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## THE RUDIST FAUNA OF THE CÁRDENAS FORMATION, MAASTRICHTIAN, SAN LUIS POTOSÍ STATE, MEXICO

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**ABSTRACT**—A Maastrichtian rudist fauna composed of the radiolitids *Biradiolites aguilerae* Böse, *B. Cárdenasensis* Böse, *Huasteca ojanchalensis* (Myers), *Tampsia floriformis* Myers, and *Trechmannites rudissimus* (Trechmann), the hippuritids *Caribbea muellerriedi* (Vermunt) and *Praebarrettia sparcilirata* (Whitfield) sensu lato, and the plagioptychids *Coralliochama gbohemi* Böse and *Mitrocoprina tschoppi* (Palmer) is described from the Cárdenas Formation in San Luis Potosí State, Mexico. Abundant fossil material and excellent preservation of a number of specimens allowed observation of both the internal and external shell characters and their ontogenetic and eco-phenotypic variability. The description of some hitherto insufficiently known species has been enhanced and/or completed, making easier their subsequent identification and allowing their unequivocal generic assignation. Two new genera, *Huasteca* and *Trechmannites*, are proposed for two already known species of radiolitids. The Cárdenas Formation exhibits a continuously exposed sequence in the vicinity of Cárdenas. Thus, precise stratigraphic location of all fossil localities and their rudist associations, ranging from the early to the early late Maastrichtian, has been possible.

## INTRODUCTION

THE LITERATURE on American Late Cretaceous rudists is extensive (e.g., Woodward, 1862; White, 1885; Whitfield, 1897; Böse, 1906; Stephenson, 1922; Trechmann, 1922, 1924; Adkins, 1930; Palmer, 1933; MacGillavry, 1937; Chubb, 1955, 1956a, 1956b, 1967, 1971; Myers, 1968; Alencáster, 1971, 1990; van Dommelen, 1971; Mitchell, 2003, 2007; Grubić, 2004; Oviedo, 2005; Pons et al., 2010). Rudists are considered good biostratigraphic markers, allowing reasonably high resolution in the shallow water platform sediments of the margins of the Tethys. Nevertheless, many American rudist taxa are still insufficiently known concerning both the internal and external shell characters and their ontogenetic and eco-phenotypic variability, and for that reason, their subsequent identification in different localities may become doubtful. Moreover, several species are based on specimens collected in single isolated localities whose precise stratigraphic position and correlation with other rudist localities is uncertain.

The main objective of this study is the complete description of the rudist fauna from several localities of the Cárdenas Formation. The abundance of specimens and the excellent preservation of a number of them allow enhancing and/or completing the knowledge of the shell characters of some species, describing ontogenetic and eco-phenotypic variability, recognizing synonymies, and identifying unequivocal generic attributions. The relative stratigraphic position of the different localities may be easily recognized thanks to the continuously exposed sequence of the Cárdenas Formation around Cárdenas. Published data on chronostratigraphically relevant fossils (ammonites and planktic foraminifers) and Sr-isotope stratigraphy help date the different units of the sequence.

## LOCALITIES AND STRATIGRAPHY

The studied area is located in San Luis Potosí State, East-Central Mexico, about 100 km east of San Luis Potosí City.

Localities (Fig. 1) are in the municipalities of Cárdenas ('Arroyo la Atarjea', 'Cárdenas 1', 'Cárdenas 2', and 'Cárdenas 3') and Rayón ('Amoladeras', 'Cuchilla Las Palomas', 'Arroyo Los Terrerillos', and 'Arroyo el Terrero').

The stratigraphy of the Upper Cretaceous rocks around Cárdenas, known as 'division Cárdenas' or 'Cárdenas beds', was first attempted by Böse (1906), Böse and Cavins (1927), Burckhardt (1930), Heim (1940), Müllerried (1941), and Wade in Imlay (1944), where the term 'Cárdenas formation' was used. Myers (1968), after producing a detailed map of the region evidencing its structure, collecting fossils, and measuring sections, showed that previously published sections contained a repetition of lithologic units, a partly inverted sequence, or both.

Myers (1968) defined the Cárdenas Formation, divided it into three informally designated members, and subsequently recognized three assemblage zones. The Cárdenas Formation (Fig. 2) is a thick unit predominantly of fine clastic sedimentary rocks, overlying the thick to medium-bedded Tamasopo limestones, and unconformably overlain by the red and tan unfossiliferous siltstone, shale, sandstone, and conglomerate of the Tabaco Formation. The lower member of the Cárdenas Formation consists of alternating shale, sandstone and limestone, the middle member of shale and siltstone, and the upper member of siltstone, sandstone and limestone. The lowermost zone in the Cárdenas Formation is the *Durania ojanchalensis* Zone, characterized by a long list of bivalve species, but also gastropods, echinoids, and serpulids. The middle zone is the *Arctostrea aguilerae* Zone, less fossiliferous, only ostreids are abundant, and is coincident with the local range of *Exogyra costata*. The *Tampsia floriformis* Zone is the highest zone and has by far the richest fauna. These zones are not coincident with the members of the Cárdenas Formation nor are the boundaries of the members and zones parallel.

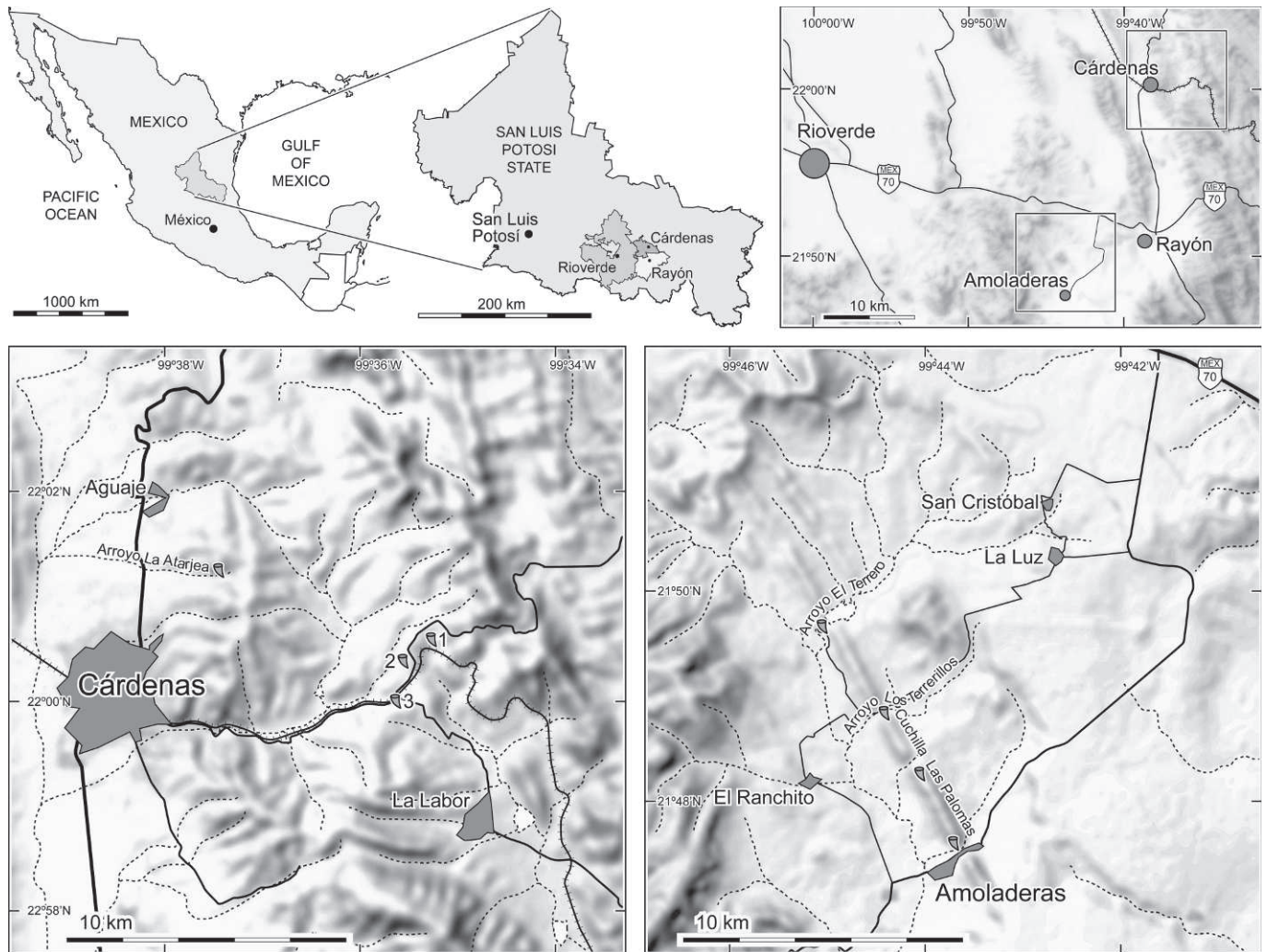


FIGURE 1—Location of studied outcrops. Shaded relief maps modified from Google Maps.

Among the studied localities of the Cárdenas Formation (Figs. 1, 2), ‘Arroyo La Atarjea’ is situated in the uppermost part of both the upper member and the *Tampsia floriformis* Zone. ‘Cárdenas 3’ is situated in lower beds of the former member and zone. ‘Cárdenas 2’ is situated in still lower beds of the upper member, but in the uppermost part of the *Arctostrea aguilerae* Zone. ‘Cárdenas 1’, ‘Amoladeras’, ‘Cuchilla Las Palomas’, ‘Arroyo los Terrerillos’, and ‘Arroyo El Terrero’, are situated in the upper part of the lower member, in the *Durania ojanchalensis* Zone.

Several relatively recently published papers contributed biostratigraphic data relevant to the chronostratigraphy of the Cárdenas Formation (Caus et al., 2002; Omaña and Pons, 2003; Ifrim et al., 2005; Schafhauser et al., 2007; Omaña et al., 2009). The most complete account on the age of the Cárdenas Formation (Schafhauser et al., 2007) dates the upper part of the lower member as early Maastrichtian, by ammonites, the middle part of the middle member as late early Maastrichtian, by planktic foraminifers, and the upper part of the upper member as early late Maastrichtian, by the  $^{87}\text{Sr}/^{86}\text{Sr}$ -isotope ratio measured in plagiopychid rudist shells. The rudist fauna of the Cárdenas Formation is thus considered to range from the early Maastrichtian to the early late Maastrichtian.

#### SYSTEMATIC PALEONTOLOGY

Specimens used for this study are kept in the Paleontological Collections of the Universitat Autònoma de Barcelona (PUAB), the Colección Nacional de Paleontología at the Instituto de Geología de la UNAM (IGM), and the Museo de Paleontología de la Facultad de Ciencias de la UNAM (FCMP). Specimens were sectioned and polished at the laboratories of the three institutions and thin sections were prepared at the UAB.

Some of the specimens identified, which were previously published with the acronym PUAB, are definitively deposited at the IGM. Thus, they were assigned new identification numbers (equivalences in the Appendix).

*Other abbreviations and conventions.*—Abbreviations used here include: AF=anterior radial fold, AG=anterior radial groove, AM=anterior myophore, AT=anterior tooth, CT=central tooth, IMG=inner marginal groove, L=ligament ridge, LV=left valve, MC=main pallial cavity, MS=medial septum, P1=first pillar, P2=second pillar, PB=posterior radial band, PC=posterior cavity, PF=posterior radial fold, PM=posterior myophore, PRS=posterior radial structure, PS=posterior radial sinus, PT=posterior tooth, RV=right valve, VB=ventral radial band, VF=ventral radial fold, VRS=ventral radial structure, VS=ventral radial sinus.

Thin sections observed with transmitted light were used in the study of the outer shell layer structure, and also in the

Myers 1968		Stratigraphic position of studied rudist localities	
LITHOSTRATIGRAPHY	BIOSTRAT.	CÁRDENAS AREA	AMOLADERAS AREA
Tabaco Formation			
Cardenas Formation ± 1050 m	Upper Member ± 400 m	<p><b>'Arroyo La Atarjea'</b> <i>Caribbea muellerriedi</i> <i>Coralliochama gboehmi</i> <i>Tampsia floriformis</i></p> <p><b>'Cárdenas 3'</b> <i>Biradiolites aguilerae</i> <i>Biradiolites cardenasensis</i> <i>Coralliochama gboehmi</i> <i>Tampsia floriformis</i> <i>Trechmannites rudissimus</i></p>	
	Middle Member ± 450 m	<p>ostreids</p> <p><b>'Cárdenas 2'</b> <i>Coralliochama gboehmi</i> <i>Mitrocaprina tschoppi</i> <i>Tampsia floriformis</i></p>	
	Lower Member ± 200 m	<p>ostreids</p> <p><b>'Cárdenas 1'</b> <i>Huasteca ojanchalensis</i></p>	<p><b>'Amoladeras', 'Cuchilla Las Palomas', 'Arroyo Los Terrerillos', 'Arroyo El Terrero'</b> <i>Huasteca ojanchalensis</i> <i>Mitrocaprina tschoppi</i> <i>Præbarrettia sparcilirata s.l.</i> <i>Trechmannites rudissimus</i></p>
Tamasopo Limestone		Not to scale	

FIGURE 2—Lithostratigraphy, biostratigraphy and rudist occurrences in the Cárdenas Formation.

figures unless indicated. All transverse sections are figured in standard orientation, that is, in adapical view and with the dorsal side up. In the drawings of transverse sections, the outer shell layer of the RV is in black, in hippuritids, and pale gray with black lines indicating growth lamellae sets, in radiolitids; the inner shell layer is in light gray; and the myocardinal apparatus elements of the LV are in dark gray. The morphoconstructional approach and terminology proposed by Pons and Vicens (2008) for the structure of the outer shell layer of the radiolitids is followed in the descriptions. Particularly, besides using growth lamellae structure types, radial structures, that is: “areas of the outer shell layer where inclination, width, and folding, taken one by one or together, of the growth lamellae are different than at the rest of the valve perimeter”, are clearly differentiated from their aspect at the outer surface (radial bands, ribs, sinuses, furrows), because correlation between both is not straight forward.

Family RADIOLITIDAE d’Orbigny, 1847

(originally misspelled as RADIOLIDAE, emended to RADIOLITIDAE by Gray 1848)

BIRADIOLITES d’Orbigny, 1850

BIRADIOLITES AGUILERAE Böse, 1906

Figure 3.1–3.7

1906 *Biradiolites Aguilerae* Böse, p. 58, pl. 5, fig. 4, pl. 8, figs. 1–4, pl. 9, figs. 1, 2, pl. 12, figs. 2, 4.

1968 *Biradiolites aguilerae* Böse; MYERS, p. 44, pl. 5, figs. 1–4.

*Material*.—Two slabs with numerous specimens each: PUAB 0856 588, 589.

*Description*.—Small long conical *Biradiolites*, right valve less than 50 mm high and 20 mm in maximum diameter. The outer surface bears five unequal ribs (two flat ribs limited by three acute ribs) at the ventral-posterior side. The remaining shell

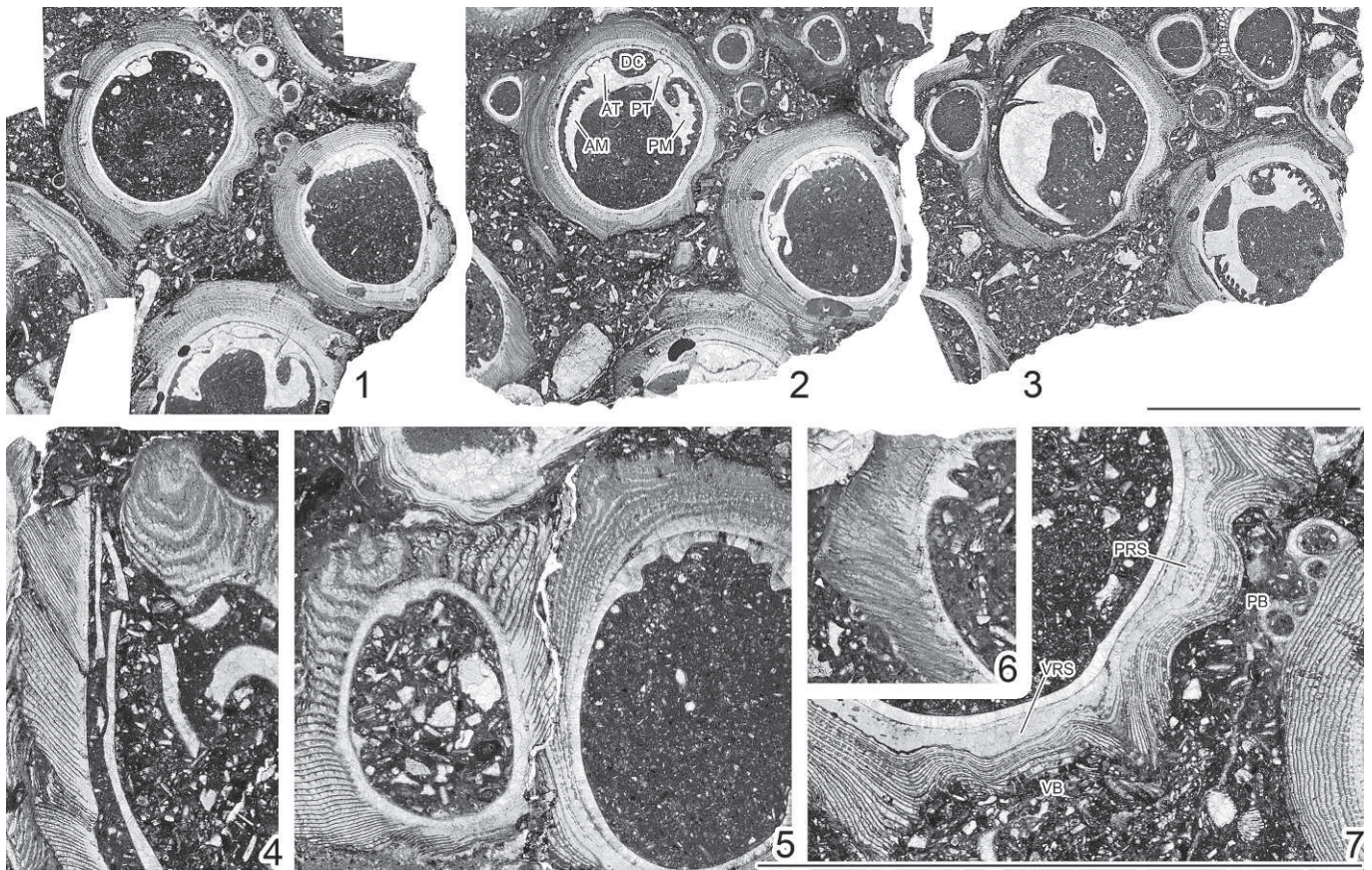


FIGURE 3—*Biradiolites aguilerae* Böse, 1906, PUAB 0856 589, thin sections of a bouquet included in bioclastic matrix, Cárdenas 3, scale bars=10 mm, note that scale bars are different for upper and lower figure rows: 1–3, serial transverse sections of right valves, adult specimens are cut close below the commissural plane showing myocardial elements of both valves, young specimens show different growth stages; 4, radial section (left) and oblique section (upper right) of right valve fragments; 5, oblique section of two right valves; 6, oblique section of right valve, detail of the groove for the anterior tooth; 7, transverse section of right valve, detail of the radial structures zone.

surface is nearly smooth, only growth lamellae are evident. Left valve is flat or slightly convex.

The growth lamellae of the outer shell layer of the right valve are inclined inwardly, developing a faint inner marginal groove (Fig. 3.4), and are radially folded at the ventral-posterior side. The structure of the growth lamellae is mostly compact, very small and low cells develop only in more expanded parts.

The radial structures (Fig. 3.7) are two down-and-outward folds. VRF is wide and flat and PRF is narrower, also flat, but slightly more pronounced. They are limited by three narrow and acute down-and-outward folds, particularly well developed the middle one. These folds are responsible for the five unequal ribs already mentioned at the outer shell surface; the radial structures correspond to the two flat ribs (bands).

The inner shell layer of the right valve is very thin. It thickens faintly near the dorsal side, developing two striated furrows where the teeth of the left valve glide (Fig. 3.1–3.3, 3.5, 3.6). As seen in a transverse section of the right valve close to the commissural plane, the myocardial apparatus of the left valve forms a typical radiolitic arch (Fig. 3.1, 3.2). Teeth are quadrangular in section and show striated outer margins. A wide dorsal cavity is left between them. Myophores are thin and have striated outer margins. AM extends all along the anterior inner shell margin and PM surpass the PRS. A conspicuous outer embayment is developed between PT and PM. There is no ligament ridge.

