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Environment related morphological variation in Early Silurian tabulate corals from the Baltic area

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Abstract. The morphology of two species, *Halysites catenularius* (Linnaeus, 1767) and *Paleofavosites asper* (d'Orbigny, 1850), is statistically analysed based on numerous specimens. The specimens of *H. catenularius*, collected from the biostrome at Ireviken 3, Gotland show no particular change in intracolony variation, but shape and size of lacunae are variable. However *P. asper* from the Slite Beds in Gotland shows very large variation of corallite size and corallum shape both within and among localities. Species with large morphological variation are widespread and difficult to deal with taxonomically.

Key words : Gotland, *Halysites*, morphological variation, paleoenvironment, *Paleofavosites*, Silurian Tabulata

Introduction

The taxonomy of the tabulate corals from the Silurian of Baltoscandia, as studied by Klaamann and Stasinska, was based on a typological approach (Klaamann, 1961, 1962, 1964, 1982, 1983 ; Stasinska, 1967). They did not pay much attention to intraspecific variation, which is common among tabulate corals. It is difficult to observe the species limits, when the descriptions are based on randomly selected material and measurement methods are poorly explained.

In the last few decades intraspecific variation of tabulate corals has been studied by several authors and it has become well known that species cannot generally be distinguished by measurement of a few diagnostic characters (Tesakov, 1978 ; Scrutton, 1989, 1997 ; Young and Elias, 1997, 1999). Intraspecific variation in tabulate coral species from Gotland has been described only by Stel (1978) and Young and Scrutton (1991).

The author has studied a number of collections of tabulates from Gotland housed in the Swedish Museum of Natural History, but intraspecific variation could not be studied in detail because material had been randomly collected (Mõtus, 1995). Fossil material not carefully documented in the field cannot provide satisfactory information about paleoenvironment, typical shapes and sizes of coralla, or the percentage of different species in a particular locality. For the purpose of the present paper it was important to provide measurements on a substantial collections of specimens from each locality. Sufficient numbers of specimens belonging to *Halysites catenularius* (Linnaeus, 1767) and *Paleofavosites asper* (d'Orbigny, 1850) from different localities on Gotland were collected and statistically analysed, to consider variation in their corallum shape and internal characters.

Material and methods

Twenty-eight specimens of *Halysites catenularius* were collected for study from 100 meters laterally along a biostrome of Lower Visby Beds at the locality Ireviken 3, Gotland. Specimens were sampled systematically, every three meters along the exposure from the lower part of the biostrome. Specimens of *Paleofavosites asper* were collected on Gotland from the localities Hide 1 (Slite Beds, unit g), Klintsbrovik 1 (Slite Beds, unit e), Alnäse 1 (Slite Beds, unit f), Tjeldersholm 1 (Slite Beds, *Pentamerus gothlandicus* layer) and Stora Myre 1 (Slite Beds, unit d). Twenty-six specimens of *P. asper* were analysed in all. Seven specimens morphologically similar to *P. asper*, but distinct in character from the others mentioned above, were collected from Asfaltverket of Gotland (Slite Beds), Simunds (Slite Beds) and Sepise, Island of Saaremaa in Estonia (Jaagarahu Stage, Pangamägi Member).

Transverse- and longitudinal thin sections were made from each specimen. All quantitative characters used to describe species were measured. For statistical analysis, tabularium diameters of halysitids and corallite diameter of favositids were based at least on 20 measurements per specimen. In favositids, smaller corallites with fewer than 5 sides were not measured. Technical methods of measurement were made according to Young and Elias (1995). The terminology of corallum shape is based on Young and Scrutton (1991).

Stratigraphic and geographic information on most localities is taken from Laufeld (1974) ; Hide 1-Slite Beds, unit g ; Tjeldersholm 1-Slite Beds, Pentamerus gothlandicus layer ;

Stora Myre 1-Slite Beds, unit d. The locality Alnäse 1-Slite Beds, unit f, is referred to in Jaanusson (1986), and at Klintsbrovik 1-Slite Beds, unit e, is based on personal communication (L. Jeppsson).

The collection of specimens studied is housed at the Swedish Museum of Natural History, Stockholm (abbreviated as RM below) and at the Institute of Geology, Tartu University (abbreviated as TUG).

