

Convergences and divergences between two European mountain dung beetle assemblages (Coleoptera, Scarabaeoidea)

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Abstract

Convergences and divergences between two European mountain dung beetle assemblages (Coleoptera, Scarabaeoidea).— We analyzed the altitudinal change in dung beetle species richness and the relative proportion of higher taxa, as well as the turnover in the type of distribution and range size of species in two mountain chains located at the two extremes of Europe (Western Rhodopes Mountains and the Iberian Central System). Both mountain ranges showed a clear substitution among higher taxa (Aphodiinae–Geotrupinae vs. Scarabaeidae) and species richness variation with the altitude was similar. We suggest that East European dung beetle assemblages are conditioned by a horizontal colonization process in which mountains had been reached in relatively recent geological time by elements coming from different latitudes. In spite of these convergences, Rhodopes dung beetle assemblages are characterized by a significantly lower proportion of narrowly distributed species and a lower relevance of Aphodiinae species in lowland places. Although these divergences can be partially attributed to the dissimilar sampling effort accomplished in both regions, we suggest that the low number on narrowly distributed species could be due to the different role of these two mountain zones as refuges during glacial–interglacial Pleistocene cycles.

Key words: Scarabaeoidea, Dung beetles, Altitudinal variation, Rhodopes mountain range, Iberian Central System, Refuges.

Resumen

Convergencias y divergencias entre dos comunidades coprófagas de montaña europeas (Coleoptera, Scarabaeoidea).— Compilando toda la información faunística disponible sobre los coleópteros coprófagos de dos zonas montañosas desconectadas, ubicadas a ambos extremos de Europa (los Rhodopes Occidentales y el Sistema Central Ibérico), hemos analizado el cambio altitudinal en la riqueza de especies, la modificación en la proporción relativa de los principales grupos taxonómicos implicados, así como el relevo en el tipo de distribución y el tamaño del rango geográfico de las especies implicadas. Ambas zonas de montaña muestran un patrón evidente de sustitución entre taxones de alto rango (Aphodiinae–Geotrupinae vs. Scarabaeidae) y también parecidas tasas de variación en la riqueza de especies con la altura. Sugerimos que las comunidades coprófagas del este de Europa están también condicionadas primordialmente por un proceso de colonización horizontal, en el cual las montañas serían colonizadas en periodos geológicos recientes por elementos procedentes de latitudes septentrionales. A pesar de estas convergencias, las comunidades de los Rhodopes se caracterizan por una significativa menor presencia de especies con rangos de distribución restringidos y una escasa relevancia de las especies de Aphodiinae en las zonas de menor altitud. Aunque estas divergencias pueden atribuirse parcialmente a diferencias en el esfuerzo de colecta realizado en ambas regiones, consideramos el escaso número de especies con distribución restringida estaría relacionado con el distinto papel ejercido por estas montañas como refugio durante los ciclos glaciares del Pleistoceno.

Palabras clave: Scarabaeoidea, Escarabajos coprófagos, Variación altitudinal, Rhodopes, Sistema Ibérico Central, Refugios.

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Introduction

Altitudinal variations in species richness and faunistic composition are unavoidably related with the environmental gradients provided by differences in elevation. However, it is currently widely accepted that historical factors such as recent Pleistocene climatic cycles have played an important role in the conformation of mountain assemblages (Brown, 1995; Brown & Lomolino, 1998; Hewitt, 2000; Lobo & Halffter, 2000). The relevance of these historical factors is based on the degree of isolation of mountain areas (i.e., on the accessibility for the biota of surrounding regions; Janzen, 1967; Brown & Lomolino, 1998; Channell & Lomolino, 2000).

Study of elevational variation in West Palaearctic dung beetle assemblages has shown that mountain faunas are influenced by a horizontal colonization process; the geographical displacement of some taxa or ancestors in relatively recent geological times seems to have generated a clear pattern of altitudinal substitution among higher taxa with different evolutionary histories (Martín-Piera et al., 1992; Jay-Robert et al., 1997; Errouissi et al., 2004). Three dung beetle lineages are present in Palaearctic dung beetle assemblages: Scarabaeidae, Geotrupinae and Aphodiinae. Scarabaeidae are largely restricted to the southern Mediterranean part of Europe, whereas Geotrupinae and Aphodiinae dominate northern assemblages, although they are also present in south temperate localities (Hanski, 1986, 1991; Lumaret & Kirk, 1991; Hortal-Muñoz et al., 2000; Lobo et al., 2002). The latitudinal turnover between these taxa (Scarabaeidae vs. Geotrupinae–Aphodiinae) is analogous to the altitudinal gradient observed in Central and Southern European mountain ranges (Jay-Robert et al., 1997), and also in the Mexican Transition Zone (Halffter et al., 1995; Lobo & Halffter, 2000). This pattern is probably the result of the southward shift of northern lineages during Quaternary climate changes (Elias, 1994), highlighting the important role of spatial shifts in species ranges (Hengeveld, 1997) and the minor influence of adaptive evolutionary changes promoted by the isolation of populations after these colonization events (Cruzan & Templeton, 2000; Hewitt, 2000; Moritz et al., 2000). In contrast, such a turnover pattern does not appear at dung beetle assemblages of Southeastern Asia islands (Hanski, 1983; Hanski & Niemelä, 1990; Hanski & Krikken, 1991), at the Andean communities of South America (Escobar et al., 2005), or even at the southernmost mountain assemblages of the Iberian Peninsula (see Jay-Robert et al., 1997). This is probably a consequence of the isolation of these areas from northern temperate zones.

