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GEOGRAPHIC VARIATION IN THE AFRICAN-IBERIAN GROUND BEETLE *RHABDOTOCARABUS MELANCHOLICUS* (COLEOPTERA: CARABIDAE) AND ITS TAXONOMICAL AND BIOGEOGRAPHICAL IMPLICATIONS

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ABSTRACT

A study of morphological variation among populations from southern Spain and northwestern Africa of *Rhabdotocarabus melancholicus* (Fabricius, 1798) shows that there is statistical support for the recognition of three taxa: *R. m. submeridionalis* (Breuning, 1975) distributed over southeastern Spain, *R. m. dehesicola* n. ssp. from southwestern Spain and southern Portugal and *R. m. melancholicus* geographically restricted to northwestern Africa. This new arrangement changes previous biogeographic pictures for the genus, since *R. m. melancholicus* is not present in Europe and the range of variation observed within Iberian *R. melancholicus* is increased with new endemic taxa. We propose that the current differentiation among taxa is the result of successive vicariance events caused by dramatic paleogeographic changes which have occurred in the western Mediterranean region since the Mio-Pliocene boundary.

Key words: Coleoptera, Carabidae, morphological variation, Biogeography, Mediterranean region.

RESUMEN

Variación geográfica en el carábido íbero-africano *Rhabdotocarabus melancholicus* (Coleoptera: Carabidae) y sus implicaciones taxonómicas y biogeográficas

Un estudio de la variación morfológica de poblaciones del sur de España y del noroeste de África de *Rhabdotocarabus melancholicus* (Fabricius, 1798) permite reconocer estadísticamente la existencia de dos taxa en las porciones meridionales de la Península Ibérica: *R. m. submeridionalis* (Breuning, 1975) distribuido por la región suroriental ibérica y *R. m. dehesicola* n. ssp. del suroeste de España y sur de Portugal; un tercer taxon, *R. m. melancholicus*, antes incluido en la fauna ibérica se considera ahora exclusivo del noroeste de África. Esta nueva estructura taxonómica cambia el cuadro biogeográfico previamente considerado para el género, ya que *R. m. melancholicus* no se encuentra en Europa, mientras que la diversidad taxonómica observada en Iberia se incrementa con dos táxones endémicos. Proponemos que la diferenciación observada es el producto de eventos vicariantes sucesivos resultado de los amplios cambios paleogeográficos producidos en la región mediterránea occidental desde el límite Mio-Pliocénico.

Palabras clave: Coleoptera, Carabidae, variación morfológica, Biogeografía, región mediterránea.

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Introduction

The geographic range of *Rhabdotocarabus melancholicus* (Fabricius, 1798), the only species in the genus, includes the Rif mountains and adjacent areas of northern Morocco in northwestern Africa and the Iberian Peninsula in southwestern Europe (Breuning, 1935). Three geographic units are currently recognized along its range, *R. m. melancholicus* (Fabricius, 1798), distributed over northern Morocco and southeastern Spain on both sides of the Strait of Gibraltar; *R. m. submeridionalis* (Breuning, 1975), restricted to the areas not occupied by *R. m. melancholicus* in the southern half of the Iberian Peninsula; and *R. m. costatus* (Germar, 1824) widely distributed over the northern half of the Iberian Peninsula (Breuning, 1935; Jeanne, 1969; Krätschmer, 1983; Zaballos & Jeanne, 1994).

