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RUGOSE CORALS FROM THE UPPER SILURIAN OF SCANIA, SWEDEN

by

Makoto Kato and Yoichi Ezaki

(with 5 text-figures and 3 plates)

Abstract

Four species of rugose corals including two new species, Pilophyllum keimori and Phaulactis variabilis are described from the upper Ludlovian Öved-Ramsåsa Group of Scania, southern Sweden. An attempt is made at re-classifying and synonymizing genera belonging to the Streptelmatidae, Lykophyllidae and Kyphophyllidae.

Introduction

In Scania, southern Sweden, Silurian sediments are extensively developed along NW-SE trending outcrop belts (Text-fig. 1). Shales are predominant, and they have been stratigraphically classified as below (Regnell, 1960):

- Öved-Ramsåsa Group
  - Colonus Shale
  - Cyrtograptus Shale
  - Rastrites Shale

The topmost sequence, the Öved-Ramsåsa Group is further divided into 4 units. The lowermost unit, division 1, the Björsjölagård limestone and shale, is composed of gray marls with lenses of limestone. Rugose and tabulate corals are known to occur in division 1, but none has been described as yet.

In 1968 Mori collected some fossils from a fossiliferous layer of division 1 rocks exposed along a ditch about 30 m WNW of the bridge on the road from Björsjölagård to Djupadal, Scania. A sketch of the outcrop by Mori (1969) is here reproduced (Text-fig. 2). The biostromal layer, rich in stromatoporoids within a marly matrix, also yields some corals.

The following three stromatoporoids were described by Mori (1969): Plexodictyon? irregulare Mori, Plectostroma scaniense Mori and Parallelopora ornata Mori. The latter two species were later described by Mori (1970) from the island of Gotland, where Plectostroma scaniense is known from the Hemse, Hamra and Sundre Beds, while Parallelopora ornata is known from the Eke and Hamra Beds.

Specimens of rugose corals collected by Mori were later entrusted to the senior author for study. Corals are small to medium in size, mostly with marly matrix attached to their coralla and lacking tips representing young growth stages. We have identified the following species from the above mentioned locality and horizon.
Text-fig. 1 Index and simplified geological map of Scania, southern Sweden (after Regnell, 1960 and Mori, 1969).

Text-fig. 2 Diagrammatic sketch of an outcrop, showing the occurrence of fossils (after Mori, 1969).
Dinophyllum involutum Lindström
Phaulactis variabilis, sp. nov.
Pilophyllum keimorii, sp. nov.
Cystiphyllum sp.

Number of specimen(s)
1
13
2
1

Total 17

The occurrence of Dinophyllum involutum here is unusual, since it has been described from the Lower Silurian of Eurasia (Latypov, 1982). Pilophyllum keimorii resembles Pilophyllum weissermeli, which was first described by Wedekind (1927) from his “Pilophyllum Stufe” in Gotland. A preliminary study on Gotlandian corals by the senior author reveals its occurrence in the Hemse and Hamra Beds. Phaulactis with morphology comparable to our Phaulactis variabilis is also known from the Sundre Beds.

Therefore the corals and stromatoporoids indicate that the Öved-Ramsåsa Group (probably its division 1) is correlative with the Hemse to Sundre Beds of Gotland. These beds have been correlated on the basis of conodonts with the all of the Ludlovian (Fåhraeus, 1969). If the Öved-Ramsåsa Group is younger than the Monograptus leintwardinensis Zone, as suggested by Regnell (1960), the stromatoporoid-coral bed of Scania herein described would be correlated with the Hamra and Sundre Beds and assigned to the Whitcliffian, the Upper Ludlovian.

Mori (1969) concluded that the stromatoporoid-coral bed was a biostromal layer deposited within the photic zone, mostly calm but with occasional turbulence.

Systematic Description
Family Streptelasmatidae Nicholson, 1889

For corals having lamellar tissue investing trabecular septa Wang (1947) introduced the family Dinophyllidae. But this character may be found not only in Streptelasmatids but also in many other coral groups. This character alone does not warrant separation of the group from the Streptelasmatids with trabecular septa.

