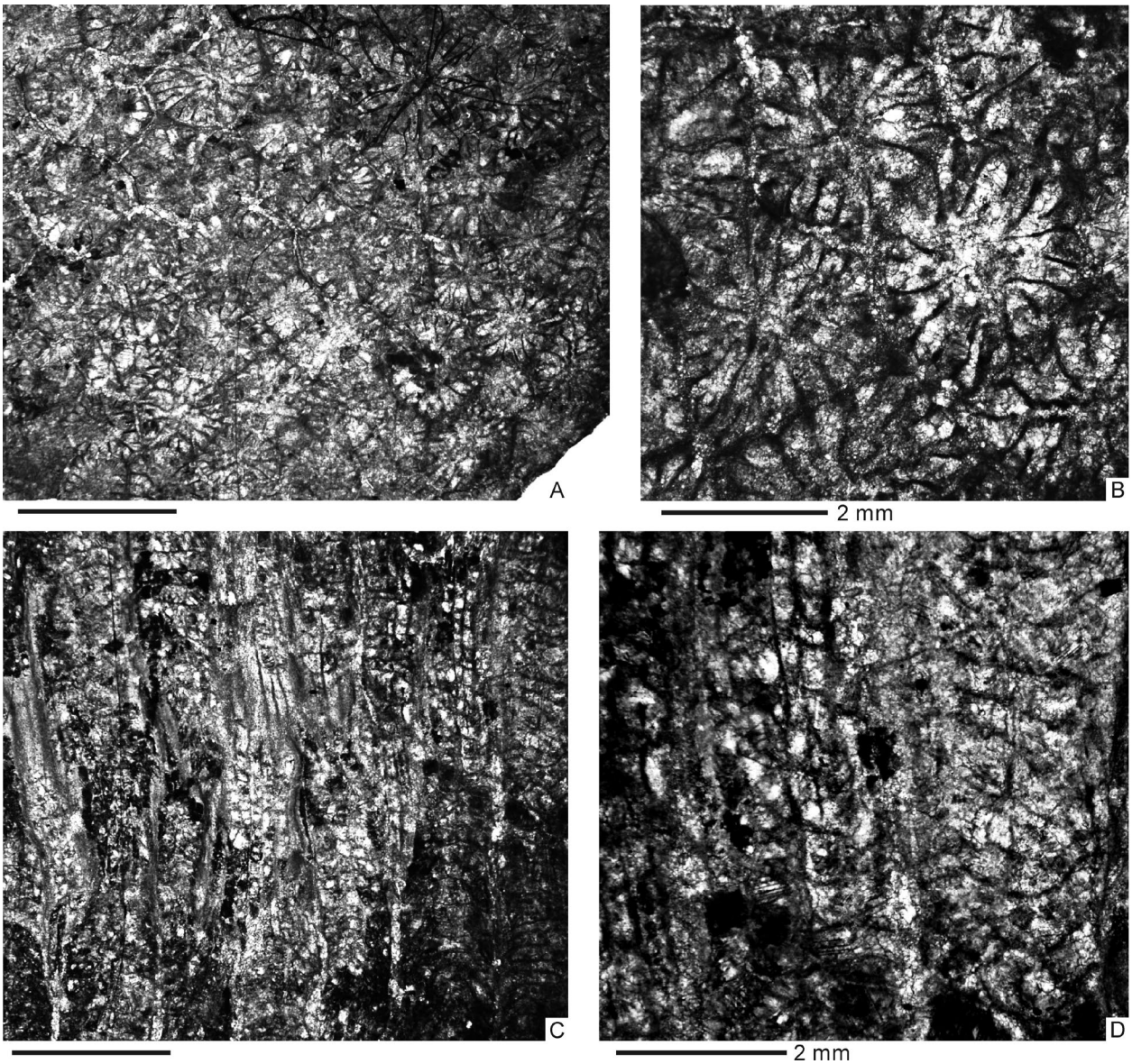


Fig. 42. Crenulites minor (Lin, 1963). XACGS-R-039, holotype of *Favistella* (*Favistella*) *shifosiensis* Cao in Cao & Lin, 1982, Liangchakou Formation (probably middle Katian), Shifosi, Shanyang, southeastern Shaanxi Province. **A, B,** TS and an enlarged portion. **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

corallite walls, or rarely long, up to 1/3 of corallite radius. Tabulae complete, flat, slightly wavy, concave or convex, well spaced (Ta5 = 5–11).

Remarks. – The description and diagnosis of *Crenulites minor* presented above are based on several specimens considered here as synonymous, including holotypes of *Agetolites minor* Lin, 1963, *Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, 1982, and *F.* (*F.*) *shifosiensis* Cao in Cao & Lin, 1982, and a further specimen described by Lin (1963) as *A. minor*. The reason for their synonymy is that they have similar corallite size [ACDs (6+) = 2.54–3.14, 2.40–2.92, 2.32–3.32, and 2.35–3.28 mm, respectively], slightly amplexoid septa, and tabular development (Ta5 = 7–9, 5–9, 5–11, and 6–11, respectively). Although assigned originally to *Agetolites*, Lin (1963, p. 120) mentioned that "the size of its mural pores are unclear". The present reassessment of the holotype confirms the lack of mural pores and the development of amplexoid septa, warranting a reassignment to *Crenulites*.

The materials that were previously described as *Agetolites minor* Lin 1963 but are true agetolitids include that documented by Kim (1966) and

Kim & Apekin (1978) from the Archalyk Member (uppermost Katian) of the Shahriomon Formation in Zeravshan–Hissar, and by Khayznikova (1978) from the top part (upper Katian) of the Baraninsky Formation in Sette-Daban area of the Verkhoyansk region, northeastern Russia. A detailed discussion as to these forms can be found in Wang & Cui (2025).

The specimens described by Deng (1987) and Lin & Wang in Wang (1991) as *Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982) come from middle Shiyanhe Formation (middle Katian) of Shiyanhe, Xichuan, southwestern Henan Province. They are now revised as *Favistina* sp. B., as considered above. Similarly, *Favistina* sp. of Lin & Wang in Wang (1991), from the middle Shiyanhe Formation (middle Katian) of the same area, may be included within *Favistina pachytheca* Deng, 1984, redescribed above.

Crenulites? sp.

1963 *Favistella alveolata* (Goldfuss); Smelovskaya, pp. 178, 179, pl. 27, figs 1–4.

Remarks. – This form occurs in the basal Akchaul Formation (middle Katian) of the Tarbagatai area. Although not mentioned in its original description, slightly amplexoid septa appear to be present in its illustrations (Smelovskaya 1963, pl. 27, figs 1–3), supporting a possible reassignment to *Crenulites*. Its distinguishing features include corallite diameters of 3–5 mm, 12–14 major septa extending close to the corallite axis, short minor septa that do not extend beyond the corallite walls, and complete, slightly arched, well-spaced tabulae (Ta5 = 10–12). Until a modern revision confirms its identity, this form is tentatively classified as *Crenulites*? sp.

Crenulites sp. B

1965 *Favistella alveolata* (Goldfuss); Ivanovskiy, pp. 110, 111, pl. 27, fig. 1a, b.
1969 *Favistella alveolata* (Goldfuss); Ivanovskiy *pars*, pp. 66, 69–71, pl. 3, fig. 2a, b [refig. Ivanovskiy 1965, pl. 27, fig. 1a, b], *non* pl. 3, figs 1a, b, 3a, b.
1969 *Favistella rigida* (Billings); Ivanovskiy, pp. 71–73, pl. 4, fig. 1a, b.
1979a *Favistina stellata* (Hall); Sytova, p. 172, pl. 36, fig. 2a, b.

Remarks. – The specimens included here in *Crenulites* sp. B were formerly described as various species, as listed in the synonymy above, all from the Dolborian Horizon (middle Katian) of the Podkamennaya Tunguska River Basin. This species is characterised by highly amplexoid septa and large corallites (5–6 mm in diameter), a combination of which distinguishes it from all other *Crenulites* species. The limited knowledge of its intraspecific variation precludes the erection of a new taxon.

Crenulites australis Hall, 1975

1975 *Crenulites australis* Hall, pp. 82, 83, pl. 2, figs e, f.
1975 *Crenulites australis minor* Hall, p. 83, pl. 2, figs g, h.
?1976 *Crenulites discreta* Bolton in Workum *et al.*, p. 168, pl. 1, figs 9, 10.
1979a *Favistina rozmanae* Sytova, pp. 172, 173, pl. 36, fig. 3a, b.
2021 *Crenulites australis* Hall; Wang *et al.*, p. 56, figs 3a–f, 4a–h.

Remarks. – *Crenulites australis* (holotype, UNE-F11705; paratype, UNE-F11706) was originally described by Hall (1975) from allochthonous limestones informally termed the 'Trelawney Beds', of the New England Region in northeastern New South Wales. Wang *et al.* (2021) revised the species based on ten topotypes, and considered *C. australis minor* Hall, 1975 documented from the same horizon as its synonym. According to their revision, the specific features of *C. australis* include small corallites (1.26–3.12 mm in diameter), well-developed minor septa, and widely spaced tabulae (Ta5 = 3–9, rarely 10–12 in number).

Crenulites discretus Bolton in Workum *et al.*, 1976, from the Maysvillian (middle Katian) of Akpatok Island, Canada, represents the only form outside Australia showing corallite size (1.5–2.3 mm in diameter) comparable to *C. australis*. The main differences are the slightly thinner corallite walls and more strongly arched tabulae of the former, and the two forms are very likely conspecific.

Crenulites rozmanae (Sytova, 1979a) comes from the Dolborian Horizon (middle Katian) of the Tungus Basin, Siberia. This species has amplexoid major septa and is clearly attributable to *Crenulites*. It is regarded herein as a synonym of *C. australis* notably because of similar small-sized corallites (less than 3–3.5 mm in diameter) and septa extending almost to the corallite axis.

Crenulites discretus Bolton in Workum *et al.*, 1976

?1975 *Crenulites australis* Hall, pp. 82, 83, pl. 2, figs e, f.
1976 *Crenulites discreta* Bolton in Workum *et al.*, p. 168, pl. 1, figs 9, 10.

Remarks. – *Crenulites discretus* (holotype, GSC 41179), from the Maysvillian (middle Katian) of Akpatok Island, Canada, has corallite diameters of 1.5–2.3 mm, long major septa extending close to the corallite axis, short minor septa, and widely spaced tabulae (commonly 1 mm apart).

Crenulites australis Hall, 1975, discussed above, shows comparable corallite size (1.26–3.12 mm in diameter), and the latter differs only in having slightly thinner corallite walls and more strongly arched tabulae. The two species may be synonymous (Wang *et al.* 2021, p. 56).

Crenulites akpatokensis Flower, 1961, considered above, from the Upper Ordovician of the same area, differs from *C. discretus* in having larger corallites (about 4–6 mm in diameter), shorter major septa, and less distinctly downturned tabulae, as noted by Workum *et al.* (1976, p. 168).

Crenulites guyuanensis (Lin in Cao & Lin, 1982)

1982 *Favistella* (*Parafavistella*) *guyuanensis* Lin in Cao & Lin, p. 32, pl. 11, fig. 2a, b.

Remarks. – *Crenulites guyuanensis* (Lin in Cao & Lin, 1982), the type species of *Favistella* (*Parafavistella*) Lin in Cao & Lin, 1982, is based on the holotype and only known specimen from the Beiguoshan Formation (lower–middle Katian) of Yindonggou, Guyuan area, southern Ningxia. This specimen (numbered 75-85-3) is now stored at Geological Museum of China, Beijing (Baoyu Lin pers. comm.). However, regrettably, it could not be located for the present study. According to Cao & Lin's (1982) original description and figures, this species has corallite diameters of 4–6 mm, thin corallite walls (0.2 mm in thickness), few, strongly amplexoid major septa (9–11, generally 10 in number) that almost extend to the corallite axis, weak minor septa represented by rare, rather short stubs, and complete, widely spaced tabulae (Ta5 = 4–6). The small number of septa and rather weak minor septa appear to be sufficient to separate *C. guyuanensis* from all other known species of the genus.

Crenulites formosus (Deng, 1984)

(Figs 43–46)

1984 *Favistina dybovskii* Soshkina in Ivanova *et al.*; Deng, p. 317, pl. 3, fig. 4a, b.
1984 *Favistina formosa* Deng, p. 317, pl. 3, fig. 3a, b.

Referred material. – NIGP 63628 (TS) and NIGP 63629 (LS), holotype, original of Deng (1984, pl. 3, fig. 3a, b), refigured here (Fig. 43); NIGP 63630 (TS) and NIGP 63631 (LS), described by Deng (1984) as

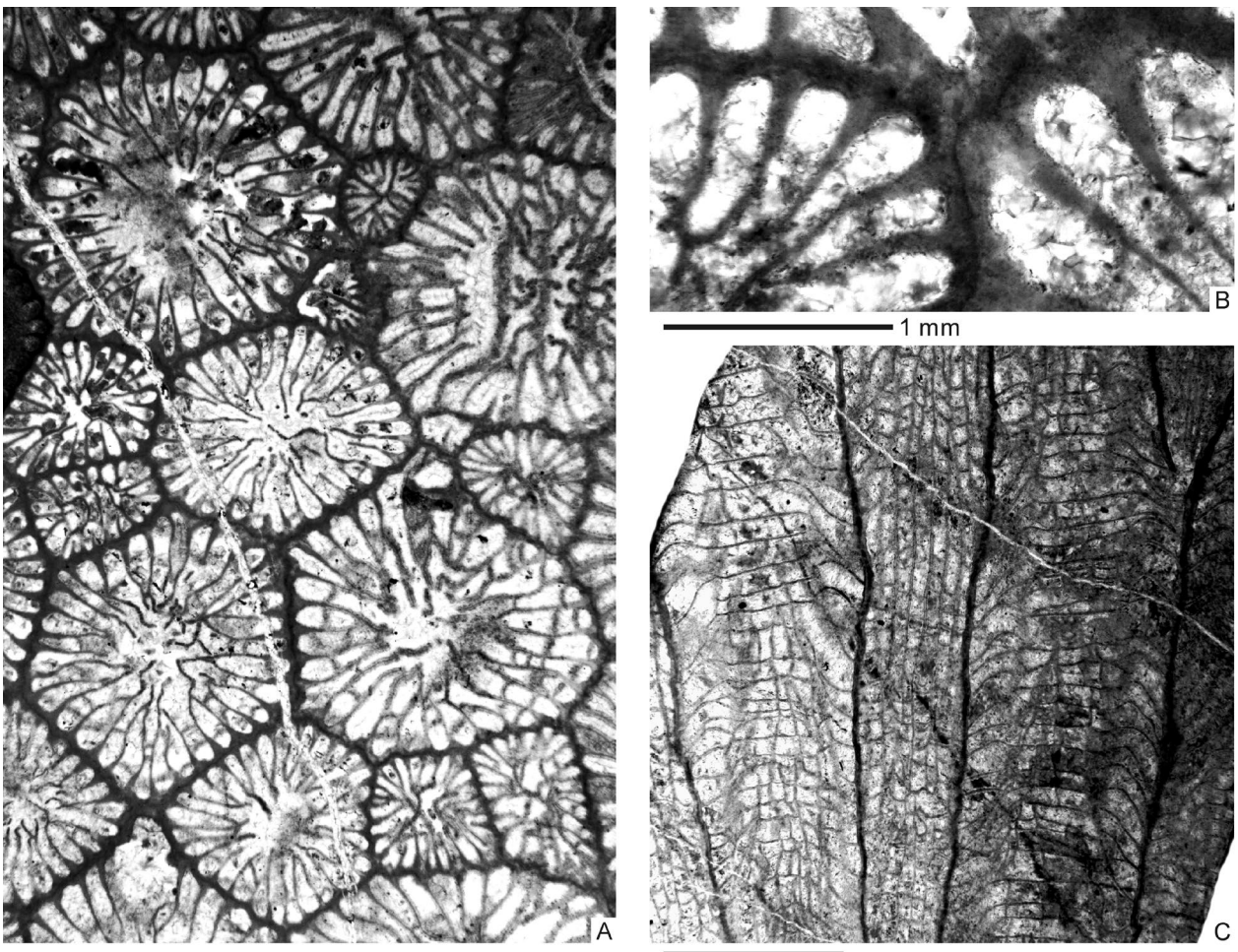


Fig. 43. Crenulites formosus (Deng, 1984). NIGP 63628 (TS) and NIGP 63629 (LS), holotype, Taoqupo Formation (lower–middle Katian), Taoqupo, Yaozhou (formerly Yaoxian) area, central Shaanxi Province. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

Favistina dybovskii Soshkina in Ivanova *et al.*, 1955, original of Deng (1984, pl. 3, fig. 4a, b), refigured here (Fig. 44); both from the Taoqupo Formation (middle Katian), Taoqupo, Yaozhou (formerly Yaoxian) area, central Shaanxi Province. NIGP 205570, and NIGP 205571, two new specimens, figured here in Figs 45 and 46, respectively, both from the same horizon at nearby Tiewadian of the same area, central Shaanxi Province.

Diagnosis. – *Crenulites* with medium to large-sized corallites [ACDs (6+) = 4.35–6.39 mm], thin corallite

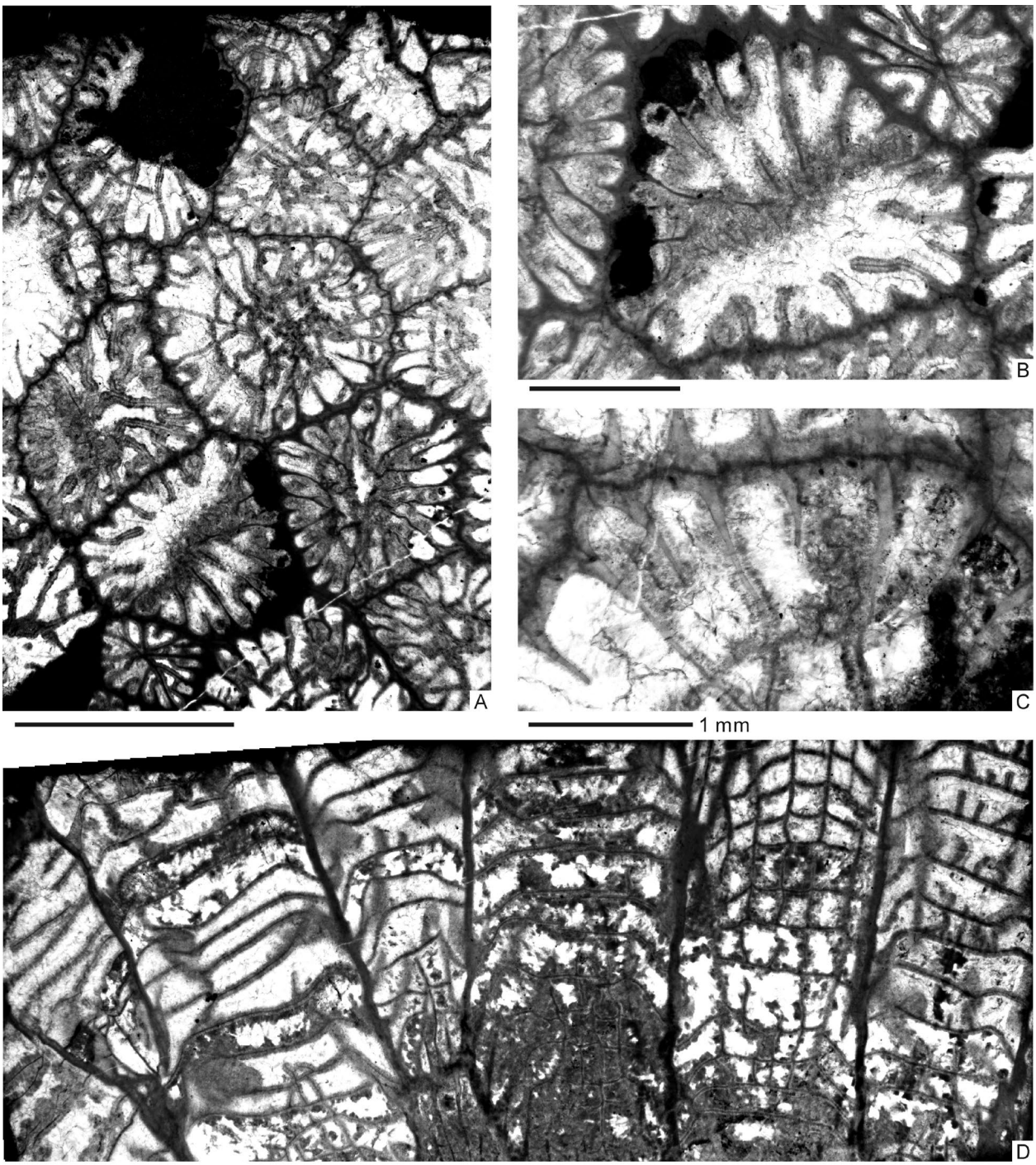


Fig. 44. Crenulites formosus (Deng, 1984). NIGP 63630 (TS) and NIGP 63631 (LS) from one corallum, described by Deng (1984) as *Favistina dybovskii* Soshkina in Ivanova *et al.*, 1955, Taoqupo Formation (lower–middle Katian) of Taoqupo, Yaozhou (formerly Yaoxian) area, central Shaanxi Province. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

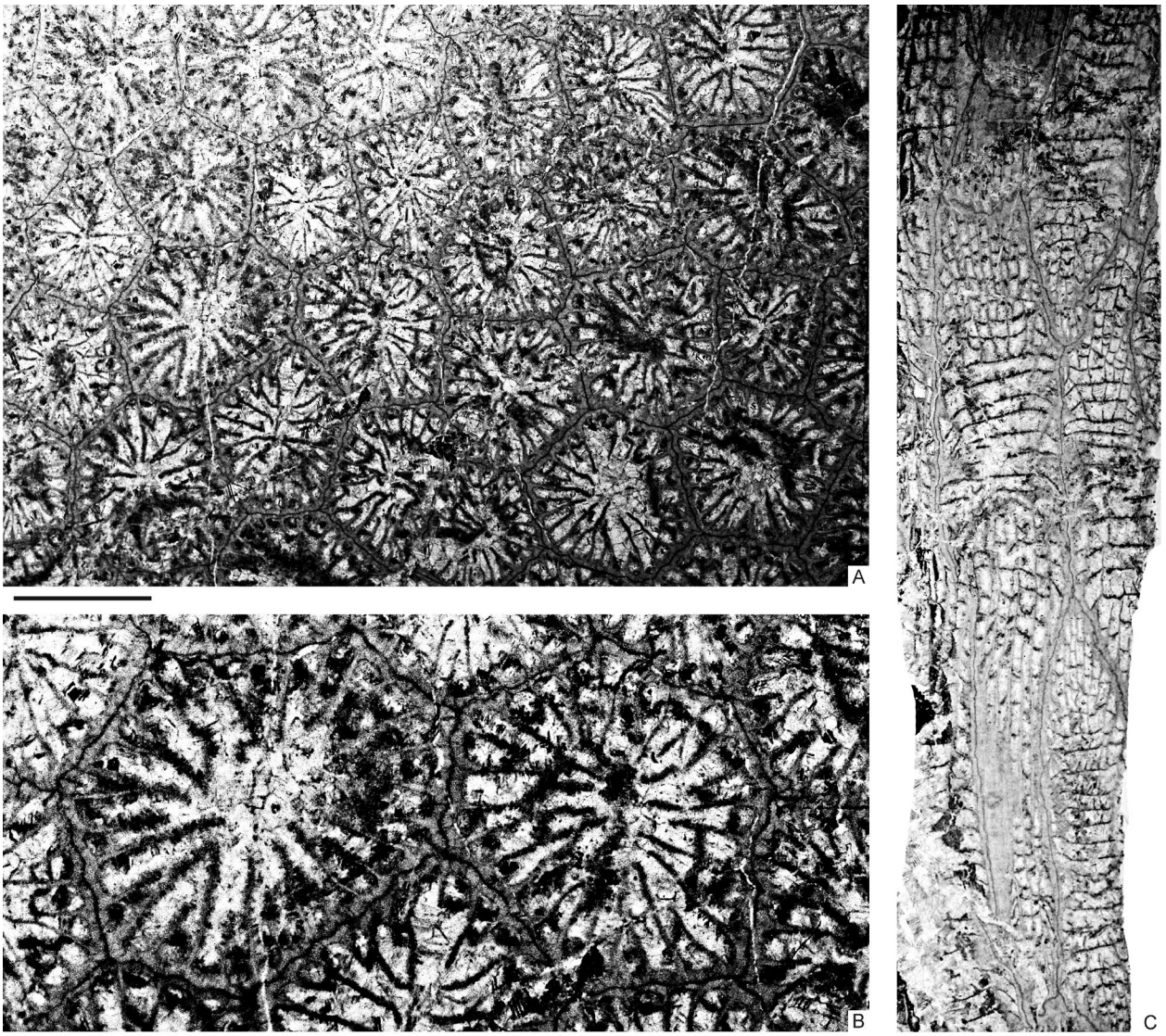


Fig. 45. Crenulites formosus (Deng, 1984). NIGP 205570, new specimen, Taoqupo Formation (lower–middle Katian), Tiewadian, Jingyang area, central Shaanxi Province. **A, B,** TS and an enlarged portion; **C,** LS. Scale bars are 5 mm.

walls (WT = 0.07–0.18 mm), major septa that are amplexoid in axial regions, and well-developed minor septa (generally up to 50–80% of corallite radius), and variably spaced tabulae (Ta5 = 3–8).

Description. – Modified from Deng (1984, p. 317). External form and size of coralla unknown. Corallites polygonal, with mature ones commonly 6–8 sided, medium to large-sized [ACDs (6+) = 4.35–6.46 mm]. Corallite walls generally slightly wavy, thin to slightly thick, 0.07–0.18 mm in thickness, separated by prominent dark lines. Septa of two orders, amplexoid in axial regions. Major septa of mature corallites 12–17 in number, long, extending to, or almost to the corallite centre. In some early-stage corallites, the axial ends of some major septa meeting in the axis but without forming an axial structure. Minor septa well developed, relatively long, generally up to 50–80% of corallite radius. Tabulae complete, or rarely incomplete, commonly slightly arched with a broad, slightly concave central platform, variably spaced (Ta5 = 3–8).

Remarks. – The revised description and diagnosis of *Favistina formosa* given above are based on a reassessment of the holotype, the specimen described by Deng (1984) as *Favistina dybovskii* Soshkina in Ivanova *et al.*, 1955, and two newly obtained specimens, all from the Taoqupo Formation (lower–middle Katian) of the Yaozhou (formerly Yaoxian) area, central Shaanxi Province. These fossils are clearly conspecific, since

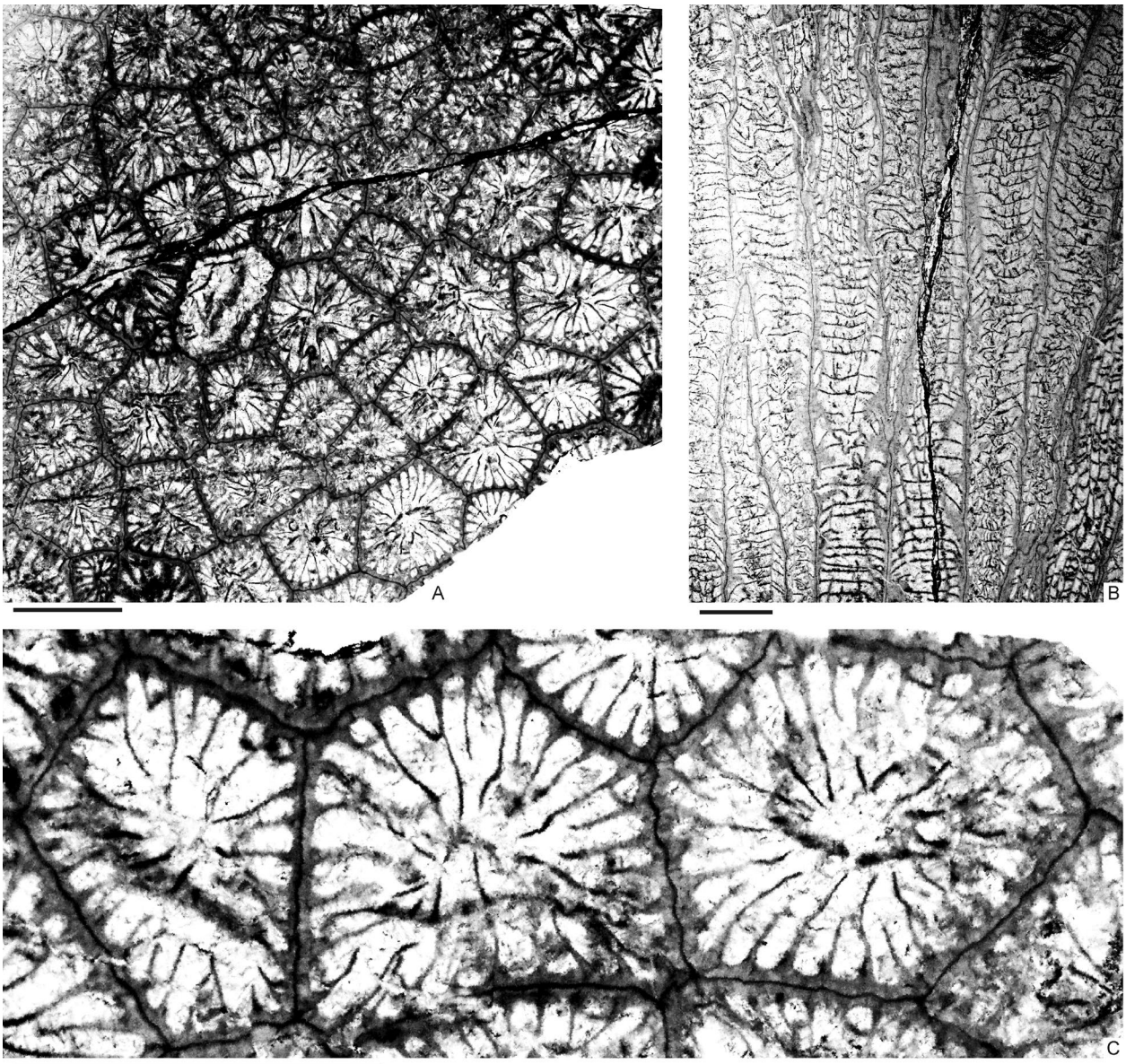


Fig. 46. Crenulites formosus (Deng, 1984). NIGP 205571, new specimen, Taoqupo Formation (middle Katian), Tiewadian, Jingyang area, central Shaanxi Province. **A, C,** TS and an enlarged portion; **B,** LS. Scale bars are 5 mm.

they have almost identical corallite size [ACDs (6+) = 4.35–6.29, 4.64–6.39, 4.95–6.46, and 5.17–6.11 mm, respectively], and septal and tabular development (Ta5 = 6–8, 4–7, 3–5, and 3–6, respectively).

***Crenulites* sp. C**

(Fig. 47)

1984 *Favistina* aff. *dybovskii* Soshkina in Ivanova *et al.*; Deng, p. 316, pl. 2, fig. 2a, b.

Referred material. – NIGP 63620 (TS) and NIGP 63621 (LS), described by Deng (1984) as *Favistina* aff. *dybovskii* Soshkina in Ivanova *et al.*, 1955, original of Deng (1984, pl. 2, fig. 2a, b), refigured here (Fig. 47), Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province.

Description. – Modified from Deng (1984, p. 316). The single corallum massive, with external form and size unknown. Corallites moderately alveolitoid, medium-sized [ACDs (6+) = 4.74–5.77 mm]. Corallite walls straight, or slightly wavy, separated by thin dark lines. Corallite walls moderately thick, varying from 0.11 to 0.23 mm. Major septa amplexoid, typically numbering 12–14 in mature corallites, relatively short, not extending to the corallite axis. Minor septa

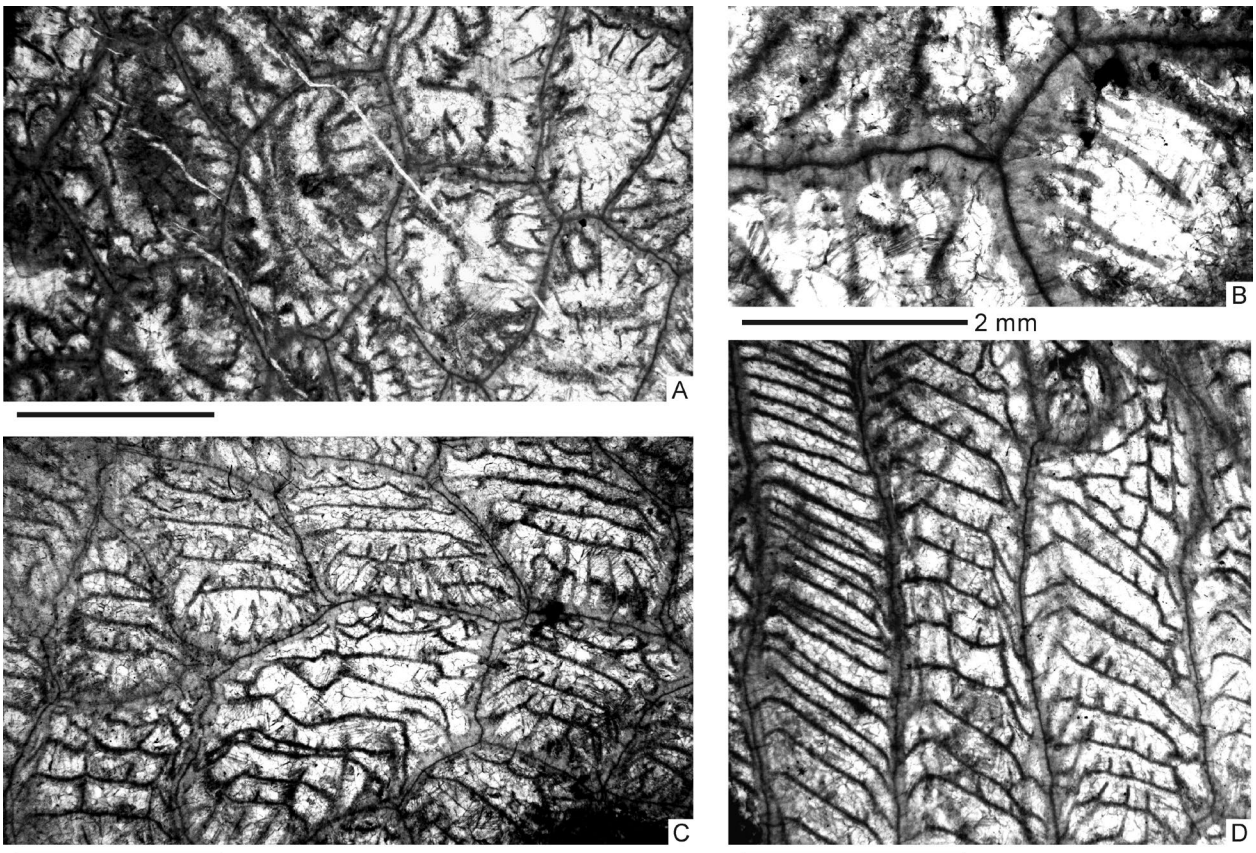


Fig. 47. Crenulites sp. C. NIGP 63620 (TS) and NIGP 63621 (LS) from one corallum, described by Deng (1984) as *Favistina* aff. *dybovskii* Soshkina, 1955, Longmendong Formation (lower Katian), Heiyingsigou, Longxian area, western Shaanxi Province. **A–C,** TSs (A, C) and an enlarged portion (**B**) of **A**; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

well developed, up to 1/2 of corallite radius. Tabulae complete, flat to moderately arched, commonly with flat central platform and downturned edges, variably spaced (Ta5 = 5–9).

Remarks. – The presence of alveolitoid corallites and relatively short major septa serves to separate this form from all other species of *Crenulites*. However, it seems wise to erect a new species only after a proper evaluation of its intraspecific variation.

Genus *Palaeolithostrotion* Lavrusevich, 1975

1975 *Palaeolithostrotion* Lavrusevich, pp. 31–33.

Type species. – *Palaeolithostrotion zachonense* Lavrusevich, 1975, "Archalyk Horizon", now Archalyk Member (uppermost Katian) of the Shahriomon Formation (Ghobadi Pour *et al.* 2023), Zeravshan–Hissar.

Diagnosis. – Phaceloid to partly cerioid coralla with lateral increase. Major septa are long and generally show a distinctive cardinal-counter axis with one prominent septum, possibly the cardinal septum, extending to or beyond the corallite centre and sometimes forming a prominent columella. Additional major septa tend to join the cardinal-counter axis at or near the corallite centre, sometimes contributing to the formation of axial structures. Tabulae complete or incomplete, moderately to strongly arched, sometimes with a broad central platform that may be flat or concave. Modified after Lavrusevich (1975, pp. 31–33) and Hill (1981, p. F138).

Remarks. – *Palaeolithostrotion* was originally defined to encompass *Palaeophyllum*-like forms characterised by the development of a prominent columella formed by one, probably the cardinal septum, or more major septa, as typically observed in the type species of the genus, *Palaeolithostrotion zachonense*

Lavrusevich, 1975, discussed below. In this study, the genus is expanded to further include forms that have a distinctive cardinal-counter axis that is generally joined by additional major septa at or near the corallite centre, regardless of whether a prominent columella develops. This approach is justified partly by the evolutionary significance of this septal feature, as evidenced by its relatively late emergence in cyathophylloidid evolution, and partly by the inconsistency of columellar development in the type species. The generally arched tabulae are another characteristic feature of this genus. Regarding its taxonomic placement, *Palaeolithostrotion* exhibits a lateral increase, warranting its original classification within the Cyathophylloididae Dybowski, 1873a.

Palaeophyllum Billings, 1858a is separated from *Palaeolithostrotion* by its lack of bilateral symmetry and generally arched tabulae. *Crenulites* Flower, 1961 and *Cyathophylloides* Dybowski, 1873a are distinguished by their cerioid coralla, with *Crenulites* further differing in its amplexoid septa.

The species included or potentially included in *Palaeolithostrotion* are discussed below, except for a form illustrated by Oliver *et al*. (1975a, p. 26) as *cf. Palaeophyllum* sp. from "early Wenlockian" strata in the Porcupine River area, Alaska. This Alaskan specimen is represented only by a fragment of a single specimen, illustrated through two thin sections of variably oriented corallites. The figures suggest the presence of moderately arched tabulae; however, the existence of a cardinal-counter axis remains uncertain. This uncertainty, combined with the unknown mode of growth, leaves its true identity unresolved.

Palaeolithostrotion zachonense Lavrusevich, 1975

1975 *Palaeolithostrotion zachonense* Lavrusevich, pp. 33, 34, pl. 2, fig. 1a–c.
1981 *Palaeolithostrotion zachonense* Lavrusevich; Hill, fig. 74, 2a, b [refig. Lavrusevich 1975, pl. 2, fig. 1a, b].
1991 *Palaeolithostrotion zachonense* Lavrusevich; Lavrusevich, pp. 23, 24, pl. 53, fig. 1a–c [refig. Lavrusevich 1975, pl. 2, fig. 1a–c].
1995 *Palaeolithostrotion zachonense* Lavrusevich; Lin *et al*., pl. 2, fig. 6a, b [refig. Lavrusevich 1975, pl. 2, fig. 1a, b].

Remarks. – *Palaeolithostrotion zachonense* (holotype, UpG 1101/14-17), the designated type species of the genus, occurs in the Archalyk Member (uppermost Katian) of the Shahriomon Formation in the Zeravshan–Hissar region. This form exhibits a lateral increase (Lavrusevich 1975, pl. 2, fig. 1a, b). Its major septa extend to the corallite centre, where "a more or less massive rounded or oval column is usually developed", which "may be associated with all or most of the major septa, but more often with one of them" (Lavrusevich 1975, p. 33). Additional specific features include small corallites (0.5–2.5 mm in diameter), 12 major septa, and complete, convex, widely spaced tabulae (8 in 10 mm).

Palaeolithostrotion zachonense is distinguished from *P. voruense* Lavrusevich, 1975, which occurs within the same horizon and general area, chiefly by the latter possessing significantly larger corallites (around 3.5 mm in diameter) and greater number of septa (15–17), also noted below.

Palaeolithostrotion multicaule (Hall, 1852)

1852 *Syringopora*? *multicaulis* Hall, p. 119, pl. 33, fig. 3a–g.
1963 *Palaeophyllum multicaule* (Hall); Oliver, p. G-5, pl. 4, figs 1–7.

Remarks. – *Palaeolithostrotion multicaule* is based on the material from the Gasport Formation of Homerian age (Laub 1983, pp. 16, 17, 28; Brett *et al*. 1995, p. 50), Lockport, New York. A lectotype (AMNH 1695) was later chosen and figured in thin section for the first time by Oliver (1963, p. G-5), who noted that its major septa "extend nearly to the axis". However, the illustrations clearly show that some major septa are connected, with their arrangement sometimes exhibiting apparent bilateral symmetry (Oliver 1963, pl. 4, figs 1, 2, 4). This, along with its later increase and strongly convex tabulae featuring an axial notch, supports its reassignment to *Palaeolithostrotion*. Key specific characteristics include small corallites (2.0–3.2 mm in diameter) and a prominent septal stereozone (0.2–0.3 in thickness). This form is the youngest known record of *Palaeolithostrotion* and the entire cyathophylloidid group worldwide.

Palaeolithostrotion vaurealense (Twenhofel, 1928)

1928 *Columnaria*? (*Palaeophyllum*) *vaurealensis* Twenhofel, pp. 122, 123, pl. 4, fig. 1.
1972 *Palaeophyllum vaurealensis* (Twenhofel); Bolton, pl. 3, figs 6, 11.
1973 *Palaeophyllum sinclairi* Caramanica, pp. 327–333, pl. 16, figs 6–10.
1976 *Palaeophyllum* cf. *vaurealensis* (Twenhofel); Fedorowski & Jull, pp. 61, 62, pl. 8, fig. 3a–b, pl. 10, fig. 1a–s, text-figs 7, 8.
1976 *Palaeophyllum vaurealensis* (Twenhofel); Fedorowski & Jull, pp. 64, 66, pl. 8, fig. 4a–c, pl. 9, fig. 1a–p, text-fig. 9.
1976 *Palaeophyllum* sp., Fedorowski & Jull, p. 66, pl. 8, fig. 5a, b, pl. 9, fig. 2a–g, text-fig. 10.
1979 *Palaeophyllum vaurealensis* (Twenhofel); Bolton, p. 7, pl. 1.3, figs 1–10.
?1985 *Palaeophyllum gracile* Flower; Gierlowski & Langenheim, p. 7, pl. 1, figs 1–4.
?1985 *Palaeophyllum humei* Sinclair; Gierlowski & Langenheim, pp. 7, 8, pl. 1, figs 5, 6, pl. 2, figs 1–5, pl. 3, figs 1–3.
1992 *Palaeophyllum sinclairi* Caramanica, pp. 75–79, pl. 6, figs 1–5.
2004 *Palaeophyllum vaurealense* (Twenhofel); Melzak, pp. 275–284, pl. 18, figs 5–7, pl. 19, figs 1–8, pl. 20, figs 1–9.

Remarks. – Both the holotype (YPM 20495) and paratype (YPM 7845) of *Palaeolithostrotion vaurealense* designated by Twenhofel (1928) occur in the upper Vauréal Formation of Anticosti Island (Bolton 1979, p. 7), of late Katian age (Desrochers *et al.* 2023), and only the former was originally figured externally. Thin sections of the types were first photographically illustrated by Bolton (1979, pl. 1.3, figs 4, 7–9), and those of a few hypotypes were also examined (Bolton 1972; Fedorowski & Jull 1976; Melzak 2004). According to these studies, *P. vaurealense* is characterised by having lateral increase, almost completely phaceloid to tollinaform/subcerioid coralla, long major septa with some uniting in the corallite centre, corallites ranging from 2.5–4.4 mm in diameter, well-developed minor septa, and strongly convex tabulae with wide central platform and sharply downturned margins. Its transfer to *Palaeolithostrotion* in this work is justified by the presence of phaceloid to tollinaform/subcerioid coralla, axially fused major septa, and generally arched tabulae.

Palaeophyllum sinclairi Caramanica, 1992, also established as a new species in Caramanica's (1973, unpublished PhD thesis), is based on the holotype (UND 13706) from the slightly older, upper Bighorn Formation (middle Katian–? basal upper Katian) of Bighorn Mountains, northern Wyoming, USA. It is characterised by lateral increase, small cateniform coralla with cerioid patches, small corallites (2.46–4.60 mm in diameter), 13–17 major septa "commonly extending to corallite axis and fusing about septal plane of bilateral symmetry", short but prominent minor septa, and convex tabulae with wide central platform, agreeing well with the concept of *Palaeolithostrotion vaurealense*. Therefore, *Palaeophyllum sinclairi* is regarded here as a probable synonym of the latter.

The material documented by Gierlowski & Langenheim (1985) as *Palaeophyllum humei* Sinclair, 1961 occurs in the similar stratigraphic level (Horseshoe Mountain Member of the Bighorn Formation) of the Sawmill Flats area, northern Wyoming. It differs from the true *P. humei* from the Farr Formation (lower Katian) of Ontario, discussed above, in having bilaterally arranged major septa with axial ends of some fused in places, and convex tabulae. Instead, it is almost identical to *Palaeolithostrotion vaurealense* and is best included in the latter species.

Palaeolithostrotion? *troedssoni* (Poulsen, 1941)

1928 *Columnaria* (*Palaeophyllum*) *stokesi* (Milne-Edwards & Haime); Troedsson, p. 111, pl. 27, fig. 1a–d.
1941 *Palaeophyllum troedssoni* Poulsen, pp. 11, 12, pl. 1, figs 9, 10.

Remarks. – This species comes from the Telychian Offley Island Formation at Cape Madison of western North Greenland (Poulsen 1941, p. 12), rather than the "Cape Calhoun beds" (Troedsson 1928, p. 111) of Ordovician age. It does not belong to *Columnaria* (*Palaeophyllum*) *stokesi* (Milne-Edwards & Haime, 1851), as initially identified by Troedsson (1928), since the true *stokesi* has since been recognised as a member of *Acinophyllum*, as discussed above. Consequently, Poulsen (1941) introduced the name *Palaeophyllum troedssoni* for this form and designated a specimen from the same level as the holotype, housed in the Mineralogical and Geological Museum of the University of Copenhagen without a registered number.

According to Troedsson (1928) and Poulsen (1941), key features include corallites with a maximum diameter of 8 mm, somewhat bilaterally arranged major septa that are occasionally fused at the corallite centre, long minor septa extending to half the corallite radius, and well-spaced, arched tabulae. The combination of septal and tabular characteristics supports its tentative placement within *Palaeolithostrotion*, though uncertainty surrounding its growth pattern renders this classification provisional.

Palaeolithostrotion radugini (Tcherepnina, 1960)

1936a *Columnaria halysitoides* Radugin, pp. 100, 101, pl. 2, fig. 12.
1936b *Columnaria* (?) *halysitoides* Radugin, pp. 44–46, fig. 17a, b.
1960 *Favistella radugini* Tcherepnina, p. 391, pl. O-11, fig. 3a, b.
?1963 *Palaeophyllum raduguini* Nelson, p. 32, pl. 6, fig. 7.
?1979 *Palaeophyllum raduguini* Nelson var.; Bolton & Nowlan, p. 6, pl. 3, figs 1, 2, 5.
?1985 *Palaeophyllum gracile* Flower; Pandolfi, p. 37, pl. 15, fig. 1, pl. 23, figs 1, 2.
?1985 *Palaeophyllum* sp. cf. *P. raduguini* Nelson; Pandolfi, pp. 38, 39, pl. 14, figs 1, 2, pl. 15, fig. 2.

Remarks. – The complex nomenclatural history of this species was presented by McLean & Copper (2013, p. 57), and is briefly outlined below. *Columnaria halysitoides* Radugin, 1936a, also introduced as a new species by Radugin (1936b), is based on the holotype numbered 504, with its repository remains to be confirmed. This specimen comes from the upper Amzas Formation of the Amzas River basin, Shoria Mountain. Tcherepnina (1960) renamed the species *Favistella radugini*, presumably because this specific name is preoccupied by *Columnaria halysitoides* Troedsson, 1928. Nelson (1963) later proposed the name *Palaeophyllum raduguini* as replacement since he believed that Radugin's species is attributable to *Palaeophyllum* and therefore homonymous with Wilson's (1926) form. Since both the names *radugini* and *raduguini* are "based simply

on different translations of the same Russian word, and are applied to the same original material" (McLean & Copper 2013, p. 57), Tcherepnina's new name has priority and should be retained.

Based on Radugin's (1936a, b) original description, *Palaeolithostrotion radugini* is characterised by somewhat cateniform growth habit with lateral increase, small mature corallites (3.5–4.0 mm in diameter), long major septa extending to the corallite centre with axial ends of some fused, short but prominent minor septa, and variably spaced tabulae (0.3–2.0 mm apart). These features support its present attribution to *Palaeolithostrotion*.

Possibly conspecific forms include *Palaeophyllum radugini* of Nelson (1963) from the middle Katian Churchill River Group of northern Hudson Bay Lowland and *Palaeophyllum raduguini* Nelson var. of Bolton & Nowlan (1979) from the rocks of similar age in the Keewatin area, as well as *Palaeophyllum gracile* Flower, 1961 and *Palaeophyllum* sp. cf. *P. raduguini* Nelson, 1963 *sensu* Pandolfi (1985) from the coeval Lost Canyon Member of the Ely Springs Dolomite of Nevada. Like Radugin's type material, exhibit a fasciculate to cateniform growth pattern, axially fused major septa, and short minor septa, with primary distinctions in corallite size and septal count. However, their conspecific status remains uncertain and requires further clarification through a comprehensive study of larger material.

Palaeolithostrotion macrocaule (Webby, 1972)

1972 *Palaeophyllum macrocaule* Webby, pp. 154, 155, pl. 9, figs 4–10.

Remarks. – *Palaeolithostrotion macrocaule* (holotype, SUP 43236) occurs in the uppermost Malachis Hill Formation (uppermost Katian) of the Bowan Park area, central NSW (Webby 1972, 1988; Wang *et al.* 2020). This species has a lateral increase, long major septa with one extending to the corallite centre in places and forming an "axial, columella-like structure", and convex, closely spaced tabulae (Ta5 = 8–13) (Webby 1972, p. 154, 155, pl. 9, figs 6, 8), supporting its transfer to *Palaeolithostrotion*. Other defining characteristics include variable corallite size (2.5–7.0 mm in diameter) and well-developed minor septa (Webby 1972).

Palaeolithostrotion voruense Lavrusevich, 1975

1975 *Palaeolithostrotion voruense* Lavrusevich, p. 34, pl. 2, fig. 2.
1991 *Palaeolithostrotion voruense* Lavrusevich; Lavrusevich, p. 24, pl. 53, fig. 2 [refig. Lavrusevich 1975, pl. 2, fig. 2].

Remarks. – *Palaeolithostrotion voruense* (holotype, UpG 1101/20) from the same strata and general area as the type species *P. zachonense* Lavrusevich, 1975, considered above. It closely resembles the latter in general aspects, and their major differences lie in the corallite size and septal number, as discussed above.

Palaeolithostrotion lyterion (Bolton, 1979)

1972 *Cyathophylloides* sp., Bolton, pl. 3, figs 2, 10.
1979 *Cyathophylloides lyterion* Bolton, p. 4, pl. 1.4, figs 1, 4, 6, 7.
1979 *Palaeophyllum clion* Bolton, p. 7, pl. 1.4, figs 2, 3, 5.
1981 *Palaeophyllum clion* Bolton; Bolton, pl. 2, figs 1, 2.
1981 *Cyathophylloides lyterion* Bolton; Bolton, pl. 2, figs 8, 9.
2004 *Palaeophyllum lyterion* (Bolton); Melzak, pp. 265–275, pl. 15, figs 1–8, pl. 16, figs 1–9, pl. 17, figs 1–5, pl. 18, figs 1–4.

Remarks. – The holotype of *Palaeolithostrotion lyterion* (GSC 61625) comes from the Prinsta Member of the Ellis Bay Formation (lower Hirnantian?) at Vauréal River, Anticosti Island, eastern Canada, whereas most of its paratypes (GSC 61626–61630) occur in the stratigraphically higher Laframboise Member (upper Hirnantian) of the same formation at Vauréal River or Salmon River of the same area. Note also that one of the paratypes (GSC 29588) is derived from the Mill Bay Member of the Vauréal Formation at the main highway of the island. This specimen was transferred by Melzak (2004) to *Palaeolithostrotion vaurealense* (Twenhofel, 1928), considered above.

In the holotype of this species, "curving major septa either almost reach the centre, frequently their tips joining in groups of two or three, or actually reach centre of corallite where the tips meet and twist slightly" (Bolton 1979, p. 4). This arrangement frequently displays clear bilateral symmetry (Bolton 1979, pl. 1.4, figs 1, 6). Other defining features include phaceloid to cerioid coralla with lateral increase, a mean corallite diameter of 3.3–5.3 mm, 15–18 major septa, long minor septa, and generally arched with a distinctive concave centre (Melzak 2004, p. 266). The combination of septal and tabular characteristics supports the reassignment of this species to *Palaeolithostrotion*, rather than *Palaeophyllum* suggested by previous authors (Melzak 2004; McLean & Copper 2013).

Palaeophyllum clion Bolton, 1979 (holotype, GSC 61646; paratypes, GSC 61647, 61648), from the same horizon and general locality as *Palaeolithostrotion lyterion*, was considered by Melzak (2004) as a junior synonym of the latter, with which I agree.

Palaeolithostrotion? sp. A

1995 *Palaeophyllum* sp., Young & Elias, pp. 101, 102, pl. 21, figs 1–14.

Remarks. – This species occurs in the lower Keel Formation (upper Hirnantian) of south–central Oklahoma and the coeval Kissenger Limestone Member of the Bryant Knob Formation of northeastern Missouri, east–central USA. According to Young & Elias (1995, pp. 101, 102), it possesses fasciculate to cateniform growth habit, corallites 2.2–4.2 mm in diameter, major septa typically 15–17 in number that "usually join together in pairs or in small groups at or near the axis", variably thick peripheral stereozone, and highly arched tabulae. Given the presence of a distinctive cardinal counter plane, which is occasionally joined by certain major septa, along with strongly arched tabulae, this species is likely to belong to *Palaeolithostrotion*. However, this attribution remains uncertain owing to its unknown mode of increase.

***Palaeolithostrotion*? sp. B**

2007 *Palaeophyllum cateniforme* Flower; Erina, p. 36, pl. 37, fig. 3a–c.

Remarks. – Initially described by Erina (2007) as *Palaeophyllum cateniforme* Flower, 1961, this species comes from the uppermost Archalyk Member (uppermost Katian; Ghobadi Pour *et al.* 2023) of the Shahriomon Formation in Zeravshan–Hissar. Major septa are "long, but only 2 or 3 reach up to the axis where they are fused and together with the tabulae occasionally form an axial structure" (Erina 2007, p. 36). One of the illustrations (Erina 2007, fig. 3a) clearly shows that four major septa are connected near the corallite centre, two of which appear to be cardinal and counter septa. This septal characteristic, combined with the generally arched tabulae, suggests that this form is likely to be reassigned to *Palaeolithostrotion*. However, the uncertainty surrounding its mode of increase makes this conclusion somewhat tentative, leading to the use of an open nomenclature. Other distinguishing features of this species large corallites (6–10 mm in diameter), weakly developed minor septa, and irregularly arched, widely spaced tabulae (Ta10 = 9–10).

***Palaeolithostrotion cumerense* (McLean & Copper, 2013)**

2010 "*Palaeophyllum*"; Nestor *et al.*, fig. 24a–d.
2012 *Palaeophyllum*; Copper & Jin, fig. 7h.
2013 *Palaeophyllum cumerense* McLean & Copper, pp. 60, 61, pl. 19, figs 1–9.

Remarks. – The type material of *Palaeolithostrotion cumerense* (holotype, GSC 129537; paratypes, GSC 134971) comes from the East Point Member (upper Aeronian) of the Menier Formation, Anticosti Island, eastern Canada. The paratype, enclosed in a stromatoporoid specimen bearing the type number GSC 127806, was previously illustrated by Nestor *et al.* (2010) and Copper & Jin (2012).

According to McLean & Copper (2013, p. 60), this species is characterised by mainly dendroid coralla, corallites 4–5 mm in diameter, major septa extending to the corallite centre or slightly withdrawn, weak minor septa, variably thick peripheral stereozone, and moderately to strongly convex tabulae. An additional feature that was not explicitly mentioned is the presence of a distinctive cardinal-counter plane, which may or may not be connected to the axial ends of other major septa, as shown in McLean & Copper (2013, pl. 19, figs 1–9). This characteristic, coupled with the commonly arched tabulae, warrants the reassignment of this species to *Palaeolithostrotion*.

Family Stauriidae Milne-Edwards & Haime, 1850

1850 Stauriidae Milne-Edwards & Haime, p. lxiv (*nom. correct.* Bronn 1860, p. 44, *pro* Stauridae Milne-Edwards & Haime).

Diagnosis. – Stauriida with phaceloid to cerioid coralla and septal parricidal increase. Dissepiments may occur, in 1–2 persistent or intermittent rows.

Definition. – Many previous authors adopted a broad concept of the family (or its synonyms) that includes a few forms lacking septal parricidal increase (Nicholson & Lydekker 1889; Zittel 1903, 1913; Hill 1956, 1981; Lin *et al.* 1995). Meanwhile, some grouped those with such a distinctive increase pattern as a separate family (Lavrusevich 1965; He & Li 1974, 1983; He 1980), or a subfamily of the Stauriidae *sensu lato* (Ivanovskiy 1965; He *et al.* 1989; Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013), the former of which is favoured herein due to the distinctiveness of the septal parricidal increase.

Note that the original incorrect spelling of the family (i.e. Stauridae) was corrected by Bronn (1860, p. 44) rather than Hill (1951, p. 13) as stated by some workers (e.g. Hill 1981; McLean & Copper 2013).

Generic composition. – Lavrusevich (1965) and Ivanovskiy (1965) placed *Stauria* Milne-Edwards & Haime, 1850 and *Ceriaster* Lindström, 1883 in the Stauriidae, with a subsequent addition of *Battersbyia* Milne-Edwards & Haime, 1851 by Ivanovskiy (1975). A few genera have since been further included based on the Silurian material of South China, including *Eostauria* He & Li, 1974, *Cystostauria* He & Li, 1974, *Parastauria* He & Li, 1974, *Fascistauria* He &

Li, 1974, *Neostauria* He, 1980, *Neoceriaster* He, 1980, *Paraceriaster* He, 1980, and *Massparaceriaster* Tang in Tang *et al.*, 2008b. However, uncertainty remains as to the identity of several (Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013).

In the present study, *Fletcheria* Milne-Edwards & Haime, 1850 and *Battersbyia* Milne-Edwards & Haime, 1851 are removed from the Stauriidae, as suggested by most previous authors. The former, with the type species *F. tubifera* from the Silurian of Gotland, Sweden, has axial parricidal increase (Stasińska 1967; Hill 1981), which led Ivanovskiy (1965) to synonymise it with *Ceriaster* Lindström, 1883. However, the increase of this form is of aseptal nature, and very different from that of stauriids. I therefore agree with its exclusion to either tabulates or tryplasmatid rugosans (Stasińska 1967; Ivanovskiy 1975; Hill 1981; Lin *et al.* 1988). *Battersbyia* has *B. inaequalis* from the Devonian of Teignmouth, UK, as its type species. Despite the limited knowledge of its type species, this genus has long been regarded as synonymous with *Fasciphyllum* Schlüter, 1885 (e.g. Hill 1981; Coen-Aubert 1992; Zhen 2007), a form unrelated to stauriids. This synonymy was recently reinforced by a re-examination of the lectotype thin sections of *B. inaequalis* by McLean (2018) and is also adopted in this study.

Among the genera assigned, the following are regarded here as valid, with synonyms indicated in square brackets: *Stauria* Milne-Edwards & Haime, 1850 [= *Neostauria* He, 1980], *Ceriaster* Lindström, 1883, *Eostauria* He & Li, 1974 [= *Fascistauria* He & Li, 1974], *Cystostauria* He & Li, 1974, *Parastauria* He & Li, 1974, *Paraceriaster* He, 1980, and *Massparaceriaster* Tang in Tang *et al.*, 2008b. In addition, two new genera, *Heina* and *Yuina*, are added to the Stauriidae. For a detailed discussion on their concept and scope, see remarks under them below.

Subfamily classification. – No attempts have thus far been made for a subdivision of the Stauriidae. In this study, three subfamilies, Stauriinae Milne-Edwards & Haime, 1850, Paraceriasterinae n. subfam. and Heininae n. subfam. are recognised, characterised by KAC, KA, and KLAC septal parricidal increase modes, respectively. Their generic composition is discussed under these taxa below.

Excluded species. – Several species were previously assigned to the Stauriidae based on the mistaken belief that their increase mode is of the same type, including the Ordovician forms *Palaeophyllum proliferum* Webby, 1972, and *P. jugatum* McLean & Webby, 1976, and the Silurian form *P. schuchertense* McLean, 1977. For detailed discussion about these taxa, see remarks on the Cyathophylloididae above.

Transferred species. – The following two species, both of early Silurian age, are reassigned to the Stauriidae, with their present revision indicated in square brackets.

Elizabethia occulta Sytova in Sytova & Ulitina, 1983, from the lower Alash Horizon (Rhuddanian; Sennikov *et al.* 2015) on the right bank of the Khemchik River, western Tuva [= *Parastauria occulta* (Sytova in Sytova & Ulitina, 1983)].

Elizabethia modica Sytova in Sytova & Ulitina, 1983, from the upper Alash Horizon (upper Rhuddanian–lower Aeronian; Sennikov *et al.* 2015) on the left bank of the Alash River, western Tuva [= *Parastauria modica* (Sytova in Sytova & Ulitina, 1983)].

Stauriids requiring revision. – The following stauriids remain inadequately unknown, and a critical revision is necessary to clarify their identity.

Stauria (?) *minor* Chen, 1959, refigured by Yu *et al.* (1963), is based on the material from strata now assigned to the lower member (lower Telychian; Rong *et al.* 2019) of the Wengxiang Formation in the Lushan area, eastern Guizhou (Chen 1959). This species has a fasciculate form, small corallites (1.6–2.0 mm in diameter), and moderately to strongly arched tabulae, and may be a synonym of *Paraceriaster fasciculatus* (Cao, 1975), considered below. However, without the knowledge of its increase mode, the identity of this species remains uncertain. In view also of the probable loss of its type material, this taxon is regarded here as *nomen dubium*.

Ceriaster calamites minor Cao, 1975 occurs in the "middle Ningqiang Group" (now probably the Wangjiawan Formation, lower Telychian) at Tianchiliang of the Nanzheng area, southwestern Shaanxi, the holotype of which is not traced for the present study. The key features include cerioid corallum, small corallites (1.5–2.0 mm in diameter), about 9–10 major septa in mature corallites, one intermittent series of dissepiments, and complete, axially arched, densely spaced tabulae (Ta5 = 12) (Cao 1975). The cerioid form and the development of one intermittent series of dissepiments led Tang *et al.* (2008b) to reassign this form to *Stauria*. However, I consider it here as *nomen dubium* since its increase pattern remains uncertain.

Stauria (*Ceriaster*) *hubeiensis* Wu in Jia & Wu, 1977, refigured by Liu (1984) and Zhu & Ma (2019), occurs in the Lojoping Formation (upper Aeronian) of Pingluo, Changyang area, southwestern Hubei Province. According to Wu in Jia & Wu (1977), it has small corallites (1.7–2.0 mm in diameter), 10–12 major septa connected in the corallite axis, well-developed minor septa (up to half the length of major septa), and complete, moderately spaced tabulae (about 10 in 5 mm). Considering that the increase

mode and tabular feature are still unknown and that its type material is probably lost, this species is treated here as *nomen dubium*.

Ceriaster minor (Chen, 1959) of Kong & Huang (1978) comes from the lower Shihniulan Formation (now upper Xiangshuyuan, lower Aeronian) at Wenjiadian, the Sinan area, northeastern Guizhou. It was said to have small corallites (1.5–2.0 mm in diameter), 13–14 major septa mostly extending to the corallite axis, short minor septa, and complete tabulae, and is likely to be synonymous with *Eostauria micropora*. However, the unclear illustrations cannot confirm its increase mode, and their synonymy remains uncertain.

Ceriaster weiganensis He & Huang in Kong & Huang, 1978 occurs in "the lower part of the lower member of the Shihniulan Formation" (now Xiangshuyuan Formation, upper Rhuddanian–lower Aeronian; Rong *et al*. 2019) at Weigan of Wengxi, southern Sinan area, northeastern Guizhou, with its knowledge entirely from the poorly documented holotype. This species has cerioid growth with "axial quadripartite increase" (Kong & Huang 1978, p. 65), small corallites (2–3 mm in diameter), 13–16 major septa with more than five meeting in the corallite axis, and complete, axially arched tabulae, and lacks dissepiments. Since the increase mode cannot be confirmed from unclear illustrations, and because features of minor septa and tabular spacing were not mentioned in the description, I regard this form as *nomen dubium*.

Stauria (*Ceriaster*) *hubeiensis* Wu in Jia & Wu, 1977 of Xiong & Gu (1978) was figured but not described from the Lojoping Formation (upper Aeronian) of Fenxiang, Yichang area, southwestern Hubei Province, with its increase mode and hence identity unknown.

Neoceriaster shiqianensis He, 1980, the type species of the genus, comes from the Leijiatun Formation (upper Aeronian) at Leijiatun, Shiqian area, northeastern Guizhou. Part of her type material was refigured by Lin *et al*. (1995). Based on He (1980), it may be synonymous with *Yuina columellata* (Ge & Yu, 1974) from the same horizon and locality. However, given that its increase pattern is uncertain, and that its type material is probably lost, this species is best treated as *nomen dubium*.

Ceriaster minor (Chen, 1959) *sensu* Jiang (1982), from "the lower Silurian" of Shimaxi, the Cili area, northwestern Hunan Province, was figured without description, and illustrations are insufficiently clear to make a proper identification.

Ceriaster minor (Chen, 1959) of Deng *et al*. (1983) occurs in "the lower Silurian" (now Chenxiacun Formation, upper Aeronian; Qian, 1978) of the Hanshan area, central–eastern Anhui Province. The increase mode of this form was neither mentioned in the description nor shown in illustrations, and a revision is needed.

Paraceriaster sp. of Tang (2006), from the Shihniulan Formation of Dongkala, the Fenggang area, northern Guizhou, lacks data on its increase, and hence requires a further study.

Subfamily Stauriinae Milne-Edwards & Haime, 1850

1850 Stauriinae Milne-Edwards & Haime, p. lxiv (*nom. transl.* Ivanovskiy 1965, p. 81, *ex* Stauridae Milne-Edwards & Haime).

Revised diagnosis. – Stauriidae with septal parricidal increase mode occurring at the counter, two alar, and cardinal septa (i.e. KAC septal parricidal increase).

Remarks. – Based on the revised concept, the following genera are considered as members of the Stauriinae: Stauria Milne-Edwards & Haime, 1850 [= *Neostauria* He, 1980], *Eostauria* He & Li, 1974 [= *Fascistauria* He & Li, 1974], and *Cystostauria* He & Li, 1974.

Paraceriaster He, 1980 was considered by McLean & Copper (2013) as a junior synonym of *Fascistauria* (= *Eostauria* He & Li, 1974; this study). However, as demonstrated below, its type species, *P. daguanensis* He, 1980 [= *P. major* (Fan in He, 1978); this study], shows a KA septal parricidal increase, and this justifies the validity of this genus and a transfer to Paraceriasterinae n. subfam., considered below.

Genus *Stauria* Milne-Edwards & Haime, 1850

1850 *Stauria* Milne-Edwards & Haime, p. 64.
1980 *Neostauria* He, p. 34.

