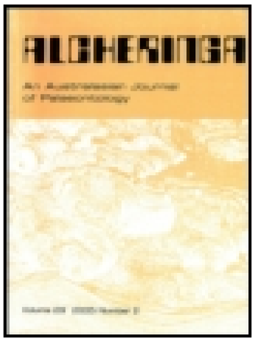

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Reassessment of *Neovenericor* Rossi de García, Levy & Franchi, 1980 (Bivalvia: Carditidae) using a geometric morphometric approach, and revision of planicostate carditids from Argentina

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Various systematic approaches have been applied to the Neogene planicostate carditids of Patagonia. Some authors have included these species within *Venericor* (known from the Eocene of North America and Europe) or in *Megacardita* (recorded from the Miocene of Europe). By contrast, Rossi de García *et al*. erected the endemic *Neovenericor* in 1980 for Patagonian species. The three proposed genera have variable outlines and similar hinge teeth configuration. Two geometric morphometric analyses were performed, which included the type species of the following taxa: *M. jouanneti* (middle Miocene, Mediterranean Basin), *V. planicosta* (middle Eocene, Paris Basin) and *N. austroplata* (early Miocene, Chenque Formation, Chubut Province). In the first approach, an Elliptic Fourier Analysis was used to test the general variability of outlines. In the second, a landmark-based method was employed to analyse the hinge configuration, followed by a Discriminant Function Analysis. The outline analysis discriminated *Megacardita* from the other two taxa based on its more elongate and rectangular shells. The Landmark Analysis distinguished the three taxa based on both, left and right hinges. The Discriminant Function Analysis showed significant values for this differentiation. *Neovenericor* has a higher hinge plate, broader and less posteriorly inclined teeth, and a less sinuous ventral edge than *Megacardita*; and it has larger and more posteriorly inclined teeth than *Venericor*. Other morphological characters of the genus include an intermediate number of radial ribs that do not dissipate ventrally, and wide and deep intercostal spaces. Thus, *Neovenericor* is clearly a distinct taxon. All Argentinian planicostate carditids were revised and included in this genus because they embrace its diagnostic features.

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Key words: Patagonia, Eocene, Miocene, Planicostates, *Venericor*, *Megacardita*.

CARDITIDAE is one of the most poorly studied and systematically unresolved families of Patagonian bivalves. The family was recently redescribed by Coan *et al.* (2000), and it includes a diverse group of bivalves that range from the Devonian to present, and which peaked during the Paleogene (Chavan 1969). Conrad (1830) and Harris (1919) described two main lineages within the family. The first includes the species allied to *Claibornicardia alticostata* (Conrad 1833) ('alticostate' carditids), and the second incorporates species related to *Venericor planicosta* (Lamarck 1801). Harris (1919) named the second group 'planicostate'carditids, incorporating species from the Paleogene of North America and Europe. Members of this group include bivalves with large shells, flat and smooth radial ribs, and long cardinal teeth. Conrad (1830) also mentioned that *Venericor planicosta* (Lamarck 1801) constitutes a 'fingerprint' of the Eocene, and emphasized the biostratigraphic importance of the group. Subsequently, Stewart (1930) formalized this group and erected *Venericor*. Gardner & Bowles (1939) studied taxa from this lineage, and described '*Venericor*' *austroplata*, which represents the first planicostate carditid from Patagonia.

'*Venericor*' *austroplata*, was subsequently assigned to *Megacardita* Sacco, 1899 by Feruglio (1954), and reassigned to *Venericor* by Camacho & Fernandez (1956), who described two new species: '*Venericor*' *abasolensis* and '*Venericor*' *wichmanni*. These last authors highlighted the use of this species as an Eocene index fossil for Patagonia, and this has been emphasized in later works (del Río 2004, and references therein). Rossi de García *et al*. (1980) erected *Neovenericor* for this species, but Camacho (1981) concluded that this taxon is not valid. Recently, Reichler (2011) proposed the validity of *Neovenericor* as a subgenus of *Venericor*. Other Argentinian planicostate carditids include '*Venericardia*' *crassicosta* Borchert, 1901 (Parana Formation, late Miocene, Entre Rios Province) and '*Venericardia*'

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carrerensis Griffin, 1991 (Rio Turbio, Man Aike and Rio Foyel formations, Eocene, Santa Cruz and Rio Negro provinces). The systematic placement of these species was not discussed in detail.

The arguments in favour of placing '*V. austroplata* in *Megacardita* include the elongate outline of its shells, the few radial ribs and the hinge configuration (Feruglio 1954). Gardner & Bowles (1939) and Camacho & Fernández (1956) argued for its inclusion within *Venericor* based on the possession of large ovate shells and a hinge configuration similar to that of the type species (*Venericardia planicosta* Lamarck, 1801). Supporting the validity of *Neovenericor*, Rossi de García *et al*. (1980) and Reichler (2011) highlighted the following diagnostic features: prominent umbos (an outline character), posterior area with the same convexity as the rest of the valve, few radial ribs that do not dissipate ventrally, juvenile radial ribs with subrectangular section, and hinge configuration with two cardinal teeth. Camacho (1981) explained that Rossi de García *et al*. (1980) misinterpreted the hinge configuration. Consequently, the placement of the Patagonian planicostate carditids remains uncertain. These arguments (on the variable outline and hinge configuration) have been used for the assignment of '*V*.' *austroplata* to three alternative genera. This study aims to review these two important morphological characters of *Venericor*, *Megacardita* and, the putatively valid *Neovenericor*, using a morphometric geometric approach. The remaining morphological characters are analysed and studied together with the outline of the shell and hinge configuration. A subsequent objective is the systematic revision of the planicostate carditids from Argentina.

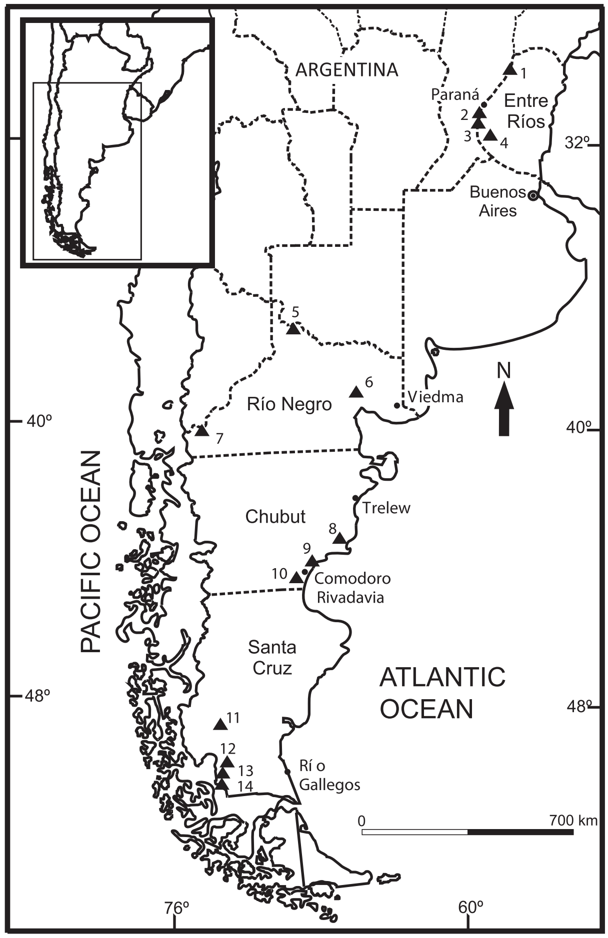

Fig. 1. Localities mentioned in the text. 1, La Paz. 2, Diamante. 3, Punta Gorda Sur. 4, Victoria. 5, Yacimiento Rinconada. 6, Gran Bajo del Gualicho. 7, Río Foyel. 8, Dos Pozos. 9, Pico Salamanca. 10, Estancia Busnadiego. 11, Cerro Castillo. 12, Cerro Palique. 13, Cancha Carreras. 14, Yacimiento Río Turbio.

