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

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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: Marciaflahy new genus to include M. inflata new combination, and Adelfinia new genus, which includes A. austrolissa 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 Proptes.

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 Möhr, 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) austrolissa 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 austrolissa 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) (Marenssi, 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 (Marenssi 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 (Porębski, 1995; Marenssi et al., 1998b), in which the allomembers represent different sedimentation stages related to sea level fluctuations (Marenssi 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
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 Marenssi 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 Marenssi (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.PI); 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).
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 Meretri-cinae 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 2. Stratigraphic column of La Meseta and Submeseta formations, showing the new stratigraphic range of the studied species. *Isotopic age in Ma from Marenssi (2006), **Isotopic age in Ma from Ivany et al. (2008).
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 Katelysia** Römer, 1857

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

*Other species.* — *Katelysia florentinoi* (Zinsmeister, 1984), La Meseta and Submeseta formations (Ypresian–Pliocene, 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,
wider than the interspaces. Some species have very fine radial ribs.

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

**Remarks.**—The genus *Katelysia* 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 (*Rerretapex exalbidus* sensu del Rio, 1997) and selected *Venus scalarina* as type species of *Katelysia*. *Katelysia* 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 *Katelysia* expands the stratigraphic and geographic ranges of the latter genus to the Eocene of the Antarctic Peninsula. *Katelysia* 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

**Figure 4.** (1–9) *Katelysia* 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) *Katelysia* scalarina (Lamarck, 1818), MACN-In 40943, interior, lateral, dorsal and anterior views (Recent, Victoria, Australia). Scale bars = 1 cm.
the hinge plate margin, 1 and 2a teeth bifid, and shorter pallial sinus. *Katelysia* 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.

*Katelysia florentinioi* (Zinsmeister, 1984) new combination

**Figure 4.1–4.9**

1984 *Eurhomalea florentinioi* Zinsmeister, p. 1520, figs. 8 K–M.
1984 *Eurhomalea carlosi* Zinsmeister, p. 1521, figs. 8 Q–S.
1992 *Eurhomalea florentinioi*; 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 florentioi*; 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. Umbro 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 florentinioi* 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. florentinioi*. 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. florentinioi*. The specimens of *E. carlosi* (Fig. 4.9) have four to six annual growth lines, whereas specimens of *E. florentinioi* 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. florentinioi*.

Most of the new specimens of *K. florentinioi* (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 grow 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 florentinioi* does not belong to the genus *Eurhomalea* (type species *E. rufa*) because this genus has a large and subquadrate shell, with sub-central umbro, 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 *Katelysia* 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. florentinioi* 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 *Katelysia* and *Retrotapes* are discussed.
above. Still, *Katelysia florentinoi* cannot be assigned to *Frigichione* because of its smaller and thinner shells, suboval shape, with narrow escutcheon and thinner teeth.

*Katelysia 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. *Katelysia 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, Burtonian–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.**—Burtonian–Priabonian. Submeseta Formation, Marambio Island, Antarctica.

**Etymology.**—*Marci* of the mist. The name refers to Marciac 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 *Rerotapes* 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 *Rerotapes*, but is ventrally oriented in *Marciachlys* n. gen. This genus is distinguishable from *Katelysia* 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**

2009 *Rerotapes 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* Coissman, 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) austroliissa* 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*
**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 nympha 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.

**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 austrolissa* 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 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.
Figure 6. (1–9) Adelphi australisra (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) Adelphia arenosa (Ortmann, 1899) n. comb., right valve, interior and lateral views (late Eocene, Loreto Formation, Punta Arenas, Chile). (12–15) Adelphia 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 austrolissa 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 austrolissa 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 Katelysia 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 Marciaclhys 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 austrolissa** (Stilwell and Zinsmeister, 1992) new combination

Figure 6.1–6.9

1992 *Eumarcia (Eumarcia) austrolissa* Stilwell and Zinsmeister, p. 82, pl. 8., figs. r, s.
2009 *Atamarcia austrolissa*; 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; postero-dorsal 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 austrolissa (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 austrolissa** 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. austrolissa* 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. austrolissa* 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 austrolissa* n. comb.
Occurrence.—Priononian. 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 nympha 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 austroliissa 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 austroliissa n. comb.

