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The species description process of North and Central American Geotrupinae (Coleoptera: Scarabaeoidea: Geotrupidae)

Proceso de descripción de especies de Geotrupinae norte y centroamericanos (Coleoptera: Scarabaeoidea: Geotrupidae)

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Abstract. The description process for North and Central American species of Geotrupinae was analyzed and compared with that of Western Palaearctic species. This process was fitted to an asymptotic function to explore when the curve stabilized. By means of GLMs, the influence of some variables from 3 different groups (body size, geographic range and location) was examined, taking into account both pure and combined effects on the development of the process of species description. The accumulation curve of North and Central American Geotrupinae showed that probably 84-91% of the total number of species is already known and 10-20 species remain yet to be described. Body size has not shown any influence on Geotrupinae species description for either region. The most influential elements were the pure effect of the geographic range, followed by the pure effect of the geographic location, and their combined effect. These same variables were also the most influential in the Western Palaearctic region, although with a different significance. As this species inventory remains yet to be completed, it is possible that some factors, such as distribution, could become progressively more important, as for the Geotrupinae species in the Western Palaearctic region.

Key words: body size, distribution range, dung beetles, geographic location, geotrupids, Nearctic region, species description.

Resumen. Se analizó el proceso de descripción de especies de Geotrupinae de América del Norte y Central y se comparó con el de las especies del Paleártico Occidental. Este proceso se ajustó a una función asintótica para explorar cuándo la curva terminaba estabilizándose. A través de GLMs, se examinó la influencia de 3 tipos diferentes de variables (tamaño corporal, rango geográfico y localización) en el proceso de descripción, teniendo en cuenta sus efectos puros y combinados. La curva de acumulación de Geotrupinae de América del Norte y Central mostró que probablemente se conoce un 84-91% del número total de especies y que quedarían 10-20 especies por describir. El tamaño corporal no mostró ninguna influencia en los procesos de descripción de Geotrupinae. Los elementos más influyentes fueron el efecto puro del rango geográfico, seguido por el efecto puro de la localización geográfica y el efecto combinado entre ambos. Éstos fueron también los más significativos en el proceso de descripción de Geotrupinae en el Paleártico Occidental, aunque con una importancia relativa diferente. Como el inventario de especies de Geotrupinae norte- y centroamericanos aún se encuentra incompleto, es posible que algunos factores, como el rango de distribución, sean progresivamente más importantes, como sucede en las especies de Geotrupinae del Paleártico Occidental.

Palabras clave: descripción de especies, escarabajos coprófagos, geotrúpidos, localización geográfica, rango de distribución, región Neártica, tamaño corporal.

Introduction

The subfamily Geotrupinae groups approximately 1 000 species around the world in 4 tribes: Lethrini, restricted to the Old World, and Athyreini, Bolboceratini, and Geotrupini, which are also distributed in America where there are roughly 227 species (Howden, 2003). Of these, a total of 102 species have been described in North and Central America: 83 belonging to North America, 10 to Central America, and 9 shared by both areas. Geotrupinae have been relatively less studied in America, compared to other groups, such as Scarabaeidae (Howden, 1955). Nevertheless, the study of Scarabaeoidea has undergone a great development lately (Onore et al., 2003), so there

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are some recent taxonomic publications describing and revising Geotrupinae from this region. Recently, Howden (1955, 1964, 2003) carried out a taxonomic review of the group; Halffter and Martínez (1962) also wrote a taxonomic review for the Mexican *Ceratotrupes* Jekel 1866; and Woodruff (1973) presented a review of Floridan Geotrupinae. Moreover, some ecology and biogeography studies have appeared recently, whose aim has been to define the geographical ranges and their causes for these species (Trotta-Moreu et al., 2007, 2008).

The percentage of species yet to be described and the magnitude of the total number of species are at present unknown. To answer this question it would be useful to analyze the historical development of the discovering and naming of species in this region, as well as the factors that have influenced it (in other words, the species description process; Cabrero-Sañudo and Lobo, 2003). Additionally, estimating the geographic and morphologic species characteristics related to their description could be very valuable to establish effective strategies to locate new species (Arnett, 1967; Medellín and Soberón, 1999). The possible influence of several factors on the species description process, such as species size, geographic range, and geographic location, has been previously analyzed (for instance, Hammond, 1992; Patterson, 1994; Gaston, 1996; Allsopp, 1997; Cabrero-Sañudo and Lobo, 2003). In these studies it has been noted, for example, that larger species tend to be described before smaller ones (Gaston, 1991), and that species with wider geographic ranges also tend to be described earlier (Allsopp, 1997). It has also been observed that geographic location influences the description process: generally, more faunal studies been carried out in places where taxonomists reside or have easy access so that these species have been described before those from more isolated or less accessible places (Dennis and Hardy, 1999; Cabrero-Sañudo and Lobo, 2003). Regarding Geotrupinae, Cabrero-Sañudo and Lobo (2003) studied the species description process in the Western Palaearctic region. In this study it was observed that the process had been almost completed and probably few species remained to be discovered (Tables 1, 2; Figure 1a). Species size hardly influenced the species description process, but geographic range and location explained a high percentage of variation of the year of description, with geographic location being the factor which justified explaining the highest percentage (Figure 2a; Cabrero-Sañudo and Lobo 2003).

Our objective is to analyze how the Geotrupinae description process has occurred for the North and Central American species, and to examine which factors have probably influenced this process. Moreover, considering the previously obtained results for the Western Palaearctic, the processes and data related to the species authors for both regions are compared to emphasize their similarities and their differences.