Materials and methods

Argentinian carditids included in the present analysis come from Cenozoic marine rocks of the Río Turbio, Man Aike, Río Foyel, Chenque, Vaca Mahuida, Gran Bajo del Gualicho and Paraná formations (Fig. 1). The Río Turbio and Man Aike formation exposures are located in the southwest of Santa Cruz Province. The fossil carditids derive from the lower section (Yacimiento Río Turbio) and from the upper section (Cancha Carreras) of the Río Turbio Formation (Griffin 1991). Fossils from the Man Aike Formation derive from Cerro Palique and Cerro Castillo (Camacho *et al*. 2000). Carditid bivalves were recovered in Estancia Troncoso, from exposures of the Río Foyel Formation (Chiesa & Camacho 2001). Each of these units has been assigned to the Eocene (Malumián *et al*. 2000, Camacho *et al*. 2000, Chiesa & Camacho 2001).

The fossil carditids studied by Gardner & Bowles (1939) and Camacho & Fernández (1956) were obtained from outcrops of the Chenque Formation at Punta Malaspina, Estancia Busnadiego, Pico Salamanca and Dos Pozos, located in the southeast of Chubut province. This unit has been studied extensively by previous authors (Camacho & Fernández 1956, Bellosi 1990, Bellosi & Barreda 1993, del Río & Camacho 1998). Its age has been debated, but there is consensus that the exposed strata are of latest early–earliest middle Miocene age (del Río 2004, and references therein).

Fossil planicostate carditid shells were collected from the Gran Bajo del Gualicho and Vaca Mahuida formations, both units exposed in eastern Río Negro Province. The carditids derive from the Saladar Member of the Gran Bajo del Gualicho Formation, at the localities of Puesto Arriola and Puesto Astorga (Reichler 2010), and from the Vaca Mahuida Formation at Yacimiento Rinconada. These units were assigned an early Miocene age (del Río 2007, Reichler 2010).

Some carditid specimens derive from outcrops of the Paraná Formation at the La Bajada, La Paz, Diamante, Victoria and Punta Gorda Sur localities (Entre Ríos Province: Pérez *et al*. 2013). Pérez (2013) interpreted this formation to be of late Miocene age.

The studied material comes from various collections, such as the Cátedra de Paleontontología of the Universidad de Buenos Aires, Argentina (CPBA), Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' of Buenos Aires, Argentina (MACN-Pi and CIRGEO-PI), Museo de La Plata, Argentina (MLP), Museo de Historia Natural of Santa Rafael, Argentina (MSR.Pi), Museo de Ciencias Naturales y Antropológicas 'Prof. Antonio Serrano' of Paraná, Argentina (MAS-Pi), Centro de Investigaciones Científicas y de Transferencia Tecnológica a la Producción of Diamante, Argentina (DMT-Pi), Natural Museum of Natural History, Smithsonian Institution of Washington, DC, USA (USNM.Mo), and Naturhistoriska Riksmuseet of Stockholm, Sweden (PZ-NRM.Mo).

To test the morphological variability of the two key traits, we performed two geometrical morphometric analyses: an analysis of valve outlines using an Elliptic Fourier Analysis (EFA), and hinge configuration using a landmark-based (LM) approach of both, left and right hinges. These two traits are not suitable for a single comprehensive analysis owing to the small number of complete specimens with both, entire outline and hinge.

All analyses include the type species of each studied genus: *Megacardita jouanneti* (Basterot, 1825), *Venericor planicosta* (Lamarck, 1801) and '*Venericor*' *austroplata* (Gardner & Bowles, 1939) (='*Venericor*' *abasolensis* Camacho & Fernández, 1956). For EFA we used 31 adult valves, including 17 specimens of '*V.*' *austroplata*, seven valves of *M. jouanneti*, and seven valves of *V. planicosta*. For LM analyses we selected 60 valves of '*V.*' *austroplata* (32 left and 28 right valves), seven valves of *V. planicosta* (four left and three right valves), and six valves of *M. jouanneti* (three left and three right valves).

In the EFA, all specimens were digitized in lateral view, and right valves were mirrored. The outlines were processed with the software Shape v1.3 (Iwata & Ukai 2002) to obtain the chain-coded data, and then the Fourier coefficients were calculated. The outlines were standardized for size and position and the longest radius was the preferred alignment method. Following Crampton (1995), the number of harmonics (n) was calculated and the Fourier series was truncated at n = 9, with an average cumulative power of 99.99% of the total average power. Subsequently, we performed a Principal-Component Analysis (PCA) on the Fourier coefficients using PAST v2.15 (Hammer *et al*. 2001).

For the LM analysis, we chose ten landmarks on the left hinge, and fifteen on the right hinge (Fig. 2A, B). The landmark configuration includes type I and type II landmarks (Bookstein 1991). On the left hinge, type I landmarks are (1) umbo, (2) anterior apex of lunule, (4) anterior apex of anterior tooth, (5) posterior-dorsal apex of anterior tooth, (6) anterior-dorsal apex of anterior tooth, (7) anterior apex of posterior tooth, (8) posterior-dorsal apex of posterior tooth and (9) posterior-ventral apex of posterior tooth, and type II landmarks are (3) deepest point of lunule and (10) nymph projection. On the right hinge, type I landmarks include (1) umbo, (3) dorsal fold of lunular margin, (4) anterior apex of anterior tooth, (5) posterior-ventral apex of anterior tooth, (6) posterior-dorsal apex of anterior tooth, (7) anterior apex of middle tooth, (8) posterior-ventral apex of middle tooth, (9) posterior-dorsal apex of middle tooth, (10) anterior apex of posterior tooth, (11) posterior-ventral apex of posterior tooth, (12) posterior-dorsal apex of posterior tooth, and type II landmarks are (2) deepest point of lunule, (13) nymph projection, (14) shallowest point of ventral margin edge sinuosity and (15) deepest point of ventral margin edge sinuosity. The configurations were processed with tpsUtil v1.46 and tpsDig2 v2.16 (Rohlf 2004), and analysed with MorphoJ v1.06c (Klingenberg 2011). Procrustes was the alignment employed. Both analyses were followed by a PCA and, subsequently, we performed a Discriminant Function Analysis (DFA) with a permutation test (1000 replications). This analysis was implemented for two pairs of taxa: '*V.*' *austroplata* and *M. jouanneti* or *V. planicosta*. A cross-validation test followed the DFA.

