UPPER ORDOVICIAN STREPTELASMATID CORALS FROM SCANDINAVIA

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Abstract. The present paper deals with the morphology, ontogeny, and taxonomy of solitary rugose corals belonging to the family Streptelasmatidae from the Upper Ordovician (Harjuan) sequence of central Sweden and southern Norway. The internal structures of the corallites have been examined by means of serial peel sections and special attention paid to the ontogeny of the various species. The variation of the morphological structures within the various genera are discussed and diagrammatically illustrated. Four new genera viz. Helicelasma n.g., Bodophyllum n.g., Densigrewingkia n.g., and Borelasma n.g. are proposed. Altogether 17 species are described of which 11 are new. Examination of the syntypes of Streptelasma corniculum Hall, 1847, the type species of Streptelasma, revealed that this genus is a senior subjective synonym of Brachyelasma. A lectotype of S. corniculum is selected and described.

INTRODUCTION

In Scandinavia representatives of the family *Strept-elasmatidae* entirely dominate the rugose coral faunas during the Upper Ordovician (Harjuan) epoch with respect to frequency of individuals as well as to the number of species.

In this study great emphasis has been laid on the ontogenetic development of the corallite. In the writer's opinion, the characters connected with the ontogenetic changes of the structures in the corallite have great phylogenetical importance and furnish a reliable foundation for the classification of rugose corals, at least at the species and genus level. Usually one longitudinal and a few transverse sections of the corallite are not sufficient for a safe characterization of the species. The variation of different morphological elements within a corallite as well as between different individuals is considerable in many species. Without making many closely spaced transverse sections of one corallite and examining a number of different corallites, it is difficult to find reliable criteria for the definition of the species.

Material

In the lithologically varied Upper Ordovician (Harjuan) sequence of Scandinavia rugose corals occur abundantly in only a few divisions. Those parts of the sequence which consist of mudstones or calcilutites are almost devoid of corals and other large sessile organisms. In addition to the divisions listed below, rugose corals are not rare in the calcarenitic beds of the lower Harjuan Slandrom Formation in those places where this formation overlies the Kullsberg Limestone. These rugose corals have not here been investigated as it was deemed advisable to treat them together with the Middle Ordovician (Viruan) coral faunas.

Material from the following formations and areas is treated here.

1. Boda Limestone, Siljan district. The Boda Limestone occurs as thick reef-like lentils surrounded by a normal sequence which mainly consists of finely nodular argillaceous limestones and mudstones. The base of the reef-like bodies is of post-*Pleurograptus linearis* age, and the top of the reefs coincides with the boundary between Ordovician and Silurian. The main extension of the reefs seems to correspond with the *Dalmanitina* beds in the interreef sequence. Numerous knolls of Boda Limestone are known within the Siljan district (Thorslund, 1936), and many of them are extensively quarried. The reef core is massive and contains few rugose corals. The flank deposits consist of stratified, variegated calcarenites with

Table 1

Stages		Dalarna			
Estonia	Sweden	Interreef facies	Reef facies	Oslo area	
Porkuni	Tommarp	Dalmanitina Beds	Boda	5 b	
Pirgu	Jerrestad	Nittsjö F. Jonstorp F.	Limestone	$\begin{array}{c} 5 \text{ a} \\ 4 \text{ d} \\ 4 \text{ c} \beta - \gamma \end{array}$	

Upper Ordovician (Harjuan) stratigraphy mainly after Jaanusson (1963).

argillaceous intercalations, locally with numerous corals. The bulk of the material from the Boda Limestone described in this paper comes from the flank deposits; the main collecting locality has been the northeast end of the large quarry of Osmundsberget. In addition, specimens from a number of other reef knolls have been available.

The rich fauna of rugose corals of the Boda Limestone has previously been treated only in two papers by Lindström (1873, 1880) who recorded the following species:

Cyathophyllum mitratum (Hisinger). Not figured nor identifiable on the basis of available information nor material from the locality. Ptychophyllum craigense M'Coy (= Grewingkia bilateralis n.sp., G. contexta n.sp., Streptelasma primum (Wedekind), and S. cyrtum n.sp.)

As a result of the writer's studies, the following species of rugose corals may be listed from the Boda Limestone:

Streptelasma primum (Wedekind) Streptelasma cyrtum n.sp. Grewingkia bilateralis n.sp. Grewingkia contexta n.sp. Bodophyllum osmundense n.sp.

Among non-streptelasmatid rugose corals, *Tryplasma* n.sp. and *Paliphyllum* n.sp. have been recorded and described recently (Neuman, 1968).

2. Dalmanitina Beds in the Siljan district. These beds form the topmost Ordovician division in the interreef area of the district. They correspond to the main, upper part of the Boda Limestone and consist of mudstone with some intercalations of limestone and calcareous sandstone, mainly in the basal part of the formation (Thorslund, 1935). Rugose corals occur in the limestone beds but are not common.

Lindström (1880, p. 35) and Thorslund (1935,

pp. 12–13) reported *Ptychophyllum craigense* M'Coy from these beds. The present study showed that specimens referred to this species belong to *Streptelasma primum* and *?Borelasma* sp. which are the only rugose corals hitherto found in these beds in the Siljan district.

3. Dalmanitina Beds, Östergötland. A large fauna, including rugose corals, has been collected mainly during the last century in an exposure at Borenshult on the northern bank of Göta Canal. This exposure is no longer accessible. The bulk of the material seems to come from the Dalmanitina Beds, but the material may also include specimens which are possibly of Lower Llandoverian age. In addition to Borenshult, the available material also included specimens from Råsnäs (lowermost Llandovery?).

Lindström (1880) described *Ptychophyllum* craigense M'Coy (=*Streptelasma ostrogothicum* n.sp.) from Borenshult. According to the present investigation, the Borenshult fauna includes the following species:

Streptelasma primum (Wedekind) Streptelasma ostrogothicum n.sp. Helicelasma simplex n.sp. Borelasma crassitangens n.sp.

4. Dalmanitina Beds, Västergötland. In the Billingen area, these beds consist mainly of calcilutites and mudstones; corals are very rare. In the southern part of the Falbygden area, parts of the formation are developed as calcareous siltstone with occasional beds which are calcarenitic. At Allebergsände, one bed abounds in rugose corals (cf. Troedsson, 1921, p. 8), representing one single species described by Lindström (1873, 1880) as Ptychophyllum linnarssoni (= Streptelasma linnarssoni (Lindström)). No other rugose coral has hitherto been identified from these beds in Västergötland.

5. Upper Ordovician erratic boulders from Oil ("Öjle") Myr, Gotland. These boulders of finegrained limestone are derived from the bedrock somewhere north of Gotland and are probably of Porkuni (Dalmanitina) age. The fauna described by Wiman (1901) is extensively silicified. The examined rugose corals were etched out by Wiman.

The most common species of rugose corals in these boulders was referred to by Wiman (1901, p. 186) as *Lindströmia dalmani* (E. & H.) and is redescribed here as *Bodophyllum oilense* n.sp.

6. Division 5a, Oslo region. This limestone division is very rich in corals (Kiær, 1899). Some rugose corals have been described by Wedekind (1927), and an attempt at a monographic treatment of the whole rugose coral fauna was made by Scheffen (1933). The types of the species erected by these authors have here been restudied. A large number of rugose corals from these beds was available for the present work. The bulk of the material comes from Stavnæstangen, Bjørkeåsen, and Vestre Svartøy of Ringerike. Additional material from Herøy of the Langesund-Skien area has been studied. Rugose corals were previously not described from this division in the latter area.

Wedekind (1927) described two species from 5a at Stavnæstangen, viz. *Kiaerophyllum kiaeri* Wedekind (= *Grewingkia buceros* (Eichwald)) and *Dybowskia prima* Wedekind (= *Streptelasma primum* (Wedekind)).

A large number of new species were described by Scheffen (1933) from 5a of Stavnæstangen and Vestre Svartøy. The present examination of Scheffen's types showed that most of his species are synonyms of other species. Scheffen also established a number of species which were provided with a brief description but not figured. These species ought to be considered *nomina nuda* in agreement with the decision of the second International Geological Congress at Bologna that fossil species published after 1882 are not valid if not accompanied by a figure (Weissermel, 1934). The following species were described by Scheffen (1933):

Streptelasma saelaboni Scheffen

Dybowskia prima Wedekind (= Streptelasma primum (Wedekind))

- Dybowskia radiata Scheffen (= Streptelasma saelaboni Scheffen)
- Dybowskia gravis Scheffen, nomen nudum (= Grewingkia buceros (Eichwald))
- Dybowskia euryacantha Scheffen, nomen nudum (= Grewingkia buceros (Eichwald))
- Dybowskia rostrata Scheffen, nomen nudum (= Streptelasma primum (Wedekind))
- Dybowskia concamerata Scheffen (= Streptelasma primum (Wedekind))
- Dybowskia solida Scheffen, nomen nudum (=Streptelasma primum (Wedekind))
- Dybowskia undulata Scheffen (=Streptelasma primum (Wedekind))
- Dybowskia complanata Scheffen (= Streptelasma primum (Wedekind))
- Dybowskia collucata Scheffen (= Streptelasma primum (Wedekind))
- Dybowskia luminosa Scheffen, nomen nudum (= Streptelasma primum (Wedekind))
- Kiaerophyllum equinum Scheffen, nomen nudum (= Grewingkia buceros (Eichwald))
- Kiaerophyllum injunctum Scheffen, nomen nudum (= Grewingkia buceros Eichwald))
- Kiaerophyllum compactum Scheffen, nomen nudum (= Grewingkia buceros (Eichwald))
- *Kiaerophyllum dumosum* Scheffen (= *Grewingkia buceros* (Eichwald))
- Kiaerophyllum pyrgoideum Scheffen, nomen nudum (= Densigrewingkia pyrgoidea n.sp.)
- *Kiaerophyllum semilunatum* Scheffen (=*Grewingkia buceros* (Eichwald))
- Kiaerophyllum kiaeri Wdkd (=Grewingkia buceros (Eichwald))
- Kiaerophyllum kiaeri Wdkd var. insaeptum Scheffen (= Grewingkia buceros (Eichwald))
- *Kiaerophyllum anguineum* Scheffen (= *Grewingkia anguinea* (Scheffen))

The writer's studies show that the following species of streptelasmatid corals can be recognized in division 5a:

Streptelasma primum (Wedekind) Streptelasma eccentricum n.sp. Grewingkia buceros (Eichwald) Grewingkia anguinea (Scheffen) Densigrewingkia pyrgoidea n.sp. Bodophyllum euthum n.sp.

7. Division 5b, Oslo region. The topmost Ordovician division of the Oslo region consists mostly of calcareous sandstone. Rugose corals are not unusual in these beds but it is difficult to obtain complete corallites from the hard rock. From the localities in Ringerike, Scheffen (1933) recorded the following species.

Lindströmia laevis Nich. & Eth. (=Bodophyllum euthum n.sp.)

Stegophyllum densum Scheffen



Fig. 1. A, External measurements of the corallite (a, length; b, diameter of the calice). B, Measurements of the transverse section (c, the diameter in cardinal-counter direction; d, the diameter in alar-alar direction).

Tyria incertum Scheffen Tyria emaciata Scheffen, nomen nudum

The two latter species are compound corals, the two former have not been identified by the present writer in the material available from 5b. *Stegophyllum densum* has not been seen by the author since Scheffen's types could not be found. Scheffen's illustrations yield little information on this species.

The bulk of solitary rugose corals from 5b of Ringerike examined by the writer belongs to a *Borelasma* sp. The material is too fragmentary for a safe identification.

Spjeldnæs (1961) described silicified material of *Holophragma duncanae* (=Bodophyllum duncanae (Spjeldnæs)) from division 5b of the Lange-sund-Skien area. His material has been redescribed in the present paper.

The coral specimens studied originate from various collections and the following abbreviations are used in order to indicate the whereabouts of particular specimens:

- AMNH = American Museum of Natural History, New York
- OM = Palaeontological Museum, Oslo (Paleontologisk Museum).
- RM = Palaeozoological Department, State Museum of Natural History, Stockholm (Naturhistoriska Riksmuseet).
- SGU = Museum of the Geological Survey of Sweden, Stockholm (Sveriges Geologiska Undersökning).

UM = Museum of the Paleontological Institute, University of Uppsala.

Methods

Most of the specimens examined were cleaned by means of a vibratool and needle.

In order to study the ontogeny of various specimens it was necessary to make serial transverse sections at small intervals. For this purpose the peel method and the equipment described by Minato (1961, pp. 40-43) have been used.

Most of the sections figured were drawn from directly enlarged projections in a modified Edinger apparatus. Here all the structures of the corallites are shown in black, and the loculi, as well as observable sutures between dilated septa, are in white.

A Leitz Panphot or comparable apparatus was used for photographing the corallite exterior. Most of the specimens photographed were whitened with ammonium chloride. The photographs of the sections were made with an enlarging apparatus with the peel or thin sections serving as negatives. All transverse sections figured, as well as the calicular views of the specimens, were oriented with the cardinal side downwards.

The external measurements of the corallites were made with sliding calipers. The length of the specimens is defined as the distance between the apex and the rim of the calice on the most convex side of the corallite (Fig. 1 A).

The internal structures observed in the sections were measured with an ocular micrometer in a stereomicroscope. The following measurements were made of most transverse sections examined: diameter of the sections measured from cardinal to counter side as well as from alar to alar side of the corallites; width of the stereozone; length of the major and minor septa; the width of the axial structure (see Fig. 1 B). The number of septa was also counted.

TERMINOLOGY

The terminology of the morphological features of the solitary streptelasmatid corals described in this paper corresponds in most cases to that recommended by Hill (1935, 1956).

The main morphological features are diagrammatically illustrated in Fig. 2 A-G. A few terms have been introduced in this paper or used in another sense than by Hill (1956).

Remarks on the terminology of the external morphological features

Transverse, wrinkle-like growth lineations on the epitheca are in this paper called *growth-lines*. When rejuvenescence is present, the strongly marked constriction of the diameter of the corallite, usually with a clear ledge of the older calice around the constricted part (see Hill 1956, p. F 245, Fig. 173, 1) is here called a *line of rejuvenescence*.

Fixing structures, anchoring the corallites directly into the substratum or onto various objects in the substratum, are often present. In this paper the term *fixing structures* includes both a *fixing groove*, mostly situated on the



Fig. 2. Terminology of streptelasmatid corals. A-B, Morphological features of the epitheca. A shows the pattern of the alar side (lateral view of the corallite), and B that of the cardinal side. C, Longitudinal section showing the axial structure and the calicular boss. D, Longitudinal section showing the tabularium. E-G, Transverse sections showing the internal structures.

convex side near the apex of the corallite, and the buttressing outgrowths, the *talons*, along its borders (see Fig. 2 A and B).

Remarks on the terminology of the internal morphological structures

In order to indicate various elements of septal origin, mostly constituting the only elements in the formation of an axial structure, the terms *septal lobes* and *lamellae* are used. A *septal lobe* is the irregularly lobate and undulate axial edge of a septum, strongly bent in quite a different direction from that of the main growth direction of the septum (see Fig. 2 F). Hill (1956, p. F 241) uses this term in another sense.

The term *septal lamella* is used (in conformity with Hill) to denote a paliform lamella (see Fig. 2 F).

The *stereozone* is either formed exclusively by the dilated minor septa, which are in contact laterally with the likewise dilated peripheral parts of the major septa (septal stereozone), or by the septa together with a variable amount of stereoplasmatic deposits. Consequently, the term *stereozone* includes both these types in the following descriptions.

The term *fossula* has been used in various meanings by different authors. Here the term is used in the sense recommended by Schouppé & Stacul (1959). Thus a *fossula* is characterized by a marked depression of the tabulae (or dissepiments) at those points of the corallite where the septal insertions take place during ontogeny. Consequently, a fossula is found only in connexion with the cardinal septum and alar septa, and is usually further marked by interseptal chambers of unusual shape and size on each side of these septa. Such interseptal chambers may, however, also be present when a depression of the tabulae is lacking; sometimes they are to be found in parts of the corallite where no insertion of the septa takes place. Such a structure is called a *pseudofossula*.

The complementary plates (see Fig. 2 D) are small tabellae in the periphery of the corallite assisting in buttressing the complete tabulae. Other tabelloid elements are *incomplete tabulae*.

ONTOGENY

The specimens of rugose corals, examined, are often badly preserved. No efforts have, however, been spared in the study of the ontogeny of the various species. The present writer has used the most widespread terminology to indicate different ontogenetic stages of the life cycle of the rugose corals: the brephic, neanic, and ephebic stages.

During the brephic stage the six protosepta (cardinal, counter, two alar, and two counterlateral septa) are developed in the corallite (prototheka). This stage begins with the formation of the cardinal and counter septa which in most cases fuse into a median septum, and somewhat later the other protosepta grow out. The boundary between the brephic and the neanic stages is quite obvious as it is based on a limited number of septa. Sometimes it may be difficult to observe the septal number in transverse sections, especially when the septa are strongly dilated and the sutures between them are indistinctly marked. Unfortunately, the brephic stage is missing in most specimens examined. In the neanic stage, which is the stage of adolescence of the corallites, all the morphological structures are under development and gradually become more and more like those found in the ephebic stage. During the latter, all morphological structures characteristic of the different species have been formed, and only alternations in connexion with growth are to be noticed. Sometimes it may be difficult to distinguish the neanic stage from the ephebic stage.

In order to examine in detail the ontogeny of several rugose corals from the Silurian of Gotland, Minato (1961) used series of transverse peel-sections made at frequent intervals; he also measured the most common structures, such as the length of the cardinal and counter septa. In his reconstructions the cardinal septum of most species examined showed a rather sudden decrease in length during the earliest phases of the ephebic stage, and became again somewhat longer in later phases. As he could observe this temporary decrease of the cardinal septum in several species it seems to be a good criterium for a limit between the neanic and the ephebic stages as it is reflected in the development of other morphological structures as well. Unfortunately it was not possible to observe this decrease of the length of the cardinal septum in the species examined in this paper, as exact measurements of the structures could not be obtained on account of the poor state of preservation. The writer had to use the development of other morphological structures for defining the limit between the neanic and ephebic stages in different species.

