

CENOMANIAN–CONIACIAN (UPPER CRETACEOUS) BIVALVES OF THE SERGIPE BASIN, BRAZIL: ORDER PHOLADOMYIDA

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ABSTRACT – Twenty-two species of the bivalve order Pholadomyida, belonging to six genera and seven subgenera of the families Pholadomyidae, Pleuromyidae and Poromyidae are described from the Cenomanian–Coniacian Cotinguiba Formation of the Sergipe Basin, north-eastern Brazil. Eleven species, *Pholadomya* (*Ph.*) cf. *agriensis* Weaver, *Ph.* (*Ph.*) *kasimiri* Pusch, *Ph.* (*Ph.*) *nodulifera* Münster, *Ph.* (*Ph.*) *occidentalis* Morton, *Ph.* (*Procardia*) *vignesi* Lartet, *Pleuromya ligeriensis* (d'Orbigny), *Pl. servesensis* Choffat, *Liopistha* (*L.*) *aequivalvis* (Goldfuss), *L.* (*Psilomya*) *elongata* Stanton, *L.* (*P.*) *globulosa* (Forbes) and *L.* (*Sergipemya*) *gigantea* (J. Sowerby) are recorded from the Sergipe Basin for the first time. The new subgenus *Sergipemya* of the genus *Liopistha*, family Poromyidae, is erected on the basis of morphological characters such as numerous commarginal ribs, large and highly inflated valves, a well-developed rounded umbonal anterior ridge bordering a deep depression on the anterior part, and the presence of two unequal cardinal teeth with a cardinal tear-shaped socket in the left valve. The pholadomyid fauna of Sergipe closely resembles that of other Tethyan regions in western and southern Europe, northern and western Africa and the Middle East. The distribution patterns of the taxa were probably influenced by east–west-directed currents. Southern Tethyan pholadomyids reached western Africa and north-eastern South America via the Trans-Saharan Seaway.

Key words: Pholadomyida, taxonomy, palaeobiogeography, Cretaceous, Cotinguiba Formation, Brazil.

RESUMO – Vinte e duas espécies de bivalvídeos da ordem Pholadomyida pertencentes a seis gêneros e sete subgêneros das famílias Pholadomyidae, Pleuromyidae e Poromyidae são descritas do Cenomaniano–Coniaciano da Formação Cotinguiba, bacia de Sergipe, nordeste do Brasil. Onze espécies são registradas na bacia pela primeira vez: *Pholadomya* (*Ph.*) cf. *agriensis* Weaver, *Ph.* (*Ph.*) *kasimiri* Pusch, *Ph.* (*Ph.*) *nodulifera* Münster, *Ph.* (*Ph.*) *occidentalis* Morton, *Ph.* (*Procardia*) *vignesi* Lartet, *Pleuromya ligeriensis* (d'Orbigny), *Pl. servesensis* Choffat, *Liopistha* (*L.*) *aequivalvis* (Goldfuss), *L.* (*Psilomya*) *elongata* Stanton, *L.* (*P.*) *globulosa* (Forbes) e *L.* (*Sergipemya*) *gigantea* (J. Sowerby). Foi proposto o novo subgênero *Sergipemya* do gênero *Liopistha*, família Poromyidae, com base em caracteres morfológicos tais como: valvas grandes e fortemente infladas, costelas comarginais numerosas, uma área umbonal anterior bem desenvolvida e arredondada margeando uma depressão profunda sobre a parte anterior, e a presença de dois dentes cardinais diferentes com um soquete cardinal em forma de ranhura na valva esquerda. A fauna de pholadomyídeos de Sergipe assemelha-se fortemente àquela de outras regiões tetianas no oeste e no sul da Europa, no norte e oeste da África e no Oriente Médio. Os padrões de distribuição dos táxons foram influenciados provavelmente por correntes no sentido leste–oeste. Os pholadomyídeos tetianos da parte sul alcançaram a África ocidental e o nordeste da América do Sul pela via transsaariana.

Palavras-chave: Pholadomyida, taxonomia, paleobiogeografia, Cretáceo, Formação Cotinguiba, Brasil.

INTRODUCTION

Taxonomy of the bivalve order Pholadomyida is, in general, difficult and in part confused. The difficulties result from the great variation in shell outline and number of radial ribs. During the first half of the past century, a large number of new species and varieties were described on the basis of variations in ribbing pattern (Weaver, 1931, p. 316), many of which were considered synonyms by later workers. For instance, Dhondt (1987, p. 89) regarded some species and varieties, such as *Pholadomya rostrata* Matheron, 1843, and *Ph. elisabethae* Moesch, 1875, as synonyms of *Ph. (Ph.) nodulifera* Münster, 1841. In fact, taphonomic processes and weathering may strongly modify the ribbing pattern (number and character of ribs) and the shell outline. Most fossil species of pholadomyids appear to have had a prismatic outer shell layer and nacreous middle and inner shell layers, all layers consisting of aragonite (Runnegar, 1972), which commonly has been completely dissolved during diagenesis. In addition, rib characteristics seem to be influenced by, or related to, the grain size of the substrate; in coarse-grained sediments, ribs are fewer, stronger and more subdivided than in fine-grained sediments (Dhondt & Jagt, 1989). In addition, distortion caused by compaction makes it difficult to reconstruct the original shell outline.

The Sergipe Basin in north-eastern Brazil is the best exposed and arguably the most fossiliferous of the Brazilian continental margin basins. It contains one of the most extensive middle Cretaceous marine successions among the northern South Atlantic basins (e.g. Smith & Bengtson, 1991; Koutsoukos & Bengtson, 1993). The Cenomanian–Coniacian succession (Cotinguiba Formation) is well exposed and contains a rich macroinvertebrate fauna dominated by molluscs (Bengtson, 1983). Parts of this fauna were illustrated and described in the classical monographs of White (1887) and Maury (1925, 1937). More recently, selected groups of molluscs such as oysters, pinnids, pectinids, inoceramids, gastropods, and ammonites have been documented (e.g. Hessel, 1985, 1988; Seeling, 1999; Seeling & Bengtson, 1999, 2003a,b; Andrade *et al.*, 2004; Andrade, 2005; Gale *et al.*, 2005; Andrade & Santos, 2011; Lexen, 2013); however, the bivalve order Pholadomyida has so far been little studied from a taxonomic point of view (Seeling, 1999; Andrade *et al.*, 2011; Ayoub-Hannaa *et al.*, 2013).

Specimens of Pholadomyida occur in Sergipe in beds dated with ammonites as Cenomanian to early Coniacian (Bengtson, 1983; Smith & Bengtson, 1991; Koutsoukos & Bengtson, 1993; Gale *et al.*, 2005; S.I. Bengtson *et al.*, 2005) and are here the subject of taxonomic study. In addition, species of Pholadomyida from Sergipe identified and illustrated by earlier workers (e.g. White, 1887; Maury, 1925, 1937) are revised. We also discuss the stratigraphic ranges and palaeobiogeographical affinities of the identified taxa.

GEOLOGICAL SETTING

The Sergipe Basin is located in the eastern, coastal part of the state of Sergipe in north-eastern Brazil (Figures 1A,B).

The basin is structurally one of four sub-basins composing the Sergipe-Alagoas Basin, viz. the Cabo, Alagoas, Sergipe and Jacuípe sub-basins (Souza-Lima *et al.*, 2002).

As a result of the strong tectonic activity that affected north-eastern South America since the beginning of its separation from Africa in the late Mesozoic, a series of half-grabens were formed, with a regional dip averaging 10–15° to the south-east. The Sergipe Basin extends offshore and is limited to the south-east by the continental slope and to the north-west by a system of normal faults. Sedimentation was strongly controlled by differential subsidence and half-graben development along the NE–SW extensional faulting (Koutsoukos *et al.*, 1993). For details about the geological evolution and the development of the marine Cretaceous of the Sergipe Basin, see, for example, Ojeda & Fugita (1976), Ojeda (1982), Bengtson (1983), Koutsoukos & Bengtson (1993), Koutsoukos *et al.* (1993), Feijó (1995) and Souza-Lima *et al.* (2002).

The Mesozoic–Cenozoic sedimentary record of the Sergipe Basin comprises an extensive Tithonian–Aptian non-marine and Aptian–Miocene marine succession (Feijó, 1995; Souza-Lima *et al.*, 2002; Campos Neto *et al.*, 2008). Thicknesses vary between 1 and 3 km onshore, whereas offshore the succession may reach a thickness of 8 km (Ponte *et al.*, 1980). The marine succession, in particular, is widely exposed and comprises the dominantly carbonate Aptian–Albian Riachuelo and Cenomanian–Coniacian Cotinguiba formations, overlain by the siliciclastic Santonian–Miocene Calumbi Formation (Figures 2A,B; Feijó, 1995). The Cotinguiba Formation, from where the material studied here derives, averages 200 m in thickness but may locally reach 1000 m in the onshore part of the basin (Schaller, 1970). The formation consists mainly of grey to blue-grey (cream or yellowish where weathered), massive, fossiliferous, bioturbated, fine-grained limestones with sparse siliciclastic intercalations at the base (Bengtson, 1983). The rich macroinvertebrate fauna is dominated by bivalves (e.g. inoceramids, oysters, pholadomyids, pinnids, pectinids), gastropods, ammonites, echinoids, and crustaceans. The 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 onshore, exposed part of the succession represents predominantly deposition on structural highs in shallow-water neritic conditions.

The biostratigraphic zonation for the marine succession of the Sergipe Basin is based primarily on ammonites, inoceramid bivalves and foraminifers and derives essentially from the work of Bengtson (1983), Kauffman & Bengtson (1985), Hessel (1988), Smith & Bengtson (1991), Koutsoukos & Bengtson (1993), Seeling (1999), Seeling & Bengtson (1999), Gale *et al.* (2005), Andrade (2005) and S.I. Bengtson *et al.* (2005). The currently most detailed scheme for the Cenomanian–Coniacian interval comprises 13 ammonite zones (Figure 2C) and is based on Smith & Bengtson (1991), Koutsoukos & Bengtson (1993), Seeling & Bengtson (1999) and S.I. Bengtson *et al.* (2005). The position of

the Cenomanian–Turonian boundary in the basin is well correlated with the GSSP for the base of the Turonian Stage at Pueblo, Colorado, USA (Gale *et al.*, 2005). By contrast, the position of the Turonian–Coniacian boundary is provisional, as the base of the Coniacian Stage has not yet been formally defined by a GSSP (Andrade, 2005; Bengtson *et al.*, 2005). Hence, the late Turonian and early Coniacian ages attributed to some of the specimens described here should, for the present, be regarded as tentative.

MATERIAL AND METHODS

The bulk of the material studied here was collected by P. and S.I. Bengtson in 1971–1972, with complementary sampling by P. Bengtson in 1977, J. Seeling (Heidelberg University) in 1995–1996 and E.J. Andrade in 2001–2004. The

material comprises 133 specimens from 33 localities (Figure 1C) of the Cenomanian–Coniacian Cotinguiba Formation. Locality descriptions are given as follows: Alto Verde 5, Cajaíba 7, Cruzes, 6, 8, Itaporanga 2, 3, Japarutuba 4, 6, 11, Jericó 3, Laranjeiras 21, 22, Machado 2, Mata 9, Muçuca 1, Mucuri 10, Pedra Branca 1, Pedra Furada 3, 4, 5, 7, 8, 16, Pedro Gonçalves 2, São Pedro 1, São Roque 2, 5, Sergipe 5 and Timbó 4 in Bengtson (1983, appendix 1); Retiro 26 in Hessel (1988), Andrade (2005) and Manso & Andrade (2008); Japarutuba 16 in Seeling (1999), Walter (2000) and Walter *et al.* (2005); Jardim 31 in Seeling (1999), Walter (2000) and Andrade *et al.* (2004); Laranjeiras 28 is described below (also in Seeling (1999) and Walter (2000) as “C652”). One specimen (NRM-PZ Mo 167942) was collected in 1969 by R. A. Reymont (Uppsala University) from locality “2/20” (Reymont & Tait, 1972) in the area of localities Cajaíba 7–10.

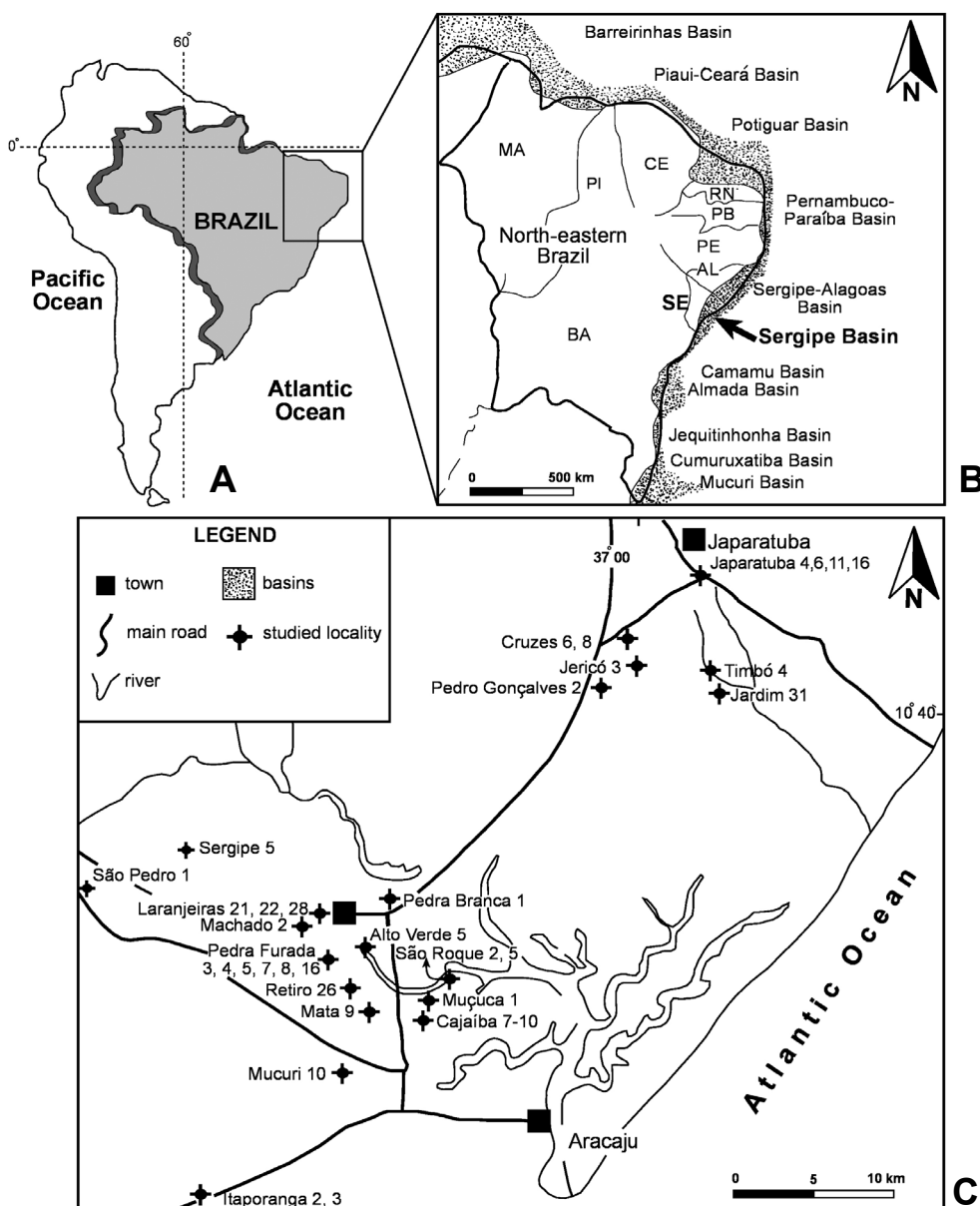


Figure 1. A-B, location of the Sergipe Basin in north-eastern Brazil. C, locality map. Abbreviations of state names: AL, Alagoas; BA, Bahia; CE, Ceará; MA, Maranhão; PB, Paraíba; PE, Pernambuco; PI, Piauí; RN, Rio Grande do Norte; SE, Sergipe.

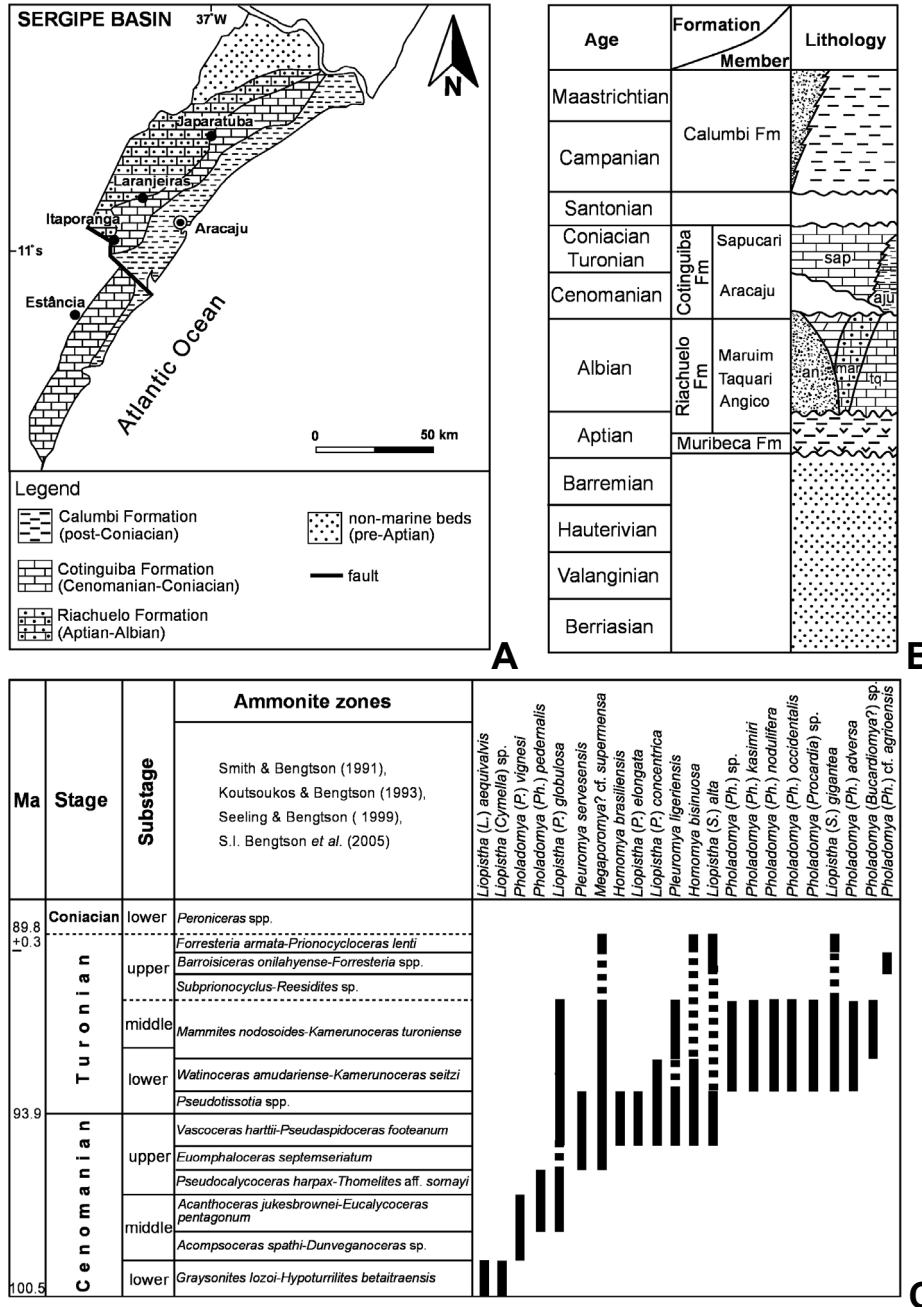


Figure 2. A, generalized geological map of the Sergipe Basin (modified after Koutsoukos & Bengtson, 1993). B, simplified Cretaceous stratigraphic framework for the Sergipe Basin (modified after Bengtson, 1983; Hessel, 1988; Smith & Bengtson, 1991; Feijó, 1995; Souza-Lima *et al.*, 2002). C, range chart for Cenomanian-Coniacian pholadomyid taxa of the Sergipe Basin. Ammonite zonation after Smith & Bengtson (1991), Koutsoukos & Bengtson (1993), Seeling & Bengtson (1999), S.I. Bengtson *et al.* (2005).

Most of the specimens are preserved as composite or internal moulds showing ornament and even muscle insertion areas. In a few cases, parts of the originally aragonitic shell are preserved, recrystallized as calcite. Some specimens are laterally deformed due to compaction.

The specimens were prepared mechanically, cleaned and photographed. A principal components analysis (PCA) was carried out to clarify the morphological relationships of some taxa, using the PAST software, version 2.16 (Hammer *et al.*, 2001) on a variance-covariance matrix of the log-transformed variables. Non-metric multidimensional scaling (nMDS) was

used to investigate biogeographic relationships. In agreement with Kiessling *et al.* (2011), although metric multidimensional scaling (MDS) makes fewer assumptions on the nature of the data, it always finds a globally optimum solution, whereas non-metric scaling iteratively seeks the best solution, which may just represent a local optimum. For details about the mechanism and utility of the latter multivariate techniques, see Huntley (2011, p. 28-37).

Linear measurements (taken with a Vernier caliper) are in millimeters. The orientation of measurements is shown in Figure 3.

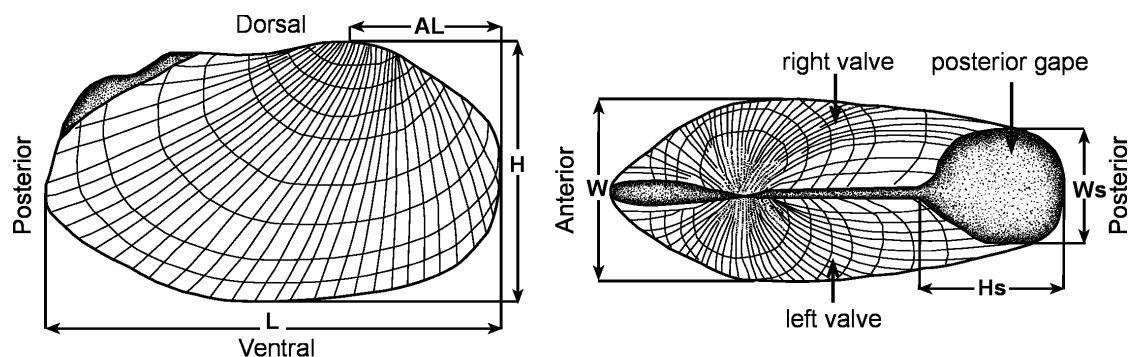


Figure 3. Orientation and measurements of pholadomyid bivalves. **A**, right lateral view; **B**, dorsal view. **Abbreviations:** L, shell length; H, shell height; W, inflation; AL, anterior length; Hs, height of siphonal gape; Ws, width of siphonal gape.

Abbreviations: L, shell length; H, shell height; W, width of articulated valves; nr, number of ribs; AL, anterior length; Hs, height of siphonal gape; Ws, width of siphonal gape; L/H, elongation; W/L, inflation; AL/L, length of anterior area; Hs/Ws, elongation of siphonal gape.

The systematic classification of the bivalves follows that of Bieler *et al.* (2010). For an alternative classification, see Carter *et al.* (2011). The morphological terminology follows the glossary of Cox (1969a) in the *Treatise on Invertebrate Paleontology*. The synonymy lists in the present work contain only entries considered to be of major importance for the study and which have been carefully checked by the authors. More comprehensive synonymies can be found in the references cited. Generic diagnoses and remarks are given in cases of ambiguity in the diagnostic features.

Identifiable specimens previously described by Seeling (1999, 2004) are listed in Appendix 1, with the revised determinations herein.

The specimens are housed in the collections of the Swedish Museum of Natural History in Stockholm, Sweden (collection acronym NRM-PZ) and the Universidade Federal de Sergipe, Aracaju, Brazil (collection acronym CPUFS-GEO).

Locality description

LARANJEIRAS 28: UTM 8 805 800N/700 600E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z- B-IV-4 Aracaju.

Section on hillside facing SE, extending laterally *ca.* 50 m. Altitude *ca.* 25-35 m.

Kcsp: Hard, locally bioturbated or coquinoid, light brown to yellowish Laranjeiras limestones.

SYSTEMATIC PALAEOLOGY

- Class BIVALVIA Linnaeus, 1758
- Subclass AUTOBRANCHIA Grobben, 1894
- Order PHOLADOMYIDA Newell, 1965
[= ANOMALODESMATA Dall, 1889]
- Superfamily PHOLADOMYOIDEA King, 1844
- Family PHOLADOMYIDAE King, 1844
[= ARCOMYIDAE P. Fischer, 1887]

Pholadomya G.B. Sowerby, 1823

Type species. *Pholadomya candida* G.B. Sowerby, 1823, by subsequent designation of Gray (1847).

