



## Incorporating palaeogeography into ancestral area estimation can explain the disjunct distribution of land snails in Macaronesia and the Balearic Islands (Helicidae: Allognathini)

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### ABSTRACT

The systematics and biogeographical history of the Eastern Mediterranean and Macaronesian land snail tribe Allognathini (Helicidae: Helicinae) is investigated based on mitochondrial and nuclear DNA sequence data. Our molecular phylogenetic analyses indicate that the genus-group systematics of the tribe needs to be revised. We show for the first time that the narrow-range endemics *Lampadia* and *Idiomela* from the Madeira Archipelago belong to Allognathini and represent together the sister group of the diverse Canary Island *Hemicycla* radiation. We therefore suggest synonymising *Lampadiini* with Allognathini. Sister to these Macaronesian genera was the Balearic Island *Allognathus* radiation. *Pseudotachea* was not recovered as a monophyletic group and the two currently recognised species clustered in *Iberus*. Similarly, *Adiverticula* was not recovered as a monophyletic group and clustered in *Hemicycla*. We therefore suggest synonymising *Pseudotachea* with *Iberus* and *Adiverticula* with *Hemicycla*. The six genera in Allognathini, which we distinguish here (*Cepaea*, *Iberus*, *Allognathus*, *Hemicycla*, *Idiomela* and *Lampadia*), originated in Western to South-western Europe according to our ancestral area estimation and the fossil record. The disjunct distribution of the Balearic Islands and Macaronesian sister clades and the mainly Iberian *Iberus* clade that separated earlier can be explained by the separation of the Betic–Rif System from the Iberian Peninsula during the late Oligocene to early Miocene, along with independent Miocene dispersals to the Balearic Islands and Macaronesia from the Iberian Peninsula, where the ancestral lineage became extinct.

### 1. Introduction

In recent decades, the Macaronesian Archipelagos (Azores, Cape Verde, Madeira, Savages and Canary Islands) in the eastern Atlantic Ocean off the European and African coasts and the Balearic Islands in the Mediterranean Sea close to the coast of the Iberian Peninsula have been the subject of an increasing number of studies addressing patterns of colonisation and speciation of different terrestrial plants (e.g. [Mort et al.,](#)

[2002](#); [Carine et al., 2004](#); [Magri et al., 2007](#); [García-Maroto et al., 2009](#); [Vitales et al., 2014](#)) and animal lineages, including arthropods ([Stüben and Astrin, 2010](#); [Amorim et al., 2012](#); [Husemann et al., 2014](#); [Machado et al., 2017](#)), vertebrates ([Nogales et al., 1998](#); [Arnold et al., 2008](#)) and molluscs ([Van Riel et al., 2003](#); [Greve et al., 2010, 2012](#); [Harris et al., 2013](#); [Chueca et al., 2015, 2017](#); [De Mattia, et al., 2018](#); [Caro et al., 2019](#); [Brozzo et al., 2020](#)).

The palaeogeographical history of the Macaronesian Archipelagos

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and the Western Mediterranean region is comparatively well-known and placed within a well-defined timeframe (Geldmacher et al., 2000, 2005; Rosenbaum et al., 2002; Klügel et al., 2005; Jolivet et al., 2006; Fernández-Palacios et al., 2011). While active or passive overseas dispersal is the only mode of colonisation for the Macaronesian Archipelagos for terrestrial species because all islands are of oceanic origin and have never been connected to the mainland (Fernández-Palacios et al., 2011), the origin of the endemic biota of the Balearic Islands has been attributed to three primary events: 1) the Tyrrhenian vicariance hypothesis in the Oligocene (Pfenninger et al., 2010; Bidegaray-Batista and Arnedo, 2011; Lázaro et al., 2011), 2) colonisation across a land bridge connection during the middle Miocene (Bover et al., 2008; Chueca et al., 2015) and 3) the Messinian salinity crisis (Chueca et al., 2017; Delicado et al., 2014; Fromhage et al., 2004; Laluzza-Fox et al., 2005).

When analysing the biogeographical history of the Balearic Islands endemic land snail genus *Allognathus* Pilsbry, 1888 in the family Helicidae Rafinesque, 1815, Chueca et al. (2015) uncovered an unusually disjunct distribution pattern, with *Allognathus* recovered as the sister group of the Canary Islands endemic genus *Hemicycla* Swainson, 1840. Two different scenarios were discussed by these authors that may explain the colonisation of the Canary Islands: 1) from the Iberian Peninsula after the colonisation of the Balearic Islands by the ancestor of *Allognathus* during the middle Miocene, or 2) from the Balearic Islands, once ancestral forms of *Allognathus* plus *Hemicycla* had colonised these. Accordingly, the latter would have involved a long-distance dispersal event from the Balearic Islands to the Canary Islands. In contrast, the former would require the extinction of the last common ancestor of *Hemicycla* and *Allognathus* in the Iberian Peninsula. Quintana Cardona et al. (2015) opposed this view, criticising in particular that the biogeographical hypothesis favoured by Chueca et al. (2015) about the origin of *Hemicycla* relies on a too recent divergence time estimate between *Allognathus* and *Hemicycla* and consequently does not adequately explain the area from which the ancestor of *Hemicycla* colonised the Canary Islands.

Quintana Cardona et al. (2015) therefore proposed an alternative scenario, under which the last common ancestor of *Allognathus* and *Hemicycla* and the related genera *Pseudotachea* Boettger, 1909 and *Iberus* Montfort, 1810 in the helicid tribe Allognathini Westerlund, 1903 would have inhabited the northern part of the Western Mediterranean during the Oligocene before the fragmentation of the Hercynian belt into the blocks corresponding to the Balearic Islands, the Kabylia, the Rif–Betic Cordillera, Corsica, Sardinia and Calabria began (Esu and Kotsakis, 1983; Rosenbaum et al., 2002). The fragmentation of the Hercynian belt into these blocks in the Oligocene to Miocene would then have resulted in the divergence of the lineages including *Iberus* and *Pseudotachea* (inhabiting parts of the Iberian Peninsula) from that including *Allognathus* and *Hemicycla* (inhabiting the Balearic Islands and the Kabylia block) through vicariance. The vicariance event separating the Balearic Islands and the Kabylia in the early Miocene (Bourrouilh, 1983; Rosenbaum et al., 2002) would accordingly have triggered the separation of *Allognathus* and *Hemicycla*, with the ancestor of the latter colonising the Canary Islands from North Africa once the Kabylia block had collided with the African continent during the early to middle Miocene (Esu and Kotsakis, 1983; Rosenbaum et al., 2002; Quintana Cardona et al., 2015).

