Vermetid Buildups from Grand Cayman, British West Indies

Brian Jones and Ian G. Hunter

ABSTRACT

Vermetid buildups, formed primarily of Dendropoma, are found in the coastal areas near Bodden Town and Great Bluff Estates on Grand Cayman. These gastropods are commonly encrusted by foraminifera (Homotrema rubum, Acrasina? sp.), coralline algae, and cyanobacteria. Spaces between the gastropods are filled with silt- to sand-sized sediment derived from the nearby lagoon. Bioerosion by echinoids, bivalves, worms, algae, and fungi substantially modified these buildups. C14 dating of the gastropod shells suggests that the in situ buildups died during the period of 1625-1740 AD. The presence of vermetids at these localities on Grand Cayman is not consistent with the high-energy conditions in which these gastropods usually thrive. Today, there are no living vermetids at these localities and the active biological processes are bioerosion and encrustation. The demise of the in situ vermetid buildups during the period of 1625-1750 AD may have been related to changes triggered by the Little Ice Age. Alternatively, their demise may have been caused by a change in sea-level or a significant reduction in the wave energy that was impinging on the coastlines.

INTRODUCTION

Vermetid buildups are generally found in marginal areas of the tropics (Safriel, 1975) such as Bermuda (Stephenson and Stephenson, 1954, 1972; Ginsburg et al., 1971; Shinn, 1971; Schroeder, 1972; Ginsburg and Schroeder, 1973; Safriel, 1974, 1975), the Mediterranean (Peres and Picard, 1952; Safriel, 1966, 1974, 1975; Tzur and Safriel, 1978; Ayal and Safriel, 1980; Barash and Zenziper, 1985), the Cape Verde Islands (Crossland, 1905), the Fernando de Noronha Islands and the Brazilian coast (Kempf and Laborel, 1968; Laborel, 1977, 1979; Jindrich, 1983), West Africa (Laborel and Delibrias, 1976; Laborel, 1977), and Florida (Stephenson and Stephenson, 1950; Warmke and Abbott, 1962; Shier, 1969). Vermetids are also common throughout the subtropical part of the Pacific (e.g., Yonge, 1932; Cramwell and Moore, 1938; Hadfield et al., 1972; Brattström, 1980; Hopper, 1981; Keen, 1983; Hughes, 1983; Colgan, 1985). Although present throughout the Caribbean (Table 1), buildups of vermetids have only been reported from Curacao (Focke, 1977), Barbados (Lewis, 1960), and Grand Cayman (Jones and Hunter, 1988). Many Caribbean intertidal zones, where vermetids should be present, are characterized by algal ridges that include only a few of these gastropods (Glynn, 1973; Adey, 1975; Adey and Burke, 1975).

Buildups formed of vermetid gastropods are present at two localities on Grand Cayman (Figures 1, 2). This paper describes the biological components involved in the construction of these buildups and comments on their geological setting.

VERMETID BIOLITHITES OF GRAND CAYMAN

The buildups are formed of tightly coiled to loosely sinuous or almost straight vermetid shells that are at least 1.5 cm long with an average inside diameter of 1.3 mm and average shell thickness of 0.3 mm (Tongpenyai, 1989; Figures 3, 4, 5). Shells that initially had a tightly coiled shell tended to straighten out during ontogeny (Figure 4). These shells typically have weakly developed lamellar striae on their exterior (Figure 5A) and a dendropomatid operculum with a well-developed axial mammilla and flange (Figure 5B). The taenioglossate radula, found in the shells, have a squarish to rectangular transverse rachidian tooth with its posterior corners turned down to form distinct cusps (Figure 5C). The lateral
Table 1. Recorded distribution of vermetids in the Caribbean.

