

MORPHOLOGICAL–PHYLOGENETIC ANALYSIS OF THE LATE CENOZOIC CHLAMYDINI VON TEPPNER (BIVALVIA, PECTINIDAE) OF SOUTHERN SOUTH AMERICA

by MARÍA BELÉN SANTELLI , MAXIMILIANO J. ALVAREZ  and CLAUDIA J. DEL RÍO 

División Paleoinvertebrados, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, CONICET, Av. Ángel Gallardo 470 (C1405DJR), Buenos Aires, Argentina; mbsantelli@gmail.com, maxialvarez82@gmail.com, claudiajdelrio@gmail.com

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Abstract: The tribe Chlamydini was highly diversified in the marine Neogene of southern South America, reaching its maximum taxonomic diversity during the Miocene. However, the evolutionary relationships of South American taxa remain uncertain. This is the first phylogenetic analysis based on a large morphological matrix on Pectinidae, which focuses on South American taxa and species related to *Chlamys* s.s. The phylogenetic analysis is based on a matrix composed of 145 shell-characters scored for 48 species, and multiple searches were conducted using equal and implied weighting. Two new monophyletic clades are defined, Multiplicata and Pauciplicata. The first includes *Dietotenhosen*, *Ckaraosippur*, *Zygochlamys*, *Moirechlamys* (South America), the North-West Pacific *Azumapecten*, and the North-East Pacific *Chlamys hastata*. Pauciplicata is represented by *Chokekenia* (Patagonia, Argentina), *Laevichlamys* (tropical Atlantic and Indo-Pacific), *Semipallium* (Indo-Pacific),

Swiftopecten (South America and North Pacific), and *Jorgechlamys* + *Reticulochlamys* (Patagonia, Argentina). All of these genera are monophyletic except for the paraphyletic *Jorgechlamys*. The oldest documented occurrence of the tribe is *Semipallium foulcheri* from the lower Oligocene, a derived taxon that pushes the divergence time of basal genera to the Eocene–Oligocene boundary, generating ghost lineages in all clades, except *Jorgechlamys* + *Reticulochlamys*. Pauciplicata and Multiplicata diverge in the early history of the tribe, at the Eocene–Oligocene boundary. Future analyses are necessary to gain a better understanding of the taxonomic arrangement of this poorly understood tribe. Further insights into the relationships of its deepest nodes may well resolve many ghost lineages.

Key words: Chlamydini, phylogeny, morphological analysis, late Cenozoic, South America.

THE taxonomy of Pectinidae Rafinesque, 1815 is unstable because of a lack of well-defined diagnostic traits (Serb 2016), phenotypic plasticity in response to environmental conditions (Orensanz *et al.* 1991; Waller 1991, Wilbur & Gaffney 1997; Culver *et al.* 2006; del Río *et al.* 2016; Trovante *et al.* 2019) and morphological convergence of shell shape (Stanley 1972; Waller 1991; Alejandrino *et al.* 2011; Serb *et al.* 2011; Sherratt *et al.* 2016; Serb *et al.* 2017). Pectinidae includes in the order of 400 (Brand 2006), 275 (MolluscaBase 2021a) or 250 (Raines & Poppe 2006) recognized extant species, with the subfamily Chlamydinae von Teppner, 1922 and particularly the tribe Chlamydini von Teppner, 1922, taxonomically the largest groups. Chlamydinae has around 98 extant species (MolluscaBase 2021b) from which 75 or 73 belong in Chlamydini (Alejandrino *et al.* 2011; MolluscaBase 2021c; respectively).

The subfamily embraces different morphologies ranging from chlamydoid shells such as those of *Chlamys* Röding, 1798 and *Talochlamys* Iredale, 1929 to the fan-shaped shells of the byssally-attaching, nestling and facultative boring *Pedum* Bruguière, 1792, and the highly variable shell shape of *Crassadoma* Bernard, 1986 that adapts due to its cementing life habit. Until now, the most complete phylogenetic studies of Chlamydinae include 37% and 47% of the extant species (Alejandrino *et al.* 2011; Sherratt *et al.* 2016; respectively), but as the internal phylogenetic relationships of this group are unclear, its evolutionary history is currently poorly understood. The tribe Chlamydini is probably a waste-basket taxon that clusters phylogenetically unrelated lineages, and is therefore probably a non-monophyletic group (Alejandrino *et al.* 2011; Sherratt *et al.* 2016). Moreover, Chlamydinae

is resolved as a paraphyletic group according to Alejandrino *et al.* (2011). The internal relationships of this group therefore need to be reviewed.

Phylogenetic background of pectinids

Previous morphological analyses. In recent decades, the taxonomy and systematics of scallops have been revolutionized by the innovative morphological phylogenetic analyses based on extant and fossil species developed by T. Waller, who proposed a taxonomic scheme that is currently followed by most taxonomists, with few modifications. Based on microsculpture traits and hinge teeth type, Waller (1991, 1993) subdivided pectinids into four subfamilies: Camptonectinae Habe, 1977, Palliolinae Korobkov *in* Eberzin, 1960, Chlamydiae and Pectininae Rafinesque, 1815. Waller (1993) also proposed that Chlamydiae is represented by the tribes Chlamydini, Mimachlamydini Waller, 1993, Aequipectinini Nordsieck, 1969, and Crassadomini Waller, 1993, according to several synapomorphies, but he failed to provide a morphological matrix to support his results. Later, Waller (2006a) published a matrix for the superfamily Pectinoidea Rafinesque, 1815, that includes 14 morphological characters with controversial definitions, one of which refers to the ctenolium (char. 10) as having three states: presence, primary absence, and secondary absence. This contradicts the proposal of de Pinna (1991), who stated that secondary homologies are those that resist phylogenetic analysis; however, Waller (2006a) established his character states before carrying out a phylogenetic analysis and therefore this homology was not properly tested.

Relevant recent molecular analyses. Molecular phylogenetic studies such as those of Puslednik & Serb (2008), Serb *et al.* (2011), Alejandrino *et al.* (2011), Sherratt *et al.* (2016) and Serb *et al.* (2017) were based on a large taxonomic sample of the Pectinidae and adequately proved the monophyly of this family through the addition of many taxa into the outgroup. The first three analyses included 46, 52 and 81 species, respectively, and the studies of Sherratt *et al.* (2016) and Serb *et al.* (2017) considered 143 species. Puslednik & Serb (2008) compared their results with the tribes scheme of Waller (1993); the other analyses did not.

The phylogenetic status and position of the subfamily Chlamydiae remain unclear according to current molecular evidence, which provides contradictory results. As new more comprehensive analyses are performed, with an increasing sampling of taxa, the status of Chlamydiae is continuously changing. Alejandrino *et al.* (2011) suggested that Chlamydiae is a paraphyletic and basal group. In contrast, Sherratt *et al.* (2016) found that

Chlamydiae is a monophyletic lineage well-distinguished from other Pectinidae, and diverging early during the evolutionary history of the group. The monophyly and arrangement of the Chlamydiae tribes have been barely debated in previous works (Puslednik & Serb 2008). The most comprehensive studies on Pectinidae comprise large-scale phylogenies with under-sampled genera and do not discuss the composition of tribes or subfamilies (Alejandrino *et al.* 2011 (81 species); Sherratt *et al.* 2016 (143 species); Serb *et al.* 2017 (143 species)). The phylogenetic status of the tribe Chlamydini is also unresolved. Alejandrino *et al.* (2011) distinguished three clades in the subfamily Chlamydiae that are not directly equivalent to the tribes defined by Waller (1993). Although the traditional taxonomic definitions of Chlamydiae and Chlamydini of Waller (1993) seem to describe paraphyletic groups, the clade containing *Chlamys s.s.* (Chlamydini) is monophyletic, and is the sister group of a lineage constituted by *Azumapecten* Habe, 1977, *Laevichlamys* Waller, 1993 *s.l.* and *Crassadoma*. In contrast, Sherratt *et al.* (2016, fig. S1) found a monophyletic Chlamydiae with four major lineages, including a monophyletic Chlamydini (but differing from that of Waller 1993) and composed of a clade containing *Chlamys* and *Swiftopecten* Hertlein, 1936. The latter clade is related to a group that clusters *Azumapecten*, *Scaeoichlamys* Iredale, 1929, *Crassadoma gigantea* (Gray, 1825), and some *Laevichlamys* (polyphyletic) and could also be considered as Chlamydini (Sherratt *et al.* 2016, fig. S1).

The tribe composition of Chlamydiae as erected by Waller (1991, 1993) was subsequently modified following the results of molecular phylogenies, with the tribe Aequipectinini separated from Chlamydiae and placed within Pectininae (Alejandrino *et al.* 2011; Serb *et al.* 2011; Sherratt *et al.* 2016; Serb *et al.* 2017). This new consensus was accepted by Waller (2006b, 2011). Modern molecular evidence also reveals that the taxonomic arrangement proposed by Waller (1993) needs to be reviewed and it is likely that several undescribed lineages could be recognized in future.

Taxonomic status of the tribe Chlamydini

Dijkstra & Beu (2018) challenged the validity of Chlamydini (and consequently of Chlamydiae) replacing it with Pedini Bronn, 1862, while stating that the correct name for the subfamily should be Pedinae Bronn, 1862. These authors claimed that the name Pedini takes priority based on the Waller's (1993) association of *Pedum* with other Chlamydini, and on the phylogenetic tree obtained by Dufour *et al.* (2006), in which *Pedum* falls into the tribe Chlamydini, being closely related to *Chlamys islandica* (Müller, 1776) (type species of *Chlamys*). However, that

assertion deserves further discussion since other molecular phylogenies do not support it (Alejandrino *et al.* 2011; Sherratt *et al.* 2016).

Initially, Waller (1993) pointed out that *Pedum* probably evolved from *Laevichlamys squamosa* (Gmelin, 1791) and stated that *Pedum* belonged in the tribe Chlamydini. Accordingly, the subfamily name Peduminae Habe, 1977 (emended to Pedinae) would be a junior synonym of Chlamydiae. Subsequently, Matsumoto & Hayami (2000) recovered a similar relationship, with *Pedum* showing a close affinity and basal to *L. squamosa*. Later, Carter *et al.* (2011) considered Pedini to be a distinctive tribe, separated from Chlamydini and containing only *Pedum*.

Comprehensive molecular studies are still insufficient to elucidate the internal relationships of Chlamydini and show *Pedum* separated from *Chlamys* s.s. (Alejandrino *et al.* 2011; Sherratt *et al.* 2016). Alejandrino *et al.* (2011) found *Pedum* to be nested in a clade containing the type species of Mimachlamydini (*Mimachlamys asperrima*), whereas, according to Sherratt *et al.* (2016), Mimachlamydini is basal to *Pedum*. In sum, according to the phylogenetic study of Alejandrino *et al.* (2011), *Pedum* would be included in Mimachlamydini rather than Chlamydini but following Sherratt *et al.* (2016), *Pedum* and *Chlamys* belong in separate and distantly related clades. Therefore, Pedini and Chlamydini cannot be synonymized as proposed by modern molecular phylogenies.

Settling a nomenclatural act based upon a small phylogenetic study is unsuitable, especially when more comprehensive phylogenetic studies are available (Alejandrino *et al.* 2011; Sherratt *et al.* 2016). The phylogenetic analysis presented by Dufour *et al.* (2006) includes five Chlamydiae species that are recovered in a polytomy in which *Pedum* is related to *Chlamys* as well as to *Mimachlamys* Iredale, 1929, a genus belonging in a different tribe. Therefore, the study of Dufour *et al.* (2006) does not solve the relationships among the tribes of Chlamydiae. According to the results achieved by Alejandrino *et al.* (2011), the tribe Chlamydini is unrelated to *Pedum*, whereas according to Sherratt *et al.* (2016), *Chlamys* and *Pedum* belong in clades distantly related but contained in the same lineage. Not only do molecular phylogenies present such conflicting results but most of the systematic and phylogenetic works carried out over almost a century have used Chlamydiae and Chlamydini. We therefore endorse nomenclatural stability (Art. 23.9.3, ICZN 1999).

