Early Pliocene tracer of North Atlantic and South Pacific sea surface currents: *Janthina typica* (Bronn, 1860) (Mollusca: Gastropoda)

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ABSTRACT

Janthina typica is an extinct, rare, floating species of gastropod from the early Pliocene whose fossils have an unusual geographic distribution, appearing in the eastern North Atlantic archipelagos (Canary, Azores, Madeira and Selvagen Islands), Morocco, and Pacific (New Zealand, Australia and Japan). This study examines the origin of this biogeography and how the species may have dispersed via sea surface currents. We have considered the published ecological aspects of the genus *Janthina*, the *Janthina typica* fossil localities, and ocean palaeocurrents. Abundant specimens of *J. typica* are found in marine deposits on Gran Canaria island (northeast Atlantic), $^{40}Ar/^{39}Ar$ dated at 4.2 Ma. These deposits therefore accumulated just before the end of the early Pliocene warm climate and closely predate the start of global changes that gave rise to the world's present climate. In the early Pliocene, the cold Canary Current did not yet exist. The subtropical northeastern Atlantic Ocean was warmer than today and its waters would have met the Circumtropical Current that crossed the Central American Seaway from the Caribbean to the Pacific. From there, the South Equatorial Current flowed towards the eastern coast of Indonesia before splitting north towards Japan and south as the East Australian Current. The latter must also have extended along the southern coast of Australia, crossing the Bass Strait before reaching the area of modern-day Perth in southwestern Australia. The reverse journey (from Australia to the eastern Atlantic Ocean) would have posed far more obstacles, and is considered improbable. *J. typica* therefore likely originated in the East Atlantic. The main causes for its extraordinary geographic distribution are its ecology as a floating animal in warm water, tectonic plate movements that permitted an open Central American Seaway and a restricted Indonesian Seaway, and Earth's rotation and its influence on marine currents.

Key words: pelagic mollusk; warm water species; Pliocene climate; plate tectonics; Coriolis effect; early Pliocene currents.

RESUMEN

Janthina typica es un molusco gasterópodo flotante, extinguido y raro del Plioceno. Sus fósiles presentan una distribución geográfica inusual apareciendo en los archipiélagos del este del Atlántico norte (Islas Canarias, Azores, Madeira y Salvajes), en Marruecos y en el oeste del Pacífico (Nueva Zelanda, Australia y Japón). En el presente trabajo se estudia la causa de esta biogeografía y de su dispersión mediante corrientes marinas de superficie. Para ello se han considerado los aspectos ecológicos del género Janthina, las localidades fósiles de J. typica y las paleocorrientes oceánicas. Abundantes ejemplares de J. typica se han encontrado en depósitos marinos de la Isla de Gran Canaria que han sido datados en 4.2 Ma. Esta época es justamente anterior a la terminación del clima cálido del Plioceno inferior y se aproxima al comienzo de los cambios globales que van a dar lugar al modelo climático actual. En el Plioceno inferior la corriente fría de Canarias no existía. El Atlántico norte subtropical era más cálido que en la actualidad y sus aguas se encontrarían con la Corriente Circumtropical que cruzaba el Paso de América Central desde el Mar Caribe al Océano Pacífico. Desde ahí, la Corriente Ecuatorial del Sur fluye hacia las costas de Indonesia en donde se divide, al norte hacia Japón y al sur hacia las costas de Australia llegando a alcanzar una posición frente a la actual ciudad de Perth tras atravesar el Estrecho de Bass. El trayecto inverso (de Australia al este del océano Atlántico) encontraría más obstáculos y puede considerarse altamente improbable. De ello se deduce que J. typica se originó en el Atlántico europeo. Las principales causas de su extraordinaria distribución geográfica son su ecología, por ser un animal flotante en aguas cálidas, los movimientos de las placas tectónicas, que permitieron el paso de América Central y un estrechamiento del paso de Indonesia, y el movimiento de rotación de la Tierra y su influencia sobre las corrientes marinas.

