# Morphology, Microstructure and Stratigraphy of Some Late Cretaceous Radiolitid Rudists from Jamaica

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**Key words:** Rudist bivalves, Cretaceous, Maastrichtian, Taxonomy, Jamaica.

**Abstract** 

Radiolitid rudists from the Upper Maastrichtian of Jamaica include genera Bournonia, Biradiolites and Thyrastylon. Three species of Bournonia are recognised, B. cancellata WHITFIELD, B. barretti TRECHMANN and B. thiadensi VERMUNT. B. cancellata evolves into B. barretti by the acquisition of costae on the anterior side. The species of Bournonia are characterised by a distinctive cardinal apparatus, a thick inner shell layer, and an outer shell layer composed of cellular microstructure. Two species of Biradiolites are recognised - B. rudissimus TRECHMANN has an outer layer composed of cellular microstructure with occasional bands of compact microstructure, particularly in the radial bands, and B. jamaicensis TRECHMANN has a very well organised outer layer with an inner band of cellular microstructure and an outer band of compact microstructure. Biradiolites and Thyrastylon have a similar dentition, a thin inner layer and similar wall structures in the outer layer. Thyrastylon is distinguished from Biradiolites by the infolding of the radial bands in RV and by the presence of oscules in LV. The evolutionary change from Bo. cancellata to Bo. barretti, and the first appearance of Bi. jamaicensis are probably useful biostratigraphic markers of the Upper Maastrichtian.

#### 1. INTRODUCTION

Radiolitid rudists belonging to the genera *Bourno-nia* FISCHER, *Biradiolites* D'ORBIGNY and *Thyras-tylon* CHUBB are abundant in the Upper Maastrichtian, *Titanosarcolites* Limestones (Guinea Corn Formation and other formations) of Jamaica. Although there is a large literature on these Jamaican forms (e.g., WHIT-FIELD, 1897; TRECHMANN, 1924; CHUBB, 1956, 1967, 1971), little information on their microstructure, or their detailed stratigraphy has been published. Indeed, there have been few studies on the microstructure of rudists, although those there have been indicate that the microstructures have high taxonomic significance (e.g., AMICO, 1978; STEUBER, 1999). This paper presents

a detailed study of the morphology, microstructure and stratigraphy of some of these radiolitid rudists, and a revision of some species.

#### 2. GEOLOGY

In the Central Inlier of Jamaica (Fig. 1), the Guinea Corn Formation (Titanosarcolites-yielding limestones) forms the middle (marine) portion of the major transgressive-regressive Kellits Sythem (unconformity bounded stratigraphic unit) (MITCHELL, in press). These limestones are up to 200 m thick and contain subordinate mudrocks and sandstones (COATES, 1965; MITCHELL, 1999, in press; MITCHELL & GUNTER, 2002). The thickest section through the Guinea Corn Formation is exposed in the Rio Minho between Grantham and Frankfield and can be divided into rhythms up to about 10 m in thickness (MITCHELL, 1999, 2002). Each rhythm consists of a lower clastic unit with diverse infaunal molluscs, a middle clastic/ carbonate unit with diverse corals and/or recumbent antillocaprinid rudists, and an upper part consisting of limestones with abundant radiolitid and antillocaprinid rudists. A bed lettering scheme, with the beds labelled from A to G (Fig. 2) based on the relative proportions of limestone and clastics, was introduced by MITCH-ELL (1999). STEUBER et al. (2002) used Sr-isotope geochronology to suggest a mid to late Late Maastrichtian age for the Guinea Corn Formation of the Central Inlier, an age that agrees with the few well-determined ages based on other biostratigraphic groups (e.g., sharks UNDERWOOD & MITCHELL, 2000).

#### 3. METHODOLOGY

For this study, rudists were systematically collected from two sections (Fig. 1). Extensive collections were made from the Rio Minho section between Grantham and Guinea Corn (Guinea Corn in Fig. 1) for which a detailed lithostratigraphy has been developed (MITCH-ELL, 1999; MITCHELL & GUNTER, 2002). Additional material was collected from sections at Slippery Rock River, Green River, Logie Green and Pindars River (Fig. 1). The section at Pindars River (described by COATES, 1965) is important because many of the rud-

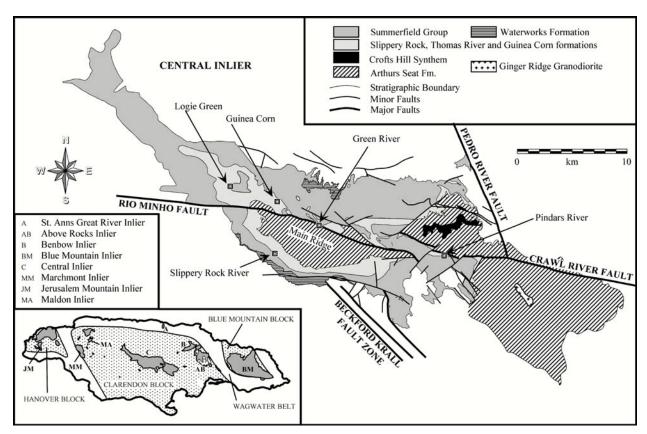


Fig. 1 Location of sections in the Central Inlier from which rudists have been collected. Inset, map of Jamaica showing inliers (additional material from the Marchmont and Maldon Inliers).

ists are embedded in relatively soft mudstones allowing excavation of the cardinal apparatus. Where particular species were common, populations were collected to aid with determining the range of variation within each rudist morphospecies. The terminology of microstructures follows AMICO (1978) and STEUBER (1999).

Longitudinal and transverse sections were cut through selected specimens, and the sections polished to show internal features. The polished surfaces were then etched with a 10% solution of HCl for 10 seconds, and allowed to dry. Acetate peels were prepared from the etched surfaces. Negative photographic prints were then developed from the acetate peels.

All material, including acetate peels, is deposited in the Geological Museum at the University of the West Indies (UWIGM numbers). Additional material studied is in the American Museum of Natural History (AMNH) in New York, and the Natural History Museum (BMNH), London.

