

Composition and Distribution Patterns of Species at a Global Biogeographic Region Scale: Biogeography of Aphodiini Dung Beetles (Coleoptera, Scarabaeidae) Based on Species Geographic and Taxonomic Data

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1. Introduction

1.1 Current distributions as a consequence of history

Hypotheses about ancient processes are not testable by direct observation or manipulative experiments. However, their resulting present patterns can potentially be observed, approached from an inductively point of view, and, therefore, tested. Today, many historical biogeographical hypotheses of many taxa are often drawn from phylogenetic analyses or from fossils. Although biogeographical hypotheses may be presented in those cases simply as a narrative addendum of results, they are supported by the evolutionary relationships or dating of fossils, and are generally considered valid (but see Crisp et al., 2011). Nevertheless, sometimes an evolutionary basis to explain the past biogeography of concrete species groups is not available. This could be the case of hyperdiverse taxa, for example, many groups of insects; in groups with a high diversity of species it may be difficult in the short term to have a complete phylogeny to help us answer some biogeographical questions (for example, the location of areas with a high supraspecific-taxa diversity). This could be aggravated when no significant fossils have been found. Moreover, insufficient biogeographical knowledge exacerbates this problem although such groups may have an important ecological role and interest in conservation.

Current distribution is a consequence of past historical processes, and some basic biogeographical questions can be answered by analysis of contemporary geographic distribution of a species group. Under this assumption and having only geographical and taxonomic information, we need statistically robust methods to frame testable hypotheses and provide valid, scientifically rigorous answers. The set of approaches herein presented may be especially important when dealing with a group of species for which we have little or not at all phylogenetic information, although both the alpha taxonomy (not necessarily the beta taxonomy) and the taxon distribution are well known.

Using taxonomic and geographical information available about Aphodiini dung beetles species as an example, I examine their general current distribution and variation in diversity, taking into account the six major biogeographic regions worldwide. A similar procedure already was conducted in a previous paper by Cabrero-Sañudo & Lobo (2009), although Aphodiini genera were used rather than species. The faunal similarities and structure among the regions also will be evaluated to explore biogeographic relationships. In addition to elucidating major biogeographic patterns of this group, this study also proposes hypotheses about the historical processes operating in each biogeographic region and worldwide based on the supported results.

1.2 Sample study group: Aphodiini dung beetles

Dung beetles are a coleopteran group of species mostly constituted by representative taxa from the Scarabaeoidea (Insecta, Coleoptera) superfamily. Together with Diptera, they are the most abundant species group at dung communities on a worldwide scale (Hanski, 1991a). While most Aphodiini species show special morphological, behavioural and ecological adaptations to the consumption of mammal excrements (mainly from ungulates), others are also known to feed on detritus, fungi, decaying plants or roots (Hanski, 1991a). These insects are of great ecological interest, as they increase the soil permeability and recycle organic matter, favouring the fertility of pastures (Bornemissza, 1976; Ridsdill-Smith & Edwards, 2011; Rougon et al., 1988). Also, they are the main controllers of hematophagous insects and disease vectors of cattle (McQueen & Beirne, 1975; Ridsdill-Smith & Edwards, 2011; Waterhouse, 1974). Moreover, dung beetles have been also used as indicator taxa in conservation studies (A.L.V. Davis et al., 2004; McGeoch et al., 2002; Nichols & Gardner, 2011).

Within Scarabaeoidea, the tribe Aphodiini (Scarabaeidae: Aphodiinae), together with Scarabaeinae and Geotrupinae (Scarabaeidae and Geotrupidae families, respectively), comprise a significant majority of the known species of dung beetles (Halffter & Edmonds, 1982; classification *sensu* Smith, 2006). Aphodiini are distributed worldwide in every biogeographical region (G. Dellacasa et al., 2001; M. Dellacasa, 1988a, 1988b, 1988c, 1991, 1995), showing a remarkably high generic and specific diversity compared to other close groups within Aphodiinae.

Since the last Aphodiini revision by G. Dellacasa et al. (2001), some genera present in previous bibliographic sources have been later reconsidered or some other new sources have contributed new genera (Ádám, 1994; Bordat, 1999, 2003, 2009; Bordat et al., 2000; M. Dellacasa & G. Dellacasa, 2000a, 2000b, 2005; M. Dellacasa et al., 2002, 2003, 2004, 2007a, 2007b, 2008, 2010, 2011; Gordon & Skelley, 2007; Hollande & Thérond, 1999; Koçak & Kemal, 2008; Masumoto & Kiuchi, 2001; Ochi & Kawahara, 2001; Skelley, 2007; Skelley et al., 2009; Stebnicka, 2000; Tarasov, 2008; Ziani, 2002), although with limited phylogenetic support. Thus, after Cabrero-Sañudo & Lobo's (2009) paper, which considered described genera through 2005, the number of genera increased by more than 18% (36 more genera, for a total of 234), so those previous results may have changed somewhat. Moreover, although genera analyses can be used to detect genealogical relationships and to answer some biogeographical questions, internal phylogenetic relationships among Aphodiini lineages are not well identified yet (Cabrero-Sañudo, 2007; Cabrero-Sañudo & Zardoya, 2004; Forshage, 2002; Smith et al., 2006). This implies that, for the Aphodiini tribe, a species-level

study may be currently more reliable than a genus-level analysis in revealing biogeographical patterns, although compilation of all the taxonomic and biogeographic data at the species level is a laborious task.

2. Material and methods

2.1 Data sets

A matrix (AphoSpes) containing information about distribution and body size of every Aphodiini species was built. Data were obtained from several bibliographic sources, including original species descriptions, which are referenced in Table 1 and Appendix 1), as well as other taxonomic and biogeographic revisions (Baraud, 1985, 1992; Cabrero-Sañudo et al., 2007; G. Dellacasa & M. Dellacasa, 2006; G. Dellacasa et al., 2001; Veiga, 1998) and databases (Bisby et al., 2011; Schoolmeesters, 2011). The body size of species was calculated as the mean between minimum and maximum lengths (mm). In 6 cases it was not possible to obtain the species body length, and the mean size for the genera was used instead. Species distribution data were included according to the presence (1) and absence (0) of species for the six worldwide biogeographical regions (Palaeotropical, Australian, Nearctic, Neotropical, Oriental and Palaearctic) proposed by Cox (2001). The area of each biogeographical region was calculated using the Idrisi Kilimanjaro GIS program (Clark Labs, 2003).

2.2 Descriptive examination and basic analyses

Simple descriptive statistical analyses and calculations were carried out to characterize the fauna of the different biogeographical regions, using Statistica (StatSoft Inc., 2006). For each region, several data were considered, including: (1) total number of species and endemic species, (2) number of species shared with other regions, (3) mean number of regions per species, (4) mean body size per species and endemic species, (5) mean percentage of species and endemic species from genus, and (6) mean number of species and endemic species per genus. Possible correlations and differences among the considered data were analysed using nonparametric statistical tests and the relationship between the number of species and region area was also analysed, considering several potential nonlinear fits (Fattorini, 2006; Flather, 1996; Soberón & Llorente, 1993).

2.3 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 was a biogeographical signal in the data set (Connor & Simberloff, 1979; Diamond, 1975). The number of species 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 (Stone & Roberts, 1990).

In order to identify the presence of nested patterns within regional faunas (Darlington, 1957), in which species-poor regions constitute a subset of those present within richer regional faunas, three different analyses were performed (Ulrich et al., 2009). The nestedness temperature of the presence-absence species matrix was calculated by means of the temperature index, which is a descriptor of the matrix disorder (0° for a completely nested matrix, 100° for a completely random matrix) (Atmar & Patterson, 1993). The BR (Brualdi) index was