Type species. – *Stauria astreiformis* Milne-Edwards & Haime, 1850 (= *Madrepora favosa* Linnaeus, 1758), "Stage f" (Lindström 1888), now belonging to the lower Slite Group of late Sheinwoodian (Wenlock) age (Calner *et al*. 2004), Gotland, Sweden, by original designation.

Diagnosis. – Stauriinae with cerioid to partly fasciculate coralla. Dissepiments are present, in 1–2 persistent or intermittent series.

Remarks. – *Neostauria* He, 1980 was proposed for *Stauria*-like forms but with persistent, solid columellae, with *Madrepora favosa* Linnaeus, 1758 selected as its type species. However, this species has been widely considered as synonymous with the type species of

Stauria, *S. astreiformis* Milne-Edwards & Haime, 1850, as discussed below under *S. favosa*, and *Neostauria* is as a result a junior synonym of *Stauria*.

Prior to the 1960s, *Ceriaster* Lindström, 1883 was regarded as a junior synonym of *Stauria* (e.g. Hill 1956) or a subgenus of the latter (e.g. Wang 1950), but later elevated to a full genus rank and believed to differ from *Stauria* by the lack of dissepiments (Yu 1963; Lavrusevich 1965; Ivanovskiy 1965), a view widely followed (Hill 1981; Lin *et al.* 1995; He & Tang 2013; McLean & Copper 2013). In this work, *Ceriaster* is viewed as a valid member of Paraceriasterinae n. subfam. due to its KA septal increase pattern.

Parastauria He & Li, 1974, with the type species *P. polygonalis* He & Li, 1974 from the Shihniulan Formation (upper Aeronian) of the Meitan area, northern Guizhou, was considered by McLean & Copper (2013) as a probable synonym of *Stauria*. However, due to its KLAC septal increase mode, this genus is removed here to the Heininae n. subfam., considered below.

Stauria is separable from the other two genera of the subfamily (i.e. *Eostauria* He & Li, 1974 and *Cystostauria* He & Li, 1974) by being cerioid. *Eostauria* further differ in lacking dissepiments.

Stauria favosa (Linnaeus, 1758)

1745 *Madrepora aggregata* Fougt; Linnaeus, pp. 26, 27, fig. 16.
1758 *Madrepora favosa* Linnaeus, p. 796.
1850 *Stauria astreiformis* Milne-Edwards & Haime, p. lxiv.
1851 *Stauria astreiformis* Milne-Edwards & Haime, p. 316, pl. 1, figs 1, 1a–d.
1879 *Stauria astreiformis* Milne-Edwards & Haime; Zittel, fig. 145 [refig. Milne-Edwards & Haime 1851, fig. 1c].
1883 *Stauria favosa* (Linnaeus); Koch, pp. 329, 330, pl. xli, figs 12–16, pl. xliii, fig. 30.
1889 *Stauria astreiformis* Milne-Edwards & Haime; Nicholson & Lydekker, text-figs 151 [refig. Milne-Edwards & Haime 1851, fig. 1a], 152.
1903 *Stauria astreiformis* Milne-Edwards & Haime; Zittel, fig. 133 a–c [a, c, refig. Milne-Edwards & Haime 1851, fig. 1c, a; b, refig. Nicholson & Lydekker 1889, text-fig. 152].
1927 *Stauria favosa* (Linnaeus); Smith & Ryder *pars*, pl. 9, fig. 4, text-fig. 2, *non* pl. 9, figs 1–3.
1950 *Stauria favosa* (Linnaeus); Bassler, pl. 19, fig. 3.
1981 *Stauria favosa* (Linnaeus); Hill, fig. 68, 1a, b.
1995 *Stauria favosa* (Linnaeus); Lin *et al.*, fig. 125a, b [refig. Hill 1981, fig. 68, 1b, a].
2004 *Stauria favosa* (Linnaeus); Ezaki & Yasuhara, text-figs 3–5, 7, 8, 10, 11, 14–16.
2005 *Stauria favosa* (Linnaeus); Ezaki & Yasuhara, figs 2–5.

Remarks. – As pointed out by Lindström (1895), *Stauria astreiformis* Milne-Edwards & Haime 1850 originally included material not only from the Silurian of Gotland but also from the Chazy Limestone of North America, without a designated type. For this reason, Lang *et al.* (1940, p. 122) selected the Gotland specimen illustrated by Milne-Edwards & Haime (1851, pl. 1, fig. 1) as its lectotype to refer "solely to the Baltica fossil". *Stauria astreiformis* was consequently widely regarded as a junior synonym of *Madrepora favosa* Linnaeus, 1758 (e.g. Hill 1981; Lin *et al.* 1995; Ezaki & Yasuhara 2004, 2005). The synonymy of the two species seems very likely, although types of both have not been traced for confirmation (Hill 1981, p. F133).

Stauria favosa is known to have a limited stratigraphic distribution. According to Lindström (1888), this form is restricted to "Stage f" of Gotland, Sweden, a level now referred to the lower Slite Group of late Sheinwoodian (Wenlock) age (Calner *et al.* 2004).

Stauria favosa was previously described by many authors (Milne-Edwards & Haime 1850; Koch 1883; Nicholson & Lydekker 1899; Smith & Ryder 1927; Hill 1981; Ezaki & Yasuhara 2004, 2005). According to Ezaki & Yasuhara's (2004) summary, the species is typified by having cerioid to partly fasciculate coralla, typical KAC septal parricidal increase, corallites of up to 6.0 mm in diameter, up to 25 major septa with four protosepta (i.e. counter, two alar and cardinal septa) meeting in the corallite axis and forming a prominent cross-shaped structure, 1–2 rows of dissepiments, and mostly complete tabulae.

Among the *Stauria* species, only *Stauria qijiangensis* He, 1980, considered below, from the much older, Shihniulan Formation (upper Aeronian) of the Qijiang area, southern Chongqing, exhibits similar septal development, but is distinguished by having smaller corallites [ACDs (6+) = 2.48–4.94 mm], and weaker development of dissepiments which occur only in one single intermittent series.

The material previously described by Smith & Ryder (1927) as *Stauria favosa* contains a specimen BM-R23801 from the "Silurian, Rejio, east of Angelin". This fossil shows a similar KAC septal parricidal increase mode but has a phaceloid form, and is therefore identified here as *Cystostauria* sp. A, considered below.

Stauria qijiangensis He, 1978

(Figs 48, 49)

1978 *Stauria qijiangensis* He, p. 142, pl. 71, fig. 1a, b.
1980 *Stauria qijiangensis* He; He, p. 38, pl. 1, fig. 3a, b [refig. He 1978, pl. 71, fig. 1a, b].
1980 *Ceriaster guanyinqiaoensis* He, p. 41, pl. 1, fig. 2a, b.

Referred material. – NMRFC-Scr650, holotype, original of He (1978, pl. 71, fig. 1a, b), refigured here (Fig. 48). NMRFC-Scr792, holotype of *Ceriaster guanyinqiaoensis* He, 1980, original of He (1980, pl. 1, fig. 2a, b), refigured here (Fig. 49). Both specimens from the Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

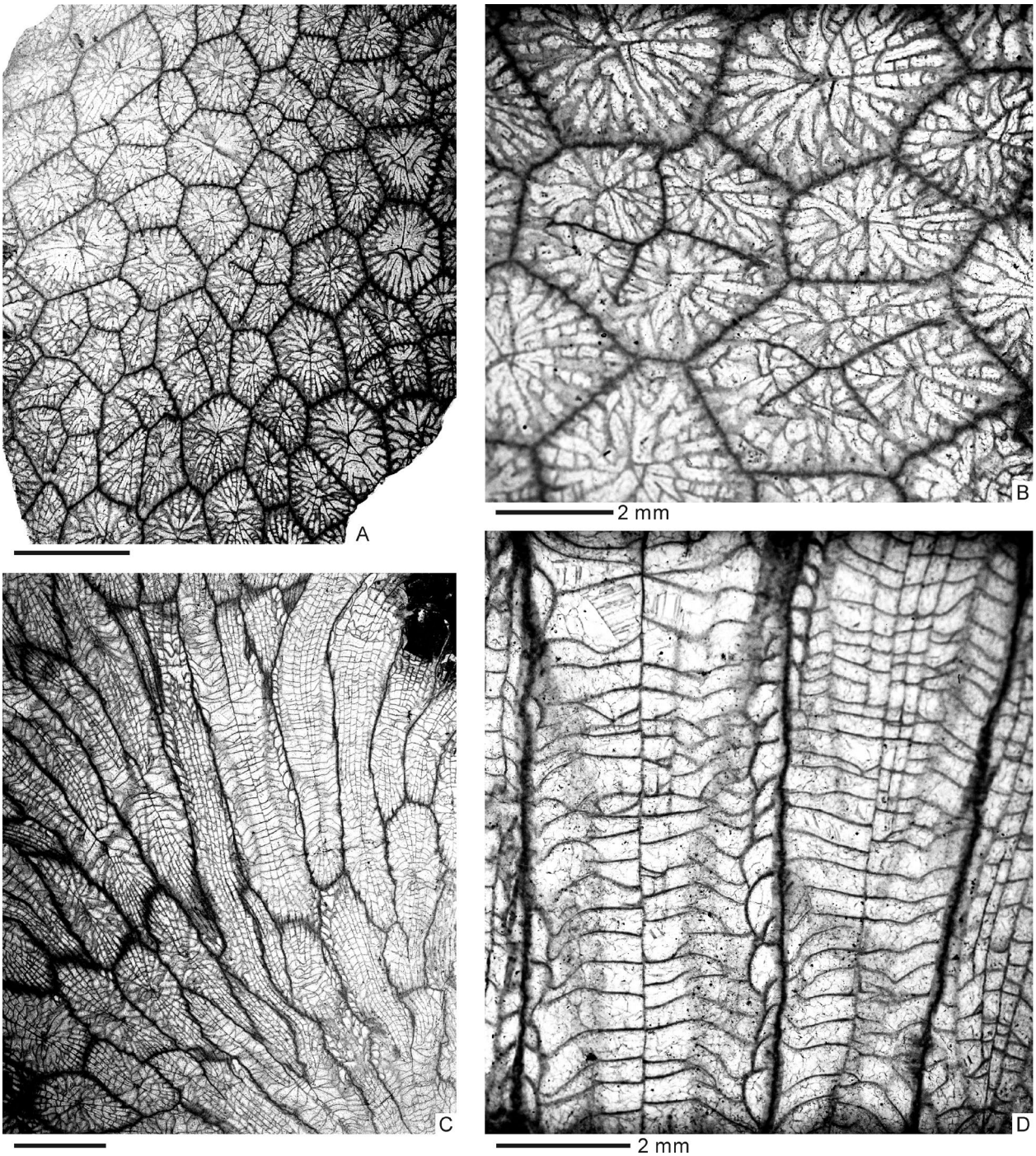


Fig. 48. Stauria qijiangensis He, 1978. NMRFC-Scr650, holotype, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B,** TS and an enlarged portion; **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Diagnosis. – *Stauria* species with medium to large-sized corallites [ACDs (6+) = 2.48–4.94 mm]. Four protosepta (i.e. counter, two alar and cardinal septa) meeting in the corallite axis and forming a cross-shaped structure. Dissepiments uncommon to almost absent, globose to subglobose, in one intermittent row.

Description. – Modified from He (1978, p. 142; 1980, pp. 38, 41). The external size and shape of coralla

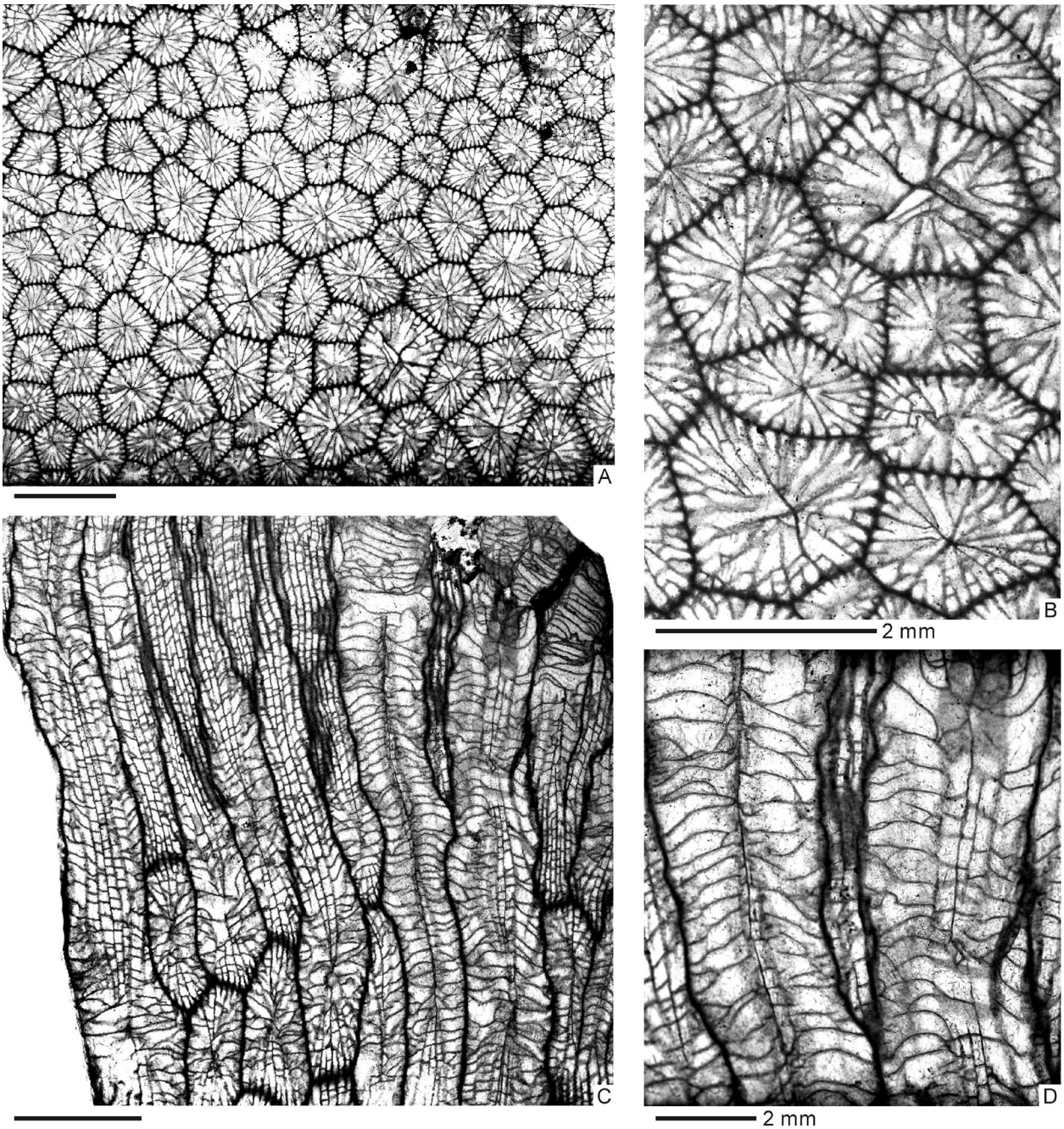


Fig. 49. Stauria qijiangensis He, 1978. NMRFC-Scr792, holotype of *Ceriaster guanyinqiaoensis* He, 1980, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B,** TS and an enlarged portion; **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

unknown. Increase of typical KAC septal parricidal type. Corallites polygonal, 4–8 sided, medium to large-sized [ACDs (6+) = 2.48–4.94 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders. Major septa 16–18 in number, long, with four protosepta (i.e. counter, two alar and cardinal septa) meeting in the corallite axis and forming a cross-shaped structure. Minor septa well developed, long, up to 1/2 of corallite radius. Dissepiments uncommon to almost absent, globose to subglobose, in one intermittent row. Tabulae complete or rarely incomplete, slightly arched, with a wide, flat or slightly concave platform, well-spaced (Ta5 = 10–13).

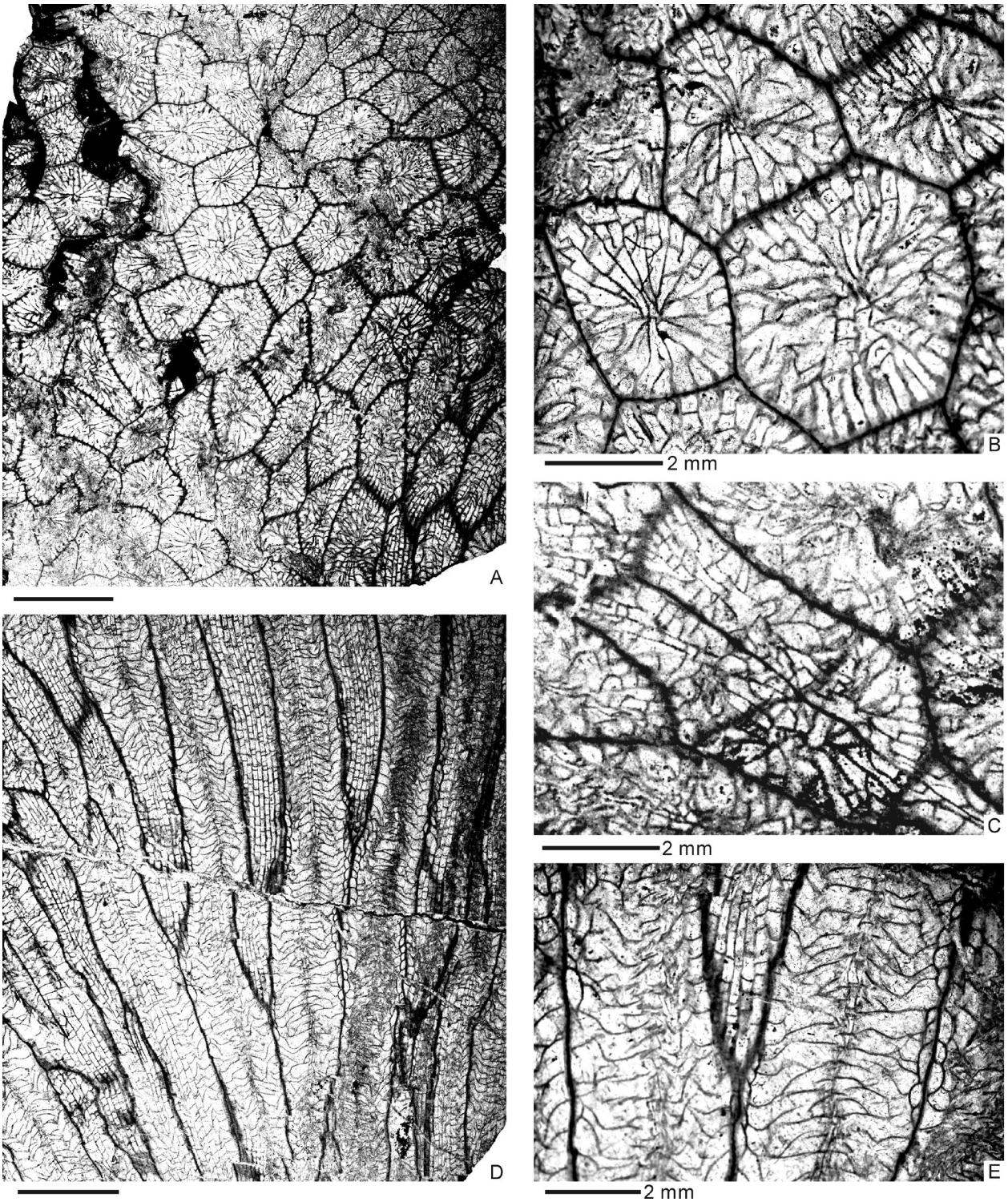


Fig. 50. Stauria tenuisepta He, 1980. NMRFC-Scr794, holotype, Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Remarks. – The revised diagnosis and description given above are based on the holotypes of *Stauria qijiangensis* He, 1980 and *Ceriaster guanyinqiaoensis* He, 1980, both from the Shihniulan Formation (upper Aeronian) of the Qijiang area, southern Chongqing. As noted by He (1980, p. 41), the major difference lies in "the absence of dissepiments" of *Ceriaster guanyinqiaoensis*. However, although rare, dissepiments are in fact present in this species (Fig. 49C, D), thus justifying their synonymy.

Stauria tenuisepta He, 1980, from the coeval Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, shows closest similarities to *S. qijiangensis*. It has comparable corallite size [ACDs (6+) = 2.82–5.03 mm] and dissepimental development but can be separated by possessing many more major septa that are connected in the corallite axis and hence lacking a prominent cross-shaped axial structure.

Stauria favosa Linnaeus, 1758, from the lower Slite Group (upper Sheinwoodian) of Gotland, resembles *S. qijiangensis* particularly in the development of a prominent cross-shaped axial structure, differing in having larger corallites (up to 6.0 mm in diameter) and better development of dissepiments, as also discussed above.

***Stauria tenuisepta* He, 1980**

(Fig. 50)

1980 *Stauria tenuisepta* He, p. 41, pl. 1, fig. 4a, b.
2006 *Stauria sinensis* (He & Huang); Tang, p. 156, pl. 28, fig. 2a–c, pl. 32, fig. 4a, b.
2008b *Stauria sinensis* (He & Huang); Tang *et al*., p. 435, pl. 1, fig. 2a–c [refig. Tang 2006, pl. 28, fig. 2a–c].

Referred material. – NMRFC-Scr794, holotype, original of He (1980, pl. 1, fig. 4a, b), refigured here (Fig. 50), Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China.

Diagnosis. – *Stauria* species with medium to large-sized corallites [ACDs (6+) = 2.82–5.03 mm]. Major septa 16–20 in number, long, generally meeting in the corallite axis. without forming a prominent columella. Four protosepta (i.e. counter, two alar and cardinal septa) occasionally meeting in the corallite axis, forming a cross-shaped structure (Fig. 50C). Dissepiments moderately developed in one intermittent series. Tabulae complete or rarely incomplete, slightly arched, with a wide, flat or slightly concave platform, well-spaced (Ta5 = 11–14).

Description. – Modified from He (1980, p. 41). The external size and shape of the holotype unknown. Increase of KAC septal parricidal type. Corallites polygonal, 4–8 sided, medium to large-sized [ACDs (6+) = 2.82–5.03 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders. Major septa 16–20 in number, long, generally meeting in the corallite axis without forming a prominent columella. Four protosepta (i.e. counter, two alar and cardinal septa) occasionally meeting in the corallite axis, forming a cross-shaped structure (Fig. 50C). Minor septa well developed, relatively long, up to 1/4–1/3 of corallite radius. Dissepiments moderately developed, globose to subglobose, in one intermittent series. Tabulae complete or rarely incomplete, slightly arched, with a wide, flat or slightly concave platform, well-spaced (Ta5 = 11–14).

Remarks. – The diagnosis and description of *Stauria tenuisepta* given above are based on its holotype. *Stauria sinensis* (He & Huang in Kong & Huang, 1978) *sensu* Tang (2006) and Tang *et al*. (2008b), from the same formation at nearby Baisha of the Shiqian area, was stated to primarily exhibit a "quadripartite parricidal increase", as also clearly shown in their illustrations (Tang 2006, p. 156, pl. 28, fig. 2a; Tang *et al*. 2008b, p. 435, pl. 1, fig. 2a). This characteristic supports its inclusion within *Stauria*, revised herein. However, it is clearly not true *Stauria favosa sinensis* He & Huang in Kong & Huang, 1978, since the latter has a pentapartite increase mode and is now treated as synonymous with *Parastauria leijiatunensis* (Ge & Yu, 1974), revised below. Instead, the form described by Tang (2006) and Tang *et al*. (2008b) as *Stauria sinensis* is regarded as synonymous with *Stauria tenuisepta* in view of their striking morphological similarities.

Closest similarities lie with *Stauria fonganensis* He & Li, 1983, from the lower Shihniulan Formation (upper Aeronian), Dongkala, Fenggang area, northern Guizhou, which has comparable septal number and length. However, it is separable by having much larger corallites [ACDs (6+) = 5.75–7.71 mm], and better development of dissepiments generally occurring 1–2 persistent series.

***Stauria fonganensis* He & Li, 1983**

(Fig. 51)

1983 *Stauria fonganensis* He & Li, pp. 394, 395, pl. 2, fig. 2a, b.

Referred material. – NMRFC-KS8011 (TS) and NMRFC-KS8012 (one TS and one LS), holotype, original of He & Li (1983, pl. 2, fig. 2a, b), refigured here (Fig. 51), lower Shihniulan Formation (upper Aeronian), Dongkala, Fenggang area, northern Guizhou, southwestern China.

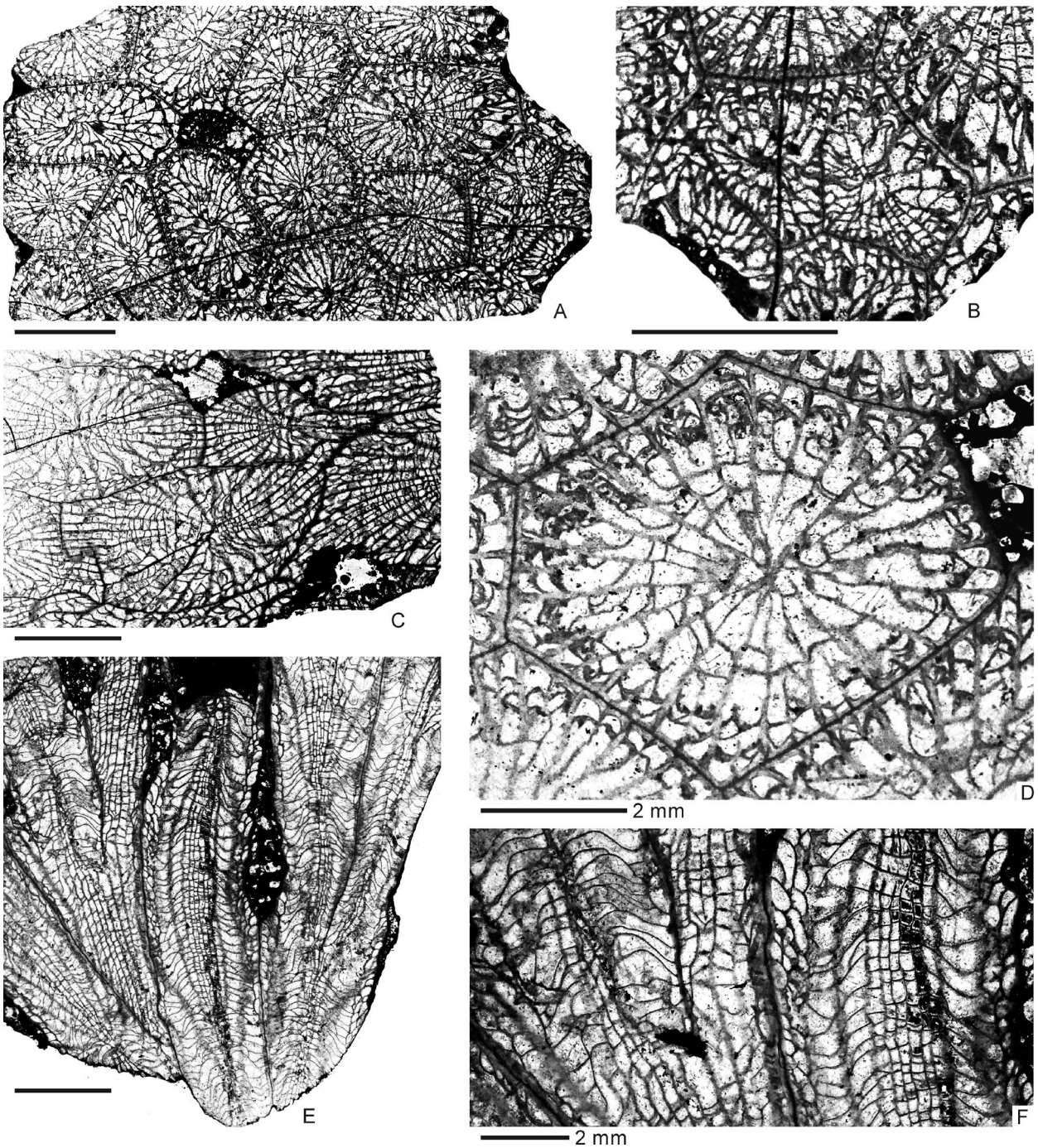


Fig. 51. Stauria fonganensis He & Li, 1983. NMRFC-KS8011 (TS) and NMRFC-KS8012 (one TS and one LS), holotype, lower Shihniulan Formation (upper Aeronian), Dongkala, Fenggang area, northern Guizhou, southwestern China. **A–D**, TSs (**A, C**) and two enlarged portions of **A** (**B, D**); **E, F,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Diagnosis. – *Stauria* species with large corallites [ACDs (6+) = 5.75–7.71 mm], and 1–2 rows of dissepiments.

Description. – Modified from He & Li (1983, pp. 394, 395). The external size and shape of the holotype unknown. Increase of KAC septal parricidal type. Corallites polygonal, 4–8 sided, large [ACDs (6+) = 5.75–7.71 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders. Major septa 22–25 in number, long, generally meeting in the corallite axis without forming a prominent columella. Minor septa relatively short, up to 1/4 of corallite radius. Dissepiments well-developed, globose to subglobose, in 1–2 series. Tabulae complete or incomplete, slightly to moderately arched, with a wide, flat or slightly concave platform, closely spaced (Ta5 = 9–14).

Remarks. – The present revision of *Stauria fonganensis* is based on a restudy of its holotype. *Stauria tenuisepta* He, 1980, considered above, from the coeval Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, closely resembles *S. fonganensis* in septal development, but differs in having significantly smaller corallites [ACDs (6+) = 2.82–5.03 mm] and weaker development of dissepiments consisting of only one single intermittent series (see also remarks on *Stauria tenuisepta*, above).

Another similar form is *Stauria favosa* Linnaeus, 1758, from the lower Slite Group (upper Sheinwoodian) of Gotland, Sweden. This species has similar septal number (up to 25) and dissepimental development. However, a combination of smaller corallites (up to 6.0 mm in diameter) and only four major septa meeting in the corallite axis to form a prominent cross-shaped axial structure distinguishes it from *S. fonganensis*, the latter having additional prominent major septa that meet in the axis (Fig. 51B–D).

Stauria sp. nov. of Scrutton & Deng, 2002

(Figs 52, 53)

1996 *Stauria leijiatunensis* He; Deng & Scrutton, pl. 12, figs 3, 4.
2002 *Stauria* sp. nov. Scrutton & Deng, fig. 80M, N [refig. Deng & Scrutton 1996, pl. 12, figs 3, 4].

Referred material. – NIGP 205572, formerly figured by Deng & Scrutton (1996) as *Stauria leijiatunensis* He, 1980 and refigured by Scrutton & Deng (2002) as *Stauria* sp. nov., original of Deng & Scrutton (1996, pl. 12, figs 3, 4), refigured here (Fig. 52); NIGP 205573, new specimen from Deng & Scrutton's collection,

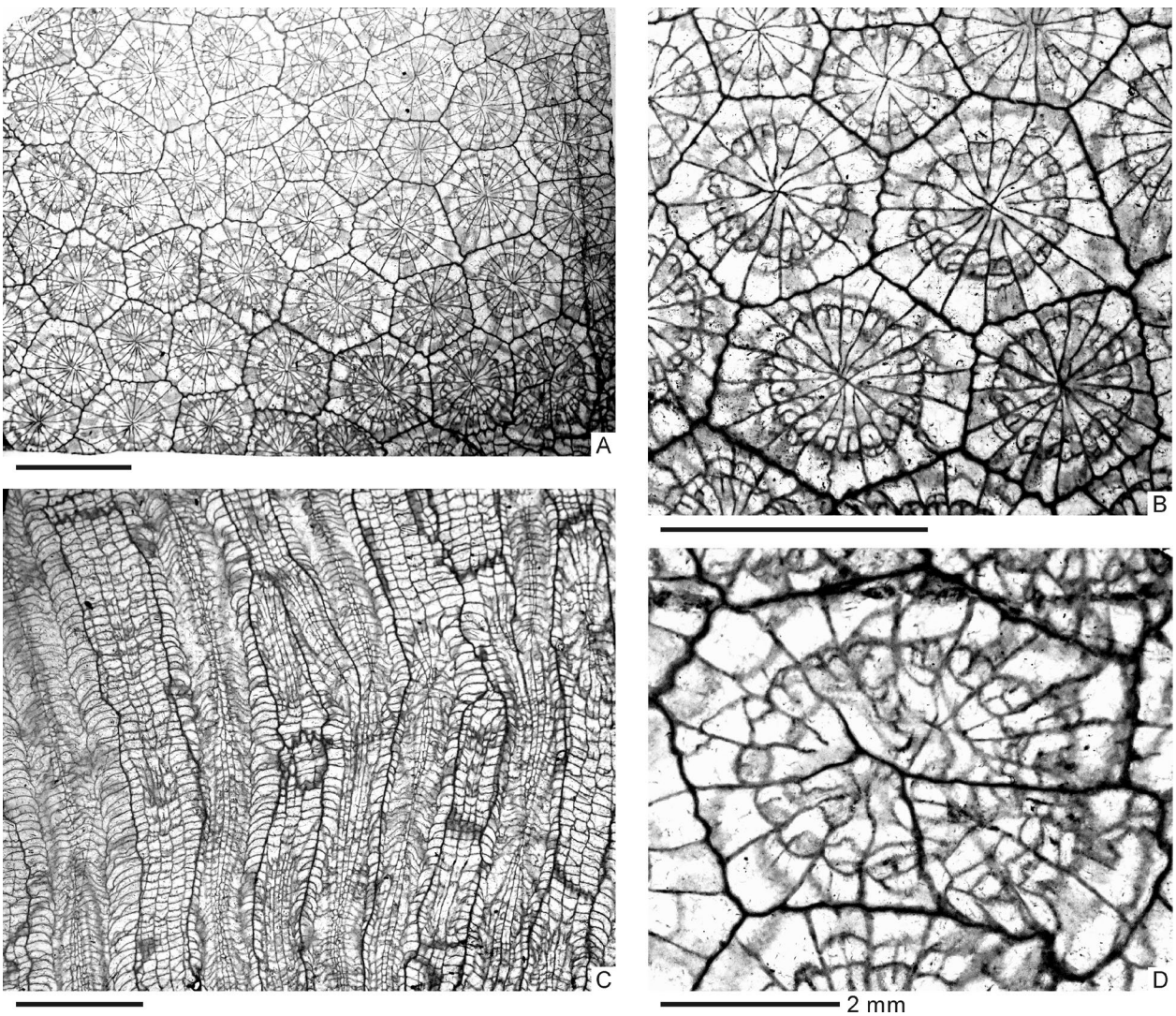


Fig. 52. Stauria sp. nov. of Scrutton & Deng (2002). NIGP 205572, described previously by Deng & Scrutton (1996) as *Stauria leijiatunensis* He, 1980, Shihniulan Formation (upper Aeronian), Hanjiadian, Tongzi area, northern Guizhou, southwestern China. **A, B, D,** TS and two enlarged portions; **C,** LS. Scale bars are 5 mm unless otherwise indicated.

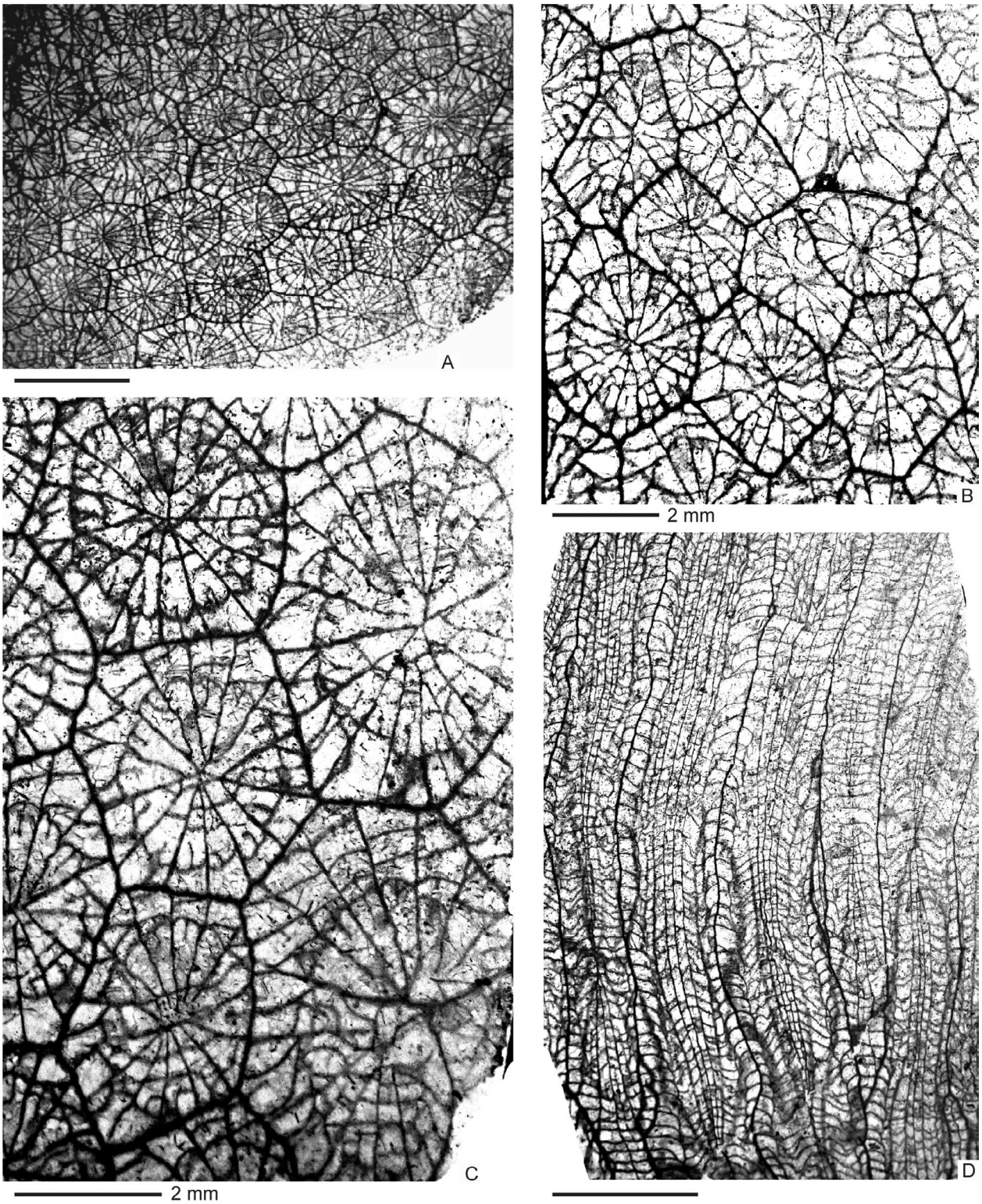


Fig. 53. Stauria sp. nov. of Scrutton & Deng (2002). NIGP 205573, new specimen, Shihniulan Formation (upper Aeronian), Hanjiadian, Tongzi area, northern Guizhou, southwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

figured here (Fig. 53). Both specimens come from the Shihniulan Formation (upper Aeronian), Hanjiadian, Tongzi area, northern Guizhou, southwestern China.

Description. – The external size and shape unknown. Increase of KAC septal parricidal type. Corallites polygonal, 4–9, commonly 6–7 sided, medium to large-sized [ACDs (6+) = 3.09–5.58, commonly 4.84–5.05 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders. Major septa 13–18, commonly 15–16 in number, long, extending to, or close to, the corallite axis, with four protosepta (i.e. counter, two alar, and cardinal septa) and sometimes more meeting in the corallite axis but without forming a prominent columella. Minor septa well developed, relatively long, generally extending slightly beyond the dissepimentarium, up to 1/2 of corallite radius. Dissepiments moderately developed, globose to subglobose, in one almost persistent series. Tabulae complete or rarely incomplete, slightly arched, with a wide, flat or slightly concave platform, moderately to closely spaced (Ta5 = 11–18).

Remarks. – Apart from the specimen figured by Deng & Scrutton (1996) and refigured by Scrutton & Deng (2002), a further one from the same horizon and locality is used for the present revision of this species. This form is clearly distinct from *Stauria leijiatunensis* He, 1980 from the Leijiatun Formation (upper Aeronian) of northeastern Guizhou, which follows a KLAC septal parricidal increase and is reassigned in this study to *Parastauria* (see discussion under that species, below).

This species shows closest similarities to *Stauria qijiangensis* He, 1978, revised above, in general aspects, but appears to be separable by having almost persistent dissepiments. Therefore, it is viewed as a distinct species, but is placed in open nomenclature because the possibility that the two species are synonymous cannot be completely ruled out.

Genus *Eostauria* He & Li, 1974

1963 *Eostauria* He & Li, pp. 55, 56 *nomen nudum*.
1974 *Ceriaster* (*Eostauria*) He & Li, pp. 4, 5.
1974 *Fascistauria* He & Li, pp. 10, 11.
1983 *Ceriaster* (*Eostauria*) He & Li, pp. 392, 393.
1989 *Eostauria* He & Li; Wang & Chen, p. 37.

Type species. – *Ceriaster* (*Eostauria*) *micropora* He & Li, 1974, "lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Fengxiang, Shiqian area, northeastern Guizhou, southwestern China, by original designation.

Diagnosis. – Like *Stauria* but having fasciculate growth form and lacking dissepiments. Tabulae complete to partly incomplete, which are locally differentiated into axial and peripheral zones.

Remarks. – *Eostauria* was first mentioned by He & Li (1963) as a new genus but without accompanying description and illustration. When formally established later (He & Li 1974, 1983), *Eostauria* was treated as a subgenus of *Ceriaster* Lindström, 1883, but is now widely accepted as an independent genus (Wang & Chen 1989; Lin *et al.* 1995; Tang *et al.* 2008a, b; He & Tang 2013; McLean & Copper 2013).

Eostauria was initially proposed to accommodate forms like *Ceriaster* Lindström, 1883 but having fasciculate growth form. With the subsequent recognition of taxonomic importance of differentiation of tabulae into axial and peripheral zones, this genus was restricted to species with complete, non-differentiated tabulae (Lin *et al.* 1995; Tang *et al.* 2008a, b; He & Tang 2013). However, as demonstrated below, incomplete tabulae that are well differentiated into axial and peripheral zones are present locally in the type species, *E. micropora* He & Li, 1974. This observation obscures the generic significance of such a tabular feature. Instead, the significance of increase modes is highlighted in this study, and *Eostauria* is revised here as consisting of forms with fasciculate growth and a KAC septal parricidal increase pattern, no matter whether tabulae are differentiated or not.

Fascistauria He & Li, 1974, with the type species *F. queizhouensis* He & Li, 1974 [= *Eostauria prolifera* (Yin, 1944)], is from "the lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian) of Pugou, the Shiqian area, northeastern Guizhou. This genus was originally proposed to embrace *Eostauria*-like forms with prominent axial connection of four major septa. Later, the differentiation of its tabulae into axial and peripheral zones was considered taxonomically more significant, and *Fascistauria* was consequently widely accepted as a synonym of *Paraceriaster* He, 1980 (e.g. He & Li 1974, 1983; He *et al.* 1989; Tang *et al.* 2008a. b; Lin *et al.* 1995; He & Tang 2013; McLean & Copper 2013). However, if the feature of increase is considered, *Fascistauria*, which has a KAC increase mode, agrees well with the revised concept of *Eostauria*, discussed above. Rather, *Paraceriaster*, with the type species *P. daguanensis* He, 1980 [= *P. major* (Fan in He, 1978); this study] from the Sifengya Formation (lower Telychian) of the Daguan area, northeastern Yunnan, has a very different, KA septal parricidal increase pattern, and is included in Paraceriasterinae n. subfam.

Neoceriaster He, 1980 has *N. shiqianensis* He, 1980, from the Leijiatun Formation of the same age at Leijiatun, Shiqian area, northeastern Guizhou, as its type species. This species resembles the type species of *Eostauria*, *E. micropora*, particularly in the well-differentiated tabulae, which led some workers (Tang 2006; Tang *et al*. 2008a, b; McLean & Copper 2013) to synonymise *Neoceriaster* with *Eostauria*. However, *Neoceriaster* is regarded here as *nomen dubium* in view of the uncertainty as to its increase mode (see also remarks under the latter, below).

Several Ordovician and (or) Silurian forms resemble *Eostauria* in being fasciculate and non-dissepimented. *Palaeophyllum* Billings, 1858a is distinguished by having a lateral, non-parricidal increase pattern. *Paraceriaster* He, 1980 and *Yuina* n. gen. differ from *Eostauria* in having KA and KLAC septal parricidal increase modes, respectively.

Eostauria has now proven to be an exclusively Silurian form from the Llandovery strata in South China and South Tien Shan, as discussed elsewhere in this study. Several Ordovician or Silurian species previously assigned to *Eostauria* should be excluded due to the absence of septal parricidal increase characteristic of stauriids. They include *Palaeophyllum proliferum* Webby, 1972, *P. jugatum* McLean & Webby, 1976, and *P. schuchertense* McLean, 1977 (He & Chen 2004; Tang *et al*. 2008a, b; McLean & Copper 2013) (see remarks on the Cyathophylloididae, above).

Eostauria prolifera (Yin, 1944)

(Figs 54, 55)

1944 *Stauria prolifera* Yin, pp. 16–19, pl. 1, figs 1–4.
1955 *Stauria prolifera* Yin; Wang *et al*., p. 26, pl. 22, figs 4, 5 [refig. Yin 1944, pl. 1, figs 2, 1].
1963 *Stauria prolifera* Yin; Yu *et al*., p. 153, pl. 42, fig. 4a, b [refig. Yin 1944, pl. 1, figs 1, 2].
1974 *Stauria prolifera* Yin; He & Li, p. 8, pl. 5, fig. 1a, b. non 1974 *Stauria* aff. *prolifera* Yin; He & Li, pp. 8, 9, pl. 5, fig. 3a, b.
1974 *Fascistauria queizhouensis* He & Li, pp. 10, 11, pl. 2, fig. 2a–c.
1978 *Ceriaster shiniulanensis* He, p. 143, pl. 71, fig. 4a–c.
1978 *Stauria prolifera* Yin; Kong & Huang, p. 63, pl. 21, fig. 6a, b.
1980 *Ceriaster shiniulanensis* He, p. 41, pl. 4, fig. 2a, b.
1983 *Paraceriaster queizhouensis* (He & Li); He & Li, p. 394, pl. 2, fig. 4a, b [refig. He & Li 1974, pl. 2, fig. 2a, b?], text-fig. 2a, b.
1989 *Stauria prolifera* Yin; He *et al*., p. 91, pl. 3, fig. 10, pl. 27, figs 1–4.
?2006 *Paraceriaster queizhouensis* (He & Li); Tang, pl. 30, fig. 4.

Referred material. – NMRFC-KS008 (TS/LS) and NMRFC- KS009 (TS/LS), holotype (not traced), Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Pugou, Shiqian area, northeastern Guizhou. NMRFC-Scr653, holotype of *Ceriaster shiniulanensis* He, 1978, original of He (1978, pl. 71, fig. 4a–c), refigured here (Fig. 54); NMRFC-Scr804, described by He (1980) as *Ceriaster shiniulanensis* He, 1978, original of He (1980, pl. 4, fig. 2a, b), refigured here (Fig. 55); both specimens from the Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang area, southern Chongqing, southwestern China. Note that the transverse section figured as Fig. 55C, D was probably mislabelled by He (1980) as "Scr804", which probably belongs to *Eostauria qijiangensis* (He, 1980), considered below, whose holotype (NMRFC-Scr805) originates from the same horizon and locality.

Diagnosis. – *Eostauria* with fasciculate to partially cerioid coralla, mature corallites 3.76–4.49 mm in diameter, a distinct peripheral stereozone, 18–20 major septa mostly extending to the corallite axis, short minor septa, and partly incomplete tabulae that are moderately arched and differentiated into peripheral and axial zones.

Description. – Modified from He (1978, p. 143; 1980, p. 41). Corallum fasciculate to partially cerioid, with external size and shape unknown. Increase of KAC septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 3.76–4.49 mm. Marginarium a narrow but distinct peripheral stereozone, composed of peripheral septal ends and lamellar stereome, with a maximum thickness up to 16% of corallite radius. Septa of two orders, thin to slightly dilated, tapering axially. Major septa 18–20 in number, generally extending to, or close to the corallite axis, with four (i.e. counter, two alar and cardinal septa) and sometimes some others meeting in axis but without forming a prominent columella. Minor septa well-developed, relatively short, generally less than 60% of the length of major septa. Tabulae complete, or incomplete, generally in moderately arched series. When incomplete, peripheral and axial zones are recognisable, with widths of axial zone variably accounting for 36–64% of corallite diameter. Tabular spacing relatively wide (Ta5 = 8–12) in peripheral zone, and slightly denser (Ta5 = 14–17) in axial zone. Dissepiments absent.

Remarks. – The revised diagnosis and description of *Eostauria prolifera* presented above are based on two specimens considered conspecific with the holotype of the species, including the holotype and a topotype of *Ceriaster shiniulanensis* He, 1978 documented by He (1978, 1980) from the same Shihniulan Formation (upper Aeronian) in the Qijiang area, southern Chongqing.

The specimens used by Yin (1944) to propose *Eostauria prolifera* come from the Shihniulan Formation (upper Aeronian) of northern Guizhou,

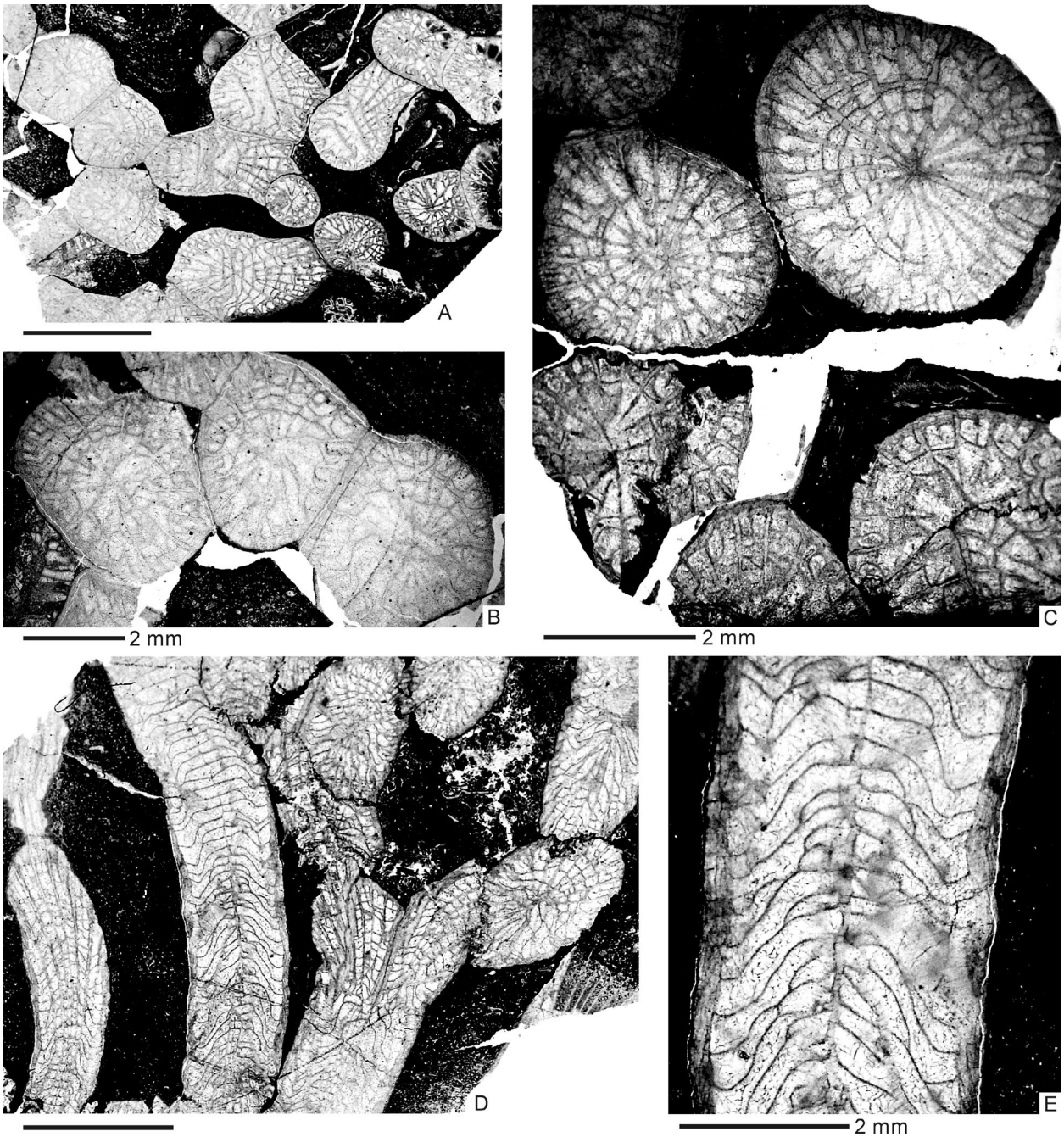


Fig. 54. Eostauria prolifera (Yin, 1944). NMRFC-Scr653, holotype of *Ceriaster shiniulanensis* He, 1980, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A–C**, TSs (**A, C**) and an enlarged portion of **A** (**B**). **D**, **E**, LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

specifically Xinglong and Suomikong in the Meitan area, as well as Honghuayuan in the Tongzi area. The specimen AB102e from Suomikong was designated as the holotype. However, the repository for Yin's material, including the holotype, was not specified and has likely been lost. This species exhibits fasciculate to partially cerioid coralla, a typical KAC increase mode (Yin 1944, pl. 1, figs 1, 3, 4), and generally arched, weakly to moderately differentiated tabulae (Yin 1944, pl. 1, fig. 2). It has mature corallites measuring 3–4 mm, occasionally reaching 5 mm in diameter, with 16–20 major septa.

Notably, Yin (1944, p. 18) also noted the presence of dissepiments, though only in "one of the

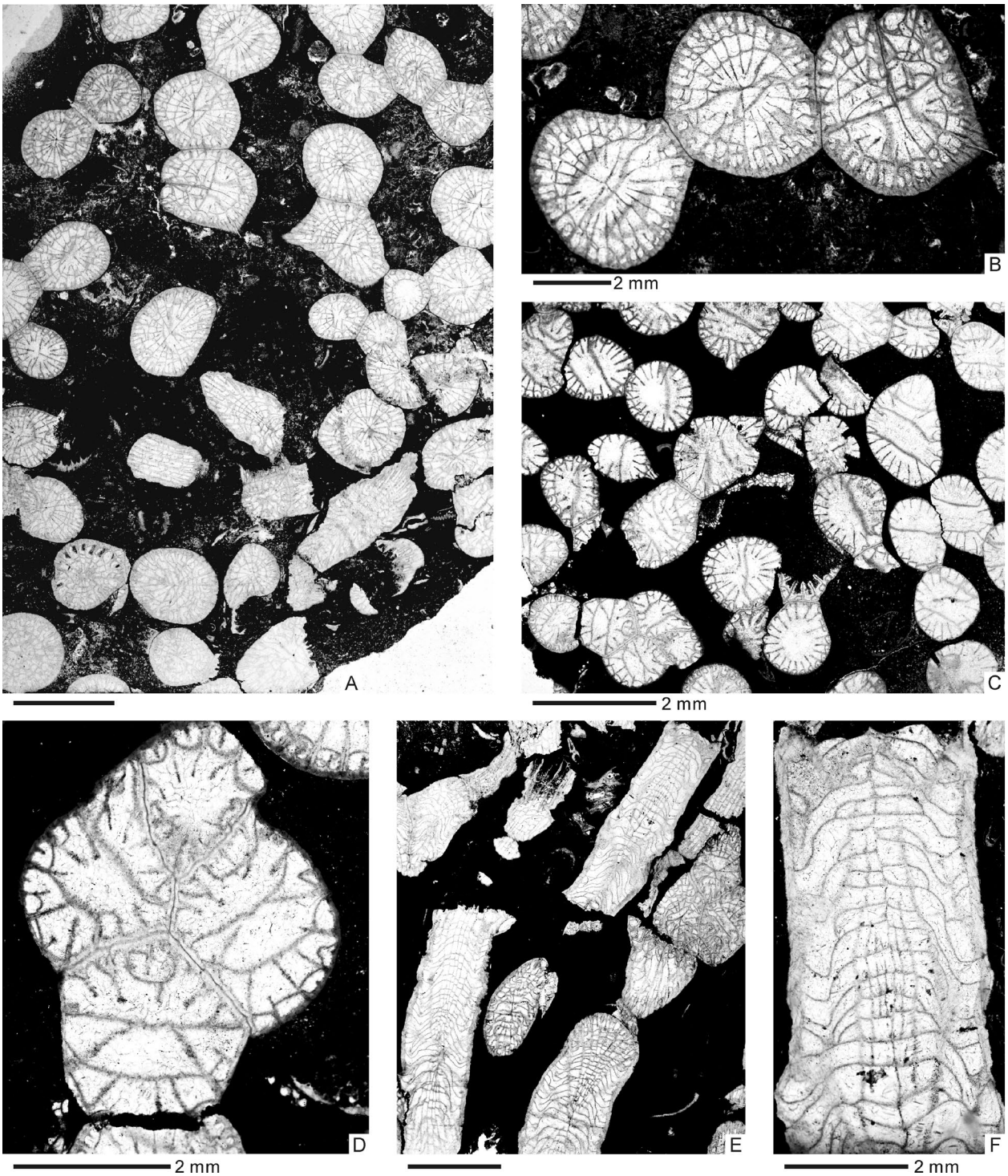


Fig. 55. *Eostauria prolifera* (Yin, 1944). NMRFC-Scr804, described by He (1980) as *Ceriaster shiniulanensis* He, 1980, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A–D,** TSs (**A, C**) and enlarged portions (**B, D**), respectively. **E, F,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated. Note that the TSs (C and its enlarged portion D) were probably mislabelled by He (1980) as "Scr804", which probably belongs to *Eostauria qijiangensis* (He, 1980), whose holotype (NMRFC-Scr805) originates from the same horizon and locality

four vertical sections so far prepared," forming "a discontinuous row of vesicles convex inward at the periphery of one of the four corallites included in that slice (AB102d-I)," which is evidently not the holotype (AB102e). This observation led Tang *et al.* (2008b) to reassign the species to *Cystostauria*. However, as demonstrated below, true dissepiments in *Cystostauria* species with a single intermittent row are distinct and easily recognisable. Thus, the rare "dissepiments" identified by Yin (1944) likely represent a misinterpretation of steeply axially inclined sections of differentiated tabulae within the peripheral zone.

Fascistauria queizhouensis He & Li, 1974, refigured by He & Li (1983), has its holotype [NMRFC-KS008 (TS/LS) and NMRFC- KS009 (TS/LS)] from the upper Xiangshuyuan Formation (lower Aeronian) of the Shiqian area, northeastern Guizhou. As this specimen has presumably been lost, it is included in the present study. This species exhibits a fasciculate growth habit with a typical KAC septal parricidal increase (He & Li 1983, text-fig. 2a), a corallite size of 2.80–4.00 mm in diameter, 18–20 major septa, and differentiated tabulae, and is best treated as a synonym of *Eostauria prolifera*. Also probably included within *Eostauria prolifera* are the materials described as this species by He & Li (1974) and He *et al.* (1989) from the same formation and general locality as the holotype, along with a specimen described by Kong & Huang (1978) from the slightly older, upper Xiangshuyuan Formation (lower Aeronian) of Dongkala, the Fenggang area, northern Guizhou.

The specimen figured by Tang (2006) as *Paraceriaster queizhouensis* (He & Li, 1974), from the Shihniulan Formation (upper Aeronian) of the Fenggang area in northern Guizhou, resembles the holotype of *Eostauria prolifera* in overall aspects and is probably a member of this species. However, its inclusion remains tentative due to insufficient knowledge regarding its increase mode.

Stauria aff. *prolifera* Yin, 1944 *sensu* He & Li (1974) comes from the upper Xiangshuyuan Formation (lower Aeronian) of Fengxiang, the Sinan area, northeastern Guizhou. It is now regarded as belonging to *C. multiseptata*, redescribed below.

Eostauria micropora He & Li, 1974

1974 *Ceriaster* (*Eostauria*) *micropora* He & Li, p. 5, pl. 1, fig. 1a, b.
1983 *Ceriaster* (*Eostauria*) *micropora* He & Li, p. 393, pl. 1, figs 1a, b [refig. He & Li 1974, fig. 1a, b], 2a, b, text-fig. 1a, b.
1995 *Eostauria micropora* He & Li; Lin *et al.*, fig. 135a, b [refig. He & Li 1983, text-fig. 1a, b].
2006 *Eostauria micropora* He & Li; Tang, pl. 29, fig. 3a–f.

Remarks. – As noted above, *Eostauria micropora* is the type species of the genus. Its type material consists of the holotype [NMRFC-KS001 (TS), NMRFC-KS002 (LS)], and a specimen later designated by He & Li (1983) as the paratype [NMRFC-KS041 (TS), NMRFC-KS042 (LS)], both from the upper Xiangshuyuan Formation (lower Aeronian) of Fengxiang, the Shiqian area, northeastern Guizhou. However, these specimens have likely been lost and are therefore unavailable for the present study. In addition, the specimen more clearly figured by Tang (2006) from the same horizon and locality has an almost identical increase pattern, fasciculate growth, corallite size, and septal and tabular development, and is undoubtedly an example of *E. micropora.*

Eostauria micropora was stated by He & Li (1974, p. 5; 1983, p. 393) to have "a quadripartite increase", indicative of a KAC septal parricidal increase mode, which is further confirmed by clearer figures of Tang's (2006, fig. 29, fig. 3a, e) material. Regarding the tabulae of this species, He & Li (1974, p. 5; 1983, p. 393) described them as being "complete" and "strongly arched axially". However, somewhat differentiated tabulae are locally observed in the clearer figures of the longitudinal sections of both the holotype (He & Li 1983, fig. 1a, b) and the specimen figured by Tang (2006, fig. 29, fig. 3b). Other features of *E. micropora* include very small corallites (less than 2 mm in diameter), 8–11 major septa that mostly meet in the corallite axis, well-developed minor septa, lack of dissepiments, and well-spaced tabulae (0.2–0.4 mm apart) (He & Li 1974, 1983; Tang 2006).

Eostauria menakovae (Lavrusevich, 1965)

1965 *Ceriaster menakovae* Lavrusevich, pp. 29, 30, pl. 1, figs 1a, b, 2a, b.
1965 *Fletcheria*? *menakovae* (Lavrusevich); Ivanovskiy, text-fig. 48a, b [refig. Lavrusevich 1965, pl. 1, fig. 1a, b].
1971 *Ceriaster menakovae* Lavrusevich; Lavrusevich, p. 71, text-fig. 4a–c [refig. Lavrusevich 1965, pl. 1, figs 2a, 1a, b].

Remarks. – The type material of this species (holotype, UpG 4208; paratype, UpG 4215) comes from the "lower–middle Llandovery" of the Zeravshan–Hissar region. The fasciculate coralla and KAC septal parricidal increase warrant its transfer to *Eostauria*, as also suggested by He & Li (1974, p. 5) and Tang *et al.* (2008b, p. 431). Its specific features include small corallites (1.5–2.0 mm in diameter), 10–12 major septa that are commonly connected in the corallite axis, short minor septa, and complete, flat to slightly convex, widely spaced tabulae (1.0–1.2 mm apart) (Lavrusevich 1965).

Closest resemblance lies with *Eostauria micropora* He & Li, 1974, considered above, especially in the corallite size and septal development, but *E. menakovae* is readily separable by having exclusively complete and significantly sparser tabulae.

***Eostauria qijiangensis* (He, 1980)**

(Figs 56, 57)

1980 *Ceriaster qijiangensis* He, p. 42, pl. 4, fig. 3a, b.
1983 *Stauria simplex* He & Li, p. 395, pl. 1, fig. 5a, b.

Referred material. – NMRFC-Scr805, holotype of *Ceriaster qijiangensis* He, 1980, original of He (1980, pl. 4, fig. 3a, b), refigured here (Fig. 56). NMRFC-SS8001 (TS) and NMRFC-SS8002 (one TS and one LS), holotype of *Stauria simplex* He & Li, 1983, original of He (1980, pl. 1, fig. 5a, b), refigured

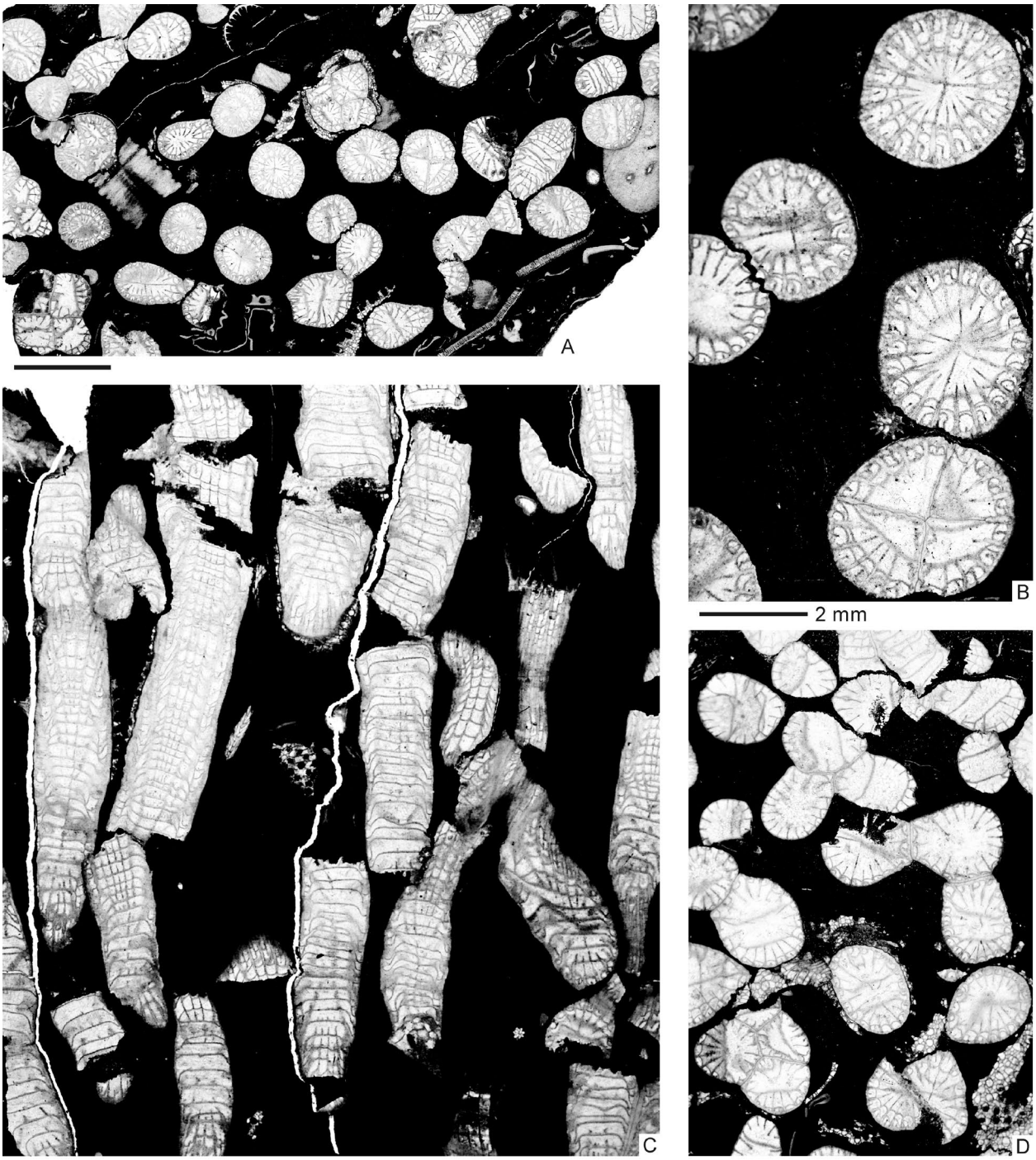


Fig. 56. Eostauria qijiangensis (He, 1980). NMRFC-Scr805, holotype of *Ceriaster qijiangensis* He, 1980, lower Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B, D,** TSs (**A, D**) and enlarged portions of **A** (**B**). **C,** LS. Scale bars are 5 mm unless otherwise indicated.

