Journal of Paleontology, 91(6), 2017, p. 1148–1165

0022-3360/17/0088-0906
doi: 10.1017/jpa.2017.69

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

The family Carditidae (Bivalvia) in the early Danian of Patagonia (Argentina)

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Abstract.—The first systematic analysis of the Danian carditids of Patagonia is presented, which includes four genera—one new genus and the first records of three other genera in South America. They consist of *Clairbornicardia paleopatagonica* (Ihering, 1903), a widely distributed species occuring in the Jagüel, Roca and Salamanca formations (Neuquén, Río Negro and Chubut Provinces); *Rotundicardia* Heaslip, 1968, represented by the new species *R. mariobrosorum* n. sp., which is restricted to the Roca Formation (Río Negro Province); *Cardites feruglioi* (Petersen, 1846) (Roca and Lefipán formations, Río Negro and Chubut Provinces); and by *Kalelia* new genus, which includes *K. burmeisteri* (Böhm, 1903) from the Salamanca and Roca formations (Río Negro and Chubut Provinces), which is related to the Paris Basin species *K. multicostata* (Lamarck, 1806) n. comb. and *K. pectuncularis* (Lamarck, 1806) n. comb. '*Venericardia*' *iheringi* (Böhm, 1903), a species known only from internal molds, is described and regarded as a carditid with uncertain affinities. The presence of *Claibornicardia*, *Rotundicardia*, and *Cardites* in Patagonia constitutes the most ancient record of these genera and confirms biogeographical connections previously established between the Danian Argentinian and North American/European fossil faunas.

Introduction

The family Carditidae Férussac, 1822 comprises a large group of heterodont bivalves worldwide, ranging from Devonian to modern times (Chavan, 1969), becoming a highly diversified group in the Eocene of the Gulf Coastal Plain (GCP) of the U.S.A. (Gardner and Bowles, 1939; Heaslip, 1968), and the Paris Basin (Cossmann and Pissarro, 1904; Cossmann and Peyrot, 1912). The Carditidae are placed in the recently defined clade Archiheterodonta, the sister group of true heterodont bivalves (Euheterodonta) (Giribet, 2008). The carditids constitute an important component of this group, in which systematic and phylogenetic relationships are poorly understood (Giribet, 2008; González and Giribet, 2014). The generic placement of carditids is complicated. For example, the genus *Venericardia* Lamarck, 1801 is a highly diversified taxon represented by more than 50 recent and several fossil species included in numerous subgenera. The assignments of recent species to this genus is uncertain and many of these assignments, both fossil and recent, were never reviewed. Therefore, the generic diversity of carditids is underestimated (Huber, 2010).

Only a few species of Paleocene carditids have been recorded in the Bassin de Brive and Sables de Bracheux (France; Cossmann and Pisarro, 1904; Lhomme and Freneix, 1993), in the Wangaloa Formation (New Zealand; Beu and Maxwell, 1990; Stilwell, 2003), in the Pebble Point Formation (Australia; Darragh, 1994), in the Kincaid, Lodo, and Clayton formations (USA; Gardner, 1935; Moore, 1992; Cope et al., 2005), and in the Soldado Formation (Trinidad and Tobago; Rutsch, 1943).

Although an abundant and greatly diversified group in Patagonia, Cenozoic carditids, and particularly those of Danian age, remain almost completely unstudied. Initial work was conducted by Burckhardt (1900, 1902) who, based on internal casts, recognized the presence of the Brazilian Paleocene species *Cardita morganiana* Rathbun, 1875 in the southern latitudes of Patagonia. Subsequent studies carried out by Böhm (1903), Ihering (1903, 1907), Feruglio (1936), Petersen (1946), and Masiuk (1967) increased the number of Danian species endemic to Patagonia to four, all of which were included in the Eocene European genus *Venericardia*. More recently, and without any justification for the generic placement, the genus *Glyptoactis* Stewart, 1930 was proposed by Rodríguez et al. (1995) for material from the Coli Toro Plateau area (Río Negro Province). Scasso et al. (2012) mentioned carditids from the Lefipán Formation (Chubut Province), placing them in the genus *Pacificor* Verastegui, 1953. A systematic revision of these species has not been carried out, so the relationships of this carditid fauna have remained poorly known.

Carditids recently collected in new localities allow the first systematic revision of the group in Patagonia. This is essential for a better understanding of the evolution of the family Carditidae and contributes to increasing the knowledge of the composition of the Danian assemblages of the southern hemisphere.

Geological setting

Carditids included in the present analysis were recovered from the Danian marine rocks of the Neuquina, Cañadón Asfalto and

San Jorge basins (Fig. 1.1) where they are common to abundant components of the faunas that inhabited the Rocaguelian and Salamancan bioprovinces (del Río and Martínez, 2015). The fossiliferous stratigraphic sequences of each of these basins have been summarized by del Río et al. (2007, 2011), del Río (2012), and del Río and Martínez (2015). An accurate stratigraphic scheme for the type area of the Roca Formation was provided by del Río et al. (2011) based on calcareous nannoplankton assemblages associated with the molluscs.

Neuquina Basin.—Carditids included in the present paper come from the Roca Formation exposed at Malargüe (Mendoza Province), Cerros Bayos (La Pampa Province) and the surroundings of the city of General Roca (Río Negro Province), and from the Jagüel Formation exposed at Opaso section (Neuquén Province) (Fig. 1.1, 1.2).

Fossils from General Roca have been recorded in the NP1–NP4 biozones recognized in Cantera Cholino, Picada Sísmica and Zanjón Roca sections, where abundant internal molds of carditids have been collected (Fig. 2.1–2.3). Assemblages constitute parauthochtonous accumulations. Carditids are associated with dense concentrations of the gastropod *Rostellaria rothi* Ihering, 1903 and the oyster *Cubistostrea ameghinoi* (Ihering, 1902) (Cantera Cholino samples 15 and 17, respectively), and of turritellids in Picada Sísmica, where the carditids are found alone with the infaunal soft-bottom dewelling bivalves *Neilo* sp. and *Dosinia burckhardti* Ihering, 1907 (del Río et al., 2011).

Carditids are rare at Cerro Bayos, where only one species has been found. Material comes from basal (CB31 and CB32 samples) and uppermost limestones (CB47 samples) of the Roca Formation where the NP1 and NP3 biozones are identified, respectively (Fig. 2.8). In the basal limestones, fossils are infrequent, carditids are rare, and the bivalves *Pycnodonte* (*Phygrea*) *burckhardti* (Böhm, 1903), *Delectopecten*, *Parvamussium*, and unidentified veneroids dominate the fauna. In contrast, horizons at the top of the section are highly fossiliferous, and comprise up to 8 m thick amalgamated yellowish, massive limestones with a dense accumulation of *Cubitostrea ameghinoi*, *Turritella* spp. and subordinate representatives of the carditids and the bivalves *Gryphaostrea callophyla* (Ihering, 1903) and *Jupiteria* sp. (del Río et al., 2007).

Strata exposed in the vicinities of Puesto Pircala (Mendoza Province, Neuquina Basin) record the only Maastrichtian carditids mentioned in this paper and only a brief explanation will be provided herein (Fig. 2.9). These exposures comprise 30 m of intercalation green and white mudstones and highly fossiliferous yellowish limestones with the gastropod '*Turritella*' sp., and the bivalves *Musculus aprilis* (Feruglio, 1935), *Ambigostrea clarae* (Ihering, 1907), *Amphidonte mendozana* Ihering, 1907, *Pinna* sp., *Camptonectes* sp., *Acesta* sp., *Yoldia*? sp., *Paraesa*? sp. and *Pterotrigonia* sp.

Cañadón Asfalto Basin.—Carditids are very abundant in the Roca Formation exposed in the Bajo de Colitoro Grande, Bajo Hondo, and Bajo Lenza Niyeu (Río Negro Province) (Fig. 1.3). However, while they are rare components of the fauna in the uppermost horizons of the Lefipán Formation at the middle Chubut River, they are common bivalves in the Salamanca Formation exposed in Sierra de los Guanacos area (Chubut Province).

Fossiliferous horizons in the Bajo Hondo and Bajo Lenza Niyeu are exposed at Puesto Nahuel Cheo and Puesto Carmelo

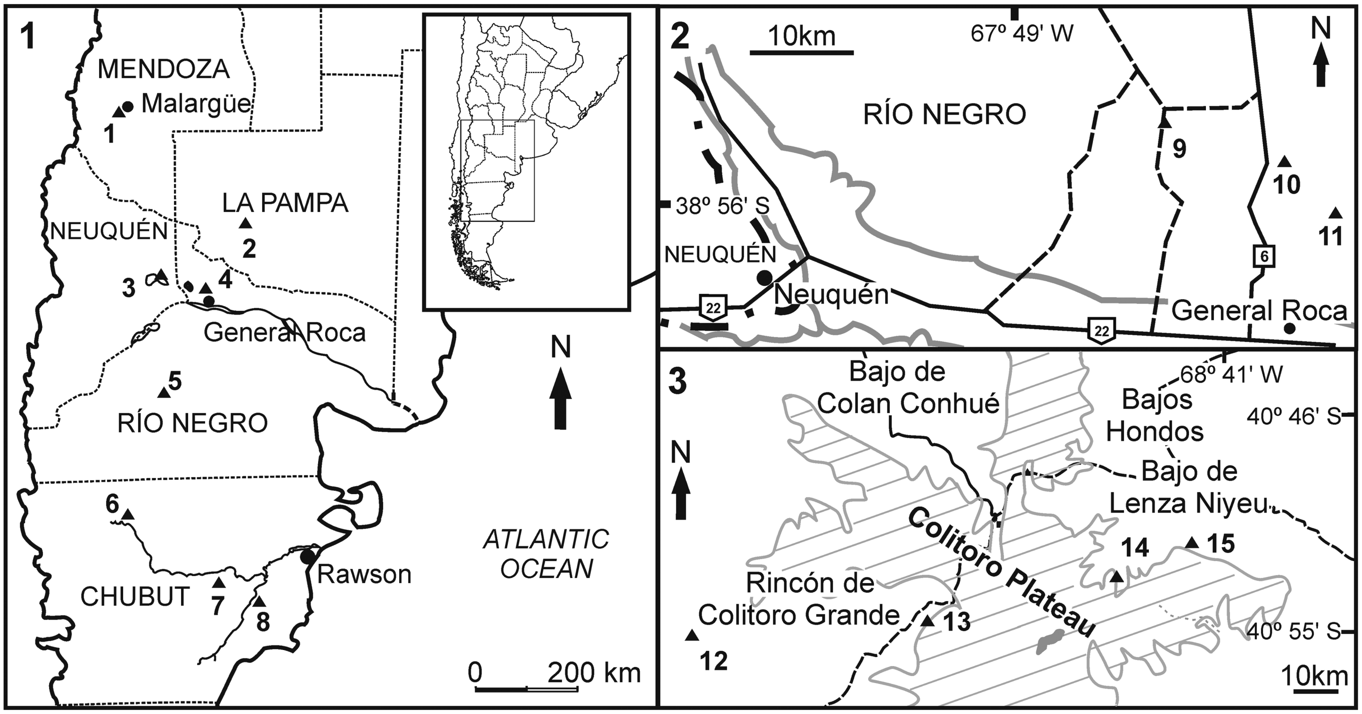


Figure 1. (**1**) General placement of study areas. (**2**) Fossiliferous sites at General Roca. (**3**) Fossiliferous sites at Colitoro Plateau. 1 = Puesto Pircala, 2 = Cerros Bayos, 3 = Opaso, 4 = General Roca area, 5 = Coli Toro Plateau area, 6 = Puesto Crettón, 7 = Puesto Ramírez, 8 = Puesto Álvarez, 9 = Cantera Cholino, 10 = Picada Sísmica, 11 = Zanjón Roca, 12 = Cerro Tiltilco, 13 = Puesto Ñancucheo, 14 = Puesto Nahuel Cheo, 15 = Puesto Carmelo Ibañez; (**2**) and (**3**) modified from del Río, 2012.

