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Dendroid morphology and growth patterns: 3-D computed tomographic reconstruction

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ABSTRACT

This paper analyzes the growth patterns of dendrolite in the Zhangxia Formation (Middle Cambrian), Shandong Province, China, using the technique of 3-D computed tomographic reconstruction. Dendroids are classified into V-dendroids, columnar dendroids, and arborescent dendroids, based on morphological characteristics. The means of interconnection between dendroids are classified into trunks, nodules, shoots, and fingers. Stacking and tiering control the gross morphology and structural framework of dendrolite. Stacking is a process of vertical growth, in which V-dendroids create a staircase-like structure. Tiering occurs when a layer of dendroids is covered by sediment, and then partially eroded, allowing a new layer of dendroids to form.

A comprehensive blueprint of the structural divisions of dendrolite is presented, according to scale, being divided into micro-, meso-, macro-, and megastructures. The mesostructure, which includes individual dendroids and their combined structures, is subsequently divided into primary (V-dendroid), secondary (columnar and arborescent dendroid), and tertiary (stair and tier) structures and a basic growth model is provided for V-dendroids. The stages of V-dendroid growth are: 1) trunk extension and base expansion, 2) divergence, 3) expansion and convergence, followed by repetition of stages 2 and 3, until 4) growth completion, followed by the subsequent emergence of a new dendroid by either stacking or tiering. This development of systematically ordered structures is suggestive of the reaction of microbial colonies to external environmental conditions.

1. Introduction

Dendrolite was first introduced by Riding (1991a) to describe microbialites which are neither laminated nor clotted, but rather composed of dendritic clusters of calcimicrobes, such as *Epiphyton*, *Renalcis*, and *Angusticellularia* (a.k.a. *Angulocellularia*) (Shapiro, 2004) found in Cambrian and Lower Ordovician reefs in association with sessile metazoans (Riding, 1991a). The descriptive term "dendritic" refers to upward bifurcating or widening bushy clusters and patterns of calcified microbial structures. The individual structures, referred to as "dendroids", occur on a millimetric scale. They occur in large meter-scale bioherms (Kruse et al., 1995; Riding and Zhuravlev, 1995) in association with reef-constructing organisms, such as archaeocyaths (Hamdi et al., 1995; James and Gravestock, 1990; Shapiro and Rigby, 2004; Spincer, 1996) or in relation to the sudden widespread appearance of calcimicrobes in the Neoproterozoic (Grotzinger et al., 2000; Shapiro, 2004; Turner et al., 1997, 2000a,b).

Observations of microbialite morphology and growth patterns have been essentially limited to 2-D observations alone. Riding (1991a) initially developed a classification scheme for microbial structures including dendrolite according to internal structures, which he subsequently re-modified (Riding 2000). These 2-D classifications are useful for identifying and describing dendritic structures in thin-section, but are ill-adapted to 3-D morphology. The purpose of this paper is to reveal the three-dimensional morphology of dendroids and related dendritic structures using 3-D computed tomographic reconstruction, a technique which has been successfully applied to a variety of fossilized specimens embedded in matrix (Ketcham and Carlson, 2001; Schopf and Kudrayavtsev, 2005; Torres, 1999; Watters and Grotzinger, 2001). This technique involves the combination of serial, cross-sectional images into a coherent three-dimensional model. The 3-D model generated from the tomographic reconstruction provides a unique view of dendritic structures observable from any perspective. This allows for the development of a general classification scheme for dendroids, and their means of interconnection and growth. This information can be particularly useful when combined with other 2-D observational techniques.

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2. Stratigraphical and geological settings

The Cambrian succession of the North China Platform is represented by shallow marine, mixed siliciclastic-carbonates formed in an extensive intracratonic platform (Meng et al., 1997). The succession in Shandong Province consists of six formations: Liguan, Zhushadong, Mantou, Zhangxia, Gushan, and Chaomidian formations, in ascending order (Bureau of Geology and Mineral Resources of Shandong Province, 1996; Woo, 2009; Fig. 1). The basement (Precambrian metasedimentary rock and granitic gneiss) is overlain by sandstone of

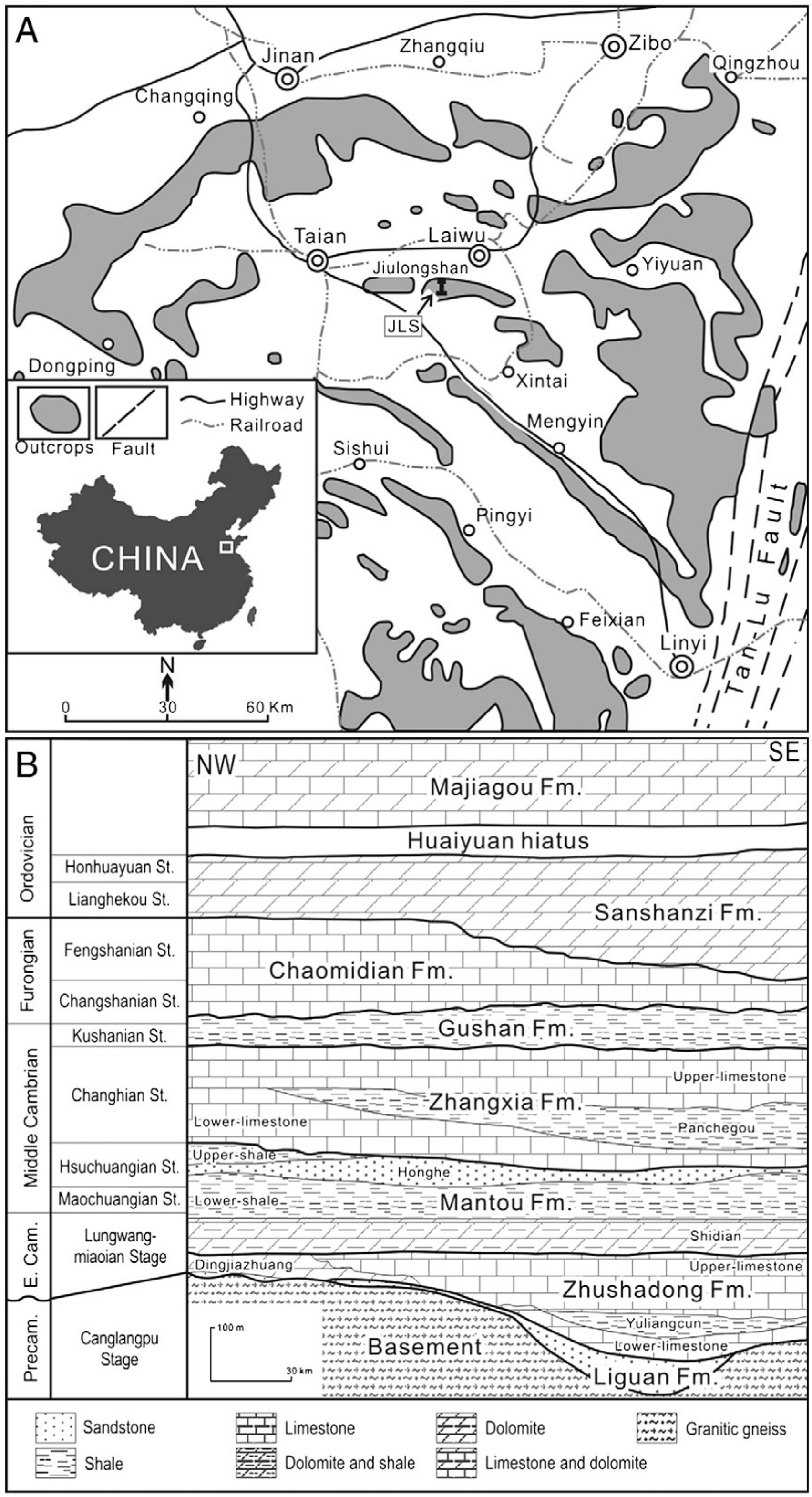

Fig. 1. (A) Geologic map of the studied area showing distribution of the Cambrian succession. (B) Spatio-temporal distribution of the Cambrian succession in Shandong Province (Bureau of Geology and Mineral Resources of Shandong Province, 1996; Woo, 2009).

the Liguan Formation in the east, and limestone and dolostone of the Zhushadong Formation in the west. The overlying Mantou Formation is characterized by reddish mudstones in the lower part and siltstone with thin sandstone interbeds and cross-stratified sandstones in the upper part with lesser amounts of limestone beds. In eastern Shandong Province the Zhangxia Formation consists of thick limestone beds in the lower part, and alternating layers of shale and thin limestones in the upper part. In contrast, in western Shandong the Formation is represented by a thick succession of limestones. Thin and extensive shale of the Gushan Formation overlies the Zhangxia Formation and transitions upward into the thick limestone succession of the Chaomidian Formation (Lee et al., 2010). This Cambrian mixed carbonate and siliciclastic succession gradually changes upward into the dolostone of the Sanshanzi Formation (Ordovician).