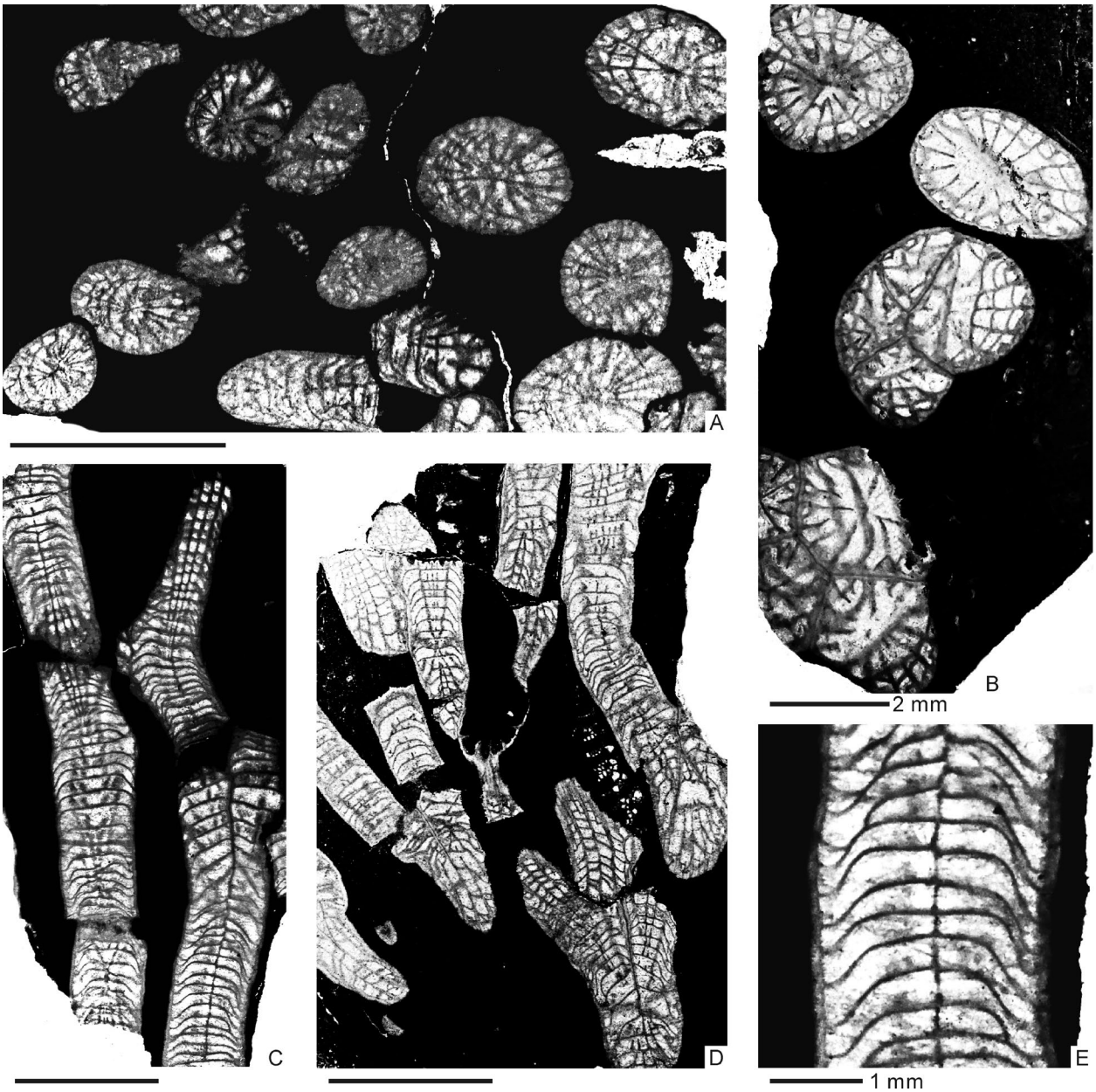


Fig. 57. Eostauria qijiangensis (He, 1980). **A–C, E,** NMRFC-SS8001 (TS) and NMRFC-SS8002 (one TS and one LS), holotype of *Stauria simplex* He & Li, 1983; **A, B,** TSs; **C, E,** LS and an enlarged portion. **D,** NMRFC-SS-8003, paratype of *Stauria simplex* He & Li, 1983, LS. Both specimens from the Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. Scale bars are 5 mm unless otherwise indicated.

here (Fig. 57A–C, E). NMRFC-SS8003, paratype of *Stauria simplex* He & Li, 1983, figured here for the first time (Fig. 57D). All the specimens from the "Qiaogou Formation" (now lower Shihniulan Formation, upper Aeronian), Guanyinqiao, Qijiang area, southern Chongqing, southwestern China.

Diagnosis. – *Eostauria* with small corallites that have adult diameters of 2.46–3.31 mm. Major septa 16–21, partly amplexoid, with only four protosepta (i.e. counter, two alar and cardinal septa) meeting in the corallite axis and forming a cross-shaped structure. Tabulae complete or rarely incomplete, slightly to moderately arched. Dissepiments absent.

Description. – Modified from Yin (1944, pp. 16–19), He (1980, p. 42) and He & Li (1983, p. 395). Coralla fasciculate, with external size and shape unknown. Increase of KAC septal parricidal type. Corallites cylindrical to subcylindrical, small, with adult

diameters of 2.46–3.31 mm. Septa of two orders, slightly to moderately dilated, tapering axially. Major septa 16–21 in number, partly amplexoid, with only four protosepta (i.e. counter, two alar and cardinal septa) meeting in the corallite axis and forming a cross-shaped structure. Minor septa well-developed, extending up to 1/3 to 1/2 of the major. Tabulae complete or rarely incomplete, slightly to moderately arched, with wide, flat or slightly concave platform. In some cases, weak tabular differentiation into peripheral and axial zones observed. Tabular spacing variable, TA5 = 8–15. No dissepiments observed.

Remarks. – The revised concept of this species, as presented above, is based on the holotypes of *Ceriaster qijiangensis* He, 1980 and *Stauria simplex* He & Li, 1983, along with the paratype of the latter, all from the lower Shihniulan Formation (upper Aeronian) of the Qijiang area, southern Chongqing. The synonymy of these two species is supported by their nearly identical holotypes, as both specimens exhibit the same increase mode, comparable corallite size (with adult diameters of 2.67–3.31 mm and 2.46–3.10 mm, respectively), and septal and tabular development (TA5 = 9–15 and 8–14, respectively).

Notably, He & Li (1983) described the presence of sporadic dissepiments in the holotype of *Stauria simplex*, a feature not confirmed by the present re-examination of this specimen. Additionally, the amplexoid septa observed in both specimens, which was not mentioned in their original descriptions, is regarded here as a key diagnostic feature of the revised species. This characteristic, combined with relatively small corallites (2.46–3.31 mm in diameter) and weakly differentiated tabulae, distinguishes it from other known *Eostauria* species.

Eostauria sp. A

(Fig. 58)

2002 *Ceriaster* sp. nov., Scrutton & Deng, fig. 80O, P.

Referred material. – NIGP 205574, original of Scrutton & Deng (2002, fig. 80O, P), refigured here (Fig. 58), Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou.

Description. – Corallum fasciculate, with external size and shape unknown. Increase of KAC septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 1.21–1.96 mm. Corallite walls thick, with a maximum thickness up to about 10% of corallite radius. Septa of two orders, thin to moderately dilated, tapering axially. Major septa 6–8, generally 8 in number, commonly extending to the corallite axis and forming a prominent, solid columella. Minor septa short, slightly extending beyond corallite walls. Tabulae complete, subhorizontal, wary, or slightly convex, widely spaced (Ta5 = 16–20). Dissepiments absent.

Remarks. – This species, formerly only figured by Scrutton & Deng (2002) under *Ceriaster* sp. nov., is described for the first time based on a re-examination of the original specimen. The presence of a KAC septal parricidal increase mode and the lack of dissepiments support its transfer to *Eostauria*. It distinguishing features include small corallites, few major septa (commonly 8 in number) and well-developed columellae. However, given the limited material available, the variability of this species remains insufficiently established, and this warrants the use of open nomenclature at present.

Eostauria stauriata Tang in Tang *et al.*, 2008b

1956 *Stauria prolifera* Yin; Qin, pp. 625, 626, pl. 2, fig. 1a, b.
1959 *Stauria prolifera* Yin; Chen, p. 296, pl. 7, fig. 1a–c.
2006 *Eostauria stauriata* Tang, p. 148, 149, pl. 32, figs 1a–e, 2, text-fig. 5.2, a–f.
2008b *Eostauria stauriata* Tang in Tang *et al.*, pp. 433, 434, pl. 2, figs 1a–e, 2 [refig. Tang 2006, pl. 32, figs 1a–e, 2].

Remarks. – *Eostauria stauriata*, also described by Tang (2006, unpublished PhD thesis) as a new species, has its holotype (CUGB-GSL0194) and paratype (CUGB-SCQ1599) from the Shihniulan Formation (upper Aeronian) of the Fenggang area in northern Guizhou, and of the Qijiang area in southern Chongqing, respectively. This form exhibits a KAC septal parricidal increase, corallites 2.5–3.0 mm in diameter, 16–18 major septa that mostly extend to the corallite centre, and complete, generally flat, closely spaced tabulae (Ta5 = 13–15).

Stauria prolifera Yin, 1944 *sensu* Qin (1956) and Chen (1959) occurs in the "Middle Silurian" (now Kaochaitien Formation, lower Telychian) of the Guiyang area, central Guizhou. Both forms exhibit quadripartite increase (= KAC septal parricidal increase, as defined in this study), a fasciculate growth habit, and a lack of dissepiments, supporting their reassignment to *Eostauria*. Their further identification as *Eostauria stauriata*, as also suggested by Tang *et al.* (2008b), is based on their close resemblance to the holotype of that species, particularly regarding comparable corallite size (3.0–3.5, and 2.5–3.4 mm, respectively) and a non-amplexoid septal type, as well as a similar major septal number (15 and 15–17, respectively).

Eostauria qijiangensis (He, 1980), considered above, has corallite size (2.46–3.31 mm in diameter)

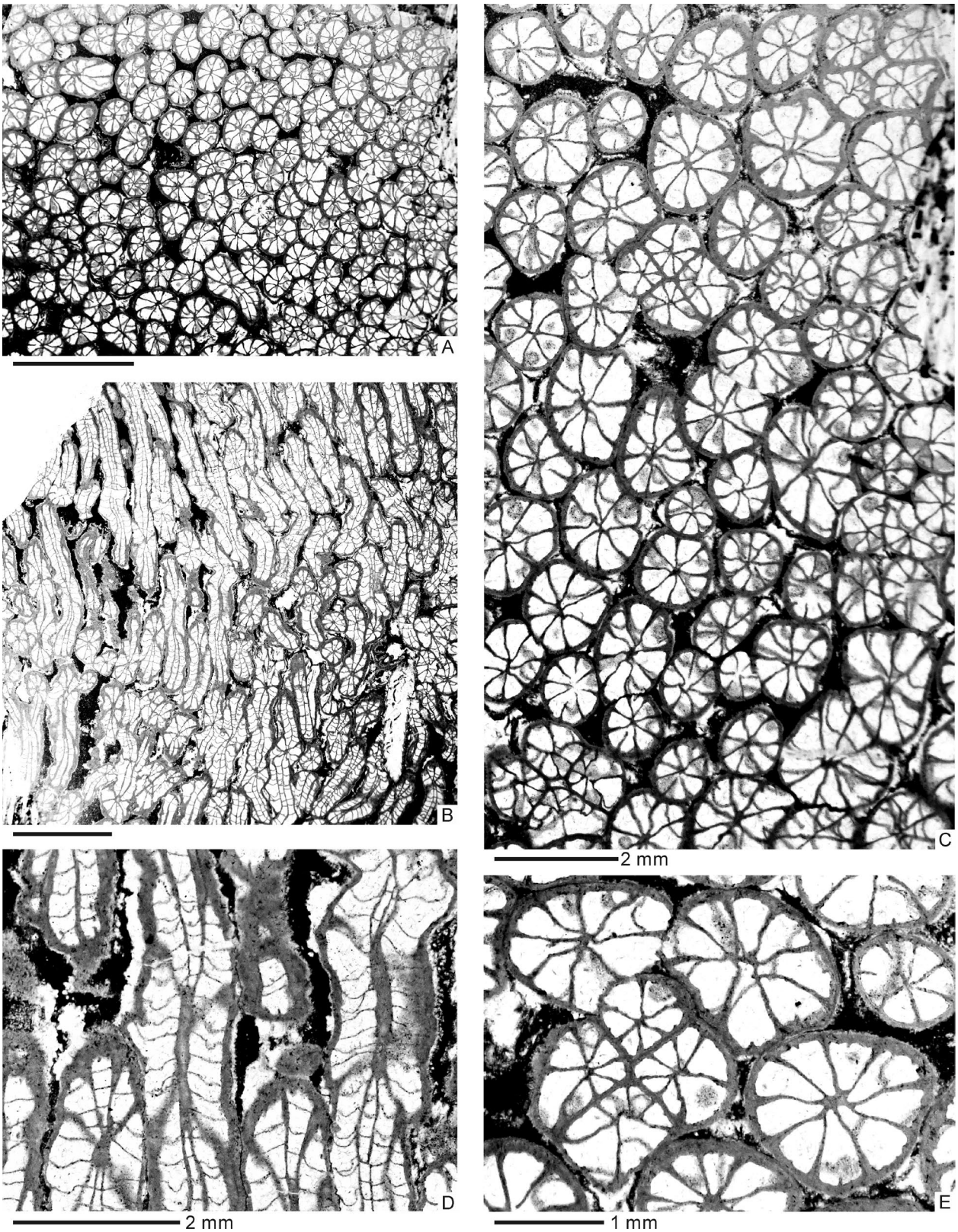


Fig. 58. Eostauria sp. A. NIGP 205574, described by Scrutton & Deng (2002) as *Ceriaster* sp. nov., Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A, C, E,** TS and two enlarged portions. **B, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

comparable to *E. stauriata*, differing in lacking amplexoid septa and somewhat differentiated tabulae.

Eostauria sp. B

2006 *Paraceriaster fasciculatus* (Cao); Tang, pp. 152, 153, pl. 29, figs 1, 4a–c.
2008b *Paraceriaster fasciculatus* (Cao); Tang *et al*., pp. 434, 435, pl. 2, figs 3, 4a–c [refig. Tang 2006, pl. 29, figs 1, 4a–c].

Remarks. – The material described by Tang (2006) and re-illustrated by Tang *et al*. (2008b) as *Paraceriaster fasciculatus* (Cao, 1975) consists of two specimens, with one coming from the Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China, and the other from the coeval Shihniulan Formation of Wenshui, Xishui area. This form is clearly not true *P. fasciculata* (Cao, 1975), revised below, from the Wangjiawan Formation (lower Telychian) of the Mianxian area, Shaanxi, and is instead transferred here to *Eostauria* due to its KAC septal parricidal increase mode. The specific features include a prominent peripheral stereozone, small corallites (2–3 mm in diameter), 16–18 major septa mostly meeting in the corallite axis, weakly developed minor septa and a narrow axial tabular zone composed of axial parts of strongly arched tabulae (Tang 2006; Tang *et al*. 2008b). Among these, the presence of strongly arched tabulae is particularly distinctive, suggesting that this form may represent a new species. However, given the lack of sufficient information regarding its variability, an open nomenclature is preferable.

Eostauria prolifera (Yin, 1944), revised above, shows closest similarities to *E.* sp. B, with both species having major septa meeting in the corallite axis, and incomplete, differentiated tabulae. However, *Eostauria prolifera* is separable by possessing larger mature corallites (3.76–4.49 mm in diameter) and better development of complete tabulae that results in weaker tabular differentiation.

Genus *Cystostauria* He & Li, 1974

1974 *Cystostauria* He & Li, p. 9.
1983 *Cystostauria* He & Li, pp. 395, 396.

Type species. – *Cystostauria normalis* He & Li, 1974, "upper part of the lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Pugou, Shiqian area, northeastern Guizhou, by original designation.

Diagnosis. – Like *Stauria*, but with entirely fasciculate growth.

Remarks. – *Cystostauria* is essentially a fasciculate edition of *Stauria* Milne-Edwards & Haime, 1850. Apart from the type species, three additional forms—*Stauria prolifera* Yin, 1944, *S. simplex* He & Li, 1983, and *S. multiseptata* He, 1978—all from the Llandovery of South China, were formerly included in *Cystostauria* (He & Li 1974, 1983; Tang *et al*. 2008b). Of these, the first two are revised herein as *Eostauria prolifera* (Yin, 1944) and *E. qijiangensis* (He, 1980), respectively, both of which have been discussed above.

From outside South China, two Gotland corals that should be reassigned to *Cystostauria* are part of *Stauria favosa* (Linnaeus, 1758) *sensu* Smith & Ryder, 1927, and *Stauria* sp. *sensu* Ting (1940), which are revised respectively as *C.* sp. A, and *C.* sp. B. In addition, the form figured by Oliver *et al*. (1975a) as *Stauria* sp. is revised as *Cystostauria* sp. C. A detailed discussion of these three species is as follows.

Cystostauria normalis He & Li, 1974

(Fig. 59)

1974 *Cystostauria normalis* He & Li, p. 9, pl. 4, fig. 2a–c.
1983 *Cystostauria normalis* He & Li, p. 396, pl. 2, figs 1a, b [refig. He & Li 1974, fig. 2a, c], 3a, b, text-fig. 3a, b.
2006 *Fascistauria* sp., Tang, p. 158, pl. 28, fig. 3a–c.
2008b *Cystostauria* sp., Tang *et al*., p. 436, pl. 1, fig. 3a–c [refig. Tang 2006, pl. 28, fig. 3a–c].

Referred material. – NMRFC-KS022 (TS) and NMRFC-KS023 (two LSs), holotype, original of He & Li (1974, fig. 2a–c), refigured here (Fig. 59), "upper part of the lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Pugou, Shiqian area, northeastern Guizhou.

Diagnosis. – *Cystostauria* with adult diameters of 3.95–5.20 mm, 15–19 major septa mostly extending about 80–90% of corallite radius, well-developed minor septa, and small, subglobose to slightly elongate dissepiments in one single, almost persistent series.

Description. – Modified from He & Li (1974, p. 9; 1983, p. 396). Corallum fasciculate, with external size and shape unknown. Increase of KAC septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 3.95–5.20 mm. Corallite walls thin. Septa of two orders, thin to slightly dilated, tapering axially. Major septa 15–19, commonly 19 in number, most extending up to 80–90% of corallite radius. Counter, two alar and cardinal septa generally meeting in axis and forming a cross-shaped structure. Minor septa well developed, relatively long, accounting for 1/3–1/2 of corallite radius. Dissepimentarium narrow, consisting of a single, almost persistent series of dissepiments. Dissepiments relatively small, subglobose to slightly elongate. Tabularium sharply delineated from dissepimentarium. Tabulae complete, or incomplete, generally in slightly arched series, with broad, flat or slightly concave platform, Ta5 = 15–18.

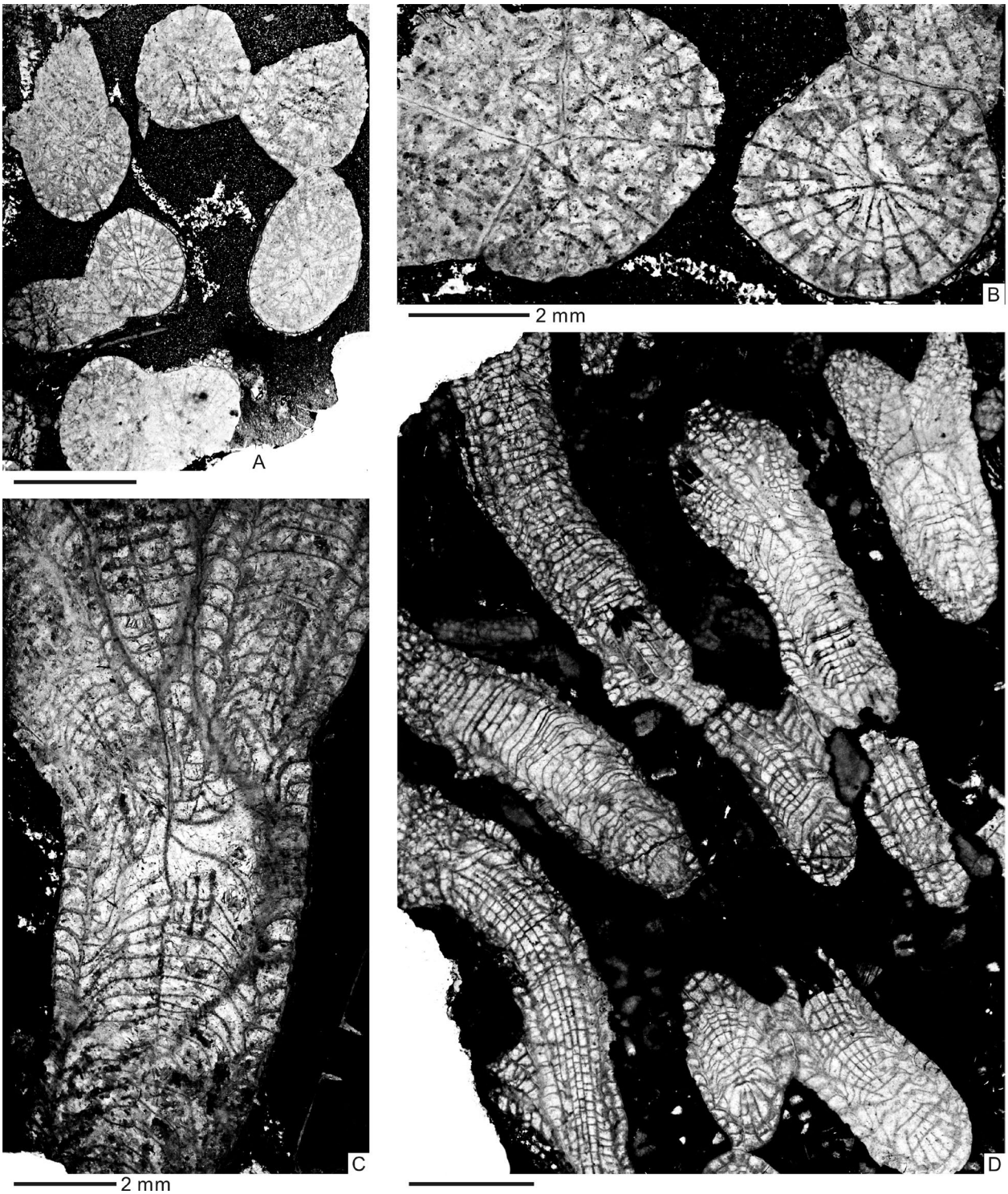


Fig. 59. Cystostauria normalis He & Li, 1974. NMRFC-KS022 (TS) and NMRFC-KS023 (two LSs), holotype, "upper part of the lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Pugou, Shiqian area, northeastern Guizhou. **A, B,** TS and an enlarged portion; **C, D,** LSs. Scale bars are 5 mm unless otherwise indicated.

Remarks. – *Cystostauria normalis* is the type species of the genus. In addition to the holotype, a paratype [NMRFC-KS043 (TS) and NMRFC-KS044] was subsequently selected by He & Li (1983) from the same rock unit at Dongkala of the Fenggang area, northeastern Guizhou. Unfortunately, this specimen has not been located in the repository for the present study. The revised concept of this species is hence based on a re-examination of its holotype.

A form regarded here as synonymous with *Cystostauria normalis* is *C.* sp. *sensu* Tang *et al.* (2008b), figured earlier by Tang (2006) as *Fascistauria* sp., from the Leijiatun Formation (upper Aeronian) of Baisha, the Shiqian area, northeastern Guizhou. The presence of KAC septal parricidal increase and dissepiments supports its attribution to *Cystostauria*. According to these authors, this form has corallite size (commonly 4.0–5.2 mm) and many other aspects comparable to *C. normalis*, differing in having "longer minor septa that extend up to 1/3–1/2 of corallite radius", and "more persistent development of dissepiments" (Tang 2006, p.158; Tang *et al.* 2008b, p. 436). However, these differences fall well within the normal variation of *C. normalis*, revised above.

Cystostauria sp. A

1927 *Stauria favosa* (Linnaeus); Smith & Ryder *pars*, pl. 9, figs 1–3, *non* pl. 9, fig. 4, text-fig. 2.

Remarks. – This form is represented solely by a single Gotland specimen (BM-R23801), formerly described by Smith & Ryder (1927) as *Stauria favosa* from the "Silurian, Rejio, east of Angelin", with its exact horizon unknown. As demonstrated by these authors, it has a typical KAC septal parricidal increase mode and a phaceloid growth form, and this warrants its transfer to *Cystostauria* He & Li, 1974. Its major specific features include large corallites (8 mm in diameter on average) and weakly developed dissepiments that sporadically occur in one single series (Smith & Ryder 1927). However, the insufficient understanding of the variability of this form prevents the formal establishment of a new species.

In corallite size and septal development, *Cystostauria* sp. A closely resembles *C.* sp. B considered below, from the Lower and Upper Visby formations (uppermost Telychian–lower Sheinwoodian), but the latter differs in having far better developed dissepiments that commonly occur in two series.

Cystostauria sp. B

1940 *Stauria* sp., Ting, pl. 1, figs 1–4.

Remarks. – This species was said by Ting (1940) to come from "Visby, Gotland", where the strata now referable to the Lower and Upper Visby formations of latest Telychian–early Sheinwoodian age (Calner *et al.* 2004) occur. The fasciculate growth led He & Li (1974) to reassign it to their new genus *Cystostauria*. Considering its KAC septal parricidal increase, I agree with such a reassignment. Based on Ting (1940), the specific features include large corallites (up to 8 mm in diameter), short minor septa, complete, or rarely incomplete tabulae, and well-developed dissepiments occurring in 1–2 series. However, given the insufficient knowledge of its variability, adopting an open nomenclature at present appears to be prudent.

A similar species is *Cystostauria multiseptata* (He, 1978), redescribed below, from the Shihniulan Formation (upper Aeronian) of the Qijiang area, southern Chongqing. It has comparable corallite size (5.13–7.93 mm in diameter) but is readily distinguished by having a much thicker peripheral stereozone, more major septa meeting in the corallite axis and without a prominent cross-shaped axial structure, and only one single intermittent series of dissepiments. Comparison of *Cystostauria* sp. B with the other Gotland form, *C.* sp. A, is discussed above under the latter.

Cystostauria sp. C

1975a *Stauria* sp., Oliver *et al.*, p. 26, pl. 10, figs 1, 2.

Remarks. – Identified by Oliver *et al.* (1975a) as *Stauria* sp., this species was based on a single specimen from the "Ludlovian" rocks of the eastern Brooks Range, Alaska. However, the precise age of this horizon remains uncertain, since the original dating by Oliver *et al.* (1975a) relied solely on the presence of *Stauria*, which this study demonstrates was no younger than the early Wenlock.

Cystostauria sp. C was initially illustrated with a brief comment noting that it "has a wide dissepimentarium (unlike the type species) but is very similar to the type in all other morphologic details" (Oliver *et al.* 1975a, p. 26). However, its partly fasciculate growth habit, KAC septal parricidal increase, and wide dissepimentarium, as observed in illustrations, indicate that it represents a distinct species of *Cystostauria*. Given the currently limited knowledge of its intraspecific variability, the use of open nomenclature is warranted.

Cystostauria multiseptata (He, 1978)

(Fig. 60)

1974 *Stauria* aff. *prolifera* Yin; He & Li, pp. 8, 9, pl. 5, fig. 3a, b.
1978 *Stauria multiseptata* He, p. 143, pl. 71, fig. 2a–c.
1980 *Stauria multiseptata* He; He, pp. 38, 39, pl. 5, fig. 4a, b [refig. He 1978, pl. 71, fig. 2a, b].
2006 *Fascistauria multiseptata* (He); Tang, pl. 33, figs 1a–c, 3a–c.
2008b *Cystostauria multiseptata* (He & Li); Tang *et al.*, pl. 2, figs 5a–c, 6a, b [refig. Tang 2006, pl. 33, figs 1a–c, 3a, b].

Referred material. – NMRFC-Scr651, holotype, original of He (1978, pl. 71, fig. 2a–c), refigured here (Fig. 60), Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

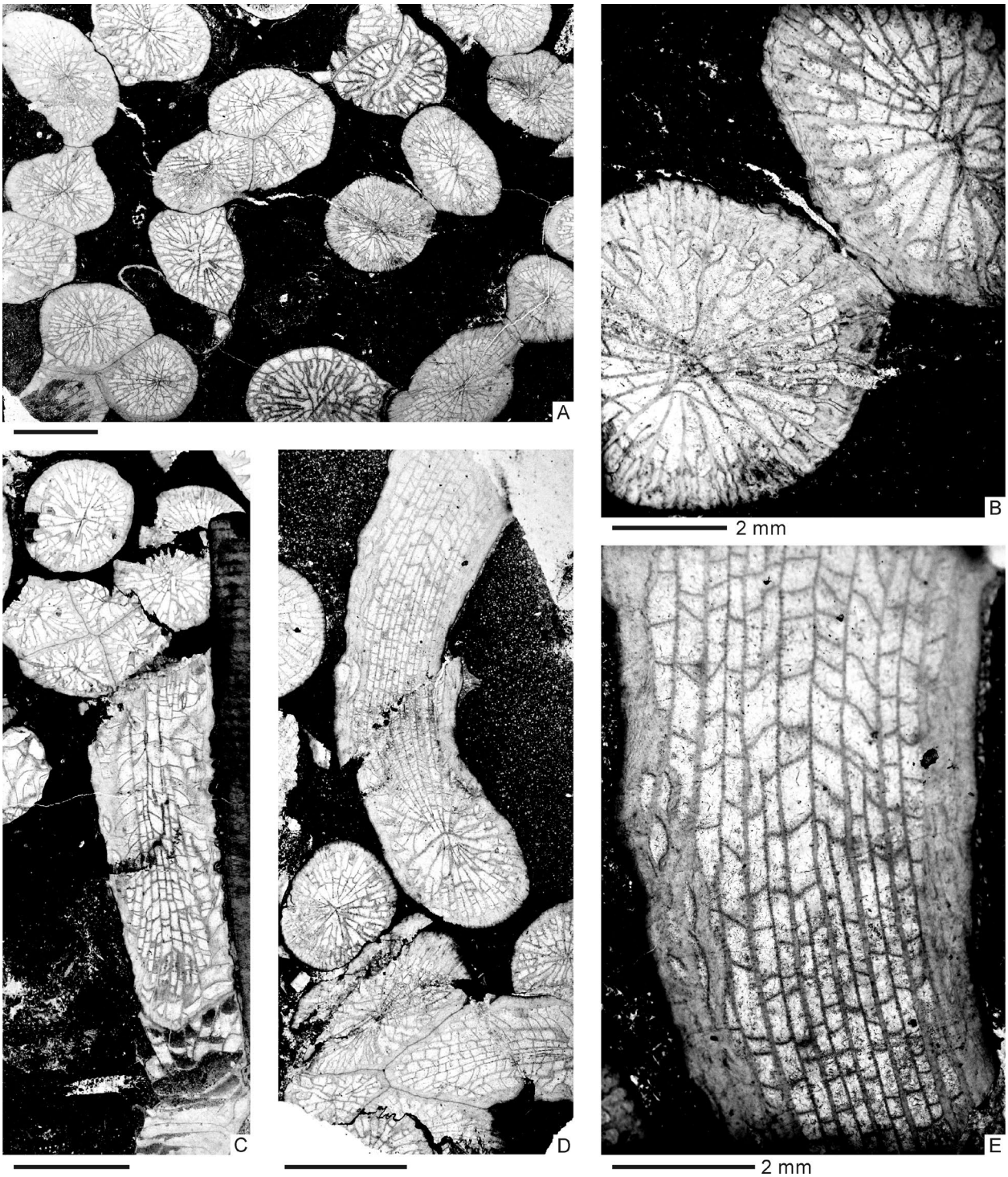


Fig. 60. Cystostauria multiseptata (He, 1978). NMRFC-Scr651, holotype, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B,** TS and an enlarged portion; **C–E,** two mainly LSs and an enlarged portion of **D**. Scale bars are 5 mm unless otherwise indicated.

Diagnosis. – *Cystostauria* species with adult diameters of 5.13–7.93 mm, a wide peripheral stereozone, 20–22 major septa mostly meeting in the corallite axis, long minor septa, a single intermittent series of dissepiments, and widely spaced tabulae (Ta5 = 7–10).

Description. – Modified from He (1978, p. 143; 1980, pp. 38, 39). Corallum fasciculate, with external size and shape unknown. Increase of KAC septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 5.13–7.93 mm. Marginarium a wide peripheral stereozone, consisting of dilated peripheral septal ends and thick lamellar stereome, with a maximum thickness up to 26% of corallite radius. Septa of two orders, thin to slightly dilated, tapering axially. Major septa 20–22 in number, four protosepta (counter, two alar and cardinal septa) and a few others meeting in axis and occasionally forming a prominent cross-shaped structure. Minor septa relatively long, extending up to 26% of corallite radius. Dissepimentarium narrow, consisting of one or rarely two intermittent series of dissepiments. Dissepiments comparatively large, slightly to moderately elongated. Tabularium sharply delineated from dissepimentarium. Tabulae complete, or rarely incomplete, slightly arched, Ta5 = 7–10.

Remarks. –The revised diagnosis and description of *Cystostauria multiseptata* presented above are based on a reassessment of its holotype. A combination of the large corallite size, wide peripheral stereozone, and one single intermittent row of dissepiments is sufficient to distinguish it from all other congeneric species.

Stauria aff. *prolifera* Yin, 1944 of He & Li (1974), from the upper Xiangshuyuan Formation (lower Aeronian) of Fengxiang, the Sinan area, northeastern Guizhou, exhibits comparable corallites (diameter 3.0–5.5 mm), major septal number (16–20), length of minor septa (up to 1/2–1/3 of the major), and wide peripheral stereozone. It is thus consistent and hence synonymous with *C. multiseptata*.

The material figured but not described by Tang (2006) and Tang *et al*. (2008b) as *Cystostauria multiseptata* (He, 1978) consists of two specimens from the Shiqian area, northeastern Guizhou, one (CUGB-GSL0090) occurring in the Xiangshuyuan Formation (lower Aeronian) and the other (CUGB-GSL0436) the Leijiatun Formation (upper Aeronian). From the clearer illustrations in Tang (2006, pl. 33, figs 1a–c, 3a–c), their inclusion within *Cystostauria multiseptata* seems very likely.

The two Gotland species revised above, *Cystostauria* sp. A, and *C.* sp. B, both have large corallites like *C. multiseptata*. The former differs in having generally four protosepta meeting in the corallite axis, and thinner peripheral stereozone, whereas the latter has much better development of dissepiments that commonly occur in two persistent rows.

Subfamily Paraceriasterinae n. subfam.

Diagnosis. – Stauriidae with septal parricidal increase occurring at counter and two alar septa (i.e. KA septal parricidal increase), and without dissepiments.

Remarks. – Based on the definition given above, the new subfamily is regarded here as consisting of *Paraceriaster* He, 1980, *Ceriaster* Lindström, 1883, and *Massparaceriaster* Tang in Tang *et al.*, 2008b (see remarks on these genera below for further discussion). Although *Ceriaster* is the older genus within this group, *Paraceriaster* serves as the basis for the establishment of the new subfamily, as its increase pattern is currently much better understood, as demonstrated below.

Genus *Ceriaster* Lindström, 1883

1883 *Ceriaster* Lindström, p. 61.

Type species. – *Ceriaster calamites* Lindström, 1883, "upper Silurian" (now probably the Wangjiawan Formation, lower Telychian), Guangyuan–Ningqiang area, Sichuan–Guizhou border region, by original designation.

Diagnosis. – Paraceriasterinae n. subfam. with cerioid growth and complete tabulae that are not differentiated into axial and peripheral zones.

Remarks. – The type material of the type species *Ceriaster calamites* was stated by Lindström (1883) to occur in the "bed l" of the Guangyuan–Ningqiang area, which was later believed to be of "middle Silurian" age (e.g. Yu *et al*. 1963; Hill 1981). However, since the later stauriid records of the area are now known to be restricted to the Wangjiawan Formation (lower Telychian, Rong *et al*. 2019), the occurrence of *Ceriaster calamites* is most likely from this unit.

Since its erection, *Ceriaster* was long considered as comprising all non-dissepimented stauriids (e.g. Lavrusevich 1965, 1971; Ivanovskiy 1965, 1975; Hill 1981). Since the 1970s, similar forms with fasciculate growth were transferred to later-erected *Eostauria* He & Li, 1974 (or its synonym *Fascistauria* He & Li, 1974), and *Massparaceriaster* Tang in Tang *et al.*,

2008b, *Ceriaster* was consequently restricted to the cerioid, non-dissepimented forms that lacks tabular differentiation. In this work, *Ceriaster* is further limited to those with KA septal parricidal increase type, as discussed above.

Ceriaster is now known to be solely represented by the type species, *C. calamites*. As discussed elsewhere in this work, Tang *et al*. (2008b) included within *Ceriaster* three further species from the Aeronian (middle Llandovery) of South China, *C. weiganensis* He & Huang in Kong & Huang, 1978, *C. guanyinqiaoensis* He, 1980, and *Neoceriaster rarisepta* He, 1980, all of which are now excluded. Also excluded is the material previously identified by some workers (He & Li 1974; Kong & Huang 1978; Tang *et al*. 2008b) as *Ceriaster calamites* from the older, Xiangshuyuan Formation (upper Llandovery–lower Aeronian) of Liangshuijing, Sinan area, northeastern Guizhou, which is transferred here to *Heina* sp., considered below.

Ceriaster calamites Lindström, 1883

1883 *Ceriaster calamites* Lindström, pp. 61, 62, pl. 5, figs 2–5.
1963 *Stauria* (*Ceriaster*) *calamites* Lindström; Yu *et al*., p. 154, pl. 42, fig. 5a–c [refig. Lindström 1883, pl. 5, figs 2–4].
non 1974 *Ceriaster* (*Ceriaster*) *calamites* Lindström; He & Li, pp. 7, 8, pl. 3, fig. 1a, b, pl. 5, fig. 2a, b.
non 1975 *Ceriaster calamites* Lindström; Cao, p. 188, pl. 41, figs 1a, b, 2a, b.
? 1975 *Ceriaster calamites minor* Cao, pp. 188, 189, pl. 41, fig. 3a, b [*nomen dubium*].
1978 *Ceriaster calamites* Lindström; He, pp. 143, 144, pl. 70, fig. 12a, b [refig. Lindström 1883, pl. 5, figs 2, 3].
non 1978 *Ceriaster calamites* Lindström; Kong & Huang, p. 64, pl. 20, fig. 7a, b [refig. He & Li 1974, pl. 3, fig. 1a, b].
1981 *Ceriaster calamites* Lindström; Hill, fig. 68, 3a–c [refig. Lindström 1883, pl. 5, figs 2–4].
non 1982 *Ceriaster* (*Ceriaster*) *calamites* Lindström; Cao & Lin, p. 33, pl. 10, fig. 7a, b [refig. Cao 1975, pl. 41, fig. 1a, b].
1995 *Ceriaster calamites* Lindström; Lin *et al*., fig. 127a–c [refig. Lindström 1883, pl. 5, figs 2–4].
non 2006 *Ceriaster calamites* Lindström; Tang, p. 146, pl. 28, fig. 1a–c.
non 2008b *Ceriaster calamites* Lindström; Tang *et al*., pl. 1, fig. 1a–c [refig. Tang 2006, pl. 28, fig. 1a–c].

Remarks. – As noted above, this is the type and only named species of *Ceriaster*, with "syntypes in Richthofen Coll., HU" (Hill 1981, p. F134) probably from the Wangjiawan Formation (lower Telychian) of the Guangyuan-Ningqiang area. The key features include a KA septal parricidal increase pattern, small corallites (less than 3 mm in diameter), 7–12, commonly 9–10 major septa extending to the corallite axis, weakly developed minor septa that are short or absent, and complete, widely spaced tabulae (Lindström 1883).

Ceriaster calamites minor Cao, 1975, from the rocks now probably assigned to the Wangjiawan Formation (lower Telychian) at Tianchiliang of the Nanzheng area, southwestern Shaanxi, is considered in this work as *nomen dubium* because of the lack of information as to its increase mode (see remarks on the Stauriidae above for further discussion).

The specimens identified as *Ceriaster calamites* Lindström, 1883 by He & Li (1974), Kong & Huang (1978), Tang (2006), and Tang *et al*. (2008b) all occur in the older, Xiangshuyuan Formation (upper Llandovery–lower Aeronian) of Liangshuijing, Sinan area, northeastern Guizhou. This form is reassigned to *Heina* sp. due to its KLAC increase pattern, discussed below.

The specimen described by Cao (1975) and refigured by Cao & Lin (1982) as *Ceriaster calamites* Lindström, 1883 comes from the "middle Ningqiang Group" (now Wangjiawan Formation, lower Telychian), Tianchiliang, Nanzheng area, southwestern Shaanxi. Re-examination of this fossil supports a reassignment to *Massparaceriaster ningqiangensis* (Ge & Yu, 1974), discussed under the latter species below.

Genus *Paraceriaster* He, 1980

1980 *Paraceriaster* He, p. 35.

Type species. – *Paraceriaster daguanensis* He, 1980 [= *Paraceriaster major* (Fan in He 1978), redescribed below], Sifengya Formation (lower Telychian), Liangfengya, Huangjingba, Daguan area, northeastern Yunnan, southwestern China, by original designation.

Diagnosis. – Paraceriasterinae n. subfam. with fasciculate coralla and tabulae that are differentiated into axial and peripheral zones.

Remarks. – *Paraceriaster* was previously regarded as synonymous with *Fascistauria* He & Li, 1974 (= *Eostauria* He & Li, 1974 in this work). Its present separation as a valid genus is based on its KA septal parricidal increase, which is quite different from the KAC increase mode of *Eostauria*.

Paraceriaster major (Fan in He, 1978)

(Figs 61–63)

1978 *Ceriaster minor* (Chen); He, p. 143, pl. 71, fig. 3a, b.
1978 *Ceriaster major* Fan in He, p. 144, pl. 71, fig. 5a, b.
1980 *Paraceriaster daguanensis* He, pp. 42, 43, pl. 4, fig. 4a, b.
1995 *Paraceriaster daguanensis* He; Lin *et al*., fig. 134a, b [refig. He 1980, pl. 4, fig. 4a, b].
2006 *Paraceriaster daguanensis* He; Tang, pl. 30, fig. 5.

Referred material. – NMRFC-Scr654, holotype, original of Fan in He (1978, pl. 71, fig. 5a, b), refigured here (Fig. 61), "Lojoping Formation" (probably equivalent to the Huanggexi Formation, upper Aeronian), Shichong,

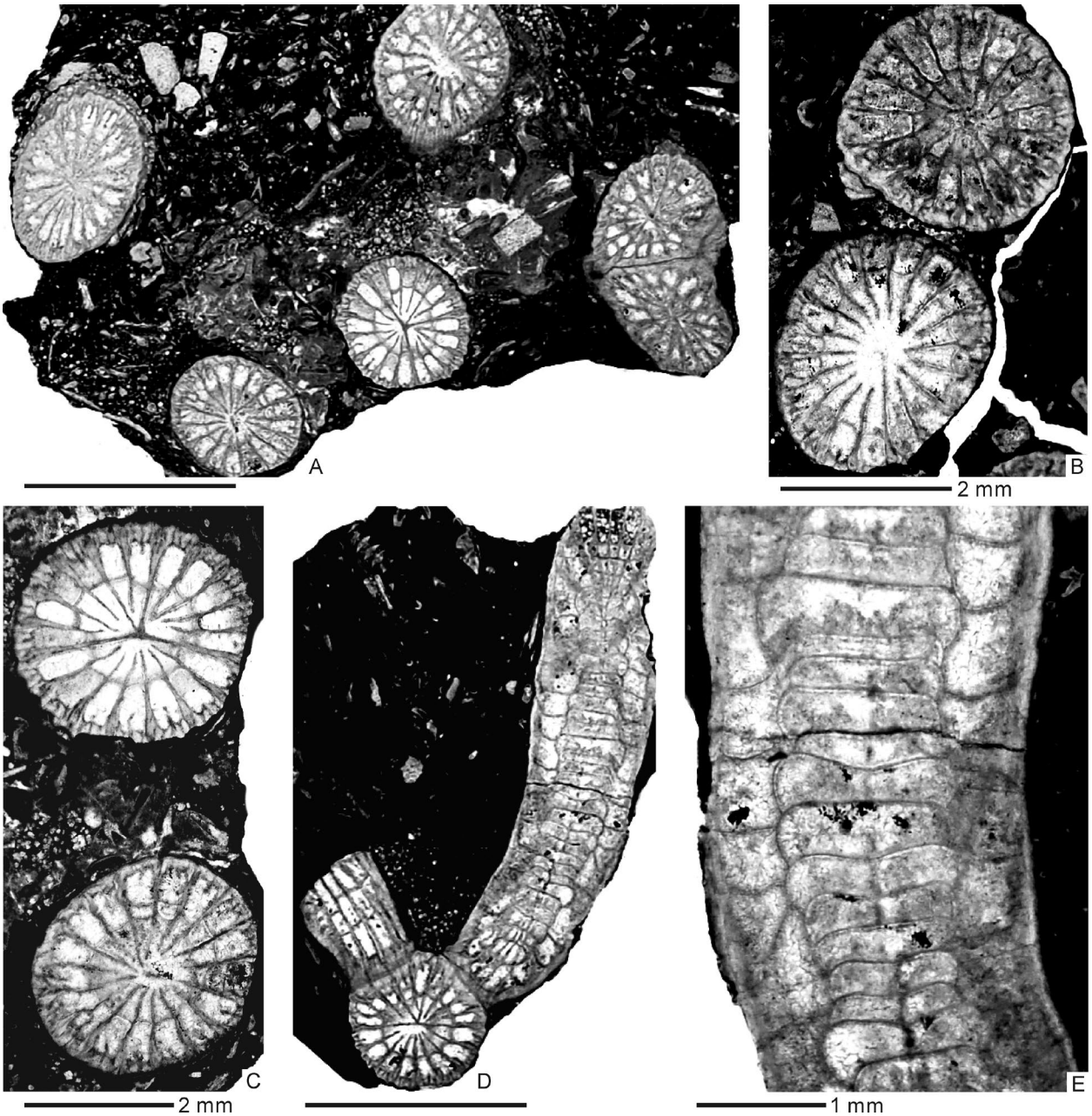


Fig. 61. Paraceriaster major (Fan in He, 1978). NMRFC-Scr654, holotype, "Lojoping Formation" (upper Aeronian), Shichong, Leibo area, southwestern Sichuan, southwestern China. **A–C,** TSs (**A, B**) and an enlarged portion of **A** (**C**). **D, E,** TS/LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

Leibo area, southwestern Sichuan, southwestern China. NMRFC-Scr652, described by He (1978) as *Ceriaster minor* (Chen, 1959), original of He (1978, pl. 71, fig. 3a, b), refigured here (Fig. 62), "Qiaogou Formation" (now lower Huanggexi Formation, Aeronian), Huangjingba, Daguan area, northeastern Yunnan, southwestern China. NMRFC-Scr806, holotype of *Paraceriaster daguanensis* He, 1980, type species of *Paraceriaster* He, 1980, original of He (1980, pl. 4, fig. 4a, b), refigured here (Fig. 63), Sifengya Formation (lower Telychian), Liangfengya, Huangjingba, Daguan area, northeastern Yunnan, southwestern China.

Diagnosis. – *Paraceriaster* species with a maximum corallite diameter of 3.29 mm. Septa of two orders, somewhat amplexoid. Major septa 16–18 in number, long, with three protosepta (i.e. counter and two alar) generally meeting in the corallite axis. Minor septa

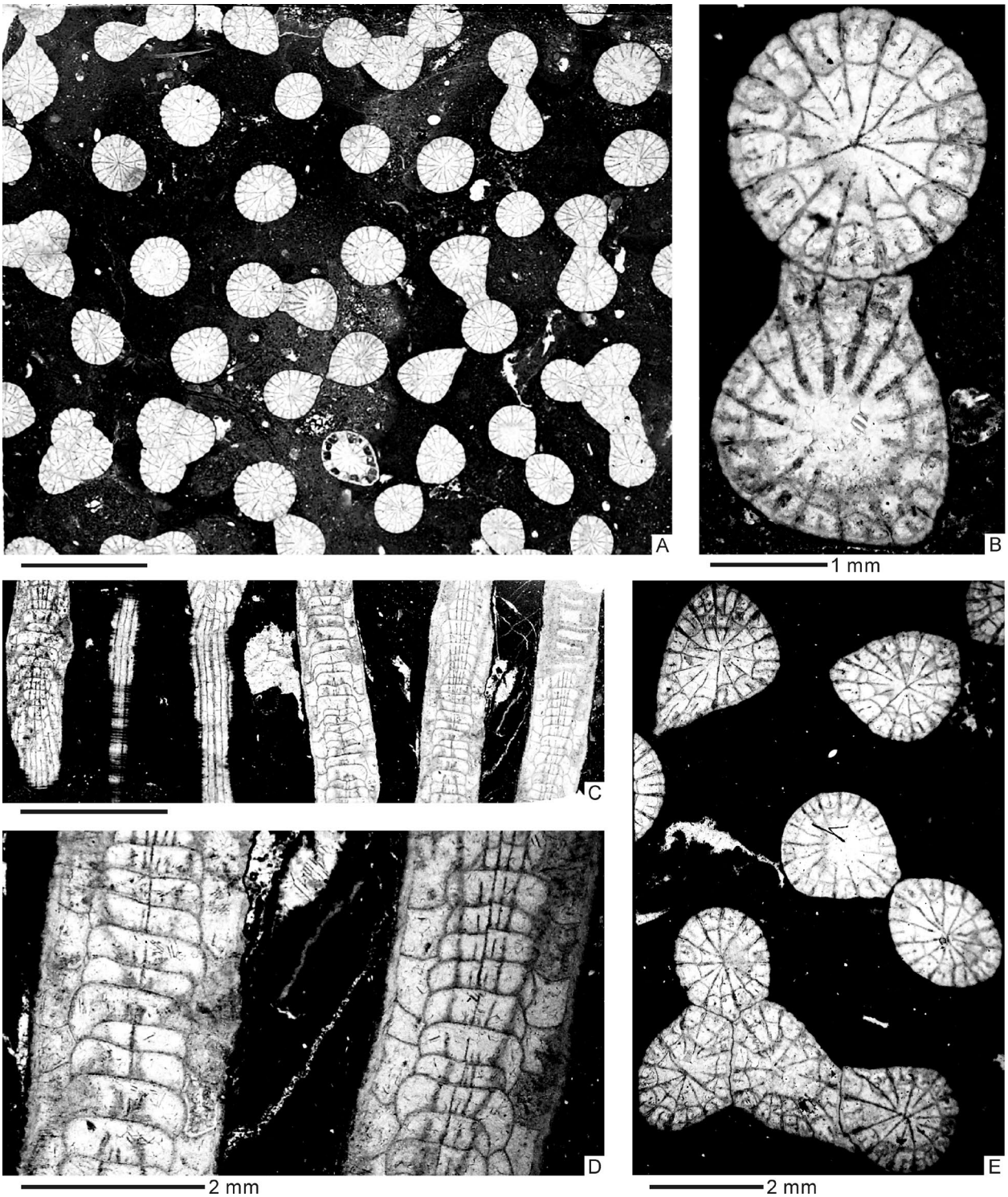


Fig. 62. Paraceriaster major (Fan in He, 1978). NMRFC-Scr652, described by He (1978) as *Ceriaster minor* (Chen, 1959), "Qiaogou Formation" (now lower Huanggexi Formation, Aeronian), Huangjingba, Daguan area, northeastern Yunnan, southwestern China. **A, B, E,** TS and two enlarged portions. **C, D,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

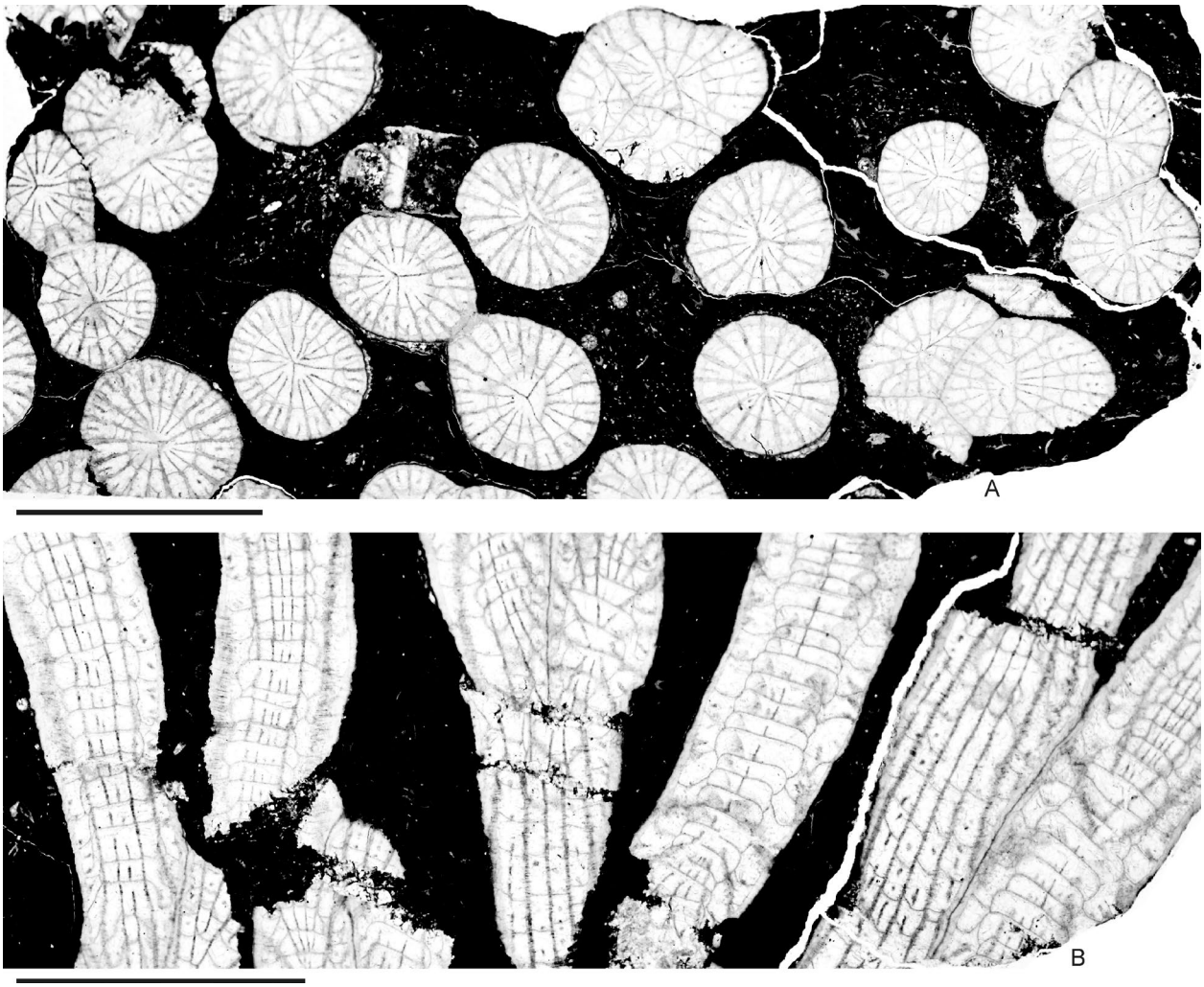


Fig. 63. Paraceriaster major (Fan in He, 1978). NMRFC-Scr806, holotype of *Paraceriaster daguanensis* He, 1980, Sifengya Formation (lower Telychian), Liangfengya, Huangjingba, Daguan area, northeastern Yunnan, southwestern China. **A,** TS. **B,** LS. Scale bars are 5 mm.

confined to peripheral tabular zone. Tabulae widely spaced (Ta5 = 8–9) in peripheral zone, and denser (Ta5 = 14–15) in axial zone.

Description. – Modified from Fan in He (1978, p. 144) and He (1980, p. 42). Corallum fasciculate, with external size and shape unknown. Increase of KA septal parricidal type. Corallites cylindrical to subcylindrical, with a maximum corallite diameter of 3.29 mm. Septa of two orders, somewhat amplexoid. Major septa 16–18 in number, long, extending to, or close to the corallite axis, with three protosepta (i.e. counter and two alar septa) generally meeting in the corallite axis but without forming a prominent columella. In some instances, major septa are all relatively short, accounting for about 47–60% of corallite radius. Minor septa well developed, short, confined to the peripheral tabular zone. Tabulae well differentiated into peripheral and axial zones, with axial zone accounting for 29–39%, or rarely 60% of corallite diameter. Tabular spacing wide (Ta5 = 8–9) in peripheral zone, and slightly denser (Ta5 = 14–15) in axial zone. Dissepiments absent.

Remarks. – The revised diagnosis and description presented above are based on the holotypes of *Ceriaster major* Fan in He, 1978 and *Paraceriaster daguanensis* He, 1980. The two specimens are considered here as conspecific, since they have comparable maximum corallite diameters (3.25 and 3.29 mm, respectively), somewhat amplexoid septa, width of axial zone (29–39%, 26–60% of corallite diameter, respectively), and tabular spacing in axial (Ta5 = 15, 14–15, respectively) and peripheral (Ta5 = 8, 8–9, respectively) zones. Note that the corallite size of the holotype of *Paraceriaster major* was originally said by Fan in He

(1978) to be 4–5 mm in diameter and hence considered as one of its key distinguishing features, a statement not supported by the present study.

The specimen described by He (1978) as *Ceriaster minor* (Chen, 1959), from the "Qiaogou Formation" (now lower Huanggexi Formation, Aeronian) of the Daguan area, northeastern Yunnan, is re-examined in this study. It shows slightly smaller corallites (up to 2.52 mm in diameter) but is otherwise identical to *Paraceriaster major*. This fossil is thus regarded here as a further example of the latter species.

Among the named *Paraceriaster* species, only *P. shiqianensis* (He & Li, 1974), considered below, has comparable corallite size (adult diameters being 2.82–3.22 mm). However, it is distinguishable from *P. major* by lacking amplexoid septa, and by having more major septa meeting in the corallite axis, and partly complete, much denser tabulae.

***Paraceriaster shiqianensis* (He & Li, 1974)**

(Figs 64, 65)

1974 *Ceriaster* (*Eostauria*) *shiqianensis* He & Li, pp. 6, 7, pl. 3, fig. 2a, b.
1974 *Ceriaster* (*Eostauria*) *songkanensis* He & Li, p. 7, pl. 3, fig. 3a–c.
non 1978 *Ceriaster shiqianensis* He & Li; Kong & Huang, pp. 64, 65, pl. 20, fig. 6a, b.
1983 *Paraceriaster shiqianensis* (He & Li); He & Li, p. 394, pl. 1, fig. 4a, b, pl. 2, fig. 6 [refig. He & Li 1974, pl. 3, fig. 2b].
1989 *Paraceriaster songkanensis* He & Li; He *et al.*, p. 91, pl. 3, fig. 9, pl. 27, figs 5–10.
2006 *Paraceriaster shiqianensis* (He & Li); Tang, pl. 29, fig. 2a–e.
2006 *Paraceriaster baishaensis* Tang, pp. 153, 154, pl. 30, fig. 3a–d.
2008b *Paraceriaster baishaensis* Tang in Tang *et al.*, p. 434, pl. 3, fig. 3a–c [refig. Tang 2006, pl. 30, fig. 3a–c].

Referred material. – NMRFC-KS016 (TS/LS) and NMRFC-KS017 (TS), holotype, original of He & Li (1974, pl. 3, fig. 2a, b), refigured here (Fig. 64), "Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Fengxiang, Shiqian area, northeastern Guizhou. NMRFC-KS8005 (TS/LS) and NMRFC-KS8006 (TS) from one corallum, described by He & Li (1983) as *Paraceriaster shiqianensis* (He & Li, 1974), original of He & Li (1983, pl. 1, fig. 4a, b), refigured here (Fig. 65), "lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Liangshuijing, Sinan area, northeastern Guizhou.

Diagnosis. – *Paraceriaster* with adult diameters of 2.82–3.22 mm, and 13–16 major septa mostly meeting in the corallite axis. Tabulae densely spaced (Ta2 = 4–5) in peripheral zone, and slightly denser (Ta2 = 7–10) in axial zone.

Description. – Modified from He & Li (1974, pp. 6, 7; 1983, p. 394). Corallum fasciculate, with external size and shape unknown. Increase of KA septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 2.82–3.22 mm. Septa of two orders, slightly to moderately dilated, tapering axially. Major septa 11–17, commonly 13–14 in number, mostly meeting in the corallite axis without forming a prominent columella. Minor septa well-developed, relatively long, extending well beyond peripheral stereozone, up to 40% of corallite radius. Tabulae incomplete or rarely complete, generally in arched series, differentiated into peripheral and axial zones. Tabular spacing variable, Ta2 = 4–5 in peripheral zone, and slightly denser (Ta2 = 7–10) in axial zone. Dissepiments are absent.

Remarks. – The revised diagnosis and description of *Paraceriaster shiqianensis* given above are based on the holotype and a further specimen considered by He & Li (1983) and herein as conspecific. *Paraceriaster shiqianensis* was also figured by Tang (2006) from the younger, Leijiatun (upper Aeronian) of Leijiatun, the Shiqian area, northeastern Guizhou. A comparison with *P. major* (Fan in He, 1978), which has comparable corallite size, is discussed above under that species.

Ceriaster (*Eostauria*) *songkanensis* He & Li, 1974, from the Shihniulan Formation (upper Aeronian) of Songkan, the Tongzi area, northern Guizhou, was transferred by He & Li (1983) to *Paraceriaster*. This reassignment is accepted here in view of its KA increase mode, as shown in its illustrations and indicated by their statement that "two or three corallites are commonly grouped together" and their illustrations (He & Li 1974, p. 7, pl. 3, fig. 3a–c). Compared with *P. shiqianensis*, it shows similar septal and tabular development, but was stated to be distinguishable by having "larger corallites" (2.3–3.5 mm in diameter), slightly more major septa (18–20 in number), and slightly denser tabulae (Ta2 = 12–13) (He & Li 1974, p. 7). However, the present revision of *P. shiqianensis* makes the distinction between the two very minor, and it is preferred here that they be synonymised. In addition, *Paraceriaster songkanensis* (He & Li, 1974) of He *et al.* (1989), from the same horizon of Wenshui, the Xishui area, northern Guizhou, is included within *P. shiqianensis* for the same reason.