The current geographic substructure within southern *R. melancholicus*, poses both biogeographic and taxonomic problems. Land connection in the western Mediterranean Region between African and European coasts was definitively interrupted by the opening of the Gibraltar Strait, 5.5 million years ago (Fernix, *et al*., 1967; Hsü, 1983). Connections among lands in southern Iberia during early Pliocene, were mostly interrupted with the flooding of the deeply incised Guadalquivir River Bassin about 3-4 Ma ago. The formation of deep fluvial drainages during the Pliocene (López Martínez, 1989) has been considered important as speciation events in different Iberian taxa (Arntzen & García-París, 1995; Busack, 1986; Doadrio, 1988). Therefore we expect differentiation between African and European taxa begining at least 5 Ma ago, while differentiation among southern Iberian taxa may have occur throughout most of the Pliocene and the Pleistocene, with many possibilites for genetic exchange among incipient lineages. The current taxonomy of *Rhabdotocarabus* however, suggests that morphological differentiation within *R. melancholicus* has been much larger between two adjacent groups of southern European populations than between European and African populations separated by the Strait of Gibraltar. This is based on the fact that populations from southern Iberia are grouped into two morphologically defined subspecies, *R. m. submeridionalis* and *R. m. melancholicus*, while both African and southeastern Iberian populations are included in the single morphological unit, *R. m. melancholicus*. Various explanations can account for this pattern of morphological differentiation, including morphological stasis in some areas but not in others, or recent (i.e. Pleistocene) dispersal across sea barriers. Alternatively, we suggest that morphological differentiation between African and European populations of *Rhabdotocarabus* simply has been underestimated, since they share a general color pattern and no morphometric studies have been attempted to discriminate among them. Therefore, closer examination and analysis of morphological differentiation should result in a clear distinction among African and European groups.

An additional taxonomic problem results from the designation of the *R. m. submeridionalis* holotype. The name *R. m. submeridionalis* was applied to a group of morphologically distinct populations distributed over central and southwestern Iberia (Breuning, 1975; Krätschmer, 1983); however the type locality (Estepona, Málaga) is

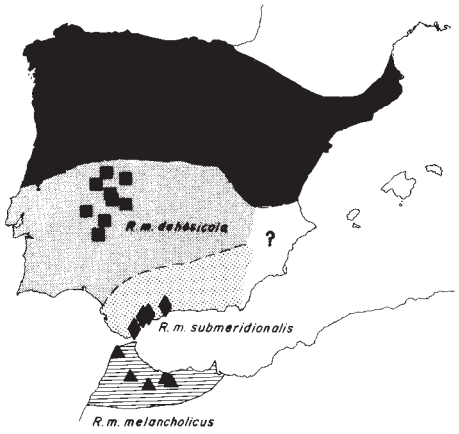

Fig. 1. Map of the Iberian Peninsula and northwestern Africa showing the localities of material examined and the geographic range of *R. melancholicus*. Triangles indicate *R. m. melancholicus*; diamonds *R. m. submeridionalis*; and squares *R. m. dehesicola* n. ssp.

Fig. 1. Mapa de la Península Ibérica y noroeste de África donde se muestran las localidades del material examinado y la distribución geográfica de *R. melancholicus*. Los triángulos indican *R. m. melancholicus*, los rombos *R. m. submeridionalis* y los cuadrados *R. m. dehesicola* n. ssp.

clearly included within the range of *R. m. melancholicus* in southeastern Spain (Krätschmer, 1983; Zaballos & Jeanne, 1994) (Fig. 1). Therefore, if the southwestern and southeastern populations are in fact distinct, a new name would be required for the southwestern group. The problem is complicated by the fact that currently recognized *R. m. melancholicus* may be composed of two taxonomic entities. If so, the name *R. m. submeridionalis* would be available for populations in southeastern Spain while *R. m. melancholicus* would be applied exclusively to the populations of northwestern Africa.

Before the biogeographic problem can be resolved it is necessary to discriminate between the following hypotheses: whether a single morphological unit inhabits both Africa and Europe, or if there are two differentiated units, an African and an European one. In order to test these alternative hypotheses, we present the results of a quantitative analysis of prothoracic and elitral measurements from the populations in question, providing morphological characters for taxon recognition. We redescribe the taxon inhabiting western Spain and southern Portugal as *R. m. dehesicola* n. ssp., and provide a discriminant function to ascribe additional material to each taxon. We also propose a new biogeographic hypothesis for morphological evolution within *Rhabdotocarabus* in congruence with current paleogeographic models of the western Mediterranean region.

Material and methods

Sixty-eight specimens of *R. melancholicus* from 18 populations in southern Spain and northern Morocco were grouped for the analysis into three geographic units, based on the characters provided by Breuning (1975) and Krätschmer (1983). Group 1: includes 30 specimens from Morocco corresponding to typical *R. m. melancholicus*; Group 2: includes 11 specimens collected near the type locality of *R. m. submeridionalis* on the coast of the provinces of Málaga and Cádiz (Spain); Group 3: includes 27 individuals from western Spain populations corresponding to *R. m. dehesicola* n. ssp., previously considered *R. m. submeridionalis* (Krätschmer, 1983) (Fig. l) (see Appendix 1 for precise collection data). All the material studied is in the collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain) (col. MNCN) except some of the *R. m. submeridionalis* that are in the private collections of M. Soler (col. MS) and J.A. Fernández-Cortés (col. FC).

