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Stromatoporoid morphology in the Devonian of the Holy Cross Mountains, Poland, and its palaeoenvironmental significance

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ABSTRACT:

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Stromatoporoid skeletons from polished slabs of stromatoporoid- and coral-bearing limestones of the Upper Devonian Kowala Formation from the Holy Cross Mountains in central Poland have been measured using a classic parameterization method, introduced by KERSHAW & RIDING (1978) and improved by KERSHAW (1984, 1998). The stromatoporoid shape appeared to be strongly dependent on its size – the V/B ratio decreases along with increasing B. The relation can be well matched by a curve described by a formula: $f(x) = 5.7103\,x^{0.81633}$. The size of the measured specimens must therefore be taken into account in those studies of the stromatoporoid morphology, where it is concerned a palaeoenvironmental indicator. The stromatoporoids adopted several types of initial surfaces, corresponding to various growth strategies in the first phase of their growth in response to various environmental conditions, such as substrate consistency and sedimentation rate. Latilaminae arrangement well records the stromatoporoid growth history and therefore its studies are crucial in environmental interpretations, as the conclusions inferred from the shape alone might be very misleading.

Key words: Stromatoporoids, Morphometric features, Depositional environment, Devonian, Holy Cross Mountains.

INTRODUCTION

The potential of stromatoporoid shapes and their taphonomic attributes as palaeoenvironmental indicators is widely accepted (BROADHURST 1966; ABBOT 1973; KOBLUK 1975, 1978; KERSHAW & RIDING 1978; MEYER 1981; KAŹMIERCZAK 1980; KERSHAW 1981, 1984, 1987, 1990, 1998; KÖNIGSHOF & *al.* 1991; SWAN & KERSHAW 1994; ŁUCZYŃSKI 1998a, b; KERSHAW & BRUNTON 1999). Most of the stromatoporoid external features are to a great extent unrelated to taxonomy, which is based on the internal microstructure (pillae and laminae arrangement). The advocates of the sponge nature of stromatoporoids agree that in the case of this group the coloniality existed on a cellular rather than on an individual level (STEARN 1993; WOOD 1990, 1991; STEARN & PICKET 1994; SWAN & KERSHAW 1994). Great influence of the environmental conditions on the stromatoporoid morphology is suggested also by authors who assume that stromatoporoids are coccoid cyanobacteria cell aggregates (KAŹMIERCZAK 1976, 1980; KAŹMIERCZAK & KEMPE 1990). Environmental factors most commonly regarded to influence the stromatoporoid growth include: deposition rate (e.g. BROADHURST 1966; KERSHAW 1981, 1987, 1990; KÖNIGSHOF & *al.* 1991; ŁUCZYŃSKI 1998a), water turbulence (e.g. ABBOT 1973; KERSHAW 1981, 1990; KÖNIGSHOF & *al.* 1991; MACHEL & HUNTER 1994), bottom currents (BROADHURST 1966;

KAPP 1974), and substrate consistency (HARPER 1970; KAŹMIERCZAK 1971; KERSHAW 1980, 1990). KERSHAW & RIDING (1978) introduced a simple method of stromatoporoid shape parameterization, improved subsequently by KERSHAW (1984, 1998). This allows a quantitative and statistical approach to stromatoporoid morphology.

Polished slabs of Devonian limestones covering interiors of public buildings in Warsaw displaying cross-cuts through stromatoporoids offer a perfect opportunity for quantitative studies of stromatoporoid morphometric features. The performed analysis, apart from the overall shape, concentrated also on basic macroscopic internal structures, such as arrangement of latilaminae. The main aim of this work was to investigate the various biological and environmental factors that might influence the stromatoporoid shape. Special attention was paid to early growth stages and the dependence of shape on specimen's dimension.

MATERIAL AND METHODS

The stromatoporoid- and coral-bearing limestones of the Kowala Formation from the Bolechowice-Panek Quarry are widely used in Poland as decorative stones. In Warsaw they cover inner walls of numerous public buildings. The present studies were carried out in the "Muranów" cinema, Palace of Culture and Science, the National Theatre, and in the National Philharmonic.

The Bolechowice-Panek Quarry is located in the southern Holy Cross Mountains (Text-fig. 1). It lies in the southern (Kielce) tectonic region of the Holy Cross Mountains and belongs to their central (Kielce) facies-paleotectonic region (*sensu* SZULCZEWSKI 1977). The topmost Sitkówka Beds and Detrital-Stromatoporoid Beds of the Middle-Upper (?) Frasnian (SZULCZEWSKI 1981, NARKIEWICZ & *al.* 1990, RACKI 1993) are exploited in the quarry. The slabs used as decorative stones come from the Sitkówka Beds, and are composed of micritic fossiliferous biostromal limestones. Besides massive and dendroid stromatoporoids, which often are the only macrofossils present, the rocks also contain corals, brachiopods, massive bivalves (megalodons) and ostracods (RACKI 1993). The limestones represent the shoal domain neighbouring the Dyminy reef. They were deposited in relatively quiet water, with depth presumably not exceeding 10 m (KAŹMIERCZAK 1971, RACKI 1993).

The stromatoporoid assemblage from the Sitkówka Beds was described as a massive, non-dendroid community (KAŹMIERCZAK 1971). The author (ŁUCZYŃSKI 1998a) measured 88 specimens from the Sitkówka-Kowala Quarry, which represents a slightly lower part of the Sitkówka Beds in comparison to that exposed in the Bolechowice-Panek Quarry.

