

## *Carnets Geol.* 20 (18)

E-ISSN 1634-0744 DOI 10.2110/carnets.2020.2018

## Exceptionally well-preserved silicified hippuritid rudist bivalves from the lower Maastrichtian of Puerto Rico

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**Abstract:** Exceptionally well-preserved (silicified) hippuritid rudists occur in the El Rayo Formation (lower Maastrichtian) of south-western Puerto Rico. Three species belonging to three different genera are present: *Caribbea muellerreidi* (VERMUNT), *Laluzia peruviana* (GERTH) and *Parastroma guitarti* (PAL-MER). Acid digestion of the limestones has resulted in a collection with numerous three-dimensional left and right valves many with the preservation of the minute details of the pore system. The morphological features of each species are described, and many features are illustrated for the first time. The new material, coupled with descriptions from other studies, demonstrates that six genera of endemic hippuritids evolved in two separate radiations in the New World: an older radiation of forms that had pallial canals in their left valves (*Barrettia, Whitfieldiella* and *Parastroma*) and a younger radiation of forms lacking pallial canals in their left valves (*Laluzia, Caribbea* and *Praebarrettia*). The exquisite preservation also reveals that in these endemic New World hippuritids the sockets for the teeth consisted of slots into which ribs on the teeth fitted; this contrasts with Old World hippuritids that have true sockets formed from upfolds of the tabulae for the teeth. The distinctive morphology of the tooth sockets is here used to define a monophyletic subfamily for which the name Barrettiinae CHUBB is available.

#### **Key-words:**

- exceptional preservation (silicification);
- rudist bivalves;
- Laluzia;
- Caribbea;
- Parastroma;
- Hippuritidae;
- Puerto Rico;
- Cretaceous

**Citation:** MITCHELL S.F. (2020).- Exceptionally well-preserved silicified hippuritid rudist bivalves from the lower Maastrichtian of Puerto Rico.- *Carnets Geol.*, Madrid, vol. 20, no. 18, p. 333-366.

Résumé : Les rudistes (Bivalvia) silicifiés et exceptionnellement bien conservés du Maastrichtien inférieur de Porto Rico .- Des rudistes hippuritidés exceptionnellement bien conservés (silicifiés) sont observés dans la Formation d'El Rayo (Maastrichtien inférieur) du sud-ouest de Porto Rico. Trois espèces appartenant à trois genres différents sont représentées : Caribbea muellerreidi (VERMUNT), Laluzia peruviana (GERTH) et Parastroma guitarti (PALMER). La dissolution par de l'acide des matrices calcaires a fourni une collection de nombreuses valves senestres et dextres en trois dimensions, dont de nombreuses présentant les menus détails du système de pores. Les caractéristiques morphologiques de chaque espèce sont décrites, et nombre de ces traits sont illustrés pour la première fois. Ce nouveau matériel, associé aux descriptions présentes dans d'autres études, montre que six genres d'hippuritidés endémiques ont évolué en deux radiations distinctes dans le Nouveau Monde : une radiation plus ancienne avec des formes qui comportent des canaux palléaux dans la valve senestre (Barrettia, Whitfieldiella et Parastroma) et une radiation plus récente de formes dépourvues de canaux palléaux dans cette même valve senestre (Laluzia, Caribbea and Praebarrettia). La délicate conservation montre également que, chez ces hippuritidés endémiques du Nouveau Monde, les alvéoles pour les dents consistaient en des fentes dans lesquelles les côtes des dents s'ajustaient ; cela contraste avec les hippuritidés de l'Ancien Monde qui présentent de véritables alvéoles constituées par les replis des tabulae pour les dents. La morphologie unique de ces alvéoles dentaires est utilisée ici pour définir une sous-famille monophylétique pour laquelle le nom de Barrettiinae CHUBB est disponible.

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Published online in final form (pdf) on November 11, 2020 [Editor: Robert W. Scott; technical editor: Bruno GRANIER]



#### Mots-clefs :

- conservation exceptionnelle (silicification) ;
- bivalves rudistes ;
- Laluzia ;
- Caribbea ;
- Parastroma ;
- Hippuritidae ;
- Porto Rico ;
- Crétacé

## 1. Introduction

Multiple-folded hippuritid rudists, exemplified by Barrettia WOODWARD, 1862, are amongst the most distinctive fossils of the tropical Upper Cretaceous of the New World, and many different forms have now been described. Yet, the lack of complete morphological descriptions, particularly the details of the left valve (LV) construction and its pore system have led to difficulties in understanding the relationships between the various forms as well as their relations with other hippuritids of the Americas and the Old World. Although the pore systems are now known (to a certain degree - although most have suffered significantly from some amount of weathering) in most forms (e.g., PALMER, 1933; DOMMELEN, 1971; MIT-CHELL, 2010; MUNUJOS et al., 2016, 2020), other details of the construction of the left valve have only been reconstructed using cut sections, which, because of their complexity, are often difficult to interpret. Norman SOHL's studies of New World Cretaceous gastropods (e.g., Sohl & KOLLMANN, 1985; SOHL, 1992, 1998) led him to collect vast quantities of material from Puerto Rico, much of which resides in the United States National Museum collection at the Smithsonian Institution. Amongst this material is a large collection of silicified specimens from the El Rayo Formation of Puerto Rico. In 2009, I was invited to the Smithsonian to study the rudist material and was able to carry out a detailed investigation of this material. This unique collection includes exceptionally preserved specimens of rudist bivalves with the shell partially or completely silicified. It presents an unrivalled opportunity to understand the morphology of various rudists, particularly the hippuritids which are represented by three species belonging to three different genera. This paper presents the results of that study.

#### 2. Stratigraphy

The collection site ('Locality 14') of the rudist (and gastropod) material from the El Rayo Formation in the Sabana Grande Quadrangle was described by SOHL and KOLLMANN (1985), SOHL (1992) and in the posthumous publication by SOHL (1998, p. 24). These descriptions are similar. The locality (Fig. 1) is described as being situated on a 125-m-high hill (1985 and 1998 papers) or 147-m-high hill (1992 paper) east of Quebrada Jicara, 4.75 km S-SW of Sabana Grande, Barrio Lajas Arriba, Municipio de Lajas (approximately Puerto Rico metre grid 23,900 N; 93,400 to 93,600 E), and has the USGS Mesozoic locality numbers 28664, 28748, 29075, 29088 and 29361. The material was collected by N.F.



**Figure 1:** Location map from which the silicified rudists were obtained. Locality 14 from SOHL (1998, p. 24). A, detailed locality. B, location in Puerto Rico (white square).

SOHL, E.G. KAUFFMAN and W.O. Ross in 1963 and 1964 (SOHL, 1992, p. 433).

The succession exposed on the hill was divided into three parts by SOHL (1998): the lower part consisted of massive, grey limestone with ostreid bivalves and other molluscs; the poorly exposed middle part of the hill consisted of inter-bedded brownish shale and limestone, and it was blocks from here that yielded the silicified material described here; and the top of the hill was capped by light-grey limestones containing the rudists *Parastroma* sp. and *Titanosarcolites giganteus* (WHITFIELD).

The silicified residue was separated from the limestone by acidization (SOHL, 1998, p. 25). Since material from here was described in KAUFFMAN and SOHL (1974, Fig. 7F-H) and SOHL and KOLL-MANN (1985), the acid digestion must have been done before those dates (presumably in the late 1960s). It is assumed that this was done using dilute hydrochloric acid, but no further details of the procedure have been recorded in the literature (KAUFFMAN & SOHL, 1974; SOHL & KOLLMANN, 1985; SOHL, 1992, 1998).

The silicified fauna is highly diverse, and SOHL recognized nearly 80 (1998)genera of gastropods and bivalves including the rudists Antillocaprina, Plagioptychus, Parastroma, Orbignya, Durania, and various other smaller radiolitids. The Durania in this list would now be referred to Macgillavryia, and Orbignya to Caribbea. SOHL (1998) assigned a Maastrichtian age to this assemblage. The presence of Caribbea and Laluzia in association with Parastroma guitarti (PAL-MER), Coralliochama cf. gboehmi Böse and a single specimen of Oligosarcolites monotubularis (MITCHELL & GUNTER) (MITCHELL, 2013, Fig. 12.1-2; SKELTON, 2013, Fig. 14a-b) would suggest assignment to the early Maastrichtian (e.g., MITCHELL, 2013; Pons et al., 2013).



## 3. Systematic palaeontology

The hippuritid rudists described here, *Caribbea muellerriedi* (VERMUNT), *Laluzia peruviana* GERTH and *Parastroma guitarti* (PALMER), have very complex shells and numerous terms have been introduced to describe their morphology (*e.g.*, WOOD-WARD, 1862; WHITFIELD, 1897; DOMMELEN, 1971) together with standard terms (*e.g.*, MOORE, 1969). The Appendix provides a list and brief description of these morphological terms. For higher level classification, see SKELTON (2013). Abbreviations used in the descriptions are listed in Table 1. **Table 1:** Abbreviations used in description of species

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 (see Appendix for details).

- AM anterior myophore
- ATS anterior tooth socket
- AT anterior tooth
- CT central tooth
- LV left valve
- P0 ligamental infold
- P1 first pillar/infold
- P2 second pillar/infold
- PM posterior myophore
- PTS posterior tooth socket
- PT posterior tooth
- RV right valve

Specimens reside at the following repositories: Naturalis, Leiden, The Netherlands (NL); Smithsonian National Museum of Natural History, Washington - D.C. (SNMNH); Museum of Paleontology, Institute of Geology, Universidad Nacional Autónoma de México (UNAM), Ciudad Universitaria, México (IGM); The Natural History Museum London (BMNH); The University of the West Indies Geology Museum (UWIGM). Specimens in the collection at Washington also have an NS number, which was assigned to specimens as they were being studied/photographed; these numbers are retained here for cross-referencing purposes. Species synonymy lists use marginal annotations (e.g., 'v.', '.', '\*') as used by MATHEWS (1973).

#### **Order HIPPURITIDA NEWELL, 1965**

#### Suborder HIPPURITIDINA NEWELL, 1965

## Superfamily RADIOLITOIDEA ORBIGNY, 1847

#### Family HIPPURITIDAE GRAY, 1848

**Discussion.** The family has been variously split into subfamilies based on the presence/absence of pores (*e.g.*, GRUBIĆ, 1979), presence/absence of multiple infolds (*e.g.*, CHUBB, 1971) and differences in right valve outer shell structure (*e.g.*, GRUBIĆ, 2004). This study of the silicified material from Puerto Rico and investigation of other New World and Old World specimens indicates that three subfamilies can be recognized within the Hippuritidae: the Hippuritinae MAc GIL-

LAVRY, 1937, the Barrettiinae CHUBB, 1971, and the Torreitinae GRUBIC, 1979.

#### Subfamily BARRETTIINAE CHUBB, 1971

**Diagnosis.** Hippuritidae in which the sockets for each tooth are formed by two pairs of slots on the inner shell wall.

