Clarification of the distribution, conchological diversity, and taxonomic status of the Iberian snail *Iberus globulosus* C.R. Boettger, 1913 (Gastropoda: Stylommatophora: Helicidae)

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Abstract. The taxonomic status of *Iberus globulosus* has been unsatisfactorily resolved since its original description, but in 2008 a molecular phylogenetic study of the genus *Iberus* suggested that it could be a valid species. However, limited information on both its geographic distribution and its conchological variability has made it difficult to properly delineate the species. Our exhaustive sampling throughout the potential area of its geographic distribution and the morphological study herein, together with pre-existing genetic evidence, allow us to confirm the validity of *I. globulosus*. Consequently, we improve the characterization of *I. globulosus* by redescribing it. Additionally, we provide information on the potential for hybridization among *I. globulosus* and geographically and phylogenetically close congeneric species.

Key words. *Iberus alonensis, Iberus carthaginiensis, Iberus campesinus*, integrative taxonomy, Andalusia, Spain

Introduction

In the scientific literature, the most cited taxon of the Iberian endemic genus *Iberus* Montfort, 1810 is likely *Iberus alonensis* (A. Férussac, 1821). This is largely because it is the most widely distributed *Iberus* species, extending beyond the regions of Andalusia and Murcia along the Mediterranean coast to the north-eastern half of the Iberian Peninsula (Robles & Martínez-Ortí 2009; Alba *et al.* 2011; Chueca *et al.* 2018; Cadevall *et al.* 2020; Zaldívar-Ezquerro 2022). A rather wide spectrum of *Iberus* populations, which are characterized by their 30–40 mm globose shells, have been identified as *I. alonensis* (e.g. Aguilar Amat 1925, 1930; García San Nicolás 1957; Arrébola 1995; Elejalde *et al.* 2005; Liétor 2014; Neiber *et al.* 2021). However, these populations—the *I. alonensis* morphospecies—do not belong to a single biological species, and

consequently, species delineation in this morphospecies has been controversial, resulting in great uncertainty of synonymy (Martínez-Ortí & Robles 2012).

Elejalde *et al.* (2008a) have partially clarified the taxonomy of the *I. alonensis* morphospecies by identifying two genetically well-defined lineages in the southern Spanish region of Andalusia; these were provisionally named *I. alonensis*-like 01 and *I. alonensis*-like 02. However, more research is needed to resolve the species-level taxonomy of the genus, as suggested by Bank & Luijten (2014), especially given the high proportion of cryptic species in *Iberus* (Elejalde *et al.* 2008a; Moreno-Rueda 2012; Liétor *et al.* 2024; Liétor *et al.* submitted).

Among the taxa contained in the *I. alonensis* morphospecies is *I. globulosus*, which was described as a subspecies of *I. gualtieranus* (Linnaeus, 1758) from an ambiguous type locality, "Um Almeria", translated as "around Almeria" (Boettger

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1913). Boettger's description of *I. gualtieranus globulosus* is certainly confusing. Although Boettger was familiar with forms intermediate between *I. gualtieranus* and *I. alonensis*, he placed *I. gualtieranus globulosus* at the end of a transitional series starting from *I. gualtieranus alonensis* (Appendix Fig. A1A) without suspecting that intermediate forms might be involved. Interestingly, none of the shells in Boettger's series would be currently classified as *I. alonensis* (Appendix Fig. A1B). The specimen of *I. globulosus* from Boettger's series shows the typical features of hybrid populations between *I. globulosus* and *I. alonensis*-like 02 (Appendix Fig. A1C).

After studying five specimens from Almería Province, García San Nicolás (1957) considered *I. globulosus* to be a valid species. However, various authors (e.g. Puente 1994) have more recently assigned it to a particular morphotype of *I. alonensis*, thus with no taxonomic validity. We have substantial doubts that the shells examined by García San Nicolás correspond to Boettger's *I. gualtieranus globulosus*, since the traits of the shells she illustrated suggest that the material could have been misidentified or at least belong to an intermediate form (Appendix Fig. A2).

The first complete phylogeny of *Iberus* (Elejalde *et al.* 2008a) showed a clade (named A2) grouping together populations with *I. alonensis*-type shells. This clade was divided into two divergent subclades, one (named A2b) including several topotypes of *I. carthaginiensis* (Rossmässler, 1853), and another (named A2a) including a topotype of *I. globulosus*. Presumably, based on this duality of sister lineages but without providing any additional argument, Bank & Luijten (2014) defined a new subspecies, as *I. carthaginiensis globulosus*, for Elejalde *et al.*'s subclade A2a, which is the currently accepted name for this taxon in MolluscaBase (2024). However, Bank & Luijten's (2014) taxonomic assignment does not agree with Elejalde *et al.*'s conclusion, which is that subclade A2a might be considered an operational taxonomic unit under the name *I. globulosus*. Indeed, Neiber *et al.* (2021) in their phylogenetic review of the Helicidae of Macaronesia and the Balearic Islands, presented *I. globulosus* as a valid species. The lack of sufficient information on the geographical distribution and morphological variation of subclade A2a populations prevented Elejalde *et al.* from formally redescribing *I. globulosus*.

The aim of the present work is to clarify the taxonomic status of the lineage traditionally known as *I. globulosus* using an integrative approach, by combining systematic sampling of the taxon throughout its potential geographic distribution, morphometric analysis of a large number of shells, and molecular evidence from the literature.

Materials and Methods

Field sampling and mapping of populations of *Iberus*

Given the controversy surrounding the geographic distribution and the diversity of morphotypes associated with the name *I. globulosus*, we undertook intensive sampling throughout the south-eastern part of the Iberian Peninsula where this species is typically considered to occur. Our sampling program covered the eastern provinces of Andalusia (Granada, Jaén, and Almería), the region of Murcia, and the provinces of Alicante (Valencian Community) and Albacete (Castilla la Mancha region).

Our dense network of sampling sites allowed us to inventory the presumed populations of *I. globulosus* and tentatively also those of other *Iberus* taxa to which *I. globulosus* may be phylogenetically (P), geographically (G), or morphologically (M) related:

- **I. alonensis** (G, M): this species presumably occupies the coastal strip east of the geographic distribution of *I. globulosus* (Tudela *et al.* submitted). The shells of *I. globulosus* and *I. alonensis* have often been confused.
- **I. alonensis-like 02** (*sensu* Elejalde *et al.* 2008a) (G, M): it likely inhabits areas to the west of *I. globulosus* (Elejalde *et al.* 2008a). Since its distribution is very extensive, reaching the western part of the province of Málaga (Torres-Alba 2010), in this study we have only considered the easternmost populations of this taxon.
- **I. campesinus** (L. Pfeiffer, 1846) (P, G): Elejalde *et al.* (2008a) placed *I. campesinus* and *I. globulosus* in phylogenetically close clades. *Iberus campesinus* occurs south of *I. globulosus* (García S. Nicolás 1957).
- **I. carthaginiensis** (P, G): following Elejalde *et al.* (2008a), *I. globulosus* and *I. carthaginiensis* are sister lineages and have close geographic distributions.

Figure 1 shows photographs of representative specimens of the species addressed in this work.

