Biometric analysis of corallite size in the colonial rugosan *Crenulites*

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Abstract: Based on detailed study of the cerioid rugosan *Crenulites* from the Upper Ordovician of southern Manitoba, we developed a standardized biometric technique yielding reproducible measurements and tightly constrained values of corallite size for characterization of coralla and distinction of taxa. Transverse sections of high- and low-density cyclomorphic bands were scanned to produce digital images for the measurement of corallite areas using image-analysis software. From results of statistical analyses, we recommend data collection only from six-sided corallites, to reduce variability of mean corallite area among sections. Sections considered to be anomalous, which have either low or high values of mean corallite area, can be excluded in order to confine the data to sections representing normal growth. Also, because anomalous sections commonly occur in the basal and top portions of coralla, and because values from peripheral margins may be greater than those from central axes, these positions can be excluded to expedite data collection. Combining data from remaining sections in the central growth axis yields a large sample with minimal variation and an overall mean value of corallite area that is representative of the corallum. In this study, we distinguished two species of *Crenulites*, differing in corallite size, intracorallum variability, and intraspecific variability.

Key words: corals, biometry, corallite size, variation, species distinction

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1. INTRODUCTION

Corallite size is an important criterion for species distinction and recognition in colonial corals. In studies of cerioid coralla, "diameter" has commonly been used to represent the size of polygonal corallites. Different values, however, may result from the varying conventions that previous workers have employed for the measurement of diameter (SUTTON, 1966; STEL, 1978; YOUNG & ELIAS, 1999). We agree with workers who consider area to be a more constrained, reproducible parameter that better reflects corallite dimensions (STEL, 1978; SCRUTTON & POWELL, 1980). Another issue in studies of corallite size involves the selection of corallites to be measured. It has become common to measure 20 corallites, which is considered to adequately represent a corallum (OLIVER, 1968; DIXON, 1974). Recently, however, YOUNG & ELIAS (1993) suggested that 20 mature corallites (having six or more sides) in a contiguous region should be measured. It was thought that data for mature corallites could be grouped because corallites with six and more sides did not differ significantly in size. Compounding the problems of corallite measurement and selection, the methodology used in many studies is unspecified. The present study evaluates and further refines techniques for biometric analysis of corallite size, based on the cerioid rugosan *Crenulites* FLOWER, 1961. The objective is to develop a standardized methodology yielding tightly constrained values for the characterization of coralla and distinction of taxa.

2. MATERIAL AND METHODS

This study is based on detailed analyses of six well-preserved, complete specimens of *Crenulites* (corallum numbers 1 to 6, assigned catalogue numbers MM I-3477 to MM I-3482, respectively; deposited in the Manitoba Museum, Winnipeg, Manitoba, Canada). The specimens are from the Selkirk Member of the Upper Ordovician Red River Formation at Garson in southern Manitoba, Canada (for maps and stratigraphic columns, see ELIAS, 1981; WESTROP & LUDVIGSEN, 1983). The Selkirk Member is considered to be mid-Maysvillian to early Richmondian in age (ELIAS, 1991). At Garson, it consists of lithologically homogeneous, dolomite mottled, carbonate wackestone and packstone (KENDALL, 1977). Deposition occurred in a shallow marine environment with occasional storm-generated currents (ELIAS, 1981; WESTROP & LUDVIGSEN, 1983).

Crenulites is characterized by tabulae with crenulate edges that are strongly downturned between amplexoid septa (FLOWER, 1961) (see Fig. 1). Coralla at Garson range from tabular to low domical in form (for definition of growth forms, see YOUNG & ELIAS, 1995). Corallum diameters and heights are up to about 80 cm and 15 cm, respectively. The selected specimens represent the seemingly broad range in variation of corallite sizes among coralla in this unit.