Discussion. This division of the Hippuritidae into subfamilies is based on major morphological features - differences in the sockets for the teeth and differences in the construction of the left valve - which are ascribed to taxonomic differentiation at a level above that of genus but below that of family. CHUBB (1971) based his subfamily Barrettiinae on the presence of multiple infolds (rays) and included within it all the American multiple-fold hippuritids, but excluded the Old World multiple-fold Pironaea MENEGHINI, which he distinguished based on the radial distance between the two principle pillars (P1 and P2), which was small in Pironaea and large in the Barrettiinae. However, MITCHELL (2010) demonstrated that this distance was too highly variable in three New World species to even distinguish species let alone genera or subfamilies, and the radial distance is an unsound criterion upon which to erect a subfamily. GRUBIĆ (2004) resurrected the subfamily Barrettiinae CHUBB and gave a revised diagnosis based on the structure of the outer shell layer of the right valve. Yet, both MITCHELL (2010) and PONS et al. (2010) have subsequently demonstrated that the structure described by GRUBIĆ (2004) does not exist and is an erroneous interpretation of previous descriptions.

Here, the subfamily Barrettiinae is defined on differences in the socket construction in the right valve of Caribbean and Central American Barrettiinae as compared with Old World Hippuritinae (Fig. 2). In the Barrettiinae, the socket for each tooth is formed by a pair of slots, one pair each for the posterior and anterior tooth (Fig. 2.1-4). When preserved in three-dimensions, it is obvious that the teeth are open to the body cavity in the right valve, and furthermore, the slots are formed from the inner wall of the right valve and do not involve the tabulae. In some ways this mimics the slots developed for the teeth in many genera in the family Radiolitidae. In contrast, in the Hippuritinae MAC GILLAVRY, 1937, the sockets for the teeth in the right valve are formed by a lamina that encloses the region where the teeth would fit (DOUVILLÉ, 1891, Pl. 1, fig. 6; DECHA-SEAUX, 1952, Pl. 2; Fig. 2.5-8); the laminae represent an upfolding of the tabulae that fill the body cavity. The form of the sockets is clear in threedimensional forms of both the Barrettiinae and the Hippuritinae but cannot always be resolved in transverse sections cut close to the commissure of the right valve. Sections cut close to the commissure of the right valve typically miss the lamina forming the socket in the Hippuritinae and do not allow the form of the socket to be determined. In such cases more adapical trans-







Figure 2: Form of sockets for teeth in Old Word (Hippurites) hippuritids (formed by cavities) and New World (Carribea) hippuritids (formed by paired slots). 2.1, Caribbea muellerriedi (VERMUNT, 1937), UWIGM. 2010.01.0001 (same specimen as MITCHELL, 2010, Fig. 3A, Guinea Corn Formation (lower upper Maastrichian), Central Inlier, Jamaica. 2.4, Caribbea maldonensis (CHUBB), no number (UWIGM collection), Maldon Formation (upper upper Maastrichtian), Maldon Inlier, Jamaica. 2.5, Hippurites sp. no number (BMNH collection), Turonian, I'iltarium, Uchaux, Vancluse, France. 2.6-7, Hippurites lapeiroussii (GOLDFUSS, 1840), interior mould of the body cavity preserving the form of the sockets for teeth and posterior myopohre, BMNH. 81722, Maastricht Chalk (Md zone, Maastrichtian), ENCI Quarry, St. Pietersburg, The Netherlands. 2.8, Hippurites radiosus DES MOULINS. BMNH.PI RU 21, Campanian, Barbezieux, Charente, SW France. P0, P1, P2, pillars; AT, PT, anterior and posterior teeth in slots; ATS, PTS, anterior and posterior sockets for the teeth, PM, PMS, posterior myophore and socket, respectively.

verse sections need to be cut in order to distinguish between members of the two subfamilies.

GRUBIĆ (1979) erected the subfamily Torreitinae to distinguish *Torreites* from the Hippuritinae. The subfamily is accepted here and has sockets formed in the same way as the Hippuritinae but lacks a pore system in the left valve. Table 2 shows a revision of the Hippuritidae as recognized here.

**Table 2:** Classification of the Hippuritidae with a revision of New World forms.

Hippuritinae Mac GILLAVRY		Hippurites LAMARCK, 1801 Pironaea MENEGHINI, 1868 Pseudovaccinites Sénesse, 1946 Tetracionites ASTRE, 1931 Vaccinites FISCHER, 1887 Yvaniella MILOVANOVIĆ, 1938
Barrettiinae Снивв	<i>Caribbea</i> Clade	<b>Caribbea</b> GRUBIĆ, 2004 Laluzia GÖTZ & MITCHELL, 2009 Praebarrettia TRECHMANN, 1924
	<i>Barrettia</i> Clade	<b>Barrettia</b> Woodward, 1862 <b>Parastroma</b> Douvillé, 1926 <b>Whitfieldiella</b> Mitchell, 2010
Torreitinae GRUBIĆ		<b>Praetorreites</b> PHILIP & PLATEL, 1994 <b>Torreites</b> PALMER, 1933 <b>Polytorreites</b> MITCHELL & SKELTON, 2013

## Caribbea Clade

**Diagnosis.** Barrettiinae that lack pallial canals in the inner layer of the left valve.

**Remarks.** This clade contains three genera: *Caribbea* GRUBIĆ, 2004, *Laluzia* GÖTZ & MITCHELL, 2009, and *Praebarrettia* TRECHMANN, 1924.

## Genus Caribbea GRUBIĆ, 2004

**Type species.** Orbignya muellerriedi VERMUNT, 1937, from the lower Maastrichtian of the Province of Pinar del Rio, Cuba.

Emended Diagnosis. A hippuritid with two primary infolds (P1 and P2) and an incipient ligamental ridge. The PT and AT have ridges that fit into channeled grooves (sockets) on the CT and inner shell layer of the RV. The PM fits into an embayment in the inner shell layer and is not separated from the body cavity by a lamina. The AM is attached directly to the inner shell layer. The outer shell layer of the RV is composed of funnel plates that are separated by irregular dendritic radial muri or pustules. Pallial canals are absent from the inner shell layer of the LV. The radial canals of the LV are overlain by a pore system characterized by thin-walled irregular to polygonal canals that are subdivided to form porules by merging denticles. The pores are irregularly arranged in the central part of the LV, but form radial lines over numerous narrow radial canals in the limbal zone.

**Discussion.** The generic placement of the simple hippuritids of the Maastrichtian of the Americas has long been debated. Most authors have used the pillar arrangements (prominent P1 and P2, incipient P0) to place the American forms grouped around *muellerriedi* within *Hippurites* LA-MARCK, 1801 (=*Orbignya* FISCHER, 1887). MAC GIL-LAVRY (1937, p. 111) also described *muellerriedi* under the generic name *Hippurites*, but suggested it might belong to *Hippuritella* DOUVILLÉ. MITCHELL (2010) illustrated the pores in the LV of a specimen of *muellerriedi* from Jamaica and placed the species in *Hippuritella*. GRUBIĆ (2004) erected the genus *Caribbea* based on the structure of the outer shell layer of the RV.

The RVs of *Hippurites* species from the Old World have well-developed P1 and P2, but incipient development of P0; furthermore, their pore systems are characterized by round, linear or vermicular pores that are clearly distinct from the American *muellerriedi*. The RV of *Hippuritella* is superficially similar to that of *Hippurites*, but instead of simple (round, linear or vermicular) pores, the pore system consists of polygonal pores, and a placement of the American *muellerriedi* in *Hippuritella* based on the pore system would appear attractive (MITCHELL, 2010).

GRUBIĆ'S (2004) character of vertical canals in the outer shell layer of the RV is now known to be incorrect. This is due to a misunderstanding of the sections and descriptions of the shell wall given by CHUBB (1956) for '*Parastroma' maldonensis* and by MAC GILLAVRY (1937) for '*Hippurites' muellerriedi*. Because MAC GILLAVRY (1937) stated that the shell structure of *muellerriedi* might be similar to some Old World forms (*e.g.*, '*Hippurites' cornucopiae* DEFRANCE figured by DOUVILLÉ, 1910, Pl. 41, fig. 3, and *Hippurites* lapeirousei GOLDFUSS of PARONA, 1900, Pl. 1, fig. 2), the structure of the outer shell layer of the RV would appear to be an unsuitable criterion for erecting a new genus.







 Figure 3: Caribbea muellerriedi (VERMUNT, 1937), El Rayo Formation (lower Maastrichtian), Puerto Rico. 3.1-2, RV (NS32; USNM 547510) attached to conjoined specimen of Antillocaprina suboccidentalis Chubb: 3.1, showing grooves on exterior surface of RV; 3.2, adapical view showing pillars, slots for teeth, and outer shell layer wall structure. 3.3-4 (NS71: USNM 547518), bouquet of two conjoined RVs, 3.3, adapical view showing single tabula closing off the body cavity, note that the sockets for the teeth are not formed by folding of the tabula; 3.4, flank with outer shell layer broken away showing the tabulae in body cavity. 3.5-6 (NS33: USNM 547548), bouquet of four RVs: 3.5, flank showing grooves on exterior surface with rounded costae between; 3.6, adapical view of interior of RV showing outer shell layer structure, thin inner shell layer, and myocardinal arrangement; note that sockets for teeth are formed by slots on the central tooth and that the 'socket' for the PM is open to the body cavity. P1 and P2, first and second pillars; ATS, anterior socket; PTS, posterior socket; PMS, posterior myophore socket; ISL, inner shell layer; OSL, outer shell layer. Scale bar = 10 mm.

However, the construction of the sockets for the teeth and PM in *muellerriedi*, now apparent from the Puerto Rican material described here, contrasts markedly with both Hippurites and Hippuritella. In the latter two genera (together with Vaccinites FISCHER), the sockets in the RV for the teeth and PM are vertical cavities developed within the inner shell layer. Transverse sections through the RVs of Hippurites, Hippuritella and Vaccinites, depending on orientation relative to, and distance from the commissure, show the teeth and PM of the LV partially or completely surrounded by the inner shell layer of the RV. In specimens preserved in three-dimensions, such as Hippurites radiosus DES MOULINS from the Maastrichtian of France (DECHASEAUX, 1952, Pl. 2) or Vaccinites petrocoriensis (DOUVILLÉ) from the middle-upper Turonian of Gourd-del-Arche (Dou-VILLÉ, 1891, Pl. 1, fig. 6), the sockets for the teeth and PM are clearly formed from the tabulate infilling of the adapical part of the body cavity of the RV. In contrast, each socket in C. muellerriedi is represented by an embayment in the dorsal inner shell wall with slots (defined by two thin laminae) developed from the shell wall and the CT; on the ventral side, each tooth is open to the body cavity for its entire length, whereas on the dorsal side each tooth is flanked by an embayment of the inner shell layer. Thus, the quite different construction of the sockets of the RVs of New World Caribbea (slots on the inner layer of the RV) and Old World Vaccinites, Hippurites and Hippuritella (cavities in the tabulate infilling of the adapical body cavity of the RV) justifies the placement of *muellerriedi* in a separate genus.

