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MEGAPOROMYA REYMENTI GEN. ET SP. NOV. (BIVALVIA, PHOLADOMYIDA) FROM THE UPPER TURONIAN (UPPER CRETACEOUS) OF THE SERGIPE BASIN, NORTH-EASTERN BRAZIL

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ABSTRACT – *Megaporomya*, a new genus of the bivalve family Poromyidae (order Pholadomyida), is erected and the type species *Megaporomya reymenti* gen. et sp. nov. described from the upper Turonian of the Cotinguiba Formation, Sergipe Basin, north-eastern Brazil. The main morphological features of the new genus are the large to very large shell, wide umbonal area, large posterior gape, strongly inflated valves, and faint, irregular commarginal ribs crossed by radial tubercles. The hinge of the right valve consists of one large, inverted, U-shaped cardinal tooth, one straight and narrow cardinal tooth and two unequal sockets. *M. reymenti* gen. et sp. nov. differs from other related species from the Cretaceous of Sergipe by its large size, surface ornamentation, valve inflation, and hinge features. The life position of *M. reymenti* gen. et sp. nov. is reconstructed on the basis of a functional interpretation of its morphology and by comparison with closely related Recent forms. *Megaporomya* gen. nov. was a semi-infaunal selective predator which probably fed on crustaceans and burrowed in soft sediments, extending slightly above the sediment-water interface. It detected its prey with the help of specialized tentacles surrounding the large inhalant siphon. The palaeoenvironmental setting of the Sergipe Basin during the late Turonian is interpreted on the basis of the associated fauna and facies.

Key words: bivalves, *Megaporomya reymenti* gen. et sp. nov., palaeoecology, Upper Cretaceous, Sergipe Basin, Brazil.

RESUMO – *Megaporomya* é um novo gênero da família Poromyidae (ordem Pholadomyida, Bivalvia) designado a partir da espécie-tipo *Megaporomya reymenti* gen. et sp. nov., descrita do Turoniano superior da Formação Cotinguiba da bacia de Sergipe, nordeste do Brasil. As principais características morfológicas do novo gênero são: concha de tamanho grande a muito grande, área umbonal ampla, abertura posterior grande, valvas fortemente infladas, costelas comarginais fracas e irregulares atravessadas por tubérculos radiais, e a presença na valva direita de um dente cardinal grande, invertido, em forma de U, um dente reto e delgado e duas fossetas desiguais. *M. reymenti* gen. et sp. nov. difere de outras espécies aparentadas do Cretáceo de Sergipe pelo seu tamanho, ornamentação, valvas muito infladas e características da charneira. O modo de vida de *M. reymenti* gen. et sp. nov. foi interpretado a partir da morfologia da concha e comparação com formas recentes. *Megaporomya* gen. nov. era um predador semi-infaunal seletivo, que provavelmente se alimentava de crustáceos e se enterrava em substratos moles, estendendo-se pouco acima da interface água-sedimento. Detectava suas presas com ajuda de tentáculos especializados, localizados ao redor do grande sifão inalante. O paleoambiente da bacia de Sergipe, durante o final do Turoniano, foi interpretado com base na fauna associada e facies sedimentar.

Palavras-chave: biválvios, *Megaporomya reymenti* gen. et sp. nov., paleoecologia, Cretáceo Superior, bacia de Sergipe, Brasil.

INTRODUCTION

The Cenomanian to lower Coniacian Cotinguiba Formation of the Sergipe Basin in north-eastern Brazil contains a rich macroinvertebrate fauna dominated by molluscs. Ammonites and bivalves are generally the most common and diverse groups. Koutsoukos & Bengtson (1993) pointed out a number of problems in establishing a macrofossil

zonation for the Sergipe Basin, which are mainly due to the discontinuous and small outcrops (normally only a few metres of section or less) in relation to the total thickness of the succession (well over 500 m). This, in combination with local shifts in strike and dip, makes stratigraphic positioning of individual specimens difficult.

The Cretaceous macrofauna of Sergipe was initially monographed by White (1887) and Maury (1925, 1937) and subsequently, particularly in the past decades, has been the subject of taxonomic and biostratigraphic revision. Bengtson (1983) pointed out that the ages of specimens given by the earlier workers are often uncertain because of imprecise locality indications. In the past decades, studies have been carried out on different groups of bivalves from the Cotinguiba Formation, such as inoceramids, oysters, pinnids and pectinids (*e.g*. Hessel, 1985, 1988; Seeling, 1999; Seeling & Bengtson, 1999, 2003a, b; Andrade *et al*., 2004; Andrade, 2005; Andrade & Santos, 2011). In particular, members of the order Pholadomyida are abundant and well-preserved, though as yet poorly investigated.

Bengtson (1983), Kauffman & Bengtson (1985), Hessel (1988), Smith & Bengtson (1991), Koutsoukos & Bengtson (1993), Seeling (1999), Seeling & Bengtson (1999), Andrade (2005) and Bengtson *et al.* (2005) contributed to establishing a biostratigraphic scheme for the Cenomanian-Coniacian interval of the basin on the basis of ammonites, inoceramid bivalves, and foraminifers. The most detailed biostratigraphic zonation is based on ammonites, which enable a subdivision of the succession into seven biozones.

The purposes of this paper are (i) to erect the new poromyid bivalve genus *Megaporomya* and to compare it with the morphologically closest genera of the family Poromyidae, (ii) to describe the new species *Megaporomya reymenti* from the upper Turonian of the Sergipe Basin, (iii) to reconstruct the growth position and autecology of *Megaporomya* gen. nov., and (4) to reconstruct the palaeoenvironmental setting of the Sergipe Basin during the late Turonian on the basis of facies relationships and associated faunal elements, such as inoceramids, pinnids, gastropods and echinoids.

GEOLOGICAL SETTING

The Sergipe Basin is situated in the eastern, coastal part of the state of Sergipe in north-eastern Brazil. It comprises an area of approximately 11,000 km^2, of which 6,000 km^2 are onshore (Figures 1A,B). Structurally, the basin forms a sub-basin of the Sergipe-Alagoas Basin, which comprises, from north to south, the Cabo, Alagoas, Sergipe, and Jacuípe sub-basins (Souza-Lima *et al*., 2002). The localities where the specimens were collected are indicated in Figure 1C.

The Sergipe Basin is one of the numerous extensional rift basins bordering the South Atlantic Ocean, which were formed during the late Mesozoic rifting and separation of South America and Africa. The basin forms a half-graben bounded to the south-east by the continental slope and to the north-west by a system of normal faults. The geological evolution and the development of the marine Cretaceous of the Sergipe Basin have been discussed by several authors, (*e.g*. Ojeda & Fugita (1976), Ojeda (1982), Bengtson (1983), Koutsoukos & Bengtson (1993), Koutsoukos *et al*. (1993), Feijó (1995) and Souza-Lima *et al.* (2002)).

STRATIGRAPHY

The sedimentary fill of the Sergipe Basin varies in thickness between 1 and 3 km onshore, whereas offshore it may reach 8 km (Ponte *et al.*, 1980). The Cretaceous succession (Figure 2A) consists of non-marine clastic deposits overlain by the marine, dominantly carbonate Riachuelo (Aptian-Albian) and Cotinguiba (Cenomanian-Coniacian) formations and the siliciclastic Calumbi Formation (Santonian-Miocene) (Feijó, 1995; Souza-Lima *et al.*, 2002). The thickness of the Cotinguiba Formation averages 200 m but may reach over 1000 m in the onshore part of the basin (Schaller, 1970). The rocks consist mainly of grey to blue-grey (cream or yellowish where weathered), fine-grained, massive, bioturbated limestones with sparse siliciclastic intercalations at the base of the formation (Bengtson, 1983). The Cotinguiba succession accumulated on a carbonate ramp system in neritic to upper bathyal environments with intermittent dysoxic-anoxic bottom conditions and well-oxygenated epipelagic waters (Koutsoukos *et al*., 1991, 1993).

The ammonite zonation used herein (Figure 2B) is that of Smith & Bengtson (1991), Koutsoukos & Bengtson (1993), Seeling & Bengtson (1999) and Bengtson *et al.* (2005). The specimens were collected from quarries exposing the upper Turonian *Barroisiceras onilahyense-Forresteria* and *Forresteria armata-Prionocycloceras lenti* zones (Figure 2B). Because the stage boundary has not yet been definitely identified in the Sergipe Basin (Bengtson *et al*., 2005; Andrade, 2005), the possibility that some specimens may be of early Coniacian age should not be excluded. The specimens occur associated with other benthic macrofaunal elements such as inoceramid and pinnid bivalves, gastropods and irregular echinoids.

Bengtson (1983) provided a summary of the literature on the Cenomanian-Coniacian succession of the basin. More recent data are found, for example, in Andrade (2005).

MATERIAL AND METHODS

The specimens described here derive from fieldwork in the Sergipe Basin by P. and S.I. Bengtson in 1971-1972, with complementary sampling by P. Bengtson in 1977 and E.J. Andrade in 2001-2004. For details of the fieldwork, see Bengtson (1983) and Andrade (2005). A total of 75 specimens from nine localities, all quarries, are studied here (Figure 1C). Localities Cajaíba 7, Mata 9, Mata 10, Mucuri 7, Mucuri 10, Mucuri 12, Oiteiro 8 and Oiteiro 17 are described in Bengtson (1983, Appendix 1) and Mata 11 in Seeling (2004), Andrade (2005) and Manso & Andrade (2008). Two of the specimens were collected in 1969 by R.A. Reyment (Uppsala University, Sweden) from locality "1/19", a quarry in the Mucuri area (Reyment & Tait, 1972), probably Mucuri 7.

