

Cenomanian–Turonian (Cretaceous) heterodont bivalves from the Sergipe Basin, Brazil

Wagih S. AYOUB-HANNA¹, Peter BENGTON², Franz T. FÜRSICH³ & Edilma J. ANDRADE⁴

¹ Geology Department, Faculty of Science, Minufiya University, El-Minufiya, Shibin El Kom, Egypt. Current address: GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Friedrich-Alexander Universität Erlangen-Nürnberg Loewenichstr. 28, D-91054 Erlangen, Germany. E-mail: wagih_hannaa@yahoo.com

² Institut für Geowissenschaften, Universität Heidelberg, Im Neuenheimer Feld 234, D-69120 Heidelberg, Germany. E-mail: peter.bengtson@geow.uni-heidelberg.de

³ GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Friedrich-Alexander Universität Erlangen-Nürnberg Loewenichstr. 28, D-91054 Erlangen, Germany. E-mail: franz.fuersich@gzn.uni-erlangen.de

⁴ Departamento de Geologia, Universidade Federal de Sergipe (UFS), Cidade Universitária, Campus Prof. José Aloísio de Campos, Avenida Marechal Rondon s/n – Jardim Rosa Elze, 49100-000 São Cristóvão, SE, Brazil. E-mail: edilmaa@gmail.com

Abstract

Fifty heterodont bivalve species, belonging to 35 genera, 15 families and six orders, from the Cenomanian–Coniacian Cotinguiba Formation of the Sergipe Basin, north-eastern Brazil, are systematically described and figured. Thirty-three species are recorded from the basin for the first time. The new species *Callucina* (*C.*) *itaporangensis* sp. nov. from the lower Cenomanian is characterised by its heart-shaped to sublanceolate and slightly asymmetric lunule, narrow, shallow and elongated escutcheon, widely spaced comm marginal ribs crossed by faint radial striations, rod-like anterior adductor muscle scar (separated ventrally from the pallial line) and straight postero-dorsal and posterior margins with an angular junction. The fauna shows little endemism, which indicates that the larvae were long-lived and possessed a high dispersal potential. The fauna occurred across a wide geographic area, from the Middle East, northern Africa and southern Europe to western Africa and the Pacific rim of South America, with some taxa also known from India. The biogeographic pattern suggests that many groups migrated via the trans-Saharan seaway, which connected the southern Tethys with the incipient South Atlantic Ocean.

Keywords

Bivalves, Taxonomy, Palaeobiogeography, Cretaceous, Cenomanian, Turonian, Sergipe Basin, Brazil.

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1. INTRODUCTION

The Heterodontia (Cohort Cardiomorphi) form the most diverse group of the Class Bivalvia, with many species-rich families (e.g., Taylor *et al.*, 2007). Most fossil heterodonts are preserved as articulated internal and composite moulds, and their internal characters such as cardinal and lateral teeth and muscle scars are not preserved or only partly preserved. This type of preservation is particularly true of shallow- and deep-infaunal bivalves, because their shells have been entirely dissolved early in diagenesis. Externally, many heterodonts show similar shell outlines, which often makes identification of fossil taxa on the basis of external morphology highly subjective. As a result, many heterodont taxa have been regrouped and reassigned through time (e.g., Dhondt, 1987; Dhondt & Dieni, 1988; Ayoub-Hannaa *et al.*, 2013, 2014). Without taking internal structure and characters into account, precise identification is in general not possible.

The Sergipe Basin in north-eastern Brazil contains one of the most extensive marine Cretaceous successions (Aptian to Maastrichtian) among the northern South

Atlantic basins, yielding a rich macroinvertebrate fauna (e.g., Bengtson, 1983; Koutsoukos & Bengtson, 1993). The large number of discontinuity surfaces, stratigraphic gaps and the predominance of small outcrops (normally only a few metres of section or less exposed) in combination with local shifts in strike and dip, makes stratigraphic positioning of individual specimens difficult (Koutsoukos & Bengtson, 1993; Ayoub-Hannaa *et al.*, 2013). However, owing to the extensive total thickness of the succession (well over 500 m), it can be assumed that specimens collected from one and the same small outcrop are largely coeval.

The Cenomanian–Turonian macroinvertebrate fauna of Sergipe is dominated by molluscs, in particular ammonites and bivalves. Parts of this fauna were studied by earlier workers (e.g., White, 1887; Maury, 1925, 1937). More recently, oysters, pinnids, pectinids, pholadomyids, inoceramids, gastropods and ammonites have been documented (e.g., Hessel, 1988; Seeling, 1999; Seeling & Bengtson, 1999, 2003a, b; Andrade *et al.*, 2004, 2011; Andrade, 2005; Gale *et al.*, 2005; Andrade & Santos, 2011; Lexen, 2013; Ayoub-Hannaa *et al.*, 2013, 2015; Bengtson *et al.*, 2015). Heterodont bivalves are widely

distributed throughout the basin but still poorly known and in need of major revision. The present study comprises taxonomic descriptions and revisions, with discussion of the palaeobiogeographic distribution of the taxa.

2. LOCATION AND GEOLOGICAL SETTING

The Sergipe Basin is located in the south-eastern, coastal part of the state of Sergipe in north-eastern Brazil (Fig. 1A–B). It is limited by the Japoaí–Penedo High to the north and by the Rio Real High to the south. The basin comprises an area of approximately 11,000 km², of which 6,000 km² are onshore. The offshore portion extends to water depths exceeding 2,000 m (Koutsoukos *et al.*, 1993; Koutsoukos, 1998). Structurally, the Sergipe Basin is a subbasin of the Sergipe-Alagoas Basin (Souza-Lima *et al.*, 2002), one of the numerous South Atlantic continental margin basins formed during the Late Jurassic–Early Cretaceous as a result of rifting and drifting between South America and Africa (Ponte & Asmus, 1976; Asmus, 1981; Ojeda, 1982; Asmus & Baisch, 1983). The basin consists of a series of half-grabens with a regional dip averaging 10–15° to the south-east, resulting from NE–SW-trending normal faults. Sedimentation within the basin was strongly controlled by changes in subsidence and by the formation of a half-graben along NE–SW-trending extensional faulting. The geological evolution and the development of the marine Cretaceous of the Sergipe Basin have been discussed by several authors, e.g., Ojeda & Fugita, 1976; Ojeda, 1982; Bengtson, 1983; Koutsoukos & Bengtson, 1993; Koutsoukos *et al.*, 1993; Feijó, 1995; Souza-Lima *et al.*, 2002; and Campos Neto *et al.*, 2008.

3. STRATIGRAPHY

The sedimentary fill of the Sergipe Basin comprises a non-marine, Carboniferous–Lower Cretaceous (Barremian) succession and a marine, upper Barremian–Holocene succession (e.g., Feijó, 1995; Souza-Lima *et al.*, 2002; Campos Neto *et al.*, 2008; Bengtson *et al.*, 2018), forming the most complete and extensively exposed succession among the South Atlantic continental margin basins. The Aptian–lower Coniacian succession is divided into an Aptian–Albian mixed carbonate–siliciclastic platform system (Riachuelo Formation) with an average thickness of c. 500 m and a Cenomanian–lower Coniacian carbonate ramp system (Cotinguba Formation) consisting of a massive succession of dominantly fine-grained, deeper-water limestones, with an average thickness of c. 200 m, locally reaching 1,000 m (Fig. 2). The overlying Santonian–Holocene siliciclastic succession (Calumbi Formation) may reach more than 2,000 m in thickness and is mainly represented offshore; onshore, probably only upper Campanian rocks are exposed (Souza-Lima *et al.*, 2002).

The Cotinguba Formation was deposited in neritic to upper-bathyal environments under moderately dysoxic to fully anoxic bottom conditions and well-oxygenated epipelagic conditions (Berthou & Bengtson, 1988; Koutsoukos *et al.*, 1991; Bengtson & Lindgren, 2005; Ayoub-Hannaa *et al.*, 2014). The Cenomanian succession is poorly exposed and incomplete, whereas the Turonian and lower Coniacian are well represented, although the large number of discontinuity surfaces suggests stratigraphic gaps. The proposed shift upwards of the Turonian–Coniacian boundary (e.g., Kauffman *et al.*, 1996) has led to a reassignment of most of the previously assigned lower Coniacian beds (Bengtson, 1983) to the upper Turonian (S.I. Bengtson *et al.*, 2005). The stratigraphy and depositional history of the marine Cretaceous of the basin have been described, for example, by Schaller (1970), Ojeda & Fugita (1976), Bengtson (1983), Berthou & Bengtson (1988), Lana (1990), Koutsoukos & Bengtson (1993), Koutsoukos *et al.* (1993), Feijó (1995), Souza-Lima *et al.* (2002) and Campos Neto *et al.* (2008). For the current biostratigraphic zonation, see Bengtson *et al.* (2018).

Most of the heterodont specimens described here were collected from Turonian beds (*sensu* S.I. Bengtson *et al.*, 2005), with only a few specimens from the Cenomanian (and possibly even upper Albian). One single specimen – *Lucina fallax* Forbes, 1846, from locality Mucuri 7 – is possibly referable to the lower Coniacian.

4. MATERIAL AND METHODS

The material for this study comprises 471 specimens from 32 localities of the Sergipe Basin (Fig. 1C). Most of the localities were described by Bengtson (1983, appendix 1), with localities Jardim 29, Jardim 31, Retiro 26 and Laranjeiras 28 subsequently described by Seeling & Bengtson (1999, appendix), Andrade *et al.* (2004, appendix A), Hessel (1988, p. 9) and Ayoub-Hannah *et al.* (2015, p. 35), respectively. The bulk of the present material derives from fieldwork by P. and S.I. Bengtson in 1971–1972, with complementary sampling by P. Bengtson in 1977, S. Übelaker and A. Herrmann in 1995, J. Seeling in 1995–1996 and E.J. Andrade in 2001–2004. Locality designations “Itaporanga 2/3” and “Cruzes 8/11” refer to specimens where the exact provenance is uncertain (Itaporanga 2 or 3, and Cruzes 8 or 11, respectively). The uncertain Itaporanga specimens were collected mainly by locals and the Cruzes specimens as float. Preservation of the heterodont bivalves of Sergipe is highly variable. Most of the specimens are preserved as internal or composite moulds. The shape and/or ornamentation of composite moulds normally allow for species identification, whereas internal moulds commonly lack important characters needed for a reliable identification. A few specimens occur in shell preservation. Specimens with shell preservation often reveal the hinge structure, a key element for precise assignment of taxa.

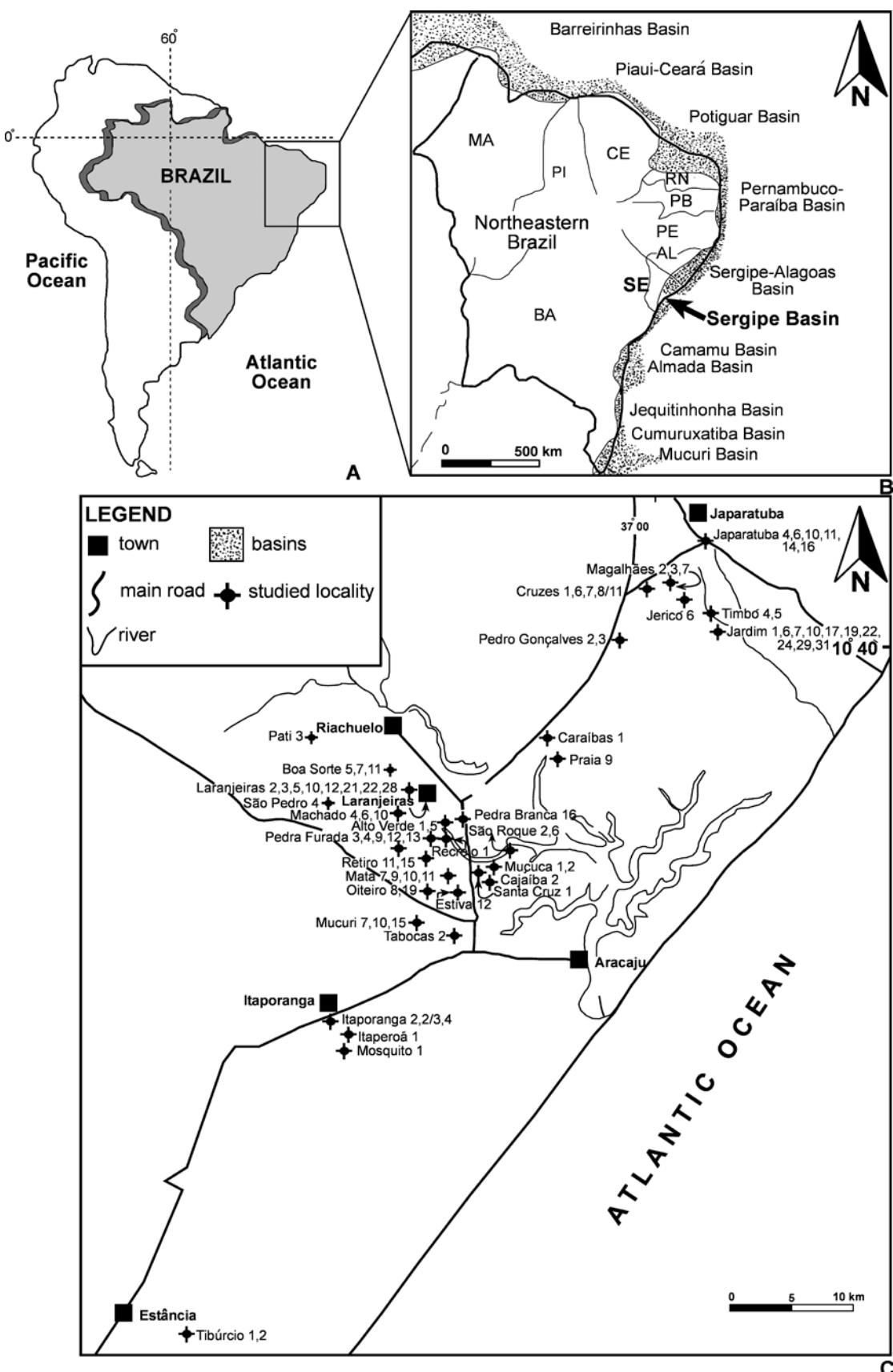


Fig. 1: A-B, Location of the Sergipe Basin in north-eastern Brazil. C, Locality map of the sections studied. Abbreviations of state names: AL, Alagoas; BA, Bahia; CE, Ceará; MA, Maranhão; PB, Paraíba; PE, Pernambuco; PI, Piauí; RN, Rio Grande do Norte; SE, Sergipe.

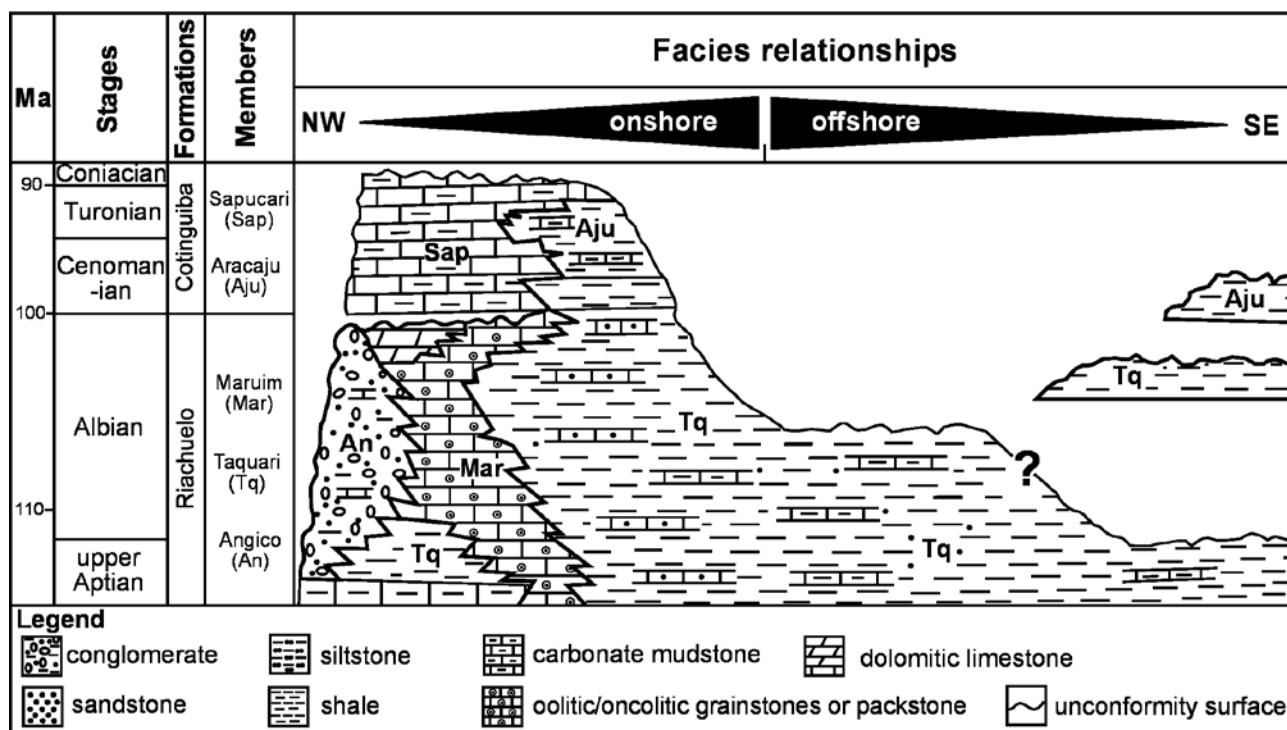


Fig. 2: Simplified stratigraphic framework of the marine middle Cretaceous succession of the Sergipe Basin (modified after Bengtson, 1983; Smith & Bengtson, 1991; Koutsoukos & Bengtson, 1993; Feijó, 1995; Souza-Lima *et al.*, 2002).

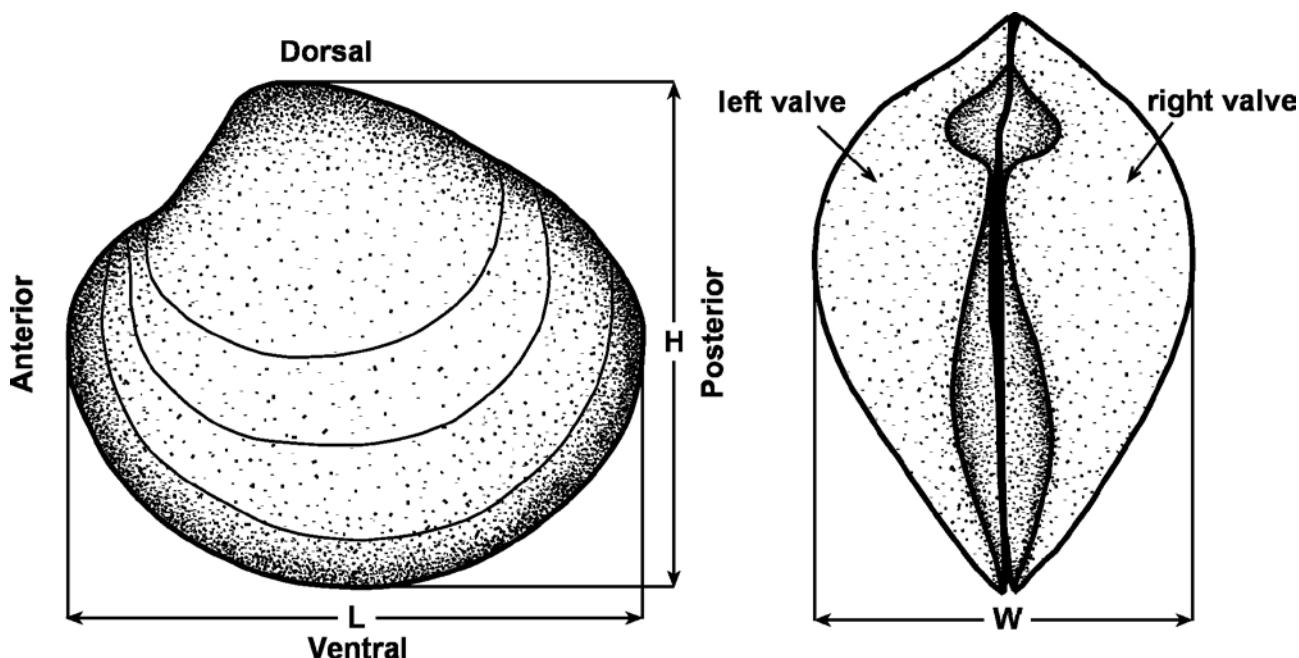


Fig. 3: Orientation and measurements of an articulated heterodont specimen. Abbreviations: L – shell length, H – shell height, W – inflation.

The specimens were prepared mechanically and cleaned. However, cleaning of small specimens (less than 10 mm in length) is risky and may cause damage. Most specimens, except the smaller ones, were whitened with magnesium oxide to enhance the finer details of ornament. In addition, silicone rubber moulds and polished sections were made in order to facilitate study of the hinge structure. Only well-preserved specimens were used for identification.

A principal component analysis (PCA) using the PAST software, version 2.16 (Hammer *et al.*, 2001), on a variance-covariance matrix of the log-transformed variables was carried out to clarify the morphological relationships of some taxa.

Classification follows that of Carter *et al.* (2011) and the terminology the glossary of Cox (1969) in the *Treatise on Invertebrate Paleontology*. For the Subfamily Opinae Chavan, 1952, the term “corcelet” is used, as defined by Carter (1967, p. 261) as “a further differentiated area posterior to the umbones, outside of the escutcheon”.

The synonymy lists and the sections “Occurrence” contain only records 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. For open nomenclature and abbreviations in synonymy lists, see Matthews (1973) and Bengtson (1988).

For diagnoses and stratigraphic ranges of genera and subgenera, see, for example, Cox (1969).

In the sections “Discussion”, reference to page and figures is given only for taxa that do not appear in the synonymy lists.

Linear measurements (taken with a Vernier caliper) are in millimetres. Abbreviations: **L** – shell length, **H** – shell height, **W** – width of articulated valves, **nr** – number of ribs, **L/H** – elongation and **W/L** – inflation. Orientation of measurements is shown in Fig. 3.

Repository: The specimens are housed in the collections of the Swedish Museum of Natural History, Stockholm, Sweden (collection prefix: NRM-PZ Mo). The single holotype and a series of paratypes are kept in the collections of the Museu Nacional, Rio de Janeiro, Brazil (collection prefix: MN).

5. SYSTEMATIC PALAEONTOLOGY

- Phylum Mollusca Linnaeus, 1758
- Class Bivalvia Linnaeus, 1758
- Infraclass Heteroconchia Hertwig, 1895
- Cohort Cardiomorpha Férussac, 1822
 (= Heterodonta of authors)
- Subcohort Carditioni Dall, 1889
- Order Carditida Dall, 1889
- Superfamily Crassatelloidea Férussac, 1822
- Family Crassatellidae Férussac, 1822

Subfamily Crassatellinae Férussac, 1822

Genus *Crassatella* Lamarck, 1799

Type species: *Crassatella tumida* Lamarck, 1805 (= *Venus ponderosa* Gmelin, 1791; *non Mactra cygnea* Chemnitz, 1782, see Wingard 1993, p. 51).

Subgenus *Crassatella* Lamarck, 1799

Crassatella (Crassatella) pusilla Coquand, 1862

Pl. I, figs A-C

1862. *Crassatella pusilla* H. Coq.– Coquand, p. 198, pl. 11, figs 12-13.

1882. *Crassatella pusilla* Coquand.– Seguenza, p. 137.

1912. *Crassatella pusilla* Coquand.– Pervinquière, p. 247.

1919. *Crassatella pusilla* Coq.– Greco, p. 34 [216], pl. 4 [20], figs 8-9.

Material: One internal mould (NRM-PZ Mo167949) from the middle–upper Cenomanian of locality Cruzes 8, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 1.

Description: Shell small, elongate oval, strongly inequilateral, equivalved and moderately inflated ($W/L=0.41$). Antero-dorsal margin strongly concave. Postero-dorsal margin straight, and gradually oblique posteriorly. Posterior margin truncated, almost perpendicular to ventral margin. Ventral margin slightly convex. Lunule small, heart-shaped and moderately deep. Escutcheon narrowly elongated and shallow. Umbones wide, slightly convex, located one-third of total valve length from anterior end. Beaks prominent, slightly prosogyrate. Posterior umbonal ridge well developed, separating slightly concave posterior flank from rest of valve (Pl. I, fig. B). Ornament not visible, except for faint commarginal ribs near ventral margin.

Discussion: With respect to shell size, outline, inflation, ornamentation and the presence of a posterior umbonal ridge, the Brazilian specimen agrees with *Crassatella pusilla* Coquand, 1862, from the “Senonian” of Algeria, whereas the co-occurring *C. tenoukensis* Coquand (1862, p. 198, pl. 11, figs 14-15) differs in being highly elongate, slightly larger ($L=20$ mm, as opposed to 16 mm) and in having a straight antero-dorsal margin and a wide and deep lunule. *Crassatella chargensis* (Quaas, 1902) from the Maastrichtian of the Western Desert, Egypt (Quaas, 1902, p. 211, pl. 24, figs 1-3) resembles the present species in having an elongate oval shell and a truncated posterior margin but differs in being larger, more inflated and in having a posterior umbonal keel, terminal umbones and a deep lunule and escutcheon.

Table 1: Dimensions (in mm) of *Crassatella (Crassatella) pusilla* Coquand, 1861.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167949	16.0	12.0	6.5	0.75	0.41

Occurrence: Cenomanian of Tunisia (Pervinquier, 1912), Italy (Seguenza, 1882) and Egypt (Greco, 1919); “Senonian” of Algeria (Coquand, 1862); Cenomanian of the Sergipe Basin (this study, first record).

***Crassatella (Crassatella) vadosa* Morton, 1834**

Fig. 4, Pl. I, figs D-G

1834. *C. vadosa* (S. G. M.)—Morton, p. 66, pl. 13, fig. 12.
 1858. *Crasatella* [sic] *ripleyana*.—Conrad, p. 327, pl. 35, fig. 3.
 1872. *C. Ripleyana*, Conrad [subgenus *Pachythaeerus*].—Conrad, p. 50, pl. 1, fig. 7.
 1885. *Crassatella vadosa*.—Whitfield, p. 116, pl. 17, figs 13-15, 12(?).
 1885. *Crassatella subplana*.—Whitfield, p. 121, pl. 18, figs 14-16.
 1907. *Crassatellites subplanus* (Conrad).—Weller, p. 553, pl. 61, figs 1-4.
 1916. *Crassatellites vadosus* (Morton) Johnson.—Gardner, p. 649, pl. 39, figs 1-4.
 1916. *Crassatellites linteus* (Conrad) Johnson.—Gardner, p. 653, pl. 39, figs 6, 7.
 1926. *Crassatellites vadosus* (Morton).—Wade, p. 79, pl. 25, figs 6-8.
 1955. *Crassatella vadosa ripleyana* (Conrad).—Stephenson, p. 117, pl. 19, figs 11-16.
 ? 1958. *Crassatellites vadosus* (Morton) 1834.—Richards, p. 189, pl. 29, fig. 10.
 1958. *Crassatellites linteus* (Conrad) 1860.—Richards, p. 190, pl. 30, figs 1-2.
 1993. *Crassatella vadosa* Morton, 1834.—Wingard, p. 63, pl. 1, figs 1-17; pl. 5, figs 1, 3, 4, 6; pl. 7, figs 1-15; pl. 8, figs 1-16; pl. 9, figs 1-13; pl. 10, figs 1-17; pl. 11, figs 1-13; pl. 12, figs 1-5; pl. 21, figs 6, 8.

Material: Three internal and composite moulds (NRM-PZ Mo167950-167952) from the lower-middle Turonian of locality Pedra Furada 4, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 2.

Description: Shell medium-sized, trigonally subovate, inequilateral, equivalved and moderately inflated ($W/L=0.67$, on average). Antero-dorsal margin subtruncated to slightly concave and steeply oblique anteriorly. Postero-dorsal margin straight, steeply inclined posteriorly, perpendicular to posterior margin. Posterior margin narrow, truncated, almost perpendicular to ventral margin. Anterior margin convex, meeting ventral margin in rounded angle. Ventral margin strongly rounded

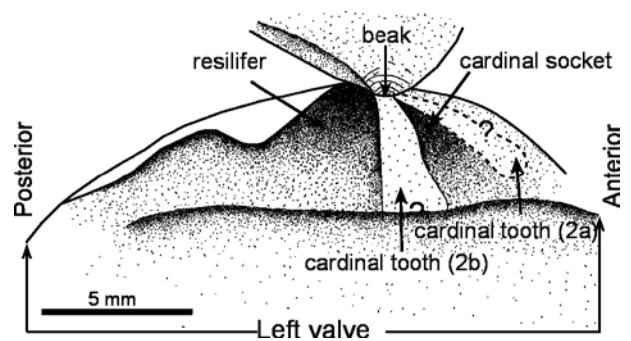


Fig. 4: Incomplete hinge of *Crassatella (Crassatella) vadosa* Morton, 1834, showing a deep trigonal socket separating two cardinal teeth with wide resilifer (NRM-PZ Mo167950). Locality Pedra Furada 4, lower-middle Turonian, Sergipe Basin.

anteriorly, slightly convex to straight towards posterior side and crenulated internally (Pl. I, fig. E). Posterior flank separated from the rest of valve by a weakly-developed umbonal ridge. Umbones triangular in outline, convex, located approximately one-fourth of total valve length from anterior end. Beaks prominent, slightly prosogyrate. Lunule relatively short, narrow and ovate. Hinge of left valve poorly preserved and incomplete but showing deep trigonal socket separating two cardinal teeth with wide and subovate resilifer extending directly below beak (Fig. 4). Ornament consisting of numerous irregular commarginal ribs with faint threads in interspaces. Commarginal ribs well developed and irregular ventrally with crenulated inner margin (Pl. I, fig. E).

Discussion: *Crassatella (C.) vadosa* is distinguished by its (1) narrow and truncated posterior margin, (2) fine and numerous commarginal striae, which become coarser and irregular towards the ventral margin, (3) internal radial ribs, preserved as denticulations along the ventral margin (Pl. I, fig. E), (4) prominent, slightly prosogyrate beaks and (5) subovate resilifer, which extends directly below the umbones of the left valve with two strong cardinal teeth (Fig. 4). According to Wingard (1993, p. 67), *C. (C.) vadosa* Morton is a highly variable species, the most obvious variation occurring in the shape of the posterior margin and the resulting effects on the general outline of the individuals (trigonally suboval, $L>H$; subquadrate, $L=H$). Therefore, some species, e.g., *C. ripleyana* Conrad, 1858, *C. subplana* Conrad, 1886, and *C. linteus*

Table 2: Dimensions (in mm) of *Crassatella (Crassatella) vadosa* Morton, 1834.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167950	53.0	44.0	?38.0	0.83	0.72
NRM-PZ Mo167951	45.0	34.0	28.0	0.76	0.62
Range	45-53	34-44	28-?38	0.76-0.83	0.62-0.72
Mean	49.0	39.0	?33.0	0.79	0.67

(Conrad, 1860) are considered synonyms of *C. vadosa*. For more detailed information about diagnostic features of *C. (C.) vadosa*, see Wingard (1993, pp. 64–68).

Corbula ganguararica Maury, 1937, from the Estância area of the Sergipe Basin (Maury, 1937, p. 87, pl. 8, figs 4–5), reassigned to *Crassatella (Sublandinia)* by Lefranc (in Bengtson, 1983, table 2) and presumed to be from the upper Cenomanian (Bengtson, 1983, table 2), differs in being smaller ($L=10$, $H=9$ mm of Maury's figured specimen, as opposed to $L=49$, $H=39$ mm, on average, of the present specimens) and in having regular, strong, widely spaced comm marginal ribs and inconspicuous beaks. *Crassatella zitteli* Wanner, 1902, from the Upper Cretaceous of Libya (Wanner, 1902, p. 121, pl. 18, figs 3–4) differs in being smaller ($L=7.5$ – 31 , $H=6$ – 25 mm) and in having subterminal umbones and numerous fine comm marginal ribs.

Occurrence: Campanian to Maastrichtian of the southern and north-eastern USA (Morton, 1834; Conrad, 1872; Whitfield, 1885; Weller, 1907; Gardner, 1916; Wade, 1926; Stephenson, 1955; Turonian of the Sergipe Basin (this study, first record).

Family Astartidae d'Orbigny, 1844
Subfamily Astartinae d'Orbigny, 1844

Genus *Astarte* J. Sowerby, 1816

Type species: *Venus scotica* Maton & Rackett, 1807 (= *Pectunculus sulcatus* da Costa, 1778 var. *scotica* Maton & Rackett, 1807), by original designation.

Subgenus *Astarte* J. Sowerby, 1816

Astarte (Astarte) cf. numismalis d'Orbigny, 1844

Pl. I, figs H-I

- cf. 1842. *Astarte laticosta* (à larges côtes), Desh.– Leymerie, p. 4, pl. 4, figs 4–5 (non *A. laticosta* Deshayes, 1839).
- cf. 1844. *Astarte numismalis* d'Orbigny.– d'Orbigny, p. 63, pl. 262, figs 4–6.
- cf. 1844. *Astarte striato-costata* d'Orbigny.– d'Orbigny, p. 64, pl. 262, figs 7–9 (non *A. striato-costata* Roemer, 1836).
- cf. 1906. *Astarte subcostata* d'Orbigny, 1850.– Woods, p. 109, pl. 14, figs 29–36; pl. 15, figs 1–2.
- v p 1983. *Astarte similis* Münster.– Lefranc in Bengtson, pp. 44–45.

- cf. 1988. *Astarte (Astarte) numismalis* d'Orbigny, 1844.– Dhondt & Dieni, p. 47, pl. 11, fig. 1 (with extended synonymy).
- cf. 1997. “*Astarte*” *porrecta* Reuss, 1846.– Smettan, p. 127, pl. 6, fig. 9.
- v p 1999. *Astarte (Astarte) cf. tenuicosta* (Seguenza, 1882).– Seeling, p. 121 (only specimen no. 585.7).

Material: Six composite moulds (NRM-PZ Mo167953–167958) from the lower–middle Turonian of localities Boa Sorte 11, Pedra Branca 16 and Alto Verde 1, Cotinguiba Formation, Sergipe Basin.

Measurements: cf. Table 3.

Description: Shell small, subtriangular, inequilateral, nearly as high as long ($H/L=1.10$, on average), relatively convex. Antero-dorsal margin concave. Postero-dorsal margin slightly convex, meeting posterior margin in obtuse angle. Anterior and ventral margins rounded. Posterior margin acute. Umbones wide, elevated, moderately convex, subterminal (one-third of total valve length from anterior end). Beaks prominent, prosogyrate. Ornament consisting of four to six prominent comm marginal ribs separated by wide, deep, concave interspaces containing riblets, visible in well-preserved specimens (Pl. I, fig. H).

Discussion: *Astarte (A.) numismalis* d'Orbigny is distinguished by its concave antero-dorsal margin, triangular subterminal umbones, few comm marginal ribs (five to seven), wide and concave interspaces (Pl. I, fig. I), fine intercalaries and by its small size and inflation. However, owing to the great variability of the species, many authors prefer splitting it into different species, such as *A. subcostata*, *A. laticosta* and *A. striatocostata*. According to Dhondt & Dieni (1988, p. 47), the differences between these latter “species” are probably expressions of intraspecific variability and changes in shape during ontogeny. Based on the taxonomic features of *A. (A.) numismalis*, specimen no. 585.7 (renumbered here NRM-PZ Mo167958), described by Seeling (1999, p. 121) as *A. (A.) cf. tenuicosta* (Seguenza, 1882) from the lower Turonian of locality Boa Sorte 11, is much closer to *A. (A.) numismalis* than to *A. (A.) tenuicosta*. Forbes (1845) remarked that specimens of his “*Venus? [striato-costata]*” from the Lower Greensand of England were identified by d'Orbigny as *A. numismalis*; however, the same specimens were later referred to *A. subcostata*.

Table 3: Dimensions (in mm) of *Astarte (Astarte) cf. numismalis* d'Orbigny, 1844.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167956	3.0	3.7	?1.5	1.23	?0.50
NRM-PZ Mo167957	5.0	6.0	--	1.20	--
NRM-PZ Mo167958	7.0	6.2	--	0.88	--
Range	3.0–7.0	3.3–6.2	?1.5	0.88–1.23	?0.50
Mean	5.0	5.30	?1.50	1.10	?0.50

by Woods (1906). For more details about the species, see Dhondt & Dieni (1988, p. 47). *Astarte defreitasi* Rennie, 1943, from the Upper Cretaceous of Buzi, Sofala Province (Mozambique) (Rennie, 1943, p. 40, pl. 4, figs 25, 26) differs in being larger ($L=23$, $H=18$ mm, as opposed to $L=3.0\text{--}7.0$, $H=3.3\text{--}6.2$ mm for the Brazilian specimens), and in having a crenulated antero-dorsal margin and more numerous, closely spaced commarginal ribs.

The Brazilian specimens show strong similarities to *A. subcostata* d'Orbigny, 1850, from the Lower Cretaceous of England (Woods, 1906) in size ($L=5.9$, $H=4.75$ mm, on average, as opposed to $L=7.5$, $H=5.3$ mm, on average, for the present material), concave antero-dorsal margin, subterminal umbones and wide and concave interspaces, but *A. subcostata* differs in having more numerous commarginal ribs (seven to nine). "*Astarte*" *porrecta* Reuss, 1846, from the Cenomanian of Germany (Smettan, 1997) closely resembles *A. subcostata* in having fewer commarginal ribs (six), wide and concave interspaces, terminal and triangular umbones and a concave antero-dorsal margin but differs in being slightly more elongate ($H/L=0.80$, as opposed to a mean of 1.10). Therefore, Smettan's single specimen is probably a variety of *A. (A.) numismalis*. *Astarte formosa* Fitton, 1836, from the Upper Cretaceous of England (Fitton, 1836, p. 4, pl. 16, fig. 16) resembles *A. subcostata* in general outline and size but has more numerous well-developed commarginal ribs covering the entire valve. *Astartemya (Freiastarte) similis* (Münster, 1837) from the Upper Cretaceous of Germany (Münster in Goldfuss, 1837, pl. 134, fig. 22) differs in having rounded margins, nearly central umbones and more numerous commarginal ribs. *Astarte subnumismalis* Thomas & Peron, 1889, from the Santonian of Tunisia (Thomas & Peron, 1890, pl. 28, figs 7-8) differs in having nearly central umbones, numerous commarginal ribs, narrow and smooth interspaces and in being slightly more elongate ($H/L=0.91$, as opposed to a mean of 1.10).

Occurrence: *Astarte (Astarte) numismalis* d'Orbigny, 1844, has been recorded from the Lower Cretaceous of

England (Woods, 1906) and Sardinia (Dhondt & Dieni, 1988), Valanginian–Aptian of France (Leymerie, 1842; d'Orbigny, 1844), Germany, Poland, Switzerland, Spain, Bulgaria, Algeria, Somalia and Tanzania (Dhondt & Dieni, 1988), Cenomanian–Campanian of Germany (Smettan, 1997) and here provisionally from the Cenomanian–Turonian of the Sergipe Basin (first record).

Astarte (Astarte) tenuicosta Seguenza, 1882

Pl. I, figs J-K

1882. *Astarte tenuicosta* n. sp.– Seguenza, p. 136, pl. 7, fig. 8.
 ? 1890. *Astarte Seguenzae* Thomas et Peron.– Thomas & Peron, p. 269, pl. 28, figs 9-10.
 1962. *Astarte (Tridonta) tenuicostata* [sic] (Seguenza).– Abbass, p. 102, pl. 16, figs 13-14, non fig. 9.
 v p 1983. *Astarte similis* Münster.– Lefranc in Bengtson, pp. 44-45.
 v p 1999. *Astarte (Astarte) cf. tenuicosta* (Seguenza, 1882).– Seeling, p. 121, pl. 4, fig. 20 (specimen 585.7 = *Astarte (A.) cf. numismalis*).
 v p 1999. *Astartemya (Freiastarte) similis* (Münster in Goldfuss, 1837).– Seeling, p. 122 (only specimens 253.11a-f and 328.4).

Material: 31 composite moulds (NRM-PZ Mo167959–167989) from the upper Cenomanian to middle Turonian of localities Jardim 6, Laranjeiras 3, São Pedro 14, Machado 4 and 10 and Boa Sorte 5 and 7, Cotinguba Formation, Sergipe Basin.

Measurements: cf. Table 4.

Description: Shell small, subtriangular, inequilateral, somewhat inflated ($W/L=c. 0.4$, on average; Table 4) with length slightly exceeding height ($H/L=0.80$, on average). Antero-dorsal margin slightly concave. Postero-dorsal margin straight to slightly convex, higher than antero-dorsal margin, meeting posterior margin in obtuse angle. Anterior and posterior margins convex, meeting ventral valve in rounded angles. Ventral margin broad and slightly rounded. Umbones triangular, subcentral, strongly elevated, slightly convex and prosogyrate (Pl. I,

Table 4: Dimensions (in mm) of *Astarte (Astarte) tenuicosta* (Seguenza, 1882).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167960	5.5	4.5	--	0.82	--
NRM-PZ Mo167970	5.2	4.0	2.6	0.77	0.50
NRM-PZ Mo167971	4.2	3.5	--	0.83	--
NRM-PZ Mo167976	7.0	6.0	?3.0	0.85	?0.43
NRM-PZ Mo167977	7.0	5.7	2.5	0.82	0.35
NRM-PZ Mo167975	6.2	5.0	--	0.81	--
NRM-PZ Mo167988	3.8	2.8	--	0.74	--
Range	3.8-7.0	2.8-6.0	2.5-3.0	0.74-0.85	0.35-0.50
Mean	5.56	4.50	2.70	0.80	0.43

fig. K). Ornament consisting of well-developed commarginal ribs (14), separated by narrow, deep, and smooth interspaces (Pl. I, fig. J).

Discussion: *Astarte (Tridonta) tenuicosta*, as described by Abbass (1962, pl. 14, figs 13-14) from the Turonian of Egypt, differs in having stronger commarginal ribs (with rounded crests), wide and smooth interspaces, triangular, not subterminal umbones and truncated postero-dorsal and posterior margins. Abbass (1962) considered *A. subnumismalis* Thomas & Peron, 1889, from the Santonian of Tunisia (Thomas & Peron, 1890, p. 268, pl. 28, figs 7-8) and *A. seguenziae* Thomas & Peron, 1889, from the Turonian of the same area (Thomas & Peron, 1889, p. 269, pl. 28, figs 9-10) synonyms of *A. (T.) tenuicosta*. In fact, *A. seguenziae* shows some similarities to *A. subnumismalis* in its well-developed commarginal ribs and rounded anterior and posterior margins, but differs in being more elongate and in having sharp beaks, narrower, triangular, subcentral umbones and a widely truncated postero-dorsal margin. *Astarte subnumismalis* differs from *A. (T.) tenuicosta* in being triangular in outline, less elongate and in having nearly central umbones, sharp beaks and straight antero-dorsal and postero-dorsal margins. *Astartemya (Freiastarte) similis* (Münster, 1837) (Münster in Goldfuss, 1837, pl. 134, fig. 22) differs from *A. (A.) tenuicosta* in having broader, non-triangular umbones, fewer commarginal ribs and narrow and ornamented interspaces.

Occurrence: Upper Cretaceous of Italy (Seguenza, 1882); Turonian of Tunisia (Thomas & Peron, 1890), Egypt (Abbass, 1962); Cenomanian–Turonian of the Sergipe Basin (Seeling, 1999; present study).

Astarte (Astarte) cf. upwarensis Woods, 1906
Pl. I, fig. L

- cf. 1906. *Astarte upwarensis*, sp. nov.– Woods, p. 105, pl. 14, figs 10-12.
- v p 1983. *Astarte similis* Münster.– Lefranc in Bengtson, pp. 44-45.
- v 1999. *Astarte (Astarte) cf. upwarensis* Woods, 1906.– Seeling, p. 121, pl. 4, fig. 19 (with incorrect specimen number, 252.16 for 252.9).

Material: Two composite moulds (NRM-PZ Mo167990–167991) from the upper Cenomanian–lower Turonian of localities Laranjeiras 2 and 5, Cotinguba Formation, Sergipe Basin, Brazil.

Table 5: Dimensions (in mm) of *Astarte (Astarte) cf. upwarensis* Woods.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167990	3.5	3.2	--	0.91	--
NRM-PZ Mo167991	6.0	5.0	3.0	0.83	0.50
Range	3.5-9	3.5-5	3.0	0.83-0.91	0.50
Mean	4.75	4.1	3.0	0.87	0.50

Measurements: cf. Table 5.

Description: Shell small, ovate to subtriangular, inequilateral, slightly longer than high ($H/L=0.87$, on average) and moderately inflated. Postero-dorsal margin broadly convex, higher than antero-dorsal margin, meeting posterior margin in rounded curve. Antero-dorsal margin slightly concave. Ventral margin regularly and strongly rounded. Umbones narrow, triangular, elevated, located slightly anterior to mid-length of valve. Beaks prominent, prosogyrate. Ornament consisting of thick, widely spaced commarginal ribs (Pl. I, fig. L).

