

Reconciling the molecular clock and biogeography: an alternative view of the divergence process between *Allognathus* Pilsbry, 1888 and *Hemicycla* Swainson, 1840 (Pulmonata Helicidae)

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ABSTRACT

The fragmentation of the Hercynian shield, which occurred between the Oligocene and Miocene explains satisfactorily the process of divergence between the Helicoidea genus *Allognathus* (endemic to the Balearic Islands) and *Hemicycla* Swainson, 1840 (endemic to the Canary Islands). The process of divergence of the common ancestor of *Allognathus* Pilsbry, 1888 and *Hemicycla* began with the separation of the Balearic islands and Kabylias. Our alternative biogeographic hypotheses suggest that the ancestor of *Hemicycla* colonized the Canary Islands from North Africa, once the Kabylias joined the African continent.

KEY WORDS

Hercynian shield; Balearic and Canary Islands; Kabylias; North African malacofauna.

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INTRODUCTION

In a recent study on the Helicoidea of the western Palaearctic, Razkin et al. (2015) considered that extant genera *Allognathus* Pilsbry, 1888 (endemic to the Balearic Islands) and *Hemicycla* Swainson, 1840 (exclusive to the Canary Islands) are sister taxa and estimated their divergence age at 9.1 Ma. (Tortonian, late Miocene).

Based on the molecular clock, Chueca et al. (2015) considered that the divergence between these genera occurred somewhat earlier, during the Langhian-Serravalian (ie, in the middle Miocene, ca, 15.97-11.60 Ma), and they proposed that the Iberian Peninsula or the Balearic Islands were the geographical areas from which the ancestor of

Hemicycla colonized the Canary Islands. The biogeographic hypothesis of Chueca et al. (2015) is based exclusively on the average divergence time estimated from the molecular clock, and hence it does not take into account the age uncertainty as defined by the maximum and minimum range of estimates. This may be correct from a methodological view point, but should not be taken as the exclusive basis for a biogeographical hypothesis on the origin of *Hemicycla*, especially since it contradicts currently available palaeogeographic data. Genetic changes do not necessarily accumulate steadily over time and at the same rate along various lineages depending on many factors and circumstances (Pulquério & Nichols, 2006). Thus, when evaluating alternative biogeographic hypotheses, the molecular

clock should be considered as one among various sources of data. It needs to be reconciled with other data, as illustrated by the contrasting results obtained by Razkin et al. (2015) and Chueca et al. (2015). In particular, the events that define the palaeogeographic evolution of a given area must not be ignored, but rather taken as the reference starting point when proposing a biogeographic hypothesis.

In our opinion, the biogeographic hypothesis favored by Chueca et al. (2015) about the origin of *Hemicycla* relies on a too recent divergence time between *Allognathus* and *Hemicycla* and consequently, it does not adequately explain the area from which the ancestor of *Hemicycla* colonized the Canary Islands.

Here we propose an alternative biogeographic hypothesis on the origin of *Hemicycla* that is based on the previous works by Esu & Kotsakis (1983), Bourrouilh (1983), Gelabert et al. (2002), Rosenbaum et al. (2002) and Waldén (1984).

AN ALTERNATIVE BIOGEOGRAPHICAL HYPOTHESIS

The last common ancestor of *Allognathus*, *Hemicycla*, *Pseudotachea* Boettger, 1909 and *Iberus* Montfort, 1810 (Chueca et al., 2015: see Figure 4) would have inhabited the northern part of the western Mediterranean during the Oligocene, before fragmentation of the Hercynian shield (into the blocks corresponding to the Balearics, Kabylas, Rif-Betic cordillera, Corsica, Sardinia and Calabria) began (Esu & Kotsakis, 1983; Rosenbaum et al., 2002). This fragmentation, which occurred during the Oligocene and Miocene, would have resulted in the divergence of the clade including *Pseudotachea* and *Iberus* (inhabiting the Iberian Peninsula area) from that including *Allognathus* and *Hemicycla*, according with the molecular study of Chueca et al. (2015: see fig. 4). In accordance to this, the common ancestor of *Allognathus* and *Hemicycla* would

