An Acad Bras Cienc (2024) 96(Suppl. 3): e20230733 DOI 10.1590/0001-3765202420230733
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ANIMAL SCIENCE

A new genus of the *'Pitar'* group (Bivalvia: Veneridae) from the Western Atlantic Ocean revealed by geometric morphometric analysis

MAXIMILIANO J. ALVAREZ, MARÍA BELÉN SANTELLI, MARÍA BELÉN VON BACZKO, DAMIÁN E. PÉREZ & ALEJANDRA ROJAS

Abstract: Understanding shell morphology is central to taxonomic and evolutionary studies of bivalves. When traditional systematic studies find limitations in the recognition and classification of taxa, geometric morphometrics methods become a tool to tackle these uncertainties. Taxonomic difficulties are frequently found in systematics studies of the generally homoplastic Pitarinae (Venereidae). Recent contributions have proposed that Neogene-Recent South American species traditionally assigned to *Pitar* sensu stricto showed a distinguishable morphology that allowed separating them from that genus, including them in *Proteopitar*. In this contribution, we perform two morphometric analyses: elliptic Fourier analysis (EFA) and 2D landmark analysis with the aim of evaluating the intra- and interspecific variation of these taxa from the Western Atlantic Ocean included in *Pitar* s.s. to evaluate its doubtful generic assignments. EFA results show a highly variable outline in *Proteopitar patagonicus*, superimposed in the morphospace of all other taxa. The three analyzed groups, *Pitar*, *Proteopitar*, and extant Western Atlantic Ocean species, are statistically differentiable in hinge morphologies (landmark analysis), as corroborated by the Discriminant Function Analysis. The latter taxa are also distributed in a restricted portion of morphospace in EFA and along with the recognition of additional morphological differences allow us to define the new genus *Jasypitar*.

Key words: elliptic fourier analysis, landmark analysis, *Pitar, Proteopitar, Jasypitar.*

INTRODUCTION

The Pitarinae Stewart, 1930 is the largest subfamily within the highly diverse Family Veneridae (Bivalvia), with more than 70 genera (Mikkelsen et al. 2006), a cosmopolitan distribution, and a stratigraphic range extending from Late Cretaceous to the Recent (Keen 1969). It is characterized by the presence of shells with smooth or commarginal sculpture, often smooth and glossy periostracum, cardinal teeth parallel (not radiating) on the right valve, anterior lateral tooth present, and usually smooth inner margin (Mikkelsen et al. 2006). Following the proposal of Alvarez et al. (2019), where the doubts regarding the use of Callocardiinae Dall, 1895 instead of Pitarinae Stewart, 1930 were discussed, we prefer to continue using Pitarinae as the name of the subfamily that includes the species of *Pitar* ss. As a reinforcement of this decision, in the most updated classification of venerids based on molecular phylogenies, proposed by Liu et al. (2022), Pitarinae is considered a valid group, separated from Callistinae Habe & Kosuge, 1967 which is synonymized with Callocardiinae.

The study of the southern South American Pitarinae began in the middle 19th Century with the contributions of d'Orbigny (1843, 1844) and Koch (in Philippi 1844). However, it was not until the beginning of the following century that von Ihering (1907) performed one of the most complete analyses of the fossil and extant mollusk species of South America, including this subfamily, and proposing that the Pitarinae of this region would be represented by *Amiantis* Carpenter, 1864 and *Pitar* Römer, 1857. The study of the Pitarinae from northern South America, Caribbean, and North America have a similar background with detailed revisions of the group performed by Römer (1857), Dall (1902), and Palmer (1927).

Pitar is one of the taxa with the most complex systematics due to its presumptive worldwide distribution and high diversity, having more than 30 extant species (Huber 2010). This genus dates back to the Late Cretaceous according to bibliographic references (Keen 1969, Skelton & Benton 1993) but a complete revision of the fossil and extant taxa is still lacking. The genus *Pitar* is highly homoplastic, which has increased the difficulty of performing an accurate systematic study. Jukes-Browne (1913) and Marwick (1938) argued about the characteristics of the genus, questioning whether the election of *P. tumens* (Gmelin, 1791, Recent, Senegal, pl. 8, Figs. 12-13) as its type species was proper or not due to the presence of several morphological differences with other members of *Pitar*. All these systematic issues are reflected in the intricate taxonomic history of the extant taxon *Pitar patagonicus* (d'Orbigny, 1844) from the southern West Atlantic Ocean, previously better known as *P. rostrata* (Koch in Philippi 1844) (junior synonym, see Alvarez et al. 2019), which was included in *Pitar* by von Ihering (1907) (see below). Another species from Argentina, the fossil *P. mutabile* del Río & Martínez, 1998 from the middle Miocene–late Miocene, is also placed in *Pitar* due to its similarities with *P. patagonicus*. Both taxa have several features in common (e.g., conic anterior lateral tooth in adults, lunule very wide in its central region which gives it a subcircular appearance, high hinge plates with thick cardinal teeth, grooved tooth 2a, and 4b separated from the nymph by a groove in all its extension) that are absent in *Pitar tumens*. Based on these differences and supported by a phylogenetic study, Alvarez et al. (2019) included these two species in their new genus *Proteopitar*. These authors also discussed the high intraspecific variation of the outline of both species, the extant species *Pr. patagonicus* being the most variable, with subquadrate, subtriangular, or subrounded outlines. This feature was taken into account in the name *Proteopitar*, alluding to the Greek sea-God Proteus, who was able to change his appearance at will. A third taxon was erected by von Ihering (1907), *Pitar rostrata* var. *ortmanni*, which was later synonymized with *Proteopitar patagonicus* by Aguirre (1994), synonymy subsequently validated by Alvarez et al. (2019).

Alvarez et al. (2019) also pointed out the notorious morphological differences between three species from the Western Atlantic Ocean traditionally assigned to *Pitar* [*P. albidus* Gmelin, 1791 (Caribbean Sea to northern Brazil), *P. fulminatus* Menke, 1828 (North Carolina, USA to Santa Catarina, Brazil), and *P. palmeri* Fischer-Piette & Testud, 1967 (Cabo Frio to Santa Catarina, Brazil) (distributions after Huber 2010)] and the type species of the genus, *Pitar tumens*, raising doubts about the inclusion of these American taxa in *Pitar*.

The main goal of this contribution is to analyze the intra- and interspecific variation of the taxa from the Western Atlantic Ocean formerly included in the genus *Pitar* to clarify their doubtful generic assignments, as well as to evaluate the possible presence of a new genus. In addition, we studied the extreme shell outline variation of the species within the genus

Proteopitar to investigate its reliability as a character in systematic analyses.