The tribe Chlamydini in South America

The tribe Chlamydini constitutes one of the most highly diversified groups in Cenozoic strata of southern South America where it is represented by the endemic genera

Moirechlamys Santelli & del Río, 2019a, *Pixiechlamys* Santelli & del Río, 2019a, *Chokekenia* Santelli & del Río, 2019a (Argentina), *Zygochlamys* Ihering, 1907, *Reticulochlamys* del Río, 2004, *Jorgechlamys* del Río 2004, *Ckaraosippur* Santelli & del Río, 2019b (Chile and Argentina) and *Dietotenhosen* Santelli & del Río, 2019b (Chile, Argentina, and Peru). Another member of this group is the genus *Swiftopecten* from Asian and North American coasts of the North Pacific (Yoshimura 2017), which has also been found in Miocene strata of Argentina (del Río 1995, 2004; Santelli & del Río 2019a, b) and Chile (MBS, pers. obs. 2015).

According to Santelli & del Río (2019a, b) this tribe occurred from the late Oligocene to the early middle Pliocene or early Pleistocene, when it became extinct in the southern South American region. This statement was based on the assumption that the Recent *Psychrochlamys patagonica* (King, 1832) (= *Ps. amandi* (Hertlein, 1935) = *Zygochlamys phalara* (Roth, 1975); synonymized by Jonkers 2003) and *Ps. delicatula* (Hutton, 1873) do not belong to the chlamydini genus *Zygochlamys* (Santelli & del Río 2019a, p. 137) as believed by Beu (1995), who had previously proposed that *Ps. patagonica* evolved from *Zygochlamys geminata* Tavera Jerez, 1979 (non *Z. geminata* (G. B. Sowerby I, 1846); Beu 1985). That proposal was strengthened by the results of the two most comprehensive phylogenetic studies based on molecular data sets, Alejandrino *et al.* (2011) and Sherratt *et al.* (2016), which found that *Psychrochlamys* Jonkers, 2003 is clearly unrelated to Chlamydini. In the first work, *Psychrochlamys* is unrelated to Chlamydiae, whereas according to Sherratt *et al.* (2016), the clade containing *Ps. patagonica* and *Ps. delicatula* is the sister group or even a member of this subfamily, although certainly not a member of Chlamydini. Therefore, the evolutionary relationships of this genus still remain unknown. As already discussed by Santelli & del Río (2019a), *Psychrochlamys* is a non-Chlamydini genus because of the presence of orbicular shells with a wide umbonal angle, very short and symmetrical auricles, having a very shallow byssal notch, minute and few ctenolium teeth, and lacking the byssal sinus. Other distinguishing traits are the absence of shagreen microsculpture, typical of Chlamydini, and the presence of coarse commarginal lamellae on the entire disc, which are thinner and developed as patches in Chlamydini (Santelli & del Río 2019a).

The main goal of this contribution is to establish phylogenetic hypotheses for the Cenozoic and extant species of Argentina, Chile and Peru, which have historically been referred to the tribe Chlamydini (Beu 1985; Morra 1985; Waller 1991; del Río 1992; Beu 1995; Jonkers 2003; del Río 2004, Santelli & del Río 2019a, b). Moreover, we aim to test whether the genera recently described by Santelli & del Río (2019a, b) are

monophyletic or not, and to explore their relationships with the Recent *Psychrochlamys*, and analyse its placement within Chlamydini. Based on current phylogenetic evidence, Chlamydini (*sensu* Waller 1993) seems to be a waste-basket taxon. Our phylogenetic analysis is taxonomically restricted to those Chlamydini genera that have been closely related to *Chlamys s.s.* (the eponymous taxon of Chlamydini) according to morphological and molecular evidence, such as *Swiftopecten* and *Azumapecten*. Also, this analysis includes South American taxa which have been recently revised or identified. It is performed avoiding the inclusion of taxonomically uncertain species or those that are morphologically dissimilar to *Chlamys*, in order to recognize the hypothetical relationships among true Chlamydini and southern South American groups. Other taxa traditionally mentioned as Chlamydini from the Indo-Pacific and South Pacific oceans, and the Caribbean Sea (*Semipallium* Jousseume *in* Lamy, 1928, *Laevichlamys* and *Talochlamys*) are also considered in this study to test their affinities with southern American taxa.

Because large morphological matrices on pectinids have never been published, a secondary goal of this contribution is to provide a morphological matrix with broad sampling for use in future phylogenetic analyses of this group.

MATERIAL AND METHOD

The present contribution is focused on 17 species of Chlamydini from the late Cenozoic of Argentina, Chile and Peru, and the analysis comprises 48 species of pectinids in total. Two South American species of *Psychrochlamys* are also included. Most of those taxa were studied from specimens in hand and some using high-quality images following comparisons with detailed systematic descriptions.

Institutional abbreviations. The studied material is listed in the Santelli *et al.* (2021, appendix S1) and is housed at the following repositories: AMS, Australian Museum, Sydney, Australia; BAS (ROW.BAS), British Antarctic Survey, Cambridge, UK; CPBA, Cátedra de Paleontología of the Universidad de Buenos Aires, Buenos Aires City, Argentina; EASPU (Ortmann collection, see del Río 2004), Purdue University, West Lafayette, Indiana, USA; GNS (GNS WM, GNS TM), Institute of Geological & Nuclear Science, Lower Hutt, New Zealand; MACN-In, División Invertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires City, Argentina; MACN-Pi and CIRGEO-PI, División Paleoinvertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires City, Argentina; MGGC, Giovanni Capellini Geological Museum, Bologna, Italy; MLP, Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata, Buenos Aires Province, Argentina; MNHN (MNHN IM, MNHN.F.), Muséum national

d'Histoire naturelle, Paris, France; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; NHMUK (NHM, NHML), Natural History Museum, London, UK; NMR, Natural History Museum of Rotterdam, Rotterdam, The Netherlands; NMV, Museum Victoria, Melbourne, Australia; PMBP 2004, 2004 Panglao Marine Biodiversity Project (PMBP) to Panglao, Philippines (see Dijkstra 2013); PRI, Cenozoic Marine Mollusks, Paleontological Research Institution, Ithaca, New York, USA; RMNH.MOL, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; SAM (F), South Australian Museum, Adelaide, Australia; SGO.PI, Colección Paleoinvertebrados, Museo de Historia Natural, Santiago, Chile; SNSB-BSPG, fossile Wirbellose collection, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; UNISTRA, Collection de Paléontologie, Université de Strasbourg, France; USNM MO, Mollusk Collection, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; WAM, Western Australian Museum, Perth, Australia; ZMA.MOLL, Zoologisch Museum Amsterdam, The Netherlands.

Phylogenetic analysis

Definition and character sampling. General morphological traits of pectinids are summarized in Fig. 1. Terminology follows Waller (1991, 1993). The matrix comprises 146 morphological characters corresponding to 132 discrete and 14 continuous traits of the external and internal shell morphology (Santelli *et al.* 2021, appendix S2, S3).

Discrete characters (chars 14–145) are grouped into categories according to the shell structure or trait: general shell-outline and shell shape (chars 14–32), shell convexity (chars 33–36), byssal notch (chars 37–39), ctenolium (chars 40–41), auricular denticles (chars 42–43), auricles shape (chars 44–57), sculpture on auricles (chars 58–65), microsculpture on auricles (chars 66–72), microsculpture on disc (chars 73–90), growth lines (chars 91–92), radial plicae (chars 93–109), radial ribs (chars 110–123), interspaces (chars 124–127), hinge (chars 128–132), internal sculpture (chars 133–134), scales (chars 135–142), growth ledges (chars 143–144) and nodes (char. 145) (Santelli *et al.* 2021, appendix S3). Microsculpture and macrosulpture features on pectinids have traditionally been considered to be useful tools in systematic and phylogenetic studies (Waller 1991, 1993, 2006a, 2011), and herein correspond to 51% of the discrete characters. Some of these characters or related structures are shown in detail in Fig. 2, including linear measurements and angles of morphological features used to define continuous characters.

The continuous characters refer to values of average shell height, umbonal angle, number of radial ribs on left and right auricles (ranges), number of plicae on each valve (ranges), number of ctenolium teeth (ranges), and ratios as hinge length/shell length (Santelli *et al.* 2021,

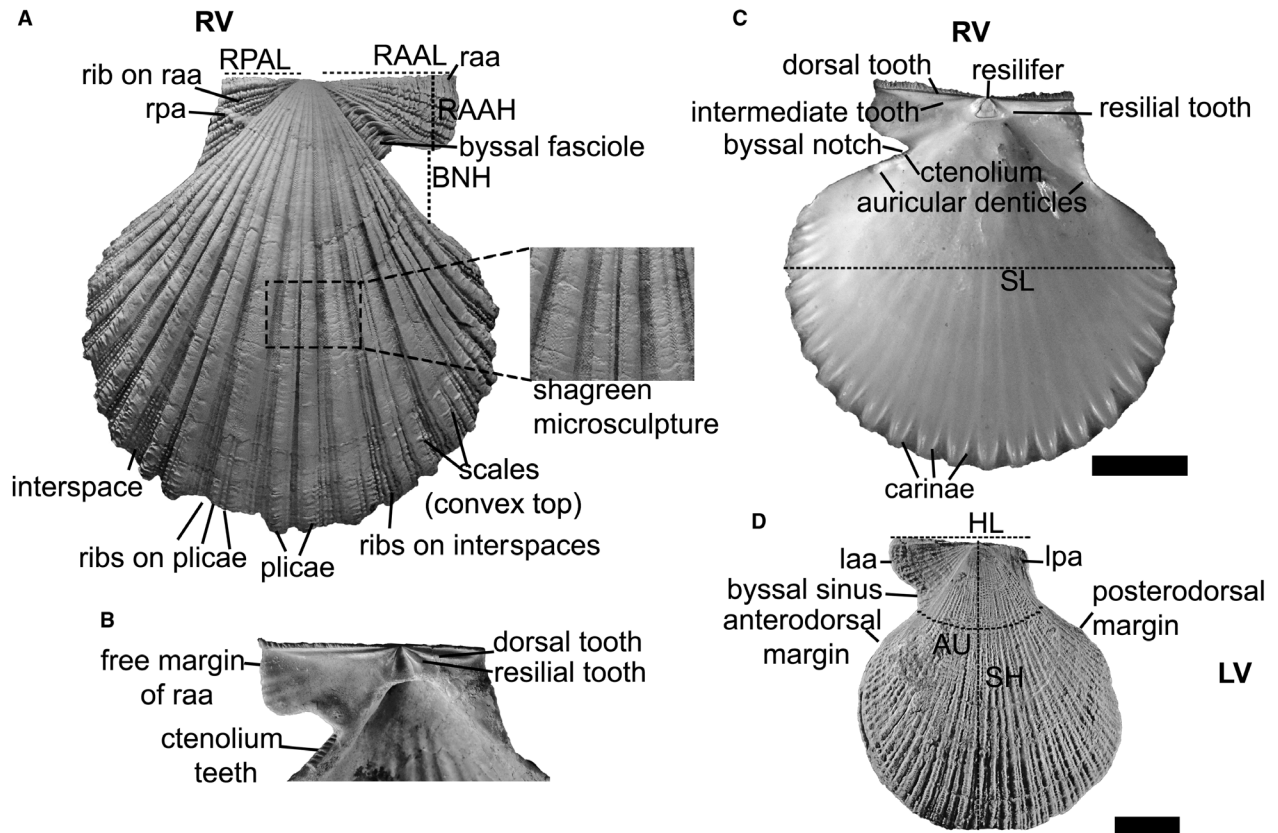


FIG. 1. General traits of pectinid shell. A–B, *Zygochlamys geminata* (G. B. Sowerby I, 1846), MACN-Pi 5813; right valve: A, external view; B, hinge and teeth. C, *Aequipecten opercularis* (Linnaeus, 1758), MACN-In 29083; left valve, internal. D, *Pixiechlamys quemadensis* (Ihering, 1897) MACN-Pi 6403; left valve, external. *Abbreviations:* AU, umbonal angle; BNH, byssal notch height; HL, hinge length; laa, left anterior auricle; lpa, left posterior auricle; LV, left valve; raa, right anterior auricle; RAAH, raa height; RAAL, right anterior auricle length; rpa, right posterior auricle; RPAL, right posterior auricle length; RV, right valve; SH, shell height; SL, shell length. Scale bars represent 10 mm.

appendix S2). Ratios of continuous characters were logarithmized following Mongiardino Koch *et al.* (2015).

