Speciation in the desert: A new endemic *Iberus* land snail restricted to the southeastern Iberian Peninsula

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ABSTRACT

Arid habitats constitute harsh environments for hydrophilic animals such as land snails. Still, several land snail species appear to inhabit arid environments and such species present an array of adaptations needed to minimise water loss in dry habitats. However, different species may have found different solutions for the same problem. Here, we describe *Iberus xerophilus* sp. nov., a new species of arid-dwelling land snail from southeastern Spain, on the basis of phylogenetic analyses. Moreover, we show a detailed morphological description as well as a characterization of its habitat. A comparison with the shell morphology of other aridity resistant *Iberus* land snails casts the question of how this snail can succeed in such harsh arid environments. Southeastern Spain constitutes a hotspot for *Iberus* arid-dwelling species, displaying a plethora of shell morphologies. The description of this new species might contribute to our understanding of the evolution and diversification of land snails specifically adapted to drought and arid conditions.

1. Introduction

Arid environments characteristically present low moisture and scarce vegetation, imposing restrictive living conditions on animals (Pianka, 2000). Arid environments are especially restrictive for hydrophilic animals such as land snails, which have permeable skin and hence undergo high rates of dehydration (Luchtel and Deyrup-Olsen, 2001). In fact, land snail distribution is strongly affected by moisture, with dry environments typically harbouring fewer individuals (Martin and Sommer, 2004). Still, several snail species inhabit arid zones, where they present behavioural, physiological, and/or morphological adaptations to minimise the risk of dehydration (Arad et al., 1989; Giokas et al., 2005; Moreno-Rueda, 2008; Giokas et al., 2014; Köhler et al., 2021). Therefore, land snails inhabiting arid environments are of special interest as they typically present evolutionary solutions to a challenging environment, helping us to understand the adaptive frontiers of life.

The arid ecosystems of the southeastern Iberian Peninsula are characterised by high temperatures (often near 50 °C in the shade) and low rainfalls (below 200 mm annually; Capel-Molina, 1995). Quaternary cycles and climate has strongly impacted current conditions, especially

throughout the Holocene (Carrion et al., 2010; Wackenheim et al., 2023), although the arid conditions prevailed since the Mid-Miocene (Carrion et al., 2010). Forests and shrublands of Mediterranean plants prevailed except in humid places near rivers where riparian forests remained (Valle, 2003). These riparian forests became lineal corridors for Mediterranean and Euro-Siberian flora and fauna, increasing biodiversity in the southeastern Iberian Peninsula (Valera et al., 2011). However, the region suffered heavy deforestation during the Bronze Age (~2000 B.C.) and even before, causing desert vegetation to spread (Pantaleón-Cano et al., 2003; Carrion et al., 2010). Therefore, the vegetation that prevails today in southeastern Spain consists mainly of therophyte and chamaephyte grassland and shrubland, in general lacking tree vegetation (Valle, 2003; Molero and Marfil, 2017).

Despite the harsh conditions for land snails, southeastern Spain constitutes a biodiversity hotspot for land snails of the genus *Iberus* Montfort, 1810 (Graells, 1846; García San Nicolás, 1957; Cobos, 1979; Alonso et al., 1985; Elejalde et al., 2005, 2008). The genus *Iberus* evolved from land snails that dwelled in zones with non-arid climates (Neiber et al., 2021). However, similarly to other land snails more typical of deserts, such as *Sphincterochila*, *Iberus* land snails have evolved a number

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of behavioural and morphological innovations to inhabit arid environments that differentiate them from other helicids (Moreno-Rueda, 2007; Moreno-Rueda et al., 2009). The finding of Greve et al. (2017) that the ability of four desert taxa of the genus *Theba* to cope with desiccation played an essential role on their distribution patterns, lead us to hypothetise that adaptation to xeric environments might be acting as a driver for diversification of the genus *Iberus* in the southeastern tip of Spain.

The taxonomic relationships between the *Iberus* species from southeastern Spain started to be clarified by the molecular study of Elejalde et al. (2008). Their work revealed that some assumed species based on their shell morphology were genetically too close to be considered valid species. In their study, they reported a clade, clade A4, which grouped the *Iberus* populations from the southeastern extreme of the Iberian Peninsula (Cabo de Gata and Sierra de Alhamilla). This clade did not correspond to a formally described species, but the morphology and the geographical origin did correspond to the specimens described as "alonensis form Epsilon" by A. Férussac (1821). Thus, the authors suggested that this clade, provisionally named *Iberus alonensis*-like 01, was a new Molecular Operational Taxonomic Unit for science, potentially being a new species.

The aim of this work is to make a formal description of the taxon known until now as *I. alonensis*-like 01, as well as a detailed mapping of the populations throughout its potential distribution area, a morphometric study, and new molecular analyses of specimens sampled in key locations. This data will elucidate key information of the phylogenetic relationships of a desert *Iberus* to its remaining genus species and let us to understand the evolutionary processes involved for such harsh climatic conditions.

2. Material and methods

2.1. Field samplings and sample processing

To precisely delineate the distribution of *I. alonensis*-like 01 we sampled intensively and systematically the whole potential distribution area throughout southeastern Spain. Most sampling was conducted between January and September 2023. The planning of sampling was based on previous citations documented in specialised literature and the prior knowledge and field experience of the research team. Finally, 60 localities were sampled, although the presence of the species was not detected in 9 sampling points (Fig. 1). The following information was compiled at each sampling point: (i) Geographic coordinates and locality. (ii) Representative photographs of the habitat. (iii) A group of shells representative of the species. Good quality specimens were cleaned, and the best samples were photographed. All the shells, including those sun-bleached and subfossils, were measured to obtain a set of morphometric parameters to characterise the species. (iv) Two live specimens were collected and their tissue samples extracted in the laboratory for molecular analyses.