Intraspecific variation in *Halysites catenularius* (Linnaeus, 1767)

Halysites catenularius is the main biostrome builder in the Lower Visby Beds at the locality Ireviken 3, associated with a few specimens of *Catenipora*, *Heliolites* and *Angopora*. Twenty-eight specimens of *H. catenularius* were measured. Mean range of tabularium diameters and the range of minimum and maximum values are shown in Table 1. The neotype (PMU G 681, Gotland, Silurian, deposited in Uppsala University Paleontological Museum) was redescribed by Klaamann (1979) and has the same diagnostic characteristics as specimens at Ireviken 3 (1.1-1.3×1.4-1.7 mm for tabularium diameter, 0.5×0.75 mm for tubule diameter, 0.15-0.2 mm for wall thickness and the occurrence of 3 to 12.5 tabulae per 5 mm length of corrallite). Minimum and maximum values overlap with measurements of the neotype.

No remarkable variation in statistical indices was observed along the 100 m length of the biostrome outcrop. The frequency distribution curve of tabularium diameters is close to normal (Figure 1). The only significantly variable characters are the size and shape of lacunae. These change from polygonal to meandroid and both forms may occur together (Figures 2A, 3A). This is explained as being dependent on astogenetic changes by several authors (Lee and Noble, 1990; Lee and Elias, 1991).

Table 1. Measurements of *Halysites catenularius* (Linnaeus, 1767) from 28 specimens of Ireviken 3, RM Cn 68853–RM Cn 68881. TAL-tabularium length (mm), TAW-tabularium width (mm), TUL-tubule length (mm), TUW-tubule width (mm), WT-thickness of wall (mm), SL-length of septa (mm), TA5-number of tabulae per 5 mm.

	TAL	TAW	TUL	TUW	WT	SL	TA5
Range of mean values	1.16-1.5	0.8-1.05	0.16-5.41	0.16-0.36	0.16-0.28	0.06-0.23	12.75-18.8
Range of minimum values	0.7-1.25	0.6-0.9	0.05-0.35	0.05-0.2	0.1-0.2	0.05-0.15	10-17
Range of maximum values	1.35-1.85	0.95-1.45	0.2-0.7	0.2-0.5	0.23-0.45	0.08-0.35	12-22