For each corallum, a block measuring about 5 by 7.5 cm in cross section was cut parallel to the growth direction from both the central axis and peripheral margin. A longitudinal surface on a side of each block was polished, and a digital image (600 dpi) was obtained using a flatbed scanner (e.g. Fig. 2). For each block, a transverse polished section was prepared of each well-preserved high-density and low-density cyclomorphic band (e.g. Fig. 1). A total of 127 transverse sections were prepared; each was scanned

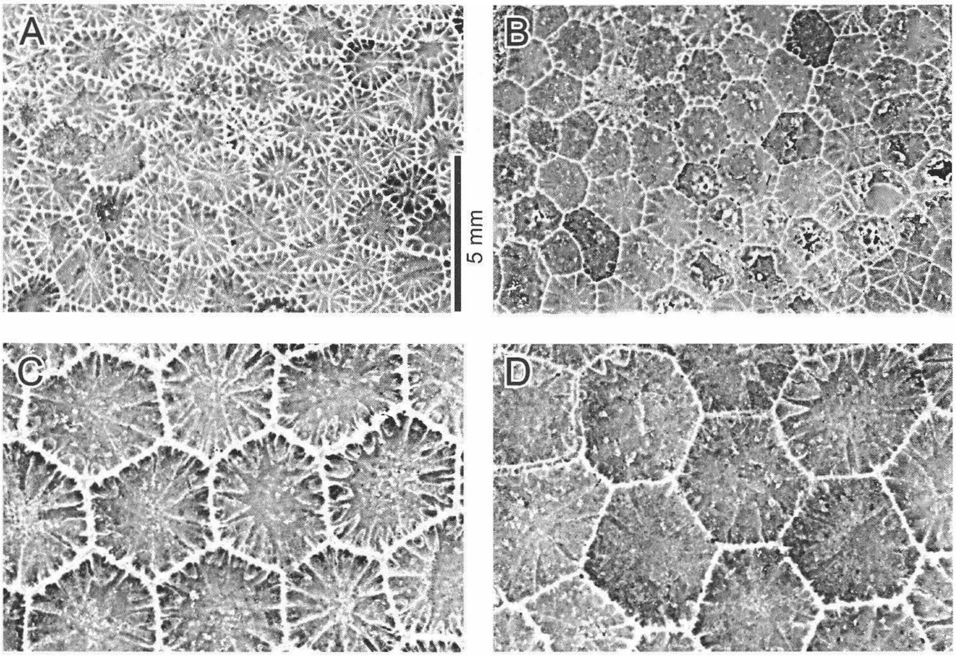

Fig. 1: Transverse polished sections of *Crenulites* (to scale shown in A) from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba.
A, B: *Crenulites* group A, corallum 3 (MM I-3479); high-density band (A) and overlying low-density band (B) in central-axis block.
C, D: *Crenulites* group B, corallum 2 (MM I-3478); high-density band (C) and overlying low-density band (D) in central-axis block.

at 2100 dpi. The position of each section and its height relative to the corallum base were recorded on the corresponding longitudinal image.

Image-analysis software (SigmaScan/Image) was utilized to measure area for 20 mature corallites within a contiguous region for each section. For measurement, the corallite was outlined along the midwall between it and adjacent corallites. In addition, we recorded the number of neighbours in contact with each corallite (polygonality; see YOUNG & ELIAS, 1995). In this study, 2540 measurements of area and determinations of polygonality were obtained. For each section, SigmaStat was used to calculate the mean area and standard deviation of all corallites within each polygonality class, and the overall mean area and standard deviation of all mature corallites. For statistical analyses, nonparametric procedures were applied in all cases for consistency, because the accompanying normality tests failed in some instances. SigmaStat was used to perform Kruskal-Wallis One-Way Analysis of Variance on ranks (ANOVA test) and All Pairwise Multiple Comparison Procedures (Dunn's Method); when less than three groups were being compared, Mann-Whitney Rank Sum Test was used. A P value of 0.05 was selected for all tests.