The ZooBank Life Science Identifier (LSID) of this publication is: urn:lsid:zoobank.org:pub:83C065BF-5C02-461D-904E-073118AB3913.

MATERIALS AND METHODS

One hundred and thirty-nine left valves of species of *Pitar and Proteopitar*: *P. tumens* (4), *P. albidus* (12), *P. fulminatus* (22), *P. palmeri* (1), *P. rostrata* var. *ortmanni* (2), *Proteopitar mutabilis* (12), and *Pr. patagonicus* (86) were digitized (shell interior) with a Nikon digital SLR camera (Appendix). We examined shell shape variation through shape variables generated from two 2D geometric morphometric methodologies: outline and landmark (LM) analyses. For the outline analysis, the overall shape was studied by means of elliptic Fourier analysis (EFA; Kuhl & Giardina 1982) of the contour coordinates. The principles of the EFA methodology have been described by previous authors (Crampton 1995, Lestrel 1997). For each individual, chain codes were registered along the contour to calculate the elliptic Fourier descriptors (EFDs). The number of harmonics (n) was calculated following Crampton (1995) and the series was truncated at n=7 with an average cumulative power of 99.99% of the total average power. Based on the first harmonic ellipse, the different outlines were normalized regarding orientation, size, and starting point (Kuhl & Giardina 1982). Three of the four EFDs describing the first harmonic ellipse were constant for all the outlines (Crampton 1995) and were not included in posterior analyses. The software Shape 1.3v (Iwata & Ukai 2002) was used for all the EFA analyses. Subsequently, a Principal Component Analysis (PCA) of the Fourier coefficients was computed using PAST v3.25 (Hammer et al. 2001).

For the LM analysis, twelve landmarks were used to explore the morphological variation of the left hinge plate of the studied specimens. These landmarks were: (1) umbo position, (2) dorsal apex of the 2a and 2b teeth, (3) ventral apex of the 2a tooth, (4, 5) anterior and posterior apices of the ventral side of the 2b tooth, (6) dorsal apex of the 4b tooth, (7) ventral apex of the 4b tooth, (8) posterior end of the nymph, (9) dorsal apex of the AII tooth, (10, 11) anterior and posterior apices of the ventral side of the AII tooth, (12) anterior end of the lunule (Fig. 2b). The configurations were processed with tpsUtil v1.61 and tpsDig2 v2.30 (Rohlf 2017) and analyzed with MorphoJ v1.07a (Klingenberg 2011). Generalized Procrustes Analysis (GPA) was the alignment method employed. The analysis was followed by a PCA and, subsequently, a Discriminant Function Analysis (DFA) with a permutation test (1000 replications) was calculated. This analysis was implemented for three pairs of taxa: *Proteopitar* versus Brazilian *Pitar* species, *Proteopitar* versus *Pitar* s.s., and Brazilian *Pitar* species versus *Pitar* s.s.

RESULTS

Geometric morphometrics

Outline analysis. The PCA performed with the Fourier coefficients shows three significant components that explain 89.29% of the total variation. Variation along the first component (PC1; 51.33%) corresponds to the elongation of the shell through its axis of maximum growth, ranging from triangular (more negative PC1 scores) to suboval shapes (more positive PC1 scores). The second component (PC2; 25.36%) highlights variation between outlines with large umbones and ventrally oriented anterior margins (more negative PC2 scores) and small umbones and anteriorly extended anterior margins (more positive PC2 scores) (Fig. 1). The

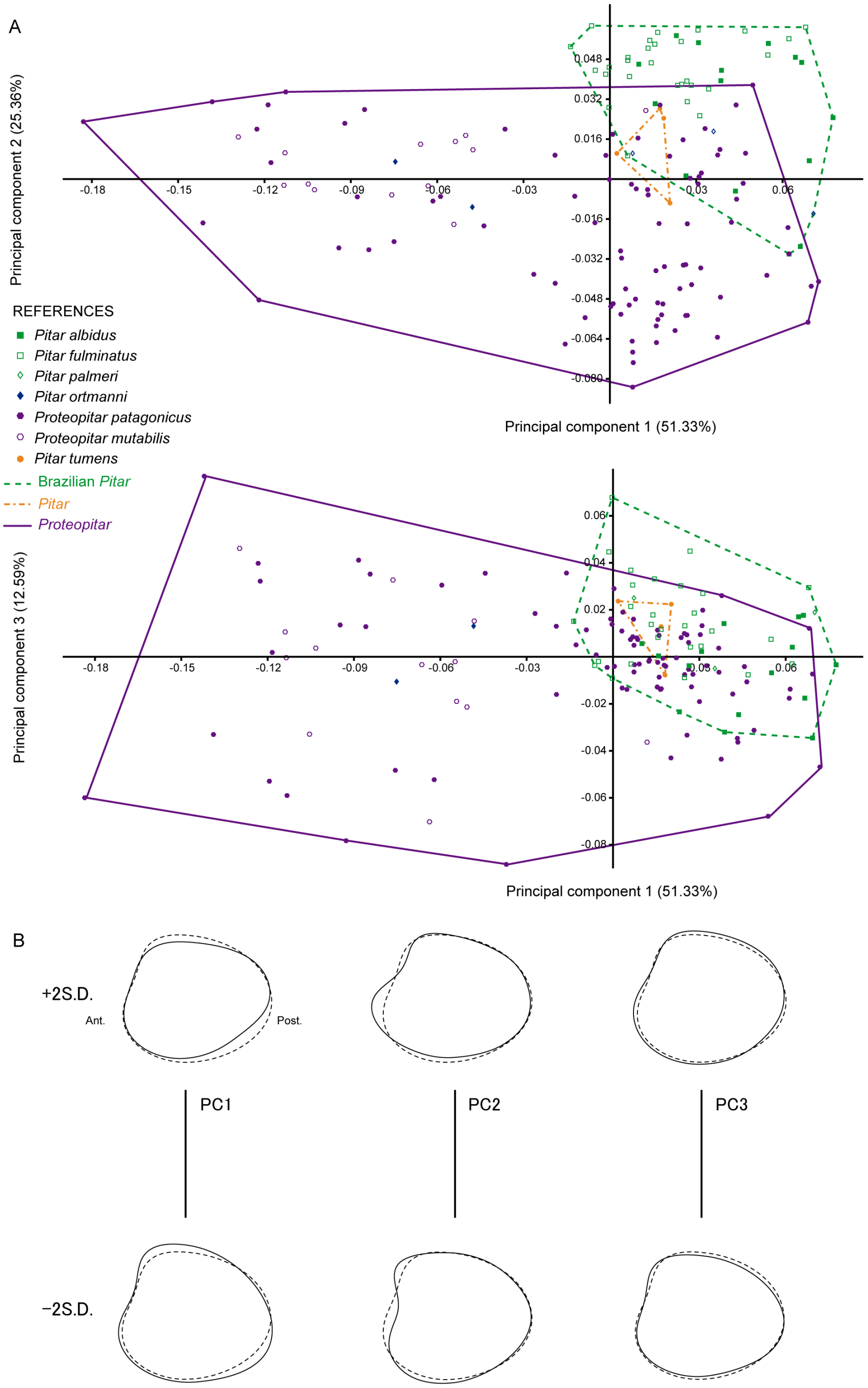

Figure 1. Results of morphometric analysis (EFA). a) Analysis of the overall shell shape variation along the first three PC axes. b) Extreme configurations for each axis (doted lines) and its corresponding mean (entire line). S.D. (Standard Deviation).