- Ádám, 1983, 1994
Ahrens & Stebnicka, 1997
Akhmetova & Frolov, 2008
Allibert, 1847
Aubé, 1850
Ávila, 1986
Báguena, 1930
Ballion, 1870, 1878
Balthasar, 1929, 1931, 1932a, 1932b, 1932c, 1932d, 1932e, 1933a, 1933b, 1933c, 1935a, 1935b, 1935c, 1935d, 1936, 1937a, 1937b, 1938a, 1938b, 1938c, 1939, 1941a, 1941b, 1941c, 1942a, 1942b, 1943, 1945a, 1945b, 1945c, 1946, 1952a, 1952b, 1952c, 1955, 1960a, 1960b, 1960c, 1961a, 1961b, 1963a, 1963b, 1965a, 1965b, 1965c, 1965d, 1966, 1967a, 1967b, 1970, 1971a, 1971b, 1971c, 1973
Balthasar & Hrubant, 1960
Baraud, 1971, 1973, 1975, 1976a, 1976b, 1976c, 1977, 1978, 1980, 1981a, 1981b, 1982
Barrett, 1931, 1932
Bates, 1887, 1889, 1890
Baudi di Selve, 1870
Bedel, 1904, 1907
Berlov, 1989
Berlov, Kalinina & Nikolajev, 1989
Blackburn, 1892a, 1892b, 1895, 1897, 1904
Blanco, 1986
Boheman, 1857
Bonelli, 1812
Bordat, 1983, 1984, 1985, 1986, 1988, 1989a, 1989b, 1989c, 1990a, 1990b, 1990c, 1990d, 1992a, 1992b, 1992c, 1992d, 1993, 1994a, 1994b, 1995, 1996a, 1996b, 1997a, 1997b, 1999, 2003, 2005, 2008, 2009
Bordat, Cambefort & Bruneau de Miré, 1991
Bordat, Dellacasa, G. & Dellacasa, M. 2000
Bordat, Paulian & Pittino, 1990
Boucomont, 1928, 1929, 1930, 1932, 1936
Boucomont & Gillet, 1921
Brahm, 1790
Branco & Baraud, 1984, 1988
Brisout de Barneville, 1866
Brown, 1927, 1928a, 1928b, 1928c, 1928d, 1929a, 1929b, 1929c
Brullé, 1832
Carpaneto, 1973, 1976, 1978, 1986
Carpaneto & Piatella, 1989, 1990
Cartwright, 1939, 1944a, 1944b, 1957, 1972
Castelnau, 1840
Červenka, 1994a, 1994b, 1995, 2000, 2003, 2005
Chromy, 1993
Clément, 1928, 1958a, 1958b, 1969, 1975, 1976, 1981, 1985, 1986
Clouët des Pesruches, 1896, 1898
Cooper & Gordon, 1987
Creutzer, 1799
Csiki, 1901
Daniel, J., 1902
Daniel, K., 1900
DeGeer, 1774
Deloya & Ibáñez-Bernal, 2000
Deloya & Lobo, 1995
Deloya & McCarty, 1992
Dellacasa, G., 1982, 1983a, 1983b, 1984, 1986, 1990
Dellacasa, G. & Dellacasa, M., 1997a, 1997b, 2009
Dellacasa, G. & Johnson, 1983
Dellacasa, G. & Pittino, 1985
Dellacasa, M., 1988a, 1988b, 1988c, 1991, 1995
Dellacasa, M., Dellacasa, G. & Gordon, 2007, 2008, 2009, 2011
Dellacasa, M., Dellacasa, G. & Skelley, 2010
Dellacasa, M., Gordon & Dellacasa, G., 2003, 2007
Dellacasa, M., Dellacasa, G., Gordon & Stebnicka, 2011
Dellacasa, M., Gordon, Harpootlian, Stebnicka & Dellacasa, G., 2001
D'Orbigny, 1896
Duftschmid, 1805
Emberson & Stebnicka, 2001
Endrödi, 1955, 1956a, 1956b, 1957, 1960a, 1960b, 1961, 1964, 1967a, 1967b, 1968, 1969, 1971, 1973, 1976a, 1976b, 1977a, 1977b, 1978, 1979a, 1979b, 1980, 1982, 1983a, 1983b, 1991
Erichson, 1834, 1842, 1843, 1848
Eschscholtz, 1922, 1923
Fabricius, 1775, 1781, 1787, 1792, 1798, 1801
Fairmaire, 1849, 1871, 1881, 1882, 1883, 1886, 1888, 1892, 1893a, 1893b, 1894, 1897, 1903
Fairmaire & Coquerel, 1860
Fairmaire & Germain, 1860
Faldermann, 1835a, 1835b
Fall, 1901, 1927, 1932
Fall & Cockerell, 1907
Frivaldszky, 1879
Frolov, 1997, 2001a, 2001b, 2001c, 2001d, 2001e, 2002a, 2002b, 2006

- Galante, Stebnicka & Verdú, 2003
Garnett, 1920
Gebler, 1848
Germar, 1813, 1824
Germar & Kaulfuss, 1817
Gerstaecker, 1871, 1883
Gestro, 1895
Given, 1950
Gordon, 1974, 1976, 1977a, 1977b, 2006
Gordon & Howden, 1972
Gordon & Salisbury, 1999
Gordon & Skelley, 2007
Graëlls, 1847
Gridelli, 1930
Gusakov, 1997, 2004, 2006
Gyllenhal, 1808, 1827
Haldeman, 1843, 1848
Harold, 1859, 1860, 1861, 1862a, 1862b, 1863, 1866,
1867, 1868a, 1868b, 1868c, 1869a, 1869b, 1870,
1871a, 1871b, 1871c, 1874a, 1874b, 1875, 1876a,
1876b, 1877a, 1877b, 1879, 1880a, 1880b, 1881
Hatch, 1971
Herbst, 1783, 1789
Heyden, 1887
Heyden & Kraatz, 1881
Hinton, 1934a, 1934b, 1934c, 1934d, 1938
Hope, 1846
Horn, 1870, 1871, 1875, 1887
Hrubant, 1961
Hubbard, 1894
Iablokov-Khuzorian, 1972
Ilcikova & Kral, 2004
Illiger, 1798, 1803
Islas, 1945, 1955a, 1955b
Jacobson, 1897, 1911
Jacquelin du Val, 1863
Johnson, 1978
Kabakov, 1996
Kabakov & Frolov, 1996
Karsch, 1881
Käufel, 1914
Kawai, 2004
Kieseritzky, 1928
Kim, 1986, 1996
Klug, 1835, 1845, 1855
Klug & Erichson, 1859
Kolbe, 1886, 1908
Kolenati, 1846
Koshantschikov, D., 1891, 1894a, 1894b, 1894c,
1894d
Koshantschikov, W., 1910, 1911, 1912, 1913a,
1913b, 1916
Kral, 1995, 1996, 1997a, 1997b, 1997c, 2000, 2002
Krikken & Kaas, 1984
Kugelann, 1792
Küster, 1854
Laicharting, 1781
Landin, 1949, 1956, 1959, 1967, 1974
Lansberge, 1886
Laxmann, 1770
Lea, 1923
Lebedev, 1911, 1932
LeConte, 1850, 1857, 1858, 1872, 1878
Lewis, 1895
Linell, 1896
Linnaeus, 1758, 1761, 1767
Lucas, 1846
Mannerheim, 1843, 1849, 1853
Masumoto, 1975, 1977, 1981, 1984a, 1984b, 1988,
1991, 1992, 1996
Masumoto & Kiuchi, 1987, 2001, 2003
Maté, 2007, 2008
Medvedev, 1928, 1968a, 1968b, 1968c
Medvedev & Dzambazish, 1977
Melsheimer, 1845
Ménétrières, 1832, 1849
Miwa, 1930
Moll, 1782
Motschulsky, 1849, 1858, 1860, 1863, 1866, 1868
Müller, G., 1940, 1941, 1942
Müller, O.F., 1776
Mulsant, 1842, 1851
Mulsant & Godart, 1879
Mulsant & Rey, 1869, 1870
Nakane, 1951, 1956, 1960, 1967, 1977, 1983
Nakane & Shirahata, 1957
Nakane & Tsukamoto, 1956
Nikolajev, 1979, 1983, 1987, 1998
Nikolajev & Frolov, 1996
Nikolajev & Puntsagdulam, 1984
Nikritin, 1969, 1971, 1973, 1979
Nikritin & Kabakov, 1979
Nomura, 1973
Nomura & Nakane, 1951
-