Remarks. The generic diagnosis and the stratigraphic distribution of the type species were discussed in detail by Runnegar (1972).

Subgenus *Pholadomya* J. de C. Sowerby, 1823

Pholadomya (Pholadomya) adversa Riedel, 1933
(Figures 4A-C)

1933 *Pholadomya adversa* n. sp.: Riedel, p. 149, pl. 6, fig. 1.
1957 *Pholadomya adversa* Riedel: Darteville & Freneix, p. 211, pl. 33, fig. 4.

?2008 *Pholadomya* cf. *P. adversa* Riedel, 1932: Benaim & Senra, p. 92, fig. 5.

Material. One composite mould (CPUFS-GEO-643) from the lower-middle Turonian of locality Retiro 26, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 1.

Description. Shell large, oblong to elliptical, equivalved, strongly inequilateral, moderately inflated and elongate posteriorly ($L/H = 1.75$; Table 1). Postero-dorsal margin concave, nearly parallel to ventral margin. Antero-dorsal margin straight and steeply oblique towards anterior margin. Anterior margin strongly convex, joining ventral margin in a rounded angle. Posterior margin truncated and slightly gaping (Figure 4C). Ventral margin broad, slightly convex and crenulate. Umbonal area wide and convex. Beaks less prominent, nearly orthogyrate, in contact, and situated more than one-third of the total valve length from the anterior end. Lunule wide and concave (Figure 4C). Ornament consisting of well-developed, tuberculate radial ribs (20 ribs with sharp crests) separated by wide interspaces. Radial ribs crossed by thick and irregular commarginal ribs forming reticulate pattern. Anterior and posterior flanks smooth, except for commarginal growth lines.

Discussion. *Pholadomya (Pholadomya) adversa* is easily distinguished from other pholadomyid species described here by its thick, irregular, commarginal ribs, wide and deep

Table 1. Dimensions (mm) of *Pholadomya (Pholadomya) adversa* Riedel, 1932.

Specimen	L	H	W	AL	Hs	Ws	nr	L/H	AL/L	Hs/Ws	W/L
CPUFS-GEO-643	86	49.2	41	30.5	28	23	20	1.75	0.35	1.22	0.48

lunule, wide umbonal area, rounded anterior margin, truncated posterior margin, and less prominent beaks.

Pholadomya elliptica Münster, 1841, from the “Senonian” of Germany (Münster in Goldfuss, 1841, pl. 158, fig. 1) resembles *Ph. (Ph.) adversa* in having elliptical and moderately inflated valves but differs in its straight to slightly concave postero-dorsal margin, rounded posterior end, shorter anterior area and less developed commarginal ribs. *Ph. nodulifera* var. *elliptica* from the Maastrichtian of Poland (Krach, 1931, pl. 7, fig. 10) resembles *Ph. (Ph.) adversa* in having rounded anterior and ventral margins and a wide umbonal area but differs in being less elongate and in having irregular and thick radial ribs with rounded crests. *Ph. elongata* Münster, 1841, from the “Senonian” of Germany (Münster in Goldfuss, 1841, pl. 157, fig. 3) is more inflated and has more numerous radial ribs, subterminal beaks, and a rounded and narrow anterior margin. *Ph. agrioensis* Weaver, 1931, from the Valanginian of Argentina (Weaver, 1931, p. 316, pl. 36, figs. 205-206) has fewer (11) and thicker radial ribs, a less convex anterior margin and a straight postero-dorsal margin.

Occurrence. Turonian of Sergipe, Brazil (this study); Coniacian of Gabon (Darteville & Freneix, 1957), Cameroon (Riedel, 1932) and possibly the Potiguar Basin, Brazil (Benaïm & Senra, 2008); Coniacian-Campanian of Angola and Congo (Darteville & Freneix, 1957).

Pholadomya (Pholadomya) cf. P. agrioensis Weaver, 1931 (Figures 4D-E)

cf. 1931 *Pholadomya agrioensis* n. sp.: Weaver, p. 316, pl. 36, figs. 205-206.

cf. 2007 *Pholadomya agrioensis* Weaver, 1931: Lazo, p. 380, fig. 6F-H.

Material. One composite mould (NRM-PZ Mo 167818) from the upper Turonian of locality Mata 9, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 2.

Description. Shell large, rectangular-ovate, strongly inequilateral, moderately inflated and elongate posteriorly (L/H = 1.64; Table 2). Maximum inflation below umbonal area, gradually decreasing towards the posterior end. Umbonal area wide and elevated above hinge line. Antero-dorsal margin short and straight. Postero-dorsal margin wide and slightly concave. Posterior margin strongly convex, joining

ventral margin in rounded angle. Ventral margin broad, slightly convex, crenulate and nearly parallel to hinge line. A wide and deep sulcus extending from the dorsal side to the antero-ventral margin. Beaks less prominent, prosogyrate, without point of contact, situated approximately one-fourth of the total valve length from the anterior end. Ornament consisting of 12 thick radial ribs (with sharp crests) separated by wide, concave, regular and smooth interspaces (Figure 4E). Posterior flank occupying approximately one-fourth of the total valve length from the posterior end; anterior flank (one-fifth of valve length from the anterior end) smooth.

Discussion. The Sergipe specimen resembles *Pholadomya agrioensis* from the Valanginian of Argentina (Weaver, 1931, p. 316, pl. 36, figs. 205-206) in general outline and number of radial ribs but differs in being larger (L = 95 mm, H = 58 mm as opposed to L = 54 mm, H = 33 mm; Table 2) and in having regular interspaces across the valve (decreasing towards the posterior flank in Weaver’s specimens). In addition, and comparing with *Ph. agrioensis* as figured and described by Lazo (2007) from the Berriasian-Valanginian of Argentina, the Sergipe specimen differs in being less inflated, larger (L = 95 mm as opposed to < 60 mm), and in having radial ribs with sharp crests. Because of the poor preservation of the Sergipe specimen, species identification remains uncertain. In addition, the specimen was collected from a considerably higher stratigraphic level than the Argentine occurrences.

Pholadomya bulgarica Toulou, 1889, from the Cenomanian of south-eastern Europe (Toulou, 1889, p. 64, pl. 2, fig. 5) resembles the Sergipe specimen in ornament and outline but differs in being less elongate (L/H = 1.08 as opposed to 1.64) and in having a concave postero-dorsal margin. Dhondt & Dieni (1988, p. 59) considered *Ph. agrioensis* a synonym of *Ph. gigantea* (Sowerby, 1836) from the Lower Cretaceous of Sardinia (Italy). However, *Ph. agrioensis* clearly differs from *Ph. gigantea* in shell size and ornament. *Ph. gigantea* from the Lower Cretaceous of England (Sowerby, 1836; Fitton, 1837, pl. 14, fig. 1) has numerous straight and regular radial ribs (38-45 with sharp crests), whereas *Ph. agrioensis* has few, thick radial ribs (12, with rounded crests), separated by wide and smooth interspaces.

Pholadomya (Ph.) salzbergensis (Andert, 1934) from the Maastrichtian of central Poland (Abdel-Gawad, 1986, p. 179, pl. 44, figs. 1-4), resembles the Sergipe specimen in possessing few radial ribs but differs in having subterminal beaks, well-developed commarginal ribs and a high anterior area (higher than the posterior area). *Ph. (Ph.) pedernalis*

Table 2. Dimensions (mm) of *Pholadomya (Pholadomya) cf. agrioensis* Weaver, 1931.

Specimen	L	H	W	AL	nr	L/H	AL/L	W/L
NRM-PZ Mo 167818	95	58	45	25	12	1.64	0.26	0.47

Roemer (1852, p. 45, pl. 6, fig. 4) from the Turonian of Texas differs in having fewer (5) and thicker radial ribs, subterminal beaks and in being less elongate.

Occurrence. Berriasian–Valanginian of Argentina (Weaver, 1931; Lazo, 2007); possibly Turonian of Sergipe, Brazil (this study).

Pholadomya (Pholadomya) kasimiri Pusch, 1837
(Figures 4F–H, 5A–G)

1837 *Pholadomya kasimiri mirim*: Pusch, p. 88, pl. 8, fig. 13.
1841 *Pholadomya Esmarki* [sic] Pusch [sic]: Goldfuss, p. 272, pl. 157, fig. 10a-c,d(?).

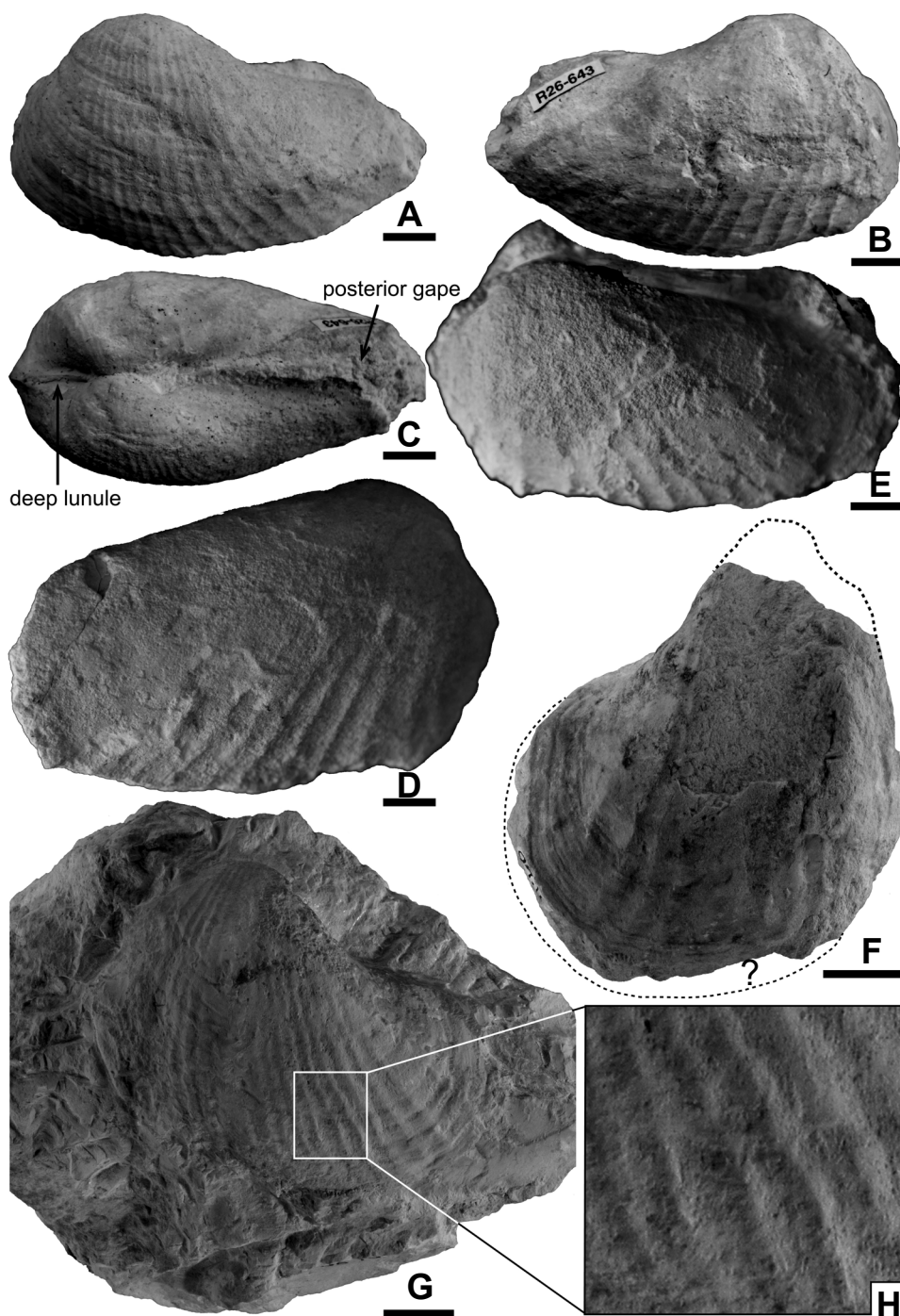


Figure 4. A–C, *Pholadomya (Pholadomya) adversa* Riedel, 1932 from the lower–middle Turonian of locality Retiro 26 (CPUFS-GEO-643). A, lateral view of left valve; B, right lateral view; C, dorsal view. D–E, *Pholadomya (Pholadomya) cf. agrioensis* Weaver, 1931, from the upper Turonian of locality Mata 9 (NRM-PZ Mo 167818). D, right lateral view of articulated composite mould; E, left lateral view showing the wide, smooth and concave interspaces between the radial ribs. F–H, *Pholadomya (Pholadomya) kasimiri* Pusch, 1837, from the lower-middle Turonian. F, right lateral view of incomplete composite mould showing the trigonal form; locality Pedra Furada 3 (NRM-PZ Mo 167819); G, left lateral view of composite mould; H, close-up showing the tuberculate radial ribs; locality Pedra Furada 4 (NRM-PZ Mo 167820). All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

?1916 *Pholadomya occidentalis* Morton: Gardner, p. 630, pl. 37, figs. 1-3.

1931 *Pholadomya Esmarkii* [sic] Nilss.: Krach, p. 361, pl. 7, fig. 15; pl. 8, fig. 1.

1986 *Pholadomya (Pholadomya) kasimiri* Pusch: Abdel-Gawad, p. 176, pl. 45, figs. 3-4; pl. 46, figs. 4-5.

Material. Nineteen composite moulds (NRM-PZ Mo 167819-167837) from the lower–middle Turonian of localities Pedra Furada 3, 4 and 16, São Pedro 1, Laranjeiras 22, and Alto Verde 5, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 3.

Description. Shell medium-sized to large, variable in outline, subtrigonal, trapezoidal to elongate-ovate, equivalved, strongly inequilateral, highly inflated and posteriorly elongate ($L/H = 1.32$ on average; Table 3). Anterior area short ($AL/L = 0.21$ on average). Maximum inflation slightly below umbonal area, valves increasingly compressed posteriorly. Anterior margin slightly convex to truncated, joining ventral margin in rounded curve. Posterior margin subtruncated and slightly gaping. Antero-dorsal shoulder short, higher than postero-dorsal margin, forming an obtuse angle with anterior margin (Figures 5C,D). Postero-dorsal margin concave, bordered by dorsal umbonal ridges and forming a high posterior edge in some individuals (Figures 5D,E). Ventral margin broadly arched and feebly crenulate. Umbonal area wide and moderately convex. Beaks pointed, prosogyrous, positioned near anterior end (one-fifth of total valve length from anterior end). Escutcheon shallow and smooth (Figure 5F). Ornament consisting of 14-18 well-developed, tuberculate radial ribs separated by wide, shallow and concave interspaces. Ribs absent along flattened anterior part, except for commarginal ribs. Faint tubercles present at intersections of radial and commarginal ribs; tubercles well developed dorsally (granular appearance; Figure 4H).

Discussion. The Sergipe specimens show strong similarities to *Pholadomya kasimiri* from the Campanian-Maastrichtian of central Poland (Pusch, 1837; Abdel-Gawad, 1986) with respect to general outline, size, and number and development of radial ribs. The species is characterized by subterminal beaks, an expanded oval posterior side, and a well-developed umbonal ridge with distinct tuberculate radial ribs, which are absent along the anterior flank.

Goldfuss (1841) considered *Pholadomya kasimiri* Pusch a synonym in part of *Cardita esmarkii* Nilsson, 1827. However, he wrongly attributed *C. esmarkii* to Pusch (1837) (see synonymy herein). In addition, he also described and figured *C. esmarkii* Nilsson (Goldfuss, 1841, p. 187, pl. 133, fig. 14). Abdel-Gawad (1986) placed the two species in separate subgenera, as *Ph. (Pholadomya) kasimiri* and *Ph. (Bucardiomya) esmarkii*. *Ph. esmarkii* indeed shows similarities to *Ph. kasimiri* but differs in having subcordate valves, a less expanded posterior area, no umbonal ridge, closely spaced, faint, non-tuberculate radial ribs and in being taller. In addition, *Ph. esmarkii* possesses a deep umbonal-ventral sulcus in the middle part of the valve (Nilsson, 1827, pl. 10, fig. 8C). The latter, distinct morphological character is

absent in *Ph. esmarkii*, as figured and described by Goldfuss (1841, p. 272, pl. 157, fig. 10d) and Krach (1931, p. 361, pl. 8, fig. 1). Therefore, their specimens are closer to *Ph. kasimiri* than to *Ph. esmarkii*.

On the basis of the H/L ratio, Krach (1931, p. 362) described three forms of *Pholadomya esmarkii* from the Campanian–Maastrichtian of Poland, viz. (i) an elongate, trapezoidal form ($L = 85$, $H = 47$, $W = 44$ mm, $L/H = 1.81$) with an expanded posterior part, terminal to subterminal beaks, and ornament consisting of 19 radial ribs; (ii) a taller, trigonal form ($L = 83$ mm, $H = 60$ mm, $W = 53$ mm, $L/H = 1.38$) ornamented with more numerous radial ribs (30); and (iii) a form similar to the trigonal form but differing in being much taller ($L = 63$ mm, $H = 72$ mm, $W = 50$ mm, $L/H = 0.87$) and having closely spaced radial ribs, which are less sharp than in the two other forms and restricted to the middle part of the valve.

Abdel-Gawad (1986) also described three forms of *Pholadomya kasimiri* (a short, elongate, and an intermediate form) based on the H/L ratio. In the present study, two forms are recognized, an elongate form, with an expanded posterior area and terminal to subterminal beaks, and a taller, trigonal form. *Ph. (Ph.) kasimiri* is highly variable in general outline (L/H) and anterior length (AL/L). The best separation of the two forms is obtained from the first three principal components that account for a cumulative variance of 95.33% (PC1: 58.89%; PC2: 22.53%; PC3: 13.91%) (Figure 6E). The anterior length (AL) and its ratio to shell length (AL/L) shows a strong positive correlation with PC1. Low PC1 is associated with wider anterior areas, whereas narrow anterior areas and a terminal to subterminal beaks are characterized by high PC1. Both varieties occur in the two forms of *Ph. (Ph.) kasimiri* illustrated in Figure 6A, whereas *Ph. (Ph.) nodulifera* differs in having a wide anterior area (high PC1 scores) and the umbonal area situated one-third of the total shell length from the anterior end. Other variables such as height (H) and width (W) are positively correlated with PC2. This means that individuals with high PC2 scores are much taller and thicker than individuals with low PC2 scores. PC3 accounts for the elongation of the shell (L/H) and the separation of the two forms. High PC3 values characterize very elongate specimens, whereas specimens with low PC3 values are shorter (trigonal) (Figures 6C,D). Thus, by plotting PC1 vs. PC2 and PC1 vs. PC3 scores of individual specimens, two forms of *Ph. (Ph.) kasimiri* are recognized on the basis of shell outline (L/H) and position of the umbonal area. However, with respect to other variables such as shell height, inflation, number and distribution of radial ribs, shell margins, and curvature of the umbonal area, the two forms are similar and best referred to the same species.

Pholadomya elliptica Münster, 1841, from the Upper Cretaceous of Germany (Münster in Goldfuss, 1841, p. 275, pl. 158, fig. 1) differs from *Ph. (Ph.) kasimiri* in being more elongate and in having a wide anterior area, truncated antero-dorsal margin, and a high posterior end. *Ph. occidentalis* Morton, 1833, from the Upper Cretaceous of the USA (Gardner, 1916, p. 630, pl. 37, figs. 1-3), resembles *Ph. (Ph.)*

Table 3. Dimensions (mm) of *Pholadomya (Pholadomya) kasimiri* Pusch, 1837.

Specimen	L	H	W	AL	Hs	Ws	nr	L/H	AL/L	Hs/Ws	W/L
NRM-PZ Mo 167819	55	57	40	13	31	12	14	0.96	0.24	2.58	0.73
NRM-PZ Mo 167820	66	60	50	13	26	10	17	1.10	0.20	2.60	0.76
NRM-PZ Mo 167821	59	55	34	13	27	15	18	1.07	0.22	1.80	0.58
NRM-PZ Mo 167822	66	48	40	14	27	16	18	1.38	0.21	1.69	0.61
NRM-PZ Mo 167823	38	21	20	5	21	7	17	1.81	0.13	3.00	0.53
NRM-PZ Mo 167824	58	60	42	14	33	11	15	0.97	0.24	3.00	0.72
NRM-PZ Mo 167825	73	47	42	13	33	11	16	1.55	0.18	3.00	0.58
NRM-PZ Mo 167826	72	52	43	17	34	17	14	1.38	0.24	2.00	0.60
NRM-PZ Mo 167827	40	40	37	10	26	13	15	1.00	0.25	2.00	0.93
NRM-PZ Mo 167828	69	42	36	13	29	10	16	1.64	0.19	2.90	0.52
NRM-PZ Mo 167829	57	33	32	9	27	12	15	1.73	0.16	2.25	0.56
NRM-PZ Mo 167830	58	39	35	14	26	12	17	1.49	0.24	2.17	0.60
NRM-PZ Mo 167831	53	39	28	13	23	12	18	1.36	0.25	1.92	0.53
NRM-PZ Mo 167832	37	40	28	8	--	--	14	0.93	0.22	--	0.76
NRM-PZ Mo 167833	63	42	33	15	31	15	18	1.50	0.24	2.07	0.52
Range	37-73	21-60	20-50	5-17	21-34	7-17	14-18	0.93-1.81	0.13-0.25	1.69-3.00	0.52-0.93
Mean	57.6	45	36	12.27	28.14	12.35	16.13	1.32	0.21	2.36	0.63

kasimiri in general outline, shell size, and ornament and is probably a synonym of *Ph. esmarkii*.

Occurrence. Turonian of Sergipe, Brazil (this study); Campanian-Maastrichtian of Germany (Goldfuss, 1841), Poland (Pusch, 1837; Krach, 1931; Abdel-Gawad, 1986), Bulgaria and Ukraine (Abdel-Gawad, 1986).

Pholadomya (Pholadomya) nodulifera Münster, 1841
(Figures 5H-J, 7A-G)

1841 *Pholadomya nodulifera*: Münster in Goldfuss, p. 273, pl. 158, figs. 2a-b.

?1841 *Pholadomya albina* Reiche: Roemer, p. 75, pl. 10, fig. 7.

1864 *Pholadomya rostrata* Matheron: Zittel, p. 115, pl. 2, fig. 2.

1864 *Pholadomya rostrata* Matheron var. *royana* d'Orbigny: Zittel, p. 115, pl. 2, fig. 1.

?1883 *Pholadomya nodulifera* Münster: Frič, p. 107, text-figs. 75a-c, 76.

1889 *Pholadomya nodulifera* Münster: Holzapfel, p. 155, pl. 15, fig. 1.

1897 *Pholadomya nodulifera* Münster: Frič, p. 60, text-fig. 71c, ?a-b.

?1931 *Pholadomya nodulifera* Münster var. *elliptica* Münster (Scupin, 1913): Krach, 360, pl. 7, figs. 10-11.

1934 *Pholadomya nodulifera* Münster: Andert, p. 328, pl. 15, figs. 3-4.

1934 *Pholadomya nodulifera* Münster var. n. *fritschi*: Andert, p. 332, pl. 15, fig. 5.

1934 *Pholadomya nodulifera* Münster var. n. *salzbergensis*: Andert, p. 333, pl. 15, figs. 6-7.

1962 *Pholadomya safrensis*: Abbass, p. 160, pl. 24, fig. 2.

?1962 *Pholadomya vignesi* Lartet: Abbass, p. 157, pl. 24, fig. 7.

v1983 *Pholadomya* aff. *esmarki* [sic] Nilsson: Lefranc in Bengtson, p. 45.

1986 *Pholadomya (Pholadomya) salzbergensis* Andert: Abdel-Gawad, p. 179, pl. 44, figs. 1-4.

1987 *Pholadomya nodulifera* Münster: Dhondt, p. 89, pl. 5, figs. 4-5. (With additional synonymy).

2003 *Pholadomya (Pholadomya)* cf. *nodulifera* Münster: Szente, p. 167, pl. 1, fig. 26.

Material. Sixteen composite moulds (NRM-PZ Mo 167838-167852; CPUFS-GEO-1300) from the lower-middle Turonian of localities Pedra Branca 1, Laranjeiras 22, Pedra Furada 4, 7 and 8, Muçuca 1, and Pedro Gonçalves 2, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 4.

