

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

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ARTICLE INFO

Keywords:

Ameghinomya
Cenozoic
Drake Passage Gateway
Long-distance dispersals
Protothaca

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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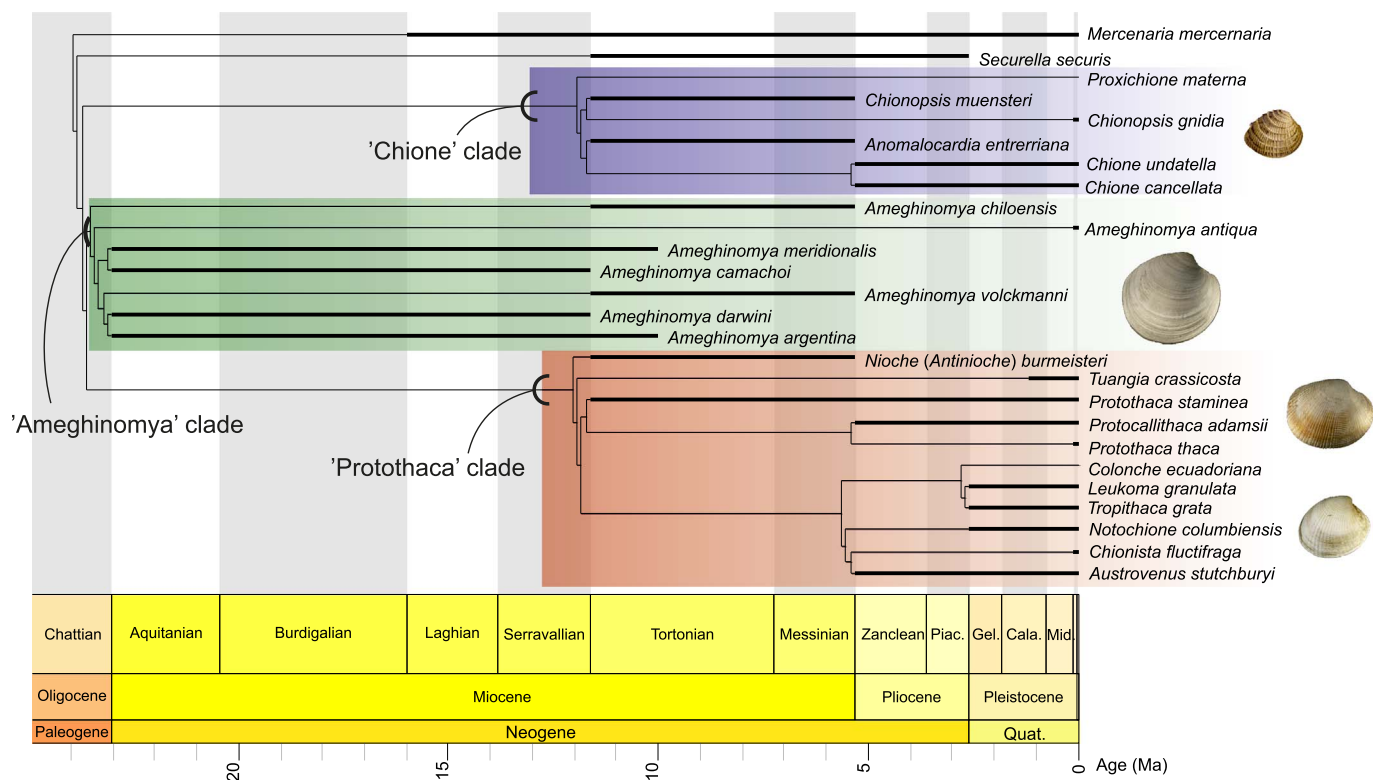


Fig. 1. Time calibrated phylogenetic tree used in the analyses. Quat. = Quaternary, Piac. = Piacenzan, Gel. = Gelasian, Cala. = Calabrian, Mid. = Middle Pleistocene. Age axis in million years. Illustrated taxa from top bottom: *Chione cancellata* (Linnaeus, 1767), *Ameghinomya argentina* (Ihering, 1897),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

using AICc and AICc model weights (Burham and Anderson, 2002) –AICc model weights were calculated with the function `akaike.weights()` of the package `qpcR` written for R. We considered all possible dispersal events as equally probable.

