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Interrelations between stromatoporoid morphometric features – a quantitative approach based on specimens from the Silurian of Podolia (Ukraine) and the Devonian of the Holy Cross Mountains (Poland)

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ABSTRACT:

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Morphometric attributes of 705 stromatoporoid specimens from a number of exposures from the Silurian of Podolia (Ukraine) and the Devonian of the Holy Cross Mountains (Poland), representing a wide array of shallow water carbonate sedimentary environments, have been analysed. Taken into account were such parameters as: general shape of the skeleton, shape of the final growth form (living surface profile), upper surface character, latilaminae arrangement, burial ratio and type of initial surface. A number of new ratios has been introduced, designed mainly to improve the mapping of the outlines of the stromatoporoids upper surfaces. All studied specimens were treated as belonging to one group, and relations between particular attributes were tested. The results were analysed in terms of potential environmental factors influencing stromatoporoid morphometric features. Most of the distinguished attributes are common in the studied group and occur in various combinations, with an important exception of parameters designed to reflect the shape of the skeleton's upper surface, which are distinctly predominated by convex variants. This indicates that surface concavity was a highly undesired feature among stromatoporoids. Upper surface convexity is interpreted herein as a response to the hazard of clogging of the animals pores by tiny sediment particles suspended in the bottom turbid water layer. Common low burial ratios of final living surface profiles and the occurrence of specimens with a smooth upper surface but a non-enveloping latilaminae arrangement are other reflections of this phenomenon. Burial by sediments and redeposition were also important factors governing stromatoporoid development. No direct arguments indicating photosensitivity of stromatoporoids can be deduced from the presented results. The hitherto postulated allometric tendency among stromatoporoids of starting growth as laminar forms and later adopting consecutively higher profile shapes has not been confirmed here. On the contrary, a tendency for gradual elimination of very high profile forms with increasing stromatoporoid size has been observed. The final shape of a stromatoporoid skeleton was always an effect of a combination of various agents.

Key words: Stromatoporoids; Morphometric features; Quantitative analysis; Palaeoenvironmental interpretations; Clogging.

INTRODUCTION

As pointed out by Kershaw (2012, 2013), there are two principal objectives of stromatoporoid studies: (i) to determine how stromatoporoids lived, what controlled them and how they varied through geological time, and (ii) to apply stromatoporoids in palaeoenvironmental interpretations at a variety of spatial scales. The focus here is on the second objective.

Application of stromatoporoids in palaeoenvironmental reconstructions requires understanding of the relations between various features of the stromatoporoid skeleton and particular environmental factors. In the case of an extinct group of animals, such as Palaeozoic stromatoporoids, it can be done either by theoretical modelling of various influences, or by comparison with living organisms displaying similar features (Hickmann 1988). Unfortunately, both approaches are extremely difficult to be applied here.

Stromatoporoids have no obvious modern analogues, with which they could be directly compared. The existing functional interpretations are based on the presumption of a poriferan affinity of Palaeozoic stromatoporoids (Stearn 2010a) – an opinion not shared by everyone, with e.g., Kaźmierczak strongly opting for their cyanobacterial nature (e.g., Kaźmierczak 1976; Kaźmierczak and Kempe 1990). With the discovery of modern hypercalcified sponges in the deep waters of Jamaica (Hartman and Goreau 1970), a living counterpart of stromatoporoids has been found, however significantly different in many important ecological aspects (Vacelet *et al.* 2010). Modern hypercalcified sponges, in a similar manner to stromatoporoids, secrete a massive basal skeleton with the living tissue restricted to its upper surface. However unlike stromatoporoids, they are not important reef builders, but instead inhabit refuge habitats, such as caves and bathyal cliffs (Basile *et al.* 1984). Also their growth rates seem to be significantly lower than those of reef builders (Wood 1990), which all point to a different growth strategy and different interrelations with the sedimentary environment (Königshof and Kershaw 2006). The slowly built skeleton of the modern hypercalcified sponge *Ceratoporella nicholsoni* (Hickson, 1911) is extremely hard and resistant (Schuhmacher and Plewka 1981), whereas the relatively light stromatoporoids were much more fragile and vulnerable to overturning and redeposition. It is likely that after the destruction of the soft tissue and prior to crystallization of sparry calcite, the internal voids of their skeletons were filled with water (Stearn and Picket 1994). Therefore, modern hypercalcified sponges cannot be treated as good analogues that would allow one to study the complex relations of stromatoporoids with the sedimentary environment.

Many aspects of the functional morphology of the stromatoporoid skeleton are still not fully understood, mainly because of the lack of a reliable modern analogue as described above. The discussion on the function and meaning of particular skeletal features is based on the predication that Palaeozoic stromatoporoids were suspension-feeding filtrators belonging to the Porifera (Stearn 2010b). However, the exact relation of the skeleton to the living tissue, as well as the process of its secretion remain dubious. There is even no unanimity whether particular stromatoporoids should be treated as individuals or as colonial (modular) organisms (e.g., Wood 1990). Therefore, reliable theoretical modelling of the skeleton's external features, such as shape, is very difficult, and only few attempts have been made so far. The function of mamelons and astrorhizae were analysed biomechanically by Boyajian and LaBarbera (Boyajian and LaBarbera 1987; LaBarbera and Boyajian 1991) and a computer model of stromatoporoid growth was presented by Swan and Kershaw (1992).

STROMATOPOROID MORPHOMETRIC FEATURES AS PALAEOENVIRONMENTAL INDICATORS

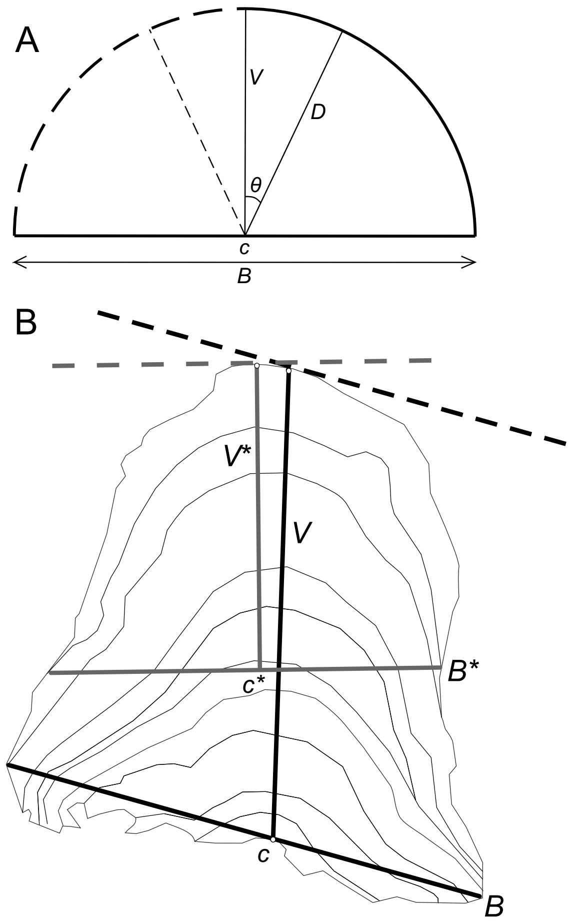
Together with corals, stromatoporoids were the most important constructors of carbonate organic buildups in the Palaeozoic (e.g., Riding 1981). They are most common in the Silurian and in the Devonian up to the Frasnian/Famennian boundary, living in a wide variety of settings, ranging from deeper shelf to intertidal. Stromatoporoids built bioherms, commonly referred to as reefs (Flügel and Flügel-Kahler 1992; Flügel and Kiessling 2002), but also inhabited level bottom environments, forming in various types of biostromes (Kershaw 1994). As soft substrate bottom dwellers, they also lived scattered individually in the sediment. Stromatoporoid facies of various types are well described i.a. from the Silurian of Gotland (e.g., Kershaw 1981, 1990; Kershaw and Keeling 1994; Sandström 1998; Sandström and Kershaw 2002), Estonia (e.g., Tuuling and Flodén 2013) and Podolia (e.g., Skompski *et al.* 2008; Łuczyński *et al.* 2009, 2014, 2015), and from the Devonian of Ardennes (e.g., Da Silva and Boulvain 2004; Boulvain 2007), Rhenish Massif (e.g., Königshof *et al.* 1991; Braun *et al.* 1994), Morocco (e.g., Königshof and Kershaw 2006), and the Holy Cross Mountains (e.g., Racki 1993; Łuczyński 1998b, 2008, 2009; Racki and Sobstel 2004).

Stromatoporoids occur in a wide variety of shapes. As is the case with every sessile benthic organism, the stromatoporoid animal built its skeleton simultaneously with the accumulation of sediments in its vicinity, and with a substantial feedback between the two processes. Although some general growth tendencies of stromatoporoid species are determined by taxonomy (e.g., Stearn 1982, 1993; Stearn *et al.* 1999), the external shapes and sizes are thought to be governed mainly by various environmental factors. The most important factors influencing the stromatoporoid morphometric features are: deposition rate and dynamics (e.g., Broadhurst 1966; Kershaw 1981, 1994, 1998; Łuczyński 1998a, 2003, 2006, 2008), water turbulence (e.g., Kershaw 1990; Königshof *et al.* 1991; Machel and Hunter 1994; Königshof and Kershaw 2006), substrate consistency (e.g., Kaźmierczak 1971; Kershaw 1980; Kershaw *et al.* 2006), directional water flow (e.g., Broadhurst 1966; Łuczyński 2008) and palaeotopography of the sea bottom (Łuczyński 2009). Swan and Kershaw (1994) presented a computer model simulating stromatoporoid growth governed by variable sedimentation patterns, and obtained shapes similar to real fossil specimens. Stromatoporoids are thus considered useful palaeoenvironmental indicators (e.g., James and Bourque 1992; Machel and Hunter 1994).

Various environmental factors influenced the stromatoporoid growth in various ways. In the morphometric analyses taken into account are such attributes of the skeleton as: the overall shape of the specimen (e.g., Broadhurst 1966; Königshof *et al.* 1991; Kershaw 1998; Sandström 1998; Łuczyński 2003; Königshof and Kershaw 2006) and the shape of its growth form (living surface profile) above the sediment surface (e.g., Kano 1990; Kershaw and Brunton 1999; Łuczyński 2006, 2008), as well as the relation between the two, expressed by the calculated burial ratio (Łuczyński 2006). Latilaminae arrangement (growth bands within the skeleton), upper surface character and occurrence of internal sediment increments are other important features interpreted in terms of stromatoporoid growth environment (e.g., Kershaw 1984; Young and Kershaw 2005; Łuczyński 2006, 2009). Analysed are also such attributes as: asymmetry (e.g., Broadhurst 1966; Kapp 1974; Łuczyński 2009) and type of initial surface (Kershaw 1980, 1998; Łuczyński 2003; Kershaw *et al.* 2006).

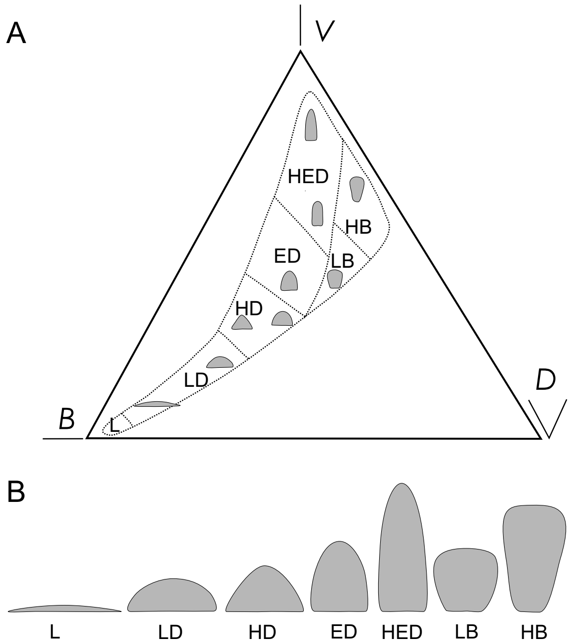
STROMATOPOROID MORPHOMETRY – A REAPPRAISAL

Parameterization of stromatoporoid shapes was first introduced by Kershaw and Riding (1978) and later improved by Kershaw (1984). Earlier, a wide variety of descriptive terms indicating particular shapes

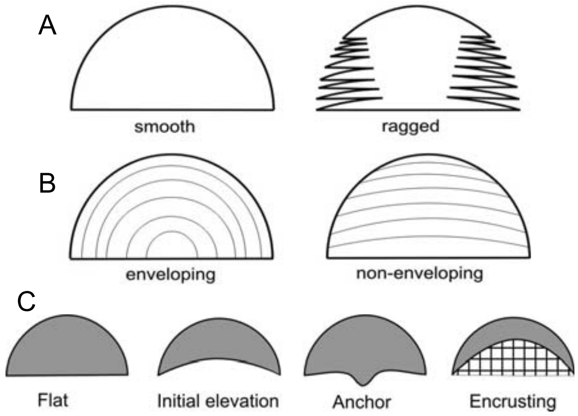


Text-fig. 1. Parameterization of stromatoporoid shapes. A – Original method introduced by Kershaw and Riding (1978, fig. 6); *B* – basal length, *V* – vertical height, *D* – diagonal distance. *V* and *D* are plotted from a central point (*c*) on *B*. *D* is measured at an angle of θ = 25º from the vertical; B – Measurements of basal length and vertical height of the whole stromatoporoid skeleton (*B*, *V*) and of the living surface profile – the final growth form (*B**, *V**); after Łuczyński (2005, 2008), simplified.

has been used, however without any clear definitions (e.g., Kaźmierczak 1971; Abbott 1973; Kapp 1974, 1975; Kobluk 1978). The parameterization applies to massive (non-dendroid) forms. A stromatoporoid skeleton is measured in a vertical crosscut running through its main axis (for discussion on the methodology of identifying such a crosscut and for methods of measuring stromatoporoid skeletons preserved as three-dimensional specimens and exposed on palaeobottom surfaces see Łuczyński 2005 and 2008). Three dimensions of the skeleton are examined (Text-fig. 1A; after Kershaw and Riding 1978): *basal length – B*, *vertical height – V*, and *diagonal distance – D* (measured at an angle θ = 25º from the



Text-fig. 2. Stromatoporoid shapes. A – Display of stromatoporoid shapes on a triangular array (after Kershaw and Riding 1978; improved). *B* – basal length, *V* – vertical height, *D* – diagonal distance. Various fields are occupied by basic stromatoporoid morphotypes: laminar (L), low domical (LD), high domical (HD), extended domical (ED), highly extended domical (HED), low bulbous (LB) and high bulbous (HB); B – Basic stromatoporoid morphotypes (symbols as in A).



Text-fig. 3. Basic macroscopic stromatoporoid morphometric features. A – Upper surface character; B – Arrangement of latilaminae; C – Initial surface. See text for references.

vertical). In the case of asymmetrical specimens, two diagonal measurements *D*1 and *D*2 are made, and the mean value is taken into account in further analysis. The results are presented on a triangular array, on which particular fields are ascribed to certain shapes (Text-fig. 2A). Originally distinguished were *laminar*, *domical* and *bulbous* forms; the *domical* further divided into *low*-, *high*- and *extended domical* varieties. Later, Łuczyński (2005) supplemented the categorization by adding a category of *highly extended domical* forms and by dividing the bulbous forms into *low*- and *high bulbous* (Text-fig. 2B). Commonly, to simplify the analysis, the *D* measurements are skipped and the stromatoporoid shape is characterised by the *V/B* ratio, referred to as the *shape profile*.

Apart from the specimens' dimensions, the analysed stromatoporoid macroscopic morphometric features include also the *upper surface character* (Text-fig. 3A), which can be either *smooth* or *ragged* (with sediment increments protruding into the skeleton), and the *arrangement of latilaminae* (major growth bands visible within the skeleton; Text-fig. 3B). These are described as *enveloping* (with the following latilaminae completely covering the preceding) and *non-enveloping* (Kershaw and Riding 1978). The *initial surface* (basal surface) is also an important feature, particularly when analysing early stages of the specimens ontogeny, and occurs in varieties referred to as: *flat*, *initial elevation*, *anchor* and *encrusting* (Text-fig. 3C; Łuczyński 2003). Kershaw (1984) supplemented the original method by adding measurements of vertical and horizontal raggedness – *RV* and *RH* for ragged forms with lateral sediment intrusions.

Łuczyński (2005) improved the parameterization method by giving strict definitions of particular parameters and pointing out that the definitions used so far leave a broad field of uncertainty and can be differently understood by various authors. Such situation could result in ascribing particular stromatoporoid specimens to different shape categories, which in turn could lead to different palaeoenvironmental interpretations (compare e.g., Kershaw 1984 and Sandström 1998). The uncertainties included the way of identifying the basal surface and thus performing the *B* measurement, the way of determining the central point (*c* in Text-fig. 1A), from which the *V* and *D* values are measured, and the way of making the *V* measurement.

