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Phylogenetic analysis of the genus *Retrotapes* del Río, 1997 (Bivalvia, Veneridae) and systematic analysis of its taxa from Chile

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Abstract.—Since the genus *Retrotapes* was erected, some authors have favored or opposed its validity, or argued about the assignment of the extant species *R. exalbidus* and *R. lenticularis* to *Retrotapes*. Some authors synonymized *Retrotapes* with the Miocene genus *Frigichione*, and others with the extant genus *Eurhomalea* to which most of the species that belong to *Retrotapes* were previously assigned. In the present contribution, a phylogenetic analysis of the genus is performed to test these controversies. In addition, a systematic revision of the Chilean species of the genus is performed to complete the analysis of *Retrotapes* taxa from Patagonia and Antarctica started by previous authors. This study demonstrates that *Retrotapes* is a monophyletic genus, which is not closely related to *Frigichione* or *Eurhomalea*. Instead, *Retrotapes* is closely related to some Austral taxa from Kerguelen Island (*Paleomarcia*), New Zealand (*Atamarcia*), and Australia (*Katelysia*), a relationship previously unknown. Besides, the extant species *R. lenticularis* and *R. exalbidus* belong to *Retrotapes* and were recovered as part of a clade closely related to the type species of the genus, *R. ninfasiensis* (Miocene, Patagonia). *Retrotapes* is reported in Chile beginning in the late Eocene, where it was represented by *R. difficilis* n. comb., which is a taxon that resembles some Eocene species of the same genus from Antarctica. In the late Oligocene–early Miocene, it was represented by *R. navidadis* and later in the Pliocene by three species: the fossil *R. fuenzalidae* and the two extant ones.

Introduction

The genus *Retrotapes* was erected by del Río (1997), describing four Miocene Patagonian species and proposing the inclusion of some Cenozoic Chilean and Antarctic taxa within it (species that were previously included in the genus *Eurhomalea* Cossmann, 1920). Several authors confirmed the assignments of del Río (1997) for the Chilean taxa and proposed additional inclusions of species into the genus from Chile (Griffin and Nielsen, 2008; Nielsen and Valdovinos, 2008; Nielsen, 2013) and from Antarctica (Beu and Taviani, 2014). Alvarez et al. (2014) reassigned three Eocene species from La Meseta Formation to *Retrotapes* that previously were considered as species of *Eurhomalea* by Zinsmeister (1984) and Stilwell and Zinsmeister (1992), and recognized the validity of the previous assignments of Chilean and Antarctic species as *Retrotapes*.

Jukes-Browne (1909) emphasized the necessity to erect a new genus in order to separate *Eurhomalea exalbida* (Dillwyn, 1817) and *E. lenticularis* (Sowerby, 1835) from *E. rufa* (Lamarck, 1818) (type species of *Eurhomalea* Cossmann, 1920). Later, Ramorino (1968) erected a new species, *E. salinensis*, from Valparaíso Bay, and stated that *E. lenticularis* and *E. salinensis* have several differences that allowed them to be distinguished from *E. rufa*. Del Río (1997) erected the genus *Retrotapes*, including *E. exalbida* and *E. lenticularis* in it, based on the presence of a concave lunule bounded by a deep groove, non-divergent teeth, some of them bifid, and a ventral margin of the hinge plate curved behind the teeth. Moreover, according to the illustrations and descriptions of Ramorino (1968) that match with the characters of *Retrotapes*, Alvarez

et al. (2014) included *E. salinensis* within this genus. *Eurhomalea*, only represented by its type species *E. rufa*, is characterized by its thin hinge plate with slightly curved margin and thin and divergent cardinal teeth, some of them entire and others slightly grooved. It is also characterized by the absence of an escutcheon and the presence of a very narrow lunule, bounded by a very shallow groove, which in some adult specimens could be absent, as illustrated by del Río (1997).

The genus *Retrotapes* also has been accepted by other authors (Gordillo, 2006; Beu, 2009), but some have questioned its validity (Lauriat-Rage et al., 2002; Huber, 2010). Lauriat-Rage et al. (2002) compared some hinge plate characters of *Retrotapes* and *Frigichione* Fletcher, 1938 (Miocene, Kerguelen Island), and proposed that the latter taxon is a senior synonym of *Retrotapes*. *Frigichione permagna* (Tate, 1900) (type species of *Frigichione* Fletcher, 1938, pl. 1, fig. 3) differs from *Retrotapes* because of its thicker and subtriangular shells, slightly developed escutcheon, straight and short lunule that is bounded by a very shallow groove, and a hinge plate with straight margin and thicker cardinal teeth.

Huber (2010, p. 717), based on a misinterpretation of Jukes-Browne (1909), Ramorino (1968), and del Río (1997), synonymized *Eurhomalea* and *Retrotapes* considering unnecessary the creation of the latter one, at least to include the extant species *R. exalbidus* and *R. lenticularis*.

Gallardo et al. (2003) analyzed the allozyme variation of 12 loci of *Retrotapes exalbidus*, *R. lenticularis* (included in *Eurhomalea* by these authors), and of *Eurhomalea rufa*, and they concluded that *R. lenticularis* and *R. exalbidus* are grouped together in a clade with a high support value of 100 bootstrap frequencies.

This close connection between these two extant species and among other fossil taxa of *Retrotapes*, as well as its separation from *Eurhomalea rufa*, also was supported by the results of the geometric morphometric analysis performed by Alvarez et al. (2014), which supports the validity of *Retrotapes*.

There is some doubt about the inclusion of *Retrotapes lenticularis* into the subfamily Tapetinae. Recent phylogenetic proposals of Veneridae would seem to indicate that *R. lenticularis* is closely related to the subfamilies Venerinae and Chioninae, and not with Tapetinae, as traditional classification suggested (Kappner and Bieler, 2006; Mikkelsen et al., 2006). In both mentioned works, the studied specimen is the same (FMNH 301912), and it was described with a crenulated inner ventral margin (Kappner and Bieler, 2006), a character that matches with the inclusion of it in Venerinae or Chioninae. However, none of the several shells studied in the present contribution has a crenulated inner ventral margin, which on the contrary is smooth, as in the rest of species of the *Retrotapes* and *Eurhomalea*. In the mentioned papers, *R. lenticularis* is the sister taxon of *Tawera spissa* (Deshayes, 1835) with high values of support in all searches. Thus, it is possible that the tissues sample used to perform the molecular analysis would be of a *Tawera* species, for example *T. gayi* (Hupé, 1854), which inhabits the same locations as *R. lenticularis* and has a crenulated inner ventral margin. Unfortunately, specimen FMNH 301912 has no associated valves (J. Gerber, Field Museum of Natural History, personal communication, 2013), so the characteristics of its shell could not be corroborated. This is why until doubts about this specimen are clarified, *R. lenticularis* should be considered as a Tapetinae.

The main goal of the present contribution is to perform a cladistic analysis of the genus *Retrotapes* to test its monophyly and study relationships with others taxa of the subfamily. In addition, a revision of the extant and fossil species of Chile is carried out to have a complete knowledge of the systematics of the genus, continuing with the analysis started by del Río (1997), who studied the fossil species of Patagonia (Argentina), and Alvarez et al. (2014), who analyzed the fossil taxa from Antarctica.

Materials and methods

The studied Tapetinae come from the marine Cenozoic outcrops of Argentina, Antarctica, and Chile, known as San Julián (late Oligocene), Centinela (late Oligocene–early Miocene), 25 de Mayo (late Oligocene–early Miocene), Monte León (early Miocene), Carmen Silva (middle Miocene), and Puerto Madryn (late Miocene) formations from Argentina; La Meseta Formation (Eocene) from Antarctica; and Loreto (late Eocene), Guadal (late Oligocene–early Miocene), Navidad (early Miocene), Bahía Inglesa (late Miocene–late Pliocene), Coquimbo (late Miocene–late Pliocene), La Cueva (early Pliocene), and Tubul (Pliocene–Pleistocene) formations from Chile. Geological settings of the *Retrotapes* taxa from Argentina are summarized in del Río (1997), and those from Antarctica in Alvarez et al. (2014). Fossiliferous localities from Chile are displayed in Figure 1.

Specimens collected by J.B. Hatcher from the Loreto Formation (late Eocene) come from the outcrops exposed to the north of Punta Arenas. The late Oligocene–early Miocene
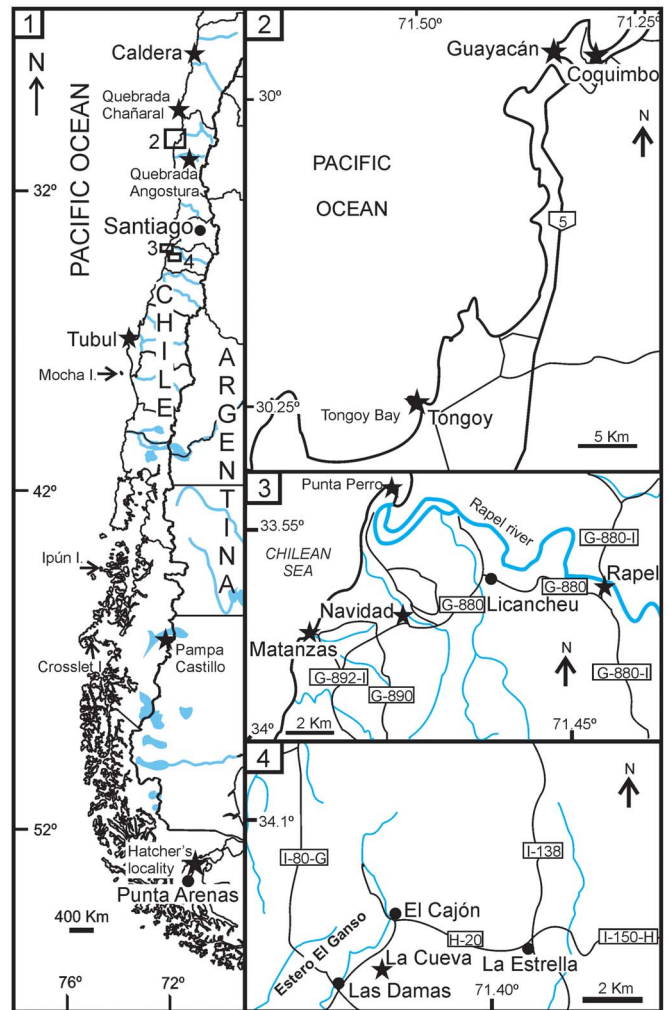

Figure 1. (**1**) Geographic location of the samples; (**2**) area of Coquimbo and Tongoy; (**3**) area of Navidad; (**4**) area of La Estrella. The black stars mark the localities.

sediments that contain the studied material are exposed at Pampa Castillo (Guadal Formation).

