

# A new rudist bivalve, *Polytorreites* gen. nov., from the Campanian of Puerto Rico demonstrating iterative evolution of American multiple-ray Hippuritidae

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**ABSTRACT.** The new hippuritid rudist *Polytorreites sohli* gen nov., sp. nov. is described from the Miramar Formation of Puerto Rico and is considered to be derived from the Cuevas Limestone which dates to around the early-middle Campanian boundary in the North American tri-part division of the Campanian Stage. The genus is particularly significant because it shows the presence of multiple rays in the *Torreites* branch of the Hippuritidae, something that has never been shown before. The presence of at least four independent originations of multiple infolds in the Hippuritidae (the New World *Laluzia* and *Praebarrettia*; the New World *Barrettia*, *Whitfieldiella* and *Parastroma*; the Old World *Pironaea*; and the New World *Polytorreites*) demonstrates that the development of multiple rays is of functional significance and should not be used as a character to define subfamilies within the Hippuritidae.

**Key words:** *Polytorreites*, Hippuritidae, Puerto Rico, Rudist Bivalves, Campanian.

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## 1. INTRODUCTION

Chubb (1971) erected the subfamily Barrettiinae for the American multiple-fold hippuritids, thus implying a monophyletic grouping, and included within it *Barrettia* Woodward, *Praebarrettia* Trechmann and *Parastroma* Douvillé, but excluded the Old World *Pironaea* Meneghini, which while having developed multiple rays had the three pillars close together. In contrast, van Dommelen (1971, p. 64) considered that the multiple-fold hippuritids of the Americas which had pallial canals in the inner layer of their left valve (*Barrettia* and *Parastroma*), and those that lacked pallial canals (*Praebarrettia*), were separate radiations from different *Pseudovaccinites* ancestors. Grublic (2004) went further and redefined the family Barrettiinae {sic} according to a misunderstanding of the microstructure of the outer shell layer in the right valve (see Mitchell, 2010), and included not only the American multiple-ray hippuritids, but also forms with three pillars that had previously been referred to *Hippurites* Lamarck, which were placed in the new genus *Caribbea* Grubić. There are therefore divergent views on whether the American multiple-fold hippuritids represent a single monophyletic radiation or are polyphyletic.

In this paper we describe a new hippuritid genus, *Polytorreites* gen. nov., from the Campanian of Puerto Rico, and discuss how this form fits into American hippuritid evolution.

## 2. SYSTEMATIC PALEONTOLOGY

### Family Hippuritidae Gray, 1848

#### Genus *Polytorreites* gen. nov.

**Type species.** *Polytorreites sohli* sp. nov. from the Miramar Formation (reworked from the Campanian), Coamo Quadrangle, Puerto Rico.

**Origin of name.** From “Poly” (=many) in combination with the genus “*Torreites*”.

**Diagnosis.** A hippuritid bivalve with multiple infoldings in the RV, a long ligamentary infold, a medial zigzag pattern along the infolds, and cortical infolds in the outer shell layer. The left valve has slots indented from the margin corresponding to the infolds and lacks a pore system. The teeth (anterior tooth, *at*, and posterior tooth, *pt*) and posterior myophore (*pm*) form a line, the axis of which is at an angle of 120° to the ligamentary infold. The anterior myophore (*am*) is set approximately perpendicular to the dental axis.