The slabs exposed inside the buildings were cut perpendicularly to the faint bedding visible in the quarry. This provides an opportunity to observe a great number of vertical cross-cuts through stromatoporoids. Clearly visible is the arrangement of internal growth-bands – the latilaminae – allowing easy orientation of the cross-sec-

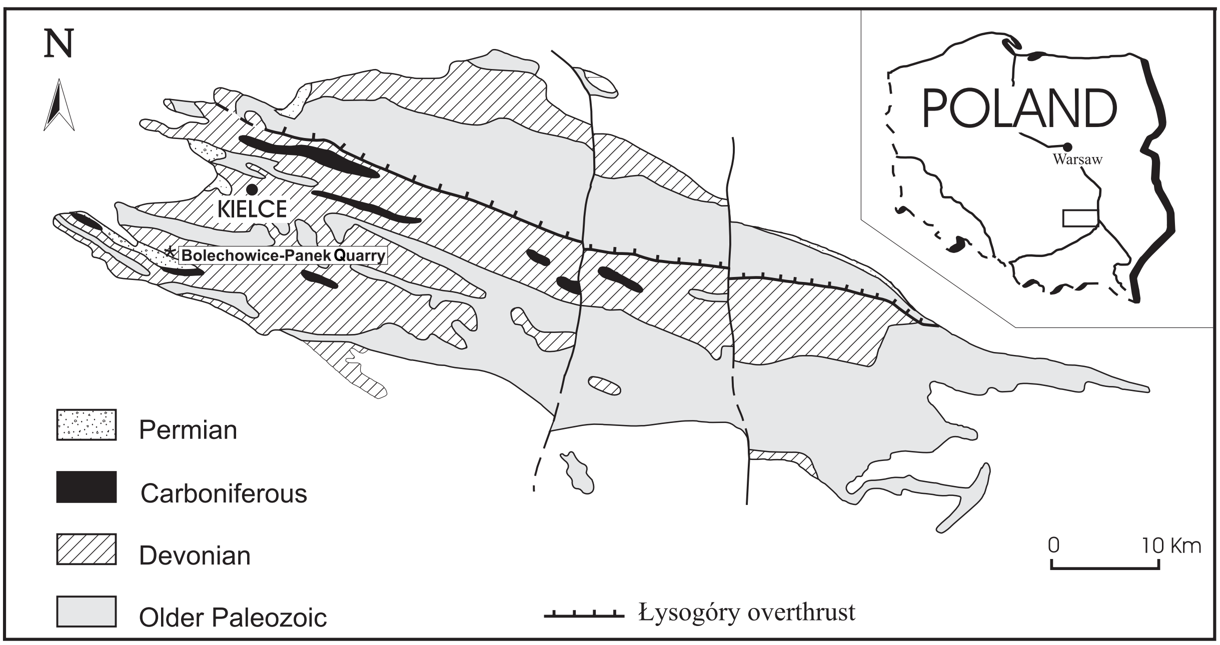

Fig. 1. Location of the Bolechowice-Panek Quarry on a sketch geological map of the Holy Cross Mountains

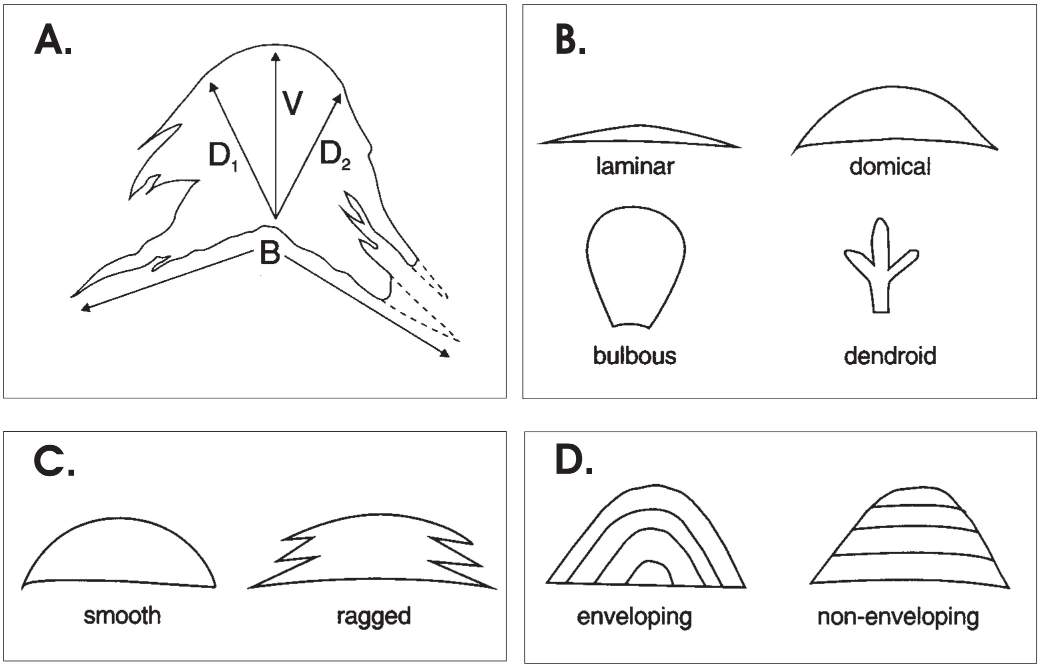

Fig. 2. Stromatoporoid shapes (after Kershaw & Riding 1978). **A.** Measurements of the stromatoporoid shape; B – basal length, V – vertical height, D_1, D_2 – diagonal distance (at an angle of ? = 25º from the vertical). **B.** Stromatoporoid shapes. **C.** Surfaces. **D.** Arrangements of latilaminae

tion. The studies focused on massive forms. The very abundant dendroid stromatoporoids (*Amphipora*, *Stachyodes*) are not considered here. The cross-section best suited for measurements should be vertical (perpendicular to the specimen's base), running through the skeleton's centre (include its main axis). Unfortunately, because of common changes in the growth direction of a stromatoporoid, it is not a common case. Only specimens apparently complete were selected for measurements. Also measured were overturned skeletons, when complete. These constraints excluded a majority of the observed specimens, but despite that, 151 cross-cuts met these basic requirements. Partly oblique cross-cuts, or running not perfectly centrally through the skeleton were also valuable sources of various information concerning their specific morphometric features. Some of these specimens, although not measured, are illustrated herein as examples of some of the described phenomena.

