Microarchitectural change in density bands of the scleractinian *Montastraea faveolata,* Looe Key Reef, Florida Keys, USA: a preliminary report

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Abstract: Scanning Electron Microscope (SEM) study of microarchitectural features of *Montastraea faveolata* provides new data on density banding. Couplets of dense and less dense bands have formed annually, and differences in the microarchitecture of septal and costal flanks, and of both upper and lower surfaces of dissepiments allow recognition of their position within dense and less dense bands. Exothecal areas of the coral skeleton show the most pronounced density changes, suggesting that skeletogenesis differs between the area within the corallite wall, beneath the individual polyp (endothecal), and the area outside the wall, underlying colonial tissue (exothecal). We have determined that aragonite crystal arrangement and secondary thickening (or lack thereof) on a microarchitectural scale determines the overall density and appearance of skeletal structural features in *Montastraea faveolata.*

Key words: Annual density banding, *Montastraea faveolata*, microarchitecture, Looe Key Reef, Florida

Contents

1. INTRODUCTION

Annual density banding occurs prominently within massive colonial corals, and presents an opportunity for measuring their health and vitality and thus, that of coral reef sys-

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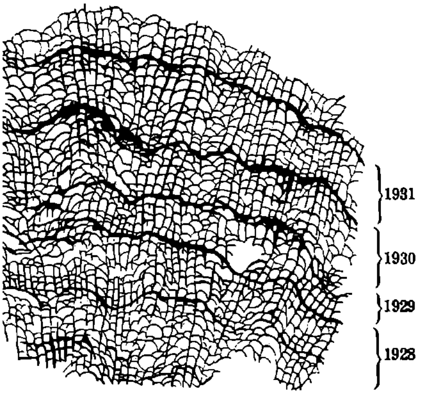

Fig. 1:
Illustration of annual banding in *Favia speciosa* by Ma (1934, p. 174) based on skeletal density (Ma's Fig. 6).

tems. Part of the importance of annual banding results from clues it provides about growth, disease and water temperature. Study of annual growth banding in massive coral colonies had as its inception the ground-breaking work by T.Y.H. Ma (1934, 1937), who recognized and measured annual density band spacing in corals from the western Pacific, relating it to water temperature (Fig. 1). Little was done to follow up on Ma's work until the 1970's, when Knutson et al. (1972) rediscovered growth banding, pioneered the use of x-radiography to illustrate it, and showed that without a doubt banding is annual. This was accomplished by calibration of x-radiographs with auto-radiographs of the same colonies with radioactive isotopes incorporated into their skeletons during atomic testing in the Pacific. Stimulated by this work, a number of important papers have been published in the 1970's and since.

Hudson (1981) used density banding to study growth of *Montastraea annularis* s.l. in changing environments. Variation in growth, as shown by density banding in *M. annularis* s.l., was evaluated statistically by Dodge & Brass (1984). Dodge et al. (1992) treated many aspects of growth banding in these much studied corals, including spacing of skeletal elements, geochemistry, identification of stress bands, and amount of thickening, and emphasized that changes in skeletal density are most marked in the exothecal area. Additionally, much of our understanding of annual banding depends on the contributions of Barnes & Lough (1992, 1993) and Lough & Barnes (1997, 2000), whose studies have been concentrated on massive species of *Porites* from the Great Barrier Reef.

One of the important observations regarding the *M. annularis* species group (Knowlton et al., 1992) is that banding is best developed in exothecal dissepiments (Macintyre & Smith, 1974; Dodge et al., 1992). Additionally, when one looks at microarchitectural details of these corals, there are features that reflect seasonal variation and provide data that aid in understanding causes of banding and the methods by which it forms. These are, 1) thickness contrast between endothecal dissepiments and exothecal dissepiments, 2) surface microarchitecture and aragonite crystallization characteristics of septal and costal flanks in less dense and more dense bands of the annual couplet, and 3) growth