The original stromatoporoid parameterization method was based on the measurements of the *post mortem* shapes of the whole skeletons. However, the stromatoporoids grew on a sea bottom simultaneously with sediment accumulation, which means that only a part of the skeleton stood above the sediment surface. It is therefore essential to discriminate the *shape* and the *growth form* (*living surface profile*). The final shape is an effect of overlapping of growth forms in consecutive stages of the individuals' development, and is therefore commonly distinctly different than the surface profile of a living stromatoporoid. The discrimination between the final shape and the living surface profile was made e.g., by Kershaw (1987, 1998), and Sandström and Kershaw (2002). Determination of the growth form can be made by analysing the latilaminae arrangement.

Despite the fact that it is the living surface profile which is ecologically more significant than the final *post mortem* shape of the skeleton, originally the growth form has not been parameterized. Łuczyński (2005) has proposed a method of measuring the growth form and introduced the definitions of particular parameters – B^*, V^* and D^*, being counterparts of the measurements made for the whole skeleton. In later studies, the D^* parameter has been abandoned and therefore the growth form is characterised by its shape profile, represented by the calculated V^*/B^* ratio. Moreover, discrimination of the shape and the growth form allowed the introduction of a new parameter, the *burial ratio* (BR) = $(V-V^*)/V$ (Łuczyński 2006), indicating the proportion of the skeleton standing above the sediment surface and buried beneath it.

Further improvements of stromatoporoid parameterization include the methodology of measuring specimens that are accessible for studies not in vertical crosscuts (which is most common), but as three-dimensional domes exposed on palaeobottom surfaces (Łuczyński 2008). Calibration of the results obtained by both methods, which enables their comparison, has been presented. Skeleton asymmetry and changes in the specimens' growth direction were also studied and quantified (Łuczyński 2009). These specific features were, however, not analysed in the present study.

AIM OF STUDIES

Throughout the years, a large number of stromatoporoid specimens have been subjected to morphometric analyses, the results of which were described in my consecutive papers (Łuczyński 1998b, 2003; Łuczyński *et al.* 2009, 2014). Although particular studies were focused on different aspects of stromatoporoid morphometry, most skeletons were measured according to the same procedure, and the same parameters, ratios and descriptive features were determined, which resulted in the collection of a big amount of stromatoporoid morphometric data that could be statistically analysed. In the present study, in order to make all the results comparable, only those stromatoporoids were analysed where all the parameters had been determined, which resulted in many specimens being excluded from the analysis.

Detailed palaeoenvironmental interpretations based on stromatoporoid shapes require analysis of a combination of growth forms, low-level taxa and sedimentary data (Kershaw 2013). Some fine attempts to establish the relations between species, environments and growth forms have been made, e.g., by Kershaw (1981, 1984, 1990) from the Silurian stromatoporoid biostromes of Gotland or by Da Silva *et al.* (2011a, b). However, stromatoporoids can rarely be identified taxonomically on external appearance alone, while basic morphometric measurements can be done directly in the field (e.g., Stearn 2010c). Moreover, after the discovery of modern hypercalcified sponges, it has become evident that the calcareous skeleton-based classification of stromatoporoids is not consistent with the spicule-based classification used for living sponges (Vacelet 1985) and that different species may produce an identical calcareous skeleton (Reitner and Engeser 1987). All these issues have made the problems of stromatoporoid taxonomy and of the taxa-environment-growth form relations even more complicated (Kershaw 2013; Kershaw *et al.* 2018).

All the above lead to a common situation, in which a lot of morphometric data is available however without specific taxonomical affiliation of the particular specimens measured, as it is in this case. In my opinion it would be inappropriate to treat all such data as invalid, as particular morphometric features of the skeleton can be interpreted independently of its taxonomic identification. One of the lesser aims of this study was to present evidence that easily gained, field collected stromatoporoid morphometric data can carry important information, which can be interpreted in terms of various ecological factors, and as such should not be ignored even in the case when taxonomical determinations of the measured specimens are missing.

The most important goal of this study, which is based on a big set of data representing various sedimentary settings, was to find all the potentially existing interrelations between particular stromatoporoid morphometric features. For example, does a particular type of an initial surface, or of latilaminae arrangement typically match with a particular shape of the skeleton, or with a particular growth form? Some of these attributes can easily be linked with a particular environmental factor, and their nature is clearly understood, whereas the origin of others is not so obvious. A specimen with enveloping latilaminae (such an arrangement of macroscopically visible growth bands within the skeleton, in which every consecutive band completely covers – envelopes – the preceding; Text-fig. 3B), univocally points to a low rate of sediment accumulation. In such case, the whole upper surface of the skeleton remained uncovered and was inhabited by the living tissue (e.g., Kershaw 1984; Łuczyński 2006). The rate and character of sediment accumulation are commonly treated as factors influencing both the stromatoporoid overall shape, as well as its living surface profiles (e.g., Kobluk 1978; Kano 1990; Sandström 1998; Königshof and Kershaw 2006; Łuczyński 2006), however in the latter case the issue is much more complicated. On the other hand, the type of the stromatoporoid's initial surface is a feature, which is difficult to interpret, and which may be associated with various factors. If indeed these basic morphometric characteristics were governed by some specific palaeoenvironmental factor, or sets of factors, it can be expected that features governed by a given factor should coincide; and on the contrary – features related to the opposite environmental conditions, e.g., low and stable *vs.* punctuated rate of sediment accumulation, should not meet in the same specimen. An analysis revealing the existence of statistically relevant interrelations between particular stromatoporoid morphometric features would indicate that these features result from the same set of environmental conditions. On the one hand, this would allow the validation of the influence of environmental conditions on those stromatoporoid morphometric characteristics that are less evident in this matter. On the other hand it would enable a better understanding of the nature of these features and of the factors that govern them.

Morphometric analysis of a large number of stromatoporoids allowed also the addressing of such important and persisting questions of stromatoporoid paleoecology as:

– What were the main factors terminating stromatoporoid growth?
– Did Palaeozoic stromatoporoids act photosensitively?
– How the shape of stromatoporoid skeletons changed during their growth?

MATERIAL AND METHODS

The studied stromatoporoids come from the Silurian (Ludlow to Pridoli) of Podolia, western Ukraine, and the Devonian (Frasnian) of the Holy Cross Mountains, central Poland (see Appendix 1 for list of localities). All localities represent an environment of shallow-water carbonate platforms and shoals (e.g., Racki 1993; Radkovets 2015), although varying in detail in terms of, for example, distance from land, depth of deposition, water turbidity, rate of sediment accumulation, etc.

A total number of 705 stromatoporoid specimens were analysed (Table 1; Appendix 2 – Supplementary Table available only in the online version). Amongst these, 413 came from the Devonian of the Holy Cross

Category \ Locality	Kadzielnia	Karwów	Sitkówka-Kowala	Bolechowice-Panek	Zubravka	Kubachivka	Podpilip'e
Total number	25	150	87	151	125	112	55
Shape profile							
Laminar	–	4 (3%)	–	–	–	3 (3%)	1 (2%)
Low domical	15 (60%)	80 (53%)	3 (3%)	14 (9%)	23 (18%)	33 (29%)	11 (20%)
High domical	10 (40%)	64 (43%)	28 (32%)	44 (29%)	76 (61%)	37 (33%)	32 (58%)
Extended domical	–	2 (1%)	36 (41%)	26 (17%)	15 (12%)	9 (8%)	8 (15%)
Highly extended domical	–	–	2 (2%)	28 (19%)	1 (1%)	12 (11%)	1 (2%)
Low bulbous	–	–	5 (6%)	22 (15%)	–	13 (12%)	2 (4%)
High bulbous	–	–	13 (15%)	17 (11%)	–	5 (4%)	–
Initial surface							
Flat	14 (56%)	73 (49%)	13 (15%)	64 (42%)	49 (39%)	34 (30%)	29 (53%)
Initial elevation	9 (36%)	69 (46%)	58 (67%)	28 (18%)	64 (51%)	48 (43%)	17 (31%)
Anchor	2 (8%)	8 (5%)	16 (18%)	33 (22%)	12 (10%	30 (27%)	9 (16%)
Encrusting	–	–	–	16 (17%)	–	–	–
Surface character							
Smooth	9 (36%)	128 (85%)	85 (98%)	62 (41%)	46 (37%)	77 (69%)	50 (91%)
Ragged	16 (64%)	22 (15%)	2 (2%)	89 (59%)	79 (63%)	35 (31%)	5 (9%)
Latilaminae arrangement							
Enveloping	8 (32%)	124 (83%)	61 (70%)	69 (36%)	41 (33%)	41 (37%)	43 (78%)
Non-enveloping	17 (68%)	26 (17%)	26 (30%)	82 (54%)	84 (67%)	71 (63%)	12 (22%)

Table 1. Quantity and percentages of stromatoporoids representing various morphometric features from particular localities studied.

Mountains, from the exposures in Karwów (150), Kadzielnia (25) and Sitkówka-Kowala (87) quarries and from polished slabs of decorative stones exposed in several public buildings of Warsaw and quarried in Bolechowice-Panek Quarry (151). 292 specimens came from the Silurian of Podolia (western Ukraine), from Zubravka (125) and Kubachivka (112) quarries and from natural exposures on the banks of Zbruch River in Podpilip'e (55). For detailed information on localities, stratigraphy and environmental interpretations of particular settings see Łuczyński (1998b – Karwów, Kadzielnia and Sitkówka-Kowala; 2003 – Bolechowice-Panek), and Łuczyński *et al.* (2009 – Zubravka and Kubachivka; 2014 – Podpilip'e).

In the papers cited above and dedicated to particular Silurian and Devonian localities, stromatoporoid morphometric features were confronted with facies and sedimentary data, and interpreted in terms of palaeoenvironmental conditions. In the present study, however, all the specimens that were measured according to the same procedure were treated as one homogeneous group. This resulted in the assembly of a large set of data, in which each discerned category of any particular analysed feature is represented by a large number of specimens, which in turn allows for a quantitative statistical approach. In this case, however, only interrelations between particular parameters and ratios are a subject of interest, as stromatoporoids representing different localities meet in the same discerned groups characterised by particular morphometric features.

All specimens were measured according to the parameterization method first introduced by Kershaw and Riding (1978), and later improved by Kershaw (1984), Łuczyński (2005, 2006) and Łuczyński *et al.* (2009). Three dimensions of a vertical cross-section through a skeleton were measured: B – *basal length*, V – *vertical height* and D – *diagonal distance*. All field measurements were made with a 1 cm accuracy, based on the presumption that a vertical cross-section through a specimen is only a rough approximation of its real three-dimensional shape and thus more precise measurements are inadequate (for discussion on the comparability of measurements made in vertical cross-sections and in three dimensions see Łuczyński 2008). The V/B and V/D ratios were used to ascribe particular specimens to various shapes (Text-fig. 2A). All forms with V/B ratio (shape profile) < 0.1 are referred to as *laminar*. Forms with $0.1 \leq V/B < 1$ are termed *domical* and subdivided into *low domical* ($0.1 \leq V/B < 0.5$) and *high domical* ($0.5 \leq V/B < 1$). Specimens with a V/B ratio ≥ 1 are divided based on the V/D ratio. All forms with $V/B \geq 1$ and $D \geq V$ are termed *bulbous*, and are further divided into *low bulbous* ($V/B < 2$) and *high bulbous* ($V/B \geq 2$). Forms with $V/B \geq 1$, but with $D < V$ are included into domical forms and referred to as *extended domical* ($1 \leq V/B < 2$) or *highly extended domical* ($V/B \geq 2$).

Apart from the measurements of the whole stromatoporoid skeletons, also the living surface profiles in the final growth stage, deciphered based on the arrangement of latilaminae, were analysed for each specimen. Measured were the basal length (B^*) and the vertical height (V^*) of the final growth form (Text-fig. 1B), and the V^*/B^* ratio was calculated. In this case, the diagonal dimension of the final growth form has not been determined (due to often occurring difficulties in obtaining equivocal and comparable field measurements of the diagonal parameter, and in determining the c^* point, from which such measurement should be made). The ascription of stromatoporoids to particular shape categories is based on the shape profile ratio V^*/B^*.

The measurements of the skeletons and the living surface profiles (quantitative data) were supplemented by determination of qualitative macroscopic stromatoporoid morphometric features, which are also considered to be environmentally significant. This includes the types of basal surface, with four distinct distinguished categories of the *initial surface* referred to as *flat*, *initial elevation*, *anchor* and *encrusting* (Łuczyński 2003; Text-fig. 3C). The upper *surface character* is described either as *smooth* or *ragged* with distinct sediment increments on the sides (Text-fig. 3A). If a specimen shows any raggedness, e.g., only on one side, it is treated as ragged. The feature is strictly related to the *latilaminae arrangement*, which can be either *enveloping* or *non-enveloping* (Text-fig. 3B). All ragged forms obviously have a non-enveloping arrangement of latilaminae, whereas specimens with a smooth upper surface occur in both varieties (Text-fig. 3A, B). In the latter case, the arrangement of the last latilamina or latilaminae set was taken into account, as the feature can change during ontogeny (Łuczyński 2006).

Based on the performed measurements, several additional quantitative parameters were calculated and a number of further categories have been introduced. The skeleton's *capacity* was calculated according to the formula $C = 4/3\pi(B/2)^2V$, in which the stromatoporoid shape is approximated by a half of a rotatory ellipsoid (Łuczyński *et al.* 2009). Determined was also the parameter of *burial ratio* in the final growth stage, described by the formula $BR = (V{-}V^*)/V$ (Łuczyński 2006), which indicates the proportion of the skeleton standing above the sediment

Category \ Parameter	Mean	Median	Standard deviation	Mean confidence interval	Maximum	Minimum	Skewness	Kurtosis
Basal length – *B*	15.7	13	12.7	0.0301	113	1	2.66	11.01
Vertical height – *V*	10.7	9	7.6	0.0181	77	1	2.81	14.15
Diagonal distance – *D*	9.9	8	6.9	0.0162	73	1	2.73	14.47
Shape profile – *V/B*	1.0	0.69	1.1	0.0026	8.50	0.05	3.08	11.72
Capacity (cm^3) – *C*	8313	1442	42014	99.2234	655212	4	11.19	168.07
Growth form basal dimension – *B**	14.0	11	11.5	0.0273	103	1	2.85	11.97
Growth form vertical height – *V**	8.5	7	6.7	0.0159	68	1	3.03	16.23
Growth form shape profile – *V*/B**	0.8	0.64	0.7	0.0016	5.5	0.04	2.30	8.06
Burial ratio – *BR*	0.2	0.14	0.3	0.0007	0.83	-0.67	0.12	-0.94
Upper surface curvature – *V/D*	1.1	1.00	0.2	0.0004	3.50	0.67	4.65	42.17
Overhangs – ½B/DB	2.4	1.83	2.3	0.0053	23	0.17	3.71	17.14
Shape of sides – *X/D*	0.7	0.71	0.2	0.0005	2.24	0.15	0.22	3.96
Upper surface convexity – *V/DV*	1.2	1.14	0.2	0.0005	3.50	0.73	3.65	27.97

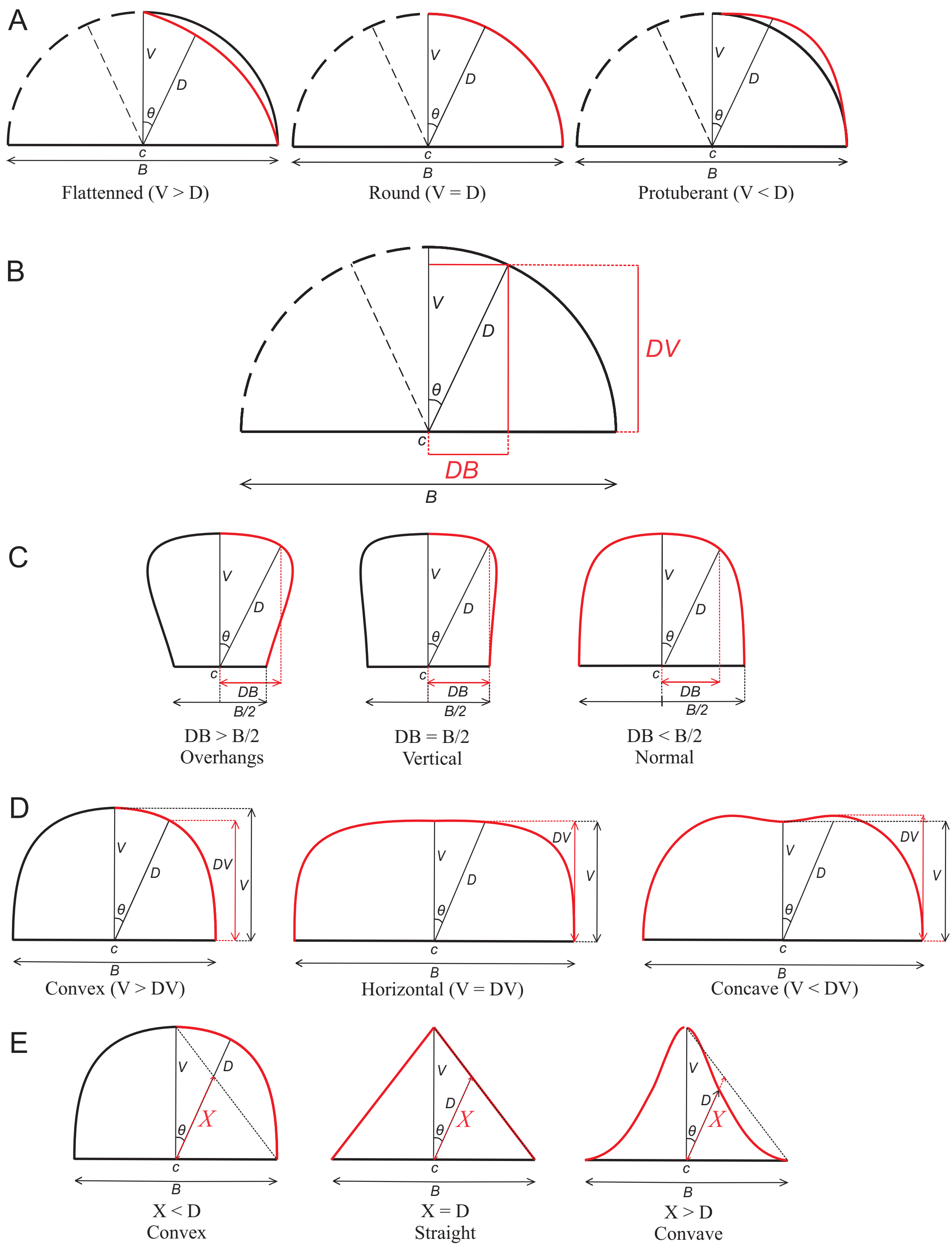
Table 2. Summary of the results of morphometric measurements and basic statistical attributes of the measured collection – quantitative categories. $C = 4/3\pi(B/2)^2V$, $BR = (V-V^*)/V$, $DB = \cos65°D$, $DV = \sin65°D$, $X = V/(\sin65°+2V/B\cos65°)$. All direct measurements are given in centimetres and with a 1 cm accuracy.