Included taxa. Taxon sampling of Chlamydiae was designed considering the phylogenetic results of Waller (1991, 1993) and Alejandrino *et al.* (2011), and taxa of each tribe ever placed in Chlamydiae have been incorporated into the study.

The phylogenetic analysis was performed using 48 species-level terminals, including the type genera of the tribes and their type-species along with co-generic species. The outgroup consists of 17 species, including representatives of the tribes: Pectinini Rafinesque, 1815 (subfamily Pectiniinae) (*Pecten maximus* (Linnaeus, 1758), *P. jacobaeus* (Linnaeus, 1758)); Amusiini Ridewood, 1903 (subfamily Pectiniinae) (*Euvola ziczac* (Linnaeus, 1758), *Leopecten oblongus* (Philippi, 1893), *Leopecten pyramidesius* (Ihering, 1907)); Aequipectinini (subfamily Pectiniinae) (*Aequipecten opercularis* (Linnaeus, 1758), *A. tehuelchus* (d'Orbigny, 1842), *A. paranensis* (d'Orbigny, 1842)); Adamussiini

Habe, 1977 (subfamily Pallioliinae) (*Adamussium colbecki* (Smith, 1902)); Crassadomini (subfamily Chlamydiae) (*Caribachlamys sentis* (Reeve, 1853)); Mimachlamyidini (subfamily Chlamydiae) (*Mimachlamys asperrima* (Lamarck, 1819), *M. crassicostata* (G. B. Sowerby II, 1842), *M. varia* (Linnaeus, 1758)); and Fortipectinini Masuda, 1963 (subfamily Chlamydiae) (*Mizuhopecten yessoensis* (Jay, 1857)). The outgroup also includes *Psychrochlamys patagonica*, *Ps. delicatula* and *Ps. moerickei* (Hertlein, 1936) (subfamily Chlamydiae), species historically related to the extinct Chlamyidini from southern South America. Members of the studied genera are illustrated in Figures 2–4. It is commonly accepted that representatives of Chlamydiae are closely related to the tribe Chlamyidini; therefore, they are the most useful taxa to establish the relationships within the ingroup. The root was fixed on *P. maximus*.

The ingroup comprises 31 species traditionally assigned to Chlamyidini (Santelli *et al.* 2021, appendix S1), including all late Cenozoic Argentinean and south-eastern Pacific Ocean taxa. This temporal and geographical category

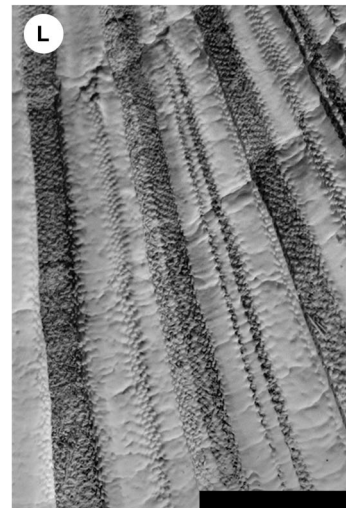
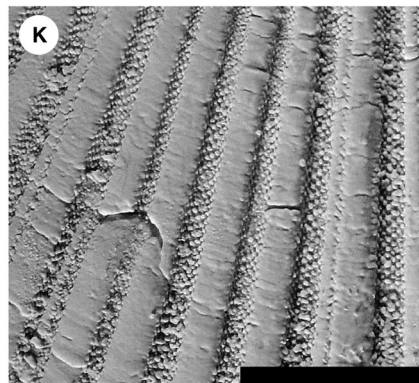
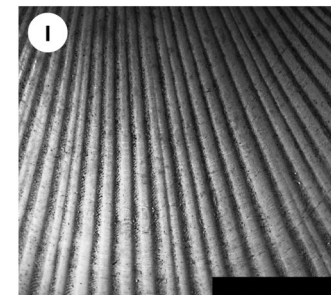
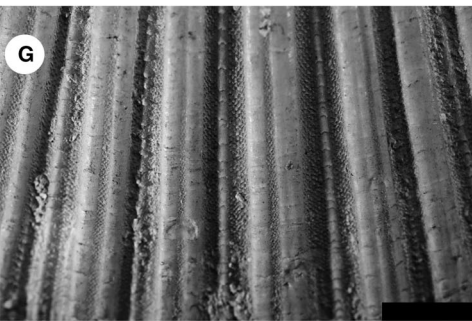
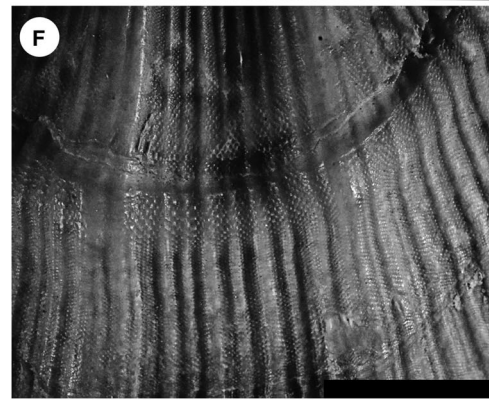
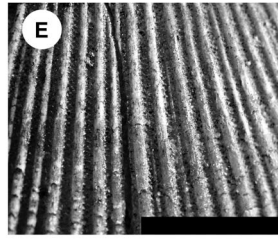
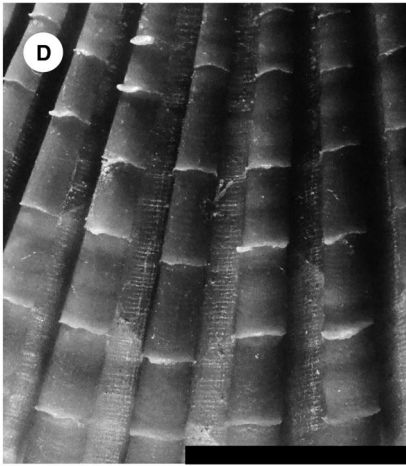
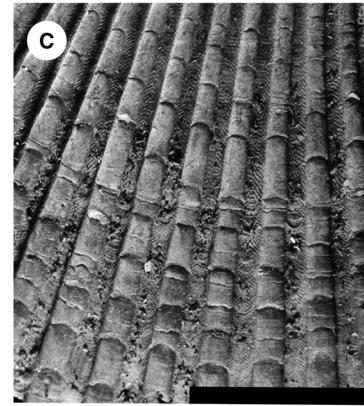
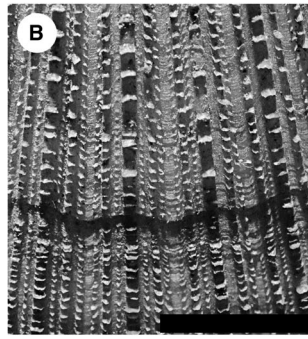
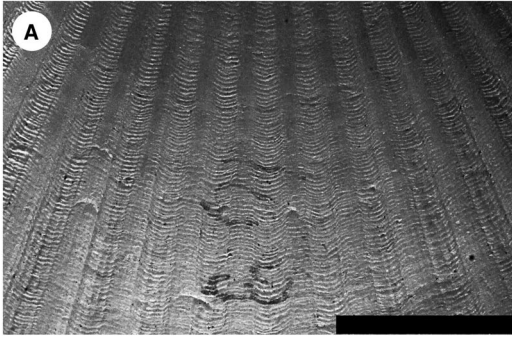


FIG. 2. Details of disc macrosculpture and microsculpture. A, commarginal microsculpture with waved lamellae on *Aequipecten opercularis* (Linnaeus, 1758), MACN-In 29083; left valve, external. B, commarginal and antimarginal ridgelets, scales with convex top surface and secondary ribs formed alongside each primary rib or plica; *Mimachlamys asperrima* (Lamarck, 1819), MNRJ 4768; right valve, external. C, herringbone (divaricating) microsculpture on *Mimachlamys varia* (Linnaeus, 1758), MACN-Pi 7098; right valve, external. D, reticulate pattern and bi-lobed scales on *Mimachlamys crassicostata* (G. B. Sowerby II, 1842), MACN-In 28824; right valve, external. E, shagreen microsculpture on the left valve of *Ckaraosippur calderensis* (Möricke, 1896), SGO.PI 4815e. F, shagreen microsculpture, nodes and growth ledges on *Swiftopecten swiftii* (Bernardi, 1858), MACN-In 8215. G, shagreen microsculpture on grooved plicae and interspaces on the right valve of *Dietotenhosen hupeanus* (Philippi, 1887), SGO.PI 656a. H, shagreen and antimarginal microsculpture on the left valve of *Azumapecten farreri* (Jones & Preston, 1904), syntype provided by V. Héros, MNHN-IM-2000-24314. I, shagreen microsculpture and bifurcation of radial primary ribs on *Chlamys rubida* (Hinds, 1845), MACN-In 2371; right valve, external. J, shagreen microsculpture on early radial stage and umbonal area on the left valve of *Chokekenia nicolasi* (Morra, 1985), MACN-Pi 6407. K, shagreen microsculpture on the right valve of *Moirechlamys actinodes* (G. B. Sowerby I, 1846), MACN-Pi 4796a. L, shagreen microsculpture on the right valve of *Zygochlamys geminata* (G. B. Sowerby I, 1846), MACN-Pi 5813. Scale bars represent 4 mm.

included: *Zygochlamys geminata* (G. B. Sowerby I, 1846) (type species), *Z. jorgensis* Ihering, 1907, *Z. sebastiani* Morra, 1985; *Pixiechlamys quemadensis* (Ihering, 1897); *Chokekenia nicolasi* (Morra, 1985); *Moirechlamys actinodes* (G. B. Sowerby I, 1846) (type species), *M. aurorae* (Ferguson, 1954); *Dietotenhosen hupeanus* (Philippi, 1887) (type species), *D. remondi* (Philippi, 1887); *Ckaraosippur calderensis* (Möricke, 1896) (type species), *C. camachoi* Santelli & del Río 2019b; *Jorgechlamys juliana* (Ihering, 1907) (type species), *J. centralis* (G. B. Sowerby I, 1846); *Reticulochlamys proximus* (Ihering, 1907) (type species), *R. borjasensis* del Río, 2004, *R. zinsmeisteri* del Río, 2004, and *Swiftopecten iheringii* del Río, 1995. The north-eastern Pacific type species of *Swiftopecten* (*S. swiftii* (Bernardi, 1858)) was also included as well as three representatives of *Chlamys* s.s.: *Ch. islandica* (type species), *Ch. rubida* (Hinds, 1845) and *Ch. hastata* (G. B. Sowerby II, 1842). The ingroup also contains some Australian and New Zealand taxa: *Semipallium flavicans* (Linnaeus, 1758) (type species), *Se. hallae* (Cotton, 1960), *Se. foulcheri* (Tenison-Woods, 1865), *Talochlamys pulleineana* (Tate, 1887) (type species), *T. dichroa* (Suter, 1909), *T. badioriva* Beu & Darragh, 2001, and *T. laticostata* Beu & Darragh, 2001. Finally, this group also comprises the north-western Pacific species *Azumapecten farreri* (Jones & Preston, 1904) (type species) and two species of *Laevichlamys*, the Caribbean *L. multisquamata* (Dunker, 1864) (type species), and the Indo-Pacific *L. squamosa*. *Talochlamys* is here considered to be part of the ingroup because taxonomists have traditionally referred it to Chlamydini and molecular phylogenetic studies have suggested incongruent relationships (Alejandrino *et al.* 2011; Sherratt *et al.* 2016). Alejandrino *et al.* (2011) showed that *Talochlamys* is unrelated to the clade *Chlamys* s.s., while Sherratt *et al.* (2016) suggested that *Talochlamys* is polyphyletic and that one of its clades with several *Talochlamys* spp. is the sister group of *Chlamys* s.s. The taxonomic composition and affinities of *Talochlamys* are poorly understood because *T. pulleineana* (its type species) was omitted by the two

mentioned studies. All genera studied herein are illustrated in Figures 2, 4–5, except for *Laevichlamys*.