#### 4. SYSTEMATIC PALAEONTOLOGY

In the following account, long synonymy lists are not given. These are available in other publications (e.g, CHUBB, 1971; ALENCASTER, 1971; STEUBER, 2002). Here, only important synonyms are provided,

and these are linked to the morphospecies concepts adopted/developed in this work.

Rudist morphospecies are here defined using populations of specimens, where possible, collected from the same level. This provides a more objective method of defining morphospecies that in the published literature where many species have been erected on one or two individuals. When the stratigraphic distribution of populations is examined, a better understanding of the time relationships of morphospecies becomes apparent. Genera are defined on major morphological criteria, species on more subtle criteria.

# Family RADIOLITIDAE D'ORBIGNY, 1847 Genus *Bournonia* FISCHER, 1887

**Type species:** *Sphaerulites bournoni* DES MOULINS, 1826.

**Diagnosis:** Right valve (RV) conical with relatively thick inner aragonite layer. Outer calcitic layer composed of funnel plates with rectangular cells, compact cell layers absent, no cortical layer observed. Surface ornamented with strong costae and intervening furrows. Radial bands represented by more prominent, or flattened costae. Prominent, narrow anterior furrow (AF) developed. Left Valve (LV) cap like, or a low cone. Cardinal apparatus of type A (Pl. 1).

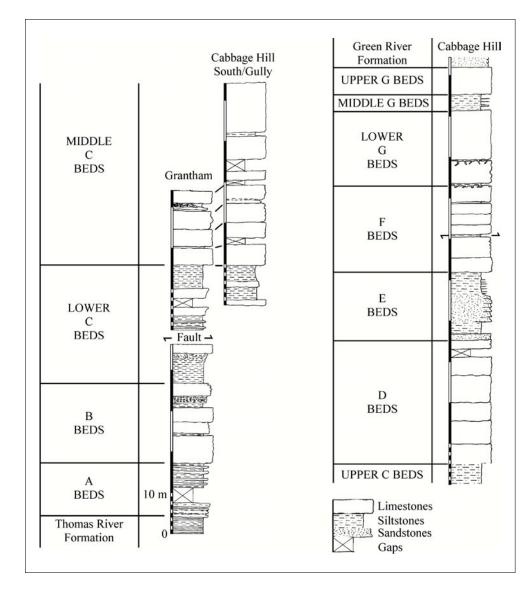


Fig. 2 Simplified succession through the Guinea Corn Formation in the Rio Minho between Grantham and Guinea Corn showing bed divisions (after MITCHELL, 1999; MITCHELL & GUNTER, 2002). The boundary between the Middle and Upper C Beds falls within a faulted gap in the section.

Three Maastrichtian species are recognised in Jamaica: *B. cancellata* (WHITFIELD), *B. barretti* TRECH-MANN and *B. thiadensi* VERMUNT.

# Bournonia cancellata (WHITFIELD, 1897)

Pls. 1, 2, 3d-f, 4a, c-d

- v. 1897 *Radiolites cancellatus*: WHITFIELD, p. 190, pl. 12, fig. 4, pl. 13, figs. 3–7.
- v. 1924 *Biradiolites subcancellatus*: TRECHMANN, p. 403, pl. 26, fig. 3.

**Diagnosis:** A species of *Bournonia* in which the anterior side lacks costae.

**Type specimens:** The original material of WHITFIELD (1897) is preserved in the AMNH; it was collected from Logie Green in the Central Inlier. WHITFIELD (1897) figured several specimens, his pl. 13, figs. 3–5 is here selected as lectotype.

**Material:** Extremely abundant material from the A and B Beds of Guinea Corn Formation in the Rio Minho at Grantham. Also abundant specimens from the lowest limestone in the Pindars River Section.

**Description:** RV conical to cylindro-conical. Ranging in height up to 14 cm and in diameter up to 7 cm. The external ornament consists of prominent costae which represent downfolds of the funnel plates, the intervening furrows corresponding to upfolds; both are obvious in transverse sections (Pl. 1). The costae number between 7 and 10 and are limited in extent to the ventral, posterior and dorsal sides. The radial bands (posterior band - Pb and ventral band - Vb) are represented by broader costae with flat tops. The anterior side is devoid of longitudinal costae, and bears a single prominent anterior furrow. This furrow corresponds to a prominent downfold of the funnel plates. Growth lines, corresponding to the outer edges of the funnel plates, are well-developed on all aspects; no cortical layer has been seen.

Transverse sections of the right valve indicate two well defined layers. The inner layer is up to 2 mm thick, and is represented by calcite spar. This is interpreted to be a replacement fabric after the original aragonitic inner layer. The outer layer is formed of funnel plates showing a quadrangular cellular microstructure; compact microstructural elements are lacking. Longitudinal cross-sections show that the funnel plates are orientated upwards, with different degrees of upward extension producing the costae and furrows. Conical tabulae, now represented by calcite menisci, fill the lower part of the body chamber (Pl. 1f).

LV ranges from flat to strongly arched. It has a similar microstructure to the RV, with a thick inner aragonite layer and an outer layer of quadrangular cellular microstructure (Pl. 1e–f).

The cardinal apparatus is of type A, and is seen in transverse and longitudinal sections, and also in a specimen excavated from the enclosing matrix (Pls. 1a–d, 3d–f). The teeth of the left valve project deeply into the body cavity of the right valve (Pl. 1e–f). They fit into sockets developed from the inner layer of the right valve (Pl. 1a–d). The teeth are distinctly separated and connected by a strong yolk. The myophores extend from the teeth towards the ventral side, and are broadly parallel to one another (Pl. 1a–d). Posterior myophore (PM) is connected by a narrow neck, and anterior myophore (AM) by a wide neck to the teeth (Pl. 1).

Specimens occur in weakly conjoined bouquets of up to 10 individuals when found in growth position. However, most specimens occur as isolated, transported or toppled individuals in rudstone beds (MITCHELL, 2002).