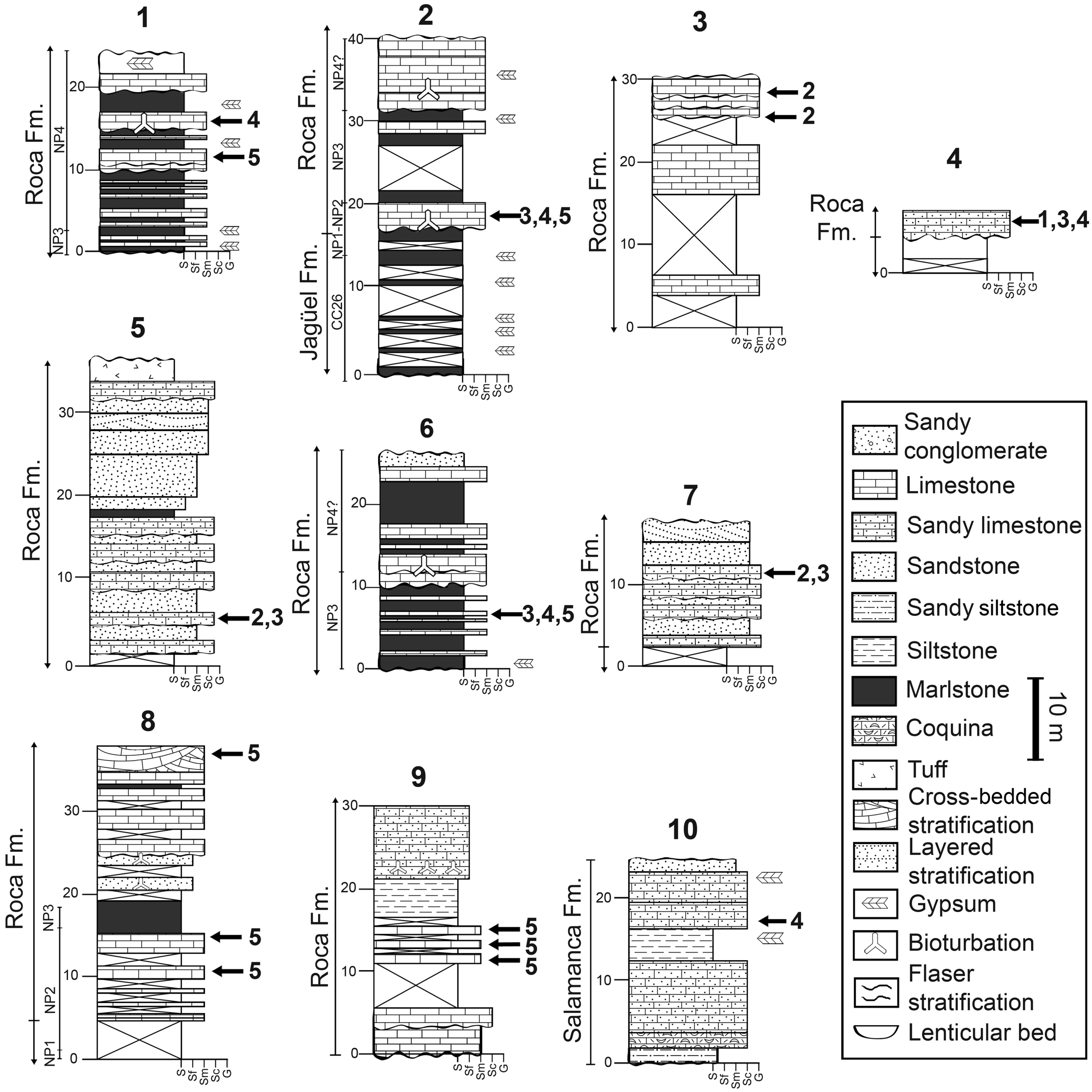


Figure 2. Lithological sections. (**1**) Cantera Cholino. (**2**) Zanjón Roca. (**3**) Puesto Ñancucheo. (**4**) Cerro Tiltilco. (**5**) Puesto Carmelo Ibañez. (**6**) Picada Sísmica. (**7**) Puesto Nahuel Cheo. (**8**) Cerros Bayos. (**9**) Puesto Pircala. (**10**) Puesto Álvarez, 1 = *Claibornicardia paleopatagonica*, 2 = *Rotundicardia mariobrosorum* n. sp., 3 = *Cardites feruglioi*, 4 = *Kalelia burmeisteri*, 5 = '*Venericardia*' *iheringi*; (**1, 2, 4–7**) after del Río, 2012; (**8**) after del Río et al., 2007; (**10**) after Masiuk, 1967.

Ibañez sections (Fig. 2.5, 2.6). Here, carditids come from hard, thin, pinkish massive grainstones, constituted by amalgamated, multi-event shell beds with internal discontinuities. *Cardites feruglioi* (Petersen, 1946) and a new species of *Rotundicardia* (Heaslip, 1968) herein described are commonly associated with dense concentrations of *Pycnodonte* (*Phygraea*) *sarmientoi* Casadío, 1998, and *Ostrea neuquena* Ihering, 1907 or *Turritella malaspina* Ihering, 1903. In both cases a rich gastropod fauna is represented by *Tejonia tapiae* (Feruglio, 1935), *Microfulgur concheyroae* del Río, 2012, *Heteroterma carmeloi* del Río, 2012, *Rocalaria alani* del Río, 2012, *Cavoscala* sp., *Gyroscala daniana* del Río, 2012, *Sulcobuccinum prominentum* del Río, 2012, *Austrophaera patagonica* (Feruglio, 1936) and by the echinoid *Cidarina lenzaniyeuensis* del Río, 2012 (del Río, 2012).

Carditids from Bajo del Colitoro Grande come from Cerro Tiltilco and Puesto Ñancucheo sections where the uppermost horizons (Fig. 2.4, 2.7), consisting of thick ochreous and whitish massive coquinas, yield *Claibornicardia paleopatagonica* (Ihering, 1903), *R. mariobrosorum* n. sp., *C. feruglioi*, and *Kalelia burmeisteri* (Böhm, 1903). Associated with the carditids are the bivalves *Glycymeris feruglioi* Celeste, 1940, *Ostrea neuquena* Ihering, 1907, *Panopea* spp., and the gastropods *Tejonia tapiae* (Feruglio, 1935), *Priscofiscus* cf. *P. gracilis* (Wilckens, 1905), *Sulcobuccinum prominentum* del Río, 2012, and *Austrophaera patagonica* (Feruglio, 1936) (del Río, 2012).

The Salamanca Formation exposed in the surroundings of Sierra de los Guanacos (Fig. 1.1) consists of an intercalation of siltstones, sandstones and coquinas with a poorly diversified fauna (Chebli and Serraioto, 1974) with abundant representatives of *C. paleopatagonica* associated with the bivalves *Nucula pervicax* Feruglio, 1936, *Ostrea neuquena*, *Bathytormus chubutensis* (Feruglio, 1936), and the gastropods '*Turritella*' *ameghinoi* Ihering, 1903, *Darwinices claudiae* Griffin and Pastorino, 2013, *Pseudamaura dubia* (Petersen, 1946), '*Cominella iheringi*' Feruglio, 1936, *Austrophaera patagonica* (Feruglio, 1936), *Gyroscala daniana* del Río, 2012, *Turritella malaspina* Ihering, 1903 (del Río and Martínez, 2015).

San Jorge Basin.—The studied material was recorded by C. Ameghino from Río Chico, in an area supposedly situated 50 km south of Puesto Alvarez (Fig. 2.10) (Chubut Province). This section was assigned to the Salamanca Formation and consists of an intercalation of gray or yellow calcareous sandstones with siltstones and whitish coquinas. The species *K. burmeisteri* is associated with the bivalves *Glycymeris feruglioi*, *Panopea thomasi* Ihering, 1914, and the gastropods *Turritella* aff. *T. soaresana* Hartt in White, 1887, *Polinices* sp., *Arrhoges* sp. and *Cimomia camachoi* Masiuk, 1967.

Materials and methods

Measurements of carditid shells include lenght and height and follows Heaslip (1968). Specimens were whitened using magnesium oxide before photography. Repositories are listed below.

Repositories and institutional abbreviations.—MACN-Pi and CIRGEO-PI, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' División Paleoinvertebrados, Buenos Aires; CPBA, Cátedra de Paleontología of the Universidad de Buenos Aires, Buenos Aires; MLP, Museo de La Plata, La Plata; GHUNLPam, Facultad de Ciencias Exactas y Naturales of Universidad de La Pampa, Santa Rosa; MHNSR. Pi, Museo de Historia Natural of San Rafael, San Rafael; SGN, Servicio Geológico Minero of Argentina, Buenos Aires; MNHM, Muséum National d'Histoire Naturelle of Paris, France; GMNH, Muséum d'Histoire Naturelle de Genève, Switzerland.

Systematic paleontology

Morphological terminology agrees with Heaslip (1968), who described the tripartite (='fasciculate' for Maxwell, 1969) sculpture as radiating costae with a central rib flanked by paracostal ones on each side (Heaslip, 1968, text-fig. 4.D), and used the term 'funginated' for the closely placed flaring scales, resembling bracket fungi, placed on central ribs of *Rotundicardia* Heaslip, 1968.

Terms such as 'planicostates' and 'alticostates' will be used with the phylogenetical meaning proposed by Gardner and Bowles (1939) and Heaslip (1968), who properly described and illustrated them. Planicostates include a lineage of carditid bivalves with large shells, flat and smooth radial ribs, and long cardinal teeth, and alticostates refer to species with small valves, tripartited and sculptured radial ribs, and short cardinal teeth.

Order Archiheterodonta Giribet, 2008
Family Carditidae Férussac, 1822

Remarks.—The systematics of carditids is complex because there is no consensus about the distinction among genera and subgenera. On one hand, for some authors, the family includes a few genera (*Venericardia* Lamarck, 1801 and *Cardita* Bruguière, 1792) with a large number of subgenera (e.g., *Megacardita* Sacco, 1899; *Venericor* Stewart, 1930; or *Claibornicardia* Stenzel and Krause, 1957). Other authors treat some of these subgenera as genera (for a comparison, see Sacco, 1899; Dall, 1903; Chavan, 1969; Moore, 1992; McClure and Lockwood, 2015). The use of subgenera implies close phylogenetic relationships, most of which are poorly understood at present. Therefore, until a complete quantitative phylogenetic study of the family is performed, we consider all carditid genera or subgenera previously proposed to have generic status, thereby discarding all phylogenetic inferences. McClure and Lockwood (2015) proposed that *Claibornicardia* and *Rotundicardia* are possible paraphyletic genera based on a phylogenetic study of some GCP carditid species. Because they included relatively few species of both taxa in their analysis, we prefer to keep the monophyletic status until a complete revision is performed.