Although populations of *I. guiraoanus* (L. Pfeiffer, 1853) are located just west of the expected distribution of *I. globulosus* (Ruiz-Ruiz *et al.* 2006), we excluded it from this study, since its phylogenetic position according to Elejalde *et al.* (2008b) and shell morphology (Liétor 2014) are quite divergent from *I. globulosus*. Although Elejalde *et al.* (2008a) assigned *I. gualtieranus* to a clade phylogenetically close to *I. globulosus*, we also excluded this species because of the pronounced morphological differences between *I. gualtieranus* and *I. globulosus* and the long distance (*c.* 60 km) between their closest populations.
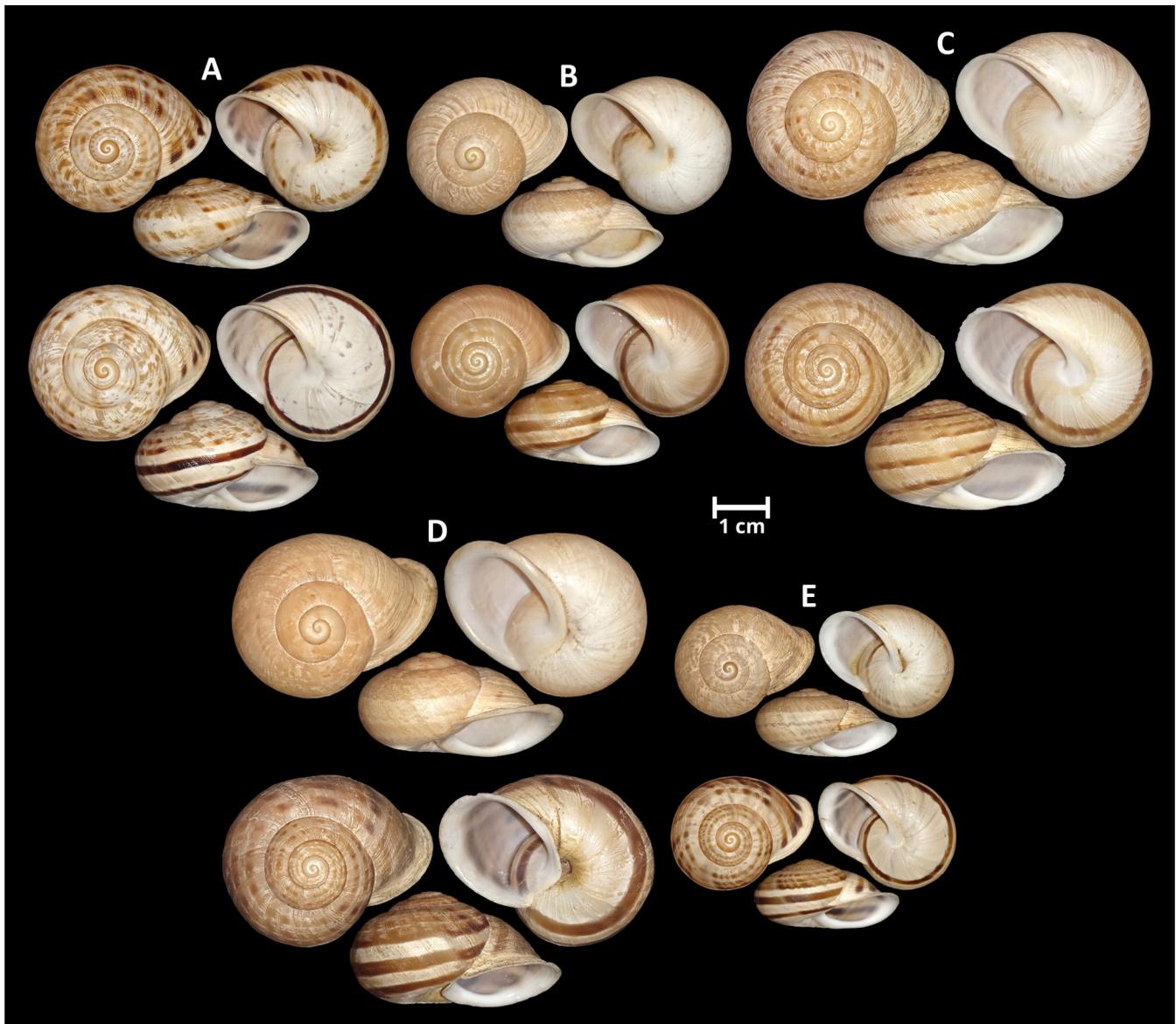
Figure 1. Representative shells of the two common morphotypes (discontinuous and continuous bands) of the five species examined in this work. **A**, *Iberus globulosus* (Albacete Province). **B**, *I. alonensis* (Murcia Province). **C**, *I. alonensis*-like 02 (Almería Province). **D**, *I. campesinus* (Almería Province). **E**, *I. carthaginiensis* (Murcia Province).

We planned the sampling by consulting the specialised geological literature to determine areas having calcareous or, at least, sedimentary lithology—the need for lithologies that provide adequate levels of calcium to form the shells of land snails is widely known (Fournié & Chétail 1984). We also considered the existence of undisturbed mountain karst habitats, and our own prior knowledge and field experience.

Although priority was given to sampling sites which were accessible by road, sites on long routes (>10 km) on foot were also sampled. We recorded the geographical coordi-nates and the names of the localities visited, photographed habitats and live animals, and collected series of empty shells of the studied species. The shells in best condition were cleaned, and we photographed some of these for the figures presented here.

Morphometric shell analysis

All specimens collected in the field, including sun-bleached and subfossil shells, were measured for our morphometric study. Altogether, 1,509 shells attributable to the typical morphotypes for each species were measured: 286 for *I.*

globulosus, 357 for *I. alonensis,* 310 for *I. alonensis*-like 02, 245 for *I. campesinus,* and 311 for *I. carthaginiensis.* Additionally, 363 shells tentatively classified as forms intermediate between *I. globulosus* and *I. alonensis*-like 02 were included in our morphometric analysis, with the aim of identifying morphological discrepancies between the typical specimens of the nominate species and potential hybrids. Our methods to obtain morphometric measurements of shells follow Jowers *et al.* (2024).

Statistical comparisons between morphometric measurements were carried out with ANOVA tests when the variables were homoscedastic and normally distributed, or otherwise used the non-parametric Kruskal–Wallis test. In addition, two principal component analyses (PCA) were carried out, the first to determine the clustering of the populations of taxa along the morphospace defined by the set of 11 morphometric indicators, and the second to evaluate the morphological divergence of *I. globulosus* and *I. alonensis*-like 02 shells with respect to shells tentatively classified as intermediate.

Genitalia

As we discuss later, several studies have reported hybridization within the genus *Iberus* (Moreno-Rueda 2006; Rodríguez-Perochena 2006; Elejalde *et al.* 2008b; Martínez-Ortí & Robles 2012; Liétor 2014; Jowers *et al.* 2024), which we have confirmed by our own intensive sampling (unpublished data). Therefore, there is sufficient evidence that genital anatomy is not taxonomically relevant in *Iberus.* Indeed, the genus *Tartessiberus* Altaba & Ríos-Jiménez, 2021 was based solely on anatomical and radular morphology, but subsequent molecular analyses have confirmed its synonymization with *Iberus* (Jowers *et al.* 2024).

RESULTS

Molecular evidence

The genetic distances obtained by Elejalde *et al.* (2008a) between the subclades A2b (*Iberus carthaginiensis*) and A2a (the lineage attributed to *I. globulosus*) ranged between 5.89% and 7.63% for the mitochondrial cytochrome c oxidase subunit I gene (COI) and between 3.17 and 3.46 % for the mitochondrial ribosomal RNA gene (16S rRNA). The genetic distances between the clade A2 (A2a + A2b) and clade G1 (*I. gualtieranus*) were 8.92–11.31% for the COI gene and 3.97–6.88% for the 16S rRNA gene. The distances between the clades A2 and C3 (*I. campesinus*) were 8.12–10.67% for the COI and 3.98–6.92% for the 16S rRNA.

Geographical evidence

Our sampling network included 253 sampling sites over 4.7 million hectares (Fig. 2). At 19 sites in the easternmost part of our study area, we found *I. alonensis.* To the south of these sites and to the west of the city of Cartagena, 19 sites had *I. carthaginiensis.* Along the westernmost coastal strip of the province of Murcia and in the easternmost part of the province of Almería, *I. campesinus* was found in 38 sites. Where *I. carthaginiensis* and *I. campesinus* come into contact, we found four populations having intermediate conchological traits between these species. In the western part of our study area, *I. alonensis*-like 02 was present at 71 sites, and populations with shells intermediate with neighbouring taxa were found in another 17 sites.

The locations of samples sequenced by Elejalde *et al.* (2008a) were included in our study to allow us to better understand the limits of the distribution of *I. globulosus* and its contact with other congeneric taxa (Fig. 2). We assigned *I. globulosus* to 39 sites within the provinces of Granada, Albacete, and Murcia. Further south, another 46 sampling points had shells with traits intermediate between *I. globulosus* and other neighbouring taxa. We note that embedded among these intermediate populations in this southern area were several sites with typical *I. globulosus* (Table 1). The site with *I. globulosus* and intermediate populations covered 42% of the study area.