After a survey for qualitative diagnostic morphological characters for each group based on the examination of mounted dry specimens and male genitalia, five measurements (A to E) were taken on camera lucida drawings of the prothorax in dorsal view, as indicated in Fig. 2. Elytra length (F) from the base of the scutellum to the posterior end, and maximum width of each elytron, were measured using a digital micrometer with accuracy of 0.001 mm (Nikon). Elytron width (G) was estimated as the mean of right and left measurements. All specimens were measured by the same person.

Discriminant analyses were performed to describe the degree of effective separation of the previously defined groups and to provide discriminant functions. Males and females were analyzed separately . The discriminant analyses must be interpreted with caution since sample sizes are not equivalent for all taxa. The statistical analyses were carried out using the Systat 5 Statistical Package (Wilkinson, 1989) on a Macintosh computer.

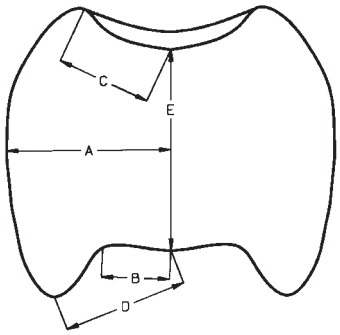

Fig. 2. Schematic drawing of a *R. melancholicus* prothorax showing the measurements taken. Reference points for measurements are defined by connections between structures, points of maximum inflexion, and the tangent to the prothoracic margin that is parallel to the median line.

Fig. 2. Esquema del protórax de *R. melancholicus*, donde se indican las medidas tomadas. Los puntos de referencia para dichas medidas están definidos por conexiones entre estructuras, puntos de inflexión máxima y la tangente del margen protorácico que es paralela a la línea media.

Table I. Mean and standard deviation of seven morphometric variables in *R. m. melancholicus, R. m. submeridionalis* and *R. m. dehesicola* (see text and Fig. 2 for explanation).

Tabla I. Media y desviación estándar de siete variables morfométricas en *R. m. melancholicus, R. m. submeridionalis* and *R. m. dehesicola* (para más información ver texto y Fig. 2).

		A	B	C	D	E	F	G
R. m. melancholicus	Mean	6.6	1.3	3.4	1.9	2.0	3.7	1.8
n= 30	SD	0.29	0.10	0.28	0.12	0.13	0.19	0.12
R. m. submeridionalis	Mean	6.3	1.3	3.3	1.7	1.9	3.4	1.7
n= 11	SD	0.34	0.13	0.26	0.14	0.18	0.21	0.10
R. m. dehesicola	Mean	6.7	1.3	3.8	1.8	1.9	3.7	1.8
n= 27	SD	0.27	0.10	0.28	0.10	0.32	0.13	0.11

Results

Rhabdotocarabus m. submeridionalis was diagnosed as an intermediate form between *R. m. melancholichus* and *R. m. costatus* (Breuning, 1975), while Krätschmer (1983) provided additional diagnostic characters to distinguish *R. m. submeridionalis* from *R. m. melancholicus,* based on prothorax shape and coloration pattern. However, both authors (Breuning, 1975; Krätschmer, 1983) included the type locality of *R. m. submeridionalis* in the supposed geographic range of the Iberian *R. m. melancholicus* (southeastern Spain). Moreover, the external characters provided by Krätschmer (1983) to characterize *R. m. submeridionalis* completely match the characters of our western sample (*R. m. dehesicola*) (group 3), but do not apply to material from *R. m. submeridionalis* type locality (group 2). A characterization of the different groups is thus needed. To avoid further nomenclatorial problems we use from here on the name *R. m. submeridionalis* to the group of populations living around its type locality in southeastern Spain, previously considered *R. m. melancholicus* (group 2); the name *R. m. dehesicola* n.ssp. to the populations inhabiting southwestern Spain and Portugal, previously considered *R. m. submeridionalis* (group 3); while *R. m. melancholicus* is only used for the North-African populations (group l) (Fig. 1).