Chavan (1969) outlined a subfamiliar classification for the Carditidae on the basis of taxonomic criteria. He recognized seven subfamilies, six newly introduced by him: Carditinae, Carditamerinae, Miodomeridinae, Palaeocarditinae, Venericardiinae, Carditesinae, and the previously proposed Thecaliinae Dall, 1903, based mainly on shell shape and hinge morphology. Members of the planicostates and alticostates were indistinctively included in Carditamerinae, Venericardiinae, or Carditesinae by Chavan (1969). In this paper, we reject the subfamiliar classification proposed by Chavan (1969) because his scheme ignored the phylogenetic proposals of other authors (Gardner and Bowles, 1939; Heaslip, 1968), as indicated by the analysis of Pérez and del Río (2016), and prefer these proposals instead.

Genus *Claibornicardia* Stenzel and Krause, 1957

Type species.—*Cardita alticostata* Conrad, 1833 (by original designation). Gosport Sand, McBean and Black Mingo formations, early–middle Eocene of Alabama, United States of America (USA).

Diagnosis.—Carditid with a highly convex shell and an elongated subrectangular outline, posterior area defined by a change in the convexity. Ventral margin of right hinge sinuous. Right anterior tooth thin dorsally or anteriorlly placed to the anterior socket for the left anterior tooth, left anterior tooth broad and triangular. External sculpture of 28–33 tripartite radial ribs covered with nodes. Nodes and paracostal ribs suppressed in advanced members of the genus (modified from Heaslip, 1968, p. 98).

Remarks.—The genus *Clairbornicardia* was erected by Stenzel and Krause in Stenzel and Krause, 1957 to include few carditids from the middle Eocene of the GCP geological province (*C. alticostata* [Conrad, 1833], *C. complexicostata* [Meyer and Aldrich, 1886], *C. nasuta* [Dall, 1890], *C. sillimani* [Lea, 1833], and *C. trapaquara* [Harris, 1895]) and *C. acuticostata* (Lamarck, 1806) from the Eocene of the Paris Basin (France). According to Stenzel and Krause (1957), the key characters of the genus are the elongate-rectangular outline with a faint posterior area, and the development of tripartite radial ribs.

Heaslip (1968) reviewed the genus, and extended its stratigraphic range in the southeastern region of the USA from the early Eocene to the middle Oligocene with the addition of several new species (*C. blandingi* [Conrad, 1830]; *C. coloradonis* [Harris, 1919]; *C. linguinodifera* Heaslip, 1968; *C. natchitoches* [Harris, 1919]; *C. perantiqua* [Conrad, 1865]; and *C. trapaquaroides* Heaslip, 1968), and synonymized *C. sillimani* with *C. alticostata*, stating that it is a case of sexual dimorphism. All American species are characterized by variable outlines, with diverse degrees of elongation and posterior margin acumination (*C. nasuta*, *C. trapaquara*, and *C. trapaquaroides*) and/or ventral margin acumination (*C. blandingi*, *C. complexicostata*, and *C. perantiqua*). Particularly, *C. alticostata* shows strong morphological variation (as shown by Heaslip, 1968, pl. 26, figs. 6–11). Cases of allometric growth are recognized within carditids (Stanley, 1972), where the shell outlines can vary throughout ontogeny. Combining allometry with sexual dimorphism and the wide geographical distribution of certain species (e.g., *C. alticostata*), it is possible that the true intraspecific variation of *Claibornicardia* is misunderstood and some proposed American species are part of the variation of other species.

Moore (1992) included within *Claibornicardia* four species from California and Baja California: *C. keenae* (Verastegui, 1953) (late Paleocene), *C. domenginica* (Vokes, 1939), *C. marksi* (Verastegui, 1953), and *C. sandiegoensis* (Hanna, 1927), the last three all being Eocene. These taxa have less elongate outlines and more convex shells than the eastern American species, but have the characteristic tripartite radial ornamentation.

Claibornicardia aalterensis Vervoenen and van Nieulande, 2010, *C. asperrima* (Wood, 1861), *C. carinata* (Sowerby, 1821), and *C. obovata* (Wood, 1861), from the Eocene of England, France, and Belgium, also have been placed within *Claibornicardia* (Pacaud and Le Renard, 1995; Tracey et al., 1996; Vervoenen and van Nieulande, 2010). These species, together with *C. acuticostata*, should potentially be assigned to a different genus converging with the American species, because they have less elongated outlines with a less well defined posterior area and a fewer radial ribs. There are other records from the Eocene of Colombia and Jamaica that are doubtfully assigned to *C. alticostata* because they are based on incomplete specimens in which the diagnostic characters cannot be recognized (Anderson, 1928; Cox, 1941). Kafanov et al. (2001) recorded *C. keenae* from the late Paleocene Getkilninskaya Formation (Kamchatka, Russia; Kafanov and Ogasawara, 2006). This record, together with *C. keenae* from the late Paleocene Lodo Formation (California, USA, Johnson and Graham, 2007), are the most ancient records known for the genus *Claibornicardia*.

Claibornicardia paleopatagonica (Ihering 1903)
Figure 3.1, 3.2, 3.4, 3.5

1903 *Cardita paleopatagonica* Ihering, p. 215, pl. 2, fig. 12.
1907 *Venericardia paleopatagonica* (Ihering); Ihering, p. 47.
1914 *Venericardia paleopatagonica* (Ihering); Ihering, p. 44.
1936 *Venericardia paleopatagonica* (Ihering); Feruglio, p. 232, pl. 23, figs. 28, 29.
1938b *Venericardia paleopatagonica* (Ihering); Fossa Mancini, p. 261.
1977 *Venericardia camachoi* Vigilante, p. 20, pl. 1, fig. 6.
1987 *Venericardia paleopatagonica* (Ihering); Farinati et al., p. 154, pl. 1, fig. 5.
1995 *Glyptoactis paleopatagonica* (Ihering); Rodríguez et al., p. 243, pl. 2, fig. G.
1995 *Glyptoactis* sp. (Ihering); Rodríguez et al., p. 243, pl. 2, fig. H.
1996 *Cardita paleopatagonica* Ihering; Parodiz, p. 246.
2012 *Venericardia* (*Pacificor*) *iheringi* (Böhm); Scasso et al., p. 43, fig. 4G.

Type specimen.—Holotype MACN-Pi 360, articulated shell from ‘Río Chico’ (Chubut Province, Salamanca Formation).

Diagnosis.—Outline subrectangular to subovate with rounded posterior margin. Lunule deep. Right anterior tooth inclined backwards, placed on anterior side of left anterior socket. Radial ribs (30–33) sculptured with closely spaced subcircular nodes and with narrow intercostal spaces.

Occurrence.—General Roca and Coli Toro Plateau areas (early Danian, Roca Formation, Río Negro Province), Opaso (early Danian, Jagüel Formation, Neuquén Province), and Río Chico’s area (early Danian, Salamanca Formation, Chubut Province).

Description.—Shell thick, medium-sized, subrectangular to subovate in anterior-posterior direction, with elongate outline; posterior rounded, slightly curved ventral and gently inclined dorsal margins; posterior area defined by smooth convexity change starting from the eighth rib. Small umbones placed near anterior fifth of valve length. Lunule small, vertical, slightly concave, demarcated by an incised groove from remaining surface of shell, sculptured with fine commarginal growth lines.

Right valve hinge with sinuous ventral edge below middle tooth; small, short anterior tooth inclined backwards, thin, parallel to middle tooth, placed on anterior side of left anterior socket; middle tooth triangular, inclined strongly backwards, with narrow base, fine striations on dorsal surface, higher towards apex in lateral view; posterior tooth thin, slightly curved, taller than anterior one but shorter than middle tooth.

Left valve hinge with almost straight ventral edge; anterior tooth elongate, triangular, inclined backwards, slightly curved, with straight anterior and curved posterior sides; posterior tooth elongate, narrow, straight, with narrow base and acute apex, equal in height to anterior tooth.

