THE RUGOSE CORAL GENERA *STREPTELASMA* HALL, *GREWINGKIA* DYBOWSKI AND *CALOSTYLIS* LINDSTRÖM FROM THE LOWER SILURIAN OF NEW SOUTH WALES

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(Plates I and II)

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Synopsis

Streptelasma recisum sp. nov. is described from the Late Lower or Early Middle Llandoverian Bridge Creek Limestone of the Four Mile Creek area, central New South Wales. *Grewingkia parva* sp. nov., *G. neumani* sp. nov. and *Calostylis panuarensis* sp. nov. are described from the Brown Mudstone Horizon near Angullong, central New South Wales, this unit being probably stratigraphically equivalent to the Bridge Creek Limestone. Possible affinities between the genera *Grewingkia* Dybowski and *Calostylis* Lindström are discussed.

Introduction

The rugose corals described occur in horizons of the Panuara Group south-west of Orange in central New South Wales. A summary of the stratigraphy of these horizons (Bridge Creek limestone at Four Mile Creek and Brown Mudstone Horizon at Angullong) together with evidence for their late Lower or early Middle Llandoverian age are given by McLean (1974). Their distribution is illustrated in Text-fig. 1.

This paper presents the first description of the genera *Streptelasma* Hall, *Grewingkia* Dybowski and *Calostylis* Lindström from Australia. The species "*Streptelasma*" *australe* (Foerste, 1888) from the Upper Silurian of the Yass district, New South Wales, is not a representative of *Streptelasma* as that genus is currently defined (see discussion below).

Systematic Palaeontology

The morphological terminology used is that employed by Hill (1956) and Neuman (1969).

All numbers of specimens in the University of Sydney Palaeontological Collections bear the prefix SUP. Where more than one section has been prepared from the one specimen, the numbers bear the suffix *a*, *b*, etc.

Text-figures have been prepared from tracings of photographs.

Family STREPTELASMATIDAE Nicholson *in* Nicholson and Lydekker, 1889

Diagnosis (based on Hill, 1956, p. F268). Solitary or fasciculate coralla generally with short minor septa and with septal stereozone often developed. Dissepiments lacking and tabulae usually domed, complete and incomplete.

Subfamily STREPTELASMATINAE Nicholson *in* Nicholson and Lydekker, 1889

Diagnosis. Septal stereozone may or may not be developed. Septa lamellar, complete throughout ontogeny.

Discussion. The generic composition of this subfamily is considered here as that given by Hill (1956, pp. F268–F269), although *Coelostylis* Lindström

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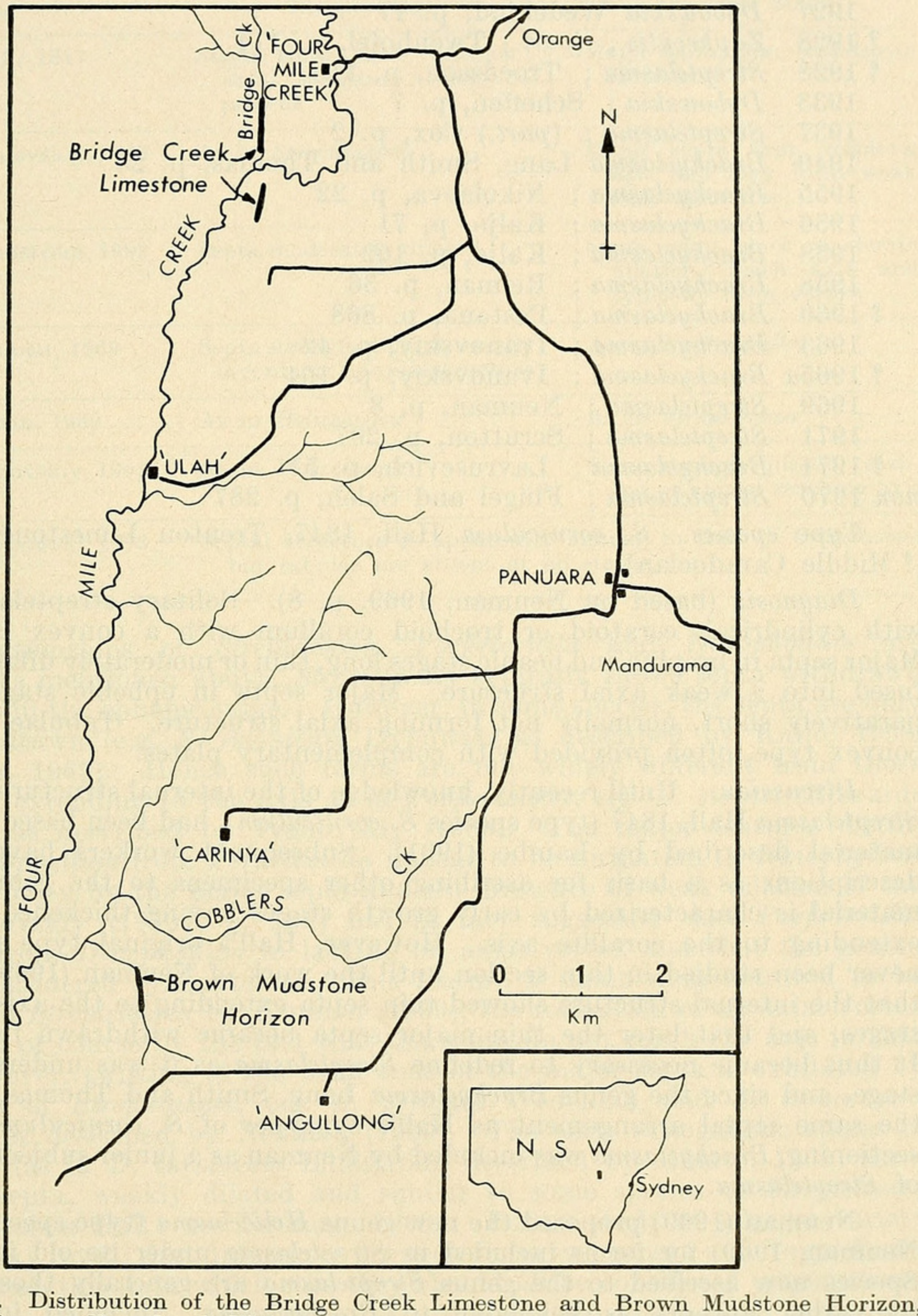
has been shown to possess monacanthine septa and has been transferred to the family Tryplasmatidae Etheridge (Neuman, 1967). Genera subsequently described and considered here as representatives of the Streptelasmatinae include *Porfirieviella* Ivanovskiy, 1963 ; *Helicelasma* Neuman, 1969 ; *Borelasma* Neuman,



Text-fig. 1. Distribution of the Bridge Creek Limestone and Brown Mudstone Horizon, South-east of Orange, New South Wales.

1969 ; *Crassilasma* Ivanovskiy, 1962 ; and *Kenophyllum* Dybowski, 1873. The relationships of these latter genera to the type genus *Streptelasma* Hall, 1847, are discussed below.

Genus STREPTELASMA Hall, 1847

1847 *Streptelasma* Hall, p. 69
1873 *Calophyllum* Dybowski, p. 75
1873 *Streptelasma*; Dybowski, p. 384
? 1901 *Zaphrentis*; Lambe, p. 118 (*non* Rafinesque and Clifford, 1820)
? 1901 *Zaphrentis*; Lambe, p. 119
1927 *Dybowskia* Wedekind, p. 17
? 1928 *Zaphrentis*; (*part.*) Twenhofel, p. 114
? 1928 *Streptelasma*; Troedsson, p. 110
1933 *Dybowskia*; Scheffen, p. 7
1937 *Streptelasma*; (*part.*) Cox, p. 2
1940 *Brachyelasma* Lang, Smith and Thomas, p. 28
1955 *Brachyelasma*; Nikolaeva, p. 22
1956 *Brachyelasma*; Kaljo, p. 71
1958 *Brachyelasma*; Kaljo, p. 102
1958 *Brachyelasma*; Reiman, p. 36
? 1960 *Brachyelasma*; Pestana, p. 868
1963 *Brachyelasma*; Ivanovskiy, p. 42
? 1965*a* *Brachyelasma*; Ivanovskiy, p. 104
1969 *Streptelasma*; Neuman, p. 8
1971 *Streptelasma*; Scrutton, p. 207
? 1971 *Brachyelasma*; Lavrusevich, p. 51
non 1970 *Streptelasma*; Flügel and Saleh, p. 287

Type species. *S. corniculum* Hall, 1847, Trenton Limestone, New York (? Middle Caradocian).