The family Dinophyllidae was, however, employed by many subsequent authors using a different definition. For example, Ivanovsky (1975) in his classification of rugose corals recognized the Streptelasmatidae, Dinophyllidae and Densiphyllidae within the Streptelasmatids. The family Dinophyllidae was said to be characterized by thin septa and incomplete tabulae [ibid]. This definition has not proved to be useful. Hill (1981) considered the Dinophyllids as constituting a subfamily in the family Streptelasmatidae. She placed ten subfamilies within the family Streptelasmatidae. Distinguishing features between the Streptelasmatinae and Dinophyllinae are unclear. Latypov (1982) did not recognize any subfamilies within the family Streptelasmatidae. Neuman (1977) listed 10 distinguishing characters for the classification of Streptelasmatids, using characters which are more or less gradational. Therefore clean cut
distinction among genera and species is sometimes difficult. McLean (1974) stated that
the relationships among *Streptelasma*, *Porfirieviella* and *Dinophyllum* are uncertain. *Streptelasma* has comparatively short and thin major septa, while major septa in *Porfurieviella* are thin but long enough to reach the axial region. In *Dinophyllum* the major septa are moderately thick, extending to the axis, and are rotated to form an axial vortex. Neuman (1977) described complete tabulae in *Streptelasma*, while they are incomplete in *Dinophyllum* and *Porfirieviella*. These distinctions, however, hold true only for typical forms of these genera. In view of great variation revealed during the course of ontogeny in Streptelasmatids, generic or specific definition appears to be a difficult task.

Genus *Dinophyllum* Lindström, 1882

1882 *Dinophyllum* Lindström, p. 21.
1982 *Dinophyllum*, Latypov, p. 82. (for further synonymy)

*Type species*: *Dinophyllum involutum* Lindström, 1882

*Generic diagnosis*: Corallum solitary, ceratoid. Septal grooves and interseptal ridges prominent on the epitheca. Axial structure made up by rotated axial ends of major septa and conically elevated tabulae which are complete or incomplete. Moderately thick stereowall present. Minor septa short. Major septa thin in early growth stages, becoming moderately thickened, extending to the axis and rotated anti-clockwise to form a weak or stout axial structure. Cardinal fossula on the convex side of the corallum.

*Remarks*: The following species have been ascribed to the genus *Dinophyllum*, or once placed in it.

- *Clisiophyllum hisingeri* Milne-Edwards & Haime, 1851
- *Zaphrenthis stokesi* Milne-Edwards & Haime, 1851
- *Clisiophyllum danaeum* Milne-Edwards & Haime, 1851
- *Zaphrenthis conigera* Rominger, 1876
- *Zaphrenthis umbonata* Rominger, 1876
- *Dinophyllum involutum* Lindström, 1882
- *Streptelasma hoskinsoni* Foerste, 1890
- *Dinophyllum minimum* Ryder, 1926
- *Paterophyllum praematurum* Smith, 1930
- *Dinophyllum involutum* var. *fissum* Scheffen, 1933
- *Dinophyllum flagellatum* Scheffen, 1933
- *Dinophyllum yunnanense* Wang, 1947
- *Paterophyllum aperture* Soshkina, 1955
- *Streptelasma latum* Nikolaeva, 1955
- *Dinophyllum lundarensense* Stearn, 1956
- *Dinophyllum brevisepatum* Ivanovský, 1960
- *Dinophyllum? irregulare* Ivanovský, 1960
- *Neobracchyleasma balchashica* Nikolaeva, 1960
- *Pseudophaulactis lasius* Ivanovský, 1965
This list of species demonstrates the different conceptions of the genus *Dinophyllum*. We interpret the genus as diagnosed above. The genera *Streptelasma* and *Helicelasma* differ from *Dinophyllum* in having thick major septa in their early growth stages. *Tenuilasma* has very thin major septa, while major septa are much dilated in cardinal quadrants of *Pseudophaulactis*. *Porfirieviella* may be synonymous with *Dinophyllum* if we interpret the type species, *Zaphrenthis stokesi* Milne-Edwards & Haimé in the sense of Shrock & Twenhofel, 1939 (fide Hill, 1981). *Neobrachyelasma* differs from *Dinophyllum* in having a central tabular depression, and the genus may prove to be related to *Pilophyllum*. *Crassilasma* is easily distinguished from *Dinophyllum* by its greatly thickened major septa throughout ontogeny. For *Streptophyllum* Grabau Lang, Smith & Thomas (1940) selected *Clisiophyllum hisingeri* Milne-Edwards & Haimé as type species. This species has generally been considered as synonymous with *Dinophyllum involutum*, thereby implying synonymity of *Streptophyllum* and *Dinophyllum*.