third component (PC3; 12.59%) emphasizes minor changes in the concavity of the ventral and dorsal margins. Although in the PC1 there is a clear separation of the specimens of *Proteopitar mutabilis* from those of *Pitar* sensu stricto and the Brazilian *Pitar* species, there is no clear separation between specimens of *Proteopitar patagonicus* and all of the remaining species, because specimens of this last taxon occupy almost the entire morphospace. There is a minor overlap in the PC2, with most of the specimens of *Pr. patagonicus* dispersed along the negative values of this axis while *Pitar* s.s. and the Brazilian species of *Pitar* tend to be distributed in positive values. There are no differences in the morphospace distribution along PC3 among the specimens a priori assigned to *Proteopitar*, *Pitar* s.s., and the Brazilian *Pitar*.

Landmark analysis. The PCA results reveal three significant components that explain 70.59% of the shape variation. The first component (PC1; 44.58%) is related to changes in the distance between the teeth, inclination of the lunule, and length of the nymph. The second component (PC2; 17.19%) explains the variation in the inclination of the 4b tooth, length of the 2b, width of the AII and length of the nymph. The third component (PC3; 8.81%) shows differences in the length of the AII, width of the 2b, and length of the lunule (Fig. 2).

In the Landmarks morphospace, *Proteopitar* and the Brazilian species of *Pitar* are at opposite

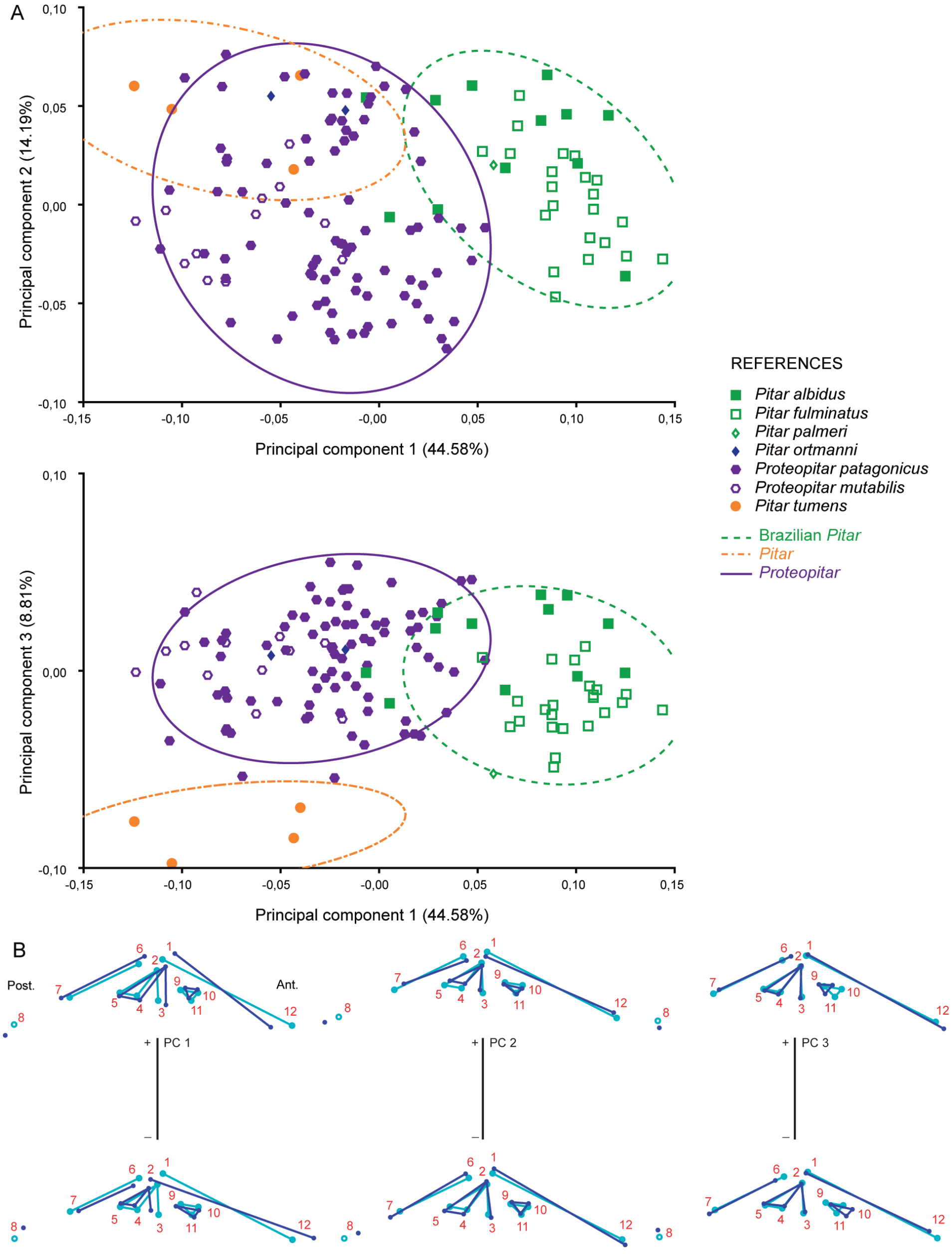

Figure 2. Results of morphometric analysis (LM). a) Hinge morphospace generated by PCA, including PC1, PC2 and PC3. b) Comparison of the mean hinge configuration (grey lines) and the extreme configuration for each axis (black lines).

ends of the PC1 with a small overlay area, *Pitar* s.s. has negative values and partially overlaps with *Proteopitar* specimens. Negative values of PC1 are characterized by the following features: the nymph is larger, cardinal teeth are also shorter, AII is lamellar, the hinge plate is lower, the umbo is more backwardly placed, and the lunule is more horizontal. In the PC2, the main difference is observed at specific level, with *Pr. mutabilis* placed mostly along negative values, *Pitar tumens*, *P. albidus* and *P. palmeri* within positive values, whereas *Pr. patagonicus* and *P. fulminatus* are placed on both sides of the axis (Fig. 2). The main variation in PC2 is related to small changes in orientation of the cardinal and lateral teeth, being both more anteriorly inclined through positive values. Along the PC3 there is a clear distinction between the morphospace occupied by the two American groups (*Proteopitar* and Brazilian *Pitar*) and the African *Pitar* (*Pitar* s.s.), which is placed at extreme negative values. At positive values of this PC the lunule is larger, the AII tooth is less distant from the cardinal teeth, and the 2b tooth is thinner than those placed on negative values (Fig. 2).