Matrix scoring. The matrix (Santelli *et al.* 2021, appendix S4) was scored in Winclada 1.61, the character states were recorded as polymorphic when different states of a single character are present in different specimens of a single taxon, using the notation: (state A, state B, state C). Unknown characters states were scored as missing data (?), such as those of the unknown right valve of *Ckaraosippur camachoi*, and microsculpture characters of pre-radial and early radial stages of most fossil taxa in which the umbonal area is frequently broken or abraded. Microsculpture traits on auricles of *T. pulleineana* (studied using Beu & Darragh 2001, fig. 29) were also scored as unknown. Inapplicable characters states are those that correspond to subsidiary characters of some structures absent in some taxa, such as the byssal notch, ctenolium, ribs on right posterior auricles, shagreen and commarginal microsculpture, plicae, radial ribs, bifurcation of radial ribs or plicae, and ribs and scales on plicae and they were scored with a hyphen (-). Few characters correspond to juvenile stages, and most of them were defined on well-preserved adult shells.

Phylogenetic searches, branch supports, and tree calibration. The software TNT v1.5 (Goloboff & Catalano 2016) was used to conduct heuristic tree searches because the high number of herein included taxa. Space was configured for 20 000 trees in memory and the searches were conducted applying maximum parsimony criterion, starting from 100 replicates of Wagner trees with random addition sequence (RAS) of taxa, which is followed by the Tree Bisection and Reconnection (TBR) branch-swapping algorithm saving 10 trees per replication. To minimize the effect of the homoplasy, characters were weighted (as suggested by Goloboff *et al.* 2003; Goloboff *et al.* 2008), which allows obtaining more reliable and stable results when a complex matrix that includes a high number of homoplastic characters is analysed.

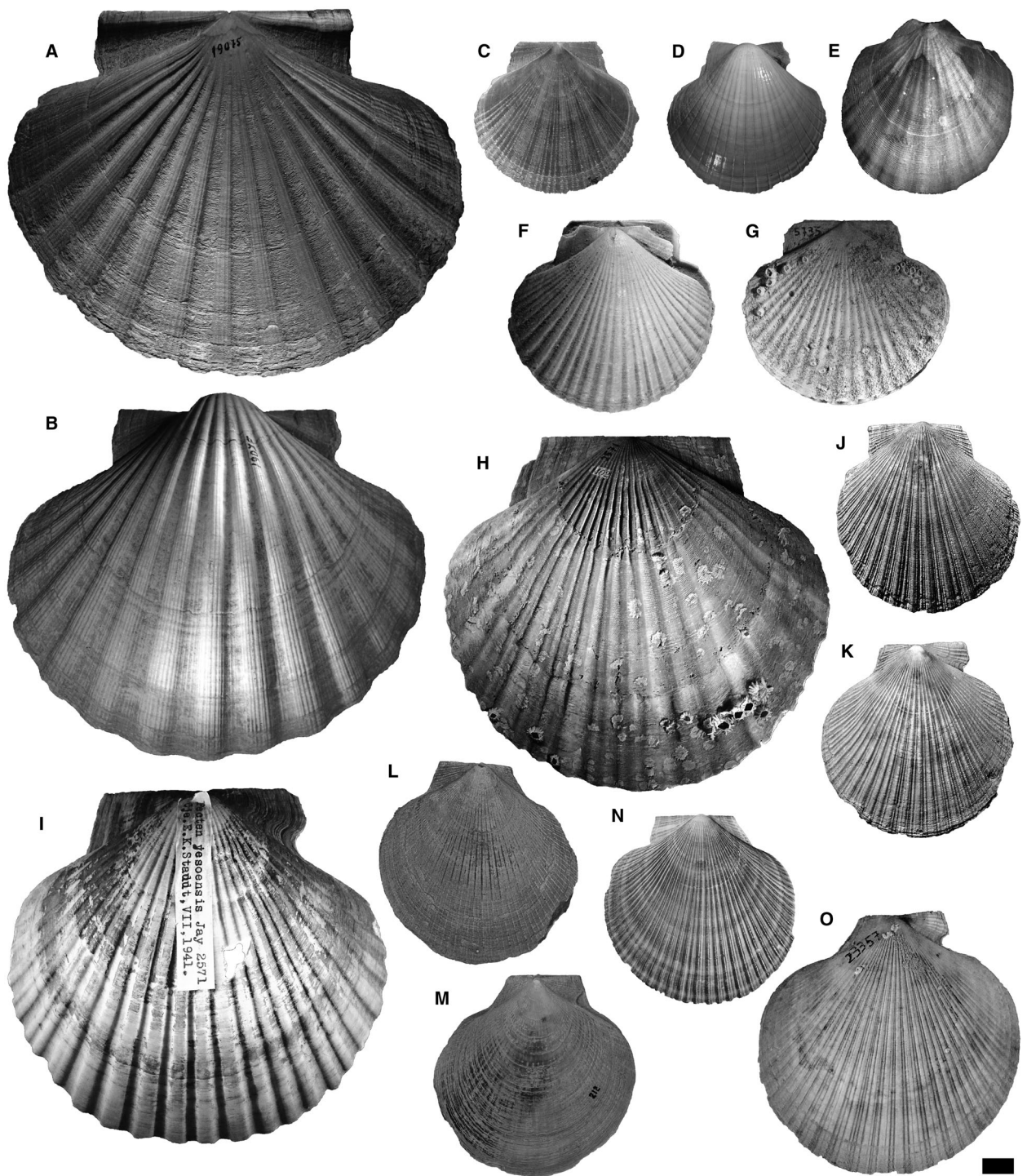


FIG. 3. Outgroup species. A–B, *Pecten maximus* (Linnaeus, 1758), MACN-In 19075: A, left valve, external; B, right valve, external. C–D, *Euvola ziczac* (Linnaeus, 1758), MACN-In 29684: C, left valve, external; D, right valve, external. E, *Adamussium colbecki* (Smith, 1902), MACN-In 17875, left valve, external. F–G, *Leopecten pyramidesius* (Ihering, 1907), MACN-Pi 5735: F, right valve, external; G, left valve, external. H–I, *Mizuhopecten yessoensis* (Jay, 1857), MACN-In 2571: H, left valve, external; I, right valve, external. J–K, *Psychrochlamys delicatula* (Hutton, 1873), hypotypes provided by M. Tereзов: J, GNS TM 2837, left valve, external; K, GNS TM 2836, right valve, external. L–M, *Psychrochlamys moerickei* (Hertlein, 1936), SGO.PI 212: L, left valve, external; M, right valve, external. N–O, *Psychrochlamys patagonica* (King, 1832): N, lectotype NHMUK 1980037, left valve, external; K, MACN-In 23357, right valve, external. Scale bar represents 5 mm.

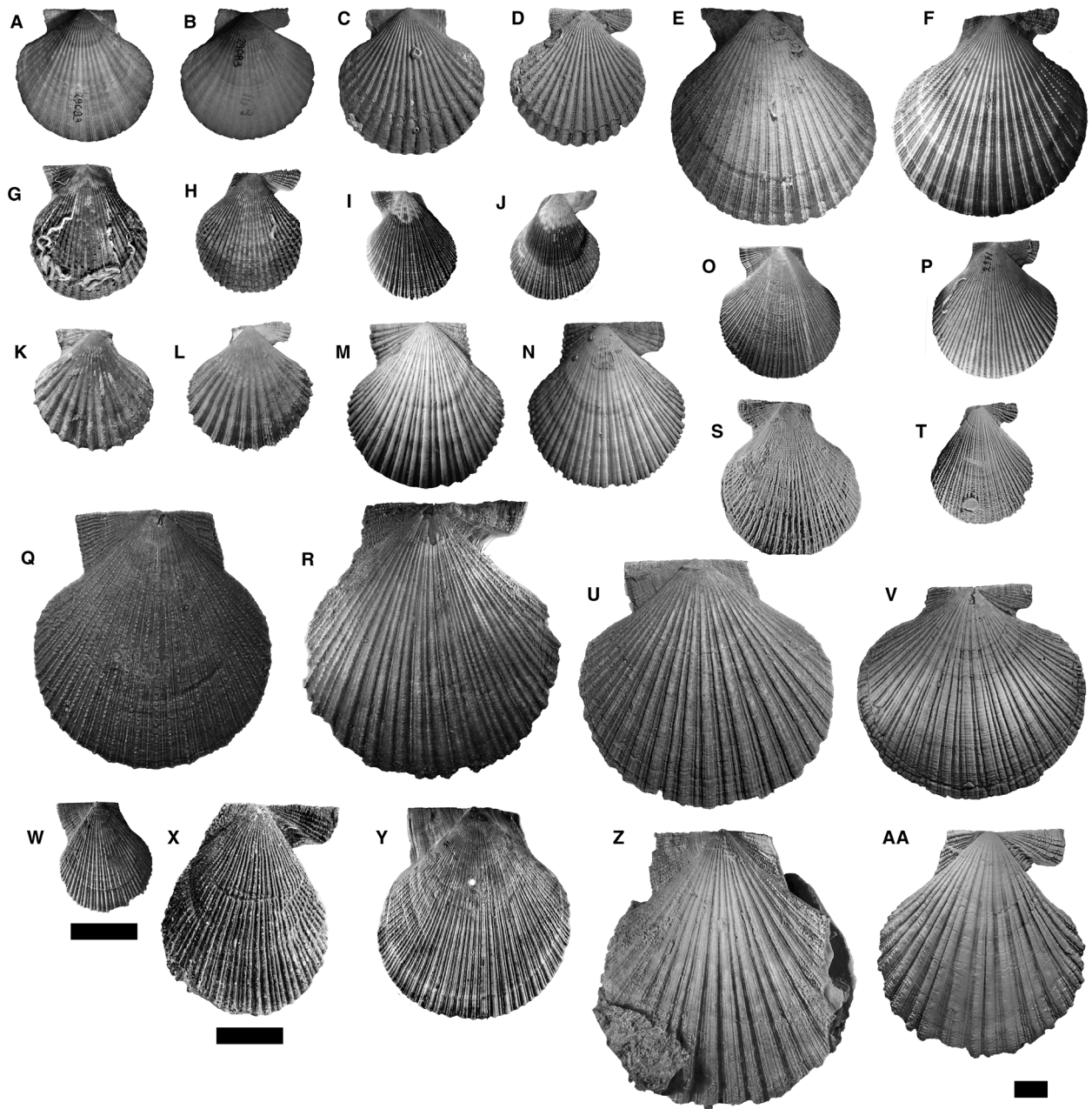


FIG. 4. A–N, outgroup species. A–B, *Aequipecten opercularis* (Linnaeus, 1758), MACN-In 29083: A, left valve, external; B, right valve, external. C–D, *Aequipecten paranensis* (d'Orbigny, 1842), MACN-Pi 5736: C, left valve, external; D, right valve, external. E–F, *Mimachlamys asperrima* (Lamarck, 1819), MNRJ 4768: E, left valve, external; F, right valve, external. G–H, *Mimachlamys varia* (Linnaeus, 1758), MACN-Pi 7098: G, left valve, external; H, right valve, external. I–J, *Caribachlamys sentis* (Reeve, 1853), MNRJ 41537: I, left valve, external; J, right valve, external. K–L, *Talochlamys dichroa* (Suter, 1909), GNS TM 211 provided by M. Terezow: K, left valve, external; L, right valve, external. M–AA, ingroup species. M–N, *Chlamys islandica* (Müller, 1776), MACN-In 29167: M, left valve, external; N, right valve, external. O–P, *Chlamys rubida* (Hinds, 1845), MACN-In 2371: O, left valve, external; P, right valve, external. Q–R, *Dietotenhosen remondi* (Philippi, 1887): Q, SNSB-BSPG 1966 IV 15 provided by W. Werner, left valve, external; R, SGO.PI 1024a, right valve, external. S–T, *Pixiechlamys quemadensis* (Ihering, 1897): S, MACN-Pi 6403, left valve, external; T, holotype MACN-Pi 272, right valve, external. U–V, *Dietotenhosen hupeanus* (Philippi, 1887): U, SGO.PI 5928b, left valve, external; V, SGO.PI 5910, right valve, external. W–X, *Ckaraosippur calderensis* (Mörnicke, 1896): W, SGO.PI 4815b, left valve, external; X, SGO.PI 4815a, right valve, external. Y, *Ckaraosippur camachoi* Santelli & del Río 2019b, holotype CPBA 8604b, left valve, external. Z–AA, *Zygochlamys geminata* (G. B. Sowerby I, 1846): Z, CPBA 21584, left valve, external; AA, MACN-Pi 5813, right valve, external. Scale bar at lower left represents 5 mm for all specimens except W and X (separate bars represent 10 mm).