**Distribution:** The genus *Dinophyllum* ranges from the Lower Silurian to Middle-Silurian. The present occurrence from the Upper Silurian of Scania is exceptional. The genus has been recorded from Sweden, USSR, China, USA, U.K., Norway, & Australia.

*Dinophyllum involutum* Lindström

(Pl. 1, fig. 1; Text-fig. 3)

1882 *Dinophyllum involutum* Lindström, p. 21.
1982 *Dinophyllum involutum*, Latypov, p. 83. (for synonymy)

**Material:** Single corallite. UHR 30639

**Description:** The corallum is solitary, ceratoid. Septal grooves and interseptal ridges are distinct on the epitheca. The specimen attains 23 mm in calicular diameter. A weak cardinal fossula is on the convex side of the corallum. The calicular floor is centrally elevated by rotated axial ends of the major septa.

In transverse sections, the peripheral stereozone formed by lateral fusion of septa is prominent and is already developed even in relatively early growth stages, becoming gradually thickened as the coral grew upward. Septa are platy and continuous, radially
arranged in two orders. Major septa extend to the axial part and there some are curved and twist anti-clockwise, but no true axial structure was constructed. Septa are moderately thick, tending to taper axially. Septal length is longer in the cardinal quadrant, and in the early growth stage in the counter quadrant. As many as 35 major septa occur in the 23 mm diameter corallite. Major septa are very short even in the mature stage. A dissepimentarium is absent. In longitudinal section, tabulae are complete, distant and axially elevated. The axial portion of the tabularium is incorporated with the axial ends of major septa, and is not differentiated from the rest.

Remarks: The specific description is based on a single well-preserved specimen.

The specimen is characterized by its long and thick major septa which twist anti-clockwise in later growth stages. The species also has a relatively thick peripheral sterezone. Lindström (1882) described a new species, *Dinophyllum involutum* and illustrated this in 1896. The calicular boss is high and distinct in Lindström's form. While it is not so prominent in the present material. This feature is, however, much related to the degree of septal twisting, which varies with growth stages. *Dinophyllum semilunus* Laub (1979) resembles *D. involutum*. But it has a relatively thin sterezone and long minor septa. *Dinophyllum brevisepatum* Ivanovsky (1960) differs from *D. involutum* in having more numerous major septa.

Family Lykophyllidae Wedekind, 1927

Hill (1981) presented a new classification of Lykophyllids, to which *Novactis* Sytova (1983) may be added. The genus *Pseudophaulactis* Zaprudskaya (in Ivanovsky, 1963) may be a Streptelastmatid, and is best excluded from the Lykophyllidae. The systematic position of *Schizophaulaetis* Laub (1979) is not well understood by us.
Genus Phaulactis Ryder, 1927

Type species: Phaulactis cyathophylloides Ryder, 1926

Generic diagnosis: Corallum solitary, trochoid, ceratoid to curved cylindrical. Cardinal side on the convex side of the corallum. Septa in two orders. In early stages of ontogeny, cardinal septum long, all septa pinnately arranged and much dilated to leave no interseptal space. In later stages, dissepiments introduced, septa attenuated from the periphery, with intrathecal dilation of major septa only prominent in cardinal quadrants; eventually septa becoming thin and even shortened to form an axial open space. Septa occasionally discontinuous in dissepimentarium; minor septa degenerate in some forms. No axial structure. Dissepiments numerous, generally small, concentric, anguloconcentric to herringbonal in transverse section. In some forms distinct lonsdaleoid dissepiments developed. Inner wall sometimes developed. Differentiation between tabularium and dissepimentarium distinct or indistinct. Tabulae incomplete to subcomplete; tabular floor subhorizontal or slightly to strongly concave upwards.

