

Phylogeny of the Eocene Antarctic Tapetinae Gray, 1851 (Bivalvia, Veneridae) from the La Meseta and Submeseta formations

Maximiliano Jorge Alvarez  and Claudia Julia del Río

Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Angel Gallardo 470, 1405, Buenos Aires, Argentina <maxialvarez82@gmail.com> <claudiajdelrio@gmail.com>

Abstract.—Systematic analysis shows that the Southern Hemisphere bivalve genus *Retrotapes* includes the Antarctic species *R. antarcticus*, *R. newtoni*, and *R. robustus* and recognizes for the first time the presence of *Katelysia* represented by *K. florentinoi*. Two new genera were erected in this study: *Marciachlys* new genus to include *M. inflata* new combination, and *Adelfia* new genus, which includes *A. australissa* new combination and *A. omega* new species from the Eocene of Antarctica, and the late Eocene Chilean *A. arenosa* new combination. *Eurhomalea carlosi* was synonymized with *K. florentinoi*; *Cyclorismina marwicki* with *R. antarcticus*; *Gomphina iheringi* was considered an indeterminate species; and *Cockburnia lunulifera* was excluded from the Tapetinae. These systematic assignments are supported by a phylogenetic analysis, which recognizes an Austral clade of Tapetinae, comprising all the genera mentioned above, along with *Marcia*, *Paleomarcia*, *Atamarcia*, and *Protapes*.

UUID: <http://zoobank.org/a8c91a9f-99ec-4235-8416-d398771a3eb2>

Introduction

The subfamily Tapetinae is the only venerid group recorded in the Eocene of Antarctica. *Cytherea antarctica* Sharman and Newton, 1894 was one of the first fossil invertebrates described and illustrated from the Cenozoic of the Antarctic Peninsula, later included in the first systematic study of the Eocene molluscan Antarctic fauna by Wilckens (1911). However, it was not until the late twentieth century that Zinsmeister (1984) resumed the analysis of this fauna, recognizing eight species of Tapetinae included in the genera *Eurhomalea* Cossmann, 1920 (*Cytherea antarctica* Sharman and Newton, 1894; *Venus newtoni* Wilckens, 1911; *E. florentinoi* Zinsmeister, 1984; *E. carlosi* Zinsmeister, 1984; *E. inflata* Zinsmeister, 1984), *Gomphina* Mörch, 1853 (*G. iheringi* Zinsmeister, 1984), and one species doubtfully placed in *Cyclorismina* Marwick, 1927 (“*C.*” *marwicki* Zinsmeister, 1984). Afterwards, Stilwell and Zinsmeister (1992) added two new Antarctic species, *Eumarcia* (*Eumarcia*) *australissa* Stilwell and Zinsmeister, 1992 and *Eumarcia* (*Atamarcia*) *robusta* Stilwell and Zinsmeister, 1992.

Later, del Río (1997) included *E. antarcticus* and *E. newtoni* in *Retrotapes* del Río, 1997, and Beu (2009) placed all the Antarctic species of Zinsmeister (1984) into *Retrotapes*, considering *Gomphina iheringi* as an indeterminate taxon because of the lack of diagnostic characters since the species was based on a single fragmented and eroded valve. More recently, Alvarez et al. (2014) agreed with these authors in assigning *R. antarcticus*, *R. newtoni*, and *R. robustus* to *Retrotapes*.

Because *E. florentinoi*, *E. carlosi*, *E. inflata*, and *Cockburnia lunulifera* were defined on articulated specimens, *Cyclorismina marwicki* has a hinge plate with very similar characters to those of *Retrotapes antarcticus*, and *Eumarcia australissa* is

known through one partially eroded valve with broken cardinal teeth, it is necessary to carry out a full revision of these species in the light of the new material collected by MJA in the 2014 field season performed by the Instituto Antártico Argentino (IAA; Argentinean Antarctic Institute).

Materials and methods

Studied Tapetinae come from the marine Eocene outcrops of Marambio Island (also known as Seymour Island), Antarctica (Fig. 1). The La Meseta Formation (Fig. 2) is an unconformity-bounded unit (Elliot and Trautman, 1982; Ivany et al., 2008) ~560 m thick, deposited between the upper Thanetian (ca. 58.4 Ma) and the lower Lutetian (ca. 45.8 Ma) (Marensi, 2006; Ivany et al., 2008; Montes et al., 2013, 2019a, b), although recent research proposed a late early Eocene (Crame et al., 2014) or middle Eocene age (Douglas et al., 2014) at the beginning of deposition, Amenábar et al. (2019) determined a middle Lutetian to Priabonian age (46.2–36 Ma). This unit includes mudstones and sandstones with interbedded conglomerates, and it is organized into seven allomembers (Marensi et al., 1998a): Valle de Las Focas, Acantilados I, Acantilados II, Campamento, Cucullaea I, Cucullaea II, and Submeseta. It is interpreted as estuarine and shallow marine environments as part of a tectonically controlled incised valley system (Porebski, 1995; Marensi et al., 1998b), in which the allomembers represent different sedimentation stages related to sea level fluctuations (Marensi et al., 2002).

The Submeseta Formation was informally named by Montes et al. (2013) (Fig. 2), being the uppermost part of the former La Meseta Formation and is dated 43.4–33.9 Ma according to Montes et al. (2013). However, a new chronologic scheme for

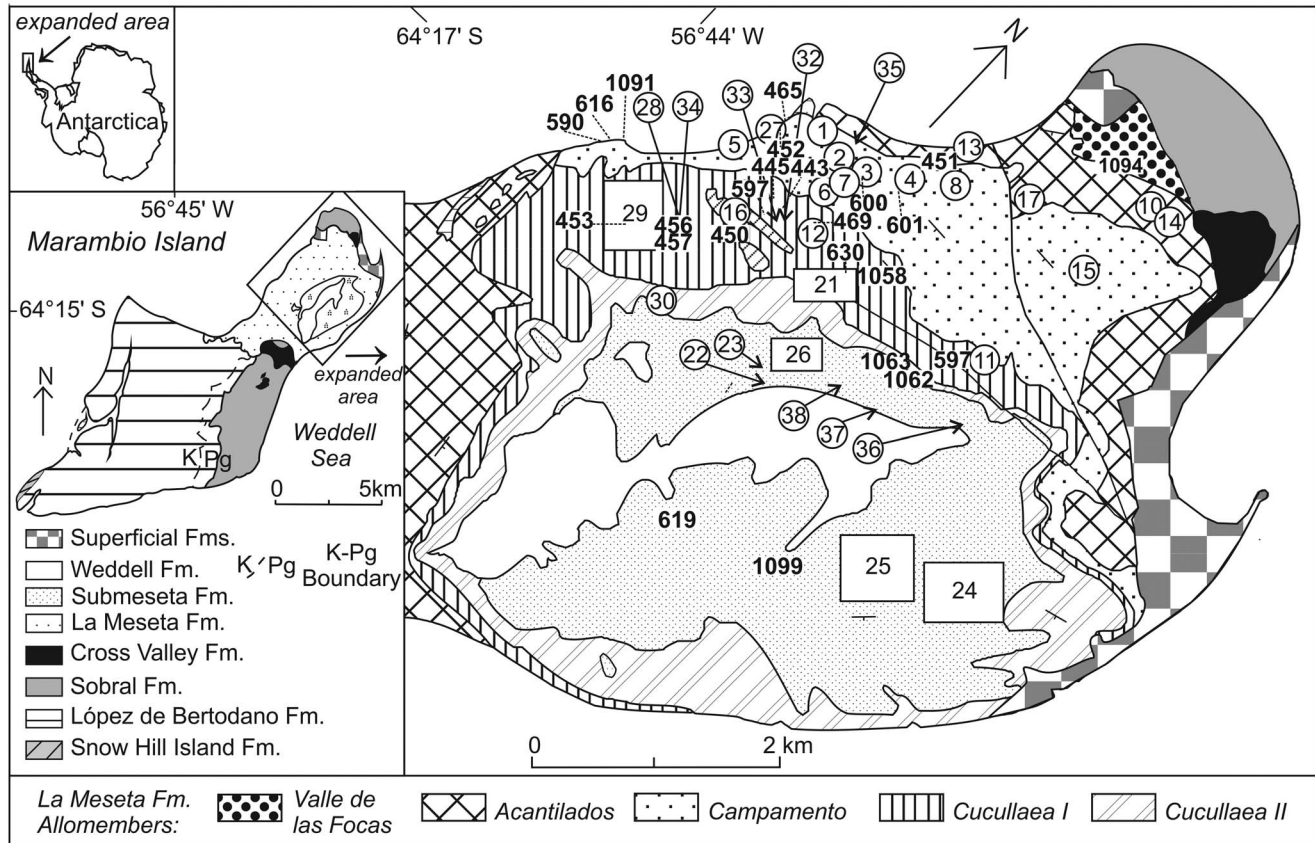


Figure 1. Geographic location of the samples collected during the 2014 expedition to Marambio Island. Details of the localities are given in the Appendix 1, and the list of samples and where they were collected is clarified in the Supplementary Data Set 1. Numbers in bold correspond to localities of Stilwell and Zinsmeister (1992).

the La Meseta Formation (Amenábar et al., 2019) suggests that the Submeseta Formation could be late Eocene to Oligocene in age. This unit corresponds to the Submeseta Allomember of Marensi et al. (1998a), and is characterized by a uniform sandy lithology that represents a tidal shelf influenced by storms (Cenizo et al., 2015). The Submeseta Formation is organized into three allomembers: Submeseta I, Submeseta II, and Submeseta III (Montes et al., 2013).

During the 2014 expedition to Marambio Island, more than 640 specimens of the studied species were collected at 33 localities (Fig. 1) distributed along all the allomembers defined by Marensi (1998a). Precise information about the mentioned localities is available in Appendix 1. We also used the material donated by W. Zinsmeister to the MACN-Pi collection, which was collected during the field seasons 1990–1994. Most of the materials collected by W. Zinsmeister and J. Stilwell are housed at the Paleontological Research Institute (PRI), and were recently studied by CJR, who noted that said materials are currently being reclassified and renumbered. For this reason, we decided to not include these specimens in our analysis, considering that the materials housed at the MACN-Pi collection and the new materials collected in the Field Season 2014 deposited in the IAA are sufficient to perform the present study.

Geographic and stratigraphic distributions of each studied species are summarized in Supplementary Data Set 1, and the materials corresponding to taxa used for comparison and phylogenetic analysis are summarized in Supplementary Data Set

2. The method used for the phylogenetic analysis is described in the corresponding section of this study.

Repositories and institutional abbreviations.—Material included in the present contribution is housed at: Repositorio Antártico de Colecciones Paleontológicas y Geológicas del Instituto Antártico Argentino, San Martín, Buenos Aires, Argentina (IAA-Pi); División Paleoinvertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN-Pi); División Invertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN-In); Museo de La Plata, Argentina (MLP); Cátedra de Paleontología de la Universidad de Buenos Aires, Buenos Aires, Argentina (CPBA); Colección Paleoinvertebrados, Museo de Historia Natural, Santiago, Chile (SGO.PD); Field Museum of Natural History, Chicago, USA (FMNH); Paleontological Research Institution, Cornell University, Ithaca, New York, USA (PRI); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Natural History Museum Rotterdam, Netherlands (NMR); Samling Paleobiologi, Naturhistoriska Riksmuseet, Stockholm, Sweden (PZ-NRM Mo); Natural History Museum, London, United Kingdom (NHMUK); Natural History Museum of Denmark (Zoology), Copenhagen, Denmark (ZMUC); Auckland Museum, Auckland, New Zealand (AM); South Australian Museum, North Terrace, Adelaide, Australia (SAM).

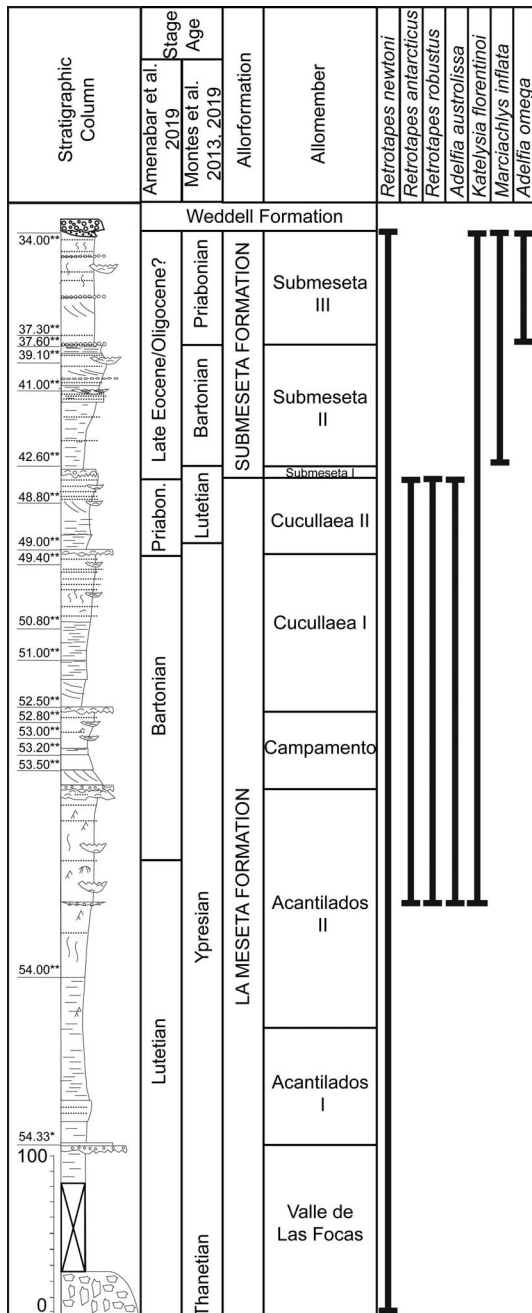


Figure 2. Stratigraphic column of La Meseta and Submeseta formations, showing the new stratigraphic range of the studied species. *Isotopic age in Ma from Marensi (2006), **isotopic age in Ma from Ivany et al. (2008).

Systematic paleontology

Family Veneridae Rafinesque, 1815
 Subfamily Tapetinae Gray, 1851

Remarks.—Some controversial taxa were erected by Zinsmeister (1984) from the La Meseta Formation, including the genus *Cockburnia*. The type species elected for the latter genus was *Cytherea lunulifera* Wilckens, 1911 (p. 17, pl. 1, fig. 13a, 13b; PZ-NRM MO 2029), however its internal characters were unknown and its assignment is therefore arguable.

