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# Quantitative palaeobiogeographical analysis of South American Neogene Chioninae (Bivalvia: Veneridae)

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## ABSTRACT

Chionine bivalves are one of the most important components of Neogene and Recent molluscan faunas in southern South America, but it was not until recently that their phylogenetic relationships has been explored quantitatively. Based on this robust framework, we analyzed the palaeobiogeographical history of the group. The geographic areas used in this analysis were discretized using a multivariate K-means cluster analysis based on the palaeocoordinates of chionine-bearing localities. Statistical comparison of quantitative, event-based biogeography models using likelihood suggests that our data best fits models that include long-distance jump dispersal (+J), with a slight preference for a model that also gives increased weight to vicariance. The ‘Chione’ clade (including the genera *Chione*, *Anomalocardia*, and *Chionopsis*) is mainly a Caribbean and central Eastern Pacific lineage with expansions to California and the southern Western Atlantic coast. The ‘Protothaca’ clade (including *Protothaca*, *Nioche*, *Austrovenus*, and *Chionista*) is mainly an Eastern Pacific lineage–with a proposed southern South American origin–with occasional dispersals to the western Pacific (Oceania and East Asia). A new alternative dispersal route is proposed across the North Pacific from California and the north Eastern Pacific to East Asia and Oceania, as shown by *Austrovenus stutchburyi*, *Tuangia crassicosta*, and *Protocallithaca adamsii*. The ‘Ameghinomya’ clade (including all *Ameghinomya* species) is a southern South American lineage–south Eastern Pacific origin–that subsequently dispersed into the southern Western Atlantic. The ‘Protothaca’ and ‘Ameghinomya’ clades show opposite histories, the former being mainly Pacific and the latter mainly Atlantic. The distribution of both clades on both sides of South America may have been allowed by the opening of the Drake Passage Gateway around the Oligocene-Miocene boundary.

## 1. Introduction

The Family Veneridae is the most taxonomically diverse group of bivalves in extant seas and they are represented in southern South America by the subfamilies Dosiniinae, Pitarinae, Tapetinae, and Chioninae (Carcelles, 1950; Bernard, 1983; Ríos, 1994). The latter subfamily is one of the most abundant components of Neogene and Recent molluscan faunas (del Río, 1990; Pérez et al., 2013). Their record in the region begins in Eocene times (Camacho et al., 2000) and their taxonomical and morphological diversification took place around the Paleogene-Neogene boundary, after the opening of the Drake Passage at end of the Oligocene (Barker and Burrell, 1977; Barker and Thomas, 2004). Most of the Chioninae taxa found in southern South America dispersed to more northern latitudes during and after the late Miocene (e.g. *Anomalocardia*, *Chionopsis*) (Aguirre, 1990; del Río, 1990; Gordillo, 1998; Gordillo et al., 2014). Nowadays, Chioninae are represented in southern South America by *Ameghinomya antiqua* (King, 1832), *Tawera gayi* (Hupé, 1854), and *Protothaca thaca* (Molina, 1782). The phylogenetic interrelationships of the genus *Tawera* are currently unknown, but the biogeographical history of *T. gayi* was discussed by Gordillo (2006). However, the systematic position and phylogenetic relationships of other Chioninae have received little attention (Roopnarine, 1996, 1997, 2001; Roopnarine and Vermeij, 2000; Pérez et al., 2013). Particularly, several authors proposed that *Protothaca* Dall, 1902 and *Ameghinomya* Ihering, 1907 are closely related to each other (Herm, 1969; Beu et al., 1997; Beu, 2004; Pérez et al., 2013) and biogeographic pathways for both taxa were proposed (Olsson, 1961; Beu et al., 1997; Beu, 2004). A recent quantitative phylogenetic analysis of these groups (Pérez et al., 2013) provides a robust framework to conduct a modern quantitative event-based palaeobiogeographical analysis of southern South America chionines for the first time, which is the aim of the present contribution.