3. Results

The inclusion of *Protothaca (Notochione) columbiensis* did not modify the tree topology recovered by Pérez et al. (2013) (Fig. 1). This species is placed as the sister-taxon of *Chionista flutifraga* + *Austrovenus stutchburyi*. Three major clades are clearly defined: the ‘Chione’ clade, the ‘Protothaca’ clade, and the ‘Ameghinomya’ clade. The ‘Chione’ clade was defined by Roopnarine (1996) and includes the ‘Chione’ subclade (*Chione sensu stricto* and *Chionista*) and the ‘Lirophora’ subclade (*Anomalocardia*, *Lirophora*, *Ilio-chione*, and *Panichione*). The presence of *Chione sensu stricto* and *Anomalocardia* allow us to assign the name ‘Chione’ clade to the former. The ‘Protothaca’ clade comprises *Protothaca* species (including *Protothaca* subgenera) + *Austrovenus* + *Chionista*, and the ‘Ameghinomya’ clade includes *Ameghinomya* species, as it was defined by Pérez et al. (2013).

All models used in the analysis show similar palaeobiogeographic histories, which bolsters the results of the analysis. In particular, DIVALIKE+J was the model that best fit our data (LnL = -88.29; AICc = 184.76; wAICc * 100 = 79.94%), whereas the second best model is DEC+J but with a wAICc of only 18.4%. As a consequence, we used only DIVALIKE+J to describe the palaeobiogeographic history of the studied group (Fig. 2; Table 1), but history estimated by DEC+J is extremely similar. In all the +J models both dispersals contribute

distinctly, but in all cases the value of jump dispersals (j) is an order of magnitude higher than range-expansions (d). After these results, the ‘Chione’ clade has a Neogene South American or Oceanian origin, with subsequent dispersals to northern latitudes in both Pacific and Atlantic oceans. Extant members of the ‘Chione’ clade inhabit a broad geographic range in America, from Brazil to North America in the Atlantic coast, and from central South America to California in the Pacific Coast. The ‘Protothaca’ clade has a Neogene South Western Atlantic origin in our results, mainly as a result of the biogeographic distribution of *Nioche (Antinioche) burmeisteri*, with a subsequent expansion to Oceania (due to *Tuangia crassicoستا*) and later to the North Eastern Pacific + California (but this event has low likelihood percentages) (Fig. 3). Next, two lineages split within the remaining genus of the ‘Protothaca’ clade, the first remains in the North Eastern Pacific and California, and the second expands to the Central Eastern Pacific, and from here two species dispersed to Oceania and East Asia (*Austrovenus stutchburyi* and *Protocallithaca adamsii*, respectively). In summary, despite its possible Atlantic origin, the ‘Protothaca’ clade is mainly an eastern Pacific lineage with occasional dispersals to the western Pacific (Fig. 3).

The ‘Ameghinomya’ clade is a completely southern South America lineage. According to our results, its origin occurred in the South Eastern Pacific and subsequently the clade dispersed to the South Western Atlantic, a geographic distribution that was retained until the late Miocene. In Recent times, this clade inhabits both South Western Atlantic and South Eastern Pacific areas, being represented by *Ameghinomya antiqua* (Fig. 3).