*Occurrence*.—Cárdenas 3', upper part of the Upper Member of the Cárdenas Formation, in the *Tampsia floriformis* Zone.

*Remarks*.—The external characters of the species were already described in detail, first by Böse (1906) and subsequently by Myers (1968). The myocardinal apparatus and the structure of the outer shell layer are first described herein and the radial structures identified. Both authors reported that shells of all specimens collected were recrystallized. Our specimens, included in a bioclastic matrix, preserve the inner characters allowing their study and description. Previous attribution of the species to *Biradiolites* is confirmed, by its radial structures pattern, myocardinal apparatus, outer shell layer structure, and absence of a ligament ridge.

#### BIRADIOLITES CARDENASSENSIS Böse, 1906

Figures 4.1–4.5, 5.1–5.10, 6.1–6.9

- 1906 *Biradiolites cardenasensis* BÖSE, p. 59, pl. 11, fig. 3, pl. 12, fig. 3.  
 1906 *Biradiolites potosianus* BÖSE, p. 60, pl. 5, figs. 2, 3, pl. 11, fig. 4, pl. 12, fig. 5.  
 1924 *Bournonia barreti* TRECHMANN, p. 405, pl. 26, figs. 2, 2a.  
 1968 *Biradiolites cardenasensis* Böse; MYERS, p. 45, pl. 4, figs. 1–4.  
 1971 *Bournonia cardenasensis* (Böse); ALENCASER, p. 43, pl. 7, figs. 5–7, pl. 19, figs. 2–4.  
 1971 *Bournonia barreti* Trechmann; CHUBB, p. 194, pl. 40, figs. 4, 5 (4 copy Trechmann).

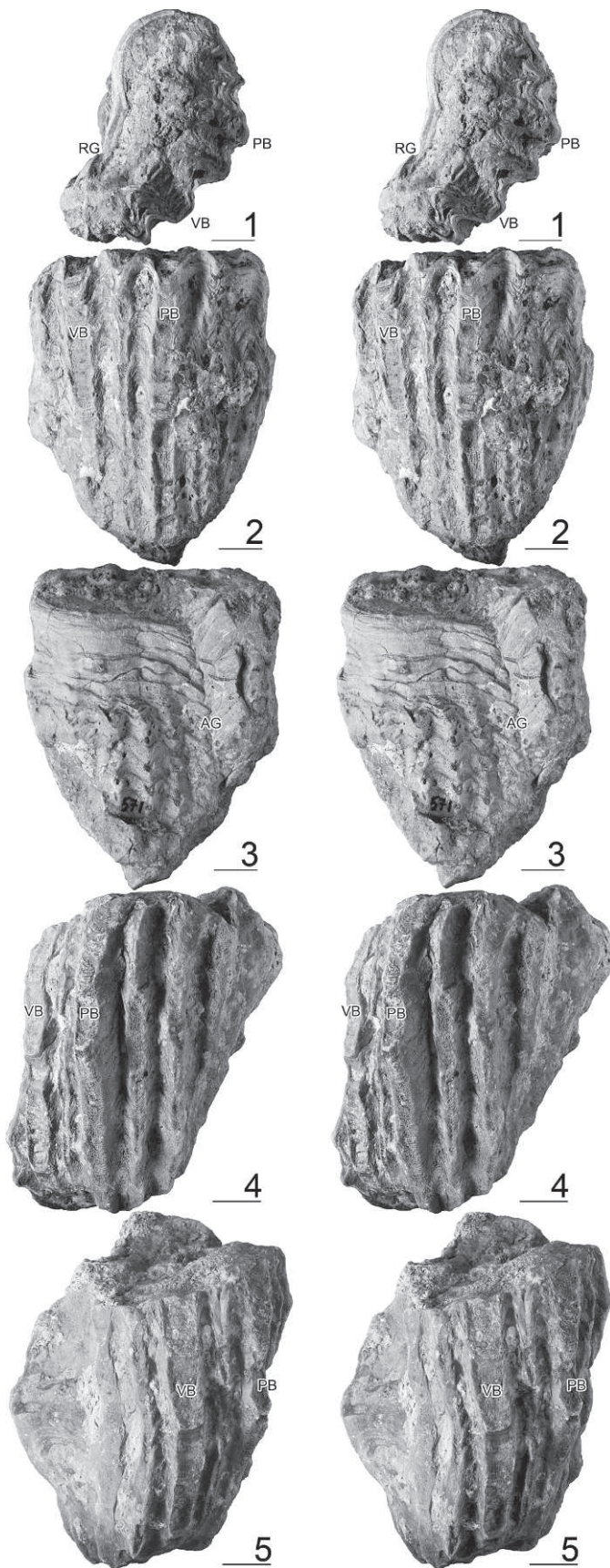


FIGURE 4—*Biradiolites cardenasensis* Böse, 1906, stereo pairs, Cárdenas 3, scale bar=10 mm: 1–3, PUAB 0856 571, upper, ventral-posterior, and anterior views, respectively, of a crushed bivalve specimen; 4, 5, IGM 9442, posterior and ventral views, respectively, of right valve.

- 1990 *Bournonia cardenasensis* (Böse); ALENCASER, p. 64, pl. 2, fig. 4.  
 1996 *Bournonia cardenasensis* (Böse); SCOTT, p. 303, text-fig. 6E, pl. 2, figs. 5, 6.  
 2003 *Bournonia cancellata* (Whitfield, 1897); MITCHELL, p. 151, pl. 1, pl. 2, pl. 3, figs. d–f, pl. 4, figs. 4a, 4c, 4d.  
 2003 *Bournonia barreti* Trechmann; MITCHELL, p. 152, pl. 3, figs. a–c.  
 2005 *Bournonia cardenasensis* (Böse); OVIEDO, p. 23, fig. 14.  
 2006 *Bournonia cardenasensis* (Böse); SCHAFFHAUSER, p. 59, pl. 16, figs. 1–5.

*Material.*—Forty-three specimens: PUAB 0720 257; PUAB 0733 266, 277, 282–285; PUAB 0856 559–575; PUAB 81119–81125, 81132; IGM 9437–9442.

*Description.*—Right valve is short conical in juveniles becoming cylindrical in adult shells. Maximal diameter is normally dorsal-ventral and reaches 70 mm in larger specimens. Longer specimens may measure 150 mm. The outer surface bears numerous acute radial ribs limited by deep radial sinuses. Ribs and sinuses are always very pronounced, close, and evident at the ventral, posterior and dorsal side while they may be more spaced or reduced to gentle undulations at the anterior side (Figs. 4, 5). A radial groove (AG) is commonly developed at this side. Left valve is from slightly convex to gently concave, shows the same ribs and sinuses than the right valve, and appears collapsed in most collected specimens.

The growth lamellae of the outer shell layer of the right valve are inclined inwardly, presenting acute down-and-outward radial folds and slightly less acute up-and-inward radial folds (Figs. 5, 6.3–6.6). The structure of the growth lamellae is non-compact with more or less discontinuous radial ridges, although nearly compact structure may be locally present. The transverse section of the right valve cuts the growth lamellae with different angles in different parts, because of their inclination and radial folding (Fig. 6.2–6.6, 6.8, 6.9). The growth lamellae are cut at a lower angle in major down-and-outward folds, and thus, quite continuous ridges may appear in the radial structures (Fig. 6.4, 6.5, 6.9) while only isolated pillars (very discontinuous ridges) are seen in other folds (Fig. 6.8). The radial section of the right valve evidences an inner marginal groove and the discontinuous radial ridges (Fig. 6.1, 6.7). At the inner marginal groove, or close to it, the continuously growing part of the growth lamellae may be particularly thicker than the discontinuously growing one, appearing nearly as compact structure (Fig. 6.4–6.6). The structure of the growth lamellae in the left valve is like in the right one.

Radial structures are two down-and-outward radial folds with a flat apical end. A down-and-outward radial fold, bounded by two up-and-inward radial folds, is developed between both radial structures. Ventral radial structure is located slightly posterior (Figs. 5, 6.4). Radial structures appear at the outer shell surface as two flat ribs (radial bands) with an acute rib between them (Fig. 4). In a transverse section, their position is marked by a slight outwards inflexion of the inner shell margin (Figs. 5, 6.4).

Transverse sections of the right valve close to the commissural plane show the outer and inner profile of the shell, the radial folding of the growth lamellae, and a robust myo-cardinal apparatus (Fig. 5). The myo-cardinal arch is located far from the dorsal margin, producing a large dorsal cavity. There is no ligament ridge. Teeth are rectangular in section and their undulated outer margin glides along similarly undulated furrows in the inner wall of the inner shell layer. Myophores are developed asymmetrically. The anterior myophore extends along the anterior side of the shell and the posterior myophore reaches the posterior margin of the ventral radial structure. A wide outer embayment is developed between posterior tooth and posterior myophore. The

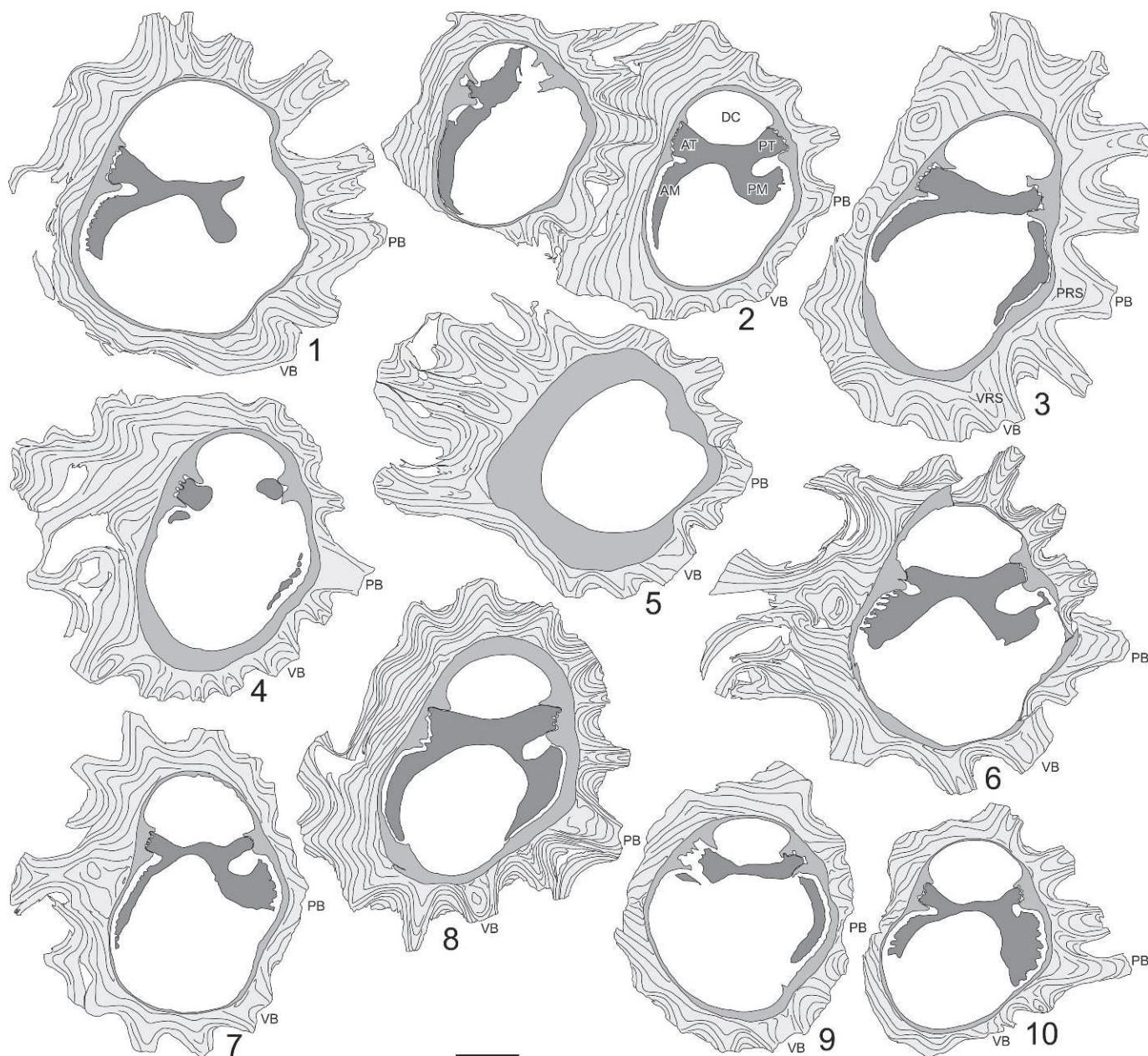


FIGURE 5—*Biradiolites cardenasensis* Böse, 1906, transverse sections of right valves close below the commissural plane, Cárdenas 3, scale bar=10 mm: 1, IGM 9440; 2, IGM 9441; 3, PUAB 0733 271; 4, PUAB 81124; 5, IGM 9442; 6, IGM 9437; 7, PUAB 81123; 8, IGM 9439; 9, PUAB 0856 573; 10, PUAB 81125.

outer margin of the myophores appears undulated only in sections close to the commissure, being smooth in the lower ones.

**Occurrence.**—‘Cárdenas 3’, upper part of the Upper Member of the Cárdenas Formation, in the *Tampsia floriformis* Zone. The species has also been reported from the Ocozocoautla Formation in Chiapas, southern Mexico, from the Campur Formation in Guatemala, and, under a different name (*B. barretti* and *B. cancellata*), from the Guinea Corn Formation in Jamaica.

**Remarks.**—The species has been ascribed in literature either to *Biradiolites* or *Bournonia* (Böse, 1906; Myers, 1968; Alencaster, 1971, 1990; Scott, 1996; Oviedo 2005). The main argument for *Bournonia* arises from MacGillivray’s (1937) observation that left valve teeth glide along striated grooves on the inner wall of the left valve, instead of being inserted in sockets. This was described for *Bournonia* but is a common trait in adult specimens of most radiolitid genera, including *Biradiolites*. The pattern of the radial structures, having a well developed down-and-outward fold in the

interband (a rib at the outer surface), is characteristic for *Biradiolites* but not for *Bournonia*. Myers (1968) first noticed the synonymy between *B. potosianus* and *B. cardenasensis*, the two species described by Böse (1906) from Cárdenas. Several specimens attributed to *Bournonia cancellata* (Whitfield, 1897) from Jamaica, particularly those more completely described and recently published (e.g., Chubb, 1971; Mitchell, 2003) show identical characteristics to *B. cardenasensis* Böse, 1906 and, in our opinion, correspond to the same species. Subsequent taxonomical consequence, apparently, should be the consideration of *B. cancellata* as the senior synonym. Nevertheless, Whitfield’s specimens of *Radiolites cancellatus* have only a sinus and no rib between the two radial bands as Mexican *B. cardenasensis* specimens and other Jamaican specimens, in our opinion erroneously named *B. cancellata*, have. We collected in both Rio Minhó section (Jamaica) and Chiapas (Mexico) specimens without a rib in the inter-band as Whitfield’s types. Thus, both

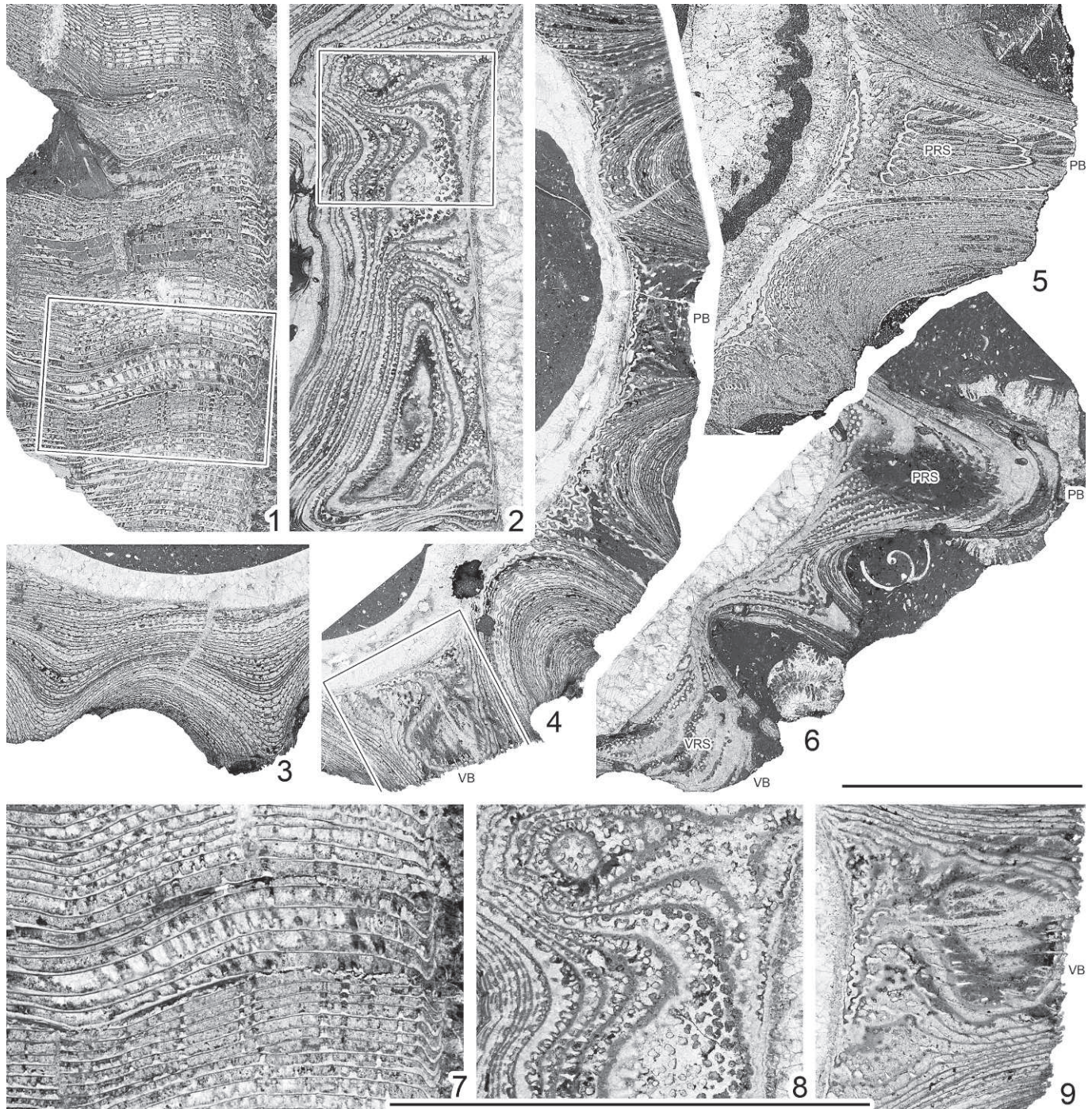


FIGURE 6—*Biradiolites cardenasensis* Böse, 1906, thin sections of outer shell layer of right valves, enlarged areas are indicated, Cárdenas 3, scale bar=10 mm, do note that scale bars are different for upper and lower figure rows: 1, PUAB 0856 568, radial section, inner margin at right; 2, PUAB 81124, transverse section, inner margin at right; 3, 4, PUAB 0856 573, transverse sections; 5, IGM 9438, transverse section (peel); 6, PUAB 81124, transverse section; 7, 8, 9, enlargements indicated in 1, 2, and 4, respectively.

species exist and are identified in Jamaica and Mexico. Other probably related species from Jamaica, namely *B. sanctannae* Chubb, 1967 and *B. sanctmariae* Chubb, 1967 are too poorly known to be certainly assigned as synonyms of *B. cardenasensis*. *B. cubensis* Douvillé, 1926, from Cuba seems related to these species but, besides being larger, has a more developed inter-band, with a higher number of ribs (see Rutten, 1936, text-figs. 2, 3). The presence of an anterior radial groove is a common feature observed in other radiolitids, including European representatives.

#### HUASTECA new genus

*Type species*.—*Durania ojanchalensis* Myers, 1968, by monotypy, Cárdenas Formation, Maastrichtian, Cárdenas, San Luis Potosí, Mexico.

*Diagnosis*.—Right valve, with very thick outer shell layer (except at the radial structures zone), has normal cellular structure, and lacks a ligament ridge. Radial structures are two wide up-and-inward radial folds, separated by a down-and-outward radial fold. At the outer shell surface, that is regularly



ribbed, they produce two wide smooth non-ribbed, slightly or deeply concave, radial bands separated by a regularly ribbed inter-band. Left valve, with compact structure at the outer shell layer, has a convex centre with sub-central apex and a very thin margin covering the wide commissural lip. Teeth and particularly myophores with striated outer margin are very short.

*Etymology.*—Refers to the Huasteca, a region in eastern San Luis Potosí State, central Mexico.