The most conspicuous difference is the size, with A. austroliissa 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 Retroptotes 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. Retroptotes 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 Retroptotes. The results allowed him to argue about the possibility of the existence of an Austral Tapetinae clade that includes the genera Retroptotes, Atamarcia, Paleomarcia, and Katelysia. 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 Retroptotes (Alvarez et al., 2014) were included in the matrix: the three Eocene Antarctic species (R. antarcricus, R. robustus, R. newtoni) and the type species, R. ninfasiensis del Río, 1997, the type species of the genera Adelfia (A. austroliissa 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 Katelysia (K. scalarina) and K. florentinii. Other austral taxa that share some features with Retroptotes 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 Tapesinae were included in the matrix, using in most cases only the type species, namely: Neotapes undulata (Born, 1778), Polititapes 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
*Euromalea 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 homoplasic
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., *Katelysia,*
and *Retrotapes* (closely related to *Paleomarcia* and *Atamarcia*)
are monophyletic groups. *Marciacllys* n. gen. is the sister taxon
of the clade *Marcia + Prototapes,* 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)
sulpture 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 *Katelysia* 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 palli-
lar 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 ven-
tral 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. *Marciacllys* n. gen. is recovered as the sis-
ter taxon of the clade *Marcia + Prototapes* with low values of sup-
port 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
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 pos-
terior 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 *Neo-
tapes* for the searches with equal weighting and with $k$
values of 29–100, and the clade *Politittapes + Eurohomalea + Verenu-
ritis + 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 recov-
ered. Within this group, *Adelfia* n. gen. and *Katelysia* (including
its type and extant species from the South Australia, *K. scalar-
ina*) 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. infrasiiensis* (late Mioc-
ene, Patagonia). In all searches, *Marciacllys* n. gen. is basal to a
clade that includes the genus *Marcia* and *Prototapes.* 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 scen-
ario for the evolution of Tapetinae is that this subfamily, as a
whole, had a subtropical origin and later migrated to higher lati-
itudes, 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 austrofossilis*, 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 *Retroptases* 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. sulcirostra* 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 lunifera* (Wilckens, 1911) is not a Tapetinae, but probably a Corbiculidae. *Eurhomalea carlosi* Zinsmeister, 1984 and ‘Cyclorismina’ marwicki Zinsmeister, 1984 are synonymized with *Katelysia florentinoi* (Zinsmeister, 1984) and *Retroptases 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 *Katelysia* Römer, 1857, which nowadays inhabit the marine coast of the Southern Australia.

Two new genera are named: *Marciaexyls* n. gen., which is represented by *M. inflata* (Zinsmeister, 1984) n. comb., and *Adelfia* n. gen., which is represented by *A. austrofossilis* (Stilwell and Zinsmeister, 1992) n. comb., *A. opera* n. gen. n. sp., and the late Eocene taxon from Punta Arenas (Chile), *A. arenosa* (Ortmann, 1902) n. comb.

*Retroptases*, *Katelysia*, *Adelfia* n. gen., and *Marciaexyls* n. gen. are grouped together in a clade with other Austral taxa, such as *Paleomarcia* and *Atamarcia*, and with two subtropical taxa, *Marcia* and *Retroptases*, 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 *Katelysia*, represented by the Eocene Antarctic *K. florentinoi* and the extant *K. scalarina* (Southern Australia). *Marciaexyls* n. gen. is basal to the clade, formed by the extant genera *Marcia* and *Retroptases*. The fossil genera *Paleomarcia* (Miocene, Kerguelen Island) and *Atamarcia* (Miocene, New Zealand) are the sister groups of *Retroptases*. 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.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cxpnvx2.

