New and Revised Llandovery (Early Silurian) Rugose Corals from Central Western New South Wales

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Revision of some of the early Silurian rugose coral faunas from central western New South Wales and study of additional new collections warrants the introduction of a number of new taxa and some previous generic assignments need to be updated. The new cystiphyllinid genus *Gephyrelasma* McLean is proposed, comprising type species *Dentilasma ramosum* McLean and *G. stevensi* McLean sp. nov. The new kodonophyllid genus *Vitiliphyllum* McLean, with type species *V. jenkinsi* McLean sp. nov., and the new arachnophyllid genus *Latomiphyllum* McLean, with type species *Arachnophyllum? epistomoides* Etheridge, are introduced. Additional new species include the tryplasmatids *Aphyllum ulahense* McLean and *A. picketti* McLean, as well as the ptychophyllinid *Ptychophyllum sutorense* McLean. *Grewingkia neumani* McLean is now regarded as a probable representative of the kodonophyllid *Cyatholasma* Ivanovskiy, while *Dentilasma honorabile* Ivanovskiy sensu McLean is now only tentatively assigned to that species. Since the original studies of the coral faunas, there has been considerable revision of the lithostratigraphy and biostratigraphy of the relevant sequences. The most current interpretations are reviewed and summarized here.

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INTRODUCTION

The early Silurian rugose corals of central western New South Wales were the subject of a thesis study by McLean (1973), and description of much of the fauna was published by McLean (1974a-c; 1975b; 1985). Since that time, it has become apparent that a number of those taxa require re-assessment of their taxonomic assignment. In addition, a considerable amount of subsequent lithostratigraphic and biostratigraphic study of the relevant sequences, particularly in terms of conodont and graptolite distributions, has led to better understanding of the ages of the coral-bearing units. Consequently, a revision of certain of the previously studied coral taxa has been undertaken in the present work, and the fauna as a whole has been reviewed in terms of its current lithostratigraphic and biostratigraphic distribution.

Fauna from a newly recognized locality in the study area is also included here. Corals were first

collected from a debris bed west of Panuara Rivulet in the Ulah area, southwest of Orange (see below) by AJW in 2004. Both of us revisited this locality in 2016 and collected extensively from the abundant coral material. The fauna includes the new colonial taxa *Gephyrelasma stevensi*, *Aphyllum ulahense* and *Vitiliphyllum jenkinsi*, which are apparently unique to this locality. In addition, the distinctive solitary form *Cyatholasma*? *neumani* is present, known previously from elsewhere in the study area, and this new material helps to provide a better understanding of that species.

LITHOSTRATIGRAPHIC AND BIOSTRATIGRAPHIC FRAMEWORK

Angullong-Bridge Creek area

This area lies southwest of Orange and south of the Miocene Canobolas Volcanic Complex (Figs 1, 3). The first attempts to map and subdivide the

stratigraphically and structurally complex Silurian and Devonian strata were by Stevens and Packham (1953) in the northern Bridge Creek portion, followed by Stevens (1954) in the Angullong-Ulah area to the south. The general distribution of the major units was determined and initial attempts at identifying the rich graptolite faunas of the shaly parts of the sequence were undertaken. Silurian strata were referred to the mostly shaly Panuara Formation, initially defined in the Bridge Creek area (Stevens and Packham 1953), but including a carbonate unit low in the sequence that they named the Bridge Creek Limestone Member. Use of the Panuara Formation was then extended south by Stevens (1954) for the Silurian strata of the Angullong-Ulah area. Significant time breaks within the Panuara Formation were noted by Packham (1969), and this interpretation was expanded upon by Jenkins (1973) in his BSc (Hons) thesis project, subsequently published in part (Jenkins 1978). In this important study, Jenkins remapped the area and introduced a number of new groups, formations and members within the old "Panuara Formation", the groups being separated by the hiatuses earlier identified by Packham (see correlation chart, Fig. 2, herein). Jenkins (1978) provided rather poorly reproduced maps and correlation diagrams of various parts of the area, but they were redrafted more clearly in a later summary (Jenkins 1986). Outcrops are patchy and largely confined to isolated, often faulted creek sections, and so while Jenkins' work generally provides an excellent basis for interpretation of the sequence, some detailed remapping is needed. However, such remapping and consequent revised lithostratigraphic and biostratigraphic synthesis of the area is beyond the scope of the present contribution.

The lowest group defined by Jenkins (1978) was the Cadia Group, later renamed Ashburnia Group by Pogson in Pogson and Watkins (1998, pp. 103, 105) because of name conflict with a constituent formation, the Cadia Coach Shale. It disconformably overlies Late Ordovician volcanics of the Angullong Formation, separated from that unit by the Cobblers Creek hiatus (Fig. 2). Stevens and Packham's Bridge Creek Limestone Member was retained, but as a member of the newly defined Bagdad Formation. Jenkins extended use of the member south from its type area, but conodont-based studies by Bischoff (1987) suggested that while equivalent strata do occur in the Angullong Syncline (Fig. 2), much of the Ashburnia sequence there may be slightly older and of a different, more muddy facies (Bischoff 1987, text-fig. 5). The Ashburnia Group is developed best in the Angullong Syncline, where it was subdivided by Jenkins into a lower Bagdad Formation and upper

Cadia Coach Shale. Within the Bagdad Formation in the northern part of the syncline, some of the constituent informal units of Bischoff (1987, textfig. 5) contain rugose corals. Strata referred here to his "nodular mudstone member", of upper cyphus Zone, late Rhuddanian age in the "Trevenas Creek" area (informal topographic name of Jenkins 1978, although also used by Krynen and Pogson in Pogson and Watkins 1998; see Fig. 3, herein), contain the rugosans Cystiphyllum cylindricum Lonsdale, 1839, Grewingkia parva McLean, 1974c, Calostylis panuarensis McLean, 1974c, Amplexoides gephyra 1985, Cystipaliphyllum conspersum McLean, McLean, 1985 and Tchinghizophyllum webbyi (McLean, 1985). Dentilasma honorabile Ivanovskiy, 1962 of McLean (1974b) is revised here as Dentilasma cf. honorabile.

A bioclastic lens immediately overlying the "nodular mudstone member" at "Trevenas Creek" is referred here to Bischoff's "upper clastic member" of the Bagdad Formation, regarded by him as being of late *cyphus* Zone to early *triangulatus* Zone, latest Rhuddanian–earliest Aeronian age. It is the type locality and horizon for "*Grewingkia*" *neumani* McLean, 1974c, revised herein and regarded as probably best assigned to *Cyatholasma* Ivanovskiy, 1961.

Some 5 km north of the Angullong Syncline, a bed of coarse, cross-bedded, pebbly, haematitic sandstone is exposed in a gully west of Panuara Rivulet, approximately 1 km southwest of "Ulah" homestead (33° 21' 11" S, 148° 53' 09" E; Fig. 3 herein), and the upper few metres of this bed have yielded a rich, previously mostly undescribed rugose coral fauna. A striking feature of many colonial (including halysitid) and solitary coral specimens from this locality is that many calices are intact, often being filled with mud, indicating minimal transport from their life position, quite probably in traction currents carrying a slurry of volcanogenic debris, metasedimentary clasts and entire or fragmental shelly material. The bed is overlain and underlain by apparently conformable limestone units, which may be equivalent to at least some of the limestones shown on Stevens' (1954, text-fig. 1) map. However, stratigraphic assignment of those limestones has not been attempted as they have not been adequately mapped or sampled, and lack biostratigraphic data. Based on general descriptions by Jenkins (1978), the coral beds seem most likely to also be referrable to Bischoff's "upper clastic member", and this view is supported by the common presence of Cyatholasma? neumani as in the northern Angullong Syncline. The Ulah fauna also includes the new taxa *Gephyrelasma* stevensi McLean, *Aphyllum ulahense* McLean and *Vitiliphyllum jenkinsi* McLean.

The Bridge Creek Limestone Member of the Bagdad Formation in its type area at Bridge Creek (Fig. 3) was correlated by Bischoff (1987) with the late cyphus Zone to early triangulatus Zone, late Rhuddanian to earliest Aeronian, and thus approximately coeval with his "upper clastic member" in the Angullong Syncline and Ulah area. It is a distinctly different facies, however, consisting of rhythmically bedded, calcareous mudstones to wackestones, and contains a different, presumably facies-controlled rugosan fauna. Currently recognized taxa include Cystiphyllum khantaikaense (Zaprudskaya in Zapruskaya and Ivanovskiy, 1962), Brachyelasma recisum (McLean, 1974c), Amplexoides gephyra McLean, 1985 and Aphyllum picketti McLean sp. nov. Dentilasma ramosum McLean, 1974b is revised here as type species of the new genus Gephyrelasma.

The Ashburnia Group is overlain disconformably by the Waugoola Group (Jenkins 1978), with the time gap referred to as the Panuara hiatus (Packham 1969). The hiatus appears to be variable in duration, but extends from the mid Aeronian to at least early Telychian (Jenkins 1978, Bischoff 1987; Fig. 2, herein). In the northern Angullong Syncline the basal unit is the Cobblers Creek Limestone, comprising basal conglomerates of reworked Ashburnia Group and Angullong Formation, grading up to pebbly, lenticular packstones and grainstones with abundant pentamerid brachiopods. The unit is regarded as probably turriculatus Zone, early Telychian (Jenkins 1978, Bischoff 1987). Rugose corals are uncommon, with only Cystiphyllum cylindricum Lonsdale, 1839 and Angullophyllum warrisi McLean, 1974b currently recorded from outcrops on Cobblers Creek (Fig. 3). It is overlain by the dominantly shaly Glendalough Formation, which bears graptolites ranging from crispus Zone to probable centrifugus Zone, mid Telychian to earliest Sheinwoodian (Jenkins 1978, 1986). The Cobblers Creek Limestone is absent to the north in the Ulah and Bridge Creek areas, where the basal unit of the Waugoola Group is the Glendalough Formation. Several laterally discontinuous members were recognized within the Glendalough Formation by Jenkins (1978), the lowest being the Burly Jacky Sandstone Member, which at Cobblers Creek is actually dominantly limy and contains the rugosans Cystiphyllum cylindricum Lonsdale, 1839 and Ptychophyllum cf. sibiricum Ivanovskiy, 1963 of McLean (1975b), with the latter revised herein as Ptychophyllum sutorense McLean sp. nov. In the

Cobblers Creek area, the unit was regarded as *crispus* Zone to possibly *crenulatus-griestoniensis* Zone, mid Telychian (Jenkins 1978, Bischoff 1987), but as noted by Jenkins (1978, 1986), it is highly diachronous and in the Bridge Creek area could be as young as late Telychian or basal Sheinwoodian, although the graptolite faunas require re-assessment.

The Wenlock-Ludlow shaly sequence disconformably overlying the Waugoola Group is separated by the Quarry Creek hiatus of Packham (1969), and was referred to his new Ulah Formation by Jenkins (1978). This unit and the overlying Wallace Shale of Stevens and Packham (1953) were assigned by Jenkins to the "Panuara Group". However, in an article written before Jenkins' (1978) stratigraphic terminology was introduced, but not actually published until much later, Pickett (1982c) proposed restricting the original Panuara Formation of Stevens and Packham (1953) to just its upper portion above the Quarry Creek hiatus, and thus it is equivalent to Jenkins' Ulah Formation. Pickett then assigned the restricted Panuara Formation and Wallace Shale to the Mumbil Group of Vandyke and Byrnes (1976), extending that unit south from its type area near Wellington (see Pickett 1982b, fig. 18 for correlation of the various formations included in this group). We prefer to follow Pickett's interpretation of the revised Panuara Formation and Mumbil Group in the present work. In the Ulah area, graptolite faunas were more recently (2004) obtained from shales (33° 29' 11" S, 148° 53' 23" E) at least 50 m higher than the coral beds west of Panuara Rivulet, discussed above. This previously unpublished fauna was identified by the late Barrie Rickards as: Monograptus flemingii cf. warreni Burns and Rickards, M. flemingii elegans Elles, M. sp (slender) serexiguous group (3 forms), Pseudoplectograptus praemacilentus (Bouček and Münch), Cyrtograptus sp., Cometagraptus sp. nov., Monoclimacis? sp. nov., Dendrograptus sp. and Dictyonema sp. The age of the graptolites was assessed as "possible lundgreni" Zone in Rickards' field note book, and Dr Lucy Muir has also commented "overall I would place this assemblage in the lundgreni Zone" (pers. comm. 2019). Such a basal Homerian assignment indicates these shaly beds should be assigned to the lowest part of the revised Panuara Formation (see Fig. 2, herein). While Waugoola Group strata are recognized elsewhere in the general Ulah-Bridge Creek area (Fig. 2), whether they are actually present west of Panuara Rivulet in the sequence between the coral beds of the "upper clastic member" and the Panuara Formation graptolitic shales considered here cannot be confirmed at present.

Spring and Quarry Creeks area

The Silurian succession in this area (Figs 1, 4), approximately 22 km west of Orange, has had a long history of study, beginning with the work of Süssmilch (1907), who provided a basic map and stratigraphic sequence and noted the occurrence of fossiliferous limestones. The first major study was by Packham and Stevens (1955), who produced a detailed map and noted the outcrops of three limestone bodies in Quarry Creek, beds A-C from east to west in the terminology of Süssmilch (1907). They determined these limestones were actually strike fault repeats of the same unit, which they named the Quarry Creek Limestone Member of the Panuara Formation. A further well-exposed outcrop of the unit occurs to the south on Spring Creek, approximately 500 m northwest of its junction with Gap Creek (Fig. 4), noted by Packham and Stevens (1955) and with corals discussed by McLean (1973). The limestone is currently regarded as a separate formation and disconformably overlies Late Ordovician volcanics of the Malachis Hill Formation. The fine-grained sandstones and shales disconformably overlying the limestone were initially assigned to the Panuara Formation by Packham and Stevens (1955), but we prefer here to use the at least partially equivalent Mirrabooka Formation of Sherwin (1971), the type locality of which is in the Boree Creek area immediately to the north (see Fig. 4), and is significantly closer than the type area of the Panuara Formation near Bridge Creek to the south (see above). The Mirrabooka Formation in the Quarry Creek area contains a number of graptolite-bearing horizons, and a few elements of that fauna were identified by Packham and Stevens (1955) and Jaeger (1991). Their work was revised by Rickards et al. (1995), supplemented by considerable additional collecting and formal description of the rich assemblage. Rickards et al. recognized graptolite zones ranging from mid Sheinwoodian riccartonensis Zone to basal Gorstian nilssoni Zone in this sequence overlying the limestone.

The preserved Quarry Creek Limestone reaches about 6 m in thickness and mainly consists of coarsely bedded, massive wackestones with abundant skeletal material, especially rugose and tabulate corals. The age of the unit is still not fully constrained, although it has been recognized as early Silurian since the studies of Packham and Stevens (1955). Conodonts were first studied by Bischoff (1987), who assigned the unit to his *amorphognathoides-latus* Assemblage Zone (regarded as equivalent to the standard amorphognathoides Zone by Simpson 1995) and considered to be late Telychian-early Sheinwoodian, He also recognized the overlying early Sheinwoodian rannuliformis Zone in a loose limestone block with shale partings overlying the bedded in situ limestone. The age of this apparently allochthonous block suggests that the top beds of the autochthonous limestone may have originally extended into the basal Sheinwoodian, but have been removed by subsequent erosion in the early Quarry Creek hiatus (see Fig. 2), as there is no evidence of the rannuliformis Zone or possibly even the highest amorphognathoides Zone in the preserved in situ limestone (Bischoff 1987). The coral-bearing beds of interest here are all from the autochthonous sequence and thus are likely to be late Telychian.

It should be noted that some small isolated limestone bodies in the area south of Bowan Park Road and immediately northwest of the Quarry Creek outcrops discussed above (Fig. 4) were mapped as Quarry Creek Limestone by Packham in Jenkins (1986, fig. 34) and Rickards et al. (1995, fig. 2). Bischoff (1987, WT section) regarded conodonts from these limestones to be older than those of the Quarry Creek Limestone, and assigned them to his antiquus-staurognathoides Assemblage Zone (equivalent to the standard staurognathoides Zone according to Simpson 1995) and latest Aeronianearly Telychian in age. These limestones were restudied by Percival and Wright (2005), who simply referred to them as "unnamed limestone". Whether this unit was originally in sequence with the later Quarry Creek Limestone or separated by the Panuara hiatus is unknown, as it is fault-bounded. It may be at least partially equivalent to the Cobblers Creek Limestone in the Angullong Syncline to the south or slightly younger (see above and Fig. 2). Percival and Wright (2005) described a new species of Trimerella from the unit, and discussed and illustrated some accompanying fragmentary, silicified, indeterminate corals.

Current determinations of the rugose coral fauna of the Quarry Creek Limestone comprise *Mictocystis endophylloides* Etheridge, 1908 (revised by McLean 1974a), *Conophyllum crebrum* (McLean, 1974b), *Rhizophyllum antiquum* McLean, 1974b, *Ptychophyllum auctum* McLean, 1975b and *Labechiellata currani* (Wright in Wright and Bauer, 1995). *Arachnophyllum? epistomoides* Etheridge, 1909, type material of which is from the Quarry Creek Limestone, was revised by McLean (1975b). It is further revised herein and designated type species of the new genus *Latomiphyllum* McLean.

Boree Creek area

The Silurian sequence in this area, south of The Escort Way between Orange and Cudal, and approximately 17 km west-northwest of Orange (Figs 1, 4), has had a complex history of study, and a brief summary is given here to help place the coral fauna in stratigraphic and biostratigraphic context. It was first mapped and discussed in any detail by Walker (1959), who produced a very generalized map (fig. 1), and introduced the term Rosyth Limestone for the lowest Silurian carbonate unit. This unit was described as being composed of fossiliferous, marly limestones, with interbedded shales and sandstones, and overlain by massive carbonates of the Borenore Limestone in the east and by shales of the "Panuara Formation" to the west. No type section was designated or described. The area was mapped in more detail in an unpublished study by Partridge (1967), and that mapping was largely used by McLean (1973, 1974a, 1974b, 1975b) in collection and analysis of the rich rugose coral fauna of the unit. Partridge (1967) and Sherwin (1971) recognized that Walker's loosely defined Rosyth Limestone may include some beds now included in the lower Boremore Limestone, although that has not been proven. Consequently, Sherwin (1971) preferred to introduce a new unit in place of the Rosyth, the Boree Creek Formation, although again no type section was selected or described. His study was largely confined to the Cheesemans Creek area (Fig. 4), mostly north of the area mapped by Walker and Partridge and considered here. He proposed a three-fold subdivision of the new unit into Limestone A, tuffaceous trilobite bed and Limestone B, in ascending order, based primarily on the western succession, east of Wattle Creek and about 1.5 km north of Boree Creek (Sherwin 1971, fig. 15). The new terminology was also applied by Sherwin to the western outcrops of "Rosyth Limestone", south of Boree Creek as mapped by Partridge, where it is overlain by shales Sherwin named Mirrabooka Formation and underlain disconformably by siltstones and volcanics of the Late Ordovician Cheesemans Creek Formation. The numerous subsequent authors who have discussed the stratigraphic sequence or who described various aspects of the conodont, trilobite, brachiopod and foram faunas of the "Rosyth Limestone" have used the Boree Creek Formation, and that terminology is followed here (see Fig. 2).