- Novikov, 1996
 Obenberger, 1914
 Ochi, 1986, 1991
 Ochi & Kawahara, 2001
 Ochi & Kon, 2004, 2008
 Ochi, Kawahara & Kawai, 2002
 Ochi, Kawahara & Kon, 2006
 Olivier, 1789
 Olsoufieff, 1918
 Palisot de Beauvois, 1805
 Panzer, 1795, 1798, 1799, 1823
 Pardo-Alcaide, 1936
 Paulian, 1933, 1934, 1936a, 1936b, 1938, 1939a, 1939b, 1939c, 1942a, 1942b, 1942c, 1945, 1954, 1980, 1984
 Paulsen, 2006a, 2006b
 Penecke, 1911
 Péringuey, 1901, 1908
 Petrovitz, 1954, 1955, 1956, 1958a, 1958b, 1959a, 1959b, 1961a, 1961b, 1961c, 1961d, 1961e, 1961f, 1962a, 1962b, 1963a, 1963b, 1964, 1965a, 1965b, 1966a, 1966b, 1967a, 1967b, 1967c, 1967d, 1968a, 1968b, 1968c, 1969a, 1969b, 1970a, 1970b, 1970c, 1970d, 1971a, 1971b, 1971c, 1971d, 1972a, 1972b, 1972c, 1973a, 1973b, 1974, 1975a, 1975b, 1975c, 1976, 1980
 Peyerimhoff, 1907, 1925, 1929, 1939, 1949
 Pilleri, 1953
 Pittino, 1978, 1984, 1988, 1995, 1997, 2001a, 2001b, 2004
 Pittino & Ballerio, 1994
 Quedenfeldt, 1884
 Raffray, 1877
 Rakovič, 1977, 1984, 1991
 Ratcliffe, 1988
 Reiche, 1847
 Reiche & Saulcey, 1856
 Reitter, 1887a, 1887b, 1889, 1890a, 1890b, 1891, 1892, 1894, 1895, 1897, 1898, 1899, 1900a, 1900b, 1901, 1904, 1906a, 1906b, 1907, 1908, 1909
 Robinson, 1938, 1939, 1940, 1946, 1947
 Roth, 1851
 Ruiz, 1998
 Sahlberg, 1908
 Say, 1823, 1824, 1825, 1835
 Saylor, 1935, 1940
 Schaeffer, 1907
 Schmidt, A., 1906, 1907a, 1907b, 1908a, 1908b, 1908c, 1908d, 1908e, 1908f, 1908g, 1909a, 1909b, 1909c, 1909d, 1909e, 1909f, 1909g, 1909h, 1909i, 1910, 1911a, 1911b, 1911c, 1911d, 1911e, 1912, 1913, 1916, 1920, 1922a, 1922b
 Schmidt, W., 1840
 Schönherr, 1806
 Schoolmeesters & Vandenheuvel, 1999
 Scopoli, 1763
 Seidlitz, 1891
 Semenov, 1898a, 1898b, 1903a, 1903b, 1903c
 Semenov & Medvedev, 1927, 1928, 1929
 Sharp, 1878
 Sietti, 1903
 Skelley & Gordon, 1995, 2001
 Skelley & Woodruff, 1991
 Solsky, 1874, 1876
 Stebnicka, 1973, 1975, 1978, 1981a, 1981b, 1981c, 1981d, 1982, 1983, 1985, 1986a, 1986b, 1988a, 1988b, 1989, 1990, 1992, 1993, 1994, 1997, 1998
 Stebnicka & Galante, 1991, 1992
 Stebnicka & Howden, 1994, 1995
 Stebnicka & Skelley, 2005
 Sturm, 1800, 1805
 Tesař, 1945, 1969
 Théry, 1918, 1925
 Thunberg, 1818
 Van Dyke, 1918, 1928, 1933
 Veiga, 1984
 Villiers, 1950
 Všetečka, 1939
 Walker, 1858, 1871
 Walter & Endrödi, 1981
 Walzl, 1835
 Warner & Skelley, 2006
 Waterhouse, 1875
 Westwood, 1839
 Wickham, 1913
 Wiedemann, 1823
 Ziani, 2002
 Zinchenko, 2003

Table 1. List of references consulted about original descriptions of Aphodiini species

also used to measure the degree of nestedness, which considers the number of discrepancies (absences or presences) that must be erased to produce a perfectly nested matrix (Brualdi & Sanderson, 1999). A third calculated index, NODF (nestedness based on overlap and decreasing fill), enabled me to differentiate between portions of overall nestedness introduced by species differences (NODFr) and site differences (NODFc) (Almeida-Neto et al., 2008).

These calculations were carried out using NODF program (Ulrich, 2010). To measure these indexes, fixed row and column constraints (Gotelli, 2000) and 1000 matrices for computing confidence limits of the null model were chosen, while the rest of parameters were those recommended by the NODF program.

2.4 Relationships among biogeographical traits

The relationship between the number of biogeographical regions in which each species is present and its mean body size was analyzed. The independence between these variables was tested using a chi-squared test and the shape of the relationship was analyzed by a boundary test. 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, 2011) by selecting 1,000 iterations, an asymmetrical data distribution with an upper left triangle shape, constraints defined by data, and upper right boundary tests, according to the relationship studied.

2.5 Similarity analyses

A sequential agglomerative, hierarchical and nested clustering (SAHN; Sneath & Sokal, 1973) was carried out for a simple examination of the faunistic similarities among biogeographical regions. This analysis takes into account information on the presence-absence of each species in the six biogeographical regions. A Jaccard similarity coefficient was calculated for regional pairs and Ward's linkage rule was applied. An analysis of similarities (ANOSIM) was used to test statistically whether there was a significant difference between the groups derived from the cluster analysis. Primer v.6 software was used in these calculations (Clarke & Gorley, 2005). In this analysis, the statistic *Global R* measures the difference of mean ranks of distance between and within groups. The maximum number of possible permutations was selected ($n = 60$).

A parsimony analysis of endemism (PAE; Rosen, 1988; Rosen & Smith, 1988) was also carried out, which allows a grouping procedure of areas as if species were synapomorphies and regions were taxa. PAE offers an opportunity to assess relationships between different faunas in the absence of more comprehensive data. A hypothetical region containing no taxa was considered as an out-group. Winclada (Nixon, 2002) and TNT programs (Goloboff et al., 2003) were used to search for the most parsimonious tree by means of a ratchet procedure and to determine confidence levels using bootstrap and Bremer support methods.

2.6 Mantel tests

Simple non-partial Mantel tests (Mantel, 1967) were carried out to check possible correspondences of Aphodiini species regional composition to other characteristics of the

biogeographical regions. A dissimilarity matrix for the six biogeographical regions based on Aphodiini species (APH) was built from the Aphodiini species-region matrix. Similarity among regions was based on the Jaccard index, and later changed to dissimilarity (1-similarity index). According to the indicated procedure of Cabrero-Sañudo & Lobo (2009), four other different dissimilarity matrices were obtained: two additional biological traits, Scarabaeinae genera (SCA; A.L.V. Davis et al., 2002) and mammal families (MAM; Smith, 1983); one ecological trait, Bailey ecoregions (ECO; Bailey, 1998); and one historical trait, land continuity (LC; Sanmartín & Ronquist, 2004). Mantel tests were carried out to compare the five matrices using the PASSaGE program (Rosenberg & Anderson, 2011). Simple Bonferroni *P*-values adjusted for multiple statistical tests, sequential Bonferroni values and original probabilities were jointly examined in order to interpret correlation results (Moran, 2003).

3. Results

3.1 Basic data by biogeographical region

Table 2 lists the descriptive data for each biogeographical region worldwide, based on the information obtained for a total of 2,052 Aphodiini species described up to date.

According to subtribes, these species are distributed into 1,958 Aphodiina, 45 Didactyliina and 49 Proctophanina. The Palaearctic region has the highest number of Aphodiini species (almost 41% of the total), followed by the Palaetropical (more than 36%), Nearctic (around 15%), Oriental (7%), Neotropical (6.7%) and Australian (more than 3%) regions. The Palaearctic region is the richest for Aphodiina species, while the Palaetropical region is the richest for Didactyliina and Proctophanina species.

A relationship between the number of species and area was observed. After examining different nonlinear procedures, a simple linear fit between the number of species and area ($R = 0.81$, $R^2 = 66.06\%$, $F = 7.79$, $P < 0.05$) was the best test. The linear relationship between the number of species and area shows that around 15.94 species are added per million square kilometres. Also, the Oriental and Palaetropical regions have a comparatively higher number of species than predicted in relation to area, while the Palaearctic, Australian, Nearctic and Neotropical regions have comparatively lower numbers (Figure 1). The variation in the number of species among biogeographical regions differs significantly from a uniform distribution (expected species [mean] = 373.17, $\chi^2 = 1498.70$, d.f. = 5, $P < 0.00001$), but also from the number of species expected according to the previously obtained area-species relationships (species: $\chi^2 = 545.38$, d.f. = 5, $P < 0.0001$).

The mean percentage of species from genus varies among regions (Kruskal-Wallis ANOVA by ranks test; $KW = 61.06$, $P < 0.0001$), the Palaearctic and the Palaetropical regions holding the highest values (more than 30% of species per genus). After applying Bonferroni criteria ($P < 0.0033$), the analyses show that the percentages are significantly different among the faunas of the Palaearctic and the Neotropical, Oriental and Australian regions, the Nearctic and the Oriental regions, and among the Palaetropical and the Oriental and Australian regions. In fact, a significant positive relationship has been observed between the mean percentage of species from genus and the number of species ($R = 0.97$, $R^2 = 93.82\%$, $F = 60.68$, $P = 0.001$), so that those regions with higher numbers of species also have a better representation of within-genus diversity.