Navidad Formation exposures are located at Navidad, Rapel Norte, Punta Perro, and Matanzas. Recent papers indicated a late Miocene–early Pliocene age for this unit based on foraminifera fauna (Finger et al., 2003, 2007; Encinas, 2006; Encinas et al., 2006), but the molluscan fauna recorded there is reworked (Finger et al., 2007) and belongs to the early Miocene (DeVries and Frassinetti, 2003; Nielsen and Glodny, 2009). Later, Finger et al. (2013) revised those assignations and reidentified several foraminifera, indicating an early Miocene–middle Miocene age for this unit. Outcrops from Ipún Island have an early Miocene–middle Miocene age (Frassinetti, 2004; Nielsen and Encinas, 2014) and the suggested age for the sediments from Crosslet Island is middle Miocene–late Miocene (Frassinetti, 2006). Late Miocene–late Pliocene sediments that contain the fossil material studied are exposed at Caldera (Atacama Region, Bahía Inglesa Formation) (Guzmán et al., 2000; Le Roux et al., 2016).

Pliocene beds that contain the fossil material studied are exposed at Coquimbo, Tongoy, Guayacán, Quebrada de

Chañaral, and Quebrada Angostura (Coquimbo Formation; late Miocene–late Pliocene), La Cueva and Estero del Ganso (La Cueva Formation; early Pliocene), Tubul, Cerro Las Lomas, and Tubul River (Tubul Formation; Pliocene–Pleistocene).

The Recent fauna analyzed comes from the Tropical East Pacific, Magellanic, Argentinean, and Caribbean Malacological Provinces.

Geographic and stratigraphic distributions of each studied species, fossils and extant, are summarized in Supplementary Data Set 1, and the materials of other taxa used for comparison and phylogenetic analysis are summarized in Supplementary Data Set 2. The methodology applied to perform the phylogenetic analysis is described in the corresponding section.

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

Phylogenetic analysis

Characters.—A matrix of 80 characters was developed (Supplementary Data Sets 1 and 2), describing the whole shell morphology, including: shape (13), hinge (30), umbo (1), lunule (6), nymph (3), escutcheon (5), pallial sinus (7), muscles scars (7), and sculpture (8).

Some characters concerning the shell shape, hinge plate, pallial line, and muscles scars were based on Mikkelsen et al. (2006) and Pérez et al. (2013), but their states were completely modified. In addition, 25 continuous characters were built based on ratios and inclinations of some structures used in classic systematic works to compare different taxa (e.g., height/length of the valve, length of the lunule and nymph, pallial sinus inclination, teeth inclination, teeth length) (Fig. 2).

In order to minimize the lack of information, most of the reviewed materials were studied first hand. The taxon *Retrotapes andrillorum* Beu and Taviani, 2014 (McMurdo Sound, Antarctica, Miocene) was not included in the analysis because it was only reviewed through published pictures and some inner characters of the shell were not visible due to the sedimentary matrix

that fills it, increasing therefore the amount of missing data in the matrix. The taxa *R. difficilis* (Ortmann, 1899) and *R. scutatus* (Ihering, 1907) also were not included because only a few characters of the hinge were useful in both species due to the incompleteness of the specimens. The same problem occurred with *Frigichione permagna* (Tate, 1900), however this taxon was considered in the analysis to test the synonymy with the genus *Retrotapes* del Río, 1997 proposed by some authors. The percentage of missing entries is 2.92%.

Ingroup.—In addition to the type species of the genera *Frigichione* and *Eurhomalea* (*F. permagna* and *E. rufa*), 10 of the 13 known species of the genus *Retrotapes* were included to build the matrix: *R. antarcticus* (Sharman and Newton, 1894), *R. robustus* (Stilwell and Zinsmeister, 1992), *R. newtoni* (Wilckens, 1911), *R. ninfasiensis* del Río, 1997, *R. striatolamellatus* (Ihering, 1897), *R. fuegoensis* del Río, 1997, *R. navidadis* (Philippi, 1887), *R. fuenzalidae* (Philippi, 1887), *R. lenticularis*, and *R. exalbidus*. Other austral taxa that share some features with *Retrotapes* were included: *Atamarcia sulcifera* (Marwick, 1927) (type species of *Atamarcia*), *Eumarcia fumigata* (Sowerby, 1853) (type species of *Eumarcia*), and *Katelysia scalarina* (Lamarck, 1818) (type species of *Katelysia*).

Outgroup.—Several genera of the subfamily Tapetinae were included to build the matrix considering only their type species in most of the cases, namely: *Gomphina undulosa* (Lamarck, 1818), *Neotapes undulatus* (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), *Paleomarcia tatei* (Fletcher, 1938), *Paphia rotundata* (Linnaeus, 1758), *Tapes literatus* (Linnaeus, 1758), *Notopaphia elegans* (Deshayes, 1854), and *Irus carditoides* (Lamarck, 1818).

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 to 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. The support measures 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.

In this analysis, *Retrotapes* is represented by 10 species, whereas the other genera included are only represented by one or two species, which generates an oversampling of *Retrotapes*. This design of the matrix could cause *Retrotapes* to direct the transformations of the characters in such a way that the phylogenetic relationships would be spurious. To solve this problem, two different analyses were performed. The first one was performed
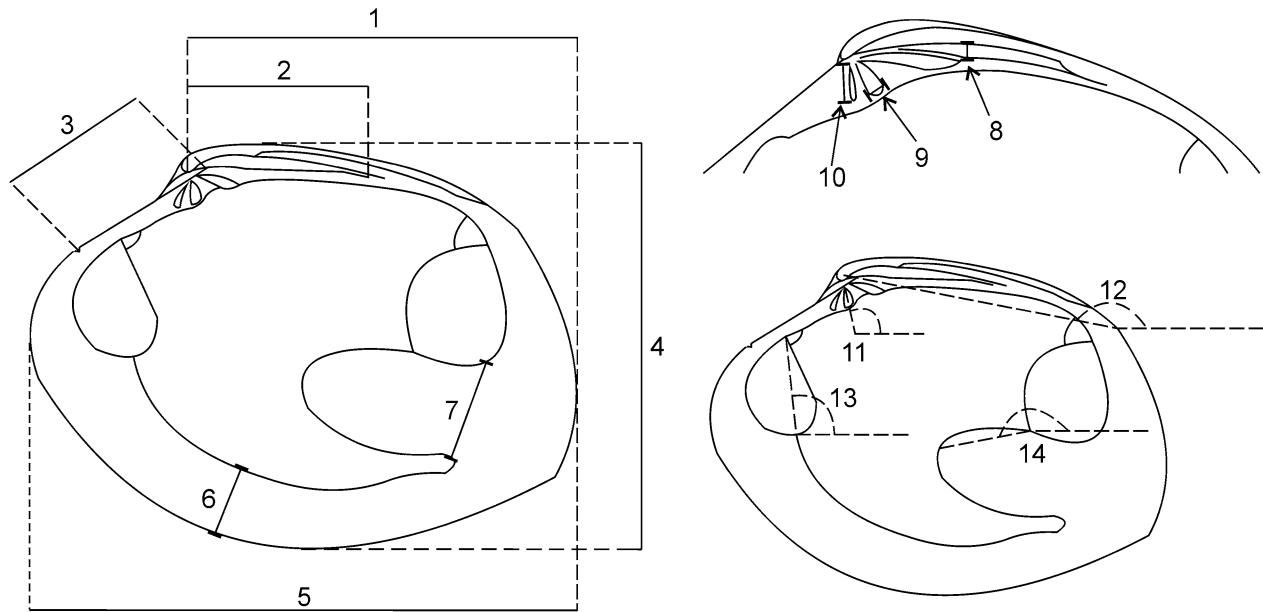
Figure 2. Measures and angles used to build continuous characters. (**1**) Length from the umbo to the posterior margin; (**2**) length of the nymph; (**3**) length of the lunule; (**4**) height of the shell; (**5**) length of the shell; (**6**) distance between the ventral margin and the pallial line; (**7**) width of the pallial sinus; (**8**) height of the nymph; (**9**) width of the teeth; (**10**) length of the teeth; (**11**) inclination of the teeth with respect to the horizontal axis; (**12**) inclination of the dorsal margin measured as a tangent that passes through the umbo and the contact between the dorsal and posterior margins; (**13**) inclination of the abductor muscles; (**14**) inclination of the dorsal side of the pallial sinus, measured as a tangent that joins the apex of the pallial sinus and the contact of it with the posterior abductor muscle scar.

to test the relationships of *Retrotapes* with the other genera, reducing the active taxa of *Retrotapes* to only three terminals: its type species *R. ninfasiensis* (Puerto Madryn Formation; late Miocene) and the extant taxa *R. lenticularis* and *R. exalbidus*, whose assignment to the genus was recently questioned by Huber (2010). The other search was performed to test the inner relationships of the genus including the 10 taxa mentioned above.

Results

Analysis with the reduced matrix.—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 trees have different topologies for *k* values 3, 9, and 22 (Fig. 3). The BS and JK values were calculated and informed on each topology (Fig. 3). The tree obtained for the *k* value 22 is the most abundant topology, and it is the same one obtained in an exploratory search performed without implied weighting, it also has the best BS and JK values, therefore the discussion is based on it.

In all the performed searches, *Frigichione* is recovered as a basal taxon, and *Eurhomalea* is closely related with *Venerupis* and *Ruditapes*. Meanwhile, *Retrotapes* is monophyletic and closely related to *Atamarcia* and *Paleomarcia*.