Iberus globulosus is distributed over approximately 2 million hectares. Liétor *et al.* (in press) estimated an area of *c.* 800,000 ha for *I. marmoratus marmoratus* (A. Férussac, 1821), the second most widely distributed *Iberus* species after *I. alonensis.* Based on our new data, the rank of second most widespread species should now go to *I. globulosus.*

Morphological evidence

Iberus globulosus has a well-defined morphological identity, as shown in our morphometric comparison (Table 2). Shells of *I. globulosus* are larger, both in terms of shell length and area, and taller than those of *I. alonensis* and *I. carthaginiensis,* but they are smaller than those of *I. alonensis*-like 02 and *I. campesinus.* In addition, *I. globulosus* is more globose than *I. campesinus* and *I. carthaginiensis,* but less globose than *I. alonensis*-like 02. *Iberus alonensis*-like 02 and *I. globulosus* have the most circular shells (ratio between major and minor shell diameters closest to 1). Only *I. campesinus* has a more circular peristome than *I. globulosus.* The shell of *I. globulosus* has the smallest peristome in proportion to the whole area of the shell.

These morphological differences are captured by the first two principal components (PCs) of our PCA which repre-
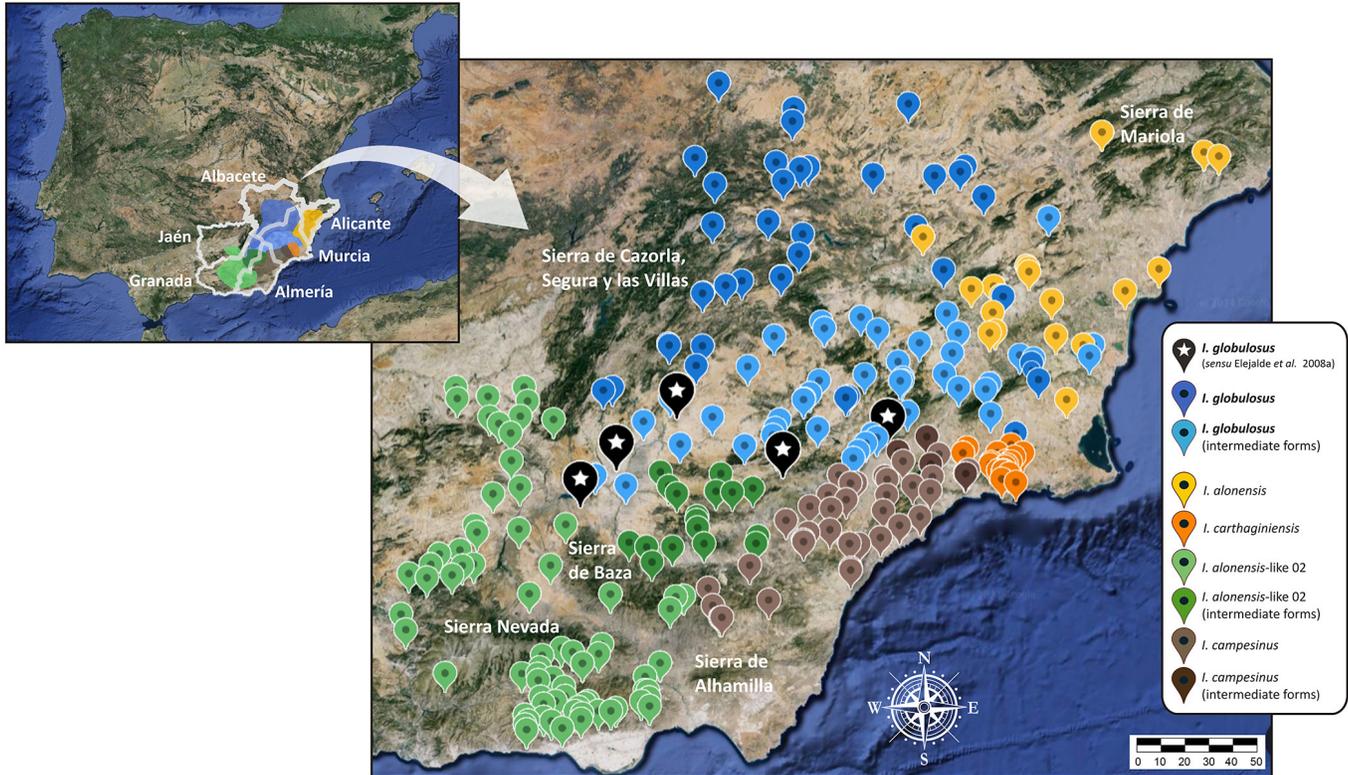
Figure 2. Distribution map of *Iberus globulosus* and other morphologically and geographically close taxa in the southeast of the Iberian Peninsula. Scale in kilometers. The thumbtacks marked with a star represent localities where samples from Elejalde *et al.* (2008a) involving COI and 16S rRNA analyses were available, thus confirming the presence of mitochondrial genes of *I. globulosus*. The samples from Ejejalde *et al.* (2008a) were referenced on the map by the centre point of the 10 × 10 km UTM grids reported by the authors. The entire territory was intensively sampled. Spaces of more than 20 km² remaining unmarked on the map indicate that no populations of the studied taxa were found. Only the easternmost populations of *I. alonensis*-like 02 were considered (*sensu* Elejalde *et al.* 2008a).

Table 1. Isolated localities of *Iberus globulosus* located to the south of its main area of distribution and surrounded by populations classified as intermediate to *I. alonensis*-like 02.

Province	Municipality	Sampling site	Latitude (N)	Longitude (W)	Altitude a.s.l. (m)
Granada	Castril	Entrance to the tunnel of the Portillo reservoir, Solana	37°48′16″	002°47′08″	940
Murcia	Lorca	Near Perigallo street, La Tercia	37°51′41″	001°00′51″	190
		Near Cañada del Burro, La Paca	37°48′36″	001°47′43″	760
	Cartagena	Near rambla del Saladillo, Los Simonetes	37°41′31″	001°06′38″	150
	Murcia	Puerto el Garruchal, Sierra de la cresta del Gallo, Garres y Lages	37°54′39″	001°02′32″	260

sents the morphospace resulting from combining the 11 morphometric parameters and ratios in this study (Fig. 3). PC1, which discriminates shells based on their size, explains the cluster of populations much better than PC2, which is attributable to shell shape (the total data variance explained by PC1 is almost five times greater than that of PC2). *Iberus globulosus* occupies a central position in the morphospace, with an average shell larger than those of *I. carthaginiensis* and *I. alonensis*, although smaller than those of *I. alonensis*-like 02 and *I. campesinus* (Table 2). The coordinates of centroids for *I. globulosus*, *I. alonensis*, and *I. alonensis*-like 02 are very close along PC2, revealing a high morphological similarity, which is consistent with their overlapping clouds in the morphospace.

On a metapopulation scale, other morphological traits allow for the discrimination of *I. globulosus* from the other species in this study (and these other species from one

Table 2. Morphometric comparisons among the shells of *Iberus globulosus* and other *Iberus* species. Data are expressed as means ± standard deviations. Parameter abbreviations: ØC (major diameter of the shell), Øc (minor diameter of the shell), H (shell height), ØP (major diameter of the peristome), Øp (minor diameter of the peristome), A (shell area), a (peristome area). Different letters indicate significant differences (*p*-value < 0.05) according to one-way ANOVA (A) followed by Tukey's HSD or Kruskal–Wallis (K) followed by two-tailed multiple comparison tests. *N* represents the number of populations from which shells were measured and *n* the total number of shells measured; "ns" means "not significant". The "Tests" column shows the four statistical tests applied to compare the parameters and ratios of *I. globulosus* with those of *I. alonensis*, *I. alonensis*-like 02, *I. campesinus*, and *I. carthaginiensis*, respectively. Similarly, the four letters in the column of *I. globulosus* represent statistical significance when comparing this species with the remaining, in the same order in which they are shown in the table. Letters in the four columns at the right of the table show the result of the statistical comparisons with *I. globulosus*.

