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First record of buccinid genus *Chauvetia* (Mollusca: Gastropoda) from the fossil record of the New World (Miocene, Venezuela) and its paleobiogeographic implications

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Abstract.—Until now, the buccinid genus *Chauvetia* was considered of European or West African origin, and is still endemic to these areas today. This paper describes the oldest representative of the genus, *Chauvetia inopinata* nov. sp., from the upper Burdigalian-lower Langhian transition Cantaure Formation of Venezuela. This surprising record suggests a New World tropical origin to the genus and subsequent immigration to the Old World before the earliest known Old World record, which is upper Tortonian. We postulate that this pre-late Tortonian (pre-8.12–7.42 Ma) dispersal of the tropical Gatunian west-Atlantic *Chauvetia* into the tropical East Atlantic European-West African Province most probably happened during the 10.71–9.36 Ma interval (early–mid Tortonian) during which the Circum-Tropical Current weakened, and the northward Intra-Caribbean Current had started, enhancing the Gulf Stream and the North Atlantic Current. This new data constitutes compelling evidence of a pre-Pliocene eastward dispersal of New World shallow marine organisms across the Atlantic.

Introduction

The rich Lower to Middle Miocene marine fossiliferous deposits of the Cantaure Formation, Paraguaná Peninsula, northern Venezuela (e.g., Jung, 1965; Gibson-Smith and Gibson-Smith, 1974; Landau and Petit, 1996; Landau et al., 2007) continue to astound us and to yield interesting results as well as surprising findings. In this paper, we report and discuss the unexpected presence of the buccinid genus *Chauvetia* Monterosato, 1884 in the Cantaure assemblage, with the description of a new species.

Chauvetia encompasses a group of buccinid species with small shells, a few millimetres to one centimetre tall, usually slender fusiform in shape, with both axial and spiral sculpture, forming a reticulate pattern, often with small tubercles developed at the intersections. The protoconch in these gastropods is very characteristic, paucispiral with a large nucleus. Although traditionally placed within the Buccinidae, *Chauvetia* species are not particularly similar to any other buccinid genus. Unpublished preliminary molecular studies are not conclusive and do not exclude alternative relationships (e.g. Muricidae: personal communication, M. Oliverio, 2014).

The genus comprises a fairly large number of extant species (approximately 43) occurring in the southern North Sea, the English Channel, and along the Atlantic coasts of continental Europe (Graham, 1988; Rolán, 1983) and West Africa, as far south as the Ivory Coast, the Macaronesian Islands, and also the Mediterranean (Rolán, 2005; Oliver and Rolán, 2008; Wirtz, 2011). The most southwestern Recent record seems to be that for *Chauvetia helenae* (E.A. Smith, 1890), from the Island of Saint Helena in the eastern South Atlantic, although the validity of this taxon is unclear (Bouchet, 2013). Recent species inhabiting the Mediterranean were reviewed by Micali (1999), those from the Canary Islands by Nordsieck and García-Talavera (1979), and those from West Africa by Ardovini (2008), Oliver and Rolán (2008, 2009) and Gofas and Oliver (2010).

The genus has sometimes been placed in the subfamily Donovaniinae Casey, 1904. This subfamily was originally introduced as a "tribe" within the Pleurotomidae and Casey (1904) did not explicitly introduce Donovaniinae as replacement for Lachesinae Bellardi, 1877 (based on *Lachesis* Risso, 1826, invalid, junior homonym of *Lachesis* Daudin, 1803 [Reptilia]), and therefore it was considered invalid by Bouchet and Rocroi (2005).

The oldest occurrence of the genus *Chauvetia* comes from the Old World fossil record, from the Atlantic Upper Miocene of southern Portugal, with one undescribed species present in the Tortonian of the Cacela Formation of the Algarve Basin (Cacela locality, BL collection, and personal observations).

This paper reports a new Miocene species of *Chauvetia*; the oldest record for the genus and, so far, the only one in the New World, in the Caribbean. This occurrence sheds new light on the geological history and the biogeography of the genus, challenging its accepted "European origin."