The DFA shows significant statistical values (Mahalanobis and Procrustes distances), and the Permutation and Cross-Validation tests indicate a few misclassified specimens (Table I).

Taxonomy

Family Veneridae Rafinesque, 1815

Subfamily Pitarinae Stewart, 1930

Jasypitar nov. gen.

Type species. *Venus albida* Gmelin, 1791, Recent, Caribbean Sea to Northern Brazil. Middle Pleistocene, Goaigoaza clays, Carabobo, Venezuela.

ZooBank Life Science Identifier (LSID) - urn:lsid:zoobank.org:act:3347C132-D494-451F-A63A-66C32D3706B0

Other included species. *Jasypitar fulminatus* (Menke, 1828) n. comb., Pleistocene-Recent, North Carolina (USA) to Santa Catarina (Brazil). *Jasypitar palmeri* (Fischer-Piette & Testud, 1967) n. comb., Recent, Cabo Frio to Santa Catarina (Brazil), and Late Pleistocene, Chuy Formation, La Coronilla, Uruguay.

Stratigraphic Range. Middle Pleistocene–Recent.

Diagnosis. Low umbones, short and thin cardinal teeth, elongated AII tooth, and short nymph. Ventral margin of the hinge plate strongly concave below 2a tooth, and parallel to the lunule margin and the AII tooth.

Derivation of name. “*Jasy*” means Moon in Guaraní, a native language commonly spoken in Paraguay, eastern Bolivia, northeastern Argentina, and southern Brazil. *Pitar* is the original name of the genus in which the species

Table I. **Results of DFA for pair analyzed.**

	Brazilian *Pitar*/*Pitar*	**Brazilian *Pitar*/*Proteopitar***
Procrustes distance	<.0001	<.0001
Mahalanobis distance	<.0001	<.0001
Permutation test (%)	100/100	97/99
Cross-validation test (%)	97/100	97/99

P-values are given for distances, and the percentage of correct classifications by taxa is noted for tests.

of *Jasypitar* were included by previous authors, and a common suffix of many Pitarinae. The grammatical gender of *Pitar* is masculine, *Jasy* is an addition to it, so *Jasypitar* should be treated as masculine.

Remarks. The three species of the genus are well known taxa inhabiting the tropical Atlantic coast of North and South America and the Caribbean Sea (Rocha & Matthews-Cascon 2015). The oldest record for a taxon of this genus belongs to a juvenile specimen of *Jasypitar albidus* reported by Weisbord (1964, p. 291, pl. 42, Figs. 7, 8) from the Goaigoaza clays, Carabobo, Venezuela of a Middle Pleistocene age (Macsotay & Caceres Hernandez 2005). There are some Pleistocene mentions of *J. fulminatus* from Grand Cayman Island (Rehder 1962), Bermudas Island (Spencer's Point Formation) (Richards et al. 1969) and a late Pleistocene record of *J. palmeri* from the Chuy Formation, La Coronilla, Uruguay, further south than its extant distribution (Rojas & Martínez 2016, Rojas et al. 2018).

Jasypitar and *Pitar* (type species *P. tumens*, Fig. 3a-c) are very similar in morphology, but it is possible to differentiate them by the lower and less inflated shells of *Jasypitar*, which also have a less prominent dorsal ligament, shorter nymphs, larger lunule, lower hinge plate, and the margin of the hinge plate, AII tooth and lunule are parallel to each other (Table II).

Jasypitar is distinguishable from *Proteopitar* (type species *Pr. patagonicus*, Fig. 3d-f) by its shorter nymph and cardinal teeth, lamellar AII, which is also placed closer to the cardinal teeth,