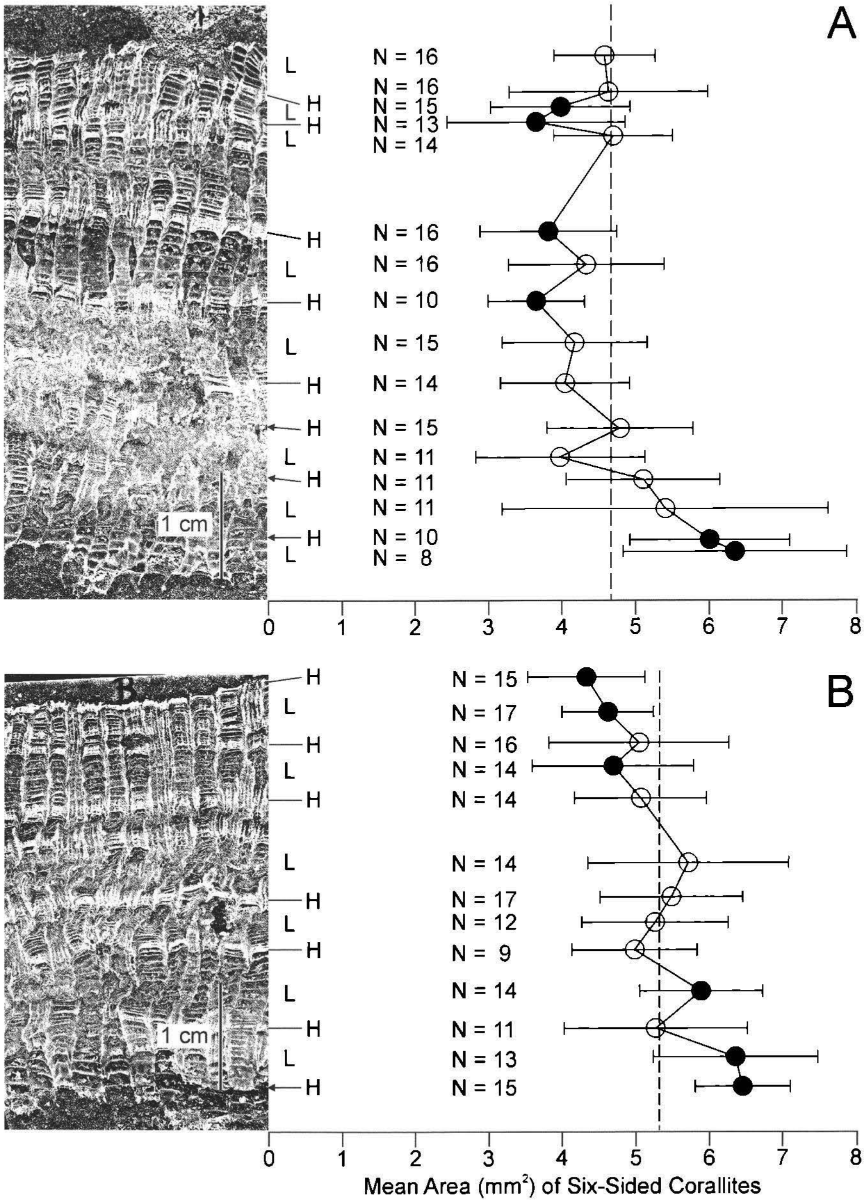

Fig. 2: Plots of mean area of six-sided corallites for successive transverse sections in the central-axis block (A) and peripheral-margin block (B); *Crenulites* (corallum 5; MM I-3481) from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba. Longitudinal polished surfaces (to scale shown); H = high-density band; L = low-density band. Open circle = value for non-anomalous section, solid circle = value for anomalous section, horizontal bar = standard deviation, N = number of measurements, vertical dashed line = overall mean value for block.

3. RESULTS AND ANALYSES

In this study of *Crenulites*, we observed that mean corallite area generally increases with an increase in polygonality (e.g. Fig. 3). This was confirmed statistically by comparing corallite areas among all polygonality classes, based on each measurement of area in each class for each entire block. We also found that corallite frequency within each polygonality class varies among sections in a corallum, and thus, the overall mean size of mature corallites tends to be variable among sections (e.g. Fig. 3). Furthermore, in the majority of sections, the standard deviation of mean area for the six-sided class is less than the standard deviation for the overall mean area of all mature corallites. In most sections, the six-sided class has the highest frequency; this class represents the equilibrium configuration in a cerioid corallum (Young & Elias, 1993). Therefore, in order to reduce variability within and among sections while still maintaining a relatively large number of measurements in the samples, data collection from this class alone is recommended.