<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Author</th>
</tr>
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<tbody>
<tr>
<td>Bahamas</td>
<td>Spirogyalus irregularis</td>
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</tr>
<tr>
<td>Bahamas</td>
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</tr>
<tr>
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<td>Barbados</td>
<td>Petalectonchus cf. varians</td>
<td>Lewis, 1960</td>
</tr>
<tr>
<td>Bermuda</td>
<td>Petalectonchus (Macrophragma) erectus</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Bermuda</td>
<td>Petalectonchus (Macrophragma) variana</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Bermuda</td>
<td>S. (S.) annulatus = D. corrodens</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Bermuda</td>
<td>Spirogyalus (Novastoa) irregularis</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Bermuda</td>
<td>Dendropoma sp.</td>
<td>Bromley, 1978</td>
</tr>
<tr>
<td>Brazil</td>
<td>Serpulorhesis decussatus</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Caribbean</td>
<td>Dendropoma (D.) nebulosum</td>
<td>Keen, 1961</td>
</tr>
<tr>
<td>Caribbean</td>
<td>Petalectonchus (Macrophragma) variana</td>
<td>Keen, 1961</td>
</tr>
<tr>
<td>Caribbean</td>
<td>Serpulorhesis (S.) decussatus</td>
<td>Keen, 1961</td>
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<tr>
<td>Cuba</td>
<td>Dendropoma (D.) corrodens</td>
<td>Keen, 1961</td>
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<tr>
<td>Florida</td>
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<td>Keen, 1961</td>
</tr>
<tr>
<td>Florida</td>
<td>Petalectonchus (Macrophragma) mcgintyi</td>
<td>Keen, 1961</td>
</tr>
<tr>
<td>Florida Keys</td>
<td>Dendropoma irregularis</td>
<td>Morton, 1965</td>
</tr>
<tr>
<td>Florida Keys</td>
<td>Spirogyalus sp.</td>
<td>Stephenson and Stephenson, 1972</td>
</tr>
<tr>
<td>Florida to Brazil</td>
<td>Petalectonchus (Macrophragma) erectus</td>
<td>Abbott, 1974</td>
</tr>
<tr>
<td>Florida to Brazil</td>
<td>Petalectonchus (Macrophragma) variana</td>
<td>Abbott, 1974</td>
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<td>Grand Cayman</td>
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<td>Petalectonchus (Macrophragma) variana</td>
<td>Glynn, 1968</td>
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<td>Puerto Rico</td>
<td>Petalectonchus mcgintyi</td>
<td>Warmke and Abbott, 1962</td>
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<td>SE Florida to Brazil</td>
<td>Spirogyalus (Novastoa) irregularis</td>
<td>Abbott, 1974</td>
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<td>SE Florida to Lesser Antilles</td>
<td>S. (S.) annulatus = D. corrodens</td>
<td>Abbott, 1974</td>
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<td>St. Croix</td>
<td>Dendropoma sp.</td>
<td>Adey, 1975</td>
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<td>West Caribbean</td>
<td>Stephopoma myrakeenae</td>
<td>Abbott, 1974</td>
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<tr>
<td>West Indies</td>
<td>Petalectonchus floridanus</td>
<td>Warmke and Abbott, 1962</td>
</tr>
<tr>
<td>West Indies</td>
<td>Serpulorhesis risiei</td>
<td>Warmke and Abbott, 1962</td>
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</table>

Teeth appear to have one cusp on their inner edge whereas the marginal teeth are simple hooked cones with a broad rounded base. The apical region of the shell has one, two, or three columella laminae (Figure 5D). The aragonite shell is formed of up to 12 alternating prismatic and crossed-lamellar layers (Figure 5E, F).

Individual shells may be segregated from neighbouring shells, cross-cut neighbouring shells, or share a compromise margin with another shell (Figure 5F, G). Collectively, the shells form large honeycombed masses that encrust hard substrates.

Most Cayman vermetids are considered to be Dendropoma because their opercula are the same size as their apertures (cf. Barash and Zenziper, 1985) and have well-developed axial mammilla comparable with those figured for Dendropoma by Keen (1961, Figure 33), Hadfield et al. (1972, Figures 3, 9), Morton (1965, Figure 5D, E), Hughes (1978, Figure 3), and Barash and Zenziper (1985, Figure 4). The Cayman vermetids corrode the surrounding limestone and neighbouring shells in the manner reported for other Dendropoma (cf. Keen, 1961; Morton, 1965; Bromley, 1978; Barash and Zenziper, 1985). Radula from the Cayman vermetids are similar to Dendropoma and Petalectonchus radulas described by Morton (1965). According to the classification of Keen (1961), the Cayman vermetids belong to the subgenus Novastoa because they form honeycombed sheets that encrust exposed rock surfaces.

Species of Dendropoma are identified by their colour, soft-part anatomy, shell morphology, operculum structure, and radula structure (e.g.,
The best examples of vermetid buildup are found near Great Bluff Estates (Figure 1) where energy levels are low because of an offshore reef (Figure 2). During periods of high winds and storms, however, there can be considerable wave activity in this area.
The cliff near Great Bluff Estates, formed of dolostones that belong to the Miocene Cayman Formation, is characterized by a ‘wave-cut notch’ (up to 1.0 m deep and 0.3 m high). The vermetids form an upper ledge and a lower ledge (Figure 2). In addition, there is a large (2 m × 1.5 m × 0.75 m) block of vermetid buildup on the beach (Figures 3B, 4).

