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# Intraspecific variation in the genus *Stelidioseris* (family Actinastraeidae, suborder Archeocaeniina, order Scleractinia; Jurassic-Cretaceous)

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**ABSTRACT.** The genus *Stelidioseris* (= *Actinastrea* s.l.) is one of the most common genera in the Late Jurassic and Early Cretaceous and has a high number of species. Species separation is generally based on calicular dimensions, septal symmetry, and septal number. To obtain better insight into intraspecific variation and results for species separation, systematic measurements of the corals were taken and statistically analysed. As a preliminary study, ten type specimens were selected for analysis. In thin sections a large number of calices (up to 200) were measured, including their diameter, distance and the thickness of the wall and coenosteum. For all values, the arithmetic mean, standard deviation and the coefficient of variation were calculated. In *Stelidioseris*, the calicular diameter is the character with the lowest variation. The distance of the calicular centres, the thickness of the wall, and the number of calices per a given area show a much higher variation and are therefore less suitable for distinguishing samples within a population or species of different faunas. It was found that about 70% of all values of the lumen diameter fall in the first interval (range of the arithmetic mean ± standard deviation). Hence, the first interval is a good representation for most types of measured values in fossil corals. The results are compared to traditional methods by remeasuring published material. It is concluded that the application of systematic measuring should be extended to other species rich coral genera.

**KEYWORDS:** Corals, statistics.

## 1. Introduction

The Late Jurassic to Cretaceous *Stelidioseris* Tomes, 1893 (= *Actinastrea* s.l., see Löser, 2012) belongs to the most common genera in the Late Jurassic and Early Cretaceous. The large number of 120 described species (Löser, 2012) reflects the abundance of the genus in the fossil record. Most species were established on the base of complete unsectionned specimens and / or without proper comparison to existing species. *Stelidioseris* taxa are generally distinguished by their calicular dimensions and the number of septal systems and septal cycles. To handle the high number of taxa and to create a base for a revision of the genus, type material of ten species has been systematically examined. Various statistical methods were applied to understand the variation of the calicular dimensions within individual colonies and obtain a better idea about the limits of species.

## 2. Abbreviations

BGS, The British Geological Survey, Keyworth (England);
ERNO, Instituto de Geología, Estación Regional de Noroeste, Universidad Nacional Autónoma de México, Hermosillo