	Palaeotropical	Australian	Nearctic	Neotropical	Oriental	Palaeartic
Approximate area (x 10 ⁶ km ²)	22.1	7.7	22.9	19.0	7.5	54.1
Species						
Aphodiini	748	68	306	137	145	835
Aphodiina	681	59	302	126	145	827
Didactyliina	26	0	3	10	0	8
Proctophanina	41	9	1	1	0	0
Number of endemic species	721	57	222	60	80	751
Percentage of endemic species	96.39	83.82	72.55	43.80	55.17	89.94
Ratio of endemic/non-endemic species	26.70	5.18	2.64	0.78	1.23	8.94
Endemic Aphodiina	656	49	220	51	80	744
Endemic Didactyliina	25	0	2	9	0	7
Endemic Proctophanina	40	8	0	0	0	0
Number of regions per species (± SD)	1.06 ± 0.38	1.46 ± 1.15	1.32 ± 0.63	1.67 ± 0.80	1.59 ± 0.86	1.12 ± 0.43
Body size per species (± SD) (mm)	4.81 ± 2.19	5.90 ± 1.99	5.45 ± 1.54	5.19 ± 1.69	4.92 ± 2.07	5.39 ± 1.90
Body size per endemic species (± SD) (mm)	4.81 ± 2.21	5.95 ± 2.03	5.44 ± 1.53	4.98 ± 1.96	4.56 ± 1.93	5.39 ± 1.88
Number of species per genus (± SD)	7.79 ± 13.54	4.00 ± 7.93	4.94 ± 6.50	2.85 ± 3.79	3.54 ± 3.49	6.90 ± 9.64
Number of species per endemic genus (± SD)	4.08 ± 4.61	8.50 ± 12.77	3.00 ± 2.83	1.82 ± 1.40	1.00 ± 0.00	3.79 ± 5.40
Percentage of species from genus (± SD)	30.64 ± 42.83	2.90 ± 15.26	18.73 ± 36.99	12.15 ± 30.74	5.14 ± 16.12	42.20 ± 46.09
Percentage of endemic species from genus (± SD)	74.57 ± 34.75	33.08 ± 44.69	57.25 ± 46.61	41.87 ± 47.57	17.83 ± 24.50	79.42 ± 32.52

Table 2. Characteristics of worldwide regional faunas of Aphodiini according to species (unless specified, values are referred to species numbers).

The mean body size of species also varies among regions (Kruskal-Wallis ANOVA by ranks test, KW = 125.01, $P < 0.0001$), and considering Bonferroni criteria ($P < 0.0033$) the size of species present in the Palaeotropical and Oriental regions is smaller and significantly differs from species size at the Palaeartic, Nearctic, Australian and Neotropical (only for the Palaeotropical) regions. Also, the mean body size of endemic species is different among regions (Kruskal-Wallis ANOVA by rank test, KW = 125.43, $P < 0.0001$): Palaeotropical and Oriental endemic species are significantly (Bonferroni corrected) smaller than those in Nearctic, Australian and Palaeartic (only those Palaeotropical) regions.

3.2 Endemic species

Within Aphodiini, Proctophanina is the subtribe with the highest percentage of endemic species (98%), followed by Didactyliina (96%) and Aphodiina (92%). Both Palaeartic and

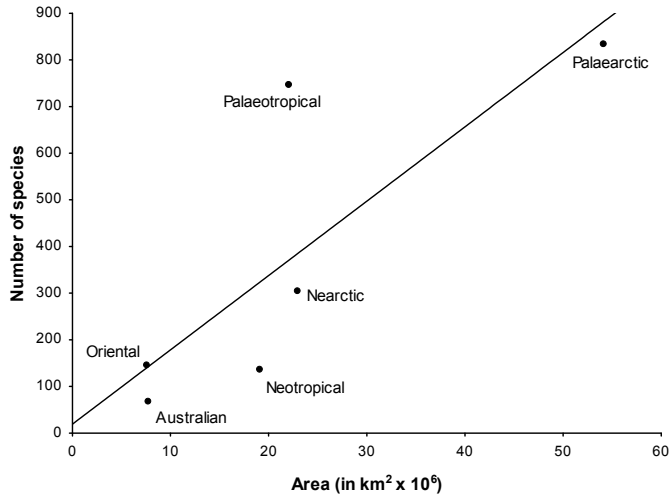


Fig. 1. Linear regression between area and richness of Aphodiini species, according to biogeographical regions ($r_s = 0.81$; $P = 0.05$). Number of sps. = $19.11 + 15.94 \cdot \text{area (km}^2 \times 10^6)$

Palaeotropical regions have the highest numbers of endemic Aphodiina species. The Palaeotropical region contains the maximum numbers of endemic species from Didactyliina and Proctophanina subtribes. Most of the Aphodiini species are only present in one biogeographical region (90%, 1,851 species), with the Palaeartic (751 species) and Palaeotropical (721 species) regions having the highest percentage (around 80%) of total endemic species (Figure 2).

The number of endemic and total species richness are related ($r_s = 0.996$, $P < 0.0001$), while the number of endemic and non-endemic species are not related ($r_s = 0.04$, $P = 0.94$). The ratio between endemic and non-endemic species is low in the Australian, Nearctic, Neotropical and Oriental regions, but is high in the Palaeartic region and very high in the Palaeotropical region (Table 2). Around 90% or more of total species in each of these two latter regions are endemic. As expected, the numbers of endemic species are significantly different from a uniform distribution among regions (expected species [mean] = 315.17, $\chi^2 = 1746.36$, d.f. = 5, $P < 0.0001$).

Body size differs significantly between endemic and non-endemic species (Mann-Whitney U-test, $U = 136.768$, $n_1 = 1,891$, $n_2 = 161$, $P < 0.05$, endemic species size = 5.15 ± 2.01 mm, non-endemic species size = 5.36 ± 1.84 mm), with non-endemic species usually larger than endemic species. Moreover, the boundary test shows that 2,048 (out of 2,052) data points have been observed within the left triangle of the relationship between species body size and number of biogeographical regions (Figure 3). However, this test confirms that the upper right-hand 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 ($P = 0.61$). There is a tendency for endemic Aphodiini species to have more variable body sizes while non-endemic species are progressively smaller as biogeographical range increases; however, this pattern is not statistically significant.

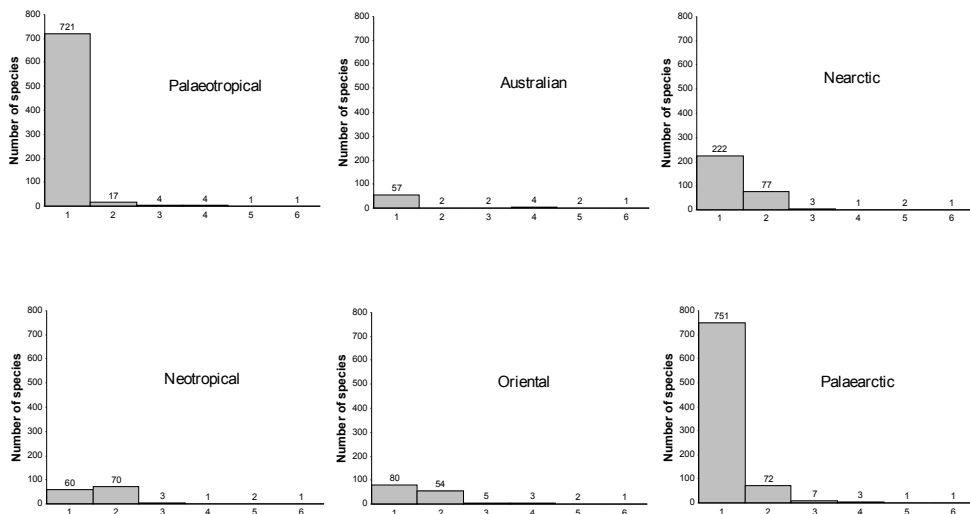


Fig. 2. Distribution of Aphodiini species in each biogeographical region, according to categories representing the number of regions in which each species occurs

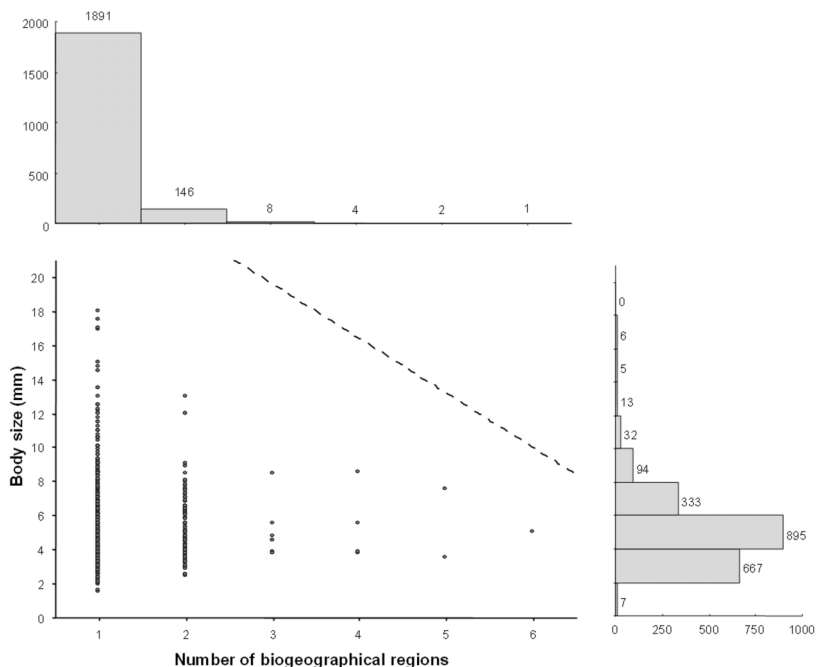


Fig. 3. Relationship between number of biogeographical regions in which Aphodiini species are present and their body size. The broken line represents a possible constraint on this relationship, according to a boundary test (upper-right corner of space, observed points not significantly lower than the number of simulated points, $P = 0.61$)

The mean percentage of endemic species from genus also varies among regions (Kruskal-Wallis ANOVA by ranks test, $KW = 54.66$, $P < 0.0001$): again the Palaearctic and the Palaetropical regions showed the highest numbers (more than 74% of endemic species from each genus). Taking into account Bonferroni criteria ($P < 0.0033$), Palaearctic, Palaetropical, Nearctic and Neotropical percentages differ significantly from those of the Oriental region. A positive and significant relationship between the mean percentage of species from genus and the mean percentage of endemic species from genus also exists ($R^2 = 0.76$, $F = 12.51$, $P < 0.05$), meaning that regions with a higher number of species from a genus will have more endemic species from that genus.