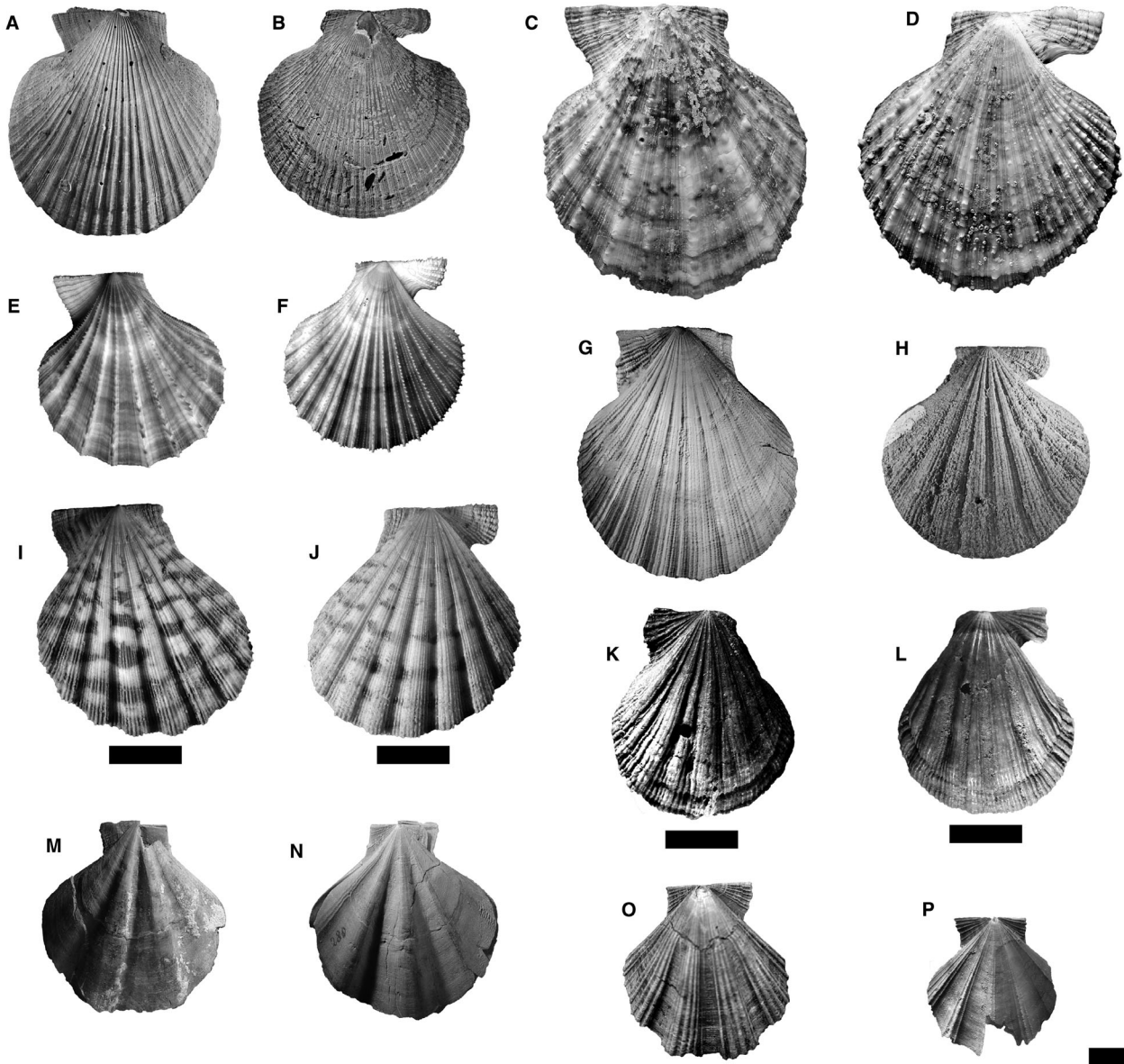


FIG. 5. Ingroup species. A–B, *Moirechlamys actinodes* (G. B. Sowerby I, 1846): A, CPBA 14421, left valve, external; B, CPBA 7832, right valve, external. C–D, *Azumapecten farreri* (Jones & Preston, 1904), syntype NHMUK 1903.12.20.6: C, left valve, external; D, right valve, external. E–F, *Chlamys hastata* (G. B. Sowerby II, 1842), FMNH 183450 provided by Jochen Gerber: E, left valve, external; F, right valve, external. G–H, *Chokekenia nicolasi* (Morra, 1985): G, MACN-Pi 6407, left valve, external; H, holotype CPBA 12465, right valve, external. I–J, *Semipallium flavicans* (Linnaeus, 1758), MACN-In 29154: I, left valve, external; J, right valve, external. K–L, *Swiftopecten iheringii* del Río, 1995, holotype MACN-Pi 252: K, left valve, external; L, right valve, external. M–N, *Jorgechlamys juli-ana* (Ihering, 1907), holotype MACN-Pi 280: M, left valve, external; N, right valve, external. O–P, *Reticulochlamys proximus* (G. B. Sowerby I, 1846): O, CPBA 16.891, right valve, external; P, CPBA 16892, left valve, external. Scale bar at lower left represents 5 mm for all specimens, except I–J and K–L (all 10 mm).

Search strategies involve two weighting arrangements: equal weights and implied weighting (Goloboff 1993), the latter using concavity (k) values from 1 to 100 in increments of 1, and both strategies under traditional searches.

Clades recovered in different search strategies were illustrated using sensitive grids (Wheeler 1995; Pérez 2019). To

measure branch support, the resampling method was used by means of frequency differences (GC), and the Jackknife index (Farris *et al.* 1996) was computed with $p = 0.14$ (equivalent to removing 10% of the characters) (Goloboff *et al.* 2003) for 1000 pseudo-replicates. The consistency (CI) and retention (RI) indices were computed (Farris

1989). Common synapomorphies of the selected topology ($k = 48-68$) are described and listed below in the results section.

Phylogenetic time-scaling

One of the most frequent topologies (implied weighting, $k = 48-68$, recovered for 20 values of concavity) was selected to be temporally calibrated using R (R Core Team 2019). The packages *paleotree* (Bapst 2012), *ape* (Paradis *et al.* 2004; Popescu *et al.* 2012) and *strap* (Bell & Lloyd 2014) were loaded to read the matrix and tree topology, and implement different functions in R. The functions *timePaleoPhy* and *geoscalePhylo* were applied by means of the minimum branch length (mbl) method of calibration with an mbl of 0.1 myr, in which a minimum branch duration is setting *a priori*. The mbl method guarantees preservation of the temporal structure of events (Laurin 2004). The stratigraphic ranges of each analysed taxon are specified in Santelli *et al.* (2021) and were considered to be the lower (FAD, first appearance datum) and upper (LAD, last appearance datum) bounds of the geological stages.

Phylogenetic nomenclature

New phylogenetic definitions are proposed using stem-based definitions according to the principles of phylogenetic nomenclature (de Queiroz & Gauthier 1990, 1992, Sereno 1999). These definitions were based on unambiguous synapomorphies, although supporting ambiguous synapomorphies are also indicated for both clades (see Systematic Palaeontology, below).

RESULTS

The tribe Chlamyidini is the most diverse group of Pectinidae and its evolutionary history is poorly understood; it is therefore likely that some taxa traditionally referred to the tribe are unrelated. However, it must be specified that our results are restricted to the hypothetical relationships among the scallops of southern South America. Two most parsimonious trees (MPTs) were obtained in the search under equal weights with a tree length of 1888 steps (CI = 0.29; RI = 0.65) and their strict consensus is figured in Santelli *et al.* (2021, appendix S6). Searches applying implied weighting showed eight different tree topologies from $k = 1$ to $k = 100$, and these correspond to the following ranges of concavity: $k = 1-2$, $k = 3-4$, $k = 5-7$, $k = 8-23$, $k = 24-39$, $k = 40-47$, $k = 48-68$, $k = 69-100$. The two more frequent topologies correspond to a k

value of 48–68 (Fig. 6), with a fit of 14.58877 (CI = 0.27; RI = 0.61) and $k = 69-100$ (Santelli *et al.* 2021, appendix S6) with a fit of 45.54514 (CI = 0.27; RI = 0.60). We illustrate and shall discuss in detail the first topology because it also has the highest support values for all clades under study. The relationships obtained under the $k = 48-68$ weighting scheme are contrasted with those of other topologies under different concavity (k) values; their main differences are described in this section and examined further in the Discussion, below. Jackknife supports are shown for the topology under $k = 40-48$ (Fig. 6). Figure 6 corresponds to the sole topology obtained under $k = 48-68$, and shows sensitive grids outlined on the nodes of each clade of interest, representing whether that clade is recovered or unrecovered for each of the strategy of search implemented (equal or implied weighting) and for each k value (Fig. 6). Alternative tree topologies and Jackknife supports are detailed in Santelli *et al.* (2021, appendix S6).

The ingroup is represented by Chlamyidini taxa (*Chlamys*, *Semipallium*, *Azumapecten*, *Laevichlamys*, *Zygochlamys*, *Reticulochlamys*, *Swiftopecten*, among others) and is recovered as a monophyletic group in all trees (Fig. 6; Santelli *et al.* 2021, appendix S6). *Talochlamys* is found outside Chlamyidini except in the search under equal weights, where *Mimachlamys* and *Caribachlamys* Waller, 1993 (members of other tribes) are also recovered within Chlamyidini. The sister clade of the ingroup changes through different values of k under implied weighting (see Santelli *et al.* 2021, appendix S6).