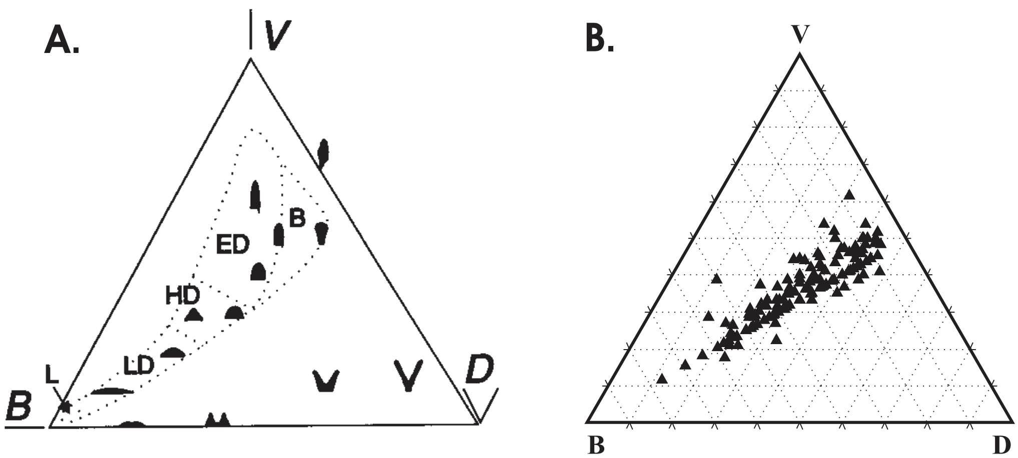

Fig. 3. Display of stromatoporoid morphology on a triangular array. **A.** Triangular array (after Kershaw & Riding 1978); *B* – basal length, *V* – vertical height, *D* – diagonal distance (at an angle of 25º from the vertical). Various fields are occupied by basic stromatoporoid morphotypes: laminar (L), low domical (LD), high domical (HD), extended domical (ED) and bulbous (B). **B**. Triangular display of the morphology of studied stromatoporoids

The stromatoporoids were studied using a classic method of parameterization and classification introduced by KERSHAW & RIDING (1978). The specimens are measured in three directions (Text-fig. 2): B – basal length, V – vertical height and D – diagonal distance (at an angle of 25° from the vertical). The results are plotted on a triangular array (Text-fig. 3), where each triangle apex represents one of three measurements (B, V, D), and where B + V + D = 100%. This defines the position of the point representing the stromatoporoid shape within the triangle, where particular areas are ascribed to certain shapes.

The simplest parameter describing the shape of a massive stromatoporoid is V/B ratio (KERSHAW 1984, 1998). Specimens with V/B < 0.1 are referred to as *laminar*. Skeletons with V/B ≥ 0.1 are termed *domical* and are subdivided further into *low* (0.1 < V/B < 0.5), *high* (0.5 ≤ V/B < 1) and *extended* (V/B ≥ 1) varieties (after KERSHAW 1984). In the present study, a variety of *highly extended domical* forms is additionally distinguished, with V/B ≥ 2, to encompass forms with particularly high profiles. The term *bulbous* is redefined here and refers to specimens with V/B ≥ 1 and D ≥ V. The bulbous forms are subdivided further into *low bulbous* (V/B < 2) and *high bulbous* (V/B ≥ 2).

A very important feature in all environmental considerations based on stromatoporoids is the arrangement of latilaminae. Careful examination of latilaminae enables tracking all shape changes during ontogeny of a specimen. Two basic arrangements of latilaminae are distinguished (after KERSHAW & RIDING 1978): *enveloping*, with the successive latilaminae entirely covering the preceding and reaching the skeletons' base (Text-fig. 2; Pl. 1, Fig. 1), and *non-enveloping*, with the successive latilaminae not covering entirely the preceding, restricted usually to the uppermost parts of a specimen (Text-fig. 2; Pl. 1 Fig. 2). The external surface is described as *smooth* or *ragged* (Text-fig. 2).

Apart from the features listed above, attention was paid to stromatoporoid abundance in a given slab. Three classes of occurrence density are distinguished: *rare* (single specimens per 1 m^2), *common* (few specimens per 1 m^2) and *dense* (> 10 specimens per 1 m^2). Also noted were substrates, on which the stromatoporoids grew, as well as encrustations on them.

The measured group may be slightly biased when related to the living community. Apart from taphonomical processes, this may be caused by a number of reasons connected with the process of selection of the specimens for the measurements, such as:

– the elimination of especially large forms, exceeding the dimensions of the examined slabs,
– excluding of shapes more susceptible for breakage – e.g. ragged varieties (KERSHAW & BRUNTON 1999),
– the possibility that equidimentional forms were more often considered to fulfil the preconditions concerning the cross-section then specimens with other shapes, and
– excluding of forms that were preferentially redeposited and overturned (e.g. bulbous) that resulted in their unsuitable orientation for the measurements.

DISCUSSION OF DATA

Results of the stromatoporoid measurements are presented in Table 1. The most striking feature is a very high participation of varieties with high profiles – V/B > 1. Laminar forms (V/B < 0.1) do not occur. The mean V/B value – 1.78, corresponds to an extended domical/low bulbous shape. The most common profiles are, however, those with the V/B ratio between 0.8 and 1 (Text-fig. 4), representing the high domical shape. The participation of specimens with enveloping and non-enveloping latilaminae, as well as with smooth and ragged surfaces, are close to equal. The obtained results correspond well to those of other studies of stromatoporoids from the Sitkówka Beds (compare ŁUCZYŃSKI 1998a; see also KAŹMIERCZAK 1971).