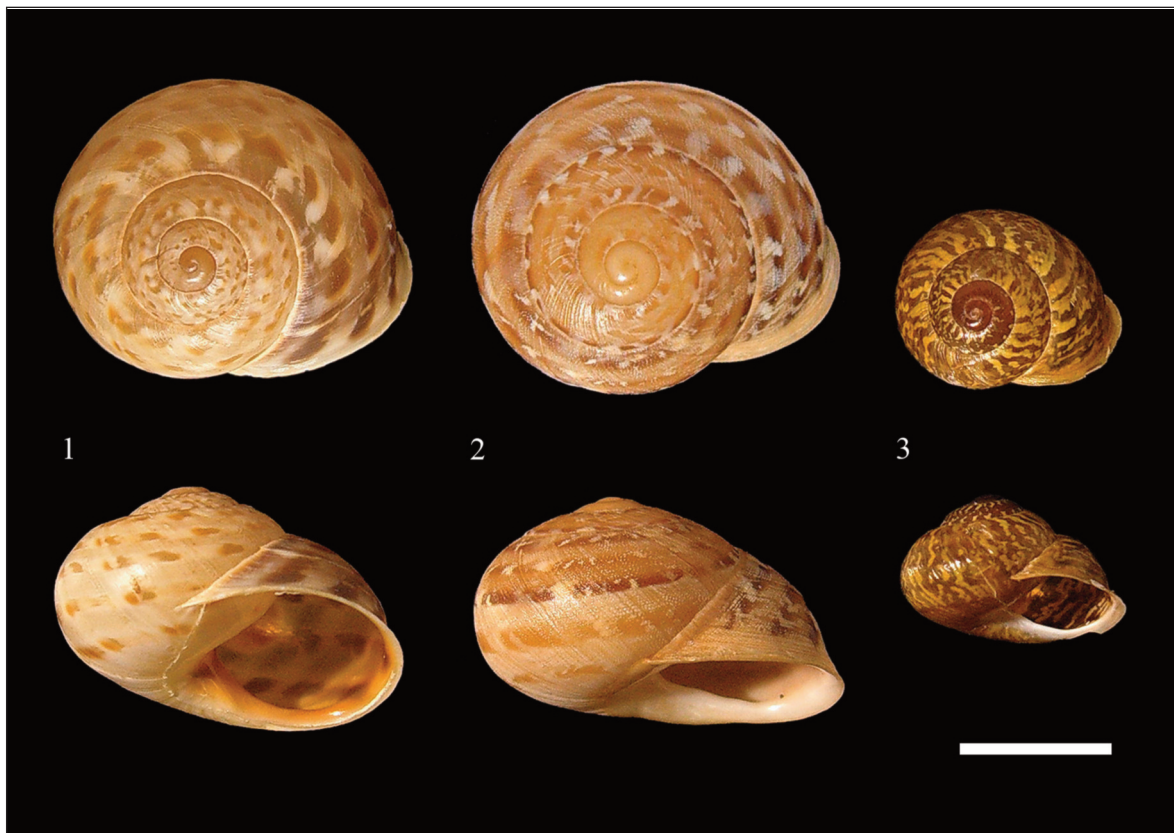


Figure 1. *Allognathus* (*Allognathus*) *graellsianus* (Pfeiffer, 1848) from Pollença (Mallorca). Figure 2. *Alabastrina* (*Loxana*) *beaumieri* (Mousson, 1873) from Ait Atab (High Atlas, Morocco). Figure 1. *Hemicycla* *laurijona* Alonso et Ibáñez, 2007 from La Gomera (Canary Islands). Scale: 10 mm.

have occupied the geographical area constituted by the Balearic Islands and the Kabylean block (see Esu & Kotsakis, 1983: fig. 2). The divergence between these genera would thus have resulted from the separation of these two blocks, which occurred in the early Miocene (Bourrouilh, 1983: p. 593). According to this scenario, the ancestor of *Hemicycla* would have colonized the Canary Islands from North Africa, once the Kabylean block joined the African continent during the early to middle Miocene (Esu & Kotsakis, 1983).

Unlike in other Macaronesian archipelagos, part of the Canary malacofauna (17%) shows affinities with the terrestrial molluscs of northwestern Africa (Waldén, 1984). According to this author, in the eastern Canary Islands there would have been an ancient continental malacofauna that was subsequently partly destroyed due to extensive volcanism during the late Tertiary (while the western islands were being formed). Many of the extant endemic species from the Canary Islands apparently evolved from immigrant species that dispersed from northwestern Africa and Madeira, during the late Tertiary. The colonization of Madeira by European Tertiary taxa (there are no fossil taxa of African origin in this archipelago) could have taken place during the middle Miocene, although an early colonization in the Oligocene, when the archipelago was considerably farther from Africa, seems more likely (Waldén, 1984). If correct, this conclusion is incompatible with the divergence time between *Allognathus* and *Hemicycla* proposed by Chueca et al. (2015).

CONCLUSIONS

According to Chueca et al. (2015): "*The position of Hemicycla as the sister group of Allognathus makes it difficult to pinpoint the colonization age of the Balearic Islands by Allognathus. Hemicycla is endemic to the Canary Islands, and there are no fossil records of Hemicycla in the Iberian Peninsula or the Balearic Islands*". Such claim is somewhat surprising, because Chueca et al. (2015) do not contemplate the possibility that *Hemicycla* diverged from a western Palaearctic helicid not included in their cladogram.

The alternative biogeographic hypothesis proposed here does not require this fossil record, since

it is based on the progressive fragmentation of the Hercynian shield as the main event that determined the divergence between *Allognathus* and *Hemicycla*. According to our hypothesis, one may expect to find the common ancestors of *Pseudotachea*+*Iberus* as well as *Allognathus*+*Hemicycla* in the fossil record of the Iberian Peninsula and the Balearic Islands. In contrast, our hypothesis is incompatible with the presence of fossil *Hemicycla* in these two geographical areas.

Based on the palaeobiogeographical hypothesis proposed above, the divergence times proposed by Chueca et al. (2015: fig. 4) for *Allognathus* and *Hemicycla* (as well as the common ancestors of *Pseudotachea*+*Iberus* and *Allognathus*+*Hemicycla*) are too recent. Instead, the divergence between *Allognathus* and *Hemicycla*, and the arrival of the *Hemicycla* ancestor to the Canary Islands from northwest Africa would have occurred earlier, sometime between the late Oligocene and early to middle Miocene. The absence of the ancestor of *Hemicycla* from the North African fossil record might be attributed to an insufficient knowledge of the fossil land snails from this area, as suggested by Waldén (1984). This is supported by the anatomical similarities between *Allognathus* and some extant terrestrial molluscs from North Africa, such as *Alabastrina (Loxana) beaumieri* (Mousson, 1873) as already noted by Hesse (1931).

We therefore agree with Forés & Vilella (1993) that more in-depth studies on the phylogenetic relationships between North African genera would be required to shed more light on the biogeographic history of *Allognathus*, *Hemicycla* and the Canary Island's malacofauna.

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