



Biogeography of Aphodiinae dung beetles based on the regional composition and distribution patterns of genera

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ABSTRACT

Aim To examine current biogeographical patterns of Aphodiinae dung beetles (Coleoptera: Scarabaeoidea: Scarabaeidae) in order to reveal relationships among regions and their potential impact on the diversification of this group.

Location Worldwide.

Methods Information about all Aphodiinae genera was obtained from the literature. An occurrence matrix was built for the six worldwide biogeographical regions, and their faunas were characterized through simple statistics. Regional variations and similarities were further explored using co-occurrence and nestedness analyses, sequential agglomerative, hierarchical and nested clustering (SAHN), and a parsimony analysis of endemism (PAE). Mantel tests were also employed to assess the relationships between several characteristics of the regions and their faunas.

Results The Palaearctic and Palaeotropical regions showed the highest total numbers of Aphodiinae genera and the greatest generic endemism. Both these regions and the Oriental also showed higher numbers of genera than would be expected according to their size. Co-occurrence and nestedness analyses confirmed the non-randomness of the distribution of genera. Clustering and PAE showed that the Palaearctic and Oriental regions are the most similar, followed by the Palaeotropical region. Regional dissimilarity in genera composition was related to biological and historical traits, but not to ecoregions.

Main conclusions A structured geographical pattern for Aphodiinae was confirmed. Land continuity and proximity in the long term could have played a unifying role in regional faunas. We suggest that the different biogeographical regions have acted as either macroevolutionary sources (basically the Palaearctic and the Palaeotropical regions) or sink regions, according to their role as diversification centres. We review the processes and events that could account for current patterns of Aphodiinae diversity.

Keywords

Biogeographical patterns, biogeographical regions, Coleoptera, diversification, faunistic similarity, genera distribution, historical factors, macroevolutionary patterns, nestedness, species richness variation.

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INTRODUCTION

The subfamily Aphodiinae (Coleoptera: Scarabaeoidea: Scarabaeidae), together with Scarabaeinae (family Scarabaeidae) and Geotrupinae (family Geotrupidae), comprise a significant

majority of the known species of dung beetles (Halffter & Edmonds, 1982; classification *sensu* Dellacasa *et al.*, 2001). Most of the species from these three subfamilies show special morphological, behavioural and ecological adaptations to the consumption of mammal (mainly herbivore) excrements

(Hanski, 1991a). Unlike Scarabaeinae and Geotrupinae, which basically have paracoprid or telecoprid habits (bury portions of dung either beneath or away from dung pats, respectively), most Aphodiinae have dweller (endocoprid) behaviour: they usually eat and reproduce within the dung pats (Halffter & Edmonds, 1982; Cambefort, 1991a). Previous phylogenetic analyses support the monophyly of an aphodiine line (containing Scarabaeinae; see Browne & Scholtz, 1996, 1998), with the status of the subfamily Aphodiinae still under debate (Forshage, 2002; Grebennikov & Scholtz, 2004; Smith *et al.*, 2006), probably due to the inclusion of some independent basal lineages within the group. Aphodiinae show a worldwide distribution (Dellacasa, 1987, 1988a,b, 1991, 1995), showing remarkably high generic and specific diversity compared with other close groups within Scarabaeidae. There are more than 2000 described species (see Dellacasa, 1991) and around 200 recognized genera (Dellacasa *et al.*, 2001).

In this study, we examine the worldwide biogeographical patterns of the Aphodiinae faunas. Although internal phylogenetic relationships among Aphodiinae lineages are not well identified (Cabrero-Sañudo & Zardoya, 2004; Smith *et al.*, 2006; Cabrero-Sañudo, 2007), this paper intends to answer some basic biogeographical questions, assuming that (1) the taxonomy is able to reflect genealogical relationships reasonably well, and (2) current distributions are the consequence of past historical processes. Using the available taxonomic and faunistic information, we examine the general distribution and diversity variation of the Aphodiinae genera. We also assess the faunistic similarity among biogeographical regions in order to study the relationships among them. Although our study is directed mainly at disentangling the main biogeographical patterns of this group, we propose a hypothesis regarding the role played by each biogeographical region on its diversification, and identify further research needs.

MATERIALS AND METHODS

Data set

To carry out genus-level analyses, Dellacasa *et al.*'s (2001) classification was selected for Aphodiinae to account for the different lineages present within each biogeographical region. Information about distribution, body size, and species number of the Aphodiinae genera was obtained from several bibliographic sources (Dellacasa, 1987, 1988a,b, 1991, 1995; Bordat, 1999, 2003; Dellacasa & Dellacasa, 2000a,b, 2005; Stebnicka, 2000; Dellacasa *et al.*, 2001, 2002a,b, 2004; Masumoto & Kiuchi, 2001; Ochi & Kawahara, 2001; Ziani, 2002). A matrix was built for the presence (1) and absence (0) of genera for the six worldwide biogeographical regions (Palaeotropical, Australian, Nearctic, Neotropical, Oriental and Palearctic; see Appendix S1 in Supporting Information). We used the biogeographical regions proposed by Cox (2001) as, although they were based on major divisions in mammal faunas, it is with mammals more than any other vertebrate group that dung beetles are mainly associated. The area of each region was

calculated using the Idrisi Kilimanjaro GIS program (Clark Labs, 2003).

Basic analyses

Simple descriptive statistical analyses and calculations were carried out to characterize the fauna of the different biogeographical regions, using the Statistica program (StatSoft, Inc., 2006). For each region, several data were considered, including: (1) total number of genera and endemic genera, (2) number of genera shared with other regions, (3) mean number of species per genus, (4) mean body size per genus, and (5) mean number of regions where a genus is present. Possible correlations and differences among these data were analysed by nonparametric statistical tests. The relationship between the number of genera and area was also analysed, considering several potential nonlinear fits (Soberón & Llorente, 1993; Flather, 1996; Fattorini, 2006).

Species co-occurrence and nestedness

To confirm the existence of possible distribution patterns of regional faunas, a co-occurrence analysis was carried out to test if there is a biogeographical signal in the data set (Diamond, 1975; Connor & Simberloff, 1979). Five thousand random matrices were built from the original presence-absence matrix of genera per biogeographical region, each of these matrices having the same row and column totals as the original matrix (the number of regions in which each genus is present and the number of the genera in each region), in order to retain as properties of the simulations both the evolutionary colonization capacity of each genus, and the regional ability to sustain different numbers of genera (Gotelli, 2000). The number of genera that never co-occur in the same biogeographical region (checkerboards) was estimated and the *C*-score was calculated as the average number of all possible checkerboard pairs, considering genera that were present at least once in the matrix (Stone & Roberts, 1990). If the observed *C*-score was significantly higher than that expected by chance, then we may conclude that the genera tended not to occur together, suggesting the existence of independent macroevolutionary processes in each biogeographical region. All calculations were carried out using the co-occurrence module of the EcoSim package (Gotelli & Entsminger, 2004).

In order to identify the presence of a nested pattern (Darlington, 1957) of regional faunas, in which genera-poor regions constitute a subset of those present within richer regional faunas, two different analyses were performed. The nestedness temperature of the presence-absence genera matrix was calculated with the *Binary Matrix Nestedness Temperature Calculator* algorithm (BINMATNEST; Rodríguez-Gironés & Santamaría, 2006). This temperature index is a descriptor of the disorder of a matrix (0° for a completely nested matrix, 100° for a completely random matrix) (Atmar & Patterson, 1993). To calculate the statistical significance of the matrix temperature, 100 null matrices were chosen, while the

parameter values were those recommended by Rodríguez-Gironés & Santamaría (2006) (population size 30, number of individuals seven, number of generations 2000).

As temperature sometimes overestimates nestedness by adding non-nested endemic taxa to matrices that are not perfectly nested, the presence-absence matrix was also analysed with the Nestedness Calculator Program (Greve & Chown, 2006), which produces the discrepancy index d_1 , a small modification of temperature that standardizes the matrix by occupancy (Greve & Chown, 2006). In total, 1000 randomizations were conducted, conserving the column and row sums of the original matrix (as in the co-occurrence analysis).

Relationships among biogeographical traits

The relationships between the number of species of each genus (a measure of current diversification rate), the number of biogeographical regions in which each genus is present (a measure of distribution), and the approximate body size of each genus were analysed. The independence among these variables was checked by a chi-squared test and the shape of the relationships was studied by a boundary test. The latter test assesses whether data are significantly concentrated or sparse in each of the four 'corners' of the bivariate space (upper right, upper left, lower right and lower left). So if some corners of the defined space are unusually empty, the observed number of points and/or the sum of squares in the real data set will be significantly less than in the simulated data sets. These simulated random matrices were built by reshuffling the observed values of each pair of variables analysed with a similar number of data points, as in the original data set. Thus, the variances and distributions of the original variables were retained, while the covariance between them was eliminated. These analyses were accomplished using the Macroecology module of the EcoSim package (Gotelli & Entsminger, 2004) by selecting 1000 iterations, an asymmetrical data distribution with a left triangle shape, constraints defined by data, and boundary tests (upper and lower right) according to the relationships studied.

Similarity analyses

New coefficients (Henning & Hausdorf, 2006) and clustering strategies (Hausdorf & Henning, 2003, 2007) have been proposed to examine more complex situations. These new strategies consider the geographical relationships of the spatial units analysed. For our simple approach (faunistic similarities among biogeographical regions), we preferred to carry out a classical sequential agglomerative, hierarchical and nested clustering (SAHN; Sneath & Sokal, 1973), which takes into account the information on the presence-absence of each genus in the six biogeographical regions recognized. A Jaccard similarity coefficient was calculated for regional pairs; this index measures the relationship between two regions on the basis of shared presences, and excludes shared absences (Legendre & Legendre, 1998). Since the Jaccard index is

considered to be problematic when comparing nested subsets (Hausdorf & Henning, 2003), the congruence of cluster analysis results was examined according to the previously mentioned nestedness analysis. Ward's linkage rule was applied (increase in sum of squares; Legendre & Legendre, 1998), because it is considered to be a very efficient method of recovering few, but well supported, clusters of similar size (StatSoft, Inc., 2006). An analysis of similarities (ANOSIM) was used to test statistically whether there was a significant difference between the groups derived from the cluster analysis. ANOSIM is a nonparametric technique analogous to an F -test, in which differences are compared within and between groups, and P -values are determined through a randomization procedure (Clarke & Warwick, 1994; Legendre & Legendre, 1998). The ANOSIM global R statistic measures the difference of mean ranks of distance between and within groups. The maximum number of possible permutations was selected ($n = 60$). PRIMER ver. 6 software was used in these calculations (Clarke & Gorley, 2005).

A parsimony analysis of endemism (PAE; Rosen, 1988; Rosen & Smith, 1988) was also carried out, which allows the grouping of areas as if species were synapomorphies (character states shared by two or more terminal groups and inherited from their most recent common ancestor). PAE is a useful method for recovering historical relationships among areas, especially when phylogenetic information is lacking and other methods cannot be applied. Although it has recently been strongly criticized (Brooks & Van Veller, 2003; Santos, 2005), PAE shares the same problems with other analytical methods in historical biogeography (Porzecanski & Cracraft, 2005), but nevertheless offers an opportunity to assess relationships between different faunas in the absence of more comprehensive data. A hypothetical region containing no taxa was considered an outgroup. The NONA program (Goloboff, 1999) was used to search for the most parsimonious tree by means of a heuristic procedure (tree bisection-reconnection). Also, the WINCLADA program (Nixon, 2002) was used to contrast results by means of a Ratchet procedure.

To check confidence limits for the nodes, two different procedures were employed: bootstrap and Bremer support. The use of bootstrapping to assess the degree of support of phylogenies has been questioned (e.g. Kluge & Wolf, 1993; Carpenter, 1996). However, the fact that fundamental statistical assumptions may not be met in the phylogenetic context (such as that of independent, identically distributed characters) could not prevent the bootstrap from becoming the most popular method to assess their reliability (Müller, 2005). That is the reason why bootstrap support has been considered in this analysis. Nevertheless, in response to the criticism that the inclusion of uninformative characters (autapomorphies) in bootstrapping commonly leads to a loss of significance (Carpenter, 1996), two bootstrapping analyses were carried out, one that included the distribution of all genera, and another that excluded genera that were only distributed in one region.