*Occurrence.*—As the type species, Cárdenas Formation, Maastrichtian, Cárdenas, San Luis Potosí, Mexico. Also reported from the Ocozocoautla Formation in Chiapas, southern Mexico.

*Remarks.*—The new genus is distinguished from *Durania*, also a radiolite with ribbed thick outer shell layer, with normal cellular structure, and lacking a ligament ridge, by its radial structures, wide up-and-inward radial folds producing smooth radial bands instead of finely ribbed radial bands at the outer surface. Additionally, *Huasteca* is characterized by very short myophores with striated outer margins.

HUASTECA OJANCHALENSIS Myers, 1968

Figures 7.1–7.5, 8.1–8.5, 9.1–9.4

?1930 *Durania huasteca* ADKINS, p. 96, pl. 6, figs. 1–4.

1968 *Durania ojanchalensis* MYERS, p. 48, pl. 8, figs. 1, 2.

1971 *Durania ojanchalensis* MYERS; ALENCASTER, p. 50, pl. 9, figs. 1–4, pl. 23, figs. 1, 2.

1990 *Durania ojanchalensis* MYERS; ALENCASTER, p. 64, pl. 2, figs. 1, 2.

2005 *Durania ojanchalensis* MYERS; OVIEDO, p. 31, figs. 21, 22.

*Material.*—Forty specimens: PUAB 0701 25, 31, 34, 36–55; PUAB 0735 298; PUAB 0854 485–491; PUAB 81091–81098, 81165; IGM 9451–9455.

*Description.*—Right valve is conical in young specimens and cylindrical in adults (Fig. 7). Larger specimens are 230 mm in height and 130 mm in maximum diameter. The outer surface presents regular, close, and rounded ribs, about 6 per 10 mm, limited by narrower furrows, and two radial bands separated by an inter-band with similar ribs. Number of ribs in the inter-band increases with specimen's size. VB is wider than PB. Both bands are smooth, without ribs but only visible growth lines, and slightly concave in most specimens although deep concave in some. Commissural lip is flat or slightly inwardly inclined, measures up to 40 mm wide in larger specimens, and thins considerably at radial bands. Left valve has a convex centre with sub-central apex, above the main cavity, and a very thin margin covering the wide commissural lip. Outer surface is smooth.

The growth lamellae of the outer shell layer of the right valve are flat, horizontal or slightly inclined inwardly, developing a conspicuous inner marginal groove. Small radial folds, only in the most marginal part, are responsible for the outer surface ribbing. Radial structures are two up-and-inward folds reducing considerably the thickness of the outer shell layer. VRS is wide and flat while PRS is narrower and deep, both separated by a large down-and-outward fold (Figs. 8, 9.2). The structure of the growth lamellae is normal cellular (Fig. 9). The structure of the growth lamellae in the left valve is compact.

The inner shell layer of the right valve is very thin. It thickens faintly near the dorsal side and at the anterior and posterior sides, fitting with the two teeth and the two myophores of the left valve, respectively. In a transverse section of the right valve close to the commissural plane (Fig. 8.2), the two teeth are rectangular and quite close one to another, but allowing the development of a narrow dorsal cavity. The myophores are thick and have a striated outer margin, fitting with the striated inner wall of the inner shell layer of the right valve. AM extends laterally to the ventral side and PM reaches the ventral margin of the PRS. A deep

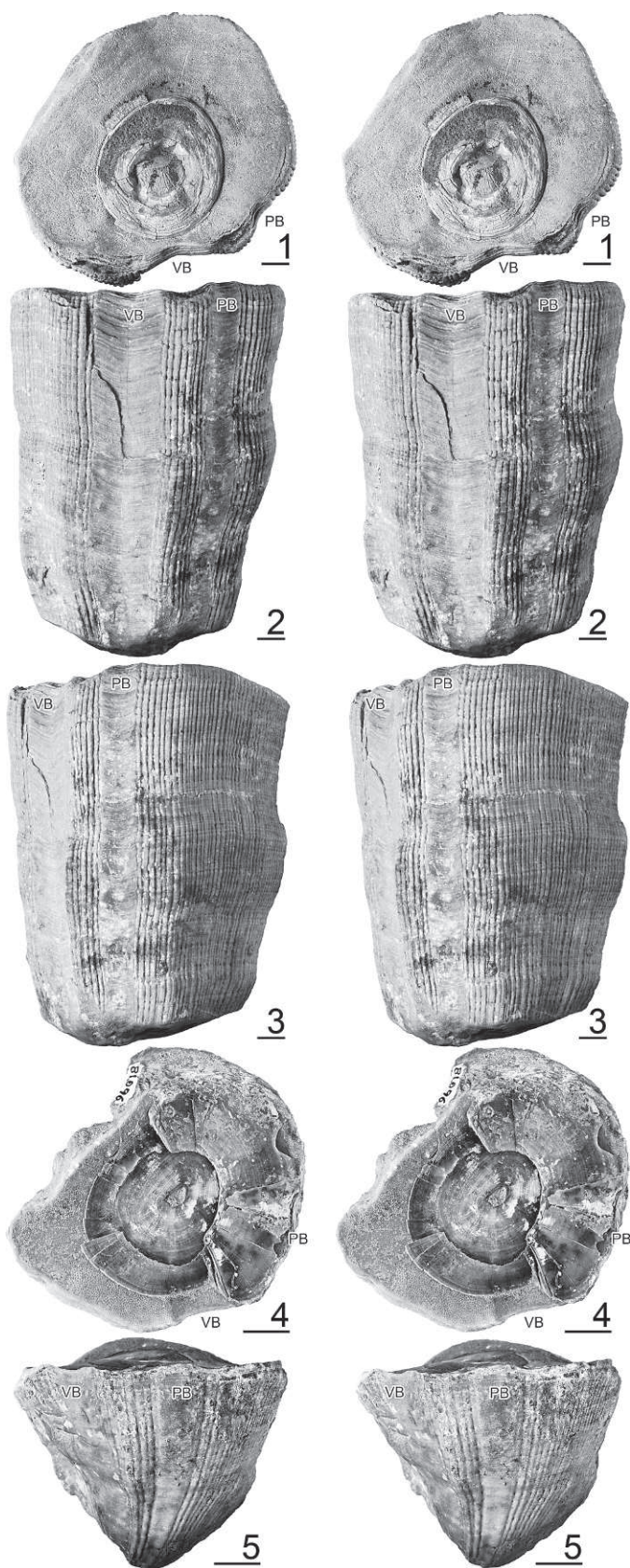


FIGURE 7—*Huasteca ojanchalensis* (Myers, 1968), stereo pairs of bivalve specimens, scale bar=10 mm: 1–3, IGM 9455, Arroyo El Terrero, upper, ventral, and posterior views, respectively; 4, 5, PUAB 81096, Amoladeras, upper and posterior views, respectively.

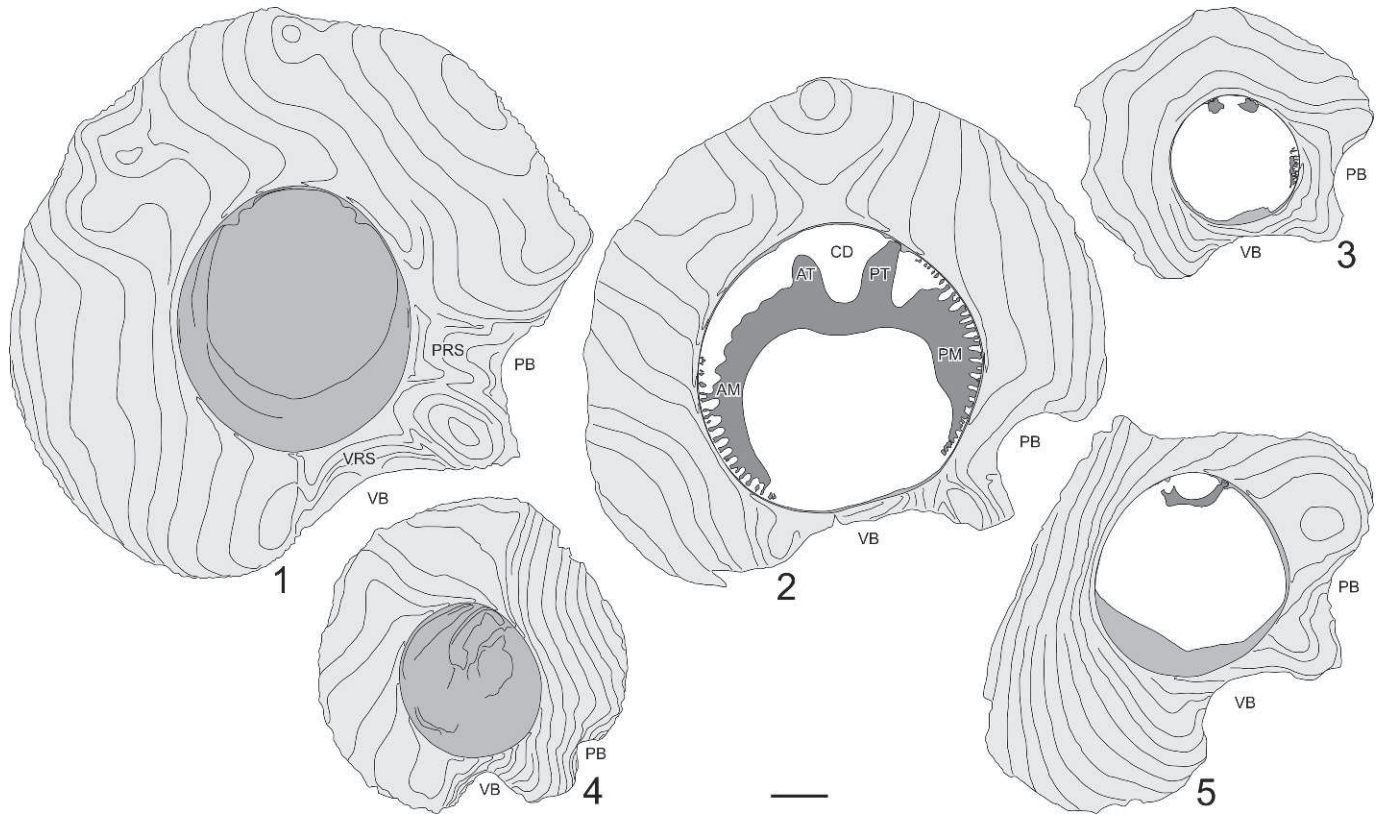


FIGURE 8—*Huasteca ojanchalensis* (Myers, 1968), transverse sections of right valves, scale bar=10 mm: 1, IGM 9454, Arroyo El Terrero; 2, IGM 9451, Amoladeras; 3, PUAB 0701 44, Amoladeras; 4, IGM 9453, Amoladeras; 5, IGM 9452, Amoladeras.

embayment develops between PT and PM. There is no ligament ridge. Teeth and particularly myophores are very short, as far as they are never cut in transverse sections of the right valve located a few mm below the commissural plane.

**Occurrence.**—‘Cárdenas 1’, ‘Amoladeras’, ‘Cuchilla Las Palomas’, ‘Arroyo El Terrero’. Lower Member of the Cárdenas Formation, in the *Durania ojanchalensis* Zone. The species has also been reported from the Ocozocoautla Formation in Chiapas, southern Mexico.

**Remarks.**—In our opinion, all characters of this species fit with the original description and figures of *Durania huasteca* Adkins, 1930, based on a single specimen from the Mendez Formation, Maastrichtian, Hacienda Cacalilao, Tamaulipas, Mexico. Thus, *huasteca* should have priority over *ojanchalensis*. Nevertheless, the specimen, although registered as TMM BEG 20666 in the non-vertebrate paleontology collections at Texas Natural Science Center, The University of Texas at Austin, cannot be tracked, no record existing since the mid-1960s (Ann Molineux, personal commun., June 2012) and our hypothesis cannot be ascertained. For that reason, and also because *huasteca* has not been recognized since Adkins (1930), we consider *ojanchalensis* as the senior specific name and propose it as type species for *Huasteca* new genus.

Genus *TAMPSIA* Stephenson, 1922  
*TAMPSIA FLORIFORMIS* Myers, 1968  
 Figures 10.1–10.6, 11.1–11.7, 12.1–12.9

- 1968 *Tampsia floriformis* MYERS, p. 46, pl. 5, fig. 5, pl. 6, figs. 1, 2, pl. 7, fig. 1.  
 1968 *Tampsia poculiformis* MYERS, p. 47, pl. 5, figs. 6, 7, pl. 7, fig. 1.  
 1971 *Tampsia floriformis* Myers; ALENCASER, p. 55, pl. 10, figs. 1, 2, pl. 11, fig. 1, pl. 22, figs. 1–3.

2005 *Tampsia floriformis* Myers; OVIEDO, p. 45, fig. 33.

2006 *Tampsia poculiformis* Myers; SCHAFFHAUSER, p. 60, pl. 15, figs. 1–10.

**Material.**—Thirty-three specimens PUAB 0719 231–235; PUAB 0720 252–256; PUAB 0733 265; PUAB 0856 583, 587, 590–604; PUAB 81130, 81131, 81163–81164; IGM 9456, 9458–9461, 9539.

**Description.**—Right valve is conical and can be very large (Fig. 10). Larger specimens are 280 mm in height and 220 mm in maximum diameter. Nevertheless, bouquets of cylindrical specimens with a maximum diameter of 50 mm each individual are also found. The outer surface presents coarse acute ribs, limited by wider round sinuses, and one or two radial bands separated by a very coarse rib. PB is always evident, more or less deeply concave and smooth (non-ribbed), and only growth lines are apparent. VB appears as a smooth V shaped sinus with a furrow in its middle part, only as a furrow, or is not recognizable at all (Fig. 10). Commissural lip, is flat or slightly inwardly inclined, radially undulate, measures up to 80 mm in larger specimens, and thins at radial bands; a radial scar, reaching close to the inner margin, is noticeable in some specimens in corresponding with VB. Left valve has a gently convex centre with sub-central apex, above the main cavity, and a very thin margin covering the radial folds of the wide commissural lip. Outer surface is smooth.

The growth lamellae of the outer shell layer of the right valve are horizontal or slightly inclined inward and radially folded. Radial folds become stronger from the inner to the outer margin, where they are responsible for the coarse ribbing at the outer surface; acute downward folds produce the ribs and gentle upward folds the sinuses. In a transverse section of the right valve close to the commissural plane (Fig. 11), besides radial folding of

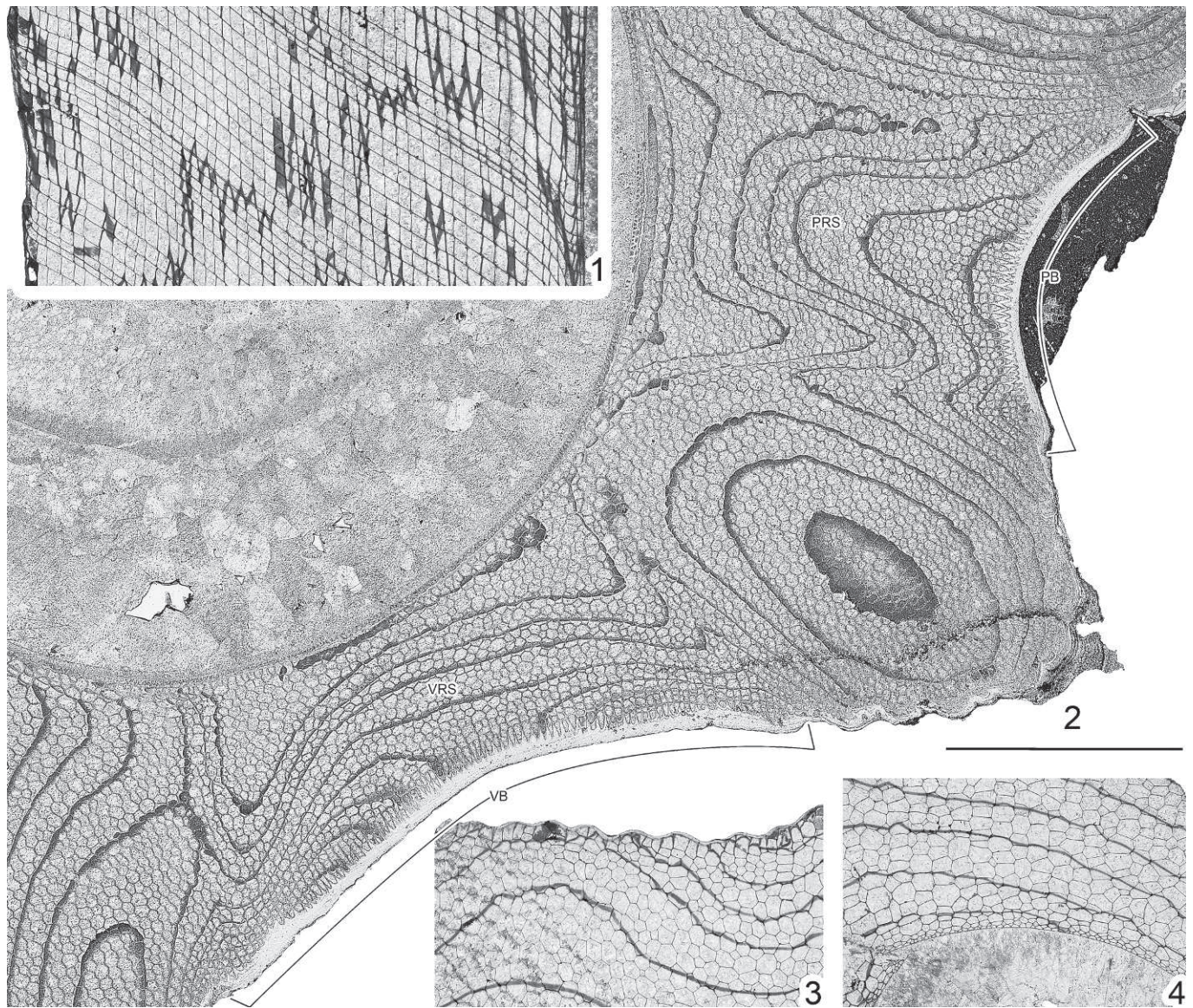


FIGURE 9—*Huasteca ojanchalensis* (Myers, 1968), thin sections of outer shell layer of right valves, scale bar=10 mm: 1, 3, 4, PUAB 81095, Amoladeras: 1, radial section, inner margin at right; 3, 4, transverse sections, inner margin at bottom; 2, IGM 9454, transverse section (peel), Arroyo El Terrero, transverse section at the radial structures part.

the growth lamellae, the myocardial apparatus is also evident. It is very similar to that of *Huasteca ojanchalensis* as described above, also having a striated outer margin.

An inner marginal groove is well developed (Fig. 12.1, 12.3, 12.6, 12.7). The structure of the growth lamellae is not homogeneous, differing among specimens. Normal cellular structure is common, but also compact and discontinuous cellular structures occur. Compare Figure 12.1, 12.6 with Figure 12.3, 12.7 and Figure 12.2, 12.8 with Figure 12.4, 12.5, 12.9, radial and transverse sections of normal cellular structure and compact and discontinuous cellular structures, respectively. The area close to the inner marginal groove is almost always compact or nearly compact.

Radial structures are two up-and-inward folds reducing the thickness of the outer shell layer. PRS may be subdivided, VRS is partially or completely infolded, and both are separated by a large down-and-outward fold (Figs. 11, 12.2, 12.4). Their manifestation

at the outer shell surface, or at the commissural lip, was already described above.

The structure of the growth lamellae in the left valve is compact.

**Occurrence.**—‘Cárdenas 2’, ‘Cárdenas 3’, and ‘Arroyo La Atarjea’. Upper part of the Middle Member and Upper Member of the Cárdenas Formation, in the *Tampsia floriformis* Zone. The species has also been reported from the Ocozocoautla Formation in Chiapas, southern Mexico.