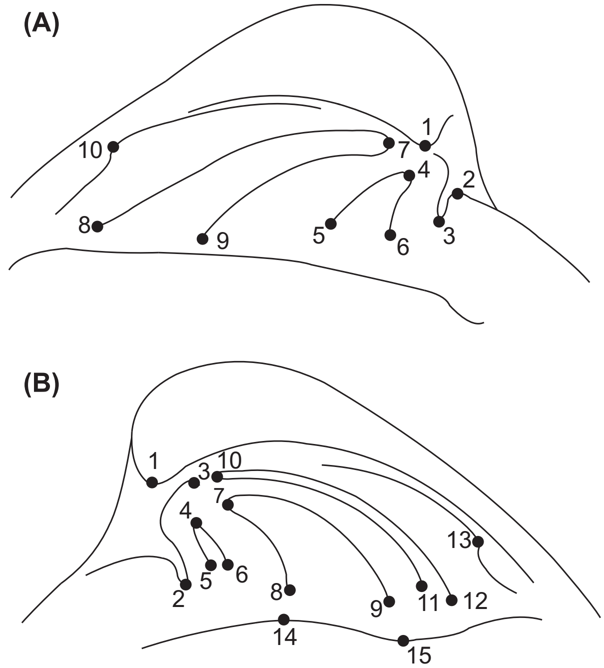

Fig. 2. Landmark configurations used for the LM analysis and hinge morphospaces generated by the PCA, including PC1 and PC2. **A**, Left hinge LM configuration. **B**, Right hinge LM configuration. Explanation of points is given in the text.

The remaining morphological characters were analysed using the terminology proposed by Verastegui (1953), Heaslip (1968) and Cox (1969), and including the other Argentinian planicostate carditids mentioned. The synonymy lists follow the proposals of Matthews (1973).

Results

Outlines

The PCA performed with the Fourier coefficients shows three significant components that explain 90.47% of the total variation. Variation along the first component (PC1; 53.61%) corresponds to the anterior–posterior elongation of the shell, with narrow triangular shapes to the left and more subrectangular shapes to the right. The second component (PC2; 32.16%) highlights variation between short and elongate outlines with subcentrally or anteriorly placed umbos, respectively. The third component (PC3; 4.70%) emphasizes the change in concavity in the lunular area. Although there is no morphological separation along PC1, there is discrimination between two groups along PC2 (Fig. 3). The specimens of *M. jouanneti* plot with positive values, whereas the '*V.*' *austroplata* and *Venericor planicosta* specimens are grouped towards negative values, and these last two taxa have very similar distributions in the morphospace. With respect to the first component, the specimens are not grouped in distinct clusters but the *M. jouanneti* specimens plot with higher values on average, compared with the other species.

Hinge configuration

The PCA highlights two significant components that explain 73.50% of the variation for the left hinge (Fig. 4A). The first component (PC1; 63.06%) is linked to the variation from more to less backwardly inclined teeth, and a shallower to deeper lunule; whereas the second component (PC2; 10.41%) explains the variation from elongate to short posterior teeth, wider to narrower anterior teeth and more to less pronounced nymph projection.

The PCA emphasizes two significant components that explain 55.5% of the total variation in the right hinge (Fig. 4B). The first component (PC1; 38.18%) is associated with the change between wider and more backwardly inclined to narrower and less backwardly inclined teeth, and by a more sinuous to straighter ventral hinge edge. The second component (PC2; 17.33%) highlights the variation from shorter to longer teeth, wider to narrower middle tooth, and deeper to shallower lunule.

In the morphospaces generated from both hinges, *Megacardita* specimens are clearly separated from the other species. *Venericor* and '*V.*' *austroplata* specimens share a minor proportion of both morphospaces, but remain well differentiated. The DFA shows significant statistical values for all analyses (Mahalanobis and Procrustres distances); on both hinges, the Permutation and Cross-Validation tests indicate a few misclassified specimens (Table 1). The main differences among the three taxa include inclination and width of the teeth, sinuosity of the ventral hinge edge, and depth of the lunule (Fig. 5).

Other morphological characters

Other morphological characters used in past studies to assess the taxonomic separation or inclusion of '*V.*' *austroplata* (Fig. 6A–D) within *Venericor* (Fig. 6E, F, I) or *Megacardita* (Fig. 6G, H, J) include the number of radial ribs, the sharpness of radial ribs towards the ventral margin, and the features of the posterior area.

Megacardita species have few radial ribs (18–21), whereas *Venericor* species have many (30–34). The Patagonian species have an intermediate number (21–26 radial ribs).

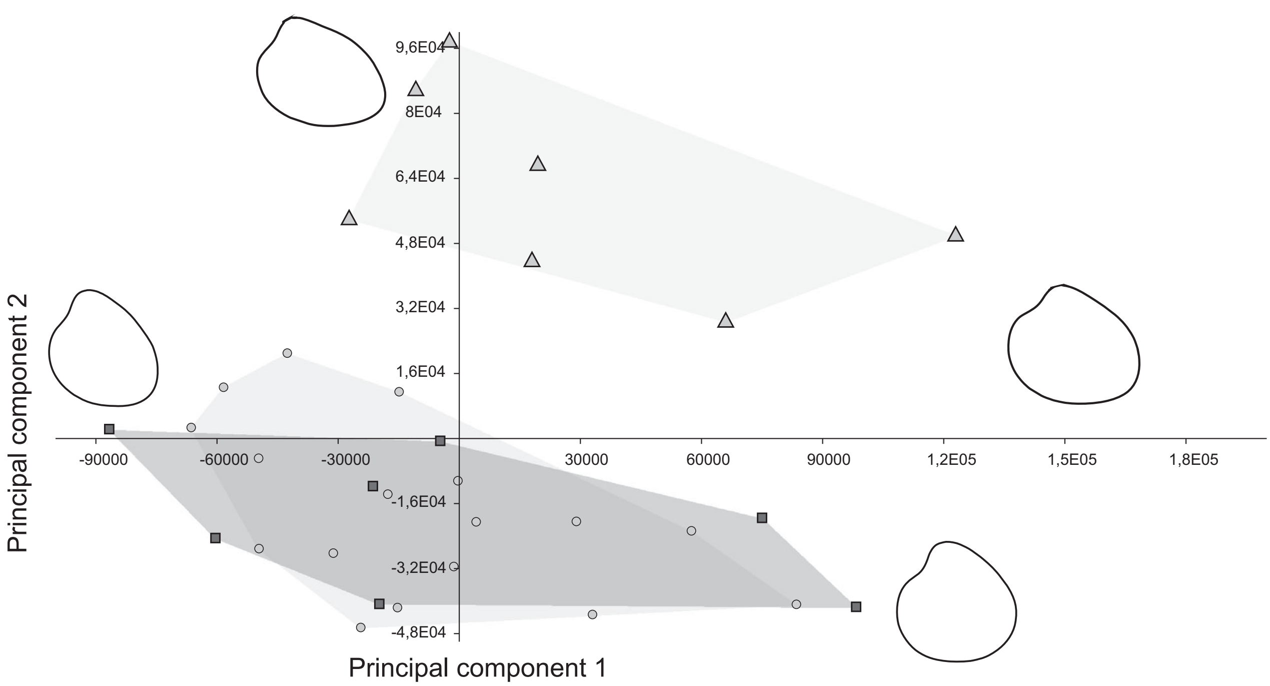

Fig. 3. Valve outline morphospaces generated by the PCA, including PC1 and PC2. The outlines show the extreme configurations of each axis. Triangles: *Megacardita jouanneti*. Squares: *Venericor planicosta*. Circles: '*Venericor*' *austroplata*.