Upper Ledge

The buildup (Figure 3B) on the upper ledge, which can be traced along the coastline for 200–300 m, is presently covered by water that is 10 to 30 cm deep. Its top is just below the base of the ‘wave-cut notch’. This buildup, formed of vermetids (Figure 5), coralline algae, and *H. rubrum* (Figure 6A, C, D, E), has been modified through bioerosion by *Echinometra*, sponges (*Cliona*) worms, bivalves, algae, and fungi. This buildup is presently encrusted by abundant green and fleshy algae.

C14 dating of the shells gave an age of 278 ± 90 years BP.

Lower Ledge

The vermetid buildup of the lower ledge, in water 0.6 to 0.8 m deep, is up to 1.5 m wide and extends along the coastline for 50 m. The buildup

Figure 3. Hand samples of the vermetid buildups from the lower ledge at Great Bluff Estates (A) and the loose block at Great Bluff Estates (B) showing vermetid shells (v), sediment (white) and laminae formed of *Homotrema rubrum* (arrows).
Figure 4. A and B, General views of part of block on beach at Great Bluff Estates showing the density of the vermetid shells which are either straight to slightly sinuous (A) or tightly coiled (B).

has a core of densely packed *Dendropoma* and an outer layer formed of *H. rubrum* and *Acervulina?* sp. (Figure 6B, F, G, H) with lesser numbers of coralline red algae and partly calcified cyanobacteria (Figure 3A). The *Dendropoma*, which colonized the rocky substrate, built up a honeycombed mass of tightly coiled shells. Although most shells are well preserved, others are partly replaced by fluorescent calcite. Areas between the shells are filled by encrusting organisms and sediment. The lower ledge has suffered little bioerosion and is therefore harder than the buildup of the upper ledge.

$^{14}C$ dating of the shells gave an age of 318 ± 90 years BP.

Loose Block on Beach

This vermetid buildup is a complex intermixture of *Dendropoma, H. rubrum, Acervulina?* sp. and sediment (Figure 4A, B). The *H. rubrum* and *Acervulina?* sp. commonly form collars around the vermetid shells (Figure 7). The *H. rubrum* are conspicuous because their red colour contrasts sharply with the amber vermetid shells and the white to cream sediment (Figure 3A). The numbers of *H. rubrum* are variable even in the context of a small hand sample. In many cases the *H.*

Figure 5. Morphology of *Dendropoma (Novastoa) irregularae.* A-E, SEM photomicrographs. F and G, thin section photomicrographs. (A) Shell exterior with transverse growth lines. (B) Operculum with well developed central mammilla and flange. (C) General view of radula. (D) Two columnellar laminae in terminal region of shell. (E) Alternating cross-lamellar layers and prismatic layers of shell. (F and G) One shell cross-cutting a neighbouring shell, note that the part of the shell not affected by neighbouring shell continued to grow.
**Figure 6.** Encrusting foraminifers that occur around the vermetid shells (V). (A and B) Thin section photomicrographs. (C to H) SEM photomicrographs. (A) Vermetid shell encrusted by *Homotrema rubrum*. (B) Vermetid shell encrusted by *Acervulina*? sp. (C) Concentric growth pattern of *H. rubrum* between two vermetid shells. (D) Interior of *H. rubrum* showing imperforate walls and isolated cribrate aerolae. (E) Outer surface of *Homotrema rubrum* showing cribrate aerolae between imperforate walls. (F) *Acervulina*? sp. encrusting a vermetid shell. (G) General morphology of *Acervulina*? sp. (H) Perforate walls of *Acervulina*? sp.

*H. rubrum* and/or *Acervulina* sp. fill the intra-shell spaces and bind the shells together (Figure 7).

Some vermetid shells are encased by a thin (< 0.5 mm) layer of dense, dark coloured, fluorescent micrite that formed by destructional and constructional processes. Destructional envelopes, less than 0.2 mm thick, are formed by the boring-filling-boring mechanism of micrite envelope formation (cf. BATHURST, 1966; KOBLUK and RISK, 1977a,b). In this case, boring algae and fungi appear to be responsible for the boring. Constructional envelopes, formed by the combination of microbe calcification in the body chambers of encrusting *H. rubrum*, and micritization of *H. rub-
Figure 7. General view of thin section of vermetid buildup from the loose block, Great Bluff Estates, showing *Homotrema rubrum* (H) and sediment (S) that occurs between the vermetid shells (v) which form the framework.