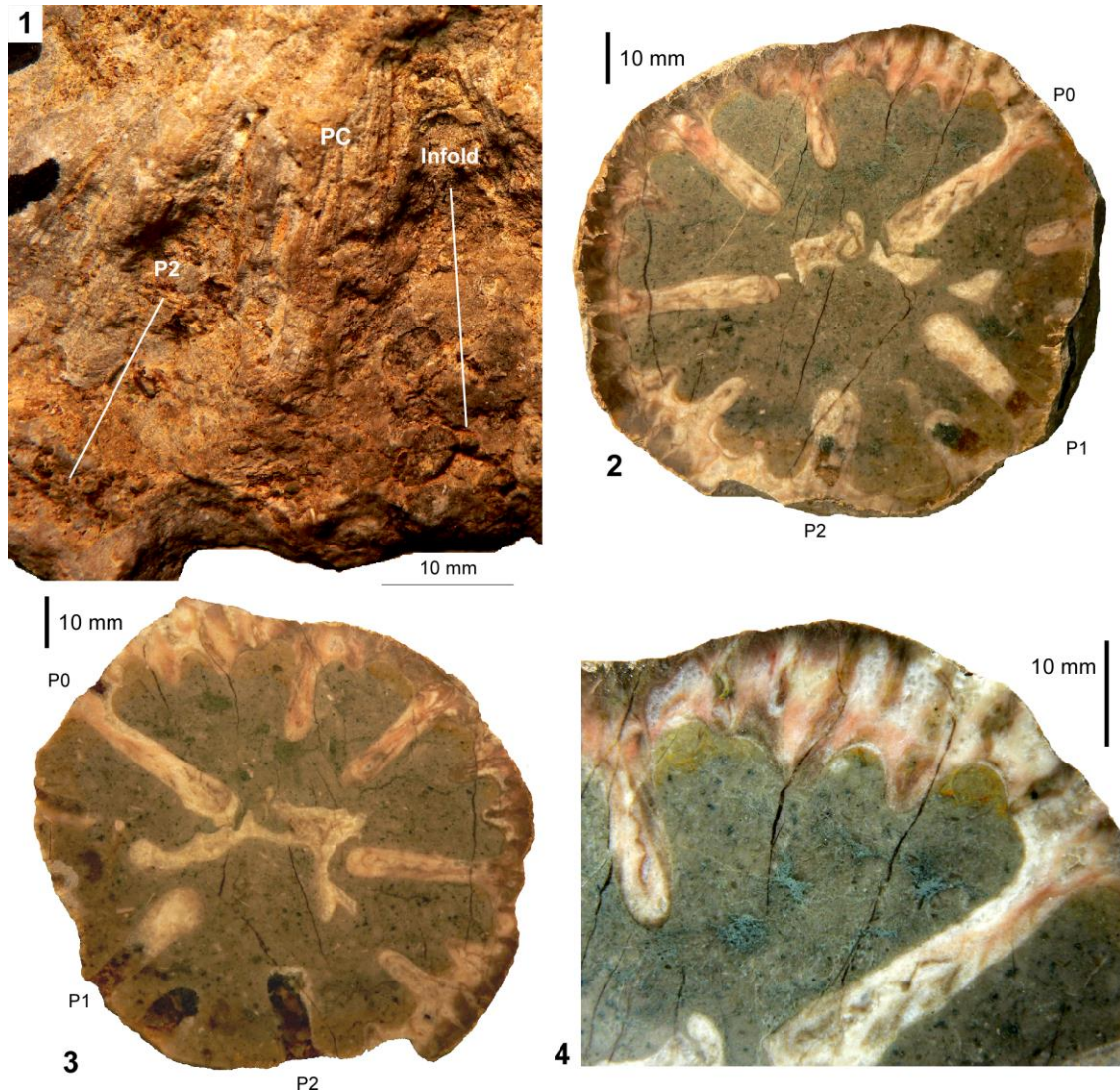


Figure 1. *Polytorreites sohli* Mitchell & Skelton 2010, holotype (USNM 547508), Miramar Formation, Puerto Rico. 1, LV showing infolds (including P2) and pallial canals (PC). 2, RV sectioned about 15 mm below commissure, adapical view, showing primary and secondary infolds and myocardinal elements (*pt*, *at* and *pm*). 3, RV, sectioned about 10 mm below commissure, abapical view showing primary and secondary infolds and myocardinal ‘arc’ with a few supporting buttresses. 4, detail of RV looking adapically showing pillars with zigzag patterns and details of the cortical folds in the outer shell layer. P0, ligamental infold; P1, first pillar; P2, second pillar.

*Polytorreites sohli* gen. nov. sp. nov.

#### Figures 1-2

**Origin of name.** Named in honour of Norman Sohl for his work on the Cretaceous rocks of the Caribbean region.

**Diagnosis.** See genus description.

**Holotype.** Smithsonian Institute number USNM 547508 (Mitchell and Skelton number CS31), from USGS field locality number 29323 (Norm Sohl field locality S-1400), Miramar Formation, Coamo Quadrangle, Puerto Rico.

**Description.** The holotype is an articulated specimen that has had its right valve (RV) transversely sectioned a short distance adapically from the commissure. The RV is fairly large, with a broadly circular commissure, and is conical in profile. The outer shell layer of the RV is thick (~10 mm), and composed of compact microstructure, with numerous small radially orientated cortical infolds. The exterior is worn but rounded costae are partially preserved in places, with furrows corresponding to the cortical infolds. P0, P1 and P2 are represented by prominent infolds: P0 is the longest; P1 is of intermediate length; and