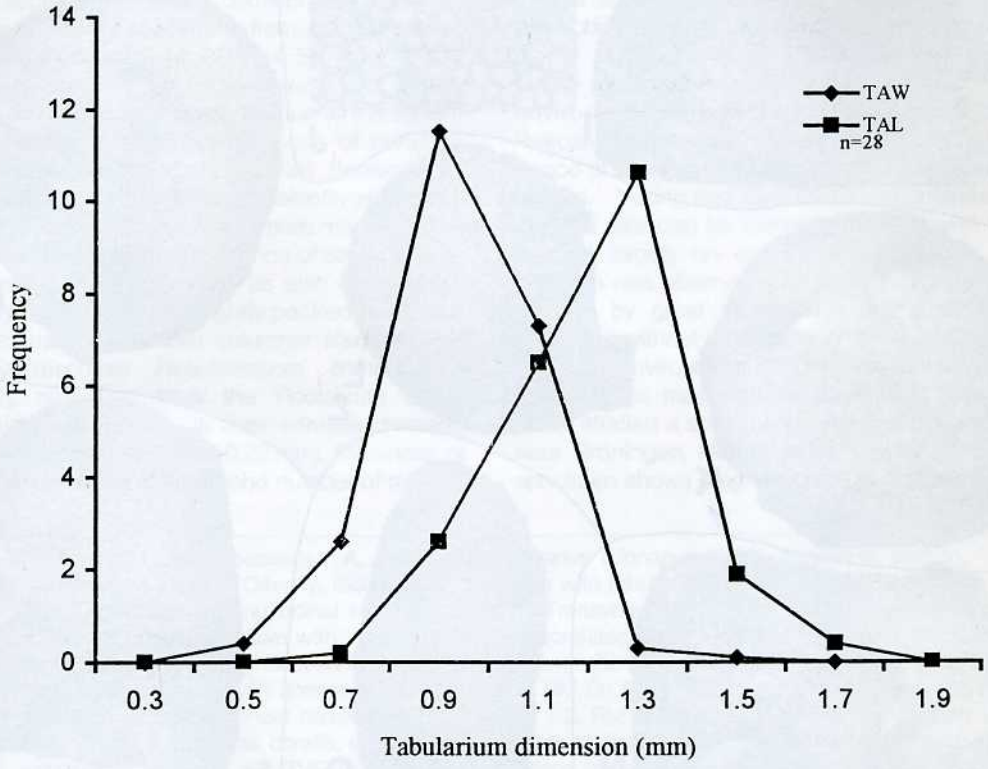
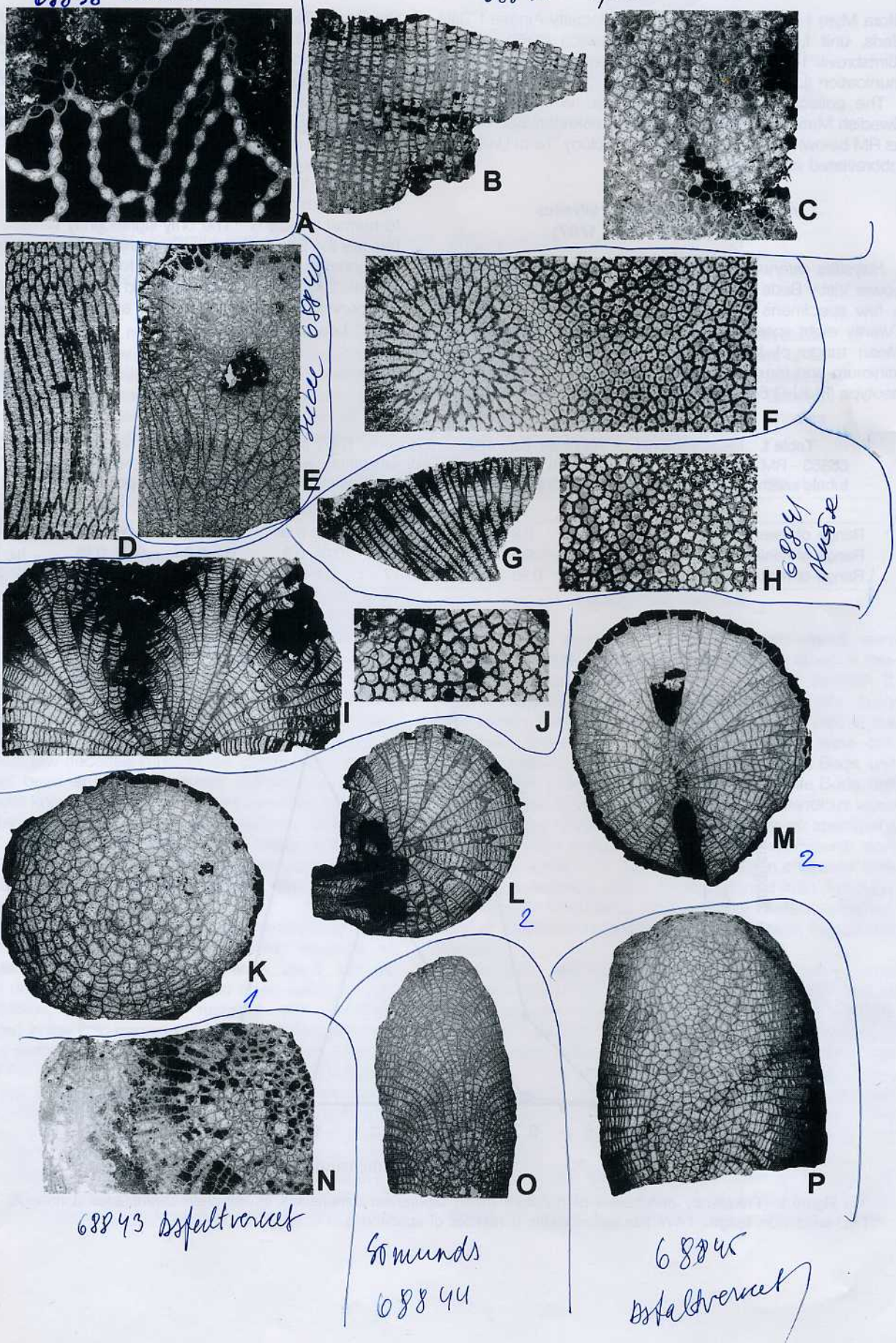