Research in the past 15 years has considerably increased our understanding of the evolution and composition of Allognathini, with *Cepaea* Held, 1838 aside from *Allognathus*, *Hemicycla*, *Iberus* and *Pseudotachea* currently considered to belong to the tribe among extant Helicidae (Neiber and Hausdorf, 2015; Razkin et al., 2015). Nordsieck (2014, 2016, 2017) considered the Western and Central European fossil genera *Parachloraea* Sandberger, 1873 (late Eocene to late Oligocene), *Palaotachea* Joos, 1912 (incl. *Megalotachea* Pfeffer, 1930) (early Oligocene to late Miocene), *Creneatachea* Zilch, 1960 (early Miocene), *Frechenia* Schlickum & Strauch, 1971 (Pliocene), *Schlickumia* Truc, 1971 (Pliocene) and possibly *Tithodomus* Pfeffer, 1930 (early Miocene) to be

affiliated with the *Cepaea*-group, which suggests that these taxa may belong to the Allognathini or its stem-group. Furthermore, Mandahl-Barth (1950) considered the endangered short-range endemic *Lampadia webbiana* (Lowe, 1831) (Neubert et al., 2019) from Porto Santo and several of its satellite islets (Madeira Archipelago) to be related to *Hemicycla*. The critically endangered *Idiomela subplicata* (Sowerby, 1824) (Neubert et al., 2019), the only other endemic helicid from the Madeira Archipelago, may also be related to this group based on published anatomical data (Cockerell, 1921; Hemmen and Groh, 1984), but this has not been tested so far.

Some North African helicids, e.g. species assigned to the nominal genus-group taxa *Atlasica* Pallary, 1917, *Loxana* Pallary, 1899, *Massylaea* Möllendorff, 1898, *Rossmassleria* Hesse, 1907 or *Maurohelix* Hesse, 1917, have been considered as being possibly related to *Iberellus* or *Hemicycla* (Hesse, 1931; Odhner, 1931; Forés and Vilella, 1993; Quintana Cardona et al., 2015). Aside from few species belonging to the helicid subfamilies Ariantinae Mörch, 1864 (Sattmann, 1992) or Murellinae Hesse, 1918 (Ezzine et al., 2018), the latter introduced, or the tribe Helicini (Neubert, 2014; Psonis et al., 2014; Korábek et al., 2015; Ketmaier and Glaubrecht, 2015; Fiorentino et al., 2016), phylogenetic studies have shown that the remaining North African helicids either belong to Otalini Pfeffer, 1930 or Thebini Wenz, 1923 and that none are closely related to Allognathini (Greve et al., 2010, 2017; Guillier and Madec, 2010; Colomba et al., 2011, 2015; Neiber and Hausdorf, 2015; Ali et al., 2016; Walther et al., 2016; Bouazziz-Yahiatene et al., 2017, 2019; Neiber, 2017; Holyoak et al., 2018, 2020; Sherpa et al., 2018; Kneubühler et al., 2019).

Considering the advances in helicid systematics and recent developments of methodological approaches in phylogenetic biogeography (see, e.g., Lamm and Redelings, 2009; Ronquist and Sanmartín, 2011; Lawing and Matzke, 2014; Sanmartín and Meseguer, 2016 for reviews), it is possible to compare different scenarios regarding Allognathini biogeography. The present contribution, therefore, aims at 1) testing the monophyly of Allognathini and the genera currently assigned to the tribe using an increased taxon sampling compared to the study of Chueca et al. (2015), 2) inferring the phylogenetic placement of *Idiomela* Cockerell, 1921 and *Lampadia* Albers, 1854, 3) inferring a time frame for the diversification of Allognathini and 4) re-evaluating the biogeography of the tribe incorporating palaeogeographical data.

## 2. Material and methods

### 2.1. Taxon sampling

To resolve the phylogenetic relationships of genus-group taxa included in the Allognathini and to infer the historical biogeography of the group, representatives of all five currently accepted genera (plus two subgenera) were included in the study. Additionally, *L. webbiana* and *I. subplicata* were also included in the analyses. Aside from newly generated sequences, data from the following studies were included in the analyses: Elejalde et al. (2005, 2008a, b), Neiber et al. (2011), Neiber and Hausdorf (2015), Chueca et al. (2015), Ali et al. (2016), Neiber (2017) and Bober et al. (2021). Species belonging to the tribes Helicini, Otalini and Thebini, respectively, were included as an outgroup. The classification and the collection data of the used specimens are compiled in Supplementary Table S1. Species belonging to *Hemicycla* were determined based on the taxonomic works and revisions by Odhner (1931, 1937), Groh (1985), Ibáñez et al. (1987, 1988, 2007), Alonso et al. (1991), Groh et al. (1992, 1996), Neubert and Gosteli (2003), Vega-Luz and Vega-Luz (2008), Yanes et al. (2009), Neiber et al. (2011, 2017), Castro et al. (2012), Verbinnen and Swinnen (2014), Bober et al. (2021). In cases where species have not been revised, early synopses of the land snail fauna of the Canary Islands (Mousson, 1872; Wollaston, 1878; Mabille, 1884, 1885) were used for determinations.

## 2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted following a slightly modified version of the protocol of Sokolov (2000) as detailed by Scheel and Hausdorf (2012). Parts of the mitochondrial cytochrome *c* oxidase subunit 1 (*cox1*) and the 16 S rRNA (16S) genes, as well as parts of the nuclear ribosomal gene cluster including parts of the 5.8 S rRNA (5.8S) gene, the complete internal transcribed spacer 2 (ITS2) and parts of the 28 S rRNA (28S) gene were amplified by polymerase chain reaction (PCR). The primer pairs LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') plus HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer et al., 1994), 16Scs1 (5'-AAA CAT ACC TTT TGC ATA ATG G-3') plus 16Scs2 (5'-AGA AAC TGA CCT GGC TTA CG-3') (Chiba, 1999) and LSU1 (5'-CTA GCT GCG AGA ATT AAT GTG A-3') plus LSU3 (5'-ACT TTC CCT CAC GGT ACT TG-3') (Wade and Mordan, 2000) were used, respectively.

PCR amplifications were carried out based on the protocols described in Neiber et al. (2017) with slight modifications, i.e. in 25  $\mu$ L volumes containing 18.3  $\mu$ L ddH<sub>2</sub>O, 2.5  $\mu$ L DreamTaq Green Buffer (Thermo Fisher Scientific, Waltham, MA, USA), 1  $\mu$ L dNTP mix (5 mM each, biolabproducts, Bebensee, Germany), 1  $\mu$ L of each primer (10  $\mu$ M), 0.2  $\mu$ L DreamTaq DNA polymerase (Thermo Fisher Scientific) and 1  $\mu$ L of the template DNA under the following reaction conditions: an initial denaturation step at 94 °C for 2 min, 40 PCR cycles (94 °C for 30 s, 50–58 °C for 30–40 s, 72 °C for 30 s) and a final extension step at 72 °C for 5 min. Both strands of the amplified products were sequenced at MacroGen Europe Laboratory (Amsterdam, The Netherlands). ChromasPro 1.7.1 (Technelysium, Tewantin, Australia) was used to assemble forward and reverse sequence reads. Sequences were deposited at GenBank (see Supplementary Table S1 for information on vouchers and GenBank accession numbers).