Moroccan (*R. m. melancholicus*) and southeastern Spanish (*R. m. submeridionalis*) populations have a prothoracic shape characterized by a subquadrangular pronotum, with almost parallel posterior edges in Moroccan individuals, and slightly convergent in southeastern Spanish individuals. Moroccan and southeastern Spanish populations

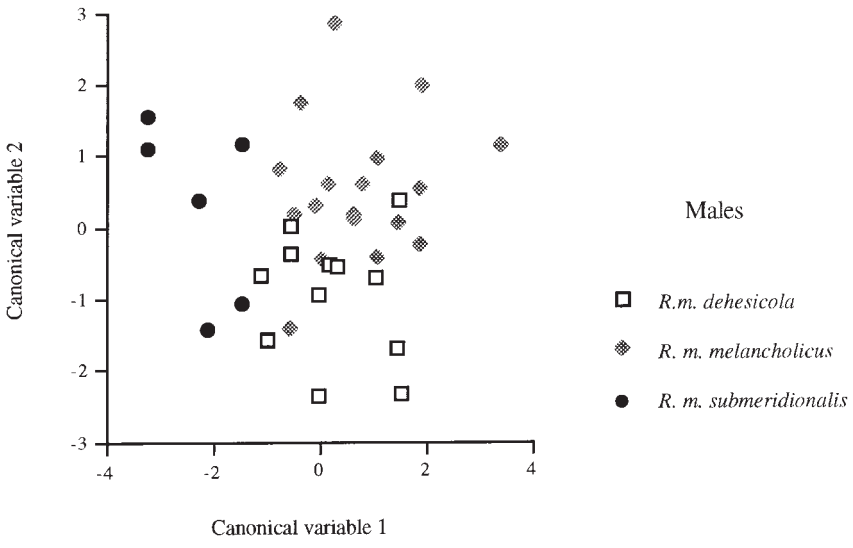

Fig. 3. Plot of the discriminant scores for male *R. m. melancholicus*, *R. m. submeridionalis* and *R. m. dehesicola* obtained from the analysis of seven morphometric variables (see Table II).

Fig. 3. Análisis discriminante para machos de *R. m. melancholicus*, *R. m. submeridionalis* y *R. m. dehesicola* obtenido a partir de siete variables morfométricas (ver Tabla II).

Table II. Discriminant function to distinguish among males of the southern subspecies of *R. melancholicus*. The analysis is based in seven prothoracic and elytral measurements.

Tabla II. Función discriminante para distinguir entre los machos de las subespecies sureñas de *R. melancholicus*. El análisis está basado en siete medidas protorácicas y elitrales.

A. Group classification function coefficents. *Rmm = R. m. melancholicus*; *Rms = R. m. submeridionalis*; *Rmd = R. m. dehesicola*.

Variable	*Rmm*	*Rms*	*Rmd*
A	-25.35	-22.24	-15.22
B	-55.39	-71.52	-60.15
C	29.91	25.09	20.42
D	92.52	82.96	91.86
E	120.28	105.67	112.00
F	26.92	28.92	23.81
G	-63.51	-52.98	-52.91
Constant	-407.31	-366.93	-401.66

B. Classification success among groups (males)

	Predicted group		
Actual group	*Rmm*	*Rms*	*Rmd*
Rmm (n = 17)	14 (82.4%)	O (0%)	3 (17.6%)
Rms (n = 6)	0 (0%)	6 (100%)	0 (0%)
Rmd (n= 12)	0 (0%)	1 (8.3%)	11 (91.7%)

Table III. Discriminant function to distinguish among females of the southern subspecies of *R. melancholicus*. The analysis is based in seven prothoracic and elytral measurements.

Tabla III. Función discriminante para distinguir entre las hembras de las subespecies sureñas de *R. melancholicus*. El análisis está basado en siete medidas protorácicas y elitrales.

A. Group classification function coefficents. *Rmm = R. m. melancholicus*; *Rms = R. m. submeridionalis*; *Rmd = R. m. dehesicola*.