In the brephic and neanic stages of many of the species of Ordovician rugose corals the septa are often strongly dilated. This also applies to those belonging to the family Streptelasmatidae. During ontogeny these septal dilations gradually disappear, at least towards the beginning of the ephebic stage. Not until the most remarkable dilations have disappeared are structures like stereozone, axial structure, interseptal chambers, tabularium, etc., developed in their final shape as found in the ephebic stage. When a species is provided with a dissepimentarium, this structure rarely appears before the late phases of the neanic stage or the ephebic stage. Within the family Streptelasmatidae especially, the septa are usually arranged in a somewhat tetrameral pattern during the neanic stage, and gradually show a more radial arrangement during the ephebic stage.

In conclusion it is possible to state that the limit between the neanic and ephebic stages must be defined individually for the different species using the variations of various morphological structures. Thus, general rules which can fit all species seem to be hard to establish.

STRATIGRAPHICAL REMARKS

The faunas of rugose corals treated in this paper indicate that their distribution is to a large extent controlled by ecological factors. The Pirgu Stage of Estonia is approximately contemporaneous with division 5a in the Oslo region (Jaanusson, 1956) and with the lower part of the Boda Limestone (see Table 1). These beds in the Siljan district, the Oslo region, and northern Estonia have, however, only one species in common, viz. *Streptelasma primum* (Wedek.). This species occurs frequently at most Swedish and Norwegian localities but is found only rarely in Estonia (Kaljo, 1958). It has also been reported from beds of similar age in the Ural Mountains and in N. America by Ivanov & Mjagkova, 1955 (cf. Kaljo, 1958 b). The type species of *Grewingkia*, *G. buceros* (Eichw.), is a common form in the Pirgu Stage of Estonia and in division 5a of the Oslo region but it has never been found in Sweden.

The main part of the Boda Limestone is contemporaneous with the division 5b of the Oslo Region and the Porkuni Stage of Estonia. These divisions have no known species of solitary rugose corals in common. However, the rugose corals of the Porkuni Stage of Estonia have not yet been exhaustively described (Dr. D. Kaljo, personal communication), and extensive collecting in the exposures of division 5b of Ringerike may increase the number of species of rugose corals known in these beds.

The main part of the Boda Limestone is comparable in time to the *Dalmanitina* Beds in the interreef facies of Sweden. These two main facies display a different composition of the rugose coral faunas on the species level. Again, *Streptelasma primum* has a wider distribution than any other species and is further the only species which these facies have in common. This species has been found in the *Dalmanitina* Beds of the Siljan district and Östergötland but not of Västergötland. The common species at this level in Västergötland is *Streptelasma linnarssoni* Lindstr. This which occurs in one bed in great abundance has never been found outside the Falbygden area.

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DESCRIPTIVE PART

Family Streptelasmatidae Nicholson, 1889

Remarks

It is evident that the Upper Ordovician material of streptelasmatid corals from Balto-Scandia constitutes a comparatively small part of the entire Ordovician material of this group in the world, and it is evident, too, that many of the hitherto described Ordovician and Silurian streptelasmatids outside Balto-Scandia ought to be revised before our knowledge of the variation of the morphological characters is reasonably complete. However, it may be anticipated already at this stage of our knowledge that it seems unnatural that genera with a dissepimentarium are included in the same family as genera which lack a dissepimentarium but invariably possess a well-developed stereozone. The material studied as well as reliable statements and figures in the literature suggest that the forms with a dissepimentarium may be distinguished as a major systematic unit in addition to Streptelasma and allied genera.

As an introduction to the systematic treatment in this paper some recent trends in streptelasmatid systematics may be summarized:

Wang (1948, 1950) treated Lambeophyllum, Kiaerophyllum (= Grewingkia), Brachyelasma (= Streptelasma), and Palaeophyllum as subgenera of Streptelasma (= Helicelasma n.g.) Palaeophyllum was included in the family Favistellidae by Bassler (1950), but it was retained within the family Streptelasmatidae by Hill (1955). On account of its different ontogeny Brachyelasma (= Streptelasma) was distinguished by Kaljo (1956, 1958) as a separate genus belonging to the family Streptelasmatidae. On the other hand, Kaljo (1958, 1961) considered Kenophyllum, Grewingkia, Rectigrewingkia Kaljo (= Grewingkia), Lambeophyllum, and Leolasma Kaljo to be subgenera of the genus Streptelasma (=Helicelasma). Several English and American workers, e.g. Smith (1930), Wilson (1934) and Cox (1937), did not fully accept Grewingkia as a separate genus and described typical species of Grewingkia as belonging to Streptelasma (=Helicelasma). Duncan (1957) described the genus Bighornia and Nelson (1963) the genus Lobocorallium for species, previously included in Streptelasma (=Helicelasma).

Several writers, e.g. Hill (1956), regarded Streptelasma (= Helicelasma), Grewingkia, Brachyelasma (= Streptelasma), Lambeophyllum, and others, as independent genera of the family Streptelasmatidae and this is also the opinion of the present author.

In the present paper *Brachyelasma* is shown to be a junior subjective synonym of *Streptelasma* as defined by the lectotype (designated herein) of the type species. The author also considers *Kiaerophyllum* (cf. Kaljo, 1961) and *Rectigrewingkia* to be junior subjective synonyms of *Grewingkia*. For *Streptelasma* as currently defined the new generic name *Helicelasma* is proposed. Further new streptelasmatid genera here described are *Bodophyllum*, *Densigrewingkia*, and *Borelasma*.

Genus Streptelasma Hall 1847

(Fig. 3)

1847 Streptelasma Hall

1927 Dybowskia Wedekind

1940 Brachyelasma Lang, Smith & Thomas

1948 Streptelasma (Brachyelasma) Wang

1956 Brachyelasma Kaljo

Type species

Streptelasma corniculum Hall, 1847, selected by Roemer in 1861.

Diagnosis

Solitary streptelasmatid corals with cylindrical, ceratoid or trochoid corallite with a convex cardinal side. Major septa in the brephic and neanic stages long, thin, or moderately dilated, normally fused into a weak axial structure. Major septa in the ephebic stage thin, comparatively short, normally not forming an axial structure. Stereozone and interseptal chambers present throughout the ontogeny. Tabulae of complete convex type mostly provided with complementary plates.

Nomenclatural notes

Streptelasma corniculum Hall, 1847, was designated as the type species of Hall's genus Streptelasma by Roemer (1861). In the original description of this species Hall (1847) figured the lateral view of three ceratoid corallites (Pl. 25, figs. 1 a, 1 b, and 1 c, respectively). None of the specimens was sectioned by him, nor did subsequent writers attempt to examine sections of Hall's syntypes. A formal designation of a lectotype among the syntypes has not previously been made.

The species was redescribed by Lambe (1901, p. 108, Pl. VI, figs. 7, 7 a, b) based on material from Canada. He described for the first time the internal characters of the species and figured a longitudinal and a transverse section. Subsequent definition of *S. corniculum* has been largely based on the information given by Lambe, and the genus *Streptelasma* has been defined to accord with this definition.

At the present writer's request Dr. W. Oliver Jr. of the U.S. Geological Survey kindly prepared photographs and series of peel sections of the syntypes of S. corniculum deposited in the American Museum of Natural History. Examination of the peels showed that the syntypes include at least two different species. The large corallite figured by Hall (1847, Pl. 25, fig. 1 b) is not conspecific with the two small corallites (Hall 1847, Pl. 25, figs. 1a and 1c). None of these specimens belong to Streptelasma as currently defined (Cox 1937, Hill 1956) but they represent species of Brachyelasma in the current taxonomy of the streptelasmatids. Thus, if the definition of the species S. corniculum is based on Hall's syntypes, the genus Brachyelasma becomes a junior subjective synonym of Streptelasma, and the group of species currently referred to Streptelasma is without a valid generic name.

The above implies an unfortunate change of the concept of the well-known generic name Streptelasma. This could only be avoided by suspension of the rules and a treatment of Streptelasma corniculum in Lambe's sense as a nomen conservandum. The present writer believes this to be impractical for several reasons. Lambe's material does not seem to be better than Hall's as a base for the definition of a type species, since the exact locality and the exact stratigraphic horizon are unknown (Trenton Formation at Ottawa, cf. Lambe, 1901, p. 108). Secondly, Streptelasma and Brachyelasma are closely related and no change is expected at the family level; the definition of the genus Streptelasma has for a long time been broad enough to include also species currently referred



Fig. 3. Schematic illustrations of the ontogeny of the genus Streptelasma Hall. A shows 'the type of ontogeny represented, e.g., by S. primum, and B that represented, e.g. by S. estonicum. Stippled areas indicate stereoplasmatic deposits.

to *Brachyelasma*. Thus no serious confusion can be expected if the genus *Streptelasma* is redefined as a consequence of basing the type species on syntypes. For this reason the present writer here designates one of the syntypes as the lectotype of *S. corniculum*.

Species

The following list is incomplete because data of the ontogenetic development are lacking from many *Streptelasma*-like species, and a correct generic reference of these species is difficult without these data.

Streptelasma corniculum Hall, 1847 Ptychophyllum linnarssoni Lindström, 1873 Calophyllum duncani Dybowski, 1873 Streptelasma estonica Dybowski, 1873 Dybowskia prima Wedekind, 1927 Streptelasma cylindricum Troedsson, 1928 Brachyelasma oanduensis Kaljo, 1956 Brachyelasma concavum Kaljo, 1956 Brachyelasma fevida Kaljo, 1958 Brachyelasma hiumica Reiman, 1958 Streptelasma eccentricum n.sp. Streptelasma cytrum n.sp. Streptelasma ostrogothicum n.sp.

Remarks

As diagrammatically illustrated in Fig. 3, this genus includes species which vary with regard to the internal structures during ontogeny. Principally two lines of development are distinguishable in this respect, apparently due to the fact that the major septa become shorter earlier during ontogeny in some species than in others. In one group of species characterized by S. corniculum, S. primum, S. duncani and S. linnarssoni, the axial structure disappears during the late phases of the neanic stage (Fig. 3 A). Thereby a wide central zone later becomes free from the major septa except for one or two septal lamellae which are sometimes present within this zone.

In another group, including *S. estonicum* and *S. cyrtum*, the central zone without septal extremities does not appear until the precalicular phase of the ephebic stage is reached (Fig. 3 *B*). Earlier during the ontogeny of this group a weak axial structure is formed by twisted and temporarily fused axial ends of the major septa. Intermediate phases between these two groups are also represented by various species.

The degree of the septal dilations in the neanic stage can vary as the study of numerous specimens of *S. primum* has revealed. During this stage most of the specimens examined have thin septa and a narrow axial structure. A few specimens, however, have considerably dilated septa and consequently a fairly solid axial structure, the width of which is influenced by the degree of septal dilations.

During the ontogeny some species show great variation in the shape of tabulae, in the frequency of tabulae and also in the width of the stereozone.

Discussion

As mentioned above the study of transverse and longitudinal peel sections and photographs of syntype specimens of *Streptelasma corniculum* figured

by Hall (1847, pl. 25, fig. 1 a-d) has revealed that they represent at least two different species. The present author has selected the largest of Hall's syntypes (Hall 1847, Pl. 25, fig. 1 b) as lectotype of S. corniculum. The study of the ontogeny of this specimen revealed that the septa were only moderately dilated and consequently comparatively large interseptal chambers were present. Moreover, this specimen is provided with a weak axial structure present only during the neanic stage. This structure which consists of very feebly fused axial ends of some of the major septa disappears in the ephebic stage where the major septa gradually become shorter. Few or no septal lamellae are present in this axial structure. All these morphological features are characteristic of the genus Brachyelasma Lang, Smith & Thomas 1940 as currently defined. The genus Streptelasma is currently restricted to include species with heavily dilated septa, normally without interseptal chambers during the early stages of growth, and with long, thin major septa forming a feeble axial structure in late phases of ontogeny. If based on the lectotype of the type species as selected herein, Brachyelasma becomes a junior subjective synonym of Streptelasma, and the group of species with the ontogenetic characters of Streptelasma in the current sense must be included in a new genus. For this genus the name Helicelasma n.g. is proposed in this paper.

Occurrence

Species of *Streptelasma* have been described from Middle and Upper Ordovician and Lower Silurian beds from most parts of the world. However, many of those species have not been investigated in detail and may belong to other related genera.

Streptelasma corniculum Hall 1847

(Figs. 4 A-B, 5 A-H, and 6 A-H)

1847 Streptelasma corniculum Hall, p. 69, Pl. 25, fig. 1 b.

Lectotype

The specimen, American Museum of Natural History, No 645/1 (*a*) figured by Hall 1847 as Pl. 25, fig. 1 *b* and in this paper as figs. 4, 5 and 6.

Type stratum and locality

According to the original label of the lectotype, lower part of the Trenton Limestone, Upper Middle Ordovician (Champlainian); Middleville, New York, U.S.A.

Diagnosis

Corallite medium-sized, of curved ceratoid type without fixing structures. Major septa in the neanic stage long, a minority of them fused into a feeble axial structure. Major septa in the ephebic stage comparatively short; axial structure lacking. Minor septa short and stereozone narrow throughout the ontogeny. Tabulae numerous, of complete type with faintly concave central parts and convex margins. Complementary plates present.

Description of the lectotype

The following description is based on the lectotype only, as at present no further topotype material is available. Consequently no observations concerning the variations of the morphological features within the species could be made.

The corallite of the lectotype is of curved ceratoid type with a convex cardinal side 39.5 mm high and with a calice diameter of 18.5 mm. The transverse growth-lines and the longitudinal interseptal ridges are fairly well marked on the epitheca. The calice is rather deep and measures about 1/4 of the height of the corallite.

The brephic stage is missing in the lectotype. Six transverse sections of one half of the corallite and two longitudinal sections reveal the following data of the internal structures.

In late phases of the neanic stage the major septa are long and some of them reach the centre of the corallite where they seem to be fused into a feeble axial structure (Figs. 5 G-H and 6 F-G). The minor septa are short and do not reach beyond the narrow stereozone (0.4 mm). The septa are moderately dilated and fairly large interseptal chambers are present.

In early phases of the ephebic stage the major septa have become shorter and the axial structure has disappeared. Most of the major septa, however, are laterally joined with their axial ends in groups with 3 or 4 septa in each group (Figs. 5 E-F and 6 D-E). The minor septa have become somewhat longer and most of them reach just beyond the stereozone, which is still narrow.

In late phases of the ephebic stage (Figs. 5 C-Dand 6 B-C) the major septa have become still shorter and a large central zone of the corallite measuring about half the diameter of the corallite just below the calice is free from septa. At this



Fig. 4. Streptelasma corniculum Hall. Lectotype A.M.N.H. No. 645/1 (a). Trenton Limestone; Middleville, New York, U.S.A. Lateral views from opposite alar sides of the corallite. Magnification of A and B is $\times 2$.

stage the septa are somewhat dilated just inside the calice only. The minor septa have become longer (reaching 1 mm in length) but the stereozone is still comparatively narrow (0.4 mm). The septa are somewhat more dilated in the cardinal quadrants than in the counter ones. It is impossible to observe whether this is a true specific character, or due to the uncertainty of the exact orientation of the transverse sections. The tabulae are of complete type with faintly concave or nearly plain central parts and highly convex margins (Figs. 5 A-B and 6 H). Complementary plates are fairly common.

Affinities

Streptelasma corniculum differs from S. primum in having a ceratoid corallite without fixing structures, in having a weaker axial structure in the neanic stage, and in having fewer tabulae, shorter minor septa and a narrower stereozone.

Occurrence

See data for type.

Streptelasma primum (Wedekind, 1927) (Figs. 7 *A*–*H*, 8 *A*–*F*, 9 *A*–*H*, 10 *A*–*B*)

1880 Ptychophyllum craigense M'Coy-Lindström, p. 35; Pl. 1, figs. 16 and 17.

- 1927 Dybowskia prima—Wedekind, pp. 17–18; Pl. 1, figs. 10–11.
- 1933 Dybowskia prima Wedekind-Scheffen, p. 7.
- 1933 Dybowskia rostrata n.sp.—Scheffen, pp. 9-10, nomen nudum.
- 1933 Dybowskia concamerata n.sp.—Scheffen, pp. 10-11, Pl. 1, fig. 5.
- 1933 Dybowskia solida n.sp.—Scheffen, p. 11, nomen nudum.
- 1933 Dybowskia undulata n.sp.—Scheffen, p. 15, Fig. 1 a, and Pl. 1, fig. 7.
- 1933 Dybowskia complanata n.sp.—Scheffen, p. 15, Pl. 1, fig. 6.
- 1933 Dybowskia collucata n.sp.—Scheffen, p. 15, Fig. 1 b.
- 1933 Dybowskia luminosa n.sp.—Scheffen, p. 15, nomen nudum.
- 1955 Brachyelasma primum n.sp.—Ivanov & Mjagkova, p. 34, Pl. 17, fig. 2 a-d.
- 1958 Brachyelasma primum (Wdkd)—Kaljo, pp. 105-106, Pl. 1, figs. 14-15.

Holotype

Deposited in Senckenberg Museum (numbers unknown). One transverse and one longitudinal thin section figured in Wedekind (1927, Pl. 1, figs. 10-11).

Type stratum and locality

Upper Ordovician, division 5a; Stavnæstangen, Ringerike area, Norway.



Diagnosis

Corallite medium-sized to large, nearly straight or irregularly curved, cylindrical with a trochoid or ceratoid apex. Fixing structures sometimes present. Major septa in the neanic stage long, some of them fused into a feeble axial structure. Major septa in the ephebic stage comparatively short; axial structure lacking. Minor septa short, stereo-



Fig. 6. Streptelasma corniculum Hall. Lectotype A.M.N.H. No. 645/1 (a). Trenton Limestone; Middleville, New York, U.S.A. B-G, Transverse sections of the ephebic stage (subcalicular part) and of late phases of the neanic stage

zone narrow. Tabulae numerous and complete with flat or faintly concave central parts and convex margins.