Description. Shell medium-sized to large, variable in outline, elongate-ovate to oblong, strongly inequilateral, equivalved, highly inflated, and posteriorly expanded. Maximum inflation at approximately one-half of total shell length (W/L = 0.59 on average; Table 4). Anterior and posterior margins convex, joining ventral margin in rounded curves. Ventral margin broadly rounded and crenulate. Some individuals bearing wide and deep dorso-ventral sulcus (Figure 7A). Umbonal area wide and strongly convex. Beaks prominent, slightly incurved anteriorly, situated more than one-third of the total valve length from the anterior end. Escutcheon wide, concave and smooth (Figure 5J). Posterior and anterior ends gaping. Ornament consisting of 13-22 radial ribs separated by wide, irregular and smooth interspaces. Radial ribs well developed, irregularly distributed, tuberculate, crossed by irregular commarginal ribs. Intersection of radial and commarginal ribs forming a reticulate pattern, well developed towards the dorsal area. Posterior flank smooth except for commarginal growth lines (Figure 5I).

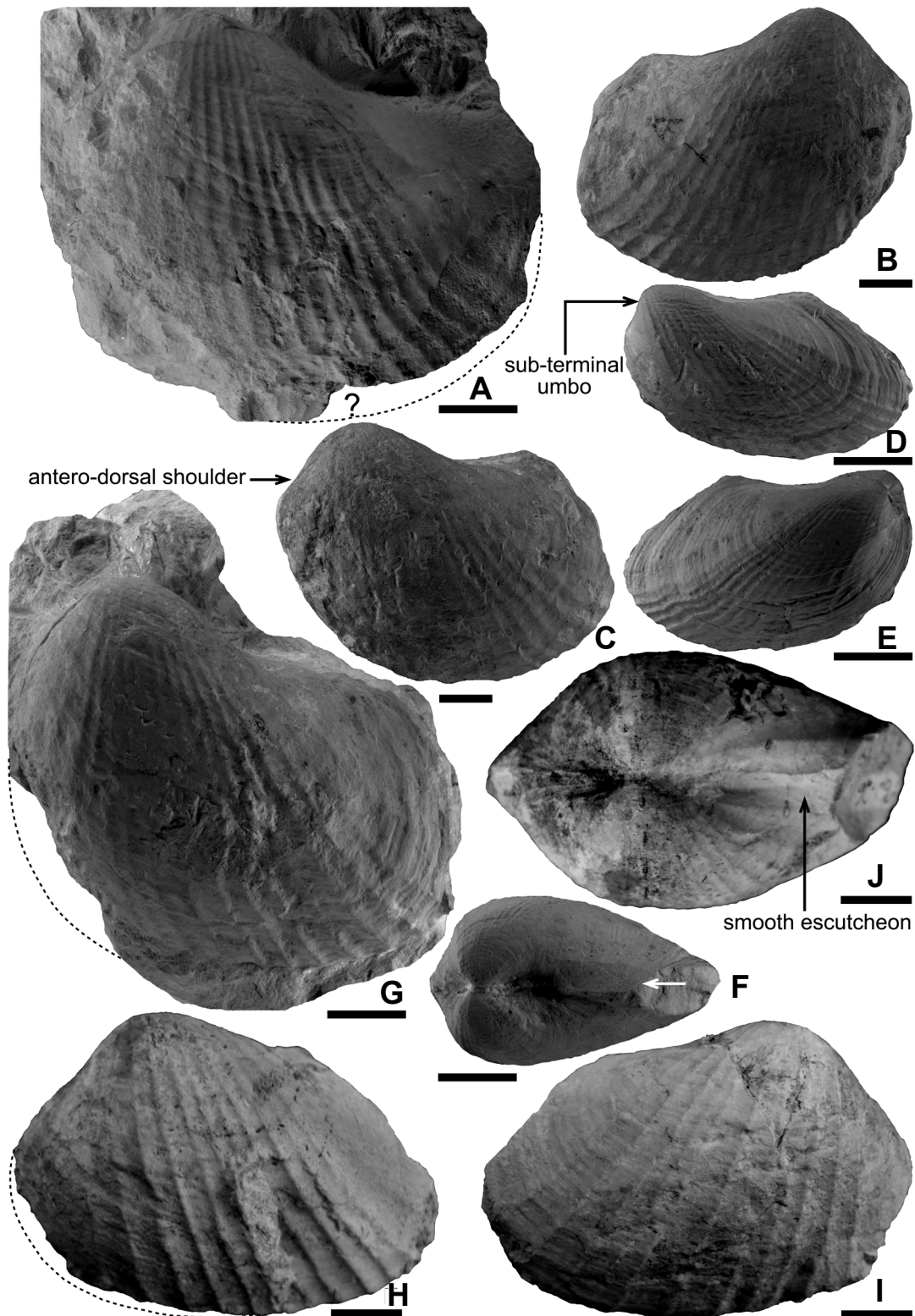


Figure 5. A-G, variation in outline of composite moulds *Pholadomya* (*Pholadomya*) *kasimiri* Pusch, 1837, from the lower–middle Turonian. **A**, left lateral view, trigonal form with subterminal beaks; locality Pedra Furada 3 (NRM-PZ Mo 167821); **B**, side view of right valve; **C**, left lateral view showing anterior shoulder (arrowed); locality Pedra Furada 4 (NRM-PZ Mo 167822); **D**, side view of left valve showing an elongate form with expanded posterior area and subterminal beaks; **E**, side view of right valve showing the smooth anterior and posterior flanks; **F**, dorsal view showing the smooth and shallow escutcheon (arrowed); locality Laranjeiras 22 (NRM-PZ Mo 167824); **G**, left lateral view, trigonally shaped variety; locality São Pedro 1 (NRM-PZ Mo 167823). **H-J**, composite mould of *Pholadomya* (*Pholadomya*) *nodulifera* Münster, 1841, from the lower-middle Turonian of locality Pedro Gonçalves 2 (CPUFS-GEO-1300). **H**, side view of left valve showing well-developed radial ribs with sharp crests, separated by wide and strongly concave interspaces; **I**, right lateral view; **J**, dorsal view of both valves showing wide and smooth escutcheon with wide posterior gape. All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

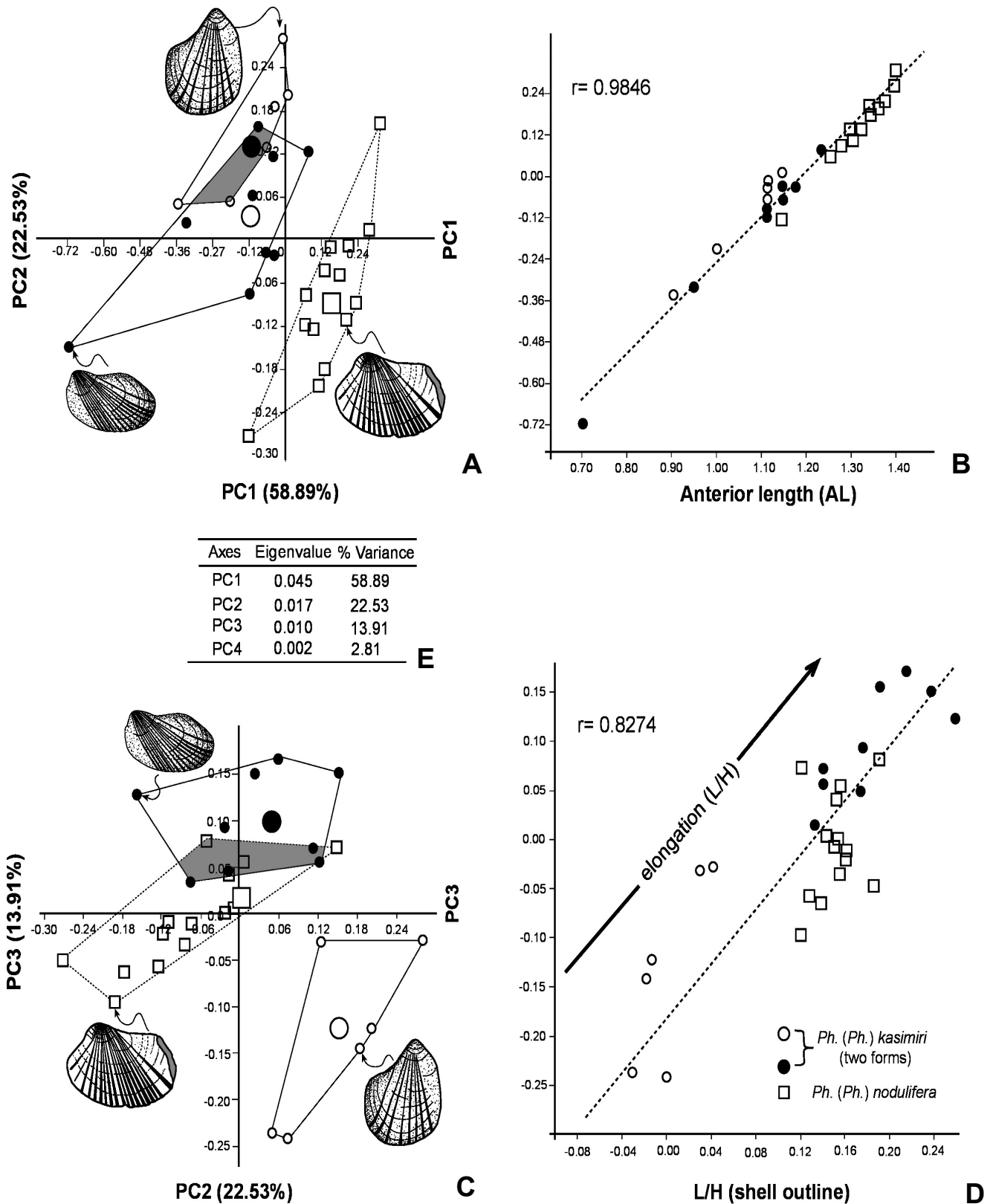


Figure 6. Principal component analysis (PCA) of *Pholadomya (Pholadomya) kasimiri* Pusch, 1837, and *Ph. (Ph.) nodulifera* Münster, 1841, using the PAST software (Hammer *et al.* 2001). **A**, scatter plot of PC1 vs. PC2 showing the separation between the two species on the basis of the anterior length (AL) and A/L ratio; **B**, relationship between PC1 and anterior length (AL) showing that *Ph. (Ph.) nodulifera* has a much greater anterior length (PC1 score ranges from -0.12 to 0.30) than the two forms of *Ph. (Ph.) kasimiri*; **C**, scatter plot of PC2 vs. PC3 showing the separation between the two species based on shell outline (H/L); **D**, relationship between PC3 and shell outline (H/L) showing that the elongate form of *Ph. (Ph.) kasimiri* is taller than the trigonal form and *Ph. (Ph.) nodulifera* (PC3 scores range from 0.0 to 0.15); **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.

Discussion. *Pholadomya (Ph.) nodulifera* is a highly variable species but is readily distinguished by its comparatively few and irregular radial ribs, rounded margins, crenulate ventral margin, well-developed umbonal ridge, wide anterior area (high PC1 scores, Figures 6A,B), wide siphonal gape, dorso-ventral sulcus (in some individuals) and smooth posterior flank, except for commarginal growth lines.

As a result of the high variability, the species has been split into varieties. For instance, Andert (1934) described the varieties *fritschii* and *salzbergensis*, separated by differences in number and sharpness of radial ribs (var. *salzbergensis* has few, sharp, radial ribs). In agreement with Dhondt (1987), these two varieties and some other species such as *Pholadomya albina* Reiche in Roemer, 1841, *Ph. elisabethae* Moesch, 1875, and *Ph. micronodulifera* Sobetski, 1977, are here regarded as junior synonyms of *Ph. (Ph.) nodulifera* (Figure 8). *Ph. nodulifera* var. *elliptica* Krach, 1931, from the Maastrichtian of Poland differs in having well-developed, irregular, rounded radial ribs, which cover the entire valve surface. Krach's variety *elliptica* is considered here a possible synonym of *Ph. (Ph.) nodulifera*.

The general outline and ribbing pattern of *Pholadomya vignesi* Lartet, 1877, from the Cenomanian of the Eastern Desert of Egypt (Abbass, 1962, p. 158, pl. 24, fig. 7) are closely similar to those of *Ph. (Ph.) nodulifera*. Abbass (1962, p. 160, pl. 24, fig. 2) described the new species *Ph. safrensis* from the Cenomanian of the Sinai Peninsula on the basis of a wide posterior gape, truncated posterior margin and highly inflated valves. However, with respect to shell outline, size, inflation, and ornament, *Ph. safrensis* is identical to *Ph. (Ph.) nodulifera* and here considered a junior synonym.

Pholadomya (Ph.) kasimiri resembles *Ph. (Ph.) nodulifera* in possessing an umbonal keel and rounded margins but differs in its terminal to subterminal beaks, narrow posterior gape, well-developed, tuberculate radial ribs covering the entire valve, and in being less elongate ($L/H = 1.32$ vs. 1.42 on average for the Sergipe specimens).

Pholadomya speetonensis Woods, 1909, from the Lower Cretaceous of England (Woods, 1909, p. 248, pl. 41, fig. 4) closely resembles *Ph. (Ph.) nodulifera* in general outline ($L/H = 1.38$), number of radial ribs and rounded shell margins but has less prominent and nearly orthogyrate beaks, thick, flat-crested radial ribs with wide, smooth, and flat interspaces. *Ph. agrioensis* Weaver, 1931, from the Valanginian of Argentina (Weaver, 1931, p. 316, pl. 36, figs. 205-206) resembles *Ph. (Ph.) nodulifera* in possessing a dorso-ventral sulcus but differs in being more elongate and in having thick, rounded radial ribs. *Ph. umbonata* Roemer, 1841, from the Upper Cretaceous of Germany (Roemer, 1841, pl. 10, fig. 6) is also similar to *Ph. (Ph.) nodulifera* in its elongate-ovate valves but differs in having fewer ribs covering only the anterior third of the flank.

Occurrence. Cenomanian of Egypt (Abbass, 1962) and central Asia (Dhondt 1987, p. 91); Turonian of Sergipe, Brazil (this study); Turonian-Coniacian of Germany (Roemer, 1841; Holzappel, 1889), north-eastern Alps (Zittel, 1864), and the Czech Republic (Andert, 1934); upper Santonian of Austria

(Dhondt, 1987; Szente, 2003); Maastrichtian of Poland (Krach, 1931; Abdel-Gawad, 1986).

Pholadomya (Pholadomya) occidentalis Morton, 1833
(Figures 7H-K, 9A)

1833 *P. occidentalis*, (S.G.M.): Morton, p. 292, pl. 8, fig. 3.
1907 *Pholadomya occidentalis* Morton: Weller, p. 513, pl. 56, figs. 1-3.

1926 *Pholadomya occidentalis* Morton: Wade, p. 72, pl. 23, figs. 13-15.

1954 *Pholadomya occidentalis* Morton: Groot *et al.*, p. 45, pl. 5, fig. 1.

1958 *Pholadomya occidentalis* Morton: Richards, p. 158, pl. 26, figs. 3-4.

1972 *Pholadomya occidentalis* Morton: Pickett, pl. 3, fig. 1.

Material. Seven composite moulds (NRM-PZ Mo 167853-167859) from the lower-middle Turonian of localities Laranjeiras 22, Pedra Furada 4 and 5, and Machado 2, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 5.

Description. Shell large, equivalved, strongly inequilateral, highly inflated and extended posteriorly; lateral outline elliptical. Maximum inflation slightly below umbonal area, gradually decreasing towards posterior side ($W/L = 0.58$ on average; Table 5). Length of nearly horizontal postero-dorsal margin two-thirds of valve length and parallel to ventral margin. Antero-dorsal margin short ($AL/L = 0.11$ on average; Table 5), rounded, steeply oblique, joining anterior margin in rounded angle. Ventral margin broadly rounded, crenulate, joining posterior margin in rounded angle. Posterior margin slightly rounded, higher than anterior margin and widely gaping. Umbonal area wide and highly inflated. Beaks prominent, terminal, incurved anteriorly, elevated above hinge line, situated less than one-sixth of the total valve length from the anterior end (Figures 7H, J). Ornament consisting of 14-18 irregular, spinose, radial ribs, crossed by irregular commarginal growth lines forming a dorsal grid-like pattern (Figure 7I). Radial ribs thick, rounded, serrated, widely separated towards postero-ventral side and becoming finer and closely spaced dorsally and anteriorly. Commarginal ribs well developed towards ventral side and separated by wide interspaces. Hinge and other internal features not visible. Specific determination of specimen NRM-PZ Mo 167859 uncertain due to poor preservation.

Discussion. *Pholadomya (Pholadomya) occidentalis* is readily distinguished from other pholadomyid species from the Sergipe Basin by the following features: (i) large shell, (ii) terminal beaks; (iii) wide posterior gape; (iv) irregular, tuberculate radial ribs, fine and closely spaced anteriorly, thick and widely spaced posteriorly; (v) small anterior area; (vi) broadly rounded ventral margin; (vii) maximum shell height near the posterior end; (viii) crenulate ventral margin. *Pholadomya tippiana* Conrad, 1858, from the Upper Cretaceous of Owl Creek, Missouri, USA (Stephenson, 1955, p. 115, pl. 8, figs. 8-13), shows strong similarities to *Ph. (Ph.)*

Table 4. Dimensions (mm) of *Pholadomya (Pholadomya) nodulifera* Münster in Goldfuss (1841).

Specimen	L	H	W	AL	nr	Hs	Ws	L/H	AL/L	Hs/Ws	W/L
CPUFS-GEO-1300	63	44	38	24	13	31	19	1.43	0.38	1.63	0.60
NRM-PZ Mo 167838	86	65	50	25	17	--	--	1.32	0.29	--	0.58
NRM-PZ Mo 167839	54	40	32	19	16	29	14	1.35	0.35	2.07	0.59
NRM-PZ Mo 167840	68	48	41	22	22	37	17	1.42	0.32	2.17	0.60
NRM-PZ Mo 167841	64	46	40	20	18	35	21	1.39	0.31	1.67	0.63
NRM-PZ Mo 167842	63	44	37	20	15	28	14	1.43	0.32	2.00	0.59
NRM-PZ Mo 167843	55	38	34	18	19	30	16	1.45	0.33	1.87	0.62
NRM-PZ Mo 167844	62	44	35	23	18	--	--	1.41	0.37	--	0.56
NRM-PZ Mo 167845	50	38	30	20	18	26	11	1.32	0.40	2.36	0.60
NRM-PZ Mo 167846	58	40	35	18	15	45	25	1.45	0.31	1.80	0.60
NRM-PZ Mo 167847	75	52	43	25	18	36	16	1.44	0.33	2.25	0.57
NRM-PZ Mo 167848	54	39	30	21	15	31	14	1.38	0.39	2.21	0.56
NRM-PZ Mo 167849	70	45	38	22	17	--	--	1.56	0.31	--	0.54
NRM-PZ Mo 167850	43	28	25	14	18	23	11	1.54	0.33	2.09	0.58
Range	43-86	28-65	25-50	14-25	13-22	23-45	11-25	1.32-1.56	0.29-0.40	1.63-2.36	0.54-0.63
Mean	61.78	43.64	36.28	20.78	17	31.90	16.18	1.42	0.34	2.01	0.59

occidentalis in ribbing pattern, inflation, and development of the umbonal area but differs in being less elongate (L/H = 1.23-1.26 as opposed to 1.55 on average for the Sergipe specimens; Table 5) and in having subterminal beaks. *Ph. conradi* Gardner, 1916, from the Upper Cretaceous of the USA (Gardner, 1916, p. 632, pl. 38, fig. 1) closely resembles *Ph. (Ph.) occidentalis* in having terminal beaks, elliptical valves and a broad and rounded ventral margin but lacks radial ribs on the anterior and posterior thirds of the valve. *Ph. conradi* is probably a synonym of *Ph. (Ph.) occidentalis*, and the presence or absence of radial ribs depends mainly on the state of preservation. *Ph. gigantea* (J. de C. Sowerby, 1836), recorded from the Lower Cretaceous of France, Germany, Mexico, Argentina, Chile and Oman (see Lazo, 2007, p. 380), resembles *Ph. (Ph.) occidentalis* in general outline and shell size but differs in having a wide anterior area, subterminal beaks (situated one-fourth of the total shell length from the anterior end) and numerous regular and straight radial ribs (38-45; see Weaver, 1931, p. 314). In addition, *Ph. gigantea* is recorded from a lower stratigraphic level, viz., Tithonian?–Valanginian to upper Aptian (Dhondt & Dieni, 1988; Lazo, 2007). *Ph. elongata* Münster, 1841, from the Upper Cretaceous of Switzerland (Münster in Goldfuss, 1841, p. 270, pl. 157, fig. 3) resembles *Ph. (Ph.) occidentalis* in having terminal beaks but is less inflated and more elongate and has a narrower anterior area and more numerous radial ribs (34) with intercalatories.

Occurrence. Turonian of Sergipe, Brazil (this study); Upper Cretaceous, mainly Campanian-Maastrichtian of the United States Atlantic coastal plain (Morton, 1833; Weller, 1907; Richards, 1958; Pickett, 1972; Sohl & Koch, 1984), Tennessee (Wade, 1926), and Mexico (Vega *et al.*, 1995).

Pholadomya (Pholadomya) pedernalis Roemer, 1852
(Figures 9B-E)

1852 *Pholadomya pedernalis* n. sp.: Roemer, p. 45, pl. 6, fig. 4.

1912 *Pholadomya pedernalis* Roemer: Pervinquierè, p. 288, pl. 21, figs. 5-7.

1957 *Pholadomya cf. pedernalis* Roemer: Dartevèlle & Freneix, p. 210, pl. 33, fig. 3.

1958 *Pholadomya aff. pedernalis* Roemer: Barber, p. 28, pl. 8, fig. 5; pl. 9, figs. 8-9.

1962 *Pholadomya pedernalis* Roemer: Abbass, p. 161, pl. 24, fig. 4.

1999 *Pholadomya (Pholadomya) cf. pedernalis* Roemer: Seeling, p. 134, pl. 5, fig. 19.

2004 *Pholadomya pedernalis* Roemer: Abdel-Gawad *et al.*, pl. 4, fig. 5.

?2004 *Pholadomya pedernalis* Roemer: Akpan & Ntekim, p. 30, fig. 6q.

?2006 *Pholadomya (Pholadomya) pedernalis* Roemer: El Qot, p. 90, pl. 18, figs. 4, 5a-b.

?2007 *Pholadomya (Pholadomya) pedernalis* Roemer: Mekawy, p. 236, pl. 5, figs. 16-17.

2008 *Pholadomya (Pholadomya) pedernalis* Roemer: Mekawy & Abu-Zied, p. 314, pl. 3, fig. 13.

2014 *Pholadomya (Pholadomya) pedernalis* Roemer, 1852: Ayoub-Hannaa *et al.*, p. 125, pl. 12, fig. 5.

Material. Six composite moulds (NRM-PZ Mo 167860-167865) from the middle-upper Cenomanian of localities Cruzes 6 and 8 and the upper Cenomanian of Timbó 4, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 6.