Microbial carbonates such as stromatolites, thrombolites, and dendrolites are present throughout the entire Cambrian succession. Meter-scale domal, egg-carton shaped, and flat stromatolites make up a portion of the shallow marine peritidal facies associations in the Zhushadong and Mantou formations. Microbial carbonates formed a thick succession of the Zhangxia Formation in the western part of Shandong Province during the Middle Cambrian, whereas they formed independent beds intercalated in the shale successions of the eastern part. Thick microbial biostromes with domal, columnar, and maceria-shaped (*sensu* Shapiro and Awramik, 2006) internal structures occur in the lower middle part of the Chaomidian Formation. Dendrolites, among the other microbial carbonates, occur mainly in the Zhangxia Formation (Middle Cambrian). They usually form small-scale bioherms or thin biostromes associated with coarse skeletal grainstone.

3. Dendrolite

Although Riding's (1991a) definition lacks strict morphological constraints, there seems to be a general consensus regarding dendrolite morphology. Most reported dendrolites are characterized by branching, narrow clusters of microbial colonies on a millimetric-scale, visible with the naked eye (e.g., Shapiro and Awramik, 2000; Shapiro and Rigby, 2004) (Fig. 2A). Some dendrolites have coarser branches which coexist with simple columnar colonies (Webb et al., 1998) or reverse triangular colonies (Riding, 2000) (Fig. 2B). This suggests that dendroid morphology can vary as indicated by Riding (2000). Individual thromboids of thrombolite are known to show a large variation in morphology ranging from spherical to irregular clots (e.g., Armella, 1994; Kennard, 1994; Riding, 2000). The morphological variation of dendroids and thromboids may result in an overlapping transitional zone in the morphologic spectrum, which causes some degree of confusion concerning the recognition of each type of microbialite. This calls for a more specific classification of dendrolite morphology.

Dendrolite, in this study, consists of dendroids formed by the accretion of peloidal micrites (*Angusticellularia*-like), chambered micrites (*Renalcis*-like), and other micritic structures of uncertain origin. Individual dendroids are about 1 to 3 mm in width and branch from the upper surface, or corners, of other dendroids, resulting in a branching gross morphology (Fig. 2C). These are similar to those dendrolites reported by Shapiro and Awramik (2000) and Shapiro and Rigby (2004) (Fig. 2A). They are, however, different from Riding's (2000) (Fig. 2B) dendrolite in that they have neither a well-layered macrostructure, nor a *Gordonophyton* microstructure. Two different states of dendroid preservation are recognized on the weathered surface and under the microscope. One is characterized by micritic dendroids and the other is characterized by re-crystallized "crystalline" dendroids (Fig. 2C and D, respectively). The former possesses a well-preserved internal structure; the latter, however, has lost its internal structures during diagenesis (see 2-D analysis section for detailed description).

A typical dendrolite bioherm of the lowermost part of the Zhangxia Formation is approximately 3 m in diameter and 0.5 m in height and consists of 8 clearly identifiable units (Fig. 3A). The bioherm rests upon a foundation of sandstone represented by the first two non-microbial units. The overlying microbial units, in turn, consist of several layers, each composed of a lateral array of dendroids with carbonate and siliciclastic grain matrices. These microbial units may be either tabular or domal in shape. The tabular microbial units tend

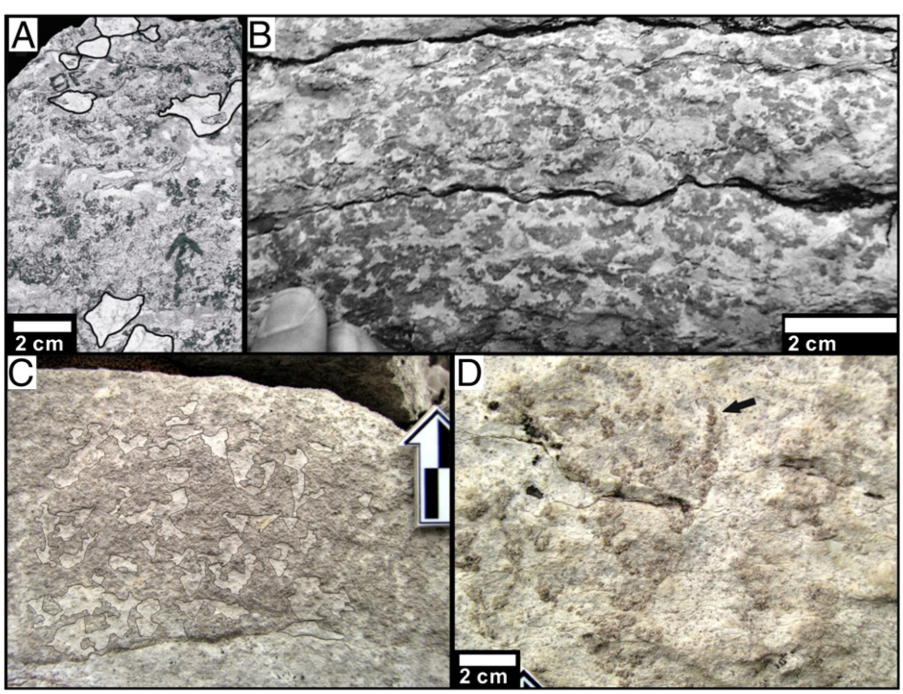

Fig. 2. Dendrolite comparison. (A) Dendrolite composed of *Renalcis* (Shapiro and Rigby, 2004; Fig. 2) from the Bonanza King Formation (Upper Cambrian), USA. (B) A sample of dendrolite from the Zhangxia Formation (Riding, 2000; Fig. 12). (C) Dendrolite with micritic dendroids which appear as a recessive and powdery surface (outlined in black). From the Zhangxia Formation. Scale is 2 cm. (D) Dendrolite with crystalline dendroids which have positive relief and granular appearance (arrow indicates one branch). From the Zhangxia Formation.

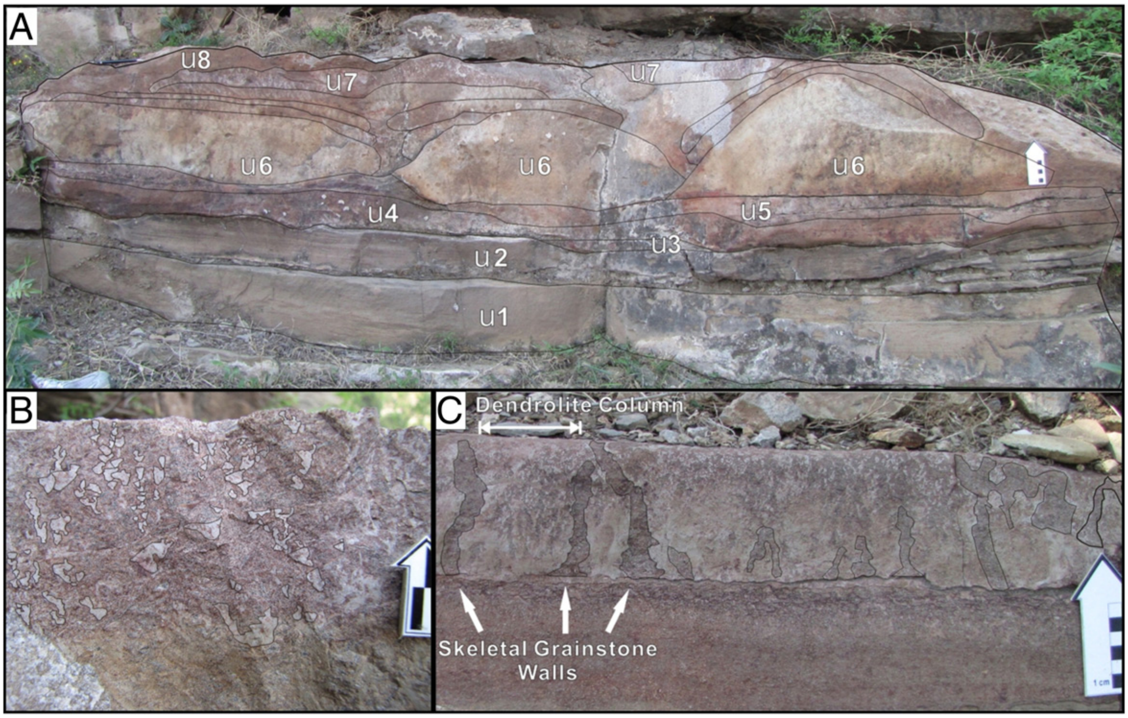

Fig. 3. Examples of dendrolite bioherms (located at the base of the Zhangxia Formation, Jiulongshan section) and associated lithologies. (A) Biohermal units: (U1) non-microbial parallel laminated medium-grained sandstone; (U2) non-microbial darker sandstone; (U3) non-microbial purple mudstone (high hematite concentration); (U4) tabular microbial unit of purple mudstone mixed with grainstone (few dendritic structures); (U5) tabular microbial unit of light-pink grainstone (pronounced, small-scale dendritic structure); (U6) domal microbial unit (large scale dendritic structure). Overhangs rest upon these domes and contain dendritic structures oriented perpendicular to the domes; (U7) tabular microbial unit of purple grainstone (small-scale dendritic structure); (U8) non-microbial orange grainstone cover. Scale is in cm. (B) Enlarged view of unit 7. Purple grainstone makes up the rock matrix, whereas white micrite (fine-grained calcite) comprises the dendritic structures (outlined in black). Scale is 2 cm. (C) Dendrolite bioherm containing columnar, instead of domal, microbial units. Skeletal grainstone walls are outlined in black.