Diagnosis (based on Neuman, 1969, p. 8). Solitary streptelasmatid coral with cylindrical, ceratoid or trochoid corallum with a convex cardinal side. Major septa in brephic and neanic stages long, thin or moderately dilated, normally fused into a weak axial structure. Major septa in ephebic stage thin, comparatively short, normally not forming axial structure. Tabulae of complete, convex type, often provided with complementary plates.

Discussion. Until recently, knowledge of the internal structure of the genus *Streptelasma* Hall, 1847 (type species *S. corniculum*), had been based on Canadian material described by Lambe (1901). Subsequent workers have used these descriptions as a basis for ascribing other specimens to the genus. Lambe's material is characterized by early growth stages having thickened major septa extending to the corallite axis. However, Hall's original type material had never been studied in thin section until the work of Neuman (1969), who found that the internal structure showed thin septa extending to the axis in the early stages, and that later the thin major septa became withdrawn from the axis. It thus became necessary to redefine *Streptelasma* as it was understood at that stage, and since the genus *Brachyelasma* Lang, Smith and Thomas, 1940, shows the same septal arrangement as Hall's syntypes of *S. corniculum* revealed on sectioning, *Brachyelasma* was included by Neuman as a junior subjective synonym of *Streptelasma*.

Neuman (1969) proposed the new genus *Helicelasma* (type species *H. simplex* Neuman, 1969) for forms included in *Streptelasma* under its old interpretation. Species now ascribed to the genus *Streptelasma* are generally those interpreted by earlier authors as belonging to *Brachyelasma*. Included in the family Streptelasmatidae are a number of genera that are obviously very closely related to *Streptelasma*. Distinctions between these genera can normally only be made by study of the character of their early ontogenetic stages. Such studies have generally been done only by recent workers (e.g. Kaljo, 1956, 1958; Reiman, 1958; Ivanovskiy, 1963; and Neuman, 1969). Hence, of the many streptelasmatid species described in the past, only a relatively small proportion may be ascribed to a particular streptelasmatid genus with certainty. The genera showing closest similarities to *Streptelasma* are listed in Table 1, together with their distinguishing features.

TABLE 1

Distinguishing Features of Streptelasma *and Related Genera*

Genus	Neanic Stage	Ephebic Stage
Streptelasma Hall, 1847 ..	Septa show little dilation ; axial structure may be present	Major septa, thin, withdrawn from axis
Porfirieviella Ivanovskiy, 1963	As in *Streptelasma*	Major septa thin, reaching axis and may form weak axial structure
Dinophyllum Lindström, 1882	Septa moderately dilated	Septa may show moderate dilation, reach axis and typically form vortex
Helicelasma Neuman, 1969	Septa strongly dilated, usually in contact ; no axial structure	As in *Porfirieviella*
Borelasma Neuman, 1969 ..	As in *Helicelasma*	As in *Streptelasma*
Crassilasma Ivanovskiy, 1962	As in *Helicelasma*	Septa strongly dilated, reaching or almost reaching axis
Kenophyllum Dybowski, 1873	Septal structure is apparently similar to that of *Crassilasma* but tabulae are absent at all stages.	

The relationships of *Streptelasma*, *Porfirieviella* and *Dinophyllum* are uncertain. As mentioned above, *Streptelasma* typically shows septa withdrawn from the axis in the ephebic stage. However, in some species, the septa are only slightly withdrawn (e.g. *S. estonicum* Dybowski as described by Kaljo, 1958, and Neuman, 1969). Hence such forms are not widely different from those having septa extending to the axis as in *Porfirieviella*, e.g. *P. stokesi* (Edwards and Haime) as described by Ivanovskiy (1963). The major features distinguishing *Dinophyllum* from *Porfirieviella* appear to be formation in *Dinophyllum* of an axial vortex by the major septa and the presence of weak dilation of the septa. Ivanovskiy (1970*a*, p. 121) has in fact suggested that *Porfirieviella* differs only from *Dinophyllum* in lacking an axial vortex and that the genera should be considered synonymous. This feature is again demonstrated to be gradational in *Streptelasma* by Neuman (1969), the formation of an axial vortex being limited of course by the fact that the septa do not reach the axis in that genus. However, twisting of the axial ends of the major septa is exhibited by some species of *Streptelasma*, e.g. *S. primum* Wedekind and *S. linnarssoni* (Lindström) as described by Neuman (1969). The early ontogenetic stages of *Dinophyllum* (as in *D. involutum* Lindström, described by Minato, 1961) show long major septa, weakly dilated and similar to some species of *Streptelasma* (e.g. *S. corniculum* Hall ; see Neuman, 1969). Future study of a larger variety of material may reveal that differences between these two genera and *Streptelasma* are merely gradational, in which case they should all be considered synonymous.

In a restudy of the composition of the genus *Streptelasma*, it is evident that many species, although similar to *Streptelasma* in their ephebic stage, are not well enough known in their earlier growth levels to be classified in that genus with certainty.

Brachyelasma fervida Kaljo, 1958, from the Oandu Horizon (Caradocian) of Estonia, possesses long, thin major septa in both ephebic and ? neanic stages

(Kaljo, 1958, Pl. I, figs 5, 6) but in the ephebic stage some septa reach the axis and there appears to be a weak axial structure of septal lobes and lamellae rather reminiscent of the genus *Grewingkia* Dybowski. Kaljo (1958, p. 104) also stated that major septa reach the axis. Ivanovskiy (1965*b*) listed *B. fervida* as a species of *Porfirieviella*, but Neuman (1969) included it in his revised genus *Streptelasma* (no mention was made by Neuman of *Porfirieviella*). The incomplete nature of Kaljo's material makes it difficult to classify the species with certainty. Similarly, *B. oanduensis* Kaljo, 1956, from the Keyla Horizon (Caradocian) of Estonia has long, thin major septa in the ? ephebic stage (Kaljo, 1956, Pl. I, fig. 10), but was included in his revised *Streptelasma* by Neuman (1969). It too was included in *Porfirieviella* by Ivanovskiy (1965*b*) but lacks sufficient illustration of its growth stages for definite classification. Ivanovskiy (1963) described the new Siberian Platform species *Brachyelasma siluriense* and *B. fossulatum* from the Upper Llandoverian, and *B. nikiforovae* from the Upper Caradocian. While all possess short, thin major septa in the ephebic stage, no figures were given of the earlier stages and their inclusion in *Streptelasma* cannot be certain. Ivanovskiy (1970*b*) later included all three species in the Upper Llandoverian *B. sibiricum* Nikolaeva from the Siberian Platform, but the synonymy of *B. siluriense* at least appears doubtful. More material, particularly of the younger stages, is necessary before a definite classification of these forms is possible. Similarly, *Brachyelasma concavifundatum* Ivanovskiy, 1965*a*, from the Upper Llandoverian of the Siberian Platform, lacks illustration of its early growth stages. However, it has thin, short major septa in the ephebic stage. Ivanovskiy (1970*b*) listed it as a subspecies of *B. sibiricum*.

Two new species of *Brachyelasma* were described from Tadzhikistan by Lavrusevich (1971). *B. agbaschiricum* from Horizon A (Upper Ordovician) has not been studied in its early growth stages. It has strongly dilated, short major septa in the ephebic stage, however, and may be a representative of *Streptelasma*, although the septa are thicker than is typical of that genus. *B. digitiforme* from Horizon H (Upper Llandoverian) also has been described only from ephebic sections, but these appear typical of *Streptelasma*, and the species when fully studied should probably be included in that genus.

Although no North American representatives of *Streptelasma*, as now defined, have been described (except the type species), several species show some similarities to that genus. *Zaphrentis affinis* Billings, 1865 (Lambe, p. 118, Pl. VII, fig. 6) from the Ellis Bay Formation (? Lower Llandoverian) of Anticosti Island shows thin major septa withdrawn from the axis in the ? ephebic stage, but earlier ontogenetic stages have not been described. Also *Zaphrentis patens* Billings, 1865, from the Jupiter Formation (Upper Llandoverian) of Anticosti Island (Lambe, 1901, p. 119, Pl. VIII, fig. 2) has thin, short major septa at the calice, but early ontogenetic stages are unknown. *Zaphrentis anticostiensis* Twenhofel, 1928, from the Gun River-Jupiter Formations (Middle-Upper Llandoverian) of Anticosti Island has thin, major septa somewhat withdrawn from the axis at the calice but extending to the axis below this level (Twenhofel, 1928, p. 114, Pl. I, figs 6–8). Unfortunately no sections of early growth stages have been figured, but it is likely that the species belongs to *Streptelasma*. *Brachyelasma bassleri* Pestana, 1960, from the Johnson Spring Formation (? Trenton) of California has thin major and minor septa strongly withdrawn from the axis in ephebic sections, but the early ontogenetic stages are not described and the species cannot be assigned to *Streptelasma* with certainty.