**Remarks.**—We consider, after the study of a large number of specimens from Cárdenas, that the two species proposed by Myers (1968) from the same locality, *T. floriformis* and *T. poculiformis* may be included within the variability range of a single species. *T. floriformis* was described first in the same publication and has priority. The occurrence of discontinuous cellular structure in radiolitids was reported by Pons and Vicens (2008), who indicated this structure seemed restricted to American radiolitids. The co-occurrence of normal cellular and discontinuous cellular structures in a single specimen has been

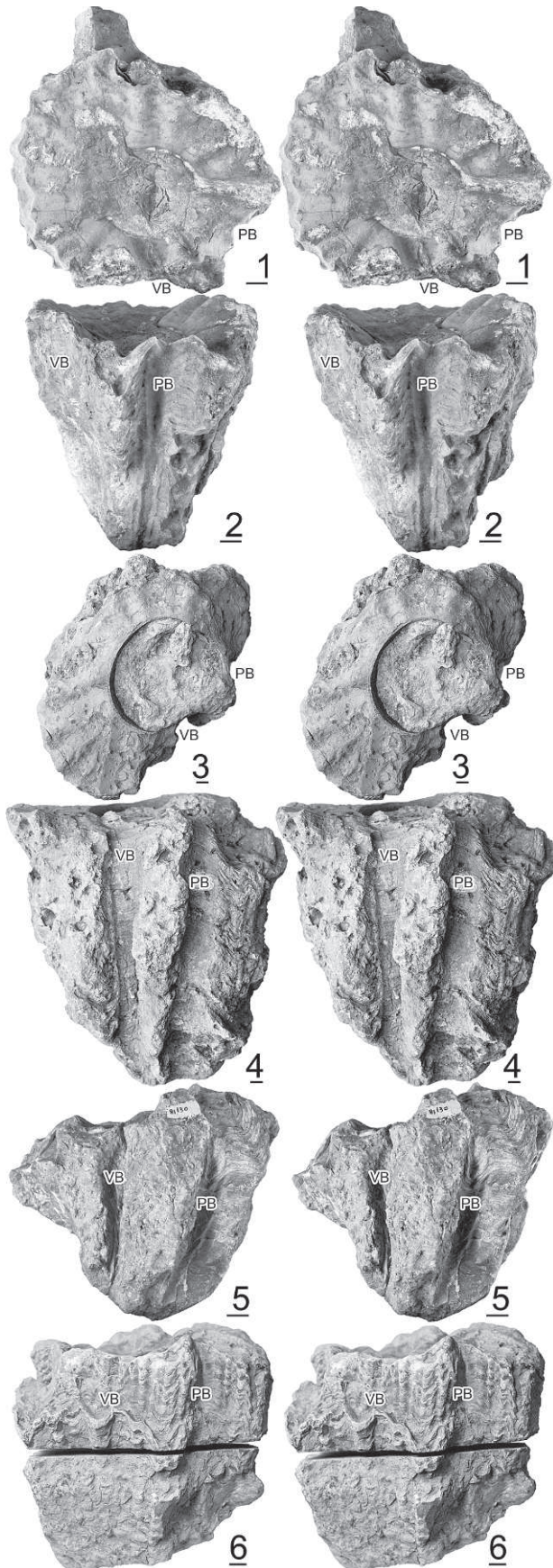


FIGURE 10—*Tampsia floriformis* Myers, 1968, stereo pairs of right valves, Cárdenas, scale bar=10 mm: 1, 2, PUAB 81131, upper and posterior view, respectively; 3, 4, IGM 9459, upper and posterior view, respectively; 5, PUAB 81130, ventral-posterior view; 6, IGM 9461, ventral-posterior view.

documented in American radiolitids as old as Early Campanian (Pons et al., 2010). In our opinion, this particular structure should be considered in phylogenetic analyses among radiolitids. In the other species of *Tampsia* described by Stephenson (1922), *T. bishopi* and *T. chocoyensis*, the growth lamellae are only slightly undulated and the outer surface of the shell is nearly smooth, contrasting with the strong radial folds and coarse ribbing in *T. floriformis*. *T. lopeztrigoi* Palmer, 1933 and *T. ruteni* Vermunt, 1937, are based on very few and incomplete specimens and are insufficiently known, but they seem more related to Stephenson's species than to *T. floriformis*.

#### TRECHMANNITES new genus

*Type species*.—*Biradiolites rudissimus* Trechmann, 1924, from the Titanosarcolites Limestone at Catadupa, St. James, Jamaica.

*Diagnosis*.—Radiolitid having both normal cellular and discontinuous cellular outer shell layer structures and lacking a ligament ridge. Growth lamellae of the right valve are inwardly inclined in long fast-growing specimens and nearly horizontal in short-conical expanded specimens. Left valve is concave in the former and slightly convex in the latter. Radial structures are two up-and-inward folds of the growth lamellae. VRS is wide and flat and bounded by two narrow and acute down-and-outward folds. PRS is narrow and acute and is followed posteriorly by a wide down-and-outward fold. In expanded short-conical specimens all these folds become similarly developed, causing a *Praeradiolites*-like external aspect, while two close unequal flat radial bands, with conspicuous growth lines, characterize long fast-growing specimens.

*Etymology*.—In honor of Charles Taylor Trechmann (1866–1947), expert on the geology of Jamaica who described its Cretaceous mollusc fauna.

*Occurrence*.—Jamaica and Mexico.

*Remarks*.—The exclusive combination of shell characters, absence of ligament ridge, pattern of radial structures (up-and-inward folds), and outer shell layer structure (normal cellular and discontinuous cellular) justify the proposal of a new genus. The type species was originally attributed to *Biradiolites*. Radial structures in *Biradiolites* are two flat down-and-outward folds separated by a well developed acute down-and-outward fold. At the outer surface, they appear as two smooth slightly protruding radial bands in the middle of two furrows separated and limited by acute ribs. Its outer shell layer has radial ridges structure and/or normal cellular structure.

#### TRECHMANNITES RUDISSIMUS (Trechmann, 1924)

Figures 13.1–13.7, 14.1–14.8, 15.1–15.8

- ?1897 *Radiolites rudis* WHITFIELD, p. 189, pl. 11, fig. 4.  
 1924 *Biradiolites rudissimus* TRECHMANN, p. 402, pl. 26, figs. 4, 5.  
 1924 *Biradiolites minhoensis* TRECHMANN, p. 402, pl. 26, figs. 1, 1a.  
 1956b *Biradiolites forbesi* CHUBB, p. 15, pl. 3, figs. 1, 2.  
 1967 *Biradiolites riograndensis* CHUBB, p. 27.  
 1971 *Biradiolites rudissimus* Trechmann; ALENCASTER, p. 40, pl. 6, figs. 1–6, pl. 24, figs. 4, 5.  
 1971 *Biradiolites rudissimus* Trechmann; CHUBB, p. 187, pl. 36, figs. 5–8.  
 1971 *Biradiolites* cf. *rudissimus* Trechmann, CHUBB, p. 188, pl. 36, fig. 9.  
 1971 *Biradiolites forbesi* Chubb; CHUBB, p. 188, pl. 37, figs. 1, 2 (copy Chubb).  
 1971 *Biradiolites minhoensis* Trechmann; CHUBB, p. 189, pl. 37, figs. 3, 4 (copy Trechmann).  
 1971 *Biradiolites riograndensis* Chubb; CHUBB, p. 189, pl. 37, figs. 9–11.

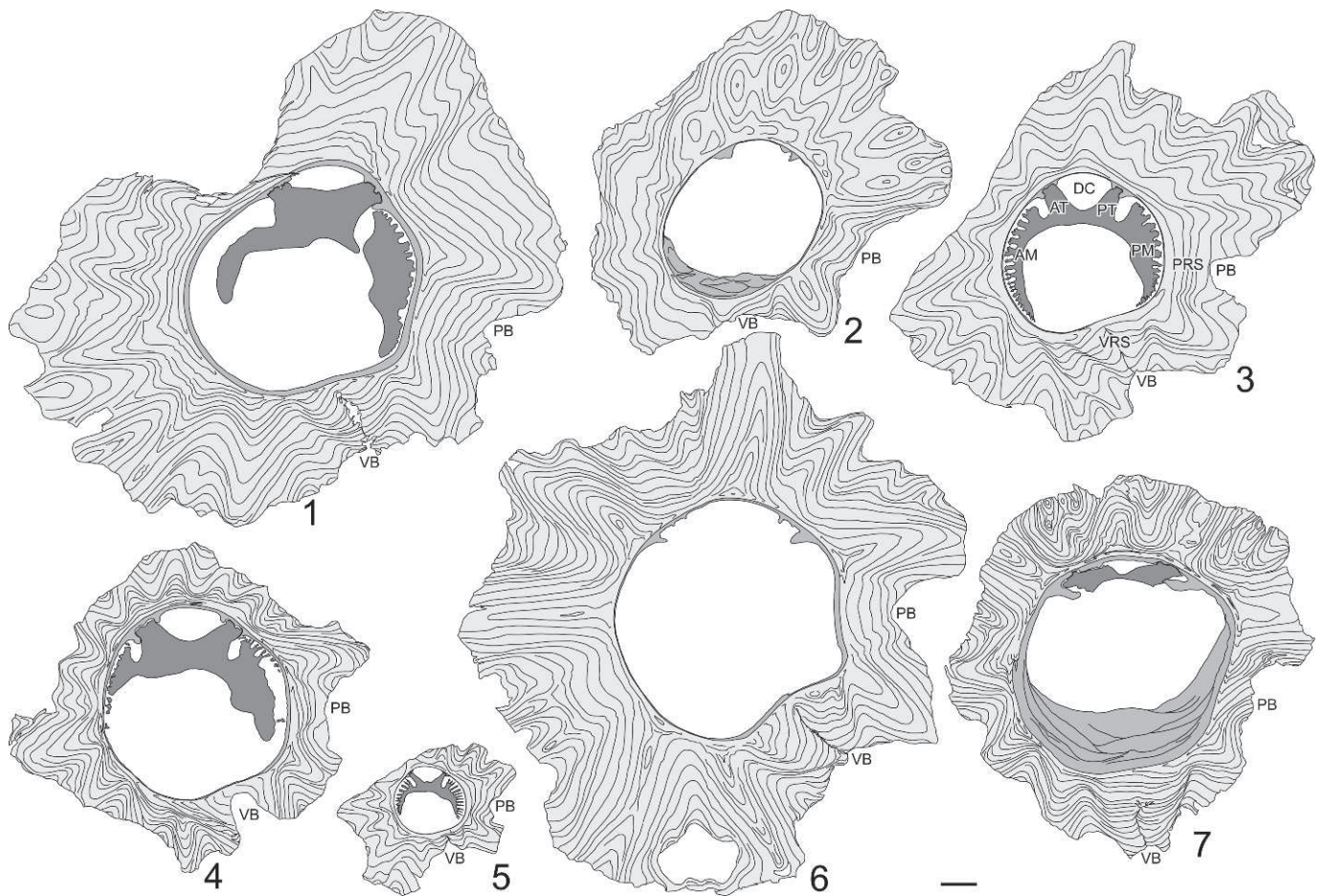


FIGURE 11—*Tampsia floriformis* Myers, 1968, transverse sections of right valves close below the commissural plane, scale bar=10 mm: 1, IGM 9460, Cárdenas 3; 2, IGM 9456, Cárdenas 3; 3, IGM 9539, Cárdenas 3; 4, PUAB 81129, Cárdenas 3; 5, PUAB 0856 583, Cárdenas 3; 6, PUAB 81163, Arroyo La Atarjea; 7, IGM 9458, Cárdenas 3.

- 1990 *Biradiolites rudissimus* Trechmann; ALENCASER, p. 64, pl. 2, fig. 5.  
 2003 *Biradiolites rudissimus* Trechmann; MITCHELL, p. 153, pl. 5, figs. b, c, pl. 6, figs. c, d, f.  
 2005 *Biradiolites rudissimus* Trechmann; OVIEDO, p. 21, fig. 12.  
 2007 *Biradiolites rudissimus* Trechmann; MITCHELL, p. 83, fig. 4A, 4B.

**Material.**—Seventy-six specimens: PUAB 0701 56–89, PUAB 81099–81109; PUAB 0733 280, 281; PUAB 0738 358, 359; PUAB 0852 484; PUAB 0855 519–521; PUAB 0856 576–582, 584–586; PUAB 81118, 81126; IGM 9443–9450.

**Description.**—Right valve is conical in juveniles, becoming cylindrical or wide conical in adult shells (Fig. 13). Maximum diameter is normally anterior-posterior and reaches up to 105 mm in larger specimens. Longer specimens may measure up to 140 mm. The outer surface is smooth at dorsal and anterior sides, although with evident growth lamellae sets, and folded at the ventral-posterior side (Figs. 13, 14). Dorsal and/or anterior sides may be much expanded. Left valve is more or less concave and shows the same ventral-posterior folds as the right valve. It may be slightly convex in specimens with extremely expanded growth lamellae (Fig. 13).

The growth lamellae of the outer shell layer of the right valve are inclined inwardly, developing a conspicuous inner marginal groove (Fig 15.1, 15.2, 15.5, 15.6), and presenting normal cellular and/or discontinuous cellular structure. Compare Figure 15.1,

15.5 with Figure 15.2, 15.6 and Figure 15.3, 15.7 with Figure 15.4, 15.8, radial and transverse sections of normal cellular structure and discontinuous cellular structures, respectively.

Radial structures are two unequal up-and-inward radial folds. Ventral radial structure is wide and flat and bounded by two very narrow down-and outward radial folds. Posterior radial structure is narrow and acute, thus slightly protruding, and a diversely developed down-and outward radial fold follows it posteriorly (Figs. 14, 15.3, 15.4). Radial structures appear at the outer surface as a wide flat radial band and as a flat slightly protruding narrower band, respectively (Fig. 13.2, 13.3). No inter-band is evident because other folds do not exist. Some specimens with highly expanded growth lamellae reach a wide conical form. Width of both ventral and posterior radial folds, as well as of their limiting folds, becomes similar in these specimens. Their external aspect reminds that of some *Praeradiolites*, although more asymmetrical (Fig. 13.4–13.7).

Transverse sections of the right valve close to the commissural plane show the outer and inner profile of the shell, the radial folding of the growth lamellae, and the myo-cardinal apparatus (Fig. 14.1). The myo-cardinal arch encloses a regular sized dorsal cavity. There is no ligament ridge. Inner shell layer is very thin, and develops two striated furrows where the teeth of the left valve glide. Teeth are rectangular with striated outer margins, AT is larger and PT is smaller. A conspicuous embayment develops between PT and PM. Myophores present a striated outer side and are asymmetrically developed. AM extends along the anterior

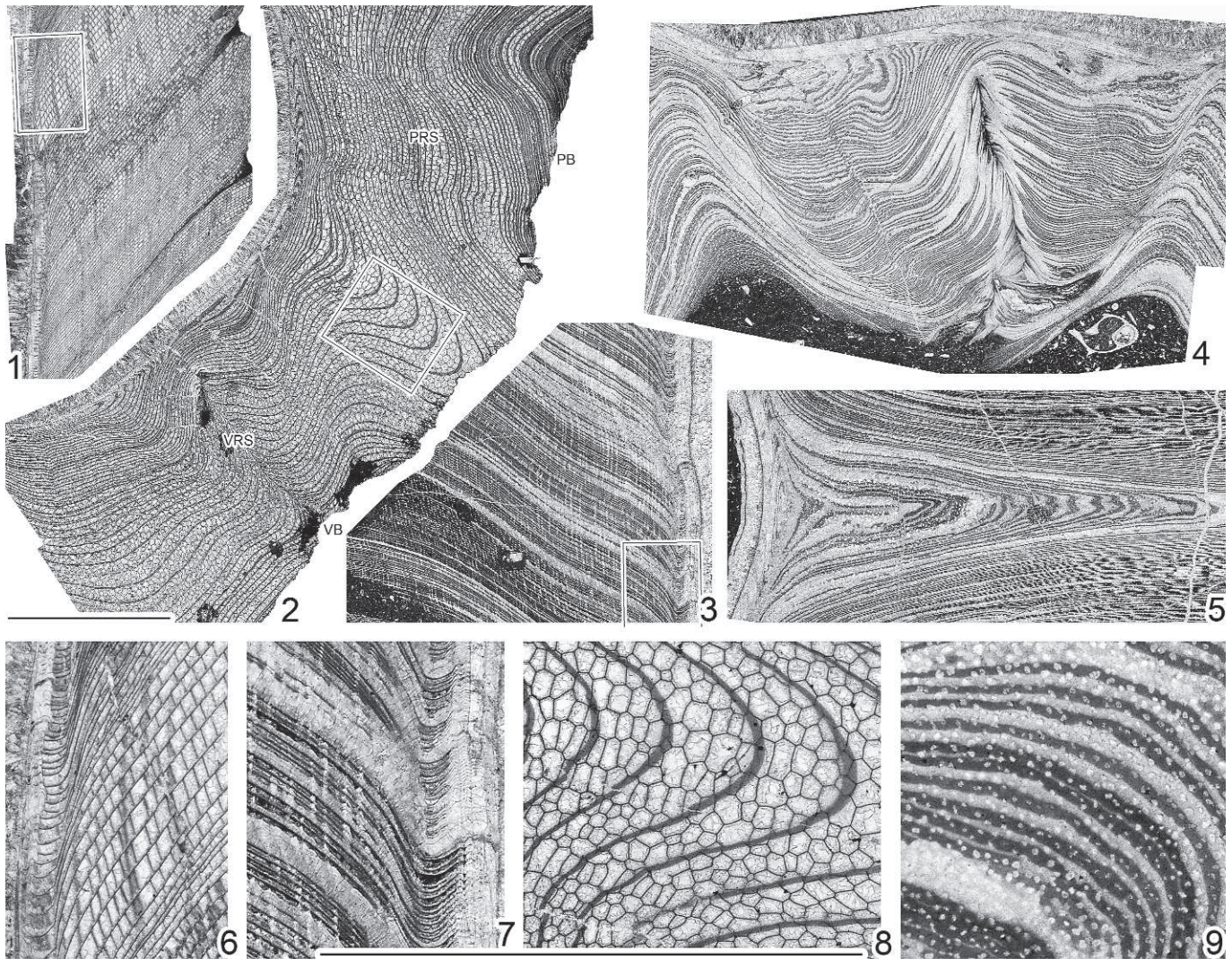


FIGURE 12—*Tampsia floriformis* Myers, 1968, thin sections of outer shell layer of right valves, enlarged areas are indicated, Arroyo La Atarjea, scale bars=10 mm, note that scale bars are different for upper and lower figure rows: 1, 2, 6, 8, PUAB 81164; 3, 4, 5, 7, 9, PUAB 81163; 1, radial section, inner margin at left; 2, transverse section at the radial structures part; 3, radial section, inner margin at right; 4, transverse section at the ventral radial structure part, inner margin at top; 5, transverse section at an anterior acute down-and-outward fold, inner margin at left; 6, 7, detail of radial sections, inner margin at left and at right, respectively; 8, 9, detail of transverse sections.

side of the shell and PM reaches the posterior margin of the ventral radial structure.

**Occurrence.**—‘Amoladeras’, ‘Arroyo Los Terrerillos’, and ‘Arroyo El Terrero’. Lower Member of the Cárdenas Formation, in the *Durania ojanchalensis* Zone. ‘Cárdenas 3’. Upper Member of the Cárdenas Formation, in the *Tampsia floriformis* Zone. The species has also been reported from the Ocozocoautla Formation in Chiapas, southern Mexico and from the Guinea Corn Formation in Jamaica.

**Remarks.**—The relationship between *Radiolites rudis* Whitfield and *Biradiolites rudissimus* Trechmann was discussed by Mitchell (2003), resulting that the type and only specimen of *R. rudis* must be regarded as indeterminate and questionably placed in the synonymy list of *B. rudissimus*. Also, the type material of *B. minhoensis* Trechmann and *B. riograndensis* Chubb were considered by this author to fall within the variability range of *B. rudissimus*. Synonymy between *B. forbesi* Chubb and *B. rudissimus*, already considered likely by Chubb (1971), was also accepted by Mitchell (2003).

Family HIPPURITIDAE Gray, 1848

Genus CARIBBEA Grubić, 2004

CARIBBEA MUELLERRIEDI (Vermunt, 1937)

Figures 16.1–16.11, 17.1–17.7, 18.1–18.3

- 1924 *Hippurites* (*Orbignya*) spp. TRECHMANN, p. 396, pl. 23, fig. 5.
- 1930 *Hippurites* (*Hippuritella* Douvillé; *Orbignya* Toucas) cf. *incisus* Toucas; MÜLLERRIED, p. 165, figs. 1, 2.
- 1937 *Orbignya müllerriedi* VERMUNT, p. 261, text-fig. 3a–3d, pl. 36, figs. 1–3.
- 1937 *Hippurites müllerriedi* (Vermunt); MACGILLAVRY, p. 111, pl. 5, fig. 6.
- 1956a *Hippurites* (*Orbignya*) *mullerriedi* (Vermunt); CHUBB, p. 9, 13.
- 1956b *Hippurites* (*Orbignya*) *mullerriedi* (Vermunt); CHUBB, p. 19, pl. 4, figs. 4, 8.
- 1956b *Hippurites* (*Orbignya*) *ceibarum* CHUBB, p. 19, text-fig. 4, pl. 4, figs. 9, 10.