The external surface of the RV of specimens of *Caribbea* from the New World is variable with three contrasting morphotypes. The first morphotype is exhibited by *C. muellerreidi* and *C. maldonensis* (CHUBB) from the Maldon Inlier (Jamaica: GUNTER, 2002); it is rounded other than for three sulci corresponding to the principal folds and a

few more sulci between as described below. The second morphotype is shown by 'H. perkinsi' MYERS from Cardenas (Mexico) and the Jerusalem Mountain Inlier (Jamaica) and most C. maldonensis from the Central Inlier (Jamaica); these have angular costae developed between the sulci. The third morphotype seen in specimens from the Jerusalem Mountain Inlier (Jamaica) is characterized by fine longitudinal riblets (similar to those described below in Laluzia peruviana). Given the change in outer shell microstructure from C. muellerriedi to C. maldonensis and the corresponding existence of two of the three morphotypes in both species, it is clear that the morphotypes are phenotypic and have little taxonomic value. For descriptive purposes these might be referred to as (in roman text) the 'muellerriedi' morphotype, the 'perkinsi' morphotype and the 'peruviana' morphotype, but without implying any taxonomic significance. As such, only a limited number of species of Caribbea need to be recognized in the Maastrichtian of the Caribbean: C. muellerriedi from the lower to lower upper Maastrichtian of Mexico, Cuba, Jamaica and Puerto Rico, C. maldonensis from the mid upper Maastrichtian of Jamaica, and an undescribed giant form from the uppermost Maastrichtian of Jamaica.

#### Caribbea muellerriedi VERMUNT, 1937

(Figs. 3.1-6, 4.1-4, 5.1-6, 4.1-4, 5.1-6, 6.1-6, 7)

- v. 1924 *Hippurites (Orbignya)* sp.; TRECHMANN, p. 396, Pl. 23, fig. 5.
- . 1930 Hippurites (Hippuritella DOUVILLE; Orbignya TOU-CAS) cf. incisus (DOUVILLE); MÜLLERRIED, p. 165, Figs. 1-2.
- \*. 1937 Orbignya müllerriedi VERMUNT, p. 261, Fig. 3ad; Pl. 36, figs. 1-3.
- v. 1937 *Hippurites muellerriedi* (VERMUNT); MAC GILLA-VRY, p. 110, Fig. 2 (on p. 123); Pl. 5, fig. 6.
- . 1937 Hippurites mullerriedi (VERMUNT); MAC GILLAVRY, p. 111, Pl. 5, fig. 6.
- v. 1956 Hippurites (Orbignya) mullerriedi (VERMUNT); CHUBB, p. 19, Pl. 4, figs. 4-8.
- v. 1956 *Hippurites (Orbignya) ceibarum*; Снивв, р. 19, Pl. 4, figs. 9-10.
- v. 1968 *Hippurites muellerriedi* (VERMUNT); MYERS, p. 42, Pl. 3, figs. 4-6.
- v. 1968 *Hippurites perkinsi*, n.sp.; Myers, p. 43, Pl. 4, figs. 5-6.
- v. 1971 Orbignya mullerriedi VERMUNT; CHUBB, p. 204, Pl. 49, figs. 1-2.
- v. 1971 Orbignya ceibarum (Снивв); Снивв, р. 204, Fig. 6; Pl. 49, fig. 3.
- v. 1974 Orbignya KAUFFMAN and SOHL, p. 413, Fig. 7F-H.
- . 1975 *Hippurites muellerriedi* (VERMUNT); LUPU, p. 240, Fig. 20.
- v. 2004 *Caribbea muellerriedi* (VERMUNT); GRUBIĆ, p. 147, Pl. 2, fig. 1.
- v. 2004 *Caribbea ceibarum* (Снивв); GRUBIĆ, p. 147, Pl. 2, fig. 2.
- v. 2004 Caribbea sladici GRUBIĆ, p. 148, Pl. 2, fig. 4.
- v. 2006 *Hippurites perkinsi* MYERS; SCHAFHAUSER, p. 62, Pl. 16, figs. 8-9.
- v. 2010 *Hippuritella muellerriedi* (VERMUNT); MITCHELL, Fig. 3A.







✓ Figure 4: Caribbea muellerriedi (VERMUNT, 1937), El Rayo Formation (lower Maastrichtian), Puerto Rico. 4.1, 4.4 (NS33: USNM 547548), bouquet of four RVs (same as Fig. 3.5-6, also figured by SKELTON, 2018, Fig. 7.6), 4.1, detail of LV in position in RV, showing radial canals, pores and porules; note that three or four pores are over each radial canal in the central region and narrow radial porules in the limbal region; 4.4, adapical view of bouquet. 4.2-3 (NS7: USNM 547513), LV showing myocardinal arrangement in juveniles, 4.2, oblique view, 4.3, adapical view. O1 and O2, oscules for first and second pillars; AT, anterior tooth; PT, posterior tooth; PM, posterior myophore. Scale bar = 10 mm.

- . 2013 Caribbea muellerriedi (VERMUNT); PONS et al., p. 738-742, Figs. 16.1-16.11, 17.1-17.7, 18.1-18.3.
- . 2018 *Caribbea muellerriedi* (VERMUNT); SKELTON, Fig. 7.6 (= Fig. 3.4 herein).

**Holotype.** The holotype (Min.-Geol. Inst., Univ. Utrecht, W. C. 1933, 6, now in Naturalis, Leiden, The Netherlands) from the lower Maastrichtian, Locality L818, province of Pinar del Rio, Western Cuba was figured by VERMUNT (1937, Pl. 36, figs. 1-2). A new photograph of it is illustrated in Figure 7 and it shows no apparent differences from the material included in this species from Jamaica, Puerto Rico or Mexico.

**Material.** Many specimens in the USNM. Material specifically referred to and placed in the type collection: NS31 (USNM 547509) (Locality 1202, USNM 187687), NS32 (USNM 547510) (Locality 1202, USNM 187687), NS35 (USNM 547511) (Locality 1202), NS39 (USNM 547512) (Locality 1445-3), NS7-10 (USNM 547513-547516) (Locality 1202?), NS70 (USNM 547517) (Locality 1202? draw 131, pores), NS33 (USNM 547548) (Locality 1202, USNM 187687), and NS71 (USNM 547518) (draw 131, Locality 1202, tabulae). All from the El Rayo Formation, Puerto Rico.

Extensive comparable material is available from Cuba (Naturalis, Leiden, The Netherlands), Jamaica (UWI Geology Museum) and Mexico (Texas Memorial Museum, The University of Texas at Austin). All this material agrees very well with the material from Puerto Rico described here.

**Diagnosis.** A small to medium sized species of *Caribbea* with a wall structure defined by radial muri on funnel plates of the outer shell layer throughout growth.

**Description.** The RV is conical gradually increasing in diameter. Its surface is marked by regular furrows (Fig. 3.1-2, 3.5), the three deepest corresponding to the three pillars (P0, P1 and P2). Between P0 and P1 there is one (rarely two) further weak furrow(s), and between P1 and P2 another weak furrow; weak furrows also occur around the remainder of the shell's circumference, but are generally not as well developed as the ones between the pillars. The surface between the furrows is regularly convex and smooth.

The inner layer of the RV is thin (Fig. 3.2); the outer layer of the RV is composed of funnel plates with irregular dendritic radial muri (Fig. 3.2, 3.5). The funnel plates are directed outwards and upwards at an angle of about 60° to 70° to the horizontal. P1 and P2 are strong infolds of the outer shell layer into the body cavity and have a microstructure identical to the remainder of the RV outer shell wall. PO is a very weak (incipient) infold into the body chamber to which the central tooth is attached (Figs. 3.6, 4.4, 5.2); the central tooth is an inward projection of the inner shell layer and has two laminae each on the posterior and anterior sides that create slots for the PT and AT to fit into; single strong vertical laminae extend on the ventral-side of the wall of the body cavity where the teeth would fit together with very weak ribs on the dorsal side to form the sockets for the PT and AT (Fig. 5.2). The interior of the RV contains only incipient (weak to very weak) secondary folds into the body cavity. There is no socket for the PM, which simply fits between the lamina for the PT and P1 (Figs. 3.5, 4.4, 5.2). No socket is present for the AM, which must attach directly onto the interior wall of the RV. The tabulae in the body cavity are plate-like and widely spaced (Fig. 3.3-4). The last tabula is inserted adapically of the point to which the teeth and PM penetrate the RV, so that transverse sections of a RV never show the teeth and tabulae at the same level (Fig. 3.3).

The LV is weakly concave, flat or very gently convex (Figs. 4.1, 4.4, 5.1, 5.4, 6.1-2). The AT, PT and PM are arranged in a straight line (Figs. 4.2-3, 6.3-6). The AT is broadest and longest and is generally two-pronged (Figs. 4.2, 6.3-4) and has a rectangular transverse cross-section. The PT is about as wide as broad (Fig. 6.3-6); in transverse cross-sections it is strongly curved with its posterior-ventral aspect highly convex and its anterior-dorsal margin straight to gently concave. The PM is a narrow to relatively narrow radially orientated blade (Fig. 6.3-4). The AM extends anteriorly from the AT and gently slopes towards the ventral aspect adapically; it forms a curved blade that extends outwards and abapically at an angle of about 45° (Figs. 4.3, 5.3, 5.6, 6.5). The teeth and myophores are connected to a circular myocardinal yoke, which lacks openings (Figs. 5.3, 5.6, 6.3-6). The PM is constructed on a strong buttress that extends radially and is supported by two or three very weak radial buttresses (Fig. 6.4). A strong buttress also extends between the openings for P1 and P2 and bifurcates towards the margin of the valve (Figs. 5.2-3, 6.3); it may be supported by a few radiating incipient buttresses. A weak buttress extends along the ventral side of the opening (O2) above P2 (Fig. 6.2, 6.5). The myocardinal yoke below the AM is supported by incipient to weak radially directed buttresses, which may number 7, 8 or 9 (Fig. 6.3, 6.5-6). The LV contains a series of radial canals that extend to the margin of the valve



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 Figure 5: Caribbea muellerriedi (VERMUNT, 1937), El Rayo Formation (lower Maastrichtian), Puerto Rico. 5.1 (NS10: USNM 547516), LV, abapical view, showing radial canals and pores. 5.2 (NS50: USNM 547542), RV of a specimen from a bouquet showing sockets for anterior and posterior teeth and posterior myophore. 5.3-4 (NS35: USNM 547511), LV: 5.3, oblique view showing teeth and myophores; 5.4, abapical view showing radial canals and partially preserved pores. 5.5-6 (NS31: USNM 547509), LV, 5.5, abapical view showing radial canals (no pores preserved); 5.6, oblique view showing teeth and myophores. P1, first pillar; O1 and O2, oscules for first and second pillars; AT/ATS, anterior tooth/socket; PT/PTS, posterior tooth/socket; PM/PMS, posterior myophore/myophore socket; CT, central tooth; RF, radial canals; B, buttress. Scale bar = 10 mm.

and are visible when the pore system is not preserved (Figs. 4.1, 5.4-5). The canals have maximum widths of 2 mm and the walls between adjacent canals are 0.3 mm thick. New canals are intercalated between earlier formed canals during growth (Fig. 4.1). The canals open onto the apertural surface of the RV (Fig. 4.2-3). In large individuals the limbal zone is different: the large canals continue as thin canals and many additional thin limbal canals are inserted. The limbal canals have widths of 0.3 to 0.4 mm and are separated by walls with thicknesses of 0.3 to 0.4 mm (Figs. 4.1, 6.1-2). The larger radial canals open onto the adapical portion of the apertural surface of the outer layer of the RV, the limbal canals open onto the abapical portion of the apertural surface of the outer layer of the RV (Fig. 6.5-6). The arrangement of apertural openings of the radial and limbal canals around the margins of the shell agrees with the pattern previously described for various Old World hippuritids (e.g., SKELTON, 1976, Fig. 2; SCHUMANN, 2010). The radial canals are overlain by the pore system which is uniform across the central region of the LV (that is no pustules are developed above the inner terminations of newly intercalated radial canals as in many Old World hippuritids). The pores in the inner zone covering the normal radial canals are polygonal with diameters of 0.3 to 0.5 mm and with three or four pores situated concentrically over each radial canal (Fig. 6.2). The walls between the pores are about 0.1 mm thick. Each pore has three or four denticles that in well-preserved regions of well-preserved specimens merge to form a fine reticulate covering consisting of three or four porules in each pore (Figs. 4.1, 6.2). It is likely that originally all pores were subdivided to form porules, but the finer denticles have been damaged or were not silicified. The limbal canals are overlain by pores which are radially elongate (Figs. 4.1, 6.1-2). These radially elongate pores also have fine denticles that would have subdivided them into two porules, which are arranged radially (Figs. 4.1, 6.1). The 'oscules' for P1 and P2 are surrounded by a single line of vertical canals with a reticulate covering; 'oscules' may

even have been completely covered by a reticulate cover as some specimens preserve part of this (Fig. 6.2).