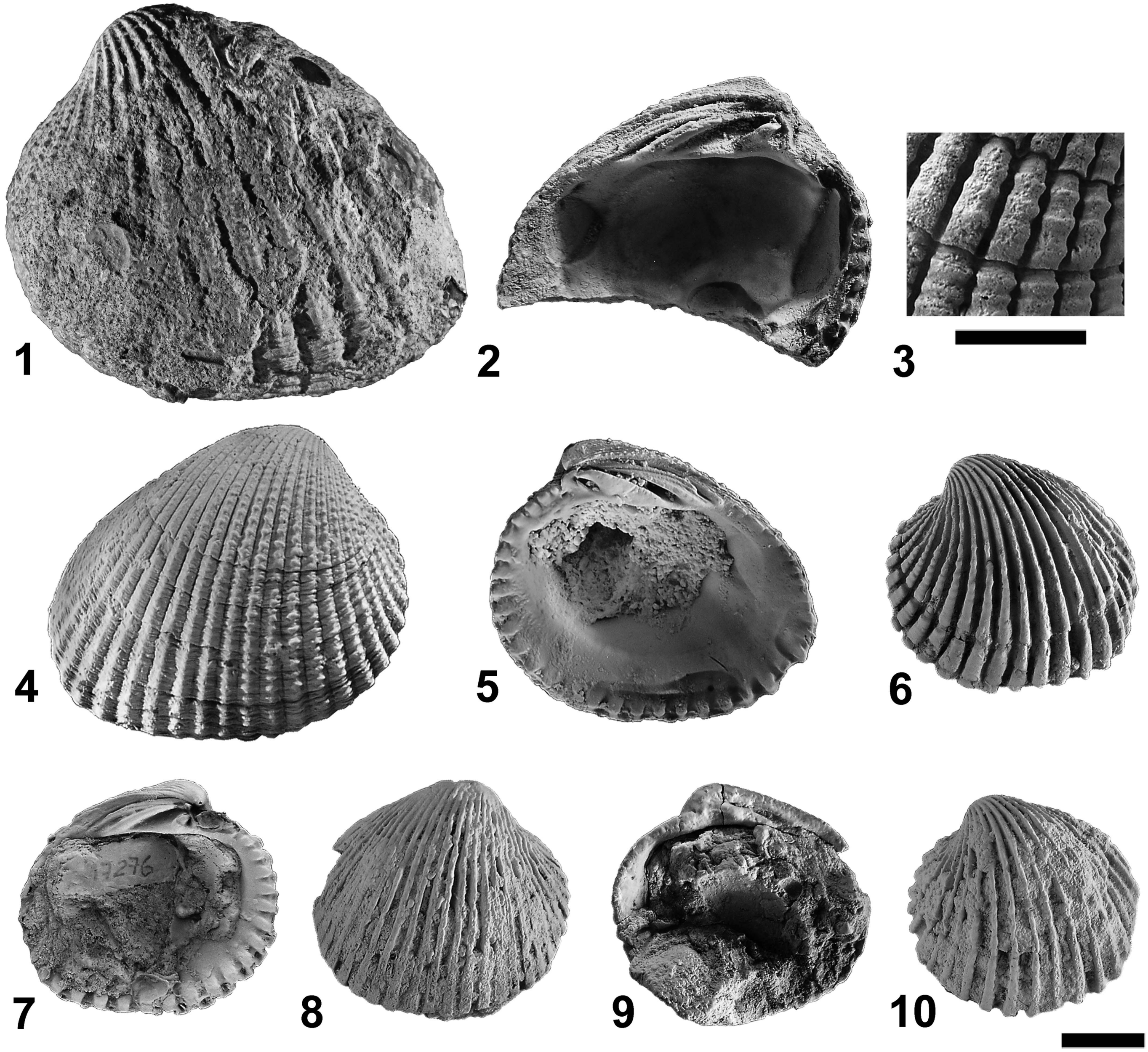


Figure 3. *Claibornicardia paleopatagonica* (Ihering, 1903) (**1, 2, 4, 5**): (**1**) external view of left valve, holotype MACN-Pi 360, from 'Río Chico'; (**2**) internal view of left valve, MACN-Pi 5197, from Puesto Ramírez; (**4**) external view of right valve, MACN-Pi 5197, from Puesto Ramírez; (**5**) internal view of right valve, MACN-Pi 5197, from Puesto Ramírez. *Rotundicardia mariobrosorum* n. sp. (**3, 6–10**): (**3**) detail of sculpture, MACN-Pi 5762, from Puesto Carmelo Ibañez: (**6**) external view of left valve, holotype CPBA 17276, from Cerro Tiltilco; (**7**) internal view of left valve, holotype CPBA 17276, from Cerro Tiltilco; (**8**) external view of right valve, Paratype MACN-Pi 5758, from Puesto Ñancucheo; (**9**) internal view of right valve, Paratype MACN-Pi 5758, from Puesto Ñancucheo; (**10**) external view of left valve, Paratype MACN-Pi 5758, from Puesto Ñancucheo. All scale bars represents 10 mm.

External sculpture with 30–33 radial ribs having a subtriangular transverse section, widening in ventral direction; elevated central costal rib covered by nodes with subcircular transverse section; smooth paracostal ribs of rounded transverse section, as wide as central rib; narrow intercostal spaces delimited by deep, narrow groove; posterior area sculptured with eight weaker, less-high ribs, with less pronounced tripartition, first three ribs with stronger, more elevated nodes than the remainder.

Pallial line at a quarter of total valve height. Inner ventral margin strongly crenulated; crenulations triangular, truncated, covering entire margin to posterior adductor muscle scar, becoming smaller over posterior.

Materials.—CPBA 17286, 17288, 21027, 21028, MACN-Pi 4289, 5197, MLP 1475, 3731, 3732, and 3734 (26 left valves, 25 right valves, one articulated shell, one internal mold, and two external molds).

Remarks.—Ihering (1903) described *C. paleopatagonica* based on a shell with conjoined valves from 'Río Chico' (Salamanca Formation), stating that the type specimen did not allow the description of hinge features. Ihering (1907) mentioned other specimens of *C. paleopatagonica* from 'Rocanense' exposures from an unspecified locality, but only the type specimen is present in Ihering's collection.

Feruglio (1936, pl. 23, figs. 28, 29) described and illustrated specimens from Puesto Ramírez (Danian, Salamanca Formation, Chubut Province) and later, Vigilante (1977, pl. 1, fig. 6) assigned one of the juvenile specimens collected by Feruglio to *V. camachoi* Vigilante, 1977. Both authors referred their species to *Venericardia* Lamarck, 1801 (type species *V. imbricata* Lamarck, 1801, Eocene, Paris Basin) (see La Perna et al., 2017, fig. 3). However, *C. paleopatagonica* is placed in *Clabornicardia* because of its subrectangular outline, sinuous ventral hinge margin, thin right anterior teeth, and the presence of wide paracostal ribs with narrow intercostals spaces.

Rodríguez et al. (1995, pl. 2, figs. G, H) illustrated *C. paleopatagonica* from Cerro Tiltilco (Roca Formation, Río Negro Province), and included it in *Glyptoactis* Stewart, 1930, (type species *V. hadra* Dall, 1903, Miocene, Florida, USA) (Heaslip, 1968, pl. 27–29), but this genus has a triangular outline, larger and more recurved umbones, a deeper lunule with the ventrally projecting lunular margin, right hinge ventral edge inverted 'V'-shaped, right middle and left posterior teeth more curved, fewer radial ribs with wider paracostal ribs, and narrower intercostal spaces.

Claibornicardia paleopatagonica differs from *C. alticostata* (Stenzel et al., 1957, pl. 13, figs. 1–9; Heaslip, 1968, pl. 26, figs. 6–11) by its rounded posterior margin, deeper lunule, weaker left anterior tooth, a right anterior tooth that is inclined backwards and placed on the anterior side of the left anterior socket, and by its stronger radial nodes. Juvenile specimens of *C. paleopatagonica* have subquadrate outlines, while adults are more elongate. The same variation can be observed in *C. alticostata* (syntypes ANSP 30562 include elongate adults and subquadrate juveniles) (Stenzel et al., 1957).

Species from the middle Eocene of the USA are mainly distinguished from each other and from *C. paleopatagonica* by their outlines. *Claibornicardia linguinodifera* Heaslip, 1968 (Stenzel et al., 1957, pl. 14, figs. 6–11; Heaslip, 1968, pl. 24, figs. 1, 2; Bashi and Reklaw formations), *C. coloradonis* (Harris, 1919) (Heaslip, 1968, pl. 24, figs. 3–6; Weches, Wautubbee, and Reklaw formations), and *C. natchitoches* (Harris, 1919) (Heaslip, 1968, pl. 25, figs. 4–7; Weches Formation) have less elongated outlines, with truncated posterior margins, wide intercostal spaces, and more closely spaced nodes than *C. paleopatagonica*. *Claibornicardia perantiqua* (Conrad, 1865) (Heaslip, 1968, pl. 25, figs. 8–11; Shark River Formation), *C. trapaquara* (Harris, 1895) (Stenzel et al., 1957, pl. 14, figs. 6–11; Heaslip, 1968, pl. 24, fig. 8, pl. 25, figs. 1–3; Stone City Beds), and *C. trapaquaroides* Heaslip, 1968 (Heaslip, 1968, pl. 24, fig. 7; Weches Formation) can be distinguished from the Patagonian species because their shells have a more acuminated postero-ventral margin, less rounded nodes, and wider intercostal spaces.

Claibornicardia paleopatagonica differs from *C. complexicostata* (Meyer and Aldrich, 1886) (Stenzel et al., 1957, pl. 15, figs. 1–4; Heaslip, 1968, pl. 26, figs. 3–5; Wautubbe Formation) by having a subrectangular to subovate shell instead of the subtriangular outlines of the American species.

Claibornicardia blandingi (Conrad, 1830) (Heaslip, 1968, pl. 26, figs. 1, 2; Lower Santee Limestone Formation) and *C. paleopatagonica* have similar shell-shapes, but can be distinguished by the larger shells sculptured with a greater number of radial ribs in the Patagonian species.

Claibornicardia paleopatagonica can be distinguished from *C. keenae* (Verastegui, 1953) (Moore, 1992, pl. 8, figs. 6, 8, 10, 12, 13, 15; Lodo Formation, late Paleocene–early Eocene, California, USA, and Getkilninskaya Formation, late Paleocene, Russia) by having a deeper lunule, and more numerous radial ribs.

Genus *Rotundicardia* Heaslip, 1968

Type species.—*Venericardia rotunda* Lea, 1833 (by original designation). Gosport Sand, Lisbon, Wautubbee, McBean, Cook Mountain, Weches and Yegua formations, middle Eocene of the USA and Laredo Formation, middle Eocene of México.

Diagnosis.—Carditid with a moderately convex shell, subrounded outline, and slightly truncated posterior margin. Umbones small, placed subcentrally. Lunule reduced or absent. Right middle tooth prominent, broad; left anterior tooth strong, triangular. Radial ribs (25–26) high, covered with funginate nodes, and paracostal ribs reduced or absent in many species (modified from Heaslip, 1968, p. 90).

Remarks.—According to Heaslip (1968), the main features of *Rotundicardia* are the subrounded shell shape with centrally placed umbones, and the funginated nodes. Heaslip (1968) included seven species from the GCP in *Rotundicardia*: *R. carsonensis* (Dall, 1903), *R. crenaea* (Gardner, 1935), *R. diversidentata* (Meyer, 1885), *R. eoa* (Gardner, 1935), *R. eutawcolensis* (Harris, 1919), *R. flabellum* (Harris, 1919), and *R. rotunda* (Lea, 1833). He also recognized the presence of sexual dimorphism within *R. rotunda* and *R. diversidentata*, identified by the development in males of less convex shells than in females, which are more strongly sculptured.

Beal (1948) recorded *Venericardia* cf. *V. rotunda* (Tepetate Formation, middle Eocene, Baja California, Mexico) and Woodring (1982) recorded *Rotundicardia* sp. for the late Eocene of Panamá. Darragh (1994) included two species from Australia within *Rotundicardia*: *R. petraea* (Darragh, 1994) from the middle Paleocene, and *R. latissima* (Tate, 1886) from the middle Eocene. The latter was placed within *Fasciculardia* by Maxwell (1969).

The oldest known record for the genus is the late Danian *R. crenaea* (Gardner, 1935) from the Kincaid Formation (Tehuacana Member, Texas, USA), assigned to this age by Barnes et al. (1992).

Rotundicardia mariobrosorum new species
Figure 3.3, 3.6–3.10

1995 *Glyptoactis feruglioi* (Petersen): Rodríguez et al., p. 243, pl. 2, fig. 1.

Type specimens.—Holotype CPBA 17276, one left valve from Cerro Tiltilco (Río Negro Province). Paratype MACN-Pi 5758, right and left valve from Puesto Ñancucheo (Río Negro Province).

Diagnosis.—Shells with a subquadrate outline. Lunule absent. Right anterior tooth minute; left anterior tooth small, short, and inclined backwards. Radial ribs (25–27) increasing in width towards ventral margin, without paracostal ribs, and with strongly funginated nodes.

Occurrence.—General Roca and Coli Toro Plateau areas (Danian, Roca Formation, Río Negro Province).

Description.—Shell medium-sized to small, subquadrate to subrounded, with rounded anterior and ventral margins, convex dorsal margin, and almost straight posterior margin. Umbones placed near middle of valve length. Lunule absent. Right valve hinge with straight or slightly curved ventral edge; right anterior tooth reduced, thin, straight, in contact with middle tooth; middle tooth triangular, inclined backwards, with wide base, higher than other teeth; posterior tooth straight, thin. Left valve hinge with nearly straight ventral edge; anterior tooth small, short, inclined backwards, with short anterior and convex posterior edges; posterior tooth narrow, slightly curved, higher than anterior tooth, with sharp dorsal tip, ventral surface finely striate. External sculpture of 25–27 radial ribs of triangular transverse section, without paracostal ribs, wider towards ventral margin; high central costal cord with subrectangular funginated nodes, more numerous towards ventral and anterior margins; intercostal spaces of 'V'-shaped transversal section, each narrower than one radial rib. Pallial line at one-quarter of total valve height. Inner ventral margin strongly crenulate, crenulations triangular, with sharp tips, covering entire margin to dorsal edge of adductor posterior muscle scar.