Figure 1. Frequency distribution of corallum mean tabularium dimensions in *Halysites catenularius* (Linnaeus, 1767). TAL-tabularium length, TAW-tabularium width, n-number of specimens.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Intraspecific variation in *Paleofavosites asper* (d'Orbigny, 1850)

Specimens of *P. asper* were collected from a number of localities on Gotland and on Saaremaa. Apparently the only characters of the species showing significant variation are the size of corallites and the shape of coralla.

The measured specimens showed no significant variation in other diagnostic characters, such as pore diameter, wall thickness, length of septa and spacing of tabulae. Only some specimens of *P. asper* from Gotland are very similar to the descriptions of the holotype, which has the mean corallite diameter range of adult corallites of 0.87–1.13 mm (Powell and Scrutton, 1978). Differences in typical corallite size of the specimens from different localities are illustrated by frequency distribution curves (Figure 4). Corallites of smaller size are common in coralla with tabular, nodular-domical, bulbous and columnar shapes. They are smaller in tabular coralla where corallites have regular growth and are parallel to one another in longitudinal section (Figures 2B, C). Coralla with multiple centres of increase (irregular growth) have more variable corallite sizes (Figures 2D, E, F, 3G). This is obvious in example of measured mean corallite diameters of some specimens from the locality Hide 1. There, all coralla are tabular, but the mean corallite size varies (Table 2). Similar variation in corallite size is seen also in the specimens from Klintsbrovik 1, where only bulbous and nodular-domical coralla are present (Figure 3C) and irregularly growing corallites are observed. The mean corallite diameter is larger in coralla of domical and spherical shape, as demonstrated by specimens from Alnäse 1, Stora Myre 1 and Sepise (Figures 2G–M, 3D–F, 4, 5).

Specimens from the localities Stora Myre 1 and Sepise have the largest corallite sizes, apparently due to the spherical shape of coralla and radial growth mode of corallites (Table 3). Specimens similar to these from Sepise were assigned by Klaamann to his species *Paleofavosites collatatus* (corallite diameters 0.9–2.2 mm, pore diameter 0.2 mm, wall thickness 0.06–0.08 mm, presence of septa, and 4–13 tabulae in 5 mm). At Asfaltverket, as also at Simunds, there is a laterally extensive bed of tightly packed striatoporids, branching tabulate corals with columnar shape. Taxonomically they resemble *Parastriatopora commutabilis* Klaamann (1962), described from the Rootsiküla Stage (uppermost Wenlock) of Estonia, in their corallite diameter (0.5–1.2 mm), diameter of pores (0.15–0.22 mm), thickness of wall (0.05–0.3 mm), presence of septa and number of tabulae (4–17 per 5 mm). However, these characters are also comparable to those of *P. asper* as shown above; they differ only in corallum shape (Figures 2N–P, 3B). It is noteworthy that the mean corallite diameter in specimens from Asfaltverket can be much smaller than in those from other localities only because of the columnar shape of coralla (Table 3, Figure 5). Similarly the specimens from Sepise have large mean corallite diameters (Figure 5).

Discussion

A number of the *Halysites catenularius* specimens, collected from different coralla forming the biostrome, show remarkable variation in lacuna size and shape.

According to Hamada (1959), halysitid lacunae form by the fusing together of new corallite chains produced by peripheral and interstitial increase.

Recently, Lee and Noble (1990) noted two different types of corallum growth: the monoplanulate mode, when the corallum develops from a single planula larva, and the polyplanulate mode, which describes the growth of a corallum from several larvae. According to this concept, the size and shape of lacunae depends on the astogenetic stage of the corallum, which is also different in the two growth modes. The regeneration pattern in halysitids demonstrates that growth of coralla is controlled both genetically and environmentally (Lee and Elias, 1991). As it is seen in number of specimens of *H. catenularius* from Ireviken 3, intraspecific variation is low in general. Additionally, the variation of lacuna size and shape can be explained by the factors mentioned here, due to regeneration or corallum growth mode.