Remarks: The above listed synonymy is not intended to be exhaustive, but is rather to show a number of genera which we believe to be synonymous with Phaulactis. In view of the extremely variable nature of the species described below, we feel it necessary to extend the generic diagnosis of Phaulactis to accommodate the listed forms. Ryder's (1926) original definition of the genus was to include forms which retain intrathecal dilation of major septa in cardinal quadrants. Lang and Smith (1927) soon extended its diagnosis to include species with no septal dilation even in the brephic stages. In a recent classification Hill (1981) merges such genera as listed in the above synonymy to Phaulactis. Our diagnosis is to further add forms with partially developed lonsdaleoid dissepiments to the genus. Hill (1981) placed Phragmophyllulll Scheffenn (1933) in the synonymy of Phaulactis, but the former possesses arched tabellae and may not be a Lykophyllid. At the same time she placed Stratiphyllum Scheffenn in the same synonymy with a query, it is possible that Stratiphyllum is a Streptelasmatid. The genera Pycnactis, Holophragma, and Onychophyllum have no dissepiments. The genera Zeravschania and Pseudocystphylllum have extensively developed lonsdaleoid dissepiments. The genus Strephophyllum has compound coralla. Thus these genera are easily distinguishable from Phaulactis. The genera Camurophylllum and Ryderophyllum are possibly Cyathactids. The genera Plasmophyllum and Lamprophyllum have no lonsdaleoid dissepiments and major septa appear to have retreated from the
axial region even in early growth stages. The genus *Rukhinia* has long and slightly thickened major septa throughout ontogeny and dissepiments are ill developed. The genus *Svetlania* has fewer septa, and a well differentiated tabularium in which tabulae are concave and distantly spaced. Therefore these genera are again easily distinguished from *Phaulactis*. The genus *Novactis* resembles *Phaulactis*, but in the former minor septa are ill developed if at all. *Mesactis glevensis* Ryder (1926) somewhat resembles some *Novactis* species.

Range: Llandoverian to Ludlovian.

*Phaulactis variabilis* Kato and Ezaki sp. nov.

(Pl. 2, figs. 1-2; Text-fig. 3)

**Derivation of Name:** After the extremely variable features of the internal skeleton.

**Material:** Holotype UHR 30640; paratypes UHR 30641, 30642, 30643, 30644, 30645, 30646, 30647, 30648, 30649, 30650, 30651, and 30652.

**Diagnosis:** Medium sized Phaulactids with little or no septal dilation. Minor septa usually degenerate. Tabularium and dissepimentarium normally well differentiated. Lonsdaleoid dissepiments sometimes developed.

**Description:** The corallum is solitary, trochoid to curved cylindrical. The surface character is unclear, but faint transverse wrinkles and interseptal ridges are observed in some corallites. The largest specimen attains 19 mm in diameter and 85 mm in length as far preserved. Calicular features are unknown. The cardinal septum is on the convex side of the corallum.

In transverse section, corallites are round with a generally thin, crenulated wall composed of alternating septal grooves and interseptal ridges. The thickness of the wall is variable, even within one corallite. No axial structure was observed. Septa are radially arranged in two orders. The fossula is indistinct. Septal dilation is lacking or only feebly recognized in the tabularium. Major septa start from the wall, extend a long distance into the axial region in early growth stages. The length of major septa is variable from corallite to corallite, but in general they retreat from the axial region to leave a wide, open space at the centre in the mature stage. Major septa show a tendency to rotate centrally. The number of major septa may be as many as 40 in a corallite 15 mm in diameter.

In the early growth stage, the cardinal septum is elongated and comparatively thick. Slight intrathecal dilation on the septa and at the boundary between the tabularium and dissepimentarium may form a distinct inner wall. Minor septa alternate with the major, and are extremely variable in length; some may intrude into the tabularium, while they are almost absent in some corallites. Septal fine structure is obscured by recrystallization. Tabulae are seen as concentric rings between the septa in the tabularium. The dissepimentarium is composed of many rows of concentric dissepiments when minor septa develop. Dissepiments become inosculating to herringbonal in case of weakly developed minor septa. In some specimens lonsdaleoid dissepiments are partly developed. They may be only the discontinuation of minor septa to begin with, but
fairly large lonsdaleoid dissepiments may be also developed, which appear in an early stage, but disappear in later stages in some corallites.

In longitudinal section, the differentiation between tabularium and dissepimentarium may be clear or sometimes indistinct. The dissepimentarium consists of several rows of small globose and large flattened dissepiments. The tabular floor is centrally sagging; tabulae are incomplete or nearly complete, and they are well spaced and deeply concave in some corallites, while they may be closely and evenly spaced and subhorizontal in others.