Figure 8. SEM photomicrographs showing components of the *Homotrema rubrum* crust that occurs on the lower ledge at Great Bluff Estates. (A and B) Coralline red algae. (C) Surface with partly calcified cyanobacteria. (D-F) Detailed views of calcified cyanobacteria.
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Table 2. Environmental setting of Dendropoma (Novastoa).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Species</th>
<th>Zone</th>
<th>Location Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Africa</td>
<td>D. corallinaceum</td>
<td>1 m tidal height centered on M.W.M.</td>
<td>Exposed coastline</td>
<td>Hughes (1978, 1979)</td>
</tr>
<tr>
<td>Brazil</td>
<td>Dendropoma sp.</td>
<td>Just below H.W.M.</td>
<td>Exposed ledges</td>
<td>Sanlaville (1972)</td>
</tr>
<tr>
<td>Israel</td>
<td>Dendropoma sp.</td>
<td>At mean sea level</td>
<td>Exposed wave swept areas</td>
<td>Safriel (1966, 1975)</td>
</tr>
<tr>
<td>Israeli</td>
<td>Dendropoma sp.</td>
<td>Exposed wave swept areas</td>
<td>Hard substrate in strong wave action</td>
<td>Tzur and Safriel (1978)</td>
</tr>
<tr>
<td>Curacao</td>
<td>Dendropoma sp.</td>
<td>Surf zone</td>
<td>Exposed wave swept areas</td>
<td>Focke (1977)</td>
</tr>
<tr>
<td>Not specified</td>
<td>Dendropoma sp.</td>
<td>Upper infra-littoral</td>
<td>Exposed ledge in strong wave action</td>
<td>Kempf and Laborel (1978)</td>
</tr>
<tr>
<td>Fernando de Noronha Islands</td>
<td>Dendropoma irregular</td>
<td>Centered on M.W.M.</td>
<td>Exposed ledge in strong wave action</td>
<td>Jindrich (1983)</td>
</tr>
</tbody>
</table>

The fluorescent micrite of these envelopes contrast sharply with the non-fluorescent aragonite of the vermetid shells.

Sediment between the vermetid shells is formed of poorly sorted silt- to sand-sized skeletal grains embedded in a dense, dark-coloured, fluorescent micrite (Figure 7). Recognizable skeletal grains include Halimeda plates, red algae, fragments of vermetid gastropods, bivalves, and foraminifera. All grains show evidence of boring by algae and/or fungi and most are micritized to the extent that identification is impossible. Peloids are present locally. Although most chambers in the vermetids contain fine-grained sediments, some contain coarse-grained sediment like that around the gastropods. Some chambers in the vermetid shells are lined with high-Mg calcite cement.

C¹⁴ dating of shells from this block yielded an age of 678 ± 90 years BP suggesting that it was not derived from the lower or upper ledges. Despite extensive searches in the surrounding area, the place of origin of this block is not known.

**HOMOTREMA RUBRUM CRUST ON LOWER VERMETID BIOLITHITE, GREAT BLUFF ESTATES**

The upper and seaward surfaces of the vermetid buildup in the lower ledge at Great Bluff Estates are coated by a layer, up to 2 cm thick, formed of H. rubrum (50–90%) with lesser numbers of coralline red algae and partly calcified cyanobacteria (Figure 3B). Vague laminations are defined by the colour contrast between the red H. rubrum and the thin white laminae of coralline algae and micrite (Figure 3B). The coralline red algae forms thin layers (Figure 8A, B), generally less than 2 mm thick, that directly overlie the H. rubrum. The red algae skeletons are not altered and have no sediment or cements in their cells.

Exposed surfaces of the buildup are green because they are covered with a mat formed of cyanobacteria and coralline red algae (Figure 8). This combination was probably responsible for the other white laminae that are present between the H. rubrum laminae (Figure 3B). Many cyanobacteria filaments in the surface mats are partly or totally calcified (Figure 8C, D, E) by irregularly shaped calcite crystals up to 4 μm long. Associated with the filaments are hemispherical spores (Figure 8F) that are akin to those described by Jones (1987, Figure 6C, D). There is no evidence of filaments trapping grains. Locally, the laminae appear to be formed mostly of micrite and it is difficult to detect the presence of filaments even at high magnifications on the SEM. Extensive calcification may have disguised the original filaments (cf. Jones and Motyka, 1987).