Unfortunately, due to the lack of standardized studies of dung beetles at elevational gradients in Asia and East Europe we can not ascertain whether the altitudinal replacement of high level lineages with those of a different origin and evolutionary history is general for the Palaearctic region. Here, we analyzed the elevational turnover of the dung beetle assemblages located near of the eastern

border of the Euro-Mediterranean region. To do this, we compiled all the available faunistic information of a mountain range located in Eastern Europe, for the first time (Western Rhodopes mountains). We analyzed the change in species richness, the relative proportion of high level taxonomic groups, the turnover in distribution and the range size of species. Finally, we compared these results with those obtained in a Western European mountain range (the Iberian Central System) which is also located in the boundary between Mediterranean and Eurosiberian domains.

Methods

We studied two distant European mountain regions (separated by 4,000 km approximately): the Western Rhodopes (South-Central Bulgaria) and the Iberian Central System. The Rhodopes mountain range covers an area of around 14,000 km² (from 200 to 2,000 m in altitude) while the area studied in the Iberian Central System covers approximately 34,000 km² (see fig. 1) (from 500 to 2,200 m in altitude). We compiled all the faunistic information available for both regions. The information compiled for Bulgarian Rhodopes comes from 17 works, comprising the period between 1904 and 2005 (Ioakimov, 1904; Nedelkov, 1905, 1909; Stolfa, 1938; Pittioni, 1940; Goljan, 1953; Mikšić, 1957, 1959; Angelov, 1965; Zacharieva, 1965a, 1965b; Zacharieva & Dimova, 1975; Mariani, 1980; Král & Malý, 1993; Bunalski, 2001a, 2001b; Rossner, 2005). All data taken from those references refers to precise localities, except for Mariani (1980), where *Aphodius montanus* is cited without an exact location. In addition, we included the data from twelve localities placed along an altitudinal transect (662–2,016 m) in three seasons: 10–19 V 04; 14–21 X 04; 15–21 VII 06 (Lobo et al., in press). Five of these localities were sampled by 10 baited pitfall traps (see Lobo et al., 1988; Veiga et al., 1989) in each season, while the other seven were sampled using a standardized (and comparable) sampling effort: over a 45-minute period, three investigators (JML, BG and ECh) collected all beetles found within and beneath cattle, sheep or horse excrements. Localities were selected on the basis of the presence of cattle. The non-parametric estimates of total species richness for this study indicate that around 94% of the total regional species pool had been collected, while the mean percentage of completeness for the localities is 83% (see Lobo et al., in press). In the case of the Iberian Central System data came from several publications (Martín-Piera et al., 1986; Martín-Piera et al., 1992; Lobo, 1992; Lobo & Hortal, 2006; Hortal et al., 2006) as well as from BANDASCA, a database which originally compiled all the available biological and geographical information from museums, private collections, published and unpublished data about Iberian Scarabaeidae dung beetles (Lobo & Martín-Piera, 1991). This database has recently been updated to include a large amount of records on

