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Iberus alonensis **dans son milieu naturel, dans la région de Cabo de Gata (prov. Almeria, Andalousie, Espagne) © Cristian R. Altaba**

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Taxonomic revision of the Iberian Allognathini (Mollusca, Gastropoda, Helicidae)

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http://zoobank.org/References/dc1176fa-28a4-427a-88ee-cc22d8fc1af2

Abstract – Land snails traditionally grouped under the genus *Iberus* comprise a variety of conspicuous taxa belonging to the Allognathini. They are restricted to southern and southeastern Iberia, and in need of a taxonomic update. Recent anatomical and molecular genetic studies strongly suggest that this not a natural group. In addition, there have been several nomenclatural errors propagating through the literature. A maximum-likelihood tree inferred from mitochondrial DNA (COI) sequences strongly supports its paraphyletic nature, as the radiations on the Balearic Islands and Macaronesia include well-defined genera that exhibit a degree of differentiation comparable to that among Iberian clades, and are nested within the latter. Morphologically identifiable species can be delineated in this phylogeny, with allopatric (or parapatric) taxa showing morphological distinctiveness but very small genetic differentiation being recognized as subspecies. Seven subtribes are recognized (six of them new, including one for the Canarian clade). Sister to the insular clades (Allognathina and Hemicyclina), the large species of *Iberus* (including its type species) constitute a monophyletic lineage (Iberina) including six subgenera (three of them new) and 13 species (three new), three of which include a total of nine subspecies (four new). The smaller snails belong to clades best treated as separate genera: *Pseudotachea* and *Herculiberus* gen. nov. are basal monotypic lineages (Pseudotacheina and Herculiberina), whilst the remaining species are grouped in two clades; Oretaniina includes *Oretanius* gen. nov. and *Cazorliberus* gen. nov., each with three species (one and two new, respectively); and Tartessiberina comprises *Marmoratus* with two subgenera (one new), three species and nine subspecies (two new), as well as *Angustiberus* gen. nov. (three species, one of them new and another one with a new name), and two monotypic genera, *Nescaniberus* gen. nov. and the distinctive *Tartessiberus.* The widespread European *Cepaea* is probably not an allognathine. Nomenclatural revision leads to rejection of 49 nominal taxa; stability is promoted through a reversal of precedence and designation of two neotypes and five lectotypes. The resulting taxonomic scheme may foster further research into the systematics, evolution and conservation of this extraordinary animal group.

Keywords – land snails, *Iberus*, Allognathini, phylogeny, taxonomy, nomenclature, Iberia

Résumé - Les escargots terrestres traditionnellement regroupés sous le genre *Iberus* comprennent une variété de taxons remarquables appartenant aux Allognathini. Ils sont limités au sud et au sud-est de la péninsule Ibérique et nécessitent une mise à jour taxonomique. Des études anatomiques et génétiques moléculaires récentes suggèrent fortement qu'il ne s'agit pas d'un groupe naturel. De plus, plusieurs erreurs de nomenclature se sont propagées dans la littérature. Un arbre de vraisemblance maximale déduit des séquences d'ADN mitochondrial (COI) appuie fortement sa nature paraphylétique, car les radiations des îles Baléares et Macaronésie incluent des genres bien définis qui présentent un degré de différenciation comparable à celui des clades ibériques, et sont imbriqués dans ces derniers. Cette phylogénie permet de délimiter des espèces morphologiquement identifiables, les taxons allopatriques (ou parapatriques) présentant une distinction morphologique mais une très faible différenciation génétique étant reconnus comme sous-espèces. Sept sous-tribus sont reconnues (dont six nouvelles, dont une pour le clade Canarien). Soeur des clades insulaires (Allognathina et Hemicyclina), les grandes espèces d'*Iberus* (y compris son espèce type) constituent une lignée monophylétique (Iberina) comprenant six sous-genres (dont trois nouveaux) et 13 espèces (trois nouvelles), dont trois comprennent un total de neuf sous-espèces (quatre nouvelles). Les plus petits escargots appartiennent à des clades qu'il vaut mieux traiter comme des genres séparés: *Pseudotachea* et *Herculiberus* gen. nov. sont des lignées monotypiques basales (Pseudotacheina et Herculiberina), tandis que les espèces restantes sont regroupées en deux clades; Oretaniina comprend *Oretanius* gen. nov. et *Cazorliberus* gen. nov., chacun avec trois espèces (une et deux nouvelles, respectivement); et Tartessiberina intégre *Marmoratus* avec deux sous-genres (un nouveau), trois espèces et neuf sous-espèces (deux nouvelles), ainsi qu'*Angustiberus* gen. nov. (trois espèces, dont une nouvelle et une autre avec un nouveau nom), et deux genres monotypiques, *Nescaniberus* gen. nov. et le distinctif *Tartessiberus*. Très répandu en Europe, *Cepaea* n'est probablement pas un allognathine. La révision nomenclaturale conduit au rejet de 49 taxons nominaux; la stabilité est favorisée par un renversement de la préséance et la désignation de deux néotypes et cinq lectotypes. Le schéma taxinomique qui en résulte pourrait favoriser de nouvelles recherches sur la systématique, l'évolution et la conservation de ce groupe animal extraordinaire.

Mots clés - escargots terrestres, *Iberus*, Allognathini, phylogénie, taxinomie, nomenclature, Ibérie

Introduction

The earliest scientific treatment of an Iberian allognathine (Gastropoda: Stylommatophora: Helicidae: Helicinae: Allognathini) was by Gualtieri (1742: fig. 60E), who shows a most strange shell of unknown origin; so strange it seemed in comparison to other snails, that he thought it should be marine. This species was described under the binominal system as *Helix gualtierana* Linnaeus, 1758 and thus correctly recognized as an odd-shaped pulmonate snail, although still of unknown provenance (Linnaeus, 1758: 770). Odd also is the fact that it was described again, on the basis of the same drawing by Gualtieri, just twenty years later (Born, 1778: 376). Nevertheless, its origin remained as "patria ignota" (Born, 1780: 368). Later on it was supposed to be terrestrial and living in India (Gmelin, 1791: 3621), even though claims had been made that it should also be found in Spain (Roissy, 1804-1805: 388). Its unusual shell lead Montfort (1810) to propose for it the genus *Iberus*, a name reflecting his discovery that this beautiful species lives indeed in Spain. Some years later, Férussac (1821: 36) was able to point at its actual range, limited to only in a small area close to Almería, in southwestern Andalusia. This early tale of mistakes and corrections was just a prelude to the chaotic history of *Iberus*.

The current understanding of *Iberus* needs revision. Several species from eastern and southeastern Iberia, mostly from the Betic area, are now included therein, but their phylogenetic relationships remain unclear (Rossmässler, 1854-1859; Schmidt, 1853, 1855; Kobelt, 1910; Serradell, 1912; Boettger, 1913; García San Nicolás, 1957; Cobos, 1980; Aparicio & Ramos, 1988; Elejalde et al., 2008a,b; Schileyko, 2006; Welter-Schultes, 2012; Polo Roldán, 2016; Jowers et al., 2024). This is reflected in the varying number of species accepted, reaching the unrealistic extreme of just one (Puente Martínez, 1994). The chaotic state of current taxonomy is also reflected in the various ways of naming taxa. As a case in point, both Serradell (1912) and Boettger (1913) thought all *Iberus* could be arranged on a continuum variation of a single polymorphic species; yet each described one extreme species and subspecies, respectively. The unsettled vagaries in nomenclature remain, for example when Martínez-Ortí et al. (2004) list "*Iberus gualtierianus* morfotipo *guiraoanus*" but mention "*Iberus gualtierianus guiraoanus*" in their figure caption; these two species-level names refer to distinct lineages that are definitely not conspecific. Recent work by Liétor et al. (2024a,b,c,d) and Tudela et al. (2024) has introduced further noise. A partial overview of nominal taxa was presented by Bank and Luijten (2015; the date 2014 printed on the first page of the paper is corrected in the journal cover), but hitherto a comprehensive revision has been lacking.

It is clear that "*Iberus*" is a heterogeneous group, whose limits and lineages should be reflected in a revised taxonomy. Thus, the genus *Tartessiberus* Altaba & Ríos Jiménez, 2021 was erected for a highly specialized, phenotypically divergent species (Altaba & Ríos, 2021); this surely makes the traditional *Iberus* an oddly diverse, paraphyletic group. This set of clades clearly belong within the Allognathini, a small tribe of helicines (Kneubühler et al. 2019; Holyoak et al., 2020) including the Western Mediterranean *Pseudotachea* Boettger, 1909 and also a few genera endemic to two southwestern Palaearctic archipelagos: in the Balearic Islands, *Allognathus* Pilsbry, 1888, *Iberellus* Hesse, 1908 and *Tramuntanicola* Altaba, 2022; and in Macaronesia, *Hemicycla* Swainson, 1840, *Lampadia* Albers, 1854, and *Idiomela* Cockerell, 1921; all these insular genera are morphologically and ecologically distinct (Welter-Schultes, 2012; Neiber et al., 2021; Altaba, 2022a, b; Juárez-Ruiz & Altaba, 2022), their recognition standing in stark contrast with the lumping within *Iberus* as hitherto recognized. The European *Cepaea* Held, 1838 may constitute a basal lineage, but this is questionable.

Although shells of all these land snails are relatively rich in taxonomically useful characters, there has been a general neglect of morphological data to evaluate the phylogenetic relationships within the Allognathini. Shells of *Iberus* and allied genera are recognizable by their depressed shape, enlarged last whorl, more or less reflected lip, and medium to fairly large size (roughly from 17 to 45 mm in maximum diameter). The surface bears a fine (in some instances very fine, albeit usually quite conspicuous) reticulate sculpture made of very thin colabral ridges and dense, fine spiral incisions. There is a distinct columellar callus, often covering entirely the narrow umbilicus. The color ranges from whitish to deep brown, generally with a marbled pattern of irregular geometric blotches coalescing into spiral bands, which may even become continuous and well contrasted. Within these basic parameters, the shells vary widely in almost every feature. However, intrapopulation variation is generally limited to individual size (usually rather uniform), spire height (more or less depressed) and coloration pattern (bands more or less marked or broken); diagnostic traits are conspicuous. *I. gualtieranus* represents an extreme morphology with a much depressed, strongly keeled and intricately sculptured shell; much variability occurs throughout the tribe.

Reliable, detailed anatomical data are available for just a handful of species. In spite of extensive anatomical work by Emilia García San Nicolás (1957) and Ana Puente Martínez (1994), interpretation of their dissections is hampered by lack of sufficient detail. Likewise, linear shell measurements predictably yield no reliable means of identifying specimens belonging to (even closely related) lineages delineated on a molecular tree (as attempted by Liétor *et al.*, 2024a). In the case of the Balearic clade, it is now clear that anatomical structures differ substantially among genera (Altaba, 2022a); for the Iberian taxa, there is a conspicuous paucity of accurate data, even though there is also a wealth of useful characters to be studied (Altaba & Ríos Jiménez, 2021).

In contrast to the morphological record, there is now a fairly high number of DNA sequences, produced by various teams working on the phylogenetics of *Iberus* and related taxa (Elejalde et al., 2008a,b; Groenenberg et al., 2011; Martínez-Ortí & Robles, 2013; Neiber et al. 2021, 2022; Liétor et al., 2024a; Jowers et al., 2024). The analyses thus far performed, however, often suffer from sparse taxon sampling, and more importantly equivocal methods. It is unclear why distance-based or maximum-parsimony methods were often applied, when it is widely accepted that neither of these approached can yield a correct phylogenetic inference based on nucleic acid sequences. Also, Bayesian algorithms, in spite of the apparent advantage of being able to yield absolute dates of divergence, are prone to artifacts, especially long-branch attraction. Taxonomic proposals derived from such error-prone trees are questionable. One such nomenclatural act is the synonymization of the distinctive *Pseudotachea* with *Iberus*, given that in one tree the former falls within the latter (Neiber et al. 2021); such topology has negligible support. Another proposal is the synonymization of *Tartessiberus*, based on a very wide (and paraphyletic) concept of *Iberus* that was favored under the assumption that genera should be of Miocene age (Jowers et al., 2024); lacking sound grounds, it appears as an untenable suggestion. A reanalysis of molecular phylogenies of allognathines seems timely.

The taxonomy of *Iberus* has also suffered from misinterpretations of the original literature. Such mistakes, either long-standing or fairly recent, need to be corrected. Currently, inadequate usage spans from invalid junior synonyms to unjustified new names and nomina nuda. Names applied to taxa in this group often do not correspond with what was originally described. For example, it is most unclear why the amazing combination *Allognathus hispanicus* (Rossmässler, 1838) was employed to include all Balearic *Iberellus* species (Chueca et al., 2013, 2015; Neiber et al., 2021, 2022), when the original description and illustration of *Helix hispanica* clearly show this is the same as the species known in recent literature as *Iberus angustatus* (Rossmässler, 1854) from northern Andalusia (Altaba, 2022b). Likewise, the eccentric name changes by Martínez.Ortí and Robles (2012) have been partially revised by Bank and Luijten (2015), who in turn take the mention of a common name by Aguilar-Amat (1921) as the proposal of a species name, effectively creating the unavailable name *Iberus carragines*. Recently, Liétor et al. (2024a) described three new species of *Iberus*, but these are indistinguishable and lacking any diagnostic traits. Also, Liétor et al. (2024b,c,d) and Tudela et al. (2024) revise the identity and distribution of several *Iberus* from southeastern Spain, but their work includes mistakes that must be addressed, and is also contrary to some provisions in the International Code of Zoological Nomenclature. Thus, a critical reevaluation of published names seems desirable. As a result, a few corrections are presented herein, affecting even well-known taxa; in order to minimize changes, additional nomenclatural acts are introduced: a reversal of precedence, as well as designation of two neotypes and five lectotypes.

A further problem to be confronted when dealing with the taxonomy of Iberian allognathines is confluent with their conservation status. Unfortunately, these land snails are all intensively sought for as food items (Mayoral et al., 2007). The fondness of southern Spaniards for eating *Iberus*, and moving live animals around, was already well documented in the early 19th century (Rossmässler, 1834) and surely dates from prehistorical times (Mannino Thomas, 2023). It is now clear that the occurrence of *Iberus gualtieranus* in three areas far from its long-known, highly restricted native range is not the outcome of any unusual evolutionary process (as discussed by Alonso et al., 1985), but rather the result of intentional introductions of a highly prized species (Elejalde et al., 2008b; Arrébola et al., 2011). Unfortunately, intermediate phenotypes in the areas affected by such introductions, as well as isolated instances of disagreement between species identification based on maternally inherited mtDNA and shell phenotype (Elejalde et al., 2008b), highlight the potential harm caused by species translocations. There is thus an added urgency for an updated, evidence-based and useful taxonomy.

Material and methods

This taxonomic revision is circumscribed to taxa of the Allognathini living in the Iberian peninsula. It is largely based on the author's experience in the field and at different museums, during almost fifty years of research; I performed my first dissection of an *Iberus* 44 years ago. Three lines of evidence have been taken into account: morphological distinctness of shells, location and length of branches leading to distinct taxa in a molecular phylogeny, and geographical and ecological distribution of putative species and subspecies. In addition, a thorough revision of the nomenclatural history of this group allowed translation into a binominal classification, including the description of new subtribes, genera, subgenera, species and subspecies.

A molecular phylogeny was built using available COI sequences (Table 1). This mitochondrial DNA fragment allows discrimination and identification of metazoans; its use is now widespread, and is called "barcoding" (Hebert et al., 2003; Guo et al., 2022). There is a wealth of information for taxonomy and the study of evolution in the large amount of homologous sequences already available in public databases (Pentinsaari et al., 2016; Andújar et al., 2018). COI barcoding has been proven to be an accurate tool, especially in densely sampled taxa and based on previous understanding of their taxonomy (Meyer & Paulay, 2005). It clearly provides a powerful basis for identification of discontinuous evolutionary groupings and species delimitation (Pons et al., 2006; Orosco et al., 2024). Of course, it might be argued that single-locus mtDNA data and small sample sizes make interpretations risky, but these limitations can be dismissed when the molecular tree is not the only criterion for species discovery, being used instead only as a scaffold for taxonomy (Kekkonen & Hebert, 2014; Wüster et al., 2024). In contrast with COI, other published short sequences (including nuclear genes) provide very limited phylogenetic information (Elejalde et al., 2008a,b; Jowers et al., 2024); although trees inferred from these other sequences agree widely with the COI tree, adding them would only increase the amount of noise over signal, and thus have not been considered. Outgroup taxa for the phylogenetic analysis include several helicines that fall outside, but more or less close to the Allognathini, and the more distantly related *Helix* Linnaeus, 1758.

The phylogenetic analysis was performed on the NGPhylogeny.fr platform (Lemoine et al., 2019). Sequences were aligned with MUSCLE (version 3.8.1551-0; Edgar, 2004), and the resulting alignment was curated with Gblocks (version 0.91.1; Castresana, 2000). Trees were inferred with PhyML+SMS, an efficient maximum-likelihood algorithm (version 1.8.1-1; Guindon et al., 2010; Lefort et al., 2017). Branch support was calculated as SH-like aLRT after 100 bootstraps (Lemoine et al., 2018). The optimal tree was redrawn with iTOL (Interactive Tree of Life, version 6; Lecunic & Bork, 2024), collapsing nodes with support below 0.5.

All algorithms devised for phylogenetic inference are prone to artifacts, often unavoidable (Venditti et al., 2006; Altaba, 2009). In particular, long-branch attraction (Bergsten, 2005) is of special concern when branch lengths differ widely (Parks & Goldman, 2014), a common situation when taxon sampling is uneven and insufficient; it is also a real threat when there is across-site compositional heterogeneity (Szánthó et al., 2023), even when data are partitioned (Susko & Roger, 2021). In order to detect and avoid such artifacts, numerous trees were inferred, adding taxa stepwise and controlling for any topological changes, until a stable pattern remained.

Delimitation of species has been performed taking into account three lines of evidence: morphological distinctiveness, appreciable genetic differentiation, and biogeographic separation. There is of course no "magic bullet" to delimitate species, even with genomic data or the various algorithms already devised (Rannala & Yang, 2020); in fact, a completely non-arbitrary method for species delimitation is simply impossible (Zachos, 2018). Herein a more natural-history approach is followed, obviously open to further refinements with more intensive sampling and additional genomic data (such as the process-based method devised by Smith & Carstens, 2019). Taxa considered as subspecies fail to meet the above three requirements, often in the form of evidence of geographic subdivision with very small genetic divergence; these lowest-rank taxa have allopatric or even parapatric distributions, likely with narrow transition areas.

The nomenclature revision follows the International Code of Zoological Nomenclature (ICZN, 1999; onwards the Code). A few changes are needed in order to correct persistent mistakes; in one case it is proposed to maintain prevailing usage through a reversal of precedence (Article 23.9). Revision of type material in museums has been possible through the kind help of curators in Geneva and Barcelona, leading to the designation of two lectotypes. These, together with three further lectotypes, two neotypes, a new

name and 28 new taxa, are dealt with in the systematic section below. The new species and subspecies are identifiable on the basis of shell characters that appear to be diagnostic and unequivocal. I use the term "monotypic" at the family level in its taxonomic sense (following Potter & Freudenstein, 2005). Shell terms and measurements follow the standard set in previous research on allognathines (Altaba & Ríos, 2021; Altaba, 2022a). Anatomical data and the resulting phylogenetic analyses are in progress and will be provided separately. The new material on which this study is based has been deposited in the author's Museographic Collection (CRA), recognized by the Council of Mallorca.

Two kinds of citations have been omitted. First, taxa that have been placed into the Allognathini have been revised, resulting in the exclusion of some. In addition, erroneous citations have been a recurrent problem for allognathine taxonomy: *Iberus* species have been reported from many extant and archaeological locations, due to confusion with species belonging to other genera or even families. Several such instances have already been corrected (Aguilar-Amat, 1925; García San Nicolás, 1957; Cobos, 1980; Groenenberg et al., 2011), whereas others remain dispersed throughout the literature (e.g., Coll Monteagudo et al., 2022); they have not been taken into account herein.

The geographical distribution of species-level taxa is shown in maps, without extensive locality data. A more thorough monograph is in preparation. The goal of this paper is to establish the framework for a much more extensive treatment of the Allognathini.

Results

Taxa excluded and relocated

Nominal taxa that have been attributed to the Allognathini have been examined, setting aside those that do not belong into this clade. Some instances are rather straightforward, being genus-level names introduced to indicate a superficial resemblance to *Iberus*. For example, *Pseudiberus* Ancey, 1887, *Tyrrheniberus* Kobelt, 1904 and *Exiliberus* Iredale, 1942 have shells deceptively similar to *I. gualtieranus*, but are closely related to species in the Murellinae, Camaenidae and Thebini, respectively (Ancey, 1887; Kobelt, 1904; Fiorentino et al., 2010; Neiber et al., 2021, 2022). *Transiberus* Monterosato, 1892 has been shown to refer to murelline species, besides being unavailable (Schileyko, 2013).

In a similar way, it is now easy to sort out cases of explicit, phylogenetically inappropriate usages of the name *Iberus*. For example, *Elona* H. Adams & A. Adams, 1853 was proposed within *Iberus* with subgeneric rank (Adams & Adams, 1853-1858), but it is now known that these two genus-level taxa are quite distantly related, the former being in Elonidae. Likewise, *Murella* Pfeiffer, 1877 and *Levantina* Kobelt, 1871 were included as sections within *Iberus,* treated as subgenus of the large Linnean *Helix* by Westerlund (1889); currently they belong into Murellinae and Helicini, respectively. Likewise, *Dupotetia* Kobelt, 1904 and *Alabastrina* Kobelt, 1904 were also proposed as subgenera (Kobelt, 1904), but these are junior synonyms of *Loxana* Pallary, 1899 and *Otala* Schumacher, 1817, respectively; recent research shows these are sister taxa and belong into the Helicini (Bouaziz-Yahiatene et al., 2017; Kneubühler et al. 2019; Holyoak et al., 2020; Neiber et al., 2021, 2022).