Materials and methods

For the analyses on the estimation of the number of species known at present and the factors that have influenced the description process, several taxonomic studies related to this Coleopteran group from North and Central America were consulted (Howden, 1955, 1964, 1974, 1985, 1995, 1999, 2003, 2005; Woodruff, 1973; Howden and Gill, 1984). 102 species were included: 38 Geotrupini, 15 Athyreini, and 49 Bolboceratini (6 of them *Eucanthus* Westwood 1848). In the last 10 years, many changes of nomenclature have been proposed. Some authors have considered the Geotrupidae as a subfamily (Howden, 2003). Scholtz and Browne (1996), supported by phylogenetic hypotheses, proposed that the Bolboceratini, including the Athyreini, must be raised to family rank (Bolboceratidae) and separated from the rest of Geotrupidae. Because of this, when the analyses were carried out for this study, the tribes proposed by Howden (2003) were taken into account individually. Moreover, *Eucanthus* species were considered as an independent taxon, as a consequence of being differentiated by some authors as an older group with a different origin with regard to Bolboceratini (Nikolajev, 1982; Browne, 1991).

After the compilation of a Geotrupinae species inventory for North and Central America, 9 information variables were also gathered for each species: year of description, species body size (in mm.), geographic range size (according to the criteria observed at Lumaret and Lobo (1996)), and the mean, maximum, and minimum latitude (in ºN) and longitude (in ºW) of the species distribution range. Geographic location variables were estimated with an approximate maximum error of 2.5º. The number of species described was fit to the description year by means of polynomial curves (linear, quadratic, cubic) and several functions used in studies of species accumulation curves (Soberón and Llorente, 1993; Flather, 1996). The fit was estimated by means of the Simplex and Quasi-Newton non-linear estimation method (Guil and Cabrero-Sañudo 2007). Statistical analyses based on generalized linear models (GLM; McCullagh and Nelder, 1989; Crawley, 1993) were carried out to explore the relationships between the year of species description (dependent variable) and the rest of the information variables (independent). So, the statistical significance of the linear, quadratic, or cubic functions was examined for each of the independent variables, choosing the ones with all terms simultaneously significant. The goodness of fit of the models was evaluated by means of the deviance statistic and comparing it with an F-test. Subsequently, the influence of these possible explanatory variables on the description year was analyzed to discriminate the variables, or their portions, with important effects from possible casual relationships (Legendre and Legendre, 1998; Guisan and Zimmermann, 2000; MacNally, 2000, 2002). After recognizing the groups of independent variables with important effects, a variance hierarchical decomposition process (MacNally, 2000, 2002) and a variance partition process (Legendre and Legendre, 1998) were employed to evaluate the relative importance of each variable group. For the variance partition process, an equation system of 3 interdependent variables was considered (Cabrero-Sañudo and Lobo, 2003).

Statistical analyses were carried out with Statistica 7.1 (StatSoft, 2006). To compare the results for North and Central American Geotrupinae with those of Western Palaearctic Geotrupinae, data from previous analyses have been also included (Cabrero-Sañudo and Lobo, 2003).

Results

Between 1758 and 2005, 102 Geotrupinae species from North and Central America (NCA) were described, which represent an average of 0.41 species per year. There were no species descriptions for about four-fifths of the years and more than 1 described species for only 4% of the years. The total number of authors for the NCA Geotrupinae species was 34, for a mean number of more than 3 described species per author. Half of these authors described only 1 species, whereas only 15% of authors described 5 or more species. The author with the highest number of descriptions was Howden with 35 (Table 1).

Taking into account the first half of the description period (from 1758 to 1881; 124 years), almost a third of NCA Geotrupinae species were described, for a mean of around a species every 4 years. There were no species descriptions for 85% of years, and only 2% of years with 2 or more described species. There were 15 different authors, three-fifths of them describing only 1 species and most of them less than 5. The mean number of descriptions per author was around 2 species, but Jekel was the author with the highest, with a total of 8 (Table 1). During the second half of the description period (from 1882 to 2005; 124 years), more than two-thirds of NCA Geotrupinae species were described, for a mean of around 3 species every 5 years. There were no species descriptions for 77% of years, and 6% of years with 2 or more descriptions. A total of 19 authors described new NCA Geotrupinae species, for a mean of more than 4 described species per author. However, around two-fifths of authors described only 1 species, whereas only one fifth of authors 5 or more species. Howden was the most prolific author in this period, with a total of 35 described species (Table 1).

Among all the functions examined, the Beta-p

Table 1. Compared descriptive statistics of the Geotrupinae species for Western Palaearctic (WP) and North and Central America (NCA) regions. Data for WP Geotrupinae species is from Cabrero-Sañudo and Lobo (2003) and also from unpublished analyses (Cabrero-Sañudo)

	Description process		*From 1758 to 1881*		*From 1882 to 2005*	
	WP	*NCA*	*WP*	*NCA*	*WP*	*NCA*
Number of described species	72	102	50	30	22	72
Mean number of described species per year (±SE)	0.29 ± 0.76	0.41 ± 1.36	0.40 ± 0.96	0.24 ± 0.85	0.18 ± 0.46	0.58 ± 1.72
Percentage of years without descriptions	80	81	74	85	85	77
Percentage of years with more than 2 described species	2	4	3	2	0	6
Number of authors	35	34	28	15	8	19
Mean number of descriptions per author (±SE)	2.09 ± 1.96	3.24 ± 5.92	1.86 ± 1.69	2.00 ± 1.89	2.75 ± 2.66	4.21 ± 7.69
Percentage of authors with only 1 description	60	47	61	60	63	37
Percentage of authors with at least 5 descriptions	11	15	7	7	25	21
Maximum number of descriptions per author	9	35	9	8	8	35
Author with maximum number of descriptions	Jekel	Howden	Jekel	Jekel	Reitter	Howden
Number of coincident authors between regions	4		4		0	