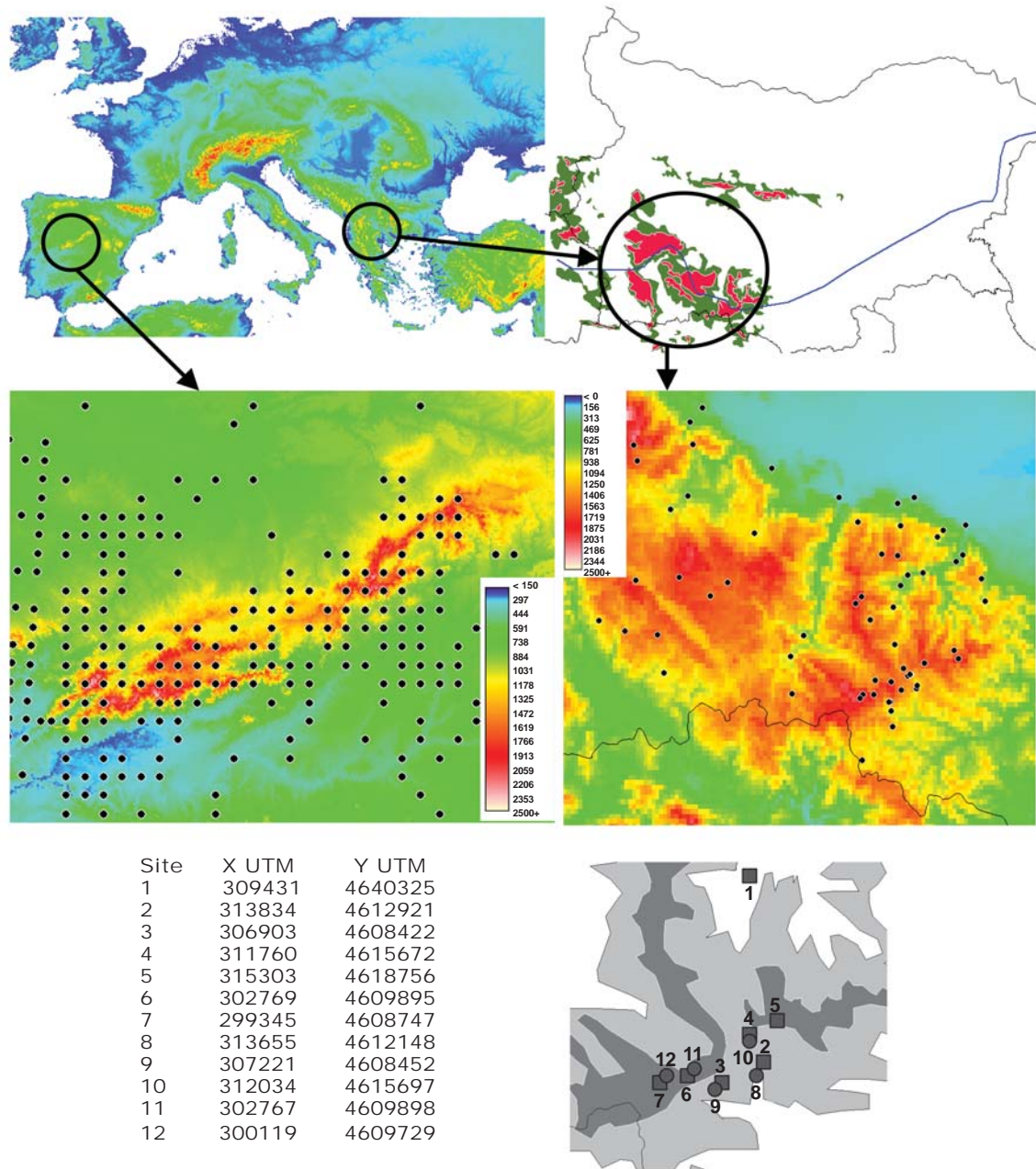


Fig. 1. Location of the two studied mountain areas in Europe (Iberian Central System and Western Rhodopes); darkest areas represent mountain areas, and white lines are the main rivers. The continuous line in the map of Bulgaria represents the Mediterranean–Eurosiberian climate boundary. The location of sites with faunistic data in both regions is shown on a topographic map with grey tones varying in accordance to altitude. Squares in the Western Rhodopes identify recently sampled localities (Lobo et al., in press), specifically located (reference system UTM–36n) and numbered on the lower part of the figure (black areas, more than 1,500 m altitude; grey areas, 1,000–1,500 m altitude).

Fig. 1. Localización general de las dos zonas de montaña estudiadas en Europa (Sistema Central Ibérico y Rhodopes Occidentales). Las áreas más oscuras corresponden a zonas montañosas, mientras que los principales ríos se muestran como líneas blancas. La línea continua en el mapa de Bulgaria representa el límite entre el clima Mediterráneo y el Eurosiberiano. Situación de las localidades con datos faunísticos dentro de un mapa topográfico en el que los tonos de gris reflejan la altitud. Los cuadrados en el mapa de los Rhodopes Occidentales identifican aquellas localidades recientemente muestreadas (Lobo et al., in press), las cuales aparecen localizadas (sistema de referencia UTM–36n) y numeradas en la parte inferior de la figura (áreas oscuras, más de 1.500 m de altitud; áreas grises, entre 1.000 y 1.500 m de altitud).

Table 1. Checklist of the species present at the Western Rhodopes mountain chain according to available bibliography and a recent survey carried out in twelve localities (J. M. Lobo, B. Guéorguiev & E. Chehlarov, unpublished). The altitudinal range of each species was established assuming that the species occurs along the whole range between minimum and maximum recorded altitude. The type of distribution of each species is included according to the criteria of La Greca (1964): EU. Euroasian; EA. Euroasiatic; E. European; M. Mediterranean; CA. Centralasiatic; EM. Euromediterranean; ET. Euroturanian; T. Turanian; H. Holarctic. Distribution range size (Rs) was estimated taking six classes into account and considering the percentage of the total western Palaearctic region area ($12 \times 10^6 \text{ km}^2$) occupied by each species (see Lumaret & Lobo, 1996). * A. (*Neagolius montanus*) is cited at the Rhodopes by Mariani (1980), but without any specific locality.

Tabla 1. Listado de las especies presentes en los Rhodopes occidentales de acuerdo a la literatura disponible y un reciente estudio de campo realizado en una docena de localidades (J. M. Lobo, B. Guéorguiev & E. Chehlarov, datos inéditos). El gradiente altitudinal para cada especie fue establecido asumiendo que la especie aparece en todas aquellas altitudes situadas entre la mínima y máxima altitud en que ha sido observada. El tipo de distribución se estimó de acuerdo al criterio de La Greca (1964): EU. Euroasiática; E. Europea; M. Mediterránea; CA. Centroasiática; EM. Euromediterránea; ET. Euroturanica; T. Turanica; H. Holártica. El tamaño de la distribución de cada especie (Rs) se estimó considerando seis categorías de distribución que consideran el porcentaje del área de distribución de cada especie respecto al área total del Paleártico occidental ($12 \times 10^6 \text{ km}^2$) (ver Lumaret & Lobo, 1996). * A. (*Neagolius montanus*) fue citada por Mariani (1980) sin localidad específica.

Species	Lobo et al. unpublished	Ioakimov 1904	Nedelkov 1905	Nedelkov 1909	Stoffa 1938	Pitton! 1940	Golian 1953	Mikšić 1957	Mikšić 1959	Angelov 1965	Zacharëva 1965a	Zacharëva 1965b	Zacharëva & Dimova 1975	Král & Malý 1993	Bunalski 2001a	Bunalski 2001b	Rossner 2005	Distribution	Rs
<i>Aphodius (Acanthobodilus) immundus</i> Creutzer																		EA	6
<i>A. (Acrossus) depressus</i> (Kugelann)	X						X		X									ES	6
<i>A. (Acrossus) luridus</i> (Fabricius)	X						X		X									EA	6
<i>A. (Acrossus) rufipes</i> (Linnaeus)	X								X									ES	6
<i>A. (Agoliinus) satyrus</i> Reitter													X					E	3
<i>A. (Agrilinus) ater</i> (De Geer)	X																	ES	6
<i>A. (Agrilinus) scybalaris</i> (Fabricius)	X						X		X									ES	6
<i>A. (Amidorus) cribrarius</i> Brullé													X					M	6
<i>A. (Amidorus) obscurus</i> (Fabricius)	X								X									E	6
<i>A. (Ammoeclus) brevis</i> Erichson													X					ES	6

Table 1. (Cont.)