As explained by Bengtson (1983, p. 29), most of the specimens were collected by quarry workers from unknown horizons within the quarries. However, owing to the small thicknesses of exposed successions (generally less than 20 m), in relation to the total thickness of the succession, and the absence of unconformities, specimens from the same locality can be assumed to be of approximately the same age. Preservation is variable; in most cases the specimens are preserved as composite or internal moulds showing ornamentation and even muscle insertion areas. In a few cases, parts of the originally aragonitic shell are preserved, recrystallized as calcite.

The specimens were prepared mechanically, cleaned, and photographed. Silicone rubber moulds were made to enable study of the hinge structure of the valves.

A principal components analysis (PCA) was carried out to clarify the morphological relationship between the three distinct morphs of the new species *Megaporomya reymenti*. The analysis was performed using the PAST software, version 2.07 (Hammer *et al*., 2001) on a variance-covariance matrix of the log-transformed variables.

The systematic classification follows Bieler *et al*. (2010) and the morphological terminology that of Cox (1969, p. 102-109).

Linear measurements (taken with a Vernier caliper) are in millimetres. Orientation of measurements is shown in Figures 3A,B. Abbreviations for dimensions are as follows: **L**, shell length; **H**, shell height; **W**, width of articulated valves; **C**, convexity of valves; **Al**, anterior length (measured from the umbones to the anterior margin); **Hs**, height of siphonal gape (measured perpendicular to the hinge axis). For measurements of individual specimens, see Appendix.

The holotype and paratypes are kept in the collections of the Museu Nacional in Rio de Janeiro, Brazil (MN). Additional specimens are housed in the Staatliches Museum für Naturkunde Karlsruhe, Germany (SMNK-PAL).

SYSTEMATIC PALAEONTOLOGY

Class BIVALVIA Linnaeus, 1758
Subclass AUTOBRANCHIA Grobben, 1894
Superorder HETEROCONCHIA Gray, 1854
Order PHOLADOMYIDA Newell, 1965
[= ANOMALODESMATA Dall, 1889]
Clade SEPTIBRANCHIA
Superfamily POROMYOIDEA Dall, 1886
Family POROMYIDAE Dall, 1886

Genus *Megaporomya* gen. nov.

Type species. *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian (Upper Cretaceous) of the Sergipe Basin, Brazil.

Etymology. *Megas* (Greek) = large, referring to the very large shell. *Poromya* (fem.): for the family Poromyidae, to which the new genus belongs.

Diagnosis. Thin-shelled, large to very large; variable in outline; strongly inflated anteriorly (cordate in cross-section), posteriorly elongate and compressed; umbones wide, strongly convex, enrolled; posterior siphonal gape wide; anisomyarian with shallow pallial sinus; hinge of right valve consisting of one large, inverted, U-shaped cardinal tooth, one straight and narrow cardinal tooth and two unequal sockets; hinge of left valve with two unequal teeth and sockets.

Species included. *Megaporomya reymenti* gen. et sp. nov., probably *Isocardia supermensa* White, 1887, and *Liopistha* (*Psilomya*) *walkeri* Whitney, 1952.

Remarks. The Sergipe specimens are placed in the family Poromyidae on the basis of (i) their very thin shells, (ii) a sub-truncated and sloping posterior margin, (iii) the presence of granules arranged in radial rows, and (iv) a posterior umbonal ridge, which separates the posterior flank from the rest of the shell.

Comparison with other genera. *Megaporomya* gen. nov. differs from other genera of the family Poromyidae (*e.g. Poromya* Forbes, 1844; *Liopistha* Meek, 1864; *Psilomya* White, 1874; *Cymella*, Meek, 1864) in its exclusive combination of characters. These include the large to very large size, broad and distinct umbonal area, strong inflation, and the hinge structure. The hinge of the right valve of *Megaporomya* consists of one large, inverted, U-shaped cardinal tooth, one straight and narrow cardinal tooth and two unequal sockets. The hinge of the left valve possesses, correspondingly, two unequal teeth and sockets. In contrast, the hinge of the genus *Liopistha* is more complicated and composed of two large cardinal teeth with one thin, tooth-like partition in the right valve and one large and one small cardinal tooth with one thin, tooth-like partition in the left valve (Dhondt & Jagt, 1989, p. 489, pl. 1, fig. 7; pl. 2, fig. 1). According to Yonge & Morton (1980), the hinge of *Poromya* has simple teeth, which are presumed to be secondary. *Megaporomya* gen. nov. is ornamented with fine, irregular commarginal ribs separated by wide interspaces bearing fine growth lines. The commarginal ribs are crossed by widely spaced radial rows of minute tubercles (tuberculate appearance). In *Liopistha*, radial and commarginal ribs are equally developed, but towards the ventral margin only the radial ornamentation remains.

Compared to *Megaporomya*, *Psilomya* is characterized by a less developed radial ornamentation. The commarginal ribs of *Megaporomya* are less pronounced than in *Cymella*, where they cover the entire surface and are crossed by less developed radial ribs on the central part of the valve. Other diagnostic features of *Megaporomya* include shell size and inflation; the genus is much larger and more inflated than *Liopistha* and related genera.

Megaporomya gen. nov. is similar to the genus *Pholadomyocardia* Szajnocha, 1889 (family Ceratomyidae Arkell, 1934) in having strongly inflated valves, a wide umbonal area, and a truncated anterior margin, but differs in lacking the wing-like postero-dorsal extension and in possessing a radial ornamentation, whereas in *Pholadomyacardia* the surface is ornamented with only a few commarginal ridges (concentric rugae).

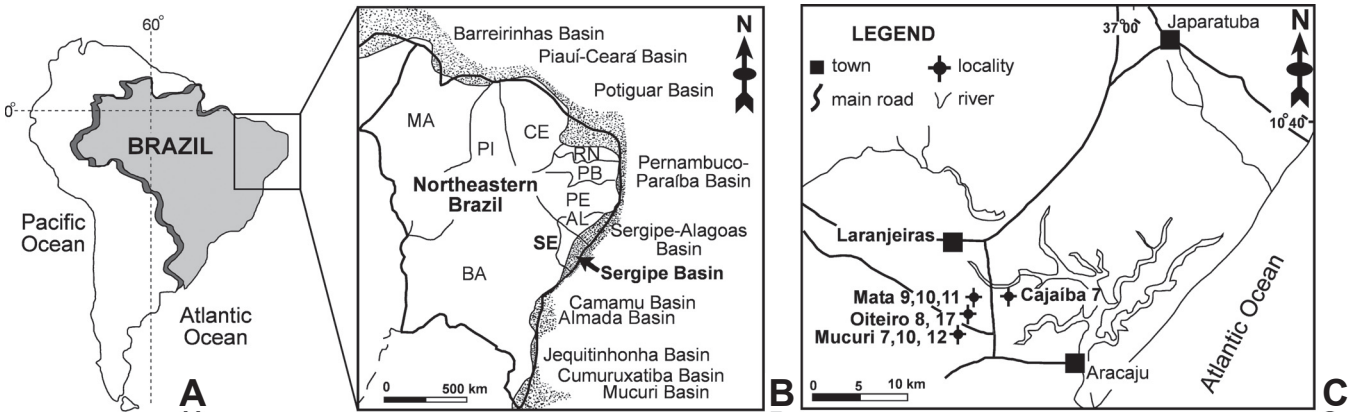

Figure 1. A-B, location of the Sergipe Basin and adjacent continental margin basins. **C**, map of central part of the Sergipe Basin showing localities with *Megaporomya reymenti* gen. et sp. nov. **Abbreviations: AL**, Alagoas; **BA**, Bahia; **CE**, Ceará; **MA**, Maranhão; **PB**, Paraíba; **PE**, Pernambuco; **PI**, Piauí; **RN**, Rio Grande do Norte; **SE**, Sergipe (modified from Seeling & Bengtson, 2003a).

Stratigraphic range. *Megaporomya* gen. nov. is so far recorded with certainty only from the upper Turonian.

Megaporomya reymenti gen. et sp. nov.
(Figures 4-6, 9)

v1983 *Liopistha* (*Psilomya*) *supermensa* White [sic]. Bengtson, p. 47.
v2005 *Psilomya ligeriensis* (d'Orbigny, 1845). Andrade, p. 49.
v?2011 *Liopistha* (*Psilomya*) *supermensa* (White, 1887). Andrade & Santos, p. 234, figs. 2: 5-7.
v?2011 *Liopistha* (*Psilomya*) *ligeriensis* (d'Orbigny, 1945 [sic]). Andrade & Santos, p. 233-234, figs. 2:3-4.