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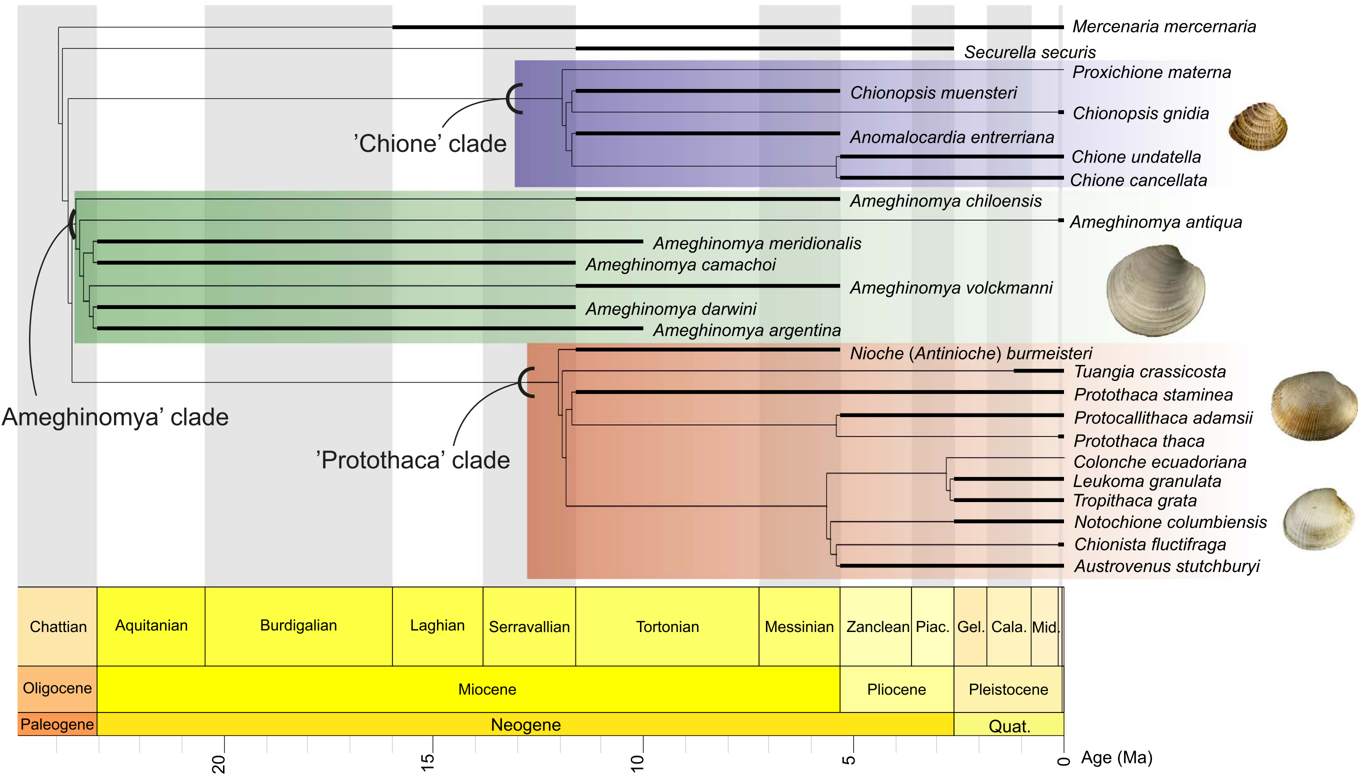

**Fig. 1.** Time calibrated phylogenetic tree used in the analyses. Quat. = Quaternary, Piac. = Piacenzan, Gel. = Gelasian, Cala. = Calabrian, Mid. = Middle Pleistocene. Age axis in million years. Illustrated taxa from top bottom: *Chione cancellata* (Linnaeus, 1767), *Ameghinomya argentina* (Ihering, 1897), *Protothaca thaca* (Molina, 1782), *Austrovenus stutchburyi* (Finlay, 1927).