A Bremer support procedure was also applied to the PAE to assess confidence limits on nodes, supplementing the bootstrap

results. A criticism of Bremer's support has been that it basically measures tree stability, which is not a goal of cladistics (Kluge, 1997). Additionally, unlike bootstrapping, the Bremer support provides an absolute quantitative measure, which could be more difficult to interpret. However, this index has been addressed in detail, and it has been confirmed that its use presents more advantages than bootstrapping (Oxelman *et al.*, 1999; DeBry, 2001). The WINCLADA (Nixon, 2002) and NONA (Goloboff, 1999) programs were used to calculate bootstrap and Bremer support indexes, respectively.

Mantel tests

To check possible correspondences of Aphodiinae regional distributions to other characteristics of the biogeographical regions, simple non-partial Mantel tests (Mantel, 1967) were carried out. Partial Mantel tests were not used because their application when the matrices are not independent has been strongly criticized (Raufaste & Rousset, 2001; Castellano & Balleto, 2002; Rousset, 2002); this is a very frequently encountered situation, and is even more likely when more than three matrices are simultaneously compared, as in our case. Five different dissimilarity matrices for the six biogeographical regions were compared: three biological traits, Aphodiinae genera (APH), Scarabaeinae genera (SCA) and mammal families (MAM); one ecological trait, Bailey ecoregions (ECO); and one historical trait, land continuity (LC). Mantel test results are used here in an exploratory way to examine whether the composition of Aphodiinae genera is correlated with the environmental, historical, mammal or Scarabaeinae similarity among biogeographical regions. Mantel tests attempt to discern whether the relationships among a set of objects (expressed as dissimilarity matrices) are linearly independent of the relationships among the same objects in another matrix.

APH was obtained from the Aphodiinae genera–region matrix (Appendix S1). Similarity among regions was based on the Jaccard index, and later changed to dissimilarity ($1 - \text{similarity index}$). SCA was also developed with the Jaccard index from the Scarabaeinae genera presence–absence data of Davis *et al.* (2002) (Appendix S2); again, similarity was based on the Jaccard index and subsequently changed to dissimilarity. MAM was built from a matrix of similarities of mammal faunas based on the results of a non-metric multidimensional scaling ordination analysis (Smith, 1983). All the observed values were converted to positive values by adding a fixed number to them. Later, these results were transformed into percentages and changed to dissimilarity values (Appendix S3). To obtain the ECO data layer, a digitized map of Bailey's (1998) ecoregions was used (CEOS, 2000). The Bailey ecoregional framework is based on global-scale biophysical data, and is used here to reflect the environmental similarity among biogeographical regions. For each biogeographical region, the percentage of the 30 ecoregions (divisions) was estimated and the dissimilarity among regions calculated with Euclidean distances (Appendix S4). LC was calculated as the geological time since any two biogeographical regions were separated.

In general, the time of vicariance among regions was taken from Sanmartín & Ronquist (2004), and from a corresponding matrix of dissimilarities that was based on calculated percentages (Appendix S5). To calculate percentages, different times of vicariance were divided by the maximum vicariance among regions: 160 Myr. A distance of 0.013 Myr, for the Nearctic–Palearctic regions, and 0 Myr, for the Palaeotropical–Oriental–Palaeartic regions, was assumed.

Mantel tests were carried out using the NTSYSPC program (Applied Biostatistics, Inc., 2002). Simple Bonferroni *P*-values that were adjusted for multiple statistical tests, which are stricter than those provided by a sequential Bonferroni procedure, sequential Bonferroni values and original (uncorrected) probabilities, were jointly examined in order to interpret correlation results (Moran, 2003).

RESULTS

Basic data by biogeographical region

A total of 198 Aphodiinae genera were compiled for all the biogeographical regions worldwide, and were divided into 186 Aphodiini, four Didactyliini and eight Proctophanini genera (see final paragraph). Table 1 lists the general data for each region and an overview of the results. The Palaeartic region has the highest number of Aphodiinae genera (around 55% of the total), followed by the Palaeotropical (35%), Oriental (21%), Nearctic (19%), Neotropical (9%) and Australian (6%) regions. The Palaeartic region is also the richest for the Didactyliini genera, while the Palaeotropical region is the richest for the Proctophanini genera (Table 1).

A relationship between the number of genera and area was observed. After examining the variability explained by different nonlinear procedures, a simple linear fit between the number of genera and area was the best test ($R = 0.85$; $R^2 = 72.68\%$; $F = 10.64$; $P < 0.05$). The linear relationship between the number of genera and area shows that around 1.8 genera are added per million square kilometres. Also, the Palaeartic, Oriental and Palaeotropical regions have a comparatively higher number of genera than predicted in relation to area; while Australian, Nearctic and Neotropical regions have comparatively lower numbers (Fig. 1). The variation in the number of genera among biogeographical regions differs significantly from a uniform distribution (equal number of genera in each region; $\chi^2 = 240.57$, d.f. = 5, $P < 0.0001$), but also from the number of genera expected according to the previously obtained area–genera relationship ($\chi^2 = 53.57$, d.f. = 5, $P < 0.0001$).

Endemic genera

Within Aphodiinae, the Aphodiini tribe represents approximately 69% of the endemic genera. Didactyliini is the tribe with the lowest percentage of endemic genera (50%), whereas Proctophanini has the highest (75%). These last two tribes

Table 1 Characteristics of worldwide regional faunas of Aphodiinae according to genera (unless specified, values refer to genera numbers).

	Palaeotropical	Australian	Nearctic	Neotropical	Oriental	Palaeartic
Aphodiinae	70	12	37	17	42	109
Aphodiini	62	9	35	15	42	106
Didactyliini	1	0	1	1	0	3
Proctophanini	7	3	1	1	0	0
Approximate area ($\times 10^6$ km ²)	22.1	7.7	22.9	19.0	7.5	54.1
Number of endemic genera	43	4	12	9	7	67
Percentage of endemic genera	61.43	33.33	32.43	52.94	16.67	61.47
Ratio of endemic/non-endemic genera	1.6	0.5	0.5	1.1	0.2	1.6
Endemic Aphodiini	38	3	12	9	7	65
Endemic Didactyliini	0	0	0	0	0	2
Endemic Proctophanini	5	1	0	0	0	0
Number of regions per genus (\pm SD)	1.76 \pm 1.18	2.83 \pm 1.90	2.27 \pm 1.33	2.12 \pm 1.69	2.55 \pm 1.17	1.66 \pm 1.04
Body size per genus (\pm SD) (mm)	5.82 \pm 2.77	6.48 \pm 3.01	5.69 \pm 1.98	5.60 \pm 2.04	5.49 \pm 2.07	5.52 \pm 1.76
Number of species per genus (\pm SD)	11.06 \pm 15.81	12.83 \pm 10.36	15.59 \pm 22.48	11.88 \pm 17.54	24.60 \pm 26.83	12.52 \pm 18.95
Number of species per endemic genus (\pm SD)	4.42 \pm 5.15	4.25 \pm 2.63	5.75 \pm 5.17	9.00 \pm 22.15	2.14 \pm 1.95	4.95 \pm 6.24

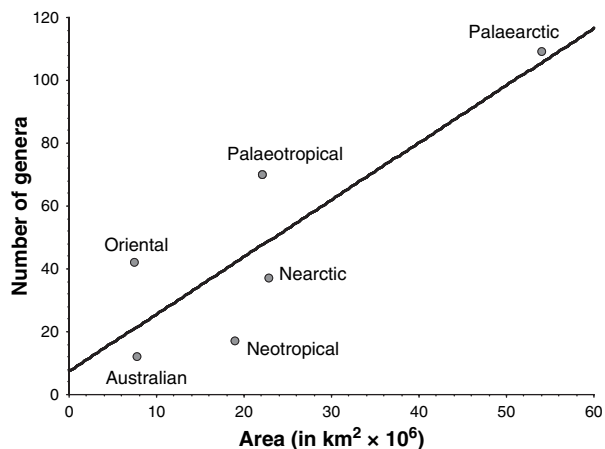


Figure 1 Linear regression between area and richness of Aphodiinae genera according to biogeographical region ($r_s = 0.85$; $P = 0.03$). Number of genera = $7.43 + 1.81 \cdot \text{area}$ ($\text{km}^2 \times 10^6$).

represent maximum numbers of endemic genera for the Palaeartic and Palaeotropical regions, respectively. A high percentage of the entire genera are endemic to a unique biogeographical region (around 72%, 142 genera), with the Palaeartic (67 genera) and Palaeotropical (43 genera) regions harbouring the highest percentage (77%) of total endemic genera (Fig. 2).

The numbers of endemic and total genera richness are correlated ($r_s = 0.83$, $P < 0.05$), whereas the numbers of endemic and non-endemic genera are uncorrelated ($r_s = 0.61$, $P = 0.20$). The ratio between endemic and non-endemic genera is low in the Oriental, Australian and Nearctic regions (a higher relative importance of non-endemic genera), but high in the richest Palaeotropical and Palaeartic regions (Table 1). More than 60% of total genera in each of these regions are endemic. As expected, the number of endemic genera is significantly different from a uniform distribution among regions ($\chi^2 = 137.86$, d.f. = 5, $P < 0.0001$).

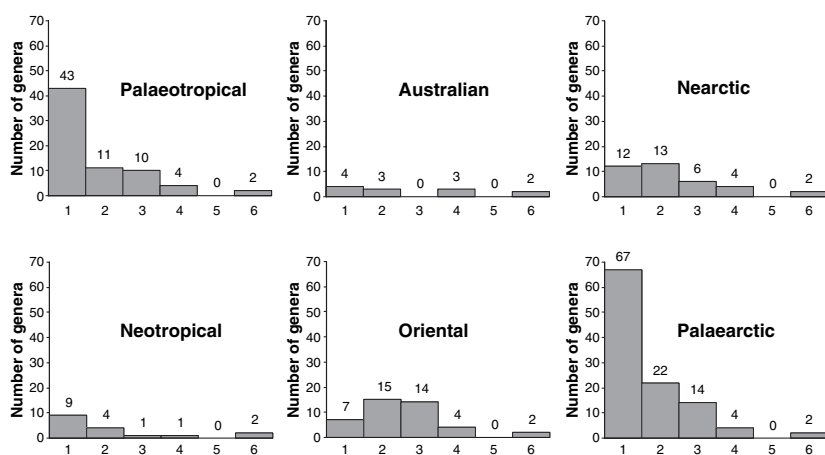


Figure 2 Distribution of Aphodiinae genera in each biogeographical region, according to categories representing the number of regions in which each genus occurs.

Body size does not differ significantly between endemic and non-endemic genera (Mann–Whitney U -test, $U = 3377$, $n_1 = 56$, $n_2 = 142$, $P < 0.10$). However, the number of species is significantly lower within the endemic genera ($U = 1474$, $P < 0.00001$). Thus, the median number of species in the endemic genera is 2.0 (upper quartile = 5.0, lower quartile = 1.0), while the median number of species in non-endemic genera is 17.5 (upper quartile = 27.5, lower quartile = 6.0). The number of species does not differ significantly among regions in either of the endemic genera (Kruskal–Wallis ANOVA by ranks test; $KW = 6.40$, $P < 0.27$; Table 1).

Non-random patterns of genus distribution

The number of regions in which each genus occurs (biogeographical extent) was calculated and the distribution of the different extent categories was estimated for each biogeographical region (Fig. 2). The mean number of regions per genus was also reported in Table 1. The biogeographical extent of the genera differed significantly among the biogeographical regions ($KW = 31.95$, $P < 0.0001$). *Post hoc* comparisons show that the extents are significantly different only among the faunas of the Palaearctic and Oriental regions, as well as among the faunas of the Palaetropical and Oriental regions ($P < 0.001$ in both cases), due to the relatively greater extent of Oriental genera (Table 1). This mean biogeographical extent is negatively and almost statistically significantly correlated with the number of genera present in each region (Spearman's rank correlation coefficient, $r_s = -0.80$; $P = 0.056$). Furthermore, the number of species per genus is positively correlated with the number of biogeographical regions in which the genera occurs ($r_s = 0.50$; $P < 0.00001$). These results suggest (1) that regions with higher numbers of Aphodiinae genera seem to sustain narrowly distributed genera, and (2) that the rate of species diversification could increase when many regions have been colonized.