Discussion: The Brazilian specimens closely resemble *Astarte upwarensis* as described and figured by Woods (1906) from the Lower Cretaceous of England in having strongly rounded margins, a concave antero-dorsal margin and elevated triangular umbones, but differ in being smaller ($L=6.14$, $H=4.10$ mm, as opposed to $L=13-24$ mm, $H=15-25$ mm) and in having fewer and thick commarginal ribs. *Astarte* sp., described and figured by Rennie (1929, p. 29, pl. 2, fig. 3) from the Albian of Angola, differs in having nearly central umbones and fewer and widely spaced commarginal ribs.

Occurrence: *Astarte (Astarte) upwarensis* Woods, 1906, has been recorded from the Lower Cretaceous of England (Woods, 1906) and here provisionally from the Cenomanian–Turonian of the Sergipe Basin (Seeling 1999; present study).

Genus *Tridonta* Schumacher, 1817

Type species: *Tridonta borealis* Schumacher, 1817 (= *Venus borealis* Chemnitz, 1784 [invalid, non-binomial, ICZN]).

Remarks: The genus *Tridonta* is characterised by (1) elongate quadrangular to rounded shells, (2) numerous and closely spaced commarginal ribs covering the entire valve, (3) slightly prosogyrate umbones; (4) a slightly concave antero-dorsal margin; (5) a narrow and truncated posterior margin, (6) a slightly convex postero-dorsal margin, (7) a lanceolate lunule and escutcheon, (8) a smooth inner margin and (9) the absence of lateral teeth. According to Marinovich *et al.* (2002, p. 241), the hinge of *Tridonta* is wide and carries prominent cardinal teeth.

Subgenus *Tridonta* Schumacher, 1817

Tridonta (Tridonta) cf. gigantea (Deshayes, 1842)
Pl. I, figs M-N

- cf. 1842. *Astarte gigantea* (gigantesque), Desh.– Leymerie, p. 5, pl. 4, fig. 3.
 cf. 1846. *Astarte gigantea* Deshayes.– d'Orbigny, p. 58, pl. 258, figs 1-6.
 cf. 1962. *Astarte (Tridonta) gigantea* (Deshayes).– Abbass, p. 103, pl. 16, figs 8, 10-12, 15a.
 cf. 2006. “*Astarte*” *gigantea* Deshayes, 1842.– El Qot, p. 74, pl. 15, fig. 9.
 cf. 2007. *Astarte gigantea* Deshayes, 1842.– Mekawy, p. 230, pl. 5, fig. 2.

Material: Six composite moulds (NRM-PZ Mo167992–167997) from the middle Cenomanian to upper Turonian of localities Jericó 6, Pedra Furada 4 and Mata 7, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 6.

Description: Shell small, variable in outline from subquadrangular, rounded, to subtriangular, inequilateral and moderately inflated. Antero-dorsal margin slightly concave below umbones. Postero-dorsal margin straight, meeting posterior margin in obtuse angle. Anterior margin rounded, meeting ventral margin in rounded curve. Posterior margin subtruncated, almost perpendicular to ventral margin. Ventral margin broad and regularly rounded. Umbones wide, moderately inflated, located one-third of total valve length from anterior end. Beaks small, inconspicuous, prosogyrate. Posterior umbonal ridge weakly developed (Pl. I, fig. M). Hinge of left valve with two cardinal teeth (2a, 2b), separated by a triangular cardinal socket (Pl. I, fig. N). Ornament consisting of numerous commarginal ribs, separated by narrow interspaces.

Discussion: The Brazilian specimens closely resemble *Astarte (T.) gigantea* from the Maastrichtian of the Eastern Desert, Egypt (Abbass, 1962) in having a subtruncated posterior margin, a moderately well-developed umbonal posterior ridge, weakly inflated valves and faint, numerous commarginal ribs, but differ in being larger (L= 20, H= 18 mm, as opposed to L= 11, H= 9.43 mm, on average).

Crassatella minima Seguenza, 1882, from the Upper Cretaceous of Italy (Seguenza, 1882, pl. 7, fig. 9)

differs in being more elongate and in having subterminal umbones and fewer, thick commarginal ribs. With respect to general outline and ornamentation, *C. zitteli* var. *lucinoides* Quaas, 1902, from the Upper Cretaceous of the Western Desert, Egypt (Quaas, 1902, p. 208, pl. 23, figs 22-23, 29) strongly resembles *T. (T.) gigantea* and is possibly a synonym. *Tridonta (T.) gigantea* (Deshayes, 1842) also resembles *Astarte gabae* from the Upper Cretaceous of Algeria (Coquand, 1862, p. 197, pl. 8, figs 27-28) but differs in having a strongly rounded posterior margin and narrow, triangular umbones. *Astarte deletrei* Coquand, 1862, from the Upper Cretaceous of the same area (Coquand, 1862, p. 197, pl. 8, figs 31-32) closely resembles the Brazilian specimens but is larger.

Occurrence: *Tridonta (Tridonta) gigantea* (Deshayes, 1842) has been recorded from the Lower Cretaceous of France (Leymerie, 1842; d'Orbigny, 1846), Coniacian–Maastrichtian of Egypt (Abbass, 1962; El Qot, 2006; Mekawy, 2007) and here provisionally from the Cenomanian–Turonian of the Sergipe Basin (first record).

Subfamily Eriphyllinae Chavan, 1952
Genus *Astartemya* Stephenson, 1941

Type species: *Astartemya fentressensis* Stephenson, 1941, by original designation.

Subgenus *Freiastarte* Chavan, 1952
Type species: *Astarte coelata* Müller, 1847 (= *Astarte similis* Münster in Goldfuss, 1837).

Astartemya (Freiastarte) similis
(Münster in Goldfuss, 1837)
Pl. I, figs O-Q

- p 1837. *Astarte similis* Münster.– Goldfuss, p. 193, pl. 134, fig. 22a (*non* fig. 22b, *fide* J. Böhm, 1891).
 1864. *Astarte laticostata* Desh.– Zittel, p. 52 [156], pl. 8, fig. 5.
 1864. *Astarte similis* Münst.– Zittel, p. 53 [157], pl. 8, fig. 6.
 1889. *Astarte similis* Mnstr.– Holzapfel, p. 194, pl. 19, figs 11-15.
 1912. *Astarte similis* Münster.– Pervinquier, p. 246, pl. 19, figs 1-7.
 1934. *Astarte similis* Münster.– Andert, p. 242, pl. 11, fig. 44.
 1957. *Astarte similis* Münster.– Darteville & Freneix, p. 132, pl. 23, fig. 5.

Table 6: Dimensions (in mm) of *Tridonta (Tridonta) cf. gigantea* (Deshayes, 1842).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167992	12.2	9.5	5.4	0.78	0.44
NRM-PZ Mo167993	10.8	9.8	4.7	0.91	0.43
NRM-PZ Mo167994	10.0	9.0	8.0	0.90	0.50
Range	10.0-12.2	9.0-9.8	4.7-8.0	0.78-0.91	0.43-0.50
Mean	11.0	9.43	6.03	1.12	0.46

1974. *A. similis* (Münster).— Oekentorp & Siegfried, p. 156, pl. 15, fig. 6.
- v p 1983. *Astarte similis* Münster.— Lefranc in Bengtson, pp. 44-45.
- ? 1986. *Astarte (Astarte) similis* v. Münster, 1840.— Abdel-Gawad, p. 167, pl. 40, figs 1-2.
1987. *Astarte s. l. similis* (Münster in Goldfuss, 1837).— Dhondt, p. 75.
- v p 1999. *Astartemya (Freiastarte) similis* (Münster in Goldfuss, 1837).— Seeling, p. 122, pl. 4, figs 21-22 [specimens 253.11a-f and 328.4 = *Astarte (Astarte) tenuicosta*].
2003. *Astarte similis* Münster.— Szente, pl. 1, figs 16-18.

Material: Twenty-seven composite moulds (NRM-PZ Mo167998-168024) from the middle Cenomanian to middle Turonian of localities Caraíbas 1, Mosquito 1, Jardim 19, Timbó 4, Boa Sorte 5, Laranjeiras 12, Machado 6, Pedra Furada 4, 12 and 16, Pedro Gonçalves 3, and São Roque 2, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 7.

Description: Shell small to very small, trigonal to subovate, slightly longer than high ($H/L=0.87$, on average; Table 7), slightly inequilateral, weakly inflated. Antero-dorsal margin slightly concave below umbones. Postero-dorsal margin straight to slightly convex, meeting posterior margin in obtuse angle. Ventral margin strongly rounded, meeting anterior and posterior margins in rounded curves. Umbones weakly convex, triangular, prosogyrate. Beaks small, inconspicuous, slightly prosogyrate. Lunule elongate ovate and shallow. Ornament consisting of strongly rounded commarginal ribs (6-11) separated by wide interspaces (Pl. I, figs O, P). Commarginal ribs well developed ventrally and faint towards the dorsal margin. Interspaces wide towards ventral margin and in some well-preserved specimens bearing fine radial riblets.

Discussion: *Astartemya (Freiastarte) similis* (Münster in Goldfuss) is distinguished by its small size ($L=3.0-6.0$,

$H=3.0-5.0$ mm), triangular, faintly convex umbones, inconspicuous beaks, strongly convex ventral margin and the presence of few, strong, rounded commarginal ribs. The present specimens are very similar to *A. (F.) similis* as described and figured by Holzapfel (1889) and Pervinquier (1912) from the Upper Cretaceous of Germany and Tunisia, respectively.

Zittel (1864) described *A. laticostata* and *A. similis* from Coniacian-lower Maastrichtian beds of the north-eastern Alps. The co-occurrence of closely related taxa strongly suggests conspecificity (see also Dhondt, 1987, p. 76). *Astartemya sergipensis* Maury, 1937, from the middle Albian of Sergipe (Maury, 1937, p. 63, pl. 8, fig. 3) differs in being larger than *A. (F.) similis* ($L=25$, $H=22$ mm, as opposed to $L=3.0-6.0$, $H=3.0-5.0$ mm) and in having rounded margins and numerous, fine, commarginal ribs. *Astartemya planissima* Forbes, 1846, from the Upper Cretaceous of South India (Forbes, 1846, p. 143, pl. 15, fig. 23) closely resembles the present species in general outline except for its inconspicuous commarginal ribs and is probably a junior synonym. *Astarte awensis* Woods, 1911, from the lower Turonian of Nigeria (Barber, 1958, p. 23, pl. 7, fig. 2) differs only in having strongly rounded margins. With respect to ornamentation, *Astarte* sp. of Rennie (1929, p. 29, pl. 2, fig. 5) from the Albian of Angola is strongly similar to *A. (F.) similis*, but the Angolan specimen differs in having prominent and strongly prosogyrate umbones, strongly rounded margins, a wide and deep lunule, and in being much wider.

Occurrence: Turonian-Campanian of Germany (Holzapfel, 1889; Andert, 1934; Oekentorp & Siegfried, 1974); Coniacian of Cameroon (Darteville & Freneix, 1957); Santonian-Maastrichtian of Austria (Dhondt, 1987; Szente, 2003); Campanian-Maastrichtian of Poland (Abdel-Gawad, 1986); Maastrichtian of Tunisia (Pervinquier, 1912); Cenomanian-Turonian of the Sergipe Basin (Lefranc in Bengtson, 1983; Seeling, 1999; this study).

Table 7: Dimensions (in mm) of *Astartemya (Freiastarte) similis* (Münster in Goldfuss, 1837).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo167998	3.0	3.0	--	1.0	--
NRM-PZ Mo168004	4.0	3.0	--	0.75	--
NRM-PZ Mo168005	4.0	3.5	--	0.87	--
NRM-PZ Mo168006	4.5	3.0	--	0.67	--
NRM-PZ Mo168007	5.0	5.0	--	1.0	--
NRM-PZ Mo168009	5.0	5.0	--	1.0	--
NRM-PZ Mo168010	6.0	5.0	--	0.83	--
NRM-PZ Mo168011	3.8	3.70	2.0	0.97	0.53
NRM-PZ Mo168012	4.2	3.3	2.3	0.79	0.55
Range	3.0-6.0	3.0-5.0	2.0-2.3	0.67-1.00	0.53-0.55
Mean	4.39	3.83	2.15	0.87	0.54

Subfamily Opinae Chavan, 1952

Genus *Opis* Defrance, 1825

Type species: *Trigonia cardissoides* Lamarck, 1819, by monotypy (Bigot, 1895).

Subgenus *Hesperopis* Squires & Saul, 2009

Type species: *Corbula triangulata* Cooper, 1894, late Campanian to early late Maastrichtian of California.

Remarks: Squires & Saul (2009) erected the subgenus *Hesperopis* for moderately small to large, broadly trigonal species, with high to very high umbones, a weak to strong posterior umbonal ridge, large and cordiform lunule, high to very high hinge, weak corcelet (*sensu* Carter, 1967) and two strong cardinal teeth in each valve. The ligament of *Hesperopis* consists of two parts, an external and an internal part. The external part is referred to as the ligament groove and the internal part as the internal ligament pit. *Hesperopis* resembles *Opis* (*Opis*) Defrance, 1825, but differs in being larger, in having two cardinal teeth in each valve and an elongated internal ligament. *Trigonopsis* Fischer, 1887, differs in lacking an internal ligament pit and in having a shallower lunule and lower beaks. Chavan (1952, 1969) recognised seven genera and five subgenera in the subfamily Opinae. Squires & Saul (2009, pp. 1319–1321) discussed in detail the differences between these genera and subgenera and regarded several as not belonging to the Opinae. Stratigraphically, the subgenus *Hesperopis* is known from the middle Turonian to the lower upper Maastrichtian. The Brazilian specimens derive from the lower to upper Cenomanian and thus extend the range of the subgenus from the lower Cenomanian to the upper Maastrichtian.

Opis (Hesperopis) triangulata (Cooper, 1894)

Fig. 5; Pl. II, figs A-E

1894. *Corbula triangulata* n. sp.– Cooper, p. 49, pl. 2, fig. 42 (not pl. 4 as stated).
 1897. *Opis triangulata* (Cooper).– Cooper, p. 332, pl. 47, figs 7–9.
 1958. *Opisoma pacifica* Anderson n. sp.– Anderson, p. 122, pl. 26, figs 5–6.
 2009. *Opis (Hesperopis) triangulata* (Cooper, 1894).– Squires & Saul, p. 1329, pl. 1, figs 1–9; pl. 2, figs 1–10.

Material: Three articulated composite moulds (NRM-PZ Mo168025–168027) from the middle–upper Cenomanian of localities Jardim 22 and 24 and Tibúrcio 1, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 8.

Description: Shell small to medium-sized, narrowly triangular, cordate in cross-section, equivalved, inequilateral, higher than long ($H/L=1.48$, on average; Table 8) and strongly inflated ($W/L=1.38$, on average). Anterior margin regularly rounded (beyond lunule), meeting ventral margin in rounded curve. Posterior margin truncated. Posterior umbonal carina well developed, broadly rounded, separating posterior third of the flank from rest of valve (Fig. 5A). Umbones high, triangular, narrow and strongly convex. Beaks projecting above hinge, narrow, sharply pointed and strongly prosogyrate. Corcelet ridge moderately weak (Pl. II, fig. D, Fig. 5A). Corcelet furrow wide and shallow. Lunule large, cordate, moderately deep. Escutcheon long, smooth, ovate. Ornament consisting of strong, regular commarginal ribs with irregularly spaced growth halts that become more conspicuous ventrally (Pl. II, figs A–B). Commarginal ribs closely spaced, covering entire valve and separated by narrow, deep and smooth interspaces. Posterior third of flank covered only by faint growth lines (Pl. II, fig. D). Teeth and other internal structures not visible.

Discussion: The Brazilian specimens closely resemble juvenile individuals of *Opis (Hesperopis) triangulata* from the upper Campanian–Maastrichtian of the Pacific Coast of North America (Squires & Saul, 2009, pl. 2, figs 1–2; text-fig. 10C, D) in having narrowly trigonal and elongate shells, prosogyrate umbones, a weak corcelet ridge, a truncated posterior margin and well-developed commarginal ribs with growth halts.

Opis (H.) triangulata is somewhat similar to *O. californica* Stanton, 1895, from the Lower Cretaceous of the Pacific slope of North America (Stanton, 1895, p. 58, pl. 7, figs 1–4) in having a narrowly triangular shell, a rounded anterior margin, a well-developed umbonal posterior ridge, narrow and elevated umbones and a poorly developed corcelet ridge, but differs in having strong and regular commarginal ribs, well-developed annual growth halts and in being strongly inflated ($W/L=1.38$, on average). *Opis (H.) vancouverensis* Whiteaves, 1879, from the middle Campanian of the Pacific slope of North America

Table 8: Dimensions (in mm) of *Opis (Hesperopis) triangulata* (Cooper, 1894).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168025	10.0	15.0	13.0	1.50	1.30
NRM-PZ Mo168026	11.0	18.0	16.0	1.63	1.45
NRM-PZ Mo168027	13.0	17.0	18.0	1.31	1.38
Range	10–13	15–18	13–18	1.31–1.63	1.30–1.45
Mean	11.33	16.0	15.67	1.48	1.38

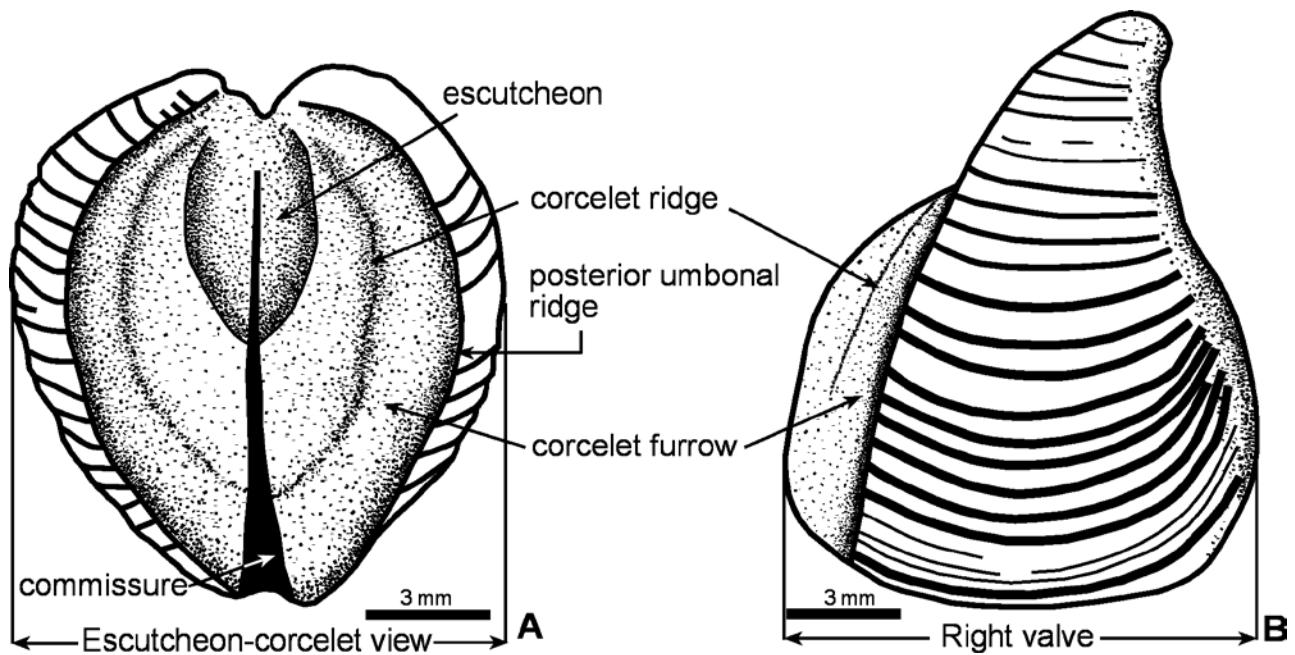


Fig. 5: Outline and ornament of *Opis (Hesperopis) triangulata* (Cooper, 1894). A, posterior view showing the well-developed corcelet and posterior umbonal ridges; B, right lateral view showing well-developed and irregular commarginal ribs (NRM-PZ Mo168025). Locality Jardim 24, middle Cenomanian, Sergipe Basin.

(Squires & Saul, 2009, p. 1328, text-figs 3a, 9) differs in having less developed commarginal ribs and in being smaller. *Opis (H.) popenoei* Squires & Saul, 2009, from the middle–upper Turonian of North America (Squires & Saul, 2009, p. 1321, text-figs 3C-E, G) differs in being larger than the present species ($H>49$, $L=35$ mm) and in having a deep lunule, strong corcelet and less developed commarginal ribs. *Opis (H.) triangulata* is also similar to some extent to *Opis neocomiensis* d'Orbigny, 1844, from the Lower Cretaceous of England (Woods, 1906, p. 118, pl. 17, figs 8-12), but the latter species differs in having a strong corcelet ridge, a deep corcelet furrow, a wider and rounded lunule and in having faint irregular commarginal ribs. *Opis* sp. from the Upper Cretaceous of the same area (Woods, 1906, p. 120, pl. 17, figs 13, 14) differs in having a smooth posterior flank, numerous, faint commarginal ribs, less developed beaks and in being smaller ($L=7.5-8.0$ mm, as opposed to $L=10-13$ mm).

Occurrence: Campanian–Maastrichtian of the Pacific Coast of North America (Cooper, 1894, 1897; Anderson, 1958; Squires & Saul, 2009); Cenomanian of the Sergipe Basin (this study, first record).

Opis (Hesperopis) sp.

Pl. II, figs F-I

Material: One composite mould of a right valve (NRM-PZ Mo168028) from the lower Cenomanian of locality Itaporanga 2/3, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 9.

Description. Shell medium-sized, triangular, slightly higher than long ($H/L=1.16$; Table 9), inequilateral, and moderately inflated. Anterior margin rounded, meeting ventral margin in rounded curve. Posterior margin subtruncated, almost perpendicular to ventral margin. Umbonal posterior ridge poorly developed. Corcelet ridge moderately weak. Corcelet furrow shallow and smooth (Pl. II, fig. I). Lunule cordate and shallow. Umbones wide, strongly convex, and located slightly anterior to mid-length of valve. Beaks sharply pointed and prosogyrate (Pl. II, fig. G). Ornament consisting of numerous and irregular commarginal ribs, well developed dorsally (Pl. II, figs H-I).

Discussion: With only one valve available, a precise identification is difficult. The specimen differs from known coeval *Opis* species by its small and broad shell, weak umbonal posterior ridge and irregular commarginal ribs. It is somewhat similar to *Opis (Hesperopis) holzana* Squires & Saul, 2009, from the uppermost Santonian to lower Campanian of the Pacific slope of North America (Squires & Saul, 2009, p. 1322, text-figs 3b, 6) in having a broad shell, wide and convex umbones and poorly developed commarginal ribs but differs in being smaller

Table 9: Dimensions (in mm) of *Opis (Hesperopis)* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168028	19.0	22.0	8.0 (RV)	1.16	?0.84

($L=19$, $H=22$ mm, as opposed to $L=47$, $H>52$ mm) and in having pointed beaks. *Opis haldonensis* Woods, 1906, from the Lower Cretaceous of England (Woods, 1906, p. 119, pl. 18, fig. 1) differs in being smooth, larger ($L=43$, $H=58$ mm) and higher than the present species ($H/L=1.35$, as opposed to 1.16) and in having a strong corcelet ridge, a deep corcelet furrow and narrower umbones.

Occurrence: Cenomanian of the Sergipe Basin, Brazil (this study).

Family Carditidae Féruccac, 1822
Subfamily Carditiniae Féruccac, 1822
Genus *Maghrebella* Frenex, 1972

Type species: *Cardita niceisei* Coquand, 1862.

Remarks: On the basis of the hinge of the right valve, *Maghrebella* was erected by Frenex (1972) to accommodate some carditid species from the Cenomanian of Morocco, e.g., *Cardita forgemoli* Coquand, 1862, *C. niceisei* Coquand, 1862, *C. deserti* Douvillé, 1916, and *Venericardia subparallela* Gerhardt, 1897.

***Maghrebella?* *forgemoli* (Coquand, 1862)**
Pl. II, fig. J

- 1862. *Cardita Forgemoli* H. Coq.– Coquand, p. 199, pl. 14, figs 14-15.
- 1862. *Cardita Delettrei* H. Coq.– Coquand, p. 200, pl. 14, figs 18-19.
- 1862. *Cardita Beuquei* H. Coq.– Coquand, p. 200, pl. 15, figs 1-2.
- 1912. *Cardita Forgemoli* Coquand.– Pervinquier, p. 238, pl. 17, figs 5-12.
- 1916. *Cardita Dupini* d'Orbigny, var. *deserti*.– Douvillé, p. 162, pl. 21, figs 1-2.
- 1919. *Cardita Forgemoli* Coq.– Greco, p. 32 [214], pl. 4 [20], figs 4-7.
- 1934. *Cardita forgemoli* Coq.– Blanckenhorn, p. 219.
- 1937. *Cardita Forgemoli* Coq.– Trevisan, p. 94, pl. 7, figs 10-13.
- 1962. *Cardita (Pteromeris) forgemoli* (Coquand).– Abbass, p. 112, pl. 17, figs 10-12.
- v 1999. *Cardita* aff. *forgemoli* Coquand, 1862.– Seeling, p. 120, pl. 4, fig. 18.
- 2004. *Venericardia forgemoli* (Coquand).– Abdel-Gawad et al., pl. 2, fig. 10.
- 2006. *Maghrebella forgemoli* (Coquand, 1862).– El Qot, p. 73, pl. 15, figs 6-8.
- 2007. *Maghrebella forgemoli* (Coquand, 1862).– Mekawy, p. 230, pl. 5, fig. 1.
- 2014. *Venericardia?* *forgemoli* (Coquand 1862).– Ayoub-Hannaa et al., p. 112, pl. 10, fig. 1.
- 2014. *Venericardia forgemoli* (Coquand, 1862).– Hewaidy et al., p. 224, pl. 2, fig. 7a-b.

2018. *Venericardia forgemoli* (Coquand, 1862).– Aouissi et al., p.17, fig. 5.8.

Material: One composite mould (NRM-PZ Mo168029) from the uppermost Cenomanian of locality Japaratuba 4, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 10.

Description: Shell medium-sized, subquadrate, elongate, strongly inequilateral, longer than high ($H/L=0.65$) and moderately inflated. Maximum inflation below umbones, abruptly decreasing posteriorly. Shallow sulcus extending along antero-ventral area (Pl. II, fig. J). Postero-dorsal margin straight, nearly parallel to ventral margin, almost perpendicular to posterior margin. Antero-dorsal margin short, straight, steeply oblique anteriorly. Posterior margin broadly convex, meeting ventral margin in rounded curve. Anterior margin narrow and rounded. Ventral margin slightly concave anteriorly, becoming strongly rounded postero-ventrally. Umbones broad, weakly convex, prosogyrate. Ornament consisting of fine, tuberculate radial ribs (30), separated by wide and smooth interspaces. Ribs crossed by faint growth lines, towards ventral and posterior margins more clearly developed, closely spaced and slightly imbricated (Pl. II, fig. J).

Discussion: The Brazilian specimen is an articulated valve, and internal structures are not visible. The generic assignment is therefore doubtful. The specimen closely resembles *Cardita forgemoli* Coquand, 1862, from the lower Turonian of Algeria (Coquand, 1862, p. 199, pl. 14, figs 14-15) in general outline and position and curvature of umbones but differs in being larger ($L=23$ mm, as opposed to 14 mm), and in having a shallow antero-ventral sulcus. With respect to ornamentation and general outline, the specimen is also very similar to *Venericardia santonensis* Müller, 1888, from the Upper Cretaceous (Coniacian?) of Germany (Oekentorp & Siegfried, 1974, pl. 15, fig. 4), but the latter species has a strongly rounded anterior margin, large anterior area, truncated posterior margin and a less elongate valve ($H/L=0.78$, as opposed to 0.65). *Cardita niceisei* Coquand, 1862, from the Cenomanian of Algeria (Coquand, 1862, p. 200, pl. 14, figs 16-17) differs in being strongly elongate ($H/L=0.50$, as opposed to 0.65), more inflated ($W/L=0.60$, as opposed to 0.48) and in carrying fewer radial ribs. *Cardita tenuicosta* (J. de C. Sowerby, 1836) from the Lower Cretaceous of England (Woods, 1906, p. 124, pl. 18, figs 7-14) is similar to the Brazilian specimen in having subquadrate valves and a compressed posterior margin but differs in having more numerous radial ribs (47-57, as opposed to 30). *Cardita beuquei* Coquand,

Table 10: Dimensions (in mm) of *Maghrebella?* *forgemoli* (Coquand, 1862).

Specimen	L	H	W	Nr	H/L	W/L
NRM-PZ Mo168029	23.0	15.0	?11.0	30.0	0.65	?0.48

1862, and *C. delettrei* Coquand, 1862, from the Upper Cretaceous of England strongly resemble *Maghrebella forgemoli* in general outline, size and ornamentation. In agreement with Pervinquier (1912), El Qot (2006) and Ayoub-Hannaa *et al.* (2014), these two species are therefore considered junior synonyms of *M. forgemoli*. *Cardita dupini* d'Orbigny var. *deserti* Douvillé, 1916, differs in having fine tuberculated radial ribs (with sharp crests). The strength of the radial ribs is not a viable character for separating species, as it appears related to ecological factors, such as substrate type. Moreover, Cox (1969, p. N555) pointed out changes in the radial ribs during ontogeny; in juveniles they are numerous and sharp, becoming flattened and enlarged in adults. Thus, *C. dupini* d'Orbigny var. *deserti* Douvillé (1916) is considered conspecific with *M. forgemoli*.

Occurrence: Albian–Cenomanian of Egypt (e.g., Douvillé, 1916; Greco, 1919; Abbass, 1962; Abdel-Gawad *et al.*, 2004; El Qot, 2006; Ayoub-Hannaa *et al.*, 2014; Hewaidy *et al.*, 2014); Cenomanian of Algeria (Aouissi *et al.*, 2018), Tunisia (Pervinquier, 1912), Syria (Blanckenhorn, 1934) and Italy (Trevisan, 1937); Turonian (“l'étage Carentonien”) of Algeria (Coquand, 1862); Cenomanian–Turonian of the Sergipe Basin (Seeling, 1999; present study).

Subcohort Cardioni Féussac, 1822
 (= Euheterodonta Giribet & Distel, 2003)
 Infrasubcohort Lucinidia J. Gray, 1854
 Order Lucinida J. Gray, 1854
 Superfamily Lucinoidea J. Fleming, 1828
 Family Lucinidae J. Fleming, 1828
 Subfamily Lucininae J. Fleming, 1828
 Genus *Lucina* Bruguière, 1797

Type species: *Venus jamaicensis* Spengler, 1784.

Lucina dachelensis Wanner, 1902

Fig. 6; Pl. II, figs K-O

1902. *Lucina Dachelensis* n. sp. – Wanner, p. 123, pl. 18, fig. 6.
 1902. *Lucina dachelensis*, Wan.– Quaas, p. 213, pl. 24, figs 8–12.
 ? 1917. *Lucina dachelensis*, Wanner 1902.– Fourtau, p. 76, pl. 1, fig. 9.
 1957. *Lucina dachelensis* Wanner.– Darteville & Freneix, p. 163, pl. 28, fig. 6.
 1962. *Lucina (Dentilucina) dachelensis* (Wanner).– Abbass, p. 107, pl. 22, fig. 2.
 2013. *Lucina dachelensis* Wanner, 1902.– El Qot *et al.*, p. 214, pl. 4, fig. 5.

Material: Fifty-seven specimens (NRM-PZ Mo168030–168086) from the lower–upper Cenomanian of localities Itaporanga 2 and 2/3, Cruzes 7 and 8 and Timbó 4, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 11.

Description: Shell small, ovate to subcircular, length and height nearly equal (Fig. 6A), almost equilateral, equivalved, moderately inflated ($W/L=0.52$, on average). Postero-dorsal margin straight to slightly convex, meeting posterior margin in an obtuse angle. Anterior margin rounded, meeting ventral margin in rounded curve. Posterior margin subtruncated. Ventral margin irregularly rounded. Umbones broad, subtriangular, weakly inflated, located near mid-length of valve. Beaks small, inconspicuous, slightly prosogyrate. Lunule ovate, wide and shallow. Escutcheon long, narrow and shallow. Posterior umbonal ridge well developed, extending from umbones to postero-ventral junction, separating the faintly concave posterior flank from rest of valve (Pl. II, figs K-L). Ornament consisting of widely spaced commarginal ribs;

Table 11: Dimensions (in mm) of *Lucina dachelensis* Wanner, 1902.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168030	10	9.3	5.0	0.93	0.50
NRM-PZ Mo168031	9.2	8.8	5.5	0.96	0.60
NRM-PZ Mo168034	8.6	9.0	5.0	1.05	0.58
NRM-PZ Mo168035	9.3	9.0	5.1	0.97	0.55
NRM-PZ Mo168037	9.5	8.9	4.7	0.93	0.49
NRM-PZ Mo168038	7.3	7.0	3.3	0.96	0.45
NRM-PZ Mo168039	8.2	9.1	5.1	1.11	0.62
NRM-PZ Mo168054	11.2	11.5	5.5	1.03	0.49
NRM-PZ Mo168055	6.0	6.0	2.7	1.00	0.45
NRM-PZ Mo168068	8.5	8.6	3.7	1.01	0.44
NRM-PZ Mo168069	8.8	7.4	4.9	0.84	0.56
NRM-PZ Mo168070	7.0	6.9	3.3	0.99	0.47
Range	6.0–11.2	6.0–11.5	2.7–5.5	0.84–1.11	0.44–0.62
Mean	8.63	8.45	4.48	0.98	0.52

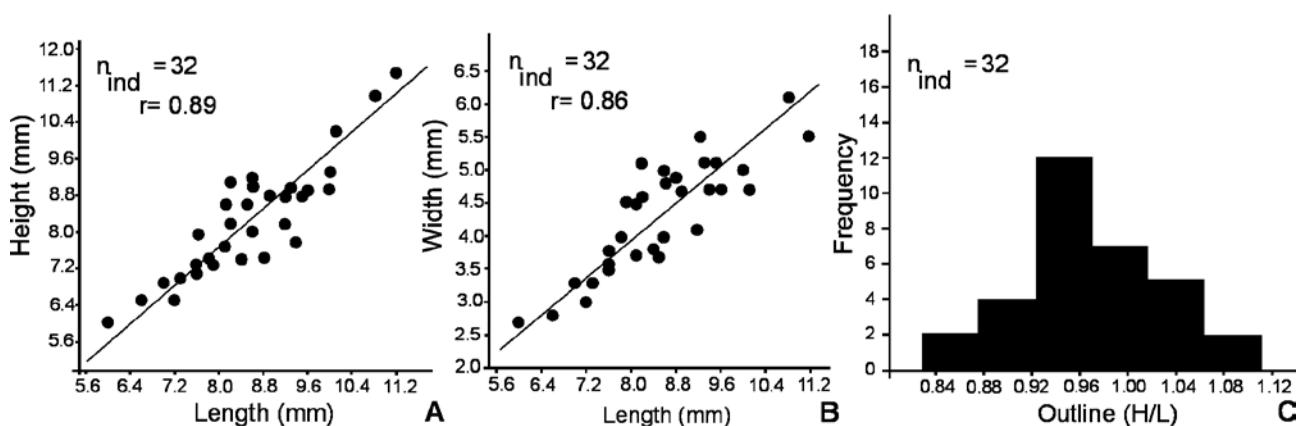


Fig. 6: *Lucina dachelensis* Wanner, 1902. A, length/height ratio; B, length/width ratio; C, histogram of the length/height ratio (outline) and number of individuals (frequency). Cenomanian, Sergipe Basin.

interspaces occupied by fine riblets, more strongly developed ventrally.

Discussion: *Lucina dachelensis* Wanner, 1902, is a highly variable species with respect to general outline (Fig. 6C), shell size and ornamentation (Quaas, 1902, pl. 24, figs 8–12), but is distinguished by its well-developed posterior umbonal ridge, faintly concave posterior flank (Pl. II, figs K–L), straight postero-dorsal margin, near-mesial umbones, a narrowly subtruncated posterior margin and wide interspaces.

Lucina glebula Conrad, 1875, from the Upper Cretaceous of North Carolina, USA (Conrad, 1875, p. 7, pl. 1, fig. 18) closely resembles *L. dachelensis* in having a well-developed posterior umbonal ridge, a compressed posterior flank and a truncated posterior margin but differs in having faint and fewer commarginal ribs separated by wide interspaces and smooth umbones. *Lucina subnumismalis* d'Orbigny, 1850, from the Upper Cretaceous of France and Tunisia (d'Orbigny, 1850, p. 241; Pervinquier, 1912, p. 252, pl. 19, fig. 14, respectively) differs in having a small lunule, numerous well-developed commarginal ribs and in being more elongate. *Lucina fallax* Forbes, 1846, from the Upper Cretaceous of India (Forbes, 1846, p. 143, pl. 17, fig. 8) differs in having triangular umbones and poorly developed commarginal ribs. *Lucina laminosa* Reuss, 1844, from the Upper Cretaceous of Germany (Andert, 1934, p. 254, pl. 12, figs 6–7) closely resembles *L. dachelensis* in size and outline but differs in having well-developed commarginal ribs and an umbonal anterior ridge that ends before the antero-ventral margin. *Lucina cretacea* (Conrad, 1870) from the Upper Cretaceous of New Jersey (Whitfield, 1885, p. 129, pl. 18, figs 23–25) closely resembles *L. dachelensis* in ornamentation and in having a straight antero-dorsal margin, a truncated posterior margin and small, inconspicuous beaks, but differs in having strongly rounded anterior and ventral margins.

Occurrence: Upper Cretaceous of Libya (Wanner, 1902; El Qot *et al.*, 2013); Santonian–Campanian of Cameroon

(Dartevelle & Freneix, 1957); Campanian–Maastrichtian of the Western Desert, Egypt (Quaas, 1902; Fourtau, 1917; Abbass, 1962); Cenomanian of the Sergipe Basin (this study, first record).

Lucina fallax Forbes, 1846

Fig. 7; Pl. II, figs P–R

- 1846. *Lucina fallax*, sp. nov.—Forbes, p. 143, pl. 17, fig. 8.
- 1871. *Lucina fallax*, Forbes.—Stoliczka, p. 256, pl. 14, figs 3–5, 7–8.
- 1953. *Lucina fallax* Forbes.—Baroni *et al.*, p. 95, pl. 6, fig. 1.
- v p 1999. *Paraesa faba* (J. de C. Sowerby, 1827).—Seeling, p. 130 (only specimen 507.F2).
- 2006. *Lucina fallax* Forbes.—El Qot, p. 70, pl. 14, figs 7–10.
- ? 2009. *Lucina* (*Lucina*) cf. *fallax* Forbes, 1846.—Jaitly & Mishra, p. 252, fig. 4a.
- 2014. *Lucina fallax* Forbes, 1846.—Ayoub-Hannaa *et al.*, p. 110, pl. 9, figs 7–8.
- 2014. *Lucina fallax* Forbes 1846.—Kumar, p. 506, fig. 2i.
- ? 2018. *Lucina fallax* (Forbes, 1846).—Aouissi *et al.*, p. 17, fig. 5.6.

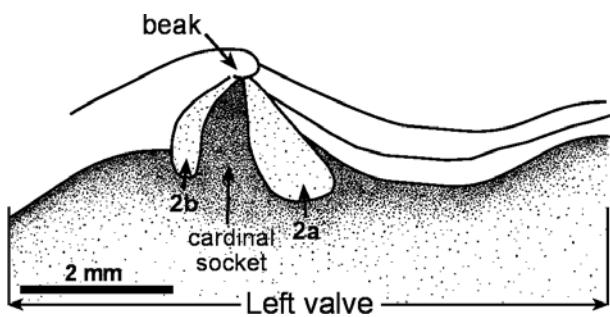
Material: Six internal and composite moulds (NRM-PZ Mo168087–168092) from the upper Cenomanian to upper Turonian (possibly also lower Coniacian) of localities Japaratuba 11, Retiro 15, Estiva 12, Tabocas 2 and Mucuri 7, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 12.

Description: Shell medium-sized, subrounded, inequilateral, moderately inflated ($W/L=0.47$, on average; Table 12). Postero-dorsal margin straight and higher than antero-dorsal margin. Antero-dorsal margin slightly concave. Anterior margin rounded, meeting regularly convex ventral margin in rounded curve. Posterior margin strongly convex. Umbones low, moderately inflated, located almost at midlength of valve. Valve of one specimen showing faint and irregular commarginal ribs near

Table 12: Dimensions (in mm) of *Lucina fallax* Forbes, 1846.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168087	14.5	12.8	?7.0	0.88	0.48
NRM-PZ Mo168088	19.0	16.0	--	0.84	--
NRM-PZ Mo168089	17.0	15.0	8.0	0.88	0.47
Range	14.5-19	12.8-16	?7-8	0.84-0.88	0.47-0.48
Mean	16.83	14.6	7.5	0.87	0.47

Fig. 7: Hinge of left valve of *Lucina fallax* Forbes, 1846 (NRM-PZ Mo168089). Locality Tabocas 2, upper Turonian (possibly lower Coniacian), Sergipe Basin.

ventral margin. Other specimens carrying numerous, faint, commarginal ribs, separated by narrow interspaces (Pl. II, fig. P). Beaks small, inconspicuous, slightly prosogyrate. Hinge of left valve with two cardinal teeth (bifid 2a, 2b) and triangular socket (Fig. 7, Pl. II, figs Q-R). Anterior tooth 2a triangular, wide, larger than posterior cardinal tooth. Lunule narrow, elongate oval.

Discussion: With respect to general outline, valve inflation and development of commarginal growth lines, *Lucina fallax* Forbes, 1846, is a highly variable species. Accordingly, Stoliczka (1871) subdivided this species into four varieties. In the present study, one specimen from the Cenomanian–Turonian boundary beds of locality Japaratuba 11 is characterised by having well-developed elevated umbones, moderately inflated valves and poorly developed commarginal ribs. This specimen agrees in all aspects with the holotype of *L. fallax* Forbes from the Upper Cretaceous of India. The other specimens, from the Turonian of locality Retiro 15 and the upper Turonian or lower Coniacian of Tabocas 2 and Mucuri 7, have well-rounded margins, less inflated valves, numerous commarginal ribs and slightly elevated umbones (Pl. II, fig. P). The latter characters closely resemble those of the *forma typica* of Stoliczka (1871, pl. 14, figs 3-5) from the Aptian–Turonian of southern India.

The specimens from the Cenomanian of Algeria described by Aouissi *et al.* (2018) as *L. fallax* are tentatively placed in synonymy because of their poor preservation and lack of information on the hinge structure. *Lucina ripleyana*

Wade, 1926, from the Maastrichtian of the south-eastern USA (Wade, 1926, p. 82, pl. 25, figs 19-21) closely resembles *L. fallax* in size, inflation and ornamentation but differs in having a strongly concave antero-dorsal margin (notched appearance). The latter character is also observed in *L. aquensis* Holzapfel, 1889, from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 188, pl. 19, fig. 4). *Lucina pisum* J. de C. Sowerby, 1936, from the Lower Cretaceous of England (Woods, 1907, p. 156, pl. 24, figs 16-19) is also similar to *L. fallax* but is smaller ($L=4.5$, $H=4.0-4.9$, $W=2.9-3.5$ mm) and strongly inflated ($W/L=0.70$, as opposed to a mean of 0.47). *Lucina cenomanensis* Abbass, 1962, from the Cenomanian of the Sinai Peninsula of Egypt (Abbass, 1962, p. 108, pl. 22, fig. 1) differs in being larger ($L=26.5$, $H=24.5$, $W=15$ mm) and in having subcentral umbones and faint radial ribs. *Lucina subnumismalis* d'Orbigny, 1850, from the Upper Cretaceous of France and Tunisia (d'Orbigny, 1850, p. 241; Pervinquier, 1912, p. 252, pl. 19, fig. 14) differs in having well-developed commarginal ribs, separated by wide and smooth interspaces. The irregular commarginal ribs of *Lucina reineckeii* Rennie, 1929, from the Albian of Angola (Rennie, 1929, p. 32, pl. 2, figs 18-19) distinguishes it from *L. fallax*, whereas *L. angolensis* Rennie, 1929, from the Albian of the same area (Rennie, 1929, p. 31, pl. 1, figs 1, 2), differs in being larger and more inflated and in having a subquadrate shell. With respect to ornamentation, *L. egitoensis* Rennie, 1945, from the Upper Cretaceous ("Senonian") of Angola (Rennie, 1945, p. 37, pl. 2, fig. 13) resembles *L. fallax* but differs in having an oval shell, a strongly concave antero-dorsal margin, more prominent and strongly prosogyrate umbones, and a distinct umbonal postero-ventral keel. The deep, wide and long lunule and large size of *L. masylaea* Coquand, 1862, from the Cenomanian of Algeria (Coquand, 1862, p. 203, pl. 12, figs 7-8) distinguish this species from *L. fallax*. With respect to shell dimension and hinge structure, specimen 507.F2 (renumbered here NRM-PZ Mo168089), described by Seeling (1999, p. 130) as *Paraesa fava* (J. de C. Sowerby, 1827) from the Cenomanian–Turonian boundary succession of locality Japaratuba 11, is better referred to *L. fallax*.