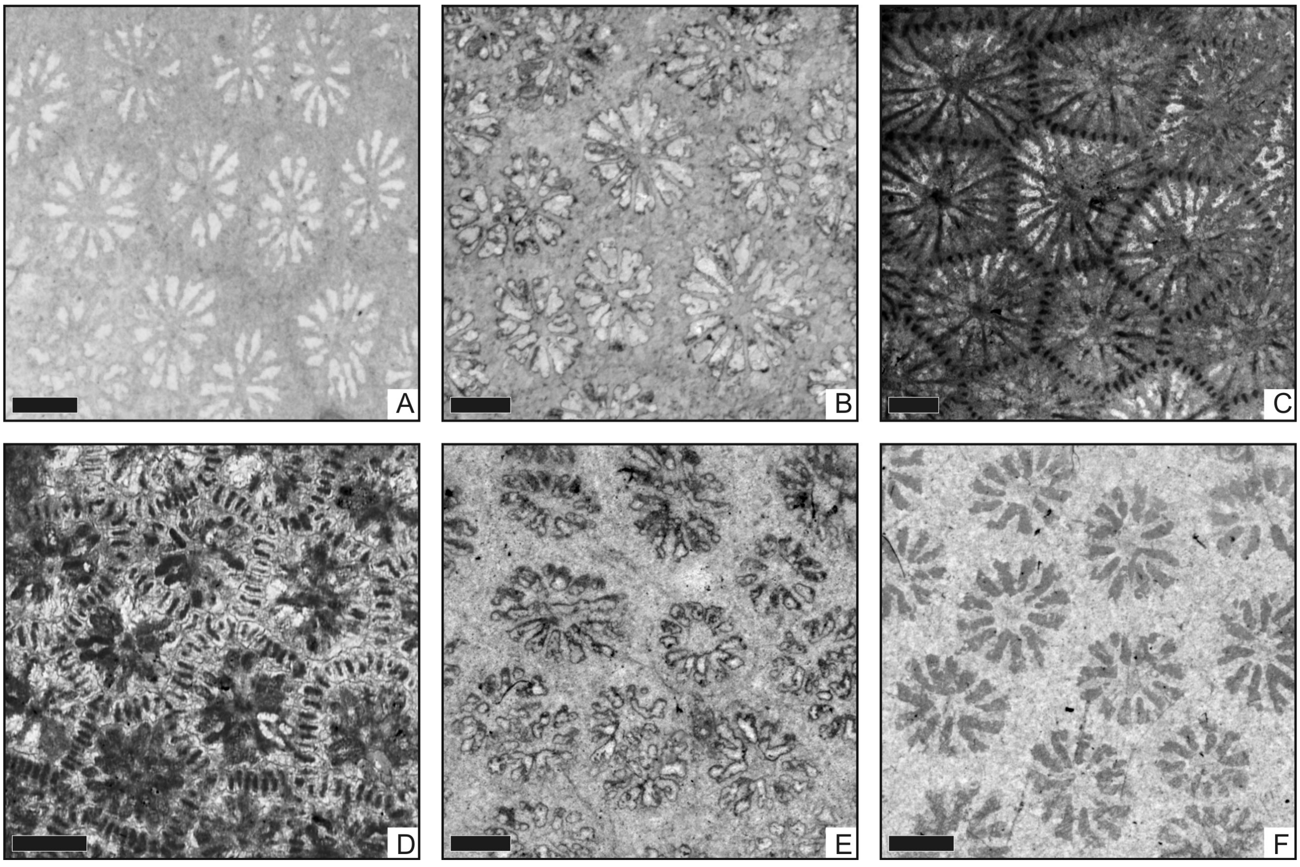


**Figure 1**. A: *Astrocoenia bernensis explanata* Dietrich, 1926, holotype MB K1330, thin section. B: *Astrocoenia bernensis sphaeroidalis* Dietrich, 1926, lectotype MB K1328, thin section. C: *Thamnasteria harrisoni* Gregory, 1927, lectotype GLAHM C4140, thin section. D: *Astrocoenia japonica* Eguchi, 1951, lectotype TUM 56502, thin section. E: *Holocoenia polymorpha* Prever, 1909, lectotype PU 18062, acetate peel. F: *Astrea ruvida* Prever, 1909, holotype PU 17933, acetate peel. Scale 1 mm.

(Mexico);
GLAHM, Hunterian Museum, Glasgow (England);
MB, Museum für Naturkunde der Humboldt-Universität Berlin (Germany);
PU, Museo di Geologia e Paleontologia dell‘ Università di Torino (Italy);
TUM, Tohoky University Museum, Sendai (Japan);
UJ, Jagiellonian University, Instytut Nauk Geologicznych, Kraków (Poland).

## 3. Material

Numerous *Stelidioseris* samples were examined in preparation of this study. The following ten type specimens of *Stelidioseris* species were selected for detailed examination to demonstrate the methods:

- *Astrocoenia bernensis explanata* Dietrich, 1926, holotype (by monotypy) MB K1330 (Fig.1A);
- *Astrocoenia bernensis sphaeroidalis* Dietrich, 1926, lectotype (here designated) MB K1328 (Fig.1B);
- *Stelidioseris gibbosa* Tomes, 1893, lectotype (by subsequent designation) BGS 5161;
- *Thamnasteria harrisoni* Gregory, 1927, lectotype (here designated) GLAHM C4140 (Fig.1C);
- *Astrocoenia japonica* Eguchi, 1951, lectotype (here designated) TUM 56502 (Fig.1D);
- *Actinastrea minima irregularis* Morycowa, 1964, holotype (by original designation) UJ 4P7#1;
- *Columastrea paucipaliformis* Baron-Szabo & González-León, 1999, holotype (by original designation) ERNO 2153;
- *Holocoenia polymorpha* Prever, 1909, lectotype (here designated) PU 18062 (Fig.1E);
- *Astrea ruvida* Prever, 1909, holotype (by monotypy) PU 17933 (Fig.1F);
- *Astrocoenia tendagurensis* Dietrich, 1926, (lectotype by subsequent designation) MB K1337.

