SOOSIANA, 13: 1 – 10, 1985

ALONSO, M. R., LÓPEZ ALCÁNTARA, A., RIVAS, P. AND IBAÑEZ, M.:

A BIOGEOGRAPHIC STUDY OF *IBERUS GUALTIERIANUS* (L.) (PULMONATA: HELICIDAE) – AZ *IBERUS GUALTIERIANUS* (L.) (PULMONATA: HELICIDAE) ÁLLATFÖLDRAJZI VIZSGÁLATA

ABSTRACT: In this work we show that *I. gualtierianus* and *I. alonensis* are ecotypes of the same species and conclude that the form *gualtierianus* has been originated iteratively, and it is an ecological variant of the form *alonensis*, as a result of the adaptations it manifests in relation to its karstic substrate.

INTRODUCTION

Some taxa of the genus *Iberus* MONTFORT 1810, endemic to the Iberian Peninsula, show a high degree of variability in their shell form, there are a large number of intermediate forms (GARCÍA S. NICOLÁS, 1957; ALONSO y IBÁÑEZ, 1978); on the other hand, the existing differences between their reproductive apparatus and radulas are very small, to such an extent that cases of hybridization are known (GARCÍA S. NICOLÁS, 1957).

This is the case with *I. gualtierianus* (LINNAEUS 1758) (very ornamented and keeled shell; see Figs. 1-5) and *I. alonensis* (FÉRUSSAC 1820) (practically smooth globose shell; Fig. 7) which, owing to the marked differences in their shell form, were considered to represent separate species, although some authors (BOETTGER, 1913; COBOS, 1979) maintained the opinion that both taxa belong to the same species: *I. gualtierianus*, as a consequence of the existence of intermediate forms (Fig. 6). Equally, BARTOLOME (1982) on comparing the globose and keeled forms of closely related taxa of Mediterranean Helicids, postulated that *I. gualtierianus* is a form adapted to life in rocky environments possibly deriving from the globose form of *I. alonensis*.

Recently we have carried out a biometric study of the reproductive apparatus and the external and internal forms of the shell of both taxa, (LÓPEZ ALCÁNTARA *et al.*, in press), in conjunction with a study of the chemical compositon and laminar structure of the respective shells, reaching the conclusion that both taxa belong to the same highly polymorphic species, being denominated „form *gualtierianus*" and „form *alonensis*", respectively.

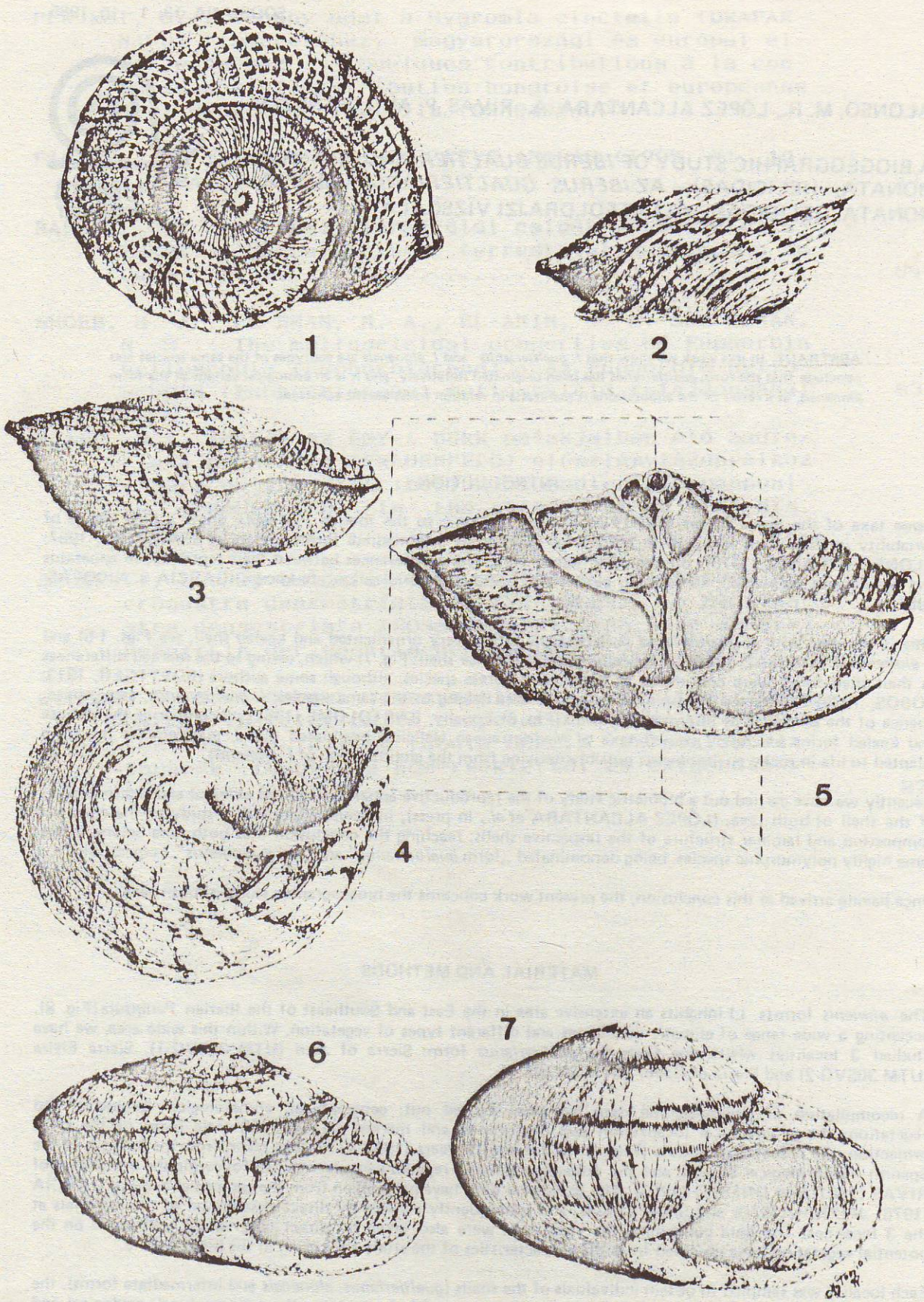
Once having arrived at this conclusion, the present work concerns the biogeographic study of both taxa.