During the 2014 field season several specimens were collected from concretionary facies of Cerro Jonas (Acantilados II Allomember, La Meseta Formation). This new material has a hinge plate with long and thin anterior and posterior cardinal teeth, a very short middle one, and an anterior lateral tooth in the left valve. These features are not coincident with those of Tapetinae, and added to the presence of a sub-central umbo and a very large and wide lunule, suggest it belongs to the Family Corbiculidae; but more studies are being carried out to confirm this assignment.

As previously mentioned, *Gomphina iheringi* Zinsmeister, 1984 (Fig. 3.10, 3.11) has no internal diagnostic characters because the only known specimen is filled with sedimentary matrix, and Zinsmeister placed it in *Gomphina* because of its shape. However, this feature is similar to that of some Meretricinae or Corbiculidae species; for that reason, we follow the proposal of Beu (2009) and consider this specimen nomen dubium.

Zinsmeister (1984, p. 1522, figs. 10A–10C) named the species ‘*Cyclorismina*’ *marwicki* (Fig. 3.3–3.6) (Eocene; La Meseta Formation) based on its subcircular shells, adducing that although the generic position is uncertain, the combination of the shell-shape and internal features are similar to those of the genus *Cyclorismina* Marwick, 1927 (type species *C. woodsi* Marwick, 1927, figs. 185–187; Late Cretaceous, New Zealand; Fig. 3.7–3.9). *Cyclorismina* has circular-shaped valves, a small umbo, sunken lunule, unbounded from the rest of the shell, absent escutcheon, almost vertical nymphs, divergent cardinal teeth, entire 1, and long pallial sinus, which is triangular, ascendant, and with a sharp apex. The type material illustrated by Zinsmeister (1984), as well as those specimens donated by this author to the MACN-Pi collection, do not have any of the features described for *Cyclorismina*, even the shape of both species is not similar; therefore the Eocene species do not belong to this genus. In the present contribution, ‘*C.*’ *marwicki* is synonymized with *Retrotapes antarcticus* (Fig. 3.1–3.3) because of its similarity to the globoid morphotypes of this species analyzed by Alvarez and Pérez (2016). The only significant difference is that the contacts between the anterior and posterior margins with the dorsal and ventral ones are slightly more rounded, giving the subcircular shape described by Zinsmeister (1984); but it is within the range of shapes observed in the globoid morphotypes of *R. antarcticus*.

Another species from the Eocene of Antarctica included in the genus *Eurhomalea* is ‘*Eurhomalea*’ *claudiae* Stilwell, 2000, from McMurdo Sound (Ross Sea). Stilwell (2000) tentatively included this species in *Eurhomalea* due to its similarity to the shape of *Retrotapes newtoni* (Wilckens, 1911) and *Katelysia florentinoi* (Zinsmeister, 1984), both previously considered as *Eurhomalea* by Zinsmeister (1984) and Stilwell and Zinsmeister (1992), but mentioned that it might belong to *Retrotapes* del Río, 1997 instead. However, ‘*E.*’ *claudiae* has divergent cardinal teeth, which means that it does not belong to *Retrotapes*. The teeth are very small, the middle one is vertical and the posterior is slightly curved, resembling those of *K. florentinoi*. However, it is not possible to determine if the middle teeth of both valves are bifid, a diagnostic character of *Katelysia*, either in the material illustrated or in the description provided by Stilwell (2000). In addition, neither muscular characters nor the pallial sinus can be observed. A search of the type material

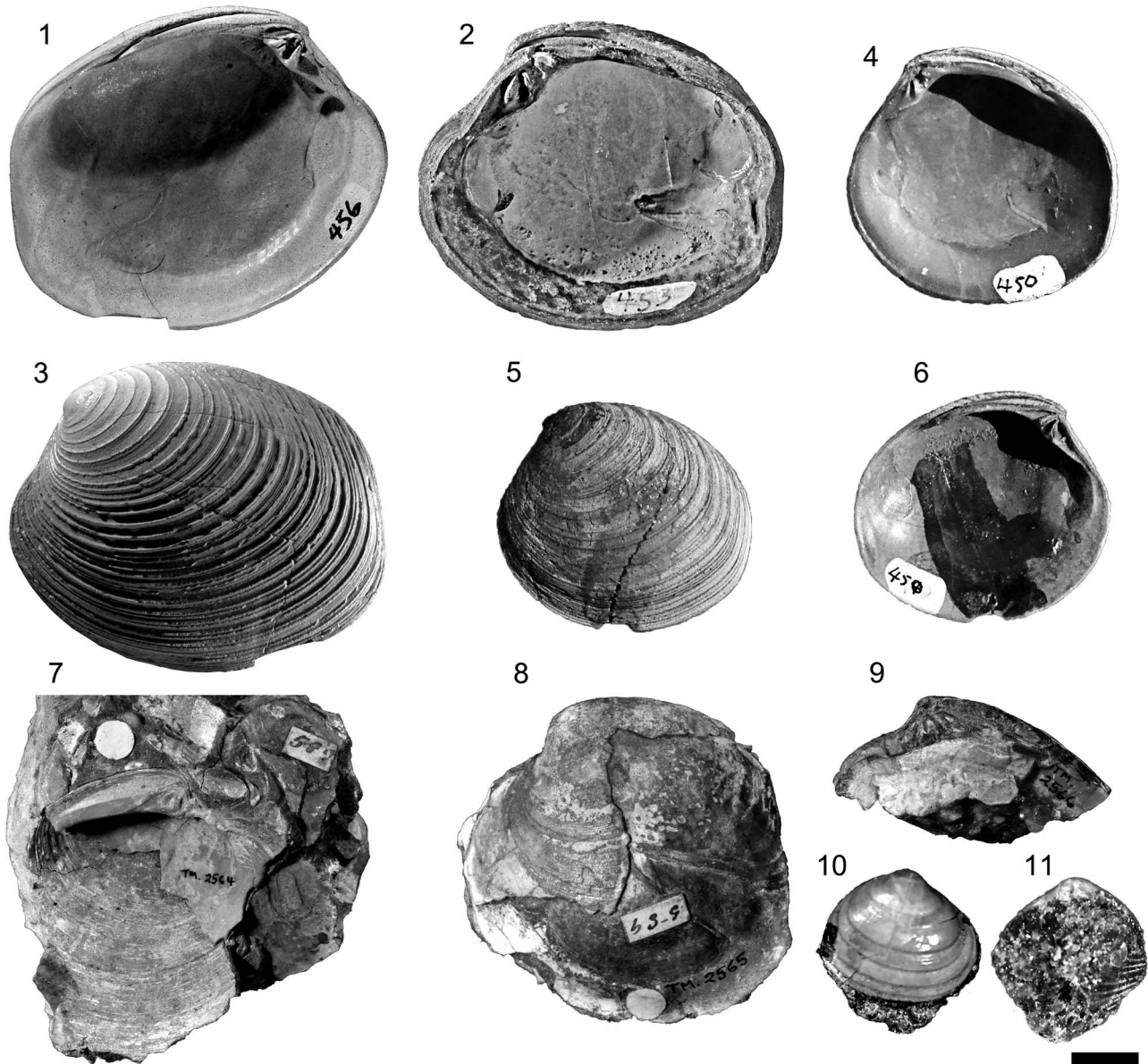


Figure 3. (1–6) *Retrotapes antarcticus* (Sharman and Newton, 1894). (1, 3) MACN-Pi 5303a, a left valve: interior and exterior views (Cucullaea I Allomember); (2) MACN-Pi 5413a, a left valve: interior view (Cucullaea I Allomember); (4–6) MACN-Pi 6374, subrounded specimens of *Cyclorismina marwicki* Zinsmeister, 1984: (4) right interior view; (5, 6) left valve, lateral and interior views (Cucullaea I Allomember). (7–9) *Cyclorismina woodsi* Marwick, 1927. (7) TM 2564, left hinge plate; (8) TM 2565, right valve and internal cast; (9) TM 2566, right hinge plate (Late Cretaceous, New Zealand). (10, 11) *Gomphina iheringi* Zinsmeister, 1984, USNM 365531 (holotype), left valve, lateral and interior views (Acantilados II Allomember). Scale bar = 1 cm.

supposedly housed at Smithsonian Museum of Natural History was made, but the specimens were not in the collection, and are presumably lost. Therefore it is possible that ‘*Eurhomalea claudiae*’ belongs to a new genus, but the lack of key features and any type material makes it impossible to determine.

Genus *Katelsia* Römer, 1857

Type species.—*Katelsia scalarina* (Lamarck, 1818) Pliocene–Recent; South Australia (by subsequent designation of Dall, 1902) (Fig. 4.10–4.14).

Other species.—*Katelsia florentinoi* (Zinsmeister, 1984), La Meseta and Submeseta formations (Ypresian–Priabonian,

Antarctica); *K. corioensis* (Tate, 1887), Fyansford Formation (middle Miocene, Australia); *K. lunulata* Marwick, 1931, Tutamoe Formation (middle Miocene, New Zealand); *K. rhytiphora* (Lamy, 1935), Ascot Formation (Pliocene, southeastern Australia) and Recent from South Australia; *K. peronii* (Lamarck, 1818), Recent, South Australia; *K. victoriae* (Tenison-Woods, 1878), Recent, South Australia.

Diagnosis.—Shell medium to small sized, suboval, laterally compressed. Lunule very narrow, bounded by a line. Escutcheon very narrow, wider in the left valve. Hinge plate narrow, with short cardinal teeth that do not exceed the hinge plate margin; 1 and 2a bifids. Pallial sinus very short, with apex rounded. Shell sculptured with low commarginal ribs,

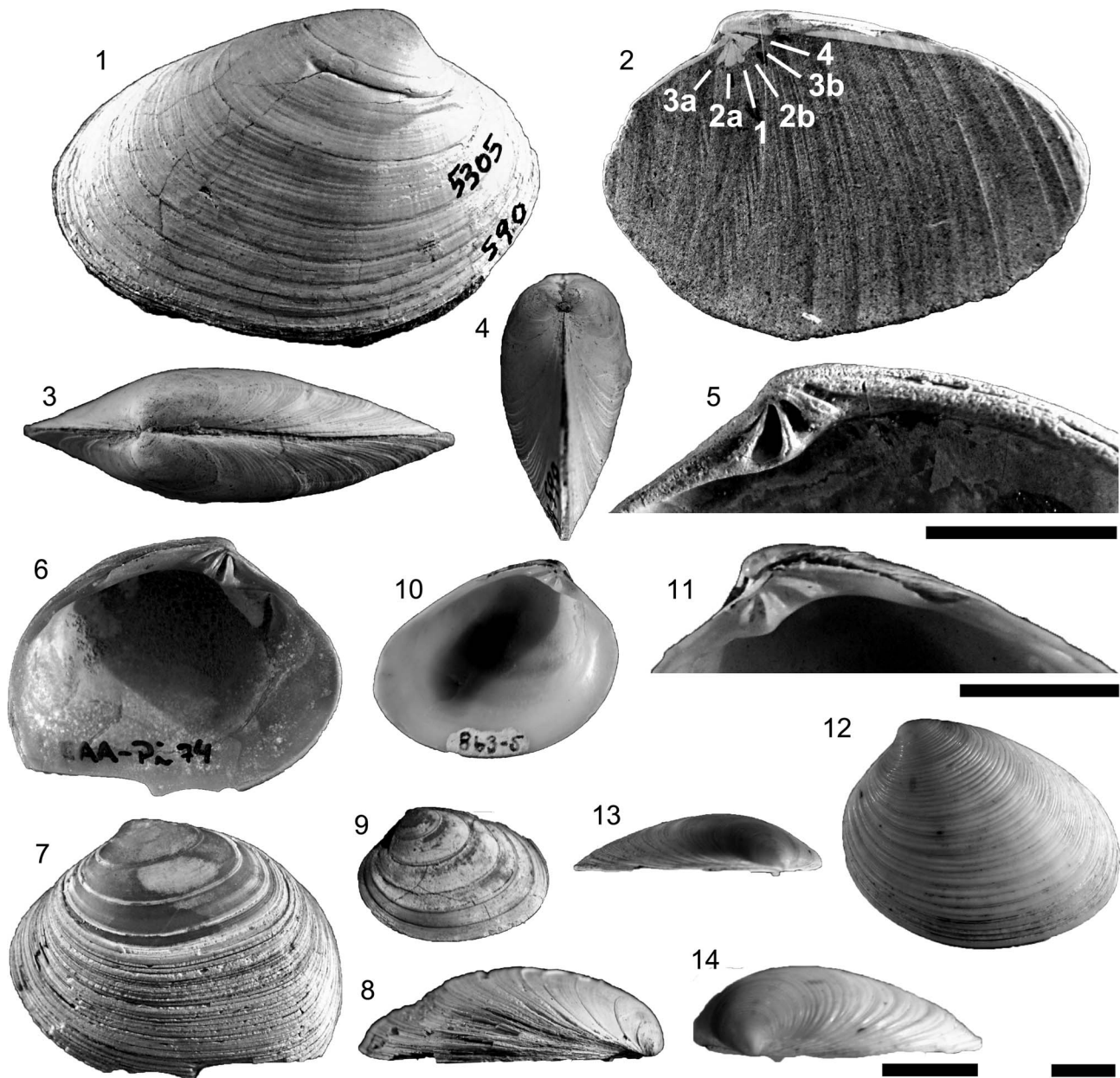


Figure 4. (1–9) *Katelaysia florentinoi* (Zinsmeister, 1984). (1, 2) MACN-Pi 5305 right valve, lateral view and longitudinal section showing the hinge configuration (Campamento Allomember); (3, 4) MACN-Pi 5304 articulated specimen, dorsal and anterior views (Campamento Allomember); (5) MACN-Pi 6367 right hinge plate (Campamento Allomember); (6–8) IAA-Pi 74 left valve, interior, lateral and anterior views (Campamento Allomember); (9) IAA-Pi 63 right valve of a *Eurhomalea carlosi* specimen. (10–14) *Katelaysia scalarina* (Lamarck, 1818), MACN-In 40943, interior, lateral, dorsal and anterior views (Recent, Victoria, Australia). Scale bars = 1 cm.

wider than the interspaces. Some species have very fine radial ribs.

Occurrence.—Ypresian–Recent. West Antarctica, New Zealand, and South Australia.

Remarks.—The genus *Katelaysia* was erected by Römer (1857), including *Venus scalarina* Lamarck, 1818 and *Venus exalbida* Dillwyn, 1817, without clarifying which was the type species. Dall (1902) reassigned *Venus exalbida* into the genus *Marcia* Adams and Adams, 1857 (*Retrotapes exalbidus* sensu del Río, 1997) and selected *Venus scalarina* as type species of *Katelaysia*.