## 4. Methods

The distinction of species in Mesozoic scleractinian corals is almost entirely based on (1) dimensions of the corallites, distance of corallites, and width of calicular rows in meandrinoid corals, respectively, (2) the number of regular septal systems (if present), and (3) the number and/or density of septa. Corallite dimensions indicated in the literature, or their ranges between a lower and an upper value, are generally not based on statistically significant measurements. While skeletal dimensions are indispensable for species determination, almost nothing is known about the variation of these dimensions within single colonies, species or populations of Mesozoic corals apart from a few empiric studies (Lathuilière, 1988, 1990; Lathuilière & Gill, 1998; Pandey et al., 1999) on mainly Jurassic corals. In contrast to Tertiary corals where systematic measurements of skeletal dimensions serve as an important tool for understanding taxonomy, phenotypic plasticity and palaeoecology (for instance Budd Foster, 1979, 1980, 1983, 1984), the dimensions of the coral skeleton are generally not systematically measured in Mesozoic corals.

The Mesozoic coral genus *Stelidioseris* and its synonyms, which are the subject of this study, counts according to the literature with up to 120 species (Lathuilière, 1989; Löser, 2000; Löser, 2012). These species were established during the previous 150 years, based on different ideas and concepts. The species are generally distinguished by (1) calicular dimensions, (2) the number of septal systems and cycles, (3) number of septa, and (4) number of septa reaching the columella. Whereas septal systems and the number of septa remain relatively constant within one colony, the calicular dimensions (calicular diameter, distance and thickness of wall) vary within one colony. The knowledge about the ranges and variation of these dimensions and consequences for the separation of species is limited. For this reason, more attention is paid to skeletal dimensions in the framework of this study.

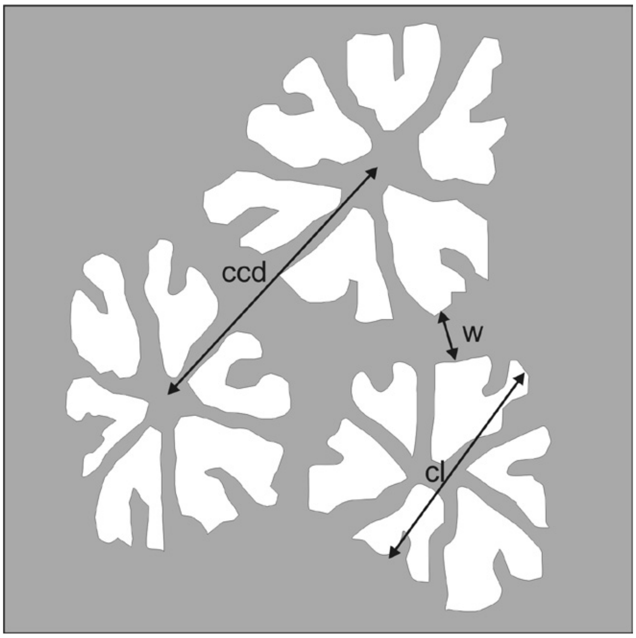


**Figure 2**. Schematic illustration showing how the calicular diameter (cl), distance (ccd) and wall thickness (w) values were measured.