function provided the best fit to the whole process of NCA Geotrupinae species description. The asymptotic fit of the relationship between the year of description and the number of accumulated species explained more than 98% of the variation. According to this curve, the description process tends towards an asymptote, reaching a total of 122 described species (Fig. 1). This implies that the estimated percentage of described species at present is around 84% and that 20 species remain yet to be described. Moreover, it predicts that 90% of total species would be described by the year 2012, 95% by 2021 and 100% by 2024 (Table 2). The number of species described per year has been quite constant since the most recent revision for NCA Geotrupinae species was published (Howden, 1964). So, taking into account the final forty years considered (1965-2005), a new analysis of the relationship between the year of description and the number of accumulated species showed that the Beta-p function was again the best fit, explaining up to 96% of the variation. This curve tends to an asymptote of 24 accumulated species since 1965, giving a predicted total number of 112 NCA Geotrupinae species (Fig. 1). This result gives a result of 91% of described species in 2005 and predicts that 95% of species would be described by year 2028, 99% by 2094, and all the NCA Geotrupinae species by 2134 (Table 2).

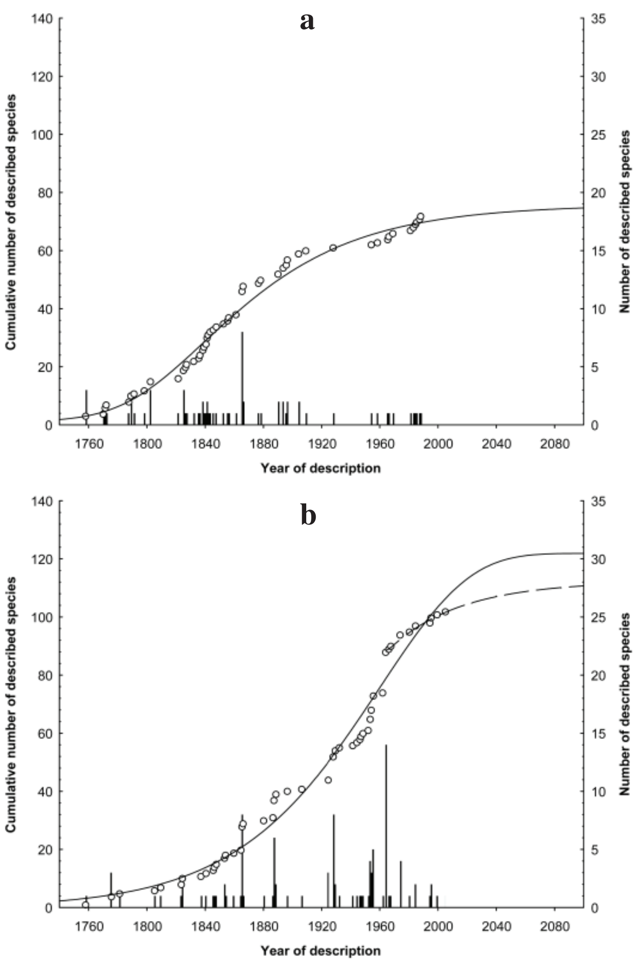

Figure 1. Accumulated number of described Geotrupinae species from 1758 to 2005. Number of described species by year in bars. The Beta-p functions with the best fit for the curves are also represented as solid lines. a) West Palaearctic Geotrupinae (Cabrero-Sañudo and Lobo, 2003); b) North and Central America Geotrupinae. The broken line corresponds to the Beta-p fit based on data for the years 1765 to 2005.

The results of GLM for Geotrupinae showed that 6 of 8 variables seemed significantly related to the species description process. Minimum and mean longitudes were significant (explaining 16.67% and 5.84% of deviance, respectively) and were positively related to the year of description, so those species whose minimum and mean longitudes were lower (species distributed more to the east) would have been described earlier. Maximum, minimum, and mean latitudes, as well as the geographic range were also significant, being related negatively to the description process (explaining 17.99%, 8.32%, 15.22%, and 10.81% of deviance, respectively), so that species distributed at higher latitudes (more northern) and with wider ranges would have been described earlier. A general explanatory model for NCA Geotrupinae containing all the significant variables selected only the minimum longitude and the

Table 2. Compared estimations of the Geotrupinae species description process for Western Palaearctic (WP) and North and Central America (NCA) regions. The relationships of the accumulated number of described species with respect to the year of description have been fitted to Beta-p functions. Data for WP Geotrupinae species is from Cabrero-Sañudo and Lobo (2003) and also from unpublished analyses (Cabrero-Sañudo). NCA* and NCA** correspond to the whole description process (from 1758 to 2005) or to the last forty years of the curve (from 1965 to 2005), respectively

	WP	*NCA**	*NCA***
Explained variance (R^2 X 100) by the asymptotic model	98.51	98.50	95.98
Total number of species predicted by the asymptote	76	122	112
Estimated percentage of current described species	95	84	91
Date to describe 50% of predicted species	1860	1952	1941
Date to describe 90% of predicted species	1979	2012	1999
Date to describe 95% of predicted species	1988	2021	2028
Date to describe 99% of predicted species	2092	2024	2094
Date to describe all the predicted species	2188	2024	2134

Table 3. Relationships between the species description process for the Geotrupinae and the explanatory variables considered in this study. BS: body size; GL: geographic location; GR: geographic range

Geotrupinae	*Selected terms*	*Abbreviation*	*Deviance*	*d.f.*	*Change in deviance*	*F*	*Sign*	*% Explained deviance*
BS	.	.	.	.	.	.	.	.
GL	Minimum longitude	Lonmin	294590.0	100	58870.49	0.20	+	16.67
	Mean longitude	Lonmed	332808.3	100	20652.23	0.06	+	5.84
	Maximum latitude	Latmax	289864.3	100	63596.24	0.22	-	17.99
	Minimum latitude	Latmin	324041.8	100	29418.72	0.09	-	8.32
	Mean latitude	Latmed	299658.3	100	53802.18	0.18	-	15.22
	GL explanatory model	Lonmin+Latmax	267529.2	100	85931.30	0.32	+ / -	24.31
GR	Geographic range	Range	315239.0	100	38221.54	0.12	-	10.81
	General explanatory model	Lonmin+Latmax	267529.2	100	85931.30	0.32	+ / -	24.31

maximum latitude, explaining almost a quarter of the total variation (24.31%; Table 3).