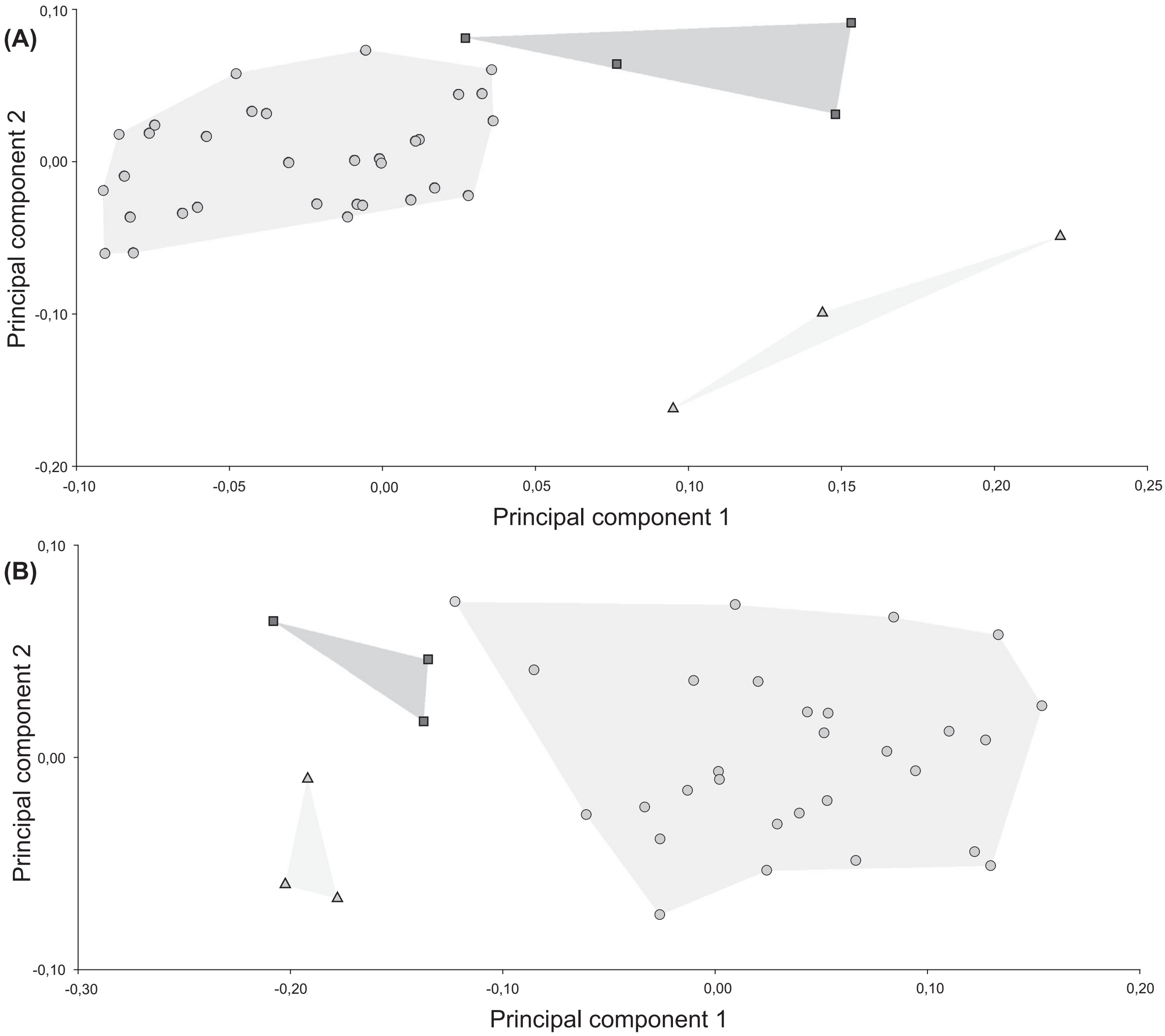

Fig. 4. Hinge morphospaces generated by the PCA, including PC1 and PC2. **A**, Left hinge morphospace. **B**, Right hinge morphospace. Triangles: *Megacardita jouanneti*. Squares: *Venericor planicosta*. Circles: '*Venericor*' *austroplata*.

	'*V.*' *austroplata*/*M. jouanneti*	'*V.*' *austroplata*/*V. planicosta*
Left hinge		
Procrustes distance	<.0001	<.0001
Mahalanobis distance	<.0001	0.002
Permutation test	0	0
Cross-validation test	0	3
Right hinge		
Procrustes distance	<.0001	<.0001
Mahalanobis distance	<.0001	<.0001
Permutation test	0	0
Cross-validation test	3	1

Table 1. Results of DFA for pairs analysed.
P-values are given for distances, and the number of misclassified specimens is noted for tests.

Both Northern Hemisphere genera have radial ribs that dissipate ventrally. This feature is more pronounced on *Venericor* species, but this is not the case in '*V.*' *austroplata*.

The posterior area is similar in the three genera. Another morphological character, not mentioned by previous authors, is the width of intercostal spaces. In *Venericor* and *Megacardita*, these spaces are reduced,

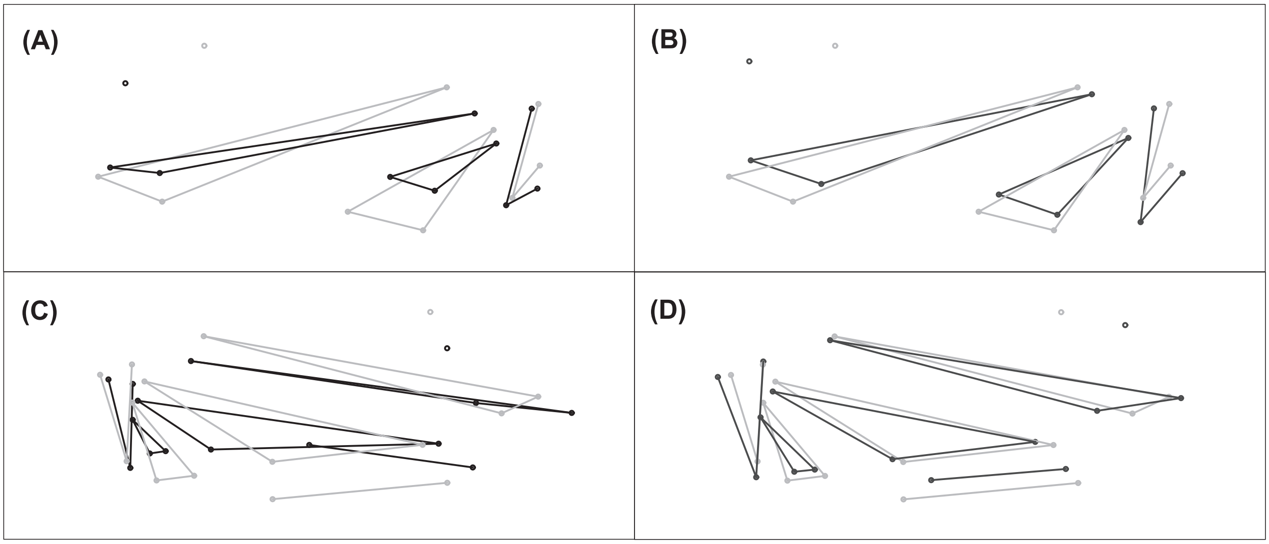

Fig. 5. Mean hinge configurations compared. **A**, '*Venericor*' *austroplata* and *Megacardita jouanneti* left hinges. **B**, '*V.*' *austroplata* and *Venericor planicosta* left hinges. **C**, '*V.*' *austroplata* and *M. jouanneti* right hinges. **D**, '*V.*' *austroplata* and *V. planicosta* right hinges. Grey lines represent '*V.*' *austroplata* in all schemes.

but in '*V.*' *austroplata*, the intercostal spaces are deeper and wider.