Etymology. Named after Professor Richard A. Reyment (Uppsala University, Sweden), who in 1969 collected two well-preserved specimens from locality "1/19" in the Mucuri area, probably Mucuri 7 (specimens MN 8748-I and MN 8749-I herein); see Reyment & Tait (1972).
Diagnosis. *Megaporomya* with large to very large valves (L = *c*. 85-150 mm), elongate-ovate to ovate; oblong or rounded (H/L= *c*. 0.6-1.0); strongly inflated (W/L= *c*. 0.6-0.9); sub-truncated to slightly convex anterior margin, meeting the ventral margin in a blunt angle; posterior margin sub-truncated and sloping; anterior umbonal ridge moderately well-developed, forming boundary of shallow depression on anterior part; posterior umbonal ridge faint, separating concave posterior flank from rest of shell; commarginal ribs irregular, crossed by radial rows of minute tubercles (tuberculate appearance).
Holotype. Composite internal mould of articulated specimen no. MN 8711-I (Figures 4A,B) collected by E.J. Andrade in 2003 from the upper Turonian of locality Mata 11, Cotinguiba Formation, Sergipe Basin, Brazil.
Paratypes. 38 composite and internal moulds (MN 8712-I-8749-I) of articulated specimens illustrated in Figures 5A-F, 6A, and 9C from the upper Turonian of localities Mucuri 7, 10, 12 and Mata 11, Sergipe Basin, Brazil.
Other material. 36 composite and internal moulds (SMNK-PAL 11001-11036) from the upper Turonian of localities Cajaíba 7, Mata 9, 10 and Oiteiro 8, 17, Cotinguiba Formation, Sergipe Basin, Brazil.
Type locality. Mata 11 (Nassau Quarry), 12 km northwest of Aracaju, Sergipe Basin, Brazil (Figure 1C; described in detail by Seeling, 2004; Andrade, 2005; Manso & Andrade, 2008).
Type horizon. *Forresteria armata-Prionocycloceras lenti* Zone, upper Turonian, Cotinguiba Formation.
Measurements. See Table 1 and Appendix.
Description. Large to very large (L = 85-150 mm) shell, varying in outline from elongate-ovate to broadly ovate or rounded, slightly equivalved, strongly inequilateral, strongly inflated (W/L= 0.74 on average) and posteriorly elongate (H/L= 0.80 on average). Maximum inflation below the umbones; shell slightly compressed posteriorly. Antero-dorsal margin slightly convex, meeting the anterior margin in a rounded angle. Anterior margin sub-truncated to slightly convex, meeting the ventral margin in a blunt, nearly right angle (Figure 5D). Postero-dorsal margin slightly convex, slightly sloping, forming an obtuse angle with the posterior margin. Posterior margin obliquely truncated, forming an acute angle with the ventral margin. Posterior end strongly gaping. Ventral margin irregularly broad, slightly convex. Rounded ridge extending from front of umbones to middle of anterior margin, forming boundary of shallow depression on anterior part (Figure 4B). Posterior concave area (10-17% of total valve length from posterior end) separated from rest of shell by a faint posterior umbonal ridge. Umbonal area wide and strongly convex. Lunule cordate in outline, wide, and shallow. Umbones large, prominent, pointed, enrolled, elevated above hinge line and slightly incurved anteriorly. Hinge of right valve consisting of one large, inverted, U-shaped cardinal tooth, one straight and narrow cardinal tooth and two unequal sockets (Figures 5C; 8A-C). Hinge of left valve with two unequal teeth and sockets. Posterior adductor muscle scar elongate ovate, larger than anterior muscle scar, located near postero-dorsal side; anterior scar circular to oval, located antero-dorsally (Figure 8D). Small anterior and posterior pedal retractor muscle scars attached to respective adductor scars. Pallial line oblique to ventral margin,

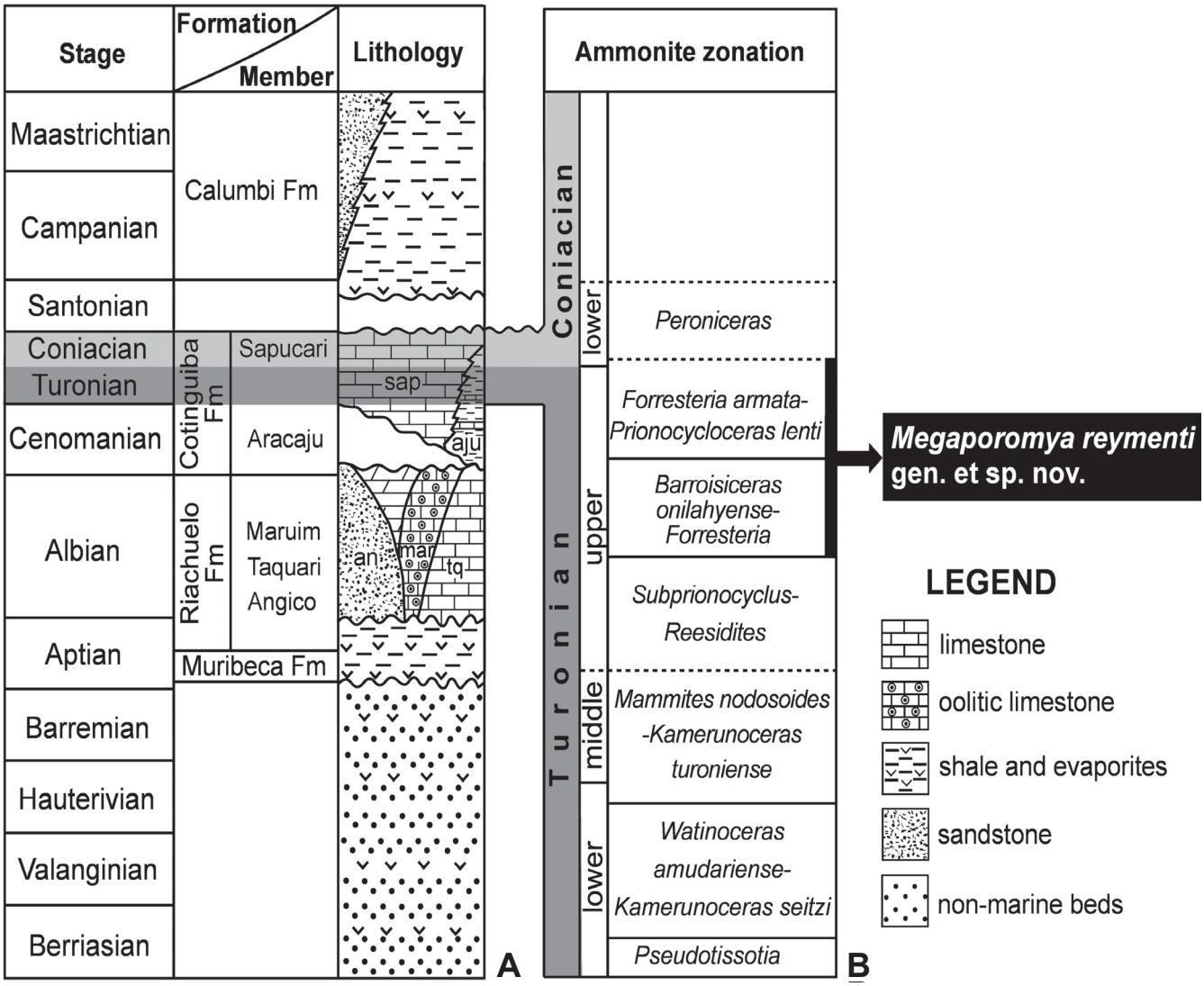

Figure 2. A, Simplified Cretaceous stratigraphic framework for the Sergipe Basin (modified from Bengtson, 1983; Hessel, 1988; Smith & Bengtson, 1991; Feijó, 1995; Souza-Lima *et al*., 2002). **B**, Ammonite zonation for the Turonian-Coniacian of Sergipe (after Smith & Bengtson, 1991; Koutsoukos & Bengtson, 1993; Seeling & Bengtson, 1999; Bengtson *et al*., 2005).

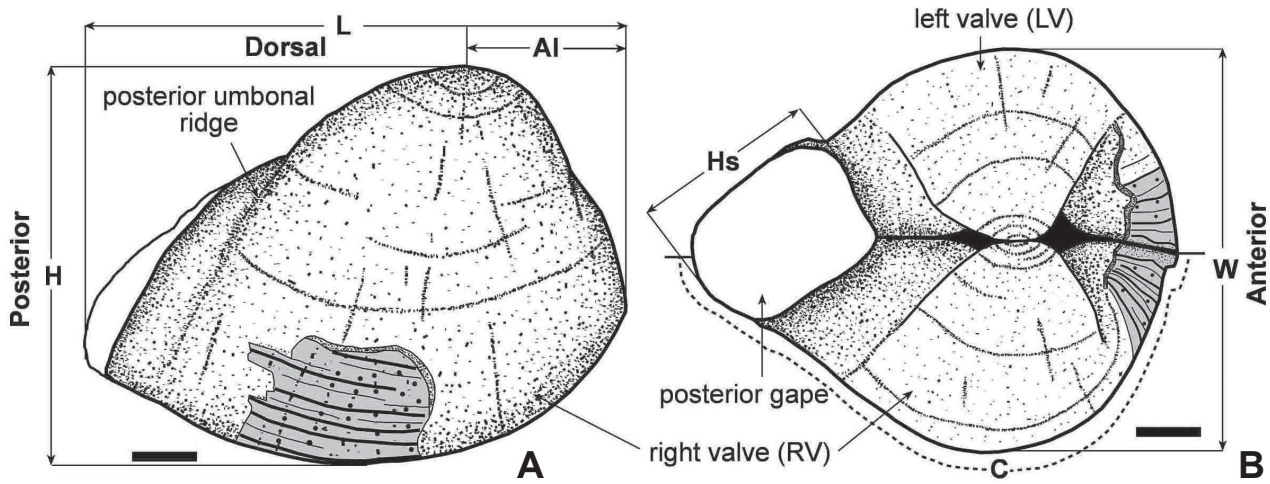

Figure 3. Measured parameters of *Megaporomya reymenti* gen. et sp. nov. **A**, lateral view of right valve; **B**, dorsal view. The grey parts refer to preserved shell material. **Abbreviations: L**, shell length; **H**, shell height; **W**, width of articulated valves; **C**, convexity of valve; **Al**, anterior length; **Hs**, height of siphonal gape. Scale bars = 20 mm.