## 2.3. Sequence alignment and phylogenetic analyses

Sequences were aligned with MAFFT (Katoh and Standley, 2013) using the Q-INS-i iterative refinement algorithm and otherwise default settings. PartitionFinder 2.1.1 (Lanfear et al., 2017) was used to select the best evolutionary models for the Bayesian inference (BI) and maximum likelihood (ML) analyses of phylogenetic relationships, conducting exhaustive searches with a separate estimation of branch lengths for each partition and with the Bayesian information criterion to select among models. The models were limited to those available in MrBayes 3.2.6 (Ronquist et al., 2012) as well as in Garli 2.1 (Zwickl, 2006). The data set was initially divided into two partitions corresponding to 1) mitochondrial data and 2) the partial sequences of the nuclear ribosomal gene cluster. Each of these partitions was further subdivided and analysed with PartitionFinder separately. The mitochondrial data set was subdivided into 16S and the codon positions of *cox1*. The nuclear ribosomal data set was subdivided into 5.8S, ITS2 and 28S.

The BI analysis was performed using MrBayes. Metropolis-coupled Monte Carlo Markov chain (MC<sup>3</sup>) searches were run with four chains in two separate runs with 50,000,000 generations under default priors, trees sampled every 1,000 generations using default heating and the evolutionary models and data partitions as suggested by the PartitionFinder analyses. The first 50,000 generations of each run were discarded as a burn-in. Diagnostics obtained from the MrBayes output were used to assess stationarity and convergence, i.e. it was ensured that the average standard deviation of split frequencies was smaller than 0.01, potential scale reduction factors were close to 1 and effective sample sizes were greater than 200 for all estimated parameters.

The ML analysis was performed using Garli with evolutionary models and data partitions, as suggested by the PartitionFinder analyses and otherwise default settings. Support values were calculated by bootstrapping with 1,000 replications.

Heuristic maximum parsimony (MP) searches were conducted with

Paup\* 4.0b10 (Swofford, 2002) with unordered characters, 100 random sequence addition replicates, tree bisection reconnection (TBR) branch-swapping, and gaps treated as missing data. Support for internal branches was assessed in Paup\* by bootstrapping with 1,000 replications, using full heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and one tree held at each step during stepwise addition.

Bootstrap support (BS) values from the ML and MP analyses as well as posterior probabilities (PP) from the BI analysis were mapped on the BI 50% majority-rule consensus tree with SumTrees 3.3.1, which is part of the DendroPy 3.8.0 package (Sukumaran and Holder, 2010). PP values  $\geq 0.95$  and BS values  $\geq 70$  were interpreted as positive support for a node and PP values  $\geq 0.99$  and BS values  $\geq 90$  as strong support for a node.

## 2.4. Inference of divergence times

Divergence times within Allognathini were dated using the Bayesian algorithm implemented in Beast 2.4.1 (Bouckaert et al., 2014) based on the concatenated mitochondrial and nuclear data assuming an uncorrelated relaxed log-normal molecular clock and using the same partitioning scheme and nucleotide substitution models as in the BI analysis described above. As tree prior, the Birth–Death model was chosen. Calibration was based on late Eocene (Priabonian) fossils of *Parachloraea* assigned to the Helicinae by Wenz (1923) and Nordsieck (2014, 2017), and assumed to be closely related to the *Cepaea* group by Nordsieck (2014). We therefore specified a log-normal distribution for the most recent common ancestor of the Helicinae and a minimum age of 33.9 Ma corresponding to the Eocene/Oligocene boundary and otherwise default settings. The Beast analysis was run for 100,000,000 generations with a sampling frequency set to 50,000. Tracer 1.7.1 (Rambaut et al., 2018) was used to check whether effective sample sizes for the relevant estimated parameters were above 200. Ten per cent of the generations were discarded as burn-in, and a maximum clade credibility tree with median node heights was constructed with TreeAnnotator 2.4.1, which is part of the Beast 2.4.1 distribution.

## 2.5. Ancestral range estimation

Putative historical distributions patterns were evaluated using ancestral range estimation. The biogeographical analyses were limited to species lineages belonging to Allognathini by pruning replicate species tips off the dated maximum clade credibility tree and removing outgroups using Phytools (Revell, 2012) in R 4.0.2 (R Core Team, 2020). For biogeographical analyses, the R package BioGeoBEARS (Matzke, 2013) was used. The following discrete areas were considered: 1) Iberian Peninsula (I) (excl. the Betic System), 2) Continental Europe (E) (excl. the Iberian Peninsula), 3) Betic System (B), 4) Rif System (R) (northern Morocco), 5) Balearic Islands (Ba) and 6) Macaronesian Archipelagos (M) (Madeira Archipelago, Canary Islands). Species distributions were obtained from own observations and gathered from the following literature sources (Mousson, 1872; Wollaston, 1878, Mabille, 1884, 1885; García San Nicolás, 1957; Hemmen and Groh, 1984; Ibáñez et al., 1987, 1988; Altonaga et al., 1994; Puente Martínez, 1994; Bank et al., 2002; Elejalde et al., 2005, 2008a, b; Manganelli et al., 2005; Beckmann, 2007; Ibáñez and Alonso, 2007; Seddon, 2008; Yanes et al., 2009; Welter-Schultes, 2012; Liétor Gallego, 2014; Chueca et al., 2013, 2015; Cadevall and Orozco, 2016; Neiber et al., 2017). Probably human-mediated introductions of *Allognathus* to the Iberian Peninsula and southern France (Chueca et al., 2015; Cadevall and Orozco, 2016) or the possible introduction of *Pseudotachea* to the Balearic Islands (Gasull, 1964; Altonaga et al., 1994) were not considered in the analyses.

The complex geological history of the Western Mediterranean region with considerable displacement along with collisions and break-ups of terranes (Rosenbaum et al., 2002) and dramatic sea-level fluctuations during the Messinian salinity crisis (Krijgsman et al., 1999) was

incorporated into the analyses by time-stratification and choice of dispersal multipliers. Based on the palaeogeographical reconstructions of Rosenbaum et al. (2002) and the extent of the Messinian salinity crisis the following time periods were considered: 1) present to 5.33 Ma (geographical settings approximately as today), 2) Messinian salinity crisis (5.33–5.96 Ma; Ba + I, Ba + R, B + R connected), 3) late Miocene, 5.96–11.6 Ma (Ba + I and B + R not connected), 4) 11.6–12 Ma (Ba + B presumably connected via the Betic–Balearic corridor (Riba, 1981; Fontboté et al., 1990; Roca, 1996), B + R not connected), 5) middle Miocene, 12–16 Ma (Ba + B and B + R connected), 6) late Oligocene/early Miocene 16–25 Ma (B + I and B + R connected, Ba + B not connected), 7) middle Oligocene, 25–29.5 Ma (B, Ba, I, R very close together or connected) and 8) > 29.5 Ma (B, Ba, R connected to I forming part of the Hercynian shield). Rate multipliers for areas with direct connections were set to 1.0, those for regions separated by short stretches of water to 0.1, those for areas separated by wide stretches of water to 0.05 and those for areas not directly connected or separated by vast stretches of water to 0.000001 (Supplementary Table S2). Macaronesia was assumed to have been colonisable from Iberia throughout the considered time periods (rate multiplier 0.05) because emerged islands were probably always present in the region from the Oligocene to the present (Fernández-Palacios et al., 2011). The colonisation of Macaronesia was also assumed to have been possible from 16 Ma to the present time from B and R, when these microplates moved towards their present-day positions. The maximum areas allowed was set to three. However, as most extant taxa have ranges restricted to one area only, only ranges spanning three areas that are observed today, were allowed. Additionally, two area states which encompassed areas not directly adjacent during any of the selected time periods or that were separated by wide stretches of water during any of the selected time periods were not allowed.