Although 193 out of the 198 data points fell within the left triangle of the relationship between species richness and number of biogeographical regions (Fig. 3), a boundary test confirms that the upper-right corner of the space is not unusually empty, and the observed number of points is not significantly lower than the number of randomly estimated points ($P = 0.89$). This is because there are few genera present in more than four regions, and few genera with more than 40 species (Fig. 3). On the other hand, the observed number of points in the lower-right corner ($n = 2$) is significantly lower than the mean number of simulated points (5.6; $P = 0.0001$), showing that this space is unusually empty. There are no genera with more than 60 species present at the same time in fewer than three biogeographical regions.

Most data points (194 out of the 198) fell within the left triangle of the relationship between body size and number of species (Fig. 4), but again, the boundary test confirms that the upper right-hand corner is not unusually empty (0 observed points and 0.10 simulated points; $P = 0.89$). With regard to the relationship between number of biogeographical regions

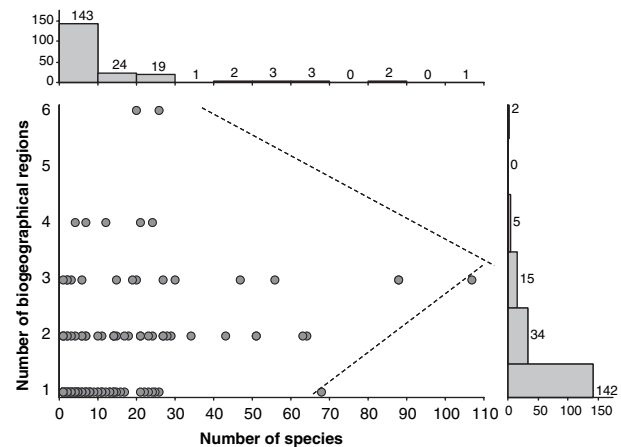


Figure 3 Relationship between the number of species for each Aphodiinae genus and the number of biogeographical regions in which each genus is present. Broken lines stand for possible constraints on this relationship, according to a boundary test (upper-right corner of space, observed number of points not significantly lower than the number of simulated points, $P = 0.89$; lower-right corner, observed number of points significantly lower than the number of simulated points, $P = 0.0001$).

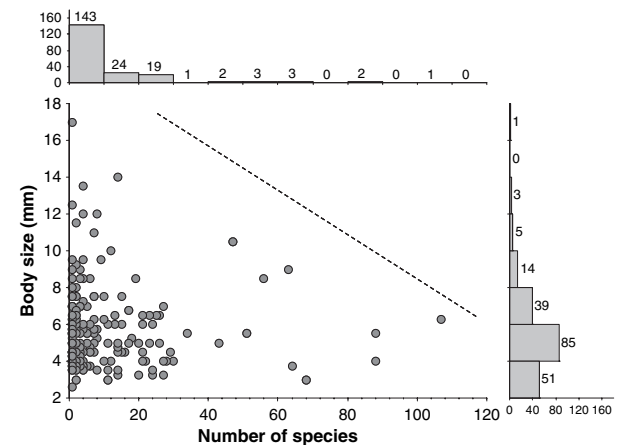


Figure 4 Relationship between number of species and body size of each Aphodiinae genus. The broken line stands for a possible constraint on this relationship, according to a boundary test (upper-right corner of space, observed points not significantly lower than the number of simulated points, $P = 0.89$).

and body size (Fig. 5), the boundary test also shows that the number of observed points (0) is not significantly lower than the mean number of simulated points ($P = 0.87$).

The total number of possible relationships among the six biogeographical regions is 63. However, only 23 different distributions have been observed (Fig. 6a). For example, no genera are distributed simultaneously and exclusively in the Palaetropical and Nearctic regions, or in the Palaearctic and Neotropical regions, so observed frequencies do not fit with the expected, under the supposition that all possible combinations of relationships among regions are equally probable

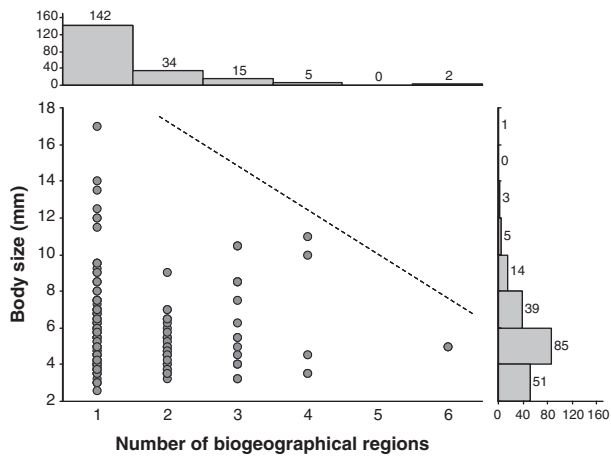


Figure 5 Relationship between number of biogeographical regions in which an Aphodiinae genus is present and its body size. The broken line stands for a possible constraint on this relationship, according to a boundary test (upper-right corner of space, observed points not significantly lower than the number of simulated points, $P = 0.87$).

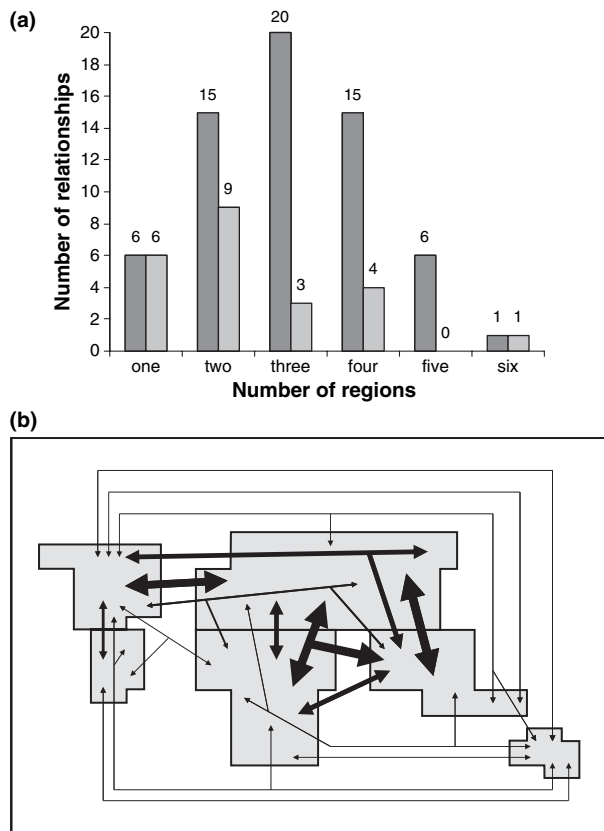


Figure 6 Patterns of distribution for Aphodiinae genera. (a) Expected (left) vs. observed (right) numbers of combinations of shared regions according to genera distributions. (b) Representation of the different regional relationships for Aphodiinae genera. Region size is proportional to the number of endemic Aphodiinae genera. Arrow and box widths are proportional to the number of genera with similar patterns for each relationship.

($\chi^2 = 30.9$, d.f. = 5, $P = 0.0001$). This result highlights the existence of concrete and non-random distribution patterns for the Aphodiinae genera. In fact, the co-occurrence analysis provided an observed C -score that was significantly higher than randomly expected ($C_{\text{observed}} = 0.85$; $C_{\text{expected}} = 0.83$; $P = 0.01$). This indicates that some groups of genera were repeatedly present in specific biogeographical regions, and therefore showed coincident diversity patterns (Fig. 6b).

Nestedness temperature in the data matrix was 11.37° , which was statistically lower than the estimated temperature of 36.05° (variance of 16.25°) provided by the null model 3 (recommended by Rodríguez-Gironés & Santamaría, 2006; $P < 0.00001$). However, the observed discrepancy index d_1 of 0.47 did not differ significantly from the estimated one (0.45 ± 0.01 SD; z -score = 1.51 ; $P_{(z\text{-score})} = 0.93$). So, although the temperature indicated that there was a pattern of nestedness in the regional faunas, the discrepancy index suggests that this effect is produced by the number of non-nested endemic genera, so each regional fauna shows an independent identity.

Similarity analyses

The dendrogram of faunistic similarity based on all genera showed that the Palearctic and Oriental regions are the most similar, and the Palearctic region is the next most highly associated region (Fig. 7a). The Neotropical and Australian regions are also similar, and together are closer to the Nearctic region. The ANOSIM test shows that the most probable similarity configuration is with the following three groups (global R was 0.636 , $P = 0.08$): I (Palearctic–Oriental), II (Palearctic), and III (Neotropical–Nearctic–Australian).

The dendrogram of faunistic similarity, based on exclusive genera, showed a unique tree (length = 231; consistency index = 0.85 ; retention index = 0.55 ; autoapomorphies included; Fig. 7b). The closest regions are the Palearctic and Oriental, followed by the Palearctic, and subsequently by the Australian, Nearctic, and Neotropical regions. Bootstrap validation supported the clade of the Palearctic and Oriental regions (82%), and their clade together with the Palearctic region (81%). Although the Nearctic and Neotropical regions also initially appeared to be linked, there was not enough statistical support to confirm their similarity (53%) and their node was consequently collapsed.

Independence of regional traits

The regional dissimilarity in the Aphodiinae genus composition was significantly and positively correlated with (1) the composition of the Scarabaeinae dung beetles, (2) the geological time of separation among the biogeographical regions (when a simple Bonferroni correction is applied), and (3) the mammal composition (when a sequential Bonferroni correction is used; Fig. 8; Table 2). Regional distribution of Scarabaeinae behaved similarly, and was also positively correlated with the mammal composition and the geological time of

Figure 7 Dendrograms of faunistic similarity among worldwide regions based on worldwide distributions of Aphodiinae genera. (a) Sequential agglomerative, hierarchical, and nested clustering analysis (SAHN). (b) Parsimony analysis of endemism: $L = 231$; $CI = 0.85$; $RI = 0.55$. Left values refer to bootstrap support; right values to Bremer support. Regions: PTR, Palaeotropical; AUS, Australian; NEA, Nearctic; NEO, Neotropical; ORI, Oriental; PAR, Palearctic.

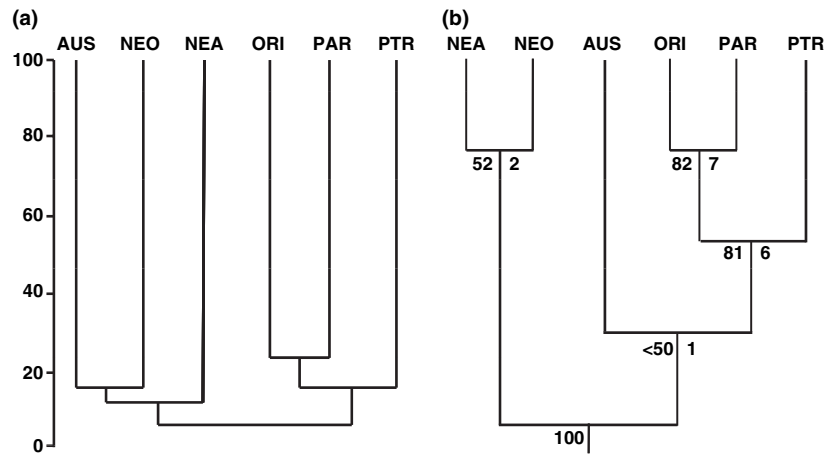


Figure 8 Trees based on an unweighted pair group method with arithmetic mean (UPGMA) clustering for the different matrices considered in the Mantel tests. Scale corresponds to dissimilarity index values. APH, Aphodiinae; SCA, Scarabaeinae; MAM, Mammals; ECO, Ecological; LC, Land continuity. Regions: PTR, Palaeotropical; AUS, Australian; NEA, Nearctic; NEO, Neotropical; ORI, Oriental; PAR, Palearctic (Table 2).