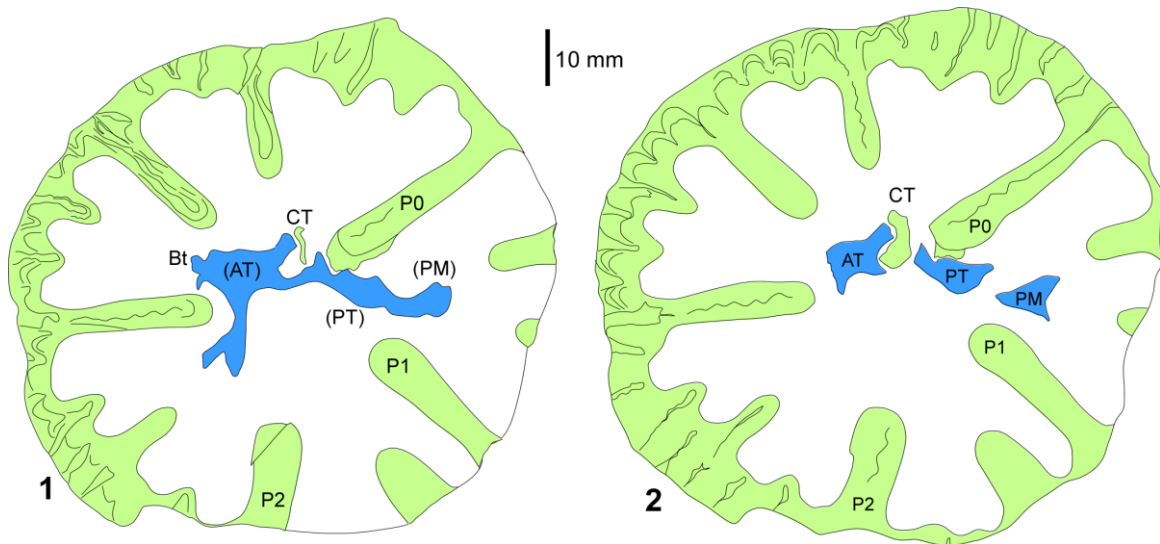


Figure 2. *Polytorreites sohli* Mitchell & Skelton 2010, holotype, Miramar Formation, Puerto Rico. Drawings of RV sections shown in Figure 1 both orientated looking apically with myocardinal elements and pillars identified. P0, P1, P2, pillars; PM, posterior myophore; AT, CT, PT, anterior, central and posterior teeth.

P2 (which is tentatively identified) is the shortest. The angles between them are  $P0-P1 = 83^\circ$  and  $P1$  to  $P2 = \sim 60^\circ$ . The tip of  $P1$  is gently swollen; whereas the tips of  $P0$  and  $P2$  are rounded. Two secondary infolds occur between  $P0$  and  $P1$ , one between  $P1$  and  $P2$ , and a further four longer secondary pillars between  $P2$  and  $P0$ . A few orimal infolds occur between the primary ( $P0$ ,  $P1$ ,  $P2$ ) and secondary infolds. A zigzag pattern is visible in section along the centres of the longer infolds. The inner shell layer is thin, as the transverse cross section cuts through the abapical portion of the body cavity.

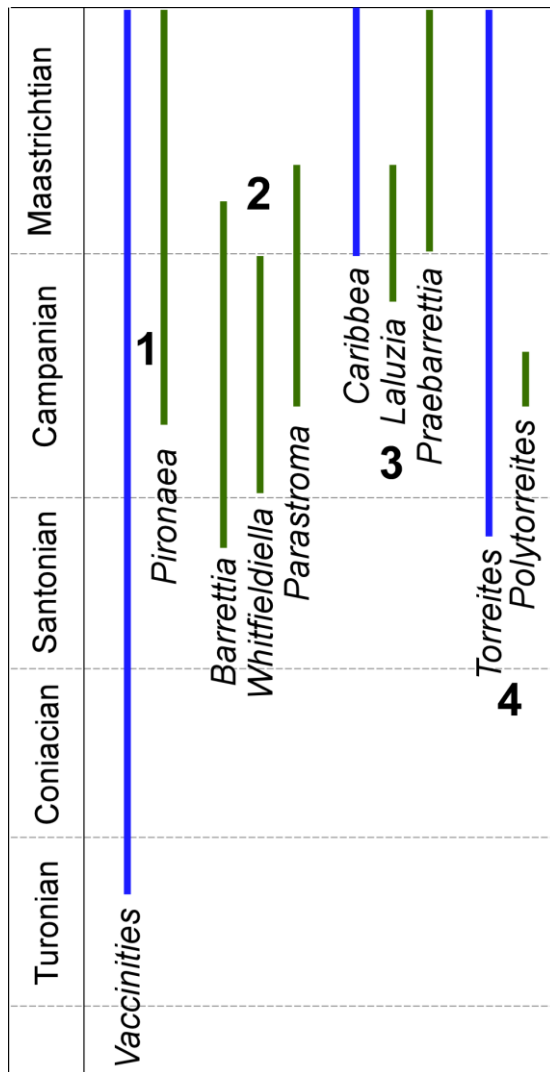
The left valve (*LV*) is low and conical, and its outer layer has been weathered away. The inner layer contains thin radiating pallial canals with diameters of about 0.5 mm. Slit-like grooves penetrate the *LV* from its margin and correspond to the infoldings seen in the *RV*. The myocardinal arrangement is visible in cross section. The central tooth (*ct*) is situated at the end of the ligamental infold. The *pt* and *at* are about the same size; and the line joining the teeth intersects the long axis of the ligamental at an angle of  $120^\circ$ . The *pm* is situated in line with the *pt* and *at*; it is narrow anteriorly and broader towards the posterior; it may be forked, but the cut does not show the ventral prong. The *am* is thin and concave towards the anterior side.