Description. Shell small to medium-sized, elongate-ovate, equivalved, strongly inequilateral and posteriorly expanded. Greatest inflation slightly below umbonal area (W/L = 0.69 on average; Table 6). Anterior end nearly as high as posterior end. Anterior margin truncated, sloping steeply to

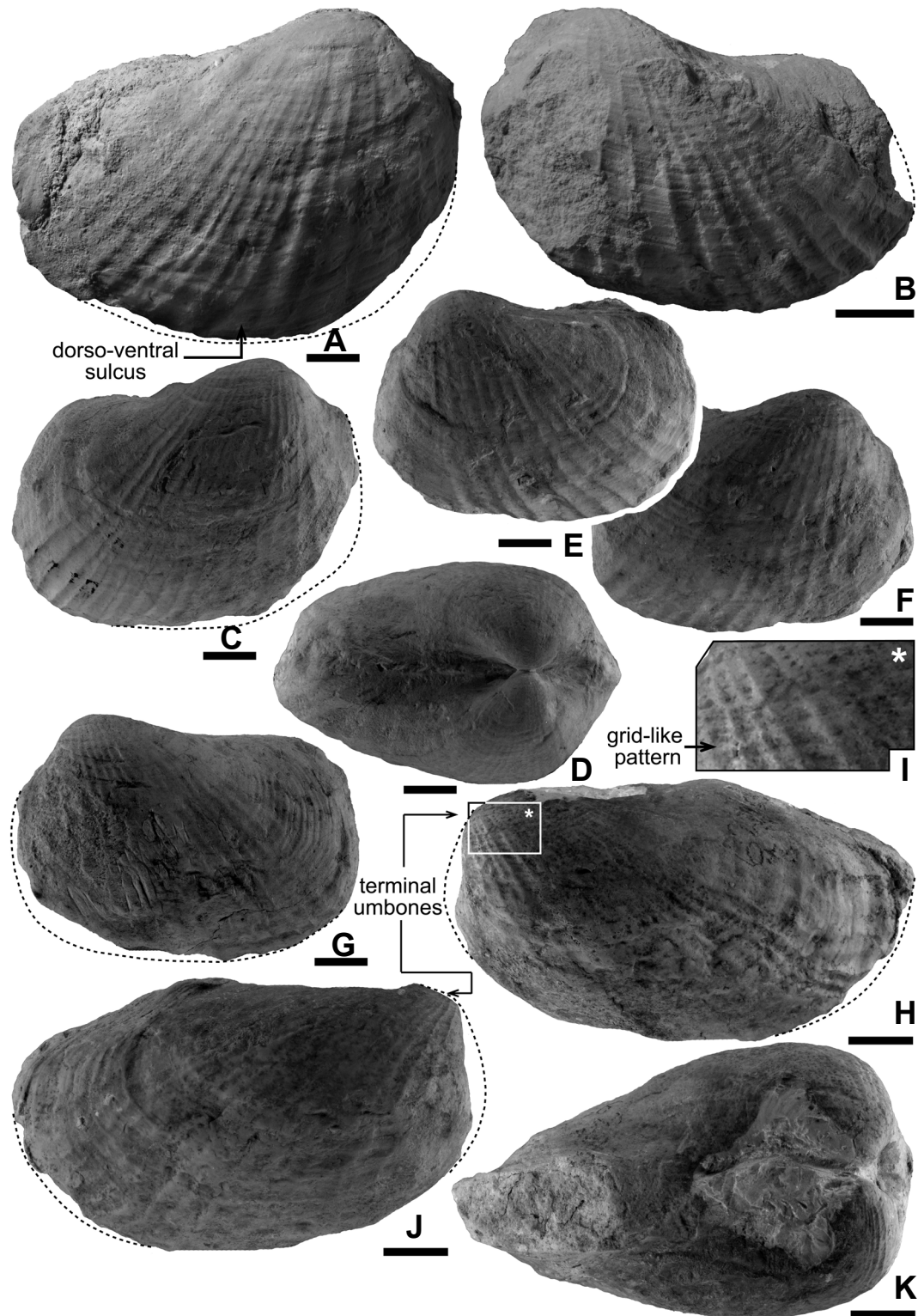


Figure 7. A-G, variation in outline of *Pholadomya* (*Pholadomya*) *nodulifera* Münster, 1841; composite moulds from the lower–middle Turonian. **A**, right lateral view showing the deep umbonal-ventral sulcus; locality Pedra Branca 1 (NRM-PZ Mo 167838); **B**, side view of left valve showing irregular and sharp radial ribs; locality Laranjeiras 22 (NRM-PZ Mo 167839); **C**, right lateral view; **D**, dorsal view showing deep escutcheon and highly inflated valves; locality Pedra Furada 4 (NRM-PZ Mo 167840); **E**, side view of left valve; **F**, side view of right valve showing a wide umbonal area; locality Pedra Furada 4 (NRM-PZ Mo 167841); **G**, left lateral view showing the oblong outline of the left valve and smooth posterior flank (covered only with commarginal growth lines); locality Muçuca 1 (NRM-PZ Mo 167842). **H-K**, *Pholadomya* (*Pholadomya*) *occidentalis* Morton, 1833; composite mould from the lower–middle Turonian of locality Laranjeiras 22 (NRM-PZ Mo 167853). **H**, side view of left valve showing the extreme terminal beaks and strongly extended posterior area; **I**, close-up showing grid-like pattern on the dorsal surface of left valve; **J**, Right lateral view showing irregular tuberculate radial ribs; **K**, dorsal view of highly inflated, articulated specimen. All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

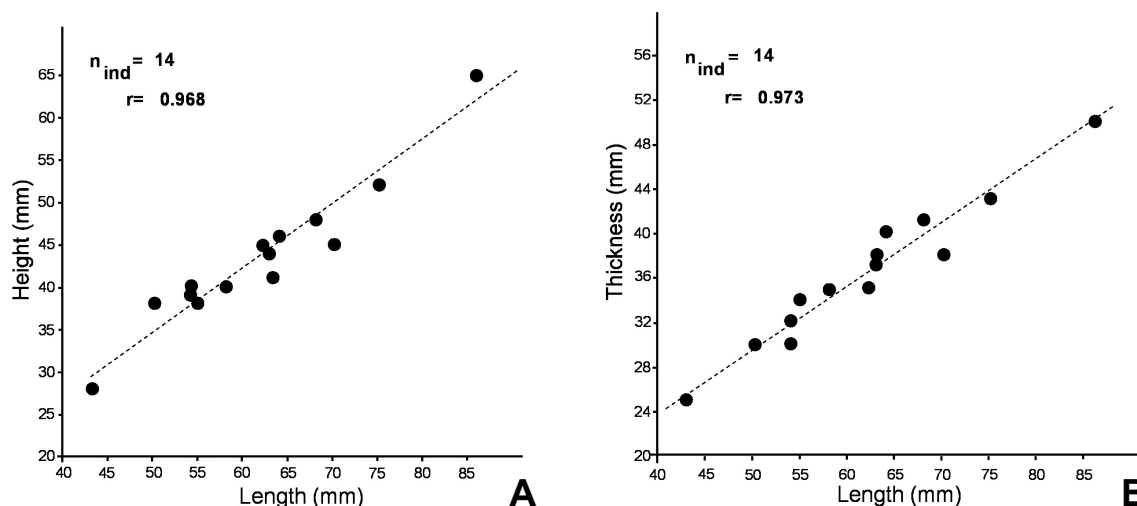


Figure 8. Length/height ratio (A) and length/inflation ratio (B) of *Pholadomya (Pholadomya) nodulifera* Münster, 1841, from the lower–middle Turonian of the Sergipe Basin, Brazil.

Table 5. Dimensions (mm) of *Pholadomya (Pholadomya) occidentalis* Morton, 1833.

Specimen	L	H	W	AL	Hs	Ws	nr	L/H	AL/L	Hs/Ws	W/L
NRM-PZ Mo 167853	76	45	35	7	36	15	18	1.69	0.09	2.40	0.46
NRM-PZ Mo 167854	81	48	42	8	35	21	16	1.69	0.10	1.67	0.52
NRM-PZ Mo 167855	63	40	43	8	28	15	16	1.58	0.13	1.87	0.68
NRM-PZ Mo 167856	56	35	31	7	19	12	14	1.60	0.13	1.58	0.55
NRM-PZ Mo 167857	52	39	32	6	25	13	16	1.33	0.12	1.92	0.62
NRM-PZ Mo 167858	54	38	35	7	32	19	18	1.42	0.13	1.68	0.65
Range	52-81	35-48	31-43	6-8	19-36	12-21	14-18	1.33-1.69	0.09-0.13	1.58-2.40	0.46-0.68
Mean	63.66	40.83	36.33	7.17	29	16	16	1.55	0.11	1.85	0.58

join ventral margin in obtuse angle. Ventral margin broadly rounded, joining the posterior margin in a rounded angle. Postero-dorsal margin slightly concave to straight. Posterior end slightly gaping. Umbonal area wide and slightly convex. Beaks subterminal, situated approximately one-fifth of the total valve length from the anterior end, prosogyrate, and not very prominent. Ornament consisting of sparse tuberculate radial ribs (four to six) separated by wide, concave interspaces (Figure 9C) and crossed by numerous, strong, commarginal ribs, becoming finer, more numerous and closely spaced towards the dorsal side.

Discussion. Although the Sergipe specimens are poorly preserved, they show strong similarities to *Pholadomya pedernalis* from the Turonian of Texas, USA (Roemer, 1852) in having comparatively few and tuberculate radial ribs, wide interspaces, well-developed and numerous commarginal ribs, a short anterior end, subterminal beaks and a wide umbonal area.

Pholadomya connectans Forbes, 1846, from the Upper Cretaceous of southern India (Forbes, 1846, p. 140, pl. 17, fig. 5) resembles *Ph. (Ph.) pedernalis* in having few radial ribs (eight) but differs in its strongly rounded anterior and ventral margins and more prominent and nearly orthogyrate beaks.

Ph. (Procardia) fontannesi Choffat, 1886, from the upper Cenomanian of Algeria (Collignon & Roman, 1983, p. 105, pl. 15, figs. 3-4), differs in having finer and more numerous radial ribs and in being more inflated and less elongate (L/H = 1.07 as opposed to 1.39 on average for the Sergipe specimens; Table 6). According to Barber (1958, p. 29), *Ph. nauliensis* Cox, 1952, from the Campanian of Ghana (Cox, 1952, p. 28, pl. 2, fig. 7) can be easily distinguished from *Ph. (Ph.) pedernalis* by the less anteriorly located umbonal area.

Abbass (1962, p. 161-162) discussed the differences between *Pholadomya (Ph.) pedernalis* and other European and American pholadomyid species such as *Ph. parvula* Roemer, 1846, and *Ph. papyracea* Meek & Hayden, 1862, described by Stanton (1894).

Occurrence. Cenomanian of Sergipe, Brazil (this study); Cenomanian–Turonian of the Sinai Peninsula and the Eastern Desert, Egypt (e.g. Abdel-Gawad *et al.*, 2004; El Qot, 2006; Mekawy, 2007; Mekawy & Abu-Zied, 2008; Ayoub-Hannaa *et al.*, 2014); Turonian of Texas (Roemer, 1852), Gabon (Darteville & Freneix, 1957), Nigeria (Barber, 1958; Akpan & Ntekim, 2004), Tunisia (Pervinquière, 1912) and Syria (Blanckenhorn, 1934); also reported from the Aptian of France and Algeria and the “Vraconian” (uppermost Albian) of Texas

Table 6. Dimensions (mm) of *Pholadomya (Pholadomya) pedernalis* Roemer, 1852.

Specimen	L	H	W	AL	Hs	nr	L/H	AL/L	W/L
NRM-PZ Mo 167860	20	13	11	6	9	6	1.54	0.30	0.55
NRM-PZ Mo 167861	22	17	13	4	11	6	1.29	0.18	0.60
NRM-PZ Mo 167862	24	18	15	5	13	4	1.33	0.21	0.62
Range	20-44	13-18	11-15	4-6	9-13	4-6	1.29-1.54	0.18-0.30	0.55-0.62
Mean	22	16	13	5	11	5	1.39	0.23	0.69

(Pervinquière, 1912, p. 289) and from the Santonian of the Sinai Peninsula (Ziko *et al.*, 1993, p. 142).

Pholadomya (Pholadomya) sp.
(Figure 9F)

Material. One composite mould (NRM-PZ Mo 167866) from the lower–middle Turonian of locality Pedra Furada 4, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 7.

Description. Shell medium-sized, elongate-ovate, strongly inequilateral, compressed posteriorly. Antero-dorsal margin slightly convex, higher than postero-dorsal margin, joining anterior margin in rounded angle. Postero-dorsal margin slightly concave. Anterior and posterior margins strongly rounded, joining ventral margin in rounded curves. Ventral margin broad and rounded. Umbonal area moderately convex, wide, situated approximately one-third of the total valve length from the anterior end. Ornament consisting of well-developed, tuberculate radial ribs (five), separated by irregular, smooth and wide interspaces. Radial ribs restricted to posterior flank, situated one-third of the total valve length from the posterior end. Central and anterior parts of shell bearing only commarginal growth lines (Figure 9F).

Discussion. The present specimen differs from the other pholadomyid species described here by its wide and strongly rounded anterior margin, narrow and strongly rounded posterior margin and in possessing few and tuberculate radial ribs separated by wide and smooth interspaces. The radial ribs are restricted to the posterior flank, whereas the rest of the valve surface is covered with commarginal growth lines. The specimen may represent a new species, but more material is needed before its status can be determined.

Pholadomya pedisulcata Stoliczka (1870, p. 81, pl. 4, fig. 1; pl. 1, fig. 2G) from the Upper Cretaceous of India resembles the present specimen in having few but well-developed radial ribs, though restricted to the anterior area (approximately 15% of the total valve length from the anterior end), and in being much larger (L = 45 mm as opposed to 15 mm for the Sergipe specimen; Table 7) and more elongate.

Table 7. Dimensions (mm) of *Pholadomya (Pholadomya) sp.*

Specimen	L	H	W	AL	nr	L/H	AL/L	W/L
NRM-PZ Mo 167866	15	13	--	6	5	1.15	0.33	--

Occurrence. Turonian of Sergipe, Brazil (this study).

Subgenus *Bucardiomya* Rollier, 1912

Type species. *Pholadomya bucardium* Agassiz, 1842, by subsequent designation of Cox (1969b).

Remarks. The subgenus *Bucardiomya* is characterized by its tall, subtrigonal shell, sharply pointed, orthogyrate to prosogyrate beaks, truncated posterior margin, and absence of escutcheon and lunule. Ornament consists of radial ribs intersecting with concentric growth lines, forming a reticulate pattern. The Brazilian specimens are incomplete and distorted composite moulds and therefore only tentatively assigned to *Bucardiomya*.

Pholadomya (Bucardiomya?) sp.
(Figures 9G-M)

Material. Two composite moulds (NRM-PZ Mo 167867-167868) from the lower–middle Turonian of locality São Roque 2, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 8.

Description. Shell small, subtrigonal, equivalved, inequilateral, slightly higher than long (L/H = 0.90 on average; Table 8) and highly inflated (W/L = 0.71 on average). Maximum inflation below umbonal area, sharply diminishing towards posterior side. Valves in anterior view subcordate. Ventral margin strongly rounded, joining anterior and posterior margins in rounded curves. Postero-dorsal margin concave and steeply oblique towards posterior end. Antero-dorsal margin slightly convex and higher than postero-dorsal margin. Umbonal area trigonal, narrow, and strongly convex. Beaks prominent, sharply pointed, slightly prosogyrate to orthogyrate, situated approximately one-third of the total valve length from the anterior end, with moderately well-developed posterior umbonal ridge. Escutcheon and lunule lacking (Figure 9I). Ornament consisting of 8-12 radial ribs crossed by thick commarginal ribs. Numerous fine, radial and commarginal elements intersecting towards the umbonal area, forming reticulate pattern. Further away from the

umbonal area, radial and commarginal ribs becoming thicker, irregularly distributed and separated by wide interspaces occupied by intercalatories (Figures 9G,K).

Discussion. The two specimens differ from the other pholadomyid species described here in having sharply pointed and orthogyrate beaks, thick and irregular commarginal ribs

with intercalatories (Figures 9H,K-L), strongly rounded anterior and ventral margins, and in lacking a lunule and escutcheon. Because the specimens are distorted composite moulds, a species determination is not possible.

The Sergipe specimens closely resemble *Pholadomya distorta* Anderson, 1938, described from the Lower

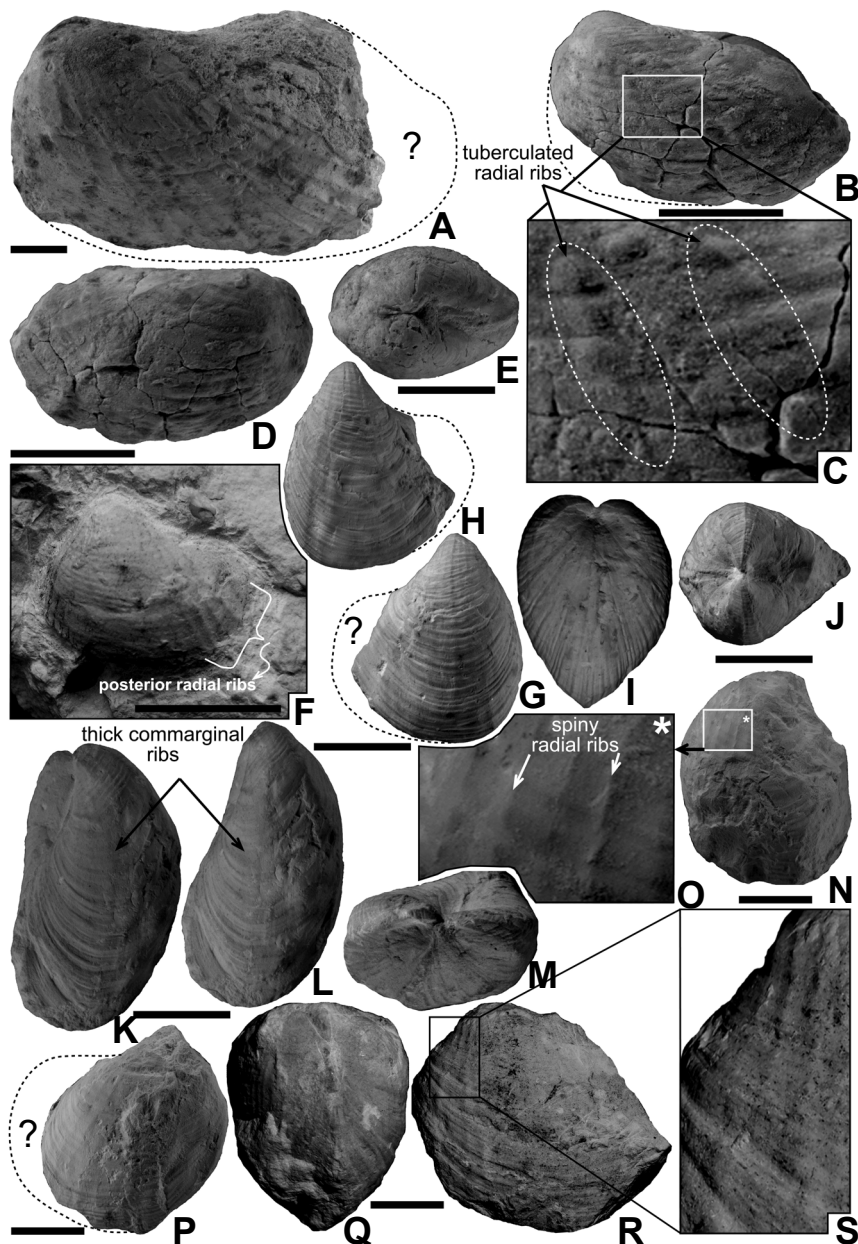


Figure 9. A, *Pholadomya (Pholadomya) occidentalis* Morton, 1833; left lateral view of incomplete composite mould from the lower–middle Turonian of locality Pedra Furada 5 (NRM-PZ Mo 167854). B–E, *Pholadomya (Pholadomya) pedernalis* Roemer, 1852 from the middle–upper Cenomanian. B, incomplete distorted composite mould of left valve; C, close-up view of left valve showing tuberculate radial ribs; D, Side view of right valve; locality Cruzes 8 (NRM-PZ Mo 167860); E, dorsal view of articulated valves; locality Timbó 4 (NRM-PZ Mo 167861). F, *Pholadomya (Pholadomya)* sp.; left lateral view of composite mould from the lower–middle Turonian of locality Pedra Furada 4 (NRM-PZ Mo 167866). G–M, *Pholadomya (Bucardiomya?)* sp. from the lower–middle Turonian. G, right lateral view; H, left lateral view; I, anterior view of articulated valves with thick anterior commarginal ribs; J, dorsal view of articulated composite mould showing narrow, sharply pointed beaks; locality São Roque 2 (NRM-PZ Mo 167867); K, posterior view of articulated valves; L, right lateral view of distorted composite mould showing thick, irregular growth rugae; M, dorsal view showing sharply pointed beaks with shallow anterior depression; locality São Roque 2 (NRM-PZ Mo 167868). N–P, *Pholadomya (Procardia) vignesi* Lartet, 1877, from the middle Cenomanian of locality Jericó 3 (NRM-PZ Mo 167869). N, left lateral view of incomplete composite mould; O, close-up showing spinose radial ribs near the antero-dorsal area of left valve; P, side view of right valve; Q–S, *Pholadomya (Procardia)* sp. from the lower–middle Turonian of locality Laranjeiras 22 (NRM-PZ Mo 167870). Q, anterior view of articulated valves; R, lateral view of incomplete left valve; S, close-up showing fine growth lines crossed by tuberculate radial ribs along the dorsal area. Both radial ribs and growth lines increase in strength ventrally. All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

Cretaceous of California (Anderson, 1938, p. 117, pl. 3, figs. 9,10) in general outline and in having orthogyrate and sharply pointed beaks but differ in being smaller (L = 23.5 mm, H = 26 mm, W = 16 mm (Table 8) as opposed to L = 35 mm, H = 40 mm, W = 27 mm on average) and showing faint radial ribs along the dorsal region (reticulate pattern) that disappear ventrally. According to Anderson (1938), *Ph. distorta* has well-developed commarginal ribs and lacks radial ribs. *Ph. esmarkii* (Nilsson, 1827) differs in possessing less developed commarginal ribs and more numerous, regular radial ribs with two well-developed anterior ventral keels with a sulcus in between. *Ph. decussata* (Mantell, 1822) from the Upper Cretaceous of England (Mantell, 1822, p. 125, pl. 25, fig. 3) differs in having a posteriorly truncated, incurved umbonal area, a shallow anterior cavity, and in being larger and more inflated.

Occurrence. Turonian of Sergipe, Brazil (this study).

Subgenus *Procardia* Meek, 1871

Type species. *Isocardia? hodgei* Meek, 1871, by monotypy.

Remarks. The subgenus *Procardia* is characterized by highly inflated valves, a strongly rounded posterior margin, a narrow and slightly convex anterior margin, tuberculate radial ribs, and strongly prosogyrate beaks.

Pholadomya (Procardia) vignesi Lartet, 1877
(Figures 9N-P)

- 1877 *Pholadomya vignesi*: Lartet, p. 126, pl. 11, fig. 9.
 1912 *Pholadomya vignesi* Lartet: Pervinquière, p. 290, pl. 21, figs. 8-9.
 1917 *Pholadomya vignesi* Lartet: Fourtau, p. 93, pl. 7, fig. 6.
 1928 *Pholadomya vignesi* Lartet: Shalem, p. 83, pl. 4, fig. 14.
 ?1957 *Pholadomya cf. vignesi* Lartet: Darteville & Freneix, p. 213, pl. 33, fig. 5.
 1962 *Pholadomya vignesi* Lartet: Abbass, p. 157, pl. 24, fig. 8, non fig. 7.
 1981 *Pholadomya (Procardia) vignesi* Lartet: Collignon & Roman., p. 82, pl. 2, figs. 3-4.
 2002 *Pholadomya vignesi* Lartet: Abdel-Gawad & Gameil, p. 97, pl. 4, fig. 11.
 2006 *Pholadomya (Pholadomya) vignesi* Lartet: El Qot, p. 91, pl. 18, fig. 8.
 ?2006 *Pholadomya sp.?* Perrilliat *et al.*, p. 104, figs. 29-30.
 2012 *Pholadomya (Pholadomya) vignesi* Lartet: Benyoucef *et al.*, pl. 3, fig. 14.

Material. One incomplete composite mould (NRM-PZ Mo 167869) from the middle Cenomanian of locality Jericó 3, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 9.

Description. Shell medium-sized, elongate-ovate, equivalved, inequilateral, slightly longer than high, highly inflated (W/L=0.81; Table 9) with maximum inflation below umbonal area. Anterior area short, higher than posterior area. Anterior margin convex, joining ventral margin in rounded angle. Ventral margin strongly convex. Postero-dorsal margin straight, gradually sloping towards posterior end. Umbonal area wide, moderately convex, situated anteriorly. Beaks strongly prosogyrate. Ornament consisting of well-developed commarginal ribs separated by narrow interspaces and crossed by seven widely spaced radial ribs. Ribs tuberculate, well developed in middle and dorsal parts and separated by wide, smooth, concave interspaces (Figure 9O).

Discussion. *Pholadomya (Procardia) vignesi* is readily distinguished by its comparatively few radial ribs, thick and well-developed commarginal ribs, highly inflated valves, wide umbonal area and rounded margins.

Pholadomya (Bucardiomya?) sp. described above resembles *Ph. (P.) vignesi* in having well-developed commarginal ribs and rounded margins but differs in being less inflated and in having a narrow trigonal umbonal area and more numerous radial ribs (13). *Ph. incurvata* Riedel, 1933, from the Cenomanian of Cameroon (Riedel, 1933, p. 65, pl. 5, fig. 2) differs in being more elongate and in having a large anterior area. In addition, the radial ribs of *Ph. incurvata* are restricted to the middle part of the valves. *Ph. (Ph.) pedernalis* Roemer, 1852 has approximately the same number of radial ribs (five) but differs in being much more elongate (L/H = 1.43 as opposed to 0.90; Table 9) and in having less prominent and subterminal beaks and less developed commarginal ribs. *Ph. aff. pedernalis* from the lower Turonian of Nigeria (Barber, 1958, p. 28, pl. 8, fig. 5; pl. 9, figs. 8-9) is closer to *Ph. vignesi* than to *Ph. (Ph.) pedernalis*. *Ph. umbonata* Roemer, 1841, from the Upper Cretaceous of Germany (Roemer, 1841, pl. 10, fig. 6) differs in being larger (L = 75 mm, H = 64 mm as opposed to L = 27 mm, H = 30 mm) and in having numerous, fine, commarginal ribs and the radial ribs restricted to the anterior flank of the valves. Blanckenhorn (1934, p. 261) distinguished *Ph. vignesi* and *Ph. syriaca* Conrad, 1852, from the Cenomanian of Syria (Conrad, 1852, p. 231, pl. 2, fig. 17) on the basis of number and strength of radial ribs (7-14 sharp ribs in *Ph. syriaca* and 16-24 in *Ph. vignesi*). However, Vokes (1941, p. 9) regarded *Ph. syriaca* and *Ph. vignesi* as probable varieties of the same species. *Ph. (Procardia) fontannesi* Choffat, 1886, from the upper

Table 8. Dimensions (mm) of *Pholadomya (Bucardiomya?)* sp.