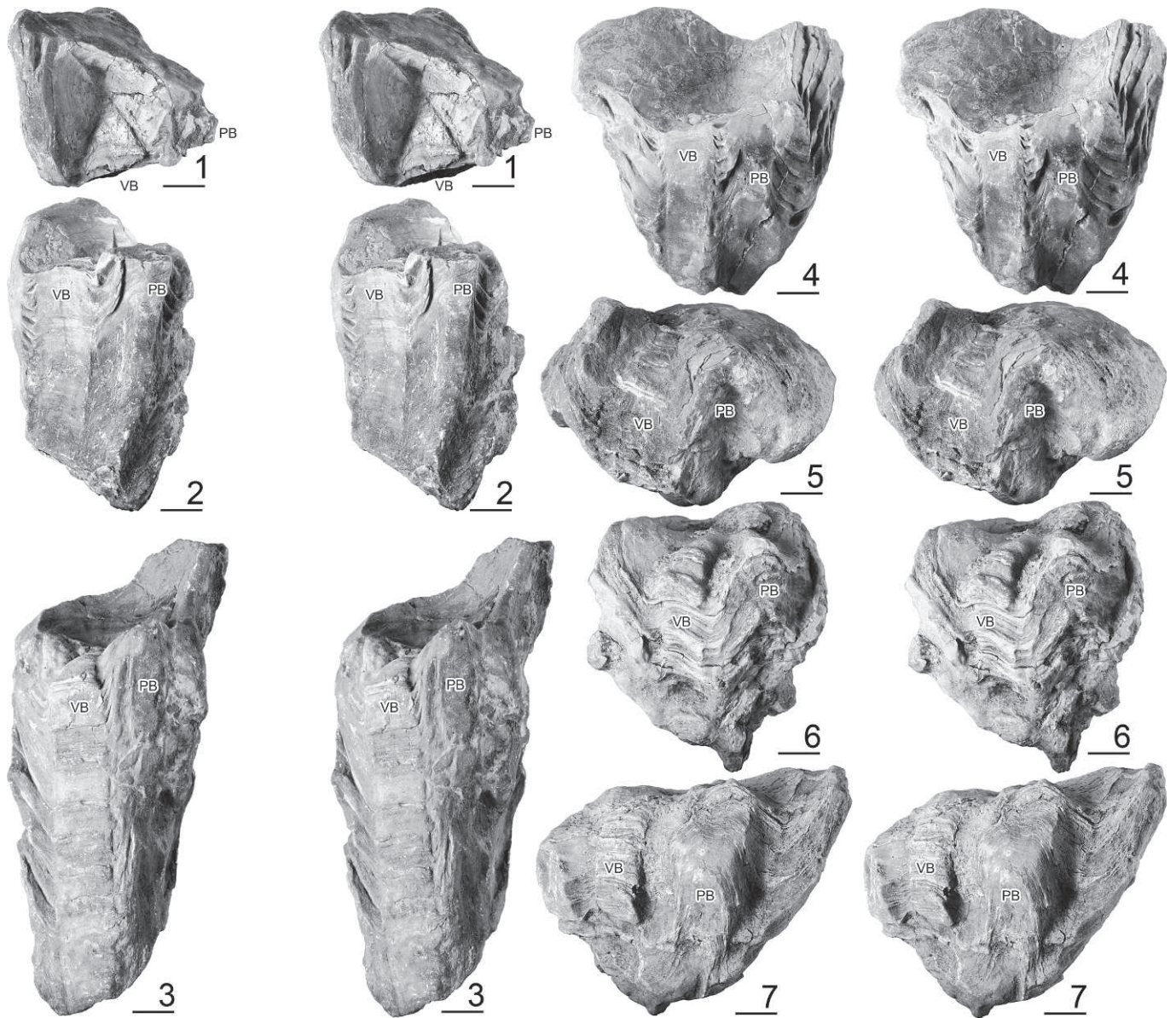


FIGURE 13—*Trechmannites rudissimus* (Trechmann, 1924), stereo pairs of bivalve specimens, scale bar=10 mm: 1, 2, PUAB 81099, Amoladeras, upper and ventral-posterior views respectively; 3, IGM 9448, Amoladeras, ventral-posterior view; 4, PUAB 81104, Amoladeras, ventral-posterior view; 5, IGM 9446, Amoladeras, ventral-posterior view; 6, PUAB 81126, Cárdenas 3, ventral-posterior view; 7, PUAB 81118, Cárdenas 3, ventral-posterior view.

- 1968 *Hippurites muellerriedi* (Vermunt); MYERS, p. 42, pl. 3, figs. 4–6.  
 1968 *Hippurites perkinsi* MYERS, p. 43, pl. 4, figs. 5, 6.  
 1971 *Orbignya mullerriedi* Vermunt; CHUBB, p. 204, pl. 49, figs. 1, 2.  
 1975 *Hippurites muellerriedi* (Vermunt); LUPU, p. 240, fig. 20.  
 1981 *Hippurites mullerriedi* (Vermunt); SÁNCHEZ, p. 20.  
 1993 *Hippurites mullerriedi* (Vermunt); DAVIS-STRICKLAND AND DONOVAN, table 1.  
 1996 *Hippurites mullerriedi* (Vermunt); ROJAS ET AL., p. 285, table 2.  
 1996 *Hippurites mullerriedi* (Vermunt); ROJAS AND ITURRALDE-VINENT, p. 293.  
 2004 *Caribbea muellerriedi* (Vermunt); GRUBIĆ, p. 147, pl. 2, fig. 1 (drawing on Vermunt, 1937, pl. 36, fig. 2).

- 2004 *Caribbea ceibarum* (Chubb); GRUBIĆ, p. 147, pl. 2, fig. 2 (drawing on Chubb, 1956b, pl. 4, fig. 9).  
 2004 *Caribbea sladici* GRUBIĆ, p. 148, pl. 2, fig. 4 (drawing of Trechmann's, 1924, pl. 23, fig. 5 specimen).  
 2006 *Hippurites muellerriedi* (Vermunt); OVIEDO ET AL., p. 62.  
 2007 *Hippurites muellerriedi* (Vermunt); OVIEDO ET AL., p. 311.  
 2006 *Hippurites perkinsi* Myers; SHAFHAUSER, p. 62, pl. 16, figs. 8, 9.  
 2007 *Hippurites perkinsi* Myers; SHAFHAUSER ET AL., table 1.  
 2011 *Caribbea muellerriedi* (Vermunt); MITCHELL ET AL., p. 40.

*Material*.—Twenty-eight specimens: PUAB 81133–81160, most of them are right valves of isolated individuals but some bouquets with several shells.

*Description*.—Right valve is cylindrical in adults, with a

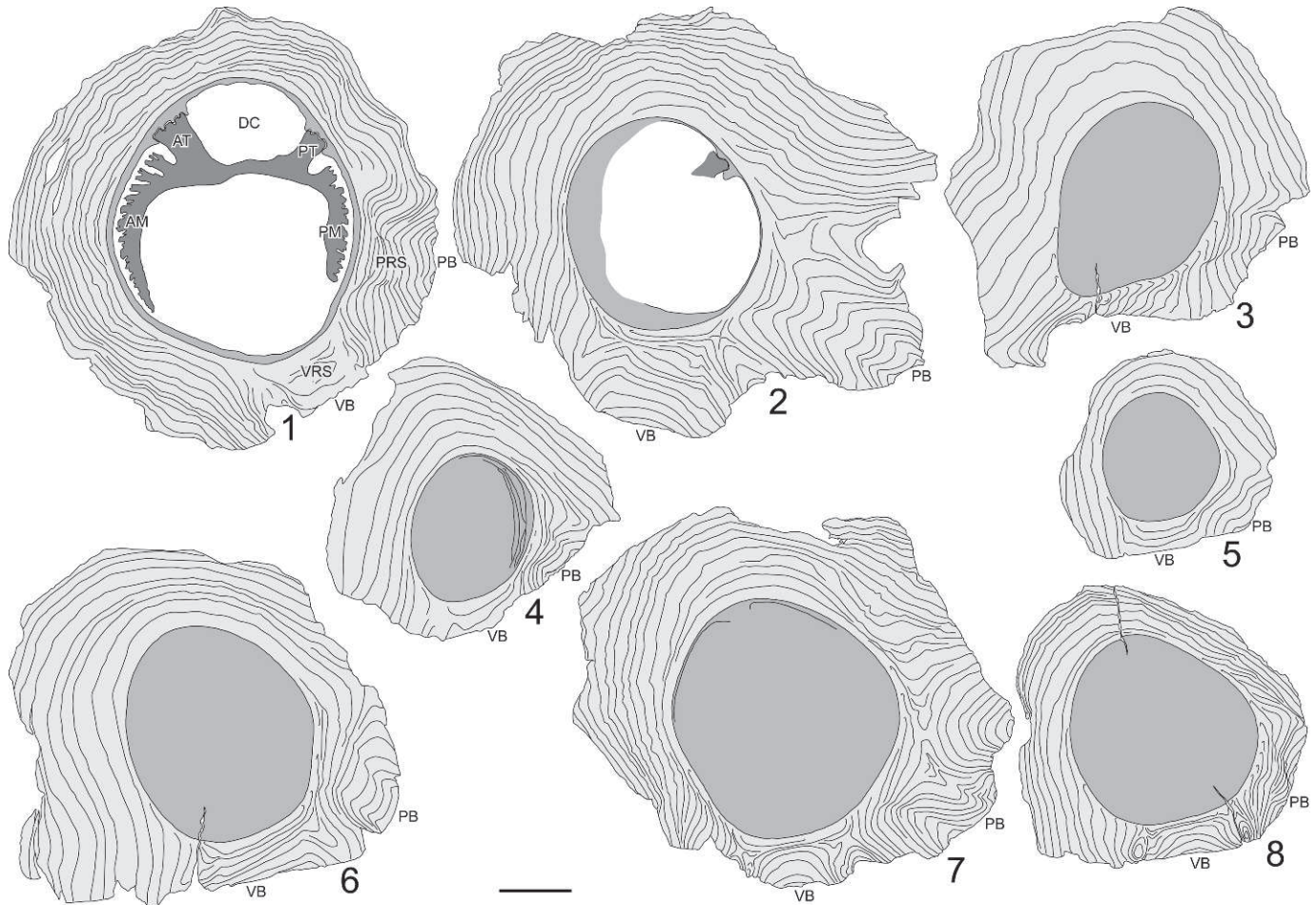


FIGURE 14—*Trechmannites rudissimus* (Trechmann, 1924), transverse sections of right valves, scale bar=10 mm: 1, PUAB 81128, Cárdenas 3, close below the commissural plane showing myocardial elements; 2, IGM 9449, Amoladeras; 3, IGM 9445, Amoladeras; 4, IGM 9443, Amoladeras; 5, IGM 9450, Amoladeras; 6, PUAB 81108, Amoladeras; 7, IGM 9447, Amoladeras; 8, IGM 9444, Amoladeras.

maximum diameter of 40 mm. The longest collected specimen measures 140 mm. Bouquets of several individuals with their valves attached one to another, or thickets of hundreds with variable amount of sediment between them, are common although isolate individuals are also found. The outer surface may be provided with rounded ribs separated by grooves as wide as ribs, with narrow ribs separated by wide grooves, or lack ribs. The three internal hippuritid folds commonly correspond with differently developed grooves at the outer surface (Fig. 16). No isolated specimens with preserved left valves were found, but serial sections made on bouquets revealed some specimens preserving the myocardial apparatus. Internally (Fig. 16), the ligament ridge (L) is only a wide inward fold of the outer shell layer which does not increase its thickness. In some specimens the inward fold is narrower, and the ligament ridge becomes slightly triangular, although always with a clear rounded end. The first pillar (P1) is from short and parallel-sided to longer, curved, and pinched at the base. The second pillar (P2) is longer, normally curved and/or pinched, although straight and parallel sided in some specimens. The inner and outer profile of the shell in transverse section is extremely irregular, thus, it is difficult to measure accurately the L-P2 angle, since it has been observed to be highly variable but always higher than  $120^\circ$ . The cardinal apparatus is located dorsally, close to the ligament ridge with AT and PT at its anterior and posterior side, respectively. PM is aligned slightly dorsal from the AT-PT axis (Fig. 16.1).

The outer shell layer structure is not compact (Fig. 17). The growth lamellae are steeply inwardly inclined and closely radially folded. Upward folds are deep and very narrow, while downward folds are shallower and wider. Consequently, successive growth lamellae are in contact at upward folds while an empty space is left between successive growth lamellae at downward folds. In transverse sections observed at low magnification, differently colored more or less sinuous and off-branched lines seem to traverse radially the shell (Fig. 17.1). At medium magnification, differences in the pattern of the lines are observed from the inner to the outer margin of the shell (Fig. 17.2), or between different specimens (Fig. 18). At higher magnification, it becomes evident that these lines correspond to the more or less aligned upward folds of the successive growth lamellae, cut oblique because of the inward inclination of the lamellae. The downward folds of the successive growth lamellae also become visible. Both upward and downward folds are more numerous, regular, and stronger at the outer margin than at the inner margin, this fact explaining the differences in the observed pattern in the transverse section. Tangential and radial sections (Fig. 17.4–17.7) both confirm these interpretations of the shell structure.

The inner shell layer may develop tabulae. Tabulae are concave upward, more or less spaced, and the space between tabulae is currently filled with fine sediment. Inner casts, formed by several pieces corresponding to the successive infillings, are preserved from specimens lacking its outer and inner shell layer.



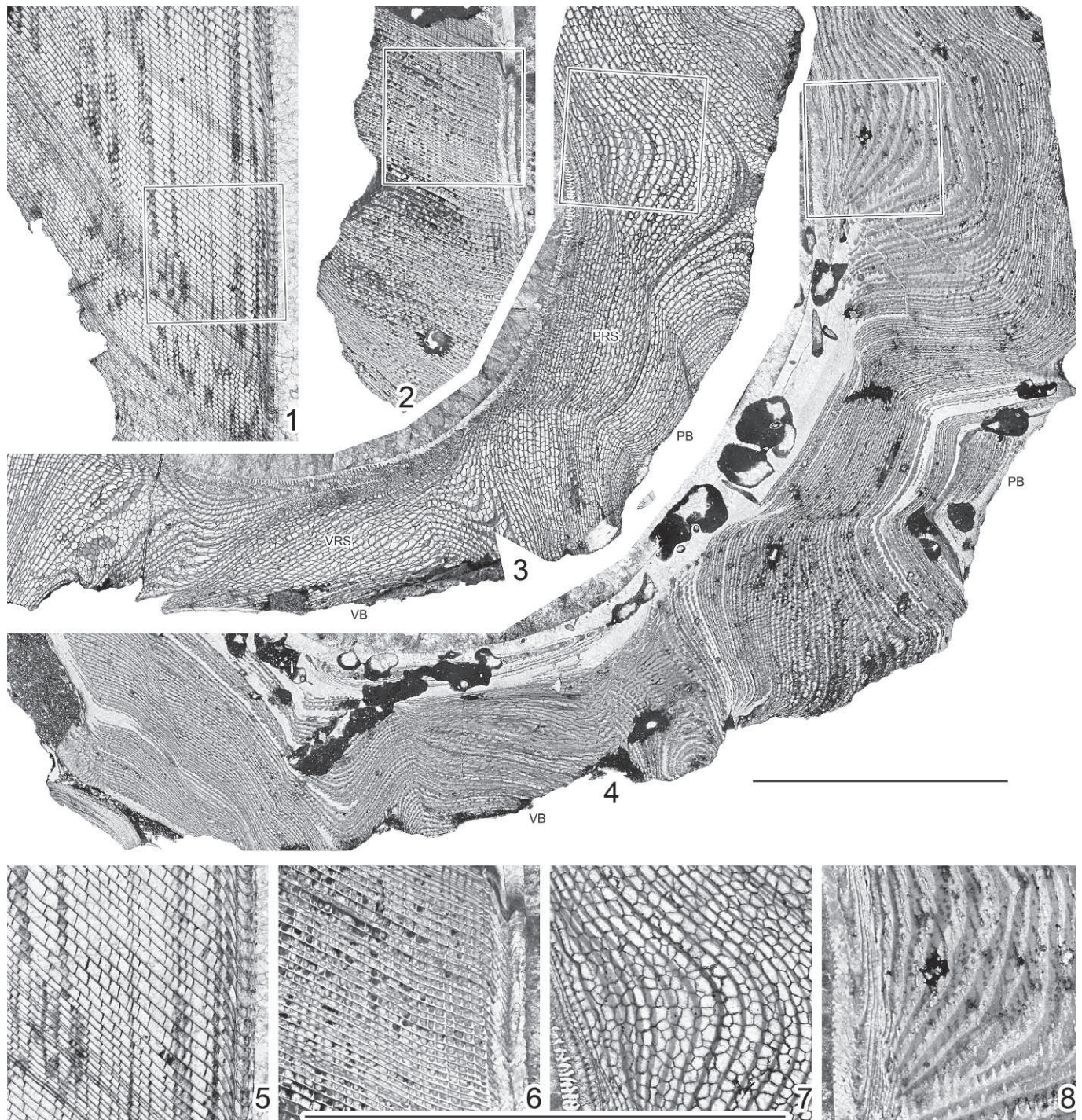


FIGURE 15—*Trechmannites rudissimus* (Trechmann, 1924), thin sections of outer shell layer of right valves, enlarged areas are indicated, scale bars=10 mm: 1, 3, 5, 7, PUAB 81108, Amoladeras; 2, 4, 6, 8, PUAB 81128, Cárdenas 3; 1, 2, radial sections, inner margin at right; 3, 4, transverse sections at the radial structures part; 5, 6, details of radial sections, inner margin at right; 7, 8, details of transverse sections, inner margin at left.

**Occurrence.**—‘Arroyo La Atarjea’. Uppermost part of the Upper Member of the Cárdenas Formation, in the *Tampsia floriformis* Zone. This species, under the same or different name, has also been reported from Jamaica and Cuba.

**Remarks.**—Differences in external ribbing, undulation of the inner margin of the outer shell layer, and separation of the three main infolds, in *ceibarum*, *perkinsi* and *sladici* fit within the variability range of *C. muellerriedi* and, in our opinion, considering them different species is not justified.

The genus proposed by Grubić (2004) differs from other hippuritid genera with short ligament ridge and high L-P2 angle, like *Hippurites* and *Hippuritella*, by its PM alignment slightly dorsal from the AT-PT axis, besides its outer shell layer structure.