The most complete published map of the distribution of the Boree Creek Formation south of The Escort Way is that of Holloway and Lane (2012, fig. 1), although outcrops do continue a little further east, south of "Rosyth" homestead (Fig. 4 herein; Partridge 1967, McLean 1973). A type section for the

formation was eventually nominated by Scott et al. in Pogson and Watkins (1998, p. 111), who selected the "Boree section" measured by Bischoff (1987, pp. 35-38, text-fig. 8) in the vicinity of the "BOC section" of Cockle (1999, text-fig. 1) and "BM section" of Molloy and Simpson (2012, text-figs 1, 2), near "Kalinga" homestead between The Escort Way and Boree Creek in the eastern part of the outcrop area. In that area, other measurements of the section have recognized up to six units within the Boree Creek Formation (Molloy and Simpson 2012, fig. 3, pp. 621-623), and the original three-fold subdivision of Sherwin (1971) is considered here to have limited practical regional application. The lowest, coral-rich unit is sometimes referred to as Sherwin's Limestone A, but is regarded here simply as the lower Boree Creek Formation. The coral unit has a thickness of approximately 40 m in the type area and comprises rubbly, yellow to light grey weathering, thinly bedded, dark grey to brown wackestones and packstones, with abundant partially silicified corals, which are commonly weathered out.

There have been numerous studies of conodonts from throughout the Silurian sequence of the area, starting with the regional work of Bischoff (1987). He concluded that all the equivalent beds of Sherwin's (1971) Limestone A in his "Boree section" (now the type section, see above) belonged to the late Telychian-basal Sheinwoodian amorphognathoides Zone, and this view was supported by later sampling by Cockle (1999) and Molloy in Valentine and Brock (2003, p. 233, fig. 3). In contrast, Simpson (1995, p. 335) suggested almost all of the lower coral unit (most of "Limestone A") in Bischoff's "Boree section" may belong to the underlying celloni Zone, based on review of Bischoff's fauna. This interpretation was followed by Valentine et al. (2003) and Molloy and Simpson (2012), who, with further resampling, recognized possible juvenile specimens of Pterospathodus celloni (Walliser) in the lower coral unit, and thus assigned it to the celloni Zone (Molloy and Simpson 2012, fig. 3), with the amorphognathoides Zone restricted to the remaining thin uppermost interval of "Limestone A". The most recent work (Molloy and Simpson 2012) regards the higher Boree Creek Formation as ranging through the early Sheinwoodian ranuliformis Zone, with the disconformably overlying basal Borenore Limestone lying within the late Sheinwoodian-mid Homerian amsdeni Zone. Although the precise zonal assignment of the lower coral beds remains in contention, the most likely age appears to be late Telychian.

The rich rugose coral fauna of the lower Boree Creek Formation basal beds south of The Escort Way includes *Latomiphyllum epistomoides*

(Etheridge, 1909), revised by McLean (1975b) and herein, Ketophyllum attenuatum McLean, 1974a, Conophyllum crebrum (McLean, 1974b), Holmophyllum confertum McLean. 1974b. Rhizophyllum antiquum McLean, 1974b, fasciculate cystiphyllinid gen. et sp. undet. ("Microplasma" cf. lovenianum Dybowski of McLean, 1974b), Donacophyllum rosythense (McLean, 1975b), Ptychophyllum auctum McLean, 1975b, Cyathactis variabilis McLean, 1975b, and Nanshanophyllum multicarinatum (McLean, 1975b). The species L. epistomoides, C. crebrum, R. antiquum and P. auctum are common to the fauna of the Quarry Creek Limestone (see above) and emphasize the closely similar ages of the two units, although it is possible that the Boree Creek coral fauna may be slightly older, *celloni* (?) Zone as opposed to early amorphognathoides Zone at Quarry Creek, as discussed above.

SYSTEMATIC PALAEONTOLOGY

Morphological terminology primarily follows that of Hill (1956, 1981). Taxa in species lists are in order of publication. Locality and biostratigraphic data for those listed taxa are for the primary types.

Repositories for numbered specimens bear the following prefixes:

- AM: Australian Museum, Sydney. Original rock specimen has the additional prefix F, with thin sections prepared from that specimen having different numbers and the prefix AM FT. Where both specimen offcuts and associated thin sections are present in the collections, then both numbers are cited. If no specimen number is given with the numbered thin section, then only the thin section is preserved.
- GSC: Geological Survey of Canada Type Collections, Ottawa.
- MMF: Geological Survey of New South Wales, W B Clarke Geoscience Centre, Londonderry. Some older specimens have been transferred to the Australian Museum, Sydney and now bear AM numbers.
- SUP: University of Sydney palaeontological collections. Type specimens from these collections were subsequently transferred to the Australian Museum, Sydney, and now carry newly assigned AM F and/or AM FT numbers. If AM F numbers for such specimens are not cited, we have been unable to locate the relevant offcut material.

All material with SUP numbers was collected by R. A. McLean. With the exception of the refigured

type material of *Aphyllum delicatulum* (Etheridge, 1907) and *Latomiphyllum epistomoides* (Etheridge, 1909), all specimens bearing only AM numbers were collected by A. J. Wright and R. A. McLean. Those specimens with MMF numbers were collected by J. W. Pickett. McLean is the author of the coral systematics presented in this work.

Family CYSTIPHYLLIDAE Edwards and Haime, 1850 Subfamily CYSTIPHYLLINAE McCoy, 1851 Genus *Dentilasma* Ivanovskiy, 1962

Synonymy

Dentilasma Ivanovskiy, 1962, p. 128 Protoketophyllum Chen, He and Tang, 2005, p. 232

Type species

Dentilasma honorabile Ivanovskiy, 1962. "Upper Llandovery", Mogokta River, Siberian Platform.

Diagnosis

Cystiphyllinid with corallites either solitary or with rare calical offsets. Septa comprise sparse, short spines on corallite wall, adjacent dissepiments, or rarely tabulae. Horizontal skeletal elements consist of generally narrow zone of large dissepiments and a clearly defined, broad tabularium, containing complete and incomplete tabulae.

Discussion

Suprageneric classification of Dentilasma has a diverse history. Ivanovskiy (1962) originally assigned it to the Ketophyllidae Lecompte, 1952, based on the genus Ketophyllum Wedekind, 1927. That genus has been regarded as synonymous with Dokophyllum Wedekind, 1927 by many later authors (e. g. Wang 1944, Minato 1961, Hill 1981), with some of those authors preferring to regard Dokophyllum as the senior synonym, presumably because of supposed "page priority" (e. g. Munson and Jell 2016, p. 307). However, according to ICZN Article 24.2, synonymy of simultaneously published generic names is determined by the actions of the First Revisor, who in this case appears to be Wang (1944, p. 27), who designated Ketophyllum as senior synonym. The first three revisors in fact used Ketophyllum in preference to Dokophyllum (Wang 1944, 1950, Hill 1956), although Hill (1981) later switched to Dokophyllum without giving a reason. Further relevant discussion of First Revisor synonymy can be found in Pedder (1999, pp. 372, 373). The key feature for distinguishing Dentilasma from Ketophyllum and thus the Ketophyllidae, is the nature of the septa. In the numerous Gotland species attributed to both *Ketophyllum* and *Dokophyllum* by Wedekind (1927), he described the septa as consisting of "leistes" or ridges developed on the surfaces of dissepiments and tabulae. The most thorough later revision of some of Wedekind's material was by Minato (1961), who specifically referred to septal lamellae and not spines, even in short septate forms like *K. spinosum* Wedekind, 1927. The septa in the type species of *Dentilasma*, *D. honorabile* Ivanovskiy, 1962, were stated to be short, thick spines on the corallite wall (Ivanovskiy 1962, p. 129), and so assignment of the genus to the Ketophyllidae by Ivanovskiy (1962) and some later authors (including even Hill, 1981, although with question) cannot be justified.

Wang (1947) proposed the new cystiphyllid subfamily Holmophyllinae, based on the genus Holmophyllum Wedekind, 1927. He distinguished the subfamily by having rhabdacanthine trabeculae, noting that Holmophyllum also has a more or less distinct tabularium, although the presence of rhabdacanths in the Gotland type species, H. holmi Wedekind, 1927, was not confirmed until revision by Jell and Hill (1970). As is now commonly recognized (Hill 1981, p. F16), rhabdacanths and other primary trabecular microstructures are frequently recrystallized to a holacanthine structure, and it is as the latter that septal spines of the cystiphyllids are most generally preserved. Consequently, presence or absence of rhabdacanths cannot be realistically regarded as a consistent distinguishing feature at the suprageneric level in the cystiphyllids. Of greater significance in Holmophyllum and similar genera (see cited representatives of the Holmophyllidae in Hill 1981) is the presence of a generally welldefined tabularium and long, radially aligned septal spines. Like Hill (1981), some authors have elevated the Holmophyllinae to full family status and separated it from the Cystiphyllidae within the order Cystiphyllida Nicholson (e.g. Munson and Jell 1999, Kido 2009), but we prefer to retain it as a subfamily of the Cystiphyllidae, since it has greater affinities with other cystiphyllids than with the other families of the Cystiphyllida recognized by Hill (1981), the Palaeocyclidae Dybowski, Tryplasmatidae Etheridge and possibly Fletcheriidae Zittel (see also discussion by McLean 2021). Munson and Jell (1999, p. 19) assigned Dentilasma to the Holmophyllidae (Holmophyllinae herein) because of its discrete septal spines and well-defined tabularium. However, it is preferred here to include it in the Cystiphyllinae, because the long, radially aligned septal spines characteristic of the Holmophyllinae are absent in Dentilasma. A generally well-defined tabularium as seen in Dentilasma is not a common feature of the

Cystiphyllinae, but certainly occurs in other genera such as Coronoruga Strusz, 1961, which has been typically referred to the Cystiphyllinae (generally as undifferentiated Cystiphyllidae) by other authors (e. g. Strusz 1961, Shurygina 1970, Hill 1981). The latter genus is probably the morphologically closest solitary cystiphyllinid to Dentilasma. The type species, C. dripstonensis Strusz, 1961, is from strata now referred to the early-mid Ludlow Narragal Formation in the Dripstone area near Wellington, central western New South Wales, and was revised by McLean (1975a, 2021). It has a wide tabularium as in Dentilasma, and an unevenly developed dissepimentarium, but is distinguished by having a distinct "inner wall" at the marginarium-tabularium boundary, composed of probably rhabdacanthine trabeculae enclosed in stereome (Strusz 1961, pl. 42, figs 9, 17; McLean 1975a, pl. 10, figs 8-10; pl. 11, figs 1-3; McLean 2021, pl. 19, fig. 5).

The genus Protoketophyllum was introduced by Chen et al. (2005), with type species P. daguanense Chen et al., 2005, from the late Aeronian-early Telychian Sifengya Formation of Daguan, northeastern Yunnan. It is primarily a solitary form, although may have occasional calical offsets, and has a well-differentiated marginarium and tabularium, with short septal spines on the corallite wall and adjacent dissepiments (Chen et al. 2005, pl. 1, figs 1-3, 5; translation 2006, pp. 335, 336). These characters are also typical of Dentilasma, and Protoketophyllum is consequently regarded here as a junior synonym.

Nyhamnia Johannessen, 1999 shows general similarities to Dentilasma. The type and only assigned species, N. pusilla Johannessen, 1999, from the late Telychian–early Sheinwoodian Ygne Member, Visby Formation of Gotland, has comparable development of horizontal skeletal elements to Dentilasma, but differs in having longer, at least partially radially aligned septal spines (Johannessen 1999, fig. 2). The latter feature suggests Johannessen's assignment of the genus to the Holmophyllinae (as Holmophyllidae) rather than Cystiphyllinae is appropriate.

In addition to the type species, the following species are assigned here to *Dentilasma*.

- Dentilasma contemptum Ivanovskiy, 1962. "Upper Llandovery", Gorbiyachin River, Siberian Platform. Regarded as synonymous with type species *D. honorabile* by Ivanovskiy (1970b).
- Ketophyllum simile Ivanovskiy, 1965. Transitional beds between Llandovery and Wenlock, Sukhaya Tunguska River, Siberian Platform. Assigned to *Dentilasma* by Ivanovskiy (1970b) and McLean (1974b).

- Cystiphyllum? henryhousense Sutherland, 1965. Upper member, Henryhouse Formation, late Ludfordian–Přídolí (Barrick et al. 2011), Arbuckle Mountains, southern Oklahoma. Has rare calical offsets, but does not form the branching colonies of *Gephyrelasma* gen. nov. (see below).
- Dentilasma maximum Shurygina, 1970. Pavda Horizon, early Wenlock (Beznosova 1996), Nizhne Tura region, Is River, eastern slopes of northern Urals.
- Dentilasma indigenum and D. accessorium of Lavrusevich (1971b). Yakkakhona Beds (J), early Wenlock, Mount Daurich, Zeravshan-Gissar Mountains, Tajikistan.
- Ketophyllum subsimile Cao, 1975. Ningqiang Formation, mid Telychian (Rong et al. 2012), Nanzheng, southwestern Shaanxi.
- Dentilasma meitanense He and Huang in Kong and Huang, 1978. Lower Shihniulan Formation, late Aeronian (Rong and Cocks 2014), Meitan, Guizhou.
- Ketophyllum yanjinense and Dentilasma cylindricum of He (1978). Takuan Formation, late Aeronian– early Telychian (Rong et al. 2012), Banbiandu, northeastern Yunnan. Probably synonymous.
- *Ketophyllum shiniulanense* He, 1982. Shihniulan Formation, late Aeronian, Guanyinqiao, southern Chongqing.
- Protoketophyllum daguanense Chen et al., 2005. SifengyaFormation, lateAeronian–earlyTelychian (Rong et al. 2012, as Sifengya Member, Takuan Formation), Huanggexi, Daguan, northeastern Yunnan. Type species of Protoketophyllum. See discussion of Dentilasma, above.

Species below are regarded as possible representatives of *Dentilasma*.

- Ketophyllum equitabulatum Wang, 1944. Kuanti Formation, late Ludfordian, Qujing, eastern Yunnan (He and Chen 2004). Said to have discrete septal spines, but not apparent in longitudinal section (line drawings only), but grouped series of tabulae are more typical of ketophyllids. Requires further study.
- Holmophyllum taltiense Nikolaeva, 1949. Bobrovka Horizon (Ivanovskiy and Shurygina 1975), early Přídolí (Beznosova 1996), Tal'tiya River, eastern slopes of northern Urals. Revised and illustrated photographically by Ivanovskiy and Shurygina (1975), who included *H. heterovesiculosum* Nikolaeva, 1949, from same horizon and close to same locality, as synonym. Has large incomplete tabulae and tabellae axially and assigned to

Dentilasma by Munson and Jell (1999), but Ivanovskiy and Shurygina (1975) placed it in *Cystiphyllum*, and that is probably more appropriate.

- Holmophyllum squamosum Lavrusevich, 1960. Shikorkhona Beds, late Wenlock (Lavrusevich and Menakova 1971), Menora Pass, Zeravshan-Gissar Mountains, Tajikistan. Has short peripheral spines and assigned to *Dentilasma* by Munson and Jell (1999). Requires further study.
- Dokophyllum subelegantulum Zheltonogova, 1961. Chesnokovka Formation (Yolkin and Zheltonogova 1974), latest Telychian – basal Homerian (Yolkin et al. 2003), basin of Bol'she Chesnokovka River, Gorniy Altai. Stated to have septal spines, but not apparent in illustrations.
- Holmophyllum chalfini Zheltonogova, 1965. Chagyrka Suite, late Wenlock, Poperechnyy Stream, Gorniy Altai. Has short spines and mainly large tabellae in tabularium. Could also be representative of *Cystiphyllum* and needs study of variability.
- *Ketophyllum intermedium* Ge and Yu, 1974. Kaochaitien Formation, early Telychian (Rong et al. 2012), Guiyang, Guizhou. Has short septal spines, but appears to have some development of furrows in marginarium. Requires further study.
- Ketophyllum rariseptatum He in Kong and Huang, 1978. Lower Shihniulan Formation, late Aeronian (Rong and Cocks 2014), Sinan, Guizhou. Has well-developed septal spines, but narrower tabularium and wider marginarium than typical *Dentilasma*.
- Dentilasma kuqaense Cai, 1981. Keketiekedaban Formation, Ludlow–Přídolí (data in Ni et al. 1996), Beikule, Xinjiang. Illustrations inadequate.
- Dentilasma lindstroemi (Wedekind, 1927) of Lavrusevich (1991). Lower Isfara Horizon, late Ludlow–early Přídolí, northern slopes of Turkestan Range, Tajikistan. Not conspecific with *Ketophyllum lindstroemi* (Wedekind, 1927), from the middle Sheinwoodian Högklint Formation, Gotland.
- Dentilasma simplex Cai, 2001. Yiqikebashi Formation, "Middle Silurian", Heiyingshan, South Tianshan, Xinjiang. Indeterminate from figures.
- Dentilasma tianshanense Cai, 2001. Keketiekedaban Formation, Ludlow–Přídolí, Heiyingshan, South Tianshan, Xinjiang. Illustrations inadequate.

The species below have been assigned to *Dentilasma* by some authors, but are excluded here from that genus.