## 2. Methods

We re-analyzed the phylogenetic data matrix built by Pérez et al. (2013) with the addition of *Protothaca* (*Notochione*) *columbiensis* (G.B. Sowerby, 1835) (scorings in Supplementary Dataset I). The original search strategy conducted by Pérez et al. (2013) was kept in this iteration of the data set (i.e. WAG + TBR with 50 replications and implied weighting of k = 4–20), using TNT 1.1 (Goloboff et al., 2008). The single optimal tree found includes all proposed *Protothaca* lineages known (Dall, 1902; Olsson, 1961; Bernard, 1983) with exception of *Callithaca* Dall, 1902 (type species *Tapes tenerrima* Carpenter, 1857) because this genus shows features that probably separate it from chionines (e.g. absence of inner margin crenulation). *Protocallithaca* Nomura, 1937 is often considered a synonym or a subgenus of *Callithaca*, but this statement has been criticized (Matsubara, 2009). Further studies on the systematic position of *Callithaca* are needed. Recently, Huber (2010) proposed *Leukoma* Römer, 1867 as a valid name for *Protothaca* but the placement of *Chionista fluctifraga* (Sowerby II, 1853) and *Austrovenus stutchburyi* (Gray, 1828) in the topology of the present analysis does not allow us to conclude about the monophyly of the genus *Protothaca* and we prefer use the term 'Protothaca clade' following Pérez et al. (2013). For this reason, the species of the *Protothaca* subgenera are mentioned without genus (i.e. *Notochione columbiensis*), and the name '*Protothaca*' is used for the *Protothaca* species sensu stricto. This phylogenetic tree was temporally calibrated with the timePaleoPhy() function of the package *paleotree* (Bapst, 2012) for R (R Core Development Team, 2017) using the "mbl" calibration and a minimum branch length of 0.1 million years. We choose the latter setting in order to recover the most conservative age estimation for each branch and, as a result, ghost lineage lengths are mostly a consequence of the age of its sister-branch. The biogeographic events estimated in *BioGeoBEARS* are mostly cladogenetic rather than anagenetic and, as a result, there should not be considerable differences using different time-calibrated trees (Matzke pers. comm. 2018).

The stratigraphic range of each taxon was listed in millions of years (see Supplementary Dataset II and III) and their geographic range was sampled as palaeolatitudes and palaeolongitudes (see Supplementary Dataset IV). We conducted a k-mean multivariate cluster analysis using the palaeocoordinate data in order to determine the geographic areas to be used in the palaeobiogeographic analysis. This cluster analysis was performed in R (R Core Development Team, 2017) with 1000 replicates. This analysis discretized eight independent geographic areas: a) California (southern North American coast, Baja California, and Mexico), b) Oceania (Australia and New Zealand), c) Caribbean Sea and Gulf of Mexico, d) Eastern Asia (Japan, Korea, and East Russia), e) Central Eastern Pacific (from Central America to northern Chile), f) North Eastern Pacific (Alaska and northern North American coast), g) South Western Atlantic (from Patagonia to Brazil), and h) South Eastern Pacific (Chilean coast). Taxa were assigned to one or more areas as appropriate (i.e. we allowed widespread taxa), resulting in a taxon-area matrix (see Supplementary Dataset V). All geographic areas where Chioninae bivalves were recorded are included in our analysis.

The obtained dataset was analyzed using different palaeobiogeographic models: Dispersal-Extinction-Cladogenesis (DEC), DEC + J, Dispersal Vicariance Analysis (DIVALIKE) (with Maximum Likelihood as optimization criteria), DIVALIKE + J, BAYAREALIKE, and BAYAREALIKE + J (+ J models include founder-event speciation, for a description of all these models see Matzke, 2013) using the R package *BioGeoBEARS* (Matzke, 2013, 2014). *BioGeoBEARS* allows a + J model variant, which allows founder-event or jump dispersal events to occur during cladogenesis (Matzke, 2014). The founder event allows the occupation of a new area simultaneously with a lineage splitting (Matzke, 2014), thus contrasting with the dispersal event of DEC and DIVALIKE, which is limited to a range-expansion (Ronquist and Sanmartín, 2011). *BioGeoBEARS* also allows statistical comparison (Burham and Anderson, 2002) of the fit of different models to historical biogeography datasets, in contrast with most previous analyses that were restricted to a single model (Matzke, 2013, 2014). Model fit was assessed