To gain more insight into the intraspecific variation of genus *Stelidioseris* and to obtain a better strategy for separating species, selected thin sections and peels were systematically measured. The smaller calicular diameter (cl; inner calicular diameter), the distance between the four to five nearest calicular centres (ccd; from columella to columella) and wall thickness (w) were measured (Fig. 2). To achieve statistical significance, the largest number of possible measurements was taken. This number was mainly determined by the size and quality of the thin section. For each type of measurement (calicular diameter and distance, thickness of the walls) in one thin section the following values were obtained:

| | |
|---|---|
| n | number of measurements |
| $v_{min}$ | lowest measured value |
| $v_{max}$ | highest measured value |
| $\mu$ | arithmetic mean (average) |
| $\sigma$ | standard deviation |
| $v$ | coefficient of variation |

The coefficient of variation ($v$) according to K.Pearson (Weber, 1986) is calculated for all values to be able to compare the variability of the values cl, ccd and w. A low coefficient of variation indicates a lower variation of the values and makes them more suitable for the distinction of samples (species, populations). When there were more than 50 measurements, values were classified into ranges of 50µm or 100µm and converted into a graph to observe the distribution and asymmetry of the measured values. In addition to this, the number of calices per 25 square millimetres was counted for each thin section where possible. Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (version 1.2; http://www.paleotax.de/measure; Fig. 3).

Coral species in the fossil record are strictly morpho species that are separated on the basis of their respective calicular diameters, septal symmetry and number of septal cycles and/or septal density. The comparison of skeletal dimensions is up to now the only method to distinguish fossil species. Although some attention has been paid to intraspecific variation and a certain variation of measured values has always been admitted, there exists no quantification of this variation. In descriptions of Cretaceous corals, ranges are provided for the calicular diameter,