Occurrence: Aptian–Maastrichtian of southern India (Forbes, 1846; Stoliczka, 1871; Jaitly & Mishra, 2009; Kumar, 2014); Albian–Cenomanian of Egypt (El Qot,

2006; Ayoub-Hannaa *et al.*, 2014); possibly Cenomanian of Algeria (Aouissi *et al.*, 2018); Upper Cretaceous of Libya (Baroni *et al.*, 1953); Cenomanian–Turonian (possibly Coniacian) of the Sergipe Basin (this study, first record).

***Lucina subnumismalis* d'Orbigny, 1850**

Pl. III, figs A-B

- 1847. *V. numismalis* Müller.—Müller, p. 25, pl. 2, fig. 5.
- 1850. *Lucina subnumismalis*.—d'Orbigny, p. 241.
- 1889. *Lucina subnumismalis* [sic] d'Orb.—Holzapfel, p. 187, pl. 19, figs 1-3.
- 1891. *Lucina subnumismalis* [sic] d'Orb.—Böhm, p. 73, pl. 3, fig. 6.
- 1906. *Lucina subnumismalis* D'Orb.—Wiśniowski, p. 328, pl. 1, fig. 7.
- 1906. “...tylko pewną odmianę ...” (*Lucina* sp.).—Wiśniowski, p. 329, pl. 1, fig. 8.
- 1908. *Lucina subnumismalis* Orb.—Schmidt, p. 237.
- 1912. *Lucina (Dentilucina) subnumismalis* d'Orbigny.—Pervinquier, p. 252, pl. 19, fig. 14.
- 1931. *Lucina subnumismalis* [sic] d'Orb.—Krach, p. 358, pl. 7, fig. 3.
- 1971. *Lucina (Dentilucina) subnumismalis* d'Orb.—Collignon, p. 176, pl. H, fig. 1.
- 1986. *Lucina (Lucina) subnumismalis* d'Orbigny, 1850.—Abdel-Gawad, p. 166, pl. 39, fig. 4.
- 1994. ?“*Lucina*” *subnumismalis* d'Orbigny.—Malchus *et al.*, p. 131.

Material: Nine composite moulds (NRM-PZ Mo168093–168101) from the upper Turonian of localities Cajaíba 2 and Estiva 12, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 13.

Description: Shell medium-sized, subcircular, equilateral, length slightly exceeding height (H/L=0.98, on average; Table 13), nearly flat to slightly concave ventrally (compressed), slightly inflated dorsally. Anterior margin strongly rounded, meeting moderately convex ventral margin in rounded curve. Posterior margin subtruncated to slightly convex. Umbones little inflated, slightly prosogyrate, located slightly anterior to mid-length of valve. Ornament consisting of well-developed, regular, widely spaced commarginal ribs separated by wide and smooth interspaces (Pl. III, fig. A).

Table 13: Dimensions (in mm) of *Lucina subnumismalis* d'Orbigny, 1850.

Specimen	L	H	H/L
NRM-PZ Mo168093	20.0	18.0	0.90
NRM-PZ Mo168094	10.0	10.0	1.0
NRM-PZ Mo168095	?18.0	19.0	?1.05
Range	10-20	10-19	0.9-1.05
Mean	16.0	15.67	0.98

Discussion: The Brazilian specimens are very similar to *Lucina subnumismalis* d'Orbigny, 1850, from the Coniacian–Campanian of Germany (Holzapfel, 1889, pl. 19, fig. 3), although the hinge and other internal characters are not visible. Holzapfel's specimens show two divergent cardinal teeth (bifid 3a, 3b of right valve; 2a, 2b of left valve), which is typical of the genus *Lucina*. *Lucina subnumismalis* is distinguished from other lucinid species by its well-developed, widely spaced commarginal ribs (Pl. III, figs A-B), and rounded anterior and ventral margins.

Lucina nicesei Coquand, 1862, from the Albian of Algeria (Coquand, 1862, p. 203, pl. 12, figs 5-6) differs in having strongly rounded margins, triangular and elevated umbones, nearly orthogyrate beaks, finer, numerous commarginal ribs and in being smaller (L=12 mm, as opposed to 20 mm). *Lucina (Dentilucina) dachelen-sis* (Wanner, 1902) from the Campanian of the Western Desert of Egypt (Abbass, 1962, p. 107, pl. 22, fig. 2) differs in having fewer commarginal ribs, a well-developed posterior umbonal ridge and in being larger (L=37, H=29 mm). *Lucina (L.) laminosa* (Reuss, 1846) from the Maastrichtian of Poland (Abdel-Gawad, 1986) differs in having a higher postero-dorsal margin, a strongly concave antero-dorsal margin and fine, numerous commarginal ribs.

Occurrence: Coniacian–Campanian of Germany (Böhm, 1885; Holzapfel, 1889; Schmidt, 1908); Campanian–Maastrichtian of Poland (Krach, 1931; Abdel-Gawad, 1986); Coniacian–Santonian of SE Belgium (Malchus *et al.*, 1994); Maastrichtian of Algeria (Collignon, 1971), Tunisia (Pervinquier, 1912) and the Carpathian Mountains of eastern Europe (Wiśniowski, 1906); Turonian of the Sergipe Basin (this study, first record).

Genus *Callucina* Dall, 1901

Type species: *Lucina radians* Conrad, 1841.

Remarks: The genus *Callucina* is characterised by (1) rounded margins, (2) an elongate, narrow anterior adductor muscle scar (detached from the pallial line ventrally), (3) commarginal ribs crossed by fine radial striations, (4) an asymmetric, heart-shaped lunule, (5) crenulated inner margins and (6) two cardinal teeth in the left valve and a single tooth in the right valve, with no lateral teeth.

Subgenus *Callucina* Dall, 1901

***Callucina (Callucina) itaporangensis* sp. nov.**

Figs 8-9; Pl. III, figs C-N

- 1907. *Lucina* sp.—Woods, p. 152, pl. 24, figs 2-5.

Etymology: After the type locality of the species, Itaporanga.

Diagnosis: Small to very small *Callucina*; shell subcircular to elongate oval; valves moderately inflated; anterior

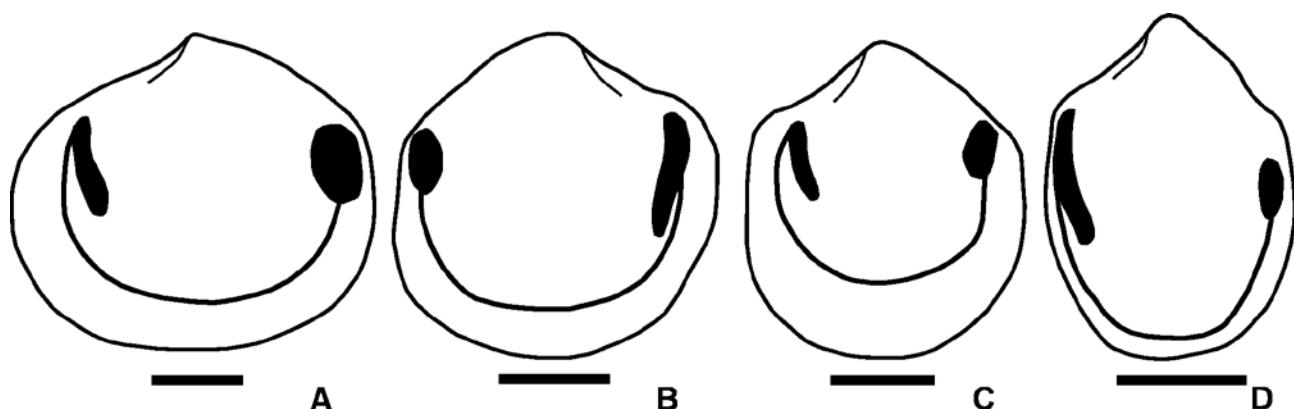


Fig. 8: A-D. Variation in outline of *Callucina (Callucina) itaporangensis* sp. nov. (A, holotype (MN8980-I); B, paratype (MN 8981-I); C, paratype (MN 8987-I); D, paratype (MN 8988-I). Locality Itaporanga 2, lower Cenomanian, Sergipe Basin. Scale bars: 3 mm.

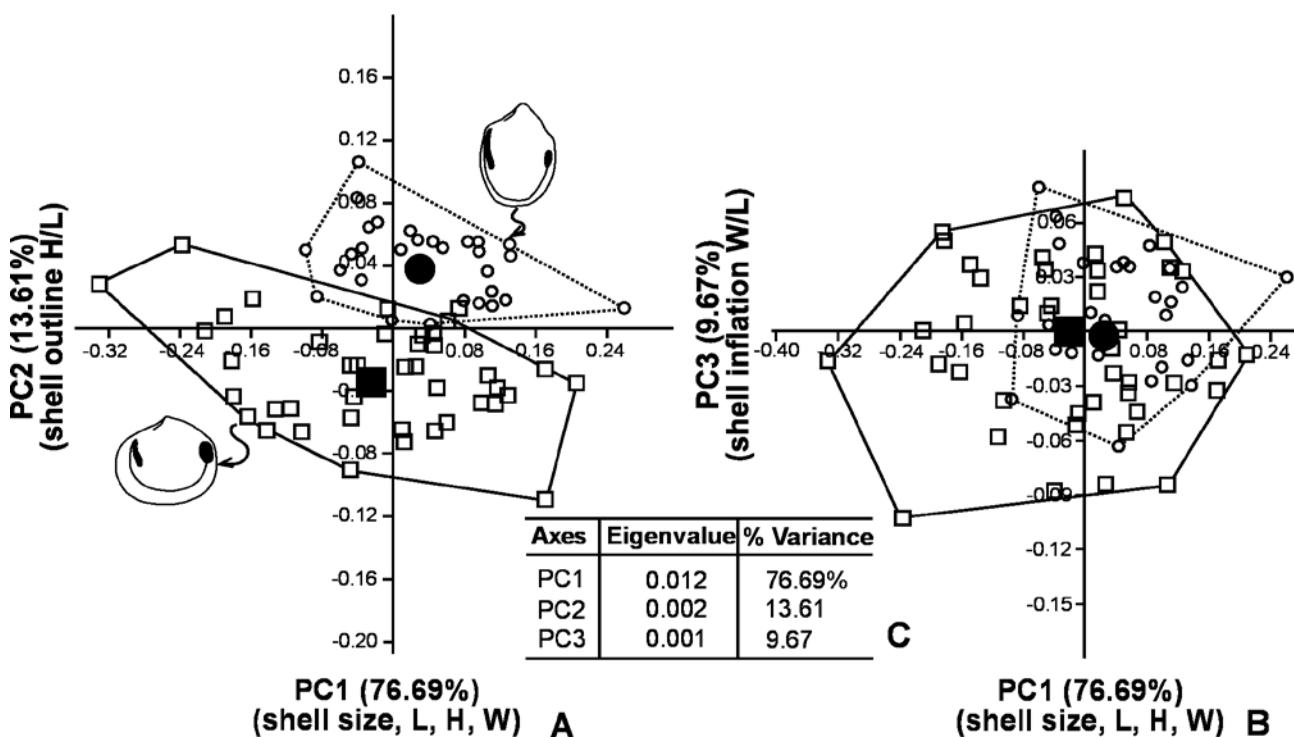


Fig. 9: Principal component analysis (PCA) of *Callucina (Callucina) itaporangensis* sp. nov., using the PAST software (Hammer *et al.*, 2001). A, scatter plot of PC1 vs. PC2 showing overlap of the elongate and suborbicular morphs (on the basis of shell outline (H/L ratio); B, scatter plot of PC1 vs. PC3 also showing overlap of the morphs based on shell inflation (W/L ratio). C, percentage of variation explained by PCA of body-size variables. The large symbols in the scatter plots represent the centroid value for the respective groups (A and B). Cenomanian, Sergipe Basin.

adductor muscle scar long, narrow, rod-like, separated ventrally from the pallial line; lunule slightly asymmetric, heart-shaped; escutcheon narrowly elongated; posterior margin subtruncated to slightly convex; pallial line irregular and entire; umbones submesial; commarginal ribs and radial striations faint; inner margin crenulated. **Holotype:** Composite articulated mould, no. MN 8980-I

(Pl. III, figs D-E), from the lower Cenomanian of locality Itaporanga 2, Cotinguiba Formation, Sergipe Basin.

Paratypes: One-hundred-and-fifty-four articulated composite moulds, nos. MN 8981-I–8990-I (Museu Nacional, Rio de Janeiro, Brazil) and NRM-PZ Mo168102–168245 (Swedish Museum of Natural History, Stockholm, Sweden) from the lower Cenomanian of

localities Itaporanga 2 and 2/3, Cotinguiba Formation, Sergipe Basin.

Type locality: Itaporanga 2 (see Bengtson, 1983, p. 65) in the south-western part of the Sergipe Basin, Brazil.

Type horizon: Lower Cenomanian *Graysonites lozoi* Zone, Cotinguiba Formation, Sergipe Basin.

Measurements: cf. Table 14.

Description: Shell small, variable in outline, subcircular, ovate to elongate oval (Fig. 8A-D), almost equilateral, moderately inflated ($W/L=0.59$, on average). Postero-dorsal margin straight, long, higher than antero-dorsal margin, slightly oblique, almost perpendicular to posterior margin (Pl. III, fig. H). Antero-dorsal margin concave, steeply oblique anteriorly, meeting anterior margin in obtuse angle. Posterior margin subtruncated to slightly convex, almost perpendicular to ventral margin. Anterior margin rounded, meeting ventral margin in rounded angle. Ventral margin regularly rounded and denticulated (Pl. III, fig. M). Umbones wide, subtriangular, slightly inflated, located slightly anterior to mid-length of valve. Beaks prominent, slightly prosogyrate. Lunule narrow, depressed, heart-shaped to sublanceolate, slightly asymmetric (Pl. III, figs F, N). Escutcheon narrow, elongated and shallow. Anterior adductor muscle scar long, rod-like, separated from pallial line ventrally (Pl. III, figs C-E, I). Posterior adductor muscle scar subrounded to ovate, located near postero-dorsal margin. Pallial line entire, irregular, running parallel to ventral margin (Pl. III, fig. D). Surface nearly smooth except for faint commarginal ribs near ventral margin, separated by irregular, smooth interspaces and crossed by faint radial striations (Pl. III, fig. E).

Remarks: *Callucina (C.) itaporangensis* sp. nov. is a highly variable species (Fig. 8A-D), with two morphs recognised, a subrounded and an elongate ovate form. Intermediate forms also occur. Principal Component Analysis (PCA) was carried out to clarify the morphological relationship between the two forms on the variance-covariance matrix of the following log-transformed variables: length (L), height (H), width (W), outline (H/L) and inflation (W/L). Plots of PC1 vs. PC2 and PC1 vs. PC3 scores of individual specimens shows that the two forms are similar in size and inflation (Fig. 9B) but differ in general outline (H/L; PC2). However, as the two forms overlap (based on H/L ratio; Fig. 9A), they are assigned to the same species.

Discussion: *Callucina (C.) itaporangensis* is distinguished from other species of lucinids by its straight postero-dorsal and posterior margins (angulated at their junction), heart-shaped to sublanceolate, slightly asymmetric lunule, narrow, shallow, elongated escutcheon, faint, widely spaced commarginal ribs crossed by faint radial striations and by its crenulated inner margin.

Callucina olea Vokes, 1946, from the Aptian of Lebanon (Vokes, 1946, p. 190, pl. 7, figs 14-17), resembles *C. (C.) itaporangensis* in having straight postero-dorsal and posterior margins and inconspicuous beaks but differs in being larger ($L=22.7-28.5$, $H=21.4-27.3$, $W=14.5$ mm, as opposed to $L=9.13$, $H=9.23$, $W=5.45$ mm, on average) and in having wider umbones and numerous, well-developed commarginal ribs with no radial striations.

Vokes (1941, p. 10, fig. 11) described the new species “*Lucina*” *hajulaensis* from the Cenomanian of Lebanon

Table 14: Dimensions (in mm) of *Callucina (Callucina) itaporangensis* sp. nov.

Specimen	L	H	W	H/L	W/L
MN 8980-I (Holotype)	11.5	11.2	6.3	0.97	0.55
MN 8981-I (Paratype)	10.7	10.0	6.8	0.93	0.63
MN 8987-I (Paratype)	9.8	10.5	6.3	1.07	0.64
MN 8988-I (Paratype)	6.2	7.8	5.0	1.26	0.81
NRM-PZ Mo168102	10.3	9.3	6.2	0.90	0.61
NRM-PZ Mo168103	10.4	11.8	6.3	1.13	0.60
NRM-PZ Mo168106	10.5	11.0	5.8	1.05	0.55
NRM-PZ Mo168107	10.0	10.8	5.8	1.08	0.58
NRM-PZ Mo168130	12.1	11.5	7.2	0.95	0.59
NRM-PZ Mo168131	7.7	8.1	4.2	1.05	0.55
NRM-PZ Mo168132	9.1	9.0	5.5	0.99	0.60
NRM-PZ Mo168138	6.2	5.7	3.0	0.92	0.48
NRM-PZ Mo168139	6.4	6.3	3.8	0.98	0.59
NRM-PZ Mo168174	10.2	10.0	6.8	0.98	0.67
NRM-PZ Mo168191	5.8	5.5	2.7	0.95	0.47
Range	5.8-11.5	5.5-11.8	2.7-6.8	0.90-1.26	0.47-0.81
Mean	9.13	9.23	5.45	1.01	0.59

on the basis of a single, poorly preserved composite mould (ventral margin missing). The species resembles *C. (C.) itaporangensis* in its truncated posterior margin and large anterior area but differs in having a well-developed posterior umbonal ridge, strongly rounded anterior margin and in being larger ($L=24$, $H=22.6$ mm) and less inflated ($W/L=0.20$). *Lucina (Dentilucina) calmoni* Pervinquieré, 1912 from the Maastrichtian of Tunisia (Pervinquieré, 1912, p. 253, pl. 19, figs 10-13), differs in having strongly rounded margins, a strongly convex postero-dorsal margin, a straight antero-dorsal margin (gradually oblique anteriorly) and well-developed commarginal ribs. Similarly, *L. saharica* Quaas, 1902, from the Upper Cretaceous of the Western Desert, Egypt (Quaas, 1902, p. 214, pl. 14, figs 5-7), has well-rounded margins, except for the short and concave antero-dorsal margin, and well-developed and widely spaced commarginal ribs, but lacks prominent beaks. *Lucina smockana* Whitfield, 1885, from the Upper Cretaceous of New Jersey, USA (Whitfield, 1885, p. 130, pl. 18, figs 21-22), differs in having a narrower lunule, a reniform anterior adductor muscle scar, long and narrow posterior adductor muscle scar, a truncated anterior margin and in being larger ($L=16$ mm). The circular outline and wide umbones of *L. benvenistii* Shalem, 1928, from the Cenomanian of Palestine (Shalem, 1928, p. 81, pl. 3, fig. 10) distinguish this species from *C. (C.) itaporangensis*. Abbass (1962, p. 108, pl. 22, fig. 1) described *L. (Loripes) cenomanensis* from the Cenomanian of Sinai, Egypt, which resembles *C. (C.) itaporangensis* in having nearly central umbones and faint radial ribs crossed by commarginal growth lines, but differs in having rounded anterior, posterior and ventral margins, concave antero- and postero-dorsal margins, a short, deep lunule and sharply pointed beaks. Moreover, *L. (L.) cenomanensis* is larger than *C. (C.) itaporangensis* ($L=26.5$, $H=24.5$, $W=15$ mm, as opposed to $L=9.13$, $H=9.23$, $W=5.45$ mm, on average).

Occurrence: Lower Cretaceous of England (Woods, 1907); Cenomanian of the Sergipe Basin (this study, first record).

Family Mactromyidae Cox, 1929 (P. Fischer, 1887)

Genus *Thetis* J. de C. Sowerby, 1826
 (= *Thetironia* Stoliczka, 1871;
 = *Fimbriella* Stoliczka, 1871)

Type species: *Thetis major* J. de C. Sowerby, 1826 (= *Corbula laevigata* J. Sowerby, 1818; non *Thetis* Oken, 1815).

Remarks: J. de C. Sowerby (1826, p. 19) erected the genus *Thetis* from the Lower Cretaceous of England on the basis of (1) its slightly inequilateral and orbicular shell, (2) external ligament, (3) slightly incurved beaks, (4) lack of a lunule and (5) three and/or four unequal teeth; the two cardinal ones are large, conical and slightly incurved, whereas the lateral teeth are smaller.

Thetis? minor J. de C. Sowerby, 1826

Pl. III, figs O-P

- 1826. *Thetis minor* J. de C. Sowerby, p. 21, pl. 513, figs 5-6.
- 1907. *Thetironia minor* (J. Sowerby).—Woods, p. 167, pl. 25, fig. 15; pl. 26, figs 1-8.
- ? 1908. *Thetironia papyracea* (Sharpe).—Kitchin, p. 142, pl. 7, fig. 11.
- 1974. *T. minor* Sowerby.—Oekentorp & Siegfried, p. 155, pl. 15, fig. 2.
- 1988. *Thetis minor* Sowerby, 1826.—Dhondt & Dieni, p. 45, pl. 7, fig. 14 (with extended synonymy).

Material: One composite mould (NRM-PZ Mo168246) from the lower Cenomanian of locality Itaporanga 4, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 15.

Description: Shell medium-sized, rounded, slightly inequilateral and moderately inflated. Anterior margin convex, meeting ventral margin in rounded curve. Ventral margin regularly convex. Antero-dorsal margin slightly concave. Umbones broad, elevated above hinge, moderately convex, located slightly anterior to mid-length of valve. Beaks prominent, slightly prosogyrate. Ornament consisting of faint commarginal growth lines at regular intervals, crossed by regular rows of faint radial ribs, with well-developed minute tubercles towards posterior margin. Intersection of radial ribs and growth lines producing a grid-like pattern (Pl. III, fig. P).

Discussion: With respect to general outline, shell size and ornamentation, the Brazilian specimen corresponds to the genus *Thetis*, but without knowledge of the hinge structure generic identification remains doubtful.

The specimen is very similar to *Thetis minor* J. de C. Sowerby, 1826, from the Lower Cretaceous of England (Woods, 1907). The species appears well differentiated from other species of *Thetis* by having (1) rounded margins, (2) strong inflated valves, (3) more prominent beaks and (4) well-developed tuberculate radial ribs along the posterior area. The specimen is somewhat similar to *Thetironia laevigata* (J. Sowerby, 1818) from the Lower Cretaceous of England (Woods, 1907, p. 169, pl. 26, figs 9-14), but the latter species differs in having narrow, high, triangular umbones and in being larger. *Thetironia papyracea* (Sharpe, 1856) from the Valanginian of South Africa (Kitchin, 1908) closely resembles *T. minor* in general outline, size, ornamentation and curvature of beaks but differs in being less inflated and is tentatively placed in synonymy with *T. minor*. According to Dhondt & Dieni (1988), there are no differences between *T. renevieri*

Table 15: Dimensions (in mm) of *Thetis? minor* J. de C. Sowerby, 1826.

Specimen	L	H	H/L
NRM-PZ Mo168246	36.0	36.0	1.00

de Loriol, 1861, from the “Neocomian” of France and *T. minor* except that the umbones of the latter species are more mesially placed. Therefore, they suggested that *T. renevieri* is a junior synonym of *T. minor*.

Occurrence: Hauterivian of Italy and Hauterivian–Albian? of France, Denmark and the Russian Platform (Dhondt & Dieni, 1988); Aptian of England (J. de C. Sowerby, 1826; Woods, 1907); Lower Cretaceous (Albian?) of Germany (Oekentorp & Siegfried, 1974); possibly Valanginian of South Africa (Kitchin, 1908); Cenomanian of the Sergipe Basin (this study, first record).

Infrasubcohort Cardiida Féussac, 1822
 Megaorder Cardiata Féussac, 1822
 (= Neoheterodontei Taylor et al., 2007)
 Superorder Cardiiformii Féussac, 1822
 Order Megalodontida Starobogatov, 1992
 Superfamily Megalontoidea Morris & Lycett, 1853
 Family Dicerocardiidae Kutassy, 1934
 Genus *Agelasina* Riedel, 1933

Type species: *Agelasina plenodonta* Riedel, 1933.

Remarks: The genus *Agelasina* is very similar to the genus *Glossus* Poli, 1795, of the family Glossidae in general outline and ornamentation but the latter has only been recorded from the Cenozoic. With respect to the hinge structure, *Agelasina* carries two large, posteriorly elongated cardinal teeth, separated by a wide socket, and has no lateral teeth. By contrast, the hinge of *Glossus* has well-developed lateral teeth. The genus *Ambocardia* Beringer, 1949, differs in having posterior and anterior umbonal ridges, a truncated posterior margin, less incurved umbones and in being much taller than *Agelasina*.

Agelasina plenodonta Riedel, 1933

Pl. III, figs Q-T; Pl. IV, figs A-D

1933. *Agelasina plenodonta* n. gen. n. sp.—Riedel, p. 58, pl. 4, fig. 1; pl. 12, figs 1, 3-5.
 1955. *Agelasina plenodonta* Riedel.—Reyment, p. 142, pl. 4, fig. 1.
 1957. *Agelasina plenodonta* Riedel.—Dartevelle & Freneix, p. 155, pl. 26, fig. 3; pl. 27, figs 1-3; pl. 28, figs 1-2.

2015. *Agelasina plenodonta* Riedel, 1932 [sic].—Musavu Moussavou, p. 316, figs 4/F, H, L, P.

Material: Six articulated specimens (NRM-PZ Mo168247–168252) from the upper Turonian of localities Mucuri 10, Oiteiro 8 and 19 and Mata 11, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 16.

Description: Shell medium to large, varying from sub-trigonal, subrounded to cordiform, inequilateral, equivalved, slightly higher than long and strongly inflated ($W/H=0.91$, on average; Table 16). Antero-dorsal margin strongly concave below umbones. Postero-dorsal margin broadly convex, higher than antero-dorsal margin, meeting posterior margin in rounded curve. Anterior margin narrow, strongly rounded, meeting ventral margin in rounded angle. Posterior margin broadly rounded, forming rounded curves with postero-dorsal and ventral margins (Pl. IV, figs A, D). Anterior and posterior adductor muscle scars equal in size, small, subrounded, located close to anterior and posterior margins respectively (Pl. IV, fig. A). Pallial line entire, close to ventral margin. Umbones broad, convex and strongly prosogyrate (Pl. IV, figs B, D). Beaks prominent, terminal, sharply pointed and strongly prosogyrate. Ornament not preserved except for faint comm marginal ribs near ventral margin.

Discussion: The Brazilian specimens are articulated and internal characters such as hinge and muscle scars are not visible. However, they are more similar to the genus *Agelasina* than to *Glossus* and *Ambocardia* in having large, strongly inflated valves, strongly incurved terminal umbones, strongly rounded margins and by lacking umbonal ridges. Despite the poor preservation of the specimens, they closely resemble *Agelasina plenodonta* from the Maastrichtian of Cameroon (Riedel, 1933; Dartevelle & Freneix, 1957) and Nigeria (Reyment, 1955).

Carvalho et al. (2000, p. 248) recorded *Agelasina plenodonta* from the Barremian–Aptian of the Campos Basin, Brazil. However, their identification must be considered doubtful, as (1) the preservation of their specimens is inadequate for identification (small, reworked, broken shells), (2) no illustrations of the specimens are provided, (3) the species is only known from higher stratigraphic

Table 16: Dimensions (in mm) of *Agelasina plenodonta* Riedel, 1932.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168247	42.0	45.0	36.0	1.07	0.86
NRM-PZ Mo168248	41.0	43.0	21.0 (RV)	1.05	?1.02
NRM-PZ Mo168249	52.0	54.0	22.0 (LV)	1.03	?0.85
NRM-PZ Mo168250	62.0	62.0	28.0 (RV)	1.0	?0.90
NRM-PZ Mo168251	50.0	50.0	23.0 (LV)	1.0	?0.92
Range	41-62	43-62	---	1-1.07	?0.85-?1.02
Mean	49.40	50.80	---	1.03	?0.91

levels (Turonian–Maastrichtian) and (4) the known specimens of *A. plenodonta* are much larger than their specimens. *Venilicardia odonneli*, Rennie, 1945, from the Upper Cretaceous of Angola (Rennie, 1945, p. 36, pl. 3, figs 2, 42) strongly resembles *A. plenodonta* in having prominent, terminal, sharply pointed, strongly prosogyrate beaks and a strongly concave antero-dorsal margin but differs in having a truncated posterior margin.

Veniella (Venilicardia) obruncata Stoliczka, 1870, from the Coniacian–Maastrichtian of South India (Stoliczka, 1870, p. 196, pl. 8, figs 4–9) is somewhat similar to *A. plenodonta* but differs in having rectangular valves ($H/L=0.83$, as opposed to a mean of 1.08), strongly incurved and terminal umbones, a well-developed posterior umbonal ridge, short and strongly convex anterior margin, straight to slightly convex postero-dorsal margin and in being strongly inflated. *Cyprina (Venilicardia) barroisi* Coquand, 1880, from the Santonian of Tunisia (Pervinquière, 1912, p. 225, pl. 16, figs 12–13; Thomas & Peron, 1890, p. 298, pl. 24, figs 8–9) closely resembles *A. plenodonta* in general outline, curvature of umbones and shell inflation but differs in having sharp and less coiled beaks, narrow umbones and in being higher than the present species. *Anisocardia hermitae* Choffat, 1885, from the Turonian of Portugal (Choffat, 1902, p. 133, pl. 9, figs 4–7) differs in being less elongate and in having a subtrapezoidal shell, less incurved umbones, a subtruncated postero-dorsal margin, an angular to truncated posterior end and a nearly straight ventral margin. *Isocardia aquilina* Coquand, 1862, from the Cenomanian of Algeria (Coquand 1862, p. 209, pl. 9, figs 11–12) differs in having a straight postero-dorsal margin, narrow umbones, sharp beaks, a wide and cordate anterior depression and in being larger ($L=65$ mm, as opposed to a mean of 46 mm) and strongly inflated.

Occurrence: Coniacian–Maastrichtian of Cameroon (Riedel, 1933; Darteville & Freneix, 1957), Nigeria (Reymont, 1955) and Coniacian–Santonian of Gabon (Musavu Moussavou, 2015); Turonian of the Sergipe Basin (this study, first record).

Genus *Ambocardia* Beringer, 1949

Type species: *Isocardia planidorsata* Zittel, 1864.

Ambocardia planidorsata (Zittel, 1864)

Fig. 10; Pl. IV, figs E–F

- 1864. *Isocardia planidorsata*.—Zittel, p. 36 [140], pl. 5, fig. 4.
- 1889. *Isocardia Zitteli* nov. sp.—Holzapfel, p. 177, pl. 15, figs 2–4.
- 1949. *Isocardia planidorsata* Zitt.—Beringer, p. 208, pl. 18, figs 4–6.
- 1949. *I. planidorsata* Zitt. var. *acutata*.—Beringer, p. 209, pl. 18, fig. 6.
- 1987. *Ambocardia planidorsata* (Zittel, 1865).—Dhondt, p. 84, pl. 5, figs 6, 7.

Material: Three articulated internal moulds (NRM-PZ Mo168253–168255) from the lower–middle Turonian

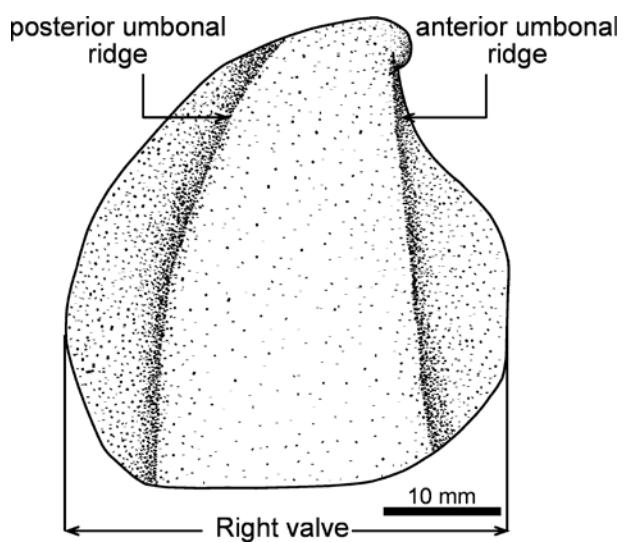


Fig. 10: Right valve of *Ambocardia planidorsata* (Zittel, 1864), showing the anterior and posterior umbonal ridges (NRM-PZ Mo168253). Locality Pedro Gonçalves 3, lower–middle Turonian, Sergipe Basin.

of locality Pedro Gonçalves 3, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 17.

Description: Shell medium to large, rectangular-ovate, higher than long ($H/L=1.20$, on average), strongly inequilateral and strongly inflated ($W/L=0.97$, on average; Table 17). Postero-dorsal margin strongly convex, higher than antero-dorsal margin, meeting posterior margin in rounded curve. Antero-dorsal margin concave (Pl. IV, fig. E). Posterior margin slightly convex to subtruncated, meeting ventral margin in rounded angle. Anterior margin slightly convex. Posterior and anterior umbonal ridges poorly preserved (Pl. IV, fig. F). Area between anterior and posterior umbonal ridge wide and nearly flat. Anterior adductor muscle scar small, rounded, located near antero-dorsal margin (Pl. IV, fig. E). Umbones broad, triangular, strongly inflated and prosogyrate. Beaks sharply pointed, subterminal and strongly prosogyrate. Ornament not preserved except for faint commarginal ribs near ventral margin.

Discussion: The specimens are internal moulds with only feeble signs of ornament preserved. However, they closely resemble *Ambocardia planidorsata* (Zittel, 1864) from the “Senonian” of the north-eastern Alps in general outline, size, curvature of umbones, shell inflation and in having posterior and anterior umbonal ridges (Fig. 10). *Isocardia zitteli* Holzapfel, 1889 from the lower Campanian of Germany (Holzapfel, 1889, p. 177, pl. 15, figs 2–4) is very similar and is here regarded as a junior synonym of *A. planidorsata*.

Occurrence: “Senonian” of the north-eastern Alps (Zittel, 1864); Santonian–Maastrichtian of Austria

(Dhondt, 1987); Campanian of Germany (Holzapfel, 1889); Turonian of the Sergipe Basin (this study, first record).

- Order Cardiida Férrusac, 1822
- Suborder Cardiidina Férrusac, 1822
- Hyporder Cardioidei Férrusac, 1822
- Superfamily Cardioidea Lamarck, 1809
 - Family Cardiidae Lamarck, 1809
 - Subfamily Protocardiinae Reuss, 1846
 - Genus *Protocardia* Beyrich, 1845

Type species: *Cardium hillanum* J. Sowerby, 1813.

Subgenus *Protocardia* Beyrich, 1845

***Protocardia (Protocardia) coquandi* (Seguenza, 1882)**

Pl. IV, figs G-J

- 1882. *Cardium Coquandi* n. sp.– Seguenza, p. 148, pl. 9, fig. 1.
- 1912. *Cardium (Protocardia) Coquandi* Seguenza.– Pervinquier, p. 266, pl. 19, fig. 23, non 22, 24.
- 1957. *Protocardia (Protocardia) coquandi* (Seguenza).– Darteville & Fréneix, p. 176, pl. 30, figs 2-3.
- 2002. *Protocardia (Protocardia) coquandi* (Seguenza, 1882).– Berndt, p. 122, pl. 6, fig. 5.

Material: Two composite moulds (NRM-PZ Mo168256–168257) from the middle–upper Cenomanian of localities Cruzes 6 and 8/11, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 18.

Description: Shell medium-sized, outline rounded quadrangular, nearly equilateral and moderately inflated ($W/L=0.64$). Antero-dorsal margin slightly concave. Postero-dorsal margin slightly convex. Anterior margin strongly rounded, meeting ventral margin in rounded curve. Ventral margin rounded, meeting posterior margin

in acute angle. Anterior adductor muscle scar subcircular, located close to antero-dorsal margin. Umbones wide, moderately convex, elevated and slightly prosogyrate. Beaks sharply pointed and slightly prosogyrate. Posterior slope ornamented with closely spaced radial ribs (10-13) (Pl. IV, figs H, I). Middle part of valve and anterior slope covered with closely spaced commarginal ribs.

Discussion: *Protocardia (P.) coquandi* (Seguenza, 1882) is distinguished from other Protocardiinae described here by having a rounded quadrangular valve, slightly convex postero-dorsal margin, sharply pointed beaks.

Protocardia shabrawitensis Abbass, 1962, from the Cenomanian of the Eastern Desert, Egypt (Abbass, 1962, p. 126, pl. 21, fig. 6) closely resembles *P. (P.) coquandi* in general outline but differs in being larger ($H=62$, $L=57$, $T=50$ mm, as opposed to $L=38.5$, $H=40$ mm, on average), more inflated ($W/L=0.81$, as opposed to a mean of 0.64) and in having numerous radial ribs (25) and a straight postero-dorsal margin (higher than the concave antero-dorsal margin). Two of Pervinquier's *P. coquandi* specimens (Pervinquier, 1912, pl. 19, figs 22, 24) are much closer to *Protocardia (Pachycardium) pauli* (Coquand, 1862, p. 204, pl. 10, figs 5-6) from the Cenomanian of Algeria than to Seguenza's species. *Protocardia (P.) pauli* differs in being larger and in having elevated umbones, a less developed posterior umbonal ridge, concave postero- and antero-dorsal margins and inconspicuous beaks. *Protocardia regulare* (Coquand, 1862) from the lower Cenomanian of Algeria (Coquand, 1862, p. 205, pl. 10, figs 13-14) closely resembles *P. (P.) coquandi* but differs in having narrowly triangular umbones, a less convex anterior margin, a slightly concave postero-dorsal margin and an elevated and truncated posterior margin. *Protocardia altum* (G. B. Sowerby, 1846) from the Upper Cretaceous of South India (G. B. Sowerby in Forbes, 1846, p. 145, pl. 15, fig. 13) differs in being taller ($H/L=1.20$, as opposed to a mean of 1.04), less inflated and

Table 17: Dimensions (in mm) of *Ambocardia planidorsata* (Zittel, 1864).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168253	42.0	49.0	20.0 (RV)	1.17	0.95
NRM-PZ Mo168254	46.0	57.0	23.0 (RV)	1.24	1.00
Range	42-46	49-57	20-23 (RV)	1.17-1.24	0.95-1.00
Mean	44.0	53	21.5	1.20	0.97

Table 18: Dimensions (in mm) of *Protocardia (Protocardia) coquandi* (Seguenza, 1882).

Specimen	L	H	W	nr	H/L	W/L
NRM-PZ Mo168256	39.0	41.0	?25.0	10	1.05	0.64
NRM-PZ Mo168257	38.0	39.0	--	13	1.03	--
Range	38-39	39-41	?25	10-13	1.03-1.05	0.64
Mean	38.5	40	?25	11.5	1.04	0.64

in having narrow umbones, a subtruncated posterior margin and a less rounded anterior margin.

Occurrence: Cenomanian of Tunisia (Pervinquière, 1912) and Jordan (Berndt, 2002); “Senonian” of Cameroon (Dartevelle & Freneix, 1957); Cenomanian of the Sergipe Basin (this study, first record).

Protocardia (Protocardia) hillana (J. Sowerby, 1813)

Pl. IV, figs K-N

- 1813. *Cardium Hillanum*.— J. Sowerby, p. 41, pl. 14.
- 1864. *Cardium (Protocardia) hillanum* Sow.— Zittel, p. 42 [146], pl. 7, fig. 2.
- 1870. *Protocardium hillanum*, Sowerby.— Stoliczka, p. 219, pl. 12, figs 8-10; pl. 13, figs 1-3.
- 1902. *Protocardia hillana*, Sow. sp.— Quaas, p. 218, pl. 24, figs 18-19.
- 1908. *Protocardia Hillana* (Sowerby, 1813).— Woods, p. 197, pl. 31, fig. 6a-c; pl. 32, figs 1-6.
- 1916. *Protocardia hillana* Sowerby.— Douvillé, p. 158, pl. 20, fig. 1.
- 1916. *Protocardia hillana* Sowerby variété *prisca*.— Douvillé, p. 158, pl. 20, figs 2-3.
- 1929. *Protocardia hillana* (J. Sowerby).— Rennie, p. 35, pl. 3, fig. 1.
- 1934. *Protocardia hillana* Sow. sp.— Andert, p. 262, pl. 12, figs 21-22.
- 1934. *Protocardia hillana* Sow.— Blanckenhorn, p. 244 (with additional synonymy).
- 1941. *Protocardia* sp. aff. *hillana* (Sowerby).— Vokes, p. 10, figs 9-10.
- 1957. *Protocardia (Protocardia) hillana* (Sowerby).— Dartevelle & Freneix, p. 178.
- 1962. *Protocardia hillana* (Sowerby).— Abbass, p. 123, pl. 21, figs 1, 3, 13.
- 1974. *P. hillana* (Sowerby).— Oekentorp & Siegfried, p. 157, pl. 15, fig. 10.
- 2005. *Protocardia (P.) hillana* (J. Sowerby 1813).— Hradecká *et al.*, p. 29, pl. 1, figs b-g.
- 2006. *Protocardia hillana* (J. Sowerby, 1813).— El Qot, p. 78, pl. 16, figs 4-6.
- 2014. *Protocardia hillana* (J. Sowerby 1813).— Ayoub-Hannaa *et al.*, p. 115, pl. 10, figs 8-9.
- 2014. *Protocardia hillana* (J. Sowerby).— Kumar, p. 509, fig. 3c.
- 2014. *Protocardia hillana* (Sowerby, 1813).— Niebuhr *et al.*, p. 145, fig. 12h.
- 2016. *Protocardia hillana* (Sowerby, 1813).— Benzaggagh, p. 201, figs 16C-I.

Material: Two composite moulds (NRM-PZ Mo168258–168259) from the upper Cenomanian–lower Turonian

of localities Tibúrcio 1 and Magalhães 7, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 19.

Description: Shell medium-sized, subrounded, equilateral and moderately inflated ($W/L=0.54$, on average). Antero- and postero-dorsal margins concave, almost perpendicular to anterior and posterior margins. Posterior margin subtruncated. Anterior margin rounded, meeting broadly convex ventral margin in rounded angle. Lunule well defined, ovate and moderately deep. Escutcheon elongate ovate and deep (Pl. IV, fig. N). Umbones moderately convex, located submesially. Beaks small, inconspicuous, slightly prosogyrate. Posterior slope with well-developed radial ribs (14-17), becoming finer posteriorly and postero-dorsally and separated by relatively broad, smooth, concave interspaces (Pl. IV, figs K-L). Commarginal ribs on flank and anterior end not preserved.

Discussion: *Protocardia (P.) hillana* (J. Sowerby, 1813) is characterised by having 10-20 radial ribs on the posterior third of the shell, fairly well-rounded margins, submesial umbones and small beaks (Ayoub-Hannaa *et al.*, 2014).

Protocardia (P.) hillana differs from *P. (P.) coquandi* (Seguenza, 1882) in having rounded margins and near-mesial umbones. *Isocardia coutinhoana* White, 1887, from the middle Albian of the Sergipe Basin (Maury, 1937, p. 69, pl. 9, figs 1-4) resembles the present species in having rounded margins, near-mesial umbones and small beaks but has fewer radial ribs (5), a well-developed posterior umbonal ridge and is more inflated ($W/L=0.78$, as opposed to a mean of 0.59). *Protocardia moutai* Rennie, 1945 from the Upper Cretaceous (“Senonian”) of Angola (Rennie, 1945, p. 40, pl. 2, fig. 16) differs in having irregular commarginal ribs and coarse radial ribs with narrow interspaces.

Occurrence: Lower Cretaceous of England (Woods, 1908); Aptian–lower Campanian of Egypt (e.g., Abbass, 1962; El Qot, 2006; Ayoub-Hannaa *et al.*, 2014); Albian of Angola (Rennie, 1929) and Morocco (Benzaggagh, 2016); Cenomanian of Lebanon (Vokes, 1941); Cenomanian–Turonian of Syria (Blanckenhorn, 1934); Turonian–Coniacian of Austria (Hradecká *et al.*, 2005) and Germany (Andert, 1934; Oekentorp & Siegfried, 1974; Niebuhr *et al.*, 2014); Coniacian–Santonian (Trichinopoly Group) of South India (Stoliczka, 1870; Kumar, 2014); Upper Cretaceous of the northeastern Alps (Zittel, 1864) and Libya (Quaas, 1902); “Senonian”

Table 19: Dimensions (in mm) of *Protocardia (Protocardia) hillana* (J. Sowerby, 1813).

Specimen	L	H	W	nr	H/L	W/L
NRM-PZ Mo168258	16.0	16.0	78.0	?11	1.0	0.50
NRM-PZ Mo168259	37.0	35.0	21.0	13	0.95	0.57
Range	16-37	16-35	78-21	?11-13	0.95-1.0	0.50-0.57
Mean	26.5	25.5	9.5	12	0.97	0.54

of Angola (Dartevelle & Freneix, 1957); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

Subgenus *Pachycardium* Conrad, 1869

Type species: *Cardium spillmani* Conrad, 1858, by subsequent designation of Dall (1900).

Remarks: The subgenus is characterised by elongate valves (height appreciably greater than length), a thick hinge plate (Schneider, 1995), narrow elevated umbones, fine radial ribs along the posterior flank and numerous irregular commarginal ribs anteriorly and in the middle part of the valve. The Brazilian specimens are assigned to the subgenus *Pachycardium* on the basis of height/length ratio and ornamentation.