Regarding Geotrupini exclusively, the results of GLM showed that 6 of 8 variables were significantly related to the species description process. Minimum and mean longitudes were significant (explaining 28.25% and 13.96% of deviance, respectively) and were positively related to the description year, so that species with lower minimum and mean longitudes would have been described earlier (as in the Geotrupinae subfamily). Maximum, minimum, and mean latitudes were also significant (explaining 29.85%, 16.45% and 27.58% of deviance, respectively) and negatively related to the year of description, so that northern species would have been described earlier. Geographic range was also significant and negatively related to the description process (explaining 23.34% of deviance), so species with smaller ranges would have been described later. The general explanatory model obtained with these variables selected only the maximum latitude, explaining almost a 30% of the total variance (29.85%; Table 4). With regard to tribe Bolboceratini, 4 variables were significant. Minimum longitude was positively related to the description process (explaining 10.24% of deviance), so species with a more easterly distribution have been described earlier. Maximum and mean latitudes and range were also significant and negatively related (explaining 13.42%, 12.74% and 12.45% of deviance, respectively), so that species with wider and more northern distributions have been described earlier. A general explanatory model also includes maximum latitude and explains 13.42% of the total variation (Table 4). None of the variables were significant for Athyreini or *Eucanthus* geotrupids. This was probably due to the low number of NCA species for each group. Most of the Athyreini species are distributed in South America, and less than half of the total number of species has a NCA distribution. With respect to *Eucanthus*, it is a small genus with only 7 species present in the NCA region.

Subsequently, because interactions among variables could frequently have a higher explanatory power than independent variables by themselves (Margules et al., 1987), a possible significant relationship between the descriptive process and all the interacting pairs among variables related to the year of description was examined. None of these significant relationships contributed by themselves more than the independent variables, so they were finally not considered.

The variance hierarchical decomposition analysis for Geotrupinae showed that the most important variables explaining the description process were those related to geographic location (GL) and range (GR), responsible for 18.58% and 5.64% of variation, respectively (Table 5). The variance partition analysis also corroborated that the pure effect of GL were in fact that which provided a substantial portion of explained variation (12.45%), followed by the combined effect between GL and GR, which covered more than 10% of total deviance (Fig. 2b).

Considering each tribe independently, the variance hierarchical decomposition for Geotrupini proved that the most important variables are those related to geographic location and range, explaining 19.03% and 12.32% of variation, respectively (Table 5). The variance partition analysis showed that the pure effects of GL provided a substantial portion of the explained variation (8.49%). However, the combined effect between these GL and GR managed to explain a total of 21.24% of variation (Fig. 2c). In the case of Bolboceratini the results are very similar. The variance hierarchical decomposition analysis showed that the most important variable groups were those related to both geographic location and range, counting for 7.85% and 7.95% of variation, respectively (Table 5). The variance partition corroborated that the pure effects of GL and GR explained some portion of variation (2.27% and 3.45%, respectively); nevertheless, the combined effects of both groups explained a higher percentage (10%). For

Table 4. Relationships between the species description process for the Geotrupini and Bolboceratini and the explanatory variables considered in this study. BS: body size; GL: geographic location; GR: geographic range

	Selected terms	*Abbreviation*	*Deviance*	*d.f.*	*Change in deviance*	*F*	*Sign*	*% Explained deviance*
Geotrupini								
BS	.	.	.	.	.	.	.	.
GL	Minimum longitude	Lonmin	110795.5	36	43626.34	14.18	+	28.25
	Mean longitude	Lonmed	132862.7	36	21559.12	5.84	+	13.96
	Maximum latitude	Latmax	108329.3	36	46092.53	15.32	-	29.85
	Minimum latitude	Latmin	129018.4	36	25403.40	7.09	-	16.45
	Mean latitude	Latmed	111830.4	36	42591.42	13.71	-	27.58
	GL explanatory model	Latmax	108329.3	36	46092.53	15.32	-	29.85
GR	Geographic range	Range	118379.2	36	36042.62	10.96	-	23.34
	General explanatory model	Latmax	108329.3	36	46092.53	15.32	-	29.85
Bolboceratini								
BS	.	.	.	.	.	.	.	.
GL	Minimum longitude	Lonmin	101797.0	41	11613.43	4.68	+	10.24
	Maximum latitude	Latmax	98194.58	41	15215.88	6.35	-	13.42
	Mean latitude	Latmed	98960.05	41	14450.42	5.99	-	12.74
	GL explanatory model	Latmax	98194.58	41	15215.88	6.35	-	13.42
GL	Geographic range	Range	99290.47	41	14119.99	5.83	-	12.45
	General explanatory model	Latmax	98194.58	41	15215.88	6.35	-	13.42

Table 5. Percentages of variance of the North and Central American Geotrupinae description process explained by body size (BS), geographic location (GL) and distribution range size (GR), according to the variance hierarchical decomposition analysis