The structure of the outer shell layer of the right valve was first noticed by Müllerried (1930) and described and correctly interpreted by MacGillavry (1937, p. 111, and fig. 2 in p. 123). Some subsequent authors erroneously interpreted this structure as a capillary structure (Grubić, 2004), while other emphasized its

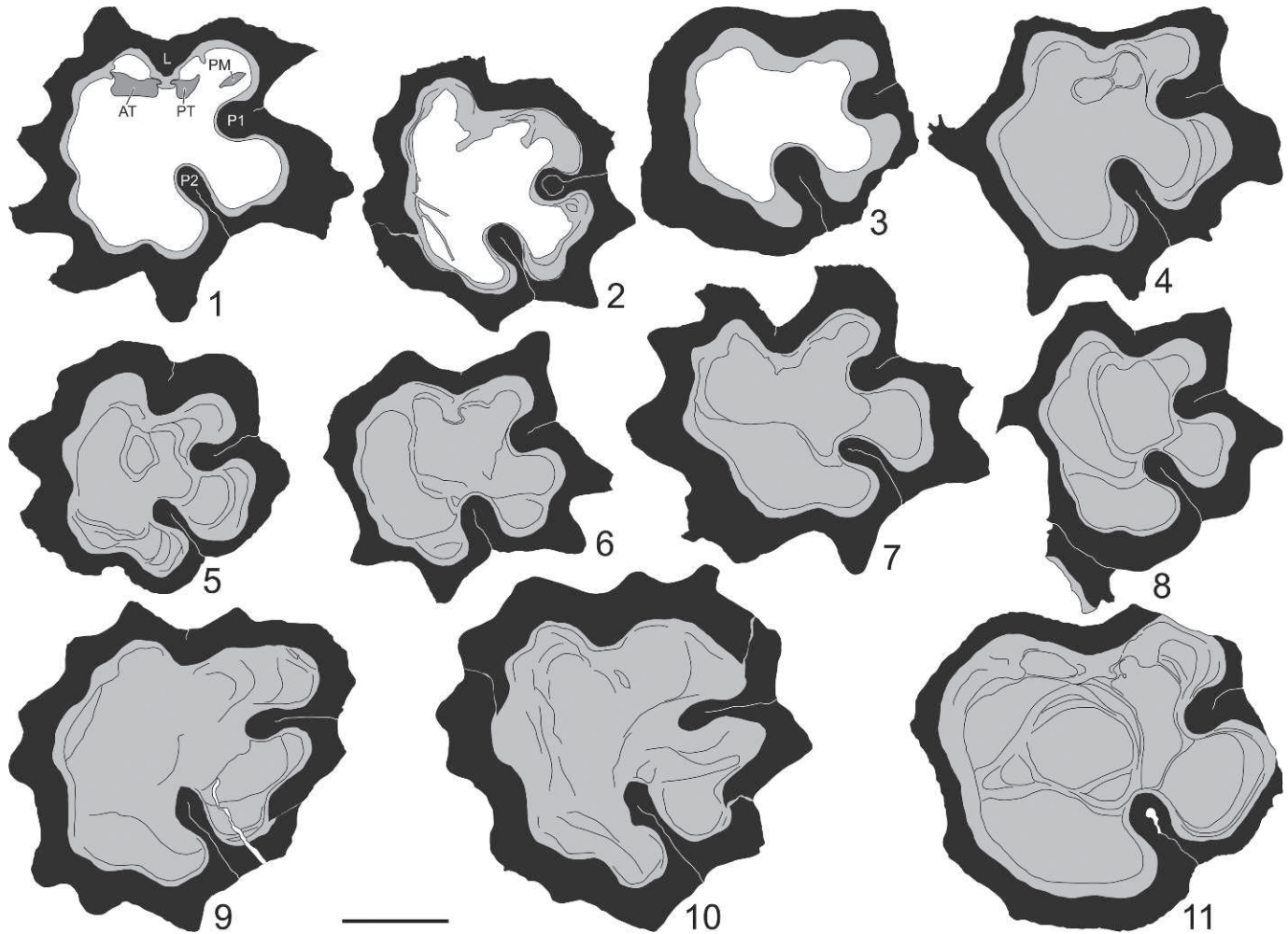


FIGURE 16—*Caribbea muellerriedi* (Vermunt, 1937), transverse sections of right valves, Arroyo La Atarjea, scale bar=10 mm: 1, PUAB 81156; 2, PUAB 81160; 3, PUAB 81142; 4, PUAB 81152; 5, PUAB 81158; 6, PUAB 81154; 7, PUAB 81136; 8, PUAB 81137; 9, PUAB 81155; 10, PUAB 81143; 11, PUAB 81148.

similarity with a cellular radiolite structure (Schaffhauser, 2006). The non-compact shell in *Caribbea* and other hippuritids is constructed in a completely different way as radiolites construct theirs. In radiolites (Pons and Vicens, 2008), two differently growing parts may be distinguished in a single growth lamella. In the first, secretion of shell is uniform (continuous growth='funnel plates' of authors). In the second, secretion of shell takes place only locally (discontinuous growth='pillars' of authors) and open spaces remain until closed by the first part of the successive growth lamella; local growth may form radial ridges, forked or not, or polygonal cell walls. In hippuritids, secretion of shell in the growth lamellae is uniform, as in the first part of radiolites, and the growth lamellae are radially undulate. Successive growth lamellae are in contact with each other only in deep and very narrow upward folds, leaving voids between them in shallower and wider downward folds, as described above in *Caribbea*. MacGillavry (1937) described in *Praebarrettia corrali* a similar structure where successive growth lamellae are in contact with each other only in the inflection points between neighboring folds, leaving voids between them in both upward and inward folds.

#### Genus PRAEBARRETTIA Trechmann, 1924

##### PRAEBARRETTIA SPARCILIRATA (Whitfield, 1897) sensu lato

Figures 19.1–19.10, 20.1–20.12, 21.1–21.6, 22.1–22.3, 23.1–23.8

- 1897 *Barrettia sparcilirata* WHITFIELD, p. 245, text-figs. 36, 37.  
 1922 *Barrettia sparcilirata* Whitfield; TRECHMANN, p. 512.  
 non1924 *Barrettia sparcilirata* (Whitfield); SÁNCHEZ-ROIG, p. 98, text-figs. 3, 4. (= *Barrettia monilifera* Woodward)  
 1924 *Praebarrettia sparcilirata* (Whitfield); TRECHMANN, p. 395, pl. 23, figs. 3, 4.  
 non1926 *Barrettia sparcilirata* (Whitfield); DOUVILLÉ, p. 128, pl. 7, fig. 1. (= *Barrettia monilifera* Woodward)  
 1928 *Pironea peruviana* GERTH, p. 235, text-figs. 2, 3.  
 1932 *Barrettia sparcilirata* Whitfield; BOISSEVAIN AND MACGILLAVRY, p. 1303, pl. 1, figs. a, b, pl. 2, figs. a, b, pl. 3, fig. a.  
 1933 *Pironea corrali* PALMER, p. 98, pl. 4, fig. 2.  
 1933 *Praebarrettia sparcilirata* var. *cubensis* PALMER, p. 98, pl. 6, figs. 1, 2.  
 1933 *Praebarrettia porosa* PALMER, p. 99, pl. 6, figs. 3–6.  
 1935 *Barrettia sparcilirata* Whitfield; MACGILLAVRY, p. 562, 563.

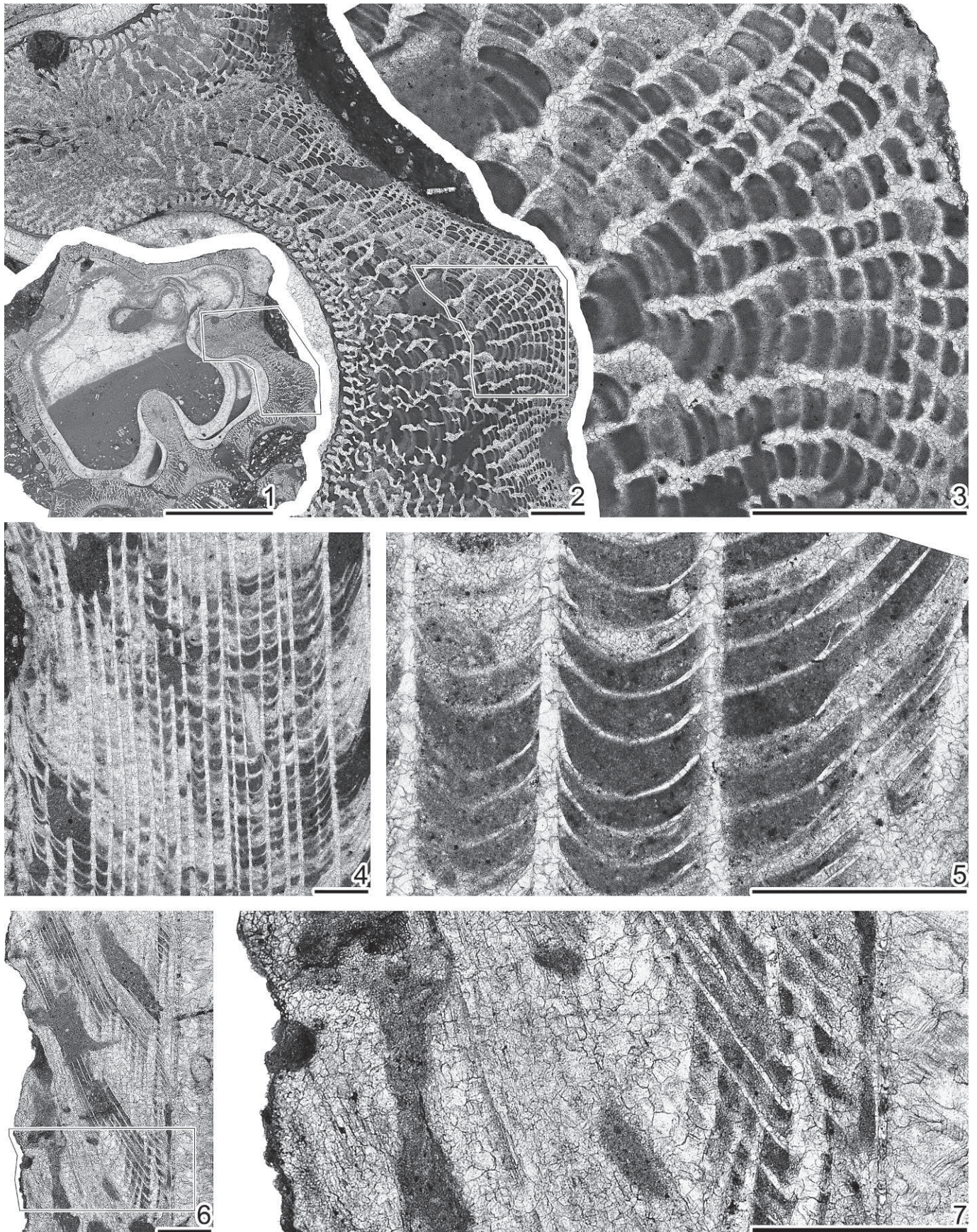


FIGURE 17—*Caribbea muellerriedi* (Vermunt, 1937), thin sections of outer shell layer of right valves, Arroyo La Atarjea, scale bars=10 mm in 1 and 1 mm in 2-7: 1-3, PUAB 81152, transverse section, enlarged area in successive figures is indicated; 4, 5, PUAB 81141, tangential section; 6, 7, PUAB 81148, radial section.

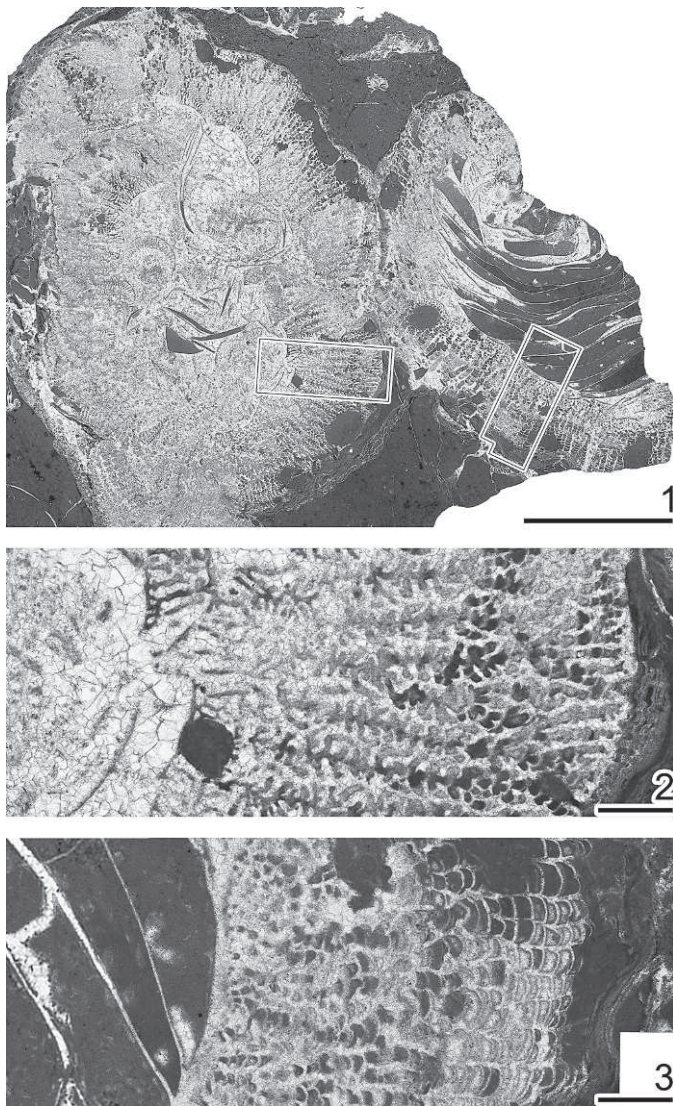


FIGURE 18—*Caribbea muellerriedi* (Vermunt, 1937), transverse thin section of outer shell layer of right valves, enlarged areas are indicated, PUAB 81217, Jerusalem Mountain, Jamaica, scale bars=10 mm in 1 and 1 mm in 2, 3.

- 1936 *Barrettia sparcilirata* Whitfield; THIADENS, p. 1011, pl. 1, fig. 2, pl. 2, fig. a–k.
- 1937 *Pironea* cf. *peruviana* Gerth; VERMUNT, p. 266, text-fig. 2i, 2j.
- 1937 *Barrettia sparcilirata* Whitfield; VERMUNT, p. 268
- 1937 *Praebarrettia* sp. MACGILLAVRY, p. 122.
- 1937 *Praebarrettia corrali* (Palmer); MACGILLAVRY, p. 122, text-fig. 1, pl. 5, fig. 3, pl. 10, fig. 3.
- 1937 *Praebarrettia sparcilirata* (Whitfield); MACGILLAVRY, p. 123.
- 1951 *Pironea macgillavryi* MÜLLERRIED, p. 88, pl. 12, fig. 5.
- 1955 *Praebarrettia sparcilirata* (Whitfield); CHUBB, p. 13.
- 1956a *Praebarrettia sparcilirata cubensis* Palmer; CHUBB, p. 13.
- non1956b *Praebarrettia coatesi* CHUBB, p. 13, pl. 58, figs. 2–4 (= *Barrettia coatesi* after van Dommelen [1971]).
- 1960 *Praebarrettia sparcilirata cubensis* Palmer; DE LA TORRE, p. 52.
- 1960 *Praebarrettia porosa* Palmer; DE LA TORRE, p. 52.

- 1971 *Praebarrettia sparcilirata* (Whitfield); ALENCASTER, p. 70, pl. 14, figs. 1–6, pl. 15, figs. 2, 3.
- 1971 *Praebarrettia sparcilirata* (Whitfield); CHUBB, p. 215, pl. 57, figs. 1, 2 (2 copy Trechmann), pl. 58, fig. 1 (copy Whitfield).
- 1971 *Prebarrettia corrali* (Palmer); VAN DOMMELEN, p. 66, text-fig. 19, pl. 3, figs. 1, 2.
- 1971 *Prebarrettia peruviana* (Gerth); VAN DOMMELEN, p. 68, text-fig. 13.11.
- 1971 *Prebarrettia sparcilirata* s.l. (Whitfield); VAN DOMMELEN, p. 69, pl. 3, fig. 3, pl. 4, figs. 1, 2, pl. 12, pl. 13, figs. 1–10, pl. 20, pl. 21, pl. 22.
- 1975 *Praebarrettia corrali* (Palmer); LUPU, p. 229, text-figs. 5, 6.
- 1975 *Praebarrettia sparcilirata albeari* LUPU, p. 233, text-figs. 10–14.
- 1975 *Praebarrettia* aff. *sparcilirata* (Whitfield); LUPU, p. 236, text-fig. 15.
- 1975 *Praebarrettia torrei* LUPU, p. 238, text-figs. 16–19.
- 1990 *Praebarrettia sparcilirata* (Whitfield); ALENCASTER, p. 64, pl. 2, figs. 7, 8.
- 2004 *Gloria vermunti* GRUBIĆ, p. 150, pl. 2, fig. 5 (drawing on Vermunt 1937, text-fig. 2i).
- 2004 *Gloria peruviana* (Gerth); GRUBIĆ, p. 150, pl. 2, fig. 7 (copy of Gerth 1928, text-fig. 3).
- 2004 *Gloria corrali* (Palmer); GRUBIĆ, p. 151, pl. 2, fig. 6 (drawing on Palmer 1933, pl. 4, fig. 2).
- 2004 *Praebarrettia porosa* Palmer; GRUBIĆ, p. 153, pl. 3, fig. 2 (copy of Thiadens 1936, text-fig. 2b).
- 2004 *Praebarrettia thiadensi* GRUBIĆ, p. 154, pl. 3, fig. 3 (copy of Thiadens 1936, text-fig. 2).
- 2004 *Praebarrettia sparcilirata* (Whitfield); GRUBIĆ, p. 153, pl. 3, fig. 1 (drawing on Whitfield 1897).
- 2005 *Praebarrettia sparcilirata* (Whitfield); OVIEDO, p. 68, fig. 51.
- 2006 *Praebarrettia?* *sparcilirata* (Whitfield); SCHAFFHAUSER, p. 63, pl. 16, figs. 6, 7, 10.
- 2009 *Laluzia armini* GÖTZ AND MITCHELL, p. 63, pl. 16, figs. 6, 7, 10.

**Material.**—Three-hundred and fifty-one specimens: PUAB 0701 1–16, 18–24, 32; PUAB 0735 288–296; PUAB 0738 299–357; PUAB 0852 481–483; PUAB 0854 492–514; PUAB 0855 522–546, PUAB 81035–81090, 81111–81117, 81166–81210; IGM 9462–9463.

**Description.**—Two different morphotypes have been recognized, differing only in size of adult shells and thickness of the outer shell layer, inward folds comprised, all other characters being identical. The two morphotypes occur in different levels, separated by a thick very fine grainstone limestone bed. Smaller shells with thinner outer shell layer are accumulated in the lower beds. Many specimens are disarticulated right valves, with epibionts both internally and externally, or inner casts also with epibionts. Most left valves, of specimens preserving it, are eroded, thus mostly lacking the pore bearing shell layer which is only preserved in very few specimens. Larger shells with thicker outer shell layer are found in the upper beds. Most specimens are well preserved and with both valves articulated. Both morphotypes have low-wide conical juvenile shells while adult shells are nearly cylindrical. Maximum diameter is 50 mm, and the tallest specimen measures 70 mm, in the (smaller) first morphotype. Larger specimens among the (larger) second morphotype measure 90 mm in diameter and 150 mm in height, although specimens measuring 30 mm and 50 mm respectively are also found.

Transverse sections of right valves (Figs. 19, 20) reveal that the ligament ridge is the longest main in-fold and P2 is longer than

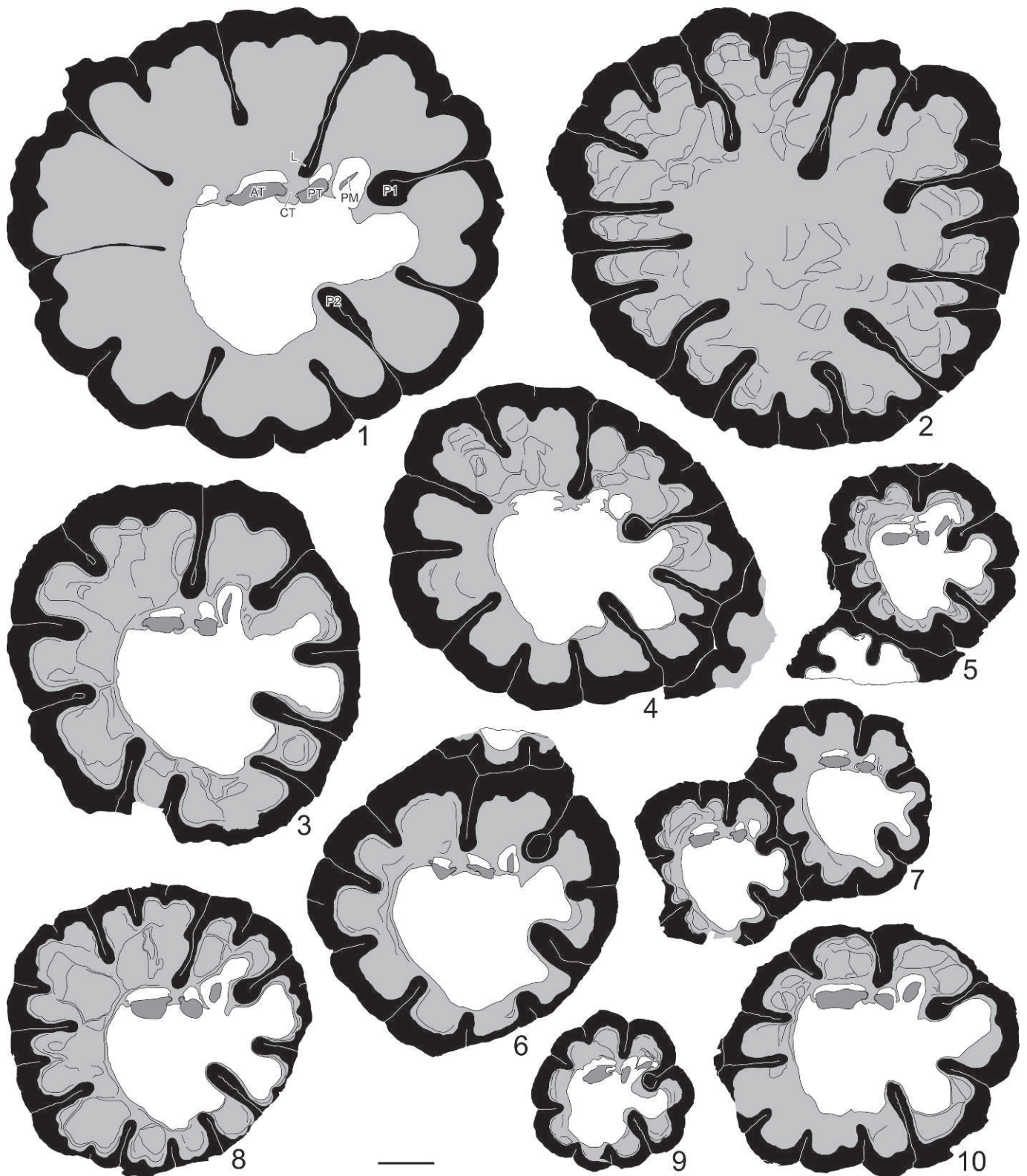


FIGURE 19—*Praebarretia sparcilirata* (Whitfield, 1897) sensu lato, larger morphotype, transverse sections of right valves close below the commissural plane, scale bar=10 mm: 1, PUAB 0701 2, Amoladeras; 2, PUAB 81116, Cuchilla Las Palomas; 3, PUAB 0701 4, Amoladeras; 4, PUAB 81111, Cuchilla Las Palomas; 5, PUAB 0854 504, Arroyo El Terrero; 6, PUAB 81112, Cuchilla Las Palomas; 7, IGM 9463, Arroyo El Terrero; 8, PUAB 81113, Cuchilla Las Palomas; 9, PUAB 0854 512, Arroyo El Terrero; 10, IGM 9462, Arroyo El Terrero.