Katelaysia currently occurs in South Australia and its known fossil record goes back to the middle Miocene, represented by *K. corioensis* (Tate, 1887) from Australia and *K. lunulata* Marwick, 1927 from New Zealand, although the specimens of both species are articulated and the internal characters remain unknown.

The assignment of *Eurhomalea florentinoi* Zinsmeister, 1984 into the genus *Katelaysia* expands the stratigraphic and geographic ranges of the latter genus to the Eocene of the Antarctic Peninsula. *Katelaysia* differs from *Eurhomalea* Cossmann, 1920 (type species *E. rufa* [Lamarck, 1818], Pacific Ocean between the central region of Chile and Panama) because of its smaller size, suboval shape, shorter cardinal teeth that do not exceed

the hinge plate margin, 1 and 2a teeth bifid, and shorter pallial sinus. *Katelsysia* is distinguishable from *Retrotapes* del Río, 1997 by having a narrower hinge plate, with divergent cardinal teeth, 1 and 2a teeth bifid, lanceolate lunule bounded by a line, and shorter pallial sinus.

Katelsysia florentinoi (Zinsmeister, 1984) new combination

Figure 4.1–4.9

1984 *Eurhomalea florentinoi* Zinsmeister, p. 1520, figs. 8 K–M.

1984 *Eurhomalea carlosi* Zinsmeister, p. 1521, figs. 8 Q–S.

1992 *Eurhomalea florentinoi*; Stilwell and Zinsmeister, p. 79, pl. 8, figs. a–c.

1992 *Eurhomalea carlosi*; Stilwell and Zinsmeister, p. 80, pl. 8, figs. d–f.

2009 *Retrotapes florentinoi*; Beu, p. 210.

2009 *Retrotapes carlosi*; Beu, p. 210.

Holotype.—Articulated specimen, USNM 365516, from the Submeseta Formation. Paratype, articulated specimen, USNM 365515, from the Submeseta Formation.

Emended diagnosis.—Pallial sinus short (but longer than that observed in extant species). Sculptured with low commarginal ribs, which are closer towards the ventral margin of the disk.

Occurrence.—Acantilados II, Campamento, Cucullaea I, Cucullaea II, and Submeseta allomembers (late Ypresian–Priabonian; La Meseta and Submeseta formations).

Description.—Shell thin, medium to small sized, suboval to elliptical. Umbo small, placed in anterior third of length. Posterodorsal and anterior margins tend to be dorsally straight and ventrally convex, ventral margin convex. Lunule lanceolate, short, bounded by a line. Escutcheon very narrow and short, wider in the left valve, with commarginal sculpture similar to the rest of the shell. Nymph narrow and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are divergent, short, and do not exceed the ventral margin of the hinge plate. Right hinge with 3a tooth lamellar, sloped forwards; 1 triangular, narrow, bifid, tilted backwards; 3b wide, bifid, sub-horizontal; posterodorsal region of right valve with a groove for the insertion of left valve. Left hinge with 2a triangular, wide, bifid, higher than the other teeth; 2b narrow, bifid; 4b lamellar, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars isomyarian, the anterior one is deeper; anterior pedal retractor scar placed below the anterior margin of the hinge plate and separated from the adductor muscle scar; posterior pedal retractor scar joined to the posterior adductor muscle scar; and small pedal elevator muscle scars under the hinge plate. Pallial sinus short, triangular, dorsal and ventral margins straight, and apex rounded. Shell sculptured with low and narrow commarginal ribs, which are closer to each other towards ventral margin of the disk, and wider than the interspaces. Some well-preserved specimens have very fine radial ribs.

Material.—One hundred and fifty nine specimens, MLP 18303 (1 specimen), SGO.PI 4959 (1 specimen), SGO.PI 4962

(1 specimen), CPBA 16778 (58 specimens), IAA-Pi 63 (7 specimens), IAA-Pi 70 (2 specimens), IAA-Pi 74 (4 specimens), IAA-Pi 85 (6 specimens), IAA-Pi 111 (2 specimens), MACN-Pi 5304 (1 specimen), MACN-Pi 5305 (1 specimen), MACN-Pi 6366 (17 specimens), MACN-Pi 6367 (9 specimens), MACN-Pi 6368 (21 specimens), MACN-Pi 6377 (1 specimen), MACN-Pi 6378 (10 specimens), MACN-Pi 6386 (6 specimens), MACN-Pi 6387 (3 specimens), MACN-Pi 6446 (8 specimens).

Measurements.—Holotype USNM 365516: length 41 mm, height 30 mm (Appendix 2).

Remarks.—Zinsmeister (1984) erected *Eurhomalea florentinoi* describing hinge plate characters, but without providing any internal images, and erected *Eurhomalea carlosi* based only on articulated specimens, considering the presence of a lunule in *E. carlosi* as the only difference from *E. florentinoi*. The revision of specimens of both species herein allows us to synonymize them because they have the same shape, sculpture, position of the umbones, and hinge plate. Regarding the presence or absence of a lunule depends on the grade of erosion of the external surface; with significant erosion, the line that bounded the lunule is not recognizable. The only difference between both species is that *E. carlosi* is smaller than *E. florentinoi*. The specimens of *E. carlosi* (Fig. 4.9) have four to six annual growth lines, whereas specimens of *E. florentinoi* have more than ten. This fact, added to the morphological evidence discussed before, indicates that the specimens of *E. carlosi* are probably young specimens of *E. florentinoi*.

Most of the new specimens of *K. florentinoi* (Fig. 4.6–4.8) have an initial shell shape that is similar in form and number of annual growth lines to those of the specimens of *E. carlosi*. However, in the same specimens, the convexity of the shell and the number of annual growth lines increases, developing a globoid shape, similar to that observed in *R. antarcticus*, which is associated with the great longevity of this Antarctic taxon (Alvarez and Pérez, 2016).

Eurhomalea florentinoi does not belong to the genus *Eurhomalea* (type species *E. rufa*) because this genus has a large and subquadrate shell, with sub-central umbo, narrow hinge plate with thin and high cardinal teeth that exceed the hinge plate margin, and a pallial sinus, which is large, triangular, and with an acute apex.

This species is included in the genus *Katelsysia* because of its medium-sized shell, suboval, laterally compressed shape, with very narrow lunule, which is lanceolate and bounded by a line. The escutcheon is very narrow, but wider in the left valve. The hinge plate is narrow, with short cardinal teeth that do not exceed the hinge plate margin and bifid 1 and 2a teeth. The pallial sinus is very short, with rounded apex. The shell is sculptured with low commarginal ribs, wider than the interspaces. Some well-preserved specimens have very fine radial ribs.

Beu (2009) assigned *K. florentinoi* to the genus *Retrotapes* del Río, 1997 and commented that the lack of lunule would support its inclusion in the genus *Frigichione* Fletcher, 1938. The differences between *Katelsysia* and *Retrotapes* are discussed

above. Still, *Katelsysia florentinoi* cannot be assigned to *Frigichione* because of its smaller and thinner shells, suboval shape, with narrow escutcheon and thinner teeth.

Katelsysia florentinoi is distinguishable from the Miocene Australian and New Zealand species (*K. corioensis* and *K. lunulata*) by its suboval shape, larger shell, and sculpture of low commarginal ribs. *Katelsysia florentinoi* differs from the extant species of the genus by its larger shell, longer pallial sinus, and sculpture of low commarginal ribs. However, its low sculpture is closer to that of *K. florentinoi polita* Nielsen, 1963 (p. 223, pl. 1, figs. 4–6). The flat morphotype of *K. florentinoi* is less inflated than the extant species, which are similar in convexity to the globoid morphotype (Fig. 4.8, 4.14).

Marciachlys new genus

Type species.—*Eurhomalea inflata* Zinsmeister, 1984, Bartonian–Priabonian, Marambio Island, Antarctica. By monotypy (Fig. 5.1–5.7).

Diagnosis.—Shell very inflated, umbo prominent and rounded. Hinge plate narrow with divergent cardinal teeth, short and straight, the anterior ones are angled forward, 1 tooth almost vertical, 2b entire. Pallial sinus short (shorter than *K. florentinoi*), ascendant, with apex rounded.

Occurrence.—Bartonian–Priabonian. Submeseta Formation, Marambio Island, Antarctica.

Etymology.—*Marcia* of the mist. The name refers to Marcia because the external similarity to this genus and *Achlys* refers to the Greek word for mist, because the new specimens of this new genus were found at the northern end of the Marambio Base airstrip in a day of thick mist.

Remarks.—*Marciachlys* n. gen. differs from *Retrotapes* in having a lunule bounded by a line, divergent cardinal teeth, with the anterior ones very much tilted forward, entire 2b, and ascendant pallial sinus. Tooth 3b is horizontal in *Retrotapes*, but is ventrally oriented in *Marciachlys* n. gen. This genus is distinguishable from *Katelsysia* in having a more convex shell, prominent and rounded umbo, wider lunule, larger hinge plate and teeth, entire 2b, and longer pallial sinus.

Marciachlys n. gen. differs from the New Zealand *Eumarcia* and *Atamarcia* by its smaller shell, prominent and rounded umbo, entire 2b, and shorter and ascendant pallial sinus. The specimens MACN-Pi 2531–2533 (Fig. 5.8) from Tolhuin in the vicinity of Kaiken Hostel (Tierra del Fuego Province, Argentina), of Paleocene age, could be assigned to *Marciachlys* n. gen. since they have similar shape, convexity, umbo, and sculpture. However, these specimens are larger and no inner characters are known.

Marciachlys inflata (Zinsmeister, 1984), new combination
Figure 5.1–5.7

1984 *Eurhomalea inflata* Zinsmeister, p. 1521, figs. 9L–9P.

1992 *Eurhomalea inflata*; Stilwell and Zinsmeister, p. 80, pl. 8, figs. g–k.

2009 *Retrotapes inflata*; Beu, p. 210.

Holotype.—Articulated specimen, USNM 365524, from the Submeseta Formation. Paratypes, an articulated specimen USNM 365525, a left valve USNM 365526, an articulated specimen USNM 365527, a right valve USNM 365528, from the Submeseta Formation.

Diagnosis.—Same as for genus, by monotypy.

Description.—Shell thick, medium sized, suboval, very inflated. Umbo prominent, rounded, placed at anterior quarter of length. Posterodorsal margin slightly convex, anterior margin tends to be dorsally straight and ventrally convex, ventral margin convex with straight central area. Lunule lanceolate, long, bounded by a line. Escutcheon very narrow and short, with commarginal sculpture similar to that of rest of the shell. Nymph narrow and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are divergent, short, and do not exceed the ventral margin of the hinge plate. Right hinge with 3a tooth thick, triangular, sloped forward; 1 triangular, narrow, entire, sub-vertical; 3b wide, bifid, sub-horizontal. Left hinge with 2a triangular, wide, entire, and higher than the other teeth; 2b narrow and bifid; 4b lamellar, straight, and separated from the nymph by a groove. Adductor muscle scars deep; anterior pedal retractor scar placed below the anterior margin of the hinge plate and separated from the adductor muscle scar; posterior pedal retractor scar joined to the posterior adductor muscle scar; pedal elevator muscle scars small and deep, placed under the hinge plate. Pallial sinus short, triangular, ascendant, with apex wide and rounded. Shell sculpture smooth with annual growth lines.

Material.—One hundred specimens, SGO.PI 4958 (1 specimen), IAA-Pi 109 (74 specimens), IAA-Pi 113 (4 specimens), MACN-Pi 6379 (21 specimens).

Measurements.—Holotype USNM 365524: length 37 mm, height 33 mm (Appendix 2).

Remarks.—Zinsmeister (1984, p. 1521, fig. 9L–9P) included *Marciachlys inflata* n. comb. in the genus *Eurhomalea* Cossmann, 1920 (type species *E. rufa* [Lamarck, 1818]), without knowing all its internal characters; new material collected during the 2014 field season, showed these features. Therefore, this species does not belong in *Eurhomalea* because of its suboval shape, prominent and rounded umbo, thicker cardinal teeth that do not exceed the hinge plate margin, and a short, ascendant, and round-ended pallial sinus.

Adelfia new genus

Type species.—*Eumarcia (Eumarcia) australissa* Stilwell and Zinsmeister, 1992, late Ypresian–Lutetian, Marambio Island, Antarctica.

Other species.—*Adelfia arenosa* (Ortmann, 1899) n. comb. (Loreto Formation, late Eocene, Punta Arenas, Chile); *Adelfia*

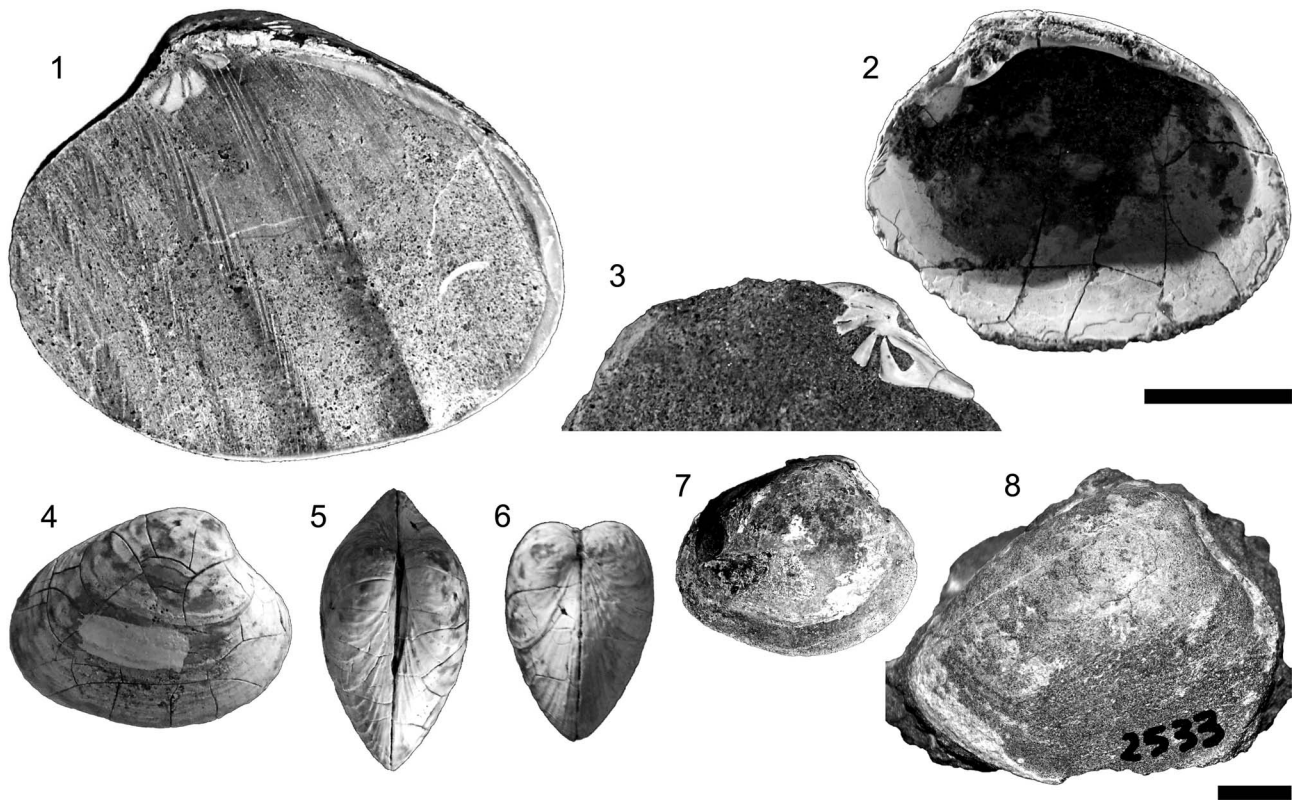


Figure 5. (1–7) *Marciachlys inflata* (Zinsmeister, 1984) n. comb. (1, 4–6) MACN-Pi 6379, longitudinal section showing the hinge configuration and lateral, dorsal and anterior views (Submeseta III Allomember); (2, 3, 7) IAA-Pi 109 interior of a right valve, left hinge plate and internal cast showing muscle scars and pallial line (Submeseta III Allomember). (8) *Marciachlys?* indet. MACN-Pi 2533 right valve, internal cast (Paleocene, Tolhuin, Tierra del Fuego Province). Scale bars = 1 cm.

omega n. gen. n. sp. (Submeseta Formation, Priabonian, Marambio Island).