**Discussion:** WHITFIELD (1897) and CHUBB (1971) suggested that two anterior furrows may be developed in some specimens. This is considered erroneous here; one furrow represents AF, whereas the other is a crack due to compaction.

TRECHMANN (1924) and CHUBB (1971) separated *B. cancellata* from *B. subcancellata*. These species differ in the relative height of their RVs, *B. cancellata* being tall and *B. subcancellata* short. The type specimen of *B. subcancellata* has the umbo of the RV broken off. Considering the populations of *B. cancellata* collected from the Guinea Corn Formation during this study, forms similar to *B. subcancellata* clearly represent extreme morphological variants of *B. cancellata*. *B. subcancellata* is therefore synonymised with *B. cancellata* here.

### Bournonia barretti TRECHMANN, 1924

Pl. 3a-c

v. 1924 *Bournonia barretti*: TRECHMANN, p. 405, pl. 26, figs. 2, 2a.

**Diagnosis:** A species *Bournonia* in which the anterior side bears from several to many costae.

**Type:** TRECHMANN (1924, pl. 26, figs. 2, 2a) figured a single specimen of *Bournonia barretti* (BMNH L63227) from the Great River Valley near Catadupa, St. James. This specimen is similar to forms occurring in the Middle C Beds in the Central Inlier, and is here selected as lectotype.

**Material:** Many specimens collected from the Guinea Corn Formation. Forms transitional between *B. cancellata* and *B. barretti* are common in the Lower C Beds, whereas typical *B. barretti* has been collected from the Middle C, Upper C, D and G Beds. It is generally rare.

**Description:** RV varies from cylindro-conical to cylindrical, and is up to 10 cm high and 7 cm in diameter. The dorsal, posterior and ventral sides bear strong costae with prominent furrows between. The anterior side in early examples (Lower C Beds of the Central Inlier) bears a few costae; in later forms (Middle C to G Beds of the Central Inlier) it bears numerous costae. Up to 17 costae may be present in total around the entire shell. When the anterior surface is strongly cemented to a smooth hard substrate (such as a valve of *Antillocaprina* or *Titanosarcolites*), costae are not developed, and the specimen cannot be distinguished from *B. cancellata*. The radial bands are marked by two prominent costae. The anterior furrow is marked by a downfold of the funnel plates between two costae. LV cap like.

Specimens usually occur as isolated individuals in growth position. Rarely specimens occur in conjoined bouquets numbering two or three individuals.

**Discussion:** *B. cancellata* and *B. barretti* appear to be part of an evolving lineage. *B. cancellata* occurs in rock-forming abundance in the limestones of the upper A and B Beds. In the Lower C Beds forms with a few weak costae on the anterior side appear, and occur together with forms of typical *B. cancellata* morphology. These are here seen as transitional forms between *B. cancellata* and *B. barretti*. In the Middle C Beds, *Bournonia* are rare, but those specimens collected have anterior sides with many costae and are typical of *B. barretti*; forms similar to *B. cancellata* are absent. *B. barretti* occurs sporadically through the Upper C and D Beds, and rarely in the G Beds.

ALENCASTER (1971) included *B. barretti* in the synonomy of *B. cardenasensis* (BÖSE, 1906). She recorded the latter species from Vega del Paso (locality 30) in the Upper Cretaceous of Mexico. The associated rudist fauna from this locality included *Titanosarcolites macgillavryi* ALENCASTER, *Barrettia monilifera* WOODWARD, *B. multilirata* WHITFIELD and *B. gigas* CHUBB. In Jamaica, the *B. gigas–B. multilirata* assemblage is of late Middle to early Late Campanian age (MITCHELL, in press), and *B. cardenasensis* is therefore older than the late Maastrichtian *B. barretti*. *B. barretti* and *B. cardenasensis* are here considered as homeomorphs.

## Bournonia thiadensi VERMUNT, 1937

Pls. 3g-h, 4b

1937 Bournonia thiadensi; VERMUNT, p. 271–272, pl. 36, figs. 4–5, text figs. 3e–g.

- v. 1967 Bournonia tetrahedron: CHUBB, p. 28-29.
- v. 1971 *Bournonia tetrahedron*: CHUBB, p. 195, pl. 40, figs. 11–12.

**Diagnosis:** A species of *Bournonia* with four, five, or rarely six, prominent costae in adults.

**Type:** Type specimens not seen.

**Material:** Moderately rare in the upper Middle C Beds, D Beds and F Beds. A single specimen also from the base of the B Beds.

**Description:** RV conical, up to 6 cm high and 7 cm in diameter. The exterior bears four very prominent costae, two broad costae representing the radial bands, and two acute costae at the ventral and dorsal margins of the flat anterior surface. A further costa may be developed, and sometimes two are seen on the dorsal side. The costae represent downfolds of the funnel plates, the furrows, upfolds. The anterior side is flat and bears the AF, represented by a sharp downfold of the funnel plates.

A single transverse section (Pl. 4b) shows that the inner layer of the RV is about 2 mm thick, and the outer layer is composed solely of quadrangular cellular layers; compact layers are absent. The cardinal apparatus is not seen.

The LV is cap like, and may bear prominent radial striations.

*B. thiadensis* occurs as isolated individuals, often cemented to valves of other rudists.

**Discussion:** CHUBB's (1967) species *Bournonia tetrahedron* is a juvenile specimen of a *Bournonia* with four costae. Similar small specimens of *Bournonia* cemented to hard substrates (usually rudist shells) are not uncommon in the upper part of the Guinea Corn Formation. Where such specimens have grown to maturity, they acquire the form of *B. thiadensi*. Thus, *B. tetrahedron* is considered a juvenile of *B. thiadensi* here.

## Genus BIRADIOLITES D'ORBIGNY, 1850

**Type species:** *Biradiolites canaliculatus* D'ORBIGNY, 1850.

**Diagnosis:** Radiolitids with no ligamental infold, radial bands situated in furrows, cardinal apparatus of type B (Pl. 5b), outer layer of RV formed of cellular and compact wall structures.