Under these assumptions, two models were implemented in BioGeoBEARS: 1) the dispersal–extinction–cladogenesis (DEC) model (Ree et al., 2005; Ree and Smith, 2008) and 2) the DEC model allowing for founder-event speciation (+J) (Matzke, 2014). Despite alleged conceptual and statistical problems with the DEC and DEC + J models and their comparison via model selection (Ree and Sanmartín, 2018, but see the response by D. J. Matzke at [www. http://phylo.wikidot.com/biogeobears-validation#DEC\\_DECj](http://phylo.wikidot.com/biogeobears-validation#DEC_DECj)), a likelihood ratio test (LRT) was conducted. However, the outcomes of the different analyses were also compared based on empirical (biological, geographical) considerations, as recommended by Ree and Sanmartín (2018). For comparison, the DEC and DEC + J models without excluding ranges up to a maximum of three allowed areas were also implemented in BioGeoBEARS and the results compared to the more constrained models.

### 3. Results

#### 3.1. Phylogenetic analyses

The final alignment had a length of 2,464 base pairs (bp): *cox1* 655 bp, 16S 924 bp, 5.8S 45 bp, ITS2 490 bp and 28S 350 bp. The PartitionFinder analyses suggested to subdivide the data into three partitions: 1st plus 2nd codon positions of *cox1* (GTR + I + G model), 3rd codon positions of *cox1* and 16S (GTR + I + G model) and 5.8S plus ITS2 plus 28S (K80 + G model).

All phylogenetic analyses recovered a clade including the genera *Allognathus*, *Cepaea*, *Hemicycla*, *Iberus*, *Idiomela*, *Lampadia* and *Pseudotachea* with strong support (PP: 1.00, BS (ML): 100, BS (MP): 97) (Fig. 1), indicating that *Lampadia* and *Idiomela* from the Madeira Archipelago belong to the Allognathini in the sense of Chueca et al. (2015). The two *Cepaea* species formed a maximally supported group that was sister to a clade including *Allognathus*, *Hemicycla*, *Iberus*, *Idiomela*, *Lampadia* and *Pseudotachea*, which was supported by BI and the ML analysis, but marginally not by the MP analysis (PP: 1.00, BS (ML): 81, BS (MP): 69) (Fig. 1). A strongly supported clade including the representatives of *Iberus* and *Pseudotachea* (PP: 1.00, BS (ML): 100, BS (MP): 96) was

recovered as the sister group of a clade including *Allognathus*, *Hemicycla*, *Idiomela* and *Lampadia* (PP: 1.00, BS (ML): 87, BS (MP): 67) (Fig. 1). While the monophyly of *Hemicycla*, *Idiomela* and *Lampadia* was only supported in the ML analysis (Fig. 1), the monophyly of *Hemicycla* (PP: 1.00, BS (ML): 99, BS (MP): 91) and *Idiomela* plus *Lampadia* (PP: 1.00, BS (ML): 100, BS (MP): 99) was supported in all three analyses. *Adiverticula*, proposed as a subgenus of *Hemicycla* and represented by *H. pouchet* (Férussac, 1821) (= *H. adansoni* Webb & Berthelot, 1833, the type species of the subgenus) and *H. mascaensis* Alonso & Ibáñez, 1988, was not supported as a monophyletic group (Fig. 1). *Allognathus* including the subgenus *Iberellus* was recovered as a monophyletic group with maximal support in all three analyses, with *Allognathus* (*A. graellsianus*) (Pfeiffer, 1848) as sister to *Iberellus* (PP: 1.00, BS (ML): 96, BS (MP): 88) (Fig. 1).

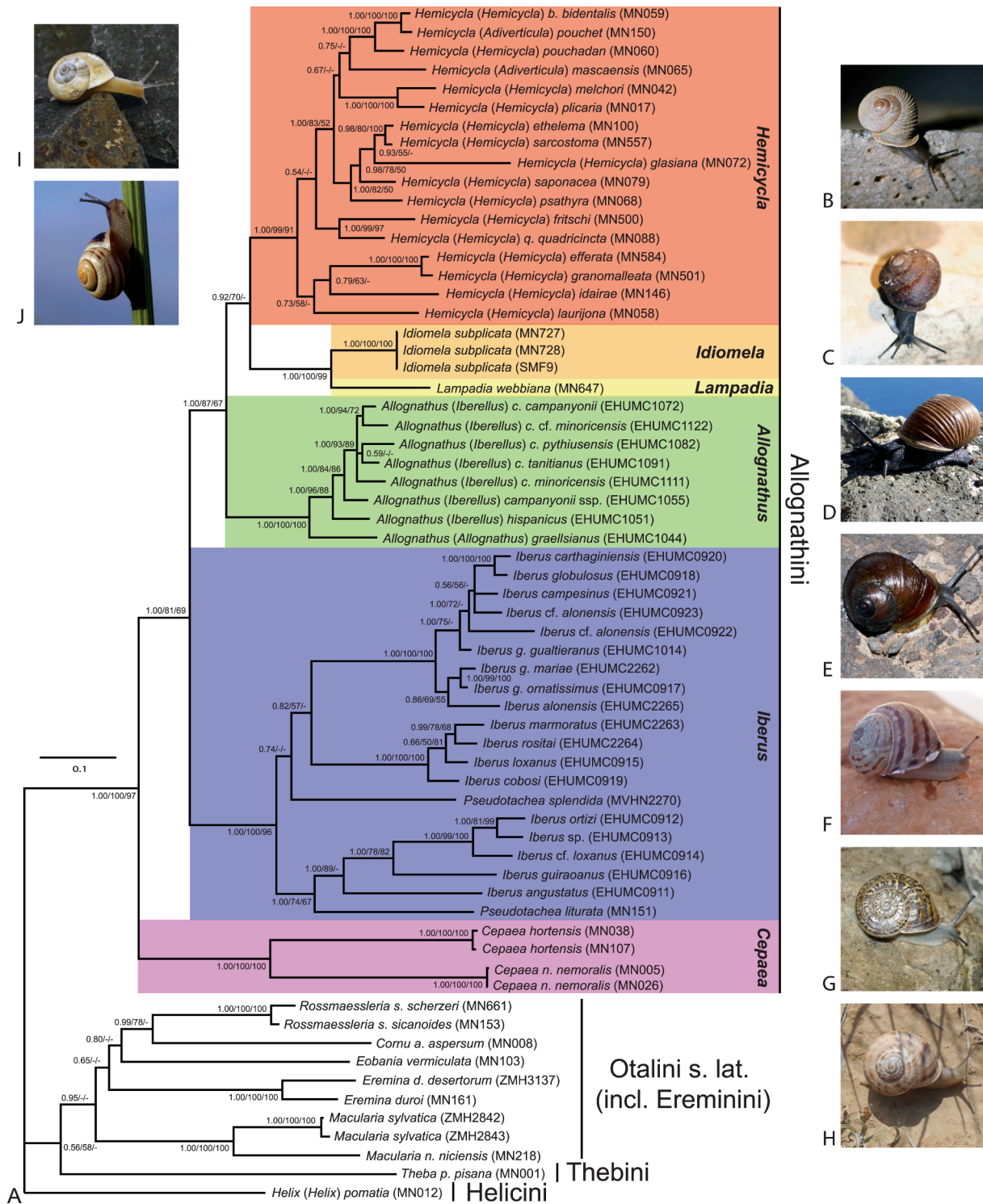
Although the clade including representatives of *Iberus* and *Pseudotachea* was strongly supported in all three analyses, the relationships of lineages within this clade were, at least concerning deeper nodes, not well-resolved (Fig. 1). *Pseudotachea splendida* (Draparnaud, 1801) and *Pseudotachea liturata* (Pfeiffer, 1851) did not form a monophylum, instead *P. liturata* was joined, albeit only supported in the BI and ML analyses (PP: 1.00, BS (ML): 74, BS (MP): 67), with a group of *Iberus* species including *I. angustatus* (Rossmässler, 1854), *I. guiraoanus* (Pfeiffer, 1853), *I. ortizi* García San Nicolás, 1957, an unnamed *Iberus* species and a specimen similar to *I. m. loxanus* (Schmidt, 1853) (Fig. 1). *Pseudotachea splendida* was weakly joined with a maximally supported clade including the type species of *Iberus*, *I. gualtieranus* (Linnaeus, 1758), and a likewise maximally supported clade including the taxa belonging to the *I. marmoratus* (Férussac, 1821) complex (Fig. 1).