Remarks: At first it would seem reasonable that there exist a number of forms within the present new species. However, by observing internal characters exemplified in a transverse section at mature stage of a specimen (Pl. 2, fig. 1g), we realized that variation was very great. In one specimen (UHR 30640), the major septum is long on one side, and short on the other. Lonsdaleoid dissepiments are developed and minor septa are degenerate in one side, but not on the other. Wall thickness is different from place to place. In a young stage of the same specimen, the central part of the corallite is wide
open, little intrathecal dilation is observed, and no lonsdaleoid dissepsiments are
developed. Assuming wide intracorallite variation in a single specimen, in other
individuals, a wide range of intercorallite populations was expected, and observed. No
Pycnactis or Mesactis stages (Ryder, 1926) have been observed in young stages of the
specimens examined, but this is apparently representative of Lykophyllids without any
or only little intrathecal septal dilation. Some parts of our specimens having well
developed, long major and minor septa, and no lonsdaleoid dissepsiments appear to
show similarity to "Hercophyllum". When minor septa degenerate, they resemble
"Neocystiphyllum". Specimens with relatively short, radially arranged major septa re­
mind of some forms of "Desmophyllum" of Wedekind (1927). But no previously
described form of Lydophyllids is identical with the present form, which is placed here
in the wider context of the genus Phaulactis. Minor septa sometimes become discon­
tinuous in Phaulactis cyathophylloides Ryder (1926), Phaulactis quebecensis Oliver
(1962) and Phaulactis onukii Murata (1977). Dissepsiments may become partly
lonsdaleoid in Neocystiphyllum keyserlingi of Ivanovsky (1965), but lonsdaleoid
dissepsiments are never as conspicuous in any other Phaulactids as in the examined
species. Septal dilation is absent and the tabularium is well differentiated in Ex­
pressophyllum krikovense Sytova (1968), “Desmophyllum” sp. (Wedekind, 1927) and
in Phaulactis onukii Murata (1977). They show some similarity to the present species.
But in these forms major and minor septa are always long. The first species cannot be a
member of the genus Expressophyllum Strelnikov (1968), which should have domed
tabulae. Neocystiphyllum sp. of Sytova (1970) somewhat resembles the present species,
but is distinguished from the latter in having no lonsdaleoid dissepsiments. The present
new species is a late representative of Phaulactis. Corals probably identical with the
present new species occur in the Sundre Beds of the Hoburgen Formation in Gotland.

Family Kyphophyllidae Wedekind, 1927

Wedekind (1927) erected the family Kyphophyllidae, and Torley (1933) introduced
the family Endophyllidae later. These two families, as interpreted by Hill (1981), are in
fact very close and difficult to distinguish. Indeed the general presence of axial depre­
sion in up-arched tabulae is a major feature of the family Kyphophyllidae distingui­
sishing it from the Endophyllidae. Apart from these families, Hill (1942) created the
family Pilophyllidae, which several subsequent authors employed in a different sense.
Hill hereself, however, merged the family Pilophyllidae into the family Endophyllidae
with a query in 1956. Later this family was made synonymous with the family Kypho­
phyllidae by Hill in 1981. For the systematic position of the genus Pilophyllum we ten­
tatively follow Hill (1981). However we notice that some forms of Endophyllids are
not unlike forms of Pilophyllum. Suprageneric classification of Kyphophyllids, En­
dophyllids and Pilophyllids needs further study.

Genus Pilophyllum Wedekind, 1927

? 1927 Kyphophyllum Wedekind, S. 19. (partim)
1927  *Pilophyllum* Wedekind, S. 39.
1942  *Sinospongophyllum* Hill, p. 20.
1944  *Pilophyllum*, Wang, p. 23. (not seen)
1952  *Pilophyllum*, Bulvanker, p. 20.
1956  *Pilophyllum*, Hill, F. 301.
1961  *Nipponophyllum*, Strusz, p. 346. (partim)
1961  *Pilophyllum*, Zheltonogova (not seen)
1963  *Pilophyllum*, Yū et al., p. 155.
1961  *Pilophyllum*, Ivanovsky, p. 60.
1965  *Pilophyllum*, Ivanovsky, p. 73. (partim)
1968  *Pilophyllum*, Goryanov, p. 22.
1968  *Pilophyllum*, Lavrushevich, p. 60.
1973  *Pilophyllum*, Pavlova, p. 36.