***Protocardia (Pachycardium) pauli* (Coquand, 1862)**

Figs 11–13; Pl. IV, figs O–R; Pl. V, figs A–E

- 1862. *Cardium pauli* H. Coq.—Coquand, p. 204, pl. 10, figs 5–6.
- 1890. *Cardium elongatum* Thomas et Peron.—Thomas & Peron, p. 275, pl. 28, fig. 15.
- 1912. *Cardium (Protocardia) Pauli* Coquand.—Pervinquière, p. 265, pl. 19, fig. 21.
- ? 1912. *Cardium (Protocardia) Coquandi* Seguenza.—Pervinquière, p. 266, pl. 19, figs 22, 24.
- 1919. *Cardium (Protocardia) Pauli* Coq.—Greco, p. 37 [219], pl. 4 [20], fig. 11.
- 1933. *Cardium (Protocardia) pauli* Coq.—Riedel, p. 53, pl. 10, fig. 3; pl. 11, figs 8–9.
- 1934. *Cardium pauli* var. *aequilaterale* n. v.—Blankenhorn, p. 240, pl. 13, fig. 125.
- 1957. *Protocardia (Protocardia) pauli* (Coquand).—Dartevelle & Freneix, p. 175, pl. 30, figs 4–6.
- v p 1983. *Protocardia pauli* (Coquand).—Lefranc in Bengtson, p. 45.
- v p 1999. *Protocardia (Protocardia) pauli* (Coquand,

1862).—Seeling, p. 125, pl. 5, fig. 3 [pl. 5, fig. 2 = *Granocardium (G.) tenuistriatum*].

- ? 2009. *Protocardia (Pachycardium) pauli* (Coquand).—Jaitly & Mishra, p. 257, fig. 3E; fig. 4L, M.
- v 2011. *Protocardia (Protocardia) pauli* (Coquand, 1862).—Andrade & Santos, p. 235, figs 2/13, 14.
- ? 2015. *Protocardia cf. pauli* (Coquand, 1862).—Musavu Moussavou, p. 318, fig. 4/G, J.
- 2016. *Protocardia (Protocardia) pauli* (Coquand, 1862).—Benzaggagh, p. 203, figs 17A–E.

Material: 37 internal and composite moulds (NRM-PZ Mo168260–168296) from the middle Cenomanian to upper Turonian of localities Magalhães 3, Cruzes 6, Japaratuba 6, Jardim 17 and 29, Recreio 1, Pedro Gonçalves 2, São Roque 2 and 6, Retiro 15, Oiteiro 19, Muçuca 1 and 2, Laranjeiras 21 and 22, Mata 9 and 10, Alto Verde 5 and Mucuri 10, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 20.

Description: Shell large, variable in outline from triangular–elongate, subtrapezoidal to elongate ovate (Fig. 11), much higher than long ($H/L=1.31$, on average), strongly inequilateral, equivalved and moderately inflated ($W/L=0.76$, on average). Posterior margin truncated, meeting ventral valve in acute angle. Anterior margin convex, narrow, meeting ventral margin in rounded angle. Ventral margin broad, irregular and slightly rounded. Postero-dorsal margin slightly convex, meeting posterior margin in acute angle. Antero-dorsal margin slightly concave, steeply oblique and lower than postero-dorsal margin. Umbones triangular, narrow, moderately convex, elevated above hinge, located one-third of total valve length from anterior end. Beaks prominent, slightly prosogyrate. Posterior umbonal ridge well developed, separating posterior third of flank (concave and steeply oblique) from the rest of valve (Pl. IV, fig. P; Pl. V, fig. A). Lunule subrounded to rounded, large and deep (Pl. V, fig. C).

Table 20: Dimensions (in mm) of *Protocardia (Pachycardium) pauli* (Coquand, 1862).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168260	26.0	32.0	18.0	1.23	0.69
NRM-PZ Mo168261	24.0	26.0	--	1.08	--
NRM-PZ Mo168262	43.0	57.0	?35.0	1.32	0.81
NRM-PZ Mo168263	34.0	43.0	--	1.26	--
NRM-PZ Mo168264	38.0	63.0	--	1.66	--
NRM-PZ Mo168265	42.0	60.0	35.0	1.43	0.83
NRM-PZ Mo168266	34.0	38.0	23.0	1.12	0.67
NRM-PZ Mo168267	49.0	67.0	37.0	1.37	0.75
NRM-PZ Mo168268	48.0	63.0	40.0	1.31	0.83
NRM-PZ Mo168269	47.0	64.0	--	1.36	--
Range	24.0–49.0	26.0–67.0	18.0–40.0	1.08–1.66	0.67–0.83
Mean	38.5	51.3	31.3	1.31	0.76

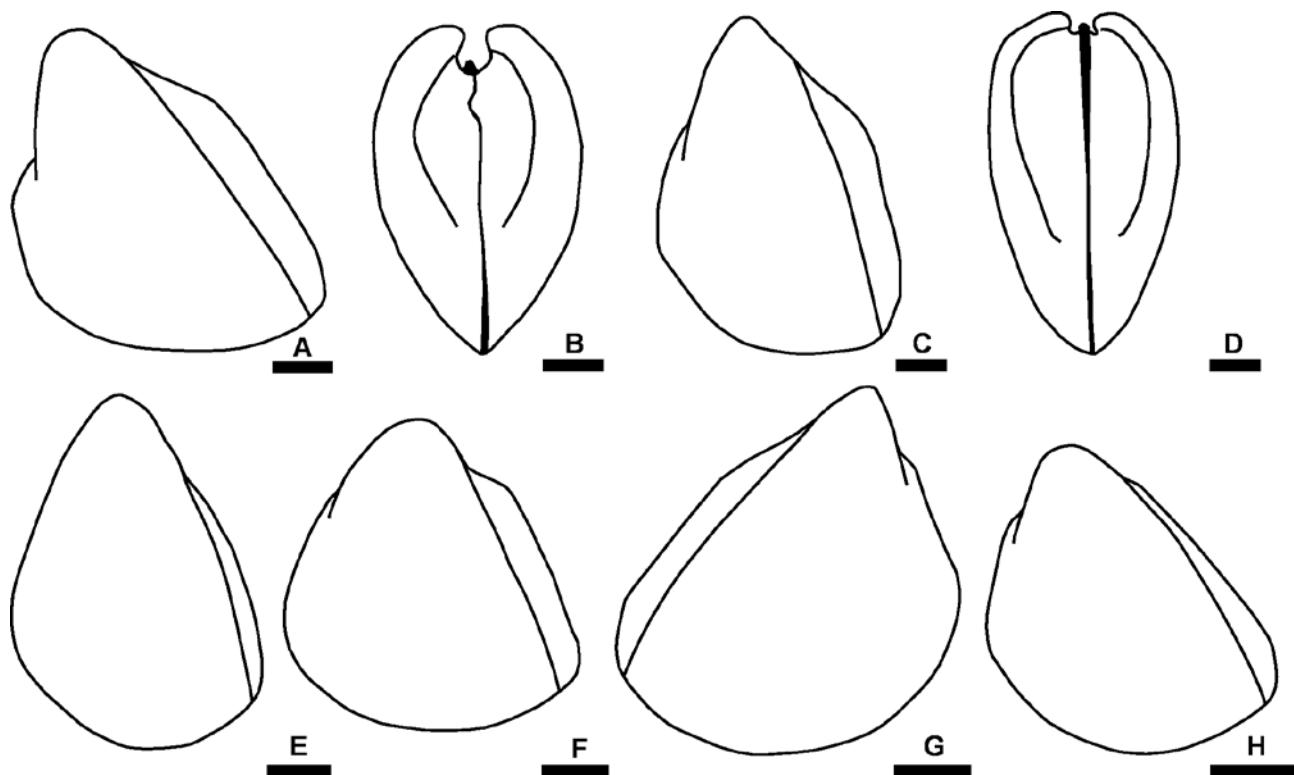


Fig. 11: A-H. Variation in outline of *Protocardia (Pachycardium) pauli* (Coquand, 1862) from different localities. A-B, NRM-PZ Mo168268; C-D, NRM-PZ Mo168267; E, NRM-PZ Mo168265; F, NRM-PZ Mo168263; G, NRM-PZ Mo168262; H, NRM-PZ Mo168260. Cenomanian–Turonian, Sergipe Basin. Scale bars: 10 mm.

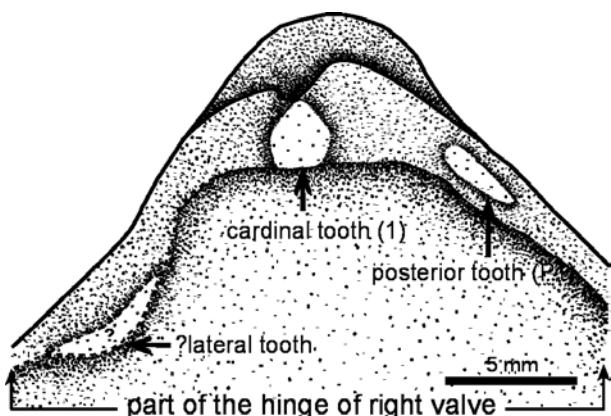


Fig. 12: Hinge of right valve of *Protocardia (Pachycardium) pauli* (Coquand, 1862) showing strong cardinal tooth and an elongate posterior lateral tooth (NRM-PZ Mo168268). Locality Cruzes 6, upper Cenomanian, Sergipe Basin.

Hinge of right valve incompletely preserved but carrying a strong cardinal tooth with elongated posterior lateral tooth (Fig. 12; Pl. V, figs D-E). Anterior adductor muscle scar small, circular, located near antero-ventral margin. Posterior third of flank ornamented with faint radial ribs (Pl. IV, fig. O). Anterior and middle parts ornamented with numerous fine, irregular commarginal ribs, well

developed towards ventral margin and separated by wide and smooth interspaces.

Discussion: Although the outline of *Protocardia (Pachycardium) pauli* (Coquand, 1862) is highly variable (Fig. 11), histogram analysis indicates that all varieties belong to the same species (Fig. 13C).

Protocardia regulare Coquand, 1862, from the lower Cenomanian of Algeria (Coquand, 1862, p. 205, pl. 10, figs 13-14) differs in being smaller and in having well-developed commarginal and radial ribs. The co-occurring *P. triangulare* Coquand, 1862 (Coquand, 1862, p. 206, pl. 11, figs 1-2) closely resembles *P. (P.) pauli* in having a trigonal valve, narrow, trigonal umbones, sharp beaks and a well-developed posterior umbonal ridge but differs in being less inflated and in having well-developed commarginal ribs and a straight anterior margin. However, development of commarginal ribs may be related to the nature of the substrate or other environmental factors. Because *P. (P.) pauli* is a highly variable species (Fig. 13), *P. triangulare* and *P. regulare* may be synonyms. In agreement with Darteville & Freneix (1957, p. 175), *Cardium elongatum* Thomas & Peron, 1890, from the Santonian of Tunisia is considered a junior synonym of *P. (P.) pauli*. *Protocardium delicatulum* Stoliczka, 1870, from the Turonian–Campanian of South India (Stoliczka, 1870, p. 220, pl. 13, fig. 8) resembles *P. (P.) pauli* in ornamentation but differs in having a less

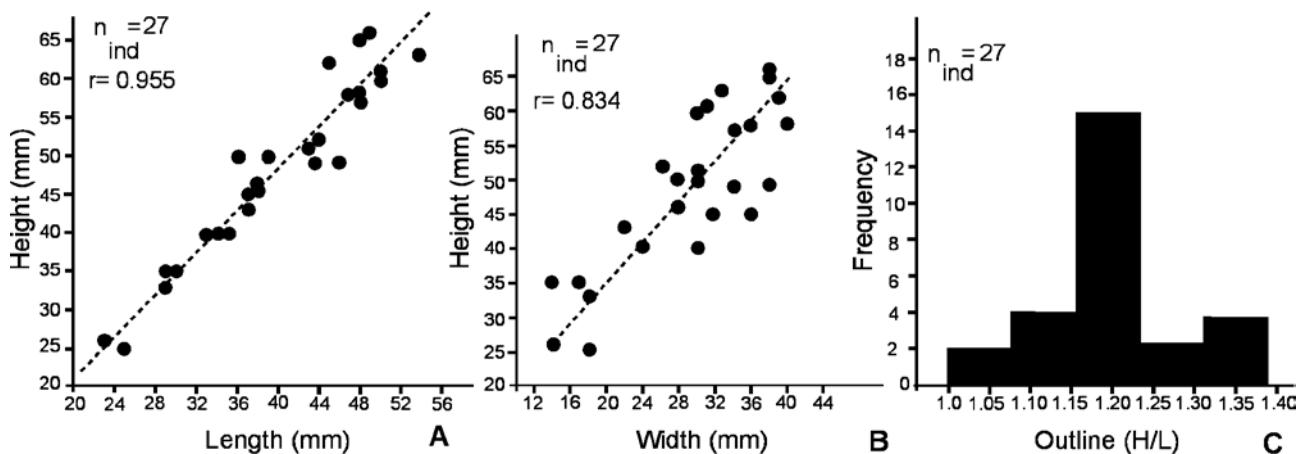


Fig. 13: *Protocardia (Pachycardium) pauli* (Coquand, 1862). A, length/height ratio; B, width/height ratio; C, histogram of the height/length ratio (outline) and number of individuals (frequency). Cenomanian–Turonian, Sergipe Basin.

elongate valve (subquadrate), a strongly rounded anterior margin and a less truncated posterior margin. Forbes (1846, p. 145, pl. 15, fig. 13) and Stoliczka (1870, p. 221, pl. 12, figs 1-3) recorded *P. altum* (G. B. Sowerby, 1853) from the Aptian–Santonian of South India, a species that differs from *P. (P.) pauli* in its narrow anterior margin, well-developed commarginal ribs that become abruptly weak dorsally and in its less elongate and much more inflated shell. *Cardium (Protocardia) coquandi* Seguenza, 1882, from the Cenomanian of Tunisia (Pervinquier, 1912, p. 266, pl. 19, fig. 22) closely resembles *P. (P.) pauli* in outline and the narrow umbones but differs in having thick commarginal ribs and in being less elongate ($H/L=1.05$, as opposed to a mean of 1.31). *Isocardia branneri* White, 1887, from the middle Albian–lower Cenomanian of the Sergipe Basin (White, 1887, p. 83, pl. 6, figs 18-20; Bengtson, 1983, table 2) differs in being less elongate and in having less incurved umbones and a straight anterior margin. Specimen 451.70 (renumbered here NRM-PZ Mo168305), figured by Seeling (1999, pl. 5, fig. 2) as *P. (P.) pauli* from the upper Cenomanian of locality Timbó 5, differs in having a truncated posterior margin, strongly inflated valves, triangular and elevated umbones and is here assigned to *Granocardium (G.) tenuistriatum* (Whitfield, 1885).

Occurrence: Cenomanian of Algeria (Coquand, 1862), Tunisia (Pervinquier, 1912), Egypt (Greco, 1919), Syria (Blanckenhorn, 1934); Albian of Morocco (Benzaggagh, 2016); Turonian–Campanian of Cameroon and Gabon (Riedel, 1933; Darteville & Freneix, 1957; Musavu Moussavou, 2015) and India (Jaitly & Mishra, 2009); Santonian of Tunisia (Thomas & Peron, 1890); Cenomanian–Turonian of the Sergipe Basin (Lefranc in Bengtson, 1983; Seeling, 1999; Andrade & Santos, 2011; this study).

Protocardia (Pachycardium) cf. moevusi (Coquand, 1862)

Fig. 14; Pl. V, figs F-G

cf. 1862. *Isocardia Mœvusi* H. Coq.– Coquand, p. 210, pl. 10, figs 3-4.

cf. 1912. *Mactra Mœvusi* Coquand.– Pervinquier, p. 281, pl. 20, figs 18-19.

Material. Two poorly preserved composite moulds (NRM-PZ Mo168297–168298) from the lower–middle Turonian of localities Laranjeiras 10 and Retiro 15, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 21.

Description: Shell medium-sized, triangular, inequilateral, strongly inflated and slightly produced posteriorly (Fig. 14A-B). Anterior margin narrow, slightly convex and lower than posterior margin. Ventral margin broad and slightly convex. Umbones triangular, narrow and strongly inflated (Pl. V, fig. G). Beak small, sharply pointed, slightly prosogyrate (Fig. 14B). Posterior umbonal ridge well developed, straight, separated from rest of valve by a narrow posterior flank. Faint radial ribs, moderately well developed near ventral margin (Fig. 14A).

Discussion: The Brazilian specimens closely resemble *Isocardia moevusi* Coquand, 1862, from the Upper Cretaceous of Algeria in their narrow umbones, sharply pointed beaks (Pl. V, fig. G), well-developed posterior umbonal ridge and strongly inflated valve but differ in being smaller ($L=17.5$, $H=14$ mm on average, as opposed to $L=45$, $H=35$ mm). In addition, the specimens are ornamented with faint radial ribs near the ventral margin. *Protocardia (Pachycardium) moevusi* shows some similarities to *P. (P.) pauli* (Coquand, 1862) in general outline and curvature of umbones but differs in being smaller, less elongate and in having strongly inflated valves and narrow umbones. *Isocardia branneri* White, 1887, from

Table 21: Dimensions (in mm) of *Protocardia (Pachycardium) cf. moevusi* (Coquand, 1862).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168297	21.0	16.0	?20.0	0.76	?0.95
NRM-PZ Mo168298	14.0	12.0	--	0.86	--
Range	14-21	12.0-16	?18	0.76-0.86	?0.86
Mean	17.5	14.0	?18	0.81	?0.86

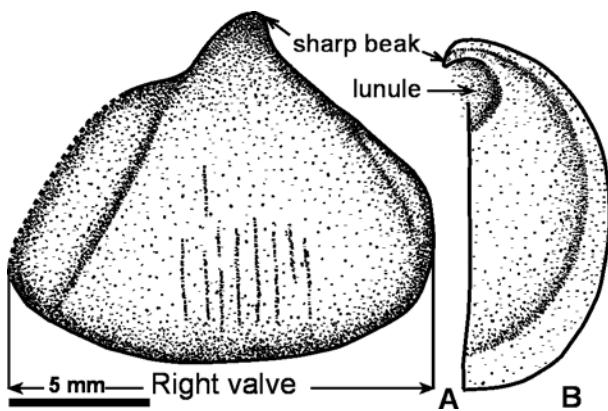


Fig. 14: Right valve of *Protocardia (Pachycardium) cf. moevusi* (Coquand, 1862) (NRM-PZ Mo168297). A, faint radial ribs and well-developed posterior umbonal ridge; B, strongly inflated valve with a sharply pointed beak. Locality Retiro 15, middle–upper Turonian, Sergipe Basin.

the middle Albian–lower Cenomanian of the Sergipe Basin (Maury, 1937, p. 67, pl. 9, figs 5-7, 10) resembles *P. (P.) moevusi* in having a slightly rounded ventral margin and inflated valves but differs in being less inflated and in having faint commarginal ribs and wider umbones, which are located more anteriorly than in *P. (P.) moevusi*. *Isocardia coutinhoana* White, 1887, from the middle Albian of Sergipe (Maury, 1937, p. 69, pl. 9, figs 1-4) resembles *P. (P.) moevusi* in being inflated and in having sharp and slightly prosogyrate beaks but differs in having strongly rounded margins, wide umbones and in being larger (L= 32, H= 30, W= 25 mm).

Occurrence: *Protocardia (Pachycardium) moevusi* (Coquand, 1862) has been recorded from the Upper Cretaceous of Algeria (Coquand, 1862) and the Coniacian of Tunisia (Pervinquier, 1912) and here provisionally from the Turonian of the Sergipe Basin (first record).

Clade Eucardiids J. Schneider, 1995

Subfamily Cardiinae Lamarck, 1809

Tribe Cardiini Lamarck, 1809

Genus *Granocardium* Gabb, 1868

Type species: *Cardium carolinum* d'Orbigny, 1844, by subsequent designation of Stewart (1930).

Subgenus *Granocardium* Gabb, 1868

Granocardium (Granocardium) productum
(J. de C. Sowerby, 1832)
Pl. V, figs H-L

1832. *Cardium productum*— J. Sowerby in Sedgwick & Murchison, p. 347, pl. 39, fig. 15.
 1850. *Cardium Olisiponense*, n. s.— Sharpe, p. 181, pl. 14, fig. 4.
 1864. *Cardium productum* Sow.— Zittel, p. 37 [141], pl. 6, fig. 1.
 1870. *Card. [Trachycardium] productum*, Sowerby.— Stoliczka, p. 217, pl. 11, figs 15-16.
 p 1889. *Granocardium productum* Sow.— Holzapfel, p. 174, pl. 17, fig. 3, non figs 1-2, 4-5.
 1890. *Cardium subproductum* Thomas & Peron.— Thomas & Peron, p. 273, pl. 28, figs 13-14.
 1912. *Cardium (Trachycardium) productum* J. de C. Sowerby.— Pervinquier, p. 259, pl. 19, fig. 25.
 1912. [*Cardium (Trachycardium) productum* J. de C. Sowerby var.] *Byzacenica*.— Pervinquier, p. 259, pl. 19, figs 26-27.
 1934. *Granocardium productum* Sow. sp.— Andert, p. 254, pl. 12, figs 10-11.
 1937. *Cardium (Trachycardium) productum* Sow.— Trevisan, p. 102.
 1957. *Granocardium (Granocardium) productum* (Sowerby).— Darteville & Freneix, p. 168, pl. 28, figs 8-10; pl. 29, fig. 1.
 1958. *Cardium (Trachycardium) productum* J. de C. Sowerby.— Barber, p. 26, pl. 9, figs 2a-b, 3.
 1971. *Trachycardium productum* J. de C. Sow. var. *byzacenica* Perv.— Collignon, p. 183, pl. H, fig. 10.
 1974. *G. productum* (Sowerby).— Oekentorp & Siegfried, p. 157, pl. 15, fig. 9.
 1986. *Granocardium (Criocardium) productum* (Sowerby, 1832).— Abdel-Gawad, p. 169, pl. 40, figs 6-7.
 1987. *Granocardium productum* (J. Sowerby, 1832).— Dhondt, p. 77, pl. 4, figs 5-6.
 1993. *Granocardium productum* (J. de C. Sowerby, 1832).— Dhondt & Dieni, p. 229, pl. 14, figs 4-9b.
 1994. *Granocardium cf. productum* (J. de C. Sowerby, 1832).— Malchus et al., p. 133, pl. 4, fig. 1.
 2004. *Granocardium hassani* Abbass.— Abdel-Gawad et al., pl. 2, fig. 11.
 2004. *Granocardium* sp.— Abdel-Gawad et al., pl. 2, fig. 12.
 2006. *Granocardium productum* (J. de C. Sowerby, 1832).— El Qot, p. 77, pl. 16, figs 2b-3.
 2006. *Granocardium (Criocardium?)* sp. — Perrilliat et al., p. 101, figs 19-24.

2012. *Granocardium productum* (J. de C. Sowerby, 1832).—Benyoucef *et al.*, pl. 3, fig. 8.
2013. *Granocardium productum* (J. De C. Sowerby, 1832).—El Qot *et al.*, p. 218, pl. 5, fig. 4.
2013. *Granocardium productum* (J. Sowerby).—Musavu Moussavou *et al.*, p. 4, fig. 3/10-14.
2014. *Granocardium (Granocardium) productum* (J. de C. Sowerby 1832).—Ayoub-Hannaa *et al.*, p. 114, pl. 10, figs 5-6.
2014. *Granocardium productum* (J. De C. Sowerby, 1832).—Hewaidy *et al.*, p. 225, pl. 2, fig. 8a-b.
2015. *Granocardium productum* (J. de C. Sowerby).—Nagm, p. 15, fig. 6J.
2018. *Granocardium (Granocardium) productum* (J. de C. Sowerby, 1832).—Aouissi *et al.*, p. 19, fig. 5.11.

Material: Four composite moulds (NRM-PZ Mo 168299–168302) from the lower Cenomanian to upper Turonian of localities Itaporanga 2/3, Japaratuba 14, Pedro Gonçalves 2 and Mucuri 10, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 22.

Description: Shell medium to large, variable in outline, elongate ovate to subquadrate, higher than long ($H/L=1.36$ on average), equivalved, slightly inequilateral and moderately inflated ($W/L=c. 0.98$ on average). Maximum inflation slightly above mid-height of valve. Dorsal margin slightly arched with squarish shoulders (Pl. V, fig. I). Anterior and posterior margins subtruncated, meeting ventral margin in rounded angles. Ventral margin crenulated and regularly rounded. Lunule ovate, small and shallow. Umbones triangular, strongly convex, located mesially. Beaks small, sharply pointed, slightly prosogyrate (Pl. V, fig. K). Hinge short and straight. Ornament consisting of numerous, well-developed, spinose radial ribs (55–60; Pl. V, fig. L) varying in strength and separated by narrow interspaces bearing sparse tuberculated riblets.

Discussion: *Granocardium (G.) productum* (J. de C. Sowerby, 1832) is distinguished from other cardiid species from Sergipe by its elongate ovate to subquadrate valves, strongly convex umbones, numerous spinose, unequal, fine, radial ribs, small beaks and small and shallow lunule.

Cardium olisiponensis Sharpe, 1850, from the Cenomanian of Portugal and *Cardium subproductum* Thomas

& Peron, 1890, from the Turonian of Tunisia are very similar to *G. (G.) productum* in general outline, ornamentation and shell inflation and are here considered junior synonyms. Holzapfel (1889) identified well-preserved specimens from the Maastrichtian of Germany as *G. productum*; however, his figured specimens (except fig. 3) differ from *G. productum* in having strong and fewer radial ribs, a truncated and crenulated posterior margin and in being more rounded and wider ($H/L=1.09$, as opposed to 1.48). Dhondt (1987, p. 79) remarked that Holzapfel's specimens are almost identical with *Cardium kuemmelii* (Weller, 1907) as illustrated by Wade (1926, pl. 26, figs 5-6) from the upper Campanian of Tennessee, USA, but assigned them provisionally to *G. productum*. *Cardium (G.) deltatum* Stephenson, 1941, and *C. (G.) bowenae* Stephenson, 1941, from the Maastrichtian of Texas (Stephenson 1941, p. 196, pl. 35, figs 1-4; p. 198, pl. 34, figs 10-12) closely resemble *G. (G.) productum* in general outline and valve inflation but their ornamentation appears somewhat different. Because the appearance of the ribs mainly depends on the preservation, Stephenson's species are probably varieties of *G. (G.) productum*. *Cardium mermeti* Coquand, 1862, from the Upper Cretaceous of Algeria (Coquand, 1862, p. 207, pl. 11, figs 6-7) differs in having strong radial ribs, narrower umbones and in being larger.

Occurrence: Aptian–Turonian of South India (Stoliczka, 1870); Cenomanian of Portugal (Sharpe, 1850) and Algeria (Collignon, 1971; Benyoucef *et al.*, 2012; Aouissi *et al.*, 2018); Cenomanian–Santonian of Egypt (e.g., Fourtau, 1917; Abdel-Gawad *et al.*, 2004; El Qot, 2006; Ayoub-Hannaa *et al.*, 2014; Hewaidy *et al.*, 2014); Libya (El Qot *et al.*, 2013), Cenomanian–“Senonian” of Cameroon, Congo, Angola and Gabon (Dartevelle & Freneix, 1957; Musavu Moussavou *et al.*, 2013); Turonian of Jordan, Tunisia and Nigeria (Perrilliat *et al.*, 2006; Thomas & Peron, 1890; Pervinquier, 1912; Barber, 1958); Coniacian–lowermost Campanian of Italy (Trevisan, 1937; Dhondt & Dieni, 1993); Santonian of Austria (Dhondt, 1987); Campanian of Germany and France and northwestern Europe (Holzapfel, 1889; Andert, 1934; Oekentorp & Siegfried, 1974); Maastrichtian of Poland (Abdel-Gawad, 1986); Santonian of SE Belgium (Malchus *et al.*, 1994); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

Table 22: Dimensions (in mm) of *Granocardium (Granocardium) productum* (J. de C. Sowerby, 1832).

Specimen	L	H	W	nr.	H/L	W/L
NRM-PZ Mo168299	30.0	48.0	33.0	60	1.60	1.10
NRM-PZ Mo168300	47.0	64.0	35.0	--	1.36	0.94
NRM-PZ Mo168301	37.0	49.0	16 (LV)	--	1.32	?0.94
NRM-PZ Mo168302	32.0	37.0	15 (RV)	55	1.15	?0.93
Range	30-47	37-64	33-35	55-60	1.15-1.60	?0.93-1.10
Mean	36.5	49.5	34.0	57.5	1.36	?0.98

Granocardium (Granocardium) tenuistriatum
(Whitfield, 1885)

Pl. V, figs M-O; Pl. VI, figs A-D

1885. *Cardium (Criocardium) dumosum*.— Whitfield, p. 133, pl. 20, figs 9-10, 13(?).
1885. *Cardium (Criocardium) multiradiatum*.— Whitfield, p. 135, pl. 21, figs 1-3.
1885. *Fragum tenuistriatum* n. sp.— Whitfield, p. 139, pl. 20, figs 15-16.
1907. *Cardium tenuistriatum* (Whitfield).— Weller, p. 591, pl. 65, figs 13-19.
1926. *Cardium tenuistriatum* (Whitfield).— Wade, p. 84, pl. 26, fig. 4.
1958. *Cardium tenuistriatum* Whitfield 1886.— Richards, p. 211, pl. 32, fig. 10.
- v 1999. *Protocardia (Protocardia) pauli* (Coquand, 1862).— Seeling, p. 125, pl. 5, fig. 2. [pl. 5, fig. 3 = *P. (P.) pauli* (Coquand, 1862)].

Material: Six composite moulds (NRM-PZ Mo168303–168308) from the lower–upper Cenomanian of localities Itaporanga 2, 2/3 and 4 and Timbó 5, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 23.

Description: Shell medium-sized, subovate to subtrapezoidal in lateral view, cordate in anterior view, nearly equilateral, equivalved, slightly higher than long ($H/L=1.13$ on average) and moderately inflated ($W/L=0.85$ on average; Table 23). Dorsal margin arched with squarish shoulders (Pl. V, fig. M). Posterior margin vertically truncated, almost perpendicular to ventral margin (Pl. V, fig. N; Pl. VI, figs A, B). Anterior margin short, regularly rounded, meeting ventral margin in rounded angle. Ventral margin regularly convex and weakly crenulated. Umbones triangular, elevated above hinge, strongly convex, located slightly posterior to mid-length of valve. Beaks sharply pointed and slightly prosogyrate. Posterior umbonal ridge well developed. Anterior adductor muscle scar large, rounded, located close to antero-dorsal margin (Pl. V, fig. O). Posterior adductor muscle scar subrounded, located close to postero-dorsal margin. Ornament consisting of numerous irregular, fine, radial ribs separated by narrow interspaces bearing faint radial tubercles near the ventral margin.

Discussion: *Granocardium (G.) tenuistriatum* (Whitfield, 1885) is distinguished from other cardiid species by its

vertically truncated posterior margin, strongly inflated valves, numerous fine, irregular, radial ribs with narrow interspaces and rounded anterior and crenulate ventral margin.

Cardium (Criocardium) dumosum Conrad, 1870, and *C. (C.) multiradiatum* Gabb, 1860, as figured and described by Whitfield (1885) from the upper Cretaceous of New Jersey, closely resemble *G. (G.) tenuistriatum* in general outline, shell size, inflation and ornamentation and are here regarded as conspecific with the latter species. *Cardium (Nemocardium) brasiliense* White, 1887, from the middle Albian of the Sergipe Basin (White, 1887, p. 91, pl. 6, figs 3-4) resembles *Granocardium (G.) tenuistriatum* with respect to ribbing but differs in having a less truncated posterior margin, a short anterior margin, narrow umbones, less inflated valves ($W/L=0.63$, as opposed to a mean of 0.85) and lacking a posterior umbonal ridge. *Cardium amphitrites* Maury, 1925, from the Turonian of the Potiguar Basin, Brazil (Maury, 1925, p. 549, pl. 22, fig. 13) differs in having numerous well-developed radial ribs and in being larger ($L=63$ mm), more elongate ($H/L=0.92$, as opposed to a mean of 1.13) and less inflated ($W/L=0.35$, as opposed to a mean of 0.85; Table 23). *Granocardium (G.) carolinum* (d'Orbigny, 1844) from the Upper Cretaceous of France (d'Orbigny, 1844, p. 245) and the Cenomanian of Algeria (Collignon & Roman, 1983, p. 75, pl. 1, figs 1-2) closely resembles *G. (G.) tenuistriatum* in general outline and ornamentation but differs in being less inflated ($W/L=0.71$, as opposed to a mean of 0.85) and in having less incurved beaks and narrow umbones. *Cardium (Pectunculus?) scrobiculatum* Stoliczka, 1870, from the Coniacian–Santonian of South India (Stoliczka, 1870, p. 219, pl. 11, fig. 14) differs from *G. (G.) tenuistriatum* in being smaller ($H=17$, $L=17$ mm) and in having well-rounded margins. *Cardium kuemmeli* Weller, 1907, from the Campanian of New Jersey, USA (Weller, 1907, p. 585, pl. 66, figs 1-3) differs in having a slightly rounded posterior margin and fewer, thick, spinose radial ribs with narrow interspaces. *Cardium uniformis* Weller, 1907, from the same beds (Weller, 1907, p. 588, pl. 65, figs 1-3) differs in being less inflated and in having narrow umbones, nearly straight anterior margin, strongly crenulated ventral margin and regular radial ribs. Because the appearance of the ribs depends mainly on preservation, Weller (1907, p. 591) and Wade (1926, p. 84) regarded *C. eufaulensis* of Whitfield (1885,

Table 23: Dimensions (in mm) of *Granocardium (Granocardium) tenuistriatum* (Whitfield, 1886).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168303	35.0	43.0	33.0	1.23	0.95
NRM-PZ Mo168304	40.0	42.0	34.0	1.05	0.85
NRM-PZ Mo168305	38.0	42.0	28.0	1.10	0.74
Range	35.0-40.0	42.0-43.0	28.0-34.0	1.05-1.23	0.74-0.95
Mean	37.67	42.33	31.67	1.13	0.85

p. 132, pl. 20, figs 18-19), *C. (Criocardium) dumosum* of Whitfield (1885, p. 133, pl. 20, figs 10-20) and *C. (C.) multiradiatum* of Whitfield (1885, p. 135, pl. 21, figs 1-3) from the Upper Cretaceous of the USA as conspecific with *G. (G.) tenuistriatum*.

Occurrence: Campanian of New Jersey, USA (Whitfield, 1885; Weller, 1907; Richards, 1958); Campanian–Maastrichtian of the south-eastern USA (Wade, 1926); Cenomanian of the Sergipe Basin (this study, first record).

Subfamily *Fraginae* R. Stewart, 1930

Tribe *Fragini* R. Stewart, 1930

Genus *Fragum* Röding, 1798

Type species: *Cardium fragum* Linnaeus, 1758.

Remarks: The genus *Fragum* is characterised by variably sized triangular valves with prosogyrate umbones, a well-developed posterior umbonal ridge, which separates a flat to slightly concave posterior flank from the rest of the shell, deeply serrated or crenulated margins, a short hinge, a poorly developed lunule and escutcheon, and ornament consisting of well-developed radial ribs, often bearing tubercles, and separated by narrow interspaces. For more details on the diagnostic characters of the genus *Fragum*, see Wilson & Stevenson (1977, p. 36).

Although *Fragum* has been mainly recorded from Miocene or younger rocks, the genus is also known from the Turonian of Cameroon (Dartevelle & Freneix, 1957, p. 173) and here from the Sergipe Basin.

Subgenus *Fragum* Röding, 1798

Fragum (Fragum) cf. perobliquum

(von Koenen, 1897)

Pl. VI, figs E-F

- cf. 1897. *Cardium perobliquum* v. Koenen.– Koenen, p. 33, pl. 4, fig. 3.
- cf. 1933. *Cardium perobliquum* v. Koen.– Riedel, p. 51, pl. 8, fig. 6.
- cf. 1957. *Fragum perobliquum* (Koenen).– Dartevelle & Freneix, p. 172, pl. 29, figs 4-5.
- 1983. *Fragum perobliquum* (von Koenen).– Lefranc in Bengtson, p. 19, table 2.

Material: Three incomplete specimens (NRM-PZ Mo168309–168311) from the lower–middle Turonian of localities Pedra Furada 3, 4 and 13, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 24.

Description: Shell small, triangular, inequilateral, higher than long ($H/L=1.55$ on average) and strongly inflated. Posterior margin subtruncated. Anterior margin rounded, meeting ventral margin in rounded angle. Posterior umbonal ridge weakly developed, separating steeply oblique and slightly concave posterior flank from rest of valve (Pl. VI, fig. F). Umbones triangular, elevated above hinge line, moderately inflated, located one-third of the valve length from the anterior end. Beaks prominent, prosogyrate. Ornament consisting of numerous (18-28), tuberculated radial ribs separated by narrow, deep interspaces. Posterior flank covered with fine radial tubercles, becoming coarser towards ventral margin.

Discussion: The Brazilian specimens are very similar to *Fragum perobliquum* from the lower Turonian of Cameroon (Riedel, 1933; Dartevelle & Freneix, 1957) in general outline, ornamentation and in having a well-developed posterior ridge but differ in being smaller ($H=10.7-11.4$ mm, as opposed to $H=16.5-21.0$ mm in Dartevelle & Freneix, 1957, p. 172). Therefore, they are here provisionally assigned to *F. (Fragum) perobliquum*. *Fragum subperobliquum* (Riedel, 1933) from the Coniacian(?) to Campanian of Cameroon (Riedel, 1933, p. 52, pl. 3, figs 2-5) closely resembles *F. perobliquum* in general outline but differs in having fewer, well-developed, spinose radial ribs, separated by wide, deep, smooth interspaces. It also differs in being strongly inflated, much taller and larger than *F. perobliquum*. *Cardium (Trachycardium) riachuelense* Maury, 1937, from the middle Albian of the Sergipe Basin (Maury, 1937, p. 73, pl. 5, fig. 10) differs in having thicker and fewer radial ribs (15) and in being less inflated. In addition, the radial ribs of Maury's specimens are spinose, thick posteriorly and fine anteriorly and separated by wide interspaces with fine intercalatories.

Occurrence: *Fragum (Fragum) perobliquum* (von Koenen, 1897) has been recorded from the Turonian of Cameroon (Koenen, 1897; Riedel, 1933; Dartevelle & Freneix, 1957) and here provisionally from the Turonian of the Sergipe Basin (Lefranc in Bengtson, 1983; Bengtson, 1983; this study).

***Fragum* sp.**

Pl. VI, figs G-H

v 1999. *Granocardium?* sp.– Seeling, p. 124, pl. 4, fig. 23.

Table 24: Dimensions (in mm) of *Fragum (Fragum) cf. perobliquum* (Koenen, 1897)

Specimen	L	H	W	nr	H/L	W/L
NRM-PZ Mo168309	7.2	11.4	3.8 (RV)	28	1.58	?1.05
NRM-PZ Mo168310	7.0	10.7	3.5 (RV)	18	1.53	?1.0
Range	7.0-7.2	10.7-11.4		18-28	1.53-1.58	1.0-1.05
Mean	7.1	11.05		23	1.55	1.02

Material: One incomplete right valve (NRM-PZ Mo168312) from the lowermost Turonian of locality Japaratuba 16, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 25.

Description: Shell medium-sized, ovate, inequilateral and moderately inflated. Ventral margin rounded, meeting posterior margin in obtuse angle. Umbones moderately inflated and located slightly anterior to mid-length of valve. Posterior umbonal ridge weakly developed, separating posterior flank from rest of valve. Ornament consisting of numerous, well-developed, tuberculated radial ribs. Towards posterior and dorsal margins ribs becoming fine, spinose and separated by narrow, deep interspaces (Pl. VI, fig. H).

Discussion: The Brazilian specimen closely resembles *Cardita beaumonti* d'Archiac & Haime, 1854, from the Upper Cretaceous of Cameroon (Riedel, 1933, p. 47, pl. 2, fig. 2) in having numerous tuberculated radial ribs (finer dorsally and posteriorly) and a rounded anterior margin, but differs in being larger ($L=36$, $H=45$ mm, as opposed to $L=22$, $H=22$ mm) and more elongate. *Fragum subperobliquum* (Riedel, 1933) from the Coniacian(?) to Campanian of Cameroon (Riedel, 1933, p. 52, pl. 3, figs 2-5) differs in having fewer and thicker radial ribs, near-mesial umbones, a well-developed posterior umbonal ridge and in being smaller. *Fragum praecurrens* Stoliczka, 1870, from the Aptian-Turonian of South India (Stoliczka, 1870, p. 222, pl. 11, figs 1-2) differs in being longer ($L>H$) and in having fewer radial ribs (crossed by commarginal ribs, thereby forming a reticulate pattern) and strongly prosogyrate umbones.

Occurrence: Turonian of the Sergipe Basin (this study).

Superfamily Tellinoidea de Blainville, 1814

Family Tellinidae de Blainville, 1814

[= Macominae Olsson, 1961;

= Arcopagiinae Kuroda, Habe & Oyama, 1971;

= Strigillinae Habe, 1977]

Genus *Arcopagella* Meek, 1871

Type species: *Arcopagella mactroides* Meek, 1871.

Remarks: Meek (1871, p. 309) erected the genus *Arcopagella* on the basis of its (1) longitudinally subovate

and moderately inflated shell (height approximately two-thirds of length), (2) deep, broadly rounded pallial sinus, (3) rounded and narrow anterior margin, (4) large anterior area (wider than the posterior area), (5) broadly convex posterior margin meeting the postero-dorsal and ventral margins in rounded curves, (6) moderately prominent, subcentral beaks and (7) numerous faint growth lines. The genus *Palaeomoera* Stoliczka (1870, p. 129; type species *Tellina strigata* Goldfuss, 1840) differs in being strongly elongate and in having a reticulate rib pattern. *Arcopagella* is somewhat similar to the genus *Tellina* (*Arcopagia*) but differs in the hinge structure.

Arcopagella sp.

Pl. VI, figs I-J

Material: One articulated composite mould (NRM-PZ Mo168313) from the middle-upper Cenomanian of locality Cruzes 6, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 26.

Description: Shell medium-sized, elongate ovate, wedge-shaped, inequilateral, equivalved and moderately inflated ($W/L=0.47$). Anterior area longer than posterior area (Pl. VI, fig. J). Postero-dorsal margin broad, convex, higher than antero-dorsal margin, meeting posterior margin in rounded curve. Antero-dorsal margin slightly convex, long and slightly oblique anteriorly. Anterior margin narrow, strongly rounded, meeting ventral margin in rounded curve. Posterior margin narrower than anterior margin, strongly convex, meeting ventral and postero-dorsal margins in rounded curves. Ventral margin broad and irregularly rounded. Umbones wide, moderately convex, located slightly posterior to mid-length. Beaks moderately prominent, slightly prosogyrate. Ornament consisting of irregular, ventrally well-developed growth lines (Pl. VI, fig. J).

Discussion: The Brazilian specimen is very similar to the type species *A. mactroides* Meek, 1871, from the Upper Cretaceous of the Western Interior Basin, USA (Meek, 1871, p. 309, figs A-B) in general outline, size and inflation ($L=20$, $H=13$, $W=7$ mm; $L=19$, $H=13$, $W=9$ mm for the Brazilian specimen). *Tellina* (*Palaeomoera*) *inconspicua* Broderip & G.B. Sowerby, 1829, from the

Table 25: Dimensions (in mm) of *Fragum* sp.

Specimen	L	H	W	nr	H/L	W/L
NRM-PZ Mo168312	36.0	?45.0	--	>40	?1.25	--

Table 26: Dimensions (in mm) of *Arcopagella* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168313	19.0	13.0	9.0	0.68	0.47

Coniacian–Santonian of South India (Stoliczka, 1870, p. 129, pl. 4, figs 6–8) resembles the Brazilian specimen in having a narrowly rounded anterior margin, strongly rounded postero-dorsal margin and moderately prominent beaks but differs in its numerous, fine commarginal ribs and in being larger and more compressed. *Tellina strigata* Goldfuss, 1840, from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 159, pl. 11, figs 6–10) differs in having numerous, fine radial ribs crossed by commarginal ribs (forming a reticulate pattern). In addition, the latter species has a well-developed posterior umbonal ridge, is larger but has less inflated valves ($W/L=0.32$, as opposed to 0.47). *Tellina reichii* Roemer, 1841, from the Upper Cretaceous of Germany (Roemer, 1841, p. 73, pl. 9, fig. 26) differs in being less elongate and in having a concave antero-dorsal margin and compressed valves.

Occurrence: Cenomanian of the Sergipe Basin (this study).

Genus *Tellinimera* Conrad, 1860

Type species: *Tellinimera eborea* Gardner, 1916.

***Tellinimera?* sp.**

Pl. VI, fig. K

v 1999. *Tellinimera?* sp.– Seeling, p. 126, pl. 5, fig. 5.

Material: Six composite moulds (NRM-PZ Mo168314–168319) from the middle–upper Cenomanian of localities Cruzes 6 and Jardim 1, 10 and 24, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 27.

Description: Shell medium-sized, ovate and subequilateral, compressed ($W/L=0.29$). Postero-dorsal margin slightly convex, meeting posterior margin in obtuse angle. Antero-dorsal margin nearly straight. Anterior and posterior margins convex, meeting regularly convex ventral margin in rounded curves. Anterior umbonal ridge faint. Umbones broad, weakly inflated and slightly prosogyrate, located at midlength of valve. Ornament consisting of numerous fine commarginal striae (Pl. VI, fig. K).