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Appendix 1

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

| Locality | Coordinates   | m.a.s.l. | Formation | Allomember |
|----------|---------------|----------|-----------|------------|
| 1        | 64°13.695'S   | 13       | La Meseta | Campamento |
|          | 56°39.585'W   |          |           |            |
| 2        | 64°13.737'S   | 41       | La Meseta | Campamento |
|          | 56°39.430'W   |          |           |            |
| 3        | 64°13'43.6''S| 31       | La Meseta | Campamento |
|          | 56°39'21.6''W|          |           |            |
| 4        | 64°13'42.1''S| 30       | La Meseta | Campamento |
|          | 56°39'16.3''W|          |           |            |
| 5        | 64°13'49.7''S| 7        | La Meseta | Campamento |
|          | 56°39'49.8''W|          |           |            |
| 6        | 64°13'48.3''S| 30       | La Meseta | Campamento |
|          | 56°39'23.8''W|          |           |            |
| 7        | 64°13'41.1''S|          | La Meseta | Campamento |
|          | 56°39'10.9''W|          |           |            |
| 8        | 64°13'41.1''S|          | La Meseta | Campamento |
|          | 56°39'10.6''W|          |           |            |
| 9        | 64°12'59.9''S| 31       | La Meseta | Campamento |
|          | 56°37'28.7''W|          |           |            |
| 10       | 64°13'58.5''S|          | La Meseta | Campamento |
|          | 56°38'15.5''W|          |           |            |
| 11       | 64°13'58.5''S|          | La Meseta | Campamento |
|          | 56°39'10.9''W|          |           |            |
| 12       | 64°12'59.9''S| 51       | La Meseta | Campamento |
|          | 56°37'28.7''W|          |           |            |
| 13       | 64°13'58.5''S|          | La Meseta | Campamento |
|          | 56°38'15.5''W|          |           |            |
| 14       | 64°13'18.5''S| 128      | La Meseta | Campamento |
|          | 56°37'28.7''W|          |           |            |
| 15       | 64°13'18.5''S| 128      | La Meseta | Campamento |
|          | 56°37'32.1''W|          |           |            |
| 16       | 64°14'02.7''S| 112      | La Meseta | Campamento |
|          | 56°39'37.9''W|          |           |            |
| Jonas Hill| 64°13'18.5''S|          | La Meseta | Campamento |
|          | 56°37'32.1''W|          |           |            |
| 21       | 64°13'45.6''S| 0        | La Meseta | Campamento |
|          | 56°39'35.9''W|          |           |            |
| 22       | 64°14'10.5''S| 61       | La Meseta | Campamento |
|          | 56°39'55.4''W|          |           |            |
| 23       | 64°13'45.6''S| 0        | La Meseta | Campamento |
|          | 56°39'35.9''W|          |           |            |
| 24       | 64°13'45.6''S| 0        | La Meseta | Campamento |
|          | 56°39'55.4''W|          |           |            |
| 25       | 64°14'01.0''S| 55       | La Meseta | Campamento |
|          | 56°39'20.9''W|          |           |            |
| 26       | 64°14'01.0''S| 55       | La Meseta | Campamento |
|          | 56°39'20.9''W|          |           |            |
| 27       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 28       | 64°14'01.0''S| 55       | La Meseta | Campamento |
|          | 56°39'20.9''W|          |           |            |
| 29       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 30       | 64°14'01.0''S| 55       | La Meseta | Campamento |
|          | 56°39'20.9''W|          |           |            |
| 31       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 32       | 64°14'01.0''S| 55       | La Meseta | Campamento |
|          | 56°39'20.9''W|          |           |            |
| 33       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 34       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 35       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 36       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 37       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |
| 38       | 64°14'16.5''S| 126      | La Meseta | Campamento |
|          | 56°39'08.5''W|          |           |            |

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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.