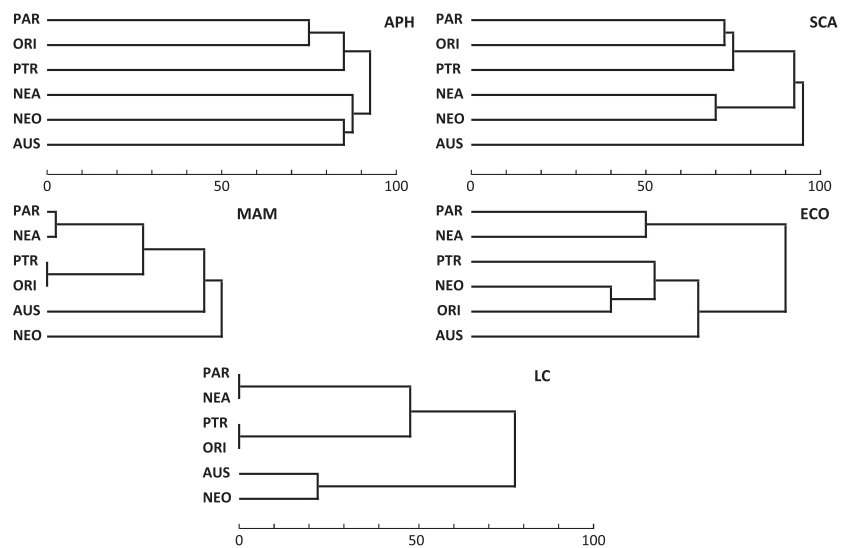


Table 2 Mantel test correlation scores (ρ) among the five considered matrices, and P -values.

	Aphodiinae	Scarabaeinae	Mammals	Ecology	Land continuity
Aphodiinae		$\rho = \mathbf{0.704}$ $P = \mathbf{0.004}$	$\rho = 0.620$ $P = 0.009$	$\rho = -0.178$ $P = 0.744$	$\rho = \mathbf{0.713}$ $P = \mathbf{0.005}$
Scarabaeinae			$\rho = \mathbf{0.685}$ $P = \mathbf{0.005}$	$\rho = -0.295$ $P = 0.865$	$\rho = \mathbf{0.767}$ $P = \mathbf{0.002}$
Mammals				$\rho = -0.082$ $P = 0.623$	$\rho = 0.628$ $P = 0.006$
Ecology					$\rho = 0.155$ $P = 0.286$

Simple Bonferroni significant probability values ($\alpha = 0.05/10 = 0.005$) are in bold. The Scarabaeinae genera data are based on data from Davis *et al.* (2002); mammal data from Smith (1983); ecology data are the percentage of Bailey ecoregions (CEOS, 2000); land continuity data represent the separation time between biogeographical regions (adapted from Sanmartín & Ronquist, 2004).

separation among biogeographical regions (when both simple and sequential Bonferroni corrections are considered). Regional mammal distribution was also positively correlated with the geological time of separation among the biogeographical

regions, when a sequential Bonferroni correction was used. The regional dissimilarity in ecoregions did not show any significant correlation with any biological or historical trait (Table 2).

DISCUSSION

Non-random distribution patterns

All observations and analyses strongly suggest that the richness of genera and endemic lineages and the faunistic composition of Aphodiinae follow a geographically structured pattern. The Palaearctic and Palaeotropical regions have the highest numbers of genera and highest endemism, and a singular faunistic composition. This result is only partially due to the area or the environmental heterogeneity of these regions, because (1) they own a higher number of genera than expected in accordance with their areas, and (2) the compositional differences do not seem to be related to ecoregional dissimilarity.

Co-occurrence and nestedness analyses suggest the singular character of regional Aphodiinae faunas; the most frequent worldwide distribution patterns of genera are indeed related to one or several of these regions (Palaearctic, Palaeotropical and Oriental). All of these characteristics make these three regions stand as a consistent group with regard to Aphodiinae (each one being, nonetheless, significantly singular on its own), as the two different similarity analyses produced a higher closeness among the Palaeotropical, Oriental and Palaearctic regions ('Old World faunas') and showed discrimination with respect to the other three regions. Long-term land continuity and proximity could have played a unifying role in these regional faunas. In fact, as the Mantel tests showed, historical and biological traits were related to regional similarities, in contrast to environmental factors.

Thus, based on these results, we hypothesize that there are two main types of region for Aphodiinae: macroevolutionary sink and source regions (Goldberg *et al.*, 2005). The first type would be characterized by the higher comparative importance of colonization processes and recent radiations in the shaping of current faunas, while the second type would be characterized by a long history as production and distribution centres for the main Aphodiinae lineages (basically the Palaearctic and the Palaeotropical regions).

Diversification and distribution range

Regions with lower Aphodiinae diversity usually have widely distributed genera. This could be interpreted as a variation of Rapoport's rule (the size of species distribution ranges increases with latitude; Rapoport, 1975). One of the explanations for this rule is that seasonal variability selects for greater climatic tolerances, and therefore for wider latitudinal ranges (Letcher & Harvey, 1994; Stevens, 1996). In the case of Aphodiinae, this relationship suggests that genera with higher environmental tolerances could have better chances of colonizing a greater number of biogeographical regions. Alternatively, and complementarily, we also hypothesize that this pattern could be due to the increase in opportunities for diversification when more than one biogeographical region is inhabited. In fact, the positive relationships between the number of described species in each genus and its distribution

suggest that those genera more widely distributed by the chance effects of lower extinction rates could have experienced higher probabilities of speciation (this could be considered as a variation of the age and area hypothesis: Willis, 1922).

It seems that there is an evolutionary limit to the possible species number for an endemic genus within a single region. Only when a genus colonizes other regions does it diversify beyond this apparent limitation. This constraint could be related to the existence of ecophysiological adaptations at higher taxonomic levels that limit the colonization of new environmental conditions (Hawkins *et al.*, 2006; Ricklefs, 2006). It could also be related to the role played by the contingent history of the biogeographical regions, meaning that the species could have environmentally favourable conditions in other biogeographical regions, but dispersal limitations prevent its colonization. In dung beetles, there are many sources of evidence of successful introductions into distant regions (Edwards, 2007), which support the lack of relevance, in some cases, of a contemporary environmental control on global distributions. However, Aphodiinae species also show clear geographical, seasonal and elevational limits, which suggest the existence of basic climatic restrictions among high-level taxonomic groups (Lobo, 2000; Cabrero-Sañudo & Lobo, 2006).

Endemic and non-endemic genera

There is a significant difference in regional species numbers between endemic and non-endemic genera. A total of 142 out of the 198 Aphodiinae genera (72%) are endemic to a single region; less than a third are shared among regions. Widely distributed genera usually correspond to those of a known wide ecological spectrum and opportunistic nature. For example, *Calamosternus* Motschulsky and *Labarrus* Mulsant and Rey, present in all biogeographical regions, show a higher climatic tolerance, are not strictly coprophagous, and can alternatively choose to behave as saprophagous or cleptoparasites (Veiga, 1998). However, the correlation between endemic and non-endemic genera is positive but not statistically significant, probably because world biogeographical regions have partially independent evolutionary histories, so the number of endemic genera can be the consequence of the barriers that have generated these regions independently of the genera numbers that they currently harbour.

Body size

Body size is not an important feature shaping the distribution patterns of Aphodiinae, although some large genera are endemic from a single region and have a small number of species. In contrast, larger species of North American mammals and birds usually tend to occupy greater areas (Brown, 1995). Larger genera, however, also could be a consequence of either insularity, as observed for island mammals (Lomolino, 1985), or the presence of ancient lineages, as in Scarabaeinae (Davis *et al.*, 2002).

Regional characteristics

The Palaearctic region presents the highest number of total and endemic Aphodiinae genera as a whole. Together with the Palaeotropical region, it also shows the highest ratio of endemic/non-endemic genera, indicating the great importance of endemics to the composition of its fauna. In fact, the genera inhabiting the Palaearctic show the lowest mean number of regions per genus compared with those of other regions. The Palaearctic is also the region with the highest number of genera and endemics for both Aphodiini and Didactyliini, but excludes Proctophanini.

Aphodiinae are usually the most common species group in dung beetle communities in the Palaearctic (Hanski, 1991b). In this region, they display the highest diversity of species (Dellacasa, 1987, 1988a,b, 1991, 1995) and the greatest abundance of individuals in northern communities compared with other scarabaeid taxa (Hanski, 1991b; Gittings & Giller, 1997, 1998; Roslin & Koivunen, 2001; Finn & Gittings, 2003). The best studied area in the world has traditionally been the Western Palaearctic, which has attracted much effort in Aphodiinae taxonomy (Báguena, 1967; Dellacasa, 1983; Baraud, 1985, 1992; Ádám, 1994; Hollande & Thérond, 1998; Veiga, 1998), although many Aphodiinae may still remain undiscovered (Cabrero-Sañudo & Lobo, 2003). The only phylogenetic studies so far on Aphodiinae evolution were based on Iberian species within the Palaearctic (Cabrero-Sañudo & Zardoya, 2004; Cabrero-Sañudo, 2007). These analyses show that most of the earlier branches of Aphodiinae are of Palaearctic or Holarctic distribution. This supports the hypothesis of a Laurasian origin of Aphodiinae, in spite of the reduced geographical and taxonomic scope of these studies. Nevertheless, the oldest known fossil evidence for Aphodiinae is the Eocene species *Aphodius charauxi*, which Piton discovered in France in 1940 (Krell, 2003). Some forms similar to the modern Aphodiinae were discovered in the UK (Scholtz, 1990) and dated also from the Eocene, in contrast to other regions, which lack recorded Aphodiinae fossils until the Oligocene.

The Palaeotropical region also shows important numbers of total and endemic genera of Aphodiinae. Its endemic/non-endemic genera ratio is the highest (together with the Palaearctic). Thus, the mean number of regions per genus is the second lowest compared with other regions. However, it probably ranks third among regions with regard to the number of species (Dellacasa, 1987, 1988a,b, 1991, 1995). Proctophanini show the highest genera richness in this region, Aphodiini are well represented, and there is also a Didactyliini genus. Interestingly, while the mean body size of the Palaeotropical genera is the largest after the Australian, the mean number of species per genus is the lowest in relation to other regions, possibly because genera with large body size and low number of species correspond to ancient lineages (as in Scarabaeinae; Davis *et al.*, 2002). Although Palaeotropical dung beetle communities are basically dominated by Scarabaeinae individuals (Cambefort, 1991b; Doube, 1991; Davis *et al.*, 2002), some studies show that the number of individuals in some

localities can sometimes be very high, or even the highest, for Aphodiinae (Bernon, 1981; Rougon & Rougon, 1991; Krell *et al.*, 2003). Together with the Palaearctic region, the Palaeotropical can be considered as a macroevolutionary source region, possibly acting as a refuge and/or a distribution centre for Aphodiinae genera. There is no record, however, for Tertiary or Quaternary Aphodiinae fossils within the Palaeotropical region (Krell, 2003), possibly a consequence of difficult fossilizing conditions, absence of prospecting studies, and/or recent Aphodiinae genera diversification.

The Oriental region is the third in terms of number of genera. Although this region hosts many more genera than expected according to its area, it is the second lowest in terms of endemic genera, showing the lowest endemic/non-endemic genera ratio and one of the greatest mean genera distribution ranges, for it shares many genera with the Palaeotropical and Palaearctic regions. In spite of this low degree of endemism, it has the greatest mean number of species per genus, and is probably the second most species-rich region after the Palaearctic (Dellacasa, 1987, 1988a,b, 1991, 1995). Thus, the majority of Oriental genera would be expected to be evolutionary successful (widely distributed and diversified). This suggests the Oriental region to be a macroevolutionary sink region for Aphodiinae lineages (Forshage, 2002), possibly explaining why the mean body size per genus is the lowest. Studies on dung beetle communities carried out in the Oriental region frequently omit results for Aphodiinae; the studies including it (Hanski & Krikken, 1991; Davis, 2000; Davis *et al.*, 2001; Shahabuddin *et al.*, 2005) show that they represent a small proportion of local Scarabaeidae richness (c. 4–10% of species). However, most of these studies have been carried out on island communities, and there is a lack of studies from continental communities considering species richness and abundances for Aphodiinae. As for the Palaeotropical region, there is no fossil evidence for Aphodiinae within the Oriental region (Krell, 2003).