Two species from the ? Llandoverian of Iran recently described by Flügel and Saleh (1970), *Streptelasma ruttneri* and *S. shirgeshtensis*, have sufficiently well-described early growth stages to permit classification. *S. ruttneri* has long, thin, major septa extending to the axis in ephebic sections, while the septa are strongly dilated and also reach the axis in the neanic stage. It is probably a representative of *Helicelasma* Neuman, 1969. *S. shirgeshtensis* on the other hand has short, thin septa in the ephebic stage, while in the neanic stage they are long and moderately dilated. This species should probably be included in the genus *Borelasma* Neuman, 1969.

The only form from Australia previously described as belonging to *Streptelasma* is " *S.*" *australe* (Foerste, 1888), represented in the " Phacops bed " of the Yass district, New South Wales (Hill, 1940, p. 410). Link and Druce (1972, p. 7) listed " *Streptelasma* " *australe* from the Rainbow Hill Marl Member (Link, 1970) at Yass, apparently the horizon referred to by Hill. The age of this unit is regarded as late Ludlovian (Link, 1970 ; Link and Druce, 1972). From the descriptions of Hill (1940) it is apparent that " *S.*" *australe* possesses dilated septa in its early ontogenetic stages, together with some development of an axial structure. Hence it is not a representative of *Streptelasma* as defined by Neuman and its systematic position needs to be resolved.

Range. Middle Caradocian of Estonia, New York, ? California ; Upper Caradocian of Estonia, ? Siberian Platform ; Ashgillian of Sweden, Norway, Estonia, Urals, ? Tadzhikistan, ? Anticosti Island, Greenland ; Lower Llandoverian of Estonia, Venezuela and N.S.W. ; Upper Llandoverian of the Siberian Platform, ? Tadzhikistan, ? Kazakhstan, ? north-east U.S.S.R., ? Anticosti Island.

Streptelasma recisum sp. nov.

Plate I, figs 1–6

Derivation of name. Latin *recisus* =reduced, referring to the nature of the septa in the ephebic stage.

Material. Holotype SUP 45167. Paratypes SUP 45168–45175. Preserved in a colony of the tabulate coral, *Priscosolenia* sp., Bridge Creek Limestone. Late Lower or Early Middle Llandoverian.

Diagnosis. Small *Streptelasma* with average calice diameter 8–10 mm. Septa in neanic stage thin, short (reaching up to 0·5 corallite radius) and few in number (average 26–30). Minor septa very weakly developed ; stereozone absent. Tabulae horizontal or sagging axially.

Description. Corallum trochoid-ceratoid, weakly curved. Specimens incomplete but dimensions are of the order of at least 25 mm in height and maximum observed diameter of approximately 15 mm. Average corallite diameter 8–10 mm towards base of calice. Epitheca thin and peripheral stereozone lacking at all stages of growth.

In neanic stage (Plate I, figs 3, 6) septa are thin and extend almost to corallite axis. No axial structure formed but a few septal lamellae may be present in axial region. ? Cardinal septum shorter than other septa in neanic stage (Plate I, fig. 6), but owing to poorer preservation this cannot be confirmed in later growth levels. In neanic stage, at diameters of 5 mm and 7·5 mm, septa number 24 and ? 25 respectively (SUP 45172, 45171). In the ephebic stage, septa are withdrawn from axis, with a common length of about 0·5 of radius of corallite (Plate I, figs 1, 5). In ephebic sections available, at corallite diameters of 7·5–9·5 mm, septa number 26–30. Minor septa are difficult to distinguish and if present occur only as very fine ridges on corallite wall. High in calice, septa are reduced greatly in length (approximately 0·2 total corallite radius).

Tabulae mainly complete, moderately downflexed peripherally, horizontal or sagging axially, particularly in late stages of growth. Average spacing of tabulae 0·4–0·6 mm in small specimen (SUP 45175) and 0·5–1·2 mm in large form (SUP 45174). Complementary plates lacking.

Remarks. An interesting feature in regard to the growth form of *S. recisum* sp. nov. is its relationship to the massive tabulate coral *Priscosolenia* in which the described material grew commensally. Small flexures in the rugosan epitheca are common, indicating mutual adjustment of both corals during growth. Invaginations of the epitheca of *S. recisum* into the *Priscosolenia* colony are evident, possibly for support of the rugosan form (Plate I, fig. 3, particularly). The corallites of the *Priscosolenia* colony have also been considerably disturbed and distorted by the presence of the *Streptelasma* (Plate I, fig. 4).

The only described species of *Streptelasma* to show any strong similarities to *S. recisum* sp. nov. is *S. sibiricum* (Nikolaeva, 1955) from the Upper Llandoverian of the Siberian Platform. It resembles the New South Wales form in having comparable corallite dimensions, thin septa almost reaching the axis in the neanic stage and major septa of similar number (up to 35) and length (up to 0·5 of corallite radius) in the ephebic stage. It is also similar in having the minor septa lacking or very short in the ephebic stage, tabulae of similar shape and little or no peripheral stereozone. However, a clear distinction between the two forms may be made, since *S. sibiricum* has rather more dilated, thin, wedge-shaped septa in the ephebic stage and possesses a very prominent cardinal fossula with very short cardinal septum in the late neanic or early ephebic stage (Ivanovskiy, 1963, Pl. IX, fig. 1B). No definite fossula has been observed in any of the Bridge Creek material. There is evidence of very short minor septa in the material of Nikolaeva (1955, Pl. XLVIII, fig. 2a).

The form described by Twenhofel (1928) as *Zaphrentis anticostiensis* from the ? Middle-Upper Llandoverian of Anticosti Island shows quite strong similarities to *S. recisum*, but lacks illustration and detail of the early ontogenetic stages and so cannot be closely compared with it. Similarities include septal number (23 at corallite diameter of 8 mm), the minor septa reduced to " spines or nodes ", very thin major septa in the ephebic stage extending half or more than half-way to the axis, and the shape of the tabulae. Twenhofel stated (p. 114) that the major septa reach the axis below the level of the calice. A cardinal fossula with a short cardinal septum on the calice floor is also reported, although this is not illustrated by Twenhofel.

Genus GREWINGKIA Dybowski, 1873

1873 *Grewingkia* Dybowski, p. 384
1901 *Streptelasma*; Lambe, p. 109 (*non* Hall, 1847)
1927 *Kiaerophyllum* Wedekind, p. 17
1933 *Kiaerophyllum*; Scheffen, p. 16
1937 *Streptelasma*; (*part.*) Cox, p. 10
1948 *Streptelasma* (*Kiaerophyllum*); Wang, p. 102
1950 *Streptelasma* (*Kiaerophyllum*); Wang, p. 213
1956 *Grewingkia*; Hill, p. F268
1956 *Grewingkia*; Duncan, Pl. 21, figs 4a, b
1958 *Grewingkia*; Reiman, p. 34
1958 *Streptelasma* (*Kiaerophyllum*); Kaljo, p. 25
1960 *Brachyelasma*; Tcherepnina, p. 387 (*non* Lang, Smith and Thomas, 1940)
1960 *Grewingkia*; Pestana, p. 868
1961 *Streptelasma* (*Grewingkia*); Kaljo, p. 62
1961 *Rectigrewingkia* Kaljo, p. 62
1961 *Cyatholasma* Ivanovskiy, p. 120
1963 *Grewingkia*; Nelson, p. 33
1965*a* *Cyatholasma*; Ivanovskiy, p. 76
1965*a* *Grewingkia*; Ivanovskiy, p. 77
1965 *Grewingkia*; Kaljo and Klaaman, p. 420
1969 *Grewingkia*; Neuman, p. 33
1970*a* *Grewingkia*; Ivanovskiy, p. 121
1970 *Grewingkia*; Flügel and Saleh, p. 291
1971 *Grewingkia*; Lavrusevich, p. 49

Type species. Clisiophyllum buceros Eichwald, 1856, Upper Ordovician, Estonia. (Type horizon unknown.)

Diagnosis (abbreviated from Neuman, 1969, p. 33). Solitary streptelasmatid coral with cylindrical, ceratoid or trochoid corallum. Septa moderately or heavily dilated early in ontogeny, major septa long, forming narrow axial structure. Later in ontogeny major septa relatively short and thin, axial structure broad, composed of numerous irregularly intertwined septal lobes and lamellae. Calicular boss present or absent. Tabulae few or numerous, complete or incomplete, with or without complementary plates.