#### 3.2. Estimation of divergence times

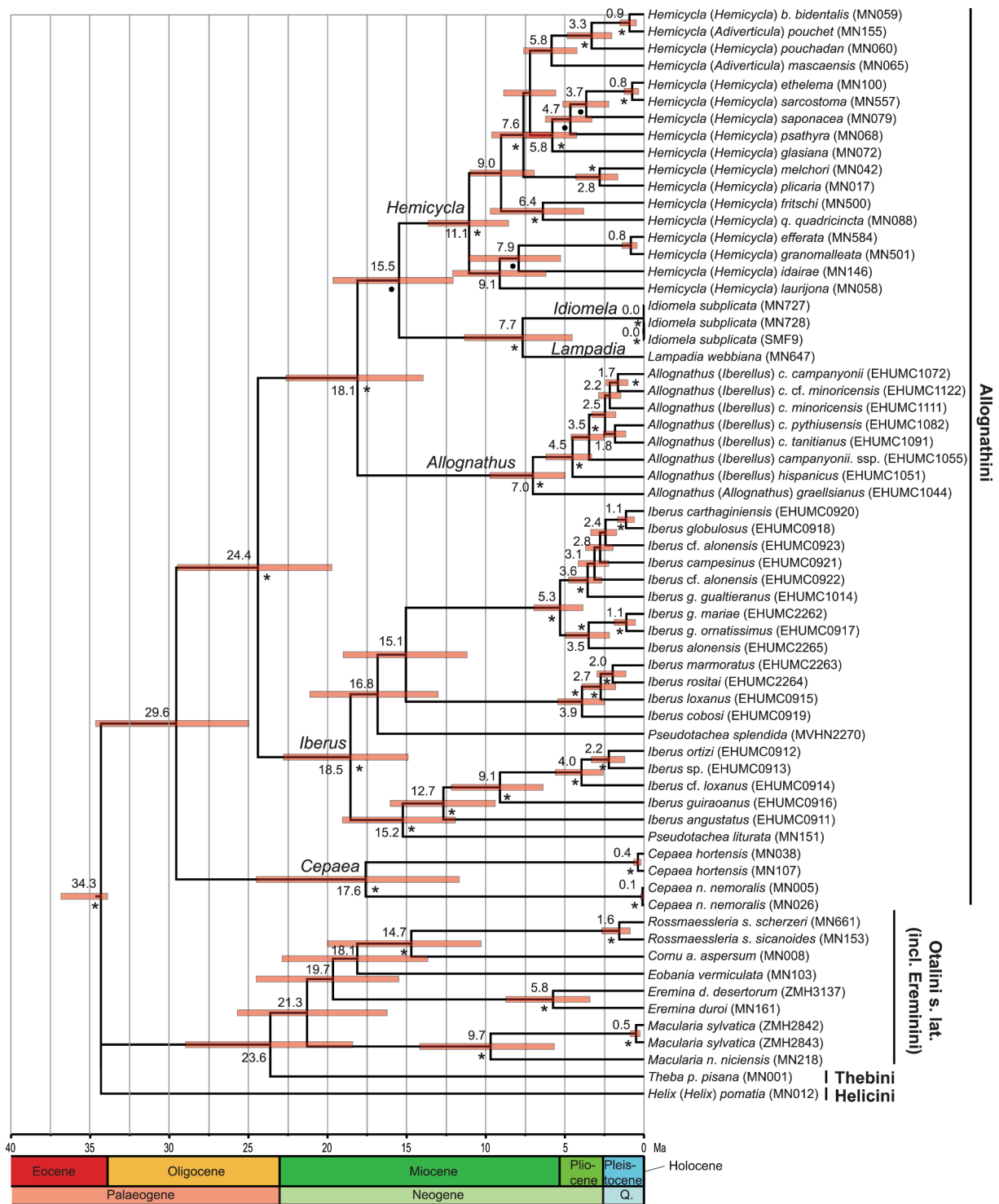
Based on the calibration of the origin of the Allognathini with the late Eocene *Parachloraea*, the onset of the diversification of extant lineages of Allognathini including *Lampadia* and *Idiomela* was inferred at 29.6 Ma (95% highest posterior density interval (HPD): 25.0–34.7 Ma) (Fig. 2). The split of *Iberus* from the lineage leading to *Allognathus*, *Hemicycla*, *Lampadia* and *Idiomela* was dated at 24.4 Ma (HPD: 19.7–29.5 Ma) in the late Oligocene, with the onset of diversification of extant lineages belonging to *Iberus* (incl. *Pseudotachea*) starting at 18.5 Ma (HPD: 14.9–22.8 Ma) in the early Miocene (Fig. 2). The separation of *Allognathus* from the lineage leading to *Hemicycla*, *Idiomela* and *Lampadia* was dated at 18.1 Ma (HPD: 14.0–22.6 Ma), with the split of *Allognathus* s. str. and *Iberellus* dated at 7.0 Ma (HPD: 5.0–9.8 Ma) and the onset of diversification of *Iberellus* dated at 4.5 Ma (HPD: 2.5–4.6 Ma) (Fig. 2). *Hemicycla* separated from *Idiomela* plus *Lampadia* at 15.5 Ma (HPD: 12.1–19.7 Ma) during the middle Miocene, with an onset of diversification of extant *Hemicycla* lineages starting at 11.1 Ma (HPD: 8.6–13.6 Ma). The split of *Lampadia* and *Idiomela* was dated at 7.7 Ma (HPD: 4.5–11.3 Ma) in the late Miocene (Fig. 2). The separation of the lineages leading to the two extant species belonging to *Cepaea* was dated at 17.6 Ma (HPD: 11.7–24.5 Ma) (Fig. 2).