On the topology with the *k* value of 22, the genus *Retrotapes* is supported by 13 synapomorphies: (character 2 [c2]) Vertical adductor muscle scar (1.953–1.957), (c3) posterior adductor muscle scar slightly oriented backwards (1.919–1.926), (c4) Tooth 3a slightly tilted backwards (1.943–1.960), (c5) Tooth 1 strongly sloped backwards (2.101–2.113), (c6) Tooth 3b sub-horizontal (2.226), (c14) umbo position (0.881–0.884), (c17) space of the hinge plate occupied by 3a tooth (0.808–0.828), (c25) ratio between length and height of the nymph (0.975–0.990), (c30) high hinge plate, (c50) comarginal elements of the sculpture spaced towards the umbo and closer to each other towards the ventral margin of the disk, (c56) lunule bounded by a deep groove, (c63) edge between dorsal and posterior margins rounded, and (c70) presence of marked growth ribs and thin ribs interspersed among them.

Analysis with the complete matrix.—Each search performed with a different *k* value (*k* between 1 and 100) resulted in a single topology, obtaining ranges of *k* in which the recovered topologies are similar to each other. The trees have different topologies for *k* values 2, 7, and 57 (Fig. 4). The BS and JK values were calculated and informed on each topology (Fig. 4). The tree obtained for *k* value 7 is the most abundant topology and has the best BS and JK values, therefore the discussion is based on it. The latter phylogenetic tree was temporally calibrated with the timePaleoPhy() function of the package paleotree (Bapst, 2012) for R (R Core Development Team, 2018) using the 'mbl' calibration and a minimum branch length of 0.1 My (Fig. 5). This setting was chosen in order to recover the most conservative age estimation for each branch. As a result, ghost lineage lengths are mostly a consequence of the age of its sister-branch (Pérez and Ezcurra, 2018).

In all the performed searches, *Retrotapes* is recovered as a monophyletic group and the Eocene Antarctic *R. newtoni* is recovered as the basal-most taxon. In most of the searches (*k* range from 1 to 56) the suboval (*R. newtoni*, *R. fuegoensis*, *R. fuenzalidae*) and subtriangular (*R. robustus*) taxa are successive sister taxa to a group of subquadrate shells in which are included the type species *R. ninfasiensis* and the extant taxa *R. exalbidus* and *R. lenticularis*, the latter being a sub-rounded one. That group of subquadrate shape is recovered in all the searches.
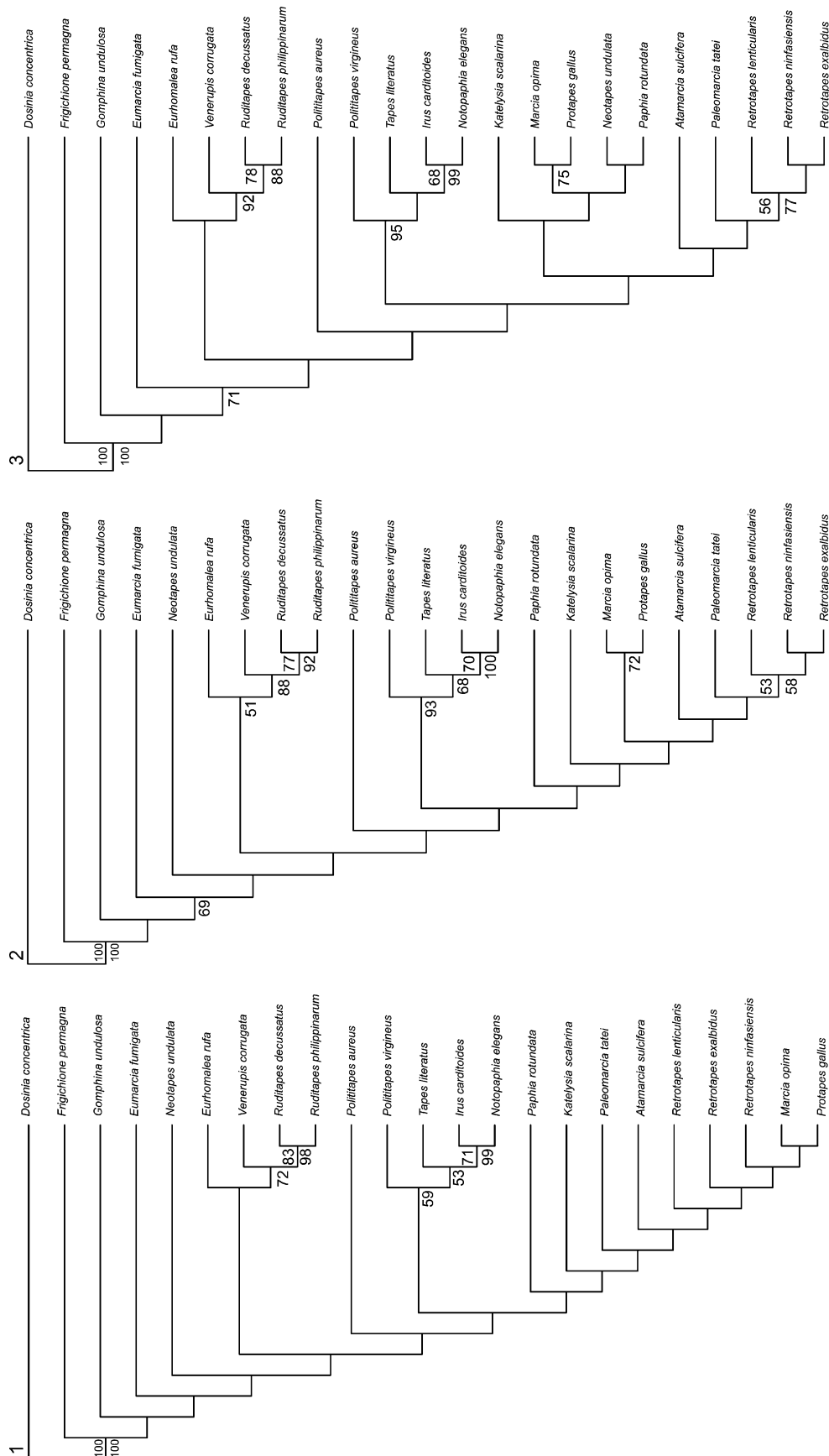
Figure 3. Topologies recovered at different *k* values from the performed analysis with the reduced matrix. (**1**) *k* = 3–8; (**2**) *k* = 9–21; (**3**) *k* = 22–100. BS values are informed over the branches; JK values are informed under the branches; only values over 50 are informed.

Systematic paleontology

Family Veneridea Rafinesque, 1815
Subfamily Tapetinae Gray, 1851
Genus *Retrotapes* del Río, 1997

Type species.—*Retrotapes ninfasiensis* del Río, 1997 (Puerto Madryn Formation, late Miocene) (Fig. 6.6–6.9).

Other included species.—*Retrotapes antarcticus*, *R. newtoni*, and *R. robustus*, La Meseta Formation (Eocene, Marambio Island, Antarctica); *R. difficilis* (Ortmann, 1899), Loreto Formation (late Eocene, Punta Arenas, Chile), *R. scutatus* (Ihering, 1907), San Julián (late Oligocene) and Centinela (late Oligocene–early Miocene) formations (Santa Cruz, Argentina); *R. fuegoensis*, Carmen Silva Formation (middle Miocene, Isla Grande de Tierra del Fuego, Argentina); *R. striatolamellatus*, early Miocene sediments of Centinela (late Oligocene–early Miocene) and Monte León formations (early Miocene) (Santa Cruz, Argentina); *R. navidadis*, Navidad (early Miocene) and Guadal formations (late Oligocene–early Miocene) and sediments from Ipún and Crosslet islands (Chile); *R. andrillorum* Beu and Taviani, 2014, McMurdo Sound (early Miocene, Antarctica); *R. fuenzalidae*, La Cueva (early Pliocene) and Tubul (Pliocene–Pleistocene) formations (Chile); *R. exalbidus* (Dillwyn, 1817) (Pliocene–Recent, from Chiloé, 42°S (Chile), Eastern Pacific Ocean, to Rio Grande do Sul, 32°S (Brazil), Western Atlantic Ocean); and *R. lenticularis* (Sowerby, 1835) (Pliocene–Recent, Eastern Pacific Ocean between 14°S in Perú and 33°S in Chile).

Occurrence.—Eocene–Recent.

Retrotapes difficilis (Ortmann, 1899) new combination
Figure 7.1–7.4

1899 *Venus difficilis* Ortmann, p. 428.
1902 *Venus difficilis*; Ortmann, p. 135, pl. 28, fig. 1.
1907 *Marcia difficilis*; Ihering, p. 350.

Holotype.—A left valve (PRI 72689) from Punta Arenas, Chile (Loreto Formation) (Ortmann, 1902, pl. 28, fig. 1; Fig. 7.1–7.4).

Diagnosis.—Shell subtriangular to suboval shaped, umbo small and slightly curved, lunule slightly concave and bounded by a shallow groove.

Occurrence.—Horizon III, Loreto Formation, late Eocene, Punta Arenas, Chile.

Description.—Shell subtriangular to suboval shaped, convex, medium to large sized, longer than high. Umbo small, slightly curved, placed at anterior 0.25 of length. Anterior, dorsal, and ventral margins convex, posterior slightly convex. Lunule concave and bounded by a shallow groove. Escutcheon wide, wider in the left valve, with comarginal sculpture similar to that of rest of the shell. Nymph short and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are not divergent and do not exceed the ventral margin of the hinge plate. Right hinge with tooth 3a slightly sloped backwards; tooth 1 thick and sloped backwards; tooth 3b thick, bifid and sub-horizontal. Left hinge with tooth 2a subtriangular, high, curved, and ventrally thickened; tooth 2b thick, rectangular, asymmetrically bifid and tilted backwards; tooth 4b lamellar, sub-horizontal, and separated from the nymph by a groove. Shell sculptured with fine comarginal ribs, which are closer to each other towards ventral margin of the disk.

Materials.—Six specimens, MACN-Pi 432, PRI 66447, 66448, 72686, 72687, 72688 (Supplementary Data Set 1).

Measurements.—Holotype PRI 72689: 71.35 mm length, 63.60 mm height.

Remarks.—The specimens of the Ortmann and Ihering collections, from Punta Arenas, which are poorly preserved, are very similar to adult specimens of the Antarctic Eocene taxon *Retrotapes robustus* (Stilwell and Zinsmeister, 1992). Unfortunately the lack of inner characters, as well as complete hinge plates, did not allow determination of whether these two taxa are synonyms or not, so it has been decided to keep *R. robustus* as a valid taxon. *Retrotapes difficilis* would be the oldest species of the genus in the American Continent.