Discussion. The genus *Grewingkia* has been interpreted in many different ways by previous workers. Representatives described as belonging to *Kiaerophyllum* (Wedekind, 1927 ; Scheffen, 1933) were considered as being a subgenus of *Streptelasma* Hall by Wang (1948). Hill (1956), however, recognized the synonymy of *Kiaerophyllum* and *Grewingkia* and considered the latter to be distinct from *Streptelasma.* Kaljo (1958) applied the classification adopted by Wang but later (1961) recognized the synonymy suggested by Hill. He still, however, considered *Grewingkia* to be a subgenus of *Streptelasma.* Kaljo (1961) also erected a new genus, *Rectigrewingkia* (see discussion below), to include the species *G. anthelion* Dybowski and *G. lutkevitshi* Reiman (possibly with *G. eminens* Eichwald and *G. formosa* Dybowski, both needing revision). Neuman (1969) in a thorough revision of *Grewingkia* considered differences between the two genera to be gradational and restored *Rectigrewingkia* to the genus *Grewingkia.* Furthermore, Neuman revived the classification of Hill (1956) and gave *Grewingkia* the status of a full genus. This classification has been adopted by the author of this paper.

Densigrewingkia Neuman, 1969, and *Lobocorallium* Nelson, 1963, are similar to *Grewingkia* in possessing a reticulate axial structure. *Densigrewingkia* may be distinguished by its concave cardinal side and the considerable amounts of sclerenchyme in its axial structure, particularly in the early ontogenetic stages. *Lobocorallium* differs in having a prominent cardinal fossula and a tri-lobed corallum with the lobes corresponding to the cardinal and alar septa. As mentioned above, *Rectigrewingkia* Kaljo, 1961, is considered by Neuman (1969), and in this paper, to be a synonym of *Grewingkia.* The major distinguishing feature of *Rectigrewingkia,* according to Kaljo, is the presence of rounded septal lamellae in the axial structure, as compared with intertwined lobes and lamellae in species of *Grewingkia.* This appears to be only a gradational feature and is not considered important enough for formation of a separate genus. Further detail on the distinction of these genera may be obtained in Neuman (1969).

The genera *Bighornia* Duncan, *Bodophyllum* Neuman, *Dalmanophyllum* Lang and Smith and *Ditoecholasma* Simpson apparently all possess a solid axial structure of fused septal lobes and lamellae, together with complete, lamellar septa peripherally. Further study of these forms is required ; they may possibly be synonymous (Ivanovskiy, 1965*a* ; and Neuman, 1969). Their solid axial structure serves to distinguish them from *Grewingkia* in any case.

The species *G. dentiseptata* Lavrusevich, 1971, from Horizon B of the Zeravshan-Gissar region of Tadzhikistan was considered as Lower Llandoverian by Lavrusevich (1971). However, Horizon B is correlated with the Porkuni Horizon of Estonia (Lavrusevich and Menakova, 1971), and the latter is generally considered as Upper Ashgillian (Männil, 1966 ; Rõõmusoks, 1970). Ivanovskiy (1965*b*) also considered the fauna of Horizon B to be more typical of the Upper Ordovician. *G. dentiseptata* shows no close similarities to the New South Wales representatives of the genus.

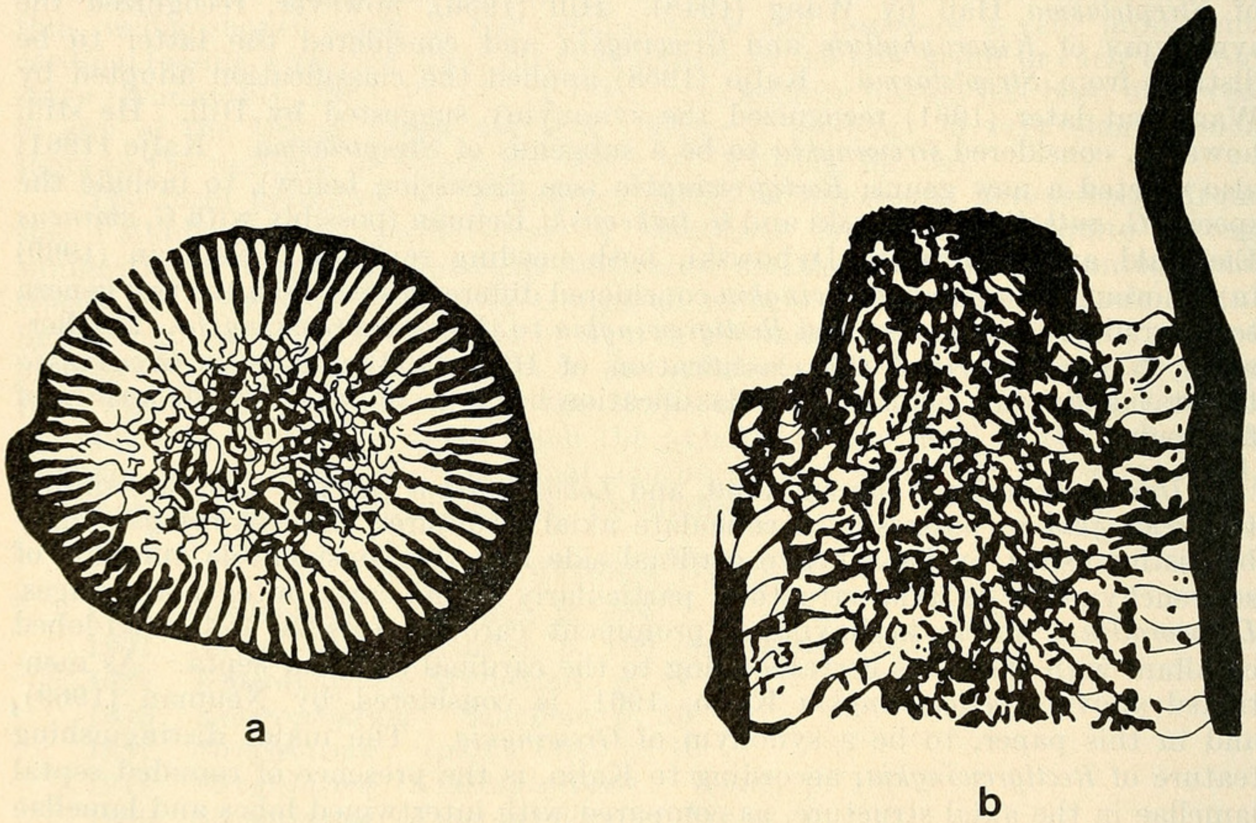
Range. Lower Caradocian of ? Scotland ; ? Middle Caradocian of California ; Upper Caradocian of Estonia, south-west Siberia, Manitoba ; Ashgillian of Ireland, Norway, Sweden, Estonia, Tadzhikistan, Quebec, Michigan ; Llandoverian of north-east Iran ; Lower or Middle Llandoverian of New South Wales.

Grewingkia parva sp. nov.

Plate I, figs 7–10 ; Text-fig. 2*a*, *b*

Derivation of name. Latin *parvus* =small.

Material. Holotype SUP 45151. Paratypes SUP 45152–45155, 63274. Brown Mudstone Horizon, Angullong district. Late Lower or Early Middle Llandoverian.



Text-fig. 2. *Grewingkia parva* sp. nov. *a*. SUP 45151a, holotype, transverse section, ×4. *b*. SUP 45152, paratype, longitudinal section, ×4.

Diagnosis. Small, subcylindrical *Grewingkia* with a prominent calicular boss and narrow peripheral stereozone. Corallite diameter up to 14 mm and maximum septal number ranges from 60 to 70. Minor septa long, up to half length of major septa, the latter typically showing dilated lobes at their axial extremities. Axial structure compact, approximately half corallite diameter. Tabulae mainly incomplete, weakly concave peripherally and strongly arched through axial zone.

Description. Subcylindrical corallum gradually tapering proximally although proximal end not preserved in any specimens. Epitheca thin, although all specimens have most of epitheca lacking. Average corallite diameter 11–14 mm with a height of at least 30 mm. Calice rather shallow with steep sides comprising stereozone and epitheca only (Plate I, fig. 9). Depth of calice 8 mm in preserved corallite height of 23 mm (total height probably at least 30–35 mm) in only specimen showing this feature (SUP 45152). Calicular boss prominent, with a height of 3 mm and diameter approximately 6 mm (SUP 45152). Calice floor flat around axial boss.