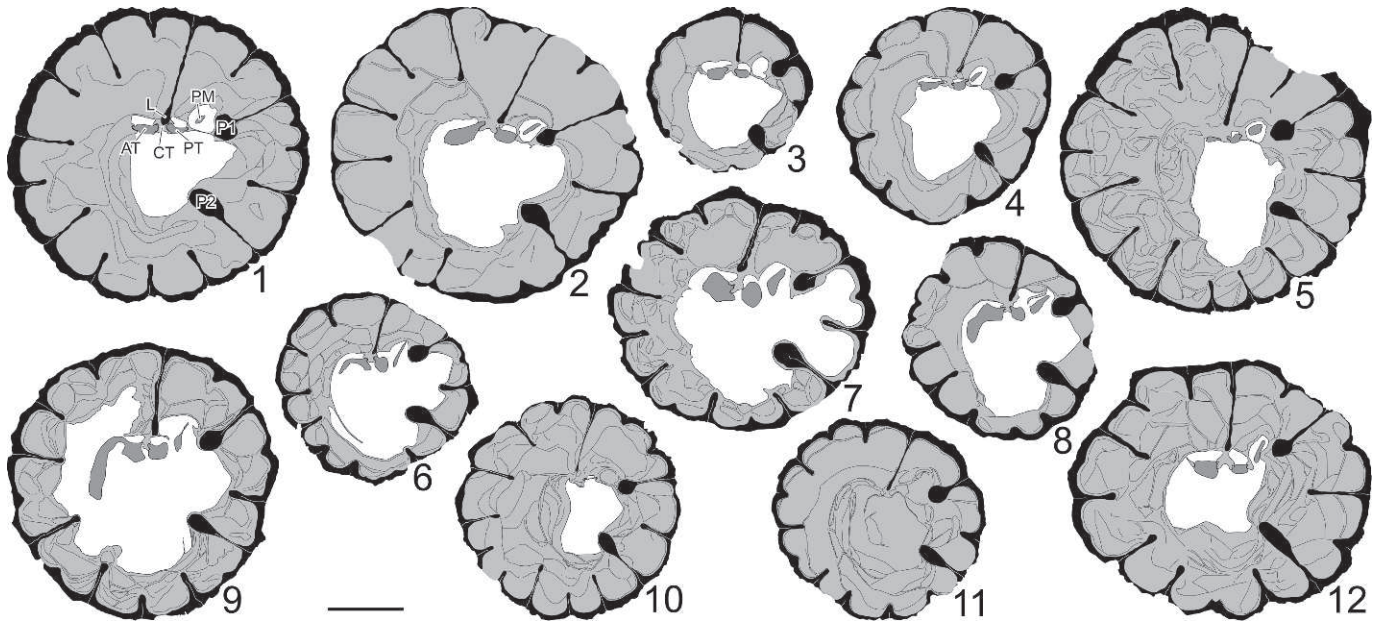


FIGURE 20—*Praebarrettia sparcilirata* (Whitfield, 1897) sensu lato, smaller morphotype, transverse sections of right valves close below the commissural plane, scale bar=10 mm: 1, PUAB 81048, Amoladeras; 2, PUAB 0738 299, Amoladeras; 3, PUAB 81197, Amoladeras; 4, PUAB 0738 305, Amoladeras; 5, PUAB 0855 533, Arroyo El Terrero; 6, PUAB 81070, Amoladeras; 7, PUAB 0738 307, Amoladeras; 8, PUAB 81082, Amoladeras; 9, PUAB 81050, Amoladeras; 10, PUAB 81200, Arroyo El Terrero; 11, PUAB 81080, Amoladeras; 12, PUAB 81057, Amoladeras.

P1. Both pillars end distally in a knob, circular in P1 and more or less slightly radially elongate in P2; this feature (pillars ending in a knob) is more accentuated in the smaller morphotype because in-folds are thinner. The angle L-P2 measures between  $100^{\circ}$  and  $140^{\circ}$ . The angle P1-P2 is equal or much wider than L-P1. Development of secondary in-folds: triangular, with parallel sides or with one constriction (rays of category 1 in van Dommelen, 1971) and in two cycles, increases with growth. At least, one first cycle secondary in-fold is developed between P1 and P2. The cardinal apparatus is located close to the distal end of the ligament ridge with CT centered and AT and PT at its anterior and posterior side, respectively. PM is aligned slightly dorsally from the AT-PT axis (dentition type B in van Dommelen, 1971).

The outer shell layer structure is non-compact, similarly as described above for *Caribbea muellerriedi* as evident from transverse, tangential and radial sections of the right valve (Figs. 21, 22). The growth lamellae are radially folded, up-folds are narrow and acute, with successive growth lamellae remaining in contact with each other, while down-folds are wide and low, with successive growth lamellae not in contact with each other. Although its outer shell layer is thinner, the same structure is observed in specimens of the smaller morphotype (Fig. 22). The inner shell layer is vesicular, both in the main body cavity and between the in-folds of the outer shell layer. Vesicles are arranged in one or more rows depending on the size of the specimen, that is, of the available space between rays.

The pore-canal system of the left valve is better observed on whitened specimens, compare Figure 23.2–22.6, 22.8 with Figure 23.1, 23.3, 23.7. Canals are radial in early growth stages and directed to each side of the outer shell layer in-folds (rays) of the right valve when these are developed, showing a herring-bone pattern similarly as in the European genus *Pironea*. Canal pattern is observed either by the convexity of the pore layer when this is well preserved (Fig. 23. 1, 23.2, 23.5) or directly by its bottom and lateral walls in eroded specimens (Fig. 23.3, 23.4, 23.6). Pores are simple polygonal (Fig. 23.2, 23.4, 23.6), although they may seem ‘subdivided’ or ‘denticulate’ in specimens with its

pore layer partially eroded (Fig. 23.5). The inner shell layer of the LV is non canalculated and projects inwards between the outer shell layer in-folds of the RV. These inward projections are indicated as radial furrows in inner casts.

**Occurrence.**—‘Amoladeras’, ‘Cuchilla Las Palomas’, ‘Arroyo Los Terrerillos’, ‘Arroyo El Terrero’. Lower Member of the Cárdenas Formation, in the *Durania ojanchalensis* Zone. *Praebarrettia* is known from Jamaica, Cuba, Puerto Rico, Northern Peru, and Mexico.

**Remarks.**—The generic name *Gloria* was proposed by Grubić (2004) for multiple-fold hippuritids with: 1) up to two cycles of secondary in-folds (rays), second cycle ones being poorly developed; 2) capillary structure of the outer shell layer (a misinterpretation of the non-compact structure described above); 3) L-P2 angle about one-third of the shell circumference; and 4) L-(AT-PT axis) angle higher than  $100^{\circ}$ . The genus included those American species originally ascribed either to *Pironea* or *Praebarrettia*, like *P. corrali* Palmer, 1933, *P. peruviana* Gerth, 1928, and *P. cf. peruviana* of Vermunt (1937). Grubić’s genus was erected to distinguish these forms from “typical” *Praebarrettia* but the generic name was not available being preoccupied by *Gloria* Barrande, 1881, synonym of *Slava*, Barrande, 1881, a praecardioid bivalve genus, and by *Gloria* Egorova and Savitsky, 1968, replaced by *Gloriagloria* Jell in Jell and Adrain, 2002, a trilobite genus.

Götz and Mitchell (2009) proposed the generic name *Laluzia* (type species *L. armini*) for specimens of the smaller morphotype described above, but did not mention, Grubić’s work. Their diagnosis and description of the genus and type species are incomplete and contain misinterpretations, because they are limited to small specimens and only eroded shells or inner casts were used in the description of the left valve characters. The outer shell layer structure of the RV is figured in a transverse section but neither interpreted nor mentioned in the diagnosis. No other known species were considered to belong to this genus. In case this genus is considered necessary, and we do not think so, *Laluzia* should formally become a replacement generic name for *Gloria* Grubić, 2004. The species *P. corrali* Palmer, 1933, *P.*

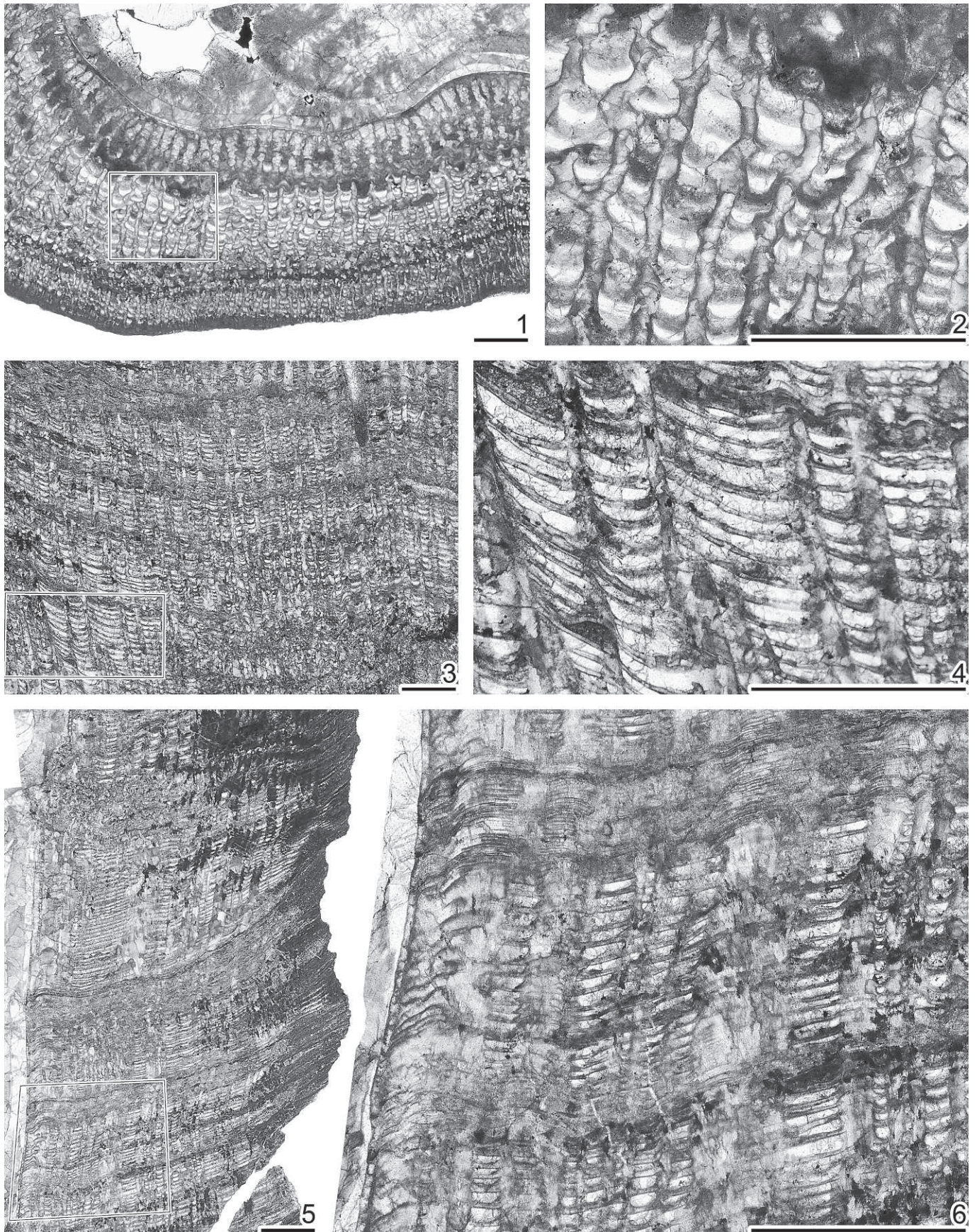


FIGURE 21—*Praebarrettia sparcilirata* (Whitfield, 1897) sensu lato, larger morphotype, thin sections of outer shell layer of right valves, enlarged areas are indicated, scale bars=1 mm: 1, 2, PUAB 0854 504, Arroyo El Terrero, transverse section; 3, 4, PUAB 81114, Cuchilla Las Palomas, tangential section; 5, 6, PUAB 81114, Cuchilla Las Palomas, radial section, inner margin at left.

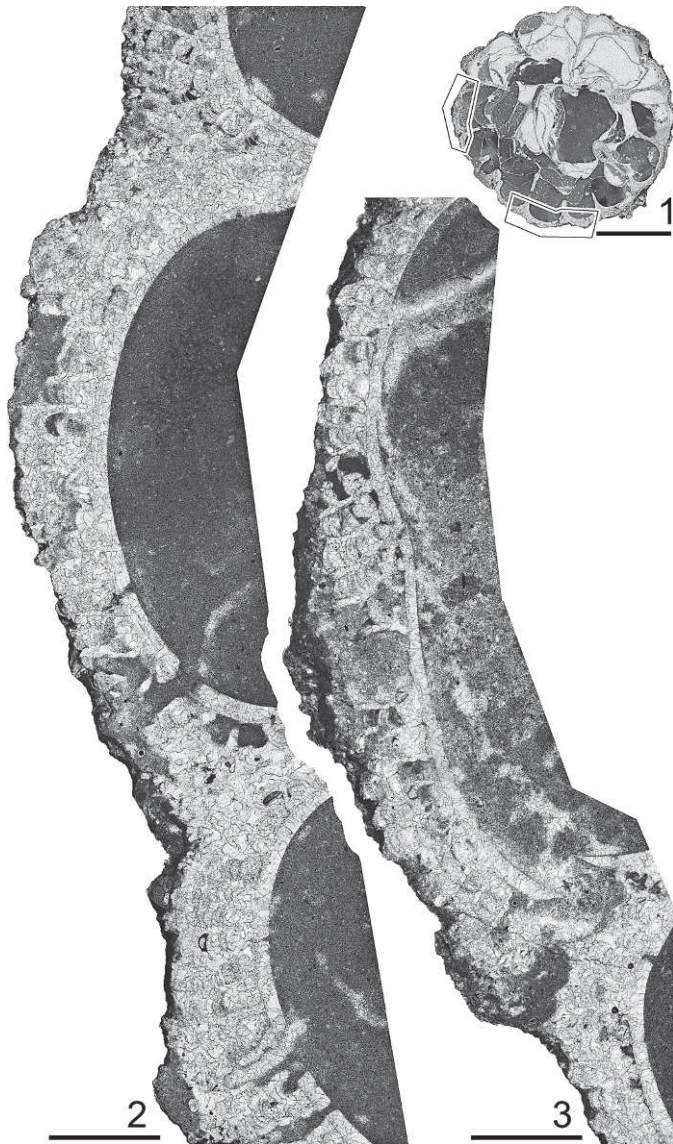


FIGURE 22—*Praebarrettia sparcilirata* (Whitfield, 1897) sensu lato, smaller morphotype, thin sections of right valve's outer shell layer, enlarged areas are indicated, PUAB 81200, Arroyo El Terrero, scale bars=10 mm in 1 and 1 mm in 2, 3.

*peruviana* Gerth, 1928, and *P. cf. peruviana* of Vermunt (1937), indicated by Grubić (2004) to correspond to this genus, are insufficiently known at present to be unquestionably considered senior synonyms of *L. armini*.

Based on sedimentological analysis, Götz and Mitchell (2009) presented this species as adapted to a low energy, relatively deep, nutrient-rich, with low-light intensity, soft-bottom environment. The dense accumulation of shells, partially eroded, disarticulated, and colonized by epibionts both internally and externally, in our opinion, suggests that the rudists inhabited a shallow bottom with, at least sporadic, moderate energy, where their shells were partly abraded, and later transported (turbiditic currents?) to a deeper environment. All specimens are small, developing an extremely thin outer shell layer and sparse vesicular inner shell layer; this could indicate growing in stress conditions.

Due to an excellent preservation of some specimens, the present description of the *Praebarrettia* from Cárdenas, including outer shell layer structure and in-folds of the RV, pattern of the

pore-canal system of the LV, myo-cardinal apparatus, and inner shell layer structure, as well as ontogenetic and eco-phenotypic variability, is by far the most complete of the genus. In our opinion, main characters as: 1) outer shell layer structure of the RV; 2) pore-canal system of the left valve; and 3) myo-cardinal apparatus, do not differ significantly from those of other *Praebarrettia* species, as far as they are known. Consequently, we think non sense and inopportune to split *Praebarrettia* into a number of genera.

Moreover, the abundance in literature of *Praebarrettia* species: *P. corrali*, *P. macgillavryi*, *P. peruviana*, *P. porosa*, *P. sparcilirata*, *P. sparcilirata albeari*, *P. sparcilirata cubensis*, *P. thiadensi*, *P. torrei*, *L. armini*, and diverse *Praebarrettia* sp., some of them only known by a single poorly informative, more or less transverse section of the RV does not help much to understand the genus.

Consequently, we include our specimens in *Praebarrettia sparcilirata* (Whitfield, 1897) sensu lato hoping that further research based on better preserved material may definitively clear up the issue of the distinction of species within *Praebarrettia*. Nevertheless, the existence of different species within *Praebarrettia* is not excluded.

Family PLAGIOPTYCHIDAE Douvillé, 1888

Genus CORALLIOCHAMA White, 1885

CORALLIOCHAMA GBOEHMI Böse, 1906

Figure 24.1–24.7

- 1906 *Coralliochama G.Boehmi* BÖSE, p. 54, pl. 6, figs. 4, 5, pl. 9, fig. 5, pl. 10, fig. 1, pl. 11, fig. 2, pl. 12, fig. 1, pl. 13, figs. 1, 9, pl. 14, figs. 5, 6.
- non1927 *Coralliochama g.boehmi* BÖSE; BÖSE AND CAVINS, p. 73 (= *Coralliochama* n. sp. after Müllerried [1931])
- 1932 *Coralliochama gboehmi* BÖSE; MÜLLERRIED, p. 175.
- 1936 *Coralliochama gboehmi* BÖSE; MUIR, p. 72.
- 1937 *Coralliochama gboehmi* BÖSE; MACGILLAVRY, p. 157.
- 1968 *Coralliochama gboehmi* BÖSE; MYERS, p. 41, pl. 3, figs. 1–3.
- 1971 *Plagioptychus agariciformis* ALENCASTER, p. 28, pl. 3, fig. 5, pl. 4, fig. 1, pl. 17, figs. 1, 2.
- 1975 *Coralliochama gboehmi* BÖSE; MARINCOVICH, p. 212.
- 1998 *Coralliochama gboehmi* BÖSE; GARCÍA-BARRERA ET AL., p. 128, pl. 4, figs. 1–5.
- 2005 *Coralliochama gboehmi* BÖSE; OVIEDO, p. 56, figs. 41, 42.
- 2006 *Coralliochama gboehmi* BÖSE; SCHAFHAUSER, p. 57, pl. 13, figs. 1, 2.

*Material*.—Twenty-four specimens: PUAB 0718 229, 230; PUAB 0719 236–237, 246; PUAB 0720 258; PUAB 0733 278, 279; PUAB 0734 286, 287; PUAB 0856 547–558; PUAB 81161, 81162.