Diagnosis.—Shell with lunule flat, narrow, and bounded by a line. Cardinal teeth narrow, divergent; 1 entire; 4b short and curved. Pallial sinus short, triangular, with the dorsal margin subhorizontal and the apex slightly truncated. Sculpture of broad, low, and flat ribs, closer to each other towards the ventral margin, separated by interspaces of equal depth throughout the valve.

Occurrence.—Late Ypresian–Priabonian. The La Meseta and Submeseta formations (Marambio Island, Antarctica) and the Loreto Formation (Punta Arenas, Chile).

Etymology.—From the Greek *Adelphos* (brother) and *ia* (action or will), in recognition of the spirit of brotherhood of the GeoMarambio camp, composed of Argentinean and Spanish geologists and paleontologists; located over sediments of the Campamento Allomember (La Meseta Formation), from which new material of the type species of this genus was collected during the 2014 field trip.

Remarks.—Stilwell and Zinsmeister (1992) included the type species of *Adelfia* n. gen. in the genus *Eumarcia* Iredale, 1924 (type species *E. fumigata* [Sowerby, 1853; Recent, South Australia]), but this species does not belong to *Eumarcia* because it does not have a posteriorly lengthened and

sharpened shell shape as *Eumarcia* has, and because of the presence of a larger umbo, well-defined escutcheon, tooth 4b separated from the nymph by a groove, entire 2a, thinner tooth 1, narrow and subhorizontal pallial sinus, and sculpture of broad, low, and flat ribs, closer to each other towards the ventral margin, separated by interspaces of equal depth throughout the valve.

Beu (2009) reassigned *Eumarcia australissa* as *Atamarcia* Marwick, 1927 (type species *A. sulcifera* Marwick, 1927; Miocene, New Zealand). Both species have similar shell shapes, but *Adelfia australissa* n. comb. does not belong in *Atamarcia* because of its flat lunule bounded by a line in its entire extension, shorter 4b, bifid 2b with a shallower groove, narrower 3b, smooth 1, and triangular, shorter, and subhorizontal pallial sinus. In addition, the interspaces of the sculpture have the same depth throughout the valve and are closer to each other towards the ventral margin in *Adelfia* n. gen., while in *Atamarcia* the interspaces are deeper in the anterior margin of the valve and are closer to each other towards the posterior one.

Ortmann (1899) erected *Venus arenosa* (PRI 72690; Fig. 6.10, 6.11) (Loreto Formation, late Eocene, Punta Arenas, Chile) based on three right valves embedded in sedimentary matrix. This taxon is included in *Adelfia* n. gen. because it shows a similar shell shape, with a hinge plate with cardinal teeth similar to those of *Adelfia australissa* n. comb., but with a margin more curved behind the teeth, and the sculpture when preserved is similar to that of *Adelfia* n. gen. The lunule is lanceolate and slightly concave, and this is the only difference

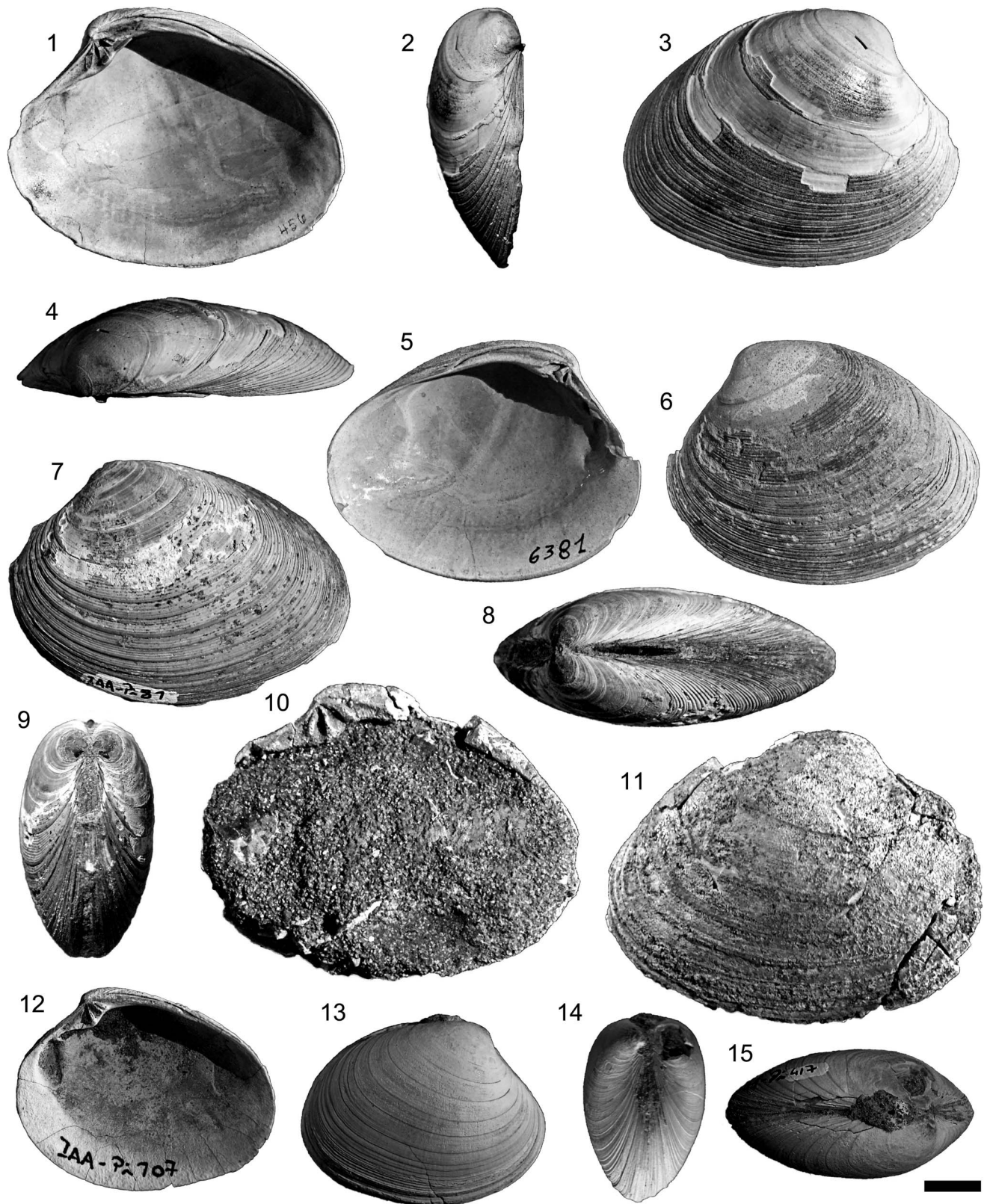


Figure 6. (1–9) *Adelfia australissa* (Stilwell and Zinsmeister, 1992) n. comb. (1–4) USNM 441638 holotype, right valve, interior, anterior, lateral, and dorsal views (Cucullaea I Allomember); (5, 6) MACN-Pi 6381 left valve, interior and lateral views (unknown allomember); (7–9) IAA-Pi 81 articulated specimen, lateral, dorsal, and anterior views (Campamento Allomember). (10, 11) *Adelfia arenosa* (Ortmann, 1899) n. comb., right valve, interior and lateral views (late Eocene, Loreto Formation, Punta Arenas, Chile). (12–15) *Adelfia omega* n. gen. n. sp. (12) IAA-Pi 416 holotype, right valve, interior view (Submeseta III Allomember); (13–15) IAA-Pi 417 paratype, articulated specimen, lateral, anterior and dorsal views (Submeseta III Allomember). Scale bar = 1 cm.

from species of *Adelfia* n. gen. The scarcity of observable characters in the eroded and matrix-embedded right valves, as well as the complete absence of left valves, plus the fact that the differences with *Adelfia australissa* n. comb. are very little, make it difficult to differentiate both species. Based on these characters and due to the geographic and stratigraphic distance between both taxa, they are recognized here as valid species. If new evidence on *Adelfia arenosa* n. comb. would appear, allowing us to synonymize them, the specific name *arenosa* would have priority over *australissa* n. comb.

Adelfia n. gen. differs from *Retrotapes* by its flat lunule bounded by a line, divergent cardinal teeth, entire 1, and narrower 3b. It is distinguishable from *Katelsysia* by its larger and more convex shell, wider escutcheon, higher hinge plate with longer teeth, entire 1, and longer and subhorizontal pallial sinus. *Adelfia* n. gen. differs from *Marciachlys* n. gen. by its less-convex shell, less-prominent umbo, narrower lunule, less-tilted forwards anterior cardinal teeth, backward sloping 1, subhorizontal 3b, and longer and subhorizontal pallial sinus. The sculpture of *Adelfia* n. gen. differs from that observed in the three compared taxa, and consists of broad, low, and flat ribs.

Adelfia australissa (Stilwell and Zinsmeister, 1992) new combination
Figure 6.1–6.9

1992 *Euamrcia* (*Eumarcia*) *australissa* Stilwell and Zinsmeister, p. 82, pl. 8., figs. r, s.

2009 *Atamarcia australissa*; Beu, p. 210.

Holotype.—One right valve, USNM 441638, from Cucullaea I Allomember, La Meseta Formation (Fig. 6.1–6.4).

Emended Diagnosis.—Shell medium to large sized. Up to 10 pedal elevator muscle scars. Pallial sinus with dorsal margin subhorizontal, ventral margin curved, and apex small and truncated.

Occurrence.—Acantilados II, Campamento, Cucullaea I, and Cucullaea II allomembers (late Ypresian–Lutetian, La Meseta Formation).

Description.—Shell thin, large size, suboval. Umbo small, placed at anterior quarter of length. Dorsal margin slightly convex; ventral, anterior, and posterior margins convex. Lunule narrow, flat, and bounded by a line. Escutcheon narrow, wider in the left valve. Nymph narrow and smooth. Hinge plate wide, slightly curved behind the cardinal teeth, which are divergent, narrow, and do not exceed the ventral margin of the hinge plate. Right hinge with 3a tooth lamellar, straight, sloped forward, and shorter and lower than the 1, which is thin, entire, and tilted backwards; 3b triangular, bifid, and sub-horizontal; posterodorsal region of right valve with a groove for the insertion of left valve. Left hinge with 2a triangular, straight; 2b triangular, bifid, and higher than 2a; 4b lamellar, curved, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars deep; anterior pedal retractor scar placed below the anterior margin of the

hinge plate and separated from the adductor muscle scar; posterior pedal retractor scar joined to the posterior adductor muscle scar; up to 10 pedal elevator muscle scars small, deep. Pallial sinus short, triangular, with dorsal margin straight and subhorizontal, and ventral margin curved, and apex small and truncated. Sculpture of broad, low, and flat ribs, closer to each other towards the ventral margin, separated by interspaces of equal depth throughout the valve.

Material.—Twenty-eight specimens, IAA-Pi 64 (2 specimens), IAA-Pi 81 (5 specimens), IAA-Pi 86 (2 specimens), IAA-Pi 100 (1 specimen), IAA-Pi 106 (1 specimen), MACN-Pi 6370 (7 specimens), MACN-Pi 6371 (7 specimens), MACN-Pi 6381 (3 specimens).

Measurements.—Holotype USNM 441638: length 60.5 mm; height 46.5 mm (Appendix 2).

Remarks.—*Adelfia australissa* (Stilwell and Zinsmeister, 1992) n. comb. was erected based on only one specimen found in the Cucullaea I Allomember (middle Eocene). During the 2014 field season, new articulated material was collected at the cliff near Campamento Point (64°13'45.6"S; 56°39'55.9"W), from the Campamento Allomember, extending the stratigraphic range of this species. Later, based on this new material, other specimens of this species were recognized in the collection of MACN-Pi from Acantilados II and Cucullaea II allomembers. The external surface of the holotype is almost smooth, and its name is derived from this fact, but the surfaces of the new material are not smooth, revealing that the holotype is partially eroded and the outer layer of the shell is almost absent.

Adelfia australissa n. comb. differs from the other Tapetinae from Acantilados II to Cucullaea II allomembers (*Retrotapes antarcticus* and *R. robustus*), by its suboval shape and characteristic sculpture. The articulated specimens of *A. australissa* n. comb. and *R. newtoni* have the same shape and they can be easily confused with each other. The difference between them is that *R. newtoni* has a concave lunule, bounded by a deep groove, whereas *A. australissa* n. comb. has a flat lunule, bounded by a line, which is not visible in eroded specimens.

