

# Dung Beetle Geographic Diversity Variation Along a Western Iberian Latitudinal Transect (Coleoptera: Scarabaeidae)

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**ABSTRACT** To explore the richness and geographic turnover of dung beetle assemblages (Scarabaeinae and Aphodiinae) inhabiting the Western Iberian peninsula, a latitudinal north-south transect was carried out in Portuguese territory. Estimators of alpha, beta, and gamma diversities were used, as well as the ratio Scarabaeinae/Aphodiinae, which puts into evidence some dung beetle community spatial characteristics. Clustering methods were also used to ascertain relationships between biogeographical Portuguese regions and geographical patterns of species replacement. Although Scarabaeinae appears mainly responsible for overall and regional richness, Aphodiinae richness was rather low everywhere except for the southernmost plot of the transect investigated. The scarcity of Aphodiinae species is reflected in the Scarabaeinae/Aphodiinae ratio, a score that is, however, clearly biased toward the Aphodiinae in almost all the Iberian Peninsula. For this reason the pairwise turnover in species composition between sites is mainly determined by the variation in Scarabaeinae species. Peaks of  $\beta$ -diversity, especially for Scarabaeinae, and clusters from dendrograms are highly consistent with physioclimatic subregions of Portugal, thus suggesting a correspondence between biogeographic and environmental boundaries.

**KEY WORDS** Scarabaeinae, Aphodiinae, dung-beetles, faunistic turnover, biogeography, Portugal

THE FAUNISTIC KNOWLEDGE of Iberian dung beetles has been notably increased over the present decade (Ávila and Sánchez-Piñero 1990; Galante et al. 1991; Sánchez-Piñero and Ávila 1991; Lobo 1992a; Martín-Piera and Lobo 1992; Martín-Piera et al. 1992; Galante and Stebnicka 1993, 1994; Lobo and Martín-Piera 1993, Martín-Piera and Lobo, 1996; Hidalgo and Cárdenas 1994; Verdú-Faraco 1994; Cartagena 1996; Menéndez and Gutiérrez 1996; Lobo et al. 1997; Sánchez-Piñero 1997; Hidalgo et al. 1998a, 1998b; Micó et al. 1998). Currently, available data allow studies to be designed to estimate both the spatial diversity and faunistic composition variation, as well as the role played by different environmental factors over these variables.

However, the use of an exhaustive database that compiles all of the specialized literature as well as museistic available information on Iberian Scarabaeinae (Lobo and Martín-Piera 1991) has demonstrated that only 32% of the 50 × 50 km UTM grid cells can be considered fairly well sampled to recover reliable richness estimations (J.M.L. and F.M.P., unpublished data). Most of the undersampled zones are located in the Western Iberian areas (mostly Portugal), where no recent faunistic studies have been carried out, the only available faunistic data being those from old catalogues (Oliveira 1894; Seabra 1907, 1909; Ladeiro 1950).

Regional variation studies of spring coprophagous community composition and richness in the Iberian Peninsula (Martín-Piera et al. 1992, Lobo and Martín-Piera 1993, Lobo et al. 1997) reveal at least 2 well

defined patterns: (1) The average richness per trap at local pastureland, estimated by a uniform sampling method (Lobo et al. 1988, Veiga et al. 1989), is usually quite homogeneous and ranges between 12 and 14 species. (2) The richness ratio of the 2 major dung beetle groups (Scarabaeinae/Aphodiinae; sensu Lawrence and Newton 1995) is either nearly 1 or clearly biased to Aphodiinae (ranging from 1.04 to 0.64) throughout the Iberian Peninsula (Lobo et al. 1997). Aphodiinae have small body sizes and are predominantly dwellers (they feed and nest inside the dung pats). Scarabaeinae species are both tunnelers (they dig a vertical tunnel below the dung pat, and carry dung into the bottom of the burrow) and rollers (they roll away a ball of dung, and dig a tunnel outside the dung pat). Aphodiinae appears to be mainly responsible for the species turnover among localities and the regional richness as well, whereas Scarabaeinae richness and abundance in local communities are higher than that of Aphodiinae (Lobo et al. 1997). Thus, it is expected that geographic turnover scores of dung beetle assemblages decrease when the Scarabaeinae/Aphodiinae ratio increases because of the scarcity of Aphodiinae species.