| Parameters and ratios	Tests	*I. globulosus* ($N = 29, n = 286$)	*I. alonensis* ($N = 15, n = 357$)	*I. alonensis*-like 02 ($N = 61, n = 310$)	*I. campesinus* ($N = 29, n = 245$)	*I. carthaginiensis* ($N = 9, n = 311$)
ØC (mm)	A,K,K,K	30.65 ± 2.37 a,b,b,a	28.01 ± 1.85 b	35.14 ± 3.24 a	34.65 ± 4.10 a	24.69 ± 1.61 b
Øc (mm)	A,K,A,K	24.88 ± 1.94 a,b,b,a	22.59 ± 1.45 b	28.44 ± 2.62 a	27.26 ± 3.14 a	19.37 ± 1.23 b
H (mm)	K,K,A,K	17.69 ± 1.92 a,b,b,a	16.12 ± 1.31 b	21.09 ± 2.43 a	19.75 ± 2.88 a	13.37 ± 1.21 b
ØP (mm)	K,K,K,K	18.09 ± 1.55 a,b,b,a	16.82 ± 1.27 b	21.79 ± 2.40 a	20.53 ± 2.69 a	15.28 ± 1.14 b
Øp (mm)	A,K,K,K	16.23 ± 1.43 a,b,b,a	14.87 ± 1.27 b	18.90 ± 1.90 a	18.63 ± 2.45 a	12.75 ± 1.04 b
H/ØC	A,A,A,K	0.58 ± 0.04 ns,b,a,a	0.58 ± 0.03 ns	0.60 ± 0.03 a	0.57 ± 0.03 b	0.54 ± 0.03 b
A (mm²)	K,K,K,K	602.49 ± 91.86 a,b,b,a	498.89 ± 64.01 b	791.45 ± 144.31 a	751.65 ± 167.94 a	377.07 ± 48.25 b
a (mm²)	K,K,K,K	232.00 ± 38.93 a,b,b,a	197.37 ± 30.40 b	326.51 ± 66.15 a	305.12 ± 74.61 a	153.65 ± 22.48 b
ØC/Øc	K,A,A,A	1.23 ± 0.03 b,ns,b,b	1.25 ± 0.03 a	1.24 ± 0.03 ns	1.27 ± 0.03 a	1.27 ± 0.03 a
ØP/Øp	A,A,A,A	1.12 ± 0.06 b,b,a,b	1.13 ± 0.06 a	1.15 ± 0.06 a	1.10 ± 0.06 b	1.20 ± 0.07 a
a × 100/A (%)	A,A,A,A	38.52 ± 2.54 b,b,b,b	39.52 ± 2.72 a	41.19 ± 2.94 a	40.47 ± 3.41 a	40.75 ± 2.99 a
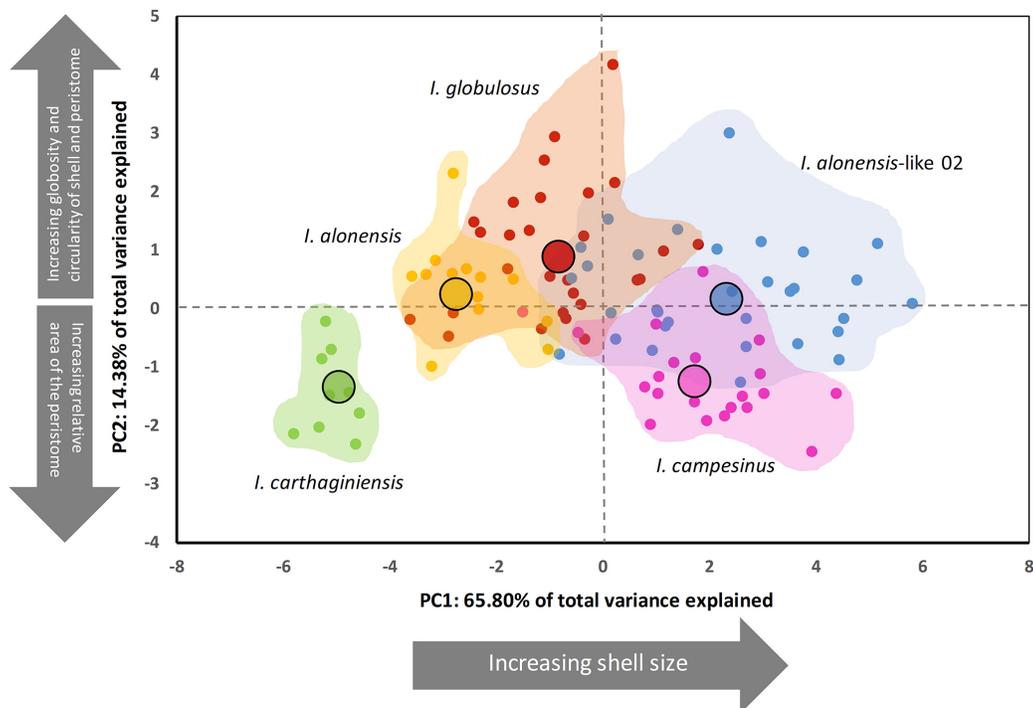
Figure 3. Clustering of *Iberus globulosus* (28 sites), *I. alonensis* (13 sites), *I. alonensis*-like 02 (32 sites), *I. campesinus* (21 sites) and *I. carthaginiensis* (9 sites) within the two-dimensional morphospace generated by the first two PCs of a PCA. Each point on the graph represents a sampling location. The coordinates of the centroids for each taxon (largest points) were calculated as the averages of the X and Y coordinates of the points within the corresponding clouds.

another); these are the ratio between the abundance of the two common banding patterns in the genus *Iberus*, and the proportion of shells showing a somewhat open umbilicus (Table 3). *Iberus globulosus* has the frequency of shells showing a continuous banding pattern (92%) 2.5 times higher than in *I. alonensis*-like 02. Furthermore, 16% of the shells of *I. globulosus* show some amount of an umbilical opening, more frequent than in both *I. alonensis* and *I. alonensis*-like 02 (6% and 0%, respectively).

Our morphometric analysis confirms that most shells intermediate between *I. globulosus* and *I. alonensis*-like 02 have dimensions halfway between these species in terms of size (diameter, height, and area of the shell, and diameter and area of the peristome) and prominence of the peristome. The only morphometric parameter in which the intermediate shells did not show significant differences with respect to typical shells was the shell circularity index (Table 4). The morphometric divergences between specimens of *I. globulosus* and *I. alonensis*-like 02 with respect to their intermediate

forms were captured within the morphospace determined by the two first principal components of our PCA (Fig. 4). The separation between the three clusters is well defined along PC1 (which orders the shells by size), so that the intermediate forms are located between *I. globulosus* and *I. alonensis*-like 02. Clustering is much less conditioned by shell shape since data variance collected by PC2 (defined by shell globosity and circularity and prominence of the peristome) is 4 times lower than that of PC1. Thereby, the separation of the three clusters along PC2 was less clear than in PC1, albeit the intermediate forms were typically located in the range of lower values of PC2 for *I. globulosus* and *I. alonensis*-like 02.

We also observed intermediate traits in the soft parts in populations in the contact zone between *I. globulosus* and *I. alonensis*-like 02. While *I. globulosus* has a greyish body and a bone-white mantle, *I. alonensis*-like 02 has characteristically lemon-yellow body and a pinkish mantle. Often, intermediate specimens retain the greyish body colour of *I. globulosus* and the pink mantle of *I. alonensis*-like 02 (Fig. 5).

Table 3. Differences in band patterns and umbilical opening among the *Iberus* species studied.

	Percentage of shells	*I. globulosus*	*I. alonensis*	*I. alonensis*-like 02	*I. campesinus*	*I. carthaginiensis*
Shell banding pattern	With continuous bands	92	82	35	76	87
	With discontinuous bands	2	12	61	24	9
Umbilical opening	With fully closed umbilicus	84	94	100	26	97
	With some degree of umbilical opening	16	6	0	74	3

Table 4. Morphometric comparisons between shells of *Iberus globulosus*, shells of *I. alonensis*-like 02, and shells of populations classified as intermediate. Data are expressed as means ± standard deviations. The abbreviations of the parameters are indicated in Table 2. Different letters indicate significant differences (*p*-value < 0.05) according to one-way ANOVA (A) followed by Tukey's HSD or Kruskal–Wallis (K) followed by two-tailed multiple comparison tests. *N* represents the number of different populations from which shells were measured and *n* the total number of shells measured; "ns" means "not significant".