At the species level, several species have been described or relocated with no justification for their taxonomic placement: for example, *Helix (Iberus) ragusae* Kobelt, 1883 from the Egadi Islands near Sicily, and *Helix (Iberus) circeja* Kobelt, 1903 and *H. (I.) melii* Kobelt, 1903 from central Italy (Kobelt, 1883a, 1903a); the latter two refer to the same population, and all three surely belong into *Marmorana* Hartmann, 1844 in the Murellinae (Fiorentino et al., 2010). The subgenus *I. (Transiberus)* Monterosato 1892 was devised to englobe several other Sicilian and Italian nominal taxa (Monterosato, 1892), albeit with the same lack of any solid basis. *Eobania vermiculata* and *Iberellus balearicus* have occasionally been placed in *Iberus* (Kobelt, 1904), but it is now clear they belong into distinct, more or less closely related clades within the large Helicinae (Bouaziz-Yahiatene et al., 2017; Neiber et al., 2021, 2022; Altaba, 2022b).

In other instances, further information is needed to clarify mistakes. This is the case of *Iberus carragines* unintentionally mentioned due to a confusion. The common name of *Iberus* land snails in southern Catalonia is "carragines", as first compiled by Aguilar-Amat (1921). It is unclear why this popular name, albeit originally written in italics, could be taken as the proposal of a Linnean species name by Bank and Luijten (2015), who erroneously attributed the nomenclatural act to the earlier author.

Shells of medium-sized helicids were recovered from muddy sediments at the Albufera lake, south of València by two prominent naturalists, Eduardo Boscá and S. Becker around 1898. Some of the specimens were sent to Wilhelm Kobelt in Frankfurt, who considered one of the species collected would be a morphological link between *Pseudotachea* and the Balearic allognathines (Kobelt, 1900). He thus coined *Helix beckeri* Kobelt, 1900 and later, as promised in the original description provided an illustration of this new species (Kobelt, 1904: p. 60 and fig. 1890 in pl. 294). Germain (1930) considered it a species of *Pseudotachea*, probably accepting Kobelt's hypothesis, but it is obvious from the description and figured specimen that this nominal species belongs into *Cepaea*. Kobelt himself might have reevaluated his initial assessment of phylogenetic affinities, as the plate showing this species depicts the variability of *Cepaea nemoralis* (Linnaeus, 1758). It appears that *H. beckeri* represents an ecophenotype in response to an environment that is marginally adequate for *Cepaea* in terms of aridity and summer temperature, resulting in unusually small shells with well marked colabral striae. The white lip of *H. beckeri*, together with its small size, suggests it is identical to *Cepaea hortensis* (Müller, 1774), a species currently absent from the Mediterranean coast (Puentre Martínez, 1994). If so, then *Helix beckeri* is a junior subjective synonym of *C. hortensis*. It is most unclear why Robles & Martínez-Ortí (2005) decided that other lots of subfossil shells collected at a different location (the Carraixet temporary stream, north of València), representing at least two species and curated in three different museums would all belong to the type series of Kobelt's species (an opinion repeated by Martínez-Ortí & Uribe, 2008). It is also unclear why they decided (without mentioning Germain, 1930) that they all belong to *P. splendida.* As a consequence of these misidentifications, these mixed lots were considered as syntypes, a specimen in the Senckenberg Museum was designated as lectotype, and *H. beckeri* was placed in synonymy of *P. splendida*; these nomenclatural acts and taxonomic consideration must be obviated.

Fossil species attributed to the allognathine clade have also been revised, acknowledging that such taxa may be hard to place in a phylogenetic scheme. Truc (1971) and Nordsieck (2014, 2016a) disentangled the confused taxonomy of Paleogene taxa similar to the extant *Cepaea* (once known as *Tachea* Turton, 1831, a junior honomym of the avian *Tachea* Fleming, 1822), showing a diversity of now extinct, probably related genera. Basal (usually fossil) lineages pose the problem of deciding whether they fall outside the clade, albeit being more or less closely related, or belong into its stem by virtue of possessing incipient character states recognizable as synapomorphies (Cela-Conde & Altaba, 2002).

Cepaea has been inequivocally present (and widespread) in Central Europe since the Middle Miocene (Salvador, 2013). The suggestion by Neiber et al. (2021) that *Palaeotachea* Joos, 1912 might belong "in Allognathini or its stem-group" is plausible, but currently appears as a mere guess. *Palaeotachea* appears in the late Oligocene and is diverse and abundant in the Middle Miocene of southern Germany (Nordsieck, 2014; Höltke et al., 2018). It lacks the diagnostic peristome of *Cepaea* and includes the subgenus *P.* (*Megalotachea)* in the Miocene (Nordsieck, 1984); through its likely descendant *Frechenia* Schlickum & Strauch, 1971 in the Pliocene, it appears closely related to the extant *Eobania* Hesse, 1913 (Truc, 1971). Thus, *Palaeotachea* most likely does not belong into the allognathine radiation. *P. (Megalotachea)* occurs also in central Portugal (Truc, 1977). Likewise, the proposal by Nordsieck (2016a) that the Pliocene *Frechenia* could be ancestral to *Cepaea* is questionable, given that the columellar trait they share is known to be homoplastic.

There is a diversity of *Cepaea*-like genera in the Miocene to Pliocene of central Europe (Truc, 1971; Nordsieck, 2014). From the Pliocene of Santa Pola, very close to Alacant (Alicante), *Otala alicantensis* Truc, 1971 was described on the basis of two molds as *?Otala (Otala) alicantensis* expressing doubts on the generic allocation; the uncertain generic allocation in the original description was justified with the need for a new genus that would include this and other fossils from southern France, Portugal and northern Italy (Montenat & Truc, 1971). Thus *Schlickumia* Truc, 1977 was erected to include an assortment of species, and hypothesized to be ancestral to *Iberus* and close to *Galactochilus* Sandberger, 1875 from the Miocene of Central Europe (Truc, 1977). However, *Schlickumia* as originally envisioned is a polyphyletic taxon. Species included therein are members of different families. *Helix aquensis* Serres, 1829 from the Upper Miocene of Provence was placed in *Galactochilus* within the Elonidae (Nordsieck, 2016b). However, the type species of the latter genus is an extant species from Indonesia and belongs into the Camaenidae (Kadolsky, 2017), so several fossils from the Central European Tertiary were grouped in *Agalactochilus* Kadolsky, Binder & Neubauer, 2016 and placed in the Ariantinae (Kadolsky et al., 2016). The type species of *Schlickumia*, *Helix gaspardiana* Paladilhe, 1873 lived in the Upper Pliocene of Occitania in southern France and is clearly different from any allognathine; it seems very close, and perhaps ancestral, to the

thebine *Eremina* Pfeiffer, 1855, currently restricted to North Africa.

Three fossil species referred to *Iberus* surely belong to non-allognathines. Although more detailed research is needed on them, they can be tentatively placed in different groups. *Helix (Macularia) torresi* Roman, 1917, described from the Miocene of central Portugal, has a rather discoidal shape and smaller size, and lacks both a sharply reflected lip and any crisscrossed microsculpture (Roman, 1917); it has been placed in *Pseudotachea* Boettger, 1909 (Wenz, 1923; Jodot, 1953, 1955, 1958), but this allocation, as that of other Neogene fossils from southern Spain and southern France, was shown to be mistaken by Truc (1971). More recently it has also been placed in *Iberus* without any justification (Neiber et al., 2021). However, the traits of this fossil support its allocation into the Ariantinae, likely as an early member of *Corneola* Held, 1838, an isolated lineage likely diverging in the Eocene and living in southwestern Europe, only in the area between Catalonia, the Pyrenees, Britanny and Provence (Groenenberg et al., 2016). This proposal implies *Corneola* had a larger geographical distribution during the early Neogene, as *Corneola torresi* (Roman, 1917) shows.

Also from a Miocene site in central Portugal, *Helix (Iberus) delgadoi* Roman, 1917 was considered a noteworthy geographical outlier of *Iberus* (Roman, 1917). Nevertheless, it has a totally different microsculpture and only resembles *I. gualtieranus* in being strongly keeled with a depressed spire; this is a shape that has appeared in many helicoid lineages and has no phylogenetic meaning. It is unlikely that this fossil would belong into the *Iberus* group. The third fossil species is *Helix bolivari* Royo Gómez, 1922 from the Miocene of eastern Spain. It has also been included in *Iberus* (Harzhauser & Neubauer, 2021), but *H. bolivari* is a large species exhibiting a thickened rib inside the aperture and lacking any spiral microsculpture (Royo Gómez, 1922). No known species within the *Iberus* group has a thickened rib in the aperture, usually a very useful diagnostic character. Species without spiral microsculpture are not known in the *Iberus* group. The two latter species do not fit into this group (the Allognathini); they are better considered to belong into the Helicini, and can be placed in the living North African genus *Loxana* Pallary, 1899, composed of large snails with a wide array of shell shapes spanning from quite globose to strongly keeled. This assessment implies that *Loxana* extended into Iberia during the Miocene, as attested by *Loxana delgadoi* (Roman, 1917) and *L. bolivari* (Royo Gómez, 1922).

Molecular phylogenetics

The phylogenetic analysis based on partial cytochrome oxidase I sequences resulted in a tree with overall high support. The selected model was GYR+γ with four categories, γ = 0.731 and 0.536 proportion of invariants. Most nodes have very high bootstrap support values; very few had support values below 0.5 (thus collapsed in Fig. 1). In contrast with previous works, better taxon sampling appears to account for stronger resolution and increased branch support.

The relationship among the various outgroup taxa supports a complex evolutionary history of the Helicinae. Two relevant points can be raised from this basal part of the tree (in black in Fig. 1). First, the Thebini (as defined by Neiber et al., 2022) appear to be paraphyletic, probably deserving a revision. Besides, *Cepaea* groups with *Otala*, so it cannot be considered an allognathine. Its inclusion as a sister group to other Allognathini by Neiber et al. (2022) is probably an artifact of long-branch attraction, likely caused by insufficient taxonomic coverage and aggravated by partitioning. A more comprehensive taxon sampling and careful analyses should shed light on its placement in the helicine phylogeny; it is probably basal to the Otalini (as defined by Holyoak et al., 2020).

It appears that *Iberus*, either in its traditional wide sense or even wider as revised in some recent literature, is a grossly paraphyletic assemblage. Given that the island clade (including both Balearic and Macaronesian subclades) is nested within, and sister to a cluster of large snails including the type of the genus, the latter needs to be considerably restricted. The smaller species fall outside its boundaries, forming different branches that deserve recognition. Thus, subtribes are erected to account for the phylogenetic groupings within Allognathini; seven new suprageneric clades are named in order to reflect diversification.

The earliest offshoot within the Allognathini is the monotypic *Pseudotachea*. The position of *Helix liturata* Pfeiffer, 1853 (until now placed in *Pseudotachea*) as a second basal lineage would make this genus paraphyletic, so a new genus is proposed for it.

A distinct clade is formed by large species attributable to the genus *Iberus*. This is divided into six subgenera (four of them new). The first subgenus, *Labioiberus* subgen. nov., includes a polytypic species readily identifiable by its large size and more or less expanded apertural lip.

The distinctive expanded lip of typical *I. campesinus* is considerably reduced in populations to the north and east of the limited species range. *H. lorcana* Rossmässler, 1853 represents populations similar in size and structure, but bearing a smaller, incomplete peristome lip. A third unnamed group has an even less developed aperture. I consider the three taxa as geographical subspecies of *I. (L.) campesinus*, presumably having parapatric distributions.

The second group, *Carthaginiberus* subgen. nov. is found from the coastal area around Cartagena, in southern Murcia region, up to the mountains of northern Almería and northeastern Granada provinces. It includes *I. carthaginiensis* (Rosmässler, 1853) and *I. bajoi* (Bourguignat in Servain, 1881). The former species includes a southern subspecies. These taxa exhibit a noteworthy variation in size, and less so in shape, attributable to the varied microclimates they live in. *I. bajoi* was shown to be a distint species by Elejalde (2008b), albeit under the synonym *I. globulosus* Boettger, 1913.

A third group of *Iberus* lives further west, in the Betic and Subbaetic areas of eastern Andalusia; this is *Nazariberus* subgen. nov. These are large snails with rather solid shells. The nominal species *Iberus rhodopeplus* Aguilar-Amat, 1925 was validly described on the basis of its red-colored mantle. It has an allopatric distribution relative to two new species. The fourth group of *Iberus* includes the type species, as well as three narrow endemics; all four are restricted to small areas in the very dry Sierra de Gádor and its foothills, in southernmost Almería province. Further east, the monotypic *Alonensis* includes only *Iberus alonensis* (Férussac, 1821), a distinctive species having a very small range in extreme southeastern Andalusia. Finally, the subgenus *Valentiberus* subgen. nov. includes *Iberus alvaradoi* García San Nicolás, 1957, whose phylogeographic structure allows distinction of four geographical subspecies (three of them new).

The two lineages of "small *Iberus*" are well defined and may constitute a clade. The subtribe Oretaniina subtrib. nov. includes species restricted to north-central and northeastern Andalusia, grouped in two separate genera: *Oretanius* gen. nov. and *Cazorliberus* gen. nov., with three species each (including one and two new, respectively). The other lineage of small snails (Tartessiberina, subtrib. nov.) is more diversified: the basal *Angustiberus* gen. nov., with two allopatric species (one of them new, and another one with a new name) living in north-central Andalusia; the narrow-range endemic, monotypic *Nescaniberus* gen. nov., restricted to a small area in south-central Andalusia; *Marmoratus* gen. nov., more widely distributed in south-central Andalusia, with two subgenera (one new), three species and nine subspecies (two new); and at the westernmost edge of the Betic ranges, the narrow endemic, monotypic *Tartessiberus*.

New taxa of Allognathini and remarks

Family Helicidae Rafinesque, 1815

Subfamily Helicinae Rafinesque, 1815

Tribe Allognathini Westerlund, 1903

Pseudotacheina subtr. nov.

Diagnosis.- Small allognathines with strongly depressed shell, completely closed umbilicus, expanded last whorl, small reflected lip, soft pink peristome, gently curving whorls, and shining surface provided with faint collabral and exceedingly fine spiral lines.

Type genus.- *Pseudotachea* Boettger, 1909 (monotypic)

http://zoobank.org/NomenclaturalActs/5138C884-FFA0-4F6F-97BD-65D1AB6F5315

Remarks.- *Pseudotachea* is clearly different from *Iberus*, both in its smooth shell (with only exceedingly

faint spiral sculpture) and genitalia including a dart with bilaterally revolving edges and multifid glands considerably more numerous, branching distally (Boettger, 1909; Aparicio & Ramos, 1988; Puente, 1994). In the molecular tree, it constitutes a basal lineage, sister to all other allognathines. The proposal to synonymize it (Neiber et al., 2021) cannot be sustained.

The only species in the genus, *P. splendida* (Draparnaud, 1801) has the largest distribution of all allognathines (Fig. 2). It lives throughout eastern Iberia (inland across the Júcar and Ebro drainages) and northwards along the Mediterranean coast of Languedoc and Provence (Haas, 1929; Germain, 1928, 1930; Gasull, 1976; Puente, 1994; Kerney et al., 2006; Bragado et al., 2010; Welter-Schultes, 2012). It is also widespread in the island of Mallorca and neighboring islets, undoubtedly as an alien introduced by humans (Sacchi, 1956; Gasull, 1964; Altaba, 1991, 1993). It has been introduced (and eradicated) in Malta in 2003 (Cilia, 2010). The genus had a wider range in the Pleistocene, attaining northern Italy (Manganelli et al., 2005).

Several varieties of *P. splendida* have been named, essentially naming individual variation in the banding pattern. Rossmässler (1838-1844: 8, pl. 17, fig. 238) mentions a few varieties indicated by Greek letters, but later on (Heft 9/10: 13) describes *Helix splendida* var. *roseolabiata* Rossmässler, 1839. Moquin-Tandon (1855: 150) gives a name to each of 13 such varieties found in France: *Penchinatia*, *Serresia*, *Dugesia*, *Tersonia*, *Webbia*, *Sarratia*, *Dunalia*, *Tournalia*, *roseo-labiata* (already descrubed by Rossmässler, 1839), *Philbertia*, *Gouania*, *Dumasta* and *sphaecelata*. None of these nominal taxa appear to have any taxonomic value (as discussed by Sacchi, 1956).

A further variety, *H. s. var. microstoma* Salvañá, 1887 was described from Camprodon (Ripollès, Catalonia) on specimens with a very small size and barely expanded aperture (Salvañá, 1887); this is typical of populations living near the species' upper altitude limit in the Pyrenees. Besides, this name is preoccupied by *Helix microstoma* Lamarck, 1822 from Cuba (Lamarck, 1833: 72). This species was well illustrated by Chenu (1842: pl. 5, fig. 9), and is obviously a member of the Cuban endemic genus *Zachrysia* Pilsbry, 1894. Pilsbry (1928: 602) refers only to the description by Lamarck, and places it in this genus, but without assigning it into any of the taxa he recognizes. It is clear from Chenu's illustration that *Helix microstoma* Lamarck, 1822 is a senior synonym of *Zachrysia auricoma* var. *havanensis* Pilsbry, 1926, restricted to northwestern Cuba (Pilsbry, 1928: pl. 30, fig. 17); it thus has precedence and the name for this Cuban snail must be *Zachrysia microstoma* (Lamarck, 1822).

In spite of its conspicuous chromatic polymorphism, *Pseudotachea splendida* has only two further synonyms. *Helix cossoni* Letourneux, 1877 was described as living together with the type species (Letourneux, 1877). It has been recognized as a separate species by some authors (Servain, 1881; Locard, 1882; Madurga, 1973), but treated as just a possible variety by Germain (1928, 1930). Later on, it was only accepted by Bech (1990), on the grounds of imaginary geographic isolation. Kerney et al. (1999) mention it as a likely synonym of *P. splendida*. Having examined numerous samples of this species from throughout its range, it is clear to me that this nominal taxon is just a morphotype with uniformly whitish color and a rather depressed spire, appearing in many disperse localities together with normal-looking *P. splendida*.

Helix calaeca Bourguignat in Fagot, 1887 is a nominal species referring to specimens intermediate between typical *P. splendida* and *H. cossoni* on conchological grounds (Fagot, 1887). The name *H. calaeca* is attributed by Fagot to Bourguignat, who provided the name, the description and a comparison with other species in a letter stated to be from 1885 at the heading of the description. The last paragraph under this species heading is surely by Fagot, who provides a few localities from the southern slopes of the Pyrenees. This paragraph starts acknowledging Bourguigant's authorship: "M.[onsieur] Bourguignat ha establecido su tipo con individuos franceses..." [Mr. Bourguignat has established its type with Frech specimens...] This name has ben used by very few authors (Fagot, 1891; Locard, 1894; Maluquer Nicolau, 1904). It was correctly placed in synonymy of *P. splendida* by Germain (1928, 1930), and also Puente and Prieto (1991).

The revision of French helicoids by Germain (1928) bears 1929 as publication date, but it was printed and distributed before the end of the preceding year (Germain, 1930).

Herculiberina subtr. nov.

Diagnosis.- Small allognathines with low domed spire, rounded whorls, last whorl well convex below,

closed umbilicus, internally thickened peristome, and dull surface provided with faint collabral and fine spiral lines.

Type genus.- *Herculiberus* gen. nov. (monotypic)

http://zoobank.org/NomenclaturalActs/24ACC250-EEAE-4E2F-9500-5265932FB444

Remarks.- This monotypic lineage is the sister group to all allognathines except *Pseudotachea*. In order to avoid a paraphyletic group (and an unnecessary multiplication of name-bearing clades), it is best recognized as a taxon of equal rank to the Pseudotacheina.

***Herculiberus* gen. nov.**

Diagnosis.- Small allognathines with thin, semiglobose, depressed shell with completely closed umbilicus, expanded last whorl, barely expanded lip, dark pink peristome and dull surface having faint but visible colabral striae and spiral lines.

Type species.- *Helix liturata* Pfeiffer, 1853.

Species included.- Monotypic (but see remarks).

Etymology.- A combination of the Hercules Columns, the classical name of the Strait of Gibraltar, and *Iberus*, a related land snail genus that is endemic to the southeastern Iberian Peninsula. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/0ac42827-0faa-4cf5-935b-92d7e855261c

Remarks.- *Herculiberus lituratus* is similar to *Pseudotachea splendida*, but differs in its shell and genitalia: it has a taller, nearly globose shell, with a considerably less expanded last whorl, rougher surface, and more visible spiral sculpture, as well as a dart with simple edges (Pfeiffer, 1853a; Hesse, 1919; Sacchi, 1956; Aparicio & Ramos, 1988; Puente, 1994; Manganelli et al., 2005). This species was often placed in *Cepaea* (Morelet, 1854; Kobelt, 1880, 1903b, 1915; Tryon & Pilsbry, 1888; Boettger, 1914; Perrot, 1938; Perrot & Perrot, 1938; Zilch, 1987), and also in *Pseudotachea* (Boettger, 1909; Hesse, 1920; Aparicio & Ramos, 1988; Puente, 1994); Sacchi (1956) pointed out it could belong into a genus of its own.

The real date of publication of the original description of *Helix liturata* is 1853, not 1851 as printed therein (Sclater, 1893: 439). The species name has often been emended as *H. litturata*, but this is both unexplained and unjustified (Welter-Schultes, 2012): although the original description doesn't include an etymology, it includes the assessment "fasciis punctatim vel lituratim interruptim rufus ornatâ" (Pfeiffer, 1853a: 253), meaning it is decorated with red, interrupted, dotted or smeared ("liturata") bands. This trait is clear in the figure of the type specimen given by Tryon and Pilsbry (1888: pl. 35).

H. lituratus is locally common, although often hard to detect, in two restricted areas: the Campo de Gibraltar, a coastal area between Tarifa and Estepona in southernmost Spain (Fig. 2), and the eastern Riff in northernmost Morocco (Germain, 1928; Perrot & Perrot, 1938; Sacchi, 1956; Puente, 1994; Arrébola et al., 2002). A question mark in the original description of *Helix liturata* indicates that the origin of the shell was unknown (Pfeiffer, 1853a), but the diagnosis and (later) figure fit well with Moroccan specimens. After a much more detailed study (but one year later), *Helix coquandi* Morelet, 1854 was described with Tarifa as type locality (Morelet, 1854). Almost all authors have assumed both nominal species refer to the same biological entity living on both sides of the Strait of Gibraltar, in spite of conspicuous differences. These were already noticed by Morelet (1854), and are clear in the figures by Tryon and Pilsbry (1888: p. 35) and Zilch (1987: pl. 1). However, this has never been adequately justified. The Riffian specimens appear to be larger and more solid, with a more completely covered umbilicus, often a more reflected lip, and usually more intense (continuous or broken) color bands. The Iberian populations may be distinct and native; in this case, the differences with their Moroccan counterpart would support the recognition of two allopatric species separated by the sea.