Species	Rs	Distribution	Lobo et al. unpublished	Ioakimov 1904	Nedelkov 1905	Nedelkov 1909	Stofa 1938	Pittioni 1940	Gollan 1953	Mikšić 1957	Mikšić 1959	Angelov 1965	Zacharčeva 1965a	Zacharčeva 1965b	Zacharčeva & Dimova 1975	Kral & Malý 1993	Bunalski 2001a	Bunalski 2001b	Rosner 2005	
<i>A. (Aphodius) fimetarius</i> (Linnaeus)	6	EA	X							X	X	X	X	X						
<i>A. (Aphodius) foetens</i> (Fabricius)	6	EA							X						X					
<i>A. (Bodius) lugens</i> Creutzer	6	T-M											X							
<i>A. (Calamosternus) granarius</i> (L.)	6	ET-M	X							X	X	X	X	X						
<i>A. (Chilothorax) distinctus</i> (Müller)	6	EA	X																	
<i>A. (Chilothorax) melanosticticus</i> W. Schmidt	6	EM-CA											X							
<i>A. (Chilothorax) sticticus</i> (Panzer)	6	E	X										X							
<i>A. (Colobopterus) erraticus</i> (Linnaeus)	6	EA	X							X	X	X	X	X						
<i>A. (Coprimorphus) scrutator</i> (Herbst)	6	EM	X							X	X	X	X	X						
<i>A. (Esymus) merdarius</i> (Fabricius)	6	ET	X							X										
<i>A. (Esymus) pusillus</i> (Herbst)	6	ES	X																	
<i>A. (Eudolus) quadriguttatus</i> (Herbst)	6	ET-M								X										
<i>A. (Eurrodalus) paracoenosus</i> Bal. & Hru.	6	EM	X														X			
<i>A. (Eupleurus) subterraneus</i> (L.)	6	ES										X								
<i>A. (Limarus) maculatus</i> Sturm	6	E	X											X						
<i>A. (Melinopterus) consputus</i> Creutzer	6	EM	X									X								
<i>A. (Melinopterus) prodromus</i> (Brahm)	6	EA	X							X	X	X	X	X						
<i>A. (Melinopterus) sphaelatus</i> (Panzer)	6	EA	X											X						
<i>A. (Neagolius) montanus</i> Erichson	6	EA							X											*
<i>A. (Nialus) varians</i> Duftschmid	6	ET-M								X										
<i>A. (Nimbus) contaminatus</i> (Herbst)	6	E	X																	
<i>A. (Nimbus) oblitteratus</i> Panzer	6	E	X																	
<i>A. (Nobius) serotinus</i> (Panzer)	4	ES													X					

Table 1. (Cont.)

Species	Lobo et al. unpublished	Ioakimov 1904	Nedelkov 1905	Nedelkov 1909	Stofa 1938	Pittioni 1940	Golian 1953	Milksić 1957	Milksić 1959	Angelov 1965	Zacharčeva 1965a	Zacharčeva 1965b	Zacharčeva & Dimova 1975	Kral & Mały 1993	Bunatski 2001a	Bunatski 2001b	Rosser 2005	Distribution	Rs
<i>A. (Otophorus) haemorrhoidalis</i> (L.)	X										X							EA	6
<i>A. (Phalacrobothus) biguttatus</i> Germar													X					E	6
<i>A. (Planolinus) borealis</i> Gyllenhal													X					H	6
<i>A. (Planolinus) uliginosus</i> (Hardy)	X							X										H	6
<i>A. (Pseudocrossus) thermicola</i> Sturm	X										X							EM	6
<i>A. (Sigorus) porcus</i> (Fabricius)	X																	E	6
<i>A. (Teuchestes) fossor</i> (L.)	X							X	X	X	X	X						ES	6
<i>A. (Trichonotulus) scrofa</i> (Fabricius)	X												X					EA	6
<i>Euheptaulacus carinatus</i> (Germar)	X										X							ES	6
<i>Euheptaulacus sus</i> (Herbst)													X					ET	6
<i>Oxyomus silvestris</i> (Scopoli)	X							X										CA-ET-M	6
<i>Pleurophorus caesus</i> (Creutzer)								X										EM-CA	6
<i>Anoplotrupes stercorosus</i> (Scriba)	X							X	X									E	6
<i>Geotrupes mutator</i> Marsham	X								X	X								EA	6
<i>Geotrupes spiniger</i> Marsham	X												X					ET	6
<i>Geotrupes stercorarius</i> (Linnaeus)	X																	EA	6
<i>Thorectes punctulatus</i> (Jekel)																		East E	5
<i>Lethrus schauimi</i> Reiter													X					East M	2
<i>Trypocopris vernalis</i> (L.)	X								X	X								E	6
<i>Caccobius schreberi</i> (L.)	X							X	X	X								ET-M	6
<i>Copris hispanus</i> (L.)									X	X	X							CA-M	6
<i>Copris lunaris</i> (L.)	X								X	X	X	X						ET	6
<i>Copris umbilicatus</i> Abeille de Perrin													X					E	5

Table 1. (Cont.)