| Parameters and ratios	Tests	*I. globulosus* ($N = 29, n = 286$)	Intermediate forms ($N = 34, n = 363$)	*I. alonensis*-like 02 ($N = 61, n = 310$)
ØC (mm)	A	30.65 ± 2.37 c	32.12 ± 3.07 b	35.14 ± 3.24 a
Øc (mm)	K	24.88 ± 1.94 c	25.98 ± 2.41 b	28.44 ± 2.62 a
H (mm)	K	17.69 ± 1.92 c	19.39 ± 2.18 b	21.09 ± 2.43 a
ØP (mm)	K	18.09 ± 1.55 c	19.20 ± 2.08 b	21.79 ± 2.40 a
Øp (mm)	K	16.23 ± 1.43 c	17.55 ± 1.99 b	18.90 ± 1.90 a
H/ØM	A	0.58 ± 0.04 b	0.60 ± 0.04 a	0.60 ± 0.03 a
A (mm^2)	K	602.49 ± 91.86 c	661.02 ± 123.35 b	791.45 ± 144.31 a
a (mm^2)	K	232.00 ± 38.93 c	267.26 ± 56.74 b	326.51 ± 66.15 a
ØC/Øc	A	1.23 ± 0.03 ns	1.24 ± 0.03 ns	1.24 ± 0.03 ns
ØP/Øp	A	1.12 ± 0.06 b	1.10 ± 0.06 c	1.15 ± 0.06 a
a × 100/A (%)	A	38.52 ± 2.54 c	40.35 ± 3.14 b	41.19 ± 2.94 a
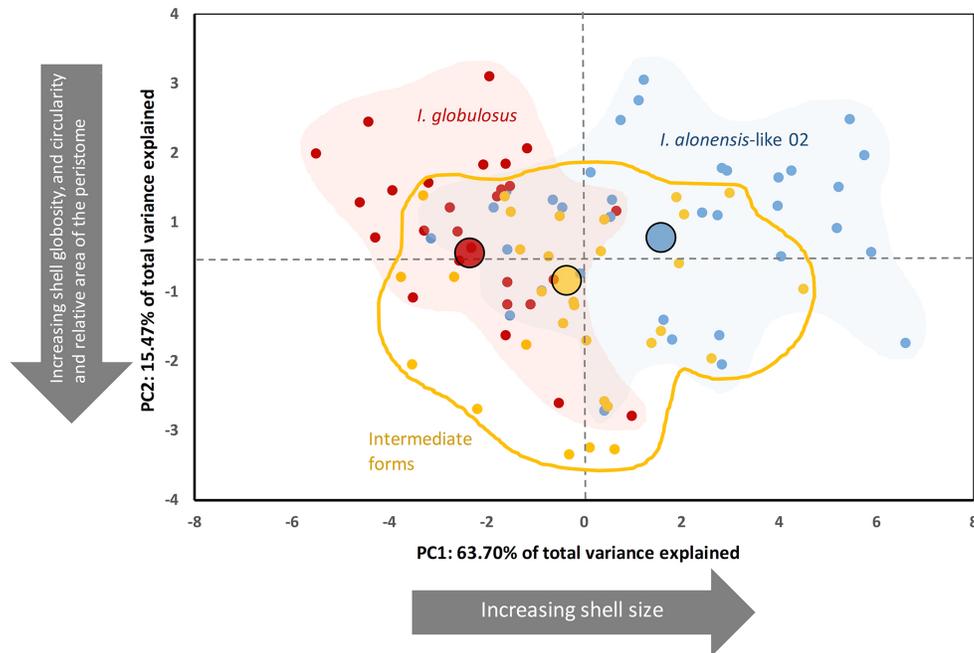
Figure 4. Clustering of *Iberus globulosus* (28 sites), *I. alonensis*-like 02 (32 sites), and the intermediate forms between both (32 sites) within the two-dimensional morphospace generated by the first two PCs of a PCA. Each point on the graph represents a sampling location. The coordinates of the centroids for each taxon (largest points) were calculated as the averages of the X and Y coordinates of the points within the corresponding clouds.

The whole body of evidence

According to Elejalde *et al.* (2008a), the genetic divergence between *I. globulosus* and *I. carthaginiensis* and between the clade formed by both with respect to the sister clades (*I. gualtieranus* and *I. campesinus*) ranges between 5.89 and 11.31% for the COI gene and between 3.17 and 6.92% for the 16S rRNA gene. Furthermore, *I. globulosus* shows a well-delimited geographical distribution which is clearly separated from *I. carthaginiensis* and *I. campesinus* (Fig. 2), as well as from *I. gualtieranus* (Ruiz-Ruiz *et al.* 2006), and a distinctive morphological identity (Fig. 3, Tables 2, 3). The only species with which *I. globulosus* shows morphological and geographical overlap are *I. alonensis* and *I. alonensis*-like 02. However, the genetic divergence between *I. globulosus* and *I. alonensis* (10.51–12.26 % for the COI gene and 5.3–7.16% for 16S rRNA gene) and between *I. globulosus* and *I. alonensis*-like 02 (10.67–14.65 % for the COI gene and 8.2–9.81 % for the 16S rRNA gene) (Elejalde *et al.* 2008a), clears any doubt abour their phylogenetic separation.

This body of evidence leads us to conclude that *I. globulosus* C.R. Boettger, 1913 is a valid species, with *I. carthaginiensis globulosus* C.R. Boettger, 1913 becoming a junior synonym. Since the available information on this species is scarce and confusing, we redescribe it below.

Redescription of *Iberus globulosus*

Iberus globulosus C.R. Boettger, 1913

Type shell and type locality. In his original description of *I. gualtieranus globulosus*, Boettger (1913) did not specify where the holotype, or any other type specimen, was deposited. Zilch (1977), in his compilation of all Boettger's publications and new taxa, explained that the holotype deposited in the Senckenberg Forschungsinstitut und Naturmuseum of Frankfurt (Germany) had been destroyed during World War II. For this reason, we select a neotype for *I. globulosus*, the shell shown in Fig. 6A, which has been deposited in the Museo Nacional de Ciencias Naturales - CSIC (Madrid, Spain), catalogue number 15.05/200534. Given the ambiguity of the type locality provided by Boettger and the plausible genetic introgression of the southernmost populations of *I. globulosus* (see Discussion), we consider it appropriate to select a neotype that is representative of a non-hybrid population from southern Albacete. With the selection of the neotype, the type locality is restricted to the limestone cliff above the Mundo River near Mirador del Diablo, Ayna, Albacete, Spain (38°33′28″N, 002°04′28″W).

It may seem unorthodox to assign a neotype having a location different from the original type locality, but the original type locality spans a territory of almost 9,000 km²,
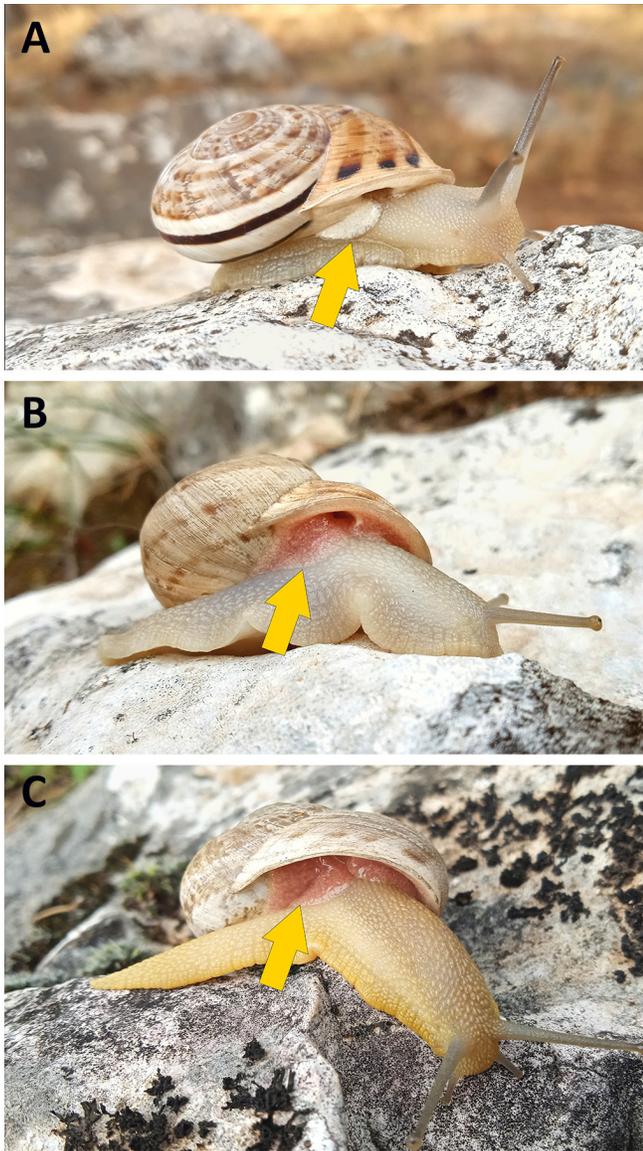
Figure 5. Colours of the soft parts of pure and hybrid specimens of *Iberus globulosus*. Arrows point to the detail of the mantle colour. **A**, *I. globulosus* (Ayna, Albacete). **B**, intermediate specimen between *I. globulosus* and *I. alonensis*-like 02 (Puerto Lumbreras, Murcia). **C**, *I. alonensis*-like 02 (Berja, Almería).

and selecting a neotype that knowingly is from a hybrid population seems inappropriate.