Etymology.—The specific epithet honors Mario and Luigi, the Mario Bros. brothers, main characters from the popular videogame Mario Bros., in which they collect mushrooms, and it is a reference to the 'funginate' nodes of the radial ribs in this species.

Materials.—MACN-Pi 4180, 5758–5762, 5766 (17 left valves, 13 right valves, and one fragment).

Remarks.—The specimen assigned to *Glyptoactis feruglioi* Petersen, 1946 by Rodríguez et al. (1995, pl. 2, fig. 1) from Cerro Tiltilco is placed in *R. mariobrosorum* n. sp. The new species differs from *G. feruglioi* by its less triangular outline with a truncated posterior margin, its smaller hinge, the presence of a right anterior tooth, and its smaller right middle tooth.

The new species is placed in *Rotundicardia* because it has a subquadrate outline with slightly truncated posterior margin, 25–27 radial ribs covered with funginated nodes, and because it lacks a lunule and paracostal ribs. *Glyptoactis* Stewart, 1930 (type species *V. hadra* Dall, 1903, Miocene, Florida, USA) (Heaslip, 1968, pls. 27–29), the genus where Rodríguez et al. (1995) placed these shells, has a more triangular outline, with larger and more prominent umbones, fewer radial ribs (19–20) covered with small subrectangular nodes.

Rotundicardia mariobrosorum n. sp. differs from *R. rotunda* (Lea, 1833) (Heaslip, 1968, pl. 22, figs. 8, 9, pl. 23, figs. 1, 2) by its subquadrate shells, smaller right anterior tooth, shorter and smaller left anterior tooth, and radial ribs becoming wider towards the ventral margin. *Rotundicardia diversidentata* (Meyer, 1885) (Heaslip, 1968, pl. 23, figs. 3–8, Jackson and Ocala Limestone formations, late Eocene, USA) differs from *R. mariobrosorum* n. sp. in having the same characters as *R. rotunda*, and a lunule and less pronounced nodes.

Rotundicardia mariobrosorum can be distinguished from *R. eoa* (Gardner, 1935) (Heaslip 1968, pl. 22, figs. 1, 2) and *R. crenaea* (Gardner, 1935) (Heaslip, 1968, pl. 22, figs. 3, 4) (Kincaid Formation, late Danian, USA) because both the latter species have fewer radial ribs (~23) covered with less pronounced nodes, and have paracostal ribs, that are absent from *R. mariobrosorum* n. sp.

Rotundicardia flabellum (Harris, 1919) (Heaslip, 1968, pl. 22, figs. 6, 7, Weches and Yegua formations, middle Eocene, USA) and *R. carsonensis* (Dall, 1903) (Heaslip, 1968, pl. 23, figs. 9, 10, Red Bluff Formation, early Oligocene, USA and from an unnamed formation, early Oligocene, Mexico) are distinguished from *R. mariobrosorum* by the presence of a lunule, by having a larger anterior right tooth, and by having radial ribs of equal width throughout the ontogeny.

Rotundicardia mariobrosorum differs from *R. petraea* Darragh, 1994 (Darragh, 1994, fig. 6E, 6F, 6I–6L, Pebble Point and Kings Park formations, late Paleocene, Australia) by having a slightly truncated posterior margin instead of the expanded posterior margin that characterizes the Australian species.

Rotundicardia latissima (Tate, 1886) (Darragh and Kendrick, 2008, fig. 1.5, Lower Browns Creek, Upper Browns Creek, Blanche Point formations and Southern Carnavon Basin, middle–late Eocene, Australia) can be distinguished from *R. mariobrosorum* because the South American species has a more subquadrate shape and radial ribs with more prominent nodes.

Genus *Cardites* Link, 1807

Type species.—*Chama antiquata* Linnaeus, 1758 (by original designation). Miocene–Recent of Europe and Northern Africa.

Diagnosis.—Carditid with very convex shell, subtriangular to subrounded in shape with a truncated posterior margin. Umbones prominent. Lunule convex. Right anterior tooth extremely faint; absent in some species. Radial ribs wide, sculptured with beaded or rectangular nodes.

Remarks.—The key character of *Cardites* is the presence of a very faint right anterior tooth (Link, 1807; Chavan, 1969), absent according to other authors (Dall, 1902; Lamy, 1921). This tooth could be present with varying degrees of development within different species of the genus (see for examples Lamy, 1921, p. 202; Chavan, 1969, fig. E56.1; Huber, 2010, p. 251). The diagnoses provided by Dall (1902), Lamy (1921), and Chavan (1969) are incomplete for a definition of *Cardites*. Because of this, we give an emended diagnosis herein.

The oldest records for *Cardites* are *C. dertopartschii* (Sacco, 1899) and *C. partschii* (Goldfuss, 1840) from the Burdigalian (early Miocene) of the Vienna Basin (Sieber, 1954). *Cardites* has a wide stratigraphical and geographical range, and has been cited from Miocene of Europe (Jimenez and Braga, 1993; Lacour et al., 2002) and North Africa (Freneix et al., 1987), from the Pliocene of

Panamá (Collins and Coates, 1999) and Ecuador (Olsson, 1941), and from the Pleistocene of East Asia (Cox, 1931), North Africa (El-Sorogy, 2002), Australia (McNamara and Kendrick, 1994), Europe (Menesini and Ughi, 1982), and Ecuador (Olsson, 1964). Most of these records have never been reviewed, and a few of these records may not be *Cardites*. For example, La Perna et al. (2017) recently placed the species *C. ignoratus* (Cossman and Peyrot, 1912) in *Megacardita* Sacco, 1899.

The only reference to *Cardites* from the USA was provided by Whitfield (1885), who mentioned *C. antiquatus* as occurring in the Shark River Formation (Eocene of New Jersey). However, Palmer and Brann (1965) pointed out that this record mistakenly confused the name with *Claibornicardia perantiqua* (Conrad, 1865).

Huber (2010) suggested that living species referred to *Cardites* include species belonging to at least two different genera. He recognizing a group of elongated species from America, including *C. floridanus* (Conrad, 1838), *C. grayi* (Dall, 1903), and *C. laticostatus* (Sowerby, 1833), and another group composed of species with triangular and subrounded shells from Europe and Asia, including *C. antiquatus* (Linnaeus, 1758), *C. bicolor* (Lamarck, 1819), *C. canaliculatus* (Reeve, 1843), and *C. ovalis* (Reeve, 1843). The American species have a notch at the posterior margin and radial ribs with squamose nodes, while the European and Asian species have radial ribs with subrectangular nodes. Therefore, Huber's (2010) hypothesis that American taxa could belong to distinct genera from European and Asian taxa could potentially be corroborated based upon morphological differences and distinct geographical distributions.

Cardites feruglioi (Petersen, 1946)
Figure 4.1–4.6

1946 *Venericardia feruglioi* Petersen, p. 126, pl. 10, figs. 3–5.
1990 *Venericardia feruglioi* Petersen; Medina et al., p. 140, pl. 1, figs. 1–3.
1992 *Venericardia feruglioi* Petersen; Camacho, p. 37.

Type specimens.—Syntypes SGN 9379 and SGN 9381. One right and one left valve, from Puesto Crettón, (Chubut Province).

Diagnosis.—Shell subtriangular to subrectangular outline, with sinuous ventral margin. Lunule small. Left anterior tooth small and triangular; right middle tooth very curved, broad, and prominent. Radial ribs (28–29) with elongated rectangular nodes, better developed on ventral and posterior regions of valves than elsewhere, and with reduced intercostal spaces.

Occurrence.—General Roca and Coli Toro Plateau areas (Danian, Roca Formation, Río Negro Province), and Puesto Crettón (Danian, Lefipán Formation, Chubut Province).

Description.—Shell medium-sized, thick, triangular to subrectangular; anterior margin rounded, ventral margin sinuous, posterior margin truncated with right angle between it and ventral one, dorsal margin inclined, slightly convex; posterior area defined by convexity change starting from seventh or eighth radial rib. Umbones large, recurved, placed near anterior third of valve length. Lunule very small. Hinge of right valve high, with sinuous ventral edge below middle tooth; anterior tooth absent; middle tooth large, high, strongly curved, inclined backwards, with broad base, dorsal tip sharp; fine striations on dorsal surface; posterior tooth long, thin, curved.

Hinge of left valve high, with straight ventral edge; anterior tooth short, triangular, inclined backwards, with straight anterior and curved posterior edges; posterior tooth long, curved, higher than anterior one. External sculpture of 28–29 broad, low radial ribs of subrectangular transverse section, covered with obsolete and elongated rectangular nodes, more strongly developed on ventral and posterior regions of valve; intercostal spaces reduced, with 'V'-shaped transverse section; posterior area covered with seven or eight lower, narrower radial ribs. Pallial line at about one-quarter of valve height. Inner ventral margin with strong crenulations that are rectangular, truncated, and extend around margin until junction of ventral and posterior margins.

Materials.—SGN 9395; MACN-Pi 4120, 4197, 5748, 5763-5765, 5767; CPBA 6411 (39 left valves, 27 right valves, one articulated shell, one internal mold, and eight fragments).

Remarks.—Petersen (1946) erected *C. feruglioi* based on a large number of shells collected from the Danian section of the Lefipán Formation, exposed in the middle Chubut River area (Chubut Province). Later, Rodríguez et al. (1995) assigned a left valve (CPBA 17276) to this species from Cerro Tiltilco (Roca Formation, Río Negro Province). This specimen does not resemble the specimens in Petersen (1946), therefore we included it in the new species. The description of *C. feruglioi* is expanded here to include new specimens from Puesto Nahuel Cheo, Puesto Carmelo Ibañez, and unspecified fossiliferous sections describe by R. Wichmann at Bajo Lenza Niyeu and Bajos Hondos. Petersen (1946) assigned this species to *Venericardia*, but that genus has subquadrate shells, strongly truncated posterior margin, and paracostal ribs sculptured with rounded nodes. The presence in *C. feruglioi* of subtriangular shells, radial ribs covered with subrectangular nodes, without paracostal ribs, and the absence of a right anterior tooth place this species within *Cardites* Link, 1807.

Cardites feruglioi differs from *C. antiquatus* (Linnaeus, 1758) (Chavan, 1969, fig. E56.1) by its larger shells with subtriangular outlines, a sinuous ventral margin, shorter left anterior and wider right middle teeth, and a greater number of radial ribs that are more strongly developed on the ventral and posterior regions of the valves.

Cardites canaliculatus (Reeve, 1843), *C. bicolor* (Lamarck, 1819) (Recent, Indian Ocean), and other subtriangular species from Europe and Asia (Huber, 2010, p. 251–252) can all be distinguished from *C. feruglioi* by having a larger lunule and sculpture with fewer radial ribs.

Cardites floridanus (Conrad, 1838) (Recent, from North Carolina, USA to Northern Brazil) and the remaining elongate American species (Huber, 2010, p. 251–252) differ from *C. feruglioi* by their elongate outlines, with more rounded umbones and large lunules.