Several varieties of *Helix liturata* were described by Kobelt (1880, 1883, 1888, 1903c; see Zilch, 1987:

226) for its chromatic polymorphism: *rufescens* Kobelt 1880; *carnea* Kobelt, 1880; *ellioti* Kobelt, 1883; *depressa* Kobelt, 1888; *nahoni* Kobelt, 1888; *nemoraloides* Kobelt, 1888; and *tarifensis* Kobelt, 1903. The latter deserves two comments. First, the publication date follows Welter-Schultes (1999). And second, this is a homonym of *Helix tarifensis* Bourguignat, 1880, a junior subjective synonym of *Xerosecta reboudiana* (Bourguignat, 1863) that apparently has not been used after 1899 (Gittenberger, 1993). None of these varieties appear to have any taxonomic meaning. Only two of these (*ellioti* and *tarifensis*) are based on Iberian specimens (Gibraltar and Tarifa, respectively).

Iberina subtr. nov.

Diagnosis.- Small to large allognathines with semiglobose to strongly depressed shells, rounded to strongly keeled whorls, closed umbilicus, small reflected lip, expanded last whorl, and surface ornamented with conspicuous spiral lines.

Type genus. *Iberus* Montfort, 1810 (monotypic).

Subgenera included.- Six subgenera are recognized within *Iberus*, five of them described below as new: *I. (Iberus)*, *I. (Labioiberus)* subgen. nov., *I. (Carthaginiberus)* subgen. nov., *I. (Nazariberus)* subgen. nov., *I. (Achatiberus)* subgen. nov., and *I. (Alonensis)* subgen. nov. The type of the genus (and the nominotypical subgenus) is *Helix gualtierana* Linnaeus, 1758.

http://zoobank.org/NomenclaturalActs/018702B8-24A1-4153-A6AD-FF82C7FAB894

Remarks.- The type species is morphologically divergent, but it is closely related to species with conservative shell morphology; the genus as a whole exhibits rather moderate genetic differentiation.

The section *Helix (Iberus (Euiberus))* Westerlund 1889 was erected as part of a practical conchological scheme (Westerlund, 1889). It is an objective synonym, as it is based by monotypy on the same type species as *Iberus* (and its nominotypical subgenus, Arts. 42.3, 44).

García San Nicolás and Alvarado (1955) proposed to divide *Iberus* into three subgenera: *Euiberus*, *Alonensis* and *Marmoratus*. The latter two were proposed as new, designating type species for each on the basis of prioty and absolute tautonimy. The latter criterion constitutes a valid stype designation (Art. 68.4). *Alonensis* is considered herein as a valid subgenus of *Iberus*, and *Marmoratus* as a valid genus in a different subtribe.

The nominotypical subgenus is restricted to the Sierra de Gádor and its foothills, near the southeastern corner of Almería province (Fig. 3). It includes *Iberus (I.) gualtieranus* (Linnaeus, 1758), *I. (I.) mariae* Cobos, 1980, *I. (I.) ornatissimus* Cobos, 1980, and *I. (I.) latissimus* spec. nov. The former three were well treated by Cobos (1980). He showed that the nominal species *Helix laurenti* Bourguignat, 1870 and *Iberus gualterianus intermedius* C.R. Boettger, 1913 are just higher-spired ecophenotypes of *I. gualtieranus* living at different altitudes in that steep range (reaching an altitude of 2,249 m). Bank and Luijten (2015) consider *I. g. laurenti* as a valid subspecies, but this is unsupported. *I. gualtieranus* occupies the eastern and south-central parts of the Sierra de Gádor, from the highlands to the coastal piedmont. It has been successfully introduced into three distant localities: Sierra Elvira near Granada, the mountains in the outskirts of Jaén, and around Huércal-Overa in eastern Almería province (Serradell, 1912; García San Nicolás, 1957; Alonso et al., 1985; Puente, 1994). In these new areas it hybridizes with native *Iberus*, but the viability of those hybrids and the possible resulting introgression remain to be assessed.

The ranges of the other three species in *I. (Iberus)* are more restricted. *I. ornatissimus* extends across the central Sierra de Gádor, from some of the northern ravines to part of its southern foothills. *I. latissimus* spec. nov. is found in the range's soutwestern slopes. *I. mariae* lives only in the near-insular tip of Punta Entinas further south; its small size may be interpreted as a case of island dwarfism.

Born (1778: 376) named *Helix obversa* based on Gualtieri (1742) and specimens he had in Vienna. This is an junior synonym of Linnés's name, which was also based on the same work. Bank and Luijten (2015) notice Born (1778) correctly introduced the name in the first edition of his catalogue, not in the second (Born, 1780: 368) as often cited. There are no specimens of this species in the Linnean collection in

London (catalogue available at https://linnean-online.org), so it is most likely that *Helix gualtierana* Linnaeus, 1758 was based solely on the illustration in Gualtieri's catalogue. In order to render *Helix obversa* Born, 1778 an objective junior synonym of *H. gualtierana*, I hereby designate as lectotype of *H. obversa* the same specimen depicted by Gualtieri (1742: pl. 68, fig. E).

http://zoobank.org/NomenclaturalActs/2B42EF17-946A-4509-8961-49BB4944E459

The form described as *Helix gualtierana umbilicata* Kobelt, 1910 was reported to have been collected at Los Millares (Kobelt, 1910). The locality seems correct, based on both Pallary's travel account and my own exploration of the area. However, this name refers to an individual abnormality without any taxonomic significance; it is thus a junior (subjective) synonym of *I. gualtieranus*. Besides, it is a junior homonym of *Helix umbilicata* Montagu, 1803, currently known as *Pyramidula umbilicata* (Montagu, 1803) in the very distantly related Pyramidulidae (Gittenberger & Bank, 1996).

The publication date of the paper by Cobos (1980) is stated in print as 1979, but this was surely falsified. Antonio Cobos Sánchez was a prolific naturalist. In his obituary, Alonso-Zarazaga (2001) states that the journal was not distributed until April 1980. The volume includes mentions to papers published and meetings held during 1979. Such mismatch between printed and actual publication dates was usual for the *Boletín de la Sociedad de Historia Natural de Baleares*, with delays ranging from one up to at least three years (Altaba, in prep.).

Liétor et al. (2024c) rank *I. (I.) ornatissimus* as a subspecies of *I. mariae* and describe a "new form" from the southwestern sector of Sierra de Gádor on the basis of linear shell measurements and the unsubstantiated hypothesis of widespread hybridization in large contact areas. *Iberus mariae mariae f. macrolabiatus* Liétor, Tudela, Jódar, Galán-Luque & Jowers, 2024 is an infrasubspecific name proposed with no type; thus it is unavailable (Art. 10.2, 45.5, 72.3).

***Iberus (I.) latissimus* spec. nov.**

Diagnosis. - A large *Iberus (I.)* with only moderately enlarged last quarter whorl, low domed spire, reduced sculpture, and suddenly downturned aperture provided with a conspicuous, greatly enlarged, flaring lip; broken, thin spiral bands of pale chestnut brown.

Description.- Shell dextral, large, moderately thick, semiglobose, with low domed spire consisting of just over four well inflated, rounded whorls, slowly growing and just moderately expanded in the last 1/8, delimited by a barely incised suture; aperture oblique, widely oval, suddenly downturned, with palatal edge thickened inside and protruding externally in a conspicuously enlarged, flaring lip; columella thick but rather indistinct, completely covering the umbilicus with a terminal, appressed callus; no parietal callus; external surface with a reduced silky shine, covered by a fine reticulate, dense sculpture made of colabral ridgelets and thin spiral lines, less marked on the lower surface; pale cream with five thin, heavily broken, pale chestnut brown bands.

Type material. - Spain, Andalucía, Almería province, Poniente Almeriense county, Dalías, 36° 48' N, 2° 51' W, ca. 320 m, under esparto grass; 12.iv.2019, Carlos Rubí col. Holotype CRA-23604, diameter 38.8 mm (Fig. 4).

Distribution.- *Iberus (I.) latissimus* spec. nov. is distributed over the southwestern slopes of the Sierra de Gádor (Fig. 3).

Habitat.- The new species lives in calcareous areas at low to mid elevation, under dry Mediterranean grassland and scrub.

Etymology.- The species name is an adjective referring to its most enlarged aperture.

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Remarks.- The expanded lip appears to be a convergent character state present in other allognathines; its adaptive value remains unclear. The color pattern of *I. (I.) latissimus* is similar to that of *I. (I.) ornatissimus*;

its general shape (albeit larger and with a flaring lip) is reminiscent of that of *I. (I.) mariae*.

***Iberus (Labioiberus)* subgen. nov.**

Diagnosis.- Medium to fairly large allognathines with relatively solid, semiglobose shell provided with a conspicuously reflected lip, making a complete or nearly complete ring around the aperture.

Type species.- *Helix campesina* Pfeiffer, 1846.

Species included.- Monotypic, with three subspecies. *Iberus (Labioiberus) campesinus lorcanus* (Rossmässler, 1854) is considered a valid subspecies, along with the nominotypical *I. (L.) c. campesinus* (Pfeiffer, 1846) and *I. (L.) c. bastetanus* subsp. nov.

Etymology.- A combination of *Iberus* and the prefix *labio* (lip) referring to its expanded peristome. It is a masculine noun.

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Remarks.- The morphological distinctness of the geographically restricted forms of *I. campesinus* does not translate into a comparable degree of genetic differentiation. There is, however, a phylogeographic structure, which supports the recognition of parapatric subspecies.

The nominotypical *Iberus (L.) c. campesinus* has a most expanded, virtually continuous peristome giving a peculiar appearance to the shell. This subspecies is found in the valley of the Almanzora River in eastern Almería and southwestern Murcia, extending further south to the much smaller Antas drainage (Fig. 3).

The authorship of *Helix campesina* was attributed by both Pfeiffer (1846) and Rossmässler (1854) to Ezquerra del Bajo, and this has been generally accepted. However, the latter was a mining engineer who never published any malacological work. He probably discovered the species during his work in the Almanzora valley, as he was a keen naturalist with wide interests (Lentisco Puche et al., 2007). Ezquerra del Bajo may have proposed the name for it, but the species was only formally and solely described by Pfeiffer, who must be credited (Art. 50.1.1; Bank & Luijten, 2015). Pfeiffer (1847: pl. 19 fig. 14-15) later provided an adequate illustration. As explained by Rossmässler (1854: 5), the species name is directly derived from the Spanish word “campesino, campesina” (meaning peasant), equivalent to the Latin adjective “campestris”. However, this Spanish word, both as masculine or feminine, can be either a noun or an adjective. It is unclear how it was used in the original description (Pfeiffer, 1846: 76), but it has been subject to gender agreement, as *Iberus campesinus* by subsequent authors (Boettger, 1913; García San Nicolás, 1957: 217; Cobos, 1980). According to Art. 31.2.2, evidence of usage must be followed, treating “campesinus, campesina” as a latinized adjective.

Helix campesina millarensis Kobelt, 1910 is based on a single specimen with a well-developed peristome. The only reason to coin the name was the reportedly isolated locality where that specimen was collected (Kobelt, 1910). However, this is a typical *I. c. campesinus,* as correctly assessed by Bank and Luijten (2015) and García Meseguer et al. (2017). The problem with a wrong locality affects also other *Iberus* described in the same work. Wilhelm Kobelt (1910) provided excellent drawings and descriptions of several shells he received from the Algerian naturalist and archaeologist Paul Pallary, who had traveled through Almería province more than twenty years earlier, in order to visit the ancient settlement at Los Millares, in the Sierra de Gádor mountains. I explored the area around Los Millares and am sure only *Iberus gualtieranus* lives there, in agreement with Cobos (1980).

Kobelt (1910) states all the shells he received, both recent and subfossil, came from Los Millares. This is surely not the case. Perhaps the mistake originated from Pallary himself, given the time elapsed since his trip in 1882; fortunately, he wrote a detailed (and picturesque) account of his travel (Lentisco Puche et al., 2007). From Águilas in southernmost Murcia province he explored a stretch of seashore on foot, and then continued on wagon to Almería, eventually reaching Los Millares. He reports two stops along the way: first at Pozo del Esparto, at the easternmost tip of Andalusia, and then at Vera further west. It is clear that the

taxa studied by Kobelt were collected at four different places. Only typical *campesinus* would be found around Vera, and that is most likely where the holotype of *H. c. millarensis* was collected.

The nominal *Helix gualtiero-campesina* Serradell, 1912 was based on two specimens collected at Cuevas de Vera, in the native range of *I. (L.) campesinus*. They were considered to be the likely outcome of hybridization with *I. gualtieranus*, translocated therein as a food resource (Serradell, 1912). Given that its hybrid origin was only hypothesised in the original description, this name is not unavailable in the sense of Art. 1.3.3; it is available under Art. 17.2. In plates V and VI, the spelling *Helix Gualterio-campesina* appears. As First Reviser (Art. 24.2), I select the correct spelling as that appearing in the text: *Helix gualtierocampesina* Serradell, 1912. Since the species was described on the basis of the single specimen illustrated, *Helix gualteriocampesina* Serradell, 1912 is an objective junior synonym.

The local subspecies *I. (L.) c. lorcanus* (Rossmässler, 1854) also has a restricted range, limited to the lowland and hills around Lorca, Puerto Lumbreras, and Águilas in southwestern Murcia province, and a small adjacent area in Almería province. It is distinguished by its less flaring and barely but conspicuously incomplete peristome. The localities plotted by Liétor et al. (2024d) near the coast may be in part due to confusion with *I. (Carthaginiberus) carthaginiensis posthumus*.

Helix pseudo-campesina Kobelt, 1910 is based on a specimen collected by Pallary. The locality of Los Millares given by Kobelt (1910) is an obvious mistake, as it was surely found at Pozo del Esparto, at the easternmost tip of Andalusia. This nominal taxon is clearly a junior (subjective) synonym of *I. (L.) c. lorcanus*.

A subset of populations living at the northeastern corner of the species range exhibit a constantly different structure of the conspicuous peristome. They are described below as a new subspecies.

***Iberus (Labioiberus) campesinus bastetanus* subspec. nov.**

Diagnosis. - A large, rather globulous *Iberus* with a prominent peristome, but less reflected and more widely discontinuous than in other subspecies of *I. (Labioiberus) campesinus*; the columellar and palatal ends of the moderately reflected lip are more distant to each other than in *I. c. lorcanus*.

Description.- Shell dextral, large, moderately thick, semiglobose, slightly depressed, broadly conical above and convex below, with well inflated whorls; pale ocher with up to five thin chestnut bands that are very pale except for irregularly placed darker spots (the two intermediate bands may be obsolete); external surface opaque, with dull shine caused by a fine reticulate, dense sculpture made of colabral ridgelets and thin spiral lines, less marked on the lower surface; spire conical, low, with about 4 slightly convex whorls, slowly and regularly growing except at the last 1/4 whorl which becomes wider; last whorl large, noticeably depressed, well rounded at periphery and suddenly descending near aperture; suture shallow but incised; umbilicus almost completely open, just partially covered by the reflected peristome; aperture oblique, nearly circular but narrowed towards the gently sloping columella; peristome widely interrupted, moderately thickened, moderately reflected, whitish, with palatal and columellar edge regularly curved, joining the parietal surface just above the columella, thus leaving a wide gap.

Type material. - Spain, Murcia region and province, Alto Guadalentín county, Lorca, Sierra de La Carrasquilla, 37° 34’ N; 1° 34’ W, ca. 650 m, under esparto grasses; 23.i.2015, J. Liétor col. Holotype CRA-15613-1, diameter 35.3 mm (Fig. 5); and 2 paratypes (CRA-15613-2 and 3).

Distribution.- Restricted to a small area extending to the south and southeast of Lorca, in Murcia province: the small ranges of Sierra de la Carrasquilla and adjacent mountains (Fig. 3).

Habitat.- The new subspecies lives in Mediterranean scrub and dry grassland areas at moderate elevation (roughly between 400 and 700 m).

Etymology.- The subspecies name is an adjective referring to its affiliation with the Bastetani, an Iberian people who lived in present-day easternmost Andalusia and southwestern Murcia, including the small area where this subspecies occurs.

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Remarks.- Specimens of this subspecies were studied by García San Nicolás (1957), but she identified them as *I. pseudocampesinus*. Cobos (1980) mentions the existence of populations differing from typical *Iberus campesinus lorcanus*. *Iberus (L.) campesinus bastetanus* subsp. nov. occurs at the northeastern limit of the species range. Between *I. (L.) c. campesinus* and the new subspecies, *I. (L.) c. lorcanus* is intermediate morphologically and geographically.

***Iberus (Carthaginiberus)* subgen. nov.**

Diagnosis.-Small to large allognathines with depressed spire, last whorl inflated below, slightly reflected lip not extending over the parietal zone, nearly completely closed umbilicus, and just subtle peripheral keel. The sculpture includes marked, regular colabral striae and fine spiral lines. Coloration usually involving broken spiral color bands.

Type species.- *Helix carthaginiensis* Schmidt, 1853

Species included.- *Iberus (Carthaginiberus) carthaginiensis* (Schmidt, 1853), including the subspecies *I. (C.) c. posthumus* Haas, 1934, and *I. (C.) bajoi (*Bourguignat in Servain, 1881).

Etymology.- A combination of *Iberus*, a genus endemic to the southeastern Iberian Peninsula, and the name of Carthaginia, the Roman name for the originally Punic city now called Cartagena. It is a masculine noun.

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Remarks.- The two species in *Iberus (Carthaginiberus)* have been treated as subspecies (Elejalde et al., 2008b; Bank & Luijten, 2015), but they are morphologically distinct. *I. (C.) bajoi* is definitely larger, and has the last whorl more inflated below and less expanded near the aperture, relative to *I. (C.) carthaginiensis*. The latter is restricted to the coastal area along the southern coast of the Murcia region; the former extends over the mountains draining into the Segura watershed, in the western part of the Murcia region and the northernmost area of Almería province (Fig. 3). In spite of moderate genetic differentiation, they are best treated as allopatric species.

Helix carthaginiensis was first mentioned by Rossmässler in 1853; one year later it was more extensively treated (Rossmässler, 1854). Acting as First Revisors (Art. 24.2 of the Code), Bank and Luijten (2015) selected Rossmässler (1853) as the author, over Schmidt (1853) who also used the name. However, Schmidt writes about his anatomical research and provides useful diagnostic traits. What Rossmässler (1853: 168-169) said about the species does not meet the minimum requirements for a valid description (Art. 12.1): “die der Schale nach zwischen H. alonensis und splendida steht, und einer kleinen Form von jener täuschend ähnlich wird. Der Pfeil is aber entscheinend.” [which in terms of the shell stands between *H[elix] alonensis* and *[Helix] splendida*, a small form of the former being deceptively similar. The dart, however, is decisive.] No trait is given for the dart, and the conchological diagnosis is too meager to allow recognition of the taxon. Bank and Luijten (2015) were not correct in treating this description as sufficient; thus there is no need to determine the precedence of authorship, and their action as First Revisers must be nullified (Art. 24.2.5).

In his extended treatment of *H. carthaginiensis*, Rossmässler (1854) states that the species lives in the mountains of the Sierra de Cartagena, all the way down to the rocky valleys close to the coastal city of Cartagena. He also mentions a variety found further west, between Cartagena and Mazarrón. Eighty years later, Fritz Haas (1934) revised several land snail taxa in the Senckenberg Museum (Solem, 1967). He examined Rossmässler’s specimens of the unnamed variety, collected in the limestone mountains near Mazarrón, and described *Iberus (Iberus) gualtieranus posthumus* Haas, 1934 (Haas misspelled the specific name as gualtierianus). The etymology of this name was not given, but obviously it is a posthumous tribute to Rossmässler. The original allocation of this subspecies within a very wide, single species of *Iberus* (as well as the typographical error) followed the scheme proposed by Boettger (1913). Although there are no DNA sequences available for this taxon, the shells suggest it is closely related to the type species of the subgenus. It differs in having a more expanded aperture and a more reflected peristome; it

usually has also a more depressed spire, a slightly more open umbilicus, and a larger size. Although it was left as an unassessed nominal taxon by Bank and Luijten (2015), its original allocation into *I. gualtieranus* can be rejected; likewise, it has been placed in the synonymy of *I. alonensis* (García-Meseguer et al., 2017), but this is also unsupported. It is best treated as a local subspecies: *Iberus (Carthaginiberus) carthaginiensis posthumus* Haas, 1934.

Helix alonensis var. *minima* Schmidt, 1855 is based on specimens provided by Rossmässler, and probably also his unnamed variety (Schmidt, 1855), upon which Haas described *posthumus*. Schmidt's name, however, is preoccupied: *Helix minima* Gmelin, 1791 was based on a species shown by Schröter (1779: t. 7, fig. 18); the description and indicated illustration refer most likely to *Valvata piscinalis* (Müller, 1774). Gmelin's name has never been used (absent even from the nomenclator of the Valvatidae by Haszprunar, 2014), but this appears to be the case also for Schmidt's. Besides, the name *minima* was repeatedly used in the early literature as a variety name within the wide Linnean *Helix*.

Ignoring the work by Haas (and others), the nominal species *Iberus calaensis* Ahuir Galindo, 2013 was described from the same area (Ahuir Galindo, 2013). Although this name was left unassessed by Bank and Luijten (2015), it has been used by some authors (García-Meseguer et al., 2017); it is clearly just a junior (subjective) synonym of *I. (C.) carthaginiensis posthumus* Haas, 1934.

A further level of noise has recently been introduced by Tudela et al. (2024), who for some reason think the name *I. carthaginiensis* should apply to specimens that do not fit the original description (and illustration), nor live anywhere near the type locality. Thus, they describe the eastern set of populations (including the area around Cartagena) as the alleged new species *Iberus punicus* Tudela, Liétor, Jódar, Galán-Luque & Jowers, 2024. This is clearly a junior (subjective) synonym of *Helix carthaginiensis* Rossmässler, 1853. What they assume should bear Rossmässler's name is unequivocally *I. (C.) carthaginiensis posthumus* Haas, 1934. Tudela et al. (2024) acknowledge there are specimens with intermediate morphology at the limit between the two taxa. They interpret this as evidence of introgression between two distinct species. However, it seems more parsimonious to consider such individuals as belonging to a narrow zone of contact between neighboring subspecies.

The two subspecies of *I. (C.) carthaginiensis* have ranges extending on either side of the Cabo Tiñoso promontory. The typical subspecies is found to the east, from Sierra Los Gómez and through Cartagena, all the way up to the southern and eastern shores of the Mar Menor lagoon. To the west, *I. (C.) c. posthumus* ranges through the Mazarrón area and southwards as far as the rugged Lomo de Bas near the shore.