The goals of this study were to determine if spring Portuguese communities richness is similar to that of other Iberian region communities sampled in the same season and to test if spatial dung beetle-species turnover, on a geographical scale, is predominantly determined by Aphodiinae species replacement, thus fitting into the patterns described for other Iberian regions.

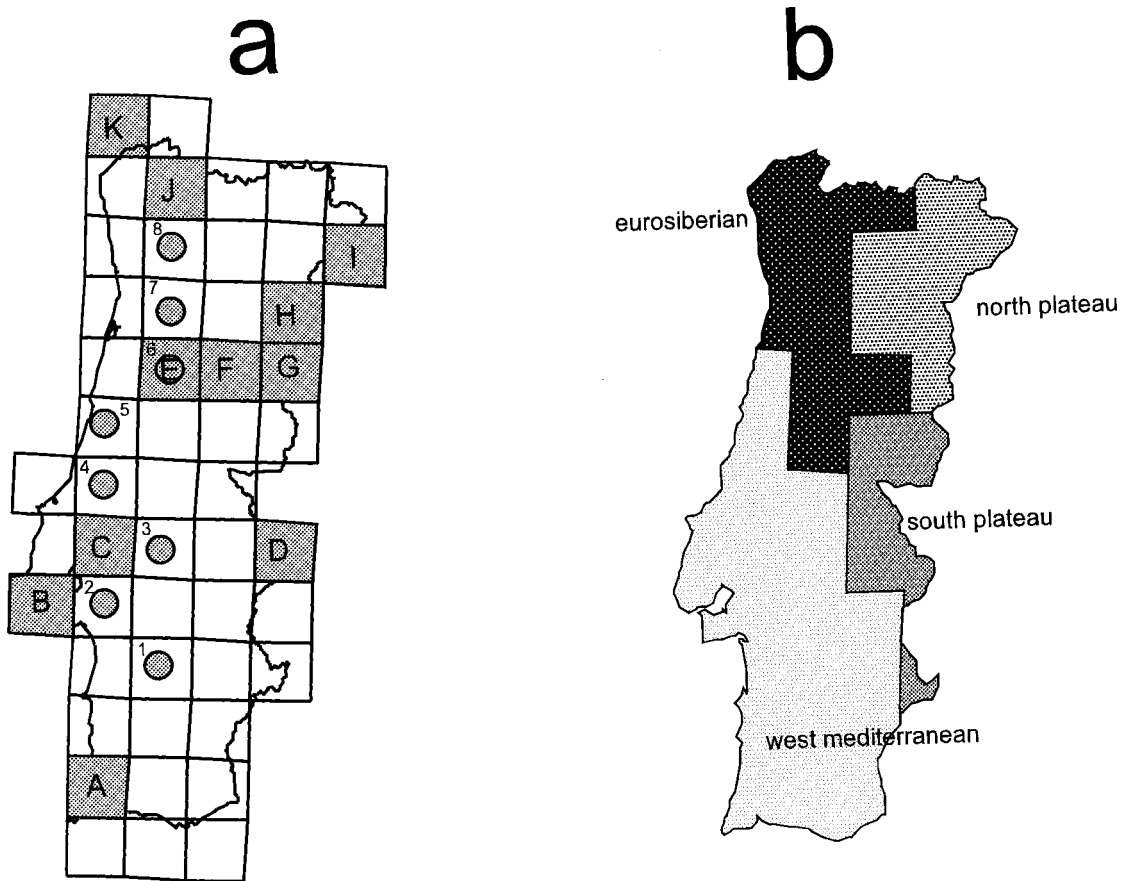


Fig. 1. Sampling sites in Portugal: (a) Sites (circles with inner dots) and  $50 \times 50$  km UTM grid cells faunistically 'well sampled' (shadow) (see text). (b) Physioclimatic subregions of Portugal covered by the climatic and topographic data for each of the  $50 \times 50$  km UTM grid cells of Portuguese territory; courtesy of W. Cramer (CLIMATE database version 2; <http://www.pik-potsdam.de/~cramer/climate.htm>).

It is expected that spatial turnover measures will succeed in recovering a pattern similar to that of the principal Portuguese biogeographic regions, or at least, to be sensitive to the biotic transition zones (Williams 1996). To achieve this, the data of a geographic transect carried out over a north-south latitudinal gradient in Portuguese territory were examined. Although site specific richness comparisons are made, the data from this transect have been mainly used to compare Portuguese species richness, Scarabaeinae/Aphodiinae ratio, and species turnover with those of other Iberian sites. Information compiled in an exhaustive database of the Iberian dung beetle was also analyzed.