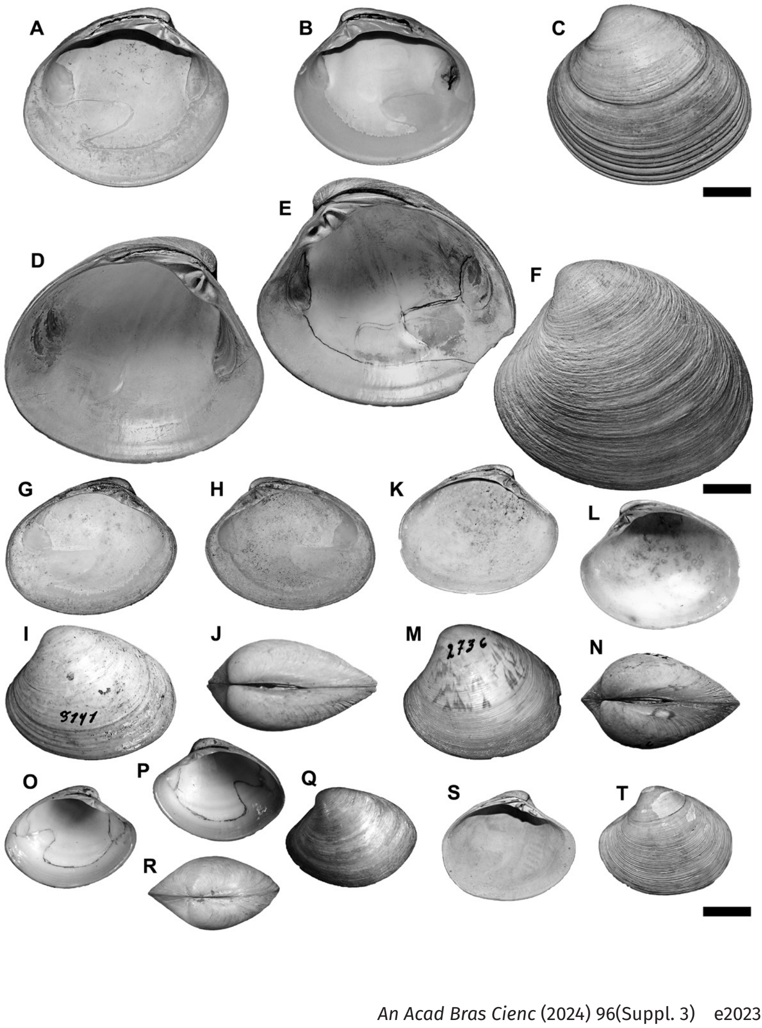

Figure 3. a), b) and c) *Pitar tumens* (Gmelin, 1791); MACN-In 40492; a) left valve, interior view; b) right valve, interior view; c) left valve, lateral view (Recent, Senegal). d), e) and f) *Proteopitar patagonicus* (d'Orbigny, 1844); NHMUK 1854.12.4.712, holotype; d) left valve, interior view; e) right valve, interior view; f) left valve, lateral view (Recent, Bahía San Blas, Buenos Aires, Argentina). g), h), i) and j), *Jasypitar albidus* (Gmelin, 1791); MACN-In 3141; g) left valve, interior view; h) right valve, interior view; i) left valve, lateral view; j) dorsal view (Recent, Kingston, Surrey, Jamaica); k), l), m) and n) *Jasypitar fulminatus* (Menke, 1828); MACN-In 2736; k) left valve, interior view; l) right valve, interior view; m) left valve, lateral view; n) dorsal view (Recent, São Sebastiao Island, São Paulo, Brazil). o), p), q), r), s) and t) *Jasypitar palmeri* (Fischer-Piette & Testud, 1967); MNHN_IM_2000-38651, holotype; o) left valve, interior view; p) right valve, interior view; q) left valve, lateral view; r) dorsal view (Recent, Grande Island, Rio de Janeiro, Brazil); s) and t), *J. palmeri*; FCDPI 4222; s) left valve, interior view; t) lateral view (Late Pleistocene, Chuy Formation, La Coronilla, Uruguay). Scale bar = 10 mm.

lower hinge plate, more central umbo, more horizontal lunule, thinner 2a tooth, and the margin of the hinge plate, AII tooth and lunule all being parallel to each other. It is also notable that the portion of the dorsal ligament visible with closed valves is thinner than in *Proteopitar*, and that the pallial sinus is a little shorter (Table II).

Jasypitar albidus (Gmelin, 1791) n. comb.

(Fig. 3g-j)
1791 *Venus albida* Gmelin, p. 3287
1853 *Dione albida* (Gmelin), Deshayes, p. 68
1864 *Venus albida* Gmelin, Krebs, p. 95
1867 *Caryatis albida* (Gmelin), Römer, vol. 1, p. 91, pl. 14, Fig. 4
1885 *Cytherea albida* (Gmelin), Dall, p. 102
1901 *Meretrix albida* (Gmelin), Dall & Simpson, vol. 20(1), p. 485
1902 *Pitaria albida* (Gmelin), Dall, vol. 26(1312), pp. 370–371
1927 *Pitaria* (*Pitaria*) *albida* (Gmelin), Palmer, vol. 1(5), pp. 25-26, pl. 6, Figs. 17, 18, 20
1933 *Cytherea* (*Dione*) *albida* (Gmelin), Trechmann, vol. 70(823), p. 35
1934 *Pitar albida* (Gmelin), Johnson, vol. 40(1), p. 47
1936 *Cytherea albida* (Gmelin), Lermond, p. 8
1949 *Pitar* (*Pitar*) *albidum* (Gmelin), Morretes, vol. 7(1), p. 35
1951 *Pitar* (*Pitar*) *albida* (Gmelin), McLean, vol. 17(1), p. 80, pl. 16, Fig. 3
1964 *Pitar* (*Pitar*) *albida* (Gmelin), Weisbord, vol. 45(204), p. 291, pl. 42, Figs. 7-8
1975 *Pitar albidus* (Gmelin), Rios, p. 229, pl. 72, Fig. 1099
1994 *Pitar albidus* (Gmelin), Rios, p. 286, pl. 98, Fig. 1401

Description. Shell small to medium sized (common size 40 mm), subquadrate to subelliptic. Umbo slightly prominent placed at anterior quarter of total length. Lunule long, occupying almost the total length of anterior margin, narrow, flat or slightly convex, and limited by a very thin line. Nymphs short and smooth. Right valve with 3a lamellar, short, inclined backwards, subparallel to tooth 1 and joined to anterior lateral AIII; 1 triangular, slightly thicker, and higher than 3a; 3b subhorizontal, short, wide, bifid; AIII lamellar, smaller, and shorter than AI, which is triangular; channel that

Table II. Genera comparison.

Pitar Römer, 1857	*Proteopitar* Alvarez et al. 2019	*Jasypitar* new genus
External ligament visible	External ligament visible	Ext. ligament barely visible
Nymph short	Nymph larger	Nymph shorter
Lunule short	Lunule larger	Lunule shorter
Pallial sinus large	Pallial sinus larger	Pallial sinus shorter
Ventral margin of the hinge plate, AII and margin of the lunule not parallel	Ventral margin of the hinge plate, AII and margin of the lunule not parallel	Ventral margin of the hinge plate, AII and margin of the lunule parallel
Hinge plate low	Hinge plate taller	Hinge plate lower
Cardinal teeth short	Cardinal teeth larger	Cardinal teeth short
AII lamellar	AII conic	AII lamellar

connects anterior lateral pit to cardinal pit deep and remarkably short. Left valve with 2a and 2b joined in an inverted V shape; 2a thin, lamellar, not grooved; 2b triangular, straight, and slightly higher than 2a; 4b short, slightly curved, higher in its middle region and separated from nymph by narrow groove; AII tall, lamellar in adults, close to cardinals. Margin of hinge plate, AII tooth and lunule parallel to each other. Dorso-posterior region of right valve with a groove for insertion of left valve. Right lunule margin with a groove for insertion of left valve. Scar of pedal retractor muscles joined to adductor scars. Pallial sinus triangular, short, ascending, and round-ended. Commarginal sculpture of growth lines.

Additional material examined. See Appendix.

Remarks. One of the differences between *Jasypitar albidus* and the other species of the genus is the periostracum colour, being chalky white in *J. albidus*, white with brown or yellow spots or markings in *J. fulminatus*, and pinkish white in the case of *J. palmeri*. *Jasypitar albidus* also has the narrowest lunule of the three species, which is less trigonal, and more compressed.

Jasypitar fulminatus (Menke, 1828) n. comb.