Geologic and stratigraphic setting

The *Chauvetia* material herein described and discussed comes from the San José de Cocodite region in the Paraguaná Peninsula of northern Venezuela (Falcon State). The collection site where it originates from is located in the Cantaure area, 3.4 km west of the church of the village of San José de Cocodite (as the crow flies), at an altitude of approximately 140 m above sea-level on an acacia and cactus covered area approximately 400 m South of Casa Cantaure with the approximate geographic coordinates: N11° 56' 24.1" W70° 01' 04.5" (Fig. 1; location of Casa Cantaure after Griffiths *et al.*, 2013: N11° 56' 35.9" W70° 01' 10.8").

The specimens were collected from a thick friable yellow fine sandstone bed containing an abundant and diversified molluscan assemblage (mostly gastropods and bivalves with rare fossils of *Nautilus* cephalopods), as well as other elements such as barnacles and corals. This bed is part of the Cantaure Formation (Jung, 1965; Hunter and Bartok, 1974) which as a whole, after Díaz de Gamero (1974), is correlated with the planktonic foraminiferal biozones *Globigerinatella insueta* and *Praeorbulina glomerosa* of Bolli (1966), biozones N7 and N8 of Blow (1969), which in turn, according to the latest geologic time scale of Gradstein et al. (2012), correspond to the Lower to Middle Miocene transition, upper Burdigalian to lower Langhian. Rey (1996) corroborates this biostratigraphic correlation stating that the Cantaure calcareous nannofossil assemblage contains the *Helicosphaera ampliaperta* and *Sphenolithus heteromorphus* markers corresponding to the biozones NN4 and NN5 of Martini (1971), which broadly correlate with the above mentioned foraminiferal zones.

In several recent papers, however, the Cantaure Formation continues to be assigned to the Lower Miocene, Burdigalian, after the traditional correlation of Díaz de Gamero (1974) and Rey (1996). Aguilera and Rodrígues de Aguilera (1999), based on planktonic foraminifera data from a personal communication by Collins, place the Cantaure Formation in the Lower Miocene, Burdigalian. Griffiths et al. (2013), based on $^{87}Sr/^{86}Sr$ isotope data obtained from corals, assign an age of between 16.3 and 16.6 Ma to the fossils of Cantaure, placing them in the Burdigalian.

These authors further comment that the isotopic results obtained are in good agreement with the traditional biostratigraphic age estimates for the Cantaure Formation based on the identification of the N7-N8 planktonic foraminiferal zones by Díaz de Gamero (1974) and the nannofossil biozones NN4-NN5 by Rey (1996). Anderson and Roopnarine (2005), on the other hand, in their Table 2, place the Cantaure Formation in the Burdigalian-Langhian, straddling the Lower-Middle Miocene boundary.

The Cantaure Formation consists of an approximately 75 m thick sedimentary sequence mainly composed of fossiliferous silts, silty sandstones and fine to medium sandstones interbedded with thin algal limestones (Hunter and Bartok 1974; Léxico Estratigráfico de Venezuela, 1997; Aguilera et al., 2013). A diverse fossil assemblage, particularly rich in molluscs, but also featuring corals, decapods and cirripedian crustaceans, and fish remains, has been identified in the sediments of the Cantaure section, especially in its lower part (e.g. Jung 1965; Nolf and Aguilera 1998; Aguilera and Rodrigues de Aguilera, 1999; Griffiths et al., 2013). Locally, decimetric boulders of limestone with in situ attached valves of the shallow marine bivalve *Spondylus* sp. may be observed within the friable fine sandstone beds. This fossil assemblage is indicative of a shallow, coastal tropical marine environment, with clear waters and marine euhaline salinity (Jung, 1965; Díaz de Gamero, 1974; Nolf and Aguilera, 1998; Aguilera et al., 2013; Griffiths et al., 2013).