Discussion: As stated by Seeling (1999), the external features and overall appearance of the Brazilian specimens

allow a provisional assignment to the genus *Tellinimera* Conrad. The lack of information on internal features makes a generic determination doubtful. The specimens also show similarities to representatives of the genus *Hercodon* Conrad in Kerr, 1875, but the latter genus has faint radial ribs. Species of the genus *Aenona* Conrad, 1870, also resemble the Brazilian specimens but differ in being more compressed, more inequilateral and in having commarginal ornamentation.

The specimens resemble *Tellinimera eborea* Conrad, 1860, from the Upper Cretaceous of Maryland, USA (Gardner, 1916, p. 695, pl. 42, figs 5–6) in style of ornamentation and shell inflation, but the latter species is more elongate and triangular in outline.

Hyporder Veneroidei J. Gray, 1854

Minorder Veneroidei J. Gray, 1854

Superfamily Arcticooidea R. Newton, 1891

(d'Orbigny, 1844)

Family Arcticidae R. Newton, 1891

(d'Orbigny, 1844)

Genus *Arctica* Schumacher, 1817

Type species: *Arctica vulgaris* Schumacher, 1817 (= *Venus islandica* Linnaeus, 1767).

***Arctica?* cordata (Sharpe, 1850)**

Pl. VI, figs L–M; Pl. VII, fig. A

1850. *Cyprina cordata*, n. s.– Sharpe, p. 182, pl. 15, fig. 2.

1912. *Cyprina cordata* Sharpe.– Pervinquier, p. 223, pl. 16, figs 1–2.

1917. *Cyprina cordata*, Sharpe 1850.– Fourtau, p. 62.

1919. *Cyprina cordata* Sharpe.– Greco, p. 41 (223).

1934. *Cyprina cordata* Sharp.– Blanckenhorn, p. 248.

1983. *Arctica cordata* (Sharpe).– Collignon & Roman, p. 78, pl. 1, fig. 7.

2006. *Arctica cordata* (Sharpe, 1850).– El Qot, p. 81, pl. 16, figs 10–11.

2014. *Arctica cordata* (Sharpe, 1850).– Hewaidy *et al.*, p. 225, pl. 3, fig. 1a–b.

Material: Two composite moulds (NRM-PZ Mo168320–168321) from the lower–upper Turonian of localities Laranjeiras 22 and Mucuri 10, Cotinguba Formation, Sergipe Basin, Brazil.

Table 27: Dimensions (in mm) of *Tellinimera?* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168314	25.0	19.0	?6.0	0.76	?0.24
NRM-PZ Mo168315	22.0	17.0	--	0.77	--
NRM-PZ Mo168316	27.0	18.0	?9.0	0.67	?0.33
NRM-PZ Mo168317	16.0	13.0	?5.0	0.81	?0.31
Range	16.0–27.0	13–19	5–9	0.67–0.81	?0.24–?0.33
Mean	22.5	16.75	?6.67	0.75	?0.29

Measurements: cf. Table 28.

Description: Shell medium-sized, subrounded, inequilateral and moderately inflated. Antero-dorsal margin concave below umbones. Postero-dorsal margin higher than antero-dorsal margin, slightly convex, meeting posterior margin in rounded curve. Anterior margin narrow, strongly rounded, forming rounded curve with ventral margin. Posterior margin relatively broad, strongly convex, meeting broad and rounded ventral margin in rounded angle. Lunule wide, subcordate and moderately deep. Umbones broad, moderately convex, subterminal, strongly prosogyrate (Pl. VI, fig. L). Beaks moderately prominent, prosogyrate. Ornament consisting of faint commarginal ribs, well developed towards the ventral margin (Pl. VII, fig. A).

Discussion: The Brazilian specimens are articulated and internal characters such as hinge and muscle scars are not seen. Therefore, only a provisional assignment to the genus *Arctica* is possible. The specimens closely resemble *Cyprina cordata* Sharpe, 1850, from the Cenomanian of Portugal (Sharpe, 1850, p. 182) in having rounded margins, subterminal beaks and a wide and subcordate lunule. *Arctica picteti* (Coquand, 1862) from the Cenomanian of Algeria (Coquand, 1862, p. 199, pl. 13, figs 10-11) differs in having a straight postero-dorsal margin and in being strongly elongate ($H/L=0.66$, as opposed to 0.89). *Arctica inornata* (d'Orbigny, 1844) from the Aptian of France (d'Orbigny, 1844, p. 99, pl. 272, figs 1-2) resembles *A. cordata* in having rounded margins but differs in its prominent beaks and shallow antero-dorsal margin.

Occurrence: Cenomanian of Portugal (Sharpe, 1850), Tunisia (Pervinquiére, 1912), Algeria (Collignon & Roman, 1983), Syria (Blanckenhorn, 1934) and Egypt (e.g., Fourtau, 1917; Greco, 1919; El Qot, 2006; Hewaidy et al., 2014); Turonian of the Sergipe Basin (this study, first record).

Genus *Etea* Conrad, 1875

Type species: *Etea carolinensis* Conrad, 1875.

Etea carolinensis Conrad, 1875

Pl. VII, figs B-D

- 1875. *E. Carolinensis*.—Conrad, p. 6, pl. 1, fig. 14.
- 1907. *Etea carolinensis* Conrad.—Weller, p. 541, pl. 59, figs 4-6.
- 1923. *Veniella (Etea) carolinensis* var. *aspera* n. var.—Stephenson, p. 266, pl. 66, figs 13-15.
- 1926. *Etea carolinensis* Conrad.—Wade, p. 81, pl. 25, figs 9-10.

Table 28: Dimensions (in mm) of *Arctica? cordata* (Sharpe, 1850).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168320	48.0	43.0	17.0 (RV)	0.89	?0.71
NRM-PZ Mo168321	52.0	?38.0	26.0	0.74	0.50
Range	48.0-52.0	?38-43	26.0	0.74-0.89	0.50-0.71
Mean	50.0	?40.5	26.0	0.81	0.60

- 1958. *Veniella (Etea) carolinensis* var. *aspera* Stephenson 1923.—Richards, p. 175, pl. 28, figs 6-7.
- 1993. *Crassatella carolinensis* Conrad, 1875.—Wingard, p. 72, pl. 2, fig. 9; pl. 5, figs 5, 8, 11, 13, 15-20.

Material: Two internal and composite moulds (NRM-PZ Mo168322-168323) from the upper Turonian of locality Oiteiro 8, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 29.

Description: Shell medium to large, oblong ovate, strongly inequilateral, posteriorly elongate and moderately inflated. Antero-dorsal margin slightly convex, meeting anterior margin in rounded curve. Postero-dorsal margin straight. Anterior margin broadly convex, meeting ventral margin in rounded angle. Posterior end broken off, slightly rostrate and narrow. Ventral margin faintly rounded anteriorly and straight to slightly concave posteriorly (Pl. VII, fig. C). Posterior umbonal ridge well developed, straight, separating a narrow and concave posterior flank from rest of valve. Umbones broad, moderately convex, located approximately one-third of total valve length from anterior end. Beaks small, orthogyrate to slightly prosogyrate (Pl. VII, fig. B). Faint commarginal ribs present near ventral margin (Pl. VII, fig. D).

Discussion: With respect to general outline, size and ornamentation, the Brazilian specimens are very similar to *Etea carolinensis* Conrad, 1875, from the Upper Cretaceous of North Carolina, USA, and *Veniella (E.) carolinensis* var. *aspera* Stephenson, 1923, from the Upper Cretaceous (Cenomanian?) of New Jersey, USA (Richards, 1958). *Veniella (E.) trapezoidea* Conrad, 1860, from the Upper Cretaceous of New Jersey (Richards, 1958, p. 175, pl. 28, figs 8-9; pl. 29, figs 7, 15) resembles *E. carolinensis* in having a subtruncated posterior margin and numerous, well-developed commarginal ribs but differs in being less elongate and in having a concave antero-dorsal margin, a slightly rounded ventral margin and umbones located slightly anterior to the midline of valve.

Table 29: Dimensions (in mm) of *Etea carolinensis* Conrad, 1875.

Specimen	L	H	Range	Mean
NRM-PZ Mo168322	63.0	42	55.0-63.0	59.0
NRM-PZ Mo168323	55.0	40	42.0-40.0	41.0
			0.66-0.73	0.69

Occurrence: Upper Cretaceous (Cenomanian?) of New Jersey, USA (Weller, 1907; Richards, 1958); Campanian of Georgia, USA (Wingard, 1993) and Campanian–Maastrichtian of Tennessee and Mississippi, USA (Wade, 1926); Turonian of the Sergipe Basin (this study, first record).

Genus *Izumia* Ichikawa & Maeda, 1963

Type species: *Izumia trapezoidalis* Ichikawa & Maeda, 1963.

Remarks: According to Ichikawa & Maeda (1963, p. 122), the genus *Izumia* is characterised by a moderately convex, trapezoidal shell, a wide lunule, lack of an escutcheon, ornament of fine radial striae and a crenulated inner ventral margin. In addition, the hinge of the left valve carries bifid cardinal teeth, one posterior tooth and anterior and posterior lateral teeth. The hinge of the right valve consists of one cardinal tooth (1), anterior and posterior cardinal teeth and two anterior lateral teeth (Ichikawa & Maeda, 1963, p. 122, text-fig. 3a-b). The hinge of *Izumia* resembles the hinge of the genus *Argenticyprina* Lazo & Damborenea, 2011 (type species: *Argenticyprina mulensis* Lazo & Damborenea, 2011, p. 733, figs 10-14 from the Barremian of the Neuquén Basin, Argentina). Superficially, *Argenticyprina* resembles *Izumia* in having a subovate to trapezoidal shell, faint radial ribs and a well-developed posterior umbonal ridge but differs in lacking ventral margin crenulations and in being larger ($L=37.64$, $H=33.87$ mm). *Izumia* is also similar to the genus *Petalocardia* Vincent, 1925 (type species: *Venus?* *pectinifera* J. de C. Sowerby, Eocene of England). *Petalocardia* was originally proposed as a subgenus of *Veniella* Stoliczka, 1870, but should be separated from the latter genus on account of the ventral crenulation and radial ornamentation. *Petalocardia* differs from *Izumia* in having stronger radial ribs with irregular commarginal ribs on the anterior margin and an angulate (not carinate) posterior end. The genus *Pharodina* Stephenson, 1953 (type species: *Pharodina ferrana* Stephenson, 1953, p. 109, pl. 27, figs 1-7) from the Cenomanian of Texas, USA, differs in having a triangular shell, a long, narrow and moderately wide escutcheon and in lacking radial ornamentation.

Izumia? *saussuri* (Brongniart, 1821)

Pl. VII, figs E-G

- 1821. *Donacites Saussuri*.— Brongniart, p. 555, pl. 7, fig. 5.
- 1856. *Cyprina Saussuri* (Brong.).— Pictet & Renevier.— Pictet & Renevier, p. 73, pl. 8, figs 1-2.
- 1865. *Cyprina Saussuri*, (Brongniart) Pictet & Renevier.— Pictet & Campiche, p. 220.
- ? 1906. *Cyprina Saussuri* (Brongniart).— Woods, p. 131, pl. 19, figs 7-13.
- 1921. *Cyprina Saussuri* (Brong.) Pictet & Renevier.— Gillet, p. 16, pl. 2, figs 5-6.
- ? 1931. *Cyprina saussuri* (Brongniart).— Weaver, p. 324.

Material: One internal mould (NRM-PZ Mo168324) from the upper Turonian of locality Mucuri 15, Catinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 30.

Description: Shell medium-sized, trapezoidal, inequilateral, equivalved and moderately inflated ($W/L=0.61$). Antero-dorsal margin short and strongly concave. Postero-dorsal margin broad and straight, higher than antero-dorsal margin, almost perpendicular to posterior margin. Anterior margin narrow and rounded, posterior margin subtruncated, both meeting ventral margin in rounded angles. Ventral margin broad, convex and slightly crenulate. Umbonal posterior ridge weakly developed, extending from postero-dorsal margin to postero-ventral side. Lunule subrounded, wide and deep (Pl. VII, fig. G). Anterior adductor muscle scar large, subrounded, located near antero-dorsal margin. Posterior muscle scar subrounded and slightly larger than anterior one, located near postero-dorsal margin (Pl. VII, fig. F). Umbones broad, inflated, prosogyrate, located approximately one-third of total valve length from anterior end. Beaks small, strongly prosogyrate. Valve with fine radial ribs, well developed ventrally (Pl. VII, fig. E).

Discussion: Externally, the Brazilian specimen resembles *Izumia* in having faint radial ribs, a crenulate ventral margin, wide lunule and a well-developed posterior umbonal ridge. However, because of the poorly preserved hinge and muscle scars, the specimen can only be tentatively assigned to *Izumia*. It closely resembles *Cyprina saussuri* (Brongniart, 1821) from the Aptian of England (Woods, 1906) in general outline ($H/L=0.84$, as opposed to a mean of 0.81), shell inflation ($W/L=0.61$, as opposed to a mean of 0.63) and in having faint radial ribs and a well-developed posterior umbonal ridge.

Izumia trapezoidalis Ichikawa & Maeda, 1963, from the Cenomanian of Japan (Ichikawa & Maeda, 1963, p. 124, pl. 10, figs 1-10; text-fig. 3a-b) resembles *I. saussuri* in having faint radial ribs, trapezoidal valves and a crenulated ventral margin, but differs in being smaller ($L=12.5-23.1$, $H=9.7-18.7$; $W=3.4-11.2$ mm, as opposed to $L=44$, $H=37$ mm), less inflated and in having a less developed posterior umbonal ridge and narrow, triangular umbones. *Argenticyprina mulensis* Lazo & Damborenea, 2011, from the Barremian of west-central Argentina (Lazo & Damborenea, 2011, p. 733, figs 10-14) is similar in general outline and ornamentation but differs in having straight to slightly concave anterodorsal margin, a small anterior muscle scar, less developed umbonal posterior keel, and in being less inflated and more elongate. *Cyprina saussuri* (Brongniart) as described by Weaver

Table 30: Dimensions (in mm) of *Izumia?* *saussuri* (Brongniart, 1821).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168324	44.0	37.0	27.0	0.84	0.61

(1931) from the Lower Cretaceous of Argentina also resembles the Brazilian specimen but differs in being smaller ($L=21$, $H=20$ mm) and less inflated ($W/L=0.52$, as opposed to 0.61). Weaver's material is, in fact, much closer to *A. mulensis* than to *C. saussuri*. *Cyprina cuneata* J. de C. Sowerby, 1836, from the Albian of England (Woods, 1907, p. 134, pl. 20, figs 7-12) shows the same style of ornamentation but differs in being triangular in outline, strongly inflated, with a straight ventral margin and narrower and higher umbones. With respect to general outline, the Brazilian specimen is also very similar to *C. (Venilicardia) angulata* (J. Sowerby, 1814) from the Albian of England (Woods, 1907, p. 141, pl. 22, figs 1-4; text-figs 23-24) but the latter species differs in lacking radial ribs and in being larger ($L=82-109$; $H=70-92$ mm, as opposed to $L=44$, $H=37$ mm).

Occurrence: Aptian of France and Switzerland (Brongniart, 1821; Pictet & Renier, 1856; Pictet & Campiche, 1865; Gillet, 1921); possibly Lower Cretaceous of Argentina (Weaver, 1931) and England (Woods, 1906); Turonian of the Sergipe Basin (this study, first record).

Genus *Proveniella* Casey, 1952

Type species: *Cyprina meyeri* Woods, 1913.

Remarks: According to Casey (1952, p. 139), *Proveniella* is a Cretaceous genus, with a number of Aptian, Albian and Cenomanian species. He suggested that *Proveniella* might be a homoeomorph of *Venilicardia*, with a hinge structure intermediate between that of *Venericyprina* and *Veniella* Stoliczka, 1871. For detailed information, see Casey (1952, p. 139, fig. 15; p. 155, figs 51-52). *Proveniella* is characterised by ovate to trapezoidal, strongly inflated and smooth shells (except for growth lines), a truncated posterior margin, a well-developed posterior umbonal ridge and a well-defined lunule. The genus *Etea* Conrad, 1875 (see above) has also a well-developed posterior umbonal ridge and inconspicuous beaks but differs from *Proveniella* in being more elongate and in having a slightly concave antero-dorsal margin and umbones located one-third of total valve length from anterior end (Pl. VII, fig. C). In addition, the lateral teeth of *Etea* are smooth (Casey, 1952, p. 140).

Proveniella cf. *testacea* (Zittel, 1864)

Fig. 15; Pl. VII, fig. H

cf. 1864. *Cypocardia testacea* Zitt.—Zittel, p. 32 [136], pl. 4, fig. 8.

Table 31: Dimensions (in mm) of *Proveniella* cf. *testacea* (Zittel, 1864).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168325	34.0	27.0	10.0 (LV)	0.79	? 0.59

- cf. 1887. *Proveniella? testacea* (Zittel, 1865).—Dhondt, p. 83, pl. 5, fig. 2.
 v 1999. *Arctica* cf. *ligeriensis* (d'Orbigny, 1844).—Seeling, p. 126, pl. 5, fig. 4.

Material: One internal mould (NRM-PZ Mo168325) from the upper Cenomanian of locality Timbó 5, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 31.

Description: Shell medium-sized, subtrapezoidal, strongly inequilateral and moderately inflated. Antero-dorsal margin strongly concave. Postero-dorsal margin convex, higher than antero-dorsal margin, almost perpendicular to subtruncated posterior margin. Anterior margin narrow and strongly rounded. Ventral margin broken off. Posterior umbonal ridge well developed, slightly curved, separating the slightly concave posterior flank from rest of valve (Pl. VII, fig. H). Umbones broad, moderately convex, prosogyrate, subterminal (one-fourth of total valve length from anterior end). Beaks small, prosogyrate. Hinge of right valve with two cardinal teeth (3a, 3b) and two well-developed lateral teeth (AI, PII). Cardinal tooth 3b bifid (3b₁, 3b₂, Fig. 15). Hinge of left valve not preserved. No ornament visible, except for faint growth lines near ventral margin.

Discussion: The hinge of the right valve of the Brazilian specimen closely resembles the hinge of species of *Proveniella*, as described and figured by Casey (1952).

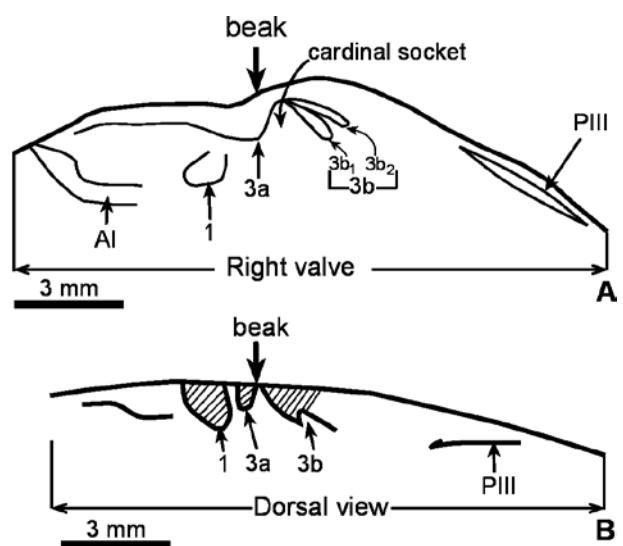


Fig. 15: Incomplete hinge of right valve of *Proveniella* cf. *testacea* (Zittel, 1864) (NRM-PZ Mo168325). A, right side view of hinge; B, dorsal view. Locality Timbó 5, upper Cenomanian, Sergipe Basin.

The lateral teeth are elongated, ridge-like and separated from the shell margin by narrow slits. On account of these similarities, the specimen is assigned to the genus *Proveniella*.

The specimen closely resembles *Cypricardia testacea* Zittel, 1864, in having subterminal umbones, a strongly concave antero-dorsal margin and a well-developed, slightly incurved posterior umbonal ridge, but it differs in being slightly larger ($L=34$, $H=27$ mm, as opposed to $L=24$, $H=20$ mm; Table 31), less inflated ($W/L=0.82$, as opposed to c. 0.59) and slightly elongate. The poor preservation of the specimen does not allow a definite species assignment. *Proveniella meyeri* (Woods, 1913) from the Aptian of England (Woods, 1913, p. 427, pl. 62, figs 2-3) is somewhat similar to the Brazilian specimen in having subterminal umbones, a truncated posterior margin and a narrow and strongly convex anterior margin but differs in being larger ($L=56$, $H=42$ mm), more elongate and in having a less developed posterior umbonal ridge.

Crassatella tricarinatum Roemer, 1841, from the Upper Cretaceous of Germany (Roemer, 1841, p. 74, pl. 9, fig. 23) is an internal mould, with no information about the hinge structure. It resembles *P. testacea* in general outline and in having subterminal umbones and a truncated posterior margin but differs in being less elongate, smaller and in having two weakly developed posterior umbonal ridges. *Cyprina ligeriensis* d'Orbigny, 1844, from the Turonian of France (d'Orbigny, 1844, p. 103, pl. 275, figs 1-4) differs in being larger ($L=90$ mm, as opposed to 34 mm) and in having a large, rounded lunule and a weakly developed posterior umbonal ridge. Therefore, *Arctica* cf. *ligeriensis* d'Orbigny, described and figured by Seeling (1999), is here assigned to *Proveniella* cf. *testacea* (Zittel, 1864). *Veniella forbesiana* (Stoliczka, 1870) from the Coniacian–Santonian of South India (Stoliczka, 1870, p. 197, pl. 9, figs 2-8) and the “Senonian” of Cameroon (Darteville & Freneix, 1957, p. 150, pl. 25, figs 5-6; pl. 26, fig. 1) closely resembles *P. testacea* but differs in having a narrower escutcheon, strongly incurved umbones, well-developed commarginal ribs and in being slightly elongate. *Arctica picteti* (Coquand, 1862) from the Upper Cretaceous of Algeria (Coquand, 1862, p. 199, pl. 13, figs 10-11) differs in being more elongate ($H/L=0.65$, as opposed to 0.79), less inflated and in having inconspicuous umbones, a truncated posterior margin and a less developed posterior umbonal ridge. *Cyprina maresi* Thomas & Peron, 1890, from the Cenomanian of Tunisia (Thomas & Peron, 1890, p. 297, pl. 29, figs 6-7) and *C. (Roudairia?) checchiae* Trevisan, 1937 from the Cenomanian of Italy (Trevisan, 1937, p. 91, pl. 6, figs 1-2) differ in being more inflated and in having higher, triangular, subterminal umbones (approximately one-third of total valve length from anterior end) and a less developed posterior umbonal ridge.

Occurrence: *Proveniella testacea* (Zittel, 1864) has been recorded from the Upper Cretaceous of the north-eastern Alps (Zittel, 1864), Santonian of Austria (Dhondt, 1987)

and here provisionally from the Cenomanian of the Sergipe Basin (first record).

Genus *Schedotrapezium* Stewart, 1930

Type species: *Trapezium carinatum* Gabb, 1864.

Remarks: The genus *Schedotrapezium* is known from the Upper Cretaceous of California, USA (Stewart, 1930). The species of this genus are small (type species: $L=9.1$, $H=5.7$ mm) and characterised by a subovate to trapezoidal shell, a well-developed posterior umbonal ridge, terminal to subterminal umbones, an obliquely truncated posterior margin and an external ligament. The species of the genus *Trapezium* Megerle von Mühlfeld, 1811 (family Trapeziidae Lamy, 1920) are larger, with valves carrying faint radial ribs restricted to the ventral area, an undulating ventral margin (sinuous), a vertically truncated posterior margin and terminal umbones.

Schedotrapezium? sp.

Pl. VII, figs I-K

Material: One internal mould (NRM-PZ Mo168326) from the upper Cenomanian of locality Tibúrcio 1, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 32.

Description: Shell large, elongate trapezoidal, strongly inequilateral, equivalved and moderately inflated ($W/L=0.45$). Antero-dorsal margin strongly concave, meeting anterior margin in blunt angle. Postero-dorsal margin higher than antero-dorsal margin, slightly convex and subparallel to ventral margin. Posterior margin oblique, truncated, meeting ventral margin in rounded angle and postero-dorsal margin in obtuse angle. Anterior margin narrowly convex, grading evenly into broad and convex ventral margin. Distinct posterior umbonal ridge (Pl. VII, fig. I) separating a slightly concave posterior flank from rest of valve. Umbones wide, moderately convex, prosogyrate, located one-fifth of total valve length from anterior end. Beaks inconspicuous, slightly prosogyrate and subterminal. Lunule small, smooth and slightly depressed. Anterior adductor muscle scar small, rounded, located near anterior margin (Pl. VII, fig. J). Posterior adductor muscle scar not seen. Ornament not preserved.

Discussion: Based on the outline, a truncated posterior margin, development and position of beaks, the Brazilian specimen appears to belong to the family Arcticidae, most probably to the genus *Schedotrapezium*. However, the large size of the specimen places doubts on the identification.

The specimen is distinguished from other Arcticidae by its elongate trapezoidal shell ($H/L=0.55$), blunt anterior and posterior ends, inconspicuous subterminal beaks, truncated posterior margin and well-developed posterior umbonal ridge. Based on the latter taxonomic features, it may represent a new species, but is too poorly preserved for precise identification.

Table 32: Dimensions (in mm) of *Schedotrapezium?* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168326	55.0	30.0	25.0	0.55	0.45

Trapezium (Schedotrapezium) coxi Darteville & Freneix, 1957, from the Maastrichtian of Cameroon (Darteville & Freneix, 1957, p. 157, pl. 28, figs 3-4) closely resembles the Brazilian specimen but differs in being less elongate ($H/L=0.74-0.84$, as opposed to 0.55, Table 33), smaller and in having convex posterior and ventral margins. The specimen also closely resembles *T. carinatum* Gabb, 1864, from the Upper Cretaceous of California, USA (Gabb, 1864, pp. 170, 232, pl. 23, fig. 150), but the latter species is smaller ($L=9.1$, $H=5.7$ mm, as opposed to $L=55$, $H=30$ mm). *Crassatella trapezoidalis* Roemer, 1841, from the Upper Cretaceous of Germany (Roemer, 1841, p. 74, pl. 9, fig. 22) differs in being less elongate ($H/L=0.68$, as opposed to 0.55), smaller ($L=22$, $H=15$ mm) and in having narrower umbones and a regularly convex ventral margin. *Sexta navicular* Stephenson, 1953, from the Cenomanian of Texas, USA (Stephenson, 1953, p. 101, pl. 24, figs 20-22) differs in being less elongate, smaller and in having more prominent and nearly centrally located umbones.

Genus *Tenea* Conrad, 1870

Type species: *Mysia parilis* Conrad, 1860.

Remarks: The hinge structure of the genus *Tenea* resembles that of the genus *Paraesa* Casey, 1952. The left valve of *Tenea* carries two cardinal teeth (2a, 2b), connected to form a chevron pattern and separated from the cardinal margin by a narrow, deep slit. Tooth 2a is curved anteriorly and apparently continuous with the basal edge of the hinge plate (Pl. VII, fig. O; Fig. 16), whereas in *Paraesa* it is nearly vertical and meets the hinge plate in an acute angle. The posterior tooth 4b is somewhat divergent from the nymph (Ichikawa & Maeda, 1963, p. 131). The type species *Paraesa faba* (J. de C. Sowerby, 1827), described below, is posteriorly elongate and slightly compressed, with well-developed beaks and a narrow, lanceolate lunule. By contrast, species of *Tenea* are rounded with less prominent beaks.

Tenea delettrei (Coquand, 1862)

Fig. 16; Pl. VII, figs L-O

- 1862. *Venus Delettrei* H. Coq.— Coquand, p. 194, pl. 8, figs 3-4.
- 1862. *Venus Forgemoli*.— Coquand, p. 194, pl. 8, figs 7-8.
- 1912. *Dosinia Delettrei* Coquand.— Pervinquier, p. 270, pl. 20, figs 4-8.
- 1917. *Dosinia Delettrei* var. *Forgemoli* Coquand 1862.— Fourtau, p. 87, pl. 7, fig. 8.

- 1919. *Dosinia Delettrei* Coq. sp.— Greco, p. 49 [231], pl. 5 [21], figs 6-10.
- 1937. *Dosinia Delettrei* Coq.— Trevisan, p. 113, pl. 7, figs 29-31.
- 1937. *Dosinia Forgemoli* Coq.— Trevisan, p. 114, pl. 7, figs 32-33.
- 1962. *Dosinia delettrei* (Coquand).— Abbass, p. 151, pl. 23, figs 8-9.
- 1962. *Dosinia forgemoli* (Coquand).— Abbass, p. 152, pl. 23, figs 6-7.
- 1983. *Dosinia delettrei* Coq.— Collignon & Roman, p. 81, pl. 1, fig. 5.
- 2004. *Dosinia delettrei* (Coquand).— Abdel-Gawad *et al.*, pl. 3, fig. 7.
- 2006. *Tenea delettrei* (Coquand, 1862).— El Qot, p. 84, pl. 17, figs 4-9.
- 2013. *Tenea delettrei* (Coquand, 1862).— El Qot *et al.*, p. 220, pl. 5, fig. 7.
- 2014. *Tenea delettrei* (Coquand, 1862).— Hewaidy *et al.*, p. 119, pl. 11, figs 5-7.
- 2014. *Tenea delettrei* (Coquand, 1862).— Hewaidy *et al.*, p. 226, pl. 3, fig. 3a-b.
- ? 2018. *Tenea delettrei* (Coquand, 1862).— Aouissi *et al.*, p. 19, fig. 6.1.

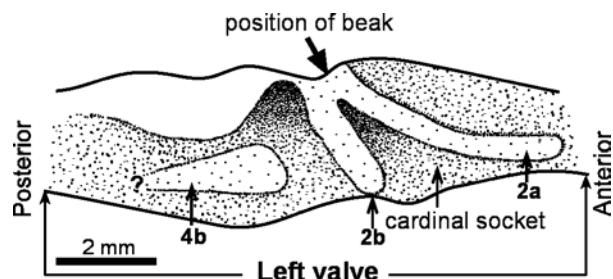


Fig. 16: Hinge of left valve of *Tenea delettrei* (Coquand, 1862) (NRM-PZ Mo168328). Locality Magalhães 2, middle Cenomanian, Sergipe Basin.

Material: Two internal moulds (NRM-PZ Mo168327–168328) from the middle Cenomanian and upper Turonian of localities Magalhães 2 and Mata 9, respectively, Cotinguba Formation, Sergipe Basin.

Measurements: cf. Table 33.

Description: Shell medium-sized, round to subrounded, inequilateral, nearly as long as high ($H/L=0.97$ on average), equivalved and moderately inflated ($W/L=0.53$ on average; Table 33). Postero-dorsal margin broadly convex, higher than antero-dorsal margin, meeting posterior margin in rounded curve. Antero-dorsal margin slightly concave below umbones. Anterior and posterior margins strongly rounded, curving into regularly rounded ventral margin. Umbones broad and prosogyrate. Beaks small, inconspicuous, prosogyrate, located slightly anterior to mid-length of valve. Anterior muscle scar large, elongate ovate, located near anterior margin. Posterior muscle scar not preserved. Escutcheon and lunule shallow and

Table 33: Dimensions (in mm) of *Tenea delettrei* (Coquand, 1862).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168327	26.0	24.0	?14.0	0.92	0.54
NRM-PZ Mo168328	37.0	38.0	20.0	1.03	0.53
Range	26.0-37.0	24.0-38.0	14.0-20.0	0.92-1.03	0.53-0.54
Mean	31.5	31.0	17.0	0.97	0.53

narrow. Hinge of left valve with three cardinal teeth. Anterior tooth 2a curved anteriorly, elongate, extending nearly parallel to the hinge plate, separated from tooth 2b by a triangular socket (Pl. VII, figs N-O; Fig. 16). No traces of ornament visible, except faint commarginal ribs near ventral margin.

Discussion: Pervinquieré (1912), Blanckenhorn (1934), El Qot (2006) and Ayoub-Hannaa *et al.* (2014) considered *Dosinia forgemoli* (Coquand, 1862) a synonym of *D. delettrei* (Coquand, 1862). Fourtau (1917) and Fawzi (1963) regarded *D. forgemoli* as a variety of *D. delettrei*. By contrast, Trevisan (1937) and Abbass (1962) separated *D. delettrei* and *D. forgemoli* on the basis of shell outline, and the latter author suggested that the difference in shell outline may be due to sexual dimorphism, as the two forms were found at the same stratigraphic level. According to Ayoub-Hannaa *et al.* (2014), *Tenea delettrei* is a highly variable species, ranging from orbicular (*T. delettrei*) to elongate (*T. forgemoli*). “*Venus*” *dutrugei* Coquand, 1862, from the Upper Cretaceous of Algeria (Coquand, 1862, p. 193, pl. 7, figs 5-6) is somewhat similar to *T. delettrei* in its inconspicuous beaks, shallow and small lunule but differs in being more elongate (H/L=0.85, as opposed to 0.97) and in having slightly elevated and triangular umbones. The specimens from the Cenomanian of Algeria described by Aouissi *et al.* (2018) as *T. delettrei* are tentatively placed in synonymy because of their poor preservation.

Occurrence: Cenomanian of Italy (Trevisan, 1937); Cenomanian–Turonian of Algeria (Coquand, 1862; Collignon & Roman, 1983), Tunisia (Pervinquieré, 1912), Egypt (Greco, 1919; Abbass, 1962; Abdel-Gawad *et al.*, 2004; El Qot, 2006; Ayoub-Hannaa *et al.*, 2014; Hewaidy *et al.*, 2014), Libya (El Qot *et al.*, 2013) and Syria (Blanckenhorn, 1934, p. 250); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

Genus *Veniella* Stoliczka, 1870

Type species: *Venilia conradi* Morton, 1833.

Remarks: The taxonomic status of the genera *Veniella* Stoliczka, 1870, *Cicatrea* Stoliczka, 1870, and *Roudairia* Munier-Chalmas, 1881 remains unclear. For instance, Darteville & Freneix (1957, pp. 138-142) considered *Cicatrea* and *Roudairia* synonyms of *Veniella*. In addition, “*Cyprina*” *forbesiana* Stoliczka, 1870, was

considered by Vokes (1954) to have a left valve hinge as in *Roudairia* and a right hinge resembling *Veniella*. Similarly, some other species, e.g., *Cicatrea cordialis* Stoliczka, 1870, from the Upper Cretaceous of South India, combine the hinge of *Veniella* and the external shape and ornamentation of *Roudairia* (Kirby & Saul, 1995, p. 28). On the basis of previous studies (e.g., Vokes, 1954; Darteville & Freneix, 1957; Kirby & Saul, 1995, pp. 30-31), two distinct generic groups, *Veniella* and *Roudairia*, can be recognised. *Veniella* is characterised by irregular commarginal ribs on the anterior margin and a posterior angulation. The hinge is characterised by an anterior lateral tooth and an internal myophoric flange on the anterior side of the posterior adductor muscle scar. *Roudairia* has a strongly carinate posterior angulation and regular commarginal ribs, which are rounded, ripple-like on the anterior portion of the shell near the beaks and disappear ventrally. In addition, the hinge carries an anterior lateral tooth and an internal myophoric flange bordering the anterior side of the posterior adductor muscle scar. For more details of the diagnostic features of the above mentioned genera, see Vokes (1954, pp. 36-54), Darteville & Freneix (1957, pp. 138-142) and Kirby & Saul (1995, pp. 28-34).

Veniella byzacenica (Pervinquieré, 1912)

Pl. VIII, figs A-D

1912. “... une variété de *R. Forbesiana* que nous appellerons *Byzacenica*”.—Pervinquieré, p. 232, pl. 15, fig. 15.
1958. *Veniella* aff. *byzacenica* (Pervinquieré).—Barber, p. 25, pl. 8, fig. 2.

Material: Nine internal and composite moulds (NRM-PZ Mo168329–168337) from the middle Cenomanian to lower Turonian of localities Jardim 24, Cruzes 8/11 and Magalhães 7, Cotinguiba Formation, Sergipe Basin, Brazil

Measurements: cf. Table 34.

Description: Shell small, subtrapezoidal, inequilateral, nearly as long as high (H/L=0.84 on average; Table 34), moderately inflated. Posterior margin obliquely truncated, meeting ventral margin in acute angle (Pl. VIII, fig. D). Anterior margin narrowly rounded and grading smoothly into ventral margin. Postero-dorsal margin straight to slightly convex, becoming oblique posteriorly,

Table 34: Dimensions (in mm) of *Veniella byzacenica* (Pervinquière, 1912).

Specimen	L	H	H/L
NRM-PZ Mo168329	10.0	6.5	0.65
NRM-PZ Mo168330	7.0	6.5	0.93
NRM-PZ Mo168331	9.0	9.0	1.0
NRM-PZ Mo168332	11.0	9.0	0.82
NRM-PZ Mo168334	10.0	7.0	0.70
NRM-PZ Mo168335	7.5	7.0	0.93
Range	7.0-11.0	6.5-9.0	0.65-1.0
Mean	9.08	7.50	0.84

meeting posterior margin in obtuse angle. Ventral margin broad and slightly sinuous. Posteroventral end angular (Pl. VIII, fig. A). Posterior umbonal ridge well developed, resulting in a large, concave posterior flank (on average, one-third of total valve length from posterior end) (Pl. VIII, fig. B) carrying faint growth lines. Umbones triangular, moderately convex, slightly prosogyrate and located slightly anterior to mid-length of valve. Ornament consisting of numerous, irregular, fine commarginal ribs separated by narrow interspaces, well developed ventrally (Pl. VIII, figs B, D), without crossing posterior umbonal ridge.

Discussion: Although the Brazilian specimens do not preserve internal structures they agree with the genus *Veniella* in ornamentation, general outline and the development of a posterior umbonal ridge. With respect to ornamentation and size, the specimens closely resemble *Roudaireia forbesiana* var. *byzacenica* (Pervinquière, 1912) from the Coniacian of Tunisia and *Veniella* aff. *byzacenica* (Pervinquière) of Barber (1958) from the lower Turonian of Nigeria in having a non-oblique trapezoidal shell, a truncated posterior margin, a straight and non-carinate posterior umbonal ridge and in being small. *Roudaireia brasiliensis* Maury, 1930 from the Campanian–Maastrichtian of the Pernambuco-Paraíba Basin, Brazil (Maury, 1930, pl. 8, fig. 10) and the Sergipe Basin (Löfgren & Oliveira, 1943, pl. 3, figs 1-2) and *R. erichseni* Santos & Castro, 1970 from the Campanian–Maastrichtian of Sergipe (Santos & Castro, 1970, p. 735, figs 6-10) differ from *Veniella byzacenica* in having thick commarginal ribs with wide interspaces and in being triangular in outline, more inflated, larger and taller. *Roudaireia drui* Munier-Chalmas, 1881, from the Campanian–Maastrichtian of Tunisia (Munier-Chalmas, 1881, p. 305, pl. 4, figs 1-7) differs in being trigonal, higher than long and in having a strongly carinate posterior and numerous thick, commarginal ribs, which become irregular towards the ventral margin. *Roudaireia squiresi* Kirby & Saul, 1995, from the Maastrichtian of California (Kirby & Saul, 1995, p. 34, pl. 1, figs 1-7; pl. 2, fig. 1) differs in its very large size (L=66.5-70, H=69-70 mm),

trigonal outline, strong posterior carina along the posterior angulation and in having strong, undulating commarginal ribs on the dorsal side, which become fainter ventrally. *Cyprina forbesiana* Stoliczka, 1870, from the Coniacian–Santonian of South India (Stoliczka, 1870, p. 197, pl. 9, figs 2-8) is a highly variable species. Some of Stoliczka's specimens (pl. 9, figs 2-4) are as small as the present species but differ in having few, regular, widely spaced commarginal ribs and strongly carinate valves. Other specimens (pl. 9, figs 5-8) are larger, obliquely trapezoidal in outline, strongly inflated and ornamented with numerous, irregular, well-developed commarginal ribs. *Veniella conradi* (Morton, 1833) from the Upper Cretaceous of the USA (Morton, 1833, p. 294; 1834, pl. 8, figs 1-2) is somewhat similar to *V. byzacenica* in having a well-developed posterior umbonal ridge and a subtruncated posterior margin but differs in having flanged commarginal ribs, narrow subterminal umbones, and in being larger (L=41, H=43 mm, H/L=1.05). *Veniella undata* (Conrad, 1852) from the Coniacian–Maastrichtian of Nigeria (Reyment, 1955, p. 142, pl. 3, fig. 2) differs in having terminal umbones, a strongly carinate posterior area and few, thick commarginal ridges.

Occurrence: Coniacian of Tunisia (Pervinquière, 1912) and lower Turonian of Nigeria (Barber, 1958); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

Veniella trapezoidea (Conrad, 1860)

Pl. VIII, figs E-G

- 1860. *Venilia trapezoidea*.—Conrad, p. 282, pl. 47, fig. 7.
- 1860. *C. Monmouthensis*.—Gabb, p. 302, pl. 48, fig. 20.
- 1862. *C. lineata*, (n. sp.).—Shumard, p. 201.
- 1885. *Veniella trapezoidea*.—Whitfield, p. 151, pl. 19, fig. 3.
- 1885. *Crassatella Monmouthensis*.—Whitfield, p. 119, pl. 17, figs 21-22.
- ? 1885. *Veniella subovalis*, Con.—Whitfield, p. 150, pl. 19, figs 1-2.
- 1907. *Etea trapezoidea* (Conrad).—Weller, p. 543, pl. 58, figs 20-21; pl. 59, fig. 7.
- 1941. *Veniella lineata* (Shumard).—Stephenson, p. 170, pl. 26, figs 16-20.
- 1958. *Veniella (Etea) trapezoidea* Conrad 1860.—Richards, p. 175, pl. 28, fig. 8.
- 1958. *V. subovalis* Whitfield = *V. trapezoidea* Conrad.—Richards, pl. 28, fig. 9.
- 1958. *Crassatella monmouthensis* Gabb (= *Veniella trapezoidea* Conrad).—Richards, pl. 29, figs 7, 15.

Material: Nine composite moulds (NRM-PZMo168338–168346) from the lower Cenomanian and possibly upper Albian of locality Praia 9, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 35.

Description: Shell medium-sized, subtrapezoidal to subovate, strongly oblique, inequilateral, moderately inflated (W/L=0.62 on average) and posteriorly elongate. Posterior margin wide, oblique, subtruncated, meeting

ventral margin in blunt angle. Postero-dorsal margin higher than antero-dorsal margin, slightly convex, gradually sloping to subtruncated posterior margin, forming obtuse angle. Anterior margin narrow, rounded, meeting faintly convex ventral margin in rounded angle. Posterior umbonal ridge well developed and separating wide and slightly concave posterior flank from rest of valve (Pl. VIII, fig. G). Umbones broad, moderately convex, prosogyrate, located one-third of total valve length from anterior end. Beaks prominent, prosogyrate. Ornament consisting of fine commarginal growth lines of variable strength (Pl. VIII, figs E-F).

Discussion: The shape of *Veniella trapezoidea* Conrad, 1860, varies throughout ontogeny (Weller, 1907, p. 545; Richards, 1958, p. 176). The ventral margin is at some stages slightly sinuous posteriorly and/or nearly straight or slightly convex. Accordingly, some species, e.g., *Crassatella monmouthensis* Gabb, 1860, and *V. subovalis* Whitfield, 1885, are considered junior synonyms of *V. trapezoidea*. Although the type of *Crassatella lineata* Shumard, 1862, from the Upper Cretaceous of North America has not been figured, on the basis of a large number of individuals, Richards (1958) concluded that *C. lineata* is a synonym of *V. trapezoidea*. *Crassatella desvauxi* Coquand, 1862, from the Upper Cretaceous of Algeria (Coquand, 1862, p. 199, pl. 13, figs 8-9) closely resembles the present species but is larger (L=60, H=35 mm) and more elongate and has numerous, well-developed commarginal ribs and subterminal umbones. “*Arca*” *acclivis* Conrad, 1852, from the upper Cenomanian–Turonian of Syria (Blanckenhorn, 1934, p. 213, pl. 10, figs 65-66, 68-69) differs in having subterminal umbones and an oblique posterior umbonal ridge. A taxodont hinge, which would indicate the genus *Arca*, is not seen in Blanckenhorn’s specimens; instead, the general outline suggests a genus of the family Arcticidae. The Cenomanian *Sexta navicula* Stephenson, 1953, from the Upper Cretaceous of Texas, USA (Stephenson, 1953, p. 101, pl. 24, figs 20-22) is similar to *V. trapezoidea*

but differs in being more inflated and in having wide umbones, faint radial ribs on the postero-dorsal slope and less prominent beaks.

Occurrence: Upper Cretaceous (Cenomanian?) of New Jersey, USA (Whitfield, 1885; Weller, 1907; Richards, 1958), Texas, USA (Stephenson, 1941) and India (Stoliczka, 1870, p. 189); Cenomanian and possibly Albian of the Sergipe Basin (this study, first record).

Genus *Venilicardia* Stoliczka, 1870

Type species: *Cyprina bifida* Zittel, 1865.

Venilicardia sp.

Pl. VIII, fig. H

v 1999. *Venilicardia* cf. *intermedia* (d’Orbigny, 1844).—Seeling, p. 127, pl. 5, fig. 6.

Material: One right valve with preserved shell (NRM-PZ Mo168347) from the Cenomanian–Turonian boundary beds of locality Japaratuba 11, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 36.