MATERIAL AND METHODS

The *alonenis* form (s. l.) inhabits an extensive area in the East and Southeast of the Iberian Peninsula (Fig. 8), accepting a wide range of climatic conditions and different types of vegetation. Within this wide area, we have studied 3 localities where one finds the *gualtierianus* form: Sierra of Jaen (UTM 30SVG-1), Sierra Elvira (UTM 30SVG-2) and Sierra of Gador (UTM 30SWF-1).

A recompilation of environmental data has been carried out: geographical, climatological, geological and vegetation; the geographical localization was determined and marked on 1:50.000 scale maps of the UTM projection; the climatological data (Figs. 9-11) for the 11 years (1963-1973) was taken from the Bulletin of the Spanish Meteorological Service, and the respective climatic regimes were determined following the procedures of RIVAS (1981) and UNESCO (1963). The geological data have been taken from the geological maps of GARCÍA (1976), JACQUIN (1970) and SANZ (1974), and subsequently verified by direct observation of the materials at the 3 localities. The data concerning the vegetation were also taken by direct observation, and those on the potential vegetation were obtained from the characteristics of the study sites given in the bibliography.

Each locality was sampled to obtain individuals of the snails (*gualtierianus*, *alonensis* and intermediate forms), the sampling procedure adopted taking into account the geographical situation, the topographical, geological and climatological characteristics, the vegetation, the localization and extension of each site.



FIGS. 1-7. Variation in shell form of *Iberus gualtierianus*; 1-5: the *gualtierianus* form, 6: intermediate form; 7: the *alonensis* form.

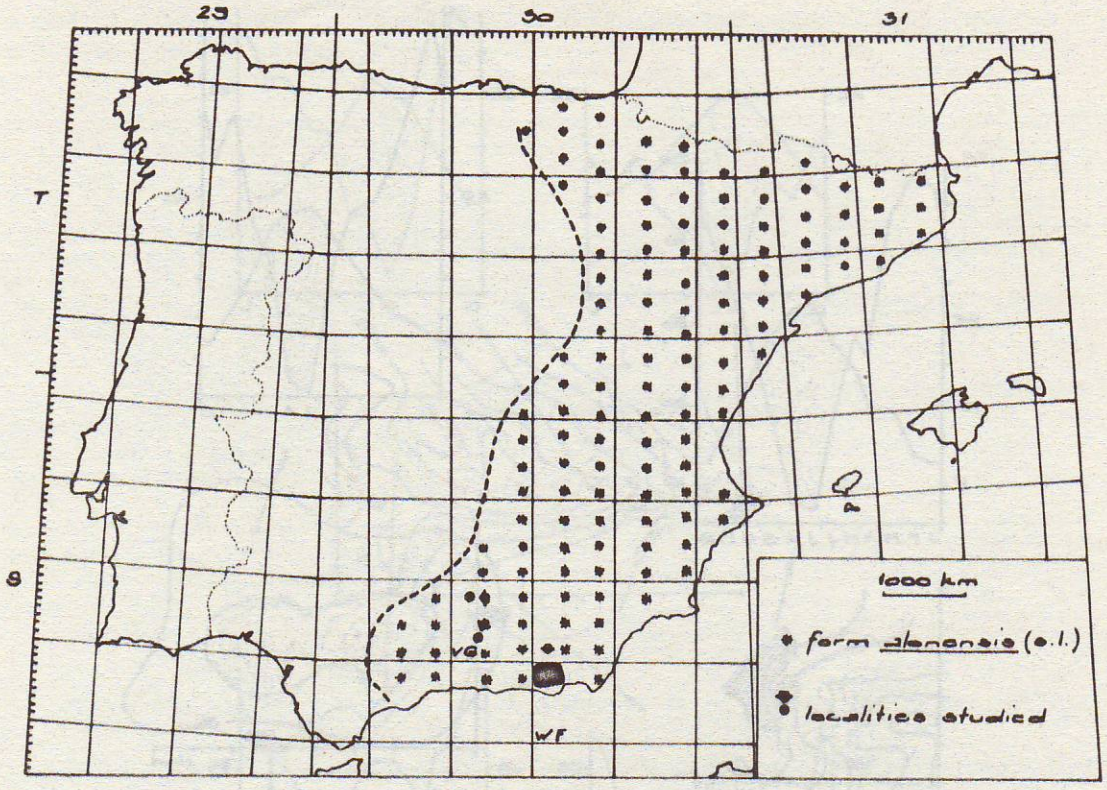


FIG. 8. Area occupied by the *alonensis* form (s. l.) (according to data taken from the bibliography) and localities studied.