The relationship between corallum internal structure and environmental conditions is easily observable in *Paleofavosites asper*. Scrutton (1997) described the dependence of corallum growth mode and shape on environmental factors. Young and Elias (1999) demonstrated that even the corallite size can be correlated with growth mode and both depend largely on environmental factors. An analogous situation was observed in *P. asper*. Therefore, corallite size marked by great variation is not a valuable diagnostic character without a description of the interaction of morphology and environment. In my opinion, *P. collatatus* and *P. commutabilis* may well be conspecific with *P. asper*. Stel (1978) studied a specimen of *P. asper* from an erratic boulder near Gröningen, Netherlands. Quantitative analysis of the specimen shows diagnostic values the same as those of the

Figure 2. Photographs of thin sections. **A.** *Halysites catenularius* (Linnaeus, 1767), transverse section, ×2.1, RM Cn 68858. **B–P.** *Paleofavosites asper* (d'Orbigny, 1850), **B, C.** Corallum with tabular shape, showing regular growth of corallites, Tjeldersholm 1, RM Cn 68838; B. longitudinal section, ×2.1. C. Transverse section showing regularly growing corallites, ×2.5. **D, F.** Sections of tabular corallum with irregularly growing corallites, Hide 1, RM Cn 68839; D. longitudinal section, ×2.1. F. transverse section, ×2.3. **E.** Section from bulbous corallum, where corallites grow irregularly, ×2.2, Hide 1, RM Cn 68840. **G, H.** Sections of corallum with domical shape, Alnäse 1, RM Cn 68841; G. longitudinal section, ×2, H. transverse section, ×2.2. **I, J.** Sections of spherical corallum, Stora Myre 1, ×2, RM Cn 68842; I. longitudinal section, J. transverse section. **K–M.** Sections from spherical coralla, showing radial growth of corallites, Sepise; K, transverse section, ×2.2, TUG 1/1066; L, M. longitudinal sections, ×2, TUG 2/1066. **N–P.** Sections of columnar coralla; N. transverse section, Asfaltverket; ×2, RM Cn 68843; O. longitudinal section, Simunds, ×2, RM Cn 68844; P. transverse section, Asfaltverket, ×2, RM Cn 68845.