The relationships between the angles P1-PM-PT and P2-P1-PM (Fig. 8) separate different genera of multiple fold hippuritids of the Caribbean region (MITCHELL, 2010). This plot requires articulated specimens so that the position of the PM can be determined (there is no enclosed socket in *Caribbea*) and it can be determined in specimens from Jamaica and Mexico, but not from Puerto Rico. *Caribbea* plots in an intermediate position between *Laluzia* and *Praebarrettia*.

Discussion. The holotype of Orbignya muellerreidi was figured by VERMUNT (1937, Pl. 6, figs. 1-2) and shows orimentary folds and slots on the CT for the reception of the teeth of the LV (Fig. The adjoining individual shows a round cavity, however this is not the cavity for the PM, but an oblique cut through a tabula filling the lower part of the body cavity. A socket is not present between the ligamentary infold and P1 for the reception of the PM and this material is fully consistent with the material described from Puerto Rico in this paper (as well as material from Jamaica and Mexico). Furthermore, specimens of RVs examined by SFM in 2009 in the collections of the Museo Nacional de Historia Natural, La Habana, Cuba, are also identical to the Puerto Rican material.

The pore system of C. muellerriedi has also been illustrated in a specimen from the Guinea Corn Formation of Jamaica (MITCHELL, 2010). This specimen shows a pore system very similar to that of the Puerto Rican material described here. The inner zone of the LV is characterized by irregular sub-polygonal pores with five or six pores arranged concentrically above each radial canal; the limbal zone has radially arranged lines of radially orientated pores. Both the central zone pores and the limbal zone pores have denticles, which divide central pores into three or four porules, and limbal pores into two porules. The only difference between the pore systems of the Puerto Rican and Jamaican specimens is in the number of pores developed concentrically above the radial canals of the inner zone of the LV; 3 or 4 in the former, and 5 or 6 in the latter. The Jamaican specimen is also larger than the Puerto Rican specimens. The increased number of pores concentrically above each radial canal may be due to phylogenetic size increase passing from the early Maastrichtian (Puerto Rican material) to mid Maastrichtian (Jamaican material). the Caribbea maldonensis is still larger, but the pore system is unknown. Given the rarity with which pores are preserved in New World specimens, it is inadvisable to use this to define species, and in any case only a single specimen from Jamaica has the pore system preserved.



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 Figure 6: Caribbea muellerriedi (VERMUNT, 1937), El Rayo Formation (lower Maastrichtian), Puerto Rico. 6.1 (NS39: USNM 547512), LV, abapical view showing radial canals and well preserved pores and porules. 6.2 (NS70: USNM 547517), LV, abapical view showing radial canals and well preserved pores and porules. 6.3 (NS9: USNM 547515), LV, oblique view, showing myocardinal arrangement; note lack of canals penetrating myocardinal yoke. 6.4 (NS35: USNM 547511), LV, oblique view showing myocardinal elements. 6.5-6 (NS8A: USNM 547514), LV showing myocardinal arrangement, oblique views; 6.5, note lack of canals penetrating myocardinal yoke, 6.6, note ridges on teeth that fit into the grooved sockets. O1 and O2, oscules for first and second pillars, AT, anterior tooth; PT, posterior tooth; Am, anterior myophore; PM, posterior myophore. Scale bar = 10 mm.

Five further species assigned to Orbignya, Hippurites or Caribbea have been erected in the Central American region. CHUBB (1956) erected Hippurites (Orbignya) ceibarum for small forms from Jamaica. They occur with normal-sized specimens of *muellerriedi*, and other than being smaller, do not appear to differ in any significant way from that species. Hippurites perkinsi was erected by MYERS (1968) for material from the Cardenas Formation which occurred together with specimens of C. muellerriedi. MYERS' specimens differ from muellerriedi in having more prominent costae on the external surface of their RVs. Numerous additional specimens of H. perkinsi collected by MYERS are preserved in the Texas Memorial Museum, Austin, Texas, and were examined by SFM in 2009. Similar forms also occur in the Jerusalem Mountain Limestone in Jamaica. As discussed earlier, these forms are interpreted as phenotypic variants and H. perkinsi is placed in synonymy with C. muellerriedi here. GRUBIĆ (2004) erected Caribbea sladici for a specimen from Jamaica that had been illustrated by TRECH-MANN (1924), based on its lack of orimentary folds. In populations of *muellerriedi*, the presence and strength of orimentary folds is variable and it is doubtful if forms that lack orimentary folds are anything other than morphological variants of C. muellerriedi.

In contrast, I point out that C. maldonensis is distinct, having a different outer shell structure (pustules rather than muri as described by CHUBB, 1956, 1971) and a different range (mid Maastrichtian, as opposed to early to early mid Maastrichtian for C. muellerriedi) in the Jamaica (MIT-CHELL, 1999; STEUBER et al., 2002; GUNTER & MIT-CHELL, 2005). Given that juvenile growth stages of C. maldonensis have an identical RV outer shell layer microstructure to adult forms of C. mueller*riedi*, it seems likely that the former is the direct descendent of the latter and that differences in outer layer shell microstructure do not warrant the erection of a separate genus for maldonensis, a move that would artificially split a single evolving lineage.

OLSSON (1934) erected *Orbignya pacifica* for a species from the Monte Grande Formation (upper Campanian - lowermost Maastrichtian?) of Peru. This form has multiple infolds and appears to be unrelated to *Caribbea*, it may represent *Laluzia peruviana* (GERTH).

Geographic and Stratigraphic Range. Caribbea muellerriedi is widely distributed in the Caribbean and Central American region. In Cuba it is reported from the Habana Formation of the province of Pinar del Rio (VERMUNT, 1937; MAC GILLAVRY, 1937) which I attribute to the early Maastrichtian based on its association with Laluzia. In Jamaica the species is widely distributed in the Jerusalem Mountain Limestone (lowermost upper Maastrichtian), the Titanosarcolites limestone of the Marchmont Inlier (CHUBB, 1971) and the lower part (A to Upper C Beds) of the Guinea Corn Formation (MITCHELL, 1999, 2010). In Puerto Rico it occurs in the El Rayo Formation which is attributed to the lower Maastrichtian (MITCHELL et al., 2011). In Mexico, it is recorded from the Cardenas Formation (MYERS, 1968; PONS et al., 2013) which has been dated by ammonites and Sr-isotope values to the lower to lower upper Maastrichtian (IFRIM et al., 2005; SCHAFHAUSER et al., 2007). Caribbea muellerriedi is therefore a widespread early to early mid Maastrichtian species.

#### Genus Laluzia Götz & MITCHELL, 2009

=*Gloria* GRUBIĆ, 2004, type species *Gloria vermunti* GRUBIĆ, 2004 (=*Pironaea* cf. *peruviana* VER-MUNT, 1937), from the Habana Formation of the Pinar del Rio Province, Cuba; non *Gloria* BARRAN-DE, 1881, which is a mid-Palaeozoic cryptodont bivalve.

**Type species.** Laluzia armini Götz & MITCHELL, 2009, from the lower Maastrichtian Cardenas Formation of San Luis Potosi, Mexico.

Diagnosis. A hippuritid with three primary infolds (P0, P1 and P2) and multiple secondary infolds. The PT and AT have ridges that fit into channeled grooves (sockets) on the CT and inner shell layer/PM lamella of the RV. The PM fits into an embayment in the inner shell layer that is separated from the body cavity by a lamella; the anterior myophore is attached directly to the inner shell layer. The outer shell layer of the RV is composed of funnel plates that are separated by irregular dendritic radial muri. Pallial canals are absent from the inner shell layer of the LV. Vertical canals penetrate the outer zone of the LV above the rays, and radial canals occur in the inner zone. The pore system consists of irregularly distributed, thick-walled irregular pores.

**Discussion.** The genus Laluzia was erected for a small hippuritid that lacks pallial canals in the inner layer of its LV and had a myocardinal arrangement different from that of *Praebarrettia*, the only other American multiple-ray hippuritid





**Figure 8:** Scatter Plots of myocardinal arrangements of selected hippuritid rudists. *Laluzia peruviana* plots in the field overlapping with *Laluzia armini* and *Barrettia* and not in the field of *Praebarrettia*. *Caribbea* with its simple infolds plots midway between the fields for *Laluzia* and *Praebarrettia*, and could be the ancestor of either or both of these genera. Fields for *Whitfieldiella*, *Praebarrettia*, *Barrettia* and *Laluzia armini* are taken from GÖTZ and MITCHELL (2009). Holotype of *Laluzia armini* (reproduced from GÖTZ and MITCHELL, 2009, Fig. 6) shown for interpretation of angles a (P2-P1-PM) and b (P1-PM-PT).



that lacks pallial canals in its LV. At that time, the affinity of the various forms referred to Pironaea (that is, P. peruviana GERTH and P. cf. P. peruviana VERMUNT) from the Americas was unknown. With the new material from Puerto Rico described here which includes details of the pore system, and which I regard as undoubtedly congeneric with Laluzia, differences can be pointed out between Laluzia and Caribbea. In Laluzia, the teeth fit into slots developed from the body cavity lining just as in Caribbea. But Caribbea and Laluzia differ in many other respects: in Laluzia the PM fits into a socket whereas in Caribbea it fits into an embayment; Laluzia and Caribbea have differences in PM locations, LV buttress formation, pore systems and secondary infolds. So, whereas the 'sockets' in the RV of Laluzia and Caribbea are similar and may indicate a common ancestry, other details indicate that the two genera have already significantly diverged.

PONS et al. (2013, 2019) considered that Laluzia was a junior synonym of Praebarrettia TRECHMANN. However, the myocardinal arrangements of Laluzia and Praebarrettia are different, with Laluzia resembling that of Barrettia and Praebarrettia resembling that of Whitfieldiella (DOMMELEN, 1971; GÖTZ & MITCHELL, 2009; MIT-CHELL, 2010). Furthermore, the outer shell layer of Laluzia consists of funnel plates with radial muri; in contrast the outer shell layer of the RV of Praebarrettia consists of funnel plates separated by pustules. Although Caribbea shows an evolutionary development of pustules from radial muri, the differences in the myocardinal arrangements are sufficient to justify separation at the generic level. The pore systems of the two genera are also different: in Laluzia, pores are randomly distributed across the reticulum; whereas in Prae*barrettia*, they are highly ordered occurring on sieve plates directly above the transverse canals (DOMMELEN, 1971). The stratigraphic distribution of the two genera is also different (Laluzia in the early Maastrichtian and Praebarrettia in the late Maastrichtian). It is possible that Laluzia evolved into Praebarrettia, but this would have required changes in both the position of the PM and the pore system. It seems advisable at the present time to maintain two separate genera.