This taxon differs from *R. antarcticus*, *R. newtoni* (Eocene; Antarctica) and the South American species of the genus by its subtriangular shape, small umbo, and its slightly concave lunule, bounded by a shallow groove.

Retrotapes navidadis (Philippi, 1887)
Figure 7.5–7.11

1887 *Venus navidadis* Philippi, p. 120, pl. 14, fig. 4.
1887 *Venus lamelligera* Philippi, p. 121, pl. 14, fig. 6.
1907 *Marcia navidadis*; Ihering, p. 304.
1974 *Venus navidadis*; Frassinetti, p. 47, fig. 4.
1979 "*Venus*" (*Marcia*) *navidadis*; Tavera, p. 80, pl. 13, fig. 20.
1997 *Retrotapes navidadis*; del Río, p. 77.
1999 *Eurhomalea*? *navidadiformis* Frassinetti and Covacevich, p. 36, pl. 7, figs. 2, 3.
2006 *Retrotapes navidadis*; Frassinetti, p. 65, fig. 6.
2014 *Retrotapes navidadis*; Alvarez et al., p. 62.

Holotype.—*Venus navidadis* Philippi, a right valve (SGO.PI 134) from Navidad (Navidad Formation, Chile) (Philippi, 1887, pl. 14, fig. 4; Fig. 7.5).

Emended diagnosis.—Shell thin, subquadrate shaped, medium sized, sculptured with thin comarginal ribs.

Occurrence.—Matanzas, Navidad, Rapel Norte, Punta Perro, (Navidad Formation, early Miocene, Chile), and Pampa Castillo (Guadal Formation, late Oligocene–early Miocene, Chile) and outcrops from Ipún and Crosslet islands (Chile).
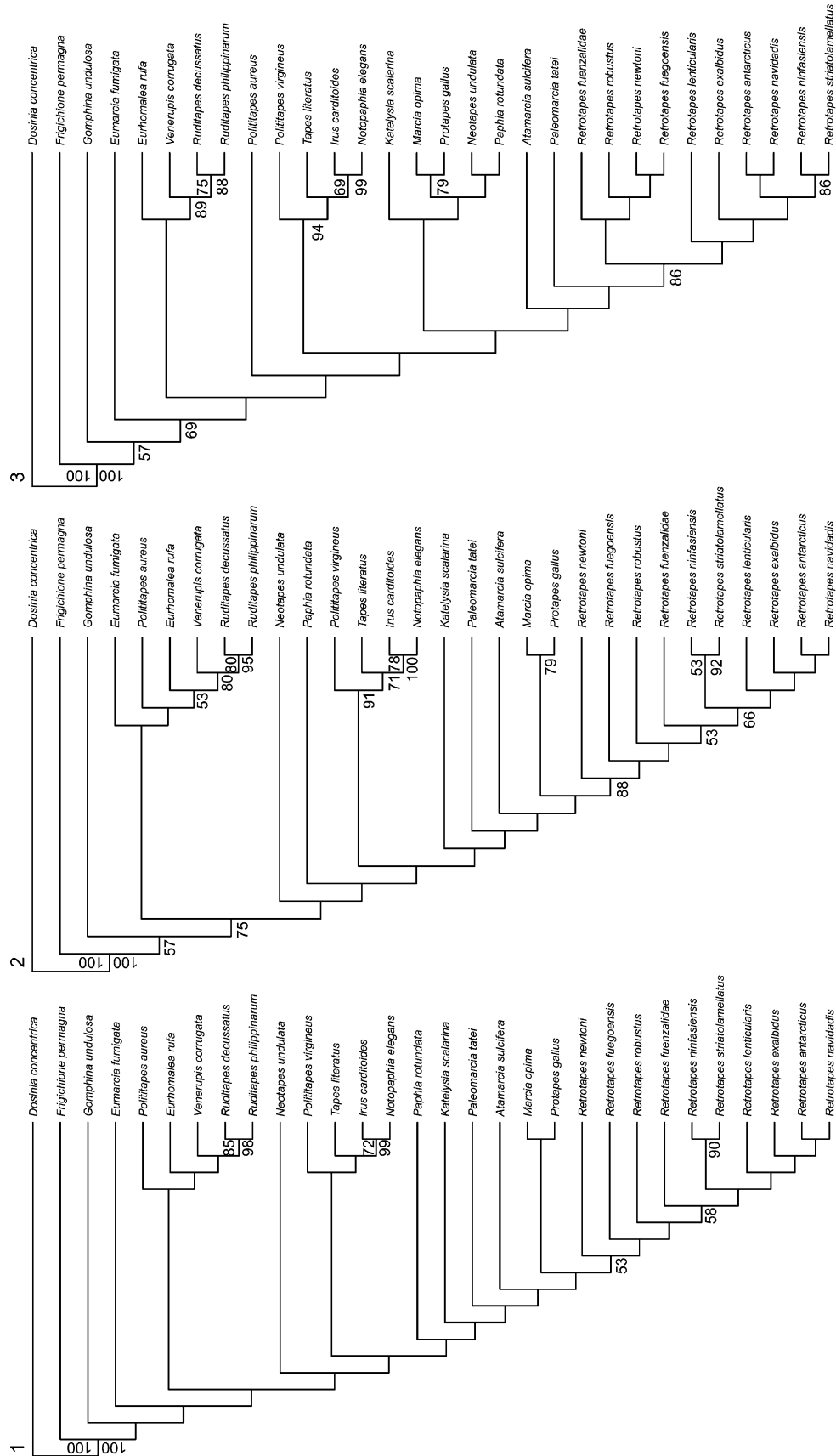
Figure 4. Topologies recovered at different *k* values from the performed analysis with the complete matrix. 1, *k* = 2–6; 2, *k* = 7–56; 3, *k* = 57–100. BS values are informed over the branches; JK values are informed under the branches; only values over 50 are informed.

Description.—Shell thin, subquadrate shaped, medium sized. Umbo small, placed at anterior 0.25 of length. Dorsal margin slightly convex, posterior margin truncated, straight to slightly convex, ventral and anterior margins rounded. Lunule concave and bounded by a deep groove. Escutcheon narrow, wider in the left valve, with comarginal sculpture similar to that of rest of the shell. Nymph short and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are not divergent and do not exceed the ventral margin of the hinge plate. Right hinge with tooth 3a lamellar, slightly sloped backwards or vertical; tooth 1 thin, slightly lower than tooth 3a, with a groove in its posterior area and tilted backwards; tooth 3b rectangular, thick, bifid and horizontal. Left hinge with all its cardinal teeth sloped backwards; tooth 2a triangular, thin, curved, higher than the other teeth, and ventrally thickened; tooth 2b thick, triangular, asymmetrically bifid; tooth 4b lamellar, sub-horizontal, and separated from the nymph by a groove. Dorsal-posterior region of right valve with a groove for the insertion of left valve. Adductor muscle scars isomyarian and 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. Pallial sinus short, with dorsal and ventral margins straight, dorsally oriented, with apex slightly sharpened. Shell sculptured with high comarginal ribs, which are closer to each other towards ventral margin of the disk, and with very fine radial ribs.

Materials.—Thirty-five specimens, MACN-Pi 433, 6353–6357, SGO.PI 92, 99, 130, 5096–5103, 5475, 5572, 6148, 6156, 6165. One external cast, SGO.PI 4292 (Holotype, *Eurhomalea*? *navidadiformis* Frassinetti and Covacevich). Four internal casts SGO.PI 4413, 4342, 5144, 5145. Thirteen fragmented shells, SGO.PI 5572 (Supplementary Data Set 1).

Measurements.—Holotype SGO.PI 134: 51.40 mm length, 43 mm height.

Remarks.—The specimens studied and identified by Ortmann (1902, p. 141, pl. 27, fig. 12) as *Venus navidadis* Philippi (1887) and later named by Ihering (1907, p. 304) as *Marcia ortmanni*, belong to young specimens of *Retrotapes striatolamellatus* (Ihering, 1907) (del Río, 1997).

Eurhomalea? *navidadiformis* Frassinetti and Covacevich (1999, p. 36, pl. 7, figs. 2, 3) (Fig. 7.11) is considered as a junior synonymy of *Retrotapes navidadis* (Philippi, 1887) because it
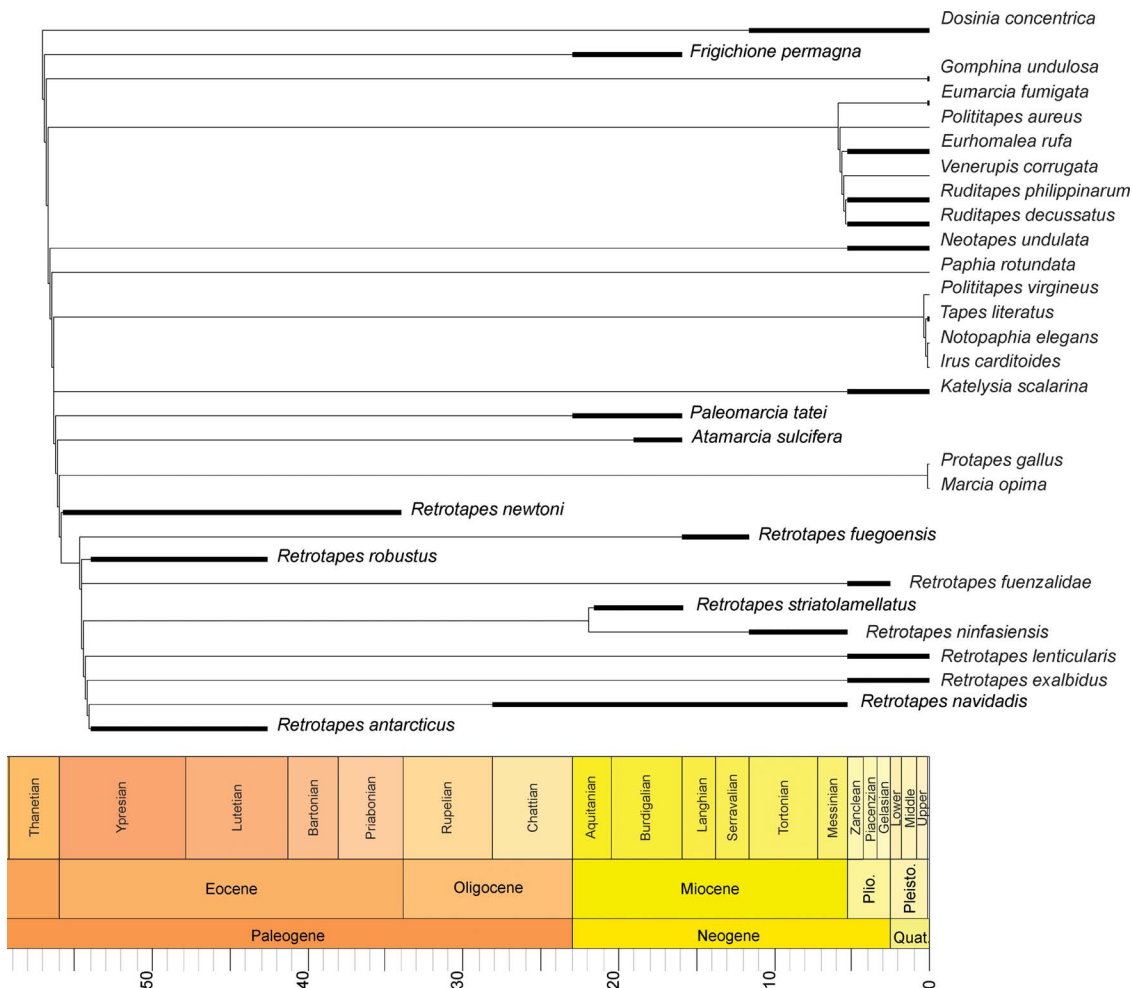