2.2. Molecular analysis

Among all the specimens found alive in the field, those from two key locations were selected for genetic analyses (individuals AP3 and AP6). These locations were considered to properly cover the genetic variability for the species since they were geographically distant and placed at the ecological extremes of its distribution, one on the coast at 80 m altitude and another in a further inland mountainous area at 500 m altitude (Fig. 1). Once in the laboratory, the specimens were sacrificed by drowning and a tissue sample was extracted for molecular analyses. Samples were stored in absolute ethanol and maintained at −20 °C.

The total alignment comprises all known *Iberus* sequences from Genbank along with *Iberellus minoricensis* and two outgroup taxa, *Rossmaessleria sicanoides* and *Eremina dillwyniana* (Supplementary Table S1).

We amplified a fraction of the mitochondrial Cytochrome Oxidase I (COI) gene and the 16S Ribosomal RNA (16S rRNA), and a fraction of the nuclear gene Large Ribosomal Subunit (LSU) following Jowers et al. (2024). Sequences were edited with Sequencher v5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA) and checked for potential contaminants using GenBank's BLASTn search (Altschul et al., 1990). Sequences were aligned in Seaview v.4.2.11 (Gouy et al., 2010) with con MAFFT (Katoh et al., 2002).

Phylogenetic tree reconstructions for the three concatenated gene fragments (total length 1984 bp) were performed using maximum likelihood (ML) and Bayesian inference (BI), through RAxML v7.0.4 (Silvestro and Michalak, 2012) and MrBayes v3.2.673 (Ronquist and Huelsenbeck, 2003), respectively. The Akaike Information Criterion (AICc) was implemented in PartitionFinder v2.1.1 (Lanfear et al., 2016), using a 'greedy' search (Lanfear et al., 2012) to select the best fit evolutionary model for each partition. The resulting models and partitions were GTR + I + G (COI pos1), F81+I (COI pos2), GTR + I + G (COI pos3), GTR + I + G (16S rRNA) and HKY + G (LSU).

From the BI, two independent runs (each with four Markov chains for 10×10^7 generations) were performed. Trees and parameters were sampled every 1000 generations. The majority-rule consensus tree was estimated by combining results from duplicated analyses, after
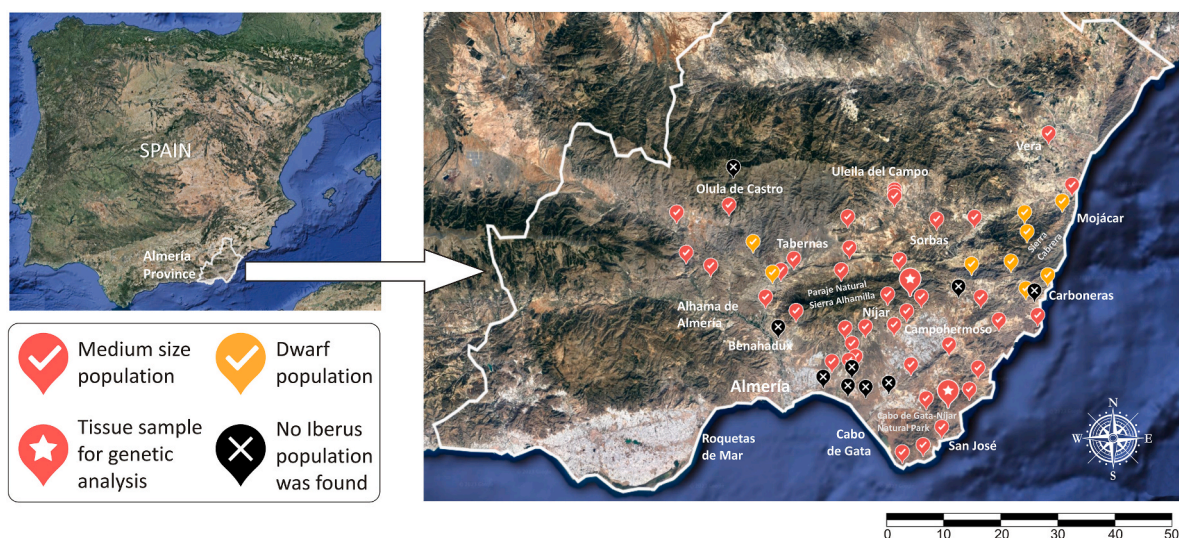

Fig. 1. Sampling area showing the distribution of *I. alonensis*-like 01. This map includes data from Landsat/Copernicus. Data SIO, NOAA, U.S. Navy, NGA, GEBCO (10/4/2013–14/12/2015). Scale in kilometers.

discarding 25 % of the total samples as burn-in. ML searches were conducted under GTRGAMMA and support was assessed by using 1000 bootstrapped replicates. All phylogenetic analyses were performed in the CIPRES platform (Miller et al., 2010). The consensus tree was visualised and rooted using FigTree v1.4.4 (Rambaut, 2018), and later prepared as a graphic with the software Inkscape v1.0.1 (http://www.inkscape.org). Uncorrected *p*-distances with partial deletion were computed in MEGA (Kumar et al., 2018).