## Laluzia peruviana (GERTH, 1928)

#### (Figs. 9.1-7, 10.1-6, 11.1-6, 12)

. 1928 Pironaea peruviana: GERTH, p. 235, Figs. 2-3.

- v. 1937 Pironaea sp. cf. P. peruviana GERTH; VERMUNT, p. 266, Fig. 2i-j.
- v. 2004 *Gloria vermunti* spec. nov.; GRUBIĆ, p. 150, Pl. 2, fig. 5.
- . 2004 Gloria peruviana (GERTH); GRUBIĆ, p. 150, Pl. 2, fig. 7.
- . 2004 Praebarrettia sparcilirata (WHITFIELD, 1897); PHI-LIP and JAILLARD, p. 45, Pl. 3, figs. 1-2.
- . 2013 *Praebarrettia sparcilirata* (WHITFIELD) *sensu lato*, larger morphotype; PONS *et al.*, p. 742-748, Figs. 19.1-10, 21.1-6, 23.1-6.

**Type.** The material described as *Pironaea peruviana* by GERTH (1928) is missing from the collections held by Naturalis in Leiden, The Netherlands. However, GERTH's illustrations are sufficient to suggest affinity and a neotype should be selected from Peru.

Material. NS6 (USNM 547519) (locality 1202-3), NS11 (USNM 547520) (locality 1202-3), NS12 (USNM 547521) (locality 1202-3), NS34 (USNM 547522) (locality 1202, NSNM 187687), NS36 (USNM 547523) (locality 1202-10), NS40 (USNM 547549) (locality 1202), NS41 (USNM 547524) (locality 1202-33), NS45 (USNM 547525) (locality 1202-5), NS48 (USNM 547526) (locality 1202-7), NS54 (USNM 547527) (locality 1202), NS48 (USNM 547528) (locality 1202-7), NS49 (USNM 547529) (locality 1202 45), NS51 (USNM 547530) (locality 1202), NS52 (USNM 547531) (locality 1202), NS53 (USNM 547532) (locality 1202), NS66 (USNM 547533) (locality 1202-5 or 17?), and NS73 (USNM 547534) (draw 118, locality 1202). All from the El Rayo Formation, Puerto Rico.

**Diagnosis.** A large species of *Laluzia* with broad, short secondary infolds.

Description. RV small to medium sized, conical to cylindrical. External surface with many rounded costae and in some specimens vertically striated (Fig. 9.6), no growth lines. The larger furrows correspond to infolds of the outer shell layer. The outer shell layer is composed of funnel plates that are orientated outwards and upwards at an angle of about 50°. The funnel plates are ornamented with radial muri (Fig. 9.1, 9.3). The outer shell layer is folded into the inner shell layer as a series of rays that may number up to 15 (Fig. 9.2, 9.7). The body chamber (body cavity lining) is formed by a continuous lamina that represents the inner shell layer, and this lamina rises above the apertural surface of the inner layer as a pronounced wall (Fig. 9.2). The inner shell layer is filled with large partitions formed by vertical radial plates extending from the rays and horizontal tabulae (Fig. 9.2). The central tooth has two laminae each on the anterior and posterior sides that form slots for the PT and AT to fit into; two thin laminae project from the interior wall both posterior (that is on the lamella separating the PM cavity from the body cavity) and anterior of the central tooth to create two further slots for the AT and PT to fit into (Fig. 9.1-2). The PM cavity is separated from the body cavity by a thin lamella (Fig. 9.1-2).

During ontogeny, P1 and P2 develop first, then incipient infoldings develop, but the ligamental ray does not develop until later in ontogeny. This suggests that the ligamental infold is an acquired character and not an ancestral character in *Laluzia* (a similar situation occurs in the upper Maastrichtian in an undescribed large species of *Caribbea*).







 Figure 9: Laluzia peruviana (GERTH, 1928), El Rayo Formation (lower Maastrichtian), Puerto Rico. 9.1 (NS12: USNM 547521), incomplete RV showing pillars, sockets for teeth, and enclosed socket for posterior myophore. 9.2 (NS40: USNM 547549), juvenile RV, showing sockets for teeth and posterior myophore and infolds. 9.3 (NS51: USNM 547530), incomplete RV, adapical view, showing infolds. 9.4 (NS52: USNM 547531), incomplete RV, adapical view, showing infolds. 9.5 (NS34: USNM 547522), articulated shell, showing the anterior tooth fitting into its socket and the anterior myophore that would attach directly onto the inner shell layer of the RV. 9.6 (NS49: USNM 547529) articulated shell showing longitudinal ribs on RV. 9.7 (NS48: USNM 547526), RV, adapical view showing infolds. PO, ligamentary infolding; P1 and P2, first and second pillars, ATS, anterior tooth socket; PTS, posterior tooth socket, PMS, posterior myophore socket; BCL, body cavity lining. Scale bar = 10 mm.

The LV is flat to gently domed and does not contain pallial canals (Fig. 9.5). The myocardinal yoke is continuous and elliptical (Figs. 10.1-2, 10.4-6, 11.1, 11.5-6). The PT is about half the size of the AT (Fig. 10.4-6). The teeth are concentrically blade-like. The PM is blade like and situated on a buttress extending posterior-dorsally from the PT (Figs. 10.4, 10.6, 11.1, 11.3, 11.6). The AM is a surface that is tilted outwards extending around a third of the yoke, it extends around the anterior side of the AT (Figs. 10.1-2, 10.4-6, 11.1, 11.6). The yoke is supported by very prominent buttresses, which are much more prominent that those in *Caribbea*. The buttresses are single, or bifurcate once. The yoke is penetrated by openings on the adapical side of the AM (Fig. 10.2, 10.5). Between each pair of buttresses, a very irregular line of double pores penetrates the LV. The terminal pore is broadly rounded, and the other pores are irregular and alternate with each other (Fig. 10.1). The adapical side of the left valve bears radial canals in the umbonal (inner) part of the shell (Fig. 10.3). The radial canals are overlain by a fine reticulate mesh that has denticles (Figs. 10.3, 11.2, 11.4-5). The radial canals pass down to the round canal at the end of the irregular pore system (Fig. 10.3). Where the canals penetrate the LV, lateral canals are developed. Lateral openings extend concentrically from the radial canals into the inter-radial areas. The inter-radial areas are covered by the same reticulate covering as the radial canals (Fig. 11.2, 11.4-5). P1 has a round oscule in the LV and P2 has an elongate oval oscule that is connected to the rim (at least in young forms; Figs. 10.3-4, 11.1, 11.6). A fine mesh extends across part of the opening for P2 suggesting it may have been covered by a reticulate mesh (Fig. 11.5).

From the arrangement of the myocardinal yoke with the interior surface of the body chamber, the AM must have been connected to the interior of the body cavity, much as in *Caribbea*.

Discussion. GRUBIĆ (2004, p. 151) stated that the type specimen of Pironaea peruviana, which came from the middle member of the La Mesa Formation of Peru (GERTH, 1928; PHILIP & JAILLARD, 2004), is missing from the collections at Naturalis, Leiden. I also could not find it in the same collection in 2010 although I made a thorough search. New material, collected from the upper member of the La Mesa Formation, Peru, was described under the name Praebarrettia sparcilirata (WHITFIELD) by PHILIP and JAILLARD (2004). They considered that their material was synonymous not only with 'Pironaea' peruviana, but also with Praebarrettia sparcilirata and Praebarrettia porosa PALMER. The age of these deposits, based on ammonites and bivalves, is either upper Campanian or lower Maastrichtian (PHILIP & JAILLARD, 2004; DHONDT & JAILLARD, 2005). PHILIP and JAIL-LARD (2004, Pl. 3, figs. 1-2) illustrated a RV that conforms to the population of L. peruviana from Puerto Rico. When plotted on scatter plots for myocardinal arrangements (Fig. 8), the upper La Mesa specimen plots in the same field as the Puerto Rican and Cardenas specimens. Although no LV was figured, it was described (PHILIP & JAIL-LARD, 2004, p. 11) as follows: "Typical radial canals covered with a thin, more or less continuous reticulate layer of small pores (0.3-0.5 mm.). Transverse furrows described by DOMMELEN (1971) not observed in our specimens". This description is also comparable with the material from Puerto Rico. I therefore consider that the type specimen of Pironaea peruviana illustrated by GERTH (1928) and the material described by PHILIP and JAILLARD (2004) as Praebarrettia sparcilirata (WHITFIELD) are the same species and are identical to the material described here from Puerto Rico; all are assigned to Laluzia peruviana here. Pons et al. (2013) described a series of specimens from the Cárdenas Formation in Mexico as Praebarrettia sparcilirata (WHITFIELD) sensu lato and recognized two successive morphotypes in the early Maastrichtian. Their smaller morphotype is the earlier form and corresponds to Laluzia armini Götz & MITCHELL, whereas their larger morphotype is equivalent to L. peruviana. In contrast to PHILIP and JAILLARD (2004) and PONS et al. (2013), I recognize both Praebarrettia porosa PALMER and P. sparcilirata as separate species and maintain them in a distinct genus, based on differences in their myocardinal-pillar arrangements and pore systems (DOMMELEN, 1971; GÖTZ & MITCHELL, 2009; Fig. 8 herein).

*Pironaea* sp. cf. *P. peruviana* from Cuba (VER-MUNT, 1937), on which GRUBIĆ (2004) erected *Gloria vermunti*, shows a very similar morphology (Fig. 12) and has a fine costation developed on the exterior surface of the RV. *Pironaea* sp. cf. *P. peruviana* is associated with *Caribbea muellerriedi* (VERMUNT, 1937), and also seems to be conspecific with the Puerto Rican material of *L. peruviana*.



✓ Figure 10: Laluzia peruviana (GERTH, 1928), El Rayo Formation (lower Maastrichtian), Puerto Rico. 10.1 (NS45: USNM 547525), LV, adapical view showing myocardinal arrangement and buttresses. 10.2-5 (NS66: USNM 547533), LV, various views showing myocardinal arrangement and buttresses: note the tunnels through the myocardinal yoke visible in 10.2 and 10.5; 10.3, abapical view showing radial furrows. 10.6 (NS41: USNM 547524), LV, oblique view showing myocardinal arrangement and buttresses. O1 and O2, oscules for first and second pillars. AT, anterior tooth; PT, posterior tooth; AM, anterior myophore; PM, posterior myophore. Scale bar = 10 mm.

Laluzia armini shows a similar myocardinal-pillar arrangement to L. peruviana but differs in the nature of the primary and secondary infolds. In L. armini, the primary and secondary infolds are narrow and comparatively elongate. In contrast, the infolds of *L. peruviana* are broad and short. Because the infold morphology in populations overlaps little, the two species appear to be separate. It is notable that L. peruviana occurs in both the Cardenas Formation (MITCHELL, pers. obs.) and El Rayo Formation, where it is associated with a highly diverse, normal-shelf rudist assemblage; yet L. armini occurs in a low-diversity rudist association in the Cardenas Formation at La Luz which was interpreted as a relatively deepwater low-light environment (GÖTZ & MITCHELL, 2009). It seems likely, therefore, that the two species may have been adapted to different environments or have been ancestor (L. armini) and descendant (L. peruviana).