Peripheral stereozone narrow, with a width of 1–1·5 mm in ephebic sections, consisting of dilated septa and indeterminate ? sclerenchyme tissue. Septa of two orders, thin, with average number 64–70 (possibly 78 in SUP 45154), typically showing small, rounded projections irregularly developed on sides of septa. Major septa also show larger dilated lobes at their axial extremities. Minor septa extend well beyond peripheral stereozone, reaching a length of approximately half that of major septa. Axial structure has mainly consistent diameter throughout visible ontogeny (approximately the distal 23 mm) and is about half the diameter of corallite. Structure composed of tightly anastomosing septal lobes and lamellae, generally of smaller diameter than septa themselves.

Tabulae mainly complete with generally constant spacing of about 0·7 mm. Individual tabulae strongly arched in axial reticulate zone, conforming in shape with profile of calicular boss. In peripheral area tabulae are weakly sagging and may be faintly traced curving distally in peripheral stereozone. Complementary plates may be present in peripheral regions.

Remarks. Owing to lack of sufficient well-preserved material, the early ontogenetic stages of this species could not be studied. However, enough material was available to allow some comparisons with other representatives of the genus. None of the described species of *Grewingkia* are closely similar to *G. parva* sp. nov. However, some relationships with *G. anguinea* (Scheffen, 1933) from Division 5A (Lower Ashgillian) of Norway as described by Neuman (1969) may be seen in its corallite size, septal number and development of long minor septa, narrow stereozone, weak dilation of septa, convex tabulae with slightly concave peripheral portions and an axial structure of comparable dimensions. It clearly does not have the ceratoid growth form of *G. anguinea*, although this growth form only appears obvious in the more proximal regions, which have not been found preserved in any of the Angullong specimens. *G. anguinea* also differs in having a deeper calice with far less steeply inclined walls, a low, broad calicular boss, as a result of less convex tabulae, no broadly dilated septal lobes at the axial extremities of the major septa and a less dense axial complex of septal lobes and lamellae.

G. contexta Neuman, 1969, from the Boda Limestone (Ashgillian) of Sweden, also shows some similarities to the local form in having similar corallite dimensions, subcylindrical growth form (but ceratoid also), and a prominent calicular boss. Like *G. parva*, it also shows a narrow stereozone, generally long minor septa late in ontogeny and comparable size and appearance of the axial structure. However, it too may be clearly distinguished by showing a greater number of septa (90–100 average), lack of large lobes on the axial septal extremities and strong septal dilation in the cardinal quadrants until quite late in ontogeny, although it is possible those early stages have not been preserved in the Angullong specimens. Other differences include a less steep-walled calice, different shape of the tabulae (Neuman, 1969, p. 47, fig. 37J) and a fixing groove and rootlets on the convex side of the corallite.

The only other Llandoverian species described (*G. alternata* Saleh *in* Flügel and Saleh, 1970, from the Niur Formation of Iran) differs from *G. parva* in having much larger size (corallite diameter 30 mm), proportionately fewer septa (n/Dc = 5 for *G. parva* and 3·5 for *G. alternata*), less tightly anastomosing elements in the axial structure and a lack of lobes on the major septa.

The specimen sectioned at the base of the calice (SUP 45154, Plate I, fig. 10), while tentatively included in *G. parva*, shows a greater number of septa (78), longer minor septa and very pronounced dilated lobes on the axial extremities of the major septa.

Grewingkia neumani sp. nov.

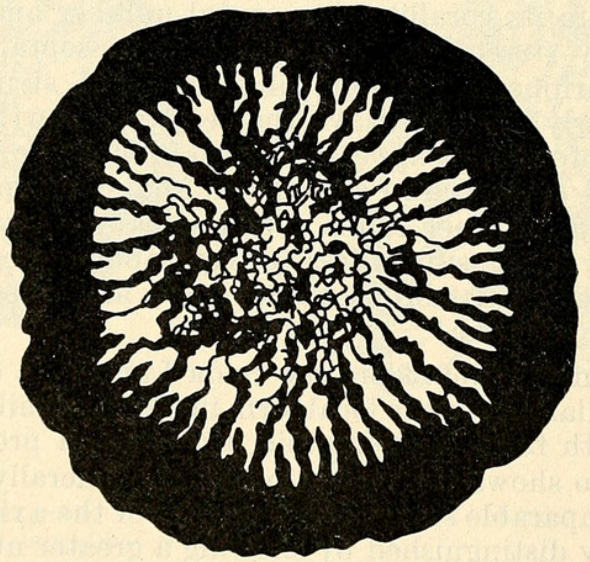
Plate I, figs 11, 12; Plate II, fig. 1; Text-fig. 3

Derivation of name. After Dr. B. Neuman, for his important studies of streptelasmatid corals.

Material. Holotype SUP 20115. Paratypes SUP 45156, 45157. Coarse calcarenite lens in Brown Mudstone Horizon, Angullong district. Late Lower or Early Middle Llandoverian.

Diagnosis. Trochoid or ? subcylindrical *Grewingkia* characterized by very deep calice, wrinkled epitheca and very broad peripheral stereozone. Corallite diameter ranges up to at least 35 mm and septal number ranges up to 96 in subcylindrical forms. Minor septa short, major septa typically showing club-like dilated lobes at axial extremities. Axial structure 0·3–0·5 corallite diameter, septal lamellae and lobes coarse in trochoid forms, more tightly intertwined and finer in smaller representatives. Tabulae slightly sagging peripherally, weakly convex axially.

Description. Corallum trochoid in two specimens while the other shows subcylindrical growth form. Epitheca smooth with transverse wrinkles evident in SUP 45157. Calice very deep and in largest specimen (holotype SUP 20115, with height of at least 30 mm) calice has approximate depth of 15 mm. Corallite diameter varies from about 50 mm at top of calice to about 30 mm near calice base in largest specimen. Subcylindrical specimen reaches diameter of 14 mm. Calical boss low and wide.



Text-fig. 3. *Grewingkia neumani* sp. nov. SUP 45156a, paratype, transverse section, ×4.

Broad peripheral stereozone of dilated septa and ? sclerenchyme. In largest specimen stereozone thins progressively from about 8 mm in width at base of calice to approximately 2 mm near its top. Maximum of about 60 septa in subcylindrical form, ranging to 94–96 in large trochoid specimen. Septa dilated so as to be in contact in stereozone where trabecular structure of septa is shown. Trabeculae, although poorly preserved, exhibit coarse fibres radiating obliquely from central axis (Plate II, fig. 1). Beyond stereozone major septa thin markedly to about 0·3 of their peripheral width and internal structure is obscured by recrystallization. Small " nodes " and undulations are evident on septa in this region in transverse section (Text-fig. 3). Minor septa barely extend beyond peripheral stereozone, while in subcylindrical form they extend approximately 0·3 of the distance between stereozone and axial structure. Width of axial structure ranges from 0·3 to 0·5 corallite diameter and it is composed of loosely intertwined septal lamellae and lobes. In subcylindrical form septal elements in axial structure are finer and more tightly reticulate. Tabulae sagging adjacent to peripheral stereozone, weakly arched in axial region. Tabular spacing approximately 1 mm.

Remarks. The only described species of *Grewingkia* to show any strong similarities to *G. neumani* is the Upper Caradocian *G. altaica* (Tcherepnina, 1960) from the Altai and Salair areas of south-west Siberia. Features in common include similar corallite dimensions and growth form (for the large, trochoid representatives), coarse, intertwined septal lamellae of the axial structure, and a broad stereozone consisting mainly of dilated septa. In particular, the transverse section illustrated by Ivanovskiy (1961, Pl. XV ; 1965*a*, Pl. XXVI, fig. 3) appears closely comparable. However, differences may be seen in the rather more irregular and wavy nature of the major septa in the region between the stereozone and axial structure of *G. altaica* although this is not as apparent in the Altai material of Tcherepnina (1960, Pl. O–X, fig. 3*b*). Also in *G. altaica* the tabulae are more strongly downflexed near the periphery and there is no development of club-shaped dilated lobes on the axial ends of the major septa such as is found in *G. neumani*.

The smaller, subcylindrical specimen assigned to *G. neumani*, while differing in possessing longer minor septa, rather wavy major septa and a more densely compacted axial structure, is included in the species because of its similarly constructed broad stereozone. If further material is found that confirms there is a sharp distinction between these two types, then it may be advisable to consider the latter form perhaps as a new species or as a subspecies of *G. neumani*. For the present, however, they are grouped together.