## Biradiolites rudissimus TRECHMANN, 1924

Pls. 5b-c, 6c-d, 6f

1897 ?*Radiolites rudis*; WHITFIELD, 189, pl. 11, fig. 4.

- v. 1924 *Biradiolites rudissimus*; TRECHMANN, p. 402, pl. 26, figs. 4, 4a, 5.
- v. 1924 *Biradiolites minhoensis*; TRECHMANN, p. 402–403, pl. 26, figs. 1, 1a.
- 1956 *Biradiolites forbesi*; CHUBB, p. 15–16, pl. 3, figs. 1–2.
- v. 1971 *Biradiolites riograndensis*; CHUBB, p. 189, pl. 37, figs. 9–11.

**Diagnosis:** *Biradiolites* with a broad, flat-topped Vb and a strongly upfolded Pb. Other costae and furrows much reduced.

**Type:** TRECHMANN (1924) figured two specimens of *Biradiolites rudissimus* from the Railway Cutting at Catadupa, St. James. TRECHMANN's (1924) pl. 26, fig. 5, is here selected as lectotype.

**Material:** Numerous individuals from the *Titanosarco-lites* Limestones of Jamaica.

**Description:** A highly variable species of *Biradiolites*. RV up to 15 cm in diameter and 11 cm high. The RV is conical and ranges from narrow, tall cones (*Radiolites rudis*- or *Biradiolites minhoensis*-like forms) to broad, low cones. The margin of the RV is usually irregular, and may be devoid of costae and furrows other than for the radial bands. The radial bands are strongly marked and very distinctive. Vb is characterised by a sunken, flat, square-topped upfold, and is broad. Pb is narrower, convex and strongly upfolded. The apertural surface may bear plications and/or vascular impressions.

Transverse sections of RV show a thin inner layer (less than 0.5 mm thick), and an outer layer formed largely of quadrangular, cellular microstructure with occasional irregular compact layers (Pl. 5b–c). Compact layers are often best developed adjacent to the radial bands. The cardinal apparatus is of type B (Pl. 5b). The teeth are relatively close together and fit into sockets in the RV. They are connected by a yoke that forms a small accessory cavity between the cardinal apparatus and the inner layer of the RV. The myophores form two arcs extending towards the ventral side (Pl. 5b).

LV cap-like, with a raised central portion (Pl. 6c), and a flat brim that extends across the apertural surface. This brim is usually broken away, although vestigaes are sometimes preserved (e.g., at the top of Pl. 6c).

*B. rudissimus* occurs as isolated individuals, or in small conjoined bouquets numbering up to three individuals.

**Discussion:** A great deal of confusion surrounds the relationship between *Radiolites rudis* WHITFIELD and

Biradiolites rudissimus TRECHMANN. The type and only specimen of *R. rudis* is in AMNH, and is embedded in a hard limestone matrix. Consequently, the form of the radial bands cannot be determined. The general morphology of the RV resembles narrow specimens of *B. rudissimus*, but in the absence of details of the radial bands the specimen must be regarded as indeterminate. *R. rudis* is therefore questionably placed in the synonymy list of *B. rudissimus* here.

Biradiolites minhoensis TRECHMANN has a shape typical of conical specimens of *B. rudissimus*, but with rather smooth radial bands. Similar specimens with smooth radial bands do occur in large populations of *B. rudissimus* (e.g., a population taken from rhythm D1 in the Central Inlier), and since *B. rudissimus* has page preference, *B. minhoensis* is placed in synonymy here. In describing *Biradiolites forbesi* and *B. rudissimus*, CHUBB (1971, p. 188) stated that "[it] appears there is little... to differentiate between the two species", and *B. forbesi* is placed in synonymy here. *B. riograndensis* CHUBB also has similar radial bands to *B. rudissimus*, and falls within the range of collected populations.

## Biradiolites jamaicaensis TRECHMANN, 1924

Pls. 5a, 5d-e, 6a-b, 6e

- v. 1924 Biradiolites jamaicensis; TRECHMANN, p. 404, pl. 24, figs. 5, 5a, 6, 6a, 7.
- v. 1967 Biradiolites robinsoni; CHUBB, p. 27.
- v. 1971 *Biradiolites robinsoni*; CHUBB, p. 187, pl. 36, figs. 1–3.

**Diagnosis:** *Biradiolites* with strong stellate transverse sections, well-organised thick cellular and compact layers, and a double costa in the interband.

**Type:** TRECHMANN (1924) figured three specimens of *B. jamaicensis*. His pl. 24, figs. 5, 5a is the most typical, and is here designated as lectotype.

**Material:** Abundant material from the Guinea Corn Formation and elsewhere in the *Titanosarcolites* Limestones of Jamaica.

**Description:** RV cylindrical, straight, twisted or gently arched. Diameter up to 4 cm, length up to 25 cm. RV bears between 7 and 12 strong angular costae, including the two costae in the interband. Minor, longitudinal ridges may be developed on some costae. The cross section ranges from triangular to square to broadly rounded. Pb and Vb are marked by flat bands on either side of the prominent double costae of the interband (Pls 5a, 6a–b, 6e). The surface of RV is smooth.

Transverse sections indicate a very well structured wall of the RV. The inner layer is very thin (less than 0.5 mm). The outer layer is divided into an inner portion with quadrangular cellular layers and an outer portion of compact layers (Pl. 5a, 5e). The compact layers correspond to the strongly upturned margin of the

funnel plates (Pl. 5d). Cardinal apparatus similar to *B. rudissimus*.

LV with a central raised portion, and a brim extending across the apertural face. The thin brim is often broken away.

Occurs as ramifying masses and well-defined bouquets of up to 100 or more individuals (MITCHELL, 2002).

**Discussion:** CHUBB (1967) erected *B. robinsoni* for a short, curved form. The type specimen is missing (Edward ROBINSON, pers. comm., 2000), although a cast of it is in the BMNH. This specimen shows the typical radial bands of *B. jamaicensis*, and *B. robinsoni* is placed in synonymy here.