#### Materials and Methods

Eight sites, separated by 50 km, were sampled along a 400-km geographic transect. Each sampling plot was located at one of the following Universal Transversal Mercator (UTM)  $50 \times 50$  km grid cells: 29SNC4, Odivelas (site 1); 29SNC1, Pegoes (site 2); 29SND4, Mora (site 3); 29SND1, Tomar (site 4); 29SNE2, Pon-

tao (site 5); 29TNE3, Tondela (site 6); 29TNF4, Castro Daire (site 7); and 29TNF3, Amarante Alto da Serra (site 8) (Fig. 1). In all cases the chosen sampling sites were open pastures with no arboreal cover. In Mediterranean conditions, open biomes have much higher abundance and richness scores than closed biomes, which do not have exclusive dung beetle species (Lumaret 1980, Lumaret and Kirk 1987). The environmental characteristics and geographic location of each site are shown in Table 1 and Fig. 1a.

To collect a spring inventory, a sampling program was carried out between 19 and 23 of May 1997. Previous studies have shown that the spring dung-beetle inventory of a local community ranges between 70 and 80% of the complete annual inventory (Martín-Piera et al. 1992, Lobo and Martín-Piera 1993, Lobo et al. 1997). The pitfall traps recommended by Lobo et al. (1988) and Veiga et al. (1989) were used. Four traps, baited with 1,000 g of fresh cow dung, were set in each of the 8 sampling sites. Baited traps were left 10 m apart for a period of 48 h.

In Mediterranean conditions, very few baited traps are needed to give a good picture of the structure and

**Table 1. Geographic location and environmental characteristics of the sampling plots across a geographic North–South transect carried out in Portugal from 19 May to 21 May in 1997**

Site no.	1	2	3	4	5	6	7	8
Locality	Odivelas	Pegoes	Mora	Tomar	Pontao	Tondela	Castro Daire	Amarante
UTM Coordinate	29SNC72	29SNC37	29SND72	29SND58	29SNE42	29TNE78	29TNF83	29TNF87
Altitude, m	75	95	200	225	400	460	1200	800
Habitat	Cork oak meadow	Cork oak meadow	Cork oak meadow	Pasture near a river	Olive tree meadow	Pasture near a pine forest	Alpine pasture with shrubs	Grassland with Erica sp.
Lithology	Sands	Sands	Sands	Muds/sands	Limestone	Granite	Granite	Granite

composition of a dung beetle assemblage. There is evidence that with only 15 traps, almost 95% of the species present at that site are collected (Lobo et al. 1998). We have chosen only 4 traps because, although they capture ≈65% of the total site species, these species represent around 92% of total dung beetle abundance and total biomass (Lobo et al. 1998). Hence, it can be assumed that the main assemblage composition is collected.

To test if total number of caught species is an underestimated figure of the true species richness along the transect, we calculated the species accumulation curve, namely, the cumulative number of discovered species as a function of the randomized number of pitfall-traps (Colwell and Coddington 1995). The total richness for all sampling plots was also estimated by applying the abundance-based coverage estimator (ACE), proposed by Chazdon et al. (1998). ACE is a modification of the Chao and Lee (1992) estimator, which tries to overcome the consistent overestimate of species richness present in Chao and Lee's estimator (Colwell and Coddington 1995). For these analyses the EstimateS package (Colwell 1997) was used. With the sampling effort developed, a nearly asymptotic richness score is obtained. The number of species caught is a high percentage of those predicted by the ACE estimator (92.6%), assuring the good quality of the faunistic and richness information provided by the transect.

The collected specimens were identified according to Dellacasa (1983), Baraud (1992), and Martín-Piera and López-Colón (2000).

We define  $\alpha$ -diversity as the species number in each sampling plot, but it is commonly agreed that the best way to determine whether species distributions are widespread or localized depends on understanding the beta diversity (the turnover in species composition with distance). The  $\beta$ -2 diversity index proposed by Harrison et al. (1992) has been used:

$$(S/\alpha_{\max}) - 1/(N - 1) \times 100,$$

where  $\alpha_{\max}$  is the maximum value of  $\alpha$ -diversity in the collection of  $N$  sites. Because in this study  $\beta$ -2 is calculated on a pairwise basis, the value of  $N$  is 2 for each comparison, so the denominator equals 1. This measure was chosen because it distinguishes true species turnover along a distance (or environmental) gradient from situations in which species drop out along the gradient without any new species being added, thus

eliminating apparent patterns in beta diversity generated by trends in alpha diversity (Harrison et al. 1992, Lawton et al. 1994). Finally, we define  $\gamma$ -diversity as the cumulative richness along the sampling sites.