	BS	GL	GR
Geotrupinae	-1.23	18.58	5.64
Geotrupini	0.41	19.03	12.32
Bolboceratini	4.29	7.85	7.95

this group, the variance hierarchical decomposition and the variance partition analyses also showed that both the general effect of body size and the pure effect of body size explained a high percentage of variation, but this percentage should not be taken into account as size was not significant in previous analyses (Table 5, Figure 2d). Figure 3 resumes the combined effects between GL and GR for Geotrupini and Bolboceratini. Within Geotrupinae 2 description tendencies have been observed. Thus, Geotrupini species with smaller geographic ranges and with southern maximum latitudes have been described even later than expected (Figure 3a); however, within Bolboceratini this fact is different, as those species with smaller ranges and northern maximum latitudes have been described even later than the rest (Fig. 3b).

Discussion

The asymptotic adjustment of the accumulated number of species provides a Beta-p model which explains a high percentage of the variation in the year of species description (98%). A subsequent partial analysis restricted to the last forty years selects also a Beta-p model which explains up to 96% of the description process for these concrete data. Although these results must be considered as an approximation, they show that the species inventory for the NCA Geotrupinae species would be almost complete. Thus, these 2 methods point that 10 to 20 NCA Geotrupinae species remain yet to be described, which represent between 9% and 16% of the total species.

Regarding Geotrupinae from the Western Palaearctic (WP), the asymptotic adjustment retained more than a 98% of variation in the accumulated number of species (Cabrero-Sañudo and Lobo, 2003). It was also adjusted to a Beta-p function and the number of known species was slightly lower than the number predicted by the asymptote (at present 95% of species would have been described, which is a higher percentage than that at the NCA region; Fig. 1a). Comparing the 2 descriptive processes, it is observed that species from the WP region were in general described earlier than the NCA species. Thus, half the total number of WP species was described by 1860, whereas

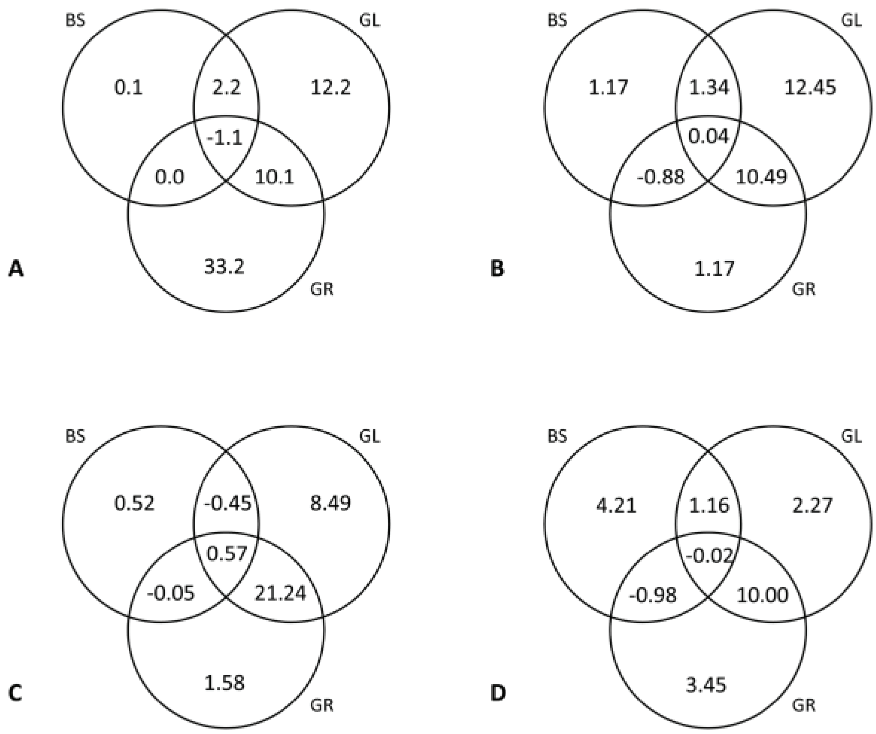

Figure 2. Percentages of variation explained through variance partitioning in the year of species description of West Palaearctic Geotrupinae (A), data from Cabrero-Sañudo and Lobo, 2003), North and Central America (NCA) Geotrupinae (B), NCA Geotrupini (C), and NCA Bolboceratini (D) between the 3 considered explanatory groups of variables: BS, GR, and GL. BS: body size; GR: geographic range; GL: geographic location.

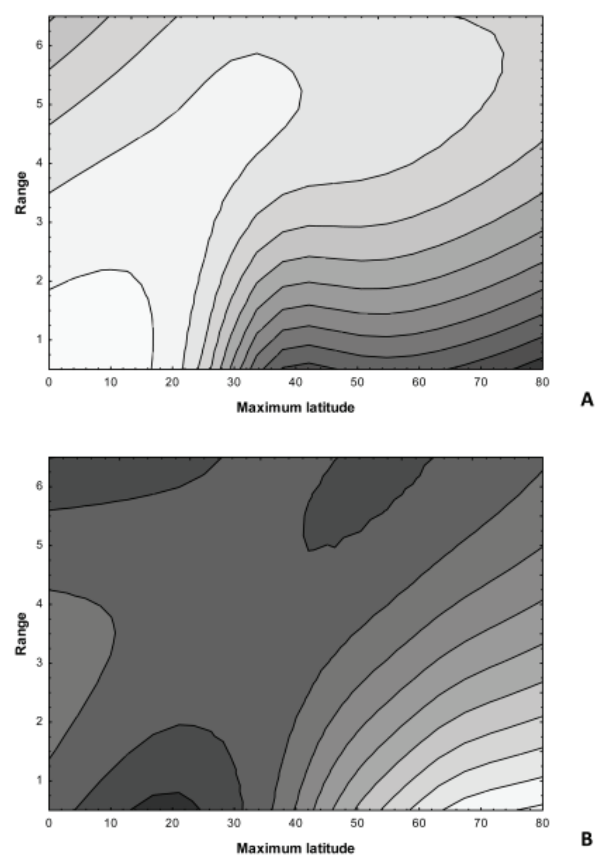

Figure 3. Contour plots of the year of species description for North and Central American Geotrupini (A) and Bolboceratini (B) in the space delimited by the scores of the geographic range and the maximum latitude. Clearer curves represent subsequent years with respect to darker ones.