Systematic paleontology

The material described here is from the Gibson-Smith collection, housed in the Naturhistorisches Museum Basel (NMB coll.), Switzerland. Abbreviations: NMB, Naturhistorisches Museum Basel, Switzerland.

Measurements taken with scanning electron microscopy photographs: dn = diameter first ½ protoconch whorl; dp = diameter protoconch; dp/hp = diameter of protoconch/height; dp1 = diameter first protoconch whorl; hp = height protoconch.

<div align="center">

Class Gastropoda Cuvier, 1797
Superfamily Buccinoidea Rafinsque, 1815
Family Buccinidae Rafinsque, 1815
Genus *Chauvetia* Monterosato, 1884

</div>

Type species.—*Nesaea mamillata* Risso, 1826, by typification of replaced name, Recent, Mediterranean.

<div align="center">

Chauvetia inopinata new species
Figure 2.1–2.7

</div>

Diagnosis.—Shell small, fusiform, with a paucispiral protoconch bearing spiral cordlets, a teleoconch composed of strongly convex whorls, with predominant axial sculpture, without tubercles formed at the sculptural intersections and a small aperture without denticles.

Description.—Shell small for genus, fusiform. Protoconch paucispiral, composed of 1.5 convex whorls, with large nucleus (dn = 190 µm; dp = 460 µm; hp = 390 µm; dp/hp = 1.18; dp1 = 330 µm). Protoconch bearing sculpture of fine, close-set
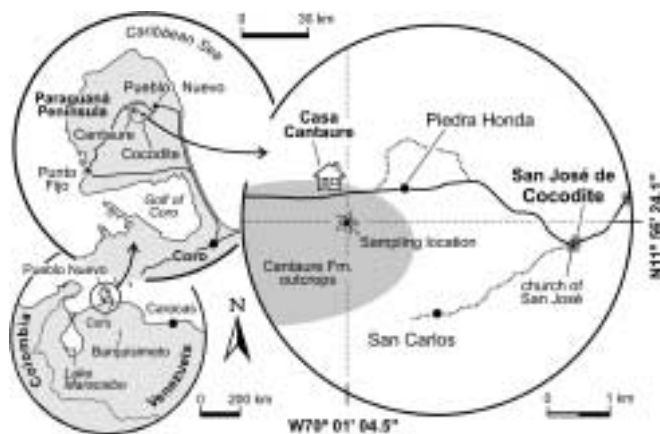