Species	Lobo et al. unpublished	Ioakimov 1904	Nedelkov 1905	Nedelkov 1909	Stofra 1938	Pittioni 1940	Gollan 1953	Miksić 1957	Miksić 1959	Angelov 1965	Zacharava 1965a	Zacharava 1965b	Zacharava & Dimova 1975	Kral & Malý 1993	Bunatski 2001a	Bunatski 2001b	Rosner 2005	Distribution	Rs
<i>Euoniticellus fulvus</i> (Goeze)	X				X	X		X	X	X	X							ET-M	6
<i>Euoniticellus pallipes</i> (Fabricius)												X						EA-M	6
<i>Euonthophagus amyntas</i> (Olivier)									X	X								EA	6
<i>Euonthophagus gibbosus</i> (Scriba)	X						X	X	X		X	X						EA	6
<i>Gymnopleurus geoffroyi</i> (Fuessly)		X			X	X	X	X	X									ET-M	6
<i>Gymnopleurus mopsus</i> (Pallas)					X	X					X							CA-M	6
<i>Gymnopleurus sturmi</i> McLeay					X													M	6
<i>Onthophagus (Furonthophagus) furcatus</i> (F.)	X				X	X		X	X	X	X							ET-M	6
<i>O. (Onthophagus) illyricus</i> (Scopoli)	X							X										ET	6
<i>O. (Onthophagus) taurus</i> (Schreber)	X				X	X		X	X	X	X	X						EA-M	6
<i>O. (Palaeonthophagus) coenobita</i> (Herbst)								X										EA	6
<i>O. (Palaeonthophagus) fracticornis</i> (Preysslter)	X	X			X	X	X	X	X		X	X						ET	6
<i>O. (Palaeonthophagus) grossepunctatus</i> Reit.	X					X	X											EM	6
<i>O. (Palaeonthophagus) joannae</i> Goljan	X					X	X											ET	6
<i>O. (Palaeonthophagus) lemur</i> (Fabricius)	X				X	X		X	X	X	X	X						E	6
<i>O. (Palaeonthophagus) ovatus</i> Linnaeus	X							X	X	X	X	X						ET	6
<i>O. (Palaeonthophagus) ruficapillus</i> Brullé	X				X	X		X	X	X	X	X						EM	6
<i>O. (Palaeonthophagus) similis</i> (Scriba)	X												X					EA	6
<i>O. (Palaeonthophagus) vacca</i> (L.)	X									X	X	X	X					EA	6
<i>O. (Palaeonthophagus) verticicornis</i> (Lairch.)	X							X	X	X	X	X						EA	6
<i>Scarabaeus (Scarabaeus) plus</i> (Illiger)					X			X										East M	6
<i>S. (Scarabaeus) typhon</i> Fischer-Waldheim					X	X	X	X										CA-M	6
<i>Sisyphus schaefferi</i> (L.)					X								X					CA-E-M	6

Geotrupinae and Aphodiinae Iberian species (around 8,000 database records). The information compiled for the Iberian Central System also involves a long period of samplings: from 1872 to 2004. All these data are freely available in the GBIF web page (<http://www.gbif.org/>).

We established the range of altitudes for each species assuming that they occur along the whole range between minimum and maximum recorded altitude. This procedure implies the existence of two assumptions: i) that the species generally have a Gaussian symmetric or skewed unimodal response along the elevational environmental gradients, and ii) that the detected upper and lower limits of species occurrence are related with true altitudinal limits. While much evidence supports the occurrence of such response curves in most species (McKenzie et al., 2003; Sanders et al., 2003; McCain, 2004; Austin, 2005), the second assumption clearly relies on the existence of reliable sampling inventories along the altitudinal interval. Here, we assume that the analysis of a long period of data collection has allowed detection of the potential altitudinal distribution of species, a similar supposition to that generally established in the estimation of species range distributions. To do this, we divided the altitudes into 100 m intervals at both regions. For each species we also considered information on its range size and type of distribution. Geographic range size was estimated considering the six classes of geographic range size suggested by Lumaret & Lobo (1996), according to the percentage of the total western Palaearctic region area covered by the distribution range of each species' ($12 \times 10^6 \text{ km}^2$). Those species with range-size classes 1–4 (i.e., ranges of approximately the same area as the Iberian Peninsula or smaller) were considered narrowly distributed. The type of distribution was defined according to the criteria of La Greca (1964) calcu-

lating the number of species with Euroturanian and Mediterranean distributions (herein, Mediterranean-centred species). Species nomenclature followed the taxonomic criteria of Dellacasa (1983) and Baraud (1992).

For each higher taxa and region we calculated the one hundred altitudinal interval with most species (i.e., the mode). Two linear regressions were calculated using two groups of data defined by this modal score (above and below) to estimate whether the increase and/or decrease in species richness with altitude (the slope) depart significantly from zero. The significance (p -level) for the difference between proportions has been calculated taking into account the sample size of each of region (total number of species) according to the t -value for the respective comparison (see StatSoft, 2003).

Results

Seventy-nine dung beetle species have been cited for the Western Rhodopes (table 1), although many of the localities surveyed were situated in the western part of this mountain chain (fig. 1). Recent field work (Lobo et al., in press) recorded 48 species (60% of total), adding seven new species to the regional inventory. In contrast, the dung beetle fauna of the Iberian Central System was richer (121 species). Almost half of these species (57 species) were present in both regions (fig. 2). Interestingly, although 57% of all the species collected in both regions were Aphodiinae (82 species) and 30% Scarabaeidae (44 species), 44% of the shared species belonged to the latter family while most of the species exclusive of the Rhodopes or the Iberian Central System were Aphodiinae (58% and 73%, respectively; see fig. 2). In the Western Rhodopes 45% of the species (36 species) had a distribution centred in the Mediterranean basin, while only 4%