Systematic palaeontology

Family CARDITIDAE Férussac, 1822

Neovenericor Rossi de García, Levy & Franchi, 1980

Type species. *Venericor* (*Venericor*) *abasolensis* Camacho & Fernández, 1956 (by original designation) (=*V. austroplata* Gardner & Bowles, 1939), early Miocene, Chenque Formation, Chubut Province.

Included species. *Neovenericor paranensis* (Borchert, 1901) (late Miocene, Paraná Formation), *N. carrerensis* (Griffin, 1991) (Eocene, Río Turbio, Man Aike and Río Foyel formations), *N. ponderosa* (Suter, 1913) (late Oligocene, Chatton Formation, New Zealand).

Emended diagnosis. Carditid with large shells, reaching 120 mm long, subtriangular to subrectangular in outline, umbos placed near to the anterior third of the total valve length. Small and shallow lunule. High hinge with low right anterior tooth, very large right middle tooth, and long and wide left anterior tooth. External sculpture represented by 21–26 wide and smooth radial ribs, with subrectangular or subovate transverse section, persistent towards ventral margin. Deep and wide intercostal spaces.

Remarks. The taxonomic validity of *Neovenericor* is based on suggested morphological differences between this taxon and the other planicostate carditids: *Megacardita* and *Venericor*. The distinctions between these taxa are discussed in the next section. *Neovenericor* has a distinctive hinge configuration, an intermediate number of radial ribs that do not dissipate ventrally, and wide and deep intercostal spaces.

'*Megacardita*' *ponderosa* (Suter, 1913) (Beu & Maxwell 1990, p. 148, pl. 12i, j) from New Zealand (late Oligocene, Chatton Formation) possibly belongs to this genus. This species has subrectangular outlines, a small lunule, 25–26 wide and smooth radial ribs that do not dissipate ventrally and wide intercostal spaces.

Neovenericor austroplata (Gardner & Bowles, 1939)
Fig. 6A–D

v*1939 *Venericardia* (*Venericor*) *austroplata* Gardner & Bowles, p. 190, pl. 42, figs 11, 12.
1954 *Venericardia* (*Megacardita*) *austroplata* (Gardner & Bowles); Feruglio, p. 31, pl. 7–10.
v.1956 *Venericardia* (*Venericor*) *austroplata* Gardner & Bowles; Camacho & Fernández, p. 43, pl. 1, fig. 2, pl. 2, fig. 2.
v.1956 *Venericardia* (*Venericor*) *abasolensis* Camacho & Fernández, p. 44, pl. 1, fig. 1, pl. 2, fig. 1.
v.1956 *Venericardia* (*Venericor*) *wichmanni* Camacho & Fernández, p. 44, lám. 4, figs 1, 2.
1975 *Venericardia* (*Venericor*) sp.; Uliana & Camacho, p. 369, pl. 2, figs 1, 2.
1980 *Neovenericor abasolensis* (Gardner & Bowles); Rossi de García *et al.*, p. 66, pl. 1, figs 1–6.
1981 *Venericardia* (*Venericor*) *austroplata* Gardner & Bowles; Camacho, p. 314, pl. 1, figs 1, 3, pl. 2, figs 1, 2, 4, 5.
1991 *Venericardia* (*Venericor*) *austroplata* Gardner & Bowles; Reichler & Camacho, p. 29, pl. 1a.
2004 *Venericor abasolensis* Camacho & Fernández; del Río, figs 14.1, 14.2.