'Pironaea' corrali PALMER, 1933, is a much more difficult form to interpret. The RV has a small number of infolds that range from non-moniliform to submoniliform. On the holotype the LV buttresses are weathered, and it is not possible to determine the myocardinal arrangement. I have not been able to work out the form of the myocardinal arrangement in any specimens of this species that I have seen (including material in Naturalis, The Netherlands, and the National Natural History Museum, Havana), and therefore its affinity and phylogenetic position remain unclear. New material will have to be analysed to determine the affinity of this form, and this I consider is one of the outstanding problems in understanding New World hippuritids.

**Geographical and Stratigraphical Distribution.** Laluzia peruviana is moderately widely distributed in lower Maastrichtian rudist assemblages of the American region. It is recorded from: the El Mesa Formation (upper Campanian, or more likely lower Maastrichtian) of Peru (PHILIP & JAILLARD, 2004); the Habana Formation *sensu lata* (the specific occurrence which I regard as likely to be of early Maastrichtian age) from Pinar del Rio, Cuba (VERMUNT, 1937), the El Rayo Formation (lower Maastrichtian) of Puerto Rico (recorded here), and the Cardenas Formation, near Rayon, San Luis Potosi State, Mexico (MYERS, 1968; MYERS Collection, Texas Memorial Museum, examined by SFM in 2009; PONS *et al.*, 2013).

The only other described species, *Laluzia armini*, occurs in the Cardenas Formation (lower Maastrichtian) at La Luz, State of San Luis Potosi, Mexico (GÖTZ & MITCHELL, 2009). Consequently, *Laluzia* appears to be a good biostratigraphic marker for the early Maastrichtian of the Central American region but could also be present in some upper Campanian assemblages of Peru.

## Barrettia Clade

**Diagnosis.** Barrettiinae that have pallial canals in the inner layers of their LVs and a pore system in the LVs.

**Remarks.** Pallial canals are also present in the LV inner shell layers of *Torreites*. The absence of pallial canals in the LV of the *Caribbea* clade could, therefore, be a derived character. The clade includes three genera: *Barrettia* WOODWARD, 1862, *Whitfieldiella* MITCHELL, 2010, and *Parastroma* DOUVILLÉ, 1926.

## Genus Parastroma DOUVILLÉ, 1926

**Type species.** Parastroma sanchezi DOUVILLÉ, 1926, from the Campanian of Arroyo Hondo, Camagüey Province, Cuba.

Diagnosis. A hippuritid with two primary infolds (P1 and P2) but with the multiple infolds represented by incipient rays. The PT and AT have ridges that fit into channeled grooves (sockets) on the CT and inner shell layer/PM lamella of the RV. The PM fits into a socket formed from the inner shell material of the RV; the anterior myophore is attached to a platform developed in the inner shell layer of the RV. The inner shell layer is composed of three elements of variable development: radial partitions with or without connellae, inter-radial partitions with or without connellae, and tabulae. Pallial canals are present in the inner layer of the LV. Vertical canals penetrate the outer zone of the LV and above each canal a sieve plate with a denticulate pore system is developed.

**Discussion.** Parastroma is distinguished from the other multiple-folded hippuritids by its lack of well-defined rays and instead contains only incipient rays. Interestingly, *Parastroma* shares its arrangement of myocardinal angles with *Whitfieldiella* but has a pore system similar to that of *Barrettia*. Until material is discovered from the Santonian (or older) it is not possible to sort out the evolutionary history of this clade at the present time. However, the silicified material from Puerto Rico allows the first detailed description of a species belonging to this clade.



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✓ Figure 11: Laluzia peruviana (GERTH, 1928), El Rayo Formation (lower Maastrichtian), Puerto Rico. 11.1-2 (NS36: USNM 547523), LV: 11.1, adapical view showing myocardinal arrangement and buttresses; 11.2, abapical view showing pores and porules. 11.3-4 (NS11: USNM 547520), incomplete LV; 11.3, adapical view showing myocardinal arrangement and buttresses; 11.4, abapical view showing pores and porules. 11.5-6 (NS41: USNM 547524), LV (same as Fig. 9.6): 11.5, abapical view showing pores and porules; 11.6, adapical view showing myocardinal arrangement and buttresses. O1 and O2, oscules for first and second pillars, AT, anterior tooth; PT, posterior tooth; AM, anterior myophore; PM, posterior myophore. Scale bar = 10 mm.



**Figure 12:** New photograph of *Pironaea* sp. cf. *P. peruviana* from Cuba (VERMUNT, 1937), NLM.P240-1953, RV, transverse cross-section, showing short rounded infolds and position of posterior myophore socket. Scale bar = 10 mm.

#### Parastroma guitarti (PALMER, 1933)

(Figs. 13.1-2, 14.1-6, 15.1-3, 16.1-3, 17.1-4)

- \*. 1933 Orbigna guitarti PALMER n. sp.: PALMER, p. 96, Pl. 1, fig. 1; Pl. 2, fig. 2; Pl. 3, fig. 1. (corrected to Orbignya in pen by the author in offprints).
- v. 1937 Parastroma guitarti (PALMER); MAC GILLAVRY, p. 126, Pl. 5, figs. 1, 5; Pl. 10, figs. 5-9.
- v. 1971 Parastroma guitarti (PALMER); DOMMELEN, p. 94, Figs. 8B, 31(1-5); Pl. 11, figs. 1-2; Pls. 12-15.
- v. 2004 Parastroma guitarti (PALMER); GRUBIĆ, p. 168, Pl. 9, fig. 2.

**Types.** PALMER (1933) figured three specimens (syntypes) of the species from Sancti Spiritus, Santa Clara Province, Cuba. His Pl. 1, fig. 1, is a view of a specimen in profile, his Pl. 2, fig. 2, is a view of a specimen showing the myocardinal arrangement, and his Pl. 3, fig. 1, shows the pore system. The specimen figured in his Pl. 2, fig. 2, shows the distinctive features of the species and is clearly the most desirable to use in stabilizing the species concept; but the whereabouts of this specimen is not known and it cannot be designated as lectotype here.

**Material.** Including NS37 (USNM 547535) (locality 1202-10), NS38 (USNM 547536) (locality 1202-25), NS42 (USNM 547537) (locality 1202), NS43 (locality 1202), NS44 (USNM 547538) (locality 1202-3), NS46 (USNM 547539) (locality 1202), NS47 (USNM 547540) (locality 2000), NS49 (USNM 547541) (locality 1202-5), NS50 (USNM 547542) (locality 1202), NS60 (USNM 547543) (locality 1202), NS61 (USNM 547544) (locality 1202), NS62 (USNM 547545) (locality 1202), NS63 (USNM 547546) (locality 1202), and NS72 (USNM 547547) (locality 1202, very nice pores). All from the El Rayo Formation, Puerto Rico.

**Diagnosis.** A species of *Parastroma* in which deep conical folds (concentric spaces) are present in the complex inner shell layer of the RV and the crests of these folds are sharp with reduced or without conellae. LV buttresses contain a single line of pallial canals, except where buttresses bi-furcate.

Description. The RV is large and generally cylindro-conical, increasing rapidly in size. Its external surface is marked by regular narrow furrows with flat-faced to gently rounded costae between. The outer shell layer is thin, but its structure is not preserved in the silicified material. The complex inner shell layer is composed of irregular, broadly rectangular concentric spaces (Figs. 13.1-2, 14.1-2), with each space being open abapically and narrowing adapically to a point. The abapical tops of the walls of the concentric spaces are sharp or very weakly beaded (conellae-bearing). Tabulae insertion in the inner shell layer produces a stack of cones giving the typical chevron patterns seen in tangential and radial longitudinal sections. In juveniles the body cavity occupies about one third of the diameter, but the proportionate size of the body cavity decreases with growth. The apertural surface is represented by radially directed ribs and furrows that are formed by the variable height of the chevron structure, and commonly the radial partitions correspond with the radial ribs (Fig. 13.1). P0 is not present; P1 is represented by an isolated circular body of outer shell material, and P2 is represented by an isolated radially elongated body of outer shell material. Consequently, the two pillars are only connected to the outer shell at the point where they developed in juveniles. The two pillars rise high above the apertural face so that they can reach toward the openings on the LV (Fig. 15.2). The sockets for the PT and AT are embayments on the margin of the body cavity (Fig. 14.1-2). The socket for the PM is tear-shaped and fully embedded within the complex inner shell layer being situated dorso-posteriorly of the PT and P1 (Fig. 13.1). The socket for the AM is represented by a broad platform developed in the inner margin of the complex inner shell layer that extends from the area opposite the dorsal side of





**Figure 13:** *Parastroma guitarti* (PALMER, 1933), El Rayo Formation (lower Maastrichtian), Puerto Rico. **13.1-2** (NS42: USNM 547537), RV, adapical view: **13.1**, inner shell layer construction; **13.2**, detail showing connellae in anterior myophore attachment area. RF, radial furrows; RR radial ribs. Scale bar = 10 mm.





**Figure 14:** *Parastroma guitarti* (PALMER, 1933), El Rayo Formation (lower Maastrichtian), Puerto Rico. **14.1** (NS37: USNM 547535), RV with teeth of LV in place. **14.2** (NS63: USNM 547546), RV with partial LV in place. **14.3** (NS62: USNM 547545), LV, adapical view showing myocardinal arrangement and buttresses with pallial canals. AT, anterior tooth; PT, posterior tooth; AM, anterior myophore, PM, posterior myophore, O1 and O2, oscules for first and second pillars; (L), deep groove corresponding to ligamental infold. Scale bar = 10 mm.







Figure 15: Parastroma guitarti (PALMER, 1933), El Rayo Formation (lower Maastrichtian), Puerto Rico. 15.1-2 (NS50: USNM 547542), articulated shell: 15.1, LV, abapical view showing domed sieve sheets; 15.2, view of flank showing pillars extending up into LV. 15.3-6 (NS38: USNM 547536), LV various views: 15.3, adapical showing myocardinal elements, rounded double-canals, and buttresses with single rows of pallial canals; 15.4, flank view showing short PM; 15.5, oblique view showing pallial canals in myocardinal yoke; 15.6, abapical view showing rounded double-canals (sieve sheets not preserved). AT, anterior tooth; PT, posterior tooth; Am, anterior myophore; PT and P2, first and second pillars; O1, oscule for first pillar. Scale bar = 10 mm.

the AT around almost half the circumference of the body cavity as far as P2 (Figs. 13.1-2, 14.1-2). The surface of the AM socket is covered with strongly developed coarse connellae (Fig. 13.2); similar connellae are seen on the surface of the PM in specimens from Cuba preserved in the collections of the USNM in Washington and the National Natural History Museum in Havana. Such structures would thereby present a salient vertical micro-relief for adductor muscle insertion similarly to those presented by the laminar vertical ridges shown in the RV AM of an exceptionally well-preserved specimen of Pseudovaccinites gosaviensis (DOUVILLÉ) illustrated in SKELTON (2018, Fig. 10a-b). Such rotations of the adductor muscle insertion surfaces can be explained as a constructional adjustment to overcome the constraint on shell accretion normal to insertion surfaces due to the histological mode of muscle insertion (SKELTON, 2018, p. 13-15).