RESULTS

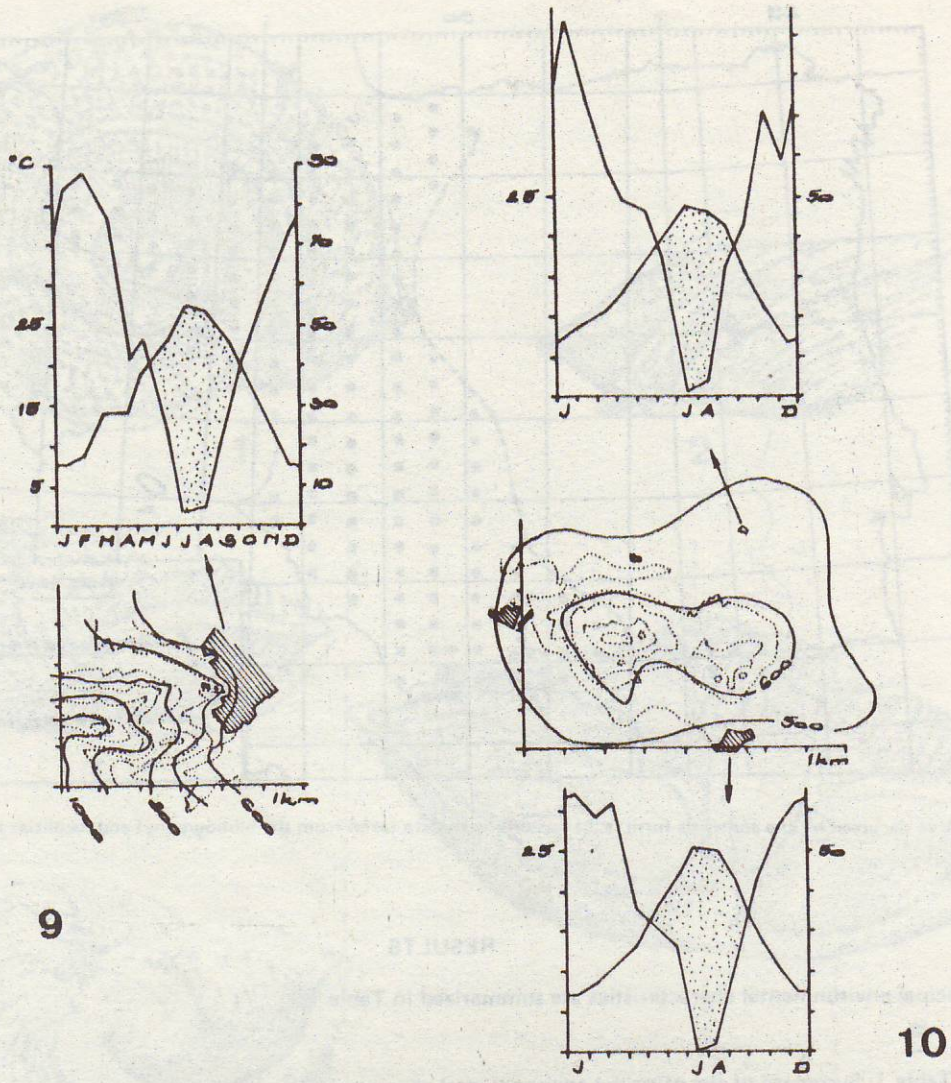
The principal environmental characteristics are summarized in Table 1.

Table 1. Summary of the principal environmental characteristics.

	Sierra of Jaen	Sierra Elvira	Sierra of Gador (eastern and southern slopes)
Chorological sector	subbetic	malacitano-almijarense	alpujarro-gadorense
Altitude (m)	700-1200	600-1100	0-1200
Bioclimatic after Rivas (1981)	dry mesomediterranean	dry mesomediterranean	dry thermomediterranean
zone after UNESCO (1963)	attenuated thermomediterranean	acentuated mesomediterranean	Xerothermomediterranean
Precipitation (mm)	500-600	600-1000	250-550
Substrate	limestone and dolomite		
Erosion	karstic, incipient		
Vegetation	degradation stage of cork oak forest, with saxicole communities		

At the 3 localities the temperature is higher than in the corresponding surroundings. All the localities possess a potential vegetation of the „mediterranean cork oak" type included within the Phytosociological Order Quercetalia ilicis (BRAUN-BLANQUET, 1963). To be more exact, that of the Jaen and Elvira Sierras is included in the Paeonio-Quercetum rotundifoliae association, whilst that of the Gador Sierra in the Oleo-Quercetum rotundifoliae association, though without woodland formations, due to its aridity.

As regards the chorological situation, the 3 localities are included within the Betic Province of the Mediterranean Region.



9

10

FIGS. 9-10. Ombrothermic graphs and maps of annual isoheytes: 9: Sierra of Jaen; 10: Sierra Elvira.

The Jaen Sierra (Fig. 12) lies in the NE of the Subbetic Sector, near to the Hispalense Sector from which it receives influences especially with respect to the high temperatures, experiencing more than 4 dry months.

It is composed mainly of Cretaceous limestones which make up the principal relief of the Pena and the Alcazar of Jaen, changing to marls and calcareous clays on passing to the North and South. The strong regional tectonics have meant that the materials are highly fractured and diaclassed and a surface karstic morphology, at least in its initial phases, has developed over them.

The population of the *gualtierianus* form is found in the drier and warmer areas on the southern slope of Alcazar of Jaen, on a substrate of limestone rocks with an abundance of narrow surface fissures and a poorly developed soil covered by a sparse vegetation composed of saxicole communities together with rosemary and thyme. It occupies a smaller area than at the other 2 localities, and its individuals are the smallest and those that present the least variation in form. The population is isolated in the northern part by a pine plantation and to the South by an olive grove. Further to the South towards the Jabalcuz mountain, some larger *gualtierianus* forms are found together with a large number of intermediate forms and a sparse number of *alonensis* forms, in amore humid habitat with rocks less limestone in character (marly), lower temperatures and a higher density of vegetation. Ascending towards the Jabalcuz mountain, the vegetation begins to take on the character of the potential vegetation, and the taxon that appears is the *alonensis* form with individuals both large in size and shell height.