Figure 1. Geographic location of the study site South of Casa Cantaure, Paraguaná Peninsula, Falcón State, Venezuela, in which the specimens of *Chauvetia inopinata* nov. sp. species were collected.
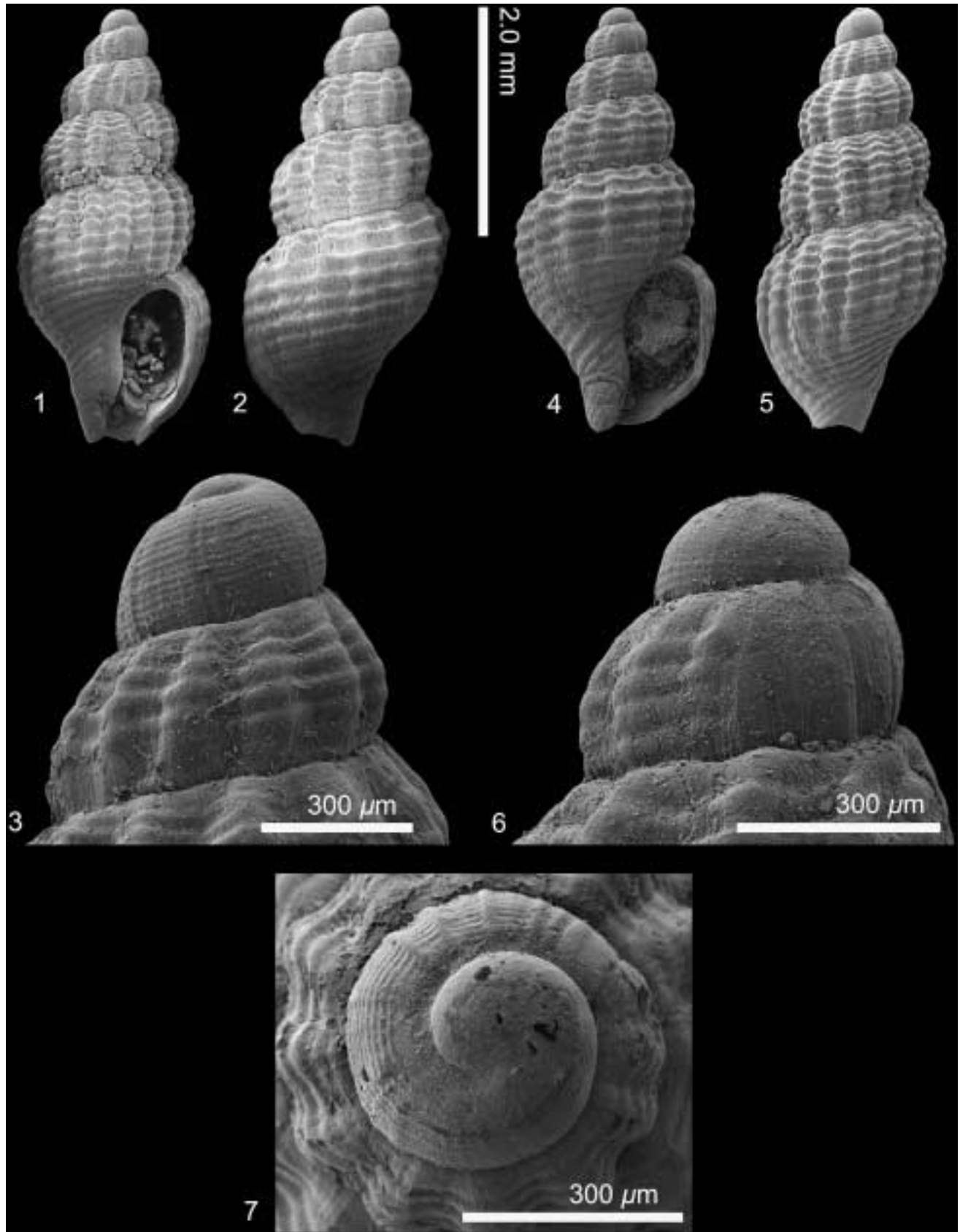
Figure 2. Specimens of *Chauvetia inopinata* nov. sp. from South of Casa Cantaure, Paraguaná Peninsula, Falcón State, Venezuela; Cantaure Formation, upper Burdigalian to lower Langhian, Miocene: (**1–3**, **7**) Holotype NMB H20317, height 3.9 mm. (**4–6**) paratype 1 NMB H20318. NMB locality 17516.

spiral cordlets. Junction with teleoconch sharply delimited by line of protoconch outer lip and beginning of adult sculpture. Teleoconch of four strongly convex whorls, with periphery just below mid-whorl. Suture linear, impressed. Axial sculpture predominant, consisting of weakly opisthocline rounded ribs, slightly narrower than their interspaces, seven on first teleoconch whorl, increasing in number abapically to 12 on penultimate whorl and 15–16 on last whorl. Spiral cords roughly equal in width to their interspaces, five on the first teleoconch whorl, increasing in number abapically to 7–8 on the penultimate whorl and 12 on last whorl. Spiral cords override axial ribs, but not swollen at sculptural intersections. Last whorl short, convex, constricted at base. Aperture small, ovate; outer lip slightly thickened at edge, smooth within; anal canal not developed, siphonal canal short, wide, open. Columella excavated, smooth. Columellar callus poorly developed, narrow, hardly thickened. Siphonal fasciole short, bearing spiral cords.