To explain possible faunistic differences along the geographic transect carried out, Portuguese faunistic subregions were investigated using only those 50 × 50 km UTM grid cells, which can be thought to be well sampled (Fig. 1a), starting from the presence/absence data of the Scarabaeinae species. The information gathered in a database that summarizes all the published and museistic information about Iberian Scarabaeinae dung beetles (BANDASCA, Lobo and Martín-Piera 1991) was used. Currently, this database contains 15,023 records belonging to 96,981 individuals. No similar database of Aphodiinae is yet available. The asymptotic relationship between the number of species and the database records in each of the grid cells, as a measure of sampling effort, provides a predictive tool to extrapolate the total number of species present in a grid cell (Soberón and Llorente 1993). Using this model it is possible to establish the well and poorly sampled Iberian grid cells. Well sampled grid cells were those in which the number of records equals, or is higher than, the records necessary to obtain at least 75% of total species expected, as calculated by the asymptotic curve (J.M.L. and F.M.P., unpublished data). Presence-absence data provided by 26 1-yr studies carried out in the Iberian Peninsula were also used (J.M.L., unpublished data).

To describe the faunistic similarity among sampling sites, a cluster analysis was performed, using the percent of dissimilarity Bray and Curtis' index as a measure of quantitative resemblance (Ludwig and Reynolds 1988), and the Ward's method as linkage rule (Statistica 1995). Cluster analysis was used again to describe the Scarabaeinae faunistic dissimilarity (presence-absence data from the BANDASCA database; (Lobo and Martín-Piera 1991) among 50 × 50 km grid cells, calculating Baroni-Urbani and Buser similarity qualitative index (Baroni-Urbani and Buser 1976) and the same linkage rule (Ward's method). Baroni-Urbani and Buser similarity index was chosen because it takes into account common absences on a pairwise comparison.

Mean comparison between sites was done by non-parametric statistics: the Kruskal-Wallis analysis of variance (ANOVA) test and the Mann-Whitney  $U$  test.

Table 2. Spring inventory of Scarabaeoidea dung beetles from Portugal, sampled across a geographic North-South transect carried out in Portugal from 19 May to 23 May in 1997

Species	1 NC4	2 NCI	3 ND4	4 NDI	5 NE2	6 NE3	7 NF4	8 NF3	Total
Aphodiidae									
Md	0	0	0	0	0	0	0	6	6
Md	1	0	2	0	0	0	0	0	3
Eu	0	0	0	0	0	25	52	2	79
Md	4	0	0	0	0	0	0	0	4
Eu	0	0	0	0	0	0	1	0	1
Md	2	0	0	0	0	2	0	0	4
Eu	58	3	2	0	0	0	0	0	63
Eu	0	0	0	0	0	7	1	11	19
Md	2	0	1	0	0	0	0	0	3
Md	3	0	36	0	1	0	0	0	40
Eu	43	1	0	1	0	1	0	0	46
Eu	0	0	0	0	6	0	0	0	6
Eu	4	0	0	0	8	18	2	29	61
Md	3	0	0	0	0	0	1	1	5
Et	0	0	0	0	0	8	0	0	8
Md	0	0	0	0	0	0	2	0	2
Scarabaeidae									
Et	4	0	2	2	3	0	0	0	11
Et	0	1	0	0	0	0	0	0	1
Et	202	0	9	0	0	1	3	0	215
Et	22	0	0	0	0	0	0	0	22
Et	0	0	0	0	1	0	0	0	1
Eu	0	0	0	0	7	0	0	0	7
Md	0	0	0	0	3	0	0	0	3
Et	0	1	1	0	0	0	0	0	2
Et	135	15	32	14	0	5	0	0	201
Eu	0	0	0	0	8	18	0	0	26
Md	0	0	0	0	16	0	0	0	16
Md	0	0	0	1	7	0	3	18	29
Eu	0	0	0	0	0	0	0	2	2
Md	4	0	0	65	2	64	9	16	160
Eu	48	4	3	31	0	284	767	93	1230
Md	0	0	0	0	0	0	1	4	5
Eu	13	0	2	1	1	0	9	0	26
Md	0	0	0	4	0	27	8	1	40
Et	0	0	0	0	0	42	0	7	49