In the latest Pleistocene the range of *I. (C.) c. posthumus* extended further south. The fossils illustrated but not identified by Kobelt (1910) exhibit diagnostic traits: depressed spire, last whorl inflated below, slightly reflected lip not extending over the parietal zone, just subtle peripheral keel, broken spiral color bands, and marked, regular colabral striae. In spite of the alleged locality given by Kobelt (Los Millares), they were collected by Pallary very close to the seashore just north-east of Cocedores, at the extreme southern tip of the Murcia region. These specimens were taken from a sediment overlying a Tortonian (Late Miocene) reef and thought to be of Pliocene age by Pallary (Lentisco Puche et al., 2007). However, they likely have a latest Pleistocene age. Also the "Tyrrhenian" (i.e., latest Pleistocene) fossils found by Gasull (1976) a little northeastwards at Cabo Cope belong to this southern subspecies.

Puente Martínez (1994) mentions *I. carthaginiensis* from three localities in Teruel (Aragón). This is surely a misidentification. The specimens she discusses belong into *I. alonensis*.

The name *Helix bajoi* Bourguignat in Servain, 1881 was based on a detailed and informative description, but has been overlooked by most authors. The authorship of this species can be determined from three lines of evidence. First, the description of this species was written by Bourguignat in a letter, as explicitly attested by Servain ("Helix Bajoi, *Bourguignat*, in Sched."). Within the text, not all the letter was copied, as suggested by the abrupt stop of characters with an "etc." A third source of information is the location of the only type specimen. The Servain collection, curated at the Muséum des sciences naturelles in Angers (France), contains no sample belonging to *H. bajoi* (Benoît Mellier, pers. comm., 21.xi.2024). The only specimen of the type series is in the Bourguigant collection (see below). Thus, Bourguignat must be credited as the author of the species description (Art. 50.1.1). This is in agreement with Gasull (1976), and contrary to later opinions (Bank et al., 2019; Bank & Luijten, 2015; García-Meseguer et al., 2017). Although, the type of *H. bajoi* was collected among flood debris near Murcia, Servain (1881: 48) correctly

inferred it must have come from the headwaters of the Segura River.

Two of the above mentioned references have incorrect publication dates. As shown by Bank et al. (2019: 88), Servain's book, although stated to be printed in 1880, was actually published in early 1881. Likewise, the work by Gasull (1976), published as the sole paper in a volume thoroughly dated as "1975", bears a false publication date. Field observations were made by Gasull as late as November 1974. The preceding and following volumes were certainly published one year after the dates printed (1975, not "1974", and 1977 instead of "1976"); in the 1970's the Boletín de la Sociedad de Historia Natural de las Baleares was published with a delay ranging from one to at least two years relative to the dates printed (Altaba, in prep.).

H. bajoi has been considered as a synonym of *I. alonensis* without any scientific argument (Gasull, 1976; Bank and Luijten, 2015; García-Meseguer et al., 2017). However, Bourguignat's description unequivocally points at a species of *Iberus (Carthaginiberus)* with depressed spire, last whorl inflated below, and relatively large size. The single specimen of *H. bajoi* in the Bourguignat collection, housed at the Muséum d'Histoire naturelle in Geneva (Switzerland) is a syntype corresponding entirely with the original description; it is most likely that the description was based on this particular and only specimen. Thus, the specimen with catalogue number MHNG-MOLL-118673 (Fig. 6) is hereby designated as lectotype of *Helix bajoi* Bourguignat in Servain, 1881.

http://zoobank.org/NomenclaturalActs/872F9225-6001-45D0-B687-736CCC907DBF

Boettger (1913) interpreted the different shell morphologies as indicating a gradual transition encompassing all *Iberus*; as an extreme form of this apparent continuum, he introduced *I. gualtieranus globulosus* Boettger, 1913 (the species name was misspelled as gualterianus). Such interpretation was based on questionable conchological and taxonomic criteria, and is not supported by the results of the present study. Moreover, Boettger didn't consider Servain's work, effectively creating a junior subjective synonym of *Helix bajoi.* Boettger's name has been used very few times, so there would be no grounds for preserving it.

Liétor et al. (2024d) propose a neotype designation for *Iberus gualtieranus globulosus*. However, the qualifying conditions of Art. 75.3 did not apply, as there was no exceptional need to designate a neotype. As stated by Zilch (1977), the holotype was destroyed during World War II. However, it is unequivocally identifiable in the work by Boettger (1913: p. 196, fig. 8), who clearly states that it comes from around Almería. This must mean the province of Almería, as he only provides this level of geographical precision for other taxa he mentions. The only part of the Almería province where *Iberus bajoi* (=*globulosus*) lives is Los Vélez county, the northernmost district; this area belongs to the eastwards flowing Segura drainage, in contrast with the remaining of the province. Although this is a mountain region, it is crossed by the main road connecting Murcia and Granada, so collecting there was easy over a century ago. Furthermore, there is an appreciable variation in shell features across the species range; Boettger's specimen matches those from Almería province, and differs from those living further north and northeast. However, Liétor et al (2024d) state:"the neotype of *I. globulosus* does not completely match the shell characters and the locality of the morphotype originally assigned to the species". Although it seems normal that a shell cannot match completely another shell, so deviating a little from the original would certainly not invalidate a neotype designation, shells were available that would match much better the original; this is in violation of Art. 75.3.5. They also state: "It may seem unorthodox to assign a neotype having a location different from the original type locality". This is a more serious issue, as specimens collected in the area given as type locality were available to the authors; this is in violation of Art. 75.3.6. Both statements show theirs is an invalid neotype designation, as it is clearly and admittedly contrary to Article 75 of the Code, which mandates that a neotype must be consistent with what is known of the former name-bearing type from the original description (Art. 75.3.5), as well as that it must come from as nearly as practicable from the original type locality (Art. 75.3.6).

A useful neotype designation is proposed herein in order to clarify and stabilize the identity and type locality of this nominal taxon, thus preventing any further arbitrary changes. This is needed, in accordance with the Code, because no name-bearing type specimen is extant, the original description is insufficient, and I consider that a name-bearing type is necessary to define the nominal taxon objectively (Art. 75.1). I think there is an exceptional need to clearly define this taxon, as the neotype is herein designated with the express purpose of clarifying both the taxonomic status and the type locality of the nominal taxon *Iberus*

gualtieranus globulosus Boettger, 1913 (Art. 75.3.1). This nominal taxon is herein considered a junior subjective synonym of *Iberus bajoi* (Bourguignat in Servain, 1881), and differs from *Iberus carthaginiensis*, its phylogenetically closest relative, in its larger size, as well as in the less expanded and more bulging last whorl (Art. 75.3.2). The data, description and illustration provided below are sufficient to ensure unequivocal recognition of the specimen designated (Art. 75.3.3). The holotype was not found, and presumed to have been destroyed (Art. 75.3.4) according to the research performed by Adolf Zilch (1977: 12), curator of Mollusca at the Senckenberg Museum in Frankfurt where all of Boettger's specimens were housed: "*Iberus gualterianus globulosus* C. Boettger 1913, Ber. senckenb. naturf. Ges., 44 (3): 187, Abb. 8 (Seite 196). - Holotypus SMF [in 2. Weltkrieg vernichtet]." The neotype is fully consistent with what is known of the former name-bearing type from the original description (Art. 75.3.5), and came from the original type locality, which although vaguely stated must have included the neotype's collecting station and a small area around it (Art. 75.3.6). The neotype is properly curated and accessible for study in the author's research collection, recognized as a Museographic Collection by the Council of Mallorca (Art. 75.3.7).

The selected type locality is in Almería province, in agreement with Boettger (1913). It is very close to Vélez Blanco, in the district of Los Vélez in the far north of Almería Province. This area is the most likely the origin of *Iberus gualtieranus globulosus* Boettger, 1913.

The neotype is fully adult; its major diameter is 32.5 mm (Figs. 7, 8). It was collected live by the author, in the early morning, after rain, crawling on rocks with scattered thorny bushes, close to a temporary stream carved in limestone, very close to the entrance to Vélez Blanco (Los Vélez district, Almería province, Andalucía, Spain), 37º 4' 21'' N, 2º 06º 06'' W, 1070 m elevation; 20.x.2023. It is cataloged with number CRA-23646-1 in the author's Museographic Collection; the shell is kept dry in a clear polystyrene box with a label written with India ink on acid-free paper, and the soft parts in a vial with 80% ethanol and a label written also with India ink on onionskin paper.

http://zoobank.org/NomenclaturalActs/88045788-A983-48F0-8EDA-FA6387CF5AD1

The citation of *Iberus (C.) carthaginiensis* in the mountains of southwestern Albacete province by Servain (1881) refers most probably to *I. (C.) bajoi*.

***Iberus (Nazariberus)* subgen. nov.**

Diagnosis.- Largest of all allognathines, with fairly solid, slightly depressed shell, umbilicus sealed by a strong callus, and conspicuously enlarged last quarter whorl.

Type species.- *Iberus alonensis rhodopeplus* Aguilar-Amat, 1925.

Species included.- *Iberus (Nazariberus) rhodopeplus* Aguilar-Amat, 1925, *I. (N.) labiatus* Ahuir Galindo, 1989, *I. (N.) turdetanus* sp. nov., and *I. (N.) selambinicus* sp. nov.

Etymology.- A combination of *Iberus* and a prefix referring to the Nazari dinasty of kings of Granada, the last muslim kingdom in Iberia, originally extending through the range of this subgenus. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/657648BF-C835-45CB-B053-3F99FA10EDDF

Remarks.- The four species of *I. (Nazariberus)* are separated by the Sierra Nevada range and adjoining, lower chains (Fig. 3). The main summit area is inhospitable to these snails, due to its extreme altitude (reaching 3,478 m) and unfriendly substrate. Thus, allopatric speciation is likely responsible for diversification in this subgenus. Two of these species are new, described below.

The description of *Iberus alonensis rhodopeplus* Aguilar Amat, 1925 was based on specimens with a conspicuous pink mantle, collected at "El Muruche" in Jaén province (Aguilar-Amat, 1925: 266). Although the sentence where the name is introduced is written in conditional, this is not a problem for nominal taxa described before 1961 (Art. 15.1). The new taxon was identified by a diagnostic trait. It is thus a fully

available name (Art. 12.1). The type series (Art. 72.4) is curated at the Museu de Ciències Naturals de Barcelona, into whose collection the syntypes were said to be incorporated. The type locality is officially spelled El Moroche, likely a transcription of the original name as pronounced in the local Spanish dialect (eastern Andalusian). This is an individualized peak rising to an altitude of 1,051 m and located south of Pegalajar, near the southern limit of Jaén province. This name must be applied to the *Iberus* species ranging from south-central Jaén province, through central Granada province, to southeastern Almería province. It belongs to the clade of large *Iberus* found in central Andalusia, and on the basis of its morphological and genetic distinctiveness is herein ranked as species: *Iberus (Nazariberus) rhodopeplus* Aguilar-Amat, 1925.

Rossmässler (1854) already noticed the existence of very large snails similar to *I. alonensis* in the range of *I. (N.) rhodopeplus*.

For unclear reasons, Liétor et al. (2024 b) decided to explicitly dismiss the description of *I. rhodopeplus* by Aguilar-Amat (1925), and describe *Iberus sumuntanus* Liétor, Tudela & Jódar, 2024 from a site located just 5 km northeast of the former's type locality. The only diagnostic traits on which *I. sumuntanus* is based are average measurements of eight specimens (smaller average shell diameter, lower average shell height, and smaller average associated measurements); however, the small type series exhibits a wide variation in size and shape, making it impossible to allocate an individual into this nominal species. The morphological record strongly suggests that *I. sumuntanus* is a junior (subjective) synonym of *Iberus rhodopeplus* Aguilar-Amat, 1925.

In order to identify the unique bearer of the name of a nominal species-group taxon and the standard for its application (Art. 74.1), the syntype from the type series of *Iberus alonensis rhodopeplus* Aguilar-Amat, 1925 with catalogue number MZB-89-2580 in the Museu de Ciències Naturals de Barcelona, and measuring 36.2 mm in maximum diameter, is herein designated as lectotype (Fig. 9). Given the individual variability observed in this species (as well as among syntypes), this designation is intended to precisely define this species-level taxon.

http://zoobank.org/NomenclaturalActs/047D78A1-2A6D-4DBD-B034-A5256FC31A2C

The description of *Iberus labiatus* Ahuir Galindo, 1989 is sufficient to consider it a distinct taxon. Morphologically it is similar to other members of *I. (Nazariberus)*, but differs in its conspicuously flaring lip. It seems restricted to the Sierra de Almijara, a coastal range located to the south and east of the distribution of other congenerics. *I. (N.) labiatus* has been found (three shells) in an Epipalaeolithic shell midden in the Nerja Cave (Jordá et al., 2011: Fig. 6, 1-3), close to the seashore at the foothill of this range. The expanded peristome appears to be a case of parallel evolution with that occurring in the nominotypical subgenus and *I. (Labioiberus)*. In both cases, this morphological trait occurs on a south-oriented coastal area.

***Iberus (Nazariberus) turdetanus* spec. nov.**

Diagnosis. - Differs from *I. (N.) rhodopeplus* in having a heavier, white peristome with a more reflected lip, and a thicker shell. It lacks the conspicuously expanded last quarter whorl of *I. (N.) selambinicus* and *I. (N.) labiatus*, as well as the expanded peristome of the latter. The shell is usually very pale.

Description.- Shell dextral, large, fairly thick, semiglobose, broadly conical above and convex below, with just over four well inflated whorls separated by a well marked suture, slowly growing except for a very moderate expansion immediately behind aperture that is strongly descending; aperture oblique, elongate oval, strongly downturned, with thickened peristome; palatal lip thickened internally but barely expanded, continuing over the enlarged columella until the umbilicus, which is completely sealed by a thickened callus; parietal callus thin but noticeable; external surface dull, with sculpture somewhat more prominent on the upper side, consisting of rather strong, irregular colabral ridgelets and thinner spiral lines; very pale ocher speckled on ivory white, diffusely forming bands but much reduced on the underside; up to five thin chestnut bands that are very pale except for irregularly placed darker spots (the two intermediate bands may be obsolete); peristome porcelain white inside, and with a vivid, thin, chestnut band that extends, diffused and lighter, all along the external edge of the columella.

Type material. - Spain, Andalucía, Jaén province, Comarca Metropolitana de Jaén county, Torredelcampo, La Mella mountain, 37° 45'3 N, 3° 49' W, ca. 1100 m, in limestone crevices covered by Mediterranean shrubs; 8.i.2013, J. Liétor, col. Holotype CRA-23566-1, diameter 34.0 mm (Fig. 10); and two paratypes (CRA-23566-2 and 3).

Distribution.- *Iberus (Nazariberus) turdetanus* sp. nov. extends over a relatively large area, from southwestern Jaén province and southern Córdoba province to central Granada province (Fig. 3).

Habitat.- The new species lives in limestone areas covered by Mediterranean scrub and brush, from low to moderate elevation.

Etymology.- The species name is an adjective refering to its affiliation with the Turdetani, an Iberian people who lived in present-day northeastern Andalusia, including much of the area where this species occurs.

http://zoobank.org/NomenclaturalActs/1CA57AA6-27FD-49A1-B8E0-18D700FECA31

Remarks.- The limits with *I. (N.) rhodopeplus* remain to be investigated in the field.

***Iberus (Nazariberus) selambinicus* spec. nov.**

Diagnosis. - Differs from *I. (N.) labiatus* in lacking an expanded, flaring peristome. It is distinguished from both *I. (N.) turdetanus* and *I. (N.) rhodopeplus* by its bulging, more expanded last quarter whorl.

Description.- Shell dextral, very large, moderately thick, semiglobose, with low conical spire consisting of $4^1/_2$ well inflated, rounded whorls, slowly growing until the last half whorl, which is expanded, more so in its last eigth, separated by a moderately incised suture; aperture oblique, widely oval, suddenly downturned close to the peristome, with palatal edge thickened inside and flaring lip; columella thick but rather indistinct, completely covering the umbilicus with a terminal, appressed callus; no parietal callus; external surface with a reduced silky shine, covered by a reticulate, dense sculpture made of colabral ridglets and thin spiral lines, somewhat less conspicuous on the lower surface; pale cream with five thin, broken, saddle brown bands diffused among numerous thin same-colored markings extending in both colabral and spiral directions; peristome ivory white.

Type material. - Spain, Andalucía, Granada province, Costa Granadina county, Salobreña, Tajo de la Virgen, 36° 47' N 3° 32' W, ca.120 m, under esparto grasses; 21.x.2015, J. Liétor, col. Holotype CRA-15612-1, diameter 40.0 mm (Fig. 11); and 1 paratype (CRA-15612-2).

Distribution.- *Iberus (Nazariberus) selambinicus* sp. nov. is restricted to the southernmost foothills of Sierra Nevada, around the lower Guadalfeo drainage and adjacent areas (Fig. 3).

Habitat.- The new species lives in rocky limestone areas at low to moderate elevation.

Etymology.- The species name is an adjective referring to its native range around the ancient Pheoenician city of Selambina (currently Salobreña), on the coast of southern Granada province.

http://zoobank.org/NomenclaturalActs/7B454790-651E-4FE1-AA61-3D099B861C4E

Remarks.- *Iberus (Nazariberus) selambinicus* may be more closely related to *I. (N.) labiatus* than other congenerics.

***Iberus (Alonensis)* García San Nicolás & Alvarado, 1955**

Remarks.- Proposed as a subgenus by García San Nicolás and Alvarado (1955), available through absolute tautonimy (Art. 68.4). It was proposed again by García San Nicolás (1957: 244), effectively as a junior

synonym.

Helix (Helicogena) alonensis Férussac (1821) was described on specimens attributed to five different varieties (Férussac, 1821-1822, p. 35, 26.05.1821). These were designated by Greek letters, from alpha to epsilon. These are only inherently numeric values (from 1 to 5) expressed by a Greek letter, and cannot be considered a zoological name (Arts. 11.2, 11.9.1). The original description was completed (Art. 10.1.1) only when plate 39 (depicting all five varieties) was published (13.vii.1821) together with the explanation of plates (21.iv.1821) in the same work (Férussac, 1819-1832). Bank & Luijten (2015) reconstructed this fragmentary description but erroneously accepted it could be published in two separate works..

Unfortunately, the original description of *Helix alonensis* suffers from two major shortcomings. First, none of the five varieties was designated as typical. It is now clear that at least two different species were included in the original description: one is represented by varieties 1 to 4 (alpha to delta) have no conspicuous banding and come from the València region (Alacant and València), and the other, much larger variety 5 (epsilon), exhibits well-defined bands and lives in Andalusia (Almería). Later authors remarked that the former has always a grey mantle, whilst the latter has a purplish red mantle when adult (Férussac & Deshayes, 1820-1851: 121; García San Nicolás, 1957: 299). They also differ in genital anatomy (García San Nicolás, 1957).

It could be claimed that Férussac considered "typical" *alonensis* (var. α) only from Alacant (Alicante). He called this species "helicogène d'Alicante" (Férussac, 1819-1832: livraison 9, p. xiv, 06.iv.1821), or "hélice d'Alicante" (Férussac & Deshayes, 1820-1851a: 120). That city, or rather a nearby settlement, was known in ancient times as Alona, so the species names is a patronym. Nevertheless, this has only a historical value. In fact, Férussac's opinion was quite the contrary, as variety 5 from Almería was deemed to be "the type" shortly after the species description, as attested by the following three sentences (Férussac & Deshayes, 1820-1851a: 121): "Nous avons une petit variété qui n'est guère plus grande que notre *Helix nemoralis*, le type de l'espèce acquiert le triple ce volume" [We have a small variety that is barely larger than our *Helix* [*Cepaea*] *nemoralis*, the type of the species acquires a volume triple than this]; "Mais dans le type de l'espèce, il existe constamment quatre ou cinq zone brunes dont les deux inférieures sont toujours plus nettes et plus foncées que les trois autres" [But in the type of the species, there exist constantly four or five brown zones, the lower two being always more neatly defined and darker than the other three]: "Le manteau est d'un beau rose légèrement purpurin" [The mantle is of a beautiful, slightly purplish rose]. It is thus clear that the intention was to restrict the "type" to variety 5; unfortunately, such use of the word "type" refers collectively to specimens fitting the mentioned traits. In fact, the above mentioned sentences stem from examination of various specimens, including several live ones, one of which was drawn crawling (Férussac & Deshayes, 1820-1851b: pl. 39B, fig. 8). Given that no individual specimen was pinpointed, this taxonomic restriction cannot be considered a valid lectotype designation (Art. 74.3).

Acknowledging the incompleteness of the description of *Helix alonensis*, Graells (1846: 3) revised the original diagnosis. Thus he states in Latin: "Hel. testa orbiculato-convexá, depresiusculâ, imperforatâ, decussatim, striatâ, albidâ, rufo-fusco fasciatâ; spirâ retusâ; labro sub-aculo, albo." [*Helix* with convex orbicular shell, rather depressed, imperforate, criss-cross striated, whitish, ornamented with dark reddish bands; spire blunt; almost sharp, white lip.] And follows in Spanish: "He modificado la frase que dá Lamarck de esta especie , porque en su descripción no hace notar su principal carácter distintivo..." [I have modified the sentence given by Lamarck for this species, because in its description he doesn't highlight its main disctinctive trait…] Three points need to be made about this redescription: Graells was erroneously attributing the description to Lamarck, he correctly noticed the conspicuous microsculpture that is typical of all *Iberus*, and he explicitly restricted the species concept only to the banded variety. He also added a further explicit mention to his restriction of the species (Graells, 1846: 4): "El *H. alonensis* tipo, tiene el fondo blanco amarillento, sobre el que se ven en su última vuelta de espira, cinco fajas de un pardo oscuro, dispuestas como en el *H. splendida*. Estas fajas no llegan al borde del labio, que es blanco y sencillo" [The type of *H. [Iberus] alonensis* has a yellowish white background, upon which five dark brown bands can be seen in its last whorl, placed as in *H. [Pseudotachea] splendida*. These bands do not reach the edge of the lip, which is white and simple]. This double, explicit restriction includes only variety 5 (epsilon), and refers to the specimen of this variety provided in the original description by Férussac (1821-1822). It thus could constitute a valid lectotype designation, acting consistently with the previous taxonomic restriction (Art. 74.1.1, Recommendation 74A). This restriction was also accepted explicitly by later authors (e.g., García San Nicolás,1957: 299; Cobos, 1980). Férussac's variety ε is thus the nominotypical species of *Iberus*

(Alonensis).