The Elvira Sierra (Fig. 13) is a small limestone massif rising above a plain with a greater array of temperatures and an earlier flowering season. The number of dry months oscillate between 4 on the North slope to 5 on the South.

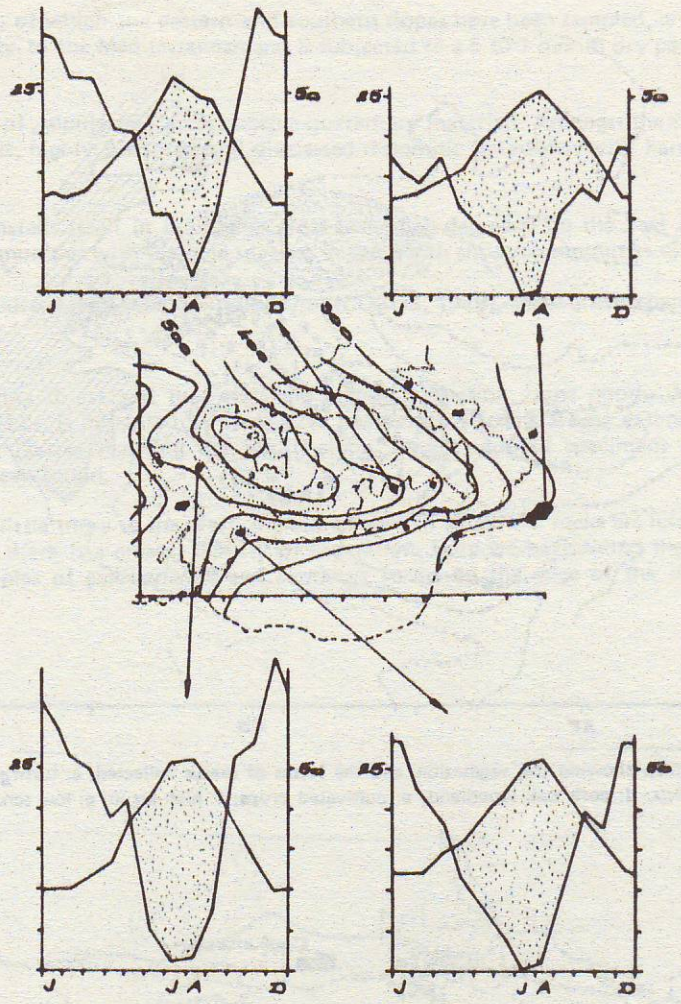


FIG. 11. Ombrothermic graphs and map of annual isoheytes of the Gador Sierra.

It is composed of Triassic, Jurassic and Cretaceous materials strongly folded and with faults, surrounded by Neogenic-Quaternary materials of the Granada Depression (BERTRAND et KILLIAN, 1889; BRAGA *et al.*, 1979; GARCÍA, 1976). The Jurassic materials occupy the greatest extension, being formed mainly of limestone and dolomite of the lower and middle Lias, and marls and calcareous limestones of the upper Lias, Dogger and Malm. The limestones and dolomites have been subjected to surface karstic erosion which has given rise to the presence of numerous narrow fissures, and they represent the only materials to have escaped agricultural working thereby conserving their surface morphology.

The potential vegetation is restricted to the northern zone; towards the South it degrades into shrubland, saxicole species being abundant on the southern and southeastern slopes as a consequence of the abudance of stony areas. The whole Sierra is surrounded by cultivation which also penetrate to the eastern sector.

The larger part of the population of the *gualtierianus* form is made up of small-sized individuals inhabiting the southwestern slope, although they also extend towards the southeastern slope and to the extreme South.Throughout all this area, surface karstic erosion is evident, accompanied by poorly developed soils, low density of vegetation, relatively high temperatures and low precipitation.

In the higher areas one finds a richer soil, insolation is less and the humidity greater and there exists a greater density of vegetation. In parallel with these environmental changes, the forms of *Iberus* similarly change, intermediate forms appearing first, which on moving higher up towards the areas of maximum vegetation cover, become more globose until the typical *alonensis* form is attained. On the North slope where the potential vegetation develops, and similarly in the cultivated areas of the Sierra and its immediate environs, only specimens of *alonensis* form have been found.