Adelfia omega new species
Figure 6.12–6.15

Holotype.—One right valve, IAA-Pi 416, from Submeseta III Allomember, Submeseta Formation. Paratypes: IAA-Pi 417, an articulated specimen; IAA-Pi 418, a right hinge plate; IAA-Pi 419, an articulated specimen with some visible cardinal teeth; IAA-Pi 420, a right valve with a broken left hinge plate, so the six cardinal teeth are articulated; IAA-Pi 421, an internally polished right valve; IAA-Pi 422, an internal mold with muscle scars, and pallial line and sinus; from Submeseta III Allomember, Submeseta Formation.

Diagnosis.—Shell small sized. Pallial sinus with dorsal and ventral margins straight, ascendant, and apex sharpened. Elements of the sculpture lower than those of *Adelfia australissa* n. comb.

Occurrence.—Priabonian. Submeseta III Allomember, Submeseta Formation, Marambio Island, Antarctica.

Description.—Shell thin, small sized, suboval. Umbo small, placed at anterior quarter of length. Dorsal margin slightly convex and ventral, anterior and posterior margin convex. Lunule narrow, flat, and bounded by a line. Escutcheon narrow, wider in the left valve. Nymph narrow and smooth. Hinge plate narrow, slightly curved behind the cardinal teeth, which are divergent, narrow, and do not exceed the ventral margin of the hinge plate. Right hinge with 3a tooth lamellar, straight, sloped forward, and shorter and lower than the 1, which is thin, entire, and tilted backwards; 3b triangular, bifid, and sub-horizontal; posterodorsal region of right valve with a groove for the insertion of left valve. Left hinge with 2a triangular, straight; 2b triangular, bifid and higher than 2a; 4b lamellar, curved, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars deep; posterior pedal retractor scar joined to the posterior adductor muscle scar. Pallial sinus short, triangular, dorsal and ventral margins straight and ascendant, and apex sharpened. Sculpture of broad, low, and flat ribs, closer to each other towards the ventral margin, separated by interspaces of equal depth throughout the valve.

Etymology.—*Omega* is the last letter of the Greek alphabet, and the name refers to some of the specimens of this taxon collected in the last bed with veneroids of the Submeseta Formation, found just below the Weddell Sea Formation (Pliocene) outcrops.

Material.—Two hundred fifty four specimens, IAA-Pi 107 (37 specimens), IAA-Pi 110 (113 specimens), IAA-Pi 114 (53 specimens), IAA-Pi 416–422 (7 specimens), MACN-Pi 6380 (36 specimens), MACN-Pi 6382 (8 specimens).

Measurements.—Holotype IAA-Pi 416: length 43.3 mm; height 33.25 mm (Appendix 2).

Remarks.—During the 2014 expedition several specimens of this new species were found in the beds with veneroids at the top of the Submeseta Formation. They have the same shape, umbo, lunule, and similar sculpture and hinge plate to those of *Adelfia australissa* n. comb., which is why this species is included in *Adelfia* n. gen.

All specimens are articulated, so it is not possible to observe internal features. However, some cracked shells were broken to have access to the inner cast and these showed some internal characters. This demonstrated that there are some differences between the pallial sinuses of both species, which are used as diagnostic characters. In addition, the elements of the sculpture of the new species are lower than those of *Adelfia australissa* n. comb.

The most conspicuous difference is the size, with *A. australissa* n. comb. being larger than *A. omega* n. gen. n. sp. (Appendix 2). This could indicate that the new species is a juvenile of the type species, but counting of the annual growth ribs observed in eroded specimens of *A. omega* n. gen. n. sp. revealed that some specimens are more than 30 years old.

Specimens of *Marciachlys inflata* n. comb. and *Retrotapes newtoni* were also collected from the beds where *A. omega* n. gen. n. sp. was found. These three species have a suboval shape and most of their specimens are eroded. Although it is very hard to identify them, there are some distinguishing features. *Marciachlys inflata* n. comb. has a larger lunule, prominent umbo, and is wider than the other two species. *Retrotapes newtoni* has a concave lunule bounded by a deep groove, and *A. omega* n. gen. n. sp. has a smaller and flatter lunule and the disk is sculptured with low, broad, and flat ribs.

Phylogenetic analysis

Characters.—A matrix of 80 characters was developed (Appendix 3), describing the whole shell morphology of extant and fossil taxa, including: shape (13), hinge (30), umbo (1), lunule (6), nymph (3), escutcheon (5), pallial sinus (7), muscles scars (7), and sculpture (8) (Alvarez, 2019).

In order to minimize the loss of information, most of the reviewed material was studied first hand. Only 3.57% of the entries are missing in the data matrix. Characters from 18 to 23 are lineal measurements (not ratios), therefore, in order to compare the measurements, these were rescaled to the average size of *Tapes literatus* (Linnaeus, 1758) (average height value of 45.9 mm). The ratios of the other continuous characters were logarithmized (log10) following Mongiardino Koch et al. (2015).

Ingroup.—Previously, Alvarez (2019) tested the monophyly of the genus *Retrotapes*. The results allowed him to argue about the possibility of the existence of an Austral Tapetinae clade that includes the genera *Retrotapes*, *Atamarcia*, *Paleomarcia*, and *Katelsysia*. With the objective of evaluating the relationships of the new genera described herein within this Austral clade, the selected terminals of the ingroup settled in Alvarez (2019) were resampled. Only four of the 13 known species of the genus *Retrotapes* (Alvarez et al., 2014) were included in the matrix: the three Eocene Antarctic species (*R. antarcticus*, *R. robustus*, *R. newtoni*) and the type species, *R. ninfasiensis* del Río, 1997, the type species of the genera *Adelfia* (*A. australissa* n. comb.) and *A. omega* n. gen. n. sp., as well as the type species of *Marciachlys* n. gen. (*M. inflata* n. comb.) and the type of *Katelsysia* (*K. scalarina*) and *K. florentinoi*. Other austral taxa that share some features with *Retrotapes* were also included: *Atamarcia sulcifera* (Marwick, 1927) (type species of *Atamarcia*), *Eumarcia fumigata* (Sowerby, 1853) (type species of *Eumarcia*), and *Paleomarcia tatei* (Fletcher, 1938).

Outgroup.—Several genera of the subfamily Tapetinae were included in the matrix, using in most cases only the type species, namely: *Neotapes undulata* (Born, 1778), *Polittapes aureus* (Gmelin, 1791), *P. virgineus* (Linnaeus, 1767), *Venerupis corrugata* (Gmelin, 1791), *Ruditapes philippinarum* (Adams and Reeve, 1850), *R. decussatus* (Linnaeus, 1758), *Protapes gallus* (Gmelin, 1791), *Marcia opima* (Gmelin, 1791), *Paphia rotundata* (Linnaeus, 1758), *Tapes literatus* (Linnaeus, 1758), *Notopaphia elegans*

(Deshayes, 1854), *Irus carditoides* (Lamarck, 1818), and *Eurhomalea rufa* (Lamarck, 1818). Two other genera previously considered as Tapetinae were included: *Frigichione permagna* (Tate, 1900) and *Gomphina undulosa* (Lamarck, 1818). *Dosinia concentrica* (Born, 1778) was used to root the tree.

Search.—A phylogenetic analysis was performed following the maximum parsimony criterion using the TNT 1.5 software (Goloboff et al., 2008) through a heuristic search of 100 replicates of Wagner trees (with addition of random sequences) followed by TBR branch swapping algorithm holding 10 trees per replicate. Characters 1–25 were considered as continuous. The methodology of character weighting was implied weighting (Goloboff, 1993), performing 100 searches for k values between 1 and 100, because bivalves and mollusks in general are a homoplastic group. However, an exploratory search without implied weighting was also performed. Support values were estimated by resampling using frequency differences under Bootstrap (BS) (Felsenstein, 1985) and Jackknife (JK) (Farris et al., 1996), with a $p=8$ (equivalent to removing 10% of the characters) (Goloboff et al., 2003), and performing 1,000 pseudo-replicates.

Results

Each search performed with a different k value (k between 1 and 100) resulted in a single topology, obtaining ranges of k where the recovered topologies are similar to each other. The ranges of trees that have similar topologies are 6–28 (Fig. 7.2) and 29–100 (Fig. 7.3). The BS and JK values were calculated and informed on each topology (Fig. 7). The tree obtained for the k value 29 is the most abundant (71 of 100 trees), and is similar to the one obtained in an exploratory search performed without implied weighting; it also has the best BS and JK values, and the discussion is based on it.

In all the performed searches, *Adelfia* n. gen., *Katelsysia*, and *Retrotapes* (closely related to *Paleomarcia* and *Atamarcia*) are monophyletic groups. *Marciachlys* n. gen. is the sister taxon of the clade *Marcia* + *Protapes*, and in the search performed with equal weighting (Fig. 7.1), which was a k value of 29, it is possible to recognize a large clade of Austral or sub-Antarctic taxa that was previously unknown.

In the topology with k values ranging from 29 to 100, the Austral clade is supported by eight synapomorphies: (character 15 [c15]) lunule long (35–36% of total height); (c20) width of the tooth 4b (0.679–0.803 mm); (c21) width of the tooth 3a (0.961–0.979 mm); (c51) well-marked escutcheon; (c52) sculpture of the escutcheon similar to the rest of the shell; (c53) slightly narrow escutcheon; (c54) wider escutcheon in the left valve; and (c55) long escutcheon, reaching halfway down the posterior side of the muscle adductor scar.

The inclusion of *K. florentinoi* in the genus *Katelsysia* is supported by high JK values in all searches. This clade has 13 synapomorphies in the topology with k values ranging from 29 to 100: (c4) inclination of tooth 3a of 69.5°; (c5) inclination of tooth 1 of 121°; (c7) width of the pallial sinus 25% of the total

height; (c9) tooth 2a thin (89% of 2b width); (c14) umbo anterior (placed at 75% of total length); (c15) lunule short (32% of total height); (c17) tooth 3a long, occupying 88% of the hinge plate area in its position; (c18) width of the 2a tooth (1.776 mm); (c24) slope of the dorsal margin of 164°; (c26) very shallow pallial sinus; (c44) pedal retractor muscle scar placed below the anterior cardinal teeth; (c50) elements of the commarginal sculpture closer towards the umbo and spaced towards the ventral margin of the disk; and (c61) adults small sized.

Adelfia n. gen. is supported by high JK values in all searches, and has four synapomorphies on the topology with k values ranging from 29 to 100: (c7) width of the pallial sinus 17% of the total height; (c30) high hinge plate; (c39) smooth tooth 1; and (c70) presence of growth commarginal ribs with thin ribs interspaced. *Marciachlys* n. gen. is recovered as the sister taxon of the clade *Marcia* + *Protapes* with low values of support in all searches and has only three synapomorphies: (c5) inclination of tooth 1 of 107–110°; (c10) tooth 4b wide (52% of 2b width); and (c63) smooth angle between the posterior and dorsal margins.

The clade *Paleomarcia* + *Atamarcia* + *Retrotapes* is recovered in all searches performed with implied weighting, and is supported by nine synapomorphies: (c3) inclination of the posterior muscle scar of 93°; (c6) inclination of tooth 3b of 163°; (c7) width of the pallial sinus 22% of the total height; (c12) tooth 3b 1.40–1.94 times wider than tooth 1; (c17) tooth 3a short, occupying 73% of the hinge plate area in its position; (c23) width of tooth 3b (1.931–2.429 mm); (c24) slope of the dorsal margin of 159–160°; (c51) well-marked escutcheon; and (c69) commarginal sculpture of low and thin ribs.

Discussion

In all the performed searches, subtropical taxa are recovered as basal for the clade Tapetinae (e.g., *Eumarcia*, *Pahia*, and *Neotapes* for the searches with equal weighting and with k values of 29–100, and the clade *Polittapes* + *Eurhomalea* + *Venerupis* + *Ruditapes* in searches performed with k values of 6–28), which suggests a possible subtropical origin for the subfamily Tapetinae. On the other hand, for the searches with equal weighting and with k values of 29–100, a clade of Austral taxa with clear affinities with Eocene Antarctic genera is recovered. Within this group, *Adelfia* n. gen. and *Katelsysia* (including its type and extant species from the South Australia, *K. scalarina*) are recovered basal to a clade that includes *Paleomarcia* (Miocene of Kerguelen Island) and *Atamarcia* (Miocene of New Zealand) as a sister taxa of *Retrotapes*. Concerning the clade *Retrotapes*, the Eocene Antarctic species are recovered basal to the type species of the genus, *R. ninfasiensis* (late Miocene, Patagonia). In all searches, *Marciachlys* n. gen. is basal to a clade that includes the genus *Marcia* and *Protapes*. These last two genera have a subtropical distribution nowadays and this result raises a possible evolutionary history connected with taxa from the Eocene of Antarctica.