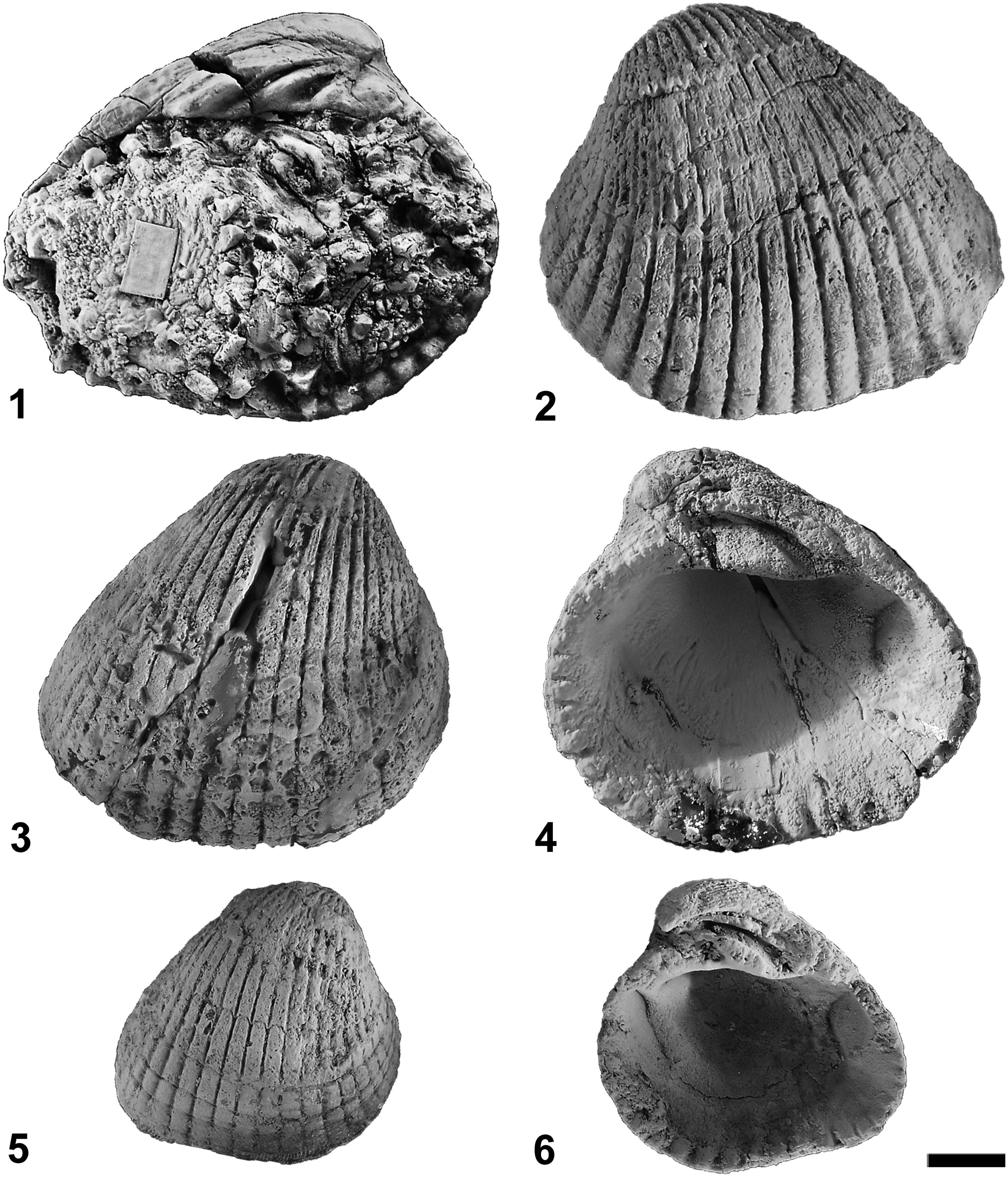


Figure 4. *Cardites feruglioi* (Petersen, 1946): (**1**) internal view of left valve, syntype SGN 9381, from Puesto Crettón; (**2**) external view of left valve, syntype SGN 9381, from Puesto Crettón; (**3**) external view of right valve, syntype SGN 9379, from Puesto Crettón; (**4**) internal view of right valve, syntype SGN 9379, from Puesto Crettón; (**5**) external view of right valve, MACN-Pi 5763, from Cerro Tiltilco; (**6**) internal view of right valve, MACN-Pi 5763, from Cerro Tiltilco. Scale bar represents 10 mm.

Cardites feruglioi can be distinguished from *C. partschii* (Goldfuss, 1840) (Miocene from Europe; Sieber, 1954, pl. 1, fig. 3) by having a larger shell with subtriangular outlines, and narrower radial ribs that become better developed on the ventral and posterior regions of the valves and are separated by wider intercostal spaces.

Genus *Kalelia* new genus

Type species.—*Cardita multicostata* Lamarck, 1806. Late Paleocene, Paris Basin, France.

Included species.—*K. burmeisteri* (Böhm, 1903), *K. pectuncularis* (Lamarck, 1806).

Diagnosis.—Carditid with large shells for the family, thick and subcircular. Posterior margin convex, large umbones and posterior area defined by an umbonal carina and a convexity change. Lunule large, vertically oriented. Hinge high, with wide ventral development. Right anterior tooth long, inclined backwards; right middle tooth thick, strongly curved, with broad base. Left anterior tooth triangular, very broad, inclined backwards, with very convex posterior edge. External sculpture of tripartited radial ribs, 25–30 wide, most prominent on anterior, intercostals spaces confined to a narrow groove.

Etymology.—The name honors Kal-El, Kryptonian name of Superman, the first superhero in comic books. This genus is one of the oldest and largest alticostate carditids.

Remarks.—*Kalelia* n. gen. is the largest member of all alticostate carditids, with shells reaching up to 60 mm in height. It is characterized by the development of a tall hinge plate, prominent teeth, a large lunule, and the presence of low radial ribs; subrectangular in cross section. These characters are shared with planicostate carditids, but the development of tripartite radial ribs places *Kalelia* within alticostates carditids. Rutsch (1936) and McClure (2009) already mentioned the possibility that '*Venericardia*' *pectuncularis* convergently developed some planicostate characters.

We proposed including in *Kalelia* n. gen., apart from the type species '*Cardita*' *multicostata* (Lamarck, 1806) (Cossmann and Pissarro, 1904, pl. 31, fig. 97–3), the late Paleocene species '*C.*' *burmeisteri* (Böhm, 1903) (Roca and Salamanca formations, early Danian, Argentina) (Fig. 5.1–5.11) and '*C.*' *pectuncularis* (Lamarck, 1806) (Cossmann and Pissarro, 1904, pl. 31, fig. 97–2) (Fig. 6.1, 6.2), from the Sables de Bracheux, France. These species have large shells with strong hinge teeth and the particular external sculpture described above. The poorly known species '*V.*' *marylandica* (Clark and Martin, 1901) (Clark and Martin, 1901, pl. 40, fig. 7; Nanjemoy Formation, early Eocene, USA) is possibly a North American representative of this genus.

Kalelia n. gen. differs from *Venericardia* Lamarck, 1801 (La Perna et al., 2017, fig. 3) in having larger shells with more nearly circular outlines, a convex posterior margin instead of a truncated one, a larger lunule, a higher hinge plate, a triangular right anterior tooth, and fewer radial ribs that are separated by intercostal spaces defined by narrow grooves.

Kalelia n. gen. can be distinguished from *Arcturellina* Chavan, 1951 (type species *C. asperula* Deshayes, 1825, Eocene, Paris Basin) (Cossmann and Pissarro, 1904, pl. 22, fig. 97-22) by having larger shells, convex posterior margin, higher hinge plate, long or straight right anterior tooth, triangular left anterior tooth, and fewer radial ribs covered with subcircular nodes instead of the subrectangular ones that characterize *Arcturellina*.

Kalelia n. gen. can be distinguished from *Clairbornicardia* Stenzel and Krause, 1957 (Heaslip, 1968, pl. 26, figs. 6–11) because *Kalelia* has larger and more nearly circular shells, a higher and more robust hinge, and fewer, lower, and wide radial ribs.

Kalelia n. gen. can be separated from *Rotundicardia* Heaslip, 1968 (Heaslip, 1968, pl. 22, figs. 8–9, pl. 23, figs. 1–2) by having a rounded posterior margin, convex umbones, a well-developed posterior area, the presence of a lunule, the higher number of radial ribs with subcircular nodes, and narrower intercostals spaces separating the ribs.

Kalelia burmeisteri (Böhm, 1903) n. comb.
Figure 5.1–5.7

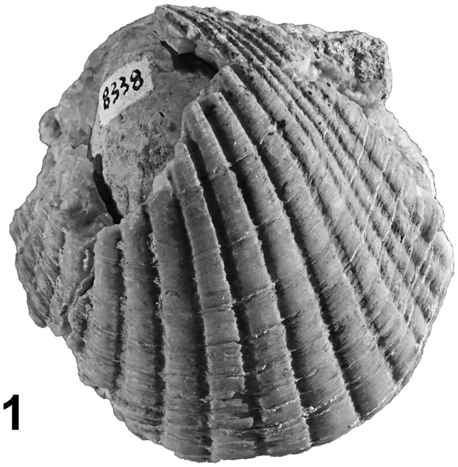
1902 *Cardita morganiana* Rathbun; Burckhardt, p. 216, figs. 1,7.
1903 *Cardita burmeisteri* Böhm, p. 72.
1903 *Cardita Burckhardti* Ihering, p. 205.
1907 *Venericardia burmeisteri* (Böhm); Ihering, p. 23.
1938b *Venericardia burmeisteri* (Böhm), 'Forma B'; Fossa-Mancini, p. 263.
1967 *Venericardia paleopatagonica* var. *australis* Masiuk, p. 243, pl. 5, fig. 2.

Type specimens.—Holotype MLP 15294a and 15294f. Two internal molds from General Roca (Río Negro Province).

Diagnosis.—Shell medium-sized, posterior margin slightly convex, dorsal margin sloping from beaks to posterior one, posterior area sculptured by three or four higher and wide radial ribs, continued by three lower and narrower other ones. Umbones subcentrally placed. External sculpture of 25 wide and low radial ribs.

Occurrence.—General Roca area (early Danian, Roca Formation, Río Negro Province) and Puesto Álvarez (early Danian, Salamanca Formation, Chubut Province).

Figure 5. *Kalelia burmeisteri* (Böhm, 1903) n. comb. (**1–7**): (**1**) external view of left valve, CPBA 8338, from Puesto Álvarez; (**2**) external view of left valve with shell removed, CPBA 8338, from Puesto Álvarez; (**3**) external view of right valve, CPBA 8338, from Puesto Álvarez; (**4**) internal view of right valve, MACN-Pi 5357, from General Roca; (**5**) left view of internal mold, CPBA 8338, from Puesto Álvarez; (**6**) left view of internal mold, holotype MLP 15294f, from General Roca; (**7**) left view of internal mold, holotype MLP 15294a, from General Roca. *Kalelia multicostata* (Lamarck, 1806) n. comb. (**8–11**): (**8**) internal view of left valve, holotype MNHN A07711, from Abbecourt, France; (**9**) external view of left valve, holotype MNHN A07711, from Abbecourt, France; (**10**) internal view of right valve, MNHN F07559, from Noailles, France; (**11**) external view of right valve, MNHN F07559, from Noailles, France. Scale bar represents 10 mm.