Shapes	Laminar	Low domical	High domical	Extended domical	Highly extended domical	Low bulbous	High bulbous
Skeleton	8 (1.1%)	179 (25.4%)	291 (41.3%)	93 (13.2%)	45 (6.4%)	55 (7.8%)	34 (4.8%)
Growth form	12 (1.7%)	239 (33.9%)	247 (35%)	95 (13.5%)	28 (4%)	71 (10%)	13 (1.8%)
Initial surface	Flat		Initial elevation		Anchor	Encrusting	
	275 (39%)		294 (41.7%)		110 (15.6%)	26 (3.7%)	
Burial ratio *BR*	Elevated (*BR* < 0)		Erect (*BR* = 0)			Partly buried (*BR* > 0)	
	167 (23.7%)		122 (17.3%)			416 (59.9%)	
Upper surface curvature *V/D*	Flattened (*V* < *D*)		Round (*V* = *D*)			Protuberant (*V* > *D*)	
	88 (12.5%)		276 (39.1%)			341 (48.3%)	
Inclination of sides ½*B/DB*	Normal (*DB* < ½*B*)		Vertical (*DB* = ½B)			Overhangs (*DB* > ½*B*)	
	555 (78.7%)		25 (3.5%)			125 (17.7%)	
Shape of skeleton sides *X/D*	Concave (*D* < *X*)		Straight (*D* = *X*)			Convex (*D* > *X*)	
	32 (4.5%)		6 (0.9%)			667 (94.6%)	
Upper surface convexity *V/DV*	Concave (*V* < *DV*)		Horizontal (*V* = *DV*)			Convex (*V* > *DV*)	
	19 (2.7%)		61 (8.7%)			625 (88.7%)	
Surface character	Smooth				Ragged		
	491 (69.6%)				214 (30.4%)		
Latilaminae arrangement	Enveloping				Non-enveloping		
	387 (54.9%)				318 (45.1%)		

Table 3. Summary of the results of morphometric measurements and basic statistical attributes of the studied collection – qualitative categories.

surface and buried beneath it. Typically, the ratio varies between 0 (totally erect) and 1 (totally buried), however different definitions of the *V* and *V** parameters result that the burial ratio can adopt negative values. Therefore, the basic distinguished categories based on this ratio are *elevated* (*BR* < 0), *erect* (*BR* = 0) and *partly buried* (*BR* > 0).

In order to better quantify the shapes of the stromatoporoids upper surfaces, which is particularly important when analysing the interplay between the living animal and the sediment accumulating around it, several additional calculated parameters (ratios) were introduced (Tables 2 and 3). One of the values reflecting the stromatoporoids *upper surface curvature* (convexity *vs*. concavity) is the *V/D* ratio. Three categories of the curvature of the upper surface were distinguished. Specimens with $V < D$ are referred to as *flattened*, with $V = D$ are termed *round* and with $V > D$ are referred to as *protuberant* (Text-fig. 4A). Moreover, calculated were the horizontal and vertical components of the measured diagonal dimensions – cos65º*D* (horizontal), later referred to as *DB*, and sin65º*D* (vertical), later referred to as *DV* (Text-fig. 4B). All calculated values are given with a



Text-fig. 4. New calculated stromatoporoid morphometric attributes. A – Upper surface curvature – categories distinguished based on the V/D ratio; *flattened* (V > D), *round* $V = D$) and *protuberant* ($V < D$); B – Horizontal and vertical components of the measured diagonal dimensions – cos65°D (horizontal) referred to as DB, and sin65°D (vertical) referred to as DV (65° = 90°−θ); C – Specimens with various ½B/DB parameter, which enables to depict specimens with overhangs; i.e., those, in which the upper parts of the skeleton protrude sideways above its base; *overhangs* (DB > ½B), *vertical* (DB = ½B) and *normal* (DB < ½B); D – Specimens with various V/DV parameter, which allows to recognise specimens with a *convex* upper surface (if the ratio exceeds 1), a *horizontal* upper surface (if it equals 1) and a *concave* upper surface with a depression (if the ratio is less than 1); E – Specimens with various shapes of the sides; *convex* ($X < D$), *straight* ($D = V$) and *concave* ($X > D$). The X value was determined according to the formula: $X = V/(\sin 65° + 2V/B \cos 65°)$.

1 cm accuracy, to make the results comparable with basic field measurements. Determined were also the ½*B*/*DB*, and the *V*/*DV* ratios. The ½*B*/*DB* ratio referred to as *inclination of sides* enables the depiction of specimens with overhangs, i.e., those, in which the upper parts of the skeleton protrude sideways above its base (Text-fig. 4C). Such a situation occurs if the ratio is less than 1. Accordingly, the *V*/*DV* ratio, referred to as *upper surface convexity.* allows for the recognition of specimens with a *convex* upper surface (if the ratio exceeds 1), a *horizontal* upper surface (if the ratio equals 1) and a *concave* upper surface with a depression (if the ratio is less than 1; Text-fig. 4D).

Finally, a hypothetical *X* value was determined, according to the formula: $X = V/(\sin 65^o + 2V/B \cos 65^o)$. The value represents the calculated diagonal dimension *D* if the side surfaces of the skeleton were straight, or in other words, if the stromatoporoid in a vertical cross-section was approximated by a triangle determined by the end points of its *B* and *V* dimensions (Text-fig. 4E). The relation between the calculated *X* value and the real measured diagonal dimension (*D*), allows for the recognition of specimens with concave sides (if the ratio exceeds 1). The ratio is here referred to as *shape of skeleton sides*.

Basic statistical attributes of the measured population, such as mean, median, maximum and minimum values, skewness and kurtosis were calculated for all quantitative parameters. The percentage share of all qualitative parameters has been determined.

RESULTS

General measurement results and proportions of particular features

The most common shape of the skeleton from among the distinguished categories is high domical followed by low domical and extended domical (Table 3). Other categories are less common, but only in the case of laminar forms, the sample is too small to be taken into account in quantitative analyses (30 considered to be a minimum value). The basal measurement proportion curves (Text-fig. 5) follow the same outline for the shapes of the whole skeletons (%*B*) and for the shapes of the final growth forms representing living surface profiles (%B^*). The proportion of *B* value graphs, also referred to as "%*B* curves", show the variabilities of shape profiles within groups characterised by given attributes. They are a convenient way of presenting arrays of stromatoporoid

Text-fig. 5. Shape profiles. *%B* curves presenting relative proportion of the basal length parameter. The curves illustrate the proportion of specimens (in percent; vertical axis) falling within 5% wide intervals of the $[B/(B+2V)]\times100\%$ ratio (in percent; horizontal axis).

shapes and allow direct comparison between various groups. Assumedly, such curves should show the proportion of the basal length value in the sum of all the measurements – $[B/(B+V+D)]\times100\%$ and $[B^*/(B^*+V^*+D^*)]\times100\%$ respectively for the whole skeletons and for the final growth forms. However, in the present studies the D^* parameter has not been measured in all localities (in some places, particularly when strongly dolomitised, the internal latilaminae array is strongly obscured and illegible, which makes a reliable determination of the c^* point impossible). In such case, in order to make all the graphs comparable, the diagonal measurements have been replaced by repeated vertical dimension values (*V* and *V**), and therefore the applied formulas are: $[B/(B+2V)]\times100\%$ and $[B^*/(B^*+2V^*)]\times100\%$ respectively.

From among the initial surface categories distinguished, encrusting is the least common and because of the number being less than 30, it is not taken into account in further considerations. Anyway, the shape of encrusting forms often follows the outline of the encrusted element, and therefore cannot be treated in the same way as the other types distinguished. Other categories are common, with roughly the same number of flat and initial elevation varieties and a much lesser number of specimens with initial surfaces described as anchor (Table 3).

More than half of the studied specimens have a positive value of the burial ratio and are classified as partly buried (Table 3). The remaining 40% is divided between specimens classified as erect (*BR* = 0) and as elevated (*BR* < 0). In this and all the other cases, the categories are based on measurements made with a 1 cm accuracy. The two categories of latilaminae arrangements (enveloping and non-enveloping) are comparably common, while the smooth upper surface character distinctly outnumbers the ragged variety (Table 3). However, in spite of the differences, all the distinguished categories of burial ratio, latilaminae arrangements, and upper surface characters constitute groups large enough to be analysed quantitatively and show that the particular features are common among stromatoporoids. As such, they can be treated as typical stromatoporoid responses to various environmental conditions.

The situation with the ratios calculated to describe various aspects of the shapes of the upper surfaces is different. In most cases, there is a single distinctly dominant category, which can be interpreted as best adapted to the whole array of conditions and changing factors, while the other theoretical possibilities in reality occur very seldom. Such is the situation with the ratio describing the upper surface convexity (Text-fig. 4D), with convex specimens constituting almost 90% of the measured population (Table 3). This suggests that for some reasons (discussed below) the horizontal and concave varieties are not easily attained by stromatoporoids. In further considerations the two latter categories are treated together. A similar situation is the case with the calculated *X*/*D* ratio (Table 3) dedicated to describe the shape of the stromatoporoid's sides by comparing its outline to a triangle (Text-fig. 4E). Only 38 specimens (5.4%) exhibit concave or straight sides (Table 3), which indicates that a convex shape of the skeletons' lateral sides is typical for the whole array of sedimentary environments, in which stromatoporoids commonly grew. Similarly, almost 80% of the measured population exhibits normal inclination of the sides (Table 3), with much fewer varieties with vertical and overhanged sides, as is indicated by the ½*B*/*DB* ratio (Text fig. 4C). Nonetheless, 125 of the measured specimens (almost 20%) indicate the existence of overhangs (obviously mainly in the bulbous shape varieties), and 25 more show sides that are at least vertical. In further considerations the two categories are treated together, and they are discussed in terms of the possible photosensitivity of stromatoporoids. The only calculated ratio describing the shape of the upper surface, in which all the distinguished categories are numerous enough to be treated separately, is the upper surface curvature (Table 3), described by the *V*/*D* ratio (Text-fig. 4A), by which a stromatoporoid is compared to a semicircle. Protuberant forms are the most common here (almost 50%), but round and flattened varieties are also numerous.

Basic correlations

Shape profile vs. upper surface character and latilaminae arrangement

The shapes of the skeletons adopted by specimens which have respectively smooth and ragged surfaces and with enveloping and non-enveloping latilaminae arrangements show only minor differences (Text-fig. 6A, B). In all these cases, practically the whole array of shapes is represented. In the case of ragged specimens, the proportion of relatively low profile varieties (laminar plus low and high domical) equals 78%, which is noticeably higher than 64% of smooth specimens representing the same shapes (Text-fig. 6A). When comparing the non-enveloping and enveloping groups, the difference is smaller (respectively 63% and 72% of relatively low profile varieties; Text-fig. 6A). The proportion of *B* value curves generally follow the same outline (Text-fig. 6B) for stromatoporoids with various types of upper surfaces and latilaminae arrangements. The ragged forms %*B* curve shows a peak of values (18% plus 16%) representing specimens, in which the *B* value falls within the 45–55% interval of the sum of the measurements. The %*B* curve of the smooth forms is more flat, however with a mode in roughly the same interval.

The case is different when the final growth form representing a living surface profile of a stromatoporoid is considered. The growth forms of specimens with non-enveloping latilaminae arrangements show distinctly lower shape profiles than the specimens with an enveloping arrangement, which is reflected in a higher component of the *B** value in the sum of the measurements (Text-fig. 6C). In the case of non-enveloping forms, most common are specimens, in which the %*B** proportion falls between 50% and 60%, whereas in the case of enveloping forms, most common values are 35% to 45%. The same, or even more distinct difference is evident when comparison is made between the %*B** curves of the final growth forms of the smooth and ragged varieties. Stromatoporoids with ragged sides adopt distinctly lower final shape profiles (Text-fig. 6C). Dominant %*B** value is 60% for the ragged forms and only 35% for the smooth forms.

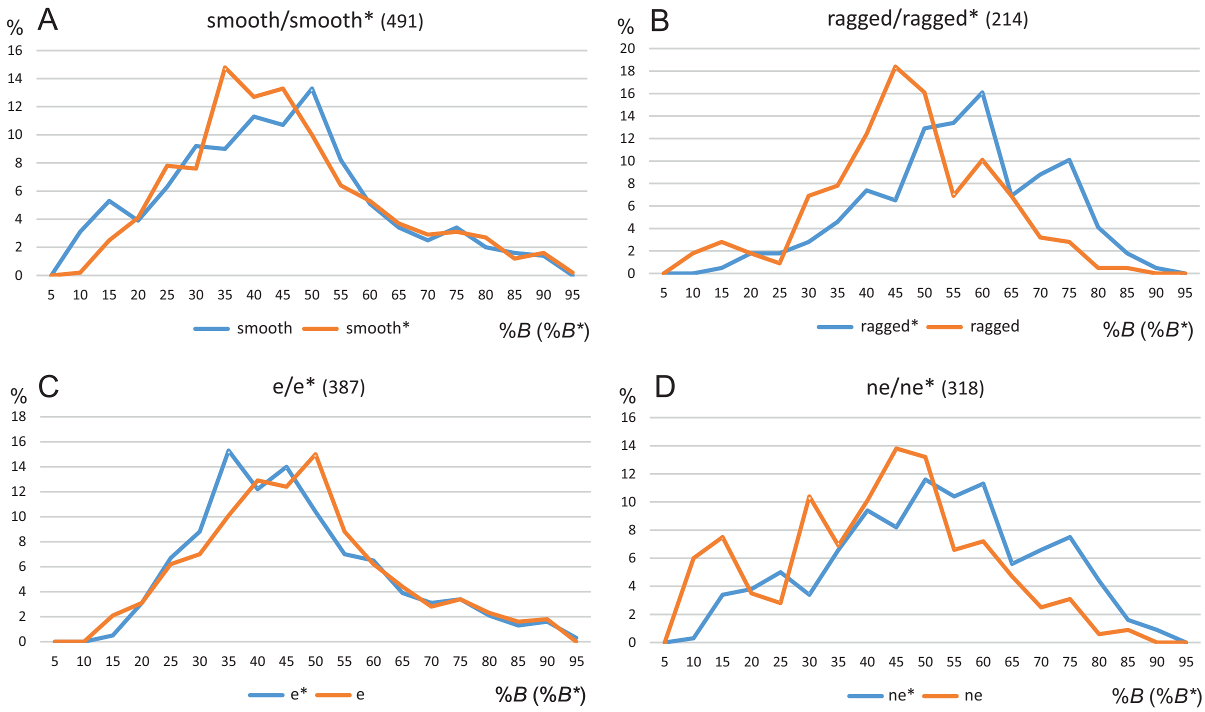
It is interesting also to compare the skeleton shapes and the final growth form profiles within particular groups. Shape profiles of the final growth forms are distinctly lower than those of the skeletons in the group of ragged specimens (Text-fig. 7B), and less distinctly also in the group of stromatoporoids with non-enveloping latilaminae arrangements

Text-fig. 6. Shape profile *vs.* upper surface character and latilaminae arrangement. A – Proportions of shape profiles among stromatoporoids with various upper surface characters and latilaminae arrangements (in percent); *L* – laminar, *LD* – low domical, *HD* – high domical, *ED* – extended domical, *HED* – highly extended domical, *LB* – low bulbous, *HB* – high bulbous. B, C – %*B* and %*B** curves presenting relative proportion of the basal length parameter (see Text-fig. 5) in stromatoporoids with various types of upper surface characters and of latilaminae arrangements among skeleton shapes (B) and final growth forms (C); *ne* – non-enveloping, *e* – enveloping; *B* values for skeleton shape and *B** values for the final growth form.