In view of the results previously discussed, a possible scenario for the evolution of Tapetinae is that this subfamily, as a whole, had a subtropical origin and later migrated to higher latitudes, in this case to the south. Once in Antarctica, the group

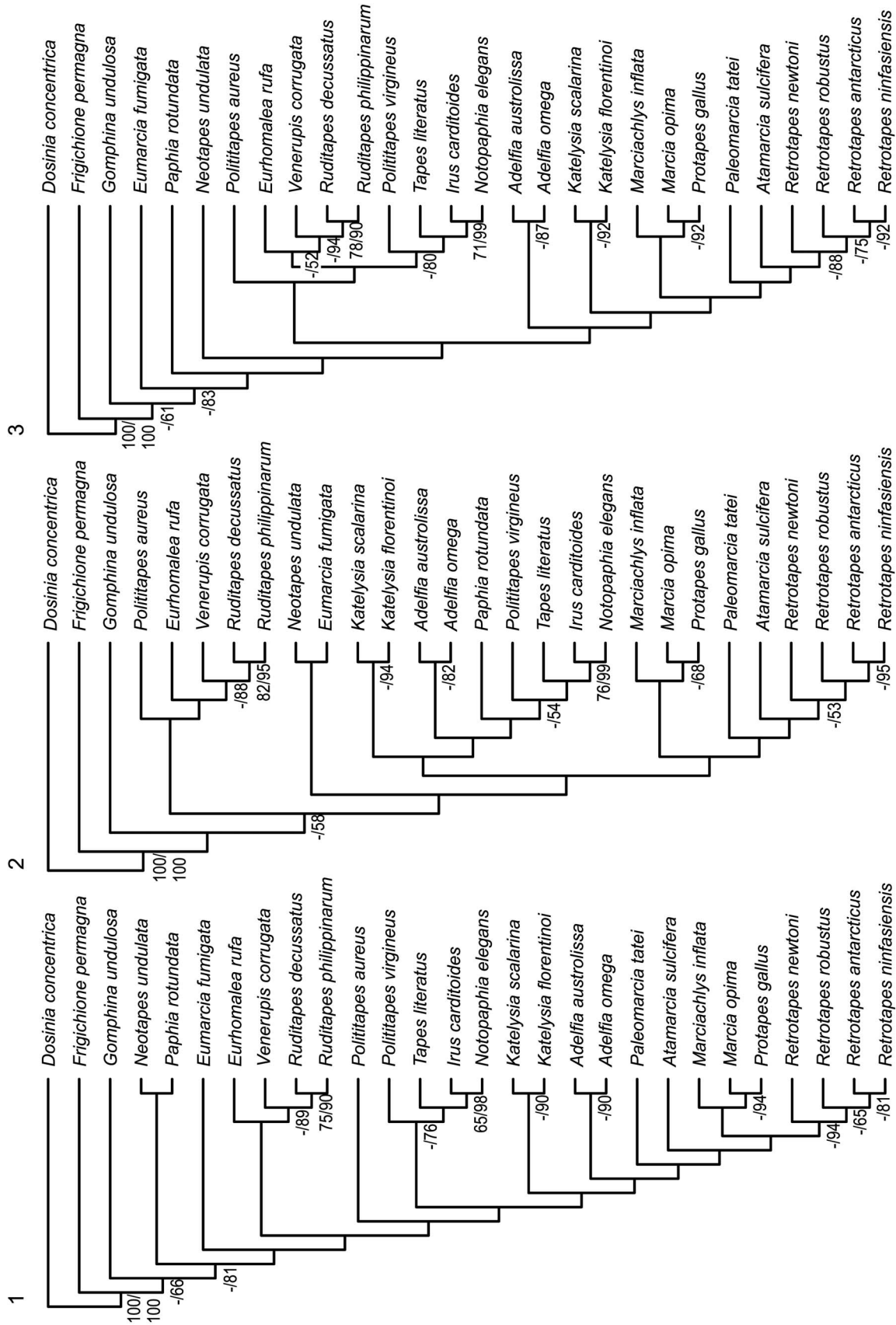


Figure 7. (1) Topology recovered with a search performed with equal weighting. (2, 3) Topologies recovered at different *k* values: (2) *k* = 6–28, (3) *k* = 29–100. Only values of BS/JK over 50 are informed.

would have diversified during the Eocene, to migrate once again, but this time towards lower latitudes, which led in part to the conformation of the Neogene Austral faunas.

As Beu (2009) argued, it may be too risky to claim an Antarctic origin for the aforementioned fauna due to the scarcity of early Cenozoic record in the southern hemisphere. But the phylogenetic results obtained here can shed light on the origin and distribution of part of the modern fauna from the Austral seas, which without a doubt has a close link with the Eocene fauna of Antarctica.

Although it is not the objective of the present contribution, it is important to discuss the phylogenetic position of the genus *Atamarcia*. This fossil genus was erected by Marwick (1927) as a subgenus of the extant *Eumarcia*. Later, Stilwell and Zinsmeister (1992) and Beu (2009) included some species from the Eocene of Antarctica within this genus, including *Atamarcia austrolissa*, which we considered as the type species of the new genus *Adelfia*. *Eumarcia* and *Atamarcia* were not grouped together in any of our phylogenetic results. *Eumarcia* is part of the tropical clade of the Tapetinae, whereas *Atamarcia* is recovered as an Austral Tapetinae. The genera *Adelfia* n. sp. and *Atamarcia* were never recovered as sister taxa. *Atamarcia* is more closely related to *Retrotapes* than to *Adelfia* n. sp., in agreement with the morphological differences recognized between the type species of *Adelfia* n. sp. and *Atamarcia* discussed in the systematic section, which in consequence led us to name the new genus for the Eocene Antarctic species. We use only the type species of *Atamarcia* for both the systematic comparison and the phylogenetic study because a preliminary search of the taxa included in *Atamarcia* allowed us to conclude that a major systematic revision of this genus is needed. There is a big morphological disparity among the species originally assigned by Marwick (1927) as *Atamarcia*. Considering only some hinge characters as an example, *A. sulcifera* has slightly curved cardinal teeth, whereas *A. benhami* (Hutton, 1874) and *A. crassatelliformis* Marwick, 1927 have straight cardinal teeth, and *A. crassa* Marwick, 1927 has a straight right anterior cardinal tooth, joined to the lunule and strongly curved middle and posterior ones.

Conclusions

Only six species of Tapetinae are recognized as valid from the original pool of 10 species described by Zinsmeister (1984) and Stilwell and Zinsmeister (1992). *Gomphina iheringi* Zinsmeister, 1984 is considered as a nomen dubium. *Cockburnia lunulifera* (Wilckens, 1911) is not a Tapetinae, but probably a Corbiculidae. *Eurhomalea carlosi* Zinsmeister, 1984 and ‘*Cyclorismina*’ *marwicki* Zinsmeister, 1984 are synonymized with *Katelsysia florentinoi* (Zinsmeister, 1984) and *Retrotapes antarcticus* (Sharman and Newton, 1894), respectively.

The presence of *K. florentinoi* (Zinsmeister, 1984) in the Eocene of Antarctica considerably extends the stratigraphic and geographic occurrences of *Katelsysia* Römer, 1857, which nowadays inhabit the marine coast of the Southern Australia.

Two new genera are named: *Marciachlys* n. gen., which is represented by *M. inflata* (Zinsmeister, 1984) n. comb., and *Adelfia* n. gen., which is represented by *A. austrolissa* (Stilwell and Zinsmeister, 1992) n. comb., *A. omega* n. gen. n. sp., and the

late Eocene taxon from Punta Arenas (Chile), *A. arenosa* (Ortmann, 1902) n. comb.

Retrotapes, *Katelsysia*, *Adelfia* n. gen., and *Marciachlys* n. gen. are grouped together in a clade with other Austral taxa, such as *Paleomarcia* and *Atamarcia*, and with two subtropical taxa, *Marcia* and *Protapes*, a relationship previously ignored. This reinforces the importance of Antarctica as a center of origin and distribution of fauna during the Cenozoic. The basal position of the clade is occupied by *Adelfia* n. gen. and *Katelsysia*, represented by the Eocene Antarctic *K. florentinoi* and the extant *K. scalarina* (Southern Australia). *Marciachlys* n. gen. is basal to the clade, formed by the extant genera *Marcia* and *Protapes*. The fossil genera *Paleomarcia* (Miocene, Kerguelen Island) and *Atamarcia* (Miocene, New Zealand) are the sister groups of *Retrotapes*. The latter is represented here by its Eocene Antarctic taxa and the Miocene Patagonian *R. ninfasiensis*, being the most ancient species of the genus, and *R. newtoni*, which is basal to the rest of the species.

Acknowledgments

The authors especially thank S.A. Marensi and S. Santillana, as well as the team of Geomarambio, for their assistance during the organization and subsequent realization of the 2014 field trip dispensed to MJA. The authors are indebted to the curators who facilitated access to paleontological and biological collections: M. Longobucco (MACN-Pi and exCIRGEO-PI), A. Tablado and M. Romanelli (MACN-In), M. Tanuz (CPBA), C. Amenábar (IAA-Pi), A. Riccardi (MLP), and C. Salazar and S. Soto (SGO.PI). We also thank everyone who sent us photographs: A. Salvador (NHMUK), G. Dietl (PRI), C. Franzén-Bengtson and J. Hagström (PZ-NRM Mo), S. Hannam (AM), M. Binnie (SAM), J. Gerber (FMNH), T. Schiøtte (ZMUC-BIV), and J. Trausel and F. Sliker (NMR). The authors would like to thank R. Pujana (MACN), C. Greppi (MACN), and M. Miñana (MACN) for their assistance in making the cuts of the new materials, O. Lehmann (MACN) for the script for multiple implied weighting searching, and M.B. von Baczko and L. Tanoni for the improvement of language. We especially thank A. Beu and an anonymous reviewer for their helpful comments and suggestions as reviewers, and to J. Jin for his suggestions as editor that improved this work. The use of TNT software is facilitated by the Willi Hennig Society. CONICET is acknowledged for the post-graduate grant given to MJA. The participation of MJA in the 2014 field trip was financially supported by the Instituto Antártico Argentino (IAA). This research was also supported by ANPCyT-PICT 57.

Accessibility of supplemental data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpvnv2s>.

References

- Adams, A., and Reeve, L., 1848–1850, Mollusca, in Adams, A., ed., The zoology of the voyage of H.M.S. Samarang, under the command of the Captain Sir Edward Belcher, C.B., F.R.A.S., F.G.S., during the years 1843–1846: London, Reeve and Benham, 87 p.

- Adams, H., and Adams, A., 1853–1858, The genera of Recent Mollusca, arranged according to their organization: London, J. van Voorst, (vol. 1, p. 1–256, 1853; p. 257–484, 1854; vol. 2, p. 1–92, 1854; p. 93–284, 1855; p. 285–412, 1856; p. 413–540, 1857; p. 541–661, 1858).
- Alvarez, M.J., 2019, Phylogenetic analysis of the genus *Retrotapes* del Río, 1997 (Bivalvia: Veneridae) and systematic analysis of its taxa from Chile: *Journal of Paleontology*, v. 93, p. 685–701. doi: 10.1017/jpa.2018.110
- Alvarez, M.J., and Pérez, D.E., 2016, Gerontic intraspecific variation in the Antarctic bivalve *Retrotapes antarcticus*: *Ameghiniana*, v. 53, p. 485–494.
- Alvarez, M.J., del Río, C.J., and Marensi S.A., 2014, Revisión del género *Retrotapes* del Río (Bivalvia: Veneridae) en el Eoceno de la Antártida: *Ameghiniana*, v. 51, p. 61–78.
- Amenábar, C.R., Montes, M., Nozal, F., and Santillana, S., 2019, Dinoflagellate cysts of the La Meseta Formation (middle to late Eocene), Antarctic Peninsula: implications for biostratigraphy, palaeoceanography and palaeoenvironment: *Geological Magazine*, v. 157 p. 351–366. <https://doi.org/10.1017/S0016756819000591>
- Beu, A.G., 2009, Before the ice: biogeography of Antarctic Paleogene molluscan faunas: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 284, p. 191–226.
- Born, I., 1778, *Index rerum naturalium Musei Caesarei Vindobonensis, pars prima. Testacea*: Wien, Officina Krausiana, 458 p.
- Cenizo, M., Acosta Hospitaleche, C., and Reguero M., 2015, Diversity of pseudo-toothed birds (Pelagornithidae) from the Eocene of Antarctica: *Journal of Paleontology*, v. 89, p. 870–881.
- Cossmann, M., 1920, Rectifications de nomenclature: *Revue Critique de Paléozoologie*, v. 24, p. 81–83.
- Crame, J.A., Beu, A.G., Ineson, J.R., Francis, J.E., Whittle, R.J., and Bowman, V.C., 2014, The early origin of the Antarctic marine fauna and its evolutionary implications: *PloS one*, v. 9, e114743.
- Dall, W.H., 1902, Synopsis of the family Veneridae and of the North American Recent species: *Proceedings of the United States National Museum*, v. 26, p. 355–412.
- del Río, C.J., 1997, Cenozoic biogeographic history of the eurythermal genus *Retrotapes*, new genus (Subfamily Tapetinae) from southern South America and Antarctica: *The Nautilus*, v. 110, p. 77–93.
- Deshayes, G.P., 1854, Descriptions of new shells from the collection of Hugh Cuming, Esq: *Proceedings of the Zoological Society of London*, v. 22, p. 317–371.
- Dillwyn, L.W., 1817, A descriptive catalogue of Recent shells, arranged according to the Linnean method; with particular attention to the synonymy: London, John and Arthur Arch, v. 2, p. 581–1092.
- Douglas, P.M., Affek, H.P., Ivany, L.C., Houben, A.J., Sijp, W.P., Sluijs, A., Schouten, S., and Pagani, M., 2014, Pronounced zonal heterogeneity in Eocene southern high-latitude sea surface temperatures: *Proceedings of the National Academy of Sciences*, v. 111, p. 6582–6587.
- Elliot, D.H., and Trautman, T.A., 1982, Lower Tertiary strata on Seymour Island, Antarctic Peninsula, in Craddock, C., ed., *Antarctic Geoscience*: Madison, University of Wisconsin Press, p. 287–297.
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D., and Kluge, A.G., 1996, Parsimony jackknifing outperforms neighbor-joining: *Cladistics*, v. 12, p. 99–124.
- Felsenstein, J., 1985, Confidence limits on phylogenies: an approach using the bootstrap: *Evolution*, v. 39, p. 783–791.
- Fletcher, H.O., 1938, Marine Tertiary fossils and a description of a Recent *Mytilus* from Kerguelen Islands: *British, Australian and New Zealand Antarctic Research Expedition Reports*, series A, p. 101–116.
- Gmelin, J.F., 1791, *Vermes*, in Gmelin, J.F., ed., *Caroli a Linnaei Systema Naturae per Regna Tria Naturae: Editio Decima Tertia, Aucta Reformata*. Tome 1, Pars 6: Leipzig, G.E. Beer, p. 3021–3910.
- Goloboff, P.A., 1993, Estimating character weights during tree search: *Cladistics*, v. 9, p. 83–91.
- Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J., and Szumik, C.A., 2003, Improvements to resampling measures of group support: *Cladistics*, v. 19, p. 324–332.
- Goloboff, P.A., Farris, J.S., and Nixon, K.C., 2008, TNT, a free program for phylogenetic analysis: *Cladistics*, v. 24, p. 774–786.
- Gray, J.E., 1851, List of the specimens of British animals in the collection of the British Museum. Part 7. Mollusca, Acephala and Brachiopoda: London, British Museum, 167 p.
- Hutton, F.W., 1874, Description of three new Tertiary shells, in the Otago Museum: *Transactions and Proceedings of the Royal Society of New Zealand*, v. 7, p. 458.
- Iredale, T., 1924, Results from Roy Bell's molluscan collections: *Proceedings of the Linnean Society of New South Wales*, v. 49, p. 179–278.
- Ivany, L.C., Lohmann K.C., Hasiuk, F., Blake, D.B., Glass, A., Aronson, R.B., and Moody, R.M., 2008, Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctica: *Geological Society of America Bulletin*, v. 120, p. 659–678.
- Lamarck, P.A., 1818, *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux etc.*: v. 5, Paris, Chez l'auteur, au Jardin du Roi, 612 p.
- Lamy, E., 1935, Sur le *Venus corrugata* Lamarck (Moll. Lamellibr.): *Bulletin du Muséum National d'Histoire Naturelle*, Paris, v. 7, p. 357–358.
- Linnaeus, C., 1758, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum...* Tomus I. Editio decima, reformata: Holmiae, Impensis Direct, Laurentii Salvii, 824 p.
- Linnaeus, C., 1767, *Systema naturae per regna tria naturae...* Editio duodecima, reformata. Tomus I: Holmiae, Impensis Direct, Laurentii Salvii, Pars II, p. 533–1327.
- Marensi, S.A., 2006, Eustatically controlled sedimentation recorded by Eocene strata of the James Ross Basin, Antarctica, in Francis, J.E., Pirrie, D., and Crame, J.A., eds., *Cretaceous–Tertiary high-latitude paleoenvironments*, James Ross Basin, Antarctica: London, Geological Society of London, Special Publication, v. 258, p. 125–133.
- Marensi, S.A., Santillana, S.N., and Rinaldi, C.A., 1998a, Stratigraphy of La Meseta Formation (Eocene), Marambio Island, Antarctica, in Casadío, S., ed., *Paleógeno de América del Sur y de la Península Antártica*: Buenos Aires, Revista de la Asociación Paleontológica Argentina, Publicación Especial, v. 5, p. 137–146.
- Marensi, S.A., Santillana, S.N., and Rinaldi, C.A., 1998b, Paleoambientes sedimentarios de la Aloformación La Meseta (Eoceno), Isla Marambio (Seymour), Antártida: *Instituto Antártico Argentino, Contribución*, v. 464, p. 1–51.
- Marensi, S.A., Casadío, S., and Santillana, S.N., 2002, La Formación Man Aike al sur de El Calafate (Provincia de Santa Cruz) y su relación con la discordancia del Eoceno medio en la cuenca Austral: *Revista de la Asociación Geológica Argentina*, v. 57, p. 341–344.
- Marwick, J., 1927, The Veneridae of New Zealand: *Transactions of the New Zealand Institute*, v. 57, p. 567–635.
- Marwick, J., 1931, The Tertiary Mollusca of the Gisborne District: Wellington, Department of Scientific and Industrial Research, Geological Survey Branch, p. 178.
- Mongiardino Koch, N., Soto, I.M., and Ramírez, M.J., 2015, Overcoming problems with the use of ratios as continuous characters for phylogenetic analyses: *Zoologica Scripta*, v. 44, p. 463–474.
- Montes, M., Nozal, F., Santillana, S., Marensi, S., and Olivero, E., 2013, Mapa Geológico de Isla Marambio (Seymour), Antártida, 1ª edición: Serie Cartográfica, escala 20.000, v. 1.
- Montes, M., Beamud, E., Nozal, F., and Santillana, S., 2019a, Late Maastrichtian–Paleocene chronostratigraphy from Seymour Island, James Ross Basin, Antarctic Peninsula: Eustatic controls on sedimentation: *Advances in Polar Science*, v. 30, p. 303–327. doi: 10.13679/j.advps.2018.0045
- Montes, M., Nozal, F., Olivero, E., Gallastegui, G., Maestro, A., Santillana S., and Martín-Serrano, A., 2019b, Serie Cartográfica Geocientífica Antártica, 1:20.000, in Montes, M., Nozal, F., and Santillana, S., eds., *Geología y Geomorfología de la isla Marambio (Seymour)*. Madrid: Instituto Geológico y Minero de España; Buenos Aires, Instituto Antártico Argentino, p. 1–250.
- Mörch, O.A.L., 1853, *Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra et Gadea, Comes de yoldi, regis Daniae cubiculariorum princeps ordinis Danebrogici in prima classe et ordinis tertii eques*. Fasc. 2, Acephala, Annulata cirripedia, Echinodermata: Copenhagen, Typis Ludovici Kleini, 74 p.
- Nielsen, B.J., 1963, Studies of the genus *Katelysia* Römer 1857 (Mollusca, Lamellibranchiata): *Memoirs of the Natural Museum of Victoria*, v. 26, p. 219–257.
- Ortmann, A.E., 1899, The fauna of the Magellanian beds of Punta Arenas, Chili: *The American Journal of Science*, v. 8, p. 427–432.
- Porębski, S.J., 1995, Facies architecture in a tectonically-controlled incised-valley estuary: La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula: *Studia Geologica Polonica*, v. 107, p. 7–97.
- Rafinesque, C.S., 1815, *Analyse de la nature, outableau de l'Universe et des corps organisées*: Palerme, Aux dépens de l'auteur, 224 p.
- Römer, E., 1857, *Kritische Untersuchung der Arten Molluschengeschlechts Marcia bei Linne und Gmelin mit Berücksichtigung der später beschriebenen Arten*: Cassel, Luckhardt, 135 p.
- Sharman, G., and Newton, E.T., 1894, Notes on some fossils from Seymour Island, in the Antarctic regions obtained by Dr. Donald: *Transactions of the Royal Society of Edinburgh*, v. 37, p. 707–709.
- Sowerby, G.B., II, 1853, *Monograph of the genus Venus*. Supplementary Veneridae. First index to Veneridae. *Thesaurus conchyliorum*, or monograph of genera of shells: London, Sowerby, v. 2, p. 703–762.
- Stilwell, J.D., 2000, Eocene Mollusca (Bivalvia, Gastropoda and Scaphopoda) from McMurdo Sound: systematics and paleoecologic significance, in Stilwell, J.D., and Feldmann, R.M., eds., *Paleobiology and Paleoenvironments of Eocene Rocks, McMurdo Sound, East Antarctica*: American Geophysical Union Antarctic Research Series, v. 76, p. 261–320.