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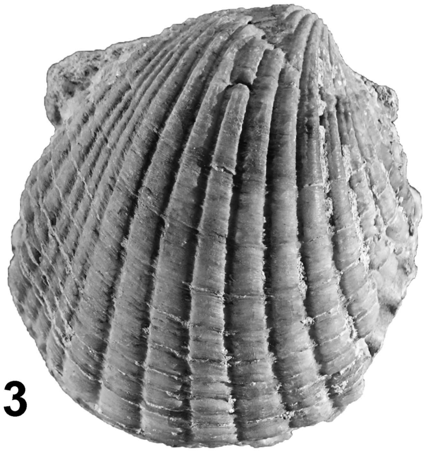

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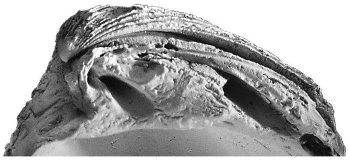

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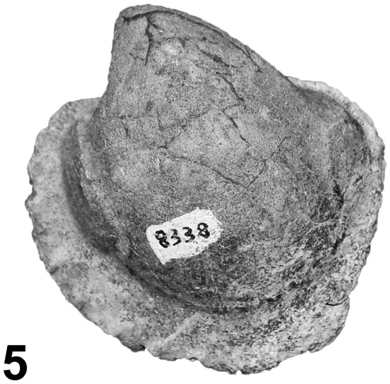

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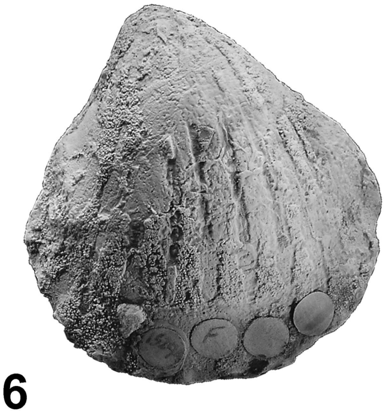

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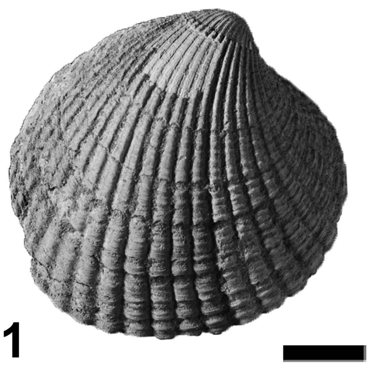

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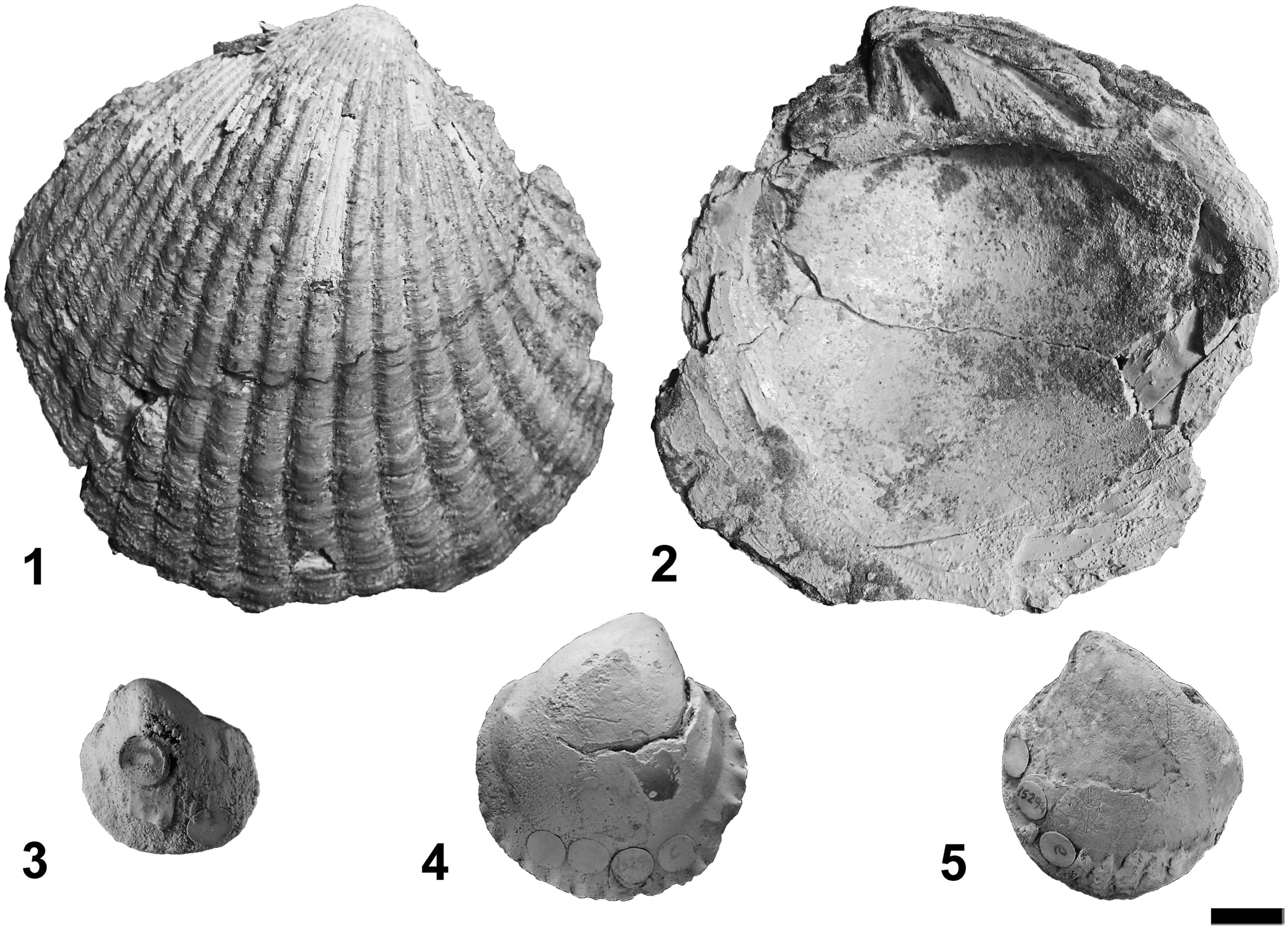

Figure 6. *Kalelia pectuncularis* (Lamarck, 1806) n. comb. (**1, 2**): (**1**) external view of right valve, holotype GMNH 46030, from Bracheaux, France; (**2**) internal view of right valve, holotype GMNH 46030, from Bracheaux, France. '*Venericardia*' *iheringi* (Böhm, 1903) (**3–5**): (**3**) left view of internal mold, MLP 10220a, from Puesto Pircala; (**4**) right view of internal mold, syntype MLP 15294c, from General Roca; (**5**) left view of internal mold, syntype MLP 15294c, from General Roca. Scale bar represents 10 mm.

Description.—Shell medium-sized, thick, subcircular in outline, with rounded anterior and ventral margins, weakly convex posterior margin, and curved dorsal margin with pronounced slope from beaks to posterior end; posterior area defined by convexity change starting from sixth or seventh radial rib. Umbones large, convex, near center of valves. Lunule large, convex, sunken, vertically oriented. Right valve hinge with straight ventral edge; anterior tooth thin, large, inclined backwards; middle tooth large, strongly curved, strongly inclined backwards, with broad base, higher towards dorsal extreme in lateral view; posterior tooth thin, curved, extending to center of middle tooth. Left hinge not seen. External sculpture of 25 wide, low, tripartite radial ribs, more prominent towards anterior region of valves, transverse section triangular in dorsal region but semicircular in central region; central radial ribs covered with nodes, subcircular transverse in cross section; paracostal ribs smooth, semicircular transverse in cross section, as wide as central radial rib; intercostal spaces, subquadrate transverse in cross section, each wider than one radial rib; posterior area sculptured with three or four higher, wider ribs, followed by three lower and narrower ones. Pallial line at about one-quarter of total valve height. Inner ventral margin with prominent crenulation; crenulations triangular, truncated, extending along entire margin to center of posterior adductor muscle scar.

Materials.—CPBA 6402-6403, 6407, 8338; MACN-Pi 341-343, 5747, 5751-5753, 5357; MLP 1876, 1878, 1882, 1897, 4098, 4475, 5517, 7286, 9108, 9416, 9724, 9725, 9768, 10504, 10505 (one left valve, two right valves, one articulated shells, and 81 internal molds).

Remarks.—Internal molds studied by Burckhardt (1902), Böhm (1903), and Ihering (1903, 1907) are characterized by their large size, subrounded outline, convex umbones, and particularly by the presence of a postero-ventral carina. The specimens collected by Masiuk (1967) and described as *Venericardia paleopatagonica* var. *australis*, include composite molds, with internal molds and valves that allowed us to identified Masiuk's variety with *K. burmeisteri*. The carina present in the molds corresponds to the change in convexity and sculpture observed in the preserved valves.

Burckhardt (1902) identified this species as *Cardita morganiana* Rathbun, 1875, a Brazilian taxon from Maria Farinha (Paleocene) and Pirabas (Miocene) formations (Penna, 1965; Tavora et al., 2010). The Brazilian species (White, 1887, pl. 8, figs. 18–21) differs from *K. burmeisteri* in having smaller and more robust shells with umbones placed more anteriorly, and in having more pronounced tripartition and the ribs sculptured with squamose nodes.

Kalelia multicostata (Lamarck, 1806) (Cossmann and Pissarro, 1904, pl. 31, fig. 97–3; Sables de Bracheux) can be separated from *K. burmeisteri* by being larger, with a more horizontal dorsal margin, anteriorly placed umbones, the posterior area sculptured with radial ribs of equal width, and by having more numerous radial ribs with better-developed tripartition over center of the valves.

Kalelia burmeisteri is distinguished from *K. pectuncularis* (Lamarck, 1806) (Chenu, 1842, pl. 2, fig. 8; Cossmann and Pissarro, 1904, pl. 31, fig. 97–2; Sables de Bracheux) by its smaller size, sloping dorsal margin, subcentrally placed umbones, and fewer and wider radial ribs.

Other Danian records of Carditidae

Some records of Danian carditids from Argentina have an uncertain taxonomic status and affinities and they are reviewed below.

'Cardita' morganiana *and* 'Cardita' beaumonti.—(Fig. 6.3; MLP 10220a–d). These two species have been mentioned frequently in the literature of the Paleocene from Argentina (Behrendsen, 1891; Burckhardt, 1900, 1902; Windhausen, 1918, 1931; Weaver, 1927, 1931; Gerth, 1935; Fossa Mancini, 1938a, 1938b).

As stated above, '*Cardita*' *morganiana* Rathbun, 1875 is a Cenozoic Brazilian species that is possibly related to *Baluchicardia* Rutsch and Schenck, 1943. '*Cardita*' *morganiana* was cited for the first time in Argentina from Puesto Pircala (Malargüe, Roca Formation, Mendoza Province) (Behrendsen, 1891), based on internal molds. These outcrops were assigned a Maastrichtian age by Parras et al. (1998). Burckhardt (1902) indicated the presence of '*C.*' *morganiana* in the type area of the Roca Formation, which is of early Danian age according to del Río et al. (2011).