**Type species** (by original designation): *Pilophyllum keyserlingi* Wedekind, 1927

**Generic diagnosis:** Corallum solitary, trochoid to conico-cylindrical. Wall thick, crenulated. Peripheral stereozone developed to varied degrees. Septa radially arranged in two orders. Fossula indistinct. Septa discontinuous in dissepimentarium where large and small lonsdaleoid dissepiments develop. Intrathecal dilation common, making the inner wall prominent. Major septa moderately thick, extending and thinning towards the axial region where rotated. Longitudinally dissepiments large. Taburarrium well differentiated from dissepimentarium. Tabulae axially domed with peripheral series of sagging tabellae. Axial parts of tabulae commonly depressed.

**Remarks:** Wedekind (1927) originally placed *Pilophyllum* in the family *Kodonophyllidae*, probably in view of the presence of thick stereozone in the type species of *Pilophyllum*.

The following is a check list of nominal species of the genus *Pilophyllum*.

*Sinospongophyllum abrogatum* Hill, 1942  
*Pilophyllum angusta* Zheltonogova, 1961 (*fide* Hill, 1981; = *Salairophylum*)  
*Pilophyllum bimurum* Sytova, 1966  
? *Neokyphophyllum calcareum* Spasskiy, 1965  
*Cyathophyllum clisiophylloides* Stepanov, 1908 (*fide* Sytova & Ulitina, 1983)  
? *Kyphophyllum conicum* Wedekind, 1927  
*Pilophyllum insolitum* Zheltonogova, 1961 (*fide* Lavrushevich, 1968) (non *Pilophyllum*)  
*Pilophyllum keyserlingi* Wedekind, 1927  
*Pilophyllum kodonophylloides* Pavlova, 1973 ( = *Ptychophyllid?*)  
*Pilophyllum moyeroense* Ivanovsky, 1963 ( = *Pseudopilophyllum*)  
*Nipponophyllum multisepatum* Strusz, 1961  
*Pilophyllum munthei* Wedekind, 1927 ( = *Grabauphyllum*)
A number of genera were placed in the family Kyphophyllidae by Hill (1981). Among these Donacophyllum (= Strombodes) is essentially fasciculate, and Wintunastraea is cerioid. Pilophylloides and Maikottaphyllum have ill developed dissepiments. Neokyphophyllum is similar to Pilophyllum, but its axial portion is more complex. Kyphophyllum is solitary, with small dissepiments, no stereolone, and no axially rotated major septa. Morphological affinity of Pilophyllum to Endophyllids, and Tabulophyllids, as noted earlier, should not be overlooked.

Apart from the above mentioned Kyphophyllid genera Pseudopilophyllum and Pilophyllia have been proposed. Pseudopilophyllum (Lavrusevich, 1971) has small dissepiments, domed tabellae without any axial depression and no lonsdaleoid dissepiment. The genus is not related to Pilophyllum. Hill (1981) placed it in Arachnophyllids in general. In 1974 a new genus, Pilophyllia was introduced by Ge & Yü, the type species of which was Pilophylloides jenggangensis, but again in the plate explanation it was changed to Pilophyllia jenggangensis. Ge (1978) diagnosed Pilophyllia and gave Pilophyllia involutus as its type species. In any case Pilophyllia has no dissepimentarium, and tabulae are not differentiated; thus it is not related to Pilophyllum.

_range_: Upper Llandoverian? to Lower Devonian

**Pilophyllum keimorii** Kato and Ezaki sp. nov.

*(Pl. 3, figs. 1-2)*

**Derivation of Name:** After Dr. K. Mori of Tohoku Univ.

**Material:** Two specimens. Holotype UHR 30653; paratype UHR 30654

**Specific diagnosis:** Large Pilophyllum with relatively thin wall, narrow dissepimentarium, ill developed inner wall, and numerous thin septa. Tabulae axially depressed and nearly complete.

**Description:** The corallum is solitary, ceratoid to curved cylindrical, and medium in size. The surface characters are unknown, except that distinct septal grooves and interseptal ridges were observed on a partially weathered out epitheca. The largest specimen attains a 28 mm diameter.