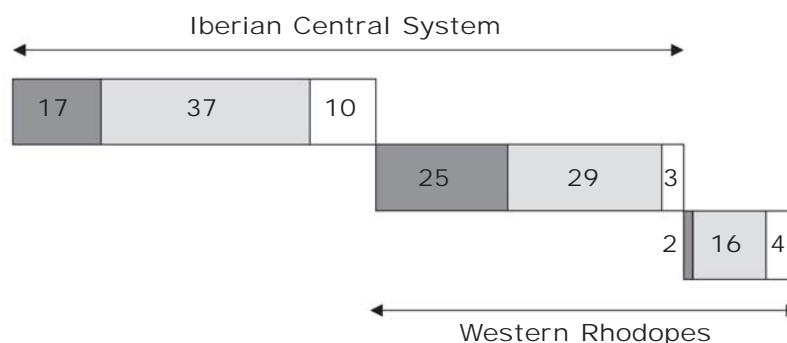


Fig. 2. Number of species shared by both regions and number of species exclusive to each of them. Scarabaeidae (dark grey), Aphodiinae (clear grey), Geotrupinae (white).

Fig. 2. Número de especies compartidas y número de especies propias de cada una de las regiones analizadas. Scarabaeidae (gris oscuro), Aphodiinae (gris claro), Geotrupinae (blanco).

Table 2. Number of species (S) belonging to each of the three main dung beetle taxonomic groups for the two mountain chains considered (the percentage of the total is shown in brackets), the 100 m altitude interval with the highest number of species (according to the Mode), and slope scores of the linear relationship between altitude and species richness, calculated considering the data above (B+) and below (B-) modal values (change in the number of species for each 100 m); *t*-value and resulting *p*-value test the hypothesis that the slope equals to 0.

Tabla 2. Número de especies (S) de cada uno de los tres principales grupos de escarabajos coprófagos en las dos regiones montañosas analizadas (porcentajes entre paréntesis), valor modal del número de especies en los intervalos de 100 m utilizados y valores de la pendiente de regresión lineal entre el número de especies y la altitud según se consideren los datos por encima (B+) y por debajo (B-) de los valores modales (número de especies por cada 100 m de altitud). Los valores de *t* tratan de comprobar si estas pendientes pueden considerarse significativamente diferentes de cero.

	S	Mode	B +	B -
Iberian Central System				
Total species	121	900	6.1 (<i>t</i> = 3.68; <i>p</i> = 0.02)	- 8.2 (<i>t</i> = 22.05; <i>p</i> < 0.0001)
Scarabaeidae	42(35%)	900	2.8 (<i>t</i> = 9.90; <i>p</i> = 0.002)	- 2.7 (<i>t</i> = 19.20; <i>p</i> < 0.0001)
Aphodiinae	66(54%)	1,000	3.2 (<i>t</i> = 8.61; <i>p</i> = 0.001)	- 4.7 (<i>t</i> = 25.18; <i>p</i> < 0.0001)
Geotrupinae	13(11%)	1,450	0.6 (<i>t</i> = 2.49; <i>p</i> = 0.03)	- 1.3 (<i>t</i> = 15.39; <i>p</i> < 0.0001)
Western Rhodopes				
Total species	80	1,000	3.9 (<i>t</i> = 5.14; <i>p</i> = 0.001)	- 3.7 (<i>t</i> = 12.75; <i>p</i> < 0.0001)
Scarabaeidae	27(34%)	700	1.1 (<i>t</i> = 1.71; <i>p</i> = 0.16)	- 1.7 (<i>t</i> = 10.42; <i>p</i> < 0.0001)
Aphodiinae	46(57%)	1,100	2.3 (<i>t</i> = 6.96; <i>p</i> = 0.0001)	- 1.4 (<i>t</i> = 9.97; <i>p</i> < 0.0001)
Geotrupinae	7(9%)	1,500	0.3 (<i>t</i> = 5.43; <i>p</i> = 0.0002)	- 0.5 (<i>t</i> = 5.00; <i>p</i> = 0.02)

could be considered narrowly distributed (3 species). The proportion of Mediterranean-centred species was similar in the Iberian Central System (58 species; 48%, *p* = 0.34) as was the percentages of species of the three main taxonomical groups (table 2). However, the percentage of narrowly distributed species was higher than in Rhodopes (16% of total; *p* = 0.005).

The elevational pattern derived for Rhodopes (fig. 3) showed a mid-elevational peak between 700 and 1,400 m. All relationships between richness and altitude (except Scarabaeidae in the 200–700 m interval) differed significantly from zero, with negative slopes above the modal altitude and positive slopes up to this modal altitude (table 2). The increase in species richness towards the modal altitude was more pronounced in Aphodiinae than in Scarabaeidae, while the two groups showed similar decays in species richness from the modal altitude. Thus, a manifest elevational turnover among the two taxonomical groups occurred (fig. 3).

A mid-elevational peak in species richness was also observed at the Iberian Central System (between 800–1,000 m), with very similar modal altitudes for each of the three dung beetle groups (table 2). Here, the rates of increment and decrease in species richness were more pronounced than at Rhodopes Mountains, probably due to the higher number of species considered. In spite of this, the emerged altitudinal pattern was quite similar (table 2). Although the relevance of Aphodiinae species in lower altitudinal levels seemed comparatively higher, the increase in the contribution of Aphodiinae and Geotrupinae species with altitude was also evident (fig. 2).

The occurrence of Mediterranean-centred species clearly diminished with altitude, both at the Rhodopes and the Iberian Central System (fig. 4), showing similar slopes. On the contrary, the number of narrowly-distributed species increased slightly but significantly with altitude in both regions (fig. 4).