The LV is generally gently to strongly domed (Fig. 15.1-2, 15.4). The myocardinal yoke varies in development around the valve; it forms the support for the PM, teeth and AM (Figs. 14.3, 15.3). The MP is a low blade-like, radially elongated plate that is situated on a strong buttress supporting the myocardinal yoke that extends along the dorsal margin of the oscule for P1 (Figs. 14.3, 15.3). The myophore expands rapidly adapically giving it concave sides when viewed in concentric profile (Fig. 15.4), but convex sides when viewed in radial profile (Fig. 15.5). It is about half the length of the AT and PT (Fig. 15.4-5). Either the PT or the AT may be slightly larger than the other; both are concentrically expanded and may be more-or-less rectangular or crudely pointed (Figs. 14.3, 15.4-5, 17.1-2). The AM curves around the dorsal side of the AT and forms an extensive platform that encircles about half the myocardinal yolk (Figs. 14.3, 15.3). The AM is flat or gently inwardly facing. A strong buttress extends from the PT on the interior side of the oscule (O1) for P1 and then extends between the openings for P1 (O1) and P2 (O2) and bifurcates twice passing towards the valves margin (Figs. 14.3, 15.3). A weaker buttress extends along the anterior side of O2 and bifurcates at least once passing towards the valve's margin (Fig. 14.3). The inner parts of the buttresses supporting the

PM, extending between O1 and O2, and on the anterior side of O2 lack pallial canals; canals only appearing level with the tips of the pillars. Small pallial canals pass below the myocardinal yoke at the end of the radial furrows for O1, O2 and the other radial furrows. The earliest formed radial canals appear to open out into the cavity inside the yoke; this however appears to be because the original shell material was very thin and has not been silicified; originally they appear to have been blind. Extensive buttresses are developed around the remainder of the shell and may bifurcate once or twice passing towards the valves margin (Figs. 14.3, 15.4). In larger specimens (Fig. 16.3), further bifurcations of the buttresses occur passing towards the valve margin, but the number of divisions becomes progressively fewer with growth. The area inside the myocardinal yoke is composed of compact shell material (Figs. 14.3, 15.34, 14.3), with holes only evident where silicification has been incomplete. The adapical base of the myocardinal yoke contains a single row of pallial canals extending around the base of the AM, the PT and the PM (Figs. 15.4, 16.1). The pallial canals of the myocardinal yoke are blind at their inner ends, and expand in diameter as they pass both radially outwards and abapically to open in a circle marginal to the base of the cardinal apparatus. Abapically of this row of pallial canals around the length of the AM platform are a series of larger tunnel canals that open out into the interior of the myocardinal yoke (Fig. 16.1-2). The buttresses are penetrated by a series of pallial canals that are blind at their adapical end, but form a linear array of openings along the abapical side of each buttress (Figs. 14.3, 15.3, 16.3). Along each buttress only a single layer of pallial canal openings is present except where buttresses branch, where two rows may be developed for a short distance (Figs. 14.3, 15.3, 16.3). Between the buttresses radial grooves are developed on the abapical side of the LV, which have broad, rounded inner ends adjacent to the myocardinal yoke (Figs. 14.3, 15.3, 16.3). The tops of P1 and P2 lie at the interior ends of two of the more prominent radial grooves. The grooves extend under the yoke and pass into radial canals. Along the adapical side of each groove is a linear series of rounded double-canals that penetrate the LV (Fig. 15.3, 15.6); these extend along the entire length of the groove/radial canal. Adapically, these canals expand to emerge in a low rectangular field on the adapical surface of the LV (Fig. 17.4). The rectangular field is overlain by a low to high domed sieve sheet (Fig. 15.1-2) with different scales of trabeculae that gives rise to the fine reticulate pore system (Fig. 17.3-4). The sieve sheets are only separated by the narrow walls of the rectangular field, and not by an imperforate zone. Denticulate margins to the pores are present where the trabeculae have been broken away or were not preserved. The pores and sieve sheets are uniform across the entire surface





**Figure 16:** *Parastroma guitarti* (PALMER, 1933), El Rayo Formation (lower Maastrichtian), Puerto Rico. **16.1-2** (NS60: USNM 547543), fragment of LV (viewed from outside yoke) showing tunnel canals and pallial canals. **16.2**, fragment of LV (viewed from inside yoke) showing tunnel canals. **16.3** (NS44: USNM 547538), LV, adapical view showing single rows of pallial canals along each buttress. Scale bar = 10 mm.



**Figure 17:** *Parastroma guitarti* (PALMER, 1933), El Rayo Formation (lower Maastrichtian), Puerto Rico. **17.1-2** (NS45: USNM 547525), LV: **17.1**, adapical view showing myocardinal elements, rounded double-canals, and buttresses with single rows of pallial canals; **17.2**, oblique view showing pallial canals in myocardinal yoke. **17.3** (NS72: USNM 547547), LV, abapical view, showing details of well-preserved sieve plates divided into pores and porules by trabeculae. **17.4** (NS43: USNM 547550), LV, abapical view, showing details of well-preserved sieve plates divided into pores and porules by trabeculae. AT, anterior tooth; PT, posterior tooth; AM, anterior myophore. Scale bar = 10 mm.



**Figure 18:** Stratigraphic distribution of selected hippuritid rudists from the Upper Cretaceous of the Old World (from STEUBER, *et al.*, 2016) and New World showing migration events of Old World taxa into the New World, and the two separate hippuritid radiations in the New World.

of the LV. The two pillars have openings above them (oscules) in the LV; the circular oscule for P1 seems to have been covered by a fine reticulate mesh similar to the other openings as part of it is preserved in places; details for P2 are not as clear and it may or may not have been covered by a reticulate mesh.

**Discussion.** The pore system of *P. guitarti* has been previously described by PALMER (1933), MAC GILLAVRY (1937) and DOMMELEN (1971). DOM-MELEN's illustrations show only the coarser trabeculae preserved in the pore system. The more poorly preserved parts of the pore system illustrated here, which show only the coarser trabeculae in each sieve sheet, resemble the illustrations of DOMMELEN, whereas the better preserved areas in the silicified material show areas where virtually all of the finest trabeculae are preserved (Fig. 17.3-4).

The pallial canals in the buttresses of *P. guitarti* are aligned in single rows that are only double where the buttresses branch. This contrasts with other multiple-rayed hippuritids. In *Parastroma trechmanni* (CHUBB), two rows of pallial canals have been illustrated (*e.g.*, DOMMELEN, 1971, Pl. 20) in agreement with extensive material collected from Jamaica in the University of the West Indies Geological Museum (UWIGM) collection. Other species of multiple-ray hippuritids, including *Barrettia* (*e.g.*, DOMMELEN, 1971, Pl. 9, fig. 1; Pl. 10, fig.1), *Whitfieldiella* (material in UWIGM) and *Parastroma sanchezi* DOUVILLÉ (material in the National Natural History Museum, Havana, Cuba), have three or more rows of pallial canals present within the buttresses. It appears that during the evolution of the lineage of *Parastroma* the number of rows of pallial canals in buttresses decreases progressively: *P. sanchezi* (3 or 4 rows of pallial canals) to *P. trechmanni* (2 rows of pallial canals) to *P. guitarti* (1 row of pallial canals).

# 4. Significance for the evolution of American hippuritids

This study indicates that a distinctive group of hippuritid rudists, the Barrettiinae, evolved in the Upper Cretaceous of the New World. The group was characterized by the development of distinctive socket morphologies for the two teeth and suggests a monophyletic subfamily. This subfamily can be divided into two distinctive clades, those that have pallial canals in the left valve (Barrettia, Whitfieldiella and Parastroma) and those that lack them (Caribbea, Praebarrettia and Laluzia). The former group appeared in the late Santonian and ranged into the early Maastrichtian, whereas the latter group appeared in the late Campanian or early Maastrichtian and ranged up to the late Maastrichtian (Fig. 18). The lower Campanian of the New World also saw the appearance of members of the Hippuritinae (Vaccinites) and the Torreitinae (Torreities), with previous Santonian ages now generally referred to the early Campanian (MITCHELL, 2020), but neither subfamily persisted into the Maastrichtian of the New World.

The pore systems are now known in at least one species of each New World barrettine genus: *Whitfieldiella* sp. (MITCHELL, 2010), *Barrettia monilifera* (MITCHELL, 2010), *Parastroma guitarti* (PALMER, 1933; MAC GILLAVRY, 1937; DOMMELEN, 1971; herein), *Laluzia peruviana* (herein), *Caribbea muellerriedi* (MITCHELL, 2010; herein), and *Praebarrettia sparcilirata* (DOMMELEN, 1971). This demonstrates that pores are different in each genus and validates the separation of species based on features of the myocardinal arrangement as suggested by MITCHELL (2010).

This work indicates that continued provincialization of the rudists of the Americas occurred even during the Late Cretaceous. While cosmopolitan and endemic forms were present (Fig. 18) in the late Turonian (*Hippurites*), early to middle Campanian (*Vaccinites* and *Torreites*), by the Maastrichtian the hippuritids of the American region were represented by endemic radiations (*Barrettia* and *Caribbea* and their allies), and cosmopolitan forms had disappeared.



## Acknowledgments

Jann THOMPSON and Brian HUBER facilitated my trip to the Smithsonian Institution for two weeks to study and sort the rudist collections in 2009. Peter Skelton accompanied me on this trip and I am extremely grateful to him for taking photographs. I thank: the late Ann MOLINEUX (former Non-Vertebrate Paleontology Collections Manager, Texas Natural Science Center, The University of Texas at Austin) who facilitated my trip to the Texas Memorial Museum in 2009, which was supported by the National Science Foundation under Grant No. 0646468 awarded to the Texas Natural Science Center at the University of Texas; Dr Jon TODD facilitated me in The Natural History Museum, London; Dr Reinaldo Rojas-Consuegra kindly allowed access and permission to photograph the collections in the National Natural History Museum, Havana, Cuba; Dra María del CARMEN PERRILLAT and Violeta A. ROMERO MAYÉN are thanked for allowing access to the type collections of the Museum of Paleontology, Institute of Geology, Universidad Nacional Autónoma de México, Ciudad Universitaria, México; Mr W.J. WILDENBERG allowed free access to work through the extensive Caribbean rudist collections at Naturalis, Leiden, The Netherlands. Hernán SANTOS facilitated me in the field in Puerto Rico and in the Geological Museum, University of Puerto Rico, Mayagüez. Mr Ian BROWN and Dr Sherene JAMES-WILLIAMSON allowed access to the collections at the University of the West Indies Geological Museum, Kingston, Jamaica. I thank Peter SKELTON for his thorough and careful review of the manuscript and for making suggestions that greatly improved it. The reviews of Robert Scott and Thomas STEUBER also helped correct errors and improve the manuscript.