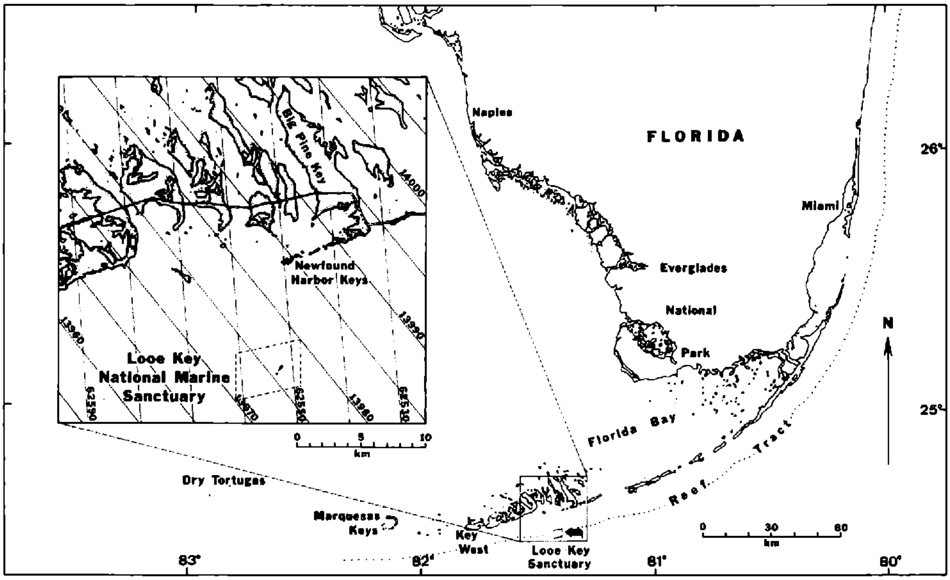

Fig. 2: Index Map showing location of Looe Key Reef in the Looe Key National Marine Sanctuary, Florida Keys, U.S.A. The keys form the southernmost part of the State of Florida. Figure is from LIDZ et al. (1985, p. 174).

lines and characteristic morphology of crystal clusters forming the underside of dissepiments.

This report focuses on details of only one species of the genus, *Montastraea faveolata,* from Looe Key Reef, Florida (Fig. 2). *M. faveolata* belongs in the *Montastraea annularis* species complex (KNOWLTON et al., 1992), which contains the most thoroughly studied corals in the Caribbean – Atlantic faunal realm. The species differs from *M. annularis* sensu stricto (ELLIS & SOLANDER, 1786), by having a differing colonial form, as determined by KNOWLTON et al. (1992), WEIL & KNOWLTON (1994) and BUDD & KLAUS (2001). The specimens from Looe Key Reef have been identified as *M. faveolata* by J. H. Hudson (personal communication, 2003). In literature older than 1994, the species name *M. annularis* only refers with certainty to the species complex, rather than to *M. annularis* s.s. as defined by later authors.

This research has focused on corals from several localities and on several corals from Looe Key. This report is illustrated by micrographs of one core only, of skeleton dated by bands as being as old as 1970 and as young as 2002. We do not deal here with variation due either to environmental changes between localities or respective health of coral colonies. Until now, there has been no scanning electron microscopic study of banding to illustrate the microstructure and microarchitecture of septa, walls, costae and both endothecal and exothecal dissepiments. The information presented here is based on preliminary research and serves to indicate the direction of our future efforts.

2. OBSERVATIONS

Dissepiments

Annual density banding is expressed best in the exothecal skeleton, and thus is seen most easily in exothecal dissepiments. Figures 1 and 2 of Plate 1 illustrate exothecal and endothecal dissepiments in *Montastraea faveolata*, and show clearly that endothecal dissepiments remain thin at the same time that thicknesses of exothecal dissepiments alter greatly. This apparently reflects a rather fundamental difference in skeletogenesis between the area within the corallite wall, beneath the individual polyp (endothecal), and the area outside the wall, underlying colonial tissue (exothecal). There is a recognizable first-formed layer (primary layer, SORAUF, 1970, 1972) of small crystals that have grown centripetally from the interior surface of the walls and septa to a central junction line. The primary layer has a similar thickness in all dissepiments, whether exothecal or endothecal, and is comprised of small crystals, comparable in size to the fine crystals forming the centers of calcification in septa. There is also an upper, secondary or thickening layer universally present in all dissepiments and seen on the upper surface. If this layer is thin, a junction ridge is generally visible, but if the dissepiment is greatly thickened, no ridge is visible. Thickening of exothecal dissepiments seen in the dense portion of annual growth bands is entirely due to the growth of crystals in the secondary layer. The presence of a central junction line on both endothecal and exothecal dissepiments indicates that skeletogenesis by basal flesh is similar both within the corallite wall and without. Organic control of mineralization was apparently the same during formation of both types of dissepiments, but the process is thought to have operated more rapidly or continued longer to produce the thicker secondary layer in some exothecal dissepiments.