(Fig. 3k-n)

1791 *Venus holosericea* Gmelin, **nomen oblitum**, p. 3290
1828 *Cytherea fulminata* Menke, **nomen protectum**, p. 91
1844 *Cytherea varians* Hanley, p. 109
1844 *Cytherea rubiginosa* Philippi, p. 19, pl. 3, Fig. 2
1858 *Cytherea holosericea* Gmelin, Menke, p. 15
1890 *Cytherea penistoni* Heilprin, p. 142, pl. 8, Fig. 4
1902 *Pitaria fulminata* Menke, Dall, vol. 26(1312), p. 371
1926 *Pitar fulminata* Menke, Peile, vol. 17, p. 95
1954 *Pitar fulminata* Menke, Abbott, p. 414, pl. 39d
1967 *Pitar* (*Pitar*) *varians* Hanley, Fischer-Piette & Testud, p. 212
1971 *Pitar* (*Pitar*) *fulminata* Menke, van Regteren Altena, p. 67
1975 *Pitar fulminatus* Menke, Rios, p. 229, pl. 72, Fig. 1101
1994 *Pitar fulminatus* Menke, Rios, p. 286, pl. 98, Fig. 1403
1994 *Pitar fulminatus* Menke, Diaz Merlano & Puyana Hegedus, p. 81, Fig. 181
2006 *Pitar fulminatus* Menke, Denadai et al., vol. 6(3), p. 3, 10A–10C
2014 *Pitar fulminata* Menke, de Freitas Tallarico et al., p. 97, pl. 3.42

Description. Shell small to medium sized (common size 40 mm), subquadrate to subtriangular. Umbo slightly prominent placed at anterior quarter of total length. Lunule long, occupying almost the total length of anterior margin, narrow, flat or slightly convex, and limited by a very thin line. Nymphs short and smooth. Right valve with 3a lamellar, short, inclined backwards, subparallel to tooth 1 and joined to anterior lateral AIII; 1 triangular, slightly thicker, and higher than 3a; 3b subhorizontal, short, thin, bifid; AIII lamellar, strikingly smaller, and shorter than AI, which is triangular; channel that connects anterior lateral pit to cardinal pit deep and very short. Left valve with 2a and 2b joined in an inverted V shape; 2a thin, lamellar, not grooved; 2b triangular, straight, or slightly curved and slightly lower than 2a; 4b short, slightly curved, higher in its middle region and separated from nymph by narrow groove; AII tall, lamellar in adults, close to the cardinals. Margin of hinge plate, AII tooth and lunule parallel to each other. Dorso-posterior region of right valve with groove for insertion of left valve, another groove for insertion of left valve in lunule margin. Scar of pedal retractor muscles joined to adductor scars. Pallial sinus triangular, short, ascending, and round-ended. Commarginal sculpture of thin commarginal ribs.

Additional material examined. See Appendix.

Remarks. As Huber (2010, p. 732) proposed the name *Cytherea fulminata* is the valid name for this species, and it has to be considered as nomen protectum. Meanwhile, the previous name *Venus holosericea* Gmelin, 1791, p. 3290, has to be treated as nomen oblitum. *Venus holosericea* was never used by other authors, except Menke (1858, p. 15), who recognized the junior synonym of *C. fulminata*.

Jasypitar fulminatus is differentiated from the other members of the genus by the portion of the dorsal ligament that is visible from outside, being an intermediate stage between *J. albidus*, and *J. palmeri*. Besides its color, the ornamentation of the shell is different from the other two species, in the case of *J. fulminatus* it consists of thin commarginal ribs, whereas *J. albidus* has commarginal lines and *J. palmeri* thin lirae.

Jasypitar palmeri (Fischer-Piette & Testud, 1967) n. comb.

(Fig. 3o-t)
1967 *Pitar* (*Pitar*) *palmeri* Fischer-Piette & Testud, p. 212, pl. 4, Fig. 24-29
1994 *Pitar palmeri* Fischer-Piette & Testud, Rios, p. 287, pl. 98, Fig. 1404
2018 *Pitar* cf. *palmeri* Fischer-Piette & Testud, Rojas et al., p. 234

Description. Shell small sized (common size 30 mm), subtriangular. Umbo slightly prominent placed at anterior quarter of total length. Lunule long, occupying almost the total length of anterior margin, wide, flat or slightly convex, and limited by a very thin line. Nymphs short and smooth. Right valve with 3a lamellar, short, inclined backwards, subparallel to tooth 1; 1 triangular, thicker, and slightly higher than 3a; 3b subhorizontal, dorsally elongated, very wide, bifid; AIII lamellar, smaller, and shorter than AI, which is also lamellar; channel that connects anterior lateral pit to cardinal pit deep and very short. Left valve with 2a and 2b joined in an inverted V shape; 2a thin, lamellar, not grooved, slightly curved; 2b triangular, narrow, straight, and slightly lower than 2a; 4b short, slightly curved, higher in its middle region and separated from nymph by narrow groove; AII tall, lamellar, close to the cardinals. Margin of hinge plate, AII tooth and lunule parallel to each other. Dorso-posterior region of right valve with groove for insertion of left valve, another groove for insertion of left valve in lunule margin. Scar of pedal retractor muscles joined to adductor scars. Pallial sinus triangular, short, ascending, and round-ended. Commarginal sculpture of very thin lamellae.

Additional material examined. See Appendix.

Remarks. Fischer-Piette & Testud (1967) remarked that *P. palmeri* has no external ligament, a characteristic that separates this species not only from others of the *Pitar* group, but also distinguishes it from the rest of the venerids. We observed that the nymph of the type material of *P. palmeri* (MNHN_IM_2000-38651; Fig. 3o-r) is the shortest of the three species and the ligament is less developed externally than in the other taxa of the genus, but still visible. If we compare this condition among the three species, we can recognize that *J. albidus* has the largest nymph and the widest separation between valves in the ligament area, *J. palmeri* has the shortest nymph and the narrowest separation, and *J. fulminatus* has an intermediate stage for both characters. Another remarkable characteristic of *J. palmeri* is its shorter and more ascending pallial sinus (Fig. 3s).

DISCUSSION

As Huber (2010) stated, there are many Caribbean species doubtfully classified and the intraspecific variation of well-known species such as *J. albidus* (Gmelin, 1791) and *J. fulminatus* (Menke, 1828) have not been studied yet, which could lead to problems of misclassification. A geometric morphometric approach (using both methodologies, EFA and LM) is demonstrated to be an adequate tool to distinguish both intra- and interspecific variation as well as intergeneric differences in bivalves in recent years. There are many examples in the bibliography applying geometric morphometric methodologies to the evolutionary and systematic study of bivalves. Some examples of these studies include analysis of the variation through ontogeny (Márquez et al. 2010, Alvarez & Pérez 2016, Pérez & Santelli 2018); sexual dimorphism (Pérez et al. 2017a); ecological morphotypes (del Río et al. 2016, Collins et al. 2019); geographical morphotypes (Getino Mamet et al. 2021); anagenetic and cladogenetic changes (Boretto et al. 2014, Milla Carmona et al. 2018, Trovant et al. 2017); and systematics (Collins et al. 2013, Pérez et al. 2017b).

According to the results of the EFA, *Jasypitar* nov. gen. has short shells with subrounded to suboval outlines. This outline is similar to that of *Pitar tumens*. The distribution of these taxa is almost completely overlapped by the position in morphospace of the subrounded to suboval specimens of *Proteopitar patagonicus*, which means that it is not possible to differentiate them by their outline itself.