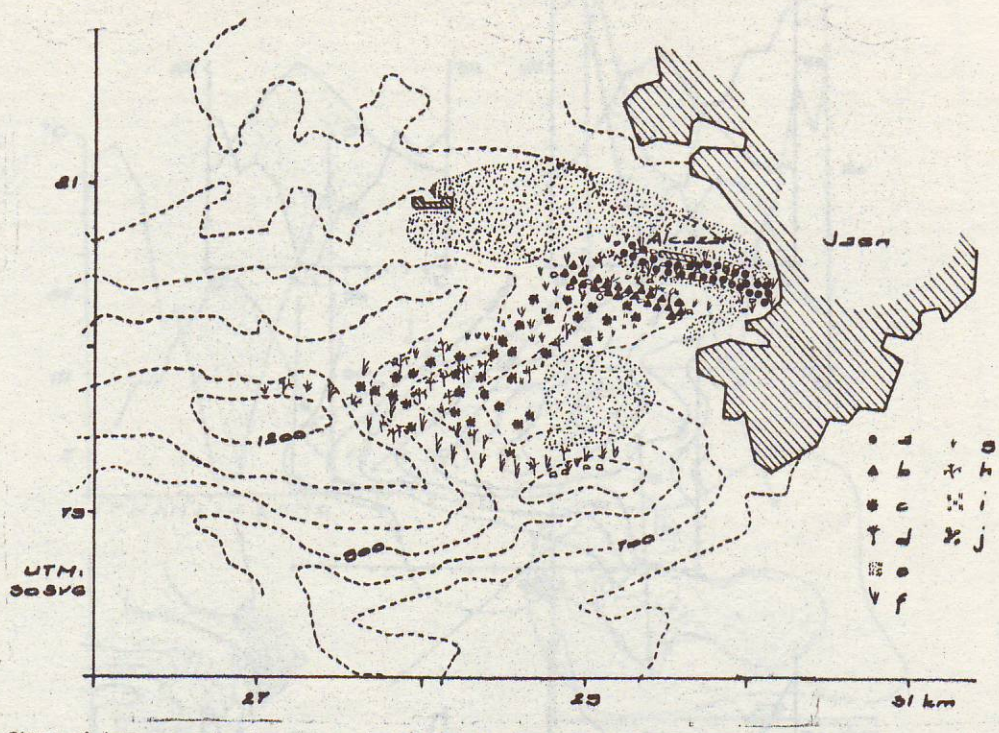


FIG. 12. Sierra of Jaen: map showing the vegetation and the forms of *Iberus* collected. a: form *gualtierianus;* b: intermediate form; c: form *alonensis;* d: cork oak woodland; e: cultivated crops; f: high scrub; g: low scrub; h: thyme; i: grassland; j: saxicole communities.

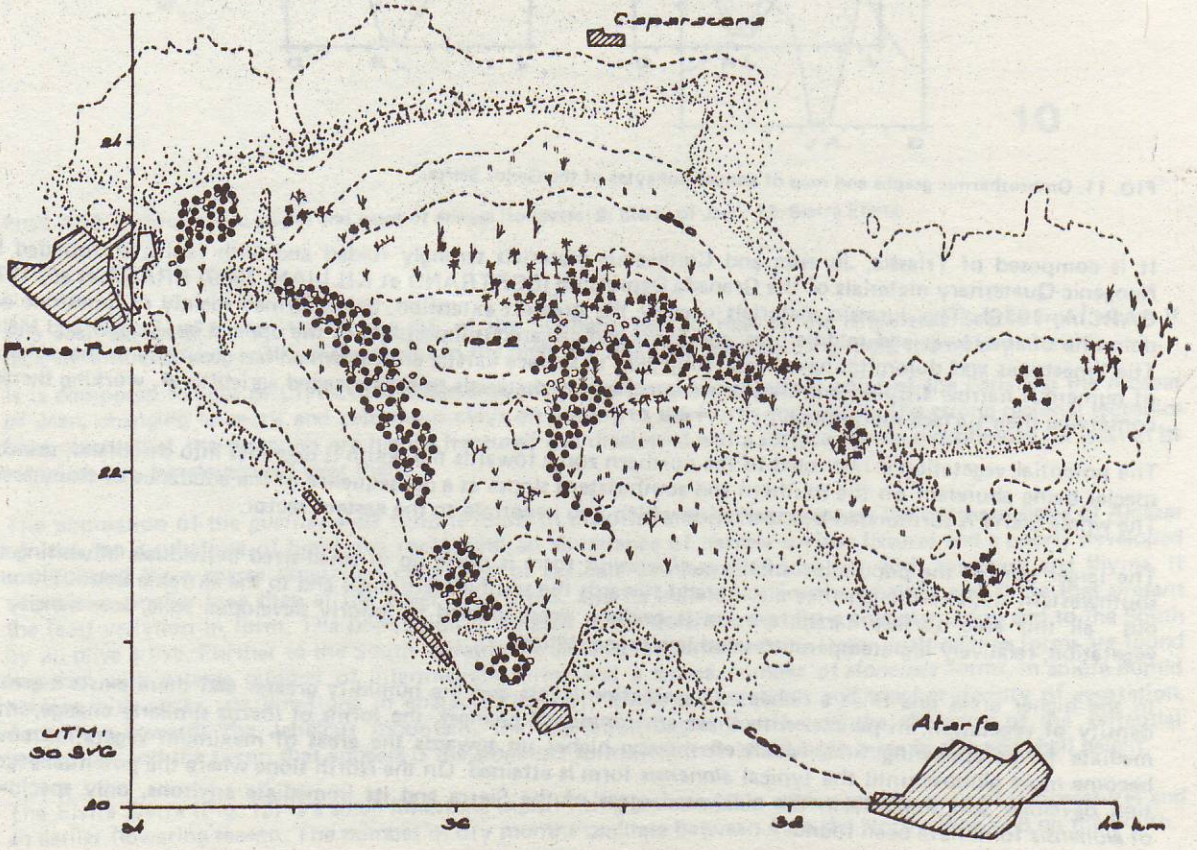


FIG. 13. Sierra Elvira: map showing the vegetation and the forms of *Iberus* collected; for the symbols, see the Fig. 12.

The Gador Sierra (Fig. 14), of which the eastern and southern slopes have been sampled, is a wide massif that in some areas descends directly to the Mediterranean and is subjected to a 5 to 7 month dry period depending upon the areas.

It is composed of outcrops of „alpujarrid" and neogenic-quaternary materials. Amongst the former, together with some none karstic materials, highly fractured and diaclassed dolomitic limestones with karstic morphology, are the most important.