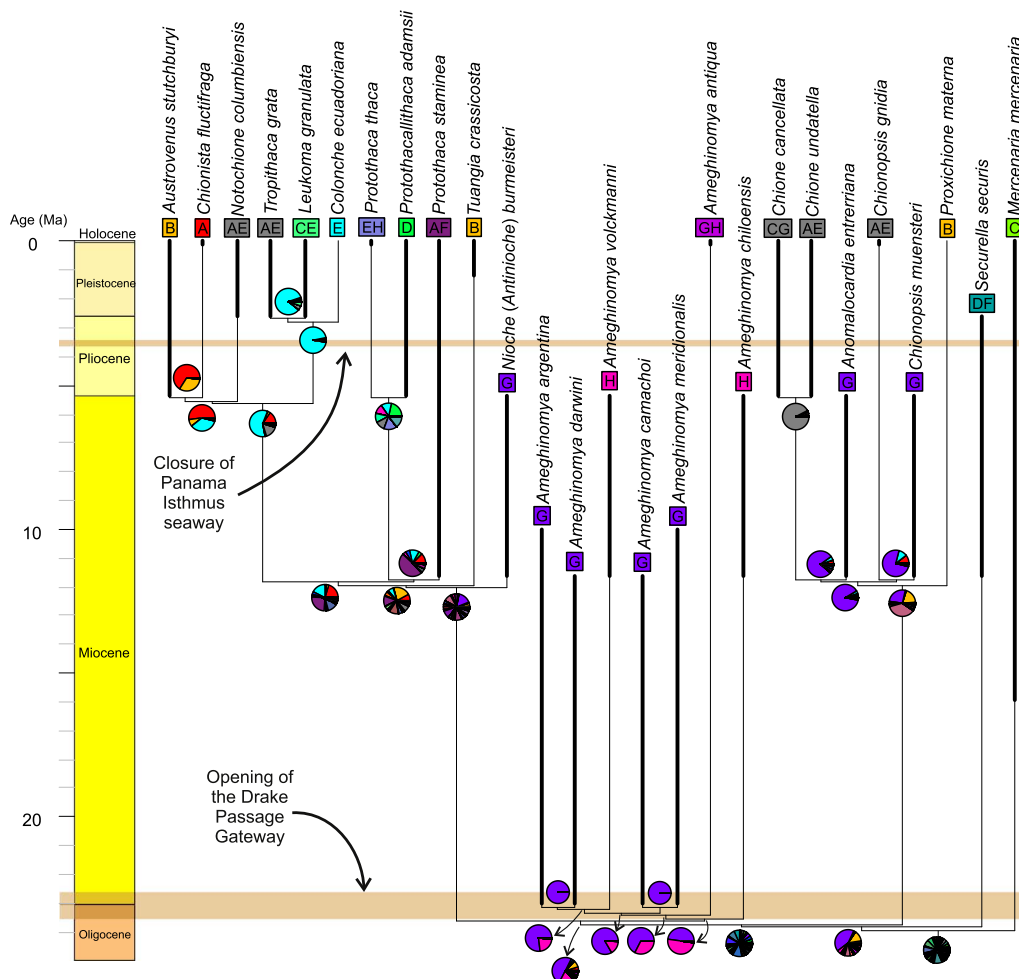


Fig. 2. Results of the DIVALIKE+J palaeobiogeographic model. A = California, B = Oceania, C = Caribbean Sea and Gulf of Mexico, D = Eastern Asia, E = Central Eastern Pacific, F = North Eastern Pacific, G = South Western Atlantic, H = South Eastern Pacific, details in the text. Age axis in million years.

Sea and Gulf of Mexico area) during the late Miocene (Petuch, 1982, 2003). Some lineages, such as the *Chione* species, dispersed to southern latitudes in both Pacific and Atlantic coasts probably during the early Pliocene. The *Chionopsis* species of the ‘Chione’ clade also dispersed to the southern Pacific coast (Olsson, 1961), reaching Patagonian latitudes during the late Miocene (del Río, 1991, 1994). Other lineages of this clade, such as the *Anomalocardia* species, did the opposite way, dispersing from southern to northern latitudes (from Patagonia to Brazil, South Western Atlantic area) (Aguirre, 1990). However, some possible *Anomalocardia* species (not included in the present phylogenetic and biogeographic analyses) now inhabit Western Pacific regions (Roopnarine et al., 2008) and may be the product of dispersal events similar to those of the ‘Protothaca’ clade members (see below). Further studies of the ‘Chione’ clade are needed, including a taxonomic revision of the genera and new phylogenetic analyses to complement the early studies of Roopnarine (1996, 1997, 2001) and Roopnarine and Vermeij (2000).

4.2. The Protothaca clade

The biogeographic history of the ‘Protothaca’ clade seems to be more complex than previous authors considered (Dall, 1902; Olsson, 1961). Our analysis indicates the origin of the group in the South Western Atlantic as a result of the presence of *Nioche (Antinioche) burmeisteri* in the upper Miocene Paraná Formation (Entre Rios Province, Argentina) (del Río, 1991). This estimation has a very low probability (approximately 15%) but the record of ‘*Chione*’ sp. in the Man Aike Formation (Eocene) (Camacho et al., 2000) bolsters this possibility. ‘*Chione*’ sp. is not assigned to any Chioninae genus but its sculpture resembles that of *Nioche (Antinioche)* species and may be an earlier representative of the *Protothaca* lineage (DEP, pers. obs.). Other *Nioche (Antinioche)* species are restricted to the Pacific coast in Neogene and Recent times, being distributed from Central Eastern Pacific to California (Olsson, 1961; Fischer-Piette and Vudikanovic, 1977). *Nioche (Antinioche)* is the sister-taxon of the *Protothaca* lineage and this latter group has an Oceanian origin in our analysis –due to *Tuangia crassica*, which ranges from the Pleistocene to the Recent–, but this result has a very low probability (< 20%). Remaining species of the *Protothaca* lineage have a Californian/North Eastern Pacific origin, with a subsequent diversification into three lineages. The high richness of *Protothaca* fossil and recent species in these areas supports this proposal (Olsson, 1961). From this area, some dispersal events occurred in this clade towards East Asia (with the Pleistocene–Recent *Protocallithaca adamsii*) (Matsubara, 2009) and the central South American regions. *Protothaca thaca* is the only *Protothaca* species that reaches the South Eastern Pacific region, and nowadays is present in the Chilean coast (Bernard, 1983).