Paraceriaster baishaensis Tang in Tang *et al.*, 2008b, also introduced earlier as a new species in Tang's (2006) unpublished PhD thesis, comes from the Leijiatun Formation (upper Aeronian) of Baisha, the Shiqian area, northeastern Guizhou. The presence

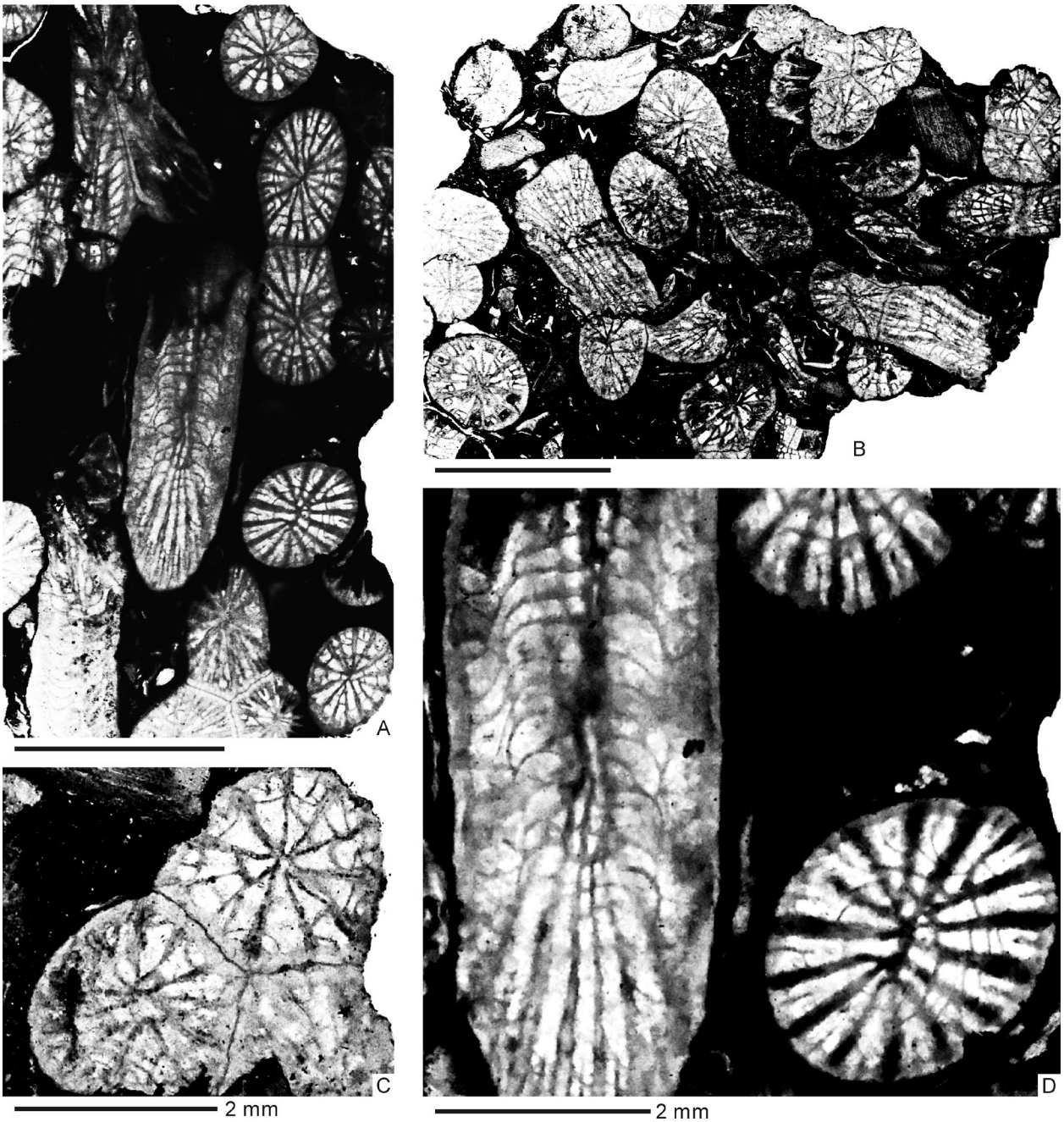


Fig. 64. Paraceriaster shiqianensis (He & Li, 1974). NMRFC-KS016 (TS/LS) and NMRFC-KS017 (TS), holotype, "Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Fengxiang, Shiqian area, northeastern Guizhou. **A, D,** TS/LS and an enlarged portion. **B, C,** TS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

of a "quadripartite, or rarely tripartite increase" was mentioned in this species (Tang *et al*. 2008b, p. 434), but the illustrations indicate a solely KA septal parricidal increase pattern (Tang 2006, pl. 30, fig. 3a–d), agreeing well with the currently revised concept of *Paraceriaster*. According to these authors (Tang 2006, p. 154; Tang *et al*. 2008b, p. 434), *P. baishaensis* has mature diameters of 3.5–4.0 mm, prominent peripheral stereozone, 18–19 major septa that extend to the corallite axis, short minor septa, and well-differentiated tabulae with Ta5 = 14–15 and 7–8 in peripheral and axial zones, respectively. It thus exhibits strong similarities to *P. shiqianensis* in general aspects, with major differences lying in "the local presence of complete tabulae and the tabulae being denser in the peripheral tabular zone" (Tang *et al*. 2008b, p. 434) of the latter. However, complete tabulae are also locally present in *P. baishaensis* (Tang 2006, pl. 30, 3b), and,

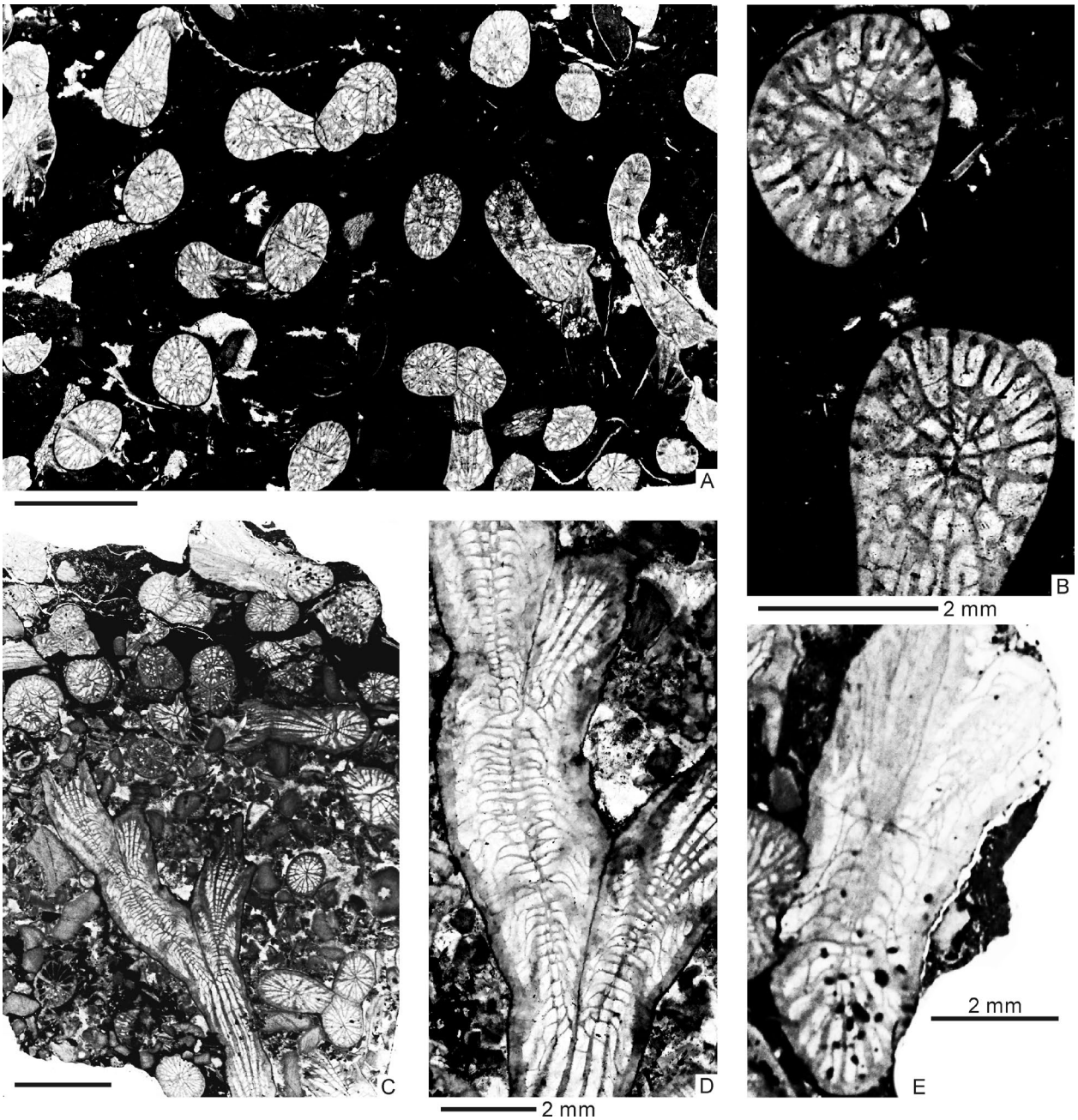


Fig. 65. Paraceriaster shiqianensis (He & Li, 1974). NMRFC-KS8005 (TS/LS) and NMRFC-KS8006 (TS) from one corallum, described by He & Li (1983) as this species, "lower member of the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian), Liangshuijing, Sinan area, northeastern Guizhou. **A, B,** TS and an enlarged portion. **C–E,** TS/LS and two enlarged portions. Scale bars are 5 mm unless otherwise indicated.

as noted above, the statement concerning the feature of tabular spacing in *P. shiqianensis* proves to be an error; the two species are consequently synonymous.

Ceriaster shiqianensis He & Li, 1974 *sensu* Kong & Huang (1978), from the lower Shihniulan Formation (upper Aeronian) of Banqiao, Zunyi area, northern Guizhou, is now reassigned to *Paraceriaster qijiangensis* (He, 1980), revised below.

***Paraceriaster fasciculatus* (Cao, 1975)**

(Figs 66–68)

?1959 *Stauria* (?) *minor* Chen, pp. 296, 297, pl. 7, fig. 2a–d. [*nomen dubium*]

?1963 *Stauria* (*Ceriaster*) *minor* (Chen); Yu *et al.*, p. 154, pl. 42, fig. 6a, b [refig. Chen 1959, pl. 7, fig. 2b, a].

non 1974 *Ceriaster* (*Eostauria*) *minor* (Chen); He & Li, p. 6, pl. 1, fig. 2a, b, pl. 2, fig. 1a, b.
1975 *Ceriaster minor* (Chen); Cao, p. 189, pl. 43, fig. 4a, b.
1975 *Ceriaster fasciculatus* Cao, p. 189, pl. 40, fig. 3a, b.
non 1978 *Ceriaster minor* (Chen); He, p. 143, pl. 71, fig. 3a, b.
non 1978 *Ceriaster minor* (Chen); Kong & Huang, p. 64, pl. 21, fig. 5a, b.
1982 *Ceriaster* (*Eostauria*) *fasciculatus* Cao; Cao & Lin, p. 34, pl. 9, fig. 7a, b [refig. Cao 1975, pl. 40, fig. 3a, b].
?1982 *Ceriaster minor* (Chen); Jiang, p. 82, pl. 46, fig. 9a, b.
?1983 *Ceriaster minor* (Chen); Deng *et al*., p. 11, pl. 10, figs 2a, b, 3, 4.
2006 *Paraceriaster micropora* Tang, p. 152, pl. 30, figs 1a–c, 2a–f.
non 2006 *Paraceriaster fasciculatus* (Cao); Tang, pp. 152, 153, pl. 29, figs 1, 4a–c.
2008b *Paraceriaster micropora* Tang in Tang *et al*., p. 434, pl. 3, figs 1a–c, 2a–f [refig. Tang 2006, pl. 30, figs 1a–c, 2a–f].
non 2008b *Paraceriaster fasciculatus* (Cao); Tang *et al*., pp. 434, 435, pl. 2, figs 3, 4a–c [refig. Tang 2006, pl. 29, figs 1, 4a–c].
2011 *Paraceriaster micropora* Tang in Tang *et al*.; Wang *et al*., pp. 456, 457, pl. 1, figs 16–19, pl. 2, figs 1, 2.
2020 *Paraceriaster micropora* Tang in Tang *et al*.; Wang & Cui, p. 230, pl. 7-79, fig. 1a, b [refig. Wang *et al*. 2011, pl. 2, figs 1, 2].

Referred material. – XACGS-G376, holotype, original of Cao (1975, pl. 40, fig. 3a, b), refigured here (Fig. 66), "middle Ningqiang Group" (now Wangjiawan Formation, lower Telychian) at Yingpanshan of the Mianxian area, Shaanxi. XACGS-G391, described by Cao (1975) as *Ceriaster minor* (Chen, 1959), original of Cao (1975, pl. 43, fig. 4a, b), refigured here (Fig. 67),

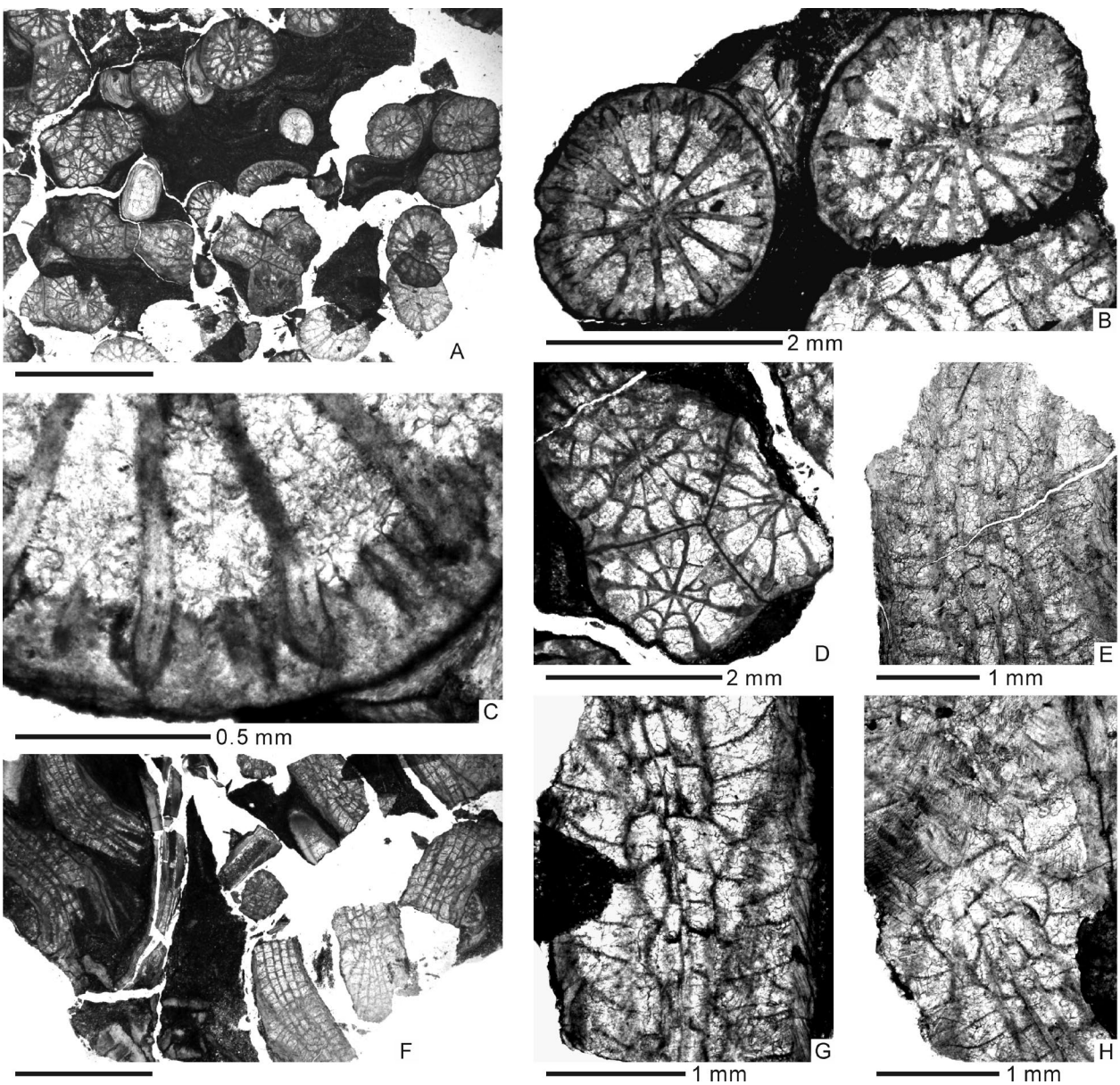


Fig. 66. Paraceriaster fasciculatus (Cao, 1975). XACGS-G376, holotype, "middle Ningqiang Group" (now Wangjiawan Formation, lower Telychian), Yingpanshan, Mianxian area, Shaanxi. **A–D,** TS and three enlarged portions. **E–H,** LS (**F**) and three enlarged portions (**E, G, H**). Scale bars are 5 mm unless otherwise indicated.

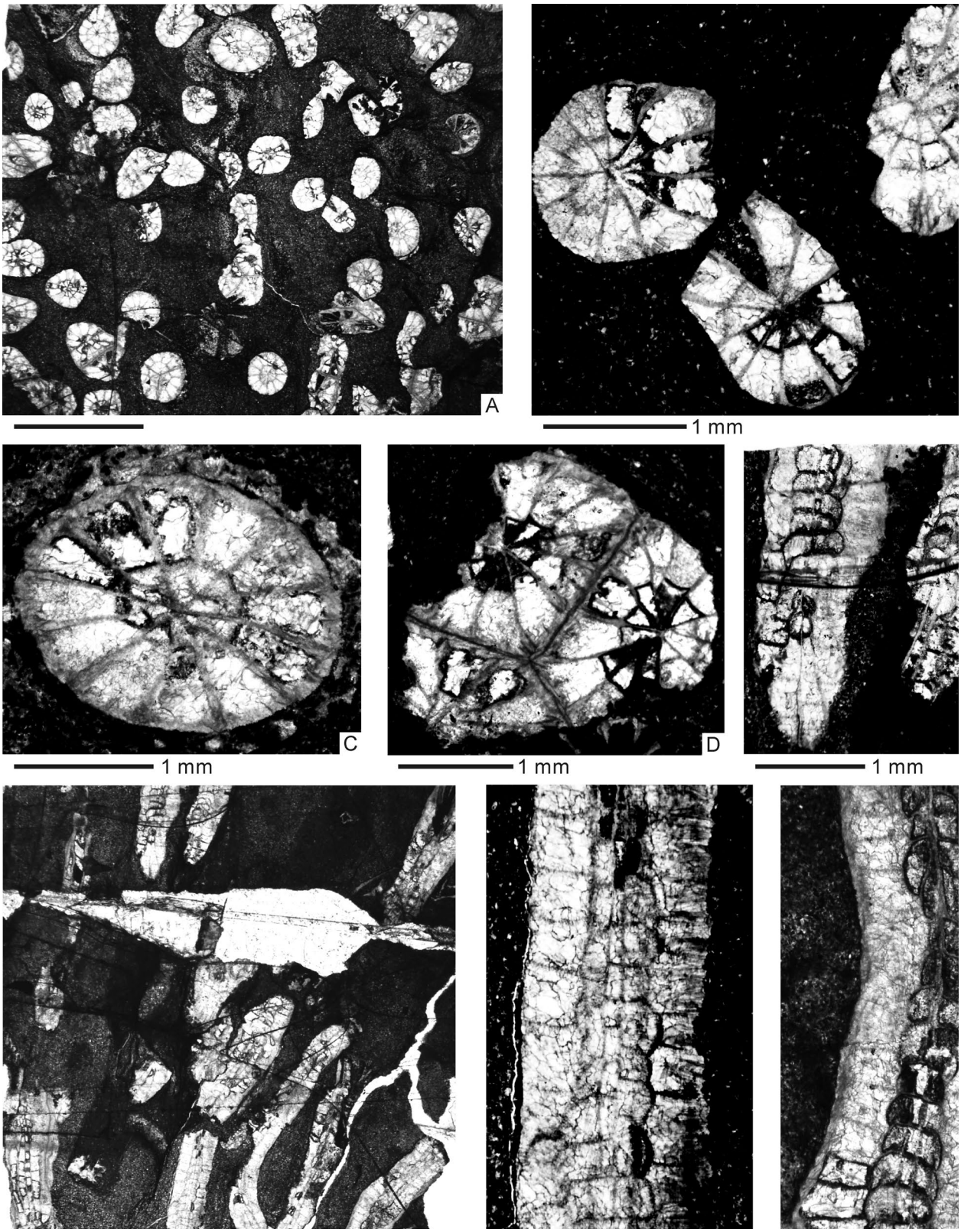


Fig. 67. Paraceriaster fasciculatus (Cao, 1975). XACGS-G391, described by Cao (1975) as *Ceriaster minor* (Chen, 1959), "middle Ningqiang Group" (probably the Wangjiawan Formation, lower Telychian) at Yingpanshan of the Mianxian area, Shaanxi. **A–D,** TS and three enlarged portions. **E–H,** LS (**F**) and three enlarged portions (**E, G, H**). Scale bars are 5 mm unless otherwise indicated.

"middle Ningqiang Group" (probably Wangjiawan Formation, lower Telychian) at Yingpanshan of the Mianxian area, Shaanxi. NIGP154128 (TS) and NIGP154129 (LS), described by Wang *et al.* (2011) as *Paraceriaster micropora* Tang in Tang *et al.*, 2008b, original of Wang *et al.* (2011, pl. 2, figs 1, 2), refigured here (Fig. 68), upper Baiyun'an Formation (lower Telychian), Sanbaiti, Huaying Mountain, eastern Sichuan.

Diagnosis. – *Paraceriaster* with very small corallites (adult diameters being 1.65–2.79 mm), 10–15 major septa generally connected in the corallite axis, minor septa weakly developed, commonly confined to peripheral stereozone. Tabulae incomplete, well differentiated into peripheral and axial zones.

Description. – Modified from Cao (1975, p. 189) and Wang *et al.* (2011, p. 456). Corallum fasciculate, with

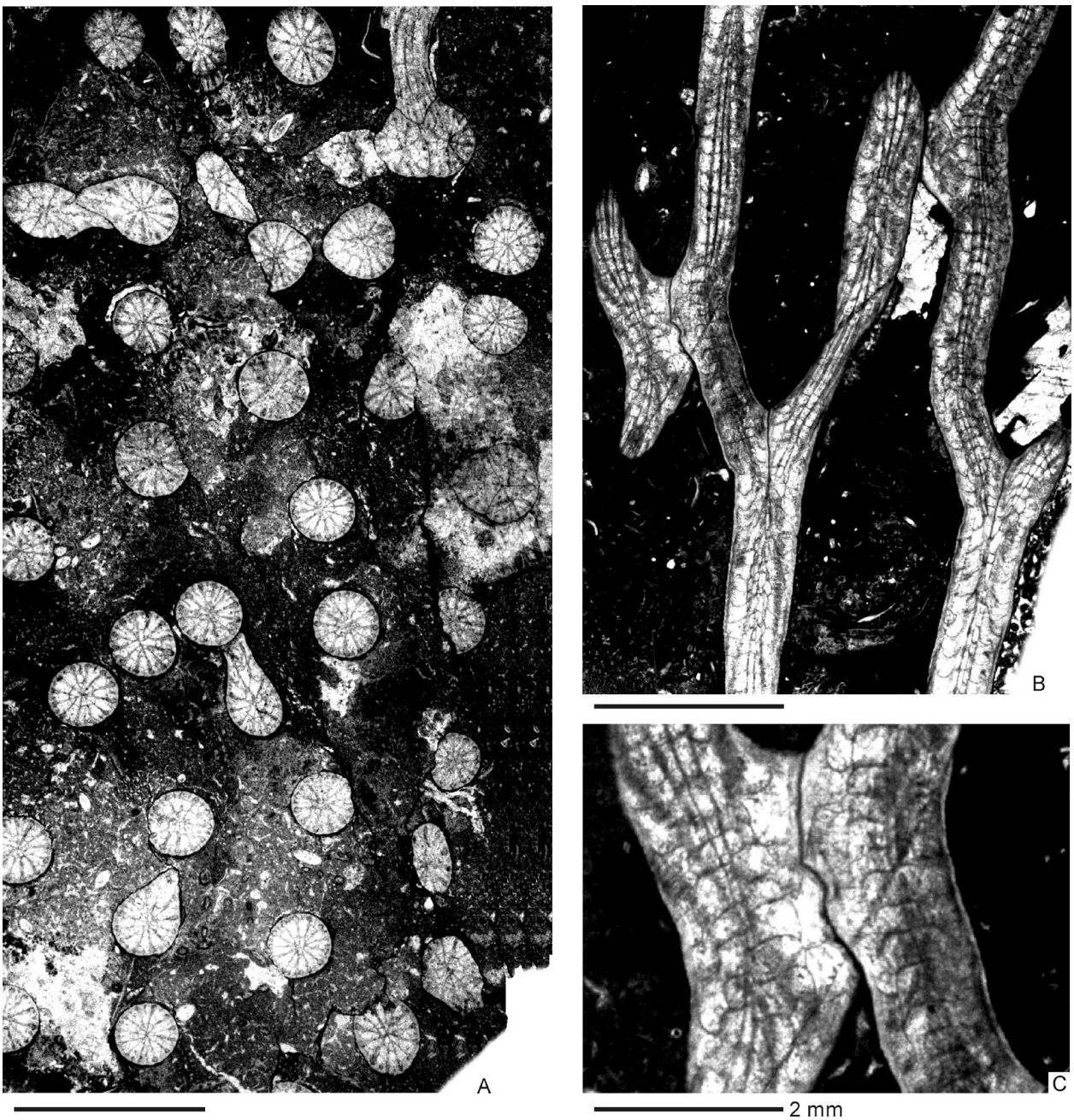


Fig. 68. Paraceriaster fasciculatus (Cao, 1975). NIGP154128 (TS) and NIGP154129 (LS) from one corallum, described by Wang *et al.* (2011) as *Paraceriaster micropora* Tang in Tang *et al.*, 2008b, upper Baiyun'an Formation (lower Telychian), Sanbaiti, Huaying Mountain, eastern Sichuan. **A,** TS. **B, C,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

external size and shape unknown. Increase of KA septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 1.65–2.79 mm. Septa of two orders, slightly to moderately dilated. Major septa 10–15, commonly 12–15, mostly connected in axis and sometimes forming a weak columella. Minor septa weakly developed, commonly confined to peripheral stereozone. Tabulae incomplete, generally arched axially, well differentiated into peripheral and axial zones. Tabular spacing wide (Ta5 commonly 10–13) in the peripheral zone, and slightly denser (Ta5 commonly 15–20) in the axial zone. Dissepiments are absent.

Remarks. – The revised diagnosis and description of *Paraceriaster fasciculatus* are based on its holotype, as well as two conspecific specimens previously described by Cao (1975) as *Ceriaster minor* (Chen, 1959) and by Wang *et al.* (2011) as *Paraceriaster micropora* Tang in Tang *et al*., 2008b, respectively, as noted above. The three specimens closely resemble one another in their increase mode, corallite size (mature diameters of 2.10–2.79, 1.63–2.34, and 1.65–2.11 mm, respectively), septal number (10–15, commonly 14–15, 11–13, commonly 12, and 10–12, commonly 12, respectively) and septal development (all having long major septa that generally meet in the corallite axis, and weak minor septa mostly confined to peripheral stereozone), as well as tabular differentiation. The differences chiefly lie in the slightly larger corallites and septal number of the former, which are best viewed as intraspecific variation.

Paraceriaster micropora Tang in Tang *et al*., 2008b, formerly also introduced as a new species in Tang's (2006) PhD thesis, has its type material (holotype, CUGB-SGM 0803; paratype, CUGB-SGM 0807) from the coeval Wangjiawan Formation (lower Telychian) of Modaoya, the Guangyuan area, northern Sichuan. It falls well within the variation of *P. fasciculatus* and is thus synonymous with the latter.

Stauria (?) *minor* Chen, 1959 comes probably from the lower member (lower Telychian) of the Wengxiang Formation in the Lushan area, eastern Guizhou. The original material forming the basis of this species comprises 5–6 well-preserved specimens housed at the "Institute of Geology, Ministry of Geology" (now Institute of Geology, Chinese Academy of Geological Sciences) (Chen 1959, p. 297; Pl. 1 caption). However, no type specimens were designated, and these specimens are not located for this work. This species may be a senior synonym of *Paraceriaster fasciculatus*, since it has comparable corallite size (1.6–2.0 mm in diameter), 10–13 thick major septa that generally extend to corallite axis, short minor septa generally confined within the peripheral stereozone, and "saddle-shaped" tabulae with Ta2 = 4–5 (Chen 1959, p. 297). However, considering that its increase mode is unknown and that its type material is probably lost, this taxon is best treated as *nomen dubium*. Also uncertain for the same reason is the status of *Ceriaster minor* (Chen, 1959) *sensu* Kong & Huang (1978), Jiang (1982) and Deng *et al*. (1983), from the upper Xiangshuyuan (lower Aeronian) of Wenjiadian, the Sinan area, northeastern Guizhou, "the lower Silurian" of Shimaxi, the Cili area, northwestern Hunan Province, and the Chenxiacun Formation (upper Aeronian) of the Hanshan area, central–eastern Anhui, respectively. For a detailed discussion on these forms, see remarks on the Stauriidae above.

The following forms are excluded here from *Paraceriaster fasciculatus*.

Ceriaster (*Eostauria*) *minor* (Chen, 1959) *sensu* He & Li (1974) comes from the Xiangshuyuan Formation of Pugou, the Shiqian area, northeastern Guizhou, and from the Lojoping Formation of Fenxiang, Yichang area, southwestern Hubei. This form is now considered as synonymous with *Yuina agglomorata* He & Li, 1974, considered below.

Ceriaster minor (Chen, 1959) of He (1978) is from the lower Huanggexi Formation (Aeronian) at Huangjingba, the Daguan area, northeastern Yunnan. Re-examination of her material indicates a reassignment to *Paraceriaster major* (Fan in He, 1978), considered above.

Paraceriaster fasciculatus (Cao, 1975) of Tang (2006) and Tang *et al*. (2008b) was recorded from the Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China, and the coeval Shihniulan Formation of Wenshui, Xishui area. It is revised here to *Eostauria* sp. B, considered above.

***Paraceriaster qijiangensis* (He, 1980)**

(Figs 69, 70; ?Fig. 71)

1978 *Ceriaster shiqianensis* He & Li; Kong & Huang, pp. 64, 65, pl. 20, fig. 6a, b.
1980 *Neoceriaster qijiangensis* He, p. 43, pl. 5, fig. 1a, b.
?1999 *Eostauria minor* (Chen); He & Chen, pp. 425, 426, pl. 1, fig. 5a, b.

Referred material. – NMRFC-Scr807, holotype of *Neoceriaster qijiangensis* He, 1980, original of He (1980, pl. 5, fig. 1a–c), refigured here (Fig. 69), Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. NIGP 205575, new specimen figured here (Fig. 70), Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou. NMRFC-TS9805 (LS) and NMRFC-TS9806 (TS) from one corallum, described by He & Chen (1999) as *Eostauria minor*

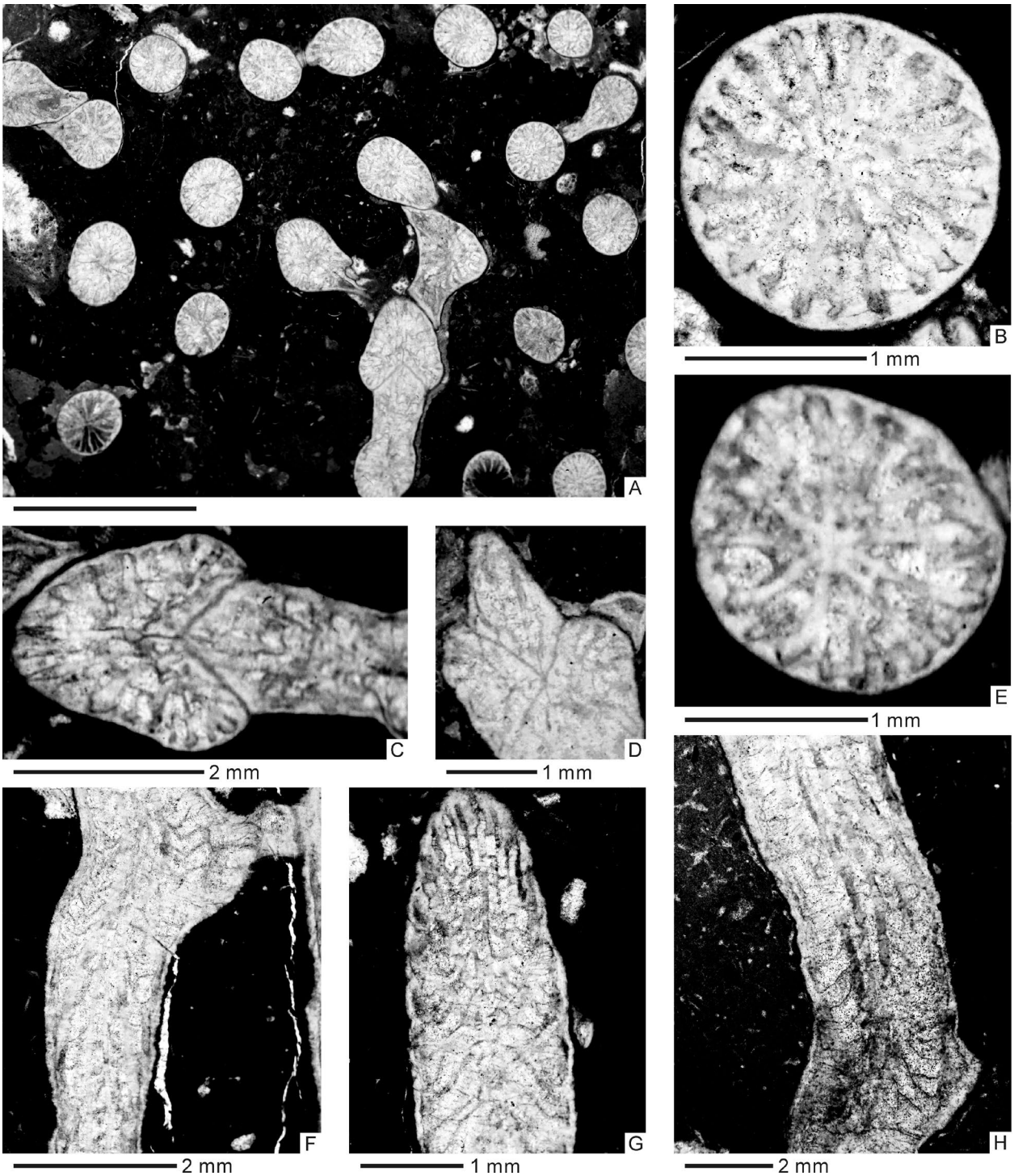


Fig. 69. Paraceriaster qijiangensis (He, 1980). NMRFC-Scr807, holotype, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B, C, E,** TS and three enlarged portions. **D,** oblique section. **F–H,** LSs. Scale bars are 5 mm unless otherwise indicated.

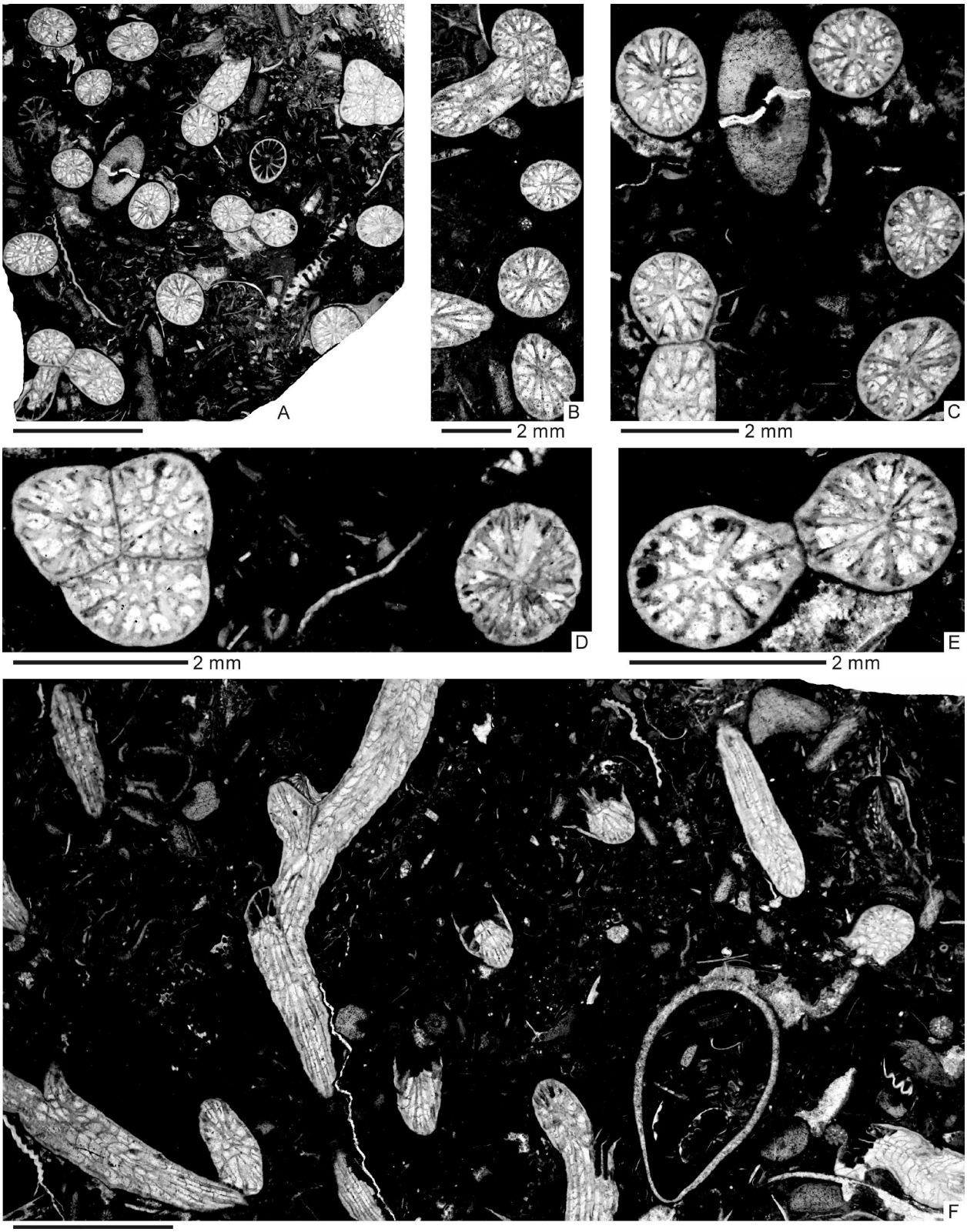


Fig. 70. Paraceriaster qijiangensis (He, 1980). NIGP 205575, Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A–E,** TSs (**A, B**) and three enlarged portions (**C–E**) of **A**. **F,** LS. Scale bars are 5 mm unless otherwise indicated.

(Chen, 1959), original of He & Chen (1999, pl. 1, fig. 5a, b), refigured here (Fig. 71), upper member (Aeronian) of the Lalong Formation, Gagu, Yiwa, Diebu area, southern Gansu Province, northwestern China.

Diagnosis. – *Paraceriaster* with very small corallites (less than 2 mm in diameter), and slightly to moderately dilated major septa. Three or more major septa connected in the corallite axis and sometimes forming a prominent columella. Minor septa well developed (up to 1/3–1/2 of corallite radius). Tabulae incomplete, well differentiated into peripheral and axial zones, widely spaced (Ta2 = 4–6).

Description. – Modified from He (1980, p. 43). Corallum fasciculate, with external size and shape unknown. Increase of KA septal parricidal type. Corallites cylindrical to subcylindrical, with adult diameters of 1.36–1.96 mm. Septa of two orders, slightly to moderately dilated. Major septa 11–14, commonly 12 in number, with three protosepta (i.e. counter and two alar) or more connected in axis and sometimes forming a prominent columella. Minor septa well developed, accounting for 1/3–1/2 of corallite radius. Tabulae generally incomplete, in arched series, well differentiated into peripheral and axial zones, widely spaced (Ta2 = 4–6).

Remarks. – The revised diagnosis and description of *Paraceriaster qijiangensis* are based on its holotype and a new specimen (NIGP 205575) that is considered here as conspecific, obtained from the coeval Leijiatun Formation (upper Aeronian) of the Shiqian area, northeastern Guizhou.

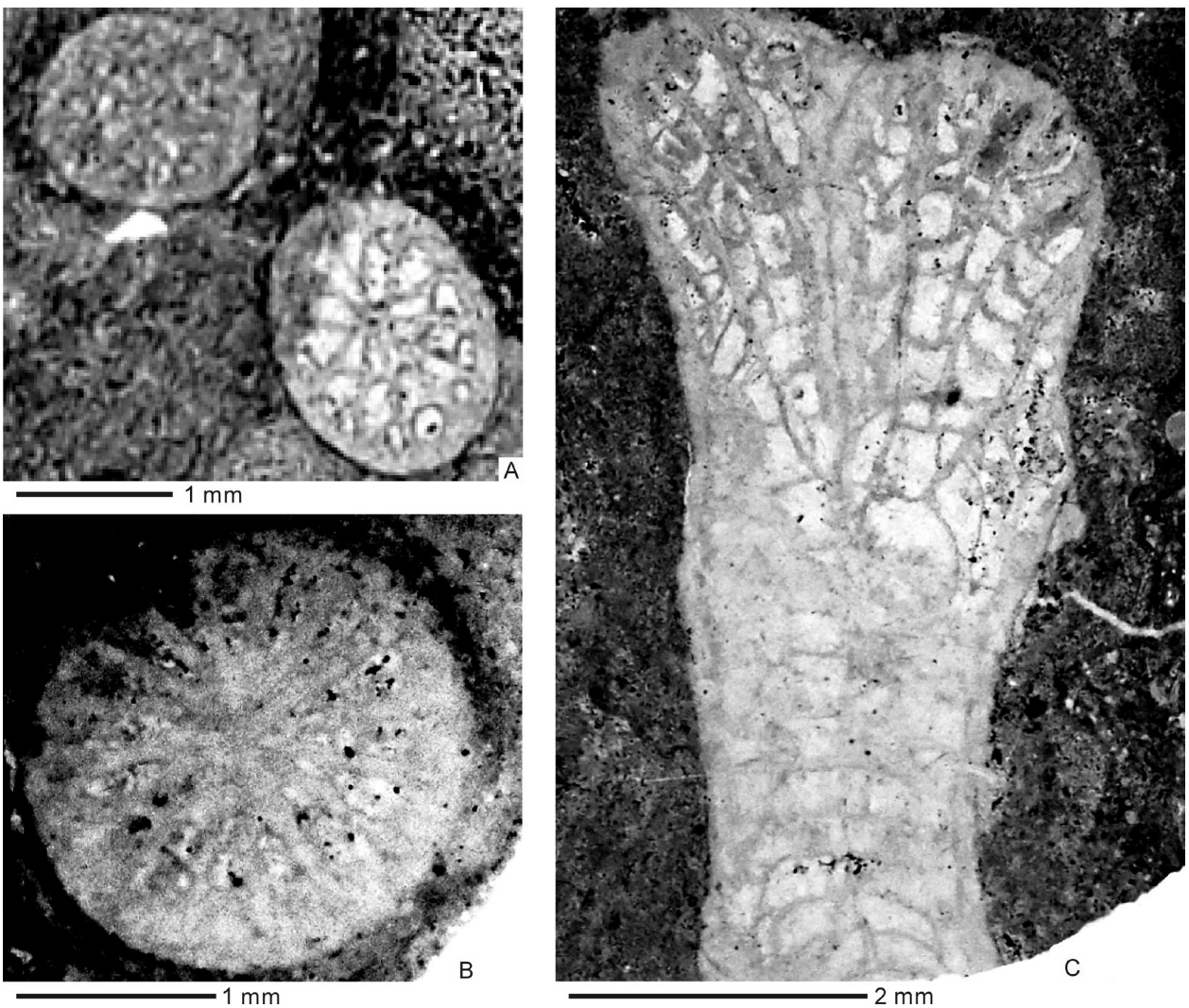


Fig. 71. Paraceriaster qijiangensis? (He, 1980). NMRFC-TS9805 (LS) and NMRFC-TS9806 (TS) from one corallum, described by He & Chen (1999) as *Eostauria minor* (Chen, 1959), upper member (Aeronian) of the Lalong Formation, Gagu, Yiwa, Diebu area, southern Gansu Province, northwestern China. **A, B,** TSs; **C,** LS.

Ceriaster shiqianensis He & Li, 1974 *sensu* Kong & Huang (1978) comes from the lower Shihniulan Formation (upper Aeronian) of Banqiao, Zunyi area, northern Guizhou. Its transfer to *Paraceriaster* is justified by the development of a KA septal parricidal increase pattern, as shown in illustrations of both the transverse and longitudinal sections (Kong & Huang 1978, pl. 20, fig. 6a, b), and the presence of tabular differentiation. Key specific features include small corallites (1.7–2.0 mm in diameter), 13–14 major septa with generally over 5 major septa meeting in the corallite axis, and well-developed minor septa (up to 1/3 of corallite radius). Consequently, this form is consistent with the concept of *Paraceriaster qijiangensis* rather than *P. shiqianensis* (He & Li, 1974), since the latter has significantly larger corallites (2.82–3.22 mm in diameter) and more septa that meet in the corallite axis.

The specimen described by He & Chen (1999) as *Eostauria minor* (Chen, 1959), refigured here (Fig. 71), comes from the coeval Lalong Formation of the Diebu area, southern Gansu, as noted above. It has similar corallite size (1.5–2.0 mm in diameter), major septal number (12), and development of weak columellae, as well as other features, and is probably a member of *Paraceriaster qijiangensis*. However, the lack of knowledge of its increase mode makes this identification tentative.

Paraceriaster cateniformis He & Li, 1983

(Figs 72, 73)

1983 *Paraceriaster cateniformis* He & Li, pp. 393, 394, pl. 1, fig. 3a, b, pl. 2, fig. 5a, b.

Referred material. – NMRFC-KS8002 (TS) and NMRFC-KS8001 (LS), holotype, original of He & Li (1983, pl. 1, fig. 3a, b), refigured here (Fig. 72), Shihniulan Formation (upper Aeronian), Dongkala, Fenggang area, northern Guizhou, southwestern China. NMRFC-KS8004 (TS) and NMRFC-KS8003 (LS), paratype, original of He & Li (1983, pl. 2, fig. 5a, b), refigured here (Fig. 73), Shihniulan Formation (upper Aeronian), Liangshuijing, Sinan area, northeastern Guizhou, southwestern China.

Diagnosis. – *Paraceriaster* with subcerioid to cateniform corallum, large corallites [ACDs (6+) = 3.58–4.38 mm], long major septa extending to, or almost to the corallite axis, long minor septa (up to about 50% of corallite radius), and narrow axial tabular zone (30–50% of corallite diameter).

Description. – Modified from He & Li (1983, p. 393). Corallum fasciculate, with external size and shape unknown. Increase of KA septal parricidal type. Corallites polygonal to subcylindrical, large [ACDs (6+) = 3.58–4.38 mm]. Marginarium a prominent peripheral stereozone, composed of dilated peripheral septal ends and thick lamellar stereome, with a maximum thickness up to about 20% of corallite radius. Septa of two orders, slightly dilated, tapering axially. Major septa 17–20 in number, extending to, or almost to the corallite axis, with three (i.e. counter and two alar) or more meeting there but without forming a prominent columella. Minor septa well-developed, variable in length, accounting for up to about 50% of corallite radius. Tabulae incomplete, moderately to strongly arched axially, well differentiated into peripheral and axial zones. The axial zone is narrow, accounting for 30–50% of corallite diameter. Tabular spacing variable, sparse (Ta2 = 2–4) in peripheral zone, and denser (Ta2 = 4–8) in axial zone. Dissepiments are absent.

Remarks. – The revised diagnosis and description of *Paraceriaster cateniformis* given above are based on a reconsideration of its holotype and paratype. A combination of its partly cerioid corallum, large corallite size, and distinctively narrow axial tabular zone serves to distinguish it from all other named species of *Paraceriaster*.

Genus *Massparaceriaster* Tang in Tang *et al.*, 2008b

2008b *Massparaceriaster* Tang in Tang *et al.*, p. 431.

Type species. – *Ceriaster ningqiangensis* Ge & Yu, 1974, Wangjiawan Formation (lower Telychian), Ningqiang area, southern Shaanxi Province, by original designation.

Diagnosis. – Paraceriasterinae n. subfam. with cerioid growth and tabulae that are differentiated into axial and peripheral zones.

Remarks. – *Massparaceriaster* is essentially a cerioid edition of *Paraceriaster*, as noted above. It differs from the other cerioid form of the Paraceriasterinae n. subfam., *Ceriaster* Lindström, 1883, in having tabular differentiation. *Massparaceriaster ningqiangensis* (Ge & Yu, 1974), from the lower Telychian of South China, is the only known species at present.

*Massparaceriaster ningqiangens*is (Ge & Yu, 1974)

(Fig. 74)

1974 *Ceriaster ningqiangensis* Ge & Yu, pp. 166, 167, pl. 74, figs 9, 10.

1975 *Ceriaster calamites* Lindström; Cao, p. 188, pl. 41, figs 1a, b, 2a, b.

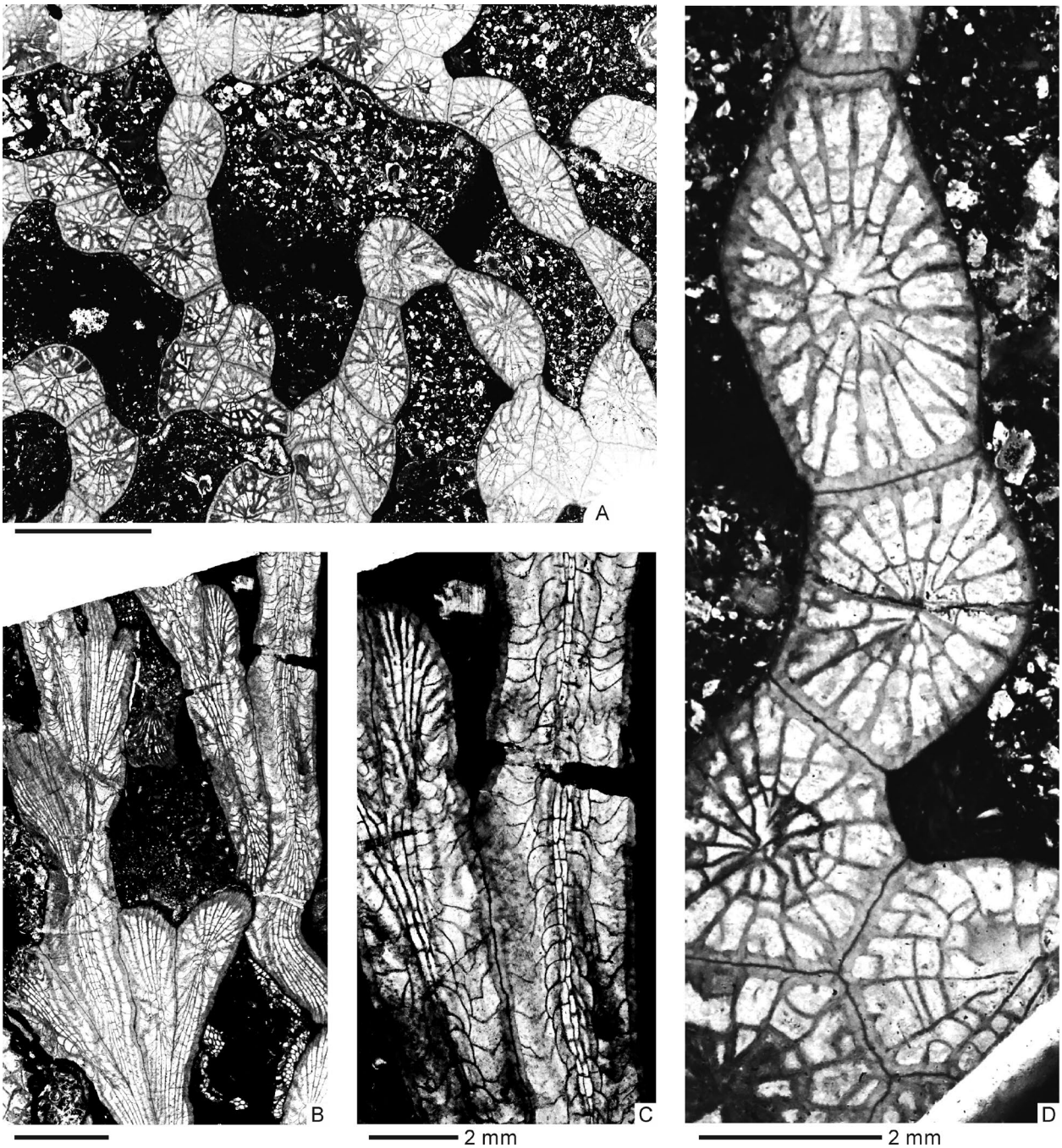


Fig. 72. Paraceriaster cateniformis (He & Li, 1983). NMRFC-KS8002 (TS) and NMRFC-KS8001 (LS), holotype, Shihniulan Formation (upper Aeronian), Dongkala, Fenggang area, northern Guizhou, southwestern China. **A, D,** TS and an enlarged portion. **B, C,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

1982 *Ceriaster* (*Ceriaster*) *calamites* Lindström; Cao & Lin, p. 33, pl. 10, fig. 7a, b [refig. Cao 1975, pl. 41, fig. 1a, b].
2006 *Massparaceriaster ningqiangensis* (Ge & Yu); Tang, p. 155.
2008b *Massparaceriaster ningqiangensis* (Ge & Yu); Tang *et al.*, p. 435, pl. 3, fig. 5a, b [refig. Ge & Yu 1974, pl. 74, figs 9, 10].

Referred material. – XACGS-G378, described by Cao (1975) as *Ceriaster calamites* Lindström, 1883, original of Cao (1975, pl. 41, fig. 2a, b), refigured here (Fig. 74), "middle Ningqiang Group" (now Wangjiawan

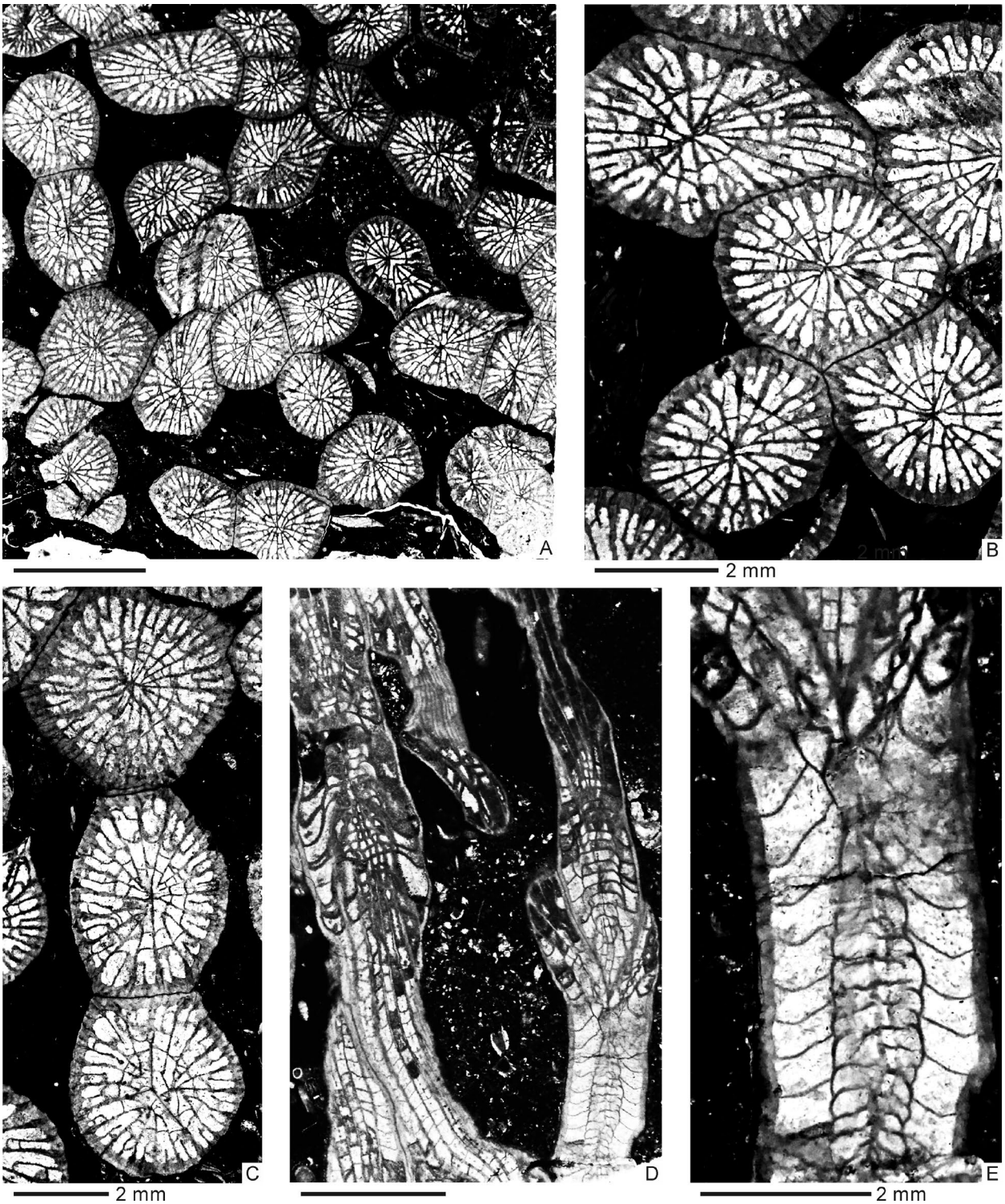


Fig. 73. Paraceriaster cateniformis (He & Li, 1983). NMRFC-KS8004 (TS) and NMRFC-KS8003 (LS), paratype, Shihniulan Formation (upper Aeronian), Liangshuijing, Sinan area, northeastern Guizhou, southwestern China. **A–C,** TS and two enlarged portions. **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

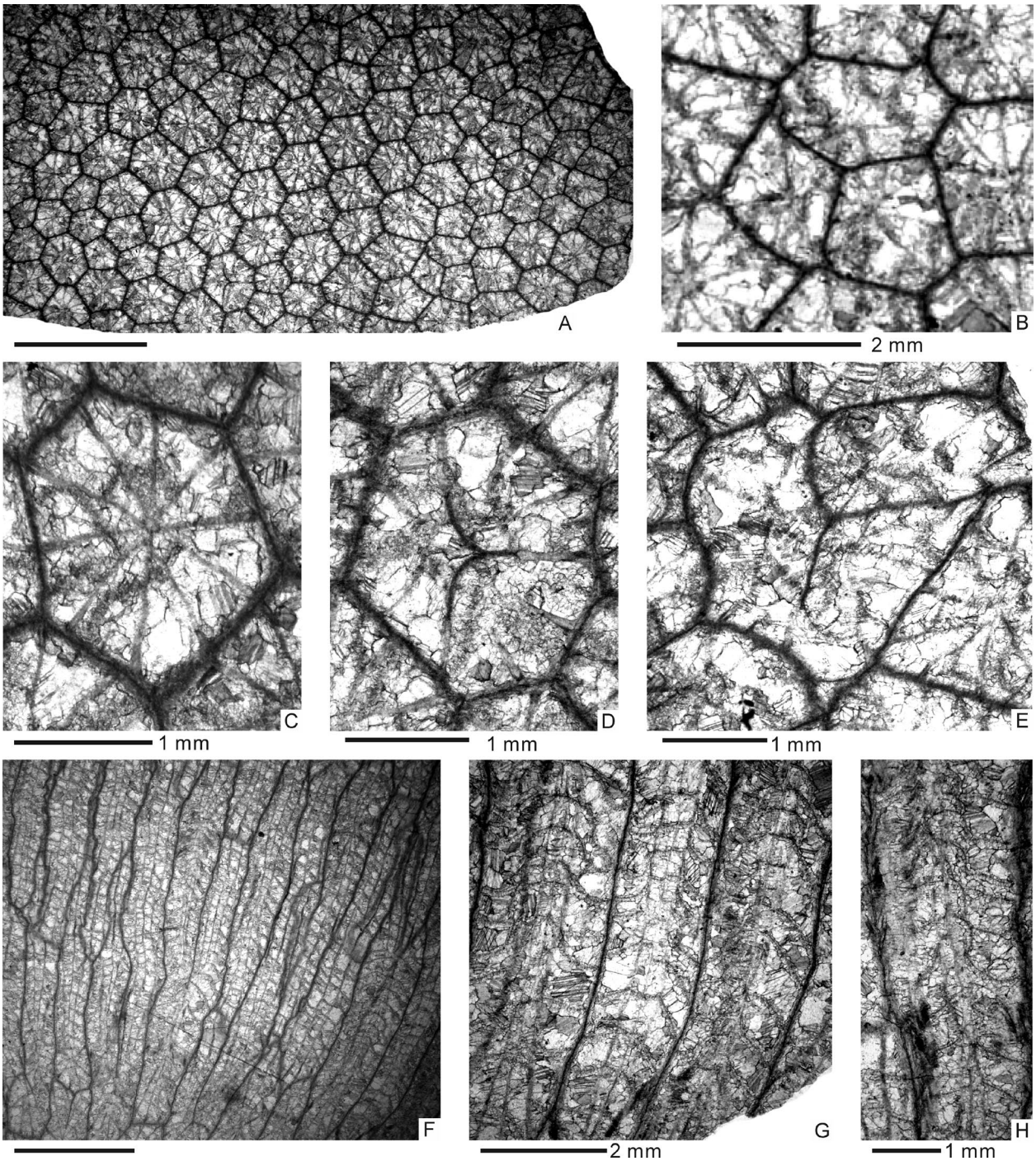


Fig. 74. Massparaceriaster ningqiangensis (Ge & Yu, 1974). XACGS-G378, described by Cao (1975) as *Ceriaster calamites* Lindström, 1883, "middle Ningqiang Group" (now Wangjiawan Formation, lower Telychian), Tianchiliang, Nanzheng area, southwestern Shaanxi. **A–E,** TS and four enlarged portions. **F–H,** LS (**F**) and two enlarged portions (**G, H**). Scale bars are 5 mm unless otherwise indicated.

Formation; Cao & Lin 1982, p. 33), lower Telychian, Tianchiliang, Nanzheng area, southwestern Shaanxi.

Diagnosis. – *Massparaceriaster* with small corallites [ACDs (6+) = 1.53–2.53 mm]. Major septa 10–12 in number, meeting in the corallite axis. Minor septa very short to almost absent. Tabulae widely spaced (Ta5 = 7–9).

Description. – Modified from Ge & Yu (1974, pp. 166, 167). The external size and shape of the holotype [NIGP22106 (LS) and NIGP22107 (TS)] unknown. Increase of KA septal parricidal type (Fig. 74B, D, E). Corallites polygonal, 5–7, mostly 6 sided, small [ACDs (6+) = 1.53–2.53 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders, thin, slightly tapering axially. Major septa 10–12 in number, meeting in the corallite axis but without forming a prominent columella. Minor septa weakly developed, very short to almost absent. Tabulae differentiated into peripheral and axial zones, widths of axial zone accounting for about 45–50% of corallite diameter. Tabulae widely spaced (Ta5 = 7–9). Dissepiments are absent.

Remarks. – As noted above, *Massparaceriaster ningqiangensis* is the type and only known species of the genus. Its holotype, refigured by Tang *et al.* (2008b), from the Wangjiawan Formation (lower Telychian) of the Ningqiang area, southern Shaanxi, has unfortunately not been located for the present study, which is probably lost. The diagnosis and description of this species presented above are chiefly based on a clearly conspecific specimen formerly described by Cao (1975) as *Ceriaster calamites* Lindström, 1883.

Subfamily Heininae n. subfam.

Diagnosis. – Stauriidae with a septal parricidal increase occurring at two counter-lateral, two alar, and cardinal septa (i.e. KLAC septal parricidal increase).

Remarks. – As noted above, Heininae n. subfam. is proposed for stauriid corals with the KLAC septal parricidal increase. The following three genera are assigned here to this subfamily: *Heina* n. gen., *Parastauria* He & Li, 1974 and *Yuina*, n. gen.

Genus *Heina* n. gen.

Type species. – *Neoceriaster rarisepta* He, 1980, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

Derivation of name. – To honour both Xinyi He and Yuanxiang He, for their outstanding work on stauriid rugose corals.

Diagnosis. – Heininae n. subfam. having cerioid coralla and lacking dissepiments.

Remarks. – The new genus differs from *Parastauria* He & Li, 1974 in lacking dissepiments, and from *Yuina*, n. gen. in being cerioid.

Heina rarisepta (He, 1980)

(Fig. 75)

1980 *Neoceriaster rarisepta* He, pp. 43, 44, pl. 3, fig. 1a, b.

Referred material. – NMRFC-Scr799, holotype, original of He (1980, pl. 3, fig. 1a, b), refigured here (Fig. 75), Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

Diagnosis. – *Heina* n. gen. with small corallites [ACDs (6+) = 1.30–2.40 mm]. Major septa consistently 5 in number, meeting in the corallite axis and forming a prominent, solid columella. Minor septa up to 3/4 of corallite radius. Tabulae slightly arched, widely spaced (Ta5 = 5–8).

Description. – Modified from He (1980, p. 43). The single specimen cerioid, with external form and size unknown. Increase mode of KLAC septal parricidal type. Corallites polygonal, 4–9, commonly 5–7 sided, small [ACDs (6+) = 1.30–2.40 mm]. Corallite walls straight to slightly wavy, moderately thick, accounting for up to 18% of corallite radius, separated by prominent dark lines. Septa of two orders, moderately thick, slightly tapering axially. Major septa consistently 5 in number, connected in the corallite axis and forming a prominent, solid columella. Minor septa well-developed, relatively long, generally up to 2/3–3/4 of corallite radius. Tabulae complete, or rarely incomplete, subhorizontal to slightly arched, widely spaced (Ta5 = 5–8).

Remarks. – The revised description and diagnosis of *Heina rarisepta* are based on a restudy of its holotype. A combination of its consistent septal number, and persistent, solid columellae serves to separate it from *Heina* sp., the other *Heina* species known from the slightly older, Xiangshuyuan Formation (upper Llandovery–lower Aeronian) of the Sinan area, northeastern Guizhou. For a further discussion, see remarks under *Heina* sp. below.

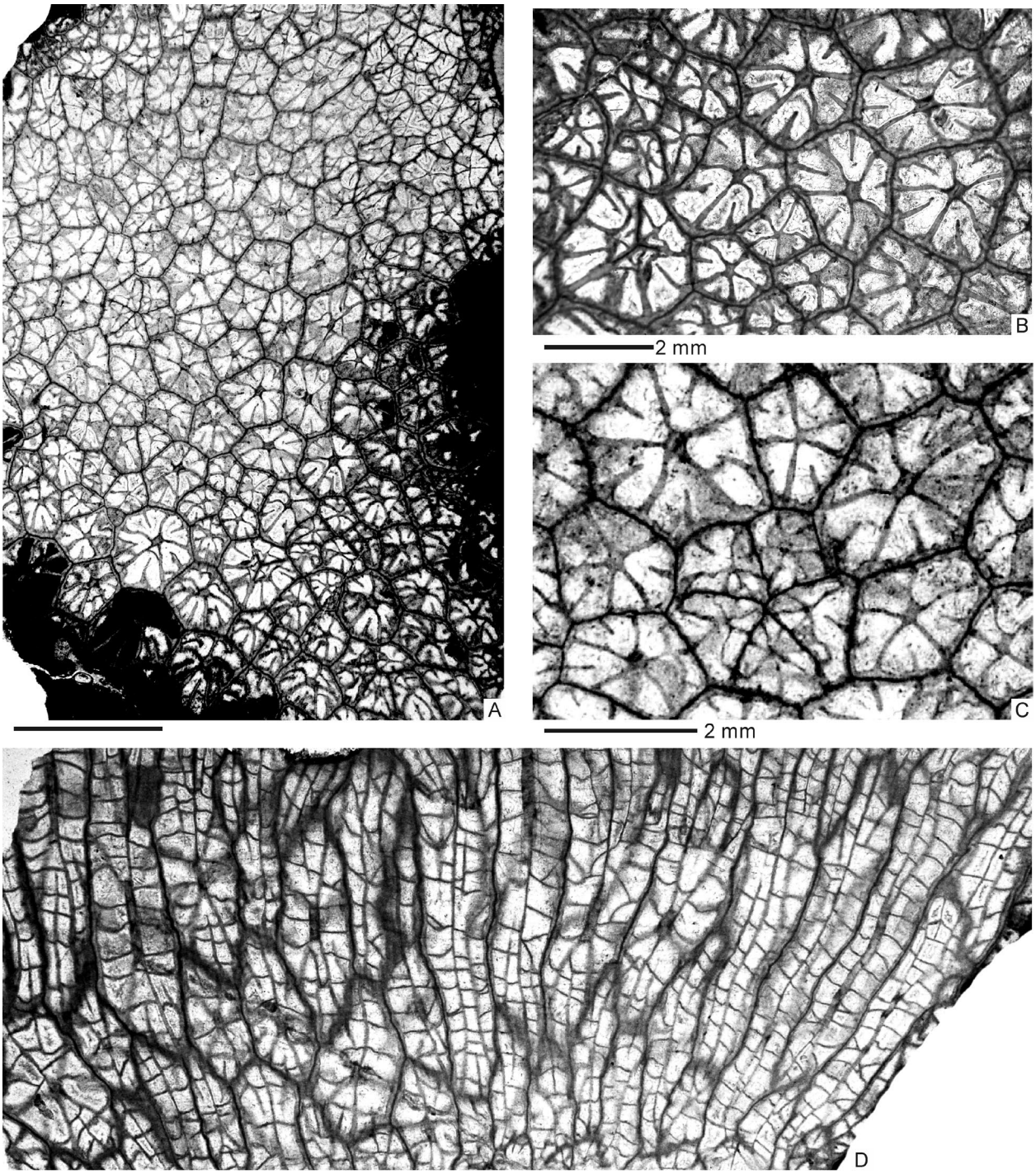


Fig. 75. Heina rarisepta (He, 1980). NMRFC-Scr799, holotype, Shihniulan Formation (upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

Heina sp.

1974 *Ceriaster* (*Ceriaster*) *calamites* Lindström; He & Li, pp. 7, 8, pl. 3, fig. 1a, b, pl. 5, 2a, b.
1978 *Ceriaster calamites* Lindström; Kong & Huang, p. 64, pl. 20, fig. 7a, b [refig. He & Li 1974, pl. 3, fig. 1a, b].
2006 *Ceriaster calamites* Lindström; Tang, p. 146, pl. 28, fig. 1a–c.
2008b *Ceriaster calamites* Lindström; Tang *et al*., pl. 1, fig. 1a–c [refig. Tang 2006, pl. 28, fig. 1a–c].

Remarks. – The conspecific materials described as *Ceriaster calamites* Lindström, 1883 by He & Li (1974) and Tang (2006) was later refigured by Kong & Huang (1978) and Tang *et al*. (2008b), respectively. Both come from the Xiangshuyuan Formation (upper Llandovery–lower Aeronian) of Liangshuijing, Sinan area, northeastern Guizhou. They exhibit a cerioid growth habit with a "pentapartite increase" (He & Li 1974, p. 7, pl. 3, fig. 1a), a feature also clearly shown in much better figures of the material given by Tang (2006, pl. 28, fig. 1a–c), and this justifies a reassignment to *Heina* n. gen. Its specific characteristics include small corallites (1.5–3.5, commonly 2.2–3.0 in diameter), 7–11, generally 10 major septa with more than 5 meeting in the axis, weakly developed minor septa (up to 1/5–1/4 of the radius), and complete, flat to axially arched, widely spaced tabulae (0.40–0.84 mm apart) (He & Li 1974).

Heina rarisepta (He, 1980), considered above, is the only other congeneric form. It comes from the slightly younger, Shihniulan Formation (upper Aeronian) of the Qijiang area, southern Chongqing, and shows comparable tabular development. However, this form is readily separated from the form described here by having smaller corallites [ACDs (6+) = 1.30–2.40 mm], consistent septal number, and more prominent columella. The latter thus represents a distinct species. However, due to the limited fossil material available, a precise definition remains unattainable, necessitating the adoption of an open nomenclature at present.