*Description*.—Plagioptychid of moderate size. Larger specimens collected measure 110 mm of maximal diameter, measured at the anterior-posterior axis, and are 150 mm high. The right valve is conical, much higher at the ventral than at the dorsal side, and slightly twisted at the first growth stages. The outer shell layer has a maximum thickness of 5 mm and the inner shell layer is finely canaliculated; canals are close and regularly tabulated, producing a fine polygonal cellular structure. The left valve is convex, with a prominent coiled prosogyrous umbo which extends below the commissural plane (Fig. 24.1, 24.2). The outer shell layer is very thin, maximum thickness is less than 1 mm. The inner shell layer presents a marginal row, 12 mm wide at maximum, of narrow and long pyriform canals. Canal walls bifurcate three times, 14 canals of the second cycle are measured



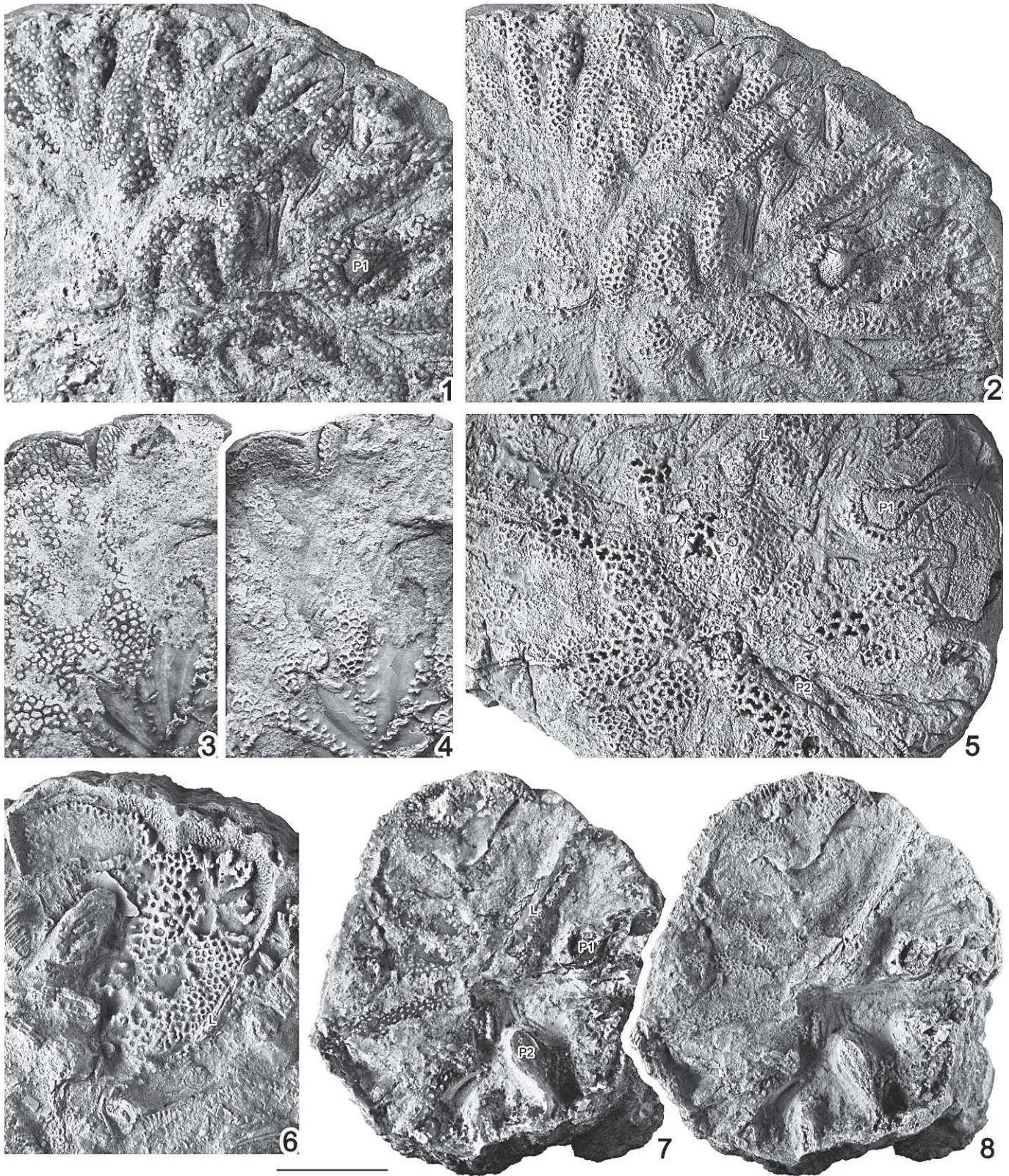


FIGURE 23—*Praebarrettia sparcilirata* (Whitfield, 1897) sensu lato, larger morphotype (1–6), smaller morphotype (7, 8), pore-canal system of outer shell layer of right valves, scale bar=10 mm: 1, 2, PUAB 0854 493, Arroyo El Terrero, detail of the area around the ligament ridge and first pillar, natural and whitened, respectively; 3, 4, PUAB 0701 13, Amoladeras, erosion of pores layer makes visible the base of canals at bottom right, natural and whitened, respectively; 5, PUAB 0854 505, Arroyo El Terrero, detail of the area around both pillars; 6, PUAB 0701 4, Amoladeras, detail at the marginal area; 7, 8, PUAB 81209, Arroyo El Terrero, natural and whitened, respectively.

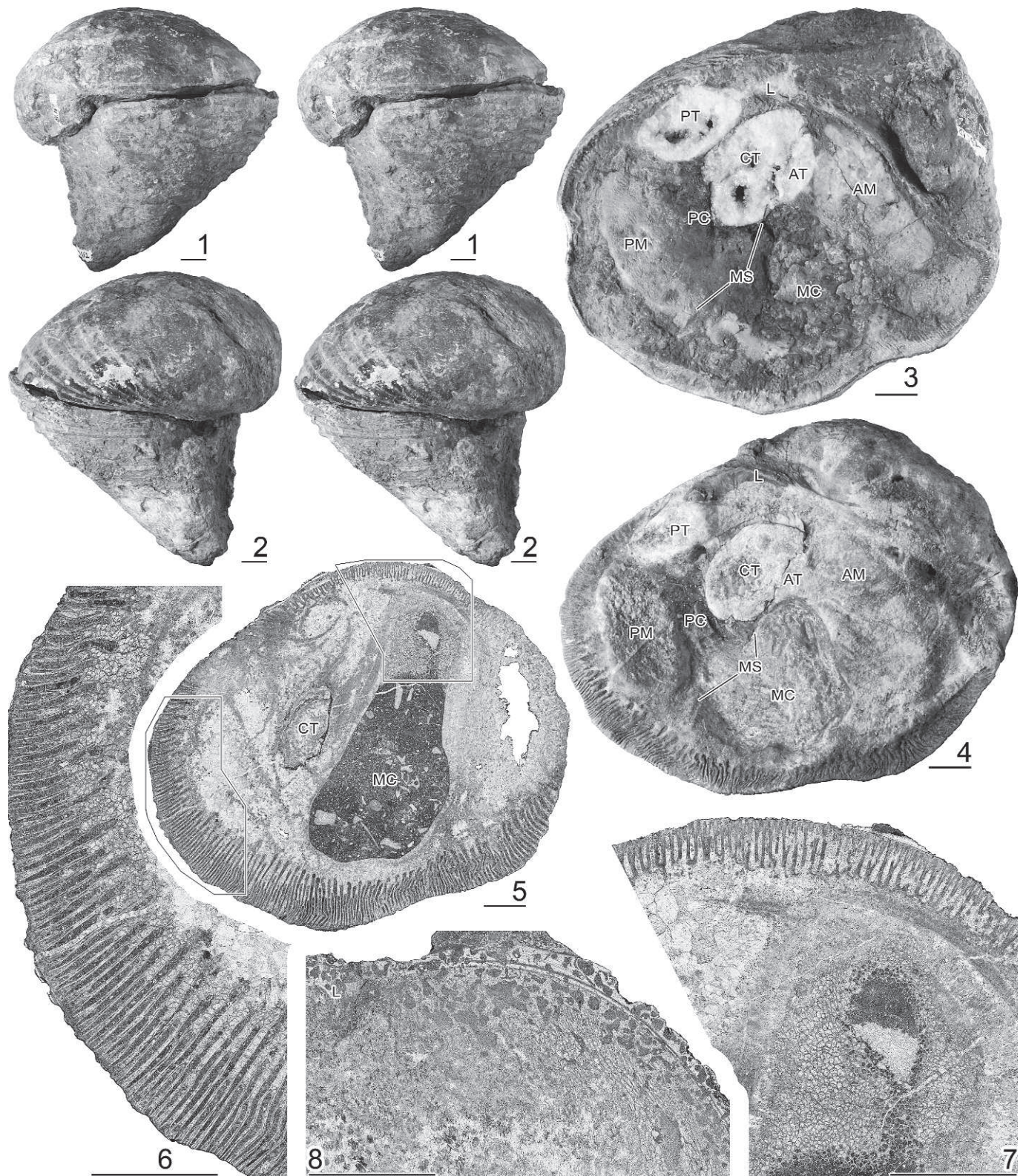


FIGURE 24—*Coralliochama gboehmi* Böse, 1906, scale bars=10 mm: 1–3, 8, PUAB 81162, Arroyo La Atarjea; 4–7, PUAB 0856 547, Cárdenas 3; 1, 2, stereo pairs of a bivalve specimen, anterior and posterior view, respectively; 3, 4, inner view of left valve, broken central tooth of right valve located in its socket; 5, transverse section (peel) of left valve, adapical view, areas amplified in following figures are indicated; 6, detail of marginal canals at posterior side; 7, detail of marginal canals and innermost canals at dorsal side; 8, transverse section (peel) of right valve at dorsal side.

in 10 mm. Canals mainly develop at the anterior, ventral, and posterior shell sides. Inner part of the LV is finely canaliculated, as in the RV (Fig. 24.6–24.8). Coarse growth lines are evident at the outer surface of both valves (Fig. 24.1, 24.2), as well as a ligament furrow along the RV. The myo-cardinal apparatus arrangement is like in other plagioptychids (Fig. 24.3–24.5). The central tooth is large and crescent-shaped, posterior tooth is located near the posterior-dorsal margin, and anterior tooth is smaller, located close to the concave anterior side of CT and continuing at its ventral margin as a central septum which reaches the marginal row of pyriform canals and forms a small posterior cavity enlarging ventrally the central socket. The posterior myophore of the LV is a large platform inclined inwards, with its outer margin invading the RV below the commissural margin. The ligament is opisthodontic, forming a short ligament ridge located behind the dorsal margin of PT.

**Occurrence.**—‘Cárdenas 2’, ‘Cárdenas 3’, ‘Arroyo La Atarjea’. Upper Member of the Cárdenas Formation, in the upper part of the *Arctostrea aguilerae* and in the *Tampsia floriformis* zones.

**Remarks.**—External and internal shell characters of *C. gbohemi* were already exhaustively described and figured by Böse (1906), who also described the main differences with *C. orcuti*, the type species of the genus. Böse reported specimens up to 200 mm high.

Genus MITROCAPRINA Böhm, 1895  
MITROCAPRINA TSCHOPI (Palmer, 1933)  
Figure 25

1933 *Plagioptychus tschoppi* PALMER, p. 103, pl. 10, figs. 1–3.

1936 Caprinid fragment; THIADENS, p. 1011, text-fig. 3.13.

1937 *Mitrocaprina tschoppi* (Palmer); MACGILLAVRY, p. 158, pl. 5, fig. 7, pl. 7, figs. 1, 4, 5, 7, 8, pl. 8, figs. 4, 7.

1937 *Mitrocaprina tschoppi* (Palmer); THIADENS, p. 43.

non1975 *Plagioptychus tschoppi* Palmer; LUPU, p. 246 (= *Plagioptychus* sp. indet.)

2005 *Mitrocaprina tschoppi* (Palmer); OVIEDO, p. 60, fig. 44.

2006 *Mitrocaprina* cf. *tschoppi* Palmer; SCHAFHAUSER, p. 56, pl. 13, figs. 3, 4.

**Material.**—Ten specimens: PUAB 0701 25, 26; PUAB 0719 238–245, 247; PUAB 0735 297.

**Description.**—Plagioptychid smaller than the above described species. Larger specimens collected measure 64 mm of maximal diameter, measured at the anterior-posterior axis, and are 110 mm high. The right valve is loosely coiled; irregular form in some specimens suggests growing attached to any irregular substrate. The prominent umbo of left valve projects below the commissural plane. Besides the typical characters of *Mitrocaprina*, its most characteristic trait is the pattern of the marginal canals in the inner shell layer of the left valve (Fig. 25). Canals are polygonal, more or less radially elongate, and arranged alternated in five rows. Width of canals decreases from the inner to the outer row, allowing the number of canals to increase from five to fifteen canals per 10 mm, and resulting in a big difference in the width of the three inner rows and that of the two outer ones.

**Occurrence.**—‘Amoladeras’, ‘Cuchilla Las Palomas’, ‘Cárdenas 2’. Lower and Upper members of the Cárdenas Formation, in the *Durania ojanthalensis* and in the upper part of the *Arctostrea aguilerae* zones. The species was only reported from Cuba.

**Remarks.**—The characters of the species, first reported by Palmer (1933), were completed by MacGillavry (1937), who also stressed the differences with the European *Mitrocaprina* species.

DISCUSSION

Rudists in the Cárdenas Formation are abundant and a number of specimens have excellent preservation, allowing observation of both the internal and external shell characters and their ontogenetic and eco-phenotypic variability, thus, enhancing



FIGURE 25—*Mitrocaprina tschoppi* (Palmer, 1933), PUAB 0719 239, Cárdenas 2, transverse section (peel) of left valve, adapical view, scale bar=10 mm.

and/or completing previous descriptions. The Cárdenas Formation exhibits a continuously exposed sequence around Cárdenas, allowing precise stratigraphic location of all successive fossil localities and their rudist associations. Available chronostratigraphic data indicate an age ranging from early to early late Maastrichtian.

**Stratigraphic importance.**—The succession of rudist faunas in the Mexican Upper Cretaceous was first studied by Oviedo et al. (2007) who distinguished five successive stratigraphic levels with hippuritids, occurring in carbonate platform intervals that are delimited by unconformities, deeper siliciclastic intervals, or tectonic boundaries: *Hippurites resectus*—Upper Turonian; *Vaccinites macgillavryi*—Santonian; *Vaccinites, Barrettia*, and *Torreites*—Lower-Middle Campanian; *Praebarrettia sparcilirata*—Maastrichtian; *Hippurites muellerriedi*—Maastrichtian. Subsequently, Pons et al. (2010) detailed that the rudist fauna of the third hippuritid level, occurring in the ‘Temazcal limestones’, is composed by the radiolitids *Potosites tristanatorresi* Alencaster and Pons and *Radiolites acutocostata* (Adkins), the hippuritids *Barrettia* cf. *ruseae* Chubb, *Torreites sanchezi* (Douvillé) and *Vaccinites vermunti* Mac Gillavry, plagioptychids and antilocaprinids, and dated as early Campanian.

The rudist fauna of the Cárdenas Formation described herein corresponds to the fourth and fifth levels of Oviedo et al. (2007) and provides a more accurate dating of both levels. The rudist fauna of the former is composed by the radiolitids *Huasteca ojanthalensis* (Myers) and *Trechmannites rudissimus* (Trechmann), the hippuritid *Praebarrettia sparcilirata* (Whitfield) sensu lato, and the plagioptychid *Mitrocaprina tschoppi* (Palmer); it is dated as early Maastrichtian. The rudist fauna of the latter is composed by the radiolitids *Biradiolites aguilerae* Böse, *B. cardenasensis* Böse, *Tampsia floriformis* Myers, and *Trechmannites rudissimus* (Trechmann), the hippuritid *Caribbea muellerriedi* (Vermunt), and the plagioptychids *Coralliochama gbohemi* Böse and *Mitrocaprina tschoppi* (Palmer); it is dated as early late

Maastrichtian. Two species occur in both rudist levels: *Trechmannites rudissimus* and *Mitrocaprina tschoppi*.

**Biogeographic relations.**—All rudist species described from the Cárdenas Formation in central Mexico are known to also occur in Chiapas, in southern Mexico, and in the Caribbean islands, thus corresponding to the Caribbean Biogeographic Province. This confirms that this province extends during the Maastrichtian further north than previously thought; its rudists occupied, besides the narrow shallow platforms surrounding the Yucatan Basin, the wide shallow margins surrounding the Gulf of Mexico Basin as already indicated by Pons et al. (2010) for the early Campanian.

**Systematics and evolutionary context.**—The original generic attribution of *Biradiolites aguilerae* Böse, 1906 and *Biradiolites cardenasensis* Böse, 1906 is confirmed, as well as the fact that *B. potosianus* Böse, 1906 and *B. barretti* Trechmann, 1924 are junior synonyms of the latter. *Biradiolites aguilerae* is a small and very simple *Biradiolites* that, like similar American representatives of the genus, has uncertain affinities. *Biradiolites cardenasensis* is clearly distinguished from *B. cancellatus*, although some specimens of the former species from Jamaica were attributed to *B. cancellatus* in literature. *Biradiolites cardenasensis* shells show close similarities with the European *B. acuticostatus* and related species, but it is still not clear if these similarities correspond to phylogenetic relationships or are only convergent traits.

The new genus *Huasteca*, type species *Durania ojanthalensis* Myers, 1968, differs from *Durania* by its radial structures, evident at the outer shell surface as smooth radial bands, and by its very short myophores with striated outer margin. Both genera have normal cellular outer shell layer structure and lack a ligament ridge. Several American radiolitid species with normal cellular outer shell layer structure and without a ligament ridge have been ascribed to genus *Durania* without taking into account other important shell characters. Similarly, other species having a ligament ridge were attributed to genus *Sauvagesia*. As a result, the stratigraphic and paleogeographic distribution of these genera might have been overestimated, with *Durania* ranging from the Turonian to the Maastrichtian, *Sauvagesia* from the Albian to the Maastrichtian, and both genera having a worldwide distribution.

*Tampsia floriformis* Myers, 1968 and *Trechmannites rudissimus* (Trechmann, 1924), belonging to different genera, share the same type of outer shell layer structure: normal cellular and/or discontinuous cellular. Discontinuous cellular structure has been observed only in American radiolitids. Both species also share with *Huasteca ojanthalensis* a similar myocardial apparatus, having very short myophores with striated outer margin.

The herein provided description of the shell characters of *Praebarrettia* from the Cárdenas Formation is by far the most complete among all available *Praebarrettia* descriptions. Nevertheless, it is placed in *P. sparcilirata* (Whitfield, 1897) sensu lato until the issue of *Praebarrettia* species distinction is cleared up. Most of the *Praebarrettia* species in literature are only known by a single poorly informative, more or less transverse section of the RV; further research is needed before confirming these species although the existence of different species within *Praebarrettia* is not formerly excluded.

The hippuritid genera *Caribbea* and *Praebarrettia*, being completely different and presumably not related, share the same type of outer shell layer structure. This is a modification of the current compact structure of hippuritids, in which the successive radially folded growth lamellae are in contact with each other in up-folds, while leaving voids in between them in down-folds, resulting in a non-compact outer shell layer structure. This has been observed only in American hippuritids.

Two species ascribed to different genera of plagioptychids are described and figured, *Coralliochama gbohemi* Böse, 1906 and *Mitrocaprina tschoppi* (Palmer, 1933). The relationships among plagioptychids, both European and American, are still not well understood.

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## APPENDIX—Equivalences among published PUAB and IGM register numbers.

Register PUAB	Register IGM	Register PUAB	Register IGM
<i>Biradiolites cardenasensis</i> Böse, 1906		<i>Tampsia floriformis</i> Myers, 1968	
PUAB 0856 563	IGM 9437	PUAB 0720 252	IGM 9456
PUAB 0856 564	IGM 9438	PUAB 0856 597	IGM 9458
PUAB 0856 567	IGM 9439	PUAB 0856 599	IGM 9459
PUAB 0856 570	IGM 9440	PUAB 0856 603	IGM 9460
PUAB 0856 574	IGM 9441	PUAB 0856 s/n2	IGM 9461
PUAB 0856 575	IGM 9442	PUAB 0856 596	IGM 9539
<i>Huasteca ojanthalensis</i> (Myers, 1968)		<i>Trechmannites rudissimus</i> (Trechmann, 1924)	
PUAB 0701 41	IGM 9451	PUAB 0701 33	IGM 9443
PUAB 0701 43	IGM 9452	PUAB 0701 56	IGM 9444
PUAB 0701 46	IGM 9453	PUAB 0701 60	IGM 9445
PUAB 0854 485	IGM 9454	PUAB 0701 61	IGM 9446
PUAB 0854 487	IGM 9455	PUAB 0701 63	IGM 9447
<i>Praebarrettia sparcilirata</i> (Whitfield, 1897)		PUAB 0701 72	IGM 9448
PUAB 0852 482	IGM 9462	PUAB 0701 74	IGM 9449
PUAB 0854 508	IGM 9463	PUAB 0701 82	IGM 9450

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