Specimen	L	H	W	AL	Hs	Ws	nr	L/H	AL/L	Hs/Ws	W/L
NRM-PZ Mo 167867	20	22	16	7	12	4	12	0.91	0.35	3.00	0.80
NRM-PZ Mo 167868	27	30	17	---	14	---	8	0.90	---	---	0.63
Range	20-27	22-30	16-17	7	12-14	4	8-12	0.90-0.91	0.35	3.00	0.63-0.80
Mean	23.50	26	16	7	13	4	13	0.90	0.35	3.00	0.71

Cenomanian of Algeria (Collignon & Roman, 1983, pl. 15, figs. 3-4) differs in having well-developed, dorsal commarginal ridges. *Ph. coxi* Abbass, 1962, from the Cenomanian of the Sinai Peninsula, Egypt (Abbass, 1962, p. 158, pl. 24, fig. 3), differs in having less developed commarginal ribs, a trigonal outline and a narrow and truncated posterior margin.

Occurrence. Cenomanian of Sergipe, Brazil (this study), the Dead Sea area (Lartet, 1877), Palestine (Shalem, 1928), Syria (Blanckenhorn, 1934), Egypt (e.g. Fourtau, 1917; Abdel-Gawad & Gameil, 2002; El Qot, 2006), Tunisia (Pervinquier, 1912) and Algeria (Collignon & Roman, 1983; Busson *et al.*, 1999; Benyoucef *et al.*, 2012); Turonian of Jordan (Perrilliat *et al.* 2006); “Senonian” of Gabon (Darteville & Freneix, 1957).

Pholadomya (Procardia) sp.
(Figures 9Q-S)

Material. Two incomplete, composite moulds (NRM-PZ Mo 167870-167871) from the lower–middle Turonian of localities Laranjeiras 21 and 22, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 10.

Description. Shell medium-sized, elongate-ovate, inequilateral, slightly equivalved and moderately inflated (W/L = 0.59; Table 10). Length and height nearly equal (L/H = 1.06). Anterior side of both valves subcordate. Anterior margin truncated. Ventral margin rounded. Umbonal area wide and convex; no lunule. Ornament consisting of sparse, tuberculate, radial ribs, becoming finer dorsally and crossed by commarginal ribs forming a reticulate pattern near umbonal area. Growth lines fine along dorsal area, thicker and more irregular ventrally (Figures 9R,S).

Discussion. The two specimens are similar in general outline and ornament to *Pholadomya decussata* (Mantell, 1822) from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 154, pl. 14, figs. 3-4) and to *Ph. cordata* Tate, 1865, from the Upper Cretaceous of England (Woods, 1909, p. 253, pl. 42, fig. 2). However, *Ph. decussata* is larger, highly inflated and has sharp, pointed, strongly incurved beaks with a well-developed anterior umbonal keel extending from the umbonal area to the antero-ventral margin, forming a shallow to deep anterior depression.

Occurrence. Turonian of Sergipe, Brazil (this study).

Homomya Agassiz, 1843

Type species. *Maetra (Lutraria) gibbosa* J. Sowerby, 1813, by subsequent designation of Herrmannsen (1847).

Homomya bisinuosa (White, 1887)
(Figures 10A-C)

1887 *Myacites bisinuosus* (sp. nov.): White, p. 104, pl. 7, figs. 6-7.

1887 *Glycimeris rathbuni* (sp. nov.): White, p. 110, pl. 7, figs. 3, 4(?).

1937 *Homomya bisinuosa* (White): Maury, p. 79, pl. 10, figs. 15-16.

1937 *Panopea rathbuni* (White): Maury, p. 83, pl. 9, figs. 12(?), 13.

1999 *Panopea (Panopea) rathbuni* (White): Seeling, p. 132-133 (*pars*, cf. Appendix 1 herein), pl. 6, fig. 4, *non* figs. 2-3.

2014 *Homomya rathbuni* (White 1887): Ayoub-Hannaa *et al.*, p. 127, pl. 12, fig. 8.

Material. Five composite moulds (NRM-PZ Mo 167872-167876) from the upper Cenomanian-lower Turonian of localities Japarutuba 6 and 16, the lower Turonian of Sergipe 5 and the upper Turonian of Cajaíba 7, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 11.

Description. Shell large, elongate-ovate, strongly inequilateral, equivalved, posteriorly elongate and moderately inflated (W/L = 0.49 on average; Table 11). Inflation decreasing gradually towards posterior end. Antero-ventral and postero-dorsal margins slightly gaping. Antero-dorsal margin short, straight to slightly concave, higher than postero-dorsal margin and joining anterior margin in nearly right angle. Postero-dorsal margin slightly concave. Anterior and posterior margins rounded, joining ventral margin in rounded angles. Escutcheon narrow, elongate and moderately deep (Figure 10C). Umbonal area broadly arched and slightly convex. Beaks less prominent, slightly prosogyrate, elevated above hinge, and situated one-fourth of the total valve length from the anterior end. Ornament consisting of thick, undulating commarginal ribs (Figure 10A). Radial ribs absent. Commarginal ribs less developed towards dorsal side.

Discussion. The species *Homomya bisinuosa* is here assigned to the genus *Homomya* on the basis of its less prominent beaks, narrow and deep escutcheon, moderately inflated valves and commarginal ribs. Although the present specimens show strong similarities in outline, size, and ornament to *H. bisinuosa*, as figured by White (1887) and Maury (1937), they differ in having a wider umbonal area.

Homomya bisinuosa (White, 1887) from the Albian of Sergipe (White, 1887; Maury, 1937) closely resembles

Table 9. Dimensions (mm) of *Pholadomya (Procardia) vignesi* Lartet, 1877.

Specimen	L	H	W	AL	nr	L/H	AL/L	W/L
NRM-PZ Mo 167869	27	30	22	12	7	0.90	0.44	0.81

Table 10. Dimensions (mm) of *Pholadomya (Procardia) sp.*

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167870	49	46	c. 29	14	1.06	0.28	0.59

H. rathbuni in having less prominent beaks, moderately inflated valves ($W/L = 0.49$ on average) and irregular and strong commarginal ribs, but differs in being less elongate and in having subterminal beaks. These differences are not considered sufficient enough to separate the species. *H. refugium* (White, 1887), from the middle Albian of Sergipe (White, 1887, p. 103, pl. 7, fig. 8) resembles *H. bisinuosa* in having a wide umbonal area and approximately the same size ($L = 72$ mm, $H = 42$ mm and $L = 65.5$ mm, $H = 40.5$ mm on average, respectively) but differs in being slightly more elongate ($L/H = 1.71$ vs. 1.61 on average for *H. bisinuosa*; Table 11) and in having a narrow and rounded posterior margin, blunt anterior margin and a regularly convex ventral margin.

Occurrence. Albian (White, 1887; Maury, 1937) and Cenomanian–Turonian (Seeling, 1999; this study) of Sergipe, Brazil; Turonian of the Sinai Peninsula, Egypt (Ayoub-Hannaa *et al.*, 2014).

Homomya brasiliensis (White, 1887)
(Figures 10D-H)

1887 *Glycimeris brasiliensis* (sp. nov.): White, p. 111, pl. 7, figs. 1-2.

1937 *Panopea brasiliensis* (White): Maury, p. 81, pl. 11, figs. 11-12.

v1999 *Panopea (Panopea) rathbuni* (White, 1887): Seeling, pp. 132-133 (*pars*, cf. Appendix 1 herein), pl. 6, figs. 2-3, non fig. 4.

v1999 *Panopea* sp.: Seeling, p. 134 (*pars*, cf. Appendix 1 herein).

Material. Three composite and internal moulds (NRM-PZ Mo 167877-167879) from the upper Cenomanian-lower Turonian of locality Japarutuba 16, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 12.

Description. Shell large, oblong to subquadrate, strongly inequilateral, equivalved, moderately inflated, posteriorly elongate ($L/H = 1.73$ - 2.02 ; Table 12). Anterior margin short, blunt, located below hinge. Posterior margin wide, ovate,

regularly rounded, joining ventral margin in rounded curve. Antero-ventral and posterior margins slightly gaping. Ventral margin slightly curved to straight, parallel to hinge line. Antero-dorsal margin short, concave, joining anterior margin in acute angle. Postero-dorsal margin straight to slightly concave. Escutcheon narrow, elongate and shallow. Umbonal area broad and moderately convex. Beaks less prominent, slightly prosogyrate, terminal to subterminal ($Al/L = 0.16$ on average; Table 12). Valve surface bearing numerous fine commarginal ribs (Figure 10D).

Discussion. *Homomya brasiliensis* is readily recognized by its very elongate valves ($L/H = 1.87$ on average; Table 12), terminal to subterminal beaks, straight postero-dorsal margin running nearly parallel to the ventral margin and being higher than the antero-dorsal side, blunt anterior end, and by having numerous fine commarginal ribs. According to Seeling (1999, p. 133) *Homomya rathbuni* and *H. brasiliensis* are similar and occur in the same stratigraphic interval and therefore synonyms. *H. brasiliensis* indeed resembles *H. rathbuni* (= *Homomya bisinuosa* herein; see above) in size, curvature of umbonal area, and in having a small shallow escutcheon, but it differs in being much more elongate ($L/H = 1.87$ on average as opposed to 1.66) and in having terminal to subterminal beaks, a blunt anterior end, and numerous, fine, commarginal ribs.

Occurrence. Albian (White, 1887; Maury, 1937) and Cenomanian–Turonian (this study) of Sergipe, Brazil.

Family PLEUROMYIDAE Zittel, 1895

Pleuromya Agassiz, 1842

Type species. *Mya gibbosa* J. de C. Sowerby, 1923, by monotypy.

Pleuromya ligeriensis (d'Orbigny, 1845)
(Figures 10I,J)

1845 *Pholadomya ligeriensis* d'Orbigny, 1844 [*sic*]: d'Orbigny, p. 355, pl. 363, figs. 8-9.

Table 11. Dimensions (mm) of *Homomya bisinuosa* (White, 1887).

Specimen	L	H	W	AL	Hs	L/H	AL/L	W/L
NRM-PZ Mo 167872	69	43	34	18	30	1.60	0.26	0.49
NRM-PZ Mo 167873	62	38	31	15	22	1.63	0.24	0.50
Range	62-69	38-43	31-34	15-18	22-30	1.60-1.63	0.24-0.26	0.49-0.50
Mean	65.50	40.50	32.50	16.5	26	1.61	0.25	0.49

Table 12. Dimensions (mm) of *Homomya brasiliensis* (White, 1887).

Specimen	L	H	W	AL	Hs	L/H	AL/L	W/L
NRM-PZ Mo 167877	76	44	40	13	24	1.73	0.17	0.52
NRM-PZ Mo 167878	71	35	33	11	21	2.02	0.15	0.46
Range	71-76	35-44	33-40	11-13	21-24	1.73-2.02	0.15-0.17	0.46-0.52
Mean	73.5	39.5	36.50	12	22.50	1.87	0.16	0.49

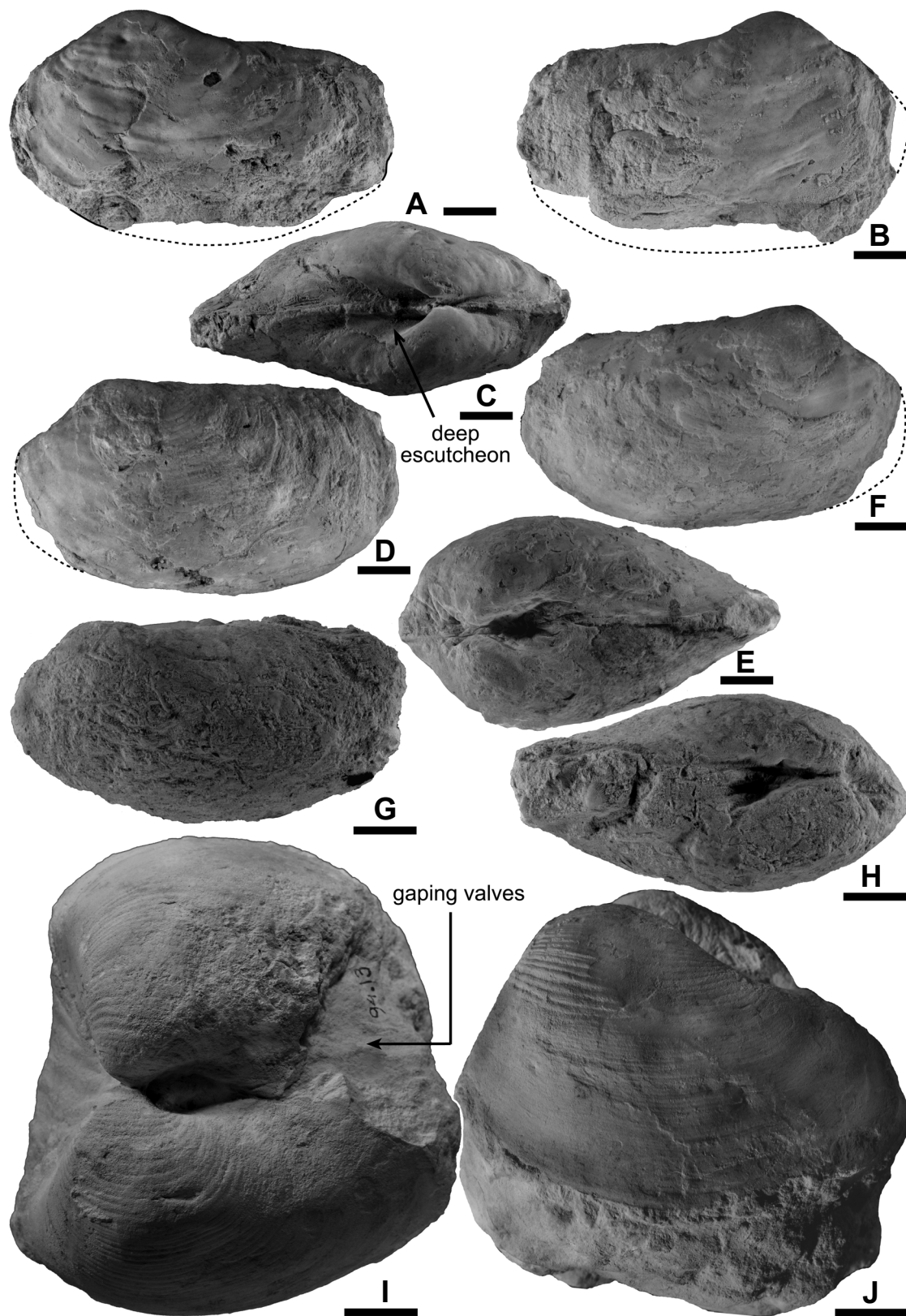


Figure 10. A-C, *Homomya bisinuosa* (White, 1887) from the upper Cenomanian–lower Turonian of locality Japarutuba 6 (NRM-PZ Mo 167872). A, left lateral view; B, side view of right valve; C, dorsal view showing depressed umbonal area and deep escutcheon. D-H, *Homomya brasiliensis* (White, 1887) from the upper Cenomanian–lower Turonian of locality Japarutuba 16. D, side view of left valve; composite mould of articulated specimen; E, Dorsal view of both valves; F, right lateral view (NRM-PZ Mo 167877); G, left lateral view; of internal mould showing the expanded posterior area; H, dorsal view of both valves showing the subterminal beaks and highly inflated valves (NRM-PZ Mo 167878). I-J, *Pleuromya ligeriensis* (d’Orbigny, 1845) from the lower–middle Turonian of locality Pedra Furada 3 (NRM-PZ Mo 167880). I, dorsal view showing gaping valves; J, left lateral view. All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

?1862 *Pholadomya Molli* H. Coq.: Coquand, p. 189, pl. 6, figs. 6-7.

1887 *Homomya profunda* (sp. nov.): White, p. 105, pl. 7, fig. 5.

1912 *Liopistha (Psilomya)* cf. *L. ligeriensis* (d'Orbigny): Pervinquière, p. 292, pl. 20, fig. 22.

1937 *Homomya profunda* White: Maury, p. 77, pl. 10, fig. 13.

1958 *Liopistha ligeriensis* (d'Orbigny): Barber, p. 29, pl. 9, fig. 7.

1997 *Pleuromya ligeriensis* (d'Orbigny): Smettan, p. 132, pl. 7, figs. 12-13.

non 1999 *Liopistha (Psilomya) ligeriensis* (d'Orbigny): Seeling, p. 136, pl. 6, figs. 5-7 [= *Liopistha (Sergipemya) alta* (Roemer, 1852)].

1999 *Liopistha (Psilomya)?* cf. *alta*: Seeling, p. 137 (*pars*, cf. Appendix 1 herein).

non 2011 *Liopistha (Psilomya) ligeriensis* (d'Orbigny, 1945 [sic]): Andrade & Santos, p. 233, figs. 2.3-4 [= *Megaporomya reymenti* Ayoub-Hannaa *et al.*, 2013].

2014 *Pleuromya ligeriensis* (d'Orbigny 1845): Ayoub-Hannaa *et al.*, p. 128, pl. 13, fig. 1.

Material. Three composite moulds (NRM-PZ Mo 167880-167882) from the upper Cenomanian–lower Turonian of locality Japarutuba 6 and the lower–middle Turonian of Pedra Furada 3, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 20.

Description. Shell medium-sized, elongate-ovate, equivalved, strongly inequilateral, elongate posteriorly, and highly inflated. Anterior margin short, truncated, joining the ventral margin in nearly right angle. Posterior margin rounded, joining ventral margin in rounded curve. Ventral margin wide and faintly convex. Postero-dorsal margin straight to slightly concave. Umbonal area wide and inflated. Beaks prominent, slightly incurved anteriorly. Ligament external. Anterior umbonal ridge moderately well developed, extending from umbonal area to middle of anterior end, forming wide, concave, anterior cavity (Figure 10I). Numerous fine, commarginal ribs separated by irregular interspaces; ribs becoming stronger and separated by narrower interspaces towards umbonal area (Figure 10J).

Discussion. *Pholadomya molli* Coquand, 1862, from the Turonian of Algeria resembles *Pleuromya ligeriensis* (d'Orbigny) in possessing numerous, fine, commarginal ribs and a well-developed anterior umbonal ridge with a deep anterior depression, but differs in its narrow and terminal beaks. White (1887) described the new species *Homomya profunda* from the middle Albian of Sergipe, which closely resembles *P. ligeriensis* in outline and ornament but is smaller (L = 36 mm, H = 30 mm, W = 22 mm; *P. ligeriensis*:

L = 57 mm, H = 49 mm, W = c. 44 mm on average; Table 13). Following Pervinquière (1912) and Barber (1958), *H. profunda* is here considered a junior synonym of *P. ligeriensis*. *P. elongata* (Roemer, 1841) from the Upper Cretaceous of Germany (Roemer, 1841, p. 75, pl. 10, fig. 5) differs from *P. ligeriensis* in being less inflated and in having a more extended posterior area and a narrow umbonal area.

The specimens described by Andrade & Santos (2011, p. 233, fig. 2.3-4) as *Liopistha (Psilomya) ligeriensis* from the Turonian of Sergipe (locality Mata 11) are poorly preserved and differ from the specimens described here in being larger (L = 65-112 mm, H = 64-102 mm), more inflated, and in having less prominent beaks. Ayoub-Hannaa *et al.* (2013) referred the specimens of Andrade & Santos (2011) to the new genus and new species *Megaporomya reymenti*.

Occurrence. Aptian(?)–Cenomanian of Germany (Smettan, 1997); Cenomanian of Tunisia (Pervinquière, 1912); Cenomanian–Turonian of Algeria (Coquand, 1862); Cenomanian of Egypt; Cenomanian–Turonian of Sergipe, Brazil (this study); Turonian of France (d'Orbigny, 1845) and Nigeria (Barber, 1958).

Pleuromya servesensis Choffat, 1902
(Figures 11A-E)

1902 *Pleuromya servesensis*: Choffat, p. 132, pl. 9, figs. 1-3.

1928 *Homomya* sp.: Adkins, p. 140, pl. 15, fig. 2.

?1958 *Liopistha* cf. *servesensis* (Choffat): Barber, p. 29, pl. 9, fig. 13.

v1999 *Panopea (Panopea) rathbuni* (White, 1887): Seeling, p. 132-133 (*pars*, cf. Appendix 1 herein); non pl. 6, figs. 2-4.

v1999 *Liopistha (Psilomya) concentrica* Stanton, 1893: Seeling, p. 135 (*pars*, cf. Appendix 1 herein).

v1999 *Panopea* sp.: Seeling, p. 134 (*pars*, cf. Appendix 1 herein).

?2004 *Pleuromya* sp. Akpan & Ntekim, p. 30, figs. 60-p.

Material. Five composite moulds (NRM-PZ Mo 167883-167887) from the upper Cenomanian of locality Jardim 31 and the upper Cenomanian–lower Turonian of Japarutuba 6 and 11, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 20.

Description. Shell large, elongate-ovate to oblong (L/H = 1.52 on average; Table 14), strongly inequilateral, nearly equivalved, inflated. Maximum inflation slightly below umbonal area (W/L = 0.47 on average; Table 14), decreasing gradually towards posterior end. Postero-dorsal margin straight to slightly concave. Posterior margin rounded, joining ventral margin in rounded angle. Anterior margin

Table 13. Dimensions (mm) of *Pleuromya ligeriensis* (d'Orbigny, 1845).

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167879	62	48	c. 44	13	1.29	0.21	c. 0.71
NRM-PZ Mo 167880	52	50	--	16	1.04	0.31	--
Range	52-62	48-50	c. 44	13-16	1.04-1.29	0.21-0.31	c. 0.71
Mean	57	49	c. 44	14.50	1.16	0.26	c. 0.71

Table 14. Dimensions (mm) of *Pleuromya servesensis* Choffat, 1901.

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167883	38	29	21	14	1.31	0.37	0.44
NRM-PZ Mo 167884	56	34	25	17	1.65	0.30	0.45
NRM-PZ Mo 167885	48	30	27	14	1.60	0.29	0.56
NRM-PZ Mo 167886	42	27	18	15	1.48	0.38	0.42
NRM-PZ Mo 167887	44	28	22	12	1.57	0.27	0.50
Range	38-56	27-34	18-27	12-17	1.31-1.65	0.27-0.38	0.42-0.56
Mean	45.60	29.60	22.60	14.40	1.52	0.32	0.47

truncated, joining wide and slightly convex ventral margin in nearly right angle. Posterior end slightly gaping; no lunule. Umbonal area wide and highly inflated. Beaks less prominent, prosogyrate, situated one-third of the total valve length from the anterior end. Ornament consisting of well-developed irregular commarginal ribs separated by wide interspaces (Figures 11A,B).

Discussion. Barber (1958) assigned *Pleuromya servesensis* to the genus *Liopistha* Meek, 1864. However, radial ribs, which are an important feature in *Liopistha* (see below), are absent in *P. servesensis*. *P. servesensis* is characterized by irregular, thick growth rugae and a wide umbonal area. *P. congoensis* Darteville & Freneix, 1957, from the Maastrichtian of Bas-Congo (Democratic Republic of the Congo) (Darteville & Freneix, 1957, p. 208, pl. 32, figs. 9,10; pl. 33, figs. 1,2) resembles the Sergipe specimens in ornament and in having elongate-ovate to oblong valves but differs in being less elongate (L/H = 1.33 as opposed to 1.52 on average for the Sergipe specimens; Table 14), more inflated (W/L = 0.64 as opposed to 0.47 on average) and in having finer commarginal ribs. *P. lynesii* (Lartet, 1877) from the Upper Cretaceous of Palestine (Lartet, 1877, p. 125, pl. 11, figs. 7,8) and the Coniacian of Egypt (Greco, 1919, p. 158, pl. 17, figs. 23,24) differs in having numerous, fine, commarginal ribs, a rounded anterior margin and a nearly central umbonal area (situated slightly anterior to the mid-line of valve). *P. orbigniana* (Rouillier, 1847) from the Upper Cretaceous of England (Woods, 1909, p. 256, pl. 43, figs. 1,2) resembles the Sergipe specimens in its less developed beaks and in being elongate-ovate but differs in having fine, irregular, tuberculate radial ribs, in addition to finer commarginal ribs, and a slightly gaping posterior end. *P. molli* Coquand, 1862, from the Turonian of Algeria (Coquand, 1862, p. 189, pl. 6, figs. 6,7) differs in being more inflated (W/L = 0.67 as opposed to 0.47 on average for the Sergipe specimens) and in having terminal beaks.