Palabras clave: moluscos pelágicos; fauna de aguas cálidas; clima del Plioceno; placas tectónicas; efecto Coriolis; corrientes del Plioceno temprano.

INTRODUCTION

On Gran Canaria (Canary Islands, Spain; Figure 1) marine deposits at La Esfinge site (Figure 2) host a considerable accumulation of *Janthina typica* (Figure 3). These deposits have been recently dated (Meco *et al.*, 2015) using $^{40}Ar/^{39}Ar$ to 4.2 Ma from samples of pillow lava that entered into contact with it. The aim of the present paper is to show the geographic distribution of *J. typica* in the Atlantic and Pacific oceans during the early Pliocene. The paper presents hypotheses that could explain its notable dispersal as a floating animal in warm water.

Meco, J., Lomoschitz A, Betancort, J.-F., 2016, Early Pliocene tracer of North Atlantic and South Pacific sea surface currents: *Janthina typica* (Bronn, 1860) (Mollusca: Gastropoda): Revista Mexicana de Ciencias Geológicas, v. 33, núm. 2, p. 192-197.

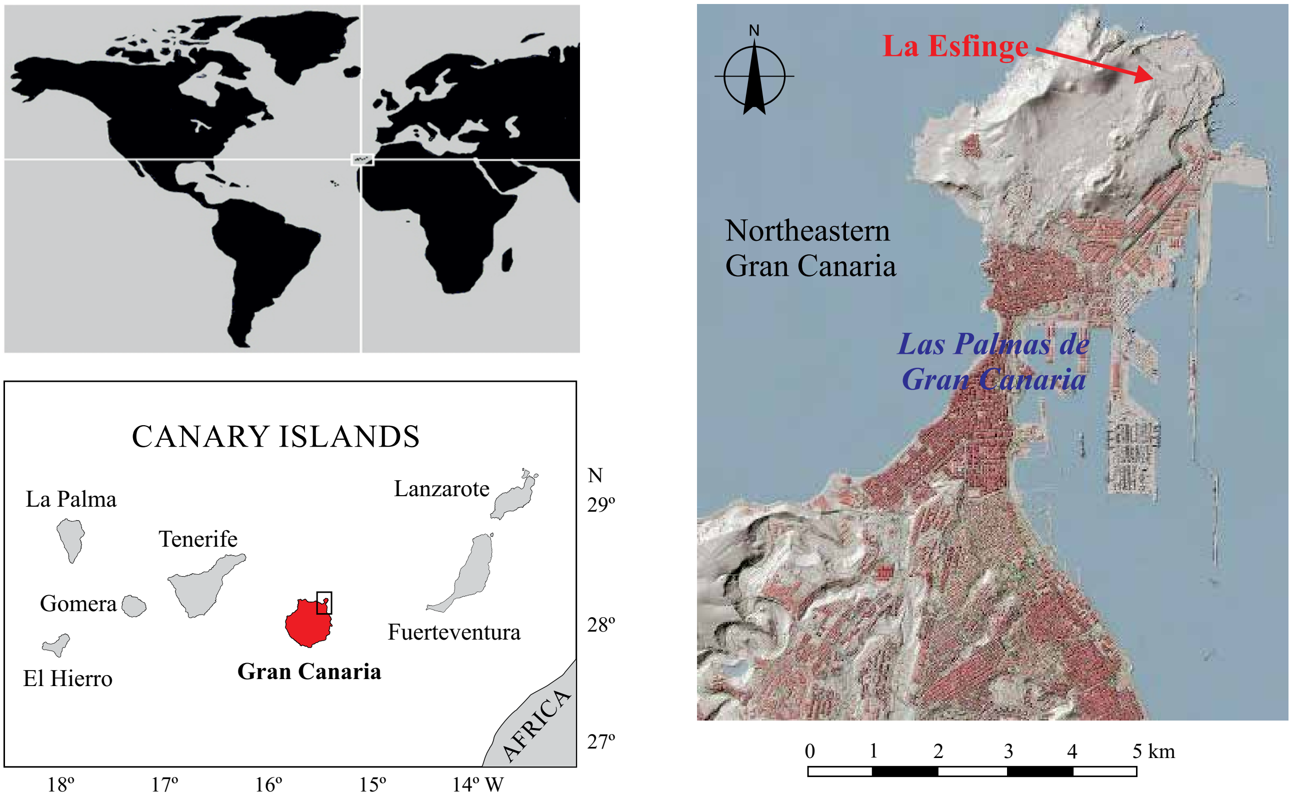

Figure 1. Location of La Esfinge site in northeastern Gran Canaria, where *Janthina typica* has been found.

***Janthina typica*: ecology and palaeodistribution**

The geographic distribution of fossil specimens of the tropical gastropod *Janthina typica* (Bronn, 1860) (= *Hartungia typica* Bronn = *Janthina Hartungi* Mayer = *Hartungia chuberti* Chavan) is striking for the great distances between the sites where this taxon has been found: from the Canary Islands (Meco *et al.*, 2015), the Azores (Bronn, 1860; Mayer, 1864), Madeira (Mayer, 1864), Selvagem Grande (Joksimowitsch, 1911) and Atlantic Morocco (Chavan, 1951) to the antipodean locations of New Zealand, Australia and Japan (Tomida and Kitao, 2002; Beu and Raine, 2009).