Variable	*Rmm*	*Rms*	*Rmd*
A	40.68	57.37	62.03
B	57.62	22.25	39.70
C	-101.73	-97.04	-111.02
D	23.78	31.41	16.50
E	4.75	-20.49	-9.77
F	0.83	6.02	-2.44
G	79.20	68.65	91.65
Constant	-336.23	-317.82	-333.88

B. Classification success among groups (females)

	Predicted group		
Actual group	*Rmm*	*Rms*	*Rmd*
Rmm (n= 13)	12 (92.3%)	0 (0 %)	1 (7.7 %)
Rms (n = 5)	0 (0%)	5 (100 %)	0 (0 %)
Rmd (n= 15)	1 (6.7%)	1 (6.7 %)	13 (86.6 %)

show narrower lateral margins and narrower posterior prothoracic expansions than southwestern Spanish populations (*R. m. dehesicola*). *Rhabdotocarabus m. dehesicola* shows a prothorax wider than it is long with concave posterior edges, expanded margins and wider posterior prothoracic

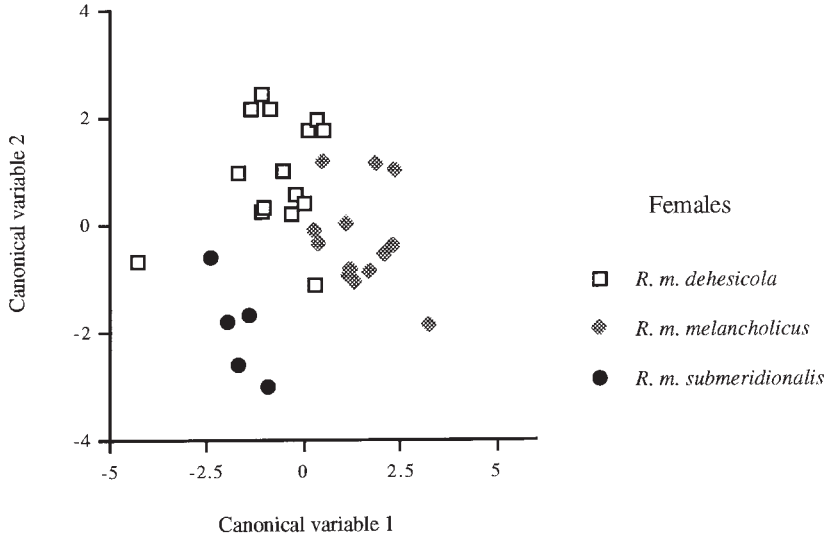

Fig. 4. Plot of the discriminant scores for female *R. m. melancholicus, R. m. submeridionalis* and *R. m. dehesicola* obtained from the analysis of seven morphometric variables (see Table III).

Fig. 4. Análisis discriminante para hembras de *R. m. melancholicus, R. m. submeridionalis* y *R. m. dehesicola* obtenido a partir de siete variables morfométricas (ver Tabla III).

expansions. Vertex punctuation is very dense and extends almost until mandibular insertion in *R. m. dehesicola*, while it is restricted to the posterior part of the head in both *R. m. melancholicus* and *R. m. submeridionalis*. General shape is elongated in *R. m. melancholicus* and *R. m. submeridionalis* while it appears stouter in *R. m. dehesicola*. General coloration is dark bronze to dark brown with metallic reflections restricted to the elytral shoulders and prothoracic margins in Moroccan populations (*R. m. melancholicus*), while it is dark brown with a more shiny background at the elytral and prothoracic margins in *R. m. submeridionalis*. General coloration of *R. m. dehesicola* is bronze-copper to dark olive green, with metallic green reflections over most of the prothorax, vertex and elytra surfaces; the reflections are more intense at the margins of the prothorax and elytra. There are no differences in male genitalia among the three groups, although all of them differ conspicuously from the northern *R. m. costatus*, as Raynaud (1972) and Krätschmer (1983) pointed out.

Mean and standard deviation of all measurements for each group are shown in Table 1. The results of the discriminant analysis show effective discrimination among the three southern groups, using both males (Fig. 3) and females (Fig. 4). The proportion of correct classifications is greater than 82% for all three groups, for both males and females (Tables 2 and 3). The existence of three morphologically differentiated groups of populations within southern *R. melancholicus*, corresponding to *R. m. melancholicus*, *R. m. submeridionalis* and a southwestern group (*R. m. dehesicola*), is thus supported.