Endothecal dissepiments are thin, with the primary layer being almost the same thickness as that in the exothecal dissepiments, but with little thickening in the upper secondary layer. The undersurface shows characteristic features, crystals in ropy clusters, growing parallel to the lower surface of the dissepiment, forming strands of acicular crystals in less dense bands (Pl. 1, Fig. 3), and denser "ropes" in dense bands (Pl. 1, Fig. 4). The upper surface microarchitecture shows rather luxurious growth of aragonite crystals in the dense band (Pl. 1, Fig. 5), and densely packed, small clusters of crystals in the less dense band (Pl. 1, Fig. 6), thus easily differentiated.

Exothecal dissepiment formation is similar to the endothecal, with crystals in strands, converging on the central junction groove. Crystals are parallel to the lower surface, and are complete and orderly within strands in dense-band dissepiments. There is great thickening above, which occurs in the upper secondary layer, in upwardly directed, expanding crystal clusters, and thickness here may reach 7 or 8 times the thickness of endothecal dissepiments. In dense bands there is very luxurious growth of the upper surface crystals in bundles, forming a characteristic microarchitecture.

Septal flanks

The most recent growth of septal surfaces (May 2002) shows discrete crystal clusters, or fasciculi (WISE, 1970; LETISSIER, 1990, 1991), as shown on Plate 2, Figure 2. The septo-costal blade is continuous over both the costal and septal sides of the wall (theca). Septal flanks are then smoothed over, with granulations the main ornamentation. Later formation of thickening carbonate on septal flanks occurred during the life of the polyps, attested to by attachment scars seen on septal flanks (Pl. 2, Fig. 1). The number and size of granulations varies within the colony (Pl. 1, Fig. 2; Pl. 2, Fig. 2). They are sparsely developed and larger at some levels, but more abundant and smaller at others, with no patterns yet discernable in their occurrence.

Septal flanks show recognizable differences between dense and less dense bands. These primarily reflect more complete growth of flank crystals in dense bands (mostly within thickening layers on the flanks) and less complete crystal development on septal flanks in less dense bands, where crystals commonly have a skeletal appearance (see below).

Dense band. – In dense bands, development of thickening crystals is more extensive than in the lighter bands. This crystal growth is a part of the thickening of septa, the thickening deposits of Cuif & Dauphin (1998) and of Stolarski (2003). This is called stereome in fossil corals (Moore et al., 1956, p. F250). Micrographs of this thickening indicate that crystal growth in *Montastraea faveolata* is more or less parallel to the pre-existing septal surface. It tends to grow in and around flank prominences (granulations), as shown in Figure 1 of Plate 2, where crystals grow around attachment scars. This apparently precedes development of thick secondary deposits, in which crystals are more commonly oriented at a high angle to the septal flank.

This development of the septal flank is considered part of development of dense bands, in that thickening of septa is part of the increase in density of skeleton at these levels. In dense bands, crystal growth is complete and oriented nearly parallel to the septal flank, consisting of small crystals with elongate shapes and terminal pyramids (as seen at the left side of Fig. 1, Pl. 2). Thus, the thickening fills in around granulations and smooths the flanks to a certain degree.

Less Dense Band. – In less dense bands, septal flanks tend to be less thickened, and crystals have a rather unique-appearing form. These are clusters of crystals, generally oriented at an angle to the septal flank, but with crystal form modified so that, rather than having well-developed terminal c-axis prisms forming a point, these have a terminal pit that is generally 3 or 4 sided, as shown at the right side of Figure 1 of Plate 2. The development of this pitted form resembles that of skeletal crystals, but further clarification of their meaning awaits additional research.

Costal flanks

The development of youthful septal and costal flanks indicates that most of dense band formation has little to do either with skeletal elongation or the formation of primary skeleton (*sensu* Cuif & Dauphin, 1998). Rather, it has most to do with thickening by later formed flank crystals on costae (just as on the upper surface of exothecal dissepiments). When first formed, the costal part of the septo-costal blade is formed together with the septal flank. Fasciculi are apparent, with individual crystal clusters visible (Pl. 2, Fig. 2), and with similar arrangement of clusters on both the septal and costal side of the blade, seen here extending above the upper margin of the theca. Coating of this continues until both flanks are relatively smooth, but thereafter, crystal growth on the costal flank is considerably more developed (Pl. 2, Fig. 3).