Table 2 (continued)

Species	1 NC4	2 NC1	3 ND4	4 ND1	5 NE2	6 NE3	7 NF4	8 NF3	Total
Eu <i>Oonthophagus (s.s.) taurus</i> (Schreber)	19	1	0	22	23	47	25	12	149
Md <i>Oonthophagus (Trichonthophagus) maki</i> (Illiger)	0	0	0	0	2	0	0	0	2
Md <i>Scarabaeus (Auteuchetus) cicatricosus</i> (Lucas)	0	0	16	0	0	0	0	0	16
Md <i>Scarabaeus (Auteuchetus) laticollis</i> L.	0	0	0	0	3	0	0	0	3
Eu <i>Sisiphus schaefferi</i> (L.)	0	0	0	0	0	1	0	0	1
Geotrupidae									
Md <i>Geotrupes ibericus</i> Baraud	0	1	0	0	0	0	0	0	1
Md <i>Sericotrupes niger</i> (Marsham)	3	0	0	2	0	1	0	1	7
Md <i>Thoretes (s.s.) lusitanicus</i> Jekel	0	0	0	0	1	0	0	0	1
Eu <i>Trypocopris (Trypocopris) pyrenaicus</i> (Charpentier)	0	0	0	0	0	0	0	2	2
Eu <i>Tiphthaeus typhtoeus</i> (L.)	0	0	0	0	0	13	0	0	13
Total N	570	27	106	143	92	564	884	205	2,591
Total S	18	8	11	10	16	17	14	15	45
Mean richness per trap	14.3 ± 0.5	2.8 ± 0.9	6.0 ± 1.1	5.8 ± 0.5	9.8 ± 1.0	12.5 ± 1.0	8.5 ± 0.3	10.5 ± 1.0	8.8 ± 0.7
Mean abundance per trap	142.5 ± 20.8	6.75 ± 2.95	26.5 ± 7.0	35.8 ± 4.6	23.0 ± 2.7	141.0 ± 19.0	221.0 ± 11.4	51.3 ± 6.8	81.0 ± 13.5
Scar/Aphod ratio	0.89	2.50	1.75	8.00	4.00	1.50	1.33	1.60	1.50
$\beta_2$	16.67		36.36	54.55	31.25	70.59	35.29	33.33	21.43

Mean values are displayed with standard errors.  $\beta_2$ -scores are calculated on a pairwise base, namely, the beta diversity between 2 adjacent sampling sites (Harrison et al. 1992). Et, species with an Euroturanian geographic distribution; Eu, Eurosiberian distribution; Md, Mediterranean distribution.

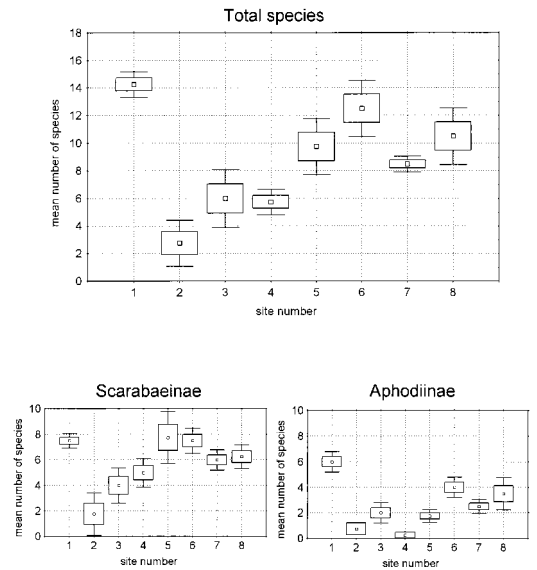


Fig. 2. Box and Whisker plots (Statistica 1995) showing the species variation between sampling sites for Scarabaeinae and Aphodiinae. The central points represent the estimated means, the bars are the standard errors, and the brackets the confidence intervals at 95%.

Results

A total of 2,591 individuals, belonging to 45 species of 3 families, was collected: 24 species of Scarabaeinae (2,217 individuals), 16 of Aphodiinae (350 individuals), and 5 of Geotrupinae (24 individuals) (Table 2).