The clade that consists of *Colonche ecuadoriana*, *Leukoma granulata*, and *Tropithaca grata* shows a Central Eastern Pacific origin. These three species are distributed from Pleistocene to Recent times in the Eastern Pacific coast (Bernard, 1983), with only one dispersal event–represented by *L. granulata*–to the Caribbean Sea. This event is probably linked to an earlier origin of the clade, previous to the closure of the seaway across the Panama Isthmus (Petuch, 1982; Bacon et al., 2015). The third ‘Protothaca’ clade, composed of *Notochione columbiensis*, *Chionista fluctifraga*, and *Austrovenus stutchburyi*, is the most interesting from a biogeographic point of view. This group is inferred to have originated in California, and a dispersal event occurred towards Oceania before early Pliocene, represented by the presence of *A. stutchburyi* in the latter area (Beu, 2004). This biogeographical link refutes the proposals of Beu et al. (1997) and Beu (2004) that stated that *A. stutchburyi* had a South American origin because it was a descendant of *Ameghinomya* species. Huber (2010) also mentioned a possible close relationship between *Austrovenus* and *Protothaca* species. The close phylogenetic relationships between *Chionista* and *Austrovenus* or *Protothaca* species have been proposed by previous authors (Marwick 1927; Kappner and Bieler, 2006; Mikkelsen et al., 2006; Chen et al., 2011). The presence of *Austrovenus* and *Tuangia* in Oceania reveals a

possible dispersal route that has not been considered by previous authors. Nevertheless, several dispersal pulses from South America to New Zealand between the late Oligocene and Pleistocene have been proposed, being driven either by the Antarctic Circumpolar Current (Beu et al., 1997) or a migration route along Western Antarctica by a shallow sea (Casadío et al., 2010). By contrast, an alternative route is inferred from our results via North Pacific waters, from California and the North Eastern Pacific to East Asia and Oceania. This biogeographic event is based on the records of *Tuangia crassica*, *Protocallithaca adamsii*, *Austrovenus stutchburyi*, and *Securella securis*. Other East Asian or Oceanian chionines not considered in the present analysis, such as *Mercenaria stimpsoni* (Gould, 1861), *Anomalocardia squamosa* (Linnaeus, 1758), and *Hinemoana acuminata* (Hutton, 1873), may also support this northern dispersal route (Beu and Maxwell, 1990; Huber, 2010; Roopnarine et al., 2008). The Alaska Current could have been acted as the dispersal mechanism of this event (Bernard et al., 1991).

4.3. The Ameghinomya clade

The ‘Ameghinomya’ clade seems to have a less complex biogeographic history. The origin of the group is inferred in the South Eastern Pacific by the presence in this area of *A. chilensis* (late Miocene) and *A. antiqua* (Pleistocene–Recent), but the latter species is also present in the South Western Atlantic. The probabilities of both regions as origin areas for the group are nearly similar. All remaining *Ameghinomya* species possess a South Western Atlantic distribution (excluding the Chilean *A. volckmanni*) and they were restricted to the late Miocene Valdesian and Paranaian provinces (Martínez and del Río, 2002). At the end of the Miocene, they disappear in the region with the exception of *A. antiqua* (von Ihering, 1907; del Río, 1994; Pérez et al., 2013). The poorly known ‘*Chione*’ *laciarina* Feruglio, 1954 (early Pliocene, Terraces of Cerro Laciara, Argentina) may represent the earliest record the latter species (DEP, pers. obs.). Nowadays, *Ameghinomya* represents cold water taxa in contrast to *Anomalocardia*, *Chione*, and other warm water taxa with tropical histories (Aguirre, 1990; Martínez et al., 2016).

The tempo of the dispersal events of the Chioninae clades in South America coincides with the complete opening of the Drake Passage Gateway around the Oligocene–Miocene boundary (Barker and Burrell, 1977; Barker and Thomas, 2004). Palaeogeographic reconstructions of this time span (Malumián and Nájuez, 2011) indicate more extensive water coverages –due to marine transgressions– than today and, therefore, shorter pathways for bivalve dispersals.

5. Conclusions

A Dispersal-Vicariance model that includes long-distance dispersals events fitted better our data, and these events may be important beyond oceanic islands systems. The ‘Chione’ clade is mainly a Caribbean lineage but further studies on this group are needed. The ‘Ameghinomya’ clade has a mostly Atlantic history in opposite to the ‘Protothaca’ clade. Both lineages may have split before Miocene times (related to the opening of the Drake Passage Gateway) and they diversified in different areas: the *Protothaca* lineage mainly in the Eastern Pacific (from North Chile to Alaska) and the *Ameghinomya* lineage mainly in the South Western Atlantic.

Acknowledgments

Thanks to M. Alvarez (MACN) for his helpful comments. CONICET is acknowledged for the post-graduate grants given to DEP and the use of TNT software is facilitated by Willi Hennig Society. We thank the Museo Argentino de Ciencias Naturales for generating an interdisciplinary place that allowed this research. We thank N. Matzke (The Australian National University) and an anonymous reviewer for their constructive comments, which helped us to improve the manuscript.

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