2.3. Morphometrics

Shell morphometric parameters were obtained following López-Alcántara et al. (1985) and Polo (2016). Measurements were taken with a digital calliper (accuracy 0.01 mm): the largest and the smallest diameters (Ø) of the shell, shell height, and major and minor external Ø of the peristome (Fig. 2). According to these data, we estimated the shell and peristome area, by considering that both the shell and the peristome may resemble an ellipse, applying the formula Area = $\pi \times$ [(major Ø)/2] $\times$ [(minor Ø)/2]. On the basis of these measurements, we estimated the subsequent set of morphological ratios: shell height/major Ø of the shell (as a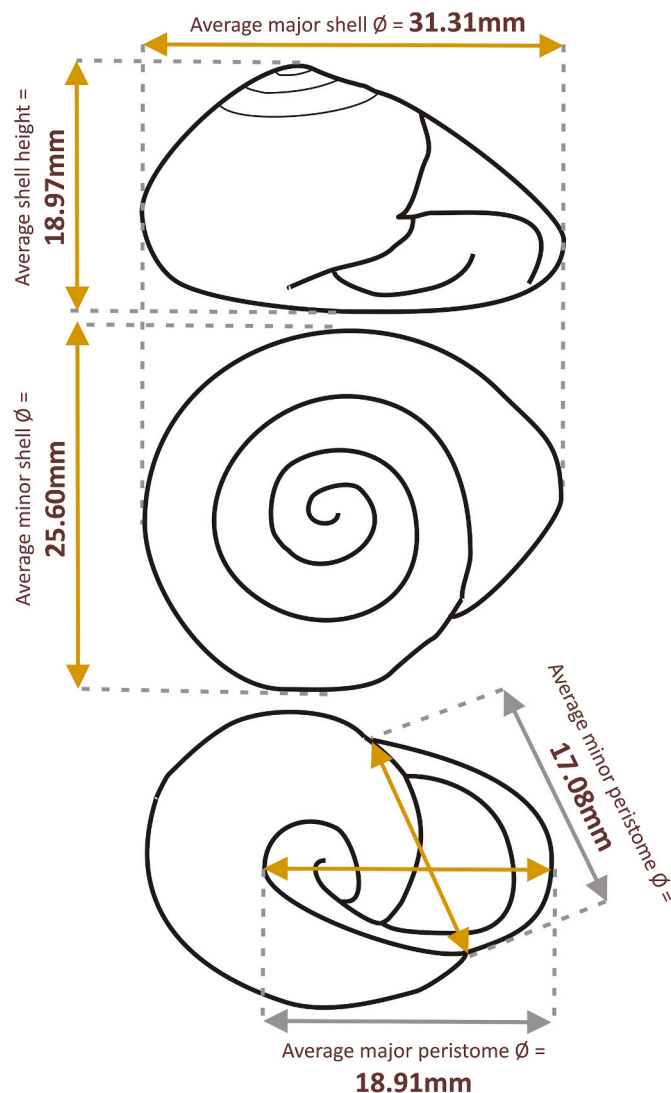n indicator of shell globosity, more globose shells having a higher ratio); major Ø of the shell/minor Ø of the shell (as an indicator of shell circularity, so that the closer this rate is to unity, the greater the degree of circularity of the shell); major external Ø of the peristome/minor external Ø of the peristome (as an indicator of peristome circularity); percentage of the total surface of the shell occupied by the peristome, calculated as (peristome area x 100)/shell area. All measurements were carried out by the same researcher (JL). The average values and the coefficients of variation for the 5 morphometric measurements tend to stabilise around 200 shells measured (Supplementary Fig. S1). Lastly, a Principal Components Analysis (PCA) was carried out to examine the intraspecific morphometric variability in the species.

3. Results

3.1. Phylogenetic analyses and genetic distances

The two samples (AP3, AP6) are recovered in a clade with *I. alonensis* 9, 10, 11, and 12 from Elejalde et al. (2008) study (Fig. 3). Therefore, our results support that our species corresponds with the potential species called *I. alonensis*-like 01 by them. The clade had a support of 78 % and 1.00 for the ML and BI analyses, respectively. This clade was grouped within a large clade that consists of several species. More specifically, this clade (see green marked clade in Fig. 3) is basal, although with low support, to *gualtieranus* (Linnaeus, 1758), *mariae* Cobos, 1979, *campesinus* (L. Pfeiffer, 1846) and *carthaginiensis* (Rossmässler, 1853), a group that as a whole was weakly supported but with strong support of internal clades. This clade was a sister clade to another clade composed of *alonensis*-like 02 sensu Elejalde et al. (2008) and *alonensis s. str.* (A. Férussac, 1821). (inferior clade). The genetic *p*-distances between the tree clades were consistent with high genetic divergence. The top clade composed of *gualtieranus, mariae, campesinus* and *carthaginiensis* had a within genetic divergence of 7.90 % for COI and 4.30 % for the 16S rRNA. The studied clade (marked in green in Fig. 3) within genetic divergence was 0.46 % for the COI and 1.08 % for the 16S rRNA. Lastly, the bottom clade composed of *alonensis*-like 02 and *alonensis s. str.* had a within-clade divergence of 9.20 % for the COI and 5.46 % for the 16S rRNA. The genetic distances between the clade of *I. alonensis*-like 01 and the larger clade (*gualtieranus, mariae, campesinus* and *carthaginiensis)* was 10.77 % for the COI and 6.09 % for the 16S rRNA, while with the *alonensis*-like 02 and *alonensis s. str.* clade was 12.20 % and 6.56 % for the COI and 16S rRNA, respectively. Genetic distances between *gualtieranus-mariae-campesinus-carthaginiensis* and *alonensis*-like 02-*alonensis s. str.* clades were 9.27 % and 8.13 % for the COI and 16S rRNA, respectively. On the basis of these genetic distances, we can consider that the clade including *I. alonensis*-like 01 and our two new samples correspond to a new species (as suggested by Elejalde et al., 2008), which we proposed to be named *Iberus xerophilus* sp. nov. and we therefore proceed to describe it below.

3.2. Systematics

Phylum MOLLUSCA Cuvier, 1795
Class GASTROPODA Cuvier, 1795
Order STYLOMMATOPHORA A. Schmidt, 1855
Family HELICIDAE Rafinesque, 1815
Subfamily HELICINAE Rafinesque, 1815
Genus *Iberus* Montfort, 1810
I. xerophilus sp. nov.

3.3. Etymology

The name of this species refers to the xeric environments of subdesert and desert areas where *I. xerophilus* sp. nov. inhabits in most of its distribution.

Fig. 2. Dimensions of *I. alonensis*-like 01 used for morphometric analyses. The largest diameter of the peristome includes the space occupied by the umbilical callus if present. The average values obtained for the selected morphometric parameters for 604 shells from 44 locations have been included.