Description

The corallites are variable in size, attaining a height of more than 150 mm and a calice diameter of 36 mm. The longitudinal interseptal ridges and the transverse growth-lines of the epitheca are moderately marked. Some of the latter, however, are strong, resembling lines of rejuvenescence. The calice is fairly shallow and has a flat or slightly concave bottom.

Ontogeny and internal structures

The brephic stage is not represented in the specimens available. An early phase of the neanic stage is represented by a transverse section with a diameter of 2.2 mm which has 10 compara-

(also in Fig. 5 C-H) and the position of these sections in A. H, A central longitudinal section (also in Fig. 5 A). Magnification of B-H is $\times 3$ and of $A \times 1$.

tively long major septa. Some of the inner ends of these septa are fused into a feeble axial structure in the center of the corallite. As a rule the septa are only slightly dilated and the interseptal chambers are fairly large. However, in some specimens with a ceratoid apex the axial ends of the major septa are conspicuously dilated, and the axial structure is fairly broad (see Fig. 8 B). A narrow stereozone is present. In the last phases of the neanic stage the major septa gradually decrease in length and the axial structure disappears. Consequently, the central zone lacks structures except one or two septal lobes and lamellae and the tabularium. Short minor septa are developed entirely enclosed in the narrow stereozone (about 0.5 mm wide).

In the neanic stage of corallites with a trochoid apex fixing structures are present along their slightly convex, cardinal side (see Fig. 7 A). In the cardinal quadrants of the corallite these specimens have somewhat more dilated peripheral



Fig. 7. Streptelasma primum (Wedekind). A, UM D 1202. Lateral view. B-C, UM D 1201. Transverse sections of a late (subcalicular) phase of the ephebic stage, and of the neanic stage, respectively. D, RM Cn 2507. Lateral view. E, UM Nor 5. Transverse section of the ephebic stage. F, UM Nor 6. Transverse section of the neanic stage. G, UM D 1201. Longitudinal section. H, UM Nor 5.

Longitudinal section. Magnification of A and $D \times 1$, B, C, E, G and $H \times 1.25$, and $F \times 3$. Specimens nos. UM Nor 5 and 6 are from division 5a; Stavnæstangen, Ringerike, Norway, UM D 1201 and 1202 from Boda Limestone; Osmundsberg NE, Siljan District, and RM Cn 2507 from Dalmanitina Beds; Borenshult, Östergötland, Sweden.

parts of the septa as well as a broader stereozone than in the counter quadrants.

During the ephebic stage the major septa gradually become shorter and somewhat thinner. They may be slightly twisted in one direction. A fairly distinct cardinal pseudofossula is present. The minor septa have increased in length and reach slightly beyond the fairly narrow stereozone. In the last precalicular phases of large (adult) specimens the major septa have a length of 1/6 to 1/3 of the diameter of the corallite, and the minor septa may reach a length of 1/4 to 1/3 of the length of the major septa but are commonly shorter. The width of the stereozone is 1.2 mm to 1.5 mm, but in the largest specimen examined it is 5.5 mm. The septal number may reach 55 of each order but is usually between 40 and 50. One or two septal lobes and lamellae, originating from the major septa, may be present in the broad central zone of the corallite.

In the neanic stage and in early phases of the ephebic stage the tabulae are, comparatively few,



Fig. 8. Streptelasma primum (Wedekind). A, UM Nor 5. Transverse section representing a late phase of the ephebic stage. B, OM 11373. Transverse section of an early phase of the neanic stage. C-F, UM Nor 6. C and D transverse sections of the ephebic and the neanic stage respectively, and E and Flongitudinal sections. Magnification of all figures $\times 3$. All specimens are from division 5a; Stavnæstangen, Ringerike, Norway.

each having a slightly concave central part and convex borders (Fig. 8 E and others). In late phases of the neanic stage and in the ephebic stage the tabulae are numerous in most specimens and have flat, sometimes slightly convex, central parts and steeply convex margins (Figs. 8 F, 9 G, 10 A). In a few specimens the types of tabulae mentioned are mixed throughout the ontogeny. In some specimens, which are curved almost at right angles, the tabulae have their growth-plane altered already below the curve of the corallite.

Affinities

S. primum differs from most other species of the genus by having very short major septa, a narrow stereozone, tabulae with flat or slightly concave

central parts and with convex borders during the ephebic stage. S. linnarssoni resembles S. primum in several respects (see the section on this species).

S. primum differs from S. duncani (Dybowski, 1873) by having a larger corallite, a larger number of septa and a comparatively broader stereozone, at least in the ephebic stage. In addition, the tabulae in S. primum seem to have less marked central concavities and the minor septa are longer throughout ontogeny.

Scheffen (1933) described as many as 9 species of *Dybowskia* (=*Streptelasma*) from Stavnæstangen, Ringerike area, Norway. The present study of the type material has revealed that 7 of these undoubtedly are synonyms of *S. primum*. Kaljo (1958) described *Streptelasma primum* from



Fig. 9. Streptelasma primum (Wedekind). A-G, UM D 1202 (see also Fig. 7 A). The position of the transverse sections B-F is indicated in A. G, a longitudinal section of the same specimen. H, UM D 1201. Transverse

section of a late phase of the ephebic stage. Magnification of A is \times 1, and that of B-H is \times 4. Both specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

Estonia, and his specimens are undoubtedly correctly identified. Only one statement in Kaljo's description, viz. that the stereozone decreases in width towards the calicular part of the corallite, is not in agreement with the conditions in the revised material of *S. primum*; this statement, however, seems to be due to the imperfect state of preservation of the Estonian material.



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Occurrence

Upper Ordovician (Harjuan). Norway, division 5a: Ringerike area-Stavnæstangen and Vestre Svartøy; Langesund-Skien area-Herøy. Sweden, Boda Limestone: Siljan district-Osmundsberg, Kallholn, Lissberg, and Östbjörka; Dalmanitina Beds: Siljan district-Nittsjö and Kullsberg; Östergötland-Borenshult and Råsnäs. Estonia, Pirgu Stage, Piirsalu beds: Haapsalu. In addition, the species has been reported from the Central Ural Mountains by Ivanov & Mjagkova, 1955 (cf. Kaljo, 1958 b).

Streptelasma linnarssoni (Lindström, 1873) (Figs. 11 A-G, 12 A-D)

- 1873 Ptychophyllum linnarssoni n.sp.-Lindström, p. 28.
- 1880 Ptychophyllum linnarssoni-Lindström, pp. 34-35. Pl. 1, figs. 12-13.

Fig. 10. Streptelasma primum (Wedekind). A-B, UM D 1203. Longitudinal sections. A illustrating a late phase, and B an early phase of the ephebic stage of this large specimen. Both figures $\times 4$. Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

Lectotype

(Selected herein.) The longitudinal section RM Cn 54660 figured by Lindström (1880) as Pl. I, fig. 12, refigured as Fig. 11 B in this paper.

Type stratum and locality

Upper Ordovician Dalmanitina Beds; Allebergsände, Västergötland, Sweden.

Diagnosis

Medium-sized or large Streptelasma with almost straight or irregularly curved cylindrical corallite possessing a ceratoid apex. Fixing structures absent. Ontogeny as in Streptelasma primum except for more pronounced septal dilations and a wider



Fig. 11. Streptelasma linnarssoni (Lindström). A, UM Vg 861. Lateral view. $\times 1$. B, Lectotype RM Cn 54660. Longitudinal section. $\times 1.25$. C, UM Vg 862. Longitudinal section. $\times 1.5$. D-E, UM Vg 863. Transverse sections of

the ephebic and the neanic stage, respectively. $\times 1.5$. *F-G*, UM Vg 864. Transverse sections, ephebic and neanic stage, respectively. $\times 1.5$. All specimens are from the Dalmanitina Beds; Allebergsände, Västergötland, Sweden.

stereozone throughout ontogeny, and except for the convex tabulae with no central depression during the neanic stage.

Description of the corallite

Unfortunately most specimens examined are poorly preserved. The corallites seem to have reached a greatest height of 20 cm with a calice diameter of 24 to 29 mm. The epitheca has moderately marked longitudinal interseptal ridges and numerous transverse growth-lines. Some of the latter may be particularly pronounced, resembling of lines of rejuvenescence. The calice is moderately deep and has an almost flat bottom.

Ontogeny and internal structures

The brephic stage is unrepresented in the specimens available.

The smallest transverse section made (not

figured), representing an early phase of the neanic stage, has a diameter of 4.5 mm and possesses 16 septa of each order. The major septa are moderately dilated, especially at their axial ends, and most of them reach the center of the corallite where they are fused into a fairly broad axial structure (1.6 mm wide in the specimen referred to). The minor septa are very short, and the stereozone is fairly narrow. Consequently, the small interseptal chambers are very peripherally situated in the corallite.

During later phases of the neanic stage the major septa gradually decrease in length and the axial structure disappears. Consequently, the central zone has no structures apart from one or two septal lamellae and the tabularium. The minor septa increase in length; they are strongly dilated and in lateral contact with the likewise dilated peripheral parts of the major septa, forming a fairly wide stereozone which almost lacks stereo-



Fig. 12. Streptelasma linnarssoni (Lindström). A, UM Vg 863. Transverse section of a late phase of the ephebic stage (also in Fig. 11 D). B-C, UM Vg 864. Transverse sections, the ephebic stage and the neanic stage, respectively (also in Fig. 11 F and G). D, UM Vg 862. Longitudinal section of late phases of the neanic stage (completely figured in Fig. 11 C). All figures \times 3. All specimens are from the Dalmanitina Beds; Ållebergsände, Västergötland, Sweden.

plasmatic deposits. During the last phases of the neanic stage the axial dilations of the major septa disappear. An indistinct cardinal pseudofossula is present.

During the ephebic stage the major septa become still shorter and are slightly turned in one direction. The stereozone is broader than before and usually reaches a width of 1.5 to 2.5 mm (in one specimen, however, no less than 3.4 mm); it still mainly consists of the dilated peripheral parts of the septa, and the amount of stereoplasmatic deposits is small. The minor septa are longer but seldom reach far inside the stereozone. The parts of the septa inside the stereozone have lost most of their dilations, especially at their extremities. The number of septa may reach 45 of each order but is usually less. The central zone of the corallite may have one or two septal lamellae in this stage too.

In the neanic stage, and in early phases of the ephebic stage, the tabulae are comparatively few and show a slightly convex central part and more steeply convex borders (Fig. 12 D). In late phases of the ephebic stage the tabulae are numerous and have flat or slightly convex or concave central parts and convex borders (Fig. 11 B and C).

Affinities

Streptelasma linnarssoni resembles S. primum in several respects but differs in having more dilated septa, especially just inside the epitheca, and a considerably broader stereozone which almost entirely lacks stereoplasmatic deposits throughout



type RM Cn 2537. Lateral and calicular view, respectively. \times 3. C, RM Cn 2504. Transverse section just below the calice showing the intracalicular budding. \times 3. D-E, SGU (no number). Transverse sections showing a late phase of the ephebic stage and an early phase of the neanic stage, respectively. \times 3. F, RM Cn 2575. A longitudinal section. \times 3. G-H, Holotype RM Cn 2537. G, Transverse section of a late phase of the ephebic stage. \times 3. H, A longitudinal section. \times 2. I, RM Cn 2530. A transverse section of a late phase of the ephebic stage. \times 3. Specimen SGU (no number) is from the Dalmanitina Beds; Råsnäs, and the other specimens are from the same beds; Borenshult, Östergötland, Sweden.

growth. Additionally the minor septa are almost entirely enclosed in the stereozone, even in late phases of the ephebic stage, and the tabulae of the neanic stage are convex and have slightly convex central parts (instead of a central depression). S. linnarssoni also has a less pronounced cardinal pseudofossula, and the major septa are less twisted than in S. primum. This species differs from other species of Streptelasma in almost the same respects as S. primum.

Occurrence

Streptelasma linnarssoni has been found only in the Upper Ordovician Dalmanitina Beds at Ållebergsände, Västergötland, Sweden. In one bed at that locality the species occurs in great profusion.

Streptelasma ostrogothicum n.sp.

(Figs. 13 A–I, 14 A–F)

1880 Ptychophyllum craigense M'Coy-Lindström, Pl. I, fig. 13.

Derivation of the name

The specific name alludes to Östergötland, the name of the province in which the type locality is situated.

Holotype

RM Cn 2537, see Fig. 13 A, B, G and H in this paper.

Type stratum and locality

Upper Ordovician *Dalmanitina* Beds; Borenshult, Östergötland, Sweden.

Diagnosis

Small or medium-sized *Streptelasma* species with a weakly curved ceratoid or cylindrical corallite possessing a ceratoid apex. Calice shallow. In the neanic stage major septa long and fused into a slender, solid axial structure. In the ephebic stage major septa comparatively long and temporarily fused and twisted into a fairly weak axial structure; stereozone comparatively broad. Tabulae numerous, of complete type with flat or moderately concave central parts and steeply convex borders. Intracalicular budding common.

Description of the corallite

The corallites are between 9 and 50 mm high and their calice diameter is between 5 and 17 mm. Unfortunately all the specimens are badly preserved and it is not possible to observe whether or not the corallites are provided with fixing structures. However, some of the specimens examined are somewhat flattened on their convex (cardinal) sides and this suggests that they may have been provided with fixing-grooves. The epitheca has very faint longitudinal interseptal ridges and transverse growth-lines. The calice is fairly shallow measuring about 5 mm in depth and has a nearly flat or weakly concave bottom. Intracalicular budding is common (see Fig. 13 B and C). As many as 6 buds have been observed in one specimen. They are peripherally placed in the calice and often laterally fused with each other.

Ontogeny and internal structures

The brephic stage is not represented by the available specimens.

The smallest transverse section examined, representing an early phase of the neanic stage, has a diameter of 2.6 mm and has 15 septa of each order (Figs. 13 E and 14 D). At this stage most of the major septa reach the center of the corallite where they are fused into a slender but fairly solid axial structure. The minor septa have already been formed though they are quite enclosed within the narrow stereozone (0.20 to 0.45 mm wide). All the septa are thin, somewhat dilated in their peripheries only, and the interseptal chambers are comparatively large.

The axial ends of the major septa may, however, be moderately dilated.

In late phases of the neanic stage the axial ends of most of the major septa are still fused into an axial structure which has commonly increased in width. At this stage some of the major septa are axially fused into small groups outside the axial structure. The stereozone has become broader and most of it is formed by the dilated and laterally fused peripheral parts of the septa. Consequently it contains very small amounts of stereoplasmatic deposits. The minor septa have increased in length and reach considerably beyond the stereozone.

In early phases of the ephebic stage most of the major septa are somewhat shorter than in earlier stages. Only some of them still reach the center of the corallite where they are fused into an axial structure, in some specimens observable only at certain levels. Due to variations in the dilation of the axial ends of the major septa, the axial structure may differ greatly in width. During this stage the stereozone gradually broadens and contains a larger amount of stereoplasmatic deposits than in the neanic stage.

In late phases of the ephebic stage the major septa are often twisted in one direction (see Figs. 13 G and 14 A). Just below the bottom of the



Fig. 14. Streptelasma ostrogothicum n.sp. A, Holotype RM Cn 2537. Transverse section of the ephebic stage (just below the calice) (also in Fig. 13 G). B, Same specimen, longitudinal section. C-D, SGU (no number). Transverse sections of the ephebic stage, and of an early phase of the neanic stage, respectively (also in Fig. 13 D and E).

E, RM Cn 2587. Transverse section of an early phase of the neanic stage. *F*, RM Cn 2422. Longitudinal section of a medium-sized specimen. All figures \times 5. Specimen SGU (no number) derives from the *Dalmanitina* Beds; Råsnäs, the other specimens from the same beds; Borenshult, Östergötland, Sweden.

calice a narrow central zone of the corallite has become free from septa. The minor septa are long and in large specimens nearly attain half the length of that of the major septa (Fig. 13 D). The stereozone reaches a width of 1.8 to 3.2 mm in most adult specimens but is narrower in small ones. The tabulae are numerous and of complete type and are provided with complementary plates. In early phases of the ontogeny they have moderately concave central parts and steeply convex borders (Figs. 13 H and 14 B). In the ephebic stage the central parts of the tabulae are less concave and often almost flat (Figs. 13 F and 14 F).

Affinities

S. ostrogothicum differs from other species of Streptelasma with comparatively long major septa in the ephebic stage, in shape and size of the corallite as it has a nearly smooth epitheca, a broad stereozone, long minor septa, and intracalicular budding with several buds in each corallite.



Fig. 15. Streptelasma cyrtum n.sp. *A*, UM D 1210. Lateral view. \times 1. *B*, UM D 1211. Lateral view. \times 1. *C*, UM D 1212. Lateral view showing part of the calice. \times 2. *D*, UM D 1213. Longitudinal section. \times 3. *E*-*G*, Holo-

type UM D 1214. E, A longitudinal section. F-G, Transverse sections of the ephebic and the neanic stage, respectively. \times 1.5. All specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

Occurrence

Upper Ordovician Dalmanitina Beds; Borenshult and Råsnäs, Östergötland, Sweden.

Streptelasma cyrtum n.sp.

- (Figs. 15 A-G, 16 A-E, 17 A-G, 18 A-E, and 19)
- 1880 Ptychophyllum craigense M'Coy-Lindström, Pl. 1, fig. 14.

Derivation of the name

The specific name alludes to the highly convex tabulae.

Holotype

UM D 1214. Sections of the holotype are figured as Figs. 15 E-G and 19.

Type stratum and locality

Upper Ordovician Boda Limestone; Osmundsberg, (NE quarry), Siljan district, Sweden.

Diagnosis

Medium-sized *Streptelasma* with moderately curved ceratoid or trochoid corallite possessing a trochoid apex. Fixing structures present on the convex cardinal side of the apex. Calice moderately deep and with a faintly concave bottom. Major septa long throughout the ontogeny, typically somewhat twisted, some of them fused into a weak axial structure which disappears somewhat below the calice. Tabulae fairly numerous, complete, with flat or faintly convex central parts and steeply inclined borders. Complementary plates are common.