### Genus Thyrastylon CHUBB, 1956

**Type species:** *Radiolites adhaerens* WHITFIELD, 1897.

**Diagnosis:** A radiolitid with no ligamental infold, quadrangular cellular and compact layers in the outer layer of RV, type B cardinal apparatus, radial bands partially infolded into the shell layer of the RV, and oscules developed in the LV.

# Thyrastylon adhaerens (WHITFIELD, 1897)

Pls. 7, 8

v. 1897 *Radiolites adhaerens*; WHITFIELD, p. 188–189, pl. 10, fig. 1, pl. 12, fig. 1.

**Diagnosis:** As for genus (but see discussion).

**Type:** WHITFIELD (1897) figured several specimens of *Radiolites adhaerens*. No lectotype is currently selected, pending revision of TRECHAMNN's (1924) and CHUBB's (1956, 1971) species concepts.

**Material:** Abundant material from the *Titanosarcolites* Limestones of Jamaica.

**Description:** RV cylindrical to conical, up to 10 cm long and 7 cm in diameter. Margin broadly rounded and irregular, with radial bands marked by wide or narrow furrows. Aperture with radial plications and/or vascular impressions.

Transverse cross sections of the RV show a thin inner layer (less than 0.5 mm) and an outer layer formed mainly of quadrangular cellular microstructure with occasional bands of compact microstructure (Pl. 7c). Compact shell layers are particularly developed around the infolded radial bands (Pl. 7d). Longitudinal sections show the upward projecting funnel plates, with occasional layers of compact microstructure, which is also concentrated adjacent to the infolded radial bands (Pl. 8a–b). The cardinal apparatus is type B as in *B. rudissimus* (see CHUBB, 1971).

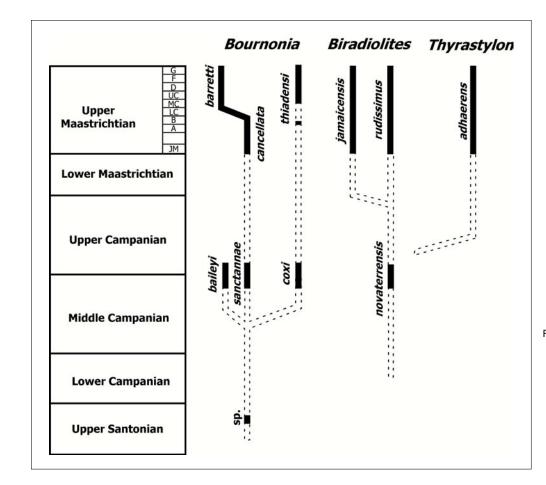


Fig. 3 Stratigraphy of radiolitid rudists from the Upper Cretaceous of Jamaica. JM = Jerusalem Mountain occurrences, A–G = Beds in Guinea Corn Formation; the gap between JM and A–G is not known at outcrop.

The LV is cap like, with a central raised/domed section and a wide thin brim that extends across the apertural face. The LV has two oscules developed above the radial bands (CHUBB, 1956, 1971).

Specimens occur as weakly to strongly attached elevators or clingers. Sometimes in bouquets numbering up to 20 or more individuals.

**Discussion:** TRECHMANN (1924) erected two further species, *Biradiolites coryi* and *Biradiolites semiannulosus*, that CHUBB (1956) placed in *Thyrastylon*. The distinction between these 'species' is remarkably difficult in many of the collected specimens. A full revision of the genus using populations is needed to sort out the species concepts in this genus.

Many of the features of *Thyrastylon* resemble those of *B. rudissimus*. The genus differs in the infolding of the radial bands and the development of oscules in the LV.

#### 5. STRATIGRAPHY

The distribution of the Maastrichtian rudists discussed in this paper, together with similar forms from the Santonian and Campanian of Jamaica is shown in Fig. 3. This demonstrates that *Bo. cancellata*-like, *Bo. thiadensi*-like and *Bi. rudissimus*-like forms occur over extend-

ed ranges. In continuous sections, in would probably be difficult to separate these 'species', which undoubtedly represent lineages. The evolutionary change from *Bo. cancellata* to *Bo. barretti*, and the first appearance of *Bi. jamaicensis* are probably useful biostratigraphic markers of the Upper Maastrichtian.

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#### 6. REFERENCES

ALENCASTER, G. (1971): Rudistas del Cretacico Superior de Chiapas [*Upper Cretaceous rudists from Chiapas* – in Spanish].– Paleontologia Mexicana, 34, 1–91.

AMICO, S. (1978): Recherches sur la structure du test des Radiolitidae [*Study of the shell structure of radiolitidae* – in French]. – Traveaux du Laboratoire de Géologie Historique et de Paléontologie, 8, 1–131.

- BÖSE, E. (1906): La fauna de moluscos del Senoniano de Cárdenas, S.L.P. [*The mollusc fauna of the Senonian of Cardenas, S.L.P.* in Spanish].– Boletín del Instituto Geológico de México, 24, 1–92.
- CHUBB, L.J. (1956): Thyrastylon, a new rudists genus from the Upper Cretaceous of Guatemala, the Antilles, and Persia, with a discussion of the function of rudists oscules and pillars.—Palaeontographica Americana, 4/27, 33–49.
- CHUBB, L.J. (1967): New rudist species from the Cretaceous rocks of Jamaica. Journal of the Geological Society of Jamaica, 9, 24–31.
- CHUBB, L.J. (1971): Rudists of Jamaica.— Palaeontographica Americana, 7, 161–257.
- COATES, A.G. (1965): A new section in the Maastrichtian Guinea Corn Formation near Crawle River, Clarendon.—Journal of the Geological Society of Jamaica (Geonotes), 7, 28–33.
- FISCHER, P. (1887): Manuel de conchyliologie et de paléontologie conchyliogique ou histoire naturelle des mollusques vivants et fossils [Manual of shell and shell paleontology and natural history of Recent and fossil molluscs — in French].— F. Savy, Paris, 1369 p.
- MITCHELL, S.F. (1999): Stratigraphy of the Guinea Corn Formation (Upper Cretaceous) at its type locality between Guinea Corn and Grantham (northern Clarendon,