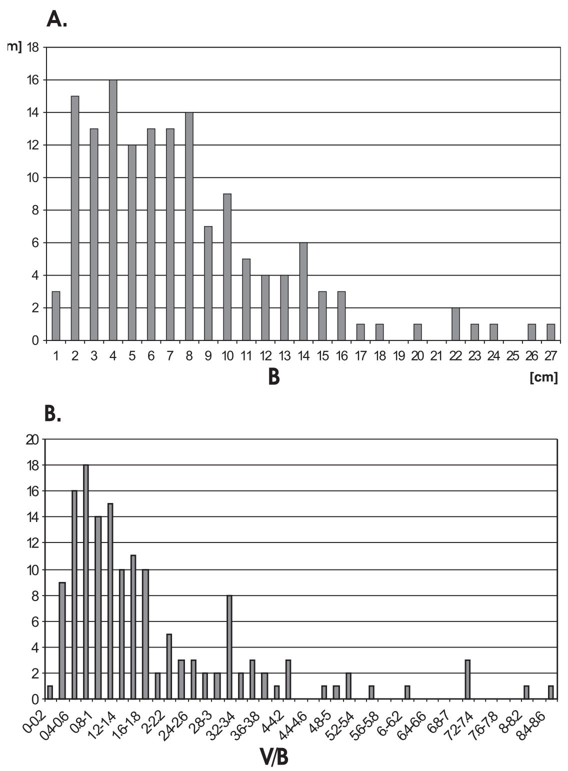

Fig. 4. Distribution histograms of: **A.** stromatoporoid basal length (B) and **B.** Vertical height versus basal length ratio (V/B), in the measured population of stromatoporoids

Sample		Total	After correction for initial elevation
Number of specimens		151	151
Composition of shapes	Laminar Low domical High domical Extended domical Highly extended domical Low bulbous High bulbous	- 14 (9.3%) 46 (30.5%) 24 (15.9%) 27 (17.9%) 22 (14.6%) 18 (11.9%)	- 10 (6.6%) 38 (25.2%) 27 (17.9%) 31 (20.5%) 27 (17.9%) 18 (11.9%)
Arrangement of latilaminae	Enveloping Non-enveloping	69 (45.7%) 82 (54.3%)	69 (45.7%) 82 (54.3%)
Surface	Smooth Ragged	89 (58.9%) 62 (41.1%)	89 (58.9%) 62 (41.1%)
Mean values	B (cm) V (cm) D (cm) V/B	7.87 9.55 8.39 1.78	7.87 10.19 9.03 1.84
Value ranges	B (cm) V (cm) D (cm) V/B	1 – 28 2 – 44 2 –31 0.15 – 8.5	1 – 28 2 – 48 2 –34 0.29 – 8.5
Occurrence density	Rare Common Dense	23 (15.2%) 74 (49%) 54 (35.8%)	23 (15.2%) 74 (49%) 54 (35.8%)
Initial surface	Flat Anchor Initial elevation Encrusting a previous colony	64 (42.4%) 33 (21.9%) 28 (18.5%) 26 (17.2%)	64 (42.4%) 33 (21.9%) 28 (18.5%) 26 (17.2%)

Table 1. Results of the stromatoporoid measurements

The latilaminae arrangement and/or surface character prove to be crucial in environmental interpretations, as the shape alone might be very misleading. For instance, in the case of specimens illustrated on Pl. 1, Figs 3, 4, the external shape in both cases has to be described as bulbous, but the depositional conditions indicated by the internal structure appear to be very different. Local variability of sedimentary environment is indicated by the occurrence of strongly asymmetric specimens, with enveloping latilaminae on one side, and a ragged surface on the other (Pl. 1, Figs 6, 7), as well as of specimens with continuous growth only on their lower sides, and their topmost part left uncovered (Pl. 1, Fig. 8). The latter, most probably, formed when strong bottom currents, possibly also carrying material abrading the substrate, prevented growth of the stromatoporoid in its upper part, and restricted it to its lower parts lying in the current's shadow. This is an opposite situation to typical ragged varieties, where the specimen's growth was often limited only to its topmost part, not smothered by sediment.

RESULTS OF DETAILED OBSERVATIONS

The studied material allowed direct inferences on the relative influence of biological and environmental factors on the shape. It appears that simple correlation of particular shapes with certain palaeoenvironmental conditions may be misleading, and other parameters must also be considered.

Size of the specimens

The V/B values of the measured specimens were plotted against the B value (Text-fig. 5). This revealed a very clear allometric tendency of decreasing V/B ratio along with B. Attempts to find the closest mathematical approximation of this relationship have shown that the regression curve described by a power function formula: $f(x) = 5.7103x^{0.81633}$ (Text-fig. 5a) gives the highest R^2 correlation coefficient – 0.5028 ($R = 0.7091$), and is therefore the best fit to the data points.

The observed allometry indicates that any environmental speculation based on stromatoporoid morphology must take into account also the size of the specimens. When studying two assemblages, only forms belonging to the same size class can reliably be compared. The interpretation should concentrate on the most abundant size classes with the widest spectrum of shapes. Very cautiously must be treated extremely large and small specimens. A formula should be developed which would enable taking the size effect into account, and which would allow the comparison of stromatoporoid assemblages with different mean sizes of the specimens. This needs further study based on material from various settings.