The cork oak woodland installs itself in the higher areas becoming degraded on the East and Southeast slopes where one finds shrub communities with saxicole species; in the South shrub communities on stony ground exist.

In this Sierra of which we possess recent basic information (COBOS, 1979), small areas separated from each other have been sampled.

The East slope which is the driest and that with the highest insolation, most poorly developed soil, sparse vegetation and dolomite rocks, is inhabited by large-sized *gualtierianus* forms. These extend over a much wider area than in the other 2 Sierras reaching the South slope. Some subfossil specimens of *gualtierianus* and *alonensis* forms have also been found.

Still on the South slope, a little more to the West, there is a valley in which the rocks are less fissured, the climate slightly more humid, and there is a greater density of vegetation. Here we have found the intermediate forms, together with some examples of *gualtierianus* and *alonensis* forms on the edge of the area occupied by this subpopulation.

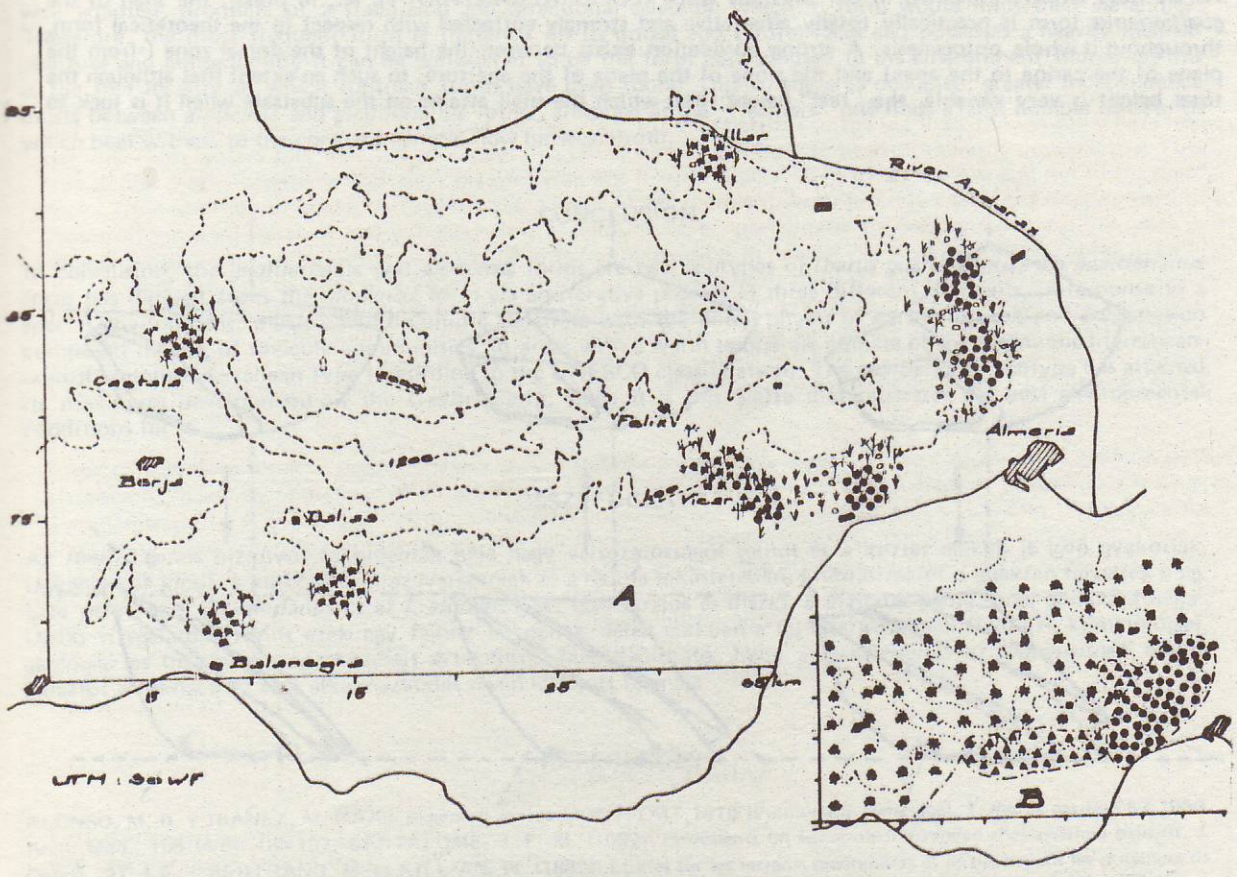


FIG. 14. Sierra of Gador. A: map showing the vegatation and the forms of *Iberus collected*. B: area occupied by *alonensis*, *gualtierianus* and intermediate forms (taken from COBOS, 1979); for the symbols, see the Fig. 12.

More towards the West, from Viacar to Balanegra and Castala, where the temperature is lower and the precipitation higher than that on the East slope, one finds a richer soil on dolomitic or limestone rocks with nuclei of calcareous clays. In this area, only the *alonensis* form has been localized with a great variety of forms and sizes, those of Castala being the largest and most globose. The taxon also extends towards the Northwest where the small-sized specimens of *alonensis* form (from Illar) live on marly materials in an area with a well developed soil, not to dry climate, low relative temperatures and dense vegetation.