to possess smaller-scale dendritic structures, whereas the domal microbial units possess larger dendritic structures. Dendroids appear as recessive white micrite within a skeletal grainstone matrix, on the weathered outcrops (Fig. 3B). Some bioherms may also contain columnar units of dendrolite (Fig. 3C). Narrow furrows filled with skeletal grainstone separate adjacent columns. The bioherms of the lowermost part of the Zhangxia Formation are supposed to have formed in high-energy, shallow, subtidal environments (Woo, 2009).

Watters and Grotzinger (2001) have suggested that studying original fossil morphology is important because it "provides an objective basis for taxonomic description and enables analysis of their functional behavior and phylogenetic affinities." Although, as stated earlier, in the case of calcified microbes taxonomic classification of the original constituent microbes can be virtually impossible due to recrystallization (Shapiro and Rigby, 2004). However, the conservation of size, shape, and habit of certain calcimicrobial structures has led to general classifications which can be fairly easily applied on the basis of morphology alone (Shapiro, 2004; e.g. Riding, 1991b; Flügel, 2004). Likewise, here we attempt to use this approach to classify individual dendroids according to their morphology, rather than in accordance with any supposed phylogenetic affinities.

4. Materials and methods

Polished dendrolite surfaces were scanned with a resolution of 1200 dpi. The contrast between dendroids and the surrounding matrix was enhanced using built-in image filters in the 3-D tomographic reconstruction software "Volview 2.0" (Kitware Inc., Clifton Park, NY) to distinguish dendroids from the matrix. A slightly etched dendrolite chip was observed under a Scanning Electron Microscope (SEM, Jeol JSM 6380) using backscattered electrons (BSE) to identify microscopic features under higher magnification. An energy dispersive spectroscopy (EDS) apparatus equipped to the SEM was used to map the distribution of major elements. Conventional thin-section observations under plain- and cross-polarized light were made for micro-scale textural analysis and identification of calcified microbes.

3-D tomographic reconstruction has been used in many instances in the field of paleontology in order to obtain true-to-life models of microfossils and other specimens too small to remove from their original rock matrix using conventional techniques without damaging the sample. This is particularly true in the case of calcified microbes, algae or simple metazoans which do not possess a skeleton (Watters and Grotzinger, 2001). The techniques used to obtain serial images may be either manual or automated, and either destructive or non-destructive. In this case, a manual, destructive method similar to the automated, destructive method used by Watters and Grotzinger (2001) is employed. Automated, non-destructive methods of obtaining serial images include Raman Spectroscopy (Schopf and Kudrayavtsev, 2005) and X-ray CT (Ketcham and Carlson, 2001; Torres, 1999) technologies.

The process begins with sample selection and the preparation of a rectangular column (Fig. 4). The sample is cut to the desired specifications and the surface is prepared and polished using 1/600 inch grinding powder. The polished surface is scanned into the computer at a resolution of 1200 dpi with a layer of water in between the surface and the scanner to increase visibility. A 0.1 mm thick layer of rock is then removed from the surface and the new surface is scanned. This process is then repeated until a total of 200 images is obtained.

In the second stage of preparation, the full complementary of images is digitally altered and manipulated using an image editing program (CorelDRAW® Graphics Suite X4; Corel Corporation Inc., Ottawa, Canada) to enhance the color contrast between dendritic

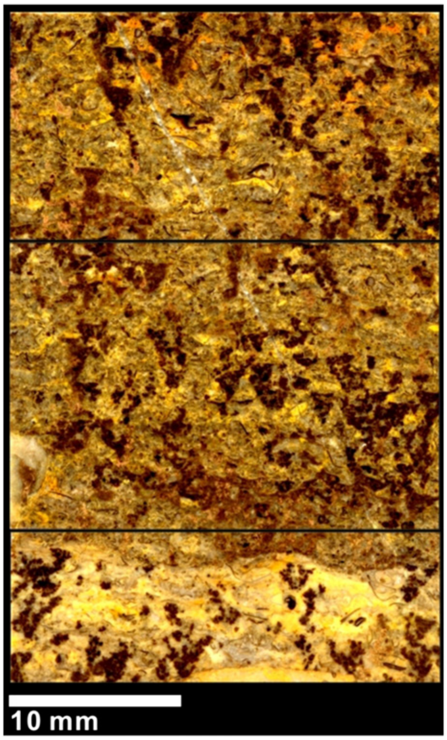

Fig. 4. An example of the scanned surface of the sample in which dimensions equal 45 mm wide, 69.1 mm high, and 20 mm thick. The scanned image is divided into three sections (upper, middle, and lower) for easy handling in Volview 2.0.

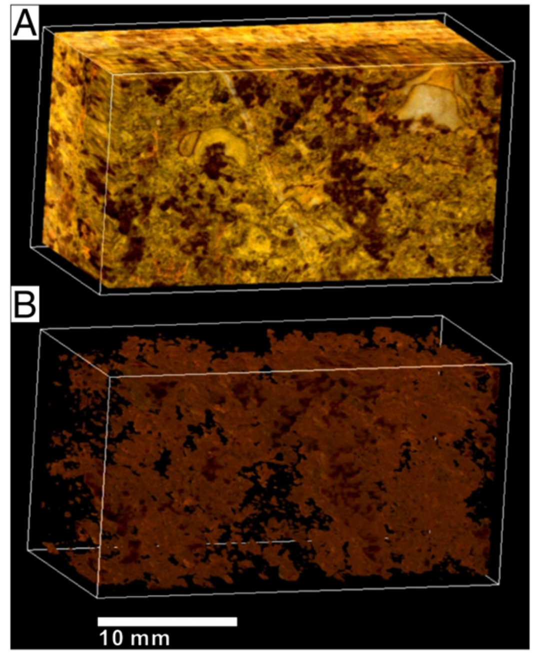

Fig. 5. (A) 3-D reconstruction of upper section of dendrolite sample. (B) 3-D rendering of the same volume with matrix removed so as to reveal calcified microbial structures alone. Structures appear a reddish-orange color.

structures and the surrounding sediment/debris. The images are then brought into perfect alignment. Due to the excessive size of the image files, the entire sample is subsequently divided into three sections and image files are saved separately for each section (Fig. 4).

In the final stage, the images from each section are combined into one coherent 3-D model "Volview 2.0". The image will first appear as a solid block. In order to begin analysis on the dendritic structures it is necessary to isolate them from the surrounding rock matrix. This can be accomplished using various tools and filters located within the software which control the opacity of each color scheme; thus, the necessity of the earlier color contrast enhancement. Once the matrix has been made transparent, analysis of the dendritic structures can begin (Fig. 5).

5. 2-D analysis

In the graphically enhanced 2-D image (Fig. 6A), approximately 60% of the calcified microbial structures appear in the regular V-shaped form. These dendroids are referred to as "V-dendroids". V-dendroids often occur in large branching sequences which grow vertically in quasi-fractal patterns. In the image, there is one base from which at least 18 other dendroids branch off. Such structures of vertically connected dendroids with a common origin can be referred to as dendroid "stairs." Irregular dendroids which do not fit the description of V-dendroid account for approximately 30% of the calcified microbial structures. The final 10% of the calcified microbes occur in spherical, rounded shapes (Fig. 6B).