Figure 5. Time calibrated phylogenetic tree performed with the topology recovered at $k = 7$ from the performed analysis with the complete matrix. Quat. = Quaternary, Plio. = Pliocene, Pleisto. = Pleistocene. Age axis in million years.
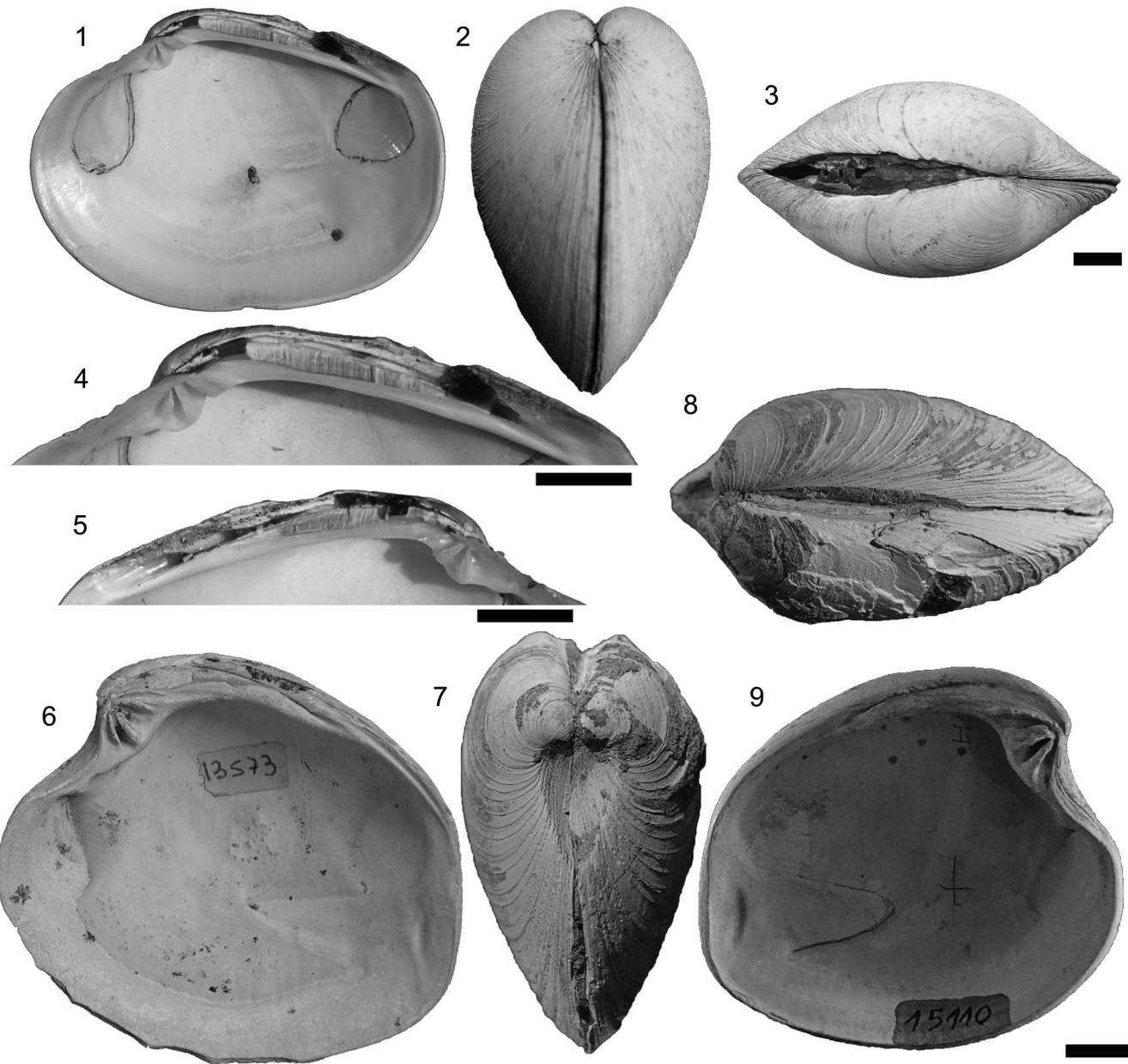
Figure 6. (**1–5**) *Eurhomalea rufa* (Lamarck, 1818): (**1, 4, 5**) MACN-In 37805: right valve interior view, and right and left hinge plate (Caldera, Chile, Recent). (**2, 3**) MACN-In 24780: anterior and dorsal views (Tongoy Bay, Chile, Recent). (**6–9**) *Retrotapes ninfasiensis* del Río, 1997: (**6**) CPBA 13573 (Holotype), a right valve, interior view (Cerro Prismático, Puerto Madryn Formation, Argentina); (**7, 8**) CPBA 15090: anterior and dorsal views (Punta Norte, Puerto Madryn Formation, Argentina); (**9**) CPBA 15110 (Paratype), a left valve, interior view (Fondeadero Ninfas, Puerto Madryn Formation, Argentina). Scale bar (**1–9**) 1 cm.

was erected based on external casts from Pampa Castillo, which have the same proportions, shape, lunule, and sculpture as those of the latter taxon. This assignment is doubtful because the lack of inner characters and because the Guadal Formation is supposed to be of Atlantic origin (Frassinetti and Covacevich, 1999; Encinas et al., 2018), which would indicate a more southern distribution than previously known for the species.

The presence of *Retrotapes navidadis* in the outcrops of Crosslet Island (Frassinetti, 2006) extended its stratigraphic range from the late Oligocene–early Miocene to the middle Miocene–late Miocene.

Retrotapes navidadis differs from the rest of the subquadrate species of the genus (e.g., *R. antarcticus*, *R. andrillorum*, *R. ninfasiensis*, *R. striatolamellatus*, *R. exalbidus*) by its smaller size, thinner shells, and curved 2a tooth. Its subquadrate shape separates it from the subtriangular species (*R. robustus* and *R. difficilis*) and from the sub-rounded *R. lenticularis*.

Retrotapes fuenzalidae (Philippi, 1887)
Figure 7.12–7.14

1887 *Venus fuenzalidae* Philippi, p. 125, pl. 19, fig. 3.
1887 *Venus colchaguensis* Philippi, p. 122, pl. 17, fig. 4.
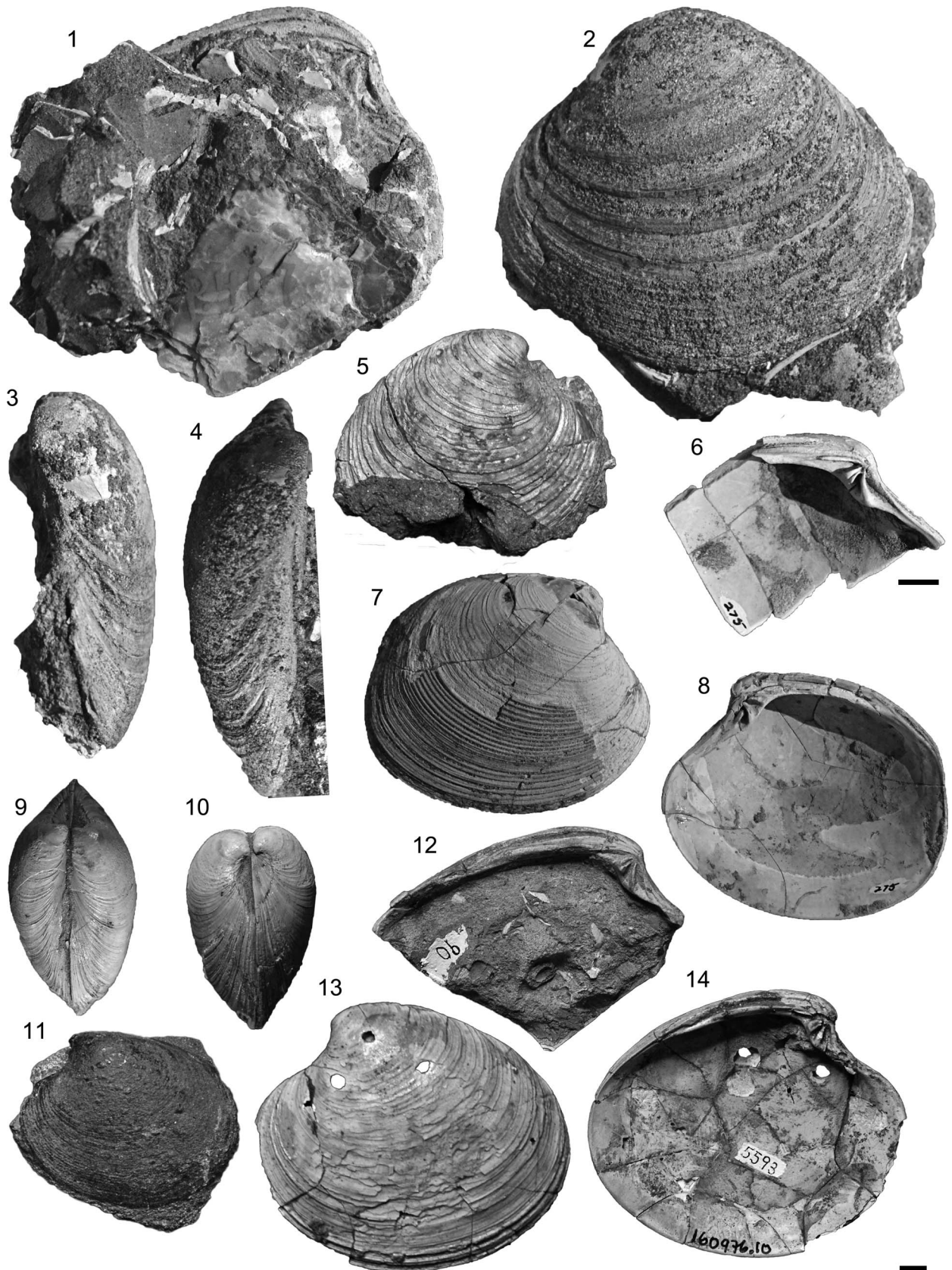
1969 *Eurhomalea fuenzalidai*; Herm, p. 128, pl. 12, figs. 15, 16.
1974 *Eurhomalea colchaguensis*; Frassinetti, p. 47.
2013 *Retrotapes fuenzalidae*; Nielsen, p. 52, pl. 9, figs. a–h.
2014 *Retrotapes fuenzalidae*; Alvarez et al., p. 64.