The current *Janthinidae* comprise a family of pelagic gastropods that live in colonies in warm and temperate seas, floating on a bubble-like raft of their own making, bound by mucus secreted from the organisms´ feet, and they feed on hydrozoans such as *Velella* and *Physalia* (Nicklès, 1950; Laursen, 1953; Powell, 1979; Janssen, 2007; Churchill *et al.*, 2011). This unusual adaptation enables them to travel enormous distances by drifting along with the currents, and sometimes they are cast onto beaches in significant numbers by on-shore winds (Beu and Raine, 2009).

J. typica is a fossil species from the early Pliocene (5.3 Ma to 3.6 Ma; Gradstein *et al.*, 2004). The other localities where *J. typica* is found span much of the Pliocene. On Santa María Island in the Azores, specimens have been found in Feteirinhas and Pinheiro on the southeastern tip of the island (Reiss and Bronn, 1863). In a nearby locality, Pedra que Pica, the marine deposits have been attributed to the Messinian based on an $^{87}Sr/^{86}Sr$ age of 5.51 Ma (Kirby *et al.*, 2007). The oldest shield of Madeira Island has yielded a $^{40}Ar/^{39}Ar$ age >4.6 Ma (Geldmacher *et al.*, 2000) to 5.3 Ma (Klügel, 2009); therefore, the marine deposits at the Sao Vicente locality are also probably early Pliocene. In Selvagem Grande the marine deposits accumulated before the Pliocene volcanic cycle occurring at 3.4 Ma (Geldmacher *et al.*, 2001). The marine deposits at Aïn Sebaa near Casablanca in Morocco are referred to the Piacenzian stage (Chavan, 1951). In New Zealand, *J. typica* has been found in deposits assigned to the Kapitean to Waipipian stages (Beu and Raine, 2009), which are roughly contemporaneous with the uppermost Messinian-Lower Zanclian to Lower Piacenzian stages (*ca*. 6 Ma to *ca*. 3 Ma). In southeastern Australia (Victoria) and western Australia (Perth) the deposits that yielded *J. typica* were included in the Kalimnan stage (Tate, 1893; Beu and Raine, 2009), which corresponds roughly to the Upper Zanclian and Lower Piacenzian (*ca*. 4.4 to *ca*. 3 Ma). The *J. typica* specimens found in Kyushu, South Japan, were included in the earliest Pliocene (Tsuma Formation *ca*. 5 Ma) and in the latest Pliocene (Takanabe Formation, 2.6–2.5 Ma; Tomida *et al.*, 2013).