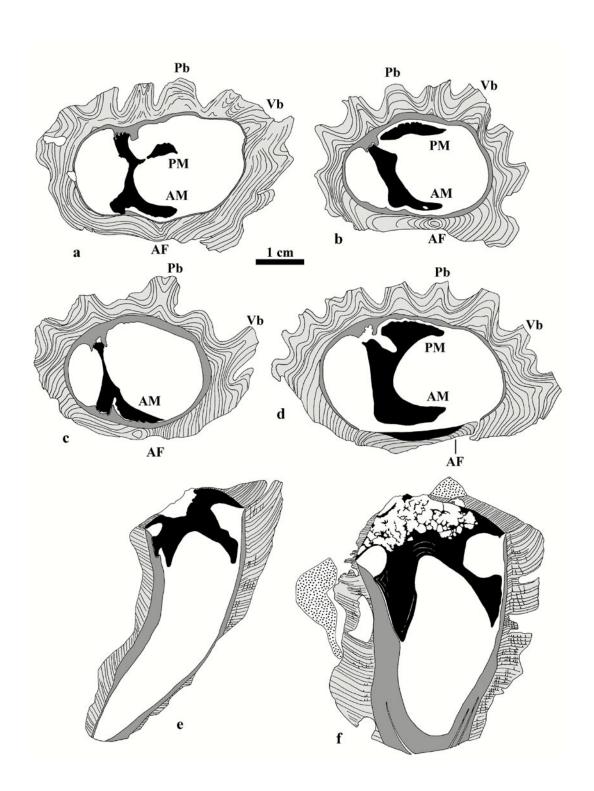
- Jamaica).— Journal of the Geological Society of Jamaica, 33, 1–12.
- MITCHELL, S.F. (2002): Palaeoecology of corals and rudists in mixed volcaniclastic–carbonate small-scale rhythms (Upper Cretaceous, Jamaica).— Palaeogeography, Palaeoclimatology, Palaeoecology, 186, 237–259.
- MITCHELL, S.F. (in press): Sedimentary and tectonic evolution of central Jamaica.— In: BARTOLINI, C., BURKE, K., BUFFLER, R., BLICKWEDE, J. & BURKART, B. (eds.): Mexico and the Caribbean Region: Plate Tectonics, Basin Formation and Hydrocarbon Habitats.— American Association of Petroleum Geologists Memoir.
- MITCHELL, S.F. & GUNTER, G.C. (2002): Biostratigraphy and taxonomy of the rudist *Chiapasella* in the *Titanosar-colites* Limestones (Maastrichtian) of Jamaica.— Cretaceous Research, 23, 473–487.
- DES MOULINS, C. (1826): Essai sur les sphérulites qui existent dans les collections de MM. F. Jouannet, member de l'Académie royale des Sciences, belle Lettres et Arts de Bordeaux, et Charles des Moulins; et considerations sur la familie à laquelle ces fossils appartiennent [Essay on the Dherulites in the collection of MMF Jouannet, member of the Royal Academy of Sciences, beautiful Letters and Arts of Bordeaux, and Charles des Moulins and consideration on the families to which these fossils belong in French].— Bulletin d'Histoire Naturelle de la Société Linnéenne de Bordeaux, 1, 148–303.

## PLATE 1

Bournonia cf. cancellata (WHITFIELD), forms with a few weak costae on anterior side, Lower C Beds, Guinea Corn

- a UWIGM.RUD.3003.3; b-e UWIGM.RUD.2003.171–174, respectively; f UWIGM.RUD.2003.2.
- a-d Transverse sections cut at various levels and angles through the cardinal apparatus.
- e-f Longitudinal sections.

Camera lucida drawings, outer layer structure simplified. Black, aragonitic inner layer of left valve; dark grey, aragonitic inner layer of right valve; light greys calcitic outer layers of left and right valves; dotted, epifornal corals. PM, posterior myophore; AM, anterior myophore; Pb, posterior band; Vb, ventral band; AF, anterior furrow. Note intense boring (*Entobia* isp.) in upper part of aragonitic inner layer of left valve in f.



D'ORBIGNY, A. (1847): Sur les brachiopods ou palliobranchs [*On the brachiopods and pallialbranchs* – in French]. – Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, 25, 266–269.

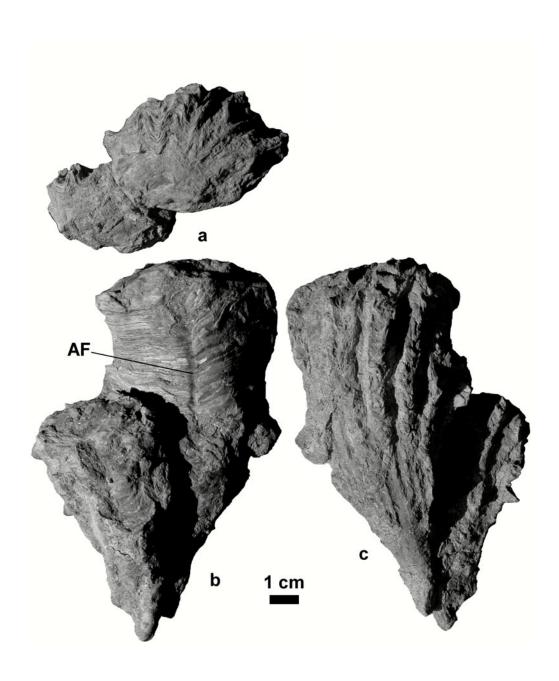
- D'ORBIGNY, A. (1850): Paléontologie Francaise, Terrains Crétacés. Vol. 4, Brachiopodes [Paleontology of France, Cretaceous rocks. Vol. 4, Brachiopods – in French].— Bertrand, Paris, 105–328.
- STEUBER, T. (1999): Cretaceous rudists of Boeotia, central Greece. Special Papers in Palaeontology, 61, 229 p.
- STEUBER, T. (2002): Depository item 2002022, List of occurrences of rudist bivalves (Hippuritoidea) in the Americas. Plate tectonic control on the evolution of Cretaceous platform-carbonate production.—Geology, 30, 259, 71 p.
- STEUBER, T., MITCHELL, S.F., BUHL, D., GUNTER, G. & KASPER, H.U. (2002): Catastrophic extinction of Caribbean rudist bivalves at the Cretaceous–Tertiary boundary.—Geology, 30, 999–1002.