Syntype.—Fragmented left valve (SGO.PI 90) from La Cueva (La Cueva Formation, Chile) (Philippi, pl. 19, fig. 3; Fig. 7.12).

Emended diagnosis.—Shell medium sized, suboval in shape, thin, laterally compressed.

Occurrence.—Pliocene beds of La Cueva and Estero del Ganso (La Cueva Formation, Chile) and Tubul (Tubul Formation, Chile).

Description.—Shell thin, suboval, medium sized, laterally compressed. Umbo small, placed at anterior 0.25 of length. Dorsal, ventral, anterior, and posterior margins convex. Lunule slightly concave and bounded by a deep groove. Escutcheon wide, wider in the left valve, with comarginal sculpture similar to that of rest of the shell. Nymph short and smooth. Hinge plate wide, curved behind the cardinal teeth, which are not divergent and do not exceed the ventral margin of the hinge plate. Right hinge with tooth 3a lamellar, and sloped backwards; tooth 1 thin, tilted backwards; tooth 3b rectangular, thin, bifid and horizontal; dorsal-posterior region of right valve with a groove for the insertion of left valve. Left hinge with all its cardinal teeth sloped backwards; tooth 2a triangular, straight, thin; tooth 2b thick, triangular, asymmetrically bifid; tooth 4b lamellar, slightly curved, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars isomyarian and shallow; 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. Pallial sinus short, linguiform. Shell sculptured with low comarginal ribs, which are closer to each other towards ventral margin of the disk.

Materials.—Seven specimens, SGO.PI 120 (Holotype, *Venus colchaguensis* Philippi), SGO.PI 4863–4866, 5091, 5593. (Supplementary Data Set 1).

Measurements.—SGO.PI 5593: 69.4 mm length, 28.1 mm height.

Remarks.—This species is assigned to *Retrotapes* because of its wide escutcheon, wider in the left valve, lunule bounded by a deep groove, hinge plate wide, curved behind the teeth, which are tilted backwards.

The suboval shape of *Retrotapes fuenzalidae* distinguishes it subquadrate taxa (e.g., *R. antarcticus* and *R. exalbidus*), from the subtriangular taxa (*R. robustus* and *R. difficilis*) and from the sub-rounded *R. lenticularis*. Its shape and the presence of a slightly concave lunule make it very similar to *R. fuegoensis* del Río, 1997 (Carmen Silva Formation, middle Miocene, Tierra del Fuego, Argentina), but its smaller size and 3a tooth strongly sloped backwards allows differentiation from them.

There is some controversy regarding the synonyms of this taxon. Herm (1969) validated the specific epithet *fuenzalidai* and Nielsen (2013) *fuenzalidae*. Here, the proposal of Nielsen (2013) was considered as correct, consequently the valid name of this taxon is *Retrotapes fuenzalidae* (Philippi, 1887).

Retrotapes exalbidus (Dillwyn, 1817)
Figure 8.1–8.5

1795 *Venus exalbida* Chemnitz, p. 225, pl. 202, fig. 1974 [not binomial].
1817 *Venus exalbida* Dillwyn, p. 170.
1842 *Venus hanetiana* d'Orbigny, p. 123, pl. 13, figs. 3–6.
1854 *Venus subalbicans* Hupé, p. 339.
1863 *Venus exalbida*; Reeve, p. 14, pl. 3, fig. 13.
1887 *Venus subalbicans*; Philippi, p. 122.
1887 *Venus araucana* Philippi, p. 117, pl. 17, fig. 6.
1887 *Venus coquimbana* Philippi, p. 125, pl. 19, fig. 2.
1887 *Venus hupeana* Philippi, p. 132, pl. 26, fig. 1.
1902 *Marcia exalbida*; Dall, p. 360.
1907 *Marcia exalbida*; Ihering, p. 297.
1938 *Samarangia exalbida*; Lamy and Fischer-Piette, p. 614.
1944 *Samarangia exalbida*; Carcelles, p. 287, pl. 12, figs. 93, 94.
1954 *Eurhomalea exalbida*; Keen, p. 54.
1957 *Venus araucana*; Tavera and Veyl, p. 170, pl. 4, fig. 13c.
1960 *Eurhomalea exalbida*; Powell, p. 182.
1969 *Eurhomalea coquimbana*; Herm, p. 127, pl. 12, fig. 9 (non figs. 10, 11).
1970 *Samarangia exalbida*; Castellanos, p. 250, pl. 22, figs. 4, 5.
1974 *Eurhomalea araucana*; Frassinetti, p. 47, figs. 1, 2.
1994 *Eurhomalea exalbida*; Ríos, p. 288, pl. 99, fig. 1412.
1995 *Eurhomalea araucana*; Frassinetti and Covacevich, p. 54, text-fig. 3c, pl. 1, fig. 18.
1997 *Eurhomalea araucana*; Frassinetti, p. 74, pl. 2, fig. 6.
1997 *Retrotapes exalbida*; del Río, p. 80, figs. 22–24.
2008 *Retrotapes exalbidus*; Griffin and Nielsen, p. 257, pl. 1, figs. 2–4, pl. 16, figs. 1–3.
2008 *Retrotapes exalbidus*; Nielsen and Valdovinos, p. 206, fig. 12.
2010 *Eurhomalea exalbida*; Huber, p. 373.
2014 *Retrotapes exalbidus*; Alvarez et al., p. 63. figs. 5.7–5.12.
2015 *Eurhomalea exalbida*; Forcelli and Narosky, p. 160.