In the early Pliocene (5 Ma to 4 Ma), Earth's climate was warm in many regions and temperate in others. The gradual cooling that followed the early Pliocene led to the establishment of modern temperature patterns (Fedorov *et al.*, 2013). Thus, the age of the Gran Canaria marine deposits with *J. typica* (4.2 Ma) falls within the early Pliocene warm period, but is close to the transition into the cooling period that followed.

The geological characteristics and sedimentary interpretation of the Gran Canaria marine deposits that contain a significant accumulation of *J. typica* shells, along with their isotopic age (4.2 Ma; Figure 2), were reported in a previous paper (Meco *et al.*, 2015). Other marine deposits of Las Palmas de Gran Canaria are also early Pliocene but these sediments provided a $^{40}Ar/^{39}Ar$ age of 4.8 Ma (Meco *et al.*, 2015) and no fossil specimens of *J. typica* have been found in them. The fossils contained indicate a coastal and littoral habitat (*e.g.*, *Patella ambroggii* Lecointre) with a warm intertropical climate (*e.g.*, *Persististrombus coronatus* Defrance), *Nerita emiliana* Mayer).

In the present paper the ecology of *Janthina* is discussed and the oceanic currents of *ca*. 4 Ma are summarized, mainly from the findings

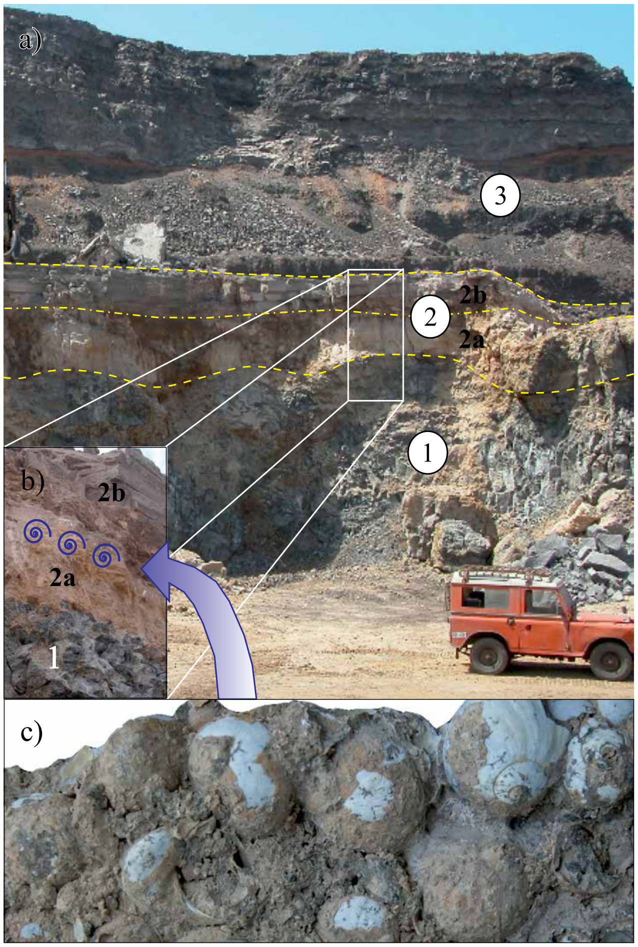

Figure 2. Geological context at La Esfinge (Gran Canaria). (a) Section showing the fossiliferous marine deposit (2) between pillow lavas with a 4.2 Ma $^{40}Ar/^{39}Ar$ age (1) (from Meco *et al.*, 2015) and Pleistocene volcanics (3); (b) detail of layer 2: 2a marine sands with fossils inside and 2b aeolian sands; (c) accumulation of *Janthina typica* at the top of layer (2).