Description of the corallite

The corallites are between 30 and 60 mm high and have a calice diameter between 20 and 30 mm. Near the apex on the convex cardinal side there is a fairly pronounced fixing groove with talons along its borders. The epitheca is provided with fairly distinct longitudinal interseptal ridges and transverse growth-lines. A few growth-lines are very distinctly marked and developed as faint lines of rejuvenescence. The calice measures about 1/5 to 1/4 of the height of the corallite and is almost funnel-shaped.

Ontogeny and internal structures

The brephic stage is not represented in the specimens available.

In early phases of the neanic stage (see Figs. 16 E, 17 E and 18 E) most of the major septa reach the center of the corallite where they are feebly and irregularly fused into a weak axial structure. The septa are moderately dilated, generally somewhat more in the cardinal quadrants than in the counter ones. Small interseptal chambers are present at least in the counter quadrants, as is a narrow stereozone measuring about 0.2 mm in width. In late phases of the neanic stage the major septa are arranged in a more pinnate fashion. The axial structure is more loosely constructed than earlier. The septal dilations are weaker but are in most specimens more marked in the cardinal quadrants than in the counter ones. Fairly large interseptal chambers are, however, present in all the quadrants of the corallite. In these phases of the ontogeny a cardinal pseudofossula is present. Short minor septa develop but are completely enclosed in the narrow stereozone (about 0.5 mm broad).

During the early phases of the ephebic stage (e.g. Fig. 18 D) the axial structure has become broader and is still more loosely constructed than in earlier stages; it consists of the irregularly twisted and occasionally fused axial ends of some of the longest major septa. In a few specimens also, a few septal lamellae occur in the axial structure. The septa are yet thinner than in earlier stages, somewhat dilated near the epitheca only. The minor septa have increased in length (1 to 1.5 mm), and reach inside the stereozone which is 0.7 to 1 mm wide. During the late phases of the ephebic stage (Figs. 15 F, 16 B-C, and 17 F-G) the major septa gradually decrease in length. Consequently the axial structure disintegrates and disappears somewhat below the calice where there is a fairly narrow central zone (about 1/6 to 1/4 of the diameter of the corallite) free from the major septa. The stereozone is, then, broader and in typical specimens measures 1.8 to 2.6 mm in width. The minor septa are at the same level fairly long, usually reaching a length of at least 1/3 of that of the major septa. During the ephebic stage of some specimens, especially in those with weak lines of rejuvenescence, the septa may be irregularly dilated in certain levels (Figs. 17 and 18), and a remarkably broad stereozone, containing very small amounts of stereoplasmatic deposits, may be present (in one specimen reaching a width of 3.9 mm). The shape of the tabulae is illustrated in Figs. 15 D-E and 19.

Affinities

Streptelasma cyrtum differs distinctly from S. primum and S. linnarssoni by having longer major septa, more convex tabulae, and an axial structure during the ephebic stage. It differs from S. cylindricum Troedsson (1929) in having a ceratoid or trochoid shape (instead of cylindrical), a less complex and narrower axial structure, and a broader stereozone. In addition, the present writer is inclined to assume that the specimen which Kaljo (1958) referred to Streptelasma cylindricum Troedsson (1929, Pl. 27, figs. 2 and 3), must belong to a new species since it has almost flat tabulae (instead of steeply convex ones). The



Fig. 16. Streptelasma cyrtum n.sp. A-E, UM D 1210. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. The position of the transverse sections B-E is indicated

present species differs from *Streptelasma concavum* Kaljo and *Streptelasma fervidum* Kaljo mainly by having much more convex tabulae, which lack a central depression.

Occurrence

Upper Ordovician Boda Limestone; Osmundsberg (N.E. quarry), Siljan district, Sweden.

Streptelasma eccentricum n.sp. (Figs. 20 A-F, 21 A-H) Derivation of the name

The name alludes to the eccentrically placed zone without major septa during the late phases of the ephebic stage.

Holotype

RM Cn 41875 figured as Fig. 20 A. A longitudinal section of the type species is figured as Fig. 20 F.

in A. A is $\times 1$, B-E $\times 4$. (Also figured in Figs. 15 A and 17 F and G.)

Type stratum and locality

Upper Ordovician, division 5a; Herøy, Langesund-Skien area, Norway.

Diagnosis

Medium-sized *Streptelasma* species with curved ceratoid corallite. Fixing structures absent. Major septa in the neanic stage long, some of them fused in the centre of the corallite into a weak axial structure. During the ephebic stage the major septa in the cardinal quadrants of the corallite increase in length, the opposite major septa become shorter, and the axial structure disappears. Minor septa fairly long, stereozone thin. Tabulae numerous, complete, and highly convex, provided with complementary plates.

Description of the corallite

The corallites are 28 to 65 mm high, and their calice diameter is 25 to 29 mm. The epitheca has



Fig. 17. Streptelasma cyr:um n.sp. A-E, UM D 1211. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. Transverse sections of the ephebic and neanic stages. $\times 3$.

Note the effect of weak rejuvenescense in the late phases of the ephebic stage. (See also Figs. 15 *B* and 18.) *F* and *G*, UM D 1210. Transverse sections. Same locality. \times 3.

faint transverse growth-lines and longitudinal interseptal ridges. The calice is funnel-shaped and measures about 1/3 to 1/2 of the height of the corallite. Its deepest part is in the counter quadrants. The cardinal side of the corallite may be either convex or slightly concave.

Ontogeny and internal structures

The brephic stage is not represented in the specimens available.

The smallest transverse section examined (Figs. 20 E, 21 G) has 18 septa. During the neanic stage most of the major septa reach the center of



Fig. 18. Streptelasma cyrtum n.sp. A-E, UM D 1211. Boda Limestone; Siljan district, Sweden. The position of the

transverse sections B-E is indicated in A. A is $\times 1$, otherwise $\times 4$.

the corallite and are, in an irregular way, fused into a feeble axial structure. These septa are straight, except at their axial ends, and show a distinct tetrameral arrangement. They are somewhat dilated, especially near the epitheca, and the interseptal chambers are fairly wide. A distinct cardinal pseudofossula is present. The stereozone is narrow.

During the early phases of the ephebic stage the major septa become somewhat shorter and bent in one direction. Consequently, the axial structure is disintegrated and, in its place in the center of the corallite a narrow zone free from the major septa appears. The minor septa develop and rapidly reach a length of about 1/4 or 1/3 of that of the major septa. All the septa are, as a rule, fairly thin but retain some of their dilations near the

epitheca. The stereozone is still very narrow. During the late phases of the ephebic stage the major septa in the counter quadrants become shorter, at the same time as those in the cardinal quadrants increase in length. Consequently, the central zone, free from the major septa, is gradually displaced towards the counter side of the corallite. All the septa are still slightly bent in one direction. The minor septa increase in length and reach a length of at least 1/3 of that of the major septa. The stereozone is somewhat wider than in earlier phases and reaches a maximum width of about 1 mm. Just below the calice the inner ends of the major septa-and in a few cases those of the minor septa-in the counter quadrants are irregularly undulate. All septa are thinner here than in earlier phases but are still dilated in their peri-



Fig. 19. Streptelasma cyrtum n.sp. Holotype UM D 1214. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. Longitudinal section. $\times 4$. (Also in Fig. 15 *E*.)

pheries. The cardinal pseudofossula is well defined and observable at the bottom of the cleaned calice. Tabulae are numerous in the ephebic stage, but less numerous in the neanic stage. They have flat or faintly convex central parts and steeply inclined convex margins. Complementary plates are very common.

Affinities

Streptelasma eccentricum clearly differs from all other species of Streptelasma by having an eccentrically placed zone free from the septa in the ephebic stage owing to the different length of the major septa in the cardinal and the counter quadrants in that stage.

Occurrence

Upper Ordovician, division 5a; Stavnæstangen, Ringerike area, and Herøy, Langesund-Skien area, Norway. Genus *Helicelasma* n.g. (Fig. 22) *Type species*

Helicelasma simplex n.sp.

Diagnosis

Solitary streptelasmatid corals with a trochoid, ceratoid or cylindrical corallite possessing a convex cardinal side. Septa in the brephic and neanic stages strongly dilated, normally in mutual contact laterally; the major ones reaching the centre of the corallite without forming an axial structure. Major septa in the ephebic stage comparatively long and thin; their axial edges normally joined into a loosely built axial structure. Stereozone present. Tabulae complete and of convex type. Complementary plates common.

Species

Streptelasma fossulatum Wang, 1948 Streptelasma whittardi Smith, 1930



Fig. 20. Streptelasma eccentricum n.sp. A, Holotype RM Cn 41875. Lateral view. $\times 1$. B-E, OM 17416. B, Lateral view $\times 1$, and C-E, transverse sections from ephebic and neanic stages. $\times 2$. F, Holotype RM Cn 41875. Longitudinal section. $\times 1.5$. The holotype is from division 5a; Herøy, Langesund-Skien area, and OM 17416 from the same division; Stavnæstangen, Ringerike, Norway.

Streptelasma corniculum Cox, 1937 Streptelasma rusticum Billings, 1858 Streptelasma giganteum Kaljo, 1958 Helicelasma simplex n.sp.

Most of the species listed above have been very briefly described and incompletely figured, and in most of them the ontogeny could not be observed by the present author. At present the number of species to be referred to *Helicelasma* is therefore incompletely known.

Remarks

The ontogeny of the genus *Helicelasma* is diagrammatically illustrated in Fig. 22. The neanic stage of this genus resembles in many respects the same stage of the genus *Borelasma* n.g. Thus both genera have strongly dilated septa and lack an axial structure. In this stage, however, the cardinal septum may be more prominent than the other major septa in *Borelasma*, which is not the normal case in *Helicelasma*. In the ephebic stage the genus *Helicelasma* differs from *Borelasma* in having long major septa some of which are normally fused into a weak axial structure. In the last phases of the neanic stage of some species of Helicelasma one or very few septal lamellae are present in or just outside the axial structure, e.g. in *H. rusticum* (Billings, 1858). The ontogeny of *Helicelasma* corresponds in most respects with the old opinion of the ontogeny of *Streptelasma* (see p. 10). The present study shows that *Streptelasma* has another type of ontogeny than earlier surmised. According to the opinion of the present author several of the forms earlier described as species of *Streptelasma* were more correctly ascribable to the genus *Helicelasma*. The most important morphological differences between *Helicelasma* and other streptelasmatid genera are summarized in Table 3 p. 70.

> Helicelasma simplex n.sp. (Figs. 23 A–G, 24 A–J, 25 A–F, 26) Derivation of the name

The specific name refers to the simple construction of the corallite morphology of this species.

Holotype

UM Ög 117. A longitudinal section of the holotype is given in Figs. 23 *B* and 26.



Fig. 21. Streptelasma eccentricum n.sp. A-H, OM 17416. Division 5a; Stavnæstangen, Ringerike area, Norway. The

position of the transverse sections *B*-*G* is indicated in *A*. *H*, A longitudinal section. *A* is $\times 0.5$, *B*-*H* $\times 3$.



Type stratum and locality

Upper Ordovician *Dalmanitina* Beds; Borenshult, Östergötland, Sweden.

Diagnosis

Medium-sized, slightly curved ceratoid corallite. Calice deep. A weak axial structure is present only during the late phases of the neanic stage. The minor septa are short, and the stereozone is narrow throughout the ontogeny. Tabulae few, incomplete or complete and of convex type.

Fig. 22. Ontogeny of the genus *Helicelasma*. A-B show the variation of the internal structures in a late phase of the ephebic stage. Stippled areas indicate stereoplasmatic deposits between septa.



Fig. 23. Helicelasma simplex n.sp. A, RM Cn 2389. Lateral view. $\times 2$. (Transverse sections in Fig. 24.) B, holotype UM Ög 117. Longitudinal section. $\times 3$ (see also Fig. 26). C, RM Cn 2862. Lateral view. $\times 3$. (Transverse sections in Fig. 25.) D and E, RM Cn 2389. Transverse

Description of the corallite

The corallites are 13 to 40 mm high and have a calice diameter 8 to 18 mm. The epitheca shows distinct longitudinal interseptal ridges and rather faint transverse growth-lines. Most specimens lack fixing structures, but some are provided with a small fixing-groove on the convex cardinal side of the corallite near the apex. The calice is very deep, beaker-like, and measures between 1/3 and 1/2 of the height of the corallite.

Ontogeny and internal structures

The brephic stage is not represented in the material available. In early phases of the neanic stage (Fig. 24 J) the major septa (numbering 9 in the smallest transverse section examined with a dia-

sections of the ephebic and the neanic stage, respectively. (Large specimen.) \times 3. F and G, RM Cn 2862. Transverse sections. \times 4. All specimens are from the *Dalmanitina* Beds; Borenshult, Östergötland, Sweden.

meter of 1.13 mm) are heavily dilated and in contact laterally. Their edges mostly reach the center of the corallite; in some specimens, however, a very small central chamber may be observed. In somewhat later phases of the neanic stage small interseptal chambers have been formed, though the septa are still considerably dilated. Short minor septa have developed and are almost entirely shut in between the thick major ones (Fig. 24 H). An axial structure is present; it is weakly constructed by the occasionally fused axial ends of some of the major septa. However, when most or all of the septa have become withdrawn from the center of the corallite the axial structure disappears at certain levels. In the last phases of the neanic stage the interseptal chambers have increased in width, though all septa are still con-



wise $\times 5$.

Fig. 24. Helicelasma simplex n.sp. A-J, RM Cn 2389. Dalmanitina Beds; Borenshult, Östergötland, Sweden. The position of the transverse sections B-J is indicated in A.

siderably dilated. The short minor septa are in contact laterally with the major septa and form a fairly narrow stereozone without stereoplasmatic



Fig. 25. Helicelasma simplex n.sp. RM Cn 2862, preadult specimen. Dalmanitina Beds; Borenshult, Östergötland, Sweden. The position of the transverse sections B-F is indicated in A. B is cut through the lower part of the calice. A is $\times 1$, otherwise $\times 4$.

deposits. The axial structure is more feebly constructed than in earlier phases.

During the ephebic stage the axial structure disappears on account of the gradual decrease of the length of the major septa and-though they are of variable length-they gradually become shorter. In this stage a fairly large part of the stereozone consists of stereoplasmatic deposits because the septa have lost most of their dilations, particularly in their axial parts. The minor septa are now longer than in earlier ontogenetic stages, and in the calice at least they are visible beyond the narrow stereozone. In the calice the major septa show a somewhat undulating appearance. In large adult specimens some few complete tabulae of highly convex type are present (see Figs. 23 B and 26). In small, preadult specimens, however, tabulae are mostly incomplete or entirely lacking.

Affinities

This species differs from other species of *Helic-elasma* in having very few convex tabulae.

Occurrence

Only found at the type locality.

Genus Grewingkia Dybowski, 1873 (Fig. 27)

- 1873 Grewingkia Dybowski (p. 384)
- 1927 Kiaerophyllum Wedekind (p. 17)
- 1933 Kiaerophyllum Scheffen (p. 16)
- 1948 Streptelasma (Kiaerophyllum) Wang (p. 102)
- 1950 Streptelasma (Kiaerophyllum) Wang (p. 213)
- 1951 Grewingkia Hill (p. 13)
- 1956 Grewingkia Hill (p. F 268)
- 1958 Streptelasma (Kiaerophyllum) Kaljo (p. 25)
- 1961 Streptelasma (Grewingkia) Kaljo (pp. 52-54)
- 1961 Rectigrewingkia Kaljo (p. 62)

Type species

Clisiophyllum buceros Eichwald, 1856, selected by Scherzer 1891 (cf. Kaljo 1961).

Diagnosis

Solitary streptelasmatid corals with cylindrical, ceratoid, or trochoid corallites possessing a convex cardinal side. Septa in the brephic stage and in the early phases of the neanic stage moderately or heavily dilated; the major septa long and feebly fused into a central narrow axial structure. Later phases of the ontogeny characterized by comparatively short and thin major septa; axial structure broad, composed of numerous, mostly irregularly intertwined septal lobes and lamellae of various shapes. Calicular boss present or absent. Tabulae few or numerous, of incomplete or complete, convex type, with or without complementary plates.

Species

Clisiophyllum buceros Eichwald 1856
Clisiophyllum eminens Fichwald 1860
Strantalasma auronaaum Boemer 1861
Streptetasma europaeam Roemen, 1801
Grewingkia anthelion Dybowski, 1873
Grewingkia formosa Dybowski, 1873
Streptelasma robustum Whiteaves, 1896
Kiaerophyllum anguineum Scheffen, 1933
Grewingkia lutkevitschi Reiman, 1958
Streptelasma (Grewingkia) europaeum hosholmensis Kaljo,
1961
Grewingkia contexta n.sp.
Grewingkia bilateralis n.sp.

3-681925 Björn Neuman



Fig. 26. Helicelasma simplex n.sp. Holotype UM ög 117. Dalmanitina Beds; Borenshult, Östergötland, Sweden. Longitudinal section (also in Fig. 23 B). × 4.

Remarks

Dybowski (1873) and Kaljo (1961) seem to have based their diagnosis of the genus Grewingkia almost entirely on those morphological structures which are characteristic of the type species only, and apparently very little attention was paid to these structures in other species of Grewingkia. The ontogeny and morphology of some wellknown species will therefore be discussed below, and their respective types of ontogeny are illustrated diagrammatically in Fig. 27. The dilations of the septa and of the elements of the axial structure are most variable in different species of Grewingkia. A comparison of some features of the corallite and the characters of the neanic stage of some thoroughly studied species are presented in Table 2. The neanic stage has been chosen because the brephic stage is not preserved in the material of most species of Grewingkia and could therefore seldom be examined.