SEM imaging provides a view of the entire morphology of a single V-dendroid, which under normal optical magnification appears as a collection of numerous micritic spheres (Fig. 7A). SEM imaging also reveals the existence of branches connecting individual dendroids (Fig. 7B), which would normally be invisible, causing adjacent dendroids to seem unconnected. Fig. 7C shows an enlarged image of the region in Fig. 7B, revealing the difference in grain sizes between the fine-grained micrite of the dendroids and the large crystalline calcite connecting them. The presence of this connection is further affirmed under EDS analysis (Fig. 7D).

The difference in chemical composition between dendroids and their surrounding matrix (Fig. 8) suggests that the matrix consists of a significant fraction of siliciclastic material, whereas the dendroids are pure calcium carbonate. This fact is significant since, according to

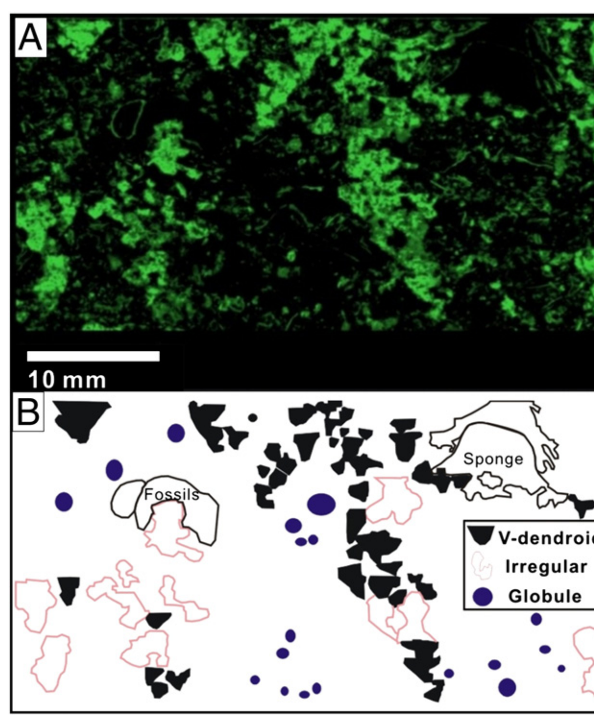

Fig. 6. (A) Graphically enhanced 2-D image with surrounding sediment removed to reveal calcified microbial structures alone. (B) Sketch showing divisions of microbial structures.

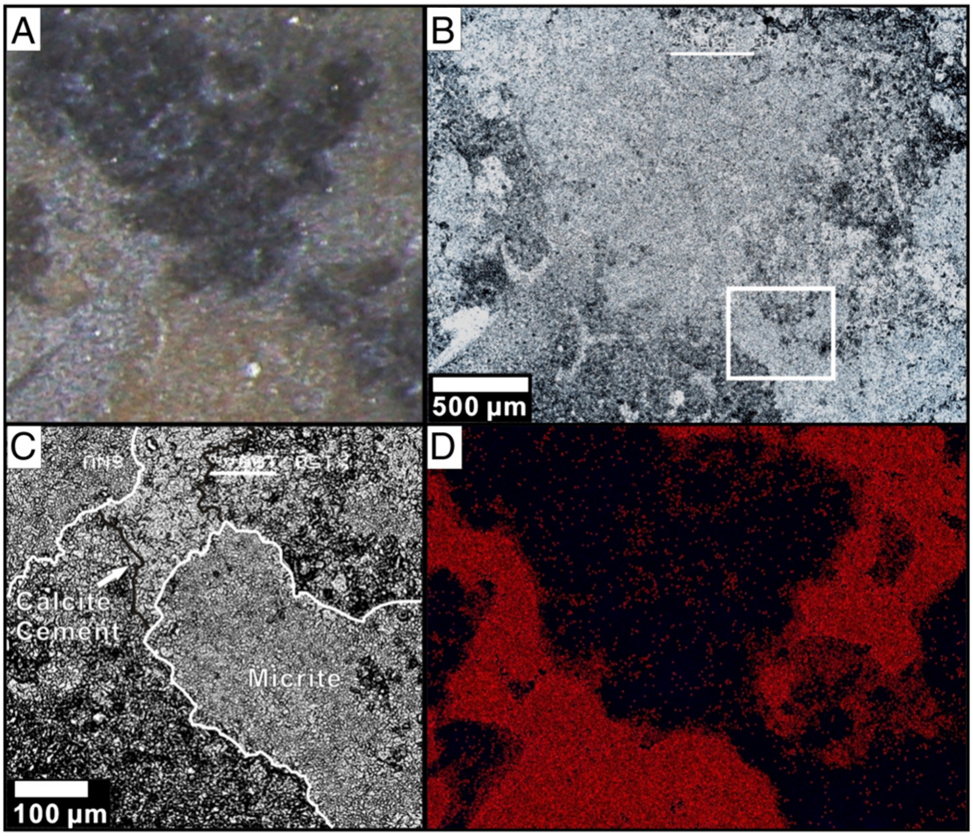

Fig. 7. (A) Original optical view of a slightly etched surface of sample dendroid. (B) SEM BSE view of same sample dendroid. Note the box indicating a branching structure and connection point which is invisible with the naked eye. (C) Enlarged image of boxed region in (A). Dendroids are composed of fine-grained micrite (outlined in white). Large calcite crystals act as cement between the dendroids (outlined in black). (D) EDS analysis of sample showing calcium carbonate in black.

Riding (2000), it is one of the defining features of dendrolite. Unlike stromatolites and thrombolites which can form in large part due to the binding and agglutination of sediment within microbial mats,

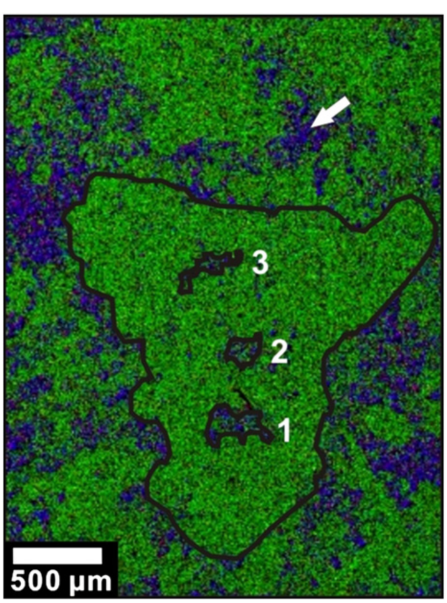

Fig. 8. A composite image of the EDS analyses for the elements calcium (green) and silicon (blue) of a single dendroid (outlined in black). Three porous regions within the dendroid are outlined and numbered in ascending order, and there is an arrow indicating an interstitial region between dendroids, all of which are filled with trapped and bound sediments (allochthonous grains). The numbered inner regions indicate three stages of development in the dendroid's growth.

dendrolites form entirely from the calcification of microbes. The EDS analysis reveals, however, that there exist both porous and interstitial regions within and in between individual dendroids, respectively, in which sediment is trapped and bound (Fig. 8). The trapping and binding of such allochthonous grains is a byproduct of the V-dendroid growth pattern.

Dendroids often appear in large, compound structures consisting of many individual dendroids (Fig. 9A). The sediment surrounding the dendroids consists of trilobite skeletal grains, *Chancelloria*, and detrital fine-grained clastics which have been dolomitized (Fig. 9B). The dendroids consist of several different microstructures. Darker areas are due to the aggregation of round micritic spheres with an average diameter of ca. 80 µm (Fig. 9C). The aggregate usually forms an erect, elongated body which resembles that of *Angusticellularia*. Lighter areas are characterized by aggregates of irregular chambers (Fig. 9D). The chambers are usually larger (ca. 100 µm in diameter) in size than the round micritic spheres and similar to botryoidal *Renalcis* (Flügel, 2004; Riding, 1991b). The chamber walls are about 15–20 µm thick and composed of micrite. One chamber shares its walls with adjacent chambers. The hollow space within chambers is filled with microspar. The aggregate forms upward-elongated and widening colonies. Dendroids of a somewhat obscure structure occasionally occur within the dendrolite buildup as well (Fig. 10A). The internal structure of these chambered *Renalcis*-like dendroids seems to be well preserved; consisting of fine tubular structures which collectively form ill-defined segments of the dendroid (Fig. 10B).