Description: Shell medium-sized, elongate ovate, strongly inequilateral and moderately inflated. Antero-dorsal margin short and slightly concave. Postero-dorsal margin faintly convex, gradually sloping towards posterior margin and higher than antero-dorsal margin. Posterior margin subtruncated, grading into the broad, regularly curved ventral margin. Anterior margin narrow, strongly rounded, meeting ventral margin in rounded angle. Posterior umbonal ridge moderately well developed, extending from umbo to postero-ventral angle. Umbo broad, moderately elevated, moderately convex, located one-third of total valve length from anterior end. Ornament consisting of fine, irregular commarginal growth lines, increasingly well developed near ventral margin (Pl. VIII, fig. H).

Discussion: The Brazilian specimen is very similar

Table 35: Dimensions (in mm) of *Veniella trapezoidea* Conrad, 1860.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168338	22.0	20.0	--	0.91	--
NRM-PZ Mo168339	34.0	24.0	?20.0	0.71	?0.58
NRM-PZ Mo168340	33.0	25.0	--	0.76	--
NRM-PZ Mo168341	33.0	24.0	?22.0	0.73	?0.67
Range	22.0-34.0	20.0-25.0	20.0-22.0	0.71-0.91	0.58-0.67
Mean	30.5	23.25	21	0.78	0.62

Table 36: Dimensions (in mm) of *Venilicardia* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168347	22.0 (RV)	16.0	?5.0 (RV)	0.73	?0.45

to *Venilicardia reyi* (Bosquet, 1860) from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 175, pl. 16, figs 1-8) in general outline, development of umbones and shell inflation, but the latter species has well-developed growth lines and is slightly taller. *Venilicardia olivensis* Vokes, 1946, from the Aptian of Lebanon (Vokes, 1946, p. 173, pl. 6, figs 12-15) differs in having a convex high postero-dorsal margin, short anterior area and in being higher ($H/L=0.82$ on average, as opposed to 0.73). *Cyprina intermedia* d'Orbigny, 1844, from the Upper Cretaceous of France (d'Orbigny, 1844, p. 107, pl. 278, figs 1-2) is larger ($L=80$ mm, as opposed to 58 mm), more inflated and has a strongly convex ventral margin. Therefore, Seeling's identification of the specimen as *Venilicardia cf. intermedia* (d'Orbigny, 1844) is not accepted. Similarly, *Cyprina bifida* Zittel, 1864, from the Upper Cretaceous of the north-eastern Alps (Zittel, 1864, p. 137, pl. 5, fig. 1) is larger ($L=60-80$; $H=50-65$ mm, as opposed to $L=22$, $H=16$ mm) and taller than the Sergipe specimen and has strongly rounded margins. *Venilicardia leonhardi* Darteville & Freneix, 1957, from the Campanian of Cameroon (Darteville & Freneix, 1957, p. 153, pl. 26, fig. 2) differs in having triangular shell and wide umbones.

Occurrence: Cenomanian–Turonian boundary beds of the Sergipe Basin (this study).

Family Trapezidae Lamy, 1920

Genus *Trapezium* Megerlé von Mühlfeld, 1811

Type species: *Trapezium perfectum* Megerlé von Mühlfeld, 1811.

Trapezium africanum (Coquand, 1862)

Pl. VIII, figs I-M

1862. *Cyprina africana* H. Coq.– Coquand, p. 202, pl. 11, figs 18-19.

Material: One internal mould with remains of shell (NRM-PZ Mo168348) from the upper Turonian of locality Mata 9, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 37.

Description: Shell large, ovate-trapezoidal, strongly inequilateral, equivalved, moderately inflated. Antero-dorsal margin distinctly concave below umbones (Pl. VIII, fig. J). Postero-dorsal margin slightly convex and higher than antero-dorsal margin. Anterior margin narrow, rounded, meeting wide and rounded ventral margin in regular curve. Posterior margin broken off. Ligament external. Umbones broad, moderately convex,

Table 37: Dimensions (in mm) of *Trapezium africanum* (Coquand, 1862).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168348	58.0	42.0	35.0	0.72	0.60

subterminal (one-tenth of total valve length from anterior end). Anterior adductor muscle scar large and rounded, located close to anterior margin (Pl. VIII, fig. J). Posterior umbonal ridge gently curved, moderately well-developed and separating smooth posterior flank from rest of valve. Beaks small, terminal and prosogyrate (Pl. VIII, fig. M). Ornament not preserved except numerous fine commarginal growth lines on a few shell fragments (Pl. VIII, fig. K).

Discussion: The specimen closely resembles *Cyprina africana* Coquand, 1862, from the Cenomanian of Algeria in general outline, strongly concave antero-dorsal margin, inconspicuous terminal beaks and moderately well-developed umbonal posterior ridge, but differs in being smaller ($L=58$ mm, as opposed to 70 mm). Thomas & Peron (1889), Pervinquier (1912) and El Qot (2006) considered *C. africana* a junior synonym of *C. cordata* Sharpe, 1850 (p. 182, pl. 15, fig. 2). However, *C. cordata* differs from *Trapezium africanum* in having subrounded valves ($H/L=0.87$, as opposed to 0.72), subterminal umbones and a wide, convex postero-dorsal margin. In addition, *T. africanum* has less prominent beaks, an external ligament, a well-developed posterior umbonal ridge, a subtruncated posterior margin and a straight postero-dorsal margin, the latter meeting the posterior margin in obtuse angle.

Crassatella trapezoidalis Roemer, 1841, and *C. picteti* Coquand, 1862, from the Upper Cretaceous of Germany (Roemer, 1841, p. 74, pl. 9, fig. 22) and Algeria (Coquand, 1862, p. 199, pl. 13, figs 10-11), respectively, are similar to *T. africanum* in general outline and in having terminal to subterminal umbones but they differ in possessing a well-developed posterior umbonal ridge separating a narrow posterior flank from the rest of valve, a less concave antero-dorsal margin and in being smaller ($L=23$, $H=14$ mm, as opposed to $L=58$, $H=42$ mm) and less elongate.

Occurrence: Cenomanian (“Rhotomagien”) of Algeria (Coquand, 1862); Turonian of the Sergipe Basin (this study, first record).

Superfamily Mactroidea Lamarck, 1809

Family Mactridae Lamarck, 1809

Subfamily Mactrinae Lamarck, 1809

Genus *Cymbophora* Gabb, 1869

Type species: *Mactra ashburnerii* Gabb, 1864.

Cymbophora? *scabellum* Stephenson, 1941

Pl. VIII, figs N-P

1941. *Cymbophora scabellum* n. sp. – Stephenson, p. 229, pl. 43, figs 8-9.

1964. “... lamelibrânquo, provavelmente pertencente aos Mactridae.” – Beurlen, p. 68, pl. 8, fig. 53.

Material: Four internal and composite moulds (NRM-PZ Mo168349–168352) from the upper Cenomanian to

lower Turonian of localities Tibúrcio 2, Alto Verde 5 and Laranjeiras 22, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 38.

Description: Shell medium-sized, varying in outline from subtrapezoidal, elongate ovate to subtriangular, nearly equilateral and weakly inflated ($W/L=c. 0.38$ on average). Postero-dorsal margin slightly convex to straight, higher than antero-dorsal margin, meeting posterior margin in obtuse angle. Antero-dorsal margin slightly concave and steeply inclined towards anterior margin. Posterior margin narrow, subangular below and truncated above. Anterior margin strongly rounded, meeting broad and slightly convex to straight ventral margin in rounded angle. Posterior umbonal ridge moderately well developed, separating small, shallow posterior flank from rest of valve (one-fifth of total valve length from posterior end). Umbones triangular, slightly inflated, located somewhat anterior to mid-length of valve. Beaks inconspicuous and slightly prosogyrate. Ornament consisting of faint, irregular commarginal ribs, well developed ventrally (Pl. VIII, fig. N).

Discussion: The Brazilian specimens probably belong to the genus *Cymbophora*, but without information on hinge structure, ornamentation and inclination of the pallial line, generic assignment remains provisional.

Cymbophora scabellum Stephenson, 1941, from the Maastrichtian of Texas, USA, is distinguished from other *Cymbophora* species by its fairly well-developed umbonal posterior ridge, less prominent beaks, broad and slightly rounded to straight ventral margin, truncated posterior margin and in being less elongate.

Cymbophora scabellum is somewhat similar to *C. tenuissima* (Gabb, 1869) from the Upper Cretaceous of California, USA (Stewart, 1930, p. 213, pl. 1, fig. 3) and to *C. stantoni* (Arnold, 1908) from the Campanian of California (Saul, 1974, p. 1076, pl. 2, fig. 4; pl. 3, figs 3-6) in general outline (H/L of Saul's material=0.65-0.81) and size but differs in being more inflated (average $W/L=0.32$, as opposed to 0.21 in Saul's specimens). In addition, the umbones of *C. tenuissima* are less triangular than in *C. scabellum*. *Cymbophora ashburnerii* (Gabb, 1864) from California (Stewart, 1930, p. 212, pl. 5, fig. 6a) differs in being larger ($L=51.5$, $H=42$, $W=25$ mm, as opposed to $L=22.30$, $H=17$, $W=c. 8.30$ mm on average), more inflated ($W/L=0.49$, as opposed to a mean of $c.$

0.38) and in having a well-developed posterior umbonal ridge. *Mactra (Schizodesma) tripartita* G.B. Sowerby, 1846, from the Coniacian–Santonian of India (G.B. Sowerby in Forbes, 1846, p. 142; Stoliczka, 1870, p. 57, pl. 5, figs 8-11) and *M. debeyana* (Müller, 1847) from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 148, pl. 10, figs 20-24) differ in being more inflated, taller and in having well-developed posterior umbonal ridges.

Occurrence: Maastrichtian of Texas, USA (Stephenson, 1941); Turonian of the Potiguar Basin, Brazil (Beurlen, 1964); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

***Cymbophora? subtilis* Stephenson, 1941**

Pl. IX, figs A-B

p 1907. *Schizodesma appressa* Gabb.– Weller, p. 634, pl. 71, figs 17-18, non figs 14-16, 19-21.

1941. *Cymbophora subtilis* n.sp. – Stephenson, p. 230, pl. 43, fig. 11.

Material: Four internal and composite moulds (NRM-PZ 168353–168356) from the middle Cenomanian to middle Turonian of localities Jardim 7, Japaratuba 10 and Muçucá 2, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 39.

Description: Shell medium-sized, elongate subtriangular, inequilateral, equivalved and moderately inflated ($W/L=0.44$). Maximum inflation at the umbones, tapering off posteriorly. Antero-dorsal margin slightly convex, steeply oblique anteriorly, meeting anterior margin in rounded angle. Postero-dorsal margin wide and slightly concave. Anterior margin slightly convex. Posterior margin strongly rounded, meeting ventral margin in rounded curve. Ventral margin slightly rounded anteriorly, becoming straight posteriorly. Posterior umbonal ridge poorly developed. Umbones triangular, convex, elevated above hinge line, located slightly anterior to mid-length of valve. Beaks prominent, sharply pointed and slightly prosogyrate. Ornament consisting of irregular commarginal ribs.

Discussion: *Cymbophora? subtilis* differs from *C.? scabellum* described above in having narrow, projecting, triangular umbones (Pl. IX, fig. A), prominent, sharply pointed beaks, a strongly rounded posterior margin, poorly developed posterior umbonal ridge and in being

Table 38: Dimensions (in mm) of *Cymbophora? scabellum* Stephenson, 1941.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168349	24.0	19.0	9.0	0.79	0.37
NRM-PZ Mo168350	24.0	18.0	8.0	0.75	0.34
NRM-PZ Mo168351	19.0	14.0	8.0	0.74	0.42
Range	19-24	14-19	8.0-9.0	0.74-0.79	0.34-0.42
Mean	22.30	17.0	8.30	0.76	0.38

Table 39: Dimensions (in mm) of *Cymbophora? subtilis* Stephenson, 1941.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168353	34.0	23.0	15.0	0.67	0.44
NRM-PZ Mo168354	24.0	18.0	--	0.75	--
NRM-PZ Mo168355	21.0	13.0	--	0.62	--
Range	21-34	13-23	15.0	0.62-0.75	0.44
Mean	26.33	18.0	15.0	0.68	0.44

more elongate. Generally, *Schizodesma appressa* Gabb differs from *C. subtilis* in the style of ornamentation and general outline. However, Stephenson (1941, p. 230) considered *S. appressa* Gabb, figured and described by Weller (1907) from the Upper Cretaceous of New Jersey, USA, as belonging to his new species *C. subtilis*, in view of the high variability of the species.

Occurrence: Santonian of New Jersey, USA (Weller, 1907); Maastrichtian of Texas, USA (Stephenson, 1941); Cenomanian–Turonian of the Sergipe Basin (this study, first record).

Genus *Geltena* Stephenson, 1946

Type species: *Geltena subequilatera* Stephenson, 1946.

Geltena subequilatera Stephenson, 1946

Pl. IX, fig. C

1946. *Geltena subequilatera* Stephenson MS.– Vokes, p. 202, pl. 10, figs 1-6.

1953. *Geltena subequilatera* Stephenson.– Stephenson, p. 126, pl. 32, figs 25-29.

Material: One left composite mould (NRM-PZ Mo168357) from the middle Cenomanian of locality Jardim 24, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 40.

Description: Shell medium-sized, subtrigonally rounded, subequilateral, slightly longer than high ($H/L=0.95$) and moderately inflated. Anterior and posterior margins strongly rounded, meeting strongly convex ventral margin in rounded curves. Umbones weakly inflated, wide and in near-mesial position. Ligament external, short and narrow. Ornament consisting of numerous, closely spaced, fine commarginal ribs, becoming stronger towards postero-dorsal and posterior margins (Pl. IX, fig. C).

Discussion: The Brazilian specimen closely resembles *Geltena subequilatera* Stephenson, 1946, in size ($L=20$, $H=17.8$, $W=11.8$ mm for Stephenson's specimens), and in having a subovate shell, numerous fine commarginal ribs (well developed posteriorly) and a narrow, short ligament.

With respect to general outline and ornamentation, *Geltena obesa* Stephenson, 1953, from the Cenomanian of Texas (Stephenson, 1953, p. 127, pl. 32, figs 30-33) closely resembles the Brazilian specimen but differs in

Table 40: Dimensions (in mm) of *Geltena subequilatera* Stephenson in Vokes, 1946.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168357	19.0	18.0	?10.0	0.95	?0.53

being larger ($L=42$, $H=38.5$, $W=15$ mm), less inflated ($W/L=0.36$, as opposed to 0.53) and in having narrower umbones. *Mactra angulata* J. de C. Sowerby, 1836, from the Lower Cretaceous of England (Woods, 1907, p. 177, pl. 27, figs 19-23) differs in having a well-developed posterior umbonal ridge, a subtriangular valve and in being smaller and more inflated ($W/L=0.82$, as opposed to 0.53). Similarly, *G. nitida* Stephenson, 1953, from the Cenomanian of Texas (Stephenson, 1953, p. 127, pl. 32, figs 21-24) differs in having a well-developed posterior umbonal ridge, slightly concave antero-dorsal margin, convex postero-dorsal margin and in being larger ($L=25.4$, $H=21.7$, $W=19.9$ mm) and more elongate ($H/L=0.85$, as opposed to 0.95). *Geltena mactriforma* Vokes, 1946, from the Upper Cretaceous of Lebanon (Vokes, 1946, p. 204, pl. 9, figs 22-25) is smaller and triangular in outline.

Occurrence: Cenomanian of Texas, USA (Stephenson in Vokes, 1946); Cenomanian of the Sergipe Basin (this study, first record).

Genus *Mulinoides* Olsson, 1944

Type species: *Mulinoides chilca* Olsson, 1944.

Remarks: The genus *Mulinoides* resembles *Cymbophora* Gabb, 1869, but differs in having rounded margins, wide and convex umbones and a posterior umbonal ridge. Based on shell outline and ornamentation, Darteville & Freneix (1957, pp. 200-201) discussed the differences between some mastrid genera, such as *Geltena* Stephenson, 1946, *Aliomactra* Stephenson, 1953, and *Priscomactra* Stephenson, 1953 (see the latter author for additional information).

Mulinoides cf. olbrechtsi Darteville & Freneix, 1957

Fig. 17; Pl. IX, figs D-F

cf. 1957. *Mulinoides olbrechtsi* nov. sp.– Darteville & Freneix, p. 199, pl. 32, fig. 2.

Material: One specimen in shell preservation (NRM-PZ Mo168358) from the upper Cenomanian or lowermost Turonian of locality Laranjeiras 28, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 41.

Description: Shell medium-sized, subrounded, slightly inequilateral and moderately inflated ($W/L=0.53$). Anterior and posterior margins rounded, meeting ventral margin in rounded curves. Ventral margin broad and slightly convex. Antero-dorsal margin slightly concave. Postero-dorsal margin straight and higher than antero-dorsal margin. Posterior umbonal ridge weakly developed (Fig. 17). Umbones wide, strongly convex, located almost centrally. Beaks small, inconspicuous, slightly prosogyrate. Ornament consisting of well-developed, slightly undulating, irregular growth lines, being weak dorsally and becoming stronger towards ventral and anterior margins (Pl. IX, fig. E).

Discussion: The specimen closely resembles *Mulinoides olbrechtsi* Darteville & Freneix, 1957, from the “Senonian” of Cameroon in its rounded anterior margin, small beaks, wide, triangular and strongly convex umbones and well-developed, irregular growth lines (thickening ventrally), but differs in having a rounded posterior margin and a poorly developed posterior umbonal ridge.

Mulinoides chilca Olsson, 1944, from the Campanian–Maastrichtian of Peru (Olsson, 1944, p. 61, pl. 7, figs 4, 7–9) resembles *M. olbrechtsi* in having rounded margins, small beaks and well-developed growth lines but differs in being larger ($L=56$ mm, as opposed to 36 mm) and in having wide and strongly convex umbones and valves strongly inflated ventrally. *Priscomactra cyma* Stephenson, 1953, from the Cenomanian of Texas, USA (Stephenson, 1953, p. 124, pl. 31, figs 6–10) resembles the Brazilian specimen in having wide umbones and thick growth lines but differs in being smaller ($L=28.8$, $H=20$, $W=13.2$ mm), subtrigonal and in having a shallow posterior umbonal sulcus. *Aliomactra compressa* Stephenson, 1953, from the Cenomanian of the same area (Stephenson, 1953, p. 125, pl. 31, figs 1–5) differs in being compressed, more elongate and in having narrowly triangular umbones and a large anterior area.

Occurrence: *Mulinoides olbrechtsi* Darteville & Freneix, 1957, has been recorded from the “Senonian” of Cameroon (Darteville & Freneix, 1957) and here provisionally from the Cenomanian or Turonian of the Sergipe Basin (first record).

Superfamily Veneroidea Rafinesque, 1815

Family Veneridae Rafinesque, 1815

Genus *Aphrodina* Conrad, 1869

Type species: *Meretrix tippana* Conrad, 1858.

Remarks: According to Jaitly & Mishra (2009, p. 260), the genera *Aphrodina* Conrad, 1869, and *Calva* Popenoe, 1937, are externally identical. However, the genus *Calva* shows a slight posterior truncation, a well-defined escutcheon and a longitudinally grooved cardinal 4b with an elongated anterior lateral tooth (AII) with crenulations on its ventral side, whereas *Aphrodina* lacks an escutcheon and a groove in cardinal 4b.

Subgenus *Mesocallista* Cox, 1952

Type species: *Meretrix andersoni* Newton, 1909.

Remarks: The subgenus *Mesocallista* includes small species with suborbicular and ovate shells and a narrow, cordate lunule while lacking an escutcheon.

***Aphrodina (Mesocallista) cf. plana* (J. Sowerby, 1813)**

Fig. 18; Pl. IX, figs G–K

cf. 1813. *Venus planus*.—J. Sowerby, p. 58, pl. 20.

cf. 1908. *Callista plana* (Sowerby), 1813.—Woods, p. 192, pl. 30, figs 1–6.

cf. 1933. *Callistina plana* Sow.—Riedel, p. 60, pl. 2, figs 1, 3; pl. 11, fig. 5; pl. 12, fig. 2.

cf. 1953. *Meretrix plana* (Sow.) var. *judaica* Picard.—Baroni et al., p. 74, pl. 4, fig. 6.

cf. 1983. *Aphrodina (Aphrodina) plana* (Sow.).—Collignon & Roman, p. 80, pl. 1, figs 3–4.

v 1999. *Aphrodina (Aphrodina) aff. plana* (J. Sowerby, 1813).—Seeling, p. 128, pl. 5, figs 7–9.

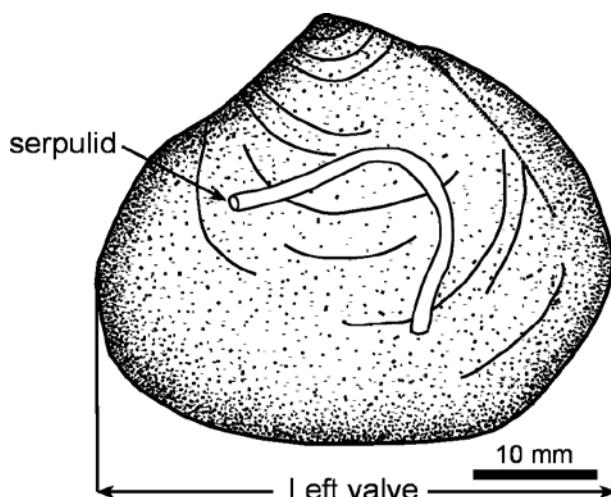


Fig. 17: Left valve of *Mulinoides* cf. *olbrechtsi* Darteville & Freneix, 1957 (NRM-PZ Mo168358). Locality Laranjeiras 28, Cenomanian–Turonian boundary beds, Sergipe Basin.

Table 41: Dimensions (in mm) of *Mulinoides* cf. *olbrechtsi* Darteville & Freneix, 1957.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168358	38.0	32.0	?20.0	0.84	?0.53

Material: One specimen with remains of shell (NRM-PZ Mo168359) from the Cenomanian–Turonian boundary beds of locality Japaratuba 11, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 42.

Description: Shell small, moderately inflated, nearly circular, inequilateral, equivalved, with length approximately equal to height ($H/L=1.05$). Maximum inflation anteriorly, below umbones. Postero-dorsal margin convex, meeting posterior margin in rounded curve. Antero-dorsal margin slightly concave, lower than postero-dorsal margin. Anterior and posterior margins convex, meeting regularly curved ventral margin in rounded angles. Lunule narrow, cordate and moderately impressed with faint border (Pl. IX, fig. K). Hinge of right valve with three cardinal teeth – (3a), (3b) and elongated (5b) – the latter nearly parallel to postero-dorsal margin (Pl. IX, fig. H; Fig. 18). Anterior lateral tooth (AI) partly preserved and apparently crenulate, running nearly parallel to antero-dorsal margin. No escutcheon. Umbones wide, moderately convex and slightly prosogyrate. Beaks inconspicuous and strongly prosogyrate. Ornament consisting of numerous irregular commarginal growth lines (Pl. IX, fig. J).

Discussion: With respect to height/length ratio, *Aphrodina (Mesocallista) plana* (J. Sowerby, 1813) is a highly variable species (subtrigonal to ovate in outline). In addition, the anterior area is slightly extended (Woods, 1908, p. 194). The Brazilian specimen is similar to *A. (M.) plana* from the Albian of England (Woods, 1908) but is smaller ($L=18$, $H=19$ mm, as opposed to $L=35-72$, $H=29-63$ mm) and less elongate and has nearly rounded margins.

The presence of a narrowly elongate, V-shaped, deep

escutcheon in Riedel's (1933) *Callistina plana* from the Upper Cretaceous of Cameroon throws some doubts on his identification. *Callistina? angustosinuosa* Riedel, 1933, from the same area (Riedel, 1933, p. 62, pl. 11, fig. 1) is larger, more elongate, has subterminal umbones and a narrowly elongate, deep escutcheon. *Aphrodina (Mesocallista) riedeli* Reyment, 1955, from the Coniacian of Nigeria (Reyment, 1955, p. 147, pl. 4, fig. 6; text-fig. 2) and *A. (Aphrodina) gabonensis* Darteville & Freneix, 1957, from the "Senonian" of Gabon (Darteville & Freneix, 1957, p. 187, pl. 31, fig. 11; pl. 34, figs 6-8) resemble the Brazilian specimen in having nearly rounded margins and in lacking an escutcheon but differ in being larger ($L=42$, $H=39$ mm for the Nigerian specimens and $L=53.3-64$, $H=39-57.5$ mm for the Gabonese specimens, as opposed to $L=18.0$, $H=19$ mm) and in having slightly extended posterior areas and triangular umbones.

Occurrence: *Aphrodina (Mesocallista) plana* (J. Sowerby, 1813) has been recorded from the Albian of England (Woods, 1908), the Upper Cretaceous of Libya (Baroni *et al.*, 1953), the Cenomanian of Algeria (Collignon & Roman, 1983), possibly from the Upper Cretaceous of Cameroon (Riedel, 1933) and here provisionally from the Cenomanian–Turonian boundary beds of the Sergipe Basin (Seeling, 1999; present study).

Tribe Dosiniini Deshayes, 1853

Genus *Cyprimeria* Conrad, 1864

Type species: *Cytherea excavata* Morton, 1833.

***Cyprimeria? discus* (Matheron, 1843)**

Fig. 19; Pl. IX, figs L-M

1843. *Lucina discus*, Math.– Matheron, p. 144, p. 13, fig. 12.
1851. *L. Geinitzii* Müller.– Müller, p. 66.

1864. *Circe discus* Math. sp.– Zittel, p. 24 [128], pl. 3, fig. 7.
? 1864. *Circe concentrica* Zitt.– Zittel, p. 26 [130], pl. 4, fig. 1.

1889. *Cyprimeria Geinitzii* Müll. sp.– Holzapfel, p. 174, pl. 12, figs 1-4.

1897. *Cyprimeria Geinitzi*, Müller sp.– Frič, p. 53, fig. 58.

1934. *Cyprimeria discus* Math. sp.– Andert, p. 273, pl. 12, figs 33-34.

1974. *C. geinitzii* (J. Müller).– Oekentorp & Siegfried, p. 160, pl. 16, fig. 7.

1987. *Cyprimeria? discus* (Matheron, 1843).– Dhondt, p. 86 (with extensive synonymy).

1994. *Cyprimeria discus* (Matheron, 1843).– Malchus *et al.*, p. 134.

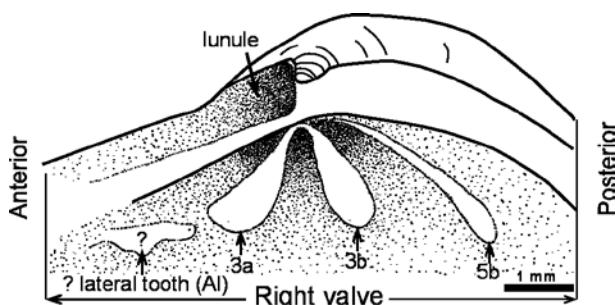


Fig. 18: Hinge of right valve of *Aphrodina (Mesocallista) cf. plana* (J. Sowerby, 1813) showing three cardinal teeth and sockets (NRM-PZ Mo168359). Locality Japaratuba 11, Cenomanian–Turonian boundary beds, Sergipe Basin.

Table 42: Dimensions (in mm) of *Aphrodina (Mesocallista) cf. plana* (J. Sowerby, 1813).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168359	18.0	19.0	11.0	1.05	0.61

Material: Three internal/composite moulds (NRM-PZ Mo168360–168362) from the lower and upper Turonian of localities Pedra Furada 4 and Mucuri 10, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 43.

Description: Shell medium-sized, rounded to subrounded, inequilateral, equivalved, moderately inflated ($W/L=0.62$ on average). Right valve slightly more convex

than left valve (Fig. 19B). Anterior margin rounded, meeting ventral margin in rounded curve. Posterior margin slightly convex to subtruncated. Postero-dorsal margin broadly convex, higher than antero-dorsal margin. Posterior umbonal ridge inconspicuous (Fig. 19A). Umbones wide, weakly inflated, slightly prosogyrate, located approximately one-third of total valve length from anterior end. Beaks small, low, inconspicuous, prosogyrate. Lunule ovate, moderately deep. Escutcheon narrow, long and V-shaped (Pl. IX, fig. M; Fig. 19B). Ornament consisting of commarginal ribs, well developed near ventral margin.

Discussion: With respect to shell outline, size, inflation and ornamentation, the Brazilian specimens closely resemble *Cyprimeria discus* (Matheron, 1843) from the Upper Cretaceous of Germany and the northeastern Alps (Zittel, 1864; Andert, 1934). The specimens are very similar to *C. geinitzii* (Müller, 1851) from the Upper Cretaceous of Germany (Holzapfel, 1889; Frič, 1897; Oekentorp & Siegfried, 1974), which is here regarded as a junior synonym of *C. discus*. *Cyprimeria concentrica* (Zittel, 1864) is also similar to the Brazilian specimens but differs in being less inflated and in having only a faint posterior umbonal ridge. *C. concentrica* is possibly a junior synonym of *C. discus*. *Cyprimeria patella* Stephenson,

1953, from the Cenomanian of Texas (Stephenson, 1953, p. 108, pl. 27, figs 12-18) differs in being more rounded, less inflated ($W/L=0.41$, as opposed to a mean of 0.62) and in having subcentral umbones. *Cyprimeria alta* Conrad, 1875, from the Maastrichtian of the south-eastern USA (Wade, 1926, p. 91, pl. 29, figs 2-4; pl. 30, fig. 1) and the Upper Cretaceous of Texas (Stephenson, 1941, p. 212, pl. 40, figs 1-2; pl. 41, figs 1-4) differs in being larger ($L=73$, $H=65$ mm for Stephenson's specimens, as opposed to $L=47.0$, $H=43.5$ mm on average), more compressed ($W/L=0.23$, as opposed to a mean of 0.62) and in having a sharp posterior umbonal ridge. *Cyprimeria densata* (Conrad, 1858) from the Upper Cretaceous of New Jersey, USA (Weller, 1907, p. 601, pl. 68, fig. 14; pl. 69, figs 1-2) differs in having subcentral umbones, a truncated posterior margin and in being larger ($L=81$, $H=66$, $W=25$ mm). *Cyprimeria major* Gardner, 1916, from the "Senonian" of Maryland, USA (Gardner, 1916, p. 689, pl. 40, figs 11-12; pl. 41, figs 1-4; pl. 42, fig. 1; pl. 43, fig. 1) resembles *C. discus* in having a truncated posterior margin and a faint posterior umbonal ridge, but differs in being less inflated ($W/L=0.27$, as opposed to a mean of 0.62) and larger ($L=86$, $H=76.5$ mm).

Occurrence: Upper Cretaceous of the north-eastern Alps (Zittel, 1864); Coniacian–Campanian of France

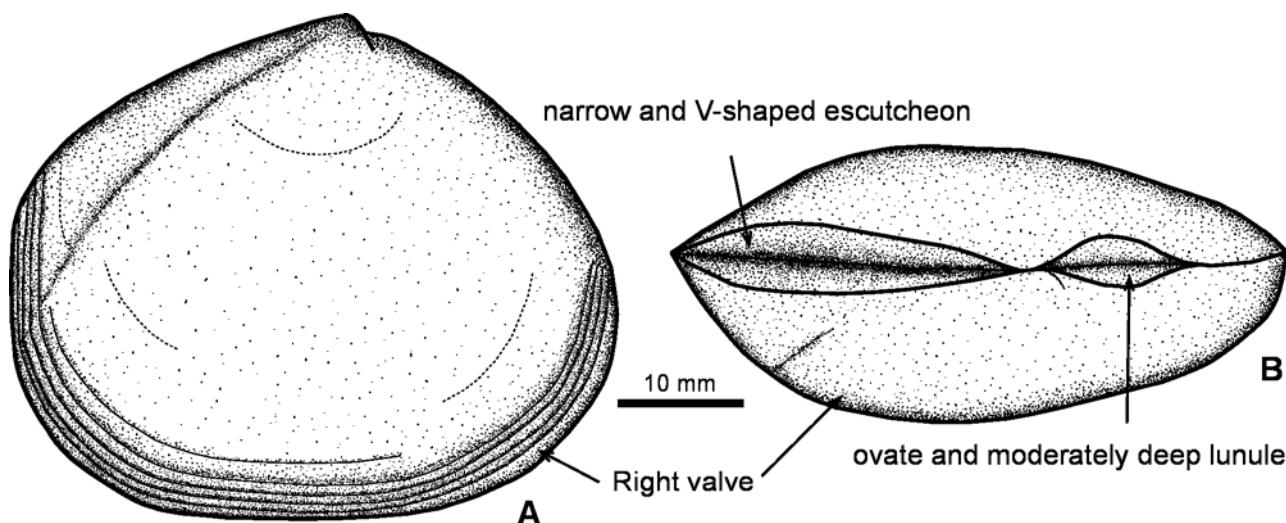


Fig. 19: *Cyprimeria? discus* (Matheron, 1843) (NRM-PZ Mo168361). A, right lateral view showing posterior umbonal ridge; B, dorsal view of articulated valves showing a narrow, V-shaped escutcheon. Locality Pedra Furada 4, lower Turonian, Sergipe Basin.

Table 43: Dimensions (in mm) of *Cyprimeria? discus* (Matheron, 1843).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168360	51.0	45.0	?35.0	0.88	0.68
NRM-PZ Mo168361	43.0	42.0	24.0	0.98	0.56
Range	43-51	42-45	24-? 35	0.88-0.98	0.56-0.68
Mean	47.0	43.5	29.5	0.93	0.62

(Matheron, 1843) and Austria (Dhondt, 1987); Santonian of south-eastern Belgium (Malchus *et al.*, 1994) and Germany (Holzapfel, 1889; Frič, 1897; Andert, 1934); Turonian of the Sergipe Basin (this study, first record)

Cyprimeria? cf. riograndensis Maury, 1934

Pl. IX, figs N-P

cf. 1934. *Cyprimeria riograndensis*, sp. nov.— Maury, p. 135, pl. 9, fig. 1.

v 1999. *Cyclorisma?* sp.— Seeling, p. 130, pl. 6, fig. 1.

Material: One composite mould (NRM-PZ Mo168363) from the upper Cenomanian of locality Jardim 1, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 44.

Description: Shell medium-sized, subrounded, length and height equal, slightly equilateral, equivalved and moderately inflated ($W/L=0.43$). Postero-dorsal margin slightly convex, meeting posterior margin in rounded curve. Antero-dorsal margin slightly concave. Anterior and posterior margins rounded, meeting ventral margin in rounded angles. Umbones broad and moderately convex. Beaks small, slightly prosogyrate and slightly elevated above hinge line, located approximately half of total valve length from anterior end. Ornament consisting of ventrally well-developed, wide growth lines; dorsal area smooth. Growth lines prominent, separated by wide interspaces carrying faint growth lines.

Discussion: The Brazilian specimen closely resembles *Cyprimeria riograndensis* Maury, 1934, from the Upper Cretaceous of the Potiguar Basin, Brazil, in having a subcircular outline and inconspicuous beaks, but differs in being smaller ($L=46$, $H=46$ mm, as opposed to $L=70$, $H=68$, $W=22$ mm; Table 44) and more inflated ($W/L=0.43$, as opposed to 0.31). *Dosinia brasiliensis* White, 1887, from the Albian of the Sergipe Basin (White, 1887, p. 97, pl. 8, figs 13-15) differs in having numerous commarginal ribs, a strongly concave antero-dorsal

margin and subterminal umbones and in being smaller ($L=35$, $H=35$, $W=17$ mm). The beaks of *Lucina discus* (Matheron, 1843 from the Coniacian–Campanian of France (Matheron, 1843, p. 144, pl. 13, fig. 12) are more prominent, sharply pointed and located more anteriorly than in *C. riograndensis* (approximately one-third of total valve length from anterior end). In addition, *C. discus* displays a faint posterior umbonal ridge and is ornamented with numerous commarginal ribs. *Cyprimeria major* Gardner, 1916, from the “Senonian” of Maryland, USA (Gardner, 1916, p. 689, pl. 40, figs 11-12; pl. 41, figs 1-4; pl. 42, fig. 1; pl. 43, fig. 1), is somewhat similar but differs in being more elongate ($H/L=0.89$, as opposed to 1.0), less inflated ($W/L=0.27$, as opposed to 0.43), larger ($L=86$, $H=76.5$ mm) and in having a faint posterior umbonal ridge.

Occurrence: *Cyprimeria riograndensis* Maury, 1934, has been recorded from the Upper Cretaceous of the Potiguar Basin, Brazil (Maury, 1934) and here provisionally from the Cenomanian of the Sergipe Basin (first record).

Tribe Tapetini J. Gray, 1851

Genus *Cyclorisma* Dall, 1902

Type species: *Cyclothyris carolinensis* Conrad, 1875.

Remarks: The genus *Cyclorisma* differs from the genus *Paraesa* Casey, 1952, in being less elongate and in having rounded margins, well-developed prominent beaks, distinct commarginal ribs and a different hinge structure.

***Cyclorisma vectensis* (Forbes, 1845)**

Pl. X, figs A-C

1845. *Venus vectensis*. Sp. nov.— Forbes, p. 240, pl. 2, fig. 4.

1908. *Cyprimeria (Cyclorisma) vectensis* (Forbes), 1845.— Woods, p. 183, pl. 28, figs 11-18.

1952. *Resatrix (Vectorbis) vectensis* (Forbes).— Casey, p. 162, pl. 8, fig. 5; pl. 9, fig. 2.

v 1999. *Cyclorisma* cf. *vectensis* (Forbes, 1845).— Seeling, p. 129, pl. 5, figs 10-12.

Material: Six composite moulds (NRM-PZ Mo168364–168369) from the lower Turonian of locality Pati 3, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 45.

Description: Shell small, subrounded, equivalved,

Table 44: Dimensions (in mm) of *Cyprimeria?* cf. *riograndensis* Maury, 1934.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168363	46.0	46.0	20.0	1.0	0.43

Table 45: Dimensions (in mm) of *Cyclorisma vectensis* (Forbes, 1845).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168364	10.0	10.5	5.5	1.05	0.55
NRM-PZ Mo168366	16.0	16.0	8.0	1.0	0.50
NRM-PZ Mo168367	15.0	14.0	6.5	0.93	0.43
Range	10-16	10-16	5.5-8.0	0.93-1.05	0.43-0.55
Mean	13.67	13.33	6.67	0.99	0.49

inequilateral and moderately inflated ($W/L=0.49$ on average). Antero-dorsal margin slightly concave and lower than postero-dorsal margin. Other margins regularly rounded. Umbones broad, little inflated, located slightly anterior to mid-length of valve. Beaks inconspicuous, prosogyrate. Lunule ovate, small and shallow (Pl. X, fig. C). Escutcheon shallow, long and narrow. Valves smooth except for faint commarginal growth lines, well developed near ventral margin (Pl. X, fig. B).

Discussion: *Cyclorisma vectensis* resembles *Cytherea ovalis* (Goldfuss, 1840) from the Upper Cretaceous of Germany (Andert, 1934, p. 287, pl. 13, fig. 3) in having rounded margins and nearly orthogyrate umbones, but the latter species differs in having well-developed commarginal ribs and wide umbones. *Cyclorisma rho-tomagensis* (d'Orbigny, 1845) from the Cenomanian of England (Cleevely & Morris, 2002, p. 154, pl. 26, fig. 9) differs in having a slightly concave antero-dorsal margin, a short anterior area and a poorly defined lunule and escutcheon. *Cyprimeria moneta* Holzapfel, 1889, from the Upper Cretaceous of Germany (Holzapfel, 1889, p. 175, pl. 12, figs 5-8) differs in being more elongate ($H/L=0.83$, as opposed to 0.96) and in having a subtruncated postero-dorsal margin and numerous, faint commarginal growth lines.

Occurrence: Albian of England (Forbes, 1845; Woods, 1908) and Cenomanian–Turonian of the Sergipe Basin (Seeling, 1999; present study).

Genus *Paraesa* Casey, 1952

Type species: *Venus faba* J. de C. Sowerby, 1827.

Remarks: In outline, the genus *Paraesa* resembles the genera *Flaventia* Jukes-Browne, 1908, *Aphrodina* Conrad, 1869, *Calva* Poponoe, 1937, *Egrona* Saul, 1993,

and *Meretrix* Lamarck, 1799. The hinge structure is a key taxonomic character to distinguish these genera. According to Casey (1952, p. 171), the hinge of the left valve in *Paraesa* has three cardinal teeth, *viz.* an anterior (2a), a posterior (4b) and a median tooth (2b₂), which form a chevron structure with the apex touching the cardinal margin. The hinge of the right valve also carries three cardinal teeth, an anterior (3a), a median (1, paired, prosocline, divergent) and a posterior (3b) tooth, consisting of two distinct lamellae. No posterior lateral teeth are present. The genera *Aphrodina* and *Calva* differ in having anterior and posterior lateral teeth.

Paraesa faba (J. de C. Sowerby, 1827)

Fig. 20; Pl. X, figs D-J

- 1827. *Venus Faba*.—J. de C. Sowerby, p. 129, pl. 567, fig. 3.
- 1836. *Venus (?) sublaevis*. M.—J. de C. Sowerby, p. 342, pl. 17, fig. 5.
- 1836. *Venus (?) immersa*. M.—J. de C. Sowerby, p. 342, pl. 17, fig. 6.
- 1862. *Venus Dutrugei* H. Coq.—Coquand, p. 193, pl. 7, figs 5-6.
- 1862. *Venus Reynesi* H. Coq.—Coquand, p. 193, pl. 7, figs 11-12.
- 1908. *Cyprimeria (Cyclorisma) faba* (Sowerby, 1827).—Woods, p. 187, pl. 29, figs 7-13.
- 1908. *Cyprimeria (Cyclorisma) sublaevis* (Sowerby, 1836).—Woods, p. 189, pl. 29, fig. 14.
- 1908. *Venus immersa*, Sowerby.—Woods, p. 189, pl. 29, fig. 15.
- 1912. *Venus (?) Reynesi* Coquand.—Pervinquier, p. 274.
- 1933. *Cyprimeria (Cyclorisma) faba* Sow.—Riedel, p. 59, pl. 11, fig. 4.
- 1934. *Venus reynesi* Coq.—Blanckenhorn, p. 251, pl. 13, fig. 151; pl. 14, fig. 154.

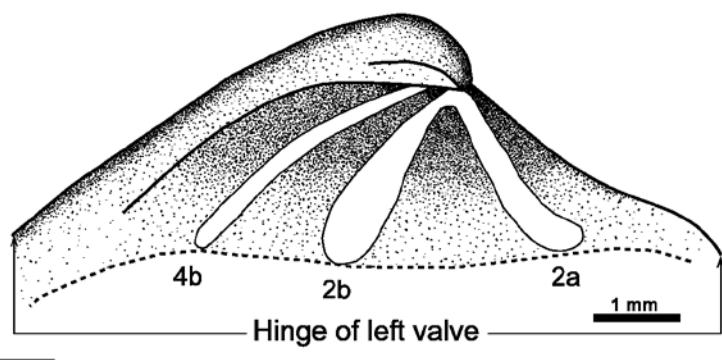
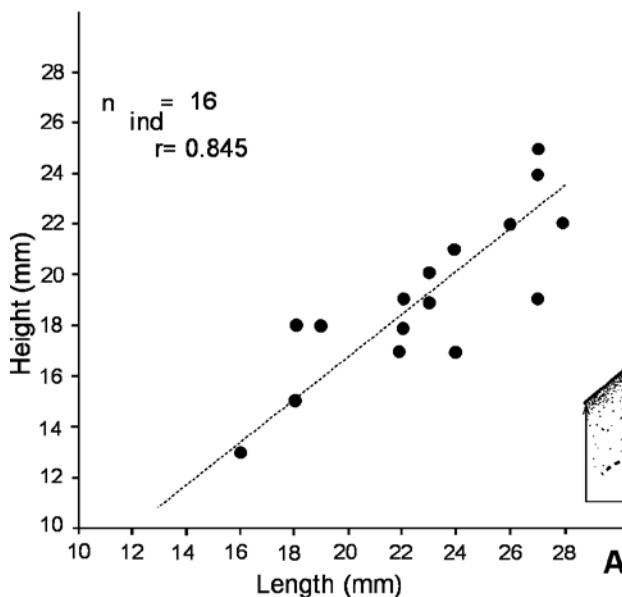


Fig. 20: *Paraesa faba* (J. de C. Sowerby, 1827) (NRM-PZ Mo168381). A, length/height ratio; B, hinge of left valve. Locality Retiro 15, middle–upper Turonian, Sergipe Basin.