DISCUSSION

From an ecological standpoint, the similarity between the 3 localities is clear, although some small differences do exist; at the 3 sites, the morphological changes between the *gualtierianus* and *alonensis* forms are correlated with the ecological changes, and they are produced in the same direction. In effect, the *gualtierianus* form has been found at each locality in the drier and warmer areas on limestone and/or dolomitic ground subjected to at least incipient karstic erosion which accounts for the presence of abundant fissures in the rocks, a poorly developed soil and a basic substrate rich in calcium carbonate upon which a low scrub vegetation grows composed of saxicole communities formed as a consequence of the degradation of the cork oak woodland. The latter attains its maximum in the Gador Sierra where at the same time the vegetation is more stable. It is precisely in this Sierra that the *gualtierianus* form has colonized a greater extension of terrain and has reached a greater size, some indivuals attaining a maximum diameter of 60 mm, the mean being 39 mm.

The *alonensis* form inhabits shadier and less warm areas on marly, limestone and/or dolomitic materials that show less karstic erosion and have a richer soil accompanied by a denser and less degraded vegetation.

The intermediate individuals are found in intermediate environments or mixtures of the former two, and their measurements fall between the means of the extreme forms of each locality. Therefore, in the Jaen Sierra they are larger than *gualtierianus* but smaller than *alonensis;* in the Elvira Sierra they are all smaller, whilst in the Gador Sierra they are larger than *alonensis* but smaller than *gualtierianus*. Consequently, their form and size depends more on the corresponding forms and sizes of *gualtierianus* and *alonensis* forms at each locality which most probably ariese from hybridization, than upon the environmental conditions.

As we have already indicated in our previous work (LÓPEZ ALCÁNTARA *et. al.*, in press), the shell of the *gualtierianus* form is practically totally adaptative and strongly corrected with respect to the theoretical form, throughout it whole ontogenesis. A strong correlation exists between the height of the dorsal zone (=from the plane of the carina to the apex) and the slope of the plane of the aperture, to such an extent that although the total height is very variable, the "real" height (that which the snail attains on the substrate when it is tuck to

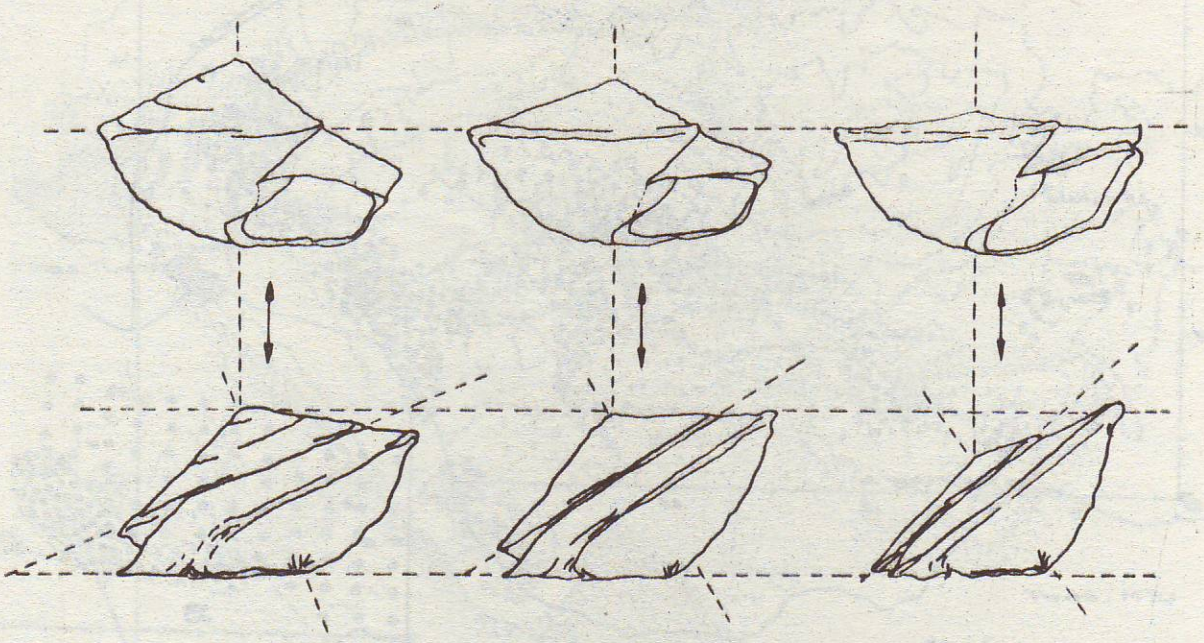


FIG. 15. Form *gualtierianus:* correction of the "real" height by inclination of the aperture.

the same by means of the epiphragma) becomes homogenized (Fig. 15) allowing the snail to introduce itself into the cracks between the rocks. Consequently, it is a taxon perfectly adapted to life in areas with indices of karstic erosion where the *alonensis* form is not to be found.

One could assume that both forms are vicariant subspecies, but the typical *gualtierianus* form is to be found at three different localities isolated geographically from one another if one considers them to be subspecies (in the sense of geographical races), each of the groups corresponding to each locality would be a subspecies, and subsequently there existing 3 subspecies with the typical *gualtierianus* morphology. This idea is unacceptable owing to the high similarity between the 3 populations, a similarity which can only be explained as the result of an iterative process, initiating from a common morphology (the *alonensis* form), and as a response to a similar environment, which is repeated at the 3 localities. Therefore, the *alonensis* and *gualtierianus* forms are ecotypes of the same species.

As regards the origin and variability of the *gualtierianus* form at these 3 localities, in our earlier work we showed that the Elvira Sierra population is that which presents the greatest variability; bearing in mind the small extension of this Sierra, we can assume that this population finds itself in a stage equivalent to a typogenesis, that is to say, commencing to expand and subjected to a disruptive selection that forces the manifestation of all the potential forms; this variability is also supported by the fact that the genetic flow between *alonensis* and *gualtierianus* forms is limited to a concrete zone where the hybrid forms are to be found, which would give a greater freedom of morphological expression to *gualtierianus* form.