**Richness Comparison.** The mean number of total species per trap differs significantly from site to site (Kruskal-Wallis ANOVA test = 27.10,  $n = 32$ ,  $P = 0.0003$ ). Both the mean number of Scarabaeinae species (Kruskal-Wallis ANOVA test = 23.46,  $n = 32$ ,  $P = 0.001$ ) and the mean number of Aphodiinae species (Kruskal-Wallis ANOVA test = 26.17,  $n = 32$ ,  $P = 0.0005$ ) differ significantly between sites. The geographic pattern of richness variation differs between Scarabaeinae and Aphodiinae (Fig. 2). The southernmost locality Scarabaeinae richness is significantly higher than those of the localities situated 150 km northward (2, Pegoes; 3, Mora; and 4, Tomar), which together constitute an impoverished region. With regard to Aphodiinae, the pattern is quite different. Once again, mean number of Odivelas (locality 1) species is significantly higher than in all other localities, which do not have more than 4 species per trap. The central segment of the transect (sites 2 Pegoes, 3 Mora, 4 Tomar, and 5 Pontao) again constitutes an impoverished region.

The total mean richness per trap, with a value of  $8.8 \pm 0.7$  (Table 2), is lower than that measured in other areas of the Iberian Peninsula (14–15) (Table 3) and is quite similar to that observed in Balearic Islands (Lobo and Martín-Piera 1993). Only the northern and southern sites (1, 6, and 8) richness values are similar to the general Iberian pattern. Scarabaeinae and

**Table 3. Mean values of abundance and richness per trap in some studies made in different areas of the Iberian Peninsula and Balearic Islands**

	Gimnesic Balears	Pitiuses Balears	Guadarrama	Gredos	Doñana	Portugal
Mean no. of individuals	45	16	211	680	291	81
Abundance range	13-125	3-39	26-886	237-1,733	50-600	1-238
Mean no. of species	7	3	14	14	15	9
Richness range	4-12	2-5	6-23	7-20	7-24	1-15

The range of abundance is also pointed out. The data for the Guadarrama Mountains come from Martín-Piera et al. (1992), those of Gredos Massif from Lobo (1992b), Balearic Islands from Lobo and Martín-Piera (1993), and Doñana from Lobo et al. (1997).

Aphodiinae mean richness per trap is also low for the Portuguese territory, with scores of  $5.7 \pm 0.4$  for the former, and  $2.6 \pm 0.3$  for the latter.

**Scarabaeinae/Aphodiinae Ratio and Species Turnover.** The ratio Scarabaeinae/Aphodiinae is 1.50, but varies highly between sites (Table 2). This ratio is  $>1$  at all the sites except for Odivelas plot (site 1). Only 4 of 26 Iberian regions (presence-absence data from 1-yr studies; J.M.L., unpublished data) have a higher number of Scarabaeinae species than Aphodiinae: Pego-Oliva (ratio 1.33;  $S = 15$ ), Sierra de Onil (ratio 2.04;  $S = 12$ ), Sierra de Salinas (ratio 2.33;  $S = 12$ ), and a general faunistic survey of the Almería province (ratio 1.33;  $S = 54$ ) (Carrión 1961, Cartagena 1996, Micó et al. 1998). All studies were carried out in the arid southeastern region of the Iberian Peninsula (the first 3 in Alicante province), and they always show a striking species impoverishment.

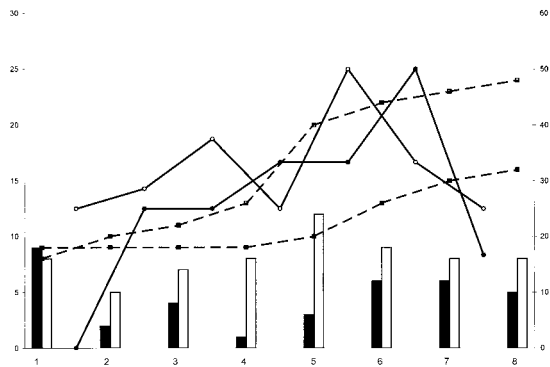
The total  $\beta$ -2 diversity scores for the entire transect are quite similar for both families ( $\beta$ -2 Scarabaeinae, 14.29;  $\beta$ -2 Aphodiinae, 11.11). The turnover in species composition between consecutive sites shows 2 well-defined peaks in the case of Scarabaeinae; one between the plots 3 and 4, and the other 1 between the plots 5 and 6 (Fig. 3). However, the Aphodiinae species turnover is more homogeneous and its higher

peak occurs between the northern localities 6 and 7. The accumulation curve of species ( $\gamma$ -diversity) is more pronounced in the case of Scarabaeinae (Fig. 3).