- TRECHMANN, C.T. (1924): The Cretaceous limestones of Jamaica and their Mollusca.— Geological Magazine, 61, 25–410.
- UNDERWOOD, C.J. & MITCHELL, S.F. (2000): Serratolamna serrata (Agassiz) (Pisces, Neoselachii) from the Maastrichtian (Late Cretaceous) of Jamaica.— Caribbean Journal of Earth Science, 34, 25–30.
- VERMUNT, L.W.J. (1937): Cretaceous rudistids of Piñar del Rio, Cuba. Journal of Paleontology, 11, 261–275.
- WHITFIELD, R.P. (1897): Descriptions of species of Rudistae from the Cretaceous rocks of Jamaica, W. I., collected and presented by Mr. F. C. NICHOLS.—Bulletins of the American Museum of Natural History, 9, 185–196.

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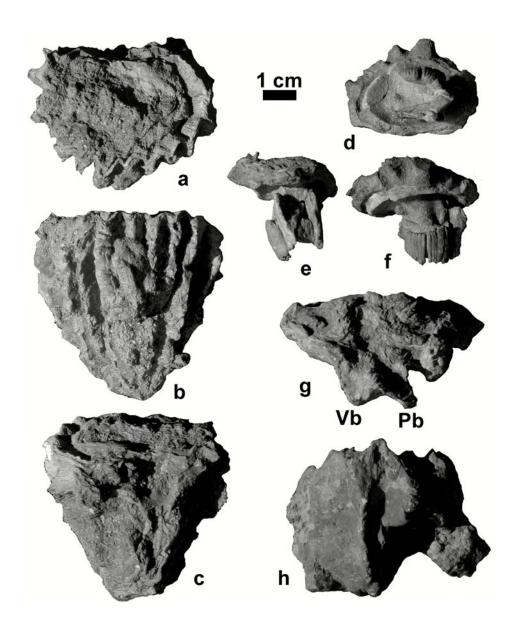
## PLATE 2

a-c Three views of conjoined specimens of *Bournonia cancellata* (WHITFIELD), bed 15 upper, upper A Beds, Guinea Corn, UWIGM.RUD.2002.89. Anterior furrow (AF) obvious in b.



# PLATE 3

- a-c *Bournonia barretti* TRECHMANN, Lower C Beds (upper part), Slippery Rock River, UWIGM.RUD. 2002.90.
- d-f Cardinal apparatus of *Bo. cancellata*, lowermost limestone, Pindars River Section, UWIGM.RUD.2003.1.
- g-h Bo. thiadensi VERMUNT, F Beds, Green River, UWIGM.RUD.2002.73. Vb, ventral band; Pb, posterior band.

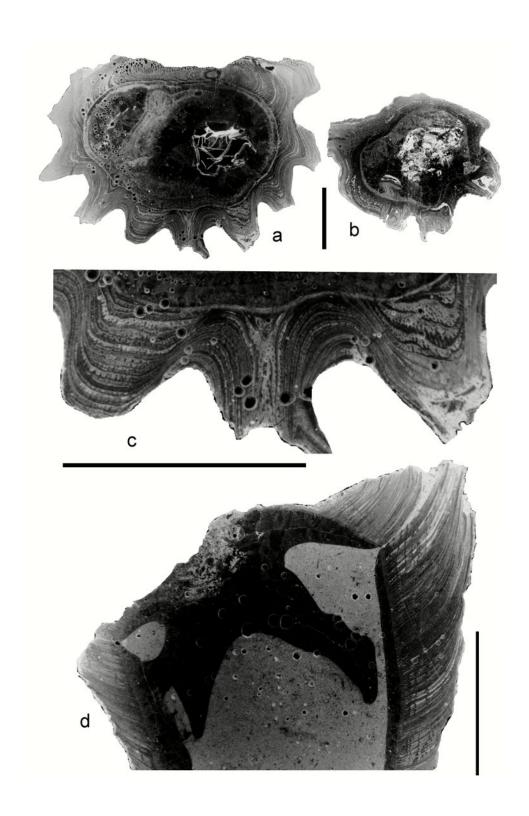


## PLATE 4

- a, c Transverse section of Bournonia cf. cancellata (same as Pl. 1b);
- b Transverse section of *Bo. thiadensi*, Marchmont Inlier, UWIGM.58CA34;
- d Longitudinal section of *Bo*. cf. *cancellata* (same as Pl. 1e).

# Negative prints of acetate peels.

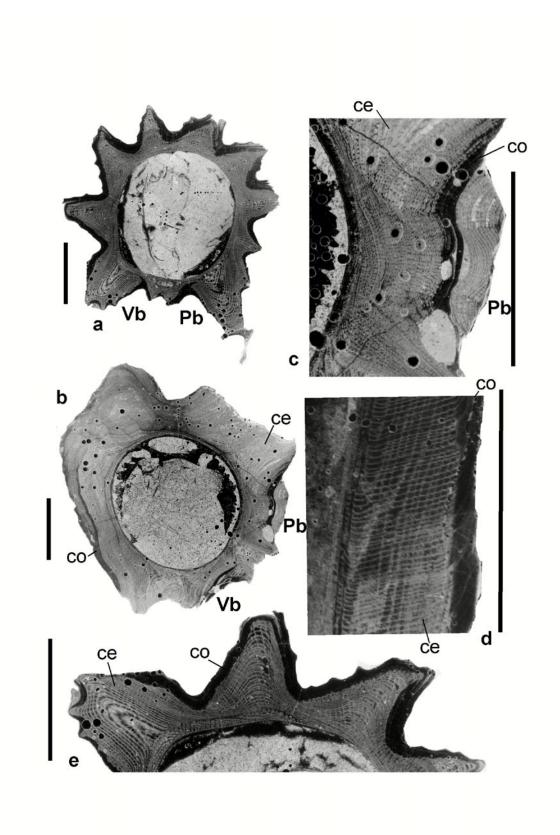
Scale bar = 1 cm; a and b show the inner aragonitic layer, and the outer calcitic layer composed of quadrangular cell structure; c, detail showing quadrangular cell structure in outer shell layer; d, showing the very thick aragonitic inner layers of the left and right valves, and the massive aragonite of the cardinal structure; note the closely spaced funnel plates in the outer layer. Aragonite of inner layer replaced by calcite.