Etymology.—From Latin *inopinatus*, adjective, meaning unexpected, unforeseen, as we did not expect to find representatives of the genus in the Miocene Caribbean assemblages. *Chauvetia* gender feminine.

Types.—Holotype NMB H20317, height 3.9 mm (Figures 2.1–2.3, 2.7), paratype 1 NMB H20318, height 3.7 mm, paratype 2 NMB H20319, height 3.6 mm (Figures 1.4–1.6), paratype 3 NMB H20320, height 3.7 mm.

Other material examined.—Known only from type material.

Occurrence.—NMB locality 17516. South of Casa Cantaure, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, upper Burdigalian to lower Langhian, Lower to Middle Miocene transition.

Differentiation.—This new Venezuelan Miocene material is very unlikely to be conspecific with any of the known Pliocene to Recent European or West African congeners. However, several of the Recent eastern Atlantic European species have shells with closely similar sculpture: i.e. *Chauvetia mamillata* (Risso, 1826); *C. procerula* (Monterosato, 1889); *C. lamyi* Knudsen, 1956 among others. The shell of *Chauvetia inopinata* nov. sp. differs from most of its congeners in being smaller in size, about half the height of most modern European *Chauvetia* specimens, and in not having denticles developed within the aperture. The protoconch of the Cantaure specimens is also significantly smaller (dp = 460 μm) than that of most Recent species with similar sculpture, which have a protoconch diameter of 600–900 μm, depending on the species (see Oliver and Rolán, 2008, 2009; Gofas and Oliver, 2010).

Discussion and conclusion

In the present day, the genus *Chauvetia* has an eastern Atlantic and Mediterranean distribution. It spans several biogeographical provinces, from the cool temperate southern part of the Boreal-Celtic Province in the North, to the tropical Mauritanian-Senegalese molluscan province of Raffi et al. (1985), in the South.

The genus *Chauvetia* makes its first appearance in the fossil record in the European Upper Miocene, with one undescribed species present in the Cacela creek outcrop of southern Portugal (BL collection, and personal observations), lower member of the Cacela Formation. According to Cachão (1995) and Cachão and Silva (2000), the calcareous nannofossils assemblage from the fossiliferous beds of the Cacela creek outcrop correlate it with the lower part of the biozone NN11 of Martini (1971) or the biozone CN9a of Okada and Bukry (1980), upper Tortonian, approximately 8.12–7.42 Ma (geochronology according to the latest geologic time scale of Gradstein et al., 2012).

There are no published records for *Chauvetia* in the rich and diversified Miocene fossil record of Italy. In the European Lower Pliocene the genus is more speciose, with two species recorded by Chirli (2000) from the Italian assemblages, two species from the Atlantic Lower Pliocene of the Guadalquivir Basin, southern Spain (Landau et al., 2011), and two in the uppermost Zanclean to lowermost Piacenzian of the Mondego Basin of central West Portugal (Silva, 2001). However, for the Pliocene, by far the greatest diversity is seen in the Zanclean Mediterranean assemblages of the Estepona Basin of southern Spain, where at least ten species occur. This material awaits description as part of the Estepona series of monographs (e.g., Landau et al., 2004, 2009; Landau and Silva, 2006).

The genus *Donovania* Bucquoy, Dautzenberg, and Dollfus, 1883 is an invalid junior homonym of *Donovania* Leach, 1814 [Crustacea]), and considered a synonym of *Chauvetia*. The Middle Miocene species *Donovania miocaenica* Boettger, 1902 (figured by Zilch, 1934, pl. 18, fig. 31) from Kostej, Romania, seems to have a multispiral protoconch and a shallow anal sinus, and is not a *Chauvetia* but a turrid. Indeed Zilch (1934, p. 261) placed the species in the genus *Haedropleura* Bucquoy, Dautzenberg and Dollfus, 1883, however, the shell has unusually strong spiral sculpture for this genus and may be closer to the horaiclavid *Anacithara* Hedley 1922 (personal communication, R. Janssen, 2014).