The most remarkable result is that South American Chlamyidini are separated into two major clades under $k = 1-7$ and $k = 24-100$ (Fig. 6), which are herein named as Multiplicata and Pauciplicata. The definition of both suprageneric clades follows the proposal of de Queiroz (1994), Sereno (2005), and Maxwell *et al.* (2020), and these clades can be distinguished by substantial morphological differences. The name Multiplicata refers to the presence of shells with numerous plicae, with 11–36 narrow plicae and sculptured with scaly ribs. This group includes *Dietotenhosen* (Chile–Peru, Miocene–Pleistocene), *Ckaraosippur* (Chile–Argentina, middle Miocene – Pliocene), *Zygochlamys* (Chile–Argentina, late Oligocene – middle Miocene) and *Moirechlamys* (Argentina, late Miocene – early Pliocene), *Azumapecten* (Pleistocene–Recent, Japanese and East China seas), and *Chlamys hastata* (late Pliocene – Recent, north-east Pacific 60°N–32°N, and the north-west Pacific, Kamchatka). The Pauciplicata clade is characterized by taxa sculptured with four to nine wide plicae that bear scaly or non-scaly ribs. This group is represented by *Chokekenia* (early Miocene, Argentina), *Laevichlamys* (Recent, North and tropical Atlantic Ocean and Indo-Pacific Ocean), *Semipallium* (Eocene–Recent, Indo-West Pacific), *Swiftopecten* (Miocene–Recent, southern South America and North Pacific),

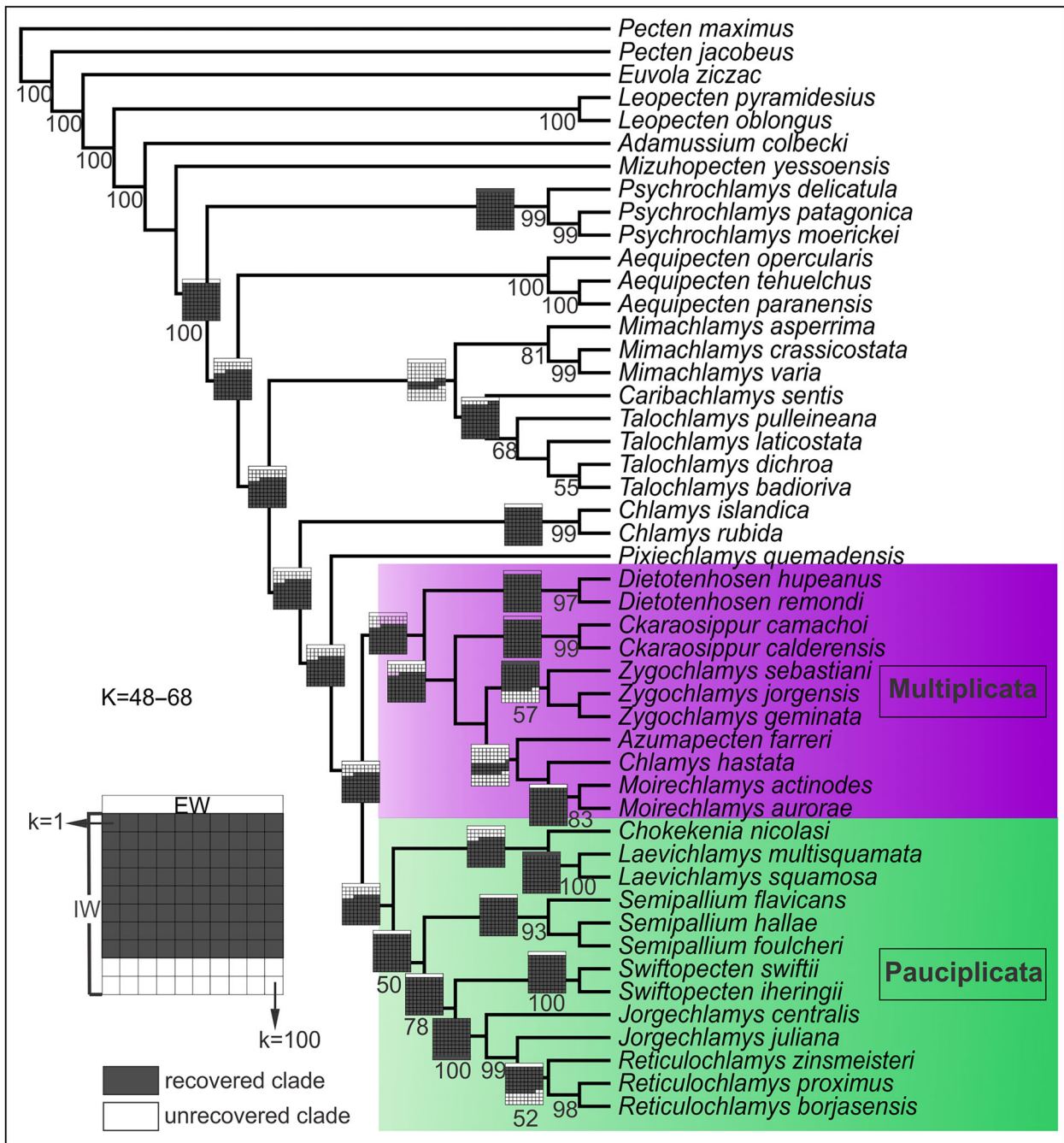


FIG. 6. Resultant topology for $k = 48-68$ displaying the two clades obtained for the ingroup, Multiplicata and Pauciplicata. Sensitive grids show presence (grey) or absence (white) of some clades under equal weighting (EW) implied weighting (IW; k values from 1 to 100) searches. Jackknife support values above 50 are reported below branches or grids.

Jorgechlamys and *Reticulochlamys* (early Miocene, Patagonia). The taxonomic composition of both major clades (Multiplicata and Pauciplicata) is consistent in topologies with k values from 24 to 100. The studied genera are monophyletic, except for *Jorgechlamys* in all searches and *Zygochlamys* for k values of 69–100. The topology under the $k = 8-23$ weighting scheme shows Multiplicata as a paraphyletic group while

Pauciplicata is recovered as a derived and monophyletic clade nested within the first, with *Dietotenhosen* as the most basal genus of the ingroup (Santelli *et al.* 2021, appendix S6). Under this tree topology, all Chlamydiina genera are monophyletic.

We find that monotypic taxa show more unstable phylogenetic positions than non-monotypic genera,

particularly the Patagonian *Chokekenia* (frequently recovered within Pauciplicata) and *Pixiechlamys*. *Chokekenia* is placed outside of Pauciplicata under $k = 1-7$ searches and it takes different phylogenetic positions, being related to *Zygochlamys* and *Moirechlamys* ($k = 1-2$) or related to *Pi. quemadensis* ($k = 3-23$) (Santelli et al. 2021, appendix S6). Nevertheless, *Chokekenia* belongs in Pauciplicata in five different tree topologies under $k = 8-100$ searches. This genus resolves as the sister group of *Laevichlamys*, and is related to the Patagonian *Reticulochlamys* and *Jorgechlamys* under $k = 24-100$ searches. However, *Chokekenia* + *Pi. quemadensis* are related to a group that contains *Chlamys* and Pauciplicata taxa (*Semipallium*, *Swiftopecten*, *Reticulochlamys* and *Jorgechlamys*), under $k = 8-23$ tree topology (Santelli et al. 2021, appendix S6). *Pixiechlamys* (monotypic genus) is recognized as the sister group of Pauciplicata and Multiplicata in the four topologies for $k = 24-100$ searches. In contrast, the $k = 3-23$ weighting scheme resulted in *Pi. quemadensis* changing its phylogenetic position within these clades (Santelli et al. 2021, appendix S6).

There are some ingroup taxa that fall outside Multiplicata and Pauciplicata, such as *Chlamys* and *Ckaraosippur* and they have also an uncertain phylogenetic position that changes for different k values (Santelli et al. 2021, appendix S6). The first genus is resolved as the sister group of Pauciplicata ($k = 1-23$) or is recovered as the most basal Chlamydini ($k = 24-100$), and *Ckaraosippur* belongs in Multiplicata ($k = 1-4$, $k = 24-100$) or is found as the most basal taxa of the ingroup ($k = 5-23$) (Santelli et al. 2021, appendix S6).

Remaining southern South America clades (non-monotypic) are more stable than the monotypic genera, although their relative positions within Multiplicata and Pauciplicata change with varying values of k , under implied weighting. *Zygochlamys* is monophyletic for equal weighting and almost 70% of the values of k ($k = 1-68$). However, it is paraphyletic and basal to the *Ckaraosippur* + *Ch. hastata* + *Moirechlamys* clade ($k = 69-100$), which comprises taxa younger than *Zygochlamys* (Santelli et al. 2021, appendix S6).

Internal relationships of Multiplicata and Pauciplicata

Southern South American Chlamydini are grouped into two well-differentiated clades under $k = 1-7$ and $k = 24-100$ (as explained above). These clades show the same taxonomic composition when $k = 24-100$, although the internal relationships of their taxa change throughout the four different topologies obtained for this range of k values. The sister taxon of both clades is *Pi. quemadensis*, and *Chlamys* is the most basal Chlamydini in these topologies ($k = 24-100$). Within these trees, the second most frequent topology

was resolved by the $k = 48-68$ weighting schemes (e.g. Fig. 6, including Jackknife supports) and has the highest support values for all clades. Moreover, this tree shows the same internal relationships for the two new clades as the topology recovered when $k = 40-47$.

The tree of the $k = 48-68$ weighting schemes indicates that *Dietotenhosen* is the most basal genus of Multiplicata, and this genus is related to the *Ckaraosippur* + *Zygochlamys* + *Azumapecten* + *Chlamys hastata* + *Moirechlamys* clade. *Ckaraosippur* is basal to *Zygochlamys*, and *Zygochlamys* is closely related to a group that contains two extant non-Patagonian taxa, *Azumapecten* and *Chlamys hastata*, and *Moirechlamys*, the most derived genus within Multiplicata ($k = 40-68$). Multiplicata also includes two extant, non-Patagonian taxa: *Azumapecten farreri* (Pleistocene–Recent, Japanese and East China seas) and *Ch. hastata* (late Pliocene – Recent, north-east Pacific 60°N–32°N, and north-west Pacific, Kamchatka) ($k = 1-7$, $k = 24-100$). The placement of *Ch. hastata* varies; it is within Multiplicata in most of found topologies ($k = 1-7$ and $k = 24-100$), being closely related to *Zygochlamys* for $k = 1-7$, whereas it is resolved as the sister group of *Moirechlamys* when $k = 24-100$. In contrast, *Ch. hastata* is basal to a large clade comprising mainly Pauciplicata taxa in the topology of the $k = 8-23$ weighting scheme (see Santelli et al. 2021, appendix S6).

The topology obtained under the $k = 48-68$ weighting scheme shows that Pauciplicata clusters to a *Chokekenia* + *Laevichlamys* group that is in turn related to *Semipallium*, *Swiftopecten* and the clade of *Reticulochlamys* (the most derived terminal taxon) and the paraphyletic *Jorgechlamys* (Fig. 6).

Synapomorphies of the ingroup ($k = 48-68$)

There are ten synapomorphies that sustain the ingroup (the taxa herein recovered as Chlamydini taxa, i.e. the smallest clade containing both *Chlamys* s.s. and *Swiftopecten*, excluding *Talochlamys* spp. and *Psychrochlamys* spp.) among which stand out: the presence of shagreen microsculpture on disc and left auricles, which extends over the entire right valve and is restricted to the left umbonal area on the left valve; and the restriction of commarginal microsculpture to umbonal areas on both valves. Also, the pre-radial stage is very short, microsculpture in advanced pre-radial and early radial stages is dominated by antimarginal striae, and the number of radial ribs increases by bifurcation and intercalation.

Pauciplicata + Multiplicata is grouped by five synapomorphies: shallow byssal sinus; a straight postero-dorsal margin of disc; concave free margin of left anterior auricle; plicae commencing at the early radial stage; and right valve with primary and secondary radial ribs.

The Multiplicata clade has seven synapomorphies in common: opisthocline valves; disc with dorsal gape; left anterior auricles sculptured with 14–16 ribs; ctenolium comprising strong and large teeth; the number of radial plicae increasing by bifurcation and intercalation on the right valve; and by intercalation on the left valve.

The Pauciplicata group is defined by eight synapomorphies: right-convex shells; eight plicae on right valve; nine plicae on left valve; right anterior auricle with seven ribs; ribs on plicae of homogenous thickness; 4–7 ribs on right central plicae; 6–7 ribs on left central plicae; and 4–5 radial ribs on left central interspaces. It is represented by the *Semipallium* + *Swiftopecten* + *Reticulochlamys* + *Jorgechlamys* clade along with the *Chokekenia* + *Laevichlamys* clade.