The Jaen Sierra population is the most homogeneous and it occupies an even smaller area by being surrounded by an adverse environment created by cultivations. Its sparse morphological variability can be compared to that existing in a stage of incipient typogenesis or typolysis (bearing in mind that its present range could have been greater in epochs prior to cultivation of the area) and it could also be due to the natural hybridizations with the *alonensis* form, which at this locality are important and consequently, the genetic flow between both forms is greater. As a result of this, the relative height of the shell of *gualtierianus* form is the greatest of the 3 localities, and in order to conserve the possibility of entering the fissures between the rocks, a smaller diameter is necessary, that is to say, a smaller size.

The Gador Sierra population shows a homogeneity of forms but not of sizes, and it occupies a wider geographic range. All these phenomena are consistent with what would appear in a stage of typostasis, where the forms are well adapted, products of a stabilizing and directional selection which in turn, would limit their variability. Therefore, the most frequent form is flattened on its dorsal and ventral faces and possesses a heavily inclined aperture and consequently it can be considered to be the form best adapted to the environment. Moreover, this is the sole locality at which subfossil forms have been found. Due to the area occupied, greater independence exists between *alonensis* and *gualtierianus* forms, although at the „frontiers" one finds a large number of hybrids which bear witness to the constant genetic flow between both.

CONCLUSION

In conclusion, the *gualtierianus* and *alonensis* forms are two ecotypes of *Iberus gualtierianus*; the *gualtierianus* form has derived from the *alonensis* form via an iterative process at three different moments, in response to a special environment: a calcareous-dolomitic substrate with the initial phases of karstic erosion and a vegetation composed mainly of saxicole communities, in areas with a warm temperate climate of the thermomediterranean--xerothermomediterranean type (according to the UNESCO classification). The *gualtierianus* ecotype has attained its maximum development in the Gador Sierra, since it is this Sierra that possesses the best environmental conditions for it.

ÖSSZEFOGLALÁS

Az *Iberus* genus bizonyos taxonjainak héja nagy változatosságot mutat és a köztes alakok is igen gyakoriak. Ugyanakkor kicsik a különbségek az ivarszervek és a radula tekintetében, s hibridizációt is gyakran figyeltek meg. Erre példa az *I. gualtierianus* és az *I. alonensis*, az első tarajos és díszes, a második pedig sima, gömbded héjjal. Újabb vizsgálatok szerint ezek egy fajhoz tartoznak. Jelen cikkben e faj elterjedésének földrajzi, klimatológiai, geológiai és botanikai vonatkozásait értékeltük. Megállapítható, hogy a *gualtierianus* az *alonensisnek* egy, a karsztos alapkőzethez való alkalmazkodás révén létrejött formája.

REFERENCES

ALONSO, M. R. y IBÁÑEZ, M. (1978): El género *Iberus* MONTFORT 1810 (Pulmonata: Helicidae). 1. *Iberus rositai* FEZ 1950. Arch. Moll., 108 (4/6): 185-192. BARTALOME, J. F. M. (1982): Comments on some mediterranean rockdwelling helicids. J. Conch., 31: 1-6. – BERTRAND, M. et KILLIAN, W. (1889): Etudes sur les terrains secondaires et tertiares dans les provinces de

Grenade et Malaga. In: Mission d'Andalousie. Mém. Ac. Sc. Paris, 30:378-582. – BOETTGER, C. R. (1913): Aus der Schausammlung. Die Veränderlichkeit der Schale von *Iberus gualtierianus* L. Bericht Senck. Naturf. Gesell., 44, 3:183-197. – BRAGA, J. C., JIMENEZ, A. P. y RIVAS, P. (1979): El Jurásico de Sierra Elvira (estudio especial del Lias medio y superior). Cuad. Geol. Granada, 10:597-604. – COBOS, A. (1979): Sobre algunos *Iberus* MONTFORT de la provincia de Almería (Gastrop. Pulmon.). Bol. Soc. Hist. Nat. Baleares, 23:35-46. – GARCIA, V. (1976): La zona subbética al Norte de Granada. Tesis Doctoral (inedited) University of Granada. – GARCIA SAN NICOLAS, E. (1957): Estudios sobre la biología, la anatomía y la sistemática del género *Iberus* MONTFORT 1810. Bol R. Soc. Esp. Hist. Nat. (B.), 55:199–390. – JACQUIN, J. P. (1970): Contribution à l'étude géologique et minière de la Sierra de Gador (Almería, Espagne). Thése Nantes, 1-501. – LÓPEZ ALCÁNTARA, A., RIVAS, P., ALONSO, M. R. y IBÁÑEZ, M.(1983):Variabilidad conquiológica de *Iberus gualtierianus* (IV Congr. espanol Malac., Gijón, 1982). Iberus (in press). – RIVAS, M. (1981): Les étages bioclimatiques de la végétation de la péninsule Ibérique. Actas III Congr. optima, Anal. Jard. Bot. Madrid, 37 (2): 251-268. – SANZ DE GALDEANO, C. (1974): Geología de la transversal Jaén-Frailes (provincia de Jaen), Tesis Doctoral, Universidad de Granada: 1-274. – UNESCO (1963): Recherches sur la zona aride: Carte bioclimatique de la zone Méditérranéenne: 1-47. Notice explicative. Paris.

M. R. ALONSO and M. IBÁÑEZ

Department of Zoology
University of La Laguna
Tenerife, Canary Isles
Spain

A. LÓPEZ ALCÁNTARA and R. RIVAS

Department of Paleontology
University of Granada
Spain