The Nearctic has the highest number of Aphodiinae genera, endemic genera, and species richness of both 'New World' regions (Dellacasa, 1987, 1988a,b, 1991, 1995), hosting representatives from the three tribes, although only Aphodiini has endemic genera. Moreover, the Nearctic region also holds the second highest mean number of species per genus. However, the ratio of endemic/non-endemic genera of this region is the lowest, together with the Australian region. Most Nearctic genera are shared with the Palaearctic, and there is also a great proportion that are either shared with the Neotropical region or show worldwide distributions. All these facts allow us to define the Nearctic as a mainly macroevolutionary sink region for Aphodiinae (however, see final paragraph). Aphodiinae are usually the dominant species group in northern dung beetle communities in the Nearctic region (Lobo, 2000, and references therein). This region has also displayed an ancient presence of Aphodiinae, the first Nearctic fossil records dating from the Oligocene, a little more recent than those of the Palaearctic (Krell, 2003).

The Neotropical region holds the second lowest richness for genera and endemic genera, and holds the least number of genera as predicted by its size. Although it hosts genera from the three different tribes, the only endemic genera are Aphodiini. It shares several Aphodiinae genera with the Nearctic region, and some of them also have Palaeotropical and Australian affinities. Its ratio of endemic/non-endemic genera is high, and the mean number of species per genus is the second lowest after the Palaeotropical region. This could be explained by the fact that it probably has acted not only as a macroevolutionary sink region, but also as a source region to a limited extent. In fact, the Neotropical region has a higher proportion of endemics than the Nearctic, and more than half of its genera are exclusive to this region. Few studies on Neotropical dung beetle communities have taken Aphodiinae into consideration. Although very few Aphodiinae species are represented in these communities, they can be very abundant (Andresen, 2002). No Aphodiinae fossil records have been found for this region.

The Australian region shows the lowest numbers of Aphodiinae genera and endemic genera, as well as the fewest described species (Stebnicka & Howden, 1995). While only two tribes (Aphodiini and Proctophanini) have representatives in this region, a third of the genera for each tribe are endemic. Nevertheless, the Australian region has the highest mean number of regions occupied per genus, so most non-endemic genera are widely distributed and shared among several regions, especially with the Palaeotropical, Neotropical and Oriental. Thus, its endemic/non-endemic genera ratio is the lowest, together with the Nearctic. The Australian region has basically acted as a macroevolutionary sink region with regard to Aphodiinae lineages. The Australian genera also display the largest mean body size per genus compared with other regions, which could point to possible gigantism for some genera caused by either a greater insularity or, more likely, the presence of ancient lineages, as in the Palaeotropical region. With regard to abundance and species richness, Scarabaeinae dominate Northern dung beetle communities, while southern Australian communities are dominated by endemic species of Aphodiinae (Doube *et al.*, 1991; Steinbauer & Weir, 2007). There is no fossil record for Aphodiinae in this region and, again, the causes could be similar to those for the Palaeotropical, Oriental and Neotropical regions.

A synthesis of Aphodiinae evolution and biogeography

The main radiation of Scarabaeoidea dates from the Mesozoic and Cenozoic ages (Scholtz & Chown, 1995; Krell, 2000; Davis *et al.*, 2002). Aphodiinae probably separated from the Scarabaeidae main lineage sometime between the Jurassic and Cretaceous (Krell, 2000). These ancestral lineages of Aphodiinae possibly had different feeding (mycetophagy or saprophagy; Scholtz & Chown, 1995) and ecological habits (forest- or sand-dwellers), as has been observed previously within earlier branches of Iberian Aphodiinae, which show

proportionally more of these tendencies than more recent groups (Cabrero-Sañudo & Zardoya, 2004; Cabrero-Sañudo, 2007). Although there are no fossil records for Aphodiinae from this period (Krell, 2003), the radiation of coprophagous beetles presumably happened as a response to an increasing rate of dung production, density and size of vertebrate droppings from dinosaurs and/or small mammals (Jeannel, 1942; Halffter & Matthews, 1966; Davis, 1990; Arillo & Ortuño, 2008), as is thought to have happened in the case of the sister group Scarabaeinae (Davis *et al.*, 2002).

The first Aphodiinae probably developed before or around the early Jurassic age (200–170 Ma), when most continents were joined in Pangea (Scotese, 2003). Most Aphodiinae have temperate to temperate-cold and/or subalpine preferences, so they may have arisen at the northern territories of contemporary Eurasia, where the climate was cool with temperate conditions compared with the rest of the world, which was very arid and hot (Scotese, 2003). Phylogenetic analyses on Iberian Aphodiinae showed that most of these earlier branches might be Laurasic in origin (Cabrero-Sañudo & Zardoya, 2004). Some of the first lineages of Aphodiinae could have spread later to other Pangean southern territories before their break-up, in contrast to Scarabaeinae, which show tropical and warmer affinities and probably dispersed northward from the Gondwanan territories (Davis & Scholtz, 2001).

After the fragmentation of Pangea (middle Jurassic to early Cretaceous; 160–130 Ma), some Aphodiinae would have remained within Laurasia, although it is possible that a few Aphodiinae lineages survived in Gondwanan continents. Some genera from the Neotropical, Palaeotropical and Australian regions show distributions that would be explained only by former relationships among continents. This is the case for the Proctophanini tribe, which currently presents a Gondwanan-like distribution.

The dinosaur extinction at the K/T boundary (late Cretaceous, c. 66 Ma) could also have affected those Aphodiinae taxa associated with their dung (if any) and many lineages could have then disappeared worldwide, especially within the Gondwanan regions. Also, the sudden extinction of the dinosaurs removed the restriction imposed by their predation over the diversification of mammals (Cox, 2000), so dung from mammals became increasingly more common, providing a resource that could be consumed gradually by new Aphodiinae taxa. Almost at the same time, and while all Gondwanian lands stayed separated, Eurasia and North America approached each other and were intermittently connected from the late Cretaceous to Eocene periods (66–38 Ma; Scotese, 2003). This could explain why the first Aphodiinae fossils registered date from these ages (see above). The faunas from the rest of the regions probably had little contact (Krell, 2003); although perhaps there were several lineage exchanges between continents, such as Africa and Eurasia, or Eurasia and the Indian peninsula, those were not as frequent as between Eurasia and North America.

Nevertheless, the main causes of the present worldwide distribution of Aphodiinae date back to the Miocene

(26–12 Ma), when Eurasia and Africa finally met. Similar to Scarabaeinae (Davis & Scholtz, 2001; Davis *et al.*, 2002), a secondary radiation of Aphodiinae could have happened as a consequence of the mixture of faunas and the opening and establishment of new dispersal routes between Africa and Eurasia (Potts & Behrensmeier, 1993). Also, prairies and savannas became more and more common as a consequence of an increase in aridity and general climate cooling (Cambefort, 1991b; Scotese, 2003), and the radiation of Artiodactyla (Bovini) associated with these events (30+ Ma; Cumming, 1982; Silva & Downing, 1995). Most of the mammal dung present on the continents until the early Eocene (54–48 Ma) was from one of three different types: pellets (in all regions) from Marsupalia, Insectivora, Rodentia, Lagomorpha and Artiodactyla; small odiferous droppings (in all regions) from Primates and Carnivora; and large fibrous droppings (only in Palaeotropical, Neotropical, Oriental and Palaeartic regions) mainly from Perissodactyla (Silva & Downing, 1995; Penny *et al.*, 1999; see classification of dung types in Davis & Scholtz, 2001; Davis *et al.*, 2002). When Bovini arose, a different, new type of dung, soft-fibrous droppings, appeared within the Palaeotropical and Palaeartic regions (Davis *et al.*, 2002), serving as a new high-quality resource for dung beetles, which boosted their rapid and massive radiation. Although currently there are many Aphodiinae species adapted to feed on dry dung, dung-specialized or euriphagic Aphodiinae generally prefer large, soft-fibrous excrement. In fact, most Aphodiinae are currently endocoprids, and are necessarily linked to large pads of dung, which maintain a higher humidity and last longer than other resources (Lumaret *et al.*, 1992). All this points to the Miocene radiation as the most significant event for the configuration of recent Aphodiinae faunas worldwide (Forshage, 2002). Here, our Mantel tests highlight the relationships between Aphodiinae and Scarabaeinae, mammal faunas and land continuity, which are probably related to these events.

For a long time, the Palaeotropical and Palaeartic regions shared several groups of ungulates (Cambefort, 1991c), migrations of which should have contributed to the radiation and interchanges of Aphodiinae lineages and species. This interchange culminated during the late Miocene period (12 Ma), when the Indian peninsula crashed against Eurasia. Consequently, several Aphodiinae taxa probably finished invading this territory from Eurasia and Africa due to greater land continuity. There was also an increase of pastures in North America, and the Beringian land bridges permitted the passage of Bovini and other mammals from Eurasia to the Nearctic region during the Miocene and, later, in the Pliocene (Potts & Behrensmeier, 1993). However, the most important event for the American continents was the final closure of the Isthmus of Panama during the late Miocene and Pliocene (13–7 Ma; Coates *et al.*, 2004), which caused the great American interchange of fauna and flora (Webb, 1985), and also range expansions of many dung beetle taxa, as seen in Scarabaeinae (Davis & Scholtz, 2001). A certain number of current Aphodiinae taxa within the South America and Mexican

transition zone showing adaptations to warmer environments are the likely survivors of the specialized and hardly diversified fauna from the Neotropical region. Many of these species have undergone the same adaptations as the Scarabaeinae inhabiting this area: they often show stenotopic preferences (they are hardly found in the tropical evergreen forest), nocturnal activity, and a higher rate of deviation towards necrophagy or other rare dung sources (Halffter & Matthews, 1966).

The principal characteristic of the Australian continent has been its isolation from the rest of the regions and the lack of placental mammals until the Pleistocene (2.5 Ma–10 ka; Cox, 2000). In spite of this, the degree of generic endemism is quite low in this region. Until that time, only two types of dung were available in this region (pellets and small-odiferous; Davis *et al.*, 2002). Hence, older Australian lineages were adapted to exploiting these excrements. Nevertheless, the appearance of land connections during the Pleistocene between Eurasia and Australia probably allowed the dispersal of mammals towards the latter region, together with a number of Aphodiinae taxa associated with them. Consequently, there was a mass extinction of monotremes and marsupials (Murray, 1984), which probably could have caused the subsequent extinction of some endemic Aphodiinae taxa.

During the middle–late Pleistocene (420–18 ka), the polar ice extended and contracted in repeated glacial–interglacial cycles (Imbrie *et al.*, 1993). These climatic changes could have played an important role as modifying factors of Aphodiinae richness and diversity, especially in the Holarctic regions (Hanski, 1991b). Fossil evidence (Lindroth, 1948; Coope & Angus, 1975; Coope, 1978, 1990) shows that insects showed substantial range shifts and colonized new habitats during the Pleistocene, according to the changes in climate and vegetation. Thus, in the Northern Hemisphere, Aphodiinae should have shifted their distribution ranges southwards during glacial periods, and northwards during interglacials (Cabrero-Sañudo & Lobo, 2006). The mixing of fauna should then have been more frequent between the Palaeartic and the Palaeotropical and Oriental regions on the one hand, and between the Nearctic and Neotropical regions on the other, since the ice sheets should have interrupted most of the interchanges across the Beringian strait. Moreover, climatic deterioration of the ice ages led to an impoverishment of the mammal faunas of the Northern Hemisphere (Cox, 2000). The Oriental region was probably isolated by the glaciated ice sheets of mountain ranges, and was not able to act as a refuge for northern Aphodiinae lineages. This possibly favoured the role of the Palaeotropical region as a refuge for a great number of Aphodiinae lineages of the ‘Old World’, and may explain the high density of Aphodiinae endemic genera in this region in comparison with others.