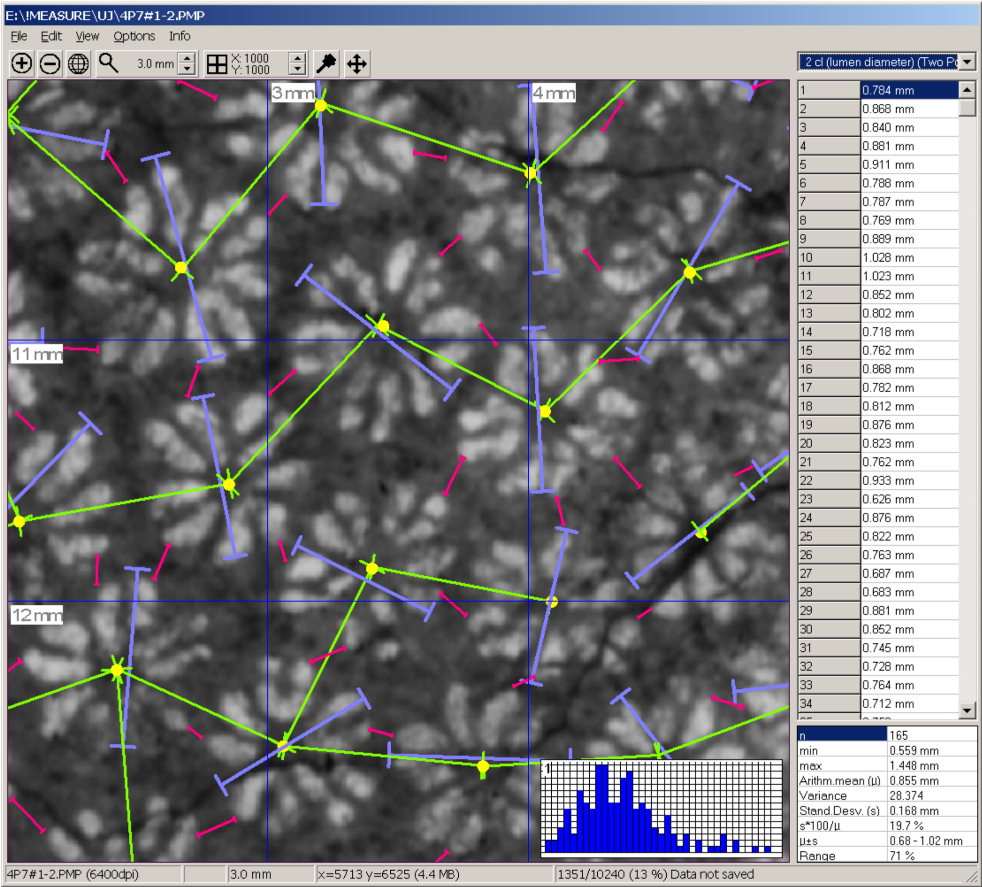


**Figure 3**. Screen shot of the program used to measure the dimensions of the corals (PaleoTax/Measure).

but it is not clear how these ranges are defined. Here, the ranges are defined as an interval of $\mu\pm\sigma$. It has been found - not only for corals but for all normally distributed values - that any observation is rarely more than a few standard deviations away from the mean (Chebyshev's inequality; Krengel, 2003). In the values observed here, about 70% of all values fit into the interval of two standard deviations ($\mu\pm\sigma$). This allows the calculation of ranges that (1) accurately reflect the measured values and (2) are comparable to values not obtained through systematic measurements.

## 5. Results

Table 1 gives for the measured samples the dimensions of the lumen diameter, the distance of the calices and the wall thickness, and the quantity of calices per 25 $mm^2$. In all specimens the calicular diameter (lumen) has the lowest variation, followed by the calicular distance and the thickness of the wall (after normalisation using the coefficient of variation $v$). The high standard deviation of the wall thickness corresponds to the high standard deviation of the calicular distance. These are correlated since the calicular distance corresponds to the sum of the values cl and w. The standard deviation of both the calicular distance and the thickness of the wall is low where the wall is thin and both are higher where the wall is thick. A thin wall can be a constant character within one colony, but in colonies where a thick wall is found, the thickness of the wall generally varies. Studies about intraspecific variation carried out on extant and Neogene corals with comparable morphology (Budd Foster, 1979, 1980, 1984) confirm that the wall thickness is a character that varies greatly depending on the palaeoecological conditions. The higher variation of the calicular distance is also shown by the different distribution of the calicular diameter and calicular distance for eight samples (Fig. 4).

## 6. Discussion

### *6.1. Variation through ontogenesis*

Varying calicular diameters are due to the ontogenesis of the individuals on the one hand and due to a certain variation, perhaps depending on the position in the colony and in relation to other individuals, on the other. Budding is mainly intracalicinal, which means that adult (large) calices divide into two or more new individuals whose calicular diameter is at first much smaller than that of the mother calice. Depending on the resulting number of new calices, these calices start with a diameter that can be very small to only slightly smaller than the average. The distribution of the calicular diameters in eight measured colonies (Fig. 4) shows that new calices relatively quickly reach the average calicular diameter, and the number of calices that are larger than average decrease with increasing diameter, because they obviously divide into new calices. All colonies show a positive skewness of the distribution of calicular diameter, so the maximum of counts in any class lies below the average.

### *6.2. Sample and species distinction*

For more than 200 years, Cretaceous corals have been described and illustrated and new genera and species created. Examination methods and ideas about what constitutes a species have changed over that time. During this period, new species have been erected based on different ideas, giving importance to different macromorphological or micromorphological features. When new species were established, already existing species were rarely considered under the specific aspects used to distinguish the new material. This procedure has produced a high number of synonymous species (from today's point of view). Another source of synonyms is that it is often easier to establish a new species than compare one's own material to all existing species of the same genus or species group (Lathuilière, 1988). The genus *Stelidioseris* is unfortunately a genus with - from today's point of view - a high number of species including many synonyms. As statistical analysis has shown, the separation of samples (populations, species) in *Stelidioseris* species should mainly be based on the dimension of the lumen in addition to the septal symmetry and number of septal cycles. The calicular distance shows a larger variation, which confirms the low importance of this value for the distinction of samples (populations, species). The density of calices per x square millimetres is controlled not only by the calicular diameter, but also by wall thickness and