The most characteristic costal microarchitecture seen in dense bands shows bundles of elongate prismatic aragonite crystals (Pl. 2, Fig. 4). These bundles resemble those developed on the upper surfaces of both endothecal and exothecal dissepiments in dense bands. In less dense bands, costal flanks tend to have sparse acicular crystals grown on them, which may even be later-formed inorganic cements (Pl. 2, Fig. 5). This area also is commonly bored by fungi, as are exothecal dissepiments (Pl. 2, Fig. 6).

3. CONCLUSIONS

The exothecal portion of the skeleton shows most recognizable variation in density, both in exothecal dissepiments and costal flanks. This suggests a different rate or duration of thickening, but not a different means of control by colonial tissue versus polypal tissue in *Montastraea faveolata*. The densest portion of the skeleton is formed in the warmest period of the year, apparently related to water temperature, as early surmised by MA (1934). Optimal temperatures for primary growth and elongation are roughly known, and during summer weather, apparently when these temperatures are exceeded, dense band formation proceeds. Changes in skeletal density are the result of differences in thickening of skeleton. This is affected by two factors, 1) the rate of extensional skeletal growth and 2) the rate of thickening of skeletal elements. Work to date makes it clear that there are a number of differences between dense and less dense band microarchitecture, as follows:

1. Aragonite crystals on costal flanks and upper surfaces of dissepiments form in clusters of elongate crystals that are much more luxurious in dense bands than in less dense bands.
2. Crystal form seen in early thickening of septal flanks varies between dense bands and less dense bands. Dense band aragonite forms "normal" elongate crystals with terminal pyramids, and light band aragonite crystals have terminal pits, resembling "skeletal" crystals.
3. Undersurfaces of endothecal dissepiments have a characteristic ropy appearance in dense bands. These are complete strands of crystals having a dense appearance, while the undersurfaces of other dissepiments (in less dense bands) generally have more visible occurrences of acicular aragonite and less ordering within crystal strands. Additionally, there is a suggestion that the time taken to form the primary layer of dissepiments in dense bands may be slightly longer (5 to 6 days) than in less dense bands (3 to 4 days), based on the number of discernible growth increments visible. The last requires further research.

The present paper reports early stages of a continuing research program.

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Plate 1

Montastraea faveolata. Scanning Electron Micrographs, magnifications as shown by scale on image.

Fig. 1: Overview of endothecal portion of corallite, central in image, with the exothecal portion to the left, showing dissepiments, septa, costae, and columella, with massive aragonite present in dense band, and exothecal dissepiments thick as compared to thin endothecal dissepiments.

Fig. 2: Showing the 3 mm deep calice and offset of equivalent, higher exothecal and lower, endothecal dissepiments (offset approximately 6 dissepiments). Note that fungal infestation occurs in the basal part of the calice, above the last dissepiment. Septal flanks are relatively smooth near the top of the calice, with granulations the only ornamentation on the septum.

Fig. 3: Undersurface of endothecal dissepiment in less dense band, with central junction line and incremental lateral growth of primary layer visible, as well as bushy acicular needles of aragonite beneath the dissepiment.

Fig. 4: Undersurface of a dense-band endothecal dissepiment shows strands of crystals growing towards central junction. Orderly crystal growth here forms ropy strands of tightly adjoined crystallites. Growth shown here is still incremental, and although growth lines are not clearly marked, they may be more numerous here (ca. 5–6) than in less dense bands.

Fig. 5: Upper surface of dense-band dissepiment has luxurious growth of aragonite crystals, showing characteristic development of lath-like acicular crystals in tight and well-defined clusters.

Fig. 6: Upper surface of less-dense-band dissepiment is shown, with more limited growth of aragonite crystals, which still occur in well-defined clusters.