Genus *Parastauria* He & Li, 1974

1974 *Parastauria* He & Li, pp. 9, 10.

Type species. – *Parastauria polygonalis* He & Li, 1974, Shihniulan Formation (upper Aeronian), Xinglong, Meitan area, northern Guizhou, by original designation.

Diagnosis. – Heininae n. subfam. with cerioid coralla and one intermittent or persistent series of dissepiments.

Remarks. – *Parastauria* was originally introduced for *Stauria*-like forms but with one persistent series of dissepiments, and McLean & Copper (2013) regarded it as possibly synonymous with *Stauria* Milne-Edwards & Haime, 1850. However, its type species, *P. polygonalis* He & Li, 1974, redescribed below, shows a distinctive KLAC septal parricidal increase, and is therefore treated as a distinct genus belonging to the Heininae n. subfam. Unlike the other two genera of the subfamily, *Heina* n. gen. and *Yuina* n. gen., *Parastauria* is separated by developing dissepiments. *Yuina* n. gen. further differs in being fasciculate.

A further similar form is *Elizabethia* Sytova in Sytova & Ulitina, 1983, with the type species *Tenuiphyllum crassum* Sytova, 1979b from the "upper Silurian" of central Tuva. It resembles *Parastauria* in its cerioid coralla and the development of dissepiments, differing in having an increase mode of "lateral budding" (Sytova & Ulitina 1983, p. 120).

Parastauria is now known to be confined to the Llandovery rocks of South China and western Tuva, as discussed below. In the former region, apart from the type species, Tang *et al*. (2008b) reassigned to this genus *Stauria leijiatunensis* He, 1980, *S. huayinshanensis* He, 1980, *S. xikouensis* He, 1980, and *S. guanyinqiaoensis* He, 1980. Additional species transferred here to *Parastauria* include *Stauria shiqianensis* Ge & Yu, 1974 and *Stauria liangfengyaensis* He, 1980. In western Tuva, *Elizabethia occulta* Sytova in Sytova & Ulitina, 1983 and *E. modica* Sytova in Sytova & Ulitina, 1983, both from the Alash Horizon (upper Rhuddanian–lower Aeronian; Sennikov *et al*. 2015), are transferred here to *Parastauria*.

Parastauria polygonalis He & Li, 1974

(Fig. 76)

1974 *Parastauria polygonalis* He & Li, p. 10, pl. 2, fig. 3, pl. 4, fig. 1a, b, pl. 5, fig. 4a, b.
1978 *Parastauria polygonalis* He & Li; Kong & Huang, p. 65, pl. 20, fig. 3a, b.
non 1980 *Stauria polygonalis* (He & Li); He, p. 39, pl. 2, fig. 2a, b.
2006 *Stauria polygonalis* (He & Li); Tang, pp. 156, 157, pl. 28, fig. 4a–d.
2008b *Parastauria polygonalis* He & Li; Tang *et al*., pp. 435, 436, pl. 1, fig. 4a–d [refig. Tang 2006, pl. 28, fig. 4a–d].

Referred material. – NMRFC-KS020 (TS) and NMRFC-KS021 (LS)], holotype, original of He & Li (1974, pl. 4, fig. 1a, b), refigured here (Fig. 76), Shihniulan Formation (upper Aeronian), Xinglong, Meitan area, northern Guizhou, southwestern China.

Diagnosis. – *Parastauria* with small corallites [ACDs (6+) = 2.28–3.24 mm]. Dissepimentarium narrow. Tabulae strongly arched axially.

Description. – Modified from He & Li (1974, p. 10). The holotype is complete, of domical external form, about 100 mm wide and 60 mm high. Increase of KLAC

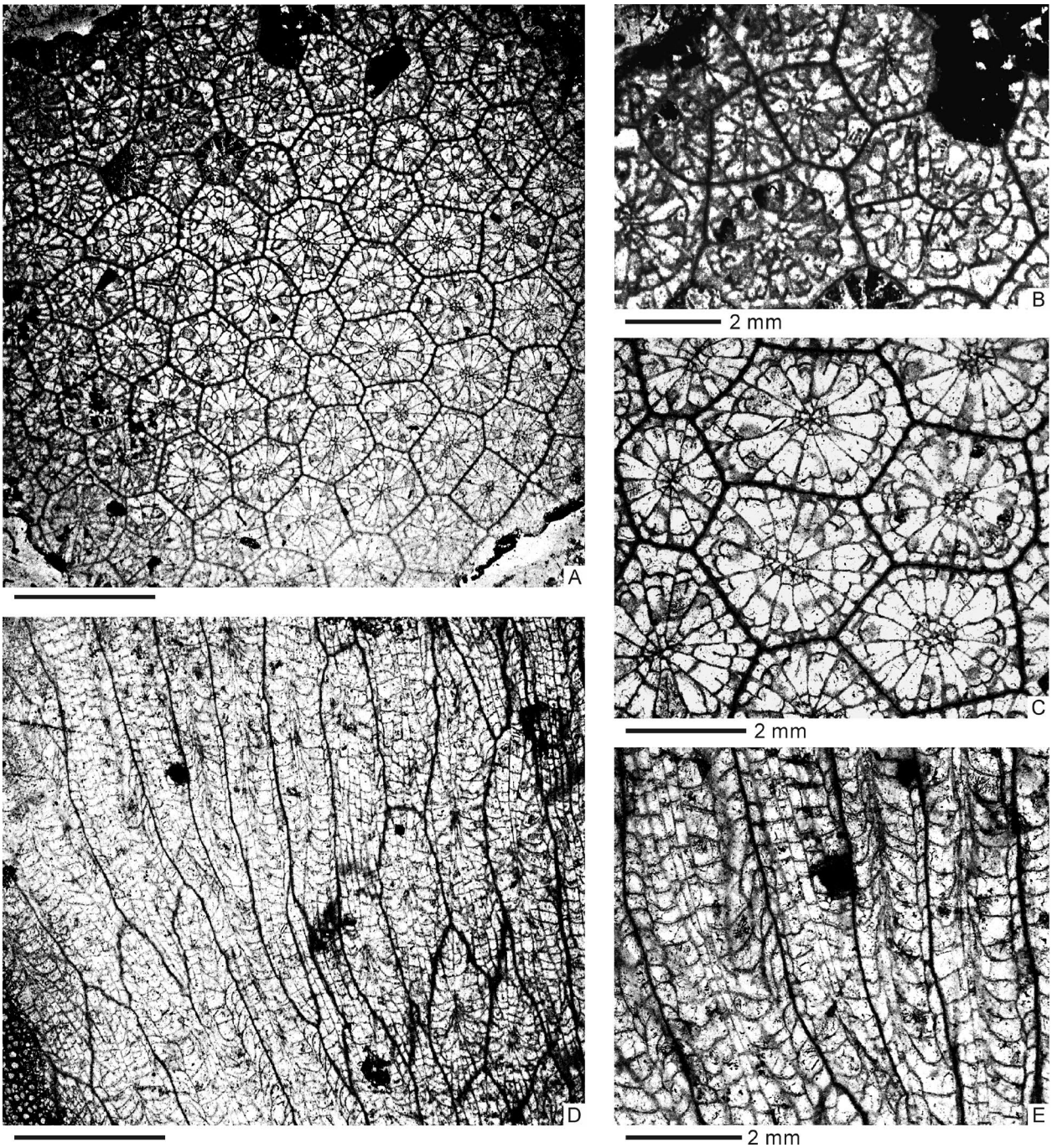


Fig. 76. Parastauria polygonalis He & Li, 1974. NMRFC-KS020 (TS) and NMRFC-KS021 (LS)], holotype, Shihniulan Formation (upper Aeronian), Xinglong, Meitan area, northern Guizhou southwestern China. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

septal parricidal type. Corallites polygonal, 4–7, commonly 6 sided, small [ACDs (6+) = 2.28–3.24 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders, thin. Major septa 8–14, commonly 12–14 in number, mostly meeting in the corallite axis but without forming a prominent columella. Minor septa well developed, relatively short, extending within, or slightly beyond the dissepimentarium. Dissepimentarium narrow, consisting of a single, almost persistent row of generally large, subglobose to strongly elongate dissepiments. Tabularium sharply delineated from dissepimentarium. Tabulae complete, strongly arched axially. Tabular spacing moderate (Ta5 = 10–12).

Remarks. – As well as one TS and LS of the holotype of *Parastauria polygonalis* documented by He & Li (1974), four additional thin sections of this specimen were illustrated by Tang (2006, pl. 28, fig. 4a–d) and refigured by Tang *et al.* (2008b, pl. 1, fig. 4a–d). However, only the former two thin sections are located, forming the basis of the present revision. Based on available data, *Parastauria polygonalis* is characterised by strongly arched tabulae and a narrow dissepimentarium consisting of a single persistent row of dissepiments, a combination of which serves to distinguish it from all other described species of the genus.

Parastauria polygonalis He & Li, 1974 *sensu* He & Li in Kong & Huang (1978) comes from the Shihniulan Formation (upper Aeronian) of the nearby Zheng'an area, northern Guizhou. Although not clearly illustrated, the description of this material indicates that it is identical to the holotype of this species. Thus, I consider it as a probable example of *P. polygonalis*.

Stauria polygonalis (He & Li, 1974) of He (1980), from the Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou was suggested by Tang *et al.* (2008b, p. 436) as a separate species. I agree with their conclusion and identify it as *Parastauria huayinshanensis* (He, 1980), discussed below.

***Parastauria shiqianensis* (Ge & Yu, 1974)**

(Fig. 77)

1974 *Stauria shiqianensis* Ge & Yu, p. 167, pl. 75, figs 5, 6.
1978 *Stauria favosa sinensis* He & Huang in Kong & Huang, p. 63, pl. 20, fig. 2a, b.
1978 *Stauria shiqianensis* Ge & Yu; Kong & Huang, p. 63, pl. 20, fig. 1a, b [refig. Ge & Yu 1974, pl. 75, figs 5, 6].
non 2006 *Stauria sinensis* (He & Huang); Tang, p. 156, pl. 28, fig. 2a–c, pl. 32, fig. 4a, b.
2006 *Parastauria tenuisepta* Tang, p. 160, pl. 32, fig. 3a–d.
non 2008b *Stauria sinensis* (He & Huang); Tang *et al.*, p. 435, pl. 1, fig. 2a–c [refig. Tang 2006, pl. 28, fig. 2a–c].
2020 *Stauria shiqianensis* Ge & Yu; Wang & Cui, p. 224, pl. 7-76, fig. 3a, b [refig. Ge & Yu 1974, pl. 75, figs 5, 6].

Referred material. – NIGP22112 (TS) and NIGP22113 (LS), holotype, original of Ge & Yu (1974, pl. 75, figs 5, 6), refigured here (Fig. 77), Xiangshuyuan Formation (upper Llandovery–lower Aeronian), Baisha, Shiqian area, northeastern Guizhou Province.

Diagnosis. – *Parastauria* with large corallites [ACDs (6+) = 3.09–4.60 mm] and one intermittent row of dissepiments. Tabulae complete or incomplete, slightly concave or convex, moderately spaced (Ta5 = 14–16).

Description. – Modified from Ge & Yu (1974, p. 167). The external size and shape of the holotype unknown. Increase of typical KLAC septal parricidal type. Corallites polygonal, commonly 6 sided, medium-sized [ACDs (6+) = 3.09–4.60 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders, thin. In mature corallites, major septa 15–17, 5 meeting in the corallite axis, whereas others relatively short, extending almost to the axis. Minor septa short, confined to dissepimentarium. Dissepimentarium narrow, consisting of a single, persistent or intermittent row of dissepiments. Where present, dissepiments subglobose to strongly elongate, variable in size. Tabularium sharply delineated from dissepimentarium. Tabulae complete or incomplete, wavy, slightly concave or convex, moderately spaced (Ta5 = 14–16).

Remarks. – The holotype of *Parastauria shiqianensis*, refigured by Kong & Huang (1978) and Wang & Cui (2020), is redescribed, and the concept of this species is thereby revised.

Stauria favosa sinensis He & Huang in Kong & Huang, 1978, from the same horizon and locality as the holotype of *Parastauria shiqianensis*, was synonymised by Tang *et al.* (2008b, p. 429) with *Stauria tenuisepta* He, 1980, considered above, whose type material comes from the slightly younger Leijiatun Formation (upper Aeronian) at Leijiatun of the same area. However, *Stauria favosa sinensis* clearly differs in having a very different, "pentapartite increase pattern" (Kong & Huang 1978, p. 63, pl. 20, fig. 2a), and fewer major septa. Instead, it is essentially identical to *Parastauria shiqianensis* apart from having slightly weaker development of dissepiments, as also noted by Kong & Huang (1978, p. 63). The two species are thus considered here as synonymous.

Parastauria tenuisepta Tang, 2006 is a further species from the same horizon and locality as the holotype of *P. shiqianensis*. It shows slightly smaller corallites (2.5–3.0 mm in diameter) but is otherwise like the latter, and this supports its placement within *P. shiqianensis*.

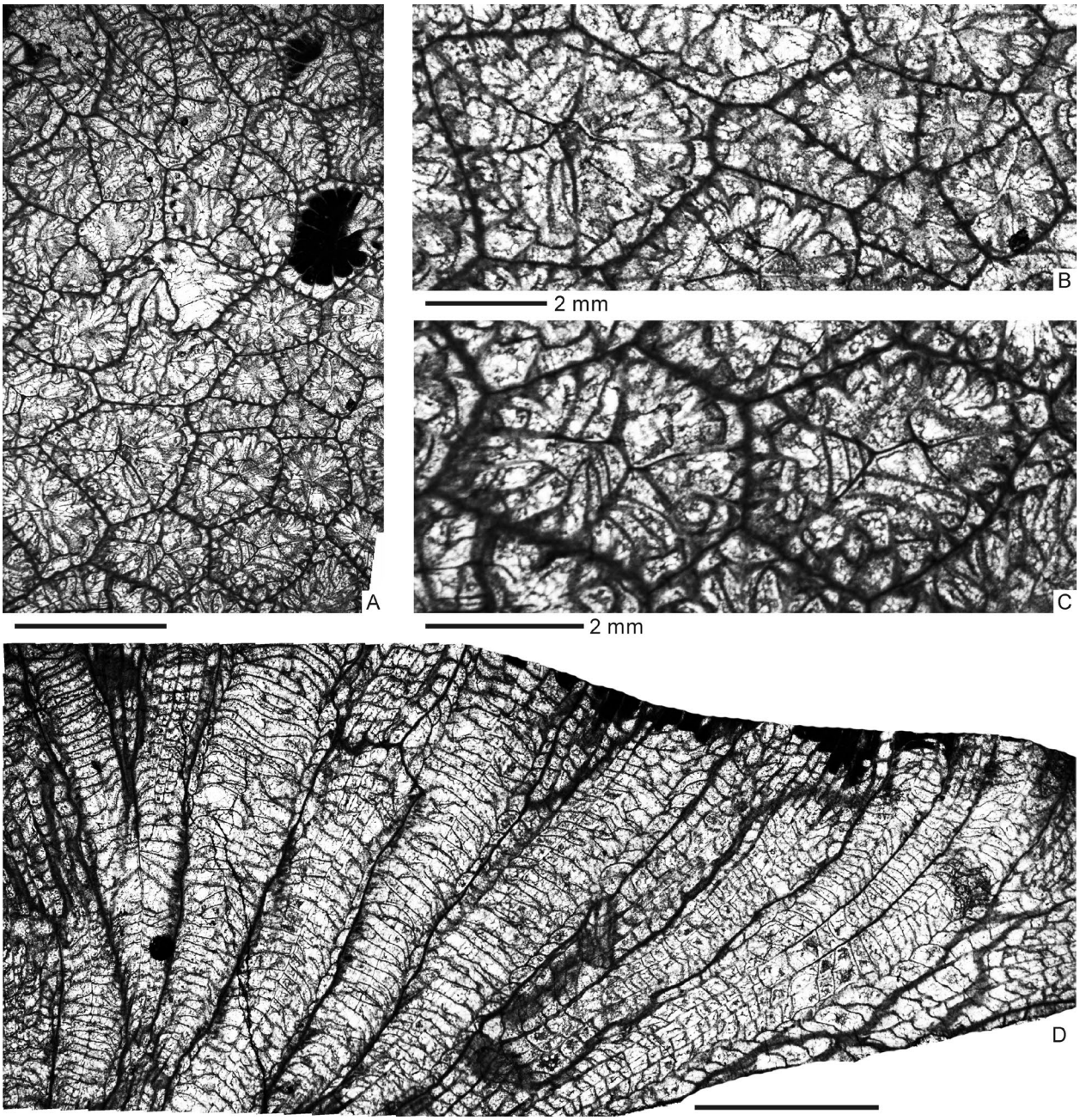


Fig. 77. Parastauria shiqianensis (Ge & Yu, 1974). NIGP22112 (TS) and NIGP22113 (LS), holotype, Xiangshuyuan Formation (upper Rhuddanian–lower Aeronian), Baisha, Shiqian area, northeastern Guizhou. **A–C,** TS and two enlarged portions; **D,** LS. Scale bars are 5 mm unless otherwise indicated.

Closest similarities lie with *Parastauria leijiatunensis* (He, 1980), considered below, from the Leijiatun Formation (upper Aeronian) of the same area. It exhibits comparable corallite size [ACDs (6+) = 1.85–4.86 mm], but is distinguishable by having much weaker development of minor septa, and a wider dissepimentarium consisting of one persistent row of dissepiments.

The material documented by Tang (2006) and refigured by Tang *et al.* (2008b) as *Stauria sinensis* (He & Huang in Kong & Huang, 1978), from the Leijiatun Formation (upper Aeronian) at Leijiatun of the Shiqian area, northeastern Guizhou, is clearly not the species itself, which is synonymised here with *Stauria tenuisepta* He, 1980, discussed above.

***Parastauria leijiatunensis* (He, 1980)**

(Fig. 78)

1980 *Stauria leijiatunensis* He, p. 39, pl. 1, fig. 1a, b.
non 1996 *Stauria leijiatunensis* He; Deng & Scrutton, pl. 12, figs 3, 4.

Referred material. – NMRFC-Scr791, holotype, original of He (1980, pl. 1, fig. 1a, b), refigured here (Fig. 78), Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China.

Diagnosis. – *Parastauria* with variably sized corallites [ACDs (6+) = 1.85–4.86 mm], and wide dissepimentarium consisting of one single persistent row of dissepiments.

Description. – Modified from He (1980, p. 39). The external size and shape of the holotype unknown. Increase of KLAC septal parricidal type. Corallites polygonal, 4–7 sided, variable in size [ACDs (6+) = 1.85–4.86 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Major septa 11–15 in number, commonly meeting in the corallite axis but without forming a prominent columella. Minor septa very weakly developed, almost absent to absent. Dissepimentarium wide, up to about 55% of corallite radius, consisting of one single, persistent row of dissepiments. Dissepiments relatively large, subglobose to flat, with somewhat flattened upper surfaces. Tabularium sharply delineated from dissepimentarium. Tabulae complete or sometimes incomplete, slightly to moderately convex, closely spaced (Ta5 = 14–16).

Remarks. – The holotype of *Parastauria leijiatunensis* is re-examined here and the concept of this species is thereby revised. Its comparison with a similar form, *P. shiqianensis* (Ge & Yu, 1974), from the Xiangshuyuan Formation (upper Llandovery–lower Aeronian) of the same area, is presented above.

The form initially described by Deng & Scrutton (1996) as *Stauria leijiatunensis* and later revised by Scrutton & Deng (2002) as a new *Stauria* species is found in the Shihniulan Formation (upper Aeronian) of the Tongzi area, northern Guizhou. Exhibiting a KAC septal parricidal increase, it is now considered a potential undescribed species of *Stauria*, as discussed above.

***Parastauria huayinshanensis* (He, 1980)**

(Figs 79, 80)

1980 *Stauria huayinshanensis* He, p. 39, pl. 2, fig. 1a, b.
1980 *Stauria polygonalis* (He & Li); He, p. 39, pl. 2, fig. 2a, b.
1980 *Stauria xikouensis* He, p. 40, pl. 2, fig. 4a, b.

Referred material. – NMRFC-Scr795, holotype, original of He (1980, pl. 2, fig. 1a, b), refigured here (Fig. 79). NMRFC-Scr798, holotype of *Stauria xikouensis* He, 1980, original of He (1980, pl. 2, fig. 4a, b), refigured here (Fig. 80). Both specimens from the "upper Lojoping Formation" (now Baiyun'an Formation, lower Telychian; Wang *et al*. 2011), Xikou, Huaying Mountain, eastern Sichuan.

Diagnosis. – *Parastauria* with small corallites [ACDs (6+) = 1.38–2.42 mm], and 6–9 major septa commonly meeting in the corallite axis. Minor septa weakly developed to almost absent. Dissepimentarium variably wide (about 30–60% of corallite diameter), consisting of one single intermittent row of dissepiments. Tabulae complete, widely spaced (Ta5 = 8–14).

Description. – Modified from He (1980, pp. 39, 40). The external size and shape of the holotype unknown. Increase of typical KLAC septal parricidal type. Corallites polygonal, 4–6 sided, small [ACDs (6+) = 1.38–2.42 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Major septa 6–9 in number, commonly meeting in the corallite axis but without forming a prominent columella. Minor septa weakly developed to almost absent. Dissepimentarium variable in width, accounting for about 30–60% of corallite diameter, consisting of one single intermittent row of dissepiments. Dissepiments small to relatively large, subglobose to flat, with somewhat flattened upper surfaces. Tabularium sharply delineated from dissepimentarium. Tabulae complete, slightly convex, widely spaced (Ta5 = 8–14).

Remarks. – The revised concept of the present form is based on a reassessment of the holotypes of *Stauria huayinshanensis* He, 1980 and *S. xikouensis* He, 1980, considered here as synonymous. As noted above, both specimens come from the Baiyun'an Formation (lower Telychian) of Huaying Mountain, eastern Sichuan. The former shows a KLAC increase pattern, small corallites [ACDs (6+) = 1.45–2.42 mm], 7–9 major septa commonly meeting in the corallite axis without forming a prominent columella, weakly developed minor septa that are almost absent, variably wide dissepimentarium (45–60%, rarely up to about 35%, of corallite diameter), one single intermittent row of dissepiments, and complete, slightly convex, widely spaced tabulae (Ta5 = 13–14). By comparison, the holotype of *S. xikouensis* He, 1980 shows no substantial difference, having the same increase mode, comparable corallite size [ACDs (6+) = 1.38–2.05 mm], major

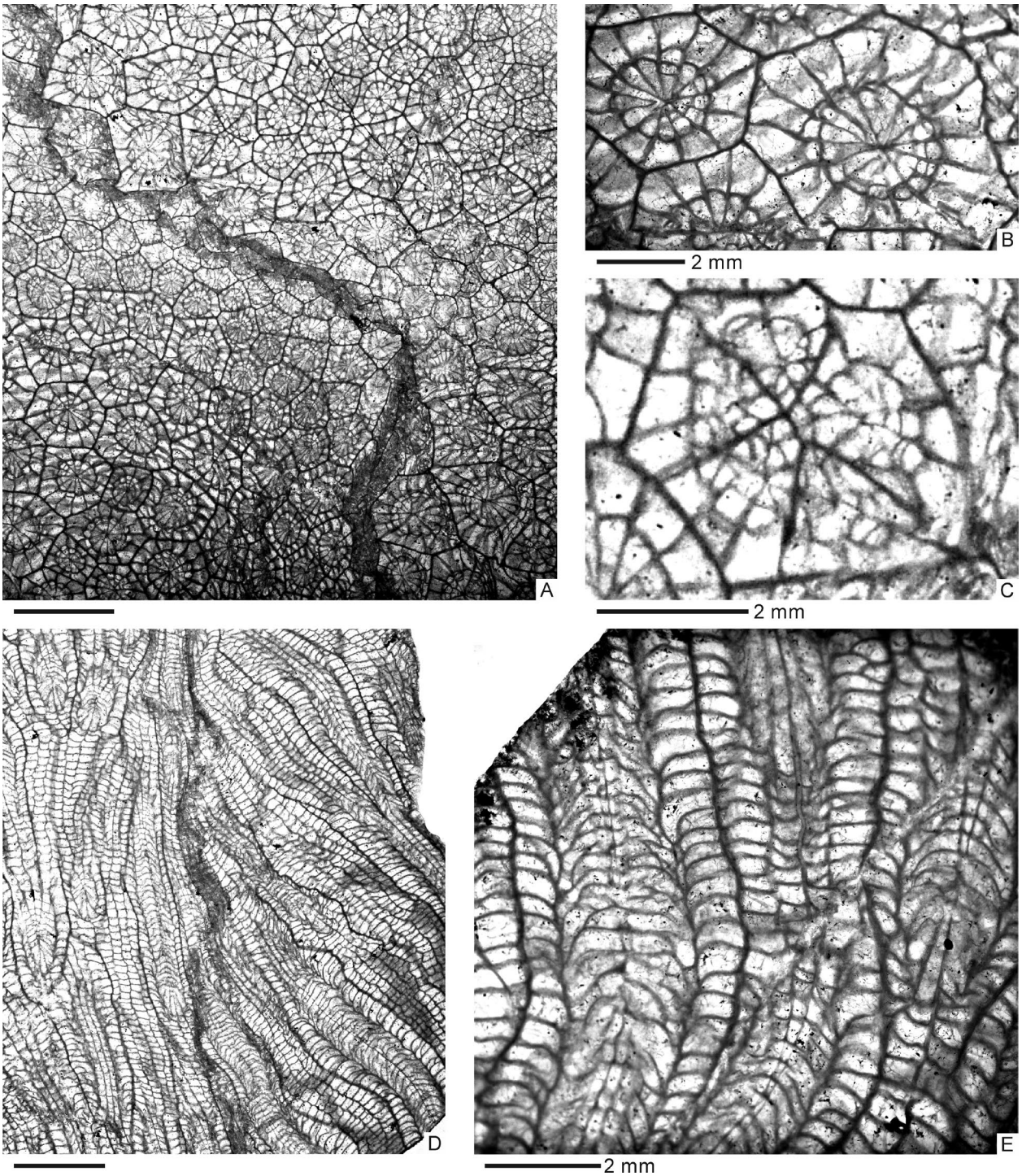


Fig. 78. Parastauria leijiatunensis (He, 1980). NMRFC-Scr791, holotype, Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

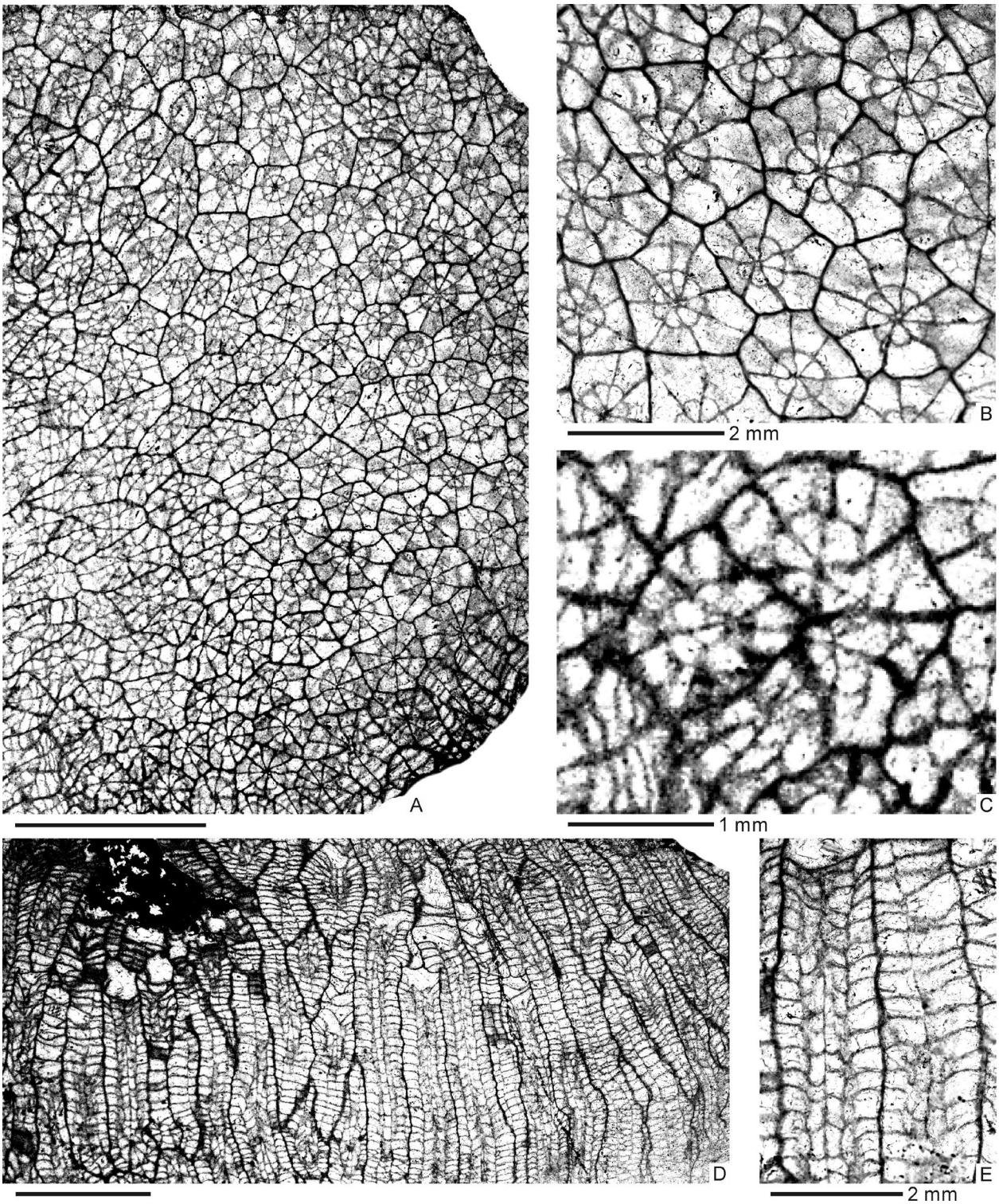


Fig. 79. Parastauria huayinshanensis (He, 1980). NMRFC-Scr795, holotype, "upper Lojoping Formation" (now Baiyun'an Formation, lower Telychian), Huaying Mountain, eastern Sichuan. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

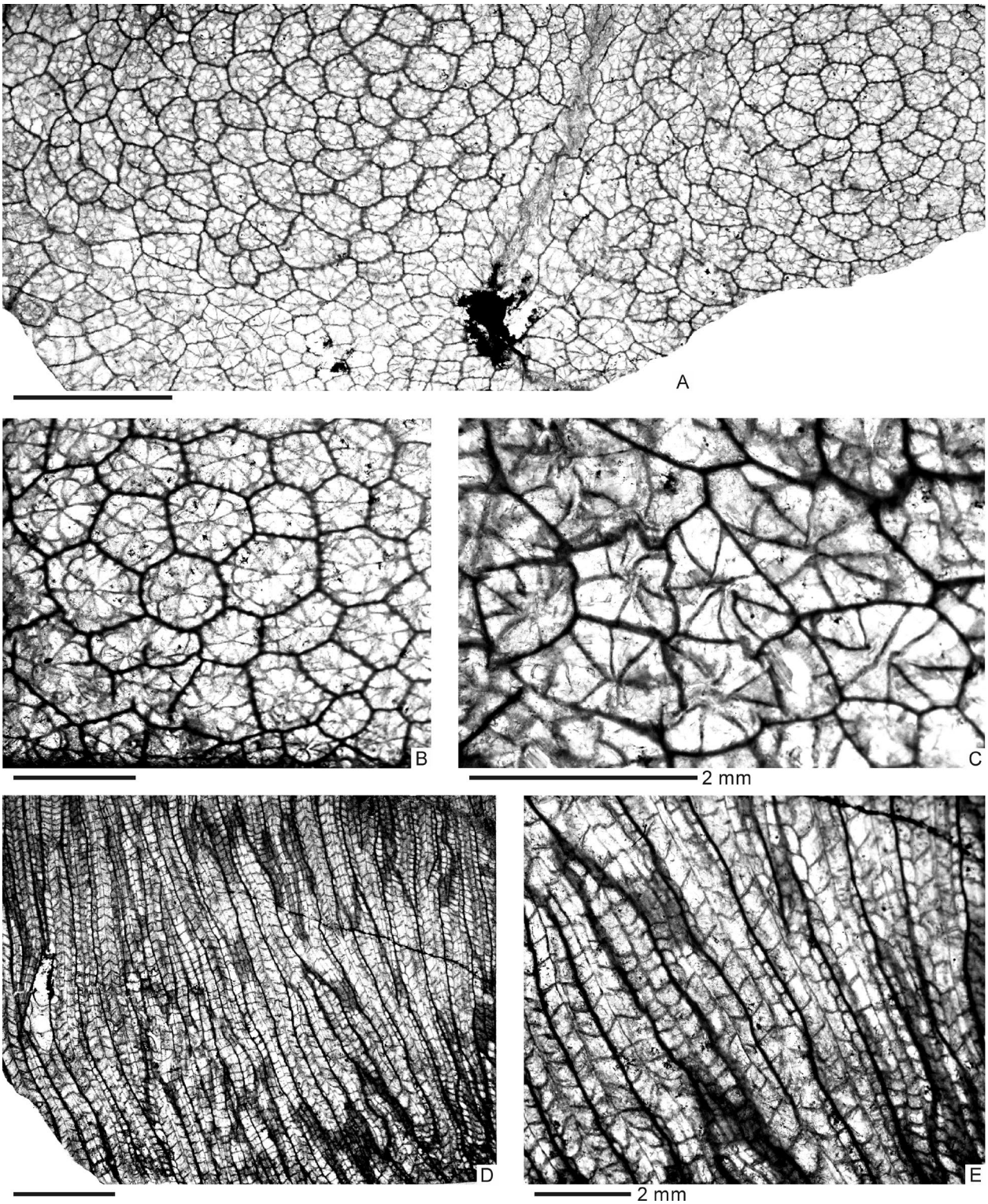


Fig. 80. Parastauria huayinshanensis (He, 1980). NMRFC-Scr798, holotype of *Stauria xikouensis* He, 1980, "upper Lojoping Formation" (now upper Baiyun'an Formation, lower Telychian), Huaying Mountain, eastern Sichuan. **A–C,** TS and two enlarged portions; **D, E,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

septal number (6–8), width of dissepimentarium (about 20–50% of corallite diameter), minor septal development and general tabular features (Ta5 = 8–12). He (1980) commented that their major difference lies in the width of dissepimentarium, which in my view is best considered as intraspecific variation. The present reassignment of this species to *Parastauria* is because of its KLAC increase pattern.

The specimen described by He (1980) as *Stauria polygonalis* (He & Li, 1974) comes from the Leijiatun Formation (upper Aeronian) at Leijiatun of the Shiqian area, northeastern Guizhou. This form has a KLAC increase type (He 1980, pl. 2, fig. 2a), corallites of 2–3 mm in diameter, about 9 major septa that are all connected in the corallite axis, weakly developed minor septa, narrow dissepimentarium consisting of one single persistent row of dissepiments, and slightly arched tabulae with Ta5 = 15. Therefore, it agrees well with the revised concept of *Parastauria huayinshanensis* and is included within the latter. Note that this specimen was formerly considered by Tang (2006) as conspecific with her *Parastauria tenuisepta* sp. nov., a species regarded here as a junior synonym of *P. shiqianensis* Ge & Yu, 1974, discussed above.

Among the species assigned to *Parastauria*, *P. liangfengyaensis* (He, 1980), considered below, from the Sifengya Formation (lower Telychian) of the Daguan area, northeastern Yunnan, shows striking similarities to *P. huayinshanensis* in many aspects, particularly in the corallite size [ACDs (6+) = 1.78–2.75 mm], long major septa commonly meeting in the corallite axis, very weak development of minor septa, dissepiments that occur in one single intermittent series, and complete, widely spaced tabulae (Ta5 = 11–13). However, it appears to be distinguishable by more major septa (7–12, commonly 10–12 in number) and much weaker development of dissepiments. The two forms may eventually prove to be conspecific but are provisionally treated as separate due to the limited knowledge of their variation.

Parastauria guanyinqiaoensis (He, 1980), revised below, from the coeval Hanchiatien Formation (lower Telychian) of the Qijiang area, southern Chongqing, shows corallite size [ACDs (6+) = 1.97–2.53 mm] similar to *P. huayinshanensis*. However, it can be easily separable by having fewer septa that meet in the corallite axis, much better development of minor septa and one persistent series of dissepiments, as well as partly incomplete, denser tabulae, as discussed under that species below.

***Parastauria liangfengyaensis* (He, 1980)**

(Fig. 81)

1980 *Stauria liangfengyaensis* He, p. 40, pl. 2, fig. 3a, b.

Referred material. – NMRFC-Scr797, holotype, original of He (1980, pl. 2, fig. 3a, b), refigured here (Fig. 81), Sifengya Formation (lower Telychian), Liangfengya, Huangjingba, Daguan area, northeastern Yunnan, southwestern China.

Diagnosis. – *Parastauria* with small corallites [ACDs (6+) = 1.78–2.75 mm], 7–12, commonly 10–12 major septa meeting in the corallite axis, narrow dissepimentarium consisting of one single, intermittent row of dissepiments, and complete, axially arched, widely spaced tabulae (Ta5 = 11–13).

Description. – Modified from He (1980, p. 40). The external size and shape of the holotype unknown. Increase of KLAC septal parricidal type. Corallites polygonal, 4–7 sided, small [ACDs (6+) = 1.78–2.75 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders, slightly dilated, tapering axially. Major septa 7–12, commonly 10–12 in number, commonly meeting in the corallite axis but without forming a prominent columella. Minor septa short to almost absent, up to about 20% of corallite radius. Dissepimentarium comparatively narrow, consisting of one single, intermittent row of dissepiments. Dissepiments relatively small, subglobose to elongate. Tabularium sharply delineated from dissepimentarium. Tabulae complete, slightly convex, widely spaced (Ta5 = 11–13).

Remarks. – The diagnosis and description of *Parastauria liangfengyaensis* given above are based on a reassessment of its holotype. A comparison with a closely similar form, *P. huayinshanensis* (He, 1980) from the coeval, upper Baiyun'an Formation (lower Telychian) of Huaying Mountain, eastern Sichuan, is discussed above under the latter species, and does not need repeating here.

***Parastauria guanyinqiaoensis* (He, 1980)**

(Fig. 82)

1980 *Stauria guanyinqiaoensis* He, p. 40, pl. 3, fig. 4a, b.

Referred material. – NMRFC-Scr802, holotype, original of He (1980, pl. 3, fig. 4a, b), refigured here (Fig. 82), Hanchiatien Formation (lower Telychian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

Diagnosis. – *Parastauria* with small corallites [ACDs (6+) = 1.97–2.53 mm], commonly 5 protosepta meeting in the corallite axis, well-developed minor septa, and one persistent row of dissepiments. Tabulae

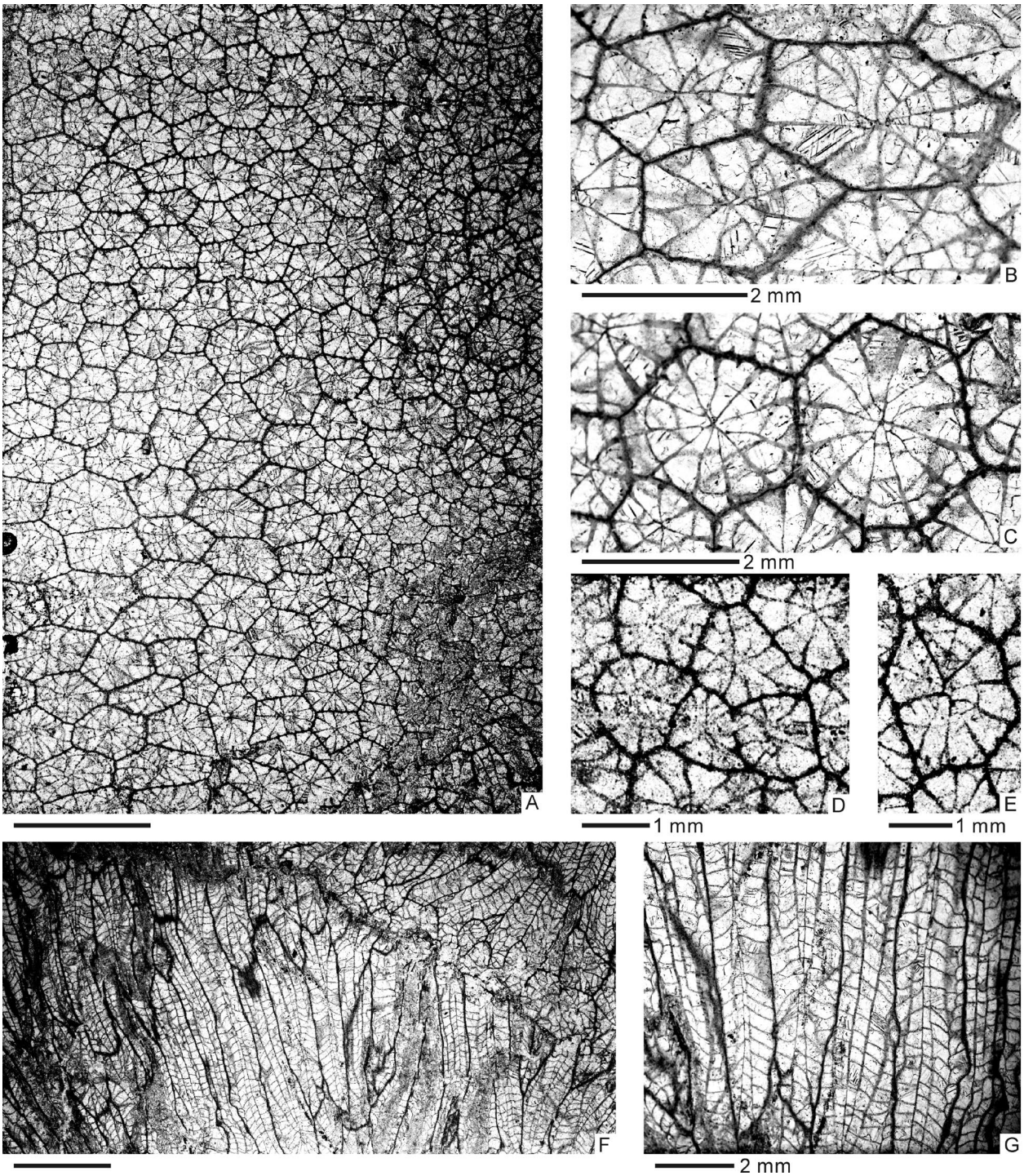


Fig. 81. Parastauria liangfengyaensis (He, 1980). NMRFC-Scr797, holotype, Sifengya Formation (lower Telychian), Liangfengya, Huangjingba, Daguan area, northeastern Yunnan, southwestern China. **A–E,** TS and four enlarged portions; **F, G,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

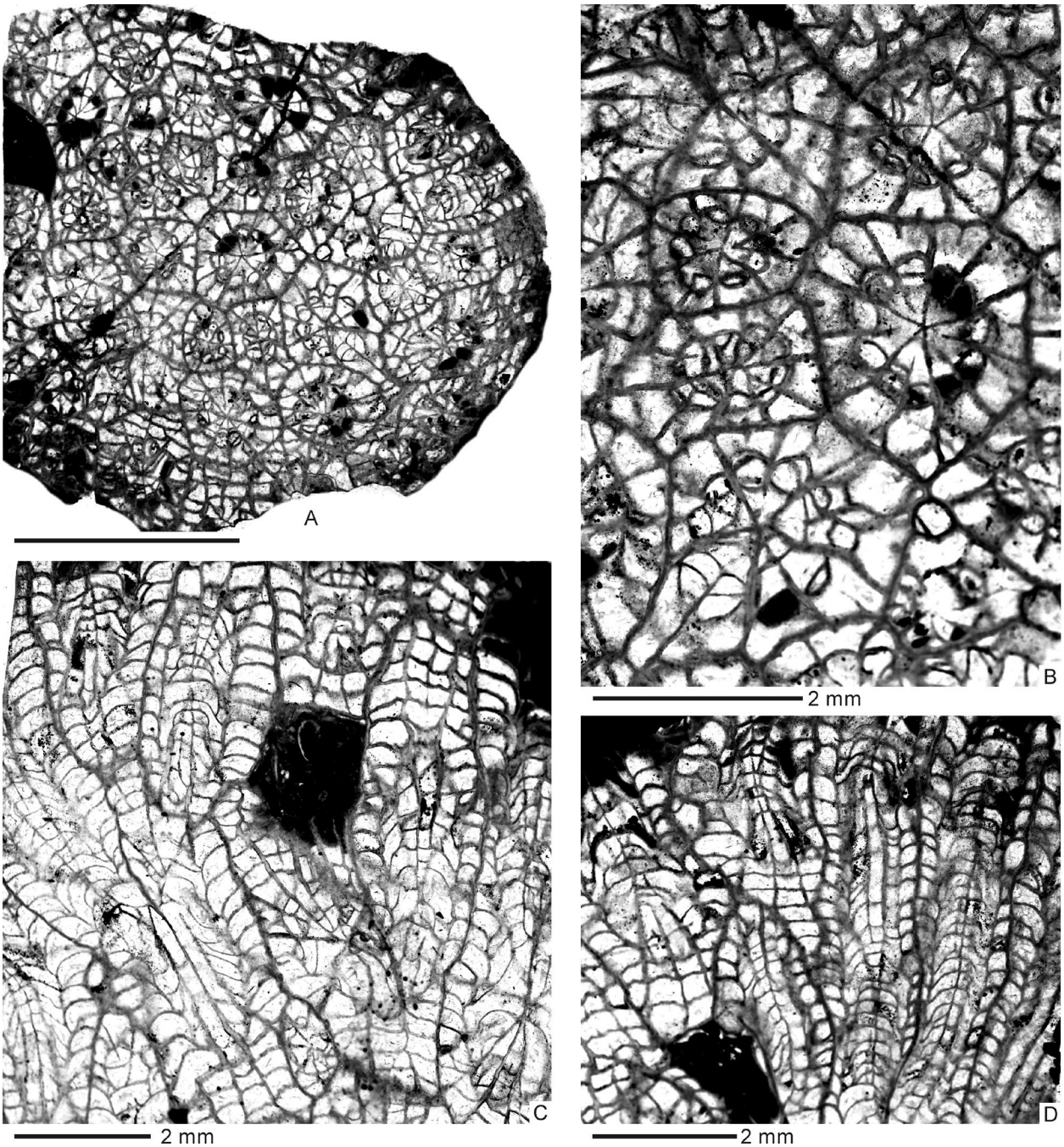


Fig. 82. Parastauria guanyinqiaoensis (He, 1980). NMRFC-Scr802, holotype, Hanchiatien Formation (lower Telychian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B,** TS and an enlarged portion; **C, D,** LSs. Scale bars are 5 mm unless otherwise indicated.

complete or incomplete, moderately to strongly arched, closely spaced (Ta2 = 8–12).

Description. – Modified from He (1980, p. 40). The external size and shape of the holotype unknown. Increase of typical KLAC septal parricidal type. Corallites polygonal, 4–7 sided, small [ACDs (6+) = 1.97–2.53 mm]. Corallite walls straight to slightly wavy, thin, separated by prominent dark lines. Septa of two orders. Major septa 8–11 in number, long, 5 protosepta (i.e. two counter-lateral, two alar and cardinal septa) and rarely few more meeting in the corallite axis but without forming a prominent columella. Minor septa short, commonly less than 1/5 of corallite radius. Dissepimentarium moderately wide, accounting for up to 50% of corallite diameter, consisting of one persistent row of dissepiments. Dissepiments variable in size, subglobose to flat, with slightly flattened upper surfaces. Tabularium sharply delineated from dissepimentarium. Tabulae complete or incomplete, moderately to strongly arched, closely spaced (Ta2 = 8–12).

Remarks. – The diagnosis and description of *Parastauria guanyinqiaoensis* given above are based on the holotype. The two species revised above, i.e. *P. huayinshanensis* (He, 1980) from the upper Baiyun'an Formation (lower Telychian) of Huaying Mountain, eastern Sichuan, and *Parastauria liangfengyaensis* (He, 1980) from the Sifengya Formation (lower Telychian) of the Daguan area, northeastern Yunnan, show comparable corallite size [both having ACDs (6+) less than 3 mm). However, they have more septa that are connected in the corallite axis, much weaker development of minor septa, and intermittent development of dissepiments, as well as exclusively complete and sparser tabulae, as also noted above under *P. huayinshanensis*.

Parastauria occulta (Sytova in Sytova & Ulitina, 1983)

1983 *Elizabethia occulta* Sytova in Sytova & Ulitina, pp. 120, 121, pl. 19, figs 3a, b, 4a, b.

Remarks. – This species (holotype, PIN 3942/311) occurs in the lower Alash Horizon (Rhuddanian; Sennikov *et al.* 2015) of the right bank of the Khemchik River, western Tuva. Based on the original description and illustrations, it exhibits a KLAC parricidal increase mode, medium-sized corallites (up to 4.5 mm in diameter), 14–16 major septa meeting in the corallite axis, well-developed minor septa (up to 50% of the major), complete, subhorizontal to slightly convex, widely spaced tabulae (Ta5 = 7–10), and one intermittent series of dissepiments. The distinctive increase mode and dissepimental development support a reassignment to *Parastauria*.

Parastauria modica (Sytova in Sytova & Ulitina, 1983), the other described species from Tuva considered below, shows similar tabular spacing to *P. occulta*. However, it is readily distinguishable by having larger corallites (up to 6 mm in diameter), irregularly sized dissepiments and subhorizontal tabulae.

Forms closely resembling *Parastauria occulta* also include *P. shiqianensis* (Ge & Yu, 1974) from the Xiangshuyuan (upper Llandovery–lower Aeronian) Formation, and *P. leijiatunensis* (He, 1980) from the Leijiatun Formation (upper Aeronian), the Shiqian area, northeastern Guizhou. Both have comparable corallite size [ACDs (6+) = 3.09–4.60, and 1.85–4.86 mm, respectively], but are separable by having incomplete and much denser tabulae (both having Ta5 = 14–16). *Parastauria leijiatunensis* is further distinguished in possessing one consistent row of dissepiments.

Parastauria modica (Sytova in Sytova & Ulitina, 1983)

1983 *Elizabethia modica* Sytova in Sytova & Ulitina, pp. 121, 122, pl. 20, figs 1a, b, 2.

Remarks. – *Parastauria modica* (holotype, PIN 3942/323) is known from the upper Alash Horizon (upper Rhuddanian–lower Aeronian; Sennikov *et al.* 2015) on the left bank of the Alash River, western Tuva. This species exhibits KLAC septal parricidal increase modes, as indicated by the statement of a division of the parent corallite into "2–5" new ones and also shown in illustrations (Sytova & Ulitina 1983, p. 122, figs 1a, 2). According to its original description, key specific features of *P. modica* include medium to large-sized corallites (up to 6 mm in diameter), 15–18 major septa connected in the corallite axis, well-developed minor septa (up to 50% the length of major septa), moderately convex, widely spaced tabulae (Ta5 = 8) and one persistent series of irregularly sized dissepiments. Its reassignment to *Parastauria* is based on a consideration of its increase mode and dissepimental development.

The large corallites and irregularly sized dissepiments of *Parastauria modica* distinguish it from all other known congeneric species. Its comparison with the other Tuva species, *P. occulta* (Sytova in Sytova & Ulitina, 1983), is discussed above.

Genus *Yuina* n. gen.

Type species. – *Ceriaster columellatus* Ge & Yu, 1974, Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China.

Derivation of name. – To honour Changmin Yu, for his outstanding work on rugose corals.

Diagnosis. – Heininae n. subfam. with fasciculate coralla that lack dissepiments.

Remarks. – The other two genera assigned to Heininae n. subfam., *Heina* n. gen. and *Parastauria* He & Li, 1974, differ from *Yuina* n. gen. in being cerioid. *Parastauria* is further distinguished by possessing dissepiments.

Yuina columellata (Ge & Yu, 1974)

(Figs 83, 84)

1974	*Ceriaster columellatus* Ge & Yu, p. 167, pl. 74, figs 11, 12.
1978	*Ceriaster columellatus* Ge & Yu; Kong & Huang, p. 64, pl. 21, fig. 7a, b [refig. Ge & Yu 1974, pl. 74, figs 11, 12].
?1980	*Neoceriaster shiqianensis* He, p. 43, pl. 5, figs 2a, b, 3a, b. [*nomen dubium*]
1980	*Neoceriaster columellatus* (Yu & Ge); He, p. 44, pl. 3, figs 2a, b, 3a, b.
?1995	*Neoceriaster shiqianensis* He; Lin *et al.*, fig. 136a, b [refig. He 1980, pl. 5, fig. 3a, b].
2006	*Eostauria columellatus* (Ge & Yu); Tang, pl. 31, fig. 4a–c.
non 2008b	*Eostauria shiqianensis* (He); Tang *et al.*, pl. 3, fig. 4a, b [refig. Tang 2006, pl. 31, fig. 1a, b].
2020	*Ceriaster columellatus* Ge & Yu; Wang & Cui, p. 226, pl. 7-77, fig. 2a, b [refig. Ge & Yu 1974, pl. 74, figs 11, 12].

Referred material. – NIGP22108 (LS) and NIGP22109 (TS), holotype, original of Ge & Yu (1974, pl. 74, figs 11, 12), refigured here (Fig. 83); NMRFC-Scr800, described by He (1980) as *Neoceriaster columellatus* (Ge & Yu, 1974), original of He (1980, pl. 3, fig. 3a, b), refigured here (Fig. 84). Both specimens from the Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China.

Diagnosis. – *Yuina* with adult diameters of 1.64–2.53 mm. Major septa 9–10 in number, with 5 protosepta or more meeting in the corallite axis and forming a prominent columella. Minor septa short to almost absent. Tabulae complete, widely spaced (Ta5 = 8–12).

Description. – Modified from Ge & Yu (1974, p. 167). The external size and shape of the holotype unknown. Increase of typical KLAC septal parricidal type. Corallites cylindrical to subcylindrical, small, with adult diameters of 1.64–2.53 mm. Corallite walls straight to slightly wavy, separated by prominent dark lines. Septa of two orders. Major septa 9–10, generally 10 in number, with 5 septa (i.e. two counter-lateral, two alar and cardinal septa) or more meeting in the corallite axis and commonly forming a prominent columella. Minor septa short to almost absent, generally less than 1/5 of corallite radius. Tabulae complete, moderately arched, widely spaced (Ta5 = 8–12). Dissepiments are absent.

Remarks. – The holotype of *Yuina columellata,* refigured by Kong & Huang (1978) and Wang & Cui (2020), comes from the Leijiatun Formation (upper Aeronian) at Leijiatun of the Shiqian area, northeastern Guizhou. Further material was later documented by He (1980) and Tang (2006) from the same horizon and locality. The present revision is based on the holotype of Ge & Yu (1974) and a topotype of He (1980).

A possible synonym of *Yuina columellata* is *Neoceriaster shiqianensis* He, 1980, with type material from the coeval Leijiatun Formation of the Shiqian area, northeastern Guizhou. However, due to the uncertainty as to its increase, this form is considered here as *nomen dubium*, as discussed in remarks on the Stauriidae above. The material described by Tang *et al.* (2008b) as *Eostauria shiqianensis* (He, 1980), from the Leijiatun Formation (upper Aeronian) of the Shiqian area, northeastern Guizhou, is revised as *Y. agglomorata* He & Li, 1974 (see remarks on the latter species, below).

Both *Y. agglomorata* (He & Li, 1974) and *Y. qiaogouensis* (He, 1980), considered below, are separable from *Yuina columellata* by the general lack of solid, prominent columellae. *Yuina agglomorata* further differs in having smaller corallites (0.45–2.00 mm in diameter), and *Y. qiaogouensis* has lager corallites (adult diameters being 2.50–3.34 mm).

Yuina agglomorata (He & Li, 1974)

1974	*Ceriaster* (*Eostauria*) *agglomorata* He & Li, pp. 5, 6, pl. 1, fig. 3a–c.
1974	*Ceriaster* (*Eostauria*) *minor* (Chen); He & Li, p. 6, pl. 1, fig. 2a, b, pl. 2, fig. 1a, b.
1978	*Ceriaster agglomoratus* He & Li; Kong & Huang, pp. 63, 64, pl. 19, fig. 3a–c [refig. He & Li 1974, pl. 1, fig. 3a–c].
2006	*Eostauria crassosepta* Tang, pp. 147, 148, pl. 31, figs 1a–c, 2a–c, 3a–d.
2008b	*Eostauria shiqianensis* (He); Tang *et al.*, pl. 3, fig. 4a, b [refig. Tang 2006, pl. 31, fig. 1a, b].

Remarks. – The holotype of *Yuina agglomorata* (KS003 and KS005, TSs; KS004, LS), refigured by Kong & Huang (1978), comes from "the Shihniulan Formation" (now upper Xiangshuyuan Formation, lower Aeronian) at Pugou of the Shiqian area, northeastern Guizhou. The statement of "pentapartite increase" and the accompanying illustrations (He & Li 1974, p. 5, pl. 1, fig. 3a, c) clearly suggest a KLAC septal parricidal increase, thereby justifying its current generic attribution. According to He & Li (1974), its specific features include small corallite size (0.45–2.00 mm in diameter),

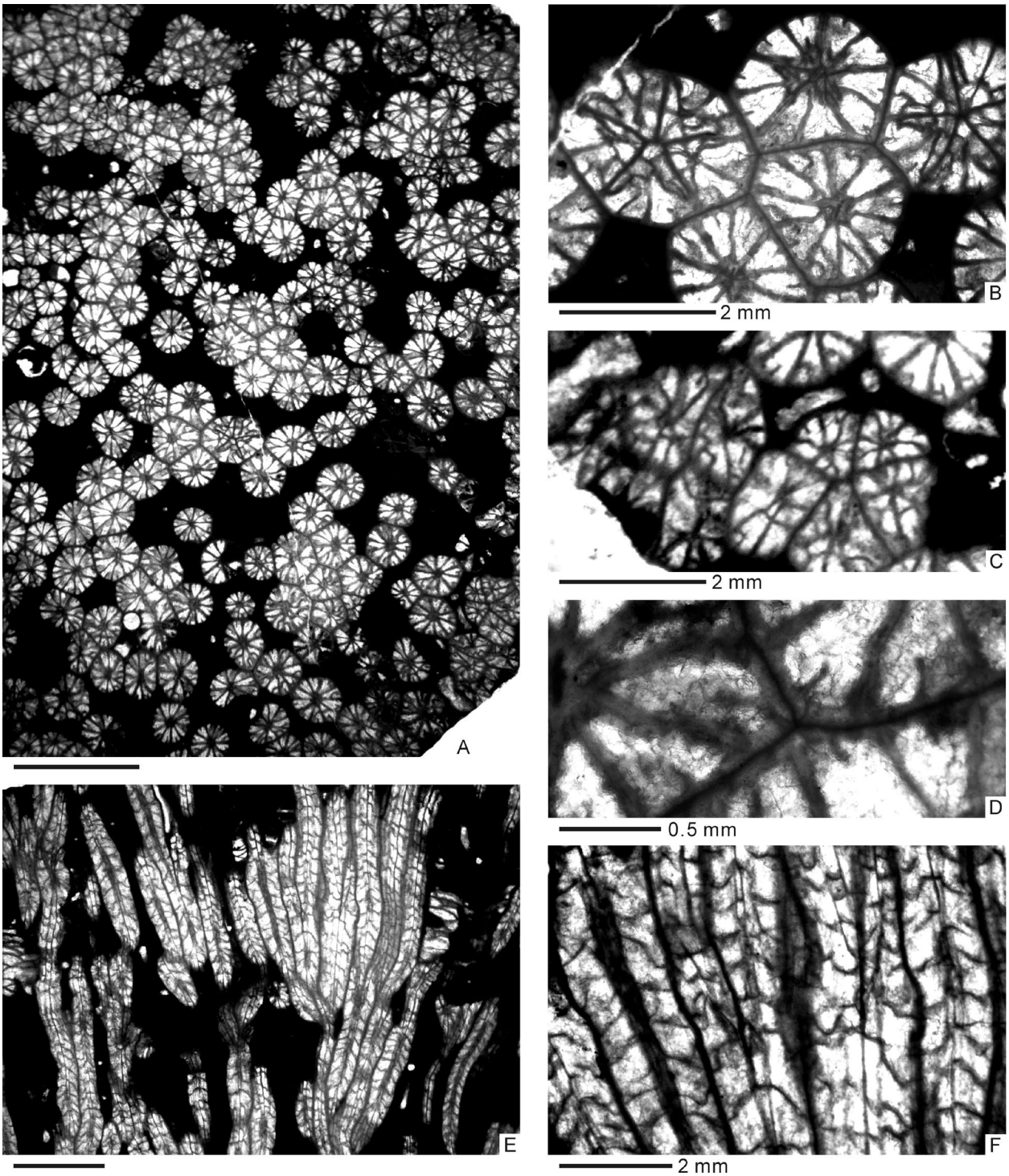


Fig. 83. Yuina columellata (Ge & Yu, 1974). NIGP22108 (LS) and NIGP22109 (TS), holotype, Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A–D,** TS and three enlarged portions; **E, F,** LS and an enlarged portion. Scale bars are 5 mm unless otherwise indicated.

10–12 major septa generally meeting in the corallite axis, short minor septa, and complete, subhorizontal or slightly convex, widely spaced tabulae (0.2–0.4 mm apart). The very small corallites serve to distinguish it from all other *Yuina* species.

Ceriaster (*Eostauria*) *minor* (Chen, 1959) *sensu* He & Li, 1974 consists of two specimens, one occurring in the same horizon and locality as the holotype of *Yuina agglomorata*, and the other from the slightly

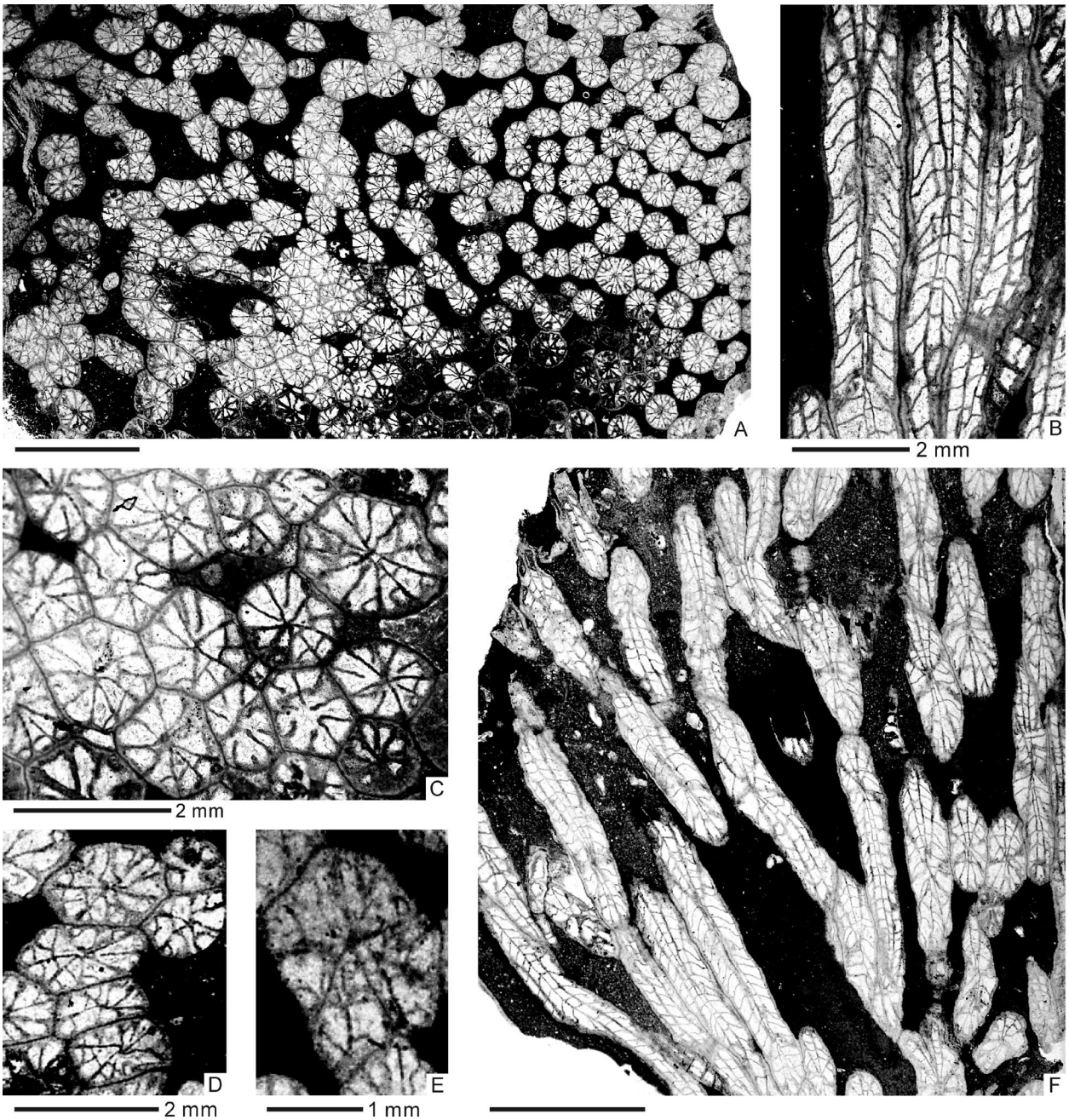


Fig. 84. Yuina columellata (Ge & Yu, 1974). NMRFC-Scr800, described by He (1980) as *Neoceriaster columellatus* (Yu & Ge, 1974), Leijiatun Formation (upper Aeronian), Leijiatun, Shiqian area, northeastern Guizhou, southwestern China. **A, C–E,** TS and three enlarged portions; **B, F,** LS (**F**) and an enlarged portion (**B**). Scale bars are 5 mm unless otherwise indicated.

younger Lojoping Formation (upper Aeronian) of the Yichang area, southwestern Hubei. Both are regarded here as conspecific with *Y. agglomorata*, since they exhibit the same increase pattern, as stated in the description and shown in the illustrations, as well as other features that are essentially identical to the holotype of the latter.

The material described by Tang (2006) as *Eostauria crassosepta* Tang, 2006, later revised by Tang *et al.* (2008b) as *E. shiqianensis* (He, 1980), comes from the Leijiatun Formation (upper Aeronian) of the Shiqian area, northeastern Guizhou. Its illustrations distinctly demonstrate a KLAC increase mode (Tang 2006, figs 1a–c, 2a–c, 3a–d), supporting a transfer to

the new genus *Yuina*. As summarised in Tang (2006), other key features of this form include small corallites (0.45–2.00 mm in diameter), 8–10 major septa meeting in the corallite axis and generally forming a prominent columella, short minor septa that are commonly confined to the peripheral stereozone, and complete, slightly arched, evenly spaced tabulae (Ta5 = 14–15). Tang (2006, p. 148) noted that it is rather similar to the holotype of *Y. agglomorata*, differing mainly in having slightly less major septa (8–9, rarely 10 in number). Since this difference is minor, Tang's material is included here within *Y. agglomorata*.

***Yuina qiaogouensis* (He, 1980)**

(Figs 85, 86)

1980 *Ceriaster qiaogouensis* He, p. 42, pl. 4, fig. 1a, b.

Referred material. – NMRFC-Scr803, holotype, original of He (1980, pl. 4, fig. 1a, b), refigured here (Figs 85, 86), "Qiaogou Formation" (now lower Shihniulan Formation, upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China.