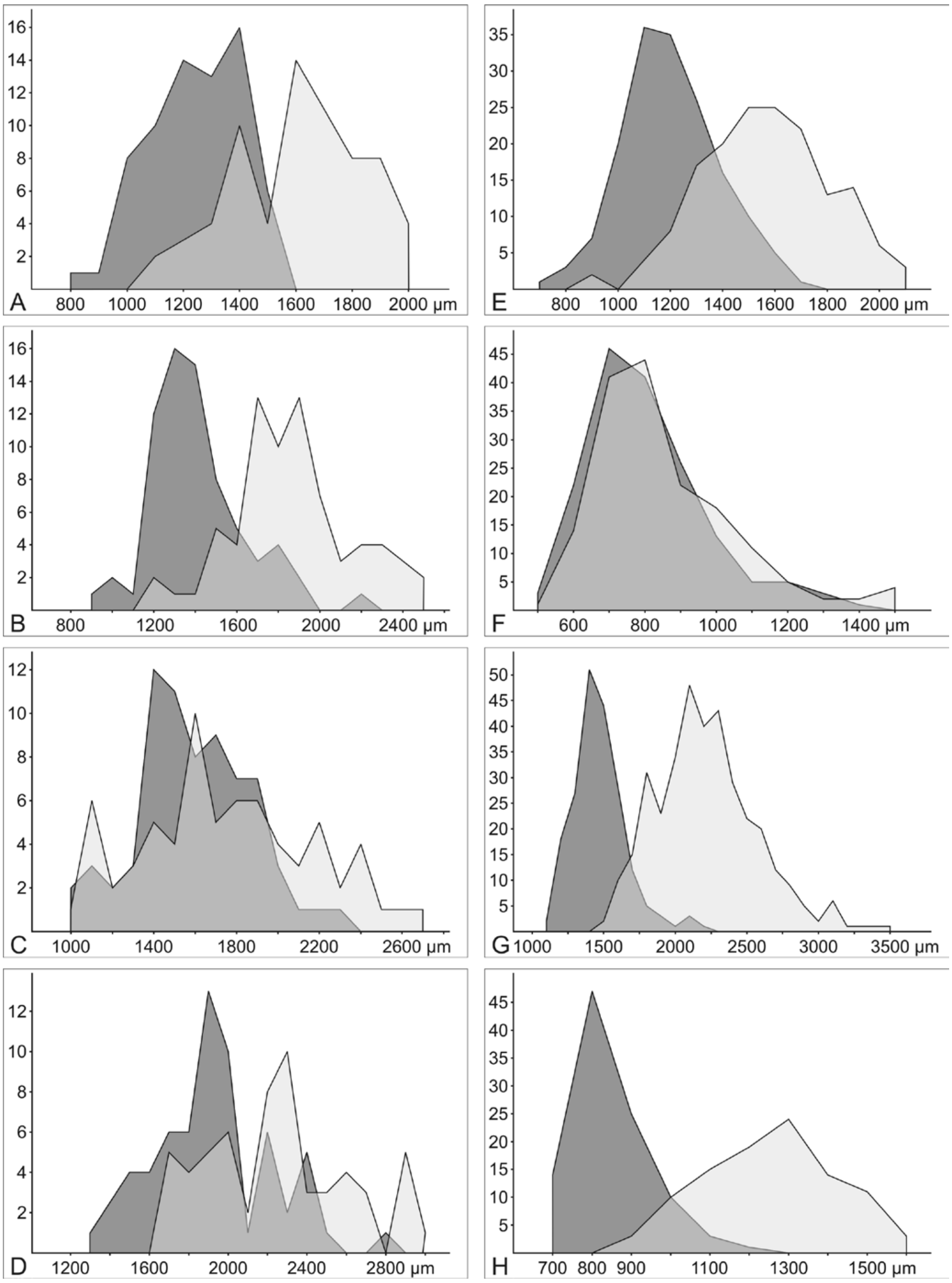


**Figure 4**. Distribution of the calicular diameters (dark grey) and distance (light grey) in eight *Stelidioseris* species. Size of classes is 100µm. A: MB K1330. B: MB K1328. C: BGS 5161. D: GLHAM C4140. E: TUM 56502. F: UJ 4P7#1. G: ERNO 2153. H: MB K1337.

therefore distance of the calices. The density of calices varies over a large range and will not help distinguish samples (populations, species) from each other.