(Text-fig. 7D). Of course, all the ragged specimens exhibit a non-enveloping latilaminae arrangement. In the cases of smooth forms and those with an enveloping latilaminae arrangement, there are no distinct differences between the arrays of shape profiles of the skeletons and of the final growth forms (Text-fig. 7A, C).

The surface character and latilaminae arrangement can also be considered together. In such a case, there are three possible combined categories – specimens with a smooth surface and an enveloping latilaminae arrangement, specimens with a smooth surface and a non-enveloping arrangement, and stromatoporoids with a ragged surface, which by definition show a non-enveloping arrangement. Most common in the studied population is the smooth/enveloping variety (Table 4), constituting more than 50% of all specimens (387). The ragged variety is also common (214), whereas smooth/non-enveloping forms are relatively rare, although also present in a substantial number (104).

The proportion of particular shapes among the smooth/enveloping and the ragged/non-enveloping specimens is very much the same (Table 4A),



Text-fig. 7. Comparison of skeleton shapes and final growth forms of stromatoporoids with various types of upper surface characters and latilaminae arrangements. %*B* and %*B** curves presenting relative proportion of the basal length parameter (see Text-fig. 5). A, B – skeletons and final growth forms of stromatoporoids with various types of upper surfaces; C, D – skeletons and final growth forms of stromatoporoids with various types of latilaminae arrangements; *ne* – non-enveloping, *e* – enveloping; *B* values for skeleton shape and *B** values for the final growth form.

A

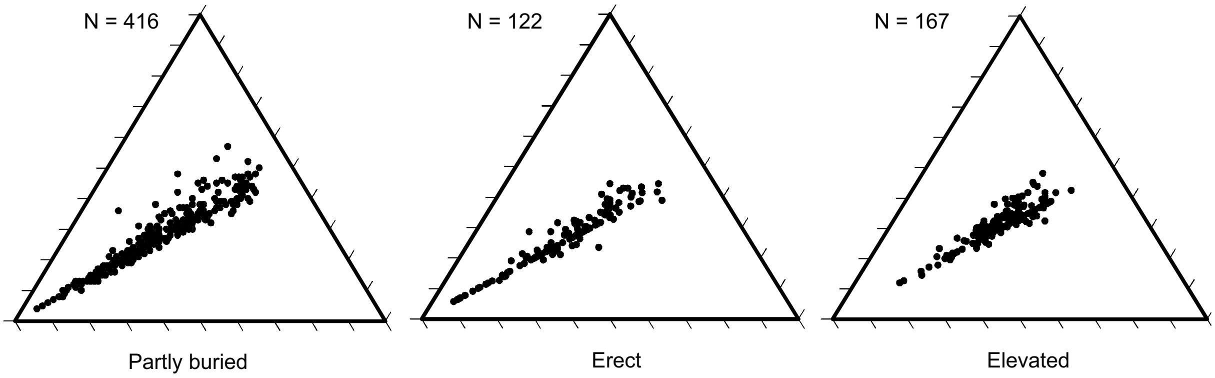
Shape \ **Upper surface**	Smooth / Enveloping	Smooth / Non-enveloping	Ragged / Non-enveloping
Laminar	0 (0%)	7 (6.7%)	1 (0.5%)
Low domical	101 (26.1%)	13 (12.5%)	65 (30.4%)
High domical	169 (43.7%)	23 (27.1%)	99 (46.3%)
Extended domical	56 (14.5%)	21 (20.2%)	18 (8.4%)
Highly extended domical	17 (4.4%)	18 (17.3%)	10 (4.7%)
Low bulbous	32 (8.3%)	7 (6.7%)	16 (7.5%)
High bulbous	12 (3.1%)	17 (16.3%)	5 (2.3%)
Total	387	104	214

B

Upper surface \ **Shape**	Laminar	Low domical	High domical	Extended domical	Highly extended domical	Low bulbous	High bulbous
Smooth/enveloping	0%	56.4%	58.1%	58.9%	37.8%	58.2%	35.3%
Smooth/non-enveloping	87.5%	7.3%	7.9%	22.1%	40.0%	12.7%	50.0%
Ragged/non-enveloping	12.5%	36.3%	34.0%	18.9%	22.2%	29.1%	14.7%

Table 4. Stromatoporoid shapes and types of upper surfaces. A – Quantities and percentiles of specimens with particular shapes among stromatoporoids with various upper surface characteristics; B – Percentiles of stromatoporoids with particular upper surfaces among stromatoporoids with various shapes.

and generally corresponds to the general proportion of the whole studied sample, with the high domical specimens constituting the most common group, followed by the low domical ones. In the case of stromatoporoids with a smooth surface but a non-enveloping latilaminae arrangement, the proportion



Text-fig. 8. Triangular displays of stromatoporoid shapes of specimens with various burial ratios (for areas on the triangles corresponding to particular shapes see Text-fig. 2).

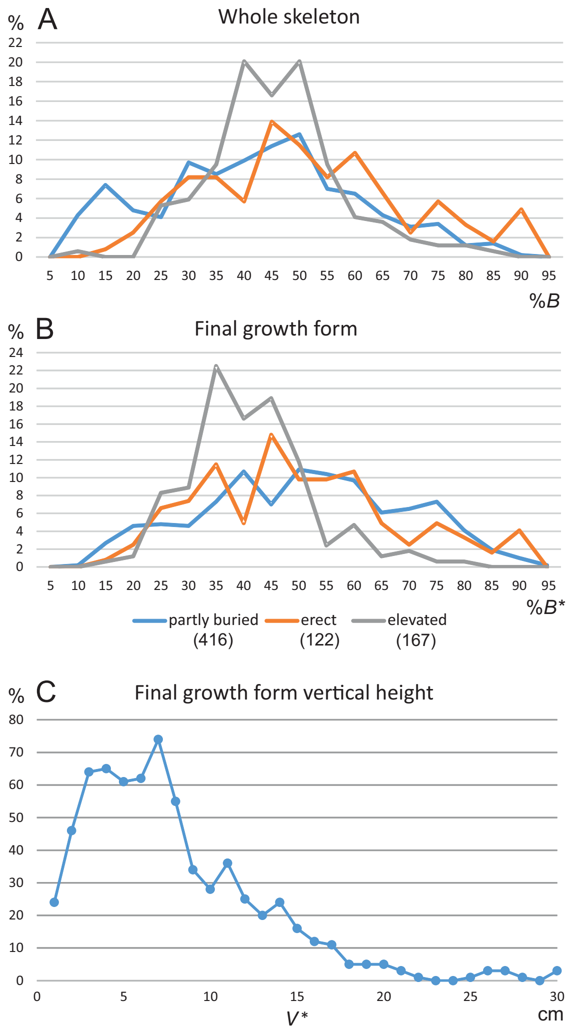
of shapes is visibly different and is devoid of a distinctly leading category.

If the proportion of various combined upper surface categories for particular distinguished shape categories is considered, three groups show a very similar picture – low domical, high domical and low bulbous (groups with a relatively low *V*/*D* ratio, reflecting the upper surface curvature). All these groups are characterised by a distinct dominance of the smooth/enveloping varieties and a relatively rare occurrence of the smooth/non-enveloping ones (Table 4B). On the other hand, very high shape profiles – high bulbous and highly extended domical, show a different proportion, with the smooth/non-enveloping forms being relatively most frequent (a group which is least numerous in the whole population).

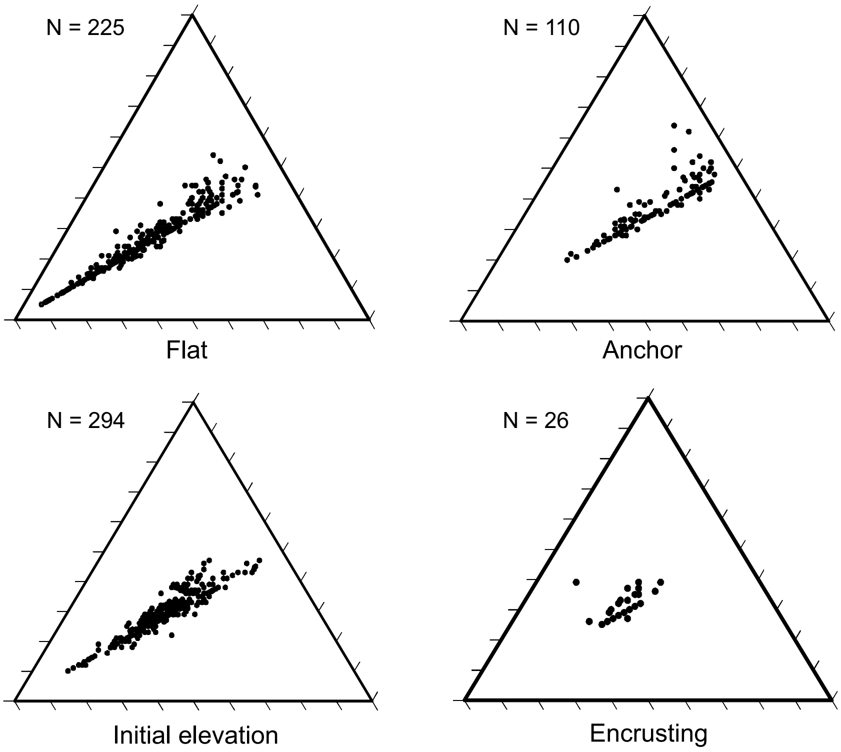
Shape profile and living surface profile (growth form) vs. burial ratio

As illustrated in Text-fig. 5, the general variabilities of the shapes of the whole stromatoporoid skeletons and of the final growth forms are almost similar in the studied sample, and a whole range of shape profiles is represented. This is somehow surprising, because a big proportion (59.9%;) of the sample is represented by partly buried specimens (Table 3), thus with particular measurements clearly differing between the skeleton and the living surface profile.

If particular burial ratio categories are considered (elevated – $BR < 0$, erect – $BR = 0$, and partly buried – $BR > 0$), a broad variety of shapes is adopted in each case, as can be seen on triangular arrays (Text-fig. 8). The proportions of *B* value curves for the whole skeletons of the erect and the partly buried forms are almost similar (Text-fig. 9A). In the case of



Text-fig. 9. Shape profiles of stromatoporoids characterised by various burial ratios. A, B – %*B* (A) and %*B** (B) curves presenting relative proportion of the basal length parameter (see Text-fig. 5); C – Quantities of specimens with certain values of the V^* parameter (vertical height of the final growth form). The ten specimens with V^* greater than 30 cm are not shown on the graph.



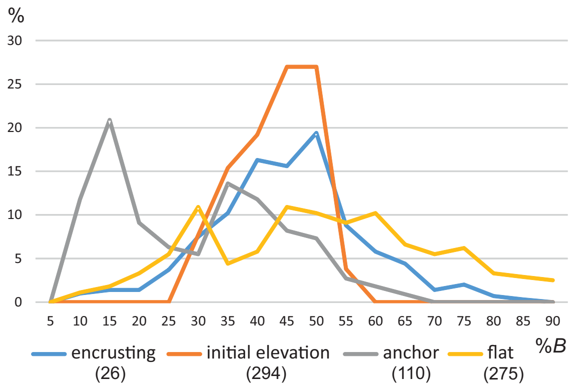
Text-fig. 10. Triangular displays of stromatoporoid shapes of specimens with various types of initial surfaces (for areas on the triangles corresponding to particular shapes see Text-fig. 2).

elevated forms there is a distinct domination of specimens with a *B* value proportion between 40% and 50%, while both very high profile (%$B \leq 20$) and very low profile forms (%$B \geq 70$) are almost completely eliminated. The same applies to %B* curves illustrating the variability of the final growth forms (Text-fig. 9B). Also in this case, the %B* curves for erect and partly buried specimens are very much alike, and without a clearly dominant category, whereas the curve for elevated stromatoporoids shows a distinct peak embracing *B* values proportion between 35% and 45%.

If %B and %B* curves drawn for particular burial ratio categories are compared, an opposite shift of the growth form profiles *vs*. the shape profiles can be observed in the cases of elevated and partly buried specimens (Text-fig. 9A, B). In the case of elevated specimens, the %B* curve is shifted to the left, which indicates that the final living surface profiles represent generally higher shape profiles than the whole skeletons. If the partly buried specimens are concerned, the %B* curve is generally shifted to the right, which means that the living surface profiles have generally lower profiles than the whole skeletons. The vertical dimension (V*) of the final growth forms most commonly falls between 3 and 8 cm (Text-fig. 9C). The two curves for the erect specimens are almost identical.

Shape profile vs. initial surface

The arrays and variabilities of shape profiles of the stromatoporoid skeletons with various types of initial surfaces shows distinct differences. Each category is represented by a range of shapes, however with different proportions, which is well illustrated on triangular arrays (Text-fig. 10). Very high profiles (very extended domical and low and high bulbous forms) are most common among specimens with an anchor. The three categories together constitute 57% of the stromatoporoids with an anchor, whereas among specimens with flat or elevated bases the proportion is in the range of few up to 15%. The domination of very high profiles among anchored specimens is clearly evident on the proportion of *B* value curve, with 15%*B* being the dominant category (over 20% of the group; Text-fig. 11). Stromatoporoids with a flat base adopt a whole array of shapes, without any %*B*



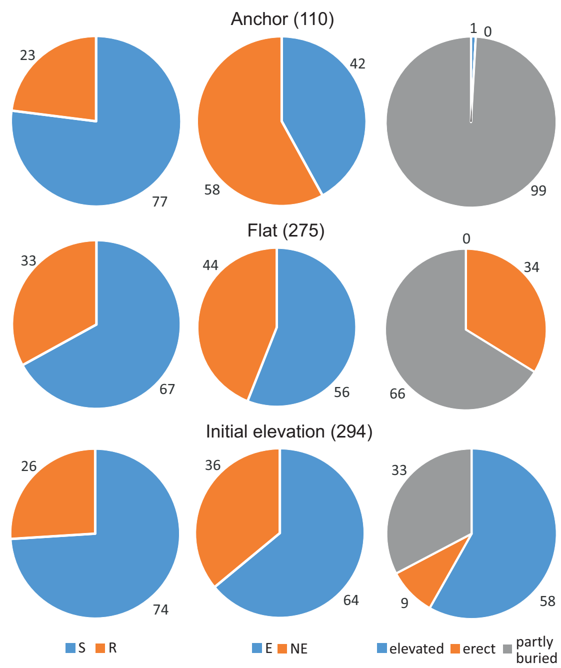
Text-fig. 11. Shape profiles of stromatoporoids characterised by various types of initial surfaces. %*B* curves presenting relative proportion of the basal length parameter (see Text-fig. 5); *E* – encrusting, *I* – initial elevation, *A* – anchor, *F* – flat.

interval distinctly dominating, however relatively low profile forms are most numerous. Specimens with an initial elevation are most commonly high domical, as are the encrusting forms (Text-fig. 10). Encrusting stromatoporoids are not common enough in the studied group to be treated separately, but in fact they can be considered as having a specific type of initial elevation, and therefore the two groups can be treated together.