Statistical comparison of corallite areas for the six-sided class, among all sections in each block, revealed that some sections were significantly different from at least one other section in the block. Such sections (identified using Dunn's Method) were considered to be anomalous; they have either low or high values of mean area (e.g. Fig. 2). This finding demonstrates that the common practice of relying on measurements from a single section does not ensure data that are truly representative of the corallum. Therefore, we recommend that data be obtained from as many sections as possible, followed by exclusion of those sections considered to be anomalous, which serves to

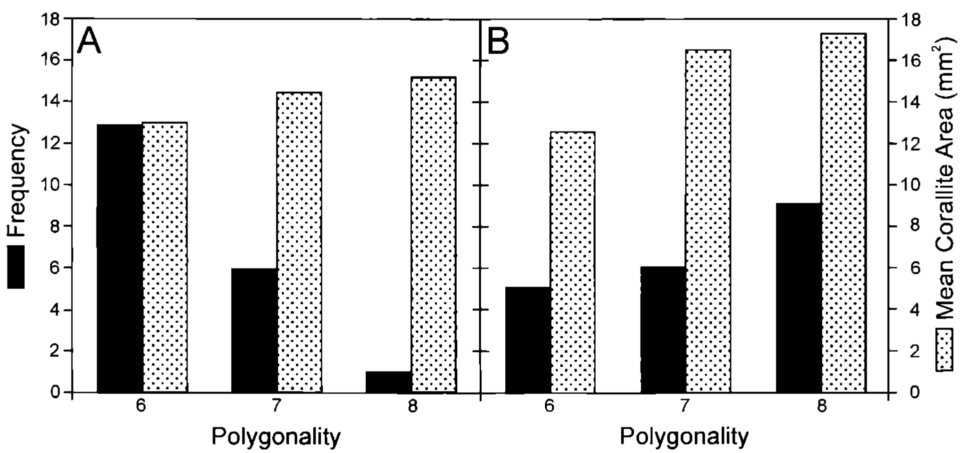

Fig. 3: Histograms of corallite frequency and mean corallite area for polygonality classes of mature corallites in two transverse sections (A, B) within the central-axis block; *Crenulites* (corallum 2; MM I-3478) from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba.
A: mean area of six-sided class = 13.10 mm^2, overall mean area of mature corallites = 13.66 mm^2; B: mean area of six-sided class = 12.41 mm^2, overall mean area of mature corallites = 15.67 mm^2.

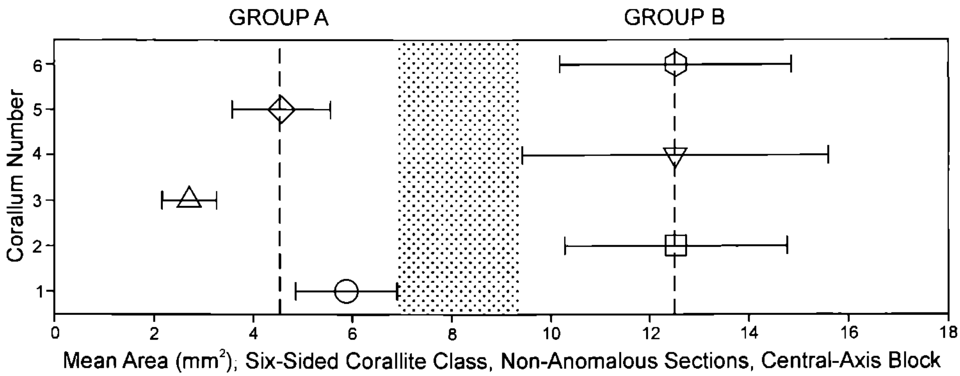

Fig. 4: Plot of overall mean areas and standard deviations based on measurements of six-sided corallites from non-anomalous sections in central-axis blocks of six coralla; *Crenulites* (coralla 1–6; MM I-3477 to MM I-3482, respectively) from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba. Two groups of coralla (A, B), separated by wide interval of non-overlapping standard deviations (shaded), are considered to represent separate species. Vertical dashed line = overall mean value for each group (A = 4.51 mm^2; B = 12.52 mm^2).