### *6.3. Methods*

This study presents results obtained from a large number of systematic measurements of colonial corals of the genus *Stelidioseris* in order to better understand intraspecific variation and the limits of species. The method is new in Mesozoic corals and two questions arise: 1) what is the optimal number of measurements and 2) how are the newly obtained values comparable to calicular dimensions obtained through traditional methods that did not quantify their obtained values?

#### *6.3.1. Number of measurements*

In fossil scleractinian corals, few previous studies have systematically measured individual colonies in order to understand the ranges of dimensions of single colonies and therefore also species. Even in previous statistical approaches, the number of measurements of the calicular diameter and distance within one colony has been low. Six calices per colony were measured by Budd Foster (1979), five to ten in Budd & Johnson (1996), ten in Budd Foster (1985) and Budd Foster (1980), and two to three in Budd Foster (1979). No quantity of measurements is provided in Lathuilière (1988), Lathuilière & Gill (1998) and Pandey et al. (1999). Whereas Scott & Aleman (1984) give the results of detailed measuring, the number of values taken is unknown. The data presented here shows that variation of important coral dimensions within one colony can be very high. Figure 5 shows the oscillations of the arithmetic mean, the standard deviation and the resulting first interval in steps of ten values for one characteristic in one colony. Whereas the oscillation is low in the arithmetic mean, it is high in the standard deviation and the first interval. To obtain a representative value for the arithmetic mean, a low number of measurements is required (< 25), but in order to obtain representative values for the standard deviation, the coefficient of variation and the first interval more values are necessary (> 50). This is the case for studies on variation in dependence on environmental factors on the one hand, and for taxonomic interpretations on the other.

#### *6.3.2. Comparison of values*

In the literature, the dimensions of coral calices are generally given as minimum-maximum value, often also based on various specimens. It is often not indicated whether these values represent the respective smallest and largest value measured