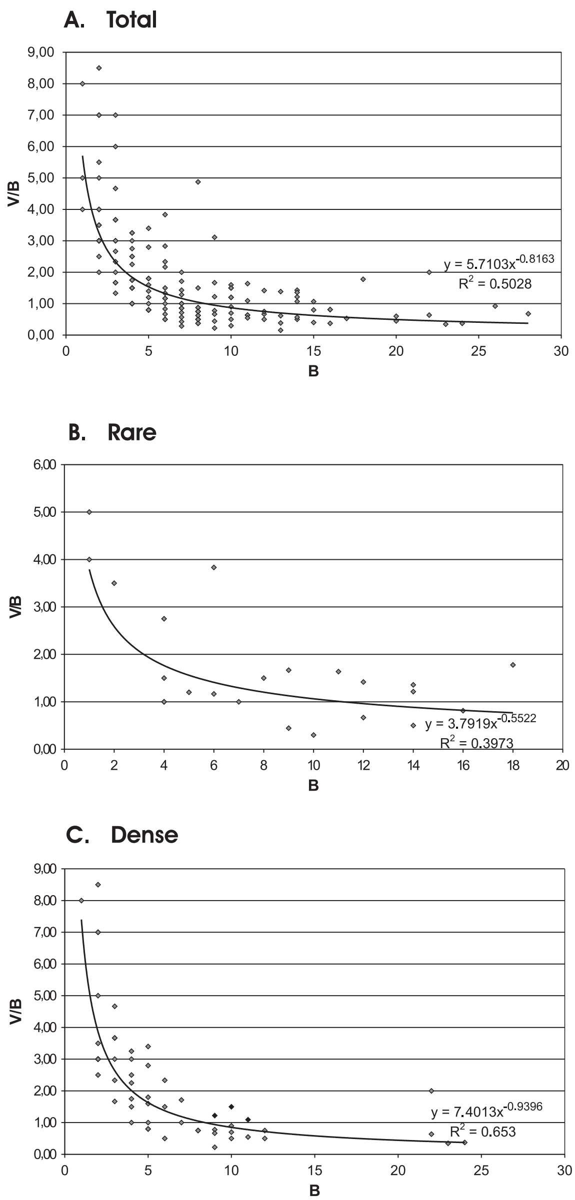

Fig. 5. Graphs presenting the V/B versus B relation (vertical height/basal length ratio versus basal length), with regression curves best approximating the relation. R^2 – correlation coefficient. **A.** – whole sample, **B**. – specimens occurring in rare densities, **C** – specimens occurring in dense concentrations

KERSHAW (1990), who also noticed that large stromatoporoids generally have low morphologies, ascribed this phenomenon to the coalescence of two or more neighbouring specimens. This, however, does not seem to be a common case in the studied material. The latilaminae arrangement, apart from a few examples, shows no multiple growth centres. What is even more convincing, a similar tendency of decreasing profile along specimens size is observed in all distinguished groups when treated separately, such as enveloping/smooth forms or non-enveloping/ragged forms. Moreover, this relationship is independent of stromatoporoid density (Text-fig. 5), although the correlation coefficient is the highest ($R = 0.81$) in the case of dense concentrations (Text-fig. 5c).

The arguments presented above indicate that the tendency of decreasing V/B ratio with increasing B is universal in the studied material. Without detailed taxonomic analysis it is impossible to judge whether it is an environmentally or biologically controlled phenomenon. The effect may be caused by a response of larger forms to soft sediment (KERSHAW *personal communication*) or may be an expression of mechanical limitations of large skeletons. However, the universal character of this tendency, and particularly its independence of other features, clearly governed by the environment (e.g. latilaminae arrangement and surface type), suggests its biological nature (ontogenetic changes). The graphs could thus be treated as stromatoporoid growth rate curves, showing that stromatoporoids grew fast when young, slowing down when getting older.

Initial surfaces

Two environmental factors have great influence on stromatoporoid shape – sediment accumulation rate and substrate consistency (e.g. BROADHURST 1966; HARPER 1970; KAŹMIERCZAK 1971; KERSHAW 1980, 1984, 1990, 1998; KÖNIGSHOF & *al*. 1991). Their importance in determining the stromatoporoid shape, particularly in early stages of ontogeny, is also evident in the studied material.

Only 64 specimens (42.4%) have a flat base. Apart from that, there are three basic types of stromatoporoid initial surfaces, corresponding to three growth strategies. The first strategy, occurring in 33 measured specimens (21.9%), is referred here to as *anchor* (Pl. 2, Figs 1, 2). A stromatoporoid started growing from almost one point, and for some time continued to grow upwards, obtaining high profile morphology, until it was well anchored in the sediment. Subsequently it started to expand laterally. This seems to be an adaptation to a relatively firm substrate and a low deposition rate, where the main hazard for the stromatoporoid was to be pulled out from the sediment by bottom currents.

The second strategy in the early stage of ontogeny is referred here to as *initial elevation* (Pl. 2, Figs 3, 4). It was recognised in 28 specimens (18.5%). The basal surface of the stromatoporoid is convex upward, which indicates its growth on a small elevation of the sea bottom. The height of the elevations ranges from 1 to 11 cm, usually, however, does not exceed 3 cm. The occurrence of lithified deposits on the sea bottom may result from either winnowing of the soft overlying sediment, or may result from microbial activity, which played an important role in surface stabilisation in the Upper Devonian organic buildups of the Holy Cross Mountains (SZULCZEWSKI & RACKI 1981; HOFFMAN & PASZKOWSKI 1992). The initial elevations provided the stromatoporoid a solid substrate, on which they could grow, but also elevated the growth surface slightly above the bottom, so they could survive burying by sediment, and finally anchored them to the substrate, which made them more stable and less susceptible for redeposition.

Existence of an initial elevation affects the shape of the stromatoporoid. The total height of the specimen measured together with the elevation is larger than the V dimension of the skeleton, and equals $V + V_1$, where V_1 is the height of the initial elevation. The same value may be added to the D measure, because the elevation is always convex upward. This feature may seriously change the profile of the stromatoporoid and cause its classification to different shape category. With this correction, the content of forms with high profile ($V/B > 1$) rises to 68.2% (Tab. 1).

The last group comprising 26 stromatoporoid specimens (17.2%), embraces forms *encrusting* other organisms – mainly other stromatoporoids (Pl. 2, Figs 5, 7) and corals (Pl. 2, Fig. 6). This strategy gives all the advantages of an initial elevation – a solid substrate, elevation over the sea bottom, and prevention from redeposition. The stromatoporoids very rarely encrust shells of large megalodon bivalves (Pl. 2, Fig. 8), locally common in the sediment. The bivalves lived however an infaunal or semi-infaunal mode of life, and during their life did not provide a substrate for growth to other organisms.