As shown in Table 2 it is evident that there are species of *Grewingkia* with heavily dilated septa located only in the cardinal quadrants of the corallite. In the corallites of these species the fixing structures along the convex cardinal side may be developed or lacking. In species provided with fixing structures, the irregular dilations seem to be



Fig. 27. Diagrammatic illustrations of the growth of four species of *Grewingkia* to show the great variation of ontogenetic characters in this genus. A, *Grewingkia buceros. B, G. anguinea. C, G. contexta. D, G. anthelion*

(the type species of *Rectigrewingkia* Kaljo). Stippled areas indicate stereoplasmatic deposits between septa. Not to scale.

developed in order to strengthen the epitheca in this portion of the corallite where the strain must have been greater than elsewhere. This is proved by the fact that the dilations begin to disappear just above the fixing structures. However, *Grewingkia europaea hosholmensis* is provided with similar septal dilations though it lacks fixing structures. Apparently, the differences in the septal dilations are due to differences of an ecological nature, such as bottom and current conditions.

In the ephebic stage the dilations of the septa and of the elements of the axial structure are

Species	Fig.	Size of the adult corallites	Fixing structures (fixing groove and talons)	Septal dilations	Interseptal chambers
Grewingkia buceros Grewingkia robusta	27 A	large large	absent absent	strong in all quadrants of the corrallite	absent (septa laterally in mutual connexion)
Grewingkia anguinea Grewingkia bilateralis	27 B	small or medium-sized medium-sized	absent present (on the convex cardinal side)	weak in all quadrants of the corallite	present
Grewingkia contexta Grewingkia europaea hosholmensis	27 C	medium-sized or large large	present (on the convex cardinal side) absent	strong in the cardinal quadrants, weak in the counter ones.	present in the counter quadrants

Morphology of the neanic stage in Grewingkia species.

mostly lacking. Septa may, however, remain dilated along the epitheca and form together with a variable amount of stereoplasmatic deposits a stereozone of varying width.

The axial structure is the most characteristic element of the genus. In the brephic stage and in the early phases of the neanic stage it is formed by feebly joined axial ends of the major septa and is always fairly narrow. In species with strong septal dilations it is sometimes difficult to distinguish an axial structure in these growth stages. Later on in the ontogeny the axial structure gradually becomes wider at the expense of the length of the major septa and consists either of septal lobes or lamellae which are mostly irregularly bent and intertwined. In most species the axial structure consists of a combination of both septal lobes and lamellae which gradually increase in number towards the calice. In various species, as well as in different ontogenetic phases of a single species, these elements of the axial structure may be very different in shape and size. In some species (e.g. G. bilateralis) the cardinal-counter plane in the axial structure (or in the calicular boss if present) is marked by a longish septal lamella, which either emanates from a median septum, or from the cardinal or counter septum. Most species of Grewingkia have a calicular boss of varying shape and size. The tabulae are of a more or less convex type, and are mostly numerous during the ephebic stage. Some species, however, have very few, often incomplete tabulae (e.g. *G. anguinea* and *G. bilateralis*), and in some immature specimens they are lacking. The variation of the morphological structures as noted above, within or between species of *Grewingkia* show that most structures when treated singly cannot be used as characteristics for defining species although in combination with each other they may help to distinguish between them. The axial structure as well as the shape of the tabulae of the ephebic stage, on the other hand, are more stable than the other features within a species of *Grewingkia*, and for this reason they have a greater taxonomic value at the species level.

Affinities

The most important morphological differences between *Grewingkia* and other Ordovician streptelasmatid coral genera are easily seen in Table 3, p. 70. Only the genera *Rectigrewingkia* Kaljo and *Lobocorallium* Nelson will be discussed briefly below because they are provided with a "spongy" axial structure like that in the genus *Grewingkia*. Structures of *Rectigrewingkia* (Kaljo, 1961, p. 62) which could be expected to indicate differences from *Grewingkia* at the generic level are (1) the round septal lamellae of one kind, (2) the moderate dilations of septa and presence of interseptal chambers during early growth, (3) the narrow stereozone, and (4) the few complete or incomplete tabulae of convex type. The ontogeny of Rectigrewingkia is illustrated diagrammatically in Fig. 27 D. From the observations made by the present writer on the variation of different morphologic characters within the genus Grewingkia it is evident that the differences between Grewingkia and Rectigrewingkia are few and unimportant, and that it is not justifiable to maintain the latter genus. The genus Lobocorallium Nelson (1963) differs from Grewingkia in having a trilobate appearance of the corallite (one cardinal and two alar lobes) and a cardinal fossula in the strict sense. This genus otherwise closely resembles Grewingkia.

Occurrence

Species of *Grewingkia* have been found in the Upper Ordovician beds of Balto-Scandia, England, North America, and Asia.

Grewingkia buceros (Eichwald, 1856) (Figs. 28 A-C, 29 A-B, 30 A-E)

- 1856 Clisiophyllum buceros m.-Eichwald, p. 108.
- 1860 Clisiophyllum buceros n.sp.—Eichwald, p. 552, Pl. XXIX, fig. 17.
- 1873 Grewingkia buceros Eichwald sp.—Dybowski, p. 386, Pl. II, fig. 7.
- 1927 Kiaerophyllum kiaeri n.sp.—Wedekind, pp. 16 and 17, Pl. I, figs. 7–9.
- 1933 Kiaerophyllum kiaeri Wdkd.—Scheffen, pp. 21–23, Pl. II, figs. 7–8, and Pl. III, fig. 1.
- 1933 Kiaerophyllum Kiaeri Wdkd. var. insaeptum-Scheffen, p. 23, Pl. III, fig. 2.
- 1933 Kiaerophyllum equinum n.sp.—Scheffen, pp. 17–19 (nomen nudum).
- 1933 Kiaerophyllum injunctum n.sp.—Scheffen, p. 18 (nomen nudum).
- 1933 Kiaerophyllum compactum n.sp.—Scheffen, p. 20 (nomen nudum).
- 1933 Kiaerophyllum falcatum n.sp.—Scheffen, pp. 18-19, Pl. II, figs. 1-2.
- 1933 Kiaerophyllum dumosum n.sp.—Scheffen, p. 20, Pl. II, fig. 3.
- 1933 Kiaerophyllum semilunatum n.sp.—Scheffen, p. 21, Pl. II, figs. 4-6.

Holotype

(By monotypy.) See Kaljo, 1961, p. 54.

Type stratum and locality

Unknown. See Kaljo, 1961, p. 54.

Diagnosis

Corallite large of curved ceratoid type. Calice moderately deep, provided with a low boss. Characters of the neanic stage: septa heavily dilated and in mutual contact laterally; axial structure narrow, consisting of a few dilated septal lamellae. Characters of the ephebic stage: major septa short, axial structure broad consisting of numerous elongated and round septal lamellae and a few septal lobes; septal dilations comparatively slight; stereozone broad, tabulae numerous, complete, with strongly convex central parts and less convex portions along their borders.

Description of the corallite

The corallites are 8 to 30 cm high and have a calice diameter of between 34 and 49 mm (seldom more than 39 mm). The epitheca has fairly indistinct longitudinal interseptal ridges and numerous transverse growth-lines. The calice measures about 20 to 30 mm in depth and is provided with a low, dome-shaped calicular boss. Septal number can reach 91 of each order but they are less numerous in most specimens examined (between 75 and 85 of each order).

Ontogeny and internal structures

The brephic stage is not represented in the specimens available.

In the early phases of the neanic stage, represented by the smallest transverse section made (see Fig. 30 E) 26 strongly dilated septa are arranged in a pinnate fashion. The cardinal septum is the most prominent of the septa and reaches the center of the corallite. No interseptal chambers are present. In somewhat later phases of the neanic stage the cardinal septum has become still more prominent, and its especially strongly dilated axial end occupies an essential part of the center of the corallite. The other major septa remain shorter. Short, wedge-shaped minor septa are present. Interseptal chambers are still absent. In the last phases of the neanic stage the prominent axial end of the cardinal septum has been split into a few free septal lamellae (see Fig. 30 C-D). Together with some septal lamellae split away from the other major septa they form a fairly narrow axial structure. The cardinal septum is in these phases of the same length as the other major septa and is situated in a distinct pseudofossula.


Fig. 28. Grewingkia buceros (Eichwald). UM Nor 12. Division 5a; Stavnæstangen, Ringerike area, Norway. A-C, Transverse sections from the ephebic and from a

late phase of the neanic stage, respectively. All figures $\times \ 2.5.$

The ontogeny of the neanic stage was studied in a fairly small (preadult) corallite. The last transverse sections of this specimen show the gradual decrease of the septal dilations. This decrease begins earliest in the counter quadrants, and in the cardinal pseudofossula where interseptal chambers first appear. The cardinal septum is still dilated axially but is otherwise very thin. Consequently the cardinal pseudofossula is open in its peripheral parts and is fairly distinct. In the moderately deep calice of this species a low and narrow calicular boss is formed by a few dilated septal lamellae (see Fig. 30 B). The minor septa are longer than before and visible beyond the stereozone.

The continuation of the ontogeny is observed in several large specimens. In the early phases of the ephebic stage the septa are still considerably dilated but narrow interseptal chambers are present in the same parts of the corallite as in the late neanic stages (Fig. 28 C). The axial structure consists of a few, elongate and irregularly bent, dilated septal lobes and lamellae. The minor septa are fairly short and completely embedded in the stereozone, often completely shut in between the heavily dilated peripheral parts of the major septa. No stereoplasmatic deposits can be recognized.

During later phases of the ephebic stage the dilations of the septa and of the elements of the axial structure gradually decrease (see Fig. 28 A and B and Fig. 29 A). The axial structure becomes broader and more loosely constructed than in earlier ontogenetic phases. It is composed of a few septal lobes and of numerous fairly small septal lamellae of both round and elongate, irregularly bent types. In some specimens the axial structure shows a lattice-like pattern as its elements are intertwined. In other corallites, however, the septal lamellae are small, of a rounded type and situated at some distance from each other. The major septa are fairly short and are comparatively little dilated with the maximum dilation close to the epitheca. The minor septa are completely embedded in the wide stereozone, which contains very small amounts of stereoplasmatic deposits. Just below the calice the cardinal septum is mostly shorter and even thinner than the other major septa (see Fig. 28 A). The cardinal pseudofossula is distinctly developed. The major septa reach a length of 1/4 to 1/3 of the diameter of the corallite and the minor septa are about half as long as the major septa. In the calice the stereozone decreases in width, and the axial ends of the minor septa reach somewhat beyond it.

The tabulae in adult specimens are numerous and complete (see Fig. 29 B).

Remarks

Comparisons between Kiaerophyllum kiaeri Wedekind and Grewingkia buceros (Eichwald), as redescribed by Kaljo (1961, pp. 54-56, Pl. I), have led the present writer to consider these two species synonymous. Unfortunately, in his examination of the type material and other specimens of Clisiophyllum buceros Eichwald, Kaljo could not observe the early ontogeny because the proximal part of the corallite was not preserved in any specimen available to him. Furthermore, the photographs published by Kaljo (1961) do not give a clear idea of the internal structures. However, Grewingkia buceros only seems to differ from Kiaerophyllum kiaeri in reaching a somewhat larger size, by its stronger septal dilations, and in having a somewhat broader and more solid axial structure. These small differences, are in the opinion of the present writer, scarcely of any taxonomic value and are probably due to intraspecific variation. Scheffen (1933) described several species of Kiaerophyllum, all from the same type locality. The study of Scheffen's collection of thin sections has clearly revealed that seven of these species are synonymous with Kiaerophyllum kiaeri and, consequently, with Grewingkia buceros. The specimens mentioned were examined by Scheffen only as disconnected thin sections. Consequently, the species described by Scheffen represent various ontogenetic stages, or even variations of the same stage of Grewingkia buceros.

Affinities

This species differs from all other species of *Grewingkia* in a combination of numerous characters, such as a large size of the corallite, the lack of fixing structures, the presence of a broad axial structure in the ephebic stage and of a very distinct pseudofossula, strong dilations of the septa and of the elements of the axial structure during the neanic stage, and the shape of the tabulae.



Fig. 29. Grewingkta buceros (Eichwald). A, OM 72976. Transverse section of a late phase of the ephebic stage. $\times 2.5$. B, UM Nor 13. Longitudinal section of the ephebic stage. $\times 2$. Both specimens are from division 5a; Stavnæstangen, Ringerike area, Norway.

Occurrence

Estonia: Pirgu and possibly also Porkuni Stage (see Kaljo, 1961, p. 56). *Norway:* Oslo region, division 5a; Ringerike area—Stavnæstangen and Vestre Svartøy; Skien-Langesund area—Herøy. *Grewingkia bilateralis* n.sp. (Figs. 31 *A*-*J*, 32 *A*-*G*, and 33 *A*-*B*)

1880 Ptychophyllum craigense—Lindström, p. 35, Pl. 1, figs. 19–20.



Fig. 30. Grewingkia buceros (Eichwald). OM 17154. Small preadult specimen. Division 5a; Stavnæstangen, Ringerike area, Norway. The position of the transverse sections B-E is indicated in A. B is sectioned through the calice. A is $\times 1$, $B-E \times 4$.

Holotype

UM D 1221. Side view of the holotype shown in Fig. 31 C and transverse sections in Fig. 31 G and H and Fig. 32.

Type stratum and locality

Upper Ordovician Boda Limestone; Osmundsberg (NE quarry), Siljan district, Sweden.

Diagnosis

Medium-sized *Grewingkia* with a slightly curved ceratoid or trochoid corallite. Fixing structures

present on the convex cardinal side. Calice shallow, with a low broad calicular boss which, together with the axial structure, has a median lamella in the cardinal-counter plane. Tabulae not numerous, incomplete or complete, and of convex type.

Description of the corallite

The corallites are 9 to 30 mm high and have a calice diameter of 11.5 to 34 mm. As many as 52 septa of each order may occur. The epitheca has distinct transverse growth-lines and weak inter-



Fig. 31. Grewingkia bilateralis n.sp. A and B, UM D 1220. Lateral and calicular view, respectively. A is $\times 4$, $B \times 3$. C, Holotype UM D 1221. Lateral view (transverse sections in Fig. 32). $\times 2$. D, RM Cn 54717. Calicular view of a large specimen. $\times 2$. E, UM D 1222. Longitu-

dinal section. \times 1.5. F, UM D 1223. Lateral view. \times 2. G and H, Holotype UM D 1221. Transverse sections. \times 2. I-J, RM Cn 54717. Transverse sections. \times 1.5. All specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.



Fig. 32. Grewingkia bilateralis n.sp. Holotype UM D 1221. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. The position of the transverse sections B-G is indicated in A. A is $\times 1$, $B-G \times 4$.

septal ridges. In a few specimens weak lines of rejuvenescence are present. A prominent fixing groove is situated along the convex cardinal side near the trochoid apex. Along its borders it is provided with well developed talons. The corallites have often been found fixed by means of these structures to crinoid stems, bryozoans, etc. The calice is shallow and reaches a depth of 5 to 7 mm. Within the very blunt calicular boss a slightly elevated median lamella along the cardinal-counter plane is, as a rule, easily distinguishable. In a few specimens, however, this lamella is recognizable only with difficulty.

Ontogeny and internal structures

The brephic stage is represented in only one of the sectioned specimens. The poorly preserved structures on the transverse section with a diameter of 0.94 mm shows 5 (or 6) moderately dilated septa which do not quite reach the centre of the corallite. Accordingly the most central zone is free from structures.

In the early phases of the neanic stage (Fig. 32 G) most of the major septa reach the center of the corallite and are fused into a weak axial structure. The inner end of the cardinal septum constitutes a substantial part of this structure. A

narrow stereozone is present. Somewhat later in the neanic stage the axial part of the cardinal septum is split, and the subsequent septal lamella constitutes throughout the ontogeny a median element in the cardinal-counter plane. In late phases of the neanic stage the axial ends of some of the major septa have become lobate, the septal lobes contributing to the increase in width of the axial structure. Short minor septa are almost entirely embedded in the stereozone which is still narrow. During the brephic and neanic stages the dilations of the septa are fairly weak, and large interseptal chambers are present. A few specimens, however, display during these stages somewhat more dilated peripheral parts of the septa and a wider stereozone in the cardinal quadrants than elsewhere in the corallite. This seems to be due to the position of the fixing structures along the convex cardinal side.

In the ephebic stage (e.g. Fig. 32 B-E) the axial structure has gradually increased in width at the expense of the length of the major septa. It consists of a gradually increasing number of septal lamellae, mostly of irregular shape, and of a few septal lobes originating from the major septa. The minor septa have become longer than in earlier growth stages and reach considerably



Fig. 33. Grewingkia bilateralis n.sp. A, RM Cn 54717. A transverse section through the lowermost part of the calice. $\times 1.5$. B, UM D 1224. A longitudinal section of a

large specimen. \times 5. Both specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

beyond the still narrow stereozone. Just below the bottom of the calice the axial structure measures more than half the diameter of the corallite. The major septa almost reach the axial structure, and the minor septa are of about half the length of the major septa. A weakly developed cardinal pseudofossula is present. The median septal lamella of the axial structure is not much separated from the inner end of the cardinal septum.

Throughout the ontogeny of typical specimens the septal lobes and lamellae of the axial structure are not particularly dilated. A few specimens, however, have fairly strongly dilated elements of the axial structure, even more strongly so than the major septa. In most large (adult) specimens the width of the stereozone is between 0.5 and 0.8. mm. In one specimen, however, the stereozone reaches a width of 2.4 mm just below the calice.

The tabularium has been studied in longitudinal sections of several specimens. In small (preadult) specimens tabulae may be lacking altogether or are of incomplete type. Larger (adult) specimens have a fairly low number of incomplete or complete tabulae of a moderately convex type (see Fig. 33 B).

Affinities

This species clearly differs from other species of *Grewingkia* by the construction of the axial structure, by the weak dilations of the septa throughout growth, and by the fairly small number of complete tabulae. In several respects *G. bilateralis* resembles *Dalmanophyllum subduplicatum* (M'Coy) described by Kaljo (1965). However, the state of preservation of the material of the latter species is too bad to allow any careful comparisons.

Occurrence

Upper Ordovician Boda Limestone; Osmundsberg and Östbjörka, Siljan district, Sweden.

Grewingkia contexta n.sp.