During the Holocene (10 ka to the present), human impact on the landscape has been significant in every region. Cattle, horses and other domesticated animals have contributed particularly to the dispersion of Aphodiinae with large fibrous and soft-fibrous dung preferences. These human-induced changes have been especially important in the Western

Palaeartic during the late Quaternary (Birks, 1986; Hanski, 1991b) and over the past centuries for the Nearctic, Neotropical and Australian regions (Delcourt & Delcourt, 1987; Doube *et al.*, 1991; Kohlmann, 1991; Mirol *et al.*, 2003). Several Aphodiinae taxa have been introduced to foreign regions as a consequence of new land uses and cattle importation (Cabrero-Sañudo & Lobo, 2006). Finally, recent agricultural changes (monocultures, progressive increase of cowshed cattle-raising, antiparasitic treatments, etc.) have negatively influenced Aphodiinae diversity (Lumaret, 1986; Lumaret *et al.*, 1993; Barbero *et al.*, 1999; Roslin & Koivunen, 2001; Lumaret & Martínez, 2005; Lobo *et al.*, 2006).

Future challenges

Current distribution patterns are a historical product of diversification (differentiation and extinction) and migration (emigration and immigration) processes. However, a coherent and reliable procedure that is able to discriminate the differential role played by each one of these macroevolutionary forces remains elusive (Ricklefs, 2006; Martin *et al.*, 2007). The lack of comprehensive fossil information and the shifts in the distribution of species makes it extremely difficult to determine past dispersal patterns, complicating the formulation of reliable hypotheses that allow explanation of current distribution by means of past events, even when phylogenetic information is available (Gaston & Blackburn, 1996; Losos & Glor, 2003; Thomas *et al.*, 2006; Pulquério & Nichols, 2007). Thus, one of the main challenges for biogeographers continues to be the formulation of reliable hypotheses about the underlying historical processes based on present-day biogeographical data. This implies that is necessary that current patterns actually hold an identifiable signature of the processes from which they originated. Some studies propose the existence of these signatures, such as the classical assumption that the region of origin of a given taxon is the one that has higher levels of species richness and endemism (Willis, 1922; Ricklefs & Schluter, 1993; Ricklefs, 2006). However, this is not always true, because sometimes regions of origin hold a high proportion of recently derived taxa (Goldberg *et al.*, 2005), probably as a consequence of young taxa having lower chances of becoming extinct in the region of origin, and also of being dispersed to other regions. The joint occurrence of ancestral and new taxa in a region of origin agrees with the point of view that tropical regions act both as 'cradles' and 'museums' of diversity (McKenna & Farrell, 2006). Another proposal is based on the concept of 'ancestral ecological zones' (Farrell *et al.*, 1992; Ricklefs, 2006), where the species are hypothesized to be best adapted to the conditions in the ecological zone of their lineages' origin, and new adaptive range shifts are difficult to evolve. In this case, both basal taxa and maximum diversity would be located in the regions that harbour the prevailing climatic conditions during the time of speciation (see Lobo, 2007, and references therein for a similar proposal in the case of dung beetles).

In this paper, we suggest that Palaeotropical and Palaeartic regions have been the main diversification centres for Aphodiinae after the break-up of Pangea, which holds the explanation of the current distribution of the main Aphodiinae tribes (Didactyliini, Proctophanini and Aphodiini). Phylogenetic data are nevertheless needed to solve both the taxonomic status of Didactyliini and Proctophanini, and their relationship with Aphodiini. Palaeotropical and Palaeartic regions have a long history of interchanges for vertebrate mammals, the group with which dung beetles are associated. Many clades originated in Africa and have expanded across the Palaeartic, where they underwent new episodes of cladogenesis and colonized Africa again (Folinsbee & Brooks, 2007, and references therein). Thus, both regions could have acted jointly as macroevolutionary source regions in different times, also suffering range shifts and extinctions that obscure the link between past events and present-day distributions. For example, if recent Pleistocene glaciations pushed Palaeartic temperate taxa southwards, some of them will now be refuged in the Palaeotropical mountains (via the so-called horizontal process of colonization; Lobo & Halffter, 2000). It would be possible to find recently derived sister taxa in Africa, originated from either ancestral Palaeotropical or Palaeartic clades. Thus, comprehensive phylogenetic and phylogeographical information is needed to determine: (1) if early diversification processes occurred in both biogeographical regions, and (2) if the main radiation events happened at different periods in both regions. Also, the climatic adaptations of ancestral Aphodiinae taxa are as yet unknown, especially in the case of Aphodiini, species of which are adapted to temperate biomes. Preliminary phylogenetic data indicate that basal Aphodiini lineages are those that adapted to temperate-cold Palaeartic conditions (Cabrero-Sañudo & Zardoya, 2004; Cabrero-Sañudo, 2007), but new and more comprehensive data are needed to estimate the relative ages of basal and derived lineages.

In addition to phylogenetic data, we also need better distributional and ecological data for Aphodiinae species, as well as reliable taxonomic revisions. During the editing of this paper, a monograph on North American Aphodiini has been published (Gordon & Skelley, 2007; see also Cabrero-Sañudo *et al.*, 2007; Skelley *et al.*, 2007) and the Aphodiinae species of southern South America have been revised (Smith & Skelley, 2007). These new revisions, not considered by the present paper, include more than 20 new Nearctic genera, increasing the relevance of temperate Holarctic Aphodiini fauna for the global distribution patterns of this group.

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SUPPORTING INFORMATION

Additional Supporting information may be found in the online version of this article:

Appendix S1 List of Aphodiinae genera.

Appendix S2 Scarabaeinae genera presence/absence matrix.

Appendix S3 Matrix of similarities of mammal faunas.

Appendix S4 Percentage of area of the 30 ecoregions.

Appendix S5 Matrix of similarities among regions according to geological time.

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Supporting Information

Appendix S1.- List of Aphodiinae genera with their number of described species, as well as their approximate body size (length) and their presence/absence in each one of the biogeographic regions. Genera classification was according to Dellacasa *et al.* (2001). Species numbers were from several bibliographic sources (Dellacasa, 1987, 1988a, b, 1991, 1995; Bordat, 1999, 2003; Dellacasa & Dellacasa, 2000a, b, 2005; Stebnicka, 2000; Dellacasa *et al.*, 2001, 2002a, b, 2004; Masumoto & Kiuchi, 2001; Ochi & Kawahara, 2001; Ziani, 2002). Regions: PTR: Palaeotropical; AUS: Australian; NEA: Nearctic; NEO: Neotropical; ORI: Oriental; PAR: Palaearctic.

Tribe	Genus	Number of described species	approximate size (in mm)	Distribution					
				PAR	NEA	PTR	NEO	ORI	AUS
Aphodiini	<i>Acanthaphodius</i>	1	3.5	-	-	-	1	-	-
Aphodiini	<i>Acanthobodilus</i>	2	5.75	1	-	-	-	-	-
Aphodiini	<i>Acrossidius</i>	4	12	-	-	-	-	-	1
Aphodiini	<i>Acrossoides</i>	2	11.5	-	-	-	-	-	1
Aphodiini	<i>Acrossus</i>	47	10.5	1	1	-	-	1	-
Aphodiini	<i>Adeloparius</i>	14	14	-	-	1	-	-	-
Aphodiini	<i>Afrodiapterna</i>	2	5	-	-	1	-	-	-
Aphodiini	<i>Aganocrossus</i>	21	4.5	1	-	1	-	1	1
Aphodiini	<i>Agoliinus</i>	27	7	1	1	-	-	-	-
Aphodiini	<i>Agolius</i>	2	7.5	1	-	-	-	-	-
Aphodiini	<i>Agrilinus</i>	51	5.5	1	-	-	-	1	-
Aphodiini	<i>Ahermodontus</i>	3	4.25	1	-	-	-	-	-
Aphodiini	<i>Alocoderus</i>	19	8.5	1	-	1	-	1	-
Aphodiini	<i>Allobodilus</i>	4	5.75	-	-	1	-	-	-
Aphodiini	<i>Amidorus</i>	24	6	1	-	-	-	-	-
Aphodiini	<i>Ammoecioides</i>	10	4	-	-	1	-	-	-
Aphodiini	<i>Ammoecius</i>	23	6.5	1	-	1	-	-	-
Aphodiini	<i>Anomalurobius</i>	1	4	-	-	1	-	-	-
Aphodiini	<i>Anomius</i>	13	6	1	-	-	-	-	-
Aphodiini	<i>Aparammoecius</i>	29	4.5	1	-	-	-	1	-
Aphodiini	<i>Aphodaulacus</i>	7	6.25	1	-	-	-	-	-
Aphodiini	<i>Aphodiellus</i>	2	7.5	1	-	-	-	-	-
Aphodiini	<i>Aphodiopsis</i>	12	4	-	-	1	-	-	-
Aphodiini	<i>Aphodius</i>	12	10	1	1	-	-	1	1
Aphodiini	<i>Aphodobius</i>	3	4.75	-	-	1	-	1	-
Aphodiini	<i>Aphodoharmogaster</i>	1	5.75	-	-	1	-	-	-
Aphodiini	<i>Apsteiniella</i>	3	7	1	-	-	-	-	-
Aphodiini	<i>Arrowiellus</i>	1	6	-	-	1	-	-	-
Aphodiini	<i>Basilewskyanus</i>	1	7	-	-	1	-	-	-
Aphodiini	<i>Biralus</i>	5	7	1	-	-	-	-	-
Aphodiini	<i>Blackburneus</i>	68	3	-	-	-	1	-	-
Aphodiini	<i>Bodiloides</i>	2	5	1	-	1	-	1	-
Aphodiini	<i>Bodilopsis</i>	3	7	1	-	-	-	-	-
Aphodiini	<i>Bodilus</i>	56	8.5	1	-	1	-	1	-
Aphodiini	<i>Boucomontiellus</i>	1	6.25	1	-	-	-	-	-
Aphodiini	<i>Brachiaphodius</i>	15	7.5	1	-	1	-	1	-
Aphodiini	<i>Calamosternus</i>	26	5	1	1	1	1	1	1
Aphodiini	<i>Calocolobopterus</i>	8	12	-	-	1	-	-	-