- *Omphyma glomeratum* Grabau, 1930. Kaochaitien Formation, early Telychian, Guiyang, central Guizhou (data in Scrutton and Deng 2002, Chen et al. 2002). Assigned to *Dentilasma* by He (1978) and Scrutton and Deng (2002), but is a fasciculate–subcerioid form with weak amplexoid septa, and regarded here as a ketophyllid.
- Dentilasma tubularium Shurygina, 1970. "Detrital limestones", Wenlock, Nizhne Tura region, Is River, eastern slopes of northern Urals. Branching form, assigned here to *Gephyrelasma* gen. nov. (see below).
- Dentilasma? aseptatum Shurygina, 1970. "Upper Wenlock", Nizhne Tura region, Is River, eastern slopes of northern Urals. Branching form and regarded here as possible representative of *Gephyrelasma* (see below).
- Dentilasma intermedium (Chernyshev, 1893) of Strel'nikov (1971). "Lower Wenlock", Kozhim River, Subpolar Urals. Diplochone intermedium Chernyshev, 1893, was revised with topotypes from the late Wenlock (Beznosova, 1996) Elka Horizon of Tura River, eastern slopes of northern Urals, by Ivanovskiy and Shurygina (1975), who assigned it to Ketophyllum.
- Holmophyllum cayugaeaforme Lavrusevich, 1972.
 "Neomphyma originatum beds" = Bursykhirman Beds (Lavrusevich 1971d), early Lochkovian (Yolkin et al. 2000), Karasu River, Zeravshan-Gissar Mountains, Uzbekistan. Assigned to Dentilasma by Munson and Jell (1999), but has very short peripheral rhabdacanthine spines and a weak" inner wall", and is probably representative of Coronoruga.
- Dentilasma apertum Strel'nikov in Strel'nikov and Zhavoronkova, 1972. Greben' Horizon, late Ludlow–Přídolí (Baarli et al. 2003), Kozhim River, Subpolar Urals. Has septal lamellae rather than spines and is probably a *Ketophyllum*.
- Dentilasma ramosum McLean, 1974b. Bridge Creek Limestone Member, Bagdad Formation, late Rhuddanian–early Aeronian, Bridge Creek area, southwest of Orange, central western New South Wales. Fasciculate form, type species of *Gephyrelasma* gen. nov.
- Dentilasma polygonalum He, 1978. Takuan Formation, late Aeronian–early Telychian, Yanjin, northeastern Yunnan. Cerioid form, possibly representative of ketophyllid *Yassia* Jones.
- Dentilasma gansuense Cao in Cao and Lin, 1982. Lower Bailongjiang Group, Maogou Formation (?), Ludlow (Rong et al. 2019), West Qinling Mountains, Gansu. Has weak tabularium of

tabellae and incomplete tabulae, and assigned to *Cystiphyllum* Lonsdale by McLean and Copper (2013).

- Dentilasma typicum Sultanbekova, 1986. Sapporipora tarbagataica beds of Koren' et al. (2003), Zhumak Formation, apparently overlying late Telychian–early Sheinwoodian Pentamerus longispinatus beds of basal Zhumak Formation sensu Nikitina et al. (2015), probably Sheinwoodian, northeastern Chingiz Range, Kazakhstan. Has amplexoid septa and is assigned here to Ketophyllum.
- Dentilasma benestratum Munson and Jell, 1999. Quinton Formation, Telychian, Broken River Province, Graveyard Creek Subprovince, northeastern Queensland. Dendroid form, assigned here to *Gephyrelasma* gen. nov. (see below).
- Dentilasma xinjiangense Cai, 2001. Keketiekedaban Formation, Ludlow–Přídolí, Heiyingshan, South Tianshan, Xinjiang. Has weak "inner wall" and probably representative of *Coronoruga*.

Dentilasma sp. cf. D. honorabile Ivanovskiy, 1962 Fig. 5

Synonymy

- cf. *Dentilasma honorabile* Ivanovskiy, 1962, p. 128, pl. 1, figs 2a, b; pl. 2, fig. 1
- cf. *Dentilasma contemptum* Ivanovskiy, 1962, p. 129, pl. 2, figs 2a, 2b, 3
- cf. Dentilasma honorabile Ivanovskiy; Ivanovskiy 1963, p. 109, pl. 26, figs 3a-v
- cf. Dentilasma contemptum Ivanovskiy; Ivanovskiy 1963, p. 110, pl. 32, figs 1a, b
- cf. *Dentilasma honorabile* Ivanovskiy; Ivanovskiy 1965, pl. 39, figs 2a, b
- cf. Dentilasma honorabile Ivanovskiy; Ivanovskiy 1967, fig. 11a
- cf. Dentilasma honorabile Ivanovskiy; Ivanovskiy 1970b, p. 14
- Dentilasma honorabile Ivanovskiy; McLean 1974b, p. 15, pl. 2, figs 10–13
- cf. *Dentilasma honorabile* Ivanovskiy; Ge and Yu 1974, p. 168, pl. 72, figs 1, 2
- cf. Dentilasma honorabile Ivanovskiy; Lavrusevich 1975, p. 126
- Dentilasma honorabile Ivanovskiy; McLean 1977a, table 2
- Dentilasma honorabile Ivanovskiy; Jenkins 1978, p. 113
- cf. *Dentilasma honorabile* Ivanovskiy; Latypov 1978, p. 89, pl. 28, figs 2a, b

- cf. *Dentilasma honorabile* Ivanovskiy; Kong and Huang 1978, p. 132, pl. 43, figs 3a, b
- cf. *Dentilasma honorabile* Ivanovskiy; Hill 1981, p. *F*219, figs 137.1a, b
- Dentilasma honorabile Ivanovskiy; Jenkins 1986, fig. 33
- Ketophylloides? honorabile (Ivanovskiy); Strusz 1989, pl. 1
- Dentilasma honorabile Ivanovskiy; Strusz 1996, p. 16, fig. 3
- Dentilasma honorabile Ivanovskiy; Strusz and Munson 1997, p. 319
- Dentilasma honorabile Ivanovskiy; Pogson and Watkins 1998, p. 375
- cf. *Dentilasma honorabile* Ivanovskiy; Munson and Jell 1999, p. 20, figs 9A–F
- cf. *Dentilasma honorabile* Ivanovskiy; Talent et al., 2002 pl. 10, figs C–F
- cf. *Dentilasma honorabile* Ivanovskiy; Chen et al., 2005 p. 233, pl. 1, figs 4a, b
- cf. *Dentilasma honorabile* Ivanovskiy; Chen et al., 2006 p. 338, pl. 1, figs 4a, b (English translation of Chen et al. 2005)

Dentilasma honorabile Ivanovskiy; Pickett 2011, p. 71

cf. *Dentilasma honorabile* Ivanovskiy; Wang and Cui in Wang et al. 2020, pl. 7-76, figs 1a, b

Material

SUP 45200 (thin sections AM FT.11665, 11666); SUP 45201 (thin section AM FT.11667); SUP 45202 (thin section AM FT.11668). "Nodular mudstone member", Bagdad Formation (sensu Bischoff 1987), late Rhuddanian, "Trevenas Creek", north flowing tributary of Cobblers Creek, approximately 33 km southwest of Orange, central western New South Wales.

Description

See McLean (1974b, p. 16).

Remarks

At the time of description of the New South Wales material assigned to the type species of *Dentilasma*, *D. honorabile* Ivanovskiy, 1962, by McLean (1974b), there was little published material available for comparison, and a fairly broad interpretation of the species was suggested. In addition to the type specimens and others from the late Llandovery of the Siberian Platform, the species can now be recognized in a number of other units and regions, including the Aeronian Xiangshuyuan Formation (Ge and Yu 1974) or Shihniulan Formation (Kong and Huang 1978) of Yingyiang, Guizhou, late Llandovery– Wenlock Kandyg Horizon of the Sette Daban Range,

northeastern Russia (Latypov 1978), Telychian Quinton Formation of Broken River Province, north Queensland (Munson and Jell 1999), and early Telychian Sifengya Formation of Huanggexi, Yunnan (Chen et al. 2005, 2006). All this material is characterized by development of short septal spines dominantly on the corallite wall, with only rare occurrences on the peripheral dissepiments. Reexamination of the three New South Wales specimens of McLean (1974b) suggests that in some at least of this material the septal spines are more common on the dissepiments than the wall (Figs 5A-C, herein), although all specimens are variably abraded. With the lack of adequately preserved material to confirm the dominant location of the septal spines in this fauna, it is considered here more appropriate to only compare the New South Wales material to D. honorabile.

Few of the species assigned here to Dentilasma (see list above) bear much resemblance to the New South Wales material compared to D. honorabile. Dentilasma yanjinense (He, 1978) and its probable synonym D. cylindricum He, 1978, from the late Aeronian-early Telychian Takuan Formation of Banbiandu, northeastern Yunnan, have similar large, elongate dissepiments and complete to incomplete tabulae, although the tabular series are not as concave as those in the New South Wales form. Dentilasma *vanjinense* itself has clear, short septal spines on some dissepiments as in D. sp. cf. D. honorabile (He 1978, pl. 82, figs 1a, b), although they appear to be more common on the corallite wall in D. cylindricum (He, 1978, pl. 82, figs 2, 3). The major difference appears to lie in the larger corallites of the Chinese material, although the diameters are within the accepted range for D. honorabile itself, based on the synonymy accepted by Ivanovskiy (1970b).

Also showing some similarity is *Dentilasma shiniulanense* (He, 1982), from the late Aeronian Shihniulan Formation of Guanyinqiao, southern Chongqing, particularly in its well-developed short septal spines on the dissepiments (He 1986, pl. 2, figs 5, 6). However, it is clearly separated by having larger corallites, with smaller, more abundant dissepiments and flat to arched tabular series (He 1982, pl. 8, figs 8a, b).

Genus Gephyrelasma McLean gen. nov.

Derivation of name

Greek, *gephyra*, a bridge, referring to the type Bridge Creek area, central western New South Wales.

Type species

Dentilasma ramosum McLean, 1974b. Bridge Creek Limestone Member, Bagdad Formation, late Rhuddanian–early Aeronian, Bridge Creek area, approximately 25 km southwest of Orange, central western New South Wales.

Diagnosis

Fasciculate to subcerioid cystiphyllinid. Septa developed as short spines on corallite walls and to varying degrees on horizontal skeletal elements, and may be enclosed in lamellar stereome. Dissepiments generally large and subglobose to elongate, mostly occurring in one to several rows, although occasionally only intermittently developed. Tabularium clearly defined, containing flat to weakly concave series of complete and incomplete tabulae, in some cases with a few accessory tabellae.

Discussion

This genus is separated from the internally comparable *Dentilasma* Ivanovskiy by having a fasciculate rather than solitary corallum. Like that of *Dentilasma*, its suprageneric assignment is contentious (see discussion of *Dentilasma*, above), but it is included in the Cystiphyllinae for the same reasons.

Two other fasciculate genera show some general similarities to Gephyrelasma. The holmophyllinid Nipponophyllum Sugiyama, 1940 (with synonyms Baeophyllum Hill, 1940; Dendroholmia Spasskiy and Kravtsov in Spasskiy et al., 1974; and probably Zhushanophyllum He, 1978) bears perhaps greatest similarity. Nipponophyllum, as exemplified by its type species, N, giganteum Sugiyama, 1940, from the Wenlock-Ludlow Kawauchi Formation of the South Kitakami Terrane of northeastern Japan, has a broad tabularium as in Gephyrelasma and a narrow zone of variably developed dissepiments peripherally, as well as acanthine septa (Sugiyama 1940, pl. 30, figs 3, 4; text-fig. 3). However, the septal spines in N. giganteum and other representatives of the genus (see lists in Kato 1982 and Kido 2009) are typically longer than in Gephyrelasma, commonly piercing more than one layer of dissepiments or tabulae, and tend to have the marked radial alignment characteristic of the Holmophyllinae and not seen in Gephyrelasma.

McLean (1985, p. 24) suggested that *Dentilasma* ramosum McLean, 1974b, designated here as type of *Gephyrelasma*, was probably a representative of *Ketophylloides* Lavrusevich, 1971b. However, further study of the ketophyllids (see discussion of *Dentilasma*, above), and *Ketophylloides* in particular, indicates that such a generic assignment for ramosum is not appropriate. As discussed above, the ketophyllids are characterized by having low septal ridges or laths developed on the inner dissepiments and variably on the tabulae. The type species of *Ketophylloides*, *Ketophyllum atlassovi* Chernyshev, 1941, from the "Lower Silurian" (Lavrusevich 1971b) of Yakutia, northeastern Russia, has such development of low septal laths (Lavrusevich 1971b, p. 94, translation provided by the Geological Survey of Canada, although they are not clear in the original illustrations of Chernyshev 1941, pl. 1, figs 1, 2) and lacks septal spines. Consequently, *Ketophylloides* can be regarded as a ketophyllid and a fasciculate equivalent of the solitary *Ketophyllum*.

In addition to the type species, the forms below are assigned to *Gephyrelasma*.

- Ketophyllum aseptatum Ivanovskiy, 1959. "Transitional beds between the Llandovery and Wenlock", Sukhaya Tunguska River, Siberian Platform. Assigned to the holmophyllinid Nipponophyllum by Ivanovskiy (1963, 1970b), but lacks the radial rows of long septal spines characteristic of that genus.
- Dentilasma tubularium Shurygina, 1970. "Detrital limestones", Wenlock, Nizhne Tura region, Is River, eastern slopes of northern Urals.
- Dentilasma benestratum Munson and Jell, 1999. Quinton Formation, Telychian, Broken River Province, Graveyard Creek Subprovince, northeastern Queensland.
- Gephyrelasma stevensi McLean sp. nov. "upper clastic member", Bagdad Formation, late Rhuddanian– early Aeronian, Ulah area, southwest of Orange, central western New South Wales.

The following species is regarded as a possible representative of *Gephyrelasma*.

Dentilasma? aseptatum Shurygina, 1970. "Upper Wenlock", Nizhne Tura region, Is River, eastern slopes of northern Urals. Apparently lacks septal spines, but requires further study.

> Gephyrelasma ramosum (McLean, 1974b) Figs 6, 7

Synonymy

- Dentilasma ramosum McLean, 1974b, p. 17, textfig. 4; pl. 3, figs 1–5
- Dentilasma ramosum McLean; McLean 1977a, p. 104
- Dentilasma rumosum (sic) McLean; Jenkins 1978, p. 113
- Dentilasma ramosum McLean; Pickett 1982a, p. 142

- Ketophylloides? ramosum (McLean); McLean 1985, p. 24
- Dentilasma rumosum (sic) McLean; Jenkins 1986, fig. 33
- Dentilasma ramosum McLean; Strusz et al., 1988 p. 29

Dentilasma ramosum McLean; Strusz 1989, plate 1

Ketophylloides? ramosum (McLean); Strusz and Munson 1997, p. 319

- Dentilasma ramosum McLean; Pogson and Watkins 1998, p. 375
- Dentilasma ramosum McLean; Munson and Jell 1999, p. 23
- Ketophyllum ramosum (McLean); Pickett 2011, p. 87

Material

Holotype, SUP 63273 (thin sections AM FT.7177–7191). Bridge Creek Limestone Member, Bagdad Formation, late Rhuddanian–early Aeronian, immediately south of junction of Bridge Creek and Panuara Rivulet, approximately 25 km southwest of Orange, central western New South Wales.

Diagnosis

Phaceloid *Gephyrelasma* with closely spaced corallites of average diameter 9.5 mm. Septal spines short, on corallite wall and irregularly on horizontal skeletal elements. Dissepiments in 1-3 rows; tabularium clearly differentiated from marginarium.

Description

See McLean (1974b, p. 17).

Remarks

Although this species is known only from the holotype, which is not particularly well preserved, a large number of thin sections were prepared so that its internal morphology is reasonably understood. As such, its distinctive morphology makes it a suitable type species for the new genus.

Amongst species included here in *Gephyrelasma* (see list above), *G. ramosum* shows perhaps closest similarities to the Wenlock *G. tubularium* (Shurygina, 1970), with large dissepiments and generally well-spaced tabulae (Shurygina 1970, pl. 23, figs 3a, b; pl. 24, figs 2a, 2b, 3). However, the latter has larger corallites (14 mm diameter) and less regularly developed dissepiments. *Gephyrelasma aseptatum* (Ivanovskiy, 1959) also has more irregularly developed dissepiments than *G. ramosum* and they are considerably smaller, while its tabularium is wider (Ivanovskiy 1959, pl. 1, figs a–d; 1963, pl. 32, figs 3a, b). *Gephyrelasma benestratum* (Munson and

Jell, 1999) has much larger corallites, with far more numerous dissepiments and more closely spaced tabulae (Munson and Jell 1999, figs 11A-L). The new species *G. stevensi* has significantly smaller, more closely spaced corallites and unevenly developed dissepiments. It is compared further in the remarks on that species, below.

Gephyrelasma stevensi McLean sp. nov. Figs 8–11

Derivation of name

In honour of Neville C. Stevens, who first mapped the general Ordovician–Devonian geology of the Panuara–Angullong area, and first recorded the Silurian carbonate outcrops in the Ulah area, type locality for this species.

Type material

Holotype, AM F.156003 (thin sections AM FT.15556, 15557). Paratypes, AM F.156004 (thin sections AM FT.15558-15560); AM F.156025 (thin sections AM FT.15561, 15562); AM F.156026 (thin sections AM FT.15563, 15564); AM F.156005 (thin sections AM FT.15565, 15566); AM F.156006 (thin section AM FT.15567); AM F.156007 (thin sections AM FT.15568, 15569); AM F.156008 (thin sections AM FT.15570.001, 15571.001; note that this specimen also has separately numbered sections of a paratype of Vitiliphyllum jenkinsi sp. nov., see below). "Upper clastic member", Bagdad Formation, late Rhuddanian-early Aeronian, western tributary of Panuara Rivulet, Ulah area, approximately 34 km southwest of Orange, central western New South Wales.

Diagnosis

Phaceloid to subcerioid *Gephyrelasma* with very closely spaced corallites, most commonly 3.5–4 mm in diameter. Septal spines very short, primarily on corallite wall and partially enclosed in stereome to form narrow stereozone. Dissepiments large, mainly elongate, in sparsely developed single row. Tabulae complete and incomplete, mostly in flat, widely spaced series.

Description

Coralla comprise very closely spaced, generally phaceloid corallites, which may locally become partially subcerioid. Corallite diameter ranges from 3–4 .5 mm, with most common values of 3.5–4 mm. Increase appears to be lateral and non-parricidal.

Septal spines are variable in length, but always short and stout, primarily developed on corallite

wall (Fig. 11E), where they are mostly at least partially enveloped in stereome to form a narrow peripheral stereozone, although occasionally stereozone may be wider (Fig. 11C). In rare instances, spines may also occur on horizontal skeletal elements (Fig. 11D).