Table 1. Dimension ranges (in mm) of *Megaporomya reymenti* gen. et sp. nov. For abbreviations, see Figure 3.

n = 58	L	H	W	Al	Hs	C	H/L	Al/L	W/L
Range	85–150	73–113	60–105	10–45	47–83	113–180	0.61–0.98	0.09–0.63	0.61–0.93
Mean	114.89	91.15	84.45	29.48	64.46	147.96	0.80	0.26	0.74

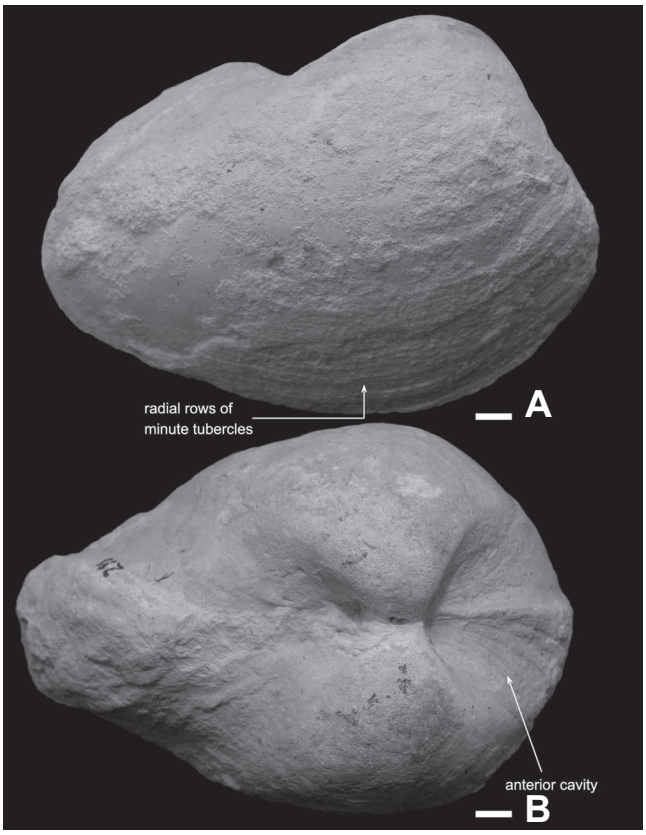

Figure 4. *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Cotinguiba Formation, Sergipe Basin (elongate form); holotype, no. MN 8711-I, from Mata 11. **A**, right lateral view of the articulated composite mould, showing radial rows of minute tubercles; **B**, dorsal view showing the strongly inflated valves and the anterior depression. Scale bars = 10 mm.

with faint posterior sinus. Ornamentation consisting of fine commarginal ribs separated by wider interspaces. Interspaces carrying fine growth lines in some individuals (Figures 5D, F). Posterior area (near posterior end) smooth. Commarginal ribs well developed on dorsal area, crossed by widely spaced radial rows of minute tubercles. Radial tubercles becoming more prominent away from umbones towards ventral margin.

Statistical analysis. Three morphs of *Megaporomya reymenti* are recognized mainly on the basis of variability in general outline (H/L ratio) and position of the umbones: elongate, suborbicular and intermediate forms. Principal Component Analysis (PCA) was performed to clarify the morphological relationship between the three forms on variance-covariance matrix of the following log-transformed variables: length (L), height (H), width (W), inflation (C), and anterior length (Al). The first principal component (PC1) accounted for 73.81% of the variation in the data, PC2 accounted for 20.16%, and PC3 accounted for 2.69% (Figure 7E). The original variables display a strong positive correlation with PC2 and, therefore, individuals with high PC2 scores have a large body size. The anterior length (Al) is positively correlated with the PC1 axis, individuals with high PC1 values having a large anterior part (Figures 7A,C). It can be seen that the three forms are similar in size but differ in general outline and length of the anterior area. The latter is confirmed by plotting of PC1 *vs.* PC3, where PC3 is positively correlated with the H/L ratio; therefore, individuals with high PC3 values have a more rounded shell than those with low values. The suborbicular form is characterized by a large anterior part (umbones situated at approximately one-third of the total valve length from the anterior end), a sub-rounded outline, and by being taller (H/L= 0.80 on average) (Figures 7C,D). In contrast, the elongate form is characterized by more elongate valves, sub-terminal umbones, a short anterior area and an expanded posterior area. However, as the three forms overlap (based on Al/L and H/L ratios), they are assigned to the same species (Figures 7A,B).

Discussion. *Megaporomya reymenti* is a variable species (elongate-ovate to ovate, rounded), characterized by very large, strongly inflated valves, a wide umbonal area, irregular commarginal ribs, crossed by radial rows of minute tubercles (Figures 4A, 6A), sub-terminal to nearly central umbones (located from one-fourth to more than one-third of the shell length from the anterior end), which are nearly in contact, a wide siphonal gape, and two cardinal teeth, one a large inverted U-shaped and one straight and narrow, and with two unequal sockets in the right valve.

The similar species *Isocardia supermensa* was described by White (1887, p. 80, pl. 6, figs. 1-2) and redescribed by Maury (1937, p. 71, pl. 9, figs. 16-17) on the basis of a single, poorly preserved specimen presumed to derive from the Albian of the Sergipe Basin. Beurlen (1971) referred this species to *Psilomya* and dated it as Coniacian, and Seeling (1999) reported it from the Cenomanian-Turonian boundary beds of Sergipe. Lefranc (*in* Bengtson, 1983, Table 2) assigned the species to *Liopistha* (*Psilomya*). Here it is tentatively referred to *Megaporomya* on account of its size, sub-terminal umbones, wide umbonal area, and strong inflation. It differs from *M. reymenti* in having a strong antero-dorsal ridge, which extends from the umbones to the middle of the anterior margin and forms a deep anterior depression, terminal and strongly enrolled umbones, and in being smaller (L= 80, H= 55, T= 62 mm *fide* Maury, 1937, p. 71. as opposed to L= 115, H= 91, T= 84 on average for *M. reymenti*) and more elongate (L/H= 1.45 as opposed to L/H= 1.27 on average). In addition, the specimen of *M.*? *supermensa* described by White (1887) and Maury (1937) lacks radial ornamentation, although this may be a preservational artefact.

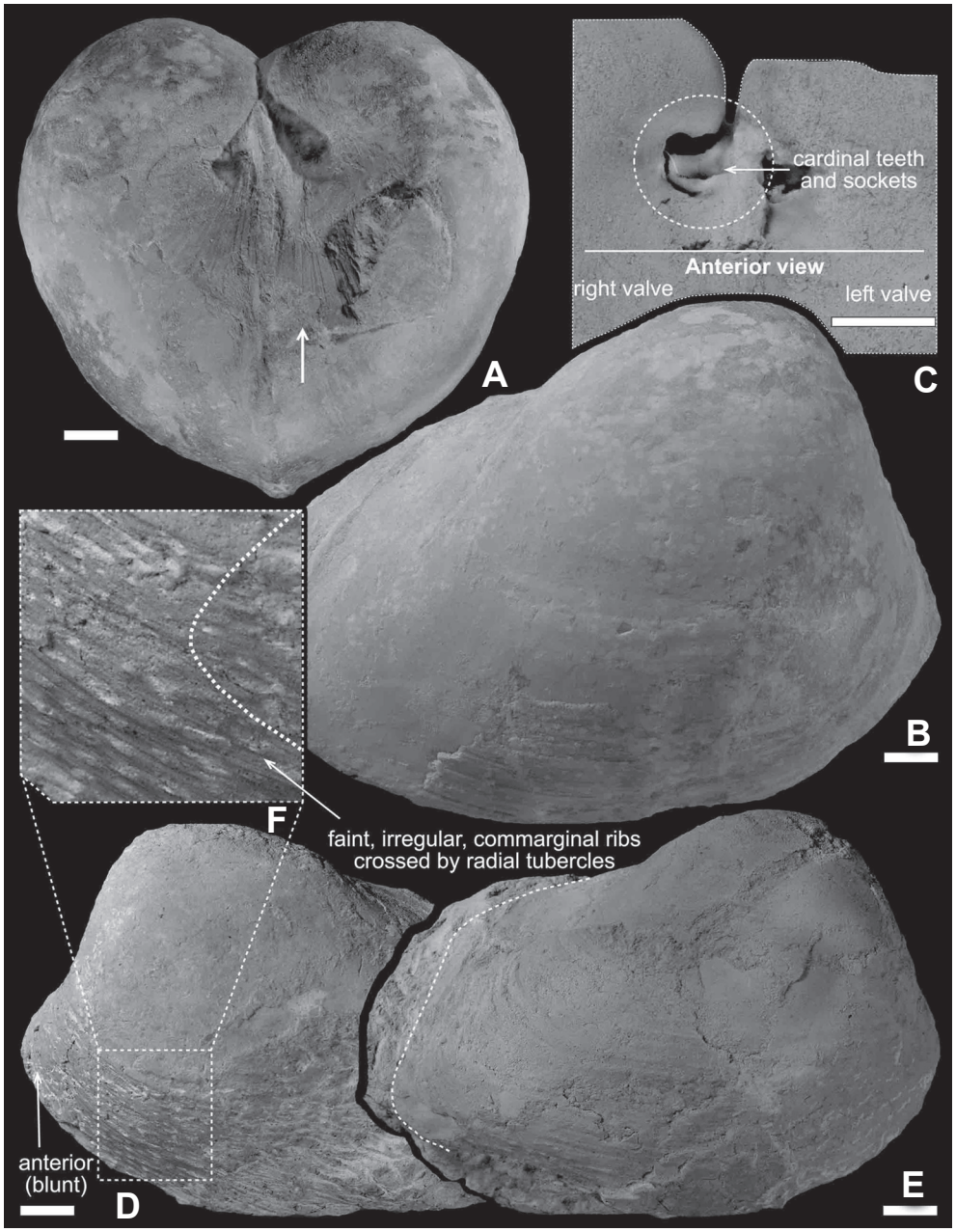

Figure 5. *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Cotinguiba Formation, Sergipe Basin (elongate form). **A-B**, articulated composite mould with remains of shell; paratype, no. MN 8748-I, from locality "1/19" of Reyment & Tait (1972), Mucuri area, probably Mucuri 7. **A**, anterior view showing the strongly inflated valves with remains of shell (arrowed); **B**, side view of right valve; **C**, anterior view of articulated composite mould, no. SMNK-PAL 11034, from Mata 10, showing the upper and lower cardinal sockets with two unequal teeth; **D-F**, composite mould with remains of shell; paratype, no. MN 8722-I from Mucuri 10; **D**, side view of left valve; **E**, side view of right valve showing the truncated posterior end; **F**, close-up showing irregular commarginal riblets and well-developed radial tubercles. Scale bars = 10 mm.