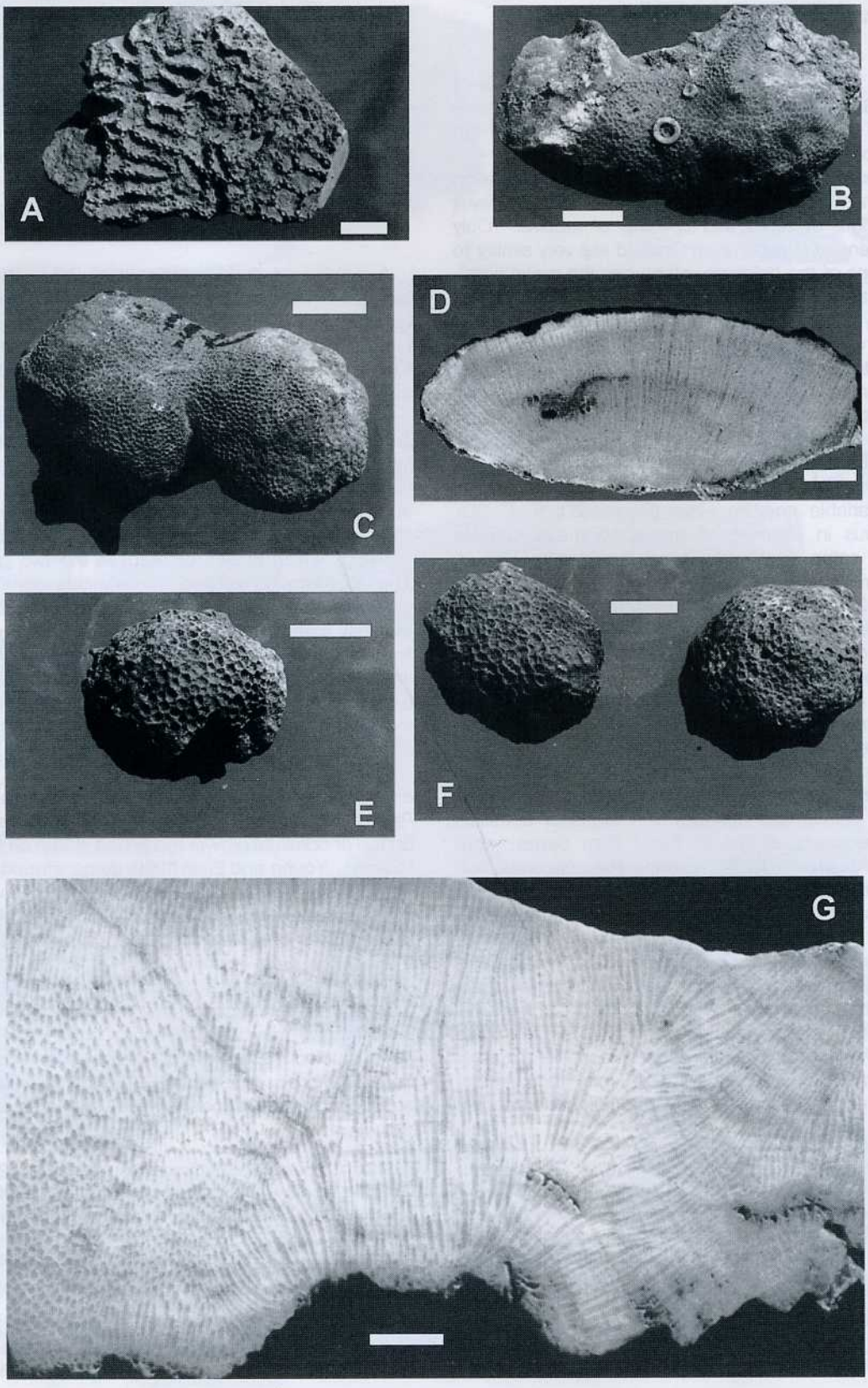
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Table 2. Measurements of corallite diameters of selected specimens of *Paleofavosites asper* (d'Orbigny, 1850) with regular and irregular growth from Hide 1. Specimen with smaller mean corallite diameter (RM Cn 68850) has regular growth of corallites and that with larger one (RM Cn 68851) has irregularly growing corallites. COD-diameter of corallites (mm).

	COD	COD
Mean value	1.02	1.45
Minimum value	0.65	1.0
Maximum value	1.3	1.75
Number of measurements	20	20
Number of specimens	1	1
Locality	Hide 1	Hide 1

Table 3. Measurements of corallite diameters of selected specimens of *Paleofavosites asper* (d'Orbigny, 1850) from Stora Myre 1 (RM Cn 68842), Sepise (TUG 5/1066) and Asfaltverket (RM Cn 68852); showing different values of corallite diameters. COD-diameter of corallites (mm)

	COD	COD	COD
Mean value	1.79	1.62	1.03
Minimum value	1.55	1.2	0.8
Maximum value	2.25	2.15	1.2
Number of measurements	20	19	22
Number of specimens	1	1	1
Locality	Stora Myre 1	Sepise	Asfaltverket