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## Appendix

## MORPHOLOGICAL TERMS APPLICABLE TO HIPPURITID RUDISTS

- **Anterior Myophore (AM).** Arc shaped muscle platform developed from the Myocardinal Yoke in the LV. The length, shape and orientation of the AM differ in different hippuritids.
- **Anterior Myophore Attachment (AMA).** The Anterior Myophore may attach directly onto the wall of the body cavity or it may attach onto an inclined ledge or surface formed in the Inner Layer shell of the RV.
- Anterior Tooth (AT). Developed on the myocardinal arc of the LV.
- **Apertural Face.** The internal surface of the RV that may be gently concave, flat of gently convex. It may be unspecialized in early forms but becomes highly complex in advanced forms.
- **Apertural Radial Ribs.** Positive features on the apertural surface of *Parastroma* which resemble the rays in ray-bearing complex multiplefold hippuritids but lack any form of rays. They are formed by the variable height of the concentric and/or radial partitions.
- **Apertural Radial Furrows.** Negative features on the apertural surface of *Parastroma* which resemble the inter ray spaces in ray-bearing complex multiple-fold hippuritids but lack any form of rays. They are formed by the variable height of the concentric and/or radial partitions.
- **Base** (DOMMELEN, 1971, p. 45). Unpinched attachment of Ray to outer shell layer.
- **Beads** (WOODWARD, 1862, p. 374). Wide parts of rays between constrictions; they may be regular or irregular.
- **Body Cavity (BC).** Cavity formed in the RV in which the animal was situated. The corresponding cavity in the LV is much reduced or absent. Same as Visceral Cavity (CV).
- **Body Chamber Layer (BCL).** A continuous layer lining the body cavity of the RV. This is directly equivalent to the inner shell layer in more primitive hippuritids but in more advanced forms the inner and outer shell layers are separated by the infolds (rays) and partitions formed from extensions of the inner shell layer. The Body Chamber Layer may rise to form a prominent wall on the apertural face.
- **Buttress.** Support between the LV and the myocardinal yoke.
- **Central Tooth (CT).** The reduced Central Tooth of the RV is represented by a support for receiving the two teeth of the LV; there is no socket in the LV other than for the gap between the two teeth.

- **Complex Inner Shell Layer.** Situation where the inner shell layer of the RV is composed of a Body Chamber Layer separated by the Outer Shell Layer by a series of cavities formed by interactions between rays (when present), various radial and/or concentric partitions and horizontal tabulae.
- **Concentric Elongate Spaces.** Regular or irregular concentrically elongated spaces developed between radial and concentric partitions in *Parastroma*.
- **Concentric Partitions.** Concentric wall-like elements representing part of the Complex Inner Shell Layer of hippuritids between the Body Cavity Lining and the Outer Shell Layer.
- **Connellae.** Small conical structures developed on tabulae or on the myocardinal areas of some complex hippuritids such as *Parastroma*. Include two types: Myocardinal Connellae and Tabular Connellae.
- **Costae.** Positive features on the outer surface of the RV.
- **Cross-Yoke Tunnels.** Tunnels that penetrate the myocardinal yoke. They may be small or large.
- **Cycles of Infolds** (GRUBIĆ, 2004). Scheme where rays are inserted successively and considered by GRUBIĆ (2004) to have taxonomic value at the genus level. Each lineage, however, tends to show an increase in number of rays and cycles of rays during both ontogeny and lineage evolution. The concept is therefore of little value in determining generic affinities.
- **Degree of Pinching** (DOMMELEN, 1971, p. 45). Ratio between minimum diameter (pinched area between beads) and maximum diameter (*i.e.*, a bead) of a ray.
- **Dendritic Radial Muri.** Irregular branching radial muri developed on surfaces of funnel plates.
- **Denticulae** (DOMMELEN, 1971, Pl. 3). Minute teeth developed on margins of the pore walls, probably the broken terminations of trabeculae.
- **Double Vertical Canal.** A vertical canal with a figure-of-eight shape that penetrates vertically through the LV of multiple fold hippuritid rudists.
- **Funnel Plates.** Plates developed in the non-compact Outer Shell Layer that are separated by radial muri or pustules in the RV of some hippuritids. The formation is analogous to the shell layer developed in radiolitid rudists.

#### Infoldings. See Rays.



#### Infolds. See Rays.

- **Interradial Plate** (DOMMELEN, 1971, p. 94). Plate developed in LV of *Parastroma* between adjacent Radial Spaces and bearing pallial canals. Same as buttresses and radial walls.
- **Inter-Radial Spaces** (WHITFIELD, 1897, p. 235). Inter-ray spaces or Quadrangular Pits.
- *Inter-Ray Partitions.* Partitions between infolded rays.
- **Inter-ray pits.** Pits developed in the inter-ray spaces by inter-ray partitions in some multiple-folded hippuritids.
- **Inter-Ray Spaces.** The area between rays which is characterized by a depression on the surface of the RV. May be broken up by inter-ray partitions to form inter-ray quadrangular pits.
- **Knob** (DOMMELEN, 1971, p. 45). Terminal bead in a ray.
- *Lacuna* (WHITFIELD, 1897, p. 234). The "first bead of the ray" or knob, obsolete.
- **Left Valve (LV).** The operculate or Free Valve that carries the pore system in hippuritid rudists.
- **Limbal Zone.** Marginal zone of the LV. In adult specimens of some species it may have different kinds of pore developed compared to the rest of the LV.
- **Marginal Canals.** Canals on the margin of the LV that open directly onto the apertural surface and not into the Radial Furrows.
- **Moniliform Rays** (Woodward, 1862, p. 373). Rays with more than one constriction and with regular sized and spaced beads.
- **Multiple-Fold** (DOMMELEN, 1971, p. 37). Term for *Barrettia* and alike forms.
- **Multiple-Ray** (DOMMELEN, 1971, p. 37). Term for *Barrettia* and alike forms.
- **Muri.** Radial features developed between the funnel plates in non-compact (cellular) outer shell layers in certain hippuritid rudists.
- **Myocardinal Connellae.** Conical to irregular features developed on the surfaces of the sockets for the PM and AM in some complex hippuritids such as *Parastroma*.
- **Myocardinal Yoke.** Thickened arc, circular or elliptical structure that supports the myocardinal (teeth and myophore) elements in the LV.
- **Non-Moniliform Rays** (DOMMELEN, 1971, p. 45). Rays with more than one constriction and with only occasional beads.
- **Orimental Folds.** Incipient folds that do not involve a tight invagination of the cortical layer of the shell.
- **Oscules.** Holes developed in the LV above the pillars.
- **Outer Shell Layer.** Calcitic shell layer of hippuritids.

- **Pallial Canals.** Canals penetrating the inner shell layer. Seen in the LV of certain hippuritids in the New World. Contain tabulae or are blind suggesting that they are related to low density construction rather than having direct physical applications (cf. Cross-Yoke Tunnels).
- **Partitions.** Wall-like elements representing part of the Complex Inner Shell Layer of hippuritids between the Body Cavity Lining and the Outer Shell Layer.
- **Pillars.** The two or three principal rays or infolds (P0, P1 and P2).
- **Polygonal Field.** Polygonal area with 4, 5 or 6 sides on the surface of the LV corresponding to a single or pair of vertical canals in multiple fold hippuritids. The Polygonal Field is defined by raised ridges that support the walls of the sieve sheet.
- **Pore System.** The arrangement of pores on the LV. The pore system is regarded as having high taxonomic value at the genus level and has been used to define various genera.
- **Pores.** Openings connecting the outside world with the radial furrows or lateral/vertical canals. Pores include simple, linear, polygonal, and dendritic.
- **Porules** (DOMMELEN, 1971, p. 38). Small divisions in pores formed by tabulae.
- **Posterior Myophore (PM).** Elliptical or forked muscle platform developed from the Myocardinal yoke in the LV. The position of the PM is different in different hippuritids and has value in distinction at the genus level.
- **Posterior Myophore Socket (PMS).** Cavity for the PM that may be connected to the body cavity or separated from the body cavity by a lamina.
- **Posterior Tooth (PT).** Tooth built on the myocardinal yoke of the LV.
- Primary Infoldings. The two or three pillars.
- **Pustules.** Bleb-like or irregular features developed between the funnel plates in non-compact (cellular) outer shell layers in certain hippuritid rudists.
- **Quadrangular Pits or Depressions** (WHITFIELD, 1897, p. 235). Inter-ray pits.
- **Radial Canals** (DOMMELEN, 1971, p. 70). Radially directed canals in the LV that exit at the RV knob of multiple-folded hippuritids or at the shell margin in simple hippuritids. They terminate at the shells outer margin and are overlain by the pore system. Some radial canals originated at the apex of the RV, others are intercalated as the valve increases in size. Where poorly preserved, the pore system is not preserved and only the radial furrows are visible.



- **Radial Grooves.** Grooves on the abapical side of the LV that correspond to the rays in multiple fold hippuritids. Same as radial spaces.
- **Radial Partitions.** Radially orientated wall-like elements representing part of the Complex Inner Shell Layer of hippuritids between the Body Cavity Lining and the Outer Shell Layer.
- **Radial Space** (DOMMELEN, 1971, p. 95). Space above ray or apertural ridge in hippuritid rudists.
- **Radial Walls/Ribs** (DOMMELEN, 1971, Pl. 11). Walls developed in LV of *Parastroma* between adjacent Radial Spaces and bearing pallial canals. Same as Buttresses.
- **Rays** (WOODWARD, 1862, p. 372). Infoldings of the outer shell layer of the RV; the term used by WOODWARD (1862) to describe *Barrettia*. Two infoldings (P1 and P2) are present in all hippuritids, in many a third (P0 of Ligamental) is developed, whereas in multiple-folded hippuritids several to hundreds of infolds may be present.
- **Reticulum** (DOMMELEN, 1971, p. 70). Pore covering in hippuritid rudists.
- **Riblets.** Thin positive features on the exterior surface of the RV of hippuritid rudists.
- Right Valve (RV). The lower or fixed valve.
- **Secondary Infoldings**. Rays other than the primary three infoldings, in multiple-ray hippuritids.
- **Sieve Pustule.** Pustule shaped covering separated from neighbouring pustules by a wide imperforate zone over a single or double vertical canal that bears various pores in multiple hippuritids such as *Whitfieldiella*.
- *Sieve Sheet/Plate.* A sheet bearing pores overlaying a Polygonal Field in multiple fold hippuritids.

- **Simple Rays**. Triangular to parallel-sided to concave sided infolds.
- **Stem** (DOMMELEN, 1971, p. 45). Interval between the knob and the base of a ray in non-simple rays.
- **Submoniliform Rays** (DOMMELEN, 1971, p. 45). Rays with more than one constriction (*i.e.*, with a stem) and with only irregularly formed beads.
- **Sulcus.** Furrow or groove on the exterior surface of the RV.
- **Tabulae Connellae.** Irregularly distributed or aligned cones on the tabulae some complex hippuritids such as *Parastroma*.
- **Tabulae.** Broadly horizontal layers in the Complex Inner Shell Layer or the Body Cavity.
- **Trabeculae** (DOMMELEN, 1971, p. 38). Division of pores into porules.
- **Transverse Furrows** (DOMMELEN, 1971, p. 70). Concentrically orientated furrows connecting the vertical canals to the sieve plates in *Praebarrettia*.
- *Transverse Walls* (WHITFIELD, 1897, p. 235). Inter-ray partitions.
- **Tunnel Canals.** Canals that pass through the Myocardinal Yoke.
- **Vertical Canals.** Canals that penetrate vertically through the LV of multiple fold hippuritid rudists. They may be single or double.
- **Vesicular.** Cell-like fill of Body Cavity by anastomosing tabulae.
- **Visceral Cavity (CV).** Cavity formed in the RV in which the animal was situated. The corresponding cavity in the LV is much reduced or absent. Same as Body Cavity (BC).