A similar situation occurs with the subtriangular specimens of *Proteopitar mutabilis* sharing their morphospace with specimens of *Pr. patagonicus*. The extremely variable outline of *Pr. patagonicus*, previously reported by Alvarez et al. (2019), clearly influences the EFA analysis, because its specimens are distributed in almost the entire morphospace. Alvarez et al. (2019) did not indicate differences between the outline of these taxa, but our results allow us to separate *Jasypitar* from *Proteopitar* based on the restricted area of the morphospace occupied by *Jasypitar*. In addition, Alvarez et al. (2019) used some outline features to distinguish *Pr. mutabilis* from *Pr. patagonicus*. In our results, *Pr. mutabilis* occupies a more restricted portion of the morphospace than *Pr. patagonicus*.

In terms of hinge configuration, the three genera *Pitar*, *Proteopitar*, and *Jasypitar* nov. gen. are easily distinguishable, as corroborated by the DFA. *Proteopitar* occupies a central position in the morphospace while *Pitar* and *Jasypitar* are found at opposite ends. The LM analysis showed that the main differences between *Pitar* s.s. and *Jasypitar* are that *Jasypitar* has lower umbones, which means a less sloped lunule, shorter and thinner cardinal teeth, a longer AII tooth, and a shorter nymph. As was indicated by Alvarez et al. (2019), differences based on hinge configuration are important among these genera, which agrees with our results, but are opposite to the proposals of Huber (2010), Rios (1975, 1985), Fischer-Piette & Testud (1967), who considered that all the studied species are members of *Pitar*.

The phylogenetic analysis performed by Alvarez et al. (2019) also corroborated the evolutionary differences among *Proteopitar*, *Pitar*, and the new genus *Jasypitar*, because they obtained these species included in three different clades. *Proteopitar mutabilis* and *Pr. patagonicus* constitute a unique clade with very high support, but Alvarez et al. (2019) questioned the inclusion of the Brazilian species *J. albidus* and *J. fulminatus* (here included in *Jasypitar* nov. gen.) in the genus *Pitar* as proposed by previous authors (Rios 1975, 1985, Huber 2010). Finally, Alvarez et al. (2019) recovered *Jasypitar albidus* and *J. fulminatus* as part of the same clade with high support values and sharing seven synapomorphies: umbo anterior; lunule length of two-thirds of total height; nymph short; tooth 3b two times longer than tooth 1; lateral margin of the nymph low; thinner valves; tooth 3a of similar height of the other cardinal teeth. In that phylogenetic analysis *Pitar tumens* is the earliest diverging taxon of the "*Pitar* clade", where *Proteopitar* is the most derived genus being the sister taxon of *Lamelliconcha*, another American genus, with *Jasypitar* species occupying an early diverging position.

CONCLUSIONS

By means of geometric morphometric analysis on hinge configuration and the consideration of other morphological characters, such as low umbones; short and thin cardinal teeth; elongated AII tooth; short nymph; ventral margin of the hinge plate below 2a tooth strongly concave, and parallel to the lunule margin and the AII tooth; and an external ligament less visible than in *Pitar* and *Proteopitar*, we erect the new Western Atlantic genus *Jasypitar* to include *J. albidus* (Gmelin, 1791), *J. fulminatus* (Menke, 1828), and *J. palmeri* (Fischer-Piette & Testud, 1967). Our results agree with the previous phylogenetic results of Alvarez et al. (2019), in which *Jasypitar*, *Pitar* and *Proteopitar* are monophyletic. The identification of the new genus *Jasypitar* allows us to better understand the taxonomy of the Pitarinae, a taxonomically complex group that has long been misunderstood because of its wide distribution, abundant diversity, and highly homoplastic shells.

Acknowledgments

We especially thank K.S. Collins and S.N. Nielsen for their helpful comments and suggestions that improved this work. We thank C.J. del Río for her assistance, and helpful comments on an early version of the manuscript. The authors are indebted to the curators who facilitated access to paleontological and biological collections: C.J. del Río (MACN-Pi), A. Tablado and M. Romanelli (MACN-In), and to V. Heros and P. Maestrati (MNHN) for the pictures of the holotype of *J. palmeri*. CONICET is acknowledged for the postdoctoral grant given to MJA. AR acknowledges PEDECIBA, and ANII FCE_1_2021_1_167109 research grant for financial support.

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Appendix.

Collection number	Valves	Species	Locality	Province	Country	Formation	Age
CIRGEO-PI 2805p	2	*Pr. mutabilis*	Cantera a 7km Ea S. Julio	Tierra del Fuego	Argentina	Carmen Silva	middle Miocene
CIRGEO-PI 2867p	2	*Pr. mutabilis*	Puesto 26	Tierra del Fuego	Argentina	Carmen Silva	middle Miocene
CPBA 15092	17	*Pr. mutabilis*	Puesto Fracaso	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12510	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12512	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12513	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 15514	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12515	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12516	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12518	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12519	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12520	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12522	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 17392	2	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14469	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14470	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene

Appendix. Continuation.

CPBA 14471	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14472	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14473	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14474	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14475	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14476	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14477	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14478	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14479	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14480	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14481	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14482	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14483	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14485	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14486	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14487	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14488	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14489	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 13284	1	*Pr. mutabilis*	Punta Norte	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14462	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14463	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14465	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14466	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14467	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14468	1	*Pr. mutabilis*	Pto. Pirámides/P. Valdés	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12507	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12508	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12509	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12511	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12517	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12487	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 12488	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14460	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 14461	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 15491	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 15492	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 15493	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene

Appendix. Continuation.