The pre-Late Miocene history of the genus in the eastern Atlantic and the Mediterranean is unknown. The hitherto known fossil record and the present day distribution of the genus would suggest an eastern Atlantic origin. Therefore, the presence of the genus *Chauvetia* in the Lower-Middle Miocene of the Caribbean is totally unexpected, and very interesting. *Chauvetia inopinata* nov. sp. from Cantaure is now not only the earliest occurrence for the genus, but also its only known Western Atlantic record, fossil or extant. This Caribbean Miocene species sheds new light on the geological history and the biogeography of *Chauvetia*, modifying all previous notions on the origin and history of the genus.

Are the origins of the genus in the western Atlantic, in the Caribbean, rather than in the eastern Atlantic? Certainly other typically western Atlantic genera with paucispiral protoconchs, and hence inferred to have non-planktotrophic development (even intracapsular in most cases), seem to have found their way across the Atlantic (Vermeij and Rosenberg, 1993; Silva et al., 2011).

For example, the extant marginelliforms *Prunum* and *Persicula* are abundant and diversified in the western Atlantic. *Prunum* is a prominent element of the Neogene fossil assemblages of tropical America (Nehm, 2001; Landau and Silva, 2010).

Persicula is known from the fossil record of both the eastern and the western Atlantic since the Eocene (Nieulande, 1981; Coovert and Coovert, 1995, respectively). In Europe, however, the genus is absent in the Oligocene and Miocene, whereas the record is continuous on the other side of the Atlantic.

As shown by Silva et al. (2011), it is plausible to assume that representatives of these genera emigrated from the western Atlantic. All marginelliform gastropods have paucispiral protoconchs and for those species in which development is known, they are direct developing and non-planktotrophic (Coovert and Coovert, 1995; Penchaszadeh and Rincon, 1996). Such types of larval development would make the west-east Atlantic immigration more difficult, but not impossible.

Ávila (2005) noted that numerous extant species found both on the western Atlantic and in the Azores also have non-planktotrophic development. Moreover, he demonstrated a correlation between bathymetric distribution of species and dispersal ability; those gastropods with non-planktotrophic development living in the tidal zone are most likely to disperse, namely by rafting, attached to algae and other floating materials, which are more common at shallower depths.

Almost all *Chauvetia* species have a shallow bathymetric distribution, subtidal, at not more than 20–30 m depth (Oliver and Rolán, 2008, 2009). The possibility of dispersal by rafting is further supported by the findings of Hergueta et al. (2002), who observed that, for example, *C. mamillata* (Risso, 1826) in the Mediterranean coasts of Spain lives typically on sea grass blades and on algae, both substrates adequate for effective rafting. It is reasonable to assume that the Miocene western Atlantic representatives of these genera would live in similar habitats, and share similar modes of life, which would facilitate dispersal by rafting, especially taking into consideration the inferred shallow, coastal marine palaeoenvironments of Cantaure.

Vermeij and Rosenberg (1993) suggest that eastward dispersal of marine gastropods across the Atlantic is a somewhat recent phenomenon, with no documented cases older than Middle Pliocene (Piacenzian). This eastward dispersal resulted from changes in northern Atlantic Ocean currents, following the final closure of the Central American Seaway (CAS) at around 3.5–3.0 Ma (Coates et al., 2004; Coates and Stallard, 2013). Before the emersion of the Isthmus of Panama, westward flowing oceanic currents —the Circum-Tropical Current— normally prevailed (Vermeij and Rosenberg, 1993). After closure, the northward Intra-Caribbean Current was activated and the Gulf Stream became more vigorous (Cronin and Dowsett, 1996), thus facilitating eastward dispersal.

What is puzzling in the eastern dispersal of *Chauvetia* across the Atlantic is that, unlike the case of the early–mid Pliocene emigration of *Prunum* and *Persicula*, it must have occurred, at the latest, before the end of the Tortonian, Late Miocene, that is, well before the emergence of the Isthmus of Panama, and the consequent demise of the CAS.