Upward widening or branching dendroid colonies have self-similar, fractal structures consisting of small-scale upward-widening colonies of calcimicrobes (Fig. 9A). The small-scale colony is sometimes topped by sharp, sub-horizontal, and undulatory surfaces from which new tiers of colonies begin (Figs. 9A, 10C). The dendroids' flat tops are

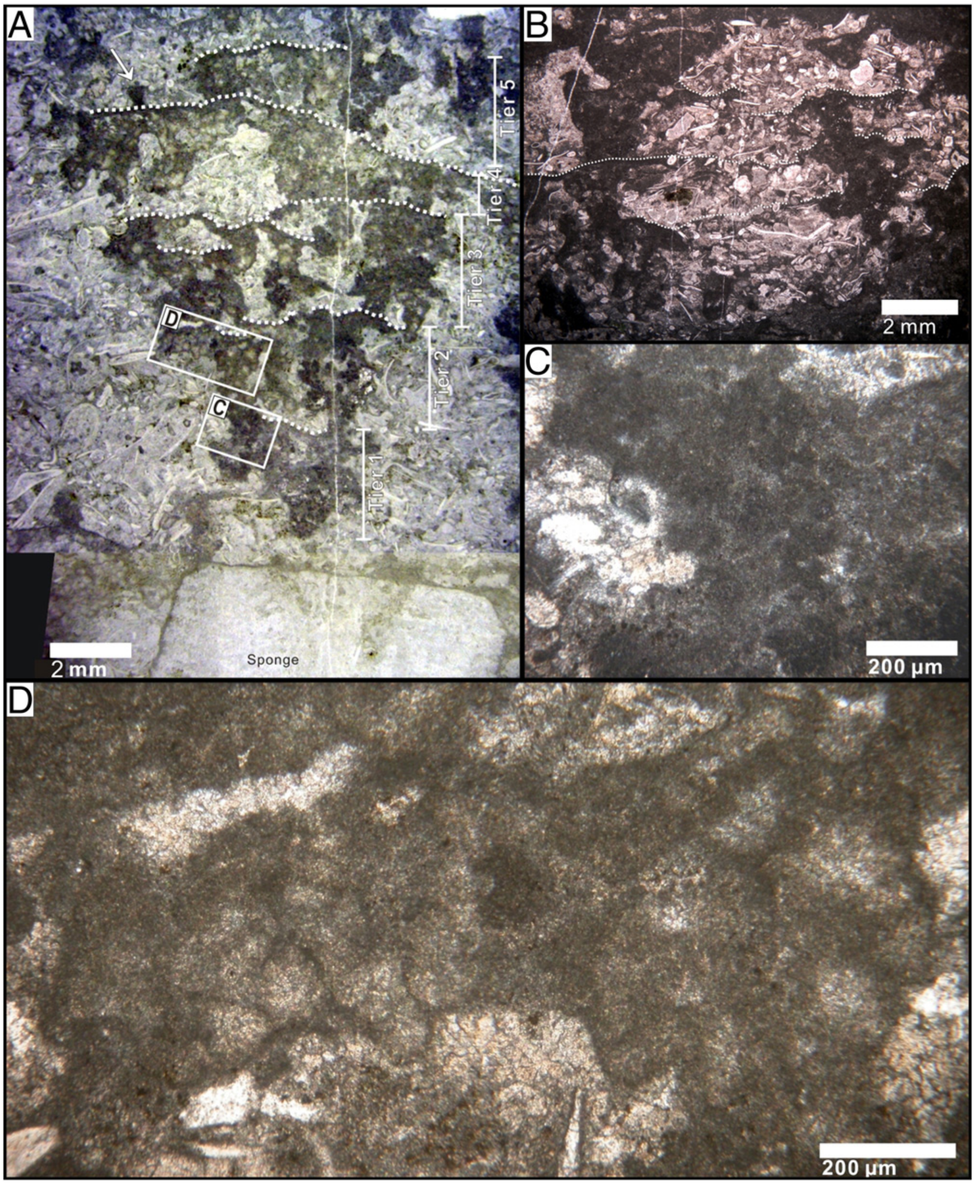

Fig. 9. Photomicrographs of dendrolite and associated sediments. (A) A colony of dendroids grown on a substrative sponge. The dendroids are characterized by two types of aggregation: round micritic spheres and irregular chambers. This whole colony consists of 5 tiers of dendroids. Note the flat surfaces marked by dotted lines and a shoot growing from the sharp surface (arrow). (B) Correlation of the flat surface between different dendroid stairs. Skeletal grains and detrital sediments associated with dendroids include allochems such as trilobite, ostracods, and *Chancelloria*. (C) Details of dendroid consisting of round micritic spheres with agglutinated peloidal texture. Upward-stretched aggregates of these micritic spheres resemble *Angusticellularia*. (D) Dendroid formed by the aggregation of micritic chambers resembling a cellular structure. These connected chambers with micritic walls appear to be botryoidal *Renalcis*.

characterized by a thin encrustation of darker dense microbial micrite (Fig. 10C). This thin layer of microbial encrustation has formed not only on the flattened dendroid surfaces, but also on the skeletal grainstone between dendroids (Fig. 10C). Some surfaces are encrusted by *Girvanella* (Fig. 10D) which was later detached and incorporated into the skeletal sediment between dendroids (Fig. 10D, E).

Some dendrolites seems to lose their pristine microstructures including microbial constituents (Fig. 11). These dendrolites, instead, consist of crystalline dendroids lacking any internal structures identifiable under the microscope (Fig. 11A). The outline of these dendroids suggests a diagenetically modified chambered morphology (Fig. 11B). Microspar fills the hollow space within the chamber. The size of the chambers ranges from 150 μm to 800 μm in diameter. The overall colony tends to be more elongated than that of common micritic dendroids. The associated sediments are a mixture of skeletal grains, fine-grained carbonate, and siliciclastic mud. The 3-D structure of these crystalline dendroids has yet to be analyzed.

6. 3-D analysis

6.1. Dendroids

The most fundamental and common structure within dendrolite is the V-dendroid (Fig. 12A–B). Many V-dendroids appear to be somewhat elongated and possess a more or less conical or prismatic shape. Dendroid surfaces are characterized by small bumps, which are round micritic masses with a diameter of ca. 100 μm and probably correspond to microbial masses (spheres and chambers) typically observed under the microscope (see Figs. 9 and 11). V-dendroids stem from a thin “trunk” (Fig. 12A). The trunk can extend for some distance