The specimens from localities Pedro Gonçalves 2 (lower or middle Turonian) and Mata 11 (upper Turonian), described and figured by Andrade & Santos (2011) as *Liopistha* (*Psilomya*) *supermensa* (White, 1887) and *Liopistha* (*Psilomya*) *ligeriensis* (d'Orbigny, 1945 [sic]) probably belong to *M. reymenti* (specimen MT11-288, erroneously given as MT11-387 on p. 233), although some of their specimens of *L.* (*P.*) *ligeriensis* are considerably smaller (L= 65 mm) than the specimens described here. The true *L.* (*P.*) *ligeriensis* differs in being smaller and less inflated, in having numerous and fine commarginal ribs, and in lacking radial ribbing. Pervinquière (1912) and Barber (1958) considered *Homomya profunda* (White, 1887, p. 105, pl. 7, fig. 5) from the middle Albian of Sergipe as conspecific with *L.* (*P.*) *ligeriensis.* Andrade & Santos (2011) followed Barber's opinion but their specimens differ in being much more inflated and larger (L= 65-112, H= 64-102 mm as opposed to L= 36, H= 30 mm).

Liopistha (Psilomya) gigantea (Sowerby, 1818), as described and figured by Woods (1909, p. 257, pl. 43,

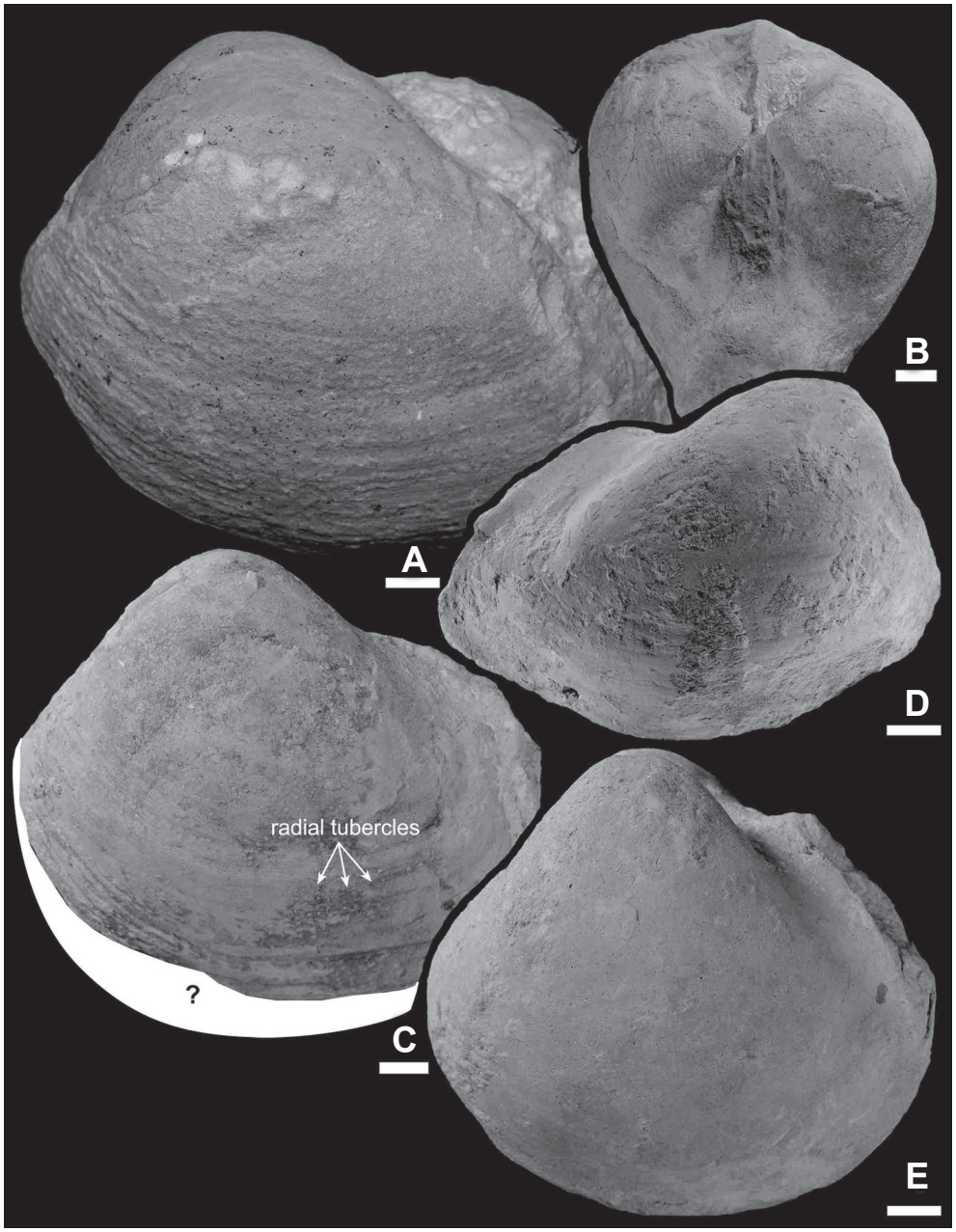

Figure 6. *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Cotinguiba Formation, Sergipe Basin (intermediate and suborbicular forms). **A**, Composite mould, side view of left valve, no. SMNK-PAL 11034, from Mata 10. **B**, Dorsal view of composite mould, no. SMNK-PAL 11022, from Mata 9. **C**, Left lateral view of composite mould, no. SMNK-PAL 11009, from Cajaíba 7. **D**, Right lateral view of composite mould; paratype, no. MN 8713-I, from Mucuri 10. **E**, Lateral view of left valve (rounded form) of composite mould; paratype, no. MN 8717-I, from Mucuri 10. Scale bars = 10 mm.

figs. 3-4; pl. 44, figs. 1-2) from the Upper Cretaceous of England, strongly resembles *M. reymenti* in size and outline but differs in having a narrow umbonal area, numerous fine, dorsally well-developed commarginal ribs, less-developed radial tubercles, restricted to the anterior area, a rounded posterior margin and in lacking a postero-dorsal ridge.

Liopistha (Psilomya) walkeri Whitney (1952, p. 68, pl. 16, figs. 5, 6) from the Albian of Texas is probably better referred to *Megaporomya*. The specimen is an internal mould without any trace of ornamentation and is too poorly preserved for species assignment. *M.*? *walkeri* is similar to *M. reymenti* in having a well-developed postero-dorsal ridge, truncated anterior margin, and a wide and rounded ventral margin, but differs in being less inflated, smaller (L= 95 mm, H= 65 mm, W= 70 mm) and more elongate. In addition, *M.*? *walkeri* is recorded from a lower stratigraphic level (Albian).

Poromya superba Stoliczka (1871, p. 48, pl. 3, figs. 2-4) from the Coniacian of India and *Liopistha superba* (Stoliczka, 1871) described and figured by Riedel (1932, p. 68, pl. 5, fig. 1) from the Santonian-Maastrichtian of Germany, resemble *Megaporomya reymenti* in size (L= 100, H= 80 mm; Stoliczka, 1871) but differ in having narrow, sharply pointed umbones, less