the NCA inventory took at least eighty years more to reach that point. These differences have been minimized as the processes went on, so the date to describe higher percentages of the WP Geotrupinae inventory would be similar or even higher to those dates for the NCA region (Table 2).

The NCA Geotrupinae description rate has been in general more irregular over the years that the WP description rate (Table 1). The first species at NCA region was described in 1758 by Linnaeus, but it was also a Palaearctic species (*Geotrupes stercorarius* Linnaeus, 1758). The first exclusively NCA species were described in 1775 (*Bolbocerosoma farctum* (Fabricius), *Cnemotrupes splendidus* (F.), and *Eucanthus lazarus* (F.)). In the following years, some species from this region were described sporadically, although since 1837 the number of described species started to increase. During this first half of the description process (until 1881), the most prominent author was Jekel, who described a total of 8 species in 1865. At the same time, almost twice as many species were described at the Western Palaeartic by around twice as many authors. Jekel was also the most prolific author, with 9 described species in 1865. In this period, a few WP authors were also working at the NCA region (around 14%). From 1882 to 2005, there was a more constant rate of description at the NCA region, in spite of the brief halt coincident with the years around the First World War.

Three years excel the rest of this period as a result of their higher number of descriptions, 1887, 1928 and 1964, as Bates, Wallis and Brown, and Howden, respectively, published almost half the number of the described species of this period. Compared to the WP description process, the number of described species in this period at the NCA region was tripled and the active authors were at least twice as many. From this period and for the whole NCA description process, Howden has been the entomologist with a higher number of described species. In fact, in the last 50 years, around 95% of the described species have been published by him, which represent almost half of the described species at this period and a third of the total NCA Geotrupinae inventory (Table 1). However, in this period none of the WP authors coincide with the NCA authors; this could be because of the fact that there was a progressively greater relationship between the authors and their region of origin.

The diversity of Geotrupinae species at the NCA region is higher than that at the WP region. A lower number of species has been described for the WP region, so consequently the mean number of described species per year is in general higher at the NCA region. However, the percentage of years without species description is similar for the WP and NCA regions. Thus, the percentage of years with more than 1 species described is necessarily lower for the WP region, and it has been more usual describing several species simultaneously at the NCA region. Then, the description process has developed more gradually at the WP region, whereas it has been more stepped for the NCA region.

The taxonomic composition of the inventories present at each region could also be a determinant for the observed differences in both description processes. Thus, there are no Athyreini species within the WP fauna and there are only a few Bolboceratini species. These 2 groups are more difficult to collect and are typically found in low numbers (Howden, 1955), so the description of these species has probably been complicated and delayed in the NCA region. In the WP region there are also only a few groups of Geotrupini, such as *Trypocopris* Motschulsky, 1858, or *Thorectes* Mulsant, 1842, etc., whose species are hard to collect; however, taking into account the habitats present in both regions, NCA areas usually are comparatively more extensive and isolated than WP ones, with worse communications and less population, which could also influence the description process.

The most influential variables on the species description process of NCA Geotrupini as well as for that of Bolboceratini were those related to GL and GR, especially the combined effect of both groups, which explains the highest percentage. For Geotrupini, species with smaller ranges at lower maximum latitudes have recently been described. Geotrupini have a Holarctic origin (Halffter, 1976) and, thus, they are predominant in the northern areas of North America (in fact, there is currently no Geotrupini species described further south than El Salvador). So, species with wider northern geographic ranges have been described earlier, because they would have been easier to locate. On the contrary, the first described NCA Bolboceratini species were those in southern latitudes, and geographic range progressively takes importance, so that the last described species where those with narrower geographic ranges and higher latitudes. Although Bolboceratini are distributed worldwide, they are found mostly in low areas with sandy or light clay soils (Howden et al., 2007), and are especially abundant in the south and south-east of the NCA region (Howden, 1955).

For NCA Athyreini and *Eucanthus* no significant variable was observed; this fact is likely due to the lower number of considered taxa for these 2 groups. Athyreini is a speciose group in South America, but only 15 reach Central America. *Eucanthus* is not represented by many species either, as there are only 6 species in the NCA region. *Eucanthus* shows low species diversity values worldwide, but its distribution is quite wide as it includes the Nearctic, the Neotropical, and the Australian regions.

Both WP and NCA species description processes are influenced primarily by location and geographic range. In the WP region, the most influential variables were the pure effect of the geographic range size (33.2%), followed by the effect of the geographic location (12.2%), and their combined effect (10.01%; Cabrero-Sañudo and Lobo, 2003; Fig. 2). For the NCA Geotrupinae those factors were also the most important, although the percentages of the explained variance varied; thus, the pure effect of geographic location was most important (12.45%), followed by the combined effect of location and geographic range (10.49%), and the pure effect of the geographic range (1.7%). There are not so many differences between the pure effects of the geographic location and the combined effects of the range and location of both regions, but the pure effect of geographic range is more influential for WP species than for NCA species. This could point to the NCA region being less surveyed than the WP region, as only recently the effect of distribution ranges is being felt, likely as a consequence of the causes previously discussed (the NCA region is larger than the WP region, less populated, less accessible) and the fact that the NCA has had a lower concentration of taxonomist per area than the WP region.