Average major shell Ø = **31.31mm**

Average shell height = **18.97mm**

Average minor shell Ø = **25.60mm**

Average minor peristome Ø = **17.08mm**

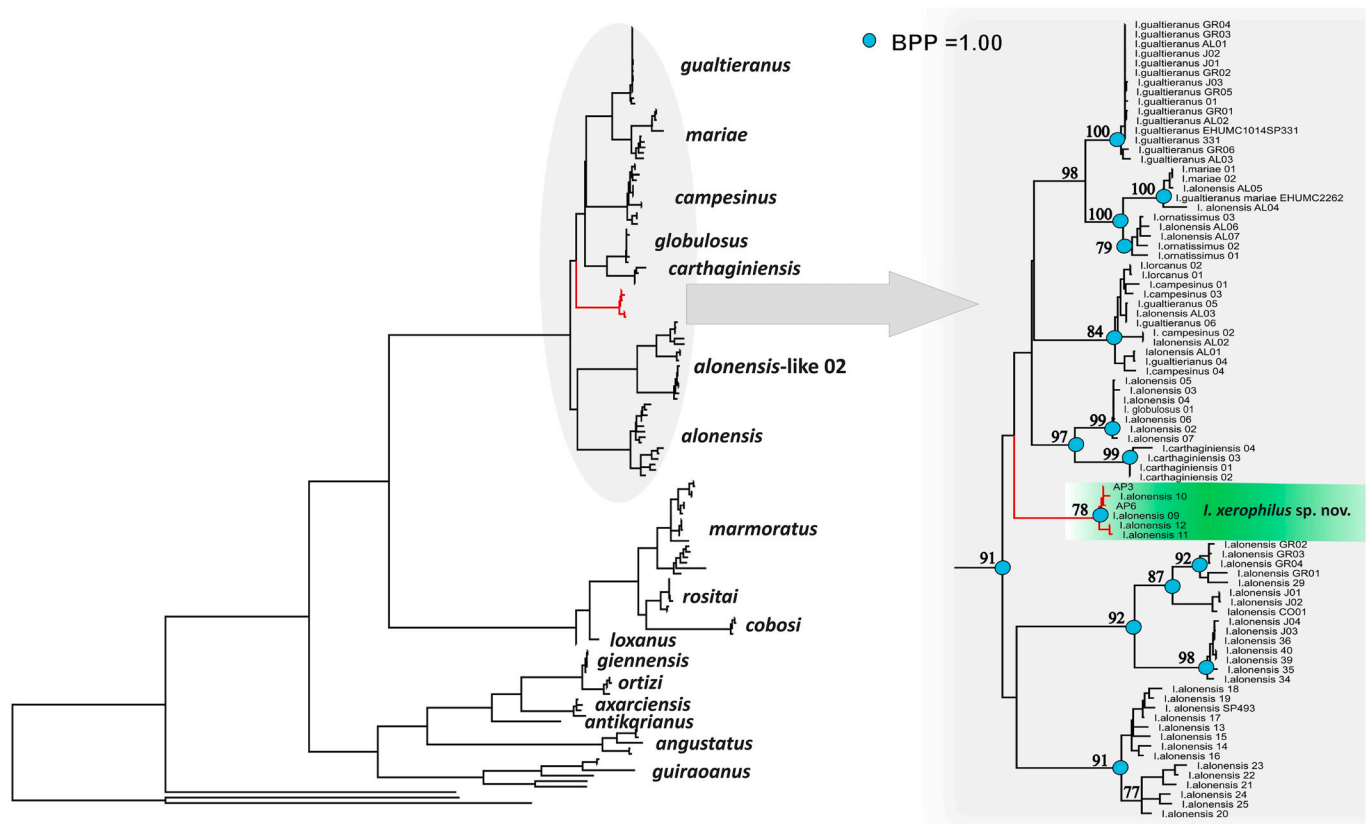Average major peristome Ø = **18.91mm**

Fig. 3. Maximum Likelihood tree of *Iberus*. Values by nodes represent bootstrap values for the ML analyses (>70 %). BI = 1.00 are represented on nodes by turquoise-filled circles in the clade of interest. Node support is not shown for terminal taxa. Important note for the reader: the provisional taxonomic designation *I. alonensis*-like 02 will soon be replaced by *I. rhodopeplus* ssp. (Liétor et al., in press).

3.4. Holotype and paratypes

Fig. 4 shows the shell photographs of the holotype and 6 paratypes assigned to *I. xerophilus* sp. nov. Information on the morphometry and locations of the holotype and paratypes is given in Table 1. Holotype and paratypes 4, 5 and 6 have been deposited within the collections of the Zoology Department of Granada University (Spain). The catalogue code for the holotype is 22772-CG (CCZ-UGR) whereas the corresponding codes for the paratypes 4, 5 and 6 are 22773-CG (CCZ-UGR), 22774-CG (CCZ-UGR) and 22775-CG (CCZ-UGR). The paratypes 1, 2 and 3 remain deposited in the private collection of Dr. José Liétor Gallego (Jaén, Spain) registered as IXP1, IXP2 and IXP3, respectively.

The type locality for *I. xerophilus* sp. nov. consists of esparto (*Macrochloa tenacissima*) grasslands devoid of tree vegetation and rock formations in El Nazareno, Níjar, Cabo de Gata-Níjar Natural Park (near the Mediterranean coast of Almeria Province, southeastern Spain), with the following coordinates: 36° 48′ 44″ N, 2° 05′ 22″ W.