A detailed description of the synapomorphies that support the clades of interest for implied weighting tree of $k = 48$ – 68 is provided in Santelli *et al.* (2021). The synapomorphies of all included taxa are also listed in this appendix (Santelli *et al.* 2021, appendix S7B).

Origin of the lineages within Chlamydini

According to the time-calibrated phylogenetic tree, our results suggest that the divergence between both Multiplicata and Pauciplicata occurred before or in the late Eocene or early Oligocene (Fig. 7). This tree shows the existence of ghost lineages for every studied genus, the shortest one for *Z. geminata*, a species that occurs in the upper Oligocene. The sole clade without ghost lineages is *Jorgechlamys* + *Reticulochlamys*, a group that is represented in the lower Miocene of Patagonia. The stratigraphic occurrence of *Semipallium* (early Oligocene to Recent), a taxon that occupies a derived phylogenetic position, sustains an early diversification in the evolutionary history of the tribe Chlamydini.

SYSTEMATIC PALAEOLOGY

CHLAMYDINI von Teppner, 1922

MULTIPLICATA nov.

Definition. The most inclusive clade containing *Dietotenhosen*, *Zygochlamys* and *Moirechlamys*, but not *Semipallium* or *Jorgechlamys*, and their descendants (stem-based).

Synapomorphies. Disc with dorsal gape; left anterior auricles sculptured with more than 14 ribs; ctenolium with strong and large teeth; number of radial plicae increases by bifurcation and intercalation on right valves and by intercalation on left valves.

Taxa included. *Zygochlamys* Ihering, 1907; *Moirechlamys* Santelli & del Río, 2019a; *Dietotenhosen* Santelli & del Río, 2019b; *Ckaraosippur* Santelli & del Río, 2019b; *Azumapecten farreri* (Jones & Preston, 1904); *Chlamys hastata* (G. B. Sowerby II, 1842).

Occurrence. Late Oligocene (*Z. geminata*) to Recent.

Remarks. This clade is resolved as paraphyletic and basal to Pauciplicata under $k = 8$ – 23 . In the topologies recovered for low values of k ($k = 1$ – 7) the monotypic genera *Pixiechlamys* and *Chokekenia* are found within Multiplicata, and *Ckaraosippur* is placed as a basal group to Multiplicata and Pauciplicata when $k = 5$ – 23 . This clade is also supported by an ambiguous synapomorphy, the presence of opisthocline shells, which is ambiguous because *Zygochlamys* is characterized by the presence of acline shells.

PAUCIPLICATA nov.

Definition. The most inclusive clade containing *Semipallium*, *Jorgechlamys*, *Reticulochlamys* and *Swiftopecten*, but not *Zygochlamys* or *Dietotenhosen*, and their descendants (stem-based).

Synapomorphies. Seven ribs on right anterior auricle; ribs on plicae of homogenous thickness.

Taxa included. *Chokekenia* Santelli & del Río 2019a; *Laevichlamys* Waller, 1993; *Semipallium* Jousseume *in* Lamy, 1928; *Swiftopecten* Hertlein, 1936; *Jorgechlamys* del Río, 2004; *Reticulochlamys* del Río, 2004.

Occurrence. Early Oligocene (*Se. foulcheri*) to Recent.

Remarks. This clade is recovered in all implied-weighting searches. The Patagonian monotypic *Chokekenia* is nested within this clade for $k = 24$ – 100 searches, whereas when $k = 1$ – 23 it is placed outside from Pauciplicata. This clade is also supported by ambiguous synapomorphies: right-convex shells; eight plicae on right valve; nine on the left one; 4–7 ribs on right central plicae; 6–7 ribs on left central plicae; and 4–5 radial ribs on left central interspaces. These are ambiguous because *Se. foulcheri* and *Se. hallae* are grouped, among other synapomorphies, by having equiconvex shells and 2–3 ribs covering plicae on the left valve, and due to *Swiftopecten* having left-convex shells. Eight plicae on the right valve; nine on the left one; 4–7 ribs on right central plicae; and 4–5 ribs on left central interspaces are also ambiguous synapomorphies because the clade *Swiftopecten* + *Jorgechlamys* + *Reticulochlamys* is recognized by having 6 and 5 plicae on the right and left valves, 7–14 ribs on right plicae and 6–13 ribs on left

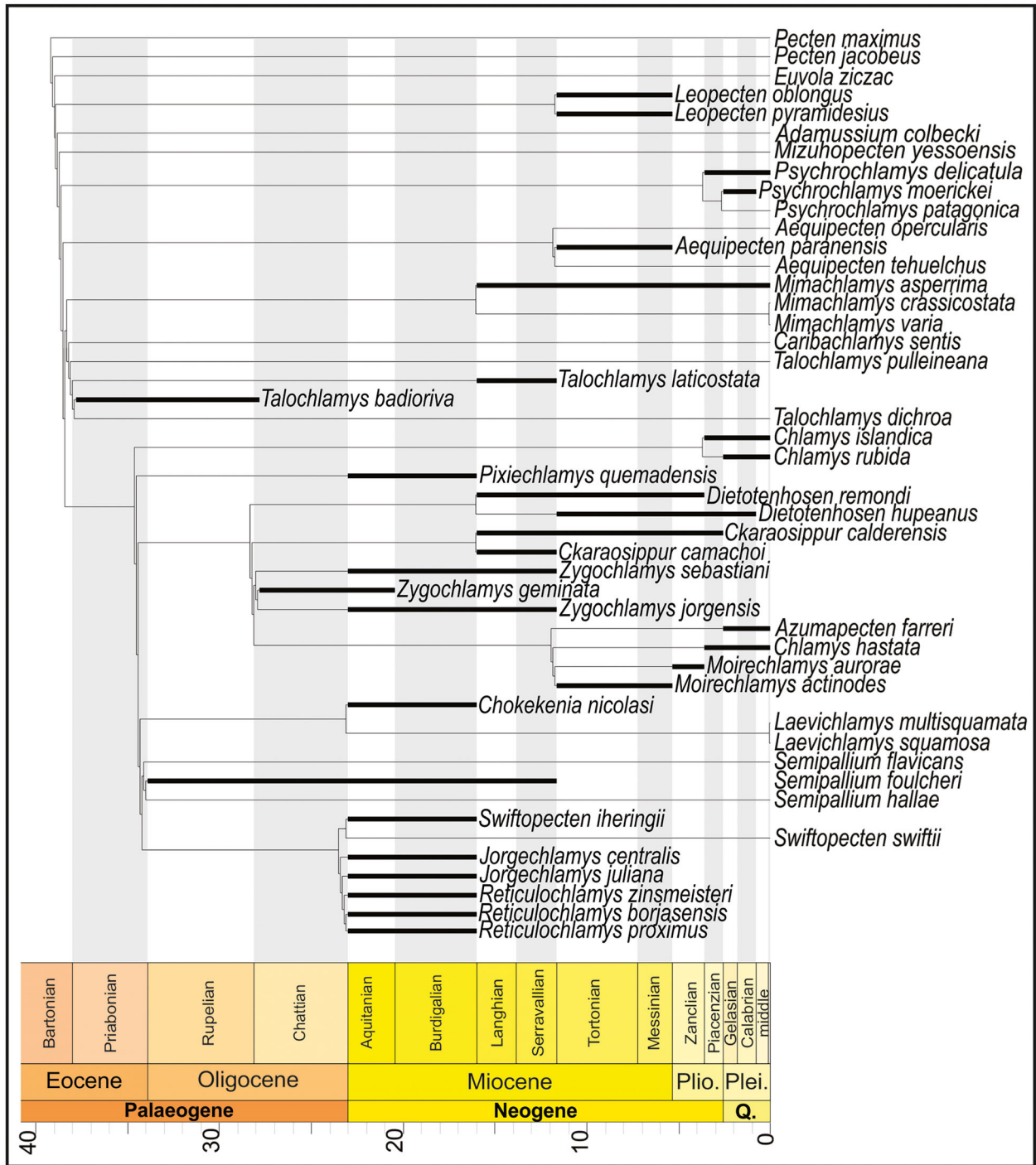


FIG. 7. Time-calibrated phylogenetic tree. Black bars represent highest and lowest stratigraphic occurrence of each taxon. Abbreviations: Q., Quaternary; Plio., Pliocene; Plei., Pleistocene. Ages are in millions of years.

interspaces, respectively. Nested within Pauciplicata, *R. borjasensis* and *R. proximus* are grouped by the synapomorphy (among others) of 7–11 ribs on the central plicae of the left valve instead of the 4–7 ribs that characterize the Pauciplicata clade, thus forming an ambiguous synapomorphy for Pauciplicata.

DISCUSSION

This phylogenetic study provides a morphological matrix and suggests possible evolutionary relationships for the species of southern South America, focusing on a high number of extinct Chlamydini taxa. The only

morphological matrix previously published was that of Waller (2006a), which comprised only 14 characters, and was developed for the superfamily Pectinoidea. Therefore, it has many plesiomorphic characters that are ineffective for resolving the phylogenetic relationships of Chlamydini. Our data matrix was completely created anew and coded herein. Several considerations arose from the results outlined above and will be discussed as follows.

Many of the southern South American Chlamydini species, such as *Z. geminata*, *Z. jorgensis*, *M. actinodes*, *M. aurorae*, *Cho. nicolasi*, *Pi. quemadensis*, *C. calderensis* and *D. hupeanus*, were historically considered to be related to or assigned to *Zygochlamys* or *Chlamys* s.s. However, as proposed by Santelli & del Río (2019a, b), they belong in six different genera that are herein recovered as monophyletic groups supporting our previous taxonomic findings. These are *Zygochlamys* (*Z. geminata*, *Z. jorgensis* and *Z. sebastiani*), *Moirechlamys* (*M. actinodes* and *M. aurorae*), *Ckaraosippur* (*C. calderensis* and *C. camachoi*), *Dietotenhosen* (*D. hupeanus* and *D. remondi*), *Pixiechlamys* (*Pi. quemadensis*) and *Chokekenia* (*Cho. nicolasi*). The latter two genera were described as monotypic taxa (Santelli & del Río 2019a), which is also sustained by our present results.

This study allows us to test the hypotheses proposed by Beu (1985) and Jonkers (2003). We reject the hypothesis of Beu (1985) that *Ps. patagonica* and *D. hupeanus* (= *Chlamys vidali* (Philippi, 1887)) as closely related species; we find that *D. hupeanus* is unrelated to *Ps. patagonica* and *Ps. delicatula*. However, our results suggest that *D. hupeanus* is clustered with *Moirechlamys actinodes*, as suggested by Beu (1985). Following Waller (1991), Beu (1995) referred both *M. actinodes* and *Ps. delicatula* to *Zygochlamys*. However, our topologies reveal that *Zygochlamys* is composed of three species, while *M. actinodes* and *Ps. delicatula* belong in *Moirechlamys* and *Psychrochlamys* respectively, and that *Ps. delicatula* is unrelated to *Zygochlamys*; this is consistent with the results of Santelli & del Río (2019a). Finally, we reject the hypothesis of Jonkers (2003) that stated that *D. remondi* (= *Chlamys coquimbensis* (Möricke, 1896)) evolved from *Z. geminata*, because our analysis shows that *Zygochlamys* is a separate and more derived group than *Dietotenhosen* in all searches. Moreover, *Dietotenhosen* and *Zygochlamys* present notable morphological differences (as detailed by Santelli & del Río 2019b).