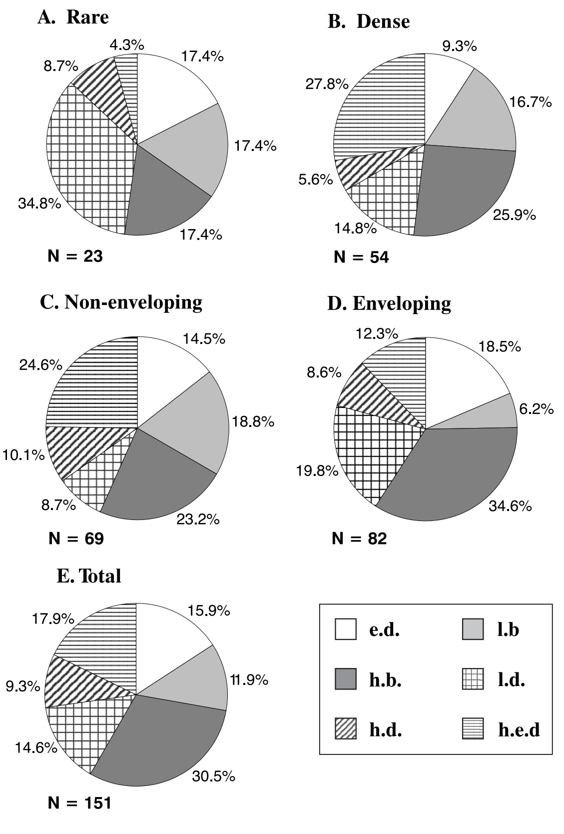

Fig. 6. Proportions of specimens with various shapes in the measured population of stromatoporoids. e.d. – extended domical, h.b. – high bulbous, h.d. – high domical, l.b – low bulbous, l.d. – low domical, h.e.d. – highly extended domical. **A.** – specimens occurring in rare densities, **B.** – specimens occurring in dense concentrations, **C.** – all specimens with non-enveloping latilaminae, **D.** – all specimens with enveloping latilaminae, **E.** – whole sample

Reworking and occurrence density

Although taphonomic analysis of stromatoporoids does not reveal features supporting their longer transport, such as e.g. breakage along latilaminae (KERSHAW & BRUNTON 1999), some features of the studied material show signs of intraformational reworking. Variously oriented specimens commonly occur on a single slab (Pl. 1, Fig. 5). The encrusting forms protrude often in other directions than the specimen they grow on. Moreover, the occurrence of decimetre size "nodules", visible mainly due to subtle colour changes and differences in the abundance of *Amphipora*, points to reworking of very poorly lithified bottom sediment.

A factor potentially influencing stromatoporoids shape is their occurrence density. In the studied material bulbous forms are over-represented in the group of specimens occurring in the low density groups (Text-fig. 6a), whereas highly extended domical forms in groups with dense concentrations (Text-fig. 6b). Stromatoporoids from dense populations show often allomorphic shapes (KISSLING & LINEBACK 1967, KERSHAW 1981). This tendency, which may be taxonomically controlled, allows better use of all available space and nutrients. On the other hand FAGERSTROM & *al.* (2000) found very little convincing evidence of spatial competition in Palaeozoic stromatoporoids. In the studied material all shapes coexist in each density group, which indicates that competition between the stromatoporoids probably did not play an important role in determining their shapes. The same may, however, be also a taphonomical feature, linked with *post mortem* redeposition.

Shape/latilaminae arrangement relation

As both the external shape of a stromatoporoid and the arrangement of latilaminae depend on environmental conditions, such as rate of deposition and water turbulence, it may be assumed that there is an interrelation between these two attributes. Indeed, in spite of the fact that the entire range of shapes is encountered in both the enveloping and non-enveloping varieties, the measured population is distinctly over-representated by forms with very high profiles (highly extended domical and high bulbous) in the non-enveloping group (Text-fig. 6c) and by slightly lower forms (extended domical and low bulbous) in the enveloping group (Text-fig. 6d).

Studies of stromatoporoid shapes together with latilaminae arrangement allow discerning shapes of the specimens *in statu nascendi* (the profile above the sea bottom during life of the stromatoporoid) and *post mortem* (the shape of the whole skeleton including its part buried in the sediment during life of the specimen), which may be very different. In many environmental considerations (e.g. response to bottom currents) it is the *in statu nascendi* profile, which is more important.

The stromatoporoids with a non-enveloping latilaminae arrangement may have grown as the sediment collected around them, with only their highest latilamina (or group of latilaminae) remaining above the sea bottom (e.g. KERSHAW 1981, 1987). Their *in statu nascendi* profile was therefore low (corresponding to laminar and low domical shapes). All stromatoporoids with ragged surfaces by definition have a non-enveloping latilaminae arrangement. However, in the measured population there is a group of 20 specimens with smooth surfaces and non-enveloping latilaminae (e.g. Pl. 1, Figs 2, 4). It is an unresolved problem, as to whether such forms grew as sediment gradually accumulated around it, or whether they grew up as a column, buried subsequently by sediment. Careful examination of the surfaces reveals that even in the case of overall smooth surface, in smaller scale it shows minor raggedness (Text-fig. 7). The same feature has been noticed by KERSHAW (*personal communication*). This indicates that the mode of life of non-enveloping stromatoporoids with ragged and smooth surfaces was quite similar, with their lower parts buried in the sediment. The same is also suggested by the co-occurrence of non-enveloping forms with both types of surfaces in the same place, or even on two sides of the same specimen (Pl. 1, Fig. 7). Presumably, the differences lie in the convexity of the upper surface of the living stromatoporoid and/or in episodic versus more gradual input of sediment. Unfortunately, any more detailed