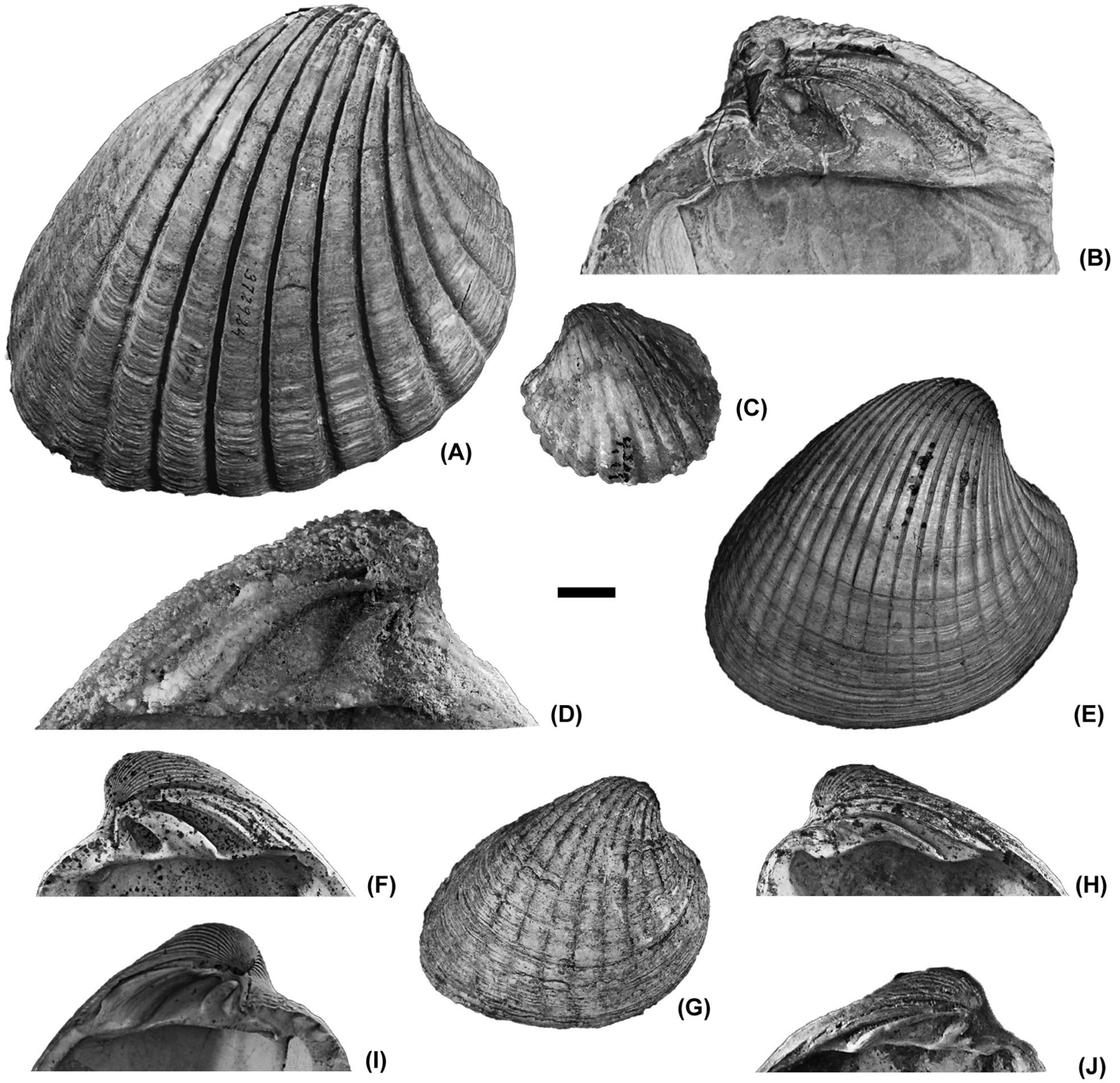

Fig. 6. **A–D**, *Neovenericor austroplata* (Gardner & Bowles, 1939). **E–F, I**, *Venericor planicosta* (Lamarck, 1801) (MACN-Pi 961 from Pévy, France). **G–H, J**, *Megacardita jouanneti* (Basterot, 1825). **A**, External view of the right valve, holotype USNM.Mo 327924 from Punta Malaspina. **B**, Right hinge, CPBA 11043 from Estancia Busnadiego. **C**, External view of the left valve, MACN-Pi 4719 from Puesto Arriola. **D**, Left hinge, MACN-Pi 4718 from Puesto Astorga. **E**, External view of the right valve. **F**, Right hinge. **G**, External view of the right valve, MACN-Pi 2355 from Sallez, France. **H**, Right hinge, MACN-Pi 2175 from Sallez, France. **I**, Left hinge. **J**, Left hinge, MACN-Pi 2350 from Sallez, France. Scale bar = 10 mm.

v.2007 *Venericor* (*Neovenericor*) *austroplata* (Gardner & Bowles); Reichler, pp. 183–188, pl. 5, figs 5, 6, pl. 7, figs 1–5, pl. 8, figs 1, 2.

v.2007 *Purpurocardia* sp.; Reichler, pp. 189–192, pl. 9, figs 10–12.

v.2011 *Venericor* (*Neovenericor*) *austroplata* (Gardner & Bowles); Reichler, p. 57, fig. 3, 1–7.

Emended diagnosis. Large shell with subtriangular to subrectangular outline. Lunule partially covered by the beaks. Right hinge with slightly sinuous ventral margin and long anterior tooth. External sculpture of 21–22 radial ribs. Intercostal spaces with U-shaped transverse section.

Type material. Holotype USNM.Mo 327924 (articulated specimen) from Punta Malaspina, Chubut Province.

Studied material. CPBA 6576, 14321–14327 ('Gran Bajo del Gualicho'), 7459, 11042, 11043 (Estancia Busnadiego), 7460, 8738 (Pico Salamanca), 15764–15772 (Yacimiento Rinconada), 21861–21870 (Dos Pozos); MACN-Pi 4718 (Puesto Astorga), 4719, 4805 (Puesto Arriola); MSR.Pi 2785, 2789 ('Gran Bajo del

Gualicho'); 67 left valves, 75 right valves, four internal moulds and 18 fragments.

Stratigraphic occurrence. Chenque (latest early–earliest middle Miocene), Gran Bajo del Gualicho (early Miocene) and Vaca Mahuida formations (early Miocene).

Description. Large shell with subtriangular to subrectangular outline, slightly convex dorsal, convex posterior and rounded ventral and anterior margins. Posterior area defined by a gentle convexity change from the sixth radial rib. Large and prominent umbos, placed near to the anterior third of the total valve length. Small and shallow lunule, convex and vertical, partially covered by the beaks. Right hinge with slightly sinuous ventral margin, long and very low anterior tooth, slightly inclined backwardly; large and triangular middle tooth, curved and very inclined backwardly with broad base; slightly curved posterior tooth. Left hinge with slightly convex ventral margin, long and broad anterior tooth, subrectangular, gently curved, and slightly inclined backwardly, with flat anterior and convex posterior sides; elongated and very curved posterior tooth, with broad base and acute apex. External sculpture of 21–22 smooth and wide radial ribs, with subrectangular transverse section, wider to ventral margin. Wide intercostal spaces with U-shaped transverse section. Posterior area sculptured by six weak and low radial ribs. Pallial line placed at a quarter of the total valve height. Ventral margin with strong and subrectangular crenulations.

Remarks. Uliana & Camacho (1975) mentioned the presence of *Venericor* specimens in the Vaca Mahuida Formation, and these valves are assigned here to *N. austroplata*. Reichler (2010) assigned two valves from Bajo del Gualicho to *Purpurocardia* sp., but these specimens correspond to juvenile individuals of this species (Fig. 6C).

Camacho & Fernández (1956) described two other planicostate carditids from the Chenque Formation ('*V.*' *abasolensis* and '*V.*' *wichmanni*) that were separated from *N. austroplata* based on some outline differences. Because of the great variability in outline of this species, these differences are not sufficient for specific differentiation, and these taxa are considered junior synonyms of *N. austroplata* here.

Neovenericor austroplata differs from *N. paranensis* (Borchert 1901) in its larger shells, lunule covered only partially by the beaks, larger right anterior tooth and fewer radial ribs.

Neovenericor austroplata can be distinguished from *N. carrerensis* by its subtriangular to subrectangular shells, narrower umbos, right hinge with sinuous ventral margin edge, and fewer radial ribs with subrectangular transverse section.

Neovenericor austroplata contrasts with *N. ponderosa* by the former's shorter and subrectangular outline, longer right anterior tooth, fewer radial ribs and intercostal spaces with a U-shaped transverse section.

Neovenericor paranensis (Borchert, 1901) Fig. 7A–F

v.1901 *Venericardia crassicosta* Borchert, p. 32, pl. 3, fig. 6.
v*1901 *Cardita paranensis* Borchert, p. 33, pl. 3, figs 7, 8.
1907 *Venericardia crassicosta* Borchert; Ihering, p. 381.
1907 *Venericardia paranensis* Borchert; Ihering, p. 382.
1939 *Venericardia* cf. *crassicosta* Borchert; Wahnish, p. 152.
v.1991 *Venericardia crassicosta* Borchert; del Río, p. 62, text-fig. 21.
vp.1991 *Venericardia* (*Purpurocardia*?) *paranensis* (Borchert); del Río, p. 60, pl. 1, fig. 6, text-Fig. 20.
2000 *Venericardia crassicosta* (Borchert); Camacho *et al*., p. 68.
2009 *Venericardia crassicosta* (Borchert); Casadío *et al*., p. 40.
v.2013 *Venericardia crassicosta* (Borchert); Pérez *et al*., p. 61, figs 2, 11.

Emended diagnosis. Large to medium-sized shell with subovate to subrectangular outline. Lunule totally covered by the beaks, with small nodules around it. Right hinge with slightly sinuous ventral margin and very backwardly inclined anterior tooth. External sculpture of 23–25 radial ribs.

Type material. Holotype MACN-Pi 2534 (one right valve) from Paraná, Entre Ríos Province.