The number of species per endemic genus does not differ significantly among regions (Kruskal-Wallis ANOVA by ranks test, $KW = 9.18$, $P = 0.10$), but the number of species per genus differs among regions (Kruskal-Wallis ANOVA by rank test, $KW = 17.64$, $P < 0.005$): both Palaetropical and Palaearctic have the highest values and differ significantly from the Neotropical region. The number of species per genus and per endemic genus is not related due to the Australian region supporting a great number of species in most of its endemic genera ($R^2 = 0.03$, $F = 0.12$, $P > 0.05$). However, when Australian data are omitted, a significant and positive relationship is detected ($R^2 = 0.85$, $F = 17.57$, $P < 0.05$), indicating that regions with high numbers of species per genus normally have more species in endemic genera.

The number of non-endemic Aphodiini species is not correlated to the number of species per genus ($P = 0.79$), but a marginally negative relationship exists between the number of non-endemic species and the mean number of species per endemic genus ($R^2 = 0.56$, $F = 5.03$, $P = 0.09$). So, those regions with more widely distributed species tend to have fewer species in each of its endemic genera.

3.3 Non-random patterns of species distribution

The number of regions in which each species occurs (its 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 species is reported in Table 2. The biogeographical extent of the species (Kruskal-Wallis ANOVA by ranks test, $KW = 391.33$, $P < 0.0001$) differed significantly among biogeographical regions. Paired *post hoc* comparisons using Bonferroni criteria ($P < 0.0033$) show that biogeographical extent differs significantly among the faunas of all regions ($P < 0.001$), except those of the Palaearctic and Australian regions, the Nearctic and the Australian regions, and the Neotropical and the Oriental regions. The mean biogeographical extent is negatively and statistically significantly related to the number of species ($R^2 = 0.83$, $F = 18.90$, $P < 0.05$) and the number of endemic species ($R^2 = 0.86$, $F = 24.62$, $P < 0.01$) present in each region. These results suggest that regions with higher numbers of Aphodiini species usually support narrowly distributed species, and *vice versa*.

The total number of possible paired relationships among the six biogeographical regions is 63. However, only 22 different species distributions were detected (Figure 4A). For example, no species are distributed simultaneously and exclusively in the Palaetropical and Australian regions, or in the Palaearctic and Neotropical regions. Therefore, observed frequencies do not fit the expected supposition that all possible combinations of

relationships among regions are equally probable ($\chi^2 = 165.64$, d.f. = 5, $P < 0.0001$). This result highlights the existence of concrete and non-random distribution patterns for the Aphodiini species. In fact, the co-occurrence analysis provided an observed C-score that was significantly higher than randomly expected ($C_{observed} = 0.78$, $C_{expected} = 0.75$, $P = 0.001$). This indicates that some groups of species were repeatedly present in specific biogeographical regions, and therefore showed coincident diversity patterns (Figure 4B).

The matrix fill (number of occupied cells divided by total number of cells) given by the NODF program was only 18.18%. Nestedness temperature in the data matrix was 38.62° , which was statistically higher ($P < 0.001$) than the estimated temperature of $34.84^\circ (\pm 0.68^\circ)$. Furthermore, the observed BR index was also higher than the expected value ($BR_{observed} = 1,360$, $BR_{expected} = 1,280.27 \pm 5.76$, $P < 0.001$). In addition, the observed NODF index was significantly lower from the estimated value ($NODF_{observed} = 5.37$, $NODF_{expected} = 8.10 \pm 0.15$, $P = 0.001$). Although NODFr sub-index values were similar to global NODF, observed NODFc (nestedness based exclusively on sites) was significantly higher than the expected value ($NODFc_{observed} = 11.24$, $NODFc_{expected} = 8.34 \pm 0.38$, $P = 0.001$). These results suggest that a genuine pattern of nestedness exists among regional faunas, although this pattern is concealed as a consequence of non-nested endemic species.

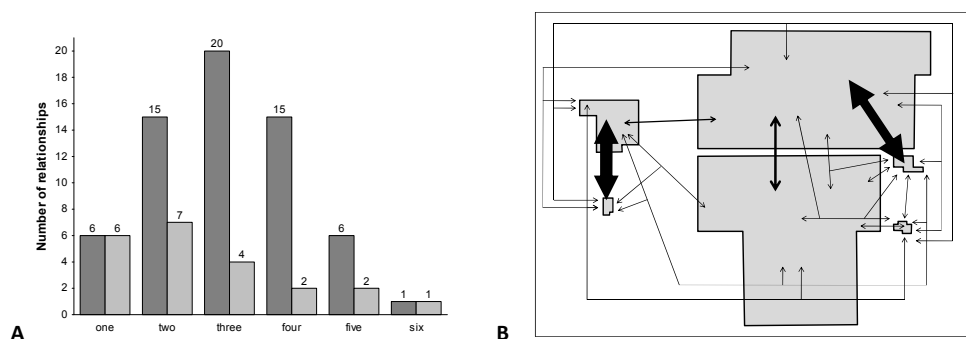


Fig. 4. Patterns of distribution for Aphodiini species. (A) Expected (left) vs. observed (right) numbers of combinations of shared regions according to genera distributions; (B) Representation of the different regional relationships for Aphodiini species. Region size is proportional to the number of endemic Aphodiini species, whereas arrow and box widths are proportional to the number of species with similar patterns for each relationship

3.4 Similarity among biogeographical regions

The dendrogram of faunistic similarity based on Aphodiini species revealed that the Nearctic and the Neotropical regions are most similar (Figure 5A). The Palaeartic and the Oriental regions also are similar, and together are closer to the Australian region, and narrowly followed by the Palaeotropical. The ANOSIM test shows that the Neotropical-Nearctic and the Palaeartic-Oriental pairs are statistically significant. According to this analysis, the most probable similarity configuration is made up of the following three groups (Global $R = 0.68$, $P = 0.08$): i) Nearctic-Neotropical; ii) Palaeartic-Oriental-Australian; and, iii) Palaeotropical.

The dendrogram of faunistic similarity based on parsimony and shared species showed a unique tree (length = 2085, consistency index = 0.98, retention index = 0.80, autapomorphies included; Figure 5B). The Palaeartic-Oriental and Nearctic-Neotropical region pairs again are observed. The Palaeartic-Oriental clade is closer to the Palaeotropical region, and together are joined in a clade that is closer to the Australian region. Bootstrap validation confirmed the Palaeartic-Oriental (100%), the Palaeartic-Oriental-Palaeotropical-Australian (76%), and the Nearctic-Neotropical clades (100%). Bremer support also showed highest number of steps (>30) for the Palaeartic-Oriental and the Nearctic-Neotropical clades. Although the Palaeotropical region appears to be closer to the Palaeartic-Oriental clade than the Australian region; however, there was insufficient data for bootstrapping or Bremer supports to confirm similarity.

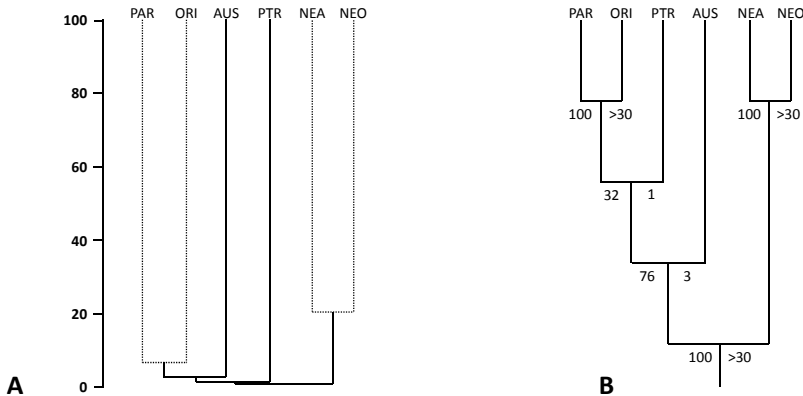


Fig. 5. Dendrogram of faunistic similarity among worldwide regions based on distributions of Aphodiini species. (A) Sequential agglomerative, hierarchical, and nested clustering analysis. Dotted clades are well supported, according to the ANOSIM test; (B) Parsimony analysis of endemicity. Left values refer to bootstrap support; right values to Bremer support. Regions: PTR, Palaeotropical; AUS, Australian; NEA, Nearctic; NEO, Neotropical; ORI, Oriental; PAR, Palaeartic

3.5 Independence of regional traits

The dissimilarity in the Aphodiini species composition among biogeographical regions was significantly and positively related to the genera composition of the Scarabaeinae dung beetles (Mantel test correlation coefficient (ρ) = 70.13%, $P < 0.005$; when both simple and sequential Bonferroni corrections are considered). A positive correlation between Aphodiini species composition and the geological time of separation among the biogeographical regions approaches significance ($\rho = 43.83%$, $P = 0.059$).