Diagnosis. – *Yuina* with adult diameters of 2.50–3.34 mm. Major septa 12–16 in number, but commonly with only 5 protosepta (i.e. two counter-lateral, two alar and cardinal septa) meeting in the corallite axis. Tabulae complete, variably spaced (Ta5 = 6–13).

Description. – Modified from He (1980, p. 42). The external size and shape of the holotype unknown. Increase of typical KLAC septal parricidal type. Corallites cylindrical to subcylindrical, small, with adult diameters of 2.50–3.34 mm. Septa of two orders. Major septa 12–16 in number, long, 5 protosepta (i.e. two counter-lateral, two alar and cardinal septa) generally meeting in the corallite axis without forming a prominent columella. Minor septa variable in length, up to about 1/4 of corallite radius. Tabulae complete, moderately arched, with a wide, flat or slightly concave central platform. Tabular spacing variable, Ta5 = 6–13. Dissepiments are absent.

Remarks. – The diagnosis and description of *Yuina qiaogouensis* given above are based on a reassessment of the holotype. Both *Y. columellata* (Ge & Yu, 1974) and *Y. agglomorata* (He & Li, 1974), considered above, differ from *Y. qiaogouensis* in having smaller corallites, and *Y. columellata* is further separated by developing solid, prominent columellae.

***Yuina*? sp.**

(Fig. 87)

1987 *Palaeophyllum* sp., He, p. 24, pl. 1, fig. 9a, b.

Referred material. – NMRFC-ZO024 (TS) and NMRFC-ZO025 (LS) from one corallum, described by He (1987) as *Palaeophyllum* sp., original of He (1987, pl. 1, fig. 9a, b), refigured here (Fig. 87), Badanjilin Formation (uppermost Katian), Danmianshan, Ejin, Inner Mongolia.

Description. – Modified from He (1987, p. 24). The single corallum is fasciculate with a possible KLAC septal parricidal increase. Corallite large, ranging from 8.65 to 9.36 mm in diameter. Septa of two orders. Major septa 28 in number, long, extending almost to the corallite axis. Minor septa well developed, accounting for 1/3 to 1/2 of the length of major septa. Tabulae complete, slightly convex, with a wide, slightly concave central platform, Ta5 = 7–8.

Remarks. – This species was based solely on a transverse and longitudinal section of an incomplete specimen, which is reassessed in this work. It exhibits a possible KLAC septal increase mode, as indicated in the transverse section (Fig. 87A), and a tentative transfer to *Yuina* n. gen. is thus preferred here. Given that this species remains poorly defined, an open nomenclature is applied.

He (1987) suggested that this species has an increase mode comparable to *Palaeophyllum proliferum* Webby, 1972, from the lower Katian of central NSW, with their major differences lying in the much smaller corallite size (2.5–5.0 mm in diameter) and less septa of the latter. However, the increase of the latter is of aseptal type, and thus very different from the Chinese form.

Cyathophylloidid record

As defined above, the Cyathophylloididae is typified by non-dissepimented Stauriida that exhibit exclusively lateral increase. This family includes *Palaeophyllum* Billings, 1858a, *Cyathophylloides* Dybowski, 1873a, *Favistina* Flower, 1961, *Crenulites* Flower, 1961, and *Palaeolithostrotion* Lavrusevich, 1975.

Cyathophylloidid corals have so far been reported from various Upper Ordovician–Wenlock stratigraphic levels in North China, South China, the Australian and New Zealand section of peri-Gondwana, Laurentia, Baltica, and Siberia, as well as a few small terranes including Qilian, Qaidam,

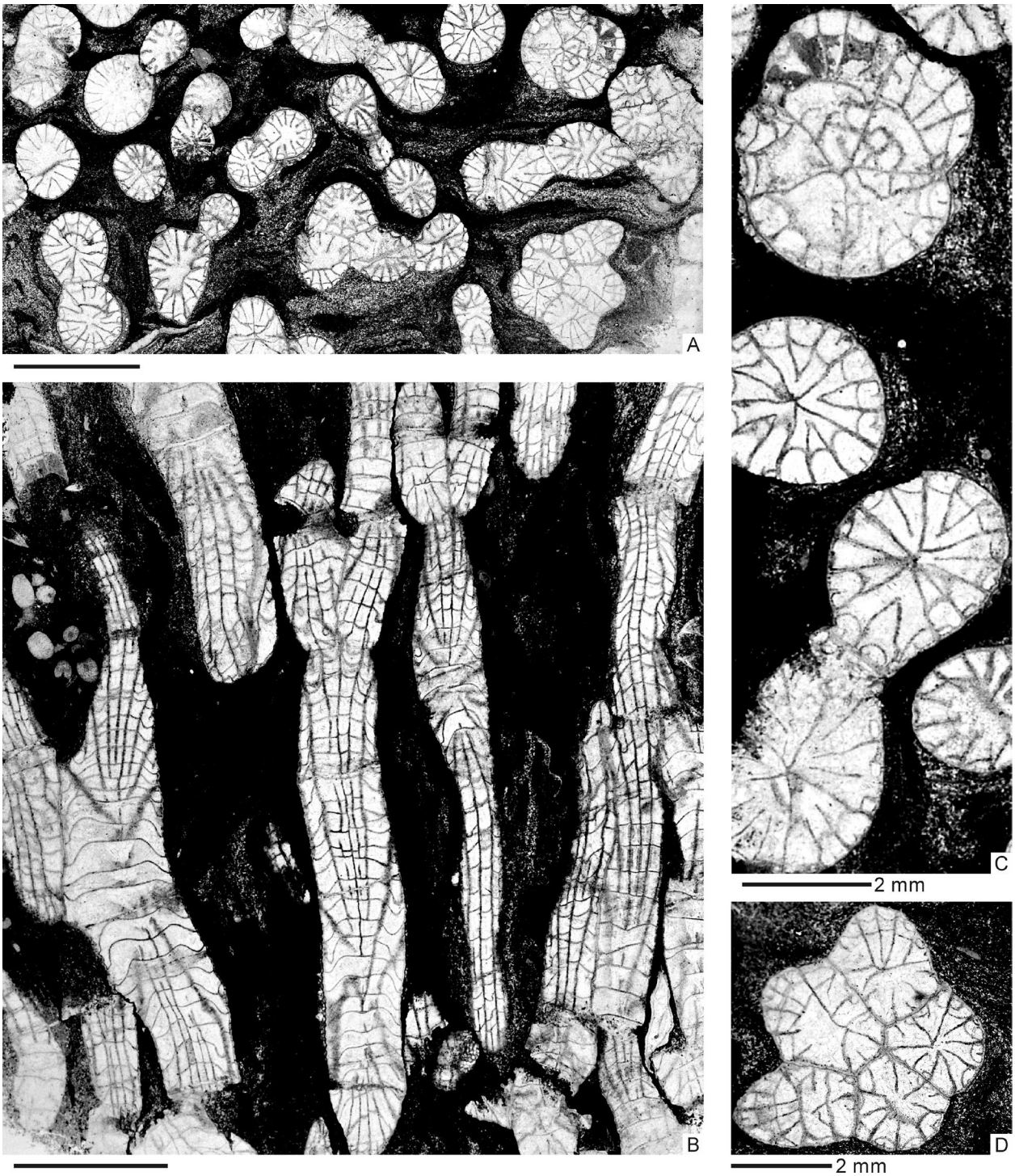


Fig. 85. Yuina qiaogouensis (He, 1980). NMRFC-Scr803, holotype, "Qiaogou Formation" (now lower Shihniulan Formation, upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, C, D,** TS and two enlarged portions; **B,** LS. Scale bars are 5 mm unless otherwise indicated.

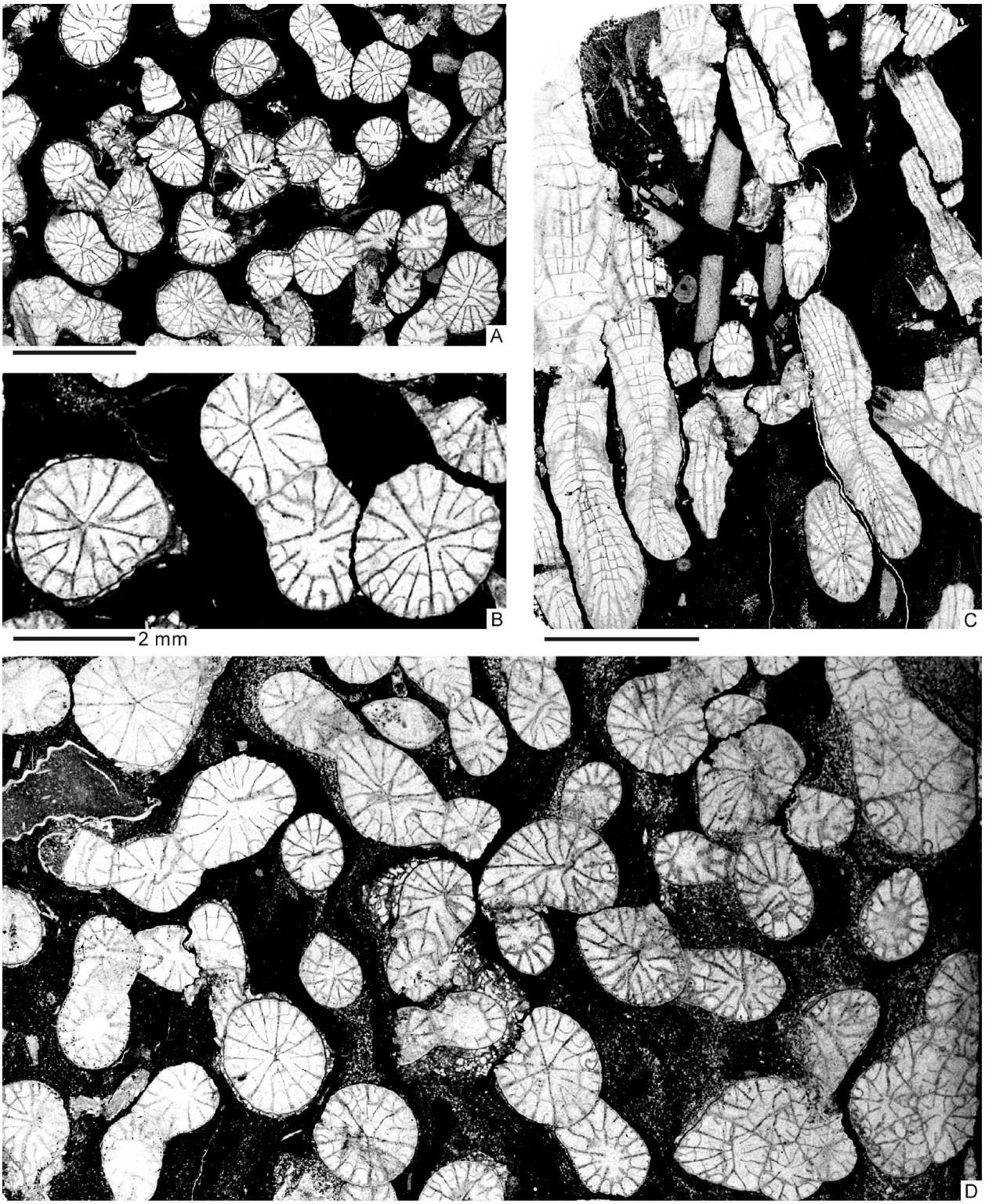


Fig. 86. Yuina qiaogouensis (He, 1980). NMRFC-Scr803, holotype, "Qiaogou Formation" (now lower Shihniulan Formation, upper Aeronian), Guanyinqiao, Qijiang, southern Chongqing, southwestern China. **A, B, D,** TSs (**A, D**) and an enlarged portion of **A** (**B**). **C,** LS. Scale bars are 5 mm unless otherwise indicated.

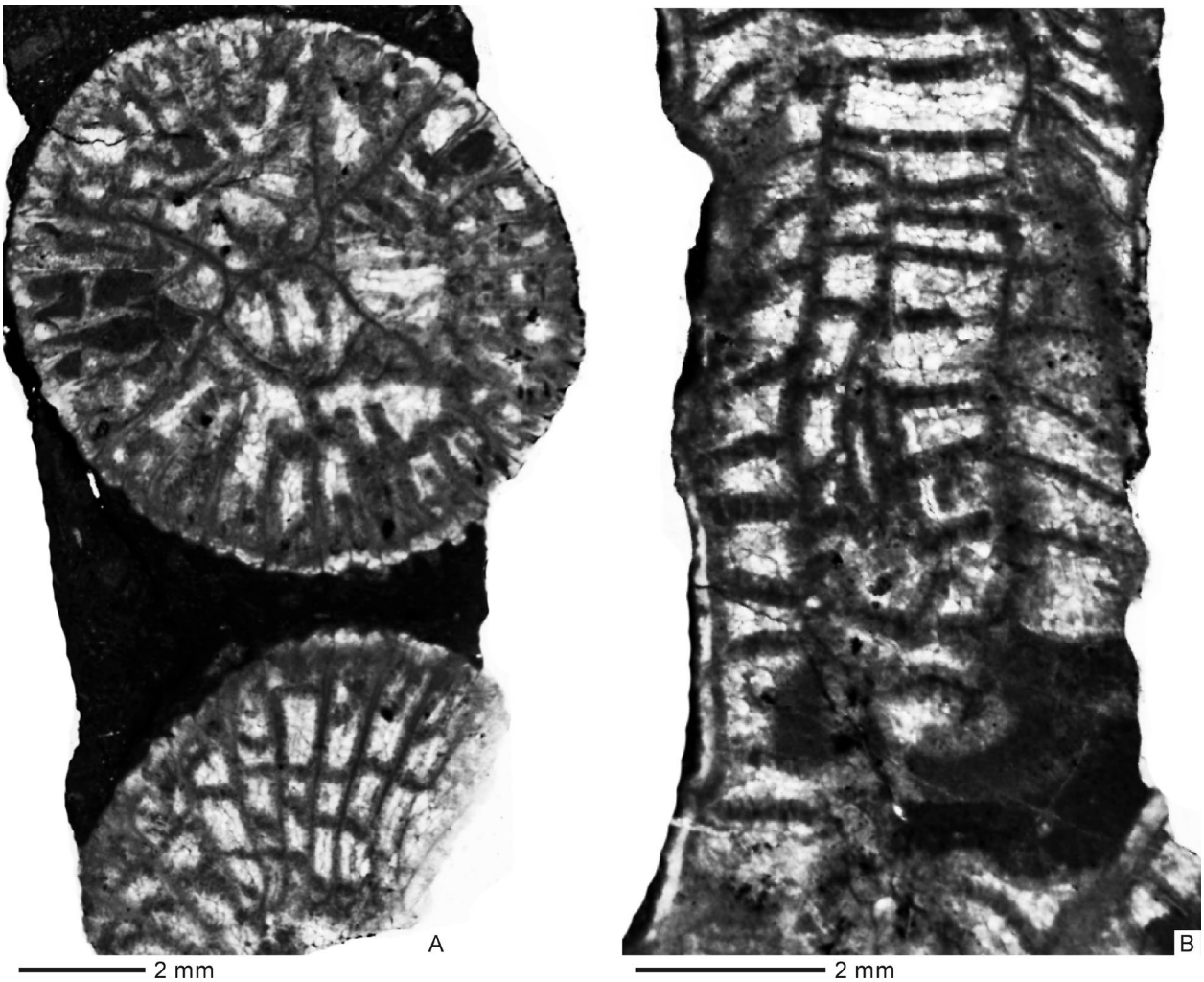


Fig. 87. Yuina? sp. NMRFC-ZO024 (TS) and NMRFC-ZO025 (LS) from one corallum, described by He (1987) as *Palaeophyllum* sp., Badanjilin Formation (uppermost Katian), Danmianshan, Ejin, Inner Mongolia. **A,** TS; **B,** LS.

Sivi, South Tien Shan, Kazakhstan terranes, York and Altai–Sayan (Figs 88, 89). Since the nature and boundaries of tectonic units in relation to present-day China remain unsatisfactorily settled (Zhou *et al.* 1996a, 2008; Xiao *et al.* 2019; Wu *et al.* 2020; Metcalfe 2021), a preferred terrane map of China is presented in Fig. 90. For the stratigraphic context of blocks/terranes outside China, that are mostly well understood, see recent summaries on South Tien Shan (Ghobadi Pour *et al.* 2023), Chu–Ili and Chingiz–Tarbagatai terranes within today's Kazakhstan (Popov & Cocks 2017; Popov *et al.* 2023), the Australian and New Zealand section of peri-Gondwana (Percival *et al.* 2023), Laurentia (Desrocher *et al.* 2023; McLaughlin & Stigall 2023), York Terrane (Dumoulin *et al.* 2023), Baltica (Nielsen *et al.* 2023; Meidla *et al.* 2023b), and Siberia (Kanygin *et al.* 2019) and its surrounding terranes including Altai–Sayan, Tuva–Mongol, Central Mongolia and Gobi Altai (Cocks & Torsvik 2007; Sennikov *et al.* 2015, 2019).

Over half a century has elapsed since Bassler's (1950) and Ivanovskiy's (1969) comprehensive appraisals of then-known cyathophylloidid records. Below is an updated summary of their distribution based on new fossil, stratigraphic and tectonic data (see also Appendix Table 1).

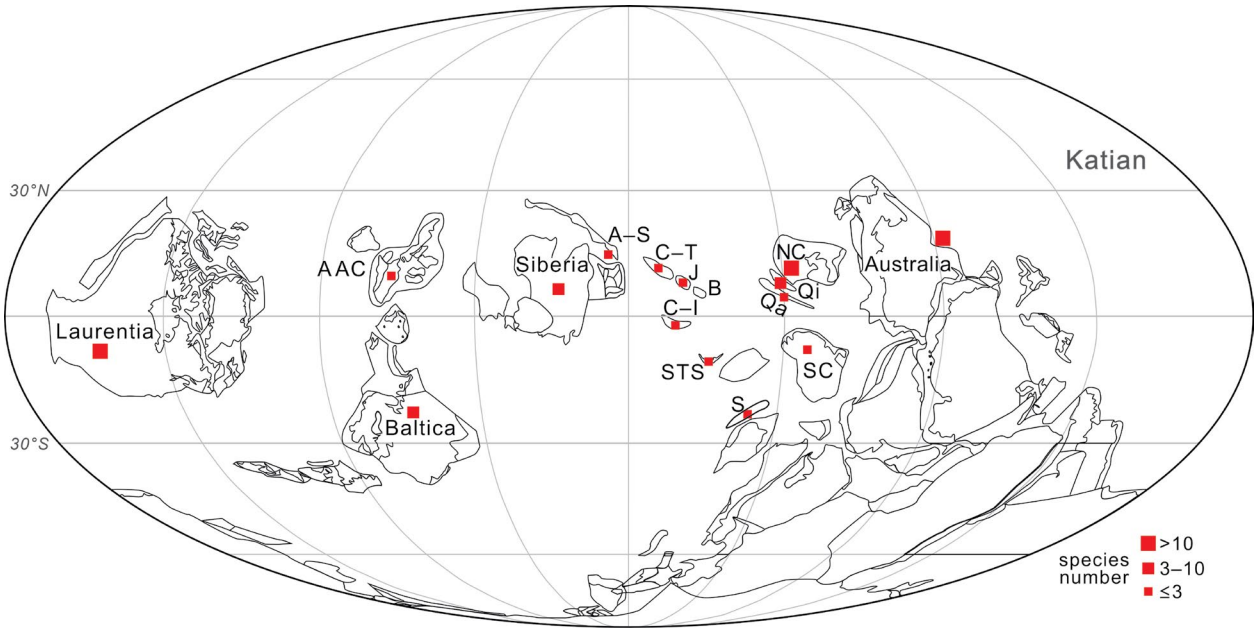


Fig. 88. Katian palaeogeographical reconstruction showing the distribution of cyathophylloidid corals. Base map modified from Torsvik & Cocks (2013) and Cocks & Torsvik (2021). AAC, Arctic Alaska–Chukotka; A–S, Altai–Sayan; B, Beishan; C–I, Chu–Ili; C–T, Chingiz–Tarbagatai; J, Junggar, comprising East and West Junggar; NC, North China; Qi, Qilian; Qa, Qaidam; S, Sivi; SC, South China; STS, South Tien Shan.

Fig. 89. Llandovery–Wenlock palaeogeographical reconstruction showing the distribution of cyathophylloidid corals. Base map modified from Torsvik & Cocks (2017). A–S, Altai–Sayan; SC, South China.

North China

Cyathophylloidid corals are reliably known to be confined to lower–middle Katian strata in the Ordos region (Fig. 90:1–3; Fig. 91), and strata possibly of similar age in the southern Pyeongnam Basin (Fig. 91), belonging to western and eastern parts of the North China block, respectively. Previous reports from younger strata of the block are all excluded here, including *Palaeophyllum* sp. of Guo (1976) from the "upper Silurian" at Daximiao, Zhenglan Banner, central Inner Mongolia, *Cyathophylloides silurica* Guo, 1976 (introduced also as a new form by Guo 1978) from the Xibiehe Formation (Ludlow) of the Bateaobao (or Bater Obo) area, south–central Inner Mongolia, and *Palaeophyllum xiashibeiense* Guo, 1980 from the Xiashibei Formation ("upper Silurian") of Naiman Banner, eastern Inner Mongolia (see remarks on the family above for discussion).

In the Ordos region, the oldest known cyathophylloidids occur in the topmost Longmendong Formation (lower Katian; Chen *et al.* 2013) of the Longxian area, western Ordos. Taxa described by Deng (1984) comprise *Favistina mediana* Deng, 1984, *F. pachytheca* Deng, 1984, *F. longxianensis* Deng, 1984, and *F.* aff. *dybovskii* Soshkina in Ivanova *et al.*, 1955, the last of which is now revised as *Crenulites*

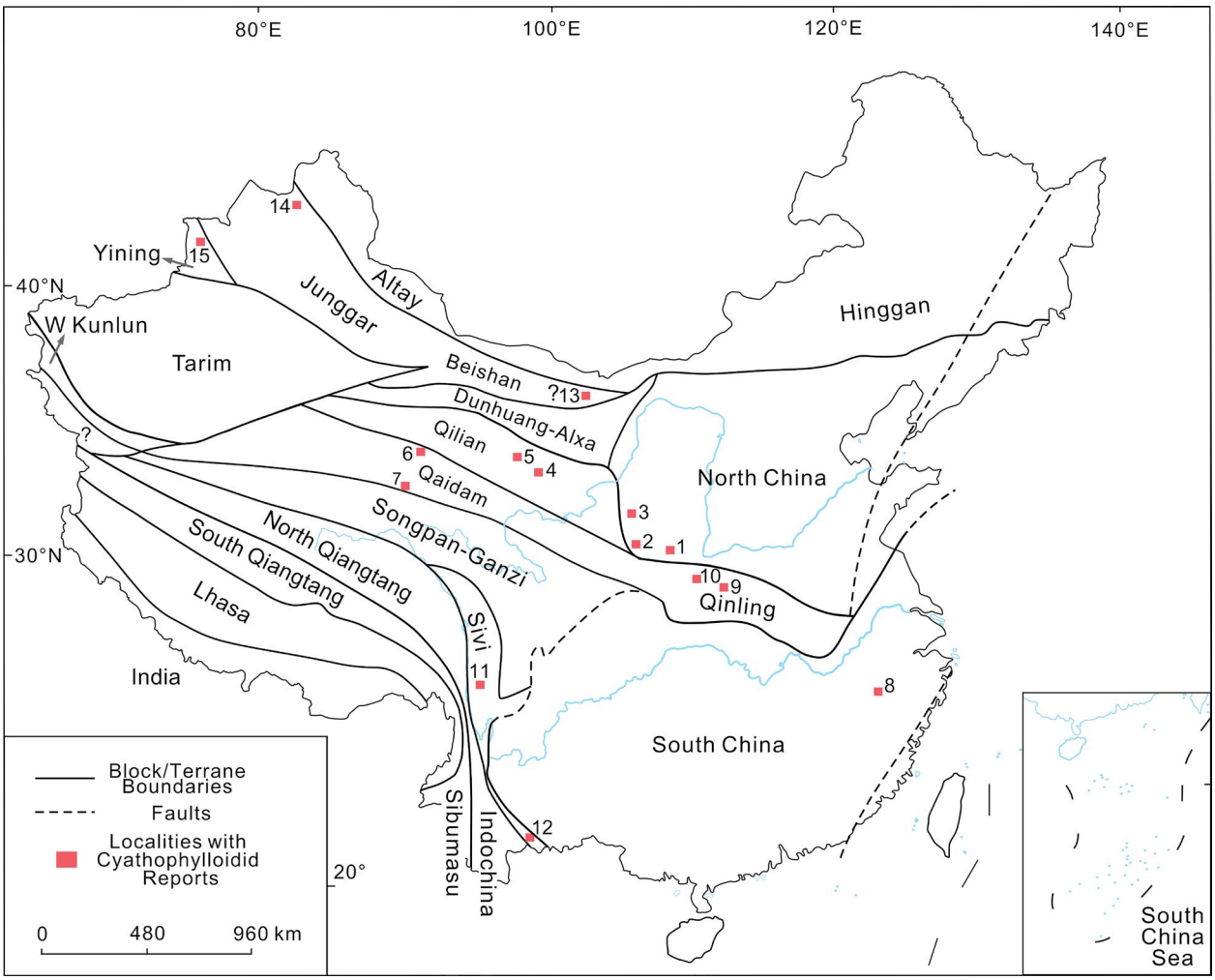


Fig. 90. Map of China showing the early Palaeozoic tectonic blocks/terranes and their boundaries. Pink squares represent approximate locations of the Ordovician strata yielding cyathophylloidid corals, the one preceded by a question mark indicating doubtful occurrence. Terrane boundaries are slightly modified after Zhou *et al.* (1996a, 2008), Wu *et al.* (2020) and Metcalfe (2021). 1, Jingyang, central Shaanxi, southwestern Ordos; 2, Longxian, western Shaanxi, western Ordos; 3, Guyuan, southernmost Ningxia, western Ordos; 4, Menyuan, northeastern Qinghai; 5, Qilian, northeastern Qinghai; 6, Dachaidan, northern Qinghai; 7, Nachitai, south of Golmud city centre, central–western Qinghai; 8, Jiangshan–Changshan–Yushan (JCY) area, Jiangxi–Zhejiang border region; 9, Xichuan, southwestern Henan; 10, Shanyang, southeastern Shaanxi; 11, Zhongza, Batang, westernmost Sichuan; 12, Dapingzi, Jinping, southeastern Yunnan; 13, Danmianshan, southeastern Ejin Banner, western Inner Mongolia; 14, Bulunggor, Hobuksar, northwestern Xinjiang; 15, southern Jinghe, western Xinjiang.

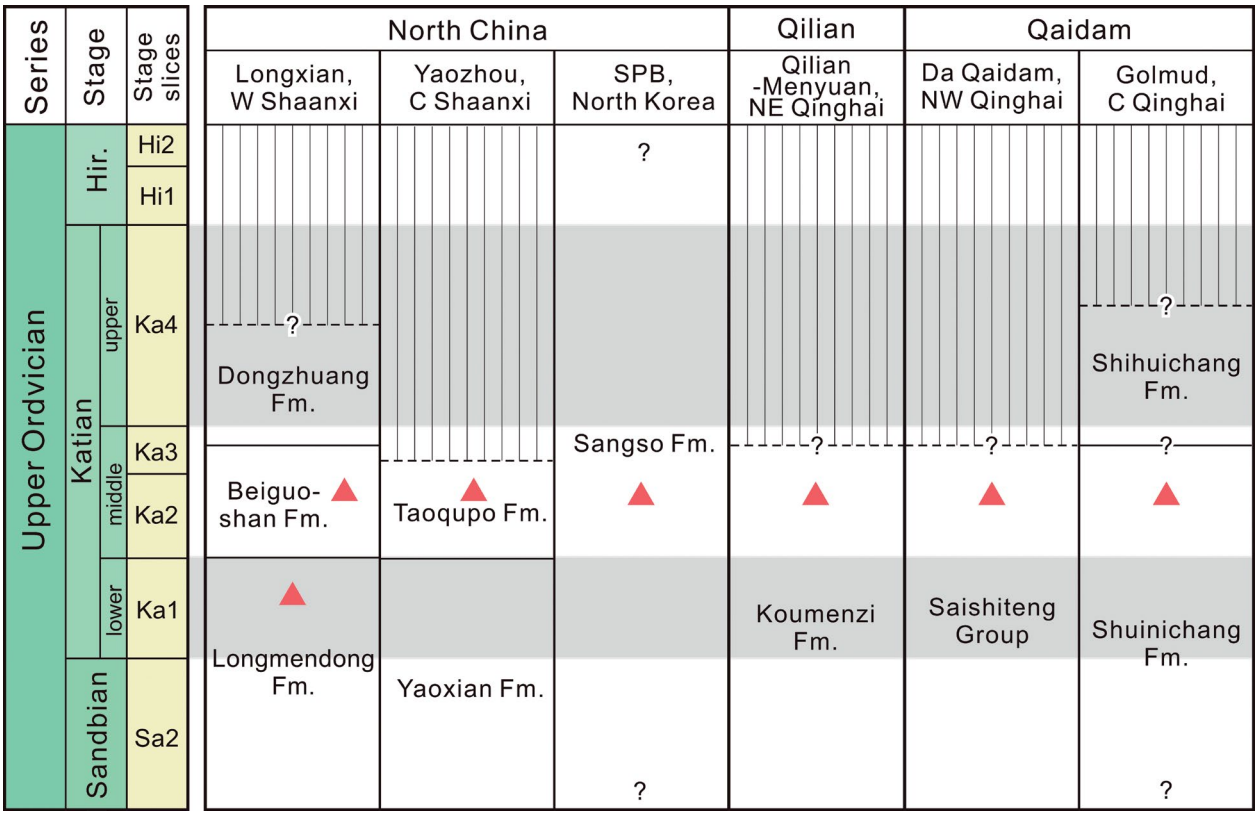


Fig. 91. Correlation of the Late Ordovician successions yielding cyathophylloidids in North China, Qilian, and Qaidam, pink triangles indicating approximate horizons bearing these corals. SPB, southern part of "the Pyeongnam Basin" (Oh *et al.* 2023). Data source: Timescale (Goldman *et al.* 2020); stratigraphic correlations (Wang & Cui 2025 and references therein).

sp. C (see above for discussion). Higher up in the lower–middle Katian, cyathophylloidids occur in the Beiguoshan Formation of the Longxian area, western Ordos (Yu 1960; Yu *et al.* 1963; Cao & Lin 1982; Deng 1984; Liang 2020), and the Taoqupo Formation of the Yaozhou (formerly Yaoxian) and Jingyang areas, southwestern Ordos (Cao & Lin 1982; Deng 1984; Jiang *et al.* 2013). The present revision shows that the Beiguoshan fauna contains *Crenulites grandis* (Yu, 1960), *C. formosus* (Deng, 1984), *C. guyuanensis* (Lin in Cao & Lin, 1982), *Palaeophyllum*? *guyuanense* Lin in Cao & Lin, 1982, and *P.*? *simplex* Deng, 1984. In the Taoqupo Formation, the taxa are revised here as including *Crenulites nanshanensis* (Yu, 1960), *C. formosus* (Deng, 1984), *Cyathophylloides taoqupoensis* Lin in Cao & Lin, 1982, *Cy. strigosus* (Deng, 1984) and *Favistina arcuta* Deng, 1984.

In the southern Pyeongnam Basin, cyathophylloidids are recorded from the Sangso Formation of possible similar age (Lee *et al.* 2017; Oh *et al.* 2023). Taxa recognised by Pak (1983) include *Favistina alveolata* (Goldfuss, 1826), *F. obliquisepta* Yu, 1960, *F. intermediata* Yu, 1960, *F. irregularis* Yu, 1960, *F. grandiformis* Pak, 1983, and *F. crussa* Pak, 1983. However, a critical revision is required to clarify their identity due to the lack of proper documentation.

Qilian

Cyathophylloidids of this block are only known from the Koumenzi Formation (probably lower–middle Katian) in the Menyuan and Qilian areas of northeastern Qinghai Province, northwestern China (Fig. 90:4–5; Fig. 91). In the former area, they were all documented from the left bank of Daliang River, near Koumenzi, including *Favistella alveolata* (Goldfuss, 1826), *F. nanshanensis* Yu, 1960, *F. obliquisepta* Yu, 1960, *F. alveolata* (Goldfuss) var. *maxima* Yu, 1960, *F. intermediata* Yu, 1960, and *F. irregularis* Yu, 1960. Of these, the first four are revised here as *Crenulites nanshanensis*, and the last two are transferred to *Crenulites*.

In the Qilian area, cyathophylloidids documented by Deng & Li (1979) and Li & Liao (1979) include *Favistina qilianensis* (Deng & Li in Li & Liao, 1979), *F.* aff. *nanshanensis* (Yu, 1960), *F.* cf. *intermediata* (Yu, 1960), *F. luotuoheensis* (Deng & Li in Li & Liao, 1979), *Agetolites rariperforatus* Deng & Li, 1979,

Saffordophyllum heiquanheensis Deng & Li, 1979, and *S. inconstus* Deng & Li, 1979. These forms are now revised as consisting of *Crenulites nanshanensis* (Yu, 1960), *C. intermediatus* (Yu, 1960), *C. irregularis* (Yu, 1960), and *C. grandis* (Yu, 1960). Note that Lin (1985b), based on the supposed development of mural pores, regarded *Saffordophyllum heiquanheensis* as an agetolitid tabulate coral, a view rejected by Wang & Cui (2025) and herein.

Qaidam

In northern Qaidam (Fig. 90:6; Fig. 91), *Palaeophyllum qinghaiense* Lin, 1985a is known from the upper Saishiteng Group ("Upper Ordovician") at Mahai, Dachaidan (or Daqaidam), northern Qinghai. From the same level, *Favistella* sp. was also listed but without description (Lin 1985a, pp. 281, 282).

To the south in southern Golmud, central–western Qinghai, on the southern margin of the Qaidam block (Fig. 90:7; Fig. 91), *Cyathophylloides shuinychangensis* Lin in Li & Lin, 1982 occurs in the Shihuichang Formation (probably middle Katian) near Shihuichang, northern Nachitai.

South China

The only Ordovician cyathophylloidid in South China is found from the Xiazhen Formation (uppermost Katian) at Zhuzhai, the Jiangshan–Changshan–Yushan (JCY) area, Zhejiang–Jiangxi border region, east China (Fig. 90:8; Fig. 92). Initially documented by Deng (1986) as *Favistina* cf. *burksae* (Flower, 1961), this coral is revised here as *Cyathophylloides* sp. B. From the same horizon and area, *Palaeophyllum minimum* Yu, 1960, refigured by Yu *et al.* (1963) and Liang (2020), has typical monacanthine septa, and should be excluded from cyathophylloidids. Further excluded for the same reason is *Palaeophyllum irregulare* Lin & Chow, 1980, also introduced as a new species by Deng *et al.* (1983), from the older, lower Yenwashan Formation (Sandbian; Wang *et al.* 2015) at Daqiaotou. Additionally, *Favistella major* Yoh, 1959 documented from the lower "Pogoda Formation" (lower Katian) of the Huangping area, northeastern Guizhou, does not belong to cyathophylloidids (see discussion above).

The only probable Silurian cyathophylloidid in South China is *Palaeophyllum*? *hubeiense* Ge & Yu, 1974 (= *P. paradoxum* Jia in Jia & Lin, 1987; this work), from the Lojoping Formation (upper Aeronian) at Dazhongba of the Yichang area, southwestern Hubei. All other previous cyathophylloidid reports of this age should be excluded, including *Palaeophyllum major* He, 1985 from the upper Xiangshuyuan Formation (lower Aeronian) of the Shiqian area, northeastern Guizhou, *Palaeophyllum fenggangense* He, 1985 from the Shihniulan Formation (upper Aeronian) of the Fenggang area, northern Guizhou, *Palaeophyllum bijishanense* He, 1978 from the "lower Silurian" of Biji Mountain, Yuexi area, southwestern Sichuan, *Palaeophyllum* sp. A and *P.* sp. B of Chen *et al.* (2005) both from the Sifengya Formation (lower Telychian) of the Daguan area, northeastern Yunnan, and *Cyathophylloides carinatus* Cao & Ouyang 1987 from the Yanglugou Formation (Pridoli) of the Zoige (Ruoergai) area, northwestern Sichuan. Their exclusion is further discussed in the remarks on the family above.

Ordovician cyathophylloidids are also known from the middle Katian rocks of the eastern Qinling region in the Xichuan area in southwestern Henan (Fig. 90:9; Fig. 92) and the Shanyang area in southeastern Shaanxi (Fig. 90:10; Fig. 92). The tectonic affinity of this region remains contested (e.g. Liu *et al.* 1991; Rong *et al.* 2015), and its present attribution to South China is therefore tentative. From the middle part (middle Katian; Jing *et al.* 2017, 2019) of the Shiyanhe Formation in Xichuan, *Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982) was described (Deng 1987; Wang 1991; Liang 2020), which is revised here as *Favistina* sp. B. In the Shanyang area, the Liangchakou Formation probably of the same age produces *Agetolites minor* Lin, 1963, *Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, 1982, and *F.* (*F.*) *shifosiensis* Cao in Cao & Lin, 1982, all of which are now included within *Crenulites minor* (Lin, 1963).

Sivi

Cyathophylloidids are present in the strata of generalized early–middle Katian age in the Zhongza area of westernmost Sichuan (Fig. 90:11; Fig. 92) and the Jinping area of southeastern Yunnan (Fig. 90:12; Fig. 92). These areas belong to the newly recognised Sivi between South China and Indochina. A comprehensive definition and discussion of this tectonic unit will be presented in a separate publication.

In the Zhongza area, cyathophylloidid-bearing strata are known as the Wuluochipu Formation, where *Palaeofavosites* cf. *grandis* Yu, 1960, revised now as *Crenulites grandis*? (Yu, 1960), was described by Deng & Zhang (1984). In the Jinping area, corals were recorded from the Dapingzi Formation, but without any cyathophylloidids reported (Zhang *et al.* 1996). However, a preliminary study on the newly obtained coral material from this horizon confirms the presence of this coral group.

South Tien Shan

In this terrane, Erina (2007) described *Palaeophyllum cateniforme* Flower, 1961, which is revised here as *Palaeolithostrotion?* sp. B (see above), from the uppermost Archalyk Member (uppermost Katian; Ghobadi Pour *et al.* 2023) of the Shahriomon Formation in Zeravshan–Hissar (Fig. 92). Additionally, Lavrusevich (1975, 1991) documented *Palaeolithostrotion zachonense* Lavrusevich, 1975 and *P. voruense* Lavrusevich, 1975 from this level.

Kazakh terranes

Kazakh terranes are an assembly of several small tectonic units, comprising Karatau–Naryn, North Tien Shan, Chu–Ili, Chingiz–Tarbagatai, Boshchekul, Selety and Kalmykkol–Kokchetav located in much of modern-day Kazakhstan and part of Uzbekistan and Kyrgystan in central Asia (Popov & Cocks 2017; Popov *et al.* 2023), as well as Yining, West Junggar, East Junggar, and Beishan in adjacent northwestern China (Chen *et al.* 1998; Zhou *et al.* 1996b, 2008). In the following discussion, only those regions with reports of cyathophylloidids are considered, namely Beishan, East Junggar, West Junggar, Chingiz–Tarbagatai and Chu–Ili (Fig. 93).

Beishan. – From the Badanjilin Formation (uppermost Katian) of the Danmianshan area, Ejin Banner, western Inner Mongolia (Fig. 90:13; Fig. 93), a specimen was described by He (1987) as *Palaeophyllum* sp. This form is tentatively reassigned here to stauriids due to its probable KLAC septal axial parricidal increase, as discussed above.

East Junggar. – *Cyathophylloides xinjiangensis* Cai, 1989, from the Kaokesirke Formation ("upper Silurian") of the Barkol area, northeastern Xinjiang, is excluded here from cyathophylloidids due to the presence of a thick peripheral stereozone and carinate septa, as also detailed above.

West Junggar. – *Favistella tachengensis* Cai, 1988 and *F. xinjiangensis* Cai, 1988, both revised here as *Cyathophylloides tachengensis* (Cai, 1988), occur in the Bulunggor Formation (possibly upper Katian),

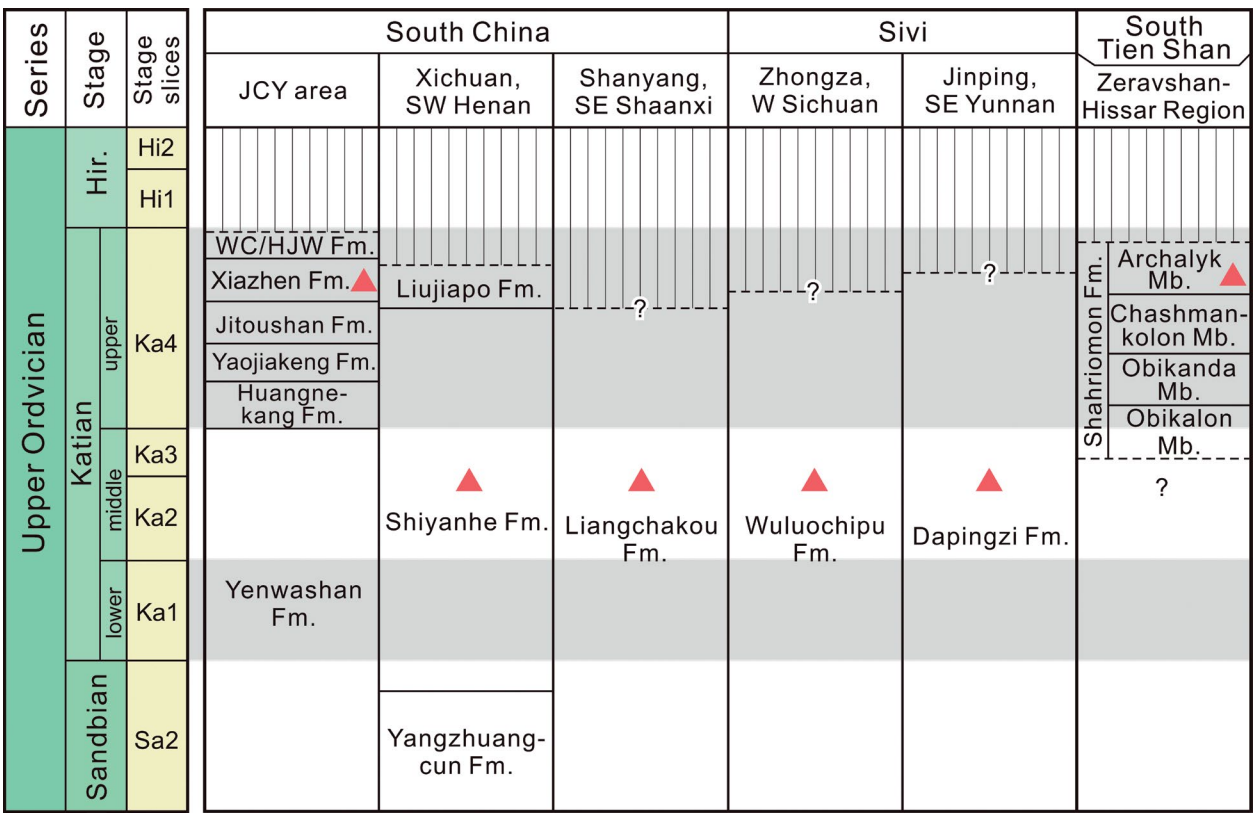


Fig. 92. Correlation of the Late Ordovician successions yielding cyathophylloidids in South China, Sivi and South Tien Shan, pink triangles indicating approximate horizons bearing these corals. Data source: Timescale (Goldman *et al.* 2020); stratigraphic correlations (Wang & Cui 2025; unpublished data). Abbreviations: WC, Wenchang; HJW, Hongjiawu.

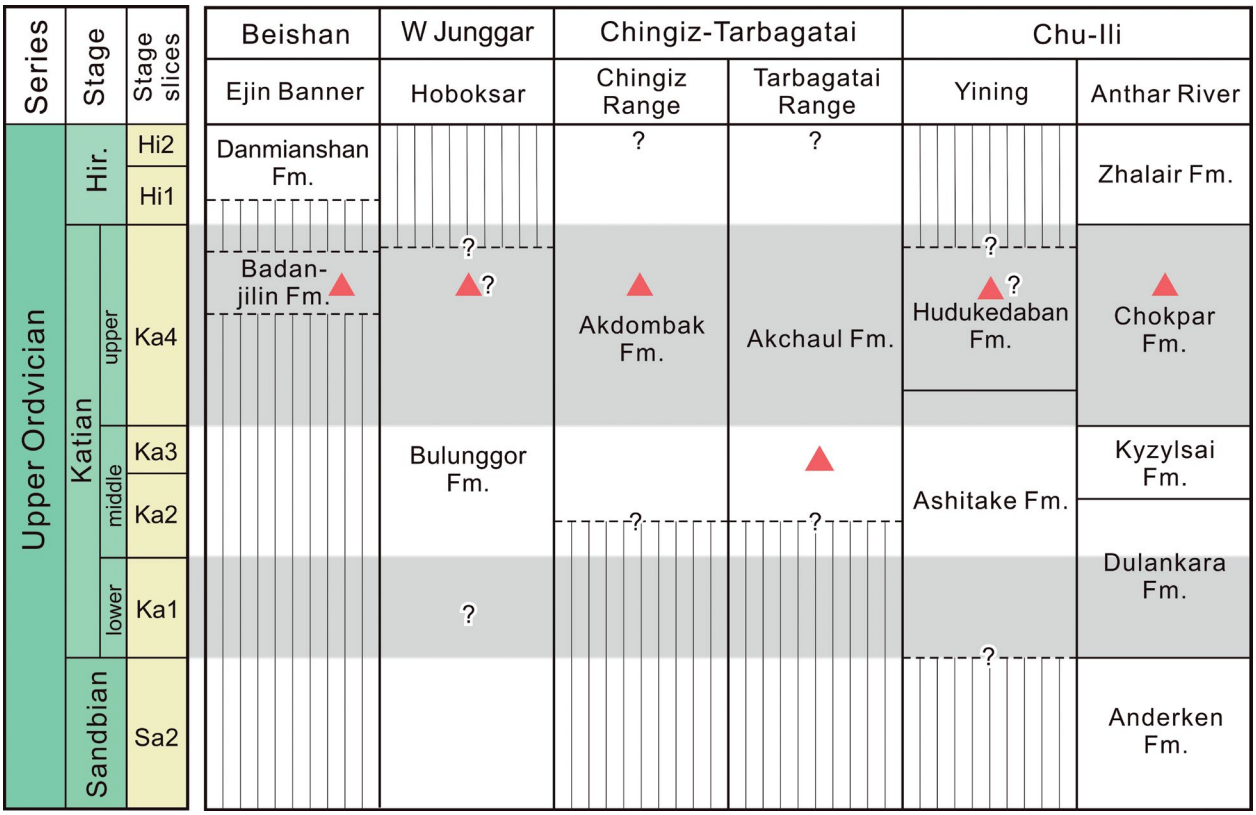


Fig. 93. Correlation of the Late Ordovician successions yielding cyathophylloidids in Kazakhstan terranes. Pink triangles indicate approximate horizons bearing these corals, those followed by question marks indicating uncertain occurrences. Data source: Timescale (Goldman *et al.* 2020); stratigraphic correlations (Wang & Cui 2025 and references therein).

southern slopes of Tarbagatai Mountains, Tacheng Prefecture, northwestern Xinjiang (Fig. 90:14; Fig. 93). Their precise stratigraphic position within this formation remains uncertain.

Chingiz–Tarbagatai. – From the basal Akchaul Formation (middle Katian) of the region (Fig. 93), Smelovskaya (1963) described *Favistella alveolata* (Goldfuss, 1826) and *Cyathophylloides aktshaulicus* Smelovskaya, 1963 in the Tarbagatai area, the former of which is revised here as *Crenulites*? sp. In addition, *Palaeophyllum fasciculum* (Kutorga, 1837) was described by Sultanbekova (1986) from the uppermost Akdombak Formation (uppermost Katian; Popov *et al.* 2023) in the Chingiz Range.

Chu–Ili. – In the Jinghe area of western Xinjiang, Cai (1981) introduced *Palaeophyllum*? *jingheensis* and *P.*? *distans* from the Hudukedaban Formation (probably upper Katian) near Hudukedaban (Fig. 90:15; Fig. 93). Additionally, *Palaeophyllum siluriense* Cai, 1981, from the Jifuke Formation ("middle Silurian") of the Nilka area, northwestern Xinjiang, may not belong to cyathophylloidids, and its identity remains to be clarified.

To the west, strata yielding cyathophylloidids are known as the Chokpar Formation in the Anthar river valley and an adjacent quarry (Fig. 93), which has been determined to be of latest Katian age by graptolites of the *Amplexograptus latus* and *Paraorthograptus pacificus* biozones and brachiopods of the *Holorhynchus giganteus* Beds (Apollonov *et al.* 1980; Popov *et al.* 2023). *Palaeophyllum fasciculum* (Kutorga, 1837) was described by Sultanbekova (1986) from this horizon.

Australia & New Zealand

Cyathophylloidids are restricted to strata of middle–late Katian age in Australia and New Zealand, which at that time formed part of equatorial peri-Gondwana (Percival *et al.* 2023) (Fig. 94). *Palaeophyllum proliferum* Webby, 1972 know from an earlier, Fauna II age (early Katian) in central NSW is now excluded from cyathophylloidids due to its probable aseptal parricidal increase mode, as also discussed above. In addition, the only Silurian cyathophylloidid report excluded here is *Palaeophyllum oakdalense* McLean, 1975, earlier described by Strusz (1961) as *Palaeophyllum rugosum* Billings, 1858a, from a horizon now known as the

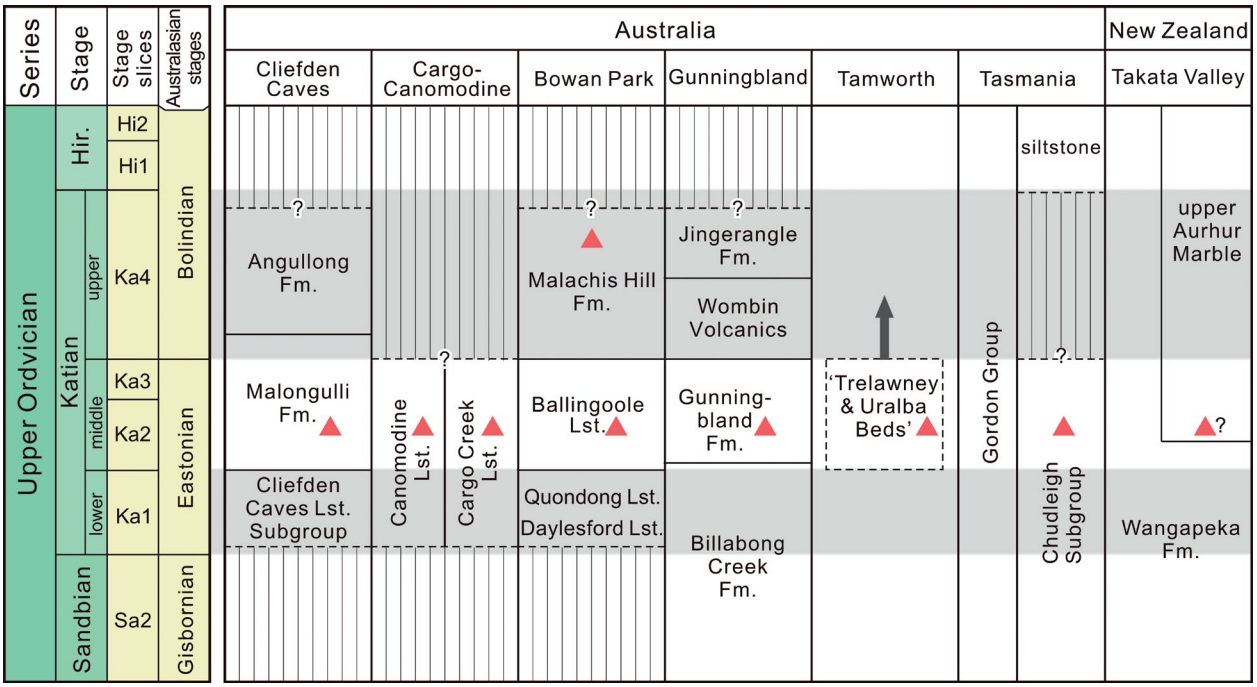


Fig. 94. Correlation of the Late Ordovician successions yielding cyathophylloidids in eastern Australia and New Zealand. Pink triangles indicate approximate horizons bearing these corals, the one followed by a question mark indicating a doubtful occurrence. Data source: Timescale (Goldman *et al.* 2020); stratigraphic framework of both Australia and New Zealand (Percival *et al.* 2023 and references therein).

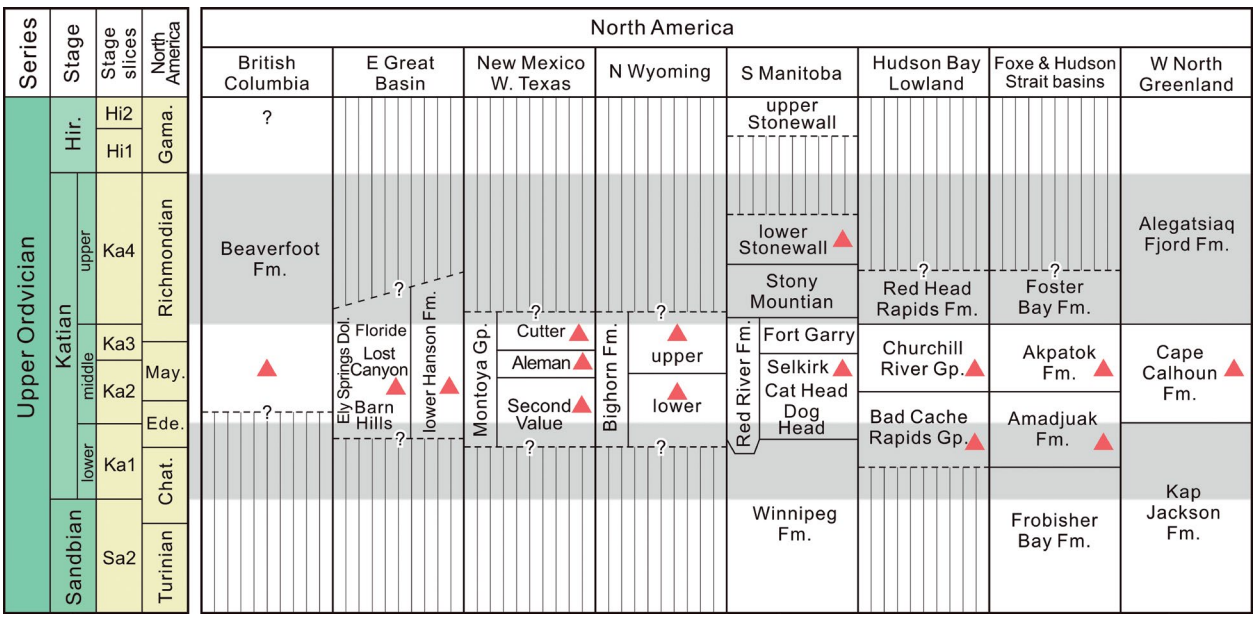


Fig. 95. Correlation of the Late Ordovician successions yielding cyathophylloidids in Laurentia, pink triangles indicating approximate horizons bearing these corals. Data source: timescale (Goldman *et al.* 2020); British Columbia (Buttler *et al.* 1988); Eastern Great Basin (Sheehan & Harris 1997; Bergström 2003; Bergström *et al.* 2010b); New Mexico and Western Texas (Sweet 1979; Elias, 1985; Bergström 2003); northern Wyoming (Sweet 1979; Caramanica 1992; Bergström 2003); southern Manitoba (Jin & Zhan 2001; Elias *et al.* 2013a); Hudson Bay Lowland (Desrochers *et al.* 2023); Foxe and Hudson Strait basins (Bolton 2000; Desrochers *et al.* 2023); western North Greenland (Rasmussen 2013).

Bell River Member (probable Homerian; McLean & Copper 2013) of the Dripstone Formation.

Middle Katian cyathophylloidids in the region are chiefly known from central NSW. In the Cliefden Caves area, *Favistina floweri* Webby, 1988, *F. gleesonensis* Webby, 1988, *F. plus* Webby, 1988, and *F.* sp. B of Webby (1988) are present in the Malongulli Formation (Webby 1988; this study). To the northwest in the Cargo–Canomodine area, the Canomodine Limestone yields *Favistina floweri* Webby, 1988, *F.* sp. A of Webby (1988), *Palaeophyllum bothroides* Hall, 1975, *P.*? *laxum* McLean & Webby, 1976, and an unnamed *Crenulites* species (McLean & Webby 1976; Webby 1988; this study). From the upper Cargo Creek Limestone southeast of a tributary of Canomodine Creek, *Favistina floweri* Webby, 1988 and *Palaeophyllum crassum* Webby, 1972 were described. In the Bowan Park area, *Palaeophyllum*? *patulum* McLean & Webby, 1976 occurs in the Ballingoole Formation at Malachi's Hill. In the Parkes area, *Favistina floweri* Webby was documented from the "lower part of the Goonumbla Volcanics" (now Gunningbland Formation; Percival *et al.* 2023) near Gunningbland, some 30 km west of Parkes. To the north, immediately west and northwest of Peak Hill, Zhen *et al.* (2022) recently recognised *Favistina plus* Webby, 1988 from carbonate intervals of comparable age intersected in a drill hole (WNDD0002).

Cyathophylloidids of middle Katian age are also found in northeastern NSW, western Tasmania, and possibly the Takaka area of central New Zealand. In the New England region of northeastern NSW, strata of this age are represented by allochthonous limestones (formerly 'Trelawney Beds') within the Devonian Drik-Drik Formation between Tamworth and Nundle, and coeval allochthonous limestones (formerly 'Uralba Beds') within the Glen Bell Formation of early Silurian or younger age in the nearby Manilla–Attunga area (Percival *et al.* 2023). The former rocks produce *Crenulites australis* Hall, 1975, *Cyathophylloides junctus* Hall, 1975, *Favistina neminghensis* (Etheridge, 1918) and *Palaeophyllum bothroides* Hall, 1975 (Hill 1942b; Hall 1975; Wang *et al.* 2021). The Uralba fauna is almost identical, apart from the absence of *Cyathophylloides junctus* Hall, 1975 (Hall 1975; Wang *et al.* 2021). In western Tasmania, *Favistina cerioides* (Hill, 1942a) was documented from the coeval strata now assigned to the top of the Benjamin Limestone and the upper Chudleigh Subgroup (Gordon Group) (Percival *et al.* 2023). In New Zealand, a form recognised as *Favistella* (= *Favistina*; this study) occurs in the upper Arthur Marble of generalised Late Ordovician age in Takata Valley (Cooper 1965, p. 55; 1968, p. 79). This coral-bearing level is more likely of middle Katian age, although a further study is needed.

Strata of late Katian age in the region yield *Cyathophylloides semeniuki* Webby, 1988 and *Palaeolithostrotion macrocaule* (Webby, 1972), both from the uppermost Malachis Hill Formation (uppermost Katian) in the Bowan Park area, central NSW (Webby 1972, 1988; Wang *et al.* 2020; this work).

Laurentia

Cyathophylloidids in Laurentia are known from Upper Ordovician–Wenlock strata, according to early summaries of Bassler (1915, 1950) and Flower (1961). More recently, Elias *et al.* (2013b) tabulated all known Laurentian coral taxa of Late Ordovician age at the genus level and assigned them to four biogeographical divisions: the Red River–Stony Mountain Province, Richmond Province, Edgewood Province, and an informal "Continental Margin" Area. In their analysis, *Favistina* was viewed as a junior synonym of *Cyathophylloides*, a position not supported in this study. Using new fossil and stratigraphic data (Figs 95, 96), an updated review of the Laurentian cyathophylloidids is outlined as follows.

Reliable cyathophylloidids recognised from the strata of late Sandbian age in North America include *Favistina discreta* (Foerste, 1914), *F. paleophylloides* Flower, 1961 and *F. undulata* (Bassler, 1950) from the upper Black River Group of Ottawa and Ontario, *F. undulata* (Bassler, 1950) from the Platteville Formation of Wisconsin (Flower, 1961), and *F. minor* (Bassler, 1932) from the upper Carters and basal Hermitage formations of Tennessee (Foerste 1914; Bassler 1932, 1950; Okulitch 1938; Flower 1961; this study). These represent the earliest cyathophylloidids both in Laurentia and globally. In addition, *Palaeophyllum mazourkense* Pestana, 1960 recorded from the Johnson Spring Formation of Inyo Mountains in California may also be of this age or perhaps the early Katian. All excluded forms of this age or older are listed in Appendix Table 1 and are not repeated here.

Cyathophylloidids of early Katian age are recorded in many areas of North America. In northern Hudson Bay Lowland, the Bad Cache Rapids Group yields *Palaeophyllum halysitoides*? (Wilson, 1926) (Nelson 1963; this study). In the Foxe Basin, a small satellite basin of the Hudson Bay Basin, *Favistina undulata* (Bassler, 1950) and a possible *Palaeophyllum* species occur in the Amadjuak Formation of Edenian–early Maysvillian (early–middle Katian) age at Silliman's Fossil Mount, southern Baffin Island, Nunavut, northern Canada (Roy 1941; Bolton 2000). At Lake Timiskaming outlier of Ontario, *Palaeophyllum humei* Sinclair, 1961, revised here as *P. rugosum* Billings, 1858a, occur in the Farr Formation. *Palaeophyllum rugosum* Billings,

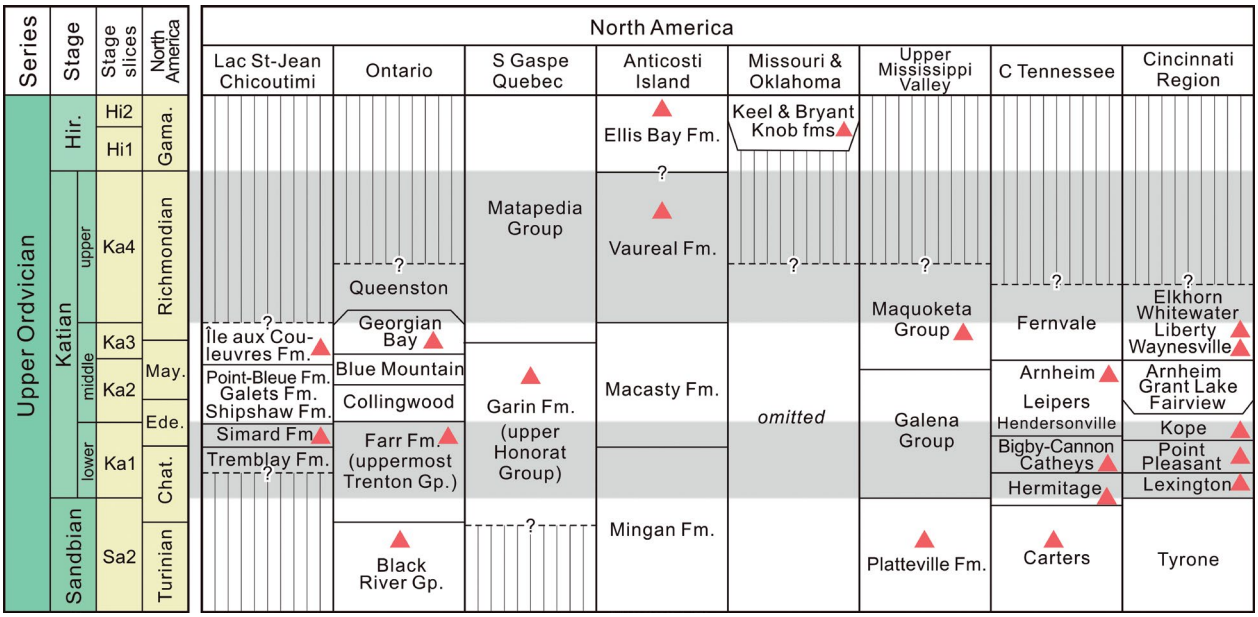


Fig. 96. Correlation of the Late Ordovician successions yielding cyathophylloidids in Laurentia, pink triangles indicating approximate horizons bearing these corals. Data source: Timescale (Goldman *et al.* 2020); Lac Saint-Jean (Desbiens and Lespérance 1989); Ontario (Copper & Grawbarger 1978; Sanford 1993; Goldman & Bergström 1997; Desrochers *et al.* 2023); southern Gaspé, Quebec (Riva & Malo 1988); Anticosti Island (Desrochers *et al.* 2023); northeastern Missouri and south–central Oklahoma (Young & Elias 1995); Upper Mississippi Valley (Goldman & Bergström 1997); central Tennessee (Patzkowsky & Holland 1999; Leslie 2000); Cincinnati Region (Bergström *et al.* 2010b; Brett *et al.* 2020; Daniel Goldman & Patrick McLaughlin pers. comm.).

1858a is also known from the Simard Formation in the Lac St-Jean outlier, Quebec (Billings 1858a, b; Lambe 1901; Bassler 1950; Hill 1959, 1961), a level now considered as the Cobourg Formation equivalent of early Edenian (early Katian) age (Desbiens & Lespérance 1989). In central Tennessee, *Favistina undulata*? (Bassler, 1950) is present in the Catheys Formation (Bassler 1932; this study). In Kentucky, *Favistina interventa* (Foerste, 1914) and *F. minima* (Foerste, 1914) are recorded from the Lexington and Point Pleasant formations, respectively (Foerste 1914; Bassler 1950); a coral recently figured externally by Harris *et al.* (2019) as *Cyathophylloides* cf. *C. burksae* comes from the stratigraphically higher Kope Formation of this region, which apparently requires a thin-section study. Note that *Columnaria erratica* Billings, 1858a, from the same general area and stratigraphic level as *Palaeophyllum rugosum* Billings, 1858a, was regarded by Lambe (1901) as a synonym of the latter but was revised by Sinclair (1961) as belonging to *Eofletcheria* Bassler, 1950. Also excluded are *Columnaria crenulata* Bassler, 1932 from the upper Hermitage Formation of central Tennessee (Bassler 1932, 1950; Flower 1961) and *Streptelasma* (*Palaeophyllum*) *aggregatum* Nicholson & Etheridge, 1878 from the Craighead Limestone of Scotland and from the Balclatchie Group at Balclatchie (Nicholson & Etheridge 1878; Wang 1948; Orita & Ezaki 2001) (see above).