Dissepiments are relatively large and typically moderately to strongly elongate. They occur in a very unevenly developed single row, which is rarely continuous for any vertical distance in any corallite. In some corallites, dissepiments are virtually absent, this being particularly so in early corallite growth stages. Tabulae are complete to variably incomplete, and are generally wellspaced, 3-8 in 5 mm, most commonly 5-6. In some specimens, part of corallum may have very closely spaced tabular series (in those cases tabulae are generally complete), and up to 17-19 may occur in 5 mm. However, in such colonies parts of the corallites may have more normally spaced tabulae (Fig. 10B). There is no clear evidence that such colonies with some more closely spaced tabulae could represent a separate species, and the variation may be related to environmental factors.

Remarks

Gephyrelasma stevensi is clearly differentiated from the geographically closely occurring, although slightly younger G. ramosum (McLean) (see above), by having distinctly smaller and more closely spaced corallites, more prominent septal spines, and much weaker dissepiment development. All other species assigned here to Gephyrelasma have even larger corallites and do not bear any close resemblance.

Family TRYPLASMATIDAE Etheridge, 1907 Genus Aphyllum Soshkina, 1937

Synonymy

- ? Aphyllostylus Whiteaves, 1904, p. 113
- Aphyllum Soshkina, 1937, p. 45
- *Holacantia* Sytova in Sytova and Ulitina, 1966, p. 208

Holacanthia Ivanovskiy, 1969, p. 31 (nom. van.)

Rhabdacanthia Ivanovskiy, 1969, p. 45

Soshkinelina Goryanov and Lavrusevich, 1972, p. 91 (nom. subst. pro *Aphyllum* Soshkina, 1937, non *Aphylum* Bergroth, 1906, a hermipteran insect)

Type species

Aphyllum sociale Soshkina, 1937. Elka Horizon, late Wenlock, Vyya River, Elka village, eastern slopes of central Urals.

Diagnosis

Fasciculate tryplasmatid with mainly calical or rarely peripheral increase. Septal spines short, rhabdacanthine or holacanthine, primarily based on corallite walls, rarely on tabulae, and may be confined to generally narrow peripheral stereozone. Tabulae mostly complete, flat to sometimes weakly arched or concave, occasionally incomplete, and may have large peripheral tabellae. Dissepiments absent.

Discussion

The genus *Soshkinelina* was proposed by Goryanov in Goryanov and Lavrusevich (1972, p. 91) as a replacement name for *Aphyllum* Soshkina, 1937, which he believed was a junior homonym of *Aphylum* Bergroth, 1906, a hermopteran insect. The generic spelling difference was noted by Ivanovskiy (1974, p. 128) and Hill (1981, p. *F*100), and ICZN Art. 56.2 clearly indicates that two generic names must have identical spelling to be regarded as homonyms. Consequently, *Soshkinelina* is a nomen vanum and junior objective synonym of *Aphyllum* Soshkina.

Aphyllum is used here for species differing from *Tryplasma* Lonsdale, 1845 only in having fasciculate rather than solitary coralla. This taxonomic approach is held by most modern workers on the tryplasmatids (e. g. Kong and Huang 1978, Hill 1981, He and Chen 1999, Munson and Jell 1999, 2016). As a result, most fasciculate forms originally assigned to *Tryplasma* are now referred to *Aphyllum* (see list below).

Aphyllostylus Whiteaves, 1904 bears very close resemblance to Aphyllum, but the name has been only rarely used since its introduction. The type species, A. gracilis Whiteaves, 1904, was not illustrated until his later work (Whiteaves 1906, pl. 24, figs 1, 1a), and then only as line drawings. The material was derived from strata now assigned to the latest Ordovician (Gamachian) Stonewall Formation of southern Manitoba (Stearn 1956), but unfortunately is heavily dolomitized, with consequent poor preservation, and lacks thin sections. However, the available figures of the holotype by Whiteaves (1906) and probable topotype by Stearn (1956, pl. 6, figs 1, 8) do show fasciculate coralla lacking dissepiments and having well-spaced, complete tabulae and clear, short septal spines on the corallite walls, typical of Aphyllum. However, no transverse view of the corallites has been illustrated and neither the true length of the septa (the short spines on the walls may be merely preserved septal bases) nor the character of the stereozone are known. Aphyllostylus was regarded as a valid genus by Lang et al. (1940, p. 18) and Bassler (1950, p. 22), but considered to be a synonym of Tryplasma (interpreted at the time to include both solitary and fasciculate forms) by Stumm (1952), Hill (1956), Stearn (1956) and Soshkina et al. (1962). Of interest, however, is the view of Duncan (1956, p. 225 and caption to pl. 25, figs 3a, b), who proposed use of *Aphyllostylus* as a subgenus of *Tryplasma* for phaceloid forms previously assigned to that genus, thus implicitly restricting *Tryplasma* to solitary species. It appears to be very likely that *Aphyllum* is a junior synonym of *Aphyllostylus*, but, until the type and preferably other, better-preserved material of *Aphyllostylus gracilis* is studied, especially in transverse sections, such a synonymy is difficult to confirm. Consequently, for the present it is preferred here to continue the current common usage of *Aphyllum*, but follow Hill (1981) in regarding *Aphyllostylus* as a possible senior synonym.

Sytova and Ulitina (1966) introduced the genus Holacantia for forms with branching coralla, holacanthine septal spines and lacking dissepiments. Madrepora flexuosa Linnaeus, 1745, from the Silurian of Gotland, was designated as type species, and is now regarded as probably from the early Sheinwoodian Upper Visby Formation. Material assigned to the species by Hill (1936, p. 209) from the late Homerian Much Wenlock Limestone Formation of Shropshire was described by Hill as having holacanthine trabeculae. Sytova and Ulitina (1966) did not mention Aphyllum when discussing Holacantia, but revision of the type material of the type species, A. sociale Soshkina, 1937 by Ivanovskiy and Shurygina (1975, p. 27, pl. 12, figs 3a, b) indicated the presence of holacanthine spines, as well as the same overall morphology as in the type species of Holacantia, and, as noted by Hill (1981), the two genera are clearly synonymous.

Ivanovskiv (1969) subsequently proposed Rhabdacanthia for similar forms, but having rhabdacanthine rather than holacanthine trabeculae. Eridophyllum? rugosum Edwards and Haime, 1851, from undetermined Silurian strata of Gotland, and with a lectotype described and illustrated by Smith and Lang (1927, p. 306, pl. 6, figs 1-7), was selected as type species. Material also from the Much Wenlock Limestone Formation and assigned to the species by Hill (1936, p. 309) was stated to have rhabdacanthine trabeculae. The trabeculae of the lectotype were not described by Smith and Lang (1927), but their diagrammatic drawings (pl. 6, figs 6, 7) suggests they are more likely to be holacanthine. As discussed by Hill (1956, 1981), recrystallization of septa during diagenesis commonly causes an original rhabdacanthine (or monacanthine) microstructure to be replaced by holacanths, so that the presence of holacanths or rhabdacanths in tryplasmatids cannot be given any taxonomic significance on its own. Consequently, Hill (1981) is followed here in regarding *Rhabdacanthia* as also being a junior synonym of *Aphyllum*.

Few genera with branching coralla show much similarity to Aphyllum. Closest resemblance lies with Pycnostylus Whiteaves, 1884, the type species of which, P. guelphensis Whiteaves, 1884, was derived from the late Homerian-late Gorstian Guelph Formation of southern Ontario. This genus is comparable to Aphyllum in all features except the septa, which in Pycnostylus are generally short and lamellar, and at least partially amplexoid adjacent to the corallite walls, as discussed in some detail by Hill (1940, p. 391). Although it is difficult to confirm the amplexoid nature of the very short septa in the poorly preserved type material of P. guelphensis, as illustrated by Whiteaves (1884, pl. 1, figs 1, 1a, 1b) and discussed by Stearn (1956) and Munson and Jell (1999), clearly amplexoid septa were described by Stearn (1956, p. 82) in material he assigned to the species from the late Telychian-early Sheinwoodian Cedar Lake Formation of southern Manitoba. The current generally accepted interpretation of the pycnostylid Pycnostylus is of having amplexoid septa (Hill 1981, p. F140), as compared to the acanthine septa of the tryplasmatid Aphyllum.

Similarities may also be seen between Aphyllum and the mucophyllid Stylopleura Merriam, 1974, although they are not as pronounced as with Pycnostylus. The type species, S. berthiaumi Merriam, 1974 is from strata now regarded as early Lochkovian upper Roberts Mountains Formation at Roberts Creek Mountain, Nevada (Pedder in Pedder and Murphy 1998). The genus has been thoroughly revised by Pedder (1976, 1985, in Pedder and Murphy 1998) and is characterized by a flaring calice in the parent corallite, from which numerous offsets generally arise, often supported by talons, in some cases forming fasciculate coralla. Septa are short and may be acanthine in the lower part of a corallite, but in the expanded calice tend to form low, broad, laterally contiguous ridges. Dissepiments are absent and the tabulae are complete and simple as in Aphyllum. These features have been illustrated best by Merriam (1974, pl. 3, figs 6-20) in the type species, and Pedder (1985, pl. 70.1, figs 2-7, 9, 11-23) in S. julli Pedder. Overall, Stylopleura can be distinguished from Aphyllum by its corallum and corallite growth forms and partial development of acanthine septa only in early growth stages.

In addition to the type species, the following are assigned to *Aphyllum*.

Madrepora flexuosa Linnaeus, 1745. "Silurian, Gotland". Lindström (1896, p. 632) stated original material (now lost) was probably from strata at Lickershamn, Gotland, which are likely to be early Sheinwoodian Upper Visby Formation (data in Laufeld 1974). Lang and Smith (1927) illustrated sections of material from Sheinwoodian "Wenlock Shale", Malvern, which they regarded as conspecific with Linnaeus' form. Type species of *Holacantia* Sytova.

- *Eridophyllum? rugosum* Edwards and Haime, 1851. "Upper Silurian, Gotland". Lectotype selected by Smith and Lang (1927) and figured in thin section for first time. Type species of *Rhabdacanthia* Ivanovskiy.
- Acanthodes tubulus Dybowski, 1873a. Tõrevere Member, Ärina Formation, lower Porkuni Regional Stage, early Hirnantian, Porkuni, northern Estonia (data in Mõtus and Hints 2007). Requires restudy.
- *Tryplasma lonsdalei* Etheridge, 1890. Hume Limestone Member, Silverdale Formation (Strusz et al. 1988), late Gorstian, Hattons Corner, Yass River, Yass Basin, southern New South Wales. Revised and lectotype selected by Hill (1940).
- Tryplasma lonsdalei var. scalariforme Etheridge, 1907. Silurian, New South Wales. Nine localities listed, but type specimen and locality not yet selected (see discussion by Hill 1940. p. 406). Hill regarded it as a possible synonym of Aphyllum lonsdalei (as Tryplasma).
- *Tryplasma lonsdalei* var. *minor* Etheridge, 1907. "Shale below limestone", Gorstian, Yass River, Yass Basin, southern New South Wales. Revised by Hill (1940), who selected a lectotype and regarded it as synonymous with *Aphyllum lonsdalei* (as *Tryplasma*).
- Tryplasma delicatulum Etheridge, 1907. Barrandella Shale Member (Brown 1941, table B), Silverdale Formation, late Gorstian, Yass River, Yass Basin, southern New South Wales. Revised and lectotype selected by Hill (1940). Regarded as synonym of *Aphyllum flexuosum* (as *Holacantia*) by Ivanovskiy (1969). Lectotype re-illustrated herein (Figs 15A, C).
- Pholidophyllum fasciculare Soshkina, 1937. Ludlow (?) (Ivanovskiy and Shurygina, 1975), Nyazepetrovsky area, western slopes of central Urals. Revised by Ivanovskiy and Shurygina (1975), who illustrated holotype photographically for first time, and regarded it as probably synonymous with Aphyllum rugosum (as Rhabdacanthia).
- Tryplasma japonicum and T. higutizawaense of Sugiyama (1940). Kawauchi Formation,

Wenlock–Ludlow (Kato et al. 1980), Kitakami Mountains, northeastern Japan. Illustrations inadequate.

- Yabeia salmoni Hill, 1942. Burdekin Formation, early Givetian, Burdekin Basin, northeast Queensland. Revised by Zhen and Jell (1996), who assigned it to Aphyllum.
- Pholidophyllum subhedstroemi Bul'vanker, 1952. Malinivtsy Group, Gorstian-mid Ludfordian (Jarochowska et al. 2016), Dneister River area, Podolia, Ukraine. Regarded as synonymous with Aphyllum flexuosum (as Holacantia) by Ivanovskiy (1969).
- *Tryplasma fascicularium* Oliver, 1960. Coeymans Formation, early Lochkovian (Denckler and Harris 1998), Mosquito Point, central New York.
- *Tryplasma lonsdalei sibiricum* Zheltonogova, 1961. Baskuskan Formation, late Telychian (Yolkin et al. 2003), Baskuskan River area, Salair.
- *Tryplasma crassiseptatum* and *T. (Stortophyllum) pustulosum* of Shurygina (1968). Lower Petropavlovsk Suite (= Severoural'sk Horizon, Shurygina et al. 1981), Přídolí, Lobva River, eastern slopes of central Urals.
- *Tryplasma concavatabulatum* Shurygina, 1968. Stratigraphy probably as above, Nizhniy Targil, eastern slopes of central Urals. Ivanovskiy (1969) included *T. crassiseptatum* Shurygina as synonym.
- *Tryplasma pakshifiense* Lavrusevich, 1971a. "Eifelian", Pakshif ravine, northern slopes of Zeravshan Range, Tajikistan.
- Rhabdacanthia rugosa sogdiana Lavrusevich, 1972. "Neomphyma originatum beds" Bursykhirman Horizon (data in Lavrusevich 1971d), early Lochkovian (Talent et al. 2001), Karasu River, Zeravshan-Gissar Mountans, Tajikistan.
- Soshkinelina magna Goryanov in Goryanov and Lavrusevich, 1972. "Lower Devonian", Yauruntuz Mountains, Alai Range, Kyrgyzstan.
- *Tryplasma minimum* Zhavoronkova in Tyasheva and Zhavoronkova, 1972. Upper Siyak Horizon, mid Lochkovian (Talent et al. 2001), Irgizly River, western slopes of southern Urals.
- Tryplasma newfarmeri Merriam, 1974. Unit 3, Roberts Mountains Formation, "Silurian coral zone C", Přídolí (Johnson and Oliver 1977), Roberts Creek Mountain, Great Basin, Nevada.
- *Tryplasma concavotabulatum* Cao, 1975. Ningqiang Formation, mid Telychian (Rong et al. 2012), Nanzheng, southwestern Shaanxi. Requires clearer illustration.
- Rhabdacanthia grandis Ivanovskiy and Shurygina, 1975. Isa Horizon, early Ludlow (Beznosova

1996), Vyya River, eastern slopes of central Urals. New name for *Stortophyllum* aff. *concavum* Wedekind of Soshkina (1937).

- Aphyllum multiseptatum Huang in Kong and Huang, 1978. Lower Shihniulan Formation, late Aeronian (Wang et al. 2019), Meitan, Guizhou.
- Aphyllum shiqianense Huang in Kong and Huang, 1978. Stratigraphy as above, Shiqian, Guizhou.
- Aphyllum siluriense He and Huang in Kong and Huang, 1978. Stratigraphy as above, Zheng'an, Guizhou.
- *Tryplasma guangyuanense* He, 1978. Ningqiang Formation, mid Telychian, Guangyuan, Sichuan.
- *Tryplasma shamotanense* He, 1978. Takuan Formation, Aeronian–early Telychian (Zhang et al. 2014), Yanjin, northeastern Yunnan.
- *Tryplasma hinganlingense* Guo, 1980. Wunur Formation, Emsian (data in Yu and Jell 1990), Wunur, Heilongjiang.
- Columnolasma gansuense Cao in Cao and Lin, 1982. Lower Yanglugou Formation, Přídolí (Cao and Ouyang 1987), Diebu, Gansu. Lacks scattered dissepiments of *Columnolasma* Pavlova, and appears to have occasional short septal spines on walls and tabulae. Assigned to *Aphyllum* (as *Holacantia*) by Cao and Ouyang (1987).
- Holacantia robusta and H. suetenkoae of Sytova in Sytova and Ulitina (1983). Khanaindolon Beds, Ludlow (Ulitina 2003), Mandal-Obo, southern Mongolia.
- Rhabdacanthia? inconspicua Sytova in Sytova and Ulitina, 1983. Kyzylchira Beds, late Aeronian (Sennikov et al. 2019c), Ara-Arga ravine, western Tuva.
- Rhabdacanthia? pachyacanthia Sytova in Sytova and Ulitina, 1983. Sukhebator Horizon, Ludlow– Přídolí, Barun-Urt, eastern Mongolia.
- *Tryplasma maoxianense* He, 1985. "Upper Miaoxian Group, late Silurian", Jiudingshan Mountains, Miaoxan County, Sichuan.
- Rhabdacanthia lailakaensis Lavrusevich, 1991. Lower Isfara Horizon, Přídolí, Isfara River, northern slopes of Turkestan Range, Tajikistan.
- "*Aphyllum*" sp. of Oliver et al. (1995). Silurian or Early Devonian, Irian Jaya.
- Aphyllum leptostylum Munson and Jell, 1999. Quinton Formation, Telychian, Graveyard Creek Subprovince, Broken River Province, northeast Queensland.
- Aphyllum tewoense He and Chen, 1999. Upper Lalong Formation, Aeronian, Tewo area, West Qinling Mountains, Gansu.
- Pycnostylus sp. of Schröder (2007). Kshtut Formation, Pragian, Shishkat area, Zeravshan

Range, Tajikistan. Stated to have holacanthine spines in peripheral stereozone.

- Aphyllum simplexum Blake, 2010. Craigilee Beds, Emsian, Yarrol Province, east central Queensland.
- Aphyllum sp. of He and Tang (2011). Sanqushan Formation, late Katian (Wang et al. 2014), Yushan, western Zhejiang.
- Aphyllum pachystele Munson and Jell, 2016. Jack Formation, late Homerian, Jack Hills Gorge, Broken River Province, northeast Queensland.
- Aphyllum sp. of Zhen and Fitzherbert (2021). Elura Limestone Member, Brookong Formation, early Lochkovian, Cobar area, central western New South Wales.
- Aphyllum ulahense McLean sp. nov. "Upper clastic member", Bagdad Formation, late Rhuddanian– early Aeronian, Ulah area, southwest of Orange, central western New South Wales.
- Aphyllum picketti McLean sp. nov. Bridge Creek Limestone Member, Bagdad Formation, late Rhuddanian–early Aeronian, Bridge Creek area, southwest of Orange, central western New South Wales.