Initial surface vs. latilaminae arrangement, upper surface character and burial ratio

The initial surface character reflects the early stages of the stromatoporoid's growth, whereas the latilaminae arrangement, upper surface character and burial ratio show the relation of the growing skeleton to the sediment accumulating around it. All initial surface categories (anchor, flat and initial elevation) show comparable proportions of specimens with smooth and ragged upper surfaces, with a distinct domination of the smooth variety, ranging between 67% for stromatoporoids with a flat base, and 77% for those with an anchor (Text-fig. 12). On the other hand, the proportion of latilaminae arrangements is somewhat different between stromatoporoids with various initial surfaces. In the case of the whole studied sample, the enveloping forms slightly outnumber the non-enveloping (Table 3). The non-enveloping latilaminae arrangement is exclusive among encrusting specimens and dominant among those with flat bases. However in the cases of stromatoporoids with initial elevations and anchors, the enveloping variety is more common (Text-fig. 12). The most distinct differences between specimens with various initial surfaces occur, however, when the burial ratio categories are considered. In the whole studied population, partly buried specimens are by far the most common category constituting almost 60% of the studied sample (Table 3). The proportions of particular burial ratio categories are completely different among stromatoporoids with various initial surfaces (Text-fig. 12). Almost 60% of the specimens with an initial elevation show a negative burial ratio (elevated), and all 167 elevated specimens ($BR < 0$) studied have an initial elevation. This is completely different than in the case of encrusting specimens, which are all partly buried ($BR > 0$). Apart from just one elevated specimen, also the stromatoporoids with an anchor are all partly buried. Partly buried specimens are also most common among stromatoporoids with a flat base (~⅔), however with a large proportion of erect specimens (~⅓).

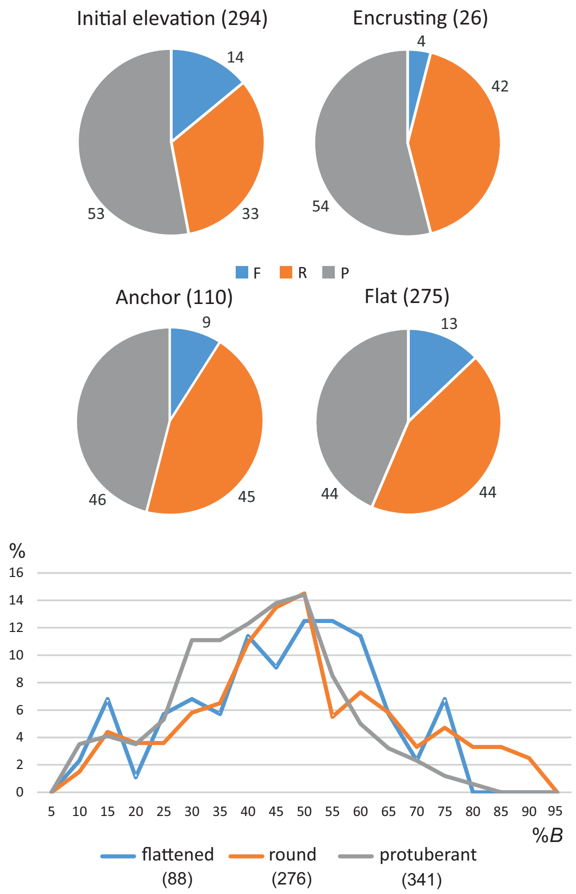
Encrusting stromatoporoids are not illustrated in Text-fig. 12 due to their small number, but also because in every case all the specimens (26) fall into the same category. All studied encrusting stromatoporoids have a ragged surface with a non-enveloping latilaminae arrangement, and thus all were partly buried in the final stage of their growth.



Text-fig. 12. Initial surface *vs.* upper surface character, latilaminae arrangement and burial ratio. Proportion of various types of upper surfaces and latilaminae arrangements among specimens with different types of initial surfaces; surface character: *S* – smooth, *R* – ragged; latilaminae arrangement: *E* – enveloping, *NE* – non-enveloping; burial ratio: elevated – $BR < 0$, erect – $BR = 0$, partly buried – $BR > 0$.

Initial surface and shape profile vs. ratios describing the shape of the upper surface

The proportion of specimens with various upper surface curvatures (described by the *V*/*D* ratio) is very much the same among all groups of initial surfaces (Text-fig. 13A). Specimens with protuberant upper surfaces constitute a little more of a half of the studied sample among stromatoporoids with initial elevations and encrusting (53% and 54%, respectively), and slightly less than a half among stromatoporoids with a flat initial surface and an anchor (44% and 46%, respectively). As in the whole studied sample, stromatoporoids with round upper surfaces are the second most common group that in case of three distinguished categories constitutes more than 40% of the measured specimens. Only in the case of stromatoporoids with an initial elevation is the proportion noticeably lower and equals 33%. In each category, the specimens with a flattened upper surface are least common, never adding up to more than a dozen or so percent.



Text-fig. 13. Upper surface curvatures *vs.* initial surfaces and shape profiles. A – Proportion of specimens with different types of upper surface curvatures among specimens with various initial surfaces; *F* – flattened, *R* – round, *P* – protuberant; B – %*B* curves presenting relative proportion of the basal length parameter (see Text-fig. 5) among stromatoporoids with various types of upper surface curvatures.

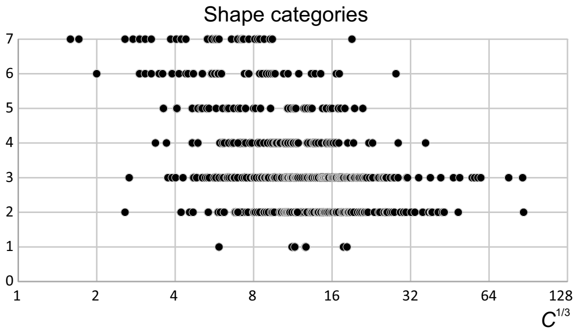
There is also no clear correlation between the shape profiles and the upper surface curvatures (flattened, round, protuberant). All three types of the upper surface occur in stromatoporoids with a wide spectrum of shape profiles, as illustrated on the %*B* curves drawn for particular curvature categories (Text-fig. 13B).

The overall shape of the final upper surface of the skeleton is difficult to determine based only on a single vertical crosscut. The ratios, which apart from the shape profile itself and the upper surface curvature, are meant to describe the upper surface are: the upper surface convexity (*V*/*DV*), inclination of sides (½*B*/*DB*), and shape of sides (*X*/*D*). In the case of two of these ratios – shape of sides and upper surface convexity, there is an overwhelming dominance of convex forms (Table 3). Varieties with straight or concave upper or side surfaces are very rare and occur in quantities that preclude reliable conclusions, especially when taking into account that the measurements are made with a 1 cm accuracy. For example, from among the 32 specimens with concave sides, only 12 have the *X*/*D* ratio ≥ 1.1, indicating a distinct concavity.

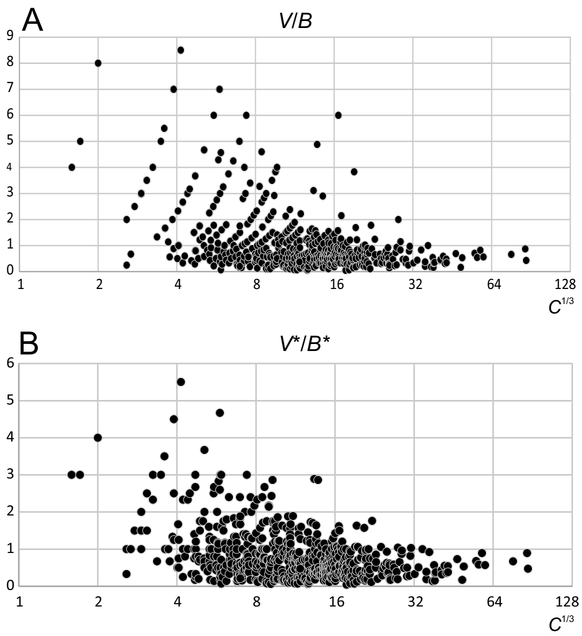
Presented above are the main relations between particular stromatoporoid morphometric parameters and calculated ratios. Obviously, more potential correlations can be tested based on the detailed data presented in the Supplementary Table.

Relation between stromatoporoid size and its morphometric features

An aspect, which is especially significant in considerations about possible applications of stromatoporoid morphometry in palaeoenvironmental analysis, is the variability of particular ratios depending on the stromatoporoid size. Stromatoporoid size allometry has been described by e.g., Łuczyński (2006) and Kershaw (2012), however with different conclusions (see Discussion). Here presented are basic allometric tendencies observed in the studied sample. The measure of a stromatoporoid size used here is the calculated skeleton capacity, obtained using a theoretical formula $C = 4/3\pi(B/2)^2V$, in which the stromatoporoid shape is approximated by a half of a rotatory ellipsoid (Łuczyński *et al.* 2009). Obviously, this is only an approximation, firstly due to a lack of three-dimensional data, and secondly because of different real shapes, which can only roughly be represented by the mentioned ellipsoid.



Text-fig. 14. Relation between stromatoporoid shapes (whole skeleton) and their sizes. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale). Particular numbers are ascribed to particular distinguished shape categories; 1 – laminar, 2 – low domical, 3 – high domical, 4 – extended domical, 5 – low bulbous, 6 – highly extended domical, 7 – high bulbous.



Text-fig. 15. Relation between stromatoporoid shape profiles and their sizes. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale). A – Whole skeleton shape profile – *V*/*B*; B – Final growth form shape profile – *V**/*B**.

Size vs. shape profile

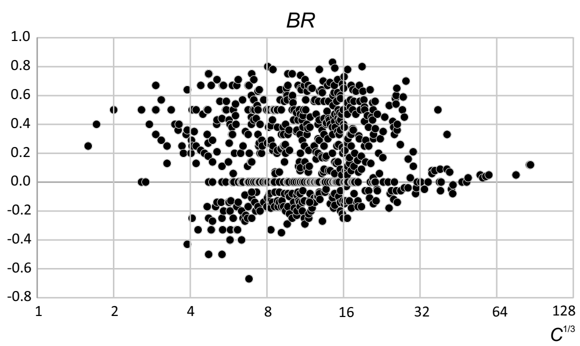
In spite of all the distinguished basic shape categories of the stromatoporoid skeleton occurring in a wide variety of sizes (Text-fig. 14), there is a an identifiable relation between size and shape in the group studied. Not taking into account laminar forms, because of the limited number of specimens, the lower the shape profile – the bigger capacities can be obtained by the skeleton. There is a clear shift towards smaller values in the scope of obtained capacities when comparison is made between consecutive shape categories characterised by an increasing shape profile. Really big specimens, with capacities exceeding 8000 cm^3 ($C^{1/3} > 20$), occur almost exclusively as low- and high domical forms, whereas high bulbous forms, with one exception, never reach a capacity of more than 1000 cm^3.

Gradual elimination of high shape profile forms together with an increasing stromatoporoid capacity can also be observed on graphs illustrating the relation between the specimens size and its shape profile (*V*/*B*; Text-fig. 15A), or its living surface profile (V^*/B^*; Text-fig. 15B). In both cases high profiles occur only to a certain dimension, and are gradually eliminated together with size, whereas low profile forms generally occur in the whole scope of recorded capacities.

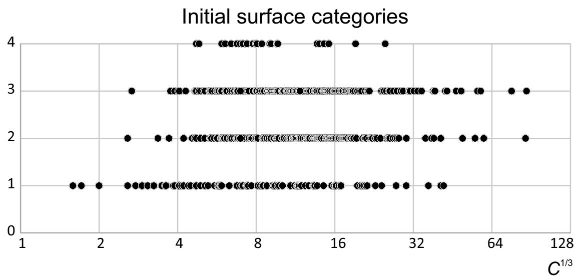
Size vs. other macroscopic morphometric features

Burial ratio. There is no distinct correlation between stromatoporoid size and its burial ratio in the final growth stage (*BR*), which indicates the proportion of the skeleton standing above the sediment surface and buried beneath it (Text-fig. 16). Specimens with a positive burial ratio (partly buried), with $BR = 0$ (erect), and with a negative burial ratio (elevated) all occur in a wide range of sizes. The only visible tendency is the elimination of both relatively high positive (> 0.2) and high negative (< −0.2) values in the group of very large specimens ($C > 27{,}000$ cm^3). High negative values indicating highly elevated specimens occur only among the smallest forms.

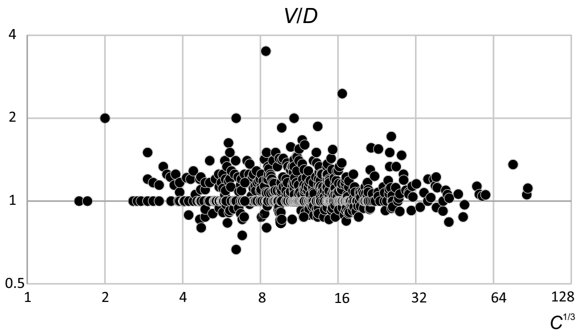
Initial surface. Stromatoporoids with all four distinguished types of initial surfaces occur in a very



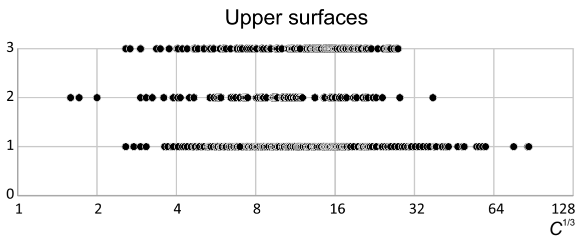
Text-fig. 16. Relation between stromatoporoid size and its burial ratio – *BR*. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale).



Text-fig. 17. Relation between stromatoporoid initial surfaces and their sizes. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale). Particular numbers are ascribed to particular distinguished initial surface categories; 1 – anchor, 2 – flat, 3 – initial elevation, 4 – incrustation.



Text-fig. 18. Relation between stromatoporoid sizes and upper surface curvature – *V/D*. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale).



Text-fig. 19. Relation between stromatoporoid upper surfaces and their sizes. The size on the x axis is represented by the cube root of the calculated capacity value – $C^{1/3}$ (logarithmic scale). Particular numbers are ascribed to particular distinguished upper surface combined categories; 1 – smooth upper surface with enveloping latilaminae arrangement, 2 – smooth upper surface with non-latilaminae arrangement, 3 – ragged upper surface.

wide range of sizes (Text-fig. 17). The biggest specimens are usually characterised by initial elevations or by flat initial surfaces, while the smallest measured specimens most commonly have an anchor. Encrusting forms, here treated as a separate category, are generally of relatively small sizes.

Upper surface curvature. The *V/D* ratio, which determines the upper surface curvature of the stromatoporoid skeleton, does not show any correlation with its size (Text-fig. 18). All categories (flattened, round and protuberant) occur in a very wide range of sizes.

Upper surface character and latilaminae arrangement. From among the three combined categories, distinguished based on the upper surface character and the latilaminae arrangement, the biggest capacities are obtained by the smooth/enveloping forms (Text-fig. 19). The non-enveloping and ragged varieties, although also occurring in a wide range of sizes are not present among the biggest specimens.

DISCUSSION

The studied sample embraces specimens measured at a number of localities representing various depositional environments in which the stromatoporoids grew. These include bioherms, auto-, autopara- and parabiostromes (*sensu* Kershaw 1994), intercalated within deposits representing environments ranging from deeper shelf to peritidal, and from agitated open shelf waters, through shoals, to calm, restricted lagoons (see Appendix 1 – List of localities). The studied material comes from two main stratigraphic horizons and palaeogeographical settings – the Frasnian of the Holy Cross Mountains in Poland and the Ludlow and Pridoli of the Podolia region in Ukraine. Thanks to combining the material from all these localities, a large data set has been created (>700 measured specimens), embracing a diversified array of stromatoporoid shapes and other morphometric features. By no means, however, can this group be treated as representing all possible varieties existing among all mid-Palaeozoic stromatoporoids, or as reflecting general quantity proportions between groups characterised by particular features.

All available complete specimens as exposed in suitable vertical crosscuts were analysed. These comprised both *in situ* and redeposited specimens. The two-dimensional insight into a three-dimensional structure, such as a stromatoporoid skeleton, can never actually reflect its whole complexity. Therefore, only in the case of specimens that were extracted from the rocks, can their shapes be unambiguously determined (for discussion on the credibility of measurements made in a two-dimensional cross-section and their comparability to the data obtained when studying three-dimensional specimens see Łuczyński 2008). However, most stromatoporoids (studied here and generally) come from solid limestones and dolomites of reef and adjacent fore- and back-reef facies, from which they cannot be easily extracted (see e.g., Stearn 2010c). Therefore, only two-dimensional stromatoporoid morphometric data can be easily collected in field and only such a method enables the gathering of large data sets, as in this study.