Studied material. PZ-NHRM Mo. 118089 ('Entre Ríos'), MACN-Pi 351, 352, 361a (La Paz), 2632 (La Bajada), 5358 (Diamante), MAS-Pi 4289, DMT-Pi 258, 505 (Punta Gorda Sur), MLP 7278 (Victoria); three left valves, two right valves, and seven internal moulds.

Stratigraphic occurrence. Paraná Formation (late Miocene).

Description. Large to medium-sized shell with subovate to subrectrangular outline, slightly convex dorsal, straight posterior and rounded ventral and anterior margins. Posterior area defined by a gentle convexity change from the eighth radial rib. Large and prominent umbos, placed near to the anterior third of the total valve length. Very small and shallow lunule, convex and vertical, totally covered by the beaks. Right hinge with slightly sinuous ventral margin, triangular, reduced and very low anterior tooth, backwardly inclined and parallel to the succeeding one; large and triangular middle tooth, curved and very inclined backwardly with broad base; slightly curved and thin posterior tooth. Left hinge with slightly convex ventral margin, long and broad anterior tooth, subrectangular, gently curved, and slightly inclined backwardly, with flat anterior and

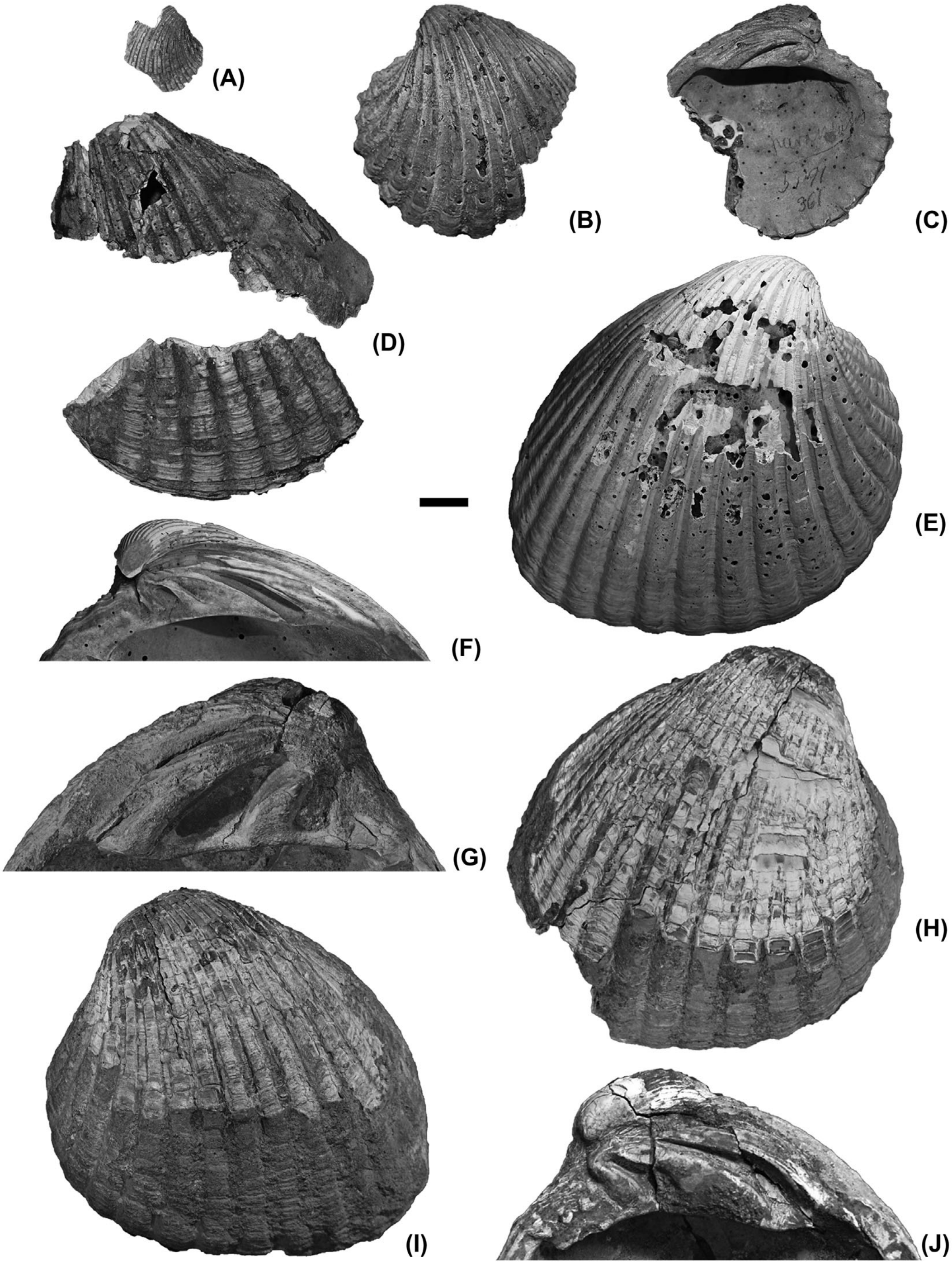

Fig. 7. **A–F**, *Neovenericor paranensis* (Borchert, 1901). **G–J**, *Neovenericor carrerensis* (Griffin, 1991). **A**, External view of the right valve, holotype MACN-Pi 2534 from La Bajada. **B**, External view of the left valve, MACN-Pi 361a from La Paz. **C**, Internal view of the left valve, MACN-Pi 361a from La Paz. **D**, External view of the left valve, MACN-Pi 2632 from La Bajada. **E**, External view of the right valve, PZ-NRM.Mo 118089 from 'Entre Ríos'. **F**, Right hinge, PZ-NRM.Mo 118089 from 'Entre Ríos'. **G**, Left hinge, CIRGEO-PI 128 from Yac. Río Turbio. **H**, External view of the right valve, holotype MLP 22934 from Cancha Carreras. **I**, External view of the left valve, CIRGEO-PI 128 from Yac. Río Turbio. **J**, Right hinge, holotype MLP 22934 from Cancha Carreras. Scale bar = 10 mm.

convex posterior sides; elongated and curved posterior tooth, with broad base and acute apex. External sculpture of 23–25 smooth and wide radial ribs, with subrectangular transverse section, wider to ventral margin. First anterior radial ribs near to lunule with small nodules. Wide intercostal spaces with subovate transverse section. Posterior area sculptured by six weak and low radial ribs. Pallial line placed at a quarter of the total valve height. Ventral margin with strong and subrectangular crenulations.

Remarks. Borchert (1901) described two carditid species from the Paraná Formation, as *Cardita paranensis* and *Venericardia crassicosta*. The first was based on a small and incomplete right valve (Fig. 6A), and the second on a large left valve (Fig. 6D). The radial ribs of both valves are smooth with subrectangular transverse sections. Despite the size difference, the two taxa correspond to the same species, at different ontogenetic stages. This potential synonymy was already suggested by Ihering (1907)

Neovenericor paranensis differs from *N. carrerensis* because it has a less ovate outline, lunule covered by the beaks with small nodules around it and a right hinge with sinuous ventral margin. *Neovenericor paranensis* can be distinguished from *N. ponderosa* by the lunule covered by the beaks and the more inclined right middle tooth on the Argentinian species.