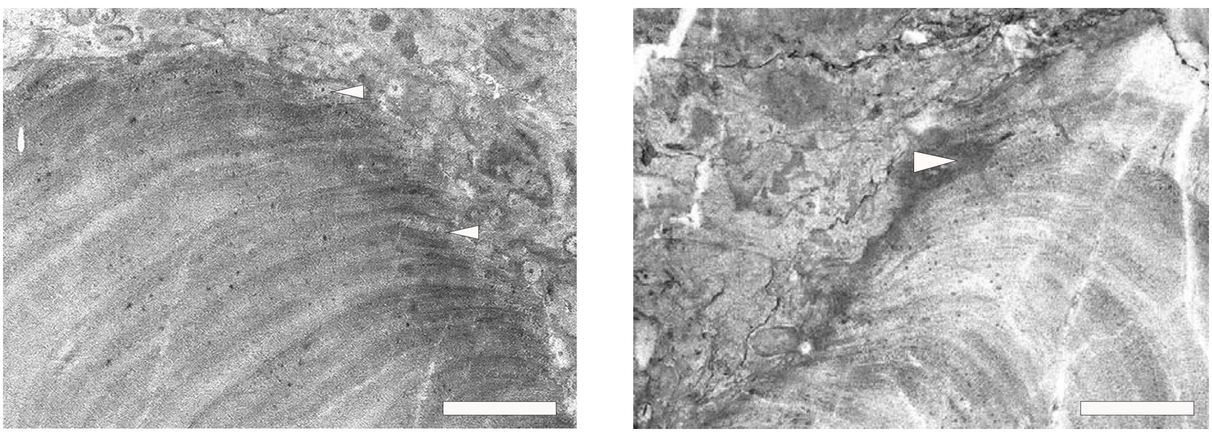

Fig. 7. Small scale surface raggedness (arrows) in specimens with overall smooth type of the surface. White bars are 1 cm long

studies, which would enable tracing the sediment bands between the latilaminae in more detail, are hindered by the character of the material.

After taking the above-presented considerations into account, the total number of low (not higher than low domical) *in statu nascendi* profile specimens equals 89 (58.9% of the measured population), and is much higher than if considering only the external shape of the skeleton. This group embraces low domical forms plus all non-enveloping forms of other shapes.

CONCLUSIONS

Analysis of stromatoporoid morphometric attributes allows for the following corollaries:

1. The shape of the stromatoporoid strongly depends on its size. Specimens with higher B values have lower V/B ratio. Therefore the size must be taken into considerations in all environmental interpretations based on stromatoporoid morphology.
2. Stromatoporoids adopted various strategies in early ontogenetic growth stages to cope with local environmental conditions, such as substrate consistency and sedimentation rate, including anchoring in the sediments, growing on initial elevations and encrusting other organisms.
3. Study of latilaminae arrangement proves to be crucial for palaeoenvironmental analysis based on stromatoporoid morphological features.

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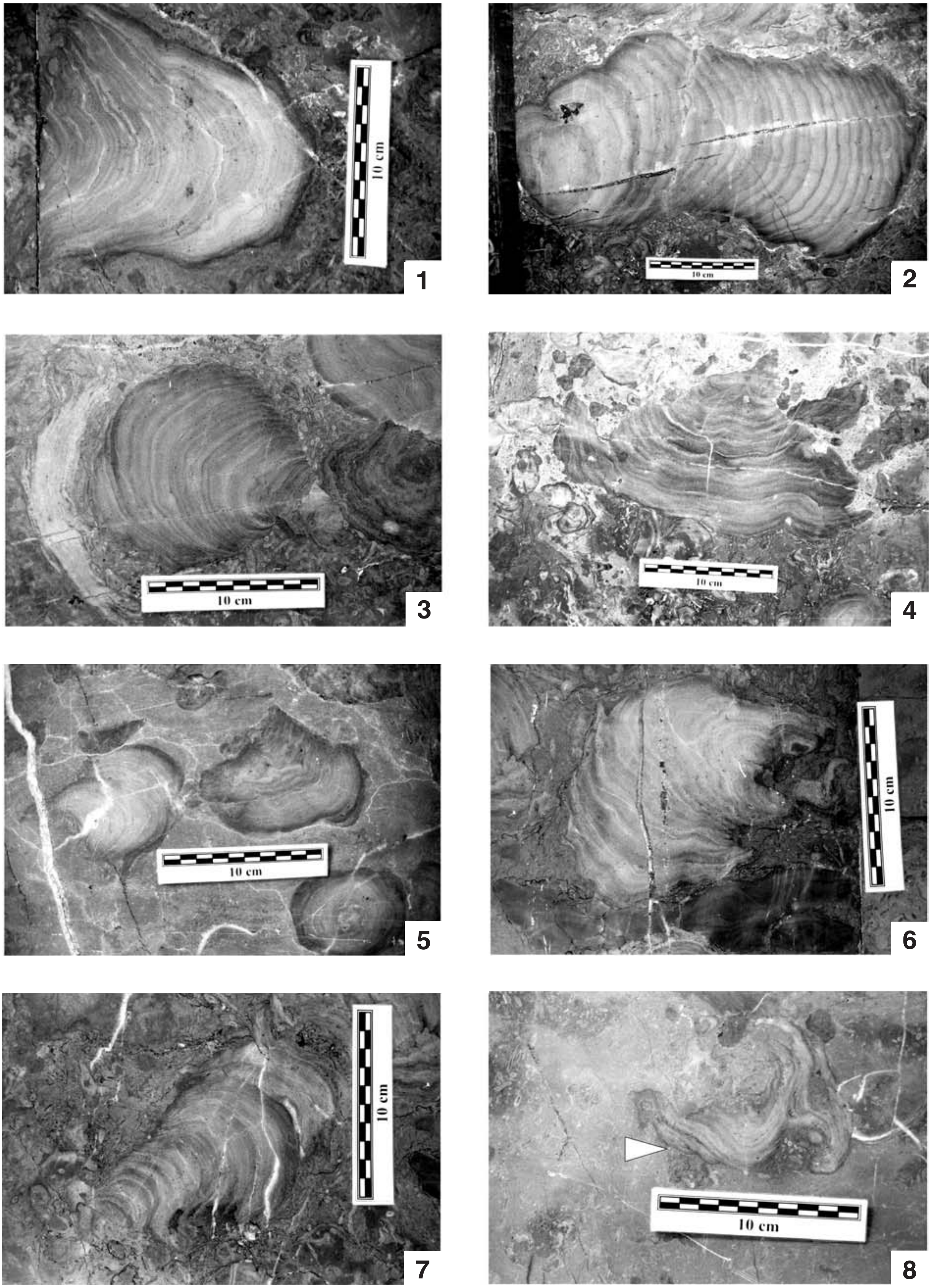
PLATES 1-2