Rossmässler (1854: 3, pl. 61, fig. 784) intentionally ignored the previous designation of a type for *H. alonensis*. However, he recognized this banded variety as a well-defined form, geographically circumscribed to Almería. He restrained from giving any name for any of the varieties he tentatively considered as part of this species. Perhaps on the basis of this work, some authors ignored the established usage and lectotype designation for *H. alonensi*s. Chevallier (1965: 482) designated as "holotype" a specimen from this origin, included in Férussac's var. α. This is a wrong usage of the term holotype, because a lectotype was designated instead. Nevertheless, under Art. 74.5 such explicit selection, even using the wrong term, could have been valid for a lectotype designation before 2000, provided Chevallier had been the first to designate a lectotype for the species, had selected this specimen personally, and had explicitly stated to have done so; he failed in the three instances. Martínez-Ortí and Robles (2012) overlooked previous works and proposed a new lectotype designation, remarkably coinciding with Chevallier's choice. Again, such act is invalid, as var. ε had already been established as the bearer of the name *Helix alonensis*. Bank & Luijten (2015) correctly consider the lectotype designation by Chevalier (1965) as invalid; they should have also considered the act by Martínez-Ortí and Robles (2012) in the same way.

The second issue regarding the original description of *H. alonensis* is that the species as such has no syntypes. This paradoxical situation stems from the fact that only each of the five (unnamed) varieties has its own syntypes: Art. 72.4.1 explicitly excludes from the type series any specimens that the author expressly refers to as distinct variants indicated as such. Bank & Luijten (2015) wrongly considered all syntypes of the five varieties as syntypes of the species. This atypical situation of the nominal taxon *H. alonensis* is certainly exceptional, but far from unique; it may cease to be a problem with a proposed change in the next edition of the Code (F. Welter-Schultes, pers. comm.). However, at present there is a risk for stability stemming from the fact that under a strict application of Art. 72.4.1 the species remains without holotype nor lectotype.

A useful neotype designation is proposed herein in order to ensure stability in the identity and type locality of *Helix alonensis* Férussac, 1821. This is needed, in accordance with the Code, because the species has no syntypes (Art. 72.4.1), the original description is insufficient, and I consider that a name-bearing type is necessary to define and stabilize the nominal taxon objectively (Art. 75.1). There is an exceptional need to clearly define this taxon, as the neotype is herein designated with the express purpose of clarifying both the taxonomic status and the type locality of the nominal taxon *Helix alonensis* Férussac, 1921 (Art. 75.3.1). This species differs from all other *Iberus* species in its very large size, semiglobous shell shape, domiform spire, incised suture, rounded downturned mouth, prominent criss-crossed sculpture, and dark brown spiral bands, continuous or broken (Art. 75.3.2). The data, description and illustration provided below are sufficient to ensure unequivocal recognition of the specimen designated (Art. 75.3.3). The holotype was not designated, no syntypes are available, and the lectotype designation by Graells (1846) appears to be thus invalid (Art. 75.3.4). The neotype is fully consistent with what is known of the former name-bearing type from the original description and subsequent taxonomic restrictions (Art. 75.3.5), and came from the original type locality, which although vaguely stated surely included the neotype's collecting station and a restricted area around it (Art. 75.3.6). The neotype is properly curated and accessible for study in the author's research collection, recognized as a Museographic Collection by the Council of Mallorca (Art. 75.3.7).

The selected type locality is in Almería province, in agreement with Férussac (1821). The neotype of *Helix alonensis* Férussac, 1821 is fully adult; its major diameter is 36.2 mm (Fig. 12). It was collected live by the author, resting under large volcanic boulders, at Las Negras (Campo de Níjar county, Almería province, Andalucía, Spain), 36° 52' 38"N, 2° 00' 21" W, 23 m elevation; 12.x.2015. It is cataloged with number CRA-16202-1, in the author's Museographic Collection; the shell is kept dry in a clear polystyrene box with a label written with India ink on acid-free paper, and the soft parts in a vial with 80% ethanol and a label written also with India ink on onionskin paper.

http://zoobank.org/NomenclaturalActs/F390DF60-B6E0-4095-9CFF-A9CEE9438252

Iberus (Alonensis) alonensis is restricted to the area of Cabo de Gata, from Retamar in the west to Níjar in the north, and Las Negras in the northeast (Fig. 3). It lives in rugged terrain and screes, in very dry areas at

low elevation on calcareous ground, volcanic rocks and limestone, under low, scanty vegetation. This is a lineage adapted to extreme xeric conditions.

***Iberus (Valentiberus)* new subgenus**

Diagnosis.- Mid-sized to large allognathines with depressed semiglobose, rather thin shell having low spire, completely (or nearly so) closed umbilicus, oblong and well inclined aperture, and reduced sculpture.

Type species.- *Iberus alvaradoi* García San Nicolás, 1957.

Species included.- Only the type species, which is considered polytypic. In addition to the nominotypical subspecies, three geographical subspecies are herein described: *I. (Valentiberus) a. turolensis* subsp. nov., *I. (Valentiberus) a. ilercaonus* subsp. nov. and *I. (Valentiberus) a. quixotei* subsp. nov.,

Etymology.- A combination of Valentia (currently València) in the eastern past of the Iberian peninsula, and the genus *Iberus*. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/377C638C-573D-443C-9299-CAD9BA9F3800

Remarks.- After restricting the description of *Helix alonensis* Férussac, 1821 to the epsilon variety in Almería (Graells, 1846), the remaining varieties α, β, γ and δ were left without any name. They belong to another species, which remained unnamed for 136 years until García San Nicolás (1957: 299) acknowledged the existence of this gap. *Iberus alvaradoi* García San Nicolás, 1957 was described on the realization that *I. alonensis* is found only in Andalusia. All Andalusian *Iberus* species differ substantially on conchological grounds from the specimens of the type series of *I. alvaradoi.* Thus, *I. alvaradoi* was erected to include all non-Andalusian populations initially included in *H. alonensis*, with a holotype from València (García San Nicolás, 1957: 350). Bank and Luijten (2015) erroneously state that no type locality was designated.

Iberus (Valentiberus) alvaradoi is the only species in extends from extreme eastern Murcia province, through the southern and central València region; its inland limits are marked by the high mountains of the Iberian Chain in the north and the Prebaetic System in the south, and by the dry plains to the north of the Ebro River and to the east of the Mancha Húmeda (Fig. 3). The existence of geographical forms deserving subspecific recognition was already mentioned by García San Nicolás (1957: 384). Compared with the three new subspecies described below, the nominotypical is more depressed and usually smaller.

***Iberus (Valentiberus) alvaradoi turolensis* subspec. nov.**

Diagnosis. - More globose than other subspecies; spire just moderately depressed, last whorl comparatively tall and a bit bulging below.

Description.- Shell dextral, medium-sized, rather thin, semiglobose, with low domiform spire consisting of a bit less than four depressed rounded whorls, moderately fast growing until the appreciably more expanding last 1/4; suture moderately incised; aperture oblique, elongate elliptical, gently downturning before the peristome, with palatal edge just a little thickened inside, and just slightly flaring lip; columella thickened but indistinct, virtually covering the umbilicus with a terminal, appressed callus; no parietal callus; external surface mate, densely sculptured with colabral ridgelets and thin spiral lines, very reduced around the umbilical area; very pale yellowish with five thin, very diffuse, dark goldenrod brown bands, which are more defined on the underside but become intermingled with pale, extensive marmorations on the upper surface; peristome porcelain white.

Type material. - Spain, Aragón, Teruel province, Comunidad de Teruel county, Orrios, El Vadillo, 40° 35' 17" N, 0° 57' 10" W, 1,189 m; 31.iii.1980, C. R. Altaba col. Holotype CRA-2617-1, diameter 29.6 mm (Fig. 13); and 2 paratypes (CRA-2617-2 and 3).

Distribution.- *Iberus (xxx) alvaradoi turolensis* appears to have a fairly wide distribution throughout central Aragón and adjoining areas, in the central Ebro valley and in the northern piedmont of the Iberian Chain (Fig. 3). Across the Ebro valley, it extends to the northwest as far as Araba (Álava) in the Basque Country, where it may have been introduced by people (García San Nicolás, 1963). The southern and eastern limits appear to be the high mountains of the Iberian Chain.

Habitat.- The new species lives in calcareous ground and limestone areas covered by Mediterranean brush, scrub or light forests, at moderate elevation.

Etymology.- The species name is an adjective, demonym referring to its distribution including the inland province of Teruel.

http://zoobank.org/NomenclaturalActs/31890c23-16e5-4070-a396-ff753e14d6a1

Remarks.- This is the relatively high-spired form reported by García San Nicolàs (1963) from the upper Ebro valley. The mention of *I. carthaginiensis* from Teruel by Puente Martínez (1994) is a misidentification for this taxon.

***Iberus (Valentiberus) alvaradoi ilercaonus* subspec. nov.**

Diagnosis. - The spire is higher than in other subspecies, and the last quarter whorl is slightly more expanded and consequently the aperture more rounded.

Description.- Shell dextral, medium-sized, rather thin, semiglobose, with low conical spire consisting of a bit less than four depressed rounded whorls, moderately fast growing until the noticeably more expanding last 1/4; suture barely incised; aperture oblique, rounded elliptical, gently downturning before the peristome, with palatal edge just a little thickened inside, and just slightly flaring lip; columella thickened but indistinct, covering the umbilicus or almost nearly so, ending in an appressed callus; no parietal callus; external surface with a soft silky sheen, densely covered with a fine sculpture of fine colabral ridgelets and thin spiral lines, much reduced on the underside; pale wheat brownish with five thin, very diffuse, sienna bands, which are generally confused among marmorations of the same color; peristome porcelain white.

Type material. - Spain, Catalunya, Tarragona province, Ribera d'Ebre county, Riba-roja d'Ebre, Pinyera de Marcel·la, 41° 14' 38" N, 0° 25' 08" E, 138 m; 12.x.2015, C. R. Altaba col. Holotype CRA-19365-1, diameter 29.2 mm (Fig. 14); and 1 paratype (CRA-19365-2).

Distribution.- *Iberus (Valentiberus) alvaradoi ilercaonus* subsp. nov. occupies the northeastern part of the species range. To the north it reaches the Baix Cinca in southernmost Huesca province (Puente & Prieto, 1991). It extends along the lower Ebro river and in the rugged mountain areas to the northeast and southwest (Fig. 3).

Habitat.- The new subspecies lives in calcareous areas at low to mid elevation, in native Mediterranean brush, scrub and light forest.

Etymology.- The subspecies name is an adjective referring to the Ilercaones, an Iberian people living until Roman times in an area roughly coinciding with this taxon's range.

http://zoobank.org/NomenclaturalActs/60FB2F4D-18AA-42CE-9F0D-F8FA14AF9373

Remarks.- The mention of a common name by Aguilar-Amat (1921) was taken as the proposal of a species name by Bank and Luijten (2015: 95), who thus mention the unavailable name "*Iberus carragines* Aguilar-Amat, 1921". Bank & Luijten (2015) did not explicitly indicate the name as intentionally new, so this is an unavailable name (Arts. 16.1, 11.6.3).

García San Nicolás (1957: 244) placed *Iberus alvaradoi* in the subgenus *Marmoratus* due to its grey mantle. Altimira (1961) cites this taxon as *Iberus (Marmoratus) alvarodoi* [*sic*] from Hospitalet de l'Infant, at the extreme northeastern limit of the species range.

***Iberus (Valentiberus) alvaradoi quixotei* subspec. nov.**

Diagnosis. - Considerably more depressed and compact than other subspecies, with very low spire and last whorl more bulging below; very finely sculptured; relatively small size (as often in the nominotypical subspecies).

Description.- Shell dextral, medium-sized, rather thin, semiglobose, with very low domiform spire consisting of around $3^3/_4$ well inflated whorls, somewhat bulging below, rather fast growing and just moderately expanding in the last 1/8; suture moderately incised; aperture oblique, elliptical, downturning before the peristome, with palatal edge just a little thickened inside, and slightly flaring lip; columella appreciably thickened but indistinct, covering much of the umbilicus before ending in an appressed callus; no parietal callus; external surface dull, sculptured with very fine colabral ridgelets and spiral lines, reduced on the underside; very pale light yellowish with five thin, well defined, pale tan bands; peristome ivory white, softly tinged with pale pink at the outer limit of the columella.

Type material. - Spain, Castilla-La Mancha, Ciudad Real province, Campo de Montiel county, Ruidera, 38° 58' N, 2° 53 W, ca. 820 m; 12.x.2015, J. Liétor col. Holotype CRA-15746, diameter 26.4 mm (Fig. 15).

Distribution.- *Iberus (Valentiberus) alvaradoi quixotei* subsp. nov. occupies the westernmost part of the species range, in the southeastern Iberian Meseta, under continental climate.

Habitat.- The new species lives in calcareous areas at moderate elevation, in Mediterranean dry scrub or light forest.

Etymology.- The species name is an adjective, referring to Don Quixote, a famous character from La Mancha.

http://zoobank.org/NomenclaturalActs/FE5E158A-C28E-4A08-B0C5-831D49E5870F

Remarks.- The eastern limits of this taxon, and its likely transition to neighboring subspecies, remain to be assessed.

Hemicyclina subtr. nov.

Diagnosis.- Small to mid-sized allognathines, with globular to discoidal shells, often with strong comarginal costulation.

Type genus.- *Hemicycla* Swainson, 1840.

Other genera included.- *Lampadia* Albers, 1854, *Idiomela* Cockerell, 1921, and *Adiverticula* Alonso & Ibáñez, 1988 (as a subgenus of *Hemicycla*).

http://zoobank.org/NomenclaturalActs/57B4001E-A406-425B-B0EA-78B851D8F3E6

Remarks.- Restricted to the Macaronesian archipelagos: *Hemicycla* in the Canary and Cape Verde Islands, and *Lampadia* and *Idiomela* in the Madeiran archipelago. The proposal to synonymize *Adiverticula* with *Hemicycla s.s.* by Neiber et al. (2021) is based on nodes with little support on a molecular phylogeny, and should not be accepted without further research.

Allognathina Westerlund, 1903

Diagnosis.- Small to large allognathines with shining, globular to depressed shell, umbilicus closed by a strong parietal callus, small reflected lip, aperture often tinged with violet, and more or less complex

pattern of broken or continuous spiral bands often intermingled with a marmoration pattern.

Type genus.- *Allognathus* Pilsbry in Tryon & Pilsbry, 1888.

Other genera included.- *Iberellus* Hesse, 1932, *Nesiberus* Haas, 1934 (as subgenus of *Iberellus*), and *Tramuntanicola* Altaba, 2022.

Remarks.- Restricted to the Balearic archipelago. Westerlund (1903) erected the monotypic family Allognathidae on the basis of shell and radula, ignoring everything else. The amazingly complex nomenclatural history of the nominotypical subtribe has recently been clarified (Altaba, 2022b).

Tartessiberina subtr. nov.

Diagnosis.- Small to mid-sized allognathines with low to strongly depressed shell, round to keeled periphery, umbilicus closed or nearly so, small reflected lip, white to violet aperture, surface with silky sheen, nearly smooth or ornamented with faint to strong colabral ribs, and often a complex pattern of marmorations, especially on the spire.

Type genus: *Tartessiberus* Altaba & Ríos Jiménez, 2021.

Other genera included: *Marmoratus* García san Nicolás & Alvarado, 1955, *Angustiberus* gen. nov., *Nescaniberus* gen. nov., and *Torcaliberus* subgen. nov. (within *Marmoratus*).

http://zoobank.org/NomenclaturalActs/B889BEC5-E1E9-46E9-AEE8-5BE1F52B75E4

Remarks.- *Tartessiberus* Altaba & Ríos Jiménez, 2021 is a restricted-range, monotypic genus including only *Tartessiberus cilbanus* Altaba & Ríos Jiménez, 2021. This is an extreme karst-adapted species, convergent with the Balearic *Allognathus* in shell shape and radula (Altaba & Ríos Jiménez, 2021). The comments aiming at invalidating this genus by Jowers et al. (2024) and Liétor et al. (2024b) are crude misrepresentations, as *Tartessiberus* cannot be synonymized with *Iberus* without completely ignoring the tribe's phylogeny, and the description of *T. cilbanus* was quite detailed and based on all morphological traits.

***Angustiberus* gen. nov.**

Diagnosis.- Small-sized allognathines with thin, strongly depressed shell, nearly closed umbilicus, and attenuated marbled pattern on the spire.

Type species.- *Helix guiraoana* var. *angustata* Rossmässler, 1854

Species included.- *Angustiberus hispanicus* (Rossmässler, 1838), *A. granatinus* nom. nov. and *A. maginensis* spec. nov.

Etymology.- A combination of *Iberus*, a related land snail genus where it has long been placed, and the previous name of its type species. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/34D8B414-17AB-45D7-9E6B-09C76BF59F08

Remarks.- There are three distinct clades within *Angustiberus*, with allopatric distributions (Fig. 16). The basal branch is described below as a new species. The other two sister species are discussed herein, one of them with a replacement name, solving a long taxonomic riddle.

The name *Helix guiraoana* var. *angustata* Rossmässler, 1854 is preoccupied by *Helix angustata* Férussac, 1822. The latter is an endemic from Hispaniola, currently known as *Hispaniolana angustata* (Férussac, 1822) in the basal helicoid family Sagdidae (Clench, 1962; Sei et al., 2017; Zhang et al., 2024). I thus propose the replacement name *Angustiberus granatinus* nom. nov. The holotype is the specimen

illustrated by Rossmässler (1854: 11, fig. 798 in pl. 63), from Dientes de la Vieja near Granada (Andalucía, Spain), following Recommendation 60A of the Code. The etimology of the new name is a patronym from Granada.

http://zoobank.org/NomenclaturalActs/1c2ecf44-5ad1-4de3-b3d2-7723eef6c970

The original description and illustration of *Helix hispanica* Rossmässler, 1838 appears to be based on a form quite similar to *Angustiberus granatinus* nom. nov.*,* but with nearly closed umbilicus (Altaba, 2022b). The similarity between these two nominal species was already suggested by Schmidt (1853: 174). Rossmässler (1854: 12) accepted the suggestion by Graells (1846) that the former name would be in conflict with *Helix hispana* Linnaeus, 1758 and proposed using the name *H. hispana* var. *balearica* Rossmässler, 1838 as the valid species name. However, this variety had been described on the basis of a specimen stated to differ in form and coloration from *H. hispanica.* Thus, that individual does not belong to the latter's type series (Art. 72.4.1), and the rank switch could not affect the status of either nominal taxon (Altaba, 2022b).

The type locality of *Helix hispanica* was given only as Spain (Rossmässler, 1838). Graells (1846) mentions he has received this species alive from Jaén, where it is common. Hidalgo (1875) also mentions this locality. However, both Spanish authors confused the Andalusian species with the true *H. balearica* from the island of Mallorca. The specimen figured by Rossmässler has the columellar callus covering the umbilicus almost completely, a markedly descending aperture and a coloration pattern consisting of five narrow, well defined bands, the lower two being continuous and the upper three broken. This combination of traits does not match any species from the Balearics. Thus, the type locality of *H. hispanica* must be continental Spain. The combinations *Iberellus hispanicus* (Rossmässler, 1838) and *Allognathus hispanicus* (Rossmässler, 1838), proposed to include Balearic species (Beckmann, 2007; Welter-Schultes, 2012; Chueca et al., 2013, 2015; Neiber et al., 2021, 2022), are erroneous. It should also be noticed that in the mid-19th century the term "Spain" was widely used in the biological literature in reference only to continental Spain. A prominent example is in the title given by Hidalgo (1875) to his compendium, as "Iconographic and descriptive catalog of the terrestrial mollusks of Spain, Portugal and the Balearics". Besides, Graells maintained a network of exchanges with several German naturalists (Reig-Ferrer, 2023), to whom he likely sent specimens from Jaén.

The combination of traits provided in the original description of *H. hispanica* is found in the small allognathine living in the mountains to the west of the city of Jaén, from the Santa Catalina castle overseeing the town to the range extending further west up to La Mella ridge. Thus the combination *Angustiberus hispanicus* (Rosmmässler, 1838) applies to this restricted-range species.

Angustiberus granatinus nom. nov. is the sister lineage to *A. hispanicus*. The range *of A. granatinus* extends from the Sierra Sur in southwestern Jaén province, through the west and south of the Guadiana Menor River, to central Granada province (Martínez-Ortí & Robles, 2012; Liétor et al., 2024a). Its type locality is the Sierra de los Dientes de la Vieja, a small, rugged mountain chain located to the north-east of the city of Granada, very close to the old road to Diezma (Schmidt, 1853; Rossmässler, 1854; Martínez-Ortí & Robles, 2013). *A. granatinus* is almost always conspicuously smaller than *A. hispanicus*, and its banding pattern is more defined. The spire of *A. granatinus* is low conical, while that of *A. hispanicus* is considerably more depressed, even almost flat.

The isolated populations of *Angustiberus* further east in the mountains of central Murcia (García-Meseguer et al., 2017) likely belong into *A. granatinus*. Another isolate at the northern edge of the genus range exhibits unique morphological traits and constitutes a basal branch of the genus in the molecular tree; it is described as a new species below.

Angustiberus maginensis spec. nov.

Diagnosis. - A small allognathine belonging to *Angustiberus*, differing conspicuously from congenerics in its almost open, clearly wider, more perspective and eccentric umbilicus. The spire is similar to that of depressed specimens of *A. hispanicus*, but the last whorl is somewhat more expanded.

Description.- Shell dextral, small, fairly thin, almost discoidal, with very low spire consisting of $3^3/_4$

strongly depressed, rounded, rather slowly growing whorls, the last one expanding more; suture moderately incised; aperture oblique oval, gently downturned but more so behind the peristome, with palatal edge just slightly thickened inside, and small but conspicuous flaring lip; columella thickened but indistinct, quite continuous with the free lip, and reflected proximally covering about two thirds of the umbilicus, which is small but perspective, widened and thus eccentric in the last whorl; no parietal callus; external surface a bit glossy, with a very fine sculpture of fine colabral ridgelets and thin spiral lines, clearly reduced around the umbilical area; ivory white peristome and underside, somewhat tinged with exceedingly pale marmorations on the upper surface, with five thin chocolate bands, the lower two continuous but the upper three nearly broken.