(Figs. 34 A-F, 35 A-C, 36 A-F, 37 A-K, and 38)

1880 Ptychophyllum craigense M'Coy-Lindström, Pl. 1, fig. 18.



Fig. 34. Grewingkia contexta n.sp. A, UM D 1231. Lateral view showing the calice and the calicular boss. \times 1. (Transverse sections in Fig. 37.) B, RM Cn 54681. Lateral view. \times 1. (Transverse sections in Figs. 35 and 36.) C, RM Cn 54676. Lateral view. $\times 2$. (Transverse sections in Fig. 37.) D, Holotype UM D 1232. Calicular view. \times 1.25. E, UM D 1234. Transverse section of a late phase of the ephebic stage. × 2. F, UM D 1233. Longitudinal section. × 1.5. All specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.



Fig. 35. Grewingkia contexta n.sp. RM Cn 54681. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. A-C, Transverse sections. $A \times 1.5$, B and $C \times 3$.

Derivation of the name

The specific name alludes to the intertwined elements of the axial structure.

Holotype

UM D 1232. Calicular view is given in Fig. 34 D.

Type stratum and locality

Upper Ordovician Boda Limestone; Osmundsberg, (NE quarry), Siljan district.

Diagnosis

Large *Grewingkia* of ceratoid or cylindrical type with a trochoid apex. Fixing structures present on the convex cardinal side of the apex. Calice moderately deep, with a prominent calicular boss. Axial structure broad, formed by numerous elongate, irregularly intertwined septal lobes and lamellae. Tabulae numerous, complete and of highly convex type, provided with complementary plates.

Description of the corallite

The corallites are either of ceratoid or cylindrical shape, both types having a trochoid apex provided with strong fixing structures. The height of the ceratoid corallites varies between 11 and 80 mm, and the diameter of the calice between 9 and 45 mm. The corresponding data for the cylindrical type are 35 and 160 mm in height and 12 and 24 mm in calice diameter. The fixing groove is generally conspicuous and restricted to the convex side of the trochoid apex. It is provided with prominent talons along its borders. The depth of the calice is not particularly great, measuring 10 to 20 mm in large specimens. The calicular boss is prominent (see Fig. 34 A and D) having a height between 5 and 10 mm. Some specimens, however, have a fairly low calicular boss.

Ontogeny and internal structures

The brephic stage is not represented in the specimens available. The examination of the other ontogenetic stages has been made on serial transverse sections of several specimens. Some of these sections are illustrated in Figs. 35, 36, and 37.

The earliest phase of the neanic stage, obtained in a section with a diameter of 1.46 mm, possesses 10 major septa. They reach the center of the corallite and are fused into a weak axial structure. Small interseptal chambers and a narrow stereozone (0.5 to 1 mm broad) are present. In later phases of the neanic stage the major septa have become shorter, and in the central zone of the corallite there is only one septal lamella, probably originating from the cardinal septum. In small (preadult) specimens the septa are, as a rule, little dilated throughout the portion of ontogeny represented by them. During the neanic stage in larger (adult) specimens, the septa in the cardinal quadrants may be heavily dilated, but the septa in the counter ones are comparatively thin.

In the early phases of the ephebic stage the axial structure has increased in width and consists of a fairly small number of irregularly bent, elongate septal lobes. One or a few septal lamel-



Fig. 36. Grewingkia contexta n.sp. RM Cn 54681. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. The

lae, mostly including the median one, may also occur. Although the septa in the cardinal quadrants are strongly dilated, the dilation of the elements of the axial structure is not particularly strong. During the late phases of the ephebic stage the dilations of the septa gradually disappear. The septa retain some of their dilations only just inside the epitheca where a narrow stereozone is formed, including fairly small amounts of stereoplasmatic deposits. As a rule the stereozone reaches a width of 1 or 2 mm but is 7 mm in one

position of the transverse sections B-F is illustrated in A. A is $\times 1$, $B-F \times 4$.

large specimen examined. The axial structure is broad and consists of numerous elongate, irregularly bent, and intertwined septal lobes and lamellae. These elements of the axial structure are either thin or moderately dilated. The minor septa are considerably longer than in earlier ontogenetic stages and reach a length of between 1/3 and 1/2that of the major septa. They may sometimes also give rise to small septal lamellae placed just beyond their axial ends. An indistinct cardinal pseudofossula is present.



Fig. 37. Grewingkia contexta n.sp. A-D, UM D 1231. The position of the transverse sections B-D is illustrated in A. E-J, RM Cn 54676. The position of the transverse sections F-I is indicated in E. J, A longitudinal section of the same specimen. K, UM D 1235. Transverse section

of the ephebic stage. Magnification of A and $E \times 1$, otherwise $\times 4$. Specimens UM D 1231 and RM Cn 54676 are from the Boda Limestone; Osmundsberg NE, and UM D 1235 from the Boda Limestone; Bodabacken, Siljan district, Sweden.

The morphological structures described above are characteristic especially of the ceratoid corallites. The cylindrical corallites display some differences (see Fig. 37 E-J). The number of the septa is smaller, and the major septa are more wedge-shaped than in the ceratoid specimens. In the neanic stage the septal dilations are comparatively weak, though more prominent in the cardinal quadrants than in the counter ones. The tabulae, highly convex in the ceratoid corallites (Fig. 38), are as a rule less convex in the cylindrical ones (see Fig. 37 J).

Affinities

Grewingkia contexta resembles G. europaea europaea and G. europaea hosholmensis as regards the construction of the axial structure, at least in late phases of the ephebic stage and, to a



Fig. 38. Grewingkia contexta n.sp. UM D 1227. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. A Longitudinal section of the ephebic stage. \times 5.

certain degree, as regards the distribution of the septal dilation. Grewingkia contexta differs by having well developed fixing structures, a prominent calicular boss, and tabulae of highly convex type (instead of moderately convex or flat tabulae). In addition, the axial structure is formed earlier than in the mentioned subspecies. The differences between Grewingkia anguinea and G. contexta are given in the description of the former species. Grewingkia robusta (Whiteaves, 1896), as figured by Troedsson (1928, Pl. 24), differs from G. contexta by its large size, by having a ceratoid (never cylindrical) shape, by a broad and low calicular boss, and by numerous convex tabulae with moderately convex central parts and convex borders forming separate peripheral elevations of the same type as in G. buceros.

Occurrence

Upper Ordovician Boda Limestone; Osmundsberg, Bodabacken, and Lissberg, Siljan district, Sweden.

Grewingkia anguinea (Scheffen, 1933) (Figs. 39 A-H, 40 A-F, and 41)

1933 Kiaerophyllum anguineum n.sp.—Scheffen, p. 23, Pl. III, figs. 3-4.

Lectotype

No. OM 73032 here chosen. A transverse thin section of the lectotype, figured by Scheffen (1933) as Pl. III, Fig. 3 (herein as Fig. 39 D), represents the ephebic stage. The transverse thin section, figured as Pl. III, Fig. 4 in Scheffen's paper is probably lost; it cannot belong to the lectotype.

Type stratum and locality

Upper Ordovician, division 5a; Stavnæstangen, Ringerike area, Norway.

Diagnosis

Small *Grewingkia* with a slightly curved ceratoid corallite. Calice deep, provided with a very low, broad calicular boss. Axial structure in the ephebic stage broad, consisting of a small number of irregularly bent and intertwined septal lobes and lamellae; minor septa fairly long; stereozone narrow. Septal dilation weak throughout the ontogeny. Tabulae few, incomplete or complete, with convex central parts and weakly concave borders.

Description of the corallite

The corallites are 23 to 50 mm high and have a calice diameter of between 11.5 and 34 mm. As



Fig. 39. Grewingkia anguinea (Scheffen). *A*, OM 18643. section Lateral view, large specimen. *B*, UM Nor 14. Lateral OM view. (Transverse sections in Fig. 40.) *C*, OM 18658. othe Longitudinal section. (See also Fig. 41.) *D*, Lectotype OM 73032. Transverse section. *E*-*H*, UM Nor 14. Transverse

sections. Figs. $A-D \times 2$ and $E-H \times 3$. OM 18643 and OM 18658 are from division 5a; Bjørkeåsen, and the other specimens are from the same division; Stavnæstangen, Ringerike area, Norway.

many as 32 septa of each order may occur near the bottom of the calice. The epitheca has moderately distinct longitudinal interseptal ridges and transverse growth-lines. Some of the latter, however, may be more pronounced and alternate with the weaker ones (see Fig. 39 A). The calice is very deep and occupies between 1/3 and 1/2 of the height of the corallite. The calicular boss is broad and very low. Fixing structures are absent.

Ontogeny and internal structures

The brephic stage is not represented in the available specimens. In early phases of the neanic stage major septa, numbering 15 in the smallest section examined with a diameter of 2.59 mm (Fig. 40 F), reach the center of the corallite and are fused into a weak axial structure. They are faintly and almost evenly dilated, and fairly large interseptal

chambers are present. There is a very narrow stereozone (about 0.25 mm broad) and an indistinct cardinal pseudofossula. In later phases of the neanic stage the major septa become shorter and only a few septal lobes reach the center of the corallite where they form a loosely built axial structure. Some of the major septa are fused axially into small groups outside this structure, others remain quite free. Short minor septa are present, though they are completely embedded in the narrow stereozone (about 0.35 mm broad).

In the early phases of the ephebic stage (Fig. 40 E) the major septa gradually become shorter, and the central zone of the corallite is occupied by the axial structure, consisting of a few irregularly bent septal lobes and a few lamellae. The minor septa have rapidly increased in length and reach inside the stereozone which is still nar-



Fig. 40. Grewingkia anguinea (Scheffen). UM Nor 14. Division 5a; Stavnæstangen, Ringerike area, Norway. The position of the transverse sections B-F is indicated in A. Magnification of A is $\times 1.25$ and of $B-F \times 5$.

row. During late phases of the ephebic stage (Fig. 40C) the axial structure gradually becomes broader and consists of a larger number of septal lobes and lamellae than in earlier stages. The elongate and irregularly bent septal lobes of the major septa constitute the peripheral parts of this structure. On the other hand, its central part consists of a fairly limited number of small, nearly round or elongate septal lamellae. The minor septa have increased in length, some of them giving off small septal lamellae, which are situated a short distance beyond the inner ends of these septa. All septa have become thinner, especially in their axial parts. During this stage, too, the cardinal fossula is inconspicuous, and the stereozone is narrow.

Tabulae are few, and only some of them are complete (see Figs. 39 C and 41).

Affinities

Grewingkia anguinea somewhat resembles G. europaea europaea (see Kaljo, 1961, pp. 54–58)

and G. contexta n.sp. in the construction of the axial structure, though it contains a much smaller number of elements. It clearly differs, however, from them in having smaller corallites and a very deep calice provided with a broad, very low calicular boss, long minor septa, and very few, highly convex, tabulae. In addition, the dilations of the septa are considerably weaker in G. anguinea and fixing structures, present in G. contexta, are altogether lacking.

Occurrence

Upper Ordovician, division 5a; Stavnæstangen and Bjørkeåsen, Ringerike area, Norway.

Genus *Densigrewingkia* n.g. (Fig. 42)

Derivation of the name

The generic name alludes to the presence of stereoplasmatic deposits making the axial structure dense and solid until late phases of the ephebic stage.

Type species Densigrewingkia pyrgoidea n.sp.

Diagnosis

Solitary streptelasmatid corals with a cylindrical, or conical corallite possessing a concave cardinal side. Ontogeny as in *Grewingkia*, but stereoplasmatic deposits connect the elements of the axial structure at least until late phases of the ephebic stage. Calicular boss present. Tabulae varying in number, of complete, convex type, with or without complementary plates.

Remarks

The genus is at present monotypic. The ontogeny is diagrammatically illustrated in Fig. 42. The neanic stage of the type species resembles in many respects this stage of *Grewingkia buceros*. The most important characters of *Densigrewingkia* are, as already mentioned, the concave cardinal side and the dense axial structure. During the last (precalicular) phases of the ephebic stage the



Fig. 41. Grewingkia anguinea (Scheffen) OM 18658. Division 5a; Bjørkeåsen, Ringerike area, Norway. Longitudinal section (also in Fig. 39 C). × 4.



Fig. 42. Diagrammatic illustration of the ontogeny of the genus *Densigrewingkia* n.g. Stippled areas indicate stereoplasmatic deposits.

stereoplasmatic deposits of the axial structure, enclosing the septal lobes and lamellae disappear, and the structure very much resembles that of *Grewingkia*. As to the microstructure, the septa consist of faint but distinguishable trabeculae which are well fused in all parts of the septa.

The most important morphological differences between *Densigrewingkia* and other important Ordovician streptelasmatid genera are easily observed in Table 3, p. 70.

Occurrence

See the type species.

Densigrewingkia pyrgoidea n.sp. (Figs. 43 A-F and 44 A-G)

1933 Kiaerophyllum pyrgoideum n.sp.—Scheffen, p. 20 (nomen nudum, not figured).



Fig. 43. Densigrewingkia pyrgoidea n.sp. A, UM Nor 19. Lateral view. $\times 2$. (Transverse sections in Fig. 44.) B, OM 73046 b. Longitudinal section in the alar plane showing the median lamella and the tabularium. $\times 1.25$. C, RM Cn 41878. Longitudinal section in the cardinal-counter

plane of a large specimen. $\times 1.5$. *D-F*, OM 72919. Transverse sections. $\times 2$. *D* shows a very late phase of the ephebic stage. RM Cn 41878 is from division 5a; Herøy, Langesund-Skien area, the other specimens from the same division; Stavnæstangen, Ringerike area, Norway.

Holotype

OM 72919. Three transverse sections of the holotype are figured in Fig. 43 D-F.

Type stratum and locality

Upper Ordovician, division 5a; Stavnæstangen, Ringerike area, Norway.

Diagnosis

Corallite medium-sized of a slightly curved ceratoid or cylindrical type. Calice moderately deep, provided with a low, elliptical calicular boss situated in the cardinal-counter plane. Septal dilations strong during the neanic stage. Axial structure in the ephebic stage consists of several round or elongate septal lamellae, during the early phases joined by stereoplasmatic deposits. Tabulae numerous, of complete, convex type with steeply inclined borders.

Description of the corallite

The corallites of this species are cylindrical to ceratoid with slightly curved apical portion and a concave cardinal side. The ceratoid corallites are 26 to 30 mm high and have a calice diameter between 15 and 17 mm. The cylindrical corallites are at least twice as high as the ceratoid ones, and their calice diameter reaches 23 mm. The transverse growth-lines and the longitudinal interseptal ridges are faint, though distinguishable on the epitheca. The calice measures between 1/4 and 1/3 of the height of the ceratoid corallites. Fixing structures are absent.

Ontogeny and internal structures

The brephic stage is unrepresented in the available specimens.

The smallest transverse section made, representing an early phase of the neanic stage, has a diameter of 1.6 mm and possesses 19 heavily dilated major septa (Fig. 44 G). These septa are distinguished only with difficulty as all loculi in the corallite are entirely filled with stereoplasmatic deposits. They are arranged in a pinnate fashion, and the cardinal and counter septa, of equal length, are incompletely fused axially. A few dilated septal lamellae form a narrow axial structure. During later phases of the neanic stage (Fig. 44 F) the counter septum decreases in length giving off a few septal lamellae which are incorporated in the axial structure. All septa are withdrawn from the axial structure with the exception of the cardinal septum which is still more prominent than in the earlier phases. Short minor septa have developed. In a somewhat later phase of the neanic stage a few small loculi have been developed between the axial structure and the inner ends of the major septa but no interseptal chambers are visible. The axial end of the cardinal septum has become detached and forms a longish median septal lamella in the cardinal-counter plane of the axial structure. This structure is broader than in earlier phases, and is still very solid, containing several heavily dilated septal lamellae. During the last phases of the neanic stage the loculi between the axial structure and the inner ends of the major septa have become wider, but this feature is subjected to great variation. The axial structure has assumed a fairly rounded outline. In addition, the cardinal septum is somewhat shorter and thinner than the other major septa, and the interseptal chambers on its sides have gradually become wider, indicating the presence of a cardinal pseudofossula. Small interseptal chambers also occur practically anywhere in the cardinal quadrants (Fig. 44 E).

In the early phases of the ephebic stage the septal dilations have gradually disappeared especially in the middle parts of the major septa, and interseptal chambers have developed in all quadrants of the corallite. By the deposition of considerable amounts of stereoplasmatic material the stereozone has become wider than in earlier stages and quite surrounds the minor septa. In addition the axial structure has become broader and very irregular in outline. It is still massive and consists of several septal lamellae in addition to the prominent median lamella; these are mostly situated at some distance from each other, though connected by a fairly large amount of stereoplasmatic deposits. The cardinal septum is thinner than most of the other major septa and the cardinal pseudofossula is distinct.

In later phases of the ephebic stage the axial structure is more loosely constructed than in earlier stages. Stereoplasmatic deposits still occur in this structure but some free septal lamellae can be observed in its peripheral parts. The elliptical median lamella is fairly conspicuous. The stereozone has decreased somewhat in width but still encloses the minor septa. This is the structural pattern in the last precalicular phases of the ontogeny in small and medium-sized specimens. In a few very large specimens, however, the stereoplasmatic deposits of the axial structure tend to disappear. Then an axial structure develops, indistinguishable from that of Grewingkia, in which free elongate septal lamellae are often radially placed around the comparatively large median lamella.

The longitudinal section (Fig. 43 B) clearly demonstrates the axial structure and its long persisting median septal lamella.

The tabulae are numerous and convex, most convex within the central parts of the corallite (Fig. 43 B and C). Sometimes they are second-arily thickened, in connexion with the deposition of stereoplasm in the axial structure.

The microstructure of the septa is weakly trabeculate, though these elements are well fused together.

Affinities

Densigrewingkia pyrgoidea differs conspicuously from all species of Grewingkia by the presence of considerable amounts of stereoplasmatic deposits within the axial structure and by having a somewhat concave cardinal side of the corallite. It resembles Grewingkia buceros by having strongly dilated septa, by the absence of interseptal chambers during early growth, and by the occurrence of a distinct pseudofossula and similar convex tabulae.

Occurrence

Upper Ordovician, division 5a; Ringerike area— Stavnæstangen and Vestre Svartøy; Langesund-Skien area—Herøy, Norway. An incomplete corralite questionably referable to this species has been found in the division 5b at Vestre Svartøy, Ringerike area.