3.5. Type shell description

Supplementary Fig. S2 shows a representative series of the conchological variability of *I. xerophilus* sp. nov. It has a globose (occasionally slightly compressed), thick, unkeeled and not umbilicated shell, with 4–5 whorls of regular growth. The suture is simple and visible in all whorls. Protoshell has 1–1.5 whorls with smooth and uniform light brown colour. The shell surface is transversely striated, except in the smooth protoshell. These radial ribs are not evenly spaced. Additionally, there is a longitudinal striation of variable intensity depending on populations and even individuals, so the shell surface of *I. xerophilus* sp. nov. shows a more or less marked reticulation. Shell aperture is large, from oval to semilunar, wider than high (equivalent to approximately

half the total width of the shell). It has a solid non-reflected peristome that sometimes can be thin and slightly sharp. In some populations, the umbilical area shows a whitish tone or white colour that sometimes becomes a slight callosity. The colour of the shell in the first three whorls (excluding the protoconch) may vary from off-white to dark brown. The colour of the protoconch is usually medium-brown, which darkens in some cases. Two morphotypes for shells of *I. xerophilus* sp. nov. can be defined. The first one represents 91 % of the shells and the second one the remaining 9 %.

(1) Morphotype 1 (Fig. S2A): The lower half usually exhibits three longitudinal brown bands of varying intensity, of which the upper one can lose width, sometimes even blurring or becoming intermittent. The upper half of the shell accumulates a variable number of bands of different thicknesses, often discontinuous and sometimes interrupted by marmorizations of varying density and intensity. Only some populations corresponding to 6 % of the measured shells of this morphotype (located mainly in the municipality of Retamar) break this typical band pattern, with the upper half of the main whorl showing continuous bands free of marmorizations that reach up to the whorl immediately preceding the protoconch. In this case, the width of the lateral bands is variable with a number ranging between 4 and 6.

(2) Morphotype 2 (Fig. S2B): The general colour of the shell becomes paler and the three bands of the lower half become intermittent or blurred. The appearance of whitish meandering transverse bands that do not penetrate the penultimate whorl of the shell is common.

The two morphotypes are found mixed in different localities so they are not grouped in distinct geographic areas.
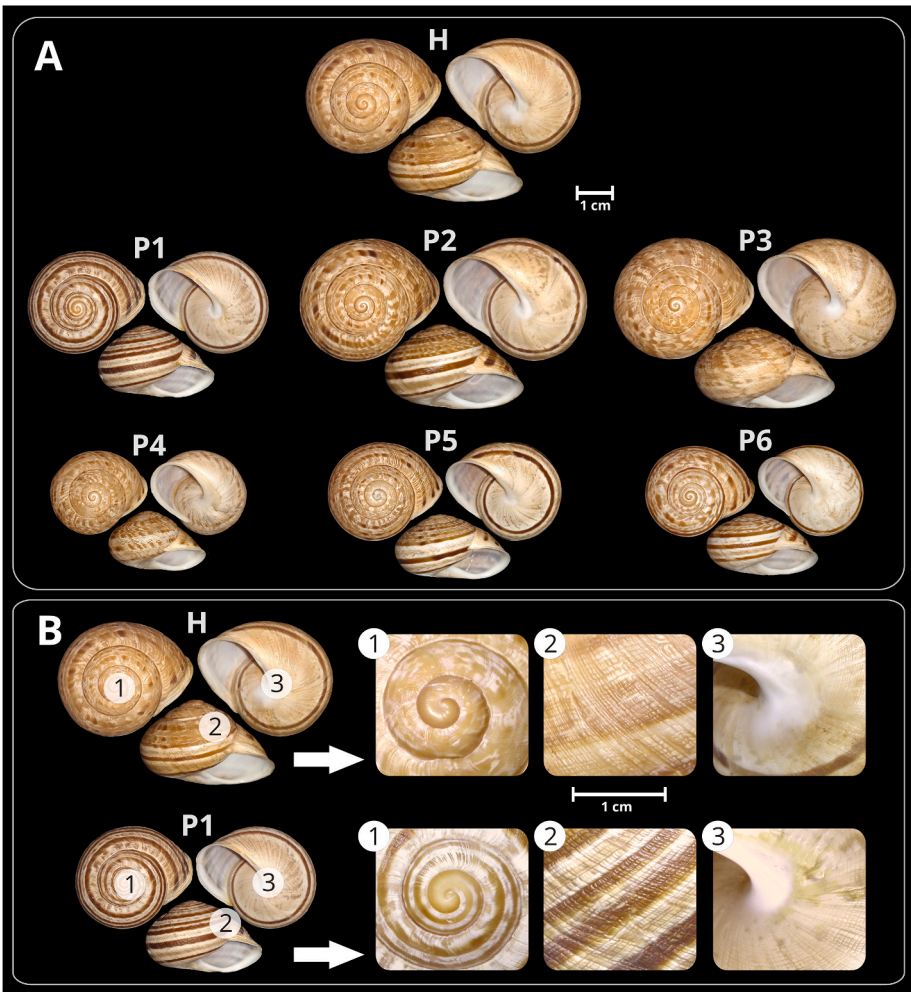
Fig. 4. A.Shell photographs of the holotype (H) and the 6 paratypes (P1 to P6) of *I. xerophilus* sp. nov. B. Microsculpture of several zones of the shell surface of the holotype and the paratype 1 (1. Protoconch and first whorls; 2. Lateral reticulation; 3. Umbilicus area).

Table 1

Location and basic morphometrics of holotype and paratypes assigned to *I. xerophilus* sp. nov.