| Species            | Collection number | Length | Height |
|--------------------|-------------------|--------|--------|
| *Katelysia florentinoi* | IAA-Pi 85a       | 31.25  | 21.95  |
|                    | IAA-Pi 85b       | 28.25  | 19.35  |
|                    | IAA-Pi 85c       | 24.45  | 18.60  |
|                    | IAA-Pi 85d       | 24.30  | 17.35  |
|                    | IAA-Pi 85e       | 28.10  | 20.40  |
|                    | IAA-Pi 63a       | 46.45  | 32.90  |
|                    | IAA-Pi 63b       | 30.25  | 21.40  |
|                    | IAA-Pi 63c       | 31.35  | 21.60  |
|                    | IAA-Pi 63d       | 20.45  | 14.60  |
|                    | IAA-Pi 63e       | 34.70  | 24.40  |
|                    | IAA-Pi 111       | 30.15  | 20.90  |
| MACN-Pi 5304       | 44.10  | 28.00  |
| MACN-Pi 5305       | 51.20  | 34.50  |
| MACN-Pi 6367a      | 38.90  | 30.10  |
| MACN-Pi 6367b      | 31.70  | 21.40  |
| MACN-Pi 6367c      | 29.60  | 21.10  |
| MACN-Pi 6367d      | 38.00  | 32.30  |
| MACN-Pi 6368a      | 31.20  | 25.30  |
| MACN-Pi 6368b      | 33.70  | 24.70  |
| MACN-Pi 6368c      | 30.80  | 22.50  |
| MACN-Pi 6368d      | 41.60  | 30.80  |
| MACN-Pi 6368e      | 34.40  | 24.10  |
| MACN-Pi 6368f      | 31.00  | 23.15  |
| MACN-Pi 6368g      | 41.00  | 29.10  |
| MACN-Pi 6368h      | 33.10  | 24.30  |
| MACN-Pi 6378a      | 39.50  | 28.70  |
| MACN-Pi 6378b      | 36.50  | 28.20  |
| MACN-Pi 6378c      | 27.20  | 25.60  |
| MACN-Pi 6378d      | 28.25  | 22.10  |
| MACN-Pi 6378e      | 22.50  | 17.40  |
| **Mean**           | **33.13** | **24.19** |
| *Adelphia austrolissa* n. comb. | USNM 441638 Holotype | 60.50  | 46.50  |
|                    | IAA-Pi 81        | 60.50  | 44.70  |
|                    | IAA-Pi 81        | 56.35  | 46.35  |
|                    | IAA-Pi 81        | 58.00  | 44.50  |
|                    | IAA-Pi 99        | 53.40  | 41.85  |
|                    | IAA-Pi 106       | 44.75  | 32.30  |
|                    | IAA-Pi 64        | 54.50  | 37.00  |
|                    | IAA-Pi 86        | 61.10  | 44.80  |
| MACN-Pi 6370a      | 47.30  | 35.60  |
| MACN-Pi 6370b      | 38.40  | 31.60  |
| MACN-Pi 6370c      | 35.50  | 34.95  |
| MACN-Pi 6370d      | 41.80  | 30.30  |
| MACN-Pi 6370e      | 40.90  | 32.20  |
| MACN-Pi 6370f      | 36.50  | 29.20  |
| MACN-Pi 6371a      | 51.80  | 40.00  |
| MACN-Pi 6371b      | 51.10  | 41.30  |
| MACN-Pi 6371c      | 51.40  | 40.70  |
| MACN-Pi 6371d      | 52.30  | 40.10  |
| MACN-Pi 6371e      | 31.60  | 24.60  |
| MACN-Pi 6371f      | 31.50  | 24.50  |
| **Mean**           | **49.46** | **38.65** |
| *Marciachlys infula* n. comb. | 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  |
| **Mean**           | **33.09** | **26.42** |
# Appendix 3. Matrix

Continuous characters:

| Species               | Continuous characters                                      |
|-----------------------|------------------------------------------------------------|
| *Gomphina undulosa*   | 2.267171728, 1.886490725, 1.857332496, 1.95635195, 2.1430148, 0.55630251, 0.479073143, 0.726998728, 0.522878745, 0.55284969, 0.132625565, 0.77619055 |
| *Paleomarcia tatei*   | 2.2636305, 1.859145, 1.84944455, 1.81744398, 2.0786064, 2.19950210, 0.65310909, 0.651321377, 0.90012053, 0.613147127, 0.954802045, 1.14206073 |
| *Paphia rotundata*    | 2.2289034, 1.851258349, 1.86332286, 1.82697134, 2.12057394, 2.12187640, 0.407742836, 0.462525789, 0.95169532, 0.447158031, 0.791149383, 0.92490725 |
| *Frugichone parvus*   | 2.2882948, 1.94610823, 1.986637396, 1.8331502, 2.037546012, 2.196286749, 0.255272505, 0.73239376, 0.62324929, 0.491361694, 0.62324929, 0.1136720567 |
| *Eumarcia fluctuata*  | 2.26351776, 1.923399466, 1.889525797, 2.03407743, 2.154789029, 0.36172836, 0.431836764, 0.81213357, 0.82607348, 0.385632724, 0.294729728 |
| *Gonphila undulosa*   | 2.25527505, 1.86952506, 2.04020662, 2.16059151, 2.189984954, 2.25527505, 2.30448291, 2.23044829, 2.23044829, 2.30448291, 2.904930007, 0.868497025 |
| *Notophacia elegans*  | 2.308120794, 1.80266795, 1.66282067, 1.537693194, 1.966096025, 2.203522417, 0.431836764, 0.462397998, 1.1222716471, 0.892094605, 1.093421685, 0.973127854, 0.755874856 |
| *Atanarica sulcifera* | 2.30252533, 1.927421695, 1.936312634, 1.795324234, 2.048083173, 2.216431945, 0.432422681, 0.556302501, 0.939512535, 0.63368456, 0.63368456 |
| *Paphia rotundata*    | 2.228403359, 1.86332286, 2.041392865, 1.814790166, 1.975247941, 2.184694131, 0.380211242, 0.59106607, 1.11058971, 0.447158031, 0.792391689, 0.104321374, 0.716003344 |
| *Venepus corniger*    | 2.26001388, 1.919078092, 2.00774777, 1.883317313, 2.046641614, 2.176467485, 0.419473348, 0.672097858, 1.012837225, 1.00697984, 0.740362689, 1.01037054, 0.832508913 |
| *Adelphi australis a. comb.* | 2.00868017, 1.830139387, 2.015778756, 2.159266331, 0.36172836, 0.62324929, 0.939512535, 0.716003344, 1.02189299, 0.897627091, 0.903809987 |
| *Adelphi australis n. sp.* | 2.28557309, 1.89546646, 1.92251786, 1.887504774, 2.06016818, 2.176765667, 0.23044829, 0.556302501, 0.919078902, 0.698970004, 0.832508913, 0.906987984, 0.892094603 |
| *Adelphi omega n. gen. n. sp.* | 2.247937266, 1.897901874, 2.012837225, 1.829506105, 2.05138391, 2.23044829, 0.23044829, 0.57983597, 0.944826726, 0.57983597, 1.05904851, 0.886490725 |
| Species                           | Coordinates | Dimensions | Description |
|----------------------------------|-------------|------------|-------------|
| Dosinia concentrica              | 0.847721299 | 0.278753601| 1.207948759 | 0.68588132  |
| Marcia opima                     | 0.861421277 | 0.531478917| 1.304960289 | 0.752845383|
| Rudites decussatus               | 0.836267799 | 0.117026175 | 0.928528247 | 1.11392606  |
| Rudites philippinarum            | 0.842454711 | 0.633468456 | 1.172405651 | 0.954361641|
| Politates aureus                 | 0.826259028 | 0.662753783 | 1.104639092 | 0.779058988|
| Politates virgineus              | 0.841716959 | 0.63242929 | 1.077439763 | 0.96906158  |
| Neotapes undulata                | 0.817340835 | 0.54312689  | 1.16192036  | 0.829418926 |
| I. carditoides                   | 0.890436125 | 0.591064607 | 1.017728767 | 0.830769231 |
| Protapes gallus                  | 0.850941519 | 0.643452676 | 1.091707376 | 0.869662323|
| Tapes literatus                  | 0.895093454 | 0.556302501 | 1.230448921 | 1.15       |
| Retrotapes antarcticus           | 0.900634955 | 0.636548176 | 1.258427594 | 0.835184494|
| Retretapes robustus              | 0.894198153 | 0.783518494 | 1.533851825 | 2.421147276|
| Retrotapes newtoni               | 0.871111292 | 0.56302501 | 1.280322532 | 0.861399917|
| Retrotapes ninfasiensis          | 0.905901493 | 0.51851394 | 1.256845685 | 0.82869216  |
| Eurhomalea rufa                  | 0.848087867 | 0.322219295 | 1.128472629 | 0.912809225|
| Katelysia scalarina             | 0.893801473 | 0.505149978 | 1.356981401 | 0.94384058  |
| Katelysia florentini             | 0.875140412 | 0.47712125 | 1.268417823 | 0.944428672 |
| Fricichone permagra              | 0.875061263 | 0.72853601 | 1.338465494 | 0.785329835|
| Paleomarcia tatei                | 0.812913357 | 0.462397998 | 0.86332286  | ?          |
| Eumarcia fusigata                | 0.851835849 | 0.672907858 | 1.033423755 | 0.998526316|
| Gomphina undulosa                | 0.785329835 | 0.51851394 | 1.322219295 | 0.72472587 |
| Notopaphia elegans               | 0.852908913 | 0.098970004 | 1.093421685 | 2.00949505 |
| Atamarcia sulcifera              | 0.851835849 | 0.643452676 | 1.283301229 | 1.796426646|
| Paphia rotundata                 | 0.860923172 | 0.69019608 | 1.385606274 | 0.857332496|
| Venerupis corrugata              | 0.869231172 | 0.579783597 | 1.041392685 | 0.919078092|
| Marcia philippinarum             | 0.819354396 | 0.633468456 | 1.113943352 | 0.943930097|
| Adeliae atrosilva n. comb.       | 0.851835849 | 0.51851394 | 1.209515015 | 0.897627091|
| Adelia omega n. gen. n. sp.      | 0.851835849 | 0.544068044 | 1.123851641 | ?          |