Fig. 44. Densigrewingkia pyrgoidea n.sp. UM Nor 19. Division 5a; Stavnæstangen, Ringerike area, Norway. The position of the transverse sections B-G is indicated in A.

Genus Bodophyllum n.g. (Fig. 45) Type species

Bodophyllum osmundense n.sp.

Derivation of the name

The generic name alludes to the old village Osmundsberg in the parish of Boda in the Siljan district.

Diagnosis

Solitary, small to medium-sized streptelasmatid corals with a ceratoid, trochoid, or subcalceoloid

B is sectioned through the calice. A is $\times 1.25$, and B-G $\times 5$.

corallite. Cardinal side convex. Calice deep; calicular boss prominent, rounded or elliptical in transverse section. Axial structure fairly narrow and solid, composed of septal lobes and very few lamellae originating from the long major septa. Minor septa short, normally confined to the narrow stereozone. Tabulae, if present, few, incomplete or complete, of convex type.

Species

Holophragma duncanae Spjeldnæs, 1961 Bodophyllum osmundense n.sp. Bodophyllum oilense n.sp. Bodophyllum euthum n.sp. Lindstroemia subduplicata M'Coy, as redescribed by Nicholson & Etheridge (1878, pp. 86– 90) and figured by them on Pl. VI, Fig. 2 c, probably belongs to the genus *Bodophyllum*, but the other specimens of this species figured by them in that paper are not congeneric. In connexion with the description of the genus *Bighornia*, Duncan (1957, p. 609) reported the occurrence of some small corals of uncertain systematic position "currently included in *Strep:elasma*". They are provided with a calicular boss and may represent one or several species of *Bodophyllum*.

Remarks

The ontogeny of Bodophyllum is diagrammatically illustrated in Fig. 45. The most characteristic features of the early growth of this genus are the weak or moderately strong septal dilations and the presence of interseptal chambers, an axial structure, and a stereozone. In the brephic stage and in early phases of the neanic stage the axial structure consists of directly joined axial ends of most of the major septa (Fig. 45 A-C). Later in the ontogeny this structure consists of joined, more or less lobate, axial ends of the major septa, and, in addition a small number of septal lamellae. The median septum (joined cardinal and counter septa) mostly constitutes an important part of the axial structure and is often distinguished as a median lamella in the calicular boss. When the boss is rounded in transverse section it is composed of some strongly fused septal lamellae often including a median lamella (Fig. 45 E); when elliptical, it is formed only by the median lamella (Fig. 45 F). The tetrameral arrangement of the septa is easily recognized during the whole ontogeny. As in most other streptelasmatid genera the microstructure of the septa is fibrous and never clearly trabeculate. The stereozone is narrow during the entire growth, and its stereoplasmatic content is either continuously or discontinuously deposited and then homogenous or clearly layered. The deep calice reaches between 1/4 and 1/2 of the height of the corallite. The calicular boss, though prominent, is never as high as the rim of the calice.

Affinities

The differences between *Bodophyllum* and certain other Ordovician streptelasmatid genera are summarized in Table 3 p. 70. Further consideration is given below together with the characters



Fig. 45. Diagrammatic illustrations of the ontogeny of the genus *Bodophyllum* n.g. E and F show the possible variation of the shape of the calicular boss. Stippled areas indicate stereoplasmatic deposits.

which distinguish Bodophyllum from Dalmanophyllum, Lindstroemia, and Coelostylis.

Dalmanophyllum Lang & Smith (1939, p. 153) differs from Bodophyllum in having a very short cardinal septum during the ephebic stage. The construction of the calicular boss, however, closely resembles that of Bodophyllum.

The genus Lindstroemia Nicholson and Thomson (1876; type species: Lindströmia columnaris Nicholson & Thomson, 1876, figured by Nicholson & Etheridge, 1878, from the Devonian of North America) includes in earlier descriptions small to medium-sized, ceratoid, trochoid, or subcalceoloid solitary corals with a deep calice which is provided with a prominent calicular boss of the most variable type. Ordovician as well as Permian species have been referred to the genus. The longitudinal and transverse sections of L. columnaris figured by Nicholson and Etheridge (1878) were thought by Lang, Smith, & Thomas (1940, p. 77) to represent the genus Metriophyllum. This opinion might seem correct if the cross-section only is considered, but the longitudinal section shows the septa to lack horizontal flanges such as in Metriophyllum. Instead, the longitudinal section resembles Stereolasma Simpson (1900, p.

205), as suggested by Edwards & Haime (1850, p. LXIX) and Stumm (1949, pp. 7-8), but the transverse section does not show the cardinal fossula so characteristic of Stereolasma. Furthermore, the axial structure is more solid in Stereolasma. After studying the two figures, the present writer suggests that Lindstroemia columnaris might belong to the family Syringaxonidae Hill, most probably a species of the genus Syringaxon Lindström (1882, p. 20). However, the possibility that it belongs to Barrandeophyllum Počta (cf. Stumm, 1949) is not quite excluded. In both cases the cross-section may have been made through a tabula in the tabulate and tube-formed axial structure (aulos). If this is the case, the dense texture of the axial structure would be accounted for. In the figure of the cross-section of the type specimen in Nicholson & Etheridge (1878, Fig. 4 b') it looks as if the central part of the axial structure were darker and thus consisted of a material different from that of the septa. The longitudinal section looks something like the subcalicular part of a corallite of one of the syringaxonid genera. Although it appears to be obliquely cut, it is possible not only to recognize what seems to be a tabulate aulos, but also most of the other structures which are characteristic of the genus. The presence or absence of a calicular boss cannot be ascertained from the figured section. In the family Syringaxonidae, the axial boss is, however, missing in all species.

The genus *Coelostylis* Lindström (1880, p. 34) must also be mentioned in connexion with corals provided with an axial boss (see Neuman, 1967). This genus has, however, monacanthine septa and is brought to the family *Tryplasmatidae*. What has been said above clearly shows that the streptelasmatid corals previously described as belonging to the genus *Coleostylis* must belong to other genera, *Bodophyllum* not excluded.

Holophragma duncanae Spjeldnæs clearly belongs to Bodophyllum. The genus Holophragma Lindström (1896, pp. 35–36; cf. Minato, 1961, pp. 70–74) lacks both the axial structure and a calicular boss.

Occurrence

Species of *Bodophyllum* have been found in the Upper Ordovician beds of Sweden, and Norway, and probably also in Scotland and North America.

Bodophyllum osmundense n.sp. (Figs. 46 A-H, 47 A-O, and 48) Derivation of the name

The specific name alludes to the type locality of the species.

Holotype

UM D 1292. Calicular view is given in Fig. 46 B.

Type stratum and locality

Upper Ordovician Boda Limestone; Osmundsberg (NE quarry), Siljan district, Sweden.

Diagnosis

Corallite of curved, ceratoid type. Calice deep; calicular boss and axial structure almost round in transverse section. In the neanic stage the septal dilations are moderate or fairly strong, though interseptal chambers always occur; a median septum is present only during this stage. Tabulae absent or few, either complete or incomplete and of convex type.

Description of the corallite

The specimens examined are 11 to 47 mm high and have a calice diameter of 5 to 30 mm. Most specimens are of a moderately curved ceratoid type, but a few specimens are almost trochoid. The longitudinal interseptal ridges and transverse growth-lines on the epitheca are not particularly distinct. No fixing structures have been observed. The deep calice is beaker-like and measures about 1/2 or 1/3 of the height of the corallite.

Ontogeny and internal structures

The brephic stage is not represented in the specimens available. In early phases of the neanic stage most of the major septa, numbering 10 in the smallest transverse section examined (with a diameter of 1.30 mm), are fused in the center of the corallite and form a slender, almost round axial structure. Some of the major septa, however, do not reach this structure. All the septa are moderately, in a few specimens considerably, dilated. However, the thin epitheca contains small interseptal chambers already in this stage (Fig. 47 H).

During later phases of the neanic stage the axial structure gradually becomes broader and more irregular in outline, being formed by some



Fig. 46. Bodophyllum osmundense n.sp. A, UM D 1291. Lateral view. $\times 2$. (Transverse sections in Fig. 47 A-H.) B, Holotype UM D 1292. Calicular view. $\times 3$. C, RM Cn 54415. Lateral view. $\times 1$. (Transverse sections in Fig. 47 I-O.) D, UM D 1293. Transverse section of the ephebic stage. $\times 3$. E and G, RM Cn 54415. Transverse sections. $\times 4$. F and H, UM D 1291. Transverse sections. $\times 3$. All specimens are from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

moderately dilated and coalesced septal lobes and a few lamellae originating from the major septa. In this stage short minor septa appear. They are dilated and form a narrow stereozone together with the equally dilated peripheral parts of the major septa. The stereozone contains only small amounts of stereoplasmatic deposits. In *Bodophyllum osmundense* the median septum is observable



Fig. 47. Bodophyllum osmundense n.sp. A-H, UM D 1291. The position of the transverse sections B-H is illustrated in A. I-O, RM Cn 54415. The position of the

transverse sections J-O is indicated in I. A and $I \times 1$, otherwise $\times 4$. Both specimens from the Boda Limestone; Osmundsberg NE, Siljan district, Sweden.

during the early phases of the neanic stage only, and never forms a prominent part of the axial structure. In other species of *Bodophyllum* the median septum is uninterrupted throughout the precalicular ontogeny and forms an important median element of the axial structure.

A cardinal pseudofossula is distinguishable already in the early phases of the neanic stage and is fairly distinct during the later phases of the ontogeny. During the ephebic stage the axial structure increases in width and is less solidly constructed, especially in its peripheral parts where there are a few free septal lamellae in typical specimens. Some of the major septa still reach the axial structure and are fused with it, the other major septa are shorter and are often joined axially with each other into groups outside this structure. All septa are thinner than in earlier ontogenetic stages especially in their axial parts. In the ephebic stage the narrow stereozone includes a larger amount of stereoplasmatic deposits than in earlier stages. The minor septa are still comparatively short and do not reach much beyond the stereozone. The width of the stereozone is mostly up to about 1 mm, but in one specimen (from Bodbacken) as much as 1.94 mm. The cardinal septum has the same length as the other major septa throughout the ontogeny and is, in most specimens examined, fused with the axial structure from the apex to the bottom of the calice. In small (pre-adult) specimens (Fig. 471-O) the septal dilations are very feeble throughout the ontogeny. Such specimens usually have either a few and as a rule incomplete, convex tabulae or lack these structures entirely. In larger (adult) specimens the septal dilations may be strong. In the ephebic stage of such specimens a few complete, strongly convex tabulae are sometimes present (Fig. 48). The prominent calicular boss is almost round in transverse section.

Affinities

Bodophyllum osmundense differs from the other species of Bodophyllum by having a ceratoid shape of the corallite and a prominent calicular boss, rounded in transverse section and without a median lamella.

Occurrence

Upper Ordovician Boda Limestone; Osmundsberg (NE quarry) and Bodbacken, Siljan district, Sweden.

Bodophyllum oilense n.sp. (Figs. 49 A-H, 50 A-H, and 51) 1901 Lindströmia dalmani E. H. n.sp.—Wiman, p. 186.

Derivation of the name

The specific name alludes to Oil Myr ("Öjle Myr"), Gotland, where the type specimen was found.

Holotype

UM G 910. Calicular and lateral views of the holotype are given in Fig. 49 A and B.

Type stratum and locality

Probably Porkuni Stage. No type locality; the holotype was found in an erratic boulder.

Diagnosis

A *Bodophyllum* with a slightly curved trochoid corallite. Calice comparatively deep. Septal dila-



Fig. 48. Bodophyllum osmundense n.sp. UM D 1294. Boda Limestone; Osmundsberg NE, Siljan district, Sweden. A longitudinal section of a large specimen. $\times 4$.

tions moderate in the apical part of the corallite. A median septum is present throughout the ontogeny, observable as a median septal lamella in the prominent, rounded calicular boss. Tabulae absent or few, incomplete or complete, and of convex type.

Description of the corallite

The corallites are 10 to 20 mm high and have a calice diameter of between 15 and 18 mm. They are, as a rule, of a moderately curved trochoid type, but a few specimens are almost ceratoid. The longitudinal interseptal ridges are fairly well marked as well as some of the transverse growthlines, which alternate with fainter ones. Fixing structures are absent. The deep calice is beakerlike and measures about 1/3 to 1/2 of the height of the corallite. As many as 25 septa of each order can occur.

Ontogeny and internal structures

All the available material is silicified and has been etched out by Wiman. By means of transverse serial sections of some of the specimens (as illustrated in one specimen in Fig. 50 B-H) the



Fig. 49. Bodophyllum oilense n.sp. A-B, Holotype UM G 910. Calicular and lateral view, respectively. $A \times 4$, $B \times 3.$ C-D, UM G 911. Calicular and lateral view. $C \times 7$, $D \times 3$. E, UM G 912. Calicular view. $\times 11$. F, UM G 913. Calicular view. \times 14.5. G, UM G 914. Lateral view. (Transverse sections in Fig. 50.) × 3. H, UM G 915. Lateral view showing the calice and the calicular boss. \times 3.6. All specimens are from erratic boulders of Upper Ordovician (Harjuan) age; Öjle Myr, Gotland, Sweden.

internal structures could be examined fairly well. The brephic stage is not represented in the specimens available. In early phases of the neanic stage the cardinal and counter septa are axially fused into a median septum. Most of the other major septa are fused with the median septum forming an axial structure which is nearly round in transverse section. In this stage the septal dilations are moderate, and small interseptal chambers are normally present. In later phases of the neanic stage short minor septa develop. Just inside the epitheca the septa are strongly dilated and in mutual contact with each other laterally. In this way a narrow stereozone is formed which also contains small amounts of stereoplasmatic deposits. The minor septa are entirely embedded in the stereozone. During the early phases of the ephebic stage the dilations of the septa gradually disappear. The stereozone becomes broader than in earlier stages, partly as a result of a larger content of stereoplasmatic deposits and partly due to the increased length of the minor septa which are still entirely embedded in the stereozone. Most of the major septa still reach the axial structure and are fused with it. The other major septa remain shorter and being joined with each other axially they form small groups outside the axial structure. The median septum, which as a rule is strongly dilated in its central part, remains continuous up to the bottom of the calice. In later (precalicular) phases of the ephebic stage the minor septa have become longer, reaching somewhat beyond the narrow stereozone. In this stage the axial structure is more loosely constructed. In small (juvenile) specimens the calicular boss is a low elliptical elevation of the median septum (Fig. 49 E and F). In large (adult) specimens the calicular boss is prominent and nearly rounded in transverse section. In these specimens some irregularly bent septal lamellae, originating from the major septa, are intimately fused with the raised portion of the median septum (Fig. 49 A). The majority of the specimens examined have a few incomplete, convex tabulae or lack these structures altogether. However, in some of the largest specimens, one or two complete convex tabulae are present (Fig. 51).

Remarks

Bodophyllum oilense differs from the other species of Bodophyllum in having a trochoid shape,



Fig. 50. Bodophyllum oilense n.sp. UM G 914. Erratic boulder of Upper Ordovician (Harjuan) age; Öjle Myr, Gotland, Sweden. The position of the transverse sections B-H is indicated in A. Magnification of A is $\times 3$ and of $B-H \times 5$.

a round calicular boss in which a median septal lamella in the cardinal-counter plane dominates and is easily distinguishable.

Occurrence

Only found in erratic boulders from Öjle Myr, Gotland, derived from Upper Ordovician Harjuan beds, probably belonging to the Porkuni Stage.

Bodophyllum euthum n.sp. (Figs. 52 A-F and 53 A-H)

1933 Lindströmia laevis Nich. and Eth.—Scheffen, p. 31, Pl. V, Fig. 1.

Derivation of the name

The specific name alludes to the straight ceratoid shape of the corallite.

Holotype

OM 72923. A longitudinal section of the holotype is given in Fig. 52 C.



Fig. 51. Bodophyllum oilense n.sp. UM G 916. Erratic boulder of Upper Ordovician (Harjuan) age; Öjle Myr, Gotland, Sweden. Longitudinal section. $\times 4$.

Type stratum and locality

Upper Ordovician, division 5a; Vestre Svartøy, Ringerike area, Norway.

Diagnosis

A small *Bodophyllum* with a nearly straight ceratoid corallite. Calice deep. Calicular boss mediumsized, elliptical in transverse section, oriented in the cardinal-counter plane. Septal dilations prominent in the apical part of the corallite. Tabulae absent.

Description of the corallite

The corallites are of a straight or slightly curved ceratoid type, 9 to 13 mm high and with a calice diameter between 5.5 and 8.5 mm. The epitheca has very distinct longitudinal interseptal ridges and weak transverse growth-lines. Fixing structures are not present. The calice is deep and measures between 1/3 and 1/2 of the height of the corallite.

Ontogeny and internal structures

The brephic stage is lacking in the available specimens.—The smallest transverse section made, with a diameter of 1.62 mm, has 11 septa of each order.



Fig. 52. Bodophyllum euthum n.sp. A, OM 18457. Lateral view. B, OM 18458. Transverse section of a late phase of the ephebic stage. $\times 4$. C, Holotype OM 72923. Longi-

tudinal section. $\times 4$. *D-F*, OM 18457. Transverse sections $\times 4$ (see also Fig. 53). All specimens are from division 5a; Vestre Svartøy, Ringerike area, Norway.



Fig. 53. Bodophyllum euthum n.sp. OM 18457. Division 5 a; Vestre Svartøy, Ringerike area, Norway. The position of the transverse sections B-H is indicated in A. B is sectioned through the calice. A is $\times 2$. $B-H \times 5$.