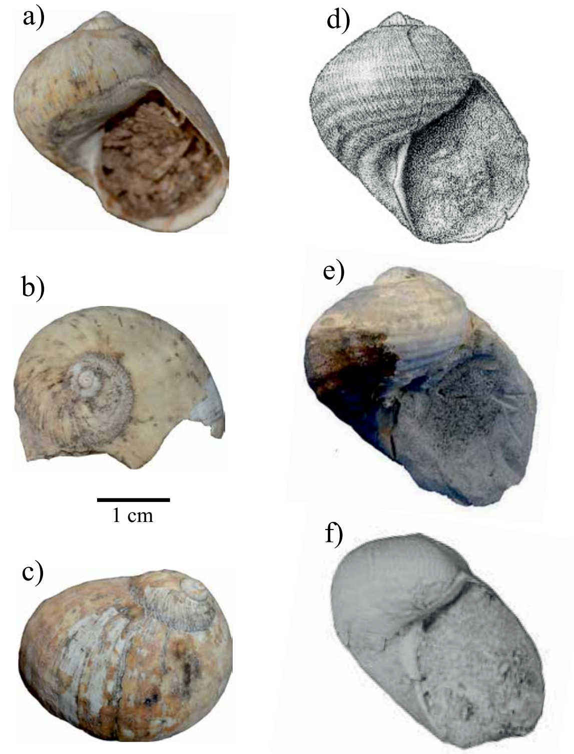

Figure 3. *Janthina typica* (Bronn, 1861) showing a) apertural view b) apical view c) lateral view (LE2051) from the early Pliocene (4.2 Ma) at La Esfinge (Gran Canaria, Spain). Note that it has faint but visible folds; d) drawing of apertural view from early Pliocene (Opoitian) at southwest Aukland, New Zealand (Beu and Maxwell, 1990); e) apertural view (MGF3472) from the Pliocene of Japan (Tomida *et al.* 2013); f) apertural view (MFM112203) from Upper Pliocene of Japan (Tomida and Kitao, 2002) as *Hartungia japonica* (Tomida and Itoigawa, 1984).

of the Ocean Drilling Program (ODP), which allow sites where fossil specimens of *J. typica* have been found to be connected. The dispersal of this species from the eastern Atlantic to the western Pacific (or *vice-versa*), must have been determined by the sea surface currents at that time, which were in turn controlled by tectonic plate movements, and pressure gradients and the effect of the Earth's rotation (the Coriolis effect).

INFLUENCE OF TECTONIC PLATE MOVEMENTS

Around 4.2 Ma ago, the geographic distribution of land masses (and so of the seas) differed significantly from today. Two important changes took place around this time that were caused by the movement of tectonic plates, and resulted in the closure of inter-ocean connections. One change caused the closure of the Central American Seaway, as the South American, Caribbean and North American plates moved closer together, and the Atlantic Ocean became isolated from the Pacific Ocean (Schmidt, 2007). In the other major change, the Indonesian Seaway closed as the Australian and Eurasian plates moved closer together, bringing about a partial isolation of the Pacific Ocean from the Indian Ocean (Gallagher *et al.*, 2009).

Closure of Central American seaway

The closure of the Central American Seaway (also called the Panamanian Seaway) can be deduced from the progressive differentiation in salinity between the Caribbean Sea and the Pacific Ocean which was taking place about 4 Ma ago (Keigwin, 1982). This change is documented in isotopic analyses of foraminifera extracted from ODP oceanic drilling samples, including ODP Site 1241 (Groeneveld *et al.*, 2006) in the eastern equatorial Pacific Ocean, and ODP Site 999 (Steph *et al.*, 2006) in the Caribbean Sea. Salinity was virtually the same on both sides of present day Panama 4.2 Ma ago (Sarnthein *et al.*, 2009), but shortly thereafter began the first phase of an increase in Caribbean salinity that concluded some 3.7 Ma ago. This time interval is considered to reflect the initial stage in the closure of the Central American Seaway (Chaisson and Ravelo, 2000). Thus, 4.2 Ma ago, the seaway still existed, and the Circumtropical Current that flowed east-to-west from the Caribbean to the Pacific, was still operative (Iturralde-Vinent and MacPhee, 1999; Mestas-Nuñez, 2014).