Aphodiini	<i>Candezeollus</i>	3	7	-	-	-	-	-	1
Aphodiini	<i>Carinaulus</i>	18	5.25	1	-	-	-	1	-
Aphodiini	<i>Cephalocyclus</i>	10	7.5	-	1	-	-	-	-
Aphodiini	<i>Cinacanthus</i>	13	6.5	-	1	-	-	-	-
Aphodiini	<i>Cnemargulus</i>	3	5.5	1	-	-	-	-	-
Aphodiini	<i>Cnemisus</i>	4	8.5	1	-	-	-	-	-
Aphodiini	<i>Coelotrachelus</i>	7	7.5	-	1	-	-	-	-
Aphodiini	<i>Colobopteridius</i>	1	9	-	-	1	-	-	-
Aphodiini	<i>Colobopteroides</i>	1	4.5	-	-	1	-	-	-
Aphodiini	<i>Colobopterus</i>	6	8.5	1	1	-	-	1	-
Aphodiini	<i>Coprimorphus</i>	1	12.5	1	-	-	-	-	-
Aphodiini	<i>Coptochiroides</i>	2	4.5	1	-	-	-	-	-
Aphodiini	<i>Craterocyphus</i>	9	9.5	-	-	1	-	-	-
Aphodiini	<i>Chilothorax</i>	88	5.5	1	1	-	-	1	-
Aphodiini	<i>Dialytellus</i>	2	3.5	-	1	-	-	-	-
Aphodiini	<i>Dialytes</i>	5	5	-	1	-	-	-	-
Aphodiini	<i>Diapterna</i>	6	6	-	1	-	-	-	-
Aphodiini	<i>Doaphius</i>	8	5.25	-	-	1	-	-	-
Aphodiini	<i>Drepanocanthoides</i>	6	4.5	-	1	-	-	-	1
Aphodiini	<i>Emadiellus</i>	5	5.5	-	-	-	-	1	-
Aphodiini	<i>Erytoides</i>	1	5.5	-	-	-	-	1	-
Aphodiini	<i>Erytus</i>	11	6	1	-	-	-	-	-
Aphodiini	<i>Esymus</i>	22	4	1	-	-	-	-	-
Aphodiini	<i>Eudolus</i>	2	4	1	-	-	-	-	-
Aphodiini	<i>Euhemicyclium</i>	2	6.75	-	-	1	-	-	-
Aphodiini	<i>Euheptaulacus</i>	6	4.75	1	-	-	-	-	-
Aphodiini	<i>Euorodalus</i>	14	4.5	1	-	-	-	-	-
Aphodiini	<i>Eupleurus</i>	2	6.5	1	1	-	-	-	-
Aphodiini	<i>Exaphodius</i>	1	17	-	-	1	-	-	-
Aphodiini	<i>Gilletianus</i>	1	4.5	-	-	-	-	1	-
Aphodiini	<i>Gonaphodiellus</i>	14	4.75	-	1	-	1	-	-
Aphodiini	<i>Gonaphodius</i>	2	6.25	1	-	-	-	-	-
Aphodiini	<i>Grandinaphodius</i>	1	4	1	-	-	-	-	-
Aphodiini	<i>Guanyinaphodius</i>	1	2.6	-	-	-	-	1	-
Aphodiini	<i>Harmodactylus</i>	1	5.75	-	-	1	-	-	-
Aphodiini	<i>Haroldaphodius</i>	3	9	-	-	1	-	-	-
Aphodiini	<i>Hemicyclium</i>	2	9.25	-	-	1	-	-	-
Aphodiini	<i>Heptaulacus</i>	8	3.5	1	-	-	-	-	-
Aphodiini	<i>Hornietus</i>	1	3.9	-	1	-	-	-	-
Aphodiini	<i>Imelda</i>	1	7.5	-	1	-	-	-	-
Aphodiini	<i>Koreoxyomus</i>	1	4.5	-	-	-	-	1	-
Aphodiini	<i>Koshantschikovius</i>	43	5	-	-	1	-	1	-
Aphodiini	<i>Labarrus</i>	20	5	1	1	1	1	1	1
Aphodiini	<i>Limarus</i>	3	5	1	-	-	-	-	-
Aphodiini	<i>Lindbergianus</i>	1	4.25	1	-	-	-	-	-
Aphodiini	<i>Liothorax</i>	7	5	1	-	-	-	1	-
Aphodiini	<i>Loboparius</i>	15	4.5	1	-	-	-	1	-
Aphodiini	<i>Longaphodius</i>	1	5.5	-	-	1	-	-	-
Aphodiini	<i>Loraphodius</i>	7	5.5	1	-	-	-	-	-
Aphodiini	<i>Loraspis</i>	1	5.5	1	-	-	-	-	-
Aphodiini	<i>Lorditormaeus</i>	26	6.5	-	-	1	-	-	-
Aphodiini	<i>Lunaphodius</i>	3	7	1	-	-	-	-	-
Aphodiini	<i>Macroretroides</i>	1	4.5	-	-	1	-	-	-
Aphodiini	<i>Macroreturus</i>	4	3.75	-	-	1	-	-	-

Aphodiini	<i>Mecynodes</i>	11	3	1	-	-	-	-	-
Aphodiini	<i>Megateloides</i>	2	3.5	-	-	1	-	1	-
Aphodiini	<i>Megatelus</i>	3	4	1	-	1	-	1	-
Aphodiini	<i>Melinopterus</i>	21	6	1	1	-	-	-	-
Aphodiini	<i>Mendidaphodius</i>	28	4	1	-	1	-	-	-
Aphodiini	<i>Mendidius</i>	51	5.5	1	-	-	-	1	-
Aphodiini	<i>Mesontoplatys</i>	24	3.25	-	-	1	-	1	-
Aphodiini	<i>Microteuchestes</i>	1	3.5	-	-	1	-	-	-
Aphodiini	<i>Mothon</i>	1	4.5	1	-	-	-	-	-
Aphodiini	<i>Mozartius</i>	4	4	1	-	-	-	-	-
Aphodiini	<i>Neagolius</i>	23	5	1	-	-	-	-	-
Aphodiini	<i>Neocalaphodius</i>	1	5.5	1	-	1	-	1	-
Aphodiini	<i>Neocolobopterus</i>	7	7.5	-	-	1	-	-	-
Aphodiini	<i>Neodipterna</i>	2	8	-	-	-	1	-	-
Aphodiini	<i>Neoemadiellus</i>	6	3.75	-	-	1	-	-	-
Aphodiini	<i>Neoheptaulacus</i>	2	5	-	-	1	-	-	-
Aphodiini	<i>Neotrichonotulus</i>	3	4.25	-	1	-	-	-	-
Aphodiini	<i>Nialaphodius</i>	2	4.5	-	1	1	1	-	-
Aphodiini	<i>Nialosternus</i>	1	4	1	-	-	-	-	-
Aphodiini	<i>Nialus</i>	17	5	1	-	1	-	-	-
Aphodiini	<i>Nimbus</i>	15	6	1	-	-	-	-	-
Aphodiini	<i>Nipponaphodius</i>	1	5	1	-	-	-	-	-
Aphodiini	<i>Nipponoagoliinus</i>	1	5.45	1	-	-	-	-	-
Aphodiini	<i>Nobiellus</i>	5	3.75	1	-	-	-	-	-
Aphodiini	<i>Nobius</i>	21	4	1	-	-	-	-	-
Aphodiini	<i>Nolicus</i>	1	6.25	-	-	1	-	-	-
Aphodiini	<i>Obaphodius</i>	1	4.25	-	-	1	-	-	-
Aphodiini	<i>Orodaliscoides</i>	2	6	-	-	-	1	-	-
Aphodiini	<i>Orodaliscus</i>	4	6	1	-	-	-	-	-
Aphodiini	<i>Oromus</i>	2	5.5	1	-	-	-	-	-
Aphodiini	<i>Osmanius</i>	3	4.75	1	-	-	-	-	-
Aphodiini	<i>Otophorus</i>	1	4.5	1	1	-	-	-	-
Aphodiini	<i>Oxyaphodius</i>	1	6	1	-	-	-	-	-
Aphodiini	<i>Oxycorythus</i>	1	4	1	-	-	-	-	-
Aphodiini	<i>Oxyomus</i>	24	3.5	1	1	1	-	1	-
Aphodiini	<i>Parabodilus</i>	1	7	1	-	-	-	-	-
Aphodiini	<i>Paracoptochirus</i>	4	7.25	1	-	-	-	-	-
Aphodiini	<i>Paracrossidius</i>	1	7.5	1	-	-	-	-	-
Aphodiini	<i>Paradeloparius</i>	4	13.5	-	-	1	-	-	-
Aphodiini	<i>Paradidactylia</i>	20	3.25	1	-	1	-	1	-
Aphodiini	<i>Parammoecius</i>	7	4.5	1	-	-	-	-	-
Aphodiini	<i>Paranimbus</i>	4	9.5	-	-	-	1	-	-
Aphodiini	<i>Paulianellus</i>	7	5.75	1	-	-	-	1	-
Aphodiini	<i>Phaeaphodius</i>	14	5	1	1	-	-	-	-
Aphodiini	<i>Phalacronothus</i>	14	3.25	1	-	-	-	-	-
Aphodiini	<i>Pharaphodius</i>	107	6.25	1	1	-	-	1	-
Aphodiini	<i>Plagiogonus</i>	27	3.25	1	-	1	-	1	-
Aphodiini	<i>Planolinellus</i>	1	3.75	1	1	-	-	-	-
Aphodiini	<i>Planolinoides</i>	1	4.25	1	1	-	-	-	-
Aphodiini	<i>Planolinus</i>	6	4.5	1	1	-	-	-	-
Aphodiini	<i>Platyderides</i>	63	9	1	-	-	-	1	-
Aphodiini	<i>Pleuraphodius</i>	88	4	1	-	1	-	1	-
Aphodiini	<i>Podotenoides</i>	1	6	-	-	1	-	-	-
Aphodiini	<i>Podotenus</i>	34	5.5	-	-	-	1	-	1

Aphodiini	<i>Pseudacrossus</i>	25	6.5	1	-	-	-	-	-
Aphodiini	<i>Pseudagoliinus</i>	3	4.25	-	-	1	-	-	-
Aphodiini	<i>Pseudagolius</i>	17	6.75	-	1	-	-	-	-
Aphodiini	<i>Pseudesymus</i>	1	5.25	1	-	-	-	-	-
Aphodiini	<i>Pseudoahermodontus</i>	1	5	1	-	-	-	-	-
Aphodiini	<i>Pseudoheptaulacus</i>	2	3	1	-	-	-	-	-
Aphodiini	<i>Pseudopharaphodius</i>	2	3.75	-	-	1	-	-	-
Aphodiini	<i>Pseudopodotenus</i>	1	9.5	-	-	-	1	-	-
Aphodiini	<i>Pseudoteuchestes</i>	1	6.5	1	-	-	-	-	-
Aphodiini	<i>Pubinus</i>	1	5.75	1	-	-	-	-	-
Aphodiini	<i>Qingaphodius</i>	2	6.5	1	-	-	-	-	-
Aphodiini	<i>Renaudius</i>	1	3.5	1	-	-	-	1	-
Aphodiini	<i>Rhodaphodius</i>	1	7.5	1	-	-	-	-	-
Aphodiini	<i>Sahlbergianus</i>	1	8	1	-	-	-	-	-
Aphodiini	<i>Siamaphodius</i>	1	4	-	-	-	-	1	-
Aphodiini	<i>Sigorus</i>	1	5	1	-	-	-	-	-
Aphodiini	<i>Simogonius</i>	4	3.75	-	-	1	-	-	-
Aphodiini	<i>Sinaphodius</i>	5	5.5	-	-	-	-	1	-
Aphodiini	<i>Sinodipterna</i>	4	4.5	1	-	-	-	-	-
Aphodiini	<i>Sitiphus</i>	3	4.5	1	-	-	-	-	-
Aphodiini	<i>Stenothorax</i>	21	6.5	-	1	-	-	1	-
Aphodiini	<i>Subrinus</i>	4	3.5	1	-	1	-	-	-
Aphodiini	<i>Sugrames</i>	3	3.75	1	-	-	-	-	-
Aphodiini	<i>Sussorca</i>	1	8.5	-	-	1	-	-	-
Aphodiini	<i>Sybax</i>	3	8.5	-	-	1	-	-	-
Aphodiini	<i>Symphodon</i>	1	7	-	-	-	1	-	-
Aphodiini	<i>Tetraclipeoides</i>	10	6.25	-	1	-	1	-	-
Aphodiini	<i>Teuchestes</i>	7	11	1	1	1	-	1	-
Aphodiini	<i>Trichaphodiellus</i>	1	7	-	-	-	1	-	-
Aphodiini	<i>Trichaphodioides</i>	16	4.5	-	-	1	-	-	-
Aphodiini	<i>Trichaphodius</i>	64	3.75	-	-	1	-	1	-
Aphodiini	<i>Trichonotuloides</i>	2	4	-	1	-	-	-	-
Aphodiini	<i>Trichonotulus</i>	30	4	1	1	-	-	1	-
Aphodiini	<i>Tristaphodius</i>	2	6.25	1	-	-	-	-	-
Aphodiini	<i>Turanella</i>	1	3.75	1	-	-	-	-	-
Aphodiini	<i>Vladimirellus</i>	1	4	1	-	-	-	-	-
Aphodiini	<i>Volinus</i>	1	4.5	1	-	-	-	-	-
Aphodiini	<i>Xenoheptaulacus</i>	1	3.75	-	-	-	1	-	-
Aphodiini	<i>Xeropsamobeus</i>	2	3.75	-	1	-	-	-	-
Aphodiini	<i>Youngaphodius</i>	1	4.25	-	-	1	-	-	-
Didactyliini	<i>Aidophus</i>	11	3.5	-	1	-	1	-	-
Didactyliini	<i>Didactylia</i>	27	4	1	-	1	-	-	-
Didactyliini	<i>Pseudomothon</i>	1	5	1	-	-	-	-	-
Didactyliini	<i>Trigonoscelus</i>	3	4.25	1	-	-	-	-	-
Proctophanini	<i>Australaphodius</i>	4	3.5	-	1	1	1	-	1
Proctophanini	<i>Coptochirus</i>	11	5	-	-	1	-	-	-
Proctophanini	<i>Drepanocanthus</i>	2	5	-	-	1	-	-	-
Proctophanini	<i>Goiginus</i>	2	3.75	-	-	1	-	-	-
Proctophanini	<i>Harmogaster</i>	5	5.5	-	-	1	-	-	-
Proctophanini	<i>Proctophanes</i>	8	5.75	-	-	-	-	-	1
Proctophanini	<i>Pseudodrepanocanthus</i>	3	3.75	-	-	1	-	-	-
Proctophanini	<i>Pseudoxyomus</i>	14	3.5	-	-	1	-	-	1

Appendix S2.-Scarabaeinae genera presence/absence matrix for each of the biogeographical regions according to Davis *et al.* (2002). Regions: PTR: Palaeotropical; AUS: Australian; NEA: Nearctic; NEO: Neotropical; ORI: Oriental; PAR: Palaeartic.