In middle Katian Laurentia, cyathophylloidids had a wide distribution. In northeastern British Columbia, *Favistina stellaris* (Wilson, 1926) and *Palaeophyllum halysitoides* (Wilson, 1926) are present in the possibly middle Katian portion of the Beaverfoot Formation (Wilson 1926; Bassler 1950; this work). In Eastern Great Basin, *Palaeophyllum rugosum*? Billings, 1858a, *Palaeolithostrotion radugini*? and species possibly assigned to *Cyathophylloides* are recorded from the Lost Canyon Member (middle Katian) of the Ely Springs Dolomite (Pandolfi 1985; this work). The specimen figured by Duncan (1956, pl. 24, fig. 6a, b) as *Cyathophylloides*, which is reclassified here as *Favistina*, comes from the coeval Burnam Formation of central Texas and the Hanson Creek Formation of Nevada. In New Mexico and western Texas, the Second Value Formation of the Montoya Group yields *Crenulites duncanae* Flower, 1961, *C. magnus* Flower, 1961, *Palaeophyllum margaretae* Flower, 1961, and *P. cateniforme* Flower, 1961. The overlying Aleman and Cutter formations (middle Katian–? basal upper Katian) produce *Palaeophyllum thomi* (Hall in Emory, 1857), *Cyathophylloides burksae* Flower, 1961 and *Favistina crenulata*? Flower, 1961 (Hall in Emory 1857; Walcott 1904; Bassler 1950; Hill 1959; Flower 1961; this study). To the west of Montoya, from strata of similar age exposed in an outlier of the Montoya at Morenci, Arizona, the coral material earlier described by Hill

(1959) was revised by Flower (1961) as including *Palaeophyllum margaretae* and *P. cateniforme*. In the Bighorn Mountains of northern Wyoming, *Crenulites rigidus* (Billings, 1858a) and *C. duncanae* Flower, 1961 are present in the lower part of the Bighorn Formation (Caramanica 1973, 1992; Porter *et al.* 2007). In the 18 meters of the "Upper Ordovician undivided" overlying the Hunt Mountain Beds, *Crenulites stellatus* (Hall, 1847) and *Palaeolithostrotion vaurealense* (Twenhofel, 1928) occur (Caramanica 1973, 1992; Gierlowski & Langenheim 1985; this study). Further north in the Williston Basin of southern Manitoba, *Palaeophyllum argus* Sinclair, 1961, *Crenulites rigidus* (Billings, 1858a) and *C. duncanae* Flower, 1961 are present in the Selkirk Member of the Red River Formation (Sinclair 1961; Caramanica 1973, 1992; Porter *et al.* 2007). In northern Hudson Bay Lowland, the Churchill River Group produces cyathophylloidids (Nelson 1963), revised in this work as *Palaeolithostrotion radugini*? (Tcherepnina, 1960) and *Favistina stellaris* (Wilson, 1926). In the Hudson Strait Basin, *Crenulites akpatokensis* Flower, 1961, *C. discretus* Bolton in Workum *et al.*, 1976 and *Palaeophyllum cateniforme* Flower, 1961 occurs in the Maysvillian (middle Katian) of Akpatok Island, Canada. From the middle Katian rocks north of Aberdeen Lake, Keewatin, *Palaeolithostrotion radugini*? (Tcherepnina, 1960) is present (Bolton & Nowlan 1979; this work). In western North Greenland, *Palaeophyllum halysitoides*? (Wilson, 1926) is recorded from the Cape Calhoun Formation (Troedsson 1928; Bassler 1950; this study).

On Snake Island, Lake St. John, Quebec, *Columnaria rigida* Billings, 1858a and *C. blainvilli* Billings, 1858a were described from the middle Katian Île aux Couleuvres Formation (Billings 1858a, b; Foerste 1924; Bassler 1950; Flower 1961), both of which were reassigned by Flower (1961) to *Crenulites*. In Ontario, *Crenulites stellatus* (Hall, 1847) and *C. calicinus* (Nicholson, 1875a) were described from the Georgian Bay Formation, with the former originating from Manitoulin Island and the latter from the Credit River (Nicholson 1875a–d; Lambe 1901; Foerste 1924; Flower 1961; Fedorowski & Jull 1976; Jull 1976a; Bolton 1979). In the Mount Saint Joseph area, southern Gaspé Peninsula, Quebec, *Favistina honoratensis* Bolton, 1979 was described from the upper Garin Formation of the Honorat Group (Bolton 1979, 1980). In Iowa, *Cyathophylloides ulrichi* Bassler, 1950, transferred by Flower (1961, p. 83) to *Crenulites*, is known probably from the middle Katian portion of the Maquoketa shale, Bristol Township. In the basal parts of the Waynesville, Liberty and Whitewater formations (middle Katian–? basal upper Katian) of Kentucky, quite a few forms were described as cyathophylloidids (Hall 1847; Rominger 1876; Foerste 1909, 1924; Bassler 1950; Flower 1961; Browne 1965; Fedorowski & Jull 1976; Jull 1976b; Bolton 1979), but those considered here as belonging to this group include *Crenulites calicinus* (Nicholson, 1875a), *C. stellatus* (Hall, 1847), *C. vacuum* (Foerste, 1909), *Favistina crenulata* Flower, 1961 and *F. magister* (Bassler, 1950).

Cyathophylloidids became rare during the late Katian, with robustly dated occurrences known in southern Manitoba and Anticosti Island. In the former area, *Palaeophyllum pasense* Stearn, 1956 and *P. pasense parvum* Stearn, 1956 are recorded in the lower Stonewall Formation, revised here as *Palaeophyllum*? *pasense* and *P.*? *parvum*, respectively. On Anticosti, *Columnaria*? (*Palaeophyllum*) *vaurealensis* Twenhofel, 1928 occurs in the upper Vauréal Formation. This form has been widely reassigned to *Palaeophyllum* (Twenhofel 1928; Bolton 1972, 1979; Fedorowski & Jull 1976; Melzak 2004), but the present author places it within *Palaeolithostrotion*.

Ordovician–Silurian boundary strata in Laurentia that yield cyathophylloidids are known from Anticosti Island of eastern Canada and east–central USA. On Anticosti, the upper Ellis Bay Formation yields *Cyathophylloides lyterion* Bolton, 1979 and *Palaeophyllum clion* Bolton, 1979 (Bolton 1972, 1979, 1981). Melzak (2004) later synonymised these forms under *Palaeophyllum lyterion* (Bolton, 1979), which is reassigned here to *Palaeolithostrotion*. In east–central USA, Young & Elias (1995) described *Palaeophyllum* sp., revised here as *Palaeolithostrotion*? A, from the lower Keel Formation of south–central Oklahoma and the Kissenger Limestone Member of the Bryant Knob Formation of northeastern Missouri. Both rock units produce elements of Transitional Benthic Fauna 3, indicative of a latest Hirnantian–earliest Silurian age (Wang *et al.* 2019; Rong *et al.* 2020).

Reliable records of Silurian cyathophylloidids are known from eastern Canada and New York. In eastern Canada, *Palaeophyllum cumerense* McLean & Copper, 2013, transferred here to *Palaeolithostrotion*, occurs in the East Point Member (upper Aeronian) of the Menier Formation, Anticosti. In New York, *Syringopora*? *multicaulis* Hall, 1852, revised here as *Palaeolithostrotion multicaule* (Hall, 1852), is recorded from the Gasport Formation (Homerian; Laub 1983; Brett *et al.* 1995), Lockport; this cyathophylloidid appears to be the youngest record worldwide. Additionally, three possible Silurian cyathophylloidid forms are noted. In western North Greenland, *Palaeophyllum* cf. *hubeiense* Ge & Yu, 1974 of McLean (1977) from the Cape Schuchert Formation (Aeronian) is revised here as *Palaeophyllum*? *hubeiense*? Ge & Yu, 1974, and *Columnaria* (*Palaeophyllum*) *stokesi* (Milne-Edwards & Haime, 1851) of Troedsson (1928) from the younger

Offley Island Formation (Telychian) is reclassified here as *Palaeolithostrotion*? *troedssoni* (Poulsen, 1941). Similarly, cf. *Palaeophyllum* sp. of Oliver *et al.* (1975a, p. 26), from an interval likely of "early Wenlockian" age in the Porcupine River area of northeastern Alaska, may represent an example of *Palaeolithostrotion*, but its identity remains to be clarified.

Several Laurentian forms previously attributed to Silurian cyathophylloidids should be removed. They include *Palaeophyllum* (*Cyathophylloides*?) *williamsi* Chadwick in Williams, 1919 and *P. umbellicrescens* Chadwick in Williams, 1919 from the Manitoulin Formation (lower Rhuddanian), Manitoulin Island; *Palaeophyllum* sp. of Bolton (1981) and Melzak (2004) from the Chabot member (Rhuddanian) of the Becscie Formation on Anticosti Island; *P. conjunctum* McLean & Copper, 2013 from the basal Merrimack and possibly uppermost Becscie formations (upper Llandovery) on Anticosti Island; *Palaeophyllum schuchertense* McLean, 1977 from the Cape Schuchert Formation (Aeronian) of Kap Schuchert, western North Greenland; and *Palaeophyllum halysitoides* (Wilson, 1926) and ?*Palaeophyllum* sp. of Scrutton 1975 from the upper part (lower Silurian?) of the Centrum Formation, northeast Greenland. Also excluded are *Cyathophylloides fergusoni* Merriam, 1973 and *C.* sp. f from the "Coral Zone A" of the Tuscarora Mountains, northern Nevada, and of the Toquima Range, central Nevada, respectively (Merriam 1973; Merriam & McKee 1976). This horizon was previously dated as late Llandovery (Johnson & Oliver 1977) but now proves to be of Lochkovian (Early Devonian) age (Pedder & Murphy 1997).

York Terrane

Strata with cyathophylloidids in this terrane are solely from a level informally known as unit Sodl on the western Seward Peninsula, Alaska (Fig. 97), which is of a probable Katian (middle Katian?) age indicated by associated solitary rugosans (Oliver *et al.* 1975a, b; Blodgett *et al.* 2002; Dumoulin *et al.* 2014, 2023). Oliver *et al.* (1975a, b) illustrated a specimen as *Cyathophylloides* sp. from this interval.

Baltica

Cyathophylloidids of pre-Hirnantian age in Baltica are recorded from southern Norway, Estonia and the Middle Urals (Fig. 97). In Norway, Kiær (1932) described *Columnaria* cf. *kassariensis* from the Kalstad Limestone (Spjeldnæs 1963) of early Katian age (Bergström 1997) in Trondheim. This form was later considered by Spjeldnæs (1963) as possibly conspecific with *C. kiaeri*, but a revision is needed. To the south, *Cyathophylloides kiaeri* Spjeldnæs, 1963 was documented from the basal Tretaspis Limestone (now upper Katian Grimsøya Formation; Nielsen *et al.* 2023) of northeastern Kalvøya, Bærum, Oslo–Asker. In the Middle Urals, *Palaeophyllum halysitoides*? (Wilson, 1926) occurs in the "middle Caradoc" (lower Katian?), while *Crenulites* sp. A is recorded in the younger Sur'ya Horizon (middle Katian?) (Ivanov & Myagkova 1950, 1955; Shurygina 1973; this study).

In the Hirnantian–lower Llandovery strata of Baltica, *Palaeophyllum fasciculum* (Kutorga, 1837) (= *Palaeophyllum tubuliferum* Reiman, 1958; this study) occurs in Estonia from the Ärina (Hirnantian; Hints *et al.* 2000; Meidla *et al.* 2023b), Varbola (lower Rhuddanian; Meidla *et al.* 2023a) and Hilliste (upper Rhuddanian–? lower Aeronian; Ursula Toom pers. comm.). *Cyathophylloides kassariensis* Dybowski, 1873a appears to be confined to the Hilliste Formation (upper Rhuddanian–? lower Aeronian). In Norway, *P. fasciculum* was listed without a description from the "Etage 5a and 5b" (upper Katian–Hirnantian?) (Kiær 1902; Kaljo *et al.* 1963), which requires confirmation.

Several Silurian forms in Baltica formerly described as cyathophylloidids are now reassigned elsewhere. They include *Dokophyllum sociale* Soshkina, 1937 from the Elkino Horizon (Wenlock) of the eastern slope of the Middle Urals, *Columnaria gothlandica* Milne-Edwards & Haime, 1851 from the lower Slite Group (formerly "Stage f"; Lindström 1888) of late Sheinwoodian (Wenlock) age (Calner *et al.* 2004) on Gotland, and "*Columnaria*" *gothlandica* Milne-Edwards & Haime, 1851 of Ivanovskiy (1969) from the "Upper Silurian" of the Dniester River, as discussed above.

Siberia

Strata in Siberia that produce cyathophylloidids are restricted to the middle–upper Katian (Fig. 97). A coral of possible pre-middle Katian age previously referred to this group is *Favistella simplex* Sokolov, 1955, from the "Middle Ordovician" of the Moyero River region; here it is reassigned to the tabulate coral *Foerstephyllum* Bassler, 1941. Also excluded are the Silurian materials described by Ivanovskiy (1965, 1969, 1992) as *Palaeophyllum tubuliferum* Reiman, 1958 and *P. fasciculum* (Kutorga, 1837) from the "Llandovery", as well as by Ivanovskiy (1988, 1992) as *Cereoelasma sibiricus* Ivanovskiy, 1988 from the "Wenlock". In addition, a form that is potentially excluded is *Palaeophyllum thomi* (Hall, 1847) of Latypov (1978) from the uppermost Baraninsky Formation of the Sette–Daban area, northeastern Russia, a level thought to correlate with the "Kety Horizon" (Volkova *et al.* 1978) of late Katian age (Kanygin *et al.* 2019).

In the Dolborian Horizon (middle Katian; Kanygin *et al.* 2019) of the Siberian Platform,

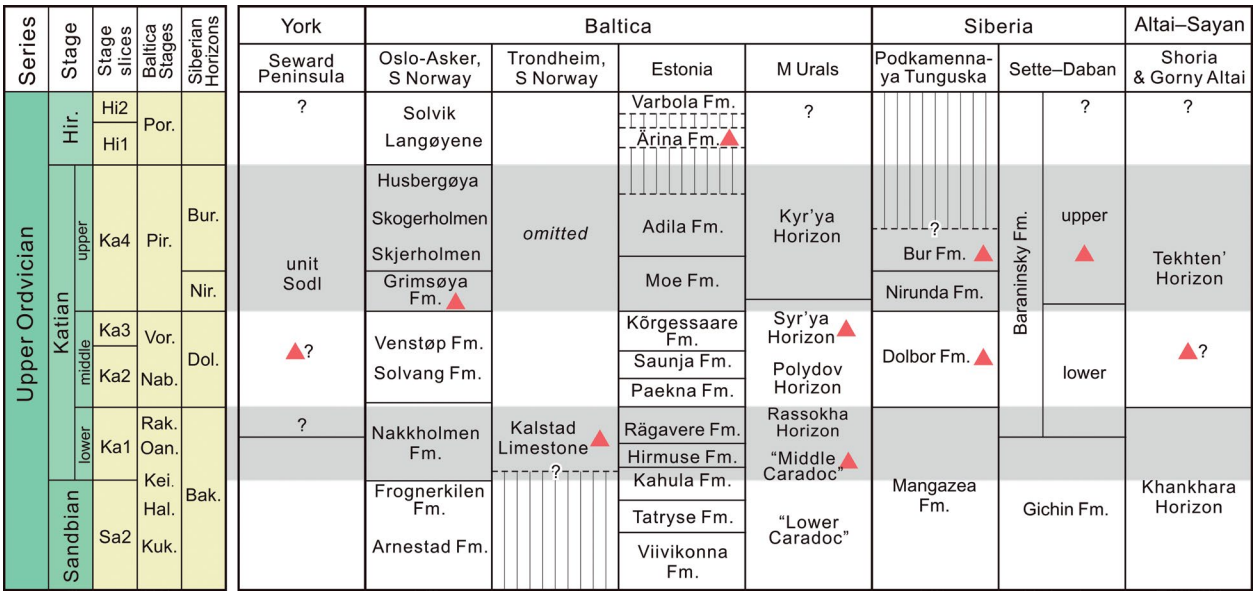


Fig. 97. Correlation of the Late Ordovician successions yielding cyathophylloidids in York Terrane, Baltica, Siberia and Altai–Sayan. Pink triangles indicate approximate horizons bearing these corals, those followed by question marks indicating uncertain occurrences. Data source: Timescale (Goldman *et al.* 2020); Seward Peninsula (Dumoulin *et al.* 2014, 2023); Oslo–Asker (Nielsen *et al.* 2023); Trondheim (Bergström 1997); Estonia (Meidla *et al.* 2023b); Middle Urals (Shurygina 1973; Antoshkina 2003); Podkamennaya Tunguska (Kanygin *et al.* 2019); Sette–Daban (Volkova *et al.* 1978); Altai & Sayan (Sennikov *et al.* 2019).

diverse cyathophylloidids were described from the Podkamennaya Tunguska River Basin (Sokolov 1950, 1955; Soshkina in Ivanova *et al.* 1955; Ivanovskiy 1965, 1969; Sytova 1979a). These corals are now revised as including *Crenulites septosus* (Sokolov, 1950), *C. asper* (Sokolov, 1955), *C. breviseptatus* (Sokolov, 1955), *C.* sp. B, *C. australis* Hall, 1975, *Cyathophylloides* sp. A, and *Favistina* sp. A.

The younger Ordovician strata in Siberia yield very few cyathophylloidids, only represented by *Palaeophyllum thomi* (Hall, 1847) from the Burian Horizon (upper Katian; Kanygin *et al.* 2019) of the Podkamennaya Tunguska River Basin (Ivanovskiy 1969; Sytova 1979; this work).

Altai–Sayan

A few corals, possibly from the middle Katian portion of the Tekhten's Horizon in the Shoria and Gorny Altai regions, were previously identified as cyathophylloidids (Fig. 97). They include *Columnaria* sp., *C. halysitoides* Radugin, 1936a, *C.* (?) *fascicularis* Radugin, 1936a, *Parabrachyelasma lebediensis* Tcherepnina, 1960, *P. virgulta* Tcherepnina, 1960, *Favistella ampla* Tcherepnina, 1960, *F. densa* Tcherepnina, 1960, *F. ainkiensis* Tcherepnina, 1960, *F. grandis* Tcherepnina, 1960, *F. radugini* Tcherepnina, 1960, and *F. calicinaeformis* Tcherepnina, 1960 (Radugin 1936a, b; Tcherepnina, 1960; Ivanovskiy 1969). Of these, only *Columnaria halysitoides* Radugin, 1936a and *Favistella calicinaeformis* Tcherepnina, 1960 are considered here as reliable cyathophylloidids, revised as *Palaeolithostrotion radugini* (Tcherepnina, 1960) and *Cyathophylloides calicinaeformis* (Tcherepnina, 1960), respectively (see above). The taxonomic status of *Columnaria* (?) *fascicularis* Radugin, 1936a remains unclear; it may belong to *Palaeophyllum*, but confirmation is needed.

The only reported Silurian cyathophylloidid of the region is *Palaeophyllum fasciculum* (Kutorga, 1837) described by Ivanovskiy & Kulkov (1974) from the upper "Chinetinsky Horizon" (upper Llandovery) of the Gorny Altai. This form is revised here *Palaeophyllum*? sp., discussed above.

Tuva–Mongol

No reliable cyathophylloidids are known from this terrane. Previous reports of this group are all from the Silurian of western Tuva, including *Favistina magna* Sytova in Sytova & Ulitina, 1983 from the Alash Horizon (Rhuddanian–lower Aeronian), and *Palaeophyllum tubuliferum* Reiman, 1958 from the Kyzylchiraa Horizon (upper Aeronian). Both are not true cyathophylloidids (see above for a discussion).

Central Mongolia

A coral was described by Sytova & Ulitina (1983) as *Palaeophyllum thomi* (Hall in Emory, 1857) from the

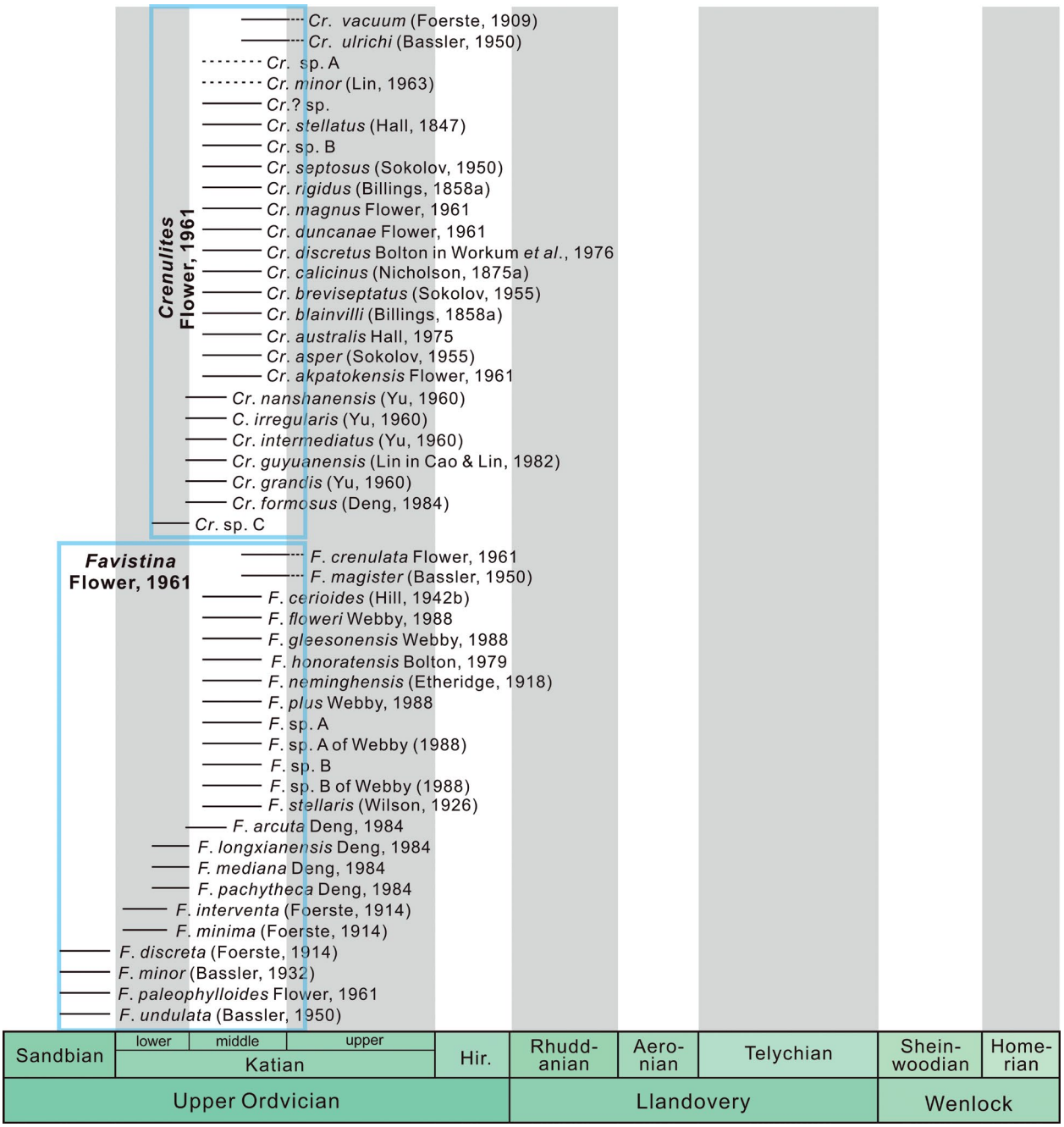
Khangai Horizon (probably upper Katian; Ulitina *et al.* 2009). It is not a cyathophylloidid due to its aseptal parricidal mode of increase.

Gobi Altai

From the Sairin Subhorizon (probably upper Katian; Ulitina *et al.* 2009) of the Khangai Horizon, southern Mongolia, Sytova & Ulitina (1983) described *Palaeophyllum crassum* Webby, 1972, *P. lebediensis* (Tcherepnina, 1960), *P. virgultum* (Tcherepnina, 1960) and *P. patulum*? (McLean & Webby, 1976), all of which are excluded from cyathophylloidids (see above).

Cyathophylloidid origin and evolution

The origin and evolution of cyathophylloidid corals are examined in the following discussion, based on the refined palaeontological and stratigraphic data summarised above and illustrated in Fig. 98.



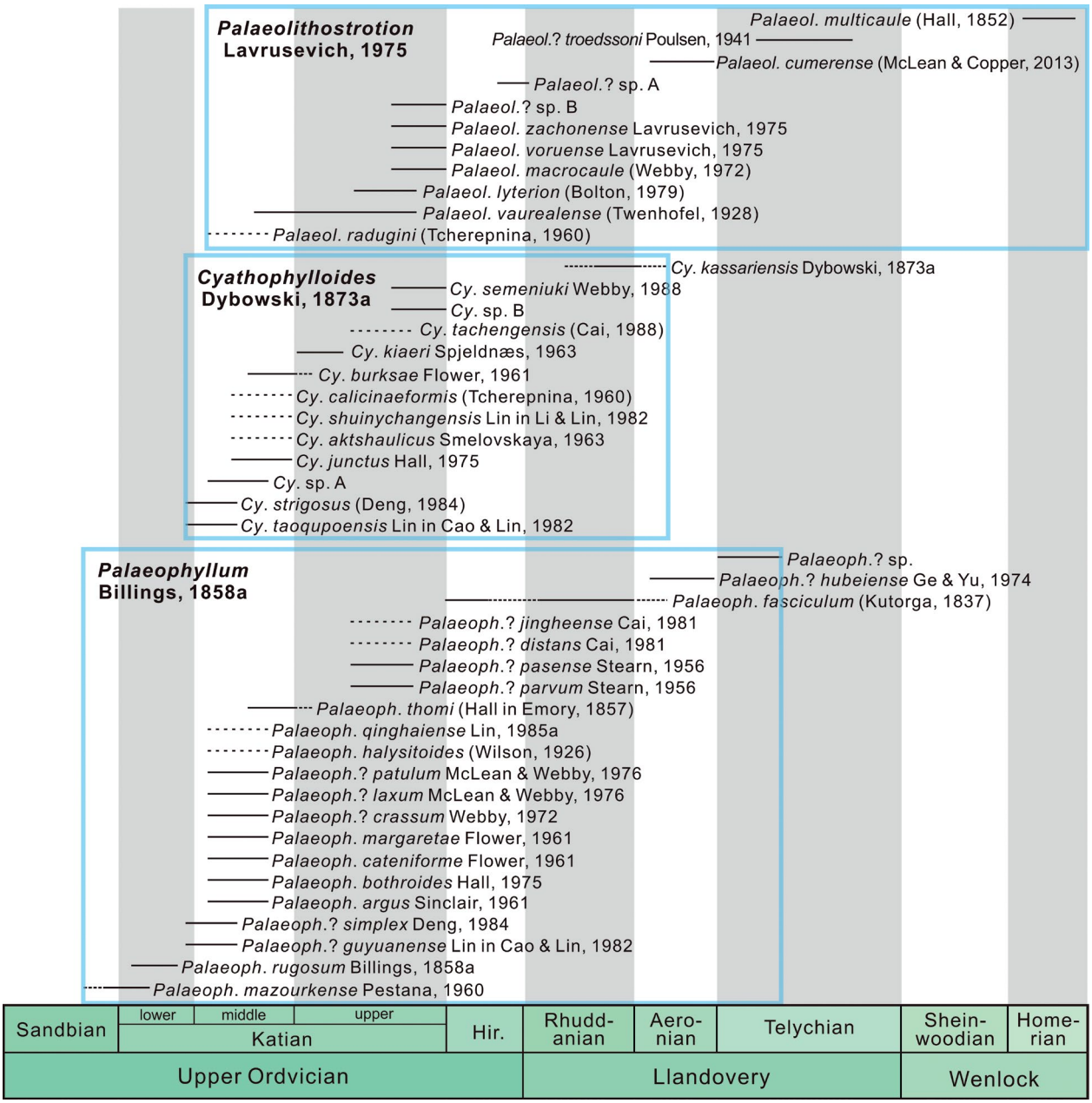


Fig. 98. Stratigraphic distribution of cyathophylloidid species, with solid and dashed black lines representing confirmed and possible ranges, respectively. Timescale after Goldman *et al.* (2020) and Melchin *et al.* (2020).

Origin

Before exploring the origin of cyathophylloidids, it is essential to first determine what constitutes their ancestral stock. The debate over whether *Favistina* or *Palaeophyllum* holds this distinction has persisted for decades. Following the view of Bassler (1941), Flower (1961) and Flower & Duncan (1975) argued that *Favistina* was the ancestral stock based on its first recorded appearance in North America within Blackriveran (Sandbian) strata, predating *Palaeophyllum*, which emerged in the early Edenian (early Katian). However, Webby (1988) challenged this scenario with stratigraphic evidence from eastern Australia. In Tasmania, *Palaeophyllum* first appeared in an assemblage associated with *Bajgolia* and *Tetradium* indicative of Fauna II (early Katian) age (Banks & Burrett 1980; Webby 1988), pre-dating the *Favistina* species recognised from his coral/stromatoporoid Fauna III (Webby 1969, 1972) of middle Katian age. This led Webby (1988, p. 141) to consider that "*Favistina* was derived from *Palaeophyllum* between faunas II and III". However, the occurrence of *Palaeophyllum* in

Tasmania is significantly later than that of *Favistina* in North America. Additionally, Lin *et al.* (1995, p. 42) proposed that *Palaeophyllum* might have first appeared in South China during the Sandbian, and later spread to other regions in the Katian, a view subsequently echoed by He & Tang (2011, p. 18). Their conclusion was based on the presumed oldest record of *Palaeophyllum*, identified as *Palaeophyllum irregulare* Lin & Chow, 1980, from the lower Yenwashan Formation (Sandbian; Wang *et al.* 2015) in the JCY area of eastern China. However, this form is now considered a probable monacanthine rugosan, as discussed above. In summary, *Favistina* is the earliest known cyathophylloidid representative, reinforcing its status as the ancestral stock for other lineages within this coral clade.

Regarding the origin for cyathophylloidids, an evaluation of previous hypotheses suggests that none are substantiated by the currently available evidence. A *Lichenaria* origin for this group was proposed by Sokolov (1955) and echoed by Kaljo (1957), among others. This form, however, now proves to be an unrelated tabulate coral (Hill 1956, 1960, 1981; Neuman 1984; Scrutton 1984, 1997; Webby *et al.* 2004), with earliest confirmed occurrences in the early Katian (Elias *et al.* 2021). Alternatively, Ivanovskiy (1965, 1969) argued that the early cyathophylloidid *Favistina* was derived from the solitary rugosan *Primitophyllum* via *Proterophyllum*, which was based on the mistaken belief that *Proterophyllum* is a ceroid cyathophylloidid but with septa typical of *Primitophyllum*. However, both *Proterophyllum* and *Primitophyllum* are considered here unrelated to cyathophylloidids. The former is likely synonymous with the tabulate coral *Foerstephyllum*, while the latter belongs to monacanthine rugosans. In my view, it remains challenging at present to confidently determine the identity of their ancestor. However, it seems possible that the ancestral stock of cyathophylloidids (i.e. *Favistina*) evolved independently from a compound soft-bodied anemone clade through the acquisition of skeletal secretion during the late Sandbian.

Evolution

Previous studies suggested that *Cyathophylloides* evolved from *Favistina* by the inward extension of major septa, resulting in a reinforced axial structure, while *Crenulites* is thought to have originated from *Favistina* through the development of amplexoid septa and *Palaeophyllum* through the adoption of a fully fasciculate growth habit (Flower 1961; Flower & Ducan 1975; Webby 1988). These evolutionary scenarios are supported by the earlier appearance of *Favistina*, highlighting its role as an ancestral form. Building on this perspective, I further suggest that these evolutionary events took place during the early Katian. Additionally, *Palaeolithostrotion* likely arose from *Cyathophylloides* during the middle Katian through the development of fasciculate growth. However, the possibility of *Palaeolithostrotion* evolving from *Palaeophyllum* via the fusion of major septa within the corallite axis remains a possible alternative. Within this phylogenetic framework, the evolutionary trajectory of cyathophylloidid corals is outlined below.

Following the initial appearance of *Favistina* in Laurentia during the late Sandbian (Foerste 1914; Bassler 1932, 1950; Okulitch 1938; Flower 1961; this study), cyathophylloidids experienced early diversification in the subsequent early Katian. This period saw the further development of *Favistina* alongside the first appearances of *Palaeophyllum*, *Crenulites* and *Cyathophylloides*. Reliable cyathophylloidid records of this interval are known in several blocks, including North China (Deng 1984), Laurentia (Billings 1858a, b; Lambe 1901; Foerste 1914; Bassler 1932, 1950; Roy 1941; Hill 1959, 1961; Pestana 1960; Flower 1961; Sinclair 1961; Nelson 1963; Bolton 2000; Harris *et al.* 2019) and Baltica (Kiær 1932; Ivanov & Myagkova 1950, 1955).

During the middle Katian, cyathophylloidids became more widespread, being known in North China (Yu 1960; Yu *et al.* 1963; Cao & Lin 1982; Pak 1983; Deng 1984; Liang 2020), Qilian (Yu 1960; Yu *et al.* 1963; Deng & Li 1979; Liang 2020), South China (Lin 1963; Cao & Lin 1982; Deng 1987; Wang 1991; Liang 2020), Sivi (Deng & Zhang 1984; Liang 2020), Chingiz–Tarbagatai (Smelovskaya 1963), the Australian and New Zealand section of peri-Gondwana (Etheridge 1918; Hill 1942a, b; Cooper 1965, 1968; Hall 1975; McLean & Webby 1976; Webby 1972, 1988; Wang *et al.* 2021; Zhen *et al.* 2022), Laurentia (Billings, 1858a, b; Nicholson 1875a–d, 1879; Rominger 1876; Lambe 1901; Walcott 1904; Foerste 1909, 1924; Wilson 1926; Troedsson 1928; Bassler 1950; Duncan 1956; Hill 1959, 1961; Flower 1961; Nelson 1963; Browne 1965; Caramanica 1973, 1992; Fedorowski & Jull 1976; Jull 1976a, b; Workum *et al.* 1976; Bolton 1979, 1980; Bolton & Nowlan 1979; Gierlowski & Langenheim 1985; Pandolfi 1985; Porter *et al.* 2007), Siberia (Sokolov 1950, 1955; Ivanova *et al.* 1955; Ivanovskiy 1965, 1969; Sytova 1979a), and possibly York Terrane (Oliver *et al.* 1975a, b), Baltica (Ivanov & Myagkova 1950, 1955; Shurygina 1973) and Altai–Sayan (Radugin 1936a, b; Tcherepnina 1960). Their diversity rose to a peak during this interval, with all five assigned genera recorded. Compared to earlier or later time intervals, the middle Katian cyathophylloidid fauna is characterised by the initial appearance of *Palaeolithostrotion* and the widespread distribution of *Crenulites*, the latter of which has so far been recorded across nearly all low-latitude blocks/

terranes, including North China, Qilian, South China, Sivi, Australia, Laurentia, Baltica, Siberia, and possibly Chingiz-Tarbagatai.

The late Katian saw a prominent decline of cyathophylloidids. *Crenulites* that had featured in the middle Katian fauna was virtually absent, while *Favistina* and *Palaeophyllum* were very rare. In contrast, *Palaeolithostrotion* and *Cyathophylloides* emerged as the dominant genera. Records of cyathophylloidids from this time interval are known from South China (Deng 1986), South Tien Shan (Lavrusevich 1975; Erina 2007), Chingiz–Tarbagatai (Sultanbekova 1986), West Junggar (Cai 1988), Chu–Ili (Cai 1981; Sultanbekova 1986), Australia (Webby 1972, 1988; Wang *et al.* 2020), Laurentia (Twenhofel 1928; Stearn 1956; Flower 1961; Bolton 1972, 1979; Fedorowski & Jull 1976; Caramanica 1992; Melzak 2004), Baltica (Spjeldnæs 1963), and Siberia (Ivanovskiy 1969; Latypov 1978; Volkova *et al.* 1978; Sytova 1979a).

Following the Late Ordovician Mass Extinction at the Katian–Hirnantian boundary, *Cyathophylloides*, *Palaeophyllum* and *Palaeolithostrotion* endured. The former was represented solely by *C. kassariensis* Dybowski, 1873a from the lower Llandovery of Baltica. *Palaeophyllum* has been rarely documented from the Hirnantian–lower Llandovery rocks of Baltica, with uncertain records from the Aeronian of South China (Ge & Yu 1974) and western Greenland (McLean 1977) and the upper Llandovery of the Gorny Altai (Ivanovskiy & Kulkov 1974). In contrast, *Palaeolithostrotion* appears to have persisted well into the Wenlock. It has been recorded from the upper Hirnantian of Anticosti Island and east–central USA (Bolton 1972, 1979, 1981; Young & Elias 1995; Melzak 2004), the Aeronian of Anticosti Island (McLean & Copper 2013), the Telychian of western North Greenland (Troedsson 1928; Poulsen 1941), and the Homerian of New York (Hall 1852; Oliver 1963).

Stauriid record

As discussed above, stauriid corals are treated here as a distinct and well-defined coral clade, distinguished by their unique septal parricidal increase. Within this framework, three subfamilies (i.e. Stauriinae Milne-Edwards & Haime, 1850, Paraceriasterinae n. subfam. and Heininae n. subfam.) are recognised, distinguished by their respective KAC, KA, and KLAC increase types. Stauriinae includes *Stauria* Milne-Edwards & Haime, 1850, *Eostauria* He & Li, 1974 and *Cystostauria* He & Li, 1974; Paraceriasterinae comprises *Paraceriaster* He, 1980, *Ceriaster* Lindström, 1883 and *Massparaceriaster* Tang in Tang *et al.*, 2008b; and Heininae contains *Heina* n. gen., *Parastauria* He & Li, 1974 and *Yuina* n. gen.

Stauriids have a comparatively restricted distribution. Most, if not all, are recorded from the Silurian of South China, South Tien Shan, Arctic Alaska, Baltica and Tuva–Mongol (Figs 99, 100), with the only possible Ordovician form from the uppermost Katian Badanjilin Formation of the Beishan terrane

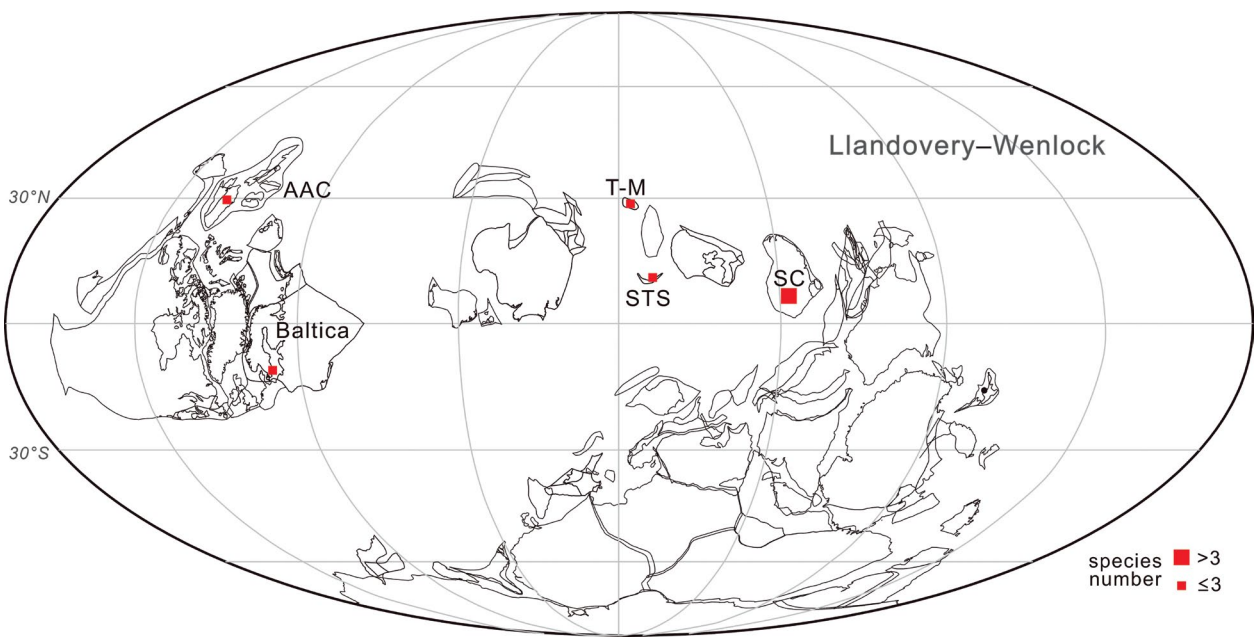


Fig. 99. Llandovery–Wenlock (Silurian) palaeogeographical reconstruction showing the distribution of stauriid corals. Base map modified from Torsvik & Cocks (2017). AAC, Arctic Alaska–Chukotka; SC, South China; STS, South Tien Shan; T–M, Tuva–Mongol.

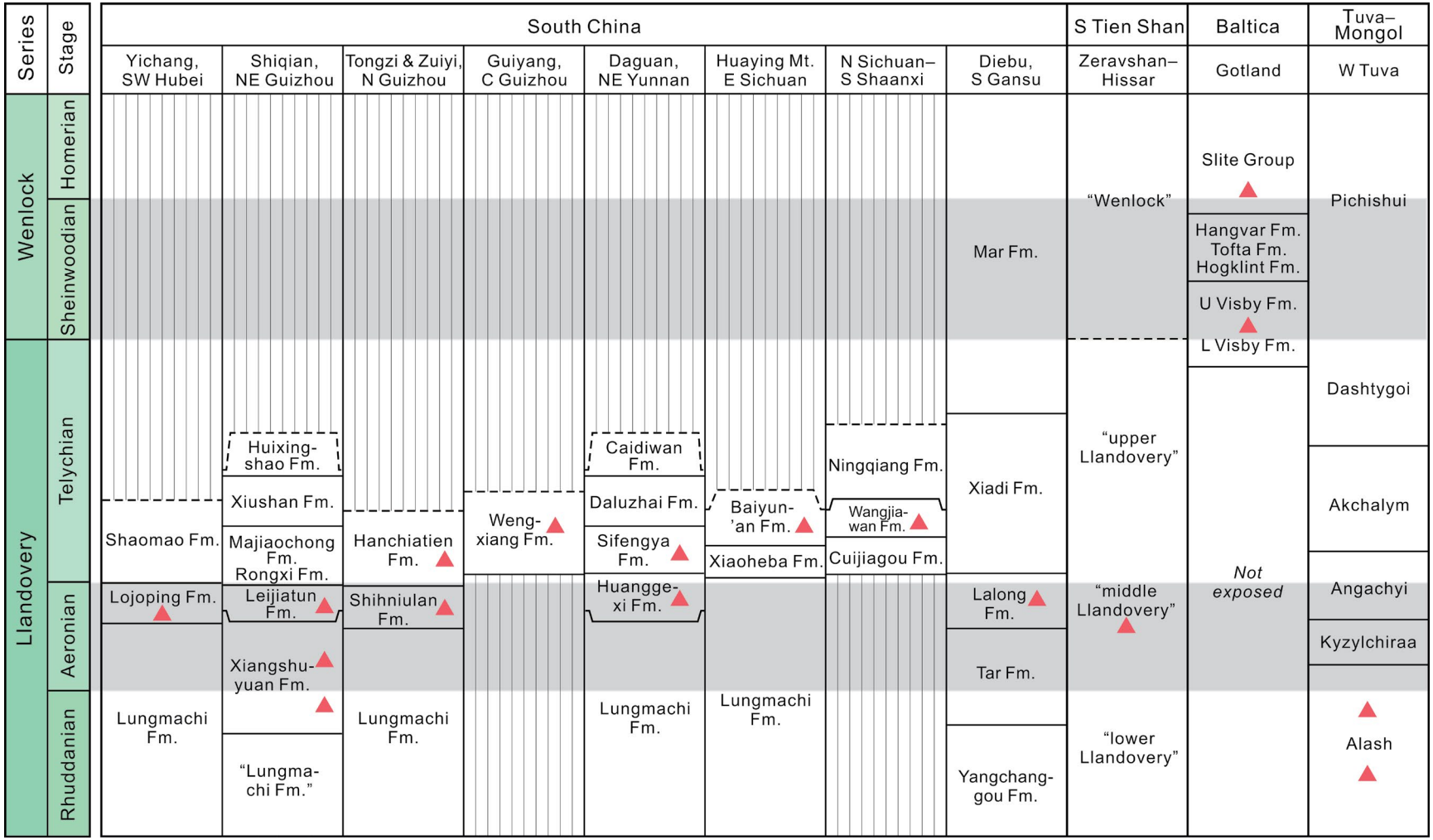


Fig. 100. Correlation of the selected Llandovery and Wenlock (Silurian) successions yielding stauriids in South China, South Tien Shan, Baltica and Tuva–Mongol. Pink triangles indicate approximate horizons bearing these corals. Data source: Timescale (Melchin *et al.* 2020); South China (Rong *et al.* 2019); South Tien Shan (Lavrusevich 1965); Baltica (Calner *et al.* 2004); Tuva–Mongol (Sennikov *et al.* 2015).

(Fig. 93). Using the new fossil and stratigraphic data, a review of their stratigraphic record is presented below (see also Appendix Table 2).

South China

Stauriids are now known from Llandovery strata on the Yangtze Platform, and a useful summary of their temporal and spatial distribution was given by Tang *et al.* (2008b). It is now clear that their earliest record in the region comes from the Xiangshuyuan Formation (upper Rhuddanian–lower Aeronian) of northeastern Guizhou (Ge & Yu 1974; Kong & Huang 1978; He & Li 1974, 1983; Tang 2006; Tang *et al.* 2008b; Wang & Cui 2020), which is revised here as consisting of *Cystostauria multiseptata* (He, 1978), *C. normalis* He & Li, 1974, *Eostauria micropora* He & Li, 1974, *E. prolifera* (Yin, 1944), *Heina* sp., *Paraceriaster cateniformis* He & Li, 1983, *P. shiqianensis* (He & Li, 1974), *Parastauria shiqianensis* (Ge & Yu, 1974), and *Yuina agglomorata* (He & Li, 1974).

The slightly younger, upper Aeronian strata of South China (i.e. the Chenxiacun, Lojoping, Leijiatun, Shihniulan, and Huanggexi formations) yield more diverse stauriid corals (Yin 1944; Wang *et al.* 1955; Yu *et al.* 1963; Ge & Yu 1974; He & Li 1974; Jia & Wu 1977; He 1978; Kong & Huang 1978; Xiong & Gu 1978; He 1980; Jiang 1982; He & Li 1983; Deng *et al.* 1983; Liu 1984; He *et al.* 1989; Deng & Scrutton 1996; He & Chen 1999; Scrutton & Deng 2002; Tang 2006; Tang *et al.* 2008b; Zhu & Ma 2019; Wang & Cui 2020). The revised faunal list includes *Cystostauria multiseptata* (He, 1978), *C. normalis* He & Li, 1974, *Eostauria prolifera* (Yin, 1944), *E. qijiangensis* (He, 1980), *E.* sp. A, *E.* sp. B, *E. stauriata* Tang in Tang *et al.*, 2008b, *Heina rarisepta* He, 1980, *Paraceriaster cateniformis* He & Li, 1983, *P. major* (Fan in He, 1978), *P. qijiangensis* He, 1980, *P. shiqianensis* (He & Li, 1974), *Parastauria huayinshanensis* (He, 1980), *P. leijiatunensis* (He, 1980), *P. polygonalis* He & Li, 1974, *Stauria fongganensis* He & Li, 1983, *S. qijiangensis* He, 1978, *S. tenuisepta* He, 1980, *S.* sp. nov. of Scrutton & Deng, 2002, *Yuina agglomorata* (He & Li, 1974), *Y. columellata* (Ge & Yu, 1974), and *Y. qiaogouensis* (He, 1980).

The youngest strata that produce stauriids in South China are of early Telychian age, represented by the Hanchiatien Formation of northern Guizhou, the Sifengya Formation of northeastern Yunnan, the Baiyun'an Formation of eastern Sichuan, and the Wangjiawan Formation of the Sichuan–Shaanxi border region (Lindström 1883; Qin 1956; Chen 1959; Yu *et al.* 1963; Ge & Yu 1974; Cao 1975; He 1978; He 1980; Cao & Lin 1982; Tang 2006; Tang *et al.* 2008b; Wang *et al.* 2011; Wang & Cui 2020). Taxa from this level are revised as including *Ceriaster calamites* Lindström, 1883, *Eostauria stauriata* Tang in Tang *et al.*, 2008b, *Massparaceriaster ningqiangensis* (Ge & Yu, 1974), *Paraceriaster fasciculatus* (Cao, 1975), *P. major* (Fan in He, 1978), *Parastauria guanyinqiaoensis* (He, 1980), *P. huayinshanensis* (He, 1980) and *P. liangfengyaensis* (He, 1980).

South Tien Shan

Ceriaster menakovae Lavrusevich, 1965, here transferred to *Eostauria* He & Li, 1974, was documented from the "middle Llandovery" of Zeravshan–Hissar, and represents the only stauriid record of South Tien Shan.

Beishan

From the Badanjilin Formation (uppermost Katian) of the Danmianshan area (Fig. 90:13; Fig. 93), Ejin Banner, western Inner Mongolia, a specimen described by He (1987) as *Palaeophyllum* sp. is tentatively reassigned here to *Yuina* n. gen. owing to its possible KLAC septal parricidal increase.

Arctic Alaska

A single specimen, originally documented by Oliver *et al.* (1975a) as *Stauria* sp., was recovered from the "Upper(?) Silurian" of the eastern Brooks Range, Alaska. Its precise age remains uncertain and requires further clarification. In this study, the specimen is reassigned as *Cystostauria* sp. C, discussed above.

Baltica

Stauriids in Baltica are solely known from the Silurian of Gotland. From the Lower and Upper Visby formations (uppermost Telychian–lowest Sheinwoodian; Calner *et al.* 2004) at Visby, Ting (1940) documented an unnamed species of *Stauria*; this form is revised as *Cystostauria* sp. B, discussed above. Higher up in the lower Slite Group (upper Sheinwoodian, Wenlock; Calner *et al.* 2004), formerly known as "Stage f" (Lindström, 1888), *Stauria favosa* (Linnaeus, 1758) (= *Stauria astreiformis* Milne-Edwards & Haime, 1850) has been recorded by various authors (Nicholson & Lydekker 1889; Smith & Ryder 1927; Bassler 1950; Hill 1981; Ezaki & Yasuhara 2004, 2005). Additionally, a specimen documented by Smith & Ryder (1927) as *Stauria favosa* from the Silurian at "Rejio, east of Angelin" is revised as *Cystostauria* sp. A, whose exact horizon remains to be verified.

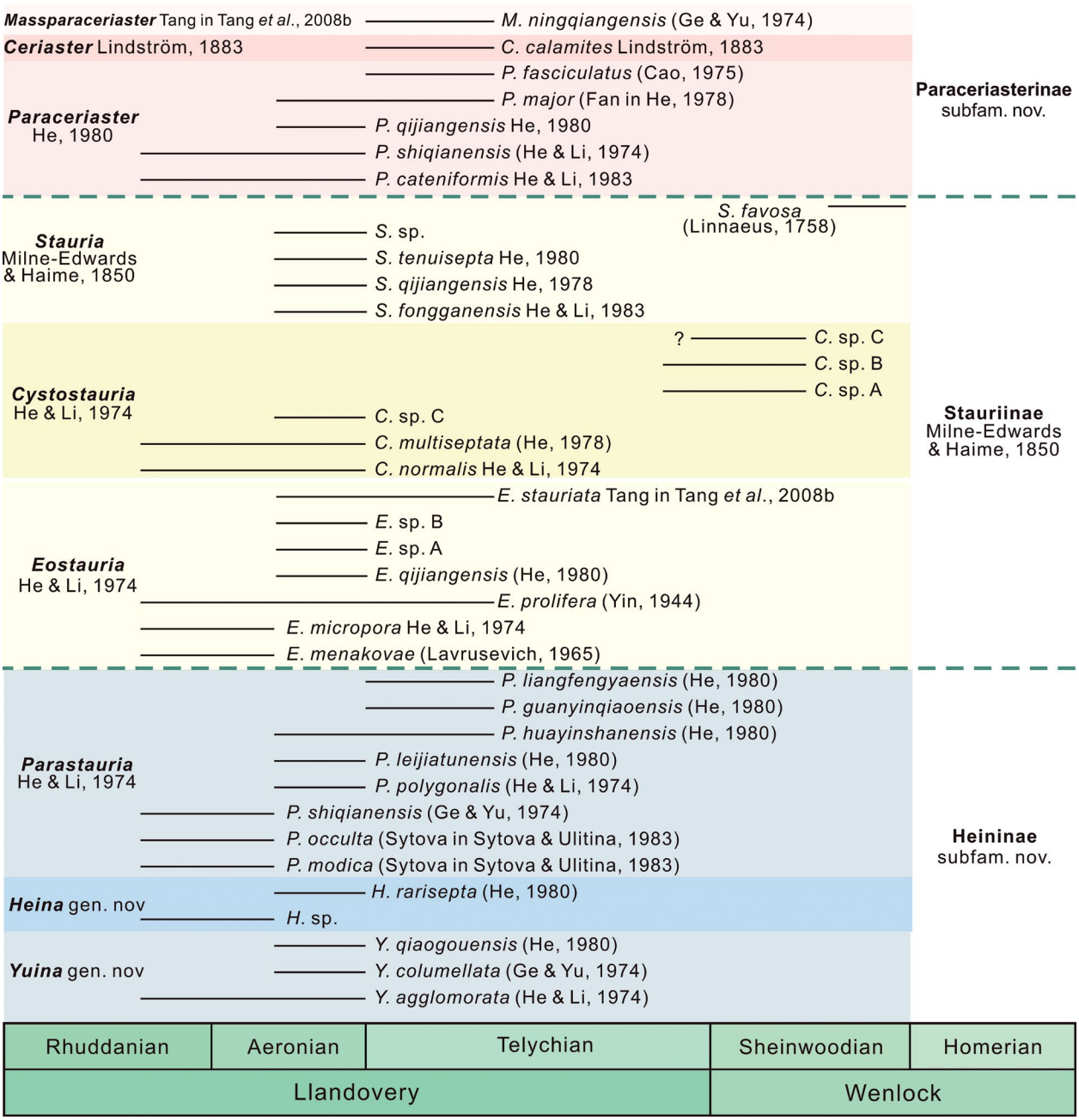


Fig. 101. Stratigraphic distribution of stauriid species, with solid black lines indicating approximate ranges. Timescale after Melchin *et al.* (2020).

Tuva–Mongol

In western Tuva, Sytova in Sytova & Ulitina (1983) described two new species, *Elizabethia occulta* and *E. modica*, from the Alash Horizon (Rhuddanian–lower Aeronian; Sennikov *et al.* 2015). Both are reassigned here to *Parastauria* He & Li, 1974 (see above).

Stauriid origin and evolution

For a long time, this group was known to be represented by just two cerioid forms, *Stauria* Milne-Edwards & Haime, 1850, and *Ceriaster* Lindström, 1883, and much attention was paid to their patterns of increase (Koch 1883; Smith & Ryder 1927; Ting 1940;

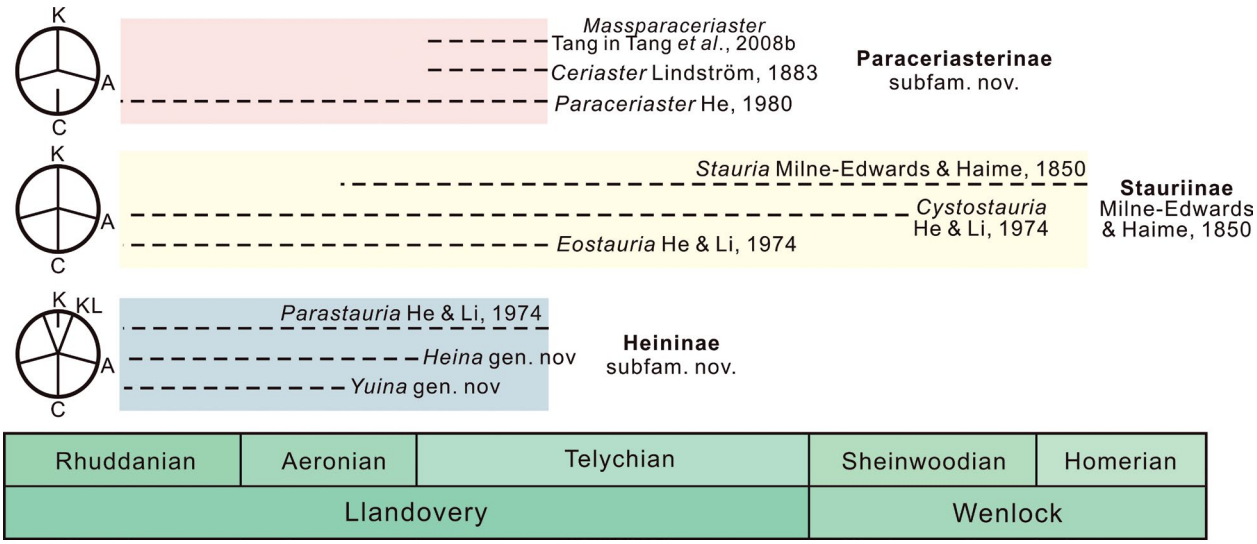


Fig. 102. Range chart of subfamilies and genera of the Stauriidae. A, alar septum; C, cardinal septum; K, counter septum; KL, counter-lateral septum. Timescale after Melchin *et al.* (2020).

Yin 1944; Ezaki & Yasuhara 2004, 2005). A comprehensive analysis of their origin and evolution was not presented until He & Li (1974), followed by He (1980), He & Li (1983), Tang *et al.* (2008a, b) and He & Tang (2013), chiefly based on the stauriid record of South China. Here, based on greatly improved stratigraphic (Fig. 100) and palaeontological (Figs 101, 102) data, an updated summary on the origin and evolutionary history of this coral group is given, including a critical reappraisal of previous views.

Origin

Okulitch (1935) proposed a tetradiid origin based on their superficially similar increase and growth patterns. A similar view was independently proposed by He & Li (1974, 1983), although they later rejected it (He *et al.* 1989; He & Tang 2013). However, it is now clear that tetradiids have an aragonitic skeleton and a distinctive four-fold longitudinal fission mode of increase, as well as growth forms ranging from massive to branching (Scrutton 1997). Furthermore, this group is now widely believed to be unrelated to the Rugosa (Hill 1981; Scrutton 1997), and is variably classified with the Tabulata (Hill 1981; Young & Elias 1995), an independent cnidarian clade (Webby in Webby *et al.* 2004), or rhodophytic algae (Steele-Petrovich 2009a, b).

With new stauriid materials documented from Llandovery strata from the 1960s onward, the possibility that stauriids evolved from cyathophylloidids has been suggested. Following the report of *Ceriaster menakovae* Lavrusevich, 1965 (reassigned here to *Eostauria*) from the "middle Llandovery" of South Tien Shan, Ivanovskiy (1965, p. 50) envisaged a *Cyathophylloides* origin of stauriids via *Ceriaster*. Subsequently, based on the fossil data from South China, a *Palaeophyllum* origin was proposed by He and colleagues (He *et al.* 1989, fig. 13; Tang *et al.* 2008a; He & Tang 2013, fig. 3). In this hypothesis, the Ordovician *Palaeophyllum*-like forms with both lateral and "axial" parricidal increase represent early members of the structurally simple stauriid *Eostauria*, which might have served as a "missing link" between *Palaeophyllum* and typical stauriids. However, I disagree with this opinion, since the increase mode shown in these Ordovician forms is of aseptal nature, as opposed to the septal increase mode characteristic of stauriids.

In short, the currently available data does not support any of the aforementioned scenarios. Instead, given that the three stauriid subfamilies first appeared around the same time in the middle Rhuddanian, as summarised above, it seems more likely that stauriids arose from forms whose protosepta tend to meet in the corallite axis, and that both *Cyathophylloides* and *Palaeolithostrotion* may therefore be candidates. In addition, since KLAC and KAC (with its variant KA) septal parricidal increase modes are so different, it is most likely that stauriid corals with these two modes might have originated from separate ancestral lineages.

Evolution

As noted above, stauriids might have originated in Beishan during the latest Katian, as evidenced by the

report of *Yuina*? sp. (He 1987; this work). However, a substantial phylogenetic radiation did not occur until the late Rhuddanian–early Aeronian, when components of all three subfamilies were present in South China (Ge & Yu 1974; Kong & Huang 1978; He & Li 1974, 1983; Tang 2006; Tang *et al*. 2008b; Wang & Cui 2020). Around the same time, stauriids apparently migrated elsewhere, as suggested by the occurrence of one *Eostauria* species in South Tien Shan (Lavrusevich 1965) and two *Parastauria* species in Tuva–Mongol (Sytova & Ulitina 1983).

The late Aeronian and early Telychian witnessed the flourishing of stauriids. Almost all the genera of the three subfamilies are recorded in South China in the upper Aeronian (Yin 1944; Wang *et al*. 1955; Yu *et al*. 1963; Ge & Yu 1974; He & Li 1974; Jia & Wu 1977; He 1978; Kong & Huang 1978; Xiong & Gu 1978; He 1980; Jiang 1982; He & Li 1983; Deng *et al*. 1983; Liu 1984; He *et al*. 1989; Deng & Scrutton 1996; He & Chen 1999; Scrutton & Deng 2002; Tang 2006; Tang *et al*. 2008b; Zhu & Ma 2019; Wang & Cui 2020), and the lower Telychian (Lindström 1883; Qin 1956; Chen 1959; Yu *et al*. 1963; Ge & Yu 1974; Cao 1975; He 1978; He 1980; Cao & Lin 1982; Tang 2006; Tang *et al*. 2008b; Wang *et al*. 2011; Wang & Cui 2020). However, such a diversification event has not been recognised from outside South China.

During the ensuing late Telychian and Sheinwoodian, the diversity of stauriids sharply declined, with only very few species of the stauriinids *Stauria* and *Cystostauria* in Gotland of Sweden (Linnaeus 1758; Nicholson & Lydekker 1889; Smith & Ryder 1927; Ting 1940; Bassler 1950; Hill 1981; Ezaki & Yasuhara 2004, 2005). The entire stauriid group went extinct by the end of the early Wenlock, as indicated by the absence of a reliable fossil record of this group in younger strata worldwide.

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Appendix

Appendix Table 1. Cyathophylloidid species and their present revision.