Species below are regarded as possible representatives of *Aphyllum*.

- Tryplasma articulatum (Hisinger, 1837) of Lonsdale (1845). Probably late Silurian, Petropavlovsk (=Severoural'sk) area, eastern slopes of northern Urals. Ivanovskiy and Shurygina (1975) regarded it as probably Aphyllum concavotabulatum (Shurygina, 1968) (as Rhabdacanthia). Not Cyathophyllum articulatum of Hisinger (1837), which is neotype of Cyathophyllum articulatum Wahlenberg, 1821, type species of Entelophyllum Wedekind (see Smith and Tremberth 1929; Jell and Sutherland 1990). Lonsdale's form may have greater septal spine development than Aphyllum, and could be a holmophyllinid.
- Amplexus cingulatus Billings, 1862. La Vieille Formation (?), late Telychian–early Homerian (Norford 1997), L'Anse à la Barbe, Baie des Chaleurs, Québec. Probably fasciculate, although not proven. Sections of syntype figured herein (Figs 15B, D) and see comments below in remarks on A. picketti McLean sp. nov.
- Acanthodes borussica Meyer, 1881. Glacial drift, Baltic area. Said by Meyer to be solitary, but considered to be colonial by Ivanovskiy (1969), who assigned it with question to *Rhabdacanthia*. Regarded as synonymous with the solitary *Tryplasma loveni* (Edwards and Haime) by Różkowska (1946). Appears to be

a tryplasmatid or holmophyllinid, but currently indeterminate.

- Aphyllostylus gracilis Whiteaves, 1904. Lower Stonewall Formation, early Gamachian (Jin et al. 1997), Stonewall, southern Manitoba. First illustrated by Whiteaves (1906). See comments in generic discussion, above.
- *Tryplasma vermiforme* Etheridge, 1907. Garra Formation, mid Lochkovian, Walker's Creek area (near or at locality BN-2 of Strusz 1963, 1967), approximately 14 km south of Molong, central western New South Wales. Known only from type material. Strusz (1963) suggested apparently spinose septa could be oblique intersections of thin, laminar septa. Possibly a representative of pycnostylid *Pycnostylus* Whiteaves.
- Holacantia sp. of Flügel and Saleh (1970). Niur Formation, Wenlock (?)–Ludlow, Ozbak-kuh, eastern Iran. Inadequately known.
- Aphyllum suiyangense Huang in Kong and Huang, 1978. Lower Shihniulan Formation, late Aeronian. Suiyang, Guizhou. Septa not clearly acanthine and could be a *Pycnostylus*.

The following species are all excluded from *Aphyllum*. They comprise fasciculate forms that have been assigned in the past to *Tryplasma*, or are species previously included in genera regarded here as synonyms of *Aphyllum*.

- Amplexus (Coelophyllum) eurycalyx Weissermel, 1894. Glacial drift, Baltic area. Assigned to Tryplasma by Różkowska (1946), who noted presence of rhabdacanthine trabeculae. Regarded as a possible Rhabdacanthia by Ivanovskiy (1969). Has flaring calice with a few calical offsets and was assigned to the mucophyllid Stylopleura Merriam by Pedder (1985).
- *Tryplasma murrayi* Etheridge, 1899. Bell Point Formation, late Pragian, Waratah Bay, southern Victoria. Holotype sectioned by Pedder (1967), although not figured, and considered to be a cyathophyllid. Regarded as a new genus by Pedder (2007, Appendix C).
- Tryplasma congregationis Etheridge, 1907. Barrandella Shale Member (Brown 1941, table B), Silverdale Formation, late Gorstian, Derringullen Creek, Yass Basin, southern New South Wales. Revised and lectotype selected by Hill (1940), who noted thin, laminar amplexoid septa and assigned it to Pycnostylus Whiteaves.
- *Tryplasma dendroidea* Etheridge, 1907. Barrandella Shale Member (Brown 1941, table B), Silverdale Formation, late Gorstian, Barbers Creek, Yass

Basin, southern New South Wales. Comments as for *T. congregationis*, above.

- *Tryplasma liliiforme* Etheridge, 1907. Stratigraphy and locality as for *T. dendroidea*, above. Revised and lectotype selected by Hill (1940), who included it in *Mucophyllum* Etheridge. Reassigned to mucophyllid *Stylopleura* Merriam by Pedder (1976).
- Holacantia gibbosa Sytova in Sytova and Ulitina. 1966. Kokbaytal Horizon (Sytova and Ulitina 1983), mid Lochkovian (Talent et al. 2001), Kara-Uzek area, southern Karaganda Basin, Kazakhstan. Solitary form, possibly representative of *Tryplasma*.
- Holacantia variaseptata Pavlova, 1973. Dal'yan Horizon, Ludlow, Mount Almala, Turkestan Range, Uzbekistan. Solitary form, included here in *Tryplasma*.
- Rhabdacanthia aculeata Ivanovskiy and Shurygina, 1975. Elka Horizon, late Wenlock, Elka village, eastern slopes of central Urals. Based in part on *Stortophyllum* aff. *simplex* Wedekind of Soshkina (1937). Has long rhabdacanthine septal spines in well-defined rows and is probably representative of holmophyllinid *Nipponophyllum* Sugiyama.
- *Tryplasma subflexuosum* Cao in Cao and Lin, 1982. Lower Yanglugou Formation, Přídolí, Diebu, Gansu. Has long septal spines and may be a holmophyllinid.
- Holacanthia insueta Cherepnina, 1987. "Maragda Suite", regarded as Přídolí by Cherepnina. Unit was divided from upper Kuimov Suite and overlain by Cherny Anui Suite (summary in Cherepnina and Krasnov 1982), but apparently not recognized by more recent workers, with Ludlow Kuimov directly overlain by Přídolí Cherny Anui (e.g Sennikov et al. 2008). If "Maragda" fauna is truly Přídolí, then it should presumably be assigned to Cherny Anui Suite. Apparently cerioid and probably representative of *Maikottia* Lavrusevich.

Aphyllum ulahense McLean sp. nov. Figs 12–14

Derivation of name

After Ulah property, which includes the type locality.

Type material

Holotype, AM F.156027 (thin sections AM FT.15572, 15573). Paratypes, AM F.156009 (thin section AM FT.15574); AM F.156010 (thin sections AM FT.15575, 15576); AM F.156011 (thin sections

AM FT.15577, 15578); AM F.156012 (thin sections AM FT.15579–15583); AM F.156013 (thin sections AM FT.15584–15586); AM F.156014 (thin sections AM FT.15587–15591). "Upper clastic member", Bagdad Formation, late Rhuddanian–early Aeronian, western tributary of Panuara Rivulet, Ulah area, approximately 34 km southwest of Orange, central western New South Wales.

Diagnosis

Aphyllum with phaceloid to dendroid corallum and calical, parricidal increase. Corallite diameter generally 2.5–3.0 mm. Peripheral stereozone highly variable in width, although narrow overall, containing stout septal spines mostly in lateral contact. Spines generally extending slightly into tabularium, although may be confined to stereozone, and rarely separable into two orders. Tabulae well-spaced, mainly flat and complete, but locally supplemented with large, peripheral, inosculating tabellae.

Description

Corallum phaceloid to dendroid, lacking connecting tubules. Increase is calical and parricidal, generally with four offsets developed.

Corallite diameter ranges from 2.5–3.5 mm, most commonly 2.5–3.0 mm. Peripheral stereozone varies greatly in width, even in the one corallum (e. g. holotype, Figs 12A, B), 0.1–0.4 mm. Septal spines composed of stout trabeculae (Figs 14C–E), with original microstructure obscured by recrystallization. Spines may be confined to stereozone where it is thinner, but otherwise extend slightly into tabularium. Major and minor septa generally not recognizable, and total number of septa, although difficult to determine, appears to be approximately 25–28. Septal spines not observed on tabulae.

Tabulae mainly widely spaced, 5–8 in 5 mm, mostly complete and flat to weakly arched. They may be rarely incomplete and also irregularly supplemented by large, globose tabellae peripherally, which inosculate onto underlying tabula.

Remarks

Aphyllum ulahense has smaller corallites than most representatives of the genus, and few species show much other similarity. Amongst those that do, closest resemblance appears to lie with *A. leptostylum* Munson and Jell, 1999, from the slightly younger Telychian Quinton Formation of north Queensland. Its corallites are generally only marginally larger (3–4 mm), and it has mostly similar stereozone width, as well as comparable complete tabulae with occasional peripheral tabellae (Munson and Jell 1999, figs 5A– E; 6A–C). It differs from *A. ulahense* primarily by having more slender and abundant septal spines set in lamellar stereome in the stereozone, as compared with the packed, stout spines of the latter. In addition, *A. leptostylum* has occasional connecting tubules, not observed in *A. ulahense*.

Aphyllum concavotabulatum (Cao, 1975), from the mid Telychian Ningqiang Formation of Shaanxi, is a further early Silurian form with small (although slightly larger) corallites, and it also shows calical, quadripartite increase. However, the septal spines extend further into the tabularium and are more readily separated into two orders than in *A. ulahense*. In addition, the tabulae are more closely spaced and more concave in *A. concavotabulatum*, and peripheral tabellae seem to be lacking, although the illustrations are inadequate (Cao 1975, pl. 43, figs 1a, b).

A further Australian species, *A. delicatulum* (Etheridge, 1907), has some general similarities to *A. ulahense*, although it is significantly younger, being from the late Gorstian Barrandella Shale Member, Silverdale Formation, of the Yass area of southern New South Wales. It has comparably small corallites, and similar development of well-spaced, flat to weakly arched tabulae with a few incomplete forms and peripheral tabellae. Major differences lie in the development of short septal spines on some tabulae in *A. delicatulum* and presence of connecting tubules (lectotype figured herein, Figs 15A, C).

Individual corallites of *Gephyrelasma stevensi* sp. nov. lacking dissepiments (see above) resemble those of *A. ulahense*. However, dissepiments are absent in all corallites of the latter, whereas corallites with intermittent dissepiments are present in all colonies of *G. stevensi*.

Aphyllum picketti McLean sp. nov. Fig. 16

Derivation of name

In honour of John W. Pickett, who collected the type material.

Type material

Holotype, MMF 31303. Paratypes, MMF 31302, 31304, 31308. Bridge Creek Limestone Member, Bagdad Formation, late Rhuddanian–early Aeronian, Bridge Creek area, approximately 25 km southwest of Orange, central western New South Wales.

Diagnosis

Aphyllum with probable calical, parricidal increase and corallite diameter ranging from 11–15 mm. Very narrow peripheral stereozone, composed

of closely spaced septal spines, which extend slightly beyond stereozone with 48–56 stout, undifferentiated septa. Tabulae very widely spaced (1–5 in 5 mm), flat to occasionally weakly concave or convex, less commonly incomplete with rare peripheral tabellae.

Description

Corallum is apparently fasciculate and lacks connecting tubules. One calical offset seen in only corallite showing mode of increase (holotype, Fig. 16G), and rejuvenescence is also present. Best preserved corallites have pronounced septal furrows on epitheca exterior.

Corallite diameter ranges from 11–15 mm in limited available material. Very narrow peripheral stereozone is developed and contains closely spaced septal spines extending slightly beyond stereozone at low to moderate angle from wall (Fig. 16D). A few short spines may rarely be seen on tabulae adjacent to stereozone. Despite poor preservation, approximately 48–56 stout septa can be recognized, without clear differentiation into major and minor.

Tabulae are variably, but generally very widely spaced, 1–5 in 5 mm. They are mostly complete, flat to weakly concave or convex. Incomplete tabulae occur occasionally, and there are rare, large, globose peripheral tabellae.

Remarks

Material of this species is unfortunately very limited, and detail of the stereozone and septa is partly obscured by recrystallization and silicification, so that the original trabecular microstructure is not preserved. However, despite the inadequacies of the material, it is a distinctive form and only a few species show much similarity.

Closest resemblance may lie with an even less well understood species, Amplexus cingulatus Billings, 1862, which is regarded here as most probably a representative of Aphyllum if it is based on a sectioned syntype figured herein and discussed below. The type material was probably derived from the late Telychian-early Homerian La Vieille Formation at l'Anse à la Barbe, Baie des Chaleurs, Québec and was collected by Sir William Logan in 1843. The syntypes of this form were examined in the collections of the Geological Survey of Canada in Ottawa, and comprise a small slab with numerous broken corallites on the surface (GSC 3038c), as well as various small fragments. One of these isolated corallites has been sectioned and polished longitudinally and transversely, the longitudinal halves numbered GSC 3038 and 3038a, and the transverse piece GSC 3038b. One of the longitudinally sectioned halves was diagrammatically illustrated by Lambe (1901, pl. 10, fig. 3), with the transverse portion in his pl. 10, fig. 3a. Also present in the collection are a subsequently prepared transverse and longitudinal thin section of another corallite fragment, presumably from GSC 3038c, although the offcuts from this sectioned specimen are not preserved. Those two thin sections are illustrated here for the first time (Figs 15B, D) and display some close similarities to A. picketti in corallite size, as well as stereozone and tabular development, but are distinctly different to the sectioned corallite figured by Lambe, which has long septa (? spines) and unusual closely spaced tabulae, which are peripherally strongly arched and axially concave. It is clear that more than one species or even genus is present in the Billings syntypes and further sectioning is needed to define the species and select a lectotype. Until such revision is undertaken, Billings' species name cannot be meaningfully used and we prefer to regard our Bridge Creek form as a new species. However, it should be recognized that Aphyllum picketti may ultimately prove to be a junior synonym of A. cingulatum (Billings) if that species is defined by the morphology of the syntype fragment figured herein and if that fragment or another of conspecific morphology is formally designated as lectotype. As noted above, Lambe's figured syntype material is not conspecific, and if that material should be chosen as lectotype, an alternative name for the Billings material figured here will be needed or it could perhaps be assigned to A. picketti. Such decisions are beyond the scope of the current study.

Two Chinese early Silurian species also bear resemblances to A. picketti. Aphyllum shamotanense (He, 1978), from the Aeronian-early Telychian Takuan Formation of northeastern Yunnan, has similar corallite diameters, narrow stereozone and widely spaced tabulae, but is distinguished by having fewer septa, which are composed of longer and more slender septal spines (He 1978, pl. 83, figs 3a, b). Aphyllum siluriense He and Huang in Kong and Huang, 1978 occurs in the late Aeronian lower Shihniulan Formation of Guizhou, and also has comparable corallite diameters and narrow stereozone to A. picketti, as well as only slightly greater number of short, stout septa. It differs by having largely complete tabulae, which are more closely spaced and may be arched upward (Kong and Huang 1978, pl. 22, figs 1a, b).

Family KODONOPHYLLIDAE Wedekind, 1927 Genus *Cyatholasma* Ivanovskiy, 1961

Type species

Cyatholasma perforatum Ivanovskiy, 1961 = Brachyelasma altaicum Cherepnina, 1960.Veber Horizon (?), probably Katian, Mount Orlinaya, Salair Ridge, southwestern Siberia.

Diagnosis

Solitary kodonophyllid. Broad peripheral stereozone in late growth stages, containing coarse, possibly rhabdacanthine trabeculae. Minor septa mainly confined to stereozone, major septa disrupted axially and forming variably developed, open axial structure of entwined septal lobes and lamellae. Tabulae in arched series, locally biform in rare cases of minor septa extending axially beyond marginarium. Dissepiments absent.

Discussion

The type species, Cyatholasma perforatum Ivanovskiy, 1961, is a junior synonym of Brachyelasma altaicum Cherpnina, 1960, as noted by Ivanovskiy (1965, p. 77; 1967, p. 122). The type material of the latter was derived from the Katian Tekhten' Formation (data in Sennikov et al. 2019a) in the Elanda-Chakyr rivers area of northwestern Gorniy Altai, southwestern Siberia, and the species is apparently common in that region (Sennikov et al. 2019a). Ivanovskiy (1961, 1965) originally assigned Cyatholasma to the family Calostylidae Roemer, 1883 on the assumption that the axially interrupted septa were perforate. However, the septa in that area are actually isolated septal lobes and lamellae, as pointed out by Weyer (1973, p. 28), and do not have the structure of the characteristic perforate septa of the Calostylidae (e. g. Weyer 1973, pls 1, 2).

Ivanovskiy (1967, p. 120; 1970a, p. 121) subsequently regarded Cyatholasma as synonymous with the streptelasmatid Grewingkia Dybowski, 1873a. The Streptelasmatidae Nicholson in Nicholson and Lydekker, 1889 and many of its constituent genera were considered in some detail by McLean and Copper (2013). Some streptelasmatid genera develop a significant axial structure of variably entwined septal lobes and lamellae and this is seen most notably in Grewingkia, clearly illustrated in the type species, G. buceros (Eichwald, 1856), by Kaljo (1961, pl. 1) and Neuman (1969, figs 28, 29). The axial structure of Grewingkia is very similar to that of the holotype of Cyatholasma perforatum (Ivanovskiy 1961, pl. 15, fig. 1a). Weyer (1973, p. 28) stated that an axial structure was absent in the paratype of that

species (see Ivanovskiy 1961, pl. 15, fig. 2) and in the holotype of *Brachyelasma altaicum* Cherepnina, 1960 (Cherepnina 1960, pl. O-10, fig. 3b). However, although more weakly developed, discrete axial septal elements can certainly be seen in those two specimens.

The presence of a pronounced axial structure of twisted septal lobes and lamellae in two new species from the Llandovery of New South Wales led McLean (1974c) to assign them to *Grewingkia*. One of the species, *G. parva*, is appropriately referred to that genus, but the other, *G. neumani*, has a broad peripheral stereozone, with general resemblances to *Cyatholasma altaicum* being noted by McLean (1974c, p. 47). Restudy of the type material of *neumani* as well as analysis of significant additional material of that species (see below) now suggest that earlier assignment of both *altaicum* and *neumani* to *Grewingkia* (and the Streptelasmatidae) needs to be reassessed.

Weyer (1973, p. 28) was the first to note that Cyatholasma perforatum has biform tabulae (term introduced by Weyer 1972), as seen in Ivanovskiy (1961, pl. 15, fig. 2), where the minor septa extend axially beyond the peripheral stereozone, and these are not known in Grewingkia. In "G". neumani, the minor septa are almost always confined to the marginarium, but in rare instances, the minor septa may extend a short distance into the tabularium, with associated biform tabulae (Fig. 18C). Perhaps more significantly, a further distinction from Grewingkia and the streptelasmatids lies in the nature of the trabeculae in the marginarium of neumani, which are composed of particularly coarse fibres diverging from a central axis in transverse section (McLean 1974c, pl. 2, fig. 1; Fig. 18B, herein). In longitudinal section, the trabeculae can be seen partially as isolated dark spots as well as upwardly inclined rods, suggesting that they may be rhabdacanths (Fig. 18G). This is in contrast to the relatively fine, diverging fibres of the streptelasmatids (e. g. Elias 1983, fig. 7; McLean and Copper 2013, pl. 5, fig. 6). Consequently, neither Cyatholasma altaicum nor Grewingkia neumani should be assigned to Grewingkia or the Streptelasmatidae as a whole.