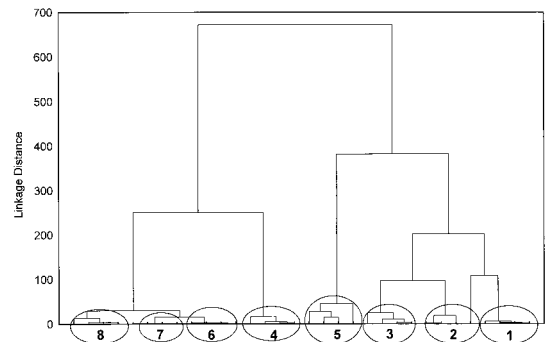
**Delimitation of Faunistic Regions.** Two well delimited faunistic regions appear when we consider the quantitative composition of each site (Fig. 4): a southern region, grouping the sites 1, 2, 3, and 5, and a northern one formed by the sites 4, 6, 7, and 8. The clustering of sites 4 and 5 to the 2 main groups appears to be marginal, thus pointing out the faunistic singularity of the central zone of the transect.

The 2 delimited faunistic regions only differ significantly in total mean abundance per trap (Mann-Whitney  $U$  test,  $Z = 3.00$ ;  $n_1 = n_2 = 16$ ;  $P = 0.003$ ), but not in mean richness per trap ( $Z = 0.77$ ;  $n_1 = n_2 = 16$ ;  $P =$  not significant), nor in the Scarabaeinae/Aphodiinae ratio ( $Z = 1.04$ ;  $n_1 = n_2 = 16$ ;  $P =$  not significant). In the southern faunistic region the mean number of individuals per trap was 49.7, and in the northern region there are 112.3 individuals per trap.

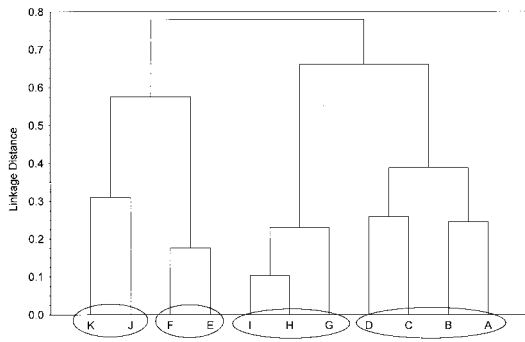
The species recorded can be assigned to 3 geographic distributional types: Mediterranean, Eurosiberian, and Euroturanian (La Greca 1964). With this assignment, it can be emphasized that faunistic differences between the 2 regions are produced by the higher number of species with a Mediterranean-type distribution (10 in the northern regions, 16 in the southern regions). However, the number of both Euroturanian-type distribution species (7 and 6, respec-



**Fig. 3.** Spatial diversity variation along a Portuguese geographic transect. Alfa diversity, measured as species richness, is represented as bars;  $\beta$ -diversity, measured as  $\beta$ -2 (Harrison et al. 1992), is shown with continuous lines and circles;  $\gamma$ -diversity, measured as the cumulative number of species, is displayed as discontinuous lines and squares. The empty symbols belong to the Scarabaeinae scores, and the black ones to the Aphodiinae.



**Fig. 4.** Cluster analysis of sampling sites, using the percent of dissimilarity Bray and Curtis' index as a measure of quantitative resemblance (Ludwig and Reynolds 1988), and the Ward's method as linkage rule (Statistica 1995). Circles group the traps from each locality.



**Fig. 5.** Cluster analysis from Iberian Scarabaeinae presence-absence data (BANDASCA database) performed with the faunistically well sampled UTM 50 × 50 grid cells of Portugal (see text). Cluster affinities were calculated as 1 - Baroni-Urbani and Buser (1976) index. Hence, the distances represented on the y-axis are dissimilarity measures. Ward's method was the linkage rule. The grid cells are as follows: A: 29SNB2. B: 29SMC3. C: 29SND2. D: 29SPD4. E: 29TNE3. F: 29TPE1. G: 29TPE3. H: 29TPF4. I: 29TQF1. J: 29TNG4. K: 29TNG1 (see Fig. 1a). Circles group the main clusters.

tively), and the Eurosiberian-type (9 in both regions) does not differ.