The taxonomic implications of these results are first that *R. m. submeridionalis* is a valid taxon distributed over southeastern Spain which includes neither the populations studied by Krätschmer (1985) under that name, nor some of the paratypes from western Spain of Breuning's (1975) type series of *R. m. submeridionalis*. Second, the well-characterized populations from western Spain require a new name. The description of these populations as a new taxon, *R. m. dehesicola* is presented below. And third, *R. m. melancholicus* is endemic to north-western Africa.

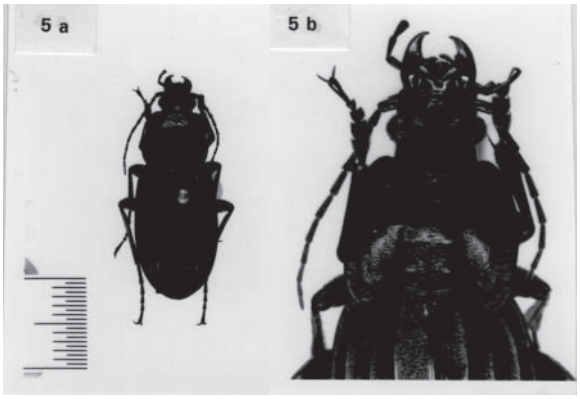

Fig. 5. Dorsal views of the holotype of *R. m. dehesicola*. 5a: general habitus; 5b: detail of prothorax and head.

Fig. 5. Vista dorsal del holotipo de *R. m. dehesicola*. 5a: habitus; 5b: detalle de la cabeza y del protórax.

Rhabdotocarabus melancholicus dehesicola n. ssp.

MATERIAL: Holotype: Male from Torrejón El Rubio, Monfragüe, province of Cáceres (Extremadura, Spain), 3-I-1988, J. Dorda & M. Esteban leg., col. MNCN. Paratypes: Spain: Badajoz: Alburquerque, 27-XII-1989 (1 male), M. García-París leg., col. MNCN; Alconera, Puerto de Santo Domingo, 27-XII-1985 (2 males), M. García-París leg., col. MNCN; Embalse de Proserpina, Mérida, 8-XI-1988 (1 female), R. Márquez leg., l0-XI-1988 (1 male, 1 female), A. García Martínez leg., col. MNCN; Mérida, 26-III-1986 (2 males), M. García-París leg., 3-I-1986 (2 females), M. García-París leg., 5-I-1986 (1 female), J. Dorda leg., col. MNCN. Cáceres: Logrosán, l9-IV-1984 (1 female), M. García-París leg., 27-XII-1985 (1 male), M. García-París leg., 3-I-1988 (1 male, 2 females), C. Martín & M. García-París leg., col. MNCN; Navalmoral de la Mata, 4-V-1987 (1 male), C. Martín & M. García-París leg., 27-XI-1989 (1 female), M. García-París leg., col. MNCN; Pescueza, 29-III-1983 (1 male), E. Gómez Granado leg., col. MNCN; Santibáñez el Alto, 7-XII-l990 (1 female), C. Martín & M. García-París leg., col. MNCN; Torrejón El Rubio, Monfragüe, XI-1985 (1 female), J. Dorda & M. Esteban leg., 26-I-1986 (1 male, 1 female), J. Dorda &, M. Esteban leg., col. MNCN; Trujillo, l9-III-1987 (2 females), C. Martín & M. García-París leg., col. MNCN.

DIAGNOSIS.— The non-terminally constricted male aedeagus places *R. m. dehesicola* in the *R. m. melancholicus* group. *R. m. dehesicola* is distinguished from *R. m. melancholicus* and *R. m. submeridionalis* by its broader prothorax with expanded margins, coppery-bronze metallic coloration, and pits of the vertex extending from the eyes to the mandibular insertion.