Specimen	Length (mm)	Width (mm)	Height (mm)	Latitude (N)	Longitude (W)	Altitude (m a. s.l.)	Location	Sampling date
Holotype	35.11	28.37	22.32	36° 48′ 44″	2° 05′ 22″	87	El Nazareno, Níjar, Parque Natural Cabo de Gata-Níjar, Almería	16/04/2023
Paratype 1	31.67	25.25	19.91	36° 52′ 27″	2° 17′ 35″	113	Retamar, Almería	20/02/2013
Paratype 2	36.46	29.37	21.73	36° 59′ 39″	2° 09′ 58″	512	Tristanes, Níjar, Sierra de Alhamilla, Parque Natural Cabo de Gata-Níjar, Almería	15/04/2023
Paratype 3	35.51	28.48	20.47	36° 59′ 38″	2° 10′ 04″	538	Tristanes, Níjar, Sierra de Alhamilla, Parque Natural Cabo de Gata-Níjar, Almería	15/04/2023
Paratype 4 (dwarf)	24.49	19.9	13.74	37° 08′ 01″	1° 51′ 16″	231	Camino de la Fuensanta, Mojácar, Almería	06/09/2023
Paratype 5	29.58	24.05	17.01	37° 01′ 52″	2° 02′ 29″	236	Peñas Negras, Sorbas, Sierra Cabrera, Almería	15/04/2023
Paratype 6	27.04	22.31	15.49	36° 52′ 20″	2° 19′ 39″	97	Rambla de los Capeles, Retamar, Almería	28/01/2023

A significant proportion of the specimens of both morphotypes show an ornamental feature characteristic for the shells of *I. xerophilus* sp. nov.: The two lower lateral bands are bordered by thin whitish bands, which are much more evident in morphotype 1.

Table 2 gathers average morphometric data obtained for 604 shells of *I. xerophilus* sp. nov. coming from 44 sample locations. According to the stabilisation threshold shown in Fig. S1, this number of shells was considered sufficiently representative to obtain reliable morphometric data. There are two areas within the distribution of *I. xerophilus* sp. nov. (involving 9 sampling localities; Fig. 1). where the specimens exhibit sizes significantly lower than the usual standard of the species. These differences were captured in the morphospace delimited by the first two factors of a PCA (Fig. 5). Such clustering was not significantly affected by the shell shape gradient, the second factor of the PCA (p-value=0.89 for one-way ANOVA comparing the scores for the second factor of dwarf and medium-sized populations). That is to say, shells from populations with dwarf individuals showed the same shape as the standard shells, differing only in size (p-value<0.001 for the same ANOVA test applied to the first factor).

Table 2

Morphometric parameters measured and estimated in shells of *I. xerophilus* sp. nov. as well as various ratios among them. The data comes from 604 shells sampled in 44 different locations. Standard deviation (SD) and coefficient of variation (CV) are included.

|	Parameters and ratios	Minimum	Maximum	Average	SD	CV (%)
Size indicators	Major Ø of the shell (mm)	23.15	40.19	31.31	3.06	9.76
	Minor Ø of the shell (mm)	19.47	32.28	25.60	2.43	9.51
	Shell height (mm)	10.77	26.21	18.97	2.26	11.89
	Major Ø of the peristome (mm)	13.21	26.48	18.91	2.05	10.86
	Minor Ø of the peristome (mm)	11.08	22.99	17.08	1.88	11.01
	Shell area (mm^2)	354.00	1005.35	635.16	120.30	18.94
	Peristome area (mm^2)	114.96	467.52	256.31	53.66	20.94
Shape indicators	Shell height/Major Ø of the shell	0.33	0.70	0.61	0.03	5.47
	Major Ø/Minor Ø of the shell	1.12	1.32	1.22	0.02	2.01
	Major Ø/Minor Ø of the peristome	0.90	1.32	1.11	0.07	5.90
	Peristome area regarding shell area (%)	30.55	49.13	40.31	3.02	7.49
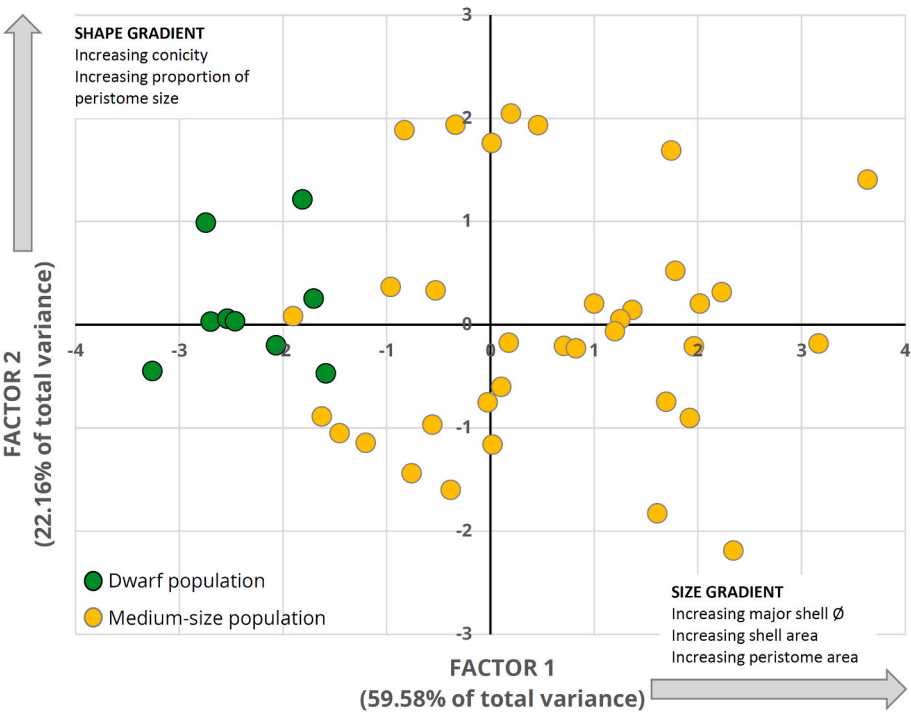
Fig. 5. PCA showing how dwarf and medium-sized populations of *I. xerophilus* sp. nov. are separately grouped in the bidimensional morphospace resulting from the two first factors (see geographical distribution in Fig. 1).

3.6. Soft parts

The body of *I. xerophilus* sp. nov. is light brown and its mantle is off-white (Fig. 6), which contrasts sharply with the lemon-yellow body and pink mantle of the geographically closest species, *I. alonensis*-like 02 (Liétor et al., in press), with which it could bear a certain conchological resemblance.

If we add to these distinctive features in the soft parts a globose shell with unmistakable banding pattern and an ornamentation with two lower lateral bands bordered by thin whitish bands, there are no other species of the genus *Iberus* which can be confused with *I. xerophilus* sp. nov.