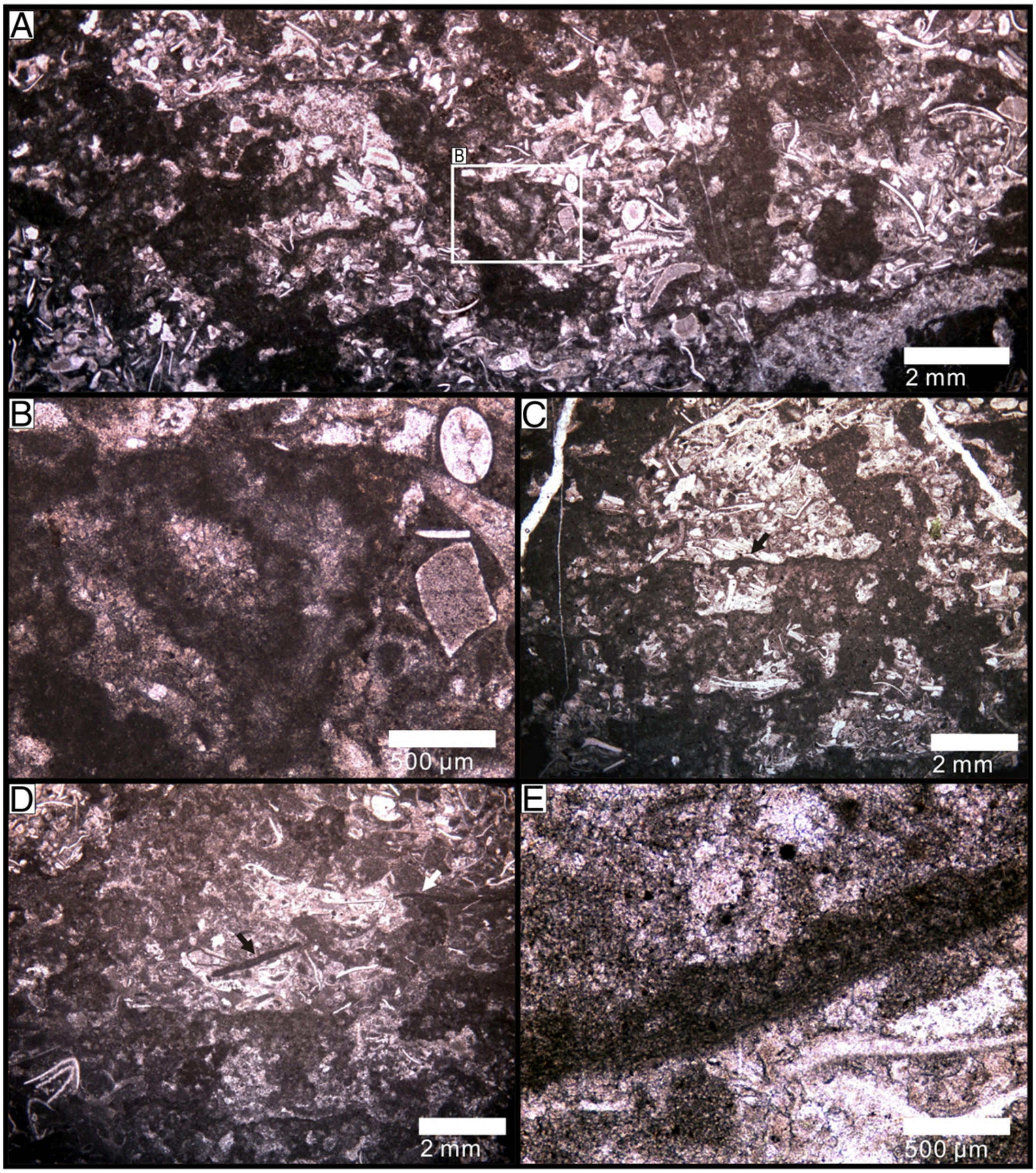

Fig. 10. Photomicrographs of dendroids displaying specific characteristics. (A) Independent dendroids partly consisting of fine-scale inner tubular structures. (B) Magnified view of boxed area in A. Note the narrow dendroid branches. (C) V-dendroid tiers. The flat dendroid surface is encrusted in dense micrite which extends to the top of the surrounding sediments (arrow). (D) *Girvanella* encrustation on dendroid surface (white arrow) and detached *Girvanella* crust (black arrow). (E) Detailed view of the detached *Girvanella* crust.

in the vertical direction (ca. 500 μm), maintaining a consistent thickness. The trunk then expands both laterally and upwardly in a “V” shape to form a base. (Note, base formation can occur with or without trunk extension, depending upon various circumstances). New V-shaped growths then appear on opposite sides of the base. This is referred to as “divergence.” Each of these growths follows the typical quasi-fractal V-dendroid pattern, expanding upwards until they merge together. This is referred to as “convergence.” A small pore space is created as a result of this growth pattern and is filled by sediments. Once convergence is complete, the top of the dendroid flattens and the process either repeats or simply ceases.

Columnar dendroids, rather than growing as separate colonies, emerge from a substrative V-dendroid. They often appear as “shoots” branching off horizontally and growing vertically, or as bulbous growths on top of the substrative V-dendroid (Fig. 12C). These shoots are merely proto-columnar dendroids. A fully developed columnar dendroid is composed of numerous columns stacked one on top of another (Fig. 12D).

Arborescent dendroids are named for their tree-like appearance and structure (Fig. 12E). Whereas V-dendroids and columnar dendroids tend to be more shrub-like in appearance, arborescent dendroids tend to more closely resemble actual trees. They begin growth from a trunk which extends vertically with little horizontal expansion. The branching pattern of arborescent dendroids is similar to that of columnar dendroids in that it begins with horizontal extension from the trunk followed by an almost 90° vertical turn, at which point vertical growth and expansion begin. These branches radiate from the trunk in a spiral manner.

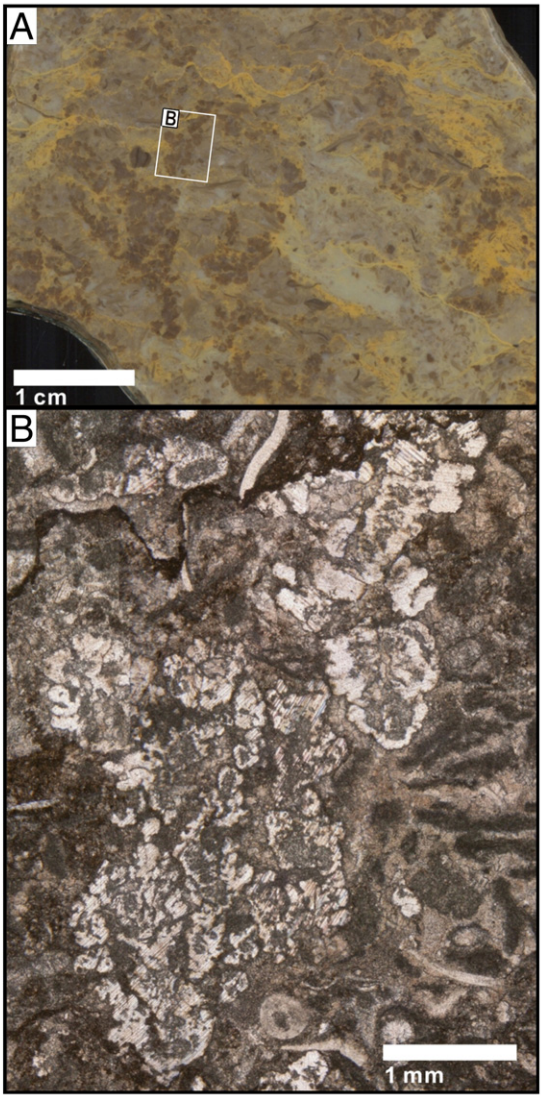

Fig. 11. A polished slab (A) and a thin-section photograph (B) of crystalline dendroids. The dendroids consist mostly of mono-crystalline calcite. The aggregation of *Renalcis*-like chambered bodies forms an upward-growing dendritic structure.

6.2. Interconnections

Dendroids typically begin growth from a substrate (Fig. 13A–B). These substrates can be either purely calcimicrobial in nature, being part of a microbial mat, or they may be fossil fragments encrusted by calcimicrobes. V-dendroids can also act as substrates for the subsequent growth of other V-dendroids (Fig. 13C). This process is called "stacking," and if it occurs successively it can lead to the formation of elaborate dendroid "stairs". These stairs can then connect to and merge with adjacent structures to form a complex web of interconnection. Dendroid stairs can also be connected vertically via "nodules" (Fig. 13C). Nodules are substrates, possibly fossil fragments, encrusted by calcimicrobes, which facilitate the growth of new dendroid stairs after previous stairs have been covered in sediment.

"Tiering" (i.e. formation of tiers) is another common phenomenon of dendrolite formation. It is defined by a series of aligned horizontal dendroid planes with flat surfaces, each stacked one upon another (Fig. 13D). "Tiers" can be distinguished from stairs in that tiers are vertically connected by new trunks, whereas stairs form directly via stacking, without trunk formation (Fig. 13D). Tiering is indicative of interrupted dendroid growth caused by fluctuations in sedimentation rates (Riding, 2000). This leaves the underlying tier abruptly covered, and thus, unable to grow normally. The flat surfaces and sharp boundaries between tiers appear to be small-scale erosional surfaces upon which new tiers of dendroids initiate growth.

Shoots are thin, vertical branching structures which often emerge from substrative V-dendroids (Fig. 13E–F). After some distance of growth shoots tend to expand horizontally and merge with adjacent structures (Fig. 13E–F), laying the foundation for future V-dendroid growth. Occasionally, adjacent dendroids may form small "finger-like" extensions which connect to each other. These "fingers" are merely minor surface outgrowths of dendroids. Fingers can emerge from both columnar and V-dendroids and merge together (Fig. 13G).

7. Structural divisions

Dendrolite is a complex organo-sedimentary rock composed of intricate microbial colonies interconnected at various structural levels. These hierarchical structures can generally be divided into micro-, meso-, macro-, and mega-scales, with differing structures apparent at each scale (Fig. 14). The microstructure refers to the calcimicrobial makeup of dendroid components (i.e., *Angusticellularia*, *Renalcis*, *Girvanella*, etc.) and the manner in which they aggregate to form discrete colonies. The biological basis for how these dendroid components interact to form a single dendroid is still unclear (see Discussion; Pratt, 1984), but it is evident from the thin-section observations that there is a significant degree of intermingling among them to the extent that a single dendroid is an amalgamation of different microbial remains and/or products. The mesostructure consists of the smallest structures visible with the naked eye and is subdivided into primary, secondary, and tertiary structures. The primary mesostructure is represented by the basic V-dendroid, which itself is a composite of repetitive micro-growth cycles. Its growth pattern can be clearly divided into four stages: 1) trunk extension and base expansion, 2) divergence, 3) expansion and convergence, followed by repetition of stages 2 and 3 until 4) growth completion (Fig. 14). The primary mesostructure constitutes the majority of dendritic structures and acts as a substrate for further development. The secondary mesostructure consists of columnar and arborescent dendroids, which possess a fully developed V-dendroid infra-structure with small columns and/or branches as accessory structures. The tertiary mesostructure involves the emergence of organized vertical arrays of dendroids by the processes of stacking and/or tiering. The macrostructure refers to the greater organization of dendritic structures into microbial units within a bioherm. These macrostructures may appear tabular, domal, or columnar in shape. The dendrolite bioherm of interest to this study consists of tabular and domal macrostructures (see Fig. 3A). The study sample was derived from the uppermost tabular unit of the dendrolite bioherm (unit 7). Macrostructures grow continuously, one on top of another, so that the dendritic structures often transition uninterrupted, or may be separated by intervening sediments. The scale and dimension of the dendritic structures within each macrostructure varies. Tabular macrostructures tend to possess small-scale (1–3 mm wide), compact dendroids, whereas domal macrostructures tend to possess large-scale (0.5–1 cm wide), vertically elongated dendroids. The megastructure refers to the scale of an entire dendrolite bioherm composed of multiple macro-structures of varying dendritic constitution.