Because there are no previous morphological phylogenetic analyses, our results can only be compared to comprehensive molecular studies of Pectinidae. Our phylogenetic analysis is restricted to shell morphological traits of a limited taxonomic sample of 35 species within Chlamydinae (27 Chlamydini species), whereas the analyses of Alejandrino *et al.* (2011) and Sherratt *et al.* (2016) are based on a limited source of molecular information,

in terms of the number of gene sequences and species (41 and 53 species of Chlamydinae in Alejandrino *et al.* (2011) and Sherratt *et al.* (2016), respectively). The current diversity of the subfamily Chlamydinae is much larger, being around 98 species (MolluscaBase 2021b; see Pedinae). Moreover, neither molecular study tests the phylogenetic placement of the type species of the polyphyletic genus *Talochlamys* (*T. pulleineana*), which is a key taxon for a better understanding of this genus. Therefore, the specific diversity of Chlamydinae is under-represented in all precedent phylogenetic analyses, which is exacerbated by the technical limitations for including fossil species of Chlamydinae related to extant species in molecular analysis. Nonetheless, there are very interesting aspects in our results that can be compared with those achieved by molecular studies, despite the limitations in both methodologies.

Some interesting differences arise when comparing our findings with the studies of Alejandrino *et al.* (2011) and Sherratt *et al.* (2016), undoubtedly arising from the different sources of information, applied methodologies and taxa sampled.

The phylogenetic position of *Swiftopecten* is partially duplicated in our topologies for low values of k ($k = 1-23$) and the molecular phylogeny of Sherratt *et al.* (2016). We resolved *S. swiftii* and *S. iheringii* within the Pauciplicata clade and related to *Chlamys* s.s., with the latter being basal to Pauciplicata ($k = 1-23$), while Sherratt *et al.* (2016) found *S. swiftii* to be the sister group of *Chlamys*. However, our trees show *Swiftopecten* and *Chlamys* to be distantly related for high values of k ($k = 24-100$), differing from Sherratt *et al.* (2016).

The present study indicates that extant species of South America that have traditionally been assigned to *Zygochlamys* (*Ps. patagonica*, *Ps. delicatula*) are unrelated to its type species (*Z. geminata*) and, therefore, to *Zygochlamys*, but that they belong in the circumpolar genus *Psychrochlamys* described by Jonkers (2003). The latter genus has an unstable phylogenetic position in different modern molecular studies (mentioned as *Zygochlamys*) that also differs from our results. However, recent molecular evidence (Alejandrino *et al.* 2011; Sherratt *et al.* 2016) and our results agree that *Psychrochlamys* is monophyletic and that it is separated from Chlamydini. Our results also show that *Psychrochlamys* is basal to *Aequipecten* ($k = 24-100$) (Pectininae according to: Waller 2006b; Alejandrino *et al.* 2011; Sherratt *et al.* 2016; MolluscaBase 2021d) and therefore presumably a non-Chlamydinae taxon. Moreover, as we previously stated in Santelli & del Río (2019a, b), *Psychrochlamys* is morphologically different from Chlamydini in having orbicular shell with symmetrical and short auricles, with the free margin of anterior auricles sloping posteriorly, shallow byssal notches; shell sculptured with coarse commarginal lamellae extended

over the entire surface, and lacking the shagreen microsculpture typical of Chlamyдини. Those remarkable morphological differences are supported by molecular phylogenies in which *Psychrochlamys* is more closely related to Pectininae and Aequipectinini than to Chlamyдини (Alejandrino *et al.* 2011). A different placement is provided by Sherratt *et al.* (2016), who found that the group containing *Psychrochlamys* is related to the lineage of Chlamyदिनाe and could even be considered part of this subfamily, but always outside of Chlamyदिनि. To summarize, morphological and recent molecular phylogenetic analyses reject the proposal of Waller (1993) that *Psychrochlamys* is related to *Chlamys s.s.* (i.e. Chlamyदिनि). Furthermore, species currently assigned to *Psychrochlamys* are unrelated to *D. hupeanus* (= *Chlamys vidali*) and *M. actinodes*, contra Beu (1985). Moreover, it is herein demonstrated that there is no close relationship between *Psychrochlamys* and any of the fossil Patagonian species traditionally considered to be members of *Zygochlamys* by Waller (1991), Beu (1995), Beu & Darragh (2001) and Dijkstra & Beu (2018), among others. Given that the type species of *Zygochlamys* and its co-generic taxa are extinct, molecular studies cannot test the phylogenetic position of *Zygochlamys* nor its relationship with *Psychrochlamys*. For that reason, morphological phylogenies are also important to study the evolutionary relationships of the present diversity. It is a methodology that allows us to assess the taxonomic assignments with better accuracy as it is frequently supported by a systematic analysis (del Río 1995, 2004; Santelli & del Río 2019a, b). For example, *Ps. patagonica* is pseudo-replicated in the analysis of Alejandrino *et al.* (2011) and Sherratt *et al.* (2016), because the synonymous *Z. amandi* (synonymized with *Ps. patagonica* by Jonkers (2003, p. 46) and accepted by Schejter & Bremec (2012)) is sequenced separately. On the other hand, our morphological analysis is biased by the study of hard-shell structures (Alvarez 2019, p. 686).

Preliminary findings that refer to non-southern South American taxa are detailed in Santelli *et al.* (2021, appendix S8). Future studies can address the relationships of these groups that are barely outlined in the present contribution.

On the divergence time of South American Chlamyदिनि

The evolutionary relationships of the tribe are still far from being completely understood. Nevertheless, the evidence presented here indicates that the earliest record of the tribe is followed by its diversification. Moreover, the topologies obtained show that *Chlamys s.s.* is basal to *Semipallium* in all searches and, because *Se. foulcheri* lived during the early Oligocene and middle Miocene (Beu & Darragh 2001), this gives rise to many ghost lineages in

groups with younger first occurrences. Most of the extinct Chlamyदिनि analysed herein are from the Neogene. Perhaps, these ghost lineages are an artefact of the limited taxonomic sampling of the tribe Chlamyदिनि being mainly restricted to Neogene southern South American taxa, hence omitting many older taxa. Therefore, our analysis probably fails to properly reconstruct the deeper nodes of these phylogenetic relationships. Therefore, the evolutionary history of the Chlamyदिनि, and the relations of its lineages, are also poorly understood. Our results indicate that *Jorgechlamys* + *Reticulochlamys* is the clade with the shortest ghost lineage, and *Zygochlamys* has a short ghost lineage, with the oldest accepted record of *Z. geminata* in the upper Oligocene. The derived position of *Semipallium* reveals that the diversification of the tribe Chlamyदिनि occurred early in its evolutionary history because it undoubtedly represents the oldest records of the tribe. It must be pointed out that there are earlier alleged representatives of the tribe mentioned in the literature, including lower or middle Eocene records of *Serripecten* Marwick, 1928, *Mesopeplum* Iredale, 1929, and *Talochlamys* (Feldmann & Maxwell 1990; Beu & Darragh 2001; Darragh & Kendrick 2008). However, since the phylogenetic relationships of the fossil taxa of the first two were not studied, we are unable to discuss their affinities, and the third taxon is disregarded because it does not belong in Chlamyदिनि according to our study (or those of Alejandrino *et al.* (2011) and Sherratt *et al.* (2016)). Because Beu & Darragh (2001) described similarities between *Serripecten* and *Psychrochlamys* (referred by them to *Z. delicatula*), it is probable that the first does not belong in Chlamyदिनि.

Our topologies indicate an earlier time of origin than the early Miocene suggested by Sherratt *et al.* (2016) who, through molecular clock techniques, estimated that the diversification of *Chlamys s.s.* and *Ch. hastata* happened at c. 20 Ma. Since our results show that *Chlamys s.s.* is basal to *Semipallium* and *Zygochlamys*, *Chlamys* might have originated earlier than the early Miocene, although its oldest documented occurrence is late Pliocene. More comprehensive future phylogenies will lead to a better understanding of the relationships of the tribe and will probably yield a more precise origin time for the Chlamyदिनि, especially if older taxa are incorporated. The study of the origin of Chlamyदिनि will also benefit from the inclusion of type taxa and type species in phylogenetic analysis, particularly those of genera with uncertain affinities.

CONCLUSION

The Cenozoic Chlamyदिनि of southern South American are separated herein into two clades that are usually recovered as monophyletic groups, named Multiplicata

and Pauciplicata in reference to the number of plicae. The low number of plicae is recognized within the set of the synapomorphies that define Pauciplicata. Multiplicata and Pauciplicata are strongly consistent groups, each having slight variations in the internal relationships of the taxa within the different tree topologies recovered here. Pauciplicata is recovered in all topologies under implied weighting (although some tree topologies include unstable taxa, such as *Chlamys* and *Laevichlamys*). All southern South American genera are monophyletic, except for *Jorgechlamys* that is paraphyletic and nested within *Reticulochlamys*; for that reason, *Jorgechlamys* should be synonymized with *Reticulochlamys*. *Zygochlamys* is paraphyletic under very high values of k ($k = 69\text{--}100$). The sister and basal group to both clades (Multiplicata and Pauciplicata) is *Pixiechlamys quemadensis*, with *Chlamys s.s.* basal to all of them, for $k = 24\text{--}100$. Multiplicata includes *Dietotenhosen*, *Ckaraosippur*, *Zygochlamys*, *Moirechlamys*, *Azumapecten* and *Chlamys hastata*; Pauciplicata is represented by *Chokekenia*, *Laevichlamys*, *Semipallium*, *Swiftopecten*, *Jorgechlamys* and *Reticulochlamys*.

This study has shown that *Zygochlamys* spp., *Moirechlamys actinodes* and *Dietotenhosen hupeanus* are closely related in the same clade (Multiplicata) and that they belong in endemic and monophyletic southern South American genera. However, the latter two species neither belong in *Zygochlamys* nor are related to *Z. patagonica* (now referred to *Psychrochlamys*), as proposed by Beu (1985, 1995). Therefore, the present evidence does not support Beu's (1985) hypothesis of a Miocene origin for the lineage of *Ps. patagonica* in South America nor its subsequent dispersion by the Antarctic Circumpolar Current (ACC) during Miocene or Pleistocene times.

Ckaraosippur and *Dietotenhosen* are the youngest survivors of the Tribe Chlamydini in the southernmost tip of South America.

Our calibrated topology allows us to confirm one of the most ancient records of a true member of the tribe (*Semipallium foulcheri*). It shows that the diversification of Chlamydini occurred early in the evolutionary history of the group, with many clades already diversified and separated at the boundary of the late Eocene and early Oligocene, such as Pauciplicata and Multiplicata. The early record of *Semipallium* generates multiple ghost lineages for all analysed clades and our results could reflect the lack of related taxa that were not incorporated in the analysis. Surely, an increased taxonomic sampling on future phylogenetic studies of Chlamydini will resolve many of the ghost lineages.

The present study shows that *Azumapecten* and *Swiftopecten* are related to *Chlamys s.s.*, which is consistent with the relationships obtained by previous modern molecular phylogenies (Alejandrino *et al.* 2011; Sherratt *et al.* 2016).

However, we found that *Semipallium* is also related to those taxa, contrary to the affinities suggested by molecular evidence (Alejandrino *et al.* 2011; Sherratt *et al.* 2016). Finally, *Ps. patagonica* and *Ps. delicatula* do not belong in *Zygochlamys* according to our study, and *Psychrochlamys* is definitely a non-Chlamydini taxon. Moreover, we question its placement in Chlamydiae. This outcome reinforces the hypotheses of Santelli & del Río (2019a, b) who proposed that the tribe Chlamydini became extinct in the southern South American region in early Pleistocene times.

A more representative sampling of the subfamily Chlamydiae could shed light on the subfamily and tribe arrangements, and its internal phylogenetic relationships. Moreover, the inclusion of additional extinct taxa in morphological analyses, as well as type species in molecular studies could contribute to clarify the evolutionary history of Chlamydini. The phylogenetic position and taxonomic status of Chlamydiae and Chlamydini within Pectinidae differ among modern molecular studies (Puslednik & Serb 2008; Alejandrino *et al.* 2011; Sherratt *et al.* 2016), encouraging researchers to enlarge the taxonomic sampling to improve our understanding of the main lineages within Pectinidae.

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DATA ARCHIVING STATEMENT

This published work has been registered in ZooBank: <http://zoobank.org/References/122AE4E3-FF79-4AC6-9185-E3E102D6754B>.

Appendices for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0zpc866vd>.

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