Geographic range size has been usually considered an important factor for species description, related linearly and negatively to the description year, as it has been confirmed that species with wider ranges from several biological groups are frequently described before those with narrower ranges (Allsopp, 1997; Blackburn and Gaston, 1995; Gaston et al., 1995a, 1995b; Patterson, 1994, 2000). With respect to geographic location, it has been observed that it usually has a curvilinear relationship to the description process (Allsopp, 1997; Gaston et al., 1995a, 1995b; Patterson, 1994, 2000), so there are specific areas where species are described earlier than in other areas, as a consequence of being more frequently sampled by taxonomists (Cabrero-Sañudo and Lobo, 2003). Body size has not shown any influence on the Geotrupinae species description process for either region. As these species live in very peculiar environments –dung, fungi, or organic litter-, normally all the specimens found are typically collected regardless of their size (Cabrero-Sañudo and Lobo, 2003). Nevertheless, other analyses show that body size could be an important factor for other beetles (Gaston, 1991), especially those with more nomadic habits.

As some Geotrupinae species probably remain yet to be discovered in the NCA region, the results could help identify the characteristics of the undiscovered species and where to locate them. According to these analyses, future searches could be mostly concentrated in narrow southern geographic enclaves for most of NCA Geotrupinae species, especially for the tribe Geotrupini. Thus, as the Geotrupini species show mountainous affinities (Trotta-Moreu et al., 2008), temperate to cold spots under latitude 30º and located in some mountain tops along the Sierra Madre and the Central American mountain ranges could be the most favorable places to discover new taxa. Contrariwise to Geotrupini, narrow northern enclaves above latitude 40º, especially those with arid or subtropical climate and lower altitudes (Trotta-Moreu et al., 2008) could be suitable places to direct survey efforts after Bolboceratini.

Certainly, the biogeographic history of species in the WP and at the NCA regions is different, although the effect of geographic and ecological factors considered was significant for the species of both regions. However, a lot of different factors could well be acting and their relative importance could vary according to regions. So, it is important to note that the explained variance for the NCA geotrupids was around half of that explained for the WP species. Nevertheless, as the NCA species inventory is less complete than the WP inventory, it is possible that some factors, such as distribution range, will progressively become more important.

We think that simple analyses like these are important to increase knowledge about a peculiar group and to help in its conservation (May, 1988; Sutton and Collins, 1991). Determining the degree of completion of the faunistic inventories from a region and estimating the geographic and morphological characteristics of a species group related to their description probability could be useful in establishing effective strategies for the search and location of new species (Arnett, 1967; Medellín and Soberón, 1999).

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Literature cited

Allsopp, P. G. 1997. Probability of describing an Australian scarab beetle: influence of body size and distribution. Journal of Biogeography 24:717-724.

Arnett, R. H. 1967. Present and future systematics of the Coleoptera in North America. Annals of the Entomological Society of America 60:162-170.

Blackburn, T. M. and K. J. Gaston. 1995. What determines the probability of discovering a species?: A study of South American oscine passerine birds. Journal of Biogeography 22:7-14.

Browne, D. J. 1991. Wing structure of the genus *Eucanthus* Westwood; confirmation of the primitive nature of the genus (Scarabaeoidea: Geotrupidae; Bolboceratinae). The Journal of the Entomological Society of Southern Africa 54:221-230.

Cabrero-Sañudo, F. J. and J. M. Lobo. 2003. Estimating the number of species not yet described and their characteristics: The case of Western Palaearctic dung beetle species (Coleoptera, Scarabaeoidea). Biodiversity and Conservation 12:147-166.

Crawley, M. J. 1993. GLIM for ecologists. Blackwell Scientific Publications. Oxford. 379 p.

Dennis, R. L. H. and P. B. Hardy. 1999. Targeting squares for survey: Predicting species richness and incidence of species for a butterfly atlas. Global Ecology and Biogeography 8:443-454.

Flather, C. H. 1996. Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. Journal Biogeographics 23:155-168.

Gaston, K. J. 1991. Body size and probability of description: The beetle fauna of Britain. Ecological Entomology 16:505-508.

Gaston, K. J. 1996. Species richness: Measure and measurement. *In* Biodiversity. A biology of numbers and difference, K. J. Gaston (ed.). Blackwell Science Ltd., Oxford. p. 77-113.

Gaston, K. J., T. M. Blackburn and N. Loder. 1995a. Which species are described first?: The case of North American butterflies. Biodiversity and Conservation 4:119-127.

Gaston, K. J., M. J. Scoble and A. Crock. 1995b. Patterns in species description: a case study using the Geometridae (Lepidoptera). Biological Journal of the Linnean Society

55:225-237.

Guil, N. and F. J. Cabrero-Sañudo. 2007: Analysis of the species description process for a little known invertebrate group: the limnoterrestrial tardigrades (Bilateria, Tardigrada). Biodiversity and Conservation, 16:1063-1086.

Guisan, A. and N. E. Zimmermann. 2000. Predictive habitat distributions models in ecology. Ecological Modelling 135:147-186.

Halffter, G. 1976. Distribución de los insectos en la zona de transición mexicana. Relaciones con la entomofauna de Norteamérica. Folia Entomológica Mexicana 35:1-64.

Halffter, G. and A. Martínez. 1962. Monografía del Género *Ceratotrupes* Jekel (Coleopt. Scarab. Geotrup.). Ciencia 11:145-159.