As showed in Cabrero-Sañudo & Lobo (2009), regional distribution of Scarabaeinae was positively related with mammal composition ($\rho = 68.45%$, $P = 0.005$) and the geological time of separation among biogeographical regions ($\rho = 76.68%$, $P = 0.002$; when both simple and sequential Bonferroni corrections are considered). Regional mammal distribution also was positively related with the geological time of separation among biogeographical regions ($\rho = 62.78%$, $P = 0.006$; when a sequential Bonferroni correction was used). The regional

dissimilarity in ecoregions did not show any significant correlation with any biological or historical trait.

4. Discussion

4.1 Existence of non-random distribution patterns

These results imply that the faunistic composition of Aphodiini species present in different biogeographical regions follows a geographically structured pattern. Co-occurrence and nestedness analyses suggest that there is a reliable relationship among Aphodiini faunas, although each biogeographical region is singular on its own and holds more endemic species than shared ones (except for the Neotropical region, with most of its species also distributed in the Nearctic region, particularly at the Mexican Transition Zone). The most frequent distribution patterns of shared species are related to the 'Old World faunas' (Palearctic, Oriental, Palaeotropical and Australian regions) or the 'New World faunas' (Nearctic and Neotropical regions), being these two groups of regions also supported by the similarity analyses. Mantel test revealed a nearly significant relationship between historical and biological traits, so long-term land continuity and proximity may play a unifying role in regional faunas. In fact, when higher taxa are tested (for example, genera, as in Cabrero-Sañudo & Lobo, 2009), this relationship turns significant.

The Palearctic and Palaeotropical regions have the highest numbers of species and endemic species. These two regions have a considerable singular faunistic composition (for example, presence of more endemic lineages or genera; Cabrero-Sañudo & Lobo, 2009), or many more species than expected (as in the Palaeotropical region). This result may be partly due to the area or the environmental heterogeneity of these regions, although results show that the compositional differences do not seem to be related to ecoregional dissimilarity. This points to historical reasons that could have influenced current distribution patterns.

Taking into account all these results, two main types of regions for Aphodiini may be considered: macroevolutionary sources – those with a long history as producers or distribution centres for many lineages – and sink regions, which are those with colonization processes and recent radiations as important shapers of current faunas (Goldberg et al., 2005). Within the first type, both the Palearctic and Palaeotropical regions may be included, although the Nearctic region to some extent and the nexus between the Nearctic and the Neotropical regions (the Mexican Transition Zone) should not be neglected. On the contrary, the Australian, Neotropical and Oriental regions, although with singular faunas, could be included within the second type, based on the lower numbers of species, endemic species and lineages (Cabrero-Sañudo & Lobo, 2009).

4.2 Diversification and distribution range

Regions with a lower Aphodiini diversity usually have widely distributed species. This may be due to the fact that the greatest percentage of regional Aphodiini faunas consists of endemic species, so those regions with fewer species will have a proportionately greater representation of widespread species. Widely distributed species are able to colonize more biogeographical regions because they usually have greater environmental tolerances. This could be interpreted as a variation of Rapoport's rule (the size of species distributional

ranges increases with latitude; Rapoport, 1975), as one explanation for this rule is that seasonal variability fosters a greater climatic tolerance, and therefore wider latitudinal ranges (Letcher & Harvey, 1994; Stevens, 1996).

Moreover, the phylogenetic relationships among species in a biogeographic region are likely higher within the region than with species from other regions. This has been indicated by the fact that regions with large numbers of species carry a greater number of species per genus and a higher percentage of species per genus. Thus, those regions with favourable environmental conditions to accommodate a greater number of Aphodiini species also could have functioned as speciation centers (macroevolutionary source regions, as the Palaearctic and Palaeotropical).

It has been pointed that the environmental tolerance of species may be related to ecophysiological adaptations at higher taxonomic levels (Hawkins et al., 2006; Ricklefs, 2006). Although the geographic distribution of a lineage (genus) could then be related to its tolerance at a large scale, favourability and diversity of environmental conditions could promote an ecological diversification (spatial, seasonal, altitudinal, feeding, etc.) even among related species (Del Rey & Lobo, 2006; Finn & Gittings, 2003; Gittings & Giller, 1997; Hanski, 1991b). This ecological diversification would act on endemic or non-endemic lineages equally, as it has been noted that the number of species per genus within a region and the number of species per endemic genus are positively related.

4.3 Endemic and non-endemic species

The total species richness and the number of endemic species are related; this is probably due to a greater percentage of endemic species *versus* non-endemic ones. Actually there is a significant difference in regional species numbers between endemic and non-endemic species. A total of 1,891 out of the 2,052 Aphodiini species (92%) are endemic to a single region; less than one tenth of species are shared among regions. Widely distributed species usually correspond to those of a known wide ecological spectrum and opportunistic nature. For example, the three most widely distributed species, *Calamosternus granarius* (Linnaeus, 1767) (present in all biogeographical regions), and *Aphodius fimetarius* (Linnaeus, 1758) and *Labarrus pseudolivinus* (Balthasar, 1941) (present in five biogeographical regions), show a higher climatic tolerance, are not strictly coprophagous, and can alternatively behave as saprophagous, fungivorous or cleptoparasites (Cabrero-Sañudo et al., 2010; Veiga, 1998).

The correlation between total numbers of endemic and non-endemic species is almost nonexistent, probably because world biogeographical regions have partially independent evolutionary histories. In fact, regions with the least number of non-endemic species are the Palaeotropical and the Australian (27 and 11 non-endemic species, respectively), while the other regions have from 65 to 84 non-endemic species registered. This may indicate that recent continental isolation of these two regions could have prevented introduction of many broadly distributed species. Moreover, regions with a lower number of non-endemic Aphodiini tend to have more species per endemic genus. This fact could point to competition between widespread, better adapted and more competitive species and endemic, more specialized species (although see Finn & Gittings, 2003) or certain speciation process that could occur in isolated territories (Gillespie & Roderick, 2002).

Another observed relationship is the positive relationship between the percentage of species from a genus and the percentage of endemic species from a genus, so regions with a greater number of species per genus do so at the expense of having a greater number of endemic species for that lineage. This again relates to the role as species generators of those regions that have showed favourable conditions for Aphodiini along the time.

4.4 Body size

Among Aphodiini genera, body size is a trait that shows no significant pattern with respect to geographical distribution, although it may be noted that some large genera are endemic to a single region (Cabrero-Sañudo & Lobo, 2009). However, species mean body size does significantly vary among different biogeographic regions. Thus, both Aphodiini species and endemic species from Palaeotropical and Oriental regions are smaller than those in other regions, especially the Australian, Nearctic or Palaearctic regions. Those species distributed in areas of temperate or cold climates (Nearctic or Palaearctic) may be larger, as a variation of Bergmann's rule for endotherm animals (Bergmann, 1847) which has also been observed for some insects (Blanckenhorn & Demont, 2004). Yet a large size also could be a consequence of the presence of ancient lineages (a possible variation of Cope's rule: taxa increase in body size over evolutionary time; Cope, 1887) or insularity (Gould & MacFadden, 2004). The first of these alternatives may occur among Palaearctic Aphodiini, as it has also been observed for Scarabaeinae in the Palaeotropical region (A.L.V. Davis et al., 2002). On the other hand, 'island' gigantism may have occurred among Australian Aphodiini, as indicated by the giant wetas of New Zealand, Madagascan cockroaches and millipedes, deep sea gastropods (McClain et al., 2006), and island vertebrates (Lomolino, 2005; but also see Meiri et al., 2008).

Nevertheless, non-endemic species are generally significantly larger than endemic ones, although endemic Aphodiini species have a greater diversity of body sizes. Aphodiini are not very good dispersers (Roslin, 2000; Roslin & Koivunen, 2001), so larger species would probably have a greater advantage to move and occupy new territories than smaller ones. In other species groups (for example, mammals or birds), larger species tend to occupy broader distributional areas (Brown, 1995).