Weaver (1927, 1931) mentioned the presence of '*Cardita*' *beaumonti* (=*Baluchicardia beaumonti*) in General Roca rocks. *Baluchicardia beaumonti* comes from Maastrichtian and Danian beds of northwestern India and Pakistan (Calcaire jaune de la chaine d'Hala, Sind Region), and North Africa (d'Archiac and Haime, 1854; Rutsch, 1936; Heaslip, 1968). According to Fossa Mancini (1938a), this species was mistakenly mentioned by Weaver (1927) because the author followed the ideas of Fritzsche (1919), who synonymized '*C.*' *morganiana* with '*C.*' *beaumonti*. Fossa Mancini (1938a) concluded that this synonymy is invalid.

The specimens from the area of General Roca (MLP 15294a–f) were used for erecting the species '*C.*' *burmeisteri* (=*Kalelia burmeisteri*) and '*C.*' *iheringi* (both discussed below) by Böhm (1903).

The only specimens found in Puesto Pircala, Malargüe ('*Cardita*' *morganiana* of Behrendsen, 1891 and Burckhardt, 1900) are small internal molds (MLP 10220a–d) with triangular outlines and very rounded margins. The absence of internal characters prevents generic and specific assignment. Casadío (1994) considered them to be juveniles of *Venericardia ameghinorum* (Ihering, 1907), but Parras et al. (1998) placed them in *V. iheringi* (Böhm, 1903). *Venericardia iheringi* is another species based on internal molds, and the Malargüe casts are very similar to this species. In this paper we accept the assignment by Parras et al. (1998), and assign the specimens MLP 10220a–c to '*Venericardia*' *iheringi*.

In this way and according to Fossa Mancini' (1938b), the presence of '*Cardita*' *morganiana* and '*C.*' *beaumonti* in Argentina is rejected.

'Venericardia' iheringi *(Böhm, 1903)*.—(Fig. 6.4, 6.5; MLP 15294b-e [Syntypes]; MLP 4298, 5377, 5387, 5517, 5125, 7625, 8866, 8955, 9455, 9726, 10506; MACN-Pi 356; CPBA 6405, 6408; MHNSR:Pi 1010, 1385, 1386, MACN-Pi 5750, MACN-Pi 5754, MACN-Pi 5749, MACN-Pi 5745). As in the previous case, this species was erected by Böhm (1903) based on the internal molds described by Burckhardt (1902, p. 219, figs. 2–6) from General Roca (Danian, Roca Formation). Ihering (1907) included it within *Venericardia*, but this assignment is not confirmed because this species lacks hinge and external sculpture, the most valuable characters required for a more precise generic placement among carditids. '*Venericardia*' *iheringi* has small to medium-sized shells with subtriangular to subquadrate outlines, rounded margins, prominent and very convex umbones placed subcentrally, and 21–22 radial ribs that are wider than their intercostals spaces. It is distinguished from casts of *Kalelia burmeisteri* (Böhm, 1903) by its smaller size with more rounded margins and by the absence of an umbonal-ventral carina. None of the other species from Roca Formation has the set of characters present in '*V.*' *iheringi*. Ihering (1907) mentioned a variation of this species, which he named *Venericardia iheringi* var. *boehmi*, with a more subquadrate outline, but it is difficult to differentiate from other specimens. Therefore, '*Venericardia*' *iheringi* is a species with uncertain affinities and we cannot assign it to any of the other species described from the Roca Formation.

Venericardia ameghinorum *(Ihering, 1907)*.—(MACN-Pi 340 [Holotype], 5213; CPBA 6406, 6409, 6410, 6412; MLP 5006, 6315, 7285, 7737, 8951, 8956, 10503, 10504, 10505; MHNSR:Pi 1398). *Venericardia ameghinorum* was erected by Ihering (1907) based on internal molds from General Roca (Roca Formation). This species has elongated shells that are easily distinguishable from other Paleocene carditid species. The elongate outlines with a sinuous ventral margin, and strongly recurved and separated orthogyrous umbones, placed this species within the genus *Arca* Linnaeus, 1758 (family Arcidae), as already mentioned by del Río et al. (2011).

cf. 'Cyclocardia' *sp. (del Río et al., 2007)*.—(GHUNLPam 22888, 22897–22900). Del Río et al. (2007) described cf. *Cyclocardia* sp. from the Roca Formation in Cerros Bayos (Danian, La Pampa Province), based on four internal molds of articulated individuals. The specimens GHUNLPam 22888 and 22898 have elongate outlines, strongly recurved umbones, and slightly sinuous ventral margin, which placed them within *Arca ameghinorum* (Ihering, 1907).

The specimens GHUNLPam 22897 and 22899 have more circular outlines, rounded margins, subcentrally placed umbones, and at least 20 radial ribs. Del Río et al. (2007) assigned them tentatively to *Cyclocardia* Conrad 1867 because of the number of radial ribs and the subcircular outline. ‘*Venericardia*’ *iheringi* Ihering, 1907 has a similar shape, but a less rounded margin, and an identical number of radial ribs. Here, these specimens are placed tentatively with ‘*V.*’ *iheringi*.

Discussion

Previous authors (Ihering, 1907; Fossa Mancini, 1938b) included Paleocene carditids from Argentina in the genus *Venericardia* Lamarck, 1801. This European taxon is based on Eocene collections from the Paris Basin. Several species ranging from Cretaceous to Recent have been assigned to this genus, but Huber (2010) indicated that *Venericardia* is an extinct taxon. Although several subgenera have been proposed within *Venericardia*, a complete systematic and phylogenetic revision is needed. Some of GCP taxa proposed by Heaslip (1968) (species of *Clairbornicardia*, *Rotundicardia*, and *Glyptoactis*) were recently reviewed by McClure and Lockwood (2015), who suggested the possible polyphyletic status of each of these genera. The authors explained that the use of few species in their analysis does not permit subgeneric reclassification. In their paper, McClure and Lockwood (2015) excluded *Baluchicardia* Rutsch and Schenck, 1943 from the analysis because Chavan (1969) included it in the subfamily Carditesine, but Chavan also considered *Claibornicardia* and *Glyptoactis* to be members of Carditesinae. In addition, Heaslip (1968) considered *Baluchicardia* as an alticostate carditid. We consider the polyphyletic status of alticostates and each of alticostate genera in the phylogeny of McClure and Lockwood (2015) to be a consequence of *Baluchicardia* outgroup status, because this genus is also an alticostate taxa. This analysis needs neither alticostates nor planicostates outgroup for a better evaluation of monophyletic status of these groups. Following the previously mentioned criteria about carditid subgenera, no species of *Venericardia* sensu stricto were found in Danian assemblages of Argentina. This revision reveals a more diverse generic composition of Paleocene carditid faunas with four different genera that have diverse affinities.

The generic composition of Paleocene Carditidae from Argentina now includes two taxa, *Claibornicardia* and *Rotundicardia*, previously reported from the GCP (Fig. 3), and a third genus, *Cardites* (Fig. 4) that previously was unrecorded from Palaeogene outcrops. The fourth genus, *Kalelia* n. gen., is a new one related to late Paleocene species from the Paris Basin (Figs. 5, 6.1, 6.2). The North American carditids were previously linked with European Paleogene species (Conrad, 1830; Clark and Martin, 1901; Dall, 1903). *Venericor* and *Claibornicardia* species were cited from both regions (Gardner and Bowles, 1939; Verastegui, 1953; Stenzel et al., 1957; Vervoenen and van Nieulande, 2010). Presumed connections previously have been established between these molluscan faunas. For example, Givens (1989) mentioned the volutid gastropod *Volutilithes* Swainson, 1829 from both regions, and Allmon (1990) proposed phylogenetic relationships between North American and European Eocene nassariid gastropods *Bulliopsis* Conrad, 1862 and *Desorinassa* Nuttall and Cooper, 1973. Givens (1989) also indicated several species with European affinities from the Paleogene of the GCP. Del Río and Martínez (2015) recorded GCP members in their Danian bioprovinces. The Rocaguelian and Salamancan bioprovinces of these authors include 12.2% and 18.8% of GCP taxa, respectively, and two of the four species described here correspond to these bioprovinces. *Claibornicardia paleopatagonica* and *R. mariobrosorum* n. sp. comprises GCP elements of the Danian Argentinian molluscan assemblages. To the relationships of this group with the Paris Basin molluscan fauna is the added presence of the genus *Kalelia* n. gen. in Patagonia. *Rotundicardia* is a genus that is also represented in the middle Paleocene of Australia (Pebble Point Formation) (Darragh, 1994), but no other Paleocene carditids are present in Australia. The species ‘*Venericardia*’ *fyfei* Finlay and Marwick, 1937 from Wangaloa Formation (Paleocene of New Zealand) was placed tentatively in the genus *Purpurocardia* Maxwell, 1969 by Maxwell (1969) and Beu and Maxwell (1990), but since ‘*V.*’ *fyfei* has some similarities in outline and external sculpture with *Claibornicardia* species, it could be also placed in this genus. *Cardites* is not present in others Danian faunas.

The fifth valid taxon included in this work is ‘*Venericardia*’ *iheringi*, which is a species based on casts (Fig. 6.3–6.5). Some internal molds were successfully assigned to *K. burmeisteri*, but in the case of ‘*V.*’ *iheringi* there are no characters that allow us to include it in any of the recognized genera. This species is the only carditid found in Maastrichtian rocks (at Puesto Pircala, in Roca Formation). The remaining carditids discussed here are restricted to early Danian beds.

Conclusions

This study has provided a revision of the Danian Carditidae bivalves from Argentina. During Danian times in Patagonia, the family Carditidae was restricted to four distinctive species representing four genera (*Claibornicardia paleopatagonica*, *Rotundicardia mariobrosorum* n. sp., *Cardites feruglioi*, and *Kalelia burmeisteri* n. comb.), and one species of uncertain affinities based on internal molds (‘*Venericardia*’ *iheringi*). The first three species constitute the first record of their respective genera from southern South America, and the most ancient record of them. One new species (*R. mariobrosorum*) is described from Roca Formation. One new genus (*Kalelia* n. gen.) is described with three species, including *K. burmeisteri* (based so far on internal molds). This revision confirms the biogeographical connections previously established between the Argentinian and North American and Europe carditid Danian faunas (del Río and Martínez, 2015).

Acknowledgments

The authors are indebted to the curators who facilitated access to collections: M. Longobucco (Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina), M.F. Rodríguez (Servicio Geológico Minero, Argentina), M. Tanuz (Facultad de Ciencias Exactas y Naturales, Buenos Aires, Argentina), M. de La Fuente (Museo de Historia Natural de San Rafael, Argentina), and A. Riccardi (Museo de La Plata, Argentina). We wish to thank J. Sime and P. Callomon (The Academy of Natural Sciences of Philadelphia), L. Cavin (Muséum d'Histoire Naturelle de Genève), and J. Pacaud (Muséum National d'Histoire Naturelle de Paris) for their help with American and European fossil materials. We thank M.S. Vázquez and L. Salgado for their help with field work at Puesto Pircala, and M. Álvarez for his help with photography. We thank M.B. von Baczko and P. Picasso by their language suggestions and we especially acknowledge and thank A. Beu for his invaluable help in polishing the English language, which highly improved the text. We also thank the editor M. Hautmann, the reviewer R. La Perna, and an anonymous reviewer for their constructive comments.

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Accepted 21 June 2017