Type material. - Spain, Andalucía, Jaén province, Sierra Mágina County, Bedmar, Torreón de Cuadros, 37° 47' N, 3° 24' W, ca. 670 m, in limestone crevices covered by Mediterranean shrubs; 12.x.2015, J. Liétor col. Holotype CRA-15568-1, diameter 22.2 mm (Fig. 17); and 1 paratype (CRA-15568-2).

Distribution.- *Angustiberus maginensis* sp. nov. appears to be restricted to Sierra Mágina, a mountain range in the Subbaetic Massif.

Habitat.- The new species lives in limestone areas at moderate elevation.

Etymology.- The species name is a patronymic adjective referring to Sierra Mágina, a mountain range in northeastern Andalusia.

http://zoobank.org/NomenclaturalActs/D5F1AA30-1282-4D13-9FDB-FC7C4629A346

Remarks.- The umbilicus may be only partially covered by the columellar callus in the other congeneric species, but the extent of such coverage is very limited in *A. maginensis*, whose umbilicus is wider and clearly more perspective.

***Nescaniberus* gen. nov.**

Diagnosis.- Small allognathines with moderately depressed to nearly flat spire, closed umbilicus, barely to strongly keeled periphery, and consequently oval to subtriangular aperture.

Type species.- *Iberus cobosi* Ibáñez & Alonso, 1978.

Species included.- Monotypic.

Etymology.- A combination of *Iberus* and Nescania, the Roman name of the small city within its very limited range. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/9F0486CD-BA64-4D6A-A27D-E268A40B619C

Remarks.- *Nescaniberus cobosi* is restricted to the Valle de Abdalajís, a narrow valley in north-central Málaga province (Andalucía; Fig. 16). There is a strong individual variation in spire elevation, with specimens having nearly flat spire, acutely angled peristome and a peripheral chord (Ibáñez & Alonso, 1978) It is unclear whether the more semiglobose shell shapes found in the lower valley represent introgression, or reflect a conspecific cline as in *Marmoratus (Torcaliberus) rositai* Fez, 1950.

***Marmoratus* García San Nicolás & Alvarado, 1955**

Diagnosis.- Small allognathines with semiglobose to strongly depressed shell, round to keeled periphery, nearly smooth to markedly ribbed surface, slightly to completely closed umbilicus, and often a well-developed pattern of marmorations on the spire.

Type species.- *Helix (Helicogena) marmorata* Férussac, 1821

Species included.- *Marmoratus marmoratus (*Férussac, 1821), *M. loxanus* (Rossmässler, 1854) and *M.*

rositai (Fez, 1951). The first two have four and three subspecies, respectively; the latter is included in the subgenus *Torcaliberus* subgen. nov.

Etymology.- A tautonym of its type species. It is a masculine noun.

Remarks.- Proposed as a subgenus by García San Nicolás and Alvarado (1955), available through absolute tautonimy (Art. 68.4). It was proposed again by García San Nicolás (1957: 244), effectively as a junior synonym.

The informal name "Marmoratus group" has been used for some Amazonian frogs (Heyer, 1969), but it has never been formally described. Instead, *Adenomera* Fitzinger in Steindachner, 1867 was found to be available, with *A. marmorata* Fitzinger in Steindachner, 1867 as type species, and deemed adequate (Heyer, 1974). The same informal name has been used for a clade of south-east Asian frogs (Pang & Liu, 1992; Lyu et al., 2019); this clade remains unnamed.

Férussac's name is preoccupied by *Helix marmorata* Gmelin, 1791. According to Art. 23.9.1 of the Code, prevailing usage must be maintained, through a reversal of precedence, if two conditions are met. The first requisite is that the senior homonym has not been used as a valid name after 1899 (Art. 23.9.1.1). This is the case, as Gmelin's name has never been used by any subsequent author. It was only listed twice in the last century, as a junior synonym of *Aplexa hypnorum* (Linnaeus, 1758), belonging into the freshwater pulmonate family Physidae (Germain, 1931; Taylor, 2003).

The second condition to be met is that the junior homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years (Art. 23.9.1.2). Such requirement is extremely restrictive for zoological groups such as mollusks. Anyway, thanks to the archaeological research in southeastern Andalusia, it can be met: *Iberus marmoratus* (Férussac, 1821) has been used as a valid name for the same taxon in the following 28 works after 1974: Ibáñez & Alonso (1978), Cobos (1980), Aparicio & Ramos (1988), Falkner (1990), Serrano et al., (1997), Lozano-Francisco et al. (2004), Steinke et al. (2004), Talaván Gómez & Talaván Serna (2006), Cortés-Sánchez et al. (2008), Elejalde et al. (2008a), Torres (2010), Jordà et al. (2010), Cortés-Sánchez et al. (2011), Groenenberg et al. (2011, although with the wrong spelling "*I. marmorana*"), Jordà et al. (2011), Talaván Serna & Talaván Gómez (2011), Welter-Schultes (2012), Torres Alba (2012), Liétor et al. (2014), Bank & Luijten (2015: 95), Vázquez Toro et al. (2015), Torres Alba et al. (2016), Neubert et al. (2019), Torres Alba et al. (2019), Ahuir Galindo (2020), Neiber et al. (2021), Jowers et al. (2024), Liétor et al. (2024a).

Thus in accordance with Art. 23.9.2 I herewith declare *Helix marmorata* Férussac, 1821 as *nomen protectum*, and *Helix marmorata* Gmelin, 1791 as *nomen oblitum*.

The type locality of *Marmoratus (M.) marmoratus* (Férussac, 1821) is Gaucín, near Gibraltar (Férussac, 1821; as revised by Bank & Luijten, 2015).

Iberus serpentinae Ahuir Galindo, 2020 is a junior (subjective) synonym of this species. Its type locality is just a few kilometers to the west of Gaucín (Ahuir Galindo, 2020), the type locality of *M. marmoratus*, from which it cannot be discriminated.

Helix balearica var. *pulchella* Rossmässler, 1854 was described on specimens collected on limestone close to the seashore between Málaga and Vélez Málaga further east (Rossmässler, 1854). Unfortunately, it is a junior homonym of *Helix pulchella* Müller, 1774, now in the stylommatophoran Valloniidae (Gerber, 1996; Altaba, 2015). Although not explicitly erected as a replacement name, but deemed identical with Rossmässler's variety, *Helix partschi* Servain, 1881 was described as coming from two areas: around Málaga and around Gibraltar (Servain, 1881). This name must be attributed to the autor of the work, who added some remarks and a bibliographical reference to the initial writing ascribed to Bourguigant (Art. 50.1.1). A syntype from Gibraltar has been figured by Bank and Luijten (2015). However, in order to minimize nomenclatural changes, I herein designate as lectotype of *H. partschi* the specimen shown in figure 797 by Rossmässler (1854), thus restricting the type locality (Art. 76.2) to La Platera, the only stretch of limestone along the (old) coastal road from Málaga to Vélez Málaga.

http://zoobank.org/NomenclaturalActs/BDF8C69F-776C-4CAF-B835-77958AB9CB11

I consider *partschi* as a subspecies of *M. marmoratus*. Specimens from this area are similar to others from the eastern part of the species range (Fig. 18), in being smaller and with a more compact build-up in comparison with those from the remaining of the species distribution. Thus, *Marmoratus (M.) marmoratus partschi* (Servain, 1881) is the name applicable to the eastern set of populations of this species. Within this eastern area there appears to be a north-south phylogeographic structure, perhaps warranting further subdivision.

Specimens from the northwestern edge of the range of *M. marmoratus* uniformly exhibit a distinctive flattened morphology. To the southwest, a peripheral isolate is inhabited by unusually small specimens. These constant differences support the recognition of two further subspecies described below.

Helix loxana Schmidt (1853) has a conspicuously depressed shape allowing discrimination from *M. marmoratus*. As correctly shown by Bank and Luijten (2015), the work by Schmidt (1853) includes valid descriptions of species whose names were used the following year by Rossmässler (1854). Although the name *loxana* was explicitly attributed by Schmidt (1853) to Rossmässler, Schmidt described the species alone (Art. 50.1.1). Later on, Schmidt (1855) added further anatomical observations.

Typical *Marmoratus loxanus* occurs in a small rugged area, the Calcareous Arc extending along an east-west direction in central Málaga province. Two southern isolates show distinctive traits and are herein recognized as subspecies, in addition to the nominotypical one. One of these is *M. (M.) l. candoni* (Ahuir Galindo, 2021), known only from the Tajo de la Cuña gorge south of Ventas de Zafarraya, in the southwestern limit of Granada province. This local form has a nearly flat spire, a strong peripheral keel and prominent colabral ridgelets (Ahuir Galindo, 2021).

To the southeast, on karstic reliefs near the coast of easternmost Málaga and southern Granada provinces, a third subspecies occurs. It was described as *Helix balearica* var. *violacea* Rossmässler, 1854 with a vague locality ("around Granada"), as it had been found among live snails on sale in Granada (Rossmässler, 1854:10). It has only been reported once after its description, from the eastern outskirts of Granada (Retgeren Altena, 1961). Specimens of *M. loxanus violaceus* (Rossmässler, 1854) differ from the nominotypical subspecies in having a strongly depressed spire, a noticeably flaring and more extended lip, a beautiful violet (fading away in dead specimens), much depressed and more downturned aperture, a shiny surface with very fine sculpture, and a lighter base color upon which the brown basal bands and upper marmoration stand out. There is no need to designate a lectotype for this taxon; its diagnostic traits are well presented in the original description (Rossmässler, 1854: 10, figs. 796 and 797 in pl. 63). This taxon has been collected in several localities, all within a small area from Granada city south to the coast of Granada province, from Motril and Lobres in the east to near Almuñécar in the west (Fig. 16), in karstified limestone areas at low elevation.

***Marmoratus (M.) marmoratus arundanensis* subspec. nov.**

Diagnosis. - A much depressed local form of *M. marmoratus*, exhibiting a strongly reflected, flaring lip.

Description.- Shell dextral, small, remarkably thin, depressed, with very low domiform spire consisting of a $3^3/_4$ depressed whorls, slightly inflated above, with rounded side and flattened below, rather fast growing; suture slightly incised; aperture rounded oval, gently downturning before the peristome, with palatal edge thickened inside, and expanding into a conspicuously flaring lip; columella thickened but indistinct, continuous with lip, completely covering the umbilicus with an appressed callus; no parietal callus; external surface a bit glossy, densely sculptured with very fine colabral ridgelets and spiral lines, reduced around the umbilical area; very pale straw yellowish with five thin, very diffuse, saddle brown bands, which are broken, more clearly visible on the underside but intermingled with dense, complex, extensive marmorations on the upper surface; peristome porcelain white, tinged with pale violet becoming more visible at its both ends.

Type material. - Spain, Andalucía, Málaga province, Serranía de Ronda county, Ronda, El Tajo de Ronda, 36° 44' 25" N, 5° 09' 51"W, 671 m, in karstified limestone covered by Mediterranean shrubs; 20.v.2022, C. R. Altaba, col. Holotype CRA-23831-1, diameter 20.8 mm (Fig. 19); and 20 paratypes (CRA-23831-2 to 21).

Distribution.- *Marmoratus (M.) marmoratus arundanensis* subspec. nov. occupies the northeastern extreme of the species range. It extends from northwesternmost Málaga province to the southeastern edge of Sevilla province (Fig. 16).

Habitat.- The new species lives in limestone areas at moderate elevation, under native Mediterranean scrub.

Etymology.- The subspecies name is a patronymic adjective referring to Arunda, the pre-Roman name of Ronda, in central-western Málaga province, Andalusia.

http://zoobank.org/NomenclaturalActs/0681DE67-4B6C-4F5C-9171-417D7F7522C5

Remarks.- The shells reported as "*Iberus* cf. *marmoratus*" by Vázquez Toro et al. (2015) in nearby mountains, already in the province of Seville, belong to this new subspecies.

***Marmoratus (M.) marmoratus gaditanus* subspec. nov.**

Diagnosis. - A semiglobose, pale, very small local form of *M. marmoratus*.

Description.- Shell dextral, quite small, somewhat thickened, semiglobose, with fairly tall domiform spire consisting of a $3^3/_4$ well-rounded whorls, appreciably inflated above and below, moderately fast growing; suture slightly incised; aperture rounded oval, rather strongly downturning before the peristome, with palatal edge thickened inside, and just moderately expanding into a barely flaring lip; columella well thickened but indistinct, completely covering the umbilicus with an appressed callus; no noticeable parietal callus; external surface glossy, densely sculptured with very fine colabral ridgelets and spiral lines, reduced around the umbilical area; ivory white with five rather wide, dark sienna to saddle brown bands, which are penetrated by white irregular lines and become almost diffused among paler marmorations on the upper surface; peristome ivory white.

Type material. - Spain, Andalucía, Cádiz province, Campiña de Jerez county, Jerez de la Frontera, Sierra de San Cristóbal, 36° 38' N, 6° 10' W, ca. 90 m; 10.xi.2012, Carlos J. Pérez col. Holotype CRA-15593-1, diameter 17.9 mm (Fig. 20); and 2 paratypes (CRA-15593-2 and 3).

Distribution.- *Marmoratus (M.) marmoratus gaditanus* subsp. nov. appears to be restricted to the Sierra de San Cristóbal, a low range near the Gulf of Cádiz, at the westernmost edge of the species distribution (Fig. 16).

Habitat.- The new species lives in limestone areas at low elevation, under Mediterranean scrub and light forest.

Etymology.- The species name is a patronymic adjective referring to the range of this species, apparently limited to a small area near Cádiz (Gades in Ancient times).

http://zoobank.org/NomenclaturalActs/5A1762D6-F88A-4B33-A765-3FB17490B637

Remarks.- This is a narrow-range endemic, whose distribution may be disconnected from the main range of the species.

***Marmoratus (Torcaliberus)* subgen. nov.**

Diagnosis.- Mid-sized allognathines with ribbed shell, barely to completely closed umbilicus, slightly to strongly keeled periphery, and consequently more or less developed peripheral chord.

Type species.- *Iberus rositai* Fez, 1950

Species included.- Monotypic, including two subspecies: *M. (T.) r. rositai* (Fez, 1950) and *M. (T.) r.*

gualtieroloxanus (García San Nicolás, 1957).

Etymology.- A combination *Iberus* and the Torcal de Antequera, the karstic massif where this taxon lives. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/151D156F-22D3-456D-BA38-9FBA55F0DCE5

Remarks.- *Torcaliberus* forms a clade together with the nominotypical subgenus in the molecular tree, albeit with low support. They are thus conservatively treated herein as congeneric.

Marmoratus (Torcaliberus) rositai (Fez, 1950) was based on a single specimen exhibiting a most pronounced keel with a small peripheral carina. The holotype has later been more adequately figured (García San Nicolás, 1957: pl. xviii, fig, 62; Martínez-Ortí & Uribe, 2008: 88). The type locality was given as Benaoján, at the western edge of Málaga province (Fez 1950). There are no known keeled allognathines in that area; instead, *rositai* matches those living in the upper Torcal de Antequera, a small, rugged karstic massif in north-central Málaga province (Alonso & Ibáñez, 1978).

García San Nicolás (1957: 382) hypothesized this would be an intermediate between *Iberus gualtieranus* and *Cazorliberus guiraoanus*, but that is just an assessment of general shell shapes. Sacchi (1957) proposed it should belong into the North African genus *Rossmaessleria* Hesse, 1907, which includes some strongly keeled shells (Walther et al., 2016); Alonso & Ibáñez (1978) correctly placed it within "*Iberus*".

The species name *rositai* was explicitly derived as a genitive of Rosita (Fez, 1950), a woman's name diminutive of Rosa, which in Latin is clearly a first declension feminine noun. Thus, it was incorrectly declined. However, patronyms should not be emended (Némésio & Dubois, 2012).

The nominal species *Iberus gualtieroloxanus* García San Nicolás, 1957 was also based on a single specimen, reported to have been collected in 1920 somewhere in the Sierra de Gádor, southern Almería province (García San Nicolás. 1957, 1986). This is surely a mistake. The holotype, well illustrated by García San Nicolás (1957: pl. xviii, fig. 63), exhibits a moderate peripheral keel. This attenuated sculpture sets it apart from *M. rositai*.

In the lower part of the Torcal there are specimens with reduced keeling, most similar to the shell described by García San Nicolás. These are not hybrids (as hypothesized by Alonso & Ibáñez, 1978), but represent intraspecific variation (Elejalde et al., 2008a). Such variation appears to have a geographical translation: a cline from more rounded shells in areas with moderate karstic development to strongly keeled specimens in the more rugged, core area of the small massif. Thus, the two forms are treated herein as subspecies: *M. (T.) r. rositai* (Fez, 1950) in the Torcal Alto (high zone), and *M. (T.) r. gualtieroloxanus* (García San Nicolás, 1957) in the Torcal Bajo (lower area).

The name *Iberus gualtieroloxanus* García San Nicolás, 1949 was introduced as a claim for priority over the work by Siro de Fez, based on a questionable account of this name being presented at a meeting in Madrid in 1949 (García San Nicolás, 1986). That may have happened, but there seems to be no written record of that presentation (Martínez-Ortí, 2006). Thus, it is a *nomen nudum*.

Oretaniina subtr. nov.

Diagnosis.- Small to mid-sized allognathines with low conical to nearly flat spire, rounded or barely keeled periphery, almost open to completely closed umbilicus, nearly smooth and moderately shining surface.

Type genus.- *Oretanius* gen. nov.

Other genera included.- *Cazorliberus* gen. nov.

http://zoobank.org/NomenclaturalActs/84EA3D05-1C40-4D72-95EF-C87CFF41A6D3

Remarks.- The two genera included differ appreciably in shell form.

***Oretanius* gen. nov.**

Diagnosis.- Small to mid-sized allognathines with very finely ribbed shell, rounded to barely keeled whorls, low conical to moderately depressed spire, and completely closed umbilicus.

Type species.- *Helix alcarazana* Rossmässler, 1854.

Species included.- *Oretanius alcarazanus* (Rossmässler, 1854), *O. ortizi* (García San Nicolás, 1957) and *O. axans* **spec. nov.**

Etymology.- Patronym of the Oretanii people, who lived until the Carthaginian and Roman conquests throughout the range of this taxon. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/5d0fa020-2786-45bd-9499-3d79ce1e55d3

Remarks.- The three species in *Oretanius* live in the central part of the Subbaetic Massif, and have allopatric distributions (Fig. 16). They live in rocky limestone areas, often hiding in crevices. *O. alcarazanus* extends through most of the Central Calcareous Arc in Málaga province, reaching the northeastern edge of Granada province and the southwestern corner of Jaén province. *O. ortizi*, smaller, paler and with whorls growing more slowly, is restricted to extreme southeastern Córdoba province. *O. axans* spec. nov., described below, is found only in a small area north of the westernmost range of the type species.

The nomenclature of species included in *Oretanius* has been loaded with mistakes, both long-standing and very recent. Bank and Luijten (2015) correctly attribute *Helix alcarazana* to Rossmässler, and partially correct other nomenclatural errors by Martínez-Ortí and Robles (2012). The latter assumed a possible swap of labels affecting the type locality of *H. alcarazana* Rossmässler, 1854. The original description states the type locality is the Sierra de Segura near Alcaraz (Albacete province, in the Castilla-La Mancha region), but the museum label indicates Castelló de la Plana (northern Comunitat Valenciana). These authors used such idea to designate a lectotype, choose a novel type locality, change the actual species involved, and attribute the name to Guirao; all four proposals are incorrect. That lectotype designation cannot be accepted, since it points at two different specimens (Art. 74.7.2). A further conspicuous mistake, developed on top of the preceding ones, is the unjustified synonymization of *H. alcarazana* with *Iberus alonensis*. Martínez-Ortí and Robles (2012: 101) state: "The conchological comparison of the specimens of *I. alcarazanus* from the Rossmässler collection with the shells of numerous individuals collected by the authors in the province of Castellón, which are attributed to *I. alonensis*, indicates that there are no significant differences between them. On the other hand, all *Iberus* samples whose DNA has been analyzed, from the northern half of the Iberian peninsula, which included the province of Castellón, have been identified as *I. alonensis* (Elejalde et al., 2008b). Therefore, the authors consider *I. alcarazanus* (Rossmässler, 1854) as a junior synonym of *I. alonensis* (Férussac, 1821)." This is puzzling, as the specimens in the Rossmässler collection and the original description cannot be confused with any form of *Iberus alonensis*. It is also unclear why Bank & Luijten (2015) accepted such misidentification and erroneous synonymization. As a matter of fact, *H. alcarazana* is an Andalusian endemic, which has never existed in the Sierra de Segura, nor anywhere near Castelló de la Plana, and is definitely quite distinct from any form of *I. alonensis*.

In order to ensure stability of nomenclature, a lectotype is herein designated for *Helix alcarazana* Rossmässler, 1854. This is the specimen figured by Rossmässler (1854: pl. 63, fig. 795).

http://zoobank.org/NomenclaturalActs/6BAFBF5B-F708-468A-A7BF-98D6AD686CD8

Within limits allowing easy identification of the species, *O. alcarazanus* exhibits a moderate variability in shell traits (Liétor et al., 2014). The three new species (*Iberus giennensis*, *I. axarcianus* and *I. antikarianus*) described by Liétor et al. (2024a) appear to be an indistinguishable subset of populations belonging to *Oretanius alcarazanus*. Remarkably, these authors explicitly acknowledge these three nominal species cannot be reliably identified, basing their descriptions on centroids in morphometric space, average

proportions, and overlapping variation in coloration patterns, plus a molecular tree that is reported to have weak support in critical nodes (the sequences are not available, so the tree cannot be assessed). They state that the average size differences are not diagnostic, and that only through molecular analysis could specimens be allocated to any of these species, but they do not provide any information as to what to look for: "All these species have to be identified by genetic distances rather than morphological features." The holotypes of the three nominal species surely look like *O. alcarazanus*, as virtually all the shells figured therein; they refer to taxa deserving to be listed as junior synonyms. However, these three species descriptions do not include any mention of a single diagnostic character, so they do not meet Art. 13.1.1 and are thus unavailable. Besides, Liétor et al. (2024a) state that *Helix alcarazana* should be rejected and substituted, but offer no valid reason for such action.

***Oretanius axans* spec. nov.**

Diagnosis. - A medium sized allognathine with fairly solid shell, strongly depressed spire, closed umbilicus, decidedly descending aperture, and fine colabral riblets.