G. neumani may be distinguished from *G. parva* sp. nov. primarily by the broad peripheral stereozone, shorter minor septa and deeper calice of the former. A feature in common, however, is the development of the dilated axial lobes on the major septa. This characteristic is apparently unique to the local representatives of *Grewingkia*. However, some Silurian species of the genus *Calostylis* show this feature, Smith (1930*a*, p. 261) recording that " individual strands of this peripheral and axial tissue . . . dilate so as to form numerous nodes, and the numerous free endings are nearly always swollen and rounded ". Possible affinities between *Grewingkia* and *Calostylis* are discussed further below.

The most useful descriptions of the septal microstructure of *Grewingkia* have been those of Kato (1963), Ivanovskiy (1967) and Wang (1950). Kato (1963, Text-fig. 10. 3) illustrated fibres diverging obliquely from a central axis in a septum of " *Grewingkia* sp.". Ivanovskiy (1967, Fig. 3*d*) showed a similar structure in *G. altaica*. The septal microstructure of the New South Wales representatives of *Grewingkia* is very poorly preserved and only the holotype of *G. neumani* (SUP 20115) shows this feature in any detail. As can be seen from Plate II, fig. 1, a rather coarse system of fibres diverging from a central axis occurs in the dilated septa of the peripheral stereozone. Beyond the stereozone recrystallization has obscured the microstructure but a similar structure on a smaller scale would be expected, according to Kato and Ivanovskiy. The septal microstructure illustrated by Ivanovskiy (1967, Fig. 3*d*) for *G. altaica* is quite closely comparable to that of *G. neumani*.

Family CALOSTYLIDAE Roemer, 1883

Diagnosis (modified from Hill, 1956, p. F296). Solitary and colonial corals with major and minor septa perforate ; axial ends of major septa lobed and reticulate, forming spongy axial structure. Tabulae generally distally arched in axial region ; dissepiments lacking. Epitheca typically not developed over entire corallum.

Discussion. The family Calostylidae is taken here to include the genera *Calostylis* Lindström, *Palaearaea* Lindström and *Helminthidium* Lindström, all characterized by possession of perforate septa. The taxonomic affinities of this group of corals, however, are open to question, as mentioned by Hill (1956), although they are generally recognized as being probably closest to the streptelasmatids.

Ivanovskiy (1961), in his discussion of the family Calostylidae, described a new genus, *Cyatholasma*, from the Upper Caradocian of the Salair region of south-west Siberia. *Cyatholasma* was characterized by complete, lamellar septa in the peripheral region of the corallite and a reticulate structure of septal lobes and lamellae at the axis. The synonymy of this form with *Grewingkia* Dybowski was recognized by Ivanovskiy (1967, 1970*a*). However, the genus *Calostylis* possesses perforate septa peripherally but an axial structure similar to that of "*Cyatholasma*". Ivanovskiy (1961) thus inferred that "*Cyatholasma*" represented a link between the Middle-Upper Ordovician Streptelasmatidae which have complete, lamellar septa throughout, and the Upper Ordovician-Silurian Calostylidae which have perforate, incomplete septa. He subsequently (1965*a*, 1968) included *Grewingkia* in the family Calostylidae, although the genus has been generally placed in the Streptelasmatidae by most workers (e.g. Dybowski, 1873 ; Hill, 1956 ; Neuman, 1969). As representatives of the Streptelasmatidae (e.g. *Streptelasma* Hall, see above and Neuman, 1969) may often show traces of septal lobes and lamellae in the axial zone at some stage of their ontogeny, it seems preferable to include *Grewingkia* in that family. However, the evident close relations of *Calostylis* to *Grewingkia* would suggest that the calostylids are most probably an aberrant branch of the Streptelasmatidae. It may in fact be best to consider *Grewingkia* and *Calostylis*, together with related forms, as representatives of a distinct subfamily of the Streptelasmatidae, characterized by forms with well-developed axial reticulate structure. Further work on these and similar forms is required before a definitive statement on the systematic position of the calostylids is possible. Particularly important in this regard would be ontogenetic studies of the species of *Calostylis* and *Grewingkia*. Hence for the present the family Calostylidae is retained for *Calostylis* and other perforate genera.

Genus Calostylis Lindström, 1868

1865 *? Clisiophyllum* Kjerulf, p. 22 (not seen)
1868 *Calostylis* Lindström, p. 421
1878 *Calostylis* ; Nicholson and Etheridge, p. 65
1906 *Calostylis* ; Foerste, p. 322
1912 *Calostylis* ; Reed, p. 123
1917 *Calostylis* ; Foerste, p. 200
1930*a* *Calostylis* ; Smith, p. 257
1930*b* *Calostylis* ; Smith, p. 294
1958 *Calostylis* ; Kaljo and Reiman, p. 27
1961 *Calostylis* ; Ivanovskiy, p. 119
1963 *Calostylis* ; (*? part.*) Ivanovskiy, p. 92
? 1965 *? Calostylis* ; Stumm, p. 47
1966 *Calostylis* ; Sytova and Ulitina, p. 243
1971 *Calostylis* ; Lavrusevich, p. 69

Type species. C. cribaria Lindström, 1868 = *? Clisiophyllum denticulatum* Kjerulf, 1865. Wenlockian, Gotland.

Diagnosis. Corallum solitary or often with lateral buds ; having perforate septa which degenerate axially and peripherally into a reticulate structure. Tabulae complete and incomplete, distally arched ; dissepiments absent. Epitheca may not be developed over entire corallum.

Discussion. A useful summary of previous work on the genus *Calostylis* has been given by Ivanovskiy (1961). He suggested a phylogenetic scheme whereby *Calostylis* was seen as a Lower Silurian intermediate between *Cyatholasma* (=*Grewingkia*), of Late Ordovician age, and the genus *Helminthidium* Lindström, a Middle-Upper Silurian form. *Helminthidium* differs from *Calostylis* in that the septa are completely broken down to a retiform condition and individual radial septa cannot be distinguished. The other member of the family Calostylidae, the early Silurian *Palaearaea* Lindström, is an astreoid form having perforate septa and " spongy " axial structure. Ivanovskiy (1961) suggested that *Palaearaea* was derived from " *Cyatholasma* " but it could equally have been derived from *Calostylis.*

The species composition of *Calostylis* is badly in need of revision. *C. tomesi* Smith, 1930, from the Wenlock Limestone (Upper Wenlockian) of Shropshire, *C. parvula* Foerste, 1917, from the " Laurel Limestone " (Wenlockian) of Ohio and *C. dravidiana* Reed, 1912, from the ? Llandoverian of Spiti, Central Himalayas, require detailed thin-section study before their affinities are known. The type species, *C. denticulata* (Kjerulf, 1865), is a very variable form, and there are several species which are very similar to it, and may in fact be found to be synonymous when they are studied in more detail. Among these forms are *C. togata* Smith, 1930, from the Purple Shales (Upper Llandoverian) of Shropshire, and *C. spongiosa* Foerste, 1906, from the Waco Limestone (Upper Llandoverian) of Kentucky, both of which were stated to be closely similar to *C. denticulata* by Smith (1930*a*). *C. concavifundatus* Reiman *in* Kaljo and Reiman, 1958, from the Porkuni Horizon (Upper Ashgillian) of Estonia and Llandoverian of the Siberian Platform is also similar to the type species and was listed as a synonym of it by Ivanovskiy (1970*b*).

C. aberrans Smith, 1930, from the Pentamerus Beds and Purple Shales (Upper Llandoverian) of Shropshire, is closely similar to *C. roemeri* Smith, 1930, differing only in its distorted growth form. There are intermediate forms between it and *C. roemeri* (Smith, 1930*a*, 1930*b*) and it may be better considered as synonymous with or a subspecies of *C. roemeri.*

The phaceloid Middle Devonian species from Kentucky, *C. ? trigemma* (Davis, 1887), as described by Stumm (1965) differs from the typical Ordovician-Silurian representatives of the genus in its growth habit and very weakly developed axial structure. Its systematic position is uncertain.

Range. Upper Ashgillian of Estonia; Lower-Middle Llandoverian of Estonia, Siberian Platform, Tadzhikistan, New South Wales; Upper Llandoverian of England, Scotland, Norway, Gotland, Estonia, Urals, Tadzhikistan, ? Central Himalayas, Kentucky; Wenlockian of England, Gotland, Tadzhikistan, Ohio; ? Ludlovian of Kazakhstan.

Calostylis panuarensis sp. nov.

Plate II, figs 2–10; Text-fig. 4*a*, *b*

Derivation of name. After the major stream in the area, Panuara Rivulet, an alternative name for Four Mile Creek.