The Kodonophyllidae Wedekind, 1927 and *Kodonophyllum* Wedekind, 1927 itself were most recently considered by McLean and Copper (2013). As discussed there, *Kodonophyllum* is characterized by a broad peripheral stereozone composed of coarse, possibly rhabdacanthine trabeculae, as illustrated in line drawings of the type species, *Streptelasma milne-edwardsi* Dybowski, 1873b =

Madrepora truncata Linnaeus, 1758, by Dybowski (1873b, pl. 13, figs 9, 10, 12), and photographically by Smith and Tremberth (1929, pl. 8, figs 6, 7a, 7b). Further illustrations of septal microstructure in Kodonophyllum have been given by McLean and Copper (2013, pl. 38, figs 13, 14), for their new species K. boltoni. The overall development of the marginarium in Kodonophyllum is comparable to that of Cyatholasma altaicum and "Grewingkia" neumani, and while the nature of the trabeculae in the Russian species is unclear in its illustrations, septal microstructure in Kodonophyllum certainly does appear similar to that in neumani. Other similarities to Kodonophyllum lie in the general character of the tabulae and lack of dissepiments. While Kodonophyllum does not develop as prominent an axial structure as neumani and some of the material of altaicum (see above), and consequently is not a suitable genus to accommodate them, it does seem appropriate to regard them as kodonophyllids.

At present, only *Cyatholasma altaicum* is definitely included in the genus, while "*Grewingkia*" *neumani* is most probably a representative. *Grewingkia xinjiangensis* Cai, 1981, which is derived from the late Katian–early Hirnantian (?) Bulongguor Formation (data in Zhou et al. 1996), Bulongguor, western Junggar, Xinjiang, has a similar broad stereozone to *Cyatholasma altaicum* and "*Grewingkia*" *neumani*, as noted by Cai (1981, p. 24; translation provided by Yong Yi Zhen), and a similar, although apparently smaller axial structure (Cai 1981, pl. 14, figs 8a, b). Unfortunately, its septal microstructure and variability are unknown, but it is certainly a possible representative of *Cyatholasma*.

Cyatholasma? neumani (McLean, 1974c) Figs 17, 18

Synonymy

- *Grewingkia neumani* McLean, 1974c, p. 46, pl. 1, figs 11, 12; pl. 2, fig. 1; text-fig. 3
- Grewingkia neumani McLean; McLean 1977a, p. 104
- Grewingkia neumani McLean; Jenkins 1978, p. 113
- Grewingkia neumani McLean; Cai 1981, p. 24
- Grewingkia neumani McLean; Jenkins 1986, fig. 33
- Grewingkia neumani McLean; Strusz 1989, pl. 1
- Grewingkia neumani McLean; Strusz 1996, p. 16, fig. 3
- Grewingkia neumani McLean; Strusz and Munson 1997, p. 318
- Grewingkia neumani McLean; Pogson and Watkins 1998, p. 375

Grewingkia neumani McLean; Munson and Jell 1999, p. 40

Grewingkia neumani McLean; Pickett 2011, p. 81

Type material

Holotype, SUP 20115 (thin sections AM FT.7242–7244). Paratypes, SUP 45156 (thin sections AM FT.11597–11599); SUP 45157 (thin section AM FT.7245). Bioclastic lens in "upper clastic member", Bagdad Formation, late Rhuddanian–basal Aeronian, west side of "Trevenas Creek", north flowing tributary of Cobblers Creek, approximately 33 km southwest of Orange, central western New South Wales.

Additional material

AM F.156015 (thin sections AM FT.15592– 15595); AM F.156016 (thin section AM FT.15596); specimen (not preserved) with thin sections AM FT.15597–15599; AM F.156017 (thin sections AM FT.15600, 15601); AM F.156018 (thin sections AM FT.15602, 15603); AM F.156019 (thin sections AM FT.15604, 15605); specimen (not preserved) with thin sections AM FT.15606–15608); AM F.156020 (thin sections AM FT.15601); AM F.156020 (thin section AM FT.15611). "Upper clastic member", Bagdad Formation, late Rhuddanian–early Aeronian, western tributary of Panuara Rivulet, Ulah area, approximately 34 km southwest of Orange, central western New South Wales.

Diagnosis

Trochoid to subcylindrical corallites, with corallite diameter at base of deep calice of 13 to approximately 22 mm. Major septa 30–45 in number, extending from broad peripheral stereozone to corallite axis, where they form large, open axial structure of coarse, entwined septal lobes and lamellae. Minor septa mainly confined to peripheral stereozone, in rare cases extending slightly beyond stereozone, where they may be associated with biform tabulae. Microstructure of dilated septa in stereozone of coarse, possibly rhabdacanthine trabeculae. Tabulae incomplete, in well-spaced, arched series, occasionally with concave gutters. Dissepiments absent.

Description

The type material was described in some detail by McLean (1974c), and is supplemented here largely on the basis of newly collected material from the Ulah area. All available material is fragmentary, but generally quite well preserved internally. The holotype (McLean 1974c, pl. 1, figs 11, 12; pl. 2, fig. 1; Figs 17A, B; 18B, herein) is by far the largest known specimen, with a diameter at base of calice of approximately 28 mm. That measurement in the other available material (13 specimens, including the two paratypes) ranges from 13–22 mm, with most common values of 13–17 mm. Lower parts of the corallites tend to be mostly subcylindrical, but above the base of the calice they generally rapidly expand to trochoid.

The broad peripheral stereozone is characteristic of the species and also tends to increase greatly in width above the base of the calice. It is composed of tightly packed, dilated septa, with a distinctly coarse microstructure of rods diverging from a central axis (McLean 1974c, pl. 2, fig. 1; Fig. 18B, herein). In longitudinal section, ends of the rods that are out of the plane of section appear as dark dots in well-preserved material (Fig. 18G), and strongly suggest an original rhabdacanthine microstructure. The holotype has approximately 45 major septa, while they range in number from 30-38 in the other specimens. The major septa consistently extend beyond the stereozone to form a broad axial structure of generally moderately dilated, entwined septal lamellae and lobes. Minor septa are mostly confined to the stereozone, but in some cases may extend slightly into the tabularium, where they may rarely be seen to be associated with biform tabulae (Fig. 18C).

Tabulae are incomplete and form strongly convex, well-spaced series, in some cases with concave gutters.

Remarks

The strong similarities between "Grewingkia" neumani and Cyatholasma altaicum (Cherepnina, 1960) were noted by McLean (1974c), although at that time the latter was also assigned to the streptelasmatid Grewingkia. Reasons for now separating them from that genus and family and referring both taxa to the Kodonophyllidae are discussed above. Through the kindness of Raliya Khabibulina (Novosibirsk) and Valeriya Moskalenko (Tomsk), photographs of thin sections of the holotype of C. altaicum were obtained, but the specimen is extensively recrystallized and the original microstructure is not preserved. A diagrammatic illustration of the microstructure of the stereozone in the holotype of synonym C. perforatum Ivanovskiy, 1961 certainly resembles that in the stereozone of C.? neumani (Ivanovskiy, 1967, fig. 3d), but unfortunately that material could not be traced to confirm this with photographic illustrations. It is preferred at present to only provisionally refer the Australian form to Cyatholasma., with formal assignment waiting until the trabecular microstructure of C. altaicum can be confirmed by study of better-

preserved material and photographic illustration of the microstructure of topotypes (preferably) of C. perforatum can be obtained. Besides the Katian type occurrence of C. altaicum (and synonym C. perforatum) in southwestern Siberia (see above), the species has also been recognized in other Katian strata, including the Typyl Horizon, Rassokha River, northern Urals (Shurygina 1973, p. 142, pl. 26, figs 1-3), Tsetsey Beds, Kadzhimy-Nuru Mountains, Mongolian Altai (Ulitina 2003, p. 63, pl. 6, figs 2, 3), and Chashmonkolon Beds of the Zeravshan Range, Uzbekistan (Erina 2007, p. 37, pl. 36, figs 7, 8), and is clearly a widespread Late Ordovician species. As such it is significantly older than the New South Wales early Llandovery species, and is also morphologically separated by having a generally broad flattening of the arched axial region of the tabular series and a less consistently developed axial structure.

Genus Vitiliphyllum McLean gen. nov.

Derivation of name

Latin, *vitilis*, interwoven, referring to the twisted axial septal lamellae and lobes characteristic of the genus.

Type species

Vitiliphyllum jenkinsi sp. nov. "Upper clastic member", Bagdad Formation, late Rhuddanian– early Aeronian, western tributary of Panuara Rivulet, Ulah area, approximately 34 km southwest of Orange, central western New South Wales.

Diagnosis

Fasciculate kodonophyllid. Moderately wide to very broad peripheral stereozone of dilated septa. Minor septa mostly confined to stereozone, occasionally extending slightly into tabularium. Major septa thin within tabularium, breaking down axially to form broad, open, irregularly developed axial structure of twisted septal lamellae and lobes. Tabulae in broadly arched series. Dissepiments absent.

Discussion

Closest resemblance to the new genus is perhaps seen in the older *Sogdianophyllum* Lavrusevich, 1971b, the type species of which is *S. karasuense* Lavrusevich, 1971b, from the late Katian (Kim et al. 2007) lower Archalyk Beds, Karasu River, Zeravshan Range, southeastern Uzbekistan. Some corallites of this fasciculate form have a similar broad peripheral stereozone and arched tabulae to *Vitiliphyllum*, but apparently only a few isolated septal lobes in the axial region (Lavrusevich 1971b, pl. 1, figs 2a–v; Erina 1978, pl. 9, figs 1a, b; Lavrusevich 1991, pl. 59, figs 2a–v), with clearest illustration by Erina (2007, pl. 38, figs 8–15). The major septa of *S. karasuense* are also significantly more dilated in the tabularium than are those of *Vitiliphyllum*, although that could perhaps be considered a specific rather than generic distinction.

Parabrachyelasma Cherepnina, 1960 is another Late Ordovician form with some resemblances to Vitiliphyllum. The holotype of the type species, P. lebediense Cherepnina, 1960, was probably derived from the late Katian upper Gur'yankova Formation (data in Sennikov et al. 2019a) on the Lebed' River, northeastern Gorniy Altai, southwestern Siberia. It is also fasciculate and was considered to be a synonym of the stauriid Palaeophyllum Billings, 1858 by Ivanovskiy (1963, 1965, 1969) and Webby (1972). However, the holotype of P. lebediense develops a weak axial structure of a few isolated septal lobes and lamellae, not seen in Palaeophyllum (Cherepnina 1960, pl. O-10, figs 4a-v; Ivanovskiy 1969, pl. 10, fig. 1a; other sections illustrated by Cherepnina and Ivanovskiv are from a separate specimen from Gornaya Shoriya). As noted by Hill (1981, p. F158), Parabrachyelasma is probably a streptelasmatid. Vitiliphyllum is primarily distinguished by its more pronounced axial structure and broader peripheral stereozone.

Closer in age to *Vitiliphyllum* is *Plektelasma* Munson and Jell, 1999, with type species *P. eurybykane* Munson and Jell, 1999, from the mid Telychian lower Quinton Formation at Gray Creek, Graveyard Creek Subprovince, Broken River Province, north Queensland. While generally similar to *Vitiliphyllum*, it is more weakly colonial, with large, trochoid corallites, a narrower peripheral stereozone, and a more weakly developed, although otherwise similar axial structure (Munson and Jell 1999, figs 23A–M, 24A–C). Most obvious distinction from *Vitiliphyllum* lies in the pronounced carinae and probable vepreculae on the septa of *Plektelasma*.

The younger *Circophyllum* Lang and Smith, 1939 also needs to be considered in relation to the new genus. The type species, *Rhysodes samsugnensis* Smith and Tremberth, 1929, was derived from strata now assigned to the late Sheinwoodian–early Homerian Slite Group (data in Laufeld 1974) at Samsugns, Gotland. It was regarded as a fasciculate equivalent of the dominantly solitary *Kodonophyllum* Wedekind, 1927 by McLean (1977b, p. 29) and also assigned to the Kodonophyllidae by Hill (1981, p. *F*173). It may develop a broad peripheral stereozone as in *Vitiliphyllum*, together with similar thinner

major septa in the tabularium, but the axial ends of the major septa tend to become entwined with the very strongly arched axial portions of the tabulae, rather than having the open structure of isolated and twisted septal lamellae characteristic of *Vitiliphyllum* (Smith and Tremberth 1929, pl. 7, figs 8–11; Hill 1981, figs 99.3*a*, *b*).

The broad, open axial structure of *Vitiliphyllum* is strongly reminiscent of that in *Cyatholasma? neumani*, revised above, with which it occurs at the type locality for the type species, *V. jenkinsi*. The septal microstructure of the latter is generally obscured by recrystallization, although in one instance traces of coarse trabeculae comparable to those of *neumani* can be seen (see below). Other internal features of the two species are also so similar that it seems likely that *Vitiliphyllum* can be considered as a fasciculate equivalent of the solitary *Cyatholasma* (in at least the latter's provisional interpretation adopted here). On that basis, *Vitiliphyllum* is also assigned here to the family Kodonophyllidae Wedekind.

Vitiliphyllum jenkinsi McLean sp. nov. Figs 19–21

Derivation of name

In honour of Christopher J. Jenkins, who provided the first detailed synthesis of the complex Silurian stratigraphy and facies of the Bridge Creek– Angullong area in central western New South Wales, including much of the currently used stratigraphic terminology.

Type material

Holotype, AM F.156028 (thin sections AM FT.15612–15614). Paratypes, specimen (not preserved) with thin section AM FT.15615; AM F.156022 (thin sections AM FT.15616–15618); AM F.156023 (thin section AM FT.15619); AM F.156008 (thin sections AM FT.15570.002, 15571.002; note that this specimen also has separately numbered sections of a paratype of *Gephyrelasma stevensi* sp. nov., see above); AM F.156024 (thin sections AM FT.15620–15623). "Upper clastic member", Bagdad Formation, late Rhuddanian–early Aeronian, western tributary of Panuara Rivulet, Ulah area, approximately 34 km southwest of Orange, central western New South Wales.

Diagnosis

Dendroid to phaceloid species of *Vitiliphyllum* with closely spaced corallites of 6.0–8.5 mm diameter. Major septa 24–26 in number, extending from wide peripheral stereozone to form broad, open axial structure of slender, loosely entwined septal lamellae

and lobes. Minor septa rarely extend slightly beyond peripheral stereozone. Coarse, irregular trabeculae may be rarely visible in largely recrystallized septa of stereozone. Tabulae incomplete, closely spaced, in broadly arched series.

Description

All available material is fragmentary and it is difficult to obtain an overall impression of corallum size and growth patterns. Corallum is dendroid to phaceloid, with generally closely spaced corallites. Increase is calical and parricidal where clearly apparent, with up to six offsets from the rim of the parent calice. There also seem to be some possible, although unconfirmed lateral offsets. Corallite diameter near base of calice ranges from 6.0–8.5 mm.

Peripheral stereozone is pronounced and may extend up to 0.5 of corallite radius, although is generally a little less. It is composed of tightly packed, dilated major and minor septa. Original microstructure is typically completely obscured by recrystallization, but in one instance traces of irregular, coarse trabeculae rather similar to those in Cvatholasma? neumani (see above) may be seen (Fig. 20F). Major septa vary from 24-26 in number in mature corallites, and rapidly thin axially from stereozone to form broad axial structure of slender, loosely entwined septal lamellae and lobes. Minor septa are mainly confined to peripheral stereozone, but may rarely extend slightly into tabularium. Tabulae are incomplete, forming broadly arched, generally closely spaced series, with approximately 13–15 tabulae in 5 mm.

Remarks

Vitiliphyllum jenkinsi is currently the only assigned species. Fragmented individual corallites bear resemblances to smaller corallites of the solitary *Cyatholasma? neumani*, with which it occurs in the Ulah area. Taxonomic distinction between such specimens can be made by the axial septal lamellae and lobes of *V. jenkinsi* tending to be thinner and more loosely arranged than the moderately dilated axial septal elements of *C.? neumani*.

Family PTYCHOPHYLLIDAE Dybowski, 1873a Subfamily PTYCHOPHYLLINAE Dybowski, 1873a

Genus Ptychophyllum Edwards and Haime, 1850

Synonymy

Ptychophyllum Edwards and Haime, 1850, p. lxixImplicophyllum Sytova in Sytova and Ulitina, 1966, p. 239

Type species

Ptychophyllum stokesi Edwards and Haime, 1850. Probably Cordell Formation, late Telychian– early Sheinwoodian, Drummond Island, Lake Huron, Michigan.

Diagnosis

Solitary ptychophyllinid with cylindrical, turbinate or more rarely patellate coralla. Calical pit generally moderately deep and may have prominent axial boss. Major septa taper towards corallite axis, where they typically form pronounced axial vortex. Dissepiments tend to be small and subglobose to elongate, in variably axially inclined layers, and lateral dissepiments may be present. Tabularium comprises arched series of numerous tabellae, with incomplete tabulae in some cases.

Discussion

The type species of Ptychophyllum, P. stokesi Edwards and Haime, 1850, is a relatively poorly known form, even though it has been recorded numerous times, and in some cases illustrated externally, from equivalent strata in the vicinity of the type locality in northern Michigan and adjacent Manitoulin Island, Ontario (e. g. Edwards and Haime 1851, pl. 3, fig. 9; Rominger 1876, pl. 44, upper tier; Williams 1919, pl. 14, fig. 4; pl. 15, fig. 3; Smith 1945, pl. 35, fig. 2a (paralectotype); Ehlers and Kesling 1957, pl. 10, figs 5, 6; Bolton 1966, pl. 5, fig. 10; Copper 1978, pl. 14, fig. 6). The lectotype of P. stokesi was designated by Lang (1926, p. 431), and identified by Smith (1945, p. 51) as the specimen illustrated in calical view as Caryophyllia sp. by Bigsby (1824, pl. 29, fig. 1, righthand figure). This seems to be the only illustration of the lectotype, as the specimen figured as lectotype by Hill (1981, fig. 201.3a) is that illustrated externally by Smith (1945, pl. 35, fig. 2a), which Smith noted was actually a "paratype" (i. e. paralectotype) and is certainly not the designated lectotype specimen figured by Bigsby. All of this externally illustrated material is heavily silicified and figures of thin sections are rare. Hill (1935, text-figs 21C, D) diagrammatically depicted a transverse and longitudinal section, which clearly show the characteristic features accepted for the species and genus, although unfortunately the source of this material was not provided. The only section illustrated photographically is the partial transverse section of a topotype by Smith (1945, pl. 35, fig. 2b). Despite the inadequate knowledge of the internal features and variability of the type species, the characteristic feature of the genus can be taken to be the axial septal vortex, and all species included here

have it developed at least to some degree (see list below). Presence of that septal vortex distinguishes *Ptychophyllum* from the otherwise closely similar *Cyathactis* Soshkina, 1955 (see full discussion of the latter by McLean and Copper 2013, pp. 65, 66).