3.7. Habitat

The habitat of *I. xerophilus* sp. nov. typically consists of esparto grasslands on variable lithologies, both calcareous (limestones) or siliceous (quartzites and slates) at an altitude between 8 and 787 m above sea level (see Fig. 6). They usually take refuge under esparto plants and in the inner side of medium-large rocks, where the shell (often greater than 3 cm) may penetrate. When rocky habitats are available (some mountain areas in the north part of its distribution), they can be found under leaf litter of Mediterranean scrubs near calcareous walls, although it is not common to see them sheltered inside rocky crevices. Climatology of the habitat range for *I. xerophilus* sp. nov. can be found in Table 3.

4. Discussion

The phylogenetic position of *I. xerophilus* sp. nov. (*I. xerophilus* hereafter), a highly divergent clade not grouped into any of the other *Iberus* species, suggests a distinct identity of this lineage. Further evidence derives from genetic distances, which recover low genetic divergence within the *I. xerophilus* clade (~0.5 % for COI and ~1 % for 16S rRNA) contrasting with high divergence to its other sister clades (>9 % for COI and >6 % for 16S rRNA). This evidence indicates, at least from a genetic perspective, the different evolutionary history of the lineage and the taxonomic identity of the clade. For these reasons, Elejalde et al. (2008) proposed it as a new Molecular Operational Taxonomic Unit (*sensu* Backeljau et al., 2001), potentially a new species. In fact, typical

Fig. 6. Some representative habitats and alive specimens of *I. xerophilus* sp. nov. within the Province of Almería (Spain). 1. Barranco Hondo, Gérgal; 2. Tristanes, Níjar, eastern Sierra Alhamilla, Cabo de Gata-Níjar Natural Park; 3. Camino de la Fuensanta, Mojácar; 4. Barranco del Aljibe, Santa Cruz de Marchena; 5. El Nazareno, Níjar, Cabo de Gata-Níjar Natural Park; 6. El Llano de Don Antonio, Carboneras.

Table 3
Weather data from three stations located in the distribution area of *I. xerophilus* sp. nov. (Almería, Tabernas, and Níjar) providing monthly maximum, average, and minimum temperatures, and average monthly rainfall during the period 2002–2020. Source: Ministerio de Agricultura, Pesca y Alimentación (Spain).

Weather station		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Almería	Minimum Tᵃ °C	4.38	4.97	5.80	8.58	11.49	14.71	17.85	18.71	15.90	11.90	8.01	5.89
	Average Tᵃ °C	12.51	13.16	14.81	17.04	20.01	23.34	26.01	26.69	24.04	20.49	16.13	13.59
	Maximum Tᵃ °C	20.64	21.52	24.04	27.42	30.95	35.51	37.11	36.51	33.27	29.73	25.05	22.00
	Rainfall mm	20.38	22.62	27.23	21.86	11.34	3.58	0.53	3.23	17.06	20.99	28.85	35.27
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tabernas	Minimum Tᵃ °C	−3.12	−2.33	−0.61	2.90	6.00	10.67	14.08	14.37	11.00	5.43	0.50	−2.23
	Average Tᵃ °C	8.33	9.39	11.79	14.42	18.18	22.77	25.44	25.17	21.3	17.14	11.85	9.03
	Maximum Tᵃ °C	21.62	22.83	26.09	27.78	32.17	36.37	38.94	38.95	34.38	30.65	24.74	22.13
	Rainfall mm	20.02	15.95	32.11	26.61	17.85	4.31	0.52	4.99	30.88	24.45	33.41	30.52
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Níjar	Minimum Tᵃ °C	2.09	3.07	4.27	7.13	10.06	13.82	17.40	18.14	15.10	10.14	5.57	3.03
	Average Tᵃ °C	11.04	11.74	13.71	16.02	19.53	23.52	26.24	26.44	23.22	19.47	14.64	12.07
	Maximum Tᵃ °C	20.88	21.36	24.93	26.42	30.50	34.19	36.40	36.37	32.92	29.71	24.65	21.99
	Rainfall mm	25.69	17.99	31.39	24.57	12.12	3.45	1.06	6.26	33.81	24.83	33.00	31.77

genetic distances for the COI used for delimiting species in land snails are between 4 and 8 % (Hebert et al., 2003; Davison et al., 2009; Köhler and Johnson, 2012), although we are aware that higher levels of variation do exist in within different groups. In addition, *I. xerophilus* presents distinctive shell and soft parts characteristics that allow it to be easily differentiated from other *Iberus* land snails. Moreover, the typical habitat for most species of the *Iberus* genus consists of mid-mountain limestone rocks with a high density of cracks and rock vegetation, which strongly differs from that of *I. xerophilus*, characterised by esparto grasslands on any type of lithology. All these characteristics (genetics, morphology, and habitat) strongly support the consideration of *I. xerophilus* as a new *Iberus* species.

I. xerophilus is a species strongly adapted (and restricted) to arid environments (Table 3). Indeed, the environment where this species inhabits is one of the most arid in which an *Iberus* species may be found. An interesting aspect of the mapped distribution of *I. xerophilus* shown from this study is its restricted presence to the eastern and southernmost region of the Iberian Peninsula. This distribution suggests a plausible expansion from northern towards southern localities, constrained today by the marine barrier. The origin of Iberian land molluscs is complex, believed to derive from ancient vicariant events, followed by subsequent dispersal events expanding species ranges, reaching areas that came into secondary contact with drifting of micro-plates (Giusti and Manganelli, 1984). In fact, the effects of Pleistocene glaciations on speciation processes and patterns of diversity have long been a subject in the Iberian Peninsula (Taberlet et al., 1998; Hewitt, 2004). Currently, there is no