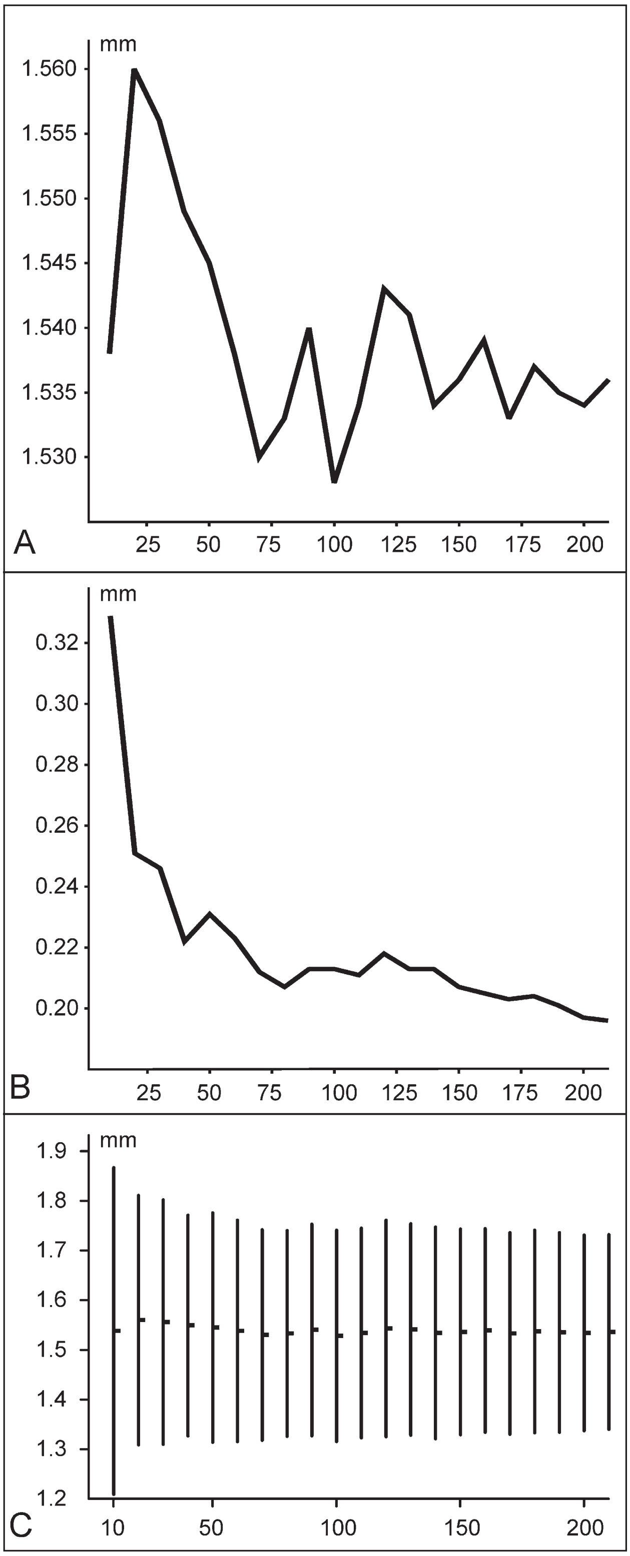


**Figure 5**. Variation of the arithmetic mean (A) standard deviation (B) and the first interval (C) in order of increasing number of measured values. The sequence of values is random. Sample ERNO 2153.

or the average range of the measured values. In order to value dimensions given in the literature, some published samples were measured systematically on the base of the originally published material. The result is given in Table 2. The general tendency is that systematically measured values limit the variation more than the published values, though not for all samples. In some samples, the obtained absolute value was higher than indicated in the literature, in some cases it was lower. Higher values obtained from recent measurements can be explained by the higher precision achieved with the computer application. Lower values are probably due to the fact that the wall in the plocoid corals is sometimes measured together with the calice by some authors. The difference between the smallest and highest value is of course higher in the measured values than in the values found in the literature because of the higher number of measurements obtained and probably also because obvious juvenile calices were discarded by other authors because they are not considered to be representative of the species.

## 7. Conclusions

Systematic statistical investigation of the Cretaceous plocoid coral genus *Stelidioseris* helps elucidate its intraspecific variation, ontogeny and taxonomy. Systematically measuring scleractinian corals can greatly assist with distinguishing species both within and between collections. The method allows for a more precise quantification of important characters because it makes a difference if only five or 50 calices are measured. It is recommended that future publications at least provide the number of measurements (n), the absolute lowest and highest value, the arithmetic mean and the standard deviation, for instance in the form "ERNO 2153, cl: (210) 1.172-2.304 (1.536, 0.196)" which allows the calculation of the first interval and the coefficient of variation. It is further recommendable to give dimensions for single specimens, not for species or populations. This makes the constitution of the given population or the separation of species within a fauna much more transparent to readers. Whereas the limits for specimens will not change, the limits of an abstract unit such as a population or species may change.

Apart from including more sample material in future studies it would also be useful to extend this research method to species of other Mesozoic species rich genera, such as *Cryptocoenia* or *Stylina* to gain more insight into intraspecific variation and to obtain more stable criteria for the separation of species. Comparisons to studies on extant corals show that non-overlapping first intervals of the calicular diameter in different samples or populations do not necessarily indicate different species, but may only represent ecotypes. This may have influence upon studies of biodiversity changes: the fossil coral species is probably not an appropriate unit to be counted and compared to extant diversity values.

The presented methods help only to analyse the variation of the calicular dimensions within one colony.

A transparent and comprehensive concept of the separation of species does not exist for fossil corals. So far species have been distinguished on the basis of their calicular dimensions, septal symmetry, septal counts, or septal density. The method of obtaining these values is not standardised nor is the process of comparing samples (populations, species) controlled by mathematical models. If fossil coral species are understood as units based on quantitative characteristics, it should be possible to apply statistical methods for easier comparison.

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