PLATE 1

Basic stromatoporoid morphometric features

1 – Highly extended domical stromatoporoid with smooth surface and enveloping latilaminae arrangement; **2** – Non-enveloping latilaminae arrangement (specimen not measured because of an unsuitable cross-section); **3** – Bulbous stromatoporoid with smooth surface; **4** – Bulbous stromatoporoid with ragged surface; **5** – Stromatoporoids protruding in different directions (not measured); **6, 7** – Asymmetric stromatoporoids (not measured); **8** – Stromatoporoid with latilaminae growing on its side (arrow), leaving its topmost part uncovered (not measured).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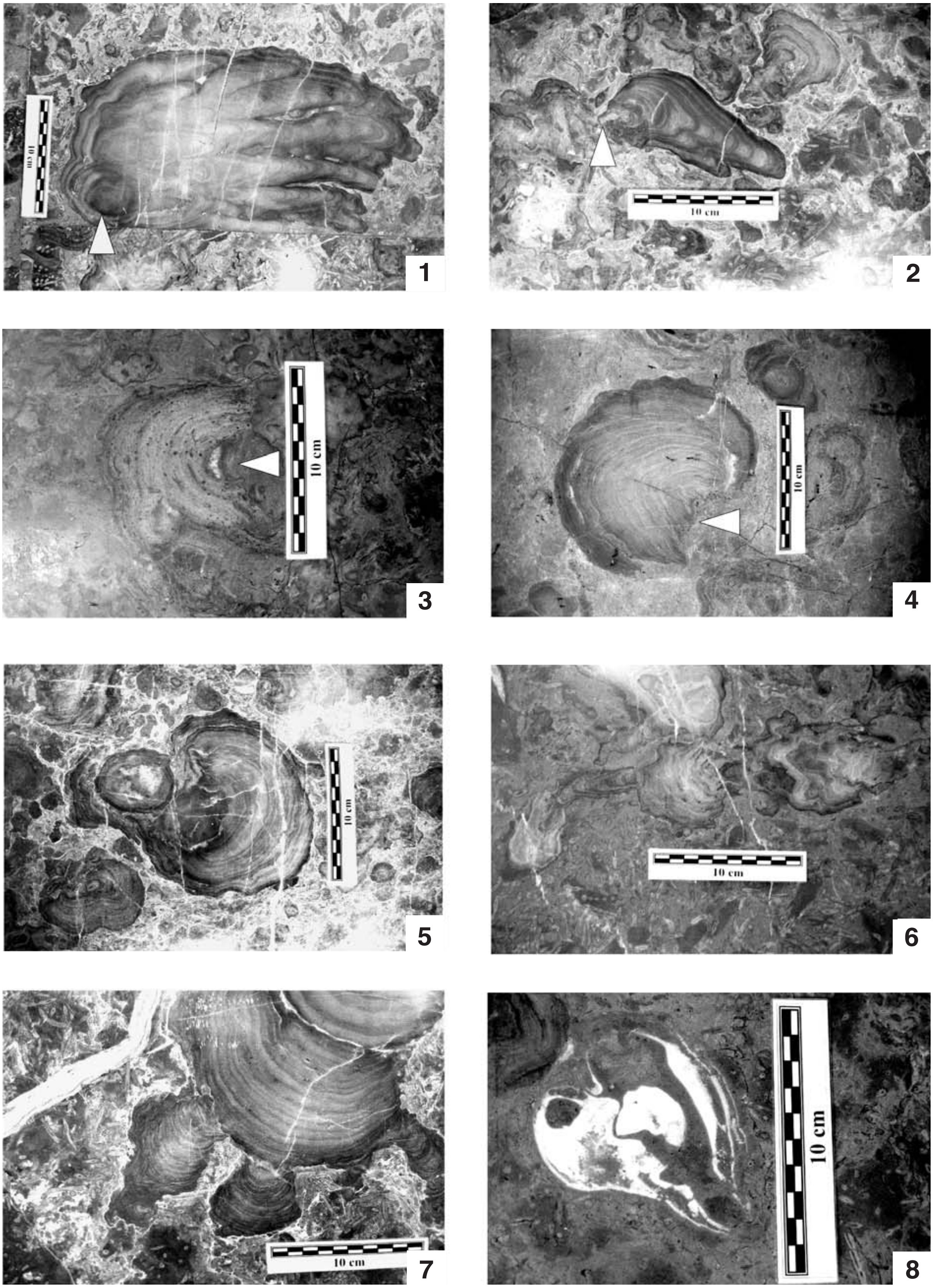
8

PLATE 2

Initial surfaces, on which stromatoporoids grew

1, 2 – Anchor (arrows); **3, 4** – Initial elevation (arrows); **5, 6,7** – Encrustation on stromatoporoids and corals; **8** – Megalodon bivalve shell (not encrusted by stromatoporoids).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