doubt that Quaternary glacial cycles were highly important factors in shaping patterns of both inter- and intraspecific diversity (e.g. Hewitt, 1996; 1999; 2000). Species expansions during glacial periods have been postulated as an important mechanism of diversification for vertebrate and invertebrate species. Such events have resulted in periods of range contraction and the generation of multiple isolated species (Hewitt, 2000). While some consider the Quaternary to have involved a period of major speciation (Johnson and Cicero, 2004), others suggest that Quaternary glaciations did not trigger major bouts of speciation and were at most responsible for modelling intraspecific diversity, with species differentiation mostly predating the Pleistocene (Klicka and Zink, 1997; Zink et al., 2004; Mas-Peinado et al., 2018). During the Early and Mid-Miocene, the literature suggests that *Iberus* species followed a southern coastal expansion from the Iberian Levant region towards the Penibetic region (Neiber et al., 2021), seeking for warmer conditions and remaining isolated at the southernmost region of its expansion. Indeed, dating the *I. xerophilus* clade would help establish possible scenarios of speciation. Considering its positioning in our tree, we can infer from Neiber et al. (2021) an approximate dating of *I. xerophilus* as ancestral to the *I. carthaginiensis* group, suggesting a likely Late Miocene origin (Neiber et al., 2021). This time would hypothetically correspond to the Messinian salinity crisis, and could suggest that coastal population might have had broader southern expansions at the time (see Chueca et al., 2015).

The correct taxonomic identification of this species may contribute to understanding the evolution of land snails in arid environments. This is especially relevant as the genus *Iberus* belongs to the Helicidae family and descendants from European land snails that inhabited milder, moister, and colder climates (Neiber et al., 2021). Therefore, this genus is not exclusive to arid environments, as others such as *Sphincterochila*. Still, the southeastern region of the Iberian Peninsula, despite its arid environment, constitutes a hotspot of *Iberus* species (Elejalde et al., 2008). The reason for such a high diversity of *Iberus* species in this arid region is unknown, but one possibility is that the evolution of different adaptations to aridity while the region was drying would result in a high morphological and behavioural (and perhaps physiological) diversification. At the same time, this diversification would result in niche adaptation, favouring genetic isolation over prolonged time. Recent exhaustive paleontological work on eastern Andalusian terrestrial molluscs has revealed an extremely rapid climate change from wet and humid in early to mid-Holocene to xeric by the end of the Holocene with contrasting effects on the biogeography of species in the region (Wackenheim et al., 2023). Thus, it becomes apparent that the distribution of *I. xerophilus* in the region is far more complex and possibly a recent adaptation to the harsh environment it inhabits.

The most studied *Iberus* species is *Iberus gualtieranus* (Moreno-Rueda, 2011). It has received substantial attention given its particular morphology, with flattened and strongly keeled and ornamented shells (López-Alcántara et al., 1985). In *I. gualtieranus*, flattened shells seem to have evolved to allow this species to be sheltered in karstic crevices (Moreno-Rueda, 2007), in this way escaping high temperatures during summer in arid environments of southeastern Spain (Moreno-Rueda et al., 2009). For this reason, this species only can inhabit karstic environments with abundant crevices resulting from rock fracturing (Moreno-Rueda, 2002; 2006a; 2014). Meanwhile, the exaggerated shell ornamentation in this species seems to have evolved to increase water retention (Moreno-Rueda, unpublished data) as has been reported in other land snails (Giokas, 2008; Giokas et al., 2014). Nevertheless, these morphological characteristics are not present in *I. xerophilus*. This opens the question of what adaptations allow *I. xerophilus* to survive in arid habitats. One possibility is that *I. xerophilus* presents behavioural adaptations to minimise water loss, as those described in the congeneric *I. gualtieranus*, which have a fine regulation of their activity patterns to avoid staying out of the shelter in the moments of highest water loss risk (see Moreno-Rueda, 2006b; 2012; Moreno-Rueda et al., 2009). Another option is that *I. xerophilus* fights against water loss by reducing the

evaporation potential through both a thick shell (Machin, 2009) and a decreasing surface-to-volume ratio posed by a globose shape (Schweizer et al., 2019). Summer aestivation during times of worst humidity conditions is another widespread strategy among land snails (Barnhart and McMahon, 1987; Withers et al., 1997) which we have observed to occur in *I. xerophilus*. Lastly, *I. xerophilus* could have physiological adaptations (such as high levels of heat shock proteins) to resist the stress of high temperatures and low humidity in its habitat, as reported in other land snails (Mizrahi et al., 2010; 2012; 2016). Habitat selection is pivotal to land snails, as sessile organisms with reduced mobility require strong adaptability to their environment. Nevertheless, the area of distribution of *I. xerophilus* suggests limited habitat heterogeneity, mostly esparto grasslands that snails likely feed on during the wetter period, and large rocks to hide during the dry season, as has been observed for other *Iberus* spp. in the south of the Iberian Peninsula (Menez, 2008).

This study adds yet another endemic snail species to the region, which fits with a pattern of endemic species locally. Indeed, from a biogeographic perspective, the south of Almería remains highly different to the remaining bioclimatic areas from Andalusia, with more representation of Mediterranean and Euro-Mediterranean species (Arrebola et al., 2006). On the contrary, hardly any of the 40 snail species from the province of Almería are hydrophilic species of broad distribution ranges (e. g., Holarctic, Palearctic) (Arrebola et al., 2006). Herein we believe that studies such as this one, with exhaustive and careful delimitation of taxa and their morphs, with accurate mapping throughout the distribution area, solving taxonomic identities and clarifying phylogenetic relationships will contribute to the knowledge of the region's biodiversity and, thus, to the implementation of conservation policies. Ultimately, *I. xerophilus* might provide new insights into the evolution of land snails to arid environments.

CRediT authorship contribution statement

José Liétor: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michael J. Jowers:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Pedro A. Jódar:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Inés Galán-Luque:** Writing – review & editing, Investigation, Formal analysis. **Antonio R. Tudela:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2024.10.008.

Data availability

Data will be made available on request.

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