4.5 Regional characteristics

The Palaearctic region presents the highest number of total and endemic Aphodiini species; however, while the Palaearctic has the highest number of species and endemics of Aphodiina, it does not support any Proctophanina. Together with the Palaeotropical region, it also shows the highest ratio of endemic/non-endemic species, indicating the great importance of endemics to the composition of its fauna. In fact, the species inhabiting the Palaearctic show the second lowest mean number of regions per species compared with those of other regions. The mean percentage of species from genus is the highest, whereas the number of species per genus is the second highest with respect to the other regions; this may be pointing to a possibly greater speciation rate for Palaearctic lineages. Also, the mean percentage of endemic species from genus is the highest in relation to the other regions. Aphodiini 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 lineages and endemic genera (Cabrero-Sañudo & Lobo, 2009) 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 Palearctic, in which Aphodiini taxonomy has attracted much attention, although many Aphodiini species may still remain undiscovered (Cabrero-Sañudo & Lobo, 2003). The only phylogenetic studies conducted on Aphodiini evolution were based on Iberian species within the Palearctic (Cabrero-Sañudo & Zardoya, 2004; Cabrero-Sañudo, 2007) and showed that most of the earlier branches of Aphodiini are of Palearctic or Holarctic in distribution. While this may support the hypothesis of a Laurasian origin of Aphodiini, the geographical and taxonomic scope of those studies was limited. Nevertheless, the oldest known fossil evidence for Aphodiini is from the Paleocene, with many other fossils from subsequent epochs (Figure 6; Krell, 2007).

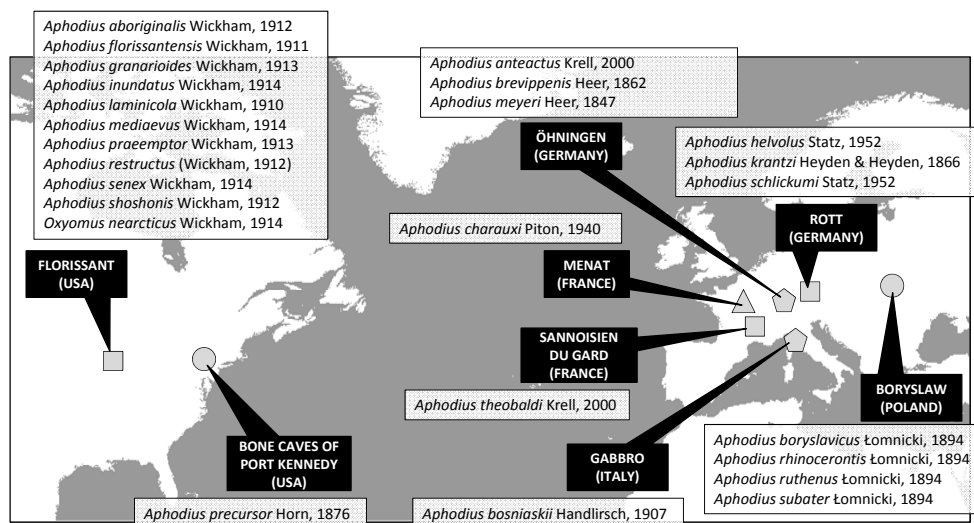


Fig. 6. Sites where extinct Aphodiini fossil species have been found, according to Krell (2007). For each site, a list of described species is provided. In most cases, the genus of the species is *Aphodius* Illiger, 1758, as they have not been yet classified into suitable genera. Geologic epoch of lagerstätten represented by geometric figures: i) triangle, Paleocene; ii) square, Eocene; iii) pentagon, Oligocene; and, iv) circle, Pleistocene.

The Palaeotropical region also shows important numbers of total and endemic species of Aphodiini. Its endemic/non-endemic species ratio is the highest and almost three times that of the next highest region, the Palearctic. Thus, the mean number of regions per species is the lowest compared with other regions. Aphodiina is well represented, with both second highest numbers of species and endemic species. Also, both Didactyliina and Proctophanina show the highest species and endemic species richness in this region. Although Palaeotropical dung beetle communities tend to be dominated by Scarabaeinae individuals (Cambefort, 1991; A.L.V. Davis et al., 2002; Doube, 1991), some studies show that the abundance of Aphodiini in some localities can sometimes be very high, or even the highest (Bernon, 1981; Krell et al., 2003; D. Rougon & C. Rougon, 1991). However, the mean body size of Palaeotropical species is the lowest in relation to other regions, and the mean body

size of endemic species is also the second lowest. The Palaeotropical region holds the second highest mean percentage of species from genus, the second highest mean percentage of endemic species from genus, and the highest mean number of species per genus. In addition, the relatively recent isolation of the Palaeotropical region with respect to other regions could explain its having the second lowest number of non-endemic species and the largest number of species per endemic genus. So, together with the Palaearctic region, the Palaeotropical region can be considered as a macroevolutionary source region, possibly acting as a refuge and/or a recent diversification centre for Aphodiini species. However, there is as yet no record for Tertiary or Quaternary Aphodiini fossils within the Palaeotropical region (Krell, 2007), possibly a consequence of limited preservation, prospecting efforts, and/or recent Aphodiini species diversification.

The Oriental region is the fourth most prominent in terms of number of species, all of which are from the subtribe Aphodiina. Although this region hosts a few more species than expected according to its area, it is the third lowest in terms of endemic species, has the second lowest endemic/non-endemic species ratio, and has one of the greatest mean species distribution ranges, sharing many species with the Palaearctic region (61 out of 65 non-endemic species). This region has the second lowest mean body size per species, the lowest mean body size of endemic species, the second lowest percentage of species from genus, the lowest mean percentage of endemic species from genus, the second lowest number of species per genus, and the lowest number of species per endemic genus. The Oriental region may have had less environmentally favourable conditions for Aphodiini species, so that widely distributed species would have been proportionately more successful. This suggests the Oriental region to be mainly a macroevolutionary sink for Aphodiini species. Studies on dung beetle communities carried out in the Oriental region frequently omit results for Aphodiini or show that they represent a small proportion of local Scarabaeidae richness (c. 4-10% of species; A.J. Davis, 2000; A.J. Davis et al., 2001; Hanski & Krikken, 1991; Shahabuddin et al., 2005). However, most of those studies were conducted on island communities, and there is a conspicuous lack of study of continental communities, particularly considering the likely species richness and abundances for Aphodiini. As for the Palaeotropical region, there is as yet no fossil evidence for Aphodiini in the Oriental region (Krell, 2007).

The Nearctic region has the highest number of Aphodiini species and endemic species in the New World, hosting representatives from the three tribes, although only Aphodiina and Didactyliina contain endemic species. In relation to the other regions, the Nearctic has the third highest number of species and endemics. Moreover, the Nearctic region supports the third highest mean percentage of species from genus, endemic species from genus, and number of species per genus. These facts define the Nearctic as a mainly macroevolutionary source region for Aphodiini. Several Nearctic species are shared with the Neotropical region (77 out of 84 non-endemic species), and many of them are endemic to the Mexican Transition Zone, although with a Nearctic or Holarctic origin (Cabrero-Sañudo et al., 2007, 2010). Aphodiini are usually the dominant species group in northern dung beetle communities in the Nearctic region (Lobo, 2000, and references therein). Also, Nearctic region total and endemic species have the second greatest mean body size per species, probably due to colder climates or presence of older lineages. This region also has displayed an ancient presence of Aphodiini, with the first Nearctic fossil records dating from the Oligocene, a little more recent than those of the Palaearctic (Krell, 2007).

The Neotropical region holds the second lowest richness for species and endemic species, and holds the least number of species on the basis of the region's land area. Although it hosts species from the three different subtribes, there are only endemic representatives from the Aphodiina and Didactyliina. It shares several Aphodiini species with the Nearctic region (all its non-endemic species), mainly endemic from the Mexican Transition Zone (Cabrero-Sañudo et al., 2007, 2010). Its ratio of endemic/non-endemic genera and the mean number of species per genus are the lowest, and the mean number of species per endemic genus is the second lowest. These facts point to the Neotropical having probably acted as a macroevolutionary sink region. Few studies on Neotropical dung beetle communities have taken Aphodiini into consideration. Although very few Aphodiini species are represented in those communities, they can be very abundant (Andresen, 2002). No Aphodiini fossil records have been found for this region.

The Australian region shows the lowest numbers of Aphodiini species and endemic species, with only two subtribes (Aphodiina and Proctophanina) represented in the region. The mean percentage of species from genus is also the lowest, whereas the mean percentage of endemic species from genus is the second lowest, after the Oriental region. However, the number of species per endemic genus is the highest, in relation to other regions. Due to its isolation, the Australian region seems to have received occasional representatives (widely distributed, generalist species) of different lineages over time. Some of these colonizing species likely led to the emergence of endemic genera, which then diversified. Consequently, the Australian region appears to have acted as a macroevolutionary sink with regard to Aphodiini lineages, but has served as a source region with regard to species. Australian species also display the largest mean body size per species and per endemic species compared with other regions, indicating a possible island gigantism or the presence of ancient lineages. With regard to abundance and species richness, Scarabaeinae dominate northern Australian dung beetle communities, while southern Australian communities are dominated by endemic species of Aphodiini (Doube et al., 1991; Steinbauer & Weir, 2007). There is as yet no fossil record for Aphodiini in this region, due to causes similar to those of the Palaeotropical, Oriental and Neotropical regions.