Occurrence. Albian of Texas, USA (Adkins, 1928); Albian-Coniacian of Nigeria (Barber, 1958; Akpan & Ntekim, 2004); Cenomanian-Turonian of Sergipe, Brazil (this study); Turonian of Portugal (Choffat, 1902).

Superfamily POROMYOIDEA Dall, 1886
Family POROMYIDAE Dall, 1886

Liopistha Meek, 1864

Type species. *Cardium elegantulum* Roemer, 1852, by original designation (*non C. elegantulum* Beck, 1842 = *Liopistha elegantulata* Vokes, 1956).

Subgenus *Liopistha* Meek, 1864

Remarks. The subgenus *Liopistha* refers to species ornamented with fine and numerous radial ribs except on the smooth dorsal part of the posterior area. Near the umbonal area, equally developed radial and commarginal ribs intersect. Towards the ventral margin only radial ribs remain.

Liopistha (Liopistha) aequivalvis (Goldfuss, 1841)
(Figures 11F-I)

1841 *Corbula aequivalvis*: Goldfuss, p. 250, pl. 151, figs. 15 a-b.

1841 *Pholadomya caudata* N.: Roemer, p. 76, pl. 10, fig. 8.

?1846 *Cardium lucerna*: Forbes, p. 145, pl. 17, fig. 10.

1870 *Pholadomya caudata* Roemer: Stoliczka, p. 79, pl. 2, figs. 10-11; pl. 16, fig. 19.

1884 *Pholadomya aequivalvis* Goldfuss: Holzapfel, p. 471, pl. 7, figs. 5a-b.

1889 *Liopistha aequivalvis* Goldfuss: Holzapfel, p. 150, pl. 9, figs. 4-5.

?1909 *Liopistha*, sp.: Woods, p. 258, pl. 43, figs. 5a-c.

1934 *Liopistha aequivalvis* (Goldfuss): Andert, p. 335, pl. 15, fig. 9; text-fig. 88.

1974 *Liopistha aequivalvis* (Goldfuss): Oekentorp & Siegfried, p. 164, pl. 18, fig. 6.

1986 *Liopistha (Liopistha) aequivalvis* (Goldfuss): Abdel-Gawad, p. 184, pl. 43, figs. 1-2.

1989 *Liopistha aequivalvis* (Goldfuss): Dhondt & Jagt, p. 188, pl. 1, figs. 1-6.

?2006 *Liopistha cf. aequivalvis* (Goldfuss): El Qot, 92, pl. 18, fig. 13.

Material. Eleven composite moulds (NRM-PZ Mo 167888-167898) from the lower Cenomanian of localities Itaporanga 2 and 3, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 15.

Description. Shell small to medium-sized, oval to rounded, nearly equilateral, inflated, with slightly extended and compressed posterior end. Length and height nearly equal (L/H = 1.14 on average; Table 15). No posterior gape.

Anterior and posterior margins strongly convex, joining ventral margin in rounded curves. Ventral margin widely arched. Postero-dorsal and antero-dorsal margins slightly concave, joining posterior and anterior ends in obtuse angles. Umbonal area broad and moderately convex. Beaks incurved, prominent, prosogyrate, elevated above hinge and situated near middle of valves ($AL/L = 0.42$ on average; Table 15). Ornament consisting of 17-40 unequal radial ribs crossed by commarginal growth lines (both of equal strength), forming reticulate pattern near umbonal area (Figures 11G,I). Only radial ribs persisting towards ventral margin; ribs strong near posterior side, becoming weaker towards anterior margin (Figure 11F). Posterior flank extending for approximately one-third of the total valve length from the posterior end, smooth except for fine commarginal growth lines.

Discussion. *Pholadomya caudata* Roemer, 1841, is closely similar to *Liopistha* (*Liopistha*) *aequivalvis* in shape, size and ornament and, in agreement with Dhondt & Jagt (1989), here considered a junior synonym. Similarly, *Cardium lucerna* Forbes, 1846, from the Upper Cretaceous of India (Forbes, 1846, p. 145, pl. 17, fig. 10) appears identical to *L. aequivalvis* in outline and ornament, though it differs in having wider interspaces between the radial ribs and well-developed, regular commarginal ribs. These differences are probably not significant enough to justify a separate species, so *C. lucerna* is here tentatively regarded as a junior synonym. In *L. sergipensis* (White, 1887) from the middle Albian of Sergipe (White, 1887, p. 106, pl. 7, fig. 17), ribs cover the entire valve and are well developed ventrally and finer dorsally. In addition, the reticulate pattern of *L. sergipensis* extends from the dorsal side to the middle part of the valve [restricted to the umbonal area in *L. (L.) aequivalvis*, Figure 11G]. *L. sergipensis* also has subterminal beaks and an elevated postero-dorsal side that is higher than the antero-dorsal margin. *L. inflata* Whitfield, 1885, from the Maastrichtian of Tennessee, USA (Wade, 1926, p. 76, pl. 24, figs. 7,8) has thicker radial ribs, well-developed commarginal ribs and smooth anterior and posterior flanks, except for growth lines. *L. alternata* Weller, 1907 from the Upper Cretaceous of New Jersey (Weller, 1907, p. 527, pl. 58, figs. 7-9) has a more centrally located umbonal area and more regular radial ribs. *L. (L.) ventricosa* von Koenen, 1897, from the “Senonian” of Gabon (Darteville & Freneix, 1957, p. 217, pl. 33, fig. 9) shows similarities to *L. (L.) aequivalvis*

in general outline and in having a smooth posterior flank but has fewer and stronger radial ribs, wide interspaces, and less developed commarginal ribs. *Liopistha* sp. from the Upper Cretaceous of England (Woods, 1909, p. 258, pl. 43, fig. 5) closely resembles *L. aequivalvis* but differs from the Sergipe specimens in being much smaller ($L = 4$ mm, $H = 3$ mm, $W = 2.6$ mm as opposed to $L = 28$ mm, $H = 26$ mm, $W = 19.8$ mm on average).

Occurrence. Cenomanian of Sergipe, Brazil (this study); probably Campanian of Egypt (El Qot, 2006); Campanian–Maastrichtian(?) of Germany (Roemer, 1841; Oekentorp & Siegfried, 1974) and north-western Europe (Dhondt & Jagt, 1989); Maastrichtian of Poland (Abdel-Gawad, 1986), “Senonian” of India (Stoliczka, 1870); recorded from Turonian(?)–Coniacian to Maastrichtian from England across to Crimea, possibly extending into Central Asia (Dhondt & Jagt, 1989).

Subgenus *Psilomya* White, 1874

Type species. *Liopistha* (*Psilomya*) *meekii* White, 1874, by monotypy.

Remarks. The subgenus *Psilomya* comprises species with a compressed posterior end, less developed radial ornament, and well-developed prosogyrate beaks, situated approximately one-third of the total valve length from the anterior end.

Liopistha (*Psilomya*) *elongata* Stanton, 1894 (Figures 11J-L)

1894 *Liopistha* (*Psilomya*) *elongata* n. sp.: Stanton, p. 119, pl. 26, figs. 11-12.

1900 *Liopistha concentrica*, Stanton (including *L. elongata*, Stanton): Herrick & Johnson, p. 208, pl. 41, figs. 11-12.

?1996 *Psilomya elongata* Stanton, 1893: Kirkland, p. 56, pl. 25, figs. G-J.

v1999 *Liopistha* (*Psilomya*) *concentrica* Stanton, 1893: Seeling, p. 135 (*pars*, cf. Appendix 1 herein).

2014 *Liopistha* (*Psilomya*) *elongata* Stanton, 1894: Ayoub-Hannaa *et al.*, p. 129, pl. 13, fig. 3.

Material. Three internal moulds (NRM-PZ Mo 167899-167901) from the upper Cenomanian–lower Turonian of

Table 15. Dimensions (mm) of *Liopistha* (*Liopistha*) *aequivalvis* (Goldfuss, 1841).

Specimen	L	H	W	AL	nr	L/H	AL/L	W/L
NRM-PZ Mo 167888	39	33	c. 26	17	40	1.18	0.43	c. 0.66
NRM-PZ Mo 167889	28	23	c. 21	14	34	1.22	0.50	c. 0.75
NRM-PZ Mo 167890	25	32	20	c. 12	25	1.28	0.48	0.80
NRM-PZ Mo 167891	36	32	28	c. 13	29	1.12	0.36	0.78
NRM-PZ Mo 167892	15	15	10	5	17	1.00	0.33	0.66
NRM-PZ Mo 167893	22	21	14	10	--	1.04	0.45	0.63
Range	15-39	15-33	10-28	5-17	17-40	1.00-1.28	0.33-0.50	0.66-0.78
Mean	28	26	19.83	11.83	29	1.14	0.42	0.71

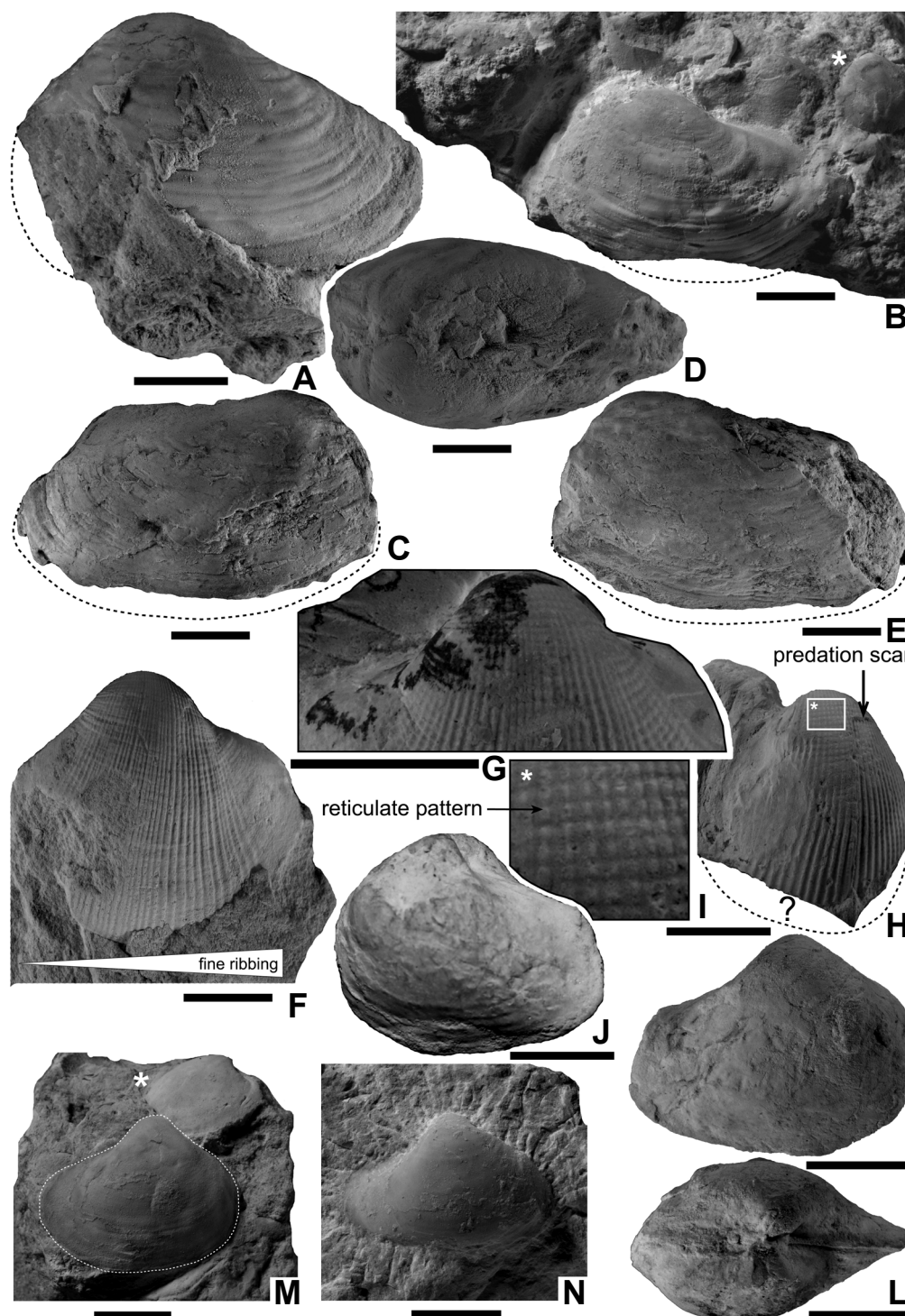


Figure 11. A-E, *Pleuromya servesensis* Choffat, 1901, from the upper Cenomanian–lower Turonian. A, side view of left valve of composite mould; locality Japaratuba 6 (NRM-PZ Mo 167883); B, left lateral view of composite mould; locality Japaratuba 11 (NRM-PZ Mo 167884); C, right valve of poorly preserved composite mould; D, dorsal view of articulated specimen; E, left valve; locality Machado 15 (NRM-PZ Mo 167885). F-I, *Liopistha (Liopistha) aequivallis* (Goldfuss, 1841) from the lower Cenomanian of localities Itaporanga 2 and 3. F, left lateral view of composite mould showing smooth posterior flank and decreasing strength of radial ribs towards the anterior side (arrowed) (NRM-PZ Mo 167888); G, close-up of the dorsal side showing the reticulate pattern (NRM-PZ Mo 167889); H, incomplete right lateral view of composite mould; I, close-up showing intersection of radial and commarginal ribs, forming a reticulate pattern (NRM-PZ Mo 167890). J-L, *Liopistha (Psilomya) elongata* Stanton, 1894, from the upper Cenomanian–lower Turonian of locality Japaratuba 16 (NRM-PZ Mo 167899). J, left lateral view of composite mould; K, side view of right valve; L, dorsal view of articulated valves showing the abrupt decrease in inflation towards the posterior end. M-N, *Liopistha (Psilomya) concentrica* Stanton, 1894, from the upper Cenomanian–lower Turonian. M, side view of right valve of composite mould; locality Japaratuba 6 (NRM-PZ Mo 167902); N, side view of right valve; locality Sergipe 5 (NRM-PZ Mo 167903). All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. White asterisks in figures B and M denote non-pholadomyid specimens [*Paraesa faba* (J. de C. Sowerby, 1827)]. Scale bars = 10 mm.

localities Japarutuba 11 and 16, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 16.

Description. Shell medium-sized, elongate-ovate, inequilateral, slightly inequivalved, strongly compressed posteriorly (Figure 11L), moderately inflated ($W/L = 0.54$ on average; Table 16) with maximum inflation slightly below umbonal area. Posterior end elongate ($L/H = 1.30$ on average). No posterior gape. Anterior end short slightly rounded, joining ventral margin in rounded curve. Antero-dorsal margin short, straight, steeply sloping towards anterior margin. Postero-dorsal margin slightly concave. Ventral margin broadly rounded. Umbonal area broad and slightly convex. Beaks prominent, elevated above hinge line, sharply pointed, prosogyrate, situated approximately one-third of the total valve length from the anterior end. Faint growth rugae visible along ventral margin, with faint axial tubercles (Figure 11J). Hinge not visible. Specific determination of specimen NRM-PZ Mo 167901 uncertain due to poor preservation.

Discussion. *Liopistha (Psilomya) elongata* Stanton is readily distinguished from other *Liopistha* species described here by its larger, elongate shell ($L = 30$ mm on average; Table 16), strongly rounded anterior margin meeting the ventral margin in a rounded angle, and its narrow and slightly convex to subtruncated posterior margin. The present specimens closely resemble *L. (P.) elongata*, as described and figured by Stanton (1894) from the Turonian(?) of Utah, USA, in general outline and ornament, but differ in being slightly smaller ($L = 30$ mm, $H = 23$ mm on average as opposed to $L = 37$ mm, $H = 28$ mm for Stanton's specimens). *L. (P.) concentrica* Stanton, 1894, from the Cenomanian of Texas, USA (Stanton, 1894, p. 119, pl. 26, figs. 8-10) differs in being smaller and in having a subtrigonal shell and a nearly centrally placed umbonal area. *L. (P.) meeki* White, 1874 from the Upper Cretaceous of Utah, USA (White, 1874, p. 26; 1877, p. 186, pl. 18, figs. 14a-d) has more inflated valves with well-developed radial ribs on the posterior side. *Psilomya elongata*, figured and described by Kirkland (1996) from the Cenomanian of northeastern Arizona, USA, resembles the present specimens in having large valves ($L = 40$ mm) but differs in being more elongate ($L/H = 1.67$, as opposed to 1.30 on average for the Sergipe specimens) and in having a well-developed umbonal posterior ridge and a strongly rounded, broad posterior margin. Kirkland's specimens are closer to *Poromya frequens* (Zittel, 1864, p. 111, pl. 1, figs. 5a-f) than to *L. (P.) elongata* and are here referred with doubt to the latter species.

Occurrence. Cenomanian of New Mexico (Herrick &

Johnson, 1900) and possibly Arizona (Kirkland, 1996); Cenomanian-Turonian of Egypt (Ayoub-Hannaa *et al.*, 2014) and the Sergipe Basin, Brazil (this study); Turonian(?) of Utah (Stanton, 1894).

Liopistha (Psilomya) concentrica Stanton, 1894
(Figures 11M,N)

1894 *Liopistha (Psilomya) concentrica* n. sp.: Stanton, p. 119, pl. 26, figs. 8-10.

1900 *Liopistha concentrica*, Stanton (including *L. elongata* Stanton): Herrick & Johnson, p. 208, pl. 33, fig. 5, pl. 41, figs. 8-10.

1953 *Psilomya concentrica* (Stanton): Stephenson, p. 92, pl. 22, figs. 13,20.

?1996 *Psilomya* sp. cf. *P. concentrica* Stanton: Kirkland, p. 56, pl. 10, fig. R.

v1999 *Liopistha (Psilomya) concentrica* Stanton, 1893: Seeling, p. 135 (*pars*, cf. Appendix 1 herein), pl. 5, fig. 20.

Material. Four composite moulds (NRM-PZ Mo 167902-177905) from the upper Cenomanian-lower Turonian of localities Japarutuba 6 and 11 and Laranjeiras 28 and the lower Turonian of Sergipe 5, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 17.

Description. Shell medium-sized, subtrigonal-ovate, slightly inequilateral; posterior area slightly elongate. Moderately inflated ($W/L = 0.42$ on average; Table 17), with maximum inflation below umbonal area. Posterior end rounded, joining ventral margin in rounded angle. Anterior margin blunt, lower than posterior end, joining ventral margin in obtuse angle. Ventral margin broadly convex. Antero-dorsal and postero-dorsal margins slightly concave, steeply sloping towards anterior and posterior ends. Umbonal area trigonal, moderately convex. Beaks prominent, prosogyrate, situated more than one-third of the total valve length from the anterior end. Ornament consisting of regular growth rugae, increasing in strength ventrally.

Discussion. *Liopistha (Psilomya) concentrica* shows some similarities to *L. (P.) meeki* White, 1874, from the Upper Cretaceous of Utah, USA (White, 1874, p. 26; 1877, p. 186-187, pl. 18, figs. 14a-d) in general outline and size but differs in being less inflated ($W/L = 0.42$ on average as opposed to 0.66) and more elongate, and in having well-developed commarginal ribs and lacking radial ribbing. In addition, the postero-dorsal slope of *L. (P.) meeki* is covered by well-developed commarginal ribs,

Table 16. Dimensions (mm) of *Liopistha (Psilomya) elongata* Stanton, 1893.

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167899	28	22	16	7	1.27	0.25	0.57
NRM-PZ Mo 167900	32	24	17	8	1.33	0.25	0.53
NRM-PZ Mo 167901	30	23	16	8	1.30	0.27	0.53
Range	28-32	22-24	16-17	7-8	1.27-1.33	0.25-0.77	0.53-0.57
Mean	30	23	16.33	7.66	1.30	0.26	0.54

crossed by faint radial ribs. *Poromya lata* Forbes (1846, p. 141, pl. 15, fig. 14) from the Upper Cretaceous of southern India closely resembles *L. (P.) concentrica* in having a subtrigonal shell but differs in having radial rows of minute tubercles separated by wide interspaces and in being more elongate posteriorly. *Psilomya* cf. *concentrica*, figured by Kirkland (1996) from the Cenomanian of northeastern Arizona, USA, differs in having a wide umbonal area, thick commarginal ribs, and a broadly curved posterior margin.

Occurrence. Cenomanian of Texas, USA (Stanton, 1894; Stephenson, 1953) and possibly Arizona, USA (Kirkland, 1996), Cenomanian–Turonian of Sergipe, Brazil (Seeling, 1999; this study).

Liopistha (Psilomya) globulosa (Forbes, 1846)
(Figures 12A–C)

1846 *Poromya globulosa*, sp. nov.: Forbes, p. 141, pl. 17, fig. 6.
1871 *Poromya globulosa*, Forbes: Stoliczka, p. 47, pl. 3, fig. 8; pl. 16, fig. 16.

Material. Three composite moulds (NRM-PZ Mo 167906–167908) from the middle-upper Cenomanian of locality Cruzes 8, the upper Cenomanian–lower Turonian of Japarutuba 11 and the lower–middle Turonian of Laranjeiras 22, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements. See Table 18.

Description. Shell medium-sized, subtrigonal-ovate, inequilateral, inflated, compressed posteriorly. Length and height nearly equal ($L/H = 1.15$ on average; Table 18). Anterior margin slightly convex. Posterior margin rounded, joining ventral margin in rounded curve. Antero-dorsal margin truncated, elevated above hinge and forming obtuse angle with anterior margin. Postero-dorsal margin concave. No lunule. Umbonal area trigonal, moderately wide, inflated and higher than hinge line. Beaks prominent, sharply pointed and slightly incurved anteriorly (Figure 12C). Ornament consisting of commarginal ribs, crossed by faint radial striae.

Discussion. *Liopistha (Psilomya) globulosa* differs from other *Liopistha (Psilomya)* species from Sergipe in having

more inflated valves ($W/L = 0.74$ on average; Table 18), a narrow and trigonal umbonal area and well-developed commarginal ribs.

According to Stanton (1894), *Liopistha (Psilomya) meeki* White, 1874, from the Upper Cretaceous of Utah, USA (White, 1877, p. 186, pl. 18, figs. 14a–d) differs from *L. (P.) globulosa* in being less globose. However, the inflation of the two species is nearly the same ($W/L = 0.74$ in *globulosa* and 0.66 in *meeki*). *L. (P.) meeki* also resembles *L. (P.) globulosa* in general outline and size but has more distinct radial striae (well developed posteriorly), a wide umbonal area, more elevated and strongly enrolled beaks and a wide lunule. *Poromya frequens* (Zittel, 1864, p. 111, pl. 1, figs. 5a–f) is larger ($L = 50$ – 60 mm, $H = 35$ – 45 mm), more elongate ($L/H = 1.38$ as opposed to 1.15 on average for the Sergipe specimens), inflated and has strongly rounded anterior and posterior margins with a broad, convex ventral margin.

It is remarkable that *Liopistha (Psilomya) globulosa* until now has not been described or reported from areas outside the Indian subcontinent, although Stanton (1894, p. 118), Rennie (1930, p. 191) and Dhondt (1987, p. 92) briefly discussed morphologically related species from the USA, South Africa and Austria, respectively.

Occurrence. Cenomanian–Turonian of Sergipe, Brazil (this study); Campanian–Maastrichtian of southern India (Forbes, 1846; Stoliczka, 1870).

Subgenus *Cymella* Meek, 1864

Type species. *Pholadomya undata* Meek & Hayden, 1856, by original designation.

Remarks. Dhondt & Jagt (1989) considered the differences between *Liopistha* and *Cymella* insufficient for generic separation. A separation at the subgeneric level is, however, justified, on the basis of differences in ornament and size. In *Liopistha (Liopistha)*, radial ribs are well developed and sharp, extending from the umbonal area to the ventral margin and bearing sparse tubercles or spines. Commarginal ribs are subordinate and restricted to the dorsal area. By contrast,

Table 17. Dimensions (mm) of *Liopistha (Psilomya) concentrica* Stanton, 1893.