It needs to be stressed that analysed here is not a statistically controlled random sample, such as received e.g., by point counting (compare Sandström 1998; Edinger *et al.* 2002; Cole *et al.* 2015). In the present study, all specimens from particular localities suitable for observations and measurements were taken into account. This is yet another reason why the results obtained, in terms of the proportions between particular groups characterised by given features, cannot be treated as representative for the studied localities, time intervals, populations, etc. Therefore, the sole aspect analysed here consists of the interrelations between particular parameters, ratios and descriptive features, and not the differences between various species (undetermined here) or between localities representing various environments. The studied sample is big enough for most of the various distinguished categories to be represented by a sufficient number of specimens to be analysed quantitatively. The few exceptions are the laminar shape of the skeleton and that of the final growth form (analysed together with the low domical shape), the shape of encrusting forms when considering the type of initial surface (analysed together with the initial elevation variety), and some of the categories describing the inclination and convexity of the upper surface and sides (usually dominated by a single variety).

Main environmental factors influencing stromatoporoid growth

As noticed e.g., by Stearn (2010a), stromatoporoids secreting a basal skeleton share the same array of growth forms with many other reef-building clonal organisms, which suggests that the growth controls were probably governed by similar agents. Among the main controlling factors are: character and rate of deposition, water turbulence and substrate consistency. All these factors are interrelated with each other, and it is commonly impossible to discern the impact of any particular one of them. In the case of photosensitively acting corals and sponges, light dependence is another important issue. It is, however, still not clear whether stromatoporoids acted photosensitively, although some of their features, such as changes of stromatoporoid growth axes inhabiting inclined surfaces towards vertical (Łuczyński 2009), fast growth and general shallowness of habitats suggest so (Brunton and Dixon 1994; Kershaw and Brunton 1999). Stearn (2010b) on one hand argues that Palaeozoic stromatoporoids must have been mixotrophs (organisms whose metabolism is based partly on digestion and partly on photosynthesis), but on the other hand points out that, unlike corals, they probably did not compete for light in the way corals did and do, which can be deduced e.g., from the generally low proportion of encrusting forms (observed also in the localities studied herein). Stromatoporoid accumulations did not construct a rigid framework even if they are composed of densely spaced specimens, and form "cluster reefs" (*sensu* Riding 1990), or level bottom communities.

Photosensitive or not, stromatoporoids were filtrators, and thus, very much as in the similar situation of modern sponges, their pores were vulnerable to clogging by tiny sediment particles (Kershaw 2012). In spite of that, they commonly grew on muddy bottoms. Therefore, one of the main roles of the basal skeleton was lifting the living soft tissue not only above the sediment surface itself, but also above the lowest part of the water column with cloudy and muddy bottom waters. Such a turbid bottom zone occurred e.g., after storms that stirred the loose fine bottom sediment. The morphometric features of the studied stromatoporoids indicate the importance of both these roles of the basal skeleton.

Much attention in this study has been paid to the shapes of the stromatoporoids' upper surfaces. Apart from the smooth or ragged surface character and the enveloping or non-enveloping latilaminae arrangement, which allow the determination of the general relation between the shape of the whole skeleton and that of the living surface profile, a number of new calculated parameters (ratios) have been designed, reflecting particular aspects of the upper surface outline (Text-fig. 4). This includes the upper surface curvature (V/D), the inclination of sides ($\frac{1}{2}B/DB$), the shape of sides (X/D) and the upper surface convexity (V/DV). The dominant characteristics of these ratios point out that getting rid of tiny sediment particles, which could clog the inhaling pores, was probably a very important factor governing the stromatoporoid shape.

The curvature of the living surface profile (V/D) is the most diversely occurring feature describing the outline of the upper surface, as indicated by the common existence of protuberant and round forms, accompanied by flattened varieties (Table 3). Two other of the calculated ratios mentioned above are distinctly dominated by a single category, regardless of the stromatoporoid's sizes, shapes or any other morphometric features taken into account here. Almost 95% of all measured specimens have convex sides ($D > X$), and almost 90% have a convex upper surface ($V > DV$; Table 3). Both of these features facilitated the discarding of fine material from the stromatoporoid's upper surface inhabited by living soft tissue. The existence of a convex upper surface indicates lack of concavities, in which fine deposits could accumulate, whereas convex sides enhanced the falling down of sediment particles. Such accumulations on the stromatoporoid's upper surfaces interrupted the growth of the living tissue, and if they existed they are preserved as sediment increments and internal banding interruptions, and are most common in large flat forms (Broadhurst 1966; Young and Kershaw 2005). Significant is the fact that convex upper surfaces or sides are much less common than overhangs, as indicated by the inclination of sides ratio (½*B*/*DB*). This suggests that these features are a response to the necessity of discarding fine sediment rather than an indication of phototrophy. The existence of bulbous forms with overhangs and with an enveloping latilaminae arrangement (Table 4) points to growth of the living tissue also on the shadowed lower sides of the skeletons.

Much easier to determine than the above discussed influence of tiny particles suspended in the bottom waters, is the impact on the stromatoporoid skeleton of the rate and character of deposition taking place around the specimen. The parameter designed to illustrate the position of the stromatoporoid's upper surface inhabited by the living soft tissue in relation to the accumulating sediment is the burial ratio (Łuczyński 2006). From among the three distinguished categories, the partly buried specimens constitute the most numerous group (Table 3, Text-fig. 8). However, erect and even elevated varieties are also common. Partial burial is of course characteristic for stromatoporoids with a non-enveloping latilaminae arrangement in both smooth and ragged varieties of the upper surface. However, the burial ratio, calculated according to the applied formula ($BR = (V-V^*)/V$) may adopt positive values also in the case of specimens with enveloping latilaminae.

Comparison of shape profiles of the whole skeletons and of the final growth forms shows surprisingly small differences if the whole studied group is taken into account (Text-fig. 5). Of course, there is a visible shift in the proportion of *B* value curves (Text-fig. 9) towards higher profiles (lower %B^* values) among elevated specimens, and towards lower profiles (higher %B^* values) among partly buried stromatoporoids, when final growth forms are compared with the whole skeletons' (*B* values). One could expect a bigger difference, as it is the final growth form which experienced a direct relation with the environment, whereas the shape of the skeleton is a composite effect of juxtaposed consecutive growth stages. Moreover, the calculated burial ratios, indicating how large a part of the skeleton protruded over the sediment surface in the final stage of the specimens' growth, very rarely adopts values close to 1, which would indicate almost total burial (Text-fig. 16). The highest calculated burial ratio value is 0.83 (mean 0.19; Table 2). The final growth forms appear to pertain a substantial elevation above the sediment surface, as is indicated by the vertical height – V^* values (Text-fig. 5D). Mean V^* value for the whole studied population equals 8.48, and more than half of the specimens (381) have V^* values between 3 and 8 (Text-fig. 9C).

All the above observations suggest that in most cases it was not the burial by sediment that was the direct cause of stromatoporoid growth termination. The specimens usually distinctly protruded above the sea floor even in the final stage of their growth, i.e., just prior to their death. Therefore, most probably clogging of the pores has to be considered as the main environmental stress factor ceasing stromatoporoid growth. The muddy carbonate bottoms in shallow waters were typical stromatoporoid habitats (e.g., Kershaw 1984; Kershaw *et al.* 2006, 2018). Temporal agitation of fine loose sediments, caused e.g., by storms, suspended small particles, and created a cloudy turbid bottom water layer. After falling down from suspension, the particles clogged the pores and foreclosed growth of the soft tissue. Convex shapes of the upper surface and maintenance of a minimal vertical dimension of the living surface profile during stromatoporoid growth are responses to such stress. The same may be deduced from the occurrence of specimens with a smooth upper surface but a non-enveloping latilaminae arrangement (see Kershaw 2012), which are most common among very high profile forms (highly extended domical and high bulbous; Table 4). In such cases, the limitation of skeleton secretion to its highest parts was not caused by burial under sediments, but was related to growth only on the area which protruded above the cloudy turbid water layer. According to Webby and Kershaw (2011), the smooth varieties are characterised by distinctly steeper lateral ends of latilaminae than their ragged counterparts, which facilitated sediment removal. Such forms enjoyed clear waters, but were very vulnerable to redeposition, in contrast to specimens with ragged margins, in which the living tissue was located in direct contact with the sediment, but which maintained a more stable position (James and Bourque 1992).

The character and rate of sediment accumulation are generally considered the most important environmental factors influencing stromatoporoid shape (e.g., Kershaw 1994, 1998; Łuczyński 2006, 2008; Webby and Kershaw 2011). The arguments presented above suggest that burial by sediments was not the main factor terminating stromatoporoid growth, nonetheless the necessity of keeping pace with the elevating surface of the sea bottom influenced the final shapes of the stromatoporoid skeletons. This is best reflected when various proportions of *B* value curves, illustrating the shape profiles of smooth, ragged, enveloping and non-enveloping varieties, are compared (Text-figs 6 and 7). Whereas, in the case of the whole skeletons, the curves show similar general outlines (Text-fig. 6B), the differences in final growth forms are very evident (Text-fig 6C). The biggest differences between the skeleton shape and the growth form occur among ragged and non-enveloping specimens (Text-fig. 7), which confirms the necessity of discerning between the two when analysing stromatoporoid shapes in terms of palaeoenvironmental reconstructions (Łuczyński 2006).

Various stromatoporoid responses to different substrate consistencies, including muddy bottoms, are reflected by the variability of initial surfaces. From among the distinguished categories, the initial elevation encrusting varieties ensured elevating the living soft tissue above the sediment surface, and possibly also above the bottom zone of cloudy waters in the early stages of the specimen's growth. In an opposite manner, stromatoporoids characterised by an anchor enjoyed better stabilization and thus resistance to redeposition.

In the studied group, specimens characterised by different types of initial surfaces adopted different shapes (Text-figs 10 and 11). The most distinct feature in this matter is the domination of very high profile forms among those stromatoporoids with an anchor. These two features clearly matched – 67% of anchored specimens have the *V*/*B* ratio exceeding 1, whereas in all other categories the proportion is around 25%. The anchor assured stabilisation in the sediment and thus allowed undisturbed growth upwards to reach the clear waters above the bottom turbid zone, in which the danger of clogging occurred. In an opposite way the same goals were achieved in the case of specimens with an initial elevation (and encrusting). Starting growth on an elevation provided sufficient initial height to lift the living tissue above the muddy turbid zone, but made the stromatoporoid very vulnerable to overturning and redeposition, which resulted in the skeleton's lateral expansion and thus adoption of generally lower shapes (preferably high domical). Forms with a flat base adopted a widest range of shapes, but what differentiates them from other groups is the domination of non-enveloping varieties (Text-fig. 12). In such case the living tissue was located low, at direct contact with the sediment surface, and was most prone to burial. There seems to be no correlation between the type of initial surface and the upper surface curvature (Text-fig. 13A), which indicated that in all initial surface groups, getting rid of sediment particles accumulating on the living tissue was equally important.

Allometric tendencies

The shape of a stromatoporoid skeleton commonly changes during its growth. Detailed reconstruction of the changing shape, reflecting ontogenic allometry of a stromatoporoid skeleton, can be done only by careful analysis of latilaminae arrangement, and by virtual removal of consecutive layers representing consecutive growth stages (Łuczyński 2006). It is, however, a very laborious and time consuming method, which is difficult to be applied for a big number of specimens. The latilaminar structure (existence of repeating growth bands separated by growth interruptions) is a dominant feature among stromatoporoids, and is usually considered to reflect annual banding (Gao and Copper 1997; Young and Kershaw 2005). However, there is still no univocal proof of such an interpretation (Stearn 2010b). Understanding the nature of latilaminae would allow the determination of the stromatoporoid growth rates, which in turn would allow better understanding of the relation between stromatoporoid growth and accumulation of sediments around it. Most authors (e.g., Meyer 1981; Gao and Copper 1997; Königshof and Kershaw 2006) estimate stromatoporoid growth between 1 and 3 mm/year. Kershaw (2012) noticed that in the Silurian and the Devonian, stromatoporoids successfully competed with corals, which probably implies that they grew in at least comparable rates. Relatively high growth rates, comparable to that of modern scleractinian corals, and completely different from that of modern hypercalcified sponges (compare Vacelet *et al.* 2010), can be inferred also from the very large sizes of some stromatoporoid specimens (Racki and Sobstel 2004).

Ontogenic allometric changes need to be analysed in relation to the specimen's age (ontogeny), which in the case of stromatoporoids arouses a number of questions. Firstly, there is a still finally unresolved, long lasting controversy whether a single stromatoporoid skeleton should be treated as an individual or as a colonial (modular or clonal) structure (for discussion see Stearn 2010a, b). The question is particularly unequivocal in the case of coalescence of closely growing specimens (Kershaw 1990; Łuczyński 2008). In spite of these controversies, in the present study all the analysed forms are treated as individuals. Secondly, if the latilaminae are not counted (and assumed to represent annual banding), the potential shape changes during growth can only be analysed in relation to the specimen's dimensions, and not against its age. Previously (Łuczyński 2003), the stromatoporoid shape profiles (V/B ratio) were plotted against the basal dimension – B. In the present study, the calculated skeleton overall capacity – C is considered to be a better measure of the specimen's size. However, due to possible growth rate variability between particular specimens in changing environmental conditions or between different species, the overall dimensions do not necessarily need to reflect the stromatoporoid's age in a simple linear relation. In such case, the shape changes described here need rather to be treated as size allometry rather than ontogenic.

Webby and Kershaw (2011) pointed out that stromatoporoids can maintain the same shape during the specimens growth or may change, and that these changes result from differentiation of growth rates in various parts of the skeleton. According to Stearn (1982), growth of the skeleton always started from one point, in which the larva settled, and proceeded in all directions on the sediment surface until limited by sediment or proximity of other organisms.

According to Kershaw (2012), stromatoporoids commonly started their growth as laminar forms, and later adopted domical shapes as the growth focused in the central part of the skeleton. The present studies do not support this observation. The graphs illustrating the relation between the shape profile of both the skeleton (V/B) and the final growth form (V^*/B^*), and the cube root of the calculated capacity values ($C^{1/3}$) show a weak tendency towards lower profiles together with size (Text-fig. 15). The tendency of gradual elimination of very high profile forms together with size is evident also in Text-fig. 14 showing capacities of specimens belonging to particular shape categories.

The described increasing domination of relatively low profile forms (low- and high domical) among larger specimens is most probably connected with their mechanical properties and lower vulnerability to overturning and redeposition. A stable position on a broad base allowed longer growth and thus the possibility of attaining bigger sizes, whereas the growth of very high profile forms with relatively small bases, such as very extended domical and bulbous, was interrupted much more easily. The stromatoporoid skeletons were probably relatively light prior to late cementation of calcite cements in their internal voids (Stearn and Pickett 1994), although Mistiaen (1994) estimated that their density was relatively highest (75%) in the Frasnian (one of the stratigraphical horizons, from which the studied specimens come). This lightness effected in the very common redeposition of stromatoporoids, which often form parabiostromal accumulations (e.g., Harrington 1987; Łuczyński *et al.* 2009, 2014). Redeposition of particular specimens is indicated i.a. by the occurrence of overturned forms, in which growth after transport continued in a different direction (Łuczyński 2006; Kershaw 2012).

Potential differences of particular stromatoporoid morphometric features according to the specimens' sizes were tested also for burial ratios (Text-fig. 16), initial surfaces (Text-fig. 17), upper surface curvatures (Text-fig. 18) and type of upper surface character and latilaminae arrangement (Text-fig. 19). In most cases, no tendencies have been noticed, which indicates that these features generally had little influence on stromatoporoid growth success. The only slight exceptions are the domination of specimens with smooth upper surfaces and enveloping latilaminae arrangements among the biggest skeletons (Text-fig. 19). Such a combination points to a slow deposition rate and calm water conditions that enabled long and undisturbed growth.

CONCLUSIONS

Stromatoporoids grew in interaction with the changing environment and sediment accumulation. It is usually impossible, and maybe even meaningless, to point out one single environmental factor responsible for the shape or other features of a particular specimen. Based on the assumption that latilaminae are annual growth bands (Young and Kershaw 2005), and that the average growth rate is in the order of few millimetres per year (Königshof and Kershaw 2006), it can be estimated that a typical stromatoporoid skeleton grew for several dozens of years, and in case of particularly big specimens (Racki and Sobstel 2004) even few hundred years or longer. Obviously, during such a time span the growth conditions could change several times, especially in such dynamic environments as the shallow fore- and back-barrier settings, which the stromatoporoids inhabited. The final shape and other features of a stromatoporoid skeleton record all these changes.