8. Discussion

3-D CT reconstruction has provided accurate observations of dendroids and their interconnections allowing for the development of a general classification scheme (Fig. 14). A question that arises is whether variations in dendroid morphology reflect differences in the microbes or in the micro-environment?

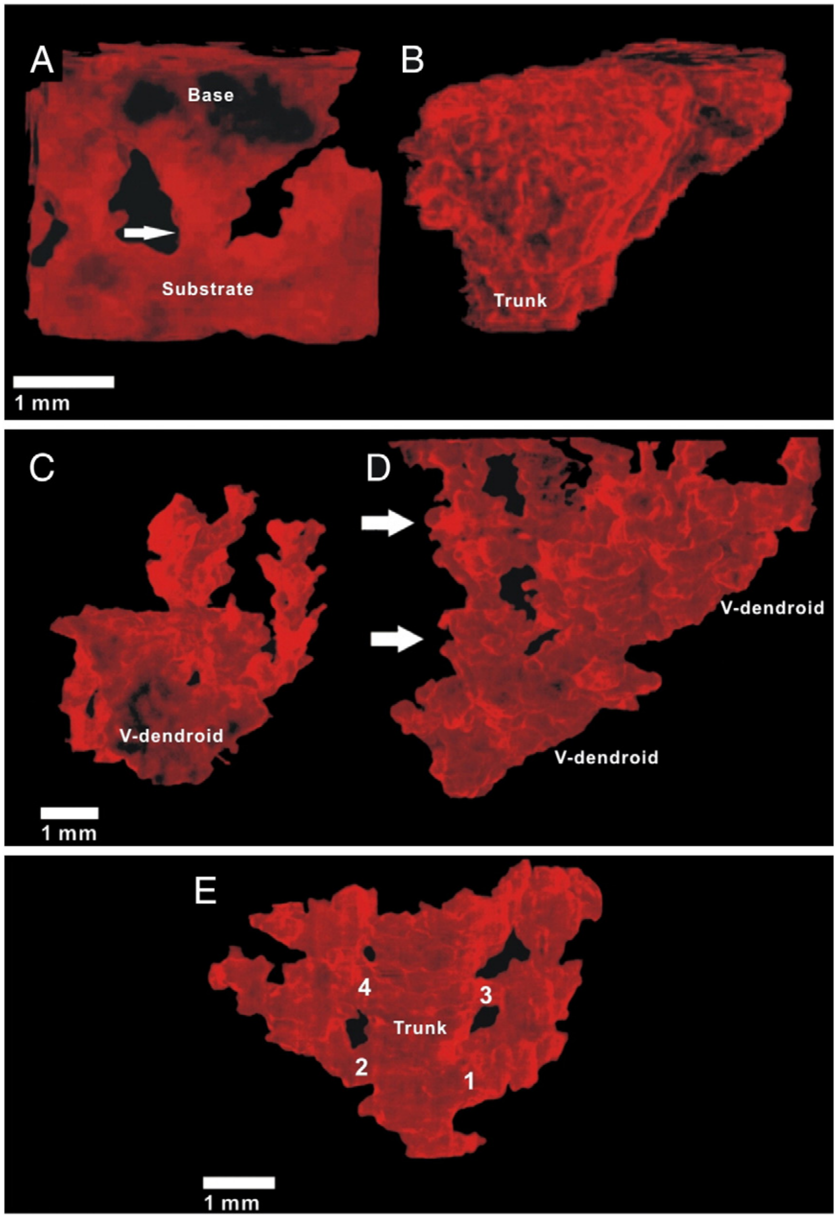

Fig. 12. 3-D reconstruction of dendroids. (A) Trunk (arrow) extending to form V-dendroid base. (B) V-dendroid with dimensions of 3.4 mm (width) × 2.7 mm (height) × 4.5 mm (depth). (C) Two small columnar dendroids emerge from a V-dendroid. A shoot emerges on the right of the dendroid, in addition to a bulbous growth on top of the dendroid. (D) Stacked columnar dendroids (arrows). The structure emerges from a V-dendroid and connects to adjacent V-dendroids horizontally as it rises. (E) Example of an arborescent dendroid possessing a trunk from which four individual branches emerge (numbered in ascending order). Branches emerge horizontally and curve upward before expanding on their own.

The basic dendroid growth pattern consists of upward widening- or branching-aggregates of microbial colonies which are also very common in some types of stromatolites, though on a smaller scale. Such stromatolite branching structures form a range of morphologies which vary in branch thickness and frequency. These variables can be influenced by factors such as the rate of sedimentation in the micro-environment as well as the rate of growth within a microbial colony. (Dupraz et al., 2006). Similarly, the basic control mechanism for dendroid morphology seems to be partial burial of microbial colonies due to fluctuations in sedimentation rates. The buried microbial colonies are unable to grow due to mechanical obstruction, which results in a shutting-down of nutrient input, as well as insufficient sunlight for photosynthesis, provided the microbes in question were phototrophs. Micro-currents may have, also, played an important role in determining dendroid growth patterns and morphology; exerting control over microbial colony sizes and encouraging calcite precipitation (Pratt, 1984).

Tertiary mesostructures, such as stairs and tiers, are formed by various means of interconnection between V-dendroids. Stacking occurs by the successive growth of V-dendroids, one directly on top of another. Excessive sedimentation, followed by partial erosion of overlying dendroids, and new growth via trunks, appears to be responsible for the formation of tiers. The eroded surface was occasionally encrusted by a thin microbial film consisting of entangled tubes of *Girvanella*. The morphologies of these microbial colonies are not directly comparable to those of trees or corals whose general morphologies are genetically programmed. New insights into bacterial colonies with specific morphologies due to physiology (Andrews, 1998; Ben-Jacob and Levine, 2006; Shapiro, 1998), however, suggest that dendroid-forming microbes might be able to