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167902	27	20	c. 11	10	1.35	0.37	c. 0.41
NRM-PZ Mo 167903	23	17	---	6	1.35	0.26	--
NRM-PZ Mo 167904	21	17	c. 9	5	1.23	0.24	0.43
NRM-PZ Mo 167905	22	16	--	7	1.37	0.32	--
Range	21–27	17–20	9–11	5–10	1.23–1.37	0.24–0.37	0.41–0.43
Mean	23.25	17.50	10	7	1.32	0.29	0.42

Table 18. Dimensions (mm) *Liopistha (Psilomya) globulosa* (Forbes, 1846).

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167906	20	17	16	8	1.18	0.40	0.80
NRM-PZ Mo 167907	26	23	18	7	1.13	0.26	0.69
Range	20–26	17–23	16–18	7–8	1.13–1.18	0.26–0.40	0.69–0.80
Mean	23	20	17	7	1.15	0.33	0.74

Liopistha (*Cymella*) is smaller and characterized by strong commarginal ribs, crossed by faint radial ribs in the middle part of the valve.

Liopistha (*Cymella*) sp.
(Figures 12D-H)

Material. Five composite moulds with remains of shell (NRM-PZ Mo 167909-167913) from the lower Cenomanian of localities Itaporanga 2 and 3, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 19.

Description. Shell small, ovate to subovate, inequilateral and moderately inflated. Length and height nearly equal ($L/H = 1.03$ on average; Table 19). Maximum inflation slightly below umbonal area; shell becoming compressed posteriorly. Antero-dorsal margin short. Postero-dorsal margin higher and slightly concave. Anterior margin regularly rounded, joining regularly rounded ventral margin in rounded curve. Umbonal area trigonal and strongly convex. Beaks prominent and strongly incurved anteriorly, situated slightly anterior to mid-length of shell. Lunule broad, smooth, moderately deep. Escutcheon narrow, long and smooth. Ornament consisting of broad, regular, commarginal ribs separated by narrow interspaces. Ribs progressively thickening towards ventral margin and crossed by 18-24 weaker radial ribs (Figures 12E,F) bearing tiny spines and separated by regular interspaces. Specific determination uncertain due to poor preservation of the specimens.

Discussion. *Liopistha* (*Cymella*) *undata* (Meek & Hayden, 1856) from the Upper Cretaceous of Idaho (Meek, 1876, p. 236, pl. 39, figs. 1a,b) and New Jersey, USA (Richards, 1958, p. 171, pl. 27, fig. 9) differs from the Sergipe specimens in being more elongate ($L/H = 0.73$ in Richards's material as opposed to 1.03 on average for the Sergipe specimens) and in having a straight postero-dorsal margin, narrow and compressed posterior side and fewer commarginal ribs. *L. (C.) bella* Conrad, 1873, from the Upper Cretaceous of North Carolina, USA (Miller, 1911, p. 96, pl. 5, fig. 10) and *L. (C.) bella texana* Stephenson, 1941 from the Upper Cretaceous of Texas, USA (Stephenson, 1941, p. 165, pl. 26, figs. 21-23) differ in having nine thick radial ribs, concentrated in the middle part of the valve, and in being more elongate ($L/H = 1.48$, as opposed to 1.03 on average for the Sergipe specimens).

Occurrence. Cenomanian of Sergipe, Brazil (this study).

Subgenus *Sergipemya* n. subgen.

Type species. *Homomya alta* Roemer, 1852.

Etymology. Named after the Sergipe Basin, from where the specimens described here derive.

Diagnosis. Large to very large *Liopistha* with highly inflated, subtrigonal to transversely oblong shell; beaks well developed, sharply pointed, strongly incurved, prosogyrate; umbonal anterior ridge well developed, extending from front of umbonal area to anterior end, forming the boundary of a deep depression; posterior gape lacking; numerous fine commarginal ribs covering the valves and crossed by faint radial tubercles; left valve with two unequal cardinal teeth, with a cardinal tear-shaped socket in-between.

Remarks. The genus *Liopistha* is characterized by radial ornament, which is clearly visible in the figures of the type species (Roemer, 1852, pl. 6, figs. 5a-c). The hinge structure of Roemer's holotype has not been described and remains unknown. Dhondt & Jagt (1989, p. 189) noted that both radial and commarginal elements are equally developed near the umbonal area but towards the ventral margin, only radial ornament remains. They described also the hinge structure of both valves, using the term "tooth-like partition" for a small cardinal tooth directly attached to the hinge margin and situated above the large cardinal tooth. They pointed out that the right valve carries two large cardinal teeth and one thin tooth-like partition, whereas the left valve has one large and one small cardinal tooth and a thin tooth-like partition (Dhondt & Jagt, 1989, pl. 1, fig. 7; pl. 2, fig. 1).

The subgenus *Psilomya* differs from the nominal subgenus mainly in its smaller size and weaker radial ribs. The Sergipe specimens of *Liopistha* (*Liopistha*) show similar hinge structures, with one large and one small cardinal tooth, separated by a tear-shaped cardinal socket in the left valve. *Liopistha* (*Sergipemya*) is readily distinguished from the other subgenera by its (i) large to very large, highly inflated valves, (ii) well-developed commarginal ribs, which cover the entire valve surface and are crossed by faint radial tubercles, (iii) well-developed anterior umbonal ridge, (iv) prominent and strongly enrolled beaks, and (v) deep and wide anterior depression.

Liopistha (*Sergipemya*) *alta* (Roemer, 1852)
(Figures 12I-M, 13A-D)

1852 *Homomya alta* n. sp.: Roemer, p. 45, pl. 6, fig. 11.

1912 *Liopistha* (*Psilomya*) *alta* Roemer: Pervinquière, p. 293, pl. 20, fig. 20.

?1919 *Liopistha* (*Psilomya*) *alta* Roemer: Greco, p. 236, pl. 5 (21), fig. 15.

Table 19. Dimensions (mm) of *Liopistha* (*Cymella*) sp.

Specimen	L	H	W	AL	nr	L/H	AL/L	W/L
NRM-PZ Mo 167909	15	15	8	7	24	1.00	0.47	0.47
NRM-PZ Mo 167910	13	13	7	4	20	1.00	0.31	0.53
NRM-PZ Mo 167911	13	12	8	4	18	1.08	0.31	0.61
Range	13-15	12-15	7-8	4-7	18-24	1.00-1.08	0.31-0.47	0.47-0.61
Mean	13.66	13.33	7.66	5.00	20.66	1.03	0.36	0.54

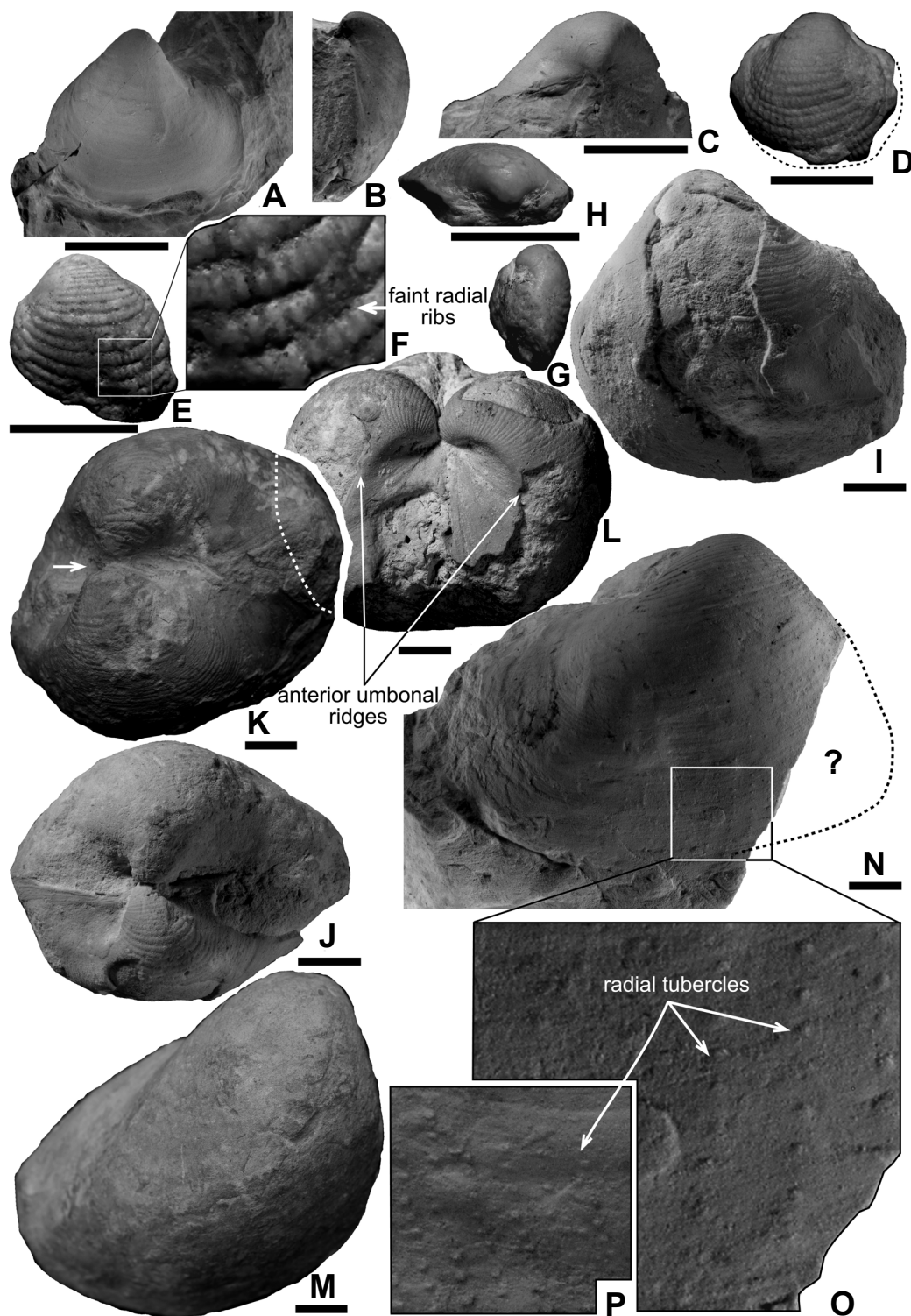


Figure 12. A-C, *Liopistha (Psilomya) globulosa* (Forbes, 1846) from the upper Cenomanian of locality Cruzes 8 (NRM-PZ Mo 167906). A, left lateral view; B, anterior view of left valve; C, close-up view showing the sharply pointed beak. D-H, *Liopistha (Cymella)* sp. from the lower Cenomanian of locality Itaporanga 2. D, side view of right valve of composite mould (NRM-PZ Mo 167909); E, left lateral view of composite mould; F, close-up view showing thick commarginal ribs crossed by faint radial ribs in the postero-ventral and central parts; G, anterior view; H, dorsal view showing the smooth umbonal area (NRM-PZ Mo 167910). I-M, *Liopistha (Sergipemya) alta* (Roemer, 1852) from the upper Cenomanian-upper Turonian. I, left lateral view with shell remains showing the ornament style; J, dorsal view of articulated valves showing lack of posterior gape; locality Japaratus 4 (NRM-PZ Mo 167914); K, dorsal view showing deep anterior depression (arrowed); locality Cajaíba 7 (NRM-PZ Mo 167915); L, anterior view showing strong anterior umbonal keels, strong anterior inflation and enrolled beaks; locality Japaratus 6 (NRM-PZ Mo 167916); M, side view of right valve of internal mould; locality Cajaíba 7 (NRM-PZ Mo 167922). N-P, *Liopistha (Sergipemya) gigantea* (J. Sowerby, 1818) from the lower-middle Turonian of locality Laranjeiras 22. N, right lateral view of incomplete composite mould; O-P, close-ups showing widely spaced radial rows of faint granules (NRM-PZ Mo 167928 and Mo 167929). All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

v1999 *Liopistha (Psilomya) ligeriensis* (d'Orbigny, 1845): Seeling, p. 136, pl. 6, figs. 5-7.

v1999 *Liopistha (Psilomya) cf. alta* (Roemer, 1852): Seeling, p. 137 (*pars*, cf. Appendix 1 herein), pl. 6, figs. 8-9.

Material. Fourteen composite and internal moulds, some of which with remains of shell (NRM-PZ Mo 167914-167927), from the upper Cenomanian–lower Turonian of localities Japarutuba 4, 6 and 16 and the upper Turonian of Mucuri 10 and Cajaíba 7, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 20.

Description. Subtrigonal to transversely oblong, equivalved, inequilateral, highly inflated ($W/L = 0.78$ on average; Figure 13D; Table 20), with thin shell wall. Length and height nearly equal ($L/H = 1.08$ on average; Figure 13C). Maximum inflation below umbonal area, with valves slightly compressed posteriorly. Anterior margin truncated, joining ventral margin in rounded angle. Antero-dorsal margin slightly convex to straight, steeply sloping towards anterior margin and forming obtuse angle. Postero-dorsal margin straight to slightly concave, gradually sloping towards posterior margin. No posterior gape. Ventral margin broad and regularly convex. Umbonal area trigonal, strongly convex. Beaks prominent, sharply pointed, enrolled (Figure 12L), anteriorly incurved, elevated above dorsal margin and situated one-fourth of the total valve length from the anterior end. Hinge of left valve composed of one large and one small cardinal teeth with a tear-shaped cardinal socket in-between (Figure 13A,B). Hinge structure of right valve not preserved. Anterior umbonal ridge well developed, extending from umbonal area to anterior end, forming boundary of deep depression on anterior part (Figure 12L). Posterior umbonal ridge moderately well developed in some specimens (Figure 12M). Ornament consisting of numerous fine, well-developed commarginal ribs, regularly distributed along dorsal area and weakening towards ventral and posterior areas. Radial ornament absent.

Discussion. *Liopistha (Sergipemya) alta* is easily recognized by its irregular commarginal ribs, absence of radial ornament, a triangular umbonal area, truncated antero-dorsal margin, highly inflated valves ($W/L = 0.78$ on average), well-

developed posterior umbonal ridge, and prominent and strongly enrolled beaks.

Liopistha (Psilomya) pervinquieri Greco, 1919, from the Cenomanian of Egypt (Greco, 1919, p. 234, pl. 5, figs. 13,14) differs in being less inflated and in having few, thick commarginal ribs and rounded margins. *L. (S.) alta* (Roemer, 1852) from the same area (Greco, 1919, p. 236, pl. 5, fig. 15) is an internal mould without preserved ornament and less prominent beaks. Therefore, identification must be considered doubtful.

Corbula gigantea Sowerby (1818, p. 13, pl. 209, figs. 5-7) from the upper Albian of England was placed by Woods (1909) and Pervinquier (1912) in *Liopistha (Psilomya)*. This species differs from the Sergipe specimens in being larger ($L = 100$ mm, $H = 80$ mm) and more elongate ($L/H = 1.32$ as opposed to 1.08) and in having fewer radial tubercles along the ventral margin.

Occurrence. Cenomanian of Texas, USA (Roemer, 1852), Egypt (Greco, 1919) and Tunisia (Pervinquier, 1912); Cenomanian–Turonian of Sergipe, Brazil (Seeling, 1999; this study).

Liopistha (Sergipemya) gigantea (J. Sowerby, 1818)
(Figures 12N-P, 14A-C)

1818 *Corbula gigantea* Sowerby, p. 13, pl. 209, figs. 5-7.

1909 *Liopistha (Psilomya) gigantea* (Sowerby): Woods, p. 257, pl. 43, figs. 3-4; pl. 44, figs. 1-2.

1912 *Liopistha (Psilomya) gigantea* J. Sowerby: Pervinquier, p. 292, pl. 20, fig. 21.

v2004 *Psilomya* sp.: Seeling, fig. 3a.

2014 *Liopistha? gigantea* (Sowerby 1818): Ayoub-Hannaa *et al.*, p. 130, pl. 13, figs. 4-6.

Material. Nine internal and composite moulds (NRM-PZ Mo 167928-167936) from the lower–middle Turonian of localities Laranjeiras 21 and 22, Pedra Furada 4 and São Roque 5 and from the upper Turonian of Cajaíba 7, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 21.

Table 20. Dimensions (mm) of *Liopistha (Sergipemya) alta* (Roemer, 1852).

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167914	60	54	45	20	1.18	0.33	0.75
NRM-PZ Mo 167915	72	66	58	20	1.09	0.28	0.80
NRM-PZ Mo 167916	64	65	53	28	0.98	0.43	0.83
NRM-PZ Mo 167917	73	65	60	20	1.12	0.27	0.82
NRM-PZ Mo 167918	85	77	67	23	1.10	0.37	0.79
NRM-PZ Mo 167919	78	70	55	28	1.11	0.35	0.71
NRM-PZ Mo 167920	76	78	65	22	0.97	0.29	0.86
NRM-PZ Mo 167921	70	66	50	18	1.06	0.26	0.71
NRM-PZ Mo 167922	68	60	48	25	1.13	0.38	0.70
NRM-PZ Mo 167923	74	70	63	15	1.06	0.20	0.85
Range	60-85	54-78	45-67	15-28	0.97-1.18	0.20-0.43	0.70-0.86
Mean	72	67.1	56.4	21.9	1.08	0.31	0.78

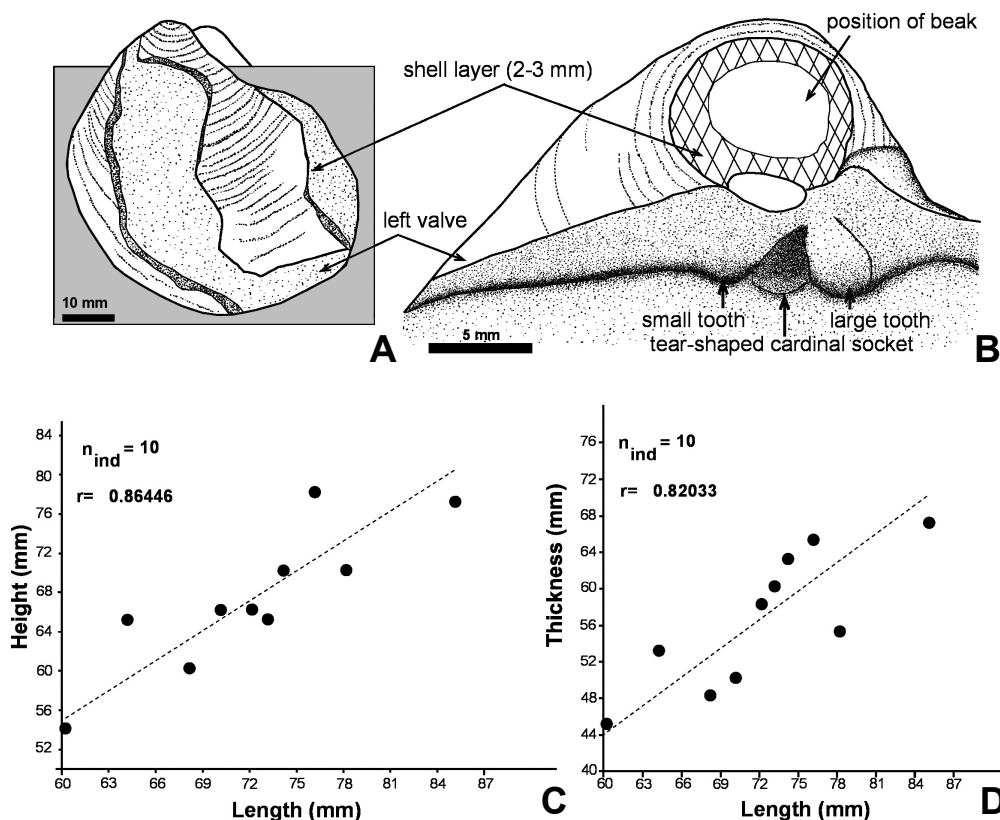


Figure 13. A-B, polished section through hinge of *Liopistha (Sergipemya) alta* (Roemer, 1852), showing one large and one small cardinal tooth with a tear-shaped socket in-between in left valve. C-D, length/height and length/thickness ratios of *L. (S.) alta* from the upper Cenomanian-Turonian of the Sergipe Basin, Brazil.

Description. Shell large, elongate-ovate to rounded-quadrangular, strongly inequilateral and inflated ($W/L = 0.60$ on average; Table 21). Maximum inflation below umbonal area; valves abruptly compressed towards posterior side. Posterior margin rounded, joining ventral margin in rounded curve. No posterior gape. Anterior margin slightly convex to straight, joining the ventral margin in rounded angle. Ventral margin broadly convex. Postero-dorsal margins slightly concave. Umbonal area broad, trigonal, moderately inflated. Beaks elevated, sharply pointed, prominent, strongly incurved anteriorly, situated one-third of the total valve length from the anterior end. Posterior adductor muscle scar nearly circular (Figure 14C). Ornament consisting of closely spaced, fine commarginal ribs, being most distinct dorsally and crossed by radial rows of faint granules further away from the umbonal area towards ventral margin (Figures 12O-P).

Discussion. The similar species *Poromya superba* Stoliczka, 1870 from the Upper Cretaceous of India (Stoliczka, 1870, p. 48, pl. 3, figs. 2-4) and Cameroon (as *Liopistha superba* STOL.; Riedel, 1933, p. 68, pl. 5, fig. 1) differs from *Liopistha (Sergipemya) gigantea* in having well-developed, regular, commarginal ribs covering the entire valve surface, the umbonal area less incurved anteriorly, numerous radial rows of faint granules separated by narrower interspaces, strongly rounded ventral and posterior margins, and in being less elongate and more inflated.

Occurrence. Aptian of Tunisia (Pervinière, 1912); Albian of England (Sowerby, 1818; Woods, 1909; Woods & Jones, 1996, p. 38) and Peru (Hillebrandt, 1970); Cenomanian of the Sinai Peninsula, Egypt (Ayoub-Hannaa *et al.*, 2014); Turonian of Sergipe, Brazil (Seeling, 2004; this study); Upper Cretaceous of South India (Stoliczka, 1870, p. 42).

Megaporomya Ayoub-Hannaa *et al.*, 2013

Type species. *Megaporomya reymenti* Ayoub-Hannaa *et al.*, 2013, by original designation.

Megaporomya? cf. *supermensa* (White, 1887)
(Figures 14D-H)

cf. 1887 *Isocardia supermensa* (sp. nov.): White, p. 80, pl. 6, figs. 1-2.

cf. 1937 *Isocardia supermensa* White: Maury, p. 70, pl. 9, figs. 16-17.

v1983 *Liopistha (Psilomya) supermensa* White [sic]: Bengtson, p. 47 (*pars Megaporomya reymenti* Ayoub-Hannaa *et al.*, 2013).

cf. 1999 *Liopistha (Psilomya) supermensa* (White): Seeling, p. 138, pl. 7, figs. 1-2.

non 2011 *Liopistha (Psilomya) supermensa* (White, 1887): Andrade & Santos, p. 234, figs. 2:5-7 (= *Megaporomya reymenti* Ayoub-Hannaa *et al.*, 2013).

Table 21. Dimensions (mm) of *Liopistha (Sergipemya) gigantea* (Sowerby, 1818).

Specimen	L	H	W	AL	L/H	AL/L	W/L
NRM-PZ Mo 167927	71	52	--	20	1.36	0.28	--
NRM-PZ Mo 167928	69	56	c. 45	28	1.23	0.40	c. 0.65
NRM-PZ Mo 167929	87	60	--	35	1.45	0.40	--
NRM-PZ Mo 167930	67	51	45	25	1.31	0.37	0.67
NRM-PZ Mo 167931	92	73	46	33	1.26	0.36	0.50
NRM-PZ Mo 167932	78	60	45	27	1.30	0.35	0.58
NRM-PZ Mo 167933	91	72	--	27	1.26	0.29	--
Range	67-92	51-73	45-46	20-35	1.23-1.45	0.28-0.40	0.50-0.67
Mean	67.28	60.57	45.25	27.86	1.31	0.35	0.60

Material. Twelve articulated composite and internal moulds (NRM-PZ Mo 167937-167948) from the upper Cenomanian–lower Turonian of localities Japarutuba 4 and 11 and Jardim 31, the lower–middle Turonian of Laranjeiras 21 and the upper Turonian of Cajuíba 7 and the area of Cajuíba 7-10, Cotinguiba Formation, Sergipe, Brazil.

Measurements. See Table 22.

Description. Shell large, elongate-ovate to oblong-elongate, slightly equivalved, strongly inequilateral, highly inflated (W/L = 0.69 on average; Table 22) and posteriorly elongate. Maximum inflation below umbonal area, with valves gradually becoming compressed posteriorly. Anterior area truncated, joining ventral margin in blunt, nearly right angle (Figure 14D). Posterior margin slightly convex, posterior end gaping. Postero-dorsal margin slightly concave and parallel to ventral margin. Ventral margin broad and slightly convex. Rounded ridge extending from front of umbonal area to middle of anterior margin, forming boundary of depression on anterior part (Figure 14F). Umbonal area wide and strongly convex. Beaks large, terminal to subterminal (AL/L = 0.20 on average, Table 22), less prominent, enrolled, and slightly incurved anteriorly. Ornament consisting of commarginal ribs, well developed along dorsal area and less well developed further away from umbonal area towards ventral side.