The presented study of macroscopic morphometric features of a large number of stromatoporoids and of the relations between particular attributes of the skeletons allows to present the following general conclusions:

- Field macroscopic studies and measurements of specimens seen in two-dimensional crosscuts are the most effective method of obtaining large amounts of stromatoporoid morphometric data that can further be interpreted in terms of environmental reconstructions.
- Stromatoporoids occur in a big variety of shapes and living surface profiles, and adopt a wide array of various macroscopic features. Most of the distinguished shapes and attributes are relatively common and occur in substantial numbers and in various combinations, with an important exception of the ratios designed to reflect the shape of the skeleton's upper surface (upper surface curvature, inclination of sides, shape of sides and upper surface convexity). Most of these ratios are distinctly predominated by convex variants, which indicates that surface concavity is a highly undesired feature among stromatoporoids.
- From among the various environmental factors terminating stromatoporoids' growth clogging of the pores by tiny suspended sediment particles in muddy bottom waters seems to be the most important. Upper surface convexity of a stromatoporoid skeleton is a response to this hazard. Common low burial ratios of final living surface profiles and the occurrence of specimens with a smooth upper surface but a non-enveloping latilaminae arrangement are other reflections of this phenomenon.
- The hazard of being buried by sediments during episodes of rapid deposition was another important factor influencing stromatoporoid morphometric features. Growth on initial elevations, high shapes and ragged margins are the most evident indications of such conditions.
- The susceptibility of living individuals to exhumation and redeposition was another important factor that strongly influenced stromatoporoid growth. The main morphometric features that allowed better resistance to such hazard were low shape profiles, high burial ratios and anchored initial surfaces.
- No direct arguments indicating photosensitivity of stromatoporoids can be deduced from the presented results. Competition for light, even if present, did not play a decisive role in governing stromatoporoid growth.
- The hitherto postulated allometric tendency among stromatoporoids of starting growth as laminar forms and later adopting consecutively higher profile shapes has not been confirmed here. On the contrary; a tendency of gradual elimination of very high profile forms together with stromatoporoid size has been observed.
- The final shape of a stromatoporoid skeleton is always an effect of a combination of various agents. Environmental factors influencing the specimens growth co-occurred at the same time or were important at different stages of its development.

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APPENDIX 1

List of localities

Kadzielnia Quarry. Abandoned quarry in Kielce town, Holy Cross Mountains, central Poland. Frasnian, Kadzielnia Limestone Member of the Kowala Formation (Szulczewski 1981; Narkiewicz *et al.* 1990; Łuczyński 1998b). Massive stromatoporoid-coral limestones forming a large organic buildup, however without a rigid framework (Szulczewski and Racki 1981; Bednarczyk *et al.* 1997), and therefore commonly described as a mud mound (or reef-mound) and interpreted as deposited in relatively calm waters and on a gentle slope (Łuczyński 2009). 25 specimens.

Karwów Quarry. Abandoned quarry in the easternmost part of the Holy Cross Mountains, central Poland. Frasnian (Godefroid and Racki 1990), Kadzielnia Limestone Member of the Kowala Formation (Łuczyński 1995, 1998b). Massive recrystallized dolomites with common stromatoporoids, which however did not construct a rigid framework, and thus are interpreted to represent a Kadzielnia-type reef mound grown in subturbulent zone, with fairly agitated waters (Łuczyński 1998b). 150 specimens.

Sitkówka-Kowala Quarry (northernmost part). Abandoned part of large conglomerate of quarries, Sitkówka, south of Kielce, Holy Cross Mountains, central Poland. Frasnian, Upper Sitkówka Beds of the Kowala Formation (Racki 1993). Varied facies representing a wave resistant reef rim and shoal domains, however the studied specimens come solely from micritic fossiliferous biostromal limestones representing a shallow water setting in a shoal domain with fairly agitated waters (Kaźmierczak 1971; Racki 1993). 87 specimens.

Bolechowice-Panek Quarry. Polished slabs exposed in public buildings of Warsaw (Muranów cinema, Palace of Culture and Science, the National Opera and the National Philharmonic) from an active quarry south of Kielce town, Holy Cross Mountains, central Poland. Frasnian, topmost Sitkówka Beds of the Kowala Formation (Racki 1993). Micritic fossiliferous biostromal limestones representing a shallow and relatively quiet water shoal domain neighbouring the Dyminy reef (Kaźmierczak 1971; Racki 1993). 151 specimens.

Zubravka Quarry. Active quarry south of Kam'janec Podil'skyj, Podolia, western Ukraine. Ludlow, Kovivka and Sokol Members of the Malynivtsy Formation (informal units; Predtechensky *et al.* 1983; Koren' *et al.* 1989). Various types of stromatoporoid-bearing biostromes representing shallow-water back-biohermal (lee) sides of shoals located at a considerable distance from shore (Skompski *et al.* 2008; Łuczyński *et al.* 2009). 125 specimens.

Kubachivka Quarry. Active quarry and natural exposures on the bank of Smotrich River, south of Kam'janec Podil'skyj, Podolia, western Ukraine. Ludlow, Kovivka and Sokol Members of the Malynivtsy Formation (informal units; Predtechensky *et al.* 1983; Koren' *et al.* 1989). Various types of stromatoporoid bearing biostromes representing shallow-water back-biohermal (lee) sides of shoals located at a considerable distance from shore (Skompski *et al.* 2008; Łuczyński *et al.* 2009). 112 specimens.

Podpilip'e. Natural exposures on the bank of Zbruch river, south of Skala Podil'ska, Podolia, western Ukraine. Pridoli, Varnytsya Member of the Skala Formation (informal units; Koren' *et al.* 1989) or upper part of the Rashkov suite (traditional local subdivision; Abushik *et al.* 1985). Stromatoporoid bearing parabiostromes forming intercalations within peritidal sediments deposited in lagoonal settings represented by limestones, marls and dolomites (Łuczyński *et al.* 2014). 55 specimens.

APPENDIX 2

Supplementary table

The supplementary table is provided only in the online version and provides all basic morphometric data of particular specimens studied. Only direct measurements and observations are presented, as all the specific artificial parameters designed to reflect various aspects of stromatoporoid morphometry can be calculated based on the provided data and the formulas given in text. Skeleton dimensions: *B* – basal length, *V* – vertical height, *D* – diagonal distance. Initial surface: *I* – initial elevation, *F* – flat, *A* – anchor, *E* – encrusting. Upper surface character: *R* – ragged, *S* – smooth, Latilaminae arrangement: *NE* – non enveloping, *E* – enveloping. Growth form dimensions: *B** – basal length, *V** – vertical height

No	*B*	*V*	*D*	Initial surface	Upper surface character	Latilaminae arrangement	*B**	*V**
1	20	12	13	I	R	NE	18	4
2	68	37	35	I	S	E	66	38
3	30	16	16	I	S	E	30	17
4	27	21	19	I	R	NE	14	13
5	61	43	38	F	S	E	60	41
6	20	12	12	F	S	E	18	8
7	28	14	13	F	S	E	24	12
8	14	4	4	F	S	E	14	4
9	13	8	7	I	S	E	13	9
10	20	13	11	I	S	E	18	14
11	28	11	11	F	S	E	28	11
12	17	10	8	F	S	E	16	8
13	23	3	3	F	S	E	23	3
14	21	4	4	F	S	E	20	4
15	15	3	3	F	S	E	15	3
16	54	26	31	I	S	E	52	28
17	61	50	48	I	S	E	54	48
18	32	16	17	I	S	E	30	17
19	35	11	11	I	S	E	34	13
20	52	24	24	A	S	E	50	16
21	14	9	8	I	S	E	14	10
22	46	2	2	F	S	E	46	2
23	20	15	15	F	R	NE	16	5
24	24	8	9	F	S	E	22	7
25	9	3	4	F	S	E	9	3
26	18	5	5	I	S	E	18	6
27	22	9	9	F	S	E	21	8
28	9	6	5	I	S	E	8	7
29	16	9	8	I	S	E	15	10
30	11	8	7	I	R	NE	10	2
31	29	11	11	I	S	E	27	11
32	9	2	3	F	S	E	8	2
33	53	23	25	F	S	E	49	21
34	17	8	7	F	S	E	17	8
35	28	11	10	F	S	NE	27	5
36	18	2	2	F	S	E	18	2
37	21	2	2	I	S	E	19	3
38	17	13	12	A	R	NE	17	8
39	60	12	12	F	S	E	57	11
40	19	14	13	F	S	NE	16	5
41	89	77	73	F	S	E	76	68
42	10	3	3	I	S	E	10	4
43	61	20	20	I	S	E	55	21

44	16	4	4	F	S	E	15	4
45	9	3	3	F	S	E	9	3
46	14	11	9	F	R	NE	12	4
47	14	9	8	I	R	NE	11	5
48	19	4	4	I	S	E	19	5
49	12	6	5	I	S	E	11	7
50	18	9	9	I	S	E	16	10
51	19	11	9	I	R	NE	14	3
52	16	5	5	F	S	E	15	5
53	21	11	11	F	R	NE	21	7
54	9	6	5	F	S	E	9	6
55	16	9	7	I	R	NE	13	5
56	13	6	6	I	S	E	11	8
57	6	5	5	I	S	E	6	6
58	3	4	3	F	S	E	3	3
59	10	6	6	I	S	E	9	7
60	14	9	8	I	R	NE	11	4
61	9	7	6	I	S	E	8	8
62	30	22	21	A	R	NE	23	9
63	13	8	8	A	S	E	13	6
64	22	2	2	F	S	E	20	2
65	33	15	15	F	R	NE	28	6
66	34	5	5	F	S	E	32	5
67	28	26	24	I	S	E	26	27
68	25	3	3	F	S	E	24	3
69	24	9	8	F	S	E	21	8
70	18	4	4	F	S	E	18	4
71	25	5	5	F	S	E	24	5
72	13	5	5	F	S	E	12	5
73	48	12	13	I	S	E	46	13
74	89	14	16	I	S	E	81	14
75	49	7	7	I	S	E	47	8
76	21	3	4	I	S	E	19	4
77	32	8	7	F	S	E	30	7
78	24	17	16	F	R	NE	20	9
79	9	4	4	F	S	E	9	4
80	20	6	7	F	S	E	20	6
81	32	9	9	I	S	E	30	10
82	20	9	7	I	S	E	17	11
83	13	6	6	I	S	E	11	8
84	11	4	5	I	S	E	11	6
85	8	3	3	I	S	E	7	4
86	38	18	17	F	S	E	32	16
87	24	12	11	F	S	NE	20	9
88	26	9	8	F	R	NE	15	4
89	17	9	8	F	R	NE	13	4
90	28	2	2	F	S	E	26	2
91	27	2	2	F	S	E	22	2
92	14	8	7	F	R	NE	12	3
93	5,5	4	5	A	S	E	5	2
94	44	3	3	F	S	E	38	3
95	9	8	6	I	S	E	9	9
96	13	2	2	F	S	E	12	2

97	21	7	6	F	S	E	20	6
98	21	4	4	F	S	E	17	3
99	70	11	9	F	S	E	66	10
100	31	3	3	F	S	E	27	3
101	46	15	13	I	S	E	45	15
102	11	2	2	F	S	E	10	2
103	28	7	6	F	S	E	26	7
104	37	17	16	I	S	E	35	17
105	25	14	13	I	R	NE	16	7
106	15	7	6	I	S	E	14	8
107	29	19	17	F	R	NE	21	8
108	14	5	5	A	S	E	13	2
109	30	9	8	F	S	E	28	9
110	16	15	14	I	S	E	16	16
111	25	5	5	I	S	E	23	5
112	14	3	3	I	S	E	12	4
113	11	7	6	I	S	E	10	9
114	20	5	4	I	S	E	18	7
115	10	6	6	F	S	E	10	6
116	22	6	4	F	S	E	21	6
117	16	3	3	F	S	E	14	3
118	12	8	7	F	R	NE	8	3
119	14	9	7	I	S	E	14	10
120	16	4	4	F	S	E	14	4
121	9	5	4	I	S	E	9	6
122	86	57	42	I	S	E	81	54
123	34	16	12	I	S	E	34	17
124	23	17	13	I	S	NE	20	11
125	55	18	19	I	S	E	54	19
126	71	40	38	F	S	E	67	38
127	10	4	4	I	S	E	10	5
128	13	7	6	I	S	E	13	8
129	7	7	6	A	S	E	7	4
130	12	9	9	A	S	E	12	6
131	24	7	7	F	S	E	22	7
132	11	6	7	I	S	E	10	7
133	19	3	3	F	S	E	18	3
134	24	13	12	I	R	NE	17	7
135	49	18	15	F	S	E	44	17
136	10	4	4	F	S	E	10	4
137	20	6	6	F	S	E	20	6
138	60	32	33	F	S	E	58	31
139	33	11	11	F	R	NE	30	6
140	21	4	4	F	S	E	20	4
141	54	19	17	I	S	E	50	19
142	36	30	28	I	S	E	30	30
143	113	49	44	I	S	E	103	48
144	31	30	29	I	S	E	29	30
145	62	19	18	I	S	E	56	20
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147	46	25	22	I	S	E	44	25
148	52	36	34	I	S	E	49	36
149	43	19	20	I	S	E	39	20

150	30	25	20	I	S	E	30	26
151	21	7	6	F	S	E	20	6
152	8	3	3	F	R	NE	7	1
153	8	3	3	F	S	E	8	3
154	9	5	4	F	R	NE	8	3
155	8	4	5	F	S	E	8	4
156	13	7	5	F	S	E	12	6
157	7	3	3	I	S	E	7	4
158	9	5	5	I	S	NE	7	4
159	10	6	5	I	S	NE	5	3
160	7	5	4	I	S	E	7	7
161	10	6	5	I	S	E	10	7
162	7	5	4	I	S	E	7	6
163	10	6	4	I	S	E	8	6
164	7	4	4	I	S	E	7	5
165	5	4	4	I	S	E	5	5
166	8	5	4	I	S	E	9	6
167	13	8	7	I	S	E	11	8
168	9	5	4	F	S	E	7	4
169	7	5	4	F	S	E	7	5
170	9	7	7	F	S	E	9	7
171	7	6	5	I	S	E	6	7
172	6	3	3	I	S	E	6	4
173	9	7	6	I	S	E	8	8
174	12	8	7	I	S	E	10	9
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176	13	7	6	I	S	E	10	8
177	9	6	5	I	S	E	8	7
178	6	5	4	I	S	E	6	6
179	12	7	6	I	S	E	10	8
180	6	5	4	I	S	E	6	7
181	6	6	4	I	S	E	6	7
182	13	9	7	I	S	E	12	11
183	9	10	7	I	S	NE	8	6
184	10	11	7	I	S	NE	9	7
185	8	11	9	I	S	NE	7	4
186	10	13	9	I	S	NE	9	8
187	9	14	10	I	S	NE	7	8
188	9	11	8	I	S	NE	5	5
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190	10	12	6	A	S	E	9	8
191	8	10	8	A	S	E	7	7
192	9	10	7	A	S	E	8	8
193	15	18	13	A	S	E	13	14
194	8	9	6	I	S	E	7	9
195	7	7	5	I	S	E	6	8
196	9	10	7	I	S	E	9	11
197	9	54	22	A	S	NE	8	12
198	14	20	15	I	S	NE	12	7
199	13	20	13	I	S	NE	11	10
200	10	15	11	I	S	NE	8	5
201	6	24	13	A	S	NE	5	6
202	14	15	11	I	S	NE	11	7

203	12	14	12	I	S	E	12	15
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205	13	14	11	I	S	E	13	15
206	14	15	12	I	S	E	13	15
207	13	14	10	I	S	E	11	14
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209	11	13	10	I	S	E	11	14
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212	14	22	16	F	S	E	13	21
213	9	16	11	I	S	E	9	17
214	9	17	11	I	S	NE	6	5
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216	7	8	7	I	S	E	7	8
217	8	12	9	I	S	E	7	12
218	10	12	9	I	S	E	9	14
219	8	8	7	A	S	E	7	6
220	4	15	16	A	S	E	5	12
221	3	15	15	I	S	NE	6	17
222	3	16	16	F	S	NE	5	15
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224	5	18	18	A	S	NE	7	11
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226	4	20	20	I	S	NE	5	12
227	4	17	18	F	S	NE	6	11
228	5	23	23	A	S	NE	5	5
229	6	19	20	A	S	E	8	14
230	5	15	15	A	S	NE	5	7
231	5	6	6	A	S	E	7	8
232	4	9	9	F	S	E	6	8
233	6	12	12	A	S	E	7	9
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236	6	11	11	A	S	E	6	8
237	3	8	8	A	S	E	6	6
238	13	2	2	I	S	E	13	3
239	9	2	2	I	R	NE	7	1
240	7	2	2	I	R	NE	6	1
241	10	3	4	I	R	NE	8	1
242	23	8	8	F	S	E	23	8
243	24	9	10	F	R	NE	18	4
244	8	3	3	I	S	E	8	4
245	8	3	3	F	R	NE	6	1
246	16	6	6	I	S	E	14	6
247	13	5	6	F	R	NE	11	2
248	15	6	6	F	R	NE	12	2
249	7	3	3	I	S	E	7	4
250	9	4	4	I	R	NE	5	1
251	20	9	8	I	R	NE	17	5
252	8	4	6	I	S	E	7	4
253	14	7	5	F	S	E	13	6
254	8	4	2	F	S	E	8	4
255	6	3	3	E	R	NE	5	1