In transverse section, the corallite is round in outline. Internally the corallite con-
consists of a moderately thick, bead-shaped wall, and dissepimentarium with large and small lonsdaleoid dissepiments and a tabularium. The width of the dissepimentarium is narrow, occupying about 1/5 of the radius of corallite. Two to three rows of large, flattened or small lonsdaleoid dissepiments are observed, but these may be small and are only indicated by discontinuous minor septa, or they are so reduced as to be replaced by stereowall (Pl. 3, fig. 1c). The inner wall is not usually very conspicuous, but dilation on the internal surface of dissepimentarium is observed in a corallite in young growth stage (Pl. 3, fig. 1a). The tabularium is wide. Septa are thin and in two orders. The fossula is indistinct. Major septa are long, extending near to the centre of corallite where they are rotated counter-clockwise. Minor septa alternate with the major, short, and are developed near the inner wall. Septal fine structure is obscured by recrystallization. All the septa become discontinuous in the dissepimentarium where they are represented by spiny projections on the dissepimental vesicles. Small tubercle-like projections are occasionally seen on both sides of major septa near the innerwall. The number of major septa is counted as many as 45 in a corallite of 26 mm in diameter. Relationship between the number of major septa and the size of corallite is shown in Text-fig. 5. No axial structure was observed. In a transverse section of young growth stages (Pl. 3, fig. 1a) a hollow, triangular projection on the corallite shows the presence of a talon on the corallum surface.

In longitudinal section, differentiation between the dissepimentarium and tabularium is clear. The wall is moderately thick and wavy. The dissepimentarium consists of 2 to 3 rows of large and small dissepiments rather steeply inclined inward. The tabular floor is centrally domed with a peripheral trough composed of sagging tabellae. Axial parts of tabulae are more or less complete and gently depressed. Remarks: The present form resembles Pilophyllum weissermeli and P. progressum. Pilophyllum weissermeli has a similar size and numerous septa as compared with the present form but is different from the latter in having a conspicuous sterezone and incomplete tabulae which are not prominently depressed in their axial region. P. weissermeli described by Różkowska (1962) has more similarity to the present form; it reveals a not very conspicuous sterezone as in the holotype of the species (Wedekind, 1927). However, it has large, steeply dipping dissepiments and incomplete tabulae, just as in the holotype. P. progressum closely resembles the present form especially in features apparent in transverse section, but P. progressum is a fasciculate form, and has smaller corallites having less numerous septa compared to the present form.

Family Cystiphyllidae Milne-Edwards & Haime, 1850
Genus Cystiphyllum Lonsdale, 1839

1839 Cystiphyllum Lonsdale, p. 691.
1974 Cystiphyllum, McLean, p. 5. (for further synonymy)
1977 Cystiphyllum, Latypov, p. 31. (for further synonymy)
1981 Cystiphyllum, Hill, F. 112.

Type species (by subsequent designation of Milne-Edwards & Haime, 1850):
Cystiphyllum siluriense Lonsdale, 1839

Remarks: In view of extreme variation experienced in the group of *Cystiphyllum*, the authors would like to retain a broad definition of the genus, yet include only solitary forms having short septal spines.

![Graph showing relationship between number of major septa and diameter of corallite](image)

**Text-fig. 5** Relationship between number of major septa and diameter of corallite in *Pilophyllum keimori* n. sp. • — UHR 30653 (Holotype); ■ — UHR 30654; ★ — *Pilophyllum weissermelii* Wedekind; ○ — *Pilophyllum keyserlingi* Wedekind; ▲ — *Pilophyllum progressum* Wedekind.

*Cystiphyllum* sp.

(Pl. 1, fig. 2; Text-fig. 3)

**Material:** Single specimen with auloporoid coral covering the external surface of the corallum. UHR 30655.

**Description:** The corallum is solitary, curved, and cylindrical. The surface characters cannot be directly observed since the corallite is covered by marly matrix and an auloporoid coral. The tip is missing, but the preserved part of corallum measures 6 cm in length along the convex side of corallum. The largest calicular diameter is 18 mm.