In the early phases of the neanic stage the comparatively long cardinal septum and the shorter counter septum are incompletely fused into a median septum. The other major septa are fused with it in the center of the corallite into an axial structure. All septa are heavily dilated, and only very narrow interseptal chambers occur. Consequently the axial structure is comparatively broad. In a somewhat later phase the axial structure, as a rule, becomes still wider by the incorporation of small deposits of stereoplasm in the interseptal chambers just outside this structure (Fig. 53 E). The stereoplasm has also been deposited in small loculi within the structure. During late phases of the neanic stage the septa become less dilated allowing greater width for the interseptal chambers. Moreover the stereoplasmatic deposits in the inner parts of the interseptal chambers gradually disappear and the axial structure decreases in width. The minor septa are still fairly short and are in contact laterally with the major septa. A stereozone including very small amounts of stereoplasmatic deposits is then developed. The cardinal septum is still the longest and most conspicuous of the major septa and is mostly in contact axially with the shorter counter septum. An indistinct cardinal pseudofossula is present.

In the early phases of the ephebic stage the axial structure is formed mainly by the dilated axial part of the cardinal septum which may be detached, forming a median lamella, which as a rule, is in near contact with both the cardinal and counter septa. Also the axial ends of most of the other major septa, as well as a few small septal lamellae have become fused with the median lamella and take part in forming the axial structure. During the late phases of the ephebic stage (just below the calice) most of the major septa become somewhat shorter than in earlier stages and are axially fused with each other in smaller groups outside or in the periphery of the axial structure. This structure is therefore more loosely constructed than before and is dominated by the median lamella, which is often still in contact with both the cardinal and the counter septum. The minor septa have become longer and are visible beyond the stereozone. The septa are thinner and the septal dilations have become restricted only to the parts just inside the epitheca. The stereozone, however, has decreased gradually in width and contains larger amounts of stereoplasmatic deposits than before. During these phases the cardinal pseudofossula becomes more distinct than in earlier stages.

The calicular boss is an elliptical raised portion from the median lamella (see Fig. 53 B). In the calice the stereozone is narrower than further below, and substantially consists of stereoplasmatic deposits.

In large specimens the cardinal pseudofossula may be more pronounced and the dilations of the septa and of the median lamella stronger than in smaller specimens.



Fig. 54. Bodophyllum duncanae (Spjeldnæs). A, UM Nor 23. Division 5b; Gunneklev, Langesund-Skien area, Norway. Calicular view, small specimen. \times 9. B, UM Nor

24. Calicular view, large specimen. \times 4. Same division and locality.

Affinities

Bodophyllum euthum differs from the other species of Bodophyllum by having a fairly straight ceratoid corallite, by the elliptical calicular boss, by the comparatively strong septal dilations, and by lacking tabulae. Scheffen's figure (1933, p. 31, Pl. V, Fig. 1) of Lindstroemia laevis, which according to the author represents B. euthum, shows a transverse section through the upper precalicular part of a medium-sized specimen. Dalmanophyllum subduplicatum (M'Coy) described by Kaljo (1965) differs in several respects from B. euthum, e.g. in having a broad axial structure, thin septa and convex tabulae.

Occurrence

Upper Ordovician, division 5a; Stavnæstangen and Vestre Svartøy, Ringerike area, Norway (see also p. 3).

Bodophyllum duncanae (Spjeldnæs, 1961) (Figs. 54 A-B and 55 A-C)

1961 Holophragma duncanae sp.n.—Spjeldnæs, pp. 81-84, figs. 2 and 3.

Holotype

PMO 154 (Spjeldnæs, 1961, Figs. 2a and b).

Type stratum and locality

Upper Ordovician, division 5b; Gunneklev, Langesund-Skien area, Norway.

Diagnosis

A small *Bodophyllum* with an almost straight, subcalceoloid corallite. Calice moderately deep.

Calicular boss medium-sized, elliptical in transverse section. Septa only slightly dilated in the apical part of the corallite. Median septum present throughout the ontogeny. Tabulae absent.

Description of the corallite

The most apical part of the corallite of this species is ceratoid and nearly circular in transverse section. During a late phase of the neanic stage the cardinal side is flattened, and the corallite becomes calceoloid in shape. This is the final appearance in small, preadult specimens. In the few large adult specimens available the calicular part of the corallite is, however, elliptical or rounded in transverse section. In a few specimens small talons are present along the borders of the flattened cardinal side. Most specimens, however, lack fixing structures. The calice reaches a depth of about 1/3 of the height of the corallite. It is provided with a fairly low, elliptical calicular boss placed in the cardinal-counter plane. As many as 27 septa of each order have been observed.

Ontogeny and internal structures

All specimens are strongly silicified. Examinations of the calice in specimens of various size and of transverse serial sections of some specimens have made it possible to follow the ontogeny fairly well in spite of the silicification. In the brephic stage (see Fig. 55 A and B) the cardinal and counter septa are fused into a median septum. When at a somewhat later stage the alar septa are formed, their axial ends become fused with the median septum. Still later, the two counter-lateral septa develop, and the alar septa are gradually shifted from the cardinal side towards the middle of the alar sides where they remain during the rest of the ontogeny. In the last phases of the brephic stage the axial ends of the protosepta are fused with the centre of the median septum and form a solid, fairly slender, axial structure. Throughout the ontogeny the septa are only slightly dilated, and comparatively large interseptal chambers are present already in the early phases of the brephic stage.

In the neanic stage (see Fig. 55 C) short minor septa appear. They form, together with small amounts of stereoplasmatic deposits, a narrow stereozone. In this ontogenetic stage a conspicuous cardinal pseudofossula develops. The axial structure is nearly circular in transverse section of typical specimens but in a few specimens it is somewhat extended in the plane of the alar septa. It still consists of the fused axial ends of most of the major septa including the central part of the median septum. Some of the major septa, however, fail to reach the axial structure, and most of them have instead been fused axially with each other into groups outside this structure.

During the ephebic stage the major septa become more lobate and a few septal lamellae are sometimes separated from them. Most of these septal lobes and lamellae are directly fused with the center of the median septum and constitute the axial structure, which has then become broader than in earlier ontogenetic stages. The number of the major septa, which are free from the axial structure, gradually increases during the ephebic stage, and as mentioned above the septa are often assembled in smaller groups outside this structure. The minor septa have become longer and are observable inside the narrow stereozone. The septa have completely lost their dilations except in their most peripheral parts. The calicular boss is formed by a central, raised portion (median lamella) of the median septum (Fig. 54 A and B).

Affinities

Bodophyllum duncanae differs from other species of *Bodophyllum* in having a subcalceoloid corallite and very feebly dilated septa in the early phases of growth.

Occurrence

This species has been found at the type locality only.



Fig. 55. Bodophyllum duncanae (Spjeldnæs). A, UM Nor 20. Transverse section of an early phase of the brephic stage. \times 33.5. B, UM Nor 21. Transverse section of a late phase of the brephic stage. \times 27.5. C, UM Nor 22. Transverse section of the neanic stage. \times 25. All specimens are from division 5b; Gunneklev, Langesund-Skien area, Norway.

Genus Borelasma n.g. (Fig. 56)

Derivation of the name

The generic name refers to Lake Boren (stem *bor*-) on the western shore of which the type locality is situated.

Type species

Borelasma crassitangens n.sp.—Upper Ordovician Dalmanitina Beds; Borenshult, Östergötland, Sweden.

Diagnosis

Solitary, streptelasmatid corals with a trochoid, ceratoid or cylindrical corallite possessing a convex cardinal side. Septa in the brephic and neanic stages strongly dilated, normally in mutual contact laterally, the major septa reaching the center of the corallite without forming an axial structure. The cardinal septum normally more prominent than the other major septa. Major septa in the ephebic stage short and thin. Stereozone contains small amounts of stereoplasm. Tabulae numerous, complete, with or without complementary plates.

Species

Streptelasma (Streptelasma) orientalis Kaljo, 1958 Streptelasma (Streptelasma) giganteum Kaljo, 1958 Borelasma crassitangens n.sp.

Remarks

The ontogeny of the genus *Borelasma* is diagrammatically illustrated in Fig. 56. The brephic and neanic stages closely resemble those of the genus *Helicelasma* n.g. Contrary to that genus, in *Bor*-



Fig. 56. Diagrammatic figures of the ontogeny of the genus *Borelasma* n.g. Stippled areas indicate stereoplasmatic deposits.

elasma the major septa in the ephebic stage become gradually shorter and thinner, and a characteristic feature is a central zone of the corallite free from septa. In this respect the ephebic stage in *Streptelasma* (e.g. *S. primum* (Wedekind)) resembles the corresponding stage in *Borelasma*.

Affinities

The most important morphological differences between *Borelasma* and other important Ordovician streptelasmatid genera are easily observed in Table 3, p. 70.

Occurrence

Species of *Borelasma* have been found in the Upper Ordovician beds (Vasalemma-Porkuni) of Baltoscandia.

Borelasma crassitangens n.sp. (Figs. 57 A-G, 58 A-K, and 59 A-O)

Derivation of the name

The specific name alludes to the fact that the septa are dilated where they are in contact with some thick tabulae during the ephebic stage.

Holotype

RM Cn 2055. Figured in Fig. 57 A and D-G, and in Fig. 58.

Type stratum and locality

Upper Ordovician *Dalmanitina* Beds; Borenshult, Östergötland, Sweden.

Diagnosis

Medium-sized species with a slightly curved ceratoid or cylindrical corallite. In the ephebic stage the major septa have lobate axial edges. In typical specimens they are heavily dilated at certain levels, where they are in contact with some of the tabulae which are especially thick. Tabulae complete, flat or slightly concave, with convex borders.

Description of the corallite

The specimens examined are 9 to 50 mm high and have a calice diameter between 5 and 25 mm. They have a straight or moderately curved ceratoid or cylindrical corallite with a ceratoid apex. Fixing structures are, as a rule, absent. A few specimens, however, are provided with a small fixing groove near the apex. The cardinal side of the corallites is convex in various degree. The epitheca is smooth and only a few fairly distinct growth-lines can be distinguished.

Ontogeny and internal structures

The brephic stage is preserved in some small (preadult) specimens. During this stage the inner ends of the cardinal and counter septum are fused and constitute a median septum. This septum and the other protosepta, formed somewhat later, are strongly dilated and fill up the whole lumen of the corallite (see Fig. 59 O).

In early phases of the neanic stage the median septum is split into separate cardinal and counter septa, though they still remain in axial contact with each other.

During the late phases of the neanic stage, the cardinal septum gradually becomes longer and



Fig. 57. Borelasma crassitangens n.sp. A, Holotype RM Cn 2055. Lateral view. $\times 1$. (Transverse sections in Fig. 58.) B, UM ög 127. Lateral view, small specimen. $\times 3$. (Transverse sections in Fig. 59.) C, UM ög 128. Lateral view. $\times 3$. (Transverse sections in Fig. 59.) D-G, Holo-

type RM Cn 2055. D, Longitudinal section, and E-G, transverse sections. \times 3. RM Cn 2055 is from the Dalmanitina Beds; Borenshult, the other specimens from the same beds; Råsnäs, Östergötland, Sweden.

G

thicker than the other major septa and is situated in a distinct pseudofossula. It may reach a length of nearly 2/3 of the diameter of the corallite, and its inner end overlaps that of the counter septum (Fig. 58 *H*). In spite of the fact that the septa are strongly dilated some irregularly distributed interseptal chambers and small central loculi are present within the corallite.

In the early phases of the ephebic stage the

major septa gradually become shorter and the dilations, especially in their axial parts, begin to disappear, in some specimens in a very irregular way. As a result the central zone of the corallite lacks other structures than the tabularium and gradually increases in width during the ephebic stage. A fairly wide stereozone has been developed, consisting of the dilated medium-sized minor septa and the likewise dilated peripheral



Fig. 58. Borelasma crassitangens n.sp. Holotype RM Cn 2055. A-K, The position of the transverse sections. B-J is indicated in A. K, A longitudinal section. Dalmanitina

parts of the major septa which are in mutual contact laterally with each other. Consequently the stereozone contains very small amounts of stereoplasmatic deposits. This is the last phase in the growth of most of the small (preadult) specimens.

In late phases of the ephebic stage the major septa have become still shorter than in earlier stages though they often are of somewhat varying length. The minor septa have increased in length,

Beds; Borenshult, Östergötland, Sweden. A is $\times 1$, otherwise $\times 4$.

and their axial ends reach beyond the fairly wide stereozone which still contains only small amounts of stereoplasmatic deposits. During the ephebic stage the comparatively thin parts of the septa inside the stereozone become strongly dilated at points where they are in mutual contact with some of those tabulae which are unusually thick.

The axial edges of the septa are clearly lobate, as may be observed easily, particularly during the



Fig. 59. Borelasma crassitangens n.sp. A-H, UM ög 128. The position of the transverse sections. B-H is indicated in A. I-O, UM ög 127. The position of the transverse

neanic stage. The microstructure of the septa consists of well fused fairly thin trabeculae which, however, are distinguishable during the whole ephebic stage. The calice in large (adult) specimens is fairly shallow and has a nearly flat bottom formed by the uppermost tabula. On the contrary, smaller (preadult) specimens, which lack tabulae, have a fairly deep and funnel-shaped calice, delimited only by the axial ends of the major septa. The tabulae which are present only during the ephebic stage are numerous and are of complete type, provided with complementary plates. The central parts of the tabulae are flat or weakly concave, and their borders are convex (Fig. 58 K).

sections J-O is indicated in *I*. A and *I* are $\times 1.25$, otherwise $\times 5$. Both specimens are from the *Dalmanitina* Beds; Råsnäs, Östergötland, Sweden.

Occurrence

Upper Ordovician *Dalmanitina* Beds; Borenshult and Råsnäs, Östergötland, Sweden.

SUMMARY

Table 3 summarizes the differences between the genera of streptelasmatid corals discussed with regard to the different stages in the ontogeny. The abbreviations S and MS signify *septum* (or septa) and *major septa*, respectively. The symbols + and - denote presence and absence, respectively, of a morphological feature. *Septal dilations* are abbreviated as S. dilat., *deposits* as dep.

Table 3

		Shape of the cardinal	Brephic stage	Neanic stage	Stance	Axial	
Genus	Type species	corallite		Septa	zone	struc- ture	Tabulae
<i>Helicelasma</i> n.g.	H. simplex n.sp.	Convex	Not examined	MS long All S strongly dilated	mostly —		-
Grewingkia Dybowski 1873	Clisiophyllum buceros Eichwald 1856	Convex	Not examined	MS long in early phases, later gradually shorter. S. dilat. weak or strong	+ or -	+	+ or -
Streptelasma Hall 1847	S. corniculum Hall 1847	Convex	Not examined	MS long in early phases, later often shorter. S. dilat. weak	+	+ At least in early phases	+
<i>Lambeophyllum</i> Okulitch 1938	Cyathophyllum profundum Conrad 1843	Convex	Not examined	MS short, strongly dilated	+ or -	-	-
<i>Leolasma</i> Kaljo 1956	<i>L. sociale</i> Kaljo 1956	Convex	Not examined	MS long. All S moderately dilated	mostly +	+	-
<i>Kenophyllum</i> Dybowski 1873	K. subcylindricum Dybowski 1873	Concave	Not examined	MS long. All S strongly dilated	_	_	_
Bighornia Duncan 1957	<i>B. parva</i> Duncan 1957	Concave	Not examined	MS long. All S strongly dilated		+	-
Lobocorallium Nelson 1963	Streptelasma rusticum var. trilobatum Whiteaves 1895	Convex	Not examined	MS long in early phases, later gradually shorter. S. dilat. moderate or strong	+ or -	+	-
<i>Bodophyllum</i> n.g.	B. osmundense n.sp.	Convex	Median septum and the proto-S fused into an axial structure	MS long. S. dilat. weak or fairly strong	+	+	_
Densigrewingkia n.g.	D. pyrgoidea n.sp.	Concave	Not examined	MS long in early phases, later gradually shorter. S. dilat. moderate or strong	+ or -	+	+ or – when + only in late phases
Borelasma n.g.	B. crassitangens n.sp.	Convex	Median septum, no axial struc- ture, all S strongly dilated	MS long in early phases, later gradually shorter. S. dilat. moderate or strong	8 <u></u>	(<u>)</u>	2

Interseptal chambers	Stereo- zone	Axial structure	Calicular boss	Tabulae	Fossula (real)	Ontogeny diagram- matically figured in this paper
+ Gradually increasing in width	+	+ (At least at some lev- els)	-	+ Complete, convex	-	Fig. 22 p. 30
+ Large	+	+ broad, composed of numerous S. lobes and lamellae	+ or -	+ Complete or incomplete, convex	-	Fig. 27 p. 34

Ephebic stage

MS long, all S comparatively

Septa

thin	increasing in width		els)		convex		
MS short, all S comparatively thin	+ Large	+	+ broad, composed of numerous S. lobes and lamellae	+ or -	+ Complete or incomplete, convex	_	Fig. 27 p. 34
MS short or fairly long. S. dilat. weak or -	+ Large	+	(+) or - when + composed of few weakly fused ends of MS, - in the last phases	-	+ Complete, convex or flat	_	Fig. 3 p. 9
MS short S. dilat. weak or strong	+	+	-	-		_	
MS long all S comparatively thin	+ Large	+	+ Composed of fused ends of MS	-	-	-	
MS long all S strongly dilated	+ Only in the last phases	+ Only in the last phases	_	-	_	– Cardinal pseudo- fossula marked	
MS fairly long. S. dilat. weak	+ Only in late phases	+	+ Composed of fused S. lobes and a few lamellae	+ Prominent, elliptical in outline	+ or - when + few, incomplete, complete, and convex	+ or – cardinal fossula	
MS short S. dilat. weak	+ Large	+	+ broad, composed of numerous S. lobes and lamellae	Probably —	+ Complete or incomplete, convex	+ Cardinal fossula	
MS long S. dilat. weak	+ Large	+	+ Composed of fused S. lobes and a few lamellae	+ Prominent, circular or elliptical in outline	+ or - when + few, incomplete, complete, convex	_	Fig. 45 p. 55
MS short S. dilat. fairly weak	+ Fairly large	+	 + broad, comp- osed of numerous S. lobes and lamellae in early phases connec- ted by stereoplasmatic de 	+ p.	+ Complete convex	-	Fig. 42 p. 51
MS short S. dilat. fairly weak	+ Gradually increasing in width	+	-	-	+ Complete convex or plane	-	Fig. 56 p. 66

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