	References	Original identification	This study
N China	uppermost Longmendong Fm. (lower Katian), Longxian area, W Ordos		
	Deng 1984	*Favistina mediana* Deng, 1984	*Favistina mediana* Deng, 1984
		Favistina aff. *dybovskii* Soshkina, 1955	*Crenulites* sp. C
		Favistina pachytheca Deng, 1984	*Favistina pachytheca* Deng, 1984
		Favistina longxianensis Deng, 1984	*Favistina longxianensis* Deng, 1984
	Taoqupo Fm. (lower–middle Katian), Liquan, Yaozhou (formerly Yaoxian) & Jinagyang areas, SW Ordos		
	Cao & Lin 1982	*Favistella* (*Favistella*) *dybovskii* Soshkina, 1955	*Crenulites nanshanensis* (Yu, 1960)
		Favistella (*Favistella*) *multiseptata* Cao in Cao & Lin, 1982	*Crenulites nanshanensis* (Yu, 1960)
		Cyathophylloides taoqupoensis Lin in Cao & Lin, 1982	*Cyathophylloides taoqupoensis* Lin in Cao & Lin, 1982
	Deng 1984	*Favistina dybovskii* Soshkina, 1955	*Crenulites formosus* (Deng, 1984)
		Favistina formosa Deng, 1984	*Crenulites formosus* (Deng, 1984)
		Favistina arcuta Deng, 1984	*Favistina arcuta* Deng, 1984
		Favistina strigosa Deng, 1984	*Cyathophylloides strigosus* (Deng, 1984)
	Jiang *et al*. 2013	*Favistella alveolata* (Goldfuss, 1826)	revision required
		Favistella intermediata Yu, 1960	revision required
	Beiguoshan Fm. (lower–middle Katian), Guyuan & Longxian areas, W Ordos		
	Yu 1960	*Palaeofavosites grandis* Yu, 1960	*Crenulites grandis* (Yu, 1960)
	Yu *et al*. 1963	*Palaeofavosites grandis* Yu, 1960	*Crenulites grandis* (Yu, 1960)
	Cao & Lin 1982	*Favistella* (*Favistella*) *yindonggouensis* Lin in Cao & Lin, 1982	*Crenulites formosus* (Deng, 1984)
		Favistella (*Parafavistella*) *guyuanensis* Lin in Cao & Lin, 1982	*Crenulites guyuanensis* (Lin in Cao & Lin, 1982)
		Palaeophyllum guyuanense Lin in Cao & Lin, 1982	*Palaeophyllum*? *guyuanense* Lin in Cao & Lin, 1982
	Deng 1984	*Palaeophyllum thomi simplex* Deng, 1984	*Palaeophyllum*? *simplex* Deng, 1984
	Liang 2020	*Palaeofavosites borealis* Tchernychev, 1937	*Crenulites grandis* (Yu, 1960)
	Upper Ordovician, S Pyeongnam Basin, North Korea		
	Pak 1983	*Favistina* spp. (6)	revision required
	"upper Silurian", Daximiao, Zhenglan Banner, C Inner Mongolia		
	Guo 1976	*Palaeophyllum* sp.	excluded from cyathophylloidids
	Xibiehe Fm. (Ludlow), Bateaobao, Darhan–Muminggan area, Inner Mongolia		
	Guo 1976	*Cyathophylloides silurica* Guo 1976	excluded from cyathophylloidids
	Guo 1978	*Cyathophylloides silurica* Guo 1978	excluded from cyathophylloidids
	Xiashibei Fm. (Ludlow?), Xiashibei, Naiman Banner, E Inner Mongolia		
	Guo 1980	*Palaeophyllum xiashibeiense* Guo 1978	excluded from cyathophylloidids
Qilian	Koumenzi Fm. (lower–middle Katian), Menyuan area, NE Qinghai		
	Yu 1960	*Favistella alveolata* (Goldfuss, 1826)	*Crenulites nanshanensis* (Yu, 1960)
		Favistella nanshanensis Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella obliquisepta Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella alveolata (Goldfuss) var. *maxima* Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella intermediata Yu, 1960	*Crenulites intermediatus* (Yu, 1960)
		Favistella irregularis Yu, 1960	*Crenulites irregularis* (Yu, 1960)
	Yu *et al*. 1963	*Favistella alveolata* (Goldfuss, 1826)	*Crenulites nanshanensis* (Yu, 1960)
		Favistella alveolata (Goldfuss) subsp. *maxima* Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella intermediata Yu, 1960	*Crenulites intermediatus* (Yu, 1960)
		Favistella irregularis Yu, 1960	*Crenulites irregularis* (Yu, 1960)
		Favistella nanshanensis Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella obliquisepta Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)

(Continous)

Appendix Table 1. *(Continous)*

	References	Original identification	This study
	Liang 2020	*Favistina obliquisepta* (Yu, 1960)	*Crenulites nanshanensis* (Yu, 1960)
	Koumenzi Fm. (lower–middle Katian), Qilian area, NE Qinghai		
	Deng & Li 1979	*Agetolites rariperforatus* Deng & Li, 1979	*Crenulites intermediatus* (Yu, 1960)
		Palaeofavosites grandis var. *infidus* Deng & Li, 1979	*Crenulites grandis* (Yu, 1960)
		Saffordophyllum heiquanheensis Deng & Li, 1979	*Crenulites grandis* (Yu, 1960)
		Saffordophyllum inconstus Deng & Li, 1979	*Crenulites grandis* (Yu, 1960)
		Favistella qilianensis Deng & Li, 1979	*Crenulites irregularis* (Yu, 1960)
		Favistella aff. *nanshanensis* Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella cf. *intermediata* Yu, 1960	*Crenulites nanshanensis* (Yu, 1960)
		Favistella luotuoheensis Deng & Li, 1979	*Crenulites nanshanensis* (Yu, 1960)
	Liang 2020	*Saffordophyllum inconstus* Deng & Li, 1979	*Crenulites grandis* (Yu, 1960)
		Saffordophyllum heiquanheensis Deng & Li, 1979	*Crenulites grandis* (Yu, 1960)
Qaidam	upper Saishiteng Group ("Upper Ordovician"), N Qinghai		
	Lin 1985a	*Palaeophyllum qinghaiense* Lin, 1985a	*Palaeophyllum qinghaiense* Lin, 1985a
	Shuinichang Fm. (Katian), S Golmud, central Qinghai		
	Li & Lin 1982	*Cyathophylloides shuinychangensis* Lin in Li & Lin, 1982	*Cyathophylloides shuinychangensis* Lin in Li & Lin, 1982
S China	lower "Pogoda Fm". (lower Katian), Huangping area, NE Guizhou		
	Yoh 1959	*Favistella major* Yoh, 1959	excluded from cyathophylloidids
	Yu *et al.* 1963	*Favistella major* Yoh, 1959	excluded from cyathophylloidids
	Yenwashan Fm. (lower Katian), JCY area		
	Lin & Chow 1980	*Palaeophyllum irregulare* Lin & Chow, 1980	excluded from cyathophylloidids
	Deng *et al.* 1983	*Palaeophyllum irregulare* Lin & Chow, 1980	excluded from cyathophylloidids
	Xiazhen Fm. (uppermost Katian), JCY area		
	Yu 1960	*Favistella* (*Palaeophyllum*) *minimum* Yu, 1960	excluded from cyathophylloidids
	Yu *et al.* 1963	*Favistella* (*Palaeophyllum*) *minimum* Yu, 1960	excluded from cyathophylloidids
	Deng 1986	*Favistina* cf. *burksae* (Flower, 1961)	*Cyathophylloides* sp. B
	Liang 2020	*Palaeophyllum minimum* Yu, 1960	excluded from cyathophylloidids
	upper Xiangshuyuan Fm. (lower Aeronian), Fengxiang, Shiqian area, NE Guizhou		
	He 1985	*Palaeophyllum major* He, 1985	excluded from cyathophylloidids
	upper Xiangshuyuan Fm. (lower Aeronian), Dongkala, Fenggang area, NE Guizhou		
	He 1985	*Palaeophyllum fenggangense* He, 1985	excluded from cyathophylloidids
	Lojoping Fm. (upper Aeronian), Yichang area, S Hubei		
	Ge & Yu 1974	*Palaeophyllum hubeiense* Ge & Yu, 1974	*Palaeophyllum*? *hubeiense* Ge & Yu, 1974
	Jia & Wu 1977	*Palaeophyllum hubeiense* Ge & Yu, 1974	*Palaeophyllum*? *hubeiense* Ge & Yu, 1974
	Liu 1984	*Palaeophyllum hubeiense* Ge & Yu, 1974	*Palaeophyllum*? *hubeiense* Ge & Yu, 1974
	Jia & Lin 1987	*Palaeophyllum paradoxum* Jia in Jia & Lin, 1987	*Palaeophyllum*? *hubeiense* Ge & Yu, 1974
	Zhu & Ma 2019	*Palaeophyllum hubeiense* Ge & Yu, 1974	*Palaeophyllum*? *hubeiense* Ge & Yu, 1974
	Huanggexi Fm. equivalent (upper Aeronian), Biji Mountain, Yuexi area, SW Sichuan		
	He 1978	*Palaeophyllum bijishanense* He, 1978	excluded from cyathophylloidids
	Sifengya Fm. (lower Telychian), Daguan area, NE Yunnan		
	Chen *et al.* 2005	*Palaeophyllum* sp. A	excluded from cyathophylloidids
	Chen *et al.* 2005	*Palaeophyllum* sp. B	excluded from cyathophylloidids
	Yanglugou Fm. (Pridoli), Putonggou, Ruoergai area, NW Sichuan		
	Cao & Ouyang 1987	*Cyathophylloides carinatus* Cao & Ouyang, 1987	excluded from cyathophylloidids
South China?	Middle Katian part of the Shiyanhe Fm., Xichuan area, SW Henan		
	Deng 1987	*Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982)	*Favistina* sp. B
	Wang 1991	*Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982)	*Favistina* sp. B?
	Liang 2020	*Favistina* aff. *shifosiensis* (Cao in Cao & Lin, 1982)	*Favistina* sp. B
	Liangchakou Fm. (Katian), Shanyang area, SE Shaanxi		
	Lin 1963	*Agetolites minor* Lin, 1963	*Crenulites minor* (Lin, 1963)
	Cao & Lin 1982	*Favistella* (*Favistella*) *shanyangensis* Cao in Cao & Lin, 1982	*Crenulites minor* (Lin, 1963)
		Favistella (Favistella) shifosiensis Cao in Cao & Lin, 1982	*Crenulites minor* (Lin, 1963)

	References	Original identification	This study
Sivi	Wuluochipu Fm. (Katian), Zhongza, W Sichuan		
	Deng & Zhang 1984	*Palaeofavosites* cf. *grandis* Yu, 1960	*Crenulites grandis*? (Yu, 1960)
	Liang 2020	*Palaeofavosites grandis* Yu, 1960	*Crenulites grandis*? (Yu, 1960)
South Tien Shan	Archalyk Mb. (uppermost Katian), Shahriomon Fm., Zeravshan–Hissar region		
	Lavrusevich 1975	*Palaeolithostrotion zachonense* Lavrusevich, 1975	*Palaeolithostrotion zachonense* Lavrusevich, 1975
		Palaeolithostrotion voruense Lavrusevich, 1975	*Palaeolithostrotion voruense* Lavrusevich, 1975
	Hill 1981	*Palaeolithostrotion zachonense* Lavrusevich, 1975	*Palaeolithostrotion zachonense* Lavrusevich, 1975
	Lavrusevich 1991	*Palaeolithostrotion zachonense* Lavrusevich, 1975	*Palaeolithostrotion zachonense* Lavrusevich, 1975
		Palaeolithostrotion voruense Lavrusevich, 1975	*Palaeolithostrotion voruense* Lavrusevich, 1975
	Lin *et al.* 1995	*Palaeolithostrotion zachonense* Lavrusevich, 1975	*Palaeolithostrotion zachonense* Lavrusevich, 1975
	Erina 2007	*Palaeophyllum cateniforme* Flower, 1961	*Palaeolithostrotion*? sp. B
Beishan	Badanjilin Fm. (uppermost Katian), Danmianshan, W Inner Mongolia		
	He 1987	*Palaeophyllum* sp.	excluded from cyathophylloidids
E Junggar	Kaokesirke Fm. ("upper Silurian"), Barkol area, NE Xinjiang		
	Cai 1989	*Cyathophylloides xinjiangensis* Cai, 1989	excluded from cyathophylloidids
W Junggar	Bulunggor Fm. (upper Katian?), Hobuksar area, NW Xinjiang		
	Cai 1988	*Favistella tachengensis* Cai, 1988	*Cyathophylloides tachengensis* (Cai, 1988)
		Favistella xinjiangensis Cai, 1988	*Cyathophylloides tachengensis* (Cai, 1988)
Chingiz-Tarbagatai	basal Akchaul Fm. (middle Katian), Tarbagatai		
	Smelovskaya 1963	*Favistella alveolata* (Goldfuss, 1826)	*Crenulites*? sp.
		Cyathophlloides aktshaulicus Smelovskaya, 1963	*Cyathophlloides aktshaulicus* Smelovskaya, 1963
	uppermost Katian part of the Akdombak Fm., Chingiz Range		
	Sultanbekova 1986	*Palaeophyllum fasciculum* (Kutorga, 1837)	*Palaeophyllum fasciculum*? (Kutorga, 1837)
Chu–Ili	Hudukedaban Fm. (upper Katian?), Jinghe area, W Xinjiang		
	Cai 1981	*Palaeophyllum jingheense* Cai, 1981	*Palaeophyllum*? *jingheense* Cai, 1981
		Palaeophyllum distans Cai, 1981	*Palaeophyllum*? *distans* Cai, 1981
	Chokpar Fm. (uppermost Katian), Anthar River		
	Sultanbekova 1986	*Palaeophyllum fasciculum* (Kutorga, 1837)	*Palaeophyllum fasciculum*? (Kutorga, 1837)
	Jifuke Fm. ("middle Silurian"), Nilka area, NW Xinjiang		
	Cai 1981	*Palaeophyllum siluriense* Cai, 1981	revision required
Australia	Cliefden Caves Limestone Subgroup (lower Katian), Cliefden Caves area; coeval Bowan Park Limestone Subgroup, Bowan Park area		
	Webby 1972	*Palaeophyllum proliferum* Webby, 1972	excluded from cyathophylloidids
	Malongulli Fm. (middle Katian), Cliefden Caves area		
	Webby 1988	*Favistina floweri* Webby, 1988	*Favistina floweri* Webby, 1988
		Favistina gleesonensis Webby, 1988	*Favistina gleesonensis* Webby, 1988
		Favistina plus Webby, 1988	*Favistina plus* Webby, 1988
		Favistina sp. B	*Favistina* sp. B of Webby (1988)
	upper Canomodine Limestone (middle Katian), Cargo–Canomodine area		
	McLean & Webby 1976	*Palaeophyllum*? *laxum* McLean & Webby, 1976	*Palaeophyllum*? *laxum* McLean & Webby, 1976
		Palaeophyllum arrectum McLean & Webby, 1976	*Palaeophyllum bothroides* Hall, 1975

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Appendix Table 1. *(Continous)*

	References	Original identification	This study
	Webby 1988	*Favistina floweri* Webby, 1988	*Favistina floweri* Webby, 1988
		Favistina sp. A	*Favistina* sp. A of Webby (1988)
		an unnamed *Crenulites* species	not figured, and revision required
	upper Cargo Creek Limestone (middle Katian), Cargo–Canomodine area		
	Webby 1972	*Palaeophyllum crassum* Webby, 1972	*Palaeophyllum*? *crassum* Webby, 1972
	McLean & Webby 1976	*Palaeophyllum* cf. *crassum* Webby, 1972	*Palaeophyllum*? *crassum* Webby, 1972
	Webby 1988	*Favistina floweri* Webby, 1988	*Favistina floweri* Webby, 1988
	Ballingoole Fm. (middle Katian), Bowan Park area		
	McLean & Webby 1976	*Palaeophyllum*? *patulum* McLean & Webby, 1976	*Palaeophyllum*? *patulum* McLean & Webby, 1976
	Gunningbland Fm. (Middle Katian), Parks area		
	McLean & Webby 1976	*Palaeophyllum jugatum* McLean & Webby, 1976	excluded from cyathophylloidids
	Webby 1988	*Favistina floweri* Webby, 1988	*Favistina floweri* Webby, 1988
	Middle Katian, drill hole (WNDD0002), immediately northwest of Peak Hill, central NSW		
	Zhen *et al.* 2022	*Favistina plus* Webby, 1988	*Favistina plus* Webby, 1988
	'Trelawney Beds' & 'Uralba Beds' (middle Katian), NE NSW		
	Etheridge 1918	*Columnaria neminghensis* Etheridge, 1918	*Favistina neminghensis* (Etheridge, 1918)
	Hill 1942b	*Favistella neminghensis* (Etheridge, 1918)	*Favistina neminghensis* (Etheridge, 1918)
	Webby 1988	*Favistina neminghensis* (Etheridge, 1918)	*Favistina neminghensis* (Etheridge, 1918)
	Hall 1975	*Palaeophyllum* sp. cf. *P. rugosum* Billings, 1858a	*Palaeophyllum bothroides* Hall, 1975
		Palaeophyllum bothroides Hall, 1975	*Palaeophyllum bothroides* Hall, 1975
		Palaeophyllum sp. cf. *P. thomi* (Hall, 1857)	*Palaeophyllum bothroides* Hall, 1975
		Palaeophyllum trelawneyense Hall, 1975	*Palaeophyllum bothroides* Hall, 1975
		Cyathophylloides sinuata Hall, 1975	*Favistina neminghensis* (Etheridge, 1918)
		Cyathophylloides juncta Hall, 1975	*Cyathophylloides junctus* Hall, 1975
		Crenulites australis Hall, 1975	*Crenulites australis* Hall, 1975
		Crenulites australis minor Hall, 1975	*Crenulites australis* Hall, 1975
	Wang *et al.* 2021	*Favistina neminghensis* (Etheridge, 1918)	*Favistina neminghensis* (Etheridge, 1918)
		Crenulites australis Hall, 1975	*Crenulites australis* Hall, 1975
		Cyathophylloides juncta Hall, 1975	*Cyathophylloides junctus* Hall, 1975
		Palaeophyllum bothroides Hall, 1975	*Palaeophyllum bothroides* Hall, 1975
	uppermost Benjamin Limestone & upper Chudleigh Subgroup (both being middle Katian), W Tasmania		
	Hill 1942a	*Favistella cerioides* Hill, 1942a	*Favistina cerioides* (Hill, 1942a)
	upper Arthur Marble ("Upper Ordovician"), Takata Valley, New Zealand		
	Copper 1965	*Favistella*	description required
	uppermost Malachis Hill Fm. (uppermost Katian), Bowan Park area, central NSW		
	Webby 1972	*Palaeophyllum macrocaule* Webby, 1972	*Palaeolithostrotion macrocaule* (Webby, 1972)
	Webby 1988	*Cyathophylloides semeniuki* Webby, 1988	*Cyathophylloides semeniuki* Webby, 1988
	Bell River Mb. of the Dripstone Fm. (probable Homerian), Mumbil area, central–western NSW		
	Strusz 1961	*Palaeophyllum rugosum* Billings, 1858a	excluded from cyathophylloidids
	McLean 1975	*Palaeophyllum oakdalense* McLean, 1975	excluded from cyathophylloidids
Laurentia	glacial drift of unknown age, North America		
	Goldfuss 1826	*Columnaria alveolata* Goldfuss, 1826	indeterminate
	Stumm 1964	*Columnaria alveolata* Goldfuss, 1826	indeterminate
	upper Black River Gp. (upper Sandbian), Ottawa & Ontario		
	Lambe 1901	*Columnaria alveolata* Goldfuss, 1826	*Favistina undulata* (Bassler, 1950)
	Foerste 1914	*Columnaria alveolata discreta* Foerste, 1914	*Favistina discreta* (Foerste, 1914)
	Okulitch 1938	*Columnaria discreta* (Foerste, 1914)	*Favistina discreta* (Foerste, 1914)
	Bassler 1950	*Favistella alveolata discreta* (Foerste, 1914)	*Favistina discreta* (Foerste, 1914)
	Flower 1961	*Favistina discreta* (Foerste, 1914)	*Favistina discreta* (Foerste, 1914)
		Favistina paleophylloides Flower, 1961	*Favistina paleophylloides* Flower, 1961

References	Original identification	This study
Ivanovskiy 1969	*Favistella alveolata* Goldfuss, 1826 *(pars)*	*Favistina undulata* (Bassler, 1950)
Platteville Fm. (upper Sandbian), Wisconsin, USA		
Bassler 1950	*Favistella undulata* Bassler, 1950	*Favistina undulata* (Bassler, 1950)
Hill 1981	*Favistella undulata* Bassler, 1950	*Favistina undulata* (Bassler, 1950)
Lin *et al.* 1995	*Favistella undulata* Bassler, 1950	*Favistina undulata* (Bassler, 1950)
upper Carters & basal Hermitage fms (upper Sandbian), Tennessee, USA		
Bassler 1932	*Columnaria alveolata* var. *minor* Bassler, 1932	*Favistina minor* (Bassler, 1932)
Bassler 1950	*Favistella alveolata minor* (Bassler, 1932)	*Favistina minor* (Bassler, 1932)
other reports from pre-Katian strata, North America		
Salter 1852	*Favistella franklini* Salter, 1852	reassigned to *Saffordophyllum*
Billings 1859	*Columnaria parva* Billings, 1859	reassigned to *Billingsaria*
Billings 1859	*Columnaria incerta* Billings, 1859	reassigned to *Eofletcheria*
Safford 1869	*Columnaria carterensis* Safford, 1869	reassigned to *Lichenaria*
Nicholson 1879	*Columnaria*(?) *halli* Nicholson, 1879	reassigned to *Foerstephyllum*
Lambe 1901	*Columnaria halli* Nicholson, 1879	excluded from cyathophylloidids
Troedsson 1928	*Columnaria parvituba* Troedsson, 1928	reassigned to *Nyctopora*
Bassler 1932	*Columnaria halli* Nicholson, 1879	excluded from cyathophylloidids
Okulitch 1936	*Columnaria simplissima* Okulitch, 1936	reassigned to *Foerstephyllum*
Okulitch 1938	*Columnaria magnifica* Okulitch, 1938	reassigned to *Foerstephyllum*
Johnson Spring Fm. (upper Sandbian–lower Katian), Inyo Mountains, California		
Pestana 1960	*Palaeophyllum mazourkense* Pestana, 1960	*Palaeophyllum mazourkense* Pestana, 1960
	Palaeophyllum rugosum Billings, 1858a	excluded from cyathophylloidids
Bad Cache Group (lower Katian), N Hudson Bay Lowland		
Nelson 1963	*Palaeophyllum halysitoides* (Wilson, 1926)	*Palaeophyllum halysitoides*? (Wilson, 1926)
Amadjuak Fm. (lower Katian), southern Baffin Island, Nunavut		
Roy 1941	*Favistella* sp.	*Favistina undulata* (Bassler, 1950)
Bolton 2000	*Palaeophyllum* sp.	revision required
Farr Fm. (lower Katian), Lake Timiskaming outlier, Ontario		
Sinclair 1961	*Palaeophyllum humei* Sinclair, 1961	*Palaeophyllum rugosum* Billings, 1858a
Simard limestone (lower Katian) in the Lac St-Jean outlier, Quebec		
Billings 1858a	*Palaeophyllum rugosum* Billings, 1858a	*Palaeophyllum rugosum* Billings, 1858a
	Columnaria erratica Billings, 1858a	excluded from cyathophylloidids
Billings 1858b	*Palaeophyllum rugosum* Billings, 1858b	*Palaeophyllum rugosum* Billings, 1858a
	Columnaria erratica Billings, 1858b	excluded from cyathophylloidids
Lambe 1901	*Columnaria rugosa* (Billings, 1858a)	*Palaeophyllum rugosum* Billings, 1858a
Bassler 1950	*Palaeophyllum rugosum* (Billings, 1858a)	*Palaeophyllum rugosum* Billings, 1858a
Hill 1959	*Palaeophyllum rugosum* Billings, 1858a	*Palaeophyllum rugosum* Billings, 1858a
Hill 1961	*Palaeophyllum rugosum* Billings, 1858a	*Palaeophyllum rugosum* Billings, 1858a
Ivanovskiy 1965	*Palaeophyllum rugosum* Billings, 1858a	*Palaeophyllum rugosum* Billings, 1858a
Lin *et al.* 1995	*Palaeophyllum rugosum* Billings, 1858a	*Palaeophyllum rugosum* Billings, 1858a
upper Hermitage Fm. (lower Katian), Tennessee, USA		
Bassler 1932	*Columnaria crenulata* Bassler, 1932	excluded from cyathophylloidids
Catheys Fm. (lower Katian), Tennessee, USA		
Bassler 1932	*Columnaria alveolata* Goldfuss, 1826	*Favistina undulata*? (Bassler, 1950)
Lexington and Point Pleasant fms (lower Katian), Kentucky		
Foerste 1914	*Columnaria alveolata interventa* Foerste, 1914	*Favistina interventa* (Foerste, 1914)
Foerste 1914	*Columnaria alveolata minima* Foerste, 1914	*Favistina minima* (Foerste, 1914)
Bassler 1950	*Favistella alveolata interventa* (Foerste, 1914)	*Favistina interventa* (Foerste, 1914)
Bassler 1950	*Favistella alveolata minima* (Foerste, 1914)	*Favistina minima* (Foerste, 1914)
Kope Fm. (lower Katian), N Kentucky		
Harris *et al.* 2019	*Cyathophylloides* cf. *C. burksae*	revision required
Craighead Limestone (lower Katian), Girvan area, Scotland		
Nicholson & Etheridge 1878	*Streptelasma* (*Palaeophyllum*) *aggregatum* Nicholson & Etheridge, 1878	excluded from cyathophylloidids
Orita & Ezaki 2001	*Palaeophyllum aggregatum* Nicholson & Etheridge, 1878	excluded from cyathophylloidids

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Appendix Table 1. *(Continous)*

References	Original identification	This study
Balclatchie Group (lower Katian), Balclatchie, Scotland		
Wang 1948	*Streptelasma* (*Palaeophyllum*) *aggregatum* Nicholson & Etheridge, 1878	excluded from cyathophylloidids
lower Beaverfoot Fm. (middle Katian?), Macdonald Platform, NE British Columbia		
Wilson 1926	*Columnaria alveolata* var. *stellaris* Wilson, 1926	*Favistina stellaris* (Wilson, 1926)
	Diphyphyllum? *halysitoides* Wilson, 1926	*Palaeophyllum halysitoides* (Wilson, 1926)
Bassler 1950	*Favistella alveolata stellaris* (Wilson, 1926)	*Favistina stellaris* (Wilson, 1926)
Lost Canyon Mb. (middle Katian) of the Ely Springs Dolomite, Nevada & Utah		
Pandolfi 1985	*Palaeophyllum humei* Sinclair, 1961	*Palaeophyllum rugosum*? Billings, 1858a
	Palaeophyllum gracile Flower, 1961	*Palaeolithostrotion radugini*? (Tcherepnina, 1960)
	Palaeophyllum sp. cf. *P. raduguini* Nelson, 1963	*Palaeolithostrotion radugini*? (Tcherepnina, 1960)
	Cyathophylloides spp. A, B	revision required
"Burnam limestone of central Texas & the Hanson Creek Formation of Nevada"		
Duncan 1956	Cyathophylloide	Favistina
Second Value Fm. (middle Katian) of the Montoya Group, New Mexico & W Texas		
Hill 1959	*Palaeophyllum thomi*? (Hall, 1857)	*Palaeophyllum margaretae* Flower, 1961
	Palaeophyllum? sp.	*Palaeophyllum margaretae* Flower, 1961
Hill 1959	*Palaeophyllum* sp.	*Palaeophyllum cateniforme* Flower, 1961
Flower 1961	*Crenulites duncanae* Flower, 1961	*Crenulites duncanae* Flower, 1961
	Crenulites magnus Flower, 1961	*Crenulites magnus* Flower, 1961
	Palaeophyllum gracile Flower, 1961	excluded from cyathophylloidids
	Palaeophyllum margaretae Flower, 1961	*Palaeophyllum margaretae* Flower, 1961
	Palaeophyllum cateniforme Flower, 1961	*Palaeophyllum cateniforme* Flower, 1961
Hill 1981	*Crenulites duncanae* Flower, 1961	*Crenulites duncanae* Flower, 1961
Lin *et al*. 1995	*Crenulites duncanae* Flower, 1961	*Crenulites duncanae* Flower, 1961
Aleman & Cutter fms (middle Katian–? basal upper Katian), New Mexico & W Texas		
Emory 1857	*Columnaria thomi* Hall in Emory, 1857	*Palaeophyllum thomi* (Hall in Emory, 1857)
Walcott 1903	*Cyathophylloides thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
Bassler 1950	*Palaeophyllum thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
Hill 1959	*Palaeophyllum thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
Flower 1961	*Palaeophyllum thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
	Cyathophylloides burksae Flower, 1961	*Cyathophylloides burksae* Flower, 1961
	Favistina stellata (Hall, 1847) *(pars)*	*Favistina crenulata*? Flower, 1961
	Cyathophylloides (?) sp.	*Cyathophylloides* (?) sp.
lower Bighorn Fm. (middle Katian), Bighorn Mountains, N Wyoming		
Caramanica 1973	*Crenulites rigidus* (Billings, 1858a) (*pars*)	*Crenulites rigidus* (Billings, 1858a)
	Crenulites duncanae Flower, 1961 *(pars)*	*Crenulites duncanae* Flower, 1961
upper Bighorn Fm. (middle Katian–? basal upper Katian), Bighorn Mountains, N Wyoming		
Caramanica 1973	*Palaeophyllum pasense* Stearn, 1956	excluded from cyathophylloidids
	Palaeophyllum sinclairi Caramanica, 1973	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
	Cyathophylloides hollandi Caramanica, 1973	*Crenulites stellatus* (Hall, 1847)
Caramanica 1992	*Palaeophyllum sinclairi* Caramanica, 1992	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
	Cyathophylloides hollandi Caramanica, 1992	*Crenulites stellatus* (Hall, 1847)
Gierlowski & Langenheim 1985	*Palaeophyllum gracile* Flower, 1961	excluded from cyathophylloidids
	Palaeophyllum humei Sinclair, 1961	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
Selkirk Mb. (middle Katian) of the Red River Fm., Williston Basin, S Manitoba		
Sinclair 1961	*Palaeophyllum argus* Sinclair, 1961	*Palaeophyllum argus* Sinclair, 1961
Caramanica 1973	*Palaeophyllum argus* Sinclair, 1961	*Palaeophyllum argus* Sinclair, 1961
	Crenulites rigidus (Billings, 1858a) (*pars*)	*Crenulites rigidus* (Billings, 1858a)
	Crenulites duncanae Flower, 1961 *(pars)*	*Crenulites duncanae* Flower, 1961

References	Original identification	This study
Churchill River Group (middle Katian), N Hudson Bay Lowland		
Nelson 1963	*Palaeophyllum stokesi* (Milne-Edwards & Haime, 1851)	revision required
	Palaeophyllum raduguini Nelson, 1963	*Palaeolithostrotion radugini*? (Tcherepnina, 1960)
	Favistella alveolata var. *stellaris* (Wilson, 1926)	*Favistina stellaris* (Wilson, 1926)
middle Katian, Hudson Strait Basin		
Flower 1961	*Crenulites akpatokensis* Flower, 1961	*Crenulites akpatokensis* Flower, 1961
Workum *et al*. 1976	*Crenulites discreta* Bolton in Workum *et al*., 1976	*Crenulites discretus* Bolton in Workum *et al*., 1976
	Palaeophyllum cateniforme Flower, 1961	*Palaeophyllum cateniforme* Flower, 1961
middle Katian, north of Aberdeen Lake, Keewatin		
Bolton & Nowlan 1979	*Palaeophyllum raduguini* Nelson var.	*Palaeolithostrotion radugini*? (Tcherepnina, 1960)
Cape Calhoun Fm. (middle Katian), W North Greeenland		
Troedsson 1928	*Columnaria halli* Nicholson, 1879	excluded from cyathophylloidids
	Columnaria franklini Salter, 1852	*Saffordophyllum franklini* (Salter, 1852)
	Columnaria halysitoides Troedsson, 1928	*Palaeophyllum halysitoides*? (Wilson, 1926)
Bassler 1950	*Saffordophyllum franklini* (Salter, 1852)	*Saffordophyllum franklini* (Salter, 1852)
Île aux Couleuvres Fm. (middle Katian), Couleuvres Island (formerly Snake Island), Lake St. John, Quebec		
Billings 1858a	*Columnaria goldfussi* Billings, 1858a	reassigned to *Nyctopora*
	Columnaria blainvilli Billings, 1858a	*Crenulites blainvilli* (Billings, 1858a)
	Columnaria rigida Billings, 1858a	*Crenulites rigidus* (Billings, 1858a)
Billings 1858b	*Columnaria goldfussi* Billings, 1858b	reassigned to *Nyctopora*
	Columnaria blainvilli Billings, 1858b	*Crenulites blainvilli* (Billings, 1858a)
	Columnaria rigida Billings, 1858b	*Crenulites rigidus* (Billings, 1858a)
Foerste 1924	*Columnaria alveolata rigida* (Billings, 1858a)	*Crenulites rigidus* (Billings, 1858a)
	Columnaria alveolata blainvilli (Billings, 1858a)	*Crenulites blainvilli* (Billings, 1858a)
Bassler 1950	*Favistella alveolata rigida* (Billings, 1858a)	*Crenulites rigidus* (Billings, 1858a)
Flower 1961	*Crenulites rigidus* (Billings, 1858a)	*Crenulites rigidus* (Billings, 1858a)
	Crenulites blainvilli (Billings, 1858a)	*Crenulites blainvilli* (Billings, 1858a)
Georigan Bay Fm. (middle Katian), Manitoulin Island & Credit River		
Nicholson 1875a	*Favistella* (*Columnaria*) *calicina* Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)
Nicholson 1875b	*Columnaria* (*Favistella*) *calicina (*Nicholson, 1875a)	*Crenulites calicinus* (Nicholson, 1875a)
Nicholson 1875c	*Favistella calicina* Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)
Nicholson 1879	*Columnaria calicina* Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)
Lambe 1901	*Columnaria calicina* Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)
Foerste 1924	*Columnaria calicina* Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)
Flower 1961	*Favistina calicina* (Nicholson, 1875a)	*Crenulites calicinus* (Nicholson, 1875a)
Fedorowski & Jull 1976	*Favistina calicina* (Nicholson, 1875a)	*Crenulites calicinus* (Nicholson, 1875a)
Jull 1976a	*Favistina calicina* (Nicholson, 1875a)	*Crenulites calicinus* (Nicholson, 1875a)
Bolton 1979	*Favistina stellata* (Hall, 1847) *(pars)*	*Crenulites stellatus* (Hall, 1847)
upper Hunorat Group (middle Katian), Mount Saint Joseph area, S Gaspe Peninsula, Quebec		
Bolton 1979	*Favistina honoratensis* Bolton, 1979	*Favistina honoratensis* Bolton, 1979
Bolton 1980	*Favistina honoratensis* Bolton, 1979	*Favistina honoratensis* Bolton, 1979
Maquoketa shale (middle Katian–? basal upper Katian), Bristol Township, Fillmore Co., Minn, Iowa, USA		
Bassler 1950	*Cyathophylloides ulrichi* Bassler, 1950	*Crenulites ulrichi* (Bassler, 1950)
Waynesville, Liberty & Whitewater fms (middle Katian–? basal upper Katian), Kentucky		
Hall 1847	*Favistella stellata* Hall, 1847	*Crenulites stellatus* (Hall, 1847)
Rominger 1876	*Columnaria herzeri* Rominger, 1876	*Crenulites calicinus*? (Nicholson, 1875a)
Foerste 1909	*Columnaria vacua* Foerste, 1909	*Crenulites vacuum* (Foerste, 1909)
Foerste 1924	*Columnaria alveolata* (Goldfuss)	revision required
	Columnaria calicina Nicholson, 1875a	*Crenulites calicinus* (Nicholson, 1875a)

(Continous)

Appendix Table 1. *(Continous)*

References	Original identification	This study
Bassler 1950	*Foerstephyllum vacuum* (Foerste, 1909)	*Crenulites vacuum* (Foerste, 1909)
	Favistella alveolata (Goldfuss, 1826)	*Favistina crenulata*? Flower, 1961
	Favistella alveolata calicina (Nicholson, 1875a)	*Crenulites calicinus* (Nicholson, 1875a)
	Favistella magister Bassler, 1950	*Favistina magister* (Bassler, 1950)
Duncan 1956	*Favistella stellata* Hall, 1847	*Crenulites stellatus* (Hall, 1847)
Flower 1961	*Favistina stellata* (Hall, 1847) (*pars*)	*Crenulites stellatus* (Hall, 1847)
	Favistina stellata (Hall, 1847) (*pars*)	*Favistina crenulata*? Flower, 1961
	Favistina magister (Bassler, 1950)	*Favistina magister* (Bassler, 1950)
	Favistina crenulata Flower, 1961	*Favistina crenulata* Flower, 1961
Browne 1965	*Foerstephyllum vacuum* (Foerste, 1909)	*Crenulites vacuum* (Foerste, 1909)
	Foerstephyllum vacuum magnum Browne, 1965	*Crenulites vacuum* (Foerste, 1909)
	Cyathophylloides stellata (Hall, 1847)	*Crenulites stellatus* (Hall, 1847)
	Cyathophylloides cf. *burksae* Flower, 1961	*Favistina crenulata*? Flower, 1961
	Cyathophylloides wellsi Browne, 1965	*Crenulites calicinus* (Nicholson, 1875a)
	Cyathophylloides crenulata (Flower, 1961)	*Favistina crenulata* Flower, 1961
	Cyathophylloides magister (Bassler, 1950)	*Favistina magister* (Bassler, 1950)
Fedorowski & Jull 1976	*Favistina stellata* (Hall, 1847)	*Crenulites stellatus* (Hall, 1847)
Jull 1976b	*Foerstephyllum vacuum* (Foerste, 1909)	*Crenulites vacuum* (Foerste, 1909)
Bolton 1979	*Favistina stellata* (Hall, 1847) *(pars)*	*Crenulites stellatus* (Hall, 1847)
Hill 1981	*Favistina stellata* (Hall, 1847)	*Crenulites stellatus* (Hall, 1847)
lower Stonewall Fm. (upper Katian), S Manitoba		
Stearn 1956	*Palaeophyllum pasense* Stearn, 1956	*Palaeophyllum*? *pasense* Stearn, 1956
	Palaeophyllum pasense parvum Stearn, 1956	*Palaeophyllum*? *parvum* Stearn, 1956
upper Vauréal Fm. (upper Katian), Anticosti Island, E Canada		
Twenhofel 1928	*Columnaria*? (*Palaeophyllum*) *vaurealensis* Twenhofel, 1928	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
Bolton 1972	*Palaeophyllum vaurealensis* (Twenhofel, 1928)	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
Fedorowski & Jull 1976	*Palaeophyllum* cf. *vaurealensis* (Twenhofel)	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
	Palaeophyllum vaurealensis (Twenhofel)	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
	Palaeophyllum sp.	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
Bolton 1979	*Columnaria*? (*Palaeophyllum*) *vaurealensis* Twenhofel, 1928	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
Melzak 2004	*Palaeophyllum vaurealense* (Twenhofel, 1928)	*Palaeolithostrotion vaurealense* (Twenhofel, 1928)
upper Ellis Bay Fm. (upper Hirnantian), Anticosti Island, E Canada		
Bolton 1972	*Cyathophylloides* sp.	*Palaeolithostrotion lyterion* (Bolton, 1979)
Bolton 1979	*Cyathophylloides lyterion* Bolton, 1979	*Palaeolithostrotion lyterion* (Bolton, 1979)
	Palaeophyllum clion Bolton, 1979	*Palaeolithostrotion lyterion* (Bolton, 1979)
Bolton 1981	*Palaeophyllum clion* Bolton, 1981	*Palaeolithostrotion lyterion* (Bolton, 1979)
	Cyathophylloides lyterion Bolton, 1981	*Palaeolithostrotion lyterion* (Bolton, 1979)
Melzak 2004	*Palaeophyllum lyterion* (Bolton, 1979)	*Palaeolithostrotion lyterion* (Bolton, 1979)
	Palaeophyllum n. sp.	excluded from cyathophylloidids
lower Keel Fm. (upper Hirnantian), Oklahoma & the coeval Kissenger Limestone Mb. of the Bryant Knob Fm., NE Missouri		
Young & Elias (1995)	*Palaeophyllum* sp.	*Palaeolithostrotion*? sp. A
Manitoulin Fm. (lower Rhuddanian), Manitoulin Island, SE Canada		
Williams, 1919	*Palaeophyllum* (*Cyathophylloides*?) *williamsi* Chadwick in Williams, 1919	excluded from cyathophylloidids
	Palaeophyllum umbellicrescens Chadwick in Williams, 1919	excluded from cyathophylloidids
Chabot Mbr. (Rhuddanian) of the Becscie Fm., Anticosti Island, E Canada		
Bolton 1981	*Palaeophyllum* sp.	excluded from cyathophylloidids
Melzak 2004	*Palaeophyllum* sp. Bolton, 1981	excluded from cyathophylloidids
basal Merrimack & possibly uppermost Becscie fms (upper Llandovery), Anticosti, E Canada		

	References	Original identification	This study
	McLean & Copper 2013	*Palaeophyllum conjunctum* McLean & Copper, 2013	excluded from cyathophylloidids
	East Point Mb. (upper Aeronian) of the Menier Fm., Anticosti, E Canada		
	McLean & Copper 2013	*Palaeophyllum cumerense* McLean & Copper, 2013	*Palaeolithostrotion cumerense* (McLean & Copper, 2013)
	Cape Schuchert Fm. (Aeronian), Kap Schuchert, western N Greenland		
	McLean 1977	*Palaeophyllum schuchertense* McLean, 1977	excluded from cyathophylloidids
		Palaeophyllum cf. *hubeiense* Ge & Yu, 1974	*Palaeophyllum*? *hubeiense*? Ge & Yu, 1974
	Offley Island Fm. (Telychian), western N Greenland		
	Troedsson 1928	*Columnaria* (*Palaeophyllum*) *stokesi* (Milne-Edwards & Haime, 1851)	*Palaeolithostrotion*? *troedssoni (*Poulsen, 1941)
	strata of "early Wenlockian" age, Porcupine River area, Alaska		
	Oliver 1975a	cf. *Palaeophyllum* sp.	revision required
	Gasport Fm. (Homerian), Lockport, New York		
	Hall 1852	*Syringopora*? *multicaulis* Hall, 1852	*Palaeolithostrotion multicaule* (Hall, 1852)
	Oliver 1963	*Palaeophyllum multicaule* (Hall, 1852)	*Palaeolithostrotion multicaule* (Hall, 1852)
	"Coral Zone A" ("upper Llandovery"; now Lochkovian, Lower Devonian) of the Roberts Mountains Fm., Nevada		
	Merriam 1973	*Cyathophylloides fergusoni* Merriam, 1973	excluded from cyathophylloidids
	Merriam 1976	*Cyathophylloides* sp. f	excluded from cyathophylloidids
	upper part (Silurian?) of the Centrum Fm., NE Greenland		
	Scrutton 1975	*Palaeophyllum halysitoides* (Wilson)	excluded from cyathophylloidids
		?*Palaeophyllum* sp.	excluded from cyathophylloidids
York Terrane	unit Sodl (middle Katian?), w Seward Peninsula, Alaska		
	Oliver 1975a, b	*Cyathophylloides* sp.	revision required
Baltica	Kalstad Limestone (lower Katian), Trondheim		
	Kiær 1932	*Columnaria* cf. *kassariensis* Dybowski, 1873a	revision required
	"middle Caradoc" (lower Katian?), Middle Urals		
	Ivanov & Myagkova 1950	*Columnaria halysitoides* Troedsson, 1928	*Palaeophyllum halysitoides*? (Wilson, 1926)
	Ivanov & Myagkova 1955	*Columnaria halysitoides* Troedsson, 1928	*Palaeophyllum halysitoides*? (Wilson, 1926)
	Sur'ya Horizon (middle Katian?), Middle Urals		
	Ivanov & Myagkova 1950	*Columnaria alveolata* Goldfuss, 1826	*Crenulites* sp. A
	Ivanov & Myagkova 1955	*Columnaria alveolata* Goldfuss, 1826	*Crenulites* sp. A
	Shurygina 1973	*Favistella alveolata* (Goldfuss, 1826)	*Crenulites* sp. A
	Grimsøya Fm. (upper Katian), Oslo–Asker, southern Norway		
	Spjeldnæs 1963	*Cyathophylloides kiaeri* Spjeldnæs, 1963	*Cyathophylloides kiaeri* Spjeldnæs, 1963
	Ärina Fm (Hirnantian), Estonia		
	Kutorga 1837	*Cyathophyllum fasciculus* Kutorga, *1837*	*Palaeophyllum fasciculum* (Kutorga, 1837)
	Hirnantian–lower Llandovery, Estonia		
	Dybowski 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Weissermel 1897	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Bassler 1950	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Reiman 1958	*Palaeophyllum tubuliferum* Reiman, 1958	*Palaeophyllum fasciculum* (Kutorga, 1837)
	Ivanovskiy 1965	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Ivanovskiy 1969	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Fedorowski & Gorianov 1973	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a

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Appendix Table 1. *(Continous)*

	References	Original identification	This study
	Hill 1981	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Lin *et al*. 1995	*Cyathophylloides kassariensis* Dybowski, 1873a	*Cyathophylloides kassariensis* Dybowski, 1873a
	Elkino Horizon (Wenlock), eastern slope of Middle Ural		
	Soshkina 1937	*Dokophyllum sociale* Soshkina, 1937	excluded from cyathophylloidids
	Ivanovskiy 1969	*Palaeophyllum*(?) *sociale* (Soshkina, 1937)	excluded from cyathophylloidids
	lower Slite Group (upper Sheinwoodian, Wenlock), Gotland, Sweden		
	Milne-Edwards & Haime 1851	*Columnaria gothlandica* Milne-Edwards & Haime, 1851	excluded from cyathophylloidids
	Bassler 1950	*Cyathophylloides gothlandicus* (Milne-Edwards & Haime, 1851)	excluded from cyathophylloidids
	"upper Silurian", Dniester River		
	Ivanovskiy 1969	"*Columnaria*" *gothlandica* Milne-Edwards & Haime, 1851	excluded from cyathophylloidids
	"Middle Ordovician", Moyero River, Siberian Platform		
	Sokolov 1955	*Favistella simplex* Sokolov, 1955	excluded from cyathophylloidids
	Ivanovskiy 1969	*Proterophyllum simplex* (Sokolov, 1955) *(pars)*	excluded from cyathophylloidids
	Dolborian Horizon (middle Katian), Podkamennaya Tunguska River Basin		
	Sokolov 1950	*Columnaria alveolata* Goldfuss, 1826	*Crenulites septosus*? (Sokolov, 1950)
		Columnaria septosa Sokolov, 1950	*Crenulites septosus* (Sokolov, 1950)
		Columnaria septosa var. *major* Sokolov, 1950	*Crenulites septosus* (Sokolov, 1950)
		Columnaria vaqua? Foerste, 1909	*Crenulites breviseptatus*? (Sokolov, 1955)
	Sokolov 1955	*Favistella breviseptata* Sokolov, 1955	*Crenulites breviseptatus* (Sokolov, 1955)
		Cyathophlloides asper Sokolov, 1955	*Crenulites asper* (Sokolov, 1955)
	Ivanva *et al.* 1955	*Favistina dybovskii* Soshkina, 1955	*Crenulites septosus* (Sokolov, 1950)
	Ivanovskiy 1965	*Favistella alveolata* (Goldfuss, 1826)	*Crenulites* sp. B
		Favistella breviseptata Sokolov, 1955	*Crenulites breviseptatus* (Sokolov, 1955)
		Favistella dybovskii Soshkina, 1955	*Cyathophylloides* sp. A
	Ivanovskiy 1969	*Proterophyllum simplex* (Sokolov, 1955) *(pars)*	*Crenulites breviseptatus* (Sokolov, 1955)
		Favistella alveolata Goldfuss, 1826 *(pars)*	*Crenulites* sp. B
		Favistella alveolata Goldfuss, 1826 *(pars)*	*Favistina* sp. A
Siberia		*Favistella rigida* (Billings, 1858a)	*Crenulites* sp. B
		Cyathophylloides septosum (Sokolov, 1950) (*pars*)	*Cyathophylloides* sp. A
		Cyathophylloides septosum (Sokolov, 1950) (*pars*)	*Crenulites septosus* (Sokolov, 1950)
	Sytova 1979a	*Favistina breviseptata* Sokolov 1955	*Crenulites breviseptatus* (Sokolov, 1955)
		Favistina stellata (Hall, 1847)	*Crenulites* sp. B
		Favistina rozmanae Sytova 1979a	*Crenulites australis* Hall, 1975
		Cyathophylloides dybowskii (Soshkina 1955)	*Crenulites septosus* (Sokolov, 1950)
	Burian Horizon (upper Katian), Siberian Platform		
	Ivanovskiy 1969	*Palaeophyllum thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
	Sytova 1979a	*Palaeophyllum thomi* (Hall, 1857)	*Palaeophyllum thomi* (Hall in Emory, 1857)
		Palaeophyllum sp.	*Palaeophyllum thomi* (Hall in Emory, 1857)
	uppermost Baraninsky Fm. (upper Katian), Sette–Daban area, NE Russia		
	Latypov 1978	*Palaeophyllum thomi* (Hall, 1857)	tentatively excluded from cyathophylloidids
	"Llandovery", Morkova River, Siberian Platform		
	Ivanovskiy 1965	*Palaeophyllum tubuliferum* Reiman, 1958	excluded from cyathophylloidids
	Ivanovskiy 1969	*Palaeophyllum fasciculum* (Kutorga, 1837) *(pars)*	excluded from cyathophylloidids
	Ivanovskiy 1992	*Palaeophyllum fasciculum* (Kutorga, 1837)	excluded from cyathophylloidids
	Yaralin Fm. (Wenlock), Siberian Platform		
	Ivanovskiy 1988	*Cereoelasma sibiricus* Ivanovskiy, 1988	excluded from cyathophylloidids
	Ivanovskiy 1992	*Cerioelasma sibiricus* Ivanovskiy, 1988	excluded from cyathophylloidids

	References	Original identification	This study
Altai–Sayan	lower part ? (middle Katian?) of the Tekhten' Horizon, Shoria & Gorny Altai		
	Radugin 1936a	*Columnaria* sp.	excluded from cyathophylloidids
		Columnaria halysitoides Radugin, 1936a	*Palaeolithostrotion radugini* (Tcherepnina, 1960)
		Columnaria (?) *fascicularis* Radugin, 1936a	revision required
	Radugin 1936b	*Columnaria* (?) *halysitoides* Radugin, 1936b	*Palaeolithostrotion radugini* (Tcherepnina, 1960)
	Tcherepnina 1960	*Parabrachyelasma labediensis* Tcherepnina, 1960	excluded from cyathophylloidids
		Parabrachyelasma virgulta Tcherepnina, 1960	excluded from cyathophylloidids
		Favistella radugini Tcherepnina, 1960	*Palaeolithostrotion radugini* (Tcherepnina, 1960)
		Favistella ampla Tcherepnina, 1960	excluded from cyathophylloidids
		Favistella densa Tcherepnina, 1960	excluded from cyathophylloidids
		Favistella grandis Tcherepnina, 1960	excluded from cyathophylloidids
		Favistella ainkiensis Tcherepnina, 1960	excluded from cyathophylloidids
		Favistella calicinaeformis Tcherepnina, 1960	*Cyathophylloides calicinaeformis* (Tcherepnina, 1960)
	Tcherepnina 1962	*Modesta prima* Cherepnina, 1962	excluded from cyathophylloidids
	Ivanovskiy 1969	*Palaeophyllum fasciculum* (Kutorga, 1837) *(pars)*	excluded from cyathophylloidids
		Palaeophyllum lebediensis (Tcherepnina, 1960)	excluded from cyathophylloidids
		Palaeophyllum ex gr. *lebediensis* (Cherepnina, 1960)	excluded from cyathophylloidids
	upper Llandovery, Gorny Altai		
	Ivanovskiy 1974	*Palaeophyllum fasciculum* (Kutorga, 1837)	*Palaeophyllum*? sp.
Tuva–Mongol	Alash Horizon (Rhuddanian–lower Aeronian), W Tuva		
	Sytova & Ulitina 1983	*Favistina magna* Sytova in Sytova & Ulitina, 1983	tentatively excluded from cyathophylloidids
	Kyzylchiraa Horizon (upper Aeronian), W Tuva		
	Sytova & Ulitina 1983	*Palaeophyllum tubuliferum* Reiman, 1958	excluded from cyathophylloidids
C Mongolia	Middle Kandel layers, C Mongolia		
	Sytova & Ulitina 1983	*Palaeophyllum thomi* (Hall, 1857)	excluded from cyathophylloidids
Gobi Altai	Sairin Subhorizon (upper Katian), Gobi Altai, S Mongolia		
	Sytova & Ulitina 1983	*Modesta gobiensis* Ulitina in Sytova & Ulitina, 1983	excluded from cyathophylloidids
		Palaeophyllum crassum Webby, 1972	excluded from cyathophylloidids
		Palaeophyllum lebediensis (Tcherepnina, 1960)	excluded from cyathophylloidids
		Palaeophyllum virgultum (Tcherepnina, 1960)	excluded from cyathophylloidids
		?*Palaeophyllum patulum* (McLean & Webby, 1976)	excluded from cyathophylloidids
	Ulitina 2003	*Modesta gobiensis* Ulitina in Sytova & Ulitina, 1983	excluded from cyathophylloidids
		Palaeophyllum crassum Webby, 1972	excluded from cyathophylloidids

Appendix Table 2. Stauriid species and their present revision.

	References	Original identification	This study
	Xiangshuyuan Fm. (upper Rhuddanian–lower Aeronian), Leijiatun, Shiqian area, NE Guizhou		
	Tang 2006	*Fascistauria multiseptata* (He, 1978)	*Cystostauria multiseptata* (He, 1978)
	Tang *et al*. 2008b	*Cystostauria multiseptata* (He & Li, 1974)	*Cystostauria multiseptata* (He, 1978)
	Xiangshuyuan Fm. (upper Rhuddanian–lower Aeronian), Fengxiang & Wude, Shiqian area, NE Guizhou		
	He & Li 1974	*Ceriaster (Eostauria) micropora* He & Li, 1974	*Eostauria micropora* He & Li, 1974
	He & Li 1974	*Ceriaster* (*Eostauria*) *agglomorata* He & Li, 1974	*Yuina agglomorata* (He & Li, 1974)
	He & Li 1974	*Ceriaster* (*Eostauria*) *minor* (Chen, 1959)	*Yuina agglomorata* (He & Li, 1974)
	He & Li 1974	*Ceriaster* (*Eostauria*) *shiqianensis* He & Li, 1974	*Paraceriaster shiqianensis* (He & Li, 1974)
	He & Li 1974	*Stauria* aff. *prolifera* Yin, 1944	*Cystostauria multiseptata* (He, 1978)
	He & Li 1974	*Cystostauria normalis* He & Li, 1974	*Cystostauria normalis* He & Li, 1974
	He & Li 1974	*Fascistauria queizhouensis* He & Li, 1974	*Eostauria prolifera* (Yin, 1944)
	Kong & Huang 1978	*Ceriaster agglomorata* He & Li, 1974	*Yuina agglomorata* (He & Li, 1974)
	He & Li 1983	*Ceriaster* (*Eostauria*) *micropora* He & Li, 1983	*Eostauria micropora* He & Li, 1974
	He & Li 1983	*Paraceriaster cateniformis* He & Li, 1983	*Paraceriaster cateniformis* He & Li, 1983
	He & Li 1983	*Paraceriaster shiqianensis* (He & Li, 1974)	*Paraceriaster shiqianensis* (He & Li, 1974)
	He & Li 1983	*Paraceriaster queizhouensis* (He & Li, 1974)	*Eostauria prolifera* (Yin, 1944)
	He & Li 1983	*Cystostauria normalis* He & Li, 1983	*Cystostauria normalis* He & Li, 1974
	Lin *et al*. 1995	*Eostauria micropora* He & Li, 1974	*Eostauria micropora* He & Li, 1974
	Tang 2006	*Eostauria micropora* He & Li, 1974	*Eostauria micropora* He & Li, 1974
	Xiangshuyuan Fm. (upper Rhuddanian–lower Aeronian), Baisha, Shiqian area, NE Guizhou		
	Ge & Yu 1974	*Stauria shiqianensis* Ge & Yu, 1974	*Parastauria shiqianensis* (Ge & Yu, 1974)
	Kong & Huang 1978	*Stauria favosa sinensis* He & Huang in Kong & Huang, 1978	*Parastauria shiqianensis* (Ge & Yu, 1974)
	Kong & Huang 1978	*Stauria shiqianensis* Ge & Yu, 1974	*Parastauria shiqianensis* (Ge & Yu, 1974)
	Tang 2006	*Parastauria tenuisepta* Tang, 2006	*Parastauria shiqianensis* (Ge & Yu, 1974)
	Wang & Cui 2020	*Stauria shiqianensis* Ge & Yu, 1974	*Parastauria shiqianensis* (Ge & Yu, 1974)
	Xiangshuyuan Fm. (upper Rhuddanian–lower Aeronian), Sinan area, NE Guizhou		
S China	He & Li 1974	*Ceriaster* (*Ceriaster*) *calamites* Lindström, 1883	*Heina* sp.
	Kong & Huang 1978	*Ceriaster calamites* Lindström, 1883	*Heina* sp.
	Kong & Huang 1978	*Ceriaster minor* (Chen, 1959)	inadequately known
	Kong & Huang 1978	*Ceriaster weiganensis* He & Huang in Kong & Huang, 1978	*nomen dubium*
	He & Li 1983	*Paraceriaster shiqianensis* (He & Li, 1974)	*Paraceriaster shiqianensis* (He & Li, 1974)
	Tang 2006	*Ceriaster calamites* Lindström, 1883	*Heina* sp.
	Tang *et al*. 2008b	*Ceriaster calamites* Lindström, 1883	*Heina* sp.
	Chenxicun Fm. (upper Aeronian), Hanshan area, E Anhui		
	Deng *et al*. 1983	*Ceriaster minor* Chen, 1959	inadequately known
	Lojoping Fm. (upper Aeronian), Yichang area, SW Hubei		
	He & Li 1974	*Ceriaster* (*Eostauria*) *minor* (Chen, 1959)	*Yuina agglomorata* (He & Li, 1974)
	Jia & Wu 1977	*Stauria* (*Ceriaster*) *hubeiensis* Wu in Jia & Wu, 1977	*nomen dubium*
	Xiong & Gu 1978	*Stauria* (*Ceriaster*) *hubeiensis* Wu in Jia & Wu, 1977	*nomen dubium*
	Liu 1984	*Ceriaster hubeiensis* Wu in Jia & Wu, 1977	*nomen dubium*
	Zhu & Ma 2019	*Ceriaster hubeiensis* Wu in Jia & Wu, 1977	*nomen dubium*
	"lower Silurian", Cili, NW Hunan		
	Jiang 1982	*Ceriaster minor* (Chen, 1959)	inadequately known
	Leijiatun Fm. (upper Aeronian), Leijiatun & Baisha, Shiqian area, NE Guizhou		
	Ge & Yu 1974	*Ceriaster columellatus* Ge & Yu, 1974	*Yuina columellata* (Ge & Yu, 1974)
	Kong & Huang 1978	*Ceriaster columellatus* Ge & Yu, 1974	*Yuina columellata* (Ge & Yu, 1974)
	He 1980	*Stauria leijiatunensis* He, 1980	*Parastauria leijiatunensis* (He, 1980)
	He 1980	*Stauria polygonalis* (He & Li, 1974)	*Parastauria huayinshanensis* (He, 1980)
	He 1980	*Stauria tenuisepta* He, 1980	*Stauria tenuisepta* He, 1980
	He 1980	*Neoceriaster shiqianensis* He, 1980	*nomen dubium*
	He 1980	*Neoceriaster columellatus* (Yu & Ge, 1974)	*Yuina columellata* (Ge & Yu, 1974)
	Lin *et al*. 1995	*Neoceriaster shiqianensis* He, 1980	*nomen dubium*
	Scrutton & Deng 2002	*Ceriaster* sp. nov.	*Eostauria* sp. A

References	Original identification	This study
Tang 2006	*Eostauria crassosepta* Tang, 2006	*Yuina agglomorata* (He & Li, 1974)
Tang 2006	*Eostauria columelletus* (Ge & Yu, 1974)	*Yuina columellata* (Ge & Yu, 1974)
Tang 2006	*Paraceriaster fasciculata* (Cao, 1975)	*Eostauria* sp. B
Tang 2006	*Paraceriaster baishaensis* Tang, 2006	*Paraceriaster shiqianensis* (He & Li, 1974)
Tang 2006	*Paraceriaster shiqianensis* (He & Li, 1974)	*Paraceriaster shiqianensis* (He & Li, 1974)
Tang 2006	*Stauria sinensis* (He & Huang in Kong & Huang, 1978)	*Stauria tenuisepta* He, 1980
Tang 2006	*Fascistauria* sp.	*Cystostauria normalis* He & Li, 1974
Tang 2006	*Fascistauria multiseptata* (He, 1978)	*Cystostauria multiseptata* (He, 1978)
Tang *et al*. 2008b	*Stauria sinensis* (He & Huang in Kong & Huang, 1978)	*Stauria tenuisepta* He, 1980
Tang *et al*. 2008b	*Cystostauria* sp.	*Cystostauria normalis* He & Li, 1974
Tang *et al*. 2008b	*Cystostauria multiseptata* (He, 1978)	*Cystostauria multiseptata* (He, 1978)
Tang *et al*. 2008b	*Paraceriaster baishaensis* Tang in Tang *et al*., 2008b	*Paraceriaster shiqianensis* (He & Li, 1974)
Tang *et al*. 2008b	*Eostauria shiqianensis* (He, 1980)	*Yuina agglomorata* (He & Li, 1974)
Tang *et al*. 2008b	*Paraceriaster fasciculata* (Cao, 1975)	*Eostauria* sp. B
Wang & Cui 2020	*Ceriaster columellatus* Ge & Yu, 1974	*Yuina columellata* (Ge & Yu, 1974)
Shihniulan Fm. (upper Aeronian), Zunyi, Tongzi, Xishui, Meitan & Zheng'an areas, N Guizhou		
Yin 1944	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
Wang *et al*. 1955	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
Yu *et al*. 1963	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
He & Li 1974	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
He & Li 1974	*Ceriaster* (*Eostauria*) *songkanensis* He & Li, 1974	*Paraceriaster shiqianensis* (He & Li, 1974)
He & Li 1974	*Parastauria polygonalis* He & Li, 1974	*Parastauria polygonalis* He & Li, 1974
Kong & Huang 1978	*Ceriaster shiqianensis* He & Li, 1974	*Paraceriaster shiqianensis*? (He & Li, 1974)
Kong & Huang 1978	*Parastauria polygonalis* He & Li, 1974	*Parastauria polygonalis* He & Li, 1974
He *et al*. 1989	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
He *et al*. 1989	*Paraceriaster songkanensis* He & Li, 1974	*Paraceriaster shiqianensis* (He & Li, 1974)
Deng & Scrutton 1996	*Stauria leijiatunensis* He, 1980	*Stauria* sp. nov. of Scrutton & Deng, 2002
Scrutton & Deng 2002	*Stauria* sp. nov.	*Stauria* sp. nov. of Scrutton & Deng, 2002
Tang 2006	*Paraceriaster fasciculata* (Cao, 1975)	*Eostauria* sp. B
Tang 2006	*Stauria polygonalis* (He & Li, 1974)	*Parastauria polygonalis* He & Li, 1974
Tang *et al*. 2008b	*Paraceriaster fasciculata* (Cao, 1975)	*Eostauria* sp. B
Tang *et al*. 2008b	*Parastauria polygonalis* He & Li, 1974	*Parastauria polygonalis* He & Li, 1974
Shihniulan Fm. (upper Aeronian), Guanyinqiao, Qijiang, S Chongqing		
He 1978	*Stauria qijiangensis* He, 1978	*Stauria qijiangensis* He, 1978
He 1978	*Stauria multiseptata* He, 1978	*Cystostauria multiseptata* (He, 1978)
He 1978	*Ceriaster shiniulanensis* He, 1978	*Eostauria prolifera* (Yin, 1944)
He 1980	*Stauria qijiangensis* He, 1980	*Stauria qijiangensis* He, 1978
He 1980	*Stauria multiseptata* He, 1978	*Cystostauria multiseptata* (He, 1978)
He 1980	*Ceriaster guanyinqiaoensis* He, 1980	*Stauria qijiangensis* He, 1978
He 1980	*Ceriaster shiniulanensis* He, 1980	*Eostauria prolifera* (Yin, 1944)
He 1980	*Ceriaster qijiangensis* He, 1980	*Eostauria qijiangensis* (He, 1980)
He 1980	*Ceriaster qiaogouensis* He, 1980	*Yuina qiaogouensis* (He, 1980)
He 1980	*Neoceriaster qijiangensis* He, 1980	*Paraceriaster qijiangensis* He, 1980
He 1980	*Neoceriaster rarisepta* He, 1980	*Heina rarisepta* (He, 1980)
He & Li 1983	*Stauria simplex* He & Li, 1983	*Eostauria qijiangensis* (He, 1980)
Tang 2006	*Eostauria stauriata* Tang, 2006	*Eostauria stauriata* Tang in Tang *et al*., 2008b
Tang *et al*. 2008b	*Eostauria stauriata* Tang in Tang *et al*., 2008b	*Eostauria stauriata* Tang in Tang *et al*., 2008b
Shihniulan Fm. (upper Aeronian), Dongkala, Fenggang area, N Guizhou		
Kong & Huang 1978	*Stauria prolifera* Yin, 1944	*Eostauria prolifera* (Yin, 1944)
He & Li 1983	*Paraceriaster cateniformis* He & Li, 1983	*Paraceriaster cateniformis* He & Li, 1983
He & Li 1983	*Stauria fongganensis* He & Li, 1983	*Stauria fongganensis* He & Li, 1983
He & Li 1983	*Cystostauria normalis* He & Li, 1983	*Cystostauria normalis* He & Li, 1974
Tang 2006	*Eostauria stauriata* Tang, 2006	*Eostauria stauriata* Tang in Tang *et al*., 2008b
Tang 2006	*Paraceriaster guizhouensis* (He & Li, 1974)	*Eostauria prolifera*? (Yin, 1944)
Tang 2006	*Paraceriaster* sp.	inadequately known

(Continous)

Appendix Table 2. *(Continous)*

	References	Original identification	This study
	Tang *et al*. 2008b	*Eostauria stauriata* Tang in Tang *et al*., 2008b	*Eostauria stauriata* Tang in Tang *et al*., 2008b
	Huanggexi Fm. (upper Aeronian), Daguan area, NE Yunnan		
	He 1978	*Ceriaster minor* (Chen, 1959)	*Paraceriaster major* (Fan in He, 1978)
	Huanggexi Fm. equivalent (upper Aeronian), Shichong, Leibo area, SW Sichuan		
	He 1978	*Ceriaster major* Fan in He, 1978	*Paraceriaster major* (Fan in He, 1978)
	Lalong Fm. (upper Aeronian), Yiwa, Diebu area, S Gansu		
	He & Chen 1999	*Eostauria minor* (Chen, 1959)	*Paraceriaster qijiangensis*? He, 1980
	Kaochaitien Fm. (largely lower Telychian), Guiyang area, C Guizhou		
	Qin 1956	*Stauria prolifera* Yin, 1944	*Eostauria stauriata* Tang in Tang *et al*., 2008b
	Chen 1959	*Stauria prolifera* Yin, 1944	*Eostauria stauriata* Tang in Tang *et al*., 2008b
	Chen 1959	*Stauria* (?) *minor* Chen, 1959	*nomen dubium*
	Yu *et al*. 1963	*Stauria* (*Ceriaster*) *minor* (Chen, 1959)	*nomen dubium*
	Hanchiatien Fm. (lower Telychian), Guanyinqiao, Qijiang, S Chongqing		
	He 1980	*Stauria guanyinqiaoensis* He, 1980	*Parastauria guanyinqiaoensis* (He, 1980)
	Sifengya Fm. (lower Telychian), Daguan area, NE Yunnan		
	He 1980	*Stauria liangfengyaensis* He, 1980	*Parastauria liangfengyaensis* (He, 1980)
	He 1980	*Paraceriaster daguanensis* He, 1980	*Paraceriaster major* (Fan in He, 1978)
	Lin *et al*. 1995	*Paraceriaster daguanensis* He, 1980	*Paraceriaster major* (Fan in He, 1978)
	Tang 2006	*Paraceriaster daguanensis* He, 1980	*Paraceriaster major* (Fan in He, 1978)
	Baiyun'an Fm. (lower Telychian), Huayingshan Mountain, E Sichuan		
	He 1980	*Stauria huayinshanensis* He, 1980	*Parastauria huayinshanensis* (He, 1980)
	He 1980	*Stauria xikouensis* He, 1980	*Parastauria huayinshanensis* (He, 1980)
	Wang *et al.* 2011	*Paraceriaster micropora* Tang in Tang *et al*., 2008b	*Paraceriaster fasciculatus* (Cao, 1975)
	Wang & Cui 2020	*Paraceriaster micropora* Tang in Tang *et al*., 2008b	*Paraceriaster fasciculatus* (Cao, 1975)
	Wangjiawan Fm. (lower Telychian), Guangyuan & Ningqiang areas, N Sichuan & S Shaanxi		
	Lindström 1883	*Ceriaster calamites* Lindström, 1883	*Ceriaster calamites* Lindström, 1883
	Yu *et al*. 1963	*Stauria* (*Ceriaster*) *calamites* Lindström, 1883	*Ceriaster calamites* Lindström, 1883
	Ge & Yu 1974	*Ceriaster ningqiangensis* Ge & Yu, 1974	*Massparaceriaster ningqiangensis* (Ge & Yu, 1974)
	Cao 1975	*Ceriaster calamites* Lindström, 1883	*Massparaceriaster ningqiangensis* (Ge & Yu, 1974)
	Cao 1975	*Ceriaster calamites minor* Cao, 1975	*nomen dubium*
	Cao 1975	*Ceriaster minor* (Chen, 1959)	*Paraceriaster fasciculatus* (Cao, 1975)
	Cao 1975	*Ceriaster fasciculatus* Cao, 1975	*Paraceriaster fasciculatus* (Cao, 1975)
	He 1978	*Ceriaster calamites* Lindström, 1883	*Ceriaster calamites* Lindström, 1883
	Hill 1981	*Ceriaster calamites* Lindström, 1883	*Ceriaster calamites* Lindström, 1883
	Cao & Lin 1982	*Ceriaster* (*Ceriaster*) *calamites* Lindström, 1883	*Massparaceriaster ningqiangensis* (Ge & Yu, 1974)
	Cao & Lin 1982	*Ceriaster* (*Eostauria*) *fasciculata* (Cao, 1975)	*Paraceriaster fasciculatus* (Cao, 1975)
	Lin *et al*. 1995	*Ceriaster calamites* Lindström, 1883	*Ceriaster calamites* Lindström, 1883
	Tang 2006	*Paraceriaster micropora* Tang, 2006	*Paraceriaster fasciculatus* (Cao, 1975)
	Tang *et al*. 2008b	*Paraceriaster micropora* Tang in Tang *et al*., 2008b	*Paraceriaster fasciculatus* (Cao, 1975)
	Tang *et al*. 2008b	*Massparaceriaster ningqiangensis* (Ge & Yu, 1974)	*Massparaceriaster ningqiangensis* (Ge & Yu, 1974)
South Tien Shan	"lower–middle Llandovery", Zeravshan–Hissar region		
	Lavrusevich 1965	*Ceriaster menakovae* Lavrusevich, 1965	*Eostauria menakovae* (Lavrusevich, 1965)
	Ivanovskiy 1965	*Fletcheria*? *menakovae* (Lavrusevich, 1965)	*Eostauria menakovae* (Lavrusevich, 1965)
	Lavrusevich 1971	*Ceriaster menakovae* Lavrusevich, 1971	*Eostauria menakovae* (Lavrusevich, 1965)
Beishan	Badanjilin Fm. (uppermost Katian), Danmianshan area, Ejin Banner, W Inner Mongolia		
	He 1987	*Palaeophyllum* sp.	*Yuina*? sp.

	References	Original identification	This study
Arctic Alaska	"Ludlovian", eastern Brooks Range, Alaska		
	Oliver 1975a	*Stauria* sp.	*Cystostauria* sp. C
Baltica	"Silurian, Rejio, east of Angelin", Gotland, Sweden		
	Smith & Ryder 1927	*Stauria favosa* (Linnaeus, 1758) (*pars*)	*Cystostauria* sp. A
	Lower & Upper Visby Fms (uppermost Telychian–lower Sheinwoodian), Gotland, Sweden		
	Ting 1940	*Stauria* sp.	*Cystostauria* sp. B
	Slite Group (upper Sheinwoodian), Gotland, Sweden		
	Fougt 1749	*Medrepora aggregata* Fougt, 1749	*Stauria favosa* (Linnaeus, 1758)
	Milne-Edwards & Haime 1850	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Milne-Edwards & Haime 1851	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Dybowski 1874	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Koch 1883	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
	Zittel 1879	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Nicholson & Lydekker, 1889	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Zittel 1903	*Stauria astreiformis* Milne-Edwards & Haime, 1850	*Stauria favosa* (Linnaeus, 1758)
	Smith & Ryder 1927	*Stauria favosa* (Linnaeus, 1758) (*pars*)	*Stauria favosa* (Linnaeus, 1758)
	Bassler 1950	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
	Hill 1981	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
	Lin *et al*. 1995	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
	Ezaki & Yasuhara 2004	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
	Ezaki & Yasuhara 2005	*Stauria favosa* (Linnaeus, 1758)	*Stauria favosa* (Linnaeus, 1758)
Tuva–Mongol	Alash Horizon (Rhuddanian–lower Aeronian), W Tuva		
	Sytova & Ulitina 1983	*Elizabethia occulta* Sytova in Sytova & Ulitina, 1983	*Parastauria occulta* (Sytova in Sytova & Ulitina, 1983)
		Elizabethia modica Sytova in Sytova & Ulitina, 1983	*Parastauria modica* (Sytova in Sytova & Ulitina, 1983)

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