Figure 5 shows the results of a cluster analysis performed with the 11 faunistically well sampled UTM 50 × 50 grid cells located in Portugal (J.M.L. and F.M.P., unpublished data) (Fig. 1a). Four groups can be distinguished from this cluster. A west Mediterranean one that brings together the 4 southern grid cells (A to D), subdivided into 2 groups of coastal and interior grid cells. A second one, composed of grid cells G, H, and I fits into the northern plateau subregion (Fig. 1b). A 3rd group (E, F) geographically located at central Portugal in the boundary delimited by the 4 physioclimatic subregions (west-Mediterranean, Eurosiberian, south, and north plateaus), and, finally, a Eurosiberian one, which includes the grid cells J and K. Total richness in each of these groups ranges from 31 species recorded in the west-Mediterranean subregion to 21 species recorded in the Eurosiberian subregion.

The 2 main clusters in Fig. 4 match 2 of the biogeographic Portuguese clusters recovered from the well sampled UTM grid cells data (Fig. 5): (1) the southern subregion identified in the transect (sites 1–3) fits into the west-Mediterranean area (grid cells A, B, C, and D); and (2) sites 6–8 of the transect correspond to the group of J and K grid cells, belonging to the Eurosiberian subregion. Grid cells E and F constitute a cluster faunistically related with the Eurosiberian grid cells J and K (Fig. 5). This group, placed at central Portugal among the 4 physioclimatic subregions (Fig. 1b), looks like a transition zone between Eurosiberian and Mediterranean faunas. Sites 4 and 5 of the transect, placed at central Portugal (Fig. 1a), might also belong to this faunistic transition zone. The cluster grouping the G, H, and I grid cells draws a biogeographic zone of the inner continental Iberian Peninsula out of the investigated transect.

**Discussion**

The Portuguese area investigated, especially the sites 2, 3, and 4 located in the Tajo valley, appears to be poorer in spring species richness than the majority of the surveyed regions in the Iberian Peninsula. Only some of the Iberian faunistic studies, performed in the southeastern arid region of the Iberian Peninsula, show a similar poverty (Carrión 1961, Cartagena 1996, Micó et al. 1998).

This poverty in dung beetle assemblages arises from the scarcity of Aphodiinae species, as is reflected by the Scarabaeinae/Aphodiinae ratio. This ratio is clearly biased toward the Aphodiinae in almost all the Iberian Peninsula, contrary to that found here. That is why the turnover in species composition between sites is mainly determined by the variation in Scarabaeinae species. The greater slope of the Scarabaeinae  $\gamma$ -diversity curve (Fig. 3) also shows that this group is mainly responsible for compositional changes across the transect. Again, a completely different pattern has been established in other Iberian studies (Lobo et al. 1997), where the spatial turnover among habitats and localities arises from the Aphodiinae species replacement.

Hence, it should be emphasized that the poorness of the Iberian dung beetle assemblages, where it occurs, is mainly the result of the scarcity of Aphodiinae, thus suggesting that low richness values, high scores of the Scarabaeinae/Aphodiinae ratios, and low species turnover appear to be closely interdependent. This pattern may be interpreted as a consequence of the differential environmental tolerances of both taxonomic groups: Iberian Scarabaeinae species are more habitat generalist than Aphodiinae species. The former are thought to be mainly responsible for community richness of a single dung-pat, whereas Aphodiinae mainly contribute to local and regional pool richness (Lobo et al. 1997). Briefly, the poorest Iberian localities predominantly have habitat generalist species with good dispersal abilities, regardless of the historical or environmental circumstances of that impoverishment. Commonly, a lot of Scarabaeinae and a very few Aphodiinae species inhabit these sites.

However, the data indicate the probable existence of a faunistic "shadow zone," specially for the Aphodiinae, in the middle of Portugal, located between the lower course of the Tajo River and the foothills of the Iberian Central System. This region is poor in abundance and richness, and is located in the inner west-Mediterranean subregion (Fig. 1b).

The data also allow one to postulate 2 major biogeographic regions, corresponding to western Mediterranean and Eurosiberian Portuguese faunas, between which a transitional faunistic boundary can be detected. The arbitrary "border lines" between biogeographic regions are not realistic representations of the ecological reality, because they can be wider than the grid cell sizes (Williams 1996). However, in the case analyzed here, peaks of  $\beta$ -diversity, especially for Scarabaeinae (Fig. 3), and clusters from dendrograms (Figs. 4 and 5) are highly consistent with the physio-

climatic subregions of Portugal (Fig. 1b). This suggests a correspondence between biogeographic and environmental boundaries.

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