**DISCUSSION**

Significance has been given to the positions of fossil vermetids because they may record sea-level standstills over the last 5,000 years (e.g., Van Andel and Laborel, 1964; Kempf and Laborel, 1968; Delibras and Laborel, 1971; Sanlaville, 1972; Laborel and Delibras, 1976; Laborel, 1977). Kempf and Laborel (1968) and Laborel (1977, 1979) also drew attention to the fact that vermetids seem to be disappearing from the coastlines of Brazil and West Africa. Although the reason for such a decrease is not known, Laborel (1977) suggested that it might be related to increased turbidity of coastal waters, oil pollution, or some unknown biological phenomenon. Grand Cayman appears to follow a similar pattern because there are fossil, but few living, vermetids.

Modern Dendropoma typically thrive in a narrow zone (< 1 m) centered on mean sea level where there is a rocky substrate and exposure to strong onshore waves (Table 2). Depending upon the viewpoint taken, this ecological niche offers
distinct disadvantages or advantages to the vermetids (Table 3). From a global perspective, their ecological niche appears hostile because of the problems associated with feeding, reproduction, and competition in such high energy conditions (cf. Hughes, 1979—Table 3). Nevertheless, vermetids are successful in this niche and their adaptation to the so-called hostile conditions are actually to their advantage (cf. Barash and Zenziper, 1985—Table 3). Despite their ability to take advantage of this niche, their sedentary, attached mode of life means that they cannot overcome adverse environmental conditions caused by external factors (cf. Hughes, 1979—Table 3). A change in sea level or energy levels, for example, usually leads to their demise.

The vermetids at Bodden Town and Great Bluff Estates are not alive today. Indeed, these buildups are currently the sites of other biological activity. Bioerosion is evident at both localities. At Great Bluff Estates maximum bioerosion is found in the buildup of the upper ledge where the water is shallow and more active. The vermetid buildup located on the lower ledge shows significantly less bioerosion. At Bodden Town, the vermetid buildup has suffered considerable bioerosion (cf. Jones and Goodbody, 1984) with the chief agents of bioerosion being echinoids, sponges (Cliona), worms (sipunculids and siphonids), bivalves (Lithophaga), Lithotrya, algae, and fungi. The exposed surfaces of the vermetid buildups commonly provide ideal substrates on which other organisms can colonize. At Great Bluff Estates, for example, the surfaces of the lower vermetid biolithite are covered with a crust formed of Homotrema rubrum and cyanobacteria filaments.

The reason(s) for the demise of the in situ vermetid buildups at Great Bluff Estates and Bodden Town are not really apparent. Today, the coastal areas at Great Bluff Estates and Bodden Town are characterized by relatively calm waters because they are separated from the open ocean by off-shore reefs (Figure 2). Such settings are not normally conducive to vermetid growth. If the C14 dates are taken at face value, then the death of the vermetid buildups would correspond to a date of 1625 to 1750 AD, an age that would coincide with the height of the Little Ice Age (1675–1800 AD—Glynn et al., 1983). If this correlation is correct, the demise of the vermetids could be attributed to temperature changes or circulation changes caused by the Little Ice Age. Such an hypothesis would parallel the explanation that Glynn et al. (1983) offered for the demise of the corals found in a Central America reef that died between 1650–1800 AD. An alternate explanation for the demise of the Cayman vermetids, which may or may not be related to the Little Ice Age, would involve a reduction in energy conditions. There are two ways in which such changes could have been triggered. First, a slight change in sea level may have led to the demise of the vermetids as in other settings. A simple change in sea-level, however, would not necessarily cause a reduction in the energy levels of the waves that reach the coastline. Thus, a second possibility involves significant changes in energy conditions rather than a simple change in sea-level. For example, the vermetids may have grown at Bodden Town and Great Bluff Estates before the off-shore reef had completely separated the lagoons from the open ocean. At that time, onshore waves would have created high-energy conditions along the coast. Increase in coral growth may have led to the development of an off-shore barrier reef that prevented wave energy from reaching the coast. That reduction in energy levels may have caused the demise of the vermetids.

CONCLUSIONS

Vermetid colonies once flourished near Great Bluff Estates and Bodden Town on Grand Cay-
man. These gastropods, along with encrusting foraminifera, red algae, and cyanobacteria, produced buildups that covered rocky substrates. Comparison with modern vermetids suggests that they must have flourished when those coastlines were characterized by higher energy conditions. The fact that those localities are now characterized by quiet-water conditions and include different biological communities suggests that coastal conditions must have changed. C\textsuperscript{14} dating of the in-situ vermetids suggests that such changes may have taken place in the period of 1625–1750 AD, possibly because of temperature changes brought about by the Little Ice Age. An alternative cause, which may or may not be related to the Little Ice Age, would be related to reduced energy levels along these coastal areas.

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