4.6 A synthesis of Aphodiini evolution and historical biogeography

The main radiation of Scarabaeoidea dates from the Mesozoic and Cenozoic ages (A.L.V. Davis et al., 2002; Krell, 2000; Scholtz & Chown, 1995), but Aphodiini probably did not separate from the Scarabaeidae main lineage and from the other Aphodiinae subfamilies until the Jurassic or Cretaceous (Krell, 2000). The radiation of coprophagous beetles presumably happened as dung from vertebrates (dinosaurs and/or small mammals) increased (Arillo & Ortuño, 2008; A.L.V. Davis, 1990, 2002; Halffter & Matthews, 1966; Jeannel, 1942; Philips, 2011). The first Aphodiini probably developed before or around the early Jurassic age (200-170 Ma), when most continents were joined in Pangea. Most Aphodiini have temperate to temperate-cold and/or subalpine preferences, so they may have arisen at the northern territories of contemporary Eurasia (Cabrero-Sañudo & Zardoya, 2004), where the climate was cool with temperate conditions, compared to the rest of the world, which was very arid and hot (Scotese, 2003). Some of the first lineages of Aphodiini could have spread later to other Pangean southern territories before their break-up. After the fragmentation of Pangea (middle Jurassic to early Cretaceous; 160-130 Ma), most

Aphodiini would have remained within Laurasia, although it is possible that a few Aphodiini lineages survived on Gondwanan continents, as shown by some genera and species distributions.

Due to the extinction of dinosaurs (K/T boundary, late Cretaceous, c. 66 Ma) dung from mammals became increasingly more common, providing a resource that could be consumed gradually by new Aphodiini taxa. Eurasia and North America approached each other and were intermittently connected (from late Cretaceous to Eocene periods, 66-38 Ma; Scotese, 2003), helping explain why the first Aphodiini fossils registered in North America date from these ages. The faunas from the rest of the regions probably had little contact in these periods.

During the Miocene (26-12 Ma), Eurasia and Africa collided and a secondary radiation of Aphodiini (similar to that of Scarabaeinae; A.L.V. Davis & Scholtz, 2001; A.L.V. Davis et al., 2002) may have resulted as a consequence of mixing faunas and the establishment of new dispersal routes between the two continents (Potts & Behrensmeyer, 1993). This interchange culminated during the late Miocene period (12 Ma), when the Indian peninsula collided against Eurasia and several Aphodiini taxa probably colonized that territory. Also, prairies and savannas became more common as aridity and climate cooling increased (Cambefort, 1991b; Scotese, 2003), and the radiation of Artiodactyla (Bovini) (30+ Ma; Cumming, 1982; Silva & Downing, 1995) brought new high-quality soft-fibrous droppings. Mantel tests results highlight the relationships between Aphodiini and Scarabaeinae, mammal faunas, and land connectivity, all of which are probably related to these events.

An increase in prairie lands also occurred 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 Pliocene (Potts & Behrensmeyer, 1993). However, the most important American event was the 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 species (Webb, 1985), and also range expansions of many dung beetle taxa, such as the Scarabaeinae (A.L.V. Davis & Scholtz, 2001). A certain number of current Neotropical Aphodiini species are the likely survivors of a specialized and hardly diversified fauna previously present at this region.

The principal characteristic of the Australian continent has been its prolonged isolation from the rest of the regions, and the lack of placental mammals until the Pleistocene (2.5 Ma-10 ka; Cox, 2000). Hence, older Australian Aphodiini lineages would have been adapted to exploiting excrements from marsupials. Land connections during the Pleistocene between Eurasia and Australia probably allowed the dispersal of mammals towards the latter region, together with a number of Aphodiini species associated with them. The mass extinction of monotremes and marsupials (Murray, 1984) may have caused the extinction of some endemic Aphodiini, but newcomer Aphodiini species may have proliferated with the advent of soft-fibrous droppings.

Middle-late Pleistocene (420-18 ka) glacial-interglacial cycles (Imbrie et al., 1993), could have played an important role as modifying factors of Aphodiini distributions and diversity, especially in the Holarctic regions (Hanski, 1991b). Fossil evidence (Coope, 1978, 1990; Coope & Angus, 1975; Lindroth, 1948) confirms that insects underwent range shifts during the Pleistocene in relation to changes in climate and vegetation. Thus, in the Northern

Hemisphere, Aphodiini 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 among Old World regions and between New World regions, as the ice sheets interrupted the interchanges across Beringia. The Oriental region probably was isolated by the glaciated ice sheets of mountain ranges, and therefore may not have served as a refuge for northern Aphodiini lineages. This possibly favoured the role of the Palaeotropical region as a refuge and recent diversification centre for a great number of Old World Aphodiini lineages, helping explain its high levels of endemism.

During the Holocene (10 ka to the present), cattle, horses and other domesticated animals, as well as human movements, have contributed particularly to the dispersion of Aphodiini. Human-induced changes have been especially important in the Western Palaearctic during the late Quaternary (Birks, 1986; Hanski, 1991b) and over the past few centuries for the other regions (P.A. Delcourt & H.R. Delcourt, 1987; Doube et al., 1991; Kohlmann, 1991; Mirol et al., 2003). Recent changes in soil uses, modifications through livestock and agricultural practices, chemical contamination and urban development have negatively influenced Aphodiini diversity, distribution and populations (Barbero et al., 1999; Gittins & Giller, 1999; Gittings et al., 1994; Hutton & Giller, 2003; Lobo et al., 1997, 2001, 2006; Lumaret, 1986, 1990; Lumaret & Kirk, 1911; Lumaret & Martínez, 2005; Lumaret et al., 1993; Romero-Samper & Lobo, 2006; Roslin & Koivunen, 2001).

5. Conclusions

Even when phylogenetic information is available, the lack of comprehensive fossil information and shifts in the distribution of species makes it extremely difficult to disentangle past dispersal patterns, complicating the formulation of reliable hypotheses that allow explanation of current distribution by means of past events (Gaston & Blackburn, 1996; Losos & Glor, 2003; Pulquério & Nichols, 2007; Thomas et al., 2006). 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. In this chapter, through statistical tests and a simple methodology, I have attempted to show that it is possible to identify signatures of the processes from which current distributional patterns originated, and to elucidate a likely past biogeography of the Aphodiini.

In relation to Aphodiini, it has been suggested that Palaeotropical and Palaearctic regions, together with the Nearctic, have been primary diversification centres after the break-up of Pangea. Consequently, these three regions may have acted jointly as macroevolutionary source regions in different times, also sustaining migration processes and extinctions that obscure linkage between past events and present-day distributions. Future phylogenetic data are needed to more completely resolve taxonomic issues and confirm internal relationships among the Aphodiini lineages. Such results also will help to confirm or to reject the hypotheses herein presented.

6. Acknowledgment

This chapter was supported by a MCI project (CGL 2010-16944) and an UCM-BSCH project (GR35/10-a). I thank Fernando Zagury Vaz de Mello and Paul Schoolmeesters, who

indirectly provided most of the Aphodiini description references by means of the bibliography databases they have compiled. I wish to dedicate this chapter to Julieta, my newborn daughter and future 'bug lover' (I hope so...).

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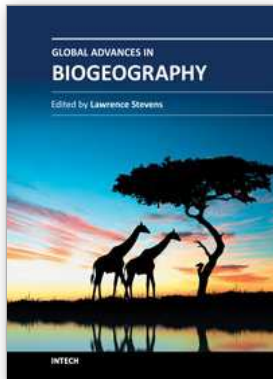
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Global Advances in Biogeography

Edited by Dr. Lawrence Stevens

ISBN 978-953-51-0454-4

Hard cover, 360 pages

Publisher InTech

Published online 30, March, 2012

Published in print edition March, 2012

Global Advances in Biogeography brings together the work of more than 30 scientific authorities on biogeography from around the world. The book focuses on spatial and temporal variation of biological assemblages in relation to landscape complexity and environmental change. Global Advances embraces four themes: biogeographic theory and tests of concepts, the regional biogeography of individual taxa, the biogeography of complex landscapes, and the deep-time evolutionary biogeography of macrotaxa. In addition, the book provides a trove of new information about unusual landscapes, the natural history of a wide array of poorly known plant and animal species, and global conservation issues. This book is well illustrated with numerous maps, graphics, and photographs, and contains much new basic biogeographical information that is not available elsewhere. It will serve as an invaluable reference for professionals and members of the public interested in global biogeography, evolution, taxonomy, and conservation.

How to reference

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Francisco José Cabrero-Sañudo (2012). Composition and Distribution Patterns of Species at a Global Biogeographic Region Scale: Biogeography of Aphodiini Dung Beetles (Coleoptera, Scarabaeidae) Based on Species Geographic and Taxonomic Data, Global Advances in Biogeography, Dr. Lawrence Stevens (Ed.), ISBN: 978-953-51-0454-4, InTech, Available from: <http://www.intechopen.com/books/global-advances-in-biogeography/what-composition-and-distribution-patterns-of-species-at-a-global-biogeographic-region-scale-can-tel>

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