- Stilwell, J.D., and Zinsmeister, W.J., 1992, Molluscan systematics and biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula: American Geophysical Union, Antarctic Research Series, v. 55, p. 1–192.
- Tate, R., 1887, Descriptions of some new species of South Australian marine and freshwater Mollusca: Transactions of the Royal Society of South Australia, v. 9, p. 62–75.
- Tate, R., 1900, Description of new genera and species of Australian Mollusca (chiefly Tasmanian): Transactions of the Royal Society of South Australia, v. 24, p. 104–108.
- Tenison-Woods, J.E., 1878, On some Tertiary fossils from Muddy Creek, Western Victoria: Proceedings of the Linnean Society of New South Wales, v. 3, p. 222–240.
- Wilckens, O., 1911, Die Mollusken der Antarktischen Tertiär formation: Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition, v. 3, p. 1–62.
- Zinsmeister, W.J., 1984, Late Eocene bivalves (Mollusca) from the La Meseta Formation, collected during the 1974–1975 joint Argentine-American Expedition to Seymour Island, Antarctic Peninsula: Journal of Paleontology, v. 58, p. 1497–1527.

Appendix 1

Explored localities of the La Meseta and Submeseta formations. during the field season 2014 in Marambio Island.

Localities	Coordinates	m.a.s.l.	Formation	Allomember
1	64°13.695'S 56°39.585'W	13	La Meseta	Campamento
2	64°13.737'S 56°39.430'W	41	La Meseta	Campamento
3	64°13'43.6"S 56°39'21.6"W	31	La Meseta	Campamento
4	64°13'42.1"S 56°39'16.3"W	30	La Meseta	Campamento
5	64°13'49.7"S 56°39'49.8"W	7	La Meseta	Campamento
6	64°13'48.3"S 56°39'23.8"W	30	La Meseta	Campamento
7	64°13'41"S 56°39'23.9"W		La Meseta	Campamento
8	64°13'41"S 56°39'10.6"W		La Meseta	Campamento
10	64°12'59.9"S 56°37'28.7"W	31	La Meseta	Acantilados I
11	64°13'58"S 56°38'15"W		La Meseta	Cucullaea I
12	64°13'56.4"S 56°39'0.86"W	51	La Meseta	Cucullaea I
13	64°13'24.2"S 56°38'43.7"W	2	La Meseta	Acantilados II
14	2 m from locality 10		La Meseta	Scouring from Campamento Allomember Campamento
15	64°13'18.5"S 56°37'32.1"W	128	La Meseta	Campamento
16	64°14'02.7"S 56°39'37.9"W	112	La Meseta	Cucullaea II
17	Jonas Hill		La Meseta	Acantilados II (Concretional beds)
21			La Meseta	Cucullaea I
22			Submeseta	Unit 39: South header of the aircraft landing strip. west slope of the plateau
23			Submeseta	Bed below of that of locality 22
24			Submeseta	Unit 37: east slope of the plateau
25			Submeseta	Unit 38: east slope of the plateau
26			Submeseta	Unit 38: west slope of the plateau
27	64°13'45.6"S 56°39'55.9"W	0	La Meseta	Campamento: Campamento point beach
28	64°14'10.5"S 56°39'55.4"W	61	La Meseta	Cucullaea I
29			La Meseta	Cucullaea I: white beds of the valley that ends in Sergios point
30	64°14'16.5"S 56°39'08.5"W	126	La Meseta	Cucullaea II: Unit 36
32	64°14'01.6"S 56°39'23.1"W	55	La Meseta	Cucullaea I
33	64°14'01.0"S 56°39'20.9"W	55	La Meseta	Cucullaea I
34	64°14'10.5"S 56°39'55.4"W	61	La Meseta	Cucullaea I
35			La Meseta	Campamento: plain in the north side of La Traición creek
36			Submeseta	Last bed of veneroids; north header of the aircraft landing strip. west slope of the plateau
37			Submeseta	Last bed of veneroids just below Weddell Fm. halfway of the aircraft landing trip. west slope
38			Submeseta	Between localities 22 and 37

Appendix 2

Measures of the studied species collected during the Field Season 2014 by MJA housed at the Instituto Antártico Argentino, and donated material of Stilwell and Zinsmeister to the Museo Argentino de Ciencias Naturales from previous field trips. All the measured specimens are adults and were randomly selected, except in the case of type materials.

				Continued.				
Species	Collection number	Length	Height	Species	Collection number	Length	Height	
<i>Katelysia florentinoi</i>	IAA-Pi 85a	31.25	21.95		IAA-Pi 107l	33.80	24.80	
	IAA-Pi 85b	28.25	19.35		IAA-Pi 110a	40.20	31.70	
	IAA-Pi 85c	24.45	18.60		IAA-Pi 110b	35.20	26.40	
	IAA-Pi 85d	24.30	17.35		IAA-Pi 110c	35.05	25.70	
	IAA-Pi 85e	28.10	19.40		IAA-Pi 110d	34.95	26.00	
	IAA-Pi 63a	46.45	32.90		IAA-Pi 110e	32.10	26.20	
	IAA-Pi 63b	30.25	21.40		IAA-Pi 110f	34.40	25.60	
	IAA-Pi 63c	31.35	21.60		IAA-Pi 110g	29.80	21.60	
	IAA-Pi 63d	20.45	14.60		IAA-Pi 114a	36.25	28.20	
	IAA-Pi 63e	34.70	24.40		IAA-Pi 114b	35.00	27.35	
	IAA-Pi 111	30.15	20.90		IAA-Pi 114c	32.00	25.00	
	MACN-Pi 5304	44.10	28.00		IAA-Pi 114d	43.45	32.50	
	MACN-Pi 5305	51.20	34.50		IAA-Pi 114e	39.50	29.20	
	MACN-Pi 6367a	38.90	30.10		IAA-Pi 114f	31.90	25.30	
	MACN-Pi 6367b	31.70	21.40		IAA-Pi 114g	48.75	37.10	
	MACN-Pi 6367c	29.60	21.10		IAA-Pi 417 Paratype	43.40	34.35	
	MACN-Pi 6367d	38.00	32.30		IAA-Pi 419 Paratype	38.70	30.10	
	MACN-Pi 6368a	31.20	25.30		IAA-Pi 420 Paratype	39.40	31.40	
	MACN-Pi 6368b	33.70	24.70		Mean	38.25	26.40	
	MACN-Pi 6368c	30.80	22.50		<i>Marciachlys inflata</i> n. Comb.	IAA-Pi 109a	37.90	30.05
	MACN-Pi 6368d	41.60	30.80			IAA-Pi 109b	32.80	27.95
	MACN-Pi 6368e	34.40	24.10			IAA-Pi 109c	30.70	25.75
	MACN-Pi 6368f	31.00	23.15			IAA-Pi 109d	31.35	25.20
	MACN-Pi 6368g	41.00	29.10			IAA-Pi 109e	32.40	25.00
	MACN-Pi 6368h	33.10	24.30			IAA-Pi 109f	34.00	27.50
	MACN-Pi 6378a	39.50	28.70			IAA-Pi 109g	28.00	23.30
	MACN-Pi 6378b	36.50	28.20			IAA-Pi 109h	34.40	27.60
	MACN-Pi 6378c	27.20	25.60			IAA-Pi 109i	35.40	29.60
	MACN-Pi 6378d	28.25	22.10			IAA-Pi 109j	36.10	32.40
	MACN-Pi 6378e	22.50	17.40			IAA-Pi 109k	32.20	24.80
	Mean		33.13	24.19		IAA-Pi 109l	30.10	23.60
	<i>Adelfia australissa</i> n. comb.	USNM 441638 Holotype	60.50	46.50		IAA-Pi 109m	31.40	25.90
		IAA-Pi 81	60.50	44.70		IAA-Pi 109n	33.00	25.60
		IAA-Pi 81	56.35	46.35		IAA-Pi 109o	32.00	27.30
IAA-Pi 81		58.00	44.50		IAA-Pi 109p	32.90	27.80	
IAA-Pi 99		53.40	41.85		IAA-Pi 113a	30.10	25.00	
IAA-Pi 106		44.75	32.30		MACN-Pi 6379a	38.00	30.70	
IAA-Pi 64		54.50	37.00		MACN-Pi 6379b	40.80	33.40	
IAA-Pi 86		61.10	44.80		MACN-Pi 6379c	35.20	34.80	
MACN-Pi 6370a		47.30	35.60		MACN-Pi 6379d	30.60	24.10	
MACN-Pi 6370b		38.40	31.60		MACN-Pi 6379e	40.05	30.60	
MACN-Pi 6370c		35.50	34.95		MACN-Pi 6379f	32.55	20.60	
MACN-Pi 6370d		41.80	30.30		MACN-Pi 6379g	30.30	23.50	
MACN-Pi 6370e		40.90	32.20		MACN-Pi 6379h	48.70	31.40	
MACN-Pi 6370f		36.50	29.20		MACN-Pi 6379i	38.95	31.00	
MACN-Pi 6371a		51.80	40.00		MACN-Pi 6379j	32.00	24.05	
MACN-Pi 6371b		51.10	41.30		MACN-Pi 6379k	34.70	25.70	
MACN-Pi 6371c		51.40	40.70		MACN-Pi 6379l	35.40	28.60	
MACN-Pi 6371d		52.30	40.10		MACN-Pi 6379m	32.80	27.30	
MACN-Pi 6371e		31.60	24.60		Mean	33.09	26.42	
MACN-Pi 6371f		31.50	24.50					
Mean			49.46	38.65				
<i>Adelfia omega</i> n. gen. n. sp.		IAA-Pi 416 Holotype	43.30	33.25				
		IAA-Pi 107a	47.95	36.70				
		IAA-Pi 107b	41.90	32.20				
	IAA-Pi 107c	43.60	36.10					
	IAA-Pi 107d	50.70	39.50					
	IAA-Pi 107e	45.30	36.10					
	IAA-Pi 107f	40.90	32.40					
	IAA-Pi 107g	35.35	26.40					
	IAA-Pi 107h	34.10	27.50					
	IAA-Pi 107i	42.20	33.70					
	IAA-Pi 107j	30.50	25.30					
	IAA-Pi 107k	28.00	24.80					