#### 3.3. Ancestral range estimation

The results of the more and the less constrained ancestral area estimations (concerning allowed areas) under the DEC and DEC + J models, respectively, mainly differ in the estimation of the most likely ancestral range at the root of extant Allognathini (incl. *Lampadia* and *Idiomela*), the ancestral range of this clade excluding *Cepaea* and the ancestral range of the clade including *Allognathus*, *Hemicycla*, *Lampadia* and *Idiomela* (Fig. 3). The results of the less constrained analyses under the DEC and DEC + J models yielded identical most probable states across all nodes (Table 1, Fig. 3). In these analyses, the ancestral range of Allognathini (incl. *Lampadia* and *Idiomela*) and the ancestral range of this group excluding *Cepaea* was estimated as B + Ba + M (Fig. 3), with an estimated range contraction to B along the branch leading to *Iberus* (incl. *Pseudotachea*) and an estimated range contraction to Ba + M along the



**Fig. 1.** Phylogeny and diversity of Allognathini. **A.** Bayesian 50% majority-rule consensus tree from the analysis with MrBayes. Numbers at nodes correspond to Bayesian posterior probabilities (left), maximum likelihood (middle) and maximum parsimony (right) bootstrap values. Only nodes with posterior probabilities  $\geq 0.5$  and bootstrap values  $\geq 50$  are annotated. **B.** *Hemicycla (Hemicycla) plicaria* (Lamarck, 1816), Spain, Tenerife, 28°20'44" N, 16°22'17" W, 9.6.2000, M. T. Neiber. **C.** *Hemicycla (Adiverticula) pouchet* (Férussac, 1821), Spain, Tenerife, 28°30'27" N, 16°14'53" W, 26.8.2011, M. T. Neiber. **D.** *Idiomela subplicata* (Sowerby, 1824), Portugal, Ilhéu de Baixo, 33°00'17" N, 16°23'07" W, 20.10.2013, D. Teixeira. **E.** *Lampadia webbiana* (Lowe, 1831), Spain, Porto Santo, 33°5'29" N, 16°18'13" W, 31.3.2017, F. Walther. **F.** *Allognathus (Allognathus) graellsianus* (Pfeiffer, 1848), Spain, Mallorca, 39°47'23" N, 2°53'27" E, 24.9.2010, A. Martínez-Ortí. **G.** *Allognathus (Iberellus) hispanicus* (Rossmässler, 1838), Spain, Mallorca, 39°49'42" N, 2°50'15" W, 7.12.2011, L. J. Chueca. **H.** *Iberus alonensis* (Férussac, 1821), Spain, Navarra, 42°10'47" N, 1°27'24" W, 12.6.2015, L. J. Chueca. **I.** *Pseudotachea splendida* (Draparnaud, 1801), Spain, Navarra, 42°03'35" N, 1°21'18" W, 4.8.2020, L. J. Chueca. **J.** *Cepaea hortensis* (Müller, 1774), Germany, 52°20'35" N, 9°53'7" E, 1.6.2014, M. T. Neiber.

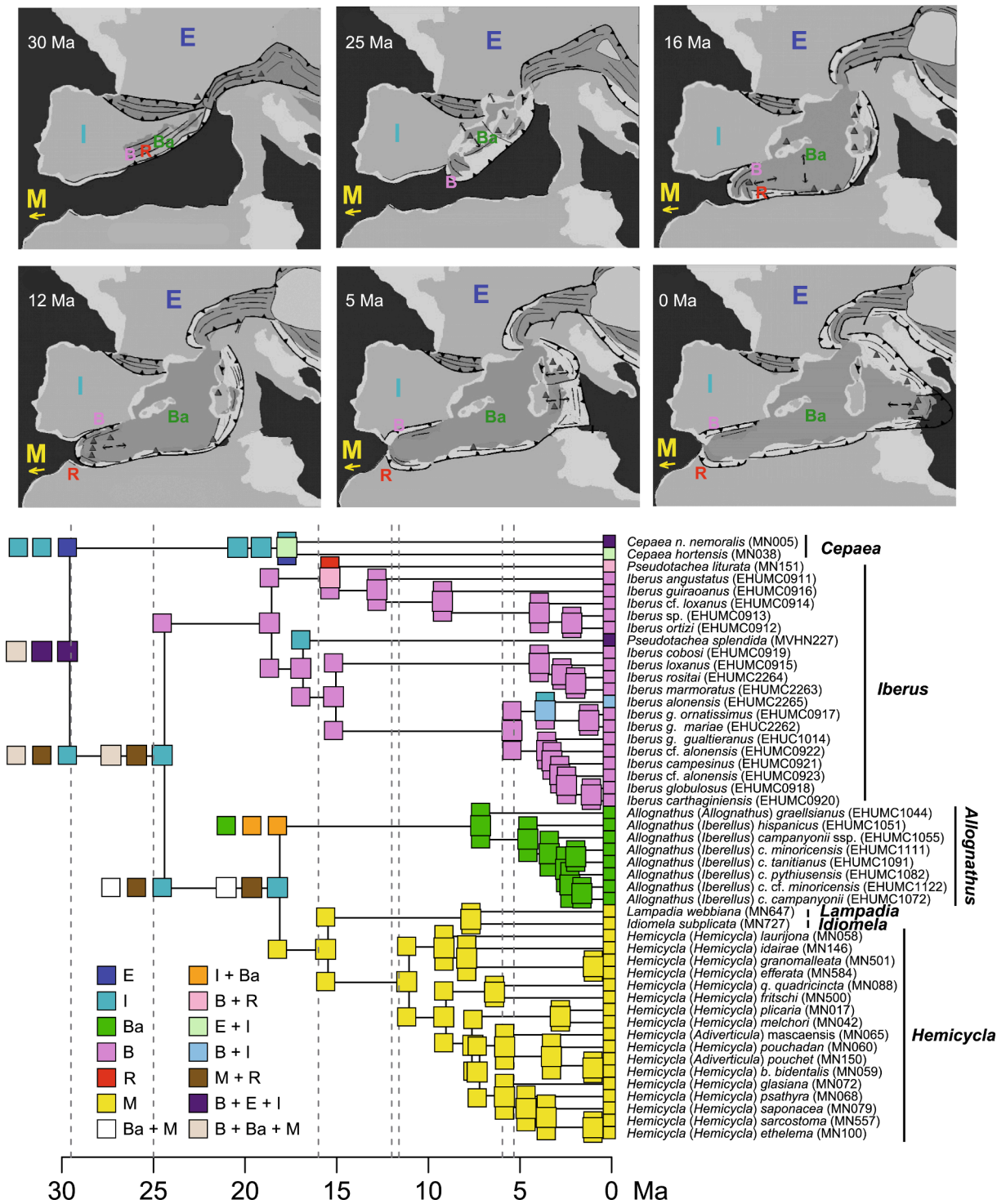


**Fig. 2.** Dated phylogeny (maximum clade credibility tree) showing the relationships and divergence times in the tribe Allognathini. Numbers at nodes refer to median node ages in Ma and the symbols indicate posterior probabilities (PP) (asterisk: PP  $\geq$  0.90, dot: PP  $\geq$  0.95). Bars represent 95% highest posterior density intervals for node age estimates. Q.; Quaternary; \*: node used for calibration.