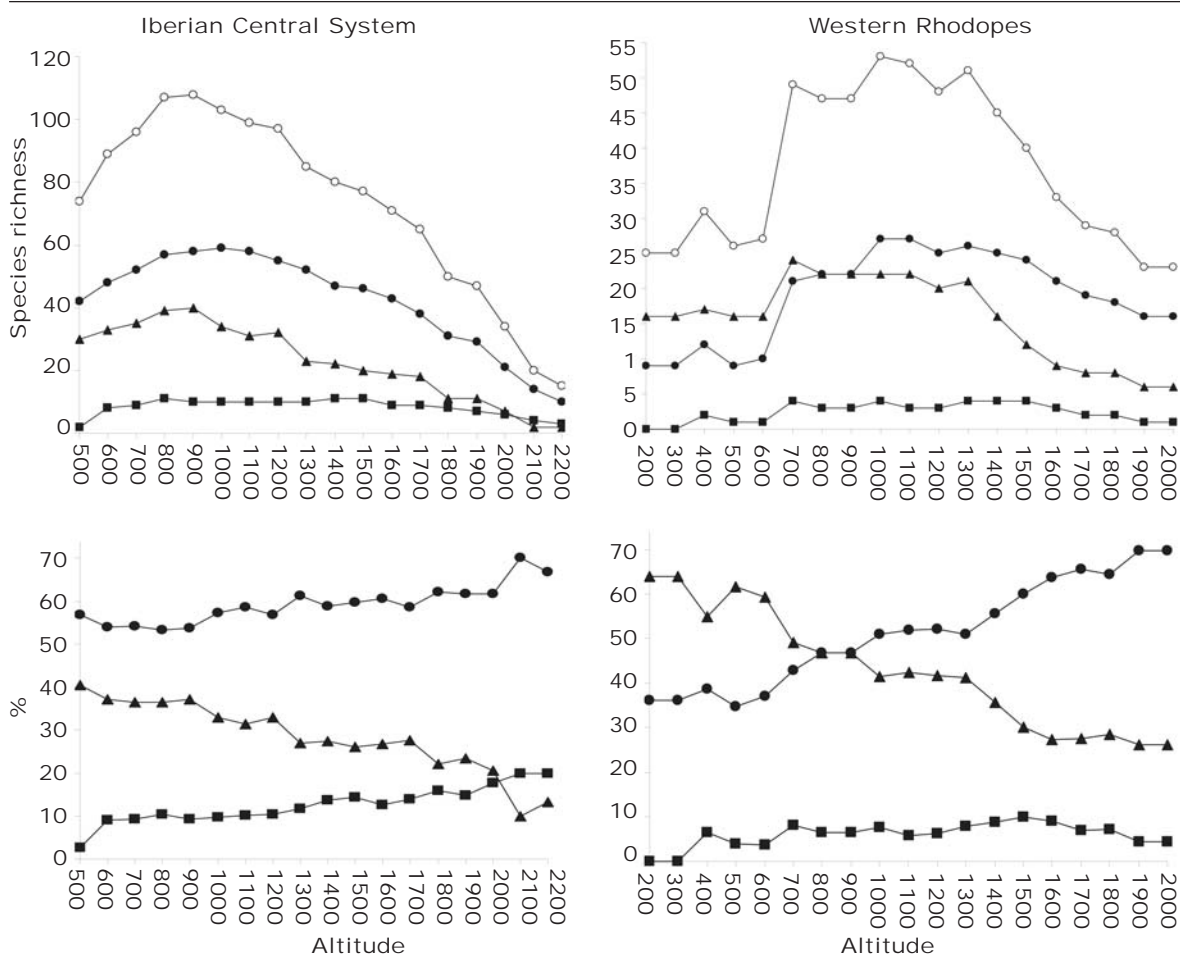


Fig. 3. Relationships between altitude and number of collected species in both mountain regions, and relationships between altitude and percentage of species from the three taxonomic groups. All dung beetles (white circles), Scarabaeidae (black triangles), Aphodiinae (black circles) and Geotrupinae (black squares).

Fig. 3. Relaciones entre altitud y el número total de especies (círculos blancos), número de especies de Scarabaeidae (triángulos negros), Aphodiinae (círculos negros) y Geotrupinae (cuadrados negros) para cada una de las dos regiones montañosas y relaciones entre altitud y el porcentaje de especies de estos tres grupos taxonómicos.

Discussion

Our results suggest that Eastern European dung beetle assemblages have similar patterns of compositional turnover and species richness variation with altitude as those observed in Western Europe and North America (Martin-Piera et al., 1992; Jay-Robert et al., 1997; Errouissi et al., 2004; Halffter et al. 1995; Lobo & Halffter, 2000). In spite of the relatively low proportion of shared species (40%), dung beetle assemblages at the Iberian Central System and Rhodopes Mountains show: (i) relatively similar proportions of species belonging to their three main taxonomic lineages

(Scarabaeidae, Aphodiinae and Geotrupinae), (ii) comparable frequencies of species with Mediterranean-centred distribution (around 45%–48%), (iii) analogous modal species richness altitudes, and (iv) similar rates of richness increase and/or decrease with altitude (both for total species and for Mediterranean or narrowly distributed species). The evident pattern of altitudinal substitution among higher level taxa (Aphodiinae–Geotrupinae vs. Scarabaeidae) at Rhodopes Mountains suggests that East European dung beetle assemblages are also conditioned by a horizontal colonization process, where mountains were colonized in relatively recent geological times by elements coming from