Typical shell description. Figures 6–8 show conchological variation in a series of typical and intermediate shells, as well as live specimens of *I. globulosus.* Because the neotype of *I. globulosus* does not completely match the shell characters and the locality of the morphotype originally assigned to the species, we redescribe *I. globulosus*.

Shell typically globose (occasionally semi-compressed or compressed), unkeeled, non-umbilicate or slightly umbili-

cate, with apex acute and with 4½–5 regularly enlarging whorls. Suture simple. Protoconch of 1–1½ whorls, smooth, uniformly light to dark brown. Teleoconch radially striate; radial ribs irregularly distributed, with intermittent varicose veins and evenly spaced spiral striation, resulting in marked reticulation. Aperture large, oval to semilunar, wider than tall. Shell height approximately half of greatest diameter. Peristome white, solid, slightly reflected. Umbilicus usually fully closed or slightly open in 16% of specimens studied. No callus in umbilical area. First three teleoconch whorls whitish to dark brown; main background colour bright white (most common) to beige or light brown. Last whorl with five continuous, dark-brown bands or with discontinuous bands (dotted lines) in *c.* 2% of specimens studied; two lowermost bands wider, more marked, and with a greater separation from each other than three upper bands. Two lowermost bands variable in their widths: sometimes equal, but most commonly with lower band 2–3 times narrower than upper band; upper band up to 7–8 times width of lower band in some western populations; two lower bands merged in some western populations. Bands not reaching lip edge. Three uppermost bands somewhat narrower on penultimate and antepenultimate whorls, less marked, and occasionally interrupted by soft marmorations. Distance between three upper and two lower bands 2–4 times the space between the three upper ones. Ventral area sometimes with irregular greyish to dark-brown spots.

Habitat. *Iberus globulosus* inhabits a broader range of habitats than *I. carthaginiensis*, the phylogenetically closest species. It occurs in xeric shrublands to mid-mountain Mediterranean forests, at 150–1,370 m altitude a.s.l. (Fig. 9). Unlike *I. carthaginiensis*, which is restricted to semi-arid coastal bushlands and grasslands with esparto and palmettos, *I. globulosus* can utilize broken limestone walls, which are the optimal niches for most *Iberus*.

DISCUSSION

All the pieces fit

There are compelling reasons to conduct a study reviewing the taxonomic status of *I. globulosus*:

(**1**) *Iberus globulosus* was ambiguously described from shells collected in the area currently inhabited by hybrid populations, therefore showing intermediate features with other neighbouring congeneric species (Appendix Fig. A1).

(**2**) García San Nicolás (1957) illustrated a shell that does not fit that of *I. globulosus s. str.* For instance, the illustration shows a dilated lip which becomes expanded and detached
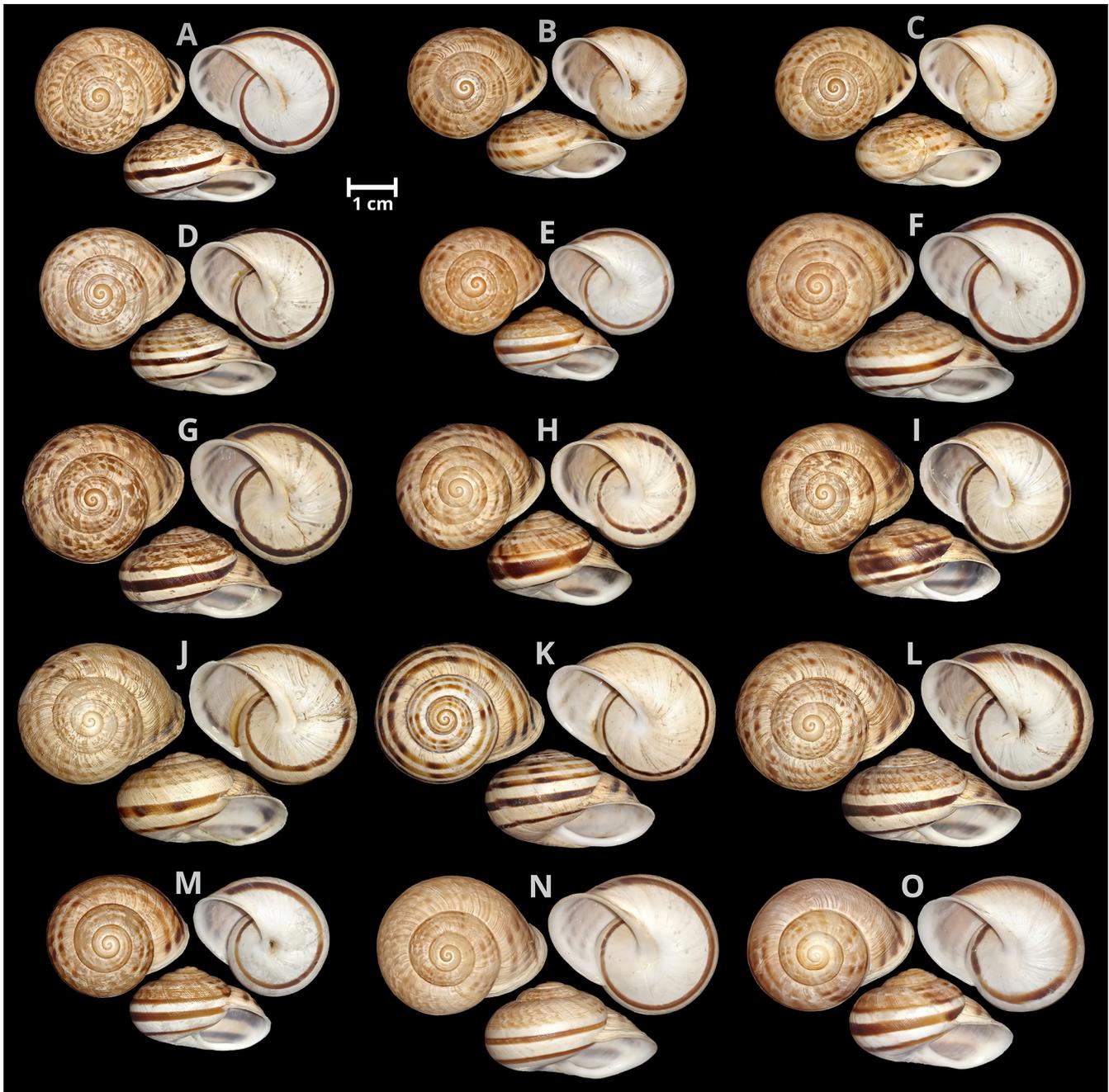
Figure 6. Series of conchological variation of *Iberus globulosus*. Albacete Province: **A–C**, Ayna (Specimen A represents the neotype of *I. globulosus*); **D**, Pedro Andrés, Nerpio; **E**, Letur; **F**, Chinchilla de Monte Aragón; **G**, Liétor. Granada Province: **H, I**, Puebla de Don Fadrique; **J**, Solana, Castril. Murcia Province: **K**, Puerto del Garruchal; **L**, La Paca, Lorca; **M**, Los Valientes, Molina de Segura; **N**, Moratalla; **O**, Cieza.

from the umbilicus in the columellar area, which is typical of *I. campesinus* but absent in *I. globulosus s. str*. (Appendix Fig. A2). Moreover, the shell dimensions provided by García San Nicolás are 25–35% smaller than those we obtained for *I. globulosus.* In view of these conchological features and the location of Garcia San Nicolás' shells within the province

of Almería, we conclude that the specimens studied by the author should be hybrids.

(**3**) No holotype of *I. globulosus* was available.