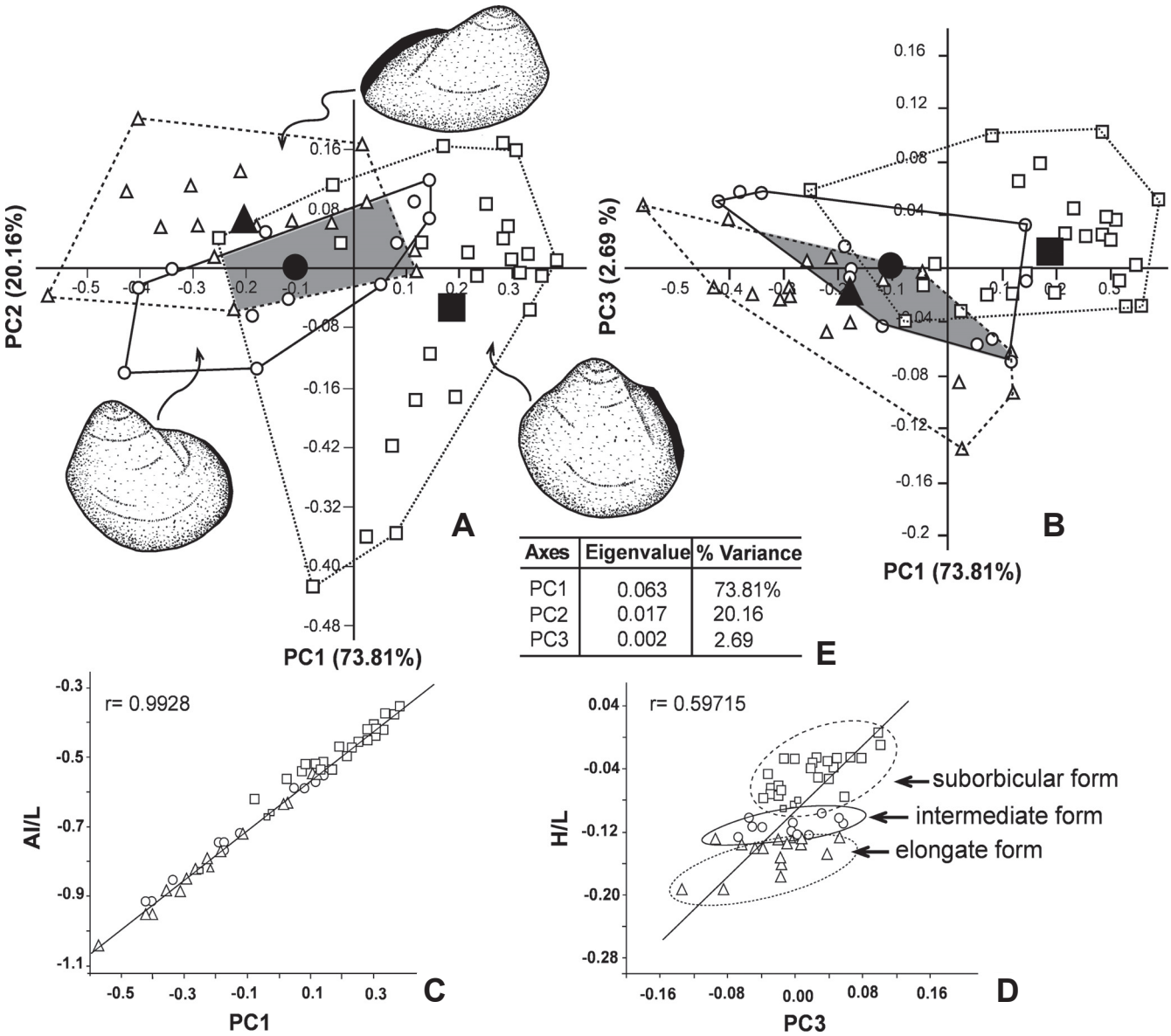

Figure 7. Principal component analysis (PCA) of *Megaporomya reymenti* gen. et sp. nov. using the PAST software (Hammer *et al*., 2001). **A**, scatter plot of PC1 *vs.* PC2 showing the overlapping of the three morphs, elongate, suborbicular and intermediate forms, of *M. reymenti* on the basis of Al/L ratio; **B**, scatter plot of PC1 *vs*. PC3 showing also the overlapping of the three morphs based on shell outline (H/L); **C**, relationship between PC1 and Al/L showing that the elongate form has sub-terminal umbones (PC1 scores range from 0 to 0.1); **D**, relationship between PC3 and shell outline (H/L) showing that the suborbicular form is taller than the elongate form (PC3 scores range from -0.04 to 16); **E**, percentage of variation explained by PCA of body-size variables. The large symbols in the scatter plots represent the centroid value for the respective groups (A and B).

inflated valves, and numerous commarginal ribs crossed by radial tubercles on the anterior area. *L.* (*P.*) *banderaensis* (Whitney, 1952, p. 67, pl. 16:1-2) from the Albian of Texas differs in being less inflated (W/L= 0.55 as opposed to 0.74 on average) and in having circular posterior and anterior muscle scars and a narrow umbonal area. In addition, Whitney's specimen is an internal mould without any signs of ornamentation.

PALAEOAUTECOLOGY

Reconstructing life habits of fossil bivalves is generally difficult, because the soft parts are decayed and the original shell is often dissolved. However, it is possible to reconstruct life habits of extinct species by analogy with the mode of life of Recent relatives and, particularly where no close relatives exist today, by applying the principles of functional morphology (Fürsich, 1980, p. 289).

All representatives of the Pholadomyida are marine organisms, some of them adapted to burrowing to varying depths in soft sediment. The burrowing depth and the degree of mobility in the sediment can be roughly estimated from their shell morphology (Runnegar, 1974, p. 909). In fossil shells, the shape and size of adductor and pedal muscle scars in combination with the hinge structure may give indications

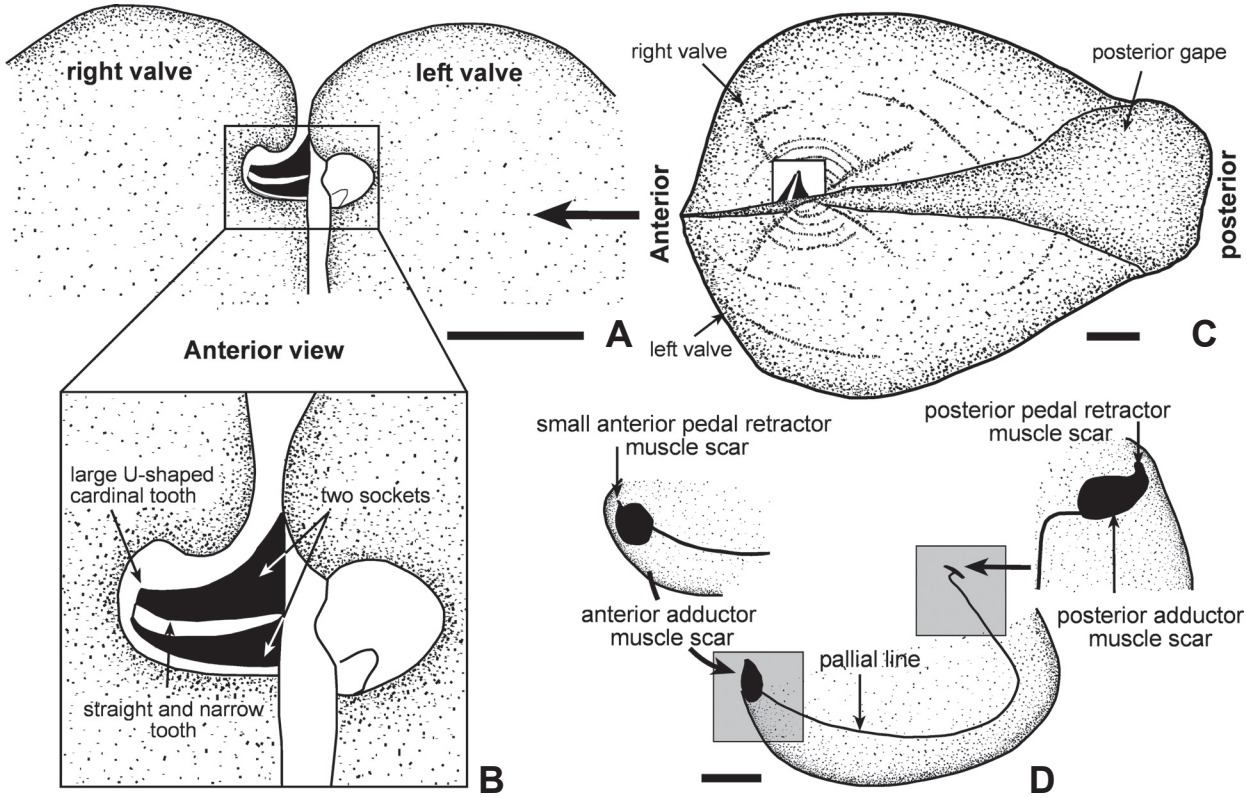

Figure 8. A-C, hinge structure of *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Cotinguiba Formation, Sergipe Basin. **A-C**, specimen no. SMNK-PAL 11034, from Mata 10. **A**, anterior view showing the cardinal teeth and sockets of the right valve; **B**, close-up showing the large, inverted, U-shaped tooth and the straight and narrow tooth with the two unequal sockets; **C**, dorsal view; **D**, adductor and pedal retractor muscle scars and pallial line of *M. reymenti*, paratype, no. MN8712-I, from Mucuri 10. Scale bars: A,C = 10 mm; D = 20 mm.

of an endobyssate or free-burrowing mode of life (*e.g.* Trueman, 1967; Stanley, 1972; Runnegar, 1974). With respect to feeding mode, representatives of several pholadomyid families live in the deep sea and have become carnivorous, showing remarkable morphological adaptations for the capture of small arthropods and polychaetes (Harper *et al*., 2006, p. 404). Species of the family Poromyidae are predators of crustaceans and/or polychaetes and show no evidence of vegetable matter in any part of the alimentary canal (*e.g.* Pelseneer, 1891; Yonge, 1928; Morton, 1981). According to Yonge (1928), *Poromya* slowly inhales small prey with the siphon, which projects only slightly above the sediment-water interface. The prey falls down onto the palps, which push it into the mouth. Morton (1981) and Allen & Morgan (1981) examined the siphonal structure of two specimens of living *Poromya granulata* and found that the inhalant siphon is surrounded by 15 tentacles, each with sensory papillae. The prey is probably detected by the siphonal tentacles, which detect mechanical disturbance in the water. For more details about the feeding mechanism of the family Poromyidae, see Morton (1981, p. 253-254).