Appendix 3. Matrix

Continuous characters:

<i>Dosinia concentrica</i>	1.872738827	1.835056102	2.076276255	2.187520721	0.424249672	0.709952153	0.680168	0.272817583	0.442965545	1.012149781	0.969346632
2.214843848	1.937517892	1.937517892	2.076276255	2.187520721	0.424249672	0.709952153	0.680168	0.272817583	0.442965545	1.012149781	0.969346632
<i>Marcia optima</i>	2.28780173	1.919078092	1.913813852	2.029383778	2.209515015	0.286306739	1.21387982	0.979796614	0.842392147	1.169751081	0.935043108
<i>Ruditapes decussatus</i>	2.256878032	1.897627091	1.929418926	2.039697324	2.184691431	0.383907396	0.590691565	0.879390433	0.467970695	0.78122584	0.856142768
<i>Ruditapes philippinarum</i>	1.946124619	1.836745966	2.056904851	2.201397124	0.432701822	0.519763082	0.81686037	0.320072817	0.692002564	0.939721605	0.883850335
<i>Politapes aureus</i>	2.273001272	1.908485019	2.015988105	1.769007871	2.066325925	2.200713734	0.395932225	0.448227688	0.84968196	0.462698788	0.889013894
<i>Politapes virgineus</i>	2.28254659	1.917330426	1.917330426	2.019808393	2.17801718	0.332473171	0.516178275	0.744472702	0.287374071	1.035779041	0.820137006
<i>Neotapes undulata</i>	2.238046103	1.86332286	2.045322979	1.73239376	2.029383778	2.149219113	0.291484678	0.416287591	1.023481096	0.522878745	0.748943979
<i>Irus carditoides</i>	2.267171728	1.908485019	1.886490725	1.857332496	1.995635195	2.1430148	0.556302501	0.479073143	0.726998728	0.522878745	0.552841969
<i>Protapes gallus</i>	2.113943352	1.886490725	1.968482949	1.707570176	2.041392685	2.190331698	0.433937662	0.528142985	1.124938737	0.756961951	0.733732111
<i>Tapes literatus</i>	2.281790638	1.960629308	1.851258349	1.884606581	2.076761772	2.213074825	0.490002829	0.551710829	0.555547862	0.038918066	0.895264649
<i>Retrotapes antarcticus</i>	2.261659304	1.979244778	1.903993826	1.945304422	2.113386207	2.229169703	0.254181681	0.68795566	0.894615228	0.476844128	0.906846277
<i>Retrotapes robustus</i>	2.280464547	1.951823035	1.857332496	1.88536122	2.063708559	2.223755454	0.303013036	0.603295957	0.809185855	0.440557414	0.823084918
<i>Retrotapes newtoni</i>	2.260071388	1.979244778	1.931966115	1.949390007	2.034762106	2.219235134	0.334406873	0.578417115	0.706248694	0.291698072	0.882432586
<i>Retrotapes ninfastiensis</i>	2.26873394	1.986771734	1.823908741	2.022565828	2.124938737	2.253661021	0.276265365	0.67309142	0.819223621	0.596924592	0.791148938
<i>Eurhormalea rufa</i>	2.262633605	1.859184501	1.849844475	1.841744398	2.07806624	2.199502018	0.460310909	0.653123774	0.900110253	0.613417137	0.954802045
<i>Katelysia scalarina</i>	2.290034611	1.851258349	1.986771734	1.86332286	2.120573931	2.212187604	0.407742836	0.466255279	0.95169532	0.499397649	0.823908741
<i>Katelysia florentinai</i>	2.24119771	1.900367129	1.932879458	1.842921121	2.083466785	2.201397124	0.397940009	0.447158031	1	0.464886798	0.819543936
<i>Frigilione permagna</i>	2.282259483	1.94610823	1.986637396	1.8831502	2.037546012	2.196286749	0.255272505	0.73239376	0.62324929	0.491361694	0.62324929
<i>Paleomarcia tatei</i>	2.259498314	1.860816964	1.967313918	1.828788748	2.042614885	2.21170775	0.146128036	0.643452676	?	?	0.812913357
<i>Eumarcia fumigata</i>	2.263517716	1.923399466	2.088809166	1.889525797	2.043047743	2.154789029	0.361727836	0.431363764	0.812913357	0.826074803	?
<i>Gomphina undulosa</i>	2.255272505	1.869252503	2.040206628	1.605951158	1.989894564	2.155062619	0.278753601	0.342422681	1	0.230448921	0.230448921
<i>Notopaphia elegans</i>	2.300812794	1.86266795	2.166282067	1.537693194	1.966986025	2.203522417	0.431363764	0.462397998	1.222716471	0.892094603	1.093421685
<i>Atanarcia sulcifera</i>	2.302525733	1.927421695	1.936312634	1.795532443	2.048053173	2.214631945	0.342422681	0.556302501	0.939519253	0.633468456	?
<i>Paphia rotundata</i>	2.228400359	1.86332286	2.041392685	1.814780146	1.975247941	2.184691431	0.380211242	0.591064607	1.11058971	0.447158031	0.792391689
<i>Venerupis corrugata</i>	2.260071388	1.919078092	2.007747778	1.883831713	2.046456142	2.176467485	0.414973348	0.672097858	1.012837225	1.06069784	0.740362689
<i>Marciachlys inflata</i> n. comb.	2.274157849	2	2.008600172	1.830139387	2.015778756	2.159266331	0.361727836	0.62324929	0.939519253	0.716003344	1.021189299
<i>Adelfia australis</i> n. comb.	2.28557309	1.896746616	1.92251786	1.887504774	2.060168812	2.176756667	0.230448921	0.556302501	0.919078092	0.698970004	0.832508913
<i>Adelfia omega</i> n. gen. n. sp.	2.247973266	1.897901874	2.012837225	1.829561056	2.051538391	2.230448921	0.230448921	0.579783597	?	0.579783597	?
2.247973266	1.897901874	2.012837225	1.829561056	2.051538391	2.230448921	2.230448921	0.230448921	0.579783597	?	0.579783597	?

<i>Dosinia concentrica</i>	1.207948759	0.68588132	1.261994985	2.654766653	0.490412559	0.568878569	2.059732748	2.079349251	2.220108088	0.914559411
<i>Marcia optima</i>	1.304960289	0.752845385	2.2032	1.3464	1.2852	0.9792	1.4076	2.0808	2.206825876	0.840132153
<i>Ruditapes decussatus</i>	1.170261715	0.928528247	1.11392606	1.530347017	0.426831481	0.801610342	1.322136559	1.186799728	2.229596528	0.921801908
<i>Ruditapes philippinarum</i>	1.172405651	0.954361641	1.476215408	2.437471952	0.514958863	0.78960359	1.922513089	1.544876589	2.223582462	0.942545583
<i>Polittapes aureus</i>	1.104639092	0.779058988	1.432894737	2.060526316	0.580263158	0.793421053	2.25	1.196052632	2.195207755	0.870431597
<i>Polittapes virgineus</i>	1.077439763	0.967906158	1.27228145	2.29989339	0.440405117	0.636140725	1.516950959	1.614818763	2.222716471	0.831491848
<i>Neotapes undulata</i>	1.164192036	0.929418926	1.458361204	1.381605351	0.460535117	0.921070234	1.151337793	1.381605351	2.225309282	0.807203047
<i>Irus carditoides</i>	1.017728767	1	0.830769231	1.557692308	0.519230769	0.519230769	1.453846154	1.973076923	2.235528447	0.788193189
<i>Protapes gallus</i>	1.091770373	0.869666232	1.306097561	0.979573171	0.559756098	0.606402439	1.119512195	1.25945122	2.195899652	0.899099504
<i>Tapes literatus</i>	1.230448921	1	1.15	3.20	0.35	1.20	1.75	3.10	2.225309282	0.888850981
<i>Retrotapes antarcticus</i>	1.274641978	0.881173429	1.811583012	2.382625483	0.702316602	1.173710074	1.466093366	2.564619165	2.215725665	0.909088191
<i>Retrotapes robustus</i>	1.292427594	0.835184494	1.533851825	2.421147276	0.660312893	0.91618414	1.378403165	1.931415213	2.198657087	0.905578594
<i>Retrotapes newtoni</i>	1.280322532	0.861399917	1.283190578	2.566381156	0.49143469	0.955567452	1.255888651	2.42987152	2.214843848	0.910172007
<i>Retrotapes ninfasiensis</i>	1.256485658	0.82869216	1.641337386	2.482522796	0.984802432	0.707826748	1.138677812	1.538753799	2.203214259	0.990460013
<i>Eurhomalea rufa</i>	1.128472629	0.912890225	1.327228916	1.67746988	0.645180723	1.078373494	1.188975904	1.631385542	2.244277121	0.88974654
<i>Katelsya scalarina</i>	1.356981401	0.943884058	1.924290999	2.150678175	0.679161529	0.905548705	1.358323058	0.905548705	2.214843848	0.862453122
<i>Katelsya florentinoi</i>	1.264817823	0.944482672	1.776774194	1.850806452	0.444193548	0.983571429	1.311428571	1.639285714	2.218797998	1.001755761
<i>Frigichione permagna</i>	1.338456494	0.785329835	0.703340484	1.680983757	0.513438553	1.146444989	2.764128103	3.79100521	2.181843588	0.93702462
<i>Paleomarcia tatei</i>	?	0.86332286	?	?	?	0.961980836	1.332219512	3.715181185	2.201397124	0.867206726
<i>Eumarcia fumigata</i>	1.033423755	?	0.998526316	1.53	1.030736842	?	?	?	2.214843848	0.929774832
<i>Gomplina undulosa</i>	1.322219295	0.72427587	1.454639175	1.447628866	0.245360825	0.418865979	2.455360825	2.206494845	2.187520721	1.187726336
<i>Notopaphia elegans</i>	1.093421685	?	2.09049505	1.249752475	0.977079208	1.431534653	1.158861386	1.090693069	2.238046103	0.800012251
<i>Atanarcia sulcifera</i>	1.283301229	?	1.796426546	2.056778219	0.893874078	?	?	?	2.198657087	0.953787894
<i>Paphia rotundata</i>	1.385066274	0.857332496	1.405102041	1.086612245	0.309122449	1.03977551	1.676755102	1.695489796	2.209515015	0.550030991
<i>Venerupis corrugata</i>	1.041392685	0.919078092	1.004628633	0.971689989	1.119913886	0.780645856	1.426243272	1.795156082	2.238046103	0.713264192
<i>Marciaeblys inflata</i> n. comb.	1.113943352	0.949390007	1.599303136	1.839198606	0.959581882	1.599303136	1.519337979	1.19477352	2.217483944	1.005701979
<i>Adelfia australissima</i> n. comb.	1.209515015	0.897627091	1.338973162	1.606767795	0.803383897	1.0996875	1.625625	1.8646875	2.212187604	0.939011759
<i>Adelfia omega</i> n. gen. n. sp.	1.123851641	?	?	?	?	?	?	?	2.209515015	0.831207915
<i>Adelfia omega</i> n. sp.	1.123851641	?	?	?	?	?	?	?	2.209515015	0.831207915

Discrete characters:*Dosinia concentrica*

3021100101011012121112100223231001100200100001000000000

Marcia opima

3120110121110312011004100100121001010011100000012012000

Ruditapes decussatus

2121010020110402021000131223231030011010202001002001020

Ruditapes philippinarum

2121010020111402001000131223231030010010202001002001020

Polittapes aureus

3021000130011301001004100223231030010200200200002021001

Polittapes virgineus

1120000130010402011013100002101030011010200210002011001

Neotapes undulata

0120000120010112001013100223231020010210200201011000001

Irus carditoides

2020000?2001?302011000120002001130011111202400002111201

Protapes gallus

3122000131010412101114100100120021011001200301012000000

Tapes literatus

1120010130010402001000100001000030001012200200002011001

Retrotapes antarcticus

1022100131112412021001102000003021011011100110002001000

Retrotapes robustus

1122111131010412021004102000023021001200100110010001000

Retrotapes newtoni

1121110131010412021013102000023021010200200110010001000

Retrotapes ninfasiensis

1122100131010412021001102000023022001001000110000000000

Eurhomalea rufa

2022000120111202020003102223231010000010200010001001001

Katylisia scalarina

0121000131010412020013103001020020020200200301012001101

Katylisia florentinoi

0121000131110412020003103102001020020210200010012000001

Frigichione permagna

1121101?0101??120210?4102223231020000200000000012000000

Paleomarcia tatei

10210?1??0??41?0?00?3100001?210200002001001000100000000

Eumarcia fumigata

1121000?2110?3120??0?3100223230020010200200000011011001

Gomphina undulosa

1110100?0110?0110?10?4102223231020021200200000112010000

Notopaphia elegans

2021011?3000?3021?11?0120001?11133021112211400002100201

Atamarcia sulcifera

202100012101?111??0?3100001022021010200100100002011000

Paphia rotundata

2221010?1110?111??10?5100001101030000200200201011000001

Venerupis corrugata

2121010?2001?4020?10?0120223231030010110201111002000010

Marciachlys inflata n. comb.

112101012101?411001003102102001020010000100000002000000

Adelfia austrolissa n. comb.

1121100?31011012011003100100021020000200100210002000000

Adelfia omega n. gen. n. sp.

10211001300110120010?3100101001020010200200210002000001