The advent of molecular analyses in taxonomic studies has provided a new tool that has notably changed our understanding of species diversity of land snails. However, in
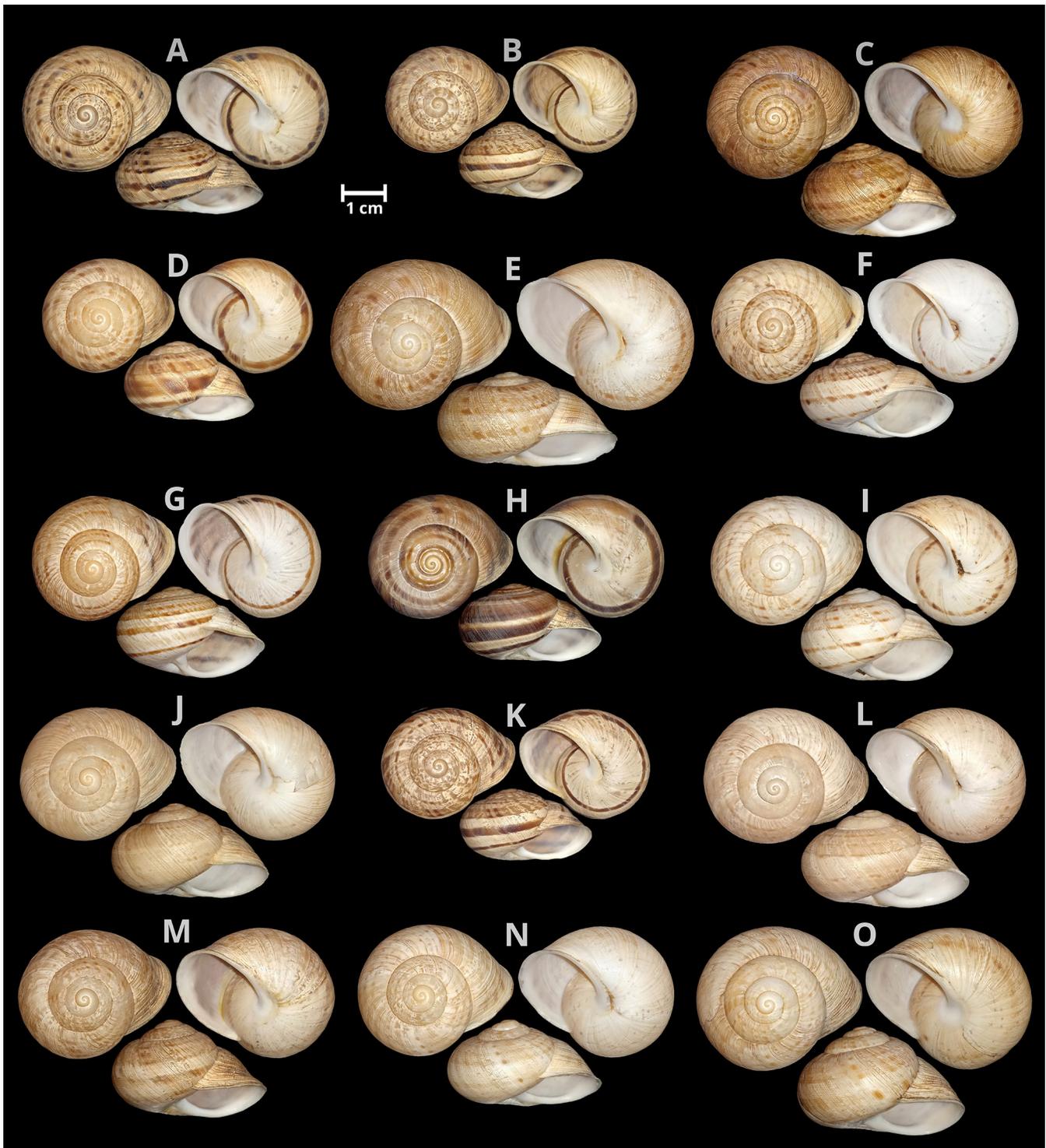
Figure 7. Series of intermediate shells showing conchological variation between *Iberus globulosus* and other nearby congeneric species (mainly *I. alonensis*-like 02). Murcia Province: **A**, Caravaca de la Cruz; **B**, Lorca; **C**, Pliego; **D**, Puerto Lumbreras; **E**, La Murta; **F**, Zarcilla de Ramos, Lorca; **G**, Casas Nuevas; **H**, Barqueros. Almería Province: **I–K**, Vélez Blanco. Granada Province: **L**, Baza; **M, N**, Zújar; **O**, Huéscar.

Figure 8. Live specimens of *Iberus globulosus* (**A–L**) and an intermediate specimen between *I. globulosus* and *I. alonensis*-like 02 (**M–O**) photographed *in situ*. **A–C**, Ayna (Albacete); **D–F**, Nerpio (Albacete); **G–I**, Liétor (Albacete); **J–L**, Puebla de Don Fadrique (Granada); **M–O**, Puerto Lumbreras (Murcia).

numerous recent studies on terrestrial gastropods, molecular data do not always agree in full or in part with the conchological or anatomical data (Fiorentino *et al.* 2008). Taxa that are almost indistinguishable in their shells may be genetically well separated or vice versa (Giusti & Manganelli 1992; Alonso *et al.* 2006; Liétor *et al.* 2024). Although species of land molluscs should not exclusively be defined by morphological characters (Collado *et al.* 2019), conchological study is still relevant in taxonomic studies when applied within a phylogenetic framework (Korábek *et al.* 2015). Indeed, behaviour and metabolism have been reported to be linked to shell morphology in land snails (Schweizer *et al.* 2019), and particularly in some species of the genus *Iberus* (Moreno-Rueda, 2006, 2007, 2009). Geography is another valuable taxonomic consideration, since in some cases there is greater agreement of phylogeny with geography than with conchology (Uit de Weerd *et al.* 2004; Stankowski & Johnson 2014). Furthermore, the geographical distribution allows us to understand the phylogeographic and evolutionary history of land snails (Neiber *et al.* 2021), as well as to know the conservation status of their populations (Moreno-Rueda 2011).

Figure 9. Some typical habitats of *Iberus globulosus*. Albacete Province: **A**, Castillo de Peñas de San Pedro; **B**, Las Anorias, Chinchilla de Monte Aragón; **C**, Fuente Librilla, Hellín; **D**, Elche de la Sierra, E, Liétor; **F**, Microrreserva de Ardal y Tinjarra, Yeste; **G**, Fuente de la Plata, Quejigal, Molinicos. Murcia Province: **H**, Arroyo Tercero, Moratalla; **I**, La Paca, Lorca; **J**, Puerto del Garruchal. Granada Province: **K, L**, Puebla de Don Fadrique.

Although there is no consensus about the magnitude of genetic divergence that land-snail species must differ, the genetic distance reported by Elejalde *et al.* (2008b) in the COI gene between *I. globulosus* and its sister taxon, *I. carthaginiensis*, is with the range accepted by various authors to distinguish species within Helicidae. For instance, Greve *et al.* (2010) found that genetic divergence of the COI gene is 3.5–8.6% in most species of the genus *Theba* Risso, 1826 from the Canary Islands and Morocco, and Colomba *et al.* (2015) determined that the genetic divergence of the same gene in the genus *Erctella* Monterosato, 1894 is 4.0–7.5%.

The morphological and geographical evidence that we provide here complements the genetic evidence, and together this integrated taxonomic approach provides support for recognizing *I. globulosus* as a valid species. The shell of *I. globulosus* has been confused with morphotypes of the *alonensis* morphospecies (*I. alonensis* and *I. alonensis*-like 02), but we find notable differences on a metapopulation scale among these taxa both in shell banding and in size, having

I. globulosus shells intermediate between *I. alonensis* and *I. alonensis*-like 02.

There is a corridor of sparsely distributed populations that connect northernmost *I. globulosus* populations and the coastal populations of *I. carthaginiensis* (Table 1). Figure 6 shows some shells from such corridor (specimens J–L) which are quite similar to the neotype of *I. globulosus*, and unpublished molecular analyses of specimens J and K reveals that they belong to the clade A2a of *I. globulosus*. Although the corridor is reminiscent of a common geological history, *I. globulosus* and *I. carthaginiensis* have developed rather divergent shell morphologies, and no intermediate populations have been found, which leads us to conclude that they are phylogenetically well separated.