DESCRIPTION OF THE HOLOTYPE.— Male (field number 305) (Fig. 5). Total length (from the tips of the mandibles to the posterior end of the elytra): 25.0

mm; pronotum length (from the anterior end to the tip of the pronotal expansions): 6.2 mm; maximum pronotum width: 7.3 mm; and elytra length: 14.8 mm. Head long and narrow. Lateral edges of the vertex delimited by a strong keel running from the posterior edge of the eye to the end of the epistome. This keel forms an angle at the mandibular insertion point. Dorsal surface of the vertex covered by dense large foveolae, decreasing in size and density towards the epistome, but reaching at least the mandibular insertion. Prothorax wider than it is long, with expanded margins and broad posterior prothoracic expansions. Pronotal surface covered by shallow pits progressively transformed to fine granuli at the posterior expansions. Median prothoracic line marked. Two large depressions in the posterior half of the pronotum. Long, convex elytra. Wide elytral margin. Continuous, pronounced dorsal ridges with smooth rounded tops. Elytral intervals with a rough surface covered by dense pointed granuli that vary in size, the median ones being bigger. Black shiny limbs. First to fourth protarsal segments expanded. Distal portion of the mesotibiae with a dense goldish hairy brush in dorsal position. Seven terminal antennae segments densely covered by short setae. Smooth shiny ventral terguites in the median region, rugous at the sides. Last ventral terguite with shallow pits that become shallow furrows at the terminal edge.

Coppery-brown dorsal coloration with green metallic reflections over the entire surface. The reflections are more intense at the margins of the elytra and prothorax, especially at the elytral shoulders. Black shiny ventral surfaces and limbs.

VARIATION.— Female paratypes similar to male but larger, with non-expanded protarsi and less developed mesotibial brushes. Measurements of a paratype female (field number 312) are: Total length: 28.3 mm; pronotum length: 6.9 mm; pronotum width: 8.2 mm; length of the elytra: 17.3 mm.

Median prothoracic line and posterior depressions can be almost invisible in some individuals. Dorsal coloration varies from dark olive green to dark brown, always with a copper or bronze metallic hue over the entire surface.

ETYMOLOGY.— The epithet "dehesicola", a substantive in apposition, is derived from the Spanish "dehesa" and the Latin "-cola" ("inhabitant"), and refers to these beetles as the inhabitants of the "dehesa", a human-modified *Quercus* savannah like forest which is the main habitat of the species in western Spain.

HABITAT AND GEOGRAPHIC DISTRIBUTION.— *R. m. dehesicola* is a riparian beetle usually found during the day under stones close to small streams or around temporary ponds. Active behavior has been observed on rainy nights when animals were seen walking on wet soil around ponds. Most of the captures have been made in flat "dehesas" of *Quercus ilex ballota* (Desf.) Samp. and *Q. suber* L., or in hilly *Q. i. ballota* forests with a high density of shrubs.

R. m. dehesicola is endemic to southern Spain and Portugal, north to the Guadalquivir River. Its distribution in Portugal ranges from the Algarve in the south to the Tajo basin in the north (Krätschmer, 1983). Its distribution in Spain ranges from the southern slopes of the Sistema Central mountains along the provinces of Cáceres and Toledo in the north, to the province of Huelva in the south, with local penetrations in western portions of Cádiz province (Zaballos & Jeanne, 1994). The northern limit of the subspecies is marked by the contact zone with *R. m. costatus*. The southern limit is defined by the contact zone with *R. m. submeridionalis* in Cádiz province, while the eastern limits of its range are not yet defined.

Discussion

Four morphologically differentiated taxa can be recognized within *R. melancholicus*. A northern form, *R. m. costatus*, well characterized based on aedeagus shape, color pattern, body proportions, and sculpturing of dorsal structures (Breuning, 1935; Jeanne, 1969; Raynaud, 1972; Krätschmer, 1983), and three distinct southern taxa statistically supported in our analysis: *R. m. melancholicus, R. m. submeridionalis* and *R. m. dehesicola*. Based on aedeagus shape and general body proportions, the affinities of the three southern groups (*R. m. melancholicus, R. m. submeridionalis* and *R. m. dehesicola*) to each other are greater than the affinities of any to the northern populations included in *R. m. costatus*. The contact zone between the northern *R. m. costatus* and the southern groups has not been studied yet, but some data support the existence of

a narrow hybrid zone between *R. m. costatus* and *R. m. dehesicola* in the western slopes of the mountains of the Sistema Central Range (Krätschmer, 1983; García-París, unpublished data). The northeastern limit of the distribution of *R. m. submeridionalis* is unknown, although the limit proposed by Krätschmer (1983), including the Sierra of Alcaraz (province of Albacete), should be considered as an initial hypothesis. The contact zones among the three southern groups are also unknown. The discriminant functions provided here can be used to assign individuals of intermediate localities to one of the two southern subspecies. However, based on their similarity in aedeagus shape and the lack of important geographic barriers, large areas of mor-phological transition are expected.