The Pacific Ocean warm pool

A comparison of foraminifera from ODP Site 806, near the Solomon Islands, and ODP Site 847, near the Galapagos Islands, reveals important changes 4.2 Ma ago that establish the timing of salinity differentiation at the latitude of Ecuador between the eastern and western sides of the Pacific Ocean. From this point onwards an enlargement of the West Pacific Warm Pool began and an eastwards lengthening of the cold tongue was initiated. The evolution of planktonic foraminifera and their ecology suggest that surface water cooling was taking place between 4.5 Ma and 4.0 Ma (Chaisson and Ravelo, 2000, Li *et al.*, 2006), which is interpreted to be a consequence of the Panamanian Seaway closure.

Indonesian Seaway closure

Foraminiferal analyses of Miocene to Holocene strata of the northwestern continental shelf off Australia have been used to chart the influence of the West Pacific Warm Pool (Gallagher *et al.*, 2009). Between 10 Ma and 4.4 Ma ago, the collision of Australia and Asia narrowed the Indonesian Throughflow. This "S" shaped current connects the West Pacific Warm Pool and the Indian Ocean, passing from south of the Philippines through the Makassar Strait (between Borneo and Sulawesi), turning southwards through the Flores Sea and the Timor Sea, ultimately heading southwest to the Indian Ocean (Figure 4). Warmer waters became trapped in the Pacific, creating a central West Pacific Warm Pool marine biogeographic province spanning a zone from the equator to 26°N (Gallagher *et al.*, 2009).

Between 4.4 Ma and 4 Ma, Indo-Pacific marine taxa migrated to waters off of northwestern Australia possibly because of a limited Indonesian Throughflow, and the absence of these taxa after 4 Ma indicates the possible restriction of this current. The Leeuwin Current, which flows from south of Java to the south of Australia along its west coast, did not begin until much later, in the Early Pleistocene (Gallagher *et al.*, 2009), and so offered no viable route for faunal migration 4.2 Ma ago. At the same time, beginning with the northward displacement of New Guinea and the emergence of the islands of Indonesia 5 Ma ago, exchange between the Pacific and Indian Oceans through the Indonesian Seaway was interrupted between 4 Ma and 3 Ma (Cane and Molnar, 2001). This had the effect of redirecting oceanic circulation from the southern Pacific warm waters northward to Japan surrounded by relatively cold waters of the northern Pacific. The presence of *J. typica* at *ca*. 5 Ma in southern Japan shows that the warm Kuroshio Currents flowed strongly in the earliest Pliocene (Tomida *et al.*, 2013).

Southern Australia

The Pliocene climatic and environmental evolution of southeastern Australia (Bass Strait) indicates that relatively stable and warmer marine conditions than the present day prevailed throughout most of the early Pliocene (Gallagher *et al.*, 2003). This corresponds to a period of low marine $\delta^{18}O$ values (corresponding to warmer waters and/or lower ice volume) from 4.2 Ma to 4.0 Ma (Shackleton *et al.*, 1995). This was also a time of relatively low ice volume in the Antarctic (Bart 2001; Gallagher *et al.*, 2003).

POSSIBLE HYPHOTHESES

There are no significant age differences among the sites where *J. typica* has been collected in the Pacific and Atlantic. This suggests that two opposing hypotheses may explain the path of its biogeographic dispersal: (a) migration from the eastern Atlantic Islands to the Australian coasts; or (b) migration from the western Australian coast to the eastern Atlantic islands.

Hypothesis 1: dispersal of *J. typica* from the eastern Atlantic Islands to the western Australian coast

At present, the Azores, Madeira, Salvagen and Canary Islands are situated within the North Atlantic subtropical gyre. Around 4.2 Ma, the waters were warmer and this gyre would have been weaker (Meco *et al.*, 2015). Nevertheless, the trade winds and associated currents likely existed, and would have allowed *J. typica* to disperse into the Caribbean Sea, and cross the Central American Seaway to the equatorial Pacific. Once it reached the equatorial Pacific Ocean, the trade winds of the intertropical zone could have carried *J. typica* westward into the southern hemisphere toward Indonesia. Because the Indonesian Troughflow was closed at the time, once the Equatorial Current reached the western Pacific, separate currents may have formed, one moving northward in the direction of Japan, and another southward to Australia and New Zealand (Figure 4).