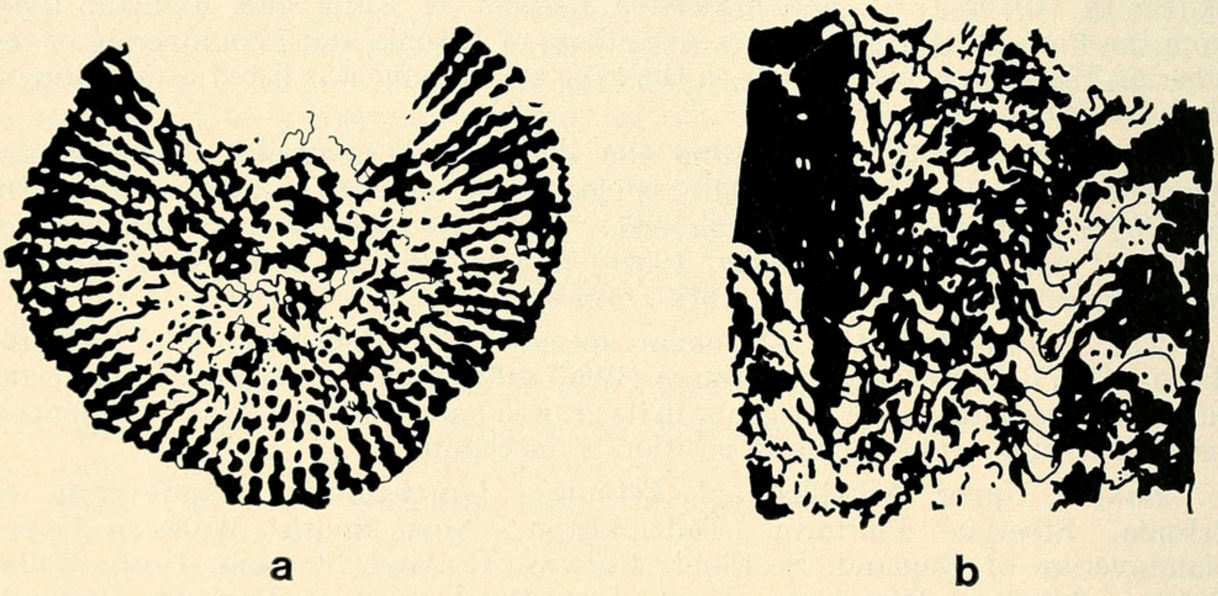
Material. Holotype SUP 69220. Paratypes SUP 45158–45166, 63275, 69221. Brown Mudstone Horizon, Angullong district. Late Lower or Early Middle Llandoverian.

Diagnosis. *Calostylis* either solitary or with rare lateral buds, cylindrical, with average corallite diameter of 12 mm. Broad axial and narrow peripheral reticulate zone; 66–76 strongly perforate septa. Tabulae sagging, with axial convex zone. Abundant sclerenchyme filling of corallite interior.

Description. Corallum solitary, in three cases (SUP 45163, 45165, 63275) showing budding. Increase is lateral and non-parricidal. Corallites cylindrical, slightly tapering proximally with sharp increase in diameter soon after budding takes place (Plate II, fig. 2). Epitheca not preserved in any specimens. Corallite diameter varies from 10·5 to 15·5 mm in material available, with an average of 12–13 mm. Weak calicular boss present but complete calice not preserved in any specimen. Disposition of layering of sclerenchyme in corallites suggests rather shallow calice.

Septa entirely perforate, 66–76 in number, breaking down axially and to a lesser extent peripherally, into anastomosing, reticulate structure. Minor septa long, extending 0·5–0·7 of length of major septa, as best illustrated by holotype SUP 69220 (Plate II, figs 8, 9; Text-fig. 4*a*). Individual septa not traceable axially beyond margin of central reticulate structure, which varies from about 4·5 to 5 mm in diameter, i.e. slightly more than 0·3 of corallite diameter. Peripheral reticulate zone, where it can be clearly differentiated, reaches diameter of about 1·5 mm, averaging 0·1 of diameter of corallite.

Tabulae generally not clearly defined, strongly sagging near margin of axial structure and prominently convex in the axial zone, although difficult to trace actual plates in this area. Tabulae may be defined by abundant sclerenchyme deposits and layers of sediment, suggestive of periodic pauses in growth (e.g. SUP 45166). Average spacing of tabulae of about 0·7–1 mm.



Text-fig. 4. *Calostylis panuarensis* sp. nov. *a*. SUP 69220b, holotype, transverse section, ×4. *b*. SUP 45158b, paratype, longitudinal section, ×4.

Remarks. Of the described species of *Calostylis*, four show some similarities to *C. panuarensis*. Of these, the type species, *C. denticulata* (Kjerulf, 1865) from the Llandoverian-Wenlockian of Scandinavia and Central Asia has perhaps the closest affinities. From the descriptions by Smith (1930*a*) of material from Gotland and Norway, similarities may be seen in the cylindrical, solitary growth form together with lateral, non-parricidal increase in some specimens, long minor septa, almost extending to the axial zone, the size and nature of axial reticulate structure and the shape and disposition of the tabulae. The transverse section illustrated by Smith (1930*a*, Pl. XI, fig. 5) in particular appears very similar to the local form. However, the general size of corallites (common diameter 20 mm, reaching 35 mm in some cases, although some may be as small as 13 mm), the usually more clearly defined and wider peripheral reticulate zone, together with a greater number of septa (average about 90, compared to 66–76 in *C. panuarensis*) serve to distinguish it from the Angullong species. According to Lindström (1868), *C. denticulata* may even have up to 140 septa.

C. denticulata has also been described from Horizon D (Lower Llandoverian) to Horizon K (Lower Wenlockian) of the Zeravshan-Gissar region of Tadzhikistan (Lavrusevich, 1971). The form from this area differs slightly in showing a greater tendency of budding, larger size with proportionally greater number of septa, generally thinner septal elements and a wide peripheral reticulate zone. It is evident that the two species are very closely related.

Several of the inadequately studied species of *Calostylis* show similarities to *C. panuarensis* also. *C. togata* Smith (1930*a*), from the Purple Shales of Shropshire, is comparable to *C. panuarensis* in the features of growth form, septal size and axial structure and is also of more comparable dimensions (average corallite diameter 13 mm). However, it too differs in having a larger number of septa (approximately 90) and a considerably broader peripheral reticulate zone. As Smith (1930*a*, 1930*b*) pointed out and was discussed above, it is quite likely that *C. togata* may represent a smaller variant of *C. denticulata*.

The two described North American species also show similarities to *C. panuarensis*. *C. spongiosa* Foerste, 1906, from the Waco Limestone (Upper Llandoverian) of Kentucky is comparable in growth form, size and axial structure but has a greater number of septa (100), weakly developed minor septa and a wide, thickened peripheral zone.

C. parvula Foerste, from the Laurel Limestone (Wenlockian) of Ohio is of comparable size, septal number and axial structure, but is more trochoid in growth form, has more clearly differentiated minor septa and the peripheral zone is not as clearly developed. However, this species has apparently not been studied in thin section and hence the internal structures are imperfectly known.

Therefore, while the local form is assigned here to a new species, further study of some of the European and North American representatives of *Calostylis* may lead to a revision of its taxonomic position. Particularly important in this respect would be a restudy of the smaller variants of *C. denticulata*.