The closure of the CAS was not a single, short-lived event. Coates et al. (1992) dated the final closure at about 3.5 Ma. Coates and Obando (1996) at 3.1–2.8 Ma and Collins (2003) at about 4 Ma, and Tiedemann et al. (in Coates et al., 2005) at 2.8 Ma. Most recent consensus view is final closure of the last seaway about 3.5–3.0 Ma (Coates and Stallard, 2013; Jackson and O'Dea, 2013). However, the process leading to the emergence of the Isthmus of Panama started earlier, much earlier. As summarized by Molnar (2008), the combination of the rise of the volcanic arc that now constitutes the southern part of Central America beginning at 25–15 Ma (late Chattian-Burdigalian) (Farris et al., 2011, Montes et al., 2012), the emergence of an archipelago by ~ 12 Ma (Serravalian) (Coates el al., 2003), and their collision with northern South America by ~7 Ma (Tortonian-Messinian transition) implies that deep water passages connecting the western Atlantic, the Caribbean, and the Pacific had vanished by the end of the Tortonian, or even slightly earlier. Shallow water connections, however, could have continued until much later.

Kameo and Sato (2000) based on nannofossil assemblages from the Caribbean Sea and the eastern equatorial Pacific Ocean inferred Neogene surface water circulation changes. According to them, in the time slab 15.83–10.71 Ma (Langhian–early Tortonian), and probably earlier, nannofossil distributions clearly show the existence of an East-West Circum-Tropical Current between the Caribbean and the eastern equatorial Pacific and no surface water communication between the northern and southern Caribbean, enhancing the Gulf Stream and the North Atlantic Current. On the other hand, during the 10.71–9.36 Ma interval (early-mid Tortonian), the Circum-Tropical Current weakened, and the northward Intra-Caribbean Current was initiated. Later, northern and southern Caribbean surface waters became separated at 8.35–3.65 Ma (late Tortonian-Zanclean) and the Circum-Tropical Current was restored. After 2.76 Ma (Gelasian-Recent), as a consequence of the rise of the Isthmus of Panama and the CAS closure, the northward Intra-Caribbean current was completely established and the Circum-Tropical Current vanished. Moreover, based on Pacific type foraminifera and the cool waters interpretation for the paleoenvironments recorded in the uppermost Miocene Chagres Formation on Panama's Caribbean side, this eastward flow continued, at least intermittently, until the Early Pliocene (Collins et al., 1996 a,b; Leigh et al., 2014).

Based on the available data on the evolution of ocean circulation in the proto-Caribbean area it is therefore possible to formulate the hypothesis that the pre-late Tortonian (pre-8.12–7.42 Ma) dispersal of the tropical Gatunian west-Atlantic *Chauvetia* into the tropical East Atlantic European-West African Province most probably happened during the 10.71–9.36 Ma interval (early–mid Tortonian) during which the Circum-Tropical Current weakened, and the northward Intra-Caribbean Current had started, enhancing the Gulf Stream and the North Atlantic Current, as described by Kameo and Sato (2000). This new data constitutes compelling evidence of a pre-Pliocene eastward dispersal of New World shallow marine organisms across the Atlantic.

The post early-mid Miocene fate of the genus in the Caribbean remains a mystery. We are aware of no other example of a species originating in tropical America that no longer lives there, but does occurs elsewhere. Furthermore, we cannot identify antecedents in either the eastern or western Atlantic or tropical American faunas for the genus. However, this may be due to us looking in the wrong place. If the taxonomic placement of *Chauvetia* were closer to the Muricidae as possibly suggested by preliminary molecular analysis (personal communication, M. Oliverio, 2014), it may be that its origins lie

within groups such as the Muricopsinae or the Ergalataxinae. One can only hope that future research on the New World Miocene molluscan fossil assemblages, especially relating to microgastropods, a clearly under-researched group, might shed more on this subject.

Acknowledgments

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