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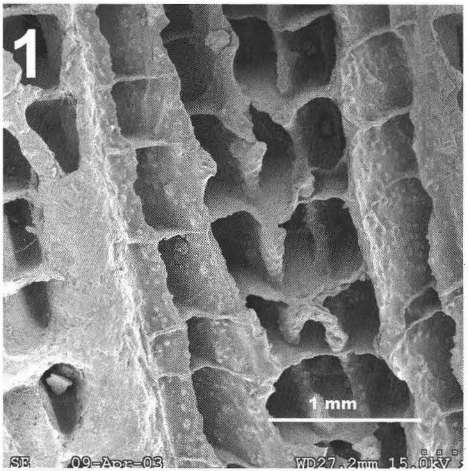
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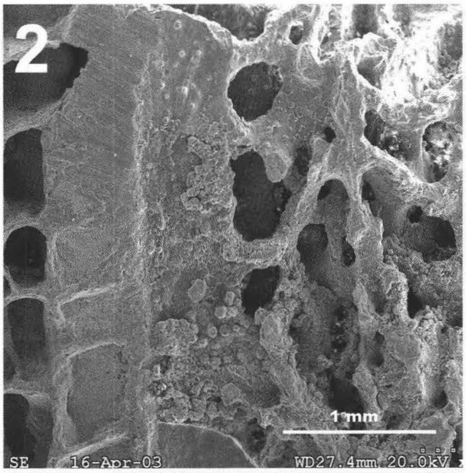
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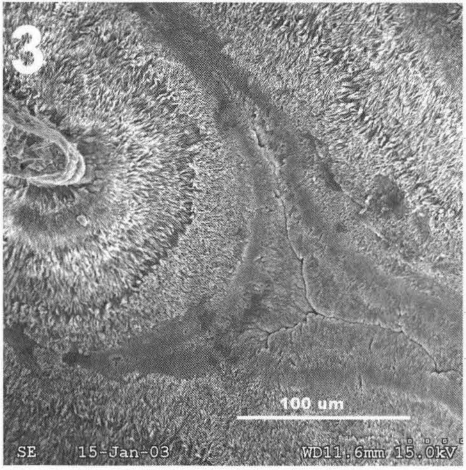
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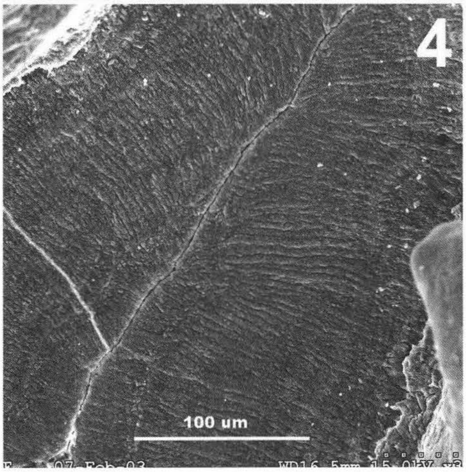
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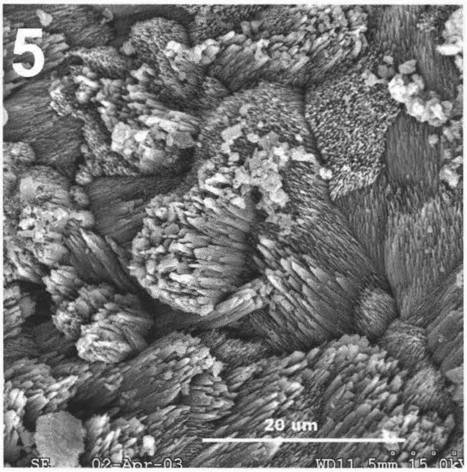
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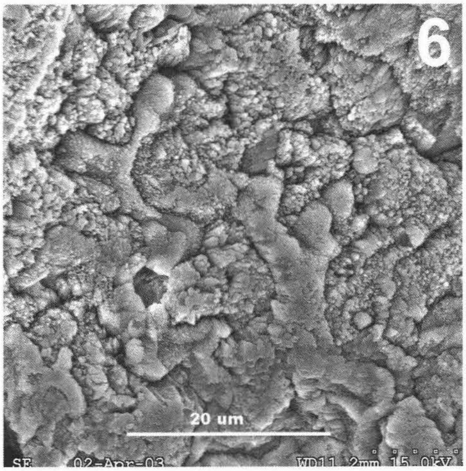
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Plate 2

Montastraea faveolata. Scanning Electron Micrographs. Magnifications as shown by scale on image.

Fig. 1: Crystals with terminal pit, here illustrated at the right side of the micrograph from less-dense-band septal flank, rather than pointed c-axis termination usual for aragonite crystallites, as seen at the left. Also note attachment scar at lower left.

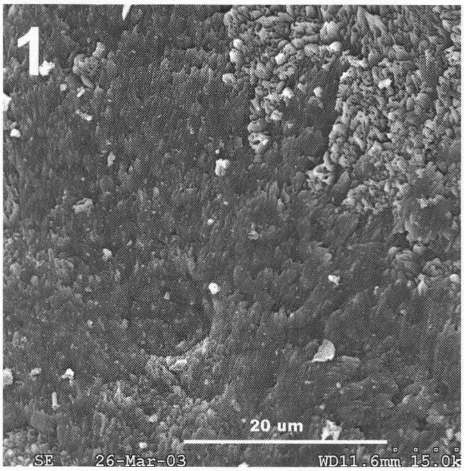
Fig. 2: Growth tip of septa and costa, with fasciculi on the new growth surface.