The genus *Implicophyllum* Sytova in Sytova and Ulitina, 1966 is based on the type species *I. vesiculosum* Sytova in Sytova and Ulitina 1966, from the early Lochkovian Aynasu Horizon of the Karaganda Basin, Kazakhstan. Sytova distinguished it from *Ptychophyllum* by its lack of lateral dissepiments, but, as noted by McLean (1977b, p. 22), the degree of development of lateral dissepiments in many genera and species can vary greatly, even in the one corallite, and their presence or absence is not considered here to be of generic significance. On that basis, the view of McLean (1977b) in regarding *Implicophyllum* as a junior synonym of *Ptychophyllum* is followed.

As interpreted here, species of *Ptychophyllum* range in age from early Silurian to Early Devonian, Rhuddanian to early Lochkovian.

In addition to the type species, the following are also assigned to *Ptychophyllum*.

- Ptychophyllum sibiricum Ivanovskiy, 1963. "Upper Llandovery" (overall range given as early Aeronian–basal Sheinwoodian by Tesakov et al. 2003), Moyero River, Siberian Platform.
- Ptychophyllum tenuiseptatum Ivanovskiy, 1963. Locality data as above. Listed as subspecies of Ptychophyllum stokesi by Ivanovskiy (1970b).
- Ptychophyllum sp. A of Stumm (1963). Hardwood Mountain Formation, late Wenlock–Přídolí (Berry and Boucot 1970), Moose River Synclinorium, Maine.
- Ptychophyllum sp. of Sytova and Ulitina (1966). Aynasu Horizon, early Lochkovian (Talent et al. 2001), Isen' River, southern Karaganda Basin, central Kazakhstan.
- Implicophyllum vesiculosum Sytova in Sytova and Ulitina, 1966. Upper Aynasu Horizon, early Lochkovian, Burnak River, southern Karaganda Basin, central Kazakhstan. Type species of Implicophyllum Sytova.
- Ptychophyllum araneosum Strel'nikov, 1972. "Wenlock", Kozhym River, Subpolar Urals.
- Ptychophyllum auctum McLean, 1975b. Quarry Creek Limestone, probably late Telychian, Quarry Creek, approximately 22 km west of Orange, central western New South Wales.
- Ptychophyllum sp. nov. of Pedder and McLean (1976). Douro Formation, late Gorstian–early Ludfordian (Norford, 1997), Grinnell Peninsula, Devon Island, Nunavut.

- Ptychophyllum orientale Guo, 1976. Chaganhebu Formation, late Přídolí (Rong et al. 2003), Bailingmiao area, Inner Mongolia. Also introduced as a new species by Guo (1978).
- Ptychophyllum tysonense, Ptychophyllum sp. A and Ptychophyllum sp. B of McLean (1977b). Offley Island Formation, early-mid Telychian (data in Norford 1972), Kap Tyson, western North Greenland.
- Ptychophyllum deibuense and P. xiawunagouense of He (1978). Probably Yanglugou Formation, Přídolí (data in Cao and Ouyang 1987), Diebu, West Qinling Mountains, Gansu.
- *Ptychophyllum guangyuanense* He, 1978. Ningqiang Formation, mid Telychian (Rong et al. 2012), Shangsi, northeastern Sichuan. Requires clearer illustrations.
- Ptychophyllum qinlingense Cao in Cao and Lin, 1982. Yanglugou Formation, Přídolí, Luqu-Tewo area, West Qinling Mountains, Gansu.
- Ptychophyllum crassiseptatum Sultanbekova, 1986. Pentamerus longispinatus beds, lower Zhumak Fornation, late Telychian–early Sheinwoodian (data in Nikitina et al. 2015; originally assigned to underlying upper Al'peis Formation by Sultanbekova), Balkybek River, Chingiz Range, Kazakhstan.
- Ptychophyllum variatum Munson and Jell, 2016. Jack Formation, late Gorstian–Ludfordian, Graveyard Creek Subprovince, Broken River Province, north Queensland.
- Ptychophyllum sutorense McLean sp. nov. Burly Jacky Sandstone Member, Glendalough Formation, early-mid Telychian, Cobblers Creek, approximately 32 km southwest of Orange, central western New South Wales.

Species listed below are regarded as possible representatives of *Ptychophyllum*.

- *Ptychophyllum floriforme* Hall, 1882. "Niagara limestone", Racine, Wisconsin. Also introduced as new species by Hall (1884). Not figured and indeterminate from description.
- Zaphrentis sp. of Chernyshev (1885). Shemakha Beds, late Llandovery (Ivanovskiy and Shurygina 1975), Ufa River, western slopes of central Urals. Revised by Ivanovskiy and Shurygina (1975) as *Ptychophyllum* ex. gr. *stokesi*. Probably weaker axial vortex than typical of *Ptychophyllum* and needs further study.
- *Ptychophyllum? cliftonense* Amsden, 1949. Brownsport Formation, Ludfordian (Barrick et al. 2011), western Tennessee. Has some stereome on dissepiments and partial development of

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presepiments. Possibly representative of the kyphophyllinid *Pilophyllum* Wedekind, as suggested by McLean (1977b).

- Ptychophyllum sp. of Norford (1962). Sandpile Group, late Rhuddanian–late Telychian (Norford 1997), Cassiar Mountains, northern British Columbia. Material inadequate.
- *Implicophyllum aitalievi* Sytova, 1966. Borovushka Suite, late Silurian or Early Devonian, Belaya River, Rudniy Altai. Weak axial vortex and may be representative of *Cyathactis* Soshkina.
- *Ptychophyllum latitabulatum* He, 1978. Probably Yanglugou Formation, Přídolí, Diebu, West Qinling Mountains, Gansu. Axial vortex unclear and may be representative of *Cyathactis*, as noted by McLean and Copper (2013).
- Ptychophyllum sibiricum araargense Sytova in Sytova and Ulitina, 1983. Upper Alash Horizon, Rhuddanian–early Aeronian, Ala-Arga River, western Tuva. Requires further study.

The following species are excluded from *Ptychophyllum*.

- Ptychophyllum canadense Billings, 1862. Lower Chicotte Formation, mid Telychian, Anticosti Island. Assigned to the arachnophyllids Chonophyllum Edwards and Haime by Lambe (1899, 1901) and Craterophyllum Foerste by Foerste (1909). Revised by McLean and Copper (2013), who illustrated thin sections of some of the type material for the first time and assigned it to the kodonophyllid Schlotheimophyllum Smith.
- Ptychophyllum pagoda Salter, 1873. "Silurian, Niagara Formation, Disaster Bay (?), Arctic America". Location unknown. Designated type species of the new genus Naos by Lang (1926), who selected a lectotype (figured externally) and illustrated sections of a specimen from Melville Island, Nunavut. Also revised by Smith (1945). Assigned to Craterophyllum by Hill (1956), McLean (1977b) and McLean and Copper (2013).
- Ptychophyllum fulcratum Hall, 1882. Louisville Limestone, late Homerian–early Gorstian (Brett et al. 2018), Louisville, Kentucky. Also introduced as new species by Hall (1884). Types first figured externally by Stumm (1965), who assigned it to Schlotheimophyllum. Not studied in thin section.
- Ptychophyllum versiforme Hall, 1882. Boyle Formation, mid Givetian (Brett et al. 2018), central Kentucky. Also introduced as new species by Hall (1884). Type first figured externally and assigned to *Schlotheimophyllum* by Stumm

(1965), who included *P. knappi* Hall, 1883 from same unit as synonym. Not studied in thin section and currently indeterminate.

- Ptychophyllum striatum Hall, 1882. "Corniferous limestone", Onondaga Formation (Bassler 1950), Eifelian, western New York. Also introduced as new species by Hall (1884), who provided exterior illustrations. Indeterminate.
- Ptychophyllum palmatum Maurer, 1885. Waldgirmes Kalk, Givetian (?), Giessen area, Germany. Probably colonial and indeterminate.
- Ptychophyllum ipomaea Davis, 1887. Louisville Limestone, late Homerian–early Gorstian, Louisville, Kentucky. Lectotype selected by Stumm (1965). Revised by Laub (1979) and assigned to Schlotheimophyllum, but not studied in thin section.
- Ptychophyllum typicum Davis, 1887. Jeffersonville Limestone, late Emsian–Eifelian (Brett et al. 2018), southern Indiana–northern Kentucky. Lectotype figured externally by Stumm (1965), who included *P. gemmatum* Greene, 1900 from same locality as synonym. Indeterminate.
- Ptychophyllum invaginatum Davis, 1887. Louisville Limestone, late Homerian–early Gorstian, Louisville, Kentucky. Not studied in thin section. Assigned to Craterophyllum by Stumm (1965), but lacks corallite morphology of that genus. Indeterminate.
- *Ptychophyllum benedicti* Greene, 1900. Stratigraphy and locality as above. Lectotype selected and first illustrated in thin section by Laub (1979), who assigned it to *Schlotheimophyllum*.
- Ptychophyllum vulcanius Foerste, 1903. Brownsport Formation, Ludfordian, western Tennessee.
 Redescribed as Chonophyllum (Craterophyllum) vulcanius by Foerste (1909). Designated type species of Craterophyllum by Lang et al. (1940).
 Holotype figured in thin section for first time by McLean (1977b).
- Ptychophyllum? kindlei Smith, 1945. Upper Kakisa Formation, late Frasnian, Redknife River, southern Northwest Territories. Revised by McLean (2007) and designated type species of the new kyphophyllinid genus *Plectophyllum*.
- *Ptychophyllum? whittakeri* Smith, 1945. Same unit, Trout River, southern Northwest Territories. Revised and assigned to *Plectophyllum* by McLean (2007).
- Ptychophyllum giganteum Sun in Wang et al., 1957. Laojiangchong Formation, late Frasnian (data in Yu et al 1990, Ma and Zong 2010), Qiziqiao, central Hunan. Also described as new species *Tabulophyllum gigantum* (sic) by Sun (1958).

Assigned to kyphophyllinid *Mictophyllum* Lang and Smith by Pedder (1965) and McLean (2007).

- Ptychophyllum orthoseptatum Ivanovskiy in Ivanovskiy and Kul'kov, 1974. Chagyrka Horizon, Sheinwoodian (Sennikov et al. 2019b), Yarkovki River, Gorniy Altai. Lacks axial vortex and assigned to *Cyathactis* by McLean (1977b) and McLean and Copper (2013).
- *Implicophyllum nodosum* Kaplan in Sytova and Kaplan, 1975. Aynasu Horizon, early Lochkovian, Mount Sagat, southern Karaganda Basin, central Kazakstan. Lacks axial vortex and possibly representative of *Cyathactis*.

Ptychophyllum sutorense McLean sp. nov. Figs 22, 23

Synonymy

- Ptychophyllum cf. sibiricum Ivanovskiy, 1963; McLean 1975b, p. 59, pl. 3, figs 3–9
- Ptychophyllum cf. sibiricum Ivanovskiy; McLean 1977a, p. 104
- Ptychophyllum cf. sibiricum Ivanovskiy; Jenkins 1978, p. 121
- Ptychophyllum cf. sibiricum Ivanovskiy; Jenkins 1986, fig. 33
- Ptychophyllum sp. cf. sibiricum Ivanovskiy; Strusz 1989, pl. 1
- Ptychophyllum sp. cf. sibiricum Ivanovskiy; Strusz 1996, fig. 3
- Ptychophyllum sp. cf. sibiricum Ivanovskiy; Strusz and Munson 1997, p. 320
- Ptychophyllum cf. sibiricum Ivanovskiy; Pogson and Watkins 1998, p. 376
- *Ptychophyllum* cf. *sibiricum* Ivanovskiy; Pickett 2011, p. 91

Derivation of name

Latin, *sutor*, a cobbler, after the type locality, Cobblers Creek, central western New South Wales.

Type material

Holotype, SUP 20111 (thin sections AM FT.7129, 7130). Paratypes, SUP 45209 (thin sections AM FT.11647, 11648); SUP 45210 (thin section AM FT.11649); SUP 45211 (thin section AM FT.11650); SUP 45212 (thin sections AM FT.11639, 11640, 11651); SUP 45213 (thin sections AM FT.11643); SUP 45215 (thin sections AM FT.11644–11646). Burly Jacky Sandstone Member, Glendalough Formation, early–mid Telychian, Cobblers Creek, approximately 32 km southwest of Orange, central western New South Wales.

Diagnosis

Cylindrical *Ptychophyllum* with corallite diameter 13.5–19.0 mm. Major septa 24–31 in number, moderately to strongly dilated peripherally, variably tapering axially to form generally prominent axial vortex. Minor septa also dilated and confined to marginarium. Dissepiments generally small, subglobose to moderately elongate, and in steeply axially inclined layers. Broad tabularium of arched series of numerous small, elongate tabellae.

Description

See McLean (1975b, p. 59) for detailed description.

Remarks

The resemblances of the above material to *Ptychophyllum sibiricum* Ivanovskiy, 1963, from Aeronian–early Sheinwoodian strata of the Siberian Platform, led McLean (1975b) to describe it simply as *P*. cf. *sibiricum*. However, restudy of the Cobblers Creek material suggests that there are sufficient differences, notably the significantly greater septal dilation, fewer septa, and consistently smaller corallites of the New South Wales form, to justify assigning it to a separate species.

Few other early Silurian species show much resemblance to *Ptychophyllum sutorense*. *Ptychophyllum tysonense* McLean, 1977b, from the Telychian Offley Island Formation of western North Greenland, has comparable corallite size and only a slightly higher septal count, but has much thinner septa and wider marginariun (McLean 1977b, fig. 4; pl. 6, figs 3, 4, 6; pl, 7, figs 2–4). *Ptychophyllum crassiseptatum* Sultanbekova, 1986, from the Rhuddanian–Aeronian Al'peis Suite of Kazakhstan, has moderate peripheral septal dilation, but thinner septa axially, as well as generally larger corallites, more septa and a wider marginarium (Sultanbekova 1986, pl. 11, fig. 2; pl. 12, figs 1a, b).

The other two representatives of *Ptychophyllum* known from eastern Australia can be easily distinguished from the new species. *Ptychophyllum auctum* McLean, 1975b occurs in the probably late Telychian Quarry Creek Limestone of central western New South Wales and has larger corallites, a greater number of septa, more pronounced peripheral septal dilation and thinner septa axially, as well as a tendency to develop lateral dissepiments (McLean 1975b, pl. 2, figs 2–12; pl. 3, figs 1, 2). The much younger *Ptychophyllum variatum* Munson and Jell, 2016, from the late Gorstian–Ludfordian Jack Formation of northeastern Queensland, has much larger corallites, a significantly wider marginarium and more septa than *P. sutorense*, with those septa also being much thinner (Munson and Jell 2016, figs 21A–F).

Family ARACHNOPHYLLIDAE Dybowski, 1873a Genus *Latomiphyllum* McLean gen. nov.

Derivation of name

Latin, latomus, a stone quarry, referring to the type locality at Quarry Creek, central western New South Wales.

Type species

Arachnophyllum? epistomoides Etheridge, 1909. Quarry Creek Limestone, probably late Telychian, Quarry Creek, approximately 20 km west of Orange, central western New South Wales.

Diagnosis

Astreoid to aphroid arachnophyllid. Septa weakly dilated in inner dissepimentarium, breaking up into isolated laths and trabeculae in tabularium. In outer dissepimentarium, septa become naotic, multitrabecular septal crests, or may be reduced to sparse trabeculae or be absent in aphroid portions of some coralla. Dissepiments are generally in strongly arched layers, broad and highly elongate and very closely spaced in central parts of dissepimentarium. Adjacent to tabularia, they are in strongly downturned layers and are smaller and less elongate. Tabularia comprise arched, mesa-shaped series of incomplete, very closely spaced tabulae axially, with deep peripheral gutters.

Discussion

As might be expected from previous generic assignment of its designated type species, the new genus Latomiphyllum is closely allied to Arachnophyllum Dana, 1846. While Etheridge (1909) originally recognized the unusual character of his species epistomoides by only doubtfully assigning it to Arachnophyllum, most subsequent authors have retained it in that genus without question (see synonymy list, below), although some have noted its atypical features. Such queries followed the thorough revision of Arachnophyllum by Scrutton (1989), with "Arachnophyllum" epistomoides being noted as atypical of true Arachnophyllum by Munson and Jell (1999, p. 51), and this point was expanded upon in discussion of the species by McLean and Copper (2013, p. 89). Scrutton (1989) emphasized the diagnostic presence of carinae on the septa in the dissepimentarium of Arachnophyllum, forming a reticulate pattern with the septa (Scrutton 1989, text-figs 7A, B, E). The absence of this septal

structure "Arachnophyllum" epistomoides in serves as a primary distinction of the new genus Latomiphyllum, proposed here to accommodate that species. Latomiphyllum is also distinguished from *Arachnophyllum* by the presence of long trabeculae in the dissepimentarium of the predominantly astreoid coralla, which tend to have greater development of naotic, multitrabecular septa than is typical of Arachnophyllum. In addition, normal septa are regularly developed in the tabularia of Arachnophyllum species, whereas in Latomiphyllum they are typically reduced to laterally and vertically discontinuous laths or trabeculae.