1937. *Venus Reynesi* Coq.—Trevisan, p. 109, pl. 7, fig. 23.
1952. *Paraesa faba* (J. Sowerby).—Casey, p. 171, pl. 9, figs 7, 8.
1957. *Paraesa cf. faba* (Sowerby).—Darteville & Freneix, p. 184, pl. 31, figs 4-5.
1962. *Meretrix faba* (Sowerby).—Abbass, p. 146, pl. 22, fig. 21.
- ? 1962. *Meretrix dutragei* [sic] (Coquand).—Abbass, p. 147, pl. 22, fig. 22.
1972. *Paraesa faba fava* (Sowerby, 1827).—Freneix, p. 178, pl. 18, figs 10-12.
- ? 1972. *Paraesa faba* (Sowerby) *subfaba* (d'Orbigny, 1850).—Freneix, p. 180, pl. 18, figs 13-14.
- v 1999. *Paraesa faba* (J. de C. Sowerby, 1827).—Seeling, p. 130, pl. 5, figs 13-17 (except specimen 507.F2 = *Lucina fallax*).
2004. *Meretrix faba* (Sowerby).—Abdel-Gawad *et al.*, pl. 3, fig. 5.
2006. *Paraesa faba fava* (J. de C. Sowerby, 1827).—El Qot, p. 88, pl. 18, figs 1, 3.
- ? 2006. *Paraesa faba subfaba* (d'Orbigny, 1850).—El Qot, p. 90, pl. 18, fig. 2.
2013. *Paraesa faba fava* (J. De C. Sowerby, 1827).—El Qot *et al.*, p. 221, pl. 5, figs 1, 6.
2014. *Paraesa faba* (J. de C. Sowerby 1827).—Ayoub-Hannaa *et al.*, p. 122, pl. 12, fig. 1.
2014. *Paraesa faba?* (Sowerby, 1827).—Niebuhr *et al.*, p. 157, pl. 14d, f.
2015. *Paraesa faba* (J. de C. Sowerby).—Nagm, p. 15, fig. 6K.

Material: Twenty internal and composite moulds (NRM-PZ Mo168370–168389) from the middle Cenomanian to upper Turonian of localities Cruzes 8/11, Japaratuba 6, 10, 11 and 16, Laranjeiras 28, Pedra Furada 9, Retiro 15 and Mata 7, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 46.

Description: Shell small to medium-sized, ovate, inequilateral, equivalved, moderately inflated ($W/L=0.45$ on

average). Postero-dorsal margin faintly to moderately convex, higher than antero-dorsal margin, meeting posterior margin in rounded angle. Antero-dorsal margin concave below the umbones. Anterior and posterior margins strongly convex and curving into the regularly rounded ventral margin. Anterior adductor muscle scar relatively large, rounded, located near antero-dorsal margin. Pallial sinus deep (Pl. X, fig. D). Umbones broad, moderately inflated, located slightly anterior of midline. Beaks weak, prosogyrate. Escutcheon elongate and narrow. Hinge of left valve with three cardinal teeth, (2a) and (2b) forming inverted “V”, separated by triangular socket and long, narrow posterior tooth (4b) (Pl. X, fig. G, Fig. 20). Ornament consisting of numerous, closely spaced, fine, commarginal growth lines.

Discussion: Although the Brazilian specimens are articulated internal or composite moulds, some polished sections show the hinge structure, which is very similar to that of Casey's (1952) specimens of *Paraesa faba* (J. de C. Sowerby, 1827).

With respect to ornamentation, Freneix (1972) subdivided *Paraesa faba* into two subspecies, *P. faba fava* (J. de C. Sowerby, 1827) and *P. faba subfaba* (d'Orbigny, 1850). The two subspecies are very similar in outline, size and ornamentation and separation is not justified. The co-occurring species *Venus dutragei* Coquand, 1862, and *V. reynesi* Coquand, 1862, from the Cenomanian of Algeria (Coquand, 1862, p. 193, pl. 7, figs 5-6 and 11-12), closely resemble *Paraesa faba* in outline and ornamentation and are here regarded as junior synonyms. As already concluded by Freneix (1972), El Qot (2006) and Ayoub-Hannaa *et al.* (2014), both *Venus(?) sublaevis* J. de C. Sowerby, 1836, and *V. (?) immersa* J. de C. Sowerby, 1836, from the Albian of England (Woods, 1908) are junior synonyms of *P. faba*.

Occurrence: Albian of England (J. de C. Sowerby, 1827, 1836; Woods, 1908); upper Cenomanian of Germany

Table 46: Dimensions (in mm) of *Paraesa faba* (J. de C. Sowerby, 1827).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168370	19.0	18.0	10.0	0.95	0.53
NRM-PZ Mo168371	27.0	24.0	?10.0	0.89	?0.37
NRM-PZ Mo168372	16.0	13.0	9.0	0.81	0.56
NRM-PZ Mo168373	18.0	15.0	--	0.83	--
NRM-PZ Mo168374	23.0	20.0	10.0	0.87	0.43
NRM-PZ Mo168375	22.0	17.0	8.0	0.77	0.36
NRM-PZ Mo168376	22.0	19.0	9.0	0.86	0.41
NRM-PZ Mo168377	23.0	19.0	11.0	0.83	0.48
NRM-PZ Mo168379	18.0	18.0	10.0	1.00	0.56
NRM-PZ Mo168380	26.0	22.0	10.0	0.85	0.38
Range	16.0-27.0	13.0-24.0	8.0-11.0	0.77-1.0	0.36-0.56
Mean	21.4	18.5	9.67	0.87	0.45

(Niebuhr *et al.*, 2014); Albian–Turonian of Morocco (Freneix, 1972); Cenomanian (“Rhotomagien”) of Algeria (Coquand, 1862), Libya (El Qot *et al.*, 2013), Tunisia (Pervinquier, 1912) and Italy (Trevisan, 1937); Cenomanian–lower Campanian of Egypt (Abbass, 1962; Abdel-Gawad *et al.*, 2004; El Qot, 2006; Ayoub-Hannaa *et al.*, 2014); Turonian of Cameroon and the Republic of the Congo (Riedel, 1933; Darteville & Freneix, 1957); Cenomanian–Turonian of the Sergipe Basin (Seeling, 1999; present study).

Superorder Pholadiformii Gray, 1854

Order Pholadida Gray, 1854

Superfamily Pholadoidea Lamarck, 1809

Family Pholadidae Lamarck, 1809

Subfamily Xylophagini Purchon, 1941

Genus *Xylophagella* Meek, 1864

Type species: *Xylophaga elegantula* Meek & Hayden, 1858.

Remarks: The genus *Xylophagella* is distinguished from other genera of the Pholadidae by its nearly straight umbonal-ventral groove and subvertical posterior ridge, and by being smaller, more inflated, globular and lacking accessory plates such as metaplax, mesoplax, protoplax and hypoplax. According to Stephenson (1941, p. 249), *Goniochasma* Meek, 1864, is more elongate than *Xylophagella* and has a mesoplax over the beaks, which is not observed in *Xylophagella*. In addition, *Goniochasma* also differs in having an oblique, deep umbonal-ventral groove, a strongly oblique posterior ridge, and in being anteriorly inflated. *Opertochasma* Stephenson, 1953, from the Cenomanian of Texas, USA, differs in having two radial umbonal-ventral grooves instead of one and less developed commarginal ribs.

Xylophagella? sp.

Pl. X, figs K-N

Material: One distorted specimen (NRM-PZ Mo168390) from the lower Cenomanian of locality Itaporanga 2/3, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 47.

Description: Shell small, subtriangular, inequilateral and strongly inflated. Maximum inflation anteriorly. Anterodorsal margin short, rounded, strongly arched, meeting anterior margin in rounded angle. Umbonal-ventral groove well developed, nearly straight, moderately depressed, extending to ventral margin (Pl. X, fig. K). Posterior ridge well developed, oblique (Pl. X, fig. M). Anterior cavity wide and deep, extending from beaks to

antero-ventral angles of both valves and separated from the rest of valve by a moderately well-developed anterior umbonal ridge. Umbones triangular, strongly convex, located approximately half of total valve length from anterior end. Beaks prominent, strongly prosogyrate. Ornament not preserved, except for faint commarginal ribs near ventral margin.

Discussion: The Brazilian specimen is distorted and poorly preserved but closely resembles *Xylophagella* in its small, inflated valves, nearly straight umbonal-ventral groove and slightly oblique posterior ridge.

Xylophagella elegantula (Meek & Hayden, 1858) from the Upper Cretaceous of North America (Meek & Hayden, 1858, p. 141) resembles the Brazilian specimen in its small size and in having prominent and strongly enrolled umbones but differs in being more inflated and in having a subvertical posterior ridge and well-developed commarginal ribs. *Goniochasma scaphoides* Stephenson, 1941, from the Upper Cretaceous of Texas, USA (Stephenson, 1941, p. 249, pl. 46, figs 1-4) is more elongate (H/L=0.53, as opposed to 0.91) and more compressed (W/L=0.47) and has numerous, faint commarginal ribs. *Opertochasma venustum* Stephenson, 1953, from the Cenomanian of Texas (Stephenson, 1953, p. 139, pl. 34, figs 13-16) is somewhat similar in outline and size but differs in having two umbonal-ventral grooves, a truncated anterior margin, a broad, straight ventral valve and a strongly oblique posterior umbonal ridge. *Martesia tundens* Stoliczka, 1870, from the Aptian–Turonian of India (Stoliczka, 1870, p. 24, pl. 2, figs 5-6) resembles the Brazilian specimen in having an umbonal-ventral groove, a well-developed posterior ridge and a rounded anterior margin, but differs in having a well-preserved mesoplax above the beaks and in being more elongate and less inflated.

Superfamily Myoidea Lamarck, 1809

Family Corbulidae Lamarck, 1818

Subfamily Caestocorbolinae Vokes, 1945

Genus *Caestocorbula* Vincent, 1910

Type species: *Corbula henckeliusiana* Nyst, 1836.

Remarks: Vokes (1946, p. 207) considered *Parmicorbula* Vokes, 1944 (*in Cox et al.*, 1969, p. N696) a subgenus of *Caestocorbula*. According to Koza (1987, p. 326), *Parmicorbula* differs from *Caestocorbula* in having a shallow, inconspicuous groove on the siphonal plate. However, Squires & Saul (2004, p. 120) regarded *Caestocorbula* (*Caestocorbula*) as very similar to *Caestocorbula* (*Parmicorbula*) and fossil specimens of *Caestocorbula* as virtually indistinguishable from *Parmicorbula*, unless their accessory siphonal plate posterior of the right valve is preserved. *Caestocorbula* is characterised by (1) small to moderately sized valves, (2) a trigonal to subtrigonal outline, (3) strongly inequilateral and moderately inflated valves, (4) a right valve extending posteriorly into a prominent rostrum, (5)

Table 47: Dimensions (in mm) of *Xylophagella?* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168390	11.0	10.0	?10.0	0.91	?0.91

strong commarginal ribs on the right valve and (6) a well-developed posterior umbonal keel on the right valve.

***Caestocorbula olivae* (Whitfield, 1891)**

Pl. X, figs O-Q

1891. *Corbula olivae*.—Whitfield, p. 386, pl. 7, figs 19-21.
 p? 1934. *Corbula substriatula* d'Orb.—Andert, p. 340, pl. 15, fig. 14, non figs 13, 15-16.
 1934. *Corbula olivae* Whitf.—Blanckenhorn, p. 263, pl. 14, figs 168-169.
 1946. *Caestocorbula olivae* (Whitfield, 1891).—Vokes, p. 207, pl. 10, figs 18-21.

Material: 12 composite moulds (NRM-PZ Mo168391–168402) from the middle Cenomanian to upper Turonian of localities Jardim 7 and 24, Cruzes 6 and 8/11, Jericó 6, Itaperoá 1, Laranjeiras 3, Ribeira 11 and Mata 7, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 48.

Description: Shell small, subtrapezoidal, elongate, longer than high ($H/L=0.70$ on average), strongly inequilateral, inflated and tapering posteriorly. Anterior margin narrow, subtruncated, meeting ventral margin in rounded angle. Postero-dorsal margin slightly concave, gradually sloping posteriorly and forming narrow posterior end (angulate appearance). Ventral margin broad, moderately rounded. Right valve extending posteriorly into smooth and short rostrum (Pl X, fig. P). Posterior umbonal ridge moderately well developed, separating posterior rostrum from rest of valve. Umbones wide, strongly enrolled (Pl. X, fig. O), located one-third of total valve length from anterior end. Beaks prominent, sharp and slightly prosogyrate. Ornament consisting of well-developed, thick, rounded commarginal ribs (weakening dorsally), separated by wide and smooth interspaces; ribs vanishing posteriorly, not extending across posterior rostrum (Pl. X, figs O-P).

Discussion: The Brazilian specimens closely resemble *Caestocorbula olivae* (Whitfield, 1891) from the Lower Cretaceous of Syria (Blanckenhorn, 1934) and Lebanon (Vokes, 1946) in having thick commarginal ribs, a smooth posterior rostrum and wide, strongly convex, enrolled umbones, but the commarginal ribs of Vokes's specimens are slightly undulating.

Table 48: Dimensions (in mm) of *Caestocorbula olivae* (Whitfield, 1891).

Specimen	L	H	nr	H/L
NRM-PZ Mo168391	7.0	5.5	15.0	0.78
NRM-PZ Mo168392	9.0	7.0	17.0	0.78
NRM-PZ Mo168393	8.0	5.5	23.0	0.69
NRM-PZ Mo168394	9.0	5.0	18.0	0.56
Range	7-8	5-7	15-23	0.56-0.78
Mean	8.25	5.75	18	0.70

Caestocorbula olivae resembles *Corbula elegans* J. de C. Sowerby, 1827, from the upper Albian of England (J. de C. Sowerby, 1827, p. 139, pl. 572, fig. 1) in having a moderately extended rostrum, a posterior umbonal ridge and sharp, slightly prosogyrate beaks, but *C. elegans* has a triangular outline and more numerous and posteriorly fine commarginal ribs. *Corbula striatula* J. de C. Sowerby, 1827, from the Albian of the same area (J. de C. Sowerby, 1827, p. 139, pl. 572, figs 2-3) differs in being more elongate ovate and in having a well-developed posterior umbonal ridge, less enrolled umbones and numerous, fine commarginal ribs. Because of the great similarity between *Corbula substriatula* d'Orbigny, 1850, from the Upper Cretaceous of Germany (Andert, 1934, pl. 15, fig. 14) and *C. olivae*, Andert's specimens are probably better referred to the latter species. *Caestocorbula semina* Vokes, 1946, from the Lower Cretaceous of Lebanon (Vokes, 1946, p. 208, pl. 10, figs 22-24) differs from *C. olivae* in having a somewhat longer posterior rostrum, a less enrolled umbo of the right valve, less developed commarginal ribs and in being smaller ($L=6.6$, $H=5$, $W=4.5$ mm). *Caestocorbula crassiplicata* (Gabb, 1860) from the Upper Cretaceous of Texas, USA (Stephenson, 1941, p. 234, pl. 44, figs 16-17) resembles *C. olivae* in size and outline, but differs in having thick, overlapping commarginal ribs separated by deep interspaces and in being less elongate. *Corbula eretzsraelensis* Shalem, 1928, from the Cenomanian of Palestine (Shalem, 1928, p. 85, pl. 4, fig. 16) differs in having fine commarginal striae and wide umbones. *Caestocorbula attina* Squires & Saul, 2004, from the Cenomanian of the Pacific slope of North America (Squires & Saul, 2004, p. 121, figs 55-57) closely resembles *C. olivae* in outline, size and ornamentation, but differs in being slightly taller. *Caestocorbula aura* Squires & Saul, 2004, from the Turonian of the same area (Squires & Saul, 2004, p. 122, figs 58-59) differs in having smooth umbones.

Occurrence: Lower Cretaceous of Syria (Whitfield, 1891; Blanckenhorn, 1934) and Lebanon (Vokes, 1946), Upper Cretaceous of Germany (Andert, 1934) and Cenomanian-Turonian of the Sergipe Basin (this study, first record).

***Caestocorbula cf. striatuloides* (Forbes, 1846)**

Pl. X, figs R-T

- cf. 1846. *Corbula striatuloides* sp. nov.—Forbes, p. 141, pl. 18, fig. 14.
 cf. 1870. *Corbula striatuloides*, Forbes.—Stoliczka, p. 43, pl. 16, figs 13-14.
 cf. 1902. *Corbula striatuloides*, Forb.—Quaas, p. 231, pl. 25, figs 12-15.

Material: Five articulated specimens in shell preservation (NRM-PZ Mo168403–168407) from the upper Cenomanian of locality Timbó 4, Cotinguiba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 49.

Description: Shell very small, oblong, inequilateral, inequivaled and moderately inflated ($W/L=0.64$ on average). Right valve larger and more inflated than left valve (Pl. X, figs S, T). Antero-dorsal and postero-dorsal margins of right valve slightly concave. Anterior margin narrow, strongly rounded, meeting strongly convex ventral margin in rounded curve. Right valve extended posteriorly, forming a short rectangular rostrum. Posterior margin of left valve non-rostrate, strongly convex, meeting ventral margin in rounded angle. Umbones triangular, strongly inflated, located one-third of total valve length from anterior end. Umbo of right valve more inflated than that of left valve and overhanging hinge line (Pl. X, fig. S). Beaks prominent, sharply pointed and slightly prosogyrate. Right valve ornamented with numerous, well-developed commarginal ribs, separated by narrow interspaces and increasing in strength towards ventral margin. Left valve recrystallized without any sign of ornamentation. Internal characters such as hinge and muscle scars not seen.

Discussion: *Caestocorbula striatuloides* closely resembles *Corbula parsura* Stoliczka, 1870, from the Coniacian–Santonian of South India (Stoliczka, 1870, p. 44, pl. 1, figs 23–24; pl. 16, figs 3–4) in size, general outline and ornamentation but differs in having a much larger left valve. *Caestocorbula eretzsraelensis* (Shalem, 1928) from the Cenomanian of Palestine (Shalem, 1928, p. 85, pl. 4, fig. 16) is somewhat similar in having small valves, a short posterior rostrum and numerous, fine, commarginal ribs, but differs in its triangular valves, narrowly triangular umbones and well-developed posterior umbonal ridge. *Caestocorbula olivae* (Whitfield, 1891), described above, differs in having fewer and thick commarginal ribs and a narrower posterior rostrum.

Occurrence: *Caestocorbula striatuloides* (Forbes, 1846) has been recorded from the Upper Cretaceous of India (Forbes, 1846; Stoliczka, 1870) and Egypt (Quaas, 1902) and here provisionally from the Cenomanian of the Sergipe Basin (first record).

Megaorder Solenata Dall, 1889

Order Hiatellida Carter *et al.*, 2011

Superfamily Hiatelloidea J. Gray, 1824

Family Hiatellidae J. Gray, 1824

Subfamily Panopeinae Brönn, 1862

Genus *Panopea* Ménard de la Groye, 1807

Type species: *Panopea glycimeris* (Born, 1778).

***Panopea* sp.**

Pl. X, fig. U

Material: One incomplete composite mould (NRM-PZ Mo168408) from the lower–middle Turonian of locality Pedra Furada 4, Cotinguba Formation, Sergipe Basin, Brazil.

Measurements: cf. Table 50.

Description: Shell large, oblong and moderately inflated. Postero-dorsal margin slightly concave, meeting posterior margin in obtuse angle. Posterior margin slightly convex, meeting ventral margin in rounded angle. Ventral margin nearly straight and parallel to dorsal margin. Faint posterior umbonal ridge separating weakly concave posterior flank from rest of valve. Umbones convex, subcentral. Beaks not preserved. Ornament consisting of irregular, faint commarginal striae.

Discussion: Based on size, outline and ornamentation, the specimen is assigned to the genus *Panopea*, but the missing beaks and the poor preservation do not allow a specific identification.

Panopea decis Conrad, 1853, from the Upper Cretaceous of New Jersey, USA (Weller, 1907, p. 646, pl. 73, figs 3–5) resembles the Brazilian specimen in size and outline but differs in having thick commarginal ribs and in being larger ($L=80$, $H=51$ mm, as opposed to $L=53$, $H=39$ mm). “*Panopea*” *monmouthensis* Gardner, 1916, from the Upper Cretaceous of Maryland, USA (Gardner, 1916, p. 722, pl. 45, figs 4–5) is similar in outline and the presence of a posterior umbonal ridge and faint commarginal ribs but differs in having near-mesial umbones and an obliquely truncated posterior margin. *Panopea mandibula* (J. Sowerby, 1813) from the Albian of Germany (Andert, 1934, p. 327, pl. 15, figs 1–2)

Table 50: Dimensions (in mm) of *Panopea* sp.

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168408	53	39	--	0.74	--

Table 49: Dimensions (in mm) of *Caestocorbula* cf. *striatuloides* (Forbes, 1846).

Specimen	L	H	W	H/L	W/L
NRM-PZ Mo168403	6.0	5.5	4.1	0.92	0.68
NRM-PZ Mo168404	6.6	5.9	4.2	0.89	0.64
NRM-PZ Mo168405	6.5	5.7	4.5	0.88	0.69
Range	6.0–6.6	5.5–5.9	4.1–4.5	0.88–0.92	0.64–0.69
Mean	6.37	5.7	4.27	0.89	0.64

and the Maastrichtian of Poland (Abdel-Gawad, 1986, p. 174, pl. 42, fig. 8; pl. 43, fig. 3) resembles the Brazilian specimen in having an oblong valve but differs in the umbonal-ventral depression and the presence of thick commarginal ribs.

Occurrence: Turonian of the Sergipe Basin (this study).

6. PALAEOBIOGEOGRAPHIC REMARKS

According to Seeling & Bengtson (2002, p. 156), a problem in palaeobiogeographic analysis of the upper Cenomanian to lower Turonian bivalve fauna of the Sergipe Basin is the scarcity and poor preservation of many taxa, in particular the heterodonts. As a result of diagenetic dissolution of the calcareous shells, most heterodonts are preserved as internal or composite moulds. However, for some better preserved specimens, identification at species level is possible.

The heterodont fauna of the Sergipe Basin is composed of geographically widely distributed taxa. The fauna shows strong Tethyan affinities, in particular with the West African coastal basins of Gabon, Cameroon and Nigeria, northern Africa (Egypt, Libya, Tunisia, Algeria), southern Europe (Portugal, Spain, southern France, Italy) and the eastern Mediterranean region (e.g., Jordan, Lebanon, Palestine, Israel, Syria) (Fig. 21A-B). The wide distribution of this group of bivalves is probably the result of long-lasting larval stages. On the basis of the close affinity between the heterodonts of the Sergipe Basin and those of the southern Tethyan regions, the basin is assigned to the Indo-Mediterranean region of the Tethyan Realm (*sensu* Kauffman, 1973) or to the Mediterranean–Caucasian Subrealm (*sensu* Westermann, 2000), as also suggested by Seeling & Bengtson (2002, p. 157).

During the Albian, the South American continent was separated from Africa by the incipient South Atlantic Ocean, although the two continents still remained in close proximity (Néraudeau & Mathey, 2000, p. 76). Consequently, faunal exchange between the South Atlantic and the western Tethys was possible, with the former becoming wider and deeper during the mid Cenomanian–early Turonian. According to Voigt (1995, p. 343), shoal ridges and extensive intraplate shelf areas formed, and the waters flooded large parts of the continents to form epicontinental seas. Heterodont bivalves were widely distributed across northern and western Africa and southern Europe (Fig. 21A). Faunal dispersal along the margins of northern and western Africa was probably facilitated by the presence of extensive shallow shelf areas during that time. In West Africa, a trans-Saharan seaway became established during the late Cenomanian–early Turonian transgression (Reyment & Tait, 1972; Collignon & Lefranc, 1974; Voigt, 1995). Most heterodont taxa of the Mediterranean Tethys colonised the northern part of the South Atlantic via the trans-Saharan seaway during the late Cenomanian, as confirmed by the great similarity

between the taxa of northern and western Africa (e.g., Algeria, Tunisia, Egypt, Cameroon, Nigeria, Angola) and north-eastern South America (Brazil). These taxa include *Astartemya (Freiastarte) similis* (Münster), *Agelasina plenodonta* Riedel, *Granocardium (G.) productum* (J. de C. Sowerby), *Protocardia (Pachycardium) pauli* (Coquand) and *Protocardia (P.) hillana* (J. Sowerby). The latter taxa have not been recorded from western South America, which suggests faunal exchange via the trans-Saharan seaway rather than the Caribbean or northern South America. The scarcity of heterodont taxa in southern North America is probably a result of the great distance and depth of the Atlantic Ocean and/or water temperature.

Dhondt *et al.* (1999) noted that during the Albian–Cenomanian and Coniacian–Santonian, dispersal of oysters was probably influenced by west–east-directed currents. By contrast, during the Santonian–Campanian, the direction of currents changed to east–west, probably as a result of tectonic activities. The present study suggests that during the late Cenomanian–early Turonian, dispersal occurred along the southern and northern margins of the Tethys mainly from east to west. The westward migration split into a southern route through the trans-Saharan Seaway and a northern route along southern Europe and northern Africa. The dispersal of heterodont taxa across Europe (e.g., Portugal, England and southern France) indicates the existence of a clockwise marine current system. Ayoub-Hannaa *et al.* (2014) suggested that the dispersal of oysters and rudists along south-eastern Europe and western Africa was probably influenced by the presence of extensive shallow shelf areas during the Cenomanian and/or narrowing of the Tethys.

7. CONCLUSIONS

1. Fifty heterodont taxa, belonging to 35 genera, 15 families and six orders are described from the Cenomanian–Coniacian Cotinguba Formation of the Sergipe Basin, north-eastern Brazil.
2. One new species, *Callucina (Callucina) itaporangensis*, is described and figured from the lower Cenomanian of localities Itaporanga 2 and 2/3 (Graysonites lozoi Interval Zone).
3. Thirty-three species are recorded from the Sergipe Basin for the first time, in beds assigned to the lower Cenomanian to upper Turonian (possibly also uppermost Albian and lowermost Coniacian) on the basis of co-occurring ammonites. They are *Crassatella (C.) pusilla* Coquand, 1862, *C. (C.) vadosa* Morton, 1834, *Astarte (A.) cf. numismalis* d'Orbigny, 1844, *Tridonta (T.) cf. gigantea* (Deshayes, 1842), *Opis (Hesperopis) triangulata* (Cooper, 1894), *Lucina dachelensis* Wanner, 1902, *L. fallax* Forbes, 1846, *L. subnumismalis* d'Orbigny, 1850, *Callucina (C.) itaporangensis* sp.

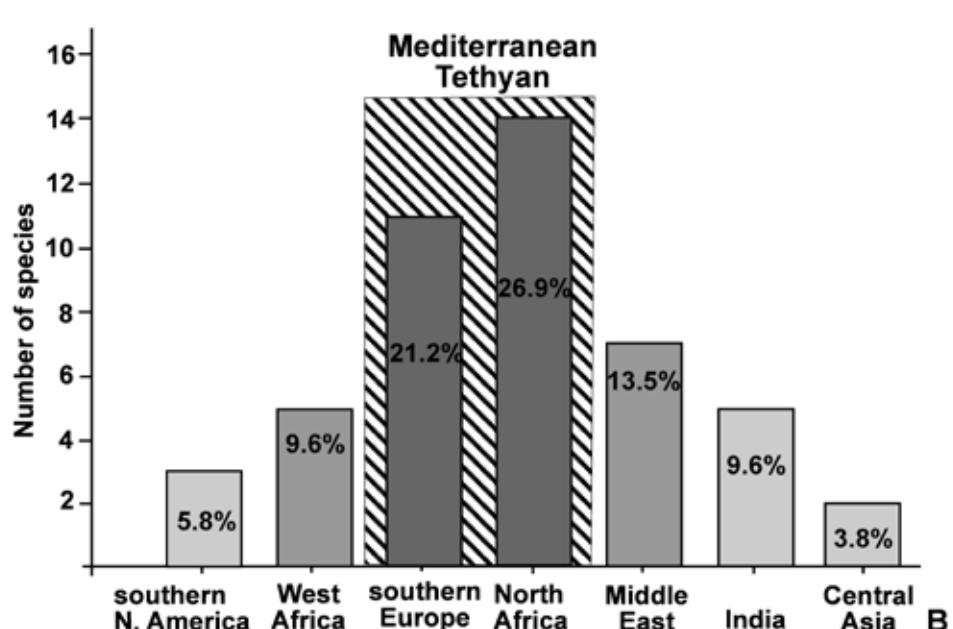
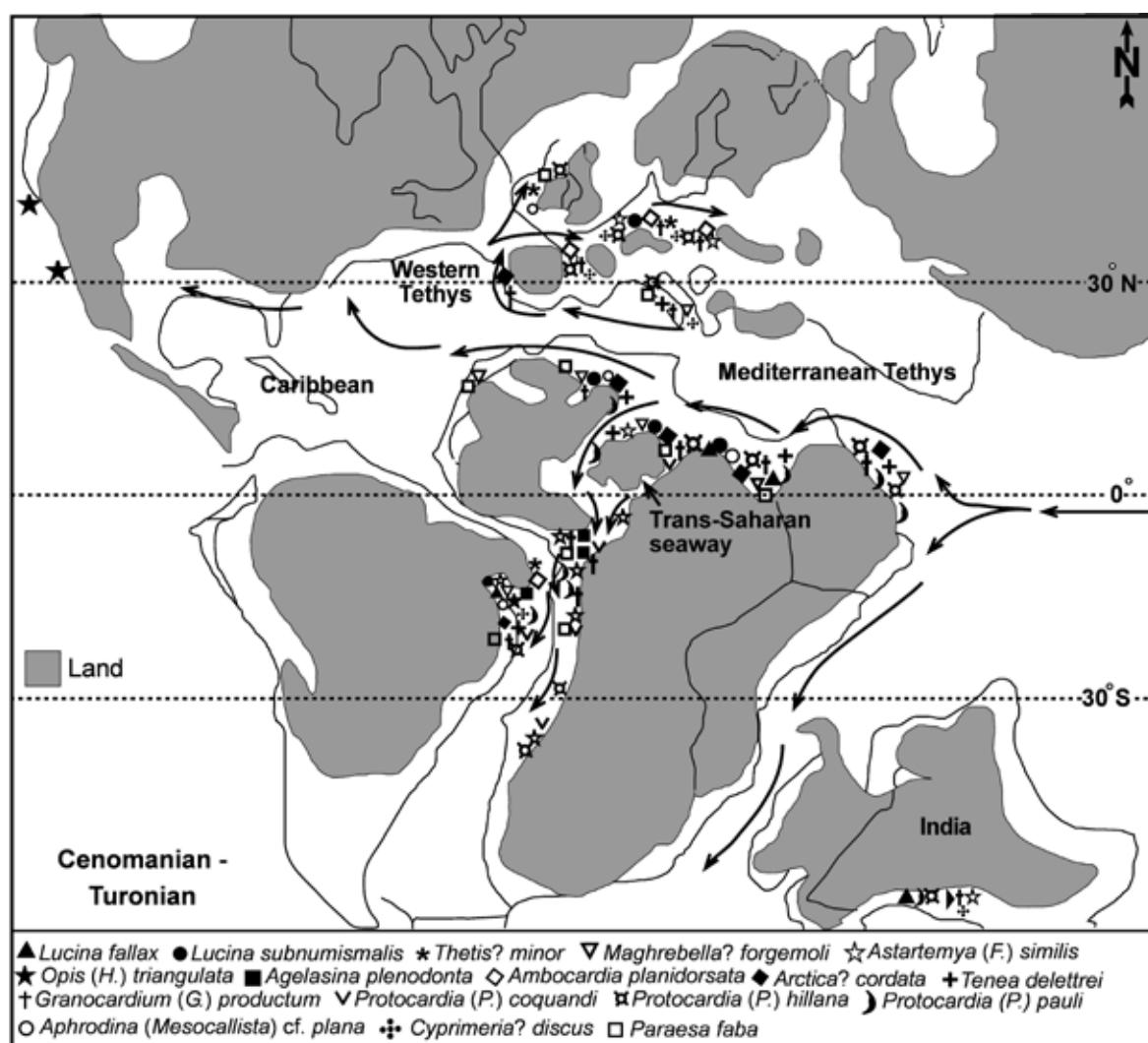


Fig. 21: A, Reconstruction of surface-water currents during the Cenomanian–Turonian, based on the distribution patterns of selected heterodont species (palaeogeographic base map after Seeling & Bengtson, 1999). B, Diversity of heterodont taxa (based on number of species) in the Mediterranean region, Middle East, South Atlantic and West Africa.

- nov., *Thetis? minor* J. de C. Sowerby, 1826, *Agelasina plenodonta* Riedel, 1933, *Ambocardia planidorsata* (Zittel, 1864), *Protocardia (P.) coquandi* (Seguenza, 1882), *P. (P.) hillana* (J. Sowerby, 1813), *Protocardia (Pachycardium) cf. moevusi* (Coquand, 1862), *Granocardium (G.) productum* (J. de C. Sowerby, 1832), *G. (G.) tenuistriatum* (Whitfield, 1885), *Arctica? cordata* (Sharpe, 1850), *Etea carolinensis* Conrad, 1875, *Izumia? saussuri* (Brongniart, 1821), *Proveniella cf. testacea* (Zittel, 1864), *Tenea delettrei* (Coquand, 1862), *Veniella byzacenica* (Pervinquier, 1912), *V. trapezoidea* Conrad, 1860, *Trapezium africanum* (Coquand, 1862), *Cymbophora? scabellum* Stephenson, 1941, *C.? subtilis* Stephenson, 1941, *Geltena subequilatera* Stephenson, 1946, *Mulinoides cf. olbrechtsi* Darteville & Freneix, 1957, *Cyprimeria? discus* (Matheron, 1843), *C.? cf. riograndensis* Maury, 1934, *Caestocorbula olivae* (Whitfield, 1891) and *C. cf. striatuloides* (Forbes, 1846).
4. The heterodont taxa of the Sergipe Basin occurred across a wide geographic area, extending from the Middle East, northern Africa and Europe to western Africa and the Pacific rim of South America, with some species also known from south-eastern India.
 5. The biogeographic pattern suggests that many groups migrated via the shallow trans-Saharan seaway, which connected the southern Tethys with the incipient South Atlantic Ocean.
 6. The wide distribution of heterodont bivalves indicates that their planktotrophic larvae were long-lived and consequently possessed a high dispersal potential.

ACKNOWLEDGMENTS

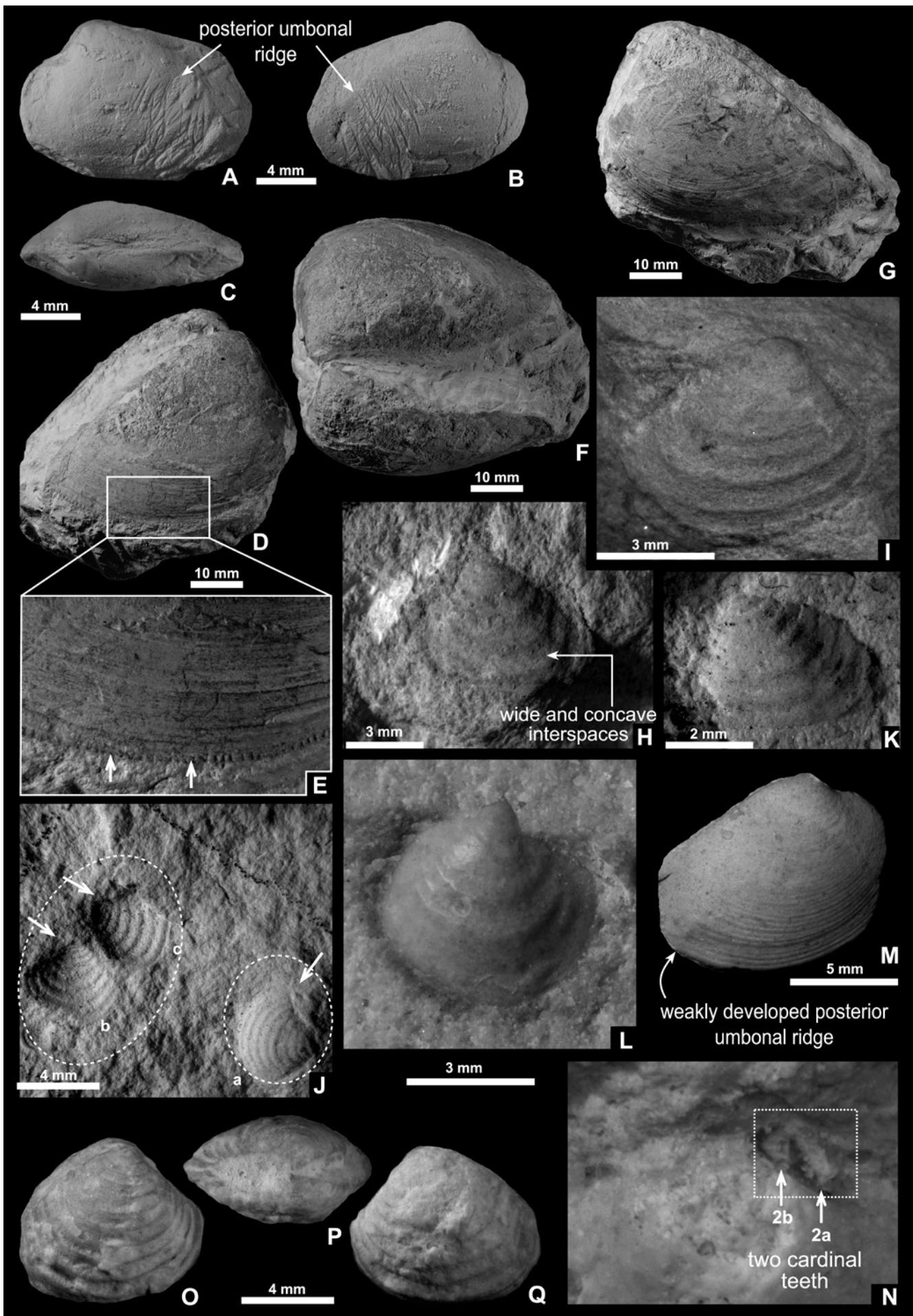
We thank Mrs Lisa Egger and Birgit Leipner-Mata (Erlangen) for the photographic work and for preparing the polished slabs and silicone moulds, respectively. P. B. thanks Suzana I. Bengtson (Heidelberg), Diógenes A. Campos (DNPM, Rio de Janeiro) and Petrobras S.A. (Aracaju and Rio de Janeiro) for field and logistic assistance. The fieldwork was financed mainly by the Swedish Natural Science Research Council (NFR, now Vetenskapsrådet, VR). E. J. A. acknowledges financial support by the German Academic Exchange Service (DAAD) and thanks Milton J. Andrade (Aracaju) for assistance in the field. We thank the two reviewers, Michael R. Cooper (Durban) and Dario G. Lazo (Buenos Aires), for their careful and constructive criticism of the manuscript.

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Plate I

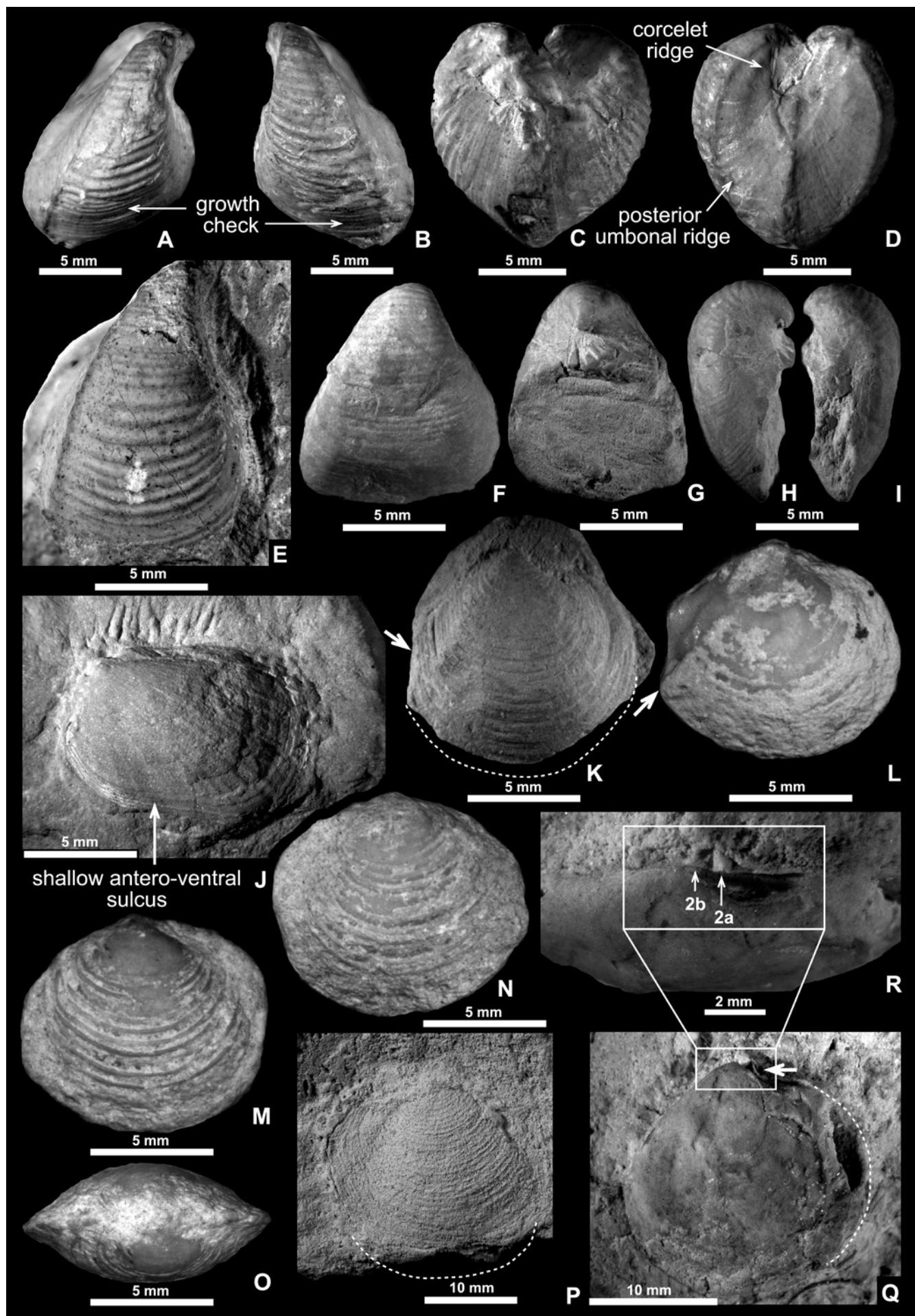
- Figs A-C: *Crassatella (Crassatella) pusilla* Coquand, 1862, articulated internal mould (NRM-PZ Mo167949). A, left lateral view. B, right lateral view showing well-developed posterior umbonal ridge. C, dorsal view, locality Cruzes 8, middle-upper Cenomanian.
- Figs D-G: *Crassatella (Crassatella) vadosa* Morton, 1834, composite mould (NRM-PZ Mo167950), locality Pedra Furada 4, lower-middle Turonian. D, right lateral view. E, close-up showing the crenulate inner margin of valve. F, dorsal view. G, left lateral view.
- Figs H-I: *Astarte (Astarte) cf. numismalis* d'Orbigny, 1844, composite moulds, locality Boa Sorte 11, lower Turonian. H, left lateral view (NRM-PZ Mo167958), showing wide, concave and deep interspaces between ribs. I, right lateral view (NRM-PZ Mo167954).
- Figs J-K: *Astarte (Astarte) tenuicosta* (Seguenza, 1882). J, left lateral views (a-b) (NRM-PZ Mo167970 and Mo167971) and right lateral view (c) (NRM-PZ Mo167972), locality Machado 4, lower-middle Turonian. K, left lateral view (NRM-PZ Mo167988), locality São Pedro 14, lower-middle Turonian.
- Fig. L: *Astarte (Astarte) cf. upwarensis* Woods, 1906, composite mould (NRM-PZ Mo167991), left lateral view, locality Laranjeiras 5, upper Cenomanian.
- Figs M-N: *Tridonta (Tridonta) cf. gigantea* (Deshayes, 1842). M, right lateral view, composite mould (NRM-PZ Mo167994), locality Jericó 6, middle Cenomanian. N, close-up (NRM-PZ Mo167995) showing two cardinal teeth with deep triangular cardinal socket in-between, locality Mata 7, upper Turonian.
- Figs O-Q: *Astartemya (Freiastarte) similis* (Münster in Goldfuss, 1837), composite mould (NRM-PZ Mo168011), locality Timbó 4, upper Cenomanian. O, right lateral view. P, dorsal view. Q, left lateral view.



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Plate II

- Figs A-E: *Opis (Hesperopis) triangulata* (Cooper, 1894), middle–upper Cenomanian. A-D, distorted composite mould, locality Jardim 24 (NRM-PZ Mo168025). E, composite mould, Jardim 22 (NRM-PZ Mo168027). A, right lateral view, showing growth checks near ventral margin. B, left lateral view. C, anterior view of articulated valves. D, posterior view showing well-developed corcelet and posterior umbonal ridge. E, right lateral view, showing well-developed posterior umbonal ridge.
- Figs F-I: *Opis (Hesperopis)* sp., composite mould of right valve, lower Cenomanian, Itaporanga 2/3 (NRM-PZ Mo168028). F, lateral view. G, hinge view. H, anterior view showing strongly enrolled umbones. I, posterior view showing a poorly developed corcelet and posterior umbonal ridge.
- Fig. J: *Magharella? forgemoli* (Coquand, 1862), composite mould, left lateral view showing posteriorly directed, shallow antero-ventral sulcus (arrowed), upper Cenomanian, Japaratuba 4 (NRM-PZ Mo168029).
- Figs K-O: *Lucina dachelensis* Wanner, 1902, lower Cenomanian. K, composite mould, right lateral view showing concave posterior flank (arrowed), Itaporanga 2/3 (NRM-PZ Mo168031). L, right lateral view (in shell preservation) showing well-developed posterior umbonal ridge (arrowed), locality Itaporanga 2/3 (NRM-PZ Mo168037). M-O: Composite mould, Itaporanga 2/3 (NRM-PZ Mo168030). M, left valve view showing well-developed commarginal ribs with wide interspaces. N, side view of right valve. O, dorsal view.
- Figs P-R: *Lucina fallax* Forbes, 1846, upper Cenomanian–upper Turonian. P, left side view, composite mould showing faint and numerous commarginal ribs with compressed valves (forma typica), Tabocas 2 (NRM-PZ Mo168088). Q, right lateral view, internal mould. R, close-up showing two cardinal teeth and one socket in-between, Japaratuba 11 (NRM-PZ Mo168089).