256	6	3	3	I	S	E	5	4
257	8	4	4	I	S	E	7	5
258	12	6	6	E	R	NE	10	2
259	10	5	4	E	R	NE	7	1
260	17	9	9	E	R	NE	14	4
261	11	6	6	E	R	NE	8	4
262	14	8	8	I	S	E	14	9
263	7	4	4	E	R	NE	6	2
264	20	12	10	I	S	E	18	11
265	13	8	7	I	S	E	13	10
266	8	5	4	F	S	E	8	5
267	8	5	5	E	R	NE	7	2
268	22	14	16	E	R	NE	18	6
269	11	7	6	I	S	E	10	7
270	11	7	6	E	R	NE	7	3
271	9	6	6	E	R	NE	8	3
272	12	8	6	I	S	E	12	9
273	6	4	4	F	S	E	6	4
274	28	19	16	E	R	NE	21	11
275	10	7	7	E	R	NE	7	3
276	7	5	5	I	S	E	7	6
277	8	6	5	I	S	E	8	7
278	12	9	7	F	S	E	12	9
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282	5	4	4	F	S	E	5	4
283	15	12	11	F	S	E	14	12
284	5	4	4	E	R	NE	3	1
285	5	4	4	F	R	NE	4	1
286	5	4	4	I	R	NE	3	1
287	16	13	10	E	R	NE	10	5
288	16	13	13	F	S	E	15	13
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292	8	7	6	I	S	E	8	8
293	8	7	7	E	R	NE	5	3
294	10	9	8	I	S	E	10	11
295	26	24	14	F	R	NE	18	11
296	4	4	4	A	R	NE	4	2
297	7	7	5	E	R	NE	5	3
298	4	4	4	A	S	E	4	3
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300	4	4	4	I	R	NE	4	3
301	4	4	4	I	S	E	4	5
302	7	7	7	F	R	NE	6	2
303	6	6	5	E	R	NE	5	2
304	7	7	6	F	S	E	7	7
305	5	5	5	F	R	NE	4	3
306	15	16	14	I	S	E	14	17
307	14	15	12	E	R	NE	11	6
308	11	12	13	I	R	NE	10	8

309	6	7	5	E	R	NE	5	3
310	6	7	7	F	S	E	6	7
311	10	12	11	F	S	E	10	11
312	5	6	6	F	R	NE	4	2
313	10	12	11	F	S	E	10	12
314	14	17	16	E	R	NE	12	5
315	9	11	9	F	R	NE	9	7
316	7	9	7	F	S	E	7	9
317	3	4	3	F	R	NE	3	2
318	6	8	7	F	S	E	6	8
319	14	19	19	F	R	NE	12	10
320	13	18	18	I	R	NE	11	6
321	5	7	7	F	S	NE	5	4
322	12	17	15	E	R	NE	11	10
323	14	20	20	F	S	E	14	20
324	7	10	10	F	S	E	7	10
325	10	15	9	F	S	E	9	14
326	6	9	9	I	S	E	6	10
327	4	6	5	F	S	NE	4	4
328	4	6	5	F	S	NE	4	3
329	8	12	11	F	S	NE	7	8
330	4	6	7	F	R	NE	3	3
331	10	15	15	F	S	E	10	14
332	10	16	10	F	S	E	10	16
333	5	8	6	F	S	E	5	8
334	11	18	12	F	S	E	10	17
335	9	15	15	F	S	E	9	15
336	3	5	5	A	S	E	3	3
337	3	5	5	A	S	E	3	3
338	7	12	12	F	S	E	7	12
339	4	7	8	F	S	E	4	6
340	4	7	6	F	S	E	4	7
341	18	32	26	F	S	E	17	30
342	5	9	7	F	S	E	5	9
343	5	9	7	F	S	E	5	9
344	7	14	10	F	S	E	6	13
345	2	4	4	A	S	E	2	2
346	3	6	6	A	S	E	3	4
347	22	44	30	F	S	NE	20	13
348	6	13	11	F	S	E	6	13
349	4	9	9	F	R	NE	4	5
350	6	14	16	F	S	E	6	14
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352	4	10	10	F	S	E	4	10
353	4	10	8	F	R	NE	4	5
354	2	5	5	A	S	E	2	3
355	3	8	9	A	S	E	3	7
356	4	11	11	A	S	NE	4	8
357	5	14	14	F	S	NE	5	7
358	6	17	13	F	S	E	6	16
359	3	9	9	A	R	NE	3	3
360	2	6	6	A	R	NE	2	3
361	4	12	11	F	S	E	4	12

362	2	6	6	A	R	NE	2	2
363	2	6	5	A	S	E	2	4
364	2	6	4	A	S	NE	2	3
365	3	9	7	A	S	E	3	7
366	9	28	15	F	S	E	9	26
367	4	13	11	F	R	NE	4	6
368	4	13	8	F	R	NE	4	7
369	5	17	15	F	R	NE	5	12
370	2	7	6	A	S	E	2	5
371	2	7	7	A	S	NE	2	3
372	3	11	9	A	S	E	3	9
373	3	11	10	A	S	E	3	8
374	6	23	27	F	R	NE	6	9
375	2	8	7	A	S	NE	2	6
376	2	8	8	A	S	NE	3	7
377	1	4	4	A	S	NE	1	3
378	3	14	12	A	S	NE	3	11
379	8	39	31	F	R	NE	7	20
380	1	5	5	A	S	NE	1	3
381	2	10	8	A	R	NE	2	6
382	2	11	9	A	S	NE	2	7
383	3	18	16	A	R	NE	3	8
384	2	14	13	A	S	NE	2	5
385	2	14	12	A	S	NE	2	9
386	3	21	15	A	S	NE	3	14
387	1	8	4	A	R	NE	1	4
388	2	17	14	A	S	NE	2	11
389	31	2	2	F	S	E	31	2
390	27	2	2	F	S	E	27	2
391	26	2	2	F	S	E	25	2
392	19	2	2	F	S	NE	17	1
393	18	2	2	F	S	NE	12	1
394	16	2	2	F	S	NE	9	1
395	36	5	5	F	R	NE	15	1
396	27	4	4	F	S	E	27	4
397	13	2	2	F	S	E	13	2
398	65	12	10	F	S	NE	43	6
399	35	7	6	F	S	NE	27	4
400	24	5	5	F	S	E	22	5
401	4	1	1	F	R	NE	3	1
402	16	4	3	F	S	NE	12	2
403	10	3	3	F	R	NE	7	1
404	20	6	6	I	R	NE	16	5
405	10	3	3	I	R	NE	9	3
406	10	3	3	I	S	E	10	5
407	23	7	8	F	R	NE	17	4
408	16	5	5	I	R	NE	14	6
409	43	14	13	A	S	E	41	11
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411	21	7	6	I	R	NE	18	7
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413	36	12	9	F	S	E	35	12
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415	17	6	5	I	R	NE	14	6
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417	11	4	4	F	R	NE	11	2
418	19	7	8	I	R	NE	17	8
419	17	7	5	F	R	NE	15	5
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421	7	3	2	F	S	NE	6	1
422	23	10	11	I	S	NE	17	10
423	16	7	7	A	S	NE	14	3
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426	12	6	6	A	R	NE	10	4
427	18	9	8	I	R	NE	15	9
428	21	11	9	I	S	E	21	13
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430	11	6	5	I	S	E	11	7
431	18	10	7	F	S	E	18	10
432	7	4	4	A	R	NE	6	2
433	24	14	14	A	S	NE	17	5
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435	16	10	9	F	R	NE	14	7
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437	3	2	2	I	R	NE	2	2
438	18	12	12	I	S	E	18	15
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445	16	12	11	F	R	NE	13	7
446	21	16	15	I	R	NE	16	17
447	5	4	5	I	S	E	5	6
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453	7	6	5	A	R	NE	5	3
454	23	20	20	F	S	NE	19	14
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456	17	15	13	F	S	NE	14	11
457	11	10	9	I	S	NE	9	9
458	12	11	10	A	R	NE	10	6
459	16	15	14	I	S	E	16	17
460	16	15	14	A	S	NE	13	12
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463	4	4	4	A	S	E	4	3
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465	16	18	18	A	S	NE	14	15
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467	10	12	9	I	R	E	10	14

468	10	12	11	A	S	E	10	12
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470	21	26	25	A	S	NE	20	17
471	10	13	13	F	S	NE	8	7
472	12	16	17	A	S	E	12	12
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477	10	14	13	A	S	NE	8	6
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487	9	20	18	A	S	NE	8	7
488	7	16	16	A	S	NE	5	7
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493	3	9	9	A	S	NE	2	5
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495	6	23	21	I	S	NE	5	8
496	12	46	48	I	S	NE	16	17
497	3	14	10	A	S	NE	2	4
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506	24	17	16	I	S	E	24	18
507	26	13	13	I	S	E	16	15
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517	13	8	8	A	R	NE	12	3
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519	13	15	14	I	R	NE	10	5
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521	16	12	13	I	R	NE	16	9
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533	14	11	11	I	R	NE	12	10
534	19	14	14	F	S	E	19	14
535	21	12	12	F	S	E	21	12
536	18	12	12	I	R	NE	15	11
537	20	17	16	I	R	NE	17	12
538	11	10	10	F	R	NE	9	5
539	16,5	11	11	I	S	NE	14	6
540	16	7	8	F	R	NE	13	4
541	14	11	11	F	R	NE	11	9
542	17	13	14	I	S	E	17	15
543	17	7	6	I	R	NE	12	4
544	22	16	17	I	R	NE	16	12
545	6	6	6	I	S	E	7	8
546	6	5	5	F	R	N	6	3
547	7	6	5	I	S	E	7	7
548	16	27	25	F	R	NE	8	13
549	12	17	16	F	R	NE	10	14
550	14	17	18	F	R	NE	14	11
551	14	17	16	F	R	NE	13	9
552	13	28	24	I	R	NE	10	12
553	12	14	15	I	R	NE	13	9
554	13	12	12	I	R	NE	13	10
555	6	6	6	I	S	E	6	8
556	5	5	5	I	S	E	6	6
557	8	6	6	A	S	E	8	4
558	17	20	20	F	R	NE	15	14
559	17	19	19	F	R	NE	18	7
560	15	19	17	F	R	NE	14	13
561	20	21	21	F	R	NE	19	14
562	14	16	17	F	R	NE	11	9
563	11	18	16	F	S	E	11	18
564	19	16	16	F	S	E	19	16
565	17	17	17	F	S	E	17	17
566	14	19	16	F	S	E	14	18
567	13	13	13	A	R	NE	11	5
568	13	16	15	I	R	NE	6	5
569	11	14	14	F	R	NE	9	11
570	20	20	20	A	R	NE	7	11
571	15	19	19	A	S	E	15	16
572	16	14	14	I	S	E	16	16
573	20	14	14	I	S	E	20	16

574	12	13	13	I	S	E	12	14
575	11	14	15	I	S	E	11	16
576	4	6	6	I	S	E	4	7
577	4	5	5	I	S	E	4	7
578	18	9	8	F	R	NE	15	6
579	19	8	6	F	R	NE	14	5
580	25	8	8	F	R	NE	17	4
581	21	10	10	I	R	NE	13	7
582	23	12	12	I	S	E	23	14
583	21	11	11	I	R	NE	15	7
584	14	10	10	I	R	NE	12	7
585	19	10	10	I	R	NE	16	8
586	17	9	8	I	R	NE	12	5
587	17	10	10	I	R	NE	13	4
588	14	10	10	I	S	E	14	11
589	14	8	8	I	S	NE	10	5
590	21	13	13	I	R	NE	18	11
591	24	12	12	F	R	NE	17	7
592	17	11	9	F	R	NE	13	6
593	19	13	13	F	S	E	19	13
594	16	9	9	A	R	NE	14	6
595	17	8	8	A	R	NE	13	5
596	13	9	9	A	R	NE	11	7
597	14	9	9	F	R	NE	11	8
598	20	9	9	F	R	NE	11	3
599	11	8	8	I	S	E	11	10
600	13	7	6	I	R	NE	11	5
601	21	11	12	I	R	NE	16	7
602	24	10	10	I	R	NE	19	7
603	16	10	10	I	R	NE	14	6
604	17	7	6	F	R	NE	14	5
605	15	9	9	I	R	NE	10	2
606	18	9	8	I	S	E	18	11
607	18	10	10	I	S	E	18	11
608	16	11	11	I	S	E	17	13
609	15	7	7	F	S	E	15	7
610	19	9	9	F	S	NE	15	4
611	17	12	12	F	S	NE	11	8
612	14	7	7	I	S	E	14	9
613	17	10	9	I	S	E	17	11
614	19	9	9	I	R	NE	16	7
615	21	4	4	I	R	NE	17	3
616	19	3	3	I	R	NE	14	2
617	16	2	2	F	S	E	16	2
618	24	6	5	F	R	NE	16	4
619	28	5	5	F	R	NE	21	3
620	14	4	4	F	R	NE	22	3
621	22	5	5	F	R	NE	8	3
622	21	4	4	F	R	NE	16	2
623	17	3	3	F	S	NE	14	2
624	12	4	4	F	R	NE	10	2
625	19	3	3	F	R	NE	11	1
626	16	9	10	F	S	NE	12	4

627	12	6	7	F	S	E	12	6
628	18	7	8	F	S	E	18	7
629	17	11	11	F	S	E	17	11
630	7	15	10	I	S	E	7	17
631	14	5	5	F	S	E	14	5
632	8	14	12	I	S	E	8	15
633	13	8	8	I	S	E	13	10
634	24	11	12	I	S	NE	21	9
635	14	8	8	F	S	E	14	8
636	14	8	7	F	S	E	14	8
637	28	11	11	F	S	E	28	11
638	9	11	9	F	S	E	9	11
639	10	6	6	F	S	E	10	6
640	14	10	10	F	S	E	14	10
641	13	15	12	F	S	E	13	15
642	12	8	8	F	S	E	12	8
643	10	9	8	A	S	E	10	7
644	5	2	2	I	R	NE	4	2
645	4	2	2	I	R	NE	3	2
646	18	9	9	F	S	E	18	9
647	6	3	3	I	R	NE	4	2
648	17	7	7	F	S	E	17	7
649	21	11	13	F	S	E	21	11
650	22	11	11	F	S	E	22	11
651	20	11	11	F	S	E	20	11
652	9	13	12	F	S	NE	7	7
653	9	15	13	A	S	NE	7	8
654	9	12	10	A	S	NE	6	5
655	17	12	12	F	S	E	17	12
656	26	17	11	F	S	E	26	17
657	11	8	7	I	S	E	11	10
658	27	31	26	I	S	E	27	26
659	6	2	2	F	R	NE	4	1
660	5	4	4	A	R	NE	4	1
661	22	16	15	I	S	E	22	17
662	22	12	11	I	S	E	22	14
663	18	22	23	A	S	E	18	19
664	36	36	35	A	S	E	36	33
665	30	17	16	I	S	E	30	19
666	14	10	9	A	S	E	14	8
667	16	7	7	F	S	E	16	7
668	24	4	4	F	S	NE	17	3
669	18	9	9	I	S	E	18	10
670	21	18	18	I	S	E	21	20
671	8	4	4	F	S	NE	5	3
672	8	6	5	F	S	E	8	6
673	4	7	7	A	S	E	7	5
674	9	4	4	I	S	E	9	5
675	4	3	3	I	S	E	4	5
676	6	2	2	F	S	E	6	2
677	6	3	3	I	S	E	6	4
678	7	3	3	F	S	E	7	3
679	8	3	2	A	S	E	8	2

680	14	1	1	F	S	E	14	1
681	45	5	5	F	R	NE	35	4
682	34	6	6	F	R	NE	26	3
683	38	11	11	F	R	NE	24	4
684	19	8	8	F	R	E	19	8
685	41	10	10	F	R	NE	35	6
686	39	11	11	F	R	NE	33	7
687	44	10	10	F	R	NE	24	5
688	23	9	9	F	R	NE	18	6
689	31	8	8	F	R	NE	26	5
690	36	7	7	F	S	E	36	7
691	43	11	12	F	R	NE	32	6
692	20	8	8	I	R	NE	17	7
693	15	5	5	I	R	NE	11	2
694	17	5	5	I	R	NE	14	3
695	27	7	7	I	R	NE	21	4
696	22	19	12	I	S	E	22	22
697	14	8	7	I	S	E	14	10
698	18	9	9	I	R	NE	15	5
699	33	26	23	I	S	E	33	27
700	20	12	12	I	R	NE	15	9
701	23	16	15	F	S	E	23	16
702	31	19	17	F	S	NE	24	14
703	27	18	16	F	S	E	17	18
704	19	10	9	A	R	NE	16	4
705	49	29	26	A	S	E	49	27