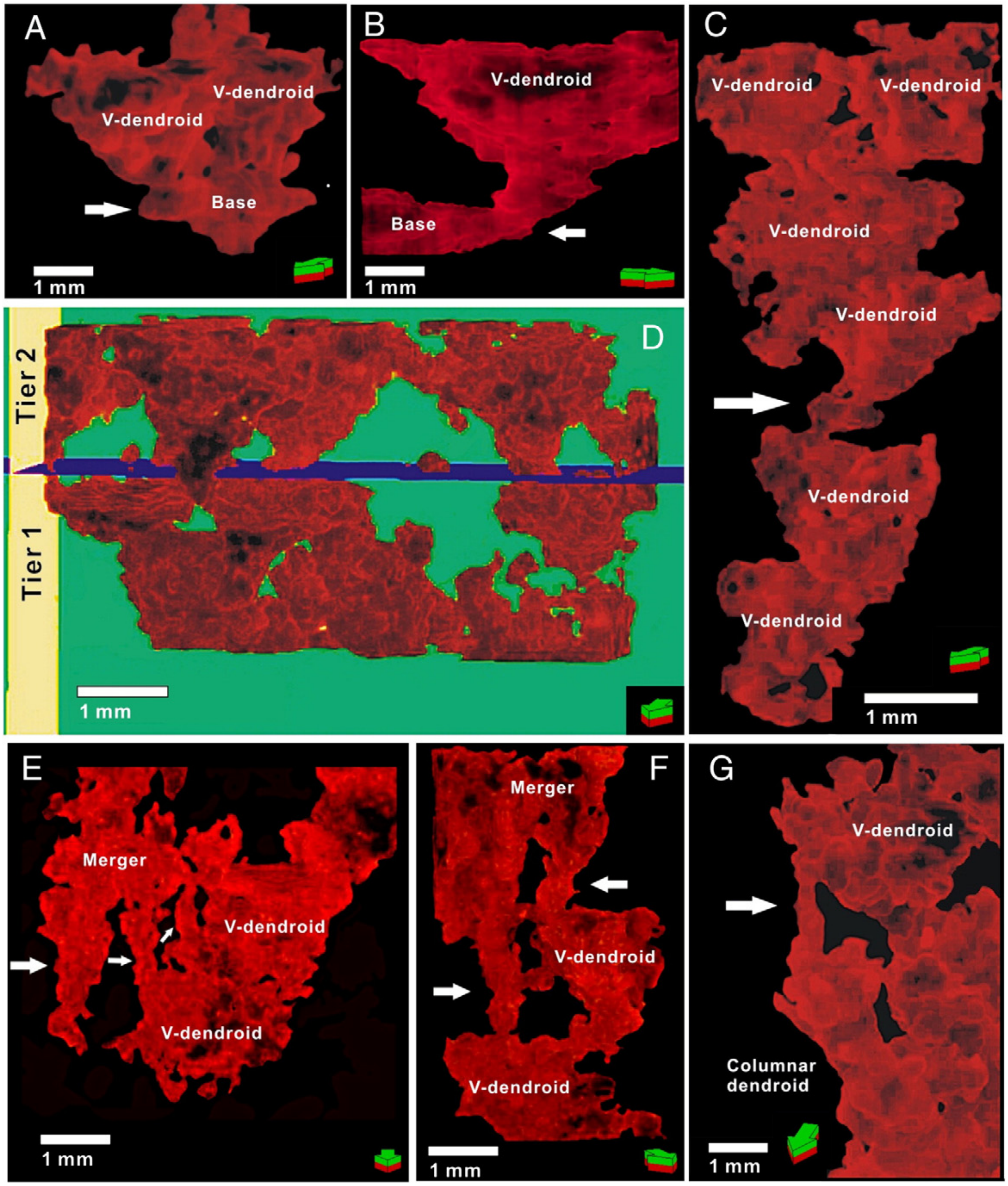

Fig. 13. 3-D reconstruction of dendroids. Arrow in corner indicates orientation (arrow points toward front of sample). (A) Substrate upon which two individual dendroids have emerged and subsequently merged together. (B) Another example of a substrate from which a single V-dendroid emerges. (C) Two dendroid stairs are vertically connected by a nodule (arrow). The nodule acts as a substrate for initiation of the upper stairs. (D) Two dendrolite tiers. Horizontal blue plane indicates boundary between tiers. (E) Two stacked V-dendroids from which two vertical shoots arise to merge with another independent vertical shoot (arrows indicate shoots). (F) Two vertical shoots (arrows) emerge from different V-dendroids. Both rise approximately 3 mm and merge horizontally. (G) Two "fingers"; one emerging from a V-dendroid, the other from a columnar dendroid. They merge together with a faint connection.

create branching morphologies in a similar manner to multi-cellular organisms.

The 2-D thin-section observations revealed *Renalcis* and *Angusticellularia* to be the main calcimicrobial constituents of the sample dendroids, with other calcimicrobes playing minor roles. It is theoretically possible that each type of dendroid (i.e., V-dendroid, columnar dendroid, and arborescent dendroid) is composed of different calcimicrobial structures or differing proportions of these structures in combination. If it were proven by thin-section correlation that there is no appreciable difference in the microbial makeup of each type of dendroid, then it might be possible to deduce that the differences in morphology are merely circumstantial and dependent upon some external factors in the micro-environment.

Pratt (1984) early on suggested that calcimicrobes (*Epiphyton*, and *Renalcis*, and *Angusticellularia*) ought to be reinterpreted as "diagenetic taxa" rather than genetically distinct organisms, citing the presence of intermediate forms, their occurrence in conjunction with one another, and their frequent intergrowth (often within a single microbial colony); something which is evident in this study. According to this interpretation, *Angusticellularia* may merely be an occluded

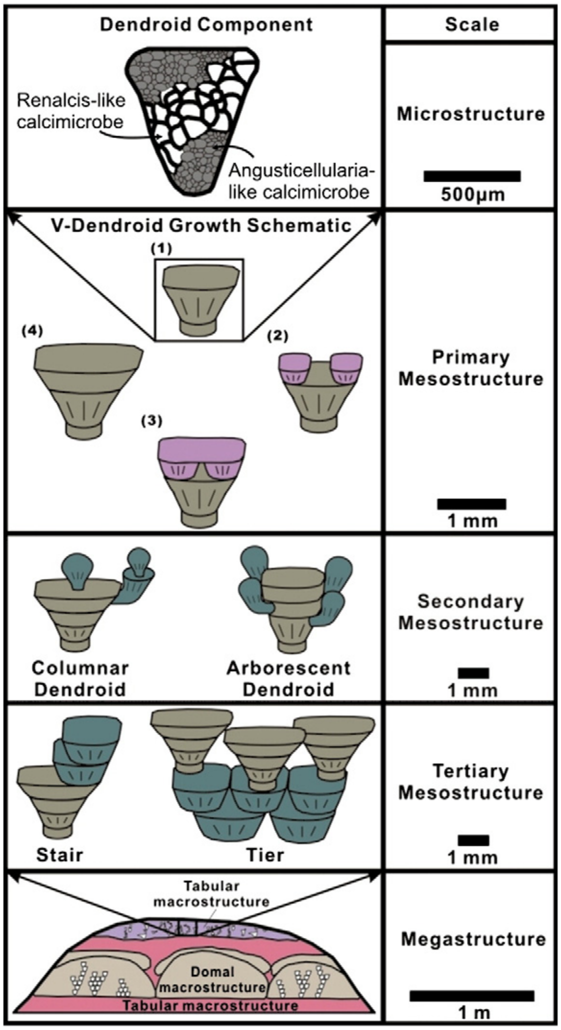

Fig. 14. Structural divisions of dendrolite bioherm according to scale. Primary mesostructure consists of the V-dendroid. V-dendroid growth schematic is divided into four stages: 1) trunk extension and base expansion, 2) divergence, 3) expansion and convergence, followed by subsequent repetition of stages 2 and 3, until 4) growth completion.

form of *Renalcis* which results from the thorough calcification of small colonies of coccoid microbes in their entirety, whereas *Renalcis*, *sensu stricto*, results when colonies of the same algae grow to larger sizes and become calcified in their exterior sheaths only (Pratt, 1984, Fig. 13).

Recent findings have affirmed the notion that *Renalcis* may in fact be a calcified exopolymeric substance (Shapiro, 2004; Stevens and Sumner, 2002). If this is true then it may suggest that the formation of *Renalcis* (and likewise the associated *Angusticellularia*) is further evidence of specific micro-environmental conditions, such as pCO_2 and alkalinity, which are linked to microbial metabolism and $CaCO_3$ precipitation. These conditions, by directly influencing the morphological development of the constituent calcimicrobial colonies, may simultaneously have an indirect affect on the regular V-dendroid growth pattern; leading to the production of a variety of different mesostructures and irregular dendritic forms. That the V-dendroid is the most common and typical form indicates that it represents the natural upward-expanding growth tendency of the constituent microorganisms. It is the dynamic interplay, however, between the natural growth tendency and the temporary micro-environmental conditions which work to produce the myriad of identifiable shapes and structures.

9. Conclusions

3-D computed tomographic reconstruction is a valuable tool for observing three-dimensional dendritic structures. It provides detailed insight into: 1) the original morphology of individual dendroids, thus allowing for adequate classification, 2) the interconnections between individual dendroids, revealing the organic interactions between the original microbes, and 3) the structural divisions of dendrolite and their developmental processes.

In addition, 2-D observational techniques, such as Volview enhanced imaging, SEM and EDS analyses, and thin section observations provide valuable insights into the physical form and chemical composition of the dendritic structures. *In situ* observation of dendrolite bioherms also provides a better understanding of the macro-scale growth patterns and the environmental conditions surrounding dendrolite growth.

Dendroid morphology is classified into three major categories: V-dendroids, columnar dendroids, and arborescent dendroids. V-dendroids are by far the most prevalent type and constitute the basis of dendritic structures. Interconnections between dendroids are divided into four basic structures: trunks, nodules, shoots, and fingers. The vertical relationships between V-dendroids are further classified into stairs and tiers, representing the two processes of stacking and tiering, respectively. The structural divisions of dendritic growth are summarily divided into the four scales: micro-, meso-, macro-, and mega, the main focus of which is the mesostructure which is further subdivided into primary, secondary, and tertiary structures. V-dendroids make up the primary mesostructure and develop in four basic stages: 1) trunk extension and base expansion, 2) divergence, 3) expansion and convergence, followed by repetition of stages 2 and 3, until 4) growth completion, and the subsequent emergence of new dendroids by either stacking or tiering.

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