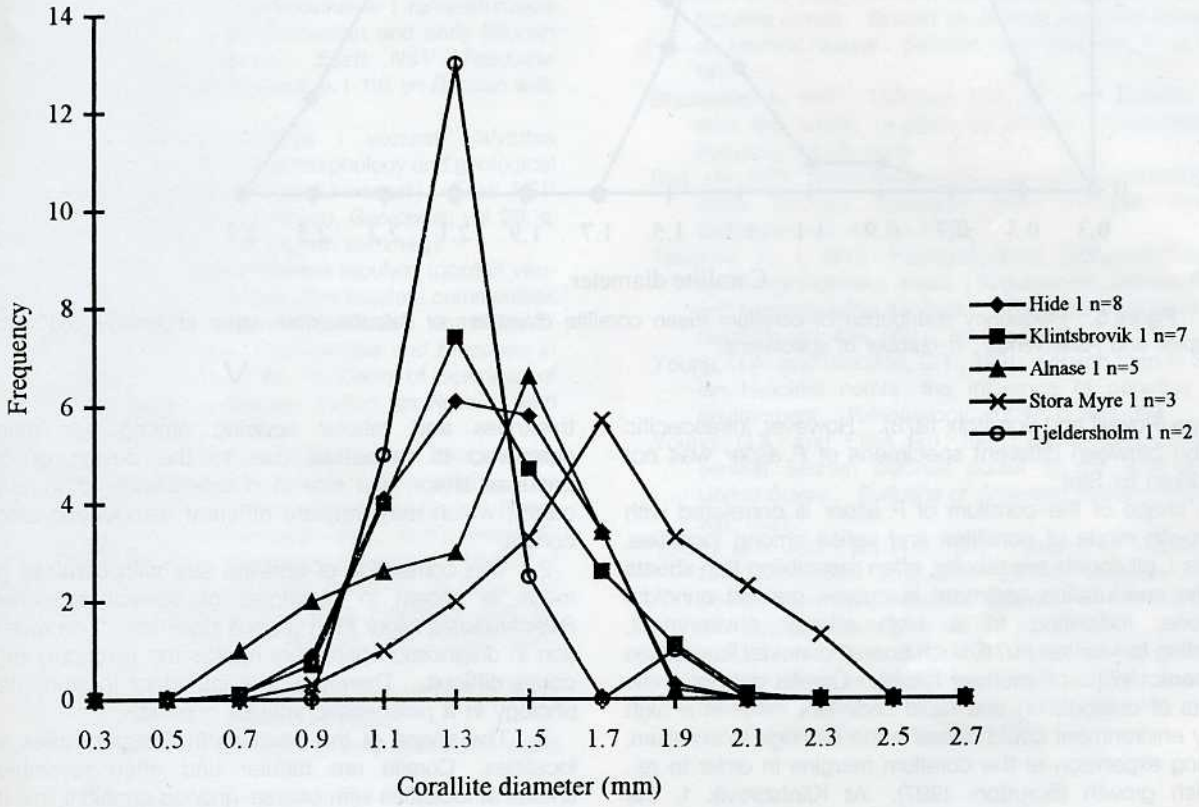

Figure 4. Frequency distribution of corallum mean corallite diameters of *Paleofavosites asper* (d'Orbigny, 1850) from Hide 1, Klintsbrovik 1, Alnäse 1, Stora Myre 1 and Tjeldersholm 1; n-number of specimens.

Figure 3. Photographs of coralla. Scale bar is 10 mm. **A.** *Halysites catenularius* (Linnaeus, 1767), lacuna have a polygonal and elongated shape, Ireviken 3, RM Cn 68854. **B–G.** *Paleofavosites asper* (d'Orbigny, 1850). **B.** Columnar corallum, Asfaltverket, RM Cn 68846. **C.** Bulbous corallum, Klintsbrovik 1, RM Cn 68847. **D.** Domical corallum, Alnäse 1, RM Cn 68848. **E.** Spherical corallum, Stora Myre 1, RM Cn 68849. **F.** Spherical coralla, Sepise, TUG 3/1066, TUG 4/1066. **G.** Tabular corallum, Hide 1, RM Cn 68839.