Hypothesis 2: dispersal of *J. typica* from the western Australian coast to the eastern Atlantic islands

The reverse route, from the western Pacific to the eastern Atlantic, would have posed significant difficulties. Two possible paths could be invoked: (1) following the oceanic gyres through the Indian Ocean into the South Atlantic, and from there into the North Atlantic. This would have endangered the survival of *J. typica*, a warm water species, as it would have required passage through long sections of cold waters in both the northern and southern hemispheres; or (2) following the Equatorial Counter Currents eastward across the Pacific, though this would have meant overcoming the obstacle of the "doldrums", the area of low pressure around the equator where prevailing winds are calm. It should be noted that the Pacific Equatorial Countercurrent originated in the west and advanced eastward as modern climate conditions began to set in (Li *et al.*, 2006). Some 4.2 Ma ago, however, the countercurrent was shorter and the oceanic gyres were only in the formative stage of their modern configurations (Li *et al.*, 2006). The Pacific currents were no doubt different from those of today and in some areas may not have even existed. It would have been difficult for *J. typica* to migrate from the western Australian coast to the eastern Atlantic Ocean *ca*. 4.2 Ma ago.

Other older species of *Janthina* are very similar morphologically to the Canary I. *J. typica* (4.2 Ma), but designated *Hartungia* instead in the literature (for a taxonomic study, see Beu and Raine, 2009). *Hartungia elegans* occurred along the Pacific coast of southern and central Japan during the Late Miocene (planktonic foraminiferal Zone N. 17, at *ca*. 6.8 Ma; see Tomida and Nakamura, 2001) and *Hartungia pehuensis* occurs at Taranaki in northwestern New Zealand also during the Late Miocene (Marwick, 1926). The Late Miocene oceanic circulation pattern (Iturralde-Vinent and MacPhee, 1999, fig. 10; Li *et al.*, 2006, fig. 8) may have set the precedent for the early Pliocene dispersal route of *J. typica* from the Atlantic Ocean to the Pacific Ocean.

CONCLUSIONS

The principal explanation for the extraordinary geographic dispersal of *J. typica* are a combination of factors of different scale: ecological, geological and astronomical. Its ecology as a floating animal in warm waters and capable of long-distance transport in a short period of time (for a modern analog, see Bryan *et al.*, 2004) and the tectonic plate configuration that permitted an open Central American Seaway and also brought about a restricted Indonesian Seaway. The ancestor of *J. typica* is unknown. The great similarity between the Pacific and Atlantic forms (Figure 3) suggests a rapid dispersal rather than a geographic speciation. Accordingly, this species must have originated in the western Atlantic during the Late Miocene or earliest Pliocene and experienced a remarkable dispersal, crossing into the Pacific during the early Pliocene before reaching the vicinity of present-day Perth in Western Australia, as well as southern Japan. The presence of *J. typica* in these diverse localities indicates that warm waters existed throughout the dispersal route, and that the Canary Current was at that time warmer. The Circumtropical Current must have extended to the western Pacific,