Genus	Distribution					
	PAR	NEA	PTR	NEO	ORI	AUS
<i>Allogymnopleurus</i> Janssens	0	0	1	0	0	0
<i>Amietina</i> Cambefort	0	0	1	0	0	0
<i>Amphistomus</i> van Lansberge	0	0	0	0	0	1
<i>Anachalcos</i> Hope	0	0	1	0	0	0
<i>Ateuchus</i> Weber	0	1	0	1	0	0
<i>Aulacopris</i> White	0	0	0	0	0	1
<i>Boletoscapter</i> Matthews	0	0	0	0	0	1
<i>Bubas</i> Mulsant	1	0	0	0	0	0
<i>Caccobius</i> Thomson	1	0	1	0	1	0
<i>Canthidium</i> Chapin	0	0	0	1	0	0
<i>Canthon</i> Hoffmannsegg	0	1	0	1	0	0
<i>Catharsius</i> Hope	0	0	1	0	1	0
<i>Cleptocaccobius</i> Cambefort	0	0	0	0	0	0
<i>Copris</i> Müller	1	1	1	1	1	0
<i>Coprophanaeus</i> Olsoufieff	0	0	0	1	0	0
<i>Coptodactyla</i> Burmeister	0	0	0	0	0	1
<i>Coptorhina</i> Hope	0	0	1	0	0	0
<i>Cyobius</i> Sharp	0	0	0	0	1	0
<i>Cyptochirus</i> Lesne	0	0	1	0	0	0
<i>Cheironitis</i> van Lansberge	1	0	1	0	0	0
<i>Delopleurus</i> Erichson	0	0	1	0	0	0
<i>Deltochilum</i> Erscholtz	0	1	0	1	0	0
<i>Demarziella</i> Balthasar	0	0	0	0	0	1
<i>Diastellopalpus</i> van Lansberge	0	0	1	0	0	0
<i>Dichotomius</i> Hope	0	1	0	1	0	0
<i>Digitonthophagus</i> Balthasar	0	0	1	0	0	0
<i>Drepanocerus</i> Kirby	0	0	1	0	1	0
<i>Epirinus</i> Reiche	0	0	1	0	0	0
<i>Euoniticellus</i> Janssens	1	0	1	0	1	0
<i>Euonthophagus</i> Balthasar	1	0	1	0	0	0
<i>Eurysternus</i> Dalman	0	0	0	1	0	0
<i>Garreta</i> Janssens	0	0	1	0	0	0
<i>Gromphas</i> Brullé	0	0	0	1	0	0
<i>Gymnopleurus</i> Illiger	1	0	1	0	1	0
<i>Haroldius</i> Boucomont	0	0	0	0	1	0
<i>Heliocopris</i> Hope	0	0	1	0	0	0
<i>Hyalonthophagus</i> Palestrini	0	0	1	0	0	0
<i>Kheper</i> Janssens	0	0	1	0	0	0
<i>Lepanus</i> Balthasar	0	0	0	0	0	1
<i>Liatongus</i> Reitter	0	0	1	0	1	0
<i>Litocopris</i> Waterhouse	0	0	1	0	0	0
<i>Lophodonitis</i> Janssens	0	0	1	0	0	0

<i>Macroderes</i> Westwood	0	0	1	0	0	0
<i>Melanocanthon</i> Halffter	0	1	0	0	0	0
<i>Metacatharsius</i> Paulian	0	0	1	0	0	0
<i>Milichus</i> Péringuey	0	0	1	0	0	0
<i>Mimonthophagus</i> Balthasar	0	0	1	0	0	0
<i>Monoplistes</i> van Lansberge	0	0	0	0	0	1
<i>Neosisyphus</i> Müller	0	0	1	0	0	0
<i>Odontoloma</i> Boheman	0	0	1	0	0	0
<i>Oniticellus</i> Serville	0	0	1	0	1	0
<i>Onitis</i> Fabricius	1	0	1	0	1	0
<i>Ontherus</i> Erichson	0	0	0	1	0	0
<i>Oxysternon</i> Castelnau	0	0	0	1	0	0
<i>Pachylomerus</i> (Hope)	0	0	1	0	0	0
<i>Panelus</i> Lewis	0	0	0	0	1	0
<i>Paragymnopleurus</i> Shipp	0	0	0	0	1	0
<i>Paraphytus</i> Harold	0	0	1	0	0	0
<i>Pedaria</i> Castelnau	0	0	1	0	0	0
<i>Pedaridium</i> Harold	0	0	0	1	0	0
<i>Phacosoma</i> Boucomont	0	0	0	0	1	0
<i>Phalops</i> Erichson	0	0	1	0	1	0
<i>Phanaeus</i> MacLeay	0	1	0	1	0	0
<i>Proagoderus</i> van Lansberge	0	0	1	0	1	0
<i>Pseudocanthon</i> Bates	0	1	0	1	0	0
<i>Pseudopedaria</i> Felsche	0	0	1	0	0	0
<i>Pseudosaproecius</i> Balthasar	0	0	1	0	0	0
<i>Sarophorus</i> Erichson	0	0	1	0	0	0
<i>Scarabaeus</i> Linnaeus	1	0	1	0	0	0
<i>Scatimus</i> Erichson	0	0	0	1	0	0
<i>Scybalocanthon</i> Martínez	0	0	0	1	0	0
<i>Sisyphus</i> Latreille	1	0	1	0	1	0
<i>Strandius</i> Balthasar	0	0	1	0	0	0
<i>Sulcophanaeus</i> Olsoufieff	0	0	0	1	0	0
<i>Temnoplectron</i> Westwood	0	0	0	0	0	1
<i>Tesserodon</i> Hope	0	0	0	0	0	1
<i>Thyregis</i> Blackburn	0	0	0	0	0	1
<i>Tiniocellus</i> Péringuey	0	0	1	0	1	0
<i>Tomogonus</i> d'Orbigny	0	0	1	0	0	0
<i>Tragischus</i> Klug	0	0	1	0	0	0
<i>Trichillum</i> Harold	0	0	0	1	0	0
<i>Uroxys</i> Westwood	0	0	0	1	0	0
<i>Xinidium</i> Harold	0	0	1	0	0	0

Appendix S3.- Matrix of similarities of mammal faunas among the biogeographical regions based on the results of a multidimensional scaling ordination analysis provided by Smith (1983). These results were converted to positive values by adding a fixed number to them. Subsequently, these results were transformed into percentages and changed to dissimilarity values. Regions: PTR: Palaeotropical; AUS: Australian; NEA: Nearctic; NEO: Neotropical; ORI: Oriental; PAR: Palaeartic.

	PAR	NEA	PTR	NEO	ORI	AUS
PAR	1.00	0.99	0.74	0.59	0.78	0.63
NEA		1.00	0.60	0.81	0.70	0.64
PTR			1.00	0.44	1.00	0.62
NEO				1.00	0.56	0.48
ORI					1.00	0.60
AUS						1.00

Appendix S4.- Percentage of the area of the thirty ecoregions (divisions) according to Bailey (1998) for each biogeographical region. These data were used to build a dissimilarity matrix among regions by using Euclidean distances. Regions: PTR: Palaeotropical; AUS: Australian; NEA: Nearctic; NEO: Neotropical; ORI: Oriental; PAR: Palaearctic.

Bailey's Ecoregions	PAR	NEA	PTR	NEO	ORI	AUS
1 Icecap Division	0.5	17.5	0.0	0.0	0.0	0.0
2 Icecap Regime Mountains	0.0	0.0	0.0	0.0	0.0	0.0
3 Subarctic Division	22.6	19.0	0.0	0.0	0.0	0.0
4 Subarctic Regime Mountains	13.1	5.7	0.0	0.0	0.0	0.0
5 Tundra Division	7.4	14.0	0.0	0.0	0.0	0.0
6 Tundra Regime Mountains	2.4	9.0	0.0	0.0	0.0	0.0
7 Hot Continental Division	2.2	1.8	0.0	0.0	0.0	0.0
8 Hot Continental Regime Mountains	0.4	0.8	0.0	0.0	0.0	0.0
9 Marine Division	2.6	0.3	0.0	0.4	0.0	0.7
10 Marine Regime Mountains	2.3	3.1	0.0	2.4	0.0	1.3
11 Mediterranean Division	1.3	0.6	0.2	0.2	0.0	1.2
12 Mediterranean Regime Mountains	2.4	0.5	0.0	0.2	0.0	0.1
13 Prairie Division	4.4	3.4	0.3	3.6	0.4	5.8
14 Prairie Regime Mountains	2.5	0.0	0.0	0.0	0.0	0.0
15 SubTropical Division	0.7	3.2	0.3	1.9	10.3	5.4
16 SubTropical Regime Mountains	0.6	0.4	0.5	0.5	6.5	1.5
17 Warm Continental Division	3.3	2.6	0.0	0.3	0.0	0.0
18 Warm Continental Regime Mountains	1.4	1.7	0.0	0.0	0.0	0.0
19 Temperate Desert Division	7.8	2.8	0.0	2.9	0.2	0.0
20 Temperate Desert Regime Mountains	1.1	0.0	0.0	0.0	0.0	0.0
21 Temperate Steppe Division	6.3	5.1	0.0	0.7	0.1	0.0
22 Temperate Steppe Regime Mountains	0.3	2.9	0.0	0.0	0.0	0.0
23 Tropical/SubTropical Desert Division	6.4	1.7	30.6	2.6	4.8	33.3
24 Tropical/SubTropical Desert Regime Mountains	2.5	0.1	1.4	4.0	4.2	0.8
25 Tropical/SubTropical Steppe Division	1.3	2.8	13.2	9.2	0.8	27.8
26 Tropical/SubTropical Steppe Regime Mountains	3.6	1.1	2.3	2.9	7.2	0.0
27 Rainforest Division	0.0	0.1	9.7	23.0	18.7	4.9
28 Rainforest Regime Mountains	0.0	0.0	0.8	5.7	13.3	5.4
29 Savanna Division	0.0	0.0	34.1	33.1	25.0	11.9
30 Savanna Regime Mountains	0.4	0.0	6.6	6.5	8.5	0.0

Appendix S5.- Matrix of similarities among the biogeographical regions according to the geological time since any two regions were separated. In general, time of vicariance among regions was taken from Sanmartín & Ronquist (2004), and a corresponding matrix of dissimilarities, based on percentages was calculated. To calculate percentages, different times of vicariance were divided by the maximum time among regions (160 Myr). A distance of 0.013 Myr for the Nearctic–Palearctic regions, and 0 Myr for the Palaeotropical–Oriental–Palaeartic regions were assumed. Regions: PTR: Palaeotropical; AUS: Australian; NEA: Nearctic; NEO: Neotropical; ORI: Oriental; PAR: Palaeartic.

	PAR	NEA	PTR	NEO	ORI	AUS
PAR	1.00	0.99	1.00	0.00	1.00	0.00
NEA		1.00	0.00	1.00	0.00	0.00
PTR			1.00	0.31	1.00	0.16
NEO				1.00	0.24	0.78
ORI					1.00	0.15
AUS						1.00