←

Figure 7. (**1–4**) *Retrotapes difficilis* (Ortmann, 1902), PRI 72689 (Holotype) left valve, interior, lateral, anterior, and dorsal views (Punta Arenas, Loreto Formation). (**5–11**) *Retrotapes navidadis* (Philippi, 1887): (**5**) SGO.PI 134 (Holotype) right valve, lateral view (Navidad, Navidad Formation); (**6–8**) MACN-Pi 6355, (**6**) left hinge plate, (**7**) right valve, lateral view, (**8**) right valve, interior view (Navidad, Navidad Formation); (**9, 10**) MACN-Pi 6356, articulated specimen: dorsal and anterior views (Navidad, Navidad Formation); (**11**) SGO.PI 4292 (holotype of *Eurhomalea? navidadiformis* Frassinetti and Covacevich, 1999), lateral view (Pampa Castillo, Guadal Formation). (**12–14**) *Retrotapes fuenzalidae* (Philippi, 1887): (**12**) SGO.PI 90 (Paralectotype) left hinge plate (La Cueva, La Cueva Formation); (**13, 14**) SGO.PI 5593, left valve, lateral, and interior views (estero del Ganso, La Cueva Formation). Scale bar (**1–14**) 1 cm.
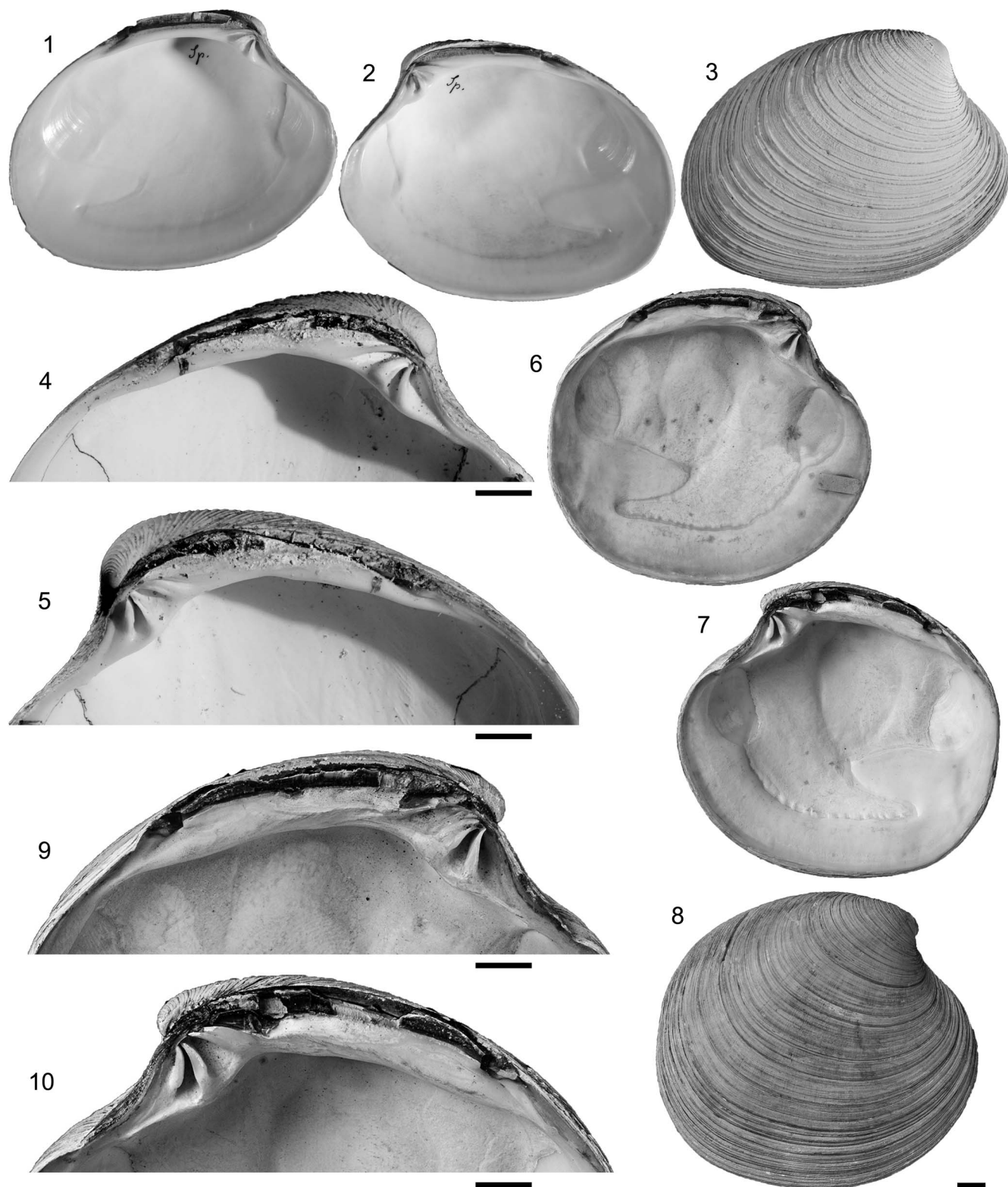
Figure 8. (**1–5**) *Retrotapes exalbidus* (Dillwyn, 1817): (**1–3**) ZMUC-BIV-388 (holotype); (**1**) left valve, interior view; (**2**) right valve, interior view; (**3**) right valve, lateral view (Malvinas Islands, Argentina, Recent). (**4, 5**) MACN-In 21170, left and right hinge plate (San Matías Gulf, Argentina, Recent). (**6–10**) *Retrotapes lenticularis* (Sowerby, 1835), NHMUK 20160316/1-2 (syntype): (**6**) left valve, interior view; (**7**) right valve, interior view; (**8**) right valve, lateral view; (**9, 10**) left and right hinge plate (Valparaiso Bay, Chile, Recent). Scale bar (**1–10**) 1 cm.

Holotype.—*Venus exalbida* Dillwyn (ZMUC-BIV-388) one left and one right valve, from Malvinas Islands (Recent) (Chemnitz, 1795, pl. 202, fig. 1974; Fig. 8.1–8.3).

Diagnosis.—Shell subquadrate, thin; hinge plate thin; lunule bounded by a shallow groove; reduced fold groove in the posterior area of the right valve; pallial sinus triangular, with dorsal margin sub-horizontal to ventrally oriented.

Occurrence.—Pliocene beds of Coquimbo, cerro Las Lomas, and La Cueva (Coquimbo and La Cueva Formation, Chile), and Plio-Pleistocene beds of Tubul Formation. Puerto San Julián (coastal ridges, Pleistocene, Argentina). Puerto Quequén, San Matías Gulf, Ushuaia, Puerto Deseado (Recent, Argentina).

Description.—Shell thin, subquadrate shaped, large sized. Umbo small, placed at anterior 0.25–0.20 of length. Dorsal margin slightly convex, posterior margin truncated, straight to slightly convex, ventral and anterior margins rounded. Lunule concave and bounded by a shallow groove that is deeper through the ventral margin. Escutcheon narrow, wider in the left valve, with comarginal sculpture similar to that of rest of the shell. Nymph short and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are not divergent and do not exceed the ventral margin of the hinge plate. Right hinge with tooth 3a lamellar, sub-vertical; tooth 1 thin, with the same height of tooth 3a, asymmetrically bifid with the posterior area larger than anterior, and sloped backwards; tooth 3b rectangular, thin, bifid and sub-horizontal; dorsal-posterior region of right valve with a groove for the insertion of left valve. Left hinge with all its cardinal teeth tilted backwards; tooth 2a triangular, thin, higher than the other teeth; tooth 2b thick, rectangular, asymmetrically bifid with larger posterior area; tooth 4b lamellar, slightly curved or straight, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars isomyarian and 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; 11–13 small pedal elevator muscle scars under the hinge plate. Pallial sinus short, triangular, with dorsal margin straight, horizontal or ventrally oriented, and ventral margin straight or slightly curved, with apex sharpened. Shell sculptured with high comarginal ribs, which are closer to each other towards ventral margin of the disk.

Materials.—Two hundred twenty five specimens, MLP 26523, SGO.PI 122 (Syntype, *Venus araucana* Philippi), 114 and 125 (Syntypes, *Venus araucana* Philippi), 164 (Holotype, *Venus coquimbana* Philippi), 983, 1308–1310, 1317, 5009, 5088–5090, 5160, MACN-Pi 6302–6304, 6320, MACN-In 19822, 21069, 21170 (Supplementary Data Set 1).

Measurements.—Holotype ZMUC-BIV-388: 76.2 mm length, 59.75 mm height.

Remarks.—The synonymy proposed with *Venus subalbicans* Hupé (1854, p. 339) and *Venus araucana* Philippi (1887, p. 117,

pl. 17, fig. 6) by Griffin and Nielsen (2008) and Nielsen and Valdovinos (2008) confirmed the presence of *R. exalbidus* in the Pliocene of the central region of Chile, nearby Concepción, which expanded its geographical and stratigraphical ranges.

Griffin and Nielsen (2008, p. 257, pl. 1, figs. 2–4) also proposed a synonymy with *Venus aerea* Hupé (1854, p. 338), but this taxon has a cancellate sculpture similar to that observed in the subfamily Chioninae (e.g., *Ameghinomya chiloensis* [Philippi, 1887]), which rejects the synonymy with *R. exalbidus*.

The specimens of *Venus coquimbana* Philippi (1887, p. 125, pl. 19, fig. 2), as well as those described by Herm (1969, p. 127, pl. 12, fig. 9), are similar to *R. exalbidus* in shape, pallial sinus, hinge, and sculpture, and therefore *V. coquimbana* is considered here as a junior synonym of *R. exalbidus*. It is important to note that the hinge plates figured by Herm (1969, pl. 12, figs. 10, 11) have divergent teeth and very small and low umbones, which differ from those of *V. coquimbana*, but are very similar to that observed in *Eurhomalea rufa*. The synonymy proposed here extends the range of *R. exalbidus* to the north of Chile during the Pliocene.

D'Orbigny (1842) erected the species *Venus hanetiana* (Coquimbo and Horcón formations, Pliocene, Chile) based on internal casts that were assigned to the genus *Retrotapes* by Griffin and Nielsen (2008). In these casts, two different morphotypes are recognized. One is mediolaterally wide, with well-developed muscle scars, and the other is mediolaterally compressed with shallow muscle scars. These two morphotypes are similar to those observed in *R. exalbidus*, in which flat and globoid morphotypes were also recognized (Alvarez and Pérez, 2016). This evidence, plus the presence of *R. exalbidus* in the same region, allows synonymy of *V. hanetiana* with *R. exalbidus*.

Retrotapes exalbidus differs from the other species of the genus by its thinner shell, shallower medial sulcus of the lunule, and shallower groove of the posterior area of the shell. Its subquadrate shape distinguishes it from the extant subcircular *R. lenticularis*, from suboval fossil taxa (*R. newtoni*, *R. fuegoensis*, *R. fuenzalidae*, and *R. scutatus*), and from subtriangular taxa (*R. difficilis* and *R. robustus*). Among the subquadrate taxa, it is more similar to the Antarctic species *R. andrillorum* Beu and Taviani (McMurdo Sound, Miocene) and *R. antarcticus* (Sharman and Newton, 1894) (La Meseta Formation, Eocene, Marambio Island), even sharing the same intraspecific variation discussed earlier with the latter species.

Retrotapes lenticularis (Sowerby, 1835)
Figure 8.6–8.10

1835 *Venus lenticularis* Sowerby, p. 42.
1887 *Venus buchanani* Philippi, p. 127, pl. 22, fig. 2.
1902 *Samarangia lenticularis*; Dall, p. 361.
1968 *Eurhomalea salinensis* Ramorino, p. 218, pl. 3, fig. 2, pl. 9, figs. 2, 3.
1969 *Eurhomalea lenticularis*; Herm, p. 128, pl. 13, figs. 1–4.
1997 *Retrotapes lenticularis*; del Río, p. 80, figs. 19–21.
2010 *Eurhomalea lenticularis*; Huber, p. 373.
2014 *Retrotapes lenticularis*; Alvarez et al., p. 64.
2014 *Retrotapes salinensis*; Alvarez et al., p. 64.

Syntype.—One right and one left valve (NHMUK 20160316/1-2) from Valparaíso Bay (Recent, Chile) (Fig. 8.6–8.10).

Diagnosis.—Shell thick, subquadrate to subcircular. Sculptured with comarginal ribs similar to other species of the genus, and with very fine radial ribs.

Occurrence.—Pliocene beds of La Cueva (La Cueva Formation, early Pliocene, Chile), Caldera (Bahía Inglesa Formation, late Miocene–late Pliocene, Chile), Guayacán, Tongoy, and Quebrada de Chañaral (Coquimbo Formation, late Miocene–late Pliocene, Chile). Puerto San Antonio and Valparaíso (Recent, Chile).