Biogeographic implications

This new taxonomic structure within southern *R. melancholicus* is congruent with current hypotheses of western Mediterranean paleogeography (López Martínez, 1989). According to such hypotheses we can reconstruct an evolutionary scenario based on vicariance processes to explain current geographic substructure within southern *R. melancholicus*. The initial stock of southern *R. melancholicus* isolated in the Betic-Riffean massif, was cut into two separate units by the formation of the Strait of Gibraltar about 5.5 Ma ago during Miocene-Pliocene transition (Fernix *et al*., 1967; Hsü, 1983). Subsequent filling of the Mediterranean Basin and the Pliocene inundation of the Guadalquivir River Basin by the sea, created a geographic barrier separating Iberian populations into two groups again, one corresponding to present day populations of *R. m. dehesicola* distributed on the northern side of the Guadalquivir river basin, the other corresponding to *R. m. submeridionalis* located south to the Guadalquivir River Valley. Isolated populations of *R. m. dehesicola* found in the southern shore of the Guadalquivir River valley in the province of Cádiz (Zaballos & Jeanne, 1994) could be the result of recent (Holocene) migration, since sediment deposits and drought could facilitate the dispersal of *Rhabdotocarabus* across the river.

Further studies including a phylogenetic analysis using a complete set of morphological or molecular characters would allow a test of the proposed biogeographic hypothesis for *R. melancholicus* differentiation. If *R. m. melancholicus*, the African taxon, is not the sister group of a southern Iberian clade formed by *R. m. submeridionalis* and *R. m. dehesicola*, the proposed model would be rejected. A review of the taxonomic position of *R. m. costatus* and of the contact zones among taxa are also needed in order to generate a more general scenario for *Rhabdotocarabus* evolution.

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Appendix I

Material examined

***R. m. melancholicus*:** Morocco: Ben Saada, El Ajmas, Yebala, VI-1930 (1 female) col. MNCN; Iguermalen, Beni Mesdui, VI-1932 (3 males, 2 females) col. MNCN; Tamorot, Beni Haled, VI-1930 (1 female) col. MNCN; Tanger (12 males, 9 females) col. MNCN; Tizi Taka, Beni Seddat, Rif, VI-1932 (2 males) col. MNCN.

***R. m. submeridionalis*:** Spain: Cádiz: Guadiaro, 9-XI-l990 (1 female) col. MNCN. Málaga: Estepona, 24-XII-1993 (1 male) col. MNCN. Los Prados, Málaga, III-1979 (1 male), 16-IX-1980 (1 male), 18-III-1981 (1 female), 7-III-1981 (1 female) col. FC; Fuente la Yedra, Málaga, without date (1 male), col. MS, 5-XI-1982 (1 male), 30-X-1982 (1 male, 1 female), col. FC; San Pedro de Alcántara, Málaga, 13-XII-1985 (1 male, 1 female) col. MS.

***R. m. dehesicola*:** Spain: Badajoz: Alburquerque, 27-XII-1989 (1 male) col. MNCN; Alconera, Puerto de Santo Domingo, 27-XII-1985 (2 males) col. MNCN; Embalse de Proserpina, Mérida, 8-XI-1988 (1 female), l0-XI-1988 (1 male, 1 female) col. MNCN; Mérida, 26-III-1986 (2 males), 3-I-1986 (2 females), 5-I-1986 (1 female), col. MNCN, ll-XI-1988 (1 female), col. MS. Cáceres: Logrosán, l9-IV-1984 (1 female), 27-XII-1985 (1 male), 3-I-1988 (1 male, 2 females) col. MNCN; Navalmoral de la Mata, 4-V-1987 (1 male), 27-XI-1989 (1 female) col. MNCN; Pescueza, 29-III-1983 (1 male) col. MNCN; Santibáñez el Alto, 7-XII-l990 (1 female) col. MNCN; Torrejón El Rubio, Monfragüe, XI-1985 (1 female), 26-I-1986 (1 male, 1 female), 3-I-1988 (1 male) col. MNCN; Trujillo, l9-III-1987 (2 females) col. MNCN.

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