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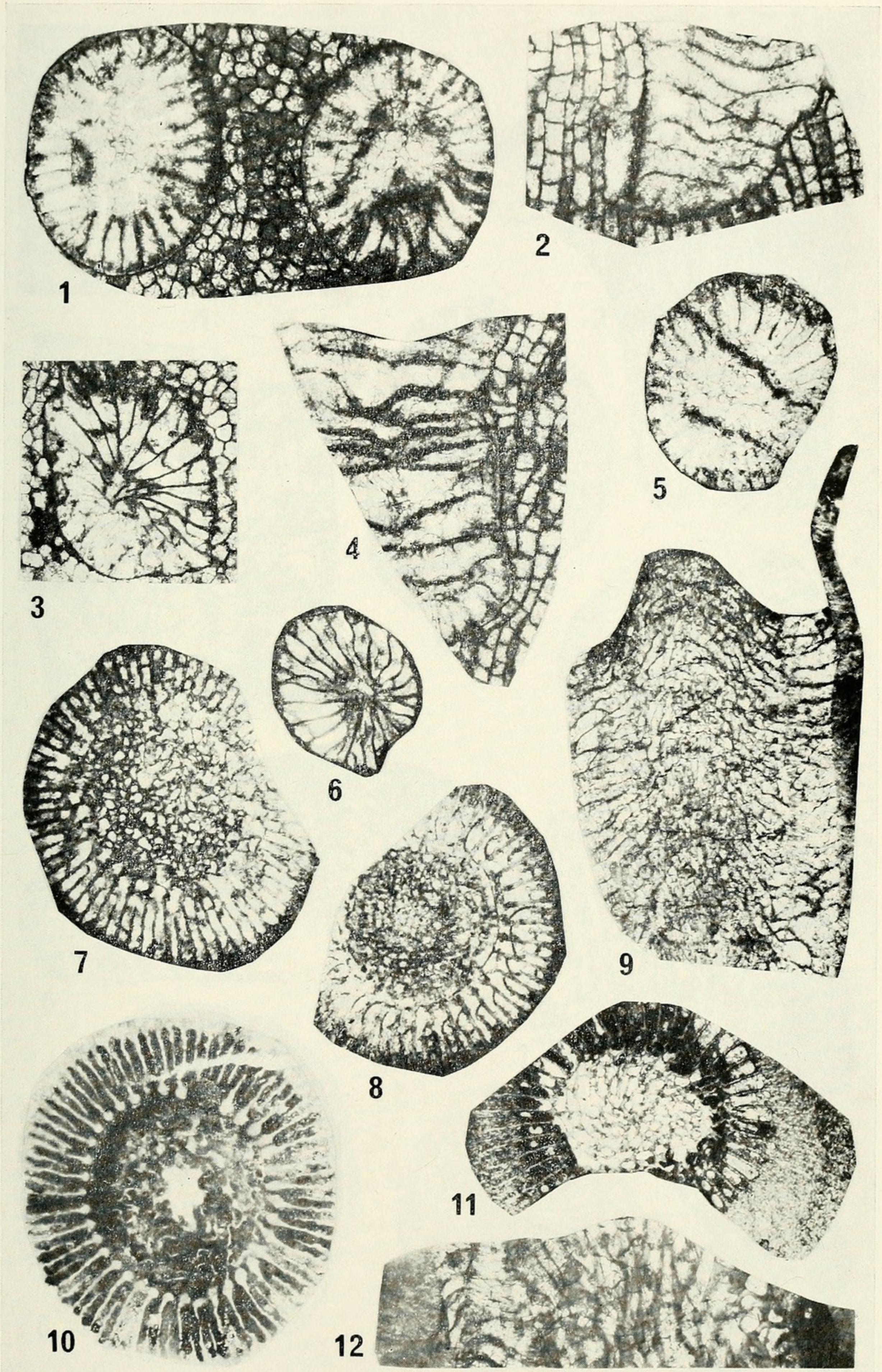
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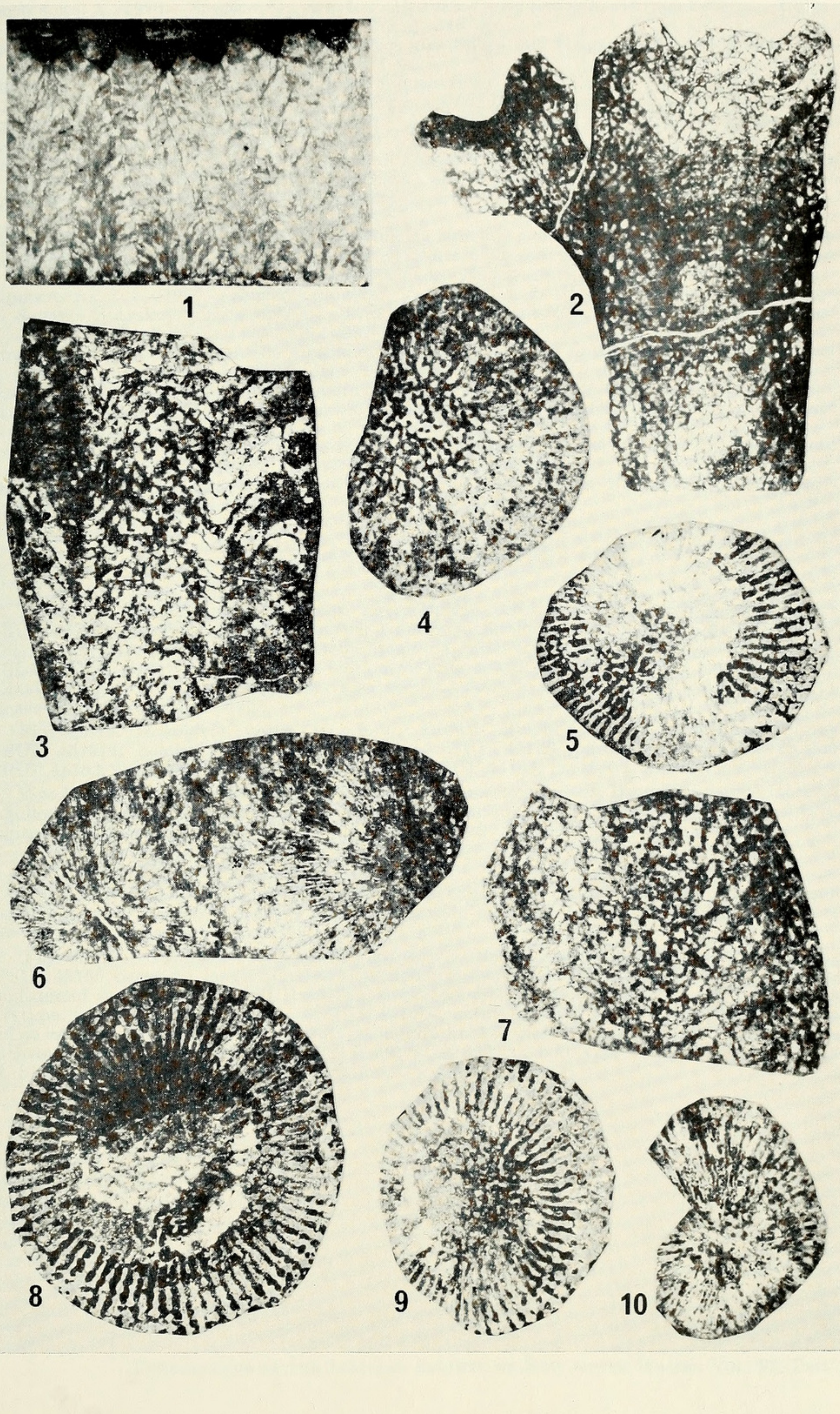
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EXPLANATION OF PLATES

PLATE I

Figs 1–6. *Streptelasma recisum* sp. nov., Bridge Creek Limestone, Bridge Creek, ×4. 1. SUP 45167 (at left of figure), holotype, transverse section, ephebic stage ; SUP 45168 (at right), paratype, transverse section, ephebic stage. 2. SUP 45175, paratype, longitudinal section. 3. SUP 45171, paratype, transverse section, neanic stage. 4. SUP 45174, paratype, longitudinal section. 5. SUP 45169, transverse section, ephebic stage. 6. SUP 45172, paratype, transverse section, neanic stage.

Figs 7–10. *Grewingkia parva* sp. nov., Brown Mudstone Horizon, Angullong, ×4. 7. SUP 45151a, holotype, transverse section. 8. SUP 45153, paratype, transverse section. 9. SUP 45152, paratype, longitudinal section. 10. SUP 45154, paratype, transverse section.

Figs 11–12. *Grewingkia neumani* sp. nov., coarse calcarenite lens, Brown Mudstone Horizon, Angullong. 11. SUP 20115a, holotype, transverse section, ×2. 12. SUP 20115c, holotype, longitudinal section, ×4.

PLATE II

Fig. 1. *Grewingkia neumani* sp. nov., coarse calcarenite lens, Brown Mudstone Horizon, Angullong. SUP 20115b, holotype, transverse section of peripheral region of corallite in calice, howing poorly preserved trabeculae, ×8.

Figs 2–10. *Calostylis panuarensis* sp. nov., Brown Mudstone Horizon, Angullong. 2. SUP 45165, paratype, longitudinal section showing lateral bud, ×3. 3. SUP 45158b, paratype, longitudinal section, ×4. 4. SUP 45162a, paratype, transverse section, ×4. 5. SUP 45161a, paratype, transverse section, ×4. 6. SUP 45163a, paratype, transverse section showing lateral bud at left, ×4. 7. SUP 45162b, paratype, longitudinal section, ×4. 8. SUP 69220a, holotype, transverse section at level of calice, ×4. 9. SUP 69220c, holotype, transverse section, ×4. 10. SUP 45158a, paratype, transveıse section, ×4.