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Discrete characters:

Dosinia concentrica
30211001101112121121002232310011002001000010000000

Marcia opima
31201101211103120110041001001210010100111000001201200

Ruditapes decussatus
212101002110402021000131223231030011010202001002001020

Ruditapes philippinarum
212101002111402001000131223231030011010202001002001020

Politapes aureus
30210001300113010041002232310300102002002000020101002000

Politapes virgineus
11220001030104020110113001101021020021001001010000001

Neotapes undulata
01220011200110210012110210012002101112012400002111201

Irus carditoides
202000002001302011000120002002100111202400002111201

Protapes gallus
3122000131010412101114100100120021011002100301012000000

Tapes literatus
11200101300104020010001000010003000101220020002011001

Retrotapes antarcticus
1022101311142120100110200000302101111001100102000010001

Retrotapes robustus
11221111031041202100140200002302101200100110010010001

Retrotapes newtoni
11221101310412021013020002302101200200110010010001000

Retrotapes ninfasiensis
1122101310412010011200002322200100100110000000000

Eurhomalea rufa
202200012011120200031022323101000001200010001001001000

Katelysia scalarina
012000131010412001114100100120021011002100301012000000

Katelysia florentinoi
0120001311041200031031020010202102020010010200000000

Frigichione permagna
1211110101011224120200000230210111011100100100000000

Paleomarcia tatei
10210000000121210011000100001000100010000000000

Eumarcia fumigata
1122100121103120000030010001001100110000000000

Gomphina undulosa
111100010110?0100100100200210202001010001010010001

Notopaphia elegans
2021011130000302111101200011133021122114000021000201

Atamarcia sulcifera
2021000121011111001022102102020100100100021110000

Paphia rotundata
2221010111111110013100001222100020020020010001000000

Venerupis corrugata
21201002011104020101202232310300110102101111102000010

Marciaclath inflata n. comb.
11210101210114100100010001001000100000000000000

Adelfia austrofissa n. comb.
112110013101101001001001000210002001000210020000000

Adelfia omega n. gen. n. sp.
1211001300110200100100100100021000200210002000001

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