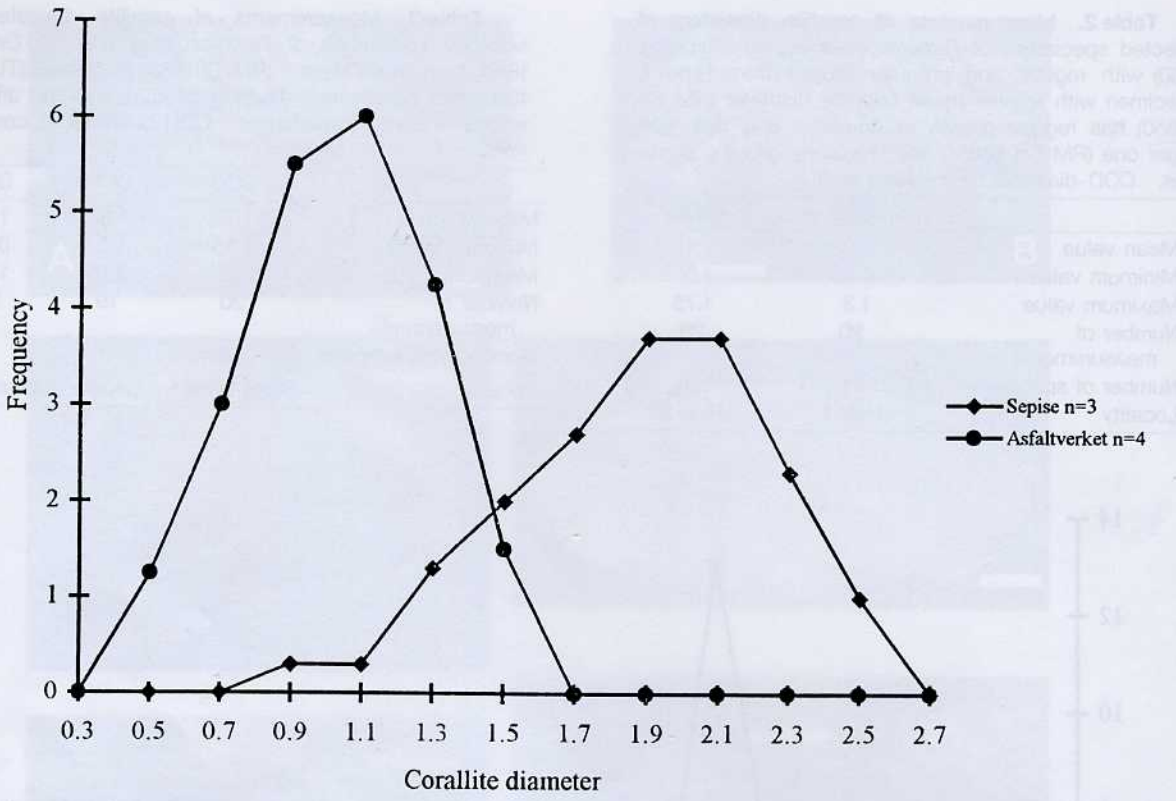

Figure 5. Frequency distribution of corallum mean corallite diameters of *Paleofavosites asper* (d'Orbigny, 1850) from Sepise and Asfaltverket; n–number of specimens.

holotype (Powell and Scrutton, 1978). However, intraspecific variation between different specimens of *P. asper* was not considered by Stel.

The shape of the corallum of *P. asper* is correlated with the growth mode of corallites and varies among localities. At Hide 1, all coralla are tabular, often resembling thin sheets and the surrounding sediment is coarse grained crinoidal limestone, indicating to a high energy environment. According to Manten (1971), such coarse crinoidal limestones are characteristic of interreef facies. Coralla did not show aspects of competition and rapid sediment influx in a high energy environment could cause some damage to corallum, following expansion at the corallum margins in order to re-establish growth (Scrutton, 1997). At Klintsbrovik 1, the coralla are bulbous and have a tendency to grow directly upwards, suggesting a lower energy environment. Here the surrounding matrix is marly limestone. It has been suggested by Young and Scrutton (1991), that coralla in a fine grained, marly sediment grew upwards because of moderate sediment influx.

Conclusions

Study of two species of tabulate corals shows that they are very differently adapted to environmental conditions.

1. Halysitids, such as *Halysites catenularius*, have comparatively low intracolonial variation in tabularium size, wall thickness and tabular spacing among specimens as compared to favositids, due to the design of coralla. Lacunae shape and size in *H. catenularius* change significantly, which may indicate different astogenetic stages of coralla.

2. The correlation of corallite size with corallum growth mode is shown in examples of several specimens of *Paleofavosites asper* from various localities. The wide variation in diagnostic characters makes the taxonomy of these corals difficult. Therefore, it is important to study its morphology in a paleoenvironmental context.

3. The shape of the corallum in *P. asper* varies among localities. Coralla are tabular and often resemble thin sheets at localities with coarse-grained crinoidal limestones. The growth of these colonies was terminated by water moving rapidly, with force. Bulbous and nodular-domical coralla are common in marly limestones, where colonies had moderate environments and could grow upwards.

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