**Geographic and Stratigraphic Distribution.** Only the holotype is known. It came from USGS field locality number 29323 (Norm Sohl field number S-1400), Miramar Formation, Coamo Quadrangle, Puerto Rico. The Miramar Formation, together with

the Cuevas Limestone, has been considered a formation of the Jacaguas Group of Eocene age (Glover and Matson, 1967); alternatively, the Miramar Formation has been considered a fault breccia below the Cuevas Limestone slide block (Krushensky, 1978). The Miramar Formation contains ‘clasts’ of the Cuevas Limestone, in a red clay, slickensided gouge (Krushensky and Monroe, 1975; Krushensky, 1978). Norman Sohl’s locality S-1400 also yields: *Barrettia* sp. nov. cf. *B. monilifera* Woodward; and *Whitfieldiella* sp. nov. These rudists are characteristic of a level around the lower-middle Maastrichtian boundary (Mitchell, unpublished) in the North American tri-part division of the Campanian Stage.

**Discussion.** *Polytorreites* differs from *Torreites* in its possession of secondary pillars and in its expanded anterior shell margin. As in *Torreites*, *Polytorreites* has a compact outer shell layer in the *RV* which has cortical infoldings, and a zigzag structure in the centre of the rays, pallial canals in the free valve and a thin curved anterior myophore. In *Torreites sanchezi* (Douvillé), the angle between  $P0$  and  $P2$  ranges from  $75^\circ$  to  $126^\circ$  (Palmer, 1933; Mac Gillavry, 1937; Skelton and Wright, 1987) whereas in *Polytorreites* it is  $143^\circ$ . The possible function of multiple infoldings in *Polytorreites* could have been to achieve an elongation of the commissure to aid in feeding, as suggested for other multiple-ray hippuritids by Skelton (1976).

With only one specimen available, we should also consider the possibility that *Polytorreites* might



**Figure 3.** Stratigraphical distribution of multiple-fold hippuritids (green) and selected other hippuritids (blue), showing four (1-4) separate iterative radiations during the Upper Cretaceous. Radiation 1 is in the Old World, radiations 2-4 are in the New World.

be a tetralogical specimen. For instance, *Tetravaccinites* Bilotte, 1981, was established for a tetralogical specimen of *Vaccinities ultimus* (Plenicar, 2004). However, the holotype of *Polytorreites sohli* gen. nov., sp. nov., shows multiple additional pillars, not just one extra one, and would therefore seem to be valid.

### 3. AMERICAN HIPPURITID PHYLOGENY

*Polytorreites* gen. nov. is clearly a very distinct rudist bivalve of the American region. Its close morphological similarity to *Torreites*, particularly in its myocardial arrangement and the construction of its left valve, leaves little doubt that the former was derived from the latter. *Torreites* and *Polytorreites* both have pallial canals in the LV as does one branch of the American multiple-fold hippuritids (*Barrettia*, *Whitfieldiella* and *Parastroma*), but other features (the myocardial arrangements in these two groups and the lack of pores in the former, and presence in the latter) demonstrates that they are not closely related. It therefore seems that there are four separate radiations that resulted in multiple ray hippuritids: 1, *Pironea* (lower Campanian-upper Maastrichtian) developing from a *Vaccinities*-like ancestor in the Old World; 2, *Barrettia*, *Whitfieldiella* and *Parastroma* (upper Santonian-lower Maastrichtian) developing from a *?Pseudovaccinities*-like ancestor in the New World; 3, *Lalluzia* and *Praebarrettia* developing from *Caribbea* or a *Caribbea*-like hippuritid in the New World; and 4, *Polytorreites* developing from *Torreites* in the New World (**Figure 3**). The development of multiple rays was clearly of functional significance for the Hippuritidae (cf. Skelton, 1976), and should no longer be seen as a reliable character for the establishment of subfamilies within the Hippuritidae.

*Acknowledgements.* We would like to thank Jann Thompson and Brian Huber for arranging our visit to the Smithsonian in summer, 2009.

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*Accepted: 16<sup>th</sup> September 2013*