Munson and Jell (1999, p. 51) suggested that "Arachnophyllum" epistomoides could be a representative of Prodarwinia Cotton, 1973. This is a substitute name for the pre-occupied Darwinia Dybowski, 1873a, and was thoroughly revised by Scrutton (1989). He primarily distinguished it from Arachnophyllum by its lack of the latter's reticulate carinate structure, with septa being only weakly carinate or non-carinate. Prodarwinia also has more pronounced crusts of trabeculae and stereome on the dissepiment layer surfaces. Latomiphyllum resembles Prodarwinia in also generally lacking carinae and developing multitrabecular layers on dissepiment surfaces. However, in Latomiphyllum these trabeculae are much longer, forming naotic crests (herein, Figs 27B, D) and generally lack associated stereome, while Prodarwinia forms irregular, vertically separated crusts of short trabeculae and stereome, as seen in the type species P. speciosa Dybowski, 1873a (Scrutton, 1989, pl. 7, 4–7). Latomiphyllum is further distinguished by its breakdown of septa in the tabularia into isolated laths and trabeculae.

McLean and Copper (2013, p. 89) noted some similarities between "Arachnophyllum" epistomoides and the inadequately known thamnasterioid form Paraphillipsastrea Jin, 1992. The type and only known species, P. jianbaoensis Jin, 1992, is from the late Telychian upper Ningqiang Formation of northern Sichuan, and is thus of comparable age to Latomiphyllum epistomoides. The published English summary in Jin (1992, p. 87) noted the presence of apparently multitrabecular septa in *P. jianbaoensis*. but unfortunately the available illustrations (Jin 1992, pl. 4, figs 1a-c; Deng and Scrutton 1996, pl. 14, figs 7-9; He and Tang 2011, pl. 2, figs 2a, b) are inadequate to demonstrate this or to recognize other characteristic features of Latomiphyllum. The affinities of Paraphillipsastrea remain unclear at present, but it does not appear to be related to Latomiphyllum.

Latomiphyllum epistomoides (Etheridge, 1909) Figs 24–27

Synonymy

- Arachnophyllum? epistomoides Etheridge, 1909, p. 305, pls 44–46
- Arachnophyllum? epistomoides Etheridge; Packham and Stevens 1955, p. 58
- Arachnophyllum epistomoides Etheridge; Packham 1969, p. 110
- Arachnophyllum epistomoides Etheridge; McLean 1975b, p. 55, pl. 1, figs 1–6, pl. 2, fig. 1
- Arachnophyllum epistomoides Etheridge; Talent et al. 1975, p. 78
- Arachnophyllum epistomoides Etheridge; McLean 1977a, table 2
- Arachnophyllum epistomoides Etheridge; Sherwin and Pickett 1982, p. 141
- Arachnophyllum epistomoides Etheridge; Pickett 1982d, p. 160
- Arachnophyllum epistomoides Etheridge; Pickett 1982e, p. 161
- Arachnophyllum epistomoides Etheridge; Jenkins 1986, p. 69
- Arachnophyllum epistomoides Etheridge; Strusz 1989, pl. 1
- Arachnophyllum epistomoides Etheridge; Strusz 1996, p. 18, fig. 3
- Arachnophyllum epistomoides Etheridge; Strusz and Munson 1997, p. 314, fig. 6
- Arachnophyllum epistomoides Etheridge; Pogson and Watkins 1998, p. 376
- Arachnophyllum epistomoides Etheridge; Munson and Jell 1999, p. 51
- Arachnophyllum epistomoides Etheridge; Pickett 2011, p. 64
- Arachnophyllum epistomoides Etheridge; McLean and Copper 2013, p. 89

Type material

Lectotype (selected by McLean 1975b, p. 55), specimen (not preserved) with thin section AM FT.4866. Paralectotype, specimen (not preserved) with thin section AM FT.4343. Quarry Creek Limestone, probably late Telychian, most easterly outcrop ("bed A" of Sussmilch 1907 and Packham and Stevens 1955; Loc. 1 of McLean 1973, text-fig. 9) in Quarry Creek, approximately 20 km west of Orange, central western New South Wales.

Additional material

Topotypes, SUP 45228 (thin section AM FT.7155); specimen (not preserved) with thin sections AM FT.15624, 15625. Possible topotype,

specimen (not preserved) with thin section AM FT.4768 (MMF 17317). SUP 45230 (thin section AM FT.7156); SUP 45231 (thin sections AM FT.7148, 7149, 7153); SUP 45232 (thin section AM FT.11663), same unit, Spring Creek, approximately 750 m east of "Mirrabooka" homestead (Loc. 4 of McLean 1973, text-fig. 9). MMF 18852, same unit, "Spring and Gap Creeks", locality uncertain. SUP 27150 (thin sections AM FT.7150, 7151, 14016); SUP 45236 (thin section AM FT.7154), lower Boree Creek Formation, probably late Telychian, midway between Boree and Barton Creeks (Loc. 2 of McLean 1973, text-fig. 11), approximately 15 km northwest of Orange, central western New South Wales. SUP 45240 (thin section AM FT.7152), same unit, Kalinga area, between Boree Creek and The Escort Way (Loc. 4 of McLean 1973, text-fig. 11).

Diagnosis

See generic diagnosis, above.

Description

Corallum is tabular, with width up to 75 cm and height 45 cm. Coralla are astreoid to at least partially aphroid, in some cases with septa partially confluent between tabularia. Distal surface of corallum shows slight swelling around calical pits, reflecting variable arching of underlying inner dissepimentarium. Pits are 5–6 mm wide and 3 mm deep, with a broad calical boss 1–2 mm high.

Major septa range from 18 to approximately 27 in number (exact number unclear), extending slightly into tabularia, where they break down to isolated, sometimes branching trabeculae, and short laths (Figs 24B, C), which extend vertically through several tabular series. Minor septa are slightly shorter than majors and confined to dissepimentarium. Septa are relatively complete in inner dissepimentarium adjacent to tabularium, but break down in outer dissepimentarium to isolated trabeculae or groups of trabeculae, which combine with stereome to form naotic, multitrabecular septa in some cases (e. g. Figs 24B, 27D). In other specimens, trabeculae may remain isolated and not radially aligned to form recognizable septa, or may be completely absent, as in the aphroid or partially aphroid coralla (Fig. 26A). Trabeculae in outer dissepimentarium are long and pierce at least several dissepiment layers, but microstructure is obscured by recrystallization in all areas.

Dissepiments are small and globose to moderately elongate in inner dissepimentarium, forming steeply downward inclined layers. In outer dissepimentarium in central area between tabularia, dissepiments are extremely elongate, with height of only 0.1–0.2 mm, and in moderately arched, flat or slightly concave series. Tabularia range in diameter from about 5–7 mm, and are spaced approximately 15–25 mm apart. Tabulae are complete and incomplete, in strongly arched, mesa-shaped series, with pronounced peripheral concave gutters. They are very closely spaced, with 12–25 in 5 mm.

Remarks

Available material of *Latomiphyllum epistomoides* is unfortunately mostly poorly preserved, with extensive recrystallization and varying degrees of silicification. However, the diagnostic morphology of the species is still clearly apparent, and the considerable intraspecific variability noted above, especially in septal development, can still be recognized. It is the only species assigned to the genus at this time.

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Figure 1. Locality map of the study area, west of Orange, central western New South Wales, with locations of detail maps, Figs 3, 4. Setting in southeastern Australia shown to the right. Silurian outcrop data from Raymond et al. (2012).

SERIES	STAGE	GRAPTOLITE ZONES AUSTRALIA	CONODONT ZONES AUSTRALIA	NORTHERN ANGULLONG SYNCLINE	ULAH - BRIDGE CREEK	SPRING and QUARRY CREEKS	BOREE CREEK
WENLOCK	HOMERIAN	ludensis	unzoned		á		6
		paradeubeli - deubeli			Panuara Em		Mirrabooka
		parvus - nassa			Mumt	Mirrabooka Fm.	Fm. ZBorenore
		lundgreni / testis	amsdeni				/ Lst.
	SHEINWOODIAN	unzoned				1	Quarry Creek hiatus
		riccartonensis		Glendalough Fm. Burly Jacky Sst. * Mbr. Cobblers Creek * Panuara hiatus	Quarry Creek hiatus	$\sim\sim\sim\sim\sim$	~~~?~~~~
		unzoned	rannuliformis		Mith Start	Quarry Creek hiatus	Boree Creek
		centrifugus	amorphognathoides				
LLANDOVERY	TELYCHIAN	unzoned					
		spiralis	celloni staurognathoides			* Limestone	*
		crenulata - griestoniensis				$\sim \sim \sim \sim \sim$	~~~?~~~~
		crispus					
		turriculatus			Panuara hiatus	F	
		guerichi					
	AERONIAN	sedgwickii	unzoned			F F	
		convolutus					
		leptotheca					
		magnus	pseudopesavis	Cadia Coach Shale	Cadia Coach Shale		
		triangulatus					
	RHUDDANIAN	cyphus					
		vesiculosus	combinatus				
		acuminatus	unzoned	Cobblers Creek	Cobblers Creek hiatus		
		ascensus					
LATE ORDOVICIAN	HIRNANTIAN	persculptus		matus			
		extraordinarius		Angullong Fm.	Angullong Fm.		
	Late KATIAN	pacificus					~~~~~~
		"pre-pacificus"				Malachis Hill Fm.	Cheesmans Creek
		uncinatus					rm.

Figure 2. Biostratigraphic correlations of Late Ordovician to mid Silurian strata in the study area. Based on data in Jenkins (1978, 1986), Bischoff (1987), Simpson (1995), Rickards et al. (1995, 2003), Percival and Wright (2005), Strusz (2007), Molloy and Simpson (2012), and Zhen and Percival (2017). Asterisks indicate approximate position of horizons bearing rugose corals described in the present work.



Figure 3. Angullong to Bridge Creek area, showing simplified, schematic distribution of major Silurian units. Based on mapping in Jenkins (1978, 1986) and modification of data in Colquboun et al. (2021) (see http://minview.geoscience.nsw.gov.au).



Figure 4. Spring and Quarry Creeks to Boree Creek area, showing simplified, schematic distribution of major Silurian units. Based on mapping in Partridge (1967), Sherwin (1971), Byrnes (1982), Percival and Wright (2005) and modification of data in Colquhoun et al. (2021) (see http://minview.geoscience. nsw.gov.au).

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Figure 5. *Dentilasma* sp. cf. *D. honorabilis* Ivanovskiy, 1962. A–C, SUP 45200; A, AM FT.11665, TS; B, AM FT.11666, portion of LS showing septal spines on dissepiment crests; C, AM FT.11666, LS. D, SUP 45202; AM FT.11668, LS. Scale bar 1 = 2 mm (Fig. B), scale bar 2 = 5 mm (Figs A, C, D).



Figure 6. *Gephyrelasma ramosum* (McLean, 1974b). SUP 63273, holotype; A, AM FT.7177, TS; B, AM FT.7191, LS showing parricidal, calical increase. Scale bar = 5 mm.

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Figure 7. *Gephyrelasma ramosum* (McLean, 1974b). SUP 63273, holotype; A, AM FT.7177, TS; B, AM FT.7191, LS showing parricidal, calical increase. Scale bar = 5 mm.



Figure 8. *Gephyrelasma stevensi* McLean sp. nov. AM F.156003, holotype; A, AM FT.15556, TS; B, AM FT.15557, LS. Scale bar = 5 mm.

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Figure 9. *Gephyrelasma stevensi* McLean sp. nov. AM F.156004, paratype; A, AM FT.15558, TS; B, AM FT.15559, LS. Scale bar = 5 mm.





Figure 10. *Gephyrelasma stevensi* McLean sp. nov. AM F.156008, paratype; A. AM FT.15570.001, TS; B, AM FT.15571.001, LS; note wide peripheral stereozone and highly variable tabular spacing. Scale bar = 5 mm.

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Figure 11. *Gephyrelasma stevensi* McLean sp. nov. A, B, D, E, AM F.156026, paratype; A, AM FT.15563, TS; B, AM FT.15564, LS; D, AM FT.15563, TS of individual corallite showing short septal spines on corallite wall and dissepiments; E, AM FT.15564, LS enlarged to show short septal spines on corallite wall. C, AM F.156025, paratype; AM FT.15561, TS of corallites showing character of thickened peripheral stereozone. Scale bar 1 = 5 mm (Figs A, B), scale bar 2 = 2 mm (Figs C–E).



Figure 12. *Aphyllum ulahense* McLean sp. nov. AM F.156027, holotype; A, AM FT.15572, TS; B, AM FT.15573, LS (see also Fig. 14E); note variation in width of peripheral stereozone. Scale bar = 5 mm.

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Figure 13. *Aphyllum ulahense* McLean sp. nov. A, B, AM F.156013, paratype; A, AM FT.15584, TS; B, AM FT.15585, LS (see also Figs 14C, D). Scale bar = 5 mm.



Figure 14. *Aphyllum ulahense* McLean sp. nov. A, B, AM F.156012, paratype; A, AM FT.15579, TS; B, AM FT.15583, LS; note parricidal, calical increase. C, D, AM F.156013, paratype; C, AM FT.15586, LS; D, AM FT.15585, LS (see also Fig. 13); note coarse, peripheral septal spines. E, AM F.156027, holotype; AM FT.15572, TS of individual corallite (see also Fig. 12). Scale bar 1 = 5 mm (Figs A, B), scale bar 2 = 2 mm (Figs C–E).

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Figure 15. A, C, *Aphyllum delicatulum* (Etheridge, 1907), lectotype; A, AM FT.742b, LS showing short septal spines on tabulae; C, AM FT.742a, TS showing septal spines on corallite walls and tabulae. B, D, *Aphyllum cingulatum*? (Billings, 1862), GSC 3038c (?), syntype; B, TS of individual corallite; D, LS and TS. Scale bar 1 = 2 mm (Figs A, C), scale bar 2 = 5 mm (Figs B, D).

Figure 16. *Aphyllum picketti* McLean sp. nov. A, B, MMF 31304, paratype; A, LS; B, TS. C, D, G, MMF 31303, holotype; C, TS; D, portion of LS showing septal spines on corallite wall at right; G, LS. E, MMF 31302, paratype, TS. F, MMF 31308, paratype, TS. Scale bar 1 = 2 mm (Fig. D), scale bar 2 = 5 mm (Figs A–C, E–G).

Figure 17. *Cyatholasma? neumani* (McLean, 1974c). A, B, SUP 20115, holotype; A, AM FT.7242, TS; B, AM FT.7244, LS (see also Fig. 18B). C, D, AM F.156015; C, AM FT.15595, LS; D, AM FT.15593, TS. E, G, AM F.156019; E, AM FT.15605, LS; G, AM FT.15604, TS. F, AM FT.15597, TS; H, same specimen, AM FT.15599, LS. Scale bar = 5 mm.

Figure 18. *Cyatholasma? neumani* (McLean, 1974c). A, C, AM F.156018; A, AM FT.15602., TS; C, portion of same section enlarged to show biform tabulae. B, SUP 20115, holotype; AM FT.7242, portion of TS showing septal microstructure in peripheral stereozone (see also Figs 17A, B). D, AM FT.15606, TS of early growth stage; E, same specimen, AM FT.15607, LS. F, G, AM F.156020; F, AM FT.15610, LS; G, portion of same section enlarged to show peripheral septal microstructure. H, AM F.156021; AM FT.15611., LS. Scale bar 1 = 3 mm (Fig. C), scale bar 2 = 2 mm (Figs B, G), scale bar 3 = 5 mm (Figs A, D, E, F, H).

Figure 19. *Vitiliphyllum jenkinsi* McLean sp. nov. A, B, AM F.156008, paratype; A, AM FT.15570.002, TS; B, AM FT.15571.002, oblique LS. C, D, AM F.156028, holotype; C, AM FT.15612, TS; D, AM FT.15613, LS. Scale bar = 5 mm.

Figure 20. *Vitiliphyllum jenkinsi* McLean sp. nov. A–D, F, AM F.156024, paratype; A, AM FT.15620, TS; B, AM FT.15622, TS; C, AM FT.15621, TS; D, AM FT.15623, LS; F, portion of section in Fig. C enlarged to show peripheral septal microstructure. E, AM F.156023, paratype; AM FT.15619, TS. G, paratype; AM FT.15615, TS and oblique LS. Scale bar 1 = 5 mm (Figs A–E, G), scale bar 2 = 2mm (Fig. F).

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Figure 21. *Vitiliphyllum jenkinsi* McLean sp. nov. A, B, AM F.156022, paratype; A, AM FT.15617, TS; B, AM FT.15618, TS. Scale bar = 5 mm.

Figure 22. *Ptychophyllum sutorense* McLean sp. nov. A, C, SUP 20111, holotype; A, AM FT.7129, TS; C, AM FT.7130, LS. B, SUP 45210, paratype; AM FT.11649, TS. D, E, SUP 45213, paratype; D, AM FT.11642, LS; E, AM FT.11641, TS. Scale bar = 5 mm.

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Figure 23. *Ptychophyllum sutorense* McLean sp. nov. A, B, SUP 45209, paratype; A, AM FT.11647, TS; B, AM FT.11648, LS. C, E, SUP 45215, paratype, C, AM FT.11644, TS; E, AM FT.11646, LS. D, SUP 45211, paratype; AM FT.11650, TS. F, SUP 45214, paratype; AM FT.11643, LS. Scale bar = 5 mm.

Figure 24. *Latomiphyllum epistomoides* (Etheridge, 1909). A, lectotype; AM FT.4866, TS (see also Fig. 27D). B, SUP 45231; AM FT.7148, portion of TS showing septal breakdown in tabularium and outer marginarium (see also Fig. 26C). C, SUP 45228, topotype; AM FT.7155, portion of TS showing septal breakdown in tabularium. Scale bar 1 = 5 mm (Fig. A), scale bar 2 = 5 mm (Figs B, C).

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Figure 25. *Latomiphyllum epistomoides* (Etheridge, 1909). A, topotype; AM FT.15624, TS; B, same specimen, AM FT.15625, LS. Scale bar = 5 mm.

Figure 26. *Latomiphyllum epistomoides* (Etheridge, 1909). A, SUP 45236; AM FT.7154, TS. B, paralectotype; AM FT.4343, LS (see also Fig. 27B). C, SUP 45231; AM FT.7153, LS (see also Fig. 24B). Scale bar = 5 mm.

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Figure 27. *Latomiphyllum epistomoides* (Etheridge, 1909). A, SUP 45230; AM FT.7156, LS. B, paralectotype; AM FT.4343, portion of LS showing divergence and branching of trabeculae adjacent to tabularium (see also Fig. 26B). C, E, SUP 27150; C, AM FT.7151, LS; E, AM FT.7150, LS. D, lectotype; AM FT.4866, portion of TS showing septal breakdown in outer marginarium (see also Fig. 24A). Scale bar 1 = 5 mm (Figs B, D), scale bar 2 = 5 mm (Figs A, C, E).