Description.- Shell dextral, mid-sized, fairly solid, almost discoidal, with very low spire consisting of $3^3/_4$ strongly depressed, rounded, rather slowly growing whorls, the last one expanding more; suture moderately incised; aperture oblique oval, gently downturned but more so behind the peristome, with palatal edge just slightly thickened inside, and small but conspicuous flaring lip; columella thickened but indistinct, quite continuous with the free lip, and reflected proximally covering about two thirds of the umbilicus, which is small but perspective, widened and thus eccentric in the last whorl; no parietal callus; external surface a bit glossy, with a very fine sculpture of fine colabral ridgelets and thin spiral lines, clearly reduced around the umbilical area; ivory white peristome and underside, somewhat tinged with exceedingly pale marmorations on the upper surface, with five thin chocolate bands, the lower two continuous but the upper three nearly broken.

Type material. - Spain, Andalucía, Málaga province, Comarca de Antequera county, Antequera, lowland near the Torcal de Antequera, 36° 58' N, 4° 29' W, ca. 820 m; 12.x.2015, J. Liétor col. Holotype CRA-23581-1, diameter 26.7 mm (Fig. 21); and 2 paratypes (CRA-23581-2 and 3).

Distribution.- *Oretanius axans* sp. nov. occupies a very small area extending from the foot of the Torcal de Antequera northeastwards to the Sierra de Archidona, in north-central Málaga province (Fig. 16).

Habitat.- The new species lives in karstified limestone areas at middle elevation.

Etymology.- The species name is an adjective, participle of the Latin verb axare (to nominate, to mention), meaning "the mentioned one".

http://zoobank.org/NomenclaturalActs/B00F55F3-87B4-479B-BA9D-A9D4BA2DC95A

Remarks.- The existence of a unique, isolated population with a depressed shell initially attributed to *Marmoratus loxanus* was noticed as an outlying branch in the molecular trees inferred by Elejalde et al. (2008a). Although the phylogenetic methods they used are inadequate, the sequence they obtained does stand out in the molecular tree. Specimens collected very near the area (UTM grid square) they reported have the general build-up of *Oretanius*, but differ in having a depressed spire that may look deceptively like that of *M. loxanus*.

Oretanius axans has a distribution limiting with that of *Marmoratus (Torcaliberus) rositai* at the base of the Torcal de Antequera. The overall similarity with the less keeled forms of the latter species was hypothesized to indicate possible hybridization with *M. loxanus* (Alonso & Ibáñez, 1978: fig. 9D, as *Iberus loxanus*), but that is a conjecture; there is no genetic trace of any such event (Elejalde et al., 2008a).

***Cazorliberus* gen. nov.**

Diagnosis.- Small-sized allognathines with rather thin shell, with strongly depressed spire, rounded whorls and open, nearly smooth surface, and deep umbilicus widely open, being just barely covered by the

thin reflected columellar callus.

Type species.- *Helix guiraoana* Pfeiffer, 1853

Species included.- *Cazorliberus guiraoanus* (Pfeiffer, 1853), *C. bovistrini* **spec. nov.**, and *C. cazorlensis* **spec. nov.**

Etymology.- A combination of *Iberus* and Cazorla, the massif where this taxon lives. It is a masculine noun.

http://zoobank.org/NomenclaturalActs/27D82EA1-640A-40EC-8074-37D0388D0F6C

Remarks.- The authorship of *Helix guiraoana* is correctly attributed to Pfeiffer (1853b) by Bank and Luijten (2015). Ludwig Georg Karl Pfeiffer received from Emil Rossmässler specimens collected by the Murcian naturalist Ángel Guirao Navarro, and validly described the species. Thus, when Rossmässler (1854) treated this taxon it already existed. The type locality provided in the original description is Castelló de la Plana, obviously a mistake, as the only allognathine near that city in the north of the València region is the clearly different *Iberus alonensis*. Martínez-Ortí and Robles (2012) examined the syntypes and proposed the mistake originated in an inadvertent mismatch of museum labels. The label stating the specimens were collected by Guirao in the Sierra de Segura near Alcaraz (Albacete province) most likely belongs indeed to *H. guiraona*. The lectotype designation by Martínez-Ortí and Robles (2012) contained errors invalidating it; a valid lectotype was designated by Bank & Luijten (2015): the specimen figured with the number 799c by Rossmässler (1854: 10).

The three species in *Cazorliberus* have allopatric distributions, restricted to the mountains of Sierra de Cazorla and adjoining ranges to the north, in the Subbaetic Massif (Fig. 16). *C. guiraonaus* ranges throughout most of the area. Two distinct taxa living to the west and south exhibit appreciable genetic and morphological differentiation, and are thus described below as new species.

***Cazorliberus bovistrini* spec. nov.**

Diagnosis. - A mid-sized allognathine with almost completely open umbilicus, larger and more depressed than *C. guiraoanus*.

Description.- Shell dextral, small, fairly thin, very strongly depressed, with very low spire consisting of almost four strongly depressed, rounded, rather rapidly growing whorls, the last half a bit expanding; suture moderately incised; aperture oblique elliptical, downturned and more so behind the peristome, with palatal edge slightly thickened inside, and very small lip, somewhat flaring along the columellar edge; columella slightly thickened, quite continuous with the free lip, and just a little reflected proximally, covering about a fifth of the umbilicus, which is medium sized and clearly perspective, widened and thus eccentric in its last whorl; no noticeable parietal callus; external surface a bit glossy, with a fine sculpture of colabral ridgelets and thin spiral lines, reduced around the umbilical area; very pale straw yellowish with five thin, nearly discontinuous chocolate to sienna bands, the lower two wider; peristome porcelain white.

Type material. - Spain, Andalucía, Jaén province, Sierra de Cazorla county, Cazorla, Cerrada del Utrero, 37° 55' N, 2° 55' W, ca. 950 m; 24.iv.2013, J. Liétor col. Holotype CRA-15574-1, diameter 26.5 mm (Fig. 22); and 1 paratype (CRA-15574-2).

Distribution.- *Cazorliberus bovistrini* sp. nov. appears to be restricted to the southernmost area of the Sierra de Cazorla (Fig. 16).

Habitat.- The new species lives in limestone areas at middle elevation, under Mediterranean forest.

Etymology.- The species name is an adjective, genitive of “bos trinus”, a young bull between two and three years old. This is called “utrero” in Spanish and gives name to the type locality: “the young bull’s pen”, a narrow valley enclosed by high walls.

http://zoobank.org/NomenclaturalActs/60F0FDE8-BD51-4D5A-A825-FFDD055B557F

Remarks.- The distribution of this species seems quite restricted, but should be better assessed.

***Cazorliberus cazorlensis* spec. nov.**

Diagnosis. - A small allognathine with partially closed umbilicus (more so than its congenerics), and dark coloration with obscure bands.

Description.- Shell dextral, small, fairly thin, strongly depressed, with low domiform spire consisting of just $3^1/_2$ depressed, rounded, rather rapidly growing whorls, the last half a bit expanding; suture moderately incised; aperture oblique, elongate elliptical, slightly downturned, with palatal edge slightly thickened inside, and small lip, reflected along the columellar edge and more strongly so over the umbilicus, about a third of which it covers; columella slightly thickened, well continuous with the free lip; umbilicus small, a bit perspective, widened and thus eccentric in its last half whorl; no parietal callus; external surface a bit glossy, with a fine sculpture of colabral ridgelets and thin spiral lines, reduced around the umbilical area; pale straw yellowish with five thin, broken, sienna to saddle brown bands, intercepted by much paler marmorations, mostly on the upper surface; peristome porcelain white with a very pale violet tinge, especially along the internal side of the columella.

Type material. - Spain, Andalucía, Jaén province, Sierra de Cazorla county, La Iruela, 37° 55' N, 2° 59' W, ca. 920 m, under live oak litter; 2.vii.2011, J. Liétor col. Holotype CRA-15578-1, diameter 22.5 mm (Fig. 23); and 2 paratypes (CRA-15578-2 and 3).

Distribution.- *Cazorliberus cazorlensis* sp. nov. is found at the westernmost part of the Sierra de Cazorla (Fig. 16).

Habitat.- The new species lives in limestone areas at middle elevation, under Mediterranean forest.

Etymology.- The species name is an adjective referring to the narrow range of this species, apparently restricted to the westernmost Sierra de Cazorla.

http://zoobank.org/NomenclaturalActs/0E0A366C-7667-4BFD-8C87-8AA9CD5447FA

Remarks.- The range of this species seems decidedly smaller than that of *C. guiraoanus*, but its limits remain to be assessed.

The revised taxonomy of the Allognathini is thus summarized (only native Iberian species mentioned; species-level taxa having neotypes and lectotypes designated herein are indicated by N or L, respectively)):

Family Helicidae Rafinesque, 1815
Subfamily Helicinae Rafinesque, 1815
Tribe Allognathini Westerlund, 1903

Pseudotacheina **subtrib. nov.**
Pseudotachea
P. splendida (Draparnaud, 1801)
(= *Helix s.* var. *penchinatia* Moquin-Tandon, 1855)
(= *H. s.* var. *serresia* Moquin-Tandon, 1855)
(= *H. s.* var. *dugesia* Moquin-Tandon, 1855)
(= *H. s.* var. *tersonia* Moquin-Tandon, 1855)
(= *H. s.* var. *webbia* Moquin-Tandon, 1855)
(= *H. s.* var. *sarratia* Moquin-Tandon, 1855)
(= *H. s.* var. *dunalia* Moquin-Tandon, 1855)
(= *H. s.* var. *tournalia* Moquin-Tandon, 1855)
(= *H. s.* var. *roseolabiata* Rossmässler, 1839)

(= *H. s.* var. *philbertia* Moquin-Tandon, 1855)
(= *H. s.* var. *gouania* Moquin-Tandon, 1855)
(= *H. s.* var. *dumasta* Moquin-Tandon, 1855)
(= *H. s.* var. *sphaecelata* Moquin-Tandon, 1855)
(= *H. s.* var. *microstoma* Salvañá, 1887, non *Helix microstoma* Lamarck, 1822)
(= *Helix cossoni* Letourneux, 1877)
(= *Helix calaeca* Bourguignat in Fagot, 1887)

Herculiberina **subtrib. nov.**
Herculiberus **gen. nov.**
H. lituratus (Pfeiffer, 1853)
(= *Helix coquandi* (Morelet, 1854)
(= *Helix liturata* var. *ellioti* Kobelt, 1883)
(= *Helix l.* var. *tarifensis* Kobelt, 1903, non *H. tarifensis* Bourguignat, 1880)

Iberina **subtrib. nov.**
Iberus Montfort, 1810
I. (Labioiberus) **subgen. nov.**
I. (L.) campesinus (Rossmässler, 1854)
I. (L.) c. campesinus (Rossmässler, 1854)
(= *Helix campesina millarensis* Kobelt, 1910)
(= *Helix gualtierocampesina* Serradell, 1912)
(=*Helix gualteriocampesina* Serradell, 1912, rejected spelling)
I. (L.) c. lorcanus (Rossmässler, 1854)
(= *Helix pseudocampesina* Kobelt, 1910)
I. (L.) c. bastetanus **subspec. nov.**

I. (Carthaginiberus) **subgen. nov.**
I. (C.) carthaginiensis (Schmidt, 1853)
I. (C.) c. carthaginiensis (Schmidt, 1853)
I. (C.) c. posthumus Haas, 1934
(= *Helix alonensis* var. *minima* Schmidt, 1853; non *H. minima* Gmelin, 1791)
(= *I. calaensis* Ahuir, 2013)
(= *I. punicus* Tudela, Liétor, Jódar, Galán-Luque & Jowers, 2024)
I. (C.) bajoi Bourguignat in Servain, 1881 **L**
(= *I. globulosus* Boettger, 1913) **N**

I. (Nazariberus) **subgen. nov.**
I. (N.) rhodopeplus Aguilar-Amat, 1925 **L**
(= *I. sumuntanus* Liétor, Tudela & Jódar, 2024)
I. (N.) turdetanus **spec. nov.**
I. (N.) labiatus Ahuir Galindo, 1989
I. (N.) selambinicus **spec. nov.**

I. (Iberus) Montfort, 1810
(= *Euiberus* Westerlund, 1903)
I. (I.) gualtieranus (Linnaeus, 1758)
(= *H. obversa* Born, 1778) **L**
(=*H. laurenti* Bourguignat, 1870)
(=*I. g. intermedius* C.R. Boettger, 1913)
(= *H. gualtierana umbilicata* Kobelt, 1910)
I. (I.) ornatissimus Cobos, 1980
I. (I.) mariae Cobos, 1980
I. (I.) latissimus **spec. nov.**
(= *I. mariae mariae* f. *macrolabiatus* Liétor, Tudela, Jódar, Galán-Luque & Joers, 2024, unavailable)

I. (Alonensis) García San Nicolás & Alvarado, 1955
(=*Alonensis* García San Nicolás, 1957)

I. (Al.) alonensis (Férussac, 1821) **N**
(=*Helix (Helicogena) alonensis* var. ε Férussac, 1821)

I. (Valentiberus) **subgen. nov.**
I. (V.) alvaradoi García San Nicolás, 1957
(= *H. (Helic.) alonensis* var. *α* Férussac, 1821)
(= *H. (Helic.) alonensis* var. *β* Férussac, 1821)
(= *H. (Helic.) alonensis* var. *γ* Férussac, 1821)
(= *H. (Helic.) alonensis* var. *δ* Férussac, 1821)
I. (Al.) a. alvaradoi García San Nicolás, 1957
I. (Al.) a. turolensis **subspec. nov.**
I. (Al.) a. ilercaonus **subspec. nov.**
(= "*I. carragines* Aguilar-Amat, 1921", inexistent but mentioned by Bank & Luijten, 2015)
I. (Al.) a. quixotei **subspec. nov.**

Hemicyclina **subtrib. nov.**
Idiomela Cockerell, 1921
Lampadia Albers, 1854
Hemicycla Swainson, 1840

Allognathina Westerlund, 1903
Allognathus Pilsbry in Tryon & Pilsbry, 1888
Iberellus Hesse, 1932
Tramuntanicola Altaba, 2022

Tartessiberina **subtrib. nov.**
Angustiberus **gen. nov.**
An. granatinus **nom. nov.**
(= Helix guiraoana var. angustata Rossmässler, 1854, non *Helix angustata* Férussac, 1822)
An. hispanicus (Rossmässler, 1838)
An. maginensis **spec. nov.**

Nescaniberus **gen nov.**
N. cobosi (Ibáñez & Alonso, 1976)

Marmoratus García San Nicolás & Alvarado, 1955
(=*Marmoratus* García San Nicolás, 1957)
M. (Marmoratus) García San Nicolás & Alvarado, 1955
M. (Marmoratus) marmoratus (Férussac, 1821)
M. (M.) m. marmoratus (Férussac, 1821)
(non *Helix marmorata* Gmelin, 1972, nomen oblitum)
(= *Iberus serpentinae* Ahuir Galindo, 2020)
M. (M.) m. partschi (Servain, 1881) **L**
(= *Helix balearica* var. *pulchella* Rossmässler, 1854, non *H. pulchella* Müller, 1774)
M. (M.) m. arundanensis **subspec. nov.**
M. (M.) m. gaditanus **subspec. nov.**
M. (M.) loxanus (Schmidt, 1853)
M. (M.) l. loxanus (Schmidt, 1853)
M. (M.) l. candoni (Ahuir Galindo, 2021)
M. (M.) l. violaceus (Rossmässler, 1854)

M. (Torcaliberus) **subgen. nov.**
M. (T.) rositai (Fez, 1950)
M. (T.) r. rositai (Fez, 1950)
M. (T.) r. gualtieroloxanus (García San Nicolás, 1957)
(= *Iberus gualtieroloxanus* García San Nicolás, 1949, nomen nudum)

Tartessiberus Altaba & Ríos Jiménez, 2022

T. cilbanus Altaba & Ríos Jiménez, 2022

Oretaniina **subtrib. nov.**
Oretanius **gen nov.**
O. alcarazanus (Rossmässler, 1854) **L**
(= *I. giennensis* Liétor, Tudela, Jódar, Jowers & Moreno-Rueda, 2024, unavailable)
(= *I. axarcianus* Liétor, Tudela, Jódar, Jowers & Moreno-Rueda, 2024, unavailable)
(= *I. antikarianus* Liétor, Tudela, Jódar, Jowers & Moreno-Rueda, 2024, unavailable)
O. ortizi (García San Nicolás, 1957)
O. axans **spec. nov.**

Cazorliberus **gen nov.**
C. guiraoanus (Pfeiffer, 1853)
C. bovistrini **spec. nov.**
C. cazorlensis **spec. nov.**

The geographic distribution of Iberian allognathines (Figs. 2, 3, 16) is largely allopatric, with different species of the same tribe rarely occurring together. Also, there is stark contrast between groups comprising narrow-range endemics and others that appear to have undergone wide range expansions.

Discussion

Describing and defining species is an explicit hypothesis of phylogenesis and must be based on various avenues of evidence and implies a significant responsibility (Padial et al., 2010; Hillis, 2019; Wüster et al., 2024). It is thus preferable to follow a conservative approach, avoiding the risk of recognizing entities that do not represent evolutionary lineages (Carstens et al., 2013). At any rate, taxonomy deals with species, not directly with the speciation process (Wheeler, 2020). The species defined herein are morphologically and genetically distinct, but undoubtedly more may be accepted in the future with adequate evidence.

This taxonomic update involves the recognition of 69 taxa of various ranks among the Iberian Allognathini (30 of these new), divided as follows: five subtribes (all new, in addition to the nominotypical and a new one in the archipelagos), nine genera (five new), eight subgenera (five new), 29 species (eight new, plus a new name) and 18 subspecies (six new). This is in stark contrast with unrealistic opinions recognizing as little as one genus with only three species. Far from representing a case of taxonomic inflation (49 taxa are considered synonyms or unavailable), this revision is an explicit recognition of biological diversity. Admittedly, it is incomplete; further research will likely show the need for recognizing additional species-level taxa.

With the advantage of hindsight, the taxonomic history of Iberian allognathines appears to have been unnecessarily complex. It appears that the pioneering work by Rossmässler (1854) was considerably more accurate in his understanding of this group than almost all subsequent workers. And in spite of her particularly complex taxonomic arrangement (including “forms” and “modifications”), and acrimonious criticism (or even overt neglect) by later authors, García San Nicolás (1957) was by far the closest to unraveling the real diversity of Iberian allognathines.

Several European fossils of Miocene and Pliocene age have been revised herein and appear to be only distantly related to allognathines, being very close to, or included in genera of the Thebini that currently occur only in North Africa. The occurrence of *Loxana* in the Miocene of Portugal and *Schlickumia* (very close to *Eremina*) in the Pliocene of southern France point at a complex biogeographic scenario for the diversification of the Helicinae. The Allognathini are restricted to just a small subset of the various terranes and volcanic hotspots involved in the Neogene formation of the Western Mediterranean and Macaronesian region. The suggestion that the Iberian taxa most closely related to the Balearic and Macaronesian clade should have become extinct (Neiber et al., 2021) is an unwarranted hypothesis, as these clades are nested within the Iberian radiation, and there is no need to assume that the only paleogeographic connection between both archipelagos must have been through southern Iberia. Besides, the Balearic *Iberellus* existed already in the Lower Pliocene (Juárez-Ruiz & Altaba, 2022), and surely

diverged earlier from *Iberus*; this fact further contradicts any hypothesized anagenetic relationship between *Schlickumia* and *Iberus.*

A taxonomic backbone should prove useful to guide insights into the systematics, evolution and biogeography of this extraordinary animal group. Several questions probably deserve in-depth examination. Why is it so uncommon to find sympatric allognathine species? Why do some groups have very narrow ranges, but others have expanded over much larger areas? What has been the tribe's historical biogeography in the dynamic Alboran area? Why do shell shapes have evolved iteratively, but not in all lineages? What are the selective pressures leading to enlarged peristomes, keeled peripheries and various chromatic patterns? Why do some lineages evolve into truly gigantic sizes, but others remain small, or even get smaller? To what extent has introgression from translocated species affected native populations? Many more questions remain open; they can now be addressed with a taxonomy that reflects the diversification of allognathines.

A solid taxonomy should also provide a solid foundation for the effective conservation of allognathine land snails. These are heavily harvested animals, and their habitats are being destroyed at an alarming rate in wide areas. As a consequence, many populations are endangered, or have already disappeared. Clear assessments of conservation status for each distinct taxon should promote reasonable, tangible protection.