In transverse section the corallite has a fine external crenulation of the moderately thick, fibrous wall from which very short holacanthine spines originate. Pl 1, fig. 2a shows a young growth stage with relatively thick wall and non-differentiated cystoseptiments. The flared part of the corallite probably indicated the presence of talon. Pl 1, fig. 2b shows the outerzone of dissepiments and the inner part of large cystosepiments; this section suggests an initial stage of rejuvenescence of corallite. Pl 1, fig. 2d is a fully grown part of a corallite which shows the outer zone of one or two series of large dissepiments, the inner zone of smaller dissepiments and still inner tabular zone which is a little excentrically situated near the concave side of corallum. In Pl 1, fig. 2e, the
uppermost section obtained, the zonal arrangement of internal features becomes obscured, and dissepiments are irregular in size and in which weak sclerenchymal thickening is observed as wavy lines. The tabular depression is filled with marly matrix.

A longitudinal section, which is made in between the sections shown as Pl. 1, fig. 2b, and Pl. 1, fig. 2d, clearly shows rejuvenescence in its lower part. The rejuvenated part of the corallite at first has a narrow, steep dissepimentarium, which is not well differentiated from tabularium. In the upper part, dissepiments grow large and the tabularium is weakly differentiated, having a relatively sparse arrangement of sagging and arched tabulae. Tabular depression is eccentrically situated close to the concave side of the corallite.

Remarks: The specimen resembles Cysticonophyllum calyxoides Ivanovsky (1963) in longitudinal section. The latter form has, however, a distinct series of small, peripheral dissepiments. Cysticonophyllum khantaiakaense described by McLean (1974) also resembles the present Scanian form, but it has more numerous septal spines. The original specimen of Cysticonophyllum khantaiakaense Zaprudskaya (fide Ivanovsky, 1963) shows very few septal spines and a shallow calicular depression. All these forms are Llandoveryan in age. On the other hand the specimen closely resembles the lower Ludlovian Cystiphyllum excentricum Zhetonogova (1965). However, as internal features vary from one growth stage to the other in our specimen, we decline a final identification of the present form.

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Explanation of Plate 1.

Fig. 1 *Dinophyllum involutum* Lindström UHR 30639
Fig. 1a Side view of a weathered surface of a corallite showing distinct septal grooves and interseptal ridges, x1.
Fig. 1b Top view of a corallite showing calyx and weak cardinal fossula. Axial vortex is observable on the calicular surface, x1.
Fig. 1c-g, i-j Serial transverse sections revealing lateral fusion of septa and major septa twisted counterclockwise, all figures, x2.
Fig. 1h Longitudinal section, x2. Note twine of major septa.

Fig. 2 *Cystiphyllum* sp. UHR 30655
Fig. 2a-b, d-e Transverse sections, all figures, x3. The presence of a talon is indicated in Fig. 2a and distinct rejuvenescence is observable in Fig. 2b.
Fig. 2c Longitudinal section showing the rejuvenated part of a corallite. The tabular depression is eccentrically situated, x3.
Explanation of Plate 2.

**Fig. 1 Phauloclis variabilis**, sp. nov., UHR 30640 (Holotype)

Fig. 1a-c, e-g Serial transverse sections from the holotype, all figures, x3. Length of major septa is variable from place to place. Note central open space of the corallites and elongate cardinal septum indicated by an arrow in Fig. 1b.

Fig. 1d Longitudinal section revealing centrally sagging tabular floor, x3.

**Fig. 2 Phauloclis variabilis**, sp. nov., UHR 30641

Fig. 2a Transverse sections in the immature part of a corallite which is provided with lonsdaleoid dissepiments, x3.

Fig. 2b Longitudinal section showing steeply sloping tabulae and dissepiments. Tabularium is well differentiated from dissepimentarium, x3.

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**Explanation of Plate 3.**

*Fig. 1 Pilophyllum keimorii*, sp. nov., UHR 30653 (Holotype)*

Fig. 1a-e Transverse sections of holotype showing well developed lonsdaleoid disseipments and distinct stereowall or innerwall. A talon is detectable on the corallum surface in Fig. 1a, all figures, x2.

Fig. 1d Longitudinal section of the holotype. The tabular floor is gently concave with peripheral trough, x2.

*Fig. 2 Pilophyllum keimorii*, sp. nov., UHR 30654

Fig. 2a Longitudinal section of the corallum, x2.

Fig. 2b-e Transverse sections of a corallum provided with much flattened lonsdaleoid disseipments, all figures, x2.
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