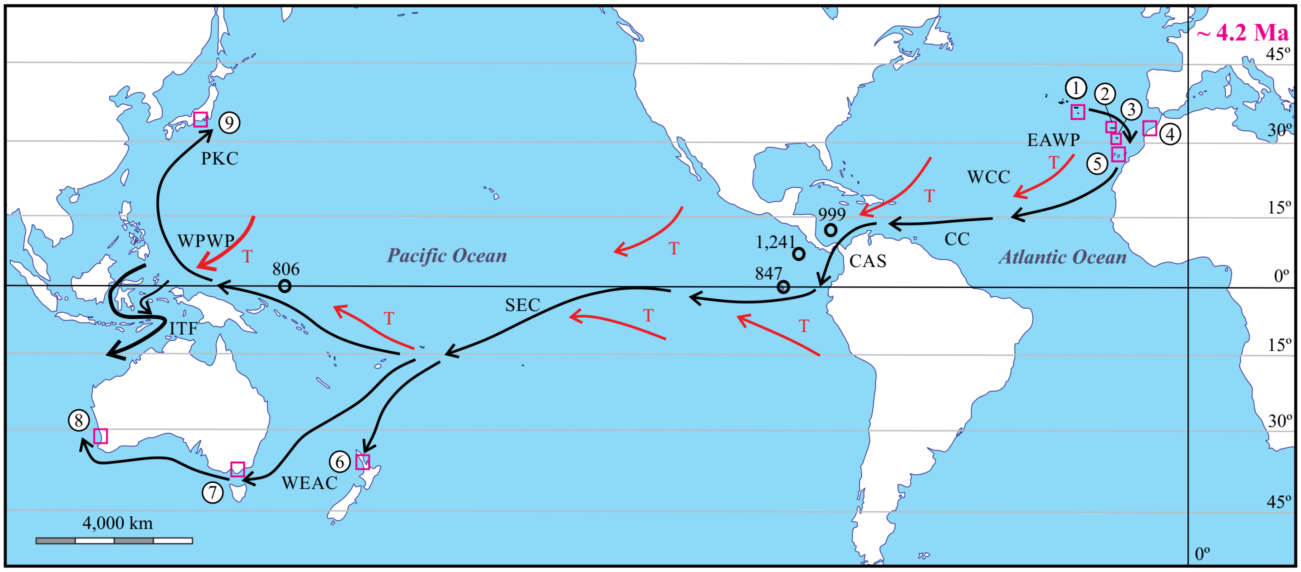

Figure 4. Biogeography of *Janthina typica* and reconstruction of the oceanographic dispersal route around 4.2 Ma in accordance with the most likely hypothesis. Important localities (pink squares) are shown with numbered circles: (1) Santa Maria I. (Azores Islands), (2) Madeira I., (3) Selvagem Grande I., (4) Casablanca (Morocco), (5) Gran Canaria I. (Canary Islands), (6) Auckland (New Zealand), (7) Victoria (Australia), (8) Perth (Australia) and (9) Kyushu (Japan). ODP Sites (black circles). Dispersal route of *Janthina typica* (black arrows) from the East Atlantic Warm Pool (EAWP), through the Warm Canary Current (WCC), the Circumtropical Current (CC), the Central America Seaway (CAS), and the South Equatorial Current (SEC), and to the Warm East Australian Current (WEAC); or trough the Western Pacific Warm Pool (WPWP) to the Proto Kuroshio Current (PKC). Indonesian Through Flow (ITF). T: Trade winds (red arrows).

while the cold Humboldt Current in the area of the Galapagos Islands must have been weak or absent. On reaching Panama, the Equatorial Countercurrent must have been deflected southward. This would allow connection with the Pacific South Equatorial Current, and end in a bifurcation in Indonesia with one branch heading north (Kuroshio Current) and the other south (East Australian Current). This latter current would extend through the Bass Strait and along the southern coast of Australia as far as modern-day Perth, which would also require some distancing of the West Wind Drift.

ACKNOWLEDGEMENTS

We are grateful to Daniel R. Muhs (U.S. Geological Survey), Alan G. Beu (GNS Science, New Zealand) and to Francisco García-Novo (Universidad de Sevilla, Spain) for comments on a draft of this manuscript. We also thank the comments from editor Thomas M. Lehman (Texas Tech University) and the suggestions of Sandra Gordillo and two anonymous reviewers.

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Manuscript received: January 26, 2016
Corrected manuscript received: April 24, 2016
Manuscript accepted: April 30, 2016