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Table 1. Partial cyochrome-oxidase I (COI) sequences used in the phylogenetic analysis of Iberian allognathines.

a) Species names according to the revised taxonomy presented herein, and Altaba (2022b).
b) 1: Fiorentino et al (2016), 2: Cadahia et al. (2014); 3: Blacket et al. (2016); 4: Grindon & Davison (2013); 5: Groenenberg et al. (2011); 6: Elejalde et al. (2008a); 7: Neiber et al. (2021); 8: Neiber et al. (2011); 9: Chueca et al (2015); 10: Elejalde et al. (2008b); 11: Jowers et al. (2024).

species[a]	GenBank accession number	ref.[b]
Helix (H.) pomatia Linnaeus, 1758	KU869801	1
Eobania vermiculata (Müller, 1774)	KF596895	2
Cornu apersum (Müller, 1774)	KX679316	3
Cepaea nemoralis (Linnaeus, 1758)	KC955095	4
Otala punctata (Müller, 1774)	JF717805	5
Otala lactea (Müller, 1774)	AY937263	6
Pseudotachea splendida (Draparnaud, 1801)	AY937265	6
Herculiberus lituratus (Pfeiffer, 1853)	MW803166	7
Idiomela subplicata (Sowerby I, 1824)	MW803162	7
Lampadia webbiana (Lowe, 1831)	MW803165	7
Hemicycla (Adiverticula) mascaensis Alonso & Ibáñez, 1988	GU598222	8
Hemicycla (H.) berkeleii (Lowe, 1861)	GU598229	8
Allognathus graellsianus (Pfeiffer, 1848)	KM592535	9
Tramuntanicola culminalis Altaba, 2022	KM592554	9
Iberellus (I.) companyonii (Companyo, 1837)	KM592561	9
Iberellus (I.) minoricensis (Mittre, 1842)	DQ822174	10
Iberellus (Nesiberus) pythiusensis (Bofill & Aguilar-Amat, 1924)	KM592577	9
Iberellus (Nesiberus) pythiusensis (Bofill & Aguilar-Amat, 1924)	KM592574	9
Iberus (Labioiberus) campesinus campesinus (Rossmässler, 1854)	DQ822164	10
Iberus (Labioiberus) campesinus campesinus (Rossmässler, 1854)	DQ822158	10
Iberus (Labioiberus) campesinus campesinus (Rossmässler, 1854)	AY928552	10

Iberus (Labioiberus) campesinus lorcanus (Rossmässler, 1854)	DQ822167	10
Iberus (Labioiberus) campesinus lorcanus (Rossmässler, 1854)	DQ822168	10
Iberus (Labioiberus) campesinus lorcanus (Rossmässler, 1854)	DQ822157	10
Iberus (Labioiberus) campesinus bastetanus subspec. nov.	DQ822156	10
Iberus (Labioiberus) campesinus bastetanus subspec. nov.	DQ822155	10
Iberus (Carthaginiberus) carthaginiensis carthaginiensis (Schmidt, 1853)	DQ822162	10
Iberus (Carthaginiberus) carthaginiensis carthaginiensis (Schmidt, 1853)	DQ822161	10
Iberus (Carthaginiberus) carthaginiensis carthaginiensis (Schmidt, 1853)	DQ822159	10
Iberus (Carthaginiberus) carthaginiensis carthaginiensis (Schmidt, 1853)	DQ822160	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822131	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822127	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822126	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822130	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822163	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822128	10
Iberus (Carthaginiberus) bajoi (Bourguignat in Servain, 1881)	DQ822129	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) rhodopeplus Aguilar-Amat, 1925	DQ822150	10
Iberus (Nazariberus) selambinicus spec. nov.	DQ822149	10
Iberus (Nazariberus) selambinicus spec. nov.	AY928500	10
Iberus (Nazariberus) selambinicus spec. nov.	AY928561	10
Iberus (Nazariberus) selambinicus spec. nov.	AY928563	10

Iberus (Nazariberus) selambinicus spec. nov.	AY928562	10
Iberus (Nazariberus) turdetanus spec. nov.	AY928565	10
Iberus (Nazariberus) turdetanus spec. nov.	AY928564	10
Iberus (Nazariberus) turdetanus spec. nov.	AY928559	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928576	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928570	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928578	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928569	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928568	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928574	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	AY928572	10
Iberus (Iberus) gualtieranus (Linnaeus, 1758)	DQ822125	10
Iberus (Iberus) mariae Cobos, 1980	DQ822170	10
Iberus (Iberus) mariae Cobos, 1980	DQ822169	10
Iberus (Iberus) mariae Cobos, 1980	AY928556	10
Iberus (Iberus) ornatissimus Cobos, 1980	DQ822173	10
Iberus (Iberus) ornatissimus Cobos, 1980	AY928558	10
Iberus (Iberus) ornatissimus Cobos, 1980	DQ822172	10
Iberus (Iberus) ornatissimus Cobos, 1980	DQ822171	10
Iberus (Alonensiss) alonensis (Férussac, 1821)	DQ822135	10
Iberus (Alonensiss) alonensis (Férussac, 1821)	DQ822134	10
Iberus (Alonensiss) alonensis (Férussac, 1821)	DQ822132	10
Iberus (Alonensiss) alonensis (Férussac, 1821)	DQ822133	10
Iberus (Valentiberus) alvaradoi ilercaonus subspec. nov.	DQ822141	10
Iberus (Valentiberus) alvaradoi ilercaonus subspec. nov.	DQ822214	10
Iberus (Valentiberus) alvaradoi ilercaonus subspec. nov.	DQ822140	10
Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822146	10

Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822147	10
Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822145	10
Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822140	10
Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822144	10
Iberus (Valentiberus) alvaradoi alvaradoi García San Nicolás, 1957	DQ822143	10
Iberus (Valentiberus) alvaradoi quixotei subspec. nov.	DQ822138	10
Iberus (Valentiberus) alvaradoi quixotei subspec. nov.	DQ822136	10
Iberus (Valentiberus) alvaradoi quixotei subspec. nov.	DQ822139	10
IIberus (Valentiberus) alvaradoi quixotei subspec. nov.	DQ822137	10
Angustiberus hispanicus (Rossmässler, 1838)	EF440241	6
Angustiberus hispanicus (Rossmässler, 1838)	EF440242	6
Angustiberus granatinus nom. nov.	EF440240	6
Angustiberus granatinus nom. nov.	EF440239	6
Angustiberus maginensis spec. nov.	EF440238	6
Nescaniberus cobosi (Ibáñez & Alonso, 1976)	EF440243	6
Nescaniberus cobosi (Ibáñez & Alonso, 1976)	EF440244	6
Nescaniberus cobosi (Ibáñez & Alonso, 1976)	EF440246	6
Nescaniberus cobosi (Ibáñez & Alonso, 1976)	EF440245	6
Marmoratus (Torcaliberus) rositai (Fez, 1950)	EF440285	6
Marmoratus (Torcaliberus) rositai (Fez, 1950)	EF440258	6
Marmoratus (Torcaliberus) rositai (Fez, 1950	EF440256	6
Marmoratus (Torcaliberus) rositai (Fez, 1950)	EF440257	6
Marmoratus (Torcaliberus) rositai (Fez, 1950)	EF440286	6
Marmoratus (Torcaliberus) rositai (Fez, 1950	EF440287	6
Marmoratus (Marmoratus) loxanus loxanus (Schmidt, 1853)	EF440259	6
Marmoratus (Marmoratus) loxanus violaceus (Rossmässler, 1854)	EF440260	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440266	6

Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440248	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440247	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440268	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440267	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440269	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440270	6
Marmoratus (Marmoratus) marmoratus partschi (Servain, 1881)	EF440271	6
Marmoratus (Marmoratus) marmoratus arundanensis subspec. nov.	EF440261	6
Marmoratus (Marmoratus) marmoratus marmoratus (Férussac, 1821)	EF440262	6
Marmoratus (Marmoratus) marmoratus marmoratus (Férussac, 1821)	EF440263	6
Marmoratus (Marmoratus) marmoratus marmoratus (Férussac, 1821)	EF440265	6
Marmoratus (Marmoratus) marmoratus marmoratus (Férussac, 1821)	EF440264	6
Tartessiberus cilbanus Altaba & Ríos Jiménez, 2022	PP384386	11
Tartessiberus cilbanus Altaba & Ríos Jiménez, 2022	PP384388	11
Oretanius ortizi (García San Nicolás, 1957)	EF440284	6
Oretanius ortizi (García San Nicolás, 1957)	EF440283	6
Oretanius ortizi (García San Nicolás, 1957)	EF440282	6
Oretanius ortizi (García San Nicolás, 1957)	EF440281	6
Oretanius ortizi (García San Nicolás, 1957)	EF440280	6
Oretanius ortizi (García San Nicolás, 1957)	EF440276	6
Oretanius ortizi (García San Nicolás, 1957)	EF440277	6
Oretanius ortizi (García San Nicolás, 1957)	EF440279	6
Oretanius ortizi (García San Nicolás, 1957)	EF440278	6
Oretanius alcarazanus (Rossmässler, 1854)	EF440274	6
Oretanius alcarazanus (Rossmässler, 1854)	EF440275	6
Oretanius alcarazanus (Rossmässler, 1854)	EF440273	6
Oretanius alcarazanus (Rossmässler, 1854)	EF440272	6

Oretanius axans spec. nov.	EF440255	6
Cazorliberus cazorlensis spec. nov.	EF440251	6
Cazorliberus cazorlensis spec. nov.	EF440252	6
Cazorliberus cazorlensis spec. nov.	EF440250	6
Cazorliberus bovistrini spec. nov.	EF440254	6
Cazorliberus bovistrini spec. nov.	EF440253	6
Cazorliberus guiraoanus (Pfeiffer, 1853)	EF440249	6

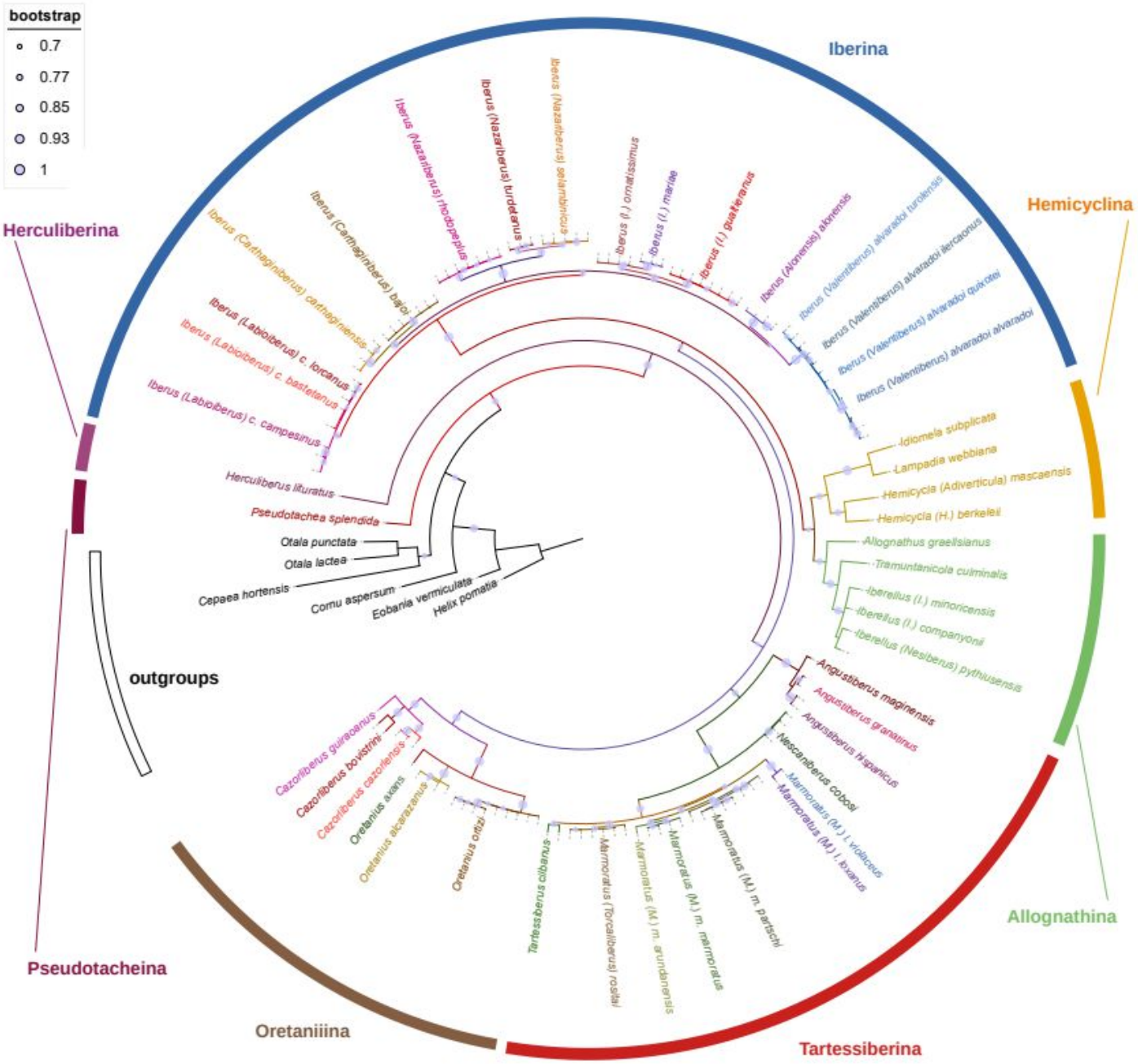

Fig. 1. Phylogenetic tree of Allognathini based on COI mtDNA sequences (Table 1) and estimated with the maximum-likelihood algorithm PhyML. Outgroup species are shown in black. Branch support (SH-like aLRT) is indicated by size of blue dots; nodes with support less than 0.5 collapsed.

Fig. 2. Geographical distribution of the Iberian allognathines belonging to tribes Pseudotacheina and Herculiberina.

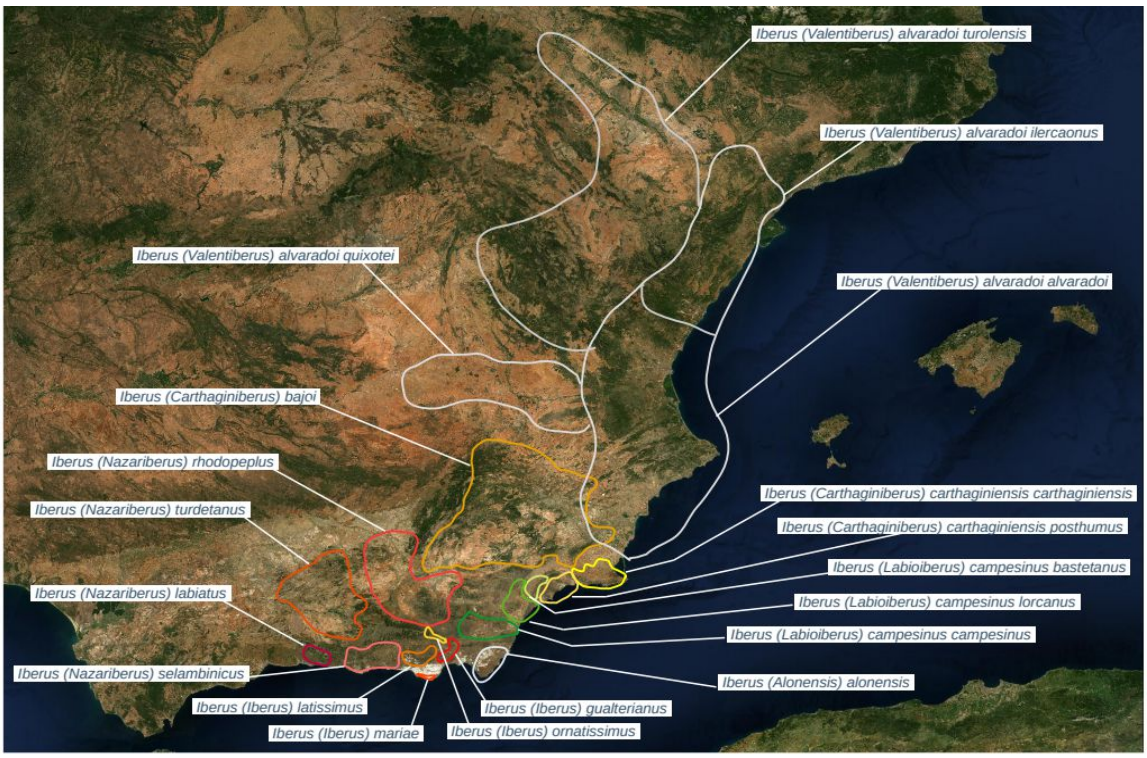

Fig. 3. Geographical distribution of the Iberian allognathines belonging to tribe Iberina.

Fig. 4. Shell of *Iberus (I.) latissimus* sp. nov. Dalías (Almería, Andalusia). Holotype, CRA-23604. Maximum diameter is 38.8 mm.

Fig. 5. Shell of *Iberus (Labioiberus) campesinus bastetanus* subsp. nov. Sierra de la Carrasquilla (Murcia). Holotype, CRA-15613-1. Maximum diameter is 35.3 mm.

Fig. 6. Lectotype of *Helix bajoi* Bourguignat in Servain, 1881 [now *Iberus (Carthaginiberus) bajoi* (Bourguignat in Servain, 1881)]. In flood debris of the Segura River near Murcia. Maximum diameter is 30.9 mm. Muséum d'Histoire naturelle de Genève (Switzerland), catalogue number MHNG-MOLL-118673. Photographs courtesy of Estée Bochud and Eike Neubert, through Emmanuel Tardy (Muséum d'Histoire naturelle de Genève).

Fig 7. Live neotype of *Iberus gualtieranus globulosus* Boettger, 1913 [= *Iberus (Carthaginiberus) bajoi* (Bourguignat in Servain, 1881)] on karstified limestone in its natural habitat. Vélez Blanco (Almería, Andalusia); 20-x-2023. CRA-23646-1. Maximum diameter of shell is 32.5 mm.

Fig. 8. Shell of the neotype of *Iberus gualtieranus globulosus* Boettger, 1913 [= *Iberus (Carthaginiberus) bajoi* (Bourguignat in Servain, 1881)]. Vélez Blanco (Almería, Andalusia). CRA-23646-1. Maximum diameter is 32.5 mm.

Fig. 9. Lectotype of *Iberus (Nazariberus) rhodopeplus* Aguilar-Amat, 1925. El Muruche (Jaén Andalucía). Museu de Ciències Naturals de Barcelona (Catalonia), catalogue number MZB-89-2580. Photographs courtesy of Museu de Ciències Naturals de Barcelona, ©MCNB-Sergi Gago, license CC BY-NC. Maximum diameter is 36.2 mm.

Fig. 10. Shell of *Iberus (Nazariberus) turdetanus* sp. nov. La Mella (Jaén, Andalusia). Holotype, CRA-23566-1. Maximum diameter is 34.0 mm.

Fig. 11. Shell of *Iberus (Nazariberus) selambinicus* sp. nov. Tajo de la Virgen (Granada, Andalusia). Holotype, CRA-15612-1. Maximum diameter is 40.0 mm.

Fig. 12. Shell of the neotype of *Helix alonensis* Férussac, 1821 [*Iberus (Alonensis) alonensis* Férussac, 1821]. Las Negras (Almería, Andalusia). CRA-16202-1. Maximum diameter is 36.2 mm.

Fig. 13. Shell of *Iberus (Valentiberus) alvaradoi turolensis* subsp. nov. Orrios (Teruel, Aragón). Holotype, CRA-2617-1. Maximum diameter is 29.6 mm.

Fig. 14. Shell of *Iberus (Valentiberus) alvaradoi ilercaonus* subsp. nov. Pinyera de Marcel·la (Ribera d'Ebre, Catalunya). Holotype, CRA-19365-2. Maximum diameter is 29.2 mm.

Fig. 15. Shell of *Iberus (Valentiberus) alvaradoi quixotei* subsp. nov. Ruidera (Ciudad Real, Castilla-La Mancha). Holotype, CRA-15746. Maximum diameter is 26.4 mm.

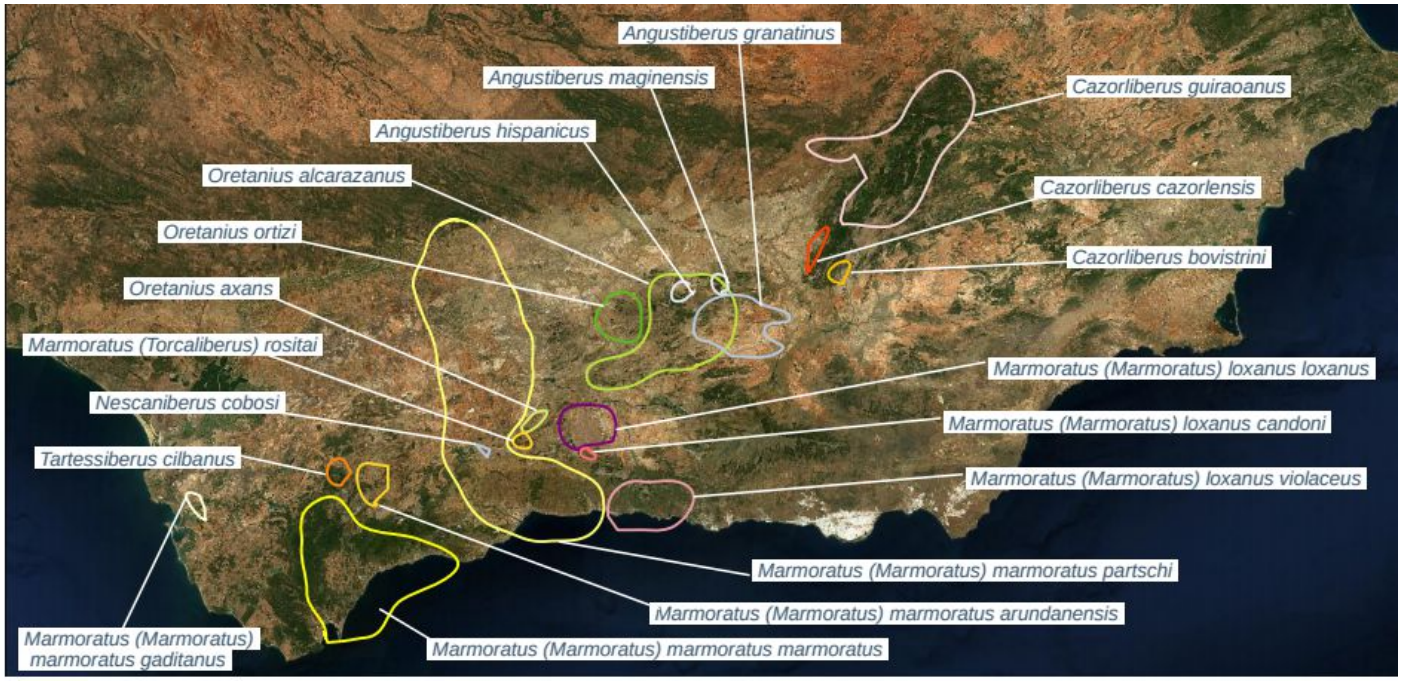

Fig. 16. Geographical distribution of the Iberian allognathines belonging to tribes Tartessiberina and Oretaniina.

Fig. 17. Shell of *Angustiberus maginensis* sp. nov. Torreón de Cuadros (Jaén, Andalusia). Holotype, CRA-15568-1. Maximum diameter is 22.2 mm.

Fig. 18. Live *Marmoratus (M.) marmoratus partschi* on an overhanging rock wall in its natural habitat. Caminito del Rey (Málaga, Andalusia); 20-x-2023. CRA-24102-1.

Fig. 19. Shell of *Marmoratus (M.) marmoratus arundanensis* subsp. nov. Tajo de Ronda (Málaga, Andalusia). Holotype, CRA-23831-1. Maximum diameter is 20.8 mm.

Fig. 20. Shell of *Marmoratus (M.) marmoratus gaditanus* subsp. nov. Sierra de San Cristóbal (Cádiz, Andalusia). Holotype, CRA-15593-1. Maximum diameter is 17.9 mm.

Fig. 21. Shell of *Oretanius axans* sp. nov. Near Torcal de Antequera (Málaga, Andalusia). Holotype, CRA-23581-1. Maximum diameter is 26.7 mm.

Fig. 22. Shell of *Cazorliberus bovistrini* sp. nov. Cerrada del Utrero (Jaén, Andalusia). Holotype, CRA-15574-1. Maximum diameter is 26.5 mm.

Fig. 23. Shell of *Cazorliberus cazorlensis* sp. nov. La Iruela (Jaén, Andalusia). Holotype, CRA-15578-1. Maximum diameter is 22.5 mm.

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