Fig. 3: Overview for comparison of septal and costal flanks and thicknesses of exothecal (right) and endothecal (left) dissepiments.

Fig. 4: Typical luxurious crystal growth on dense-band costal flank.

Fig. 5: Characteristic sparse, acicular crystals on septal flank in extreme less dense band.

Fig. 6: Exothecal dissepiments, seen from above, characterized by abundance of fungal boring within colonial skeleton.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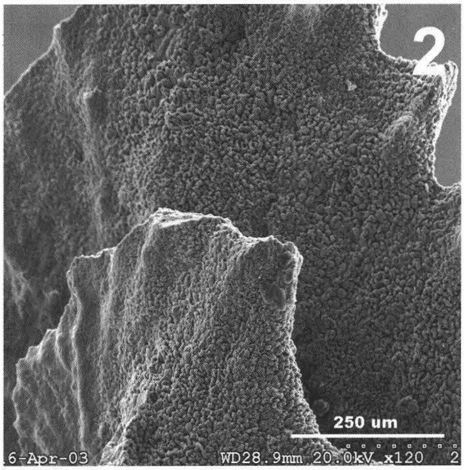
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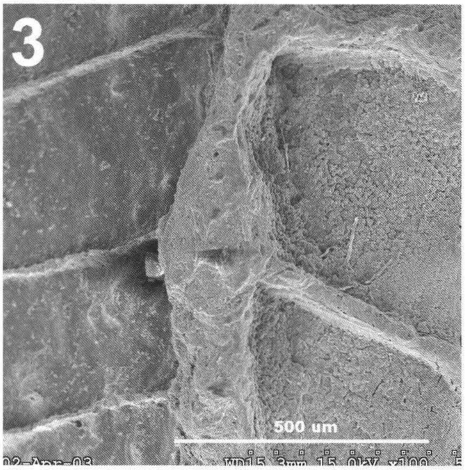
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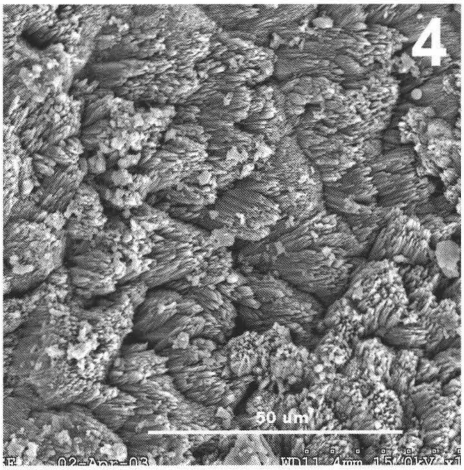
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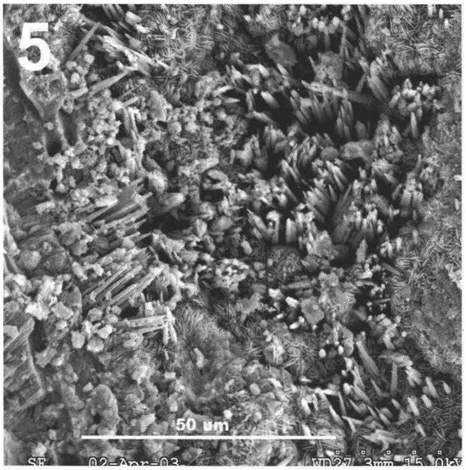
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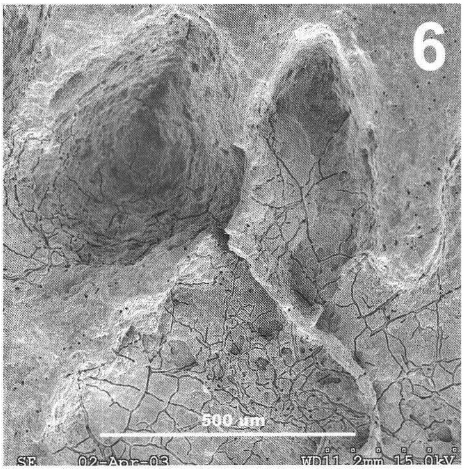
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