Description.—Shell thick, subquadrate to subcircular. Umbo small, placed at anterior 0.25 of length. Dorsal margin slightly convex, posterior slightly convex, ventral and anterior margins rounded. Lunule concave and bounded by a shallow groove that is deeper through the ventral margin. Escutcheon narrow, wider in the left valve, with comarginal sculpture similar to that of the rest of the shell. Nymph narrow and smooth. Hinge plate narrow, curved behind the cardinal teeth, which are not divergent and do not exceed the ventral margin of the hinge plate. Right hinge with tooth 3a lamellar, subvertical; tooth 1 thin, triangular, higher than tooth 3a, asymmetrically bifid with the posterior area larger than anterior, and sloped backwards; tooth 3b triangular, thick, bifid, and sub-horizontal; dorsal-posterior region of right valve with a groove for the insertion of left valve. Left hinge with all its cardinal teeth tilted backwards; tooth 2a triangular, thin, higher than the other teeth, and curved forward; tooth 2b thick, triangular, curved, asymmetrically bifid with larger posterior area; tooth 4b lamellar, slightly curved, sub-horizontal, and separated from the nymph by a groove. Adductor muscle scars shallow; 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 13 small pedal elevator muscle scars under the hinge plate. Pallial sinus short, triangular, with dorsal margin straight, ventrally oriented, and ventral margin curved, with apex rounded. Shell sculptured with low comarginal ribs, which are closer to each other towards ventral margin of the disk, and with radial ribs of nanometric thickness.

Materials.—Forty valves, SGO.PI 158 and 166 (Syntypes, *Venus buchanani* Philippi) 1022, 1094, 1115, 1118, 1123, 1144, 1233, 1256–1258, 1272, 1286, MACN-Pi 6358, MACN-In 12175, 12861. Four hinges SGO.PI 5593 (Supplementary Data Set 1).

Measurements.—Syntype NHMUK 20160316/1-2: 77.23 mm length, 71.43 mm height.

Remarks.—The current distribution of this taxon is between 24°S and 33°S on the coast of Chile (Bernard, 1983), but Paredes and Cardoso (2003) published some small valves (7.4 mm length) from Independencia Bay (Perú; 14°S) as *Retrotapes exalbidus*, which were reassigned to *R. lenticularis* by Alvarez et al. (2014), which has expanded to the north the known distribution of this species. The specimens of *Venus buchanani* Philippi, 1887 (Guayacán, Coquimbo Formation) have exactly the same characters as *R. lenticularis* (Sowerby, 1835), and this species is therefore synonymized with it.

Ramorino (1968) erected a new taxon, *Eurhomalea salinensis*, to include some small shells from Valparaíso Bay, Chile. Alvarez et al. (2014) included this species in the genus *Retrotapes* del Río, 1997 based on the characters described and illustrated by Ramorino (1968). A further revision of this species allowed it to be synonymized with *R. lenticularis*. As Ramorino (1968) mentioned, both species have exactly the same cardinal teeth, pallial sinus, and lunule bounded by a deep groove. The principal difference referred by the author to separate them is the larger shells of *R. lenticularis*, which also has a more concave lunule, but these characters probably indicate that *R. salinensis* is based on juvenile specimens of *R. lenticularis*. Similar differences are observed during the ontogeny of other species of *Retrotapes*, such as *R. striatolamellatus*, in which young specimens have a slightly concave lunule and the adults have the most concave lunule of the genus. Another difference is the sculpture of comarginal ribs in *R. lenticularis*, which is smooth in *R. salinensis* sensu Ramorino (1968), but, as the same author illustrated, the comarginal sculpture is clearly visible in it.

In order to have access to some pictures of the holotype of *R. salinensis*, Professor Bernardita Campos Maia from the Malacology Lab of the Valparaíso University where Dr. Ramorino worked was contacted. She sent some photos of specimens of that species from the personal collection of Dr. Ramorino without catalogue number. Moreover, through the contact with Dr. Ramorino himself, she confirmed (B. Campos Maia, personal communication, 2018) that the holotype of *R. salinensis* deposited in the Museum of Montemar, catalogue number 2716, has been lost.

Discussion

It is necessary to start the discussion talking about the phylogenetic position recovered for those taxa that were synonymized with *Retrotapes* by previous authors. As was previously mentioned, Lauriat-Rage et al. (2002) synonymized *Retrotapes* del Río, 1997 with *Frigichione* Fletcher, 1938. In our analysis, the type species *F. permagna* (Tate, 1900) was included, and in all the searches is recovered in a basal position, between the outgroup and *Gomphina undulosa* (Lamarck, 1818). This result coincides with the systematic history of the genus *Frigichione*, which was originally included in Cyclininae Frizzell, 1936, and later recovered as a basal Chioninae in the phylogenetic analysis performed by Harte (1998).

This background and the obtained results lead to rejection of the synonymy with *Retrotapes*, as proposed Alvarez et al. (2014), and that *Frigichione* is not a Tapetinae. This conclusion is reinforced by the position recovered for *G. undulosa*, which is the sister taxon of a clade that includes all the rest of the studied Tapetinae. This result agrees with that obtained by Mikkelsen et al. (2006) and Chen et al. (2011) based on molecular characters, in which *G. undulosa* was recovered as a Pitarinae Stewart, 1930. Thus, neither *F. permagna* nor *G. undulosa* can be considered as Tapetinae.

As was mentioned before, most of the species that are included now within *Retrotapes* were previously included within the genus *Eurhomalea*. In all the performed searches, there is no close relationship between *Retrotapes* and *Eurhomalea*. These results agree with those obtained on the geometric morphometric analysis of Alvarez et al. (2014). The genus *Eurhomalea* is only represented by its type species, *E. rufa*, which is closely related to *Venerupis* and *Ruditapes*.

The genus *Retrotapes* is a monophyletic group, which is closely related to *Atamarcia* Marwick, 1927 (Miocene, New Zealand) and *Paleomarcia* Fletcher, 1938 (Miocene, Kerguelen Island), forming a major clade that also included *Katelysia scalarina* (Recent, South Australia), *Paphia rotundata* (Recent, Indian Ocean), and *Marcia opima* and *Protapes gallus* (Recent, Indo-Pacific Region).

Among the *Retrotapes* species, the suboval Eocene Antarctic *R. newtoni*, the most ancient species of the clade (Alvarez et al., 2014), is recovered basal to the rest of the species, and other suboval and subtriangular species are successive sister taxa to a group of subquadrate-shaped ones (Fig. 5). With high values of *k* (high level of homoplastic characters), this subtriangular- and suboval-shaped species grouped together in a sister clade to the subquadrate taxa. The subquadrate group is divided into two lineages, one comprised of Miocene Patagonian species that includes the type species *R. ninfasiensis* (late Miocene, Chubut Province) and *R. striatolamellatus* (early Miocene, Santa Cruz Province) (Fig. 5), and is characterized by its strongly concave lunule and by having the most sloped backwards tooth 3a of all species. The other lineage includes taxa with slightly concave lunule and tooth 3a vertical or slightly slanted backwards. In this latter group most of the studied Chilean species are recovered, including *R. lenticularis* and *R. exalbidus*, which are closely related to the Miocene Chilean *R. navidadis* and the Eocene Antarctic *R. antarcticus* (Fig. 5). These results contradict the proposal of Huber (2010) in which the mentioned extant taxa are assigned to *Eurhomalea* and the genus *Retrotapes* is considered valid only as a fossil taxon. In addition, the close relationship between *R. exalbidus* and *R. antarcticus* was discussed by Alvarez and Pérez (2016) who studied the similarities between the two morphotypes that these species shared.

Based on its paleontological record, the genus *Retrotapes* possibly has its origin in the Eocene of Antarctica, where it is represented by three species: *R. newtoni*, *R. antarcticus*, and *R. robustus*. This last taxon has many characters (e.g., shape, hinge plate, lunule) in common with the late Eocene Chilean *R. difficilis* (Loreto Formation, Punta Arenas), which is included in the genus in the present contribution and is the most ancient record for the genus in southern South America. From this extreme Austral region, the genus diversified along both the Atlantic and Pacific coasts of the South American Continent. On the Atlantic side, it is represented by *R. navidadis* (late Oligocene–early Miocene, Pampa Castillo), *R. scutatus* and *R. striatolamellatus* (early Miocene, Santa Cruz Province), *R. fuegoensis* (middle Miocene, Tierra del Fuego Province), and *R. ninfasiensis* (late Miocene, Chubut Province). On the Pacific side, it is represented by *R. navidadis* (early Miocene, Navidad), *R. fuenzalidae* (Pliocene, La Cueva, Estero del Ganso and Tubul), and by the two extant taxa. *Retrotapes lenticularis* was present in the Pliocene beds of the La Cueva and Coquimbo formations in central and northern Chile, and today

inhabits the seashore from this zone reaching to southern Perú. In this contribution, new synonyms are assigned to *Retrotapes exalbidus*, extending its previously known Pliocene record from central to northern Chile (Coquimbo, La Cueva, and Tubul formations); this taxon is extinct in these areas today, and its distribution is restricted from Chiloé Island (South of Chile) to Rio Grande do Sul (South of Brazil).

Conclusions

The genus *Retrotapes* del Río, 1997 is a monophyletic group and is not closely related to *Frigichione* Fletcher, 1938 and *Eurhomalea* Cossmann, 1920, which rejects the synonymies proposed by some previous authors. *Retrotapes* is closely related to other Austral taxa, such as *Paleomarcia* Fletcher, 1938 (Kerguelen Island), *Atamarcia* Marwick, 1927 (New Zealand), and *Katelysia* Römer, 1857 (South of Australia).

Retrotapes was represented in Chile by three species: *R. difficilis* (late Eocene), *R. navidadis* (late Oligocene–early Miocene), and *R. fuenzalidae* (Pliocene). At present times, it is represented by two species, *R. exalbidus* (Pliocene–Recent), and *R. lenticularis* (Pliocene–Recent).

The synonymies proposed in the present contribution expand the known geographic distribution of *R. exalbidus* during the Pliocene through the north of Chile. Moreover, the validity of *R. salinensis* (Ramorino, 1968) is rejected by considering it as a juvenile of *R. lenticularis*.

The phylogenetic position here recovered for *R. exalbidus* and *R. lenticularis* confirmed that these two extant taxa belong to *Retrotapes*, as opposed to the assignments and proposals of Huber (2010).

Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.dv15kp5

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