branch leading to the genera endemic to the Balearic Islands and Macaronesia (Fig. 3). Further range contractions to Ba and M were estimated along the branches leading to *Allognathus* and the genera endemic to Macaronesia, respectively (Fig. 3). An ancestral range on the Iberian Peninsula was estimated in these analyses for *Cepaea* (Fig. 3).

The LRT (D = 8.01, df = 1, p = 0.0046, for ln-likelihoods, see Table 1) comparing the DEC and DEC + J models that were more constrained with regard to allowed ranges suggested rejecting the DEC

model in favour of the DEC + J model. The analyses under these models both estimated a range of B + E + I for the ancestor of Allognathini (incl. *Lampadia* and *Idiomela*) (Fig. 3). A most likely origin in I (DEC) or E (DEC + J) was estimated for *Cepaea*, while M + R (DEC) or I (DEC + J) were estimated for Allognathini excluding *Cepaea*, as well as for the clade including *Allognathus* and the genera endemic to Macaronesia (Fig. 3). A dispersal from M + R to I + Ba was estimated under the DEC model to have occurred after the lineage leading to *Allognathus* split off,



**Fig. 3.** Ancestral state estimation for Allognathiini in BioGeoBEARS under the DEC and DEC + J models with and without area constraints and palaeogeography of the Western Mediterranean region (modified from Rosenbaum et al., 2002). At each node, the single-most-probable state just before speciation and just after a split is shown. Where estimates differ among models, the estimates for the DEC and DEC + J models without area constraints (left; both models yielded identical most probable states across all nodes), DEC model with area constraints (middle) and DEC + J model with area constraints (right) are shown. B: Betic System; Ba: Balearic Islands; E: Continental Europe without the Iberian Peninsula; I: Iberian Peninsula (without Betic System); M: Macaronesia; R: Rif System. For node support (posterior probabilities), see Fig. 2.

with a subsequent range contraction to Ba, while the ancestral lineage of *Hemicycla*, *Lampadia* and *Idiomela* became extinct in R (Fig. 3). Under the DEC + J model, the Iberian Peninsula was estimated as the ancestral area of Allognathiini (excl. *Cepaea*), from where Macaronesia and the Balearic Islands were colonised independently (Fig. 3).

#### 4. Discussion

##### 4.1. Systematic implications

The results of our phylogenetic analyses (Fig. 1) confirm the previously published results of Neiber et al. (2011), Chueca et al. (2015),

**Table 1**

Likelihood scores and parameter estimates under different models implemented in BioGeoBEARS. L: likelihood, d: anagenetic dispersal rate, e: extinction rate, j: cladogenic dispersal rate.

Model	ln L	Number of free parameters	d	e	j
DEC (unconstrained)	-25.95	2	0.0189	$1.0 \times 10^{-12}$	0
DEC + J (unconstrained)	-25.95	3	0.0189	$1.0 \times 10^{-16}$	$1.0 \times 10^{-5}$
DEC (constrained)	-37.48	2	0.0316	0.0047	0
DEC + J (constrained)	-33.47	3	0.0244	0.0027	0.0155

Neiber and Hausdorf (2015) and Razkin et al. (2015) that the genera *Allognathus* (with subgenus *Iberellus*), *Cepaea* (in the sense of Neiber and Hausdorf, 2015), *Hemicycla* (with subgenus *Adiverticula*), *Iberus* and *Pseudotachea* belong to a clade within the Helicinae for which the name *Allognathini* is available. Additionally, our analyses suggest that the monotypic genera *Lampadia* and *Idiomela* from Porto Santo and several of its satellite islets in the Madeiran Archipelago (Hemmen and Groh, 1984; Seddon, 2008) belong to the *Allognathini* (Fig. 1). In contrast to Mandahl-Barth (1950), who argued that *Lampadia* belongs to the Helicinae and is allied to *Hemicycla*, Schileyko (2006) introduced *Lampadiini* as a tribe in the subfamily Ariantinae stating that *Lampadiini* “differs from all other tribes of Ariantinae by [the] vitrinoid shell, oxygnathous jaw and [a] peculiar combination of anatomical features” (Schileyko, 2006: 1786). Our phylogenetic analyses (Fig. 1) confirm the view of Mandahl-Barth (1950), clearly rejecting the suggested classification of Schileyko (2006). Therefore, we suggest synonymising *Lampadiini* with *Allognathini*.

*Pseudotachea* has usually been considered as a separate genus allied to *Iberus* in the last decades (e.g., Manganelli et al., 2005; Beckmann, 2007; Welter-Schultes, 2012; Chueca et al., 2015; Cadevall and Orozco, 2016). The results of our phylogenetic analyses, however, do not support the monophyly of the two living species currently assigned to *Pseudotachea*, i.e. *P. splendida*, the type species of the genus-group taxon, and *P. liturata*, but recovered both species as representing different lineages nested within a clade otherwise composed of taxa assigned to *Iberus*. According to Hesse (1920), García San Nicolás (1957), Gasull (1975) and Aparicio and Ramos (1988) *Iberus* differs conchologically mainly by the ornamentation of the shell. In *Iberus*, the shell is ornamented with incised spiral and radial lines that form a reticulate pattern. In contrast, the shell of *Pseudotachea* is almost smooth or has only very fine spiral striae. Martínez-Ortí (1999) noted though that populations of *P. splendida* with reticulate ornamentation of the shell are not uncommon and that an unambiguous separation of *Iberus* and *Pseudotachea* on the basis of shell characters alone is therefore not possible. Anatomically, *Pseudotachea* is reported to differ from *Iberus* by the cross-section of the love dart (anchor-shaped or similar to the cross of the Teutonic Order in *Pseudotachea*; cross-shaped with four sharp blades or two opposing sharp blades and the other two blades with thickened tips in *Iberus*), the larger dart sac and the higher number of terminal branches of the mucus glands (4–22 in *Pseudotachea*; 2–6 in *Iberus*) that insert near the base of the dart sac (Hesse, 1920; García San Nicolás, 1957; Aparicio and Ramos, 1988; Martínez-Ortí, 1999). These characters are known to vary considerably in other helicid genera (Hesse, 1920, 1931). Our phylogeny indicates that the blades of the dart were modified independently in the two species classified in *Pseudotachea* until now. Based on the results of our phylogenetic analyses, we therefore suggest synonymising *Pseudotachea* with *Iberus*.