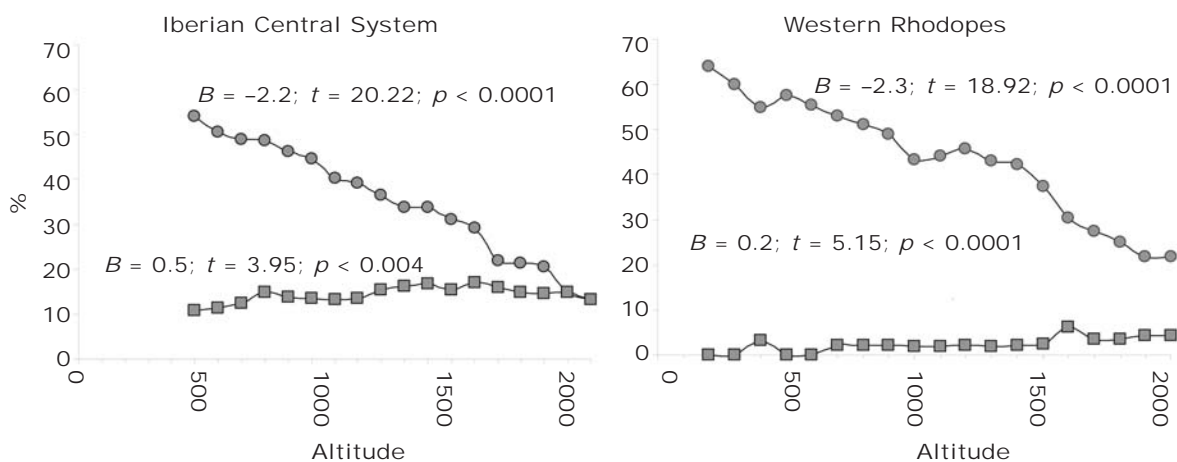


Fig. 4. Altitudinal variation in the number of Mediterranean-centred species (circles) and narrowly distributed species (squares) for both mountain areas. B is the slope of the linear relationship between altitude and the number of species, while t -value and resulting p -value test the hypothesis that the slope is equal to 0.

Fig. 4. Variación altitudinal en el número de especies con una distribución centrada en la región Mediterránea (círculos) y en el número de especies con rangos de distribución restringidos (cuadros) para ambas regiones. B es el valor de la pendiente de la regresión lineal entre altitud y número de especies, mientras los valores de t tratan de comprobar si esta pendiente puede considerarse significativamente diferente de cero.

different latitudes (Lobo & Halffter, 2000). These convergences are difficult to explain by sampling effort differences because they would imply that future new citations in Western Rhodopes should belong to taxonomically and geographically biased species.

Several differences can be observed between these two regions. Rhodopes dung beetle assemblages are characterized by a significantly lower proportion of narrowly distributed species than those of the Iberian Central System, and also by a lower relevance of Aphodiinae species in lowland places. Some of these divergences can be attributed to differences in area and differences in sampling techniques between the two regions. There is a marked variation among the area of both regions (almost 2.4 times higher in the Iberian Central System). However, species area curves for dung beetles demonstrate that the rate of species-accumulation with increasing area is low (around 0.098 species by km^2 ; see Lobo & Martín-Piera, 1999), so the inventory of Western Rhodopes could increase approximately in seven species if this region had a similar area to that of the Iberian Central System. Thus, the important difference in the total number of species at each region (41 species) would only be partially due to differences in area. The disparity in the survey techniques for the inventory in the two regions and the differences in the location of surveyed localities (few surveys in the southern part of Western Rhodopes) may also

partly explain this difference in regional species richness. For example, a recent exhaustive survey partly devoted to the Iberian Central System (Hortal, 2004) added only one new species to the regional catalogue. In contrast, our recent field work in Western Rhodopes yielded seven new citations, and sampling did not encompass a whole year. The scarcity of faunistic data from the southernmost Rhodopes localities under Mediterranean conditions probably influences the low number of species recorded for the lowlands (mainly Aphodiinae and/or species with Mediterranean distribution). The forthcoming addition of faunistic data from these places could allow us to assess the reliability of the differences in species richness between the two regions.

In spite of these limitations, we consider that the main divergence found between the two regions in this study (the lower proportion of narrowly distributed species) can not be explained by sampling effort differences (all seven new citations for the Western Rhodopes belong to the maximum range-size category; over 10% of the total area of the Western Palearctic region; see Lumaret & Lobo, 1996). There are nineteen narrowly distributed species in the Iberian Central System, some of them widely distributed in the region and with abundant populations (Lobo, 1992), but there are only three in Western Rhodopes. In our opinion, this remarkable divergence can be partially explained by the different degree of isolation and biogeographical

history of these two mountain areas. Both Iberian and Balkan Peninsulas acted as refuges during Pleistocene glacial–interglacial cycles (see Bennet et al., 1991; Hewitt, 1996; Taberlet et al., 1998; Brewer et al., 2002; Olalde et al., 2002; Petit et al., 2002 for the former and Hewitt, 2000; Bordács et al., 2001; Petit et al., 2002; Heuertz et al., 2004; Schmitt et al., 2006; Ursenbacher et al., 2006 for the latter). However, recent phylogeographic data demonstrate that, at least for butterflies, the Pyrenees could have acted as a barrier for post–glacial recolonization of European lineages, contrary to the pattern found for Italian and Balkan Peninsulas (Habel et al., 2005). Thus, the connection of Rhodopes Mountains with other European mountain chains could have hindered the isolation and subsequent speciation of the lineages sheltered there during Pleistocene climate changes. This could explain the notable divergence between eastern and western European dung beetle assemblages found in this study: the low number of narrowly distributed species inhabiting the eastern Rhodopes mountain chain.

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