Discussion. The specimens are characterized by terminal to subterminal beaks, a truncated anterior margin, highly inflated valves, lack of a radial ornament, and by a well-developed anterior umbonal ridge bordering a deep anterior depression.

The genus *Megaporomya* was erected by Ayoub-Hannaa *et al.* (2013) on the basis of specimens from the upper Turonian–lower Coniacian? of the Sergipe Basin, Brazil. *Megaporomya* differs from other genera of the family Poromyidae (*e.g.* *Poromya* Forbes, 1844, and *Liopistha* Meek, 1864) by its large to very large size, broad and marked umbonal area, highly inflated valves, strongly enrolled beaks, and its hinge consisting of two teeth, separated by a deep socket, in each valve.

The specimens described here are similar to *Megaporomya? supermensa* (White, 1887) from the upper Albian of Sergipe (White, 1887, p. 80, pl. 6, figs. 1,2; Maury, 1937, p. 71, pl. 9, figs. 16,17), in having terminal beaks, a large posterior gape, and in being elongate (L/H = 1.46 on average; Table 22) and highly inflated (W/L = 0.69 on average). However, due to the poor preservation of the present specimens

and the less developed anterior umbonal ridge, a definite identification is not possible. *M.? cf. supermensa* differs from *M. reymenti* Ayoub-Hannaa *et al.*, 2013, from the upper Turonian-lower Coniacian? of Sergipe (Ayoub-Hannaa *et al.*, 2013, p. 200, figs. 4-6,9) in being smaller (L = 80.75 mm, H = 56.12 mm, W = 57.71 mm as opposed to L = 114.89 mm, H = 91.15 mm, W = 84.45 mm on average in *M. reymenti*) and more elongate (L/H = 1.46 vs. 1.25 on average) and in having an antero-dorsal ridge with a deep anterior depression. In addition, the commarginal ribs of *M. reymenti* are well developed and crossed by widely spaced radial rows of minute tubercles. Further away from the umbonal area, towards the ventral margin, the radial tubercles are more strongly developed. *M.? supermensa* lacks radial ribs.

Occurrence. Albian–Turonian of Sergipe, Brazil (White, 1887; Maury, 1937; Seeling, 1999; this study).

PALAEOBIOGEOGRAPHIC REMARKS

A general problem when attempting to carry out palaeobiogeographic analyses of the Cretaceous marine bivalve fauna of the Sergipe Basin is the scarcity and poor preservation of many taxa, in particular the heterodonts. However, the abundance and comparatively good preservation of pholadomyid specimens have been found useful for identifying palaeobiogeographic affinities for the Cenomanian–Turonian interval.

The Sergipe pholadomyid fauna shows little endemism, with most of the taxa widely distributed in other regions such as western and southern Europe, western and northern Africa and the Middle East. Non-metric multidimensional scaling (nMDS) produces a useful ordination of regions that were geographically close to north-eastern Brazil (analysis done at the species level). For the Cenomanian, Egypt, Tunisia, Algeria and Nigeria plot close to Brazil (Figure 15A). This cluster is separated from areas along the southern margin of North America (Mexico, Arizona and Texas), India and Central Asia. The slow migration of pholadomyids across the North American Province and Indo-Pacific region (*sensu* Kauffman, 1973) was probably due to the large distance and depth of the ocean between these provinces. In addition, environmental conditions such as water temperature, salinity and substrate types may have been less favourable for

Table 22. Dimensions (mm) of *Megaporomya? cf. supermensa* (White, 1887).

Specimen	L	H	W	AL	Hs	Ws	L/H	AL/L	Hs/Ws	W/L
NRM-PZ Mo 167937	81	58	56	29	37	13	1.40	0.36	2.85	0.69
NRM-PZ Mo 167938	88	63	56	23	--	--	1.40	0.26	--	0.64
NRM-PZ Mo 167939	83	50	62	12	43	--	1.66	0.14	--	0.75
NRM-PZ Mo 167940	66	64	54	--	46	12	1.03	--	3.83	0.82
NRM-PZ Mo 167941	80	60	56	10	38	11	1.33	0.13	3.45	0.70
NRM-PZ Mo 167942	83	48	c. 42	9	35	--	1.73	0.11	--	0.51
NRM-PZ Mo 167943	77	48	53	12	--	--	1.60	0.16	--	0.69
NRM-PZ Mo 167944	88	58	67	20	40	16	1.52	0.23	2.50	0.76
Range	66-88	48-64	42-67	9-29	35-46	11-16	1.03-1.73	0.11-0.36	2.50-3.83	0.51-0.82
Mean	80.75	56.12	57.71	16.42	39.83	13	1.46	0.20	3.16	0.69

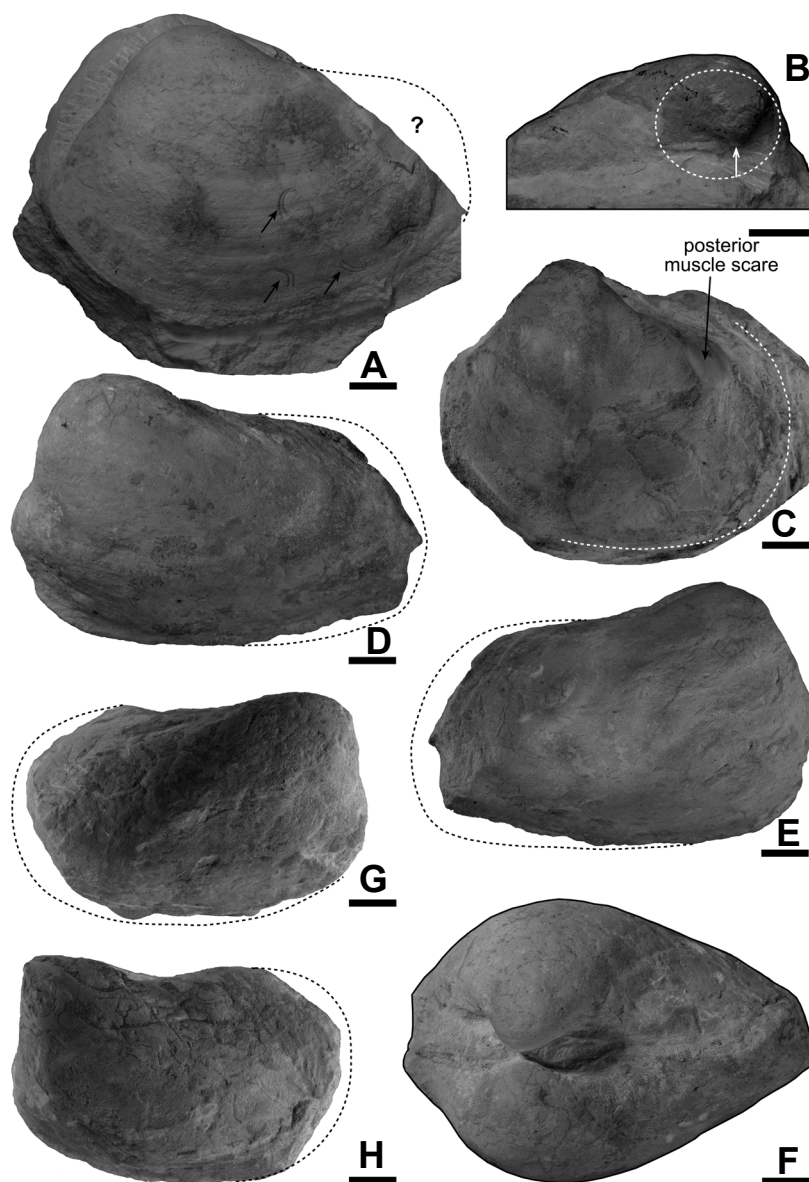


Figure 14. **A-C**, *Liopistha* (*Sergipemya*) *gigantea* (J. Sowerby, 1818) from the lower–middle Turonian. **A**, side view of left valve of incomplete composite mould, with serpulid encrustations (arrowed; cf. Seeling 2004, fig. 3a-b); locality Laranjeiras 22 (NRM-PZ Mo 167930); **B**, dorsal view of left valve of composite mould, showing strongly incurved umbonal area; locality Laranjeiras 22 (NRM-PZ Mo 167929); **C**, left lateral view of composite mould showing circular adductor muscle scar; locality Laranjeiras 21 (NRM-PZ Mo 167932). **D-H**, *Megaporomya? cf. supermensa* (White, 1887) from the upper Cenomanian–lower Turonian of locality Japaratusba 4. **D**, side view of left valve of internal mould; **E**, Right lateral view; **F**, dorsal view of articulated valves showing the deep anterior cavity and highly inflated valves (NRM-PZ Mo 167937); **G**, Side view of right valve of internal mould, showing terminal beaks; **H**, side view of left valve (NRM-PZ Mo 167938). All specimens from the Cotinguiba Formation of the Sergipe Basin, Brazil. Scale bars = 10 mm.

settling. According to Lazo (2007), the larvae were able to test the bottom substrate and postpone metamorphosis until they found a suitable substrate for adult life. As a result of the late Cenomanian–early Turonian maximum flooding, pholadomyid faunas were able to colonize increasingly the Western and Eastern Mediterranean subprovinces. A distinct clustering of points around Brazil (Figure 15B) supports the conclusion that the South Atlantic Subprovince was connected with the Western and Eastern Mediterranean Subprovinces (*sensu* Kauffman, 1973). For instance, the pholadomyids of the Gabon Basin [*Pholadomya* (*Ph.*) *adversa*, *Ph.* (*Ph.*) *pedernalis* and *Ph.* (*Procardia*) *vignesii*] show strong similarities with coeval faunas of the northwestern margins of the South Atlantic. In addition, *Ph.* (*Ph.*) *nodulifera* and *Pleuromya ligeriensis* of France, Germany, Egypt, Tunisia and Algeria indicate similarities between the northern and southern Tethys. However, Angola and Cameroon plot as far

away from Brazil as Central Asia (Figure 15B) and thus cannot be included in the latter provinces, although this pattern may be due to insufficient data from these West African regions. Kauffman (1973) discussed the palaeobiogeography of Cretaceous bivalves and concluded that the Sergipe Basin belongs to the South Atlantic Subprovince of the South Temperate Realm. However, because of the close affinity with the faunas of the southern Tethyan region, Westermann (2000) assigned the northern South Atlantic region to the Mediterranean-Caucasian Subrealm.

The distribution of pholadomyid taxa was probably influenced by east–west-directed currents and migration along a permanent north–south connection in the equatorial Atlantic from the Albian onwards (Figure 15C). During the late Cenomanian–early Turonian, connections with North African faunas were enhanced through the intermittent Trans-Saharan Seaway (*e.g.* Seeling & Bengtson 2002; Courville,

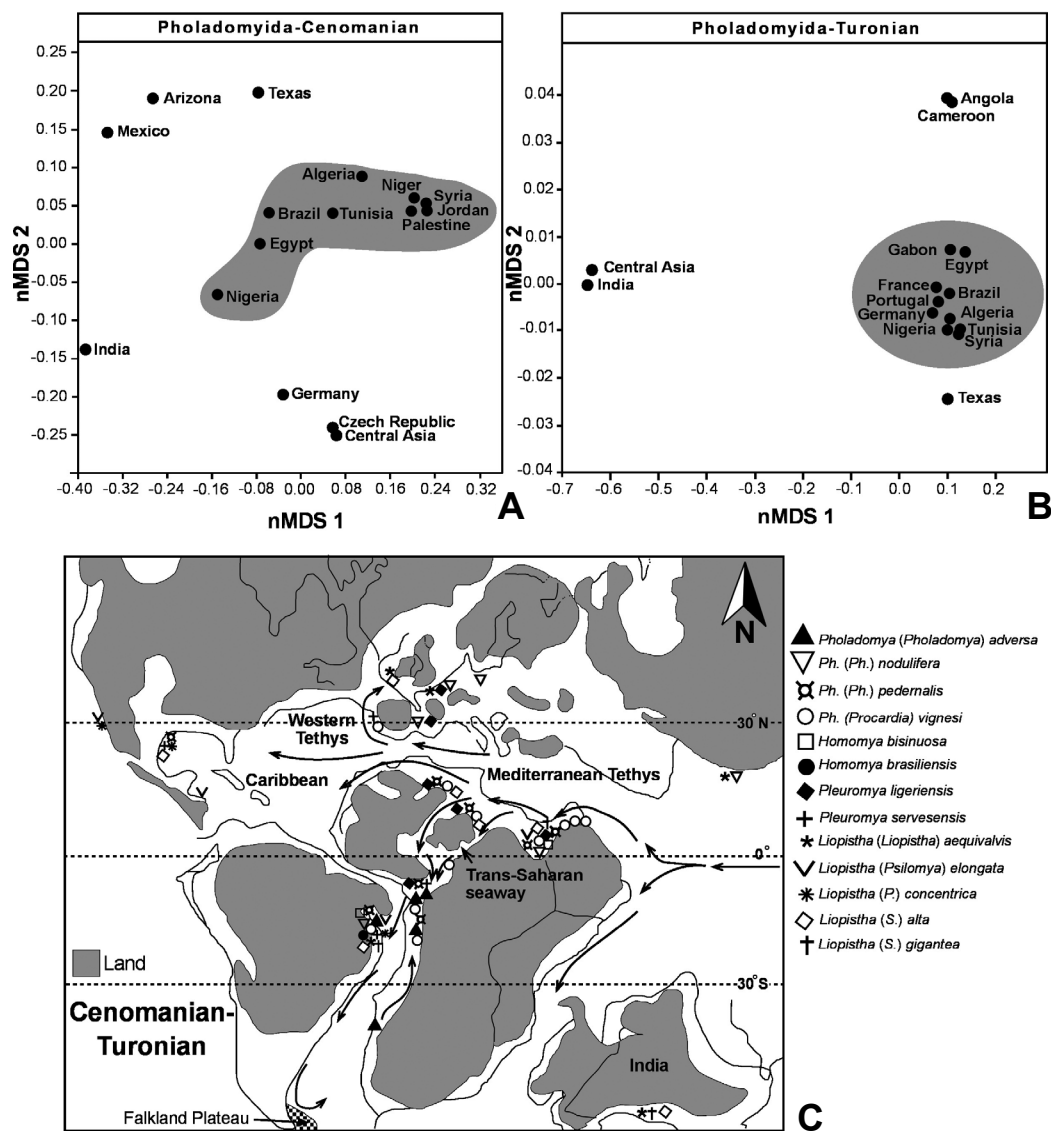


Figure 15. Non-metric multidimensional scaling (nMDS) of proportional distances of occurrences of pholadomyid taxa by country during the Cenomanian (A) and Turonian (B). C, geographic distribution and reconstruction of surface-water currents during the Cenomanian–Coniacian, based on the distribution patterns of selected pholadomyid species. Palaeogeographic base map after Seeling & Bengtson (1999).

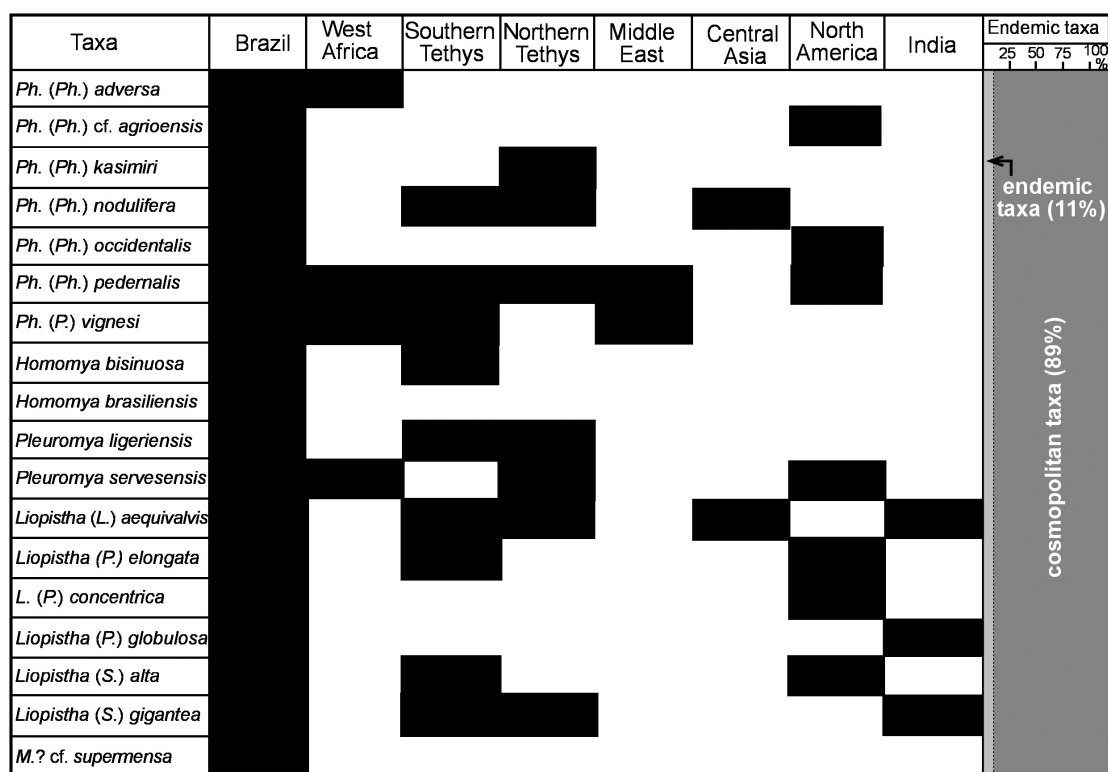


Figure 16. Geographic distribution and degree of endemism of Cenomanian-Turonian pholadomyid taxa of the Sergipe Basin, Brazil.

2007; Meister & Piuz, 2013; Ayoub-Hannaa *et al.*, 2014). The westward migration along the margins of the Tethys split into a northern route along southern Europe and northern Africa and a southern route along the eastern margins of Africa (e.g. Somalia, India, and Madagascar). However, there is no conclusive evidence for migration around the tip of southern Africa, as postulated by Néraudeau & Mathey (2000).

In conclusion, the overwhelming majority (c. 90%) of the Cenomanian–Turonian pholadomyid species of the Sergipe Basin in north-eastern Brazil show a cosmopolitan distribution, with closest ties with West Africa and the Mediterranean Province (Figure 16). The wide distribution of this group of bivalves indicates that their larvae were long-lived and possessed a high dispersal potential.

CONCLUSIONS

Twenty-two species of Pholadomyida belonging to six genera and seven subgenera of the families Pholadomyidae, Pleuromyidae, and Poromyidae are described from the Cotinguiba Formation of the Sergipe Basin, north-eastern Brazil, from beds dated with ammonites as Cenomanian–early Coniacian.

Eleven species, *Pholadomya (Pholadomya) cf. agrioensis* Weaver, 1931, *Ph. (Ph.) kasimiri* Pusch, 1837, *Ph. (Ph.) nodulifera* Münster, 1841, *Ph. (Ph.) occidentalis* Morton, 1833, *Ph. (Procardia) vignesi* Lartet, 1877, *Pleuromya ligeriensis* (d'Orbigny, 1845), *Pl. servesensis* Choffat, 1902, *Liopistha (Liopistha) aequivalvis* (Goldfuss, 1841), *L. (Sergipemya) gigantea* (J. Sowerby, 1818), *L. (Psilomya*

elongata Stanton, 1894, and *L. (P.) globulosa* (Forbes, 1846) are recorded from the Sergipe Basin for the first time.

The new subgenus *Sergipemya* of the genus *Liopistha* is erected. It is distinguished from other subgenera of *Liopistha* by its numerous commarginal ribs, lack of radial ribs, large and highly inflated valves and incurved umbonal area, a well-developed rounded ridge, deep anterior cavity and the presence of two unequal cardinal teeth with a cardinal socket in the left valve.

Most of the taxa show a cosmopolitan distribution as a result of the longevity of their larvae and the widespread marine connections in Cenomanian–Turonian times.

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Appendix 1. List of identifiable specimens described by Seeling (1999, 2004), with revised determinations herein.

Determinations by Seeling (1999, 2004)	Specimen numbers and figures of Seeling (1999)	Specimen number of Seeling (2004)	NRM-PZ number	Determinations herein, with corresponding figures
<i>Pholadomya (Ph.) cf. pedernalis</i>	452.88, pl. 5:19		Mo 167861	<i>Pholadomya (Ph.) pedernalis</i> , fig. 9E
<i>Panopea (P.) rathbuni</i>	170.25, pl. 6:4		Mo 167872	<i>Homomya bisinuosa</i> , fig. 10 ^a -C
<i>Panopea (P.) rathbuni</i>	296.13		Mo 167873	<i>Homomya bisinuosa</i>
<i>Panopea (P.) rathbuni</i>	507.P1		Mo 167884	<i>Pleuromya servesensis</i> , fig. 11B
<i>Panopea (P.) rathbuni</i>	507.P2		Mo 167886	<i>Pleuromya servesensis</i>
<i>Panopea (P.) rathbuni</i>	660.P1, pl. 6:2-3		Mo 167877	<i>Homomya brasiliensis</i> , fig. 10D-F
<i>Panopea (P.) rathbuni</i>	660.P2		Mo 167878	<i>Homomya brasiliensis</i> , fig. 10G-H
<i>Panopea</i> sp.	507.P3		Mo 167887	<i>Pleuromya servesensis</i>
<i>Panopea</i> sp.	660.P4		Mo 167879	<i>Homomya brasiliensis</i>
<i>Liopistha (P.) concentrica</i>	170.27b, pl. 5:20		Mo 167902	<i>Liopistha (P.) concentrica</i> , fig. 11M
<i>Liopistha (P.) concentrica</i>	296.12		Mo 167903	<i>Liopistha (P.) concentrica</i> , fig. 11N
<i>Liopistha (P.) concentrica</i>	507.P1		Mo 167900	<i>Liopistha (P.) elongata</i>
<i>Liopistha (P.) concentrica</i>	507.10b		Mo 167905	<i>Liopistha (P.) concentrica</i>
<i>Liopistha (P.) concentrica</i>	652.L12a		Mo 167904	<i>Liopistha (P.) concentrica</i>
<i>Liopistha (P.) concentrica</i>	660.C2		Mo 167899	<i>Liopistha (P.) elongata</i> , fig. 11J-L
<i>Liopistha (P.) cf. alta</i>	170.19		Mo 167881	<i>Pleuromya ligeriensis</i>
<i>Liopistha (P.) cf. alta</i>	660.2, pl. 6:7 (erroneously as <i>L. (P.) ligeriensis</i> in caption)		Mo 167917	<i>Liopistha (Sergipemya) alta</i>
<i>Liopistha (P.) cf. alta</i>	660:3, pl. 6:8-9 (error for no. 170.17)		Mo 167916	<i>Liopistha (Sergipemya) alta</i> , fig. 12L
<i>Liopistha (P.) cf. alta</i>	660.L5		Mo 167918	<i>Liopistha (Sergipemya) alta</i>
<i>Liopistha (P.) cf. alta</i>	660.L4		Mo 167920	<i>Liopistha (Sergipemya) alta</i>
<i>Liopistha (P.) supermense</i>	109.5		Mo 167939	<i>Megaporomya?</i> cf. <i>supermense</i>
<i>Liopistha (P.) supermense</i>	109.17		Mo 167938	<i>Megaporomya?</i> cf. <i>supermense</i> , fig. 14G-H
<i>Liopistha (P.) supermense</i>	109.27, pl. 7:1-2		Mo 167937	<i>Megaporomya?</i> cf. <i>supermense</i> , fig. 14D-F
<i>Liopistha (P.) supermense</i>	507.64		Mo 167940	<i>Megaporomya?</i> cf. <i>supermense</i>
<i>Liopistha (P.) supermense</i>	507.66		Mo 167943	<i>Megaporomya?</i> cf. <i>supermense</i>
<i>Liopistha (P.) ligeriensis</i>	109.19		Mo 167914	<i>Liopistha (Sergipemya) alta</i> , fig. 12I-J
<i>Liopistha (P.) ligeriensis</i>	109.29		Mo 167919	<i>Liopistha (Sergipemya) alta</i>
<i>Liopistha (P.) ligeriensis</i>	170.17, pl. 6:5-6, (error for no. 660.3?)			<i>Liopistha (Sergipemya) alta</i>
<i>Liopistha (P.) ligeriensis</i>	170.22		Mo 167925	<i>Liopistha (Sergipemya) alta</i>
<i>Psilomya</i> sp.		C62.126, fig. 3A	Mo 167930	<i>Liopistha (Sergipemya) gigantea</i> , fig. 14A