## PLATE 5

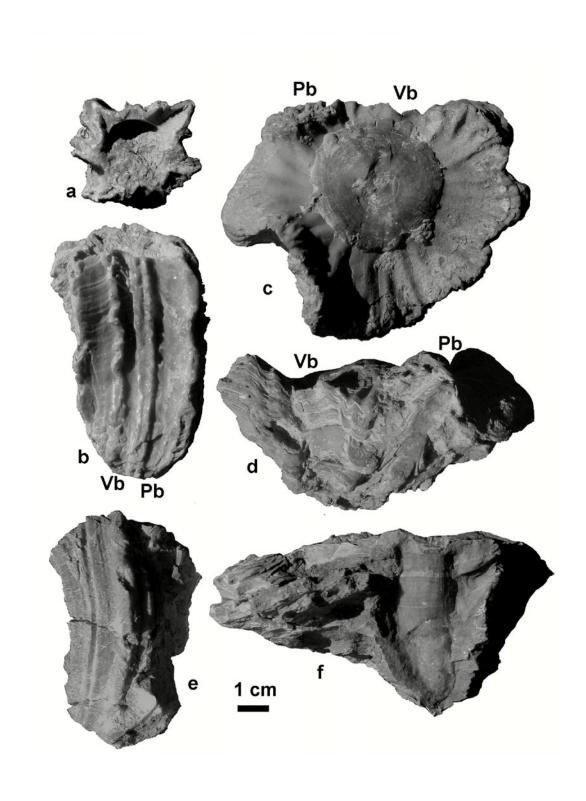
- a, e Transverse section of *Biradiolites jamaicensis* TRECHMANN, uppermost limestone, Pindars River, UWIGM.RUD.2001.114; note the well developed compact (co) and cellular (ce) structure of the outer shell layer.
- b, c Transverse section of *Bi. rudissimus* TRECHMANN, Rhythm D1, Guinea Corn, UWIGM.RUD.2001.114; b shows the cardinal structure, and alternation of compact (co) and cellular (ce) microstructure in the outer shell layer; c, detail showing compact (co) shell structure in Pb.
- d Longitudinal section of *Bi. jamaicensis*, upper part Lower C Beds, Guinea Corn, UWIGM.RUD.2002.96; note that the compact (co) shell structure corresponds to the strongly vertical upturned part of the funnel plates. Scale bar = 1 cm. Pb, posterior band; Vb, ventral band.

Negative prints of acetate peels.



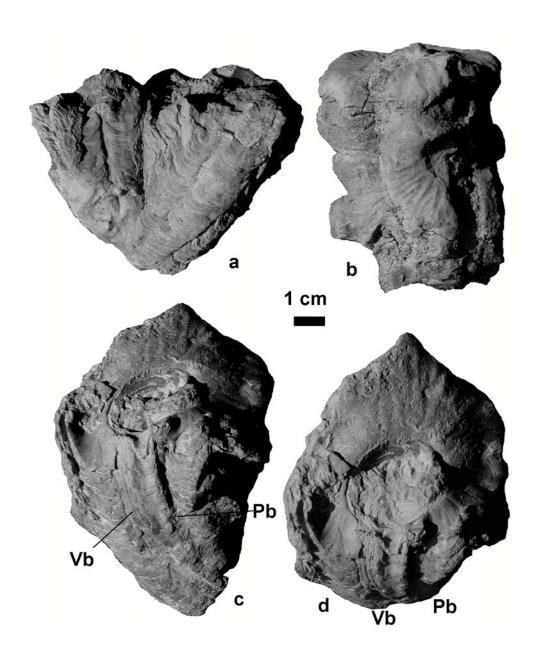
# PLATE 6

- a, b Biradiolites jamaicensis TRECHMANN, Middle C Beds, Guinea Corn, UWIGM.RUD.2001.50;
- c-d *Bi. rudissimus* TRECHMANN, Marchmont Inlier, UWIGM.RG.2001.109.MM15 (collected by Gavin GUNTER and SFM);
- e Bi. jamaicensis, Logie Green, UWIGM.RUD.2001.147;
- f *Bi. rudissimus*, Rhythm D1, Guinea Corn, UWIGM.RUD.2001.117, split showing body cavity. Pb, posterior band; Vb, ventral band.



# PLATE 7

- a-b *Thyrastylon adhaerens* (WHITFIELD); a, Lower C Beds, Guinea Corn, UWIGM.RUD.2002,143; b, UWIGM.RG.2001.96.MM16, Marchmont Inlier (collected by Gavin GUNTER);
- c–d *T. adhaerens* [form approaching *T. coryi* (TRECHMANN)], Middle C Beds, Guinea Corn, UWIGM.RUD. 2002.104. Pb, posterior band; Vb, ventral band.



## PLATE 8

- a, b Longitudinal section of *Thyrastylon adhaerens* (WHITFIELD) cut through a radial band showing compact (co) and cellular (ce) microstructure, D Beds, Guinea Corn, UWIGM.RUD.2003.175;
- c, d Detail of c: transverse section showing infolded radial bands showing compact (co) and cellular (ce) microstructure, Middle C Beds, Guinea Corn, UWIGM.RUD.2002.91. Scale bar = 1 cm.

Negative prints of acetate peels.