The most notable features of the genus *Megaporomya* are the very large shell, expanded posteriorly, the blunt anterior side, strongly inflated valves, strongly enrolled umbones, wide anterior face with shallow anterior depression and the commarginal ornamentation with radial tubercles. Burrowing was performed mainly by means of the foot, which could be extended ventrally or anteriorly (Yonge, 1928, p. 238). In vertical position, the posterior end of the valves was oriented upwards and the blunt anterior side was in wide contact with the substrate. By opening and closing the valves, *Megaporomya* could pull itself into soft sediments assisted by the acute antero-ventral margin. After the first step of burrowing, the bivalve changed to an oblique position and pushed itself downwards through jerking movements of the valves. According to Yonge (1928, p. 239), all movements of the extant *Poromya* are sudden with appreciable intervals. Finally, *Megaporomya* reached a depth at which the end of the postero-dorsal ridge was at or slightly extended above the sediment-water interface. The inhalant and exhalant siphons were never covered with sediment. The strongly convex valves with their radial rows of tubercles helped the bivalve to penetrate the soft substrate slowly. In addition, the function of the tubercles might have been to increase friction between the valves and sediment and so slowing down the burrowing rate. The commarginal ornamentation, albeit only moderately developed, most probably served to increase stability within the sediment (Stanley, 1970, 1972, 1975). According to Runnegar (1974, p. 916), prominent cardinal hinge teeth occur in several shallow-burrowing pholadomyid genera but very rarely in deep-burrowing genera. Additional evidence for the more or less vertical, shallow-infaunal growth position of *Megaporomya* is provided by the presence of serpulids and fragments of small bivalves, which encrusted only the

posterior part of some specimens (one-sixth of the specimens; Figures 9A-D). In conclusion, based on analogy with modern relatives, *Megaporomya* is interpreted as a semi-infaunal to shallow-infaunal selective predator feeding on crustaceans and/or polychaetes (Figure 11A).

PALAEOSYNECOLOGICAL REMARKS

Megaporomya reymenti is recorded from the upper Turonian (with possible occurrences in the lower Coniacian). Co-occurring faunal elements are other bivalves (*e.g.* inoceramids, plicatulids, oysters, pinnids), gastropods, echinoids and ammonites. The dominant benthic organisms of this association are bivalves (28% inoceramids and 44% other bivalves) and gastropods (24%). According to Andrade (2005, p. 49, figs. 6.9a-c), inoceramids are abundant throughout the Turonian but rare where other bivalves are abundant, as observed in the upper Turonian of locality Mata 11 (Figure 10A). Echinoids are subordinate (4%) with a monospecific occurrence of *Mecaster fourneli.* With respect to mode of life, the association contains a large number of shallow-infaunal (56%) and epifaunal (44%) organisms, whereas deeper-infaunal elements are absent (Figure 10B). Suspension-feeders dominate (72%), with carnivores and deposit-feeders as subordinate elements (16% and 12%, respectively; Figure 10C). The association occurs in fine-grained lime mudstones and wackestones (Smith & Bengtson, 1991, p. 15). The pinnids are large (L= 250 mm), articulated, and embedded in life position, as indicated by the orientation of the long axis of the shells perpendicular to bedding (Seeling & Bengtson, 2003a). Most of the pinnids show repair scars, indicating attacks by predators.

Koutsoukos *et al.* (1993) suggested that the Cenomanian-Coniacian succession accumulated in a carbonate ramp system over a relatively wide continental shelf in neritic to upper bathyal (200-500 m) environments. The approximately equal abundance of shallow-infaunal and epifaunal organisms is evidence of a biota adapted to life on a moderately soft substrate under fully marine conditions (Figure 11B). Shallow-infaunal echinoids as well as ammonites (stenohaline groups) also document euhaline conditions. Using the morphology of echinoids as a tool for palaeoenvironmental reconstruction, Smith & Bengtson (1991, p. 15) interpreted the poorly developed petals of *Mecaster fourneli* as an indication of relatively warm water conditions. With respect to the energy level, the presence of non-byssate to weakly byssate inoceramids, which lived as epifaunal recliners or semi-infaunally, suggests relatively quiet conditions (Elder, 1987). However, the dominance of suspension-feeders (72%) indicates that the energy level was sufficiently high to keep food particles in suspension under relatively low sedimentation rates. In addition, a relatively stable, low-stress environment is corroborated by intermediate diversity values (Figure 11B). According to Andrade (2005, p. 126), based on

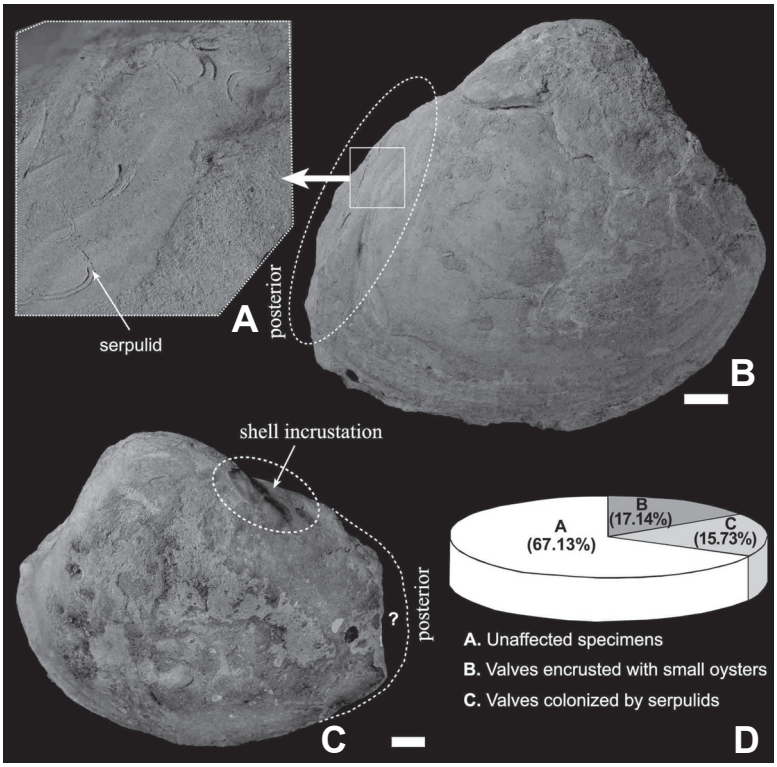

Figure 9. *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Cotinguiba Formation, Sergipe Basin. **A-B**, specimen no. SMNK-PAL 11032 from Mata 10; **A**, close-up showing the distribution of serpulids along the inner posterior side of the mould; **B**, composite mould of right valve; **C**, composite mould of left valve showing remains of cemented shells along the posterior side of the valve; paratype, no. MN8718-I, from Mucuri 10; **D**, pie diagram showing the relative abundance of epi- and endobionts in the *Megaporomya* specimens studied. Scale bars = 10 mm.

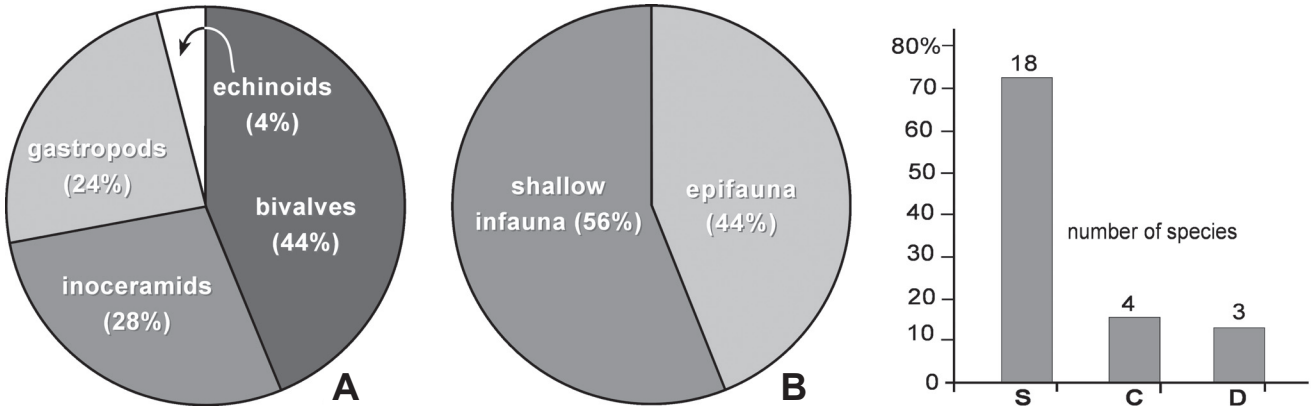

Figure 10. A-B, composition of the benthic macrofauna (number of taxa) from the uppermost Turonian of the Sergipe Basin; **C**, life habits and modes of feeding of the upper Turonian benthic macrofauna. **Abbreviations: S**, suspension-feeding; **C**, carnivorous; **D**, deposit-feeding.