CPBA 15494	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
CPBA 15495	1	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
MAS-Pi 1005	1	*Pr. mutabilis*	Ea. La Juanita	Entre Ríos	Argentina	Paraná	late Miocene
MACN-Pi 6395	6	*Pr. mutabilis*	Puesto San José Este	Chubut	Argentina	Pto. Madryn	late Miocene
NHMUK 1854.12.4.712	2	*Pr. patagonicus*	Bahía San Blas	Buenos Aires	Argentina	-	Recent
ANSP 31131	1	*Pr. patagonicus*	Plataforma Cont. Arg.	-	Argentina	-	Pleistocene
MLP 2482	13	*Pr. patagonicus*	arroyo Las Brusquitas	Buenos Aires	Argentina	-	Holocene
MLP 26232	1	*Pr. patagonicus*	Cerro de la Gloria	Buenos Aires	Argentina	-	Holocene
MLP 26253	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26297	1	*Pr. patagonicus*	Ea. Rincón de López	Buenos Aires	Argentina	-	Holocene
MLP 34020	1	*Pr. patagonicus*	Cantera Atlántida	Buenos Aires	Argentina	-	Holocene
MLP 25946	1	*Pr. patagonicus*	Ea. Rincón de López	Buenos Aires	Argentina	-	Holocene
MLP 2469	21	*Pr. patagonicus*	Cno. La Magdalena a PI	Buenos Aires	Argentina	-	Holocene
MLP 33414	1	*Pr. patagonicus*	Bahía San Blas	Buenos Aires	Argentina	-	Recent
MLP 26255	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26252	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26233	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26234	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26225	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 26254	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 2478	1	*Pr. patagonicus*	Rawson	Chubut	Argentina	-	Recent
MLP 26251	1	*Pr. patagonicus*	Mar Chiquita	Buenos Aires	Argentina	-	Holocene
MLP 2479	4	*Pr. patagonicus*	arroyo Las Brusquitas	Buenos Aires	Argentina	-	Holocene
MLP 2476	16	*Pr. patagonicus*	Bahía Sanguinetti	Santa Cruz	Argentina	-	Holocene
MLP 2480	27	*Pr. patagonicus*	Bahía Sanguinetti	Santa Cruz	Argentina	-	Holocene
MLP 34421	1	*Pr. patagonicus*	Balneario La Chiquita	Buenos Aires	Argentina	-	Recent
MLP 33805	1	*Pr. patagonicus*	Los Pocitos	Buenos Aires	Argentina	-	Holocene
MLP 1829p	1	*Pr. patagonicus*	San Antonio Oeste	Río Negro	Argentina	-	Holocene
MACN-Pi 426	1	*Pr. patagonicus*	Puerto San Julián	Santa Cruz	Argentina	-	Pleistocene
MACN-Pi 425	2	*Pr. patagonicus*	San Jorge Gulf	Santa Cruz	Argentina	-	Pleistocene
MACN-Pi 6301	1	*Pr. patagonicus*	Puerto Madryn	Chubut	Argentina	-	Holocene
MACN-Pi 6397	5	*Pr. patagonicus*	Ezeiza	Buenos Aires	Argentina	-	Pleistocene
MACN-Pi 6444	1	*Pr. patagonicus*	25 Km east of SAE	Río Negro	Argentina	B. San Matías	Pleistocene
MACN-In 35353	28	*Pr. patagonicus*	La Paloma	Rocha	Uruguay	-	Recent
MACN-In 1814	6	*Pr. patagonicus*	Ubatuba	São Paulo	Brazil	-	Recent
MACN-In 14151	8	*Pr. patagonicus*	Mar del Plata	Buenos Aires	Argentina	-	Recent
MACN-In 11191	16	*Pr. patagonicus*	Puerto Militar	Buenos Aires	Argentina	-	Recent

Appendix. Continuation.

MACN-In 21268	16	*Pr. patagonicus*	San Matías Gulf	Río Negro/Chubut	Argentina	-	Recent
MACN-In 18306	172	*Pr. patagonicus*	Puerto Quequén	Buenos Aires	Argentina	-	Recent
MACN-In 16577	38	*Pr. patagonicus*	Mar del Plata	Buenos Aires	Argentina	-	Recent
MACN-In 16145	6	*Pr. patagonicus*	Bahía Brigman	Buenos Aires	Argentina	-	Recent
MACN-In 12021	18	*Pr. patagonicus*	Necochea	Buenos Aires	Argentina	-	Recent
MACN-In 11581	14	*Pr. patagonicus*	Mar del Plata	Buenos Aires	Argentina	-	Recent
MACN-In 13041	6	*Pr. patagonicus*	Quequén	Buenos Aires	Argentina	-	Recent
CPBA 6930	1	*Pr. patagonicus*	arroyo Las Brusquitas	Buenos Aires	Argentina	-	Holocene
FCDPI 7545	6	*Pr. patagonicus*	La Coronilla	Rocha	Uruguay	-	Late Pleistocene
FCDPI 6252	1	*Pr. patagonicus*	La Coronilla	Rocha	Uruguay	-	Late Pleistocene
FCDPI 6619	1	*Pr. patagonicus*	La Coronilla	Rocha	Uruguay	-	Late Pleistocene
MACN-In 3141	20	*J. albida*	Kingston	Surrey	Jamaica	-	Recent
MACN-In 5010	4	*J. fulminata*	Isla de Guayba	Río de Janeiro	Brasil	-	Recent
MACN-In 2736	38	*J. fulminata*	Isla Sao Sebastiao	Sao Paulo	Brasil	-	Recent
MACN-6556	4	*J. fulminata*	Isla Governador	Río de Janeiro	Brasil	-	Recent
FCDPI 4222	1	*J. palmeri*	La Coronilla	Rocha	Uruguay	-	Late Pleistocene
MACN-In 40492	2	*Pitar tumens*	-	-	Senegal	-	Recent
FMNH 296352	4	*Pitar tumens*	-	-	Senegal	-	Recent

How to cite

ALVAREZ MJ, SANTELLI MB, VON BACZKO MB, PÉREZ DE & ROJAS A. 2024. A new genus of the '*Pitar*' group (Bivalvia: Veneridae) from the Western Atlantic Ocean revealed by geometric morphometric analysis. An Acad Bras Cienc 96: e20230733. DOI 10.1590/0001-3765202420230733.

Manuscript received on June 29, 2023;
accepted for publication on October 8, 2024

MAXIMILIANO J. ALVAREZ[1]
https://orcid.org/0000-0002-6435-8648

MARÍA BELÉN SANTELLI[1]
https://orcid.org/0000-0003-3077-4384

MARÍA BELÉN VON BACZKO[1]
https://orcid.org/0000-0003-2570-3418

DAMIÁN E. PÉREZ[2]
https://orcid.org/0000-0001-6771-4938

ALEJANDRA ROJAS[3]
https://orcid.org/0000-0001-6117-9217

[1]Museo Argentino de Ciencias Naturales (MACN-CONICET), Av. Ángel Gallardo, 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina

[2]Instituto Patagónico de Geología y Paleontología (IPGP CCT CONICET-CENPAT), Bvd. Brown, 2915, U9120CD, Puerto Madryn, Chubut, Argentina

[3]Universidad de la República, Facultad de Ciencias, Instituto de Ciencias Geológicas, Departamento de Paleontología, Iguá, 4225, 11400, Montevideo, Uruguay

Correspondence to: **Maximiliano J. Alvarez**
E-mail: maxialvarez82@gmail.com

Author contributions

MJA, DEP, and MBS designed the study, performed the morphometric analyses, and interpreted the results. MJA performed the systematic and statistic analyses. MBvB designed the figures, and AR collaborated with materials from Uruguay. All authors wrote and revised the manuscript.