Neovenericor carrerensis (Griffin, 1991) Fig. 7G–J

1955 *Pholadomya* sp. nov; Hünicken, p. 38.
v.1955 *Venericardia leanzai* Hünicken, p. 38.
v.1955 *Venericardia* sp. I; Hünicken, p. 38.
v.1955 *Venericardia* sp. II; Hünicken, p. 38.
1981 *Venericardia* (*Venericor*) sp.; Camacho, p. 316, figs 2a, 2b, 4.
v*1991 *Venericardia* (*Venericor*) *carrerensis* Griffin, p. 132, fig. 6.5–6.7.
v.1991 *Venericardia* sp.; Griffin, p. 132, figs 4, 6.
v.2000 *Venericardia* (*Venericor*) sp.; Camacho *et al.*, p. 68, fig. 3L.
v.2001 *Venericardia* (*Venericor*) sp.; Chiesa & Camacho, p. 309.
2009 *Venericardia* (*Venericor*) *carrerensis* Griffin; Casadío *et al.*, p. 39, fig. 6.2.
2011 *Venericor carrerensis* (Gardner & Bowles); Reichler p. 57.

Emended diagnosis. Thick shell, subovate outline. Very broad and recurved umbos. Right hinge with very concave and broad right middle tooth. Very backwardly inclined right and left anterior teeth. External sculpture of 24–26 radial ribs with subovate transverse section.

Type material. Holotype MLP 22934 (one right valve), paratype MLP 14188 (one left valve), both from Cancha Carreras, Santa Cruz Province.

Studied material. MACN-Pi 2252, 2253, 2264–2267, 2269, 2315, MLP 14201, 22916–22968 (Cancha Carreras), CIRGEO-PI 128, 159–162 (Yacimiento Río Turbio), 2253 (Cerro Palique), 3002 (Río Foyel); five left valves, six right valves, four articulated especimens, 59 incomplete valves, two internal and one external moulds.

Stratigraphic occurrence. Río Turbio, Man Aike, and Río Foyel formations (Eocene).

Description. Large and very convex shell with subovate to subrectrangular outline, very convex dorsal, slightly truncated posterior and rounded ventral and anterior margins. Posterior area defined by an abrupt convexity change from the sixth or seventh radial rib. Very large, broad and recurved umbos, placed near to the anterior third of the total valve length. Small lunule, convex and vertical. Right hinge with very concave and sinuous ventral margin, triangular, long and low anterior tooth, very backwardly inclined and parallel to the suceeding; large and triangular middle tooth, curved and very backwardly inclined with broad base; curved and thin posterior tooth. Left hinge with sinuous ventral margin, long and broad anterior tooth, triangular, gently curved, and backwardly inclined, with flat anterior and convex posterior sides; elongate and curved posterior tooth, with broad base and acute apex. External sculpture of 24–26 smooth and broad radial ribs wider to ventral margin, with subovate transverse section. Wide intercostal spaces with subovate transverse section. Posterior area sculptured by 6–7 weak, narrow and low radial ribs. Pallial line placed at a quarter of the total valve height. Ventral margin with strong and subrectangular crenulations.

Remarks. Griffin (1991) mentioned that *N. carrerensis* is a very common species in the upper section of the Río Turbio Formation, but in its lower section, he indicated the presence of *Venericardia* sp. These fossils are poorly preserved but they have the same outline and external sculpture of *N. carrerensis* and are, therefore, considered synonymous.

Camacho *et al*. (2000) and Chiesa & Camacho (2001) described two planicostate carditids from the Man Aike and Río Foyel formations, respectively. The two specimens are casts with the same external sculpture of *N. carrerensis*. *Neovenericor carrerensis* can be distinguished from *N. ponderosa* based on the more ovate outline of the former, with broader and more recurved umbos, and fewer radial ribs.

Discussion and conclusions

According to the results of EFA, *Megacardita* has elongate shells with subrectangular outlines, and is easily distinguished from *Venericor* and Argentinian species. These last two taxa are morphologically variable, with shells from subrectangular to subquadrate outlines, and they occupy a nearly identical field of the morphospace. In contrast to Feruglio (1954), we note that the outline of '*V.*' *austroplata* is not similar to that of *Megacardita*. According to Gardner & Bowles (1939) and Camacho & Fernandez (1956), this outline is more similar to *Venericor*.

In terms of hinge configuration, the three taxa are clearly differentiable, as corroborated by the DFA. The *Megacardita* left hinge teeth are more backwardly inclined than those of '*V.*' *austroplata*, and include a shorter anterior tooth. The *Venericor* left hinge teeth are relatively much shorter than those of '*V.*' *austroplata*. The Northern Hemisphere taxa have a deeper lunule and a less pronounced nymph projection. The right hinge of '*V.*' *austroplata* has teeth that are less posteriorly inclined than other taxa, and longer teeth than *Megacardita*. The ventral hinge margin is more sinuous in *Megacardita*, and the hinge height is greater in *Venericor*, than the Argentinian species. These hinge dissimilarities among the three taxa contrast with the observations of previous authors. Rossi de García *et al*. (1980) mentioned that '*V.*' *austroplata* has a particular hinge configuration, with two right teeth. Our results corroborated that proposition, but the hinge of this species differs from the description given by those authors (it has three right hinge teeth), as noted previously by Camacho (1981).

According to the results of the geometric morphometric analysis on outlines and hinge configuration, and the inclusion of other characters, *Neovenericor* has numerous distinctive features. *Neovenericor* differs from *Megacardita* and *Venericor* in the number, width and ventral definition of the radial ribs. Apart from *Venericor* and *Megacardita*, Stewart (1930) and Verastegui (1953) described two other taxa of planicostate carditids, with the same outline and radial rib features of *Venericor*: *Leuroactis* Stewart, 1930 (early Eocene, USA), and *Pacificor* Verastegui, 1953 (late Paleocene, USA). These two taxa share the differences outlined between *Neovenericor* and *Venericor*.

The numerous distinctive characters allow us to consider *Neovenericor* a valid taxon. Rossi de García *et al*. (1980) and Reichler (2011) reached the same conclusion, but used different criteria. Our more comprehensive analysis enabled us to redefine *Neovenericor*. The remaining Argentinian planicostate carditids have characters consistent with this genus, and are thus assigned to *Neovenericor*.

The features of *Neovenericor* species indicate a higher morphological variability in the planicostate carditids than recognized thus far. Previously, the only known recognized groups were *Venericor* and *Megacardita* species. The *Neovenericor* group is the only Southern Hemisphere clade, present in Oligocene fossiliferous strata of New Zealand, and Eocene and Miocene strata of Argentina. This group has a longer stratigraphic range than American planicostate carditids, which disappeared in the Paleogene (Gardner & Bowles 1939).

The outline of *Neovenericor* is easily distinguishable from that of *Megacardita* Sacco, 1899, but quite similar to that of *Venericor* Lamarck, 1801. The hinge configuration of these genera differs significantly. Therefore, *Neovenericor* Rossi de García, Levy & Franchi, 1980 is a valid taxon based on the presence of a distinctive hinge configuration, 21–26 radial ribs that do not dissipate ventrally, and wider and deep intercostal spaces. The genus includes all planicostate carditids previously described from Argentina: *N. austroplata* (Gardner & Bowles, 1939), *N. paranensis* (Borchert, 1901) and *N. carrerensis* (Griffin, 1991).

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No potential conflict of interest was reported by the authors.

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