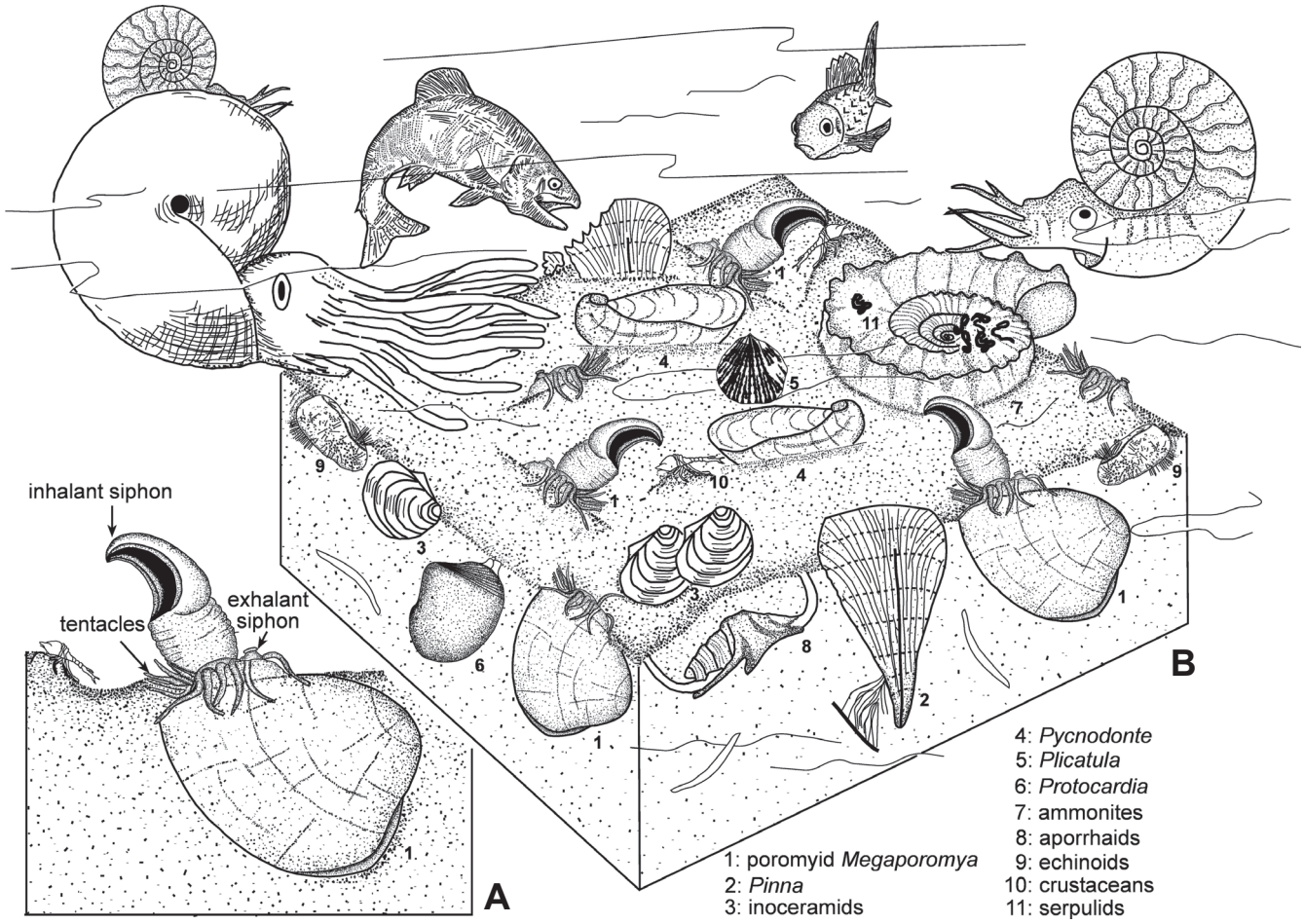

Figure 11. A, reconstruction of life and feeding modes of *Megaporomya reymenti* gen. et sp. nov. by analogy with modern relatives (*e.g.* Yonge, 1928; Allen & Morgan, 1981; Morton, 1984); **B**, environmental reconstruction showing *Megaporomya* with other bivalve groups, gastropods and echinoids.

the abundance of inoceramids, the water depth of the Sergipe Basin decreased from the early to late Turonian. In the early-middle Turonian, the fauna was dominated by inoceramids and ammonites, which decrease in abundance in the late Turonian with a corresponding increase in non-inoceramid bivalves, gastropods and echinoids.

CONCLUSIONS

The bivalve *Megaporomya reymenti* gen. et sp. nov. (Pholadomyida, Poromyidae) is described from the upper Turonian of the Cotinguiba Formation of the Sergipe Basin in north-eastern Brazil.

The main morphological features that distinguish *Megaporomya* gen. nov. from other poromyid genera are the very large size (L = 85-140 mm), wide umbonal area, thick pallial line with shallow sinus, wide posterior gape, strongly inflated valves, and the presence of one large, inverted, U-shaped cardinal tooth, one straight and narrow cardinal tooth and two unequal sockets in the right valve.

Based on analogy with Recent relatives, *Megaporomya* gen. nov. is interpreted as a semi-infaunal predator, burrowing in soft substrates with its posterior end slightly extending above the sediment-water interface. It detected its prey with the help of specialized feeding tentacles surrounding the inhalant siphon (Figure 11A).

The co-occurrence of *Megaporomya reymenti* gen. et sp. nov. with stenohaline organisms such as echinoids and ammonites indicates a fully marine environment. In addition, the dominance of suspension-feeders indicates moderately high water energy and a relatively low sedimentation rate. The nearly equal abundance of epifaunal and shallow-infaunal organisms is evidence of a moderately soft substrate.

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Appendix. Dimensions (mm) of measurable specimens of *Megaporomya reymenti* gen. et sp. nov. from the upper Turonian of the Sergipe Basin. For abbreviations, see Figure 3.

Sample no.	L	H	W	Al	Hs	C	H/L	Al/L	W/L
MN 8711-I	150	105	97	45	83	170	0.70	0.30	0.65
MN 8713-I	98	80	72	30	59	115	0.82	0.31	0.73
MN 8714-I	110	85	80	21	52	143	0.77	0.19	0.73
MN 8715-I	115	85	70	32	58	154	0.74	0.28	0.61
MN 8717-I	113	83	77	32	65	150	0.73	0.28	0.68
MN 8718-I	119	105	93	44	79	163	0.88	0.37	0.78
MN 8719-I	105	83	82	27	53	155	0.79	0.26	0.78
MN 8722-I	101	95	87	45	66	130	0.94	0.45	0.86
MN 8723-I	105	98	88	40	67	150	0.93	0.38	0.84
MN 8724-I	110	102	89	38	64	165	0.93	0.35	0.81
MN 8725-I	100	98	93	38	73	135	0.98	0.38	0.93
MN 8726-I	123	98	80	34	78	130	0.80	0.28	0.65
MN 8727-I	116	85	87	22	70	153	0.73	0.19	0.75
MN 8728-I	99	78	70	12	61	120	0.79	0.12	0.71
MN 8729-I	92	78	67	28	51	115	0.85	0.30	0.73
MN 8730-I	118	88	88	20	66	150	0.75	0.17	0.75
MN 8731-I	95	82	60	32	55	115	0.86	0.34	0.63
MN 8732-I	100	94	73	42	56	133	0.94	0.42	0.73
MN 8733-I	135	100	90	17	60	170	0.74	0.13	0.67
MN 8734-I	100	78	71	18	55	120	0.78	0.18	0.71
MN 8735-I	117	90	83	30	58	153	0.77	0.26	0.71
MN 8736-I	115	85	84	17	65	145	0.74	0.15	0.73
MN 8737-I	122	91	89	33	60	165	0.75	0.27	0.73
MN 8739-I	85	73	60	25	50	113	0.86	0.29	0.71
MN 8741-I	120	83	87	30	60	155	0.69	0.25	0.73
MN 8742-I	118	94	85	42	63	140	0.80	0.63	0.72
MN 8743-I	120	97	90	29	67	155	0.81	0.24	0.75
MN 8744-I	120	90	86	33	73	155	0.75	0.28	0.72
MN 8745-I	150	92	100	32	65	170	0.61	0.21	0.67
MN 8746-I	107	98	80	45	60	130	0.92	0.42	0.75
MN 8747-I	141	110	98	45	69	172	0.78	0.32	0.0
MN 8748-I	130	95	100	20	68	155	0.73	0.15	0.77
MN 8749-I	115	97	90	17	63	148	0.84	0.15	0.78
SMNK-PAL 11001	103	80	86	14	71	150	0.78	0.14	0.83
SMNK-PAL 11002	106	90	78	45	60	135	0.85	0.42	0.74
SMNK-PAL 11005	140	100	105	15	78	175	0.71	0.11	0.75
SMNK-PAL 11008	105	97	75	36	68	135	0.92	0.34	0.71
SMNK-PAL 11009	118	102	77	45	58	135	0.86	0.38	0.65
SMNK-PAL 11010	108	80	76	10	70	143	0.74	0.09	0.70
SMNK-PAL 11013	120	97	97	25	60	175	0.81	0.21	0.81
SMNK-PAL 11014	120	113	98	42	66	180	0.94	0.35	0.82
SMNK-PAL 11016	106	96	87	40	60	135	0.91	0.38	0.82
SMNK-PAL 11018	118	85	85	20	63	165	0.72	0.17	0.72
SMNK-PAL 11021	125	95	89	35	75	148	0.76	0.28	0.71
SMNK-PAL 11023	104	98	89	30	65	145	0.94	0.29	0.86
SMNK-PAL 11024	118	78	85	15	74	160	0.66	0.13	0.72
SMNK-PAL 11025	108	102	90	41	47	135	0.94	0.38	0.83
SMNK-PAL 11027	130	83	87	30	58	165	0.64	0.23	0.67
SMNK-PAL 11029	120	83	85	17	70	155	0.69	0.14	0.71

Appendix. Cont.

Sample no.	L	H	W	Al	Hs	C	H/L	Al/L	W/L
SMNK-PAL 11029	109	85	82	13	65	136	0.78	0.12	0.75
SMNK-PAL 11030	120	113	98	35	75	163	0.94	0.29	0.82
SMNK-PAL 11031	132	85	95	30	74	175	0.64	0.23	0.72
SMNK-PAL 11032	125	87	94	14	65	175	0.70	0.11	0.75
SMNK-PAL 11033	115	102	73	37	68	135	0.89	0.32	0.63
SMNK-PAL 11034	115	95	85	25	60	150	0.83	0.22	0.74
SMNK-PAL 11035	120	89	88	25	72	150	0.74	0.21	0.73
SMNK-PAL 11036	102	76	78	18	67	130	0.75	0.18	0.76