*Adiverticula* has been introduced as a subgenus of *Hemicycla* to accommodate species, in which the diverticulum of the bursa copulatrix is missing (Ibáñez et al. 1988; Neiber et al., 2011). Our phylogenetic tree indicates that the diverticulum was lost independently in *H. pouchet*, the

type species of *Adiverticula*, and *H. mascaensis*. Thus, we here suggest synonymising *Adiverticula* with *Hemicycla*.

#### 4.2. Historical biogeography and diversification of *Allognathini*

Chueca et al. (2015) inferred a middle Miocene colonisation of the Balearic Islands by *Allognathus* or its ancestor via the Betic–Balearic corridor that was proposed to have existed during the Langhian–Serravallian (Riba, 1981; Fontboté et al., 1990; Roca, 1996), a colonisation scenario that has also been suggested for some vertebrates (Adrover et al., 1985; Quintana and Agustí, 2007; Bover et al., 2008). Support for the inferred time frame for the diversification of *Allognathini* was mainly derived from the consistency of sea-level fluctuations that took place in the Western Mediterranean from the Messinian to the present with the diversification and secondary contacts of the phylogroups of *Allognathus*, as well as their distribution ranges in the Balearic Islands (Chueca et al., 2015).

Our age estimates are most consistent with the previously published results of Chueca et al. (2015) when considering the uncertainty in the estimates (Fig. 3). Still, median ages are slightly older than those obtained by these authors. A possible explanation is a different approach to calibration, with the estimates obtained here deriving from a fossil calibration rather than a geological event. Because of the difficulty of accurately assigning fossil Helicoidea to specific lineages, our ages may therefore represent slight overestimations of divergence times. Nonetheless, our age estimate of 23.6 Ma (HPD: 22.1–32.7 Ma) (Fig. 2) for the split of Thebini and Otalini is also congruent with the age estimate of this split of approximately 22 Ma by Teasdale (2017) based on non-helicoid fossil calibrations. Hausdorf et al., (2020) dated the split of Otalini and Thebini at approximately 33 Ma and argued that their age estimates might be about 33% too high compared to the results of Teasdale (2017), which would imply a late Oligocene origin of Helicinae. According to the discussion in Hausdorf et al. (2020), it cannot be excluded that *Parachloraea* belongs to the stem-group of Helicidae or could belong even to the Sphincterochilidae Zilch, 1960, which are known from Eocene deposits (Nordlieck, 2014). Considering that the results obtained here fit the dating of Teasdale (2017) rather well, the placement of *Parachloraea* in Helicinae and *Palaeotachea* in *Allognathini* or its stem-group may also be correct though.

The DEC model is known to estimate wide ancestral ranges (Ree et al., 2005; Lamm and Redelings, 2009). Our ancestral range estimation without putting constraints on the allowed areas, except for allowing a range to be composed of a maximum number of three areas, inferred an ancestral range of *Allognathini* excluding *Cepaea* in the Betic block, the Balearic Islands and Macaronesia during the Oligocene and an ancestral range for the lineage leading to *Allognathus*, *Hemicycla*, *Idiomela* and *Lampadia* in the Balearic Islands and Macaronesia during the late Oligocene and early Miocene (Fig. 3). Because of the large distances between at least some of these areas during the Oligocene and the Miocene (Fig. 3) and considering that most modern *Allognathini* have small to very small ranges, we consider these ranges artefacts of the analysis.

The DEC and DEC + J with constraints on permissible areas specifically allowed independent colonisations of the Balearic Islands and Macaronesia from the Iberian Peninsula and of Macaronesia from North Africa, thus allowing to test the hypotheses proposed by Chueca et al. (2015) and Quintana Cardona et al. (2015). The DEC model inferred an ancestral range of *Allognathini* excluding *Cepaea* and for the lineage leading to *Allognathus*, *Hemicycla*, *Idiomela* and *Lampadia* in Macaronesia and the Rif System during the late Oligocene to early Miocene (Fig. 3). In contrast, the DEC + J model inferred an ancestral range in the Iberian Peninsula for these clades. A range in Macaronesia and the Rif System, which would better fit the hypothesis of Quintana Cardona et al. (2015) (although these authors proposed colonisation via the Kabylias) appears not very plausible considering the geographical setting during the Oligocene and Miocene and the absence of *Allognathini* fossils from



North Africa, with the possible exception of *Pseudotachea* (Jodot, 1955; Manganello, et al., 2005). The LRT also rejected the DEC model in favour of the DEC + J model and the fossil record also seems to better support an Iberian origin of the ancestor of *Allognathus* and the ancestor of *Hemicycla*, *Idiomela* and *Lampadia*, with numerous fossil taxa currently assigned to the arguably Allognathini genera *Palaeotachea* (incl. *Megalotachea*), *Creneatachea*, *Frechenia*, *Schlickumia* and *Titthodomus* described from Central, Western to South-western European deposits (Wenz, 1923; Pfeffer, 1930; Jodot, 1953a, b, 1955, 1958; Schlickum and Strauch, 1971; Truc, 1971; Nordsieck, 1986, 2014, 2016, 2017; Harzhauser et al., 2014; Hölzke and Rasser, 2016; Salvador et al., 2016). Should the ancestral area estimation of the DEC + J model be correct, the lineages giving rise to *Allognathus* and the Macaronesian genera would have gone extinct in the Iberian Peninsula.

## 5. Conclusion

Based on our molecular phylogenetic analyses, we show that the genus-group systematics of the Allognathini needs to be revised. In particular, the narrow-range endemics *Lampadia* and *Idiomela* from the Madeira Archipelago belong to Allognathini and represent together the sister group of the diverse Canary Island *Hemicycla* radiation. *Pseudotachea* is synonymised with *Iberus* and *Adiverticula* with *Hemicycla*. The six lineages of the extant Allognathini originated in Western to South-western Europe according to our ancestral area estimation and the fossil record. The disjunct distribution of the Balearic Islands and Macaronesian sister clades and the mainly Iberian *Iberus* clade that separated earlier can be explained by the separation of the Betic-Rif System from the Iberian Peninsula during the late Oligocene to early Miocene, along with independent Miocene dispersals to the Balearic Islands and Macaronesia from the Iberian Peninsula, where the ancestral lineage became extinct.

## CRediT authorship contribution statement

**Marco T. Neiber:** Conceptualization, Methodology, Validation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Supervision, Resources, Data curation. **Luis J. Chueca:** Conceptualization, Resources, Data curation, Validation, Writing - review & editing. **Amaia Caro:** Resources, Data curation, Validation, Writing - review & editing. **Dinarte Teixeira:** Resources, Data curation, Validation, Writing - review & editing. **Kevin A. Schlegel:** Resources, Validation, Writing - review & editing. **Benjamín J. Gómez-Moliner:** Conceptualization, Resources, Validation, Writing - review & editing. **Frank Walther:** Resources, Writing - review & editing. **Matthias Glaubrecht:** Resources, Validation, Writing - review & editing. **Bernhard Hausdorf:** Conceptualization, Resources, Validation, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2021.107196>.

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