A key piece to understand hybridization processes within the genus *Iberus*

The contact zone between species of *Iberus* usually consists of mountains or hills (Moreno-Rueda 2006; Elejalde *et al.* 2008b). For instance, the only known contact zone between

I. marmoratus marmoratus and *I. loxanus* (A. Schmidt, 1853) is in Sierra de la Acebuchosa (Gilena, Seville), where intermediate shells occur (Vázquez-Toro *et al.* 2015; Liétor *et al.* in press). *Iberus globulosus* breaks this pattern. As a result of a large geographic distribution extending northeast to southwest for 190 km, and the absence of major geographic and anthropogenic barriers, *I. globulosus* easily comes in contact with neighbouring congeneric species (Fig. 2).

Various authors have hypothesised that haplotypes introduced by hybridization are a secondary source of shell variability in terrestrial gastropods (Shimizu & Ueshima 2000; Davison 2002; Teshima *et al.* 2003), which can confer an adaptive advantage (Moran *et al.* 2021). Hybridization within Helicidae and its influence on shell morphology has been widely documented. Heller (1979), Fiorentino *et al.* (2008), Chueca *et al.* (2015), Holyoak *et al.* (2018), Korábek *et al.* (2022), and Hausdorf & Xu (2023) have reported hybridization among species in the genera *Levantina* Kobelt, 1871, *Marmorana* W. Hartmann, 1844, *Allognathus* Pilsbry, 1888, *Eremina* L. Pfeiffer, 1855, *Helix* Linnaeus, 1758 and *Chilostoma* Fitzinger, 1833, respectively.

The best-known example of hybridization of two *Iberus* species is between *I. alonensis* (*I. alonensis*-like 02 according to current understanding) and *I. gualtieranus*. Rodríguez-Perochena (2006) found that these species were able to produce fertile hybrids under laboratory conditions. Moreno-Rueda (2006) found a narrow hybridization zone between populations of *I. gualtieranus* and *I. alonensis*-like 02 in Sierra Elvira (Granada), similar to that we found in the mountains surrounding the city of Jaén (unpublished data).

Hybridization, which leads to introgression of mtDNA, is manifested by intermediate characteristics in shells, as described for shells from the contact area between *I. marmoratus marmoratus* and *I. cobosi* Ibánez & Alonso, 1978 (Elejalde *et al.* 2008b). Martínez-Ortí & Robles (2012) noted the existence of areas of overlap between *I. angustatus* (Rossmässler, 1854) and *I. guiraoanus* so that hybridization cannot be ruled out. Liétor (2014) gave other plausible hybrid combinations within the genus: *I. alonensis* × *I. angustatus*, *I. gualtieranus* × *I. angustatus*, *I. gualtieranus* × *I. campesinus*, and *I. loxanus* × *I. rositai* de Fez, 1950. The populations with intermediate shells found in the present study (Table 4, Figs 4, 7) also show pigmentation of the soft parts halfway between *I. globulosus* and *I. alonensis*-like 02 (Fig. 5). This suggests that another hybrid can be added to this list: *I. globulosus* × *I. alonensis*-like 02.

Unfortunately, the available data do not allow us to confirm our hypothesis of introgression by hybridization. Other molecular approaches will be necessary (Yang *et al.* 2020; Xu & Hausdorf 2021) to address hybridization of *I. globulosus* with neighbouring *Iberus* species. Additionally, sympatric populations should be looked for. If found, these could provide evidence of genetic differentiation between species. Finally, *in situ* and captive-breeding experiments could be developed to test for viability of hybrids or to show genetic introgression.

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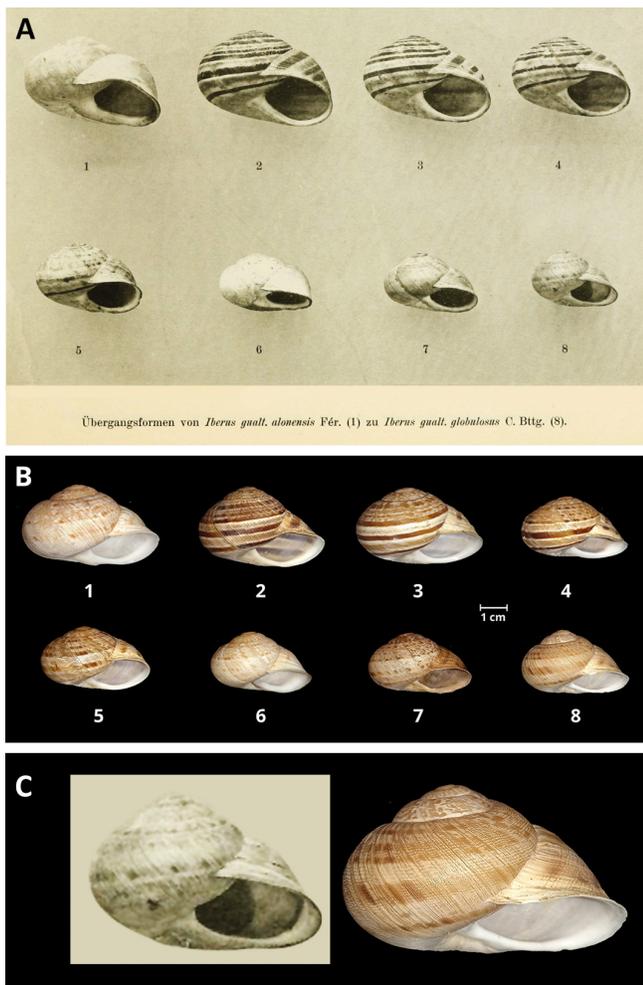
APPENDIX

Figure A1. A, original plate by Boettger (1913: 196) showing what the author claims as a transitional series of shells between *Iberus gualtieranus alonensis* (1) and *I. gualtieranus globulosus* (8). **B**, shells of *Iberus* taxa from Almería that we tentatively chose (by their similarity with those in **A**) to assign names to the shells on Boettger's plate: (1) *I. alonensis*-like 02 (Paterna del Río); (2) *I. alonensis*-like 01 (Retamar); (3) *I. alonensis*-like 01 (Sorbas); (4) *I. alonensis*-like 01 (Carboneras); (5) *I. alonensis*-like 01 (Mojácar); (6, 7) *I. alonensis*-like 01 × *I. campesinus* f. *lorcanus* (Vera); (8) *I. globulosus* × *I. alonensis*-like 02 (Vélez Blanco). **C**, comparison of Boettger's *I. alonensis globulosus* (left) and a typical specimen tentatively classified as *I. globulosus* × *I. alonensis*-like 02 in this study (right).
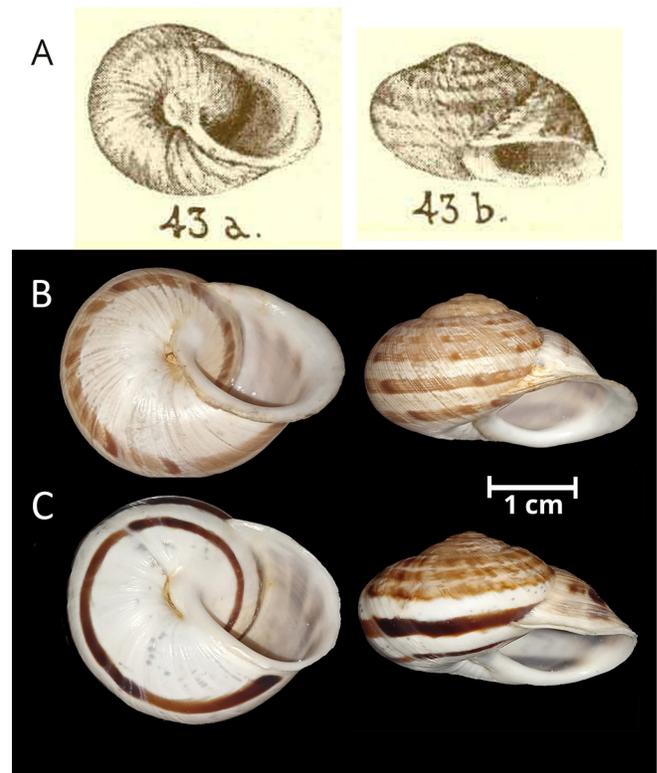

Figure A2. A, illustrations of *Iberus globulosus* reproduced from García San Nicolás (1957). **B**, *I. campesinus* f. *lorcanus* from Almería Province. **C**, *I. globulosus s. str.* described in this study (Albacete Province). Note the expansion of the lip and the columellar lip detached from the umbilicus, illustrated by García San Nicolás, which resemble *I. campesinus* f. *lorcanus* (B) rather than *I. globulosus s. str.* (C).