further reduce variability. Commonly, anomalous sections were found to occur in the basal and top cyclomorphic bands of coralla (e.g. Fig. 2). We therefore suggest that these positions be excluded in order to expedite data collection. It is thought that corallite development immediately following colony initiation and immediately prior to death may not represent typical growth during astogeny (see Scrutton, 1989). Data from all remaining non-anomalous sections were then combined to yield a larger sample of more than the standard of 20 corallite measurements per corallum, and an overall mean value of corallite area that is representative of each block. Although data collection from 20 corallites per section is recommended, our procedure maximizes data acquisition and can compensate for situations where individual sections yield fewer than 20 six-sided corallites.

For each corallum, we compared the areas of corallites belonging to the six-sided class in the central-axis block with those in the peripheral-margin blocks. In cases where the blocks differ significantly, the overall mean area for the peripheral-margin block is greater (e.g. Fig. 2). It is thought that crowding in the central axis inhibits corallite expansion, whereas expansion at the margin may be less constrained, allowing corallites to attain larger sizes (see Scrutton, 1983, 1989). Therefore, in order to reduce the potential for variability resulting from the inclusion of peripheral-margin data, we recommend that analysis be confined to the central-axis block.

Using the above methodology for each of the six coralla of *Crenulites,* we calculated an overall mean value and standard deviation for the measurements of area in the six-sided class, which is considered to be representative of the corallum. When these values were plotted for comparison, it became apparent that there are two distinct groups of coralla, separated by a wide interval of non-overlapping standard deviations (Fig. 4). Group A consists of coralla 1, 3 (see Fig. 1A, B), and 5 (MM I-3477, I-3479, I-3481). This group is characterized by small corallites (mean area 4.1 mm^2, based on combined data), with low intracorallum variability and relatively high intercorallum variability. Group B includes coralla 2 (see Fig. 1C, D), 4, and 6 (MM I-3478, I-3480, I-3482). This group is typified by large corallites (mean area 12.5 mm^2), high intracorallum variability, and very low intercorallum variability. Statistical comparison of combined data for the three coralla in group A with combined data for the three coralla in group B demonstrated that the two groups are significantly different.

Groups A and B are considered to represent separate species of *Crenulites*. In order to confirm this finding, additional coralla from the Selkirk Member at Garson should be analyzed; it is thought that a sample of 20 coralla may adequately represent a local population (OLIVER, 1968). For proper comparison and identification, the biometric methods established in this study should be applied to representatives of previously established species of this genus. Additionally, consideration of morphologic features other than corallite size will be necessary.

4. CONCLUSIONS

We have developed a standardized biometric technique yielding reproducible measurements and tightly constrained values of corallite size. This method permits effective and efficient characterization of cerioid coralla and distinction of taxa. Transverse sections of high- and low-density cyclomorphic bands are scanned to produce digital images for the measurement of corallite areas using image-analysis software. We recommend data collection only from six-sided corallites in the central growth axis, excluding the basal and top cyclomorphic bands. Data from sections considered to be anomalous are excluded from analysis. Combining data from the remaining sections can yield a large sample of more than 20 measurements, with minimal variation and an overall mean value of corallite area that is representative of the corallum.

In this study, we distinguished two species of *Crenulites* from the Upper Ordovician of southern Manitoba. One is characterized by small corallites, low intracorallum variability, and high intraspecific variability. The other species is typified by large corallites, high intracorallum variability, and very low intraspecific variability.

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