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The presence of *Tawera gayi* (Hupé in Gay, 1854) (Veneridae, Bivalvia) in southern South America: Did *Tawera* achieve a Late Cenozoic circumpolar traverse?

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Abstract

Cenozoic *Tawera* Marwick, 1927 from the Southern Hemisphere exhibits a pattern of disjunt distribution around the southern oceans. A single species, *Tawera gayi* (Hupé in [Gay, C. (1854). Historia Física y Política de Chile, Zoología 8. Paris.]) is confined to southern South America. Taking into account the occurrence of *Tawera* in the fossil record, taxonomy based on shell morphology, and available information on extant species of *Tawera*, it is plausible that the genus appeared first in southern Australia during the Early Miocene, and then expanded and radiated to New Zealand. It also appears that *Tawera* first crossed from Australasia to South America during the Early Pleistocene. This picture can be better explained if *Tawera* was able to achieve circumglobal range by means of the Antarctic Circumpolar Current. Thus, different potential factors of dispersal (i.e., larval dispersal, drifting, kelp rafting and Pleistocene cooling) are considered and discussed.

Shell morphology and overall appearance of *Tawera gayi* is very similar to *Tawera philomela* (Smith, 1885) from South Africa and *Tawera mawsoni* (Hedley, 1916) from Macquarie Island, suggesting these taxa have a close relationship. One postulated explanation, which should be confirmed by means of a phylogenetic study, is a subsequent migration of *Tawera* from South America arriving first to the Southern African Region (via the West Wind Drift Islands Province), and then probably coming back again to Australasia. It could have been mediated via the same current during the Late Pleistocene and much later during the Holocene.

Keywords: *Tawera*; Cenozoic; South America; Paleobiogeography; Dispersion; Migration routes

1. Introduction

The deep ocean that separates South America from South Africa, New Zealand and Australia represents a major barrier for the dispersal of sessile or slow mobile nearshore marine benthic taxa (Castilla and Guiñez, 2000). However, these regions, especially New Zealand and South America, share many benthic marine molluscan genus-group taxa with different biogeographic origins. Based on the fossil record, Beu et al. (1999) grouped these common mollusc faunas into three major groups, i.e., cosmopolitan genera, Gondwana genera and Cenozoic dispersers. Within the Cenozoic dispersers, they recognized a great number of taxa which migrated from New Zealand to South America during the Oligocene–Miocene interval, with only one possible exception being *Tawera*, Marwick, 1927 (type species *Venus spissa* Deshayes, 1835) which probably dispersed during the Pleistocene or the Recent.

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In the Southern Hemisphere *Tawera* displays a disjunt biogeographical distribution, with occurrences in Australasia, South America, the Mid-Atlantic islands (i.e., Tristan da Cunha and Gough Island, Nightingale Island, South Georgia) and off Southwestern Africa (Dell, 1964; Pether, 1993). In that sense, Soot-Ryen (1960) suggested that the origin of *Tawera gayi* (Hupé in Gay, 1854) from South America and *Tawera philomela* (Smith, 1885) from the Mid-Atlantic islands could have been the Magellan region; pointing out that the drift time from New Zealand around Cape Horn to Tristan da Cunha is nearly two years, and from the Straits of Magellan to Tristan da Cunha is four months with a speed of 20 miles a day.

A phylogenetic analysis on molecular data on living *Tawera* species is needed to elucidate the evolutionary history of the genus. In the meantime, however, this work attempts to reconstruct the origin and probable migration routes of *Tawera* by the analysis of the world-wide fossil and living *Tawera* distribution.

Based on the world-wide fossil record of *Tawera*, the purpose of this contribution is to reconstruct the paleobiogeographic history of *T. gayi* and to explain its arriving to southern South America during the Cenozoic. In addition, available taxonomic information on fossil and living *Tawera*, biological and ecological characteristics of *Tawera* (e.g., mode of life, pelagic stages) and paleoenvironments considerations (e.g., currents, glaciations) were also taken into account in these interpretations.

2. Material and methods

T. gayi from southern South America was studied on the basis of living and fossil specimens from Tierra del Fuego, Argentinian Patagonia and southern Chile. These specimens are housed in the Centro de Investigaciones Paleobiológicas (CIPAL), Universidad Nacional de Córdoba under prefix CEGH-UNC 22309-22358.

T. philomela specimens provided by the South African Museum Cape Town, with the permission of the South African Heritage Resources Agency were used here for comparison with *T. gayi*. These specimens are also housed in the CIPAL under prefix CEGH-UNC 20570-20587.

Tawera species from New Zealand and Australia were also revised. These specimens belong to the New Zealand Geological Survey macrofossil collections (GS numbers; additional details of these records are provided in Appendix I). The revision was completed with the description of holotypes and paratypes of the different *Tawera* species described by Smith (1885), Hedley (1916), Marwick (1927, 1928), Powell (1955) and Dell (1964), among others.

Finally, the occurrence of *Tawera* in the fossil record is also analysed and treated here within an environmental and ecological context to explain the probable dispersion and migration routes.

3. Remarks on systematics of *T. gayi* and other cogeneric species

3.1. Previous denominations for T. gayi

Tawera was proposed by Marwick (1927) for a group of New Zealand Tertiary and Recent venerid species. This author also transcribed von Ihering's statement indicating a close relationship between *Chione gayi* (i.e., *T. gayi*) from southern South America and *Chione mesodesma* (i.e., *Tawera spissa*) from New Zealand. Soot-Ryen (1959) noted that *Venus gayi* from Chile was closely related to species of the genus *Tawera* Marwick, 1927, and could well be placed in that genus. Nevertheless, Soot-Ryen (1959) referred to this taxon as *Clausinella*, Gray, 1851 (type species *Venus fasciata* da Costa, 1778). However Dell (1964), using hinge characters as diagnostic features for the genus, placed the South American species in *Tawera*. He also pointed out the reasons why he thought that the South American shells do not belong to *Clausinella*. Dell (1964) also noted that using hinge characters, the species from off Gough Island (Mid-Atlantic), identified as *T. philomela* Smith, would be included in *Tawera*. Fischer-Piette and Vukadinovic (1977) also reviewed and listed some species assigned to *Tawera*. In a revision of Cenozoic molluscs from New Zealand, and based on hinge characters as diagnostic features, Beu (2004) transferred different taxa previously assigned to *Tawera*, to *Chamelea* Mörch, 1853. This author considered that hinge differences recorded by Marwick (i.e., more or less divergent) are not more than those to be expected between congeneric species, in species groups separated since at least mid-Cenozoic time. The taxa transferred include all the New Zealand species previously referred to *Tawera*, some Australian species such as *Tawera gallinula* (Lamarck, 1818) and *Tawera lagopus* (Lamarck, 1818), and other Southern Hemisphere species such as *T. gayi* from South America and *T. philomela* from the Mid-Atlantic islands.

However, a recent molecular analysis by Kappner and Bieler (in press) constitutes new evidence that shows that *Tawera* is not synonymous with *Chamelea*, and these two genera are distinct from each other. *Tawera* is a basal Venerinae, while *Chamelea* is very