Hammond, P. 1991. Species inventory. *In* Global Biodiversity. World Conservation Monitoring Centre, B. Groombridge (ed.). Chapmann & Hall, London. p. 17-39.

Howden, H. F. 1955. Biology and taxonomy of North American beetles of the Subfamily Geotrupinae with revisions of the genera *Bolbocerosoma*, *Eucanthus*, *Geotrupes* and *Peltotrupes* (Scarabaeidae). Proceedings of the United States National Museum 104:151-319.

Howden, H. F. 1964. The Geotrupinae of North and Central America. Memoirs of the Entomological Society of Canada 39:1-91.

Howden, H. F. 1974. Additional records and descriptions of North and Central American Geotrupinae (Coleoptera, Scarabaeidae). Canadian Journal of Zoology 52:567-573.

Howden, H. F. 1985. A revision of the South American species in the genus *Neoathyreus* Howden and Martínez (Coleoptera: Scarabaeidae, Geotrupinae). Contributions of the American Entomological Institute 21:1-95.

Howden, H. F. 1995. Two new species of Geotrupinae (Coleoptera: Scarabaeidae) from Costa Rica. The Coleopterists Bulletin 49:261-266.

Howden, H. F. 1999. New Species of Central and South American Athyreini (Coleoptera: Geotrupinae). The Coleopterists Bulletin 53:339-354.

Howden, H. F. 2003. Geotrupinae. *In* Atlas de los escarabajos de México (Coleoptera: Lamellicornia: Scarabaeidae, Trogidae, Passalidae y Lucanidae) Vol. II, M. A. Morón (ed.). Argania Editio, Barcelona. p. 95-106.

Howden, H. F. 2005. Notes on Bolboceratini from Northeastern México with description of a new *Bolbocerosoma* Schaeffer (Coleoptera: Scarabaeidae: Geotrupinae). Folia Entomológica Mexicana 44:213-218.

Howden, H. F. and B. Gill. 1984. Two New Species of *Neoathyreus* Howden and Martínez from Costa Rica with distribution notes on other Athyreini from México and Central America (Coleoptera: Geotrupinae). Canadian Entomologist 116:1637-1641.

Howden, H. F., A. Howden and G. Holloway. 2007. Digging down under: Australian Bolboceratini, their habits and a list of species (Coleoptera: Scabarabaoidea: Geotrupidae). Zootaxa 1499:47-59.

Legendre, P. and L. Legendre. 1998. Numerical ecology. 2nd Edition. Elsevier, Amsterdam. 853p.

Lumaret, J. P. and J. M. Lobo. 1996. Geographic distribution of endemic dung beetles (Coleoptera, Scarabaeidae) in the Western Palaearctic region, Biodiversity Letters 3:192-199.

Macnally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between –and reconciliation of– 'predictive' and 'explanatory' models. Biodiversity and Conservation 9:655-671.

Macnally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodiversity and Conservation 11:1397-1401.

Margules, C. R., A. O. Nicholls and M. P. Austin. 1987. Diversity of *Eucalyptus* species predicted by a multi-variable environment gradient. Oecologia 71:229-232.

May, R. M. 1988. How many species are there on Earth? Science 241:1441-1449.

McCullagh, P. and J. A. Nelder. 1989. Generalized linear models. Chapman & Hall, London. 532 p.

Medellín, R. A. and J. Soberón. 1999. Predictions of mammal diversity on four land masses. Conservation Biology 13:143-149.

Nikolajev, G. V. 1982. Beitrag zur systematik der Bolbaffer arten. Deutsche Entomologische Zeitschrift 29:35-42.

Onore, G., P. Reyes-Castillo and M. Zunino. 2003. Escarabeidos de Latinoamérica: Estado del conocimiento. Monografías Tercer Milenio, vol. 3. SEA, Zaragoza. 86p.

Patterson, B. D. 1994. Accumulating knowledge on the dimensions of biodiversity: systematic perspectives on Neotropical mammals. Biodiversity Letters 2:79-86.

Patterson, B. D. 2000. Patterns and trends in the discovery of new Neotropical mammals. Diversity and Distribution 6:145-151.

Scholtz, C. H. and D. J. Browne. 1996. Polyphyly in the Geotrupidae (Coleoptera: Scaraboidea) a case for a new family. Journal of Natural History 30:597-614.

Soberón, J. and J. Llorente. 1993. The use of species accumulation functions for the prediction of species richness. Conservation Biology 7:480-488.

StatSoft, Inc. 2006. *STATISTICA (data analysis software system), version 7.1*. Tulsa, Oklahoma. www.statsoft.com

Sutton, S. L. and N. M. Collins. 1991. Insects and tropical forest conservation. *In* The conservation of insects and their habitats, N. M. Collins and J. A. Thomas (eds.). Academic Press, London. p. 405-424.

Trotta-Moreu N., E. Montes de Oca and I. Martínez M. 2007. Ecological and reproductive characteristics of *Geotrupes (Halffterius) rufoclavatus* Jekel, 1865 (Coleoptera: Scarabaeoidea: Geotrupinae) on the Cofre de Perote volcano (Veracruz, México). Coleopterists Bulletin 61:435-446.

Trotta-Moreu N., J. M. Lobo and F. J. Cabrero-Sañudo. 2008. Distribución conocida y potencial de Geotrupinae (Coleoptera: Scarbaeoidea) México. Acta Zoológica Mexicana 24:39-65.

Woodruff, R. E. 1973. The Scarab Beetles of Florida. Vol. 8. Arthropods of Florida and Neighboring Land Areas. Florida Department of Agriculture and Consumer Services. Gainesville, Florida. 220 p.