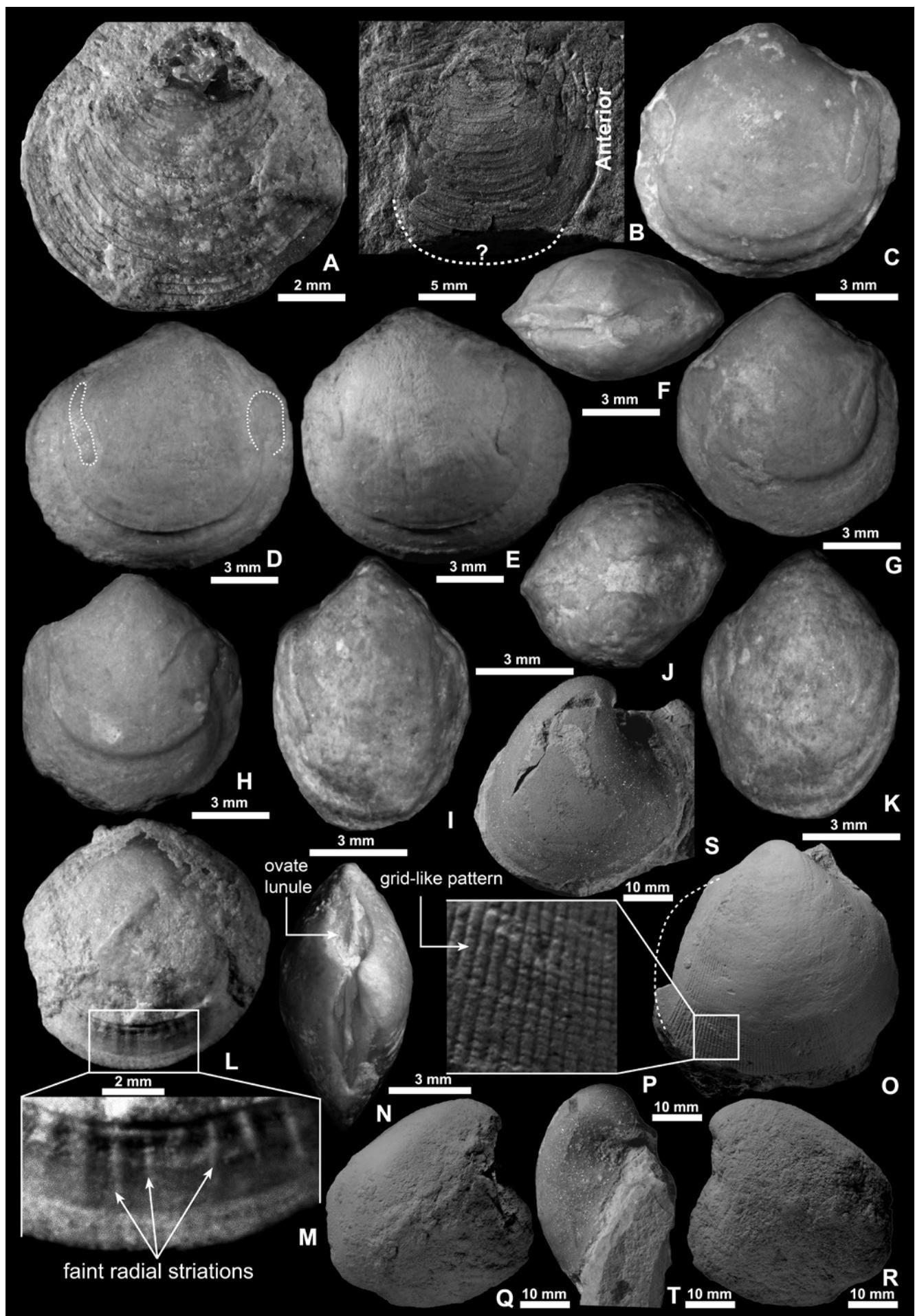


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Plate III

- Figs A-B: *Lucina subnumismalis* d'Orbigny, 1850, upper Turonian. A, left valve, lateral view, locality Estiva 12 (NRM-PZ Mo168101). B, right valve, incomplete, lateral view showing wide and concave interspaces between ribs, locality Cajaíba 2 (NRM-PZ Mo168093).
- Figs C-N: *Callucina (Callucina) itaporangensis* sp. nov., variation in outline, lower Cenomanian. C, composite mould, right lateral view, (rounded form, L=H) showing elongate, narrow anterior adductor muscle scar, Itaporanga 2/3, Paratype (MN 8981-I). D, E: Composite mould, Itaporanga 2, Holotype (MN 8980-I). D, right lateral view (subrounded form, L>H) showing entire pallial line. E, left lateral view. F-H: Composite mould of articulated specimen, Itaporanga 2/3, Paratype (MN 8987-I). F, dorsal view showing the elongated, narrow, ovate escutcheon. G, right lateral view (elongate form L<H). H, left lateral view. I-K: composite mould, Itaporanga 2/3, Paratype (MN 8988-I). I, left lateral view (elongate ovate form, L<H) showing a narrow, elongate anterior adductor muscle scar. J, dorsal view. K, right lateral view. L-M: composite mould, Itaporanga 2/3, (NRM-PZ Mo168241). L, left lateral view. M, close-up showing radial ribs and crenulate ventral margin. N, composite mould, dorsal view of articulated valves showing well-developed ovate lunule, Itaporanga 2/3, Paratype (MN 8982-I).
- Figs O-P: *Thetis? minor* J. de C. Sowerby, 1826, lower Cenomanian. O, right valve, composite mould. P, close-up showing a grid-like pattern of right valve close to ventral margin Itaporanga 4 (NRM-PZ Mo168246).
- Figs Q-T: *Agelasina plenodonta* Riedel, 1933, upper Turonian. Q, R: Internal mould, Mucuri 10 (NRM-PZ Mo168247). Q, right lateral view. R, left lateral view. S-T: Internal mould, Oiteiro 19 (NRM-PZ Mo168248). S, right lateral view, T, anterior view showing wide lunule and strongly incurved beak.

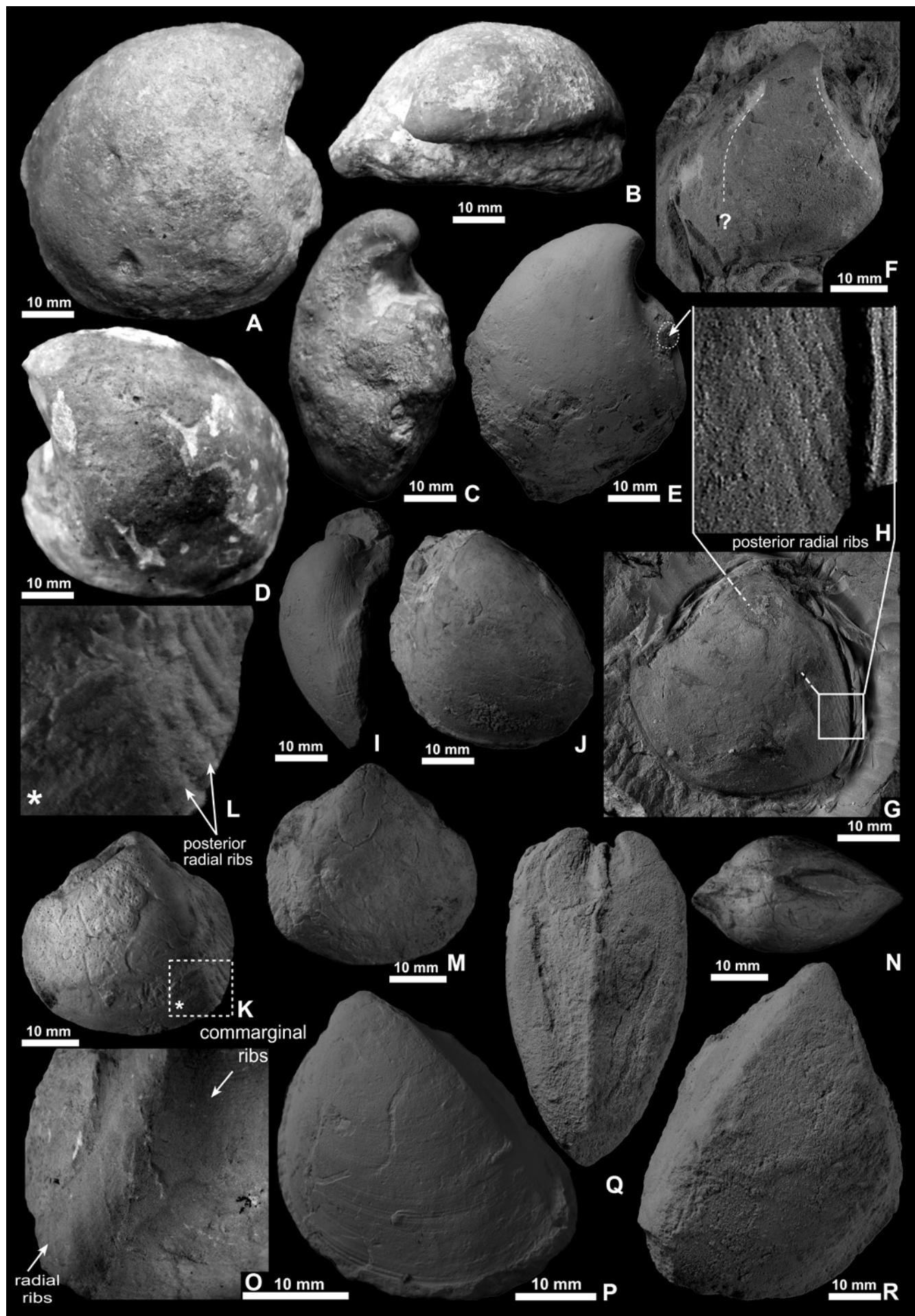
Plate III



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Plate IV

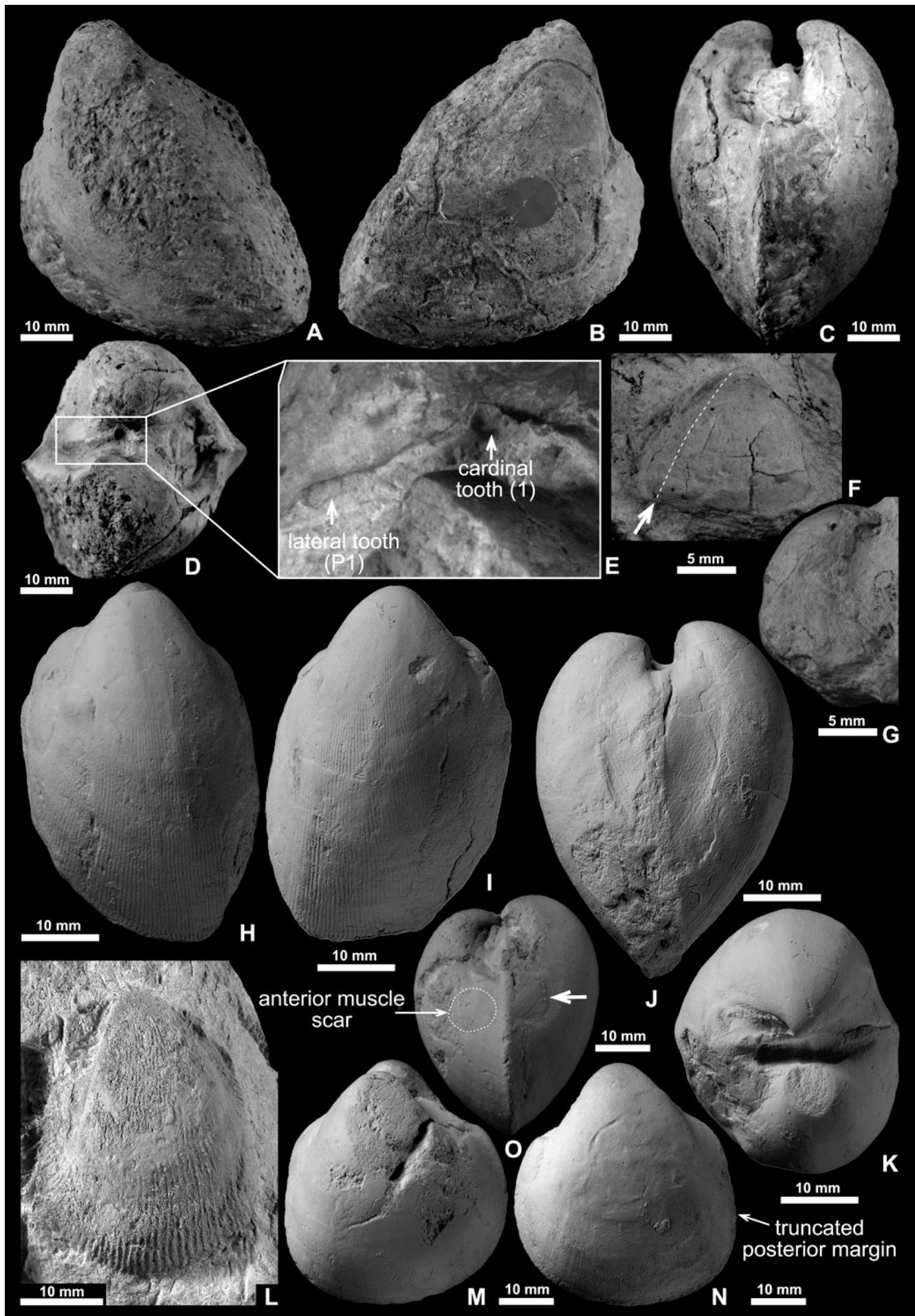
- Figs A-D: *Agelasina plenodonta* Riedel, 1933, upper Turonian. A-C: Composite mould of right valve, Mata 11 (NRM-PZ Mo168250). A, lateral view showing the small anterior and posterior adductor muscle scars (arrowed) and faint commarginal ribs close to the ventral margin. B, dorsal view showing the strongly incurved umbo. C, anterior view. D, internal mould of left valve, Mata 11 (NRM-PZ Mo168251), side view.
- Figs E-F: *Ambocardia planidorsata* (Zittel, 1864), lower-middle Turonian, internal moulds of right valves, Pedro Gonçalves 3. E, lateral view showing small, rounded anterior adductor muscle scar (arrowed) (NRM-PZ Mo168254). F, lateral view showing anterior and posterior umbonal ridges (NRM-PZ Mo168253).
- Figs G-J: *Protocardia (Protocardia) coquandi* (Seguenza, 1882), middle–upper Cenomanian, composite moulds of left valves. G, lateral view. H, close-up showing posterior radial ribs, Cruzes 6 (NRM-PZ Mo168257). I, lateral view. J, posterior view, Cruzes 8 or 11 (NRM-PZ Mo168256).
- Figs K-N: *Protocardia (Protocardia) hillana* (J. Sowerby, 1813), upper Cenomanian to lower Turonian, articulated composite mould, Tibúrcio 1 (NRM-PZ Mo168259). K, left lateral view. L, close-up showing well developed posterior radial ribs. M, right lateral view. N, dorsal view.
- Figs O-R: *Protocardia (Pachycardium) pauli* (Coquand, 1862), middle Cenomanian to upper Turonian. O, close-up showing radial ribs along posterior flank and commarginal ribs along rest of valve (arrowed), Muçucá 2 (NRM-PZ Mo168289). P, left valve, composite mould showing well-developed posterior umbonal ridge, Laranjeiras 21 (NRM-PZ Mo168263). Q-R, Articulated composite mould, Mata 9 (NRM-PZ Mo168267). Q, posterior view showing faint posterior radial ribs. R, right lateral view.



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Plate V

- Figs A-E: *Protocardia (Pachycardium) pauli* (Coquand, 1862), middle Cenomanian to upper Turonian, articulated composite mould, Cruzes 6 (NRM-PZ Mo168268). A, left lateral view. B, right lateral view. C, anterior view showing subrounded, deep lunule. D, dorsal view. E, close-up showing large cardinal tooth and imprints of lateral teeth (arrowed).
- Figs F-G: *Protocardia (Pachycardium) cf. moevusi* (Coquand, 1862), lower-middle Turonian, poorly preserved composite mould of right valve, Retiro 15 (NRM-PZ Mo168297). F, right lateral view. G, anterior view showing strongly incurved umbo.
- Figs H-L: *Granocardium (Granocardium) productum* (J. de C. Sowerby, 1832), lower Cenomanian to upper Turonian. H-K: Composite mould, Itaporanga 2/3 (NRM-PZ Mo168299). H, left lateral view, showing numerous radial ribs. I, right lateral view. J, posterior view. K, dorsal view showing small beaks. L, composite mould, Japaratuba 14 (NRM-PZ Mo168302), side view of left valve.
- Figs M-O: *Granocardium (Granocardium) tenuistriatum* (Whitfield, 1885), lower Cenomanian, articulated composite mould, Itaporanga 2/3 (NRM-PZ Mo168304). M, right lateral view. N, left lateral view showing a truncated posterior margin. O, anterior view showing anterior adductor muscle scars of both valves.

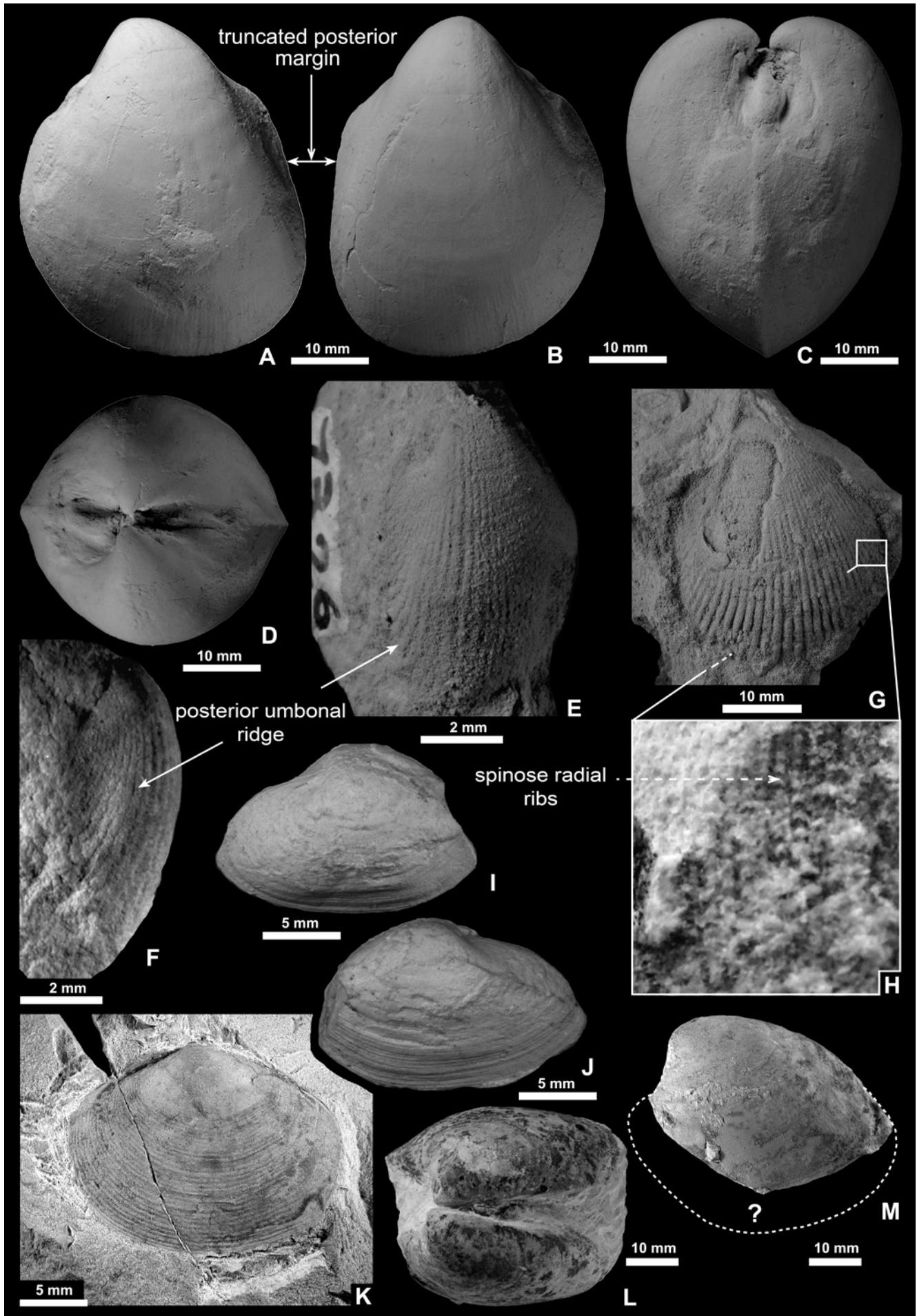


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Plate VI

- Figs A-D: *Granocardium (Granocardium) tenuistriatum* (Whitfield, 1885), lower Cenomanian, articulated composite mould, Itaporanga 2/3 (NRM-PZ Mo168303). A, left lateral view. B, right lateral view showing truncated posterior margin (arrowed). C, anterior view. D, dorsal view showing deep subcircular lunule.
- Figs E-F: *Fragum (Fragum) cf. perobliquum* (Koenen, 1897), lower–middle Turonian, composite mould of right valve, Pedra Furada 13 (NRM-PZ Mo168309). E, lateral view showing well-developed posterior umbonal ridge. F, posterior view.
- Figs G-H: *Fragum* sp., lower Turonian, composite mould of right valve, Japaratuba 16 (NRM-PZ Mo168312). G, lateral view. H, close-up showing spinose radial ribs (arrowed) along posterior flank.
- Figs I-J: *Arcopagella* sp., middle–upper Cenomanian, articulated composite mould, Cruzes 6 (NRM-PZ Mo168313). I, left lateral view. J, right lateral view showing well-developed growth lines close to ventral margin.
- Fig. K: *Tellinimera?* sp., middle–upper Cenomanian, composite mould of left valve, Jardim 1 (NRM-PZ Mo168314), side view.
- Figs L-M: *Arctica? cordata* (Sharpe, 1850), lower Turonian, incomplete articulated internal mould, Laranjeiras 22 (NRM-PZ Mo168321). L, dorsal view showing subterminal beaks. M, left lateral view.

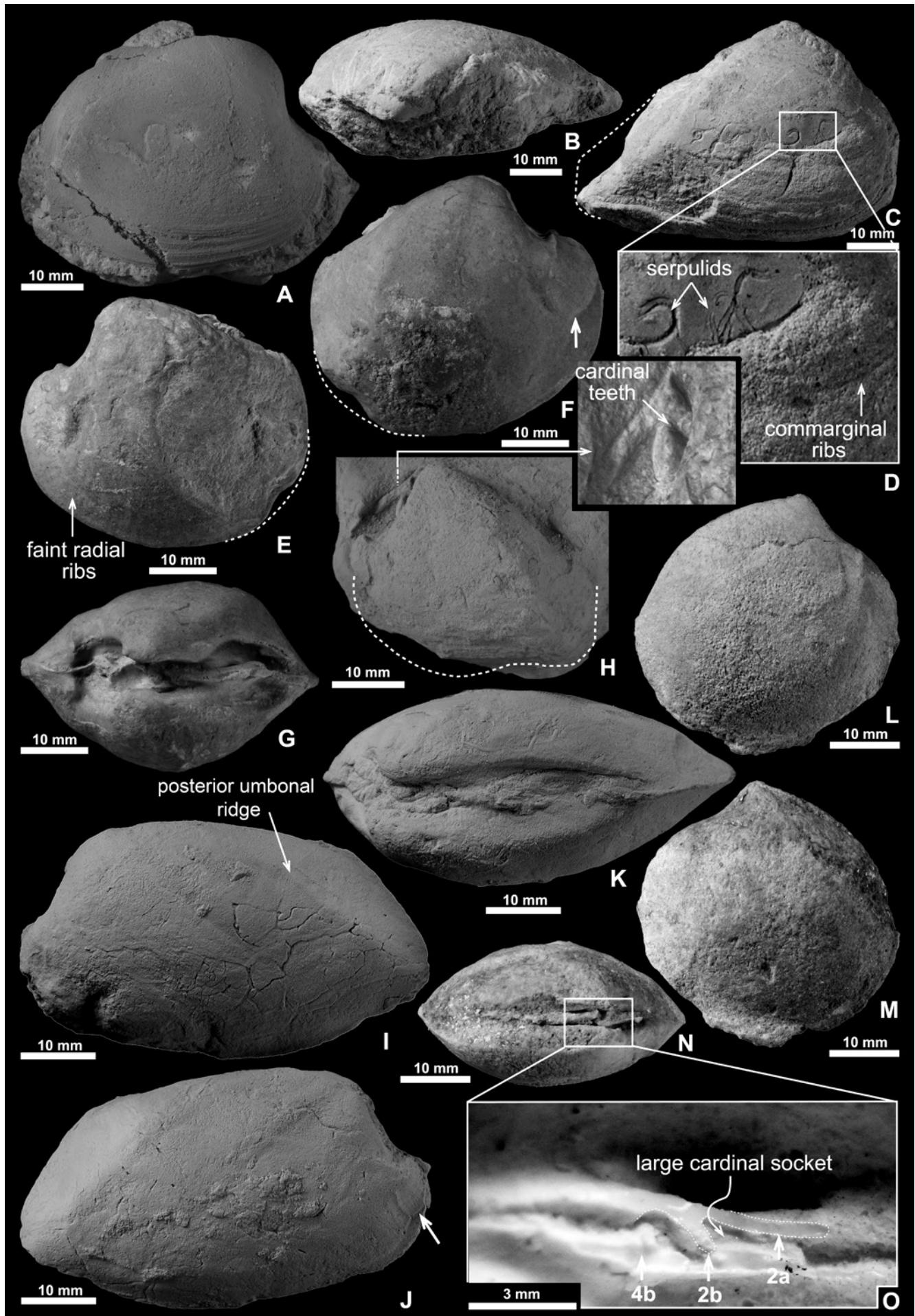
Plate VI



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Plate VII

- Fig. A: *Arctica? cordata* (Sharpe, 1850), upper Turonian, composite mould of right valve, Mucuri 10 (NRM-PZ Mo168320).
- Figs B-D: *Etea carolinensis* Conrad, 1875, upper Turonian, articulated composite mould, Oiteiro 8 (NRM-PZ Mo168322). B, dorsal view. C, right lateral view showing well-developed posterior umbonal ridge. D, close-up of commarginal ribs near ventral margin with serpulid imprints.
- Figs E-G: *Izumia? saussuri* (Brongniart, 1821), upper Turonian, articulated composite mould, Mucuri 15 (NRM-PZ Mo168324). E, left lateral view showing faint radial ribs near ventral margin. F, right lateral view showing large and rounded anterior adductor muscle scar (arrowed). G, dorsal view.
- Fig. H: *Proveniella cf. testacea* (Zittel, 1864), upper Cenomanian, left lateral view, internal mould, Timbó 5 (NRM-PZ Mo168325), showing well-developed posterior umbonal ridge and cardinal teeth (arrowed).
- Figs I-K: *Schedotrapezium?* sp., upper Cenomanian, articulated internal mould, Tibúrcio 1 (NRM-PZ Mo168326). I, left lateral view, showing well-developed posterior umbonal ridge. J, right lateral view showing small, circular anterior adductor muscle scar close to antero-dorsal margin. K, dorsal view showing the weakly developed beaks.
- Figs L-O: *Tenea delettrei* (Coquand, 1862), middle Cenomanian, articulated internal mould, Magalhães 2 (NRM-PZ Mo168328). L, right lateral view. M, left lateral view. N, dorsal view. O, rubber mould of the hinge of the left valve showing cardinal teeth and sockets.

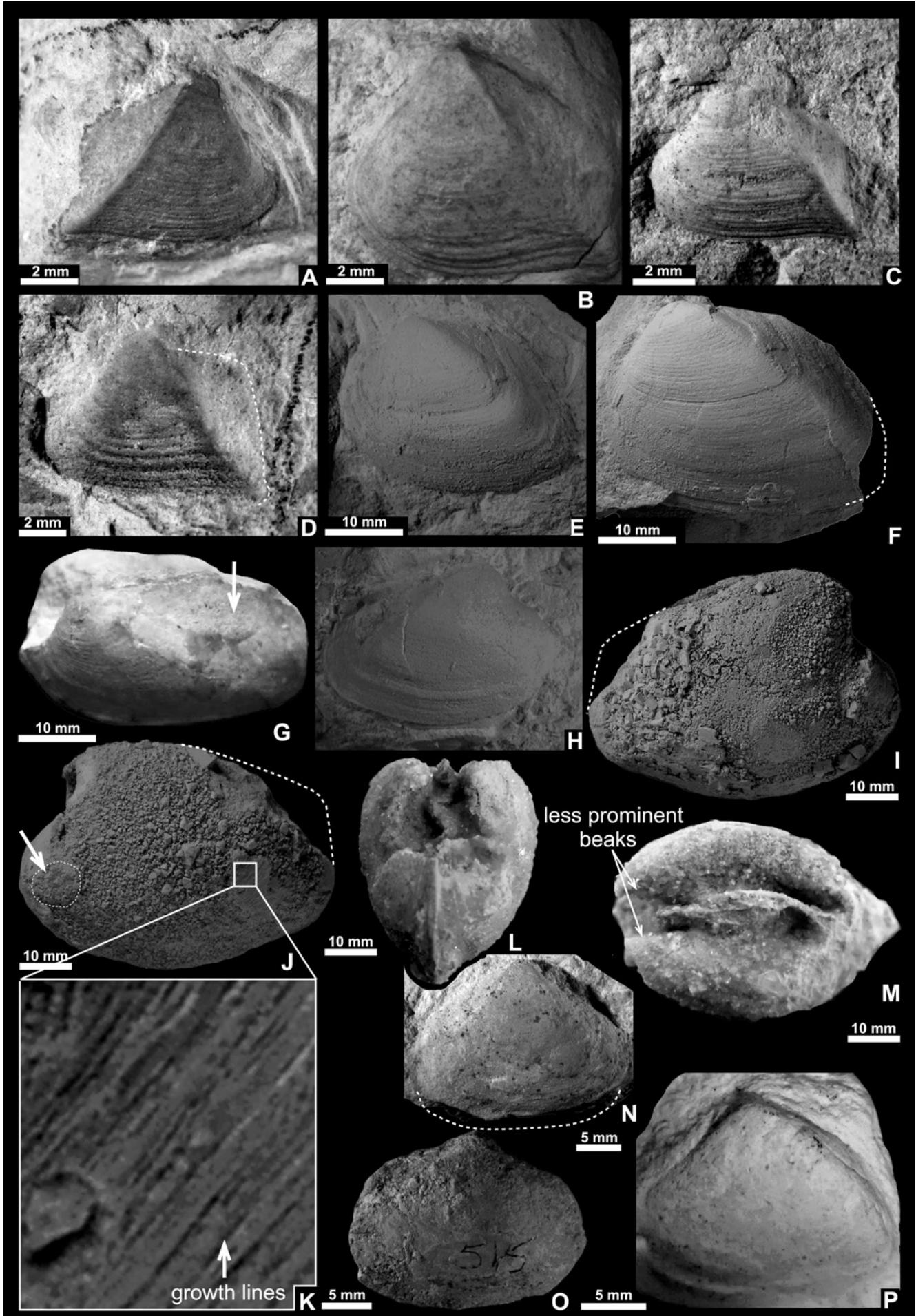


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Plate VIII

- Figs A-D: *Veniella byzacenica* (Pervinquier, 1912), middle Cenomanian to lower Turonian. A, composite mould of right valve, Magalhães 7 (NRM-PZ Mo168329), lateral view. B, composite mould of left valve, Magalhães 7 (NRM-PZ Mo168337), lateral view. C, side view of left valve, composite mould, Jardim 24 (NRM-PZ Mo168335). D, composite mould of left valve, Cruzes 8 or 11 (NRM-PZ Mo168331), lateral view showing well-developed commarginal ribs close to ventral margin.
- Figs E-G: *Veniella trapezoidea* Conrad, 1860, lower Cenomanian, Praia 9. E, composite mould of left valve, (NRM-PZ Mo168338). F, G: articulated composite mould (NRM-PZ Mo168339). F, left lateral view showing faint, irregular growth lines. G, dorsal view showing a wide and concave posterior flank (arrowed).
- Fig. H: *Venilicardia* sp., upper Cenomanian to lower Turonian, right valve in shell preservation, Japaratuba 11(NRM-PZ Mo168347), showing moderately well-developed posterior umbonal ridge.
- Figs I-M: *Trapezium africanum* (Coquand, 1862), upper Turonian, articulated internal mould, Mata 9 (NRM-PZ Mo168348). I, right lateral view. J, left lateral view with shell remains showing strongly concave antero-dorsal margin and circular anterior adductor muscle scar. K, close-up showing irregular growth lines. L, anterior view showing wide, subcircular lunule. M, dorsal view of articulated valves showing the terminal beaks.
- Figs N-P: *Cymbophora? scabellum* Stephenson, 1941, upper Cenomanian to lower Turonian. N, composite mould of right valve, Alto Verde 5 (NRM-PZ Mo168350), lateral view showing faint commarginal ribs near ventral margin. O, articulated composite mould, Tibúrcio 2 (NRM-PZ Mo168349), right lateral view. P, composite mould of left valve, Laranjeiras 22 (NRM-PZ Mo168351), side view showing moderately well-developed posterior umbonal ridge.

Plate VIII

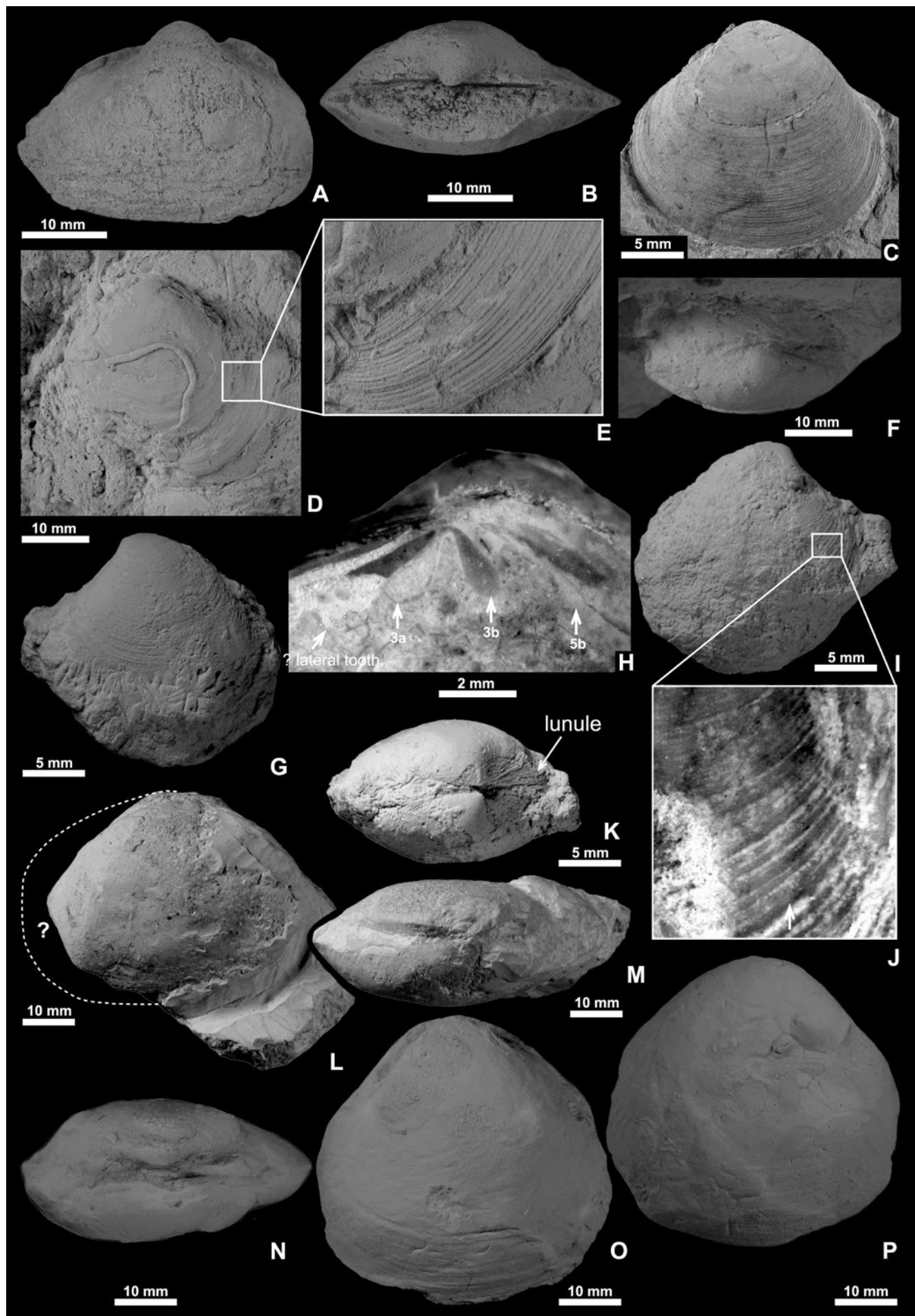


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Plate IX

- Figs A-B: *Cymbophora? subtilis* Stephenson, 1941, middle Cenomanian, Jardim 7 (NRM-PZ Mo168355). A, right lateral view. B, dorsal view of articulated valves.
- Fig. C: *Geltena subequilatera* Stephenson in Vokes, 1946, middle Cenomanian, composite mould of left valve, Jardim 24 (NRM-PZ Mo168357), lateral view.
- Figs D-F: *Mulinoides* cf. *olbrechtsi* Darteville & Freneix, 1957, upper Cenomanian or lower Turonian, left valve in shell preservation with serpulid encrustation, Laranjeiras 28 (NRM-PZ Mo168358). D, Left (?) lateral view. E, close-up showing well-developed growth lines (stronger ventrally). F, dorsal view.
- Figs G-K: *Aphrodina* (*Mesocallista*) cf. *plana* (J. Sowerby, 1813), upper Cenomanian to lower Turonian, articulated composite mould with shell remains, Japaratuba 11 (NRM-PZ Mo168359). G, Left lateral view. H, close-up showing three cardinal teeth of right valve (3a, 3b, 5b), with large sockets in-between. I, right lateral view. J, close-up showing irregular growth lines (shell part). K, dorsal view showing a cordate and moderately depressed lunule (arrowed).
- Figs L-M: *Cyprimeria?* *discus* (Matheron, 1843), lower Turonian, articulated internal mould, Pedra Furada 4 (NRM-PZ Mo168361). L, Right lateral view showing posterior umbonal ridge. M, dorsal view.
- Figs N-P: *Cyprimeria?* cf. *riograndensis* Maury, 1934, upper Cenomanian, articulated internal mould, Jardim 1 (NRM-PZ Mo168363). N, Dorsal view showing the weakly developed beaks. O, side view of right valve showing commarginal ribs close to the ventral margin. P, left lateral view.

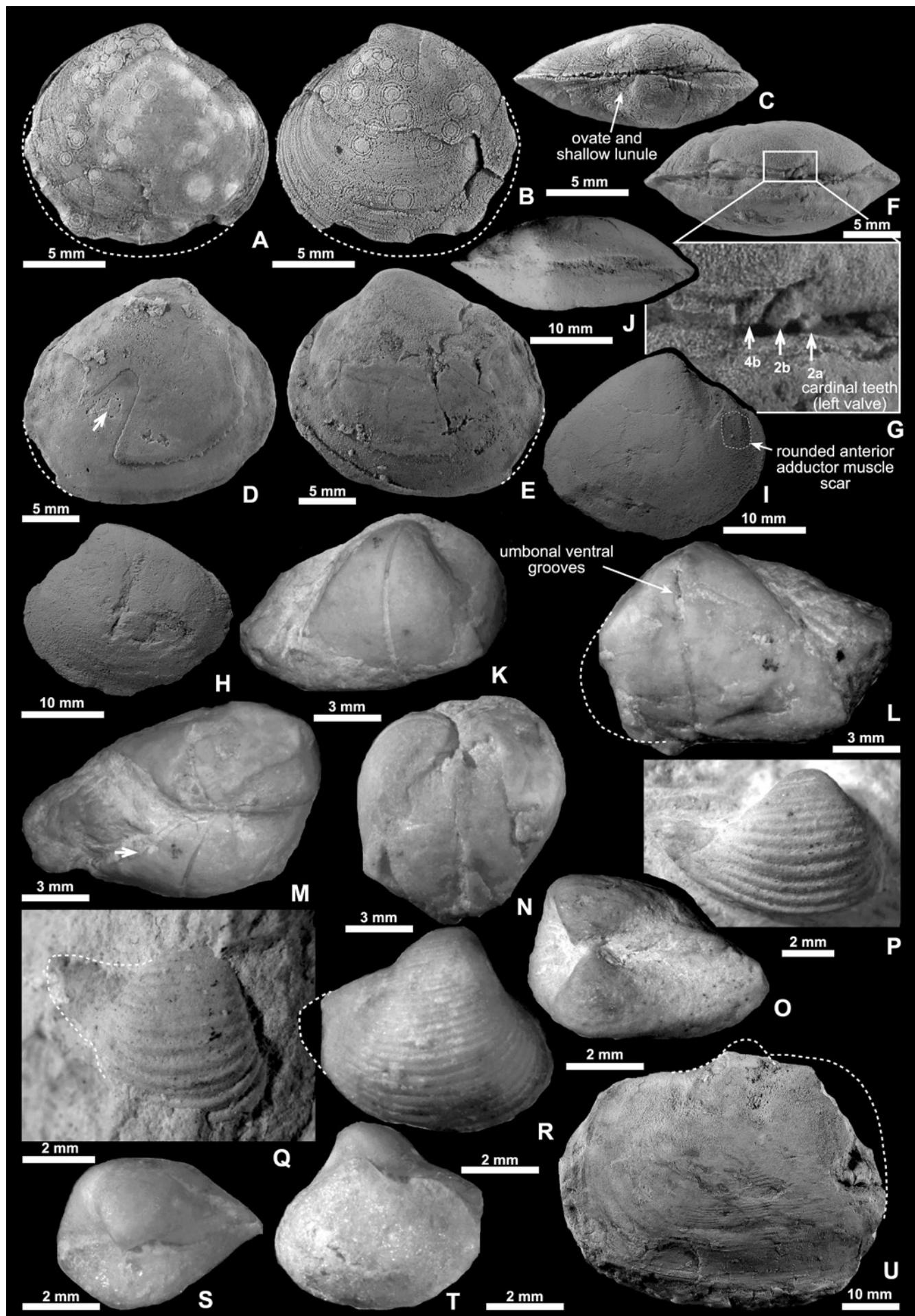
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Plate X

- Figs A-C: *Cyclorisma vectensis* (Forbes, 1845), lower Turonian, articulated composite mould, Pati 3 (NRM-PZ Mo168367). A, Right lateral view. B, left lateral view showing numerous faint commarginal ribs near ventral margin. C, dorsal view showing shallow ovate lunule and narrowly elongated escutcheon (arrowed).
- Figs D-J: *Paraesa fava* (J. de C. Sowerby, 1827), upper Cenomanian to lower Turonian. D-G: Articulated internal mould, Japaratuba 11 (NRM-PZ Mo168387). D, right lateral view showing deep pallial sinus (arrowed). E, left lateral view. F, dorsal view. G, close-up of F showing cardinal teeth and sockets of left valve (2a, 2b, 4b). H-J: Articulated composite mould, Japaratuba 16 (NRM-PZ Mo168380). H, Left lateral view. I, right lateral view showing circular anterior adductor muscle scar close to antero-dorsal margin. J, dorsal view.
- Figs K-N: *Xylophagella?* sp., lower Cenomanian, distorted composite mould, Itaporanga 2/3 (NRM-PZ Mo168390). K, Side view of right valve, showing substraight, deep ventral umbonal groove (arrowed). L, left lateral view. M, dorsal view showing well-developed posterior umbonal ridge (arrowed). N, anterior view.
- Figs O-Q: *Caestocorbula olivae* (Whitfield, 1891), middle Cenomanian. O, distorted articulated specimen in shell preservation, Jardim 24 (NRM-PZ Mo168395), dorsal view showing prominent beaks and strongly enrolled umbones. P, composite mould of right valve, Jardim 7 (NRM-PZ Mo168393), lateral view. Q, internal mould of right valve, Cruzes 6 (NRM-PZ Mo168391), side view.
- Figs R-T: *Caestocorbula cf. striatuloides* (Forbes, 1846), upper Cenomanian, articulated specimen in shell preservation, Timbó 4 (NRM-PZ Mo168403). R, Side view of right valve. S, dorsal view. T, side view of left valve.
- Fig. U: *Panopea* sp., lower-middle Turonian, articulated composite mould, Pedra Furada 4 (NRM-PZ Mo168408), right lateral view.



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